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CYLINDROPORELLA TAURICA, N. SP. URGES TO REVIEW DIFFERENT PATTERNS OF CALCIFICATION IN THE MESOZOIC DASYCLADALES (GREEN ALGAE)

BY

Marc A. CONRAD 1 et Baki VAROL 2

ABSTRACT

Cylindroporella? taurica, n. sp., is reported from the Albian in Eastern Anatolia, in the Dinarids, and from the Hauterivian-Barremian boundary in Italy. The species displays an unusual pattern of calcification that consists of a thin sheath of microcrystalline calcite. In the Mesozoic, similar features are found in a limited number of species assigned to different genera. The writers take this opportunity to review the following four post-diagenetic patterns of calcification in the Mesozoic Dasycladales:

- 1) Hyaline and colorless sheaths, of inter- or extracellular origin; they are found in most species that lived in normal marine or slightly hypersaline environments and point to the replacement of original aragonite needles.
- 2) Hyaline and yellowish, also inter- or extracellular sheaths; they point to a genuine (algal) precipitation of calcite, mainly in polyhaline habitats.
- 3) Hyaline sheaths bounded by a micritic membrane; they suggest a primary (*in vivo*) and intracellular precipitation of calcite controlled by the genotype. They are found in a few species, from the Kimmeridgian to the Berriasian.
- 4) Microcrystalline sheaths, dark in transmitted light; they cover or replace the genuine (hyaline) sheaths and presumably result from an algal/bacterial calcification process.

RÉSUMÉ

Cylindroporella taurica, n. sp., est décrite dans l'Albien de l'Anatolie orientale; elle est aussi présente dans l'Albien des Dinarides et à la limite Hauterivien-Barrémien en Italie. L'algue présente un type particulier de calcification microcrystalline que l'on trouve chez un petit nombre d'espèces appartenant à des genres différents. A titre de comparaison, les modes de calcification des Dasycladales du Mésozoïque sont passés en revue, ce qui conduit à distinguer quatre types post-diagénétiques:

- 1) Les parois hyalines incolores, d'origine inter- ou extra-cellulaire; elles sont présentes chez la plupart des espèces d'origine franchement marine et dérivent de la précipitation d'aiguilles aragonitiques.
- 2) Les parois hyalines jaunâtres, également d'origine inter- ou extra-cellulaire; elles dérivent d'une précipitation de calcite primaire, le plus souvent en milieu polyhalin.

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- 3) Les parois hyalines délimitées par une membrane microgranulaire; on admet qu'elles correspondent à des remplissages calcitiques intracellulaires, *in vivo*. Elles sont connues chez un petit nombre d'espèces évoluées, du Kimmeridgien au Berriasien, ce qui conduit à envisager un contexte phylogénétique distinct.
- 4) Les enveloppes microcrystallines, noires en lumière transmise, qui correspondent sans doute à un épiphénomène à participation microbienne, plutôt qu'à un authentique processus de biominéralisation alguaire.

Introduction

Type-locality of C. taurica, n. sp.

The *locus typicus* (fig. 1, 2) is sited about 2 km southeast of Daridere village, 5 km south of Sariz town, and 360 km southeast of Ankara, in Eastern Taurus. Greenwhich coordinates are 36°30'E, 38°26'N.

The stratum typicum was picked in Albian limestones forming the top of the Köroglutepe Fm., and dipping about 35° towards the southeast. It consists of white to greyish, weakly pelloidal wackestones containing Cuneolina gr. pavonia d'Orbigny, Cuneolina laurentii Sartoni & Crescenti and Miliolidae (foraminifers), Cylindroporella taurica, n. sp. (Dasycladales), Rivularia spp. (Porostromata), ostracods and microgastropods.

Geological setting

The type-locality belongs to the autochtonous Geyikdagi Unit, introduced by OZGUL (1986). The unit belongs to the Anatolide-Tauride Platform, a part of the passive northern margin of the Gondwana-Land. Figure 3 provides a generalized stratigraphic section of the Geyikdagi Unit, comprising Early Triassic to Maastrichtian sediments subdivided in six formations.

Time-stratigraphy

The uppermost part of the Köroglutepe Fm. belongs to the *Cuneolina* gr. pavonia zone, defined by ALTINER (1981) and by ALTINER & DECROUEZ (1982) in the Eastern Taurus. The zone ranges from the Aptian to the Cenomanian, above the *Praeorbitolina lotzei*, *Palorbitolina lenticularis* etc. subzone and below the first occurrence of *Pseudorhaphydionina dubia*.

Cenomanian and Turonian sediments are missing in the Daridere area. The Köroglutepe Fm. is overlain by the Santonian-Campanian Yaniktepe Fm., containing rudists.

Environments

Shallow marine algal-foraminiferal micrites and dismicrites, interbedded with dolomite and dolomitic limestones, are found at the top of the Köroglutepe Fm. Occa-

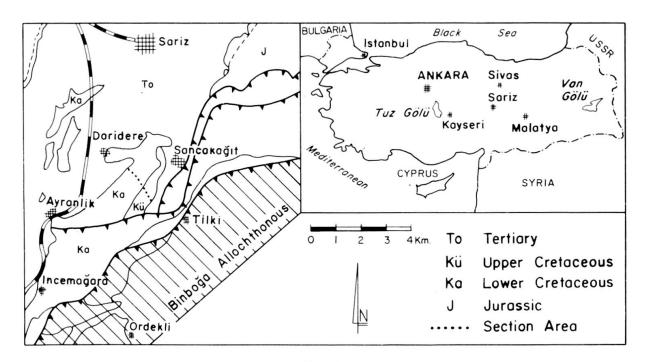


Fig. 1.

