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Microfossils of the *Tarthinia-Palaeomicrocodium* group (filamentous cyanobacteria) from the Lower Cambrian of SW-Sardinia (Italy)

Antonietta CHERCHI
Dipartimento di Scienze della Terra
Università di Cagliari

Michael FRÖHLER
Taberg Planungsbüro GmbH
Kassel

Rolf SCHROEDER
Geologisch-Paläontologisches Institut
Universität Frankfurt a.M.

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ABSTRACT – Small, irregularly spherical or cloud-like bodies with a central cavity have been found in the Lower Cambrian Gonnese Group at Cala Domestica near Buggerru (Iglesiente, SW-Sardinia). The clearly radial-fibrous aspect of the bodies suggest that these organisms may be interpreted as filamentous cyanobacteria. A morphological and structural comparison with some, mainly Paleozoic, genera reveals that the Cambrian specimens most probably belong to *Palaeomicrocodium* (including the Middle Triassic forms described as *Baccanella*). Clear affinities exist also to the Lower Cambrian genus *Tarthinia*, which is, unfortunately, insufficiently known till now. Therefore, we prefer to describe our material under the term *Tarthinia-Palaeomicrocodium* group.

RIASSUNTO – [Microfossili del gruppo *Tarthinia - Palaeomicrocodium* (cianobatteri filamentosi) del Cambriano inferiore della Sardegna Sudoccidentale] – Nel Cambriano inferiore (Gruppo di Gonnese) dell'Iglesiente (Sardegna SW) sono stati ritrovati nei pressi di Cala Domestica (Buggerru) piccoli corpuscoli irregolarmente arrotondati mostranti una cavità centrale. Per il loro aspetto chiaramente fibroso-radiale possono essere considerati cianobatteri filamentosi. Un confronto morfologico e strutturale con altri generi, soprattutto del Paleozoico, induce a ritenere che le forme cambriane appartengano molto probabilmente a *Palaeomicrocodium* (inclusendo le forme del Trias medio descritte come *Baccanella*). Forti affinità esistono inoltre con il gen. *Tarthinia* del Cambriano inferiore, che è purtroppo ancora insufficientemente conosciuto. Per questa ragione, preferiamo indicare il nostro materiale con la denominazione "gruppo *Tarthinia-Palaeomicrocodium*".

INTRODUCTION

Calcified cyanobacteria abundantly occurred in numerous Cambrian carbonate platforms. As upright bush-like structures consisting of branching rods, as encrustations around reef organisms or as pendent colonies in cavities they constitute a wide range of morphological types and took part in the construction of reefal buildups throughout this period (Zhuravlev & Wood, 1995, p. 453).

Cambrian cyanobacteria were found for the first time in Sardinia: Bornemann (1886, pp. 16-17) established the widespread «algal» genus *Epiphyton* and described from Cuccuru Contu near Iglesias *Epiphyton flabellatum*, which he found as epiphyte to an archaeocyathan. The same author (1886, pp. 16) discovered in the «red marble» of Masua the new species *Conservites primordialis*, which is, according to Riding (1991b, p. 309), «*Epiphyton*-like». *Renalcis* Vologdin is another frequently occurring, and therefore often cited, cyanobacterial genus in the Lower Cambrian of Sardinia. The intergrowth of *Epiphyton* and *Renalcis* was discussed by Cherchi & Schroeder (1985).

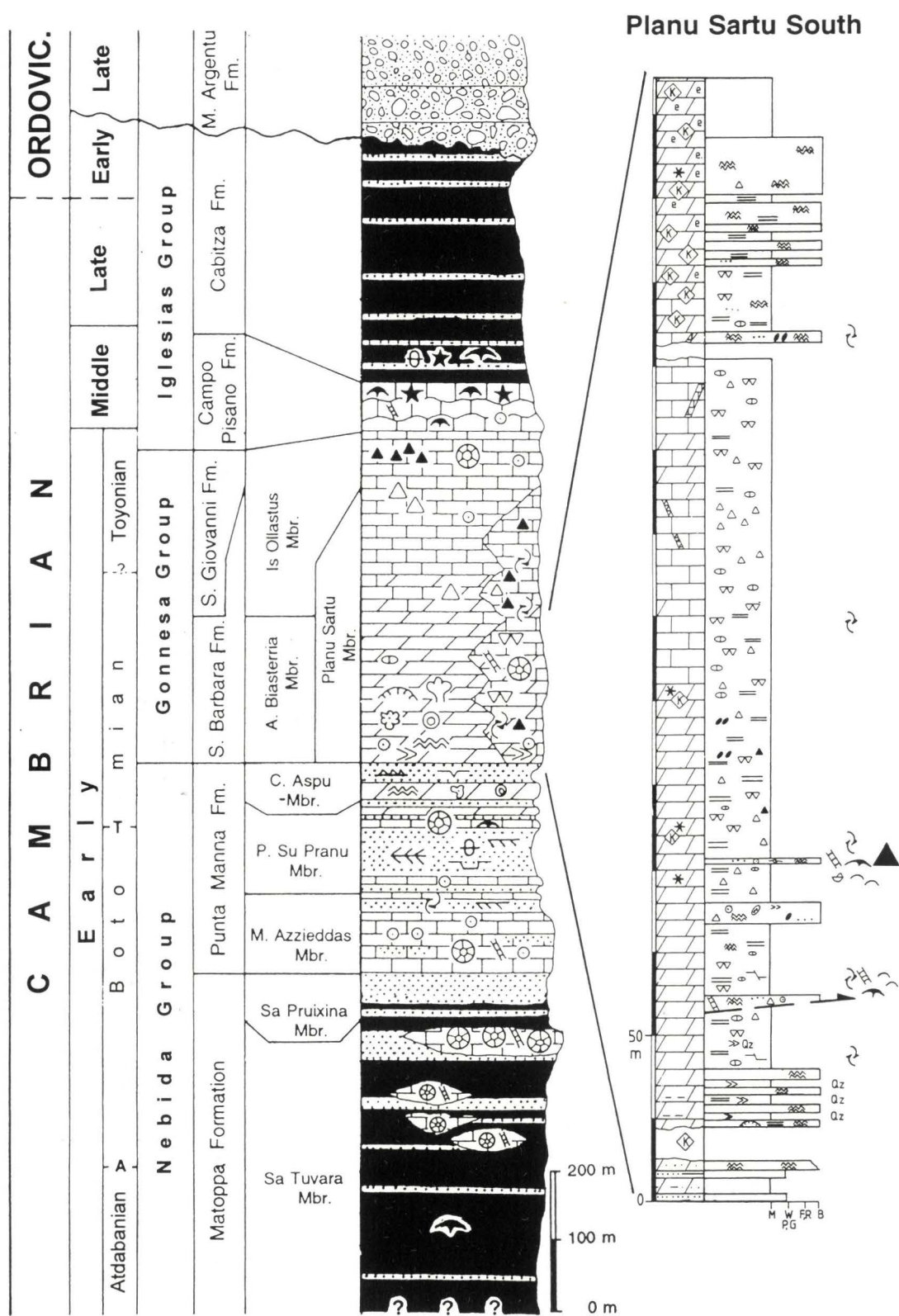
Within the scope of a doctoral thesis (1994) on the evolution of the Lower Cambrian Gonnese carbonate platform (SW Sardinia) Fröhler collected a series of samples east of Cala Domestica in the

