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# The morphology of the genus *Epiphyton* BORNEMANN

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**ABSTRACT**

*The discovery of exceptionally preserved specimens of the widespread Cambrian calcareous alga* Epiphyton *BORNEMANN enabled description of the primary structural elements, including cellular structure, and possible sporangia, plasmodesmes, nematecies, and attachment to the substrate. The new data allowed direct comparison of the fossil genus* Epiphyton *with modern red algae of the genus* Corallina *LINNAEUS, and thereby clarification of its systematic position.*

**Keywords:** Rhodophyta, calcareous algae, morphology, taxonomy, Cambrian

## 1. INTRODUCTION

Occurrences of individual calcified algal thalli are known from the Riphean (TERLEEV, 1993), but they increased in number in the Cambrian. They are taxonomically homogeneous and no Phanerozoic reef was formed without them. In the Precambrian, reefs were created by bacterial-cyanobacterial associations actively precipitating $CaCO_3$. Changes in the geochemistry of ocean waters which resulted in the increase of potassium relative to sodium began in the Phanerozoic favouring basic constructions of calcareous algae, among which *Epiphyton* (one of the most characteristic genera of the Cambrian) prevailed. It dominated Cambrian reefs (LUCHININA, 1975), almost disappeared in the Ordovician and Silurian, reappeared in the Devonian (LUCHININA, 1986), and was observed for the last time in the Cretaceous (BARATTOLO, 1990).

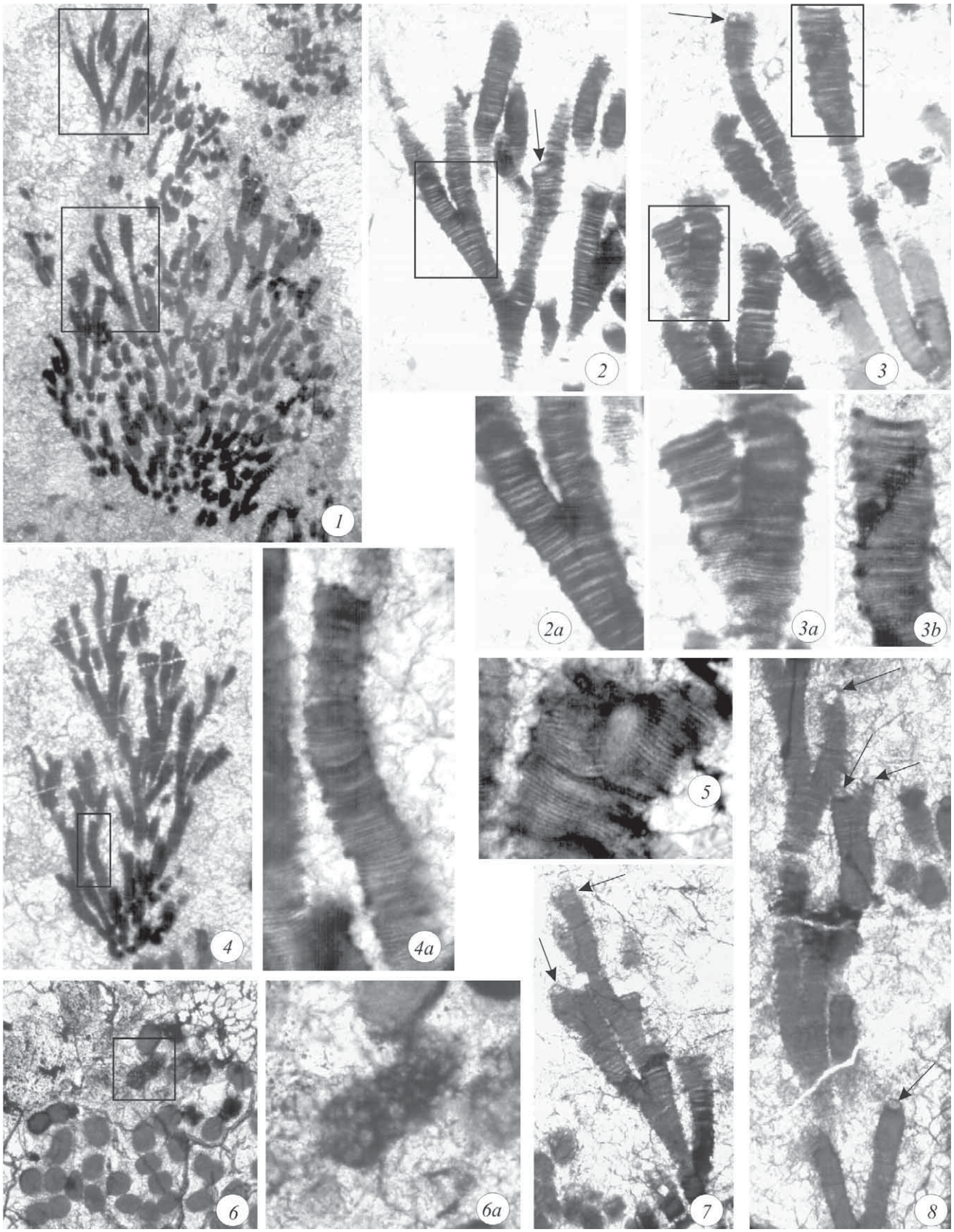
Despite the fact that the first description of the genus was more than hundred years ago (BORNEMANN, 1886), there have been many discussions regarding its taxonomy and nomenclature. These did not completely clarify the nature of the genus and until recently, its treatment remained rather inconsistent. It was placed in artificial groups (PIA, 1927), transferred to Cyanobacteria (MASLOV, 1962; LUCHININA, 1988), sometimes divided into genera, with some considered as Cyanobacteria, and others as Rhodophyceae (VORONOVA & RADIONOVA, 1976). Such different opinions were due to a lack of morphological attributes preserved by fossilization. The genus has been judged on the branching form of the thallus, the size, and the intensity of calcification of the branches. The presence of a cellular structure reported by some researchers was not substantiated by convincing material and remained hypothetical (KORDE, 1961, 1973). The situation was aggravated by difficulty in comparing Cambrian calcareous algae with modern examples. The bushy form of the genus is most reminiscent of the shape of modern red calcareous algae, but authentic traces of cellular structure, characteristic of red algae, were not clearly preserved and it was generally thought that the calcified bushes of *Epiphyton* were, as in the cases of *Renalcis* and *Girvanella*, referable to Cyanobacteria.