Type-locality of Cylindroporella taurica, n. sp. Geographical location and geological setting.

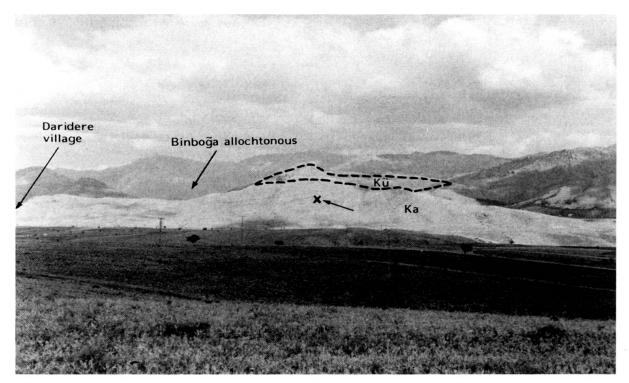


Fig. 2.

Type-locality of *Cylindroporella taurica*, n. sp. The picture looks towards the east and was taken from an area close to the Kayseri (Sariz)-Kahraman Maras highway running in low-relief, Tertiary terrains. Whitish Lower Cretaceous limestones, capped by Upper Cretaceous limestones, are seen next to the Daridere village. The Binboga allochtonous Unit, comprising ophiolites, is seen on the rear.

sionally, they include fresh water assemblages, with Charales and ostracods. Early diagenetic features include mud-cracks, solution vugs filled by meteoric sparry calcite cement, and vadose silts, suggesting fresh water flushing.

Other occurrences of C. taurica, n. sp.

Nice specimens (fig. 7) of the new species were illustrated by VELIC and SOKAC (1978) under the name of *Cylindroporella barnesii*, from the Albian of Croatia. According to these authors, the dasyclad species is found at the boundary between the Lower and the Upper Albian and the following benthonic foraminifers are found in the same interval, corresponding to the upper limit of the *Orbitolina (Mesorbitolina) texana texana* cenozone: *Cuneolina camposaurii* and *C. laurentii* (both having their maximum development here), *C. pavonia*, *C. hensoni (?)*, *Chrysalidina cf. gradata*, *Debarina hahounerensis*, *Hemicyclammina sigali*, *Nummoloculina heimi*, *Nezzazata simplex simplex*, *Pseudotextulariella? scarsellai*, *Sabaudia minuta*, *S. auruncensis*, *Trochospira avnimelechi*, and *Valvulammina picardi*, *Salpingoporella turgida* (Dasycladales), *Coptocampylodon fontis* and *C. elliotti* (incertae sedis) are also quoted from the same interval.

Another specimen probably belonging to *C. taurica*, n. sp., was illustrated by LUPERTO SINNI and MASSE (1984) from the Murge area, in continental Italy, under the name of *Montiella (?) elitzae*. It was found at the basis of the "Salpingoporella biokovensis biozone", within an interval assigned to the top of the Hauterivian or the basal Barremian.

DESCRIPTION OF THE TOPOTYPES OF C. TAURICA, N. SP.

Ordo Dasycladales (PASCHER, 1931) Familia Dasycladaceae KÜTZING, 1843 Tribus Cylindroporelleae PAL, 1976 ¹ Genus Cylindroporella JOHNSON, 1954 ¹

Cylindroporella taurica, n. sp.

Fig. 4-7

1978 Cylindroporella barnesii Johnson — VELIC and SOKAC, p. 336; pl. II, fig. 4-7. Cf. 1984 Montiella (?) elitzae Radoicic, 1980-LUPERTO SINNI and MASSE; pl. 36, fig. 1, non fig. 2-4.

Type-specimens and origin of the name

The holotype and the paratypes (fig. 4-6) are lodged in the micropaleontological collection of the Museum of Natural History, in Geneva. *Derivatio nominis:* Taurus mountain chain.

¹ The suprageneric assignments follow Deloffre (1988).

Diagnosis 2

Thallus simple, cylindrical, straight or curved. Stipe cylindrical, or slightly waxing and waning at height of verticils. Two types of first order ramifications: the R1A (simple, assumed sterile) and the R1B (modified, assumed fertile). Both are perpendicular or slightly oblique to the axis. At periphery of the thallus, they alternate in all similar, contiguous verticils. R1A funnel-like, uncompressed, first very slender, open (uncalcified) at tips. R1B supported by a short and narrow peduncle, pear-shaped or sub-spherical, closed (calcified) at tips, first almost uncompressed, then sub-polygonal at tips where mutually compressed. Thin calcareous sheath, dark and microcrystalline in transmitted light, coating the stipe and the ramifications.

Dimensions

Following measurements were made on 20 topotype specimens.

