# PERMIAN TO PALAEOCENE CALCAREOUS ALGAE (DASYCLADACEAE) OF THE MIDDLE EAST

BY

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# PERMIAN TO PALAEOCENE CALCAREOUS ALGAE (DASYCLADACEAE) OF THE MIDDLE EAST

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CONTENTS

## SYNOPSIS

The fossil flora of calcareous chlorophyte algae, family Dasycladaceae, from the Permian to Palaeocene succession of the Middle East, is described and figured. This material has been selected principally from extensive rock collections made by geologists of the Iraq Petroleum Group in Iraq, Qatar, Oman and Hadhramaut. Advantage has also been taken of much fossil comparative material from the remainder of the Middle East, the European and African circum-Mediterranean countries and elsewhere, and of herbarium specimens of Recent dasyclads from the warm seas of the Atlantic, Indian and Pacific Oceans. Dasyclad morphology, methods of study of fossil dasyclads, and the limitations of such material, are outlined, and the principles of classification employed are examined. The results are applied to the Middle East flora ; about 80 species, referred to 39 genera and 12 tribes of the family, are described and figured or discussed. Included are a small minority of fossils whose dasyclad nature is uncertain or which have been incorrectly described as dasyclads, and a few Dasycladaceae *incerta sedis*. Stratigraphically the general agreement of the Middle East dasyclad floras with those of Europe and elsewhere is confirmed, though differing local ranges for certain Upper Jurassic–Lower Cretaceous species are detailed. Geographically the homogeneity of the Tethyan dasyclad floras from west to east is confirmed at most stratigraphic levels ; the Middle East forms a central sector of this latitudinal belt. In the Palaeocene, evidence of the mixing of eastern and western elements in the Middle East area is noted. Ecologically the evidence of all the Middle East fossil dasyclads is in accord with what is known of their living descendants.

Finally, from an evolutionary point of view, the most important points of detail are the interpretation of a Palaeocene genus as possibly having been similar to the atypical living *Dasycladus* in shedding gametes direct instead of by the usual dasyclad encystment, and in the conclusion that the terminal umbrella-type fertile discs seen in the living *Acetabularia* may be of different origin though of similar morphology in the fossil *Clypeina*. Also described is a species of *Cymopolia* showing the actual transition from cladospore to choristospore organization. The views of Julius Pia on the general course of dasyclad evolution are confirmed. No detailed explanation of this evolution can be offered, but the decline of dasyclads in abundance and importance throughout geological time, and their replacement by certain calcified Codiaceae in this respect, are now considered to be due to the differing relation of calcification to reproductive bodies in the two families, this itself probably due to their differing basic morphology.

## I. INTRODUCTION

PRESENT-DAY dasyclads are small single-cylindrical segmented or umbrella-shaped green algae, calcified in varying degree, and occurring mostly in warm very shallow waters in tropical and sub-tropical seas. The family is not a large one in number of component genera, and many of these illustrate markedly the phenomenon of discontinuous distribution. *Neomeris*, for example, is largely divided in occurrence between the East and West Indies. When the fossil record is examined, the relict nature of the Recent survivors is seen at once. Ancestral forms range from the lower Palaeozoic onwards, and show a variety of strange genera now extinct. At some geological levels they occur in profusion over large areas, and are used as index fossils. Although individual sizes are small, when compared with those of some other marine algae, yet proportionally giant forms occur amongst the fossil dasyclads, and the Lower Carboniferous *Koninckopora* has been estimated to have attained a length of 50 cm. This phenomenon of former large size is also not uncommon with relict groups.

In the largely arid land-area now known as the Middle East a thick succession of ancient sediments bears witness to the former occurrence there of the old Tethyan Sea. From Upper Palaeozoic to Mid-Tertiary times conditions of repeated shallow, warm-water, limy-bottomed shelf-areas afforded suitable environments for the growth of calcareous algae, and although, palaeontologically speaking, collections are rudimentary compared with those from Europe, yet examination of routine stratigraphical samplings has shown a succession of algal floras. In these the largest single group, taxonomically if not numerically, is the Dasycladaceae. Although they do not form whole reef-like rock-masses as do the Corallinaceae, nor occasion a monotonously distinctive rock-type as do the sand-like fragmentary remains of the Chaetangiaceae, yet the dasyclads impress themselves upon the mind of the student by the seemingly endless variety of structures, all based on a common plan. In their evolution, as interpreted by the Viennese worker Julius Pia over a working lifetime of thirty years, largely from European materials, there may be traced a progressive elaboration of their verticils or whorls of side-branches, the reproductive structures moving from within the stem-cell, first to within the side-branches, and then to specialised outgrowths adjacent to the subsidiary branches. But superimposed on this was a variability of calcification, as between one genus and another, and apparently showing no progressive trend throughout geological time. Some, heavily calcified, show hollow moulds of almost the whole set of branching structures in the plant and the fossil leaves no doubt, when well-preserved, of the state of evolution attained. Others calcify daintily and capriciously, each consistent for its genus, but anywhere between the stem-cell and near the tips of the finest outer branches. Both of these extremes are known ; and whilst distinctive enough both morphologically and stratigraphically, leave doubt as to what pattern of dasyclad alga formed them, and where it should be placed within the family.

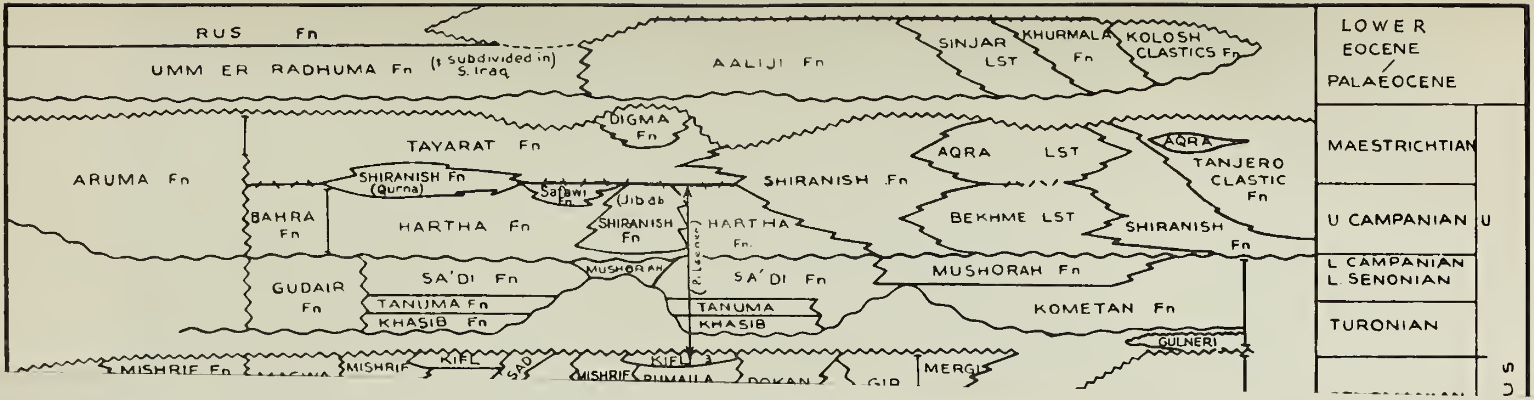
Middle Eastern Dasycladaceae were originally studied by me for their stratigraphic value, as explained below, and hence largely by comparison with those from elsewhere. In rock collections made for general survey purposes, rather than primarily for the amassing of good algal material, and showing frequently poor preservation, many occurrences have come to light which otherwise would have remained unknown, whilst on the other hand some of these specimens remain tantalisingly incomplete for palaeobotanical study. Nevertheless it may be said here that the Middle East mirrors and sometimes supplements the European record of dasyclad evolution from Permian to Eocene. Apart from very many points of detail, such as additional genera or species, extensions of generic range, and the filling in of geographical species-occurrences between East and West, there are several discoveries of especial interest, confirming earlier hypotheses or offering evidence for the probable ancestry of well-known genera.

The present work originated as part of a study of the calcareous algae generally of the Middle East, undertaken as part of my duties for Iraq Petroleum Company Ltd. Commissioned early in 1953 by Dr. F. R. S. Henson, then in charge of the Company's geological research activities, it was undertaken as a section of a project for elucidating the stratigraphical value for economic purposes of microfossil groups other than the foraminifera, and the results in this direction has been summarized elsewhere (Elliott, 1960). Many tens of thousands of thin-sections, prepared from well and surface samples, have been examined, as well as large quantities of rock and sand samples. This material came primarily from Iraq, Qatar, Oman and the Hadhramaut, where Iraq Petroleum and its associated companies operated, but much comparison material from the countries bordering the Mediterranean, and from the remainder of the Middle East, has been examined also, as well as Recent algae in the collections of the British Museum (Natural History) and elsewhere. Of those within the Company who have sent me dasyclad material for study, my thanks are offered to Messrs. H. V. Dunnington, E. Hart, D. M. Morton, K. al Naqib, A. J. Standring, W. Sugden, R. Wetzel, E. Williams-Mitchell, and Drs. R. C. van Bellen, Z. R. Beydoun, M. Chatton, and T. Harris. Of my many French friends and correspondents, I would single out for especial mention Professor J. Emberger, formerly of Algiers, who in exchanges has sent me many fine dasyclad rock-samples from the North African sector of the Tethys. At the British Museum (Natural History) members of the staffs of both Botanical and Palaeontological Departments have afforded me every facility, and I remember with gratitude the kindness and interest of the late W. N. Edwards, former Keeper of the latter department. Thanks are due to all those who have corresponded with me on dasyclad matters, from all over the world and too numerous to list here. Mr. R. C. Miller, when Senior Tech-


FIG. 1. Sketch-map of the Middle East, showing areas of provenance of principal collections examined.

nician at Iraq Petroleum's London headquarters, several times provided me with good transverse and longitudinal sections of dasyclads no larger than a few millimetres of fine pencil-lead, and Mr. J. Pope, of the Company's Photographic Department coped admirably with the problems of microphotography of largely monochromatic thin-sections : I thank them both. The distribution-maps and range-charts were prepared in Iraq Petroleum's Prodex Drawing-Office, and my thanks are due to Mr. E. G. Field and his staff for their services.

At Reading University, where these studies were continued and the present work offered as a thesis for the degree of Ph.D., I am especially grateful to my supervisors, Professor P. Allen, Dept. of Geology, and Professor T. Harris, Dept. of Botany, for


RUS Fn
UMM ER RADHUMA Fn (? subdivided in) S. Iraq
AALIJI Fn
SINJAR LST
KHURMALA Fn
KOLOSH CLASTICS Fn
LOWER EOCENE / PALAEOCENE
DIGMA Fn
TAYARAT Fn
ARUMA Fn
SHIRANISH Fn (Qurna)
Safawi Fn
(Jibab SHIRANISH Fn
SHIRANISH Fn
AQRA LST
AQRA
TANJERO CLASTIC Fn
MAESTRICHTIAN
BAHRA Fn
HARTHA Fn
HARTHA Fn.
BEKHME LST
SHIRANISH Fn
U CAMPANIAN
U
GUDAIR Fn
SA'DI Fn
MUSHORAH
SA'DI Fn
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L CAMPANIAN
L. SENONIAN
TANUMA Fn
KHASIB Fn
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KHASIB
KOMETAN Fn
TURONIAN
GULNERI
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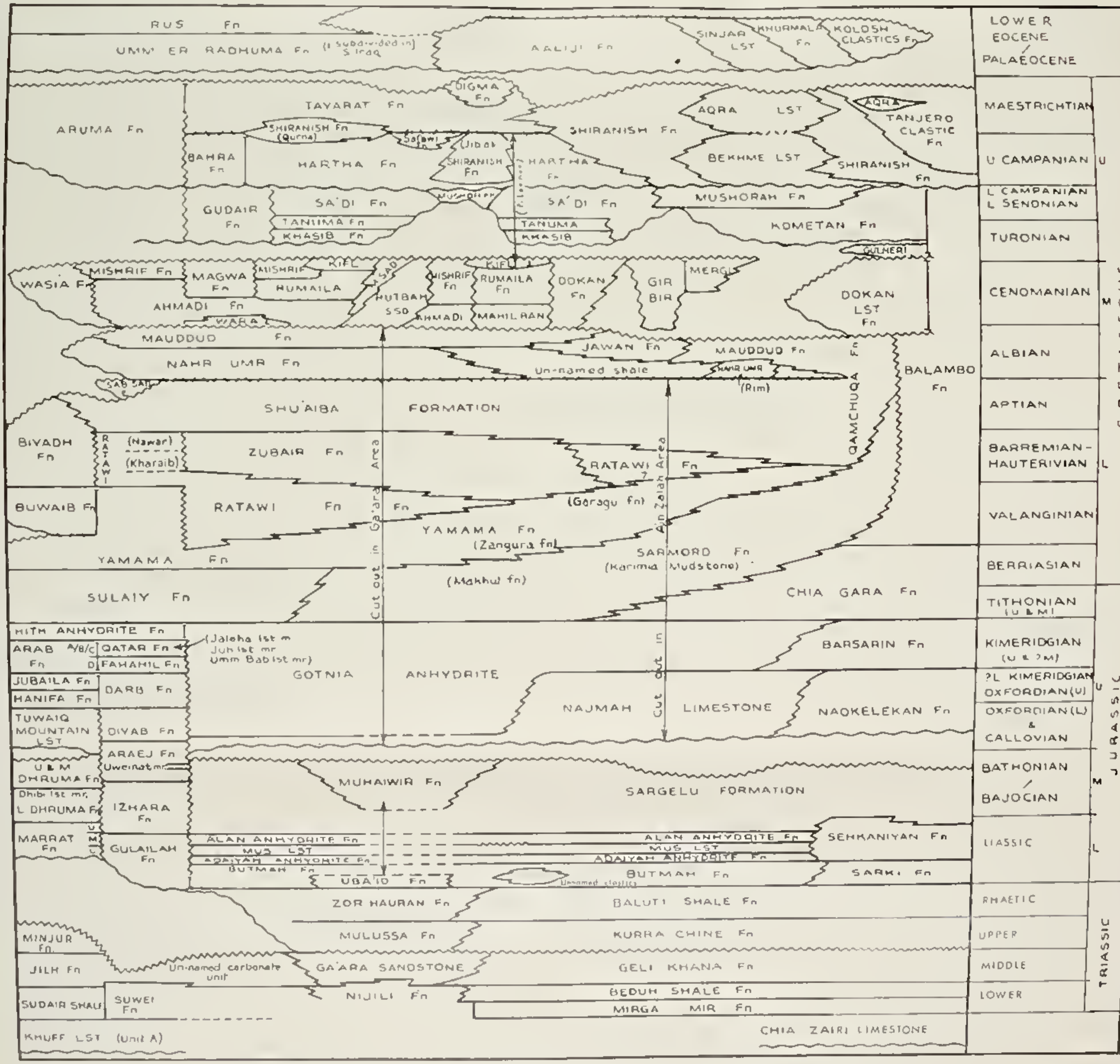


Fig. 1A. Diagrammatic stratigraphical table (Mesozoic and Palaeocene) for part of the Middle East: left to right is approximately south to north. The basal Khuff and Chia Zairi are Permian

their help and encouragement, and their very real interest in the project. Also my thanks go to my fellow-students with whom I have had many interesting discussions, and to the staff of the Sedimentological Laboratory for services of all kinds.

Finally, I would acknowledge my indebtedness to the Management of Iraq Petroleum Company, Ltd., who generously agreed to and made possible this liaison between academic and economic geology. Dr. C. Thiebaud, Exploration Manager, and Mr. H. V. Dunnington, Chief Geologist, who approved and submitted the project, I thank sincerely and gratefully for their efforts on my behalf. All the material in this paper has been presented to the British Museum (Natural History).

## II. STUDY AND CLASSIFICATION OF FOSSIL DASYCLAD ALGAE

Modern views on the botanical classification of dasyclad algae, their relationship to other green algae and the precise systematic status to be accorded them, may be found in Fritsch (1935) and more recently in Egerod (1952). Such work is necessarily based on the detailed study of structure, development and reproduction in the living plant. All the fossil forms described in this work are referred to a single family, the Dasycladaceae. Within this family the subclassification into tribes has been largely the work of palaeontologists, especially J. Pia, since the fossil forms are so numerous. Pia's classification appeared in the 1920s (Pia 1920 ; 1927) and was followed with slight modification and comment by later workers including Emberger (1944), Johnson (1954a ; 1961b) and Kamptner (1958).

Whilst it cannot be over-emphasized that as a general rule the fullest understanding of fossils is only to be obtained from an understanding of their living descendants, where skeletal structures can be studied functioning with the associated organic tissues missing in the fossil, yet much depends on how much is preserved in the latter, and how well it is preserved. In Recent members of the red algal family Chaetangiaceae, it was concluded by Svedelius (1953) that experimental spore-culture was necessary for conclusive pairing of the morphologically distinctive sexual and non-sexual generations. A morphological classification is thus inevitable with the fossil Chaetangiaceae, which in addition are notoriously fragmentary. For this general reason the account of dasyclad structure set out below stresses those structures and features of the plant which are of assistance in an understanding of the calcified remains found fossil.

Individual living dasyclads are usually small, vertically-growing algae : one observer described them as resembling " little green sausages " (Church 1895). Attached at the base by a rhizoid or holdfast, the core of the plant is a proportionally long cylindrical stem-cell, extending from rhizoid to apex. From this, whorls or verticils of lateral branches are given off at successive closely-set levels : these branches may themselves divide more than once, and they also bear the sporangial bodies. Much of the plant above the rhizoid is crusted with calcium carbonate.

The commonest fossils of dasyclads are thus small calcareous hollow cylinders with tubular pores and cavities in the thickness of the wall, the pattern of pores and cavities occurring again and again at successive levels in the wall-thickness along the cylinder. The main central tunnel represents the stem-cell, the branching tubular pores the lateral branches and the cavities the sporangia. There may be a terminal " pepper pot " structure at the apex. Determination of the fossil is made on the detail, number, arrangement and size of these structures. The essential preparations are a longitudinal cut or thin-section through the long central cylinder-axis, and a transverse section at right angles to this. More than one of the latter may be required when the lateral branches are strongly inclined relative to the horizontal plane. A whole, three-dimensional specimen, or at least a weathered surface to show surface-detail, is desirable for describing new material. A selection of such loose specimens for the preparation of orientated sections is ideal, but not always available. Once the essential structure is understood, the species may be recognized with practice in all manner of random oblique or tangential cuts. It should be noted that in exceptionally large dasyclads individual longitudinal and transverse sections, even if correctly orientated, may pass between verticil-detail and so not be diagnostic.

Exact measurements of the dimensions of thallus, stem-cell, branch- and sporangial-detail are desirable in describing dasyclad algae. It should, however, be remembered that whilst species do show average size and proportions of both thallus and component structures, they are plants and, like all plant life, variable. Dimensions are therefore a guide and not an exact character in dasyclad taxonomy.

A considerably greater variety of form has existed in dasyclads through geological time than survives at the present day. The notes which follow deal with the principal types which occur.

The stem-cell may be thin- or thick-cylindrical, club-shaped with either gradual increase of diameter or bulbous termination or greatly swollen, even to a near-spherical shape. Normally it is represented in fossils by a simple central mould, but certain cylinders whose walls are formed by hollow spherical calcareous bodies, adjacent, touching or fused, e.g. *Atractyliopsis*, are interpreted as remains of dasyclads in which the sporangia were within the stem-cell itself and calcified as a sub-dermal stem-cell peripheral zone to give the fossil seen. Occasionally there is some doubt as to whether a calcareous filling between these bodies occurred during the life-time of the plant, in the lower, older part, or is a post-mortem mineralisation feature (e.g. *Aciculella*).

Exceptional forms in which the stem-cell is creeping in habit, or modified into a thin support for a large terminal disc or discs, are dealt with separately below.

The lateral branches have been described above as occurring at successive horizontal levels in whorls or verticils. Pia (1920) recognized a tripartite classification of their relationship to the stem-cell. In the more primitive aspondyl type the pores marking the origin of branches occur irregularly, more or less over the whole stem-cell surface. In the euspondyl type single branches are set in approximately horizontal whorls, whilst in the metaspondyl arrangement tufts of branches originate from the pores of the verticils.

The lateral branches themselves may be single structures, or more commonly branched, so giving primaries, secondaries, tertiaries etc. The number of sub-branches at each point of branching or division is approximately constant within the species. These points of branching are constricted and there also occur genera in which constriction of the individual branches and branchlets occurs without division at these constrictions e.g. *Palaeodasycladus*.

The reproductive structures, usually termed sporangial cavities in the fossil literature, are often conspicuous features of the branch-detail, and are of great value in classification. They may be completely encased in the calcareous coating where this is well-developed, and indeed, in most similar living forms, gametes are only set free from resting cysts on the eventual post-mortem break-up of the calcareous structures. General classification of the condition seen in fossils is again tripartite and due to Pia. The endospore type is presumed to have had reproductive elements within the stem-cell. This is characteristic of the Palaeozoic and only such forms as the doubtful *Atractyliopsis* already mentioned and a species of *Diplopora* show any direct structural evidence of this condition. In the cladospore type, dominant throughout most of the Mesozoic, the reproductive cavities are considered to have been within swollen lateral branches. Finally, in the choristospore type the reproductive elements are located in special outgrowths, usually well-calcified, from the lateral branches. Commonly they are attached at the division of primaries into secondaries (e.g. *Cymopolia*) but various other positions characterise other genera. This type ranges from Cretaceous to Recent. Rezak (1959a) has drawn attention to the parallel between Pia's view of the migration of reproductive elements during phylogeny from stem-cell to lateral sporangia, and Egerod's summary (1952) of the migration during ontogeny of the dividing nucleus from the holdfast of the vegetative thallus into the gametangial rays of the reproductive thallus. Recent studies of the genetic mechanisms involved in this latter phenomenon in the living *Acetabularia* (Brachet 1965), do not invalidate this comparison. Summary of the chromosome mechanisms in the Dasycladaceae (Puiseux-Dao 1966) emphasizes their distinctiveness amongst green algae.

There exists a minority of dasyclads which depart from the usual pattern of a vertical calcareous cylinder described above.

*Vermiporella* and the somewhat doubtful *Pseudovermiporella* from the Palaeozoic are recumbent–irregular in form, indicating a presumed creeping thallus in life. The former branches, and the latter shows a peculiar double calcareous structure in part of the thallus. This is dealt with fully in the systematic descriptions below.

In the Palaeozoic *Mizzia* and certain later genera the stem-cell occurred as consecutive bead-like structures, almost always dissociated as found fossil. Certain Tertiary dasyclads (e.g. *Larvaria*) were of normal tubular pattern but the verticils came apart after death and usually occur fossil as separate ring-like structures.

Another and commoner growth form is where the plant appears with a thin, lightly-calcified stem supporting a specialized flower-like disc or series of discs, usually found separate as fossils, in which the radial segments or " petals " are calcified structures containing the reproductive elements in life (e.g. *Clypeina*). In *Acicularia* these segments themselves came apart after death and occur as separate microfossils, of varying form, known as spicules. Not all such spicules, however, have this origin : some, such as the Tertiary *Carpenterella*, are believed to be dissociated structures from the interiors of dasyclads of modified cylindrical form.

*Calcification*

During individual development recent dasyclads pass through several growth stages : calcification begins fairly late, often being initiated around the early reproductive structures, and thus it is the adult plant of which a fossil record is possible. Occasionally exceptional fossils, such as the Cretaceous *Trinocladus*, show differences in detail between the lower, earlier formed whorls and the upper, later ones, both being calcified. However, a combination of capriciousness in degree and occurrence of calcification for the members of the family viewed together, and constancy for the calcification of the individual species, is the rule in the Dasycladaceae.

Consequently, the reconstructions possible of the plants which originated the calcareous fossils vary enormously. With heavy calcification a record is preserved of the stem, branch and sporangial details, and also the outline of the whole plant, only the finest branchlets projecting further during life. With those which calcify, but come apart after death, a fair degree of reconstruction is possible, and chance preservation of rare complete specimens illuminates the common segments or debris. Where calcification is confined to a narrow zone, either close to the stem-cell as in *Pagodaporella*, or between the tips of the branchlets only, as with *Tersella*, the details of the plant will probably always be doubtful. Finally, such odd remains as *Aciculella*, already mentioned, or tiny dissociated elements like *Terquemella*, render necessary the description of form-genera whose components may be of diverse origin and whose position within the family is unknown.

*List of Middle Eastern Fossil Dasycladaceae*

In the list below, those genera of dasycladaceae recognized in the course of the present work are set out under the appropriate " tribes ", or subdivisions of the family. These tribes, proposed by Pia (1920 ; 1927), have been followed and modified by later workers, notably in the comprehensive schemes of Emberger (1944) and Kamptner (1958) while other workers, elements of whose classifications have been especially considered here, are Morellet (1922), Johnson (1954a ; 1961b) and Rezak (1959a).

Classification of this kind is based on structure as preserved in the fossils, and on phylogeny, which may be regarded in this connection as interpreted structure. The student of phylogeny assigns values to elements of structure in accordance with his or her experience of the group studied. Close similarities and near-identity, particularly of external form and gross structure, are often discounted in favour of smaller and less obvious features. These latter are valued on account of their persistence throughout time or their alleged significance as early or late manifestations of distinctive structures in related members of the group. In general, this interpreted structure determines the taxonomic category allotted. However, the success of a group, evidenced by numerical abundance of individuals and extensive minor variation from a common structure, as opposed to rare, but profound deviation which were evidently biologically unsuccessful or unfortunate, often leads to a taxonomic up-grading of the group being classified.

Such classification, with its very different allocation of importance to the same or similar structures in related groups, reflects attempts towards a real understanding of evolution, and dissatisfaction with rigid morphological classification, however logically contrived. The subjective elements in such reasoning, normally subordinate, become much more apparent when subdivision is attempted of a relatively homogeneous biological group. In the " small change " of evolution personal choice in detailed classification becomes obvious. Thus *Clypeina* has been referred both to the Diploporeae (Pia 1927, Emberger 1944) and to the Acetabulareae (Morellet 1913 ; 1922 ; 1939 ; Rezak 1957). Since clypeiniform remains are now recorded from the Permian (p. 36) it seems possible that the different morphological trends seen in dasyclads may have evolved more than once, and the classification of such similar forms is difficult. In the present work *Clypeina* is placed in the new tribe Clypeineae : the reasons for this and the relationship of the genus to *Actinoporella*, here left in the Diploporea, are discussed below (p. 99).

In the Dasycladaceae considered here, the increasing complexity of branch-structure, and transference of position of reproductive structures already mentioned, are noticeable evolutionary trends. It is inevitable, however, that in classifying fossil genera represented by very varied results of superimposition of localized calcification on different stages of these trends, that frequently some uncertainty should be felt as to the appropriate tribe. The Middle Eastern genera and species described below have been so referred in accordance with literature quoted. For many genera, simple or complex, e.g. *Diplopora* or *Neomeris*, there is no uncertainty. For others, e.g. *Atractyliopsis* or *Griphoporella*, the nature of the fossil ensures its relegation as *incerta sedis*. Between these extremes are several doubtful cases, assigned here to a tribe for consistency, in accordance with published accounts ; e.g. *Cylindroporella* to Diploporeae (Kamptner 1959) and *Terquemella* to Dactyloporeae (Morellet 1922 ; Emberger 1944). *Pagodaporella* is assigned to Dasycladeae, in view of its analogy with *Dasycladus*. *Mizzia* is placed under Diploporeae following Rezak (1959b), and *Acroporella* also, in view of its author's opinion on its relation to *Salpingoporella* (Praturlon 1964). The writer is in agreement with the need for subdivision of the Diploporeae expressed by Rezak (1959a : 125), but has not attempted this, still less general reclassification of dasyclad tribes, in the present study of Middle East representatives of the family. The recent discovery of a *Dissocladella* in the older Mesozoic (Ott 1965), and the phylogenetic considerations given by this writer, show how random and incomplete is the evidence for major re-classification.

The table given, therefore, represents current conventional taxonomic assignment of the genera listed, which are dealt with alphabetically in the main descriptive part of the work, where the synonymies are selected to cover primary descriptions, revisions and Middle East occurrences only.

Family **DASYCLADACEAE** Kützing 1843
orth. mut. Hauck 1884

Tribe **DASYPORELLEAE** Pia 1920
*Anthracoporella*

Tribe **CYCLOCRINEAE** Pia 1920
*Epimastopora*
*Pseudoepimastopora*

Tribe **DIPLOPOREAE** Pia 1920
*Acroporella*
*Actinoporella*
*Cylindroporella*
*Diplopora*
*Gyroporella*
*Macroporella*
*Mizzia*
*Munieria*
*Permoperplexella*
*Pianella*
*Salpingoporella*

Tribe **TEUTLOPORELLEAE** Pia 1920
*Teutloporella*

Tribe **TRIPLOPORELLEAE** Pia 1927
*Triploporella*
*Broeckella*

Tribe **THYRSOPORELLEAE** Pia 1927
*Belzungia*
*Dissocladella*
*Thyrsoporella*
*Trinocladus*

Tribe **CONIPOREAE** Pia 1920
*Palaeodasycladus*

Tribe **CLYPEINEAE** (trib. nov. ; see p. 99)
*Clypeina*

Tribe **DACTYLOPOREAE** Pia 1927
*Terquemella*

Tribe **DASYCLADEAE** Pia 1920
*Pagodaporella*

Tribe **NEOMEREAE** Pia 1920
*Cymopolia*
*Indopolia*
*Karreria*
*Larvaria*
*Neomeris*

Tribe **ACETABULARIEAE** Pia 1920
*Acicularia*

**DASYCLADACEAE** *incerta sedis*
*Atractylopsis*
*Furcoporella*
*Griphoporella*

Problematica, possibly dasycladaceae
*Pseudovermiporella* (?**DASYPORELLEAE**)
*Hensonella* (?**DIPLOPOREAE**, as *Salpingoporella dinarica*)

Algae, not dasycladaceae
*Thaumatoporella*
" *Epimastopora minima* Elliott " (= *Tauridium* sp.)
" *Griphoporella arabica* Pfender "
(= *Ovulites maillolensis* Massieux).

## III. SYSTEMATIC DESCRIPTIONS

In the descriptions which follow, the geological ages of all material mentioned are given in terms of local rock-units and standard international stages as far as possible. Every effort has been made to take account of all relevant literature up to the end of 1966. A bibliography of the geology of the Middle East is far outside the scope of the present work, but key publications may be quoted for Iraq, Qatar, Oman and the Hadhramaut from which the vast majority of the specimens were collected. For Iraq, the very detailed Lexique Stratigraphique International, listed in the present bibliography both under Bellen, R. C. van (1959), and under Dunnington, Wetzel & Morton (1959), is invaluable. The Hadhramaut material is similarly covered by Beydoun (1964). A suitable account for the much smaller and simpler Qatar is that by Qatar Petroleum Company, Ltd. (1960). Oman is covered by the general account of Morton (1959), and the detailed local papers of Hudson and collaborators are mentioned where relevant in the present study.

The regional location of the numerous small localities quoted are best gleaned from these works ; in the present text they are given with the appropriate province or administrative division. The geographical co-ordinates of these localities are listed on p. 109.

### Genus *ACICULARIA* (d'Archiac) Munier-Chalmas

Diagnosis. Calcareous spicules, typically elongate-cuneiform, circular or flattened in cross-section, set peripherally with small spherical cavities ; in life part of the fertile whorl of the plant.

*Acicularia* was proposed by d'Archiac (1843 : 386) for certain fossil spicules occurring in the Paris Basin Eocene. Referred to different animal groups by various authors, their algal origin was recognized by Munier-Chalmas (1877), and the subsequent discovery of a living species confirmed this diagnosis. Munier-Chalmas published little but the bare statements of this and other original discoveries, and the details of his species, and the subgenus *Briardina*, are to be found in later authors, notably in the classic works of L. and J. Morellet (1913, 1922), and in the paper by

Costantin (1920) which gives some of Munier-Chalmas' original figures. The recent *Acicularia* has been merged as a section *Acicularioides* of *Acetabularia* (Egerod 1952), but in the fossil state at least the remains are distinctive and the name a useful one.

Acicularian spicules are typically small elongate needle-like calcareous bodies, derived from the specialized fertile disc of the plant and containing tiny spherical sporangial cavities. (Somewhat similar discoidal or spherical bodies, *Terquemella* of Munier-Chalmas were recognized by the Morellets as sporangial structures from the walls of fossil Bornetelleae (= Dactyloporeae), which are of normal tubular dasyclad pattern and not umbrella-shaped like *Acicularia* or *Acetabularia*). Both morphological types of spicule are known from the Jurassic onwards. Whilst the attribution of the Tertiary species is as given above, the origin of the Mesozoic forms is much more doubtful. Pia (1936a, b) has described Cretaceous spicules which he referred to *Acicularia* but considered might indicate a connection between *Acicularia* and *Terquemella*, obviously using the latter in a strictly morphological sense.

In the Middle East true *Terquemella* spp. occur in the Palaeocene-Lower Eocene ; these species are dealt with below under *Terquemella*. The remaining *Acicularia* spp. are now described here.

### ***Acicularia antiqua*** Pia
(Pl. 1, figs. 1, 3)

1936a *Acicularis antiqua* Pia : pl. 3, figs. 1–14.
1955b *A*. cf. *antiqua* Pia ; Elliott : 126.

Description. Rounded, cuneiform, calcareous bodies, circular or ovoid in cross-section, containing numerous submarginal spherical hollows (sporangial cavities). Length up to 0·780 mm., with maximum diameter of 0·364 mm. The sporangial cavities are consistently about 0·040 mm. in diameter, and in thin-section appear set apart by their own diameter or a little more along the margins of the spicules.

Horizon. Cretaceous of North Africa and the Middle East.

Material. Seen in thin-section from the subsurface Garagu formation (Valanginian) of Kirkuk well No. K 116 (Kirkuk Liwa, Iraq), from the Sarmord and Qamchuqa formations (Neocomian and Aptian-Albian) of the Surdash district (Sulemania Liwa, Iraq), from the Upper Musandam formation (Lower Cretaceous, Barremian-Aptian) of the Hagab area, Oman, Arabia, and from the Maestrichtian of Diza, (Erbil Liwa, Iraq).

Remarks. Random sections of acicularian spicules are not uncommon at many levels in the Middle East Cretaceous. With few exceptions, they may be divided into two classes, on the size of the sporangial cavities. The smaller, always set in a circular section indicating a spherical spicule, is described elsewhere under *Terquemella* s.l. The larger, described above, occurs in a variety of random cuts suggesting a rounded–cuneiform spicule. For this form Pia's *Acicularia antiqua* (Pia, 1936a) appears to be available. The type material, from the Cenomanian of Libya, Northern Africa, is described as probably wedge-shaped or pointed, length probably not exceeding twice the thickness, greatest diameter 0·330 mm., diameter of sporecavities 0·040–0·055 mm., and not curved or hooked as in *A. dyumatsenae* Pia from the Indian Danian (Pia 1936b). The Middle Eastern material, on the basis of the few available dimensions and characters, seems to vary little beyond this, and the name is adopted. A few examples from the subsurface Garagu of Kirkuk show exceptional sporangial diameters of 0·065 mm., but they occur in random transverse cuts only. *A. endoi* Praturlon (1964), from the Italian lower Cretaceous, is described as a spicule, slightly larger with larger sporangial cavities, which however are more regularly and peripherally arranged to give a starred appearance in thin-section.

*A. antiqua* is more common in Lower than Upper Cretaceous in my experience, but ranges from bottom to top of the system. If the spicules are the remains of more than one botanical species in this long period, there is no apparent evidence of this in the microfossils as preserved. They should not be confused with the micro-problematicum *Coptocampylodon* (Elliott 1963a) which resembles an acicularian in transverse cut, but is readily distinguishable by the longitudinal sections normally associated.

### ?***Acicularia elongata*** Carozzi

1947 *Acicularia elongata* : Carozzi : 13, figs. 1–8.

Remarks. Carozzi's species, from the Swiss Upper Jurassic, is a distinctively elongate spicule of rather ragged outline. In the Upper Jurassic of Jabal Kaur, Oman, Arabia, remains occur which are possibly of the Swiss species, but are not well enough preserved to permit of a positive reference. They are associated with *Pianella gigantea* Carozzi and the microcoprolite *Favreina salevensis* (Paréjas), also described from the Swiss Upper Jurassic.

### ***Acicularia (Briardina)*** sp.
(Pl. 1, fig. 6)

1913 *Acicularia* section *Briardina* Munier-Chalmas ; L. & J. Morellet : 33.

Remarks. In the Palaeocene Limestones of the Batinah Coast, Oman, one or two examples of a small acicularian apparently referable to this section or subgenus have been noted. The best shows in longitudinal thin-section as a needle or narrow wedge-shaped spicule, 1 mm. long, 0·22 mm. wide at the outer end and slightly hooked at the inner (pointed) end : the sporangia are 0·078 mm. in diameter, in a double row, narrowing to a single on the upper face. The section cuts at the thinner end through the sporangia of the lower face, the elongate spicules of species of *Briardina* being thin, with flat or slightly concave upper and lower surfaces.

This may be the earliest representative of the subgenus, the Paris Basin species being Lutetian or later in age (Morellet 1913, 1922), and the acicularians from the Montian (Morellet 1940) not being referred to the subgenus.

### Genus *ACROPORELLA* Praturlon 1964

Diagnosis (after Praturlon). " Not segmented **DASYCLADACEAE** having simple, long, not ramified, akrophorous branches. Reproduction probably endospore ". " The branches are namely by no means ' gegen aussen deutlich erweitert ', as in *Salpingoporella, Pianella, Macroporella,* as well as do not incline to shut outwards as in *Oligoporella.* They are namely intermediate between the two types ". (Praturlon 1964 : 177).

### ***Acroporella assurbanipali*** sp. nov.
(Pl. 1, fig. 5)

1960 *Macroporella* sp. ; Elliott : 222.

Description. Cylindrical tubular calcified dasyclad, external diameter 1·36 mm., internal diameter 0·55 mm. (40% of external) ; successive near-horizontal verticils, probably 3 or 4 per mm. of tube-length, of perhaps twelve radial branches each. The single branches communicate with the stem-cell cavity by a pore of about 0·052 mm. diameter : they then swell out to a fig- or flask-shaped cavity of 0·182 mm. maximum diameter, narrow to a slightly curved tube of 0·078 mm. diameter, and at the outer surface flare out to a shallow terminal diameter of 0·156 mm.

Horizon. Subsurface Lower Cretaceous of Iraq.

Holotype. The specimen figured in pl. 1, fig. 5 from the subsurface Garagu Formation (Valanginian-Hauterivian) of Kirkuk Well no. 116, Iraq. V. 52032.

Remarks. *Acroporella* Praturlon (type-species *A. radoicici* Praturlon 1964) is a primitive form from the Lower Cretaceous of Italy, apparently of somewhat intermediate branch-characters, though well figured and described by him. The Kirkuk specimen exactly fits his general diagnosis for branch-structure, rather better than the type-species, in fact, but the thallus shows more than double the dimensions of the Italian species, and the shape of the peculiar branches is unique. It is therefore made the type of a new species. The exact orientation of the curved branches relative to the cylinder-axis is difficult to make out from the long tangential section : the swollen portions may have housed the sporangia in life.

The specific name commemorates a king of ancient Assyria, within whose former boundaries Kirkuk now lies.

## Genus ***ACTINOPORELLA*** Gümbel *in* Alth

Diagnosis. Verticils of several straight radial calcareous tubes, approximately in the same horizontal plane, separate for most of their length but meeting centrally in a calcareous ring, each hollow tube communicating by a single pore with the central cavity.

*Actinoporella* was created by Gümbel (Alth 1882), with type species *Gyroporella podolica* Alth (1878), which came from the Portlandian of Podolia (Cushman & Glazewski (1949) ; then in Austria, but subsequently in Poland and now included in the U.S.S.R.). This alga, represented by little impressions and hollow moulds of the verticils, was studied and reconstructed by Pia (1920 ; 1927) loose solid specimens from the same area have been seen by me. Each verticil shows numerous radial tubes, slightly curved but approximately horizontal, about 20 in number, which are interpreted as the calcareous coatings or casings of simple primary side-branches. These are free for much of their length, but touch and become fused centrally, to form a circular ring through which the stem-cell passed. Pores on the inner surface of the ring mark the old communications of side-branches with stem-cell. A succession of such verticils built up in life the peculiar plant shown in Pia's reconstruction (fig. 2).

Subsequently Carozzi (1948) figured numerous thin-sections determined as *Actinoporella podolica*, from the Swiss Portlandian-Purbeckian. It is with these sections that the Middle Eastern material has been correlated, no solid individuals having been extracted. The commonest thin-section appearance is given by tangential cuts through the finger-like projections or side-branches, which show as chains of separate or touching circles. Less commonly vertical sections along the main axis show the central stem-cell and paired opposite side-branches, and rarely, transverse cuts show a whole disc or verticil.

Although locally common in the European Portlandian, and recorded from as low as Sequanian (Francois, Lehmann & Maync, 1958), this alga is characteristic in the Middle East of the Lower Cretaceous and has never been seen there in the Jurassic. In Italy (Sartoni & Crescenti 1962) it is recorded from both Tithonian and Valanginian-Hauterivian. It appears to be slightly more common in the Middle East at a Valanginian-Hauterivian level than in the Barremian-Aptian above (Elliott 1955b), but forms a noticeable constituent of the Middle Eastern " debris-facies " (Elliott 1958a), an off-shore accumulation of fine calcareous algal fragments in fire-grained sediments.

The relationship of *Actinoporella* to *Clypeina*, and their positions within the family Dasycladaceae, are discussed elsewhere (p. 99).

## ***Actinoporella podolica*** Alth
(Pl. 1, figs. 2, 4, 7)

1878 *Gyroporella podolica* : Alth : 83, pl. 6, f. 1–8.
1882 *Actinoporella podolica* Alth : 322.
1920 *A. podolica* Alth ; Pia : 95, fig. 19, pl. 7, f. 1–7.
1948 *A. podolica* Alth ; Carozzi : 353, f. 49.
1955b *A. podolica* Alth ; Elliott : 126, pl. 1, f. 1.
1958a *A. podolica* Alth ; Elliott : 255, pl. 45, f. 1. pl. 47, f. 5.
1960 *A. podolica* Alth ; Elliott : 222, 223.

DESCRIPTION. Verticils of from 1·0 to 1·6 mm. or more total diameter, each consisting of a central calcareous ring with inner diameter of about 21% of the total diameter ; from this ring project 13 to 20 largely separate tubular elongate thin-walled cylindrical rays, outwardly directed and all very gently curved upwards on the same side of the horizontal plane. Near and at the ring the walls of the rays are fused, to give a thickened calcareous structure, and the hollow interiors of the rays communicate each by a single pore with the main central cavity.