The dark grey calcification of the thallus of *Epiphyton* obscured the original structure of the branches, and only in rare cases was light coloured calcite observed in the internal part of the branches. PRATT (1984) assumed that after the death of the algae, coccoid Cyanobacteria settled on their calcareous surface, causing secondary accretion of calcium carbonate all over the thallus. Thus *Epiphyton*, as well as *Renalcis*, was regarded as a sedimentary phenomenon comparable with stromatolites, stromatactoid structure, silicified Precam-

**PLATE I**

*Epiphyton durum* KORDE, 1961; East Siberia, East Sayan, Mana Depression, Kolba River, tributary of the Mana River, the upper part of the Anastasion Formation, Lower Cambrian, Tommotian Stage

| | |
|---|---|
| **1, 4** | General view of a dendritic colony with transverse strips on the branches; x30. |
| **2, 3** | Different aspects of the segment of *Epiphyton durum* KORDE; x100. |
| **2a, 3a, 3b, 4a** | Branches of *Epiphyton durum* KORDE, clearly showing alternation of light and dark strips. |
| **5, 6, 7, 8** | Some of the branches have single or paired rounded structures (sporangia?) at the ends. |
| **5** | Light transverse strips clearly showing a series of small cells with transverse partitions coalesced into horizontal lines. In places the cellular structure is obscured by dark carbonate masses produced by bacteria and cyanobacteria; x300. |
| **6** | Cross section of branches of *Epiphyton*; x100. |
| **6a** | Sporangia (?) with small cellules (?); x300. |
| **7, 8** | Apical cellules on the end of branches; x100. |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2
3
2a
3a
3b
4
4a
5
6
6a
7
8

