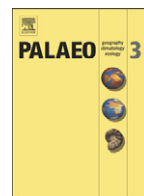




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## Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: [www.elsevier.com/locate/palaeo](http://www.elsevier.com/locate/palaeo)Late Jurassic *Epiphyton*-like cyanobacteria: Indicators of long-term episodic variation in marine bioinduced microbial calcification?Emanoil Săsăran<sup>a</sup>, Ioan I. Bucur<sup>a</sup>, George Pleș<sup>a</sup>, Robert Riding<sup>b,\*</sup><sup>a</sup> Department of Geology, Babeș-Bolyai University, Str. M. Kogălniceanu 1, 400084 Cluj-Napoca, Romania<sup>b</sup> Department of Earth and Planetary Sciences, University of Tennessee, Knoxville, TN 37996-1410, USA

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## ABSTRACT

Epiphytaceans occur in Late Jurassic shallow-marine reef limestones at several localities in the Carpathian Mountains of Romania. These calcified dendritic microfossils are well-preserved in sparry calcite as sub-millimetric radial clusters of narrow well-defined filaments, 10–30 μm in diameter that show dichotomous branching and consist of dense dark micrite, locally with tubiform structure. Epiphytaceans are widely interpreted as photosynthetic algae or bacteria, but their precise affinities remain elusive and the group may be heterogeneous. These Late Jurassic examples most closely resemble Cambrian *Tubomorphophyton* and Late Devonian *Paraepiphyton*. We interpret them to be calcified cyanobacterial sheaths. Post-Devonian records of epiphytaceans are extremely scarce. The Kimmeridgian–Tithonian specimens reported here represent one of the youngest known occurrences of epiphytaceans. Their highly sporadic geological distribution resembles that of marine calcified cyanobacteria, which show Phanerozoic abundance peaks in the Early Paleozoic, Late Devonian–Mississippian, and Late Jurassic–Early Cretaceous. We propose that Kimmeridgian–Tithonian epiphytacean cyanobacteria reflect environmental conditions that favored bioinduced calcification, in particular elevated seawater carbonate saturation state.

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## 1. Introduction

A variety of small calcified dendritic fossils, of which *Epiphyton* (Bornemann, 1886) is the best known, are locally abundant in shallow-marine Early Paleozoic limestones. Although their individual filaments are less than 100 μm in diameter and their branched thalli rarely exceed a few millimeters in size, these fossils can be important components of Cambrian (Korde, 1961; Ahr, 1971; Pratt, 1984; Riding, 2001; Woo et al., 2008; Gandin and Debrenne, 2010) and Early Ordovician (Coniglio and James, 1985, fig. 8) reefs. However, this initial Phanerozoic abundance was not maintained. Subsequent Paleozoic occurrences of epiphytaceans are sporadic and Mesozoic reports of them are very rare. Here we describe marine *Epiphyton*-like fossils from Late Jurassic (~150 Ma) shallow-marine reef limestones in Romania. They most closely resemble Cambrian *Tubomorphophyton* Korde, 1973 and Late Devonian *Paraepiphyton* Wray, 1967 and their size and morphology suggest that they are cyanobacteria. Cyanobacterial calcification is bioinduced, reflecting external environmental conditions as well as metabolic processes (Konhauser and Riding, 2012). A key environmental control on cyanobacterial calcification is ambient aquatic carbonate saturation

state (Pentecost, 1981; Kempe and Kazmierczak, 1994). Marked variations in the abundance of well-calcified cyanobacteria over geological time suggest that these fossils could be a proxy for long-term fluctuations in seawater chemistry (Riding, 1982, 2006; Arp et al., 2001). Here we explore the possibility that this previously unrecognized Late Jurassic occurrence of *Epiphyton*-like cyanobacteria represents a response to geologically long-term but nonetheless transitory conditions that favored their calcification and therefore preservation.

## 2. Location and geological setting

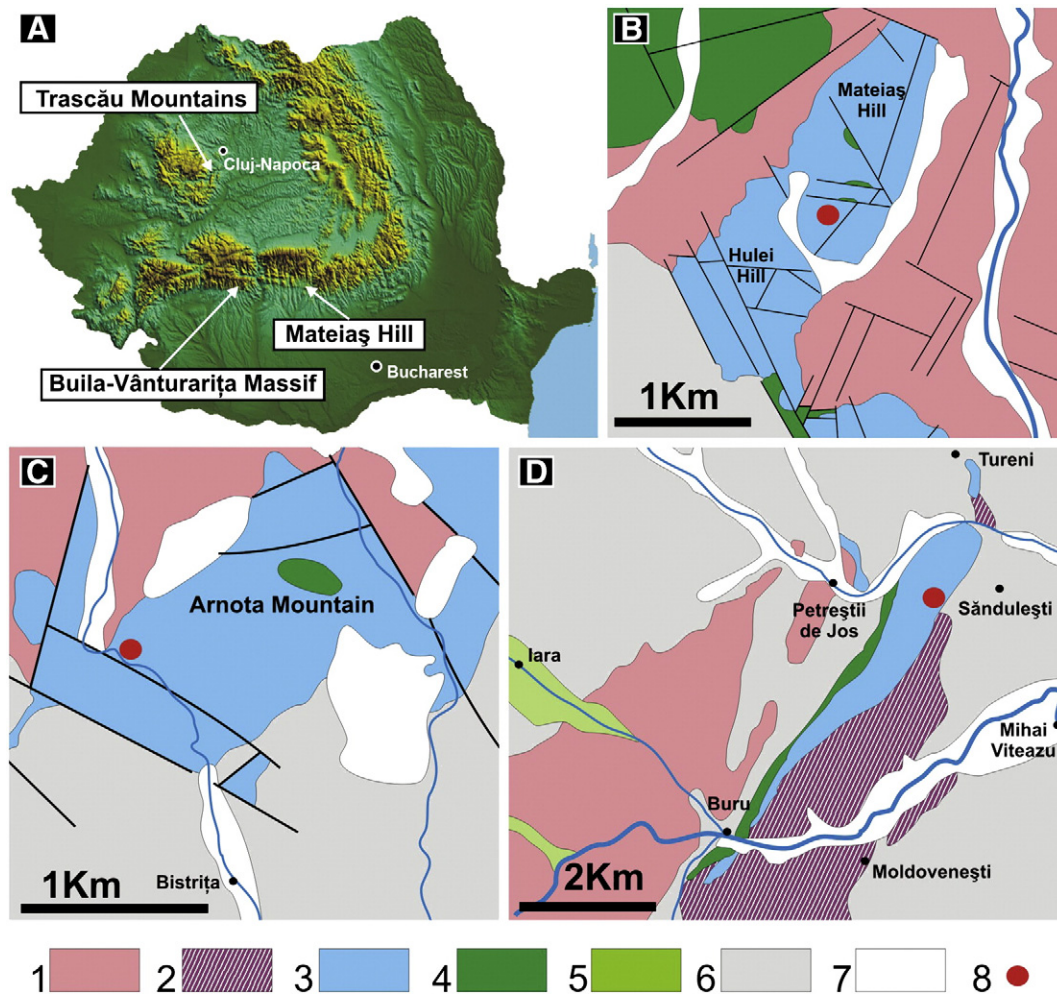
We found Late Jurassic epiphytaceans at three localities: Mateiaș-Hulei and the Vânturarița Mountains, both in the Southern Carpathians of south-central Romania, and in the Trascău Mountains of north-western Romania, on the eastern side of the Apuseni Mountains (Fig. 1). At all three locations epiphytaceans occur in reef limestones of Late Jurassic age, in the Kimmeridgian or Lower Tithonian (~150 Ma).