HORIZON. Upper Jurassic and bottom Cretaceous of Europe : Lower Cretaceous of the Middle East.

MATERIAL. Numerous random thin-sections. In Iraq seen in the Sarmord Formation (Valanginian-Hauterivian) of Jebel Gara, Mosul Liwa, and Surdash, Sulemania Liwa ; from the Garagu Formation (Valanginian) of Kirkuk well no. 116 (subsurface), of Banik (Mosul Liwa) and of Fallujah Well (subsurface : Dulaim Liwa), from the Qamchuqa Formation (Barremian-Aptian) of Kirkuk well no. 116 (subsurface) and from Zibar-Isumeran (Mosul Liwa). In the Hadhramaut (Southern Arabia), seen in Barremian-Aptian *Orbitolina*-limestone from Mintaq, Wady Hajar, and from the Aptian of Ghabar.

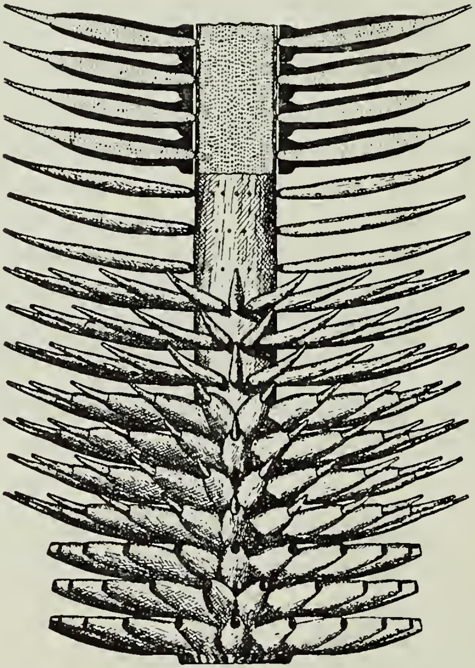

FIG. 2. Reconstruction (after Pia 1920) of *Actinoporella podolica* Alth. From top to bottom (1) vertical section (2) decalcified portion with anterior branches removed (3) decalcified portion with all branches in position (4) branches with calcareous coating in position (5) calcareous skeleton alone. ×40 approx.

REMARKS. This species, mostly Upper Jurassic in Europe, appears to be Lower Cretaceous in its Middle East occurrences. Pia, dealing with the Podolian type material, relegated *A. gümbeli* to the synonymy of *A. podolica*, regarding the differences as not significant. Carozzi referred his Swiss material to *A. podolica* likewise. This practice is now followed with the Middle East material. This latter suggests smaller verticils and possibly a lower average number of rays than in the

European fossils, but good series of solid verticils free from matrix would be needed to evaluate this decisively. Nothing like the distinctive *A. sulcata* Alth (Pia 1920 : 100, fig. 20) has been seen.

*Actinoporella podolica* is highly distinctive in random thin-section. Its thin-walled but coherent fragments cannot easily be confused with any species of *Clypeina*, whose verticils are more massive, except perhaps the Valanginian *C. marteli* Emberger, which has only about half the number of rays or branches per verticil. *Munieria*, apparently more solid, is much more fragmentary, and shows as smaller, more problematic debris : possibly its calcium carbonate was initially more fragile.

## Genus *ANTHRACOPORELLA* Pia

Diagnosis. Calcified unsegmented branched cylindrical dasyclad with close-set, aspondyl dichotomous side-branches.

*Anthracoporella*, described by Pia (1920), is a primitive dasyclad from the late Palaeozoic. The tubular thallus is exceptional in branching, often at a wide angle. The stem-cell is proportionally large in diameter to the surrounding wall-thickness in which the aspondyl dichotomous side-branches are very numerous, fine and closely set. The calcification may not have reached quite to the stem-cell, and the lateral branches probably projected considerably beyond the calcified zone.

In a later paper Pia (1937) listed occurrences of the type-species *A. spectabilis*, initially described from the Upper Carboniferous of the Austrian Southern Alps. Species of the genus are characteristic of the Upper Carboniferous and Permian of Alpine Europe and Asia, and occur also in the southwestern United States and in Madagascar.

In the revision of the Middle Eastern material for this study two species are recognized, the distinction being based mostly on size. *A. spectabilis* Pia is much the larger, with outer tube-diameters commonly up to 5 mm. or more (5·8 mm. quoted by Pia as a maximum ; Bebout and Coogan (1964) record up to 8·9 mm.). Smaller individuals or branches of this species, associated with the larger, may measure as little in diameter as 1·5 mm., but are exceptional. The second species, now described as new, is represented by solitary occurrences of tubes of diameter of less than 1 mm. This was at first considered a dwarfed variety and later in time than the large type-species, but their ranges overlap, and they seem distinct.

### *Anthracoporella spectabilis* Pia
(Pl. 2, figs. 1, 2)

1920 *Anthracoporella spectabilis* Pia : 15, fig. 3, pl. 1, figs. 7–11.
1937 *A. spectabilis* Pia ; Pia : 795, 809, 822.
1960 *A. spectabilis* Pia ; Elliott : 219.

Description. Thallus of branched tubular dasyclad pattern, up to 5–6 mm. or more in external diameter, stem-cell cavity large, d/D ratio 50–80%, the larger examples being progressively thinner-walled. Side-branches simple, about 0·040 mm. diameter, sometimes dichotomous, aspondyl in arrangement, crowded and very numerous, more or less at right angles to main axis and giving a characteristic dot and dash appearance in slightly oblique transverse cuts. About 20 of these radial pores seen in 1 mm. of wall in a large example, and a small example of 1 mm. diameter showed a total of about 60 (both in transverse section).

Horizon. Both Middle East occurrences of this species are in derived material, at Jebel Busyah and Jebel Hagab, Oman, Arabia. The former occurrence is in cobbles of derived limestone in a presumed Triassic conglomerate : associated with *Anthracoporella* are the algae *Tubiphytes* and *Pseudoepimastopora*, and the limestone of a similar cobble was dated by Dr. M. Chatton as Middle Permian on the evidence of *Parafusulina shiptoni* and other foraminifera, the fusulinid being compared with that from post-Artinskian Permian somewhat younger than the zone of *P. kattaensis* of the Salt Range (M. Permian of India). The Jebel Hagab occurrence is in derived material associated with the Mesozoic Musandam Limestone. *Tubiphytes* occurs with *A. spectabilis*, somewhat recrystallized, and this appears to be derived Permian material too.

Material. See under Horizon.

Remarks. Pia's Austrian type material was from the Upper Carboniferous-Lower Permian level ; Maslov (1956) records it from the Upper Carboniferous of the Urals, U.S.S.R. Bebout & Coogan (1964) record a large and proportionally very thin-walled form of the species from the subsurface early Permian (Wolfcampian) of Texas. Other records are discussed below under *A. mercurii* sp. nov.

### ***Anthracoporella mercurii*** sp. nov.
(Pl. 1, fig. 8)

Description. Similar in form, growth and branches to *A. spectabilis*, but much smaller, diameter 0·5–0·9 mm. ; (relatively thicker-walled, d/D 40–60% ; pores radial (branches of 0·026 mm. diameter) ; a transverse section of one individual showed about 40 such branches).

Horizon. Permian of the Middle East and Tunisia (see below).

Holotype. The specimen figured in Pl. 1, fig. 8 from the Permian, Bih Dolomite, of Wady Bih, Jebel Qamar, Oman. V. 52035. This limestone is dated in fusulinid evidence by Dr. Chatton as belonging to the " Neoschwagerina–Verbeekina zone of low Guadalupian age (Wordian) ".

Other Material. Random sections from the lower Permian of Ora and Harur, Mosul Liwa, N. Iraq (Zinnar Limestone (Artinskian) of Hudson, 1958) ; from the Permian of Jebel Qamar, Jebel Hagab, and Tawi Silaim, all Oman ; in derived Permian material in the Upper Cretaceous Hawasina formation of Juweiza Well, Trucial Oman ; and in derived Permian material associated with the Mesozoic Musandam Limestone at Jebel Hagab, Oman.

Remarks. *A. mercurii*, while much smaller than *A. spectabilis* is distinctly larger than the tiny (Upper Carboniferous) *A. kasachiensis* (Maslov 1956), and differs noticeably in proportions of the component structures. It differs in its occasionally divided branch-structure from the Japanese Lower Carboniferous *Anatolipora* (Konishi 1956), and similarly from the English Lower Carboniferous *Nanopora anglica* (Wood 1964) ; Wood refers *Anthracoporella fragilissima* to this latter genus also. Johnson's U.S.A. records of *Anthracoporella* from the Permian of New Mexico and Upper Permian of Texas (Johnson 1942 ; 1951) may well be of *A. mercurii*. Outside the Middle East, it occurs in the Upper Permian of Tebaga Well, S. Tunisia.

The species appears to be more wide-spread in scattered occurrences than the large localized *A. spectabilis*, and is dedicated to the god Mercury who presided over travel.

### *Anthracoporella magnipora* Endo

1951 *Anthracoporella magnipora* Endo : 124, pl. 10, figs. 4, 5.
1963 *A. magnipora* Endo ; Flügel : 85, pl. 1, fig. 1.

This species, originally described from the Japanese Permian, is known to me in the Middle East only from Flügel's record quoted above : Permian of the Ala Dag, Taurus Mountains, Southern Turkey.

### Genus *ATRACTYLIOPSIS* Pia 1937

Diagnosis. Fusiform, cylindrical or ovoid tubes formed of adjacent touching or fused hollow calcified spheres.

*Atractyliopsis* was proposed by Pia (1937) for certain Upper Palaeozoic algal microfossils which consist essentially of groups of adjacent, touching or fused hollow calcified spheres, occurring in the form of fusiform, cylindrical or bead-like bodies. These were regarded by him as somewhat similar to his earlier genera from the Triassic, *Aciculella* and *Holosporella* (Pia 1930). These he had interpreted as the remains of dasyclads in which the only calcified structures were the walls of endosporic sporangia set subperipherally within the main stem-cell, and he compared these with the Triassic *Diplopora phanerospora* in which these structures are seen within a normal calcified diplopore wall-structure. *Holosporella* is a hollow tube ; *Aciculella* a solid shaft, regarded as calcified internally during the lifetime of the alga.

Pia gave three figures of *Atractyliopsis*, two Carboniferous, one Permian, without assigning a type-species or species-names ; he considered these fossils as fusiform segments. The Permian form was later named *A. lastensis* (Accordi 1955), fully described from Italian topotype material, and recognized as cylindrical in form. Meanwhile Wood (1940) described the similar *Coelosporella* from the English Carboniferous, and mentioned its cylindrical form as differing from the alleged fusiform *Atractyliopsis*. *Coelosporella* however shows a much more solid wall than the other forms, and ovoid outwardly-directed sporangia, and may be regarded as valid on these grounds. *Atractyliopsis*, which differs only in larger dimensions and geological age from the earlier-described *Holosporella*, is retained here, since such fossils could originate from dasyclads of very different pattern.

In the Middle East only one species of *Atractyliopsis* is known : this occurs in a somewhat similar facies and at the same level as the type-species, but less abundantly.

### ***Atractyliopsis darariensis*** sp. nov.

(Pl. 2, figs. 3, 4, 5)

1960 *A. lastensis* Accordi ; Elliott : 219.

Description. Hollow cylindrical tubular structures, straight or gently curved, of up to 5·0 mm. observed length, 0·73 maximum external diameter : walls formed of a single layer of adjacent, touching or fused hollow spheres of 0·13 mm. internal diameter, original wall-thickness of spheres variable but 0·010–0·020 mm. in detached spheres. Primary calcification variable : the spheres may be more or less set in calcite formed by their fused walls, or almost isolated, with the outer surface of the cylinder truncating their outer curves, sometimes completely, to leave external openings, and their inner curves projecting roundly and unabraded into the cylinder-cavity.

Horizon. Upper Permian of Northern Iraq.

Holotype. The specimen figured in Pl. 2, fig. 5, from the Upper Permian Darari or Upper Chia Zairi Formation, Ora, Mosul Liwa, North Iraq ; V. 52037.

Paratypes. The specimens figured in Pl. 2, figs. 3, 4, same horizon and locality as the holotype ; V. 52015, 52037.

Other Material. Fragments in random thin-sections, same horizon and locality.

Remarks. This is very closely related to the type-species *A. lastensis* Accordi from the Upper Permian Dolomites of Northern Italy (Accordi 1956). Both occur with a similar *Gymnocodium*-flora in a rather similar facies at the same level. *A. darariensis* is described here as distinct since the cylindrical remains seem to have been markedly longer than in the Italian species, but the two are probably contemporary geographical species at most. Much depends on secondary calcification, which has to be distinguished very carefully where possible from that of the original sporangial coatings, and the Italian and Iraqi specimens are differently preserved in this respect. The measurements given above under " Description " are carefully taken from specimens without secondary calcification, or with it easily distinguishable as such when present. In the Italian topotype material available to me *Atractyliopsis lastensis* is much more abundant than in the Iraqi material, where *A. darariensis* is a minority-constituent in a flora of *Gymnocodium* and *Permocalculus*.

The Iraqi species is distinct from the Austrian *A. carnica* E. Flügel. Although described in great detail (E. Flügel 1966), the abundant material figured and described by this writer shows only circular and oval cross-sections.

Praturlon (1963a : 132) has figured a thin section which shows *Atractyliopsis* set vertically (axially) within *Permocalculus* cf. *forcepinus* (Johnson), (Chaetangiaceae or perhaps Codiaceae). He makes the interesting suggestion that this is the asexual form of the species, which is associated with other specimens of *Permocalculus* showing normal " sporangia " (?cystocarps) and regarded as the sexual form. That is, the *Atractyliopsis* is to be regarded as part of the internal structure of the *Permocalculus*, and is therefore not a dasyclad, nor indeed, a separate alga at all.

In the Iraqi material *Atractyliopsis* is associated with very abundant *Permocalculus*, but is itself rare. It is confined to the Darari Formation or top division of the Iraqi Permian, whereas *Permocalculus* ranges through the whole Chia Zairi, representing most of the system. It has never been seen inside *Permocalculus* in this material in the present study. The occasional occurrence of smaller fossils within larger ones by normal disturbance of randomly associated material on the sea-floor is not uncommon (cf. the perfect fit of the Palaeocene codiacid *Ovulites* within the dasyclad *Trinocladus* ; Pl. 23, fig. 2). With this in mind, I prefer to retain the older view of Pia (1937), that *Atractyliopsis* represents a zone of calcified sporangial structures set marginally in the dasyclad stem-cell. There is no direct proof of this for *Atractyliopsis* itself, but a comparable structure exists in *Diplopora phanerospora* Pia (Pia 1926), where both internal and external structures are calcified and the morphology is such that accidental post-mortem fitting is impossible.

### Genus ***BELZUNGIA*** Morellet 1908

Diagnosis. Hollow ovoid or elongate bead-like calcareous units, open at both ends : the thick wall perforated by verticils of radial dichotomising and swollen canals, which terminate externally as a pattern of small pores.

*Belzungia* (Morellet 1908) bears the same relation to *Thyrsoporella* as *Cymopolia* does to normal tubular dasyclads : that is, it possesses similar verticil-structure, but is organized into separate units or bodies, united in life into a jointed branching thallus, rather than the standard dasyclad single skeletal tube. *Belzungia* and *Thyrsoporella* are in fact identical in the plan of their peculiar lateral branch-structure within the calcareous wall-thickness.

In the Middle East *Thyrsoporella silvestrii* Pfender is a common Eocene fossil. Rarely, there occur isolated examples whose external morphology suggests reference to *Belzungia.* The best example seen of this was a specimen, from the Middle Eocene Pila Spi Limestone of Koi Sanjak, Erbil Liwa, Northeast Iraq. The dimensions are however those of a *Thyrsoporella* rather than of the larger *Belzungia.* L. Morellet, in an unpublished pioneer report of January 1931, compared a similar specimen from the Palaeocene of the Sulemania district (N.E. Iraq) to the smaller of the French Eocene species, *B. terquemi* Morellet, but the enlargement on the micrographs given him was inaccurate, and measurement of the actual specimen shows that it was smaller.

Note. Part 2 of Massieux (1966b), in which this author compares *Thyrsoporella* and *Belzungia* in detail, and refers *T. silvestrii* to *Belzungia*, was seen too late for proper discussion in this work. However, the specimens studied in the present work show the heavily-calcified walls of *Belzungia*, but the branch-system appears like that of *Thyrsoporella*.

### Genus ***BROECKELLA*** L. & J. Morellet 1922

Diagnosis (after Morellet). Hollow calcareous units, keg-shaped, traversed along the axis by a tube open at the extremities. Annular cavity between the outer walls and tube-walls, divided by horizontal floors into successive compartments, each of these itself divided by radial septa into several chambers each communicating by a single pore with the axial tube, and by numerous pores with the exterior, riddling the outer wall. Pores opening in the axial tube set in regular verticils ; external pores set in irregular sinuous lines.

*Broeckella* is a peculiar dasyclad described by Morellet (1922) from the Belgian Montian, and subsequently recognized from about the same level in Austria and Cuba (Keijzer 1945). These occurrences are of the type-species, *B. belgica* Morellet : *B. ranikotensis* (Walton) is known from the Indian Palaeocene (Walton 1925 ; Pia 1928), and the little *B. minuta* Carozzi from Switzerland is presumed Palaeocene.

*Broeckella* as described by Morellet (1922) is an extinct dasyclad whose skeletal remains occur as little keg- or short barrel-shaped units. Each unit contains a fairly wide central canal extending vertically from end to end, which once housed the main stem-cell of the plant. The apparently thick structure between outer surface and inner central canal is hollow, being divided by thin horizontal platforms into annular cavities, which are themselves divided into segment-shaped chambers by thin radial vertical walls. Each of these chambers (primary branches) communicates with the exterior by numerous small pores in the outer wall, said to open in sinuous lines, and with the interior canal by one large pore each, through the inner wall, arranged in horizontal rings. The distinctive thin-section appearance has been very well figured by Keijzer (1945). The numerous relatively large interior cavities between inner and outer walls have irregular surfaces to septa and partitions, made still more so by secondary calcification, and random cuts give curious irregular-radial patterns not like those of more conventional dasyclads such as *Cymopolia*, where there is a greater proportion of wall-material to original cavity in life.

The wide but scattered Tethyan distribution of this genus, its probable ancestry and its restricted geological range have been discussed (Elliott 1962b) ; I concluded that it was a primitive genus occurring uncommonly even under optimum algal conditions in the Palaeocene, and then becoming extinct.

## ***Broeckella belgica*** L. & J. Morellet

(Pl. 3, fig. 1)

1922 *Broeckella belgica* Morellet : 22, pl. 2, figs. 56, 57.
1945 *Broeckella belgica* Morellet ; Keijzer : 178, pl. 6, figs. 84–86.
1960 *Broeckella belgica* Morellet ; Elliott : 225.
1962 *Broeckella belgica* Morellet ; Elliott : 51.

Descriptions. The characters of this, the type-species, are those of the genus. The Middle Eastern material consists of random thin-sections only, similar to Keijzer's Cuban material. Of described species, the Indian *B. ranikotensis* (Walton) is the largest, and the Swiss *B. minuta* the smallest : the Belgian Cuban and Middle East specimens are all referred to *B. belgica* Morellet. Some dimensions for comparison are listed below.

Measurements and detail of ***Broeckella*** spp. Dimensions in mm.

| | *belgica* (type) | *belgica* (Cuba) | *belgica* (M.E.) | *ranikotensis* | *minuta* |
|---|---|---|---|---|---|
| Length of unit | 1·3 | up to 2·0 | 1·04 | 3·5–5·0 | 0·45–0·90 |
| Outer diam. of unit | 1·8 | 1·4–2·5 | 1·10 | 2·0–2·5 (max) | 0·25–0·45 |
| Central canal diameter | 0·6 | 0·35–0·8 | 0·4 | 0·66–0·83 (max) | 0·05–0·15 |
| No. of verticils per unit | 4 | 4–6 | 4 | 20 approx. | numerous units (fused) |
| No. of primary branches per verticil | 8–12 | 10–15 | 12 appr. | 15–20 | 15–20 |

HORIZON. Palaeocene of Europe, Cuba and Middle East.

MATERIAL. Random thin sections from the Palaeocene Sinjar Limestone of Kashti, Sulemania Liwa, North-east Iraq, and from the Palaeocene of Sahil Maleh, Batinah Coast, Oman, Arabia.

REMARKS. Both these occurrences are in rocks yielding a varied and characteristic Palaeocene algal microflora, as well as typical foraminifera for this level.

## Genus *CLYPEINA* Michelin 1845

DIAGNOSIS. Flat, saucer-, bowl- or funnel-shaped calcareous discs formed of horizontally-fused radial tubes : centrally they meet in a stout calcareous ring, each tube communicating by a single pore with the central cavity : the central ring is thickened below by the fused bases of the radial tubes and sometimes a smaller similar feature shows on the upper surface. In life these were the calcified structures of fertile dasyclad whorls.

*Clypeina* occurs as small fossil calcareous discs, saucer-, bowl- or funnel-shaped, centrally perforate, and with the solid portion composed of fused radiating tubules : communicating each by a single core with the central cavity. Usually the discs are separate, but occasionally several occur together in vertical, consecutive association. Described by Michelin (1845 : 177) from the French Oligocene as a coral, it was subsequently referred to other marine invertebrate groups by various authors until Munier-Chalmas (1877), in a brief communication, drew attention to its true algal nature.

*Clypeina* was reconstructed from Eocene material to show the probable structure and appearance of the plant in life (Morellet & Morellet 1918). These authors showed a dasyclad with central stem-cell bearing whorls of thin hair-like sterile branches below, and fused calcified cuplike fertile whorls above, each fertile whorl partially embracing the next : the plant is completed by a tuft of hair-like branches forming the terminal umbel, calcified at the base to give a perforate, " pepper-pot top ", structure (Fig. 3). The Morellets worked on loose, dissociated, elements from the unconsolidated sediments of the Paris Basin, and besides typical fertile whorls

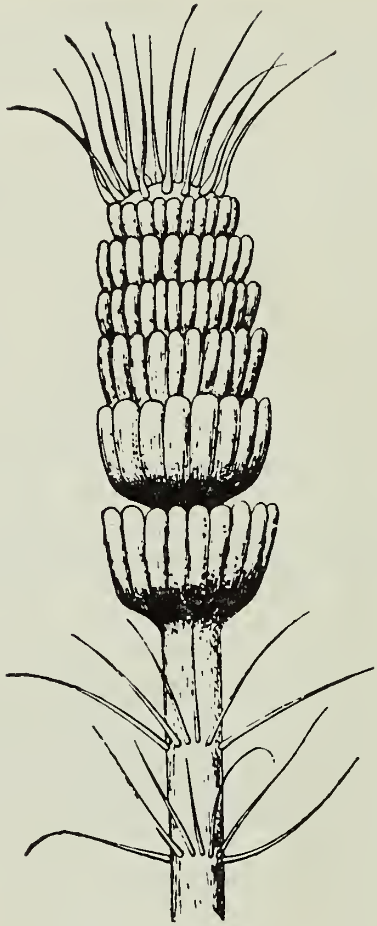

Fig. 3. Reconstruction (after Morellet 1918) of *Clypeina*. Sterile whorls below, fertile (calcified) whorls above, terminal tuft at top. ×30 approx.

they had calcified evidence of the sterile portion of the plant, of the lower, atypical fertile whorls, of the terminal structure, and of the serial association of the fertile whorls.

Pia (1927) placed *Clypeina* in the tribe Diploporeae, and he was followed in this attribution by Emberger (1944) and Kamptner (1958). The Morellets (1913 : 31 ; 1918 : 102), students of Tertiary and Recent algae, grouped *Clypeina* under Acetabulariae with *Halicoryne*, *Acetabularia* and *Acicularia*, three genera still surviving, and all showing separate sterile and fertile whorls and of somewhat similar morphology. Rezak (1957) summarizing this, agreed with the Morellets in their attribution. *Clypeina* is now placed in a new tribe Clypeineae, for its geological appearance precedes the evolution of the choristospore structures with which the terminal discs of Acetabulariae have been thought homologous. It therefore seems probable that it represents an earlier development of similar morphology, but from a different source. This point is more fully discussed below under dasyclad evolution (p. 99).

In the Middle East *Clypeina* is represented by species in the Upper Jurassic and basal Cretaceous, and again in the older Tertiary (Palaeocene and Eocene). A clypeiniform alga, still incompletely known, occurs in the Permian, and a Triassic species is now known from elsewhere (Pantić 1965). The numerous species listed throughout the Cretaceous succession in the western Mediterranean area (Algeria, France, etc.) by Emberger (1957) have not been noted in Middle Eastern material during the examination of thousands of thin-sections, often richly algal, and in fact only three records occur for this portion of the geological column.

## *Clypeina jurassica* Favre

(Pl. 3, figs. 2–5 ; Pl. 4, figs. 4, 5, 6)

1927 *Clypeina jurassica* Favre : 34, pl. 1, figs. 2, 3 ; text-figs. 10, 11.
1932 *Clypeina jurassica* Favre ; J. Favre : 12, text-fig. 2.
1951 *Clypeina jurassica* Favre ; J. Morellet : 399, pl. 22.
1955b *Clypeina jurassica* Favre and *C. hanabatensis* Yabe & Toyama ; Elliott : 125.
1958a *Clypeina jurassica* Favre ; Donze : 21.
1962 *Clypeina jurassica* Favre ; Powers : 131.

Description (from Middle Eastern material). Discs (fertile verticils), saucer to open-funnel shaped, diameter up to 2·4 mm., height up to 0·75 mm. composed of up to 24 fused radiating tubules (sporangial elements) around a central cavity of up to 0·5 mm. ; the majority of normal specimens are about 2·0 mm. diameter, with 18–20 tubules and central cavity of about 0·4 mm. The tubules widen slowly outwards, and the outer ends are open : on the external surfaces, upper and lower, the tubules are demarcated by shallow grooves. Although in normal specimens the tubules are nearly circular in cross-section, they tend to vary according to the size of the disc of which they form part, and in the larger examples, with more numerous tubules, the tubule cross-section shows the height greater than the diameter. The tubules fuse to form a conspicuous thickened central basal ring on the lower surface of the disc : this is most developed in the funnel-shaped examples. In a large example of estimated 2·5 mm. disc-diameter or more, the inner diameter of a single tubule increases from 0·130 mm. near the centre to 0·390 mm. in 1 mm. tubule-length : the diameter of the single inner communicating pore between central cavity (stem-cell) and tubule is 0·050 mm. ; and the single wall-thickness about the middle of the tubule is 0·065 mm. In random thin-section the united walls, back to back, of any two adjacent tubules show as radial fibrous calcite, clear or yellow, separated by a dark line, and in horizontal (transverse) sections these median structures project radially at the margin, to give a torn serrated appearance to the whole disc. This wall-structure and the open ends of the tubules, whatever their significance in terms of the original plant-calcification or subsequent diagenesis, are characteristic of the species, whether preserved in limestone or marl, and there is normally no confusion with the Valanginian species *C. lucasi* Emberger.

HORIZON. Upper Jurassic ; circum-Mediterranean and Middle East.

MATERIAL. Numerous solid and thin-section specimens from Qatar Peninsula, Persian Gulf, where it is abundant in the subsurface Upper Jurassic " Arab Zone " (Fahahil and Qatar Formations : Sugden *in press*) probably of Kimmeridgian-Tithonian age. Also at the same level in north-eastern Saudi Arabia (Powers 1962), and in Gezira no. 1 well, Murban, Abu Dhabi, Trucial Oman. Associated microfossils are the alga *Salpingoporella annulata* Carozzi and the microcoprolite *Favreina salevensis* (Paréjas). Thin-section material from both Kirkuk and Samawa, Iraq, where it abounds likewise in the subsurface Najmah Formation, of about the same age, with the same companions. Also seen in thin-sections from the topmost Jurassic at Haushi, Southern Oman, Arabia, accompanied by debris probably referable to *Griphoporella perforatissima* Carozzi, an alga initially described from the Upper Portlandian and Berriasian of Switzerland. The species is common in the Upper Jurassic of numerous exposures in southern Persia (Gollestaneh Coll.).

REMARKS. *Clypeina jurassica* is a common microfossil in the Upper Jurassic of southern and central Europe, North Africa and the Middle East, and records of it are very numerous. Described by Favre (Favre & Richard 1927) on thin-section material from Switzerland, and re-described for comparison with *Clypeina inopinata* (Favre 1932), the next advance was the description of Algerian material by Morellet (1951) based on both thin-section and solid (silicified) specimens. Donze (1958a) re-described material from the type-area from a good selection of solid specimens, presumably isolated by weathering or artificial breakdown of weathered material. For the present study of Middle East examples both numerous thin-sections and solid examples obtained by washing of crumbled core-material have been available.

The descriptions drawn up for this species by Favre, Morellet, Donze and myself all differ slightly in detail. The principal difference is that specimens from the type-area (Switzerland) show a lesser maximum number of sporangial tubules per verticil than do those from some other localities. For Swiss material Favre gives a relevant count of 10–17, and Donze 7–17, whereas Morellet, with Algerian examples, gives 11–20, and the Middle East material (above), shows up to 24. Although there are numerous figures in the literature of random cuts of this species conforming in this particular with the type-material, there are some which indicate a higher count (e.g. de Castro 1962, pl. 18 ; Italy, Naples area). These higher counts are from more southern areas than that of the type-material. It would seem that this is a case where the historical development of western Europe has resulted in the original description of Tethyan material being made in a marginal area, a phenomenon familiar both in stratigraphy and palaeontology.

Other differences observed in the Qatar (Middle East) specimens were the somewhat variable convexity of the verticils, and the prominence of the central thickened ring on the lower verticil surfaces. The former was however recorded by Donze on topotype material, and indeed is to be expected from our understanding of the growth of the living *Acetabularia*. The latter character was described by Morellet, but not well figured, on Algerian material.

The pioneer study on Middle East (Qatar) material was by F. R. S. Henson in an unpublished report of 1942. He distinguished a minority of *C. jurassica* conforming strictly with the type-description, and more numerous examples with a higher sporangial-tubule count. In a preliminary examination of Middle East algae (Elliott 1955b) I recorded these latter as *C.* cf. *hanabatensis* Yabe & Toyama, comparing them with this Japanese species which has a higher count (22–24, up to 27), but is a larger species (verticil-diameter up to 3·5–4·0 mm.). This determination is now abandoned.

Detailed comparative statistical studies of local populations of *Clypeina jurassica* from different circum-Mediterranean and Middle East countries have not been made to my knowledge. Such studies would have to be made on good collections of complete, isolated, verticils, since the recognition of proportional, as opposed to structural, differences, in random thin-section material is a task of great difficulty, at any rate with the small degree of difference expected in the present problem. The results would have to be interpreted in the light both of presumed salinity changes, from facies and accompanying fauna, a factor affecting living algae, and also bearing in mind possible post-mortem sorting of verticils of slightly differing size and shape from mixed assemblages of dissociated component-verticils derived from associated plants. It seems likely that the local differences revealed, at any rate in the main Tethyan basin, would depend on these secondary factors rather than on a progressive evolutionary trend.

*C. jurassica* is a frequent and characteristic fossil for much of the Upper Jurassic of the western old-world Tethys ; in the east, it is missing from rocks of this age in Borneo. The oldest level appears to be in Algeria (Rauracian-Sequanian of Morellet 1951, equalling Upper Oxfordian of current usage) ; the species occurs throughout the Mediterranean Kimmeridgian and is especially abundant at levels of Portlandian or Tithonian age over the whole of its distribution-area. In my experience it extends to the very top of the Upper Jurassic and is a good index-fossil for the upper part of the Upper Jurassic. (See also comments below (p. 87) on the Jurassic-Cretaceous boundary.)

In the Franco-Swiss area, from which the types were described, there are records from the lowest Cretaceous (infra-Valanginian and Berriasian, e.g. Donze 1958a, b). This is in an area adjacent to a region of uplift with terminal Jurassic—early Cretaceous freshwater brackish and lagoonal beds of Purbeck type : the algae are consistently smaller than those from the Jurassic. They may be a transitional form to the succeeding *C. inopinata* (rare or absent in the Middle East), their evolution a reaction to salinity-changes. Donze suggested, that they were either a different species, close to *C. inopinata*, or stunted *C. jurassica* " bad adaption to environment ". The relation of these and other algae to salinity is discussed below under environment. In Jugoslavia Kercmar (1962) has described a local variety *C. jurassica minor*, which he distinguishes from the typical *C. jurassica jurassica* mostly by the smaller size, there being little if any overlap or transition in this character.

He regards this small variety as possibly transitional to *C. parvula*. It certainly seems that *C. jurassica* was the rootstock for other and later species, and that this evolution may well have been connected with areas of late-Jurassic uplift and emergence.

### ***Clypeina inopinata*** Favre 1932

This species, described by Favre (1932) as distinct from *C. jurassica* and as succeeding it in the Swiss Valanginian, is not known to me with certainty from the Middle East, although basal Cretaceous is well-represented in available collections. Occasional qualified records in unpublished reports are based on rare and fragmentary *Clypeina* sp., and no good *C. inopinata* have been noted. The species may be a local successor to *C. jurassica* in the Franco-Swiss area only. M. Dufaure of Bordeaux informed me (personal communication 1965) that the type-occurrence of *C. inopinata* is, in fact, Upper Berriasian i.e. pre-Valanginian.

### ***Clypeina lucasi*** Emberger
(Pl. 5, fig. 4)

1956 *Clypeina lucasi* Emberger : 549, pl. 24, f. 1, 2, 7.
1960 *Clypeina lucasi* Emberger ; Elliott : 223.

DESCRIPTION (after Emberger). Fertile verticils almost flat, circular, diameter 2·5–3·0 mm. and about 0·5 mm. thick : 12–18 club-shaped sporangial chambers, of about 1·1 mm. long and max. diameter 0·5 mm., fused laterally for $\frac{3}{4}$ of their length, separated by shallow grooves, and terminally imperforate. Central cavity of 0·35–0·48 mm. diameter, margined by a feeble raised ring above and a more prominent one below.

HORIZON. Valanginian of Algeria and Oman.

MATERIAL. Thin-sections in basal Cretaceous limestones (Thamama Formation Equivalent), Hugf area, southern Oman, Arabia.

REMARKS. This distinctive species was described by Emberger (1956) from solid (silicified) specimens found in the Algerian Valanginian, where it was accompanied by *Clypeina marteli* Emberger, also new. In the Middle East the two species occur, together with the codiacid *Arabicodium aegagrapiloides* Elliott, at the same level in Southern Oman, Arabia. In the thin-sections of limestone *C. lucasi* may be recognized, the details corresponding with much of Emberger's description.

### ***Clypeina marteli*** Emberger
(Pl. 4, fig. 1)

1956 *Clypeina marteli* Emberger : 550, pl. 24, f. 3–6.
1960 *Clypeina marteli* Emberger ; Elliott : 223.

DESCRIPTION. Stellate verticils, gently curved, diameter 1–2 mm., consisting of from 7 to 12 radiating tubules, fused laterally for about the inner third of their length and then free outwards, surrounding an inner circular cavity of from 10–14% of the verticil diameter. Tubules circular in cross-section, terminally bluntly rounded, thin-walled (wall-thickness 0·026 mm. in a tubule of outer diameter 0·130 mm. ; verticil-diameter 1·5 mm. approx.), and forming a moderately developed raised central ring below, but without similar feature above : the tubules communicate with the central cavity each by a single pore.

HORIZON. Valanginian of Algeria and Oman.

MATERIAL. Found in the basal Cretaceous (Lower Thamama equivalent) of Hugf, Southern Oman, Arabia, i.e. at about the same horizon as the type-level in the Algerian Valanginian, and similarly associated with *Clypeina lucasi* Emberger, and also with the codiacid *Arabicodium aegagrapiloides* Elliott.

REMARKS. *Clypeina marteli* is highly distinctive amongst species of its genus : the only other stellate species in which the radiating tubules are similarly free for much of their length are *Clypeina digitata* (Parker & Jones) Morellet emend. Rezak, and (less closely comparable) *C. helvetica* Morellet, both Eocene. Emberger's comparison with the former drew attention to the gently concave plane of *C. marteli* as compared to the more funnel-shaped form of *C. digitata*, a valid distinction (Emberger 1956). *C. marteli*, however, does show a central fusion ring, marginal to the stell-cell cavity, on its lower surface, though this is regular in form and not irregular as that of *C. digitata* described by the Morellets (1913).

More serious risk of confusion exists with *Actinoporella podolica* Alth, which similarly occurs at about Valanginian level in the Middle East. However, although both are somewhat similar in size, *Actinoporella* shows many more tubules per verticil (18–20 as opposed to 7–12, and the former smaller in size), and a proportionally larger central cavity (d/D 20% or more, as opposed to 10–14% in *C. marteli*).

## *Clypeina parvula* Carozzi
(Pl. 5, figs. 5, 6)

1946 *Clypeina parvula* Carozzi : 24, fig. 1.
1948 *Clypeina parvula* Carozzi ; Carozzi : 355, figs. 50, 51.
1955b *Clypeina parvula* Carozzi ; Elliott : 126.
1960 *Clypeina parvula* Carozzi ; Elliott : 222, 223.

DESCRIPTION (after Carozzi). Sterile whorls in the form of straight thick-walled calcareous tubes, widening in the upper portion and with the outer surface showing a number of shallow straight vertical flutings or concavities, usually about twelve, but from ten to twenty-five recorded. The fertile whorls are similar but widen much more, terminating in a kind of peripheral fringe or collar : internally, sporangial chambers correspond to the external flutings, the actual cavities being set in the thick calcareous wall. External diameter is said to be from 0·09–0·45 mm. and the diameter of the central canal 0·03–0·12 mm. (average 0·07 mm.).

HORIZON. Upper Jurassic—bottom Cretaceous Europe (?Aptian–Albian Jugoslavia, see Radoičić 1960), bottom Cretaceous Middle East.

MATERIAL. In Iraq, from the lower part of the Cretaceous (about Valanginian level) : Sarmord Formation of Jebel Gara and Garagu Formation of Banik (both Mosul Liwa) ; also subsurface Garagu at Kirkuk.

It has also been seen in the bottom Cretaceous at Haushi, Southern Oman, Arabia, where it was accompanied by the dasyclads *Acicularia*, *Salpingoporella*, and *Griphoporella*, also by *Permocalculus* : the level was independently dated by foraminifera.

REMARKS. The details given above are summarized from Carozzi's descriptions. His reconstruction shows a somewhat peculiar little alga, consisting of inverted fluted cones inserted within one another vertically. His thin-sections substantiate the detail quoted above and also show further detail. This species, if correctly interpreted as a *Clypeina*, departs more from the usual verticil-morphology than other species. In the Swiss Purbeckian (terminal Jurassic) *C. parvula* occurs in beds interpreted as freshwater, its companion fossils being charophytes and ostracods.

In the bottom Cretaceous, marine Valanginian level, of the Middle East there occur not uncommonly in thin-section preparations sections corresponding mostly to the transverse cuts of the bases of verticils as figured by Carozzi. Occasionally vertical cuts are seen, but never the transverse cuts he figures of the upper portions of fertile verticils, which show the sporangial cavities, outer collar, and other detail. The number of flutings is usually from 8 to 10, and the size-range falls for the most part in that quoted above from Carozzi, though one large example had an external diameter of 0·6 mm.

These little fossils, with occasional charophytes and ostracods, occur in Iraq to form a subordinate element in a rich marine dasyclad and other algal flora, which includes species of *Actinoporella*, *Cylindroporella*, *Salpingoporella*, *Permocalculus*, *Lithocodium* etc., also foraminifera and microproblematica, marine mollusca and corals. They are interpreted as *Clypeina parvula* from coastal freshwater beds, which, together with the charophytes, have been washed out to sea before burial. Only the more resistant parts of the verticils survived this derivation, which would explain the absence of the more fragile reproductive structures.

## ***Clypeina*** spp. (Cretaceous)

1960 *Clypeina* spp. Elliott : 225.

Three records only of the genus may be made for the whole of the Cretaceous examined above the basal portion (Berriasian-Valanginian) yielding the species already described.

The specimen figured as " *Munieria baconica* Deecke " (Elliott 1958, pl. 48, fig. 1) is not of this species and may be a *Clypeina* ; it comes from the Aptian-Albian of Surdash, Sulemania Liwa, Iraq.

Another occurrence is in the Cenomanian, subsurface Mahilban Formation of Fallujah Well, Dulaim Liwa, Iraq. Fragmentary material indicated a *Clypeina* sp. of estimated whorl-diameter 3·25 mm., showing approximately 50 fused adjacent sporangial tubules of 1·04 mm. length, circular in cross-section and of 0·36 mm. near-terminal external diameter and 0·23 mm. internal diameter. This material is insufficient for description, and it is not known if it corresponds with any of the undescribed Cenomanian species listed by Emberger (1957). The remains were associated with fine debris of codiacid algae.

A third Cretaceous *Clypeina* occurred higher, in the Maestrichtian (Shiranish Formation) of Diyana, Rowanduz Liwa, Iraq. It showed only a transverse section of sporangial tubules of about 0·13 mm. diameter. This is quite inadequate for comparison with such species as *Clypeina sahnii* Varma (1952) from the Danian of India.

## ***Clypeina merienda*** Elliott

(Pl. 4, figs. 2, 3, 7, 8)

1955b *Clypeina merienda* Elliott : 127, pl. 1, figs. 8, 9.

DESCRIPTION. Fertile verticils disc-like, circular and flat, with diameter up to 2·5 mm., and diameter of central cavity up to 1·0 mm. The verticils consist of about 50 or more radiating hollow tubules, set nearly horizontally to the vertical axis, with the tubules united laterally and often slightly expanded at the periphery, where they are often open. Circular in cross-section, they have a transverse diameter of 0·15–0·18 mm. measured in the mid-zone of large examples, with internal diameter of 0·072 mm., but examples with smaller diameters than this are common and there would seem to be some variation in this character. The expanded and open tubule-ends at the periphery are variable, and may be an indication of spore-shedding in mature whorls. Internally each tubule communicates by a pore with the central cavity : fused calcification forms a thickening in this central zone and extends down to the next whorl. Up to six whorls have been seen in serial association as in life : these whorls, measured vertically in the mid-zone of the tubules, from centre to centre of consecutive whorls, were from 0·34–0·52 mm. apart.

HORIZON. Palaeocene–Lower Eocene of the Middle East.

MATERIAL. In northern Iraq, from the Sinjar Formation of Banik (Mosul Liwa), of Koi Sanjak (Erbil Liwa), and of Sirwan (Sulemania Liwa) ; also from the Kolosh Formation of Surdash (Sulemania Liwa). In southern Iraq, the species occurs in a fragmentary state in the Basita Beds of the Umm er Rudhama Formation (Palaeocene-Lr. Eocene) near Aidah, Diwaniyah Liwa.

