

Dasycladaleans from the Upper Turonian to Santonian of Austria (Gosau Group *pro parte*) and paleobiogeographic considerations

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Abstract Previously unreported dasycladaleans and one morpho-taxon of assumed algal origin are described from Upper Turonian to Santonian rocks of the Lower Gosau Subgroup (LGS) of the Northern Calcareous Alps. A taxonomic inventory of green-algal/benthic foraminiferal assemblages shows that assemblages of “pure” carbonate environments are more diverse than those of siliciclastic and mixed siliciclastic-carbonate settings. A comparison of the taxonomic inventory of the LGS with assemblages in similar sedimentary successions of the Alpine-Mediterranean realm shows the highest similarity with the “Mirdita Zone” of the internal Dinardids. Comparability of assemblages, however, is limited due to narrow chronostratigraphic overlap and/or because of scarcity of data from areas outside the Alps. Although higher than previously known, the total diversity of the green-algal/benthic foraminiferal assemblage of the LGS is clearly inferior to that of the peri-Adriatic carbonate platforms.

Keywords Upper Cretaceous · Gosau Group · Calcareous algae · Dasycladales · Stratigraphy · Micropaleontology · Northern Calcareous Alps

Introduction

Since the 19th century, the Upper Cretaceous of the Northern Calcareous Alps (equivalent to Gosau Group *pro parte*; cf. Wagreich and Faupl 1994) is reputed for its wealth in fossils. The tectonosedimentary cycle of the Gosau Group is subdivided into a lower subgroup characterized by neritic lithologies and an upper subgroup consisting of deeper-water facies (Wagreich and Faupl 1994; Sanders 1998). Within the Lower Gosau Subgroup (LGS), shallow-water limestones locally build intervals up to 100 m thick and at least a few kilometers in lateral extent (e.g., Sanders et al. 1997; Sanders and Höfling 2000). The micropaleontological investigation of the limestones and their closely associated lithologies, however, started at selected outcrops only (e.g., Höfling 1985; Schlagintweit 1990, 1991, 1992, 2004; Schlagintweit and Ebli 1995, 1998). In the Middle Turonian to Upper Santonian part of the LGS, calcareous algae, mainly Dasycladales, were reported from neritic limestones to marly limestones, and from rudist bioconstructions (e.g., Schlagintweit 1991; Schlagintweit and Lobitzer 2003a). Dasycladales may be quite common, and comprise associations characteristic of: (a) terrigenous-influenced shallow neritic to “lagoonal” settings, and (b) “reefal to peri-reefal” habitats with associations of corals, rudists, and sponges. The data obtained over the past decades have been compiled into an inventory of calcareous green algae, and are compared with other Late Cretaceous assemblages of the Alpine-Mediterranean realm.

Geological setting

In the area of the future Northern Calcareous Alps (NCA), Late Jurassic to Early Cretaceous tectonic convergence and

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nappe stacking were followed by exhumation and exposure of large parts of the orogen (e.g., Ratschbacher et al. 1989). Subsequent marine transgression started during the Turonian. From Turonian to Campanian times, a variegated, mixed siliciclastic-carbonate succession up to more than 2,000 m in thickness accumulated in terrestrial to neritic environments (Lower Gosau Subgroup, LGS; Wagreich and Faupl 1994) (Fig. 2). Deposition of the LGS terminated, from Santonian to Campanian times, as a consequence of deepening to bathyal to abyssal depths (Wagreich and Faupl 1994).

Both diversity and composition of macro- and microfossil assemblages indicate that during the Late Cretaceous, the area of the NCA was a transitional belt between the Tethyan and the temperate biogeographic realm, respectively (e.g., Sanders et al. 1997; Hradecká et al. 1996a, b). During deposition of the LGS, two shelf types of distinct morphology and with different prevalent sediments existed (Sanders 1998; Sanders and Höfling 2000). Type A shelves had a well-developed paralic to neritic belt, with variegated siliciclastic-carbonate facies associations. Within the inner-shelf to shore zone of type A shelves, coral-rudist limestones, rudist limestones, and bioclastic limestones accumulated in areas of low siliciclastic input (Sanders and Pons 1999). Upon persistently low terrigenous input, carbonate shelves locally developed in highstand systems tracts of depositional sequences (Sanders et al. 1997). In general, shallow-water limestones accumulated either (a) during intermittent shut-off of siliciclastic input, on siliciclastic shelves (e.g., Sanders and Pons 1999), or (b) in inner shelf settings (Sanders et al. 1997; Sanders and Höfling 2000). Type B shelves, in contrast, are characterized by a narrow paralic to neritic facies tract in front of a deep, muddy shelf. Type B shelves characterized the rapid

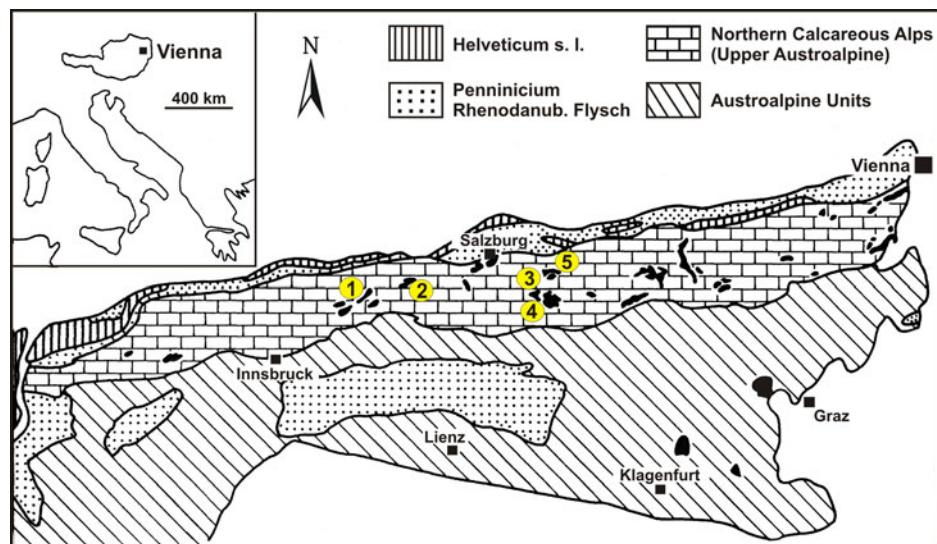
transgression and deepening that led to deposition of the Upper Gosau Subgroup (Sanders 1998). The taxa described herein are from type A shelf successions from the following localities (from west to east): Brandenberg, Pletzachalm, Theresienstein, Eisenbach, Wegscheidgraben, and Hofergraben (Fig. 1).

Brandenberg

Limestones of the LGS are located in the northern part of the Brandenberg Gosau, a larger erosional remnant of the Gosau Group located in Tyrol, approximately 10 km west of Wörgl (e.g., Sanders 1998, Fig. 2). The calcareous algae reported from the Brandenberg area occur in the Upper Turonian to ? early Coniacian carbonate succession of the Haidach Section (see Sanders and Baron-Szabo 1997; Sanders and Pons 1999, Fig. 6, for lithological column; and Steuber 2001, for Sr isotope stratigraphy), the Unterberg Section (Sanders 1998, Fig. 7A), Atzl Section (Sanders 1998, Fig. 11), and the Prinzkopf-Krumbachalm Section (Sanders 1998, Fig. 7C; Studeny 2011).

The taxa *Hungarioporella baconica* Conrad, Bodrogi and Radoičić, *Coptocamyplodon pantici* Ljubović-Obradović and Radoičić, *Milanovicella hammudai* (Radoičić) (not treated in this paper), *Cylindroporella?* aff. *kochanskya* Radoičić, *Clypeina cf. pastriki* Radoičić, and *Clypeina?* sp. were observed in wackestones with different taxa of benthic foraminifera and the gymnocodiacean *Permocalculus gosaviensis* Schlagintweit (Fig. 3a). Up-section, these limestones grade into floatstones with coral debris, and with dasycladalean algae in decreasing abundance (Fig. 3b). *Trinocladus triopolitanus* Raineri occurs in bioclastic grain- to packstones with corals, rudists, echinoderms, gastropods, calcareous algae (green algae and red

Fig. 1 Simplified tectonic map of the Eastern Alps with major occurrences of the Gosau Group and sample localities (see Wagreich and Faupl 1994). 1 Brandenberg, 2 Pletzachalm, 3 Theresienstein, 4 Russbach-Gosau (incl. Wegscheidgraben and Hofergraben), 5 Eisenbach



algae), and benthic foraminifera (textulariids, and arenaceous encrusting taxa) (Fig. 3c). The age of the algaebearing samples is Late Turonian to Early Coniacian (see Sanders 1998; Sanders and Pons 1999).

Pletzachalm

The Pletzachalm section near Kramsach, Tyrol, was first described lithologically in detail by Leiss (1988). The micropaleontological content (benthic foraminifers, calcareous algae) was studied by Schlagintweit (1991), Schlagintweit and Ebli (1995, 1998), and Schlagintweit and Sanders (2008), revealing several new taxa. Calcareous green algae occur in marly limestones that are intercalated within a succession of marls, with layers of gastropods and coalified plant remains, followed up-section by a rudist biostrome. Algal species include *Dissocladella? pyriformis* Schlagintweit, *Neomeris mokragorensis* Radoičić and Schlagintweit, and the morpho-taxon *Oroseina pletzachensis* Schlagintweit and Ebli. The age of the succession below the rudist biostrome is Late Turonian (Schlagintweit 1991, according to M. Wagreich; pers. comm.).

Theresienstein

At Theresienstein in the Strobler Weissenbach valley, the thickest and best-developed Upper Cretaceous coral reef of the Eastern Alps is exposed (Sanders et al. 1999; see Baron-Szabo 2001, for coral fauna). The reef, an interval approximately 25 m in thickness and rich in large coral colonies, is overlain by a few-meters-thick package of poorly sorted bioclastic grainstones/packstones to floatstones with toppled and coarsely fragmented rudists. These bioclastic limestones contain *Permocalculus (Pyrulites) theresiensteinensis* Schlagintweit and Sanders and *Neomeris (Drimella) cf. jerinae* Radoičić (Schlagintweit and Sanders 2007) (Fig. 3f). Based on rudists, a Coniacian age is indicated for the Theresienstein reef (Sanders et al. 1999). Strontium isotope stratigraphy of rudist shells indicates a mean age of 88.65 Ma (Steuber 2001, table 2 and fig. 4) within the early Coniacian (Walker et al. 2009).

