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BRITISH PURBECK CHAROPHYTA



BRITISH MUSEUM

(NATURAL HISTORY) *k*

BRITISH PURBECK
CHAROPHYTA

BY

THOMAS MAXWELL HARRIS *X-27*

PROFESSOR OF BOTANY IN THE UNIVERSITY OF READING

WITH SEVENTEEN PLATES AND SIXTEEN FIGURES
IN THE TEXT

LONDON :

PRINTED BY ORDER OF THE TRUSTEES OF THE
BRITISH MUSEUM

1939

Issued April 22nd, 1939]

[Price Seven Shillings and Sixpence



MADE AND PRINTED BY ADLARD AND SON, LIMITED,
21 BLOOMSBURY WAY, LONDON, W.C. 1,
ENGLAND

PREFACE

PROF. T. M. HARRIS, whose detailed study of a Rhaetic assemblage of small freshwater plants was published by the Trustees of the British Museum last year, has since turned his attention to a later Mesozoic horizon, again containing abundant material of freshwater plants. In the Middle Purbeck Cherts are the relics of a practically pure association of Charophytes, represented by only a few species; they are complex representatives of a somewhat isolated group, and with the aid of modern technical methods Prof. Harris has succeeded in unravelling their structure, thus completing the unfinished work of Clement Reid and James Groves. The specimens obtained by Reid and Groves, bequeathed to the British Museum by the latter in 1933, formed the basis of the present work; but Prof. Harris, in conjunction with Mr. P. Sylvester Bradley, has collected and prepared much additional material. The author concludes his survey of British Upper Jurassic Charophytes with an examination of the general problem of identifying Charophyte fruits, and discusses their possible stratigraphical value.

W. N. EDWARDS

Keeper of Geology

March, 1939

“ All that could fairly be claimed for the study of these fossil Charophytes would be that they had led to the clearing up of many of the problems that they themselves had raised.”

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INTRODUCTION

Fossil Charophytes were discovered in the Upper Jurassic (Purbeckian) rocks of south Dorset as long ago as 1850, and further material has been obtained at intervals. The first large collection is, however, the one made by Clement Reid, partly in conjunction with James Groves, in 1913-1916, which forms the basis of the present account.

Clement Reid and James Groves had intended to describe this material fully in a joint monograph. They published only a brief description (1916) of the commonest species, in a paper which was intended as a preliminary notice. With the help of a grant from the Royal Society they prepared numerous rock slices, which Clement Reid developed by a special process, and photographed in preparation for what would undoubtedly have been a long and important paper.

The illness and death of Clement Reid in 1916, however, led to the work remaining unfinished, for although Groves survived his friend by more than sixteen years, he did not find an opportunity to complete their joint work. The entire collection was bequeathed to the British Museum by James Groves in 1933, and in 1938 it was entrusted to me for investigation, together with Clement Reid's letters to Groves and many notes and photographs.

In the course of the reinvestigation of the material a technique was found which gave more rapid results, which moreover to me at least are easier of interpretation than those obtained by Reid's method. It therefore happens that although I have made considerable use of his preparations, nearly all the figures are of specimens newly prepared from the rough blocks.

ACKNOWLEDGMENTS

The examination of the Purbeckian Charophytes in the Department of Geology of the British Museum (Natural History) was undertaken at the suggestion of Mr. W. N. Edwards, to whom I am grateful both for this and for help in completing the catalogue.

To the Director of the Geological Survey and Museum I am indebted for the loan of some specimens which proved of the

greatest value; also to Mr. F. W. Anderson, of the Scottish Geological Survey, for lending me some material.

It is with great pleasure that I express my gratitude to Mr. P. C. Sylvester Bradley, whose help has made certain parts of this work possible. Besides giving his time in showing me the localities, he generously placed at my disposal very large numbers of tubes containing concentrates from the Purbeck rocks which he had prepared for the purpose of obtaining Ostracods. He thus made it possible to establish with reasonable certainty the horizon of the Reid and Groves Collection; the fact that Charophytes are abundant at this horizon throughout the Dorset Purbeck; and the fact that they occur, though more rarely, at certain other horizons.

Finally, I am indebted to Mr. L. C. Willis, of the University, Reading, for the skill and patience he expended in making the photographs, and to Mr. F. M. Wonnacott, of the British Museum (Natural History), for his careful assistance in checking the manuscript and seeing the work through the press.

HISTORICAL REVIEW

The Purbeck Charophytes were discovered by Edward Forbes, who was one of the first to study Purbeck stratigraphy in detail. He recorded (1851) in the Middle Purbeck Cherts for Mupe Bay region (Bacon Hole) "for the first time in the oolitic series, *Gyrogonites*, the spore vesicles of Characeae". Forbes left on record the manuscript name *Chara purbeckensis*; but there is nothing to show to what this refers.

During the second half of the nineteenth century the stratigraphy of the Purbeck was studied by the staff of the Geological Survey. Vertical sections were published by Bristow (1857), where the main Charophyte horizon is clearly shown in the Middle Purbeck. The same bed with Charophytes was referred to in the Memoirs of the Geological Survey.

In 1890 Wethered described some "*Chara*" from the Middle Purbeck Chert collected at Lulworth. He figured some thin sections through the chert in which nodes and internodes of *Clavator reidi* are clearly recognizable, but beyond some brief notes did not venture to give a botanical description. It is interesting that he used acid to dissolve some of the silicified fossils out of the cherty limestone, but he made no use of the specimens he obtained. The work is of importance in that it drew attention to the type of Charophyte fossil in the Purbeck.

Besides the references to the Charophytes of the Middle Purbeck Cherts, there have been records from the Lower Purbeck Cherts of the Fossil Forest horizon, from the classic Fossil

Forest locality near Lulworth. A map included in the Reid and Groves notes bears a manuscript entry by C. D. Sherborn, "Tree trunks with beds of Chert containing *Chara*", and Strahan (1898, p. 79) writes ". . . a seam of dark Chert in the Tufa (Purbeck 'cap') surrounding one of the tree stools in the cliff half a mile east of Lulworth is of purely fresh-water origin. It contains *Valvata naticoides* in abundance and an occasional stem of *Chara*"; and again (p. 83), discussing the Fossil Forest tufas, "*Chara* is not uncommon in the Chert bands". I was unable to find such material, despite a fairly careful search, when many chert samples were collected; the best was a piece which showed fragments of cylindrical tubes which might have belonged to Charophytes, but are indeterminable. There are plenty of fallen blocks of Middle Purbeck freshwater limestone with chert containing *Clavator* lying in the Fossil Forest locality, but it can scarcely be supposed that anyone would mistake them for Lower Purbeck Chert.

During the years 1913-1916 Reid and Groves made a considerable collection of Middle Purbeck chert and began to work out the fossils. They published a preliminary paper in 1916 in which the main features of *Clavator reidi* were brought out, but Reid's death brought the work to an end. *Clavator reidi* was referred to at some length by Groves in 1924, 1924a, and in 1933; but these accounts add nothing important to the joint paper by Reid and Groves.

The work of various authors on the Purbeck Charophytes of other countries has not proved of any special assistance in this investigation as the species concerned are all distinct.

COLLECTIONS

In 1918 Clement Reid and James Groves presented the series of etched slices from Swanage which formed the basis of their paper (1916). The remainder of the Reid and Groves Collection, bequeathed in 1933, consisted of about 150 blocks obtained from various places in Dorset. These blocks, though often containing beautifully preserved specimens, are poorly localized. Many of them were used up in the course of the present investigation.

The P. Sylvester Bradley Collection (incorporated in the Harris Collection) consists of specimens obtained incidentally during the isolation of the shells of Cyprids for stratigraphic purposes. They are well localised.

The Harris Collection (made by me in collaboration with Mr. P. Sylvester Bradley) was also made for stratigraphic purposes, but includes specimens of palaeontological value.

The above are in the Geological Department of the British Museum. In the collection of the Geological Survey and Museum

are a number of specimens obtained by various collectors ; some are well localised. I have also used a tube of Charophytes lent by Mr. F. W. Anderson, of the Scottish Geological Survey ; the specimens are in his possession.

STRATIGRAPHY

The Purbeck rocks form the uppermost part of the Jurassic series and pass conformably into the Wealden. In Dorset they are predominantly a series of non-marine shales, marls and limestones, with a few marine horizons, one of which, the Cinder Bed, is full of small oysters. The series was carefully investigated about 1850 by Bristow and others, but since then has been little studied until recent times. A good general account of the British Purbeck is given by Arkell (1933). Although Mr. Sylvester Bradley's results are not yet published, he has generously put his material and data concerning Purbeckian stratigraphy at my disposal.

Charophytes are abundant and widespread in a small region (in and near the Cherty Limestone) of the Middle Purbeck ; and, so far as is known, are frequent at no other level far removed from this. (It should be made clear that they are sometimes common in the shales at a short distance above and below the limestones.) The same species do, however, occur, though rarely, at certain levels in the Upper Purbeck, and again at much lower levels in the Middle Purbeck. No thorough search has yet been made of the Lower Purbeck rocks, apart from the Fossil Forest horizon, where the occurrence of undetermined forms was noted by Strahan and Sherborn, who must have seen far better specimens than any I found there (p. 6).

The great abundance of Charophytes at the horizon of the Middle Purbeck Cherty Limestone suggests that there was, in Dorset, a very large lake shallow enough (1-10 m. deep) for these gregarious plants to grow over large areas. The rather local occurrence of the different species suggests that they were deposited near the place where they grew.

At other periods these species were evidently growing in the same lake basin, but the rarity and the small size of the fragments found suggests that they lived at a considerable distance from the place where the sections are exposed, and it is to be expected that in some other localities they would be more abundant at another level. Thus, although in Dorset *Clavator reidi* and its associates are characteristic of a certain horizon, their abundance could not be safely used as stratigraphic evidence of this horizon in other districts.

In the Purbeck Charophyte beds there are abundant Ostracods and, as a rule, numbers of small freshwater Gastropods, and

occasional fish teeth. Here and there charcoal is frequent, and in certain localities poorly preserved petrified wood and other organs of higher plants occur.

In the Lower Purbeck Cherts of the Fossil Forest horizon in which Charophytes are recorded, but where only a few problematic specimens were obtained by me, Ostracods and freshwater Gastropods also occur and Conifer wood is abundant.

LIST OF LOCALITIES AND BEDS IN WHICH PURBECK CHAROPHYTES HAVE BEEN FOUND

The code letters and numbers of beds refer to P. Sylvester Bradley's manuscript. Only those beds which contain plants are mentioned. All the localities except the last three are in Dorsetshire.

Durlston Bay.

Material collected where the Middle Purbeck is exposed at the foot of the cliff (northern part of section).

DBE 104a' at 2' 2" below base of Cinder Bed, a white marly limestone 1' 3" thick. *Clavator grovesi* rare.

DBE 109 at about 9' below Cinder Bed. Black shale with conifer twigs and leaves; no charophytes.

DBE 111e at about 12' below base of Cinder Bed, a massive irregular marl up to 1' 6". *Clavator reidi* rare.

DBE 112 at about 12' 9" below Cinder Bed, a shell limestone 10" thick. *C. reidi* rare.

"Durlston"—no exact bed or locality; possibly one or more beach pebbles of Middle Purbeck Chert. Chert of primary origin containing vegetative organs of *Perimneste horrida*; *C. reidi* common; *C. grovesi* rare; roots and leaf fragments of higher plants occasional.

North of Anvil Point, Swanage.

Middle Purbeck Chert. Geol. Surv. and Mus. no. 5615.

Chert with *C. reidi*.

Swanage.

The specimens of *Clavator reidi* originally figured by Reid and Groves (1916) are labelled only as being from "Swanage".

Worbarrow Tout, West Side.

Material from cliff side and beach.

WT 64, below Cinder Bed, a massive limestone with chert 2' 10" thick. *C. reidi* occasional.

WT 66 massive limestone with chert 1' 4" thick. *C. reidi* occasional; silicified roots of higher plants rare.

Pondfield Cove, Worbarrow.

Middle Purbeck, under Cinder Bed. Chert with *C. reidi* common. Geol. Surv. and Mus. no. 5613-14.

Bacon Hole (Mupe Bay area).

Material from base of cliff.

BH 46 at 2' below Cinder Bed, a fine-grained limestone with chert 2' 6" thick. *C. reidi* occasional.

BH 47 at 4' 6" below Cinder Bed, a shale 7" thick. *P. horrida* gyrogonites occasional.

BH 48 at 5' 1" below Cinder Bed, a fine-grained limestone with shells and chert, 1' thick. *C. reidi* occasional.

Lulworth district.

"Fossil Forest" locality in cliff to east of Cove.

In fallen blocks of Middle Purbeck Limestone with chert (Upper Bed). *C. reidi* frequent.

Lower Purbeck; in cherts of the "Fossil Forest" tufas; undetermined stems possibly of Charophytes.

Lulworth Cove.

Outcrop on east of Cove at beach level of Cherty Limestone.

Upper Bed of Limestone with chert; *C. reidi* common.

Lower Bed of Limestone with chert; *C. reidi* frequent.

Near Lulworth.

Middle Purbeck Chert with *C. reidi*. Geol. Surv. and Mus., nos. 26338-40, 27969, and two slides, nos. 6698a, b, are similar cherts with *C. reidi* from Lulworth.

Durdle Door, East.

Outcrop of Middle Purbeck in beach.

Shale above chert, *C. grovesi* rare; *P. horrida* frequent.

Limestone with chert, *C. grovesi* abundant; *C. reidi* occasional; ? *P. horrida*.

Shale below chert, *C. grovesi* common; *C. reidi* rare; *P. horrida* occasional.

Durdle Door, West.

Outcrop in cliff of Cherty Freshwater Limestone.

Limestone with chert, *C. grovesi* abundant; *C. reidi* rare; ? *P. horrida*.

Poxwell Road Cutting.

PC 5 (Upper Purbeck) at about 36' above base of Cinder Bed and 3' below *Unio* Bed. *C. bradleyi* frequent.

PC 10 (Upper Purbeck) at about 28' above Cinder Bed. *C. grovesi*; *P. horrida* rare.

- PC 21 (top of Middle or base of Upper Purbeck) at 13' above Cinder Bed. *C. reidi* ? ; *C. grovesi* rare.
- PC 26 at 9' above base of Cinder Bed. Cf. *C. reidi* rare.
- PC 28 at about 6' above base of Cinder Bed. *C. grovesi* occasional ; *P. horrida* rare.
- (PC 30-31 is the Cinder Bed.)
- PC 33 at 1' 2" below Cinder Bed, shale and marly shale 5" thick. *C. grovesi* ; *P. horrida*.
- PC 34 at 2' below Cinder Bed, limestone and marl 11" thick. *C. grovesi* frequent ; *C. reidi* rare.
- PC 35 at 3' below Cinder Bed. Limestone and chert and cherty layer 2' 1" thick. *C. reidi* rare ; *C. grovesi* abundant.
- PC 36 at 5' below Cinder Bed, 4" marly clay. *C. reidi* rare ; *P. horrida* rare.
- PC 37 at 6' below Cinder Bed. *C. grovesi* abundant ; *C. reidi* rare.
- PC 39b at 7' 6" below Cinder Bed. *C. grovesi* rare.
- PC 43 at 14' below Cinder Bed, just above the Lower Purbeck. Utricle fragment ? *C. reidi*.

Osmington Mills (Bradley's excavation).

Middle Purbeck Limestone with chert (OMD 18). *C. grovesi* abundant ; *C. reidi* frequent ; *P. horrida* rare.

Excavation in Upper Purbeck (above *Unio* Bed) OMAX 22(1). Gyrogonites agreeing in size and shape with *C. reidi* but with about twelve ridges in lateral view.

Trial auger borings in uppermost Purbeck (above *Unio* Bed).

OMZ 3'- 6' 6". *C. grovesi* egg.

OMZ 10'- 12'. *C. grovesi* oogonium and eggs ; ill-preserved stem of *C. reidi*.

Exact position unknown ; perhaps stones from ploughed field ; *Reid & Groves Coll.*

Chert with internal casts of *C. grovesi*, *C. reidi* and possibly *P. horrida* gyrogonites.

Upwey.

Middle Purbeck outcrop in railway cutting. *C. reidi* abundant ; *Algacites clavatoris* rare.

West of Water Works. *Reid & Groves Coll.*

Various blocks of limestone with chert with *C. reidi*, *C. grovesi*, *P. horrida* and *A. clavatoris*.

Friar Waddon, near Upwey.

Middle Purbeck Chert. *F. W. Anderson Coll.*, 1938. *C. reidi* abundant ; *P. horrida* common ; *C. grovesi* rare ; *A. clavatoris* rare.

Near Coryates (Portesham district).

Loose-lying chert in ploughed field. *C. reidi* present.

Portesham or near Portesham.

Many specimens from ploughed fields, possibly in Coryates district. *Reid & Groves Coll.* *C. reidi* usually abundant; *C. grovesi* frequent to rare; *P. horrida* rare to absent; *A. clavatoris* rare. (*N.B.*—There appear to be no Middle Purbeck rocks at Portesham.)

Moigne Down.

Bradley's excavations by Bug's Lane and by water hole in Middle Purbeck Chert. *C. reidi*, *C. grovesi*, *P. horrida*.

Vale of Wardour, Wiltshire.

Teffont Evias: TE 11 *C. reidi* frequent. TE 13 *C. reidi* rare. *Sylvester Bradley & Harris Coll.*, 1939.

Swindon, Wiltshire.

Recent collections by Sylvester Bradley.

TG A' 1a: *C. reidi* abundant; *C. grovesi* frequent.

TG A' 1c: *C. reidi* frequent.

TG A' 5: *C. reidi* frequent; *C. grovesi* rare.

TG A 9: *C. grovesi* frequent.

TG B 5: *C. reidi* rare.

Kings Cross, near Haddenham, Buckinghamshire.

"*Chara*" was recorded by A. M. Davies (1899, p. 40) from the Middle or Upper Purbeck Beds in a pit (now abandoned) between Haddenham and Caddington. I have examined the only specimen extant, which is undoubtedly a gyrogonite of *C. grovesi*.

In addition to these localities where Charophytes were found, a good many were examined unsuccessfully. Even in the Middle Purbeck between rich beds, other beds can be found with few or none (as in Durlston Bay).

A large number of samples of Lower Purbeck rocks from the Fossil Forest horizon and its vicinity were examined, the number of samples being in fact as great as for the Middle Purbecks. Collections were made at the following localities:

Anvil Point (by lighthouse and Tilly Whim Valley).

Pondfield Cove and Gad Cliff.

Bacon Hole.

Poxwell Lodge Quarry.

Lulworth, Fossil Forest locality.

Many of the cherts contained wood, but only a few from Lulworth gave fragments doubtfully referable to the Charales.

MATERIAL AND TECHNIQUE

The Middle Purbeck material consists in the main of fresh-water limestone. Some of this limestone has been secondarily converted into chert, and the most valuable material is that in which the fossils have become silicified while the matrix remains unaltered limestone. There is also some material preserved in a less altered state in marls and soft shales.

This Middle Purbeck material preserved in limestone in which chert formation occurred subsequently is very characteristic. The plants had died, broken up into small pieces and decayed until all trace of organic wall material had gone, leaving only the calcareous skeleton, which either remained or was subsequently replaced by silica.

The following types of silica replacement may be distinguished, though really they intergrade and all may be found in one block.

(a) The calcite of the fossils and of the matrix is unaltered.

(b) The calcite of the fossils has been partly or completely replaced by silica, but the matrix is unaltered.

(c) The fossils are unaltered, but the matrix is partly or completely replaced by silica.

(d) Both fossils and matrix are completely silicified.

The methods most usefully employed depend on the manner of replacement ; by far the most useful is type (b), in which the fossils alone are silicified.

(a) Where no silicification has occurred, the matrix and fossils both being composed of calcite, the only methods available are probably observation of thin sections and of broken or smoothed surfaces by reflected light. The fossils do not stand out well, and it is impossible to make them show really well by etching with hydrochloric acid (Reid's and Groves's statement notwithstanding).

(b) Where a fossil has been silicified but the matrix has remained calcareous, the fossil can be very easily isolated by dissolving away the rock with acid. The procedure was simply to put the lumps of rock (500 grm. or so) in a rather large volume of 5% HCl, in which it dissolves with a gentle effervescence. This yields beautiful stems and oogonia of *Charales*, Cyprid and other shells, and no further treatment beyond washing and drying may be needed. In some cases, however, they are disfigured by ferric oxide, which can be most easily removed by adding a little oxalic acid to the hydrochloric ; and in Reid's and Groves's ploughed-field material there are often masses of fungus hyphae, which permeate the rock and entangle the fossils after acid treatment. These hyphae no doubt penetrated the rock as it lay weathering ; they occur in surprising amounts, but can be

entirely removed by subsequent treatment of the fossils with KClO_3 in concentrated HNO_3 , in which they soon dissolve.

After the acid treatment the fossils are washed with water, then alcohol, and then dried on filter-paper and sorted under a binocular dissecting microscope. The specimens may be suitably embedded and sectioned, see below.

(c) Where the matrix is silicified but the fossils are more or less calcareous, treatment with acid yields hollow moulds. From these casts can be obtained in wax or, better, in bakelite resin by impregnating the rock and then dissolving it in hydrofluoric acid.

(d) Where fossils and rock are all silicified, the methods available are the same as where it is calcareous, as in (a). The technique used is described below.

A few blocks of chert from Durlston are different; they appear to be cherts formed primarily by silicification of calcareous mud before this had consolidated, and before roots and uncalcified organs of Charophytes had lost all their organic matter. These blocks are not precisely localized, but from their fossils are probably of Middle Purbeck age.

The plant material in these cherts can be well seen in thin sections made in the ordinary way, and for most purposes can be well enough seen in the polished surface of the rock. The chert is slightly transparent, and a specimen can sometimes be traced into its smoky depths to a distance of half a millimetre, but for most purposes the only method giving entirely satisfactory results is by obtaining "serial sections", the parts exposed on the surface being drawn and the surface then being ground away and redrawn. Unfortunately there is no means of foretelling whether such a series will give anything useful; too often a stem which has been followed some way proves to be a broken piece ending without showing any new features.

For the purpose of photography it was sometimes found best to etch the polished surface of the chert with hydrofluoric acid by wiping it with 50% acid and leaving it half a minute. This makes the surface white and opaque, and the fossils sometimes show rather clearly where they meet this surface. For serial sections it is not, however, necessary to polish; the finely ground surface, smeared with a little cedar-wood oil, is as good as a polished surface.

Sectioning Isolated Specimens. Specimens isolated by maceration can be sectioned, either to give thin sections or "serial sections" if suitably embedded. For this purpose canada balsam is useless, being too weak, but the synthetic resin made from formalin and phenols is very good. The liquid resin, "R 0014", made by Bakelite Ltd., is excellent. The specimen is boiled in alcohol to rid it of air, placed in liquid resin, and then very gently baked in a drop of the liquid resin on a slide. After

several days' baking at 60° C. it is so hard that the resin cracks off as a piece when the slide is bent.

The piece of resin is then cut to a suitable shape, and if in the right position cemented on to a slide with balsam and ground in just the same way as a rock specimen. If sections at a different angle are needed, a suitable support is made by taking a block of plaster of paris; impregnating this with bakelite and baking well; drilling a suitable hole; placing the embedded specimen in the hole with more liquid bakelite and baking it again at a temperature of 90° C. For the more critical part of the embedding, slow baking at low temperatures is best, as at higher temperatures internal cavities, due to rapid contraction, appear.

Dissection of Isolated Specimens. The specimens of *Clavator* being composed purely of silica are, of course, very hard; they are, moreover, weak and brittle, and it is out of the question to dissect them in the ordinary way under the binocular microscope. It was, however, possible to chip little pieces of nodes away by applying pressure at particular points with a sharp needle. This is apt to cause breaking in the wrong planes, or else the whole specimen springs away. Both of these difficulties can be largely avoided by covering a slide with a thin film of paraffin wax and placing the specimen on this for dissection.

Reid and Groves used somewhat different methods, but the material (*b*) gave their best results also. The rock was first sliced into pieces about 3 mm. thick, and then these slices were etched to the depth of about 0.5 mm. by the "long-continued action of very dilute acid". They do not give details, and were unfortunately hampered by a misconception of the nature of the material; they supposed that the stems which stood out so beautifully in their preparations were calcite, and exposed by the differential solution of the fine-grained matrix. For this reason they made no attempt to isolate the fossils (though they noticed that this occasionally happened), and they made no experiments with stronger acids, which they assumed would have dissolved everything. Apart from its slowness, their method has the disadvantage that, instead of yielding fragments of stems and other organs, it yields sections in planes not determined by the investigator.

The material preserved in marl consists of calcareous skeletons embedded in a soft matrix. The matrix was ultimately removed by long-continued boiling with water or dilute soda. Alternate drying and wetting appears to help to disintegrate the matrix. No attempt has been made to investigate the fossils of the limestones in which no chert formation occurred.

TERMINOLOGY

Many different terms have been used by different authors in describing the same Charophyte organs, so that a statement of those employed in the present work is needed.

The *stem* or *axis* consists of *nodes* and *internodes*. They are composed of *central* cells (*nodal* and *internodal*) and *cortical* cells. In recent Charophytes the cortex also consists of alternate cells termed nodal and internodal, but for various reasons the simpler terms "long cell" corresponding to internodal cell and "short cell" corresponding to nodal cells of the cortex are used here. The short cells of the cortex may bear small "head cells" which bear clusters of small "spine cells".

The nodes bear *branches* of unlimited growth, and *leaves*; the leaves bear the reproductive organs. In *Clavator* the female organ, *oogonium*, is surrounded by a circle of elongated cells adnate to it forming the *utricle*. The oogonium wall is composed of the five *spiral cells*; its outer surface is more or less smooth, but its inner wall is strongly marked by the spiral cells. This inner part of the oogonium is the "*gyrogonite*"; it encloses the cutinised oospore membrane, which in turn encloses the egg.

Groves (1924a) rejected some of these terms, giving his reasons. In particular he preferred to call the leaves "branchlets" because of their different morphology from the leaves of some other plants. To me, however, the risk of the term "leaf" leading to error seems small, while "branchlet" is rather easily confused with a small branch. The term "gyrogonite" seems well worth reviving. It is not quite accurate to term the calcareous body found fossil the "oogonium", as most authors do, since it is but the calcareous inner part of the oogonium, and in such genera as *Lagynophora* and *Clavator*, where another layer of very different appearance is preserved, it is obviously inapplicable. Many authors have termed the gyrogonite the "nucule", though this term is also used for the non-calcareous wall found in recent Charales inside the calcareous gyrogonite, which is here termed the oospore membrane.

FLORA AND FAUNA OF THE CHAROPHYTE BEDS

The flora of the Middle and Upper Purbeck Beds consists of the following:

Clavator reidi Groves.

Clavator grovesi sp. nov.

Clavator bradleyi sp. nov.

Perimneste horrida gen. et sp. nov.

Charaxis durlstonense gen. et sp. nov. (horizon uncertain).

Algacites clavatoris sp. nov.

A minute fragment of imperfectly preserved silicified wood of coniferous type.

Some small silicified roots and leaves.

A local bed (without Charophytes) contains an undescribed flora of conifer leaves and twigs.

The fauna of this and other beds of the Purbeck series is being investigated by Mr. P. Sylvester Bradley and by Mr. F. W. Anderson, and cannot be listed at present. In most localities very numerous Cyprids of several species occur, and in addition small fresh-water Gastropods resembling in general present-day forms of *Planorbis*, *Physa*, *Valvata* and *Paludina*. A few moderate-sized Lamellibranchs occur, but they are less common than Gastropods.

SYSTEMATIC DESCRIPTIONS

CHAROPHYTA (CHARALES)

CLAVATORACEAE

Charophytes with a corticated axis ; branches arising alternately with leaves and without disturbing the cortical cell rows. Oogonia having their outer walls calcified, as well as the inner walls of the spiral cells.

Genus **Clavator** Reid and Groves emend.

EMENDED DIAGNOSIS.—Stem strongly calcified, consisting of relatively slender internodes and swollen nodes ; nodes giving rise to whorls of six equal leaves. Branches alternating with the leaves. Internode composed of a central cell surrounded by twelve series of equal cortical tubes composed of alternate long and short cells ; short cells giving rise to clusters of spine cells which more or less completely cover the cortex. Towards the node six of the cortical cell series becoming greatly enlarged and six diminishing or disappearing. Cortical cell rows uninterrupted from one node to the next.

Leaves simple, composed of a series of longer and shorter cells, the shorter giving rise to clusters of spine cells which more or less completely cover the central cells.

Oogonia borne in a single row on the adaxial side of the leaf, one on each joint. Wall of oogonium showing two calcified layers, the inner forming an ovoid gyrogonite showing five elongate, spirally-twisted cells as in recent Characeae, the outer pear-shaped, smooth or bearing a few tubercles. Oogonium usually enclosed in a utricle composed of about ten elongated adnate cells.

Antheridia not calcified, form unknown, but borne singly on the adaxial side of a leaf, one on each joint, corresponding in position to oogonia, but not found on same leaf.

