

Lower and Middle Liassic Calcareous Algae (Dasycladales) from Mt. Velebit (Croatia) and Mt. Trnovski Gozd (Slovenia) with Particular Reference to the Genus *Palaeodasycladus* (PIA, 1920) 1927 and Its Species

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Key words: Calcareous algae (Dasycladales), Lower-Middle Liassic, Croatia, Slovenia.

Abstract

Based on the characteristics of individual species, the generic characteristics of *Palaeodasycladus* have been determined and enlarged. *P. mediterraneus* (PIA, 1920) 1927 comprises a broad array of varieties that have been taxonomically distinguished on the basis of the variable shape of primary and secondary branches and the way in which the secondaries emerge. The following varieties are represented: *P. mediterraneus* (PIA, 1920) 1927 var. *mediterraneus*, *P. mediterraneus* var. *heraki* (SOKAČ & NIKLER, 1966) n. comb., *P. mediterraneus* var. *illyricus* (SOKAČ & NIKLER, 1966) n. comb., *P. mediterraneus* var. *gracilis* (CROS & LEMOINE, 1967 ex GRANIER & DELOFFRE, 1993) n. stat., *P. mediterraneus* var. *elongatulus* PRATURLON, 1966, and *P. mediterraneus* var. *calciticus* n. var., and are characterised by specific skeletal form and easily recognisable calcification pattern. Also, the generic assignment of *P. barrabei* LÉBOUCHÉ & LEMOINE, 1963 ex GRANIER & DELOFFRE, 1993 has been confirmed, in spite of its recent transferral to *Eodasycladus* by BARATTOLO et al. (1994). The following new species have been described: *Palaeodasycladus alanensis* n. sp., characterised by broadened, bowl-shaped or bushy swollen primary branch-

es; *P. multiporus* n. sp., characterised by numerous higher-order branches on each primary branch; *P. benceki* n. sp., with very large primary branches with extremely variable distal ends; and *P. asteriscus* n. sp., with loosely spaced whorls and variously directed secondary branches, often growing in opposite directions from the same primary branch. Lower Liassic species, previously ascribed to *Fanesella*, *F. dolomitica* and *F. anae*, have also been assigned to *Palaeodasycladus* with enlarged generic characteristics and are named, consequently, *Palaeodasycladus dolomiticus* (CROS & LEMOINE, 1966) n. comb. and *P. anae* (SOKAČ, 1988) n. comb., respectively. *Fanesella sokaci* BARATTOLO & BIGOZZI, 1996 is considered to be a younger synonym of *P. dolomiticus*. Phylogenetic relationships between various taxa have also been considered and a phyletic lineage *P. barrabei* - *P. alanensis* - *P. benceki* has been shown to exist.

As regards the relationship between *Palaeodasycladus* and *Eodasycladus*, the latter has been shown to have evolved directly from *P. barrabei* by enlarged and more pronounced bubble-shaped swelling of one of the secondary branches, which thus becomes a "sporangia-bearing" organ. Also, a new species tentatively assigned to the genus *Selliporella*, *Selliporella? problematica* n. sp., has been described. From its morphological characteristics it represents an intermediate form, and a phylogenetic link between Liassic *Palaeodasycladus* and Middle Jurassic *Selliporella*. Finally, a new species, *Humiella japodica* n. sp. has been described, thereby enlarging the stratigraphic range of the genus *Humiella* into the Lower Liassic.

Contents

<p>1. INTRODUCTION2</p> <p>2. TAXONOMIC DESCRIPTIONS3</p> <p> Genus <i>Palaeodasycladus</i> (PIA, 1920) 19273</p> <p> <i>Palaeodasycladus mediterraneus</i> (PIA, 1920) 1927 var. <i>mediterraneus</i>3</p> <p> <i>Palaeodasycladus mediterraneus</i> var. <i>heraki</i> (SOKAČ & NIKLER, 1966) n. comb.9</p> <p> <i>Palaeodasycladus mediterraneus</i> var. <i>illyricus</i> (SOKAČ & NIKLER, 1966) n. comb.12</p> <p> <i>Palaeodasycladus mediterraneus</i> var. <i>gracilis</i> (CROS & LEMOINE, 1967 ex GRANIER & DELOFFRE, 1993) n. stat.13</p> <p> <i>Palaeodasycladus mediterraneus</i> var. <i>elongatulus</i> PRATURLON, 196614</p> <p> <i>Palaeodasycladus mediterraneus</i> var. <i>calciticus</i> n. var.17</p> <p> Remarks on the taxonomic classification of newly established varieties18</p> <p> Distinguishing characteristics of the established varieties19</p> <p> <i>Palaeodasycladus barrabei</i> LÉBOUCHÉ & LEMOINE, 1963 ex GRANIER & DELOFFRE, 199321</p> <p> Taxonomic validation of <i>Palaeodasycladus barrabei</i> LÉBOUCHÉ & LEMOINE and its relationship with <i>Eodasycladus ogilviae</i> CROS & LEMOINE24</p> <p> <i>Palaeodasycladus alanensis</i> n. sp.25</p>	<p> <i>Palaeodasycladus dolomiticus</i> (CROS & LEMOINE, 1966) n. comb.26</p> <p> Main characteristics of the genus <i>Fanesella</i>.....26</p> <p> Comparison of the main characteristics of the genera <i>Palaeodasycladus</i> and <i>Fanesella</i> and the proposal for their unification....26</p> <p> <i>Palaeodasycladus anae</i> (SOKAČ, 1988) n. comb.28</p> <p> <i>Palaeodasycladus multiporus</i> n. sp.29</p> <p> <i>Palaeodasycladus benceki</i> n. sp.32</p> <p> <i>Palaeodasycladus asteriscus</i> n. sp.34</p> <p> Genus <i>Eodasycladus</i> CROS & LEMOINE, 1966 ex GRANIER & DELOFFRE, 199335</p> <p> <i>Eodasycladus ogilviae</i> CROS & LEMOINE, 196636</p> <p> Genus <i>Selliporella</i> SARTONI & CRESCENTI, 1962 emend. BARATTOLO et al., 198837</p> <p> <i>Selliporella? problematica</i> n. sp.37</p> <p> Genus <i>Humiella</i> SOKAČ & VELIĆ, 1981 emend. MASSE et al., 198439</p> <p> <i>Humiella japodica</i> n. sp.39</p> <p>Acknowledgements40</p> <p>3. REFERENCES40</p> <p>PLATES I-XLII42</p>
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1. INTRODUCTION

During many years of field work in the Dinaridic Karst, numerous Liassic (Lower Jurassic) outcrops were studied in an area ranging from Trnovski Gozd, Slovenia, to the north-west, to Konavoska Brda, south-east of Dubrovnik, Croatia, in the south-east. Among the abundant fossil material, calcareous algae (Dasycladales) were well represented, with the genus *Palaeodasyclus* and its type-species, *P. mediterraneus* (PIA), being the most common. For almost forty-five years the genus was represented solely by its type species, which was frequently quoted and often illustrated from Lower and Middle Liassic deposits of the peri-Mediterranean region. After a fairly long time, another species, *Palaeodasyclus barrabei*, was added by LÉBOUCHÉ & LÉMOINE (1963) and a new variety, *P. mediterraneus* var. *elongatulus* was introduced by PRATURLON (1966). At the same time, CROS & LÉMOINE (1967) described a new species, *P. gracilis*, but added, in a subsequently inserted footnote, that it probably represented a younger synonym of *P. mediterraneus* var. *elongatulus*. Putting aside, for the moment, the discussions about mutual relationships between individual species, their validity, and their distinctive features (see below, in the description of individual taxa), it remains unclear why no one attempted to perform a detailed revision of the original description of the genus (PIA, 1920) and its later emendation (PIA, 1927), in spite of numerous finds. Some workers (BOUROULLEC & DELOFFRE, 1970; DELOFFRE, 1972; LÉBOUCHÉ & LÉMOINE, 1963; CROS & LÉMOINE, 1967) commented on the typical properties of the genus and its type-species, but no new observations were added to the original descriptions. Some features mentioned by PIA, such as the club-like shape of the thallus in *P. mediterraneus* (which was never illustrated by a photograph), or the intusannulation, seemed to be passed over from one description to the next without critical checking. Thus in the monograph of BASSOULLET et al. (1978, p. 187), intusannulation was mentioned as a generic characteristic, probably influenced by the fact that it is mentioned in the descriptions of all species. Only more recently, have the genus and its species received more attention. Thus DELOFFRE & LAADILA (1990) proposed the generic description to be completed with some new characteristics, which, however, were observed in specimens (sections) which most likely do not belong to the type-species, in spite of being so assigned by the authors. They also consider *P. barrabei* LÉBOUCHÉ & LÉMOINE to be identical with *P. mediterraneus* and hence to represent its younger synonym, and for *P. elongatulus* they agree with the original authors in its being a variety of the type-species. Later, BARATTOLO et al. (1994) critically reviewed the paper by DELOFFRE & LAADILA (1990) and expressed their disagreement with some additional features ascribed by DELOFFRE & LAADILA (1990) to the type-species. They also, on the basis of abundant

material from the type locality, stated some new observations for *P. mediterraneus*, but warned that they represented only the first step towards the full understanding of the morphology of that species. They also, based on their own observations and some morphological features, revised *P. barrabei* LÉBOUCHÉ & LÉMOINE and proposed its transferral into the genus *Eodasyclus*. They reject the opinion of DELOFFRE & LAADILA (1990) that *P. barrabei* possibly represents a younger synonym of *P. mediterraneus*. For *Palaeodasyclus gracilis* CROS & LÉMOINE ex GRANIER & DELOFFRE, 1993, or, as labelled by BARATTOLO et al. (1994), *P. mediterraneus* var. *elongatulus* PRATURLON, 1966, the taxonomic status remains unclear and rather controversial. According to BARATTOLO et al. (1994), this form cannot be considered a variety or a subspecies of *P. mediterraneus*, but in order to definitely resolve whether it is a morphotype in the *P. mediterraneus* group or a distinct taxon, further detailed studies are necessary. Later, BARATTOLO & BIGOZZI (1996) again reconsidered numerous specimens (sections) of *P. mediterraneus* from Gran Sasso, but with a morphology different from the type material (as illustrated by BARATTOLO et al., 1994). BARATTOLO & BIGOZZI (1996) distinguish between two extreme morphologies, expressed in the shape of secondary and tertiary branches: the first one is smaller, with more slender secondaries and clearly phloioiphorous tertiaries, whereas the second one has large and densely packed secondaries and tertiaries. They also mention that, for the time being, and for want of a quantitative study with comparison, they consider the various morphologies as one species. In the same paper, BARATTOLO & BIGOZZI (1996) also discuss *Palaeodasyclus gracilis* (= *P. mediterraneus* var. *elongatulus* PRATURLON), adding some new observations concerning the clearly club-shaped thallus, degree of calcification, and shape of branches, which are partly different from those in the original description by CROS & LÉMOINE (1967). These features will be discussed in more detail below, in the description of individual taxa.

Because our understanding of the genus *Palaeodasyclus* is primarily based on the type-species, with only subordinate observations made on later described species, every new observation, i.e. every hitherto undescribed feature, in the type-species is of particular interest for better understanding of the genus in general. No doubt, BARATTOLO et al. (1994) and BARATTOLO & BIGOZZI (1996), in their analysis of the type-species and other species of the genus *Palaeodasyclus*, made important contributions to our greater understanding of that genus; however, some of their considerations are open for critical reconsideration, particularly regarding the interpretation of some features, valorisation of some species, and their proposed taxonomic position.

The purpose of the present paper is to discuss some open problems and to present new arguments about

some controversial opinions, based on abundant illustrated material. The work has been undertaken by examination of more than 1,000 thin sections, from Mt. Velebit (Figs. 1 and 2), which contained a large number of variously oriented specimens. In spite of the fact that the material was often recrystallised, or, more rarely, micritized, the large number of available sections made it possible to: provide a new contribution to the understanding of the genus, its type-species and the later described species; to express various opinions regarding the validity of some species and some generally accepted characteristics; to describe several new species; to establish new and to propose the abandonment of some existing genera; and to indicate some possible phylogenetic relationships within the genus and establish the sequence of evolutionary changes between some genera of the same or similar stratigraphic position.

2. TAXONOMIC DESCRIPTIONS

Order Dasycladales

Family Dasycladaceae

Genus *Palaeodasycladus* (PIA, 1920) 1927

Selected synonymy:

- 1920 *Palaeocladus* n. gen. - PIA, p. 118-122, fig. 22, pl. 6, figs. 1-5.
- 1927 *Palaeodasycladus* nom. nov. - PIA (in HIRMER), p. 79, fig. 62.
- 1963 *Palaeodasycladus* PIA, 1927 (= *Palaeocladus* PIA, 1920) - LÉBOUCHÉ & LEMOINE, p. 95.
- 1967 *Palaeodasycladus* PIA, 1927 (= *Palaeocladus* PIA, 1920) - CROS & LEMOINE, p. 250.
- 1970 *Palaeodasycladus* PIA, 1927 (= *Palaeocladus* PIA, 1920) - BOUROULLEC & DELOFFRE, p. 88.
- 1978 *Palaeodasycladus* PIA, 1927 - BASSOULLET et al., p. 187, pl. 22, figs. 8-9, pl. 23, figs. 1-2.
- 1990 *Palaeodasycladus* (PIA, 1920) PIA 1927 - DELOFFRE & LAADILA, p. 318-319, non pl. 1-3.
- 1993 *Palaeodasycladus* (PIA, 1920) - DELOFFRE & LAADILA, 1990 (= *Palaeocladus* PIA, 1920) - GRANIER & DELOFFRE, p. 36-37.
- 1994 *Palaeodasycladus* (PIA, 1920) PIA 1927 - BARRATTOLO; DE CASTRO & PARENTE, p. 1-4, pl. 1, figs. 1-4.

The original diagnosis by PIA (1920) was comparatively scant but PIA rightly emphasised that a fully adequate and reliable generic diagnosis must not be based on a single species. A concise, though somewhat more detailed, diagnosis was given by BASSOULLET et al. (1978, p. 187). Based on the present material, the gene-

ric diagnosis can be summarised as follows: The thallus may be straight or slightly bent, cylindrical or slightly club-shaped, with an even or slightly undulated or annulated outer surface. Central cavity is cylindrical or quite regularly undulated, with or without intusannulation developed to a variable degree. Primary branches arranged in clear whorls; they bear secondary, tertiary, and, sometimes, fourth-order branches. Primaries may be variously shaped, whereas the secondaries, tertiaries and fourth-order branches are acrophorous or phloio-phorous. Distal branches are more strongly phloio-phorous. Secondaries grow out of the primaries either as finger-like protrusions or are constricted at their base. Sometimes the secondaries and tertiaries may be constricted, giving a seemingly articulated appearance. The position of ramifications with regard to the longitudinal axis of growth may vary from perpendicular to steeply directed upwards, almost parallel to the longitudinal axis. It is supposed that the lower part of the thallus may show a lesser degree of ramification, so that only primaries and secondaries may be developed. The genus is basically cladosporous, but in some forms endospory cannot be excluded; still other forms indicate the beginnings of choristosporous development.

Because some characteristics of the type-species or other species are at the same time basic characteristics of the genus, they will be discussed below, in the descriptions of individual taxa.

Palaeodasycladus mediterraneus (PIA, 1920) 1927 var. *mediterraneus*

Pls. I-V; Pl. VI, Figs. 1-6; Pl. VII, Figs. 3, 5-9; Pl. VIII, Figs. 2-8; Pl. IX, Figs. 1, 8; Pls. X-XI; Pl. XII, Figs. 2-5, part. 6; Pl. XIII, Figs. 1-3, 6-7; Pl. XIV, Figs. 1-4, 7, 9, part. 8; Pl. XV, Figs. 1, 3-9;

Fig. 3

Selected synonymy:

- 1920 *Palaeocladus mediterraneus* n. gen., n. sp. - PIA, p. 118, fig. 22; pl. VI, figs. 1-5.
- 1927 *Palaeodasycladus mediterraneus* PIA -PIA; in HIRMER, p. 79-80, fig. 62.
- 1966 *Palaeodasycladus mediterraneus* PIA - RADOIČIĆ, pl. 1, figs. 1-2; pl. 19, figs. 1-2; pl. 89, fig. 1; pl. 91, figs. 1-2; pl. 110, fig. 1; pl. 143, figs. 1-2.
- 1968 *Palaeodasycladus mediterraneus* PIA - NIKLER & SOKAČ, pl. 1, fig. 1; pl. 3, figs. 1-3.
- 1978 *Palaeodasycladus mediterraneus* (PIA) 1920 - BASSOULLET et al., p. 192-197, pl. 22, figs. 8-9; pl. 23, figs. 1-2.
- non 1990 *Palaeodasycladus mediterraneus* (PIA, 1920) - DELOFFRE & LAADILA, p. 309-320, pl. 1, ?figs. 1-3; pl. 2, non figs. 1-4; pl. 3, non figs. 1-3.

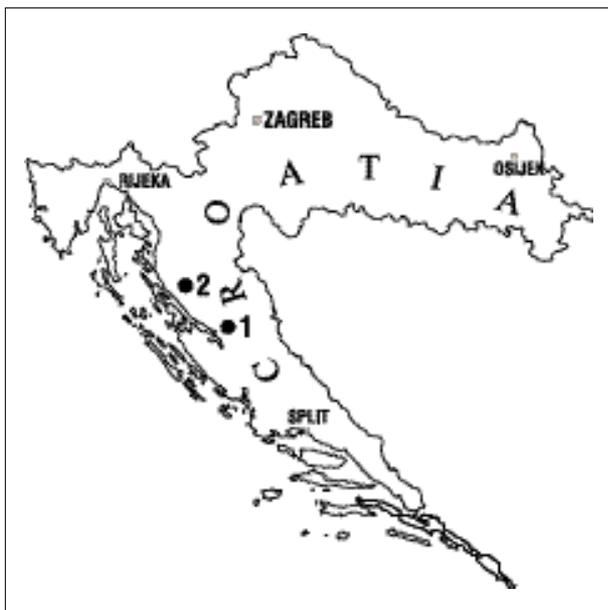


Fig. 1 General position of the localities: 1) Mali Alan; 2) Jadičevac.

- 1994 *Palaeodasycladus mediterraneus* (PIA, 1920), PIA 1927 - BARATTOLO, DE CASTRO & PARENTE, p. 1-11, pl. 1, figs. 1-4.
- 1994 *Palaeodasycladus mediterraneus* (PIA, 1920), PIA 1927 emend. DELOFFRE & LAADILA 1990 - DRAGASTAN et al., p. 59-60, pl. 1, figs. 1-2, ?7.
- 1996 *Palaeodasycladus mediterraneus* (PIA) - BARATTOLO & BIGOZZI, p. 205, pl. 44, figs. 1-2.
- 1997 *Palaeodasycladus mediterraneus* (PIA) - DE CASTRO, pl. 15; pl. 16, figs. 1-4; pl. 24, figs. 1-2; pl. 25, figs. 1-3; pl. 26, figs. 1-3.

The species was first described by PIA (1920) under the name of *Palaeocladus mediterraneus*, to be later renamed and more completely described as *Palaeodasycladus mediterraneus* PIA (1927).

The main species-specific characteristics were given in the description of the genus, which for a long time remained monospecific. In the original description, PIA (1920), probably on the basis of observations made on a number of different sections, produced a reconstruction (PIA, 1920, p. 121, fig. 22), which, as emphasised by BARATTOLO et al. (1994), may be considered hypothetical if based only on the sections figured by PIA (PIA, 1920, pl. 6, figs. 1-5) but proved to be very successful indeed if compared with other sections (e.g., DE CASTRO, 1967, pl. 15, pl. 16, figs. 1,3; present paper, Pl. I, Figs. 2, 5; Pl. II, Fig. 3). This reconstruction suggests that PIA had additional sections, perhaps even better than those figured in the original description.

BARATTOLO et al. (1994) have studied abundant material from the type-locality. They introduced a neo-

type and stated some complementary remarks and interpretations of some features, such as intusannulation and the appearance of spherical and elongated tubular structures in the branches, which they considered to be reproductive structures (BARATTOLO et al., 1994, pl. 1, figs. 1, 3).

They describe the thallus as being slightly club-shaped, in which the wall of the axial cavity is not always clearly visible. In specimens which show a broad axial cavity, they supposed that calcification did not extend to the wall of the central cell. They also mention that all specimens with a narrow central cavity (i.e. the fully calcified envelope) show three rows of branches, the primaries always being large. As a result of incomplete calcification of the primary branches, the inner wall may exhibit a toothed appearance, originally named intusannulation. In the authors' opinion, it cannot be ascribed to the alternation of calcified and non-calcified whorls of primary branches, as was put forward by PIA (1920).

Intusannulation: The usage of the term "intusannulation", which is mentioned by all authors and in all hitherto described species as a generic characteristic, seems to be rather vague, regarding both its appearance and the way it is manifested and its origin. This may be concluded from many examples, of which I shall cite the following: Intusannulation was first mentioned by PIA (1912, p. 36) in the description of *Gyroporella ampleforata* GÜMBEL and represented by broadenings in the inner side of the "skeleton" (i.e. calcareous envelope). Later PIA (1920, p. 168) interpreted the intusannulation in *G. ampleforata* as a result of incomplete calcification at irregular intervals along the axial cavity, whereas in *P. mediterraneus* he regarded it as being produced by an alternating succession of calcified and non-calcified whorls. At the same time, PIA (1920) established *Diplopora phanerospora* which shows a regular alternation of swellings and constrictions in its interior cavity and in which the inner morphology is basically of different origin and accordingly should be treated separately. HURKA (1967), interpreted the intusannulation in *Physoporella intusannulata* as a regular succession of swellings and constrictions of the inner cavity. KOCHANSKY-DEVIDÉ (1970), in the description of *Gyroporella intusannulata*, emphasised the irregularity of intusannulation, as shown by irregularly shaped (variously deep and variously broad) swellings and variously prominent and irregularly toothed constrictions of the axial cavity.

BASSOULLET et al. (1977, p. 160) mention "internal joints" or intusannulation and emphasize that it can be used as an additional detail in the description but cannot have species-specific taxonomic validity. As already mentioned above, BARATTOLO et al. (1994), in analysing *P. mediterraneus*, suppose that intusannulation occurs in specimens with a broad axial cavity as a result of incomplete calcification of the primary

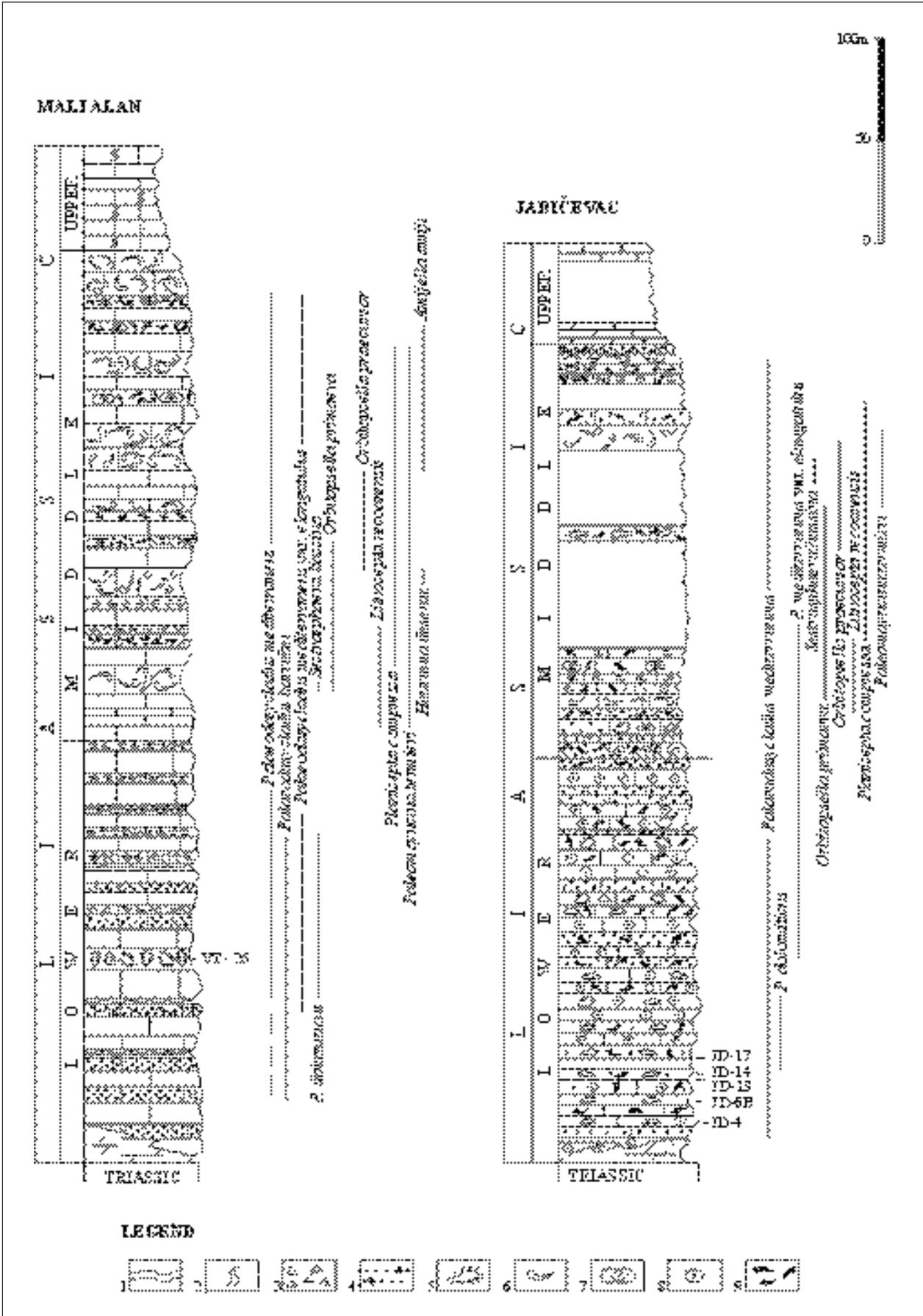


Fig. 2 Geological column of the Liassic deposits of the Mali Alan and Jadičevac localities (Velebit Mt.). Legend: 1) stromatolites; 2) bioturbations; 3) peritidal breccia; 4) peloids and intraclasts; 5) dasycladal algae; 6) bivalve *Lithiotis problematica*; 7) oncoids; 8) ooids; 9) bioclasts; VT 26 sample with algae from the Mali Alan locality; JD 4-17 samples with algae from the Jadičevac locality.

branches, i.e., when the calcification does not extend to the wall of the central cell. For the intusannulation in *P. barrabei* LÉBOUCHÉ & LEMOINE (which they transferred to the genus *Eodasycladus*), BARATTOLO et al. (1994) stated that it could be more or less pronounced or totally absent, manifesting itself as a regular alternation of swellings and constrictions of the axial cavity and producing a wavy appearance in longitudinal sections. From this it is clear that two different cases are manifestly ascribed to the same phenomenon. BERGER & KAEVER (1992, p. 10, fig 2.1e), while discussing the possible cause and origin and the shapes of that phenomenon, stated that it could show regular or irregular arrangement and could be used in defining a species, and that it deserves further study. Finally, DE CASTRO (1997, p. 187) defines the phenomenon as follows: "articulation characterised by the alternation of swellings and constrictions, along the inner surface of the skeleton, due to the different extent of calcification of the proximal lateral portions".

In an attempt to analyse this phenomenon, the following question arises: is it of primary or of secondary origin? From all that has been mentioned in the above review, it could be concluded that it is primary in all those cases in which (a) it is the result of incomplete calcification, or (b) the calcification was of varying extent, or (c) it might be environmentally induced. BARATTOLO et al. (1994), in the caption of their pl. 1, fig 4, state: "...where the stem wall is still preserved but primary branches are obliterated by the intusannulation", which may mean that intusannulation may be regarded as a secondary process. In addition to the above examples, visually similar phenomena may be observed, e.g., in *Praturlonella salernitana* BARATTOLO, in which there is no thinning of the wall between the consecutive whorls (BARATTOLO, 1978, pl. 13, fig. 4) and no intusannulation is mentioned in the original description. Similarly, in *Windosoporella radiata* MAMET & RUDLOFF, *Praturlonella nerae* (DRAGASTAN et al.) BUCUR, and in the form ascribed by SOKAČ & VELIĆ (1978, pl. 1, fig. 3), to *Selliporella donzellii* SARTONI & CRESCENTI, there is a more or less pronounced inner wavy surface. In those three forms, neither a change in wall thickness nor a pronounced toothed surface is visible, which would otherwise suggest reduced or variously extended calcification, so that the origin of that phenomenon, which may or may not occur in specimens of the same species and in the same population, remains totally obscure. In some species, e.g. *Diplopora phanerospora*, it is probably a genetic character. However, what emerges from the above review is, that features occurring on the inner wall, which may display similar or different shapes and be of the same or different origin, have been lumped together under the label of "intusannulation". This may be justified if it is regarded only as a morphological feature. However, because this phenomenon may be more or less pronounced or even totally absent, within a species, it cannot be used as a

species-specific, or, even less so, generic diagnostic taxonomic criterion. **Morphological variants**

Morphological variants: In the hitherto published papers, *P. mediterraneus* has been figured many times. Most of the published photomicrographs included more or less well preserved, often apparently heterogeneous material, without its having been analysed in more detail or mutually compared. In the material from Mali Alan Pass, Mt. Velebit, the observed variability comprises a broad array of different morphological details, occurring within one contemporaneous population thriving in the same habitat. These facts facilitated a new and more complete description of *P. mediterraneus*, which, to my mind, comprises a group of individuals with rather varying morphology and appearance, connected with transitional or intermediate forms or showing a gradual change in individual morphological characters in one specimen. The intention of this paper is to illustrate the abundant new material and thus to show the newly observed characters of individual morphological elements, their variability and interrelationships, and to explain the differing views with regard to the origin of individual morphological characters.

Description: *Palaeodasycladus mediterraneus* (PIA) includes specimens with a mostly cylindrical thallus (Pl. I, Figs. 2, 5; Pl. II, Fig. 3; Pl. III, Figs. 1-2 and others). The thallus is only seldom slightly club-shaped, i.e., its diameter slightly increases upwards; thus the thallus has no stalk and no "head" (Pl. I, Fig.1). Numerous specimens in the population show greatly varying dimensions. If specimens with a longer thallus are preserved, the thallus is often bent (Pl. II, Fig.3), which is supposed to be the result of water currents, or, alternatively, due to gravitation. The outer surface is, in general, smooth and even, perforated by circular, elliptical or polygonal pores of distal branches (Pl. I, Fig 5; Pl. II, Fig.1). Only rare specimens show a slightly undulated outer surface (Pl. III, Fig. 5). Some specimens show, on their outer surface, more or less broad or narrow fissures, arranged at regular, or, more often, irregular intervals. The depth of the fissures varies towards the centre of the skeleton resulting in the appearance of shallow, narrow and irregular annulation (Pl. III, Figs. 2, 7). Observations on numerous specimens reveal a primarily smooth and even inner surface along the central cavity; it is preserved in about 60% of observed specimens; in the others, it is more or less destroyed. The degree of destruction may vary: the walls of the primary and secondary branches may be destroyed, producing an enormously and anomalously broad central cavity (Pl. III, Fig.5), or the inner wall and part of the calcareous partitions between the primary branches may be destroyed, so that the remaining parts are visible, in longitudinal section, as shorter or longer, obliquely situated, symmetrical bars (Pl. IV, Fig. 5), or else only the inner wall at the base of the branches may be destroyed, whereas the pores of the primaries remain

completely preserved (Pl. VI, Fig. 4; Pl. VII, Fig. 6). There are specimens which show, mostly in their lower and middle parts, completely preserved inner structures (the wall of the main cell, primary and secondary branches), but, in the upper part (where the primaries are, as a rule, larger), only a part, or nothing at all, of the inner wall and the primaries may be visible, depending on the extent of the destruction (Pl. IV, Fig. 6 part; Pl. V, Fig. 4). This differs to BARATTOLO et al. (1994) in that the degree of preservation of the inner structures is regarded as being purely the result of subsequent, more or less intense, destruction, rather than being insufficient calcification. Therefore a secondary, subsequent process occurs during, and is dependent upon diagenesis and, consequently, cannot be labelled intusannulation, and, of more practical importance, cannot be regarded as a species-specific characteristic. Indeed, the extent of the destruction depends to a large degree on the dimensions (i.e., the diameter) and the shape of the primaries and on their being more or less densely arranged: the destruction is stronger and more frequent in specimens, or in parts of the specimens, having large, swollen primaries, arranged in densely packed whorls, in which the calcareous partitions between the branches and the whorls become excessively thin which is, in general, more often the case in the upper part of the thallus (Pl. IV, Fig. 1, upper part). In those observed specimens in which the inner wall is preserved, the central cavity occupies in general 20-30% of the entire diameter, rarely amounting to 40%.

Already PIA (1920) noted that the branches ramify further and that three orders of ramifications may be distinguished. Also, the branches may be more or less steeply inclined with regard to the longitudinal axis of growth; in some specimens they are more steeply inclined in the upper parts of the thallus, but they are never, in this species, perpendicular to the thallus, as incorrectly stated by DELOFFRE & LAADILA (1990). Some specimens, e.g. the sections illustrated by BARATTOLO et al. (1994, pl. 1, figs. 2, 4) and in Pl. XI, Fig. 1 below, even indicate the possibility of having four orders of branches. This depends on whether the shorter or longer, finger-like protrusions which grow out of the primary branches without basal constrictions will be regarded as a separate order of branches or not. PIA (1920) also mentions the possibility that ramifications in the basal part of the thallus may show a lesser degree of branching, which is also indicated in Pl. III, Fig. 7 below, though we still lack a unique specimen (section) in which the transition from a lower to higher degree of branching would be visible. Primary branches are arranged in clear whorls. In consecutive whorls they are positioned one above the other, thus forming vertical rows (Pl. I, Fig. 5; Pl. V, Fig. 5; Pl. X, Fig. 6), though this arrangement may be disturbed, coming closer to an alternating position. Neighbouring whorls may be either tightly packed, separated by only thin calcareous partitions (Pl. IV, Figs. 4-5; Pl. V, Figs. 3, 5), or else spaced further apart from each other and separated by thick

calcareous mass (Pl. III, Fig. 1; Pl. VI, Fig. 1; Pl. VII, Figs. 6-8).

Primary branches may exhibit various shapes, which, together with different types of secondary branching, the equally varying shapes of the secondary branches, and variable distance between the whorls, gives the impression of dealing with taxonomically heterogeneous material (Fig. 3). According to the available material (which comprises several thousand variously orientated sections), the primary branches are, as a rule, large, with minor exceptions, and may be cylindrical (tubular) or sausage-shaped (Pl. VI, Fig. 1), cone-shaped, i.e., distally tapered (Pl. V, Figs. 2-3), or very rarely completely irregular (Pl. V, Fig. 1; Pl. VIII, Fig. 2). The larger the primary branches (i.e., the greater their diameter) the tighter the package of the whorls and the thinner the calcareous partitions between the whorls, which are thus prone to destruction (Pl. I, Fig. 5; Pl. IV, Figs. 4-5). In some specimens, the primary branches increase in diameter going upwards (Pl. IV, Fig. 1); simultaneously, calcareous partitions become thinner and therefore more easily destroyed (Pl. IV, Fig. 1). Some sections show a more pronounced change in the shape of the primary branches (Pl. IV, Fig. 1; Pl. V, Fig. 4) and some primaries show even a higher degree of branching than the rest; thus, the same specimen shows both 3rd and 4th order of ramifications (Pl. I, Fig. 2; Pl. XI, Fig. 1). The number of primary branches in a whorl (previously an unknown criterion) varies from 12 to 18.

From the distal surfaces, or distal points, depending on how the terminations of primary branches are shaped, several secondaries grow out, their number varying from 3 to 8. In specimens with tapered (cone-shaped) terminations of the primaries, the secondaries seem to grow out from one place (Pl. V, Figs. 2-3) and in such cases their number seems to be restricted to 3-5 (Pl. I, Figs. 3-4). In such cases, when the secondary branches are tightly compressed at the base, they form a bundle (Pl. I, Figs. 2-5; Pl. III, Fig. 1; Pl. XIV, Fig. 7) while diverging distally. The secondaries may be either constricted at their bases (Pl. II, Fig. 3; Pl. VI, Figs. 1-4) or may form finger-shaped protrusions growing out of the primaries (BARATTOLO et al., 1994, pl. 1, fig. 4; Pl. III, Fig. 4, and Pl. V, Fig. 2, this paper). Secondaries also vary in their length and thickness, being of phloiophorous or acrophorous shape (Pl. I, Figs. 2-5; Pl. V, Fig. 2; Pl. VI, Figs. 1-4). In some specimens, the secondaries show constrictions, giving a beaded (Pl. XIII, Fig. 3) or seemingly articulated appearance (Pl. II, Fig. 3; Pl. VI, Fig. 3; Pl. XIII, Figs. 1-2). From the distal ends of the secondaries, the clearly phloiophorous tertiaries emerge; from their distal ends they seem to go through the outer rim of the skeleton (calcareous envelope) and therefore more or less widened, funnel-shaped, tubules (Pl. I, Fig. 3; Pl. XI, Figs. 1, 6-8, 13), or, sometimes, a dark, micritized layer surrounding (enveloping) the surface of the skeleton (Pl. I, Fig. 3; Pl. VII,

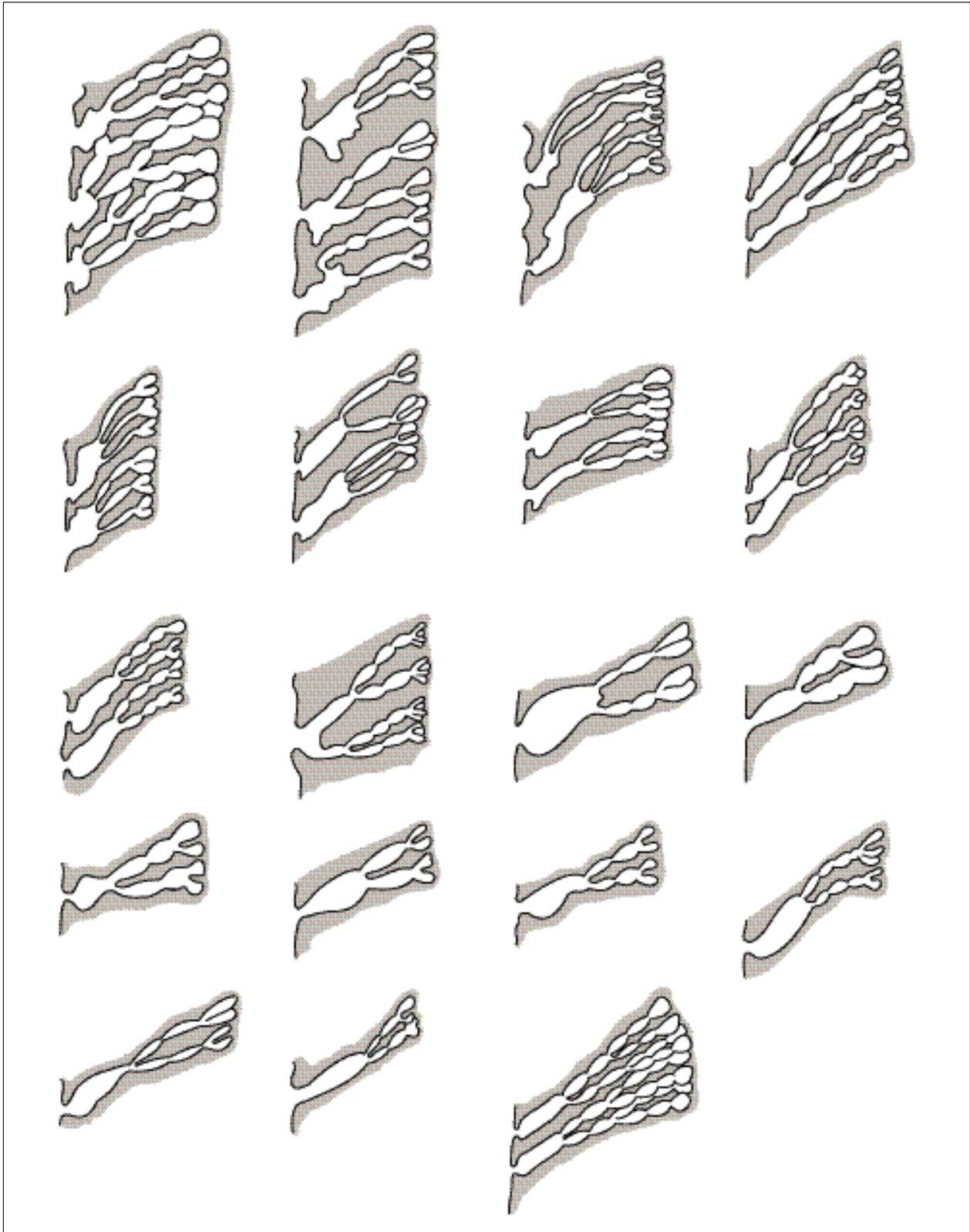


Fig. 3 Schematic review of sections of possible forms of branches in *Palaeodasycladus mediterraneus* var. *mediterraneus*.