Eisenbach

The Eisenbach Gosau occurrence is located at the eastern side of Lake Traunsee in the Upper Austrian Salzkammergut (Weber 1960; Hradecká et al. 2005) (geological map of Austria, sheet no. 66 Gmunden; Egger 2007). With its predominantly marly lithologies, this occurrence is famous for its gastropods (Zekeli 1852). From this locality, the dasycladale *Thrysoporella eisenbachensis* Schlagintweit and Lobitzer was described from marly limestones (Fig. 3d): wackestones, partly floatstones with coalified

plant remains, mollusc shells (mainly gastropods), ostracods, *Dissocladella? pyriformis* Schlagintweit, *Neomeris mokragorensis* Radoičić and Schlagintweit, and miliolid foraminifera (Schlagintweit and Lobitzer 2003a). The age is Middle Turonian, based on calcareous nannofossils, ostracods, and angiosperms (Hradecká et al. 2005).

Wegscheidgraben

Wegscheidgraben at the Pass Gschütt is located west of Gosau. Calcareous algae are reported from the Hochmoos Formation, i.e., rudist limestones and associated wackestones (Höfling 1985; Leiss 1988; Wagreich 1988; Schlagintweit and Ebli 1998). In Wegscheidgraben, Sr isotopy of rudist shells indicates a mean age of 84.1 Ma (Steuber 2001) (late Santonian; Walker et al. 2009).

Hofergraben

Hofergraben, a ravine with a creek, is situated approximately 1 km southeast of Gosau, Upper Austria (Österreichische Karte 1: 50.000, sheet no. 95 St. Wolfgang). The described material comes from two small southern tributaries of the Hofergraben, at an altitude of 900 m a.s.l. (see Schlagintweit 2004, fig. 1 for exact location). The so-called Hofergraben marls (Hofergraben Member of Sanders and Baron-Szabo 2008) belong to the Hochmoos Formation (Fig. 2). These marls are well known for their coral fauna, such as the solitary *Cunnolites* (Sanders and Baron-Szabo 2008). Calcareous green algae were described from arenitic siliciclastic-carbonate beds interpreted as storm beds (tempestites) within the marly shelf succession (Schlagintweit and Lobitzer 2003b). Calcareous algae include *Neomeris mokragorensis* Radoičić and Schlagintweit, *Trinocladus tripolitanus* Rainier, *Jodotella koradae* (Dieni, Massari and Radoičić) (Fig. 3e) and the morpho-taxon *Oroseina pletzachensis* Schlagintweit and Ebli. The age is Late Santonian (Sanders and Baron-Szabo 2008, fig. 2). In the Hochmoos Formation of the nearby Nefgraben, Sr isotopy of a rudist shell indicates a mean age of 83.88 Ma (Steuber 2001) (Late Santonian; Walker et al. 2009).

Micropaleontology

The major part of the calcareous algae is already known from the Gosau Group of the Northern Calcareous Alps. Only a few taxa, however, are fairly common. Most other taxa are rare and, in some cases, are documented as single findings only; this precludes a generic or specific assignment. Included hereunder are also a few findings of known taxa, but with morphological details not included in the original descriptions. The following taxa/morphotaxa are

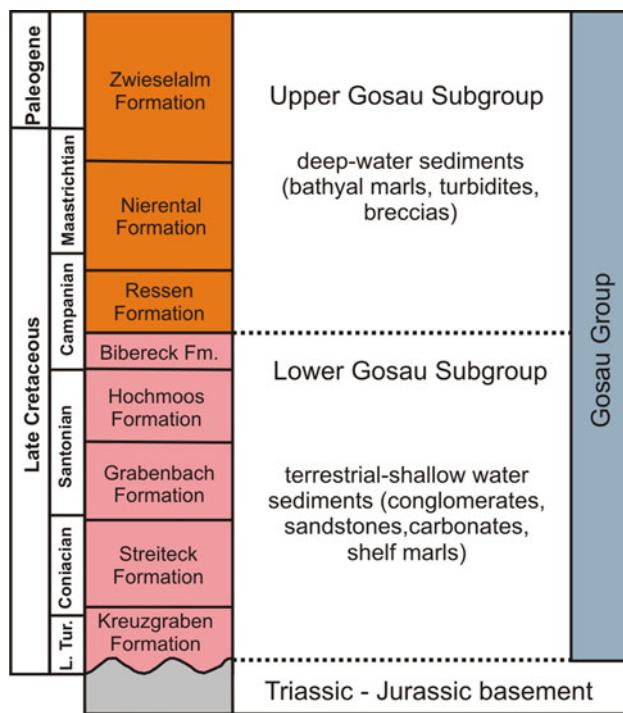


Fig. 2 Lithostratigraphic subdivision of the Gosau Group of Gosau and Russbach (redrawn from Wagreich and Decker 2001)

treated in alphabetical order (* taxa recorded for the first time from the Northern Calcareous Alps):

- Clypeina* cf. *pastriki* Radoičić*
- Clypeina?* sp.*
- Coptocampylodon pantici* Ljubović-Obradović and Radoičić*
- Cylindroporella* aff. *kochanskyae* Radoičić
- Dissoclarella?* *pyriformis* Schlagintweit
- Dissoclarella* sp.*
- Gen. et sp. indet. 1*
- Hungarioporella baconica* Conrad, Bodrogi and Radoičić *
- Neomeris (Larvaria)* aff. *oroseina* Dieni, Massari and Radoičić*
- Neomeris* sp.
- Thyrsoporella eisenbachensis* Schlagintweit and Lobitzer
- Trinocladus tripolitanus* Raineri
- Division Chlorophyta
- Genus *Clypeina* Michelin, 1845
- Clypeina* cf. *pastriki* Radoičić 1983 (Fig. 4a, b?, c–g).
- *1983 *Clypeina pastriki*, n. sp.—Radoičić: 79, pl. 4, figs. 1–4, pl. 5, figs. 1–2

Remarks *Clypeina pastriki* was described by Radoičić (1983) from the Turonian? of Libya (type level of

“*Likanella hammudai*”) and the Cenomanian of the Dinarids (Mt. Pastrik, Mirdita Zone of Kosovo). The general characters of the Gosau specimens fit well with *Clypeina pastriki*, although dimensions may be smaller ($D: 0.74\text{--}0.95$ mm, $d: 0.23\text{--}0.32$ mm vs. $0.96\text{--}1.0$ mm and $0.32\text{--}0.352$ mm). It is worth mentioning that the species is known so far only from the original paper of Radoičić (1983). Due to the findings in the Lower Gosau Subgroup, its stratigraphy range must be extended up to the Middle Coniacian.

Occurrence Gosau of Brandenberg.

Stratigraphy Lower-Middle Coniacian.

Clypeina? sp.

Figure 4h

Remarks Single finding of a small Dasycladale ($D = 0.45$ mm, $d = 0.18$ mm) represented by one transverse section showing six short almost spherical laterals ($p = 0.15\text{--}0.18$ mm) closed at tips. Without longitudinal sections showing clearly spaced-out whorls, our specimen can be attributed only tentatively to the genus *Clypeina* Michelin. Also, the transition from the laterals to the main axis is not clearly visible and could be pedunculated thus showing affinities to the genus *Holosporella* Pia with touching laterals along the axis (e.g., Granier and Hofmann 2002; Barattolo et al. 2008). If so, this would be the youngest occurrence of the genus *Holosporella*, Pia known so far until the Albian (*H. senegalensis*, Granier 1992).

Occurrence Gosau of Brandenberg.

Stratigraphy Upper Turonian-Middle Coniacian.

Genus *Cylindroporella* Johnson, 1954

Cylindroporella aff. *kochanskyae* Radoičić 1975 non 1970 (Fig. 5a–f).

*1970 *Cylindroporella kochanskyae* n. sp.—Radoičić: 359, pl. 1–6

1975 designation of lectotype by Radoičić = pl. 2, fig. 1 in Radoičić (1970)

1976 *Cylindroporella kochanskyae* Radoičić – Radoičić, pl. 5, figs. 1–4

1994 *Cylindroporella* cf. *kochanskyae* Radoičić – Kuss: 299, pl. 5, figs. 9–13

2000 *Cylindroporella kochanskyae* Radoičić – Masse and Isintek: 367, pl. 1, figs. 1–3

n.f. 2003 *Cylindroporella* cf. *kochanskyae* Radoičić – Aguilera-Franco: p. 212

Remarks Remains of a medium-sized dasycladale ($D = 0.64$ mm, $d = 0.13$ mm) with 5 (?) oval to spherical laterals (0.15–0.2 mm) interpreted as fertile ampullae.

