A CONSIDERATION OF THE TRIBE THYRSOPORELLEAE, DASYCLAD ALGAE

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ABSTRACT. The algal tribe Thyrsoporelleae Pia, 1927 (Family Dasycladaceae, Order Dasycladales) is examined in the light of later additions and discoveries. It is considered that the reasons for the earlier grouping are not now valid: *Thyrsoporella*, *Belzungia*, *Dobunniella*, and *Placklesia* now constitute the Thyrsoporelleae emend.; *Dissocladella* constitutes the Dissocladelleae trib. nov.; *Trinocladus* is transferred to the Triploporelleae. Possible ancestries are discussed, the limitations of the nature of this fossil evidence considered, and the extinction of all three reviewed against what is known and surmised of the decline of the post-Triassic Dasycladaceae generally.

THE foundations of our knowledge of fossil dasycladacean algae were laid by various workers, amongst whom Julius Pia is usually considered pre-eminent. Without discounting the pioneer work of Munier-Chalmas (1877) or the meticulously careful studies of the Morellets (1913, 1922) on a limited microflora, it was Pia who, in a series of publications from 1912 to 1943, endeavoured to interpret the fossil dasycladacean record as a whole. His sometimes bizarre reconstructions from limited thin-section evidence, and his ever-ready facility for postulating phylogenetic links, qualify but do not invalidate his achievement, which all subsequent workers have recognized. The broad outlines of his classification have been followed, or at any rate not replaced, up to the present day. A recent timely re-examination in some detail of assumed fundamentals and questioning of deductions from them by the 'Groupe français pour l'étude des algues fossiles' (Bassoulet *et al.* 1975, p. 288) paid tribute to Pia's work whilst criticizing his successors for their largely unqualified acceptance or failure to extrapolate in the light of later knowledge.

Pia's subdivision of the family Dasycladaceae (then including all taxa now placed within the Dasycladales) was into tribes (Pia 1920, p. 237). He used this term because of the relatively large number of such small divisions recognized, and because of the very unequal size of the two higher-category subfamilies, had he then proposed them. It so happens that one of these tribes, the Thyrsoporelleae (Pia 1927) is, as now constituted in 1977, of especial interest as showing unusual anomalies for a conventional taxonomic grouping. Moreover, in a considerable personal experience over the years of these particular fossils I have found that almost invariably my doubts and uncertainties were resolved neither by the literature nor by more material. It seems useful, therefore, to consider the tribe and its content anew, and this is now attempted below.

HISTORICAL

In 1927 Pia, in a textbook treatment of the algae, proposed the tribe Thyrsoporelleae (Pia 1927, p. 77). In it he placed *Trinocladus* Raineri, then known only from the Upper Cretaceous; *Thyrsoporella* Gümbel, similarly from the Eocene; and *Belzungia* Morellet, similarly from the Palaeocene–Eocene. In these genera Pia stressed the

[Palaeontology, Vol. 20, Part 3, 1977, pp. 705–714.]

conspicuous thickening of primary and secondary, and of other branch-elements if present, which he considered as evidence of their having contained reproductive elements, and he added that this tribe probably came from the Triploporelleae (Jurassic–Cretaceous).

In 1935 Pia again considered these fossils in three papers: one published in that year and two dated 1936. Both of these last must have been completed in 1935, since he refers in one to the other as 'Rama Rao and Pia 1935', and the former appeared in January 1936 (Pia 1935, 1936*a*, *b*). The information on which he amplified his concept of the Thyrsoporelleae is divided between the three. The new genus *Dissocladella* appeared in Pia 1936*b* (type species *D. savitriae* Pia): a distinctive form, discussed below, with near-spherical swollen primary branch-elements. In Pia (1936*a*) a redescription of the Upper Cretaceous *Trinocladus tripolitanus* Raineri was accompanied by detailed description of the accompanying *T. undulatus* (Raineri) Pia and its reference to *Dissocladella*. (A recent clarification of the stratigraphy at Raineri and Pia's locality is to be found in Radoičić (1975).) Pia, whilst detailing differences between *D. savitriae* and *D. undulatus*, wrote that the latter 'might very well be the direct ancestor' of the former. He regarded *Dissocladella* as the simpler genus, stating that 'its natural place in the system is near the starting-point giving origin to the Thyrsoporelleae. Whether it is better included with this tribus (taken in a somewhat wider sense) or with the Triploporelleae, I am not yet sure. This question can only be discussed when certain new Triassic species of *Diplopora*, resembling in an astonishing way *Dissocladella*, will have been described' (Pia 1936*b*; pp. 18, 19). And in 1935 Pia (p. 243), describing and discussing the Middle Triassic *Diplopora subtilis* Pia var. *dissocladelloidea* Pia, gave it as a possible origin for the line of succession of four genera: *Dissocladella*, *Trinocladus*, *Thyrsoporella*, and *Belzungia*.