Buggerru-Acqueresi region. One of them (Fröhler 12/13) has yielded abundant calcified cyanobacteria: *Renalcis*, *Botomaella* (?), and small spheroidal forms, which we assign to the *Tarthinia-Palaeomicrocodium* group. This latter group is the subject of the present paper.

REGIONAL AND STRATIGRAPHIC SETTING

The Lower Cambrian Gonnese carbonate platform, exposed in Southwest Sardinia, belongs to the late Botomian and Toyonian ages (Text-fig. 1). It is underlain by siliciclastics and carbonates of the late Atdabanian and Botomian Nebida Group. The overlaying nodular limestones and siliciclastics of the Campo Pisano Formation and Cabitza Formation represent sediments of Middle Cambrian to Lower Ordovician ages (Debrenne & Gandin, 1985; Bechstädt & Boni, 1989; Pillola, 1990). The Cambrian of Southwest Sardinia, according to a classification proposed by Pillola (1990), is subdivided in groups, formations and members (Text-fig. 1).

With the onset of Gonnese Group terrigenous input was interrupted and the platform became isolated. Flanks, occasionally very instable, occur at the southeastern and northwestern parts of the plat-



Text-fig. 1 - Generalized Cambrian stratigraphic column. The big triangle at the right border of the Planu Sartu South-column indicates the position of the microfossils of the *Tarthinia-Palaeomicrocodium* group. The Atdabanian/Botomian boundary is still in discussion (A = archaeocyathans; T = trilobites). Modified after Pillola (1990, text-fig. 2) and Fröhler & Bechstädt (1992, text-fig. 1).

form. The lower to middle part of the Gonnesa Group is subdivided in the platform sediments of the Arcu Biasterria Member («Laminated Dolomite» and «Grey Dolomite») and the platform margin dolomites and limestones of the Planu Sartu Member (*sensu* Bechstädt *et al.*, 1985).

GONNESA GROUP

The sediments of the interior platform consist of tidal to supratidal carbonates (Arcu Biasterria Member). They are arranged in shallowing upward cycles. Detailed descriptions are given by Gandin *et al.* (1974) and Bechstädt & Boni (1989). Stromatolitic boundstones with intercalated mudstones prevail, associated with oncolites, grapestones, peloids and vadose pisolites. Subordinate layers of ooids probably originated in situ within microbial mats (comp. Dahanayake *et al.*, 1985). Pseudomorphs after evaporite minerals are scattered in the mudstone. Black coloured dolomitic tufa beds indicate temporary subaerial exposition of this unit (Bechstädt & Boni, 1989). Within the Arcu Biasterria Member «Laminated Dolomite» is generally followed by the often sucrosic «Grey Dolomite», which occasionally shows structures like microbial layering or components.

In the Buggerru-Acquaressi area (Text-fig. 2) the lower to middle part of the Gonnesa Group is developed in the platform margin facies of the Planu Sartu Member. In the upper part of this Member, dolomitic sediments alternate with «Black Limestones». Near Aquaressi, the marginal facies passes into the platform facies of the Arcu Biasterria Member situated towards the east. In the Buggerru area the Planu Sartu Member is represented by low

energy microbial mats and mud laminites, with intercalated buildups in the upper part (Fröhler *et al.*, 1991a, b). The Lower Cambrian sediments of south-western Sardinia have been heavily influenced by early and late tectonics.