Maximum length of the thallus

L = up to 4.8 mm

Outer diameter of the thallus

D = 600-1,032 microns, average 854

Diameter of the stipe

d = 100-258 microns, average 161

d/D = 13-27, average 19

Total number of ramifications (R1A+R1B) in one verticil

w = 14-18

Spacing of two contiguous verticils

h = 140-193 microns, average 163

Length of the ramifications (R1A and R1B)

1 = 240-419 micron, average 336

Maximum diameter of the ramifications

p(R1A) = 96-180 microns, average 155

p (R1B) = 125-290 microns, average 198

Diameter of the peduncle supporting the R1B: about 30 microns.

Why Cylindroporella?

The dark, microcrystalline calcareous sheath is an unusual feature, so far never seen in genus *Cylindroporella*. Also, no second order ramifications are present, contrary to the diagnosis of the genus, that also includes "segments" of thallus

² Technical terms (R1A, R1B) in the diagnosis are borrowed from EXPAL/Dasycladales, a computerized expert system introduced by CONRAD and BEIGHTOL (1988).

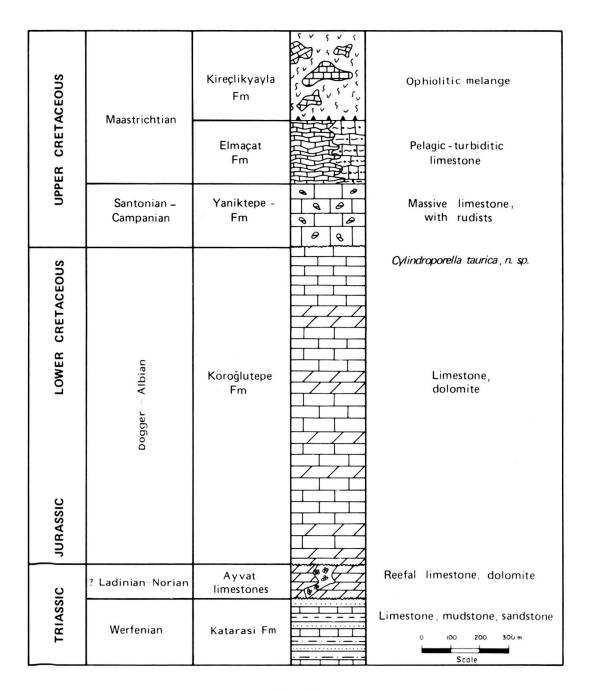


Fig. 3.

Generalized stratigraphic section of the autochtonous Geyikdagi Unit.

tapering at tips. Last but not the least, the presumably very narrow proximal part of the R1A is not seen in thin section. The *Cylindroporella*-like arrangement is seen at periphery of the thallus, not in the area surrounding the stipe, that possibly supported separate verticils of R1A and R1B, as in genus *Heteroporella*.

Comparisons

Main differences with other species of *Cylindroporella* are summarized below in an effort to consider only the "standard" taxonomic characters of the Dasycladales, such as the shape and arrangement of the organs. These characters are probably sufficient to support the creation of a new species; in addition, the microcrystalline sheath provides a clear-cut additional attribute. The writers take this opportunity to comment below on the calcification of certain Mesozoic Dasycladales, and put forward a couple of unorthodox hypothesis in an attempt to promote a discussion on the matter.

At least 14 species are currently assigned to the genus *Cylindroporella*, from the Lias to the Turonian. The type- species *Cylindroporella barnesii* JOHNSON, 1954 was first described from the Albian. It is much smaller than our new species and consists of segments of thallus tapering at tips, with spherical blisters (R1B) and clusters of secondaries arising from the R1A. *Cylindroporella arabica* ELLIOTT, 1957 (Malm-Hauterivian) is even smaller than *C. barnesii*, with same general characteristics.

Dimensions of *Cylindroporella sugdeni* ELLIOTT, 1957 (Hauterivian-Aptian) are more or less similar to our new species; but again, secondaries are present and the blisters are spherical rather than pear-shaped. In our opinion, the Barremian *Cylindroporella maslovi* SRIVASTAVA, 1973 is a junior synonym of *C. sugdeni*.

Based on available illustrations, the Barremian Cylindroporella barbui DRAGASTAN, 1978 is probably a junior synonym of Montiella? elitzae (BAKALOVA) RADOICIC, 1980. Also Cylindroporella benizarensis FOURCADE et al., 1972 (Hauterivian-Albian) looks similar to M.? elitzae; good topotypes will possibly show that it is a synonym of the latter species.

Nice specimens of a very large dasyclad were described from the Aptian by LUPERTO SINNI & MASSE (1989) under the name of *Cylindroporella lyrata*. Some of them clearly belong the genus *Cylindroporella*, whereas other specimens display a single order of fertile primaries and no secondaries.

Cylindroporella elliptica BAKALOVA, 1971 (Hauterivian-Aptian) is usually associated with Salpingoporella mühlbergii (LORENZ) PIA, 1918. In the opinion of the writers, it corresponds to fertile specimens of the latter species, because no R1A are seen, as in a true Cylindroporella, but questionable, very thin "hairs" (10-20 microns in diameter) arise from the distal end of the R1B, and possibly also from the stipe. Cylindroporella arsici RADOICIC, 1971 is also found in the same time-stratigraphic interval. It is much larger with tubular R1B, and cannot be confused with our new species.