REMARKS. This *Clypeina* is distinctive in the large number of radial tubules per whorl, in which character it somewhat resembles the larger *Orioporella* from the Belgian Montian and Indian Danian (Morellet 1922, Pia 1936b), but with no trace of the pores which perforate upper and lower surfaces of the tubules in this genus. *C. merienda* is larger than the Eocene *Clypeina* spp. described by the Morellets (1913 ; 1922) : the frequent flatness of its whorls is noticeable, though there is some variation in this character. Of Middle Eastern species, it is the one in which serially associated whorls, as in life, are most often seen in the fossils.

### *Clypeina* sp. (Palaeocene)

(Pl. 5, fig. 2)

1960 *Clypeina.* spp. Elliott: 225.

Apart from *C. merienda*, there occur rarely in the Palaeocene-Lower Eocene of the Middle East small *Clypeina* spp. inviting comparison with those from the French Eocene described by L. and J. Morellet (1913 ; 1922 ; 1939 ; see also Rezak 1957). Random thin sections of these have been noted in material from the Palaeocene Sinjar Limestone of Banik, Mosul Liwa, northern Iraq ; from the Palaeocene Ghurna Beds (Umm er Radhama Formation) of Al Ghurra, Diwaniya Liwa, southern Iraq ; from the Palaeocene-Lower Eocene of Sahil Maleh, Batinah Coast, Oman, Arabia ; and from the Palaeocene of Aqabar Khemer, Hajar, Hadhramaut. The example figured is typical and shows a verticil of 1 mm. diameter, central aperture of 0·36 mm. diameter, with about 22 adjacent sporangial tubules. None of these localities have yielded enough material for a precise determination by comparison with the similarly-sized, well-known and beautifully-preserved European material.

### ?*Clypeina* sp. (Permian)

(Pl. 5, figs. 1, 3)

1958a *Clypeina* Mich. (ou genre nouveau très voisin) Emberger : 51.
1960 ?*Clypeina* sp. Elliott : 219.
1965 *Eoclypeina* Emberger MS ; Glinzboeckel and Rabaté : pl. 74.

In a preliminary note on the Upper Permian of Djebel Tebaga, southern Tunisia, Emberger (1958a) listed a clypeiniform alga of which he proposes to describe three new species ; this has been illustrated but not described in Glinzboeckel and Rabaté (1965). Debris of the same or a similar form is now figured from the Permian of Iraqi Kurdistan, where it occurs rarely at Harur (Mosul Liwa), both from the base of the Satina Evaporite formation and from the top of the Zinnar Formation immediately below. Whether this is a true *Clypeina*, ancestral form or homoeomorph, it seems to represent an early attainment of the umbrella-like sporangial disc familiar in certain Mesozoic and Tertiary genera : it is hoped that M. Emberger's descriptions will throw light on this. The Jugoslav Permian dasyclads *Salopekiella* and *Likanella* (Milanović 1965 ; 1966) bear no close resemblance, and nothing else associated is at all comparable.

The recent description of *Clypeina besici* Pantić (1965) from the Upper Triassic of Jugoslavia is a valuable confirmatory link between the Permian *Eoclypeina* and the familiar Upper Jurassic *C. jurassica*.

## Genus *CYLINDROPORELLA* Johnson

Diagnosis. Cylindrical calcareous bodies terminally tapered or rounded, interpreted as serial dasyclad units arranged in life somewhat similarly to those of the Recent *Cymopolia*. Internally the longitudinal central canal (stem-cell cavity) is surrounded by rings of proportionally large spherical sporangial cavities alternating with whorls of infertile primary branch-canals. These are normally at right angles to the longitudinal axis, and each divides terminally into secondaries. Sporangia and infertile branches alternate in position in successive whorls.

*Cylindroporella* is a distinctive Mesozoic dasyclad first described by Johnson (1954b) : type-species *C. barnesii* from the Albian Edwards Limestone of Texas. Elliott (1957) described new species from both Upper Jurassic and Lower Cretaceous of the Middle East, and has since recognized *C. barnesii* there. The Jurassic species *C. texana* Johnson (1961a) and *C. ellenbergeri* Lebouché & Lemoine (1963), and the Upper Cretaceous *C. elassonos* (Johnson & Kaska, 1965), have not yet been identified from the Middle East.

### ***Cylindroporella barnesii*** Johnson
(Pl. 6, figs. 3, 4)

1954 *Cylindroporella barnesii* Johnson : 788, pl. 93, figs. 1–7.

Description. The characters of this, the type-species, are those of the genus. The table below gives the various measurements by which the three species recognized in the Middle East may be distinguished.

Horizon. Albian of Texas : Lower Cretaceous of Iraq.

Material. Fragmentary material referable to this species has now been recognized from two localities in Iraq : from the subsurface Garagu Formation (Valanginian-Hauterivian) of Makhul no. 2 well, Mosul Liwa, and from the Sarmord Formation (about Aptian level) at Sekhaniyan, Surdash, Sulemania Liwa.

Remarks. Both the above occurrences show a *Cylindroporella* with outer diameter of 0·468 mm., inner diameter 0·156 mm., and sporangial diameter of 0·156 mm. ; they are distinct from the larger *C. sugdeni* Elliott, which they overlap in range, and seem best referred to the type-species, described from the Albian.

Detail of *Cylindroporella* spp. (M.E.). Dimensions (in mm.)

| | *arabica* | *barnesii* | *sugdeni* |
|---|---|---|---|
| Length of segment | 1·43 | 2·8–5·1 | 3·0+ |
| Diameter of segment | 0·31–0·57 | 0·38–0·55 | 0·78–1·14 |
| Diameter of central canal | variable; 0·052–0·230 | 0·08–0·15 | 0·234–0·36 |
| Diameter of sporangia | 0·078–0·156 | 0·134–0·189 | 0·26–0·312 |
| Number of sporangia per whorl | Usually 6 in all three species | | |
| Number of sterile branches per whorl | Usually 6 in all three species | | |
| Angle of branches to stem | 90° in all three species | | |
| Number of terminal secondary branches | Probably 4 in all three species | | |
| Vertical distance between whorls | 0·13 | 0·17–0·187 | 0·39 |

### *Cylindroporella arabica* Elliott

(Pl. 6, figs. 1, 2)

1957 *Cylindroporella arabica* Elliott : 227, pl. 1, figs. 13–16.
1962 *Cylindroporella arabica* Elliott ; Powers : 131.

Description. This is the smallest of the Middle East species of the genus. *C. texana* Johnson, of about the same age from the U.S.A., shows smaller dimensions for internal structures but these occur in a very much longer slim segment.

Horizon. Upper Jurassic of Arabia.

Material. *C. arabica* occurs in the upper part of the Upper Jurassic, subsurface Arab zone, in the Dukhan wells, Qatar, Persian Gulf, also at the same level in north-eastern Saudi Arabia (Powers 1962), and in Gezira no. 1 well, Murban, Abu Dhabi, Trucial Oman ; associated algae are *Clypeina jurassica* Favre and *Salpingoporella annulata* Carozzi. It occurs at the same level, also with *S. annulata*, at Al Hamiah, coastal Wahidi, Hadhramaut.

### *Cylindroporella sugdeni* Elliott

(Pl. 6, figs. 5–7)

1957 *Cylindroporella sugdeni* Elliott : 227, pl. 1, figs. 1–6.

Description. This species shows large, thick segments, with greater sizes for internal structures than other species, if the Liassic *C. ellenbergeri* Lebouché & Lemoine is excepted : this last differs in various characters from the more homogeneous later species. *C. sugdeni* is proportionally shorter and much thicker than the type-species *C. barnesii*.

Horizon. Lower Cretaceous of Middle East.

Material. Described from the subsurface Lower Cretaceous of Fahud no. 1 well, Oman, Arabia, where it was abundant. It occurs in *Orbitolina*-limestone of probable Barremian-Aptian age at Wady Hajar and Wady Ghabar, Hadhramaut : also to the north in the subsurface Lower Qamchuqa Limestone (Hauterivian level) of Kirkuk no. 116 well, Iraq.

### *Cylindroporella* spp.

There remain various records of indeterminate *Cylindroporella*, based on random cuts in thin-section, obviously of the genus, but not diagnostic of a species : often they are small in size. These have been seen in the Lower Cretaceous Qamchuqa Formation of Chama, Mosul Liwa, northern Iraq ; subsurface in the same formation at Barremian-Aptian level in Kirkuk well no. 116, and again at this level in the Lower Cretaceous of Wady Arus, Hajar, Hadhramaut.

## Genus *CYMOPOLIA* Lamouroux 1816

Diagnosis. Thallus formed of consecutive hollow calcareous cylindrical bodies, terminally rounded ; in each the main longitudinal canal (stem-cell cavity) extends from end to end, the wall-thickness perforated by close-set more or less horizontal whorls or verticils of branch-canals. Each verticil consisting of several branch-systems of the same pattern : an inner primary branch dividing into several (usually four) secondaries, and one sporangial cavity, usually spherical : the secondaries reach the outer surface to give a dense pore-pattern.

The dasyclad *Cymopolia* is well-known from living species in the warm waters of the East and West Indies. The plant shows a branched thallus of conventional " seaweed " pattern, in which the fronds are composed of heavily calcified serial or consecutive units, united by non-calcified tissue : each of these units corresponds in general plan to the single calcified tubes of the more normal dasyclad genera. After death the units come apart, and it is in this condition that they are met with in the fossil state, being known thus from the Upper Cretaceous onwards.

### ***Cymopolia anadyomenea*** Elliott

(Pl. 7 ; Pl. 8, figs. 1, 5)

1959 *Cymopolia anadyomenea* Elliott : 218, pl. 1, figs. 1–4, 8.

Description. Elongate hollow tubular units each showing several external horizontal annular flange-like swellings or increases of diameter, more or less regularly spaced, varying in development in different individuals : external surface finely patterned with small closely-set pores. Length (incomplete), up to 6 mm. seen ; diameter varying both with absolute size and relative flange-development, 1·5–3·9 mm.(usually 2·0–2·5 mm.). Internal diameter of the main cell-cavity either constant or variable : if the latter, waxing and waning to correspond with external diameter-changes, but to a lesser extent. The d/D ratio varies correspondingly from 50–70%, being almost always 50% or more : only with extreme external flange-development can a figure of less than 50% be obtained. The wall-thickness is perforated by numerous closely-set whorls or verticils of crowded branches, 45–48 per verticil, and about 6 verticils per 1 mm. measured vertically. Each primary branch gives rise to a globular sporangium of 0·05–0·08 mm. diameter and four or more secondary branches set at an angle of 45–60° from the horizontal. The branch-systems are coarser at flange-levels, where the diameters of primary and secondary branches were 0·065 mm. and 0·039 mm. on a large specimen, and 0·039 mm. and 0·026 mm. on a small specimen.

Horizon. Maestrichtian of Northern Iraq and Afghanistan ; possibly from Maestrichtian of Tibet.

Material. Upper Aqra Formation (Maestrichtian) of Aqra and of Chalki Islam, Hadiena Formation of Chalki (top Senonian), Upper Bekhme Formation (Maestrichtian) of Chia Gara, and Aqra-Bekhme Formation of Gal-i-Mazurka, all five limestone localities in Mosul Liwa. Also in the green-rock sands (Tanjero Formation, Maestrichtian) of Diza, Erbil Liwa.

Remarks. This *Cymopolia* may be distinguished from other species of the genus by the peculiar annular flanging of the calcareous units. This " waxing-and waning " growth suggested a half-way stage between the ordinary single tubular dasyclad and the living segmented *Cymopolia*, but it seems much more likely that the units are in fact segments themselves, as in other species, and that the frequent broken pieces found are due to ordinary post-mortem mechanical fracture. The number of sporangia per verticil (45–48) is high and gives a very crowded appearance to this fossil in section, when compared with similarly-sized *C. barbata* (L.) Lmx. (Recent) and *C. elongata* (Defr.) Mun.-Chalm. (Eocene), in both of which the count is about 30.

The flanged units give outlines of striking appearance in random thin-section. It was in this condition, recrystallized in limestones, that they attracted my attention, but no description was possible until material with the internal structures well-preserved was discovered in the green-rock sand facies of the same age. In Tibet, the *Cymopolia* sp. of Morellet (1916 : 49; Maestrichtian of Kampa Dzong) may possibly be this species, as *C. tibetica* Morellet is associated with *C. anadyomenea* in Iraq.

Although *C. anadyomenea* is thus distinctive for the Maestrichtian, an apparent homoeomorph occurs in the Lower Cretaceous of Italy (Praturlon 1964). This is not yet fully described due to scarcity of material, though it appears to differ in flange-profile. This or a similar species occurs also in the Lower Cretaceous of Borneo (Bau Formation), and in the Lower Cretaceous of Jugoslavia (Radoičić *in litt.*).

### ***Cymopolia eochoristosporica*** sp. nov.

(Pl. 9, figs. 1–3)

DESCRIPTION. Tubular cylindrical thickwalled units of about 2·0–2·2 mm. external diameter (maximum seen 2·42 mm.), internal diameters 0·73–0·86 mm. (maximum seen 0·91 mm.), giving a d/D ratio of 36–40%. Estimated lengths of units up to 9 or 10 mm. Verticils of 12–14 primary branches which are probably inclined upwards at a low angle from the horizontal. Each branch communicates with the stem-cell by a very short connecting pore of 0·03–0·04 mm. diameter. These pores are set about 0·26 mm. apart measured (vertically) along the stem-cell walls. The branch then expands into the main swollen portion, seen as rounded-rectangular in near-vertical section, where it measures 0·390–0·416 mm. radially and 0·234 mm. vertically. These swollen portions occupy much of the thickness of the walls and are thus very close-set, the interstices being only 0·030 mm. thick. Finally each swollen portion divides into a small cymopoliform cluster of one spherical sporangium and four divergent secondary sterile branches. Diameter of the sporangium is 0·13 mm. ; and the diameter of the short neck or pore connecting it with the swollen primary is 0·052–0·065 mm. The secondaries have a median diameter of 0·040–0·052 mm. and expand terminally at the outer surface to shallow depressions of about 0·104 mm. diameter.

HORIZON. Maestrichtian of Trucial Oman, Arabia.

HOLOTYPE. The specimen figured in pl. 9, figs. 1, 2 from the subsurface Aruma

Formation (Maestrichtian level) of Murban No. 53 well, Abu Dhabi, Arabia. V. 52652.

SYNTYPE. The specimen figured in pl. 9, fig. 3, same locality and horizon as for holotype. V. 52653.

OTHER MATERIAL. Several incomplete random thin-sections, provenance as above.

REMARKS. This remarkable species does not at first sight appear to show the branch-structure of the genus *Cymopolia*. The large and conspicuous swollen primaries suggest a typically cladospore Mesozoic genus. However the small terminal cymopoliform branch-systems are distinctive. They are typically choristospore, and lead to the conclusion that the species shows one possible transition between cladospore and choristospore organization. Typical *C. tibetica* of the same geological age show expanded primaries, but to a very much less degree, and this feature survives not uncommonly in the Tertiary subgenus *Karreria*, and even occasionally in specimens of living *Cymopolia* (see remarks above under *C. tibetica*). In these later forms this character is best regarded as vestigial.

*C. eochoristosporica* appears to show the cladospore/choristospore transition by the appearance of a small choristospore development superimposed on the large cladospore branch, presumably with partial transference of sporangial contents. In this connection it is as remarkable an evolutionary record as Pia's suggested interpretation of his forms *trichophora* and *vesiculifera* of the Triassic *Diplopora annulata* as endospore and early cladospore respectively. Here the transition from endospore to cladospore is similarly considered to have taken place within the one species, but the separate characters are shown in different individuals with a possible geographical-environmental distribution of the two forms. The scarcity of my Maestrichtian *Cymopolia* spp., when compared with Pia's abundant Triassic diplopores, precludes an investigation of this possible subsidiary parallel for the present. Moreover, Herak's review of Pia's work on this subject (Pia 1920 ; Herak 1957), whilst clearing the taxonomic confusion involved, also shows the many uncertainties which attend evaluation of the Triassic species in its varied forms and occurrences, even with an abundance of material for study.

For these reasons the limited material now studied is described as a new species, the available individuals showing clearly in their morphology the characters on which the species is based.

### ***Cymopolia tibetica*** Morellet

(Pl. 8, figs. 3, 4)

1916 *Cymopolia tibetica* Morellet : 47, pl. 15, fig. 10, text-figs. 14–21.
1927 *Karreria tibetica* (Morellet) Pia : 83.
1940 *Cymopolia tibetica* Morellet ; Pfender : 234.
1960 *Cymopolia tibetica* Morellet ; Elliott : 223.

DESCRIPTION (summarized from Morellet). *Cymopolia* with rather straight-sided cylindrical units of up to 2·5 mm. long and diameters from 1·1 to 1·5 mm., diameter of central canal about 50% external diameter, external surface when unworn showing pattern of nearly uniform circular pores, but when worn showing pores of two sizes, the larger being the sporangial chambers. In the verticils, the normal branch-pattern of each primary giving rise to one spherical sporangial cavity and four secondaries is modified by the distal portion of the primary branch being greatly expanded immediately before branching into sporangium and secondaries : these additional cavities are conspicuous in vertical and transverse section.

Horizon. Maestrichtian of Tibet, northern Iraq, Turkey and Arabia.

Material. In northern Iraq, in the Aqra Formation of Aqra and of Zibar Isumeran, in the Hadiena Formation of Chalki, and in the Aqra-Hadiena development of Chalki Islam, all in Mosul Liwa, in limestone facies. The species is also known from the clastic Tanjero Formation of Diza, Erbil Liwa, and recorded by Naqib (1960 : 176), as a derived fossil, in pebbles occurring in Palaeocene conglomerates (Kolosh Formation) at Argosh, Mizuri Bala area, Mosul Liwa. Seen also in subsurface Maestrichtian at Murban, Abu Dhabi, Arabia.

Remarks. This species occurs not uncommonly in the Maestrichtian of Iraqi Kurdistan, usually in the limestone facies. Specimens are small (external diameter 0·75–0·85 mm.) and very often fragmentary, but show the distinctive characters of the species in section. The Zibar-Isumeran specimens are in the worn condition suggesting *Neomeris* or *Larvaria* as described by Morellet in some Tibetan material. The type-material was from the Maestrichtian of Kampa Dzong, Tibet : Pfender's record is from Sofular, Ankara, Turkey. She regarded both this Turkish and the type Tibetan rocks as Palaeocene. In the type area the species comes from an unequivocally Maestrichtian bed (Douvillé 1916), and it is not clear from her summary account which levels are represented at her Turkish locality. If the species was correctly determined, it seems likely that it is Maestrichtian in view of the Iraqi occurrences.

Fragmentary remains of an indeterminate *Cymopolia* sp. have also been noted in the Maestrichtian of Oman.

Pia's reference of *C. tibetica* to the Tertiary *Karreria* Munier-Chalmas was based on the former's recognition of this subgenus, not by the pyriform sporangia but by the expanded primary branches. Pfender, however, states that L. Morellet, dissecting Recent *Cymopolia*, found differences in this latter character between different segments of the same plant. In the present work *Karreria* is restricted to those Palaeocene *Cymopolia* showing pyriform sporangia.

### ***Cymopolia kurdistanensis*** Elliott

(Pl. 10, figs. 2–5)

1955b *Cympolia kurdistanensis* Elliott : 127, pl. 1, figs. 13–15.
1960 *Cymopolia kurdistanensis* Elliott ; Elliott : 225.

Description. Tubular cylindrical thick-walled units with rounded ends : units variable in length and diameter relationship, length up to 4·0 mm., diameter commonly about 0·75 mm. and exceptionally up to 1·5 mm. ; internal diameter (stem-cell) normally about 50% of external. Closely-set verticils of rather crowded branches, the internal openings of the primaries being 0·16–0·20 mm. apart measured vertically between successive whorls ; about 28 branches per verticil. Each branch shows a short primary of about 0·04 mm. diameter, directed upwards and outwards at about 60° from horizontal ; this gives rise to a single globular sporangial cavity of 0·10–0·13 mm. diameter (exceptionally larger), and to four secondary branches of 0·026 mm. diameter at their thinnest. These extend outwards and upwards at a lesser angle than the primaries, and at the outer surface they widen conspicuously to occasion the external pattern of closely-set rounded polygonal depressions of about 0·065 mm. diameter.

HORIZON. Palaeocene-Lower Eocene of Middle East.

MATERIAL. In Iraqi Kurdistan, from the Sinjar Formation of Banik and Kani Masa, Amadia (both Mosul Liwa) and Koi Sanjak (Erbil Liwa), from the Kolosh formation of Bekhme and Rowanduz (both Erbil Liwa), and from the Kolosh Formation of Surdash and Sinjar Formation of Pila Spi (both Sulemania Liwa). In southern Iraq, Basrah area, poorly preserved subsurface Palaeocene *Cymopolia* are probably of this species. *C. kurdistanensis* occurs in the Palaeocene/Lower Eocene Umm er Rhudhama Formation of the southwestern desert near Aidah, Diwaniyah Liwa. In south-east Arabia, from the Palaeocene of Jebel Abiad, and from the Batinah Coast, both Oman ; and from the Palaeocene of Jebel Faiyah, Sharjah, Trucial Oman. Very numerous fragmentary *Cymopolia* in the Palaeocene-Lower Eocene of the Middle East are probably referable to this, the commonest species.

REMARKS. *Cymopolia kurdistanensis* is a distinctive but typical species of its genus. Like the common European *C. elongata* (Defr.) Mun.-Chalm., it varies much in segment-size and proportions. It is, however, a smaller species ; L. & J. Morellet (1913 : 11) describe *C. elongata* segments as large as 12 mm. by 2·5 mm., and in this species the distance between successive whorls is larger (0·23–0·26 mm.) than found in *C. kurdistanensis*. An important difference lies in the secondary branches. The terminal widening described above for *C. kurdistanensis* does not occur in type area (Paris Basin) *C. elongata*. Hence the Middle East species shows an external pattern of shallow rounded-polygonal depressions (Pl. 10, fig. 2) whereas the European species is externally set with more abruptly-opening fine pores (Pl. 10, fig. 1). This is not a difference due to wear and tear, since abrasion of *C. kurdistanensis* would give a pattern more like that of *C. elongata*, and the European species is often perfectly preserved.

The Central American Eocene species *C. mayaense* (Johnson & Kaska, 1965) is said to be similar to *C. kurdistanensis* and *C. elongata*.

*C. kurdistanensis* is abundant at the localities listed and will no doubt be found elsewhere in the Middle East. Earlier Middle East records of *C. elongata* (Elliott 1955b ; 1960) are now considered to be of *kurdistanensis* (see p. 44).

### *Cymopolia barberae* sp. nov.

(Pl. 8, fig. 2)

DESCRIPTION. Units of 0·9 mm. external diameter (up to 1·22 mm. seen) internal diameter 43% of external, whorls showing 11 or 12 large near-spherical sporangia which occupy much of the wall-thickness, each sporangium associated with one very short primary branch and four secondaries. Diameter of the primary at the opening into the stem-cell 0·052 mm., sporangial diameter 0·130 mm., diameter of the outer expanded ends of the secondaries 0·055 mm.

HORIZON. Palaeocene-Lower Eocene of the Middle East.

HOLOTYPE. The specimen figured in pl. 8, fig. 2, from the Kolosh Formation (Palaeocene-Lower Eocene) of Surdash, Sulemania Liwa, Iraq. V. 52057.

PARATYPE. From the Sinjar Formation (Palaeocene-Lower Eocene) of Koi Sanjak, Erbil Liwa, Iraq. V. 52058.

OTHER MATERIAL. Fragments in the Palaeocene Umm er Rhudhama Formation of Al Ghurra, Wagsa, Diwaniyah Liwa, S.W. Iraq.

REMARKS. This dainty little species is uncommon ; when compared with *C. kurdistanensis* the lesser number of proportionally larger sporangia gives its characteristic appearance. Although only known in thin section it is distinctive. Its relation to *C. kurdistanensis* may be compared with that of the larger *C. rarifistulosa* L. & J. Morellet to *C. elongata*. *C. rarifistulosa*, also known from fragmentary material only, from the Miocene of Saucats, France, is described as having very large subspherical sporangial cavities, apparently less than half the number seen in *C. elongata*.

I have pleasure in dedicating this species to Mrs. Irene Barber, who has typed all my algal papers and reports.

## ***Cymopolia elongata*** (Defr.) Mun.-Chalm.

(Pl. 10, fig. 1)

1955b *Cymopolia* cf. *elongata* (Defr.) ; Elliott : 126.
1960 *Cymopolia elongata* (Defr.) ; Elliott : 225.

Re-examination of the numerous specimens from the Iraqi and Arabian Palaeocene/Lower Eocene, formerly referred to *C. elongata*, has shown that many may be identified as near-vertical cuts tangential to the inner surface (stem-cell surface) of *C. kurdistanensis*, or as fragments of examples showing the terminally-widening secondaries of *C. kurdistanensis*. The remainder comprises random cuts of *Cymopolia* sp. which are more likely to be *C. kurdistanensis* from their associations.

It is therefore concluded that the true *C. elongata* has not been met with in the Middle East collections studied, and that *kurdistanensis* is the typical and common Palaeocene and Eocene species of *Cymopolia* there, as *elongata* is in Europe.

## ***Cymopolia (Karreria)*** sp.

(Pl. 10, fig. 6)

1955b *Cymopolia* (*Karreria*) sp. ; Elliott : 126.

DESCRIPTION. Units of about 0·73 mm. external diameter and 0·39 mm. internal diameter, with whorls showing about 20 radially elongate, subpyriform sporangia of 0·156 mm. by 0·090 mm. each communicating with the interior by a very short primary branch, which also divides into four secondaries.

HORIZON. Palaeocene-Lower Eocene of Iraqi Kurdistan.

MATERIAL. Fragmentary thin-section material from the Kolosh Formation (Lower Eocene) of Surdash, and from the Sinjar Formation (Palaeocene-Lower Eocene) of Pila Spi, both Sulemania Liwa ; from probable Sinjar Formation, Sedelan, near Sulemania ; all localities in Iraqi Kurdistan.

REMARKS. This species is smaller than *Cymopolia* (*Karreria*) *zitteli* L. & J. Morellet from the Paris Basin Middle Eocene, shows fewer sporangia (20 against 24), and is proportionally thicker walled. By reason of the fragmentary nature of the material, the innermost layer of the wall, dividing the central stemcell from the cavities of the expanded primary branches, is usually missing. Although from the available evidence this is very probably a new species, it cannot be described as such from this material.

## Genus ***DACTYLOPORA*** Lamarck 1816

1940 *Dactylopora anatolica* Pfender : 237.
1966b *Dactylopora anatolica* Pfender ; Massieux : 118, pl. 3, figs. 1–3.

This large and handsome dasyclad, well-known from the Paris Basin Eocene, has not been met with in the collections studied by me, and the only Middle East record appears to be that of Pfender, quoted above, for the top Cretaceous (or possibly Palaeocene) of Turkey (Lutetian according to Massieux, but see p. 42 above).

## Genus ***DIPLOPORA*** Schafhäutl 1863

1960 *Diplopora* spp. Elliott : 219, 221.

The rich Triassic diplopore-limestones of central Europe and the Balkans are largely missing from the Middle East, at any rate from the areas studied by me. Although a thick development of marine Trias occurs in both Iraqi Kurdistan and Oman, original facies and subsequent dolomitization have combined to make these rocks almost completely barren of dasyclads.

The Upper Triassic Elphinstone group in Peninsular Oman yielded two alleged dasyclads during thin-section studies by M. Chatton, one of which was recorded (Elliott 1960) as *Diplopora* cf. *phanerospora* Pia. A re-examination of these specimens shows that they may not be dasyclads, and appear indeterminable. The evidence for R. G. S. Hudson's records of *Diplopora* as " not uncommon " and " occurs throughout " in different beds of the Asfal Formation of the Elphinstone Group (Hudson 1960 : 304) is not known to me, as Hudson did not make these extensive collections available for the study of the algae.

*Diplopora* sp. was also recorded (Elliott 1960) from the north Iraqi Permian. Although species of the genus have been described from the Permian of Japan, Turkey (Güvenç 1965) and elsewhere, the Iraqi specimens appear on re-examination not to be diplopores.

## Genus ***DISSOCLADELLA*** Pia 1936

Diagnosis. Small tubular dasyclads, usually thin-walled with wide stem-cell cavity and often annular, each verticil showing horizontal branches with a short distally-swollen primary dividing into a bunch of short secondaries, usually four in number and terminally widening.

### ***Dissocladella deserta*** sp. nov.

(Pl. 10, figs. 7, 8)

1960 *Dissocladella* sp. Elliott : 225.

Description. Small hollow calcareous cylinder, straight-sided with rounded ends, length about 0·75 mm., external diameter 0·39–0·47 mm., internal diameter 0·23–0·29 mm., verticils of about twelve branches each set 0·13 mm. apart vertically; branches showing a short primary, swollen to varying degree, and then dividing into four straight divergent secondaries which widen terminally to external pores.

Horizon. Palaeocene and Eocene of the Middle East.

Syntypes. The specimens figured in pl. 10, figs. 7, 8, from the Umm er Radhuma (Palaeocene-Lower Eocene) Formation of Wagsa and Aidah, Diwaniyah Liwa, S.W. Iraq. V. 52066, 67.

Other Material. Very numerous random thin-sections from the same horizon and general area, and subsurface in the Basra oilfields, S. Iraq. Also from the Palaeocene Seiyan limestone of Wady Ghabar, Hadhramaut, S. Arabia. It may occur in the Lower Eocene of Egypt (see below).

Remarks. This little *Dissocladella*, although very common, occurs in a porous microcrystalline dolomitic limestone and is always very poorly preserved, the structures showing as cavity-patterns amongst the pores and crystals. Although recognized some years ago, better material has not been found, and it is now described. It may well be the same as the " *Dactylopora* " sp. of Schwager (1883) from the Lower Eocene " Libyschen-Stufe " of Egypt, as remarked by Pia (1936b); the latter's comment on the relative sizes is an error.

### ***Dissocladella undulata*** (Raineri) Pia

(Pl. 11, figs. 4–6)

1936a *Dissocladella undulata* (Raineri) var. ; Pia : 4, pl. 1.
1960 *Dissocladella undulata* (Raineri) ; Elliott : 224.
1966b *Dissocladella undulata* Raineri ; Massieux : 115, pl. 2, figs. 2, 3.

Description (detail after Pia). Small hollow calcareous cylinder, length about 1·4 mm., external diameter 0·24–0·32 mm., internal diameter 0·08–0·10 mm., with close-set verticils showing about 8 primary branches. These are narrow at the junction with the stem-cell and widen outwards, finally dividing into about six secondaries of similar shape which widen to the outer surface.

Horizon. Upper Cretaceous, North Africa, Western Mediterranean and Middle East.

Material. From the subsurface Turonian of Musaiyib well, Hilla Liwa, Iraq ; also from the subsurface Turonian of Ras Sadr Well, Trucial Oman, Arabia.

Remarks. This little alga was described by Pia from the Cenomanian-Turonian of Libya. In the Middle East, at the two localities given above, it is fragmentary and very poorly-preserved, but in both cases is associated with *Trinocladus tripolitanus* Raineri and the codiacid *Boueina pygmaea* Pia as at the type-locality ; the range of this little algal microflorule is therefore Upper Cretaceous.

### *Dissocladella* sp.

Fragments of a small dasyclad showing branching of *Dissocladella* pattern have been noted in the north Iraq Maestrichtian, but are insufficient for description as a species. The occurrences are in the Tanjero Clastic Formation at Balambo (Sulemania Liwa), in the Aqra/Hadiena Limestone of Chalki Islam (Mosul Liwa), and in the subsurface Formation of Makhul no. 1 well (Mosul Liwa).

### *Dissocladella savitriae* Pia

(Pl. 11, figs. 1–3)

1936b *Dissocladella savitriae* Pia : 15, pl. 1, figs. 1–4, pl. 2, fig. 4, text-figs. 1–9.
1955b *Dissocladella savitriae* Pia ; Elliott : 126, 128, pl. 1, fig. 2.

Description. Thin-walled hollow calcareous cylinder, length of maximum fragment observed, 3·5 mm. ; (estimated length in life, up to 17 mm.), external diameter up to 1·7 mm., internal diameter from 69–78% of external in specimens measured, frequently about 71%. Successive verticils are represented by thin superimposed consecutive rings, of thickness up to 0·21 mm., feebly cemented together, which readily come apart and are themselves intrinsically fragile from their proportions. Rings are straight-sided within, convex without, giving the thallus an annular appearance externally. Each ring contains up to 44 globular or bluntly ovoid sporangial swellings of up to 0·13 mm. diameter : these are connected to the interior by a short primary canal of 0·026 mm. diameter and to the exterior by several bunched secondaries (4–6 from the type-description ; Middle East material does not conflict with this). The secondaries are from the sporangial swelling itself, not from the primary ; they are about 0·013 mm. in diameter and they widen to emerge on the external surface as pores.

Horizon. Palaeocene of Middle East ; " Danian " of India.

Material. Solid specimens (broken tubes) and random thin-sections from numerous localities. In Iraqi Kurdistan, from the Sinjar Formation (Palaeocene-Lower Eocene) of Banik (Mosul Liwa), Kolosh Formation (Palaeocene-Lower Eocene) of Bekhme and of Rowanduz (Erbil Liwa), and of Surdash (Sulemania Liwa). Probably present (very poor preservation) in the Palaeocene limestones of the south-western desert, Iraq. In Arabia, from the subsurface Lower Eocene, Dukhan no. 3

well, Qatar Peninsula ; from the Palaeocene of Jebel Faiyah, Trucial Oman ; and from the Palaeocene of the Batinah Coast, Oman.

REMARKS. This species was first described in great detail by Pia (1936b), his material coming from the Trichinopoly Danian, India (now regarded as Palaeocene). The Middle East material confirms his description, and also his reconstruction of the exterior, as all his material was in thin-section. His delightful reconstruction of the living algae in association with others (*op. cit.*, fig. 43) appears reasonable from the extensive Middle East material studied. It should be noted that for algae at any rate, the Tethyan Palaeocene appears to commence immediately after the Maestrichtian, the flora (including *D. savitriae*) extending up into the Lower Eocene ; this point is discussed in more detail later in this work.

## Genus *EOGONIOLINA* Endo

1953a *Eogoniolina johnsoni* Endo : 97–104, pl. 9, figs. 5–10.
1960 *Engoniolina johnsoni* Endo (*lapsus calami*) ; Elliott : 219.

REMARKS. As described by Endo, the Permian *Eogoniolina* was a club-shaped dasyclad with a lower, long cylindrical stem-like portion which extended up to a terminal expanded globular portion : this is well-shown in his reconstruction (*op. cit.*, text-fig. p. 102). His microphotographs, however, in this and later papers, usually show the pear-shaped or pyriform terminal portion only, and it was by comparison with this that the species was recognized in the Iraqi Permian by me. Subsequent re-study of this material shows that these specimens are in fact pyriform segments of *Mizzia velebitana*. At both the Iraqi and Japanese localities normal spherical examples of this common species are abundant. Without prejudice to Endo's interpretation of his original Japanese material, the Iraqi record is therefore withdrawn. *Eogoniolina pamiri* has been described from the Turkish Permian (Güvenç 1966b).

## Genus *EPIMASTOPORA* Pia 1923

DIAGNOSIS (emend. after Endo). Similar to *Pseudoepimastopora*, but with relatively long pores having the same width throughout their length.

### " *Epimastopora minima* Elliott " (= *Tauridium* sp.)

1956 *Epimastopora minima* Elliott : 327, pl. 1, figs. 1, 3.

This species was founded on fragmentary remains which occur abundantly in samples from at or near the base of the Satina Formation, or the middle evaporitic unit of the Chia Zairi or Iraqi Permian. The original remains are almost comminuted, and a re-examination in the light of subsequent studies on *Epimastopora* and *Pseudoepimastopora* suggested that the original generic allocation is doubtful. The description of the codiacid genus *Tauridium* (Güvenç 1966a) shows clearly that the Iraqi fossils are debris of a species of this genus, and not remains of a dasyclad.

### *Epimastopora* sp.

Fragmentary remains referred to the genus are said by Rezak (1959) to be abundant in the upper part of the Permian Khuff Formation (probably Upper Permian) of Dammam no. 43 well, Saudi Arabia.

## Genus *FURCOPORELLA* Pia 1918

DIAGNOSIS. Cylindrical dasyclad tube with successive verticils of horizontal paired straight radially divergent branches ; each pair of branches commences at a single opening on the interior : bifurcation occurs almost at once and the two divergent secondaries extend to the exterior.

### *Furcoporella diplopora* Pia

(Pl. 11, figs. 7–9)

1918 *Furcoporella diplopora* Pia : 209, pl. 1, figs. 1, 2 ; text-fig. 46.
1940 *Furcoporella diplopora* Pia ; Pfender : 242.
1956 *Furcoporella diplopora* Pia ; Elliott : 332, pl. 2, figs. 5, 6.
1960 *Furcoporella diplopora* Pia ; Elliott : 225.
1966 *Furcoporella diplopora* Pia ; Massieux : 121, fig. 4, pl. 4, figs. 8, 9.

DESCRIPTION. Hollow cylindrical calcareous tube, long and straight-sided ; length (incomplete) up to 5·0 mm. seen, with external diameter of up to 0·6 mm., and corresponding internal diameter of 0·325 mm. ; d/D ratio on smaller specimens from 48–55%. Numerous regular horizontally-set verticils of paired branches ; about 11 per mm. of tube-length. Each verticil shows about 8 pairs, each commencing on the inside of the tube as a single large pore : in transverse section the very short primary canal is seen to divide at once into two secondaries, which diverge at an obtuse angle varying from 45–70° and proceed, widening slightly, in a straight course to the periphery where they widen sharply to emerge as external pores. In vertical section only a succession of straight, coarse, waisted pores is seen ; in an oblique vertical cut the plane of section, traversing successive near-identical pore-pairs outwards, shows that the canals widen transversely but not vertically before splitting into two.

HORIZON. Middle Eocene of Central and Southern Europe : Palaeocene and Eocene of Middle East.

MATERIAL. In Iraqi Kurdistan, from the Sinjar Formation (Palaeocene-Lower Eocene) of Banik and (subsurface) Gullar no. 1 well (both Mosul Liwa) and Kashti (Sulemania Liwa) ; from the Kolosh Formation (Palaeocene-Lower Eocene) of Rowanduz and Koi Sanjak (both Erbil Liwa), and of Sedelan (Sulemania Liwa). In southern Iraq, fragmentary and ill-preserved remains from the Palaeocene Ghurra Beds of the Umm er Rhudhama Formation, Wagsa (Diwaniyeh Liwa) and elsewhere in the southwestern Iraqi desert. In Arabia, from the Palaeocene-Lower Eocene of the Batinah Coast, Oman ; from the Palaeocene of Jol Ba Hawar, and the Palaeocene-Lower Eocene of Aqabar Khemer, Hajar, both Hadhramaut. See also Hadhramaut record of Beydoun (1960 : 146).

REMARKS. Pia's type-material was from the Austrian Middle Eocene ; the species also occurs in the Middle Eocene of Egypt and Syria (Pfender 1940), Iraq (Sulemania district), and South Oman (Jebel Tanamir). The Middle Eastern Palaeocene-Lower Eocene examples listed above correspond in structure to the type material, but reach a larger size in many if not all examples. External diameters quoted by Pia and Pfender, for example, are 0·26–0·34 mm. and 0·35–0·45 mm respectively, whilst the older Iraqi material described above may attain a corresponding dimension of 0·6 mm.

Although *F. diplopora* is represented fossil by stout calcareous tubes, the structures preserved afford but an imperfect record of those of the living plant. The larger examples are no better than the smaller in this respect. All indicate a very short primary branch and two secondaries : presumably these latter, which are seen to expand as they reach the outer edge of the zone of calcification, branched further into a spray of uncalcified tertiary branchlets : there is no evidence at all of the sporangia. The relationships of the genus remain doubtful.

## Genus ***GRIPHOPORELLA*** Pia 1915

DIAGNOSIS. Very thin-walled cylindrical, club or ovoid shaped dasyclad calcifications, with numerous simple perforations ; so thin-walled that the perforation-structures are insufficient for elucidation of the branch-structure.

REMARKS. *Griphoporella* is an inclusive name for those dasyclads whose calcification was confined to a thin hood-like sheet which affords no clue to the detailed branch-structure, size of stem-cell, etc. of the original plant. The species referred to it range from Triassic to Palaeocene and may be quite unrelated phylogenetically; see especially under *G. arabica* below.

### ***Griphoporella*** cf. ***perforatissima*** Carozzi

(Pl. 12, fig. 4)

1955b *Griphoporella perforatissima* Carozzi : 203, text-fig. 1a–d.
1960 *Griphoporella perforatissima* Carozzi ; Elliott : 223.

DESCRIPTION. See under remarks.

HORIZON. Top Jurassic and bottom Cretaceous of Europe and Middle East.

MATERIAL. Fragments from the subsurface Upper Jurassic Najmah Formation of Kirkuk Well no. 117, Iraq ; in Arabia, from top Jurassic and bottom Cretaceous levels at Haushi, Southern Oman, and from the Lower Cretaceous of Burun, Wady Hiru Basin, Hadhramaut.

REMARKS. The material listed above is extremely fragmentary, but is of a thin-walled dasyclad, circular in cross-section, and showing very many simple pores. It is similar in age-occurrence to Carozzi's *G. perforatissima* (Portlandian-Berriasian), and has a similar appearance in random cut to the type-figures (Carozzi 1955b, fig. 1a). The pores are 0·030–0·040 mm. in diameter, and about 0·020 mm. apart. This is larger than in *G. perforatissima* (0·015–0·019 mm. diameter set 0·009–0·012 apart), and would give a pore-count per square millimetre of about one third that quoted for the type. It is however closest to this rather than to the other Upper Jurassic species *G. undulata* Pia, *G. irregularis* Pia and *G. ehrenbergi* Bachmeyer (comparison-table of Carozzi, *op. cit.*, : 206). In view of this correspondence, and of the inadequacy of the Middle East material for full description, it is given the qualified determination above.

### " *Griphoporella arabica* Pfender 1938 "<br>(*Ovulites maillolensis* Massieux)

(Pl. 12, figs. 1, 3)

1938 *Griphoporella arabica* Pfender : 69, pl. 9, figs. 5–8.
1940 *Griphoporella arabica* Pfender ; Pfender : 241.
1955b *Griphoporella arabica* Pfender ; Elliott : 126.
1966a *Ovulites maillolensis* Massieux ; Massieux : 241, pls. 1, 2.

