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Gosavisiphon gen. nov. based on *Halimeda paucimedullaris* SCHLAGINTWEIT & EBLI, 1998: a remarkable macroalga (Udoteaceae?) from the Late Cretaceous of the Northern Calcareous Alps, (Austria and Germany), with affinites to Late Palaeozoic and Late Triassic phylloids

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ABSTRACT

The new genus *Gosavisiphon* with the type-species *Halimeda paucimedullaris* SCHLAGINTWEIT & EBLI, 1998, tentatively referred to the Udoteaceae, is described from the Late Cretaceous (Middle/Late Cenomanian-Santonian) of the Branderfleck Formation and the Lower Gosau Subgroup of the Northern Calcareous Alps (Austria, Germany). It is a plurimillimetric to pluricentimetric marine, hard-substrate dwelling macroalga, with membraneous and partly fused plates and an internal siphonaceous construction but lacking a real medullary zone. Although some thallus details are still unknown, *Gosavisiphon* gen. nov. can, from a strictly morphological point of view, directly be compared with the Late Palaeozoic and Upper Triassic phylloid algae. *Gosavisiphon* gen. nov. is the first fossil record of a platy siphonal alga in the Cretaceous, since the Late Triassic *Ivanovia triassica* REID. The monotypic taxon is most probably endemic to the Northern Calcareous Alps where it dwelled in protected, terrestrially influenced lagoonal environments attaching to hard substrates, (metazoan skeletons, rudistid shells). Based on findings of the cylindrical *Halimeda*? aff. *johnsoni* PAL and another taxon described as *Halimeda* sp. with typically flattened ovate segments, some considerations on the segment-morphological phylogenetic evolution of *Halimeda* LAMOUROUX are provided. *Halimeda* species with discoidal-flattened segments, that can morphologically be compared with extant species, are not known prior to the Turonian. Forms possessing cylindrical segments date further back, but can not directly be compared morphologically with modern counterparts, thus placing doubts on the existence of long-lasting methusalemi species by uniting extant and fossil species, as proposed by both botanists and palaeontologists in recent times.

Keywords: Calcareous algae, taxonomy, Bryopsidales, Halimedaceae, Udoteaceae, phylloid algae, Phylogeny, Upper Cretaceous, Northern Calcareous Alps

1. INTRODUCTION

In the area of the Northern Calcareous Alps (NCA), Late Jurassic to Early Cretaceous convergence and nappe stacking were followed by extensional exhumation and subaerial exposure of large parts of the orogen (e.g. RATSCHBACHER et al., 1989). Within the northern part of the NCA, namely the Lechtal Nappe, the transgressive sedimentary cycle of the Branderfleck Formation started in the Lower Cenomanian with breccias, conglomerates and orbitolinid sandstones, followed succesively by deeper water lithologies (e.g. GAUPP, 1982; WEIDICH, 1984). From Turonian marls, olistolites of Late Cretaceous shallow water limestones with calcareous algae were reported from different localities (e.g. SCHLAGINTWEIT & WEIDICH, 1991; SCHLAGINTWEIT, 1992). The subsequent marine transgression affecting the higher nappe units started during the Turonian with the tectonosedimentary cycle of the Gosau Group that unconformably overlies mainly Triassic and Jurassic sediments. The Alpine Gosau Group can roughly be subdivided into a lower subgroup with neritic shelf lithologies, and an upper subgroup consisting of deeper water facies (WAGREICH & FAUPL, 1994) (Figs. 1A–B). From Turonian to Campanian times, a variegated, mixed siliciclastic-carbonate succession up to more than 2000 metres thick accumulated in a wide

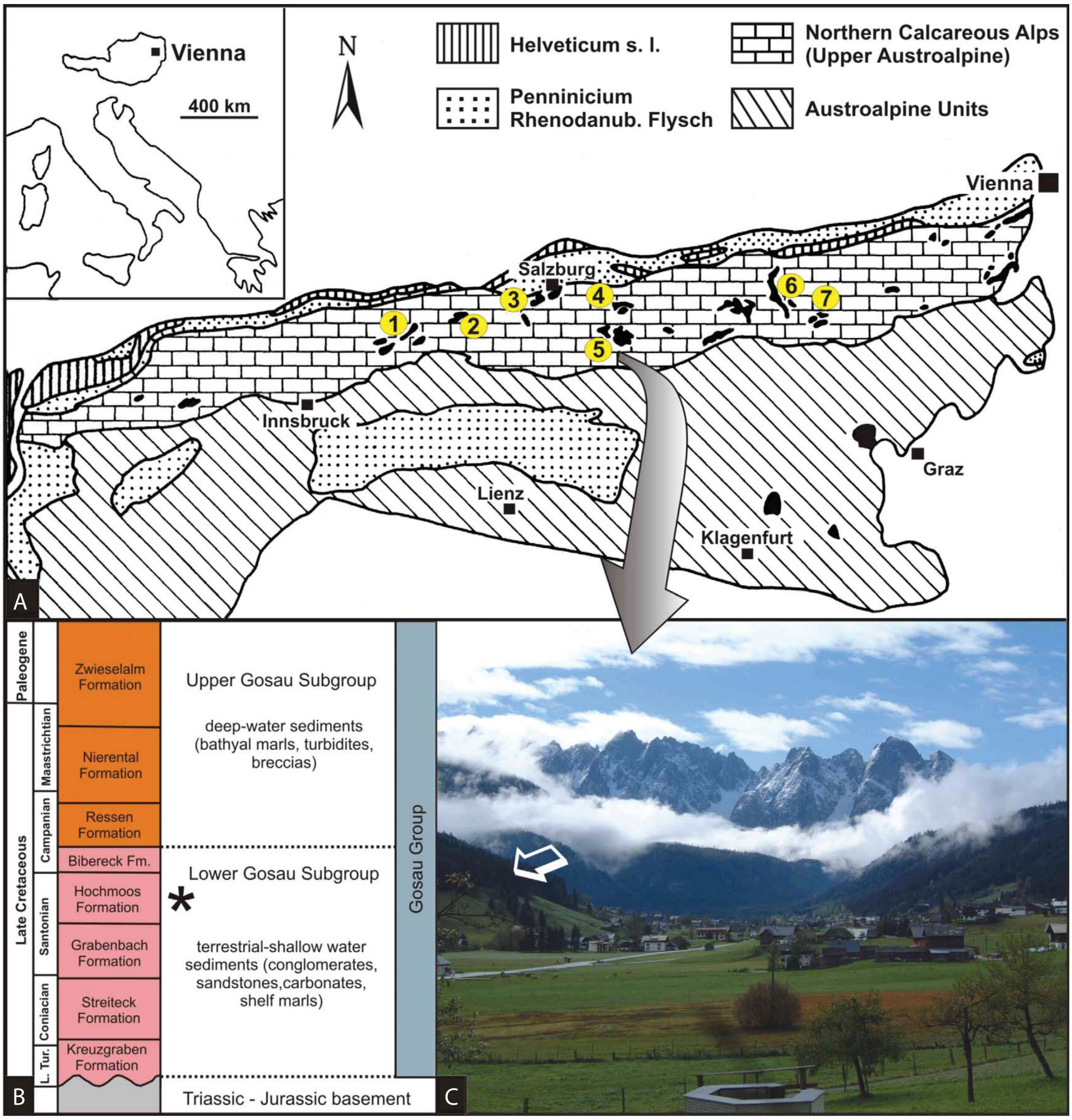

Figure 1: A) Simplified tectonic map of the Eastern Alps with the major occurrences of the Gosau Group (in black) (see WAGREICH & FAUPL, 1994). Occurrences of calcareous algae described in the present paper (yellow circles; for the distribution of individual taxa see Table 1): 1 Krumbachalm, Brandenberg, Tyrol; 2 Pletzachalm, Tyrol; 3 Lattengebirge, Salzburg, 4 Eisenbach, Lake Traunsee, Upper Austria 5 Rußbach-Pass Gschütt-Gosau (Gosau type-area), 6 Weißwasser-Unterlausa, Lower Austria, 7 Gams, Lower Austria. B) Lithostratigraphic subdivision of the Gosau Group of the type area (from WAGREICH & DECKER, 2001); asterix marks the position of the findings of *Gosavisiphon* in the area of Gosau (locality Hofergraben) and Pass Gschütt-Rußbach (locality Randobach). C) The village of Gosau (780 m altitude) with the Dachstein Mountains in the background; view towards the south. White arrow points to the Hofergraben.

spectrum of terrestrial to neritic palaeoenvironments (Lower Gosau Subgroup; WAGREICH & FAUPL, 1994). Deposition of the Lower Gosau Subgroup was terminated, from Santonian to Campanian times, by deepening into bathyal to abyssal depths (WAGREICH & FAUPL, 1994). The area around the village of Gosau (Upper Austria) and Russbach (Salzburg) represents the type locality of the Gosau Group (Fig. 1C). The lithostratigraphic division of the Gosau type area still used today is that from WEIGEL (1937) with modifications in the last decades (WILLE-JANOSCHECK, 1966; WEISS, 1977; WAGREICH, 1988; WAGREICH & DECKER, 2001) (Fig. 1B). The present occurrences (Fig. 1A) only represent the erosional remnants of a former wider distribution; preservation is often due to faulting or deposition in synsedimentary active small basins (WAGREICH & DECKER, 2001).

In the Lower Gosau Subgroup, calcareous algae, mainly Dasycladales and Halimedaceae, were reported from lagoonal limestones, rudistid limestones, and marly limestones, intercalated within marly successions of Middle Turonian to Upper Santonian age (e.g. HÖFLING, 1985; SCHLAGINTWEIT, 1991, 1992, 2004; SCHLAGINTWEIT & LOBITZER, 2003a). For an inventory of calcareous green algae of the Lower Gosau Subgroup see SCHLAGINTWEIT (2004). The alga *Halimeda paucimedullaris* was described by SCHLAGINTWEIT & EBLI (1998) from the Pletzachalm section in the Sonnwend Mountains, Tyrol. It also occurs in the Lattengebirge (Salzburg), Weißwasser-Unterlausa (Lower Austria) and Pass Gschütt-Gosau (e.g. SCHLAGINTWEIT & LOBITZER, 2003b). New material from the Gosau of Gams, Styria, and the reinvestigation of material already published, especially that from the Hofergraben near Gosau, resulted in the recognition of morphological and microstructural details that differ sufficiently from the genus *Halimeda* LAMOUROUX, to warrant establishment of a new genus of the order Bryopsidales with the generic name *Gosavisiphon* gen. nov. and the new combination *Gosavisiphon paucimedullaris* (SCHLAGINTWEIT & EBLI), described in this paper.

2. SAMPLE LOCALITIES AND MATERIAL STUDIED

Halimeda sp., *Halimeda*? aff. *johnsoni* PAL and *Gosavisiphon paucimedullaris* (SCHLAGINTWEIT & EBLI), were discovered in various outcrops of the Lower Gosau Subgroup (Fig. 1A, from west to east). The last taxon was also observed in olistolites of the Branderfleck Formation. Brief informations on geographical setting, microfacies and associations of the algal-bearing samples and stratigraphy are given for each locality. Occurrences of the described taxa are summarized in Table 1.

Table 1: Summary of the investigated sample localities with respect to the occurrence of the described calcareous algae.

Species / Localities	Krumbachalm	Pletzachalm	Lattenberg	Eisenbach	Randobach	Hofergraben	Weißwasser	Noth-Klamm
Halimeda? aff. *johnsoni*	●							
Halimeda sp.		●		●				
Gosavisiphon paucimedullaris		●	●	●	●	●	●	●

2.1. Lower Gosau Subgroup

Krumbachalm area, Brandenberg (locality 1 in Fig. 1). The outcropping limestones of the Lower Gosau Subgroup are located at the northern part of the Brandenberg Gosau, a larger erosional remnant of the Gosau Group located in Tyrol, about 10 km west of Wörgl (e.g. Fig. 2 in SANDERS, 1998).

Microfacies and associations: *Halimeda*? aff. *johnsoni* PAL occurs in bioclastic packstones with corals, rudistids, echinoderms, gastropods, calcareous algae (green algae and red algae), including *Permocalculus* (*Pyrulites*) *theresiensteinensis* SCHLAGINTWEIT & SANDERS, and benthic foraminifera (textulariids, and arenaceous encrusting taxa). The Krumbachalm area is also the type-locality of *Acanthochaetetes*? *krumbachensis* (SENOWBARI-DARYAN et. al., 2004).

Stratigraphy: Upper Turonian to Coniacian (SANDERS, 1998 and SANDERS & PONS, 1999 for details).

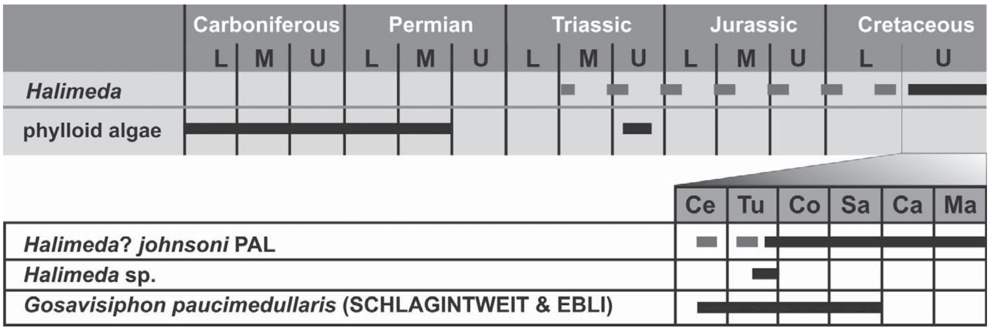

Figure 2: Stratigraphic distribution of *Halimeda*? *johnsoni* PAL, *Halimeda* sp. and *Gosavisiphon paucimedullaris* (SCHLAGINTWEIT & EBLI) in the Late Cretaceous Lower Gosau Subgroup of the Northern Calcareous Alps supplemented with literature data. It is most likely that *Halimeda* sp. has a larger stratigraphic distribution, than the two Middle-Late Turonian occurrences (see Tab. 1). The dashed dark-grey line in *Halimeda*? *johnsoni* refers to a possible synonymy with *Boueina pygmaea* PIA. For comparison, the distribution of the "phylloid algae" and the genus *Halimeda* are indicated (see Tab. 3 and details in the text).

Pletzachalm (locality 2 in Fig. 1). The Pletzachalm section near Kramsach (Fig. 1 in SCHLAGINTWEIT & EBLI, 1998, for exact location), Tyrol (Austria), was first described lithologically in detail by LEISS (1988). The micropalaeontological content (benthic foraminifera, calcareous algae) was studied by SCHLAGINTWEIT (1991, 1992), SCHLAGINTWEIT & EBLI (1998) and SCHLAGINTWEIT & SANDERS (2008), revealing several new taxa, mainly calcareous algae. Microfacies and associations: *Gosavisiphon* gen. nov. occurs in marly limestones that are intercalated within a series of marls, with layers of gastropods and coaly plant remains, followed up the section by a rudistid biostrome. *Gosavisiphon* gen. nov. is associated mainly with calcareous algae including *Dissocladella*? *pyriformis* SCHLAGINTWEIT, *Neomeris mokragorensis* RADOIČIĆ & SCHLAGINTWEIT, *Oroseina pletzachensis* SCHLAGINTWEIT & EBLI, *Halimeda* sp., and benthic foraminifera *Vidalina hispanica* SCHLUMBERGER (and other miliolids), cuneolinids and *Tetrataxiella*? *floriformis* SCHLAGINTWEIT & SANDERS.