Thus in 1936 Pia had suggested a Triassic origin for his Cretaceous–Eocene Thyrsoporelleae, with a link in the Cretaceous between *Dissocladella* and the more advanced *Trinocladus*, leading eventually (Pia 1936*a*, p. 7) to the Eocene type genus *Thyrsoporella* and its close relation *Belzungia*. All possess 'swollen branch-systems' and this may be quoted as a logical classificatory character. But the *form* of these branch-systems is conspicuously very different: *Thyrsoporella* (and *Belzungia*) show a few thickened irregular branches taking up much space in the thick calcareous wall, and divided by consequent irregular-outlined calcification; in *Trinocladus* the spindle-shaped branch-elements, long or short, usually take up much less space between consequently thicker calcification in a thick wall; and in *Dissocladella* the primaries are swollen into conspicuous spherical structures with much smaller secondaries, all within a very thin wall, occasioned by proportionally larger outer and inner thallus-diameters than with the other two.

During the subsequent forty years, up to the present, two new genera and many new species were described for the Thyrsoporelleae. They extend the total range of the tribe from Upper Triassic to Eocene: the three component elements outlined above, *Thyrsoporella*, etc., *Trinocladus* and *Dissocladella*, extending from Upper Triassic, Upper Jurassic, and Upper Trias or Lias respectively. The individual values of the various new taxa contribute unequally to the understanding of the subfamily, e.g. of my species, *T. radoicici* and *D. deserta* (Elliott, 1968) were based on very

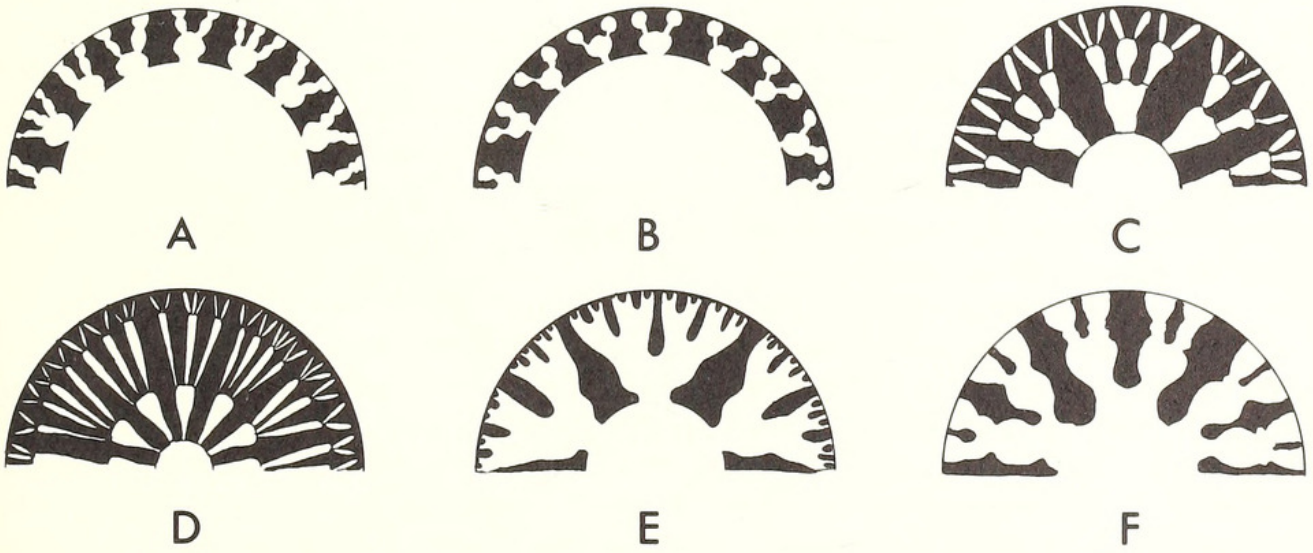
limited, and on abundant but extremely poorly preserved material, respectively. They were significant for the palaeontology of the Middle East but of no value for this present study since they occur at levels from which much better-preserved and more typical species of their respective genera occur. It is, therefore, proposed to examine now the significant taxa only, i.e. those which extend the total range or which increase our knowledge over and above the record of a new species as such, and this is attempted for the three groups, beginning with *Dissocladella* which Pia considered ancestral; then *Trinocladus*, to which he connected it, and finally *Thyrsoporella* and its related genera.

