Thaumatoporella ladders unraveled

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Abstract. *Thaumatoporella* (incertae sedis) represents a widespread constituent in Upper Triassic–Cretaceous shallow-marine carbonates of the Tethyan realm and exhibits a wide morphological variability. Seemingly monostromatic cell-layers intermingled with and incorporated into bacinellid crusts (“*Bacinella irregularis*”) were described as *Thaumatoporella* bridges or ladders in the literature. This appearance of *Thaumatoporella* also accounted for the creation of the genus *Polygonella* ELLIOTT and its misleading comparison with single-layered crustose corallinean alga, e.g., genus *Lithoporella*. In fact, these “ladders” belong to the roof part of thaumatoporellaceans encrusting microbial crusts that subsequently became overgrown and thus incorporated. Often a rudimentary thin basal layer and an elongated sparitic void corresponding to the former body of *Thaumatoporella*, are present evidencing that its morphology is that of a variously shaped organism (free or attaching) enclosed by an all-round wall. Irregular lobate and thin-walled thaumatoporellaceans occurring in “bacinellid” fabrics might be interpreted as crust-dwellers.

Keywords: *Thaumatoporella*, bacinellid textures, Calcareous algae, microbialites, Upper Jurassic, Lower Cretaceous

INTRODUCTION

Thaumatoporella parvovesiculifera (RAINERI) was a successful inhabitant of different shallow-marine carbonate environments over a period lasting more than 120 million years, from the Middle Triassic until the Early Cenozoic (Radoičić, 1960; Flügel, 1983; De Castro, 1990; Schmid, 1996). Mass-occurrences (acme intervals) are reported from the Early-Middle Jurassic and the Late Cretaceous. Concerning the systematic position of *Thaumatoporella*, an algal origin is the most widespread interpretation, although Flügel (1983) envisaged a possible animal origin. De Castro (1990) created the new order Thaumtoporellales and the new family Thaumtoporellaceae, since *Thaumtoporella* should exhibit features of both green algae (Volvocales, Cladophorales) and cyanophytes. Nevertheless, De Castro tentatively assigned these microfossils to the green algae. Remembering that with its irregular cylindrical morphology and perforated wall, the Upper Cretaceous type-species *Thaumtoporella parvovesiculifera* (RAINERI) was originally described as a dasycladalean green alga. For encrusting cell layers, Elliott (1957) created the genus *Polygonella* with the type species *P. incrustata* from the (Upper) Jurassic of Iraq followed by *Polygonella shikokuensis* (Imaizumi, 1965: Upper Jurassic of Japan) and *Thaumtoporella (Polygonella) occidentalis* (Johnson and Kaska, 1965: Upper Cretaceous of Guatemala) (Fig. 1a-b). These taxa were interpreted mainly as red algae (Corallinaceae, Solenoporaceae). There seems to be

general consensus in the literature that they represent junior synonyms of *Thaumtoporella parvovesiculifera* (RAINERI) (Sartoni and Crescenti, 1962; Radoičić, 1960; Fenninger and Hötzel, 1967; Flügel, 1983; De Castro, 1990; Düzbastilar, 1991). Internally structured Late Triassic to Early Jurassic species of *Bacinella* (*B. bicellularis*, *B. ordinata*) forming flat superimposed crust layers and exhibiting thin perforate walls, were recently interpreted as representing thaumatoporellaceans (Schlagintweit and Bover-Arnal, 2012, for details). Anyway, the problem of wide intraspecific variability of one taxon versus different species of *Thaumtoporella* and the palaeobiological classification are still unsolved and under debate (e.g., Cherchi and Schroeder, 2005). In the present contribution, thaumatoporellaceans is used to designate these microfossils without implication on the systematic nature and concrete species designation.

A peculiar structure are isolated *Thaumtoporella* cell layers incorporated into irregular pseudocellular crusts that are mostly equated with the incertae sedis *Bacinella irregularis* RADOIČIĆ [“bacinellid textures” *sensu* Maurin et al., 1985; see also Schlagintweit and Bover-Arnal, 2012)] (Fig. 1c-d). These were termed *Thaumtoporella* ladders (Schäfer and Senowbari-Daryan, 1983), *Thaumtoporella* bridges (Leinfelder et al., 1993) or suspension bridges (Senowbari-Daryan, 1984) when these span between bioclasts. These “cell layers” may also occur as isolated fragments in the sediment (Fig. 1e), e.g., in calciturbidites (Fig. 1f-g). In the present paper, new data and interpretation are provided for these enigmatic structures.