Stratigraphy: The age of the series containing *Gosavisiphon* gen. nov. below the rudistid limestones is Late Turonian.

Lattengebirge (locality 3 in Fig. 1). From this locality, the new taxon was reported for the first time as *Halimeda* sp. by HÖFLING (1985) from the so-called Krönner Reef. The biocoenosis of the lagoonal "epibenthic udoteaceandasycladacean association" and its adjacent reefal palaeoenvironments were schematically reconstructed by HÖFLING (1985) (see also MOUSSAVIAN et al., 1993). The outcrops occur at the northern side of the Lattengebirge, southeast of Bayerisch Gmain near Bad Reichenhall (Germany); topographic map no. 8243 Reichenhall (for exact location see Fig. 1 in KLINGHARDT, 1942).

Microfacies and association: *Gosavisiphon* gen. nov. occurs within marly wackestones referred to a back-reef lagoonal environment (HÖFLING, 1985).

Stratigraphy: The Krönner Reef was considered to be Santonian in age (KLINGHARDT, 1942; HÖFLING, 1985); Strontium isotope data revealed a mid Coniacian age (STEUBER, 2001), which is the same age obtained for the rudistid limestones of Weißwasser (see below).

Eisenbach, Lake Traunsee (locality 4 in Fig. 1). The Eisenbach Gosau occurrence is located at the eastern side of Lake Traunsee in the Upper Austrian Salzkammergut, ÖK 25, sheet 67 Grünau im Almtal.

The samples with *Gosavisiphon* gen. nov. belong to the type material (type locality) of the dasycladale *Thyrsoporella eisenbachensis* (see Fig. 1 in SCHLAGINTWEIT & LOBITZER, 2003a).

Microfacies and associations: *Gosavisiphon* nov. gen. was found in marly limestones; wackestones with coaly plant remains, gastropods, ostracods and *Thyrsoporella eisenbachensis* SCHLAGINTWEIT & LOBITZER, *Dissocladella*? *pyriformis* SCHLAGINTWEIT and *Neomeris mokragorensis* RADOIČIĆ & SCHLAGINTWEIT, and miliolid foraminifera (Figs. 8C–D).

Stratigraphy: Middle Turonian (based on calcareous nannofossils).

Randobach near Russbach at Pass Gschütt (locality 5 in Fig. 1). The Randobach river is located about 5 km west of the village of Gosau. Stratigraphy: Santonian (KOLLMANN & SUMMESBERGER, 1982; KOLLMANN, 1985). From this locality *Gosavisiphon* gen. nov. was reported by SCHLAGINTWEIT & EBLI (1998: see Fig. 2 for exact location).

Microfacies and associations: Brownish marly limestones with the calcareous algae: *Gosavisiphon* gen. nov., *Oroseina pletzachensis* SCHLAGINTWEIT & EBLI, *Neomeris mokragorensis* RADOICIC & SCHLAGINTWEIT, *Dissocladella*? *pyriformis* SCHLAGINTWEIT, *Terquemella*? n. sp., and benthic foraminifera *Nummofallotia cretacea* (SCHLUMBERGER) and *Vidalina hispanica* SCHLUMBERGER.

Stratigraphy: Upper Santonian.

Hofergraben, Gosau (locality 5 in Fig. 1). This locality is situated approximately 1 km southeast of Gosau, Upper Austria (ÖK 1: 50.000, no. 95 St. Wolfgang) (see Fig. 1C). The material described comes from two small southern tributaries at an altitude of 900 m above sea-level (see Fig. 1 in SCHLAGINTWEIT 2004, for exact location). *Gosavisiphon* gen. nov. was already described and illustrated by SCHLAGINTWEIT & LOBITZER (2003b) from this locality. The so-called Hofergraben marls (Hofergraben Member of SANDERS & BARON-SZABO 2007) belong to the Hochmoos Formation (see Figs. 1B–C). These marls are well-known for their coral fauna, such as the solitary *Cunnolites* (SANDERS & BARON-SZABO, 2007).

Microfacies and associations: *Gosavisiphon* gen. nov. was identified in two different types of siliciclastic-carbonate beds. One is represented by well-sorted arenites with numerous specimens with either chaotic distribution or parallel arrangement; other biotic elements are scarce (rare benthic foraminifera, shell debris) (see SCHLAGINTWEIT & LOBITZER 2003a) (Fig. 9A). The other type shows low grade sorting with different extraclasts and numerous algal remains including *Trinocladus tripolitanus* PIA, *Neomeris mokragorensis* RADOIČIĆ & SCHLAGINTWEIT, *Oroseina pletzachensis* SCHLAGINTWEIT & EBLI and *Jodotella koradae* (DIENI, MASSARI & RADOIČIĆ) (see SCHLAGINTWEIT, 2004) (Fig. 11H).

Stratigraphy: Upper Santonian (see Fig. 2 in SANDERS & BARON-SZABO, 2007).

Weißwasser-Unterlaussa (locality 6 in Fig. 1). The Weißwasser section near Unterlaussa, Lower Austria (Topographic map of Austria, ÖK 69, Großraming), was studied and illustrated by RUTTNER & WOLETZ (1955), followed by FAUPL et al. (1987) and SANDERS & PONS (1999, Fig. 17). Additional data about the microfauna from this locality were provided by SCHLAGINTWEIT (1992) and SCHLAGINTWEIT & SANDERS (2008). Outcrops from which samples were taken, are located along the forest road to the Bla-Alm (see SCHLAGINTWEIT 1992, Fig. 4).

Stratigraphy: *Gosavisiphon* gen. nov. occurs in a series below rudist limestones (the so-called Liegend-Serie of RUTTNER & WOLETZ, 1955) that have been dated biostratigraphically as Middle Coniacian (e.g. WAGREICH, 1990) and on the basis of strontium isotope stratigraphy (STEUBER, 2001). Therefore, the material with *Gosavisiphon* gen. nov. may be Early Coniacian or Late Turonian.

Microfacies and associations: Marly limestones with cuneolinids, miliolids (*Vidalina hispanica* SCHLUMBERGER).

Noth-Klamm, Gams (locality 7 in Fig. 1). The Noth-Klamm profile is located on ÖK 101 Hieflau, Styria; outcrops are located on the orographic left side of the beginning of the Noth-Klamm (KOLLMANN 1963, 1965; SANDERS & PONS, 1999, Fig. 14). A composite log of the succession of the Gosau Group of the Gams area was presented recently by SUMMESBERGER et al. (2009) and WAGREICH et al. (2009).

Microfacies and associations: The samples with *Gosavisiphon* gen. nov. come from a small interval (less than 1 m thickness), of marly limestones between two hippuritid biostromes (*Hippurites resectus* DEFRANCE). Brownish siliciclastic-influenced pack- to floatstones with stromatoporoids (?*Cladocoropsis*), rudist debris, benthic foraminifera such as *Vidalina hispanica* SCHLUMBERGER, *Quinqueloculina* sp., and cuneolinids (Fig. 8B). Calcareous algae are represented by abundant *Gosavisiphon* gen. nov. and some scattered thalli of *Marinella lugeoni* PFENDER.

Stratigraphy: Upper Turonian, with *Barroisiceras haberfellneri* (HAUER), compare SUMMESBERGER & KENNEDY, 1996) (Noth Formation of SIEGL-FARKAS & WAGREICH, 1997).

2.2. Branderfleck Formation

Urschlauer Achen, Ruhpolding. At Urschlauer Aachen in the Bavarian Alps, (topographic map of Germany no. 8241), an olistostrome is exposed, intercalated in Lower to Middle Turonian marls, (dated by nannoconids and planktonic foraminifera, SCHLAGINTWEIT & WEIDICH, 1991; SCHLAGINTWEIT, 1992). Calcareous green algae occur in different olistolites of Middle/Late Cenomanian and/or Lower Turonian age with *Heteroporella lepina* PRATURLON, *Permocalculus* sp., *Harlanjohnsonella annulata* ELLIOTT, *Salpingoporella turgida* RADOICIC, *Trinocladus tripolitanus* RAINERI.

Stratigraphy: The olistolites in which strongly recrystallized specimens of *Gosavisiphon* nov. gen. were observed are most probably of Middle/Late Cenomanian age.

3. SYSTEMATICS

The morphological features of *Gosavisiphon* gen. nov. *paucimedullaris* (SCHLAGINTWEIT & EBLI) comb. nov., originally described as a species of the genus *Halimeda*, necessitates a short introduction to the taxonomy of the siphonal calcareous green algae Halimedaceae and Udoteaceae, together with short overviews on "Fossil *versus* Recent *Halimeda* species" and "Phylloid algae", prior to the systematic description of the alga.

3.1. Taxonomic overview of fossil siphonal green algae of the Udoteaceae and Halimedaceae families.

The classification of fossil 'halimediform udoteaceans', (FLÜGEL, 2004, p. 423) (Codiaceae *versus* Udoteaceae *versus* Halimedaceae) is a matter of long lasting discussions (e.g. MU, 1991; DRAGASTAN et al., 1997). For a long time the Udoteaceae was the accepted family where *Halimeda* and allied taxa have been included. These were placed into the (segmented) Codiaceae (e.g. STEINMANN, 1899; ELLIOTT, 1965). The fossil Udoteaceae were treated systematically by BASSOULLET et al. (1983), including not only the Mesozoic and Cenozoic genera *Halimeda* LAMOUROUX, *Boueina* TOULA, *Arabicodium* ELLIOTT, *Nipponophycus* YABE & TOYAMA and *Lekhamptonella* ELLIOTT, but also Palaeozoic taxa, for example *Tauridium* GUVENC, *Lancicula* MASLOV, *Dimorphosiphon* HOEG (see BOYD, 2007) and some others (e.g. ROUX, 1985; HUBMANN, 1990, 1994; HUBMANN & FENNINGER, 1997; HUBMANN, 2000). The work of BASSOULLET et al. (1983) included only erect segmented taxa, and phylloid algae ascribed to the Udoteaceae (see following separate chapter) were excluded. Modern algal taxonomy lists the Udoteaceae AGARDH and Halimedaceae LINK as two separate families within the order Bryopsidales (former Siphonales), and *Halimeda* (with 44 species) as the only genus of the Halimedaceae (e.g. algaeBase of GUIRY & GUIRY, 2009). It is worth mentioning that DRAGASTAN et al. (1997, p. 77), included two genera in the family Halimedaceae, *Halimeda* and *Tydemania*. For the Udoteacae, on the other hand, the algaeBase mentions eighteen genera, some of which, however, are considered by some workers to be excluded from this family (e.g. CURTIS et al., 2008). In order to avoid a misleading mixing of fossil and modern taxa, this compilation should exclude *Pseudopenicillus* DRAGASTAN et al., 1997 (Late Triassic of Greece), as it represents an exclusively fossil taxon (DRAGASTAN et al., 1997). The remaining seventeen extant genera represent a rather heterogeneous group, concerning the highly diverse thallus architecture and the fact that both calcifying and non-calcifying forms are enclosed. The bauplan is generally tripartite with an anchoring holdfast, a stipe and the blade (e.g. Fig. 3A,B). In some udoteacean algae such as *Udotea* or *Avrainvillea,* the length of the bulbous holdfast can equal or even exceed the algal parts that project above the sediment surface (e.g. LITTLER & LITTLER, 1990, 1992). As for representatives of the *Halimeda*, udoteacean taxa may also show different constructional types of the anchoring holdfast as adaptations to different substrates (e.g. LITTLER & LITTLER, 1990: genus *Udotea*; LITTLER & LITTLER, 1992: genus *Avrainvillea*).

Previously, five taxa were assigned to the Halimedaceae (HILLIS-COLINVAUX, 1984; HILLIS, 1991): *Halimeda* LAMOROUX, *Penicillus* LAMARCK, *Rhipocephalus* KÜTZING, *Tydemania* WEBER-VAN BOSSE and *Udotea* LAMOUROUX. The latter four have now been included in the Udoteaceae (e.g. GUIRY & GUIRY, 2009). Extant genera of the Udoteaceae that calcify are *Penicillus* LAMARCK, *Rhipidosiphon* MONTAGNE, *Rhipocephalus* KÜTZING,

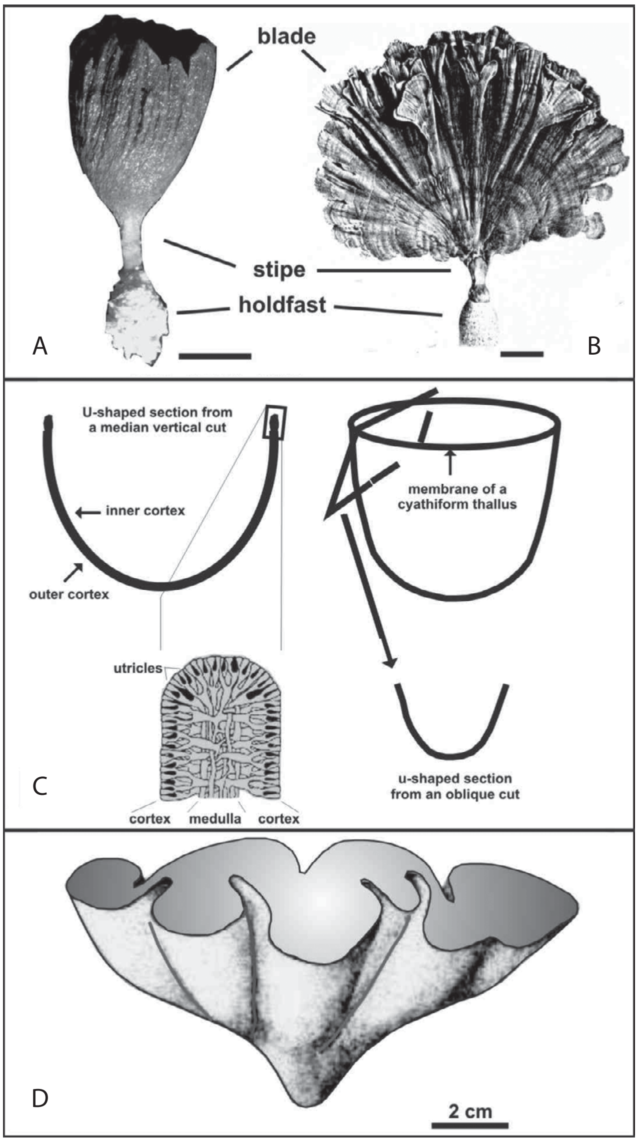

Figure 3: Examples of extant (A–B) and Palaeozoic (C–D) Udoteaceae. A) *Udotea cyathiformis* DECAISNE, Bahamas, blade without corticated filaments (= ecorticate). B) *Udotea flabellum* (ELLIS & SOLANDER), Florida (from AGASSIZ, 1880, figured as *U. flabellata* LAMOUROUX), blade corticated by branched filaments. C) *Ivanovia tebagaensis* TORRES, Permian (redrawn from TORRES, 1995). D) *Calcipatera cottonwoodensis* TORRES, WEST & SAVIN, Lower Permian of Kansas (slightly modified from TORRES et al., 1992).