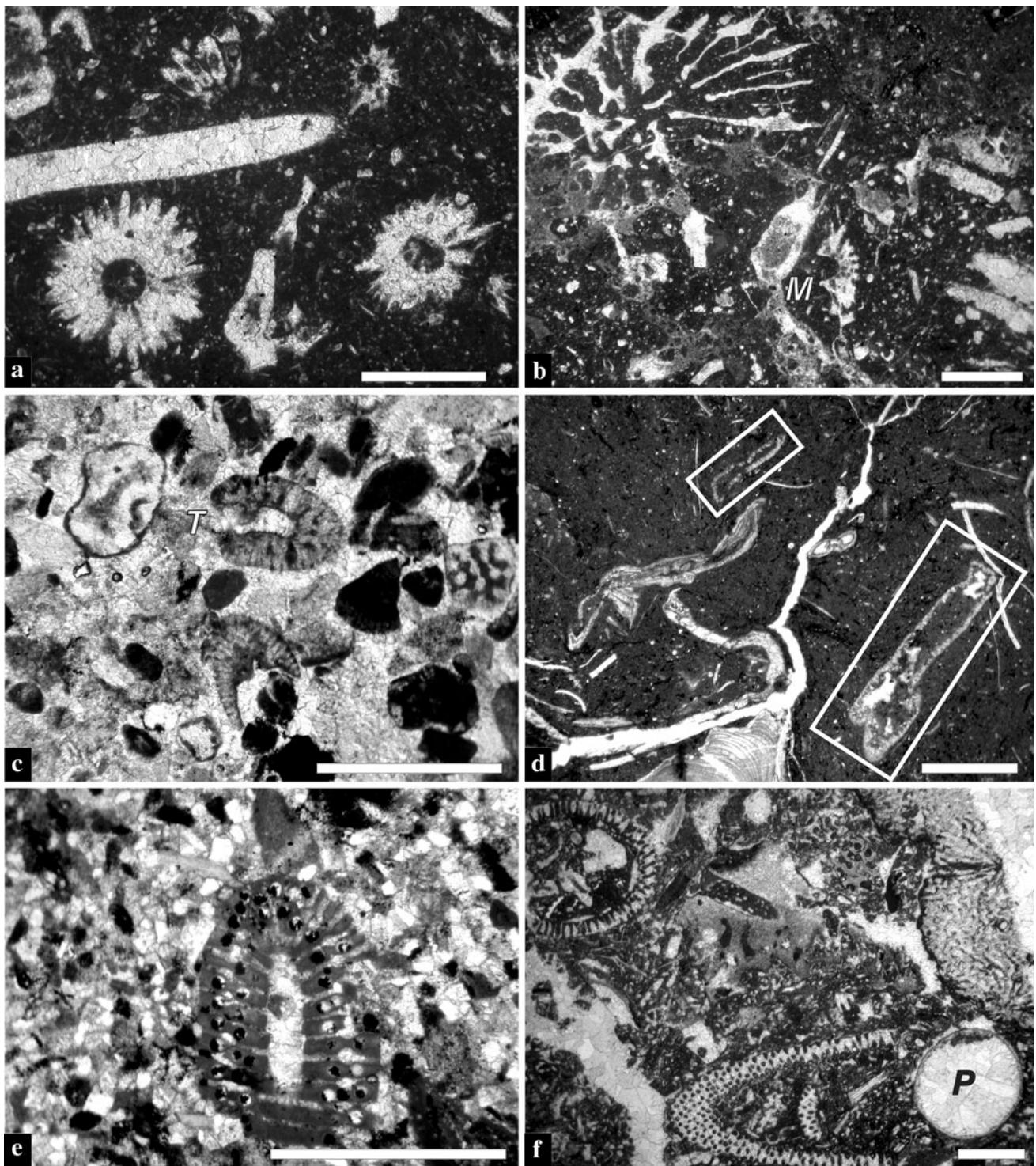


Fig. 3 Examples of microfacies types with dasycladalean algae from the Lower Gosau Subgroup of Austria. **a** Wackestone with *Milavicella hammudai* (Radoičić), Gosau of Brandenberg, sample 1659-B. **b** Floatstone with coral debris and scattered specimens of *Milavicella hammudai* (Radoičić) (*M*), Gosau of Brandenberg, sample 5495-10. **c** Grainstone to packstone with debris of corals, rudists, and *Trinocladus tripolitanus* Raineri (*T*), Gosau of Brandenberg, sample Atz 9. **d** Wacke- to floatstone with mollusc shells (mostly gastropods) and remains of *Thrysoporella eisenbachensis* Schlagintweit and

Lobitzer, Gosau of Eisenbach, sample EB 9B. White rectangles refer to detailed views shown in Fig. 9a, b, e. **e** Mixed siliciclastic-carbonate tempestite with oblique section of *Jodotella koradae* (Dieni, Massari, and Radoičić), Gosau of Hofergraben, sample HG 5B. **f** Bioclastic packstone/rudstone with corals, *Neomeris* (*Drimella*) cf. *jerinae* Radoičić and *Periocculus* (*Pyrulites*) *theresiensteinensis* Schlagintweit and Sanders (*P*), Gosau of Theresienstein, sample T6 (see Schlagintweit and Sanders 2007 for details). Scale bars 1 mm

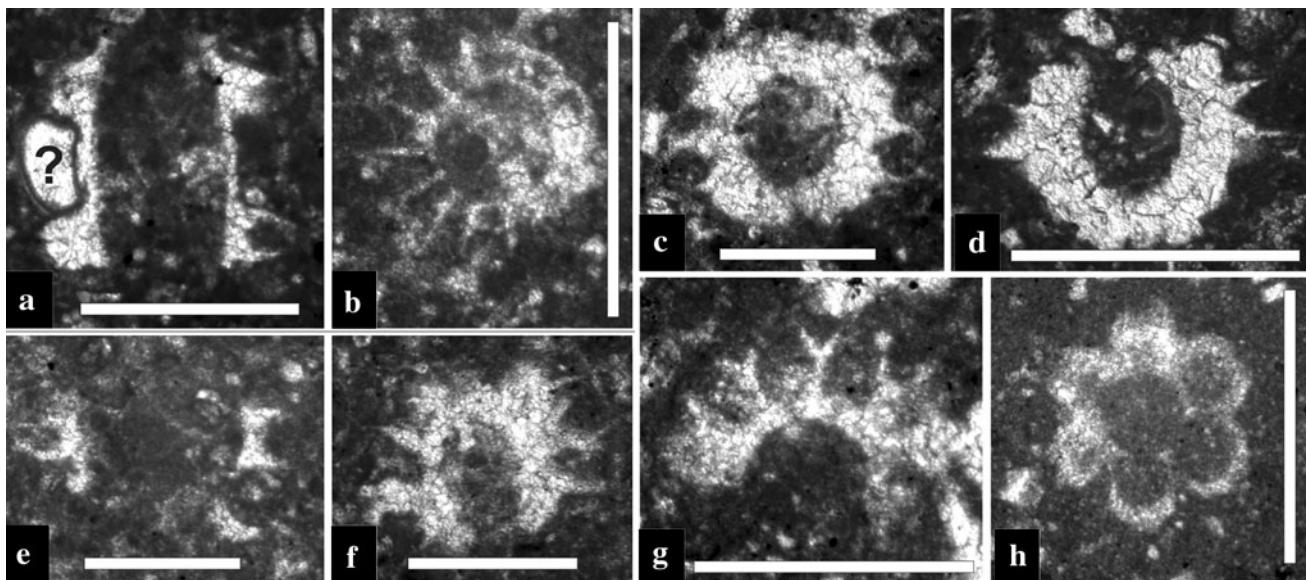


Fig. 4 Dasycladalean algae from the Lower Gosau Subgroup of Brandenberg, Austria. *Clypeina* cf. *pastriki* Radoičić, longitudinal section cutting two whorls (**a**), oblique transverse section showing an unknown organism (?; thamnoporellacean alga) attaching on the thallus between two verticils (**b**), sample 1659B; oblique transverse

section (**c–d**), sample 16795-7; oblique section (**e**), sample 1659B; oblique transverse section (**f**), sample 16795-9; oblique section (**g**), sample 5495-10. **h** *Clypeina* ? sp., transverse section, sample 16795-7. Scale bars 0.5 mm

The fragmentary state of preservation and the strong recrystallization does not allow further comments on morphological details. *C.?* *kochanskyae* is so far known from the Lower Albian-Turonian (Granier 1986; Granier and Deloffre 1993; Barattolo 2002). The attribution of this species to *Cylindroporella* is uncertain. For the taxonomy of cylindroporelliform algae, see Granier et al. (1994), Barattolo and Parente (2000), Sokač (2004), and Radoičić (2006). For example, *Cylindroporella parva* Radoičić, another Late Cretaceous representative, was transferred to the genus *Montiella* Morellet and Morellet recently by Radoičić (2006).

Occurrence Gosau of Brandenberg.

Stratigraphy Upper Turonian-Lower Coniacian.

Genus *Dissocladiella* Pia 1936

Dissocladiella? *pyriformis* Schlagintweit 1991
(Fig. 6a–b).

1988 *Trinocladus* sp. – Kuss and Schlagintweit: 84, pl. 19/4-5

*1991 *Dissocladiella?* *pyriformis* n. sp. – Schlagintweit: 193, pl. 1, figs. 1-7, pl. 2, figs. 1-7

1991 *Dissocladiella?* sp. – Kuss and Conrad: fig. 2/1-2

1998 *Dissocladiella?* *pyriformis* Schlagintweit – Schlagintweit and Ebli: 370, pl. 2, figs. 5 (pars), 6, 10

Remarks Besides the Northern Calcareous Alps, the species was reported from the Albian of Egypt (Conrad and Kuss 1991).

Originally erected as a possible representative of *Dissocladiella* (two orders of laterals), the existence of at least three orders of

laterals (or branching siphons?) necessitates a taxonomic revision. Because of the poorly calcified portion towards the central zone or region of the thallus (Fig. 6b), the generic position still remains unclear as an originally calcified central (=medullar?) zone cannot be excluded. As a further characteristic feature of this alga, not included in the original diagnosis, subparallel branching of the thallus was observed (Fig. 6a). This feature, however, occurs in both siphonous and dasycladalean algae.

Occurrences Gosau of Pletzachalm and Eisenbach.

Stratigraphy Middle Turonian-Santonian.

Dissocladiella? sp.

(Fig. 6c)

Remarks A single transverse section ($D = 0.8$ mm) showing a large number of rather small ($p = 0.03\text{--}0.04$ mm) pyriform to ovoidal primaries ($w \sim 40$) with short secondaries. The main axis is very large with respect to the total diameter ($d/D \sim 75\%$). Most likely the fragment discovered belongs to a new species, but insufficient material precludes a detailed description.

Occurrence Gosau of Brandenberg.

Stratigraphy Middle Turonian-Lower Coniacian.

Gen. et sp. indet 1.

(Fig. 6d)

Remarks One fragment of an unknown dasycladalean alga showing two orders of laterals.