Fig. 3; Pl. XI, Figs. 8-11) is visible on the outer rim. The number of tertiaries on a secondary branch varies depending on their shape: from 2-3 when the tertiaries are distinctly swollen to 4 when they are smaller and of slightly increasing diameter distally. Such branches are

said to show characteristic multiple constrictions which gives an articulated appearance. In the available material this can be seen in a small number of specimens (Pl. IV, Fig. 6; Pl. XIII, Figs. 1-2), in which, also, unambiguous distinction between the secondaries and the ter-

tiaries appears exceedingly difficult. Specimens with bundles of short phloioporous branches with no visible constrictions are much more numerous (Pl. V, Fig. 3; Pl. XI, Figs. 1, 6-8, 13). The shape of the pores of the most distal branches on the outer surface of the skeleton varies from circular-elliptical to tightly compressed, polygonal. Because of the variability in the shape and dimensions of branches, tangential sections or those in which only the third- and fourth-order branches (if developed) are preserved, are not suitable for determination. The long-held assumption of cladopority has been confirmed, in the available material, by cysts being found in the cavities of the primary branches (Pl. I, Fig. 5; Pl. XIV, Fig. 1). Sporadically, single cysts may be found within the secondary and even tertiary branches.

These occurrences of cysts question the interpretation (BARATTOLO et al., 1994, pl. 1, figs. 1, 3) of rounded and elongated structures, situated in the interior of branches of some rare specimens, as being cladoporous reproductive organs. On the basis of their shape, arrangement, their mutual relationships, and frequency of occurrence, I am inclined to assume that those features possibly develop as results of some differences during the process of calcification.

The available material contains specimens that, at first glance, give a visually heterogeneous impression and, when compared with each other, appear rather distinctly different. This impression of heterogeneity is the consequence of varying thallus size and individual parameters (Table 1): shape, size, arrangement and den-

sity of primary branches; mode of growth, shape, size, and number of secondary and tertiary branches; and general degree of ramification. However, many of these differences are frequently observed in the same specimen, which implies their genetic homogeneity, and, besides, there exist intermediary forms which morphologically connect various, visually different specimens. Therefore they have all been grouped together into one taxonomic unit. The comparatively abundant and seemingly lavish photomicrographs are deemed necessary to demonstrate the above conclusion, i.e., to show the broad array of morphological variability in this form. Even so, however, it should be emphasised that the morphological variability in the photomicrographs presented is not exhaustive for either this species or other species of that genus.

Stratigraphic position: The species is distributed throughout the southern Tethyan realm, and is particularly frequent in the peri-Mediterranean region. The compound (synthetic) stratigraphic range of the species corresponds to the Lower and Middle Liassic.

***Palaeodasycladus mediterraneus* var. *heraki*
(SOKAČ & NIKLER, 1966) n. comb .**

Pl. VII, Figs. 1-2, 4; Pl. IX, Fig. 4; Pl. XII, Fig. 1;
Pl. XIV, Figs. 5-6; Pl. XV, Fig. 2;

Fig. 4.1

1966 *Petrascula heraki* n. sp. - SOKAČ & NIKLER,
p. 7-8, fig. 1b.

		Trnovski Gozd	Mali Alan	Jadičevac
Maximum observed length of thallus	L	21.60	15.34	18.76
Outer thallus diameter	D	1.16 - 3.38	1.12 - 3.15	1.93 - 5.40
Inner thallus diameter	d	0.24 - 0.58	0.24 - 0.64	0.48 - 0.76
Relation	d/D	0.164 - 0.282	0.142 - 0.335	0.124 - 0.333
Distance between whorls	h	0.16 - 0.44	0.20 - 0.49	0.39 - 0.49
Diameter of primaries	p	0.06 - 0.24	0.08 - 0.35	0.10 - 0.34
Length of primaries	l	0.20 - 0.72	0.15 - 0.60	0.30 - 0.49
Number of primaries in a whorl	w	12 - 18	12 - 18	12 - 18
Diameter of secondaries	p'	0.10 - 0.15	0.05 - 0.20	0.09 - 0.20
Length of secondaries	l'	0.30 - 0.60	0.14 - 1.12	0.25 - 0.86
Number of secondaries on a primary	w'	3 - 5	3 - 5 (up to 8)	3 - 4
Diameter of tertiaries	p''	0.08 - 0.26	0.05 - 0.20	0.16 - 0.25
Length of tertiaries	l''	0.14 - 0.34	0.08 - 0.30	0.20 - 0.45
Number of tertiaries on a secondary	w''	3 - 4	2 - 4	3 - 4
Angle of inclination of branches		< 70°	< 70°	< 70°

Table 1 Comparison of principal biometric parameters of specimens belonging to *P. mediterraneus* (PIA) var. *mediterraneus* from three distant localities (all dimensions in mm).

1969 *Petrascula heraki* SOKAČ & NIKLER - SOKAČ & NIKLER, p. 103-112, pl. fig. 1, non figs. 2-3; pl. 2, fig. 6, non figs. 1-5; pl. 3, non figs. 1-2, 4.

non 1996 *Petrascula ?heraki* SOKAČ & NIKLER - BARATTOLO & BIGOZZI, pl. 54, fig. 7.

The remains of this alga were first briefly described by SOKAČ & NIKLER (1966) as *Petrascula heraki* n. sp. Afterwards, a more detailed description with illustrations followed later by SOKAČ & NIKLER (1969). However, both descriptions were laden with errors, in that heterogeneous material was amalgamated. Due to poor preservation it was possible only to assume the existence of trichophorous tertiary branches serving as assimilators. Later on, this uncertain taxonomic position and inadequately known characters led BASSOULET et al. (1978) to consider the form as a possible synonym of *Fanesella dolomitica* CROS & LEMOINE. The presently available material, with more numerous and better preserved sections, enabled the redetermination of the form as *P. mediterraneus* (PIA) var. *heraki* (SOKAČ & NIKLER) n. comb. The main characteristics of this variety are as follows: the rectangular shape of the primary branches, which are situated slightly obliquely (up to 25° to the growth axis), though this angle may vary on the same specimen (Pl. VII, Figs. 2, 4). The thallus is cylindrical, supposedly with a slightly club-shaped termination. The outer surface sometimes appears to be slightly wavy (Pl. XIV, Fig. 6) and clearly delineated, whereas the inner surface is more often partly destroyed. Primary branches are basically rectangular, sometimes slightly deformed and, occasionally, distally slightly widened (Fig. 4.1). They are tightly packed both within a whorl and with the respect to the arrangement of whorls. Both the whorls

and the branches within a whorl are separated by thin calcareous partitions which are prone to destruction. Secondary branches grow out of the distal end of the primaries, either in bundles or singly. The secondaries are somewhat shorter than the primaries and of slightly phloioiphorous or acrophorous shape (Pl. VII, Figs. 1-2; Pl. XIV, Fig. 5; Pl. XV, Fig. 2). Sporadic constrictions of the secondaries cannot be ruled out, though this was not clearly observed. The tertiaries, though poorly visible, are certainly present. They are short and grow out of the outer terminals of the secondaries (Pl. VII, Fig. 1). They are supposed to be phloioiphorous, numbering 3-4? (Table 2). Single cysts in the cavities of the primaries indicate the cladosporous type of reproduction in this variety (Pl. IV, Fig. 4). Some specimens may show some intermediate characters, transitional to another variety, *P. mediterraneus* (PIA) var. *illyricus* (SOKAČ & NIKLER) n. comb., or another species, *Palaeodasycladus anae* (SOKAČ) n. comb.

The main distinguishing characteristic of this variety, particularly with regard to the type-variety, is the square or rectangular shape of the primary branches due to their dense packing within a whorl and the equally dense arrangement of consecutive whorls, that are separated by thin calcareous partitions, which is almost never seen in the type variety. Further more, while the primary and secondary branches in this variety are approximately of the same length, the tertiaries are, as a rule, much shorter, as distinct from the type variety in which these relationships are highly variable. Also, the constrictions and swellings of secondaries and/or tertiaries are rarely, or never, seen in the variety, whereas they frequently occur in the type variety, in which quaternary branches also occur. Admittedly, the distinguishing characteristics of the variety, with regard to both type variety and other varieties, are clearly seen in fig-

Maximum observed length of thallus	L	9.10
Outer thallus diameter	D	1.20 - 2.66
Inner thallus diameter	d	0.24 - 0.49
Relation	d/D	0.177 - 0.300
Distance between whorls	h	0.24 - 0.48
Diameter of primaries	p	0.19 - 0.48
Length of primaries	l	0.25 - 0.58
Number of primaries in a whorl	w	12 - 16
Diameter of secondaries	p'	0.04 - 0.10
Length of secondaries	l'	0.20 - 0.54
Number of secondaries on a primary	w'	5 - 8
Diameter of tertiaries	p''	0.05 - 0.07
Length of tertiaries	l''	0.10 - 0.29
Number of tertiaries on a secondary	w''	3-4?
Angle of inclination of primaries		< 25°

Table 2 Main biometric parameters of *P. mediterraneus* var. *heraki* (SOKAČ & NIKLER) n. comb. (all dimensions in mm). Some values, such as p or l, may vary in the same specimen.

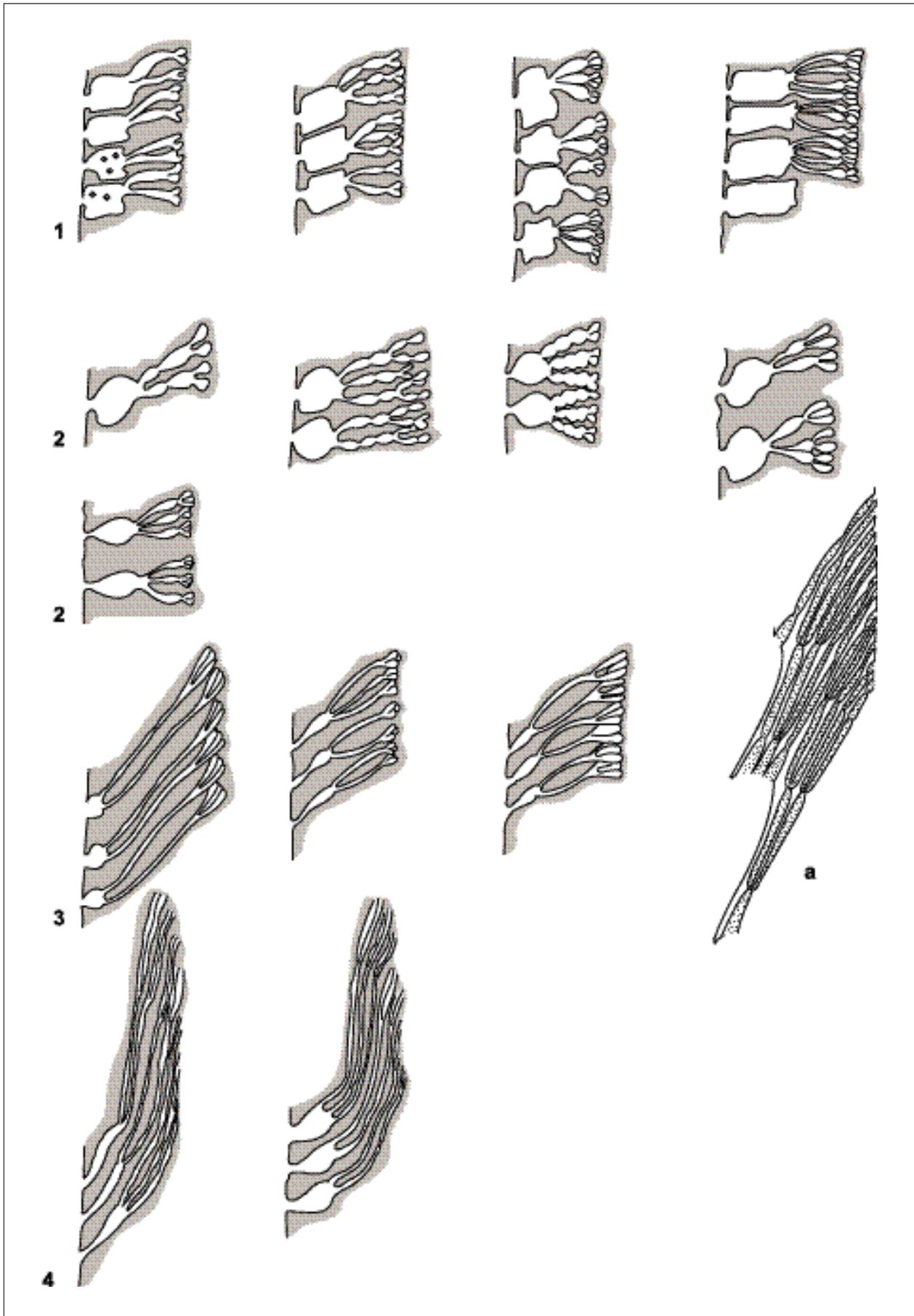


Fig. 4 Schematic review of sections of some forms of branches in: 1) *Palaeodasycladus mediterraneus* var. *heraki*; 2) *P. mediterraneus* var. *illyricus*; 3) *P. mediterraneus* var. *gracilis* (3.a: after CROS & LEMOINE, 1967); 4) *P. mediterraneus* var. *elongatulus*.

ures of thin-sections, and more easily understood than through written description. Therefore, the intention to more clearly emphasize only some more prominent morphological differences in individual specimens derived from the same or contemporary populations in order to avoid misidentification of species, is reflected in the taxonomic rank proposed.

Stratigraphic position: This variety has been found on several localities on Mt. Velebit and seems to be restricted, so far, to the Lower Liassic deposits.

***Palaeodasycladus mediterraneus* var. *illyricus*
(SOKAČ & NIKLER, 1966) n. comb.**

Pl. VI, Figs. 7-8; Pl. IX, Figs. 2-3, 5-7, 9-10;

Fig. 4.2

1966 *Petrascula illyrica* n. sp. - SOKAČ & NIKLER, p. 7-8, fig. 1c.

1969 *Petrascula illyrica* SOKAČ & NIKLER - SOKAČ & NIKLER, p. 103-109, pl. IV, figs. 1-4; pl. V, figs. 2-4, ?5, non fig. 1; pl. VI, figs. 1-2.

This form has also been previously described (SOKAČ & NIKLER, 1966, 1969), but because of insufficiently known characters it was erroneously assigned to the genus *Petrascula* and labelled *P. illyrica* SOKAČ & NIKLER. Subsequent analysis based on new finds enabled its reinterpretation and assignment to the genus *Palaeodasycladus*. The available material, primarily from the Mali Alan locality, Mt. Velebit, shows some specific characteristics (the shape of the primary branches) but also some similarities with *P. mediterraneus* (PIA) var. *mediterraneus* and also, by the intermediate

shape of some branches in some sections, with *P. mediterraneus* (PIA) var. *heraki* n. var. This new variety - *P. mediterraneus* (PIA) var. *illyricus* (SOKAČ & NIKLER) n. comb. - is proposed to include forms with elliptical or bubble-shaped primaries (Pl. IX, Figs. 2, 6) as well as those with more or less regularly spherical or nodular primaries (Pl. IX, Figs 5, 6; Pl. VI, Figs. 7-8), indicating a group of forms with closely similar though not fully identical, primary branches (Fig. 4.2). The thallus is cylindrical, perhaps slightly club-shaped, with a sharp outer surface and clearly delineated, uninterrupted, central cavity (Pl. IX, Figs. 5-6, 9). The axial cavity occupies 25-33% of the outer diameter (Table 3). Primary branches are arranged in whorls, consecutive whorls being situated approximately one above the other, thus forming more or less regular vertical rows (Pl. VI, Fig. 8; Pl. IX, Fig. 3). The density of whorls varies from specimen to specimen, though, generally, they are more widely spaced than in *P. mediterraneus* var. *heraki*. Secondary branches, 3-5, or occasionally even 6-7 in number, grow out of the distal end of the primaries, and are clearly grouped into bundles at their base, while diverging distally. They are mostly acrophorous or slightly phloioforous, either finger-shaped or constricted at their base. There are several (3-4?) tertiaries growing out from the distal end of the secondaries, which confirms the supposition of BASSOULLET et al. (1978) about their existence. The tertiaries are phloioforous, shorter than the secondaries, and, as distinct from the type-variety, do not show any constriction or apparent articulation (Fig. 4.2).

The existence of specimens with branches of intermediate characteristics on parts of the thallus, transitional to other previously described varieties, may question the justification for the varieties. However, the

Maximum observed length of thallus	L	9.60
Outer thallus diameter	D	1.45 - 2.32
Inner thallus diameter	d	0.40 - 0.64
Relation	d/D	0.234 - 0.331
Distance between whorls	h	0.30 - 0.39
Diameter of primaries	p	0.12 - 0.24
Length of primaries	l	0.20 - 0.36
Number of primaries in a whorl	w	12 - 16
Diameter of secondaries	p'	0.07 - 0.12
Length of secondaries	l'	0.17 - 0.34
Number of secondaries on a primary	w'	3 - 5
Diameter of tertiaries	p''	0.05 - 0.08
Length of tertiaries	l''	0.14 - 0.24
Number of tertiaries on a secondary	w''	3 - 4
Angle of inclination of primaries		< 20°

Table 3 Main biometrical parameters of *P. mediterraneus* var. *illyricus* (SOKAČ & NIKLER) n. comb. (all dimensions in mm).

very pronounced extreme differences, which significantly influence the general appearance of individual specimens, seem to justify their distinction and separation, admittedly at the lowest taxonomic level, in order to emphasize the total variability of the species.

Stratigraphic position: This variety, too, has been found at several localities (Mali Alan Pass, Veliko Rujno, Dušice, etc.) in the Lower Liassic deposits of Mt. Velebit.

***Palaeodasycladus mediterraneus* var. *gracilis*
(CROS & LEMOINE, 1967 ex GRANIER &
DELOFFRE, 1993) n. stat.**

Pl. XII, part. Fig. 6; Pl. XVI-XVII,
Pl. XVIII, Figs. 1-8;
Fig. 4.3

Selected synonymy:

- 1967 *Palaeodasycladus gracilis* n. sp. - CROS & LEMOINE, p. 251-253, pl. 1, figs. 2-3, 7, non fig. 4.
1975 *Linoporella buseri* sp. nov. - RADOIČIĆ, p. 277-278, fig. 1a-c.
1993 *Palaeodasycladus gracilis* CROS & LEMOINE - GRANIER & DELOFFRE, p. 37.
1996 *Palaeodasycladus gracilis* CROS & LEMOINE - BARATTOLO & BIGOZZI, pl. 54, figs. 1, 5 (oblique section, top), ?figs. 2, 5 (oblique section, bottom), ?non fig. 4.

As shown in the synonymy, this form has been variously taxonomically treated. Recently, it was discussed by several researchers, e.g.: DELOFFRE & LAADILA (1990), GRANIER & DELOFFRE (1993), BARATTOLO et al. (1994), BARATTOLO & BIGOZZI (1996). GRANIER & DELOFFRE (1993) performed its formal validation, according to the nomenclatorial rules, but without questioning the justification of its original erection. They also neglected, for formal reasons, the previously established form labelled *Palaeodasycladus mediterraneus* (PIA) var. *elongatulus* PRATURLON, 1966, for which no type-specimen was originally designated (PRATURLON, 1966, fig. 1). BARATTOLO et al. (1994) reviewed the taxonomic treatment of this form, originally described as *P. gracilis* CROS & LEMOINE, and synonymised it with *P. mediterraneus* var. *elongatulus* PRATURLON. They also stressed the controversial status of that form, which, in their opinion, cannot be considered as a variety or a subspecies of *P. mediterraneus* and, therefore, further investigation was needed in order to tell whether it was an independent taxon or a morphotype of the type-species.

Despite similarities with *P. mediterraneus*, the species was originally (CROS & LEMOINE, 1967) dis-

tinguished from it by having thinner branches, a slender cylindrical skeleton, and, as it was generally thought, often visible intusannulation which, however, may be poorly developed or even absent in the same specimen. The main error originating with the original description, was the synonymising of the form with *P. mediterraneus* var. *elongatulus* and the incorrect assignment of the illustrated sections by CROS & LEMOINE, (1967, pl. 1, figs. 2-4, 7), giving rise to some characteristic features, e.g. for example, the alleged intusannulation. However, the quoted sections, when compared mutually, show different characters. Thus, the specimen figured by GRANIER & DELOFFRE (1993) in their pl. 1, fig. 2, and designated as a lectotype, shows fine, thin primaries only in the lower part, whereas in the upper part there are cavities in the skeleton considered to represent intusannulation. However, these should be regarded as destroyed primary branches. In addition, there are evidently phloiophorous secondaries and tertiaries in the top part. That specimen, as well as the one figured in their pl. 1, fig. 7 probably belongs to specimens of *P. mediterraneus* in which the shape and the dimensions of the primaries change within the thallus. By its general characteristics the specimen figured in their pl. 1, fig. 4. certainly belongs to *P. mediterraneus*. The exceptions in the description of that form represent the sections illustrated by BARATTOLO & BIGOZZI (1996, pl. 54, fig. 1 and the oblique section in fig. 5, top), whereas other sections (pl. 54, figs. 2, 4, and 5, bottom) should be excluded from considerations, due to their secondarily enlarged axial cavity which destroyed the primary branches and thus fully obliterated their shape and dimensions.

This form is generally identical with *P. mediterraneus* var. *mediterraneus* in having a cylindrical (or, perhaps, slightly club-shaped) thallus and three orders of branches with a clear euspondyl arrangement of the primaries, but differs from other morphologically heterogeneous forms of *P. mediterraneus* on a subspecies level by its thin and slender branches (Fig. 4.3), both the first-order and the higher-order ones. The primaries are regularly narrowly tubular (Pl. XVI, Figs. 4, 7; Pl. XVII, Figs. 2, 7-8), almost ideally acrophorous, and bear three to four (never more than four) secondaries, their diameter being half that of the primaries (Pl. XVI, Figs. 3-4, 7; Pl. XVII, Fig. 8). The tertiaries, probably no more than three, grow out of the top of the secondaries (Fig. 4.3). The inner cavity is clearly and sharply delineated with visible entrance of the primaries into the central cavity (BARATTOLO & BIGOZZI, 1966, pl. 54, fig. 1 and pl. 16, figs. 4, 7-8; Pl. XVII, Figs. 3, 5, 8 this paper) and with no signs of intusannulation. The primaries are very steeply directed upwards, the angle between the primaries and the horizontal plane () amounting to 60-70° (Table 4). The secondaries generally retain the same inclination.

The unequivocal general similarity between this form and the type-subspecies (variety), represented by

Maximum observed length of thallus	L	7.12
Outer thallus diameter	D	0.63 - 1.15
Inner thallus diameter	d	0.24 - 0.38
Relation	d/D	0.250 - 0.444
Distance between whorls	h	0.20 - 0.44
Diameter of primaries	p	0.05 - 0.10
Length of primaries	l	0.24 - 0.48
Number of primaries in a whorl	w	11 - 14
Diameter of secondaries	p'	0.03 - 0.04
Length of secondaries	l'	0.24 - 0.48
Number of secondaries on a primary	w'	3 - 4?
Diameter of tertiaries	p''	?
Length of tertiaries	l''	?
Number of tertiaries on a secondary	w''	?
Angle of inclination of primaries		60-70°

Table 4 Main biometrical parameters of *P. mediterraneus* var. *gracilis* (CROS & LEMOINE) n. stat. (all dimensions in mm).

heterogeneous material, makes its separation and differentiation as an independent species, as proposed by CROS & LEMOINE (1967), rather doubtful. Contrary to the opinion of BARATTOLO et al. (1994), there seems to be no reason to exclude the form from the morphological range of *P. mediterraneus*. The aforementioned visual differences only seem to justify its determination at sub-species level, i.e., as *Palaeodasy-cladus mediterraneus* var. *gracilis* (CROS & LEMOINE, 1967 ex GRANIER & DELOFFRE, 1993) n. stat.

An additional fact supporting the separation of the variety is that it occurs in the same samples with well-developed specimens of the type variety, without observable intermediate forms (though they probably exist). As already mentioned above, the level of separation, however, may appear questionable. The separation at the variety level is suggested by the following: its main characteristic feature is the shape of the branches, which are shown to be a widely variable feature in the species, and therefore the establishment of a separate species would not seem justified. Alternatively, the designation of that form as a morphotype, as proposed by BARATTOLO et al. (1994) as a possible solution, seems insufficient to emphasize its clear differences to the type-variety.

Stratigraphic position: In the peri-Mediterranean area, the occurrence of the alga are referred to as being of Lower and Middle Liassic age. The position of algal-bearing samples and fossil assemblages in the Liassic columns of both Mt. Velebit and Mt. Trnovski Grozd supports this age.

Remarks: As can be seen from the above synonymy list, *Linoporella buseri* RADOIČIĆ (RADOIČIĆ, 1975, fig. 1a-c) is considered to be synonymous with that

variety. *L. buseri*, as noted by BASSOULLET et al. (1978, p. 147), is characterised by three orders of branches, which are not characteristic of the genus *Linoporella*. In the holotype (RADOIČIĆ, 1975, fig. 1a, upper left part), the slight constrictions and swellings of the secondary branches can be seen (although not very clearly), as well as their branching into the slightly phloiophorous tertiaries. The method of emergence of the secondaries, their grouping into bundles prior to their divergence toward the outer end, is the same as in some varieties of *P. mediterraneus* as described herein. The subsequently figured material (BASSOULLET et al., 1978, pl. 17, fig. 12), which is said to belong to Radoičić's original material, shows visible intusannulation, perpendicularly situated branches, and consecutive whorls further apart from each other, all of which clearly indicates that it belongs to *P. barrabei*. This, together with the possibility of some morphological and biometric parameters variation, unequivocally justifies the assignment of *L. buseri* to *Palaeodasy-cladus mediterraneus*, most probably to the variety *gracilis* as stated here, primarily because of the fine, tubular branches (acrophorous, with slightly phloiophorous tertiaries).

***Palaeodasycladus mediterraneus*
var. *elongatulus* PRATURLON, 1966**

Pl. XVIII, Figs. 9-12; Pl. XIX-XXI;

Fig. 4.4

Selected synonymy:

1966 *Palaeodasycladus mediterraneus* (PIA) *elongatulus* n. var. - PRATURLON, p. 169-170, fig. 1.

- 1967 *Teutoporella elongatula* (PRATURLON, 1966) SOKAČ & NIKLER - SOKAČ & NIKLER, p. 111-116, pl. I-IV, part. pl. VI.
- 1972 *Palaeodasycladus elongatula* PRATURLON, 1966 - DELOFFRE, p. 109-119, non pl. I, non pl. II.
- 1994 *Palaeodasycladus gracilis* CROS & LEMOINE 1967 ex GRANIER & DELOFFRE, 1993 (= *P. mediterraneus* var. *elongatulus* PRATURLON, 1966) - BARATTOLO et al., p. 1-2, 6-7.
- 1996 *Palaeodasycladus gracilis* CROS & LEMOINE 1967 ex GRANIER & DELOFFRE (= *Palaeodasycladus mediterraneus* var. *elongatulus* PRATURLON) - BARATTOLO & BIGOZZI, p. 205, pl. 54, figs. 1, 5 oblique section top, ?figs. 2, 4 and fig. 5 bottom.

Lectotype: PRATURLON (1966, fig. 1), oblique section, situated diagonally in upper left part of the photo.

This form, originally described by PRATURLON (1966) as a variety of *P. mediterraneus*, was subsequently variously treated, but until recently it was given priority with respect to *P. gracilis*, with which it is synonymous. BARATTOLO et al. (1994) more extensively discussed the taxonomic position and the relationships of this form to similar ones, and concluded that this form (which lost its priority) was identical to *P. gracilis*, or, according to the above, *P. mediterraneus* var. *gracilis*, respectively. The omission of designating the type-specimen (type-section) in the “group photograph” (PRATURLON, 1966, fig. 1) had the regrettable consequential loss of validity for purely formal reasons (according to I.C.B.N. rules), which led GRANIER & DELOFFRE (1993) to quote it as *P. mediterraneus* var. *elongatulus* PRATURLON 1966, nom. nud. The justification for separation of the variety is not an issue, and it would also resolve the apparent taxon *versus* morphotype dilemma posed by BARATTOLO et al. (1994). Therefore it is proposed here, in order to formally validate the variety, to select the oblique section situated diagonally in the upper left part of fig. 1 in PRATURLON (1966) as the type-section, or lectotype.

PRATURLON (1966) diagnosed the new variety as having a broad axial cavity and numerous thin, long, and dense branches situated almost parallel to the longitudinal axis of the thallus. The assimilatory filaments never widen distally; on the contrary, they seem to be trichophorous. PRATURLON (op. cit.) also mentioned the typical intusannulation.

The revalidation of the taxon has been attempted by DELOFFRE (1972). He elevated it to the rank of species, but since none of his depicted sections (DELOFFRE, 1972, pl. 1, figs. 1-5; pl. 2, figs. 1-6) belong to this variety but rather represent *P. mediterraneus*, a new description, comparison, and illustrations are required.

Description: The calcareous skeleton, of generally cylindrical shape, consists of numerous, upwardly bent, deeply concave, calcareous rings. Individual rings are shaped like deep funnels, deeply inserted and tightly squeezed one into another; therefore no annular cavities between individual rings exist; only in their proximal parts (near the central cavity) do they appear as thin fissures, visible in tangential and oblique sections (Pl. XVIII, Figs. 11-12; Pl. XIX, Figs. 2-3, 5-6). Specimens with very clearly developed annulations (see Pl. XX, Fig. 9), are extremely rare. The outer surface has a feathery (plicate) surface, due to very steep distal parts of individual rings, which are almost parallel to the growth axis (Pl. XVIII, Figs. 11-12; Pl. XIX, Figs. 1-3). It is characterised by more or less clear, slightly swollen folds, each fold corresponding to one ring (Pl. XVIII, Fig. 11; Pl. XIX, Fig. 6). The broad axial cavity, occupying up to 30% of the outer diameter, is the result of partial (Pl. XX, Figs. 2-6) or complete (Pl. XIX, Fig. 1; Pl. XX, Figs. 4-7) destruction of the primary branches.

Primary branches are elongated, cylindrical or irregularly globular in shape, more or less obliquely situated and directed upwards (Pl. XIX, Figs. 1, 4-5; Pl. XX, Fig. 2). In some specimens they may be more strongly bent in their distal ends, from where the secondaries emerge in a finger-like manner, without visible constrictions at the base. The finger-shaped secondaries quickly taper or give rise to thin, tubular, tertiary branches, which are even more steeply inclined upwards, and, in extreme cases, become parallel to the growth axis (Fig. 4.4). Some specimens suggest the possible occurrence of fourth-order branches. The number of secondaries is usually three, more rarely four (Table 5; Pl. XVIII, Fig. 9; Pl. XIX, Fig. 2; Pl. XX, Fig. 6). In this variety the secondaries and the tertiaries do not show any constrictions and swellings, which would give an impression of their being articulated. They are entirely acrophorous; nor do they show any distal widenings, as distinct from *P. mediterraneus* var. *mediterraneus*, which is characterised by phloiophorous branches. In their uncalcified parts, functioning as an assimilatory device, they perhaps assume a trichophorous shape. The exact point of bifurcation, as well as a clear distinction between the secondaries and tertiaries, is difficult to determine because they have approximately the same thickness (diameter) and cross each other in thin sections. The longest secondary branch observed reached 5.9 mm (Pl. XVIII, Fig. 10).

Similarities and differences: With regard to *P. mediterraneus*, basic similarities include: the basic morphology, the arrangement and mode of ramification of the branches, and the shape of the thallus. Differences from the type form are as follows: *P. mediterraneus* var. *elongatulus* has only two types of primary branches, elongated cylindrical ones and others which are irregularly swollen (e.g. some kind of a globular type). In this variety, the secondaries and the tertiaries never

Maximum observed length of thallus	L	13.46
Outer thallus diameter	D	1.45 - 3.96
Inner thallus diameter	d	0.38 - 0.98
Relation	d/D	0.141 - 0.266
Distance between whorls	h	0.30 - 0.58
Diameter of primaries	p	0.12 - 0.40
Length of primaries	l	0.39 - 0.72
Number of primaries in a whorl	w	?
Diameter of secondaries	p'	0.04 - 0.10
Length of secondaries	l'	5.9
Number of secondaries on a primary	w'	3 - 4
Diameter of tertiaries	p''	0.04
Length of tertiaries	l''	?
Number of tertiaries on a secondary	w''	?
Angle of inclination of primaries		50°
Angle of inclination of secondaries		90°

Table 5 Main biometrical parameters of *P. mediterraneus* var. *elongatulus* PRATURLON (all dimensions in mm).

show a seemingly articulated appearance, nor do they exhibit distal swellings, as distinct from the typical variety which always shows typically phloiophorous branches. In *P. mediterraneus* var. *elongatulus* they are distinctly acrophorous. The thallus of this variety is, in fact, annulated, but the annular depressions are mostly obliterated by calcareous rings being tightly squeezed together, or they may be partly preserved in the cortical part of the skeleton. In the type variety, the angle between the secondaries and the horizontal plane does not exceed 70°, whereas in this variety it may reach, in extreme cases, 90° whereby the secondaries become extremely long. This variety has a more massive skeleton than *P. mediterraneus* var. *gracilis* and a secondarily widened axial cavity, due to the destruction of large primary branches. In *P. mediterraneus* var. *gracilis* the primaries are either tubular, without a pronounced swelling near the axial cavity, or there is a slightly pronounced widening from which 2 or 3 secondaries immediately grow out. In such cases, the proximal swelling may be functionally regarded as being a primary branch, though visually giving the impression of metaspondility. Because of the shape and small diameter of the primaries, the central cavity in *P. mediterraneus* var. *gracilis* is clearly delineated and only very rarely secondarily enlarged, as distinct from this variety. In both varieties the branches are directed steeply upwards, but whereas in *P. mediterraneus* var. *gracilis* it is the primaries, in this variety the secondaries distally bend up and become even more steeply directed upwards, becoming longer and, in extreme cases, parallel to the thallus. In *P. mediterraneus* var. *gracilis*, the distance between the consecutive whorls is larger and more clearly expressed than in this variety (due to larg-

er primaries in the latter). Some specimens of *P. mediterraneus* var. *gracilis* show slight distal broadening of the secondaries, whereby the secondaries gradually acquire a slightly phloiophorous shape (Pl. XVI, Fig. 1), which has never been observed in this variety. However, it is sometimes difficult to avoid the question of which are the real, relevant, differences between the two varieties, though the differences clearly exist in a visual comparison. Therefore, this together with the differently shaped thallus (cylindrical or seemingly cylindrical), and the folded (plicate) outer surface resulting from original annulation (which is not of decisive significance), differentiation at the lowest taxonomic level would seem to be the most appropriate solution.

Stratigraphic position: In the original description (PRATURLON, 1966), the most common stratigraphic position of this alga is in the *Orbitopsella praecursor* subzone, or in the lower part of the *Lithiotis* facies, respectively, which should indicate, according to PRATURLON (1966), a Middle - Upper Liassic age. Subsequent synonymizing of this variety with *P. mediterraneus* var. *gracilis* (especially in absence of photographic illustrations) prohibits an unequivocal conclusion as to which one of the varieties is questionable, and therefore casts doubt on a reliable stratigraphic position. While the first finds of the alga in Mt. Velebit, quoted under the name *Teutloporella elongatula* (PRATURLON), come from an identical stratigraphic level and are accompanied by a very similar Middle Liassic fossil assemblage as that from the type locality, the newly recovered sample VT-26 indicates its occurrence in the Lower Liassic. Therefore, the total stratigraphic range of the alga is Lower - Middle Liassic.

***Palaeodasycladus mediterraneus*
var. *calciticus* n. var.**

Pls. XXXI-XXXII

Origin of the name: After well developed calcitic partitions of variable thickness, well visible in variously oriented sections.

Type locality: Mt. Velebit, on the Sv. Rok - Obrovac road, approximately 100 m from the milestone on Mali Alan Pass, in the direction of Obrovac. Greenwich coordinates: 44° 17' 24" N, 15° 39' 23" E.

Type stratum: Well-bedded, grey, Lower Liassic (Hettangian - Lower Sinemurian) limestones, represented by the alternation of skeletal-intraclastic grainstone and mudstone (micrite), with sporadically developed stromatolitic laminae. Depositional environment was probably shallow subtidal with periodic emersions into the vadose zone.

Holotype: Oblique section figured in Pl. XXXI, Fig. 3, slide VT-26/379, deposited, together with illustrated paratype-material, at the Institute of Geology, Zagreb.

Diagnosis: Being almost identical to the type variety by its main biological and morphological characteristics, this new variety is distinguished by its peculiarly developed skeleton, consisting of tightly squeezed calcareous tubules, enveloping each primary and secondary branch. The calcareous wall is irregular and of variable thickness, more pronounced toward the distal end, comprising irregular calcitic partitions, the shape and thickness of which are defined by the cavities between the branches. In tangential section, the calcareous tubes vary in shape from rectangular to polygonal.

Description: The cylindrical thallus is composed of tightly packed tubular calcareous envelopes around the branches; arranged in whorls and slightly inclined upwards, situated around the elongated central cavity. The inner cavity is originally more or less straight or with shallow depressions where the branches enter the central cavity. In such cases the inner cavity becomes slightly irregular, but always remains clearly delineated (Pl. XXXI, Fig. 8; Pl. XXXII, Fig. 8). However, the inner side of the calcareous wall, around the central cavity, is often destroyed and therefore, the central cavity is secondarily broadened (Pl. XXXI, Fig. 4; Pl. XXXII, Fig. 4), comprising 20-35% of the total diameter (Table 6). The outer surface is seldom even (Pl. XXXI, Fig. 3; Pl. XXXII, Fig. 4); instead it is more often indented, due to destruction (erosion) of the outer ends of the calcareous envelopes (Pl. XXXI, Figs. 4, 7). The main visual characteristic of the species is brought out by the irregularly and unevenly thickened walls of the branch envelopes, which then appear in sections as heavily calcified partitions.

Branches are tripartite, as in some other species or variety of the genus and each primary branch, together with its secondary and tertiaries, is situated within its own calcareous envelope. The euspondyl arrangement of branches is defined by the equally radial arrangement of tubular envelopes. The envelopes may be perpendicular to the growth axis, or, more frequently, are inclined by a small angle and directed slightly upwards (Pl. XXXI, Figs. 3, 8). Three to four secondary branches grow out from the distal ends of the primaries; however, because of poor calcification, the secondaries are not easily observable (Pl. XXXI, Fig. 3; Pl. XXXII, Fig. 7). The secondaries remain tightly pressed together within the calcareous envelope; they do not have calcified walls of their own. Additional calcification may

Maximum observed length of thallus	L	7.70
Outer thallus diameter	D	2.40 - 3.88
Inner thallus diameter	d	0.48 - 1.00
Relation	d/D	0.187 - 0.258
Distance between whorls	h	0.20 - 0.40
Diameter of primaries	p	0.16 - 0.24
Length of primaries	l	0.38 - 0.48
Number of primaries in a whorl	w	?
Diameter of secondary	p'	0.10 - 0.12
Length of secondary	l'	0.30 - 0.48
Number of secondary on a primary	w'	3 - 5
Diameter of tertiaries	p''	0.06 - 0.09
Length of tertiaries	l''	0.20 - 0.40
Number of tertiaries on a secondary	w''	?3 - 4
Angle of inclination of branches		0 - 15

Table 6 Main biometrical parameters of *Palaeodasycladus mediterraneus* var. *calciticus* n. var. (all dimensions in mm).

develop between the secondary but without being in contact with the envelope, e.g. a type of hanging calcification. The tubular envelopes are densely packed and remain in mutual contact both within a whorl and with those of the neighbouring whorls. Therefore the walls of consecutive envelopes merge together into a common recrystallised calcitic envelope and their individual existence can be only rarely observed (Pl. XXXI, Fig. 3). The tertiary branches are not visible in the material available; only an indication of their existence can be sporadically observed (Pl. XXXI, Figs. 3, 8; Pl. XXXII, Figs. 3, 7). In tangential sections, the envelopes appear as irregular rectangular or polygonal contours (Pl. XXXI, Fig. 3; Pl. XXXII, Fig. 7). This variety, too, is possibly cladosporous.