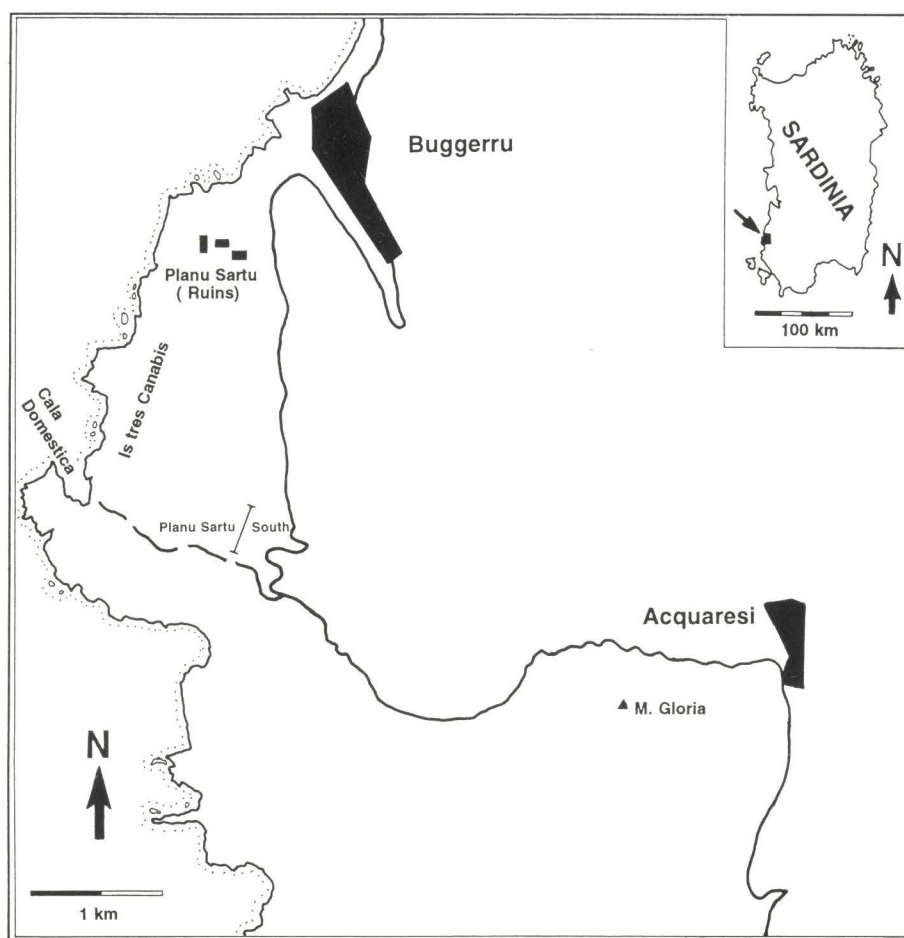
CALCIMICROBIAL-ARCHAEOCYATHAN BUILDUPS

Numerous reef-like buildups within the laminites occur about 80 to 150 m above the base of the Gonnesa Group in the Buggerru-Acquaressi region. These meter to some tens of meters thick buildups have been constructed by several groups of microbial organisms, e.g. *Epiphyton*, *Renalcis*, and *Girvanella* (Fröhler *et al.*, 1991b). The crudely laminated, dendrolitic and clotted calcimicrobial structures are comparable to low energy buildups, described by James & Gravestock (1990) from the Lower Cambrian of Australia. Transition to the enclosing laminites is frequently indistinct. Regular and irregular archaeocyathans within buildups generally show encrustations by microbial layers and *Renalcis* (Fröhler *et al.*, 1991a, b). Fragments of archaeocyathans occur within debris flows (Bechstädt & Boni, 1989). Some buildups show partial to complete silicification as well as late calcitic cements (Fröhler *et al.*, 1991b). Microfossils of the *Tarthinia-Palaeomicrocodium* group were found near Cala Domestica (sample Fröhler 12/13; Text-figs. 1, 2). Additional fragments of trilobites, echinoderms, sponges, problematic microfossils with analogies to foraminifers, and tubular fossils of uncertain affinity occur (Fröhler *et al.*, 1991a, b). The fossil content within the buildups and in associated debris indicates temporary open marine conditions during lower to middle Gonnesan time in the Buggerru

Legenda

	Conglomerates		Ooids / Peloids		Ripple marks / Parallel lamination
	Nodular Limestone		Pisolites / Oncoids		Cross-bedding / Herringbone cross-bedding
	Limestone		Lithoclasts		Desiccation cracks / Channels (erosion)
	Dolomite		Aggregates / Algal clasts		Debris flow / Mass flow / Internal Breccias
	Late Karst Late Dolomite Silicification		Stromatolites / Microbial mats		Segmented fabric / Slumping
	Sandstone		Calcimicrobes		Chert layers / Chert nodules
	Siltstone / Shale		Dolomitic tufa		Pseudomorphs after evaporites
			Burrows		? Fault
			Archaeocyathans		
			Tube-like problematical fossil		
			Trilobites / Echinoderms		
			Brachiopods / Shell hash		

M = Mudstone, W = Wackestone, P = Packstone,
G = Grainstone, F = Floatstone, R = Rudstone,
B = Boundstone



Text-fig. 2 - Map of the studied area in southwestern Sardinia.

area. None of these facies types occur at the eastern margin in eastern Sulcis.

Contrary to western areas, the eastern basin probably was much more restricted.

DESCRIPTION OF THE MATERIAL

The studied sample (Fröhler 12/13) contains thin, lens-shaped accumulations of several hundred relatively closely packed specimens embedded in a sparitic matrix, which we assign to the *Tarthinia* - *Palaeomicrocodium* group.

Typical specimens (e.g. Pl. 1, figs. 1, 3-4) are irregularly spherical or cloud-like bodies from 0.25 to 0.6 mm in diameter. Cross sections show an

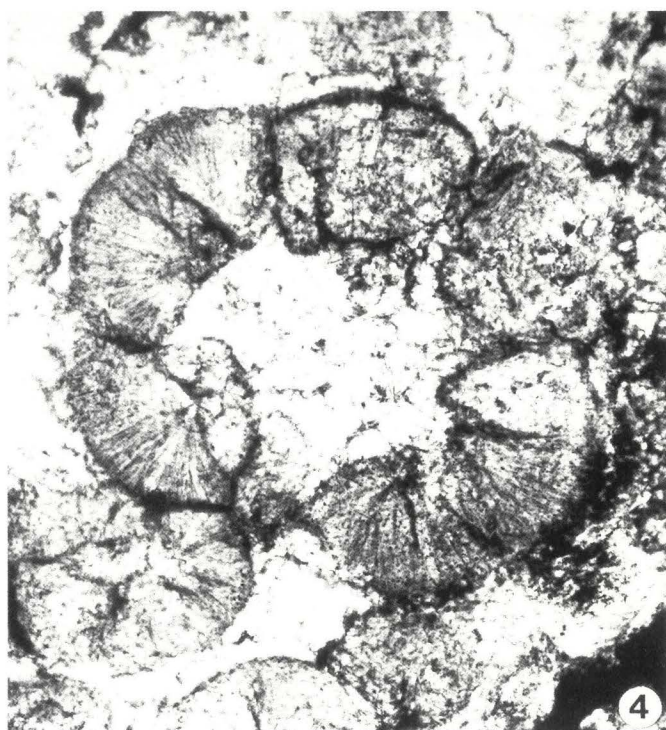
irregularly shaped and more or less well delimited central cavity, which is surrounded by a relatively thick «wall». In small specimens the central cavity is hardly developed or even lacking (Pl. 2, fig. 1: lower part).

The yellowish-brownish, sparitic «wall» is composed of numerous segments. In cross-section through a spherical body these segments are relatively broad and mostly wedge-shaped in outline showing a curved outer border (Pl. 1, figs. 1-4). In most cases the boundary between adjacent segments is well marked by a dark line, which continues in a crack enlarging towards the central cavity.