The following two species are known from the Cenomanian-Turonian interval: Cylindroporella kochanskyae RADOICIC, 1970 is smaller than our new species; it has

clusters of secondaries, and a comparatively larger stipe. Cylindroporella parva RADOICIC, 1983 is also smaller, and looks similar to C. sugdeni, although not as strongly calcified, with spherical blisters and clusters of secondaries.

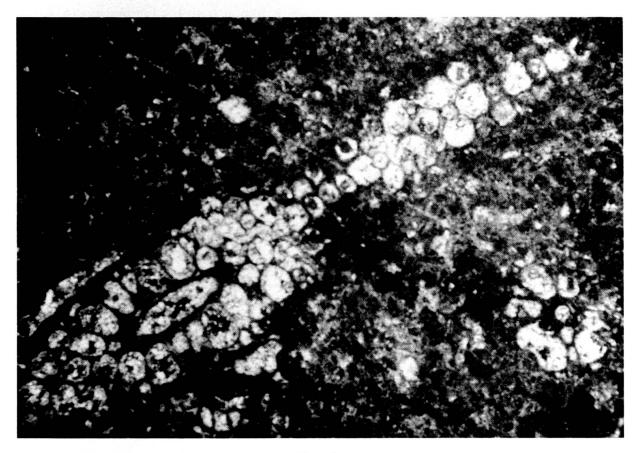


Fig. 4.

Cylindroporella taurica, n. sp. 32 X. Holotype, large oblique-tangential section of a curved piece of thallus encrusted by a? foraminifer. Pseudo-coalescent features are provided by the decay, or diagenetic removal, of the thin microcrystalline sheath coating two contiguous R1B. To the right: small perpendicular section.

Finally, let us mention that available data on the Barremian Cylindroporella adducta (MASLOV, 1960), the Cenomanian or Turonian Cylindroporella elassonos JOHNSON, 1965 and the Late Jurassic Cylindroporella texana JOHNSON, 1961 are unfortunately not sufficient for comparisons.

To sum up, considering only the "standard" characters of the thallus, Cylindroporella taurica, n. sp., is close to the frequently quoted Cylindroporella sugdeni, except for the lack of second order ramifications. In addition, it has a different pattern of calcification, that is dealt with below.

Biogenic and diagenetic features

The following sequence of biological and diagenetic events is inferred from the arrangement of the R1A and R1B, and from the patterns of calcification in topotype specimens.

- 1) Growing up of the sterile ramifications (R1A) out of the cylindrical stipe. Presumably no calcification took place at this stage.
- 2) Growing up of the fertile blisters (R1B) encircling the R1A and modifying the shape of the stipe, where touching each other. Again, no genuine (algal) biomineralization took place at this stage.
- 3) In vivo or early post-mortem algal/microbial calcification that coated the organs and the periphery of the thallus with micrite-sized crystals of Mg-calcite.
- 4) *Post-mortem* subaerial exposure providing the inner face of the R1B to be coated by sparry calcite, leaving a conspicuous moldic porosity.
 - 6) Partial infilling of geopete lime mud, or silt.
 - 7) Subsequent (? mesogenetic) clotting, or "micritization" of the sediment.

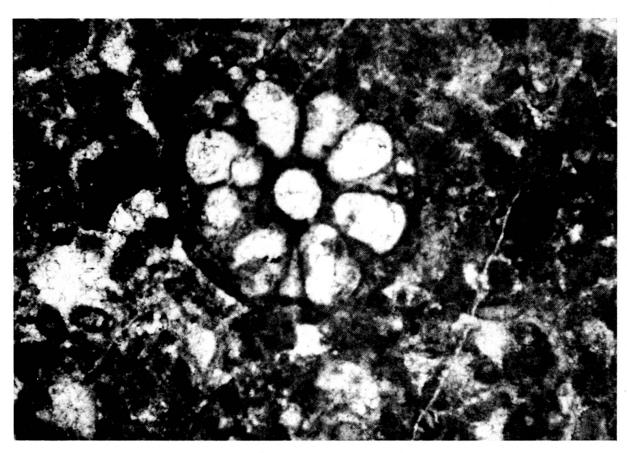


Fig. 5.

Cylindroporella taurica, n. sp. Paratype, 59 X. Almost perpendicular section cutting two verticils. Note the short peduncle supporting the R1B.

PATTERNS OF CALCIFICATION IN EXTANT AND DIAGENETICALLY UNALTERED FOSSIL DASYCLADALES — A SUMMARY

With one unconfirmed exception, calcification in the extant Chlorophyceae always takes place outside the cell wall. Marine taxa including all Dasycladales precipitate aragonite, whereas the CaCO₃ deposits of the fresh water green algae are in the form of calcite. BOROWITZA (1986), mentions the following patterns of CaCO₃ precipitation among the extant Dasycladales.

- 1) "Extracellular", that is within an external mucilage, or sheath; e.g. Acetabularia calyculus.
- 2) "Intercellular", that is within the semi-isolated space formed by appressed cell filaments, providing higher Ph and corresponding CaCO₃ precipitation; e.g. Cymopolia barbata, Neomeris annulata and Bornetella nitida.
 - 3) Simple encrustation of the cell wall; e.g. Acicularia calyculus.