Scale bars 2 cm for A, 1 mm for B, 2 mm for D.

Tydemania WEBER-VAN BOSSE and *Udotea* LAMOUROUX (Figs. 3A,B). Calcification differs between genera (and species), varying from light to medium, but in any case to a lesser extent than in the *Halimeda* (e.g. BÖHM, 1973; LIEBEZEIT & DAWSON, 1982; RIES, 2006). For example, within the genus *Udotea* LAMOUROUX we find both calcified (e.g. *Udotea flabellum*, see Fig. 3B), and non-calcified species (e.g. *Udotea petiolata*, see COLOMBO, 1978). As a consequence of this, many present day Udoteaceae have no fossil record, because of the lack of thallus calcification.

Concerning the possibilities of principal descents in the fossil record, the calcifying taxa of the Udoteaceae are worth noting. According to VERBRUGGEN et al. (2009, Fig. 4), *Udotea* should have its first appearance in the Late Jurassic, *Rhipidosiphon* in the Late Cretaceous and *Rhipocephalus* during the Cenozoic. These assumptions, however, have so far not been validated by the fossil record. KÜHNEL (1932) described *Udotea adnetensis* from the Late Triassic (Rhaetian), commented on its relationship with the genus *Mitcheldeania* JOHNSON & PIA (1942) assigned it to the so-called "porostromate algae".

Diagnosis of both the Halimedaceae and Udoteaceae families are not common in the palaeontological literature. Taking a closer look at the examples provided by DRAGASTAN et al. (1997, 2002) (see Tab. 2), the non-segmented and non-ramified character of the Udoteaceae is worth mentioning. The eponymous genus *Udotea* shows different shapes, e.g. disk-like, flattened or cyathiform (cup-shaped, *Udotea cyathiformis*), or blade morphology from uncorticated to densely corticated (see monograph of LITTLER & LITTLER, 1990 for details; COLOMBO, 1978). For example, *Udotea cyathiformis* (Fig. 3A) posseses a blade without corticated filaments, and *Udotea flabellatum* (Fig. 3B) a blade corticated by branched filaments (e.g. LITTLER & LITTLER, 1990). Another morphological type of Udoteaceae is represented by *Rhipocephalus* commonly known as the pinecone alga with an oval thallus, composed of concentric, tightly packed layered blades.

The systematics of the fossil Halimedaceae has changed considerably during recent decades. According to DRAGASTAN et al. (2002, p. 15), this family should include the following five genera: *Halimeda* LAMOUROUX, *Juraella* BERNIER, *Hydracara* DRAGASTAN, KUBE & RICHTER, *Hikorocodium* ENDO and *Collarecodium* BRANDNER & RESCH. From these, only *Halimeda* has extant representatives. *Hikorocodium* has been shown to represent an inozoid sponge (SENOWBARI-DARYAN & RIGBY, 2007), and *Hydracara* has only recently been transfered to the family Praecodiaceae DRAGASTAN (DRAGASTAN, 2008). Recently, some more new genera from the Late Triassic were

Table 2: Diagnostic characterization of the two families Udoteaceae and Halimedaceae (from DRAGASTAN et al., 1997, 2002). Note that the features refer to fossil taxa whereas in extant forms much more data (e.g. molecular data, morphology of the non-calcified parts) are available for characterization. The stipe and the holdfast of the Udoteaceae, that together with the blade are the three basic thallus components are not reported from fossil taxa.

Order Bryopsidales Suborder Halimedinae Halimedaceae	
Calcareous thallus, segmented, ramified, formed by cylindrical, oval, flabelliform or cuneate in shape, crossed by medullar and cortical siphons having different arrangements from species to species DRAGASTAN et al., 1997	Thalli segments with multishapes or morphae from cylindrical until disk-like flattened crossed by multiaxial medullar siphons and cortex with many utricle series from 2 up to 7 DRAGASTAN et al., 2002
Udoteaceae	
Calcareous thallus (= blade), flabelliform, nodular, hemispherical, more or less flattened, without segments. The genera have ecorticate, partial corticate and corticate thalli, the last ones sometimes without medullar and cortical zones DRAGASTAN et al., 1997	

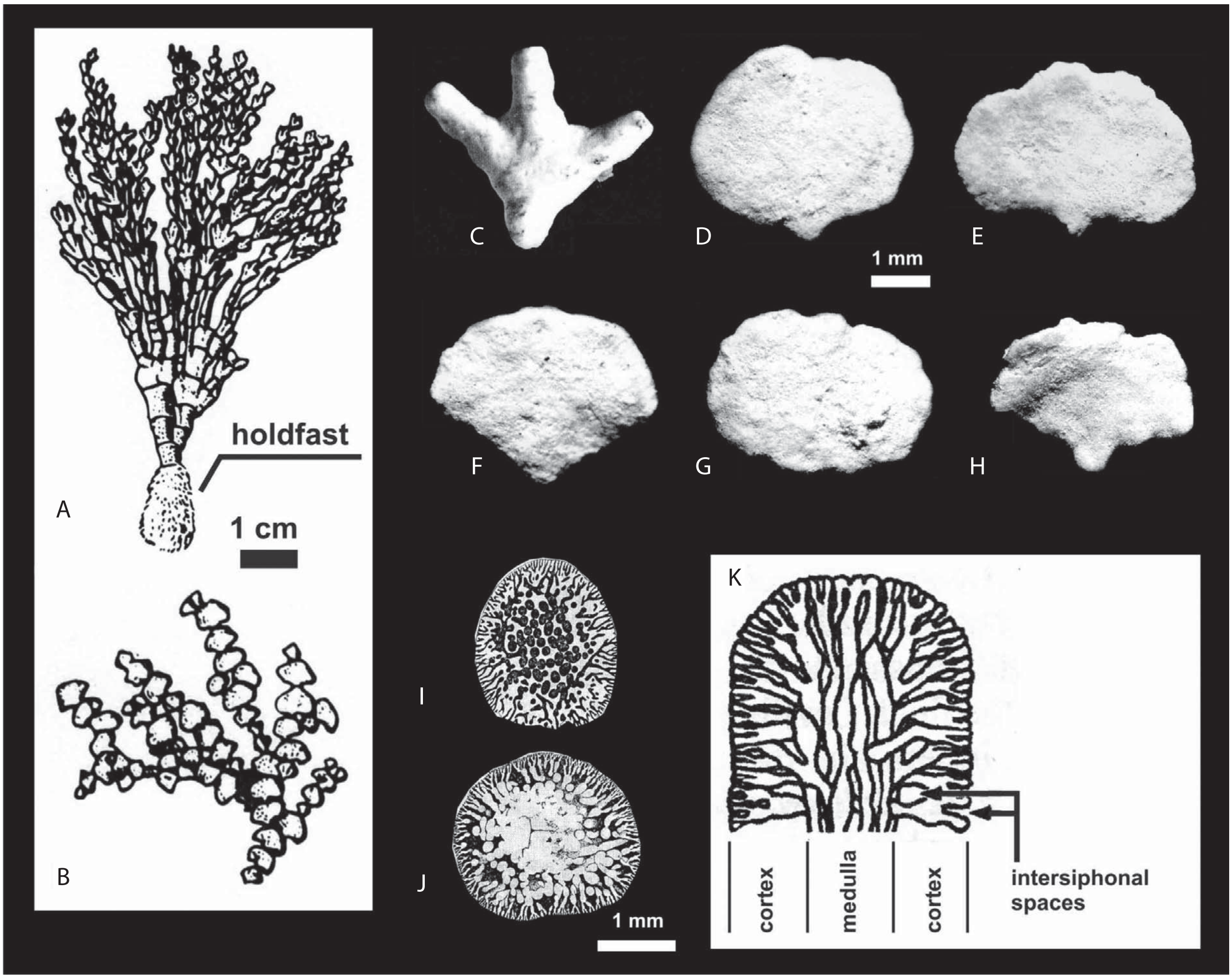

Figure 4: A–B Thallus morphology of the genus *Halimeda* LAMOUROUX (from VICKERS & SHAW, 1908). C–H Segment morphology of Recent (C) and Pleistocene (D–H) *Halimeda* species (from DRAGASTAN et al., 2002, 2003). I–J Transverse sections of *Boueina* (I) and *Halimeda* (J). A) *Halimeda incrassata* (ELLIS). B) *Halimeda opuntia* (LINNAEUS). C) deeply trilobed segment of *Halimeda opuntia* f. *trilobata* (DECAISNE). D) ovate segment of *Halimeda copiosa* GOREAU & GRAHAM. E) reniform (kidney-shaped) segment of *Halimeda gracilis* HARVEY ex AGARDH. F) rounded disc-like segment of *Halimeda tuna* (ELLIS & SOLANDER). G) elliptical-discoid segment of *Halimeda copiosa* GOREAU & GRAHAM. H) triangular rounded segment of *Halimeda tuna* (ELLIS & SOLANDER). I) Transverse section of *Boueina hochstetteri* TOULA, Aptian of Serbia; intersiphonal spaces in white, representing sparry calcite (from STEINMANN, 1899). J) Transverse section of *Halimeda cylindracea* DECAISNE, Recent, Australia; intersiphonal spaces in black (from STEINMANN, 1899). K) Schematic drawing of a longitudinal section of *Halimeda* (without scale), modified after HILLIS-COLINVAUX, 1980).

assigned to the Halimedaceae (SENOWBARI-DARYAN & ZAMPARELLI, 2005), altogether showing rather poor preservation of their internal structures, (medullary and cortical siphons) and not facilitating detailed comparisons with modern halimedaceans (Tab. 3). Except for *Boueina*, that is also known from the Late Triassic (e.g. FLÜGEL, 1975; SENOWBARI-DARYAN & HAMADANI, 1999), none of the Triassic halimedacean taxa, predominantely reef-dwelling species, survived the reef crisis at the end of the Triassic. At present, *Halimeda* is considered the only extant genus of the family Halimedaceae LINK, but there is still no consensus about the fossil members not only of the family Halimedaceae, but also the Udoteaceae.

3.2. Fossil *versus* Recent *Halimeda* species

In former times, palaeontologists dealing with *Halimeda* (and allied taxa) were exclusively referring to related fossil taxa, and biologists to extant species when discussing their material. In the last decade researchers of both fields tried to combine and synthesize the existing data of fossil and recent taxa, with some controversial results (e.g. DRAGASTAN et al., 2002, 2003; DRAGASTAN & HERBIG, 2007; KOOISTRA et al., 2002; VERBRUGGEN & KOOISTRA, 2004; VERBRUGGEN, 2005; VERBRUGGEN et al., 2005, 2009). The complex suprageneric taxonomic history of *Halimeda* has been briefly summarized in the previous chapter. As palaeontologists can only deal with the dispersed calcified parts of the alga, the understanding of the morphological bauplan of the green alga *Halimeda* is vital before going into detail. Recent representatives of *Halimeda* currently number 34 species (e.g. VERBRUGGEN & KOOISTRA, 2004) and are composed of flattened calcified segments, interconnected by non-calcified nodes that haven't yet been reported from fossil taxa (e.g. HILLIS-COLINVAUX, 1980) (Figs. 4A,B). Towards the bottom, the thallus of *Halimeda* is attached by

Table 3: Extant and fossil genus inventory of the family Halimedaceae, modified after DRAGASTAN et al. (2002) with supplementary data of SENOWBARI-DARYAN & ZAMPARELLI (2005). *Hikorocodium* included in the family Halimedaceae by DRAGASTAN et al. (2002) has been shown to represent an inozoid sponge (SENOWBARI-DARYAN & RIGBY, 2007, for details) and is therefore excluded from the compilation. DRAGASTAN et al. (1997) also included the genus *Tydemania* Weber-van Bosse as an extant genus of the Halimedaceae; more workers, however, included it within the family Udoteaceae (e.g. SILVA et al., 1996). This compilation includes 10 genera (7 when accepting the synonymy of *Arabicodium*, *Boueina* and *Nipponophycus* with *Halimeda* as suggested by DRAGASTAN et al., 2002). Note that the Late Palaeozoic *Eugonophyllum* KONISHI & WRAY was placed in the family Halimedaceae by FORSYTHE et al. (2002), most probably meaning the Udoteaceae as accepted here.

Family Halimedaceae Link	
Extant	Fossil
Halimeda Lamouroux, 1812	
	Alpinocodium Senowbari-Daryan & Zamparelli, 2005 (*A. fluegeli* Senowbari. & Zamp., Late Triassic)
	Arabicodium Elliot, 1957 (*A. aegagrapiloides* Elliot, Lower Cretaceous)
	Brandneria Senowbari-Daryan & Zamparelli, 2005 (*B. dolomitica* Senowbari-Daryan et al., Middle Triassic)
	Boueina Toula, 1884 (*B. hochstetteri* Toula, Lower Cretaceous)
	Calabricodium Senowbari-Daryan & Zamparelli, 2005 (*C. irregularum* Senowbari. & Zamp., Late Triassic)
	Collarecodium Brandner & Resch, 1980 (*B. oenipontanum* Brandner & Resch, Middle Triassic)
	Egericodium Flügel et al., 1992 (*E. hungaricum* Flügel et al., Late Triassic)
	Juraella Bernier, 1984 (*J. bifurcata* Bernier, Late Jurassic)
	Madonicodium Senowbari-Daryan & Zamparelli, 2005 (*M. noricum* Senowbari. & Zamp., Late Jurassic)
	Nipponophycus Yabe & Toyama, 1928 (*N. ramosus* Yabe & Toyama, Late Jurassic)

means of a holdfast, consisting of branching rhizoids (HILLIS-COLINVAUX, 1980; VERBRUGGEN & KOOISTRA, 2004). Depending on the sediment-type, (hard, sandy, rubble), holdfasts may be felt-like (rock grower), bulbous (sand grower) or composed of only a few branched and loose rhizoids at intervals along the plant (sprawler) (VERBRUGGEN, 2005, Figs. 7–9). The construction of the holdfast can be considered a habitat strategy (e.g. substrate, water energy) (e.g. HILLIS-COLINVAUX, 1977). Fossil holdfasts of *Halimeda* have not been reported up to now.