Similarities and differences: Main characteristics: tripartite branches, euspondyl arrangement of primary branches, relation between the outer and inner diameters, cladosporous reproduction, etc. are typical of and define the generic assignment of the variety. The main characteristic feature which distinguishes *P. mediterraneus* (PIA, 1920) 1927 var. *calciticus* from any other variety of the species is the existence of visually conspicuous calcitic partition walls of the branches, which form the calcareous skeleton of the thallus. In contrast to other *Palaeodasycladus*-species, and their varieties in which the branches grow through the calcareous mass of the skeleton, either all along their length or only as secondary and tertiary branches, in *P. mediterraneus* var. *calciticus* the branches, including the secondary and tertiary ones, remain uncalcified within their tubular envelopes. Therefore the secondaries and tertiaries of this variety remain grouped together (Pl. XXXII, Fig. 7), whereas the porous appearance, typical of other *Palaeodasycladus* species, is either undeveloped, or barely discernible.

Stratigraphic position: *P. mediterraneus* (PIA, 1920) 1927 var. *calciticus* occurs in the rich algal assemblage of sample VT-26, which contains *P. mediterraneus* (PIA, 1920) with several varieties, *P. dolomiticus* (CROS & LEMOINE) n. comb., *P. barrabei* LÉBOUCHÉ & LEMOINE, *Eodasycladus ogilviae* CROS & LEMOINE, and others; some of them prove the Lower Liassic age of the deposits. The position of the fossiliferous sample VT-26 in the stratigraphic column of Upper Triassic dolomites and Lower Liassic limestones, also including the first occurrence of a Middle Liassic foraminiferal assemblage, is shown in Fig. 2.

Remarks on the taxonomic classification of newly established varieties

The study of rich Lower and Middle Liassic algal assemblages has provided new data, in addition to that previously known regarding the visible variability of taxa. Various orientated sections of both the type species of *Palaeodasycladus* and other taxa of that ge-

nus show a broad array of morphological modifications, which, at first sight, give the impression of heterogeneous material which initially did not obviously belong to a single species. Only after a detailed study of numerous sections from one or more samples taken from the same bed, was it possible to imply the existence of contemporaneous populations derived from the same habitat (or, in cases of transported material, from several neighbouring habitats), and obtain an insight into the degree of gradual variations. These variations are manifested by the increase of the total volume of primary branches from the bottom to the top of the thallus, the variability in the shape of branches, changes in the degree of total branching orders, and varying length, method of growth, and inclination of primary, secondary and tertiary branches. All these changes can occur either in the same specimen or in related specimens of the same population. Besides, specimens occur that appear to be completely irregular, and that diverge from any group united by common characters. These specimens could only be conceived as deviants from the development of individual specimens within a species or a variety, respectively (Pl. V, Fig. 1; Pl. VIII, Fig. 2). In contrast, other specimens were observed, in which some characteristic feature (e.g., square or bubble-shaped primary branches) was more pronounced than in others, and which, then, also according to other characteristics, could be united into smaller groups. These groups could be identified, more or less reliably, and distinguished from the type species or other species of the same genus. The existence of specimens with intermediate/transitional characteristics, results in the formation of a continuous series with the type species at one end, and culminating at the other with a group of specimens with most strongly pronounced differences with regard to the type species or its type variety. Such relationships, including both observable differences and similarities, require a somewhat different approach to taxonomic interpretation. As has been already indicated, the lack of clear, valid, and generally adopted criteria of taxonomic classification in green calcareous algae means that, in such cases, every attempt of taxonomic differentiation bears the signature of a more or less subjective opinion of the author in question. Thus the main questions are: whether to carry out such a classification and at what level, e.g. genus, species or variety, and where, when, and how to fix the taxonomic boundaries, which would be subjective anyway but at least recognisable to some extent. The existence of specimens which show different morphologic features on different parts of the thallus, or a series of specimens with gradual transitions, raises the question as to the justifiability of their taxonomic separation, more so as all these changes may occur simultaneously. In contrast, there are extreme cases with strongly differing characteristics resulting in the clearly different general visual appearance of individual specimens which forces distinction between them, even if the separation is carried out at the lowest taxonomic level, in order to elucidate the

total range of variation within the species and to reduce the possibility of incorrect species identification. Therefore it is not viable to accept the species, or the variety, as an individual with sharply delimited characteristics; instead it should be considered that a group of individuals share some common characteristics whereas other characteristics may vary to a greater or lesser extent. Thus the same species, or variety, may sometimes include visually rather different specimens. The separation of varieties within the *Palaeodasycladus mediterraneus* group of species, on the basis of more or less convincing arguments, is the most convenient taxonomic approach to this data. These varieties can be distinguished, then, in spite of varying biometrical parameters, mostly on the basis of visual appearance and overall impression acquired from the study of numerous sections in extremely rich material.

Distinguishing characteristics of the established varieties

The distinguishing of the established varieties must be based on some pronounced morphological characteristics rather than on biometrical parameters, which are very variable and hence inconclusive, as can be seen from Table 7.

There follow short descriptions of the established varieties, with emphasis on differential characteristics that cannot be elucidated from the tabulated numerical values.

Palaeodasycladus mediterraneus (PIA, 1920) 1927 var. *mediterraneus*

Thallus: Cylindrical to slightly club-shaped, sometimes with visible transverse fissures in the skeleton; dimensions highly variable (D varying in relation 1:5).

Primary branches: Essentially tubular, or modified from a tubular shape, sometimes phloiophorous/club-shaped, sporadically ramified into two approximately equal branches, often varying in shape and, generally, increasing in volume toward the top parts of the thallus.

Secondary branches: More strongly phloiophorous, in general longer than the primaries, sometimes with one or two constrictions, growing out of either a constricted base, or finger-like, without basal constrictions.

Tertiary branches: Clearly phloiophorous, arranged in bundles, usually shorter, seldom longer than the secondaries; in the latter case always with several constrictions, which gives an articulated appearance. On the outer surface, pores are large, circular to polygonal in outline.

Inclination: Primary branches always clearly inclined, up to an angle () of 70°.

Ramification: Up to third, sometimes to fourth-order branches.

	<i>P. mediterraneus</i> var. <i>mediterraneus</i>	<i>P. mediterraneus</i> var. <i>heraki</i>	<i>P. mediterraneus</i> var. <i>illyricus</i>	<i>P. mediterraneus</i> var. <i>gracilis</i>	<i>P. mediterraneus</i> var. <i>elongatulus</i>	<i>P. mediterraneus</i> var. <i>calciticus</i>
L	21.60	9.10	9.60	7.12	13.46	7.70
D	1.12 - 5.40	1.20 - 2.66	1.45 - 2.32	0.63 - 1.15	1.45 - 3.96	2.40 - 3.88
d	0.24 - 0.76	0.24 - 0.49	0.40 - 0.64	0.24 - 0.38	0.38 - 0.98	0.48 - 1.00
d/D	0.124 - 0.335	0.177 - 0.300	0.234 - 0.331	0.250 - 0.444	0.141 - 0.266	0.187 - 0.258
h	0.16 - 0.49	0.24 - 0.48	0.30 - 0.39	0.20 - 0.44	0.30 - 0.58	0.20 - 0.40
p	0.06 - 0.35	0.19 - 0.48	0.12 - 0.24	0.05 - 0.10	0.12 - 0.40	0.16 - 0.24
l	0.15 - 0.72	0.25 - 0.58	0.20 - 0.36	0.24 - 0.48	0.39 - 0.72	0.38 - 0.48
w	12 - 18	12 - 16	12 - 16	11 - 14	?	?
p'	0.05 - 0.20	0.04 - 0.10	0.07 - 0.12	0.03 - 0.04	0.04 - 0.10	0.10 - 0.12
l'	0.14 - 1.12	0.20 - 0.54	0.17 - 0.34	0.24 - 0.48	5.9	0.30 - 0.48
w'	3 - 5	5 - 8	3 - 5	3 - 4?	3 - 4	3 - 5
p''	0.05 - 0.26	0.05 - 0.07	0.05 - 0.08	?	0.04	0.06 - 0.09
l''	0.08 - 0.45	0.10 - 0.29	0.14 - 0.24	?	?	0.20 - 0.40
w''	3 - 4	3	3 - 4	?	?	?3 - 4
	< 70°	< 25°	< 20°	60 - 70°	50°	0 - 15°

Table 7 Comparative table of biometric parameters of the newly established varieties of *Palaeodasycladus mediterraneus* (PIA) (all dimensions in mm).

Palaeodasycladus mediterraneus var. *heraki*
(SOKAČ & NIKLER, 1966) n. comb.

Thallus: Predominantly cylindrical; dimensions variable (D varying in relation 1:2).

Primary branches: Distinctly rectangular, densely packed both within whorls and with densely arranged consecutive whorls separated by thin calcareous partitions.

Secondary branches: Phloiophorous, approximately of the same length as the primaries, sometimes slightly swollen and constricted, giving a bumpy but never a seemingly articulated appearance; growing out of one or several places at the distal surface of a primary branch. Tertiary branches are, as a rule, clearly phloiophorous and half as long as the secondaries.

Inclination: Primary branches have a low inclination angle (), up to 25°, which is also the lower inclination limit of the type variety.

Ramification: Up to the third order.

Palaeodasycladus mediterraneus var. *illyricus*
(SOKAČ & NIKLER, 1966) n. comb.

Thallus: Predominantly cylindrical; dimensions variable (D varying in relation approximately 1:1.5).

Primary branches: Bulbous, bubble-shaped or irregularly elliptic; whorls distinctly set apart from each other, preventing the branches of neighbouring whorls (and, most frequently, also the branches within a whorl) from mutually touching.

Secondary branches: Phloiophorous, approximately of the same length as the primaries, lacking any swellings and constrictions.

Tertiary branches: Phloiophorous, visibly shorter than both the primaries and the secondaries.

Inclination of primary branches () reaching up to 20°.

Ramification: Up to third order.

Palaeodasycladus mediterraneus var. *gracilis*
(CROS & LEMOINE, 1967 ex GRANIER & DELOFFRE, 1993) n. stat.

Thallus: Cylindrical; dimensions variable (D varying in relation up to 1:2).

Primary branches: Of two types; the first type being

represented by poorly visible small irregular widenings arranged in a regular manner along the axial cavity, and giving rise to secondary branches. The second type is represented by slightly phloiophorous or, more often, elongated tubular branches (acrophorous type).

Secondary branches: As a rule, predominantly acrophorous, longer than, and half the diameter of, the primaries. Exceptionally, and only in intermediate specimens, they may acquire a slightly phloiophorous shape.

Tertiary branches: In the available material, they are not easily observed.

Inclination: Primary branches of the tubular or slightly phloiophorous shape (second type) are inclined under an angle () of 60-70°.

Ramification: Up to third order.

Palaeodasycladus mediterraneus
var. *elongatulus* PRATURLON, 1966

Thallus: Cylindrical (D varying in relation 1:2), with more or less clearly pronounced annulation becoming indistinct due to mutual contact of steeply inclined calcareous rings (segments), producing feather-like incisions on the outer surface.

Primary branches: More or less irregular, bulbous or cylindrical. Each calcareous ring bears one row of primary branches, which are always more or less steeply inclined and bent upwards.

Secondary branches: Very thin, with slightly widened proximal parts (acrophorous type); going outward they bend steeply upwards and, most frequently become almost parallel to the longitudinal growth axis.

Tertiary branches: The existence and branching of tertiary branches are difficult to discern because of long and mutually intersecting secondary branches and therefore their characteristic features cannot be defined.

Inclination of primary branches () up to 50°. The most distinguishing feature is the extremely steep inclination of the secondary branches, reaching up to 90°.

Ramification: Up to third order.

Palaeodasycladus mediterraneus
var. *calciticus* n. var.

Thallus: Cylindrical, consisting of tightly squeezed and compressed, mutually connected, tubular calcareous envelopes around each branch. This gives a pecu-

liar and easily distinguishable appearance to this variety, with clearly visible calcitic bars between the neighbouring whorls.

Primary branches: Essentially cylindrical, elongated, sometimes irregular in shape.

Secondary branches: Growing out either finger-like, or with a constricted base; of the same length as, or more frequently longer than the primaries, due to varying diameter giving bumpy appearance. The bundle of secondaries belonging to a primary branch is situated within a tubular calcareous envelope, which is internally slightly or only partially calcified (in the gaps between the branches), and secondaries are, therefore, in general, poorly visible.

Tertiary branches: Phloioporous, short, poorly visible, due to insufficient calcification.

Inclination: Primary branches, each within its own calcareous envelope, are slightly inclined (0-15°).

Ramification: Up to third order.

***Palaeodasycladus barrabei* LÉBOUCHÉ & LÉMOINE, 1963 ex GRANIER & DELOFFRE, 1993**

Pl. XIV, part. Fig. 8, Pls. XXII-XXIV;
Pl. XXXVIII, Figs. 1-3;
Fig. 5.1

Selected synonymy:

- 1963 *Palaeodasycladus barrabei* n. sp. - LÉBOUCHÉ & LÉMOINE, p. 95, 97, 99; pl. 3, figs. 1-7.
- 1970 *Palaeodasycladus barrabei* LÉBOUCHÉ & LÉMOINE - BOUROLLEC & DELOFFRE, p. 88-90; pl. 5, figs. 1-2, ?figs. 3, 6-8, non fig. 5; pl. 6, ?figs. 1-2, 7, non figs. 3-6.
- 1978 *Palaeodasycladus barrabei* LÉBOUCHÉ & LÉMOINE - BASSOULLET et al., p. 187-191, pl. 22, figs. 1-4.
- 1990 *Palaeodasycladus barrabei* LÉBOUCHÉ & LÉMOINE - GRANIER & DELOFFRE, p. 36.
- 1994 *Eodasycladus barrabei* (LÉBOUCHÉ & LÉMOINE, 1963 ex GRANIER & DELOFFRE, 1993) nov. comb. - BARATTOLO, DE CASTRO & PARENTE, p. 4-6, pl. 2, figs. 1-3, 6-8, ?4-5.

The original description (LÉBOUCHÉ & LÉMOINE, 1963) was accompanied by several illustrations of sections: pl. 3, figs. 1-7; out of which figs. 1-4 cannot be assigned with certainty to this species. This species was not frequently mentioned and even more rarely illustrat-

ed. Due to a lack of good sections it remained inadequately known, with controversial and/or uncertain taxonomic attribution. In their revision of the genus *Palaeodasycladus*, DELOFFRE & LAADILA (1990) are of the opinion that it should be considered a younger synonym of *P. mediterraneus*. However GRANIER & DELOFFRE (1990), in their critical inventory of the fossil Dasycladales (part II), amend the non existence of the holotype by selecting a lectotype and thus validate the species. BARATTOLO et al. (1994), based on the material from the type-locality, give an emended diagnosis of the species, emphasising that some specimens show strongly swollen individual secondaries, with considerably larger diameter than the remaining branches of the same bundle, whereas other specimens develop rounded pores which may be interpreted as being choristosporous reproductive organs. They also mention that each secondary branch bears four tertiaries, characterised by three segments separated by clearly pronounced constrictions. The outermost articles possibly form an enveloping crust. In addition to characteristics mentioned by LÉBOUCHÉ & LÉMOINE (1963), BARATTOLO et al. (1994) particularly discuss the intusannulation and the more or less pronounced undulation of the outer surface. They also decided to transfer this form into the genus *Eodasycladus*, primarily because an individual secondary branch may be more strongly swollen than its neighbours in the same bundle, or because of the occurrence of larger, more or less rounded pores which were assigned to bubble-shaped structures and interpreted as choristosporous reproductive organs. This means, however, that the most numerous specimens (at least in this study) which do not show any swollen secondaries or large pores assigned to choristosporous reproductive organs, were neglected. Besides, in assigning *P. barrabei* to the genus *Eodasycladus*, BARATTOLO et al. (1994) leave unresolved the relationship between this form and *Eodasycladus ogilviae*. They only pose the question of *E. ogilviae* perhaps being the younger synonym of *P. barrabei*. They suggest a possible solution by statistical comparison of biometric parameters of the two forms, based on an abundant material, though the values of individual parameters fall within the variation range of individual species (see table in BARATTOLO et al., 1994). However, in the original description of the genus *Eodasycladus* (CROS & LÉMOINE, 1966), the authors emphasise the distinction between the new genus and *Palaeodasycladus* as being the existence of fertile secondary branches in *Eodasycladus*. In the description of the species (*E. ogilviae*), CROS & LÉMOINE (1966) point out the unequivocal similarity of their sections with *P. barrabei*, but they also note the important differences in detail. These differences enable the distinction of three forms, which might be classified as three species belonging to two or three genera. CROS & LÉMOINE (1966) also put forth the supposition of their having to deal with different parts of the same plant and thus their description consists of three parts

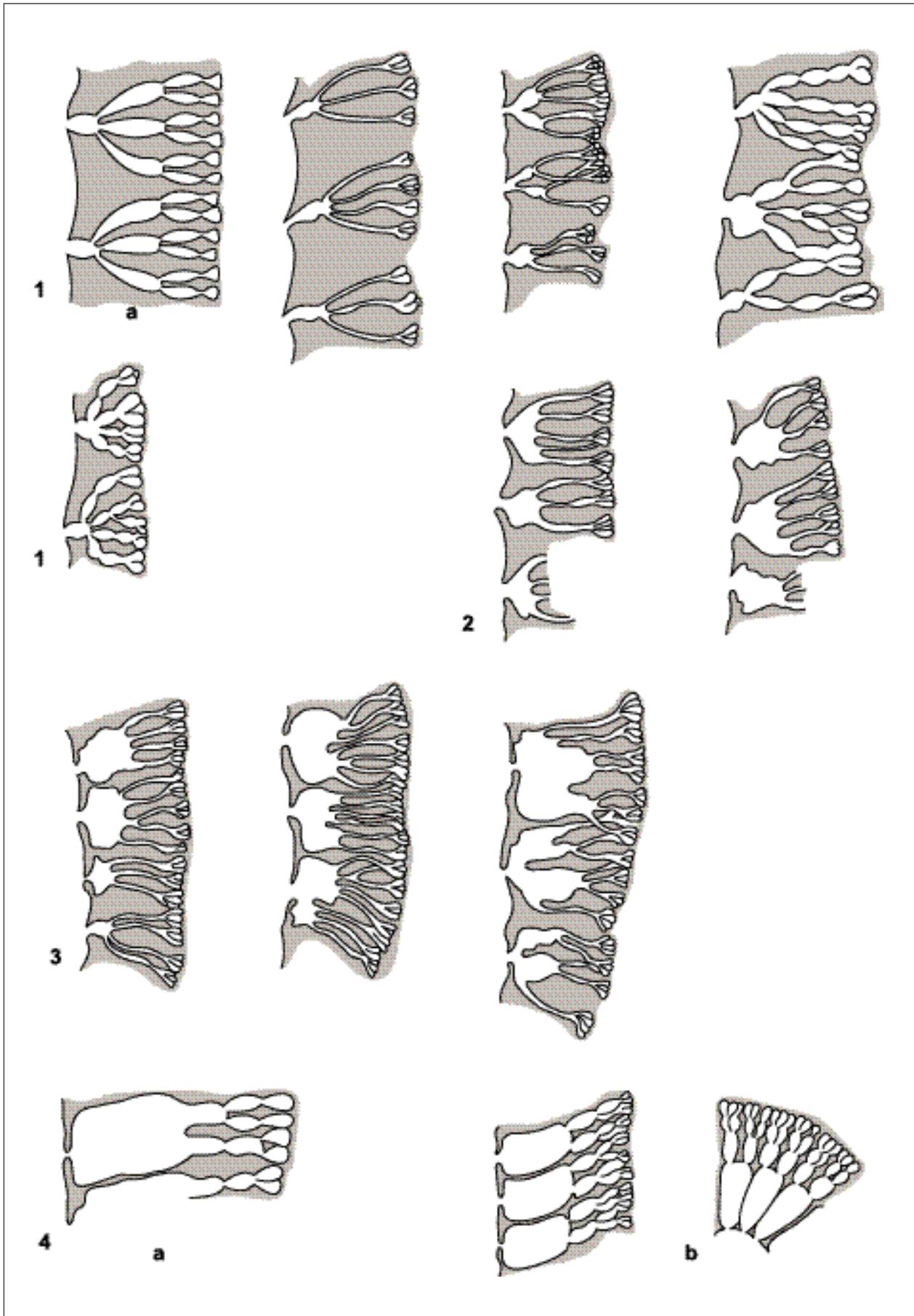


Fig. 5 Schematic review of sections of branches in: 1) *Palaeodasycladus barrabei* (1.a: after LÉBOUCHÉ & LÉMOINE, 1963); 2) *P. alanensis*; 3) *P. benceki*; 4) *P. dolomiticus* (4.a: after CROS & LÉMOINE, 1966; 4.b: after BARATTOLO & BIGOZZI, 1996).

which correspond to three types of organisation, which may be regarded as three developmental stages of the same species. While describing the three types within *Eodasycladus ogilviae*, they emphasise the similarity of their first two types with *Palaeodasycladus barrabei*, whereas the third type is distinguished by having one of the secondary branches more strongly swollen than the others and functioning, probably, as a sporangium. Because it could be established with certainty that we are not dealing with different parts of the same plant with three types of organisation, nor with three different stages of the same species, it appears necessary to give a more complete description of a great majority of the available specimens, which would correspond to the original description of *P. barrabei*.

Description: *Palaeodasycladus barrabei* LÉBOUCHÉ & LEMOINE has a cylindrical to slightly club-shaped (Pl. XXII, Fig. 1), sometimes slightly bent (Pl. XXII, Fig. 2) thallus. The outer surface of the calcareous skeleton (envelope) may show different degree of segmentation, ranging from undulation (Pl. XXII, Fig. 1) to shallow fissuration (Pl. XXII, Fig. 3; Pl. XXIII, Fig. 8) to clearly expressed annulation (Pl. XXIII, Figs. 1, 4, 9, 11-12). Therefore it is not surprising that LÉBOUCHÉ & LEMOINE (1963), in their original description of *P. barrabei*, fail to mention any outer annulation, as well as in the first type of *E. ogilviae* (which are, in fact, identical forms), whereas CROS & LEMOINE (1966) note, in the second type, a slight outer annulation producing the appearance of successive articles like a string of barrels. On the other hand, BARATTOLO et al. (1994), in their amended diagnosis mention the outer annulation but note that this feature may be obliterated or totally destroyed by micritisation and abrasion. The inner cavity is characterised by intusannulation, which is agreed by all authors regardless of whether both species, *P. barrabei* and *E. ogilviae*, or only *P. barrabei*, are considered. Intusannulation corresponds to the originally described type (PIA, 1912), in which it is featured by regular narrowings and widenings of the inner cavity, which may be clearly visible (Pl. XXII, Fig. 4; Pl. XXIII, Figs. 1-2, 11) or else only indicated (Pl. XXIII, Figs. 3, 7), or the inner cavity may have almost even rims (Pl. XXII, Figs. 1-2). The relationship between intusannulation and the outer annulation in the third type of *E. ogilviae* has been described in detail by both CROS & LEMOINE (1966) and BARATTOLO et al. (1944), in their completion of the description of *P. barrabei*.

Arrangement of the branches: The tripartite branches (Fig. 5.1) are arranged in clear, rather sparsely separated whorls. Each whorl corresponds to a segment, regardless of whether the segmentation is indicated by shallow depressions (undulation) or clear annulation, which, in some cases, may reach the wall of the central cavity (Pl. XXIII, Figs. 4, 9, 11). In specimens with clearly developed annulation, the primary branches may

be seen to enter the central cavity immediately below the tooth-like protrusion of the inner wall, directed toward the centre of the inner cavity (Pl. XXII, Fig. 4; Pl. XXIII, Fig. 1). The primaries are generally small, of varying shape (as in the type-species) ranging from short tubular (or rod-like) (Pl. XXII, Fig. 4; Pl. XXIII, Fig. 1) to short, slightly club-shaped (Pl. XXII, Figs. 2-3), to stump-like or almost bubble-shaped (Pl. XXIV, Fig. 1). In some specimens, some primaries branch off immediately after leaving the central cavity, one directed upwards, the other downwards, which produces a seemingly metaspondyl appearance (Pl. XXII, Figs. 4, 7). In some cases, there is an impression of dealing with neighbouring branches of a whorl, of which one is directed upwards, the other downwards. If this is true, then the pores of the primaries within a segment would be arranged in two rows and in alternating position. The position of the primaries has so far always been considered to be perpendicular to the longitudinal axis of growth, but they can also be directed slightly upwards, the maximum angle with the horizontal plane () amounting to 30° (Table 8; Pl. XXIII, Figs. 1-3). Depending on the inclination of the primaries and the succession of the secondaries, the ring-shaped depressions in specimens with annulation may be positioned either perpendicularly or obliquely to the growth axis, giving the same direction also to the calcareous segments (Pl. XXIII, Figs. 1, 11).

Each primary branch bears a bundle of 5-6 secondaries. Bundles with more (6-8) secondaries, as mentioned by BARATTOLO et al. (1994), have not been observed, though this does not exclude their existence. Secondaries of the same bundle diverge; some are directed upwards, some downwards. Secondaries of neighbouring bundles within a whorl cross mutually, which renders it impossible to distinguish bundles in tangential sections. In the analysed material, the secondaries are much more slender and longer than the primaries and they retain the same diameter throughout their length (Pl. XXII, Figs. 1, 3-4; Pl. XXIII, Fig. 8). The tertiaries grow out from their ends (Pl. XXIII, Fig. 8). The number of tertiaries could not be determined with certainty; it is supposed to be 3-4 (for each secondary branch), as it was stated for this species by LÉBOUCHÉ & LEMOINE (1963) and for *E. ogilviae* by CROS & LEMOINE (1966), contrary to what is visible in specimens figured by BARATTOLO et al. (1994, pl. 2, figs. 2-4). Articulation of the tertiaries was not apparent, which means that this feature, as well as the more or less pronounced swellings of the secondaries, is an unstable characteristic, which may vary from population to population and from habitat to habitat. The increase of pore diameter in the outer parts of the skeleton suggests a phloioiphorous shape of the branches. The reproduction is assumed to be cladosporous; the swellings of some branches (without a fully developed sporangial "bubble") is regarded as an adaptation necessary for the placement of cysts; owing to this, sterile specimens may also be supposed to exist.

Maximum observed length of thallus	L	11.4
Outer thallus diameter	D	1.20 - 2.54
Inner thallus diameter	d	0.34 - 0.76
Relation	d/D	0.186 - 0.331
Distance between whorls	h	0.48 - 0.76
Diameter of primaries	p	0.10 - 0.20
Length of primaries	l	0.15 - 0.24
Number of primaries in a whorl	w	20 - 26
Diameter of secondary	p'	0.05 - 0.10
Length of secondary	l'	0.20 - 0.53
Number of secondary on a primary	w'	5 - 8
Diameter of tertiaries	p''	0.05 - 0.15
Length of tertiaries	l''	0.12 - 0.48
Number of tertiaries on a secondary	w''	3 - 4
Angle of inclination of branches		< 30

Table 8 Main biometrical parameters of *Palaeodasycladus barrabei* LÉBOUCHÉ & LÉMOINE (all dimensions in mm).

Stratigraphic position: In the original description, LÉBOUCHÉ & LÉMOINE (1963) mention the finds of this alga in several levels within the stratigraphic range Lower - Middle Liassic (Lotharingian - Pliensbachian). RADOIČIĆ (1975) ascribes the same stratigraphic range to her finds, whereas BASSOULLET et al. (1978) define the general stratigraphic position of this alga as Upper Sinemurian. Revisiting the type material, BARATTOLO et al. (1994) mention only the Middle Liassic. BASSOULLET (1997, p. 339-341. pl. LXVII) assigns the species, together with some others, to the Lower Liassic, with its upper limit being below the Pliensbachian lower boundary. In Mt. Velebit, that alga has been found in the rich algal assemblage of the sample VT-26, which comes from the Lower Liassic. At some other localities in Mt. Velebit (Kubus, Jadičevac, the foothill of Mt. Crnopac), its stratigraphic position is the same. A few finds are also known from the Lower Liassic deposits of Ivanjica near Dubrovnik.

Taxonomic validation of *Palaeodasycladus barrabei* LÉBOUCHÉ & LÉMOINE and its relationship with *Eodasycladus ogilviae* CROS & LÉMOINE

As mentioned above, *P. barrabei* has been variously treated taxonomically. After the original description by LÉBOUCHÉ & LÉMOINE (1963) it was for some time regarded as valid, until DELOFFRE & LAADILA (1990), in their revision and emendation of the genus *Palaeodasycladus*, expressed the opinion that it should be considered as a younger synonym of *P. mediterraneus*. In the original description of the genus *Eodasycladus* and *E. ogilviae*, respectively, CROS & LÉMOINE (1966) consider the types I and II to be closely related to *P. barrabei*, whereas the type III is distin-

guished from *P. barrabei* by having some secondary branches more strongly swollen, and/or larger pores, interpreted as choristosporous reproductive organs. In practice this means that the specimens belonging to types I and II should be identified as *P. barrabei* if no specimens of type III are present, or if they are, then the types I and II represent sterile specimens of *E. ogilviae*, respectively. Obviously, such a situation was not satisfying, as specimens which evidently belong to the same taxon are treated as belonging to separate taxa, depending on how they occur. Because of the existence of individual more strongly swollen branches and/or rounded structures, BARATTOLO et al. (1994) transferred *P. barrabei* into the genus *Eodasycladus*, emphasising its similarity with *E. ogilviae*. Later, they stress that sterile specimens of *P. barrabei* show enough differences to *P. mediterraneus*, which was not questioned by anybody (except, erroneously, by DELOFFRE & LAADILA, 1990), in spite of the fact that primary branches in *P. barrabei* may be slightly inclined upwards. In this case, however, we may ask ourselves what had led different authors to include their own, priority-bearing species (*P. barrabei*), into the types I and II as sterile forms of *E. ogilviae*, as has been done by CROS & LÉMOINE (1966), or to transfer into the genus *Eodasycladus*, both those (relatively few) specimens with possible sporangial cavities and the sterile ones, previously described as *P. barrabei*, as has been done by BARATTOLO et al. (1994). If the above mentioned authors accept the existence of fertile and sterile forms in *E. ogilviae*, we must ask ourselves why they have not done the same thing in *P. barrabei*, which should have priority. I agree with BARATTOLO et al. (1994) that the existence of choristosporous reproductive structures, in spite of being only sporadically developed (see reconstruction by CROS & LÉMOINE,

1966, fig. 9) and rarely observed, represents a new quality which, as an extreme consequence, enables the establishment of the new genus. In spite of the obvious close relatedness between *P. barrabei* and *E. ogilviae*, which can be discussed within the framework of their phylogenetic relationships, the validity of *P. barrabei* need not be questioned, the more so because of the strongly pronounced variability of both morphologic features and biometric parameters between the species of that genus.

***Palaeodasycladus alanensis* n. sp.**

Pl. XXV; Pl. XXXVIII, Figs. 4-6;

Fig. 5.2

Origin of the name: After Mali Alan Pass, central part of Mt. Velebit, on the Sv. Rok - Obrovac road.

Type locality: On the Sv. Rok - Obrovac road (Fig. 7), about 100 m from the milestone on the Mali Alan Pass in the direction of Obrovac; co-ordinates: 44° 17' 24" N, 15° 39' 33" E. Regrettably this outcrop is nowadays inaccessible because of unmarked land-mines.

Type stratum: Grey, well-bedded fossiliferous limestone, represented by the alternation of skeletal-intraclastic grainstone and micrite with sporadically developed stromatolitic laminae. The depositional environment was probably shallow subtidal with sporadic emersions into the vadose zone. The algal-bearing samples derive from the well-documented Lower Liassic deposits within a continuous succession, as shown in the stratigraphic column in Fig 2.

Holotype: Oblique section figured in Pl. XXV, Fig. 1, slide VT-26/149. This slide, as well as others containing the figured material, are stored at the Institute of Geology, Zagreb.

Diagnosis: Calcareous alga with a cylindrical, undivided, thallus, with slight outer undulation, shallow fissuration and/or partial annulation of the outer surface. Inner cavity with well visible but not strongly pronounced intusannulation. The species-specific characteristics are bowl-shaped or irregularly swollen (nodular) primary branches, which, in deep tangential sections, appear as large, rounded to polygonal pores. Secondary branches are acrophorous, growing out from the outer margin of bowl-shaped or nodular primaries. Phloiophorous tertiary branches are barely visible.

Description: The cylindrical calcareous skeleton is characterised by a slightly undulated outer surface and, it seems, irregularly occurring shallow fissuration or annulation (Pl. XXV, Fig. 5). The inner cavity is clearly delineated, with slight intusannulation, and occupies up to 30% of the whole diameter (Table 9).

The tripartite branches are arranged in loosely spaced whorls, the distance between the neighbouring whorls being approximately equal to that in *P. barrabei*. The primary branch communicates with the inner cavity through a small pore, which is situated on or immediately below the protrusions of the inner wall that make the intusannulation and where the inner diameter is the smallest. The primary branches may have various shapes (Fig. 5.2), which may occur in different combinations in the same specimen. In well-developed specimens, the primary branches are abrupt-

Maximum observed length of thallus	L	8.18
Outer thallus diameter	D	2.08 - 3.08
Inner thallus diameter (max.)	d_{\max}	0.54 - 0.64
Relation	d_{\max}/D	0.118 - 0.302
Inner thallus diameter (min.)	d_{\min}	0.38 - 0.54
Relation	d_{\min}/D	0.123 - 0.260
Distance between whorls	h	0.64 - 0.84
Diameter of primaries	p	0.30 - 0.48
Length of primaries	l	0.20 - 0.35
Number of primaries in a whorl	w	0 - 12
Diameter of secondary	p'	0.06 - 0.12
Length of secondary	l'	0.34 - 0.58
Number of secondary on a primary	w'	5 - 7 (?8)
Diameter of tertiaries	p''	0.04 - 0.10
Length of tertiaries	l''	0.15 - 0.26
Number of tertiaries on a secondary	w''	3 - 4
Angle of inclination of branches		0

Table 9 Main biometrical parameters of *Palaeodasycladus alanensis* n. sp. (all dimensions in mm).

ly widened at their very base, whereby they acquire a bowl-like (Pl. XXV, Figs. 2-3) or nodular-bushy shape (Pl. XXV, Fig. 4). Individual branches on the same specimen may be less well-developed, similar to those in *P. barrabei*, from which this species is derived. In deeper tangential sections, the primaries appear as rounded to polygonal shaped pores which are in mutual contact both within a whorl and with neighbouring whorls (Pl. XXV, Figs. 1, 6 top). The secondary branches extend from the margins of the bowl-shaped or nodular primaries, and they diverge from one another (Pl. XXV, Figs. 1-4). These branches are acrophorous, regardless of their thickness (Pl. XXV, Fig. 4). The number of secondaries (from available sections in Pl. XXV, Figs. 1-3, 4), is estimated to be 5-7, possibly 8. Neighbouring bundles of the secondaries are not grouped separately, but are in mutual contact. Thus one cannot tell which secondary belongs to which primary branch. Tertiary branches are visible only with difficulty, because of the worn outer surface (Pl. XXV, Fig. 4). They seem to be very short. In some pores of the primary branches, single or grouped small, dark, rounded corpuscles can be seen, which are interpreted as possible cysts and which would define the species as being cladoporous.

Similarities and differences: *Palaeodasycladus alanensis* n. sp. belongs to the group of *Palaeodasycladus* species, which is characterised by having intusannulation and rather loosely spaced whorls. The phyletic connection between *P. alanensis* and *P. barrabei* (the latter being the ancestral form) is shown by the sporadic and irregular occurrence of the *barrabei*-type branches (in addition to bowl-shaped or nodular ones) in *P. alanensis*. The distinction between *P. alanensis* and *P. barrabei* is best illustrated in deeper tangential sections, in which the whorls of primary branches in *P. barrabei* appear as small pores arranged in rows which are set apart from each other (Pl. XXIII, Fig. 8), as distinct from *P. alanensis* in which the pores are large, rounded to polygonal, and in mutual contact (Pl. XXV, Fig. 1). As regards *P. mediterraneus*, the main difference concerns the shape of the primary branches and the distance between the consecutive whorls. The same differences exist in relation to *P. gracilis* and *P. illyricus* n. sp., as well as being particularly pronounced in *P. calciticus* n. sp. As regards *E. ogilviae*, the main difference concerns the shape of the primary and secondary branches: in *P. alanensis*, cysts develop in the primaries, whereas in *E. ogilviae* the development of cysts takes place in one of the secondaries, which becomes considerably thicker or even strongly swollen into a "bubble", thus becoming the choristosporous organ.

Stratigraphic position: *P. alanensis* n. sp. occurs in the algal assemblage contained in sample VT-26 which has already been shown in the preceding text to be of Early Liassic age.

***Palaeodasycladus dolomiticus*
(CROS & LEMOINE, 1966) n. comb.**

Pls. XXVI-XXVII;

Fig. 5.4

Selected synonymy:

- 1966 *Fanesella dolomitica* n. sp. - CROS & LEMOINE, p. 163-164, pl. 2, figs. 1, 3-4, 5 part.
 1969 *Petrascula heraki* SOKAČ & NIKLER - SOKAČ & NIKLER, p. 104-106, pl. 1, fig. 2, non figs. 1, 3; pl. 2, figs. 1-3, non figs. 4-6; pl. 3, fig. 1, ?fig. 2, non figs. 3-4.
 1993 *Fanesella dolomitica* CROS & LEMOINE - GRANIER & DELOFFRE, p. 22-23, 30-31.
 1996 *Fanesella dolomitica* CROS & LEMOINE - BARATTOLO & BIGOZZI, p. 201-202.
 1996 *Fanesella sokaci* n. sp. - BARATTOLO & BIGOZZI, p. 201-205, pl. 45, fig. 2; pls. 51-53.

Main characteristics of the genus *Fanesella*

In the original description of the genus *Fanesella* CROS & LEMOINE (1966) emphasise that the genus is characterised by four orders of branches. The primary branches are swollen, functioning as sporangia, and tightly squeezed, arranged in clearly developed whorls. The secondary branches grow out of the primaries like the fingers of a glove, i.e. without constrictions at the base. The third- and fourth-order branches emerge in bundles, with constrictions at the joints. In the description of the type-species, CROS & LEMOINE (1966) mention that the so-called secondary branches are, in fact, short protrusions of the primaries (Fig. 5.4a). In defining the fourth-order branches, however, the authors are not explicit, stating that in one case, when dealing with specimens with a slightly abraded outer surface, they find indications of all branches, whereas later in the text they say that in the majority of cases where the branches are visible, they appear open towards the exterior; meaning that these branches are unequivocal. BARATTOLO & BIGOZZI (1996) give a summarised diagnosis of the genus *Fanesella*, emphasising the difference toward *Palaeodasycladus* as being, mainly, the existence of four orders of branches, as distinct from the three orders in *Palaeodasycladus*, and in the primaries being somewhat thicker (Fig. 5.4b).