This diagnosis differs in the following chief particulars from that of Reid and Groves: The stem is branched ; it does not form "heads" at its termination ; the clavate processes borne on leaves and stems are recognised as distinct cells (very like

the spine cells of recent Characeae). The existence of an outer calcified wall of the oogonium is recognised. The position of the antheridia is recognised.

COMPARATIVE MORPHOLOGY

In its general organisation, *Clavator* is comparable with other Charales, in particular with the more robust species of *Chara*. There are, however, some striking differences in detail:

(1) The branches alternate with the leaves instead of being axillary.

(2) The leaves of successive whorls are superimposed instead of alternating.

(3) The cortex consists of continuous series of cells which are not interrupted in the middle of the internode, as in recent corticated Charales. Evidently it is formed in a different way.

(4) The cortex consists of six "primary" and six "secondary" series of cells; but the six "secondary" bear spine cells in exactly the same way as the "primary". In recent Charales with secondary cortical series (diplostichous) these cells are distinguished by being without spines.

(5) The swelling of the six "primary" cortical series at the node is peculiar.

The comparative morphology of the oogonium is straightforward, since its features can be readily understood in terms of those of the recent Characeae. It has the following peculiarities:

(a) The outer wall of the oogonium is calcified, as well as the inner. Its shape is slightly unusual.

(b) The outer wall of the oogonium often shows conspicuous blunt knobs.

(c) The oogonium is invested in a utricle.

In the shape of the oogonium and in its calcified outer wall, *Clavator* agrees with the Tertiary genus *Lagynophora*. It is unfortunately not known whether the agreement extends to the arrangement of leaves and branches.

In the papillae of the oogonium *Clavator* resembles *Kosmogyra*. It is true that in *Clavator* the oogonium has papillae while the gyrogonite is smooth, but in *Kosmogyra* it is apparently the gyrogonite which shows them. Their resemblance is so close, however, that they may well be of similar nature. If so it is significant that in *Clavator* the longitudinal rows of papillae have no relation to the surrounding cells of the utricle; in *Kosmogyra* therefore they may also have no relation, and there is thus no reason to suppose that *Kosmogyra* possessed a utricle.

The utricle is evidently a group of modified spine cells or bracts. Though no recent plant shows a similar calcified utricle, Groves (1924a, p. 79) states that in an African species of *Chara*

the oogonium is enclosed in a sheath of separate bracts of similar appearance.

The gyrogonite of *Clavator* is remarkably small, that of *C. grovesi* being quite the smallest hitherto described. Its structure, however, is normal.

Clavator seems to have agreed in general appearance with the recent Charophytes, and also in certain fundamental features of the organisation of the oogonium and shoot. It has, however, some very well-marked peculiarities in which it differs from every existing genus, and which seem to make it, together with *Perimneste*, well worthy to be separated as a distinct family, equal in rank to the Characeae and to the Nitelleae.

It is interesting to note that the fossil genus *Lagynophora* is in some respects at least nearer *Clavator* than is any existing genus.

HABIT OF CLAVATOR

Although very much broken, the material of *C. reidi* provides some idea of the habit of the plant; *C. grovesi* seems to have agreed with it, though rather larger in its vegetative parts.

From creeping stems with short internodes erect stems of considerable length arose. These were provided with nodes at intervals of about 1 cm. from which whorls of six short leaves sprang, and often also a single lateral branch. In certain parts of the plant the leaves bore the reproductive organs, antheridia or oogonia in a single file along their inner sides.

The plant grew in a calcareous freshwater lake, and was heavily calcified, so that it must have been very hard while alive.

Clavator reidi Groves

(Pls. I-IX; X, figs. 13-18; XVII, figs. 1-4, 7)

1916. *Clavator* Reid and Groves, p. 253, pl. viii. (Diagnosis of genus but no specific name appended.)

1924. *Clavator Reidii* Groves, p. 116. (Name alone, but intended to refer to above diagnosis of genus.)

As will be seen from the above references, the way in which the name *C. reidi* was bestowed is somewhat irregular, but there is no doubt to what fossil it applies.

DIAGNOSIS.—Internodes normally attaining a diameter of 1 mm., nodes of 2 mm. Leaves up to 0.6 mm. thick. Calcified parts of spine cells covering leaves and stem commonly short, rarely exceeding 100 μ in length, forming small and simple clusters on the internode.

Utricle of oogonium usually well developed, but sometimes feeble or absent; never laterally compressed to any considerable extent. Oogonium normally pear-shaped, swollen basal part

about 450μ wide, total length about 700μ ; surface smooth or bearing a number of very low papillae. Gyrogonite of oogonium more or less ovate, typically 500μ long, 400μ broad (extremes 650μ – 380μ long and 450μ – 250μ broad), in lateral view crossed by 9 or 10 spiral ridges (extremes 8–11). Spiral cells usually convex or flat, but sometimes concave, usually concave at the base and so forming a small "cage".

LECTOTYPE.—V. 13279. Figured Reid & Groves, 1916, pl. viii, fig. 4.

HORIZON.—Middle and Upper Purbeckian.

The description is arranged as follows:

- (1) The stem internode; the central tube; the cortex; the spine cell layer; different states of preservation.
- (2) The stem node; anatomy of node.
- (3) The leaf; oogonial and antheridial leaves.
- (4) The fructifications; the utricle; oogonium; gyrogonite; states of preservation.
- (5) The identification of the various types of organ as one species.

1. *The Stem Internode: General Remarks.* Internode fragments make up the bulk of the macerated material; in all, many thousand specimens were examined. These fragments are mostly short, averaging perhaps 2 mm., and though many are continued into a node, very few show two nodes. As one might expect, however, the specimens showing two nodes are very short, indeed shorter than some of the incomplete fragments. The normal length of the internode is thus unknown, but estimates of its length were arrived at as follows:

First method: The entire yield of *Clavator* stems from a particularly rich pebble was sorted, and the pieces of stem which included a node and those which were purely internode were put in separate piles. The total length of stem represented in both piles was measured and divided by the total number of nodes.

The following results were obtained:

$$\frac{\text{Length of stem}}{\text{number of nodes}} = \frac{550 \text{ cm.}}{471} = 12 \text{ mm. approx.}$$

This of course is an average for all parts of the stem.

Second method: This method depends on the probability of a fragment of a particular length including a node. It will be seen that if the internodes were, say, 10 mm. long and were chopped into 5-mm. lengths, half of the pieces would include a node and half be without. Had the internode been longer than 10 mm. the fraction would have been lower; so this fraction provides a basis for an estimate.

The following results were obtained:

Stem fragments 2.5 mm. or more picked out: mean length of fragment between 3.0 and 3.5 mm.

Number of pieces without nodes, 262.

Number of pieces with nodes, 75.

Ratio nearly 3·5 : 1.

This would give a length of internode of between $3\cdot5 \times 3$ and $3\cdot5 \times 3\cdot5$, *i. e.* between 10·5 mm. and 12·25 mm. This estimate is the same as that arrived at by the first method.

Both estimates depend on the assumption that the fossil material is a fair sample of the original plant. It is possible, however, that the nodes were differently transported by water and consequently were over- or under-represented.

Central Tube. The stem internode consists of a central tube representing the internodal cell, which is surrounded by the cortex consisting of twelve tubes representing the vertical files of cortical cells. The cortex is more or less encrusted with an outer mantle of spine cells of greatly varying development.

The central tube is of circular section, and shows no sign of a constriction anywhere between one node and the next. Its width is about three-fifths of the total width of the stem excluding the spine-cell layer (Pl. III, fig. 2) (the relative width of the various tubes is, of course, determined geometrically). The only local features the central tube shows, apart from those due to bad preservation, are small pores situated opposite the cortical short cells. Each of these pores may be a single oval hole (Pl. V, fig. 7), or instead there may be a group of very minute apertures.

The central tube is regarded as a single cell running from one node to the next, and provided with pits through which the protoplasm communicates with that of the cortical cells.

Cortical Tubes. The cortical tubes are invariably twelve in number and are all of the same size and structure (a specimen in which this is not true is mentioned later). They are continuous in the fossil, the transverse septa which are supposed to have existed being evidently uncalcified. The cortical tubes usually show that a distinct twist has taken place in the growth of the stem; this torsion is invariably dextral (*i. e.* like an ordinary screw).

Although the cortical tubes have thickly mineralised lateral walls they never show transverse septa in the internode. Towards the node, however, partial septa occur which make the vertical limits of the cells clear; each vertical rank of cortical cells near the node consists, as before, of a series of relatively long cells and relatively short cells. The short cells near the node appear to have been wedge-shaped, only extending a short way inwards, so that the ends of the long cells are in direct contact over most of their surface. In the internode the position of the ends of the short cells is only apparent on the surface, and it is not shown how far inwards they may have extended. There is, however, a pore in the wall of the central cell which is

situated just opposite the short cell and seems to suggest a direct communication with the short cell, in which case it is likely that the short cells extended right across the cortex, and not as in the nodal region only part way. It is noteworthy that in the nodal region no perforations in the wall of the central tube occur. The perforations seem to be constantly present in the internode.

The cortical tubes are dilated at the base of each rosette (*i. e.* the short cell is enlarged) and the outer surface is pierced by a considerable number of holes, each of which forms the base of a spine cell. These clusters of spine cells give the most obvious indication of the position of the short cells.

The short cells of the cortex seem as a rule to be roughly isodiametric. The length of the long cells of the cortex can be recognized most easily in a stem mounted in cedar-wood oil, but even in a dry stem fully covered with spine cells, the points of origin of the spine-cell groups (*i. e.* the short cells) can always be recognized. The distance between these points varies greatly; in most specimens it lies between the limits of 350μ and 900μ , but specimens with cells as short as 80μ and as long as 1200μ were noted. No correlation was noticed between the length of the cortical cells and the thickness of the stems; that is, one narrow stem will have short cells, the next long ones, and the same is true of thick stems. In any particular internode, however, they are fairly uniform.

A very significant point which was made out with certainty is that the cortical tubes run uninterruptedly throughout the internode; no specimen shows the arrangement seen in *Chara*, where one set grows up from a node and an entirely different set grows down from the node above. Although only one complete internode was studied in detail, this was established for all of a great number of internode fragments, and had any discontinuity existed it would without doubt have been found.

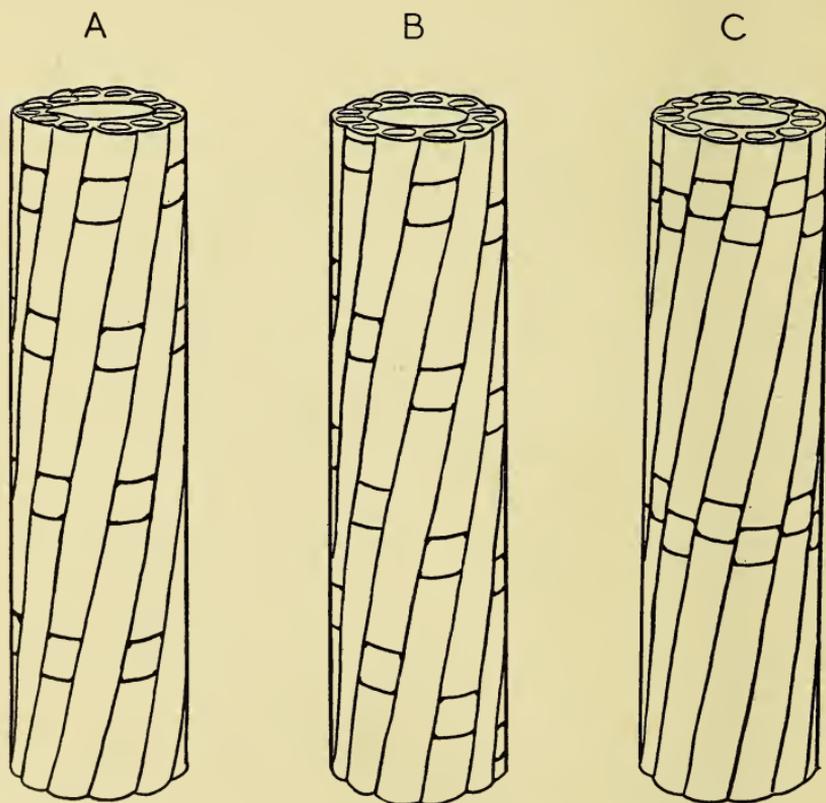
The position of the short cells, as the points of origin of the spine cells, largely determines the appearance of the internode.

Most commonly the short cells of adjacent rows alternate—each lying next to the middle of the long cell. Where the "long cells" of the cortex are fairly short this results in a quincuncial arrangement of the short cells, but where the long cells are of considerable length a pattern of interrupted rings results (Text-fig. 1A). Often the alternation is inexact, the cell on the right being slightly displaced downwards, so that instead of forming rings, the short cells form an interrupted spiral (Text-fig. 1B). The underlying differences are, indeed, very slight, and it is common to find a specimen with rings in one part, spirals in another. Very few specimens show a right-handed spiral of short cells (Pl. III, fig. 9); it is nearly always left-handed, as in Text-fig. 1.

Another rather rare arrangement—in not more than 1% of

specimens—is based on the cortical cells being nearly opposite (they are never exactly opposite). This results in a pattern of double rings at rather long intervals (Text-fig. 1c). No other regular arrangement was met.

The central cell and also the cortical cells are almost round in section. Intercellular spaces, which may be of moderate size, are therefore to be found. Towards the node much enlarged inter-

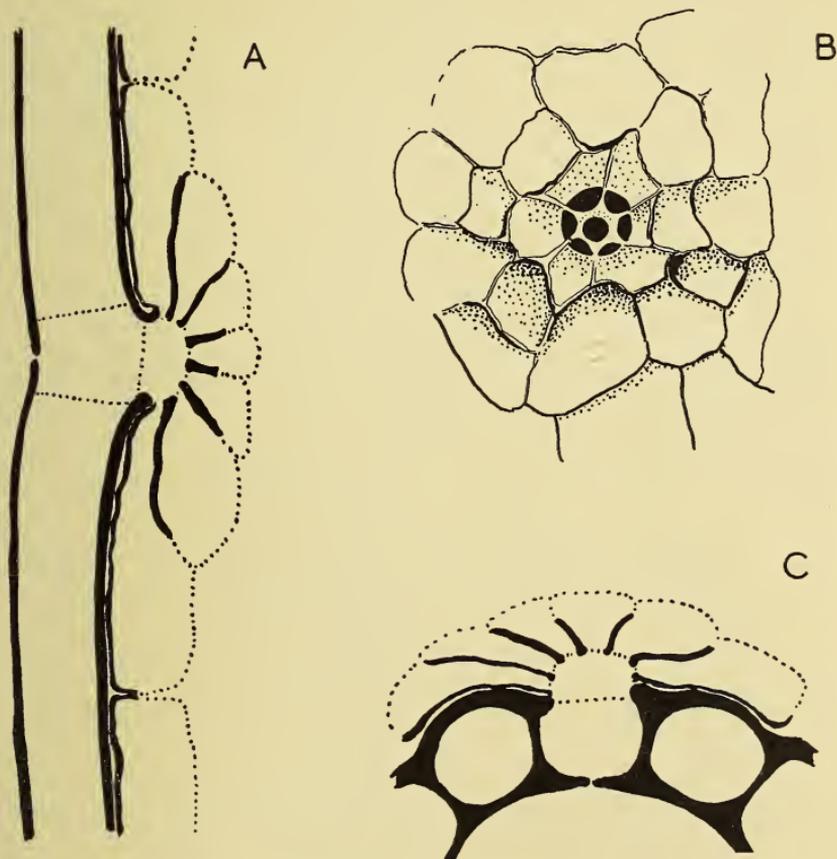


TEXT-FIG. 1.—*Clavator reidi*
Diagrams of the internode of *Clavator* illustrating the three chief patterns
made by the short cells of the cortex. $\times 20$.

cellular spaces are usually found between the central cell and the six cortical cells which diminish and vanish.

Nodal Cells. Most specimens provide no evidence bearing on the existence of a nodal cell or cell group, since transverse walls are not preserved. In occasional blocks, however, such walls are partially or completely preserved, and this was so in one specimen embedded in bakelite and subjected to serial sectioning. In this the end of the central tube of the internode below was completely shut off by a wall which was not flat, but marked by imprints which suggested that the node was occupied not by one but

rather by a group of cells. The corresponding diaphragm above the nodal group was not present in this specimen, but a slight rim was found suggesting that it existed, but was not mineralised. From such specimens it is concluded that a nodal cell or cell group is present in the stem.



TEXT-FIG. 2.—*Clavator reidi*

Diagrams showing the structure of the cortex. A, longitudinal section; the central cell is to the left. B, surface view of a spine-cell rosette. C, transverse section through a spine-cell rosette. Walls normally found preserved are shown in black; walls not preserved but presumed to exist are shown by dotted lines. V. 26060, $\times 60$.

Spine Cells. The spine cells commonly form a thick crust, which may completely conceal the cortex in a dry specimen (though after clearing in cedar-wood oil the cortex becomes obvious). The coat of spine cells might in fact be regarded as an outer cortex. Though very unevenly formed, every specimen shows at least some vestiges of this outer layer of spine cells.

In its feeblest development it consists of one to three small

cells, formed from the bulging top of a short cell of the cortex ; in its maximum development it is a thick crust of almost uniform aspect. In the great majority of specimens it consists of distinct rosettes of twelve to twenty cells, each rosette being formed from a short cell, and although the rosettes are often in contact, it is possible to make out which cell belongs to which.

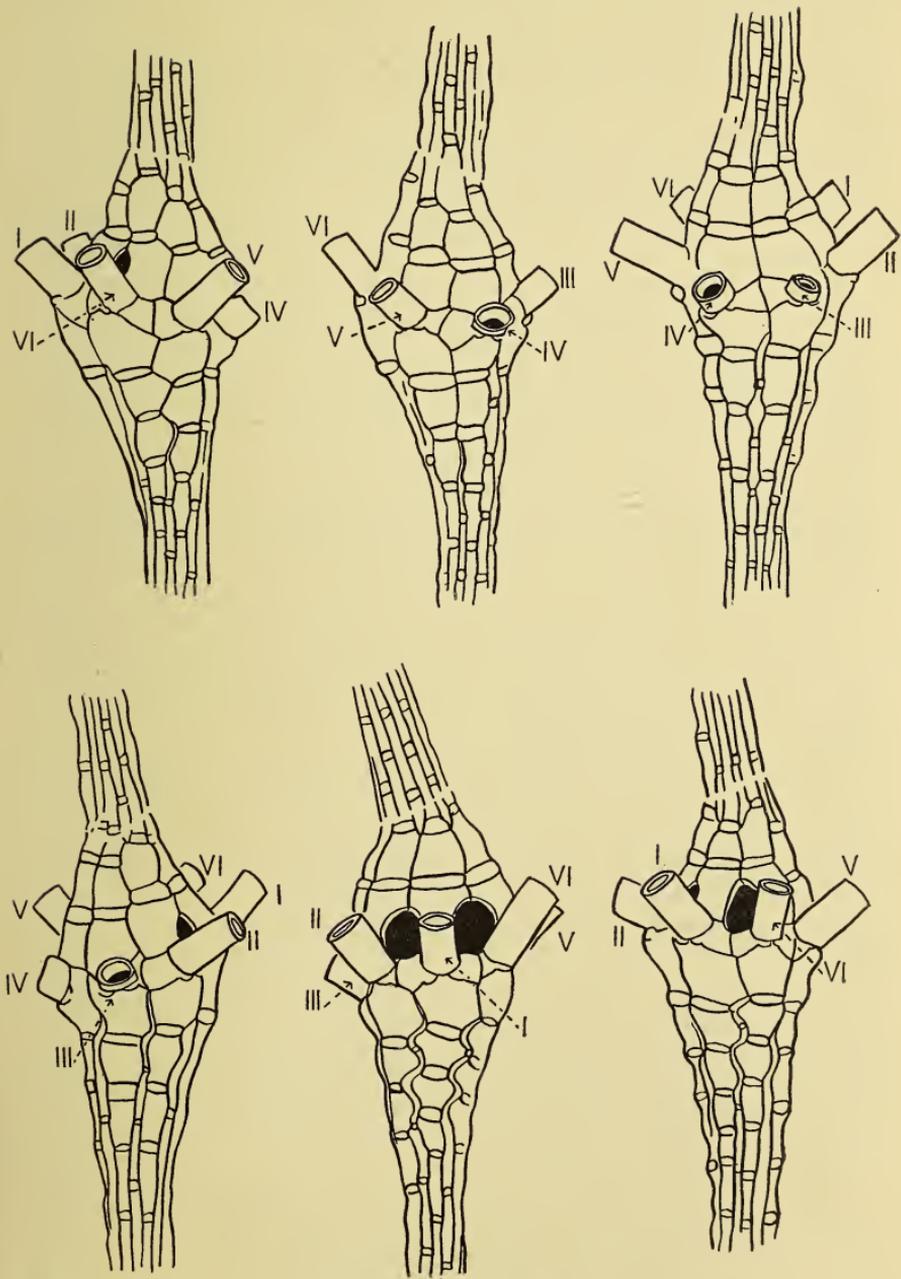
The only part of a spine cell which is usually preserved is its inner funnel-shaped half, the narrow end communicating with the cortex. At the top or centre of the rosette there is usually a single short erect cell ; round this are five or six obliquely-placed cells, and round them about twelve very oblique and irregular cells in one or two rings. In stems with rather crowded spine-cell rosettes these outer cells are everywhere in contact with the cells of other rosettes, and in such specimens the outer cells usually spread out to a less extent than usual.

Variation. Apart from the specimens in which only a few cells are produced in each rosette, the chief variations are due to (1) crowding of the rosettes, with consequent reduction in area of cortex covered by their outer cells ; (2) variation in the amount of the wall mineralised and preserved. In a few specimens almost the whole of the walls of the spine cells is mineralised and preserved (Pl. III, fig. 4). These specimens, although very unattractive, are of value in showing that the surface of the stem was nearly smooth and in giving the shape of the cortical cells. There are all intermediate forms between such specimens and those in which the wall is only mineralised at its base.

Exceptional Cortical Structure. In one internode the structure is anomalous in that six rows of cortical cells are much larger than the other six which are placed opposite them. Both sorts of cell bear spine rosettes, though these are of unequal size (Pl. III, fig. 8).

States of Preservation. It has been pointed out that the fossils described here depend for their recognition on two distinct processes of mineralisation : the primary calcification of the cell membranes which occurred during life, and then after the stem was dead and buried in calcareous silt a replacement of the calcite of the cell membranes by silica. A fully preserved specimen depends on the perfection of both processes, and the imperfection of either may result in some parts being missing. These imperfect specimens are therefore described merely as incompletely mineralised. Their importance is that they look very different from the normal stem, and need description if only to prevent their being subsequently regarded as different species or genera.

The parts most frequently missing are (a) the walls of the central cell, particularly opposite the short cells of the cortex. (b) The radial walls of the long cortical cells. This often results in the isolation of the central cell as a strongly fluted tube (Pl.

TEXT-FIG. 3.—*Clavator reidi*

Camera-lucida drawings of a node from six different aspects. The leaves are numbered; the nodal holes are shown black. The spine cells are omitted. **V. 26060**, $\times 12$.

IV, fig. 10). (c) The outer walls of the cortical cells are missing in the region of the short cells. The effect of this on the aspect of the internode depends on the arrangement of the short cortical cells and the proportion of the outer wall preserved (Pl. II, figs. 5, 7; Pl. V, figs. 1, 6, 8, 9). These specimens by no means exhaust the forms which are to be found—specimens, for example, consisting of no more than a spiral thread like a corkscrew, and many other curious forms occur.

The reasons for the identification of these different stem types are given on p. 40.

2. *Node: External Form.* The node of *Clavator* is most characteristic; a few millimetres below the node the stem begins to enlarge, and it continues to increase until it is about twice its former diameter. At this point a whorl of six leaves arises and then the stem contracts again to its former diameter. As a rule the stem contracts to its normal width much more quickly above the node than below it.

In addition to the leaves the node shows two "nodal holes"; occasionally also it bears a branch. The nodal holes and branch (if any) occur just above the leaf whorl and alternating with the leaves.

The largest node isolated measures 2·3 mm. wide at the point of departure of the leaves; the smallest are as narrow as 0·6 mm. In a few of the smallest the stem does not swell at all in reaching the node, but the cell structure, even of these specimens, appears to be quite normal.

Reid and Groves (1916) speak of the nodes as "heads", by which they mean a stem-ending such as is found in many recent Charales, in which the stem apex aborts and a crown of reproductive leaves grows out with considerable vigour. I am convinced that no such structure existed in *Clavator*, for of the great number of nodes I isolated, every one showed either the continuation of the stem or else the broken-off stump of the stem. The reason they reached their conclusions is undoubtedly that they were dealing with sections. The plane of section depended on chance, so most were decidedly oblique, and while they continued some way through the long swollen part below the node, they soon left the more quickly contracted part above. Probably the apex of *Clavator* was unspecialised and continued growth indefinitely, as in *Chara*.

The enlargement of the node is caused by the increase in size of the six rows of cells which lie above and below the leaves, while the other six grow smaller, are displaced to the surface and disappear, to appear again a little above the node. These features are usually obvious from the surface observation of a dry specimen, but are far more conspicuous in a specimen mounted in cedar-wood oil or balsam, and will be described in detail when the anatomy is considered.

As the six rows of cortical cells enlarge a change occurs in their spine-cell rosettes. Instead of being more or less round they become transversely elongated, extending right across the cortical cell, which is now about four times its former width, though the individual spine cells remain just the same.

The arrangement of the spine cells in each broad rosette shows that they now no longer form a single cluster, but two or three clusters side by side, and from the internal structure it can be seen that they spring from two or three "head" cells side by side instead of a single one. Just below each leaf there are two particularly well-developed spine-cell rosettes.

The "nodal holes" are a conspicuous feature in every specimen; they vary a good deal in size, but with the exceptions mentioned below there are constantly two, and these lie next one another (as in Text-fig. 3). Where the holes are rather large, they reduce the cortical cell between them to a mere bridge, but they are never so large as to run together.

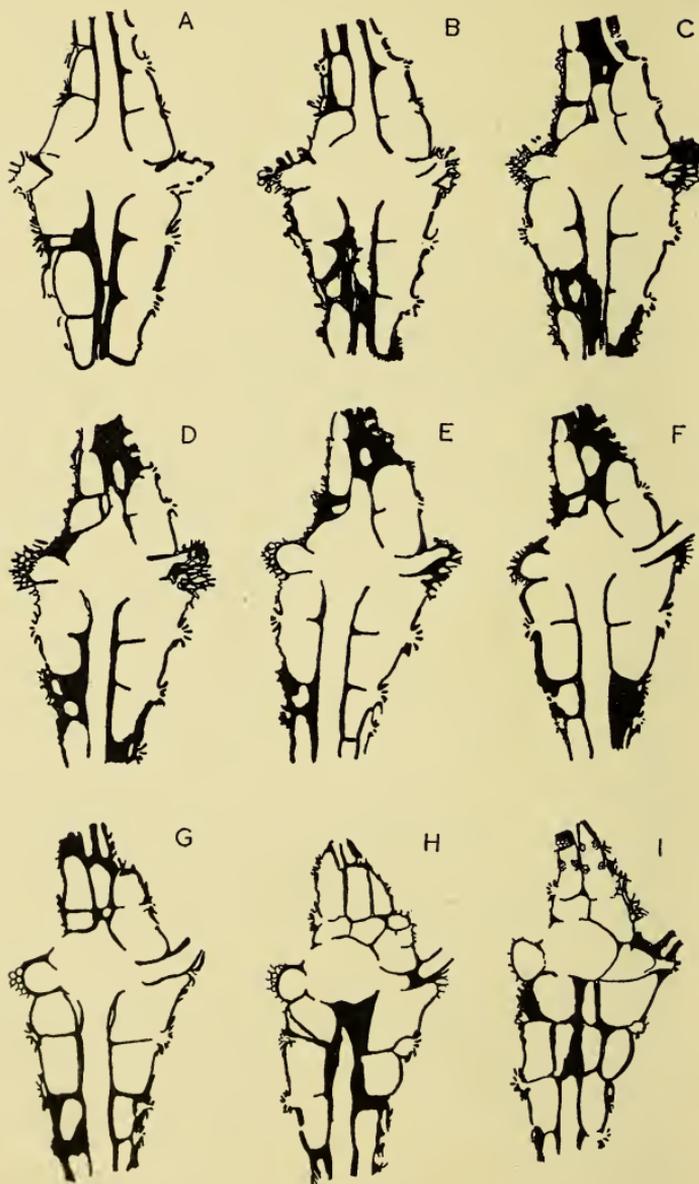
Certain rather exceptional specimens throw light on the nature of these holes. In most specimens where a small or moderate sized branch is present, it arises at one or other side of the nodal holes, so that in the intervals between four adjacent leaves are found (1) branch, (2) hole, (3) hole. Sometimes, however, only one hole is found—the branch has replaced the other.