**PLATE II**

*Epiphyton induratum* KORDE, 1961; East Siberia, Kuznetsk Alatau, Kiya River, Ust-Kundat Formation, Lower Cambrian, Tommotian – Atdabanian stages

**1** Branches of a multiaxial thallus, its surface covered by bacterial-cyanobacterial carbonate precipitate. In the more light-coloured sites, which have been not attacked by microbes, a primary cellular structure has been preserved in places; x60.

**2, 3, 4** Fragments of thallus filaments, on lateral parts of which pores with plasmodesmes are visible; x150.

**5** Thin filaments with oval cellules growing in the interstitial space. In modern algae sporangia are usually located in such bunches; x200.

**6** Structure that may have helped *Epiphyton* to attach to the substrate; x150.

**7** Thallus of recent *Corallina* LINNAEUS, 1756; x150.

**8–11** Separate fragments of thallus of recent *Corallina*. Plasmodesmes are present on either side of the filaments; x300.


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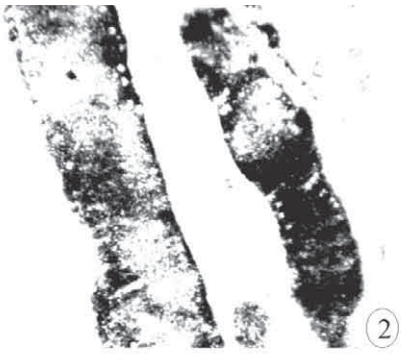
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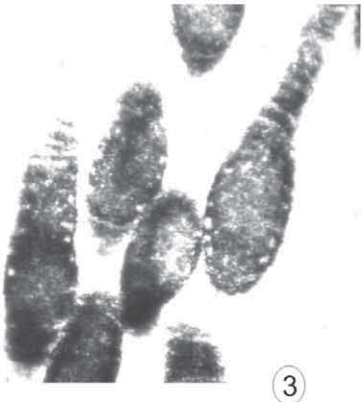
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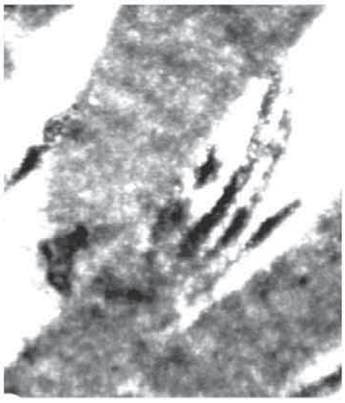
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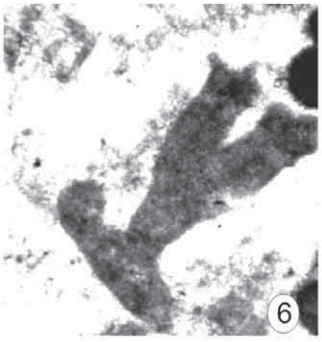
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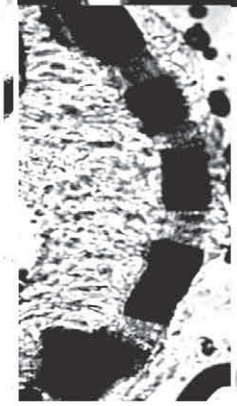
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brian microfossils, ooids, fragments of Cyanobacteria (*Girvanella*), or calcareous Fungi. In subsequent publications the conclusions of PRATT (1984) were maintained and received further development. RIDING (2000), reviews in detail the significant knowledge accrued about modern microbial carbonates, and their identification. The idea that stromatolites and *Epiphyton* were similar in nature was not new, and was suggested by MASLOV (1973), who suggested that *Epiphyton* could be regarded as a stromatolite. However, this did not clarify the nature of *Epiphyton*.