Comparison of the main characteristics of the genera *Palaeodasycladus* and *Fanesella* and the proposal for their unification

The analysis of the abundant available material of *P. mediterraneus* shows that some specimens include some characters that served as the basis for distinguishing and establishing the genus *Fanesella*. The rectangu-

lar shape of the primary branches is illustrated in several specimens of *P. mediterraneus* (Pl. VI, Fig. 3 part; Pl. VII, Figs. 1-2, 4; Pl. IX, Fig. 4), as well as the transition from cylindrical and sometimes irregularly shaped to rectangular in the same specimen (Pl. V, Fig. 4). The finger-like secondaries (i.e. without basal constrictions), which are said to be characteristic of *Fanesella*, can also be seen in some specimens of *P. mediterraneus*. It should be stressed, however, that this feature should not be given a particularly strong taxonomic significance. The main diagnostic feature of *Fanesella* is said to be the presence of four orders of branches; this feature, however, can also be present (or, at least, cannot be excluded) in some specimens of *P. mediterraneus* (e.g., pl. 1, fig. 4 in BARATTOLO et al., 1994, in which the finger-like growth of the secondaries can also be clearly seen). Specimens similar to the one shown in Pl. XI, Fig. 1, which can be visually assigned to *P. mediterraneus*, also show short, delicate protrusions which, according to the criteria adopted, can also be regarded as secondary branches. Ramification up to fourth-order branches can occur on individual branches in some whorls in *P. barrabei* (clearly visible in Pl. XXII, Figs. 4, 7 and Pl. XXIV, Fig. 2. This clearly proves the possibility of fourth-order branch development in the genus *Palaeodasycladus*. In specimens with only outer parts of the skeleton, i.e. the area of third-order and, possibly, fourth-order branches preserved, we cannot distinguish *P. mediterraneus* from *P. dolomiticus* specimens. For these reasons the alleged mor-

phological differences between *Fanesella* and *Palaeodasycladus* are insubstantial and indicate a more comprehensive description of one taxon, i.e. falling within the, admittedly broadened, variation range of the genus *Palaeodasycladus*. Therefore further retention of the genus *Fanesella* is of no benefit and therefore it is proposed that *Fanesella* be regarded as a younger synonym of *Palaeodasycladus*.

Description: *Palaeodasycladus dolomiticus* (CROS & LEMOINE, 1966) n. comb. is a seldom mentioned, and even more rarely illustrated, species, described from the calcareous Lower Liassic. It is characterised by a comparatively large, calcareous, cylindrical, sometimes bent, thallus with even outer and inner surfaces. The central cavity occupies 16-32% of the total diameter (Table 10).

Branches are tripartite to quadripartite, depending on how one interprets the morphology of the primary branches. In longitudinal sections, the primary branches are rectangular (Pl. XXVII, Figs. 2, 5, 7-8), proximally somewhat narrower, while widening distally in transverse sections (Pl. XXVI, Figs. 5-6; Pl. XXVII, Fig. 1). They are tightly compressed within a whorl, being mutually separated by thin, regular, calcareous partitions (Pl. XXVI, Figs. 5-6). Between the whorls, these partitions are somewhat more massive and more irregular (Pl. XXVII, Figs. 2, 5, 7). The primary branches are situated perpendicularly or are slightly inclined to the growth axis, the angle to the horizontal plane usually

Maximum observed length of thallus	L	16.34
Outer thallus diameter	D	1.94 - 4.34
Inner thallus diameter	d	0.48 - 1.20
Relation	d/D	0.160 - 0.321
Distance between whorls	h	0.40 - 0.60
Diameter of primaries	p	0.20 - 0.48
Length of primaries	l	0.30 - 0.85
Number of primaries in a whorl	w	14 - 20
Diameter of secondary	p'	0.08 - 0.20
Length of secondary	l'	0.14 - 0.40
Number of secondary on a primary	w'	4 - 5
Diameter of tertiaries	p''	0.06 - 0.15
Length of tertiaries	l''	0.15 - 0.38
Number of tertiaries on a secondary	w''	3 - 4
Diameter of quaternaries	p'''	0.10 - 0.15
Length of quaternaries	l'''	0.10 - 0.20
Number of quaternaries on a tertiary	w'''	3 - 4
Angle of inclination of branches		0 - 25

Table 10 Main biometrical parameters of *Palaeodasycladus dolomiticus* (CROS & LEMOINE) n. comb. (all dimensions in mm).

not exceeding 25° (Pl. XXVII, Fig.8). In some specimens, they are slightly bent in their distal parts (Pl. XXVII, Fig. 6), which becomes more strongly pronounced in secondary and tertiary branches. The primaries are connected with the central cavity through a somewhat large pore, which is situated in the lower part of the proximal end (Pl. XXVII, Fig. 8). protrusions similar to fingers of a glove or a cow's udder grow out of the distal ends of the primaries. These protrusions may be regarded as being either continuations of the primaries or representing the secondary branches. On their distal end, they bear the secondaries or tertiaries, depending on one's opinion. These, however, are clearly constricted at the base and, as is also the case in some other *Palaeodasycladus* species, may be articulated (Pl. XXVII, Fig. 6). The fourth-order of branches are seldom clearly visible, as was rightly emphasised in the original description (CROS & LEMOINE, 1966). Judging by the shape of the pores in outer parts of the tangential sections, they can be seen to be phloioiphorous. In some cases, i.e. in specimens with clearly rectangular primaries, it is difficult to distinguish between *P. mediterraneus* and *P. dolomiticus*.

In connection with *P. dolomiticus*, a short comment should be made on the recently described *Fanesella sokaci* BARATTOLO & BIGOZZI (1996), which is said to differ from *P. dolomiticus* by less massive complete calcification and its considerably larger size. However, because it is well known that the degree of calcification is not a taxonomic character but, most frequently, a consequence of environmental and diagenetic conditions, and larger size can be an extreme value within a variation range (which is perhaps supported by the fact that the finds of *P. dolomiticus* are still rare and not numerous), it is here proposed that *F. sokaci* should be considered a younger synonym of *P. dolomiticus*. As the type species of *Fanesella* is herein transferred to *Palaeodasycladus*, *Fanesella anae* SOKAČ becomes *Palaeodasycladus anae* (SOKAČ) n. comb.

Stratigraphic position: Comparatively rare finds of this alga do not permit a detailed analysis of its stratigraphic range. In the original description, CROS & LEMOINE (1966) determine the age of the algal-bearing deposits as Sinemurian, *s. str.* Lotharingian. OTT (1974) states it only very generally as Lower-Middle Liassic. BARATTOLO & BIGOZZI (1996) have discovered this alga, together with *Tersella genoti* and numerous *Palaeodasycladus* remains, in their microfacies CM3 from the upper part of the Calcare Massiccio Fm., which belongs to the Sinemurian. BASSOULLET (1997), in his summary review of the most important Jurassic dasyclads, also concurs with a Sinemurian age. In Mt. Velebit, it has already been found at the localities Dušice and Jadičevac in Lower Liassic deposits, which is supported by sample VT-26, for which a Lower Liassic age has been thoroughly documented.

***Palaeodasycladus anae* (SOKAČ, 1988)
n. comb.**

Pl. VIII, Fig. 1; Pl. XIII, Figs. 4-5; Pls. XXVIII-XXX
Fig. 6

1988 *Fanesella anae* n. sp.- SOKAČ, p. 9-14, fig. 6;
pls. 1-3; pl. 4, figs. 2-4.

This species has been recently described and well illustrated (SOKAČ, 1988). The description (SOKAČ, 1988), as well as the generic assignment, was primarily based on the shape of the primary branches and on the total degree of branching, which may reach third and fourth-order branches, often on the same specimen. In spite of the primaries frequently being of variable shape and often differing one from another in the same specimen, they may, nevertheless, generally be described as being predominantly nodular (Pl. XXVIII, Figs. 1-9; Pl. XXX, Figs. 1, 3, 5-7). The primaries connect with the central cavity either through a short stalk (Pl. XXIX, Figs. 6-7) or directly through a smaller or larger opening at their base (Pl. XXIX, Figs. 1, 4). Species-specific characters concern the distal ends of the primaries which may be variable in the same specimen. Sporadically, some branches bear irregular nipple- or horn-like protrusions (Pl. XXVIII, Figs. 2, 4-5; Pl. XXIX, Figs. 1, 5, 7). From there, some thin branches grow out, either individually or in bundles, whereas other branches grow out directly from the primary branch, so that the same type of branches may be regarded either as secondary or as tertiary branches (Pl. XXVIII, Fig. 2, top right). In some specimens, primary branches divide halfway along their length into two to three equally strong arms (Pl. XXIX, Fig. 4; Pl. XXX, Fig. 4), out of which grow thin tertiary branches, which further divide into fourth-order branches that are, undoubtedly, phloioiphorous (Pl. XXIX, Fig. 5). In some specimens, some "secondaries" grow like fingers of a glove, as in *P. dolomiticus*, or the primary branch has a conical termination and the secondaries grow out sidewise from the primary branch (Pl. XXVIII, Fig. 2, top right). It is difficult to verbally describe every variation and each possible morphological change and furthermore, it is unlikely that such an attempt would yield useful results. The best way to obtain an impression of variability is to illustrate as many differences as possible (Pl. XXVIII, Figs. 1-9; Pl. XXIX, Figs. 1, 4-7; Pl. XXX, Figs. 4-7). It should, however, be mentioned that no section (specimen) has been observed with all primaries being identical, and not even with all branches ramified to the same degree, which indicates the broad range of variation in the species. The fact that in the some specimens branches may be identical or very similar, by their shape and the degree of ramification, to those in *P. mediterraneus*; the fact that the secondaries may emerge from the primaries like fingers on a glove, without basal constrictions, as in *P. dolomiticus* or in some specimens of *P. mediterraneus* (which may have four orders

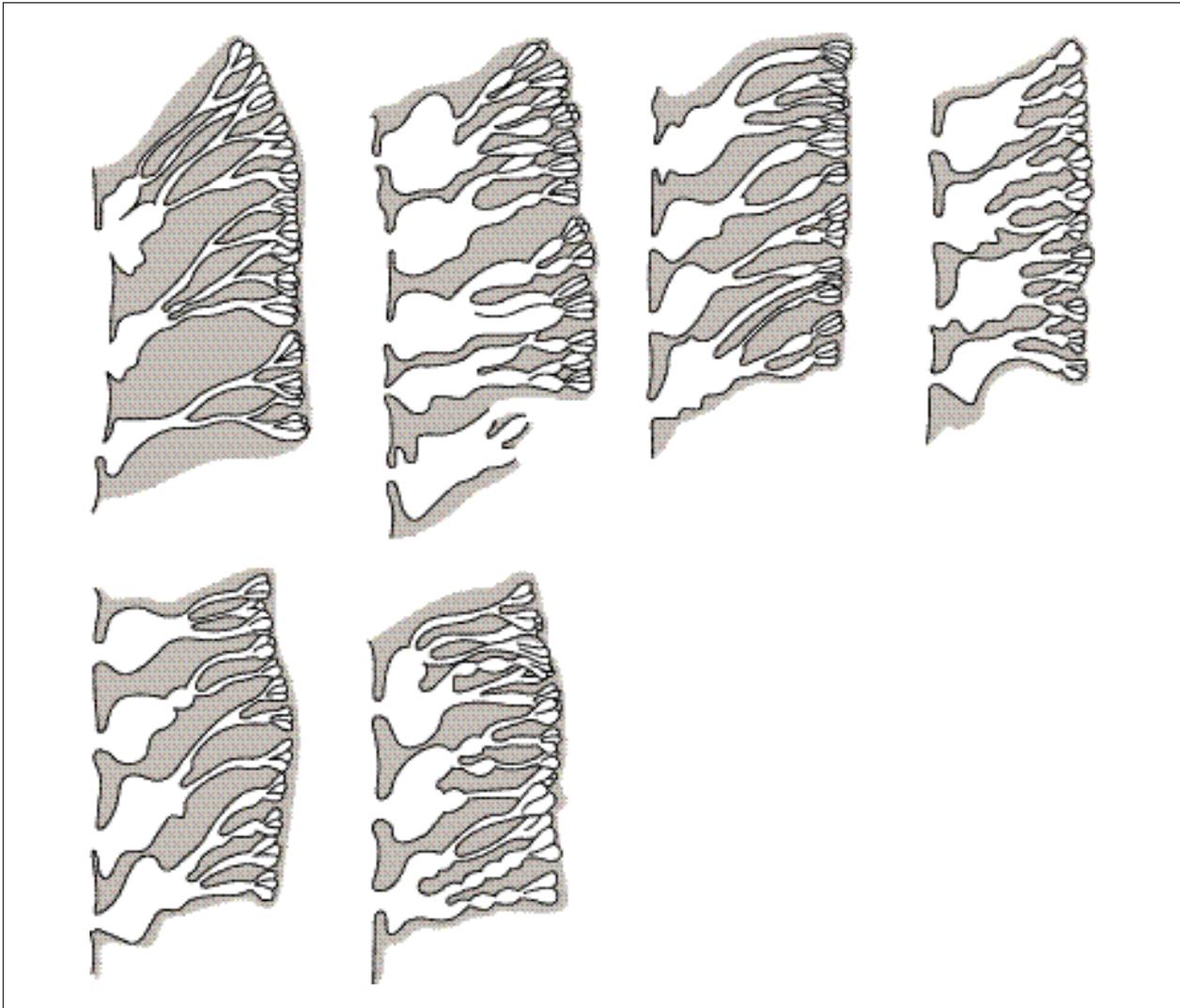


Fig. 6 Schematic review of sections of some possible forms of branches in *Palaeodasycladus anae*.

of branches), and, finally, that both species can show irregular constrictions, narrowings, etc. in the second-, third-, and fourth-order branches, suggests their common generic assignment. Basically, the main distinction between *P. mediterraneus*, *P. dolomiticus*, and *P. anae*, all three species being of approximately the same dimensions, concerns the different shape of the primary branches, particularly of their distal ends, which can clearly be illustrated: *P. mediterraneus* (Pl. I, Fig. 5; Pl. VI, Figs. 1-3; Pl. XXVII, Figs. 6-8) vs. *P. anae* (Pl. XXVIII, Figs. 1-9, Pl. XXIX, Figs. 1, 4-7), respectively. *P. anae* is cladosporous, as are other species of the genus (Pl. VIII, Fig. 1; Pl. XIII, Fig. 4). As previously mentioned, the similarities outlined above, and even with some details being identical in *P. mediterraneus* and *P. dolomiticus*, this species is also herein proposed to be transferred to the genus *Palaeodasycladus*.

The shape, diameter, and length of the first- to fourth-order branches often varies in the same specimen (Table 11). For instance, the distance between the con-

secutive whorls (“h”) in the same specimen varies, in one case, from 0.20 to 0.35, whereas in another case the length of primary branches varies from 0.29 to the extreme value of 0.76 mm.

Stratigraphic and geographic distribution: The species has been found from the central part of Mt. Velebit (localities: Jadovno, Dušice, and Mali Alan Pass). The richest sample is VT-26 from the Lower Liassic, from which it was originally described.

***Palaeodasycladus multiporus* n. sp.**

Pls. XXXIII-XXXIV

Origin of the name: After the numerous pores of the second-order to fourth-order branches. Type locality: Mt. Velebit, about 100 m from the milestone on the Mali Alan Pass in the direction of Obrovac, on the Sv.

Maximum observed length of thallus	L	12.4
Outer thallus diameter	D	1.48 - 2.90
Inner thallus diameter	d	0.34 - 0.68
Relation	d/D	0.149 - 0.293
Distance between whorls	h	0.20 - 0.48
Diameter of primaries	p	0.15 - 0.48
Length of primaries	l	0.20 - 0.76
Number of primaries in a whorl	w	12 - 18?
Diameter of secondary	p'	0.08 - 0.20
Length of secondary	l'	0.07 - 0.44
Number of secondary on a primary	w'	0 - 4
Diameter of tertiaries	p''	0.05 - 0.10
Length of tertiaries	l''	0.20 - 0.48
Number of tertiaries on a secondary	w''	2 - 6
Diameter of quaternaries	p'''	0.03 - 0.10
Length of quaternaries	l'''	0.08 - 0.35
Number of quaternaries on a tertiary	w'''	2 - 4

Table 11 Main biometrical parameters of *Pala-eodasycladus anae* (SOKAČ) n. comb. (all dimensions in mm).

Rok - Obrovac road (Fig. 7). Coordinates: 44° 17' 24" N; 15° 39' 23" E.

Type-stratum: Grey, well-bedded, Lower Liassic (Hettangian - Lower Sinemurian) limestones, represented by the alternation of skeletal-intraclastic grainstone and micrite, with sporadically developed stromatolitic laminae. The deposits probably originated in a shallow subtidal environment with sporadic emersions into the vadose zone.

Holotype: Oblique section figured in Pl. XXXIV, Fig. 2, slice VT-26/262, stored, together with illustrated paratypes, in the collection at the Institute of Geology, Zagreb.

Diagnosis: Cylindrical thallus with euspondyl arranged, more or less inclined and comparatively large primary branches, which give rise to 9-12 finger-shaped secondary branches. Tertiary and fourth-order branches are also present. The total number of secondary, terti-

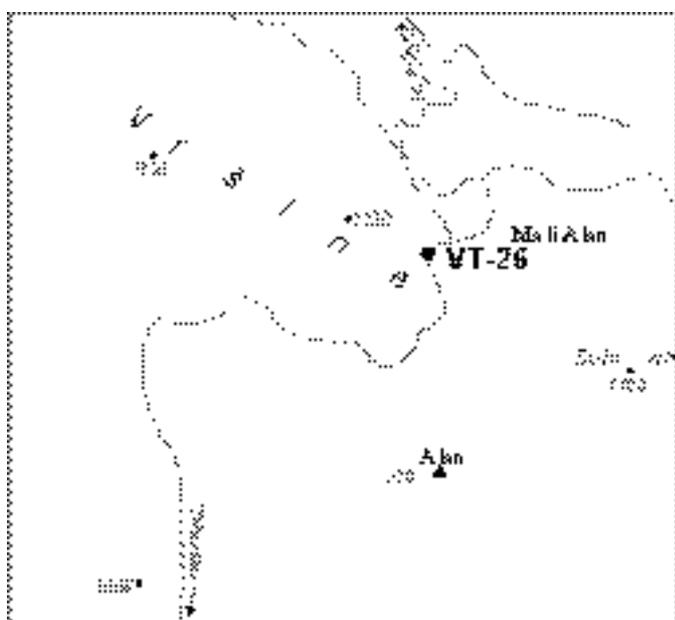


Fig. 7 Map of the Mali Alan Pass area in the south-east Mt. Velebit, type locality of the sample VT-26. Scale 1:25,000.

Maximum observed length of thallus	L	16.348.18
Outer thallus diameter	D	1.94 - 3.20
Inner thallus diameter	d	0.30 - 0.68
Relation	d/D	0.106 - 0.241
Distance between whorls	h	0.30 - 0.48
Diameter of primaries	p	0.24 - 0.48
Length of primaries	l	0.20 - 0.50
Number of primaries in a whorl	w	?9 - 12
Diameter of secondary	p'	0.08 - 0.15
Length of secondary	l'	0.20 - 0.35
Number of secondary on a primary	w'	9 - 12
Diameter of tertiaries	p''	0.04 - 0.07
Length of tertiaries	l''	0.20 - 0.35
Number of tertiaries on a secondary	w''	3 - 4
Diameter of fourth-order	p'''	0.04
Length of fourth-order branch	l'''	0.15 - 0.20
Number of fourth-order branch	w'''	2 - 4?
Angle of inclination of branches		30°

Table 12 Main biometrical parameters of *Pala-eodasycladus multiporus* n. sp. (all dimensions in mm).

ary, and fourth-order branches per primary branch amounts to 70-100 on the outer surface of the thallus.

Description: Cylindrical, non-segmented, and unbranched thallus often with a clearly delineated outer and inner surfaces. The outer surface is, in some specimens, surrounded by a partly preserved dark rim of probably organogenic micritized matter, formed in the outermost zone of the branches, where they were but weakly calcified (Pl. XXXIII, Figs. 3, 6; Pl. XXXIV, Figs. 2-3). The inner cavity has a smooth and even surface and occupies up to 25% of the total diameter.

Primary branches are generally of a rectangular shape, arranged into comparatively densely packed whorls, and tightly squeezed within a whorl. They are positioned more or less obliquely with relation to the longitudinal growth axis, and directed upwards. The main species-specific characteristic is the large number of secondaries which are finger-shaped and grow out from the distal surface of a primary branch, either from one level (Pl. XXXIII, Fig. 6; Pl. XXXIV, Figs. 2-3) or in a more irregular manner (Pl. XXXIII, Figs. 2, 4; Pl. XXXIV, Figs. 4-8). The number of secondary branches observed in one plane of section amounts to 6 (Pl. XXXIV, Fig. 4), which allows for the supposition that at least 9-12 secondaries emerge from the distal end of a primary (Table 12). The secondary branches are basically of a phloiophorous type but may be variously shaped, more swollen or more slender. From the distal end of the secondary, a bundle of 3-4 thin, phloiophorous, tertiary branches emerge, which gives a total number of approximately 35-45 tertiaries. Fourth-order

branches, which in some specimens seem to be very slender and thin, may number 70-100 per primary branch, supposing that each tertiary branch bears 2-3 fourth-order branches. As is also the case in other species of the genus, the distal ends of the primaries may vary in morphological details, and in the shape, length, and mode of emergence of the secondaries. Cysts may be occasionally preserved in the pores of the primaries, indicating that the species is cladosporous.

Similarities and differences: From its basic morphology, including the mode and degree of branching, *Pala-eodasycladus multiporus* n. sp. undoubtedly belongs to the broad group of variable forms united in the genus *Pala-eodasycladus*. In spite of its general similarity (shape of the thallus existence of tertiary and quaternary branches) with *P. mediterraneus* (including all its varieties), *P. dolomiticus*, and *P. anae*, it differs from all these forms by the larger number of secondary and, especially, tertiary and quaternary branches. Because the secondary branches grow out from the entire distal surface of the primaries, in *P. multiporus* they are not grouped into bundles as in *P. mediterraneus* (Pl. I, Figs. 3-5; Pl. III, Fig. 1; Pl. VI, Fig. 6, etc.) or *P. anae* (Pl. XXX, Figs. 1, 2, 4, 6). The large number of distal (?quaternary) branches, which are moreover much finer and incompletely or weakly calcified in the peripheral zone of the thallus, results in the loss of the conspicuous porous structure, well developed in *P. mediterraneus* and *P. dolomiticus* and, to a somewhat lesser degree, in *P. anae*. Besides, *P. multiporus* differs from *P. anae* in the shape of the primary branches, which in *P. multiporus* remain more or less rectangular, in contrast to *P.*

anae which is characterised by a broad range of morphological variety in the primaries, which are generally irregular and with nipple-like and irregular finger-shaped protrusions which represent the transition to the secondary branches. The rectangular shape of the large primaries is similar in *P. multiporus* and *P. dolomiticus*, but in *P. dolomiticus* there are only 4-5 secondary branches per primary, as distinct from at least 9-12, and possibly even more, in *P. multiporus*. With regard to *P. barrabei*, the obvious difference is in the more densely packed whorls of primary branches in *P. multiporus*, whereas in *P. barrabei* they are spaced rather far apart from each other, with a rather high *h* value. Besides, some specimens in *P. barrabei* may show a more or less pronounced intusannulation and annulation of the skeleton, but this is not a constant feature in *P. barrabei*.

Differences between *P. multiporus* and *P. alanensis* are similar to those mentioned above; in *P. alanensis* the primary branches acquire a bowl-like or irregularly bubble-like shape, which in deep tangential sections results in large alternating pores. Also, *P. alanensis* may sometimes show intusannulation and annulation, which may be regarded as a distinguishing criterion of secondary importance. With regard to *P. calciticus*, the main difference is the existence of well-developed calcitic partitions along the thallus and individualised calcitic envelopes in which are situated in all branches issuing from a primary branch in *P. calciticus*. The difference with regard to *P. benceki* n. sp. (see below) is obvious, because primary branches in *P. benceki* are enormously large and heavily deformed, with secondary branches growing out not only from the distal surface of the primaries but also from lateral parts, even proximal lateral parts, which is never observed in *P. multiporus*.

Stratigraphic position: *P. multiporus* n. sp. occurs in the algal assemblage contained in sample VT-26, which is of Early Liassic age.

***Palaeodasycladus benceki* n. sp.**

Pls. XXXV-XXXVII; Pl. XXXVIII, Figs. 7-8;

Fig. 5.3

Origin of the name: The species is dedicated to my colleague Đuro Benček, the long-serving director of the Institute of Geology in Zagreb, for his significant contribution to the development and affirmation of scientific and publicistic activities in the Institute, and, in particular, for his devotion to Mt. Velebit.

Type locality: Mt. Velebit; the locality is approximately 100 m from the milestone on Mali Alan Pass, in the direction of Obrovac, on the Sv. Rok - Obrovac road (Fig. 7); co-ordinates: 44° 17' 24" N, 15° 39' 23" E.

Type stratum: Grey, well-bedded Lower Liassic (Hettangian - Sinemurian) limestone, represented by the alternation of skeletal-intraclastic grainstone and micrite, with sporadically developed stromatolitic laminae. The strata were deposited in a shallow subtidal environment, with temporary emersions into the vadose zone.

Holotype: Oblique section figured in Pl. XXXVI, Fig. 2, thin section VT-26/436. Material containing the holotype and the paratypes figured is stored in the collection of the Institute of Geology, Zagreb.

Diagnosis: Cylindrical to slightly club-shaped thallus characterised by very large, irregular, and variously shaped primary branches, arranged in clear whorls. The distal surface of the primary branches may be curved or angular, with variously shaped (short, long, thick or thin, straight or curved) protrusions, separated by equally irregular indentations, which gives a completely irregular outline. Thin, regular, secondary branches emerge from the distal or lateral surfaces of the primaries and ramify further into the tertiaries near the outer surface. The species is cladosporous.

The measured values for *p*, *l*, *p''*, and *l''* may markedly differ (Table 13), even on the same specimen, depending on the shape and the place of emergence of a secondary branch. Thus, for instance, those secondaries which grow out from the extreme distal point of a given primary branch may be half as long as those that emerge from the lateral sides of the same primary branch.

Description: The calcareous thallus of this species has a cylindrical or slightly club-shaped form, with a gently undulating (Pl. XXXV, Fig. 2) or shallowly and irregularly annulated outer surface (Pl. XXXV, Fig. 3). Most frequently the outer surface is secondarily abraded and uneven; in some cases, it may be worn down to the distal surfaces of the primary branches (Pl. XXXV, Fig. 5 part). The inner surface clearly delineates the central cavity; it is even or slightly undulated; intusannulation may be present, but barely visible, representing a relict of its ancestral form. The central cavity occupies approximately 15-30% of the total diameter (Table 13).

The main characteristic feature of this species is the shape of its primary branches (Fig. 5.3). The primaries are arranged in whorls and are in alternating position in neighbouring whorls (Pl. XXXV, Fig. 6). They are very large, and, in well developed specimens, stretch from the very base, in the direction of specimens, stretch from the very base, in the direction of growth (Pl. XXXV, Fig. 1; Pl. XXXVII, Figs. 4-5), sometimes being of a bushy appearance (Pl. XXXV, Fig. 2), or irregular in longitudinal and oblique sections, and most frequently elliptical in transverse section (Pl. XXXVI, Figs. 5-6). Various shaped primaries may sometimes be seen on the same specimen. In some specimens, the extremely large primaries show a strongly irregular outer surface,

Maximum observed length of thallus	L	12.0
Outer thallus diameter	D	2.06 - 3.74
Inner thallus diameter	d	0.40 - 0.72
Relation	d/D	0.128 - 0.281
Distance between whorls	h	0.54 - 0.85/2
Diameter of primaries	p	0.48 - 0.80
Length of primaries	l	0.44 - 0.68
Number of primaries in a whorl	w	9 - 12
Diameter of secondary	p'	0.05 - 0.11
Length of secondary	l'	0.24 - 0.58
Number of secondary on a primary	w'	do 8
Diameter of tertiaries	p''	0.04 - 0.11
Length of tertiaries	l''	0.15 - 0.34
Number of tertiaries on a secondary	w''	3 - 4

Table 13 Main biometrical parameters of *Pala-eodasycladus benceki* n. sp. (all dimensions in mm).

with deep depressions or indentations and shorter or longer bulges, giving, in longitudinal sections, the appearance of a jagged coastline (Pl. XXXV, Fig. 3; Pl. XXXVI, Figs. 2-3). Primary branches connect with the central cavity through a short and narrow tubule (Pl. XXXVII, Fig. 4); the more swollen the branch and the nearer to the central cavity, the shorter the tubule, becoming, in some cases, only a larger or smaller pore at the base of the branch and thus enabling the direct communication. Secondary branches without pronounced basal constrictions grow out either from the distal surface and the above mentioned protrusions (Pl. XXXV, Fig. 3; Pl. XXXVI, Figs. 2-3) or, very often, sidewise, from the lateral surface of the primary branch (Pl. XXXV, Fig. 2; Pl. XXXVI, Fig. 7).

The number of the secondaries cannot be established with certainty, but it seems to be variable and to depend on the distal surface area. The secondaries are acrophorous, i.e., have the same diameter all along their length, and they extend to near the outer surface, where they branch off into short tertiaries. The fact that a secondary branch often emerges sidewise from the primaries, sometimes from near the base or even from the proximal rim (Pl. XXXVI, Fig. 7), may produce the illusion, in some sections, of sterile primary branches (Pl. XXXVI, Fig. 5; Pl. XXXVII, Figs. 2-3), arranged as in *Chinianella* in the sense of GRANIER et al. (1994) interpretation. Specimens which, in addition to large primaries as described above, also have, in the lower part of the thallus, preserved relict branches of the *P. barrabei* type (Pl. XXXVIII, Fig. 8) are exceptionally rare, which testifies to their direct phylogenetic connection. Tertiary branches are very rarely visible, due to erosion of the outer surface, but nevertheless it is evident that their diameter is larger than that of the secondary branches, which suggests that the tertiaries are of the phloiophorous type. Individual cysts, or groups

of cysts, observed in the cavities of the primary branches, indicate the cladospory of the species.

Similarities and differences: From the specific characteristics of the primary branches, *P. benceki* is distinguished from other species of the genus, though it shows unequivocal phylogenetic relationships with some. Visually, however, it is more similar to the species of the genus *Chinianella*, particularly to *Ch. macropora* (DI STEFANO & SENOWBARI-DARYAN), due to the large pores of the primaries, which are, however, much more irregular in *P. benceki*.

Besides, the intusannulation in *P. benceki* is weaker than in *Ch. macropora*. The egg-shaped thallus, as stated to exist in *Ch. macropora*, clearly differs from the cylindrical or slightly club-shaped thallus in *P. benceki*, which shows, moreover, clear signs of intusannulation and, in some specimens, annulation. These features are not mentioned in any *Chinianella* species, all of which are characterised throughout by large pores. The essential difference, however, between *Ch. carpatica* (BYSTRICKÝ), *Ch. crossi* (OTT), *Ch. zankli* OTT, *Ch. macropora* (DI STEFANO & SENOWBARI-DARYAN), *Ch. micropora* (DI STEFANO & SENOWBARI-DARYAN), and *Ch. ellenbergeri* BERNET-ROLLANDE & LEMOINE on the one hand and *P. benceki* on the other hand, is the existence of alternating whorls of fertile and sterile primary branches in all *Chinianella* species, whereas in *P. benceki* only fertile primaries are present. The illusion of sterile primaries in *P. benceki* in parts of some sections (Pl. XXXV, Fig. 4; Pl. XXXVI, Fig. 5; Pl. XXXVII, Figs. 2-3) is due, as previously stated, to the mutual crossing of those secondary branches that grow out sidewise from the primaries. The fact is, that no sterile branches could be unequivocally ascertained in *P. benceki*, and moreover, they could not be accommodated amongst the densely packed primary

branches, both within a whorl and in the neighbouring whorls (Pl. XXXV, Figs. 1, 5-6; Pl. XXXVI, Figs. 2, 4).

Stratigraphic position: *P. benceki* is one of the species contained in the algal assemblage of sample VT-26 of Early Liassic age.

***Palaeodasycladus asteriscus* n. sp.**

Pls. XXXIX-XL

Origin of the name: *Asteriscus* (lat.) = little star, diminutive of *aster*; in deeper tangential sections, cutting the distal part of the primary branch where the secondary branches emerge, the pattern is similar to the typographical asterisk mark.

Type-locality: Mt. Velebit, east of Jadičevac Hill (1,274 m), on the forest road crossing the central ridge of Mt. Velebit between Baške Oštarije and Bužimsko Bilo and merging into the longitudinal road Jadovno-Kalanjeva Ruja (Fig. 8); co-ordinates: 15°12'2"E, 44°33'20"N.

Type stratum: Grey, well-bedded limestone, often late diagenetically dolomitized; alternation of peloid-skeletal wackestone and ooid, sometimes ooid-skeletal grainstone. The algal-bearing sample has been determined as ooid-peloidal-skeletal grainstone. Skeletal particles are predominantly represented by gastropod

and algal fragments. The stratigraphic position of the holotype-bearing sample corresponds to the Hettangian-Lower Sinemurian.

Holotype: Oblique section figured in Pl. XXXIX, Fig. 2, thin-section JD-6B/5. Holotype material, as well as the illustrated paratype materials, are stored in the collection of the Institute of Geology in Zagreb. The available material includes about 30 variously oriented sections.

Diagnosis: The cylindrical skeleton with an integral inner cavity is characterised by regularly but distantly spaced whorls of primary branches. The main species-specific characteristic refers to the secondary branches, which in some specimens are directed upwards or downwards, almost parallel to the central cavity. This results in an asterisk-like section of the upper part of the primary branches, from where the secondary branches grow out. Tertiary branches are short and arranged in bundles.

Description: A comparatively large calcareous skeleton of a regularly cylindrical thallus with a clearly delineated central cavity (Pl. XXXIX, Figs. 2-3). The outer surface appears to be originally even and smooth, covered by pores of the tertiary branches; it is often subsequently eroded by shallow indentations (Pl. XXXIX, Figs. 1-3; Pl. XL, Figs. 1-4). The central cavity occupies 20-35 % of the outer thallus diameter (Table 14).

The branches are arranged in regular, rather widely spaced whorls, which is also a species-specific characteristic (Pl. XXXIX, Figs. 1-6). Primary branches are elongated, sometimes more or less regularly phloio-phorous, more often appearing to be deformed or irregularly shaped (Pl. XXXIX, Figs 2-3, 5). They are situated either perpendicularly to the growth axis, or, more frequently, directed upwards (Pl. XXXIX, Figs. 1, 5), or, more rarely, in the same specimen, they may even be inclined downwards (Pl. XXXIX, Fig. 2). The most obvious species-specific characteristic is the direction of growth and the position of the secondary branches. They grow out from the distal end or from the sides of the top of a primary branch, and soon after emerging diverge radial into opposite directions. Therefore sections cutting through this level do not show, except in very rare occasions (Pl. XXXIX, Fig. 1 top), the otherwise characteristic grouping of pores of secondary branches, typical of the type-species and its varieties. This position of secondary branches at the level of their emergence results, in tangential sections, in a large pore of the primary branch and radially arranged, elongated pores of the secondary (Pl. XXXIX, Fig. 3; Pl. XL, Fig. 1 top). In oblique and longitudinal sections, those secondary branches that are directed almost parallel to the longitudinal growth axis (Pl. XXXIX, Figs. 2-3) may be abraded to the extent that they form an inner annular cavity that seemingly separates the calcareous skeleton

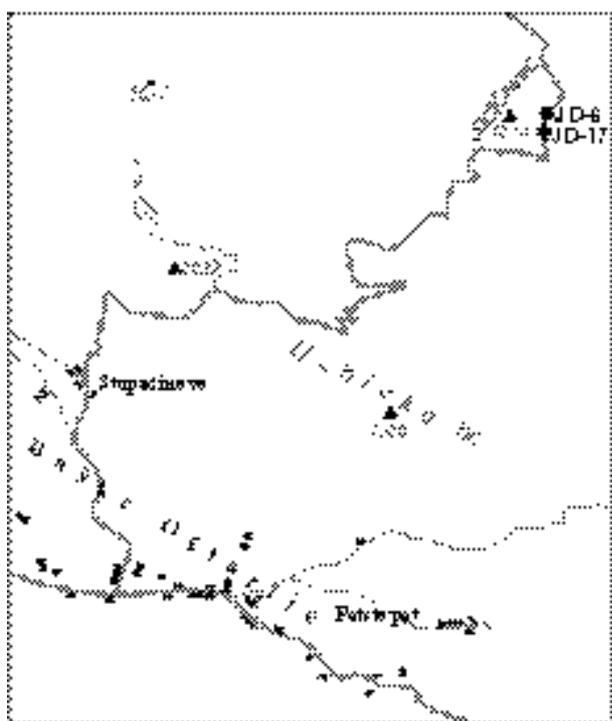


Fig. 8 Map of the Jadičevac peak area in the central Mt. Velebit, type locality of the samples JD-6B and JD-13. Scale 1:50,000.

Maximum observed length of thallus	L	12.5
Outer thallus diameter	D	1.60 - 2.70
Inner thallus diameter	d	0.35 - 0.67
Relation	d/D	0.180 - 0.350
Distance between whorls	h	0.39 - 0.72
Diameter of primaries	p	0.12 - 0.20
Length of primaries	l	0.15 - 0.35
Number of primaries in a whorl	w	
Diameter of secondary	p'	0.09 - 0.10
Length of secondary	l'	0.15 - 0.44
Number of secondary on a primary	w'	4 - 6
Diameter of tertiaries	p''	0.06 - 0.20
Length of tertiaries	l''	0.12 - 0.20
Number of tertiaries on a secondary	w''	3 - 4
Angle of inclination of branches		35°

Table 14 Main biometrical parameters of *Palaeodasycladus asteriscus* n. sp. (all dimensions in mm).

into an inner and an outer part (Pl. XXXIX, Fig. 5). A similar pattern may appear in transverse sections, in cases where the secondaries of neighbouring primaries of the same whorl converge towards each other (Pl. XL, Figs. 6-8). Those secondaries that are, due to their almost longitudinal position, confined to the interior of the calcareous envelope, lack the tertiaries, which are otherwise normally developed on those secondaries that are directed outwards (Pl. XXXIX, Figs. 1-2). The secondary branches are comparatively short, of small diameter, some with slightly widened distal ends. Because of the position of part of the secondary just described, the number of their pores in shallow tangential sections appears to be small (Pl. XXXIX, Figs. 2-4). Tertiary branches, in turn, are barely visible (if at all), due to the eroded outer surface. Those few that can be discerned, suggest that they are short, thin, and arranged in bundles that reach the outer surface. The species is supposed to be cladosporous.

Similarities and differences: From its general morphological characteristics, *P. asteriscus* n. sp. fits into the genus *Palaeodasycladus*, where it differs from other described species. The main characters distinguishing it from other *Palaeodasycladus* species are the widely spaced whorls and secondary branches of the same primary branch diverging into opposite directions. These differences are even more pronounced in those specimens of *P. asteriscus*, in which there is a secondarily developed annular cavity formed by merging of the opposingly directed secondary branches. This results, among other things, in a different arrangement of the pores of the secondary branches, in the appearance of a star-shaped cavity as opposed to bundles of pores in other species, and in a smaller number of pores per unit of the outer surface in *P. asteriscus*.

Stratigraphic position: *P. asteriscus* has been discovered in the lower part of the Lower Liassic part of the stratigraphic column, about 20 m above the dolomite/limestone boundary and about 150 m below the first occurrence of the foraminiferal genera *Orbitopsella* and *Lituosepta*. In the fossil assemblage of this part of the Lower Liassic, *Palaeodasycladus mediterraneus* and *P. dolomiticus* are the dominant species. The position of the sample with *P. asteriscus* can be therefore defined as the Lower Liassic in age, and most likely the lower part of the Lower Liassic, corresponding to the Hettangian.

**Genus *Eodasycladus* CROS & LEMOINE, 1966
ex GRANIER & DELOFFRE, 1993**

Selected synonymy:

- 1966 *Eodasycladus* n. gen. - CROS & LEMOINE, p. 161-162, fig. 8-2.
- 1978 *Eodasycladus* CROS & LEMOINE, 1966 - BASSOULLET et al., p. 97.
- 1993 *Eodasycladus* CROS & LEMOINE, 1966 - GRANIER & DELOFFRE, p. 30, 45.
- 1993 *Eodasycladus* CROS & LEMOINE, 1966 ex GRANIER & DELOFFRE, 1993 - BARATTOLO et al., p. 4-6.