The polysaccharide constituent of the cell wall has apparently no effect on the mineralogy of the CaCO₃: for example, *Acetabularia* precipitates aragonite both on the stipe and around the cysts, which walls are predominantly made up of mannose and cellulose, respectively.

Unaltered calcareous sheaths consist of more or less randomly oriented aragonite needles. They look dark and misleadingly granular under the optical microscope. Ultrastructure of 40 Recent and fossil Dasycladales was investigated by FLAJS (1977) under the scanning electron microscope (SEM). As a result, this author described three consecutive stages (termed a, b and c) of aragonite needles precipitation in the Recent and the Cenozoic specimens. Concerning the older Dasycladales, FLAJS (op. cit.) mentions the single case of a Triassic Clypeina that keeps its original ultrastructure.

PATTERNS OF CALCIFICATION IN DIAGENETICALLY-ALTERED MESOZOIC DASYCLADALES

Observations dealt with below were made using standard optical microscopes. A distinction will be first made between two different patterns of calcification:

1) the usual sheaths, or sleeves, that uninterruptedly fill the space between two contiguous ramifications; 2) the special case of sheaths bounded by a micritic membrane that it always present, even if the ramifications are joined. In the first case, the calcium carbonate presumably precipitated beyond the cell wall, as it does in extant Dasycladales; in the second case, the calcium carbonate apparently precipitated within the limits of the cell.



Fig. 6.

Cylindroporella taurica, n. sp. Paratype, 50 X. Oblique section. Outline of the stipe is obliterated by diagenesis.

HYALINE SHEATHS PRECIPITATED IN INTER- OR EXTRACELLULAR MEDIA

Final (diagenetic) product is a layer of radial-fibrous, or interlocking calcite crystals, usually colorless, sometimes yellowish. Colorless sheaths are found since the Paleozoic and are common to most species in the Mesozoic and the Cenozoic. Usually, they result from the polymorphic replacement *in situ*, of aragonite needles

produced in a variety of normal marine to slightly hypersaline environments. The original structure is usually completely lost and superficial micritization is common. Seldom (e.g. Angioporella fouryae MASSE et al., 1973) part of the thallus is coated by a thin mosaic of brownish crystal, possibly corresponding to an intermediate diagenetic stage or to the presence of organic matter. Also, the original sheath is often completely dissolved and replaced by blocky calcite cement, via a passive cavity stage.

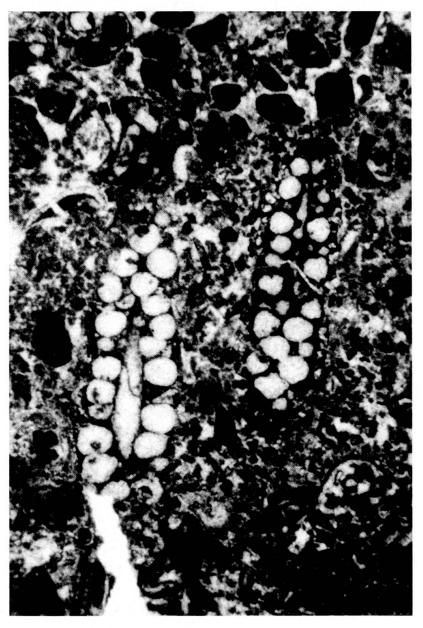


Fig. 7.

Cylindroporella taurica, n. sp. Two oblique and tangential sections, 31 X. Sokac collection, Albian, Croatia.

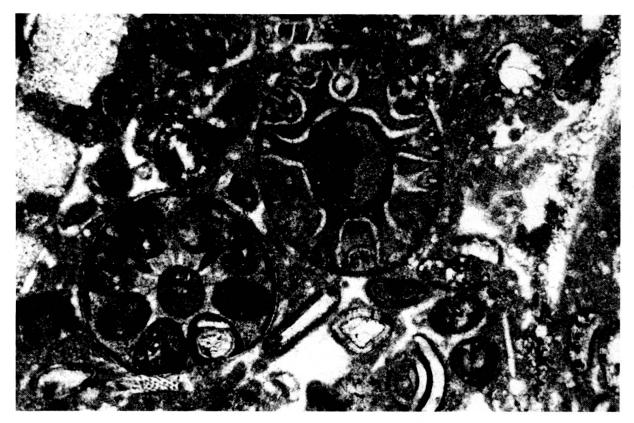


Fig. 8.

Montiella? cf. elitzae (BAKALOVA) (left): space between organs is filled in by a hyaline sheath of calcite, originally aragonite. Deloffrella quercifoliipora GRANIER (right): organs are weakly calcified, and filled in by micritic sediment. 45 X. The two specimens are coated by thin microcrystalline sheaths, presumably of algal/microbial origin. ? Hauterivian, Elburz, Iran. Material R. Fontaine.

In a small number of species belonging to different genera, the hyaline sheath is consistently yellowish in transmitted light, whatever the final depositional environment may be. It is sharply outlined against the sedimentary matrix and micritic envelopes are missing or very rare. The accompanying biota usually points to brackish or polyhaline habitats, which suggests that the calcite is original because precipitation of aragonite was inhibited. A non-exhaustive list of species having yellowish sheaths is given below.