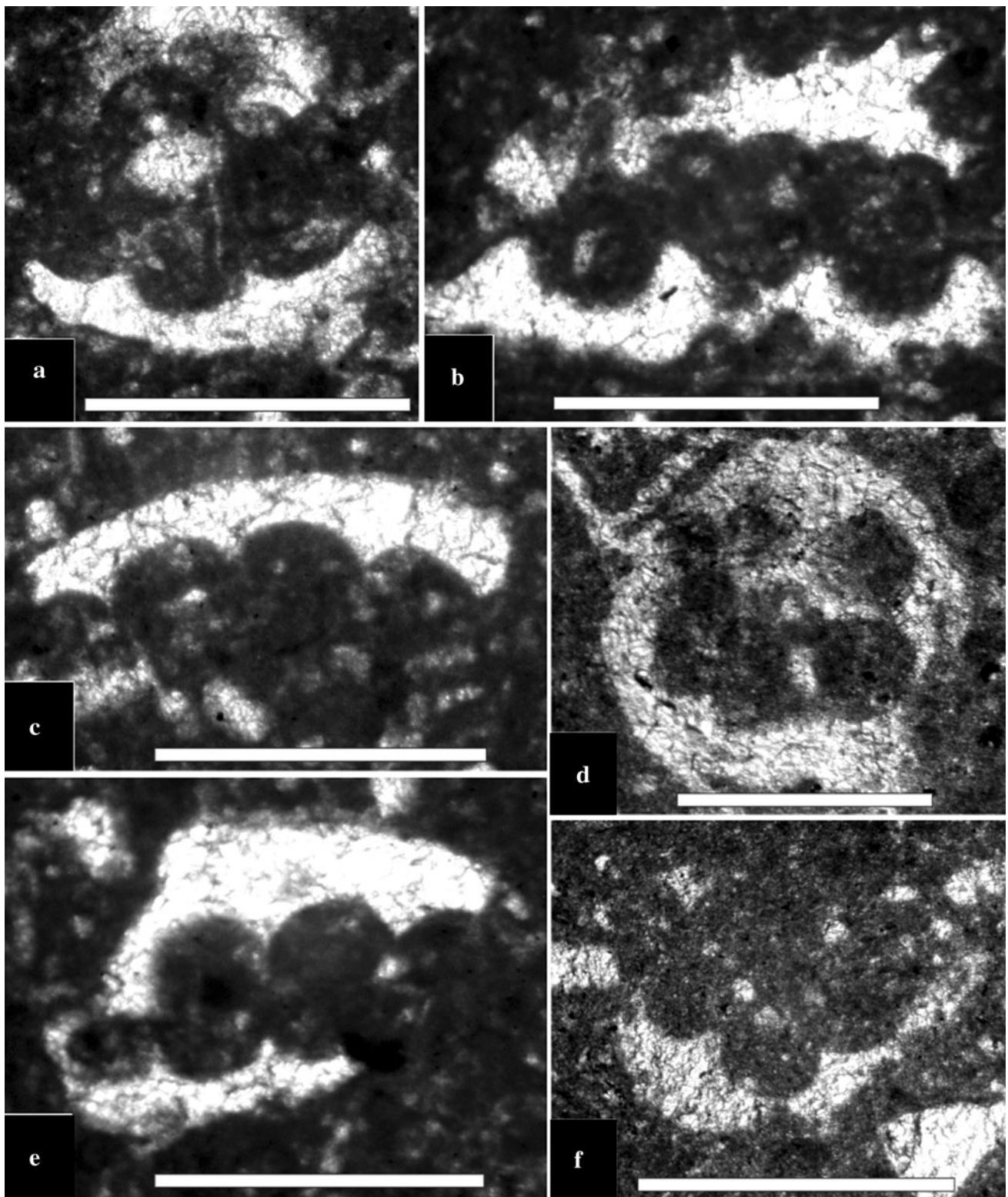


Fig. 5 Dasycladalean algae from the Lower Gosau Subgroup of Brandenberg, Austria. **a–f:** *Cylindroporella?* aff. *kochanskyaе* Radoičić. Slightly oblique transverse sections (**a, d, f**), fragmentary oblique sections (**b–c, e**), samples 1659, 5495-12, 19995-19. Scale bars 0.5 mm

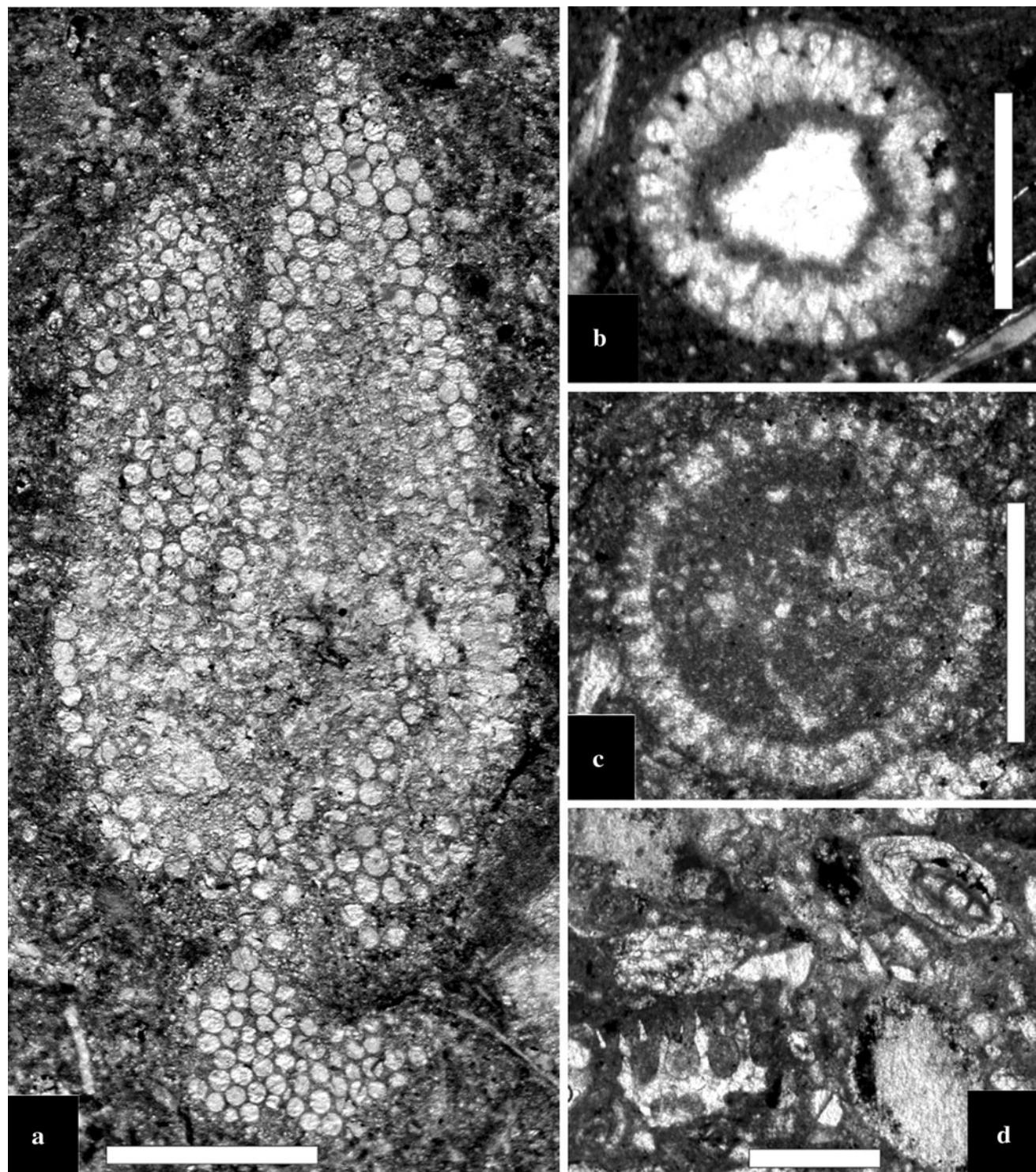


Fig. 6 Dasycladalean algae from the Lower Gosau Subgroup of Pletzachalm (**a**), Eisenbach (**b**), Brandenberg (**c**), and Wegscheidgraben (**d**), Austria. **a–b** *Dissoclarella?* *pyriformis* Schlagintweit, thallus showing low-angle, almost parallel branching (**a**), sample P-7, transverse section showing irregular inner thallus margin (**b**), sample

EB-9B. **c** *Dissoclarella* sp., transverse section showing high number of laterals and wide main axis, sample 151194-1. **d** Gen. et sp. indet. 1, fragment showing two orders of laterals and subaxial section of benthic foraminifer *Nummofallotia cretacea* Schlumberger, sample 1786. Scale bars 0.5 mm

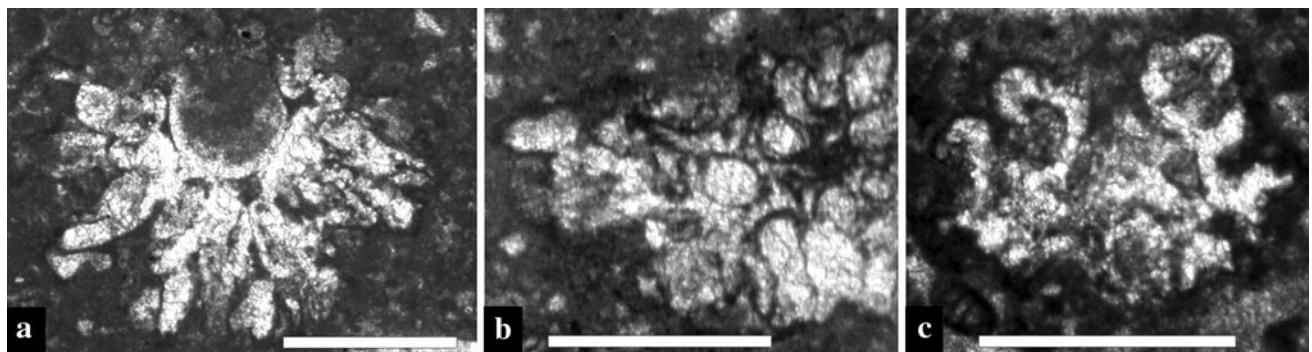


Fig. 7 Dasycladalean algae from the Lower Gosau Subgroup of Brandenberg, Austria. **a–c** *Hungariporella baconica* Conrad, Bodrogi and Radoičić, oblique transverse section (**a**), fragmentary oblique sections (**b–c**), sample 1659. Scale bars 0.5 mm

Occurrences Gosau of Russbach (locality Wegscheid-graben).

Stratigraphy Upper Santonian (Hochmoos Formation, see Fig. 2)

Genus *Hungariporella* Conrad, Bodrogi and Radoičić, 2002

Hungariporella baconica Conrad, Bodrogi and Radoičić, 2002 (Fig. 7a–c).