DESCRIPTION. Broadly club-shaped or elongate-ovoid, thin-walled, hollow calcification, external diameter up to 0·9 mm., length not known but at least three times diameter from oblique-longitudinal sections. Wall thickness up to 0·078 mm., perforated by close-set straight-sided pores of about 0·013 mm. diameter, widening very slightly at the external surface, and set 0·006–0·013 mm. apart as seen in section.

HORIZON. Paleocene and Eocene of France, North Africa and Middle East.

MATERIAL. In Iraqi Kurdistan, from the Kolosh Formation of Koi Sanjak (Erbil Liwa) and from the Sinjar Formation of Sirwan (Sulemania Liwa), both Palaeocene-Lower Eocene. In Arabia, from the Palaeocene-Lower Eocene of Sahil Maleh, Batinah Coast, Oman, and from the Seyun Limestone development of the Umm er Rhudhama Formation (Palaeocene) of Ma'adi Pass, east of the Mukulla-Shihr road, Hadhramaut.

REMARKS. The species was described by Pfender from the Lower Eocene of Morocco, and recorded by her from the Middle Eocene of Egypt and Syria ; a related species was mentioned from Madagascar. Pfender's specimens were smaller, with external diameters of up to 0·4–0·58 mm., and thinner-walled (0·040–0·050 mm. wall-thickness), but the pores and pore-spacing were similar, and it seems unnecessary to refer the Middle East specimens to a new species because some individuals attain a larger size.

In her type-description of the French Lower Eocene codiacean *Ovulites maillolensis* Massieux (1966a) records that from preliminary studies on thin-sections she determined this species as *Griphoporella arabica* Pfender. Further studies on whole (isolated) segments or articles, and comparison with the classic and beautifully-preserved Paris Basin species (Munier-Chalmas 1881) convinced her that these fossils were remains of *Ovulites*, as was also Pfender's North African material. The new species was created as Pfender's type-material could not be traced and the original description was inadequate in view of the new evidence available.

I agree with Mlle. Massieux's conclusions. The Middle Eastern material described above was identified by comparison with Pfender's accounts (1938 : 1940), and is well-known in the literature as *G. arabica*. It shows no diagnostic dasyclad characters to refute the new allocation (and indeed the genus *Griphoporella* itself is a receptacle for various inconclusive dasyclads, probably not closely related). The description of this codiacean is retained here for comparison with dasyclads as, unlike the problematic *Thaumatoporella*, it is well-known in dasyclad literature.

## Genus *GYROPORELLA* Gümbel 1872

1960 *Gyroporella* cf. *maxima* Pia ; Elliott : 219.

Many Permian species of *Gyroporella* have been described from Japan, also one from the U.S.A. (Johnson 1963), and one from Turkey (*Gyroporella* sp., Bilgütay 1959). My record of *G.* cf. *maxima* from Iraqi Kurdistan was based on a single random section : no further material has been found to substantiate this, and the determination is therefore abandoned.

## Genus *INDOPOLIA* Pia 1936

Diagnosis. Calcareous tubular dasycladacean showing verticils of branches each of which consists of one primary dividing into two secondaries set one above the other (vertically) : in fertile whorls each branch gives rise to two sporangia.

### *Indopolia satyavanti* Pia
(Pl. 12, fig. 2)

1936 *Indopolia satyavanti* Pia : 20, pl. 1, figs. 1, 5–13, text-figs. 17–19.

Description (details after Pia). Hollow calcareous elongate tubes, length unknown but perhaps 5·0 mm. or more ; external diameter (fertile part) 0·86–1·16 mm., with internal diameter of 44–49% external ; (sterile part) 0·55–0·98 mm. external, internal 47–55%. Fertile whorls of perhaps 28 branches ; each branch consists of one primary, which is set obliquely at 60–70° from the horizontal : this divides into two secondaries set nearly horizontally one above the other and reaching the outer surface almost horizontally i.e. nearly at right angles to it. The secondaries increase in diameter to become funnel-shaped and almost in contact at the external surface, and occasion a polygonal pattern there. Two small pyriform sporangia (diameter 0·09–0·12 mm.) are attached at or near the branch-junctions. The sterile whorls do not of course show sporangia, but the branches are similar.

Horizon. " Danian " of India ; Palaeocene of Middle East.

Material. In Iraqi Kurdistan, from the Sinjar Formation (Palaeocene-Lower Eocene) of Banik, Mosul Liwa, where it is uncommon. Possibly also in Arabia, from the Upper Palaeocene of the Batinah Coast, Oman (poorly preserved).

Remarks. Pia's material was from the Trichinopoly Danian of India, where the species was abundant and described as the " almost constant companion of *Dissocladella savitriae* ". In the Middle East, although *D. savitriae* is widespread, and with it the non-dasyclad alga *Parachaetetes asvapatii* Pia, also described from the same Indian locality, *Indopolia* is very rare. In Kurdistan it was found in the present investigation only at Banik, and there is possibly one other record from Oman (see above).

The Banik material shows sterile whorls only. A measured example has an external diameter of 0·455 mm., and internal diameter of 0·221 mm., or 49% ; although a little smaller, the section is closely similar to that of a sterile specimen figured from the type-material (Pia 1936b, pl. 1, fig. 11).

Although the algal sampling for the present study was far from exhaustive, the poor showing of *Indopolia* in the Middle East, when compared with its Indian associates *Dissocladella* and *Parachaetetes* is probably significant. The rare occurrence, of sterile remains only so far, suggests that it did not manage to spread westwards along Tethyan coasts. *Indopolia feddeni* Rao & Vimal (1955) is uncommon in the Palaeocene of Pakistan. Perhaps *I. satyavanti* is replaced in the algal economy by the prolific *Cymopolia kurdistanensis*, not known from the Trichinopoly beds.

## Genus ***LARVARIA*** Defrance 1822

1960 *Larvaria* sp. Elliott : 223.

The writer's 1960 record of *Larvaria* sp. from the Kurdistan Maestrichtian, is based on a worn example of *Cymopolia tibetica* Morellet (see above, under *C. tibetica*). *Larvaria* sp. was recorded by Barthoux (1920) from the Lower Eocene of Suez, Egypt.

## Genus ***MACROPORELLA*** Pia 1912

1960 *Macroporella* sp. Elliott : 219, 221.

My 1960 records of this genus, from the Permian of Iraqi Kurdistan and from the subsurface Upper Triassic of Qalian no. 1 well, Mosul Liwa, Iraq, were made on scarce and poorly-preserved material. No further specimens of either have been found. The Permian record is now discounted, and the Triassic one remains very doubtful.

Jurassic and Cretaceous species formerly referred to this genus are now described under *Pianella* and *Acroporella*.

## Genus ***MORELLETPORA*** Varma 1950

1950 *Morelletpora nammalensis* Varma : 207, figs. 1, 2.
1955 *Morelletpora nammelensis* Varma ; Varma : 101–111, 2 pls.
1960 ?*Morelletpora nammelensis* Varma ; Elliott : 225.

My 1960 record of this species (a queried determination) from the Palaeocene-Lower Eocene of Iraq, based on a random section, proves to be from material of Middle Eocene age and is not further dealt with here.

## Genus *MIZZIA* Schubert 1907

1907 *Mizzia* Schubert : 212.
1908 *Mizzia velebitana* Schubert : 382, pl. 16, figs. 8–12.
1920 *Mizzia* Schubert ; Pia : 18.
1942 *Mizzia* Schubert ; Johnson and Dorr : 63.
1959b *Mizzia* Schubert (emend) ; Rezak : 534.

Diagnosis (after Rezak). " The thallus is composed of segments joined end to end in a loosely articulated fashion. The segments are generally disaggregated and are rarely found joined together like a string of beads. Individual segments are spheroidal to cylindroidal or pyriform and are composed of a central cavity (generally barrel-shaped) through which the stipe extended. Radiating from the central cavity are simple expanding, unbranched rays arranged in regular, alternating horizontal rows. At the periphery of the segment the expanded rays are in mutual contact. The alternating nature of the rays and their crowding at the periphery gives rise to a hexagonal (honeycomb) pattern on the surface of each segment. Species are based on shapes and dimensions of the segments and their internal structures ".

### *Mizzia velebitana* Schubert 1908

(Pls. 13, 14)

1908 *Mizzia velebitana* Schubert : 382, pl. 16, figs. 8–12, text-fig. 5.
1933 *Mizzia velebitana* Schubert ; Kühn : 155.
1955a *Mizzia velebitana* Schubert ; Elliott : 83.
1959b *Mizzia velebitana* (Schubert) emend. Rezak ; Rezak : 536, pl. 72, figs. 1–3, 5, 6, 8–10, 12, 13, 15–19.
1959 *Mizzia velebitana* Schubert ; Bilgütay : 49, pl. 1, figs. 2–3, pl. 2, fig. 1.
1960 *Mizzia velebitana* Schubert ; Elliott : 219.

Description (from Iraqi material). Hollow, calcareous, bead-like segments, spheroidal, ovoid or elongate-ovoid, pear-shaped or pyriform ; length up to 2·0 mm., external diameter (maximum) up to 2·25 mm., internal diameter measured in the same transverse plane, 60–70% of external ; polar (proximal and distal) openings or gaps in the segment, from 0·18–0·36 mm. diameter in a large segment. Wall perforated by about 12 successive horizontal verticils of coarse pores (short branches), usually 20–25 per verticil over all but the polar ends of the segment. The pores of each verticil are set alternately to those of adjacent verticils, to give the external and surface-tangential section appearance of a large closely-set hexagonal mesh. In vertical section the branches are seen to be wedge-shaped, widening slowly from interior to exterior, and usually of about 0·18 mm. diameter in large examples. Externally the pores may be open or closed : in the latter case they are roofed by a thin externally-convex projecting calcareous covering.

Horizon. Permian ; North America, North Africa, Europe, Asia.

Material. In Iraq, common throughout most of the thickness of the Zinnar Formation and the Darari Formation, and occurring rarely in the intermediate Satina Evaporite Formation ; that is, probably from within the upper part of the Lower Permian to near the top of the Upper Permian (but see under Stratigraphic

Ranges) : abundant over this range in much of the material from the sampled surface sections of Ora and Harur, Mosul Liwa, and also from subsurface Upper Permian in Atshan no. 1 well, in the south of Mosul Liwa (see Hudson 1958 ; Dunnington, Wetzel & Morton 1959). Elsewhere in the Middle East Permian recorded by Kühn (1933) from Iran, by Bilgütay (1959) and Güvenç (1965) from Turkey and by Rezak (1959b) from Saudi Arabia.

REMARKS. *Mizzia velebitana* is a characteristic Permian microfossil of circum-global distribution : central and southeastern Europe and north Africa, the Middle East, Sumatra and Japan, and the southwestern United States. Its distribution was plotted and compared by Pia (1937) with that of the living warm-water codiacid alga *Halimeda tuna* Lmx. Extensive bibliographies of these occurrences have been given by Pia (1937), Johnson & Dorr (1942) and Rezak (1959b) : that given above refers mostly to the Middle East occurrencies.

Rezak (*op. cit.*) has discussed the genus and type-species in detail, and given revised diagnoses for them. That for the genus is quoted above in full : the description given here is based on the material from Iraqi Kurdistan studied by me. When compared with the equivalent species-diagnosis of Rezak, which was a synthesis of previous records and his own study of Saudi Arabian material, it is seen that the Iraqi specimens do not attain the maximum size (length breadth and pore-diameter) quoted for the species elsewhere, but are larger in size and equal in pore-diameter to the Saudi Arabian specimens.

Rezak transferred *Mizzia* to the dasyclad tribe Diploporeae, after clear demonstration of the regular arrangement of the side-branches : I agree with this. All previous workers have followed Schubert (1908 : 383) in supposing the stem-cell in each globular *Mizzia*-segment to have filled the central cavity, so that the primitive unbranched side-branches commenced approximately where the inner calcareous wall is seen in the fossil (e.g. Pia 1920 : 21 ; Rezak 1959 : 534). Theoretically it is possible that a thinner central stem-cell gave rise to thin radiating branches which thickened terminally and were calcified only around the thicker peripheral portions: a comparable arrangement exists in the Recent *Bornetella*. Although this is a much more complex dasyclad than the Permian *Mizzia* is believed to have been, it was the comparison-genus used by Wood (1943) in reconstructing the non-calcified parts of the still older dasyclad *Koninckopora* from the Carboniferous. However, the serial arrangement of connected *Mizzia*-segments (a phenomenon known from occasional short strings of consecutive fossil segments from various localities, though not yet from Iraq) is believed to indicate a jointed plant somewhat like the living *Cymopolia* (Pia 1920 ; Rezak 1959b). Mechanically, the *Bornetella*-interpretation would result in segments which would probably be extremely fragile for the assumed mode of life of *Mizzia*, even in quiet waters : *Bornetella* itself is a single non-segmented dasyclad, attached by a short holdfast. It therefore seems more likely, though not definitely known, that the older interpretation is correct. Taken in conjunction with the abundance of the fossil segments and their wide distribution, this would make *Mizzia* a common dasyclad of primitive structure, vigorous growth, and thick juicy stem-cell. This is consistent with the picture set out in the section on ecology.

Several species, other than the type-species, have been described for *Mizzia* : e.g. *M. yabei* Karpinsky, *M. japonica* Karpinsky, *M. minuta* Johnson and Dorr, *M. bramkampi* Rezak, *M. cornuta* Kochansky and Herak. These are based primarily on differences in segment shape and size, and sometimes on branch-structure. Morphologically such species are recognizable taxonomic entities. However, usually they seem to be associated with *M. velebitana*, and, so far as one can tell from the literature, to be also a minority of the local *Mizzia*-populations. Bearing in mind the variation of segments within a plant, and the environmental local variations in plant-populations, as evidenced by the study of Hillis (1959) on Recent *Halimeda*, the genus with which Pia compared *Mizzia* for distribution, it is felt that mostly they may well be, in the botanical sense, of varietal status at best. *M. bramkampi* Rezak, with its distinctive funnel-shaped branch-structure, appears the one most likely to be a distinct local species. This was described from Saudi Arabia (Khuff formation ; probably Upper Permian) : other species recorded from the Middle East are *Mizzia yabei* and *M. minuta* from Turkey (Bilgütay 1959) ; also *M. tauridiana* (Güvenç 1965).

All the Iraqi Kurdistan specimens seen are referred here to *M. velebitana*. Occasional specimens resembling *M. yabei* are considered atypical segments of the type-species. One or two specimens resemble some of Endo's figured *Eogoniolina*, but not his reconstruction, and there is no associated evidence to show that these are other than *M. velebitana*. Also in the Iraqi material are various specimens corresponding to *M. cornuta* Kochansky & Herak (1960), a species in which the external bulging terminations of the branches (or pores) are roofed over by a thin projecting convex calcareous covering. Setting aside worn material, and many fossil *Mizzia* segments are recognizably abraded, it would seem that in apparently well-preserved material the pores can be open or closed. This point was discussed in some detail by Pia (1920), who suggested that this difference in the otherwise homogeneous assemblage of segments might possibly be due to the covered pores having contained sporangia. He also drew attention to the effect of light-intensity, varied by shading due to stones, etc. on the calcification of living algae, and to the differences in the calcification of the older and younger segments of the same plant. I believe that in the case of *Mizzia* light intensity may have influenced this calcification ; in view of what is known of this phenomenon in modern algae, and the random distribution of specimens with roofed pores in *Mizzia*, the character does not seem worthy of occasioning a distinct specific name. It is true that Kochansky & Herak (*op. cit.*, text-fig. 7) give a longer range for *M. cornuta* than for *M. velebitana* in the Jugoslav Permian, but in Iraq at any rate *M. cornuta* is represented by a small minority of specimens within the main range of *M. velebitana*.

### Genus ***MUNIERIA*** Deecke 1883

DIAGNOSIS. Dasyclad with thin central stem-cell giving rise to regularly and widely spaced verticils of thin straight horizontal radial side-branches, the whole thickly calcified to give a rigid structure of centrally fused calcified successive whorls.

### *Munieria baconica* Deecke

(Pl. 15, figs. 3–8)

1883 *Munieria baconica* Deecke : 9, pl. 1, figs. 4–8.
1920 *Munieria baconica* Hantk. ; Pia : 144, pl. 7, figs. 16–26, text-fig. 25.
1948 *Munieria baconica* Hantk. ; Carozzi : 351, pl. 6, fig. 3, text-fig. 48.
1955b *Munieria baconica* Deecke ; Elliott : 126.
1955a *Munieria baconica* Deecke ; Carozzi : 47, text-figs. 10–12.
1958a *Munieria baconica* Deecke ; Elliott : 255, pl. 45, fig. 4.
1958 *Munieria baconica* Deecke ; Radoičić : 79, pl. 1, text-figs. 2, 3.
1960 *Munieria baconica* Deecke ; Elliott : 223, 224.
1962 *Munieria baconica* Hantken ; Delmas & Deloffre : 216, pl. 3.

Description (based on Pia and Carozzi). Dasyclad with external diameter (at verticil-level) of 0·6–1·6 mm., internal diameter (stem-cell) of 0·05–0·26 mm. ; verticils set apart at distances of about 66% of their diameter. Each verticil horizontal, consisting of about 16 straight radial simple branches of about 0·08–0·09 mm. median diameter. Verticils and stem-cell thickly calcified, to give successive thick horizontal discs at verticil level, joined to the thick stem-cell calcification. Occasionally calcification unites the discs peripherally.

Horizon. Upper Jurassic–bottom Cretaceous of Switzerland and Jura ; top Albian of France (Delmas & Deloffre 1962) ; Upper Jurassic–Lower Cretaceous of Italy (Sartoni and Crescenti 1962). Lower Cretaceous of Spain, central and south-eastern Europe and Middle East.

Material. In the Middle East, probably common but always fragmentary. Seen in the Lower Cretaceous of Iraqi Kurdistan, Barremian to Aptian : Sarmord Formation, Barremian level, and Qamchuqa Formation, Albian level of Surdash (Sulemania Liwa) ; Qamchuqa Formation of Ru Kuchuk and Rowanduz, Mosul and Erbil Liwas and Zibar-Isumeran, Mosul Liwa ; Aptian, Albian and Barremian–Aptian levels respectively. In southern Arabia, Lower Cretaceous of Hadhramaut (e.g. Mintaq, Wady Hajar ; Barremian–Aptian), and Lower Cretaceous of Oman (e.g. Haushi, South Oman).

Remarks. Originally described by Deecke (1883) from the Aptian of Hungary. Later Pia (1920) attempted a reconstruction of this alga from thin-section material. Carozzi (1948 ; 1955a), gave line drawings of random sections of Swiss material : he recorded it from Upper Kimmeridgian to Valanginian. Radoičić (1958) gave excellent photographs of random sections of Jugoslav material from the Valanginian-Hauterivian.

My Middle East records (Elliott 1955b ; 1958a ; 1960) record the species from Barremian to Albian.

This Middle East material is extremely fragmentary. It occurs in the Lower Cretaceous " debris-facies " (Elliott 1958a), an off-shore deposit in which small calcareous scraps, largely algal, form an appreciable part of the sediment. Much of this debris is unidentifiable, but *Permocalculus* spp., *Actinoporella podolica*, and *Salpingoporella arabica* can be recognized : their study was greatly facilitated by the occasional discovery of whole or near-complete segments, verticils or individual thalli. *Munieria* is the most fragmentary of all : it survives as little looped or hooked scraps. These have been identified by reference to the figured random cuts of debris of Carozzi (1955a), supplemented by the figures of Radoičić (1959), rather than by comparison with Pia's topotype material (1920). Since the calcification of *Munieria* is proportionally heavier than that of the comparable *Actinoporella*, it is reasonable to suppose that in life it was more porous and hence more fragile when the skeleton was dismembered.

It seems not unlikely that the combined records of the various European and Middle East occurrences, Kimmeridgian to Albian, embrace more than one species: differences in average size and proportions, number of branches per verticil, etc. are suggested by the random thin-sections of various authors (e.g. compare the figures of Radoičić 1958 with those of Delmas & Deloffre 1962). Such a revision would have to be made on much better material than has been available for the present study : the Middle Eastern debris, therefore, is here referred to *M. baconica*, the only described species. The alleged figure of a complete verticil of a Middle East *Munieria* (Elliott 1958a, pl. 48, fig. 1) is an error.

### Genus *NEOMERIS* Lamouroux 1816

Diagnosis. Calcified tubular dasyclads showing successive verticils of branches in which each primary branch divides into a stalked sporangium and two secondary sterile branches set in the same plane : the calcification surrounds the sporangia and secondaries, but not the primaries, which are weakly calcified or uncalcified.

### *Neomeris cretacea* Steinmann
(Pl. 15, figs. 1, 2)

1899 *Neomeris* (*Herouvalina*) *cretacea* Steinmann : 149, text-figs. 14–18.
1955 *Neomeris cretacea* Steinmann ; Elliott : 126, pl. 1, fig. 7.
1960 *Neomeris cretacea* Steinmann ; Elliott : 223.

Description (from Middle East material). Slightly irregular tubular calcified dasyclad of 1·10–1·25 external diameter, internal diameter 41–48% external, length (incomplete) seen to 6 mm. ; walls showing close-set verticils of neomerid groupings of sterile branches of about 0·050 mm. diameter and ovoid sporangia of 0·180 mm. length and 0·090 mm. diameter.

Horizon. Upper Cretaceous of Mexico, Iraq and possibly from circum-Mediterranean ; top Albian of France (Delmas & Deloffre 1962).

Material. Two good sections only ; from the Bekhme Formation (Maestrichtian) of Chia Gara, and from the Aqra/Bekhme Limestone development (Campanian-Maestrichtian) of Gal-i-Mazurka at Amadia ; both localities in Mosul Liwa, Iraq. Numerous random thin-sections, completely or near-completely recrystallized, possibly of the same species, possibly of other species of this genus, occur in the Upper Cretaceous Limestones of Iraqi Kurdistan.

Remarks. Steinmann's species was described from the Cenomanian of Mexico (Steinmann 1899). His specimens showed a larger size than the Iraqi material :

up to 2 mm. external diameter and an estimated length of 10 mm. Some of the indeterminable recrystallized Iraqi specimens reach this diameter. Dimensions of branches and sporangia are comparable in the two occurrences. Fragmentary Cretaceous material referred to the genus *Neomeris* has been described or recorded from the Danian of Morocco (Pia 1932), Cenomanian of Libya (Pia 1936a), Upper Cretaceous of Morocco (Pfender 1938) and Cenomanian–Turonian of Spain and Southern France (Pfender 1940). See also Massieux (1966b : 115, fig. 1).

Although the Iraqi evidence is very limited, it seems reasonable, in view of the measurements taken, especially of the sporangia, to refer the specimens to Steinmann's species. There is a resemblance between Pl. 14, fig. 2 of the present work and Steinmann's text-fig. 15, corresponding apparently to similar orientation of section and to individuals of similar development. If published dimensions and measurements on illustrations are combined, the Iraqi specimens are seen to be thicker-walled (d/D 41–48%) than the type-material (d/D 48–60%), but this is closer than the very thin-walled French Albian specimens (d/D 62–78%) of Delmas & Deloffre (1962), which should probably be referred to a new species, and which compare in this respect with the Lower Cretaceous *N. pfenderae* Konishi and Epis (1962). The difficulties of comparing species based on different kinds of fossil evidence (whole or fragmentary, few or numerous well-preserved specimens, etc.) are especially marked with Cretaceous *Neomeris*. It may be that further material would show the Iraqi form, which is Senonian-Maestrichtian, to be a different species from the type which is Cenomanian-Turonian, but it is closer to it than are the older species.

## Genus ***PAGODAPORELLA*** Elliott 1956

Diagnosis. Small calcified tubular dasyclad showing externally vertical rows of slightly alternating large pores with small interpore portions, the pores widening sharply from within outwards.

### ***Pagodaporella wetzeli*** Elliott

(Pl. 17, figs. 9, 10)

1956 *Pagodaporella wetzeli* Elliott : 333, pl. 2, figs. 3, 4.

Description. Small tubular calcified dasyclad ; observed length (incomplete) 1 mm., external diameter about 0·34 mm., internal diameter 58–66% of external, octagonal in cross-section. Successive verticils of about eight branches each, 11–14 verticils per mm. of tube-length ; branches represented by large pores, externally roughly hexagonal and separated only by narrow interstices of calcareous wall-material : internal pore-diameter 0·040–0·050 mm., widening sharply to an extrenal diameter of 0·065–0·090 mm., so that in vertical section the wall-material shows as small well-spaced triangles or wedges, the apices outward. Externally the large window-like pores give an appearance of slightly irregular vertical rows.

Horizon. Palaeocene–Lower Eocene of Iraqi Kurdistan.

Material. Solid and thin-section specimens from the Kolosh Formation

(Palaeocene) of Bekhme, Erbil Liwa ; thin-section material from the Sinjar Formation (Palaeocene–Lower Eocene) of Banik, Mosul Liwa, and from the Kolosh Formation (Palaeocene–Lower Eocene) of Sedelan, Sulemania Liwa ; all in northern Iraq.

REMARKS. *Pagodaporella* is the fossil record of a little, thick- branched dasyclad which calcified only near the stem-cell, at the base of the branches, no traces being left of branch-structure nor of sporangia : its relationships are therefore uncertain. The peculiar thin-section appearance, with more gaps than skeleton, was known for some time before the discovery of solid specimens, which when sectioned led to the elucidation of the random sections.

The living *Dasycladus* (*D. clavaeformis* (Roth) Ag. ; Mediterranean) shows a comparable limited calcification which is however not identical. Here each verticil shows 10–15 branches, branched outwardly to the third degree and also bearing sporangia : the primaries narrow markedly at their inner junctions with the stem-cell, and between their points of insertion the fleshy stem-cell wall is markedly thickened inwardly, within the stem-cell itself, and thinly calcified externally.

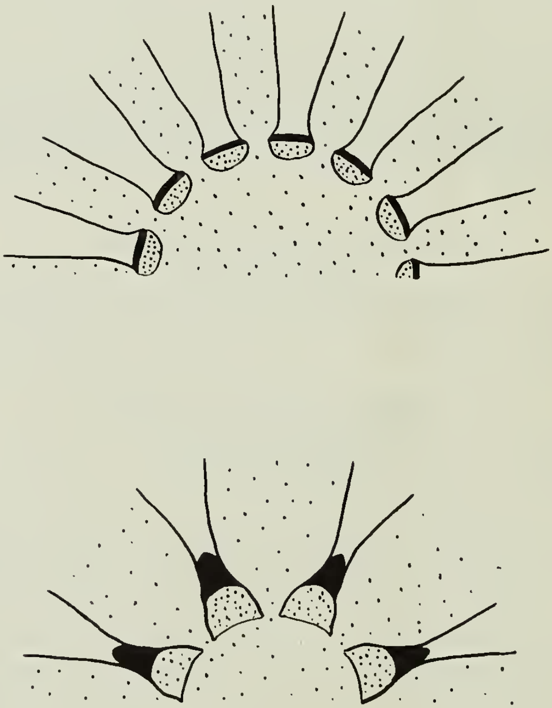

FIG. 4. Diagrammatic transverse sections of *Dasycladus* (above) and *Pagodaporella* (below, hypothetical). Greatly enlarged, ×150 approx. Spaced stipple, plant tissue ; close stipple, thickened portions of stem-cell wall ; black, calcareous structure. Each section shows half the stem-cell with branches attached. The reconstruction for *Pagodaporella* explains the possible origin of the structure found fossil.

(Fritsch 1935 : 388). If fossilized this structure would give a very thin cylindrical test perforated by alternating pores. If however calcification were to develop further outwards between the swelling primaries, wedge-shaped interstices would develop, but much closer than in *Pagodaporella*. Since dasyclad branches are normally thin at the points of origin and then swell out, it may be that *Pagodaporella* was like *Dasycladus* but with fewer, thicker branches, and that a thickened fleshy stem-cell wall bulged *outwardly* rather than inwardly between branches and was then calcified more heavily than in *Dasycladus*. (Fig. 4). If this were so the *Pagodaporella* skeleton would represent the calcification between swelling primaries, but separated from the level of their points of insertion by the thickness of the externally intermittently swollen stem-cell wall. In this way the present internal cavity of the fossil would be a record of the maximum diameters of the stem-cell, and the thin points of insertion of the primaries would have been some little distance inside the cavity.

*Pagodaporella* is therefore tentatively referred to the Dasycladeae : we know that branched choristospore laterals, seen in living genera of the tribe, had already evolved by the Palaeocene from the evidence of heavily calcified genera, e.g. *Cymopolia*. This structure may well have been present in *Pagodaporella*, even if no calcified evidence remains, and it may be that the genus is ancestral to the living *Dasycladus* : reduction of calcification and increase in number of branches seems a likely evolutionary trend.

## Genus ***PALAEODASYCLADUS*** Pia 1927
## (***PALAEOCLADUS*** Pia 1920 *non* Ettingshausen 1885)

DIAGNOSIS. Elongate near-cylindrical club-shaped calcified dasyclad, showing numerous successive verticils of strongly-inclined branches : the branches show primaries, dividing into clusters of four to six secondaries, in turn dividing into clusters of four to six tertiaries. All branch-segments slightly swollen : successive verticils show a progressive elaboration of branch-detail.

### ***Palaeodasycladus mediterraneus*** Pia
### (Pl. 16)

1920 *Palaeocladus mediterraneus* Pia : 118, pl. 6, figs. 1–5 ; text-fig. 22.
1927 *Palaeodasycladus mediterraneus* Pia : *in* Hirmer's " Handbuch der Paläobotanik ", Bd.1 79.
1960 *Palaeodasycladus mediterraneus* Pia ; Elliott : 221.

DESCRIPTION (from Middle East material). Near-cylindrical elongate club-shaped dasyclad, length 7–8 mm. or more, external diameter increasing slowly and regularly from 1 mm. or a little less at the base to about 2·4 mm. in the terminal expansion, internal diameter from about 50% of corresponding external measurement at the base to about 30% or less at the terminal expansion *i.e.* the stem-cell cavity diameter increases only slowly compared to the external measurement. Close-set successive verticils of branches, 5 or 6 per mm. of measured length in mid-thallus : each verticil with up to 20 branches, in which the primaries are inclined outwards and upwards at 45–50° from the horizontal, and the subsequent branchlets curve outwards at a lessening angle. Each primary gives rise to four or more secondaries, and these in turn to about the same number of tertiaries ; all branches and branchlets are sharply constricted terminally, slightly swollen between to give a slim sausage-shaped outline, and the tertiaries may themselves be constricted, without branching, before the final termination expansion. The branches from the lower verticils, at lesser diameters, are simpler in structure than the much larger terminal ones : the transition is gradual.

HORIZON. Lias of Southern Europe, North Africa and the Middle East.

MATERIAL. Numerous random thin-sections from one level in the median dolomitic limestone of Group *a* (Liassic) of the Lower Musandam Limestone ; Wady Bih, Jebel Hagab, Peninsular Oman (Hudson & Chatton 1959).

REMARKS. *Palaeodasycladus mediterraneus* is a characteristic and locally-

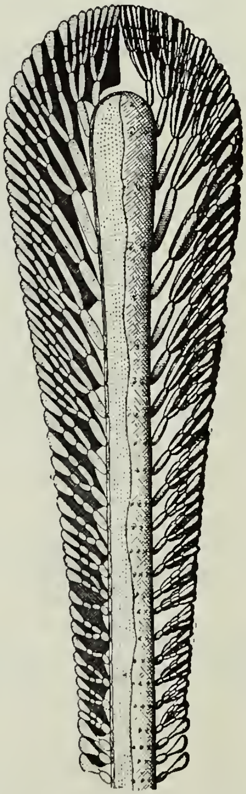

FIG. 5. Reconstruction (after Pia 1920) of *Palaeodasycladus mediterraneus* Pia. Vertical section on left ; decalcified appearance on right. ×12 approx.

abundant microfossil in the Lias of the circum-Mediterranean area, namely Spain, Italy, Greece, Morocco and Algeria. Its total range appears to be from within the upper part of the Lower Lias, through the Middle Lias, and into the lower part of the Upper Lias ; there are records from top Triassic which need confirmation (Sartoni & Crescenti 1962). The usual associated microfossil is the foraminifer *Orbitopsella praecursor* (Gümbel). In the Middle East *P. mediterraneus* is known to me only from Oman, where it is locally abundant in one bed of the Dolomitic Limestone of the Lower Musandam, associated with algal nodules, and probably of Middle Liassic age (see Hudson & Chatton 1959 : 78). *Orbitopsella* is known from S.W. Persia, but I have not seen *Palaeodasycladus* associated in this limestone, though it is likely to occur there. A. Gollestaneh has, however, recently discovered this dasyclad in the lower to middle Lias of Khaneh Kat, interior Fars province. It is interesting that in Oman, *Orbitopsella* occurred more or less throughout the Liassic rocks, whilst *Palaeodasycladus* was restricted to one bed : in southern Italy, however, the alga has a much greater vertical range than the foraminifer (Sartoni & Crescenti, 1962 ; de Castro 1962).

*P.* cf. *mediterraneus* from the subsurface Jurassic of Haifa, Israel, is Middle Jurassic in age (Maync, 1966 ; Derin & Reiss 1966).

In general, the Oman material confirms the accuracy of Pia's original reconstruction of *Palaeodasycladus* (Pia 1920 : 121). Sizes reached are less than those of large Italian specimens, for which 12 mm. length and 2·8 mm. maximum external diameter are quoted (Sartoni & Crescenti 1960 : 14). Although the dolomitised nature of the Oman specimens is not ideal for elucidation of fine detail, there appear to be several small differences. The ragged outline of the stem-cell cavity, clearly figured by Pia and ascribed by him to incomplete inner calcification on alternate verticils, was only seen on one incomplete example, where it may well be due to the dolomitisation of the stem-cell filling. The branches, although constricted as figured by Pia, appeared less swollen and slimmer than in his reconstruction, and although constriction of tertiaries without branching does occur, it was much less marked than in his figures. Finally Pia's reconstructed successive cross-sections (*op. cit.* : 121), show a reduction in the number of branches per verticil, from base to apex, 18 to 12, so accommodating the increased branch-complexity. In the Oman material this is much less obvious, if it occurs at all, and although counts of branching are difficult on sections of this crowded, highly-oblique, structure, about 20 branches have been counted at a large verticil. This is apparently to be correlated with the thinner branches already noted. It is suggested that *Palaeodasycladus* retains the number of branches per verticil during growth, or even increases them slightly like many other dasyclads, and that the reduction seen in Pia's admirable clear figures is a cartographic necessity rather than an accurate depiction.

The Oman material is referred here to *P. mediterraneus*, and there is no reason to make it a new species or variety. It is not comparable with the distinctive *P. mediterraneus elongatulus* (Praturlon 1966).

The modern appearance of *Palaeodasycladus* is striking when compared with some of Pia's other bizarre reconstructions from the Mesozoic. Probably the spores were borne in the swollen branches. It is easy to see how such an alga, with development of separate reproductive bodies, would resemble certain living genera, e.g. *Dasycladus* itself, allowing for the very different calcification.

The Oman *Palaeodasycladus*-limestone is crowded with examples of the species : presumably they grew in dense patches or thickets like the living *Dasycladus*. Their ecology is further discussed below.

### Genus ***PERMOPERPLEXELLA*** gen. nov.

DIAGNOSIS. Thin hollow calcified elongate claviform dasyclad ; walls showing consecutive horizontal verticils of large cylindrical branches, rounded in cross-section, pores (branches) of adjacent verticils set alternately, all pores separated by narrow interstices ; proximal and distal terminal openings to thallus.

HORIZON. Permian of Iraq.

TYPE SPECIES. *Permoplexella attenuata* sp. nov.

### ***Permoperplexella attenuata*** sp. nov.

(Pl. 17, figs. 1–5)

DESCRIPTION. Hollow elongate calcified club-shaped thallus, length about 2·5 mm., external diameter increasing gradually from 0·5 mm. near the base and swelling to 0·9 mm. or more sub-terminally, internal diameters 45–46% external, ends rounded, terminal apertures of about 0·156 mm. and 0·312 mm. diameter respectively. About 22 consecutive verticils each of about 20 branches, branches in successive verticils arranged alternately. The branches in vertical section are seen to communicate with the internal cavity by a narrow pore, and expand at once to a rounded rectangular section, occasionally seen as flask-shaped in the terminal expansion of the thallus. In cross-section they are rounded-polygonal, about 0·1 mm. diameter, and separated by calcareous interstices of 0·020 mm. or less. Traces of a narrow longitudinal calcified structure within the central cavity.

HORIZON. Permian of Iraqi Kurdistan.

HOLOTYPE. The specimen figured in Pl. 17 fig. 4, from the Permian Zinnar Formation ; Ora, Mosul Liwa, Iraq. V. 52085.

PARATYPES. The specimens figured in pl. 13 figs. 1–3, 5 ; same locality and horizon. V. 52084, 52085.

OTHER MATERIAL. Random sections in the same samples.

REMARKS. The little dasyclad described above, although distinctive enough in the Iraqi Permian flora studied, shows a combination of characters which are not themselves intrinsically distinctive. The pores (side-branches of the verticils) are simple and do not consistently show any of the shapes characteristic of the different genera of the diploporeae—*Diplopora*, *Gyroporella*, *Physoporella*, etc. Although the thallus is that of the conventional single dasyclad, the terminal apertures suggest that it may possibly be a unit of a serial plant ; for whilst it is true that in some of the more elaborate dasyclads of later geological periods the distal aperture is occupied by a tuft of narrow sterile branches, we do not know whether these simple-branched late Palaeozoic dasyclads were similar in this respect. The fossil is presumably not to be regarded as a new small species of *Eogoniolina* Endo, which has no distal aperture ; its branches are not those of *Gyroporella*, and it is smaller and with different shaped thallus than the somewhat doubtful *Pseudogyroporella* (Endo 1959). Although segments of *Mizzia* spp. auct. vary considerably, the fossil under discussion is outside the known range of segment-shape for this genus. It is moreover rare amongst an abundance of *Mizzia*, and the calcareous traces in the stem-cell cavity, never seen in any of very many *Mizzia*-segments examined, suggest a different internal organisation. It seems best to admit that its exact place amongst the dasyclads is at present obscure, and to describe it as a new genus, tentatively referable to the tribe Diploporeae.

### Genus *PIANELLA* Radoičić 1962

DIAGNOSIS. Calcified cylindrical dasyclad tube showing successive verticils of horizontally directed branches, alternating in position from one whorl to the next : branches simple, unbranched, widening evenly outwards from a narrow insertion at the stem-cell cavity to the anterior : i.e. differing only from *Macroporella* in the regular verticillate, instead of irregular, insertion of the branches at the stem-cell.

### *Pianella gigantea* (Carozzi) Radoičić

1955a *Macroporella gigantea* Carozzi : 43, pl. 6, fig. 4 ; text-fig. 7.
1960 *Macroporella gigantea* Carozzi ; Elliott : 221.
1962 *Pianella gigantea* (Carozzi) Radoičić ; Radoičić : 202.

DESCRIPTION (based on Carozzi). Calcified cylindrical dasyclad tube of 1·2–1·75 mm. external diameter, internal diameter 66–70% of corresponding external diameter; successive verticils of horizontally directed branches, 30–40 per verticil, widening from 0·03 mm. diameter internally to 0·09–0·20 mm. externally to give a regular external pattern of polygonal pores.

HORIZON. Upper Jurassic of Europe (Switzerland) and Arabia (Oman, Hadhramaut).

MATERIAL. Upper Jurassic of Jebel Kaur, Oman ; also in derived Upper Jurassic in the Upper Cretaceous Hawasina-complex at Jebel Buwaida, Ibri, Oman. Fragmentary remains in Upper Jurassic of the Jebel Laut area, Wahidi State, Hadhramaut, and see also Hadhramaut record of Beydoun (1960 : 140).

REMARKS. Carozzi described his species from the Sequanian-Portlandian of the Swiss Upper Jurassic. Associated fossils and stratigraphy suggest the upper part of the Upper Jurassic for the Middle East occurrences also. The species is apparently uncommon there and remains are fragmentary or poorly preserved. Praturlon (1966) relegates this species as a synonym of *P. pygmaea* (large individuals).

### ***Pianella pygmaea*** (Gümbel) Radoičić
(Pl. 17, figs. 6–8)

1891 *Gyroporella pygmaea* Gümbel : 306, text-figs. 6, 7.
1924 *Macroporella pygmaea* Gümbel spec. ; Pia : 84, pl. 1, figs. 4–7.
1955a *Macroporella pygmaea* Gümbel ; Carozzi : 40, pl. 6, fig. 3 ; text-figs. 5, 6.
1960 *Macroporella pygmaea* (Gümbel) ; Elliott : 222.
1962 *Pianella pygmaea* (Gümb.) Rad. ; R. Radoičić : 202.

Description. Calcified cylindrical dasyclad tube, external diameter 0·33–0·78 mm., internal diameter 0·10–0·34 mm. (d/D 27–43%, usually about 30%), showing consecutive horizontal verticils of branches, about 18–20 verticils per mm. of length, each verticil of 15–20 branches. The branches are straight, unbranched, near-circular in cross-section, and widen radially with straight sides to the exterior, from a very narrow insertion on the stem-cell cavity to the exterior where they have a diameter of about 0·052 mm., sometimes with a terminal widening to give a diameter of 0·090 mm.

Horizon. Upper Jurassic to bottom Cretaceous (Sequanian–Valanginian) of Central and Southern Europe (Switzerland, Italy, Southern Germany), Middle East and Borneo.

Material. In the Middle East, from the Garagu Formation (Valanginian), sub-surface at Awasil no. 5 well and Mileh Tharther no. 1 well, both Dulaim Liwa, Iraq. Also from the Upper Jurassic of the Jebel Laut area, Wahidi State, Hadhramaut, and see Hadhramaut record of Beydoun (1960 : 140).

Remarks. *P. pygmaea* from the Middle East is closely comparable in dimensions and structure with the European material described by Pia and by Carozzi (ref. Carozzi 1955a). The external diameter of the pores is usually less (0·05 mm. compared with 0·09 mm.), though not invariably so. Of comparable species, *P. grudii* Radoičić, from the Kimmeridgian of Jugoslavia, is a smaller species with proportionally wider stem-cell ; *P. tosaensis* Yabe & Toyama, from the Upper Jurassic of Japan, shows about 30 branches per verticil, and these are polygonal in cross-section, with expanded outer terminations.

### Genus ***PSEUDOEPIMASTOPORA*** Endo 1961

Diagnosis (after Endo). Thallus short-elliptical, somewhat undulating, almost circular in cross-section ; branches widening within the wall-thickness to spherical cavities (believed sporangial) and narrowing again, set at right angles and slightly ascending to the vertical axis, and may be arranged as definite verticils.