## 2.1. Mateiaș-Hulei

The Mateiaș-Hulei hills are ~4 km ENE of Câmpulung (130 km NW of Bucharest). The Jurassic limestones in this area (Fig. 1B) occur at the eastern end of the Getic Nappe (Bucur et al., 2010). They form part of the Getic carbonate platform which developed on older sediments and crystalline basement during the Late Jurassic and Early Cretaceous,

\* Corresponding author. Tel.: +1 865 974 9976.

E-mail address: [rriding@utk.edu](mailto:rriding@utk.edu) (R. Riding).



**Fig. 1.** Sample localities. A, Location of the three regions in the Romanian Carpathians with *Epiphyton*-like fossils. B to D, Geological maps of the Mateiaș–Hulei region (B), Vânturarița Massif (Arnota Mountain) (C), and Trascău Mountains (D). 1. Crystalline basement; 2. Ophiolite; 3. Upper Jurassic limestone; 4. Lower Cretaceous to Cenomanian limestone and conglomerate; 5. Upper Cretaceous; 6. Undifferentiated Cenozoic; 7. Quaternary; 8. Locations of *Epiphyton*-like fossils in the sections.

and include limestones in the Reșita and Hațeg–Pui zones, Vânturarița Mountains, Piatra Craiului Mountains, and the Dâmbovicioara Couloir.

Four main facies types can be distinguished within the Mateiaș Limestone (Fig. 2A):

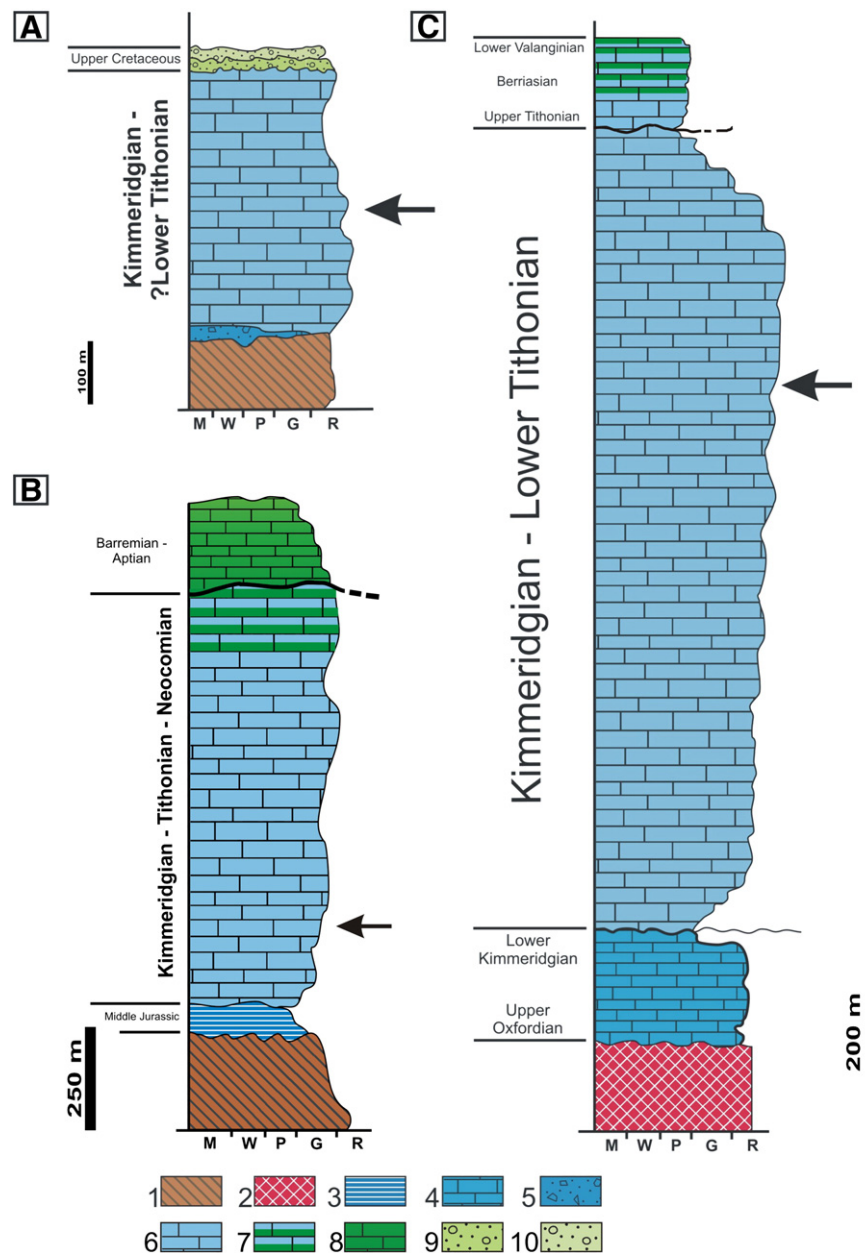
- Facies A Massive coral-microbialite reef limestones.
- Facies B Thick banks of fore-reef breccia and reef rudstone.
- Facies C Thin to thick (cm–m) bedded, mainly bioclastic, limestones, probably representing grain flows.
- Facies D Thin (cm–dm) bedded allodapic limestones, sometimes containing chert nodules and often folded, with horizons of breccia and blocks of reef limestone.