Based on the different pattern of nodal medullary filament arrangement, five sections (= groups of species that reflect fundamental phylogenetic divergences), are currently recognized (HILLIS-COLINVAUX, 1980; VERBRUGGEN & KOOISTRA, 2004), an approach impossible to conduct with fossil material. The calcified segments are highly variable in shape (often also within one and the same species), elliptical-discoid, lobed, ovate, rounded, triangular, irregularly quadrangular, reniform to ear-shaped, kidney-shaped, cuneate (e.g. DRAGASTAN et al., 2003; VERBRUGGEN, 2005, Fig. 10–18) (see Figs. 4C,H). Besides this two-dimensional segment typology, *Halimeda* segments may be distinctly undulated, keeled or ribbed (e.g. VERBRUGGEN, 2005, Figs. 19–21). In extant *Halimeda*, new segments (or daughter segments) originate terminally at the tips of the older (or mother) segments either in direct continuation of the axis or beside the axis, for instance in cases when two new segments arise, as visible in the specimen of *Halimeda opuntia* shown in Figure 4B. This construction is often termed 'serial-segmented' (details in ELLIOTT, 1982). It is noteworthy that there is a terminological dissent between botanists and palaeontologists concerning the numeration of the cortical siphons/utricles. For extant species, the numeration of the utrical series (or orders) starts from the segment surface inwards; for example, the outermost ones are termed primary utricles, and so on (e.g. HILLIS-COLINVAUX, 1980; VERBRUGGEN, 2005). By describing fossil representatives, the numeration used by the palaeontologists is simply the other way around, with the first cortical siphons arising from the meduallary siphons assigned to as primary or of first order. In the case of the Dasycladales, both the phycologists (BERGER & KAEVER, 1992) and palaeontologists (e.g. BASSOULLET et al., 1975; DE CASTRO, 1997) use the same numeration for different orders of laterals. If we bear in mind that the reduced nodal region between two subsequent segments is composed only of medullary siphons and the cortical siphons arise from the latter in the segments, the botanical method of numeration is somehow misleading, bearing in mind that the primary utricles are also called peripheral utricles. Here, the palaeontological nomenclature is followed.

There are contradicting views among phycologists and palaeontologists concerning the first appearance of *Halimeda* as a genus, or more precisely its different phylogenetic lineages. In recent times the so-called molecular clock method has been applied to decipher the phylogeny of *Halimeda* (VERBRUGGEN et al., 2009). This method needs fixed calibration points "*where a clade in the tree has a derived character that is unique to that clade and that can be traced in the fossil record. In this case one can infer that (a) the clade must have evolved on the branch of the tree leading to the the base of the clade and (b) that the clade must have evolved prior to its first occurrence in the fossil record*" (MEDLIN, 2007, p. 31). According to DRAGASTAN et al. (2002) and VERBRUGGEN et al. (2009), *Halimeda* should have its first appearance in the Permian, based on *Halimeda soltanensis* PONCET selected as the only fossil '*Halimeda*' and used as a calibration point for the phylogenetic calculations and considerations, thus not achieving the '*ideal scenario*'...."*with multiple fossil calibration points*" (VERBRUGGEN & THERIOT, 2008, p. 245). The attribution of this species to the genus *Halimeda*, however, is treated differently among palaeontologists. Whereas DRAGASTAN et al. (2002) consider it a true *Halimeda*, VACHARD et al. (2001, p. 382) treat it as a phylloid alga comparable to *Anchicodium* JOHNSON (Fig. 5; see section on phylloid algae). This view is followed here, as *H.*? *soltanensis* is obviously missing a medullar zone and only has two bilateral cortices. Moreover, the morphology of the cortical siphons with their peculiar multiple swellings is different from the inflated or cylindrical utricle structure of *Halimeda* (e.g. VERBRUGGEN, 2005). Last but not least, a cylindrical morphology has been assumed by PONCET (1989), but not evidenced by illustrations, another characteristic pointing to the phylloid *Anchicodium* (see section on phylloid algae, this work).

From the five lineages of *Halimeda* resulting mainly from gene sequencing and differences in the structure of the medullary siphons within the nodal region (e.g. HILLIS et al., 1998; KOOISTRA et al., 2002), the longest stock is referred to *Halimeda discoidea* by VERBRUGGEN et al. (2009, Fig. 4). This should date back to the Late Jurassic, or *Halimeda cylindracea* by DRAGASTAN et al. (2002) to the Late Triassic. Some of these obvious controversies are due to different interpretations of segment morphology in fossil taxa and different views concerning the group *Arabicodium-Boueina-Halimeda* with various stratigraphic ranges. It should be noted that up to now, there has been no description or illustration of a Triassic to Upper Cretaceous *Halimeda* species having flattened, e.g. discoidal segments (e.g. Fig. 4G). According to DRAGASTAN & HERBIG (2007, p. 8), such shapes should occur in latest Cretaceous times with *Halimeda*? *johnsoni* (Late Cretaceous–Paleogene of India, PAL 1971), considered a synonym of *Halimeda opuntia* (LINNAEUS) (Miocene–Pliocene, Fig. 4B). This possible synonymy has already been remarked by DRAGASTAN et al. (2002), following the description of PAL (1971) that the former should be characterized by leaf-like segments. The only figuration of *Halimeda*? *johnsoni* provided by PAL (1971), however, shows a longitudinal section of a cylindrical specimen being in accordance with Late Cretaceous sections of the NCA and the Internal Dinarides (Figs. 6A,B). Another Late Cretaceous species with cylindrical segments is *Halimeda elliotti* described by CONARD & RIOULT (1977), together with the described species of the genera *Arabicodium* ELLIOTT and *Boueina* TOULA (e.g. BASSOULLET et al., 1983, Tab. 3).

The works of DRAGASTAN et al. (2002, 2003), a co-production of palaeontologists and phycologists, provided another grouping into three phyletic lines, 'founded on the segment morphology' as the only criterion. The one with the greatest impact on fossil taxa is the proposed 'first phyletic line' of *Halimeda cylindracea*. With the synonymization of 21 Mesozoic and Cenozoic taxa, including all Late Triassic to Paleocene species of *Boueina* TOULA and most of *Arabicodium* ELLIOTT, the origin of modern *Halimeda* should date back into the Late Triassic. *Boueina hochstetteri* was thoroughly investigated using topotype material by STEINMANN (1899). He stressed a remarkable similarity to *Halimeda*. As one of the main differences STEINMANN mentions that the cortical siphons of *Halimeda* are swollen at the branching points and that the subsequent higher order siphons are mostly strongly constricted at their bases, features missing in *Boueina* (Fig. 4I). Curiously, the latter feature was stressed by CONARD & RIOULT (1977) as one outstanding feature of *Halimeda elliotti* from the Turonian of France. The fact that the Turonian *Halimeda elliotti* in turn is put in synonymy with the extant *Halimeda cylindracea* by DRAGASTAN et al. (2002), closes the circle again, leaving ample space for interpretations. The general aspect of the cortical zone of *H. cylindracea*, composed of three to five layers of utricles (HILLIS-COLINVAUX, 1980), is a more general feature shared with many other species. The synonymization of the genera *Boueina* TOULA and *Arabicodium* ELLIOTT with *Halimeda* LAMOUROUX (as having priority, see Tab. 3) is something that can be seriously discussed. However, the assumption that both type-species (*Boueina hochstetteri, Arabicodium aegagrapiloides*), with their totally different aspects of medullary and cortical zones, represent the same species *H. cylindracea*, seems to be too radical and needs further refined investigations. The more so, as *Halimeda cylindracea* does not possess real cylindrical segments with typical circular transverse sections. In DRAGASTAN et al. (2002, Figs. 3A,B), a figuration of HILLIS-COLINVAUX (1980) is shown with a thallus of *Halimeda cylindracea* whose segments were sectioned at various levels (basal, middle, top). From juvenile to adult stages, the segments become more compressed, but none shows a circular transverse section typical of the Late Triassic to Cretaceous group of halimedacean-like algae (*Halimeda, Boueina, Arabicodium*). Some transverse sections of *H. cylindracea* tend to be oval (Fig. 4J), but typical compressed sections as illustrated by DRAGASTAN et al. (2002) were not reported, for instance, from the well-known fossil *Boueina hochstetteri* (Fig. 4I). This, however, should be expected in the typical facies with abundant dispersed seg-

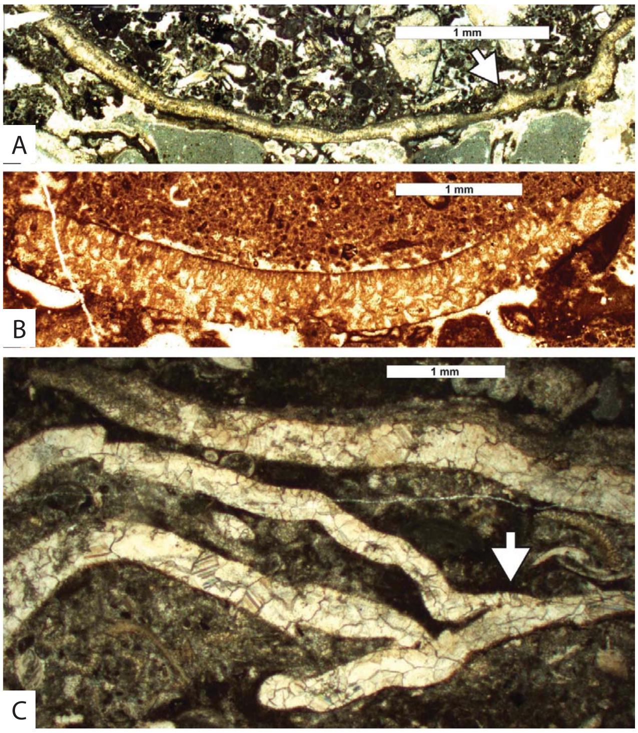

Figure 5: A–B *Anchicodium iranicum* SENOWBARI-DARYAN & RASHIDI, in press, from the Permian of Iran, note lateral protuberance/swelling (arrow) in (A), and dimorphic cortices in (B) (= inner and outer cortex sensu TORRES, 2003, Fig. 4). C) *Anchicodium* sp. from the Permian of South-China (see BUCUR et al., 2009). The lateral formation of a new plate with reduced width near the bifurcation area and the occurrence of lateral protuberances are comparable to the Late Cretaceous *Gosavisiphon* (details in the text).

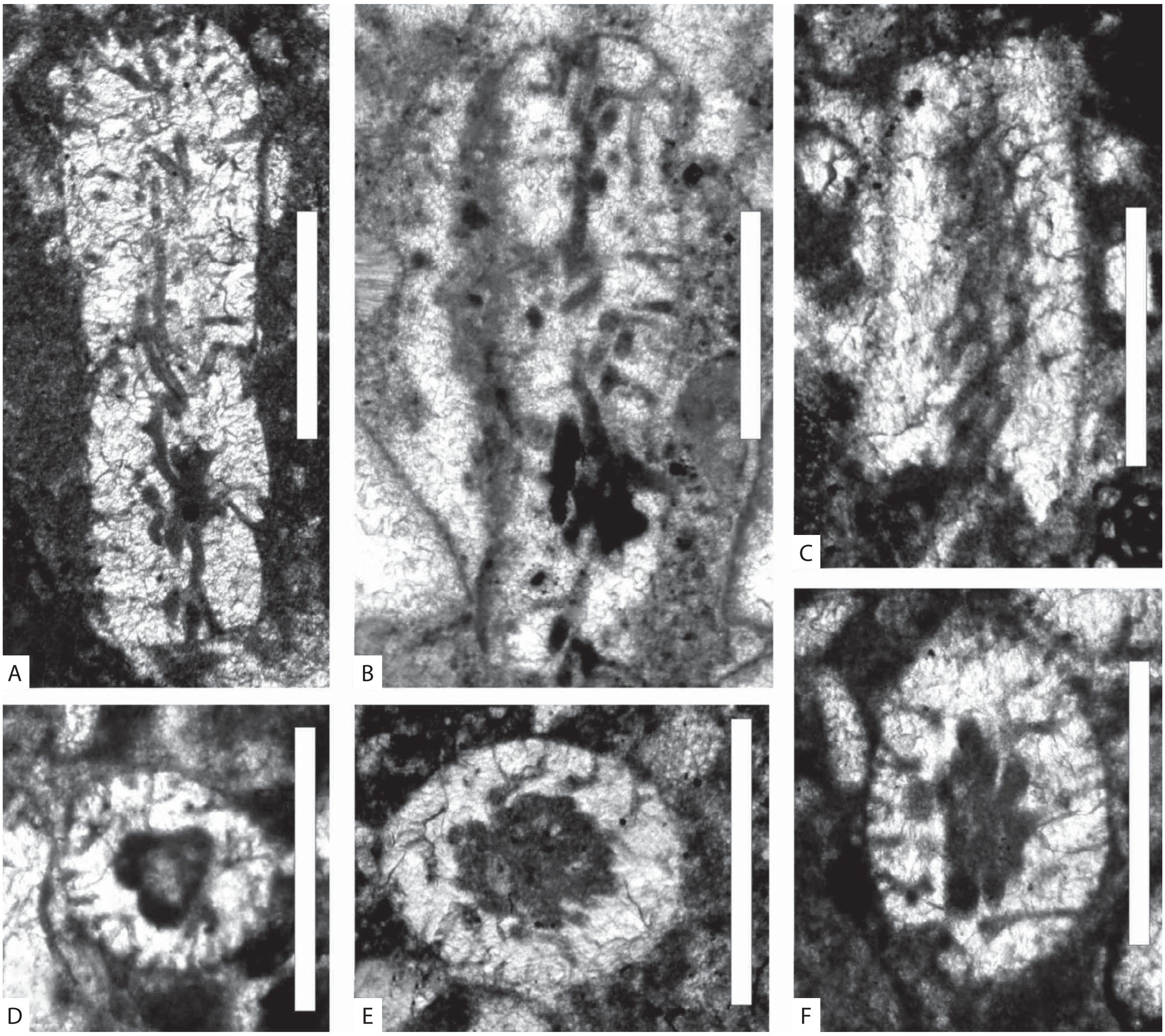

Figure 6: A–F *Halimeda*? aff. *johnsoni* PAL from the Upper Turonian-Coniacian Lower Gosau Subgroup of the Krumbachalm-Nachbergalm area (A, C–F) and the Santonian of the Inner Dinarides, Serbia (B). A) Longitudinal section; sample 20995-3. B) Longitudinal section; sample RR 2273. C) Slightly oblique longitudinal section; sample 1803. D–E) Transverse sections slightly oblique; samples 1803 and 151194/1. F) Oblique section, note comparable large medullary and distinctly smaller cortical siphons; sample 1803.

Scale bars 0.5 mm for A–C, E–F; 0.4 mm for D.

ments. Hence, the assumption as far back as the cylindrically shaped species *H. cylindracea* can be traced, is not only highly controversial but also very speculative and therefore is not accepted here. All taxa with cylindrical segments (independently of their generic position, e.g. *Boueina, Arabicodium*, some fossil '*Halimeda*' species) can not be compared purely morphologically with extant *Halimeda*, and therefore can not be used for tracing its phylogenetic origin.