*Pseudoepimastopora* was instituted by Endo (1961) to include those species of the older genus *Epimastopora* s.l. in which the pores seen penetrating the walls swell from a narrow entry to a more or less globular cavity within the wall-thickness and constrict again : these swellings were considered sporangial in origin. This left *Epimastopora* s.str. for species in which the pores traverse most of the wall thickness with little change in pore-diameter. Buri (1965) does not regard this division as significant, or of generic value. I agree that it may not be evidence of evolutionary divergence, but it forms a useful character at present in classifying these normally fragmentary and rather unsatisfactory dasyclads. Both these genera are normally represented almost entirely by wall-fragments : straight, curved or sinuous in section, and they are considered to be the broken remains of the very fragile thin hood-like outer calcification-zone of dasyclads whose stem-cell and branch-systems are necessarily unknown. A comparison has been made with the Carboniferous *Koninckopora* as restored by Wood (1943), who regarded them as very closely related. However the outer polygonal mesh of *Koninckopora* is very different in appearance to the pored walls of *Epimastopora* and *Pseudoepimastopora*, even if all three are representatives of a morphologically similarly-situated outer calcification-zone.

The fragmentary remains of the latter two genera have led to a proliferation of species based on wall- and pore-measurements (see summary in Johnson 1963). The calcified structures themselves have usually been reconstructed as originally globular or tubular. Endo (1961) cited *P. pertusus* as type-species, and referred his earlier *E. japonica* also to the genus. Subsequently H. Flügel (1963) has transferred both *E. likana* Kochansky & Herak and *E. iwaizakiensis* Endo (Permian of Jugoslavia and Japan respectively), to *Pseudoepimastopora*, figuring both from the Middle East. *P. iwaizakiensis*, from the Taurus (Southern Turkey) Permian of which the Iraqi Kurdistan Permian is a continuation, is shown intact in presumably near-longitudinal section as a very thin-walled elongate-oval. (H. Flügel 1963).

Remains of *Pseudoepimastopora*, usually fragmentary, abound in the Zinnar Formation, the lower portion of the Chia Zairi or Iraqi Permian System. Fortunately one or two whole specimens have been seen, so permitting description of a distinctive new species.

### ***Pseudoepimastopora ampullacea*** sp. nov.

(Pl. 18, figs. 1, 2, 5–7)

Description. *Pseudeopimastopora* of " waxing-and-waning " morphology, circular in cross-section, length about 4·0 mm., diameters (three successive maxima) 1·56, 1·43, 0·91 mm. : thin-walled, wall-thickness 0·078–0·104 mm., pores commencing on the inside as narrow canals, and swelling within the wall-thickness to near-spherical cavities of 0·052–0·065 mm. diameter, with outer opening of varying size, commonly about half maximum diameter ; interpore spaces (solid wall) very narrow so that there are about 16 pores per 1 mm. of wall-length, outer apertures of pores believed to be close-set in alternating levels.

Horizon. Permian of northern Iraq.

Holotype. The specimen figured in Pl. 18, fig. 1 from the Permian Zinnar Formation, Ora, Mosul Liwa, Iraq. V. 52089.

Paratypes. The specimens figured in Pl. 18, figs. 2, 7, Zinnar Formation, Ora and Harur, Mosul Liwa, Iraq. V. 52090, 52094.

Other Material. Numerous random thin-sections : many specimens fragmentary. Same formation and area.

REMARKS. This species occurs in profusion in some samples as debris ; short curved pieces of wall showing the pore-structure. These random cuts are commonly at right angles to the wall and show the near-spherical cavities well ; other, tangential, cuts may show the inner narrow initial canals, or the arrangement of larger external pore-openings. Larger pieces of wall showing much curvature are relatively uncommon, and near-complete specimens are very rare. The holotype is a longitudinal section showing two complete diameter-maxima and a third slightly crushed: detail not seen on this specimen is well-displayed by debris in the same thin-section.

*P. ampullacea* differs in its distinctively lesser wall-thickness and rather smaller pore-diameter from *P. pertunda* Endo (type), *P. japonica* Endo and *P. iwaizakiensis* Endo. Also from the coarser *P. likana* Kochansky & Herak, known from elsewhere in the Middle East (see below). In outline *P. ampullacea* is distinctive, though Endo's description of the thallus of his fragmentary *P. pertunda* and *japonica* as " somewhat undulating " may indicate a similar growth-form.

### ***Pseudoepimastopora*** cf. ***likana*** Kochansky & Herak
(Pl. 18, figs. 3, 4)

1960 *Epimastopora likana* Kochansky and Herak : 78, pl. 4, figs. 5–10.
1960 *Epimastopora* sp. Elliott : 219.

Fragments of *Pseudoepimastopora* occurring in the Permian of Jebel Qamar, Oman, show a wall-section of 0·325 mm. thickness, with well defined ovoid pores of 0·130 mm. median diameter in vertical section. In this section the pores appear oval with pointed ends, communicating with the interior by a short very narrow canal, and with the exterior by an even shorter one. They are close-set, though this feature varies in the limited material available.

This species corresponds most closely to *Ps. likana* but the dimensions seem larger. In the type-material of the Yugoslav species the wall diameter is given as 0·20–30 mm. (most frequently 0·25 and the pore-diameter maximum 0·07–0·10 mm. (misprinted as 0·7–0·10 mm.). The Oman material is insufficient to be described as new.

The specimens occurred in thin-sections of limestone boulders yielding *Anthrocoporella mercurii* sp. nov. *Pseudoepimastopora* fragments have also been seen in derived Permian material in the Lower Cretaceous Upper Musandam formation of Jebel Hagab in the same areas.

### ***Pseudoepimastopora iwaizakiensis*** Endo

1953a *Epimastopora iwaizakiensis* Endo : 120, pl. 11, figs. 7–9.
1963 *Pseudoepimastopora iwaizakiensis* (Endo) ; Flügel : 88, pl. 1, fig. 6.

Figured by Flugel (1963) from the Permian of the Taurus, Turkey.

### Genus ***PSEUDOVERMIPORELLA*** Elliott 1958

DIAGNOSIS (after Elliott). " Small gregarious meandriform calcareous tubes, showing a free inner compact-walled tube and an outer tubular layer that is pierced by numerous closely set radial pores arranged to form a regular mesh ".

*Pseudovermiporella* was described by me in some detail (Elliott 1958b) as a Permian problematicum, and an algal interpretation given of its structure. Kochansky & Herak (1960), in discussing Permian *Vermiporella* spp., agree as to the algal nature of *Pseudovermiporella*, but consider that it is not worthy of generic distinction from *Vermiporella*, and that the details described should be considered a " contribution to the knowledge of the genus *Vermiporella* ". Henbest (1963) regards *Pseudovermiporella* as a foraminifer : " A specialized, sessile form of Permian Cornuspirinae " whose originally aragonitic test has undergone a distinctive diagenetic change.

These three views depend on the interpretations made of the structure and preservation of a very distinctive microfossil.

My account (Elliott 1958b : 420) briefly discussed and discounted the possible interpretations of *Pseudovermiporella* as a foraminifer, bryozoan, serpulid, dasyclad alga of conventional structure, or hemichordate. My suggested interpretation of the problematic fossil regards the outer mesh as the main calcified layer of a dasyclad of creeping or prostrate stem-cell, perforated around lateral branches, as in *Vermiporella*. The variable inner layer or layers of grey calcite lining this in the type-material are regarded as a secondary deposit, not part of the organism, formed after death and before burial. The very distinctive thin imperforate tube found in some but not all specimens, within the main cavity of the outer mesh-tube, is considered the calcified outer surface of the early stem-cell, after the side-branches dropped off, behind the actively growing anterior branched portion.

Kochansky & Herak (1960) described Jugoslav Permian species of *Vermiporella*, including *V. nipponica* Endo, a Japanese species to which *Pseudovermiporella* was compared by me. *Vermiporella* itself has a Silurian type-species, *V. fragilis* Stolley, whose dasycladacean nature has not been disputed. There has been, however, considerable confusion over poorly-described Permian species referred to the genus, and Kochansky & Herak dealt with this. They did not record *Pseudovermiporella* (or *Vermiporella*) *sodalica* in their material, but concluded (*op. cit.* : 72–73) that the main difference between four recognized species of *Vermiporella* (including the type) and *Pseudovermiporella* is the presence of the " free inner compact-walled tube " in the latter. They quoted me correctly as not having seen this structure in all examples, and regarded this as growth-stage detail in a very full description of a species of *Vermiporella* not worthy of generic distinction.

Henbest (1963 : 33) interprets *Pseudovermiporella* as a " specialized, sessile genus of Permian Cornuspirinae " continuing a series formed by the earlier genera *Apterrinella* and *Hedraites*, with which he compares it closely. All three are interpreted as originally aragonitic foraminifera which have undergone conspicuous changes during diagenesis : it is important that in this interpretation the inner layers of grey calcite lining the outer mesh are regarded as an integral part of the test itself. In correspondence, after examining topotype material sent by me (letter of August 17, 1964) Henbest regards the free inner thin-walled tube as that of " a later individual or organism ".

The three accounts quoted should be read for a full appreciation of the differing interpretations of various minor points and comparisons : it is, however, believed that the summary above includes the essential differences.

I described *Pseudovermiporella* as a problematicum, probably algal, and believe that the presence of the inner thin-walled tube is important. It is not recorded in Permian *Vermiporella* spp. elsewhere, and although it is not seen in all specimens, its occasional presence unbroken and set in clear calcite free of the outer structures suggests that it was part of the organism and not a later inhabitant of the abandoned tube. It is, however, readily admitted that the exact nature of *Pseudovermiporella* remains unknown : its description is included here as a doubtful dasyclad of the Middle East. Güvenç (1965), who figures un-named species or forms from the Taurus, leaves it as a problematicum. The microproblematicum *Papillomembrana* from the Norwegian Precambrian (Spjeldnaes 1963) bears certain resemblances, from the type-description.

Note. The interesting study by K. B. Korde (Pal. Zhurn., 1966 no. 4) was seen too late for proper discussion here, but briefly this authoress agrees with the probable algal nature of *Pseudovermiporella*, whilst unable to place it taxonomically within the algae.

### ***Pseudovermiporella sodalica*** Elliott

(Pl. 19)

1958b *Pseudovermiporella sodalica* Elliott : 419, pls. 1, 2, 3.
1960 *Pseudovermiporella sodalica* Elliott ; Elliott : 219.
1961 *Pseudovermiporella sodalica* Elliott ; Erk & Bilgütay ; 108, pl. 1.

Description. Tubes of finely crystalline calcite, appearing white by reflected light and dark in thin section, occurring commonly with various diameters up to 1·0 mm. and sometimes attaining a diameter of 1·4 mm. The tubes are meandriform and form tangled growths several millimeters across, in which apparently more than one individual may occur. When a tube is free the cross section is circular, and remains approximately so in many coils or loops, which touch in a growth or tangle. However, when attached to others or to shell fragments, individuals occur which show in thin section as arcs applied closely to the object encrusted, whose outer surface completes the tube.

The tubes are pierced by numerous closely set radial pores, approximately at right angles to the axis of the tube, separated by interpore wall material which widens slightly outward, or terminally, as seen in transverse and vertical sections. In adult individuals the pores are about 0·030–0·040 mm. in diameter, circular in cross section, about fifty to a transverse section of the tube, and the interpores of wall material sometimes show a paired appearance in both transverse and vertical section. In tangential sections the coarsely-pored wall shows as a regular and distinctive round-pored mesh, with pores wider than interpores ; a count along a 1 mm. length of such a section gave twenty-one regularly spaced pores. Such measurements are approximate only, due to the coiled tubes, which are at best only sinuous and never straight. Smaller tubes show smaller pores.

Within the outer pored tube described above there occurs in a majority of specimens a continuous solid dark calcareous layer, attached to the inner surface of the outer mesh. In many specimens this layer is indistinguishable in colour and texture from the dark outer calcite mesh, and has the appearance of being part of the tube ; in some it shows as a lighter, obscurely banded layer of variable thickness, eccentrically placed with regard to the outer tube, i.e. much thicker on one side than on the other in transverse section ; and sometimes it is absent. This layer is interpreted as a secondary deposit formed subsequent to the death of the tube-building organism, though not after burial, for occasional specimens show other organisms attached to its inner surface. The reason for its occurrence is discussed above. Consideration of the algal dust infillings described in *Koninckopora* by Wood (1943) did not permit close comparison, but the observations of Johnson (1957 : 181) are of interest. The lining layers in *Pseudovermiporella* may be of similar origin to the granular crystalline calcite described by Johnson, and considered by him to have been formed probably almost contemporaneously with deposition, whilst objects were movable on the sea-floor.

Within some but not all specimens there occurs an innermost tube of thin dark imperforate calcite, roughly circular in cross section, and of considerably lesser diameter than the inner diameter of the outer tube from mesh to mesh. Sometimes this thin layer forms the inner boundary of the secondary layer mentioned above ; sometimes it is seen " free " within the central cavity, filled with transparent calcite and separated by the same mineral from the outer pored tube or from the dark secondary lining calcite if present. When intact, it is not invariably central in position ; not infrequently it is broken, and sometimes small organisms are seen attached to it. It is considered to be of organic origin, and its relation to the outer pored tube is discussed above.

The smallest tubes show in section as bubble-like clusters, rather like the nucleoconchs of certain foraminifera. Although some of the sections in such a cluster are a result of the plane of section cutting a meandriform tube more than once, it seems likely that more than one individual, budding from a centre, may sometimes be present. The walls of these tiny immature tubes are composed of the innermost thin dark organic calcite just described ; only when they are larger does a pored outer tube, with proportionally small pores, appear. There is considerable variation between individuals in the diameter-size at which this occurs.

In sections of the mesh of adult individuals, small bubble-like sections of the inner layer of small, usually single individuals sometimes occur, suggesting attachment or budding. Small pored tubes occur within the tubular cavities of larger individuals, attached either to the inside of the main outer mesh (rarely to the secondary calcite lining this, if present) ; or to the outside of the inner, thin-walled tube. They are never found within the latter when it is unbroken.

Horizon. Upper Permian of the Middle East.

Material. Very numerous thin-sections from Permian limestone at Jebel Qamar, Peninsular Oman, Arabia (foraminiferally dated as probably Upper Permian by Dr. M. C. Chatton). Seen also in derived Permian material in Upper Cretaceous, Tawi Silaim, Oman. In Iraq this species (or a comparable species of *Vermiporella*) occurs rarely in the Upper Permian Darari Formation of Harur, and in the subsurface Upper Permian of Atshan no. 1 well, both in Mosul Liwa. Recorded by Erk & Bilgütay (1961) from the Permian of Sarikaya, Diskaya Mountains, near Bursa, and from the Adana Basin, Turkey.

REMARKS. See discussion under " Genus *Pseudovermiporella* " above.

### ***Pseudovermiporella elliotti*** Erk & Bilgütay

1961 *Pseudovermiporella elliotti* Erk and Bilgütay : 110, pl. 2.

REMARKS. This species appears similar in many characteristics and in mode of growth to the type-species. It differs, however, in the following points, summarized from the authors' description and comparisons. It is a smaller species (external diameter up to 0·539 mm.), the pores are hexagonal, not rounded in cross-section and both smaller in diameter (0·025–0·030 mm.) and more closely set (interpores of 0·010–0·013 mm. thickness). The individuals are said to occur singly, and not tangled or closely associated as in *P. sodalica*. It is not clearly stated whether an inner thin-walled tube occurs, though small individuals occur within larger ones, as in the larger species. It is recorded from the Turkish Permian at Kozan, Adana Basin and from various localities near Ankara. In the Adana area the two species occur commonly in rocks of Middle Permian age.

## Genus ***SALPINGOPORELLA*** Pia 1918

DIAGNOSIS. Small, rod-like, thick-walled, calcified, tubular dasyclad, with regular successive verticils of relatively few simple single branches which widen to the exterior and open as simple pores : thallus not segmented, but interverticil portions sometimes outwardly slightly convex and delimited by grooves.

### ***Salpingoporella annulata*** Carozzi

(Pl. 20, figs. 3, 4, 6, 7)

1953 *Salpingoporella annulata* Carozzi ; 384, figs. 1–55.
1955b *Salpingoporella annulata* Carozzi ; Elliott : 125, 126.
1955a *Salpingoporella annulata* Carozzi ; Carozzi : 55, pl. 6, figs. 5–7, text-fig. 15.
1960 *Salpingoporella annulata* Carozzi ; Elliott : 221.

DESCRIPTION (based on Carozzi). Small, tubular, calcified dasyclad, straight or slightly curved and usually occurring in fragments of up to 1 mm. or more in length, external diameter 0·30–0·64 mm., internal diameter 0·10–0·25 mm. The thick walls perforated by horizontal verticils of branches at about 0·15–0·20 mm. apart, each verticil consisting of 8–12 simple straight radial branches which widen terminally and open in a shallow external horizontal annular groove. Pores alternate in position from one verticil to the next, and between them the external interverticil walls are gently convex.

HORIZON. Upper Jurassic–bottom Cretaceous (Kimmeridgian, Portlandian-Valanginian) of Switzerland and Southern France, Italy, Jugoslavia : and of Middle East (Arabia) ; Qatar, Trucial Oman and Hadhramaut.

MATERIAL. Solid and thin-section material from the subsurface Upper Jurassic (upper part) of the Dukhan wells, Qatar Peninsula, Arabia, where it is common ; also at the same level in Gezira no. 1 well, Murban, Abu Dhabi, Trucial Oman. Also from the Upper Jurassic of Al Hamiah, Coastal Wahidi, Hadhramaut ; and from the subsurface Lower Thamama formation (bottom Cretaceous) of Murban no. 2 well, Abu Dhabi, Trucial Oman.

REMARKS. The Qatar material corresponds with Carozzi's type material in detailed morphology, number of branches per verticil, etc. : the maximum size seen (external diameter 0·60) is a little less than Carozzi records, and the minimum measurement encountered for this dimension (0·26 mm.) is also less than that given for the type-material. Since the closely similar *S. apenninica* Sartoni and Crescenti (see below) differs mostly in its smaller size, a series of Qatar specimens were carefully measured for outer and inner diameter and spacing between verticils. Of thirteen such examples, only one fell completely within the limits given for the smaller species, and it is considered that this is best regarded as a small example of *S. annulata*. At Qatar the material consists of short lengths only of tube, occurring amongst ooliths and rounded fragments and often rolled, and it may be that sorting has occurred before burial.

### *Salpingoporella apenninica* Sartoni & Crescenti

(Pl. 20, figs. 1, 2, 5)

1962 *Salpingoporella apenninica* Sartoni and Crescenti : 266, pl. 44, figs. 1, 2, 4, 5, 6, 8.

DESCRIPTION (based on Sartoni & Crescenti). Small tubular calcified dasyclad, straight or slightly curved and usually occurring in fragments of up to 1 mm. or more in length, external diameter 0·19–0·32 mm., internal diameter 0·097–0·22 mm., the walls perforated by horizontal verticils of branches at about 0·08–0·16 mm. apart, each verticil consisting of 8–14 simple radial branches widening terminally and opening in a shallow horizontal annular groove. Pores alternate in position from one verticil to the next, and between them the external interverticil walls are gently convex.

HORIZON. Upper Jurassic–bottom Cretaceous (Kimmeridgian, Portlandian–Valanginian) of Italy : Upper Jurassic of Iraq.

MATERIAL. Abundant thin-sections from the subsurface Najmah Formation (Upper Jurassic) of Kirkuk no. 117 well ; also rarely in the subsurface Jurassic of Mileh Tharthar no. 1 well, Dulaim Liwa, believed to be a caving from the Makhul Formation (Tithonian) in this well. Both localities are in northern Iraq.

REMARKS. The Iraqi material corresponds well in morphology and dimensions with the Italian type-material (external diameters of 0·208–0·286 mm., internal diameters of 0·104–0·130 mm.). This species is very similar to *S. annulata* : the principal difference in thin-section is that whilst the stem-cell diameters are slightly less in *S. apenninica*, the external diameters are much less, so that the percentage relation of internal to external is greater (50–60% against 33–40%). In *S. annulata* the distance between the external pores of the same verticil is said to be about equal to the distance between two successive verticils (Carozzi 1955a) ; in *S. apenninica* the former is less than the latter. The two species are very similar and obviously closely related : in examining a series of either one finds atypical specimens showing measurements more usual in the other species. In Italy they occur together over the same range : in the Middle East they are apparently separate, *S. annulata* in the south at Qatar and elsewhere, and *S. apenninica* in the north in Iraq. Both these occurrences are often in a similar oolitic facies, with associated fossils in common (*Clypeina jurassica*, *Favreina salevensis*, *Cladocoropsis*, etc.).

## *Salpingoporella arabica* sp. nov.

(Pl. 21, figs. 1–3)

1955b *Salpingoporella* cf. *mühlbergii* (Lorenz) ; Elliott : 126.
1960 *Salpingoporella mühlbergi* (Lorenz), and *S. mühlbergi* var ; Elliott : 222–224.

Description. Thin-walled tubular calcified dasyclad, straight-sided with very gentle increase in diameter ; observed lengths (incomplete) up to 2·73 mm., external diameter 0·31–0·73 mm., internal diameter 0·21–0·47 mm. ; ratio of internal to external diameters 55–66% ; horizontal verticils set regularly 0·104 mm. apart, each verticil with 8–10 branches which open rapidly and widely to external pore-depressions of 0·065–0·078 mm. or more diameter. The wall calcification is thin and rather ragged : the pores have a somewhat irregular appearance, partly due to the wall-structure and partly due to slight irregular deviations from the horizontal in their orientation.

Horizon. Lower Cretaceous of the Middle East.

Holotype. The specimen figured in Pl. 21, fig. 3, from the Qamchuqa Formation (Aptian-Albian level) of Surdash, Sulemania Liwa, Iraq. V. 52102.

Paratypes. The specimens figured in Pl. 21, figs. 1, 2, from the top Qamchuqa Formation (Albian level) of Sarmord, Sulemania Liwa, Iraq, and from the Upper Musandam Formation (Lower Cretaceous) of Jebel Hagab, Peninsular Oman, Arabia. V. 52100, 52101.

Other Material. In Iraq, Qamchuqa Formation of Zibar-Isumeran, Mosul Liwa (Barremian-Aptian level) ; Sarmord Formation of Jebel Gara, Mosul Liwa (Valanginian-Hauterivian) and of Sarmord, Sulemania Liwa (Barremian). In Arabia, from Haushi, South Oman, Lower Cretaceous probably Valanginian-Hauterivian ; also from subsurface Upper Thamama Formation, ?Barremian-Aptian level, of Murban no. 2 well, Abu Dhabi, Trucial Oman.

Remarks. *S. arabica* is the Middle East form of the European *S. mühlbergii* (Lorenz) Pia, with which I earlier tentatively identified it. The European species from the Barremian-Aptian of France and Switzerland and the Lower Cretaceous of

Italy (Lorenz 1902 ; Pia 1918, 1920 ; Thieuloy 1959 ; Sartoni & Crescenti 1962), is a slightly smaller species normally (external diameter 0·3–0·5 mm.), though Thieuloy's figures appear to indicate up to 1·5 mm. for this dimension. It is however much thicker-walled, the relation of internal to external diameters being about 40% (38–45%) as against 60% (55–66%) in *S. arabica*. Because of this, the branches in the latter rarely show much of the inner narrower portion seen in the European form, if indeed this was ever present. *S. texana* from the Albian of U.S.A. (Johnson 1965), compared by its author with *S. mühlbergii*, may similarly be distinguished from *S. arabica* by dimensions and proportions.

*S. arabica* ranges from bottom Cretaceous as high as Albian ; it is wide-spread, but rarely abundant.

### *Salpingoporella dinarica* Radoičić
(Pl. 21, fig. 4 ; Pl. 22)

1959 *Salpingoporella dinarica* Radoičić : 33, pls. 3–5.
1960 *Hensonella cylindrica* Elliott : 229, pl. 8, fig. 1.

The descriptions of Radoičić (1959) and myself (Elliott 1960) refer to the same organism. Radoičić interprets this as an alga, and described it as a species of *Salpingoporella*, comparing it carefully with *S. mühlbergii* of the same age. I described it as a problematicum, since my interpretation of the wall-structure indicated that it differed very considerably from other dasyclads.

This organism is Tethyan Lower Cretaceous in age, and is especially characteristic of the Barremian-Aptian level. The type-description of *S. dinarica* lists it from numerous localities in Jugoslavia at this horizon, and Sartoni & Crescenti (1962) and de Castro (1963) figure and record it under the algal name, with *Hensonella* in synonymy, from the Aptian of Italy. Elliott (1960 ; 1962a) recorded *Hensonella* from Iraq and Oman (a full list of Middle Eastern localities is given below), Persia, Algeria and Borneo : Lower Cretaceous, various levels. It has also been seen in material from the Upper Aptian, Mededine area, S. Tunisia. Reiss (1961) recorded it from the Aptian of Galilee, Israel, and regarded it as a dasycladacean alga. Dr. M. S. Edgell (*in litt.*, May 1960) also stressed the dasycladacean nature of Iranian material.

Most of these records clearly refer to the same organism. Comparison of Radoičić's and Elliott's descriptions show that the same features are common to both, though the type-figures selected emphasize slightly different characteristics. The organism occurs as hollow cylindrical or near-cylindrical tubes, circular in cross-section, and of varying external diameters up to 0·57 mm. The internal diameter varies from 54–70% of the external : lower values up to 60% or a little more are more common. The walls show a thin inner dark amorphous layer, finely micro-crystalline under a high power, and a thick outer layer (0·013 mm. and 0·104 mm. respectively in one typical example). This latter, which occupies most of the wall-thickness, is yellowish in thin-section appearance : it shows innumerable fine radial subparallel lines or cracks, and, at intervals, coarse canals which extend to widen at the outer surface to occasion shallow pores. In specimens of regular form these are arranged at regularly-spaced levels, the pores alternating in position from level to level, and Radoičić, who figured them as dasyclad verticils of lateral branches, indicated (*op. cit.*, fig. 1) that the distance between adjacent external pores of one verticil was twice the distance between successive verticils. In Radoičić's type-figures, e.g. pl. 4, fig. 1, this regularity is very clearly shown, and other writers, e.g. Reiss 1961 (figs. 101, 105, etc.) also show this. In the types of *Hensonella* (Elliott 1960, pl. 8, fig. 1) this regularity is absent, and I drew attention to the irregularity. Reiss (*op. cit.* : 229), commenting on this, adds that the pores " occur in all suitably sectioned specimens ", meaning presumably sections taken at pore-level, and such specimens have been seen not uncommonly in slides of Middle East *Hensonella*.

The thick yellowish layer was described for *Hensonella* (Elliott 1960 p. 229) as aragonite. This was incorrect : it is calcite, and both Dr. A. Lees (Reading University) and Mr. J. McGinty (Iraq Petroleum) consider it derived from an original organic calcite structure.

Crushed examples from Algeria show the thick layer broken along radial partings, but in most cases still held together by the inner thin dark layer. If the crushing occurred during compaction, this suggests original organic nature for the thin layer, with some flexibility. Edgell (*in lit.*, 1960), who also supported the dasyclad nature of the organism, suggested that this layer may be the original algal wall, or thickened organic outer layer of the stem-cell, and this appears to be the view of Radoičić also (*op. cit.* : 38). That it was an original part of the organism is indicated both by its almost invariable presence irrespective of all but the very worst preservation, and by occasional specimens in which it is lined by a secondary inner layer of post-mortem calcite, possibly pre-burial, the actual tube-core within this being clear, transparent calcite deposited after burial from solution. The large canals which expend to the exterior are sometimes seen in random cut to reach this dark inner layer, and, following Reiss's reasoning on their external appearance, may similarly be supposed normally to do so when the sections are suitably orientated.

Summarizing, *S. dinarica* Radoičić and *Hensonella* Elliott were described from examples of the same organism, and the great majority of subsequent records refer to this same species. Slight differences in the two author's descriptions can be reconciled by examination of large sets of specimens. Since the fossil agrees in size, shape, and morphological structure with other dasyclads, and also occurs in suitable facies at suitable levels for this, Radoičić described it as a dasyclad, referring it to *Salpingoporella* and comparing it carefully with *S. mühlbergii* of the same age. A similar comparison is possible with the new *S. arabica*. This dasyclad reference seems to be the majority view of other workers, as expressed in synonymy or by comment.

In spite of this, there remain certain doubtful features which seem incompatible with a dasyclad origin. In living dasyclads, the deposition of the original aragonitic calcium carbonate is connected with the " assimilatory processes in the chlorophyll corpuscles " (Church 1895), and the calcified layers or structures built up of fine granules are amorphous. By contrast, the calcium carbonate of marine invertebrates (molluscs, brachiopods, corals, echinoderms, etc.) is deposited out of solution by a wet membrane to give normally a lamellar structure, whatever the varied microstructure (fibrous, prismatic, etc.). This difference in structure makes the algal calcium carbonate much less resistant to diagenetic changes than that of almost any other fossil, with frequent disastrous results familiar to the palaeontologist.

Ignoring near-pure limestones in which the results of calcium carbonate solution-replacement mechanisms are common, it is seen that in the marly facies in which *Hensonella* (or *S. dinarica*) abounds the undoubted dasyclads such as *Actinoporella*, *Munieria* and *Cylindroporella* and other species of *Salpingoporella*, show skeletal remains preserved as white replacement calcite, coarsely crystalline in thin-section under moderate magnification. This is interpreted as diagenetic replacement of original aragonite. *Hensonella* stands out conspicuously by its translucent yellow radially-fibrous structure. This structure represents a diagenetic alteration of original calcite, not originally amorphous as in some other algae, and not of aragonite. The radial structure is original, a point emphasized by compaction-fractured specimens, and alteration has taken place in the wall-material between these partings, and not to obliterate them. Only very rarely and incompletely has a later change affected this resistant structure, and then not to the extent seen in associated dasyclads. These undoubted dasyclads, sealed in the same matrix and subjected to the same treatment, have behaved differently.

The thin inner dark layer is also anomalous for a dasyclad. If, as suggested by Edgell, it represents the thickened cell-wall of the stem-cell, then this is unusual in living dasyclads and not seen in fossil forms. In *Hensonella* it is consistently present under varied conditions of preservation from very different localities, which suggests that it originates from an original feature of the organism, even if diagenetically altered, and not from diagenesis itself. Moreover, although localized thickening of the outer stem-cell wall is known in the living *Dasycladus*, there is no trace of this preserved in the fossil *Pagodaporella* now considered related (see above, under *Pagodaporella*), even though the former presence of the structure is inferred.

In conclusion, I consider that this organism is best classified as a problematicum. The original comparison with a scaphopod appears unlikely, but the wall-material is not that of known dasyclads, and certainly not that of the associated dasyclads in the same beds.

Appendix. List of Middle East materials referred to *Hensonella*.

In Iraq, Qamchuqa Formation (Barremian level) of Sarmord, and Sarmord Formation (Barremian-Aptian level) of Sekhaniyan, both Sulemania Liwa ; subsurface Garagu Formation (Valanginian-Hauterivian) of Kirkuk no. 116 well Bottom lower Cretaceous, probably Valanginian, at Haushi, South Oman, Arabia. Common at Barremian-Aptian level in south-west Persia, and recorded from the Aptian of Galilee, Israel (Reiss 1961).

## Genus ***TERQUEMELLA*** Munier-Chalmas 1877

1877 *Terquemella* Munier-Chalmas : 817.
1920 *Terquemella bellovacina* Munier-Chalmas ; Costantin : 1031–32.
1922 *Terquemella* Munier-Chalmas ; Morellet : 18.

DIAGNOSIS. Small, disc-like, lenticular or spherical calcareous bodies, with numerous tiny subdermal spherical sporangial cavities, the bodies themselves considered dissociated sporangial structures from Dactyloporeae (Dasycladaceae).

### *Terquemella bellovacina* Munier-Chalmas

(Pl. 23, figs. 6, 7)

1920 *Trequemella bellovacina* Munier-Chalmas ; Costantin : 1031–32, figs. 13, 14.
1922 *Terquemella bellovacensis* Munier-Chalmas ; Morellet : 18, pl. 1, figs. 67–76.
1955b *Acicularis* sp. Elliott : 126, pl. 1, figs. 11 (right-hand fig.), 12.
1956 *Terquemella bellovacina* Munier-Chalmas ; Elliott : 332.

DESCRIPTION. Flattened, discoidal, solid calcareous bodies, approximately circular or well-rounded irregular in outline, diameter about 0·57 mm. (up to 0·65 mm. maximum seen), thickness 0·117 mm. (up to 0·143 mm. maximum seen). Hollow globular cavities of about 0·045–0·055 mm. diameter occur just within the outer edge of both surfaces, so that transverse (vertical) sections show two rows each of 8 cavities, and tangential-horizontal sections show cavities scattered over the whole section.

HORIZON. Palaeocene of France and of Iraq ; possibly also Central America (Johnson & Kaska 1965).

MATERIAL. Thin-sections from the Sinjar Formation (Palaeocene–Lower Eocene) of Sirwan (Sulemania Liwa), and Banik (Mosul Liwa), Iraq.

REMARKS. The Iraqi species is compatible with the details of the Morellets' description and figures, and the Munier-Chalmas' figures as reproduced by Costantin. *T. lenticularis* Pia, Rao & Rao (1937) from the Indian Eocene is similar but smaller.

### *Terquemella globularis* Elliott

(Pl. 23, figs. 5, 8)

1956 *Terquemella globularis* Elliott : 332, pl. 2, fig. 2.

DESCRIPTION. Near-spherical or flattened ovoid solid calcareous body about 0·390 mm. in diameter, globular sporangial cavities 0·033–0·039 mm. in diameter just within outer edge over whole surface, so that equatorial sections show a circle of about eighteen of them, and tangential sections about 0·170 mm. in diameter show eight.

HORIZON. Palaeocene of Iraq.

MATERIAL. Iraq : Kolosh Formation (Palaeocene and Lower Eocene) of Bekhme and of Rowanduz, both Erbil Liwa ; Sinjar Formation (Palaeocene-Lower Eocene) of Sirwan, Sulemania Liwa, and of Chalki, Mosul Liwa.

REMARKS. Not known from outside Iraqi Kurdistan, though Praturlon (1966) records a *T.* cf. *globularis* from the same level in Italy. *T. parisiensis* Munier-Chalmas, from the Paris Basin Middle Eocene, is of similar shape but larger (diameter 0·5 mm.) and with fewer sporangial cavities.

## "*TERQUEMELLA* s.l." sp.

Minute circular cross-sections of marginally sporangial bodies have been noted not uncommonly in Upper Jurassic and Lower and Upper Cretaceous rocks. These are presumably algal remains corresponding morphologically to *Terquemella*, but are unlikely to originate from Dactyloporeae like the Tertiary *Terquemella* spp. They show insufficient detail to be of much stratigraphic value. Similar bodies have been described elsewhere e.g. from the French Jurassic (Dangeard 1931).

## Genus *TEUTLOPORELLA* Pia 1912

*Teutloporella* is mostly a Triassic genus, but Upper Jurassic species have been described from Switzerland (*T. obsoleta* Carozzi 1954) and Italy (*T. socialis* Praturlon 1963b). At Jebel Buwaida, Oman, masses of derived older rocks occur in the Upper Cretaceous Hawasina-complex. This rubble has yielded various Upper Jurassic algae, including fragmentary *Teutloporella* sp. This derived material is probably from an Oman occurrence *in situ* of one of these species, but is insufficient for description.

## Genus *THAUMATOPORELLA* Pia 1927

*Thaumatoporella* was erected by Pia (1927) as a dasyclad genus for the Upper Cretaceous alga described as *Gyroporella parvovesiculifera* (Raineri 1922). Sartoni & Crescenti (1959) have shown that *Thaumatoporella* itself, although the name is valid, is not a dasyclad, and that it is the same as *Polygonella* (Elliott 1957) and *Lithoporella elliotti* (Emberger 1958b). It is a single-layer lamellar or encrusting alga of uncertain affinities, and only occasional specimens resemble a dasyclad in section. Remarkable for its long range (Rhaetic to Senonian), it is common at many levels in the circum-Mediterranean and Middle East, but its description has no place here.

## Genus *THYRSOPORELLA* Gümbel 1872

Diagnosis. Calcified tubular dasyclad showing successive verticils of radial branches, each branch showing several repeated divisions into smaller branches and branchlets, all but the last divisions swollen.

### *Thyrsoporella silvestrii* Pfender

(Pl. 23, figs. 1–4 ; Pl. 24, fig. 5)

1940 *Thyrsoporella silvestrii* Pfender : 227.
1955b *Thyrsoporella silvestrii* Pfender ; Elliott : 129, pl. 1, fig. 10.
1960 *Thyrsoporella silvestrii* Pfender ; Elliott : 225, 226.
1966 *Thyrsoporella silvestrii* Pfender ; Massieux : 113, pl. 1, figs. 1–8. (Part 2 of this study (see Bibliography), in which Mlle. Massieux refers *T. silvestrii* to *Belzungia*, was seen too late for proper discussion in this work. However, the specimens now studied from the Middle East show the solid walls of *Belzungia*, but the branch-system appears like that of *Thyrsoporella*).

Description. Thick-walled, tubular, cylindrical calcareous dasyclad, length (observed) up to 3·5 mm., external diameter up to 0·78 mm., internal diameter from 33–50%, figures in the lower half of this range being most common ; verticils of horizontal branches close-set, about 9 per mm. of tube-length, with six or more branches per verticil. Each primary branch is considerably wider than high, and in transverse section is markedly swollen with curved sides : a thin vertical partition marks the beginning of division into two secondaries, smaller but similarly swollen, and these in turn each divide into four little swollen tertiaries. These each divide into several terminal branchlets, probably four, which reach the outer surface as pores. On a specimen of 0·754 mm. external diameter the maximum branch-diameters in transverse section were primary, 0·156 mm. ; secondary 0·117 mm., tertiary 0·039 mm., and quaternary, about 0·015 mm.

Horizon. Uncommon in Palaeocene–Lower Eocene of Middle East, but common in the Middle Eocene of the same area. Listed by Pfender (1940) from the Eocene of Madagascar.

Material. In Iraq, seen from the Palaeocene–Lower Eocene Kolosh Formation of Sedelan, Sulemania Liwa, and from the Palaeocene of the Ghurra scarp, west-southwest of Wagsa, Diwaniyah Liwa. In Arabia, from the Palaeocene–Lower Eocene of Sahil Maleh, Batinah Coast, Oman, and from the Palaeocene of Aqabar Khmer, Hajer, Hadhramaut. See also Hadhramaut record of Beydoun (1960 : 146). (The much more abundant Middle Eocene occurrences are discussed below : one of Pfender's records, however, is from the Palaeocene of Turkey.)

Remarks. *Thyrsoporella silvestrii* Pfender was described from Egyptian Middle Eocene material and compared with the European *Thyrsoporella cancellata* Gümbel from the French Middle Eocene. This latter (L. & J. Morellet 1913) is a longer, thinner, more fragile species, with a proportionally wider stem-cell (66% of external diameter). Pfender recorded her species from the Middle Eocene of Egypt and Somalia, and also from Syria, Turkey and Madagascar. In the collections now studied it has been seen commonly in the Middle Eocene of north and south Iraq, and of Oman.

In the Palaeocene–Lower Eocene occurrences studied for this work the species is rare. The records are all based on random sections, and it is possible that with a good series of specimens these older records might prove to be of a species or variety distinguishable from Pfender's species : this has not been possible so far. Pfender (1940) did not illustrate her paper, though this was remedied by Massieux (1966), and the Morellets worked on dissections of solid specimens from the French Eocene. The opportunity is now taken to illustrate *Thyrsoporella silvestrii* by figuring some good thin-sections of Arabian (Oman) material from the Middle Eocene.

### Genus *TRINOCLADUS* Raineri 1922

Diagnosis. Calcified tubular dasyclad showing successive verticils of radial branches, each branch showing outwardly-widening primaries giving rise to several similar-shaped secondaries, and these in turn to bunches of tertiaries : branches of the lower verticils may not show the full detail. Branches not alternate in position from verticil to verticil.

## *Trinocladus tripolitanus* Raineri

(Pl. 24, figs. 3, 4)

1922 *Trinocladus tripolitanus* Raineri : 79, pl. 3, f. 15, 16.
1936 *Trinocladus tripolitanus* Raineri ; Pia : 5, pl. 2, text-fig. 3.
1960 *Trinocladus tripolitanus* Raineri ; Elliott : 224.
1966 *Trinocladus tripolitanus* Raineri ; Massieux : 114, pl. 2, fig. 1.

DESCRIPTION (based on Pia). Tubular cylindrical dasyclad, probably slightly club-shaped, length (observed) up to 3·36 mm., external diameters (different parts of thallus) from 0·47–0·68 mm., corresponding internal diameters 0·16–0·19 mm. (34–28%). Successive verticils, 9 or 10 per mm. of tube-length, are each of about 8 horizontally-directed branches, which usually are not alternate in position in successive whorls. Each primary branch is club- or paddle-shaped in transverse section, widening rapidly from a narrow junction with the stem-cell and extending outwards through about half the wall-thickness : it then gives rise in turn to several smaller but similarly-shaped secondaries (perhaps five or six), and each of these in turn to a cluster of about six slim short tertiaries reaching the exterior as pores. Branches from lower verticils do not show tertiaries and may have been sterile.

HORIZON. Cenomanian or Turonian of Libya, North Africa (Raineri 1922 ; Pia 1936) : Turonian of France (Pfender 1940) and of Iraq and Trucial Coast, Arabia : Upper Cretaceous of Czechoslovakia (Andrusov 1939).

MATERIAL. Subsurface Turonian of Ras Sadr no. 1 well, Abu Dhabi, Trucial Oman, Arabia, and of Musaiyib no. 1 well, Hilla Liwa, Iraq.

REMARKS. The Middle East occurrences of this species are known only by random thin-sections, which however correspond well in dimensions and detail to those of the Libyan type-material ; external diameters observed are 0·650–0·702 mm., with corresponding internal diameters of 0·182–0·208 mm. (28–30%). Moreover, other algae associated at the type-locality are also seen in the Middle East occurrences : *Dissocladella undulata* (Raineri) Pia at both localities and the codiacid *Boueina pygmaea* Pia as well at Ras Sadr.

## *Trinocladus perplexus* Elliott

(Pl. 24, figs. 1, 2, 6, 7)

1955b *Trinocladus perplexus* Elliott : 128, pl. 1, figs. 16–18.
1960 *Trinocladus perplexus* Elliott ; Elliott : 225.