Elements of the Thyrsoporelleae

Dissocladella

D. cretica (Ott, 1965) was described from within an Upper Triassic–Lias succession. It is a thin-walled dasycladacean, ovoid-elongate, as reconstructed in Ott's fig. 4, whereas the much smaller Palaeocene *D. savitriae* Pia is annular-elongate (Pia 1936*b*, reconstruction fig. 43; Elliott 1968, solid specimen pl. 11, fig. 3). But the distinctive branch-pattern within the thin walls is closely similar: swollen near-spherical primaries followed by several short secondaries.

On morphological grounds, the attribution of these two species to the same genus is reasonable. Could they perhaps be two similar but separate evolutionary developments of which the calcification (all we have, and on which the genus is necessarily based) is closely similar, and which took place in different geological periods? Iterative evolution, repeated development in time of identical or near-identical forms from a common stock, has been postulated for some organisms. Henson (1950, p. 14) considered he had evidence for it in Tertiary peneroplid foraminifera. He had, however, a profusion of well-preserved material on which to work, which is not available



TEXT-FIG. 1. Diagrammatic representations, much enlarged, of comparable thin sections of: A, *Dissocladella savitriae* Pia. B, *D. cretica* Ott. C, *Trinocladus tripolitanus* (Raineri) Pia. D, *T. exoticus* Elliott. E, *Placklesia multipora* Bilgütay. F, *Dobunniella coriniensis* Elliott. Proportions and number of elements approximately correct in individual figures, but all figures converted to the same size for comparison. Drawn by Mr. M. Crawley.

for *Dissocladella*. It seems most likely, therefore, from the limited evidence, that *D. cretica* is a fortunate discovery of an early occurrence of a genus whose species were never very numerous. The essential importance of *D. cretica* is its closeness in geological age to Pia's Middle Triassic *Diplopora subtilis dissocladelloidea* which he postulated as an ancestor for *Dissocladella*. This was later incorporated by Ott when describing *D. cretica* (1965, text-fig. 7) as part of a scheme of diplopore phylogeny. Pia's detailed postulated ancestry is, I consider, a possibility rather than a probability, but it is marginally improved by the finding of *D. cretica*.

Given that *Dissocladella* existed from the older Mesozoic, in what light should *D. undulata* (Raineri) Pia of the Upper Cretaceous be regarded? This species was Pia's connecting link between *Trinocladus* and *Dissocladella*: he transferred it from *Trinocladus* to *Dissocladella*, so making it the earliest known *Dissocladella* at that time.

All Pia's illustrations of this species (sketches of thin-sections and reconstructions) show branch-outlines like those of *Trinocladus* (though much shorter than in other Cretaceous species of that genus and branching only to the second, not the third, degree) rather than the peculiar spherical *Dissocladella* pattern. This is confirmed by my examination of materials from various localities in the Middle East as well as North Africa from which the types came. The species should, therefore, correctly be *Trinocladus undulatus* (Raineri) Pia, as Pia (1927) first referred to it.

In most materials examined by me, *T. undulatus* is the constant associate of the larger *T. tripolitanus* Raineri. Usually both are ill-preserved: the smaller species is more numerous than *T. tripolitanus* which additionally shows tertiary branchlets. This constant association as fossils of two marine species suggests that they grew together in the same environment in life, which in turn throws doubts on the relationship. Were they in fact two species (the fossils do not suggest hybridization) or were they two forms of the same species, the smaller being either the remains of those plants, which stunted and reproducing early did not survive to achieve full growth, or possibly a record of high early mortality? Statistical analysis of large populations might throw light on this if better-preserved material can be found. Meanwhile, both species names are available for the calcifications as preserved for the palaeontologist. The important thing is that the genus *Dissocladella* is clarified by the removal and transfer of the species *undulata*.