In other specimens (*e.g.* V. 26097), which are perhaps merely well preserved, the hole is not completely open, but partly closed by a very delicate membrane, and in one of these a very minute tubular outgrowth arises from the middle of this membrane. This outgrowth I take to be an abortive branch.

These facts lead me to suppose that the nodal holes represent potential branches which did not actually grow out, but which were represented by dormant apices and which were uncalcified or very feebly calcified. If the isolated nodes were able to act as vegetative reproductive units, then new growth might perhaps take place at these points.

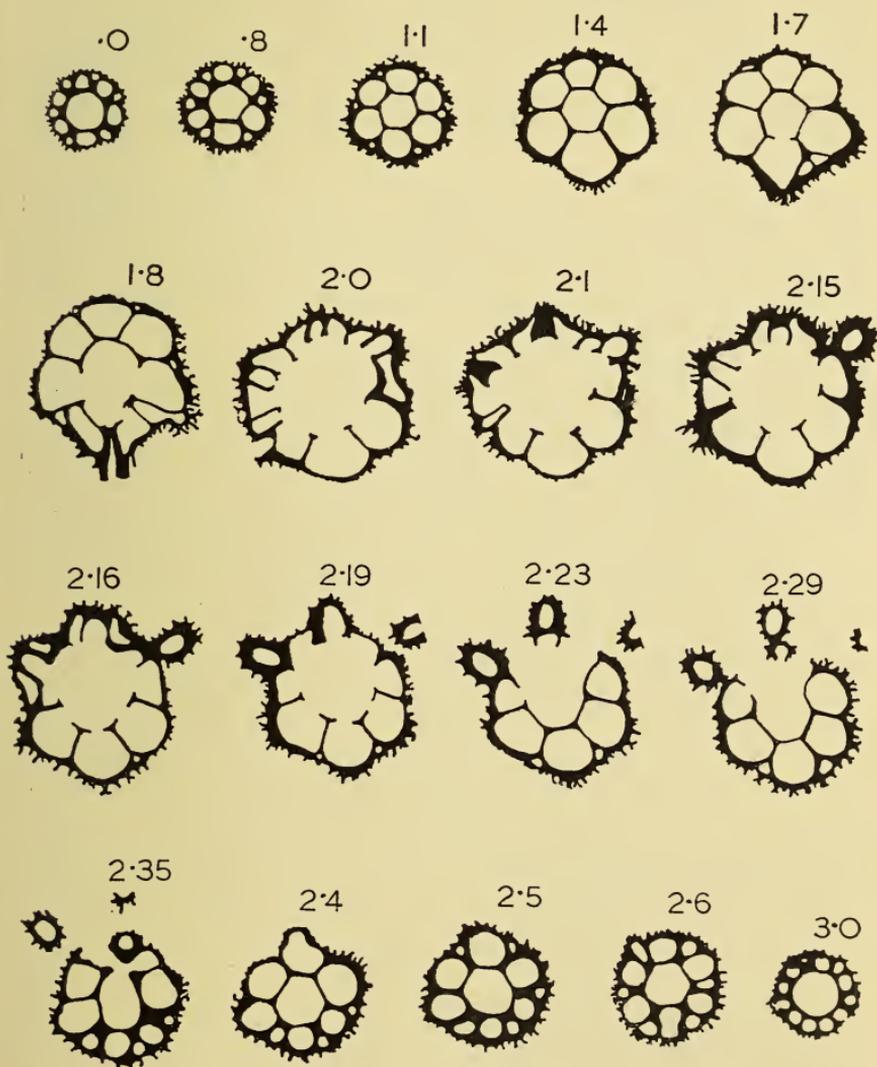
In one specimen in a single interval between a pair of leaves a branch *and* a hole occurred; this specimen might be held to provide evidence against the above interpretation of the nodal hole. In a few specimens where this point was studied the branch proved to be uncorticated at its base, consisting merely of the central cell, but immediately above its base a cortex and spine cells are developed.

Anatomy of the Node. Although nodes are common enough they are seldom preserved suitably for a study of their deeper anatomy, because the replacement of the calcite by silica has often failed in their deeper layers. Blocks differ a good deal, however, in this respect; the best yield a sufficient number of well-mineralised specimens, and on these the following description is based.

TEXT-FIG. 4.—*Clavator reidi*

Camera-lucida drawings of serial sections through the middle region of a node. Distance between successive sections about 30μ . V. 26001, $\times 13$.

In the majority of good specimens the central tube is dilated just below the leaves, but at this point its wall becomes incomplete, being calcified along the borders of the cortical cells, but not



TEXT-FIG. 5.—*Clavator reidi*

Camera-lucida drawings of serial transverse sections through a node. The levels of the sections in mm. are indicated by the figures. The sections start below the node and are all orientated similarly. V. 26022, $\times 15$.

opposite their surfaces. It thus has the form of an open funnel which has been dissected by the removal of six large pieces from its rim (Text-fig. 6A). The funnel reaches its widest point and

ends at the level where the leaves begin. Opposite the leaves the central tube appears to be continued by a wide but short length of tube; above the leaves it contracts again, forming a funnel like the one below. It may thus be pictured as having three sections—two funnels with their wide ends separated by a broad disc. The funnels, however, are dissected by six large holes, while the intervening disc is still more dissected, the only portions present being narrow bands where the walls of outer cells meet it.

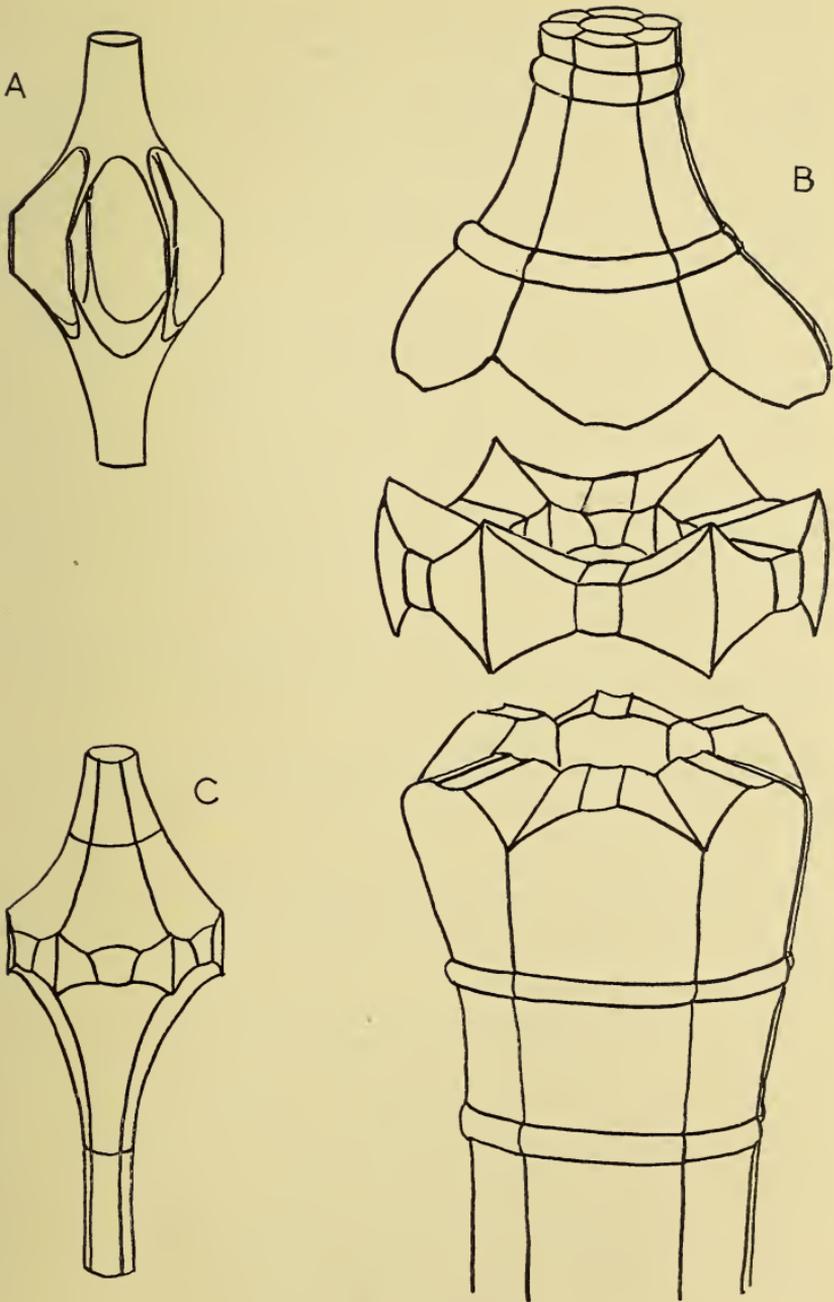
In one specimen the central tube was not at all dilated as it approached the leaves, that is to say the funnel-shaped parts are not developed, and in consequence the short portion opposite the leaves is of just the same width as the rest; here also the central tube is unusual in not being dissected, but its whole surface is mineralised.

Nodal Cell. There is usually no direct evidence for the existence of a nodal cell or cell group since no transverse wall is mineralised. There is, however, no evidence against it. The only reason for supposing that such a cell may exist would depend on analogy with recent Charales, where it is universal. The probable alternation of long (internodal) and short (nodal) cells in the cortex and in the leaves suggests that this plant is constructed throughout in the normal manner, in which case a nodal cell or cell group would exist at the stem node.

The behaviour of the cortex is most interesting. At a distance of 2 or 3 mm. below the node the six cell rows below the leaves enlarge, and the alternate six move outwards so that they lose connection with the central tube. This enlargement continues until these cells are about four times their former diameter, and as their walls are no thicker, the lumen is six or more times as wide as it was. Another change which may often be seen is that the "long cells" of the cortical rows become rather less long, making the short cells with their spine-cell rosettes rather closer, but this is not always true. What is more significant is that the ends of these cortical cells become mineralised along their inner and lateral walls to form a perforated septum between one cell and the next. Since these septa are single, it is evident that the short cells of the cortical rows did not extend right to the wall of the central tube as in *Chara*, but must have had the form of a small wedge situated in the outer part of the cortex.

Calcification has also occurred round the bases of the spine rosettes in the form of inwardly directed flanges. These flanges divide the rosette into two or three parts, which are evidently separate "head" cells formed by division of the short cell.

At each side of each leaf is a moderate-sized cell which bears at its lower end near the leaf base a particularly large spine rosette. These cells, which are termed lateral cells of the leaf base, have walls which extend inwards to meet the central tube,

TEXT-FIG. 6.—*Clavator reidi*

Diagrams representing the structure of the node of *Clavator*. A, the part of the walls of the central tube preserved in the better specimen. B, a node with the cortex dissected into three parts; the middle ring is the leaf whorl. C, restored central tube showing the imprint on it of the leaves and their lateral cells. $\times 20$.

and the walls of the leaf base itself extend inwards very close to the central tube, if not right to it. From the arrangement of the inner walls it appears natural to regard the leaf and its two lateral cells as a sort of unit, and this unit would then show a striking agreement with one of the divided short cells immediately below. In fact the alternation of long and short cells of the cortex would appear to show no essential interruption throughout the stem. This is different from what is seen in the recent Charales with cortication.

The spine rosettes of the basal cells of the leaves, although not subdivided by even incomplete partitions, yet give an indication that several small cells may be present, for the holes at the bases of the spines tend to be arranged in groups.

Above the node, the cortical cell rows rapidly diminish and become normal in size again. The nodal holes, or any branch which may exist, make the minimal disturbance, being borne at the sides of the large cortical cells immediately above the leaves. Where the two nodal holes are very large, the cortical cell between them is reduced to a rather narrow bridge, but there is no other disturbance.

The six cortical cell rows which diminish and disappear, do so at various levels, sometimes as soon as the stem begins to enlarge, sometimes just below the leaves. Often they become sinuous or irregular in their upper parts.

Above the node also they make their reappearance in a somewhat irregular way. As soon as they appear they give rise to their usual spine rosettes, though these are small and formed at rather irregular intervals.

3. *Leaf.* The leaves are invariably borne in whorls of six at the nodes, and all the leaves of a whorl are equal. They point upwards and radially outwards, and in specimens sufficiently well preserved are seen to be somewhat incurved. They never branch.

Since the leaf is very fragile and had usually broken up before preservation, its length is seldom shown. In a few complete specimens it varies from 2-6 mm., but this gives little indication of what might be the normal length. Attempts were made to determine the length by indirect means. One method was to isolate all the leaves from a rich pebble, measure their total length, and divide by the number of nodes present multiplied by six. The method gave a result of about 2 mm., which is probably too low; it was subsequently noticed that in some pebbles leaves are far commoner in relation to stems than in others, no doubt as a result of a certain amount of sorting by the action of water. This would invalidate the method.

Probably a fair picture of the length of the leaf is given by the way the fragments of it taper. By placing together suitable fragments, what would appear to be an evenly tapering leaf can

be built up (Pl. III, fig. 6). On this basis it was concluded that the normal leaf was between 5 and 10 mm. long.

As usually preserved, the leaf consists of a continuous tube, swollen at short intervals to form nodes, from which clusters of spine cells spring. Such specimens provide no direct evidence for the existence of short "nodal" and long "internodal" cells in the leaf, but the best specimens make it clear that this structure existed. Immediately below a node of the leaf is an exceedingly delicate diaphragm, and a similar one presumably occurs above (though no specimen happened to show both). The two diaphragms would delimit a lens-shaped nodal cell.

The intervals between successive whorls of spine cells on the leaf become progressively less towards the apex of the leaf, so that while in the lower part the segments of the central tube are about 800μ long \times 300μ broad, towards the apex they become as small as $150\mu \times 150\mu$.

At the point of origin of the spine cells the central tube is dilated. This enlargement is not even, but consists of six distinct bulges from which the spine cells spring. These bulges doubtless represent six distinct "head" cells. In the best specimens there is a vestige of a septum between the head cells and the nodal cell in the form of a delicate ring.

The spine cells arise in dense clusters which form globular or oval masses. They have exactly the same character as the spine cells of the stem, and like them usually show their basal parts alone mineralised, but sometimes are mineralised to their apex. In such specimens the surface of the whole mass of spines is almost smooth.

The leaf apex is rather seldom found; it is much less heavily mineralised than the lower part of the leaf. Its form is, however, well shown in a sufficient number of specimens; it is sometimes acute, or sometimes rather obtusely pointed. In oogonial leaves, oogonia are lacking from the upper few joints so that the apex of an oogonial leaf is just like that of a sterile leaf.

The most noteworthy variation in the leaf is in the relative distance between successive whorls of spine cells and in the size of the spine-cell whorls. Thus in some leaves the whole surface is almost evenly covered with spine cells; in others it is largely bare, with little spherical masses of spine cells at long intervals.

Antheridial Leaves. The specimens which are termed antheridial are very common, perhaps one-third as common as sterile leaves. They only differ from the sterile leaves in being provided with a series of exceptionally large perforations. At each joint there is a single large round hole leading to the central tube. These holes invariably occur singly and on the inner side of the curved leaf, and where present at all they seem to occur at almost every joint except those at the base and apex. The diameter of the hole varies from 60μ to 110μ .

These holes evidently mark the point of origin of a fairly large lateral organ, and from its general relations it is considered that this organ was an antheridium. No trace of the antheridium itself is preserved, but this would not be expected, because the antheridia of the recent Charales are not calcified. It is, however, very easy to imagine the appearance such a leaf with antheridia would have had if they were the usual sessile spheres found in this family.

Oogonial Leaves. Oogonial leaves are as common as antheridial, and about a third as common as sterile leaves. They are distinguished by bearing along the concave side (the upper) a single row of oogonia, one of which arises at each joint, except at the apex and base. It is very unusual for an oogonial leaf to have any sterile joints in its middle region (though one such specimen was found), but frequently some of the oogonia are of minute size.

At the point where an oogonium arises there is a much larger swelling or head-cell than the usual ones at a leaf joint, and from this the oogonium and the cells of the utricle all arise.

It is noteworthy that no specimen was found with both oogonia and antheridial holes. Evidently a single leaf bore exclusively one or other organ, and it would appear very possible that the plant was dioecious. A very few specimens were found in which two oogonia spring from the same joint, either side by side or one above the other. In such specimens one is normal, the other minute and probably abortive.

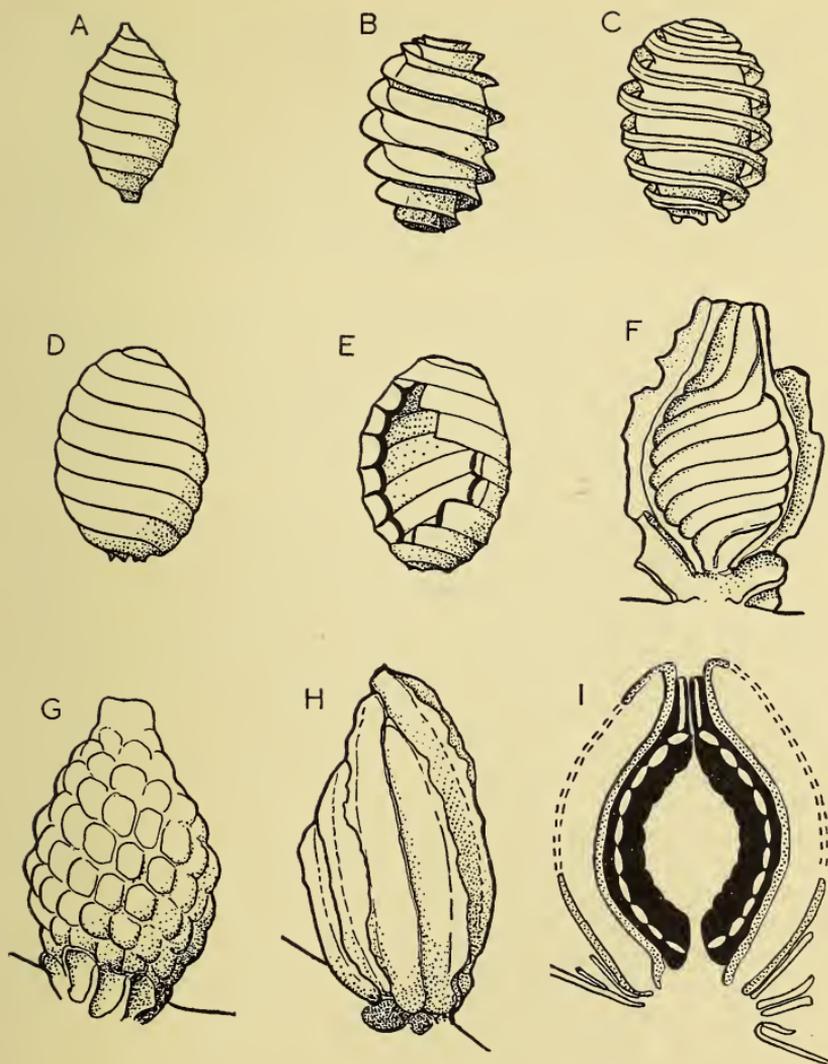
In the chert of primary origin from Durlston there are some shoots which are less broken than usual, having apparently been silicified before the plant material had rotted. In sections of this chert whorls of fertile leaves were sometimes found cut through. These sections showed that the oogonia are borne always on the adaxial side of the leaf, and also that every leaf of the whorl is oogonial. This fact provides support for the idea that *Clavator reidi* is dioecious.

4. *Oogonium and Utricle.* In *Clavator* the egg is surrounded by an oogonium composed of the usual five spiral cells, and this is surrounded by a second coat of cells, the utricle. Although thus simple in essence, the varying states of preservation and aspects in which they may be seen give a rather bewildering variety of forms to this organ. The chief of these are related to one another in Text-fig. 7.

These various forms will now be reviewed.

(1) The most complete state in which the outer walls of the utricle cells are mineralised and preserved is rarely found. In this state the utricle is a heavy and rather shapeless object very firmly attached to the leaf, and often also to other utricles of adjacent oogonia (Pl. VII, fig. 9).

(2) Normally the inner wall and some part of the lateral walls

TEXT-FIG. 7.—*Clavator reidi*

Diagrams illustrating some of the ways in which the oogonium of *C. reidi* is preserved. A, internal cast of gyrogonite (this probably corresponds to the egg). B, the cast is surrounded by flanges which are the radial separating walls of the gyrogonite. C, the cast is surrounded by spiral bands which are parts of the surface walls of the gyrogonite cells. D, the whole surface of the gyrogonite is preserved. E, a broken gyrogonite is seen in section. F, internal view of an oogonium and utricule broken open longitudinally. G, exterior of the oogonium in which the utricule is vestigial. The oogonial wall is tuberculate. H, utricule enclosing oogonium. I, ideal longitudinal section showing on the outside the utricule cell walls (stippled) parts normally missing (in broken lines), and the various parts of the oogonial wall (in black). The small white cavities in the wall represent the cells, and are the point at which the gyrogonite normally separates from the outer oogonial wall. $\times 60$.

of the utricle cells are alone mineralised. In this state the utricle is a very striking fluted body fairly firmly attached to the leaf, but sometimes isolated (Pl. VII, fig. 6; Pl. VIII, figs. 3, 8, 9; Text-fig. 7H). This is the commonest form.

(3) A considerable part of the utricle is not mineralised at all, and consequently not preserved, if indeed it was present. The part most commonly missing is on the upper side near the oogonial apex, but the whole of the upper part may be bare, while the lower part and sides are fairly well mineralised (Pl. VIII, figs. 1, 2).

(4) The utricle is unrepresented in the fossil except perhaps at the very base of the oogonium. In such cases the oogonium is only attached to the leaf by its own base and is very often found isolated. The surface of the oogonium may be smooth or tuberculate (Pl. VII, figs. 2, 4, 10; Pl. VIII, fig. 7; Text-fig. 7G). The apex of the oogonium also varies a good deal in its mineralisation; this is discussed later.

(5) The outer wall of the oogonium is fully mineralised and preserved, but the gyrogonite is not—at any rate it has not been replaced by silica, and such specimens when broken show spiral ridges on their insides (Pl. IX, fig. 11; Text-fig. 7F). Similar specimens occur in the Durlston Chert (where silicification seems to have occurred primarily). Here the gyrogonite must have been uncalcified at the time of preservation; its calcification would seem to have occurred at a late stage of development, very likely only after fertilization. The cutinised oospore wall is present as a shrunken vestige.

(6) The gyrogonite is fully mineralised, but the outer oogonial wall is not seen. In the great majority of these specimens the outer wall was certainly lost before preservation, as is shown by the frequent adhesion of isolated gyrogonites to shells, stems and other fossils they happened to lie against. A few, however, result from the outer wall being broken away in preparation, the lumen of the cells providing a line of weakness.

(7) Only a portion of the wall of the spiral cells is fully mineralised—the part of the outer wall where it meets the radial walls. This gives an egg surrounded by five spiral bands which are very easily broken away in manipulation (Text-fig. 7C).

(8) The only part of the spiral cells preserved is their radial walls, or the intercellular substance between them. This gives an egg surrounded by spiral flanges (Pl. XVII, fig. 7; Text-fig. 7B).

(9) The empty gyrogonite is well preserved, and when broken shows the structure of the spiral cells in section (Pl. IX, fig. 3).

(10) The gyrogonite has been filled up with solid silica to give an internal cast; the walls of the gyrogonite are lacking through failure of mineralisation (Pl. XVII, figs. 1, 4). Such casts may show narrow prolongations at the apex and base, which represent the cavity of the oogonial neck and basal pores. Occasionally

such gyrogonite internal casts are rather hard to distinguish from complete gyrogonites.

Utricle. The utricle is the sheath of cells round the oogonium. It is normally represented by the calcified inner walls alone; the outer walls being uncalcified are not preserved. Extremely variable in development, it may often completely invest the oogonium, even concealing its apex (but leaving an apical pore), or may leave the apex, or may leave most of the oogonial wall bare, or may be only recognisable as traces below the base of the oogonium. The extent to which the radial walls of the cells are developed also varies, so that its surface may appear nearly smooth or very strongly ribbed. These forms are all so common that they must all be regarded as normal. Exceptionally the outer walls of the cells are mineralised and preserved.

When well developed the utricle shows considerable uniformity in structure. It is composed of a ring of about twelve erect cells which closely invest the oogonial wall. Though more or less circular in section, it shows a distinct bilateral symmetry which is related to the oblique position of the oogonium on the leaf.

The lower side, which is the exposed side, is the best developed, and the lowest cell is the most deeply placed, the broadest and the longest of all. At each side of this are often a pair of rather short cells, then two longer ones and finally a shorter cell. The uppermost cells are frequently separated from the oogonial wall by a narrow space, and these cells are the least calcified of all, often their radial walls being unrepresented in a specimen in which those of the lower cells are prominent. Where these upper cells are well developed they are usually not directed to the apex of the oogonium, but converge somewhat below it.

In about a quarter of the number of oogonia the cells of the utricle are obliquely placed and form a steep spiral round the oogonium. This spiral, if shown at all, is always of the same direction as the spiral of the oogonial cells, *i. e.* left-handed. Where spiral the utricle is, as might be expected, more nearly radial in its symmetry, and the various cells are more evenly developed. Oogonia with spiral and with straight utricles may be found side by side on the same leaf.

In specimens with exceptionally well mineralised walls, the whole of the outer wall may be shown, and in these specimens a number of outer tubes can be seen enclosing the base of the utricle. Each cell of the utricle springs from a separate narrow tube at the base of the oogonium. These tubes lead into a leaf node in exactly the same way as the ordinary spine cells, and, in certain heavily mineralised specimens, cells intermediate in form between the utricle cells and the spine cells are to be found at the outside of the utricle. There is no reason to regard the utricle cells as forming a definite whorl; on the contrary, their bases are rather irregular.

The utricles cells widen considerably above their bases, and then probably remain of constant width. The shorter ones, it is true, appear to taper above, but from the appearance of the various walls it appears likely that these cells are merely departing from the oogonial wall. The parts of the utricles cells which are best calcified are those nearest the oogonium, and no part which has grown far from the oogonial wall is ever preserved. The utricles cells show no sign of septation, and may almost certainly be regarded as single cells, similar to the ordinary spine rosette cells, but more completely mineralised and a good deal longer.

In specimens where the utricles is feebly developed or absent the question arises whether this difference is due to original structure or to preservation. For some at least there is evidence that it is largely a matter of preservation. In these specimens the cell along the exposed lower side may be of normal form, but while the others appear to be only represented by their basal tubes below the oogonium, close examination shows perceptible grooves in the surface of the oogonium lying exactly where the utricles cells would be expected. In some specimens, too, with an incomplete utricles the margins of the part present are a little raised from the oogonial surface in a way which suggests that the missing part had existed, but was separated by a gap from the oogonium.

I conclude that most oogonia and possibly all were surrounded by a sheath of concrescent spine cells or bracts forming a utricles, but that the extent to which they were calcified varied greatly.

Oogonium. This term is here used for the whole of the structure composed by the five spiral cells which surround the egg; not merely for their calcified inner walls which form the gyrogonite. It happens that in *Clavator* the outer walls of the oogonial cells are calcified so that the exterior of the oogonium is commonly preserved.

The considerable majority of oogonia are enclosed in well-developed utricles, but there are plenty of specimens in which it is absent, and even when present the oogonium wall can be seen through the utricles by mounting the whole specimen in cedar-wood oil or solid balsam.

The oogonium is ovoid, being attached to a leaf node by its broad end. The free end may taper more or less abruptly, but most commonly is produced to form a distinct beak. It is always circular in section. Its surface varies a good deal: frequently quite smooth, it sometimes shows faint spiral ridges which mark the boundaries of the spiral cells; these ridges are never conspicuous, as they normally are in the gyrogonite. Most frequently the surface is roughened by a series of local thickenings: large but flattish tubercles which may be sufficiently small as to appear isolated or sufficiently large as to become hexagonal through mutual pressure. Where the outlines

of the spiral cells are clear, it can be seen that the tubercles are produced in a single series along the middle of each spiral cell.

The tubercles, being placed at even distances along the spiral cells, consequently make a pattern in the form of a secondary spiral at a large angle to the primary spiral. This secondary spiral is always right-handed; it has no relation at all to the enveloping cells of the utricle (which, if spiral at all, form a left-handed spiral. (This fact may throw some light on the morphology of *Kosmogya*, see p. 15.)

The apex of the oogonium shows a range of structure which appears to be due entirely to differences in degree of mineralisation. In the best specimens the apex is truncate, about 120μ wide, and shows a minute central pentagonal cavity $5-10\mu$ wide, surrounded by five tubes which are the transverse section (about 20μ wide) of the ends of the spiral cells. More commonly the apex shows merely a 5-cuspid aperture in the relatively thick outer wall, the inner ends of the cells being uncalcified, and more commonly still it shows merely a large round hole. In a number of oogonia the calcified wall grows thinner towards the apex and often the apex is missing. In no specimens are the tops of the spiral cells preserved, so that the form of the corona is unknown, but from the fact that the utricle when it grows beyond the oogonium leaves very little space, it can be concluded that the corona is minute.