DESCRIPTION. Tubular cylindrical calcified dasyclad, probably originally slender club-shaped. Length (incomplete) up to 2·5 mm. seen, with external diameters increasing from about 0·32 to 0·44 mm., and the proportion of internal diameter to external constant at 53%. Fragments of smaller examples of 0·26 mm. diameter show an internal diameter of only 40%. The wall shows consecutive horizontal verticils of lateral branches : in the large example quoted the verticils are spaced at about 17–19 per mm. in the lower, slimmer portion of the tube, diminishing to about 12 per mm. later. Each verticil consists of 7–10 branches : these communicate with the stem-cell cavity by rounded-rectangular pores. Each short thick primary divides into four secondaries : in the older, slimmer parts of the thallus this is all the branching seen, but in the later, wider portions each secondary divides into four tertiaries which reach the exterior as pores.

Horizon. Palaeocene–Lower Eocene of Iraqi Kurdistan.

Material. From the Kolosh Formation (Palaeocene–Lower Eocene) of Surdash, Sulemania Liwa ; Koi Sanjak, Erbil Liwa, and Sundur, Mosul Liwa : all in northern Iraq.

Remarks. *Trinocladus perplexus* is the almost invariable companion of the codiacid *Ovulites morelleti* Elliott in the clastic facies or Kolosh green-rock sands of Kurdistan, where occurrences of the two species far outnumber occasional records of other algae. *Trinocladus* is however missing from the varied, richly algal Sinjar limestone and marl facies of the same age-range, where *O. morelleti* is also abundant. This ecological distribution is considered elsewhere in this work.

*T. perplexus* has not been seen outside this limited area ; its distribution is thus very different from that of the related *Thyrsoporella silvestrii*, or indeed from the older species *Trinocladus tripolitanus*.

### ***Trinocladus radoicicae*** sp. nov.

(Pl. 24, fig. 8)

Description. Tubular cylindrical calcified dasyclad, probably originally slender club-shaped. Length unknown, fragments up to 1·0 mm. seen ; maximum observed diameter 0·75 mm. d/D ratio about 33%. Smaller transverse sections of 0·42 mm. and 0·34 mm. diameters show a verticil of seven branches : the primaries swell out markedly before dividing into thinner secondaries (probably four) and these in turn into several tertiaries. Specimens of smaller diameter show only primaries and secondaries.

Horizon. Maestrichtian of Iraqi Kurdistan and (subsurface) Dukhan, Arabia.

Syntypes. The specimens figured in Pl. 24, fig. 8 from the Tanjero Clastic Formation (Maestrichtian) of Diza, Erbil Liwa, Iraq. V. 52116.

Other Material. Several random thin-sections from the same formation and horizon, Diza, Erbil Liwa, and Balambo, Sulemania Liwa, Iraq. Also similarly from the subsurface top Aruma of Dukhan no. 1 well, Qatar, Arabia.

Remarks. Although the green-rock clastic facies continues in Iraqi Kurdistan from Tanjero Formation (Maestrichtian) to Kolosh Formation (Palaeocene), it contains different species of the codiacid *Ovulites*, *O. delicatula* Elliott and *O. morelleti* Elliott respectively. These are presumably successional in evolution. As already remarked, *Trinocladus perplexus* is the constant companion of *O. morelleti* in the Palaeocene ; *T. radoicicae* is now described as the Maestrichtian associate of *O. delicatula*. It is, however, rare and fragmentary when compared with *O. delicatula* (itself much less common than *O. morelleti*).

*T. radoicicae* is similar in form, approximate size and succession of branch-complexity within the one thallus to *T. perplexa*. It differs noticeably in the form of the branches : those of *T. perplexa* are spindly compared to the very swollen primaries of *T. radoicicae*, where each branch takes proportionally more space and hence there are fewer branches per verticil.

This species is dedicated to Mme. R. Radoičić of Belgrade, Jugoslavia, as a tribute to her many contributions to palaeophycology, and friendly correspondence with me.

### Genus ***TRIPLOPORELLA*** Steinmann 1880

Diagnosis. Club-shaped calcified dasyclads with large stem-cell, close-set verticils of numerous branches each consisting of an elongate cylindrical primary containing sporangial bodies, and dividing into several thin hair-like secondaries.

Remarks. The large and showy *Triploporella* spp. of the Upper Jurassic and Cretaceous are curiously ill-represented in the Middle East material now studied. No further material of *Triploporella fraasi* (Steinmann 1880 ; 1899) from the Lebanese Albian has been examined : most of this author's descriptive detail came from his Mexican specimens and not from the ill-preserved Lebanese fossils. Three other Middle East records of the genus known to the writer are all Cretaceous, all represented by very few random thin-sections, and none specifically determinable. Two, from the Lower Cretaceous of Burum, Wady Hiru Basin, Hadhramaut, and from the subsurface Garagu Formation (Valanginian-Hauterivian) of Makhul no. 1 well, Mosul Liwa, Iraq, are compatible in size with such a species as *T. marsicana* Praturlon from the Italian Barremian-Aptian. The third, from the Qamchuqa Formation (Aptian-Albian level) of Sarmord, Sulemania Liwa, Iraq, is much smaller than any described species.

## IV. THE STRATIGRAPHIC SUCCESSION OF DASYCLAD ALGAE

The stratigraphic ranges in the Middle East of most of the dasycladaceae described in this work are set out in Fig. 6. Before discussing these in relation to the different geological levels involved, the general reliability of the family for stratigraphic purposes must be considered.

Dasycladaceae are sessile benthos with well-defined coastal ecologic requirements, the latter discussed below (p. 92). It is, therefore, rare for them to show the limited substage range of an ammonite species, and they are inevitably influenced by facies. Against this, the Tethyan coasts and shelf-seas furnished a long succession of suitable habitats for growth and entombment, and dasyclad euryhalinity permitted frequent proliferation in emergent areas when their abundance as microfossils matched that usual with marine foraminifera, themselves scarce or banal under these conditions. In the favoured area of the Middle East, therefore, (and this probably applies to many other areas in the Tethyan belt), I have often found it possible to date to stage-level by a consideration of dasyclads in association with other algae, and their relative abundance (cf. Elliott, 1960). Supplementary confirmation from other fossils has been welcome, but rarely contradictory.

A similar conclusion was independently reached by Praturlon (1966), for the Liassic to Palaeocene algae of the central Apennines, Italy. It is of interest to compare the


Fig. 6. Stratigraphic ranges of dasyclad algae in the Middle East.

ranges of 29 dasyclads listed by him with the 45 now shown for the same time-interval in fig. 6. A general correspondence of restricted ranges, with individual, local differences, may be observed.

## Permian

The dasycladaceae recognized from the Iraqi Permian and their distribution therein are shown in Fig. 7. This Permian succession is approximately 800 m. thick, and was sampled by Wetzel and others through complete successions near the localities of Ora and Harur, in the north of Mosul Liwa, near the Turkish frontier. The general succession is set out in Dunnington, Wetzel and Morton (1959) where the whole series of thick upper and lower limestone divisions, separated by a thinner evaporitic development, is named the Chia Zairi Formation ; Hudson (1958) has named the two thick limestone divisions, so that the succession, from bottom to top, comprises Zinnar Formation, Satina Evaporite Formation and Darari Formation.

The Zinnar rests unconformably on Carboniferous (Tournaisian). The Darari, at its top, shows evidence of progressive shallowing, though the actual contact with the overlying Triassic is said to be abrupt.

Of the rich faunas collected, only two, both from the Zinnar, have been adequately investigated. A coral fauna, from the *Wentzelella* limestones at about the middle of the Zinnar, was compared by Hudson (1958) with similar faunas elsewhere in Asia, the latter often including *Neoschwagerina*, especially *N. cratulifera* (Schwager) " which could quite well be the age of the *Wentzelella*-Limestones of Iraq ". This would be Artinskian-Kungurian (or Leonard-Word). A fusulinid-fauna occurs near the base of the Zinnar : this was studied by Lloyd (1963) who thought it " somewhat older " than a comparable Iranian assemblage dated as of *Parafusulina*-zone age i.e. a possible Sakhmarian-Artinskian (Wolfcamp-Leonard) age for this lower part.

No other detailed faunal evidence for age is at present available above these levels, though the upper Darari is similar to the north Italian *Bellerophon*-limestone described by Accordi (1956). It may be that sedimentation was more or less continuous throughout, up to the Triassic contact, and that the Zinnar-Satina-Darari correspond to ?Sakhmarian (part), Artinskian-Kungurian-Tartarian, but this remains to be proved by detailed analysis of the faunas. It is unlikely that the boundaries of the Satina will correspond with stage levels. Against this lack of detail the ranges of the dasyclads are of some interest.

*Mizzia velebitana* ranges from near the base of the Iraqi Permian to near the top, accompanied by the nondasyclads *Gymnocodium bellerophontis* and some *Permocalculus* spp. The other dasyclads have very different ranges. *Anthracoporella mercurii* is confined to the basal beds of the Zinnar : *Pseudoepimastopora ampullacea* occurs in the Zinnar only, as do the non-dasyclad *Ungdarella* Maslov and the new *Permoperplexella*. *Atractyliopsis darariensis* occurs only near the top of the Darari, and *Pseudovermiporella sodalica* only within this formation. " *Clypeina* sp. " marks the emergent conditions of the Zinnar-Satina contact level.

It is probable that a fresh sampling, carried out primarily for the collection of algae, would add much to our knowledge of these fine sections and of the Permian in general, and possibly permit an algal zonation, from dasycladaceae and other families, of potentially wide application in Asia.

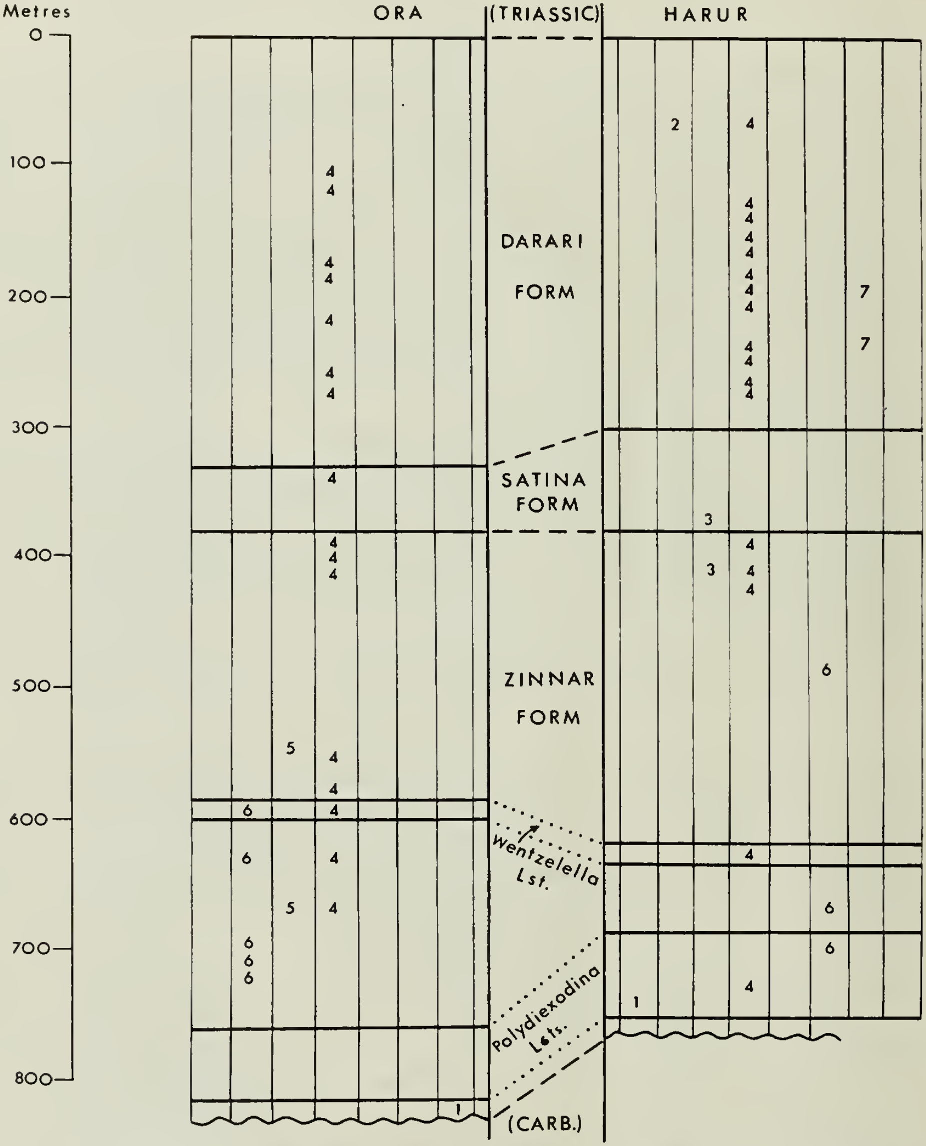


FIG. 7. The Permian dasyclads of Iraqi Kurdistan at Ora and Harur, Mosul Liwa. 1. *Anthracoporella mercurii* Elliott. 2. *Atractyliopsis darariensis* Elliott. 3. " *Clypeina* " sp. 4. *Mizzia velebitana* Schubert. 5. *Permoperplexella attenuata* Elliott. 6. *Pseudo-epimastopora ampullacea* Elliott. 7. *Pseudovermiporella sodalica* Elliott.

## Lower Jurassic

The occurrence of the Liassic *Palaeodasycladus* in the Lower Musandam of Oman is compatible with the age from other evidence (Hudson & Chatton 1959), but as the alga is so far recorded only from one level it shows no more than as an easterly occurrence of this well-known Mediterranean fossil.

## Upper Jurassic–Lower Cretaceous

The ranges of various dasyclads in the Middle East at these levels are shown on the chart. Reference to the European literature indicates different local ranges for some of these species. Thus *Actinoporella podolica* is Portlandian at the Galician type-locality, Portlandian–Valanginian in Switzerland, Portlandian-Hauterivian in Italy, and Valanginian-Aptian in the Middle East. This probably reflects facies-preference along successive Tethyan coasts, partly obscured by some occurrences being preserved in off-shore debris-facies. It is of course possible that a suite of similarly well-preserved specimens from each locality would permit successional subdivision of the species. The type-material comprises loose, dissociated verticils, whereas most of the other records are from random thin-section material. However, this must await future studies. In association with other microfossils, *A. podolica* is a useful species in the Middle East, as are most dasyclad remains. *Munieria baconica* shows a somewhat similar range, with varying local occurrences. By contrast, such species as *Clypeina lucasi* and *C. marteli* occur only at the same level in Oman as that of the Algerian types. The European ranges of a dasyclad species, and the details of its Middle East occurrences, will already have been noted under each species-description.

The algal dating of the Jurassic–Cretaceous contact in the wholly marine Tethyan succession is of some importance. Over large type-areas of western Europe a varying thickness of nonmarine Purbeck-facies strata occurs between undoubted marine Upper Jurassic and Lower Cretaceous. This Purbeckian is conventionally assigned to the Jurassic, though the studies of Donze (1958b) on the Jura area, and Casey (1963) on England, suggest that much of it is Cretaceous (see also Bartenstein, 1965). In southern France, where marine Tithonian is succeeded by marine Berriasian, the two may be distinguished by their ammonite faunas. In many other Tethyan limestone successions at this level the absence of ammonites, whether due to their non-occurrence in the fauna or their non-availability as in samples from bore-holes, necessitates estimation of the junction from microfossils in thin-section. The foraminifera give no clear picture, and tintinnids are confined to a special stratigraphical facies. Dasyclad algae are often abundant ; in my experience, if determined carefully, with a full knowledge of their recorded ranges elsewhere and used in conjunction with non-dasyclad algae such as *Permocalculus* spp. and various non-algal fossils such as the hydrozoan *Cladocoropsis*, it is usually possible to give an accurate age-determination.

## Upper Cretaceous

The dasyclads of the Middle East Upper Cretaceous are fewer in number than those of the Lower Cretaceous. The most important florules are the *Trinocladus tripolitanus* assemblage of about Turonian age, common to North Africa, Iraq, Trucial Oman and perhaps elsewhere, and the Maestrichtian assemblage of which *Cymopolia tibetica* also occurs in the Himalayas.

### Palaeocene–Lower Eocene

The rich dasyclad flora of Kurdistan and elsewhere occurs throughout the Palaeocene and Lower Eocene. In Kurdistan it has been possible to date the two stages foraminiferally in certain sections e.g. at Kashti, also at Sinjar and Koi Sanjak (Van Bellen 1959) and unpublished reports. The algae show no consistent stratigraphical differentiation throughout, though there is a sharp change from the Cretaceous below and to the Middle Eocene above. This flora contains elements known from the Indian " Danian " of the Trichinopoly coast (recently correlated on foraminiferal and other evidence with the Lower Palaeocene elsewhere : Sastry & Rao 1964, Rajagopalan 1965) and from the European Montian, and it appears that algally at any rate the Palaeocene commences with the immediate post-Maestrichtian, which is also the opinion of some workers on foraminifera (e.g. Berggren 1964). In this connection it should however be noted that the Tethyan Danian-equivalent (if and when present) may not easily be recognizable by comparison with the northern European type-development.

## V. THE GEOGRAPHICAL DISTRIBUTION OF TETHYAN ALGAE

The most casual student of Tethyan fossils is struck by the very wide east-west distribution of Tethyan facies and fossils, which occur in disconnected outcrops over enormous distances : there is often more difference between the south of England and the south of France at the same level than correspondingly between Spain and the Middle East, India or even Borneo. The algae are no exception to this : in the Permian *Mizzia velebitana* and the non-dasyclad *Gymnocodium bellerophontis* have a world-wide latitudinal distribution, and in the Cretaceous *Neomeris cretacea* occurs in both Mexico and the Middle East. The Liassic *Palaeodasycladus* ranges from Algeria to Iran, and the Upper Jurassic algal suite from France and Switzerland to the Persian Gulf, while *Terquemella* is found in the Palaeocene–Eocene of Central America, Europe, the Middle East and India. It is true that there are curious absences and near-absences from the collections studied, e.g. the Jugoslav Permian *Velebitella* (also known from Turkey, Güvenç 1965) and the Italian Cretaceous *Triploporella* spp., both of which one would expect to find conspicuously at the appropriate levels, but future collecting may well remedy this.

With this wide marginal-Tethyan distribution of the same or closely-related species it is difficult at most levels to detect evidence of directional migration. The Palaeocene–Lower Eocene of the Middle East, however, shows an apparent mingling of eastern and western elements. *Indopolia* and *Dissocladella* from the east are there, associated with *Cymopolia* from the west. These eastern and western forms quoted are otherwise mutually exclusive at this level to India-Pakistan and Europe,

Palaeocene Algae of the Middle East; Pan — Tethyan and Local types.

---- Approximate Tethyan Margin

- Broeckella } Pan — Tethyan
- Clypeina
- Terquemella
- Furcoporella } Local
- Pagodoporella
- Thyrsoporella silvestrii
- Trinocladus perplexus

FIG. 8.

Palaeocene Algae of the Middle East; Eastern and Western types.

---- Approximate Tethyan Margin

- Dissocladella savitriae } Eastern
- Indopolia
- Cymopolia — Western

FIG. 9.

Cymopolia; Upper Cretoceous and Palaeogene occurrences demonstroting Tethyan dispersal.

---- Approximate Tethyan Margin

● Upper Cretaceaus (Maestrichtian) occurrences

○ Palaeogene occurrences

FIG. 10.

Cymopolia; Neogene and living occurrences to show Tethyan origin of relict distribution.

---- Approximate Tethyan Margin

○ Neagene occurrences

● Recent occurrences

FIG. 11.


Trinocladus, an extinct dasyclad;
distribution showing relict –
occurrence in the Palaeocene.
Approximate Tethyan Margin
Trinocladus Spp.
(Upper Cretaceous)
Trinocladus perplexus
(Palaeocene — Lr. Eocene)

FIG. 12.

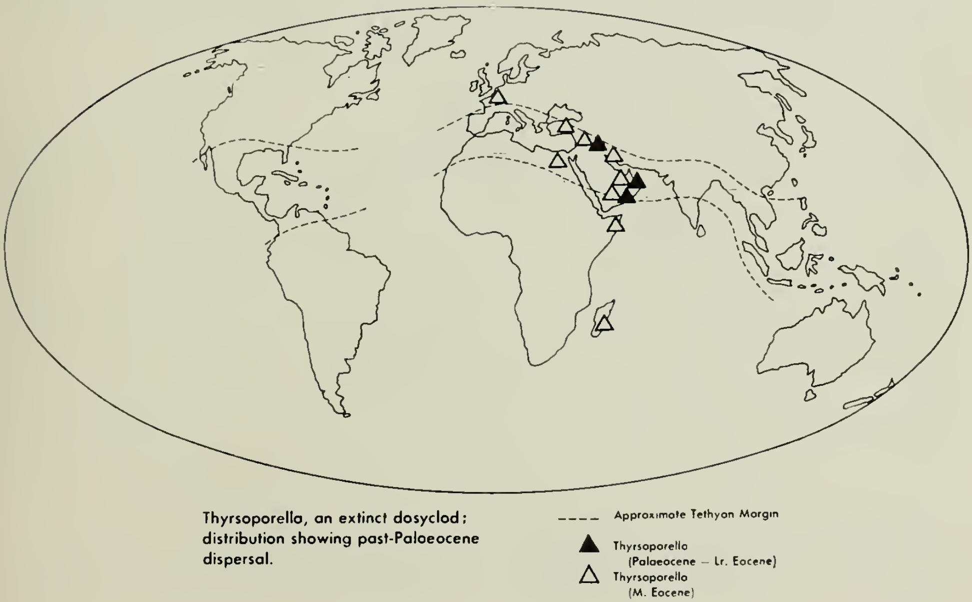
Thyrsoporella, an extinct dasyclad;
distribution showing past-Palaeocene
dispersal.
Approximate Tethyan Margin
Thyrsoporella
(Palaeocene – Lr. Eocene)
Thyrsoporella
(M. Eocene)

FIG. 13.

but *Broeckella*, *Clypeina* and *Terquemella* occur in both as well as in the Middle East, and *Pagodaporella* is so far known only from the Middle East. This assortment of genera in the very sector of the Tethys which in mid-Tertiary was to become the land barrier dividing the marine Mediterranean-Antilles from the Indo-Pacific is no doubt significant for the modern discontinuous distribution of dasyclads, even if most of the genera quoted are now extinct. The distribution-maps (Figs. 8–14) illustrate different aspects of past and present dasyclad occurrences. The value of these dated fossil occurrences may be seen by a comparison with the distribution-maps of Svedelius (1924) which, whilst taking account of former continuous sea-ways, show only Recent distribution.

The work of Kaever (1965), on the micropalaeontology of Afghanistan, contains numerous records of Tethyan algal species familiar in the Middle East. Unfortunately this paper came too late to my notice for inclusion of the detailed species records.

## VI. ECOLOGY

At the present day dasyclads are a relatively inconspicuous element in marine algal floras. Although life has sometimes taken me to warm-water shores, I have never seen or collected living dasyclads. Their ecology has been briefly summarized by Pia (1920), Cloud (1962) and Johnson (1961b), all palaeontologists, for comparison with fossil occurrences. They occur in warm shallow coastal waters in sheltered situations in tropical and subtropical seas, and in areas marginal to the latter, such as the Mediterranean. Their maximum abundance is said to be from low-tide level to 5–6 m. depth, extending down in diminishing abundance to 10 m., and with scattered occurrences below this to 30 m. or more, depending on intensity of illumination and


FIG. 14.

clearness of water. However Edelstein (1964) records *Dasycladus vermicularis* (Scop.) Krasser in the eastern Mediterranean from 18–90 m., represented by well-grown individuals larger than those in the littoral flora ; it seems clear that inferences as to exact water-depths should not be drawn from fossil dasyclads alone. The sheltered parts of coastal bays and some lagoons are favoured habitats, and they are tolerant of the reduced salinities which may occur there. Probably, like most non-stenohaline marine organisms, they are euryhaline and have a limited tolerance for temporary conditions of increased salinity. Such general conditions are associated geologically with regions of uplift, and the fossil dasyclad record confirms this. As with most marine organisms they have a scattered distribution outside the optimum habitat, and Chapman (1961 : 104, 106) gives records of *Neomeris* on mangrove roots and a stunted population of *Batophora* in an exposed situation.

Konishi & Epis (1962) gave a distribution-map showing clearly the restriction of living *Neomeris* spp. to areas within the marine isocrymes for 20 °C, and a table giving bathymetric occurrences. They discussed the implications of this evidence for the fossil occurrences, concluding that the fossil species probably occupied similar warm-water environments, then more widely-spread, as is generally accepted (e.g. Davis & Elliott 1957 : 269).

So far as can be deduced from associated fossils and the nature of the rock, the extinct dasyclad floras of the Middle East (and elsewhere) favoured exactly similar environments in the past to those now favoured by their descendants. However, at times of maximum abundance, dissociated debris of calcareous dasyclad origin forms a conspicuous element in sediments deposited further out to sea, for which the term " debris-facies " was introduced (Elliott 1958a).

In the Permian succession of northern Iraq the dasyclad *Mizzia velebitana* is abundant at many horizons through most of a thickness of over 800 m. It is accompanied throughout by profuse remains of *Gymnocodium bellerophontis* and various species of *Permocalculus*. These Gymnocodiaceae have been variously interpreted (Pia 1937 ; Elliott 1955a ; Konishi 1961) as Codiaceae (Chlorophyceae) or Chaetangiaceae (Rhodophyceae) ; whatever the taxonomic position, both the families cited are quiet-water marine algae today as compared with the reef-forming melobesioids. It is significant that amongst all the Iraq Permian algae there occurs only one solenoporoid, a group supposedly ancestral to the melobesioids (Elliott 1965a) and similarly of reef and shoal facies, and that uncommonly ; *Solenopora centurionis* Pia. The *Mizzia-Gymnocodium* association, sporadically abundant in the lower or Zinnar Formation, disappears within the lowest beds of the median Satina Evaporite, along with other algae and almost all fossils, but reappears in the uppermost beds, and so into and through the Upper or Darari Formation. At the top this latter shows signs of transition to the overlying but unconformable Lower Triassic, which is in the Werfenian alpine facies without remains of algae.

The Iraqi Permian contains some beds with a predominantly coral, brachiopod or crinoid fauna (Hudson 1958 ; Dunnington, Wetzel & Morton 1959). Moreover, in some of the algal beds the coarse colander-pore *Mizzia*- segments are worn, indicating post-mortem drifting from the position of growth. But the algal beds are sufficiently numerous to prove the continued growth of *Mizzia* and other dasyclads in coastal environments throughout the whole period of deposition, even though the sediments at the sampled successions of Harur and Ora reflect the intermittent shifting of this coastline. The minor dasyclad elements, *Anthracoporella, Atractyliopsis, Clypeina, Permoperplexella, Pseudoepimastopora* and *Pseudovermiporella* do not in any way conflict with the picture drawn from the dominant *Mizzia.* The very scarce *Clypeina* occurs at the top of the Zinnar and the bottom of the Satina Evaporite, a fact consonant with later opinions on the facies behaviour of the Mesozoic species.

Rezak (1959) dealing with the Saudi Arabian Permian, observed the occurrence-relationships and associations of *Epimastopora, Gymnocodium* and *Mizzia,* and suggested a possible algal depth zonation as explanation. In Iraq *Pseudoepimastopora* is confined to the lowest division, the Zinnar Formation, in which particularly well-marked coral and brachiopod beds occur and in which the *Gymnocodium-Mizzia* beds are more sporadic than in the later beds. From the sampling available to me, I cannot interpret my records along the lines of Rezak's suggestion, but such depth-zonation may well have existed.

The rarity of Triassic dasyclads in the Middle East has already been noted ; it forms a remarkable contrast to the diplopore-limestone of alpine Europe. The evidence of the Kurdistan Geli Khana and Kurra Chine formations (Middle and Upper Trias) suggests originally unfavourable conditions.

Two Jurassic algal occurrences give a clear picture of the original ecology. The *Palaeodasycladus*-bed in the Liassic portion of the Musandam Formation in peninsular Oman, Arabia, shows a limestone, now partially dolomitized, crowded with healthy, full-grown specimens of well-developed *P. mediterraneus,* whole and broken. Associated are concentric nodules of probable cyanophyte algal origin. The picture is of an extensive spread of the dasyclads in clear, shallow warm water, on a limy bottom: a typical habitat.

In the Upper Jurassic of Qatar and elsewhere in the Persian Gulf area the " Arab zone " (Kimmeridgian-Tithonian) yields a florule of *Clypeina jurassica, Salpingoporella annulata* and *Cylindroporella arabica* occurring in fine-grained and oolitic limestones : associated are numerous crustacean coproliths, *Favreina salevensis* (Paréjas), and small gastropods and foraminifera. The picture is again of shallow, clear limy-bottomed waters, possibly lagoonal or enclosed ; the snails and crustacean traces may be indirect evidence of an abundant growth of non-calcarous green algae of which nothing certain now remains. The modern eel-grass beds of the West Indies and Bahamas would be comparable : Chapman (1961 : 9) gave a Jamaican record of numerous Codiaceae and *Dasycladus* sp. from this environment.

In the same general area of southeastern Arabia a very different picture is given by the Lower Cretaceous algal beds penetrated in the Fahud no. 1 boring. Here the rock is formed of rounded pieces of the crusting problematic algae *Lithocodium* and *Pycnoporidium,* with similar-sized pieces of stromatoporoids and less frequent coral, and rare valves of cemented thecidean brachiopods. Associated are numerous examples of segments of the dasyclad *Cylindroporella sugdeni.* This is reef or shoal debris, current-swept and well-rounded, and washed out some distance from the organic growths which furnished it, even if to no great depth. The *Cylindroporella*, a plant believed to be possibly somewhat similar in form to the living segmented *Cymopolia*, owes its preservation to the relatively large, stumpy, well-calcified segments surviving transport : the plants themselves would have grown on the lee side of the shoals.

In the Iraqi Cretaceous, from the base up to Albian level, dasyclad remains are not uncommon and sometimes abundant. The principal genera involved are *Actinoporella*, *Cylindroporella*, *Munieria* and *Salpingoporella* ; *Acicularia*, *Acroporella*, *Clypeina*, *Pianella* and *Triploporella* also occur. The commonest non-dasyclad alga is *Permocalculus* (see Elliott 1960 for full algal lists). Complete or near-complete fossils, whether tubes, segments or verticils, are relatively uncommon and usually occur in a fragmentary condition, in limy marls and argillaceous limestones. This, the " debris-facies ", has been described by me (Elliott 1958a), where I interpreted it as off-shore sedimentation in which fragments of littoral calcareous algae were sedimented out at sea with inorganic grains of smaller size and higher specific gravity. A comparison was made with modern sediments around Pacific atolls, where fragmentary *Halimeda* and large foraminifera, roughly comparable with the Cretaceous *Permocalculus* and *Orbitolina* respectively, are washed out to sea. No exact analogy proved possible : the very extensive Cretaceous deposits were formed on inter-orogenic shelf-seas then more widely developed than with today's post-glacial submarine topography, and the wealth of Cretaceous littoral green algae proliferated before the maximum, later development in the Tertiary and present-day of reef-forming melobesioid algae. This debris-facies is very characteristic in the Middle East, and is most typical of the Lower Cretaceous, though known elsewhere from the Upper Jurassic. It occurs much more widely than remains of the littoral deposits where the algal material originated.

A completely different facies prevailed in the Upper Cretaceous of Northern Iraq. Here massive limestones, of reef or shoal and fore-reef facies, with abundant rudist remains, show the largely recrystallized remains of the dasyclad genera *Neomeris* and *Cymopolia*. Presumably these dasyclads grew in quiet situations on and around the reefs and rudist banks. In the Maestrichtian this limestone development tongues eastwards into a clastic facies (transition of Aqra Limestones into Tanjero Formation). As is usual with reef-structures, diagenesis has been active within the main calcareous mass and the best fossils occur at the junction, as with the German Upper Jurassic calcisponge and coral reefs, and the Kurdistan Maestrichtian dasyclad *Cymopolia anadyomenea* was described from this well-preserved marginal material. Within the Tanjero itself two fragmentary algae occur not infrequently ; the dasyclad *Trinocladus radoicicae* and the codiacid *Ovulites delicatula*, represented respectively by rare broken tubes and not uncommon bead-like segments. These are remains of littoral algae, sedimented not far off-shore with the sand-grains, and very similar to, say, the codiacid *Penicillus* and the dasyclad *Batophora* in the Recent Bahamas (Newell *et al.*, 1959 : 224).

Finally, the environments of the Palaeocene Dasycladaceae must be considered.

In Iraqi Kurdistan the fossils occur in two principal intergrading formations of the same age. These are the Sinjar limestones and marls, with a rich and varied dasyclad and other algal flora, and the Kolosh clastics, a coarse green-rock sand with a much more restricted flora of which only two species, only one a dasyclad, are common. Van Bellen (1959) considered the Sinjar as marking the reef-like facies of the Palaeocene (and Lower Eocene), which occurred to seaward of the near-shore Kolosh accumulation-zone of clastic detritus from the land. The Sinjar reefs and shoals did not form a continuous barrier, but a broken line of separate reef-banks and islands, sometimes backed by developments of the lagoonal Khurmala Formation, whose altered deposits sometimes contain indeterminate algal debris.

The Kolosh has yielded occasional examples of such dasyclads as *Cymopolia* and *Dissocladella*, and the codiacid *Halimeda*, etc., but the only common algae are the dasyclad *Trinocladus perplexus* and the codiacid *Ovulites morelleti*. These are presumably the descendants of the species-pair of the same genera recorded above for the lithologically similar underlying Cretaceous Tanjero, but they are much more abundant in the succeeding Kolosh. Presumably they were littoral algae from the coast : some indirect support for this is found in the complete absence of *Trinocladus* from the Sinjar, although *Ovulites* is common there. I would suggest this as possibly evidence that *Trinocladus* for some reason only grew along the coast, whence its broken tubes were wafted into the sandy offshore sedimentation, and that Sinjar shoal-conditions were unfavourable to it. By inference, the bulk of Kolosh fossils of *Ovulites* came likewise from the coastal population, and only a minority from the Sinjar shoals : no more in fact than the odd Kolosh *Cymopolia* etc. (unless indeed these came from a minority population on the coast).

Possibly *Trinocladus perplexus* was restricted to littoral waters with fresh-water dilution from the land drainage : *Teredo*-bored wood is not uncommon in the Kolosh Formation (Elliott 1963b), and this is a familiar indication of adjacent coastal or estuarine conditions, as in the English Lower Eocene London Clay.

The richer Sinjar flora seems to have been buried where it lived, more or less, amongst the pockets, pools and channels of the shoal and reef belt. Sedimentation here was more varied and irregular, and fossils are sporadically more abundant. In submerged channels and on submerged shoals, and in sheltered waters between and to the landward of the barrier-components, the dasyclads found conditions congenial to them : they are often very well-preserved and seem to have been buried where they grew, although rolled and broken material is also not uncommon. In these happy conditions a considerable variety of algae grew together : the last abundance of endospore dasyclads (*Trinocladus*, *Dissocladella*, *Thyrsoporella*) and the rare *Broeckella* co-existing with choristospore genera (*Indopolia*, *Cymopolia*), together with *Clypeina* and the more problematic *Furcoporella*. Codiaceae were represented by abundant *Ovulites*, an extinct relation of the modern *Penicillus*, and by *Halimeda*, not yet swamping the flora. But also in the Sinjar environment was a rich variety of calcareous red algae : melobesioids such as *Archaeolithothamnium* spp., *Lithophyllum*, *Mesophyllum*, *Lithothamnium* and *Lithoporella*, with surviving solenoporoids (*Parachaetetes* and *Solenomeris*), and the problematic *Pseudolithothamnium* and *Distichoplax*. Most of these were nodular or crusting forms, forming an appreciable volume of the actual reef-structures and plastering the reef-fronts in the surf zone. These two different environments, favoured by the green and red algae respectively, are strikingly demonstrated by an analysis of Palaeocene–Lower Eocene algae from Iraqi Kurdistan. Of 92 samples selected as showing well-preserved algae, from localities all along the mountain arc from Banik in the north to Sirwan-Balambo in the east, 67% show green algae only, 29% red algae only, and only 4% a mixture of the two. Moreover, in the mixed samples one or other group was a worn minority in each case. The preponderance of green-algal, back-reef samples is perhaps to be explained by the inclusion of samples from intertonguing Kolosh Formation, where only green algae occur, but there is no doubt in which environment any particular sample originated. At some localities, e.g. Sirwan-Balambo, red and green algal samples alternate, reflecting the former shifting reef and shoal pattern through time at the spot now arbitrarily revealed as a cliff-section; at others, e.g. Koi Sanjak and Kashti, green and red algae predominate respectively. These differences reflect local aspects of a palaeogeography not known in detail, but emphasize the mutual exclusiveness of the two environments.

In southwestern Iraq the desert outcrops of the Palaeocene Umm er Rhudhama Formation reveal a different picture. This was a more gently-sloping, non-orogenic shore of the Tethys than the opposite coast described above for Kurdistan : the sea extended as a shallow sheet of water on to the slopes of the Arabian landmass, and sedimentation was slow. The algae are abundant ; although abominably ill-preserved, almost all are dasyclads, and there are no red algae at all. This was a shallow-water coast with frequent sheltered bays with limy bottoms on which spreads and thickets of dasyclads proliferated : it is a much less rich flora than that of Kurdistan, and presumably provided few micro-environments like those of the Kurdistan shoal-belt.

Summarizing, with Dasycladaceae especially in mind, the principal kinds of marine algal associations in the Middle East Tethyan rocks examined indicate :

1. Reef and shoal environments, mostly exposed to rough surface water, or tide- or current-swept. The home of nodular or crusting algae (Solenoporaceae, Corallinaceae and the problematic *Lithocodium*), with dasyclads extremely rare.

2. Fore-reef or seaward shoal-slope deposits. Much debris from the environments of category 1, as well as some indigenous non-dasycladacean algae, and only exceptionally dasyclad debris from elsewhere, depending on current-patterns and sediment-transport.

3. Calm lagoonal waters behind reefs and similar barriers. Abundant Dasycladaceae and Codiaceae, few other calcareous algae, with burial on the site of growth, and only exceptionally current-transport to category 2.

4. Calm coastal bays and similar shallow, largely land-locked waters. Dasycladaceae and Codiaceae as in category 3. Burial on the site of growth, occasional current transport to category 2, and much contribution to category 5.

5. Neritic deposits out to sea on coastal shelves. Much sedimentation of broken littoral and sublittoral algal skeletal remains, largely dasycladacean, as a con-

spicuous minority-constituent of calcareous muds. This is the " debris-facies " (Elliott 1958a).

It must be emphasized that some of the local rock-facies encountered are not easily recognizable in terms of the environments set out above. Diagenesis has sometimes obscured or obliterated part of the evidence, but above all knowledge of the small-scale lateral facies-changes is insufficient for full interpretation of the ecology of the fossil-assemblages seen in hand-specimens. The original surveys were stratigraphical and structural in intent, and only much later were the algae recognized by me in thin-sections and hand-specimens of others' collecting, and then put aside for this and other studies.

The Middle East dasyclad environments reconstructed above are varied in time and space, and in the nature of the rocks which now entomb the fossil evidence. But it is noteworthy that none have yielded any evidence to suggest to me that the ecological requirements of the dasyclads of the past were essentially different to those of their living descendants.

## VII. THE EVOLUTION OF THE DASYCLADACEAE

From the introductory account given above, it will be remembered that the collection of dasyclads from the Middle East which forms the subject of this work was selected from material collected for general stratigraphical purposes. Exceptionally it proved rich in species for palaeobotanical study, but much of it yielded only sufficient evidence for identification and age-correlation with species previously described elsewhere. Nevertheless, so much material, dasyclad remains from an Upper Palaeozoic to Lower Tertiary timespan in a mid-Tethyan area favourable to them, inevitably invites the question as to whether any further light is thrown on the evolution of the family as a whole.

It may be said at once that nothing emerges seriously to modify the general picture of dasyclad evolution sketched by Julius Pia (Pia, see bibliography of : see also Rezak 1959c). The dasyclads, having achieved the verticillate branch-pattern in the Palaeozoic, proceeded to progressive and varied elaboration of the side-branches, and to the progressive shift of the reproductive structures from within the primitive thick stem-cell, into swollen lateral branches, and finally into special structures borne on the laterals, or into the specialized reproductive discs characteristic of some genera. The reproductive structures themselves are disappointing: they yield no reasonable evidence of sexual mechanisms as have the fossil Melobesioids (e.g. M. Lemoine 1961), or the Chaetangiaceae (Elliott 1961). Presumably the dasyclad reproductive bodies known conventionally in the fossils as sporangia, were similar to those of most Recent genera and so contained resting cysts from which gametes were only set free after shedding : this arose as a necessary consequence of the well-developed calcification around these organs. Release of the reproductive elements thus became only possible after the break-up of the calcified layers, and calcification is usually well-developed around the sporangia. The living *Dasycladus* with restricted stem-cell calcification only, is exceptional in shedding its gametes direct. This condition was regarded by Pia as secondary, *Dasycladus* thus bearing no more direct relation to the ancestral non-calcified proto-Dasyclad than a naked slug has to the unshelled proto-gastropod. If this is so, and if the present writer's analysis of *Pagodaporella* is correct, then this condition had arisen by the beginning of the Tertiary, but was and is uncommon.

If the fossil sporangia are intrinsically uninteresting, their progressive evolutionary movement within the dasyclad plant, from endospore to cladospore to choristospore, is the most persistent trend in dasyclad evolution. In the genera studied, an endospore genus (*Atractyliopsis*) occurs in the Permian, where it is accompanied by cladospore genera. Cladospore genera predominate in the Mesozoic and survive to the Palaeocene, where they are represented by such genera as *Trinocladus* and *Thyrsoporella*, and *Broeckella*. Choristospore types of conventional pattern appear in the Cretaceous (e.g. *Cymopolia*, which also shows a species intermediate in this character) and are dominant today. In Recent genera with terminal reproductive discs these structures are regarded (Fritsch 1935 : 397 ; Egerod 1952 : 341) as homologous with reproductive structures borne laterally on the primary branches of choristospore dasyclads *e.g.* *Bornetella*. If the extinct *Clypeina* is grouped with *Acetabularia* and *Acicularia*, as suggested by various workers (see above p. 28), then this specialized condition, expressed in *Clypeina* as serial fertile whorls rather than as a single terminal disc, arose possibly in the Permian, certainly in the Triassic. That is, it arose at the same time as, or later than, the change from endospore to cladospore and before the evolution of the choristospore type proper so far as is known. This suggests that the serial reproductive discs of *Clypeina* are homologous with the swollen branches of cladospore genera, and that the genus (?Permian, Triassic–Oligocene) is thus an earlier, different, achievement of this structure than the Acetabulareae (?Jurassic, Cretaceous–Recent) show. It is noteworthy that the radial tubules of *Clypeina* spp. do not show the calcified sporangial contents in fossils as do those of *Acicularia* ; that is they correspond in this respect to the normal swollen branches of cladospore genera, which only exceptionally display this condition e.g. *Triploporella*. Moreover, *Clypeina* became extinct in the Tertiary as did other cladospore genera, while the living dasyclad flora, of choristospore genera, includes *Acetabularia* and *Acicularia*. It seems likely, therefore, that the discs of *Clypeina* represent an earlier development in time of the condition seen in *Acetabularia*, morphologically similar but of dissimilar origin ; this is a not uncommon phenomenon in evolution. *Clypeina* is therefore placed in the new tribe Clypeineae, to include forms with reproductive discs considered to be of cladospore origin.