Heteroporella lusitanica (RAMALHO, 1970). Oxfordian, brackish or polyhaline habitats.

Heteroporella lepina Praturion, 1966. Cenomanian, open marine habitats.

Megaporella boulangeri DELOFFRE & BEUN, 1986. Bajocian-Early Kimmeridgian. Protected marine.

Salpingoporella grudii (RADOICIC, 1962). Malm. Brackish or polyhaline habitat in the type locality, where both yellowish and colorless specimens are present. Also reported from marine environments (BERNIER, 1984).

Salpingoporella dinarica RADOICIC, 1959 (alias Hensonella cylindrica ELLIOTT, 1960, alias Hensonella dinarica) — ? Valanginian-Albian in the Southern Tethys Domain. Mainly polyhaline habitats. In the type-locality, and often in micritic limestones the stipe is first outlined by a microgranular film, followed by a sheath of yellowish and radial-fibrous crystals of calcite (fig. 9). Pending detailed studies on the matter, this pattern is believed of primary origin, noting that it is often replaced by yellowish crystals of blocky calcite cement.

Salpingoporella urladanasi CONRAD et al., 1977 — Barremian-Albian. Polyhaline and protected marine habitats.

HYALINE SHEATHS, POSSIBLY OF INTRACELLULAR ORIGIN

This pattern of calcification is found in at least the following four species, that lived within a rather narrow time-stratigraphical interval straddling the Jurassic-Cretaceous boundary.

Clypeina jurassica (FAVRE, 1927) — Kimmeridgian-Berriasian. This well-known species (fig. 10) has a single order of funnel-like ramifications, arranged in regular whorls. Quoting REMANE (1969, p. 88) "the calcareous mantle enclosing the sporangial discs revealed itself as constituted of two layers (...), a thin external one with a granular texture and a thick inner layer composed of radial prisms of crystalline calcite (...). The radial array of the crystals is however purely morphological and does not correspond to an optical orientation".

In his review of the species, BERNIER (1984) mentions that *C. jurassica* keeps its primary pattern of calcification, even when flushed in fresh water diagenetic environments. Actually, the granular layer looks like a mineralized membrane enclosing the cell, unlike a *post-mortem* micritization process, as shown by the fact that it is always present, even where the ramifications are joined. An empty area filled in by sediment is left in the middle (axial) part of the ramifications, which internal sides are always coated by one or two generations of "radial prisms", made up of colorless or yellowish hyaline calcite. The ramifications are never closed (calcified) at tips, which, in the opinion of the writers, suggests a genuine, *in vivo* and intracellular algal mineralization process that followed the release of reproductive cells.

Pseudoclypeina cirici RADOICIC, 1970 — Kimmeridgian. This large and distinct species has three orders of ramifications and a pattern of calcification similar to Clypeina jurassica except that ramifications are closed. According to BERNIER (1984), P. cirici would be a ecophenotype of the latter species, which would be unusually calcified in the upper part of the thallus, owing to special environmental

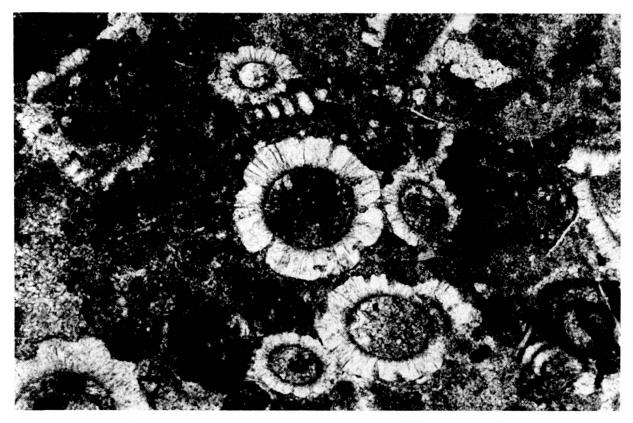


Fig. 9.

Topotypes of Salpingoporella dinarica RADOICIC, 72 X. Note the dark proximal film, followed by a solid sheath of yellowish and radial-fibrous crystals of calcite, assumed of primary origin.

conditions. This interpretation is however challenged by the fact that *P. cirici* was so far not reported from the northern Tethyan realm.

Clypeina? durandelgai JAFFREZO & FOURCADE, 1973, and Falsolikanella Campanensis (AZEMA & JAFFREZO) GRANIER, 1987. Berriasian. Patterns of calcification similar to C. jurassica are also found in these species, which main "standard" characters are spaced out verticils of diverging first order ramifications.

Indeed, essential characters are shared by these four species, which suggests some phylogenetical relationship rather than a simple coincidence: roughly same degree of evolution of the plant body, including a probable cladospory; same pattern of calcification; roughly same age; and same habitat in protected tropical pools or lagoons, as shown by the associated biota.