These limestones contain calcareous algae, benthic foraminifers, encrusting microorganisms, and calcimicrobes. The encrusters and calcimicrobes occur in the coral-microbial reef (Facies A), whereas most of the calcareous algae and foraminifers occur in the reef rudstones, bioclastic grainstones, and fine-grained grainstone-packstones (Facies B, C, and part of D). The association of algae, foraminifers and *incertae sedis* is typical of Oxfordian–Tithonian shallow marine environments. Among the stratigraphically significant taxa, only *Labyrinthina mirabilis* has a well-defined position, indicating Upper Oxfordian–Kimmeridgian, and possibly Lower Tithonian, intervals. Since the Oxfordian in this area is usually represented by radiolarites, it seems likely that the Mateiaș Limestone is Kimmeridgian, although it remains possible that its upper part could be Early Tithonian. We identified epiphytaceans in coral-microbialite reef boundstone

samples (Facies A) from a bore-hole drilled in Mateiaș Hill (Fig. 1B). All thin sections from Mateiaș were prepared from a single drill core-sample from meter 76.8 at borehole Mateiaș-5. These specimens are prefixed M in Table 1 and Fig. 3.

## 2.2. Buila-Vânturarița

The Buila-Vânturarița Massif, 75 km west of Câmpulung, and 180 km north–north-west of Bucharest, is formed by northeast–southwest trending limestones that also belong to the Getic carbonate platform and are mainly Late Jurassic (Kimmeridgian–Tithonian) and Early Cretaceous in age. The Late Jurassic limestones are reef deposits with corals, stromatoporoids, and a wide range of microbial crusts and micro-encrusters. These coral-microbial-microencruster boundstones are similar to other reef deposits of this age in the Intra-Tethyan domain (Pleș et al., 2013) that are often being termed Štramberk limestones after the locality of this name in the eastern Czech Republic (Picha et al., 2006). Štramberk limestones are latest Kimmeridgian–Berriasian in age (e.g., Houša, 1990; Eliáš and Vašíček, 1995; Houša and Vašíček, 2004) and best known in the Outer Carpathians of southern Poland, northern Slovakia, and Romania. In the Štramberk region they are generally considered reefal platform margin olistoliths (e.g., Houša, 1990). Further east, and particularly in the Romanian Carpathians, these reef facies more commonly appear to be in situ at the margins of large carbonate platforms (Bucur et al., 2005). Epiphytaceans occur in a single sample, 55A, in the Bistriței Gorges, in the south-western part of



**Fig. 2.** Stratigraphic sections and facies. A, Upper Jurassic–Cretaceous deposits at Mateiaș Hill; B, Upper Jurassic–Lower Cretaceous limestones in the Vânturarița Massif; C, Upper Jurassic–lowermost Cretaceous limestones in the Trascău Mountains. 1. Crystalline basement; 2. Ophiolite; 3. Middle Jurassic siliciclastics; 4. Upper Jurassic slope limestone; 5. Upper Jurassic conglomerate and breccia; 6. Upper Jurassic shallow-water (reef, carbonate platform) limestone; 7. Berriasian–Valanginian limestone; 8. Barremian (Urgonian-type) limestone; 9. Cretaceous carbonate conglomerates; 10. Cretaceous siliciclastic conglomerate. Arrows indicate the horizons with *Epiphyton*-like fossils. M, W, P, G, and R respectively indicate mudstone, wackestone, packstone, grainstone, and rudstone fabrics.

the Buila-Vânturarița Massif ~7 km north–northeast of Horezu (Fig. 1C), in Upper Jurassic limestones (Fig. 2B) consisting of coarse reef debris (intraclastic–bioclastic rudstone/grainstone) interlayered with coral–microbial reefs (coral–microbial–microencruster boundstone). These specimens are prefixed V in Table 1 and in Figs. 3 and 4.

### 2.3. Trascău Mountains

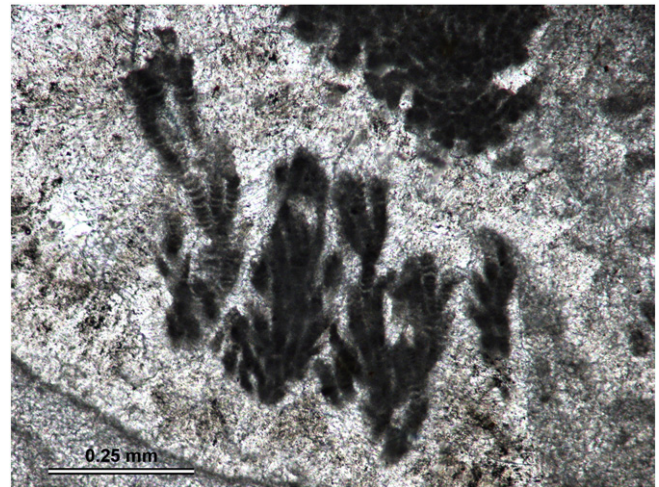
In the Trascău Mountains, 20–70 km south of Cluj-Napoca, shallow and deep-marine sediments of Late Jurassic–Early Cretaceous age occur (Fig. 1D). The shallow marine deposits are mainly Upper Oxfordian–Lower Valanginian limestones that form two north–south oriented, parallel outcrops; the northern one is shown in (Figure 1).

Kimmeridgian–Lower Tithonian limestones form the thickest interval and contain Štramberg-type reefs mainly consisting of sponges, microbial crusts, and corals. At Turzii Gorges ~20 km south of Cluj-Napoca, the reefs are small and isolated in the middle part of the succession, becoming larger towards the top. They consist of corals, microbialite, and sponges together with encrusting microorganisms that stabilized the framework, mainly bryozoans, foraminifers, calcareous algae, annelids and problematic organisms (e.g., *Radiomura cautica*, *Koskinobullina socialis*, *Lithocodium aggregatum*). The internal reef sediment is bioturbated bioclast–peloid wackestone/packstone and peloid packstone (Săsăran, 2006). Epiphyteans occur in the reefal bioconstructions in the mid-part of the succession in limestones that contain *Labyrinthina mirabilis* and *Kurnubia palastiniensis*, indicating a Kimmeridgian–Early Tithonian age.



**Table 1**  
Size data (in microns) of Romanian *Paraepiphyton*- and *Tubomorphophyton*-like epiphytaceans. Specimens M are from Mateiaş Hill; specimen V is from Vânturariţa.