The genus *Eodasycladus* has been established by CROS & LEMOINE (1966) from a Lower Liassic algal assemblage, where they observed specimens similar to, but different from, *Palaeodasycladus barrabei*. These specimens were characterised by third-order ramifications, constrictions and swellings in the tertiary branch-

es, and, most importantly, a bubble-shaped swelling of one of the secondary branches, which did not give rise to tertiary branches. Such an excessively swollen, bubble-shaped, secondary branch functioning as a choristosporous reproductive organ, was developed irregularly, but always in upper parts of the plant and in various positions with regard to other secondaries of the same whorl (CROS & LEMOINE, 1966, fig. 9). This was the main characteristic of the new genus and also the main difference from *Palaeodasycladus*. In the latter the development of fertile secondary branches is not known to exist.

***Eodasycladus ogilviae* CROS & LEMOINE,
1966**

Pl. XLI

Selected synonymy:

- 1966 *Eodasycladus ogilviae* n. sp. - CROS & LEMOINE, p. 162-163, fig. 9, pl. 1, figs. 3-4, 6-7, non fig. 5.
- 1978 *Eodasycladus ogilviae* CROS & LEMOINE - BASSOULLET et al., p. 97-100, Pl. 10, Figs. 1-3.
- 1994 *Eodasycladus ogilviae* CROS & LEMOINE, 1966 ex GRANIER & DELOFFRE, 1993 - BARATTOLO et al., p. 4-7.

As previously mentioned, only specimens that unequivocally show one of the secondary branches within a bundle transformed into a strongly swollen bubble-shaped body are assigned here to this species. Such forms correspond to the "type III" of *Eodasycladus ogilviae* by CROS & LEMOINE (1966), for which the presence of "sporangia" was said to be characteristic.

The species has a cylindrical or, possibly, slightly club-shaped thallus, with a slightly undulated or shallowly annulated outer surface (Pl. XLI, Figs. 1-2, 6, 8). More rarely, the outer surface is abraded and even. In some specimens, the skeleton seems to be composed of a row of shallow, barrel-shaped segments (Pl. XLI, Fig. 1). The central cavity may exhibit even or wavy surface, as a result of more or less developed intusannulation (Pl. XLI, Figs. 2, 6). All these characteristics represent the heritage of *P. barrabei*.

The direct descendancy of *E. ogilviae* from *P. barrabei* is evidenced by the whorls of primary branches that are spaced far apart one from another and connect to the central cavity through a pore situated at, or immediately below, the inward projecting annular bulge of the inner wall. The primary branches are perpendicular to the thallus or are directed slightly upwards. They are small, slightly club-, bubble-, or stump-shaped. Each primary branch gives rise to 5-8 tubular (acrophorous), thin, and always more or less curved and mutually diverging secondary branches (Pl. XLI, Fig. 4), which, in turn, each give rise to 3-4 short tertiaries (Table 15). The essential characteristic which served to establish the genus refers to a strongly swollen secondary branch within a bundle (Pl. XLI, Figs. 1-2, 6, 9). This bubble-shaped body, which is considered to function as a sporangium (CROS & LEMOINE, 1966) or a choristosporous reproductive organ (BARATTOLO et al. 1994), is, however, irregular; it occurs in some branches within a whorl, in some whorls, or, more often, in the younger parts of the plant. The sporangial "bubble" may be situated in the middle of a bundle or at any side (Pl. XLI, Figs. 1-2, 6). This feature gives the species a choristosporous character.

Similarities and differences: *E. ogilviae* and *P. barrabei* show a clear phylogenetic relationship, with

Maximum observed length of thallus	L	6,86
Outer thallus diameter	D	1,94 - 2,56
Inner thallus diameter	d	0,48 - 0,54
Relation	d/D	0,190 - 0,247
Distance between whorls	h	0,40 - 0,72
Diameter of primaries	p	0,07 - 0,20
Length of primaries	l	0,15 - 0,30
Number of primaries in a whorl	w	?
Diameter of secondary	p'	0,06 - 0,10
Length of secondary	l'	0,30 - 0,64
Number of secondary on a primary	w'	5 - 8
Diameter of tertiaries	p''	0,09 - 0,12
Length of tertiaries	l''	0,20 - 0,24
Number of tertiaries on a secondary	w''	3 - 4

Table 15 Main biometrical parameters of *Eodasycladus ogilviae* CROS & LEMOINE (all dimensions in mm).

numerous almost identical, or very similar, features. As early as the original description, CROS & LEMOINE (1966) emphasised the existence of transitional forms from the type II (with characteristics of *P. barrabei*) to type III (*Eodasycladus ogilviae*), in which the beginnings of swelling of individual secondary branches may be seen. The only obvious difference between the two species is the presence of swollen, bubble-shaped bodies in *E. ogilviae*, probably functioning as choristosporous reproductive organs. This was deemed to be a sufficiently significant, qualitative difference for establishing the new genus. Irrespective of acceptance, for the time being, of *Eodasycladus* as a valid genus, the question of whether a probably choristosporous reproduction, besides numerous identical features with the parent species, is sufficient for establishing the new genus, remains unanswered. When compared with the forms which are herein assigned a status of species (*P. alanensis* and *P. benceki*) and which may be aligned into a phyletic lineage *P. barrabei* - *P. alanensis* - *P. benceki* and with which *E. ogilviae* shares some visual similarity, *E. ogilviae* differs from all those species by irregularly developed "sporangia". Primary branches in *P. alanensis* are bowl-shaped or budding and in *P. benceki* they are irregularly nodular, in contrast to *E. ogilviae*, in which only one among the secondary branches swells and acquires an irregularly bubble-like shape. Statistically a dozen sections of this species, compared with several hundreds sections of other *Palaeodasy-cladus* species, all from samples from the same locality, does not suggest an infallible firm conclusion. A few specimens in a rich and diversified (on the species level) assemblage may equally indicate a possible specific adaptation of some individuals as well as the early appearance of a possibly new genus.

Stratigraphic position: In the original description, CROS & LEMOINE (1966) mention this species from the Friulian Alps in a rich algal assemblage which they consider to be of a Sinemurian *s. str.* - Lotharingian age. OTT (1974) ascribes this species to the Middle Liassic. In Mt. Velebit, the material figured in Pl. XLI derives from the rich algal assemblage of sample VT-26. Its stratigraphic position has been determined as Lower Liassic (Hettangian - Sinemurian).

**Genus *Selliporella* SARTONI & CRESCENTI,
1962 emend. BARATTOLO et al., 1988**

***Selliporella* ? *problematica* n. sp.**

Pl. XLII, Figs. 1-3

Origin of the name: After problematic taxonomic position.

Type-locality: Main ridge of Mt. Velebit, at the Sv. Rok - Obrovac road, about 100 m in the direction of

Obrovac from the milestone at the Mali Alan Pass (Fig. 7); co-ordinates 44° 17' 24" N, 15° 39' 23" E.

Type stratum: Grey, well-bedded, Lower Liassic (Hettangian - Lower Sinemurian) limestone; alternating skeletal-intraclastic grainstone and mudstone, with sporadically developed stromatolitic laminae. The strata were deposited in a shallow subtidal environment with temporary emergence into vadose zone.

Holotype: tangential-oblique section, figured in Pl. XLII, Fig. 1, thin-section VT-26/400. The holotype, and other material containing the illustrated sections, is stored in the collection of the Institute of Geology, Zagreb.

Diagnosis: Thallus cylindrical, clearly annulated, with obliquely incised annular depressions, some of which may be as deeply cut as to reach the wall of the central cavity. Calcareous annuli (rings) between consecutive annular incisions taper going outward but seem to widen again at the outer end. Each calcareous ring bears one whorl of bipartite branches. Primary branches are irregularly cylindrical, slightly swollen at the proximal ends, and sporadically with larger or smaller bag-shaped excrescences on the lower side. Secondary branches are longer than the primaries and distally widened. The species is cladosporous.

Description: The calcareous skeleton has a cylindrical shape with clearly developed annulation (Pl. XLII, Fig. 1). Annular depressions are obliquely incised into the calcareous envelope, directed downwards, and, some of them, almost reach the wall of the central cavity (Pl. XLII, Fig. 1). Calcareous segments which are inserted obliquely between the annular cavities, taper outwards but become wider at the very distal ends. In the available material, the widenings of the calcareous segments can barely be seen (e.g., Pl. XLII, Fig. 1), because they are heavily reduced due to the destruction of the outer parts of the skeleton. Therefore, the calcareous skeleton, as a whole, gives, in oblique and longitudinal sections, a many-horned appearance. The inner cavity is delimited by a smooth and clearly defined calcareous wall, which occupies about 30% of the outer thallus diameter (Table 16).

Each calcareous segment contains one whorl of branches, which are clearly divided into primary and secondary branches, whereas the third-order branches remain questionable. In Pl. XLII, Fig. 1 (lower left) a group of three pores may be seen, as well as a larger pore lower down, with a tiny pore in the immediate vicinity which may indicate a tertiary branch. Also, the possible existence of the tertiary branches is suggested by widened pores, resulting from the widened distal ends of the secondary branches, which may indicate that the development of tertiary branches has directly influenced the more swollen distal ends of the secondary branches. Primary branches are comparatively

Maximum observed length of thallus	L	11.3
Outer thallus diameter	D	2.06 - 2.40
Inner thallus diameter	d	0.48 - 0.68
Relation	d/D	0.232 - 0.287
Distance between whorls	h	0.60 - 0.96
Diameter of primaries	p	0.24 - 0.34
Length of primaries	l	0.40 - 0.48
Number of primaries in a whorl	w	10 - 12
Diameter of secondary	p'	0.15
Length of secondary	l'	0.82 - 0.86
Number of secondary on a primary	w'	?2 - 3
Diameter of tertiaries	p''	?
Length of tertiaries	l''	?
Number of tertiaries on a secondary	w''	?
Angle of inclination of branches		25° - 40°

Table 16 Main biometrical parameters of *Selliporella? problematica* n. sp. (all dimensions in mm). Remark: Because the species is very rare, the above dimensions have been measured in only three specimens.

regular, of cylindrical shape, as may be seen in the upper part of the holotype (Pl. XLII, Fig. 1), or else more or less irregularly shaped as may be seen in the lower right part of the same section, near the central cavity. There, as well as on the branches of neighbouring segments, one can see the beginning of the development of an irregular swelling, projecting from the lower surface of the proximal part of a branch. The secondary branches are more or less irregularly shaped, differing from segment to segment; they emerge in a more or less dichotomous manner from the distal ends of the primary branches, and are ?2-3 in number (Table 16). In spite of their acrophorous appearance in the figured sections, or even suggesting a slight narrowing toward the distal end, which may be an artifact of the section, they probably still widen distally and give rise to the tertiary branches, as has been mentioned above. In several pores of the primary branches indications of cysts may be found, which would support the cladospory of this species.

Similarities and differences: The distinctly segmented thallus (calcareous skeleton) and from the shape of some branches this species appears similar to *Selliporella donzellii* SARTONI & CRESCENTI. In addition to clearly developed segmentation (annulation), the similarity also refers to a comparatively small number of pores per unit of the outer surface of calcareous segments, as seen in shallow tangential (cortical) sections, and to the shape of the pores of some primary branches in deep tangential sections, near the central cavity (Pl. XLII, Fig. 1). Further similarity with *Selliporella donzellii* concerns the beginning of the development of a small, irregular excrescence projecting down from the lower surface of some primary branches, though a similar feature may also be developed in some specimens of

Palaeodasycladus mediterraneus var. *mediterraneus*. A clear difference between this species and *Selliporella donzellii* is, on the one hand, the much more strongly and regularly developed bag-shaped excrescence in the latter, hanging down from the proximal part of the primary branches (BARATTOLO et al., 1988, fig. 3); on the other hand, the new species has retained several branches very similar to those in *P. mediterraneus*. The main difference to *S. donzellii*, and at the same time a further similarity with *P. mediterraneus*, would be the existence of third-order branches, which, however, cannot be unequivocally ascertained (though the indications pointing to their existence in *Selliporella? problematica* are rather strong). All these characters clearly show the connection of *S.? problematica* with *P. mediterraneus* on the one hand and its similarity with *S. donzellii* on the other, thus giving *S.? problematica* an intermediate position. *S.? problematica* most likely evolved from *P. mediterraneus* and probably gave rise to *S. donzellii*. This alga is very rare; it is represented by only a few sections in numerous slices and among numerous sections of other species; its scarcity makes deeper analysis very difficult. However, this scarcity alone suggests that it is a new form. Thus the small number of specimens is not surprising, because it is a well known fact that new forms arise as a result of separation or, possibly, deviation of individual specimens, whereas the bulk of the ancestral forms will either keep on evolving in their own lineage or soon become extinct.

Stratigraphic position: This alga occurs in the rich algal assemblage of sample VT-26, belonging to the lower part of the Lower Liassic. This is supported by the position of the assemblage in the stratigraphic column (Fig. 2)

**Genus *Humiella* SOKAČ & VELIĆ, 1981 emend.
MASSE et al., 1984**

***Humiella japodica* n. sp.**

Pl. XLII, Figs. 4-8

Origin of name: The name recalls the ancient Illyric tribe of Iapodes, who had their settlements in the northern foothill of Mt. Velebit and also frequently settled on the mountain itself.

Type locality: Mt. Velebit, east of trigonometric point Jadičevac (1,274 m), on a forest road crossing the main ridge of Mt. Velebit between Baške Oštarije and Bužinsko Bilo and joining the longitudinal road Jadovno - Kalanjeva Ruja (Fig. 8); co-ordinates: 15°12'27" E; 44°33'18" N.

Type strata: Dark grey, well-bedded limestone, often turned into late diagenetic dolomite, represented by alternation of peloidal-skeletal wackestones and oolite, sporadically ooid-skeletal grainstone (Fig. 2). Mudstone occur as rare lenses or thin intercalations. The algal-bearing sample is an ooid-peloidal-skeletal grainstone. Skeletal particles are predominantly represented by fragments of gastropods and calcareous algae. The stratigraphic position of the algal-bearing sample, between the Upper Triassic dolomite and the first occurrence of Middle Liassic foraminiferal assemblage, is suggested to be Hettangian in age.

Holotype: The oblique-transverse section figured in Pl. XLII, Fig. 6, slide JD-13/14. This slide, as well as other slides containing the figured paratype material, is stored in the collection of the Institute of Geology, Zagreb. Because of the scarcity of the available material, the following description is based on only 7 sections.

Diagnosis: The calcareous skeleton consists of a central tube which bears individualised branches, swollen proximally and tapering distally, of a generally piriform appearance of the whole alga. Branches touch mutually where thickest, but toward the exterior they become thin, pointed, and well separated, producing the appearance of a spinose club. In neighbouring whorls, branches are arranged in alternating positions. Calcareous en-

velopes of individual branches are perforated by tiny tubules.

Description: The calcareous skeleton of this alga consists of a central cylindrical tube, which bears dense, mutually alternating, piriform-shaped branches which taper and become pointed outwards. This gives this alga the appearance of a spinose cylinder, or even a cylindrical spinose club. The central cavity looks regular and clearly delimited, occupying about 25-35% of the total thallus diameter (Table 17).

The entire structure results from the existence of undivided piriform branches with tapering ends pointing outwards (Pl. XLII, Fig. 4). Branches are comparatively large, with regard to general dimensions, with rounded bases and swollen in their lower proximal parts. At this level the branches appear tightly packed and in mutual contact (Pl. XLII, Figs. 4-5). Further outwards, the branches gradually, but apparently not uniformly, taper to a more or less pointed termination (Pl. XLII, Fig. 4). In the outer region of the thallus (in the first half of their length), the envelopes of the branches mutually touch no longer, and are fully individualised, producing smaller pores and independent circular sections of their calcareous envelopes in tangential sections. The calcareous envelopes of individual branches are perforated by numerous tiny and short tubules directed perpendicularly to the surface (Pl. XLII, Fig. 5). As a result of recrystallisation and a partly destroyed central wall, these tubules could not be seen with certainty in all sections. The species is probably cladosporeous.

Similarities and differences: Its skeletal structure, individualised branches, and overall appearance of the thallus, and particularly the existence of tiny tubules perforating the calcareous envelopes of the branches, suggest that *Humiella japodica* n. sp. unquestionably belongs to the genus *Humiella*. The existence of such perforations in the envelopes of branches and in the wall of central cavity has been established by MASSE et al. (1984) as an essential feature of the genus *Humiella*, and is illustrated by SOKAČ (1987) in a more complete description of the type-species. *H. japodica* clearly differs from all other, though not numerous species ascribed to this genus and, moreover, has the

Outer thallus diameter	D	0.62 - 1.70
Inner thallus diameter	d	0.20 - 0.48
Relation	d/D	0.241 - 0.385
Distance between whorls	h	0.15 - 0.24
Diameter of primaries	p	0.17 - 0.35
Length of primaries	l	0.28 - 0.45
Number of primaries in a whorl	w	6 - 7

Table 17 Main biometrical parameters of *Humiella japodica* n. sp. (all dimensions in mm).

lowest (= oldest) stratigraphic position. It differs from *H. teutae* SOKAČ & VELIĆ (the type-species) by being generally much smaller and by having swellings and taperings of the branches in reverse order. This latter feature is valid also in comparison with *H. sar-diniensis* (OTT & FLAVIANI), *H. dalmatarum* (SOKAČ & VELIĆ) and *H. catenaeformis* (RADOIČIĆ, 1967) MASSE et al. 1984. Moreover, those species have more strongly developed perforations of the central stem and in the envelopes of the branches. As regards the inadequately known and problematic *Humiella? pupnatensis* SOKAČ, the differences are also clear, as *H. pupnatensis* (= *Similiclypeina pupnatensis* (SOKAČ) BUCUR, 1993) is said to have 2-3 whorls of smaller branches alternating with whorls of longer, horn-like, more or less autonomous branches. And finally, in spite of the fact that the stratigraphic position has no significance for determination and differentiation of species, it nevertheless may be a useful indication in an early stage of determination.

Stratigraphic position: *Humiella japodica* n. sp. has been discovered east of Jadičevac, in the central part of Mt. Velebit, in Lower Liassic deposits containing numerous *P. mediterraneus* var. *mediterraneus*, *P. dolomiticus* and *P. asteriscus*. The position of the sample with *H. japodica* in the stratigraphic column is about 40 m above the boundary with the Upper Triassic dolomite and about 130 m below the first occurrence of the foraminiferal assemblage marking the beginning of the Middle Liassic. The age corresponds to the Hettangian.

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PLATE I

1-5 *Palaeodasycladus mediterraneus* (PIA, 1920) 1927 var. *mediterraneus*

- 1 Longitudinal, somewhat oblique, section. The gradual increase of the thallus diameter and wall thickness upwards along the thallus produces a club-shaped thallus. Short, slightly developed primary branches bear phloiophorous, seemingly articulated, secondary and tertiary branches. TG-9/5, x17.
- 2 Oblique-tangential section. Various shaped primary branches of variable size on both left and right side of the section. Long secondary branches slightly thicken distally. VT-26/252, x14.
- 3-4 Oblique sections. Large, cylindrical, primary branches bear bundles of 2-5 phloiophorous secondaries, which, in turn, give rise to short, also phloiophorous, tertiaries. 3: JD-13, x22; 4: JD-8/2, x22.
- 5 Oblique-tangential section. Slightly oblique (ca. 25°), cylindrical primary branches bear phloiophorous secondary branches which emerge without a visible basal constriction. From their distal end, tertiary branches with constricted bases emerge. In large pores of the primaries (3 lowermost rows) groups of cysts can be seen (see enlarged detail in Pl. XIV, Fig. 1). This section correlates with PIA's reconstruction (PIA, 1920, fig. 22). JD-14/1, x14.

Sample localities and ages

TG: Mt. Trnovski Gozd (western Slovenia), Middle Liassic.

VT-26: Mali Alan Pass, central Mt. Velebit, Lower Liassic.

JD-14: Jadičevac, central Mt. Velebit, Lower Liassic.

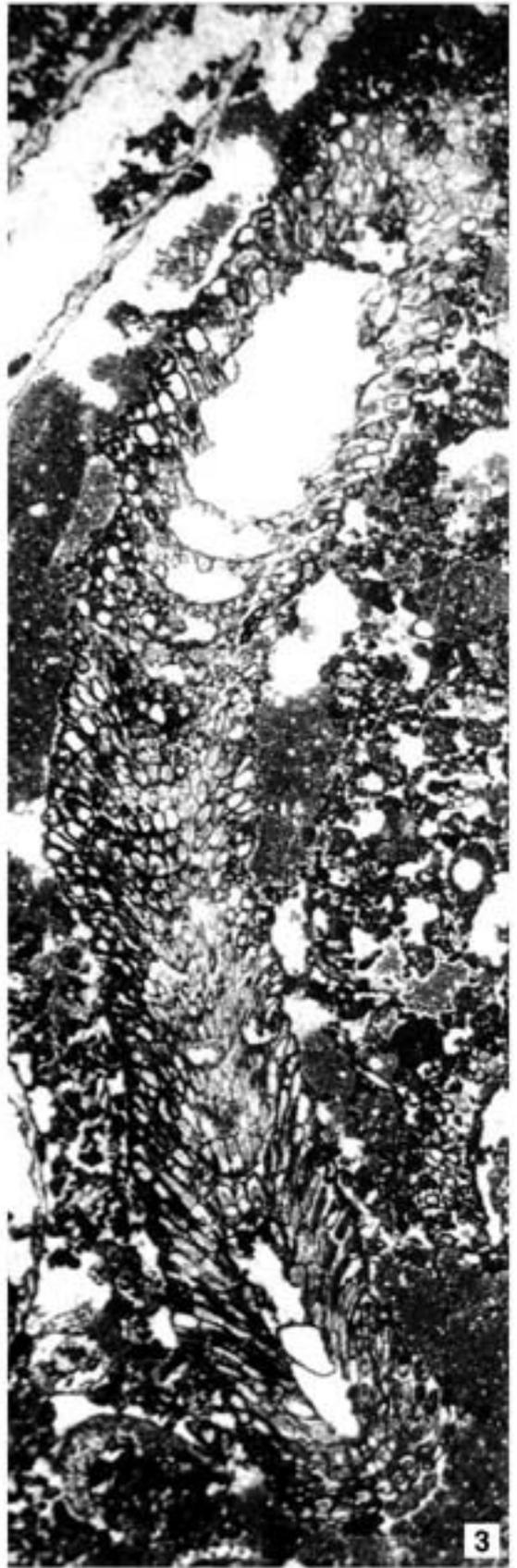
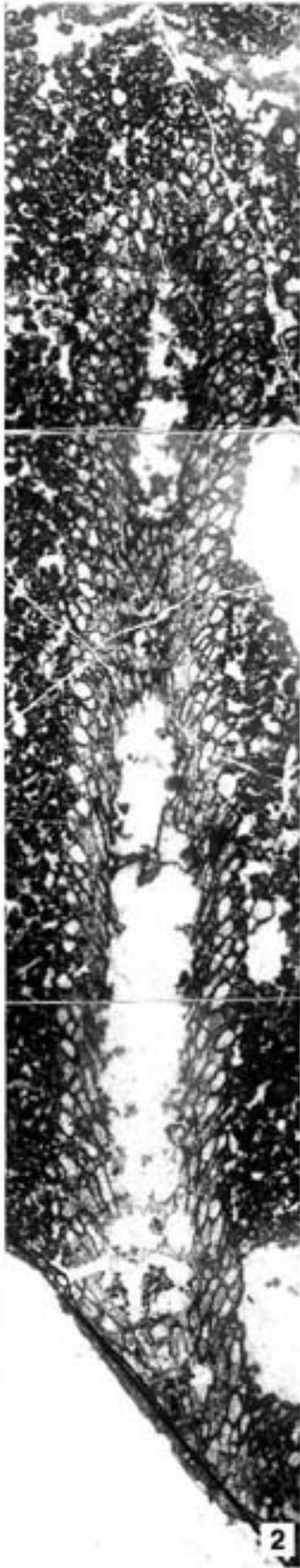


PLATE II

1-3 *Palaeodasycladus mediterraneus* (PIA, 1920) 1927 var. *mediterraneus*

- 1 Tangential section. Note the increase in diameter of the second- and third-order branches. TG-9/2, x14.
- 2 Longitudinal-oblique section. Note the second- and third-order branches with distally increasing diameter. TG-8, x14.
- 3 Oblique tangential section. In the lower part of the thallus, cylindrical, obliquely situated, primary branches are preserved, which bear seemingly articulated secondary and tertiary branches. In this part of the thallus, the inner wall of the central cavity is preserved (small inner diameter). In the upper part of the thallus, the central cavity appears much wider, because of the destruction of the inner surface and primary branches, of which only the contour is still visible. The morphology in the lower part of the thallus agrees with the reconstruction by PIA (1920, fig. 22). TG-9/3, x17.

Sample locality and age

Mt. Trnovski Gozd, western Slovenia. Middle Liassic.

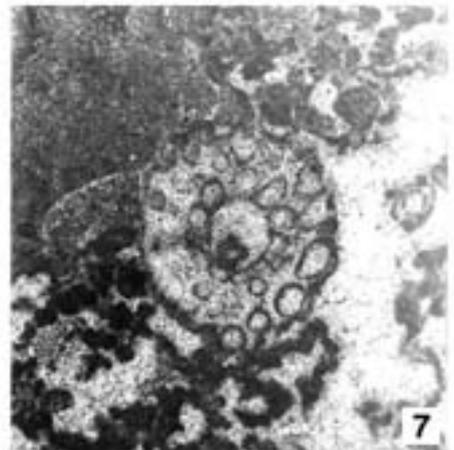
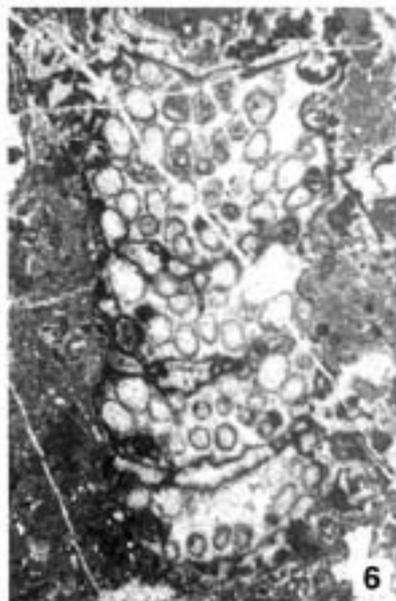
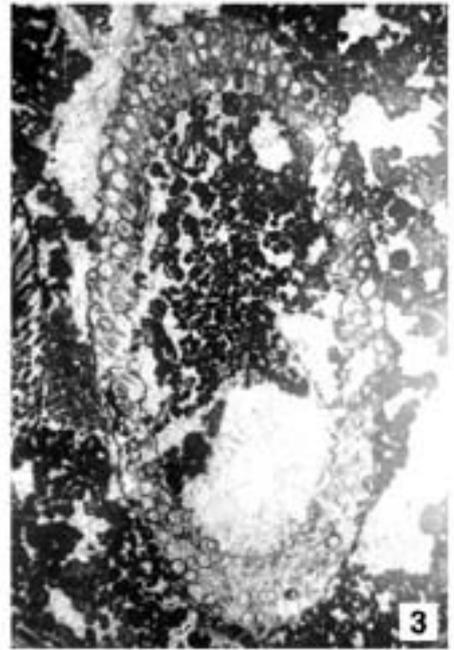
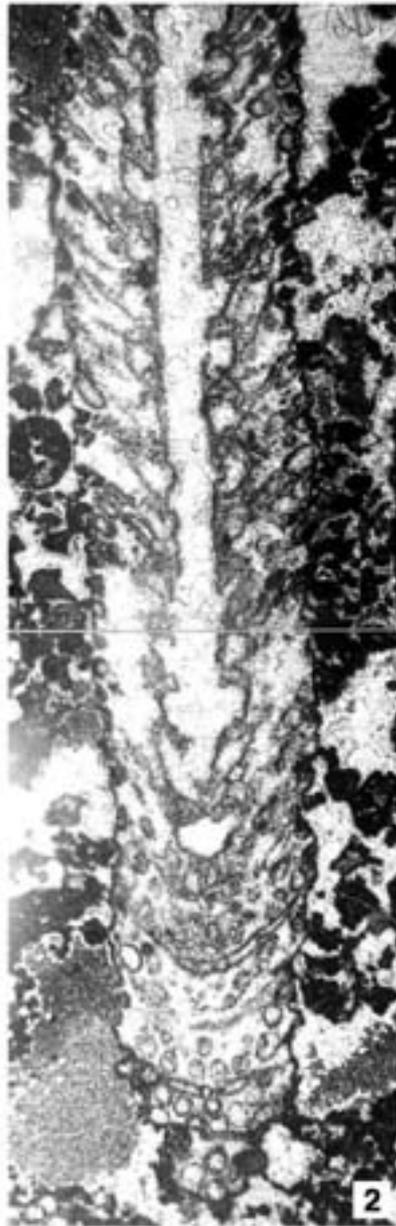


PLATE III

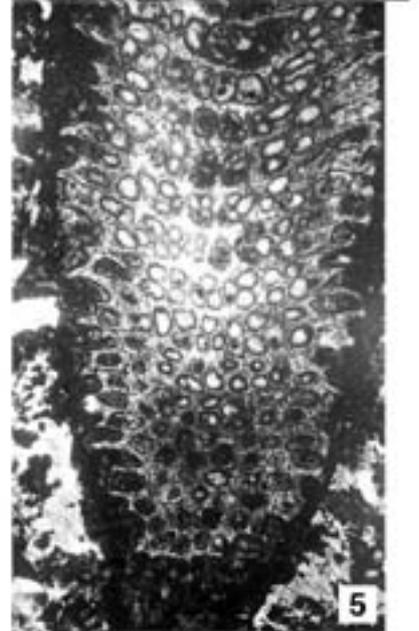
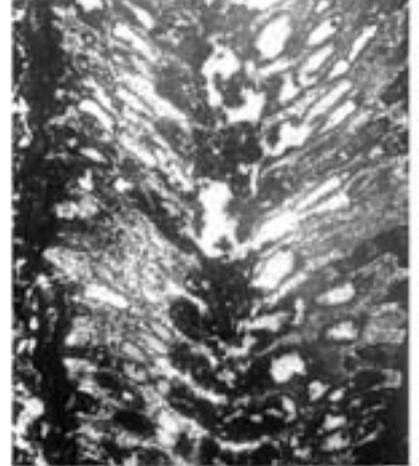
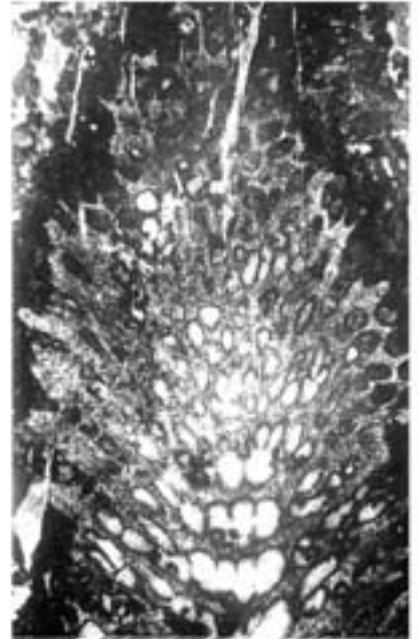
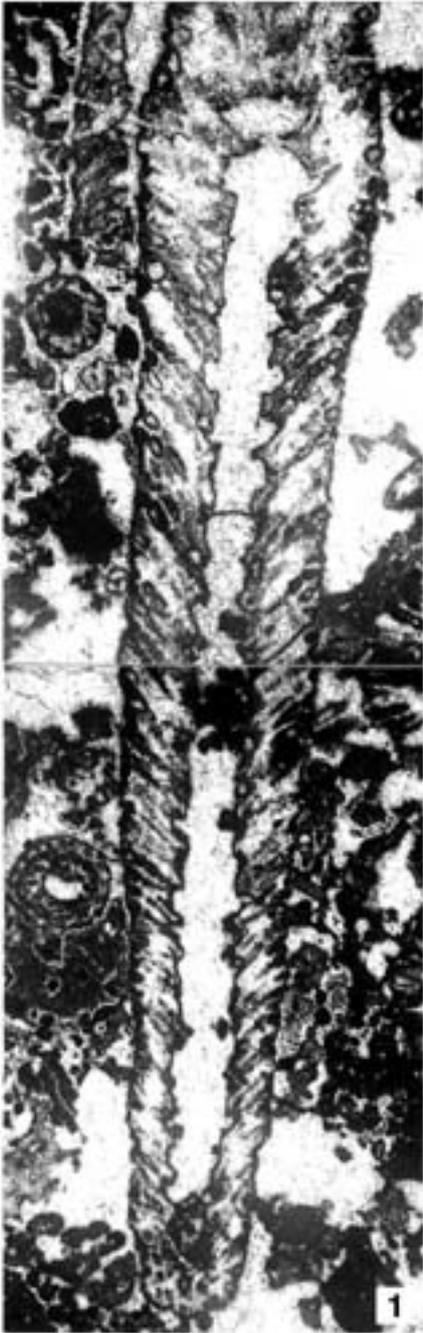
1-7 *Palaeodasycladus mediterraneus* (PIA, 1920) 1927 var. *mediterraneus*

- 1 Oblique tangential section. Cylindrical to club-shaped phloiophorous primary branches arranged in loosely spaced whorls. Bundles of 4 secondary branches can be seen in the tangential part of the section. VT-26/204, x17.
- 2 Longitudinal tangential section. Short, kidney-shaped or irregular primary branches; some are slightly bent in proximal part. In the tangential part of the section (lower part of the figure) fissures can be seen, either as inceptions or relics of possible annulation. TG-9/10, x22.
- 3 Oblique section. Specimen with destroyed primary and secondary branches, resulting in a very wide central cavity. Such sections are ill-suited for determination. TG-9/18, x14.
- 4 Oblique section. Cylindrically shaped primary branches bear clearly phloiophorous secondaries and tertiaries which seem articulated (an optical illusion). VT-26/118, x22.
- 5 Tangential section with visibly undulated outer surface of the skeleton. VT-26/17, x17.
- 6 Tangential section with irregularly spaced narrow fissures (possible inceptions or relics of annulation). TG-9, x22.
- 7 Transverse, slightly oblique section. Lower part of the thallus may have a smaller number of primary branches per whorl and lower degree of ramification. TG-9/20, x34.

Sample locality and ages

VT-26: Mali Alan pass, central Mt. Velebit, Lower Liassic.

TG-26: Mt. Trnovski Gozd, western Slovenia. Middle Liassic.



1

2

5

3

4

PLATE IV

1-6 *Palaeodasycladus mediterraneus* (PIA, 1920) 1927 var. *mediterraneus*

- 1 Oblique longitudinal section. Note the clear increase in diameter of the primary branches from bottom to top of thallus, resulting in the ever more reduced thickness of the calcareous partitions between the whorls and in the destruction in the region of primary branches. This is contrary to annulation being a primary feature (see the upper part of the thallus). VT-26/14, x22.
- 2 Longitudinal section, showing the increase of the outer thallus diameter (club-shaped thallus) and of the primary branch diameter from bottom to top of the thallus. Destroyed primary, and partly also secondary, branches in the top part of thallus do not indicate the existence of intusannulation or insufficient calcification of the primaries. VT-26/264, x17.
- 3 Longitudinal-oblique section with preserved inner wall (wall of the central cavity) and partly, and to a different extent, the destroyed region of the primary branches, producing a visual impression of intusannulation. TG-9/27, x22.
- 4 Oblique section with preserved wall of the central cavity, partly preserved proximal parts of partitions between the primary branches, and destroyed region of the primary and, partly, secondary branches. Primary branches are still partly visible. This section contradicts the existence of intusannulation and insufficient calcification. VT-26/40, x14.
- 5 Longitudinal-tangential section with preserved partitions between neighbouring whorls and erased walls of the central cavity. This feature has been incorrectly interpreted as intusannulation. VT-26/39, x22.
- 6 Longitudinal section. The right side shows the preserved wall of the central cavity and the entire region of primary and secondary branches, which is on the left side partly to completely destroyed. This section also contradicts the existence of intusannulation. Secondary and tertiary branches are visible, with sporadic indication of the existence of the fourth-order branches. VT-26/299, x17.

Sample localities and ages

VT-26: Mali Alan Pass, central Mt. Velebit, Lower Liassic.

TG: Mt. Trnovski Gozd, western Slovenia, Middle Liassic.

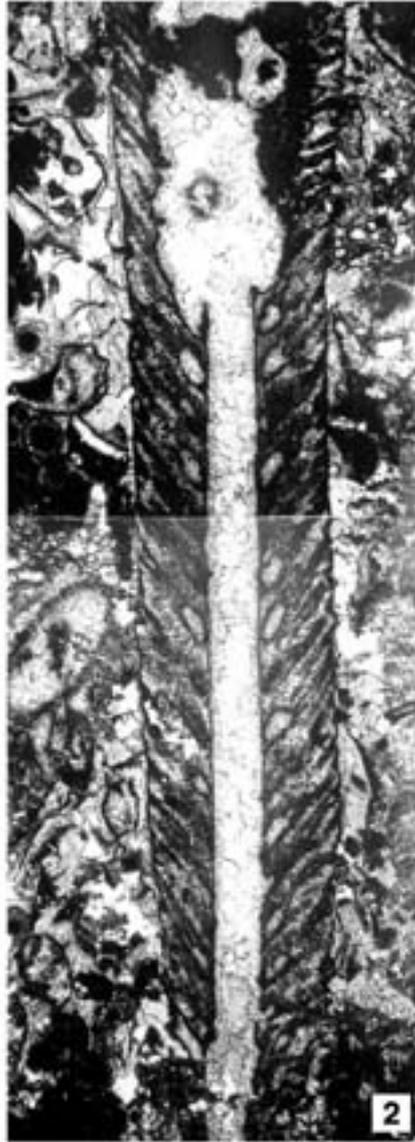


PLATE V

1-5 *Palaeodasycladus mediterraneus* (PIA, 1920) 1927 var. *mediterraneus*

- 1 Oblique tangential section of a specimen with strongly irregular primary and secondary branches. In the basal part, bundles of 4 secondary branches may be seen. This is a unique specimen amongst hundreds of more regular ones. VT-26/43, x22.
- 2 Longitudinal-oblique section of a specimen with steeply inclined primary branches the diameter of which decreases from the bottom to the top of the thallus. Primary branches taper distally and give rise to long, acrophorous to slightly phloiophorous, secondary branches. VT-26/40, x17.
- 3 Longitudinal-oblique section with cylindrical and conical primary branches, which give rise to long, slightly phloiophorous, secondary branches, which, in turn, bear short, phloiophorous tertiaries. VT-26/384, x17.
- 4 Longitudinal-oblique section. Note the increase of diameter and change in shape of primary branches from the bottom to the top of the thallus. In the basal part, primary branches are preserved. With their increasing diameter the envelopes of branches between the neighbouring whorls are destroyed whereas the wall of the central cavity is still preserved. This section denigrates the existence of intusannulation or insufficient calcification of the region of primary branches. VT-26/362, x17.
- 5 Tangential section. Pores of primary branches partly arranged in vertical rows, located one above the other, and partly approaching the alternating position. Sporadically, in the pores of primary branches, individual cysts may be seen. JD-6B/5, x17.

Sample localities and ages

VT-26: Mali Alan pass, central Mt. Velebit, Lower Liassic.

JD-6B: Jadičevac, central Mt. Velebit, Lower Liassic.