From a strictly morphological point of view, the relegation of *Actinoporella* to the synonymy of the earlier-proposed *Clypeina*, now known to contain a small minority of stellate species somewhat like *Actinoporella*, is a logical proposal. However, the earliest stellate *Clypeina*, the Valanginian *C. marteli* Emberger, is one of a group of varied species appearing after the disappearance of the Upper Jurassic *C. jurassica*, and presumably evolved from it at the time of the terminal Jurassic uplifts and lagunal developments. *Actinoporella* itself co-existed in the Upper Jurassic with *C. jurassica*. Pia's suggestion (1927 : 693) that *Clypeina* arose direct from *Actinoporella* must await understanding of the Permian *Clypeina*, and possible new

Mesozoic records. His interpretation of *Actinoporella* as similar to the Triassic *Oligoporella* but differently calcified is followed here : *Actinoporella* is regarded as a valid genus and left in the Diploporeae.

These problems apart, the evolutionary change in position of dasyclad reproductive structures is the most significant feature of their long history. It has been written (Elliott 1962) " we do not clearly know the special advantage of choristosporic structures, whether a direct one in shedding reproductive elements more easily, or an indirect one in their being produced more freely and lavishly with no greater or even less strain on the metabolism of the plant, but although not properly understood it is a main trend in dasyclad evolution ".

Although no precise elucidation of this point can be offered here, the trend itself, clearly indicated by Pia (1920), has been confirmed by subsequent work including the present study. Whatever its significance, it has not saved the Dasycladaceae from decline to a very subordinate position indeed in modern marine floras. Although growths of living dasyclads sometimes form extensive patches or thickets on the sea-floor, I know of no existing deposit in which a great thickness of sediment consisting principally of their calcareous tubes is being accumulated. A prolonged and persistent dense growth of dasyclads to build up considerable thicknesses of dasyclad limestones as are known from the Alpine Trias, e.g. the Essino Limestone of northern Italy, is apparently a thing of the past. Pia (1920 : 187) attributed this decline of the dasyclads principally to the development and spread of the articulated Corallinaceae, with different cellular organization, from the Cretaceous onwards. Much of this spread was into environments for which the dasyclads were not suited, by reason either of the mechanical effects of water movement or of lower temperatures. The appropriate modern ecological analogue comes from a related family of green algae, the Codiaceae, where *Halimeda* occurs in dense growths, notably in the lagoons of atolls and other back-reef environments once largely colonized by dasyclads. Calcified segments from generation after generation of plants pack down to form true *Halimeda*-limestones, well evidenced by borings into the reefs of these

Fig. 15. Diagrammatic vertical sections of comparable portions of the dasyclad *Cymopolia* (left) and the codiacean *Halimeda* (right). Plant tissue stippled, calcareous structure black. To show the encased dasyclad sporangia and free codiacean reproductive growth. Greatly enlarged.

islands, and by many records of *Halimeda*-limestones in the Tertiary of tropical and subtropical latitudes. Since *Halimeda* is quite heavily calcified, it is not calcification itself which has impeded the spread of dasyclads amongst more numerous non-calcified green algae in suitable environments. The explanation probably lies in the reproductive mechanism : *Halimeda* sheds abundant gametes freely from special deciduous non-calcified outgrowths from the segments. In almost all dasyclads the release of the resting cysts depends on eventual break-up of the calcareous structures. The reproductive bodies of *Halimeda* are almost unknown in a fossil state, a unique occurrence being recorded by Pfender (1940 : 245), whereas those of dasyclads survive unbroken in a majority of the specimens found fossil. There is some evidence which has been interpreted as indicating that *Halimeda* was of hybrid codiacean origin in the late Cretaceous (Elliott 1965b) ; certainly its spread and abundance in the Tertiary and at the present day is remarkable. For all their morphological elaboration, the dasyclads did not overcome the initial handicap inherent in the calcification of the reproductive bodies ; this in turn springs indirectly from the basic morphology of laterally whorled stem-cell, the Codiaceae by contrast being formed of richly-branched, agglomerated threads with largely marginal calcification between these and not encasing them, at any rate in the actively growing segments. There is some similarity with marine invertebrate evolution, where, amongst the brachiopods, progressive evolution of very complicated calcareous supports for the fleshy lophophore did not compensate for the basic inferiority of this organ when compared with the functionally comparable gill of the lamellibranch mollusca.

It is difficult, and perhaps impossible, to effect a quantitative consideration of the factors considered above, but they are considered to be in some measure responsible for the " relict group " nature of existing dasyclads, and for their general subordinate position amongst modern marine algal floras.

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## IX. APPENDIX

*Geographical co-ordinates of localities mentioned in the text.*

| | |
|---|---|
| ABIAD, J. | 56°35′E 23°35′N |
| ADANA | 35°18′E 36°58′N |
| AIDAH | 43°40′E 30°50′N approx. |
| AL GHURRA | 43°40′E 30°50′N approx. |
| AL HAMIAH | 47°40′E 14°00′N |
| ALA-DAG | 29°30′E 36°30′N |
| AMADIA | 43°29′E 37°05′N |
| AQABAR KHEMER | 48°12′E 14°48′N |
| AQRA | 43°45′E 36°47′N |
| ARGOSH | 44°10′E 37°8′ N |
| ARUS, W. | 48°20′E 14°15′N |
| ATSHAN | 42°55′E 36°20′N |
| AWASIL | 42°49′E 33°27′N |
| BALAMBO | 45°58′E 35°7′ N |
| BANIK | 42°58′E 37°12′N |
| BASRAH | 47°51′E 30°30′N |
| BATINAH | 56°57′E 24°25′N |
| BEKHME | 44°14′E 36°40′N |
| BIH, W. | 56°10′E 25°45′N |
| BURUN (BURUM) | 49°00′E 14°30′N |
| BUSYAH, J. | 56°10′E 25°45′N |
| BUWAIDA, J. | 56°20′E 23°10′N |
| CHALKI | 43°10′E 37°14′N |
| CHALKI ISLAM (see Chalki) | |
| CHAMA | 44°14′E 36°50′N |
| DAMMAM | 50°00′E 26°20′N |
| DIYANA (DIANA) | 44°33′E 36°40′N |
| DIZA | 44°18′E 36°46′N |
| DUKHAN | 50°47′E 25°26′N |
| FAHUD | 56°31′E 22°18′N |
| FAIYAH, J. | 55°50′E 25°10′N |
| FALLUJAH | 43°46′E 33°21′N |
| GAL-I-MAZURKA | 43°29′E 37°05′N |
| GARA, J. | 43°27′E 36°59′N |
| GHABAR | 48°45′E 14°13′N |
| HAGAB, J. | 56°10′E 25°45′N |
| HAJAR, W. | 48°00′E 14°30′N |
| HARUR | 43°15′E 37°14′N |
| HAUSHI | 57°40′E 21°00′N |
| HUGF | 57° E 20° N |
| JOL BA HAWAR | 48°18′E 14°25′N |
| JUWEIZA | 55°42′E 25°14′N |
| KASHTI | 45°45′E 35° 8′N |
| KAUR, J. | 58° E 22°30′N |
| KIRKUK | 44°24′E 35°28′N |
| KOI SANJAK | 44°38′E 36° 5′N |
| LAUT, J. | 47°00′E 14°15′N |
| MA'ADI PASS | 49°25′E 15°00′N |
| MAKHUL | 43°20′E 35°13′N |
| MILEH THARTHAR | 42°44′E 32°11′N |
| MINTAQ | 48°00′E 14°30′N |
| MURBAN | 53°44′E 23°53′N |
| MUSAIYIB | 44°25′E 32°49′N |
| ORA | 43°21′E 37°17′N |
| PILA SPI | 45°45′E 35°15′N |
| QAMAR, J. | 56°04′E 25°28′N |
| RAS SADR | 54°44′E 24°48′N |
| ROWANDUZ | 44°33′E 36°37′N |
| RU KUCHUK | 44° 8′E 36°56′N |
| SAHIL MALEH | 58°40′E 23°40′N |
| SARMORD | 45°02′E 35°54′N |
| SEDELAN | 45°00′E 35°45′N |
| SEKHANIYAN | 45°09′E 35°52′N |
| SIRWAN | 46°10′E 35°05′N |
| SULEMANIA | 45°26′E 35°33′N |
| SUNDUR | 43° 4′E 30°56′N |
| SURDASH | 45°06′E 35°51′N |
| TANAMIR, J. | 58°06′E 22°39′N |
| TAWI SILAIM | 58°35′E 22°25′N |
| WAGSA | 43°45′E 30°35′N |
| ZIBAR-ISUMERAN | 44° 5′E 36°52′N |

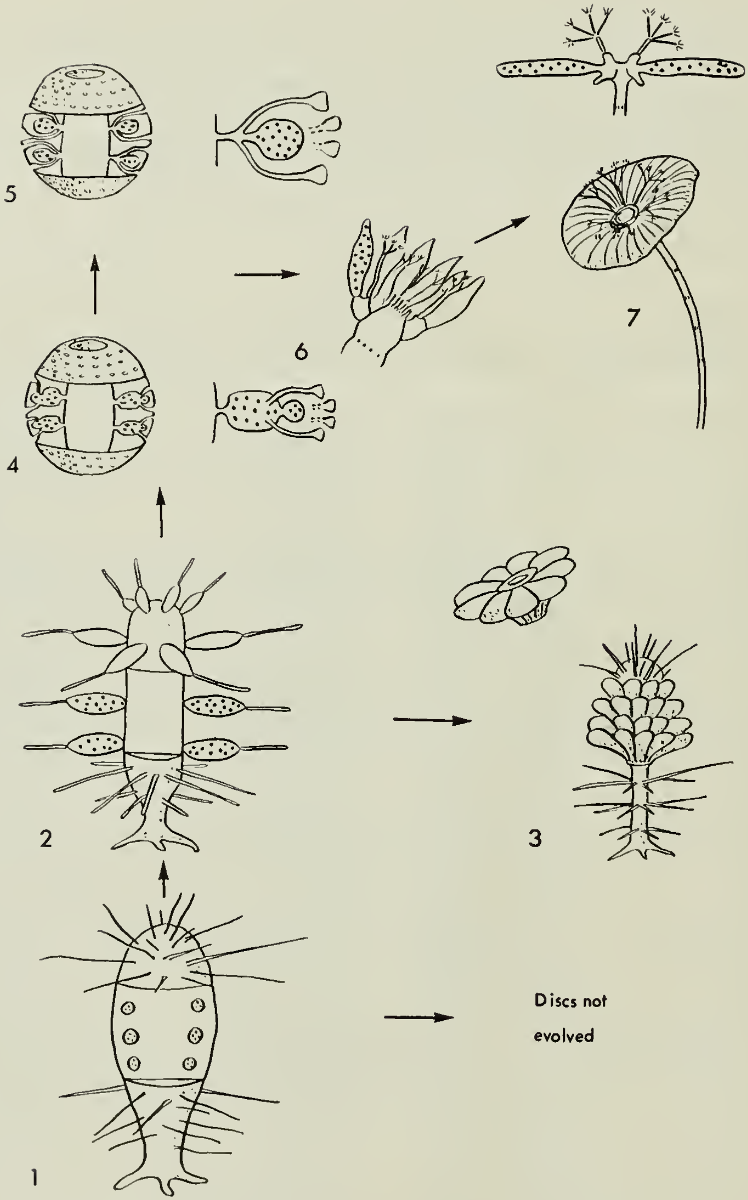


FIG. 16. Reproductive Evolution in Dasycladaceae. 1. Idealized endospore dasyclad (typically Palaeozoic), showing sporangia within the stem-cell and simple, sterile branches. No calcification shown : this feature is variable between different known genera. 2. Idealized cladospore dasyclad (typically Mesozoic), showing sporangia within swollen branches, and separate whorls of fertile and sterile branches. No

## EXPLANATION OF PLATES

Unless otherwise stated, all material is housed in the British Museum (Natural History).

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calcification shown : this feature is variable between different known genera. 3. *Clypeina* : separate fossil disc and reconstruction of living plant (Permian to Oligocene). Separate whorls of naked sterile branches and fertile whorls of fused, heavily-calcified branches. Shape and fusion of discs or cups variable between species. 4. Segment of *Cymopolia eochoristosporica* Elliott (Upper Cretaceous), and separate branch-diagram. This species transitional between cladospore and choristospore, showing as a small cymopoliform branch-system developing on the end of a swollen cladospore branch. 5. Segment of *Cymopolia* sp. (Tertiary) and separate branch-diagram, to show typical choristospore branch with separate sporangial body at junction of primary and secondary branches. *Cymopolia* is segmented and heavily calcified, but other choristospore genera exist which are single (non-segmented) and more lightly calcified. 6. Sketch of portion of *Halicoryne* (Recent) to illustrate choristosporic organization with different proportions and arrangement of the component elements. The large elongate gametangium (left) is paired with a much smaller sterile branch-system, the whole whorl grouped in a loose basket-like circular arrangement. Light incomplete calcification only. 7. *Acetabularia* (Recent). Plant showing typical mature calcified reproductive disc and stem, also diagrammatic cross-section of disc. This may be regarded as a fused calcified structure analogous to that of *Halicoryne* (note small sterile branches) : the scars of early sterile whorls may be seen on the stem. *Acetabularia* is thus the choristosporic disc-analogue to the cladosporic *Clypeina*, as now interpreted.

## PLATE 1

***Acicularia, Acroporella, Actinoporella, Anthracoporella***

FIGS. 1, 3. *Acicularia antiqua* Pia, random cuts in thin-section, ×60. Cretaceous, Barremian-Aptian, Upper Musandam Formation : Jebel Hagab, Oman, Arabia. V. 52031.

FIG. 2. *Actinoporella podolica* Alth, near-vertical section through stem-cell and two branches of one verticil, ×28. Cretaceous, Valanginian, Garagu Formation : Banik, Mosul Liwa, Iraq. V.41630.

FIG. 4. *A. podolica*, near-horizontal section through a verticil, ×45. Cretaceous, Valanginian-Hauterivian, Sarmord Formation ; Jebel Gara, Mosul Liwa, Iraq. V. 41579.

FIG. 5. *Acroporella assurbanipali* gen. et sp. nov., oblique-vertical section, ×20. Holotype. Cretaceous, Valanginian-Hauterivian, Garagu Formation ; subsurface, Kirkuk Well no. 116. V. 52032.

FIG. 6. *Acicularia* (*Briardina*) sp., thin-section along spicule, ×60. Palaeocene-Lower Eocene ; Sahil Maleh, Batinah Coast, Oman, Arabia. V. 52033.

FIG. 7. *A. podolica*, typical random tangential-vertical cut through adjacent radial tubules of verticil, ×30. Cretaceous, Valanginian-Hauterivian, Sarmord Formation ; Jebel Gara, Mosul Liwa, Iraq. V. 52034.

FIG. 8. *Anthracoporella mercurii* sp. nov., thin-section, holotype. Permian, Bih Dolomite ; Wady Bih, Jebel Hagab, Peninsular Oman, Arabia. V. 52035.

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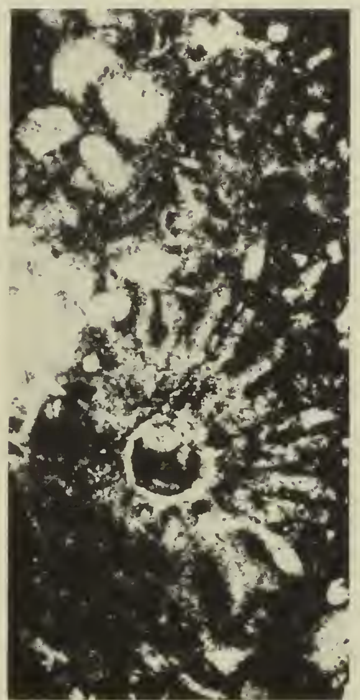

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## PLATE 2

### *Anthracoporella, Atractyliopsis*

FIGS. 1, 2. *Anthracoporella spectabilis* Pia, thin-section ×12, and portion enlarged to show wall-detail, ×24. Permian ; derived cobble in Triassic conglomerate ; Jebel Busyah, Oman, Arabia. V. 52036.

FIGS. 3–5. *Atractyliopsis darariensis* sp. nov. Thin-sections ; 3. Paratype, oblique-vertical, ×28 V. 52015 ; 4. Paratype, vertical, incomplete example, ×40 V. 52037 ; 5. Holotype, vertical, long gently-curved example, ×20 V. 52037. Upper Permian, Darari Formation; Ora, Mosul Liwa, Iraq.

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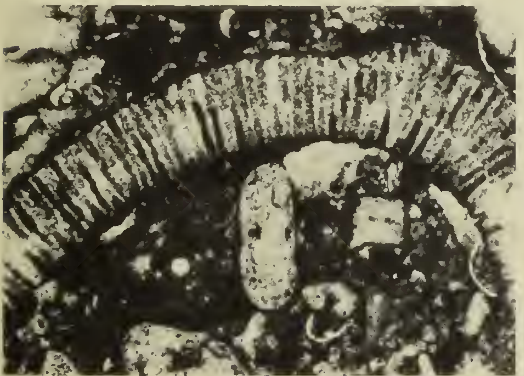

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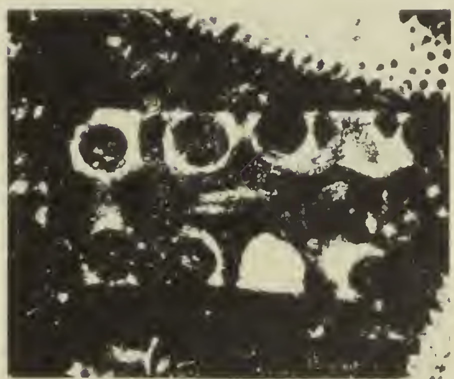

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## PLATE 3

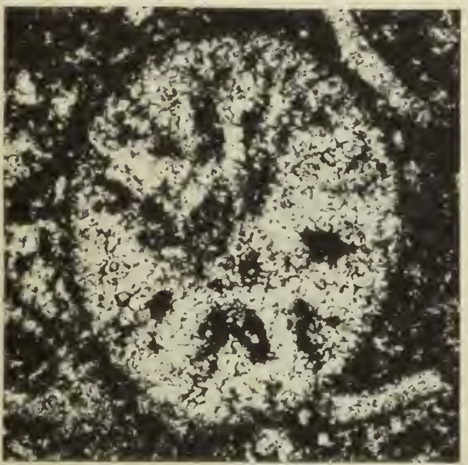
### *Broeckella, Clypeina*

FIG. 1. *Broeckella belgica* Morellet, transverse thin-section, ×50. Palaeocene ; Sahil Maleh, Batinah Coast, Oman, Arabia.

FIGS. 2, 3. *Clypeina jurassica* Favre, thin-sections, ×30. 2. Associated fragments ; above, transverse (horizontal) section of broken verticil, showing radial tubules with example of communicatory pore to stem-cell on right and distinctive thin-section appearance of adjacent tubules in this species at top centre ; below, tangential-vertical cut of thick-walled tubules at about mid-tubule zone radially. V. 52038. 3. Oblique-vertical cut of plant with successive verticils in position ; the plane of section passes from central (below) to obliquely through stem-cell wall and inner tubule-junction (middle) to outer tubules of third verticil. V. 52039. Upper Jurassic, Najmah Formation ; subsurface, Kirkuk Well No. 117, Iraq.

FIG. 4. *C. jurassica*, slightly oblique transverse cut through one verticil, ×30. Upper Jurassic, Arab Zone ; subsurface, Dukhan No. 28 Well, Qatar, Arabia. V. 52040.

FIG. 5. *C. jurassica*, transverse cut through one worn verticil, showing the resistant nature of the calcification at the fusion between adjacent tubules, ×30. Upper Jurassic, Najmah Formation ; subsurface, Kirkuk Well No. 117, Iraq. V. 52041.



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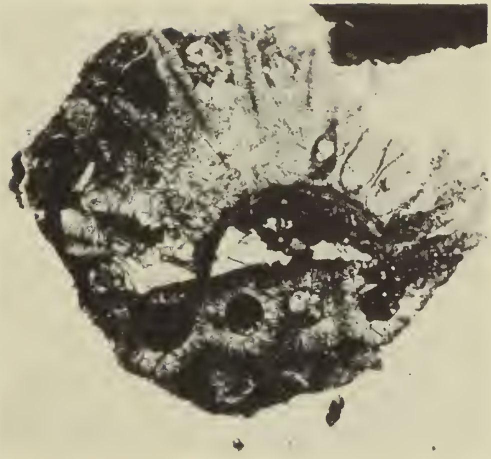

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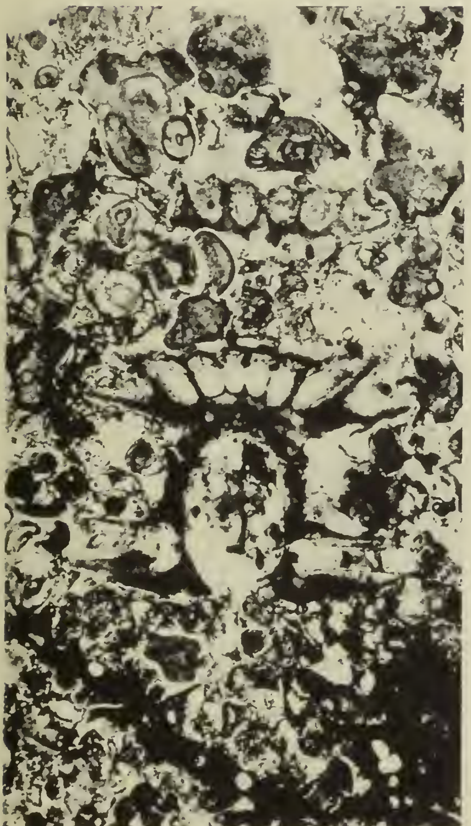

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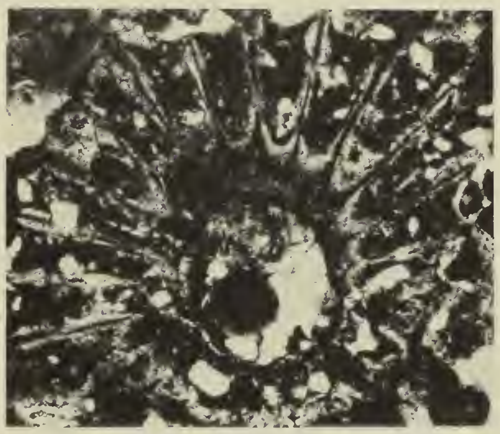

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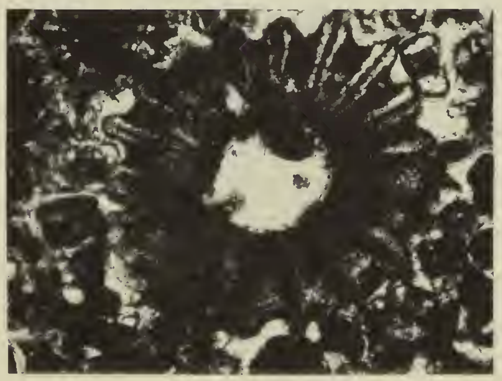

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PLATE 4

## *Clypeina*

FIG. 1. *Clypeina marteli* Emberger, transverse thin-section, ×28. Cretaceous, Valanginian ; Hugf, Southern Oman, Arabia. V. 52042.

FIG. 2. *Clypeina merienda* Elliott, oblique-transverse thin-section through verticil to show bases of tubules and part of central ring. ×35. Palaeocene, Sinjar Formation ; Koi Sanjak, Erbil Liwa, Iraq. V. 52043.

FIGS. 3, 7, 8. *C. merienda*, thin sections, ×28. Palaeocene, Sinjar Limestone. 3. Transverse cut of broken verticil. Sirwan, Sulemania Liwa, Iraq. V. 41586. 7. Oblique cut of successive verticils. Koi Sanjak, Erbil Liwa, Iraq. V. 52043. 8. Vertical-tangential cut of numerous successive verticils of one plant. Sirwan, Sulemania Liwa, Iraq. V. 41587.

FIGS. 4, 5, 6. *C. jurassica*, solid (dissociated) verticils, showing top, side and bottom appearances, ×28. Upper Jurassic, Arab zone ; subsurface, Dukhan No. 2 Well, Qatar, Arabia. V. 52044, V. 52045, V. 52046.


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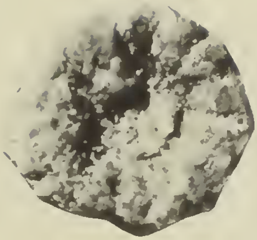
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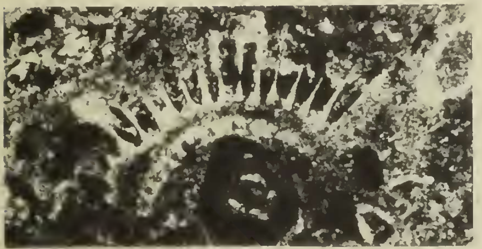
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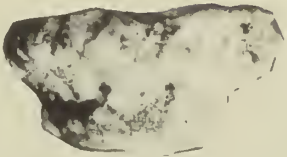
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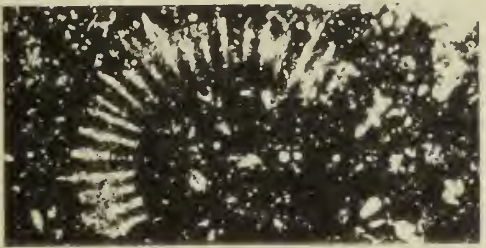
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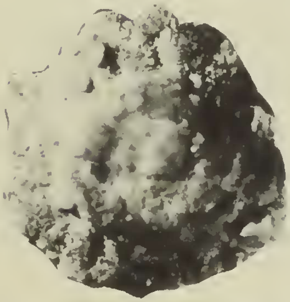
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## PLATE 5

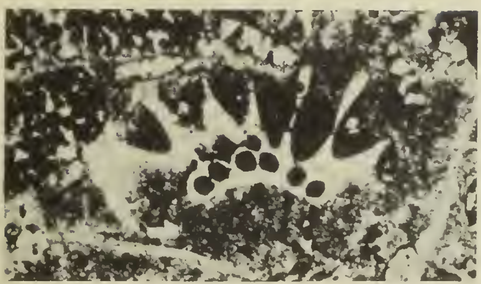
### *Clypeina*

FIGS. 1, 3. *Clypeina* (" *Eoclypeina* ") sp., thin-sections of debris, ×40. Permian, basal Satina Formation and top Zinnar Formation respectively ; Harur, Mosul Liwa, Iraq. V. 41598, V. 52048.

FIG. 2. *Clypeina* sp., slightly oblique-transverse section of verticil, ×30. Palaeocene ; Ghurra Beds, Umm er Radhama Formation ; Al Ghurra, Diwaniya Liwa, Iraq. V. 52047.

FIG. 4. *Clypeina lucasi* Emberger, oblique-transverse section of verticil, ×28. Cretaceous. Valanginian ; Hugf area, Southern Oman, Arabia. V. 52042.

FIGS. 5, 6. *Clypeina parvula* Carozzi, thin-sections showing random transverse and fragmentary longitudinal sections, ×60. Cretaceous, Valanginian, Garagu Formation ; subsurface, Kirkuk Well No. 116, Iraq. V. 52049, V. 52050.



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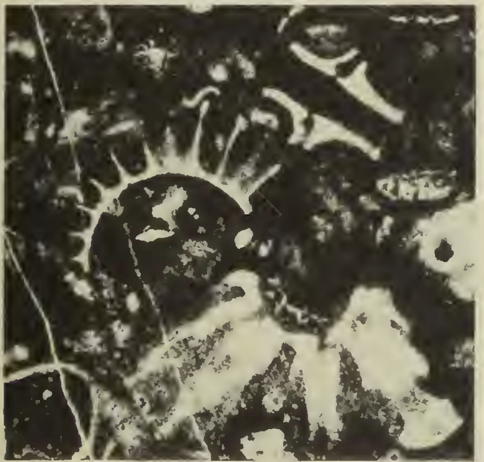

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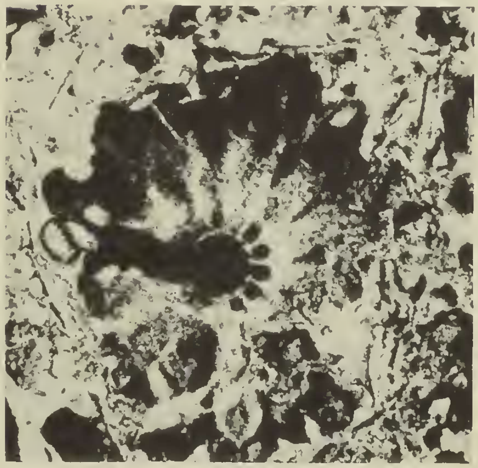

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## PLATE 6

### *Cylindroporella*

FIGS. 1, 2. *Cylindroporella arabica* Elliott, longitudinal and transverse thin-sections, ×58. Upper Jurassic, " Arab Zone " ; subsurface, Dukhan No. 28 Well, Qatar, Arabia. V. 41629.

FIGS. 3, 4. *Cylindroporella barnesi* Johnson. 3. Random oblique section, ×30. Cretaceous, Valanginian-Hauterivian, Garagu Formation ; subsurface, Makhul No. 2 Well, Mosul Liwa, Iraq. V. 52051. 4. Random tangential section, ×60. Cretaceous, about Aptian level, Sarmord Formation ; Sekhaniyan, Surdash, Sulemania Liwa, Iraq. V. 52052.

FIGS. 5–7. *Cylindroporella sugdeni* Elliott. 5. Longitudinal section, ×35. V. 52053. 6. Transverse section, ×28. V. 41623. 7. Tangential section, ×28. V. 41620. Lower Cretaceous ; subsurface, Fahud No. 1 Well, Oman, Arabia.


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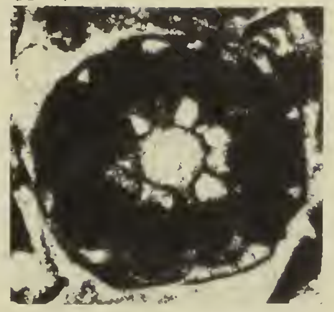
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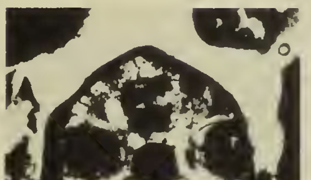
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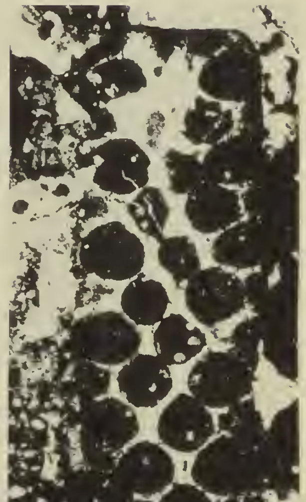
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## PLATE 7

### ***Cymopolia***

FIGS. 1–5. *Cymopolia anadyomenea* Elliott. 1. Longitudinal section, ×28. V. 41656. 2. Transverse section, ×28. V. 41656. 3, 4. Oblique sections, ×28. V. 41656, V. 41655. 5. Solid specimen on weathered surface, ×20. V. 52054. Cretaceous, Maestrichtian, Tanjero Formation ; Diza North, Erbil Liwa, Iraq.

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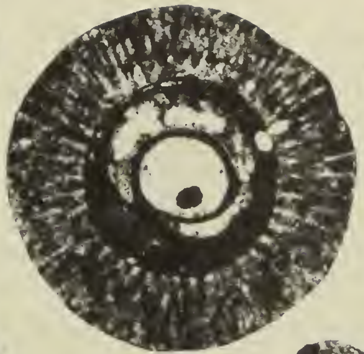

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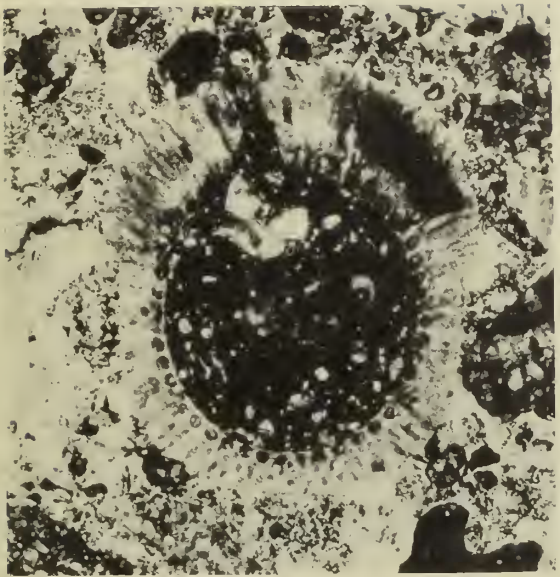
## PLATE 8

### *Cymopolia*

FIGS. 1, 5. *Cymopolia anadyomenea* Elliott. 1. Oblique-transverse section, ×28. Cretaceous, Maestrichtian, Tanjero Formaton ; Diza North, Erbil Liwa, Iraq. V. 52055. 5. Debris, in limestone facies, thin-section ×20. Cretaceous, Maestrichtian, Upper Aqra Formation ; Aqra, Mosul Liwa, Iraq. V. 52056.

FIG. 2. *Cymopolia barberae* sp. nov., holotype, transverse thin-section, ×50. Palaeocene-Lower Eocene, Kolosh Formation ; Surdash, Sulamenia Liwa, Iraq. V. 52057.

FIGS. 3, 4. *Cymopolia tibetica* Morellet. 3. Transverse section, ×60. Cretaceous, Maestrichtian, Aqra Formation ; Aqra, Mosul Liwa, Iraq. V. 52059. 4. Fragment to show branch-structure, thin-section, ×60. Cretaceous, Maestrichtian, Aqra-Hadiena Limestone Facies ; Chalki Islam, Mosul Liwa, Iraq. V. 52060.



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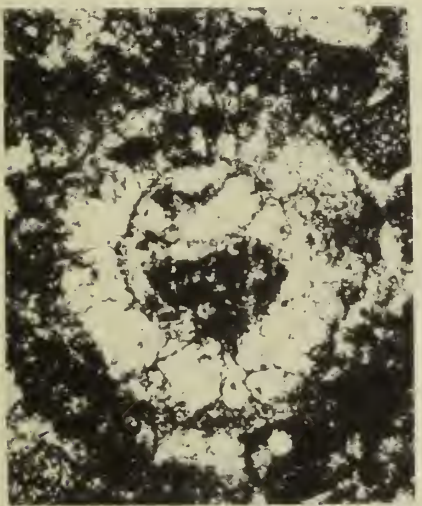

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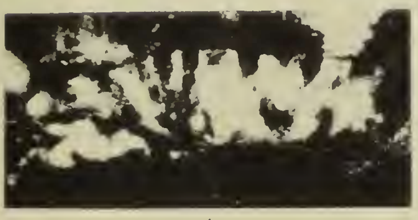

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## PLATE 9

### *Cymopolia*

FIGS. 1–3. *Cymopolia eochoristosporica* sp. nov. 1. Oblique-longitudinal thin-section, ×20. Holotype, V. 52652. 2. The same, to show branch and sporangial-detail, ×40. 3. Another oblique-longitudinal thin-section, portion ×40. Syntype, V. 52653. Both from Cretaceous, Maestrichtian, subsurface Aruma Formation ; Murban No. 53 Well, Abu Dhabi, Trucial Oman, Arabia.

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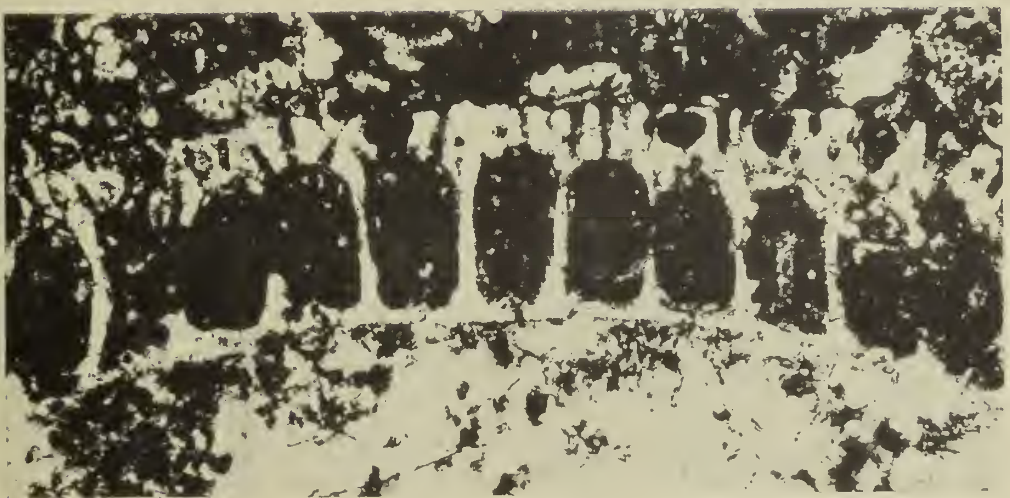

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## PLATE 10

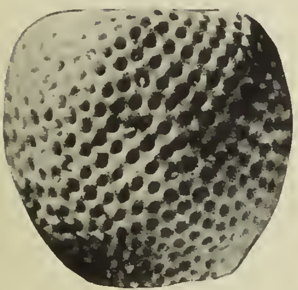
### *Cymopolia, Dissocladella*

FIG. 1. *Cymopolia elongata* (Defrance) Mun.-Chalmas. Solid specimen, small single unit or segment, ×28, for comparison of external pores (branch-openings) with those of *C. kurdistanensis* (fig. 2). Eocene, Lutetian ; Grignon, Paris, France. V. 52061.

FIGS. 2–5. *Cymopolia kurdistanensis* Elliott. 2. Solid specimen, single segment, to show detail of exterior, ×28. Palaeocene-Lower Eocene, Kolosh Formation, Bekhme, Erbil Liwa, Iraq. V. 52062. 3. Thin-section of dissociated segment, to show details of sporangia and branches, ×28. Palaeocene, Sinjar Formation ; Banik, Mosul Liwa, Iraq. V. 41593. 4. Slightly oblique transverse cut showing sporangia and branches, ×36. Palaeocene, Kolosh Formation ; Rowanduz, Erbil Liwa, Iraq. V. 52063. 5. Random transverse section at an inter-sporangial level so that only the branches are seen, ×30. Palaeocene ; Jebel Faiyah, Trucial Oman, Arabia. V. 52064.

FIG. 6. *Cymopolia* (*Karreria*) sp. Thin-section fragment to show sporangia, etc., ×50. Palaeocene-Lower Eocene, Sinjar Formation ; Pila Spi, Sulemania Liwa, Iraq. V. 52065.

FIGS. 7, 8. *Dissocladella deserta* sp. nov. Syntypes. 7. Longitudinal section, ×50. V. 52066. 8. Transverse section, ×50. V. 52067. Palaeocene-Lower Eocene, Umm er Rudhama Formation ; Aidah and Wagsa, Diwaniyah Liwa, Iraq.



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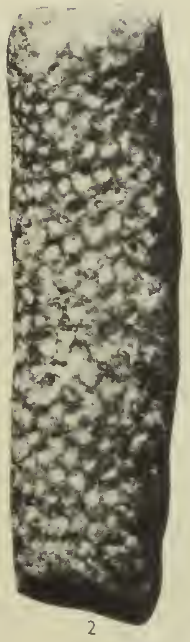

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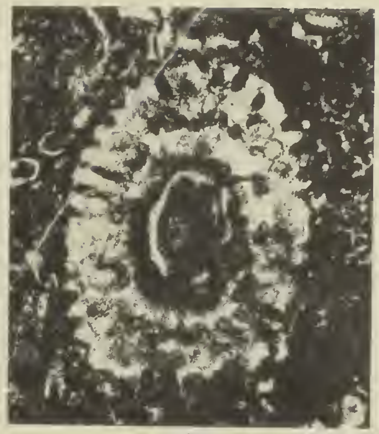

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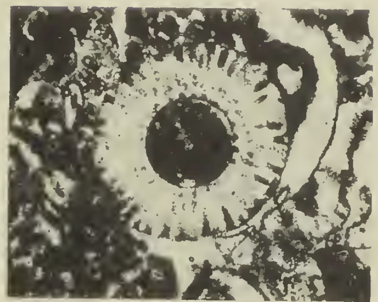

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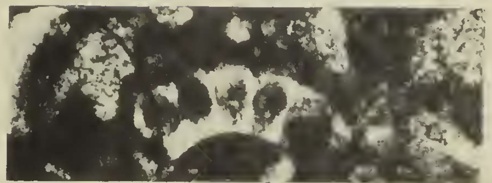

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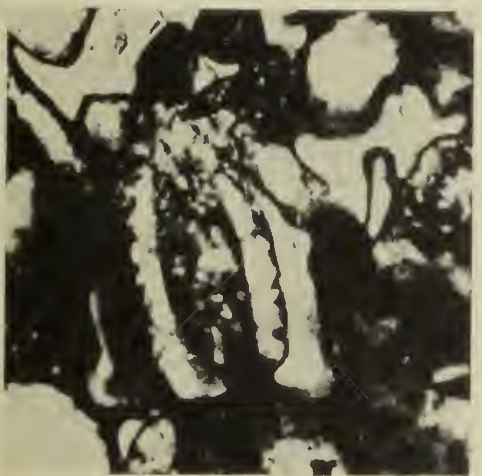

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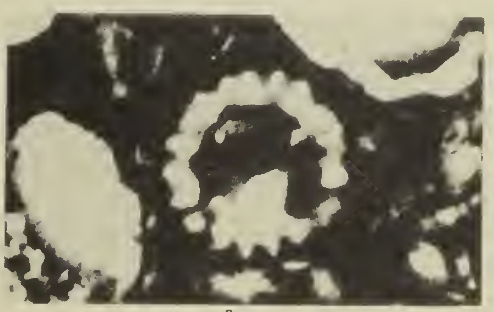

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## PLATE 11

### *Dissocladella, Furcoporella*

FIGS. 1–3. *Dissocladella savitriae* Pia. 1. Transverse section, ×28. Palaeocene, Sinjar Formation ; Banik, Mosul Liwa, Iraq. V. 41580. 2. Fragment to show enlarged wall-structure, thin-section, ×50. Palaeocene, Kolosh Formation ; Rowanduz, Erbil Liwa, Iraq. V. 52068. 3. Broken solid specimen to show nodose-annular external appearance, ×28. Lower Eocene ; subsurface, Dukhan No. 3 Well ; Qatar, Arabia. V. 52069.