Sample	Filament width		Thallus size
	Smallest	Largest	
V-06	12	24	500
	12	21	330
M-17	18	30	390
	21	30	300
M-26	11	22	300
M-35	15	26	375
M-52	12	24	400
M-65	14	23	675
M-72	12	24	520+
M-80	15	30	480
M-81	12	24	780
M-95	15	26	750
M-02	10	20	400
	10	30	500
M-09	12	20	800



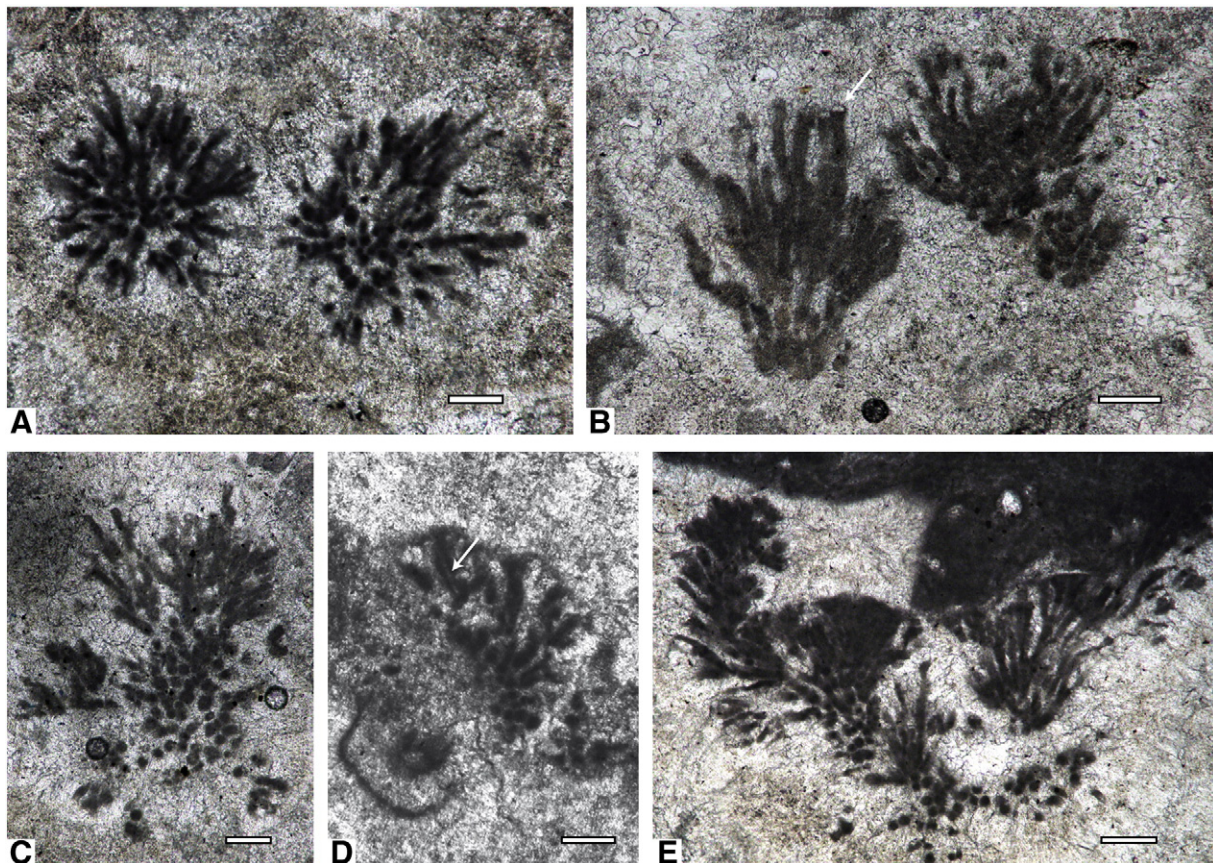
**Fig. 4.** Branched filaments with distinctive regularly spaced concave-up transverse light-colored bands that create a segmented appearance (specimen V-02, Vânturariţa).

### 3. Late Jurassic epiphytaceans

#### 3.1. Occurrences

The epiphytaceans we identified are not common but are present at the three widely spaced sites in north-western and south-central Romania described above (Mateiaş, Bistriţa and Gorges–Vânturariţa, and

Turzii Gorges in the northern Trascau Mountains). At all three locations they occur in Late Jurassic shallow marine reef limestones associated with corals, stromatoporoids and other sponges, bryozoans, calcareous algae, annelids and *Microproblematica*, with micritic and spar-rich matrices. The epiphytaceans are most conspicuous when they occur



**Fig. 3.** Thin-section photomicrographs of Kimmeridgian–Lower Tithonian specimens resembling *Paraepiphyton* and *Tubomorphophyton*. Scale bars represent 100 µm. A. Radial clusters of branched micritic filaments in sparry matrix (specimen M-02, Mateiaş Hill). B. Approximately vertical sections of clusters of sinuous filaments, with local development of hollow ovoid terminal bodies (arrow) (specimen V-06, Vânturariţa). C. Radiating branched filaments some of which show traces of tubiform structure in the cross-sections and terminations (specimen M-09, Mateiaş Hill). D. Short filaments with local tubiform structure (arrowed) (specimen M-17, Mateiaş Hill). E. Fan-like developments in erect filaments that display dichotomous, possibly trichotomous, branching that give rise to closely appressed distal clusters (specimen M-65, Mateiaş Hill).