Trinocladus

Since Pia's revision (1936*a*) of the type species *T. tripolitanus* Raineri other Upper Cretaceous species, some larger and better-preserved, e.g. *T. pinarensis* (Keijzer 1945), *T. exoticus* (Elliott 1972) have been described. In this genus the spindle-shaped primary branches, of varying length and shape according to the species, may be relatively thin and tend to be set in a thick calcareous wall, though they take up more space proportionally in the smaller species. Of these last, *T. perplexus* (Elliott 1955, 1968) was first described from the Palaeocene–Lower Eocene: surprisingly, it was later discovered in the Upper Jurassic and carefully redescribed in comparison with the original (Conrad *et al.* 1975; Peybernès 1976).

Obviously, a similar argument could be applied to these two stratigraphically separate occurrences of one species, as for the two occurrences of the genus *Disso-*

cladella discussed previously. But again, it seems reasonable to conclude that the fossil calcifications, which are all we have, do represent chance preservation of individuals of a stock whose occurrences were never more than locally abundant and whose range in time is now longer than formerly supposed.

Thyrsoporella and related genera

Pia (1927, 1936*b*) knew only of the Eocene *Thyrsoporella*, a single-tubular dasycladacean fossil and its 'serial-unit' relation *Belzungia* (Palaeocene–Eocene) with a beaded structure like *Mizzia* or *Cymopolia* spp. (Morellet and Morellet 1913). Within the calcareous walls of these fossils the verticils show characteristic thickened to swollen branch-system cavities which are somewhat irregular in outline, few in number, and, because of size and shape, take up much of the space so that the intervening calcification is conspicuously irregular in outline. The repeated branching lends itself to a simple formula indicating total number of successive primaries, secondaries, tertiaries, etc. Massieux (1966), in a detailed analysis, gave such a formula of 1:2:8:32 for *Thyrsoporella* and 1:2:4:8:16:32 for *Belzungia*.

As with *Dissocladella* and *Trinocladus* much older forms are now known: *Placklesia* from the Rhaetic (Bilgütay 1968) and *Dobunniella* from the Middle Jurassic (Elliott 1975). There are also doubtful, inadequately known forms recorded from the Jurassic (*Thyrsoporella* sp., Lower Jurassic; *T.* (?) *hatigomoriensis* and *Belzungia* sp., Upper Jurassic: Nikler and Sokač 1968; Yabe and Toyama 1949; Golonka 1970) but these do not affect the total range.

The interesting thing about these genera, all showing the peculiar thickened irregular branches of *Thyrsoporella* type, is obtained by comparing their branch-formulae with geological age:

Rhaetic	1:2:8:32:128	*Placklesia*
Middle Jurassic	1:2:4	*Dobunniella*
Eocene	1:2:8:32	*Thyrsoporella*
Palaeocene–Eocene	1:2:4:8:16:32	*Belzungia*

Thus the most elaborate branching occurs in the earliest genus, with the most simple of intermediate age, before the later medium-complicated ones. The succession in time shows no definite progression in structural detail.

In seeking an explanation of this, one must consider the effect of limited calcification in life as a factor in the selective nature of the fossil record of dasycladaceans. From living species we know that their calcification is usually near-constant in adult individuals of one species growing under normal conditions, i.e. it is usually a specific character though it may be light or heavy. It is capricious in siting between one taxon and another within dasycladaceans viewed as a whole. Thus there are all sorts of limited calcifications available for possible preservation as fossils, varying between a little calcification only around stem-cell or reproductive bodies, or a thin sheet only marginally near the tips of branches, up to a heavy calcification preserving a record of much of the plant's gross external morphology. Where the calcification is minimal, much of the plant is unknown if the species is extinct. (Cf. the interpretation of the extinct *Pagodaporella* in the light of the living *Dasycladus* (Elliott 1968, p. 60).) It is thus possible that in life the branching of *Dobunniella* continued outside the calcified

zone, perhaps as elaborately as in the other genera. There is no evidence of this at all: whether it was so or not, it seems best to regard the genus as one of the chance witnesses preserved of the *Thyrsoporella* stock, whose details would shift slowly through time with the genetic patterning consequent on small local populations. Whether the differences between these taxa should be regarded as generic or specific is a taxonomic, not an evolutionary, question. Pia considered this problem for the Thyrsoporelleae as a whole (Pia 1936*b*, p. 19). Personally I accord them generic rank, since the different calcifications preserved are all we have. New species would have the same general calcification but different sizes and proportions. The important thing is the long, if sporadic, record of that type of branching and its calcified surround, characteristic of *Thyrsoporella* and its allies.