As the segments and some internal features are the only available criteria for comparison of fossil with extant species, present knowledge (or interpretation) has not resulted in a final solution. The first fossil *Halimeda* species that shows segments that can be morphologically directly compared with modern species (see Fig. 4) is from the Early Tertiary with *Halimeda eocaenica* MORELLET & MORELLET, a species close to the recent *Halimeda opuntia* (LINNAEUS) (see BASSOULLET et al., 1983, p. 490). Although nothing is known about the internal structure of *Halimeda eocaenica* (only known as isolated segments), it was determined as synonymous with *Halimeda opuntia* by DRAGASTAN et al. (2002) and DRAGASTAN & HERBIG (2007). *H. eocaenica* has flattened, shallowly lobed segments (see MORELLET & MORELLET, 1940), a morphology previously unknown from Cretaceous halimedacean-like algae with cylindrical segments (genera *Boueina, Arabicodium*). *Halimeda* sp. described here from the Late Turonian Lower Gosau Subgroup of the NCA can morphologically be compared with *H. eocaenica* in also having disc-like flattened segments; a more closer comparison or a transfer of the Turonian form to the Eocene taxa is not possible as nothing is known about the internal structure of the latter. This is also the reason why a new species with a segment morphology so far unknown from Cretaceous representatives of *Halimeda* was not introduced. As a further consequence, the origination of *Halimeda discoidea* during the Late Jurassic as supposed by VERBRUGGEN et al. (2009), is not substantiated by fossil records; fossil *Halimeda* showing disc-like flattened segments are so far not known prior to the Middle Turonian (this study). This age of ~ 92 to 93 Ma (see GRADSTEIN et al., 2004) can be used as a calibration point for a clade of *Halimeda* with ovate flattened segments, such as *Halimeda opuntia*. According to the molecular clock approach, this morphological characteristic of modern *Halimeda* must have evolved prior to its first fossil appearance, probably around the Lower/Upper Cretaceous boundary. Such an interpretation would be in accordance with an assumption already made by ELLIOTT (1965) that *Halimeda sensu stricto* evolved in the Upper Cretaceous. For the molecular node age with the division of *Halimeda opuntia* and *Halimeda gracilis* VERBRUGGEN et al. (2009) calculated at 97 Ma, this suggests somewhere in the Cenomanian. Bearing in mind that fossil calibration data are minimum ages for the corresponding lineages, "*because newly evolved character.........do not usually fossilize until they become relatively common*" (VERBRUGGEN and THERIOT, 2008, p. 245), the observed age for Turonian *Halimeda* sp. with discoidal-flattened segments seems to fit well with the molecular age.

With respect to the incomplete original descriptions and illustrations of the Late Cretaceous '*Halimeda*' *paucimedullaris* and some Early Cenozoic species of MORELLET & MORELLET (1922), KOOISTRA et al. (2002, p. 122) state that these "*show similarity to extant groups of species*...(of *Halimeda*)...*suggesting that the extant diversity consists of living fossils*". In conclusion, these resemblances, however, are interpreted by KOOISTRA et al. (2002) as having resulted from iterative convergence therefore representing 'look-alikes'. A completely different view was advanced by HILLIS (1999, p. 186), another expert in modern halimedacean algae, suggesting that "*extant species have appeared relatively recently*". Although the present state of knowledge on fossil versus extant *Halimeda* species has advanced considerably, the topic is still a challenge for both phycologists and palaeontologists requiring further high quality, combined research for a thorough interpretation of the fossil record as a basic prerequisite when combined analysis of extant and extinct species should be conducted.

3.3. Phylloid Algae

The non-systematic, general term phylloid algae was introduced by PRAY & WRAY (1963) for a group of predominantely aragonitic algae, with poorly preserved internal features, that characterized Late Palaeozoic, (mainly Middle Carboniferous to Early Permian) reefal platform margins. They were ascribed mostly to green algae, but some also to red algae (e.g. PRAY & WRAY, 1963; KONISHI & WRAY, 1967; TOOMEY, 1976; FLÜGEL & FLÜGEL-KAHLER, 1980; WAHLMANN, 2002; GONG et al., 2007a, b). Phylloid taxa include for instance *Ivanovia* KHVOROVA, 1946 (Fig. 3C), *Anchicodium* JOHNSON, 1946, *Archaeolithophyllum* JOHNSON, 1956, *Calcifolium* MASLOV, 1956, *Eugonophyllum* KONISHI & WRAY, 1961, *Calcipatera* TORRES, WEST & SAWIN, 1992, *Kansaphyllum* BAARS, 1992, or *Kasimophyllum* MAMET & VILA, 2004. Their global dominant role and success could have been favoured by the seawater chemistry, particularly the Mg/Ca ratio, facilitating aragonite precipitation during that time (RIES, 2006). The name 'phylloid algae' comes from the greek word phyllon, meaning leaf. The thallus shape of the phylloid algae is highly variable from simple or undulose plate- or leaf-like ('corn flake-shaped'), to cyathiform (simple or folded cup-shaped, Figs. 3C–D) (e.g. TORRES, 1995, 2003; FORSYTHE et al., 2002; SAWIN & WEST, 2005). Amongst the forms with cup-shaped thalli, GONG et al. (2007a, b) further differentiated between single cup-shaped, cabbage-shaped and clustering cup-shaped forms. Some phylloid algae may show a structure of supporting plates similar to a house of cards (e.g. Fig. 9A in WAHLMAN, 2002). JOHNSON (1946) and TORRES & BAARS (1992) interpret the morphology of *Anchicodium* (see Fig. 5) not as being phylloid, but as 'distinctly cylindrical' based on extremely rare, rounded sections. Generally, when *Anchicodium* should in fact be cylindrical, circular transverse sections comon, where this alga usually occurs in special types of facies and in great abundances. However, this is not the case. Instead, long irregular curved algal thalli can be observed in thin-sections (Fig. 5). The illustrated transverse sections display an oblique radial arrangement of cortical siphons that indicate interpretation as sections cutting lateral 'rounded protuberances' that occur at irregular distances at the external side and that were also included by JOHNSON (1946) in the generic diagnosis (see Fig. 5A).

For the phylloid algae, the presence of an anchoring holdfast, comparable to that of the Halimedaceae or Udoteaceae, was assumed (TORRES et al., 1992), but has so far not been discovered fossilized, perhaps as these were not calcifying. The prostrate Archaeolithophyllaceae CHUVASHOV in CHUVASHOV et al. (1987) with internal cellular structure and conceptacles, (red algal affinities) are commonly separated from the phylloid algae with green algal characteristics, as the latter may result from the complete sparitization of the former (VACHARD et al., 2001, p. 389, Fig. 15). Other phylloid taxa were included in the family Calcifoliaceae TERMIER, TERMIER & VACHARD (see VACHARD & CÓZAR, 2006). Some of the aforementioned taxa (e.g. *Ivanovia*) have directly been compared with modern halimedacean algae (e.g. genus *Halimeda*) (e.g. HARBAUGH, 1960; CROWLEY, 1969; KIRKLAND et al., 1993). For example, *Eugonophyllum* is ascribed to the family Udoteaceae based on exceptionally well preserved specimens with primary aragonitic skeletons (KIRKLAND et al., 1993). Based on the conclusion of HILLIS-COLINVAUX (1984), that the family name Halimedaceae should have priority over Udoteaceae, the genus *Eugonophyllum* was placed in the former by FORSYTHE et al. (2002). It should be placed in the Udoteaceae as the present day Halimedaceae are monogeneric (genus *Halimeda*) (see Tabs. 2–3). For those taxa that were referred to or compared with udoteacean/halimedacean algae, the absence of a clearly delimited medullary zone (e.g. *Anchicodium*, Fig. 5) or its reduced size in some genera is striking; in these cases, a bilateral cortex, sometimes dimorphic (see Fig. 5B), may arise from the median central part of the alga. In fact, there are superficial morphological resemblances, for instance between Late Palaeozoic cup-shaped phylloid algae (TORRES, 1995, 1997; TORRES et al., 1992) and extant udoteaceans such as *Udotea cyathiformis* (see Fig. 3B, D–E). A further cross-link between phylloid and halimedacean algae is represented by the occurrence of mound structures within both groups (e.g. BRAGA et al., 1996, 'segment reefs'; GONG et al., 2007 a, b; GRAMMER & RITTER, 2008). Alternatively, Late Palaeozoic archaeolithophyllacean mounds (e.g. genus *Archaeolithophyllum*), built by an open framework were compared with Holocene deeper water *Mesophyllum*-dominated boundstones (DAVIES et al., 2004) or with encrusting peyssonneliaceans (JAMES et al., 1988). All examples mentioned clearly demonstrate that the term 'phylloid' does not imply either a particular growth habit, gross morphology or any taxonomic position, and is used as an algal waste-paper basket.

Phylloid algae have a discontinuous stratigraphic record with a main acme in the Late Carboniferous-Early, p.p. Late Permian. There is a reappearance in the Late Triassic (Norian) after a gap of about 35 to 40 MA with the single taxon *Ivanovia triassica* (REID, 1986; TORRES, 2003), one survivor of the mass extinction at the end of the Permian (e.g. PAYNE et al., 2004; JABLONSKI, 2005). Again after a considerable stratigraphic gap of more than 100 MA, another taxon with comparable morphology appears in the Late Cretaceous with *Gosavisiphon* gen. nov. A phylloid alga was described by DRAGASTAN et al. (1993) from the Bathonian of India; the illustrations, however, do not facilitate further discussion. The obvious absence of this peculiar algal morphology in post-Triassic times and the reasons for its sudden reappearance in the Late Cretaceous are unknown. Perhaps, this morphology arose independently two or more times.

4. Palaeontological Descriptions

Division Chlorophyta PASCHER
Order Bryopsidales SCHAFFNER
Family Halimedaceae LINK
Halimeda? aff. *johnsoni* PAL, 1971

Figs. 6A–F

1971 *Halimeda johnsoni*, n. sp. – PAL, pl. 1, fig. 1

Description: Small, cylindrical segments (length: 1.35–1.40 mm, diameter: 0.2–0.5 mm) with broad-rounded ends, made up of sparry calcite; calcification comprises both medullary and cortical zone. Constrictions of the segments are indicated. Medullary siphons large (diameter: 0.024–0.045 mm); cortex consists of finer, three (?four) loosely disposed utricle series (diameter: 0.016–0.035 mm), resulting in comparable large intersiphonal spaces. The ratio of segment width to length is 0.29 to 0.31 (PAL, 1971: 0.240 to 0.375).

Comparisons and discussion: In the original description, *Halimeda*? *johnsoni* was only illustrated by one longitudinal section, showing a striking analogy to specimens shown in Figs. 6A–B. As no holotype was indicated in the original paper, this specimen figured on plate 1 figure 1 by PAL (1971) is designated here as a lectotype.

Also the range of the dimensions of the Alpine specimens is comparable to those given by PAL (1971) for five segments. There are some minor variances, e.g. the diameter of segments may also be smaller than data from PAL (1971, D: 0.48–0.52 mm). From the specimen illustrated by PAL (1971), a leaf-like morphology was assumed (see DRAGASTAN et al., 2002; DRAGASTAN & HERBIG, 2007) and the species was synonymized with the extant *Halimeda opuntia*. The specimens from the Lower Gosau Subgroup, however, clearly show circular cross-sections as expected in cylindrical segments. *Halimeda*? *johnsoni* was described from the Maastrichtian-Palaeocene of India, the specimens from the Lower Gosau Subgroup are of Late Turonian-Coniacian age. *Boueina pygmaea* (PIA, 1936, Cenomanian-Turonian of Morocco), *Arabicodium tibeticum* (YU JING, 1976, Paleocene-Early Eocene of Tibet) are comparable to *Halimeda*? *johnsoni* as is *Halimeda nana* (PIA, 1932, Paleocene of Morocco) to some lesser extent. The four taxa (including *H.*? *johnsoni*) need systematic reconsideration and re-investigation for the evaluation of possible synonymies. Note that PIA (1936, p. 13) tentatively referred *Boueina pygmaea* to the genus *Boueina* rather than *Halimeda* '*as no bifurcation of the thallus was observed*', a non-diagnostic feature, the more so when only dealing with some thin-sections.

Last but not least, *Halimeda*? aff. *johnsoni* PAL appears in bioclastic packstones with corals, and rudists, and sponges, indicating an open marine paleoenvironment, whereas the other two taxa *Halimeda* sp. and *Gosavisiphon* gen. nov. *paucimedullaris* (SCHLAGINTWEIT & EBLI) comb. nov. described from the Lower Gosau Subgroup occur in lagoonal wacke- to packstones with totally different algal flora and microfauna. Another observation illustrated here in Fig. 6B is from the Santonian type-locality of *Neomeris* (*Drimella*) *jerinae* in the internal Dinarides of Serbia (see RADOIČIĆ, 1984).

Halimeda sp.

Fig. 7

Description: Weakly calcified, flattened, disc-like to broad ovate segment sections (slightly broader than high) of light brownish colour. Typically, only the segment periphery (thickness: ~ 0.08 to 0.2 mm) with up to three (? four) orders of tiny, cylindrical to cylindroconical cortical siphons is preserved; the large central part that hosted the medullar zone and the innnermost siphons is represented by a sediment-filled cavity. Therefore, nothing can be said about the internal structure. Transverse sections sometimes are bent and display varying thicknesses. For dimensions see Table 4.

Comparisons and discussion: At the Pletzachalm locality *Halimeda* sp. and *Gosavisiphon* gen. nov. *paucimedullaris* (SCHLAGINTWEIT & EBLI) comb. nov. co-occur. Due to external morphology, degree of calcification and other features, both can easily be distinguished. The ovate segment morphology was previously unknown from the Cretaceous

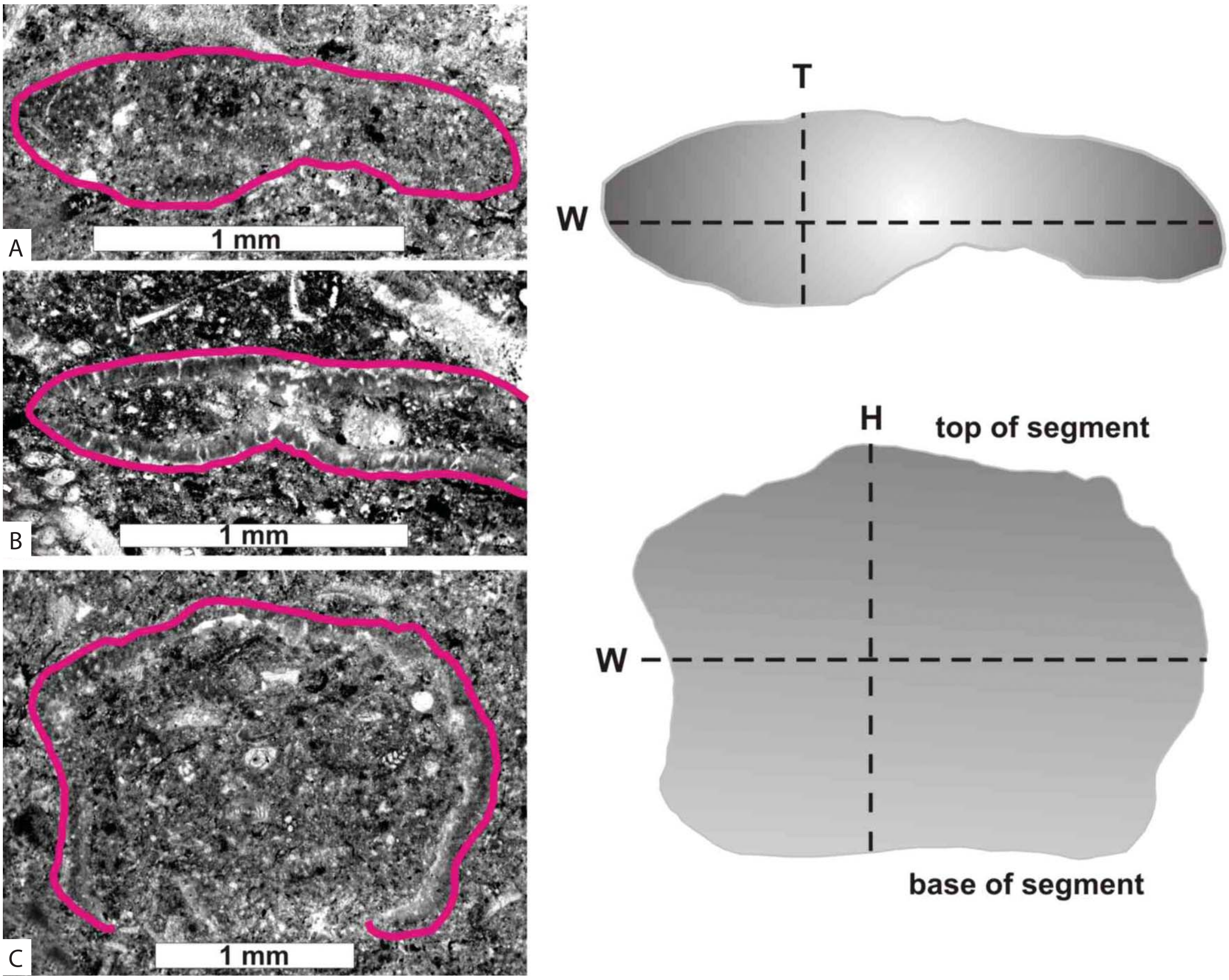

Figure 7: A–C Segment sections (outlined in red) and morphology of *Halimeda* sp., Late Turonian of Pletzachalm. A–B Transverse sections, sample Pletz 7 and sample BSP 5211a-93. C Longitudinal section in the plane of compression, sample Pletz 7. Note the totally decalcified medullary zone also affecting the innermost cortical utricles in all three specimens. Above right: Schematic segment outline from A; below: Schematic segment outline from C. H = segment height, W = segment width, T = segment thickness.