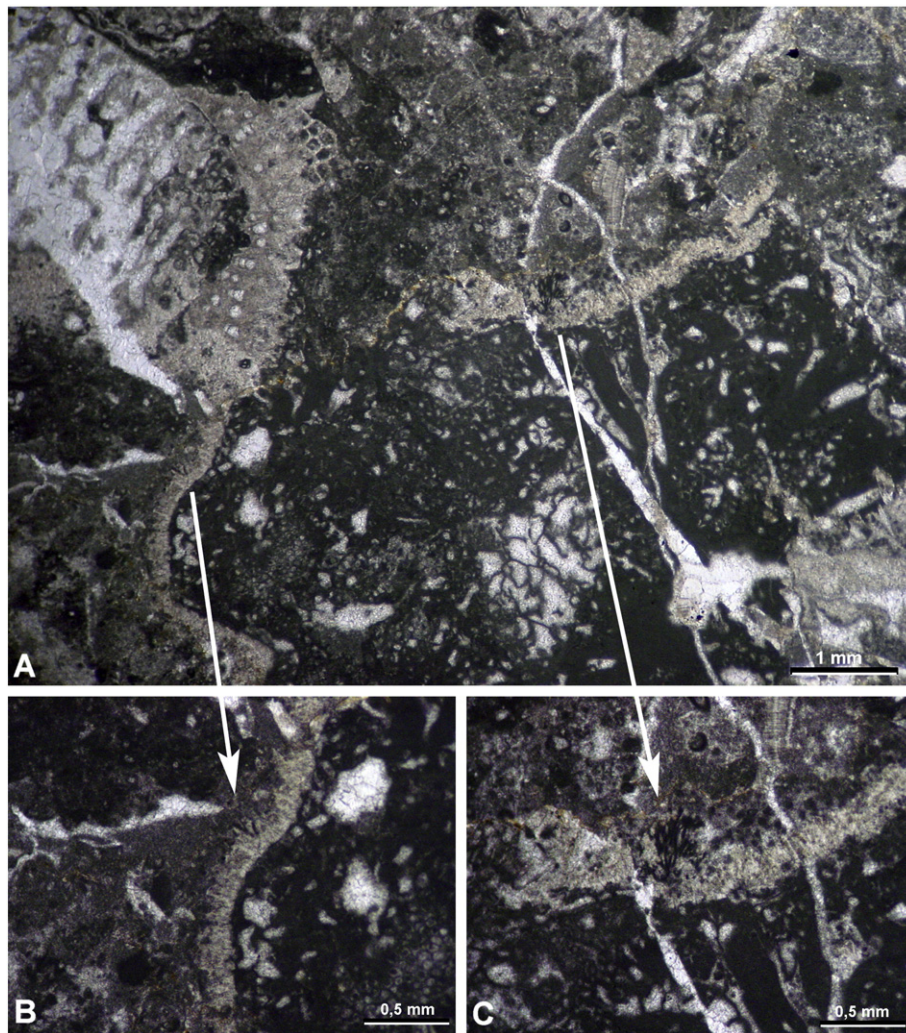


surrounded by spar. At all three locations *Epiphyton* is typically closely associated with crusts of *Koskinobullina socialis*, *Shamovella* (*Crescentiella*), *Lithocodium aggregatum* and *Bacinella*-type structures, and *Pseudorothpletzella*, together with encrusting foraminifers, and annelid tubes. It appears to be growing in place, on these crusts and skeletons. Locally, these essentially skeletal fabrics include sparry layers and patches that range from thin crusts to extensive areas up to several centimeters across, that contain isolated skeletons, including *Epiphyton*, and patches of matrix (Figs. 5–8). The surrounding spar often emphasizes *Epiphyton*, which stands out as dark filaments against the light colored background. In our examples, we see no evidence that *Epiphyton* is associated with cavities, and no evidence that *Epiphyton* grew downward. We infer that in most cases the spar is largely an overprinting recrystallization fabric in which well-preserved skeletons (including *Epiphyton* filaments), that appear to float in the spar, are remnants of the primary reef fabric. This interpretation requires confirmation, but is supported by specimens in which *Epiphyton* filaments, within a single thallus, range from well-preserved, to overprinted and destroyed (Figs. 5, 6, 8). In addition, prismatic spars locally exhibit fan-like form resembling longitudinal sections of *Epiphyton* thalli, or a radial distribution in transverse section.

### 3.2. Description and comparisons

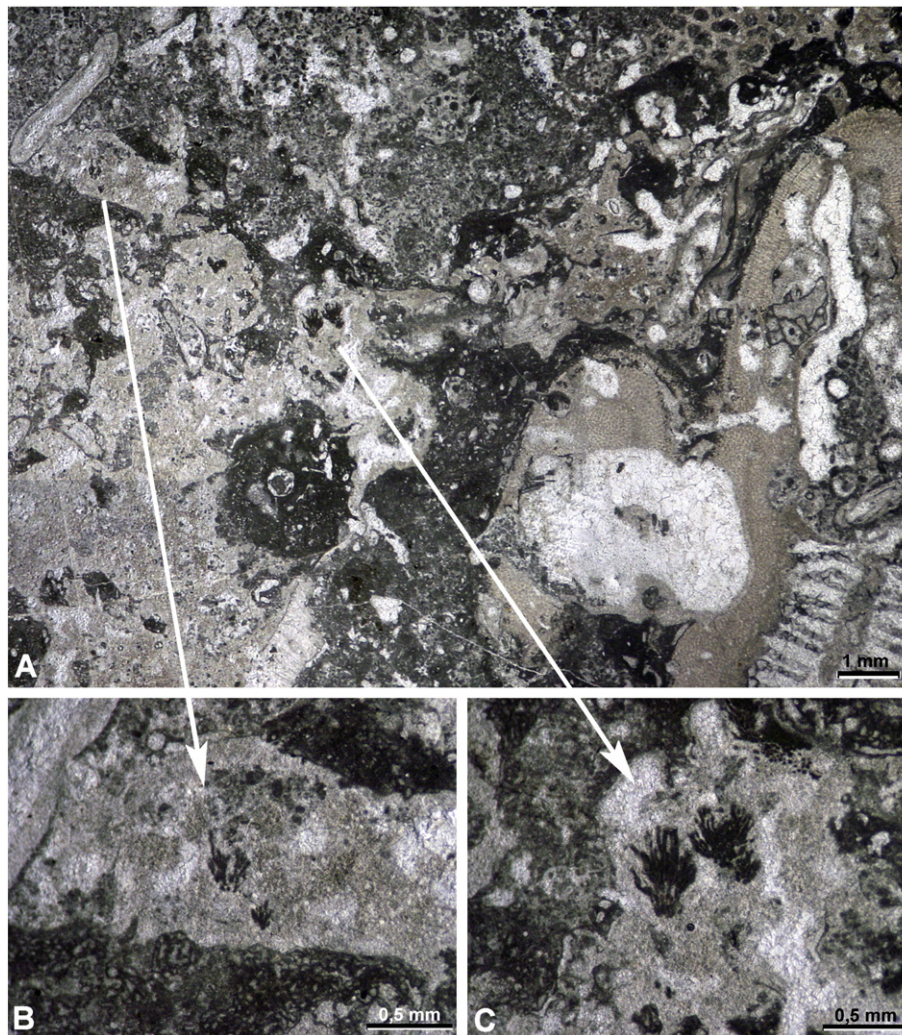
We examined fifteen epiphytacean specimens in detail. They are narrow well-defined straight to irregularly sinuous closely spaced filaments 10–30  $\mu\text{m}$  in diameter that form thalli (vertical to radial clusters) 0.3–0.8 mm in size (Fig. 3A, B). They consist of dense dark micrite that generally forms the entire filament, but locally filaments appear tubiform and have terminal rounded ovoid bodies 18–24  $\mu\text{m}$  across (Fig. 3B) (specimen V-06, Table 1) which Korde (1973) suggested are reproductive structures. The filaments maintain approximately constant widths but in places have slight distal expansion. They show dichotomous, possibly trichotomous, branching; locally this results in filaments being so close together that they almost appear to merge (Fig. 3C) (specimen M-65, Table 1).