DARK, MICROCRYSTALLINE SHEATHS OF ALGAL/BACTERIAL ORIGIN

The following discussion applies to Dasycladales having a true microcrystalline sheath, of definitely primary origin. As in the case of other organisms (e.g. molluscan

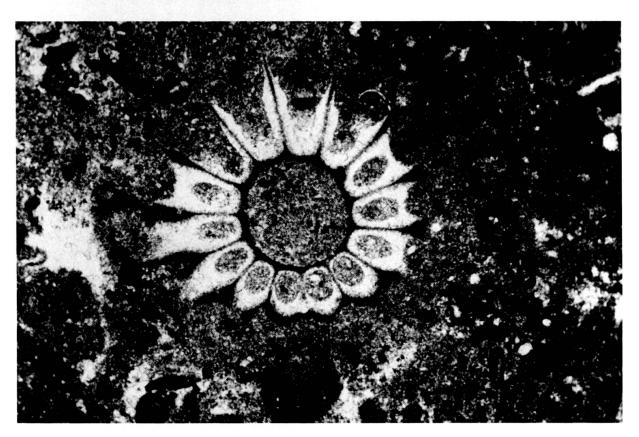


Fig. 10.

Clypeina jurassica (FAVRE). Perpendicular section, 31 X. Pierre-Châtel, SE France. A. Carozzi collection. The ramifications are open, filled in by hyaline and radial-fibrous calcite and bounded by a microcrystalline membrane, or sheath, assumed of primary origin.

shells), the usual hyaline sheaths of Dasycladales which have not been dissolved via a cavity stage, are quite often partially replaced by a micritic envelope, a well-known process that an experienced petrographer will easily detect.

Sometimes, a true microcrystalline sheath can be observed in lieu of the usual hyaline sheath, commonly seen in a given species. For example, this appears to be the case of the specimen of *Sarfatiella dubari* illustrated in figure 11, where an encrusting bryozan presumably settled while the alga was alive and is thought to be the indirect cause of a particular type of mineralization in the presence of organic matter accidentally degraded.

True microcrystalline sheaths are unusual among the fossil green algae assigned to the Dasycladales. They are known since the Paleozoic, but only Mesozoic species will be dealt with in this article. The following examples are arranged by chronological order, in addition to our new species:

Macroporella? sellii CRESCENTI, 1959. Callovian-Kimmeridgian. Primitive pattern, with a full, microcrystalline sleeve coating aspondylous, slender and appressed sterile ramifications. Habitat: protected marine.

Vermiporella? tenuipora CONRAD, 1970. An incertae sedis according to some algologists. Berriasian-Turonian. Taxonomy is similar to M.? sellii, but ramifications are much thinner. Habitat: open marine and lagoonal.

Clypeina catinula CAROZZI, 1956 — Berriasian. Thin sheath coating spaced out verticils of club-shaped ramifications, presumably fertile. Habitat: protected marine.

Clypeina nigra CONRAD & PEYBERNES, 1978. Barremian-Aptian. Conspicuous sheath coating verticils of club-shaped primaries, closed at tips, presumably fertile. Habitat: open sea and protected marine.

Mesozoic Dasycladales having a microcrystalline sheaths are generally found in sediments corresponding to very shallow marine and muddy enbayments or pools, with a low-diversity and no filter-feeder accompanying biota. In most cases the outer surface of the sheath is smooth, but certain specimens display the simultaneous presence of microcrystalline concretionary aggregates located beyond the outer limits of the thallus. These observations cautiously suggest a link between the algal habitat and this type of mineralization.

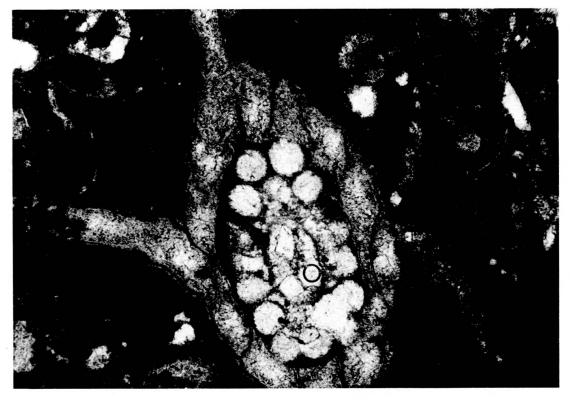


Fig. 11.

Sarfatiella dubari Conrad & Peybernes (possibly a junior synonym of Holosporella siamensis PIA), 69 X. An encrusting bryozan is thought to be the indirect cause of the unusual, microcrystalline pattern of mineralization, in the presence of organic matter accidentally degraded. Middle Jurassic, Madagascar.

On the other hand, the extent of the microcrystalline sheath looks constant in a given species. Depending on the species chosen, the sheath can form a sleeve (e.g. *Macroporella? sellii*) or, on the contrary, be limited to a relatively thin layer coating organs separately except where touching each other (e.g. *Clypeina catinula* and *Clypeina nigra*). Under this point of view, this type of mineralization appears to be a normal (skeletal) accretionary layer linked to the genotype.

As a first approximation, true microcrystalline sheaths therefore appear to be linked to the habitat, though peculiar to certain species. This is not necessarily contradictory but points at a conjunction of two phenomena, respectively exogenous and endogenous. In an attempt to explain the origin of this feature, some possible mechanisms are listed below.