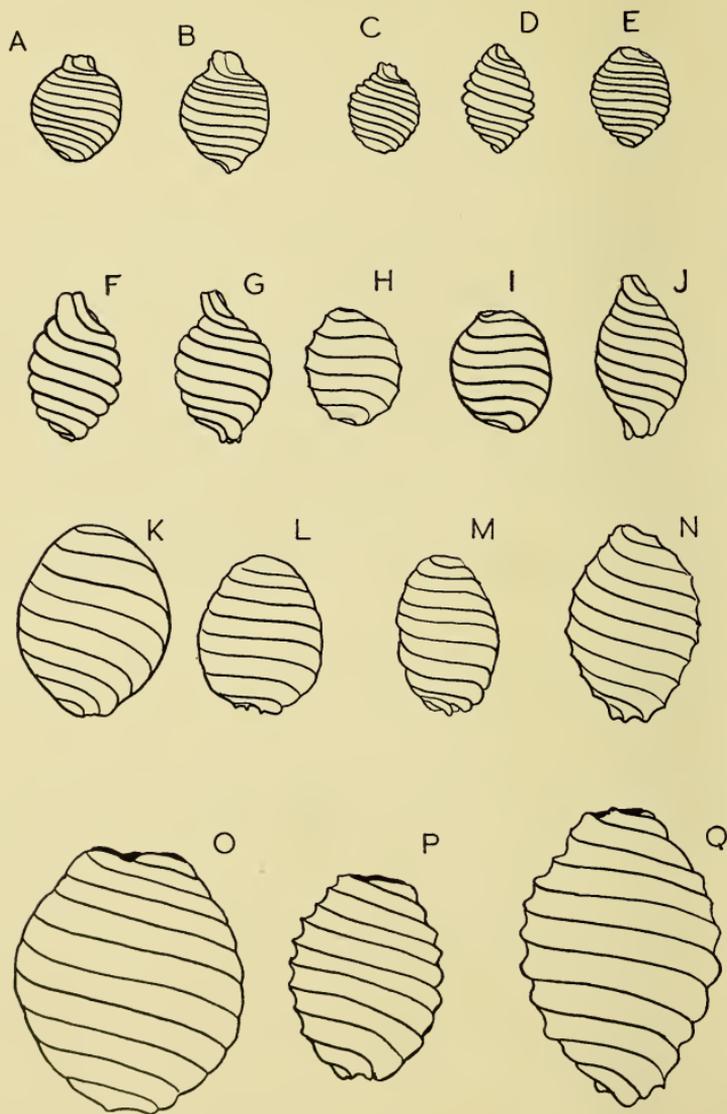
The base of the oogonium is always more or less covered by the calcified walls of the utricle or spine cells, but specimens broken off at this point show a basal hole about 50μ wide, surrounded by a thickened rim 120μ wide.

Interior of Outer Wall of Oogonium. In many pebbles the gyrogonite has failed to be replaced by silica, if indeed it ever developed, and the oogonium thus appears hollow after treatment with acid. On breaking such specimens the interior of the outer wall is seen. This wall shows conspicuous ridges which correspond to the junctions between the spiral cells (Pl. IX, fig. 11). Towards the apex the ridges change their course and bend rather abruptly outwards into the beak. Specimens in which the gyrogonite also is replaced can sometimes be dissected open, and the lumen of the spiral cells can be seen between the gyrogonite and the outer wall.

The Gyrogonite. This structure, which various authors have called the oogonium, oospore or nucule, is one or more calcified inner layers of the walls of the spiral cells which invest the egg; as explained on p. 12, it is different from the brown resistant body, also called the oospore, which is readily obtained from a recent Charophyte by vigorously cleaning the ripe fertilized oogonium.

The gyrogonite of *Clavator reidi* is oval; the two ends may appear identically similar, but often one end is slightly blunter.

The more pointed end is considered to be the apex because of two minute differences in structure from the other end, differences



TEXT-FIG. 8

Outline drawings of gyrogonites, all $\times 50$, to show the range of variation in shape. Top row, *C. grovesi*. Second row, *C. bradleyi*. Third row, *C. reidi*. Bottom row, *Perimneste horrida*. All the specimens shown have the end believed to be apical pointing upwards.

which are paralleled on the oogonia of recent Charophytes. Both ends have apertures; that of the pointed end is a rounded hole barely 10μ wide, that at the blunt end is a

pentagonal hole 30μ wide. This agrees with the base of a *Chara* calcareous gyrogonite.

In many of the best preserved specimens the spiral cells are convex in section in the top and middle, but concave at the base, their borders forming ridges. This suggests the basal "cage" seen in the oospore, and to a less extent in the gyrogonite, of many species of *Chara*.

Each spiral cell makes a little more than two complete turns round the egg, the number of cells seen crossing the mid-line in a lateral view being typically about nine or ten.

The fairly large number of specimens available facilitated a study of the variation. This falls under two heads:

(1) Variation due to structural differences:—(a) Size: The largest gyrogonite attributed to *C. reidi* measured 660μ , the smallest comparable specimen 370μ . The range of variation of size is shown in a tabular form on p. 71. (b) Shape: As has been noted the two ends may be similar, or the upper end may be very slightly sharper; no example was recognized in which the lower end is the sharper.

It occasionally happens that the hole at the apex is as large as that at the base, but in no specimens is the whole upper region open, as in Peck's genus *Aclistochara*, and as frequently occurs in *C. grovesi*, and normally in *P. horrida*.

(2) Variation in mineralisation of cell walls:—The gyrogonite of a recent Charophyte is built on the inner wall of the oogonium (oospore wall) by the impregnation of the wall substance and filling up of the cell with calcium carbonate. The extent to which this process has been carried varies in the different oogonia of a single gathering of *Chara vulgaris*, the cells sometimes appearing concave, sometimes flat if well filled, and there is every reason to suppose that similar variation occurred in *Clavator*. In addition there is, or may be, variation in the replacement of the calcite by silica, giving a whole series of interesting and striking forms.

Very commonly the spiral cells of the gyrogonite are convex in the upper and middle regions, but become flat and then concave at the base, the prominent ridges forming a little "cage". Equally commonly the spiral cells are flattened throughout, so that the outline appears quite smooth, and the individual cells can only be recognised by the slight differences in colour. Specimens in which the surface of the cells is concave throughout are rather rare. These differences are, I think, due to original differences in calcification.

In a good many specimens the surface of the gyrogonite has entirely different aspects—in one form the middle of every cell is missing, the part preserved being a very delicate band on either side of each boundary wall between adjacent cells. Sometimes such bands are free from the boundary walls and sometimes no

boundary walls are preserved, in which case the gyrogonite readily falls into a tangle of broken bands on manipulation. In another form the boundary walls alone are preserved, giving a central body representing the egg surrounded by five delicate spiral flanges. In yet another form the interior had been filled with silica, but the walls have remained calcareous so that an internal cast of the gyrogonite is all that treatment with acid yields (Pl. XVII, figs. 1, 4). Much the same appearance is obtained when a well-silicified gyrogonite with no filling is broken open. The gyrogonite wall is seen to be very thick (Pl. IX, fig. 3).

5. *The identification of the various organs as one species*: The foregoing account involves a whole chain of identifications. These are of two kinds; there is the identification of the different forms of a particular organ, and then there is the union of the different organs to build up the plant.

The identification of the various forms of a particular organ involves variants of original structure and of manner of mineralisation. It depends, in general, on the recognition that the very numerous specimens form an unbroken series in which the extremes are rare, but the average form is most abundant. It is also considerably supported by specimens which show in one part one structure, and somewhere else another structure. On this evidence the various types of internode, leaf, oogonium and gyrogonite are identified.

The identification of the different types of organ with one another depends on favourable specimens showing continuity. The best specimens of nodes show a considerable length of internode; they may also show the basal few millimetres of the leaves. The oogonia are commonly attached to the leaf, and by careful dissection typical gyrogonites can be isolated from suitably preserved oogonia. The various types of organ are in fact associated, though this would be unsafe to use as evidence, particularly in material which has undergone a certain amount of sorting by water.

On the same evidence *C. reidi* is clearly separated from *C. grovesi* (see p. 46); though fundamentally of similar construction, their organs are never of exactly similar appearance; that is, the range of form-variation for the various organs of the two species do not overlap. The gyrogonite and oogonia are always smaller, the utricle is always laterally flattened, the spine cells of the stem and leaf are always coarse.

C. bradleyi (see p. 53), which is known only from a single locality at a higher level in the Purbeckian, is in some ways intermediate, in the structure of its oogonium and utricle, between these two species and correspondingly hard to distinguish. From *C. grovesi* it differs in its far less strongly calcified but radially arranged utricle, slightly larger oogonium and gyrogonite, and

in the more gradual bend of the spiral cells at the base of the beak. From *C. reidi* it is usually distinguished by the utricle, which is normally well developed in *C. reidi*, but very feebly in *C. bradleyi*; in certain specimens of *C. reidi*, however, it is just as feebly developed. The oogonium is rather smaller, but similarly marked; the gyrogonite is rather smaller, and in well-preserved specimens has an apical beak. The gyrogonite shows somewhat fewer spiral cells in lateral view than in either species.

Few of these differences, however, are absolute. It is true that no specimen of *C. grovesi* shows a utricle approaching *C. bradleyi* in lack of calcification and no *C. reidi* gyrogonite is beaked; but the dimensions overlap those of both species. If a very few specimens of this species had been found among *C. reidi* and *C. grovesi*, it is very doubtful whether it could have been distinguished, but as quite a lot of similar specimens of the first are found together in the absence of the other two there is no doubt that it is distinct.

Perimneste horrida is a very differently organized plant, but its isolated oogonium and gyrogonite are sufficiently similar to be worth comparing. The oogonium is much larger; the enveloping leaves, which form a sort of utricle, are less regular. The gyrogonite is larger (table on p. 71), but there is a considerable overlap between the smallest of *P. horrida* and the largest of *C. reidi*. The large apical hole which is normal in *P. horrida* is not seen in *C. reidi*.

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The following specimens (V.13277-86) are those originally described and figured by Reid and Groves (1916). All from Swanage. *Reid & Groves Coll.*, 1918.

- V. 13277.** Etched slice showing sections in various planes through nodes, internodes, leaves and fruits. Utricles in section showing the inside of the outer oogonial wall (gyrogonite missing). Figured Reid & Groves, 1916, pl. viii, fig. 2. Also catalogued under *Clavator grovesi*.
- V. 13278.** Etched slice showing nodes and internodes in section. Leaf in longitudinal section bearing an oogonium. Figured Reid & Groves, 1916, pl. viii, fig. 3.
- V. 13279.** Etched chip showing nodes and internodes and a number of isolated utricles. Leaf fragment bearing three fruits with well-developed utricles. Lectotype. Figured Reid & Groves, 1916, pl. viii, fig. 4.
- V. 13280.** Etched slice showing a few isolated fruits, nodes and internodes in section. Oblique longitudinal section through a node with calcified but unsilicified inner layers. Figured Reid & Groves, 1916, pl. viii, fig. 5.
- V. 13281.** Etched slice showing nodes and internodes in section. Transverse section through a fruit, in which the utricle and the outer layer of the oogonial wall are silicified, but the gyrogonite is not preserved at all. Figured Reid & Groves, 1916, pl. viii, fig. 6.

- V. 13282. Etched slice showing nodes, internodes and leaves in section, antheridial leaf. Isolated fruits, some with well-developed, others with feebly-developed utricles. Leaf bearing a fruit (top of utricle ground away). Figured Reid & Groves, 1916, pl. viii, fig. 7. Internode in transverse section figured pl. viii, fig. 9.
- V. 13283. Etched slice in which the matrix as well as the fossils is largely silicified. Nodes and internodes seen in section. Longitudinal section through a leaf bearing a fruit with a well-preserved outer oogonial wall, but imperfectly preserved inner wall. Figured Reid & Groves, 1916, pl. viii, fig. 8.
- V. 13284. Etched slice. Nodes, internodes, leaves and fruits in various planes of section. Two internodes in longitudinal section. Figured Reid & Groves, 1916, pl. viii, fig. 10.
- V. 13285. Etched slice. Nodes, internodes, leaves and fruits in section. Transverse sections of two nodes, both showing the origin of leaves. Figured Reid & Groves, 1916, pl. viii, figs. 11, 12.
- V. 13286. Etched slice. Nodes, internodes, leaves and fruits in section. Longitudinal section through a node, showing the origin of leaves. Figured Reid & Groves, 1916, pl. viii, fig. 13. Also catalogued under *Clavator grovesi*.

Except where otherwise stated the following specimens are from a locality given as Portesham. *Reid & Groves Coll.*, 1933.

- V. 26001. Node embedded in bakelite and ground to expose interior; serial sections shown in Text-fig. 4 from this specimen. Probably Portesham.
- V. 26002. Internode cut longitudinally (Reid preparation). Pl. III, fig. 3.
- V. 26003. Leaf (rather thick). Pl. I, fig. 5.
- V. 26004. Internode; surface very incompletely mineralised. Pl. III, fig. 5.
- V. 26005. Leaf; spine rosettes well developed. Pl. I, fig. 8.
- V. 26006. Leaf; spine rosettes unusually large. Pl. I, fig. 7.
- V. 26007. Leaf apex. Pl. I, fig. 1.
- V. 26008. Antheridial leaf; antheridial holes rather small. Pl. I, fig. 2.
- V. 26009. Antheridial leaf; antheridial holes large. Pl. I, fig. 6.
- V. 26010. Antheridial leaf; holes normal. Pl. I, fig. 4.
- V. 26011. Leaf with bare internodes. Pl. I, fig. 3.
- V. 26012. Internode; also leaf in transverse section (Reid preparation). Pl. III, fig. 2.
- V. 26013. Leaf with three oogonia, the lowest very small and perhaps abortive. Pl. VIII, fig. 8. Probably Portesham.
- V. 26014. Upper part of oogonial leaf with two small-sized oogonia. Pl. VIII, fig. 10. Probably Portesham.
- V. 26015. Oogonial leaf; upper part sterile, but bearing below a small and probably abortive oogonium. Pl. VII, fig. 5. Probably Portesham.
- V. 26016. Oogonial leaf bearing two well-developed oogonia. Pl. VIII, fig. 3. Probably Portesham.
- V. 26017. Internode in longitudinal section (Reid preparation). Pl. V, fig. 7.
- V. 26018. Fragment of leaf with oogonium. The utricle is feebly developed and the oogonial wall warted. Pl. VII, fig. 8. Probably Portesham.
- V. 26019. Similar specimen to V. 26018, but utricle better developed. Pl. VIII, fig. 4. Probably Portesham.
- V. 26020. Oogonium with a very long utricle. Pl. VIII, fig. 9. Probably Portesham.
- V. 26021. Oogonium with a short thick utricle. Pl. VIII, fig. 1. Probably Portesham.
- V. 26022. Node embedded in bakelite and ground away to give serial transverse sections. Text-fig. 5. Probably Portesham.

- V. 26023. Three fragments of cortex from different nodes, embedded in balsam. Pl. VI, figs. 1-4. Probably Portesham.
- V. 26024. Oogonium; the utricle and side of the oogonium have broken away. Pl. VII, fig. 1. Probably Portesham.
- V. 26025. Node dissected open to expose the central tube and inner ends of the leaf base and leaf-base laterals. Pl. III, fig. 1.
- V. 26026. Node from above, showing the two nodal holes. Pl. IV, fig. 5.
- V. 26027. Internode in a state of incomplete mineralisation. Pl. II, fig. 5.
- V. 26028. Well-preserved internode showing a spiral pattern of rosettes. Pl. II, fig. 1.
- V. 26029. Internode; the middles of the spine rosettes are not mineralised. Pl. V, fig. 9.
- V. 26030. Internode; the spine rosettes form rings. Pl. II, fig. 2.
- V. 26031. Internode; the spine cells are of minute size. Pl. II, fig. 4.
- V. 26032. Internode; the rosettes form a pattern of double rings. Pl. V, fig. 1.
- V. 26033. Internode with very small spine cells. Pl. II, fig. 3.
- V. 26034. Unusually thick leaf. Pl. V, fig. 5.
- V. 26035. Internode; the cortical cells are of unequal size. Pl. II, fig. 8.
- V. 26036. Internode completely covered with spine cells. Pl. II, fig. 10.
- V. 26037. Internode; the spine cell layer is not preserved. Pl. II, fig. 7.
- V. 26038. Internode; the spine rosettes form a ring below but a spiral above. Pl. II, fig. 11.
- V. 26039. Internode; the spine cells are unusually small. Pl. V, fig. 3.
- V. 26040. Well-preserved internode. Pl. II, fig. 9.
- V. 26041. Internode with well-developed spine rosettes. Pl. V, fig. 10.
- V. 26042. Slender internode; spine rosettes unevenly spaced. Pl. II, fig. 6.
- V. 26043. Node; the cortex has broken away from the central tube at the top. Pl. IV, fig. 10.
- V. 26044. Unusually slender node. Pl. IV, fig. 8.
- V. 26045. Large node with leaf bases. Pl. IV, fig. 9.
- V. 26046. Node showing a branch almost as large as the axis. The spine rosettes below the leaves are well developed. Pl. IV, fig. 6; Pl. V, fig. 2.
- V. 26047. Node with a lateral branch. Pl. IV, fig. 7.
- V. 26048. Node showing nodal holes. Pl. IV, fig. 4. Probably Portesham.
- V. 26049. Node with a small branch. Pl. IV, fig. 3.
- V. 26050. Region below node, mounted in balsam. Pl. VI, fig. 6.
- V. 26051. Cortex from below node, mounted in balsam. Pl. VI, fig. 7.
- V. 26052. Node seen from above; the deeper layers are well mineralised. Pl. VI, fig. 8.
- V. 26053. Internal cast of gyrogonite. Pl. XVII, fig. 1.
- V. 26054. Leaf with two oogonia; the utricle cells are very heavily mineralised. Pl. VII, fig. 9.
- V. 26055. Oogonium with a smooth surface; the utricle is not present. Pl. VII, fig. 4.
- V. 26056. Cortex from below node, mounted in balsam. Pl. VI, fig. 5. Probably Portesham.
- V. 26057. Leaf restored from three different fragments (all from same maceration, but most probably of different stems). Pl. III, fig. 6.
- V. 26058. Small gyrogonite, only part of the radial walls of the spinal cells is mineralised. Pl. XVII, fig. 7.
- V. 26059. Leaf; the spine cells are almost completely mineralised. Pl. III, fig. 7.
- V. 26060. Node mounted in balsam. Text-fig. 3.
- V. 26061. Oogonium with strongly developed utricle. Pl. IX, fig. 5. Probably Portesham.
- V. 26062. Oogonium showing 5-cuspid state of preservation of aperture. Pl. VIII, fig. 5.
- V. 26063. Oogonium split longitudinally. Pl. IX, fig. 11.

- V. 26064. Oogonium; the utricle is absent above. Pl. VIII, fig. 2.
- V. 26065. Node; upper surface dissected away to show the central tube, which is unexpanded and mineralised right through the nodal region. Pl. VI, fig. 10.
- V. 26066. Thick abruptly tapering leaf. Pl. V, fig. 4.
- V. 26067. Oogonia; the basal cells of the utricle are conspicuous. Pl. VIII, fig. 6.
- V. 26068. Small internode and part of two nodes, mounted in balsam. Pl. VI, fig. 9.
- V. 26069. Internode; the spine cells are almost completely mineralised. Pl. III, fig. 4.
- V. 26070. Internode; the cortex is incompletely mineralised giving a spiral pattern. Pl. V, fig. 6.
- V. 26071. Oogonial leaf with four oogonia on successive nodes. Pl. VII, fig. 6.
- V. 26072. Node and base of leaf with well-developed and distinct leaf-base rosettes. Pl. IV, fig. 1. (Specimen broken.)
- V. 26073. Node and base of leaf with confluent leaf-base rosettes. Pl. IV, fig. 2.
- V. 26074. Imperfectly mineralised gyrogonite. Pl. XVII, fig. 2.
- V. 26075. Internal cast of gyrogonite. Pl. XVII, fig. 4.
- V. 26076. Imperfectly mineralised gyrogonite. Pl. XVII, fig. 3.
- V. 26077. Oogonium with a smooth surface; the utricle is undeveloped. Pl. VII, fig. 10.
- V. 26078. Gyrogonites, some drawn in Text-fig. 8.
- V. 26079. Small oogonium with a warted surface and a vestigial utricle. Pl. VII, fig. 2.
- V. 26080. Imperfectly mineralised gyrogonite. Pl. IX, fig. 10.
- V. 26081. Half of hollow gyrogonite. Pl. IX, fig. 3.
- V. 26082. Gyrogonites, one figured in Text-fig. 8.
- V. 26083. Gyrogonites, one figured in Text-fig. 8.
- V. 26084. Gyrogonite; radial walls of spiral cells alone mineralised. Pl. IX, fig. 1.
- V. 26085. Oogonium in which the spiral cells are distinct. Pl. VIII, fig. 7.
- V. 26086. Typical gyrogonite. Pl. X, figs. 13-15.
- V. 26087. Rather narrow gyrogonite. Pl. X, figs. 16-18.
- V. 26088. Oogonium split open to expose gyrogonite. Pl. IX, fig. 2.
- V. 26089. Oogonium with well-preserved apex. Pl. IX, fig. 6. Probably Portesham.
- V. 26090. Leaf in longitudinal section showing the origin of the spine cells. (Reid preparation.) Pl. III, fig. 8. (Accidentally damaged.)
- V. 26091. Leaf in longitudinal section showing large cavity below oogonium. (Reid preparation.) Pl. IX, fig. 4.
- V. 26092. Internode showing well-preserved spine cells. Pl. III, fig. 9.
- V. 26093. Imperfectly mineralised gyrogonite. Pl. IX, figs. 7-9.
- V. 26094. Node, mounted in balsam, showing a branch arising at the side of a nodal hole mentioned on p. 25. Probably Portesham.
- V. 26095. Slender node, mentioned in text, p. 24.
- V. 26096. Largest node seen.
- V. 26097. Internode with unusually well-preserved spine cells. Probably Portesham.
- V. 26098. Gyrogonite; measurements included in Table on p. 71.
- V. 26127. Abnormal stems.
- V. 26128. Leaf.
- V. 26129-30. Oogonia. Probably Portesham.
- V. 26131. Etched block showing numerous specimens in relief.

The following specimens (V. 26099-V. 26126) are all *Sylvester Bradley & Harris Coll.*, 1939.

- V. 26099, V. 26100. Gyrogonites; some measured and figures included in Table on p. 71. Upwey Railway Cutting.
- V. 26101. Stems and oogonia. Bacon Hole (Bed 48).
- V. 26102. Stems, oogonia and gyrogonites. Bacon Hole (Bed 46).
- V. 26103. Stems, oogonia and gyrogonites. Lulworth Cove East (Top bed of Middle Purbeck Chert).
- V. 26104. Stems and oogonia. Lulworth Cove East (Lower bed of Middle Purbeck Chert).
- V. 26105. Stem, male leaves and oogonia. Fossil Forest locality in cliff, near Lulworth (Thick bed of Middle Purbeck Chert).
- V. 26106. Stems, leaves and oogonia. Worbarrow Tout (Bed 64).
- V. 26107. Well-preserved leaf in longitudinal section. Worbarrow Tout (Bed 64).
- V. 26108. Stem. Worbarrow Tout (Bed 66).
- V. 26109. Stem. (Also catalogued under *Clavator grovesi*.) Durdle Door East (Middle Purbeck Chert).
- V. 26110. Stem and oogonia. (Also catalogued under *Clavator grovesi*.) Durdle Door East (Shale below Chert).
- V. 26111. Stem. (Also catalogued under *Clavator grovesi*.) Durdle Door West (Middle Purbeck Chert).
- V. 26112. Leaf. Durlston Bay (DBE 104a').
- V. 26113. Stem. Durlston Bay (DBE 111e).
- V. 26114. Stem. Durlston Bay (DBE 112).
- V. 26115. Stem, leaf, oogonium and gyrogonite. Upwey Railway Cutting (Middle Purbeck Chert).
- V. 26116. Gyrogonites. Upwey Railway Cutting (Middle Purbeck Chert).
- V. 26117. Stems, leaves, oogonia and gyrogonites. Bug's Lane, Moigne Down (Middle Purbeck Chert, not *in situ*).
- V. 26118. Stem. (Also catalogued under *Clavator grovesi*.) Moigne Down, by Water Hole (Middle Purbeck Chert).
- V. 26119. Gyrogonites (and piece of charcoal). (Also catalogued under *Clavator grovesi*.) Poxwell Road Cutting (PC 21).
- V. 26120. Gyrogonite. Poxwell Road Cutting (PC 26).
- V. 26121. Stem. (Also catalogued under *Clavator grovesi*.) Poxwell Road Cutting (PC 34).
- V. 26122. Stem. (Also catalogued under *Perimneste horrida*.) Poxwell Road Cutting (PC 36).
- V. 26123. Stem. (Also catalogued under *Clavator grovesi*.) Poxwell Road Cutting (PC 37).
- V. 26124. Oogonia. Poxwell Road Cutting (PC 43).
- V. 26125. Stem and oogonia. Teffont Evias, Vale of Wardour, Wilts.—Middle Purbeck (TE 11).
- V. 26126. Oogonium. Teffont Evias, Vale of Wardour.—Middle Purbeck (TE 13).
- V. 26239. Good longitudinal section through fertile node showing oogonium in median section. (Also catalogued under *Perimneste horrida*.) Durlston. *Reid & Groves Coll.*, 1933.
- V. 26247. Transverse section. (Also catalogued under *Perimneste horrida*.) Durlston. *Reid & Groves Coll.*, 1933.
- V. 26248. Transverse section above node. (Also catalogued under *Perimneste horrida*.) Durlston. *Reid & Groves Coll.*, 1933.
- V. 26249. Transverse section just above node with oogonia. (Also catalogued under *Perimneste horrida*.) Durlston. *Reid & Groves Coll.*, 1933.
- V. 26263. Oogonia with warted walls and feebly developed utricles. Swindon, Wilts.—TGA' 1a. *Sylvester Bradley & Harris Coll.*, 1939.
- V. 26264. Oogonia with variously developed utricles; stem fragment. Swindon, Wilts.—TGA' 1c. *Sylvester Bradley & Harris Coll.*, 1939.
- V. 26265. Oogonia with utricles. Swindon, Wilts.—TGA' 5. *Sylvester Bradley & Harris Coll.*, 1939.
- V. 26266. Oogonium with warted wall. Swindon, Wilts.—TGB 5. *Sylvester Bradley & Harris Coll.*, 1939.

Clavator grovesi sp. nov.

(Pl. X, figs. 1-12; XI, XII, XVII, figs. 8-13)

DIAGNOSIS.—Internodes normally attaining a diameter of 2 mm. Leaves up to 0.8 mm. thick. Calcified parts of spine cells covering leaves and branches often 200μ long; spine cells forming very large compound clusters on the internode.

Utricle of oogonium always well developed; more or less strongly compressed laterally, the cells being arranged in a radiating group on each side. Oogonium about 650μ long, 450μ broad. Gyrogonite ovate, with a pointed apex, typically 300μ long, 225μ broad (extremes 335μ to 225μ long and 290μ to 180μ broad). Lateral view showing about 10 (8-12) spiral cell ridges. Surface of spiral cells usually concave, occasionally flat, spiral cells bending abruptly upwards at the apex.

HOLOTYPE.—V. 26132. (Pl. XII, figs. 1-3.)

HORIZON.—Middle and Upper Purbeckian.

DESCRIPTION.—*Clavator grovesi* is far less common than *C. reidi*, but is locally very abundant, and indeed the predominant species. Its preservation is very similar to that of *C. reidi*, but perhaps because there are less samples to choose from, really good material is rather scanty, most of it being very finely broken, even where *C. reidi* is relatively good.

In the silicified material isolated by acid the deeper layers of the stem are missing. It appears that this is due to failure of the original calcification, for in the specimens preserved in primary cherts (Durlston) the wall of the central tube is of different appearance from the cortex, which is undoubtedly calcified.

The plant is organised in almost the same way as *C. reidi*; the following description is therefore similarly arranged but much abbreviated, since most of the points requiring discussion are the same.

The Stem Internode. The normal length of the internode was not estimated as there is too little really good material, but from the ratio *pieces with a node*/*pieces without a node* (see p. 17), one may conclude that it was not very long—probably between 5 mm. and 2 cm.

The central tube is missing in the specimens isolated by acid treatment, but in the primary cherts (Durlston) it appears, as far as can be judged from sections, to be like that of *C. reidi*.

The internode of *C. grovesi* is distinctly larger than in *C. reidi*, specimens narrower than 1 mm. being rare, while those as wide as 2 mm. are common. The widest seen (a fragment which was probably from the enlargement below a node) has an estimated width of 5 mm.

The cortical tubes are normally twelve in number and of equal

size, though not uncommonly six are rather smaller though otherwise similar. In a few specimens there are only six. No transverse septa are present, and the inner walls, like the central tube, are lacking in the specimens when isolated. The short cells of the cortex appear to be roughly isodiametric however. The distance between successive short cells (*i. e.* the length of the long cells) is most varied, being anything from 300μ to 1300μ , 500μ being common. As in *C. reidi*, there is no obvious correlation between the width of the internode and the length of the cortical cells.