Epiphytaceans are well-known from the Cambrian (e.g., *Epiphyton*, *Epiphytonoides*, *Gordonophyton*, *Korilophyton*, *Sajania*, *Tubomorphophyton*), Silurian (*Kosvophyton*, *Ludlovia*), and Late Devonian (*Paraepiphyton*, *Tharama*) (Bornemann, 1886; Vologdin, 1962; Korde, 1973; Voronova, 1976). Some are relatively large, with filament diameters of 100  $\mu\text{m}$  or more and dense clusters of thalli exceeding 6 mm in height. Most have filaments that appear wholly micritic but



**Fig. 5.** A. Coral-microbial-microencruster boundstone; the coral-microbial framework is encrusted by stromatoporoids and Microproblematica, mainly *Lithocodium aggregatum* and *Shamovella* (*Crescentiella*). *Epiphyton* thalli overgrow *Lithocodium aggregatum* crusts. B. Detail of A, otherwise well-preserved *Epiphyton* filaments locally replaced by adjacent prismatic sparry crust on the surface of *Lithocodium*. C. Detail of A, a few discontinuous *Epiphyton* filaments preserved in the upper part of the thin prismatic sparry crust. Locality, Turzii Gorges.





**Fig. 6.** A. Coral-stromatoporoid framework encrusted by *Koskinobullina socialis*, *Lithocodium aggregatum*, *Radiomura cautica*, *Shamovella* (*Crescentiella*), *Pseudorothpletzella*, encrusting foraminifers and annelid tubes. Patches and layers of altered sparry crust locally preserve *Epiphyton* thalli. B, C, details showing more-or-less well-preserved *Epiphyton* filaments and thalli 'floating' in spar; the left side of B shows an annelid tube. Locality, Bistri ei Gorges, Buila-Vânturari a Massif.

some are patterned by transverse bands (e.g., *Gordonophyton*) or are tubiform (e.g., *Tubomorphophyton*) and occasionally chambered.

In size and morphology, our relatively small specimens most closely resemble Late Devonian *Paraepiphyton* Wray from the Canning Basin, Australia, while those with tubiform filaments resemble Cambrian *Tubomorphophyton* Korde, based on *Epiphyton botomense* from the Early Cambrian of Siberia (Korde, 1973). *Tubomorphophyton* is similar in size to *Epiphyton*, but can show tubiform filaments, whereas *Epiphyton* appears to be wholly micritic (Riding and Voronova, 1982a). Hollow subspherical terminal bodies on filaments, similar to those recognized here (Fig. 3B) have been reported in a variety of Cambrian epiphytaceans (Korde, 1973). Antropov (1955) described *Epiphyton buldyricum* from the Late Devonian of the Russian platform with filaments 8–12  $\mu\text{m}$  in width and thalli ~0.2 mm across. *Paraepiphyton caritus* Wray, 1967 from the Frasnian and Famennian of the Canning Basin, Western Australia, is only very slightly larger than *E. buldyricum*, typically with filaments 11–13  $\mu\text{m}$  across and thalli ~1 mm across. *Paraepiphyton* was placed in synonymy with *Epiphyton* Bornemann by Riding and Wray (1972). Nonetheless, it can be distinguished from *Epiphyton* by its small size and less regular branching and until there is further clarification of epiphytaceans based on detailed comparisons of the various taxa, it seems useful to recognize *Paraepiphyton* (see Feng et al., 2010).

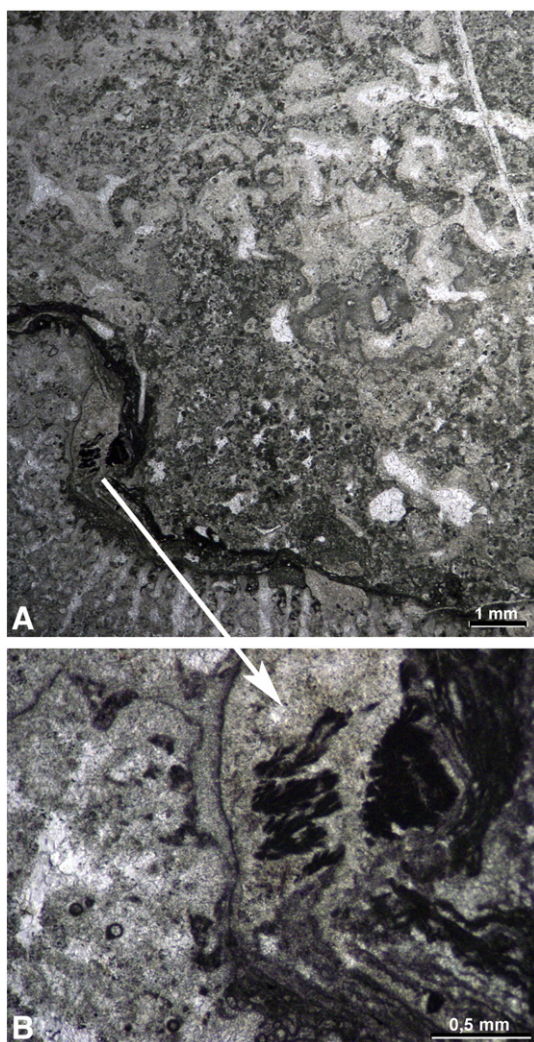
### 3.3. Cretaceous *Epiphyton*

Masse (1969, 1979, p. 688, pl. 1, fig. 5) reported *Epiphyton* from the Early Cretaceous (Barremian) of southern France. As noted by Riding (1991, p. 77), in some respects the example figured by Masse (1979) resembles the Cambrian cyanobacterium *Angulocellularia* Vologdin, 1962 (= *Angusticellularia* Vologdin, 1962). Among our material, the specimen figured by Masse most closely resembles one that shows a tendency towards amalgamated filaments (Fig. 3C).