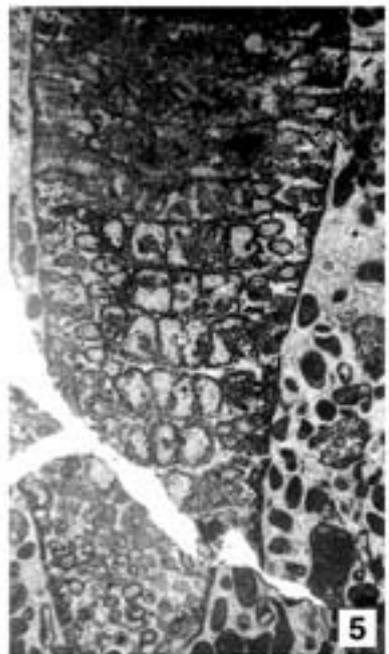
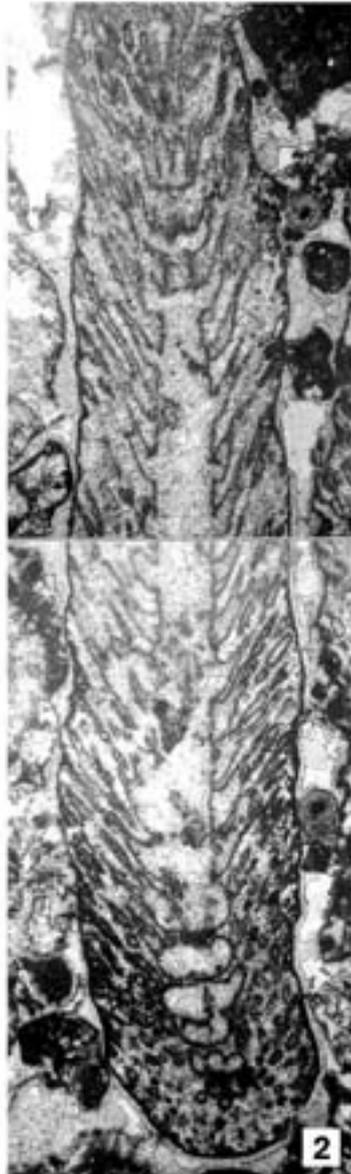
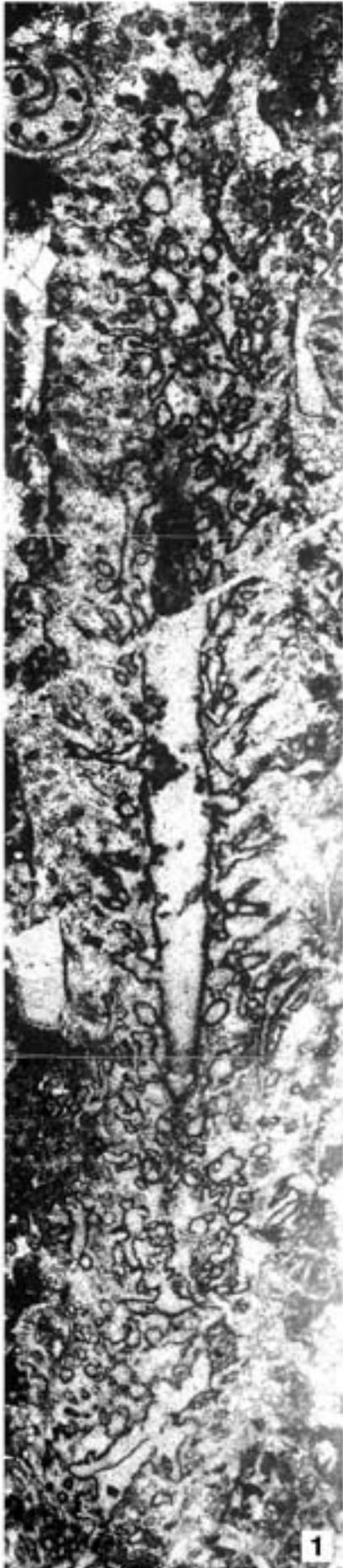


PLATE VI

1-6 *Palaeodasycladus mediterraneus* (PIA, 1920) 1927 var. *mediterraneus*

- 1 Longitudinal sections with cylindrical and kidney-shaped primary branches bearing long phloiophorous secondaries and short phloiophorous tertiaries. VT-26/27, x34.
- 2, 6 Oblique sections with elongated and comparatively thin primary branches, giving rise to phloiophorous secondary, constricted at the base. Secondary branches are grouped into bundles. 2: TG-9/12, x34; 6: VT-26/54A, x34.
- 3 Longitudinal section with cylindrical primary branches, some are curved at the base. VT-26/142, x22.
- 4 Longitudinal section with irregular, often steeply inclined, primary branches, with broad bases opening into the central cavity. The wall of the central cavity is probably partly destroyed. Short secondary branches bear "articulated", phloiophorous, tertiaries. TG-9/5, x34.
- 5 Longitudinal-oblique section of a specimen with heart-shaped and irregular short primary branches giving rise to well-developed secondary branches which, in turn, bear articulated, phloiophorous, tertiary branches. Central cavity well delineated and straight. TG-9/19, x34.

7-8 *Palaeodasycladus mediterraneus* var. *illyricus* (SOKAČ & NIKLER, 1966) n. comb.

- 7-8 Oblique sections with swollen-nodular primary branches, bearing longer, phloiophorous secondary branches, which, in turn, bear short, phloiophorous, tertiary branches. 7: VT-26/27, x34; 8: JD-4B, x17.

Sample localities and ages

VT-26: Mali Alan Pass, central Mt. Velebit, Lower Liassic.

JD-4: Jadičevac, central Mt. Velebit. Lower Liassic.

TG: Mt. Trnovski Gozd, western Slovenia, Middle Liassic.

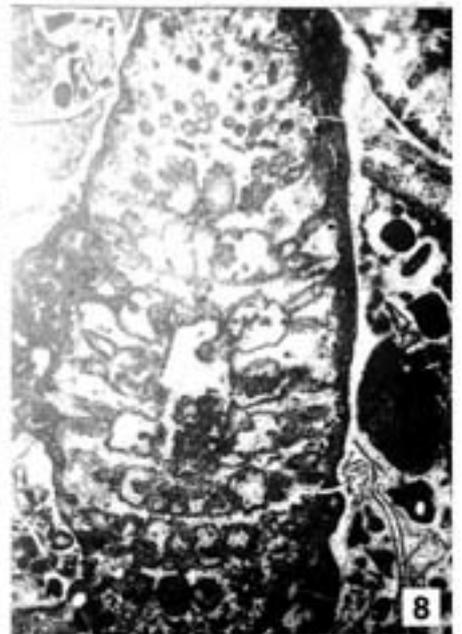
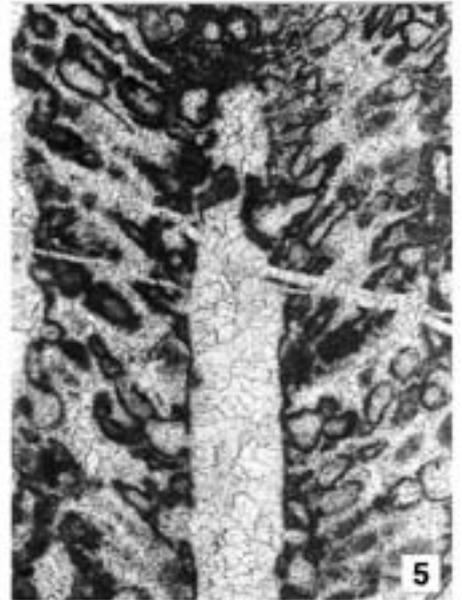
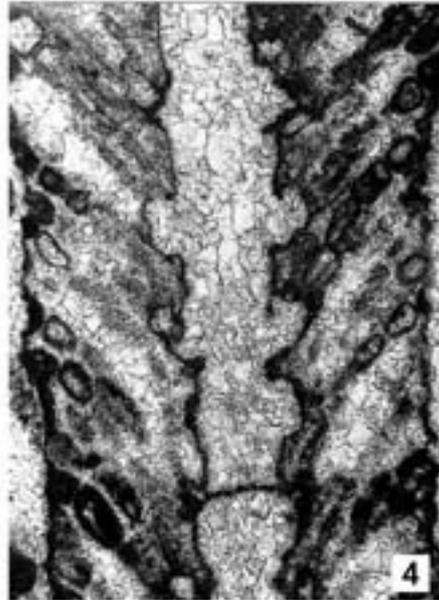


PLATE VII

1-2, 4 *Palaeodasycladus mediterraneus* var. *heraki* (SOKAČ & NIKLER, 1966) n. comb.

- 1 Oblique section. Rectangular primary branches bear bundles of secondary branches, constricted at the base. In the cavities of the primary branches, individual preserved cysts can be seen. VT-26/118, x34.
- 2 Longitudinal section. Rectangular primary branches of various size; comparatively thick, roughly shaped secondaries bear very short tertiaries. VT-26/428, x34.
- 4 Oblique section with a comparatively well-preserved central cavity and individual cysts in the pores of the primary branches. VT-26/428, x34.

3, 5-9 *Palaeodasycladus mediterraneus* (PIA, 1920) 1927 var. *mediterraneus*

- 3 Oblique section. Note club-shaped primary branches bearing equally large secondary branches. JD-17A, x22.
- 5 Longitudinal-oblique section of a specimen with preserved central cavity and elliptical-cylindrical primary branches and phloioferous to acrophorous secondaries, constricted at the base. VT-26/400, x34.
- 6-8 Longitudinal sections. Specimens with cylindrical and kidney-shaped primary branches, more or less bent in the proximal part. Long, tubular secondary branches of constant diameter bear short tertiaries. 6: VT-26/144, x22; 7: VT-26/47, x34; 8: TG-9/1, x34.
- 9 Oblique section. Note clearly club-shaped primary branches bearing bundles of comparatively short secondaries. The zone of distal branches is probably abraded. VT-26/454, x34.

Sample localities and ages

VT-26: Mali Alan Pass, central Mt. Velebit, Lower Liassic.

JD-17A: Jadičevac, central Mt. Velebit, Lower Liassic.

TG: Mt. Trnovski Gozd, western Slovenia, Middle Liassic.



PLATE VIII

1 *Palaeodasycladus anae* (SOKAČ, 1988) n. comb.

- 1 Longitudinal tangential section of a specimen with variously shaped primary branches, some of which branch off up to fourth-order branches. In the pores of some primary branches groups of cysts can be seen. VT-26/328, x14.

2-8 *Palaeodasycladus mediterraneus* (PIA, 1920) 1927 var. *mediterraneus*

- 2 Longitudinal section. Enlarged detail of Pl. V, Fig. 1, showing heavily deformed and extremely variable primary branches. VT-26/43, x34.
- 3, 5 Fig. 3. is enlarged detail of Fig. 5: oblique section of a micritized specimen with preserved central cavity and variously shaped primary branches, some of which show higher-order branching than others. VT-26/344; 3: x34; 5: x14.
- 4 Oblique-tangential section of a specimen with completely preserved central cavity and clearly visible connecting pores between primary branches and the central cavity. Primary branches have irregular and strongly widened distal terminations. VT-26/407, x22.
- 6 Transverse, somewhat oblique section, of a specimen with small primaries, large secondary, and short and thin tertiaries. VT-26/114, x22.
- 7 Part of a longitudinal section. Conical and cylindrical primary branches bear clearly phloiophorous secondaries, some of which show partial constrictions. Tertiary branches are short and have a small diameter. VT-26/35, x34.
- 8 Transverse-oblique section of a micritized specimen with thin, phloiophorous branches, clearly grouped into bundles at the second- and third- order branches. VT-26/221, x17.

Sample locality and age

Mali Alan Pass, central Mt. Velebit, Lower Liassic.

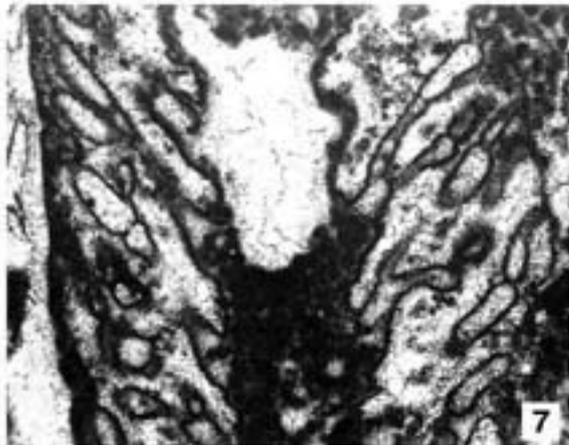
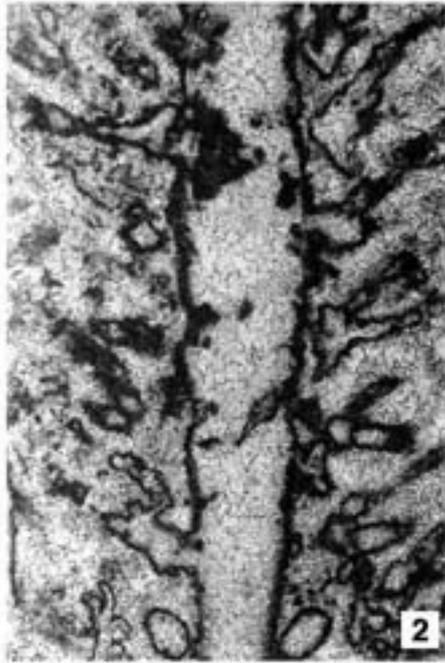
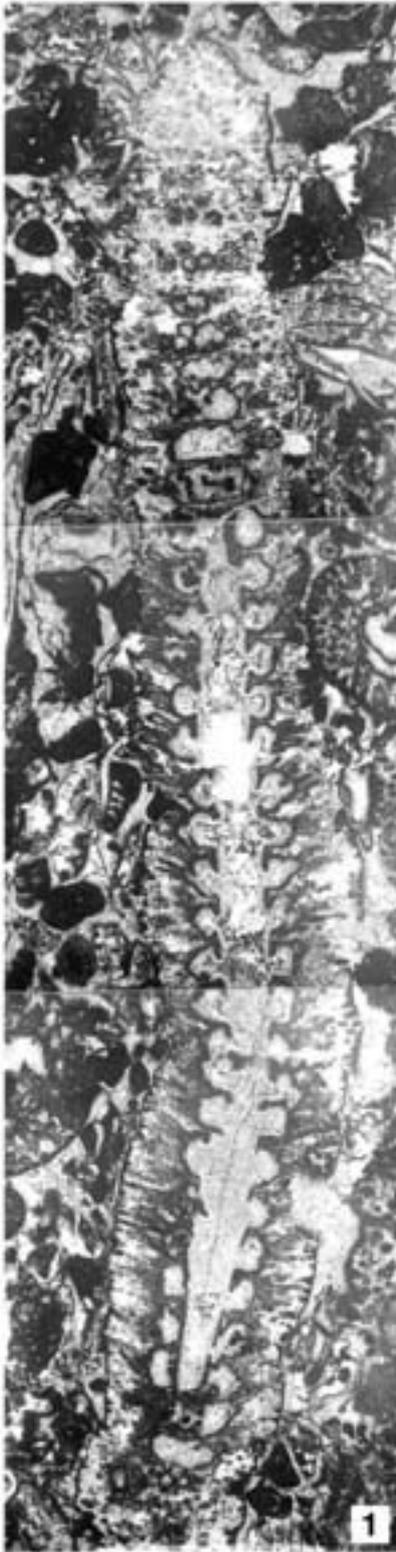


PLATE IX

1, 8 *Palaeodasycladus mediterraneus* (PIA, 1920) 1927 var. *mediterraneus*

- 1 Part of a longitudinal section of a specimen with irregular primary branches, elongated in the direction of growth. VT-26/426, x34.
- 8 Part of a longitudinal section with elongated cylindrical and irregular primary branches (left and right side are not identical). Secondary branches are either constricted at the base or finger-shaped, i.e. growing out like continuations of the primaries. VT-26/422, x34.

2-3, 5-7, 9-10 *Palaeodasycladus mediterraneus* var. *illyricus* (SOKAČ & NIKLER, 1966) n. comb.

- 2-3, 5-6, 9 Oblique sections of specimens with bubble-shaped (elliptical) primaries (?); whorls spaced at regular intervals but rather far apart from each other. Note secondary branches grouped into bundles in some specimens (Figs. 5-6, 9). 2: VT-26/88, x22; 3: VT-26/297, x17; 5: VT-26/266, x17; 6: OB-9619/42, x22; 9: VT-26/83, x17.
- 7, 10 Transverse, somewhat oblique sections. Bubble-shaped (elliptical) primary branches bear secondary branches characterised by constrictions. In the marginal part of the sections, short tertiary branches, grouped into bundles, can be seen (Fig. 7). Both sections show a comparatively small number of primary branches (11-12) per whorl. 7: GO-759/3, x22; 10: VT-26/126, x22.

4 *Palaeodasycladus mediterraneus* var. *heraki* (SOKAČ & NIKLER, 1966) n. comb.

- 4 Oblique section of a specimen with a micritized region of secondary and tertiary branches. VT-26/25, x22.

Sample localities and ages

VT-26: Mali Alan Pass, central Mt. Velebit, Lower Liassic.

OB-9619: Dušice, central Mt. Velebit, Lower Liassic.

GO-759: Rujanska Kosa, east of trigonometric point 940, Mt. Velebit, Lower Liassic.

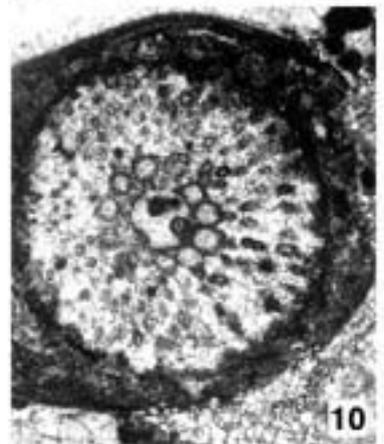
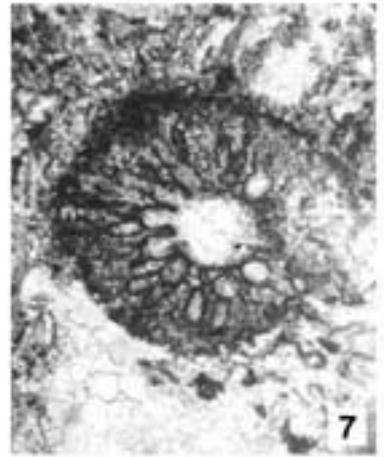
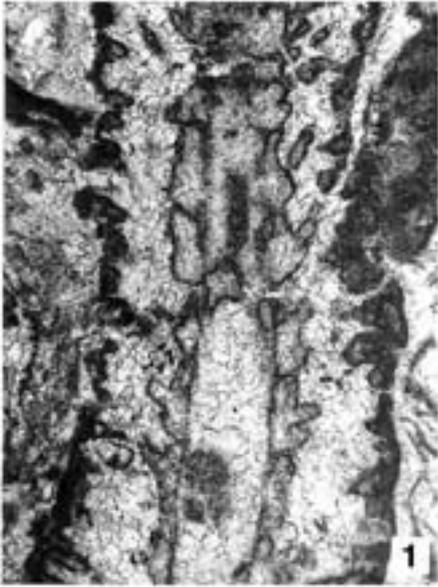


PLATE X

1-6 *Palaeodasycladus mediterraneus* var. *mediterraneus*

- 1 Oblique section of a specimen with entirely preserved central cavity, variously shaped primary branches, clearly phloiophorous secondaries, and strongly swollen tertiaries. TG-9/21, x14.
- 2 Oblique-tangential section of a specimen with short primary branches with variably shaped distal ends. Secondary branches, thinner in lower part of the thallus and thicker in the upper part, bear bundles of short, phloiophorous tertiaries. VT-26/375, x17.
- 3 Longitudinal-tangential section, with entire axial cavity and gradational diameter and shape of primary branches from the bottom to the top of thallus. Secondary and tertiary branches are phloiophorous. VT-26/408, x22.
- 4-6 Oblique sections of specimens in which the different shapes of primary branches, shorter or longer secondary and tertiary branches, more or less clearly grouped into bundles, can produce differences in the appearance of specimens in identically orientated sections. 4: VT-26/111, x34; 5: VT-26/204, x22; 6: GO-8719, x14.

Sample localities and ages

TG: Mt. Trnovski Gozd, western Slovenia, Middle Liassic.

VT-26: Mali Alan Pass, central Mt. Velebit, Lower Liassic.

GO-8719: Ivanova Draga, central Mt. Velebit (north of village Sušanj), Middle Liassic.

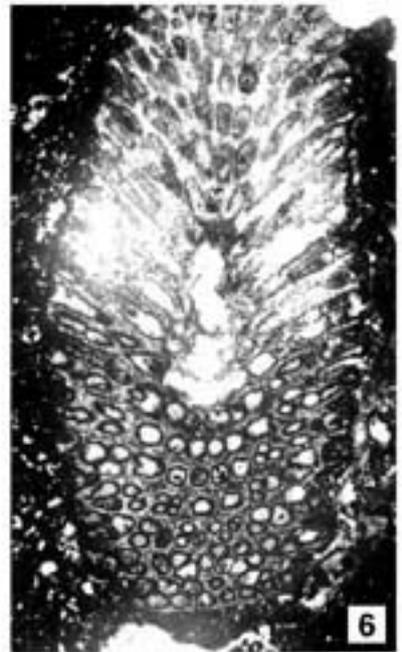


PLATE XI

1-13 *Palaeodasycladus mediterraneus* var. *mediterraneus*

- 1 Transverse section of a specimen in which some primary branches show incipient ramifications that allow possible interpretation as being very short secondary branches which give rise to thin, acrophorous tertiaries and even quaternaries. Note that the branches of the same whorl are not identical. VT-26/229, x17.
- 2-4 Transverse sections. The number of primary branches in a whorl varies from 14-16. 2: VT-26/226, x22; 3: VT-26/166, x22; 4: VT-26/102, x22.
- 5-8 Transverse sections of specimens with variously shaped primary branches. Secondary branches are, as a rule, longer than the tertiaries, which are especially short in Fig. 6. 5: VT-26/123, x22; 6: VT-26/68, x34; 7: VT-26/88, x22; 8: JD-15B, x22.
Remark: Transversal sections are not suitable for reliable determination. Thus the section in Fig. 6 may possibly belong to *P. anae*.
- 9-12 Transverse sections of specimens with secondary and tertiary branches varying in size. 9: VT-26/51, x22; 10: TG-9/24, x22; 11: VT-26/273, x17; 12: VT-26/108, x22.
- 13 Transverse section of a specimen with regular branches. Secondary branches, all of the same size and shape, bear bundles of short, phloioferous, tertiaries. OB-9619/21, x22.

Sample localities and ages

VT-26: Mali Alan Pass, central Mt. Velebit, Lower Liassic.

JD-15B: Jadičevac, central Mt. Velebit, Lower Liassic.

TG: Mt. Trnovski Gozd, western Slovenia, Middle Liassic.

OB-9619: Dušice, central Mt. Velebit, Lower Liassic.

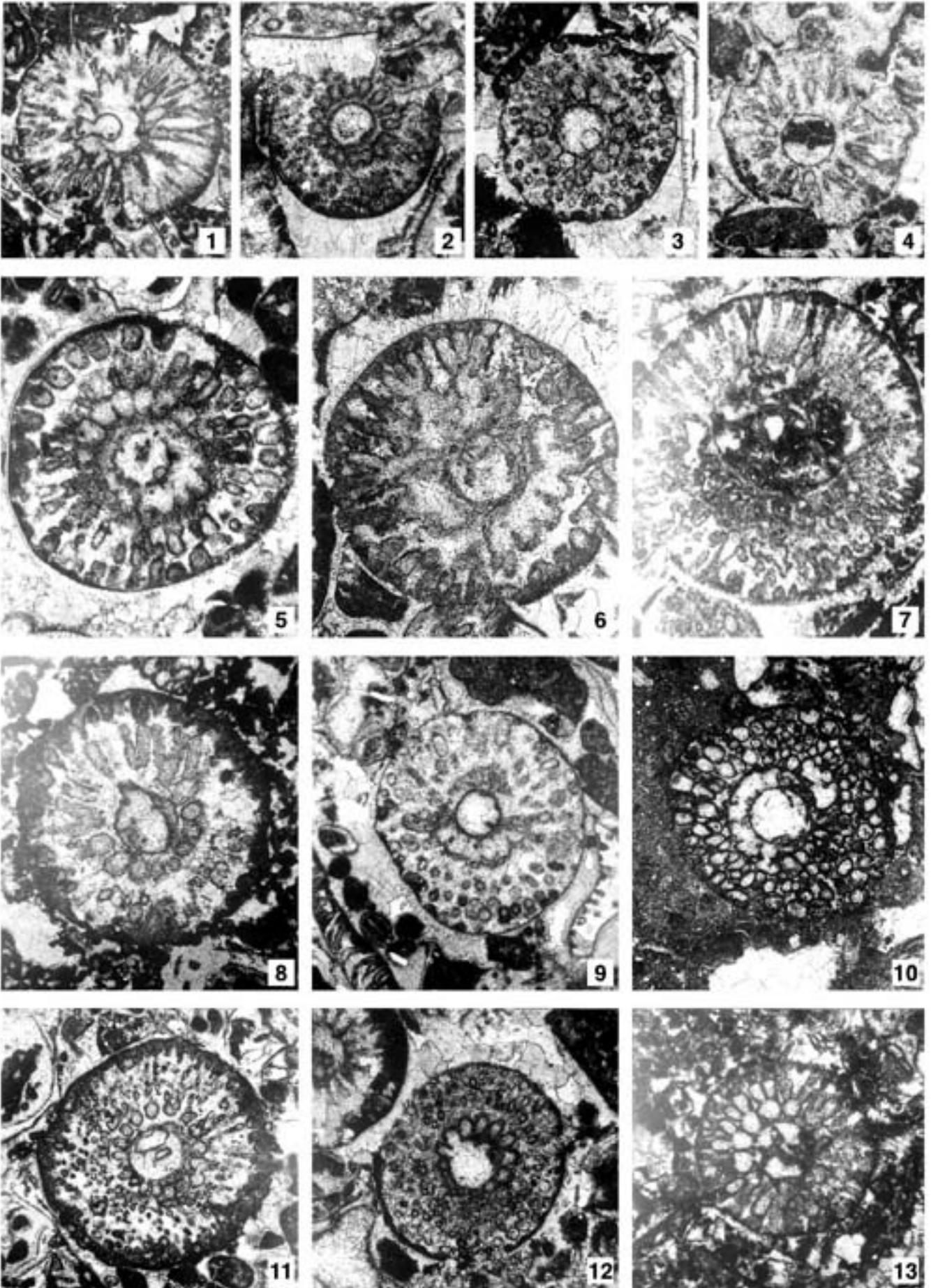


PLATE XII

1 *Palaeodasycladus mediterraneus* var. *heraki* (SOKAČ & NIKLER, 1966) n. comb.

1 Oblique tangential section. Bundles of secondary branches are clearly visible. VT-26/188, x22.

2-5, 6A *Palaeodasycladus mediterraneus* (PIA, 1920) 1927 var. *mediterraneus*

2-6A Oblique sections of specimens with similarly shaped primary branches and visible bundles of secondary branches, giving, seemingly, the appearance of articulation. 2: JD-8/6, x17; 3: TG-9/14, x34; 4: TG-9/10, x34; 5: TG-9/5, x17; 6A: TG-9/17, x34.

6B *Palaeodasycladus mediterraneus* var. *gracilis* (CROS & LEMOINE, 1967
ex GRANIER & DELOFFRE 1993) n. stat.

6B Transverse, somewhat oblique section. TG-9/17, x34.

Sample localities and ages

VT: Mali Alan Pass, central Mt. Velebit, Lower Liassic.

JD: Jadičevac, central Mt. Velebit, Lower Liassic.

TG: Mt. Trnovski Gozd, western Slovenia, Middle Liassic.

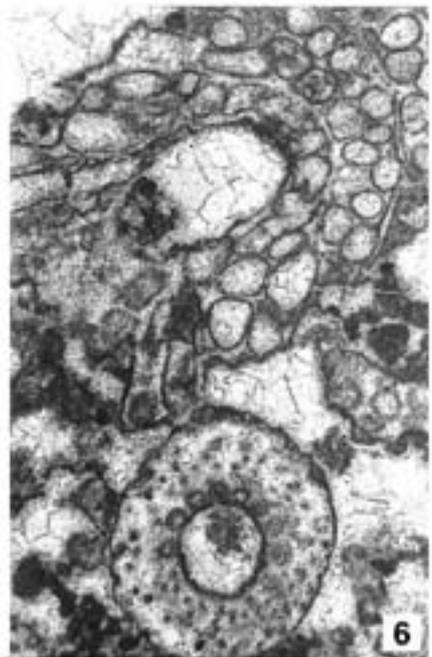
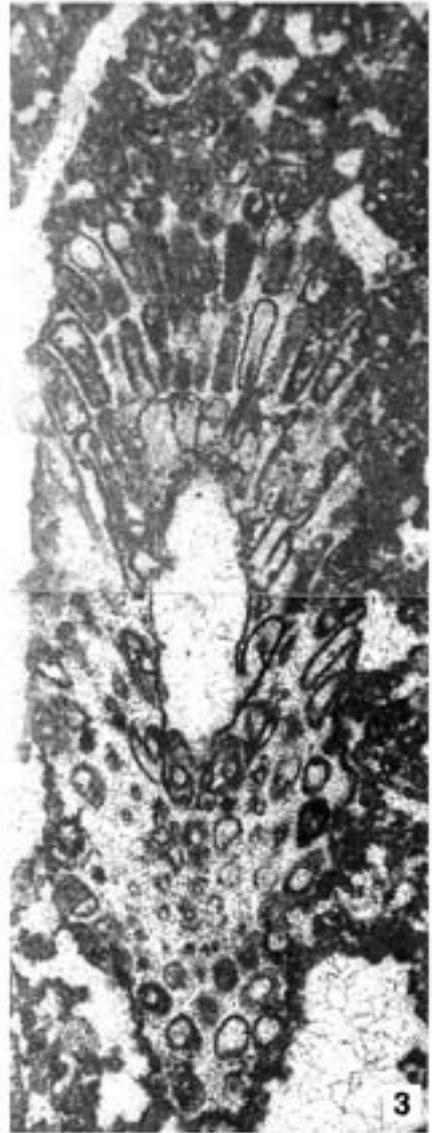


PLATE XIII

1-3, 6-7 *Palaeodasycladus mediterraneus* (PIA, 1920) 1927 var. *mediterraneus*

- 1-2 Tangential sections with well developed constrictions of secondary and tertiary branches, with apparent articulation of elongated, cylindrical segments. 1: Turska 6c/2, x17; 2: Turska 6c1, x22.
- 3 Transverse-oblique section of a fragment. Constrictions of secondary branches produce the illusion of articulation, e.g. a string of beads. VT-26/160, x22.
- 6 Oblique section. TG-9/25, x22.
- 7 Transverse section. Note the extremely short tertiary branches. Several of the secondary branches show constrictions, producing a seemingly beaded appearance. VT-26/382, x22.

4-5 *Palaeodasycladus anae* (SOKAČ, 1988) n. comb.

- 4-5 Longitudinal-oblique sections. Note primary branches of various shape and size. On the left side of the section in Fig. 4 groups of cysts in the pores of the primary branches may be seen. This is an enlarged detail of the section figured in Pl. VIII, Fig. 1. 4: VT-26/328, x40; 5: VT-26/263, x17.

Sample localities and ages

Turska: Kuyubasi-Bucak, north Antalya, Turkey, Middle Liassic.

VT: Mali Alan Pass, central Mt. Velebit, Lower Liassic.

TG: Mt. Trnovski Gozd, western Slovenia, Middle Liassic.

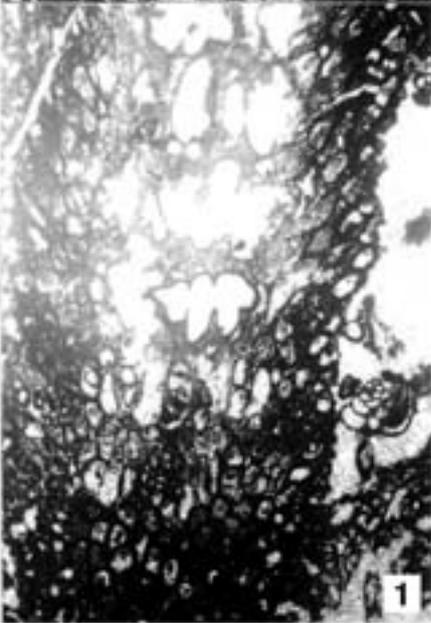
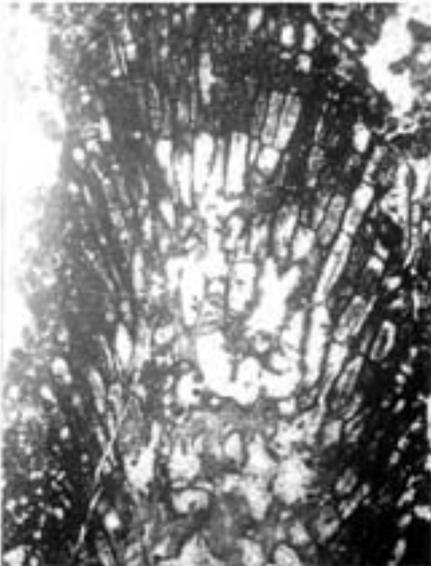


PLATE XIV

1-4, 7, 8A, 9 *Palaeodasycladus mediterraneus* (PIA, 1920) 1927, var. *mediterraneus*

- 1 Tangential section, enlarged detail of Pl. I, Fig. 1. In pores of the primary branches (central part) and secondary branches (lower part) groups of cysts can be seen. Secondary branches grow in bundles of 3-4 branches. JD-14/1, x34.
- 2-4 Oblique sections of specimens with thicker secondary branches and short tertiaries. 2: VT-26/360, x17; 3: VT-26/30, x22; 4: VT-26/327, x22.
- 7 Oblique tangential section with comparatively small primary branches arranged in loosely spaced whorls. There are bundles of 4-5 secondary branches per primary branch.

5-6 *Palaeodasycladus mediterraneus* var. *heraki* (SOKAČ & NIKLER, 1966) n. comb.

- 5-6 Tangential-oblique sections. Rectangular primary branches bear bundles of 4-5 secondary branches. Note, in Fig. 5, individual cysts in the pores of the primary branches. 5: VT-26/24, x17; 6: VT-26/386, x17.

8B *Palaeodasycladus barrabei* LÉBOUCHÉ & LÉMOINE, 1963 ex GRANIER & DELOFFRE, 1993

- 8B Oblique section. VT-26/337, x14.

Sample localities and ages

JD: Jadičevac, central Mt. Velebit, Lower Liassic.

VT: Mali Alan Pass, central Mt. Velebit, Lower Liassic.

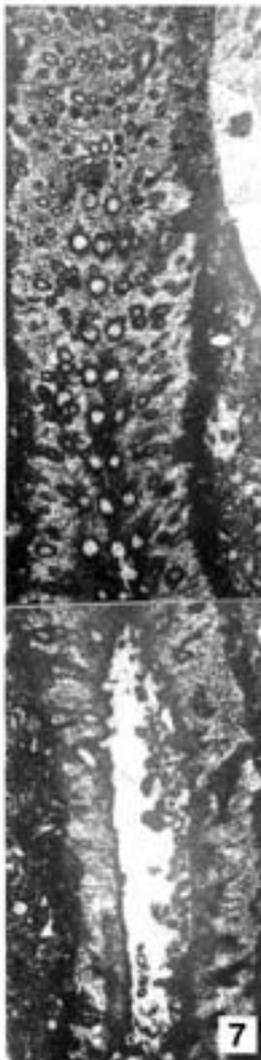
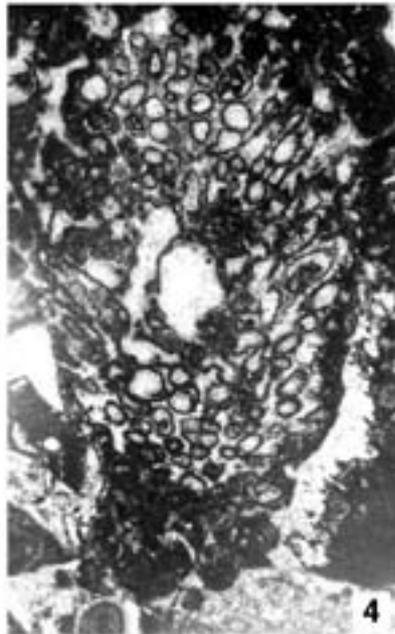
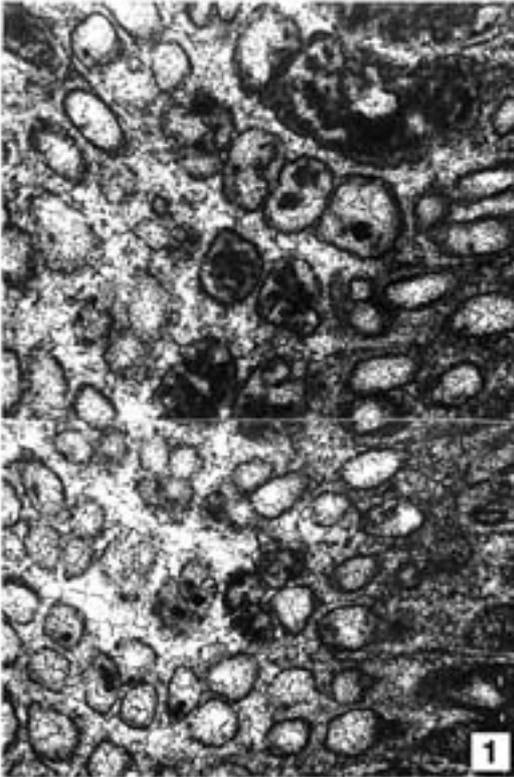


PLATE XV

1, 3-9 *Palaeodasycladus mediterraneus* var. *mediterraneus*

1, 3-9 Oblique sections of specimens with primary and secondary branches of varying size and shape. Despite of varying degree of similarity and some common features, no two specimens are identical (sections are similarly oriented). 1: TG-9/7, x17; 3: VT-26/308, x14; 4: TG-9/3, x17; 5: VT-26/78, x22; 6: TG-9/10, x22; 7: TG-9/8, x22; 8: VT-26/369, x22; 9: VT-26/52, x22.

2 *Palaeodasycladus mediterraneus* var. *heraki* (SOKAČ & NIKLER, 1966) n. comb.

2 Oblique section. Rectangular primary branches connect with the central axis through a tiny tubular pore, situated in the middle of the base of the primary branch. VT-26/283, x14.

Sample localities and ages

TG: Mt. Trnovski Gozd, western Slovenia, Middle Liassic.

VT: Mali Alan Pass, central Mt. Velebit, Lower Liassic.

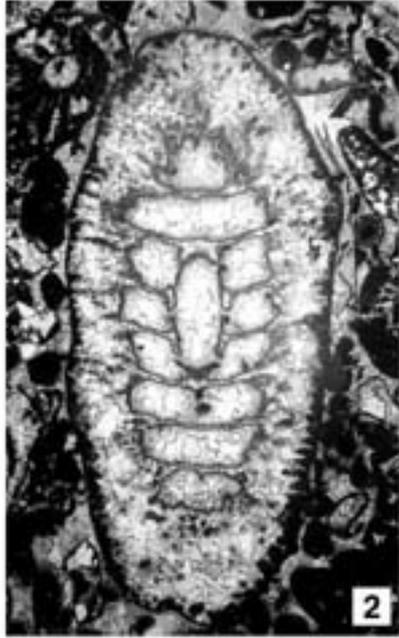


PLATE XVI

1-8 *Palaeodasycladus mediterraneus* var. *gracilis* (CROS & LEMOINE, 1967 ex GRANIER & DELOFFRE, 1993) n. stat.

- 1 Longitudinal-oblique tangential section. Comparatively thin, acrophorous, primary branches bear bundles of thin secondary branches that are slightly funnel-shaped at their distal ends (e.g. slightly phloiophorous type). Primary branches are arranged in comparatively loosely spaced whorls. The specimen may also be regarded as being intermediate between var. *gracilis* and var. *mediterraneus*. VT-26/176, x17.
- 2-3 Longitudinal sections. Primary branches are more steeply inclined and generally of an acrophorous type. The central cavity is generally preserved, sporadically destroyed by erosion and widening of the basal pores of primary branches. 2: TG-9/22, x34; 3: TG-9/2, x22.
- 4-5 Oblique sections. Primary branches tubular, slightly widened (funnel-shaped) distally, bearing thin secondaries. Tertiary branches are not clearly visible. 4: TG-9/5, x17; 5: TG-9/10, x43.
- 6 Transverse, slightly oblique section. Larger pores correspond to the sections of primary branches, each having bundle of 3-4 secondaries (e.g. smaller pores). TG-9/5, x53.
- 7-8 Oblique sections. In Fig. 7, short, tubular primary branches bear thin, longer, acrophorous secondary branches. In Fig. 8, bottom, bundles of 3 secondary branches can be seen. 7: TG-9/6, x22; 8: TG-9/18, x34.