*2002 *Hungariporella baconica* n. sp. – Conrad, Bodrogi and Radoičić: 283, figs. 3–4, pl. 1, fig. 1–6, pl. 2, figs. 1–7

Remarks *Hungariporella baconica* was reported so far only from its type-locality, the Upper Santonian of the Ugod Limestone Formation of the Southern Bakony Mountains of Hungary. The rare, mostly oblique sections do not allow further comments on the exhaustive description by Conrad et al. (2002). We note a thin micritic coating of the irregular-shaped individualized laterals. The sample with *H. baconica* comes from a bed of bioturbated, poorly sorted bioclastic wackestone with miliolids and other benthic foraminifera (e.g., *Cuneolina*, *Dictyopsella*, *Nezzazatinella*), fragments of calcareous algae (*Milanovicia hammudai*, *Coptocampylodon nikolapantici*, *Clypeina pastriki*), microgastropods, and a few crustacean pellets. Due to the findings in the Lower Gosau Subgroup of the Brandenberg Gosau (see Sanders 1998), the stratigraphic range of *H. baconica* must be enlarged to the Lower Coniacian (possibly Upper Turonian).

Occurrence Gosau of Brandenberg.

Stratigraphy Upper Turonian-Lower Coniacian.

Genus *Neomeris* Lamouroux, 1816

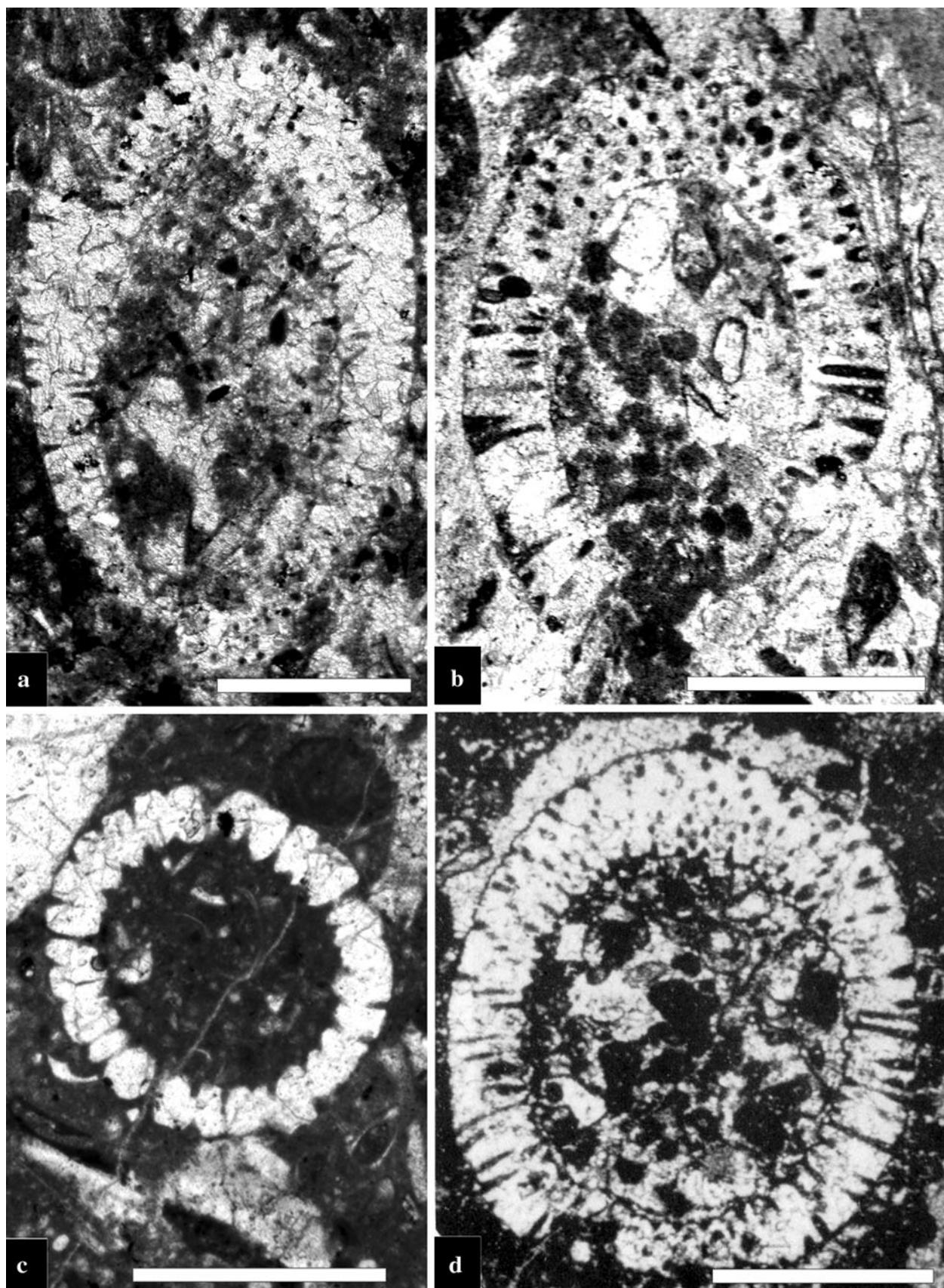
Neomeris (Larvaria) cf. oroseiana Dieni, Massari and Radoičić, 1983 (Fig. 8a–b, c?, d).

*1983 *Neomeris (Larvaria) oroseiana* n. sp. – Dieni et al.: 49, pl. 2, figs. 1–4

1985 *Neomeris (Larvaria) oroseiana* Dieni, Massari and Radoičić – Dieni et al.: 21, pl. 14, figs. 1–11, pl. 15, figs. 1–11

1998a *Neomeris (Larvaria) oroseiana* Dieni, Massari and Radoičić – Radoičić, pl. 4, fig. 4

Remarks Large specimens of *Neomeris (Larvaria)* (*D* of the Gosau specimens 1.35–2.45 mm) with densely set verticils, long secondary branches, relatively small fertile ovoid ampullae, and thick calcification. In contrast, *N. mokragorensis* Radoičić and Schlagintweit, another species recorded from the Lower Gosau Subgroup (Radoičić and Schlagintweit 2007), displays light calcification surrounding the more or less spherical ampullae. Our specimens, however, do not allow to clearly decipher the internal organization of the fertile ampullae with respect to the sterile laterals. Note that the varying degree of calcification in fossil Neomereae has been used by Génot (1985) for a more accurate species definition. The oblique section of the specimen illustrated in Fig. 8b shows striking resemblances to the specimen of *Neomeris (Larvaria) oroseiana* Dieni, Massari and Radoičić illustrated by Radoičić (1998a, b, pl. 4/4) from the Paleocene of Slovenia (Fig. 8d). This is just a further example that a taxon loses its Cenozoic monopoly and biostratigraphic importance. Similarly, *Jodotella koradae* (Dieni, Massari and Radoičić) (Fig. 3e) was also described from the Paleocene of Sardinia and was later reported from the Maastrichtian of Italy (Parente 1997) and the Upper Santonian of Austria (Schlagintweit 2004). For *N. (L.) oroseiana*, a possible Danian-Montian stratigraphy was assumed by Dieni et al. (1985). Like *Jodotella koradae*, *N. (L.) oroseiana* seems to have a wider stratigraphic range, originating in the Late Cretaceous.



◀ Fig. 8 Dasycladalean algae from the Lower Gosau Subgroup of Brandenberg, Austria (a–c) and the Lower Paleocene of Slovenia (d). a–c *Neomeris (Larvaria)* cf. *oroseiana* Dieni, Massari and Radoičić, oblique sections (a–b), sample 19995.11, and transverse section (c), sample MS 65. d *Neomeris (Larvaria) oroseiana* Dieni, Massari and Radoičić, oblique section comparable to b (from Radoičić 1998a, pl. 4, fig. 4). Scale bars 1 mm

Occurrence Gosau of Brandenberg.

Stratigraphy Upper Turonian-Lower Coniacian.

Genus *Thrysoporella* Gümbel, 1871

Thrysoporella eisenbachensis Schlagintweit and Lobitzer, 2003 (Fig. 9a–d)

*2003a *Thrysoporella eisenbachensis* n. sp. – Schlagintweit and Lobitzer: 134, pls. 1, figs. 1–10, pl. 2, figs. 1–12

Remarks The species was falsely described as *Thrysoporella eisenbachensis*; correct generic name is *Thrysoporella*. Reported from the Gosau strata of Eisenbach, it has now also been detected in the Gosau of Theresienstein (sample 1803, Fig. 9c). In the original description, the possibility of thallus branching was already mentioned and has now been verified (Fig. 9a). This feature is also known from the Upper Jurassic *Thrysoporella pseudoperplexa* (Granier and Braik 2002). *T. eisenbachensis* shows different types of calcification. Most typically, the inner part of the calcareous skeleton is not smooth but exhibits irregular indentations. In some cases, only the calcification around the highest order of laterals is preserved accounting for a comparatively large central hollow and a thin preserved calcareous sheet (Fig. 9d).

Occurrences Gosau of Eisenbach and Theresienstein.

Stratigraphy Middle Turonian-Coniacian.

Genus *Trinocladus* Raineri 1922

Trinocladus tripolitanus Raineri 1922

(Fig. 10a–c)

*1922 *Trinocladus tripolitanus* n. gen., n. sp. – Raineri: 79, pl. 1, figs. 15–16

1992 *Trinocladus tripolitanus*, Raineri – Schlagintweit: 6, pl. 2, figs. 6–9, 11

1992 *Neomeris* sp. – Moussavian: pl. 27, fig. 4

Remarks This species was found preferentially in microfacies types of medium- to high-energy settings together with debris of corals, rudists, and sponges. It may be associated with specimens of *Neomeris (Larvaria)* cf.

oroseina Dieni, Massari and Radoičić. Normally, the thalli are recrystallized to sparry calcite. In the tempestite layers of the Hofergraben marls, the thalli became rapidly buried, obviously accounting for its dark-brownish preservation (Fig. 10d–e). Here, some specimens may show a “bifurcation” at the distal end of the tertiary laterals (Fig. 10e). It is unknown whether this is simply a secondary erosional feature or points to the existence of tiny fourth-order laterals. In the latter not-proven case, the generic diagnosis including three orders of laterals should be emended.