In all specimens the «wall» has a clearly radial-fibrous aspect and shows sometimes a very thin ex-

EXPLANATION OF PLATE 1

Figs. 1-4 - *Tarthinia* - *Palaeomicrocodium* group; $\times 120$. Planu Sartu Member, Gonnese Formation (Botomian, Lower Cambrian). Cala Domestica near Buggerru, SW-Sardinia (sample Fröhler 12/13).



ternal micritic layer. The fibres of each segment are arranged fan-like. Well preserved and strongly enlarged segments suggest, that these are composed of fine tubular filaments, which are generally straight (Pl. 2, fig. 4), but sometimes also slightly curved (Pl. 1, fig. 2: uppermost part).

Frequently, the spherical bodies are subdivided in some compartments, each of them showing a pronounced convex outer border (Pl. 1, fig. 3). This structural type leads to clusters of a few or many, closely packed, irregularly spherical or hemispherical bodies, which are flattened against one another (Pl. 1, fig. 2).

In many spheres some segments seem to be not any more in their original position, but somewhat displaced (Pl. 1, fig. 4: upper right quadrant). Sometimes they are completely removed (Pl. 2, fig. 3: upper left quadrant); isolated segments are found in the sparitic matrix. These observations suggest that originally the spheres were not very solid.

DISCUSSION

The specimens described before show morphological and structural affinities to some, mainly Paleozoic, spherical or cloud-like bodies, probably formed by filamentous cyanobacteria. Unfortunately, most of them are insufficiently described and/or figured, so that a comparison becomes difficult.

1. *Palaeomicrocodium devonicum* Mamet & Roux, 1983.

The specimens studied in this paper have been determined some years ago by Cherchi and Schroeder as *Palaeomicrocodium devonicum* Mamet & Roux and were reported under this name by Fröhler *et al.* (1992, pl. 1, fig. 5), Fröhler & Bechstädt (1992, p. 274; text-fig. 4/5) and Fröhler (1994, pp. 71-72; pl. 9, fig. 6).

Mamet & Roux (1983) described *Palaeomicrocodium devonicum* as a Paleozoic representative of the family Microcodiaceae Maslov from the Frasnian of Australia. Since then, this species, which is regarded as common in marine back-reef environments (Roux, 1991, p. 366), has been found in the Givetian of Belgium (Mamet & Pr  at, 1985). The

genus *Palaeomicrocodium* was reported from the Devonian/Carboniferous transition of China (Mu & Zhang, 1988; Mamet, 1993) and of Siberia (Bogush *et al.*, 1990), from the Frasnian mud-mounds of Belgium (Mamet & Boulvain, 1992) and from the Permian of Asturias (NW-Spain) by Mamet & Martinez Garcia (1995).

According to Mamet & Roux (1983, p. 95), the thallus of *Palaeomicrocodium devonicum* is composed of an «agr  gat de rosettes de plaques calcaires radiaires et aplaties». A joined reconstruction drawing (text-fig. 5) shows that these «rosettes» (better: spheres!) consist of radially directed, slender, elongated prisms surrounding a very small central cavity. This reconstruction resembles the structure of the genus *Microcodium* (cf. Bodergat, 1974, pls. 2-7; Frey  tet & Plaziat, 1982, text-fig. 27), and indeed Mamet & Roux emphasized that *Palaeomicrocodium* may be regarded as a cluster of spherical and microscopical *Microcodium*.

However, the reconstruction of *Palaeomicrocodium devonicum* is in two respects inconsistent with the structures of the specimens figured by Mamet & Roux (1983, pl. 9), Mamet & Pr  at (1985, pl. 1) and Mamet & Boulvain (1992, pl. 4, fig. 11):