Sample localities and ages

TG: Mt. Trnovski Gozd, western Slovenia, Middle Liassic.

VT: Mali Alan Pass, central Mt. Velebit, Lower Liassic.

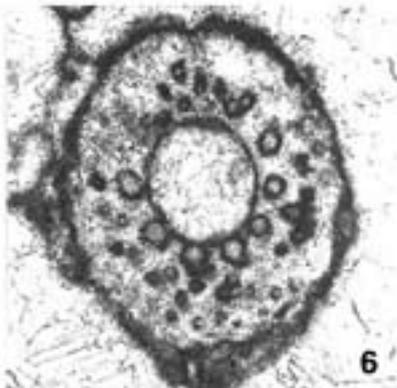


PLATE XVII

1-8 *Palaeodasycladus mediterraneus* var. *gracilis* (CROS & LEMOINE, 1967 ex GRANIER & DELOFFRE, 1993) n. stat.

- 1 Longitudinal-tangential section. Well preserved wall of central cavity, visibly perforated by larger pores of the primary branches. In the tangential part of the section, secondary branches are distinctly acrophorous. TG-9/15, x34.
- 2-3, 5 Oblique sections of specimens with preserved axial cavity and with tubular primary and secondary branches. 2: TG-9/6, x22; 3: TG-9/13, x17; 5: TG-9/2, x22.
- 4 Tangential section. Independently of the depth of the section, pores retain the same diameter throughout, indicating their acrophorous nature. TG-9/6, x22.
- 6 Transverse, slightly oblique section. TG-9/2, x43.
- 7-8 Oblique sections of specimens with preserved axial cavity and with acrophorous branches; in Fig. 8, primary branches are twice as wide as the secondary. 7: TG-9/3, x43; 8: TG-9, x22.

Sample localitiy and age

Mt. Trnovski Gozd, western Slovenia, Middle Liassic.



PLATE XVIII

1-8 *Palaeodasycladus mediterraneus* var. *gracilis* (CROS & LEMOINE, 1967 ex GRANIER & DELOFFRE, 1993) n. stat.

- 1 Longitudinal-tangential section. In the bottom part, larger pores of the primary branches are visible in the wall. Above them the destruction of these pores produces an illusion of intusannulation. Secondary branches are tubular. TG-9/6, x22.
- 2-7 Various oblique sections. In some specimens, tubular primary branches and secondary branches half their width can be observed. 2: TG-9/1, x22; 3: TG-9/3, x43; 4: TG-9/5, x54; 5: TG-9/1, x22; 6: TG-9E/22, x22; 7: TG-9/5, x22.
- 8 Transverse section. Larger pores next to the wall of the central cavity correspond to the primary branches which bear 3-4 thin secondary branches. These have a constant diameter along their length, thus being of acrophorous type.

9-12 *Palaeodasycladus mediterraneus* var. *elongatulus* PRATURLON, 1966

- 1 Longitudinal-tangential section. Axial cavity secondarily widened, due to the destruction of the proximal region of the primary branches. Secondary branches are acrophorous and, distally, more steeply inclined upwards. VT-26/220, x14.
- 10 Section of a segment with long, acrophorous secondaries. VT-26/343, x14.
- 11 Tangential section. In larger pores (of the primary branches), individual cysts and smaller groups of cysts can be seen. Secondary branches, of acrophorous type, grow out in bundles of 3-4 branches. The outer "feathery" surface results from tightly squeezed segments placed deeply one into another, and with sporadically occurring fissures indicating annulation. VT-26/296, x14.
- 12 Oblique section with contours of segments visible on the outer surface. VT-26/184, x14.

Sample localities and ages

TG: Mt. Trnovski Gozd, western Slovenia, Middle Liassic.

VT: Mali Alan Pass, central Mt. Velebit, Lower Liassic.

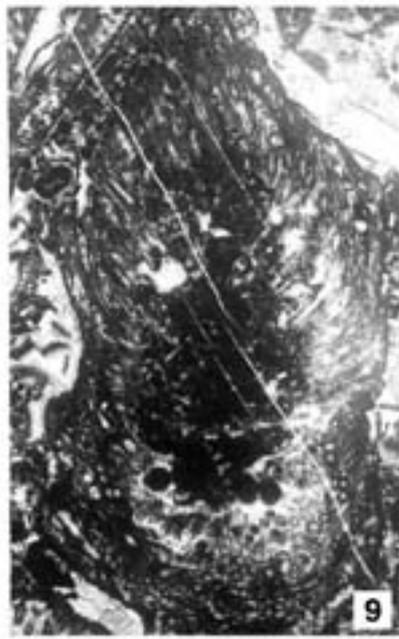
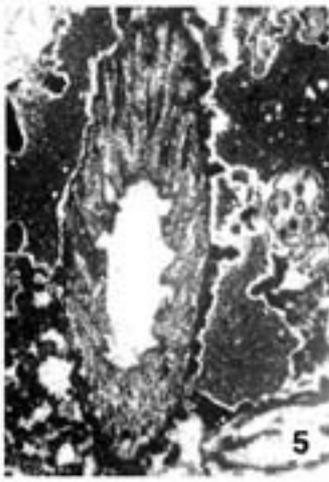


PLATE XIX

1-6 *Palaeodasycladus mediterraneus* var. *elongatulus* PRATURLON, 1966

- 1 Oblique section with destroyed proximal region of primary branches. Tubular secondary branches are more steeply inclined upwards. Possible cysts in partly preserved pores of the primary branches. VT-26/151, x14.
- 2 Tangential section passing into oblique section. In the tangential part of the section, secondary branches grouped into bundles of 3-4 branches can be seen. Uneven, "feathery", outer surface with sporadically preserved fissures (relics of annulation) indicates the segmentation in this species. VT-26/102, x14.
- 3-5 Various oblique sections. In Fig. 3 note clearly visible fissures separating the segments. The approximately equal diameter of pores indicates acrophorous secondary branches. Fissures in the skeleton are also visible in Fig. 5. 3: VT-26/280, x17; 4: VT-26/155, x14; 5: VT-26/164, x14.
- 6 Tangential-oblique section. Outer surface of the skeleton and visible fissures indicate segmentation, but with tightly squeezed segments. Long, acrophorous, secondary branches are more steeply bent in their distal part. VT-26/382, x17.

Sample locality and age

Mali Alan Pass, central Mt. Velebit, Lower Liassic.

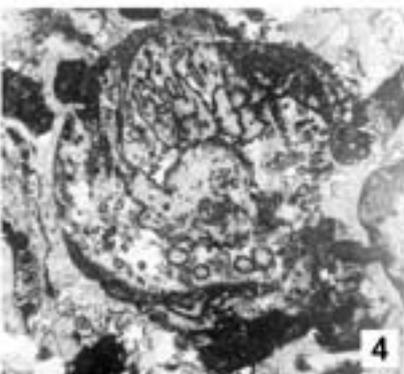
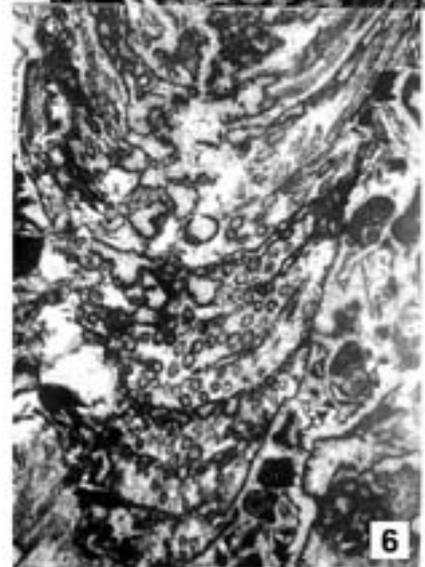
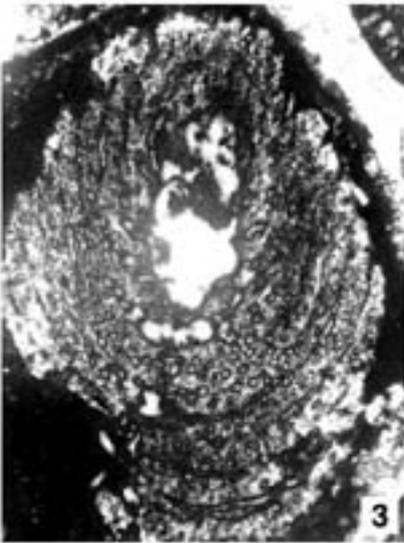
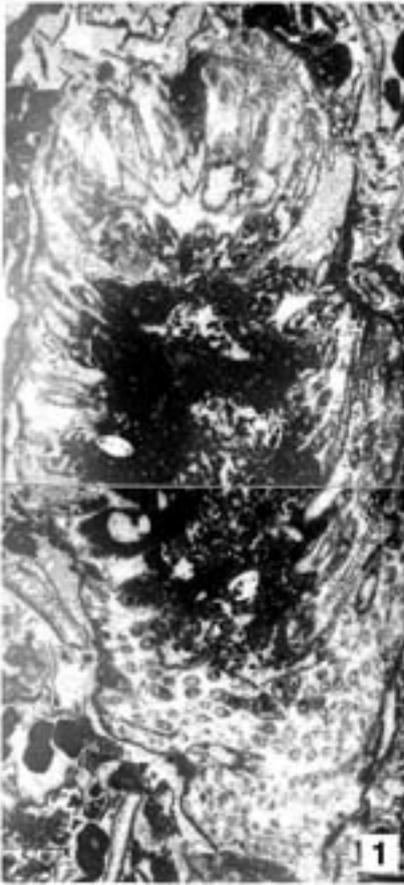


PLATE XX

1-9 *Palaeodasycladus mediterraneus* var. *elongatulus* PRATURLON, 1966

- 1-2 Oblique sections. Note, in Fig. 2, well-preserved cylindrical primary branches from which, without constrictions, secondary branches grow out in bundles of 3-4 branches. 1: VT-26/130, x14; 2: VT-26/293, x17.
- 3-5 Various oblique sections with visible traces of segmentation and with acrophorous, upwards inclined secondary branches. 3: VT-26/158, x14; 4: VT-26/190, x14; 5: VT-26/73, x14.
- 6 Transverse-oblique section with a visible arrangement and number of partly preserved primary branches in a whorl. Beside the relics of primary branches, bundles of 3-4 secondary branches can be seen, in which the diameter of the pores decreases in the distal region. VT-26/73, x14.
- 7 Oblique section with secondarily enlarged central cavity and traces of annulation. VT-26/144, x14.
- 8 Fragment with visible globular primary branches and long, acrophorous, secondaries growing out of the primaries without constrictions. GO-10096/63, x22.
- 9 Fragment of a distinctly annulated specimen in which the neighbouring segments do not fit snugly against each other. VT-26/36, x22.

Sample localities and ages

VT: Mali Alan Pass, central Mt. Velebit, Lower Liassic.

GO-10096: southern slopes of Jasenovačko brdo (elevation point 1,367), central Mt. Velebit.

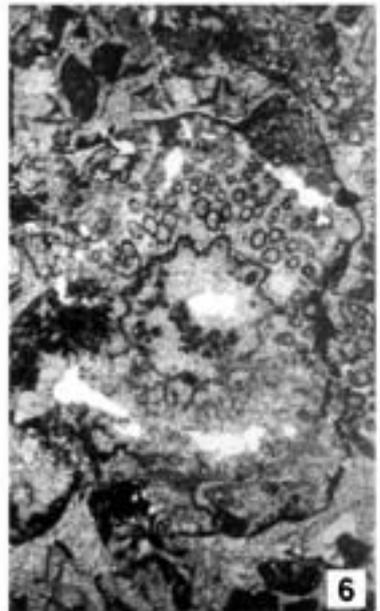
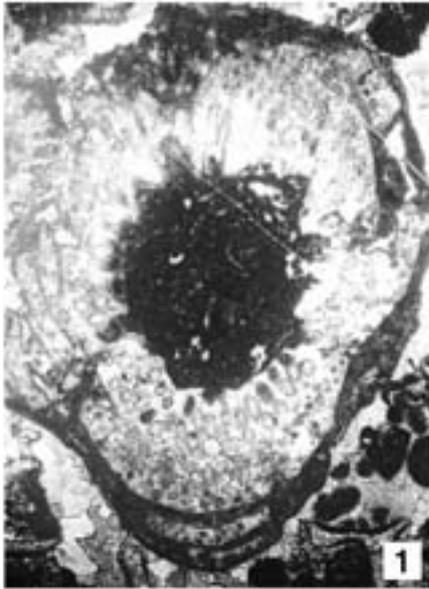


PLATE XXI

1-6 *Palaeodasycladus mediterraneus* var. *elongatulus* PRATURLON, 1966

- 1, 4 Tangential-oblique section with partly preserved primary branches and acrophorous secondary branches which are more strongly inclined in their distal part. In the bottom part of the section, traces of segmentation are clearly visible. VT-26/324, x14.
- 2-3, 5 Various oblique sections of specimens with a secondarily enlarged axial cavity and very steeply inclined acrophorous secondary branches, becoming almost parallel to the longitudinal growth axis (these specimens correspond well with those figured by PRATURLON, 1966, fig. 1). 2: G-3831/10, x26; 3: GO-3831/25, x26; 5: GO-3831/27, x22.
- 6 Tangential section with clearly marked annulation. JP-61/1, x34.

Sample localities and ages

VT: Mali Alan Pass, central Mt. Velebit, Lower Liassic.

GO-3831: east of Šarića Duplje, central Mt. Velebit, Lower Liassic.

JP: on the road to Panos, central Mt. Velebit, Lower Liassic.



PLATE XXII

1-7 *Palaeodasycladus barrabei* LÉBOUCHÉ & LEMOINE, 1963 ex GRANIER & DELOFFRE, 1993

- 1 Longitudinal, partly tangential section of a club-shaped and undulated skeleton. The club-shaped form is attained, as in the type-species, by thickening of the wall in the younger part of the thallus. Small, stump-like or globular-elliptical primary branches generally stay perpendicular to the axial cavity. Secondary branches are generally thin and slightly widened distally; they diverge from each other, being bent both upwards and downwards. The axial cavity is delimited by a smooth and even wall. VT-26/21, x14.
- 2 Oblique tangential section of a curved thallus. Primary branches are situated obliquely, as well as the segments between obliquely cut annulations. VT-26/22, x22.
- 3 Oblique section of a skeleton with incompletely developed annulation/fissuration. Primary branches perpendicular. Intusannulation not developed.
- 4 Longitudinal section of a distinctly annulated skeleton with oblique, stumpy, primary branches, some of which show apparent metaspondility (arrow). Distinctly regular intusannulation is developed. Possible individual cysts, as well as small groups of cysts, rather numerous in the central cavity, indicate possible endospority in some specimens. VT-26/33, x14.
- 5 Oblique section with larger primary branches. An upper right primary branch suggests possible ramification up to the fourth-order branches. VT-26/41, x20.
- 6 Tangential-oblique section of an annulated specimen with very slightly developed intusannulation and small, bubble-shaped primary branches. VT-26/30, x22.
- 7 Oblique section of a visibly annulated skeleton. Some primary branches show possible metaspondility (?) diverging branches. VT-26/27, x22.

Sample locality and age

Mali Alan Pass, central Mt. Velebit, Lower Liassic.



PLATE XXIII

1-12 *Palaeodasycladus barrabei* LÉBOUCHÉ & LEMOINE, 1963 ex GRANIER & DELOFFRE, 1993

- 1 Tangential-oblique section of a specimen with obliquely cut annulation and equally obliquely positioned primary branches. A slightly developed annulation is clearly visible. VT-26/155, x22.
- 2 Longitudinal, deep tangential section with pronounced intusannulation. Mutually separated, rounded to elliptical hollow spaces in the middle part of the section correspond to swellings of the axial cavity, whereas the calcareous partitions between the hollow spaces correspond to the centripetal protrusions of the wall, at the bases of which there are pores of primary branches, through which they connect with the central axis. The outer surface shows only a slight undulation. VT-26/64, x17.
- 3 Tangential-oblique section with barely visible annulation and obliquely situated primary branches. VT-26/297, x17.
- 4 Oblique tangential section of a specimen with a probably curved thallus and well-developed annulation. VT-26/60, x14.
- 5 Tangential section. Note the obliquely cut annulation. VT-26/24, x14.
- 6-8 Various oblique, partly tangential, sections of specimens without annulation (Fig. 8) or with poorly developed annulation (Fig. 6). Primary branches differ in detailed morphology and are mostly perpendicularly situated. Some primary branches (Fig. 6) are heavily deformed. 6: VT-26/267, x17; 7: VT-26/152, x14; 8: VT-26/352, x14.
- 9 Oblique section of a distinctly annulated specimen. VT-26/164, x22.
- 10, 12 Tangential sections. Fig. 10 shows an undulated specimen with barrel-shaped segments stacked one above the other. Fig. 12 shows a distinctly annulated specimen. 10: VT-26/405, x17; 12: VT-26/267, x22.
- 11 Tangential-oblique section with obliquely cut annulations and visible intusannulation. VT-26/167, x17.

Sample locality and age

Mali Alan Pass, central Mt. Velebit, Lower Liassic.

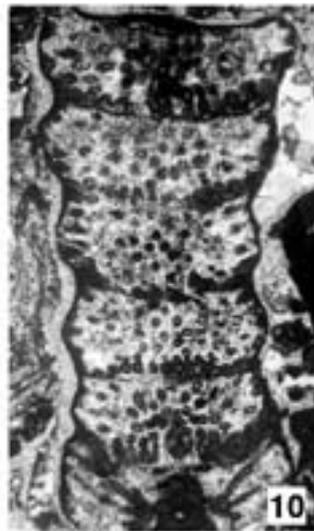


PLATE XXIV

1-10 *Palaeodasycladus barrabei* LÉBOUCHÉ & LEMOINE, 1963 ex GRANIER & DELOFFRE, 1993

- 1 Longitudinal-tangential section of a curved specimen with annulation developed only in the lower part of the skeleton. Bubble-shaped primary branches, situated perpendicular to the longitudinal growth axis, sporadically contain individual cysts. Secondary branches, diverging from each other, are of an acrophorous type and bear short, phloiophorous tertiaries. Intusannulation is well developed. VT-26/353, x17.
- 2 Enlarged detail of the oblique-tangential section figured in Pl. XXIII, Fig. 6, showing heavily deformed primary branches. VT-26/267, x34.
- 3-6, 9 Transverse sections, showing, on average, more than 20 primary branches per whorl. 3: VT-26/42, x22; 4: VT-26/436, x17; 5: VT-26/378, x22; 6: VT-26/434, x22; 9: VT-26/262, x17.
- 7 Oblique section of a specimen with distinct annulation, extending deeply into the calcareous skeleton and reaching the wall of the central cavity. VT-26/331, x22.
- 8, 10 Oblique sections of specimens showing distinct annulation and visible intusannulation. It is clearly visible that each segment bears one whorl of branches; secondary and tertiary branches diverge from each other. 8: VT-26/387, x22; 10: VT-26/199, x22.

Sample locality and age

Mali Alan Pass, central Mt. Velebit, Lower Liassic.

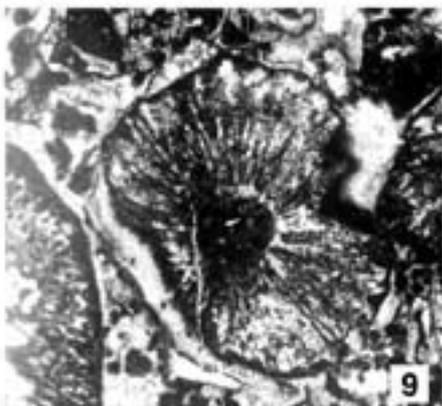
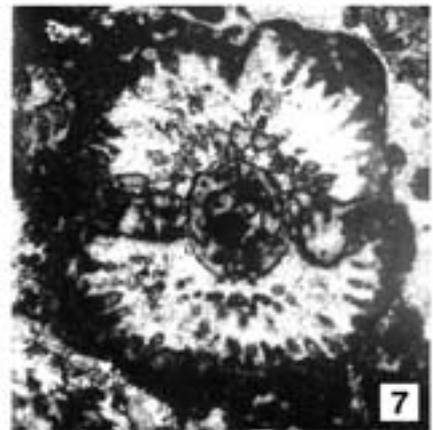
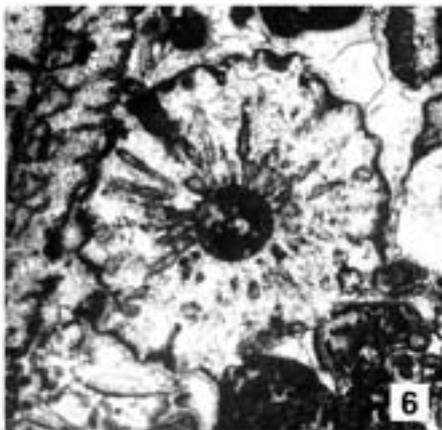
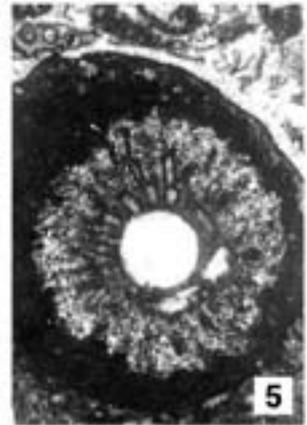
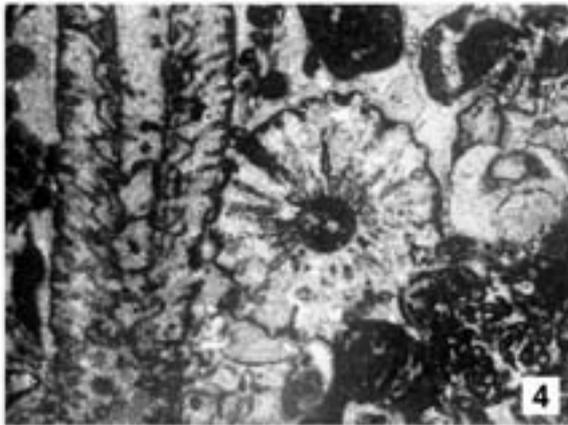
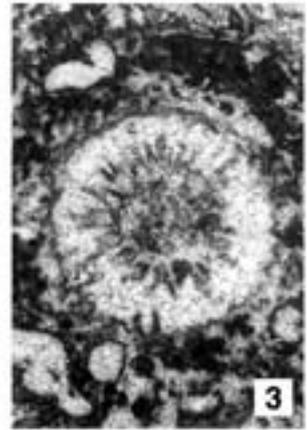


PLATE XXV

1-9 *Palaeodasycladus alanensis* n. sp.

- 1 Holotype. Oblique-tangential section. Swollen, or bowl-shaped, loosely spaced primary branches give rise, at their borders, to secondary branches. In sections nearer to the central axis, primary branches appear as large, circular pores in some of which cysts can be seen. Secondary branches are mutually divergent. VT-26/149, x17.
- 2-3 Fragments of longitudinal sections with bowl-shaped primary branches. Fig. 2 is an enlarged detail of Fig. 5. 2: VT-26/326, x34; 3: VT-26/162, x22.
- 4 Oblique section of a cylindrical skeleton. Primary branches are bushy and directly connected with central cavity; they bear thin, acrophorous secondary branches which are, at their distal ends, divided into tertiary branches. Intusannulation is poorly developed. VT-26/16, x14.
- 5 Longitudinal section of a cylindrical skeleton with visible annulation in the lower part and well developed intusannulation. Primary branches are bowl-shaped and situated perpendicular to the longitudinal growth axis. VT-26/326, x17.
- 6, 9 Tangential sections. Large pores of primary branches are approximately in alternating arrangement. 6: VT-26/150, x14; 9: VT-26/201, x14.
- 7-8 Oblique sections with bowl-shaped primary branches. 7: VT-26/403, x22; 8: VT-26/313, x22.

Sample locality and age

Mali Alan Pass, central Mt. Velebit, Lower Liassic.

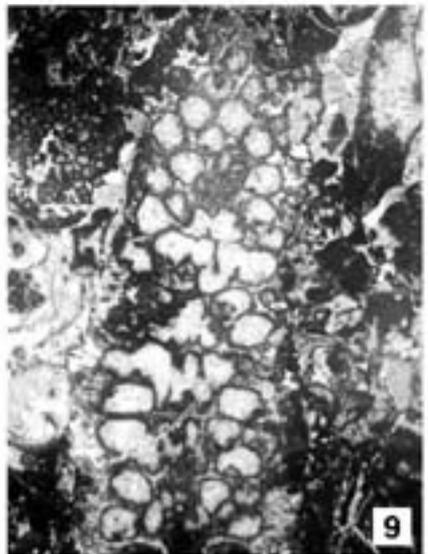
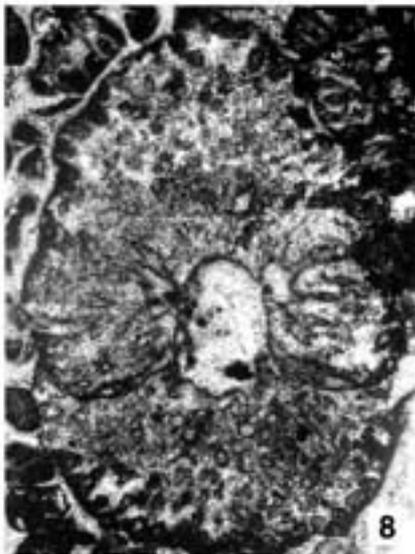


PLATE XXVI

1-7 *Palaeodasycladus dolomiticus* (CROS & LEMOINE, 1966) n. comb.

- 1-3 Oblique sections. In Fig. 1, note finger-shaped secondary branches which produce circular and polygonal pores in tangential sections. Each secondary branch bears a bundle of tertiaries. 1: TG-9/25, x22; 2: TG-9/33, x22; 3: TG-9/4, x17.
- 4, 7 Tangential sections showing well developed partitions between densely packed consecutive whorls and rectangular to elliptical pores of primary branches. Note, in Fig. 7, varying dimensions of primary branches within the same whorl and their elongation in the direction of growth. 4: OB-9619/5, x17; 7: OB-9619, x17.
- 5-6 Transverse sections. Finger-shaped secondary branches grow out of distally widened portions of primary branches. In Fig. 5, note the varying diameter of the individual primary branches of the same whorl. 5: VT-26/149, x14; 6: JD-15/2, x14.

Sample localities and ages

TG: Mt. Trnovski Gozd, western Slovenia, Middle Liassic.

OB-9619/9: Dušice, central Mt. Velebit, Lower Liassic.

JD: Jadičevac, central Mt. Velebit, Lower Liassic.

VT: Mali Alan Pass, central Mt. Velebit, Lower Liassic.

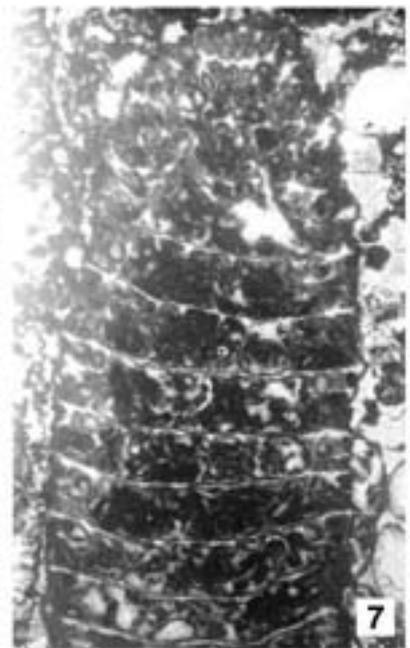
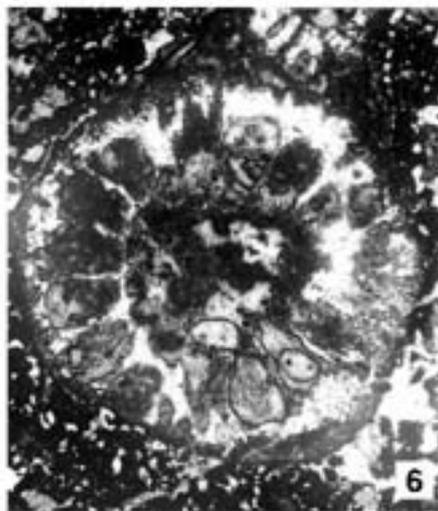
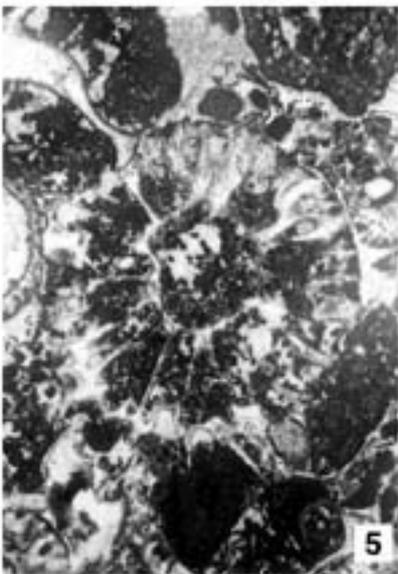
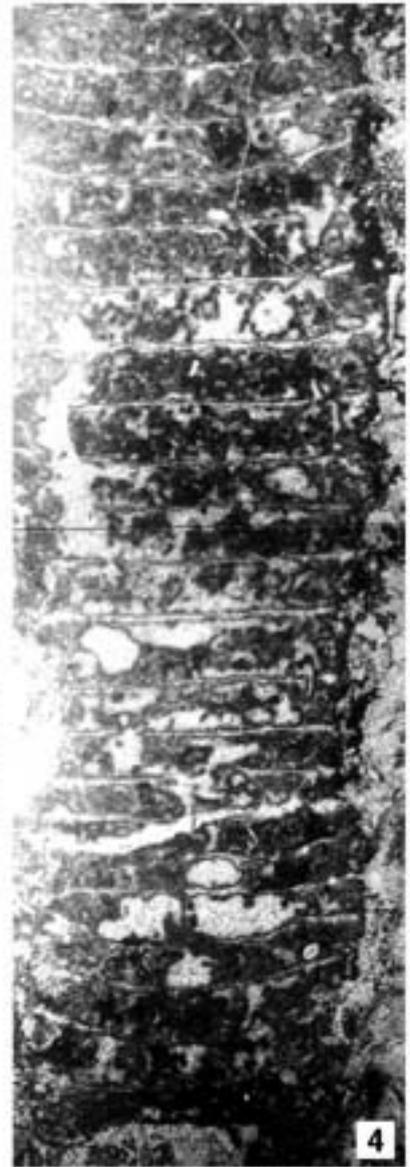


PLATE XXVII

1A, 2-3A, 4-8 *Palaeodasycladus dolomiticus* (CROS & LEMOINE, 1966) n. comb.

- 1A Transverse section. Primary branches with distally widened portions, out of which the finger-shaped secondaries emerge. OB-9619/27, x17.
- 2 Oblique section. Densely packed consecutive whorls are separated by thin partitions. VT-26/327, x14.
- 3A Part of a longitudinal-tangential section of a specimen with slightly oblique branches. VT-26/400, x17.
- 4 Oblique section. Note distinctly large rectangular branches. Outer surface of the skeleton is heavily abraded. JD-15A, x17.
- 5 Oblique tangential section. VT-26/189, x14.
- 6 Oblique tangential section of a specimen in which secondary and tertiary branches gradually become more and more steeply inclined upwards. VT-26/264, x17.
- 7-8 Oblique sections. Large rectangular, primary branches are situated obliquely to the longitudinal growth axis. 7: OB-9619/30, x17; 8: JD-15, x14.

1B, 3B *Palaeodasycladus mediterraneus* var. *mediterraneus*

1B Oblique section. OB-9619/27, x17.

3B Oblique section. VT-26/400, x17.

Sample localities and ages

OB-9619: Dušice, central Mt. Velebit, Lower Liassic.

JD: Jadičevac, central Mt. Velebit, Lower Liassic.

VT: Mali Alan Pass, central Mt. Velebit, Lower Liassic.

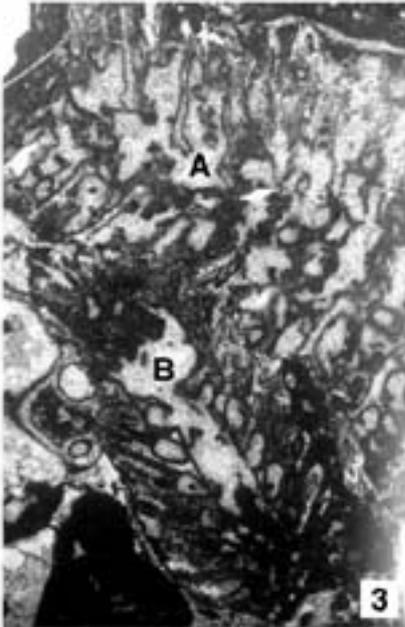
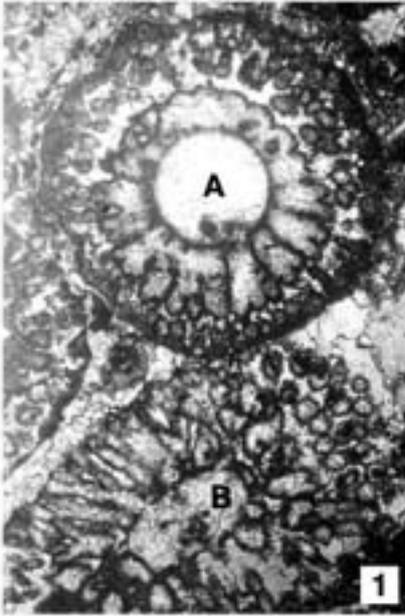


PLATE XXVIII

1-9 *Palaeodasycladus anae* (SOKAČ, 1988) n. comb.

- 1 Longitudinal section. Note variously shaped and variously large primary branches within the same whorl. VT-26/417, x34.
- 2 Oblique section. Different primary branches. Some secondary branches grow out from lateral surfaces of the primary branches, whereas other secondary branches grow out from variously shaped distal ends of the primaries. Secondary branches are phloiophorous. VT-26/275, x22.
- 3 Oblique section. Irregular branches with variously shaped distal ends from which short, horn-shaped protrusions and secondary branches grow out in a finger-like way. VT-26/275, x22.
- 4 Oblique section. Different primary branches lined up along the thallus; at their distal ends, they bear horn- or nipple-like protrusions (second-order branches?). Some primary branches lack such protrusions. VT-26/29, x34.
- 5 Oblique section. Predominantly fusiform (spindle-shaped) primary branches (*Uragiella*-type) pass into irregular and nodular ones and those with an incision at the distal end. VT-26/403, x34.
- 6 Longitudinal-oblique section. Predominantly nodular primary branches, some of which bear, at their distal ends, nipple-like protrusions that give rise to the secondary/tertiary branches. VT-26/45, x34.
- 7 Longitudinal section. Along the thallus, there are variously shaped primary branches: nodular in the lower part, fusiform (spindle-shaped; *Uragiella*-type) in the middle part, and sporadically *Physoporella*-like in the upper part. VT-26/319, x44.
- 8 Oblique section. Predominantly nodular primary branches; from their distal ends, bundles of secondary branches grow out from a common base. VT-26/209, x44.
- 9 Oblique section. Nodular primary branches; some are divided at their distal ends, into two equal forks (in the plane of section), each bearing a bundle of secondary/tertiary phloiophorous branches. VT-26/121, x34.

Sample locality and age

Mali Alan Pass, central Mt. Velebit, Lower Liassic.

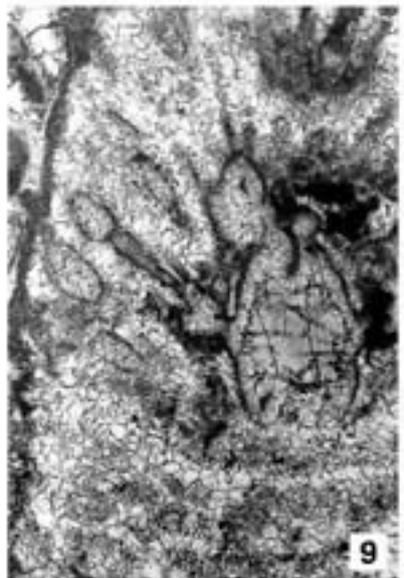
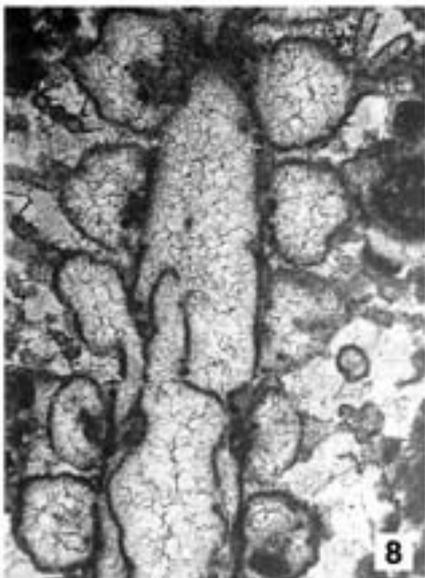
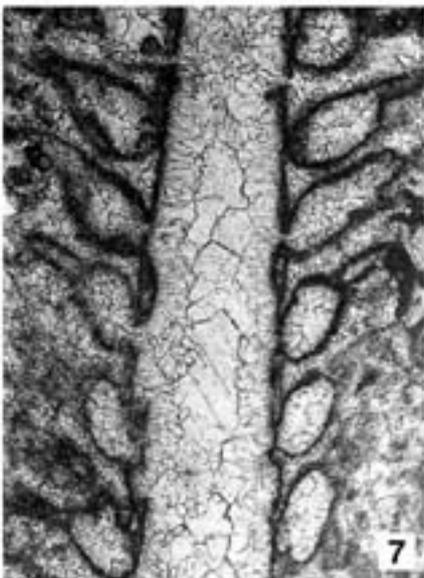
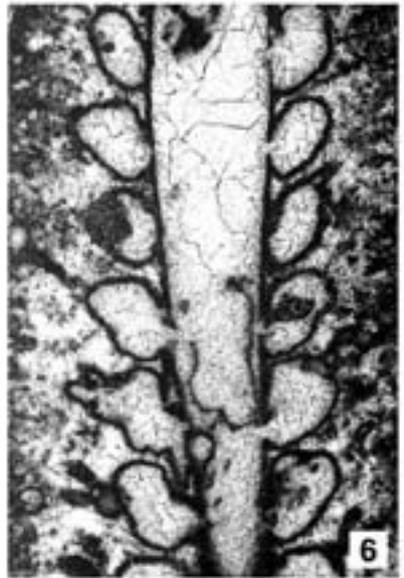
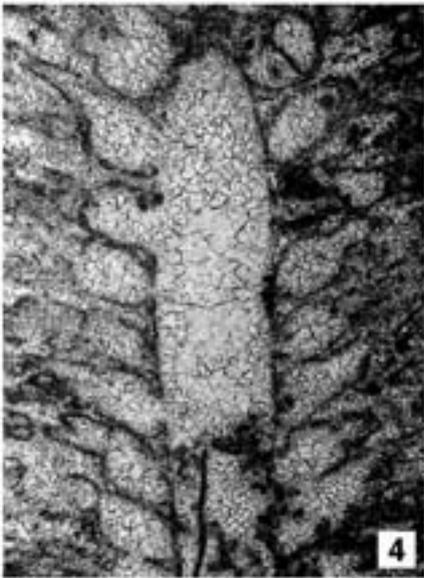
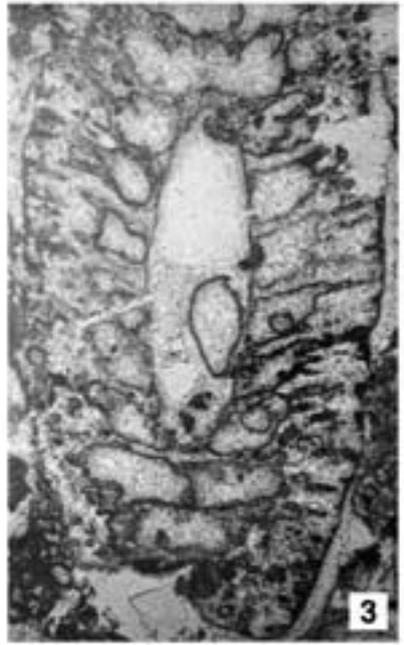
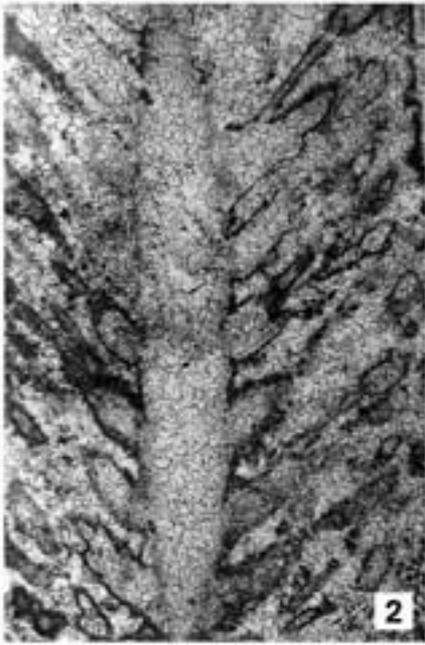
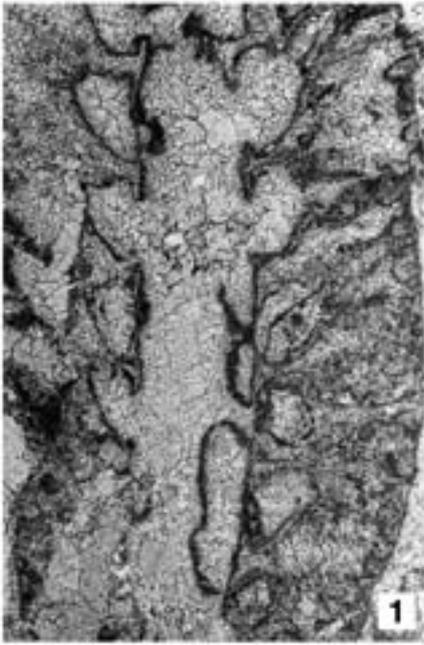


PLATE XXIX

1-7 *Palaeodasycladus anae* (SOKAČ, 1988) n. comb.