### 3.4. Affinities

Epiphytaceans have variously been interpreted as chlorophytes (Bornemann, 1886), cyanobacteria (Pia, 1927; Maslov, 1956; Luchinina, 1975) and rhodophytes (Korde, 1958). There are significant differences in detail among the various genera, and it is possible that the group is heterogeneous. For example, Luchinina and Terleev (2008), reviving Korde's earlier attribution, have proposed that some epiphytaceans are red algae. We found one similar specimen (see *Segmented specimen* section, below). Apart from this example, based on size and morphology we consider the remaining Romanian epiphytaceans to be the calcified sheaths of filamentous cyanobacteria. This is consistent with previous interpretations of the two Paleozoic



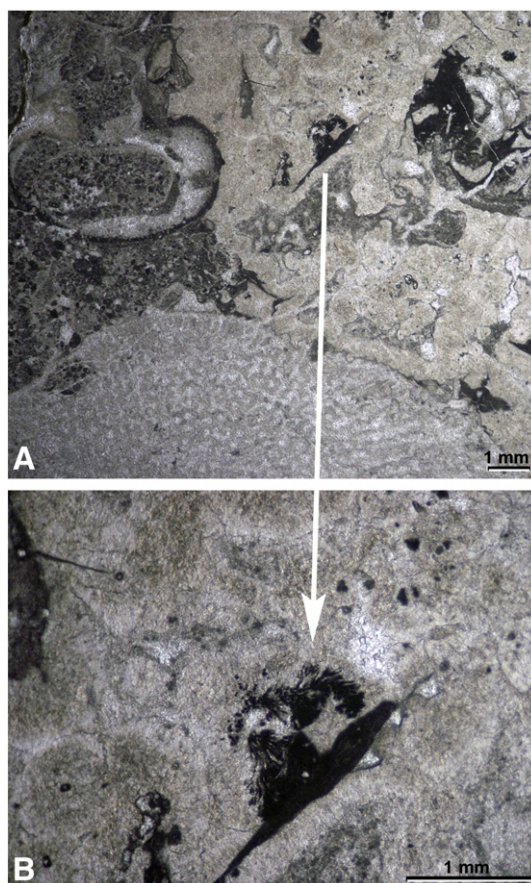


**Fig. 7.** A. Coral boundstone and matrix; laminar crust of *Koskinobullina socialis*, *Pseudorothpletzella*, and sparry calcite locally with *Epiphyton* filaments. B. Detail showing *Epiphyton* clusters (center). Locality, Bistriei Gorges, Buila-Vânturari a Massif.

forms they most closely resemble: *Paraepiphyton* and *Tubomorphophyton*. *Paraepiphyton* was considered by Wray (1967) to be a cyanobacterium, and *Tubomorphophyton*, which Korde (1973) placed in the red algae, was subsequently compared with stigonematalean cyanobacteria by Riding and Voronova (1982a, p. 875). In addition, the generally well-preserved outlines of the Romanian filaments, maintaining relatively constant dimensions and clear details of branching, suggest that they were calcified in vivo (see Riding, 2006, p. 305). This is further supported by the presence in several examples of tubiform structure (Fig. 3B, D, E). The apparently dense micritic structure of many of the other filaments could be explained if the central strands of cells (trichomes) were generally too narrow to be readily preserved (see Riding and Voronova, 1982b), and/or were obscured during syngedimentary diagenesis (see Pratt, 1984, 2001).

### 3.5. Segmented specimen

In addition to our epiphytaceans that resemble *Paraepiphyton* and *Tubomorphophyton*, a specimen from Vânturarița (Fig. 4) that has overall similar dimensions (filament width ~25–35  $\mu\text{m}$ , thallus size up to 0.56 mm) is distinguished by its regularly spaced light colored bands that interrupt the filaments and define concave-up segments (Fig. 4). This specimen shows slight resemblance to microfossils variously



**Fig. 8.** A. Boundstone (left) and an extensive area of spar (right) that appears to have largely replaced skeletal crusts and matrix. B. Partially well-preserved fan-like *Epiphyton* thalli adjacent to the microproblematic fossil *Shamovella* (*Crescentiella*). Locality, Mateia.

referred to *Sgrossoella* De Castro, 1969 (Late Cretaceous, Italy) and *Gahkumella* Zaninetti, 1978 (Permian, Iran). *Gahkumella* has a filament diameter of 60  $\mu\text{m}$  and appears to be short and unbranched; Zaninetti (1978) compared it with *Cretacicladius* and *Sgrossoella*, and with Valanginian–Aptian fossils that Masse (1976, pl. 1, figs. 3, 4) compared with the extant *Solentia*-like cyanobacterium *Hormathonema* Ercegovic, 1929 (see also Masse, 1979, p. 690, pl. 1, fig. 7, and Bucur et al., 2004, pl. 3, figs. 7, 8). Somewhat similar chambered fossils from the Oxfordian of the USA (Kopaska-Merkel and Schmid, 1999) were described by Fischer et al. (2007) as ‘*Renalcis*-like’ fossils from the Oxfordian of Mexico, and Hughes (2010) described very similar fossils from the Late Jurassic Arab Formation of Saudi Arabia. These specimens are 42–57  $\mu\text{m}$  (Kopaska-Merkel and Schmid, 1999) and 40  $\mu\text{m}$  (Hughes, 2010) in diameter and form generally short and slightly curved septate filaments/tubes that show occasional branching (Kopaska-Merkel and Schmid, 1999, fig. 7; Hughes, 2010, fig. 4g). They in turn resemble Silurian *Hecetaphyton* Riding and Soja, 1993 from Alaska, although *Hecetaphyton* is generally much larger, ranging 60–230  $\mu\text{m}$  in diameter, and shows similarities with Devonian *Shuguria* Antropov, 1950. Late Cretaceous *Cretacicladius*, suggested to be a green alga by Luperto Sinni (1979), is less chambered but also differs from our Jurassic ‘segmented’ specimen (Fig. 4) in being larger, less filamentous, and showing distinctive bowl-like laterally curved segments. With its long, narrow, dendritic form, generally small size, and poor development of chambered organization, our segmented fossil resembles some of the Cambrian epiphytaceans figured by Luchinina and Terleev (2008). It also has some similarities with the Late Jurassic tufted oncoid fabrics illustrated by Leinfelder (1985, pl. 30). Its identity and affinity remain enigmatic.

## 4. Discussion

### 4.1. Secular record of bacterially bioinduced calcification

Biological calcification can be more controlled or less controlled, and these two conditions have been termed biocontrolled and bioinduced (Lowenstam, 1981; Mann, 2001). Many organisms, including most algae and invertebrates, closely control formation of their calcified skeletons. In contrast, bacterial calcification is much less closely controlled. As a result it is not obligatory, does not appear to be fundamental to the life of the organisms, and is dependent on ambient environmental conditions (Pentecost and Riding, 1986; Konhauser and Riding, 2012). A key factor in cyanobacterial sheath calcification is carbonate saturation state (Pentecost, 1981; Kempe and Kazmierczak, 1994), which has varied through time in response to seawater and atmospheric composition (Riding and Liang, 2005). Periods of abundance of both sheath-calcified cyanobacteria (Arp et al., 2001) and reefal microbial carbonates (Kießling, 2002), during the Early Palaeozoic, Late Devonian–Mississippian and Late Jurassic–Early Cretaceous, broadly correspond with intervals when seawater carbonate saturation state is estimated to have been elevated (Riding and Liang, 2005).