The Thyrsoporelleae reconsidered as a tribe

The original definition of the Thyrsoporelleae referred to their swollen branches and to the presumed function of these as housing the reproductive elements (Pia 1927, p. 77). Some later-described species, e.g. *Trinocladus pinarensis* Keijzer are less obvious candidates for the secondary and tertiary branchlets having this function as in Pia's definition. But in no case is there direct evidence of this in Thyrsoporelleae; it is in fact very exceptional generally in fossil dasycladaceans to see remains of reproductive bodies within the branches, e.g. in some examples of *Triploporella*. Usually, where one portion of the branch-system is markedly swollen, this has been presumed to have contained the reproductive elements. How far this is to be considered a reasonable view depends on a consideration of what is known in living dasycladaceans (cf. Valet 1968, 1969) and its extrapolation to extinct forms (see discussion in Bassoulet *et al.* 1975, on Pia's terminology); it is not further dealt with here. Whether Thyrsoporelleae carried their reproductive elements within the branching of which we have evidence, or outside the calcification which is all we now have, is not known. But the distinction between the general outlines of the three branch-patterns characteristic of and persisting in *Dissocladella*, *Trinocladus*, and *Thyrsoporella*, etc., is important. Pia's reasons for uniting them are no longer valid in the light of subsequent discoveries. Is their taxonomic union still justified; if not, should they be classified apart or with other dasycladacean genera outside the Thyrsoporelleae?

Thyrsoporella, with *Belzungia*, *Dobunniella*, and *Placklesia* are together the most distinctive of the three. Ranging from Rhaetic to Eocene, there is little else like them in branch-form and calcite surround. Presumably all the dasycladaceans of the Jurassic to Recent are likely to be modified survivors of the very rich Triassic flora, but *Thyrsoporella* and the others afford no real clue to their ancestry. Dr. Ernst Ott (in correspondence, 1975) compared the branch-pattern of the Permian *Imperiella* (Elliott, 1975) to *Placklesia*. The former, with swollen crowded branch-outlines, shows a delicate lace-like calcification pattern, different to that of *Placklesia*. It is such incidental details of structure, chemistry, etc., which, carried on unmodified, often mark lines of descent, and not types of structure as observed and formulated, however important these are to progressive evolution itself. Dr. Ott's comparison of the branches is, however, valid, the preservations are different, and his suggestion is the only one I can record for a possible origin of the tribe.

These four genera therefore stay together and from the name of the type genus now constitute the Thyrsoporelleae emend. (See Appendix.)

Dissocladella, as restricted earlier in this account, is a separate stock. I have not examined material of the Triassic diplopore variety which Pia considered ancestral: from the published account (Pia 1935) it seems possible. It does in any case seem very likely that the genus arose from a Triassic ancestor. There seems now no special reason to associate it with *Thyrsoporella* and its allied genera. It can be compared with other genera showing spherically swollen branch-elements, e.g. *Cylindroporella*, where they are conventionally regarded as 'fertile' branches and where such verticils alternate with verticils of thin 'sterile' branches; or with *Sarfatiella*, showing the swollen elements only. (Did this last genus perhaps not calcify a lower, presumed non-reproductive part of the thallus?) In these two, however, there are no secondary branches from the inflated elements. Once again one is in the area of random morphological comparisons, and *Dissocladella*, as known, seems to stand by itself. For that reason the genus, although solitary, becomes the occupant of Dissocladelleae trib. nov. (see Appendix), of possible diplopore origin as shown by Ott (1965).

With *Trinocladus*, which again in this re-examination seems to stand apart from the other two, a comparison with other dasycladaceans is more fruitful. It compares well with *Triploporella* in swollen primaries and subsequent thinner branches, differing in proportions. This relationship was considered by Pia followed by Kamptner (1958) who, in a general view of dasycladaceans, derived all Pia's Thyrsoporelleae from *Triploporella*. The Upper Jurassic appearance of *Trinocladus* also accords with this, *Triploporella* being Upper Jurassic and Cretaceous. Accordingly, *Trinocladus* is here transferred to the Triploporelleae.