Occurrence Gosau of Brandenberg (« Atzl reef »).

Stratigraphy Upper Turonian-Lower Coniacian (Gosau of Brandenberg), Upper Santonian (Gosau type area).

Morphogenus *Coptocampylodon* Elliott 1963

Remarks *Coptocampylodon* Elliott has been considered a morphogenus by Ljubović-Obradović and Radoičić (2003), namely as dislocated tufts of elongated trichophorous secondary laterals of different larger dasycladalean species. The isolated holotype of the type species *Coptocampylodon lineolatus* Elliott has been considered a crustacean coprolite with grooved outer surface by Cuvillier et al. (1969) and Živković and Bogner (2006), a view considered as a case of homeomorphism by Ljubović-Obradović and Radoičić (2003). The detection of basal holdfast structures in connection with “*Coptocampylodon*”-type calcareous bodies from the Aptian of Albania represents a completely different biogenic origin as remains of octocorals, an interpretation originally favored by Elliott (1963) for *C. lineolatus* (see detailed discussion in Schlagintweit and Gawlick 2009). As obviously different “morpho species” of “*Coptocampylodon*” may belong to different taxonomic groups as a case of homeomorphism, each case has to be considered very carefully. When accepting the coprolite nature of the type species, the other representatives that according to our opinion are not consistent with such an interpretation, must belong to another genus or other genera.

Coptocampylodon pantici Ljubović-Obradović and Radoičić, 2003

(Fig. 11a–c)

*2003 *Coptocampylodon pantici*, n. morpho sp. – Ljubović-Obradović and Radoičić: 135, pl. 1, figs. 1–5, pl. 2, figs. 1–4, pl. 3, figs. 1–2

Remarks *Coptocampylodon pantici* Ljubović-Obradović and Radoičić from the Turonian of Serbia shows very

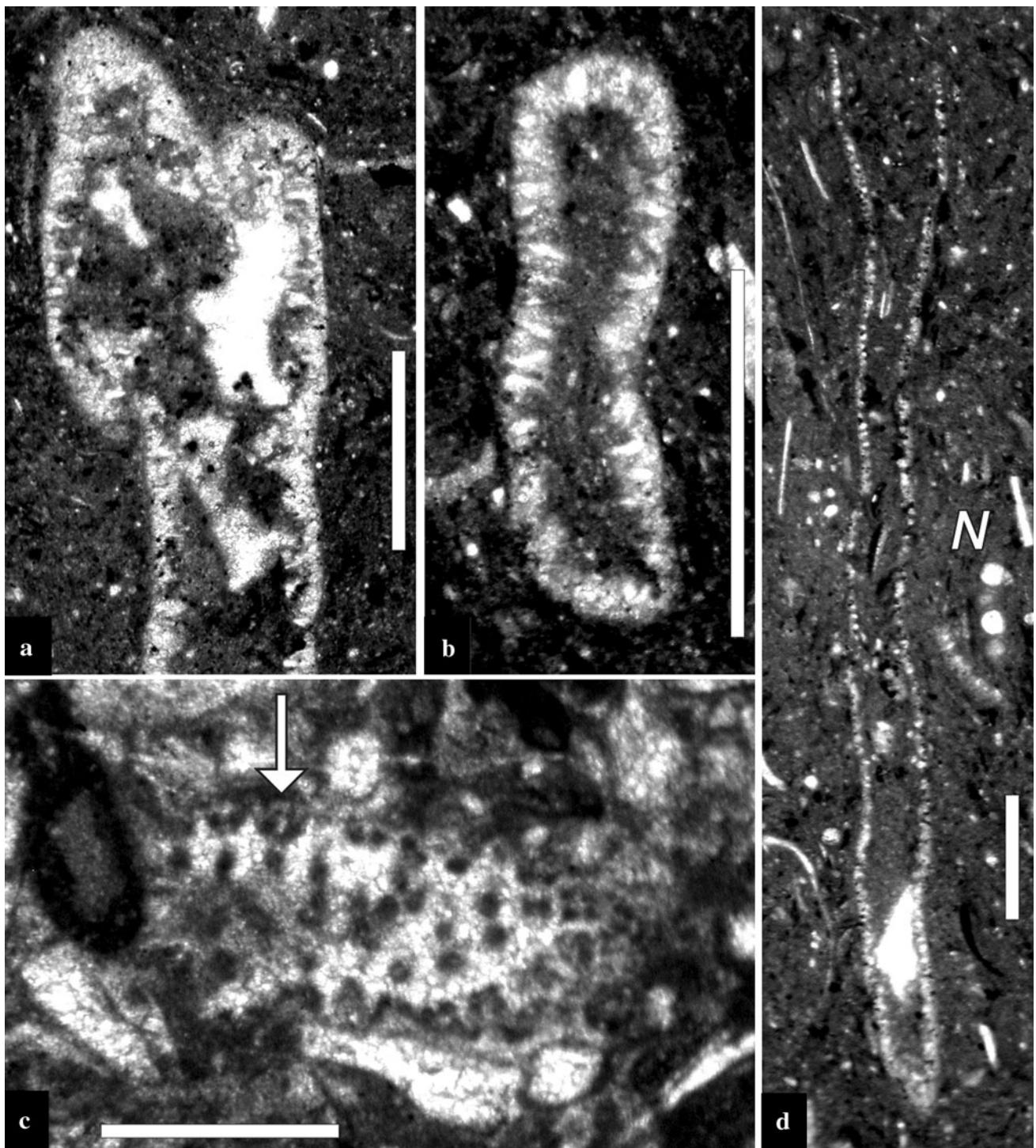


Fig. 9 Dasycladalean algae from the Lower Gosau Subgroup of Eisenbach (**a, b, d**) and Brandenberg (**c**), Austria. **a–d** *Thrysoporella eisenbachensis* Schlagintweit and Lobitzer, longitudinal section of thallus showing branching (**a**) and oblique section (**b**), sample EB 9B;

fragmentary tangential section (**c**), sample 1803; longitudinal section of the longest specimen observed ($L \sim 4.65$ mm) (**d**), note fragment of *Neomeris mokragorensis* Radoičić and Schlagintweit (**N**), sample EB 9B. Scale bars 0.5 mm

characteristic transverse sections with its four canals resembling a Maltese cross (Fig. 11b–c). Ljubović-Obradović and Radoičić (2003, p. 135) interpreted *C.?*

pantici as possible remains of larger dasycladaleans, i.e., “tufts of the secondary laterals of an indeterminate species (genus *Triploporella*? ”).

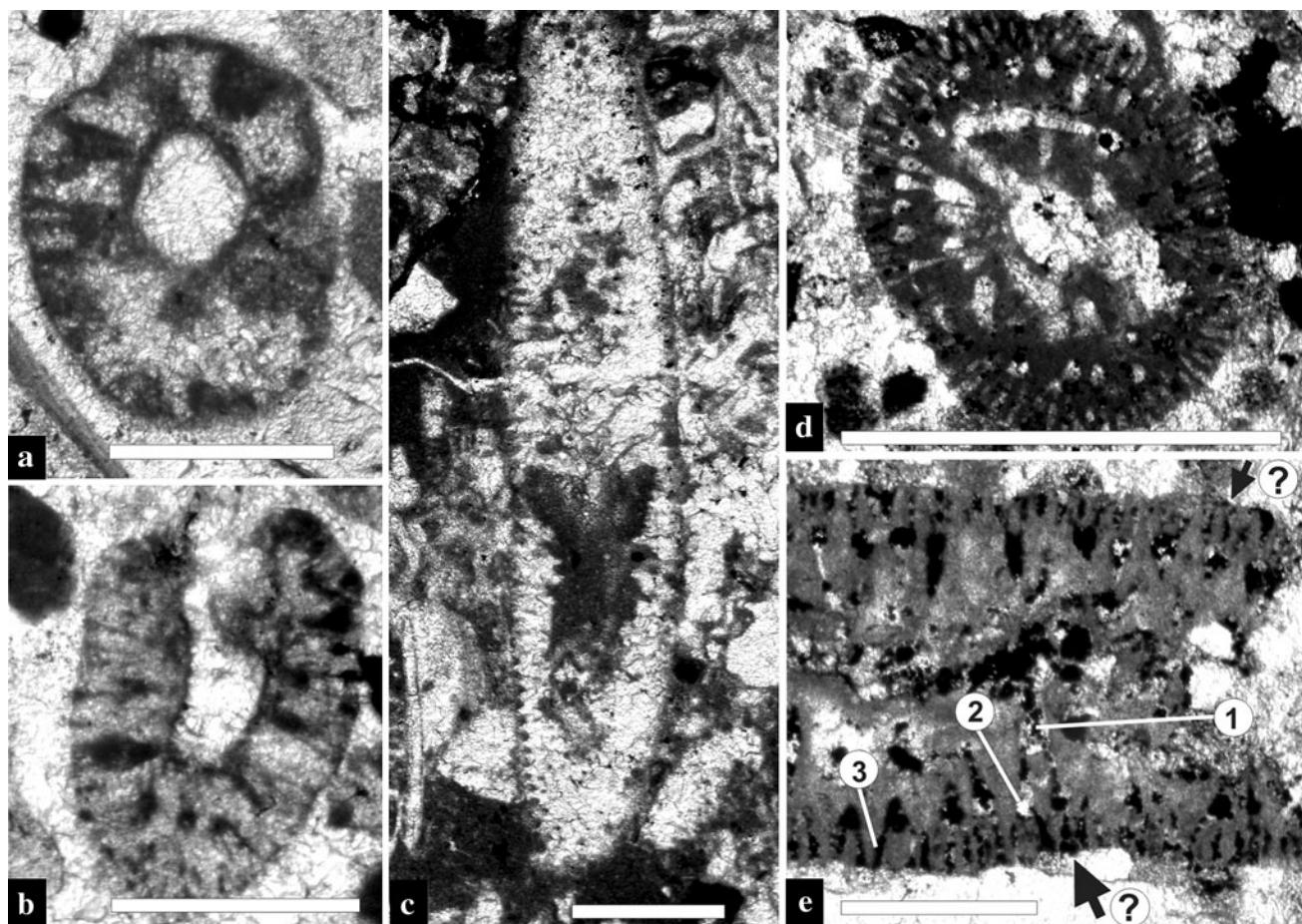


Fig. 10 Dasycladalean algae from the Lower Gosau Subgroup of Brandenberg (**a–c**) and Hofergraben (**d–e**), Austria. **a–e** *Trinocladus tripolitanus* Pia, oblique transverse (**a**) and oblique section (**b**) sample Atz 4; longitudinal-tangential section (**c**), sample Atz 11; slightly

oblique transverse section (**e**), sample HG-5B; fragmentary longitudinal section (**f**), showing three orders of phloioiphorous laterals (**1–3**) and perhaps a further, fourth order (?), sample HG-5B. Scale bars 0.5 mm

Occurrence Gosau of Brandenberg.