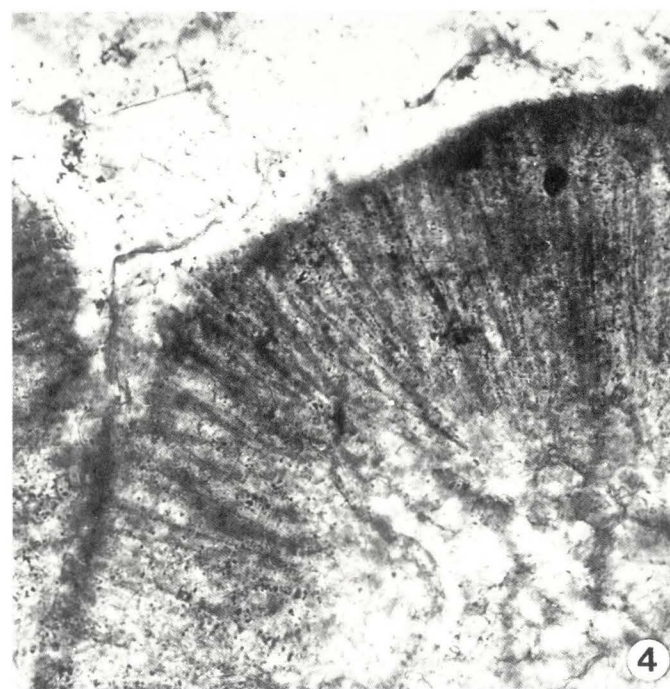
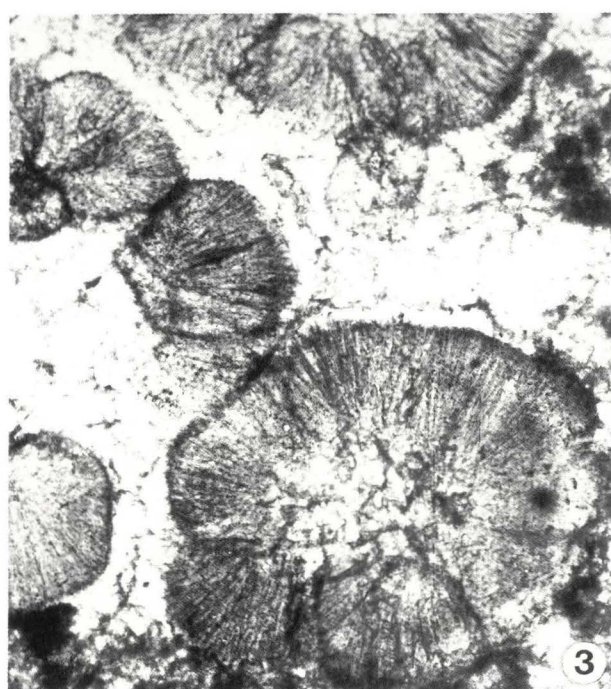
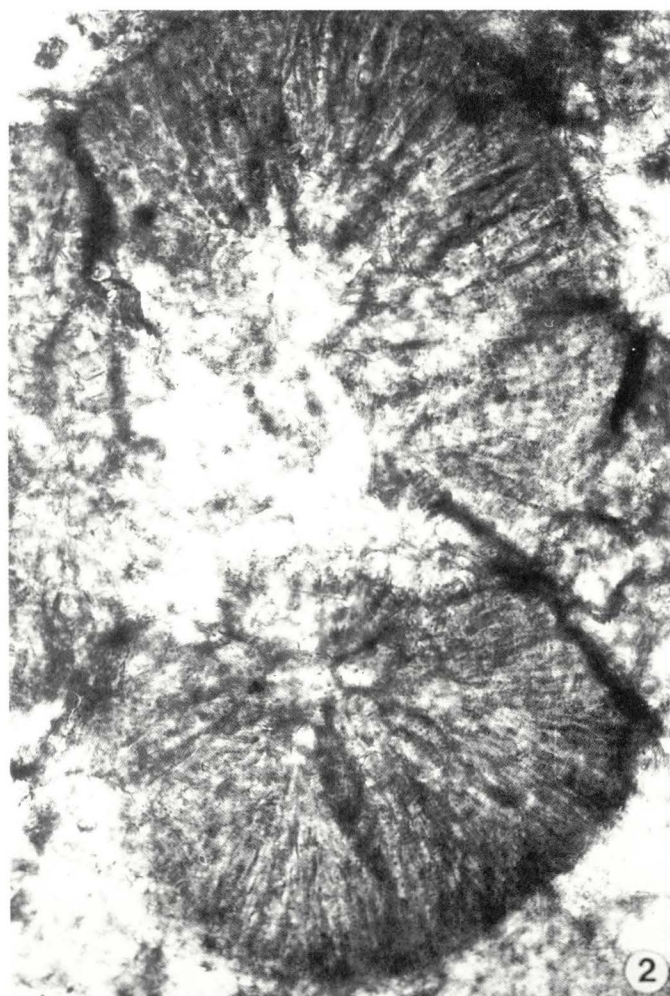
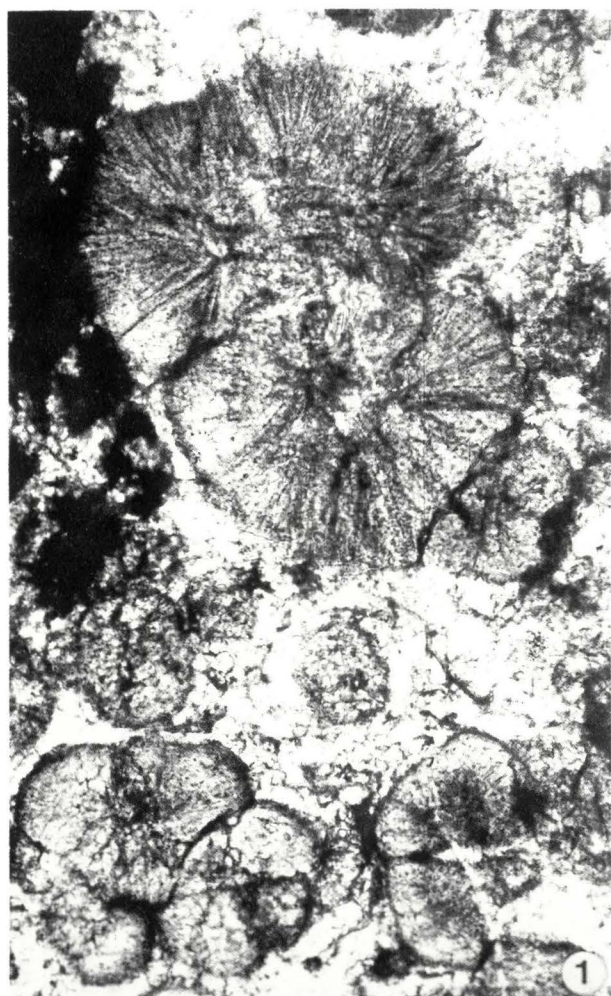
1) The calcitic segments composing the spheric bodies are generally not elongate as in *Microcodium*, but nearly always very broad (sometimes broader than long) (e.g. Mamet & Pr  at, 1985, pl. 1, fig. 1, lower part).

2) According to Mamet & Martinez Garcia (1995, p. 418), there is no trace in *Palaeomicrocodium* of an internal, non-calcified cavity. However, such a cavity is drawn in the reconstruction presented by Mamet & Roux (1983). Also the cluster of *Palaeomicrocodium* sp., figured by Mamet & Boulvain (1992, pl. 4, fig. 11) shows some spheres, which apparently are filled with micrite. Central sections of *P. devonicum* figured by Mamet & Roux (1983, pl. 9, fig. 4, lower right quadrant; fig. 7, lower half; fig. 8, center) and by Mamet & Pr  at (1985, pl. 1, fig. 1, lower half) probably show a large sparitized central cavity.

According to Mamet & Roux (1983, p. 96), the segments of *P. devonicum* show «fant  mes de fibres»; however, Mamet (1991, p. 416) rejected the opinion of Mu & Zhang (1988), that the segments are composed of radial fibrous calcite. Although this con-

EXPLANATION OF PLATE 2

Figs. 1-4 - *Tarthinia* - *Palaeomicrocodium* group; Figs. 1, 3: $\times 120$; Figs. 2, 4: $\times 300$. Planu Sartu Member, Gonnessa Formation (Botomian, Lower Cambrian). Cala Domestica near Buggerru, SW-Sardinia (sample Fr  hler 12/13).



tradition requires further studies, some sectors of the specimens figured by Mamet & Roux (1983, e. g. pl. 9, fig. 4) and Mamet & Pr  at (1985, e.g. pl. 1, fig. 7), which are not affected by the general recrystallization, show radial-fibrous structures being identical with those of the Cambrian material.