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Fig. 1. *Thaumtoporellaceans* from the Pliensbachian (a) and Bajocian (b) of Croatia, Kimmeridgian-Tithonian (c-e) and Late Tithonian (f-g) of Austria. (a) Specimen attaching to a microbial crust (see also Fig. 2a) with elucidation of the taxonomic concept of *Thaumtoporella* versus *Polygonella*. Mount Biokovo, thin-section VE 514-5. (b) Attaching specimen with “roof” (black arrow) and rudimentary basal layer (white arrow). Southern Croatia, thin-section SL 4B. (c-d) *Thaumtoporella* (oblique wall section) floating in a “bacinellid” calcimicrobial crust. Mount Plassen, thin-sections PL 88 and HW 259-22. (e) Isolated *Thaumtoporella* “ladder” within fine-grained slope sediment resulting from the erosion and transportation of a former fixed specimen as shown for example in a. Mount Krahstein, thin-section Krah 117. (f-g) Wall fragments of *Thaumtoporella* (= free specimens of *Polygonella* sensu Elliott) in calciturbidites. Note the foraminifer *Mohlerina basiliensis* (Mohler) (M) in e. Barmstein Limestone of Mount Zwerchwand, thin-section E 85 and Mount Ewige Wand, thin-section E 803. Scale bars 0.5 mm.

MATERIAL

This study is based on thin-sections from different stratigraphic levels and locations:

Lower Jurassic (Pliensbachian) of Mount Biokovo, Karst Dinarides of Croatia. The material corresponds to the type-material of *Biokovina gradacensis* (Gušić, 1977; Velić, 2007). For geographic location of the sample see Fig. 1 in Gušić (1977).

Middle Jurassic (Aalenian) of Mount Biokovo, Karst Dinarides of Croatia. For geographic location of the sample see Fig. 6 in Schlagintweit and Velić, 2011).

Upper Jurassic (Kimmeridgian-Tithonian) of the Northern Calcareous Alps of Austria: Plassen Formation of Mount Plassen (Fenninger and Hötzl, 1967; Schlagintweit et al., 2005) and Mount Krahstein (Steiger and Wurm, 1980; Gawlick et al., 2004) and turbiditic Late Tithonian Barmstein Limestone of Mount Ewige Wand and Mount Zwerchwand (Gawlick et al., 2010).

MICROPALAEONTOLOGY

Description: *Thaumtoporellaceans* are frequently associated with calcimicrobial crusts, respectively pseudo-cellular bacinellid fabrics (see Maurin et al., 1985 and Schlagintweit and Bover-Arnal, 2012 for details). The specimens within these crusts are morphologically different from the irregular cylindrical tubiform Upper Cretaceous forms on which the original description was based (Raineri, 1922; Pia, 1938; Radoičić, 1960; De Castro, 1990, 2002). Intermingled with the bacinellid textures, *thaumtoporellaceans* occur either as elongated sickle-shaped forms (length up to some mm's) that “cover” a sparitic void (Fig. 2b) or as “free” bended wall articles (Fig. 1c-d). These wall fragments (thickness about 0.08 up to 0.3 mm) have the appearance of ladders that float within the pseudocellular crusts.

Discussion: In his description of *Polygonella* (= *Thaumtoporella*), Elliott (1957: p. 230) remarked that the single-layered cells occur either “encrusting or sometimes

free". As was correctly observed by De Castro (1990), these forms do not consist of a single layer of cells like some red algae but exhibit an all-round wall enclosing a central, sparite-filled body. Whereas in irregular cylindrical morphotypes of *Thaumatoporella* an all-round perforated wall of equal thickness is well discernible, the construction is different in attaching specimens. Here the part that attaches the substrate only shows a rudimentary wall of distinctly reduced thickness mostly without discernible pores (Fig. 1a). Obviously the substrate itself partly takes the function of the stabilizing and protecting wall. Therefore, the overall bauplan of an all-round closed body remains the same in both encrusting and non-encrusting specimens. Concerning the "free specimens" sensu Elliott, they can frequently be observed in high-energy shallow-water deposits or calciturbidites within basalinal sediments (Fig. 1f-g). It is evident that they correspond to broken wall fragments that originated from the erosion and breakage of both free and attached specimens.