Table 4: Segment dimensions (in mm) of *Halimeda* sp., Upper Turonian of Pletzachalm (samples 5211a 93 and Pletz 7) and Eisenbach (sample EB 9B). H = segment height, W = segment width, T = segment thickness.

W	T	H	sample
–	0.64	–	5211a93
–	0.40	–	
2.10	0.40	–	Pletz 7
2.40	–	1.90	
1.05	0.35	–	EB-9B

(and older) *Halimeda* species, so these segments could belong to a new species. A comparable segment morphology is known from *Halimeda eocaenica* MORELLET & MORELLET; the dimensions of the Cretaceous specimens are smaller, but this feature is not diagnostic as variable sizes and also segment forms may occur in different parts of a *Halimeda* thallus (see Figs. 4A–B). The Eocene taxon is only known from isolated segments; internal structures are unknown. Isolated segments of *H. eocaenica* were also collected by GENOT (1985a, p. 210) but not studied by means of oriented sections, as these were recrystallized affecting both medullary and cortical siphons. Thus, we can not exclude but also not validate that the Turonian specimens belong to *Halimeda eocaenica* MORELLET & MORELLET. Therefore, synonymization of the fossil *Halimeda eocaenica* with the Recent *Halimeda opuntia* by DRAGASTAN & HERBIG (2007, p. 8), on the feature of comparable segment shapes alone, seems premature as the "*the cortical system with variously shaped utricle series remains the primary key for identification of fossil material and corresponding extant material*" (op. cit., p. 15).

? Family Udoteaceae AGARDH
(Remark: refering to SILVA, 1980)

Remark: Notwithstanding and obviously unaware of the common knowledge on botanical taxonomy, the Udoteaceae were introduced as a new family name with diagnosis by NIZAMUDDIN (1963) almost 80 years after the establishment of the family. *Gosavisiphon* gen. nov. surely belongs to the green alga order Bryopsidales, however, the family rank is uncertain.

Refering to fossil udoteaceans as segmented or non-segmented algae with an internal unpartitioned siphonal construction, *Gosavisiphon* gen. nov. is for reasons of pragmatism and taxonomic simplicity also placed in this family. The question of whether it belongs to the Halimedaceae can definitely be excluded (see Tab. 2). Perhaps, the combination of the external and internal morphology necessitates the establishment of a new family with at present only one genus.

Gosavisiphon gen. nov.

Origin of the name: The genus name refers to the latinized name of Gosau, named after the village of Gosau, Lower Austria (see Fig. 1C), combined with the siphonous inner structure.

Type species: *Halimeda paucimedullaris* SCHLAGINTWEIT & EBLI, 1998.

Diagnosis: Plurimillimetric to pluricentimetric, irregularly curved and twisted, non-segmented and non-branching plates, occasionally with irregularly distributed swellings; distal margins slightly thickened, rounded. Basal part stratose, attaching to hard substrates by means of flat crusts, ocassionally with small rhizoidal outgrowths. Cortication comprises both the basal and erect part. Plates partly fused laterally showing multilateral cortices separated by a thin sparitic line (?extracellular cement). The internal non-septate siphonal construction consists of an often sparitic median line (?reduced medullary zone), from which bilateral cortices originate. Cortices with 3–5 layers of utricles mostly dichotomously, sometimes also trichtomously branched, and set at right angles to slightly oblique to the median plane; internal siphons long, cylindrical to cylindroconical occasionally with a moderate terminal swelling, peripheral siphons rather short. Breakage of thallus preferentially along the median plane leading to the formation of fragments with unilateral cortices. Calcification well developed; siphons filled with blocky calcite, intersiphonal spaces of light to dark brownish appearance. Reproductive structures and exact three-dimensional thallus architecture unknown.

Composition: So far monospecific.

Comparisons and discussion: The taxon in question was originally described as a species of the genus *Halimeda* LAMOUROUX by SCHLAGINTWEIT & EBLI (1998), characterized above all by its reduced medullary zone (as reflected in the species name) and having cylindrical segments. As discussed below, the thallus organization of the gosauian taxon is on the whole completely different from *Halimeda*. In the original description of *Halimeda paucimedullaris*, the segment morphology was erroneously reported as being cylindrical because of the supposedly finger-shaped sections with parallel outer margins. Moreover, the original description was based on comparable short thallus parts only; the wavy plurimillimetric to pluricentrimetric specimens were only discovered afterwards (SCHLAGINTWEIT & LOBITZER, 2003). Already DRAGASTAN et al. (2002, p. 16) quoted that the segments of *Halimeda paucimedullaris* are not, as erroneously indicated, cylindrical, but flattened, most probable nearly discoidal. DRAGASTAN et al. (2002, p. 17) claim the species validity "*with distinct structure and morphology that cannot be referred to any of the Recent species of the genus*" (= *Halimeda*). Sections of very long (> 2 cm length) and thin (~ 0.4 to 0.5 mm) specimens led us to conclude that these are not individual segments and parts of a segmented alga like *Halimeda* (see Figs. 4A–B). The general shape and their wavy outline in cross sections are not compatible to the segment sizes and morphology (including also the ratio length/width) of any known *Halimeda*, both extant and extinct (Figs. 4C–H), and there are several indications that in *Gosavisiphon* gen. nov. instead we are dealing with plate-like phylloids (or membranes):

(a) The specimen shown on Fig. 10A, represents a section with a more or less constant thickness (~0.4 to 0.5 mm) over a length of more than 2 centimetres. This specimen is the only one observed in this thin-section and the probability that it is directly cut exactly in the middle of a cylinder along its total length is improbable (compare with the same consideration for *Anchicodium*, in the section on phylloid algae, Fig. 5). This also accounts for the large specimens shown in Figs. 8A and 9D, or very long specimens, or variously bent specimens. If a bent specimen of a small cylinder is cut in random thin-sections, we would find interruptions in the longitudinal section with tapering on both sides of the part that bends away from the cutting plane.

(b) In all thin-sections studied, we never observed a rounded/circular transverse section with a central medulla and radially arranged cortical filaments provided by cylindrical segments. The sometimes assymetric appearance of the cortices, i.e. different thicknesses on oppsite sides in sections, suggests a phylloid of reduced width comparable to a belt or plate. Thus, in oblique longitudinal sections the median plane is not centreed as would be expected when referring to a cylindrical morphology. Furthermore, several flattened-ovoid transverse sections recovered, support the inferred morphology (Figs. 14K–M).

(c) The characteristic debris of *Gosavisiphon* is composed of fragments consisting only of unilateral cortices. This type can be explained by the less well calcified median, facilitating preferential damage/breakage along this plane of the algal phylloids. Apart from this, these fragments are also formed by the lateral formation of new phylloids and their easy disintegration (see Fig. 14, for explanation).

(e) The wavy segments can morphologically directly be compared with the so-called phylloid algae.

Besides the general morphology being totally different from *Halimeda*, the internal structure also shows differences. First of all, the often total lack of a central medullary zone is striking, whereas in *Halimeda* this zone can (differing from one species to the other) make up more than 3/4 of the segment diameter, consisting of multiple longitudinally arranged medullary filaments. Only in *Halimeda cryptica* COLINVAUX & GRAHAM and *Halimeda pygmaea* VERBRUG-

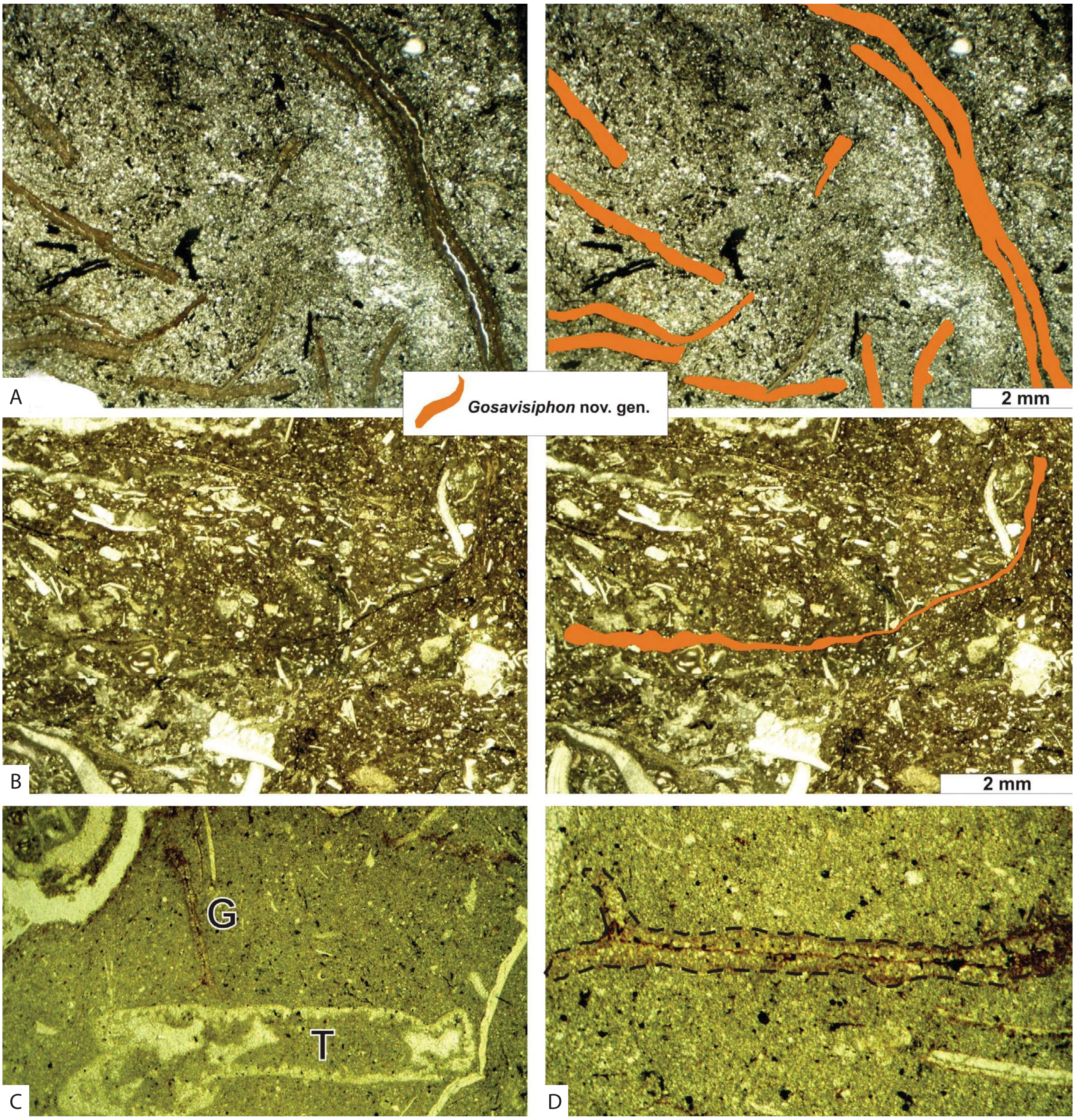

Figure 8: Microfacies with *Gosavisiphon paucimedullaris* (SCHLAGINTWEIT & EBLI) from the Lower Gosau Subgroup of the Northern Calcareous Alps.

A) Left: Mixed siliciclastic-carbonatic tempestitic layers intercalated in the Hofergraben Marls with abundant, chaotic oriented algal plates appearing as dark, brownish curves forming a floatstone facies. Locality Hofergraben, east of the village of Gosau; stratigraphy Upper Santonian, sample HG 3D. Right: Same figuration, specimens of *Gosavisiphon paucimedullaris* (SCHLAGINTWEIT & EBLI) are coloured in orange.

B) Left: Brownish marly limestone (bioclastic packstone to floatstone) with one curved specimen. Noth-Klamm, Gosau of Gams, Upper Turonian. Right: same figured specimen of *Gosavisiphon paucimedullaris* (SCHLAGINTWEIT & EBLI) coloured in orange.

C) Wacke- to floatstone with branching thallus of the dasycladale *Thyrsoporella eisenbachensis* SCHLAGINTWEIT & LOBITZER (T) and plate of *Gosavisiphon* (G). Eisenbach locality; stratigraphy Middle Turonian, sample EB-9B.

D) Close-up view of C showing plate of *Gosavisiphon*.

GEN, LITTLER & LITTLER, is the medulla composed of a single filament (COLINVAUX & GRAHAM, 1964; VERBRUGGEN et al., 2007). Finally, *Halimeda* is anchored in the sediment by means of a rhizoidal holdfast (Fig. 4A); *Gosavisiphon* in contrast represents an alga with a flat prostrate thallus portion with rhizoidal outgrowths fixed to biogenic hard substrates.

Gosavisiphon paucimedullaris (SCHLAGINTWEIT & EBLI, 1998) comb. nov.