After a comparison between the sections of *Palaeomicrocodium*, figured by the foregoing authors, and our specimens from the Lower Cambrian of Cala Domestica we come to the conclusion that the two groups are most probably congeneric. Cross-sections show the same morphology of the spherical bodies and its arrangement in clusters, the same form and outline of segments, a large central cavity, as well as radial-fibrous microstructure in the Cambrian and most probably also in the Devonian-Carboniferous specimens.

2. *Baccanella floriformis* Panti  , 1971

This species was described by Panti   (1971) as a doubtful codiacean alga from marine Ladinian beds (Middle Triassic) of the Dinarides, where it occurs together with sphinctozoans, solenoporaceans, dasycladaceans and foraminiferids. According to Senowbari-Daryan (1984, p. 27), it was found in Ladinian to Rhaetian reef sediments of SE-Europe, Sicily and Turkey.

Panti   (1971, p. 110) characterized *B. floriformis* as irregularly spherical bodies (diameter: 0.06-0.53 mm) showing a «small opening, sometimes darker in color», which is surrounded by three up to more than ten «flower-like branches», which are «divided into smaller sections» (cf. Pl. 3, figs. 7-9).

The «spherical bodies» described as *B. floriformis* show the same shape and arrangement as our Lower Cambrian material. The «small opening» corresponds to the central cavity of our specimens; it is not in the least always «small» (as drawn by Panti  , 1971, text-fig. 2), but sometimes relatively large and filled by micrite (cf. Pl. 3, fig. 9). The «flower-like branches» correspond without any doubt to the segments of the Cambrian specimens. The «smaller sections» of the «branches» of *B. floriformis* indicate perhaps the radial-fibrous aspect of the segments.

As Cherchi & Schroeder (1988, p. 80) already pointed out, the genera *Baccanella* and *Palaeomicrocodium* are identical. Unfortunately, Panti   (1971) has not designated a holotype of *B. floriformis*, the only species of that genus (six «syntypes» are named); it is, therefore, an invalid taxon (Mamet & Martinez Garcia, 1995, p. 418).

3. *Tarthinia rotunda* Drosdova, 1975

The genus *Tarthinia*, which originally was thought to be a rhodophycean alga (Drosdova, 1975a, b), comprises two species, both coming from the Lower Cambrian of western Mongolia: *T. rotunda* (the type-species) and *T. zachirica* Drosdova, 1975 (b).

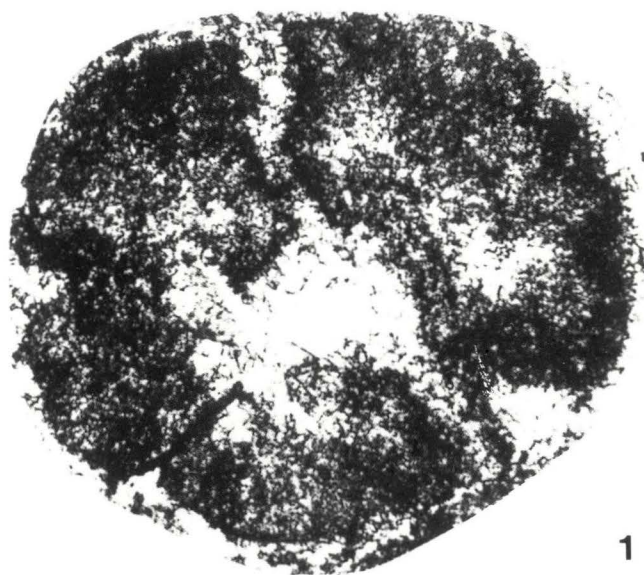
Cross-sections through the holotype of *T. rotunda* (Drosdova, 1975a, pl. 1, fig. 1; refigured by the same author 1980, pl. 3, fig. 5 and by Riding, 1991b, text-fig. 4c; cf. Pl. 3, fig. 1 of our paper) and through a second, relatively well preserved specimen (Drosdova, 1975a, pl. 1, fig. 4) show the characteristics of the species. A central, indistinctly limited and spar-filled cavity is surrounded by broad, more or less wedge-shaped segments, each of them showing a sharp convex outer surface. According to the original description (Drosdova, 1975a, p. 301), these segments are composed of thin, radially arranged filaments, sometimes showing «protosporangia» at their outer ends. These latter structures are not recognizable in the figured sections. However that may be, the segments show a radial-fibrous structure indicating the presence of filaments (Drosdova 1975a, pl. 1, fig. 3); the filamentous character of the «wall» of *Tarthinia* was also emphasized by Riding (1991a, p. 69).

According to Drosdova (1975a, p. 301), the irregularly rounded specimens of *Tarthinia rotunda* are 0.5 to 1.2-1.5 mm in diameter (mean value of 31 specimens: 0.9-1.0 mm). There is no reference to the existence of clusters of spherical or hemispherical bodies as in *Palaeomicrocodium*.

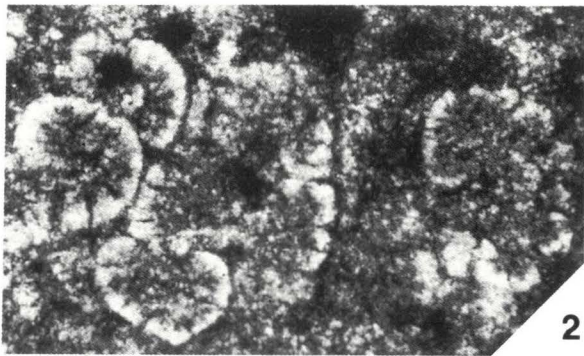
The sections of *Tarthinia zachirica* Drosdova, figured by that author (1975b, pl. 1, figs. 1-2; 1980, pl. 4, fig. 1), are so indistinct, that the exact