The short cells of adjacent rows are arranged alternately in all specimens seen, as is normal in *C. reidi*. Very commonly they show the slight displacement which results in a spiral pattern as in Text-fig. 1B.

The short cell in *C. grovesi* provides indications of the existence of a series of small cells or "head cells" at the base of the spine rosette. Instead of a single bulging projection of the outer surface there are three placed side by side, of which the outer ones are rather small in medium-sized to small stems, but just as large as the middle one in the largest stems. These bulges in small stems bear their spine cells direct, but in large ones the surface of each is divided into three or four smaller bulges, from each of which a few spine cells arise. This is interpreted as follows: the short cell cuts off a row of three cells on its outer surface, each of which may cut off a few smaller cells (arranged in a ring rather than in a row) from which the spine cells spring.

The structure of the rosette of spine cells is thus more elaborate than in *C. reidi* where the spines all arise from a single hemispherical bulge interpreted as a single head cell. The difference is not, however, fundamental, for in *C. reidi*, as the node is approached, the rosette becomes broader and shows three separate head cells, and in the very large rosettes at the base of the leaves there are indications of the existence of a ring of small head cells. The difference is probably related to the larger size of *C. grovesi*.

The spine cell rosette is thus large and complex. In a fair-sized stem the rosette includes sixty, a large one two hundred spines, which when viewed from outside may show signs of their origin from separate head cells, but often do not. In any case the centre of the rosette is occupied by the calcified bases of short erect spines, while the sides are occupied by longer oblique or horizontal ones. As a rule the rosettes are so large that they cover the whole surface of the cortex. In this species only the lower part of the spine cells is calcified and preserved as in *C. reidi*, and there is some variation in the length of this calcified part.

A few stems with an incompletely mineralised cortex were found; they are closely analogous to those of *C. reidi*, and need no discussion.

Node. The node is distinctly swollen, but in the few specimens

of adequate size not so much as in *C. reidi*; the stem swells gradually below the node and contracts even more suddenly above it. The node bears a ring of six equal leaves; none of the half dozen more complete specimens examined happened to show any branch or nodal holes. In some specimens the stem would appear to have very much narrowed in its continuation above the node, but there is no evidence that it ever terminated in producing a "head" as Reid and Groves thought was the case in *C. reidi*.

The enlargement of the node is caused by the enlargement of the six cortical cell-rows which lie above and below the leaves. The other six vary in their behaviour; they may continue as moderate-sized tubes right up to the node, to end by a sudden contraction almost at the level of the leaves, the new series beginning immediately above; they may die out about 1 mm. below the node; or in certain specimens they may be missing in the whole extent of the part below the node that happens to be present, sometimes as much as 3 mm. Such specimens, no doubt, provide the internode fragments with only six cortical tubes; whether they would ever acquire their full number is unknown.

Anatomy of the Node. The specimens isolated by acid were not suitable for a study of the anatomy because the inner layers are not mineralised; and the few stems followed by serial sections in the Durlston Chert did not happen to include a node. It is however almost certain from the surface layers of the isolated specimens that the fundamental arrangement of cells in the node is the same as in *C. reidi*, though their proportions are different. This difference mainly concerns the leaf-base laterals, which are comparatively small, sometimes hardly recognisable, their place being taken partly by the larger leaf base, partly by the six alternate or "small" cortical cells which commonly extend up to the node. The whole surface of the leaf-base laterals is bulging and divided into smaller bulges from which spine cells spring.

Leaf. All six leaves of a whorl are of equal thickness at the base. They point upwards and outwards, and appear from the larger fragments to have been nearly straight. They never branch. The length of the leaf is unknown, but from the fact that the fragments taper considerably it seems likely that they are short, that is, not much more than 1 cm. long. The width of the leaf (including the calcified parts of the spine cells) varies with the size of the stem bearing them; large specimens measure about 800 μ wide at the base, while fragments from near the apex measure about 200 μ wide.

The leaves are constructed from a continuous central tube which shows nodal swellings. No doubt the central tube is built up from a series of long cells alternating with short or nodal

cells, but the transverse walls are uncalcified. The surface of the nodal enlargement shows six very distinct bulges, better marked than those of *C. reidi*, which are regarded as head cells of the spines.

The spines are developed in a uniform manner, giving the leaf a characteristic appearance. A number of spines, about six to eight, creep up and down along the central tube, and meet those from other nodes in the middle of the internode. The rest of the spines to the number of about forty point more or less radially outwards from the node, their length, that is to say the length of their calcified bases, varying somewhat. In a number of specimens some of the spines point obliquely upward and downward, but not to a sufficient extent to alter the appearance of the leaf much. No specimens were found in which the central tube is left bare, while in *C. reidi* such specimens are common, and indeed normal. A very exceptional leaf in which the nodes are so crowded that there is no room for the creeping spine cells to develop is shown in Pl. XI, fig. 7.

Antheridial Leaf. A fair proportion of leaf fragments show a large round or oval perforation about 200μ wide at a node; other nodes show similar perforations on the same side of the leaf (Pl. XI, fig. 8). No doubt these holes are of the same nature as those of *C. reidi*, and they are considered to be antheridial.

Oogonial Leaves. Oogonial leaves are very common. They only differ from the sterile ones in bearing a single row of oogonia, one at each node. There is no evidence in this species to show whether they are borne on the outer or inner side, but probably, as in *C. reidi*, it is the inner side.

Oogonium and Utricle. The oogonium and utricle are much more uniform, both in structure and in mineralisation than in *C. reidi*.

The utricle is nearly always well developed; unlike that of *C. reidi* it is always laterally compressed, that is to say it grows more above, below and beyond the oogonium than at the sides.

The cells composing it form the following groups:

(1) Usually a large basal cell runs from the leaf right up to the utricle apex as in *C. reidi*. Occasionally no such cell is recognisable.

(2) On each side a set of about seven cells radiate from a point near the base of the oogonium. These cells normally cover the lateral and adaxial wall of the oogonium, though occasionally they fail to cover the adaxial surface. They normally extend up to the apex of the oogonium, though leaving a round hole where the oogonial apex is exposed. These lateral cells radiate from a point distinctly above the base of the oogonium, where a short cell growing out from the leaf ends. This is perhaps to be regarded as a peculiar "head cell". From this head cell a few

small erect spines usually spring, but only the bases of these are calcified.

In the majority of utricles the lateral cells meet along the distal and upper sides of the oogonium and project, forming a jagged crest. In a few, however, there are some small cells fitted in along the upper side which appear to be distal ends of spine cells from the node above, which have grown down to the oogonium.

No utricle shows any approach to the spiral arrangement of cells which is frequent in *C. reidi*, and none shows the outer walls of the utricle cells mineralised, though the extent to which the radial walls are mineralised varies.

Oogonium. Outer Wall. As the utricle is so well developed, the oogonium is comparatively seldom seen. It is oval, about 600–700 μ long (including the beak) and 450 μ wide; the apical beak is well developed and distinct. The outer wall is nearly smooth, though sometimes giving an obscure indication of the spiral cells. It never shows definite papillæ.

The apex, when well preserved, is almost identical with that of *C. reidi*, showing five little holes where the spiral cells reach the surface and a minute central canal. A few specimens were noted in which the utricle had completely covered the apex of the oogonium, leaving no pore, and presumably making it incapable of fertilisation.

Interior of Outer Wall. It is quite easy to split open the oogonium and utricle to expose the inside of the outer wall of the oogonium, and plenty of such specimens were examined. The great majority of oogonia lacked their gyrogonites, but whether because they had never calcified, as seems often to be the case in *C. reidi*, or because when calcified they had not been replaced by silica, is not known for this species. The interior of the wall shows five ridges corresponding to the boundaries between the spiral cells; at the beak these ridges turn abruptly upwards.

Gyrogonite. A few gyrogonites were found inside oogonia, but the great majority were isolated. The latter by no means always correspond in their frequency with the other organs; possibly this is due to the sorting action of water, or possibly to their lack of replacement by silica in some localities.

The gyrogonite is very minute, being probably the smallest that has been seen in any Charophyte. Though varying somewhat, it is usually broadly egg-shaped, with a pointed base, and widest just below the apex. From the rather flattened apex springs an apical beak, though in a large proportion of specimens this beak has been broken away to leave a relatively large hole.

The basal end shows a small pore 10–15 μ wide; at the apex a similar, though smaller pore can sometimes be seen. The spiral "cells" are occasionally flat, or even very slightly convex,

but in the great majority of specimens they are distinctly or strongly concave.

A number of specimens which have beaks are feebly mineralised about the base of the beak, and in some of these only part of the beak is present, or it may be broken away in preparation. Those lacking a beak altogether show an apical hole about 100μ wide, the margins of which may be either irregularly broken, as in Pl. X, fig. 11, or almost circular. The wall of the gyrogonite is a good deal thinner than is usual in *C. reidi*, being at most about 25μ thick, and usually less.

Among the lots of this gyrogonite isolated from blocks from the Portesham district, a certain amount of variation was noticed in each, but there are apparently also differences between the lots. Some, for example, tend to have a flatter upper end, and consequently a well-defined beak; others taper more gradually into the beak, which becomes indistinct. The beak itself seems longer in some lots than in others, and the gyrogonite cells are more concave in some than in others, though the dimensions are sufficiently uniform. Possibly this indicates that a number of species or varieties of gyrogonites are confused under one name, but the other organs of this plant show no corresponding variation.

The evidence for the attribution of the various organs to the one species is the same as for *C. reidi*. Although good material is less abundant, it provides very complete evidence. For comparisons, see *C. reidi*, p. 40.

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Except where otherwise stated, all specimens are from Portesham. *Reid & Groves Coll.*, 1933.

- V. 26132. Utricle of oogonium. Holotype. Pl. XII, figs. 1-3. Probably Portesham.
- V. 26133. Utricle of oogonium. Pl. XII, figs. 4-6. Probably Portesham.
- V. 26134. Fragment of node showing a leaf base and its two lateral cells. Pl. XI, fig. 6.
- V. 26135. Fragment of antheridial leaf showing perforation. Pl. XI, fig. 9.
- V. 26136. Fragment of cortex of internode showing a large spine-cell rosette. Pl. XI, fig. 3. Probably Portesham.
- V. 26137. Part of a leaf showing three leaf-internodes. Pl. XI, fig. 8.
- V. 26138. Part of a leaf with abnormally short internodes. Pl. XI, fig. 7.
- V. 26139. Utricle broken open to expose part of oogonium; oogonium broken to expose hollow interior. Pl. XII, figs. 7, 8.
- V. 26140. Fragment from nodal region showing bases of two leaves. Pl. XVII, fig. 13.
- V. 26141. Utricle broken to expose oogonium. Pl. XII, fig. 9. Probably Portesham.
- V. 26142. Gyrogonite; apex missing, giving the "Aclistochara" form. Pl. X, figs. 10-12.
- V. 26143. Gyrogonite; one-fifth of the apex is missing. Pl. X, figs. 7-9.

- V. 26144. Gyrogonite of normal form. Pl. X, figs. 4-6.
- V. 26145. Fragment of cortex of internode, showing a large rosette of spine cells. Pl. XI, fig. 5.
- V. 26146. Gyrogonite of rather small size. Pl. X, figs. 1-3.
- V. 26147. Part of oogonial leaf with two oogonia. Pl. XVII, fig. 11. Osmington Mills (Middle Purbeck Chert Bed). *Sylvester Bradley & Harris Coll.*, 1939.
- V. 26148. Part of a node, seen from within, showing some of the six large and the six small cortical cells reaching the node. Pl. XVII, fig. 12. Osmington Mills (Middle Purbeck Chert Bed). *Sylvester Bradley & Harris Coll.*, 1939.
- V. 26149. Part of a very large internode. Pl. XVII, fig. 8. Osmington Mills (Middle Purbeck Chert Bed). *Sylvester Bradley & Harris Coll.*, 1939.
- V. 26150. Fragment of internode cortex seen from within. Pl. XI, fig. 4. Osmington Mills (Middle Purbeck Chert—OM D 18). *Sylvester Bradley & Harris Coll.*, 1939.
- V. 26151. Fragment of internode showing well-developed spine rosettes. Pl. XI, fig. 1. Osmington Mills (Middle Purbeck Chert). *Sylvester Bradley & Harris Coll.*, 1939.
- V. 26152. Part of a leaf with two oogonia, mounted in balsam. Pl. XVII, figs. 9, 10. Moigne Down. *Sylvester Bradley & Harris Coll.*, 1939.
- V. 26153. Oogonium and utricle split longitudinally and seen from within. Pl. XI, fig. 2. Moigne Down, by Water Hole. *Sylvester Bradley & Harris Coll.*, 1939.
- V. 26154-61. Gyrogonites; measurements included in Table on p. 71. V. 26154, certain specimens shown in Text-fig. 8. V. 26159-60, probably Portesham. V. 26161, Upwey.
- V. 26162-71. Stem fragments. Osmington Mills (Middle Purbeck Chert—OM D 18). *Sylvester Bradley & Harris Coll.*, 1939.
- V. 26172. Stem and leaf fragments.
- V. 26173. Stem fragments.

The following specimens, except the last three, are all *Sylvester Bradley & Harris Coll.*, 1939.

- V. 26174. Oogonia. (Also catalogued under *Perimneste horrida*.) Osmington Mills (OMD 18).
- V. 26175. Internode. Osmington Mills (Middle Purbeck Chert—OMD 18).
- V. 26176. Gyrogonite. Osmington Mills (OMAX 23).
- V. 26177. Oogonium and gyrogonite. Osmington Mills (OMZ 8'-10'-12').
- V. 26178. Gyrogonites. Osmington Mills (OMZ 10'-12').
- V. 26179. Oogonium. Poxwell Road Cutting (PC 10).
- V. 26180. Oogonia. (Also stem of *Clavator* sp.) Poxwell Road Cutting (PC 28).
- V. 26181. Oogonia and cortex fragments. (Also catalogued under *Perimneste horrida*.) Poxwell Road Cutting (PC 33).
- V. 26182. Oogonia, stem and leaf. (Also catalogued under *Perimneste horrida*.) Poxwell Road Cutting (PC 35).
- V. 26109. Stem and leaf. (Also catalogued under *Clavator reidi*.) Durdle Door East (Middle Purbeck Chert).
- V. 26110. Oogonia. (Also catalogued under *Clavator reidi*.) Durdle Door East (Shale below Chert).
- V. 26118. Stem, leaf and oogonia. (Also catalogued under *Clavator reidi*.) Moigne Down, by Water Hole (Middle Purbeck Chert).
- V. 26119. Stem fragment. (Also catalogued under *Clavator reidi*.) Poxwell Road Cutting (PC 21).
- V. 26121. Oogonia. (Also catalogued under *Clavator reidi*.) Poxwell Road Cutting (PC 34).

- V. 26123. Oogonia and stem. (Also catalogued under *Clavator reidi*.) Poxwell Road Cutting (PC 37).
 V. 26267. Gyrogonites. Swindon, Wiltshire—TGA' 1a.
 V. 26268. Gyrogonites. Swindon, Wilts—TGA' 5.
 V. 26269. Gyrogonite; oogonia in utricles. Swindon, Wilts—TGA 9.
 V. 26270. Gyrogonite. Noticed A. M. Davies, 1899, p. 40. Kings Cross, near Haddenham, Buckinghamshire. Presented by A. Morley Davies, 1939.
 V. 13277. Etched slice showing a well-preserved and typical gyrogonite. Swanage. (Also catalogued under *Clavator reidi*.)
 V. 13282. Etched slice showing an isolated utricle. Swanage. (Also catalogued under *Clavator reidi*.)

Clavator bradleyi sp. nov.

(Pl. XVI, figs. 1, 3-5, 7)

DIAGNOSIS.—Oogonia borne on slender calcified leaves. Utricle consisting of about twelve narrow cells, only the bases of which are calcified. Oogonium ovoid, sometimes broadly beaked, typically about 550μ long \times 360μ broad; surface usually showing blunt papillae, and occasionally showing the spiral cells. Gyrogonites very thick walled, lower end somewhat pointed, upper end forming a prominent cylindrical beak which is, however, readily detached. Length (without the apical beak) typically about 360μ , extremes 270μ and 470μ ; beak an additional 40μ – 80μ long. Breadth about 280μ , extremes 250μ and 360μ . Spiral cells strongly convex, flat or concave, but similar in all parts of one specimen; lateral view showing about 7 or 8 spirals (extremes 6–10); spiral cells bending rather gradually to the apical beak and to the pointed base, where they often form a minute cage.

HOLOTYPE.—V. 26183 (Pl. XVI, figs. 3, 4, 7). Upper Purbeck; Poxwell Lodge, Road Cutting, bed 5b (Bradley MS.); collected by P. Sylvester Bradley, after whom it is named.

DESCRIPTION.—This species is represented by nearly fifty oogonia and gyrogonites, about half of which are well enough preserved to be useful. The material is preserved as calcium carbonate in a marl from which it was obtained by Mr. Bradley by boiling with soda.

Although the oogonia and gyrogonites are not uncommon in the marl residue where they were discovered, no leaf or stem remains are associated with them. This fact, together with the delicacy of the minute portion of the leaf attached to one oogonium, suggests that these organs may have been lightly calcified.

The chief interest in this species is that it belongs to a different horizon from the bulk of the Purbeck Charophytes. It shows nothing of botanical interest which is not shown also by *C. reidi* and *C. grovesi*. For comparisons see *C. reidi*, p. 40.

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All specimens are from Poxwell Road Cutting (Bradley's layer 5b). *Sylvester Bradley & Harris Coll.*, 1939.

- V. 26183. Gyrogonite. Holotype. Pl. XVI, figs. 3, 4, 7.
 V. 26184. Oogonium; traces of a utricle are present at the base. Pl. XVI, fig. 1.
 V. 26185. Oogonium; the wall is warted. Pl. XVI, fig. 5.
 V. 26186. Gyrogonites; measurements given in Table on p. 71.
 V. 26187. Oogonia.
 V. 26188. Gyrogonite.
 V. 26189-91. Oogonia.

PERIMNESTE gen. nov.

Stem corticated by six rows of cells, all bearing spines. Node bearing eighteen leaves in three whorls of six; one whorl of upward-pointing leaves on the same radius as the cortical cells, and two whorls of short leaves on the alternate radii, one pointing upward and one downward. Leaves uncorticated, bearing a few simple spine-like leaflets in small whorls.

Reproductive organs borne near the bases of the short upward-pointing leaves, each consisting of an oogonium surrounded at maturity with leaf segments bearing antheridia. Outer surface of oogonium (as well as inner parts of spiral cells) calcified. Antheridial wall calcified.

The name is from *περί* and *μνησθη*, meaning "surrounded by woers", and refers to the relation of the antheridia to the oogonium.

Perimneste horrida sp. nov.

(Pls. XIII-XV, XVI, figs. 6, 8, 9)

DIAGNOSIS.—Vegetative organs very thinly calcified. Spines on cortex borne in pairs, about 0.5 mm. long, sharp pointed. Shorter leaves about 1.0 mm. long, bearing one whorl of spines; longer leaves 3-5 mm. long, bearing two or three whorls of spines. Oogonium with a strongly calcified outer wall 1 mm. long, 0.8 mm. broad, strongly beaked, enclosed in an irregular investment of calcified leaflets and antheridia. Gyrogonite typically 680 μ long, 570 μ broad (extremes 580 μ and 840 μ long, and 460 μ and 700 μ broad), in lateral view, showing about 11 spirals (extremes 9 and 13). Spiral cells usually concave, but sometimes flat or slightly convex. Apex of gyrogonite uncalcified, and therefore appearing to be pierced by a hole 100 μ wide. Antheridia about 1 mm. in diameter.

HOLOTYPE.—V. 26192 (Pl. XIV, figs. 2, 7, 9).

HORIZON.—Middle and Upper Purbeckian.

The reproductive organs of *P. horrida* are widespread in the Middle Purbeck. The vegetative organs, no doubt because they

are so feebly calcified, are not generally found in the Purbeck rocks, but are confined to the chert from Durlston, where petrification occurred soon after death, and where silicification was apparently primary.

DESCRIPTION OF THE MATERIAL.—The vegetative material preserved in a chert from Durlston is unique among those I have examined. All the other cherts gave clear signs of having been formed by a replacement of limestone or calcareous shale, and in these cherts all trace of organic matter has disappeared.

This Durlston Chert includes a good deal of calcareous matter (such as Cyprid shells), small masses which appear to be altered calcareous ooze, and also sand grains which are all embedded in a homogeneous and rather transparent silica matrix. Although the calcareous fossils are largely silicified, the replacement is imperfect; their walls remain rather opaque, and are not so readily attacked by hydrofluoric acid as the matrix.

Certain layers of this chert include many specimens which seem to be much less broken up than usual; this applies both to *Clavator reidi* and *P. horrida*, and it may be that some of these specimens are preserved intact in the position of growth.

The vegetative organs of *Perimneste* and *Clavator* retain no trace of organic matter, but the oogonia often show the oospore membranes. This has characteristically shrunk away from the wall in the immature specimens, forming a collapsed sac in which the spiral cells are very obvious; sometimes both inner and outer membranes of the spiral cells are preserved.

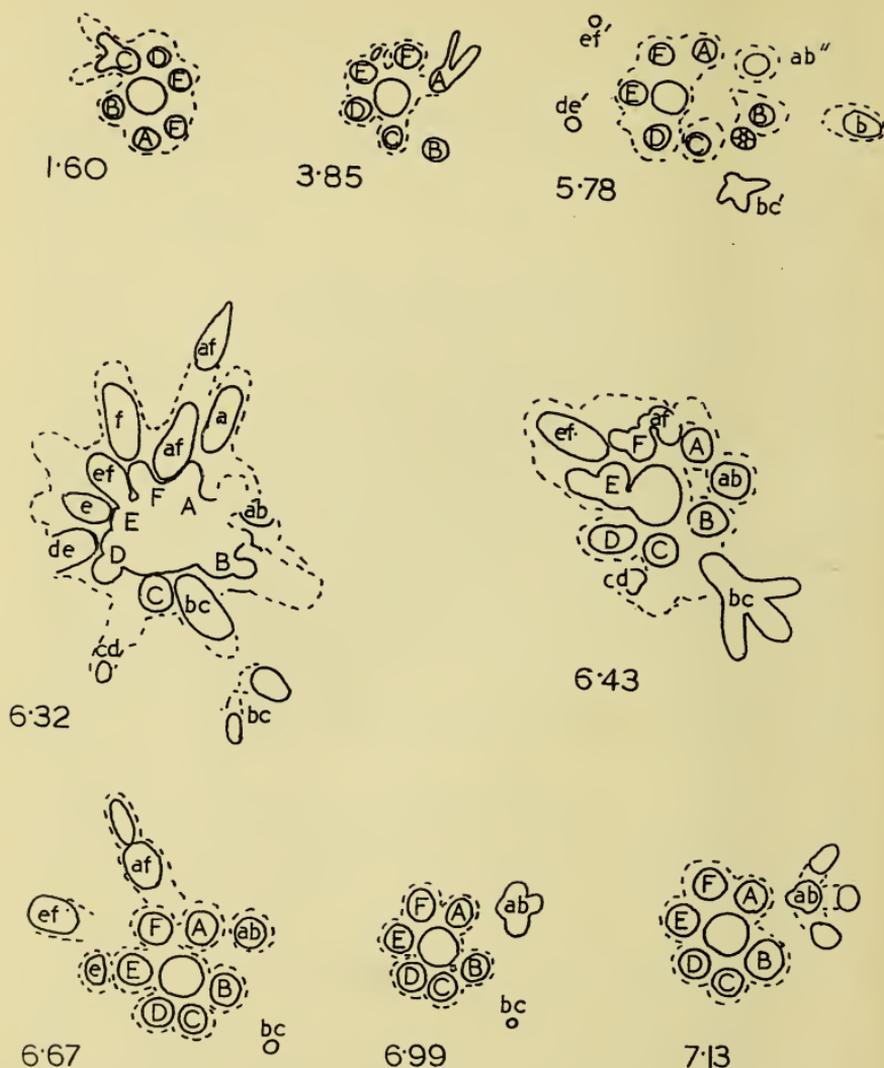
The chert contains a good many roots. These are often preserved as follows: there is a sort of cast in the somewhat impure chert representing the original outline of the root; inside this is a petrified root tissue in a collapsed state, the space being filled by pure homogeneous chert. The organic matter of the root cells is preserved, though owing to collapse the anatomy is poorly shown.

These roots suggest the following hypothesis:

- (1) The roots were growing in a sandy silt, or they were washed into such a silt.
- (2) The silt was impregnated with silica and became solid.
- (3) The roots died and contracted, in the absence of oxygen.
- (4) The space round the root and the root cells themselves were silicified.

It should be made clear that most of the chert from Durlston, including all I collected, is normal and of no special value; the peculiar and valuable chert referred to above is some collected by Reid.

Calcification. The vegetative organs of *Perimneste* had far thinner walls than either of the associated *Clavator* species, and are plainly therefore less heavily calcified. The evidence that they are to some extent calcified is provided by the way they

TEXT-FIG. 9.—*Perimneste horrida*

Outline drawings of selected sections from the series on which Text-fig. 10 is based. The numbers represent the levels in mm. from the apex where the series starts. A, B, C are cortical cell rows (lettered the same above and below the node); a, b, c are the long leaves; ab', bc', cd' are short downward-pointing leaves; ab, bc, cd are downward pointing leaves; ab'' is a leaf above ab'. The small branch is unlabelled (in 5.78). In 6.32 the cell walls are somewhat broken and displaced (especially in the region of ab). Firm line represents the cell wall, dotted line, indefinite crust of chalky silt. V. 26245, $\times 16$.

have sometimes broken in preservation ; the stems and leaves never seem bent or crushed, but very frequently show sharp breakage and a slight displacement of the two halves. This indicates that the wall was hard even after death, and the natural explanation is that it was impregnated with mineral, *i. e.* lime.

The description is arranged as follows :

- (1) Vegetative organs, ordinary stem, node, leaf.
- (2) Reproductive stem, node and leaf.
- (3) Reproductive organs.
- (4) Discussion and comparison.

Vegetative Stems. The mature stems which make up the bulk of the vegetative material are usually somewhat broken and the length of the internode is unknown ; from the large number of nodes present, however, it does not seem likely to have been much more than one centimetre, but it is known that it exceeded 5 mm. The stem is usually about 0.8 mm. (range 0.1 mm. in smallest branches to 1.1 mm.) in diameter in the internode, and is of constant structure.

There is a central axial tube about 300μ in diameter surrounded by six cortical tubes about 270μ in diameter. The tubes are all perfectly circular in section, and the cortical tubes are very loosely attached to the central tube ; sometimes one will diverge from it, but rejoin it a millimetre further on.

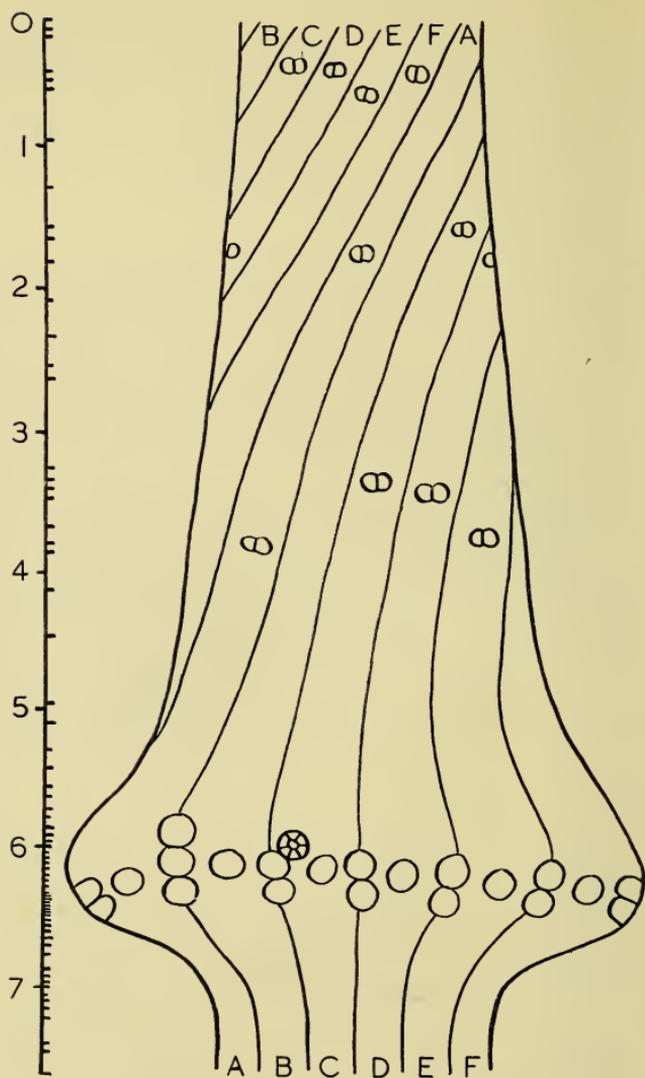
The walls of the central tube and cortical tubes are about 10μ thick ; in the best specimens they show very distinct traces of longitudinal or transverse striation. The cortical tubes have the usual dextral spiral twist, which dies out as a node is approached.