Figs. 8–12, 14E–F, K–M

1985 *Halimeda* sp. – HÖFLING, pl. 11, figs. 7–9

1993 *Halimeda* sp. – MOUSSAVIAN, HÖFLING & HERM, pl. 4, fig. 3

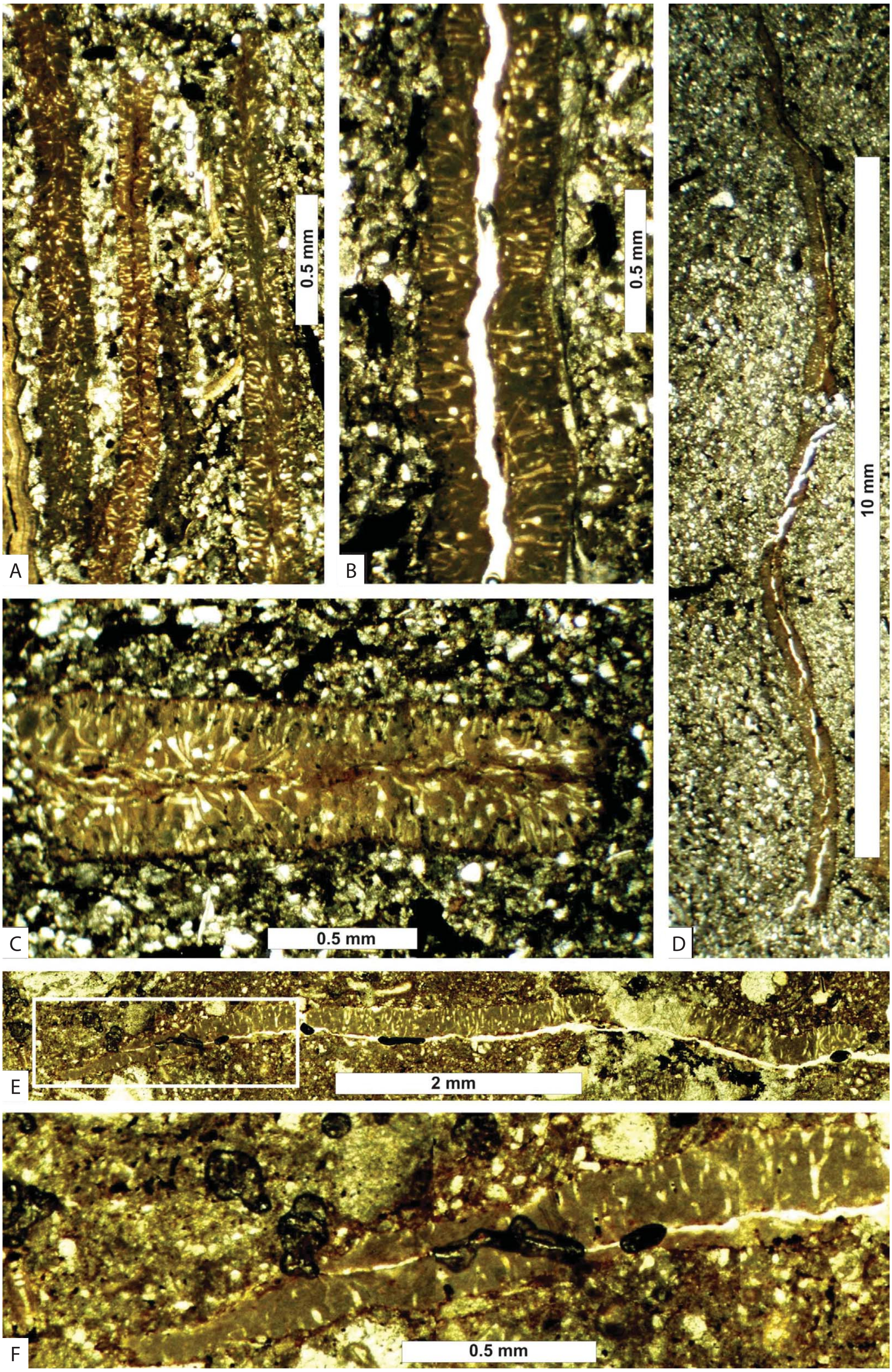

Figure 9: *Gosavisiphon paucimedullaris* (SCHLAGINTWEIT & EBLI) from the Upper Santonian Hofergraben Marls, mixed siliciclastic-carbonatic tempestite layers (A–D) and the Late Turonian Lower Gosau Subgroup of the Nothklamm, Gams (E–F). A) Four plates in parallel arrangement/orientation, sample HG-3B. B) Specimen showing a sparitic, probably monosiphonal medullary zone from which in a perpendicular manner cortical siphons of several orders originate, sample HG-3B. C) Specimen with extremely reduced to lacking medullary zone; note elongated and distally widening primary siphons (utricles), sample HG-3D. D) Long algal plate with fused plate parallely at longer distance (above) showing a little darker colour. E) Long, slightly undulating algal plate with unilateral cortex; note sparitic central line, sample HG-3D. F) Detailed view from E showing tapering and change of orientation of the cortex.

1998 *Halimeda paucimedullaris* n. sp. – SCHLAGINTWEIT & EBLI, pl. 1, figs. 1–3, 6; pl. 2, figs. 1–2

2003b *Halimeda paucimedullaris* SCHLAGINTWEIT & EBLI – SCHLAGINTWEIT & LOBITZER, pl. 1, figs. 1–3

2004 *Halimeda paucimedullaris* SCHLAGINTWEIT & EBLI – SCHLAGINTWEIT, pl. 1, fig. 3

Diagnosis: See diagnosis of the monotypic genus.

Description: The alga is well calcified with sparite filled siphons and an intersiphonal part showing a light-brownish, more seldom slightly yellowish appearance. The thallus is differentiated into a basal prostrate portion and an erect part. It was found encrusting biogenic substrates such as metazoan skeletons (e.g. stromatoporoids) or fragments of rudistid shells (Fig. 12). The crustose part (thicknesses mostly from < 0.1 mm to 0.4 mm) directly follows the substrate surface, often for lengths of several millimetres; in this connection, small rhizoidal outgrowths of the crusts may enter existing hollows (observed up to ~ 0.5 mm in depth), such as skeletal pores. Depending on the geometry of the substrate pores, these rhizoidal outgrowths may be straight or strongly bent in order to completely fill the former. Smaller shell debris can also become totally encrusted on all sides. These examples were observed without the erect part; it must remain open, whether this is due to breakage or it being a special morphotype lacking an erect part. In many cases, the crusts are diagenetically obliterated appearing as a dark brownish mass with poorly preserved internal features; a central sparitic line and fine cortical siphons, however, are discernible. Within the crusts, the sparitic line, interpreted as a strongly reduced medullary zone (?monosiphonal), can be either at the base just between the substrate and the algae (?acting as cement) or more or less in the central part. In the first case, only a simple monolateral cortex is present with siphons perpendicular to the substrate and dividing in growth direction. Alternatively, a cortex, developed on both sides (bilateral cortices) is present. Commonly, the algal thallus becomes erect, bending away from the substrate mostly gradually with low inclination. Then another plate may attach that grows in the opposite direction; the length of the attaching plane between the two plates is variable; in any case a thin sparitic crust interpreted as extracellular cement is developed. Often ends or margins of the plates seem to be broken leaving only remnants with unilateral cortices, which together with the fact that the observed plate arrangements seem to be somehow incomplete (missing of whole attaching plates), means that the three-dimensional thallus architecture is unclear. More rarely, individual plates may also bend away from the substrate in a perpendicular manner.

The plates (or phylloids, or thallus membrane) maybe more or less straight (at least along longer portions, Fig. 10a) but more often irregularly bent also showing constricted and swollen areas (e.g. Figs. 10G–J). The plates vary in thickness from 0.2 mm to 0.68 mm averaging 0.4 mm (n = 30); the greatest observed length is 2.1 centimetres (Fig. 10A). At the Eisenbach locality, very small plates with thicknesses around 0.1 mm were observed, that somehow due to their microfacies, can be interpreted as phenotypic variations (Figs. 8C–D). Anyway, the total biometric ranges can be regarded as certainly obscured by breakage and diagenetic processes (e.g. compression). Normally, a central sparitic line, that could be interpreted as a monosiphonal medulla, is present. In parts where new plates are attached, this zone moves toward the margin and finally forms the outer zone of the one plate and concurrently acts as the base of the attaching plate where a monosiphonal cortex develops (Figs. 11A–C). In these portions a multilateral (or tri-lateral) cortex is present (see Fig. 14 for explanation), meaning a bilateral cortex from the attached plate and a monolateral cortex from the fusing plate, being in contuity with the siphonal branching direction, is visible in thin-sections.

Remarks on calcification: In the investigated thin-sections, not only *Gosavisiphon* but also the accompanying dasycladalean algae namely *Neomeris mokragorensis* RADOIĆIČ & SCHLAGINTWEIT, or in the tempestite layers of the Hofergraben marls also *Trinocladus tripolitanus* RAINERI and *Jodotella koradae* (DIENI, MASSARI & RADOIĆIČ) show the same characteristic light brownish appearance (see SCHLAGINTWEIT, 2004, Pl. 1) (Fig. 13). This so-called 'brown calcification'may represent either primary calcite or aragonitic relicts (see discussion in MASSE & BUCUR, 2002, p. 160). Recent dasycladalean algae develop essentially aragonitic skeletons (e.g. BERGER & KAEVER, 1992); whereas in fossil species the original crystalline phase and microstructure have been destroyed by diagenetic recrystallization (e.g. overview in DE CASTRO, 1997, p. 165). Well preserved isolated dasycladalean thalli that have retained their original aragonite were reported by GÉNOT (1980, 1985a, b) from the Tertiary of the Paris Basin. Exceptions with skeletons of radial fibrous (?calcitic) crystals or dark micritic skeletons may also exist (e.g. CONRAD & VAROL, 1990). Hence, for the time being, a relict aragonitic preservation is put up for discussion. The reason for the diagenetic history allowing this peculiar kind of brownish preservation of originally aragonitic algae in the Late Cretaceous Lower Subgroup is not known; perhaps factors including continental influences and fluctuations in the salinity and Mg/Ca ratio could have played a role (e.g., RIES, 2006). It is noteworthy, that Miocene to Pleistocene representatives of *Halimeda* with aragonitic skeletons also show a light to dark brownish appearance in thin-sections (see DRAGASTAN et al., 2002). Older representatives of *Halimeda*, however, show recrystallized, sparitized segments (e.g. BASSOULLET et al., 1983), like the majority of the skeletons of fossil dasycladaleans.

This should be highlighted with thick and dark-grey letters same manner as on page 43 Remarks on Calcification: From all observations made in the investigated thin-sections from different localities, a hypothetical reconstruction of the thallus of *Gosavisiphon*, with interpretation of variously oriented sections, was made (Fig. 14, except B). It shows that *Gosavisiphon* was an epilithic alga growing on hard substrates such as metazoan skeletons or rudistid shells, occurring in

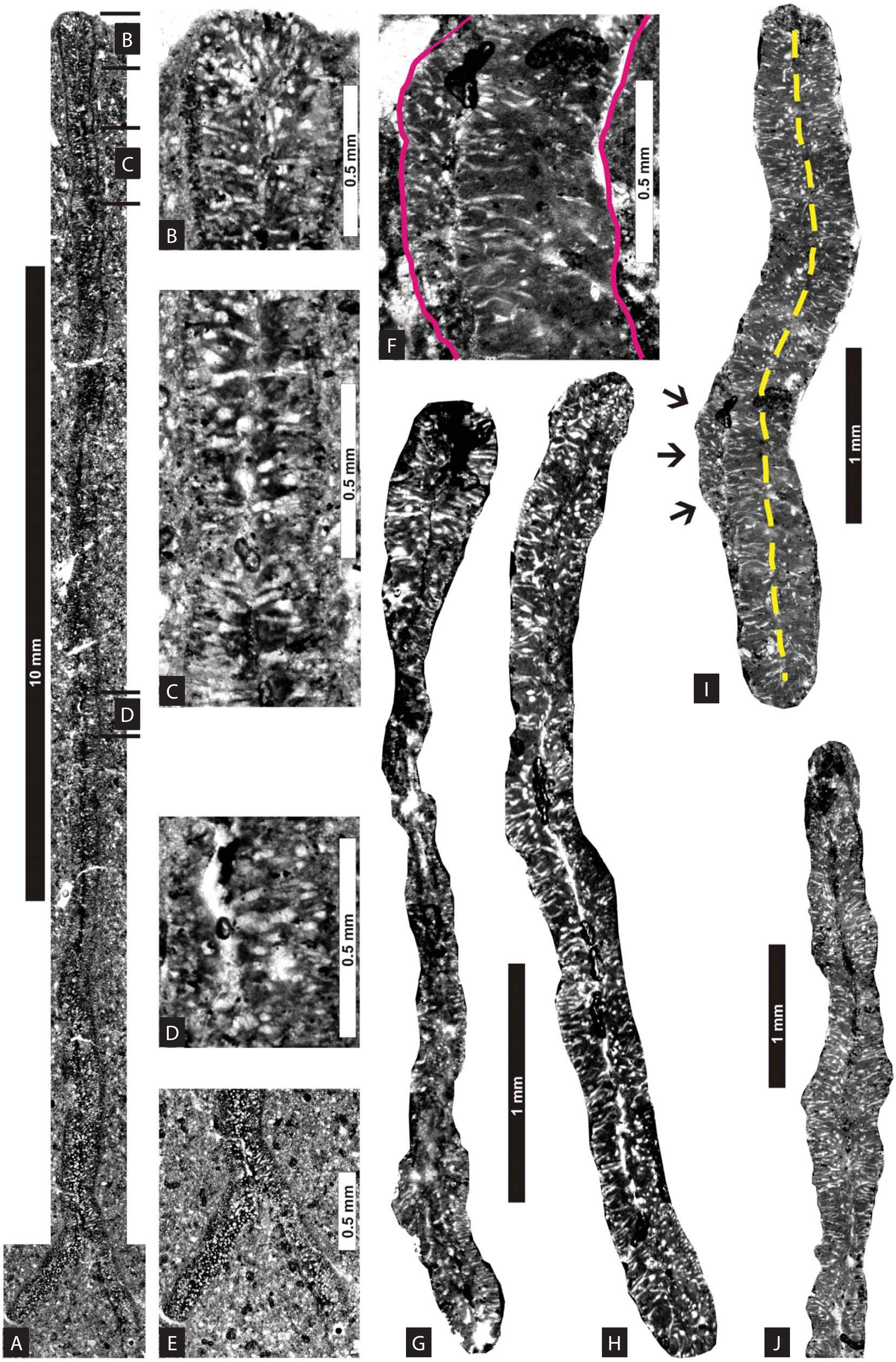

Figure 10: *Gosavisiphon paucimedullaris* (SCHLAGINTWEIT & EBLI) from the Randobach, Pass Gschütt area, Upper Santonian (A–E) and the Upper Turonian of Noth-Klamm, Gams (F–J). A) Straight to slightly undulating thallus of more or less constant thickness with rounded tip (see detail B), central sparitic line (monosiphonal medulla) in the centr (C) or excentric, random (D) and beginning of breakage at the opposite side (see detail E); total length of specimen is 2.1 cm. sample 1791. G–J Curved plates; note varying thickness in (G) and (J), lateral protuberance (arrows in I) with three-layer cortices in the area of a lateral protuberance (close up view of protuberance is shown in (F); plate outline in red). Median plane in (I) is marked in yellow.