EXPLANATION OF PLATE 3

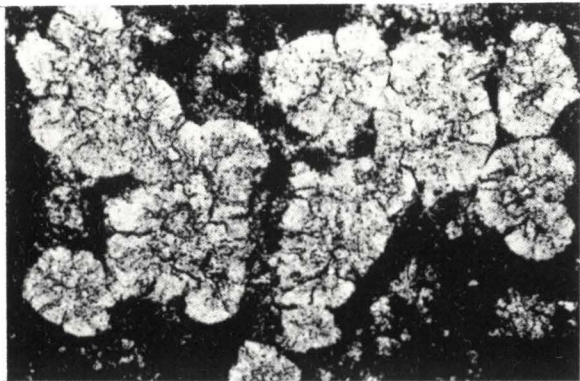
- Fig. 1 - *Tarthinia rotunda* Drosdova (holotype); $\times 66$ (after Drosdova, 1980, pl. 3, fig. 5).
 Fig. 2 - *Panomninella petrosa* Drosdova (holotype); $\times 58$ (after Drosdova, 1980, pl. 1, fig. 4).
 Fig. 3 - *Tarthinia* - *Palaeomicrocodium* group; $\times 60$. - Planu Sartu Member, Gonnese Formation (Botomian, Lower Cambrian). - Cala Domestica near Buggerru, SW-Sardinia (sample Fr  hler 12/13).
 Figs. 4-6 - *Palaeomicrocodium devonicum* Mamet & Roux; Fig. 4 (holotype): $\times 62$, Figs. 5-6: $\times 97$ (after Mamet & Roux, 1983, pl. 9, figs. 2-3, 7).
 Figs. 7-9 - *Baccanella floriformis* Panti   («syntypes»); $\times 70$ (after Panti  , 1971, pl. 2, figs. 2-4).



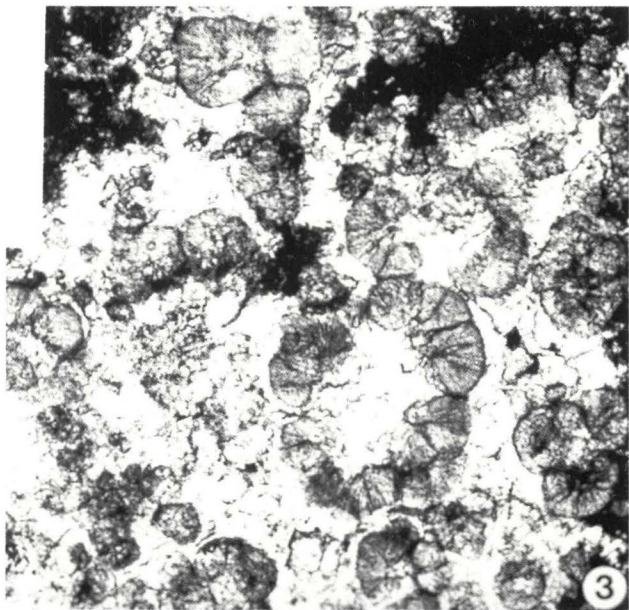
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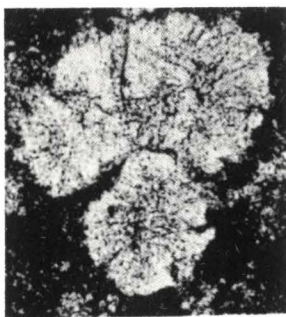
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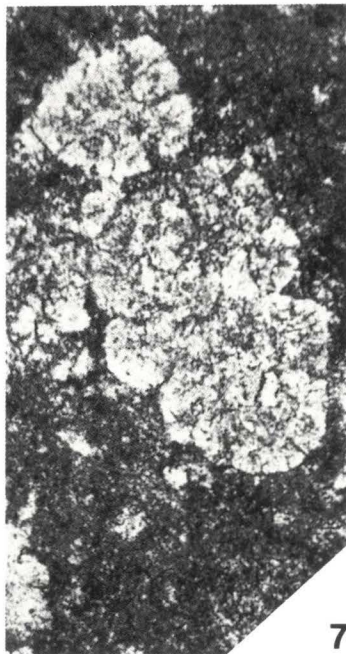
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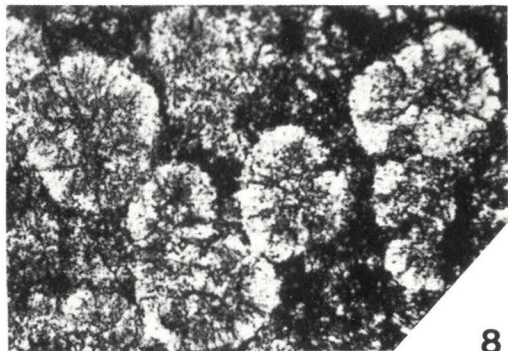
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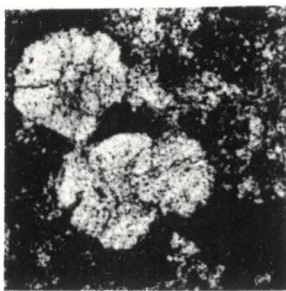
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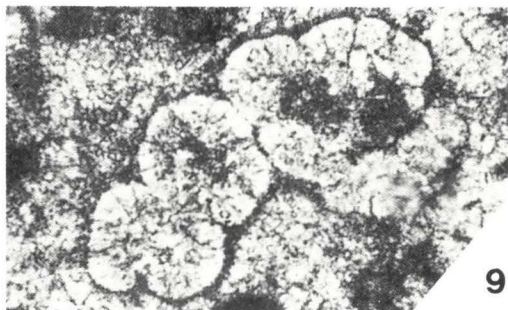
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systematic position of this species is not yet clear.

Latham & Riding (1988, p. 127; 1990, p. 752) reported *Tarthinia* together with *Renalcis* from the «Série Lie de Vin» of Morocco (western Anti-Atlas Mountains), which till now was dated of Vendian age. The discovery of *Tarthinia* provided evidence for a Cambrian age and was regarded by these authors as the first report of that genus outside Mongolia and Siberia (e.g. Olenek River, Tommotian; Riding & Voronova, 1985, p. 66). However, this genus was previously recorded (without description and figures) from the Lower Cambrian of Sardinia by Gandin & Debrenne (1984, p. 235; see also Debrenne *et al.*, 1993, p. 86).

We agree with Zhuravlev & Wood (1995, p. 456), that the organisms described by Kobluk (1985, p. 1163) as possible «globular foraminifera» (showing a «fibrous wall») from the Lower Cambrian of Virginia, are probably compartments of *Tarthinia*.