### 4.2. Episodic distribution of epiphytaceans

Although epiphytaceans are widely involved in Early–Middle Cambrian reefs (Korde, 1961; Ahr, 1971; Pratt, 1984; Riding, 2001; Woo et al., 2008; Gandin and Debrenne, 2010), including close association with archaeocyath sponges in the Early Cambrian (Bornemann, 1886),

their subsequent occurrence has been sporadic. They have been mentioned in the Early Triassic (Lehrmann, 1999), and compared with Holocene lacustrine dendritic fabrics (Laval et al., 2000), but confirmed post-Cambrian occurrences are limited to the Ordovician (Coniglio and James, 1985), Silurian (Riding and Soja, 1993), Late Devonian (Antropov, 1955; Wray, 1967; Shen et al., 1997), and Early Cretaceous (Masse, 1979) (Fig. 9). This markedly episodic secular distribution resembles that of bacterial carbonates generally, including sheath-calcified cyanobacteria (Arp et al., 2001) and reefal microbial carbonates (Kießling, 2002). Our recognition of Late Jurassic epiphytaceans validates the previously isolated and less certain identification of Early Cretaceous *Epiphyton* by Masse (1979), and our interpretation of these specimens as calcified cyanobacteria raises questions about their broad environmental significance.

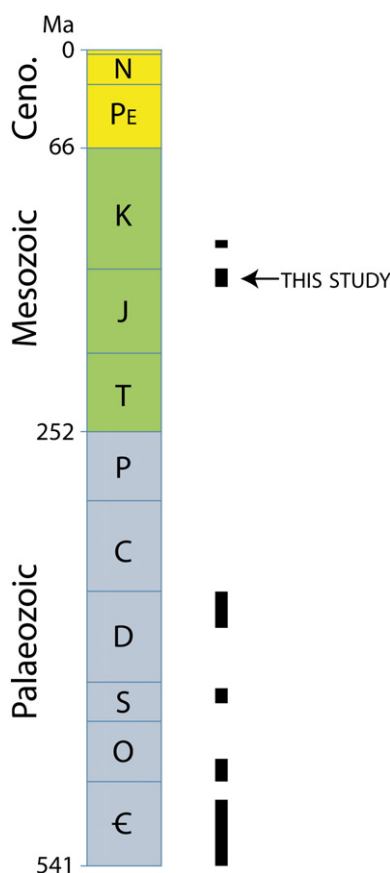
### 4.3. Late Jurassic bacterial carbonates

Calcified cyanobacteria have been recorded in marine limestones virtually throughout the Paleozoic and Mesozoic, but with strong fluctuations in abundance; their final peak of abundance was during the Late Jurassic (Arp et al., 2001, fig. 3D). Late Jurassic reefs, particularly well-documented in North America, Morocco, Europe and the Middle East, occurred in shelf seas from the Gulf of Mexico, along Atlantic margins, to areas north of Tethys (Leinfelder et al., 2002). In both the Oxfordian (Insalaco et al., 1997; Dupraz and Strasser, 1999; Olivier et al., 2004, 2012) and Kimmeridgian–Tithonian (Scott, 1988; Leinfelder et al., 1993, 1996; Ourribane et al., 2000; Olivier et al., 2003; Hoffmann et al., 2008; Rusciadelli and Ricci, 2013) they commonly contain microbial carbonates in association with corals, sponges and a wide variety of additional skeletal framebuilding and encrusting organisms, including worms and problematic organisms such as *Bacinella*, *Lithocodium*, and *Shamovella* (*Crescentiella*). In addition to leiolitic, thrombolitic and stromatolitic microbial crusts (e.g., Schmid, 1996), the microbial components in these deposits include locally abundant calcified cyanobacteria such as *Cayeuxia* and *Girvanella* (Leinfelder et al., 1993, p. 205; Shiraishi and Kano, 2004; Bádenas and Aurell, 2010, p. 99; Olivier et al., 2012).

Thus, although unexpected, Late Jurassic epiphytaceans not confidently recognized since the Late Devonian (Wray, 1967) reappear at a time when microbial carbonates generally show increased abundance and when estimates suggest that seawater carbonate saturation state was elevated (Riding and Liang, 2005, fig. 5A). Seawater carbonate saturation has declined since the Early Cretaceous and cyanobacterial calcification has become increasingly scarce in marine environments (Riding and Liang, 2005).

## 5. Conclusions

The Late Jurassic epiphytaceans reported are the first confirmed record of these distinctive microfossils since the end of the Devonian. They are present at several widely spaced localities in Romania as minor components of shallow-water coral-sponge-microbial-microencruster reef boundstones. These Late Jurassic forms are relatively small and locally preserve tubiform structure. They most closely resemble Cambrian *Tubomorphophyton* and Late Devonian *Paraepiphyton*. Although it remains possible that some Early Paleozoic epiphytaceans could be calcified algae (Korde, 1973; Luchinina and Terleev, 2008), the size and morphology of the Late Jurassic specimens suggest that they are calcified cyanobacterial sheaths. Bacterially-induced calcification reflects not only organic processes but also environmental conditions. The episodic secular distribution of post-Ordovician epiphytaceans is consistent with a bacterial affinity, and is comparable with that of Phanerozoic marine bacterial carbonates in general and calcified cyanobacteria in particular. We propose that Mesozoic *Epiphyton*-like fossils reflect environmental conditions, notably seawater carbonate saturation state, that promoted bioinduced



**Fig. 9.** Overall Phanerozoic distribution of epiphytaceans. These documented occurrences in the Early–Mid Cambrian, Early Ordovician, Silurian (Wenlock, Ludlow), Late Devonian, Late Jurassic (Kimmeridgian, Tithonian; this study), and Early Cretaceous (Barremian, see Masse, 1979) suggest a distinctly episodic development that could reflect secular fluctuations in their calcification in response to environmental controls. Time-scale from Gradstein et al. (2012).



calcification and have fluctuated over geological time-scales. Additional recognition of post-Paleozoic *Epiphyton*-like fossils would test and further explore these inferences.

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