- 1. In vivo or immediate post-mortem, biologically influenced (algal-related) skeletal or non-skeletal calcification process, presumably due to parasitic or symbiontic cyanobacteria that impregnated an algal/microbial mucilage with micrite-sized crystals of Mg-calcite. This hypothesis calls upon the concept of Microbial Framestone, a name coined by BURNE & MOORE (1987). It is supported herein.
- 2. Special to some taxa, genuine (skeletal and algal) biomineralization, that precipitated tiny crystals of Mg-calcite instead of the usual aragonite needles.
- 3. Organosedimentary deposits resulting from microbes trapping and binding detrital micrite (Microbial Boundstones).
- 4. Early diagenetic removal of an original aragonitic sheath, replaced by an endolithic microbial mat.

There is indeed a general difficulty of recognizing whether some microcrystalline features are merely of primary or secondary origin. But as far as the above-mentioned species are concerned, the first hypothesis is supported by the following arguments:

- True microcrystalline sheaths are found either alone, or together with the usual hyaline sheaths. In the first case (fig. 5) they meet the former limits of the plant matter; in the second case (fig. 8 and 12), they form a protective cover enclosing the primary hyaline sheath. This calls indeed on two very different processes of calcification.
- Species with microcrystalline sheaths may be found together with other Dasycladales having the usual pattern of calcification, even if the algal habitat looks the same. Species therefore do not react in the same way to similar environmental conditions.
- Distribution of the microcrystalline sheath is consistent: intermediate patterns combining hyaline mantles are not reported; on the other hand, the sheath may be locally replaced by patches of hyaline calcite clearly due to aggrading neomorphism.
- No internal structures are seen, even under high optical magnification. Microbial Boundstones would be expected to produce organo-sedimentary structures, such as laminations, reflecting their proper site of sediment binding.



Fig. 12.

Heteroporella? paucicalcarea Conrad, 52 X. The specimen is covered by a microcrystalline sheath capping the usual hyaline sheath and the non calcified periphery of the fertile blisters. (These are generally open and filled in by sediment). Barremian, Pyrenees. Material: B. Peybernès.

- A genuine (solely algal) microcrystalline biomineralization would be expected to be present in taxa linked by some phylogenetic relationship. Likely, this is not, or at least not obviously the case if one considers that true microcrystalline sheaths are found in several, very different genera.
- Microcrystalline sheaths or films look very resistant to the effects of the diagenesis, which is probably due to the presence of an abundant and adhesive organic matter. Providing mechanical strength, they prevent the penetration of micritic sediment inside the pores corresponding to ramifications that are filled in by sparry calcite cement.

— Finally, figure 12 shows a normally calcified specimen of *Heteroporella?* paucicalcarea covered by an additional microcrystalline sheath located both, on the hyaline sheath and on the non calcified periphery of the fertile blisters. (These are generally open and filled in by sediment). The microcrystalline sheath appears therefore to result from an autonomous phenomenon, not from the micritization of a previously calcified substratum. The same applies to other taxa illustrated in figure 8.

To sum up, we shall bear in mind that the true microcrystalline sheaths are independent adhesive layers which can either replace or cover the usual (hyaline) skeletal sheaths. In the absence of the latter, they may partially or completely fill in the space separating the fertile or vegetative organs of a specimen, acting as an exoskeleton and contributing to the bearing of the alga.

In the opinion of the writers, in many cases at least, the microcrystalline sheath should not be considered as a taxonomic character in the strict meaning of the term, but rather as a criterion for the absence of true skeletal calcification in certain taxa. Anyhow, this opinion applies to taxa whose morphological characters lead to the reasonable conclusion that they belong to known genera such as *Clypeina*, *Cylindroporella*, *Macroporella* etc. The approach may be different with primitive taxa such as *Pseudovermiporella* and *Vermiporella*, whose microcrystalline sheaths could be of merely algal origin. But are these taxa really Dasycladales, and if so, do they not belong to an entirely separate lineage?

CONCLUSIONS

Description of *Cylindroporella taurica*, n. sp., and comparisons with other taxa provide an opportunity to review briefly the following four patterns of calcification in the Mesozoic Dasycladales:

- Hyaline and colorless sheaths are common; they point to a genuine (algal) biomineralization of aragonite in normal marine or slightly hypersaline environments.
- Hyaline and yellowish sheaths are found in a few species belonging to different genera; they point to a genuine (algal) biomineralization of calcite and, in some cases, to an adaptation to brackish or polyhaline habitats.
- Hyaline calcite infillings assumed of intracellular origin are found in a few species, from the Kimmeridgian to the Berriasian. They suggest an *in vivo* algal process of mineralization, related to an extinct branch of the Dasycladales.
- Dark, microcrystalline sheaths point to a biologically influenced (algalrelated) calcification process, presumably due to cyanobacteria that impregnated an algal/microbial mucilage with micrite-sized crystals of Mg-calcite. They cover or

replace the genuine (hyaline) sheaths and are not, or only partially controlled by the genotype.

Patterns of calcification look largely independent of the morphology of the thallus. They provide significant attributes and are helpful environmental indicators, but some of them only are taxonomic characters in the strict meaning of the term. To support some of the hypothesis that are put forward in this article, it is suggested to promote detailed studies on the calcification of the Paleozoic and Mesozoic Dasycladales, using the SEM and conducting cathodo-luminescence tests.

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