The extinction of the Thyrsoporelleae (sensu *Pia*)

The possible origins of the Thyrsoporelleae (emend.) and Dissocladelleae nov., and the probable origin of *Trinocladus*, have been discussed above. One thing they still have in common: they all ended in the early Tertiary, after surviving the Cretaceous–Palaeocene transition. Is this a fact for which a common explanation can be given?

The Tethyan Palaeocene seems in certain facies to have contained favourable environments for algae of all kinds (Elliott 1968, p. 96). After the Eocene, however, with the rupture of the Tethys and continued drifting of shelf-seas as parts of their respective continental masses, the dasycladacean survivors are found as a relict flora with markedly discontinuous distribution of its component elements. It seems very unlikely that any of the numerous Palaeocene–Eocene dasycladacean genera which disappeared from the fossil record evolved into something else, so poor is the Recent flora, though a solitary exception is just possible with *Pagodaporella* and *Dasycladus*. One asks, did those genera known fossil from the Cretaceous and still living today, such as *Cymopolia* and *Neomeris*, possess some inherent advantage over Pia's Thyrsoporelleae? I think not. Few things are more striking than the way in which the teeming diplopore dasycladaceans of the Triassic lagoons have been replaced by the equally abundant codiacean *Halimeda* of the present-day atolls, as witnessed by diplopore limestones in the Alpine Trias and *Halimeda* limestones in the Indo-Pacific Tertiary. This phenomenon has been considered as possibly due to

the more efficient reproduction of the latter (Elliott 1968, p. 100). Whatever the cause, the replacement is a fact. During the long period of their gradual decline the dasycladaceans underwent a rich and varied evolution which did not improve their selectiveness for survival in any way that we can trace, since it was elaboration and diversification with their basic and constant fundamentals unchanged. It was the intra-regressive evolution to which attention has been drawn earlier in certain brachiopods (Elliott 1948, 1953). Such organisms may last a very long time geologically. Palaeontologists are prone to seek cause and effect to explain the biological changes of the past as zealously as they once sought for purpose in evolution. But chance plays a very great part in survival. Organisms long since superseded, in the sense of more highly organized competitors having evolved, will survive as relicts so long as a limited foothold can be maintained in a suitable environment. Their times of peril come when the environment changes rapidly (geologically speaking) and the few survivors have to establish their kind elsewhere. But even so, they may outlive various crises which are sporadically distributed over a very long time indeed. The algae discussed here did not survive the great changes in distribution of land and sea which began after the Eocene and which led gradually to the geography of the world as we know it today. In this they were not alone but were affected as were various other dasycladaceans. So far as we can judge, if this had not happened they could have been alive today like the surviving dasycladaceans; strange little algae of warm coastal waters, forming a very minute element indeed in the marine flora.

In conclusion, it would seem that the Thyrsoporelleae of Pia were, unintentionally, very well named. For the thyrsus was the emblem of Bacchus, whose initiates achieved, at best, an intuitive comprehension of the whole, rather than a detailed understanding of its component parts.

APPENDIX: DIAGNOSES OF EMENDED AND NEW TRIBES

Class CHLOROPHYCEAE
Order DASYCLADALES
Family DASYCLADACEAE
Tribus THYRSOPORELLEAE Pia 1927, emend.

Tubular or serial-unit calcified dasycladaceans, medium to thick walled, with verticils each usually containing six to eight branches, which divide distally up to five times; all branches and branchlets thickened or swollen; calcification weak adjacent to stem-cell. Rhaetic–Eocene. Genera: *Thyrsoporella*, *Belzungia*, *Dobunniella*, *Placklesia*. *Imperiella* (Permian) doubtfully referable to tribe.

Tribus DISSOCLADELLEAE nov.

Elongate-ovoid or annulated-tubular calcified dasycladaceans, thin walled; verticils each containing numerous small branches, each showing one near-spherical short primary communicating proximally with the stem-cell by a pore or very short stem, and distally giving rise to a small number of very small inflated secondaries. Rhaetic or Lias, to Palaeocene (?Eocene). Genus: *Dissocladella*.

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Typescript received 14 April 1976
Revised typescript received 10 June 1976