Stratigraphy Upper Turonian–Lower Coniacian.

Facies zonation: algal distribution

Figure 12 presents a schematic lateral facies zonation of green algal assemblages in the Lower Gosau Subgroup. The near-shore, terrestrial-influenced lagoon (presumably of variable salinity) is mainly characterized by *Neomeris mokragorensis* Schlagintweit and Radoičić. Shallow subtidal, “lagoonal” areas with terrigenous input are characterized by an association of *N. mokragorensis*, *T. eisenbachensis* Schlagintweit and Lobitzer (Fig. 9), *Dissocladella?* *pyriformis* Schlagintweit (Fig. 6a, b), and *Gosavisiphon paucimedullaris* (Schlagintweit and Ebli). At its type-locality in Serbia, *N. mokragorensis* is locally

associated with characean remains (Radoičić and Schlagintweit 2007). In the Lower Gosau Subgroup, *N. mokragorensis* prevails in the lower, terrestrially influenced part of transgressive successions. At Eisenbach, a normal-marine, near-shore or peri-deltaic, nutrient-rich, marly depositional setting is indicated by (a) abundance of coalified plant detritus and palynomorphs of angiosperms and gymnosperms, (b) calcareous green algae, and (c) *Vidalina* and diverse miliolids and agglutinating foraminifera. Intermittent low salinity or brackish conditions are suggested by abundant specimens of the foraminifera *Quinqueloculina angusta* and *Spirillina cretacea*, as well as by local mass occurrences of the bivalve *Protocardia* Beyrich (Hradecká et al. 2005). In “lagoonal” wackestones accumulated under low terrigenous input, *Clypeina*, *Milanovicella hammudai* (Radoičić), and *Cylindroporella?* aff. *kochanskyae* Radoičić occur (Fig. 3a). Micritic limestones with debris

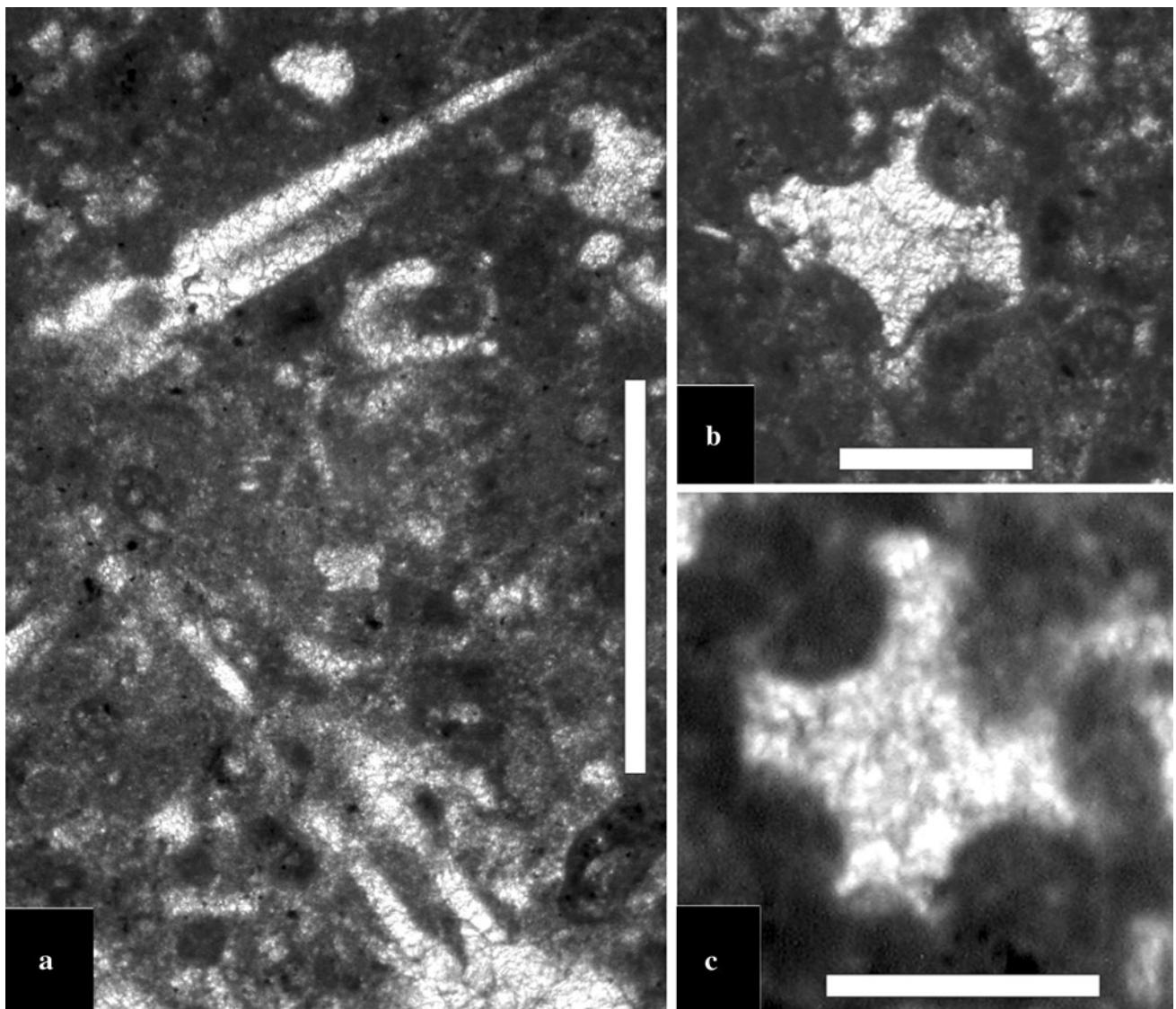


Fig. 11 Morpho-taxon of algal origin from the Lower Gosau Subgroup of Brandenberg, Austria. *Coptocampylodon?* *pantici* Ljubović-Obradović and Radoičić, transverse sections showing

characteristic Maltese-cross shape (**a, b**), sample 16795-7; longitudinal section (**c**), sample 16795-9. Scale bars 0.5 mm for **a**, 0.1 mm for **b–c**

of corals and rudists of the external “lagoonal” facies contain rare fragments of *M. hammudai* (Fig. 3b) (see also Simone et al. 2012, fig. 5c). “Reefal to peri-reefal” facies types (boundstones, rudstones to bioclastic packstones) are characterized by the large-sized algae *Neomeris* (*L.*) aff. *oroseiana* Dieni, Massari and Radoičić, *N.* (*D.*) cf. *jerinae* Radoičić, *Permocalculus* (*P.*) *theresiensteinensis* Schlagintweit and Sanders (Fig. 3f), and *Trinocladus tripolitanus* Rainieri; the latter also ranges into the wackestone facies. Besides green algae, the “reefal to peri-reefal” facies is further characterized by nodular and crust-forming red algae (corallinaceans, peysonneliaceans, solenoporaceans) (Moussavian 1992; Sanders and Baron-Szabo 1997).

Paleobiogeographic comparisons of Late Cretaceous microfloras

Aside from its defined lithostratigraphic meaning (Piller et al. 2004), the term “Gosau” is also used as an umbrella for terrestrial to deep-marine Upper Cretaceous sediments in the Carpathian arc, the Dinarids, and the Transdanubian Central Range (e.g., Haas 1999; Willingshofer et al. 1999). Gosau deposits can be traced from the NCA through the subsurface of the Vienna Basin to exposures in the Western Carpathians (e.g., Wagreich et al. 2011). The mentioned areas were part of the so-called ALCAPA (Alps-Carpathian-Pannonian) terrane or block (e.g., Csontos and Vörös 2004). Paleogeographic reconstructions of the

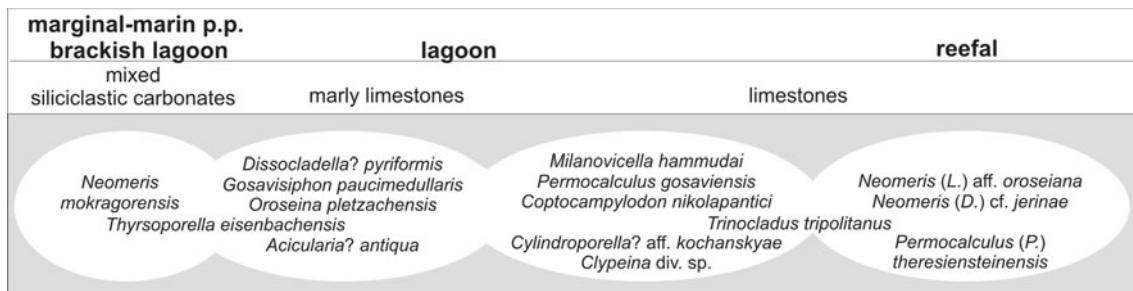


Fig. 12 Green algal associations (Dasycladales, halimedaceans, gymnocodiaceans) from the Late Cretaceous (Middle Turonian–Santonian) Lower Gosau Subgroup of the Northern Calcareous Alps

ALCAPA terrane and its environs may differ in detail (e.g., Stampfli and Borel 2004); for the purpose of data compilation and comparison presented herein (Table 1), however, these details are not relevant for the topic of the present paper.