The cortical cells bear spines at intervals of 1–2 mm. ; at these points a short cell presumably occurs, but no trace of any transverse septa is preserved. The spines are borne in pairs, and project more or less horizontally a distance of about 0.5 mm.

Node. At the node the stem is somewhat swollen ; this swelling may begin at some distance from it, but often it is confined to the node itself. This enlargement is caused partly by an increase in the central tube, and partly by the large basal cells of the leaves ; the cortical tubes increase but little in size.

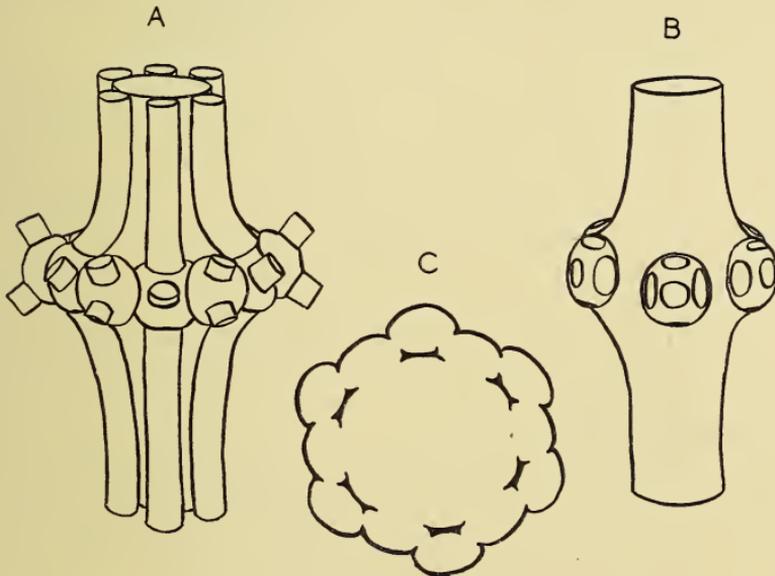
At the node three sets of leaves (eighteen in all) arise, also the cortex of the internodes, and some branches. Of these leaves one set is much the longest and arises on the same radius as the cortical cells, while the other two are equally short and arise, one above the other on the alternate radius ; on these radii too are the branches.

Internal Structure of Node. The central tube is dilated at the node to about twice its normal diameter. At this point nodal cells no doubt occur, and in certain specimens some remnants of transverse septa are recognisable, but in most no septa are present. At the outside of the dilatation

TEXT-FIG. 10.—*Perimneste horrida*

Diagrammatic analysis of a series of sections through a node of *Perimneste*. The specimen is represented as though the cortex were scored by a vertical cut and peeled off from the central tube and pressed into a plane. The double scars in the upper part represent spine-cell pairs; the swelling is the node on which are a branch, and three series of leaves represented by oval scars (an extra leaf occurs between A and B). Only the spine-cell pairs which were well enough preserved to be unmistakable are shown. The letters A, B, C represent cortical cell-rows. The vertical scale represents mm.; the marks on it indicate the levels at which sections were drawn. **V. 26245**, $\times 16$.

of the central tube it is further enlarged by six nearly hemispherical chambers, which again are not cut off by any preserved septa. On the outer surface of each of these chambers are five openings which are as follows: at the top and at the bottom are openings leading to the cortical tubes of the internode above and below. At the outside is an opening leading to the basal cell of a long leaf. At the sides are large openings which lead at once to an alternating set of round chambers; these have two further openings, one above the other, which lead to the basal cells of the short leaves. Where branches are borne, they arise



TEXT-FIG. 11.—*Perimneste horrida*

Diagrams illustrating the essential structure of the node of *Perimneste*.

A, specimen complete with cortex and inner and outer nodal chambers; the leaves are cut off short. B, similar specimen with cortex and outer chambers removed. C, transverse section through the node showing the inner and outer chambers. $\times 10$.

from these outer chambers at a point just above the attachment of the upward-pointing short leaves. The arrangement of these nodal chambers is shown diagrammatically in Text-fig. 11.

Leaves. The upward-pointing long leaves (*i. e.* of the cortical radii) are stiff and end in sharp points. They bear two, and sometimes three whorls of short pointed segments; as a rule these segments are simple and are borne in whorls of four or less, though the members of a whorl may be of very uneven size, and occasionally may themselves branch.

The short leaves are like the long leaves except for being very much shorter and in bearing only a single whorl of about four pointed ramuli. Both upward and downward-pointing short

leaves point obliquely outwards, and must have provided a formidable array of points round the node.

The only branches seen were quite small and obviously undeveloped, but their structure was normal; that is, they showed a central cell surrounded by six cortical cells. Such branches were found even on the immature reproductive stems.

Reproductive Stems. A number of small bud-like shoots have been preserved, some of which bear immature reproductive organs. It is probable that these shoots may themselves be immature, and that their structure may approach the ordinary vegetative shoots more closely at maturity; but as this cannot be proved it seems best to describe them separately.

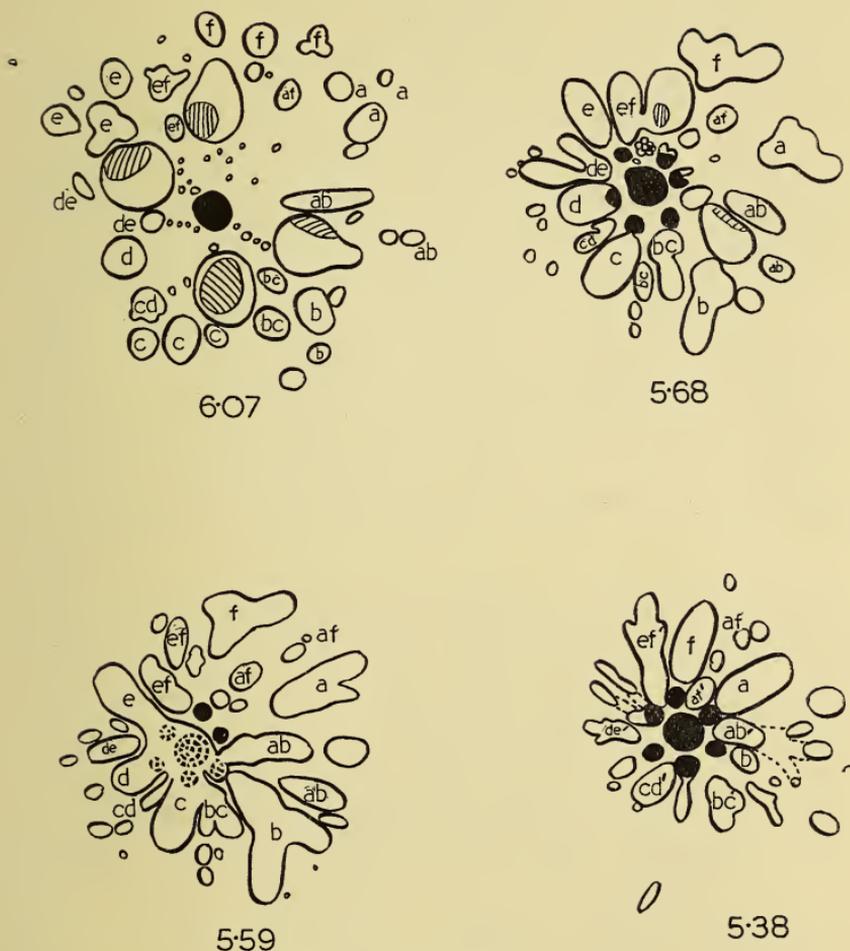
These shoots show crowded nodes; in one specimen the top internode was 1 mm. long, the next 2 mm.; another showed three internodes each about 1 mm. long. The internode is, however, of nearly the normal thickness (nearly 1 mm.). Most of these shoots are almost certainly unexpanded normal shoots, but a few are reproductive, and one of these was followed for a distance of 2 mm. (past two nodes) by serial sections.

The fundamental structure of the stem is normal; the node has the usual six inner and six outer chambers, and bears the six long leaves on the cortical radii and the twelve short leaves (upward and downward) on the other radii. The differences chiefly concern the cortex and the six upward short leaves which bear the reproductive organs.

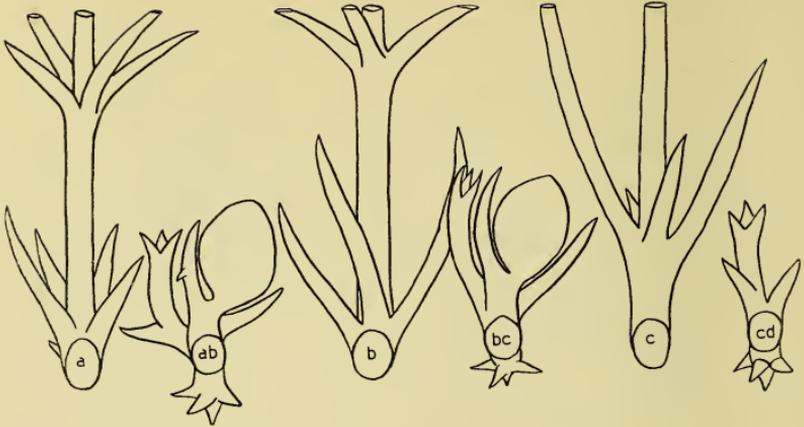
The cortex is normal just below a node, though owing to the shortness of the internode the spine pairs are very crowded. The top spines are well developed, arise very close indeed to the node, and are mixed with the short leaves. At the sides of the spine pairs a smaller spine is sometimes to be seen. The next spines below are only half the size of the top ones, and a short distance below these the cortical cells themselves disappear, about a third of the internode being uncorticated. A new cortex composed of very small cells is found a short distance above the next node; this gives rise to some upwardly directed spines, but its cells never attain the normal size.

The long leaves and the short downward pointing leaves are rather short, perhaps because young, but of normal structure. The short upward-pointing leaves are abnormally strong, if fertile, and less regularly branched than usual. The fertile leaves usually branch near the base into three parts, of which the two outer may branch again, but are sterile (at this stage), while the inner bears a large pear-shaped oogonium and continues as a sterile ramulus. In the four fertile leaves studied the oogonium appeared to be a lateral rather than a terminal organ, its base being distinctly curved.

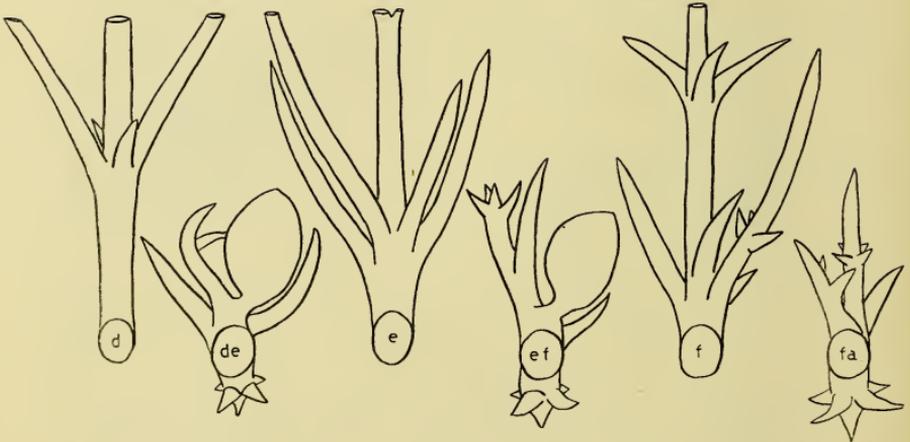
Reproductive Organs. *Perimneste* appears to be strongly protogynous, for the bud-like reproductive shoots which show

TEXT-FIG. 12.—*Perimneste horrida*

Four selected levels from a series through a fertile node (for analysis see Text-fig. 13). The axis and cortical cells are shown in solid black, except where at level 5.59 they are below the plane of section. The spiral ridges of the shrunken oospore membrane are shown inside the calcareous oogonial wall. The leaves and their main ramuli are lettered as follows: *a, b, c* refer to the long leaves; *ab, bc, cd* to the upper short leaves; *ab', bc', cd'* to the lower short leaves. At 6.07 a considerable number of spiny upgrowths from the cortical cells are present, but not lettered; at 5.68 a branch is seen, and an oogonium is seen at its attachment to *ef*; at 5.38 part of the leaf *ab'* seen through the transparent rock is shown by a broken line. Some cortical spines (between *de'* and *ef'* and again between *b* and *bc'*, and again between *bc'* and *cd'*) are shown, but are not distinguished by letters. V. 26244, $\times 12$.



a



c

TEXT-FIG. 13.—*Perimneste horrida*

Diagrammatic analysis (vertical scale shown accurately) of the appendages of a fertile node of *Perimneste* exposed by serial sections. Pl. XIII, fig. 2; Text-fig. 12). The various leaves are supposed to be cut off from the nodal cells and viewed from within; they are slightly distorted in the horizontal plane for the sake of clearness. The oval bodies on four of the short leaves are oogonia. (The lower short leaves lie very obliquely and are considerably longer than appears here.) A few of the finest ramuli which were not traced with certainty are omitted. The leaf bases are lettered as in Text-fig. 12. V. 26244, $\times 12$.

almost full-grown oogonia (though internally undifferentiated) show no sign of antheridia, and even the leaf ramuli which are to bear them are feebly developed. The oogonia at this young stage are pear-shaped or ellipsoidal, with a firm though delicate outer wall (presumably already calcified), enclosing a collapsed oospore membrane which had evidently not begun to calcify.

At maturity both internodes and reproductive leaves must have grown considerably, as there is not sufficient space for the large reproductive structures characteristic of this plant. No shoots bearing mature reproductive organs were, however, found in this Durlston chert, and knowledge of them is confined to specimens isolated by acid from the silicified limestones.

The mature reproductive organ is a compact calcified mass which must have originally been 2.0-3.0 mm. in diameter. It consists of a strongly branched calcified leaf bearing an oogonium on one of its inner ramuli, and round this a considerable number of ramuli bearing antheridia. The whole mass is roughly spherical, and shows some approach to radial symmetry in the disposition of the antheridia, though this is far from exact.

The oogonium is now provided with an apical beak which was only partly developed at the previous stage. Its outer membrane is more strongly calcified, and is surrounded by a considerable number of calcified leaf ramuli which, however, scarcely form anything definite enough to be termed a utricle. These ramuli seem particularly numerous around the apical beak (Pl. XIV, fig. 8).

The leaf ramuli are far more numerous than in the young stage, and it is evident that many new ones have been formed, though the main ones correspond well enough with those at the young stage.

The antheridia are borne at the outside of the mass. Their number is extremely varied; one specimen showed none, another about twenty-five; twelve to fifteen appears to be a normal number. They tend to be arranged in rings round the sides of the oogonial mass, leaving the apex and base free. Each antheridium has a rather strongly calcified wall, but only the part which joins the oogonium is present in the specimens examined. This is, however, enough to show that the antheridium is spherical, about 1 mm. in diameter. Its wall is composed of a small number of cells—presumably eight—which show ridges running in from the margins just as in recent charophyte antheridia. These ridges are almost impossible to see when the specimen is observed in the ordinary way, but when it is slightly moistened, so that a thin film of liquid able to reflect light is spread over the surface, they show up quite strongly. The wall cells are smooth at their middles, and no doubt here the cells bearing the sperm-producing filaments were attached.

The oogonium is usually empty just as is the case in *Clavator*; that is to say, it shows a cast of the gyrogonite, but not the gyrogonite itself. Presumably here also this is due to a failure of the oogonia to complete their development. The gyrogonite is frequently found isolated.

The Identification of the Various Organs of Perimneste with one another

1. Material in Durlston Chert: The vegetative organs (stem and leaves) are in continuity, and the agreement between the mature vegetative shoots and the young fertile shoots is so close as to leave no doubt that they are the same. The oogonia on these shoots are very immature, but the outside of their wall is already slightly calcified. These oogonia were identified with some more mature but isolated ones in the same chert in which the leaf ramuli are more numerous and better calcified.

2. Material from other localities: The more mature oogonial and antheridial masses isolated from certain cherty limestones were identified with the above specimens on the agreement between the outside of the oogonia, and on the general character of the leaf ramuli enclosed in these specimens. These oogonia show on their inner sides concave marks corresponding to the spiral cells of a fair-sized gyrogonite.

3. The gyrogonite (present at various localities, and abundant in the Durlston chert) was identified by the agreement between its surface markings and the interior markings of the oogonial wall.

The essential characters of *Perimneste* have already been described in the diagnosis. A good many were seen in section; the wall, which is thick, shows a well-marked layered construction; each spiral "cell" is formed of a thin cementing layer, inside which one or two distinct U-shaped layers can be made out. The oogonial membrane (in the immature stage) shows no sign of characteristic pits, but only the outlines of the spiral cells.

DISCUSSION. Both vegetative and reproductive organs leave no doubt that *Perimneste* is a Charophyte, but it is perhaps the most peculiar of all this class. Its reproductive organs are unique in the way the oogonium is surrounded by antheridia, and in the calcification of the antheridial wall. Its leaves, too, are unique. It is obvious that the short leaves alternating with the cortex cannot be dismissed as stipular since they are reproductive; while the long leaves, from their point of attachment, appear to be equally essential. It would not seem quite so unusual if the outer nodal chambers which form the short leaves gave rise to cortical cell rows; but there is no sign that they ever do so. Although unique, it does share certain peculiarities

with *Clavator* which may reasonably be regarded as of taxonomic importance, justifying its inclusion in the same family.

These common characters are—the calcification of the outer wall of the oogonium (which it shares also with *Lagynophora*) and the production of branches alternating with the cortical rows, instead of replacing cortical rows as in *Chara*. The main differences are in the feebler development of the cortex (which may even not be continuous from node to node), the production of additional leaves on the alternate radii, and the way in which the reproductive organs are produced. The structure of the nodes differs a good deal, but this is related to differences in leaf arrangement.

It is most unfortunate that the vegetative structure of *Lagynophora* is so little known as to allow no full comparison with this type; it seems very possible that the two genera might be closely similar. The published figures of *Lagynophora* suggest that serial sections would be a very suitable method for elucidating its structure, just as for *Perimneste*.

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Except where otherwise stated the following specimens are *Sylvester Bradley & Harris Coll.*, 1939.

- V. 26192. Oogonium surrounded by antheridia. Holotype. Pl. XIV, figs. 2, 7, 9. Moigne Down.
- V. 26193. Oogonial mass split open and seen from within. Pl. XIV, fig. 1. Moigne Down.
- V. 26194. Antheridia enclosing oogonium. Pl. XIV, figs. 3, 4. Moigne Down.
- V. 26195. Oogonium split longitudinally and seen from within. Pl. XIV, fig. 6. Moigne Down.
- V. 26196. Oogonium surrounded by antheridia. Pl. XIV, fig. 8. Specimen accidentally damaged. Moigne Down.
- V. 26197. Oogonium enclosed in a rather small mass of leaf ramuli and bearing very few antheridia. Pl. XIV, fig. 5. Durdle Door (Middle Purbeck Chert).
- V. 26198. Gyrogonite of rather small size. Pl. XV, figs. 1-3. Portesham. *Reid & Groves Coll.*, 1933.
- V. 26199. Gyrogonite of normal size. Pl. XV, figs. 4-6. Probably Portesham. *Reid & Groves Coll.*, 1933.
- V. 26200. Gyrogonite of large size. Pl. XV, figs. 7-9. Portesham. *Reid & Groves Coll.*, 1933.
- V. 26201. Oogonium divested of leaf ramuli. Pl. XV, figs. 10, 11. Probably Portesham. *Reid & Groves Coll.*, 1933.
- V. 26202-20. Gyrogonites; measurements included in Table on p. 71. V. 26202-07, Portesham, *Reid & Groves Coll.*, 1933; V. 26208-9, probably Portesham, *Reid & Groves Coll.*, 1933; V. 26210, Osmington Mills, *Reid & Groves Coll.*, 1933; V. 26211, Durdle Door East (Shale above Chert); V. 26212, Durdle Door East (Shale below Chert); V. 26213, Durdle Door East (Chert Bed); V. 26214, Durdle Door West (Chert Bed); V. 26215, Bacon Hole (Marl Bed); V. 26216-19, South of Moigne Down, by water hole (Middle Purbeck Chert Bed); V. 26220, Upwey, *Reid & Groves Coll.*, 1933.

- V. 26221. Oogonium surrounded by antheridia. Moigne Down.
 V. 26222. Oogonium split open. Moigne Down.
 V. 26223. Gyrogonite. Bacon Hole (Mupe Bay Area), Bed 48.
 V. 26224. Gyrogonite. Poxwell Road Cutting (PC 28).
 V. 26122. Gyrogonites. (Also catalogued under *Clavator reidi*.) Poxwell Road Cutting (PC 36).
 V. 26174. Gyrogonite. (Also catalogued under *Clavator grovesi*.) Osmington Mills (OMD 18).
 V. 26181. Gyrogonite. (Also catalogued under *Clavator grovesi*.) Poxwell Road Cutting (PC 33).
 V. 26182. Oogonium and gyrogonite. (Also catalogued under *Clavator grovesi*.) Poxwell Road Cutting (PC 35).

The following specimens (V. 26239–61) are all from Durlston. *Reid & Groves Coll.*, 1933.

- V. 26239. Thin section. Transverse and longitudinal sections of node. Pl. XIII, figs. 4, 6; other sections, some fertile. (Also catalogued under *Clavator reidi*.)
 V. 26240. Thin section. Transverse and longitudinal sections of node. Pl. XIII, figs. 3, 7; also transverse and longitudinal sections through other sterile and fertile nodes.
 V. 26241. Slice etched in places and mounted on glass. Transverse section of internode. Pl. XIII, fig. 1.
 V. 26242. Slice, on glass, lightly etched. Transverse section of node. Pl. XIII, fig. 5.
 V. 26243. Polished slice. On one side transverse section of node (Pl. XVI, figs. 6, 9); also other sections. Back (etched) good longitudinal section of node and internode; longitudinal section of internode, Pl. XVI, fig. 8.
 V. 26244. Etched slice on glass. Pl. XIII, fig. 2. Fertile stem from which Text-figs. 12, 13 were drawn.
 V. 26245. Slice on glass. Specimens shown in Pl. XIII, fig. 8, and Text-figs. 9, 10 were in this block, but both were destroyed by serial sectioning.
 V. 26246. Polished slice. Stems in various planes of section.
 V. 26247. Transverse section of fertile bud, sterile stem. (Also catalogued under *Clavator reidi*.)
 V. 26248. Good transverse sections. (Also catalogued under *Clavator reidi*.)
 V. 26249. Stems in various planes of section. (Also catalogued under *Clavator reidi*.)
 V. 26250. Transverse section of very slender stem.
 V. 26251. Transverse section of internode.
 V. 26252. Transverse section of poorly preserved fertile node.
 V. 26253. Transverse and longitudinal sections of vegetative stems and nodes.
 V. 26254. Transverse section of internode showing origin of spines.
 V. 26255. Stems in various planes of section.
 V. 26256. Good sections through stems.
 V. 26257. Longitudinal section through node.
 V. 26258–9. Transverse sections of nodes.
 V. 26260. Stems in various planes of section.
 V. 26261. Transverse section of well-preserved fertile node.

CHARACEAE

CHARAXIS gen. nov. (Form-genus)

DIAGNOSIS.—Vegetative Charophyte organs agreeing in so far as they are known with *Chara*. Stem consisting of nodes and internodes; internode composed of a central cell surrounded by a ring of primary cortical cells which grow up and down from the nodes; and may cut off secondary cortical cells at their sides, primary cortical cells giving rise to spine cells. Leaves as in *Chara*, either corticated in the same way as the stem, or uncorticated.

The genus is so defined as to exclude uncorticated *Nitella*-like forms which if well enough known appear to be so easily distinguished as to be worthy of being placed in a distinct form-genus. It is thus synonymous with *Characeites* Pia (*non* Tuzson).

The recent Characeae includes two genera, *Chara* and *Lychnothamnus*, in which the axis is corticated (in a few species of *Chara* it is uncorticated). As there is no generic distinction between the vegetative organs of these two genera it is clearly unjustifiable to refer an isolated fossil stem to either genus, but a form-genus is needed for such specimens. Pia (1927, p. 89) did, in fact, propose such a genus as "*Characeites*", but unfortunately this name is inadmissible because the same name was used entirely differently by Tuzson as a form-genus of fruits.

In the absence of evidence to the contrary, it is presumed that this genus belongs to the Characeae in the strict sense, but it would not be surprising if some of the species proved on closer knowledge to be widely different.

This form-genus includes the following species (list taken from Groves, 1933):

- Charaxis blassiana* (Heer) n. comb.
- Charaxis gypsorum* (Saporta) n. comb.
- Charaxis minima* (Saporta) n. comb.
- Charaxis schübleri* (Braun) n. comb.
- Charaxis zietheni* (Unger) n. comb.
- Charaxis zolleriana* (Heer) n. comb.

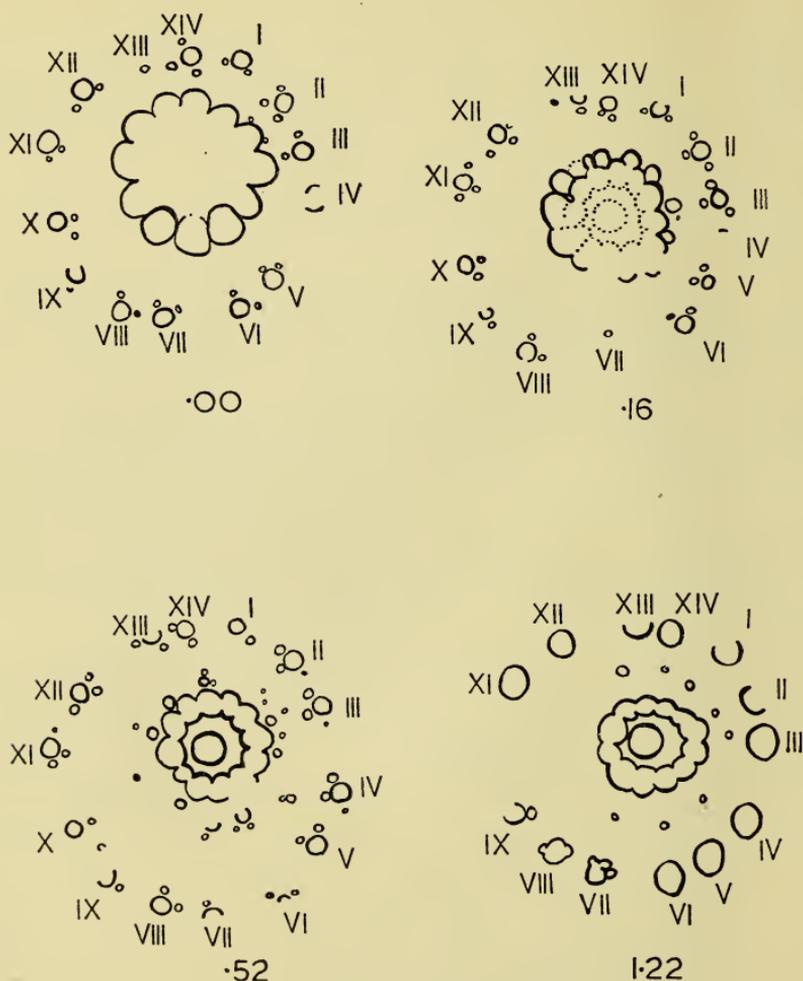
It would also include the vegetative organs described under the names *Chara langeri*, *C. medicaginula*, *C. reussiana* and *C. destructa*.

As this is probably an artificial genus, it would be meaningless to select a type-species.

Charaxis durlstonense sp. nov.

DIAGNOSIS.—Vegetative organs lightly calcified; internode about 0.8 mm. thick, showing a central cell corticated by twelve

equal cortical cells. Node bearing a whorl of twelve or more leaves; leaves very incompletely corticated below, but becoming corticated by five cells, which grow downwards from a leaf node; leaf entirely bare above.



TEXT-FIG. 14.—*Charaxis durlstonense*

Four selected levels of the series passing upwards from the nodal to the internodal regions. The numbers represent levels in mm. The roman numbers represent the fourteen leaves. V. 26262, $\times 16$.

HOLOTYPE.—V. 26262. Pl. XVI, fig. 10; Text-figs. 14, 15.

DESCRIPTION.—*C. durlstonense* is known from a single specimen preserved in Reid's and Groves's Durlston Chert. It is associated with vegetative organs of *Perimneste*. The specimen was exposed in a cut surface prepared by Reid and Groves for their investigation; they noticed it and made a photograph of it.

The specimen is a fragment which included the node. Unfortunately the first cut was right through the node and all the part below has been lost. It is not even certain in the short length investigated that the part of the internode studied was above the node—it might indeed be below; but the description is worded on the view that the specimen consists of half a node and a portion above.