Based on Upper Triassic material, Schäfer and Senowbari-Daryan (1983) described "free" thaumatoporellaceans within crusts of "*Bacinella irregularis*" assuming that these single-layered "*Thaumatoporella* ladders" became completely encrusted from all sides (Fig. 3a). Referring to the two

specimens shown in Figure 2, an alternative interpretation is favoured. It seems more likely that thaumatoporellaceans were attaching to the upper side of "bacinellid" crusts developing only a very thin basal (= attaching) wall (Fig. 3b). By subsequent ongoing growth of the "bacinellid" crusts, these *Thaumatoporella* specimens became completely incorporated. In sections perpendicular to the layers, the original sparite-filled central body is well recognizable (Fig. 2b). Specimens where the covering wall is cutted obliquely, seem to completely float inside the "bacinellid" fabric (Fig. 1c-d). Another possibility for this observation results from the encrustation of broken *Thaumatoporella* specimens (e.g., Senowbari-Daryan et al., 1994: pl. 11, fig. 3).

Fig. 2. Two examples of attaching *Thaumatoporella* unravelling the origin of the "isolated" ladders. a) Specimen (same as shown in Fig. 1a) attaching on the surface of a microbial crust as substrate. Mount Biokovo, thin-section VE 514-5. b) Specimen that was attaching to a "bacinellid" crust that became incorporated into the latter by ongoing crust formation contrasting the example shown in a). Note the preserved sparitic void (v) corresponding to the *Thaumatoporella* body, thus not representing a sheltering umbrella effect. Valanginian of Serbia, thin-section RR 4802. Scale bars 1 mm.

Fig. 3. Development of *Thaumatoporella* ladders (without scale). a) Model of Schäfer & Senowbari-Daryan (1983) with *Thaumatoporella* as single-layered boards ("einschichtige Platten") covering *Bacinella* tissue. b) This work: Specimen of *Thaumatoporella* (cement-filled body enclosed by a wall) attaching to a calcimicrobial "bacinellid" crust and becoming incorporated into the latter by crust overgrowth.

Within the “bacinellid” crusts, sometimes two different morphotypes of thaumatoporellaceans can be observed. One refers to the elongated attaching specimens with a rather thick wall exhibiting well visible pores (Fig. 2b). Another type is represented by irregular lobate bubble-shaped morphologies (Fig. 4a). Here, the wall is thinner and pores are not detectable in all cases. This observation is assumed to be due to diagenetic alteration. These irregular specimens can make up the major part of “bacinellid” crusts (Fig. 2b, 4b). A possible explanation for the different morphologies, might be that the irregular bubble-shaped forms are sediment (= crust)-dwellers. The elongated sickle-shaped forms instead are interpreted as having attached to the former crust surface (Fig. 3, right). It should be mentioned that the irregular lobate morphotype can also be found outside these crusts, e.g., in peloidal packstones (Fig. 4c-e). Here, the perforated character of the wall is mostly well discernible.

Fig. 4. Irregular-shaped thaumatoporellaceans from the Neocomian of Serbia (a-b), the Aalenian (c) and Pliensbachian (d-e) of Croatia. **a)** Irregular-shaped specimen (Th) within a “bacinellid fabric” that is interpreted as a mass agglomeration of thaumatoporellaceans. **b)** Diminished view of the fabric of thaumatoporellaceans (e.g., Th) within an indefinite fine-grained sediment exhibiting an overall microbial affinity. Note the incorporated foraminifers (arrows). See also Fig. 2b deriving from the same thin-section RR 4802. **c-e)** Specimens with numerous irregular constrictions and protuberances. Note the poorly discernible wall perforations in the specimen on the right in c. Mount Biokovo, thin-sections BST 2, VE 514-10, VE 514-2. Scale bars 0.5 mm.

CONCLUSIONS

Thaumatoporellaceans are a frequent constituent of “bacinellid” fabrics. *Thaumatoporella* “ladders” are only seemingly free, consisting of a single layer of cells as supposed in *Polygonella* ELLIOTT (= *Thaumatoporella* PIA). Also these specimens consist of a sparite-filled body that is all-round enveloped by a common wall. They are interpreted as forms that were attaching to substrates by means of a rudimentary thin basal wall, later becoming overgrown and thus incorporated.

Sometimes, thaumatoporellaceans make up the main part of bacinellid crust with attaching specimens and irregular lobate forms showing comparably thin all-round wall. These might be interpreted as crust-dwelling organisms. Therefore, the biogenic composition of these types of crusts may be rather complex deserving an individual case study rather than generalizations.

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