FIGS. 4–6. *Dissocladella undulata* (Raineri) Pia. Thin-sections. 4. Transverse section, ×50. V. 52070. 5, 6. Near-longitudinal sections, ×50. V. 52071. Cretaceous, Turonian, Sadi Formation, subsurface, Musaiyib No. 1 Well, Hill Liwa, Iraq.

FIGS. 7–9. *Furcoporella diplopora* Pia. 7. Oblique-longitudinal section to show successively divergent pore-pairs (lower part of figure), ×38. V. 41606. 8. Longitudinal section to show waisted pores, ×30. V. 41606. 9. Transverse section to show paired branches, ×45. V. 51232. Palaeocene-Lower Eocene, Kolosh Formation ; Sedelan, Sulemania Liwa, Iraq.


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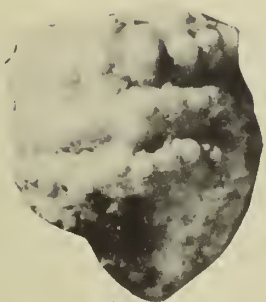
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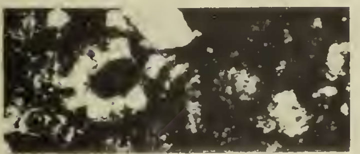
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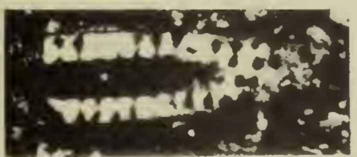
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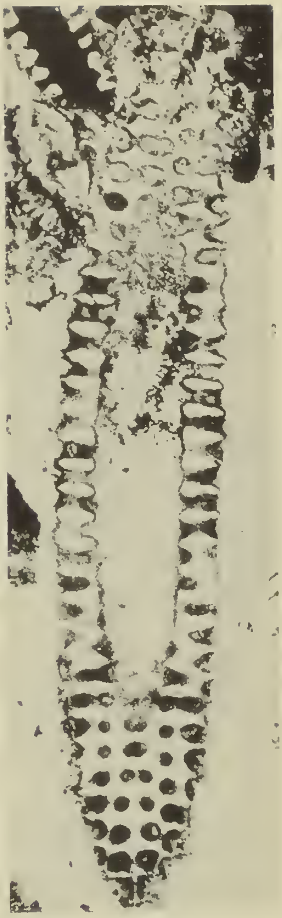
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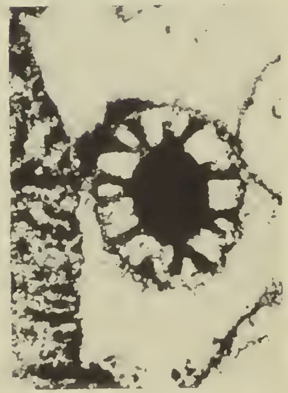
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## PLATE 12

### *Griphoporella, Indopolia*

FIGS. 1, 3. "*Griphoporella arabica* Pfender" (*Ovulites maillolensis* Massieux). Transverse and oblique longitudinal sections, ×50. Palaeocene-Lower Eocene ; Sahil Maleh, Batinah Coast, Oman, Arabia. V. 52033.

FIG. 2. *Indopolia satyavanti* Pia. Oblique-longitudinal section showing sterile whorls, ×50. Palaeocene-Lower Eocene, Sinjar Formation ; Banik, Mosul Liwa, Iraq. V. 52072.

FIG. 4. *Griphoporella* cf. *perforatissima* Carozzi. Tangential section of wall-fragment, ×50. Upper Jurassic, Najmah Formation ; subsurface, Kirkuk Well No. 117, Iraq. V. 52073.

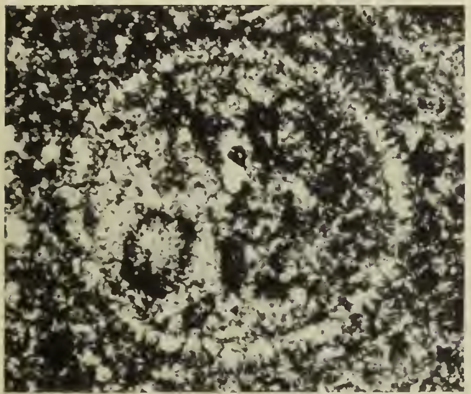

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PLATE 13

***Mizzia***

Figs. 1–5. *Mizzia velebitana* Schubert, thin-sections of separate bead-like units or segments, ×28. 1. Slightly oblique longitudinal section. V. 52074. 2, 3. Typical transverse sections near equatorial region. V. 52075, V. 41575. 4. Random sections, the lower suggests externally roofed branch-pores. 5. Three random sections : the upper is of a pear-shaped segment cut longitudinally. V. 52076. Permian, Darari Formation ; fig. 3 from Harur, the others from Ora, both localities in Mosul Liwa, Iraq.

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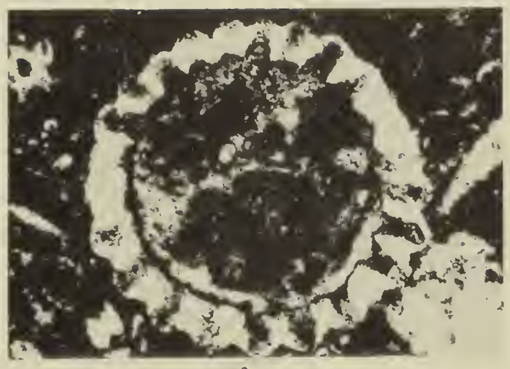

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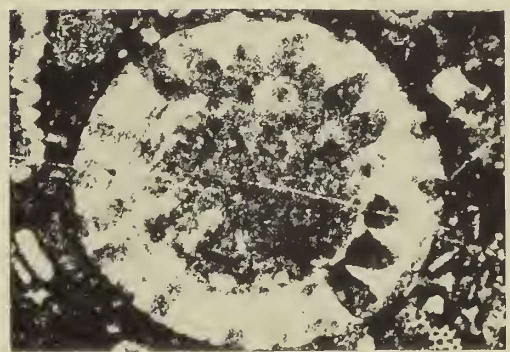

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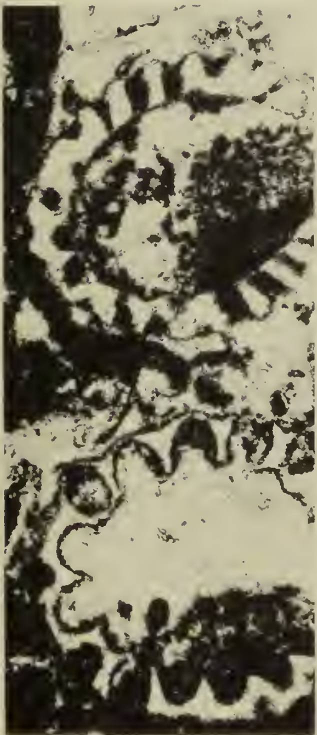

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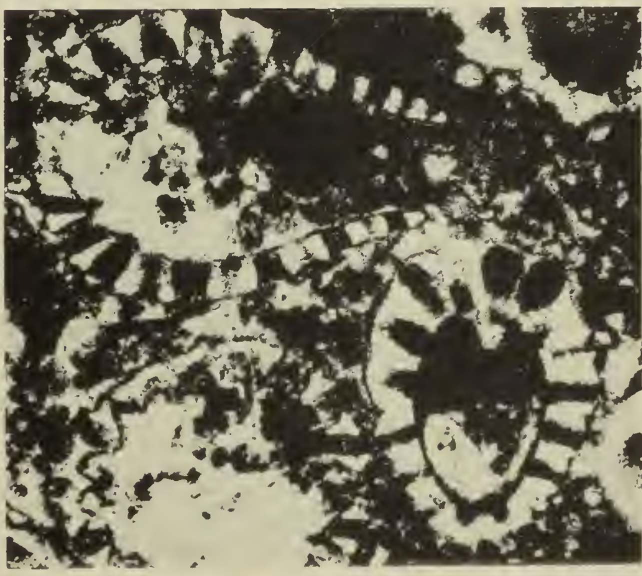

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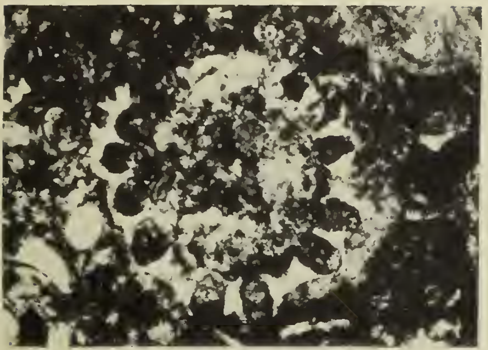
## PLATE 14

### *Mizzia*

FIGS. 1–4. *Mizzia velebitana* Schubert, thin-sections. 1. Transverse cut of unit with roofed pores, ×28. 2. Longitudinal-oblique section of unit, ×28. 3. Tangential cut to show typical coarse "colander-pore" pattern ; also longitudinal section of broken unit, ×28. 4. Random section of *Mizzia*-rock, ×20. Permian, Darari Formation ; Ora, Mosul Liwa, Iraq. V. 52076.



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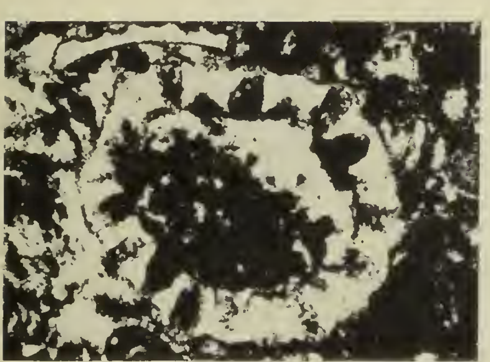

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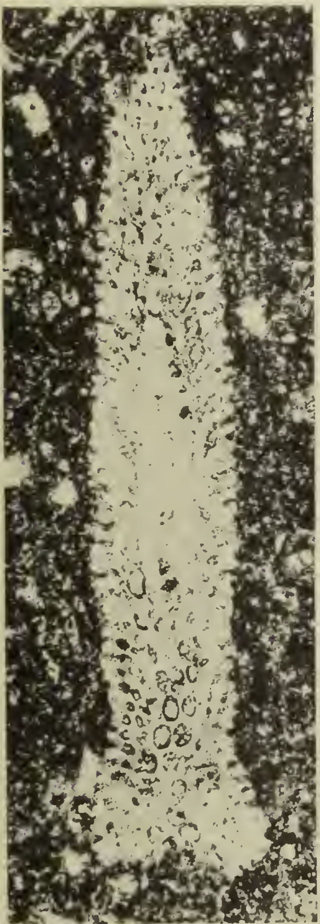
## PLATE 15

### *Neomeris*, *Munieria*

Fig. 1. *Neomeris cretacea* Steinmann. Oblique-longitudinal section, ×20. Cretaceous, Maestrichtian, Bekhme Formation ; Chia Gara, Mosul Liwa, Iraq. V. 52077.

Fig. 2. *N. cretacea.* Oblique-transverse section, ×28. Cretaceous, Campanian-Maestrichtian, Aqra-Bekhme limestone facies ; Gal-i-Mazurka, Mosul Liwa, Iraq. V. 41585.

Figs. 3–8. *Munieria baconica* Deecke. Typical fragmentary remains, thin-sections, ×50. 3, 4, 6. Cretaceous, Aptian level, Qamchuqa Formation ; Ru Kuchuk, Mosul Liwa, Iraq. V. 52078. 5, 7. Cretaceous, Barremian level, Sarmord Formation ; Sarmord, Sulemiania Liwa, Iraq. V. 52079. 8. Cretaceous, Aptian-Albian level, Qamchuqa Formation ; Surdash, Sulemania Liwa, Iraq. V. 52080.



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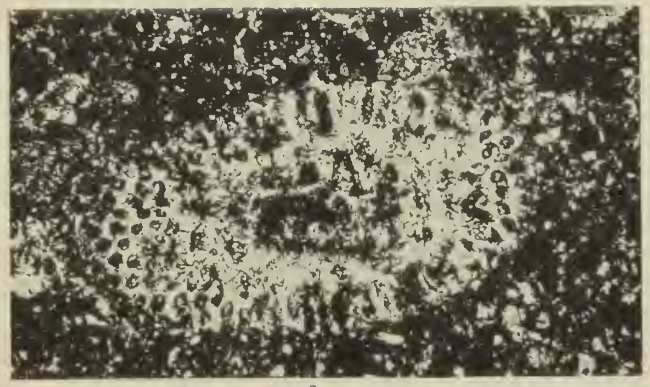

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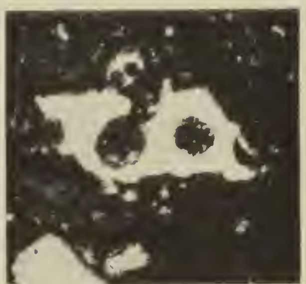

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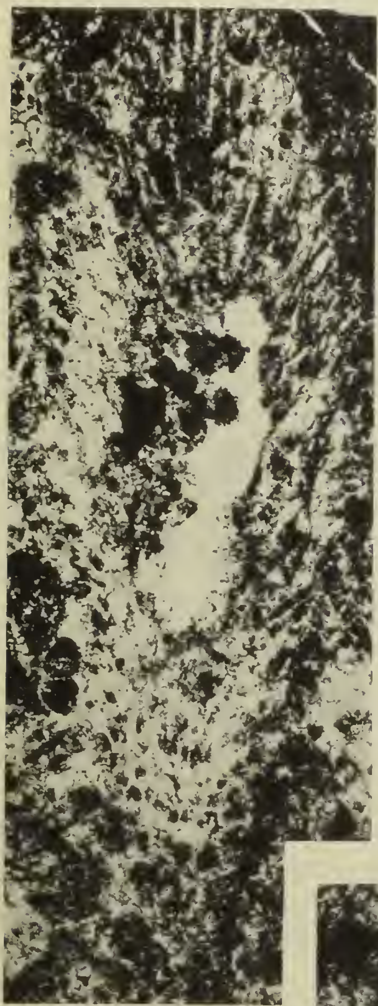
## PLATE 16

### ***Palaeodasycladus***

FIGS. 1–5. *Palaeodasycladus mediterraneus* Pia. 1, 2. Longitudinal, and two transverse sections, ×20. V. 52081. 3. Fragment to show detail of branch-constrictions, ×28. V. 52082. 4. Oblique-transverse cut to show effect of angle of branch-inclination. V. 52082. 5. Detail of terminal branches, ×20. V. 52083. Jurassic, Lias, Lower Musandam Formation ; Wady Bih, Qamar, Peninsular Oman, Arabia.



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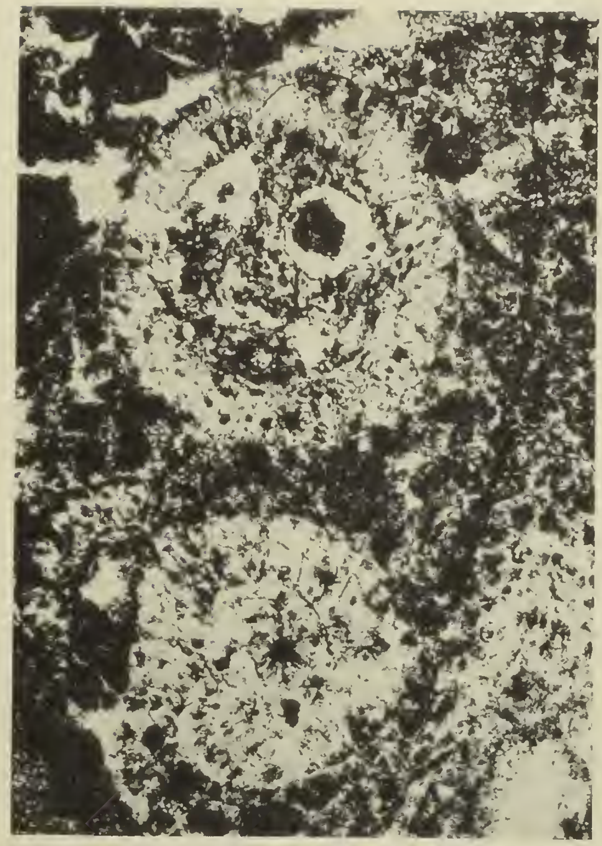

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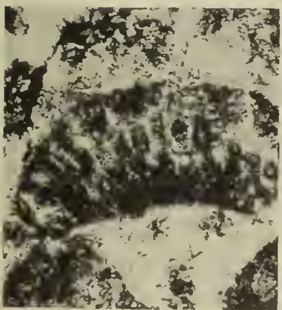

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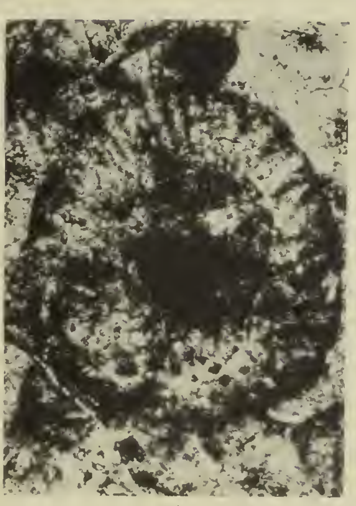

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## PLATE 17

***Permoperplexella, Pianella, Pagodaporella***

FIGS. 1–5. *Permoperplexella attenuata* gen. et sp. nov., thin-sections, ×28. 1. Paratype, oblique-longitudinal cut. V. 52084. 2, 3. Paratypes, oblique section of distal end, oblique-transverse cut near this end. V. 52085. 4. Holotype, longitudinal section. V. 52085. 5. Oblique-transverse cut near distal end. V. 52085. Permian, Zinnar Formation ; Ora, Mosul Liwa, Iraq.

FIGS. 6–8. *Pianella pygmaea* (Gümbel) Radoičić. 6. Transverse section, ×40. V. 52086. 7. Longitudinal section, ×40. V. 52087. 8. Oblique section, ×40. V. 52088. Cretaceous, Valanginian, Garagu Formation ; subsurface, Mileh Tharthar Well No. 1, Dulaim Liwa, Iraq.

FIGS. 9, 10. *Pagodaporella wetzeli* Elliott. 9. Longitudinal thin-section of solid, dissociated, example, ×60. V. 41605. 10. Solid example, external appearance, ×60. V. 41604. Palaeocene, Kolosh Formation ; Bekhme, Erbil Liwa, Iraq.

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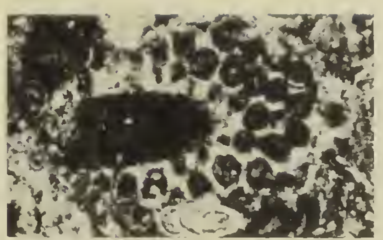

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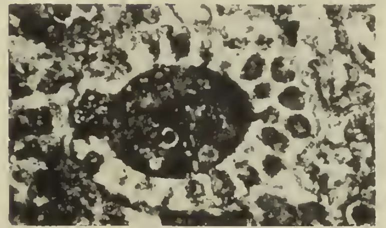

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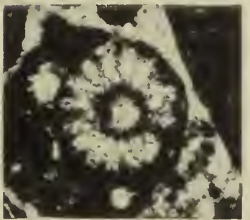

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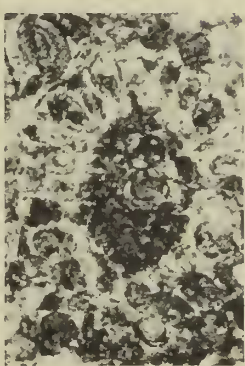

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## PLATE 18

### *Pseudoepimastopora*

Figs. 1, 2. *Pseudoepimastopora ampullacea* sp. nov. 1. Holotype, longitudinal section of "waxing-and-waning" example, ×30. V. 52089. 2. Paratype, random section of long curved piece of thallus, ×30. V. 52090. Permian, Zinnar Formation ; Ora, Mosul Liwa, Iraq.

Figs. 3, 4. *Pseudoepimastopora* cf. *likana* Kochansky and Herak. Fragments of wall-material showing large distinctive pores, thin-sections, ×30. Permian ; Jebel Qamar, Peninsular Oman, Arabia. V. 52091, 52092.

Figs. 5–7. *P. ampullacea.* 5, 6. Thin-sections of wall-fragments showing clearly the form of the pores, ×60. V. 52093. 7. Transverse section, ×60. V. 52094. Permian, Zinnar Formation ; Ora, Mosul Liwa, Iraq.


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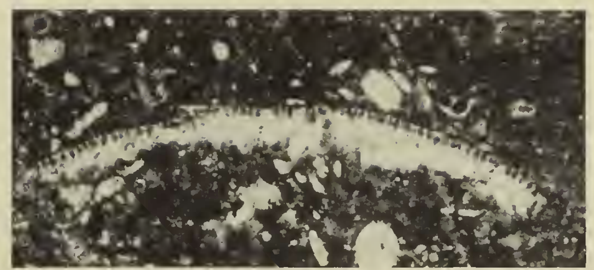
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## PLATE 19

### *Pseudovermiporella*

FIGS. 1–5. *Pseudovermiporella sodalica* Elliott. Thin-sections, ×50. 1, 2. Portions of large individuals showing typical coarse mesh of main tube, supposed diagenetic lining layers, inner tube and irregular meandriform growth ; in fig. 2 mesh of a second small individual is seen in position of growth on the inner tube of the main individual. V. 41641, V. 41645, 3. Transverse cut of typical single unattached tube. V. 41644. 4, 5. Sections of small early clusters or " nucleo-conch " structures ; in fig. 4 the reniform, calcite-filled structure is unusually large but is apparently an early inner tube. 41649, 41642. Permian; Jebel Qamar, Peninsular Oman, Arabia.

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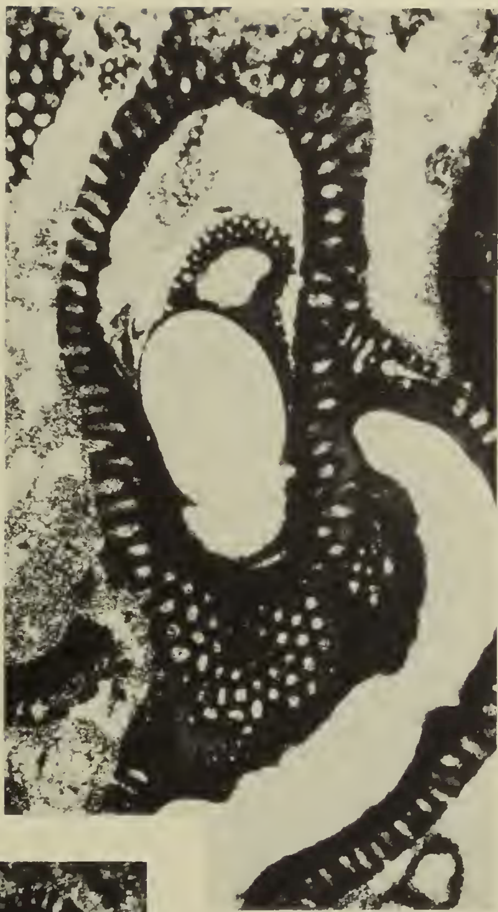

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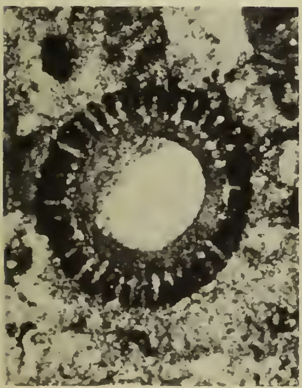

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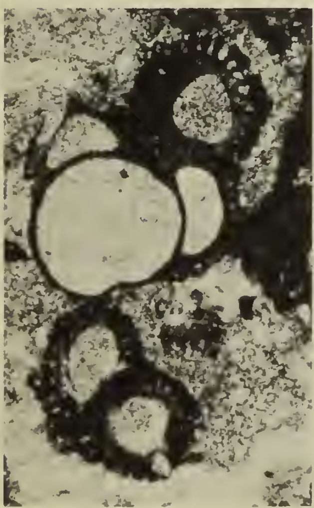

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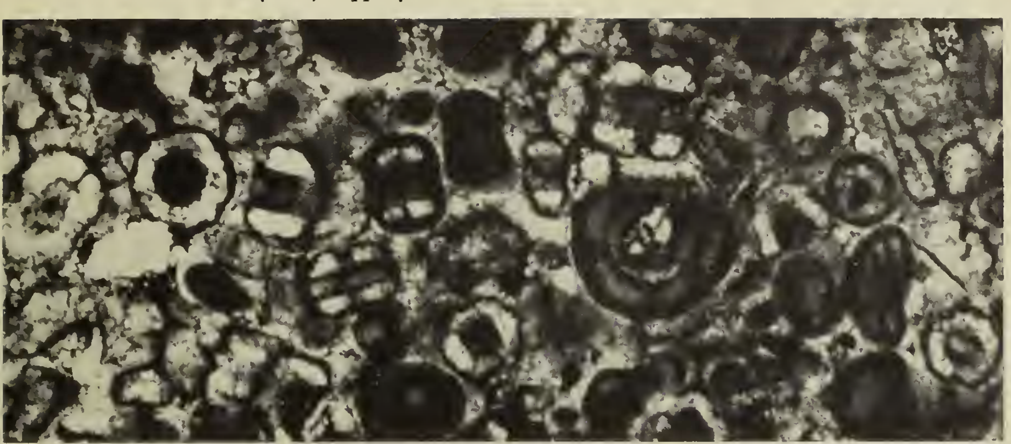
## PLATE 20

### *Salpingoporella*

FIGS. 1, 2, 5. *Salpingoporella apenninica* Sartoni & Crescenti. Thin-sections, ×50. 1. Random vertical and transverse cuts of short lengths of tube. V. 52095. 2, 5. Longitudinal sections with associated transverse sections. V. 52096. Upper Jurassic, Najmah Formation ; subsurface, Kirkuk Well No. 117, Iraq.

FIGS. 3, 4, 6, 7. *Salpingoporella annulata* Carozzi. 3. Oblique-vertical section, ×50. V. 52097. 4. Transverse section, ×50. V. 52099. 6. Solid (dissociated) specimen, external appearance, ×50. V. 52099. 7. Longitudinal thin-section, ×50. V. 52098. Upper Jurassic, " Arab Zone " ; subsurface, Dukhan Well No. 28 (figs. 3, 4, 7) and Well No. 2 (fig. 6), Qatar, Arabia.



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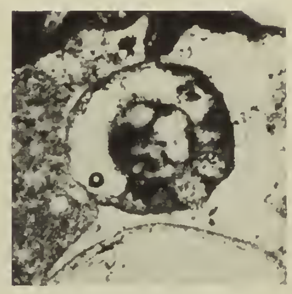

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## PLATE 21

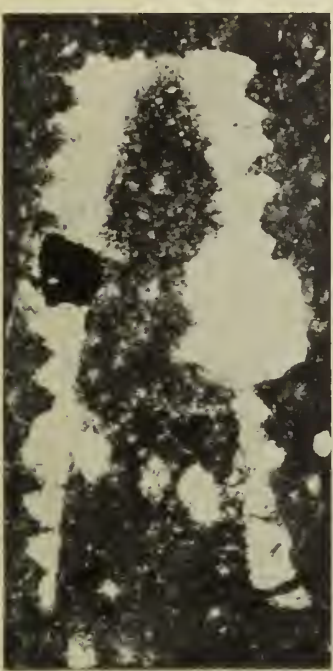
### *Salpingoporella*

FIG. 1. *Salpingoporella arabica* sp. nov. Paratype, oblique-longitudinal thin-section, wall replaced by clear calcite, ×50. Cretaceous, Albian-Cenomanian level, top Qamchuqa Formation ; Sarmord, Sulemania Liwa, Iraq. V. 52100.

FIG. 2. *S. arabica*. Paratypes, oblique-transverse sections to show simple branch-structure, ×50. Lower Cretaceous, Upper Musandam Formation ; Jebel Hagab, Peninsular Oman, Arabia. V. 52101.

FIG. 3. *S. arabica*. Holotype, longitudinal section, ×40. Cretaceous, Aptian-Albian level, Qamchuqa Formation ; Surdash, Sulemania Liwa, Iraq. V. 52102.

FIG. 4. *Salpingoporella dinarica* Radoičić (*Hensonella cylindrica* Elliott). Numerous typical random cuts in thin-section, ×50. Cretaceous, Barremian-Aptian level, Sarmord Formation ; Sekhaniyan, Surdash, Sulemania Liwa, Iraq. (Compare preservation with that of *S. arabica* above). V. 52103.



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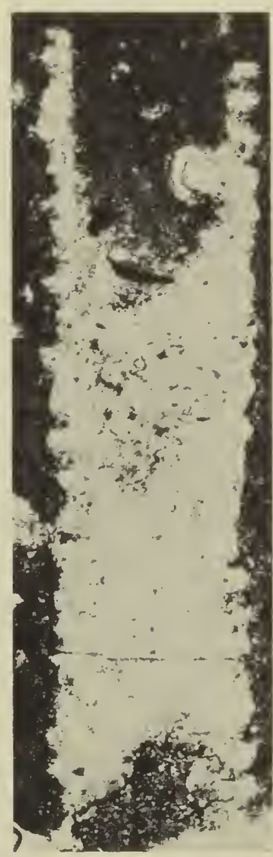

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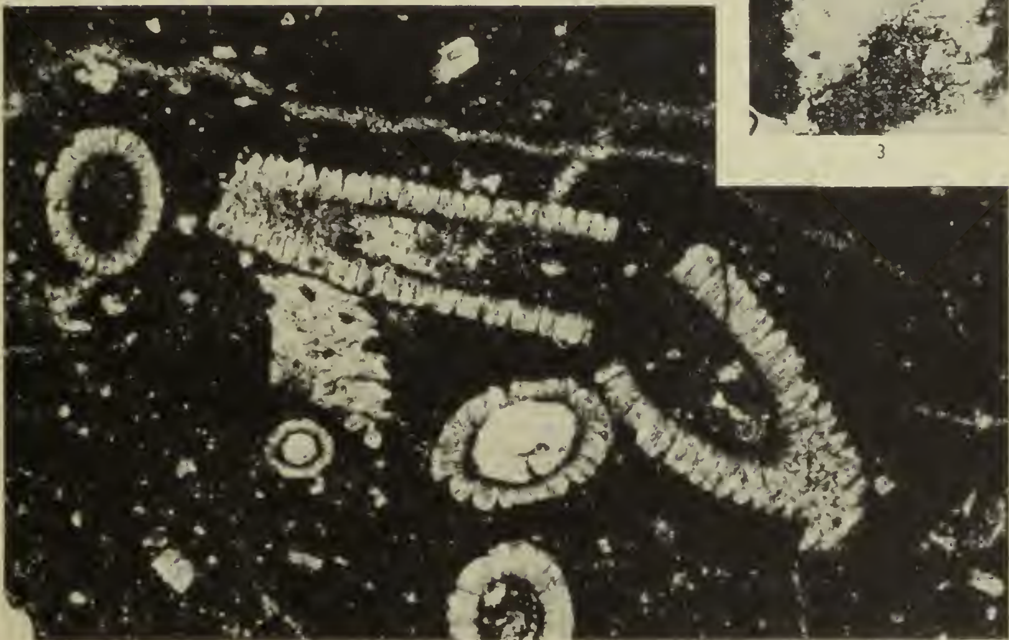

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## PLATE 22

### *Salpingoporella dinarica (Hensonella)*

FIG. 1. Part of the type thin-section, ×30, of *Hensonella cylindrica* Elliott. Cretaceous, Barremian, Qamchuqa Formation ; Sarmord, Sulemania Liwa, Iraq. Z. 902.

FIG. 2. *S. dinarica* Radoičić. Thin-section ×50, oblique-longitudinal cut, to show dasyclad branch-pore pattern as described by Radoičić. Cretaceous, Upper Aptian ; Djebel Amsid, Constantinois, Algeria. V. 52104.

FIGS. 3–6. Thin-section cuts, ×50. 3. Crushed example to show continuity of inner thin dark layer. V. 52103. 4. Random sections, one crushed. V. 52103. 5. Longitudinal and transverse sections showing very regular fibrous radial structure and coarser features with external widening interpreted as dasyclad branches. V. 52103. 6. Transverse section showing the inner dark layer of organism incrusted by a thin irregular coating of transparent calcite, the interior being filled with darker marly-calcareous matrix. V. 52105. Cretaceous, Barremian-Aptian level, Sarmord Formation ; Sekhaniyan, Surdash, Sulemania Liwa, Iraq.

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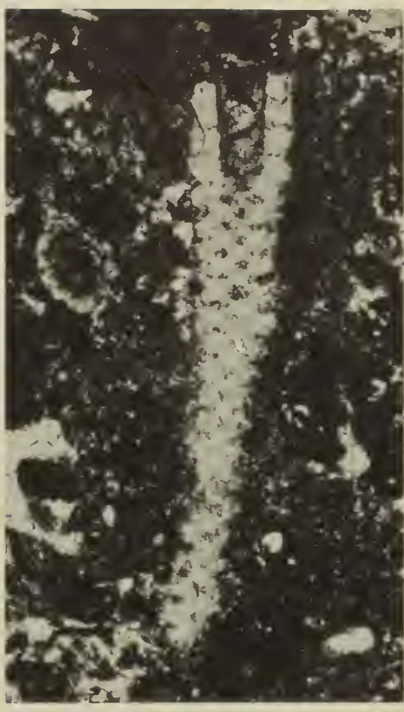

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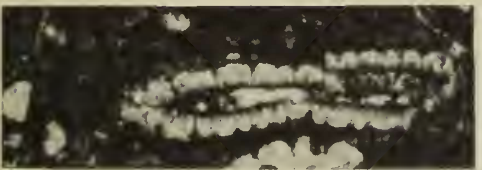

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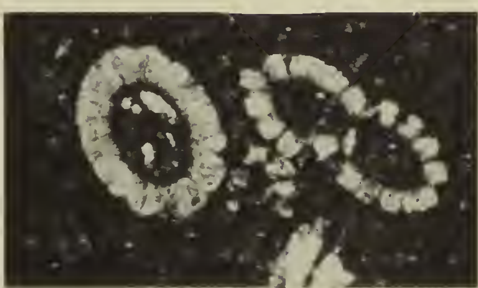

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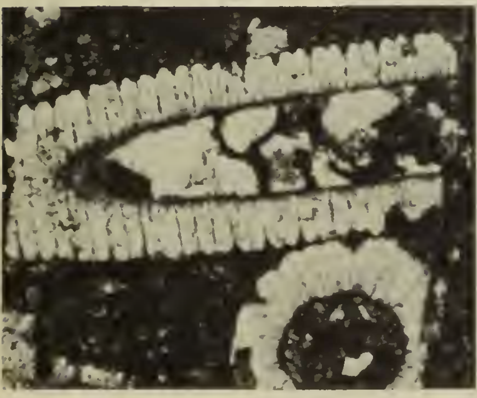

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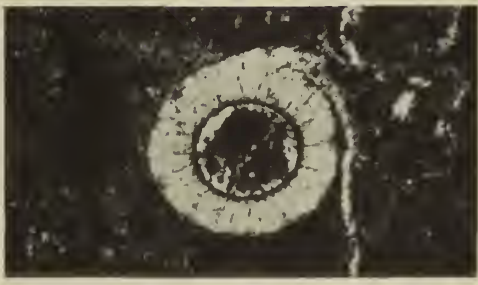

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## PLATE 23

### *Terquemella, Thyrsoporella*

FIGS. 1, 2. *Thyrsoporella silvestrii* Pfender. 1. Transverse section, ×50. V. 52106. 2. Longitudinal section, ×50. V. 52107. Middle Eocene; Jebel Tanamir, Fatah, Oman, Arabia.

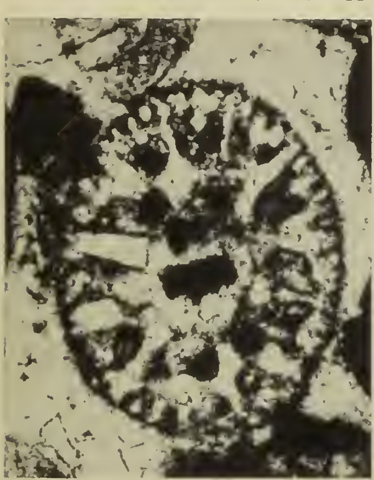
FIG. 3. *T. silvestrii.* Tangential-longitudinal section, ×50. Palaeocene-Lower Eocene, Kolosh Formation; Sedelan, Sulemania Liwa, Iraq. V. 52108.

FIG. 4. *T. silvestrii.* Longitudinal section of large individual, ×28. Middle Eocene; Jebel Tanamir, Fatah, Oman, Arabia. V. 52109.

FIG. 5. *Terquemella globularis* Elliott. Solid specimen to show exterior, ×80. Palaeocene, Kolosh Formation; Bekhme, Erbil Liwa, Iraq. V. 41603.

FIGS. 6, 7. *Terquemella bellovacensis* Munier-Chalmas. 6. Tangential-transverse section, ×55. V. 41589. 7. Vertical section, ×55. V. 41590. Palaeocene-Lower Eocene, Sinjar Formation; Sirwan, Sulemania Liwa, Iraq.

FIG. 8. *T. globularis.* Thin-sections, ×55. Palaeocene-Lower Eocene, Sinjar Formation; Sirwan, Sulemania Liwa, Iraq. V. 32496.



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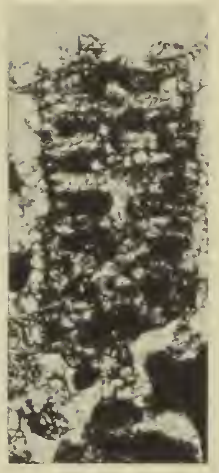

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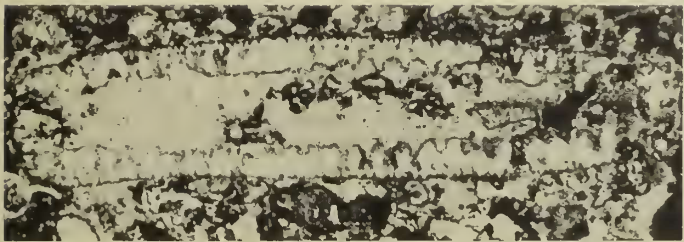

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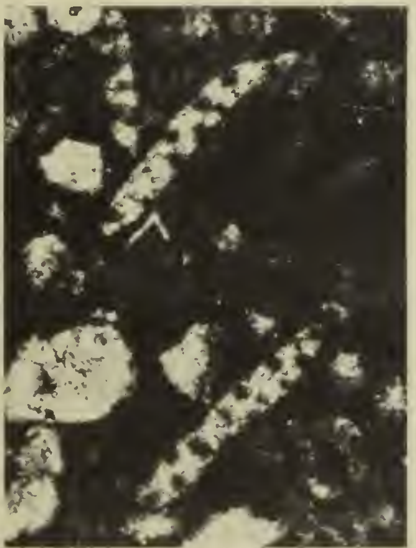

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## PLATE 24

### *Thyrsoporella, Trinocladus*

FIGS. 1, 2, 6, 7. *Trinocladus perplexus* Elliott. 1. Solid specimen to show exterior, ×50. V. 52117. 2. Longitudinal section of specimen in which an example of the codiacid *Ovulites morelleti* Elliott perfectly fits the stem-cell cavity of the larger fossil, ×50. V. 52110. 6. Oblique and transverse sections, ×50. V. 52114. 7. Near-longitudinal section to show branch-structure, ×50. V. 52115. Palaeocene-Lower Eocene, Kolosh Formation ; Koi Sanjak, Erbil Liwa, Iraq.

FIG. 3. *Trinocladus tripolitanus* Raineri. Longitudinal section, ×50. Cretaceous, Turonian ; subsurface, Ras Sadr Well No. 1, Trucial Oman, Arabia. V. 52111.

FIG. 4. *T. tripolitanus*. Oblique-transverse section, ×50. Cretaceous, Turonian, Sadr Formation ; Musaiyib Well No. 1, Hilla Liwa, Iraq. V. 52112.

FIG. 5. *Thyrsoporella silvestrii* Pfender. Thin-section fragment to show detail of branch-structure, ×50. Middle Eocene ; Jebel Tanamir, Fatah, Oman, Arabia. V. 52113.

FIG. 8. *Trinocladus radoicicae* sp. nov. Syntypes, transverse sections, ×50. Cretaceous, Maestrichtian, Tanjero Formation ; Diza, Erbil Liwa, Iraq. V. 52116.

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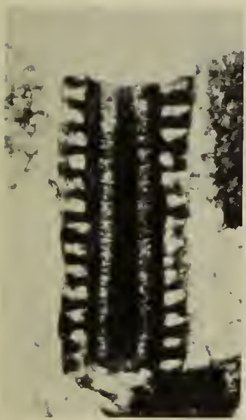

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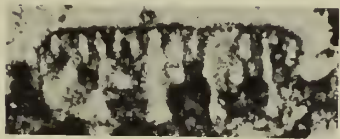

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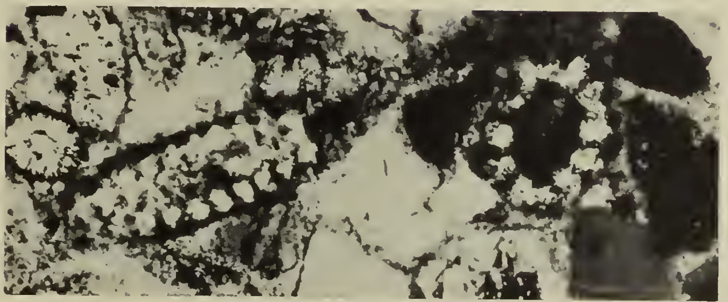

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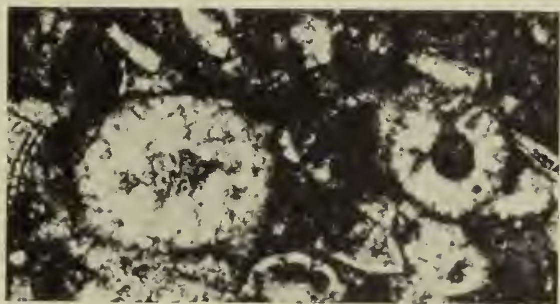

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