Above the node the stem extends into the rock for a distance of 1.2 mm., where it was followed by grinding numerous serial sections until it showed signs of coming to an end.

The specimen had been a good deal worn before preservation, the outer surface of the leaves being abraded. It was also situated at the very edge of a block of chert and the chert itself had cracked right through the specimen, but these misfortunes did not cause much difficulty in investigation. Most of the space between the leaves and stem had been filled up with fine calcareous silt before its preservation in a rather sandy chert; exactly similar specimens of *Perimneste* are associated where the outer leaves are worn away and the protected parts are choked up with silt.

The internode shows a nearly circular central axis which lies loosely in a cavity, round which is a compact tube formed by the twelve cortical cells. The central axis has a thick wall which has just the same aspect as calcified fossils in this chert (*i. e.* it is regarded as calcified). The inner and outer walls of the cortex are calcified, the radial walls are mostly uncalcified and invisible, though a few are suggested by a faint line where slight calcification seems to have occurred.

The inner walls of the cortical cells bulge inwards as might be expected; the surface of the central axis shows in places distinct fluting evidently due to the impression of (about) twelve cells.

The space between the cortex and central axis needs to be accounted for. As the central axis is regarded as calcified, it cannot be supposed to have contracted after death. The form of the inner walls of the "cortex" strongly indicates that no cells occurred between them and the axis. On the contrary the cavity appears to match closely one which may often be seen in *Chara*, where a distinct gap often exists between the central axis and cortex (at least in the preserved material I have chiefly studied).

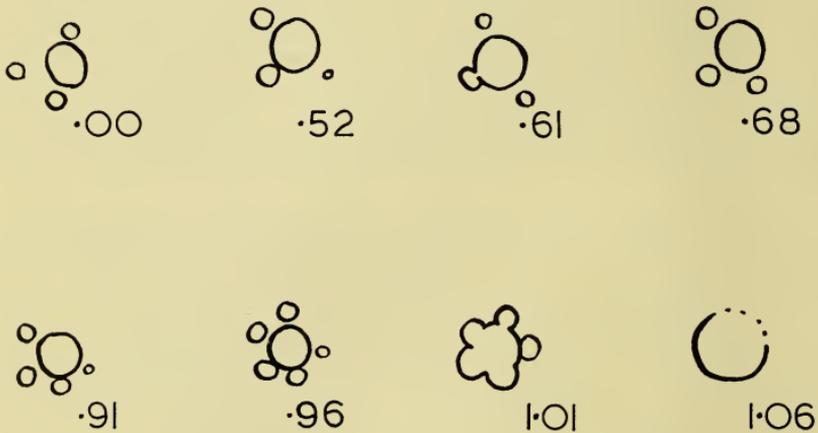
It is suggested that in *C. durlstonense* the cortex was originally in contact with the central axis, but it afterwards grew more than the central axis, breaking away from it and leaving this cavity.

The specimen shows fourteen leaves (some are damaged or missing at certain levels, but there appears to be no doubt about the number). As there are twelve cortical cells this greater

number of leaves is rather surprising; but in *Chara* a similar state of affairs is often found.

At the lowest point shown the leaves consist of a central tube accompanied by either two or three small cortical tubes. During the next millimetre new cortical tubes make their appearance so that a final number of five is attained. All the cortical tubes then pass into the central tube, which becomes considerably enlarged as it receives them. The last of the corticating cells to arrive (it is on the abaxial side) only extends for a minute distance of about 0.1 mm. They end by passing rather obliquely into the central tube.

This behaviour is closely paralleled by *Chara*, where the leaf may be corticated below, but at a certain node where it abruptly



TEXT-FIG. 15.—*Charaxis durlstonense*

Eight selected levels of a series passing through a leaf (No. II in Text-fig. 14). The numbers represent levels in mm. above that originally exposed. V. 26262, $\times 40$.

ceases to be corticated the central tube is much enlarged, being, in fact, of just the same diameter as the combined diameter of the central tube and cortex below. It thus provides one reason for the orientation of the specimen which has been adopted here.

DISCUSSION.—In such characters as this specimen shows it agrees very well with *Chara*, and there is nothing to show that it is not a species of that genus. This would seem to be the oldest fossil which there is any reason to refer to the Characeae in the narrow sense.

COMPARISON BETWEEN THE GYROGONITES OF THE BRITISH PURBECK CHAROPHYTES

The following figures give the lengths of all the Purbeck gyrogonites that have been measured. For *C. grovesi* only the well-preserved specimens (with the apical beak) were measured,

but for *C. bradleyi* all the specimens which were moderately well preserved were measured even though most lacked beaks. The four specimens with beaks measured 450, 470, 480, 430 μ respectively, and their beaks were between 40 and 80 μ long, so that some such length should be added to the others. For *C. reidi* and *Perimneste horrida* all specimens which were not either crushed or broken were measured.

It will be noticed that the different species are very unequal in abundance: *C. reidi* is represented by 238, *C. grovesi* by 131, *P. horrida* by 111, and *C. bradleyi* by 31 specimens.

Size.	Number of specimens.			Size.	Number of specimens.	
	<i>C. grovesi.</i>	<i>C. bradleyi.</i>	<i>C. reidi.</i>		<i>C. reidi.</i>	<i>P. horrida.</i>
231-240 μ	2	550	12	..
250	5	560	11	..
260	11	570	3	1
270	20	580	1	3
280	14	1	..	590	2	2
290	14	1	..	600	0	3
300	23	0	..	610	0	5
310	21	0	..	620	1	5
320	12	1	..	630	0	8
330	9	2	..	640	1	3
340	1	4	..	650	0	8
350	1	4	..	660	1	4
360	..	2	..	670	..	8
370	..	5	1	680	..	4
380	..	0	1	690	..	6
390	..	1	0	700	..	7
400	..	5	4	710	..	5
410	..	0	1	720	..	5
420	..	1	9	730	..	5
430	..	1	8	740	..	4
440	..	0	13	750	..	5
450	..	1	13	760	..	5
460	..	0	26	770	..	2
470	..	1	33	780	..	3
480	..	1	17	790	..	0
490	14	800	..	4
500	23	810	..	2
510	16	820	..	0
520	14	830	..	0
530	9	840	..	1
540	4	850	..	1

COMPARISON WITH OTHER CHAROPHYTES OF SIMILAR AGE

Pia, in Brückner and Pia (1935) described from sections some vegetative and reproductive organs in Swiss rocks of approximately Purbeck age. He recognised the close resemblance of the vegetative organs to those of the English specimens of *Clavator*; his sections through node and leaf do indeed match comparable sections through *C. reidi* perfectly. He states, however, that his specimens appear to show more than six leaves per node, though the specimens he figures give no evidence on

this point. Possibly he had a specimen which showed a small lateral branch of the same size as a leaf. The fruits he figures, though scarcely determinable, are gyrogonites which appear to be of about the same size as those of *C. reidi*. He refers to them as being of several species, but the figured specimens may well be sections in different planes through the various sized gyrogonites of this one species. He comments on the fact that no utricle is present, but it has now been shown that the gyrogonite of *C. reidi* is often preserved in isolation. It would thus appear that the evidence for referring the Swiss specimens, particularly the vegetative organs, to *C. reidi* is very strong.

Other older Mesozoic Charophytes are known from reproductive organs alone.

Chara maillardi Saporta (1891) is a very imperfectly known Purbeck fossil which, as Groves notes, might be a utricle of a *Clavator*; it might indeed be any of the species described here.

Gyrogonites jaccardi (Heer) Pia (see Groves, 1933, p. 21) is known from various Purbeck and Wealden localities. Heer's original specimens are described as oval, $600\mu \times 400\mu$, and showing six convolutions; this small number of convolutions distinguishes it clearly from the gyrogonites of *Clavator reidi* and *Perimneste horrida*. It has been stated (Loriol and Jaccard, 1865, p. 108) that *G. jaccardi* occurs in the Purbeck of Ridgeway Hill, Dorset.

Peck's (1937) Charophytes from the Morrison formation of Wyoming are of nearly the same age as the British Purbeck species. His fossils are all gyrogonites. Although several of the species are a good deal smaller than the average, none is small enough to be confused with *C. grovesi*, and none has the projecting apex of *C. bradleyi*. His *Chara verticillata*, however, is like the gyrogonite of *Clavator reidi*, and cannot be definitely distinguished from it at present. His *Aclistochara latitruncata* is rather like the gyrogonite of *Perimneste horrida*, and these two also cannot at present definitely be distinguished. The other fossils referred by Peck to *Aclistochara* are all distinctly smaller than *P. horrida*.

"*Chara purbeckensis*" Forbes (see Groves, 1933, p. 28) is a *nomen nudum*.

Older Species

"*C. gebhardi*" Ottmer, 1880 (see Groves, 1933, p. 18), is a *nomen nudum* for a Kimmeridgian Charophyte.

Kosmogyrta bleicheri (Saporta) Pia (see Groves, 1933, p. 12) is a small rounded fruit from the Oxfordian distinguished from the species described here by the small number of its convolutions, which are tuberculate.

Gyrogonites laevigatus (Upton) Pia (see Groves, 1933, p. 22) from the Inferior Oolite is an oval fruit $575-800\mu$ long with

eleven convolutions. It cannot at present be reliably distinguished from either *Clavator reidi* or *Perimneste horrida*, though from its different age it is probably distinct.

Younger Species

Chara knowltoni Seward (see Groves, 1933, p. 22) is of Wealden age. It has been by no means completely described and figured, and Groves states his opinion that it is not a Charophyte. I have examined the abundant original specimens closely and have convinced myself that it is indeed a true Charophyte gyrogonite, though a very peculiar one. It shows the usual spiral cells, and at the end of the spore it can be seen that there are five, as in other gyrogonites. It is, however, composed of organic matter and devoid of any lime shell. This evidently is an uncalcified gyrogonite, such as occurs in about half the living Charophytes, but which has been seldom if ever found fossil in any but recent deposits. It is perhaps because of the lack of a lime shell that the specimens have been crushed and rather distorted.

Gyrogonites medicaginula Lamarck is a Tertiary species, but Groves (1933, p. 25) has identified some English Wealden specimens with it. It is a spherical fruit, considerably larger than any in the Purbeck flora.

Atopochara trivolvis Peck (1938) from the Lower Cretaceous is a remarkable fruit described as an oogonium enveloped in 36 cells in groups of twelve. The present study suggests that *Atopochara* might be a utricle, and not directly comparable with a gyrogonite. Peck considers that *Atopochara* is an extremely primitive type; on this alternative interpretation it might be regarded as one of the most advanced of the Clavatoraceae in fruit structure.

COMPARISON OF THE BRITISH PURBECK GYROGONITES WITH FOSSIL CHAROPHYTES OF VARIOUS AGES

1. *Clavator grovesi* and *Clavator bradleyi*

The gyrogonites of these two species are so small that very few known species come within their size ranges, and none of these happens to show a prolonged apex. They are thus easily distinguished.

2. *Clavator reidi*

About thirty species have oospores which overlap the variation range of *C. reidi* in length, breadth and number of convolutions. Most of these, however, are frequently larger or smaller than is ever observed in *C. reidi*, and a few are excluded by differences in shape.

There remain the following, of which mention is made in Groves (1933) :

"*Chara*" (or *Gyrogonites*] *inconspicua*, *laevigata*, *petrolei*, *sadleri*, *stantoni*, and *voltzii*. There is also *G. verticillatus* (Peck) (see p. 72).

Although it is most unlikely that any of the above are specifically identical with *Clavator reidi*, it is impossible to point to any character which completely differentiates them.

3. *Perimneste horrida*

The following species mentioned in Groves (1933) are not at present clearly distinguished :

G. brongniarti (some varieties), *G. brewsteriensis*, *G. bernouli* (which has an open apex), *G. elegans*, *G. escheri*, *G. laevigatus*, *G. quinqueradiatus*, *G. politus*, *G. texensis*, *G. tornatus* (if inverted), *G. turbinatus*, *G. reussianus*. Also the following species described by Peck (1937) : "*Aclistochara*" [or *G.*] *latitruncata*, see p. 72.

The vegetative organs of *Clavator* and *Perimneste* are unique, though their character is not always shown by a single transverse section.

THE PURBECK FOSSILS AND THE EVOLUTION OF THE CHAROPHYTES

Groves and Reid had considerable hopes that the elucidation of the Purbeck fossils would throw light on the ancestry and evolution of the Charophytes. In this, however, I think the present work has proved disappointing. *Charaxis durlstonense* provides evidence that plants with the vegetative organization of *Chara*, the most elaborate of the modern forms, already grew in Upper Jurassic times.

Clavator and *Perimneste* are two of the most peculiar and, as I consider, most elaborately organized members of the whole Charophyte class. They certainly throw no light on the origin of the comparatively simple forms of to-day. It is true that they may help to explain two of the most peculiar fossil Charophytes, *Atopochara* and *Lagynophora* ; and if these forms could be brought into line it would be a certain advance. Even then all that could fairly be claimed for the study of these fossil Charophytes would be that they had led to the clearing up of many of the problems that they themselves had raised. *Perimneste* and *Clavator* slightly widen one's idea of what is a Charophyte, but do nothing to link this class up with any other group of algae.

While I would prefer to regard the "Charophytes" as being no more than a family of the green algae (Chlorophyceae), of equal rank, for example, with the Oedogoniales or the Conjugatae, this view is based on the living forms alone, for the fossils give

no help. It is indisputable that the reproductive organs of the Charophytes are quite peculiar; their cytological life-cycle, however, is that typical of the fresh-water green algae; their plant body is very like that of certain red algae, from which class they differ, however, in many obvious respects. The term "Charophyte" rather than "Charalean" is used here merely because it happens to be current.

THE STRATIGRAPHIC VALUE OF THE FOSSIL CHAROPHYTES

The Charophytes are potentially of great stratigraphic value, since they occur in lake deposits in which zone fossils apart from the shells of Cyprids are often scanty. The organ found fossilized is normally the gyrogonite; this is a strong and neatly constructed body which at first sight seems ideal for this purpose. Careful consideration of the available evidence has, however, led me to the conclusion that their value is likely to be rather small because the difficulties of recognizing the species are great.

The gyrogonites are such beautiful little fossils that they have naturally been much studied, and a large number of species have been described. A review of the literature, however, shows that little attention has been given to the normal range of variation which may be expected in a species.

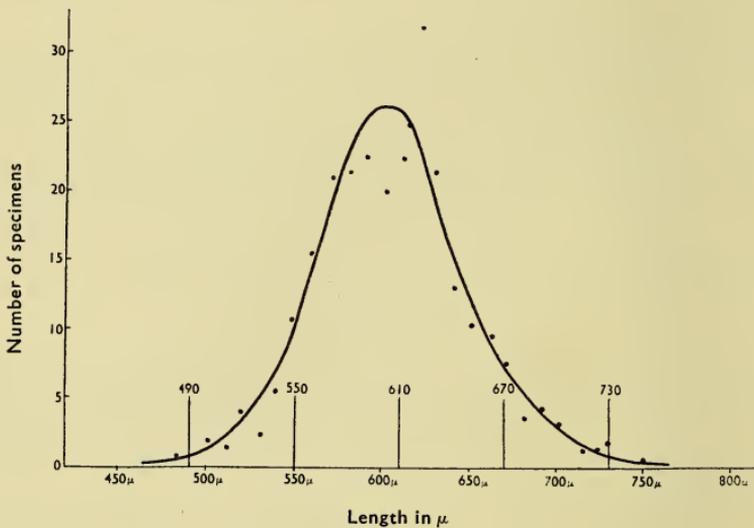
As many Charophytes are very common, such a study is easily made, and some notes are given below of the results with a single gathering of *Chara vulgaris*. A large number of gyrogonites were isolated by drying and soaking the ripe material and breaking it up. They are so hard that scarcely any suffered in preparation.

The variation noticed is grouped under the following six heads:

- (1) Length.
- (2) Breadth.
- (3) Shape (apart from that included under length and breadth).
- (4) Number of spiral cells crossing face of spore.
- (5) Character of spiral cells.
- (6) Other characters in a few special cases.

(1) Variation in length: This character was investigated in detail; the results of measuring 500 oogonia are given in Text-fig. 16. It will be seen that the figures fall as closely as could be expected to a normal curve of random variation about a mean. The mean is about 610μ ; the shortest spore is 480μ , the longest 760μ . It will be seen, however, that very nearly all lie between the limits of 730μ and 490μ , which figures are 610μ (the mean) $+20\%$ and $610\mu-20\%$. A large majority also lie between the limits of $\pm 10\%$ of the mean, that is between 670μ and 550μ ; the proportion excluded by these narrower limits is 15% .

Groves gives the limits of variation for the oospore of this species as 425μ to 675μ , "excluding the cage"; this greater range one would expect, as he must have taken into consideration many gatherings, grown under varied conditions. It would appear from his statements that other species show a rather similar range of variation, and so do the fossil gyrogonites from the Purbeck. If we take the limits of $\pm 20\%$ of the mean as the range of a species, then it would be possible to say when the sizes of two given specimens are so different that they must be distinct species. If, for example, one spore is twice as long as another they could not be the same; if one is one and a half times as long, it becomes just possible for them to be the same, one being 20% less than the mean, the other 20% greater.



TEXT-FIG. 16

Graph showing the variation in size of the spore of *Chara vulgaris*. The dots represent the number of specimens of a particular size: thus there were 40 spores 600μ to 610μ long, 45 spores 610μ to 620μ and so on. The graph is an idealised curve fitting the points as closely as possible. The vertical lines represent the mean size (610μ), and this mean $\pm 10\%$ and $\pm 20\%$. It is found that about 85% of the spores lie between the limits of $610\mu \pm 10\%$, but over 99% between the limits $610\mu \pm 20\%$. Number measured, 400. Error of individual measurement less than $\pm 10\mu$.

(2) Breadth: The breadth of the spore of *C. vulgaris* was investigated in the same way as the length, and although the number measured was smaller (100), it was sufficient to show that the variation was of just the same sort as for the length—that is to say the frequencies lay close to a probability curve with a mean at about 420μ ; most of the specimens were within $\pm 10\%$ of this mean, nearly all within $\pm 20\%$. Groves gives

a range of 225μ – 400μ , but this refers to the oospore, not the gyrogonite.

(3) Shape: There is a good deal of variation in shape, since there is no tendency for the longest spores to be also the widest, or *vice versa*. In the most slender gyrogonite measured the length was exactly twice the breadth; in the fattest spore it was 1.2 times the breadth. Besides this there is variation in the shape of the ends. Usually both ends are somewhat drawn out, the apex more so, but a number of gyrogonites have rounded ends. In a few also it is almost conical, being widest just above the base. Occasional spores in which the long axis is curved may perhaps be dismissed as abnormal.

(4) Number of spiral ridges crossing the face of the spore: This figure is not easy to count because it is most difficult to know whether to include the cell appearing at the end of the spore, and when a single spore is counted, then rolled over and counted again, the second count may be one or occasionally two more or less. Peck (1937) uses two closely related figures; the number of complete turns made by a single cell—which I find very difficult to estimate by direct observation—and the “equatorial angle” made by a spiral cell in crossing the “equator”. This is easily measured in a photograph.

I have not made a special study of these two features used by Peck, but relying on direct counts for *C. vulgaris*, the figures for the number of spiral cells seen in lateral view is 9–13, 11 being commonest in this collection, though Groves gives the range for this species as 12–15. (Groves's counts appear in many instances a little more generous than his illustrations for the same species.) For this character it would seem that the mean ± 2 gives nearly the whole range, while the mean ± 1 covers the majority of counts, though the differences due to different methods in dealing with the ends are rather serious.

(5) Character of the spiral cells: The surface is usually almost flat; in about equal numbers it is slightly concave and slightly convex.

(6) Other characters: The extent to which a “cage” is formed at the base of the spore by the projecting boundary walls varies a good deal.

Peck (1937) makes use of the failure of the apex to calcify—or its tendency to break away—to give an open hole, and bases a genus *Aclistochara* on this character. None of the gyrogonites of *C. vulgaris* examined showed this feature; Groves, however, mentions that calcification sometimes fails towards the apex in species where it is normally developed. In the fossil *Clavator grovesi* it was noticed that the apical region is sometimes rather feebly calcified, and then it is easily broken away to give a hole like that in *Aclistochara*. Peck has considered this point, and maintains that a mere breakage should be recognisable by the

irregularity of the hole, but it appears to me that in *C. grovesi* the hole, which is undoubtedly due to breakage along a line of weakness, is sometimes just as regular as in Peck's *Aclistochara* species, e. g. *A. lata*. This then would also appear to be a feature which is not fully reliable, but yet of a certain value.

The range of variation in the family will now be considered.

The range of length is from about 200μ to about 1600μ . Between these limits it would be possible to fit only about six specific groups, each differing by $\pm 20\%$ of its mean length.

The range in diameter variation is about comparable to the range of length variation, giving again six distinct groups. By combining the two features a number considerably greater than six could be distinguished, but the number would still not be large because in the Charophyta there is a considerable correlation between the two dimensions, the spores being usually ovoid and never very slender, and never much wider than long.

The variation in shape apart from that expressed by length and breadth measurements is difficult to estimate numerically either in the species or family, but it would appear from my observations that though certain shapes of spore end are rather characteristic of a species, they are far from constant. No very marked variations in shape from the normal have been described in the family.

The number of spiral cells crossing the face of the spore varies from 5 to 16, the great majority showing between 8 and 13. If we allow as before a variation within the species of ± 2 , this would allow four or five groups to be distinguished by this character with certainty.

The surface of the spiral cells may be strongly convex, flat or strongly concave. The variation in the species is, however, so considerable that very few groups could be distinguished by this character; indeed it would probably not be safe to do more than distinguish the very convex from the very concave. In the fossil group *Kosmogyra* the tubercles give an additional character, but again one which is by no means constant, as some Tertiary gyrogonites of *Kosmogyra* which I have examined seem to show.

This survey brings out the relative magnitudes of the variation ranges of the individual species and of the family. The range of the family does not appear great enough to allow a very large number of specific groups to be distinguished with any certainty. How large this number may be I cannot say, but I feel sure it is not as large as the number which are at present distinguished.

I thus consider that the Charophyte gyrogonites are likely to be very difficult to determine specifically unless exceptionally abundant material is available, and even then difficult. Specific determination of Charophytes is usually essential for stratigraphic purposes, and I am thus forced to the conclusion that these

beautiful little fossils are likely, in general, to have only slight stratigraphic value.

Genus **ALGACITES** Schlotheim

1822 *Algacites* Schlotheim, p. 45.

This designation would appear to be the valid name for fossils believed to be algae which are not fully enough understood to be classified in a definite genus. A very considerable number of fossils described under many generic names would appear to be better placed here.

Algacites clavatoris sp. nov.

(Pl. XVI, fig. 2 ; XVII, figs. 5, 6)

DIAGNOSIS.—Filamentous alga ; filaments enclosed in calcareous tubes about 100μ in diameter. Tubes branching and densely tufted, forming a cushion 0.5 mm. thick, normally growing on the stems and other organs of species of *Clavator*.

HOLOTYPE.—V. 26225 (Pl. XVII, figs. 5, 6).

HORIZON.—Middle Purbeckian.

REMARKS.—*A. clavatoris* is the only epiphyte recognised on *Clavator*. When still attached its base is slightly separated from the spine cells of the stem and leaf or utricle of the oogonium, leaving just sufficient space for the uncalcified outer walls of these cells on which it evidently grew during the life of the host. *A. clavatoris* has been found on both *C. reidi* and *C. grovesi*, but it is much more local in distribution than either of its hosts.

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All specimens are from Portesham, *Reid & Groves Coll.*, 1933.

- V. 26225. Fairly large isolated specimen. Holotype. Pl. XVII, figs. 5, 6.
 V. 26226. Figured on Pl. XVI, fig. 2.
 V. 26227. Mounted in balsam.
 V. 26228–34. Numerous specimens.

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EXPLANATION OF PLATES

[Unless otherwise stated, all specimens are in the Geology Department of the British Museum (Natural History) and are referred to by their registered numbers. Except in a few instances, which are noted, all photographs are untouched.]

PLATE I

Clavator reidi. Leaf

All $\times 50$

- Fig. 1. Apex of sterile leaf. **V. 26007.**
- Fig. 2. Part of male leaf (antheridial perforations to the left). **V. 26008.**
- Fig. 3. Part of sterile leaf with long, bare internodes. **V. 26011.**
- Fig. 4. Part of male leaf. **V. 26010.**
- Fig. 5. Part of sterile leaf showing complete spine-cell cover. **V. 26003.**
- Fig. 6. Part of male leaf with bare internodes. **V. 26009.**
- Fig. 7. Part of sterile leaf with swollen nodes. **V. 26006.**
- Fig. 8. Upper part of sterile leaf with swollen nodes. **V. 26005.**



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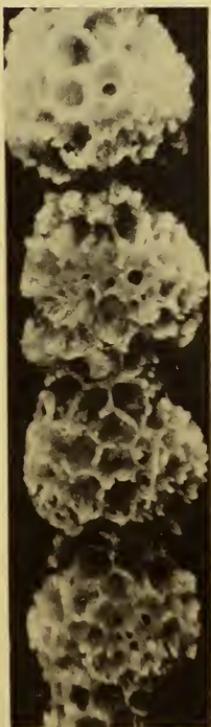
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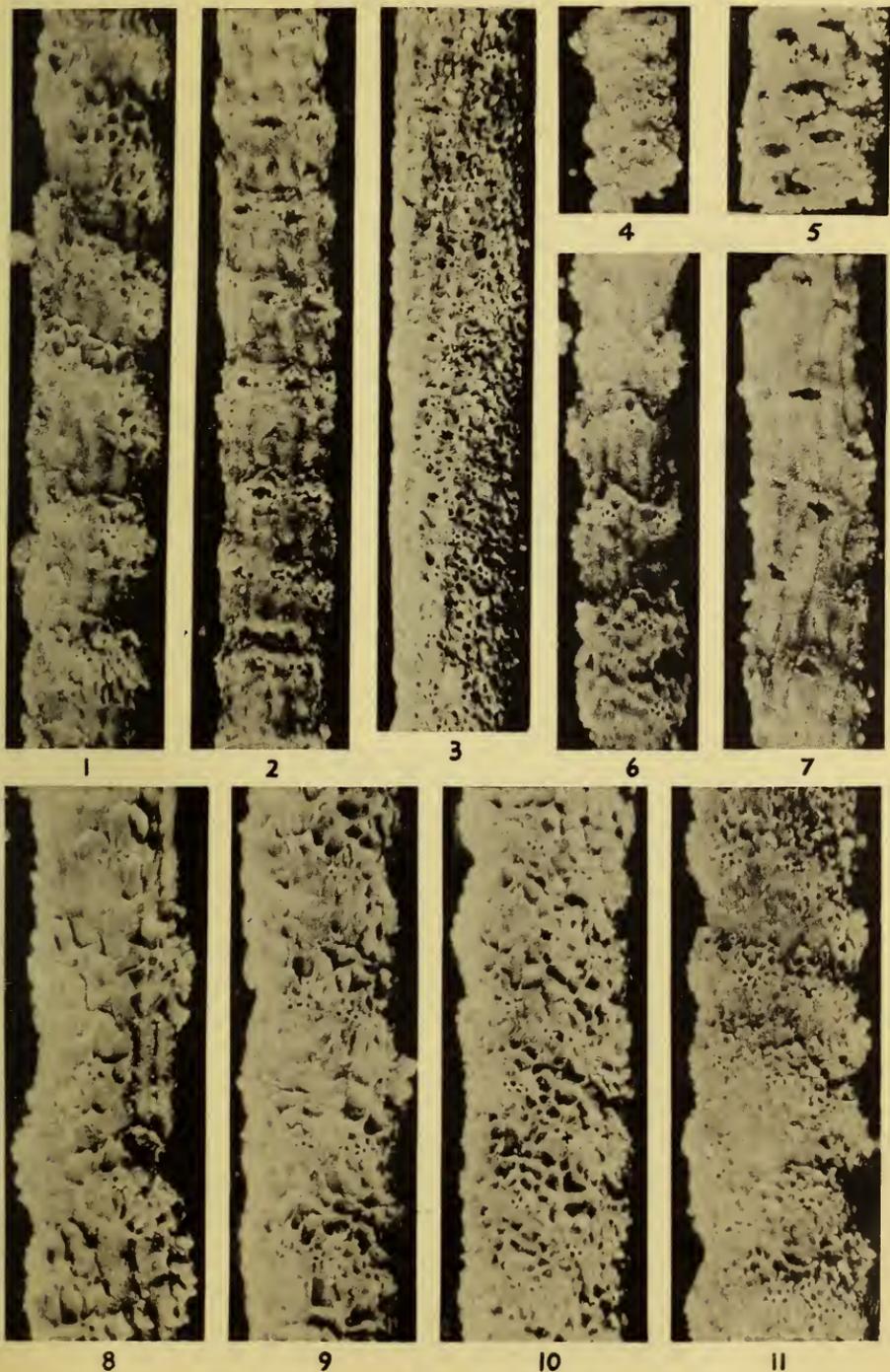
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PLATE II

Clavator reidi. Internode of axis

All $\times 30$

- Fig. 1. Cortex almost longitudinal; spine-cell layer discontinuous, forming rings below and a more or less continuous spiral above. **V. 26028.**
- Fig. 2. Cortex longitudinal; spine-cell layer incompletely mineralised. **V. 26030.**
- Fig. 3. Cortex distinctly spiral; spine-cell layer continuous and composed of rather small cells. **V. 26033.**
- Fig. 4. Slender axis bearing "rosettes" of small spines. **V. 26031.**
- Fig. 5. Incompletely mineralised axis in which the cortical cells appear to have been very short. The outer walls of the cortical cells alone are present. **V. 26027.**
- Fig. 6. Slender axis with cortex forming rings; rings distant above, crowded and continuous below. **V. 26042.**
- Fig. 7. Incompletely mineralised axis; spine-cell layer not preserved, but alternation of holes in cortex seen distinctly. **V. 26037.**
- Fig. 8. Cortex longitudinal; spine-cell layer not quite continuous of large-celled rosettes. There is a slight difference between the size of the cortical cells. **V. 26035.**
- Fig. 9. Spine-cell layer continuous but showing rings of larger and smaller cells. **V. 26040.**
- Fig. 10. As fig. 9, but larger and smaller cells form a distinct spiral. **V. 26036.**
- Fig. 11. Rather thick axis. The spine-cell layer is composed of small cells, and is spiral and incompletely covers the cortex. **V. 26038.**



CLAVATOR REIDI

PLATE III

Clavator reidi. Stem and leaf

- Fig. 1. Part of a node dissected open. The perforations leading from the central cell to the top cortical cells and the perforations of the leaf base flanked by the two laterals are seen. Above, the whole central tube is gone so that the cortical cells are exposed. **V. 26025**, $\times 30$.
- Fig. 2. Small stem internode (to the left) and leaf in transverse section. **V. 26012**, $\times 50$.
- Fig. 3. Stem internode in longitudinal section showing central and cortical tubes. **V. 26002**, $\times 30$.
- Fig. 4. Stem internode with almost completely mineralised spine cells, giving a nearly smooth surface. **V. 26069**, $\times 30$.
- Fig. 5. Stem internode with incompletely mineralised cortex showing the pores leading from the central to the cortical cells. **V. 26004**, $\times 50$.
- Fig. 6. Leaf, restored from four fragments placed end to end. **V. 26057**, $\times 10$.
- Fig. 7. Leaf; spine cells almost completely mineralised to give a nearly smooth surface. **V. 26059**, $\times 50$.
- Fig. 8. Leaf in oblique longitudinal section showing the interior of a node. **V. 26090**, $\times 50$.
- Fig. 9. Stem internode showing the details of the spine-cell rosettes. **V. 26092**, $\times 50$.