- 1 Longitudinal section. Primary branches vary in shape, particularly differing in their distal ends, which sometimes pass into nipple-like or, more often, horn-shaped protrusions, which, in turn give rise either to single secondary/tertiary branches or to bundles of these. Whether they should be called secondary or tertiary (or second-order and third-order) branches depends on how we conceive the horn-like protrusions, i.e. what status is given to them. Single cysts may be seen in the pores of the primary branches or they may be dispersed in the central cavity. VT-26/115, x34.
- 2-3 Tangential-oblique sections of specimens with different primary branches, some of which bear nipple- or horn-shaped protrusions at their distal end. The central cavity lacks intusannulation and is clearly delineated by an even and smooth wall. Primary branches are slightly oblique to the longitudinal axis of growth. 2: VT-26/290, x14; 3: VT-26/83, x14.
- 4 Oblique section. Primary branches of the same whorl show various forms and degrees of ramifications. The branch in the upper left corner ramifies into two visible forks (possibly more), each bearing a bundle of secondary/tertiary branches which divide distally. In some pores of primary branches cysts are visible. VT-26/342, x34.
- 5 Part of an oblique section. Predominantly nodular primary branches with different distal ends. VT-26/395, x34.
- 6-7 Oblique sections of specimens with differently shaped primary branches and a well preserved, uninterrupted axial cavity. 6: VT: 26/426, x22; 7: VT-26/56, x14.

Sample locality and age

Mali Alan Pass, central Mt. Velebit, Lower Liassic.

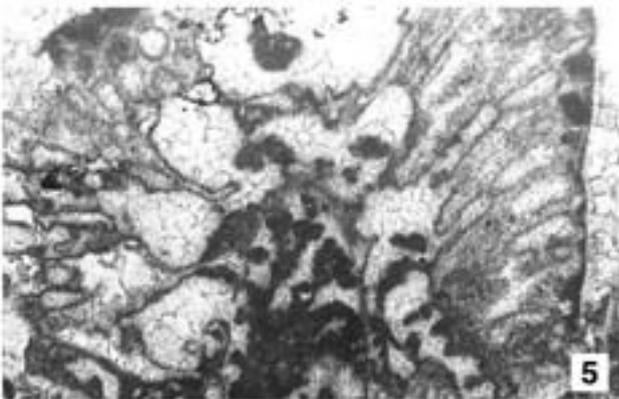


PLATE XXX

1-7 *Palaeodasycladus anae* (SOKAČ, 1988) n. comb.

- 1-2 Oblique sections. Figured specimens show variously shaped primary branches, which are particularly visible in the tangential parts of sections (upper part of figures). In Fig. 1, note the preserved uninterrupted wall of the central cavity, perforated by the entrance pores of the primary branches. Depending on the shape of their distal ends, primary branches bear one or more bundles of secondary branches (up to two in the plane of section). Some branches ramify up to the fourth-order branches. 1: VT-26/8, x22; 2: VT-26/269, x17.
- 3-7 Oblique sections of specimens with visibly different primary branches. Ramification may proceed up to the third- and fourth-order branches. All specimens show a well preserved, uninterrupted central cavity with more or less visible entrance pores or larger openings at the proximal base of the primary branches. 3: VT-26/314, x17; 4: VT-26/389, x34; 5: VT-26/454, x22; 6: VT-26/362, x17; 7: VT-26/3, x17.

Sample locality and age

Mali Alan Pass, central Mt. Velebit, Lower Liassic.

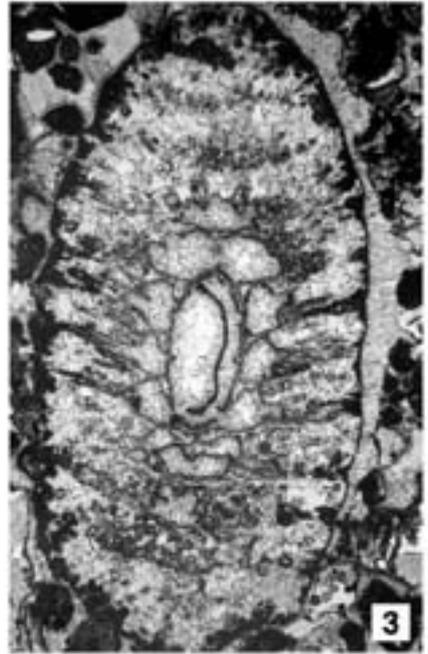


PLATE XXXI

1-8 *Palaeodasycladus mediterraneus* var. *calciticus* n. var.

- 1 Oblique section. VT-26/322, x14.
- 2 Tangential-oblique section of a specimen with well-developed calcareous partitions between neighbouring whorls. Distally widened dark pore indicates the expanding bundle consisting of 3-4 secondaries. VT-26/120, x22.
- 3 Holotype, oblique section. Well developed partitions between branches of the neighbouring whorls. Below the axial cavity, some preserved individual envelopes of primary and secondary branches or their traces delineating their square shape may be seen. Incomplete calcification of branches, with only traces of calcification in the spaces between the secondary branches, does not provide insight into their shape and mutual relationship. Porous structure is preserved only in the peripheral part of the thallus. VT-26/379, x17.
- 4, 7 Longitudinal sections of partly destroyed and secondarily enlarged axial cavities. Well developed calcareous partitions are more or less perpendicular to the longitudinal axis of growth. 4: VT-26/263, x17; 7: VT-26/399, x14.
- 5 Tangential section. VT-26/54, x22.
- 6, 8 Differently oriented oblique sections. Calcareous partitions are clearly visible. Note, in Fig. 8, the partly preserved shape of a primary branch and further ramification within the individual envelope of each branch. In the lower left part, note the bundle of 3-4 secondary branches. 6: VT-26/123, x22; 8: VT-26/205, x14.

Sample locality and age

Mali Alan Pass, central Mt. Velebit, Lower Liassic.



PLATE XXXII

1-8 *Palaeodasycladus mediterraneus* var. *calciticus* n. var.

- 1 Oblique section of a specimen with typically developed calcification without clearly visible branches. VT-26/259, x17.
- 2, 5 Parts of tangential sections with clearly developed calcareous partitions between the branches of neighbouring whorls. Note, in Fig. 2, bottom, sporadically developed calcification protruding between secondary or tertiary branches. 2: VT-26/305, x17; 5: VT-26/404, x22.
- 3, 6 Oblique, partly tangential sections with well developed, slightly inclined, calcareous partitions. In Fig. 3, bottom and Fig. 6 top, there are more or less clearly delimited pores of envelopes containing 3-4 contours of sections of secondary branches. 3: VT-26/438, x17; 6: lost slide, x17.
- 4 Oblique sections of strongly developed calcification of the envelope. Sporadically, one can see calcitic wedges and small, irregular, calcitic masses representing relics of isolated, mutually disconnected fillings (hanging calcite in the text) in the cavities between the branches within the same envelope. VT-26/87, x14.
- 7 Tangential sections with clearly delineated envelopes of the branches, within which 3-4 non-calcified secondary branches can be seen. VT-26/330, x17.
- 8 Oblique section. VT-26/330, x17.

Sample locality and age

Mali Alan Pass, central Mt. Velebit, Lower Liassic.

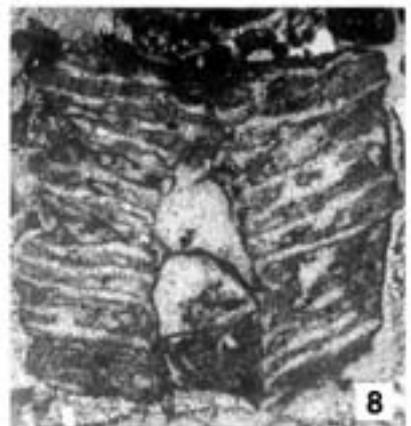
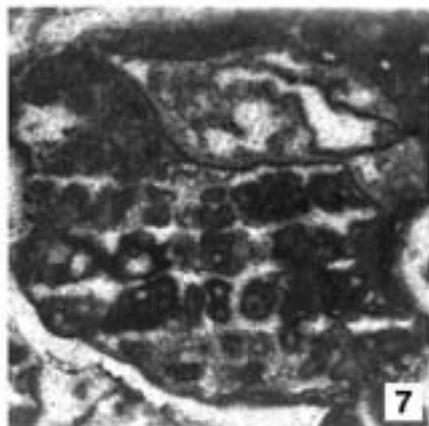


PLATE XXXIII

1-8 *Palaeodasycladus multiporus* n. sp.

- 1 Oblique, recrystallised section. VT-26/46, x22.
- 2 Longitudinal-oblique section. Rectangular primary branches bear numerous secondaries. Note the ramification of branches up to the third order. GO-10096/6, x22.
- 3, 5, 7-8 Oblique sections of specimens with numerous secondary and tertiary branches. Fourth-order ramification possibly occurs. Note characteristic lack of bundles of secondary branches in the basal part of their growth. 3: VT-26/68, x34; 5: VT-26/54, x22; 7: VT-26/448, x22; 8: VT-26/104, x22.
- 4, 6 Oblique sections. Large, rectangular primary branches bear up to 5 secondary branches (in the plane of section). In Fig. 4, the ramifications up to the fourth order may be supposed. 4: GO-100096, x22; 6: VT-26/27, x22.

Sample localities and ages

GO: 10096: Southern slopes of Jasenovačko brdo (elevation point 1,367), central Mt. Velebit, Lower Liassic.

VT: Mali Alan Pass, central Mt. Velebit, Lower Liassic.

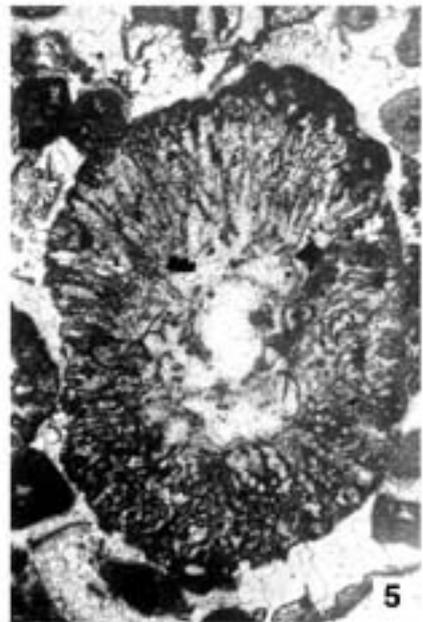
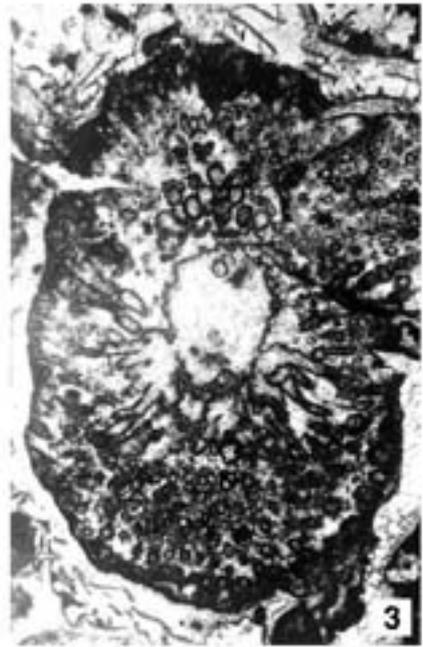


PLATE XXXIV

1-8 *Palaeodasycladus multiporus* n. sp.

- 1 Oblique-tangential section. VT-26/351, x17.
- 2 Holotype, oblique section. Quadrilateral, obliquely situated primary branches bear numerous secondary branches, which, in this species, characteristically are not grouped into bundles at the base of their growth. VT-26/262, x17.
- 3-4 Oblique section. In Fig. 4, upper right part, up to 6 secondary branches may be seen through one primary branch (in the plane of section). Ramification up to the fourth order is possibly present. Central cavity in both specimens characterised by an uninterrupted wall. 3: VT-26/319, x22; 4: VT-26/343, x22.
- 5, 7-8 Oblique sections of comparatively poorly preserved specimens. Ramification up to the fourth-order branches may be barely discerned. Large primary branches seem to bear rather numerous secondary. 5: VT-26/201, x17; 7: VT-26/303, x14; 8: VT-26/448, x22.
- 6 Oblique section. In this specimen, primary branches are somewhat more narrow and more steeply inclined; they bear numerous, thin secondary branches. Ramification up to the fourth order is indicated. VT-26/77, x17.

Sample locality and age

Mali Alan Pass, central Mt. Velebit, Lower Liassic.



PLATE XXXV

1-6 *Palaeodasycladus benceki* n. sp.

- 1 Longitudinal section of a specimen with very large primary branches, that are, moreover, elongated in the direction of growth. Whorls of primary branches are densely packed. Central cavity is straight. VT-26/192, x14.
- 2 Oblique-tangential section of a specimen with large, bubble-shaped, primary branches, that are situated somewhat more apart from each other. The distal surface is very irregular and as is the growth of the secondary branches, which may also grow out from lateral surfaces. In some cavities of the primary branches, poorly preserved cysts can be seen. VT-26/260, x17.
- 3 Oblique section of a specimen with very large and irregular primary branches and with rugged distal surfaces. In the pores, cysts are sporadically preserved. The outer surface of the skeleton is characterised by fissuration to shallow annulation. The inner wall is even, perforated by comparatively large entrance pores. VT-26/416, x17.
- 4 Transverse section. Primary branches are 9-10 in a whorl and may be variously shaped and of differing dimensions. In the left centre, note the growth of a secondary branch from the proximal lateral side of a primary branch. VT-26/361, x22.
- 5 Longitudinal section of a specimen with large and irregular primary branches which bear comparatively short secondary branches which, in turn, may be supposed to branch off distally into tertiary branches. Axial cavity is preserved, with clear intusannulation. VT-26/203, x14.
- 6 Tangential section of a specimen with large primary branches, arranged alternately in neighbouring whorls. VT-26/43, x22.

Sample locality and age

Mali Alan Pass, central Mt. Velebit, Lower Liassic.

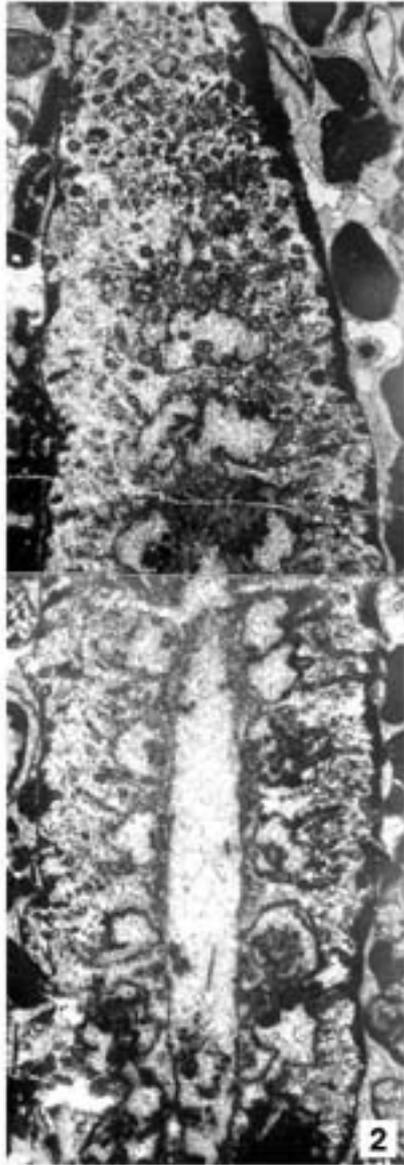
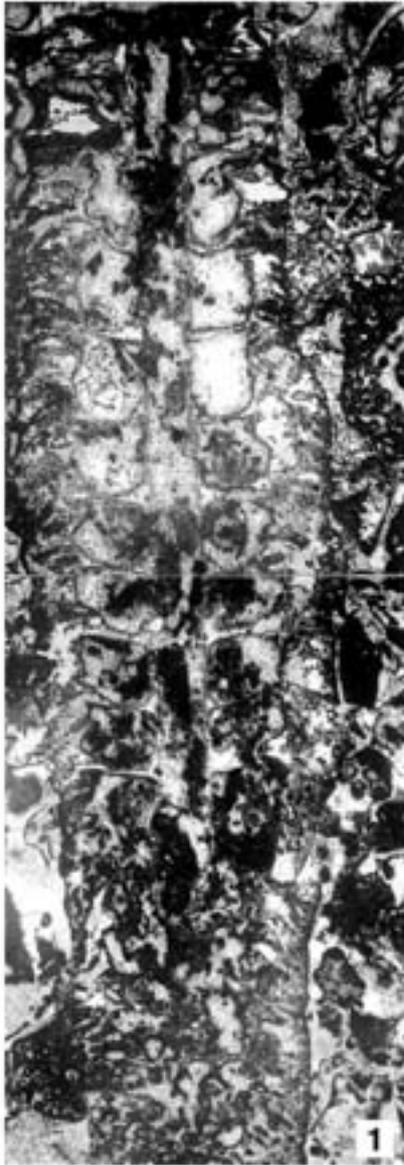


PLATE XXXVI

1-7 *Palaeodasycladus benceki* n. sp.

- 1 Longitudinal oblique section of a specimen with very large and elongated (in the direction of growth) primary branches. VT-26/223, x17.
- 2 Holotype; oblique section. Primary branches are distinctly large and visibly irregular at their distal ends. VT-26/436, x22.
- 3 Oblique section with distinctly irregular primary branches. VT-26/374, x22.
- 4 Oblique section with partly destroyed region of the primary branches. Secondary branches also grow out from the lateral sides of the primary branches, producing tiny pores of secondary branches arranged around the large pores of the primary branches. VT-26/221, x17.
- 5 Oblique section. Primary branches of various shapes and varying dimensions. Note, at the bottom, large pores of primary branches surrounded by tiny pores of secondary branches. In spite of the possible visual illusion, sterile branches do not exist. VT-26/331, x17.
- 6 Transverse section of a poorly preserved recrystallised specimen. Note the irregular, rough distal surface of the primary branches. VT-26/291, x22.
- 7 Oblique section with distinctly irregular primary branches and with secondary branches growing out of the lateral proximal surfaces of the primaries. VT-26/405, x22.

Sample locality and age

Mali Alan Pass, central Mt. Velebit, Lower Liassic.

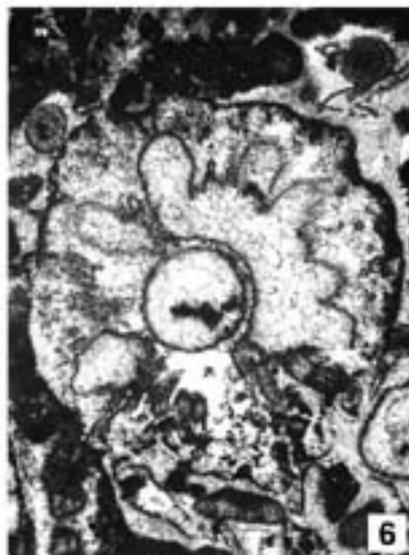
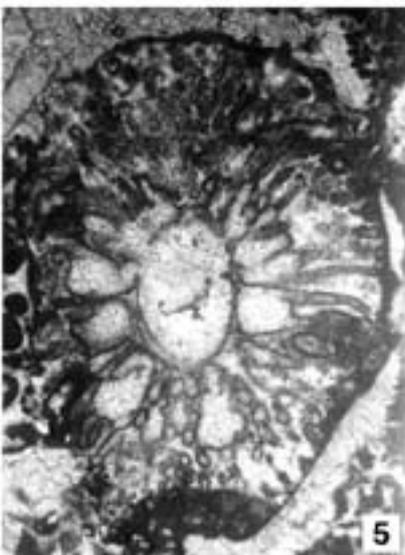
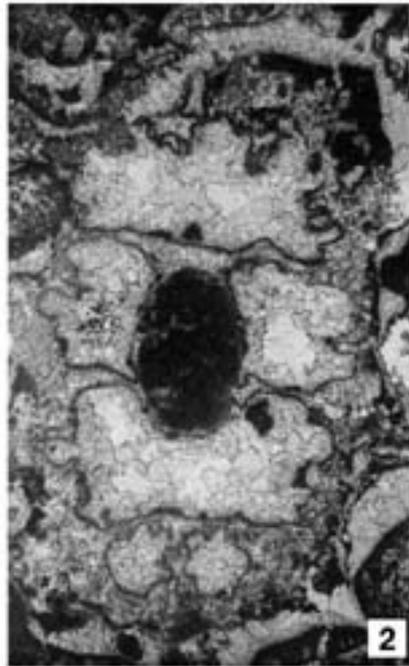
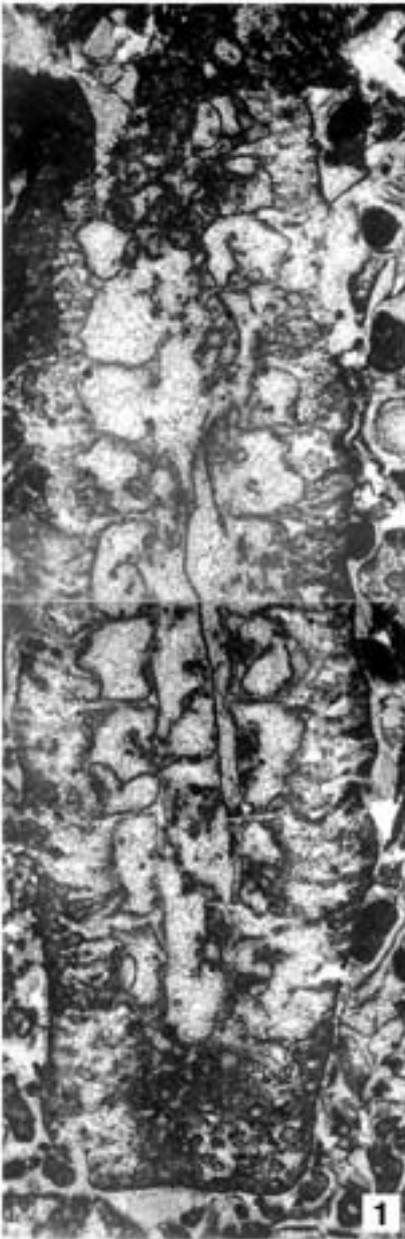


PLATE XXXVII

1-7 *Palaeodasycladus benceki* n. sp.

- 1 Oblique section of a specimen with large, comparatively regular primary branches arranged in densely spaced whorls. On the outer surface of the skeleton, fissuration to shallow annulation can be seen. VT-26/444, x17.
- 2-3 Oblique sections near to the horizontal plane. Large and irregular primary branches bear secondary branches on the edges of their distal ends (Fig. 2 left centre), which appear as tiny pores at the edge of a primary branch in the lower part of the section in Fig. 3. This may give a visual illusion of there being sterile branches arranged as in *Chinianella*. 2: VT-26/303, x17; 3: VT/378, x17.
- 4 Oblique-longitudinal section of a specimen with large, irregular and mutually different primary branches. Some primary branches in the lower part of the thallus appear, by their shape and dimensions, similar to the branches in *P. barrabei*. The central cavity shows distinct intusannulation; entrance pores to the branches are situated at or immediately below the narrowest place. VT-26/243, x17.
- 5, 7 Oblique sections of specimens with strongly irregular primary branches and secondary branches growing out from different parts of the primaries. Note, in Fig. 7 (right side), secondary branches growing out of lateral parts of the primaries. 5: VT-26/323, x17; 7: VT-26/301, x17.
- 6 Transverse section. Primary branches (9 in a whorl) are elliptical, elongated in the direction perpendicular to the direction of growth. VT-26/268, x17.

Sample locality and age

Mali Alan Pass, central Mt. Velebit, Lower Liassic.

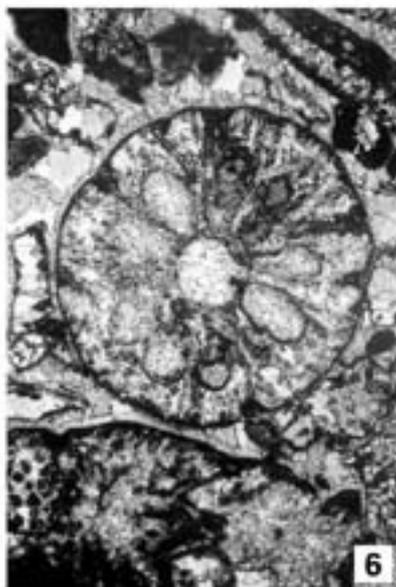


PLATE XXXVIII

1-8 Forms belonging to the phyletic lineage *P. barrabei* - *P. alanensis* - *P. benceki*

- 1 Oblique section of *P. barrabei* with distinct intusannulation and stick-like to stumpy primary branches. VT-26/224, x17.
- 2 Oblique section of *P. barrabei* with very well developed intusannulation and with primary branches showing the tendency of bubble-shaped swelling.
- 3 Longitudinal section of *P. barrabei* with primary branches showing both swellings and deformations. Note the double wall of the central cavity. VT-223, x14.
- 4 Oblique section of *P. alanensis* with swollen primary branches showing the distinct tendency of becoming bowl-shaped. VT-26/343, x17.
- 5 Oblique tangential section of *P. alanensis* with swollen, bubble-shaped, primary branches that produce large, alternately arranged pores in the tangential part of the section. Note very slight intusannulation. VT-26/149, x17.
- 6 Oblique section of *P. alanensis* with slightly developed intusannulation and bush-like widened primary branches. Three orders of branches are visible, the secondary branches being distinctly acrophorous. VT-26/16, x14.
- 7 Oblique section of *P. benceki* with visibly increasing diameter and degree of deformation of primary branches, passing upwards from the basal part of the thallus. VT-26/379, x14.
- 8 Longitudinal-tangential section of *P. benceki* showing the increasing diameter and changing shape of the primary branches from the lower to the upper part of the thallus. The lowest visible branches are typical of *P. barrabei*. VT-26/417, x17.

Sample locality and age

Mali Alan Pass, central Mt. Velebit. Lower Liassic.

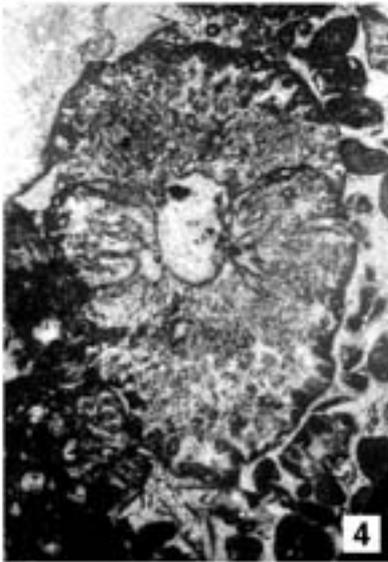
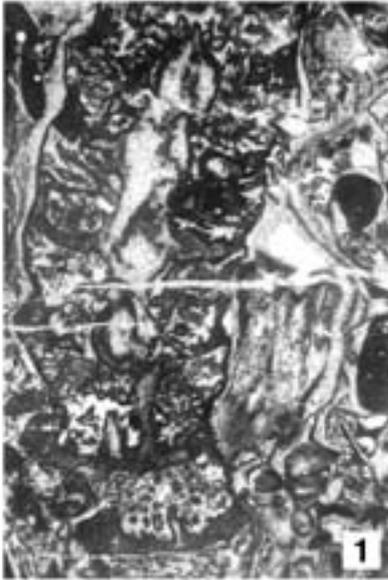


PLATE XXXIX

1-6 *Palaeodasycladus asteriscus* n. sp.

- 1 Oblique, partly longitudinal section. Oblique primary branches are situated in distinctly spaced whorls. Note partial grouping of the secondary branches in the upper part, which does not occur in the lower part of the thallus. JD-13, x14.
- 2-3 Oblique sections. Note some secondary branches of the same primary branch growing in opposite directions. Secondary branches are not grouped into bundles. The separation of the secondary branches is marked by a large pore with small radial channels (tubules; Fig. 3, upper part). 2: JD-6B/5, x17; 3: JD-14C, x22.
- 4-6 Oblique sections with a partly visible radial arrangement of secondary branch tubules (at the level of where they grow out from the primary branches). In Fig. 5, in the central part of the wall of the cylindrical skeleton, note an indication of a fissure produced by contact of branches of neighbouring whorls, directed in opposite directions. 4: JD-13/14, x22; 5: JD-4C, x17; 6: JD-13/8, x17.

Sample locality and age

The road east of Jadičevac (elevation point 1,274), central Mt. Velebit, lowermost Liassic (Hettangian).

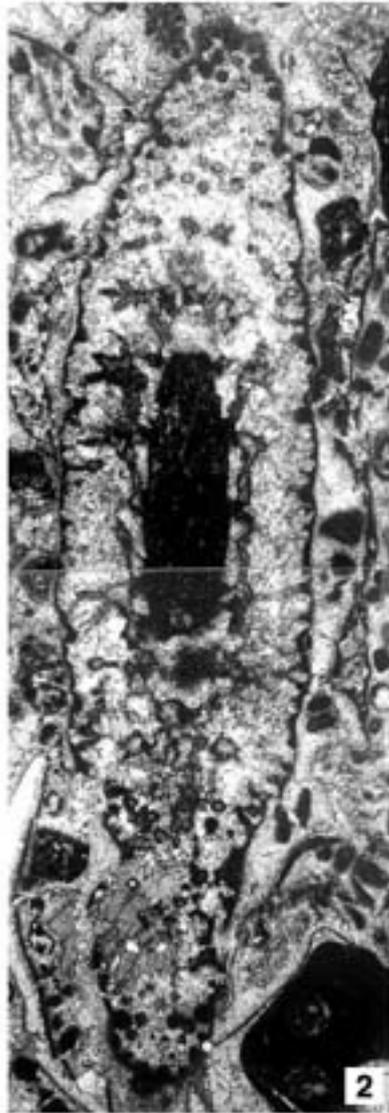


PLATE XL

1-9 *Palaeodasycladus asteriscus* n. sp.

- 1 Longitudinal-tangential section. JD-13/13, x17.
- 2-4 Oblique sections. In Fig. 2, upper part, note the tubules of secondary branches suggesting their approximately perpendicular position to the primary branch. 2: JD-13/22, x17; 3: JD-6B/3, x17; 4: JD-6B/4, x17.
- 5-9 Transverse sections. Note, in Figs. 6 and 7, an incipient fissure as a result of the direction of growth of secondary branches. 5: JD-13/21, x22; 6,8: JD-13/25; 6: x22; 8: x17; 9: JD-13/9, x22.

Sample locality and age

The road east of Jadičevac (elevation point 1,274), central Mt. Velebit, lowermost Liassic (Hettangian).

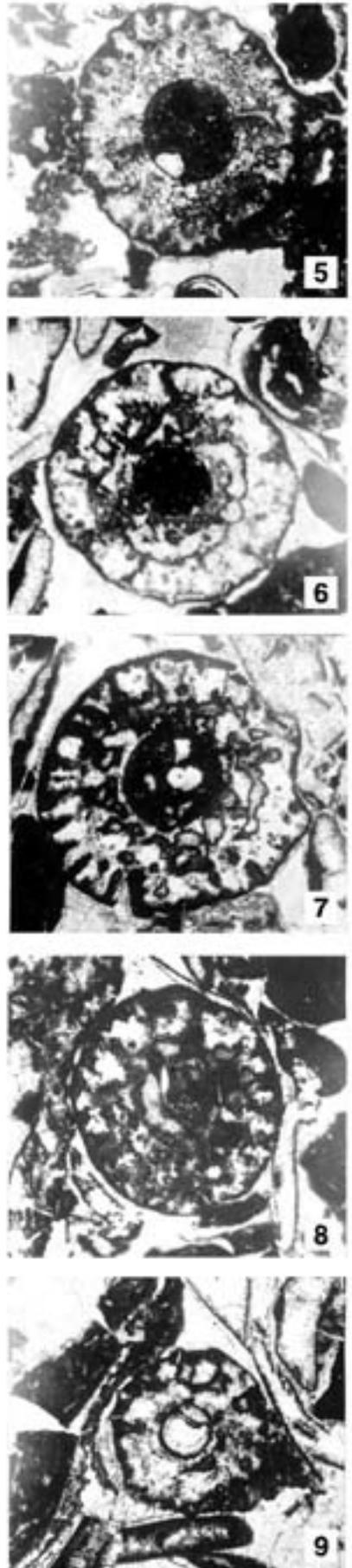
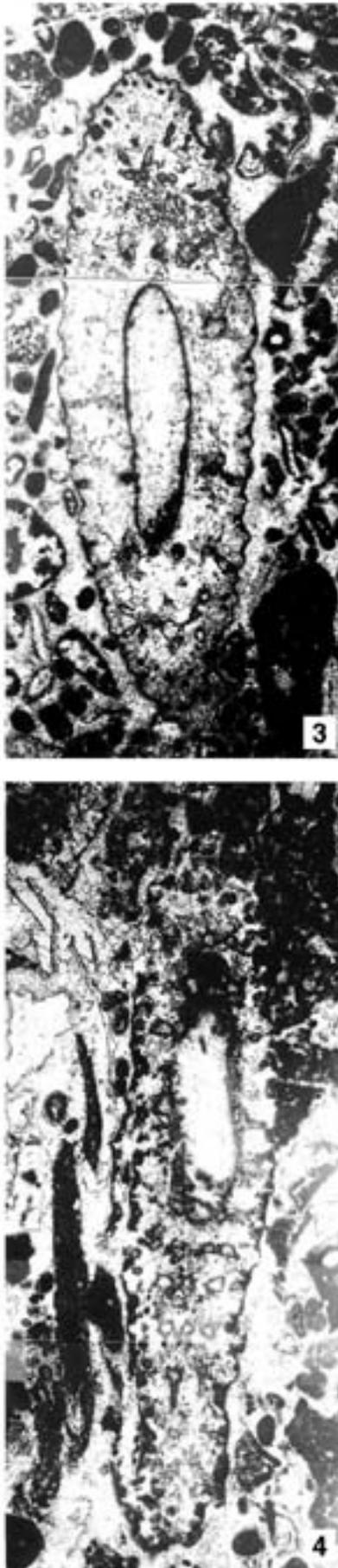


PLATE XLI

1-9 *Eodasycladus ogilviae* CROS & LEMOINE, 1966

- 1 Oblique section. Shallow fissuration of the outer surface produces a barrel-shaped appearance of segments. In the lower parts of the thallus, both primary and secondary branches are of *P. barrabei* -type; passing upwards, some secondary branches become swollen and bubble-shaped. VT-26/401, x17.
- 2 Oblique section. Outer surface of the skeleton is slightly undulated to shallowly fissurated. Intusannulation is poorly developed; secondary branches become swollen and bubble-shaped in the upper part of the thallus. VT-26/264, x14.
- 3 Tangential section of a specimen with irregularly distributed larger pores, supposedly produced by some swollen bubble-like, secondary branches. VT-26/292, x22.
- 4 Tangential section of *E. ogilviae* (?). JD-4B/6, x14.
- 5 Oblique section of *E. ogilviae* (?). Swollen branches assume a regularly alternating arrangement in neighbouring whorls only in the upper part of the thallus. One cannot tell with certainty whether these are swollen primary or secondary branches. VT-26/193, x14.
- 6 Longitudinal section of a specimen with poorly developed intusannulation and slight undulation of the skeleton. Some secondary branches are bubble-like and swollen. VT-26/202, x22.
- 7 Oblique section of a specimen in which some secondary branches are swollen and produce large pores. VT-26/30, x22.
- 8-9 Oblique-tangential sections. Note some swollen bubble-like, secondary branches and, in Fig. 9, some bubble-shaped swellings (sporangia?), located in the middle of a bundle.

Sample locality and age

VT: Mali Alan Pass, central Mt. Velebit, Lower Liassic.

JD: The road east of Jadičevac (elevation point 1,274), central Mt. Velebit, lowermost Liassic (Hettangian).

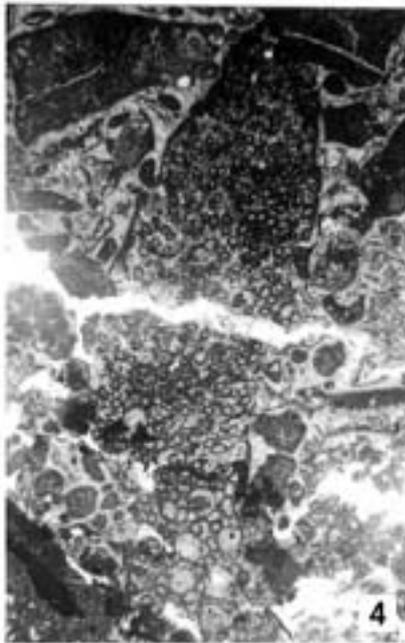


PLATE XLII

1-3 *Selliporella? problematica* n. sp.

- 1 Tangential-oblique section. Obliquely cut annular depressions are well developed. Note, in right centre, a ramified branch with a bag-shaped swelling on the lower side. In this part of the section, outer rims of the segments show a tendency of widening, suggesting distal widening of the secondary branches, or, perhaps, the existence of tertiary branches. Note, also, a reduced number of pores in the tangential section of the lower segments. T-26/400, x17.
- 2-3 Longitudinal-oblique (Fig. 2) and oblique (Fig. 3) sections. 2: VT-26/208, x14; 3: VT-26/279, x22.

4-8 *Humiella japodica* n. sp.

- 4 Oblique section. Large branches distally become narrower (in the outer half) and separate from each other. JD-13/33, x34.
- 5 Deeper tangential section, cutting through the level of maximum diameter and mutual contact of the branches. In some pores of the alternately arranged branches, dark circular sections suggest the presence of cysts. JD-13/40, x42.
- 6 Holotype - a very slightly oblique section. In the envelopes of the branches (upper part of the figure), tubules perforating the envelope can be seen. JD-13/14, x42.
- 7-8 Oblique sections. Note, in Fig. 7, the piriform shape of the branches and their individuality in the outer part and the perforations of the envelope (upper part of the figure). Fig. 8 is a heavily recrystallized specimen.

Sample localities and ages

VT-26: Mali Alan Pass, central Mt. Velebit, Lower Liassic.

JD-13: Jadičevac (elevation point 1274), central Mt. Velebit, Lower Liassic.