4. *Panomminella petrosa* Drosdova, 1980

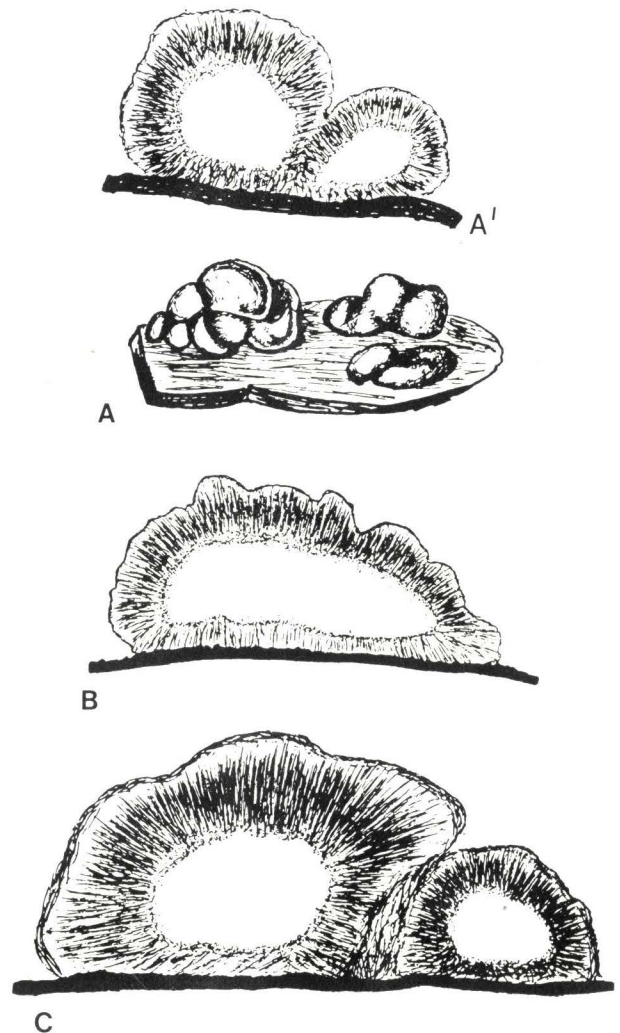
The holotype of this species coming from the Lower Cambrian of western Mongolia (Drosdova, 1980, pl. 1, fig. 4; refigured in this paper Pl. 3, fig. 2) shows a cluster of closely packed or fused, irregularly spherical and hemispherical bodies, which are partly flattened against one another. The relatively thin, sparitic outer zone of the bodies is irregularly subdivided into broad segments, frequently more or less wedge-shaped in cross-section. The inner part of the bodies is micritic, the boundary between the sparitic and micritic zones being unsharp. A radial-fibrous structure of the segments is not perceptible in the figured specimens.

The species *petrosa* was assigned by Drosdova (1980, p. 13) to the genus *Panomminella* Kolosov, 1966, an insufficiently described and figured Precambrian genus. In our opinion, this generic attribution is very questionable.

CONCLUSIONS

1 - Microfossils like *Tarthinia* and *Palaeomicrocodium* show strong morphological and structural affinities to filamentous cyanobacteria, specifically to some marine rivulariaceans. This latter group is characterized by trichomes embedded in a common gelatinous matrix to form solid colonies that are hemispherical, spherical, or irregular in shape, becoming hollow with age in some species (Text-fig. 3). These colonies are attached to different substrates.

2 - A comparison between the Lower Cambrian specimens from Cala Domestica and the sections of



Text-fig. 3 - Recent marine rivulariaceans from the French coast (reproduced from Frey, 1933, pls. 43-45).

A) *Rivularia bullata* (Poir.) Berk., view of some thalli (x1) and (A') vertical section (x5). B) *Rivularia nitida* Ag., vertical section of a thallus (x10). C) *Rivularia mesenterica* Thur., vertical section of a thallus (approx. x10).

Palaeomicrocodium figured by different authors (including the Middle Triassic forms described as *Baccanella*) has shown that the two form-groups present the same morphology and internal structure. Also *Tarthinia rotunda* shows a lobed outline in cross-section, a central cavity and a radial-fibrous microstructure suggesting a filamentous organization. However, the diameter of the *Tarthinia* spheroids seems to be more than twice as large as that of the specimens from Cala Domestica. Moreover, it is not clear whether *Tarthinia* always occurs as isolated sphaeroids or also in the form of clustered or amalgamated aggregates. This mor-

phological difference is used for instance by Senowbari-Daryan (1984, p. 28) in order to distinguish *Baccanella* from the coeval genus *Muranella* Borza. On the other hand, the growth form of some Recent rivulariaceans may depend on ecological factors. Khoja *et al.* (1984, p. 68) observed that colonies of Recent *Rivularia atra* Roth from a tidal, but relatively sheltered bay of Scotland are mostly 1 mm and seldom exceed 2 mm in diameter. «They are sometimes confluent, forming a thin substratum, especially in well-drained microhabitats. Where the colonies are permanently submerged, they tend to be separate from one another and to reach slightly larger diameters than where they coalesce to form a stratum».

However that may be, in our opinion *Tarthinia* is at present an insufficiently known genus, which requires further studies. In view of this situation we preferred to describe our Cambrian material under the term *Tarthinia-Palaeomicrocodium* group.

3 - The morphological and structural type characterized by the *Tarthinia-Palaeomicrocodium* group ranges over a long period of time: from Lower Cambrian to Middle Triassic. A similar example of a long persisting cyanobacterial taxon is the genus *Renalcis* Vologdin ranging from the Lower Cambrian to the Upper Permian (Vachard & Razgallah, 1988).

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Antonietta CHERCHI

Dipartimento di Scienze della Terra
Università di Cagliari
Via Trentino 51, 09100 Cagliari, Italia

Michael FRÖHLER

Taberg Planungsbüro GmbH
Jordanstr. 7, 34117 Kassel, Deutschland

Rolf SCHROEDER

Geologisch-Paläontologisches Institut
Universität Frankfurt a.M.
Senckenberg-Anlage 32, 60054 Frankfurt a.M. 11,
Deutschland