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PLATE IV

Clavator reidi. Node of axis

Figs. 1 and 2 $\times 30$; figs. 3-10 $\times 15$

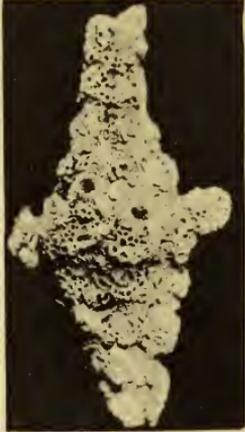
- Fig. 1. Leaf base and part of node. The spine cells form two distinct leaf-base rosettes. **V. 26072.**
- Fig. 2. Leaf base and part of node. The leaf-base rosettes are almost united. **V. 26073.**
- Fig. 3. Node showing four of the six leaves and the base of a slender branch. **V. 26049.**
- Fig. 4. Large unbranched node showing four of the six leaves and two nodal perforations. **V. 26048.**
- Fig. 5. Node viewed from above showing all six leaves, the two nodal perforations, and the broken-off end of the axis. **V. 26026.**
- Fig. 6. Node in oblique-lateral view showing bases of leaves, a nodal perforation, the base of the continued axis and a second branch almost as large as the axis. (Part of this specimen is figured also on Pl. V, fig. 2.) **V. 26046.**
- Fig. 7. Node showing bases of leaves and a strong lateral branch. **V. 26047.**
- Fig. 8. Slender axis with scarcely swollen node showing bases of leaves and a perforation (to the right). **V. 26044.**
- Fig. 9. Large node; spine cells forming prominent rosettes. **V. 26045.**
- Fig. 10. Normal node; the cortex is broken away above exposing the inner walls of the cortical cells round the central cell. **V. 26043.**



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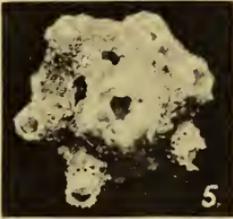
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CLAVATOR REIDI

PLATE V

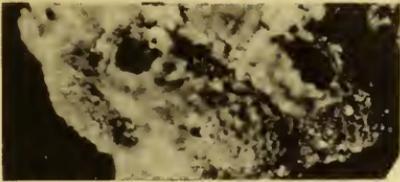
Clavator reidi. Stem and leaf

Figs. 1-3, 6-10 \times 30; figs. 4, 5 \times 50

- Fig. 1. Internode showing incomplete mineralisation of the spine cells. Note modified alternation of holes in cortex forming rings. **V. 26032.**
- Fig. 2. Portion of node showing leaves and leaf-base rosettes (one between each leaf pair). The specimen is inverted. (Also shown in Pl. IV, fig. 6.) **V. 26046.**
- Fig. 3. Internode; spine-cell layer of small uniform cells. **V. 26039.**
- Fig. 4. Apex of thick, abruptly tapering leaf. **V. 26066.**
- Fig. 5. Portion of sterile leaf with unusually thick central cells. **V. 26034.**
- Fig. 6. Internode; mineralisation of spine-cell layer incomplete. Note alternation of holes in cortex. **V. 26070.**
- Fig. 7. Stem internode in longitudinal section showing pits leading from the central tube to the cortical cells. **V. 26017.**
- Fig. 8. Internode; spine cells forming rosettes, not completely covering the cortex. Specimen accidentally destroyed.
- Fig. 9. Internode; the spine-cell layer is partly mineralised, but large perforations in the cortex are seen. **V. 26029.**
- Fig. 10. Internode; the spine-cell layer is complete and of the rosette type. **V. 26041.**



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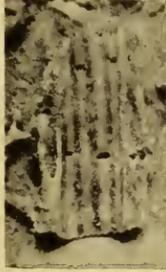
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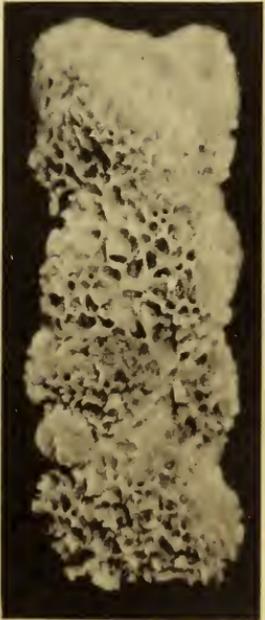
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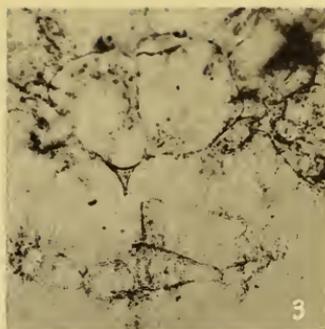
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PLATE VI

Clavator reidi. Structure of node

Figs. 1-7, 9 by transmitted light

- Fig. 1. Piece of cortex showing bases of two leaves (shown also in fig. 3). **V. 26023**, $\times 15$.
- Fig. 2. Piece of cortex with two leaf-bases; showing the leaf-base lateral cells, and the subdivided short cells. **V. 26023**, $\times 15$.
- Fig. 3. Part of specimen seen in fig. 1; two leaf-base lateral cells are seen, and below are some divided short cells. **V. 26023**, $\times 15$.
- Fig. 4. Similar specimen to those shown in figs. 1-3. **V. 26023**, $\times 15$.
- Fig. 5. Piece of cortex from just below a node showing parts of large cortical cells and the alternate cortical cell-series which disappears at the node, becoming small and irregular (as a dark band). **V. 26056**, $\times 30$.
- Fig. 6. Part of stem just below a node, with the upper surface dissected away, showing the dilated cortical cells. **V. 26050**, $\times 15$.
- Fig. 7. Part of cortex from just below a node. The dark vertical bands are the disappearing cortical cells; the short cells are subdivided. **V. 26051**, $\times 30$.
- Fig. 8. Node broken through transversely just below the leaves and the broken end seen by transmitted light, showing the large holes in the horizontal walls of the highest cortical cells, the smaller holes in those below. **V. 26052**, $\times 30$.
- Fig. 9. A small piece of stem showing parts of two nodes. **V. 26068**, $\times 15$.
- Fig. 10. A node with the upper surface dissected away, showing the imprint of the large cortical cells on the wall of the central tube; at the leaf level the imprint of smaller cells (probably the leaf bases). **V. 26065**, $\times 30$.



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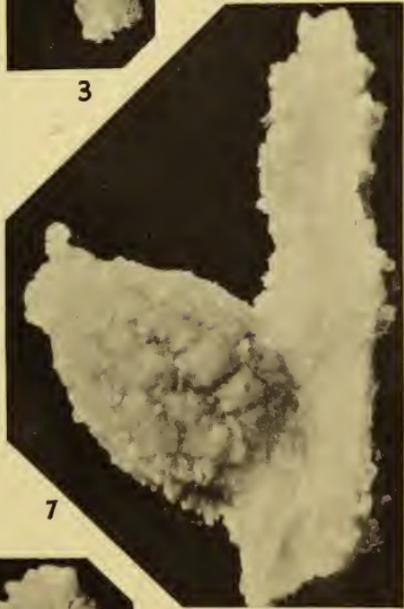
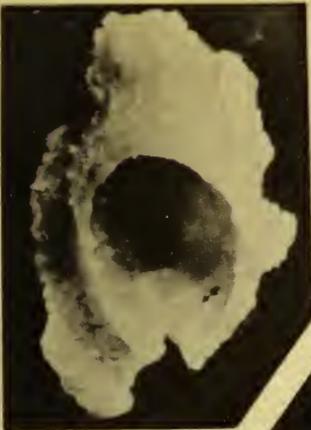
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PLATE VII

Clavator reidi. Oogonia and male branch.

Figs. 6, 9 \times 30; remainder \times 50

- Fig. 1. Interior of oogonium exposed by breaking away the utricule and part of the oogonial wall. Note on the left the ridges due to the spiral cells. **V. 26024.**
- Fig. 2. Small oogonium without utricule, outer wall warted. **V. 26079.**
- Fig. 3. Part of slender male leaf. Specimen accidentally destroyed.
- Fig. 4. Oogonium without utricule; outer wall smooth. **V. 26055.**
- Fig. 5. Apex of oogonial branch with minute (? abortive) oogonium in utricule. **V. 26015.**
- Fig. 6. Oogonial leaf with normal oogonia produced almost in contact. **V. 26071.**
- Fig. 7. Oogonium near apex of leaf. There is no utricule and the oogonial wall is warted. Specimen accidentally destroyed.
- Fig. 8. Oogonium and part of leaf in lateral view. The apex of the oogonium is curved and strongly warted; the utricule is only present at the base. **V. 26018.**
- Fig. 9. Two oogonia and part of leaf in lateral view. The utricles are abnormal in that the outer walls of their cells are mineralised. **V. 26054.**
- Fig. 10. Wide oogonium (and fragment of leaf) in lateral view. The utricule is absent and the outer wall is smooth. **V. 26077.**



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CLAVATOR REIDI

PLATE VIII

Clavator reidi. Oogonium in utricle

All $\times 40$

- Fig. 1. Lateral view. Oogonium short and wide; utricle missing from dorsal side; part of leaf present. **V. 26021.**
- Fig. 2. Lateral view. Utricle longer than oogonium, missing from dorsal side; part of leaf present. **V. 26064.**
- Fig. 3. Lateral view. Utricle well developed; internode of leaf long and bare. **V. 26016.**
- Fig. 4. Dorsal view. Utricle missing from dorsal side; oogonial outer surface warted, apex projecting beyond utricle. The leaf is in oblique section below. **V. 26019.**
- Fig. 5. Apex of oogonium showing 5-cuspid openings of outer surface. (*cf.* Pl. IX, fig. 6). **V. 26062.**
- Fig. 6. Apical and ventral view (*i. e.* surface away from leaf), showing the large ventral cell of the utricles of each oogonium. **V. 26067.**
- Fig. 7. Lateral view. Utricle only present in lower part; oogonium outer surface not warted, but showing indistinct spiral cells. Part of leaf present. **V. 26085.**
- Fig. 8. Lateral view. The two upper oogonia are normal and have developed utricles; the lowest is small (? abortive). Internodes almost completely corticated. **V. 26013.**
- Fig. 9. Lateral view. Utricle long and slender; part of leaf present. **V. 26020.**
- Fig. 10. Lateral view. Slender (? apical) part of female leaf with continuous cortex. The oogonia are minute (? abortive). **V. 26014.**



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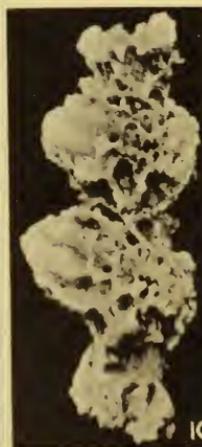
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CLAVATOR REIDI

PLATE IX

Clavator reidi. Oogonium

All $\times 80$ except figs. 4 and 5, which are $\times 40$

The figures with the exception of 1, 4 and 5 are drawings on photographs.

- Fig. 1. Egg cast showing part of the gyrogonite wall as wings. **V. 26084.**
- Fig. 2. Oogonium; part of wall dissected away to expose the egg cast. **V. 26088.**
- Fig. 3. Gyrogonite; part of the wall has been broken away to expose the interior. **V. 26081.**
- Fig. 4. Leaf in longitudinal section showing the enlargement of the central cavity below the oogonium. **V. 26091.**
- Fig. 5. Apex of oogonium completely enclosed in the utricle except for a small apical pore. **V. 26061.**
- Fig. 6. Apex of oogonium surrounded by the cells of the utricle, which do not cover its apex or dorsal side. The minute oogonial pore is surrounded by the ends of the five spiral cells, three of which have become enlarged by breakage. **V. 26089.**
- Figs. 7-9. A gyrogonite seen from below, above and from the side. The wall is incompletely mineralised. **V. 26093.**
- Fig. 10. Gyrogonite showing two states of preservation in the same specimen. **V. 26080.**
- Fig. 11. Oogonium. The upper side has been broken away to expose the interior; the gyrogonite is missing. **V. 26063.**





PLATE X

Gyrogonites of *Clavator grovesi* and *C. reidi*

All $\times 80$

Clavator grovesi

- Figs. 1-3. Side, apex and base. **V. 26146.**
Figs. 4-6. Side, apex and base. **V. 26144.**
Figs. 7-9. Side, apex and base. **V. 26143.**
Figs. 10-12. Side, apex and base. **V. 26142.**

Clavator reidi

- Figs. 13-15. Side, apex and base. **V. 26086.**
Figs. 16-18. Side, apex and base. **V. 26087.**

N.B.—The specimens shown in figs. 1, 4, 7, 10 are upside down, the apex being downward. The figures are drawings on photographs.



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PLATE XI

Clavator grovesi

- Fig. 1. Internode. **V. 26151**, $\times 10$.
Fig. 2. Oogonium split longitudinally and seen from within, showing the spiral cells and their extension into the necks. **V. 26153**, $\times 50$.
Fig. 3. Fragment of cortex showing a rosette of spine cells. **V. 26136**, $\times 30$.
Fig. 4. Fragment of cortex seen from within, showing the points of origin of the spine cells. **V. 26150**, $\times 30$.
Fig. 5. Fragment of cortex showing a rosette of spine cells. **V. 26145**, $\times 15$.
Fig. 6. Fragment from a node showing rosette from within, and the point of origin of a leaf and of the two large spine rosettes below it. **V. 26134**, $\times 30$.
Fig. 7. Fragment of a leaf with very short joints. **V. 26138**, $\times 30$.
Fig. 8. Fragment of a typical leaf. **V. 26137**, $\times 30$.
Fig. 9. Fragment of a leaf with an antheridial base. **V. 26135**, $\times 50$.



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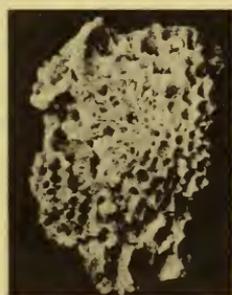
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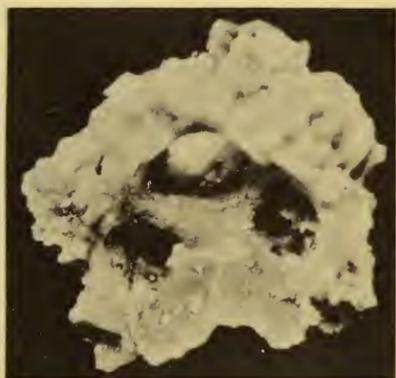
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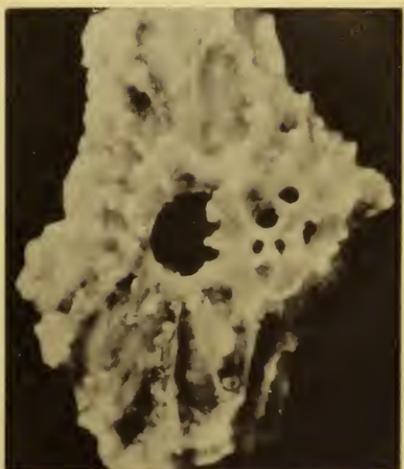
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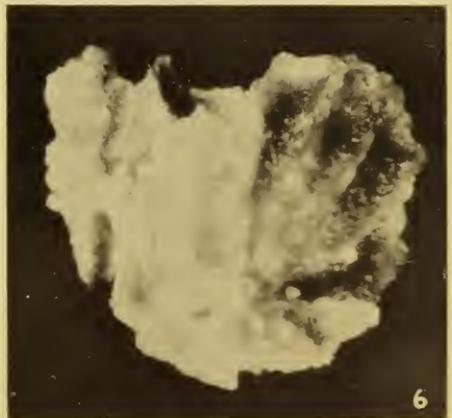
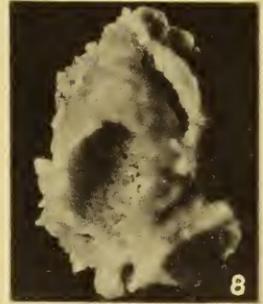
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PLATE XII

Clavator grovesi. Oogonium and utricle

All $\times 50$

- Figs. 1-3. The same utricle in three aspects. Fig. 1 from below; fig. 2 from the apex showing the aperture; fig. 3 from the side (the leaf to the left). **V. 26132.**
- Figs. 4-6. The same utricle in three aspects; fig. 4 showing the apex; fig. 5 from above; the leaf is seen in section in the lower part of the figure; fig. 6 from the side, the leaf to the left. **V. 26133.**
- Figs. 7, 8. Specimen in which half the utricle wall has been broken away to expose the oogonium, which is empty and shows its internal spiral striations in fig. 7. Fig. 7 illuminated from below; fig. 8 illuminated from above. **V. 26139.**
- Fig. 9. Specimen in which half the utricle has been broken away to expose the oogonium, which is intact. **V. 26141.**

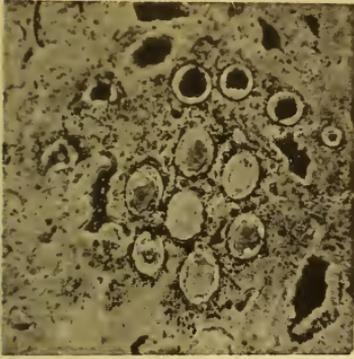


CLAVATOR GROVES!

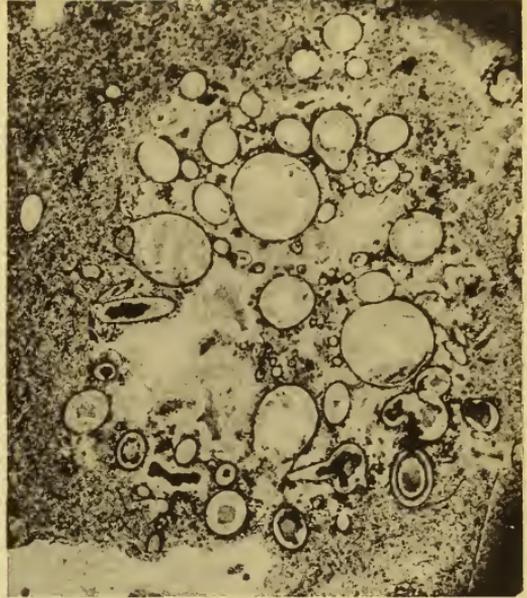
PLATE XIII

Perimneste horrida. Vegetative organs. All $\times 15$

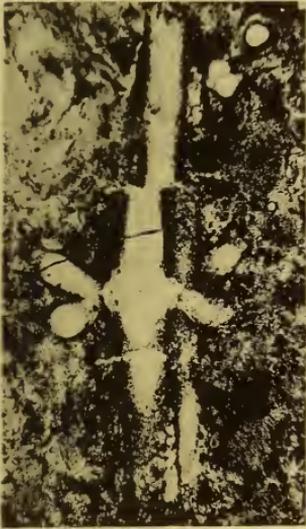
- Fig. 1. Transverse section above a node showing the stem and a number of leaves. Specimen polished, by reflected light. **V. 26241.**
- Fig. 2. Transverse section through a fertile leaf whorl; the four largest oval bodies are oogonia. This is one of the sections on which Text-fig. 12 is based. (Section at level 6.00 immediately below the one shown in Text-fig. 12.) **V. 26244.**
- Fig. 3. Longitudinal section through a node, showing the central tube giving rise to upward and downward pointing short leaves; a cortical cell is at a deeper level on the right. Thin section, by transmitted light. **V. 26240.**
- Fig. 4. Transverse section just below a node showing two of the short leaves. Thin section, by transmitted light. **V. 26239.**
- Fig. 5. Transverse section through node showing the origin of two of the long leaves. Surface whitened by hydrofluoric acid. **V. 26242.**
- Fig. 6. Longitudinal section through node, showing the central cell and passing through the cortex and a long leaf (to the right). Spine cells are seen originating below. **V. 26239.**
- Fig. 7. Transverse section just above node showing numerous leaves. **V. 26240.**
- Fig. 8. Longitudinal section through node, showing (to the left) the origin of an upward and downward pointing short leaf. Specimen exposed in grinding, afterwards destroyed. **V. 26245.**



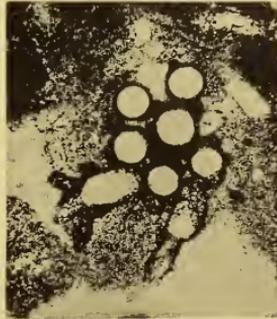
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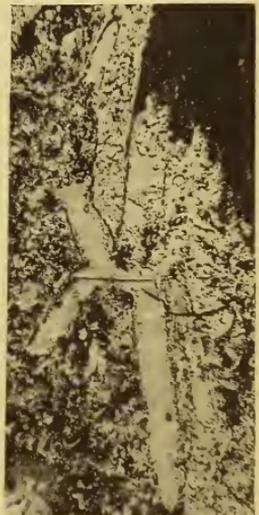
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PLATE XIV

Perimneste horrida. Fructification

- Fig. 1. Half of fructification from within showing oogonial cavity. **V. 26193**,
× 30.
- Fig. 2. Side view of fructification shown in Figs. 7 and 9. Holotype.
V. 26192, × 30.
- Figs. 3, 4. Portions of antheridial wall. **V. 26194**, × 50.
- Fig. 5. Apical view of small fruit showing oogonial neck apex. This specimen
has but few antheridia. **V. 26197**, × 30.
- Fig. 6. Inside of empty oogonium (illuminated from below) to show spiral
ridges in neck. (Retouched photograph.) **V. 26195**, × 30.
- Fig. 7. Base of specimen shown in figs. 2 and 9. **V. 26192**, × 30.
- Fig. 8. Apical view of fruit showing oogonium neck opening surrounded by
spine cells and parts of walls of several antheridia. **V. 26196**, × 30.
- Fig. 9. Apical view of fruit seen also in figs. 2 and 7. **V. 26192**, × 30.

The specimens shown in figs. 2, 3, 4, 7, 9 were photographed in a slightly moist state when the light shines on the ridges on the antheridial cells. These ridges are nearly invisible in the dry state.



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PLATE XV

Perimneste horrida. Fructification

All $\times 50$

Figs. 1-3. Side, apex and base of a rather small gyrogonite. **V. 26198.**

Figs. 4-6. Base, side, apex of a normal-sized gyrogonite. **V. 26199.**

Figs. 7-9. Side, apex and base of a gyrogonite. The spiral cells are slightly convex. **V. 26200.**

Figs. 10, 11. Half oogonium seen from the outside and the inside. **V. 26201.**

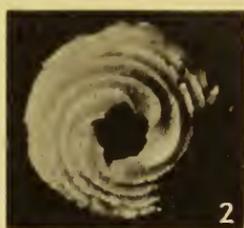


PLATE XVI

- Fig. 1. *Clavator bradleyi*; oogonium. **V. 26184**, $\times 50$.
Fig. 2. *Algacites clavatoris*. **V. 26226**, $\times 30$.
Figs. 3, 4, 7. *Clavator bradleyi*, gyrogonite. Holotype from the side, above and below. **V. 26183**, all $\times 100$.
Fig. 5. *Clavator bradleyi*; oogonium. **V. 26185**, $\times 50$.
Fig. 6. *Perimneste horrida*; longitudinal section of a node seen from within. **V. 26243**, $\times 30$.
Fig. 7. See fig. 3.
Fig. 8. *Perimneste horrida*; slightly oblique longitudinal section through internode, showing the central tube crossed by cortical tubes, some of which bear spines. **V. 26243**, $\times 15$.
Fig. 9. *Perimneste horrida*; transverse section of node. **V. 26243**, $\times 30$.
Fig. 10. *Charaxis durlstonense*; transverse section through holotype. **V. 26262**, $\times 25$.



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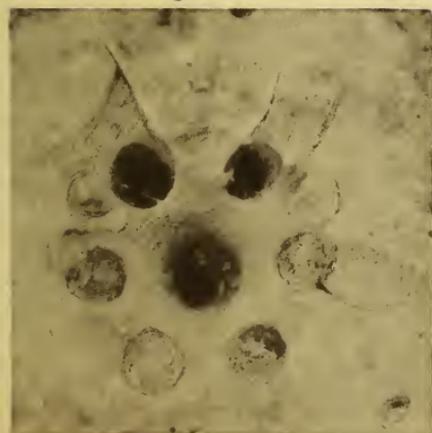
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PLATE XVII

Clavator reidi, *C. grovesi*, *Algacites clavatoris*

- Fig. 1. *C. reidi*; internal cast of gyrogonite (egg). **V. 26053**, $\times 50$.
Fig. 2. *C. reidi*; irregular gyrogonite. **V. 26074**, $\times 50$.
Fig. 3. *C. reidi*; gyrogonite cast (egg), with part of the gyrogonite wall.
V. 26076, $\times 50$.
Fig. 4. *C. reidi*; gyrogonite cast (showing cast of neck). **V. 26075**, $\times 50$.
Figs. 5, 6. *Algacites clavatoris*; holotype from outside and from inner
side. **V. 26225**, $\times 30$.
Fig. 7. *C. reidi*; small gyrogonite showing "winged" form of preservation.
V. 26058, $\times 50$.
Fig. 8. *C. grovesi*; fragment of cortex from a very large stem in end view.
V. 26149, $\times 10$.
Figs. 9, 10. *C. grovesi*; oogonia photographed dry in fig. 9, in balsam in
fig. 10. **V. 26152**, $\times 30$.
Fig. 11. *C. grovesi*; oogonia on leaf. **V. 26147**, $\times 30$.
Fig. 12. *C. grovesi*; node dissected open to show the large and the small
cortical cells. **V. 26148**, $\times 20$.
Fig. 13. *C. grovesi*; fragment of node from outer side showing two leaf bases.
V. 26140, $\times 15$.



PRESENTED

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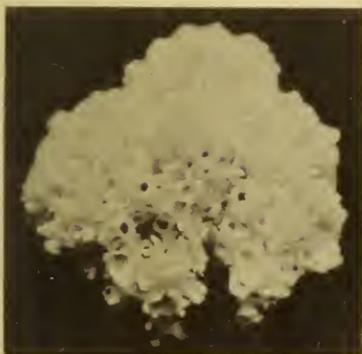
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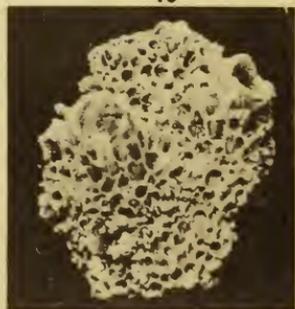
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