Clarification of the original morphological structure of *Epiphyton* was advanced by the research of A.A. Terleev in the Vendian–Cambrian of the Altay-Sayan area (SW Siberia, Russia) between 1998–2005, and the collection of uniquely preserved *Epiphyton* in East Sayan (Mana Depression) from the top part of the Anastasion Formation (Lower Cambrian, Tommotian; Plate I), and then in Kuznetsk Alatau on the Kiya River in the Ust Kundation Formation (Lower Cambrian, Tommotian-Atdabanian; Plate II). The exceptionally preserved algae occur, and are observed in dark-brown, partially phosphatized limestones.

As a result of this research it was possible to confidently observe the primary structural elements in a variety of specimens of *Epiphyton*.

## 2. RESULTS

Plates I and II show typical branching thalli of *Epiphyton*, in which the heterogenity of the calcareous thallus is visible: thin alternations of layers of dark and light calcite (Pl. I, Figs. 2, 3, 5) and single or double rounded structures (sporangia?) at the ends of branches (Pl. I, Figs. 7, 8). In some places (Pl. I, Fig. 5), thin sub-horizontal layers consisting of fine cells are present. All the cells had a flattened sub-cylindrical form. The height of a cell is 2–4 μm, and width 42–70 μm. The cell walls are composed of pelitomorphic dark calcite and their internal part by lighter calcite. In the upper part of the branch the width increases up to 98–112 μm. The dichotomizing branching of the filaments is accomplished by longitudinal division of an apical cell (Pl. I, Figs. 3, 4). Sometimes cells are obscured by areas of darker carbonates; sometimes they cover significant areas of branches.

There is also the discovery of numerous light coloured, small (5μm) ball-shaped structures located on the margins of *Epiphyton* branches (Pl. II, Figs. 2, 3, 4). These are comparable with the pores of modern red algae, through which plasmatic strings (plasmodesmes) pass that connect cells to provide intercellular transport of substances and structural durability for the thallus (SOUTH & WHITTIK, 1990).

Furthermore, detailed investigation of the thallus reveals bunches of thin strings with well preserved oval cells 5–8 μm in size. The bunches occur in internodes, and at branch ends, or along the sides of branches (Pl. II, Fig. 5). The similar forms observed in modern Red algae are referred to as nemateceae and represent knobs on the thallus surface, consisting of short strings, among reproductive bodies (ZINOVA, 1967). It is therefore possible that the cellular strings are analogous to modern Nematecies.

Finally, the structure attaching the *Epiphyton* branching thallus to the substrate has been found (Pl. II, Fig. 6) for the first time. In analogous modern algae, it appears that red algae with branching straight filiform thalli were attached to the substrate by a simple disk formed by a basal cell, or by prostrate threads (VASSER, 1989). It is possible that the structures attaching *Epiphyton* to the substrate were not calcified. The image shown in Pl. II, Fig. 6 could be an artifact, or possibly really was the point of attachment as seen in modern algae.

## 3. CONCLUSIONS

All multiaxial branching thalli of *Epiphyton* developed lengthways along the thallus by reducing numbers. The absence of transitive sites between the branches shows that they were not encased in calcium carbonate, and suggests that articulation of the thallus was similar to that in modern red algae of the genus *Corallina* (Pl. II, Figs.7–11), in which non-calcareous or weakly calcified segments consisting of axial strings and forming articulated intervals, alternated with calcified segments (VASSER, 1989; SOUTH & WHITTIK, 1990).

In modern *Corallina*, all the thallus appears black in colour, and the only light part is the non-calcified area of articulation. The dark coloring is probably caused by the ability of calcium-loving of bacterial-cyanobacterial associations to readily destroy the cellular structure of the filaments.

Discovery of the morphological elements of *Epiphyton* has allowed us to give a completely different interpretation of this genus, to recognize its similarity to modern red algae, and thereby amend its description.

The genus *Epiphyton* should be included in the family Ludloviaceae CHUVASHOV, which comprises algae with sporangia and a cellular structure of thallus (CHUVASHOV, 1987).

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