Western Carpathians

With respect to its general lithostratigraphic succession (alluvial/shallow-marine deposits overlain by deep-water and turbiditic sediments), the Upper Cretaceous of the Slovakian Western Carpathians is comparable with the Gosau Group of the NCA (e.g., Michalík and Činčura 1992; Wagreich and Marschalko 1995; Faupl et al. 1997; Aubrecht et al. 2003; Salaj 2006). These successions, starting in the ‘Senonian’ (Coniacian to Maastrichtian), also include thin beds of rudist limestones and related deposits. According to our knowledge, except for the dasycladalean *Munieria grambasti sarda*, no other algae are reported from the Santonian to Lower Campanian (Pipík et al. 2009). Another cross reference to the Gosau Group is given by the crustacean coprolite *Helicerina kainachensis*: this parataxon was described by Fenninger and Hubmann (1994) from the Gosau of Kainach, where also *Munieria* was reported (Bodrogi et al. 1994; Hofer et al. 2011).

Apuseni Mountains

Southeast of ALCAPA, Gosau-type successions are present in the Apuseni Mountains (Tisia microplate) and in the Transylvanianids of Romania (Dacia microplate) (e.g., Lupu 1976; Lupu and Zacher 1996; Săsăran and Săsăran 2007; Schuller 2004; Schuller et al. 2005, 2009; Schuller and Frisch 2006). “Gosau” deposition started diachronously from Late Turonian to Santonian times, from southeast to northeast (Schuller et al. 2009). From Santonian–Lower Campanian rudist limestones of the Gilău Mountains, eastern part of the Apuseni, Săsăran et al. (2004) reported *Neomeris* cf. *plagnensis* Deloffre, *Terquemella* sp., and fragments of unknown dasycladales. From the ‘Senonian’

(schematic) on type A shelves (cf. Sanders 1998; Sanders and Höfling 2000) (see text for description and discussion)

(Coniacian to Maastrichtian) of the Barod Basin, Apuseni Mountains, Dragastan (1978) reported *Munieria grambasti* Bystrický. We assume that the apparent scarcity of dasycladaleans in the Romanian Gosau-type successions is related to comparatively few investigations rather than to an impoverished microflora.

Internal Dinarids

The internal Dinarids consist of an ophiolite belt (see Gawlick et al. 2007; Schmid et al. 2008 for structural concepts) associated with Upper Cretaceous shallow neritic successions. The facies inventory of these successions is similar to that of the LGS in the NCA (see, e.g., Polšák 1981; Sladic-Trifunovic 1998). The “Mirdita Zone” is the type area of several taxa of calcareous algae (corallineans excluded) described by Radoičić (1970, 1983, 1997, 1998a, 2004, 2006), Ljubović-Obradović and Radoičić (2003), and Radoičić and Schlagintweit (2007).

In the Upper Cretaceous of the internal Dinarids, monospecific assemblages of *Neomeris mokragorensis* Radoičić and Schlagintweit are typical of marginal-marine to brackish settings, as indicated by remains of characean algae. So far, the ‘*mokragorensis–eisenbachensis* assemblage’ of the NCA (see above) has not been recorded from comparable successions in the “Mirdita Zone”. Both in the NCA and the “Mirdita Zone”, pure carbonate-lagoonal deposits associated with rudist limestones contain *Milanovicella hammudai* (Radoičić) (Fig. 3a), *Coptocampylodon nikolapantici* Obradović and Radoičić (Fig. 12), and *Permocalculus gosaviensis* Schlagintweit (=*Permocalculus nikolapantici* Radoičić). In addition, these settings are characterized by the benthic foraminifera *Nezzazatinella*, *Cuneolina*, *Montcharmontia*, and *Dictyopsella*. “Peri-reefal to reefal” facies with corals are characterized by *Neomeris* (*Drimella*) *jerinae* Radoičić (Fig. 3f) (Schlagintweit and Sanders 2008) and halimedaceans. From all the areas comparable to the LGS of the NCA, the internal Dinarides exhibit the most similar associations of dasycladaleans and other algae. The Late Cretaceous geographic

Table 1 Paleogeographic comparisons of the Late Cretaceous (Turonian-Santonian) microflora (corallinaceans excepted) of the Lower Gosau Subgroup of the Northern Calcareous Alps

Taxon	Lower Gosau Subgroup, Austria	Internal Dinarides, Serbia	Transdanubian Central Range, Hungary
<i>Acicularia?</i> <i>weisswasserensis</i>	X		
Schlagintweit and Sanders			
<i>Acicularia?</i> cf. <i>magnapora</i> Kuss	X		
<i>Clypeina</i> cf. <i>pastriki</i> Radoičić	X	X	
<i>Clypeina</i> <i>dusanbrstinae</i> Radoičić	?	X	X
<i>Clypeina?</i> sp.	X		
<i>Cylindroporella?</i> aff. <i>kochanskyae</i>	X	X	
Radoičić			
<i>Dissocladella?</i> <i>pyriformis</i>	X		
Schlagintweit			
<i>Dissocladella</i> sp.	X		
Gen. et sp. indet 1	X		
<i>Halimeda eliotti</i> Conard and Rioult	X	X	
<i>Heteroporella</i> <i>leptina</i>	X	X	
Praturlon			
<i>Hungariporella</i> <i>baconica</i>	X		X
Conrad, Bodrogi and Radoičić			
<i>Jodotella koradae</i> (Dieni, Massari and Radoičić)	X		
<i>Milanovicella</i> <i>hammudai</i> (Radoičić)	X	X	
<i>Munieria</i> <i>grambasti sarda</i>	X		X
Cherchi et al.			
<i>Neomeris</i> <i>mokragorensis</i>	X	X	
Radoičić and Schlagintweit			
<i>Neomeris</i> <i>(Drimella) cf.</i> <i>jerinae</i> Radoičić	X	X	

Table 1 continued

Taxon	Lower Gosau Subgroup, Austria	Internal Dinarides, Serbia	Transdanubian Central Range, Hungary
<i>Neomeris</i> <i>(Larvaria) cf.</i> <i>oroeseiana</i>	X		X (<i>Neomeris</i> sp. in Radoičić 1997, 2006)
Dieni, Massari and Radoičić			
<i>Terquemella?</i> <i>microsphaera</i>		X	
Schlagintweit and Sanders			
<i>Thrysoporella</i> <i>eisenbachensis</i>		X	
Schlagintweit and Lobitzer			
<i>Trinocladus</i> <i>tripolitanus</i>	X		X
Raineri			
<i>Vermiporella?</i> <i>tenuipora</i>		X	X
Conrad			
<i>Permocalculus</i> <i>gosaviensis</i>		X	X (sub <i>P.</i> <i>nikolapantici</i> Radoičić)
Schlagintweit			
<i>P. (Pyruvitites)</i> <i>brandenbergensis</i>		X	
Schlagintweit and Sanders			
<i>Gosavisiphon</i> <i>paucimedullaris</i>		X	
(Schlagintweit and Ebli)			
<i>Halimeda eliotti</i>		X	X
Conard and Rioult			
<i>Coptocampyloodon</i> <i>panticci</i>		X	X
Ljubović- Obradović and Radoičić*			
<i>Oroseina</i> <i>pletzachensis</i>		X	
Schlagintweit and Ebli*			

Data from the Internal Dinarides see Radoičić (1970, 1976, 1983, 1984, 1994, 1997, 1998a, b) and Radoičić and Schlagintweit (2007), data from the Transdanubian Central Range see Conrad et al. (2002) and Poignant (1984)

reconstruction of the ALCAPA area and the Dinarids (Schmid et al. 2008), however, provides no obvious reason why precisely the internal Dinarids are biogeographically

similar to the NCA. Apart from chronostratigraphic overlap, we assume that the similarity is related (mainly at least) to similar facies and relatively dense sampling in the internal Dinarids.

Transdanubian Central Range

The Upper Cretaceous succession of the Transdanubian Central Range (TCR) starts with the Ajka Formation (Upper Coniacian–Lower Santonian) (e.g., Haas 1983, 1999; Wagreich and Siegl-Farkas 1999; Siegl-Farkas and Haas 2002). In some layers, this formation contains *Munieria grambasti sarda* Cherchi, Gusic, Schmidt, and Schröder (Gellai and Toth 1982). This fossil was previously considered as a charophyte. In a morphological study, Feist et al. (2003) re-interpreted *Munieria* as a dasycladalean alga that could tolerate freshwater input.

Munieria grambasti sarda was also identified in the Upper Santonian–Lower Campanian coal-bearing succession of Miesenbach Valley, NCA (Schlagintweit and Wagreich 1992), and in C_{org}-rich beds (“Bitumenmergel”) of the Gosau of Kainach (?Campanian) (Bodrogi et al. 1994; Hofer et al. 2011). In the higher part of the Ajka Formation, the benthic foraminifer *Nummofallotia cretacea* Schlumberger is present (Sidó 1969; Siegl-Farkas and Haas 2002). This taxon is present also in the Upper Santonian Hochmoos Formation (Weiss 1977; Schlagintweit 1992) (Fig. 6d). Above the Ajka Formation, apart from basinal successions, a package of Upper Santonian–Campanian shallow-water limestones with rudists is present (Ugod Formation). From the Ugod Formation the dasycladales *Hungariporella baconica* Conrad, Bodrogi and Radoičić (Fig. 7), *?Dissocladella* cf. *undulata* Rainieri, *Clypeina dusanbrstinai* Radoičić, *Neomeris pfenderae* Konishi and Epis, and *Trinocladus tripolitanus* Rainieri are reported (Poignant 1984; Conrad et al. 2002).

Conclusions

1. In the Upper Cretaceous of the Lower Gosau Subgroup (Northern Calcareous Alps, NCA) calcareous green algae are widespread in lithologies representing different paleoenvironments. In pure carbonate deposystems, species diversity was higher relative to siliciclastic and mixed siliciclastic–carbonate settings. The assemblages of calcareous algae and/or benthic foraminifera permit characterization of different paleoenvironments of Late Cretaceous shelf areas.
2. The diversity of the algal flora from the Lower Gosau Subgroup is higher than previously documented, but still lower compared to that of the peri-Adriatic carbonate platforms of the Apennines and Dinarids.

The comparability of the Turonian–Santonian algal–foraminiferal assemblages of the NCA with other areas is limited, either because of narrow chronostratigraphic overlap (Transdanubian Central Range), and/or because of scarce data (e.g., Western Carpathians, Apuseni Mountains).

3. The highest similarity of the microfloras of the NCA exists with assemblages of the “Mirdita Zone” of the internal Dinarids. We assume that the similarity of microfloras results mainly from denser sampling and comparatively better micropaleontological documentation in the “Mirdita Zone” relative to most other areas outside the NCA.

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