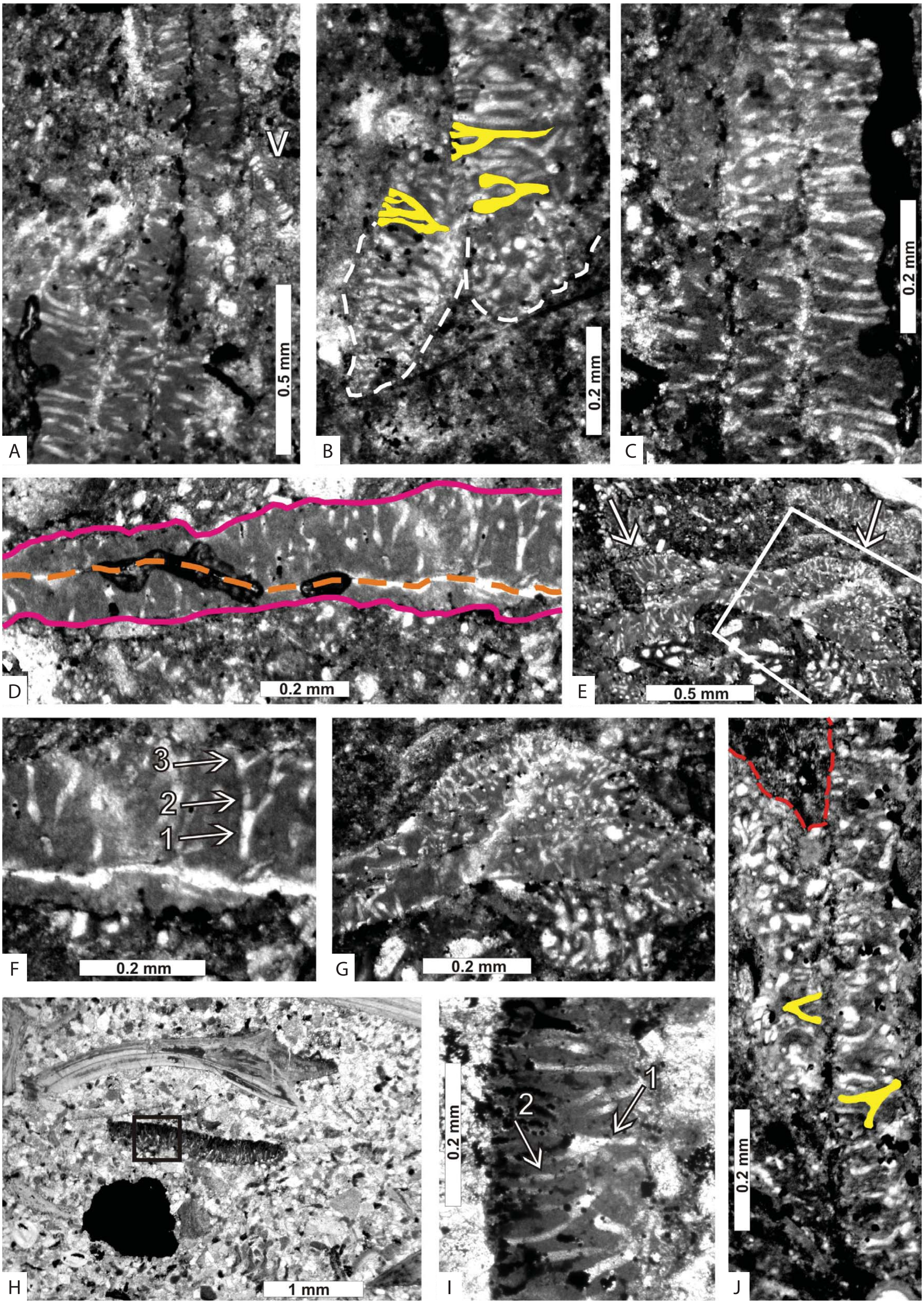

Figure 11: *Gosavisiphon paucimedullaris* (SCHLAGINTWEIT & EBLI). A–C Detailed views of laterally fused plates with three- (A, C) and two-layered cortices; note the same orientation of the cortices in (B). D, F) Portion of a plate with excentric position of monosiphonal medulla marked in orange, plate outline in red (F, detailed view of D three orders of siphons). E, G) Plate with two swelings (arrows) separated by a constricted portion (G, detailed view of E, white rectangle). H) Mixed siliciclastic-carbonatic microfacies of the Hofergraben tempestite layers with extraclasts (dark), dispersed shell fragments and a fragment of *Gosavisiphon* gen. nov. in the centre. I) Close up view of (H) (Black rectangle) showing unilateral cortex with comparable long cylindro-conical siphons of different orders (1, 2). J) two fused fragments showing opposite orientation of cortices.

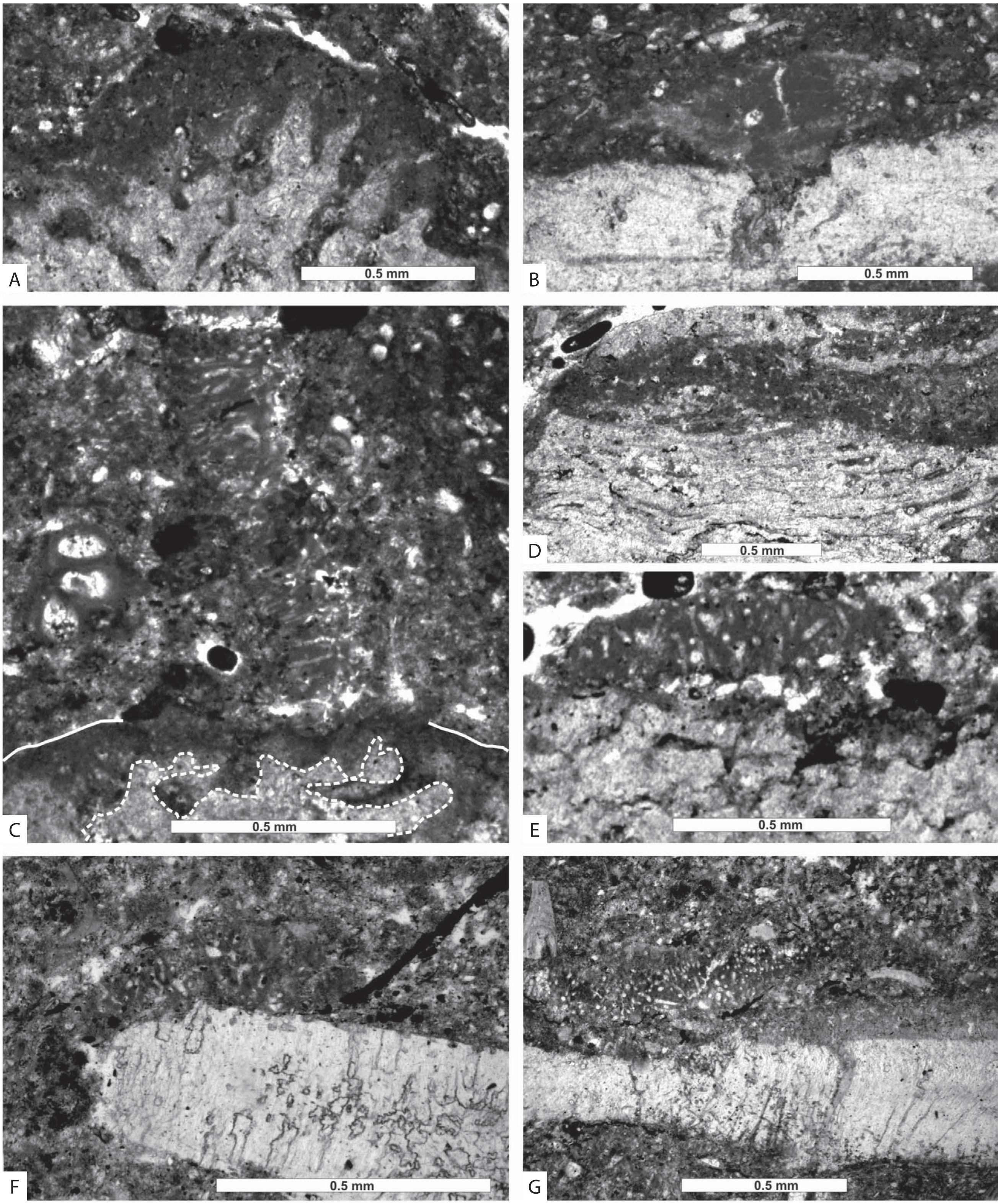

Figure 12: Basal encrusting part of *Gosavisiphon paucimedullaris* (SCHLAGINTWEIT & EBLI), Upper Turonian, Noth-Klamm, Gosau of Gams (A–E) and Upper Turonian of Pletzachalm (F–G). A Crust upon stromatoporoid skeleton, internal siphonal structure barely recognizable. B Crust fragment fixed to a cavity within the basal substrate. C Specimen fixed to a stromatoporoid skeleton (dashed line); solid line: upper crust surface. Note the infilling of the intraskeletal pores and the erect bending away from the substrate; Crust-sediment boundary solid line, rhizoidal crust outgrowths within the skeletal pores in dashed line. D Specimen flat encrusting a rudistid shell. E Crust fragment fixed to substrate; internal siphonal structure well recognizable. F–G Crust fragments fixed to pelecypod shells.

soft-bottom substrates, differentiated into a basal prostrate and an erect main part (Fig. 14A). The basal attached part directly follows the contours of the substrate surface, also infilling small depressions of the latter. In the prostrate part of the thallus, a thin sparitic layer between the unilateral cortex, with siphons dividing in direction away from the sub-

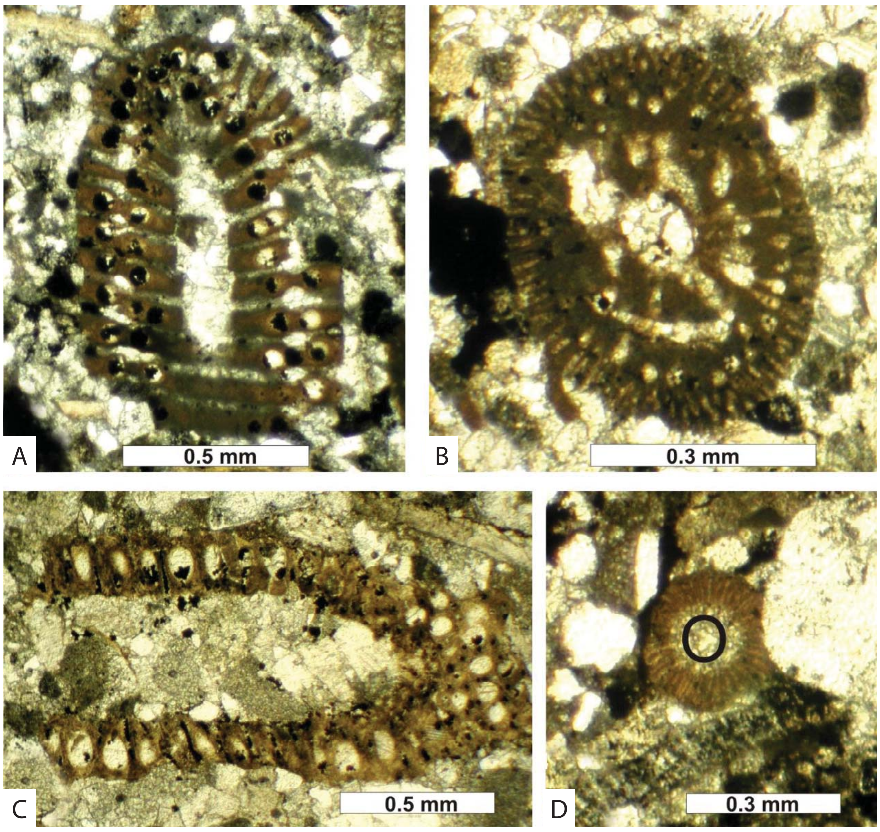

Figure 13: Brownish calcification in dasycladalean algae (A–C) and alga incertae sedis (D) associated with *Gosavisiphon paucimedullaris* (SCHLAGINTWEIT & EBLI) associated in the tempestite layers of the Hofergraben, Gosau. A) *Jodotella koradae* (DIENI, MASSARI & RADOICIC). B) *Trinocladus tripolitanus* RAINERI. C) *Neomeris mokragorensis* RADOICIC & SCHLAGINTWEIT. D) *Oroseina pletzachensis* SCHLAGINTWEIT & EBLI (O).

strate, can be observed and interpreted either as monosiphonal medulla or extracellular cement (Fig. 14D). Then, the alga bends away from the substrate either continuously at a low angle or more abrupt forming the erect part where new fused plates, separated by a thin sparitic line or zone and interpreted as extracellar cement/mucilage, occur. Within these fused parts a tri-lateral cortex (Fig. 4G) occurs composed of the unilateral cortex of the basal attached part and the bilateral cortex of the newly formed plate. Breakage and displacement of the algal plates occurred preferentially along these attachment zones commonly producing fragments with unilateral cortices of typical cylindrical to cylindroconical, long and parallel arranged siphons of several orders and reduced intersiphonal spaces (Fig. 14E). An equivalent thin sparitic zone separating adjacent and laterally fused plates also occurs in the central part of the plates (?monosiphonal medulla?), from which cortical siphons arise in both directions. Depending on the plane of section, the thin central sparitic zone doesn't always appear centreed (Fig. 14J), is also observable in the parts where plates fuse, and can occupy a random position. The plates are bent along the longitudinal axis and irregularly twisted in the plane of compression (Fig. 14H). As the plates may reach a length of several centimetres, there are of course several millimetre long straight portions. At the slightly swollen tips, the development of a small medulla consisting of several medullary siphons can be observed (Fig. 14F); these could also be terminal cortical siphons. Finally, it must be stressed that it is unkown whether the laterally fused plates all belong to one algal thallus or are just different specimens that use other algal plates as a substrate instead of metazoan skeletons or rudistid shells. The fact, that in the fused zones, the internal structure of the main plate changes, can be taken as an indication as being parts of one and the same specimen.

Comparisons: The characteristic features of the new genus *Gosavisiphon* as already discussed also account for its type-species. For instance, the special feature of *Gosavisiphon paucimedullaris* with the isolated cortical fragments was also reported from *Boueina marondei* FLÜGEL (= *Halimeda marondei* acc. to DRAGASTAN et al., 1999 = *Halimeda cylindracea* acc. to DRAGASTAN et al., 2002) from the Upper Triassic of Thailand (FLÜGEL, 1988). In this species, post-mortem disintegration was facilitated by a »distinct break in the calcification« between the medulla and the outer cortex. In *Boueina marondei*, however, the medulla is of comparable width amounting to more than half of the cylindrical segments, thus, being totally different from *Gosavisiphon paucimedullaris*.

Stratigraphy: Specimens of *Gosavisiphon paucimedullaris* (SCHLAGINTWEIT & EBLI) were detected in the Lower Gosau Subgroup within the Middle Turonian to Upper Santonian interval. Within the Branderfleck Formation it was observed within olistolites of Middle/Late Cenomanian to Early Turonian age. The observed stratigraphic range of *Gosavisiphon* is therefore Middle/Late Cenomanian – Santonian. It is most likely that this time interval does not represent its total stratigraphic range, especially at its upper boundary when neritic settings disappeared within the Gosau Group.

Palaeoenvironment: *Gosavisiphon paucimedullaris* grew in sheltered palaeoenvironments of partly sandy unconsolidated mud associated with calcareous green algae *Hali-*

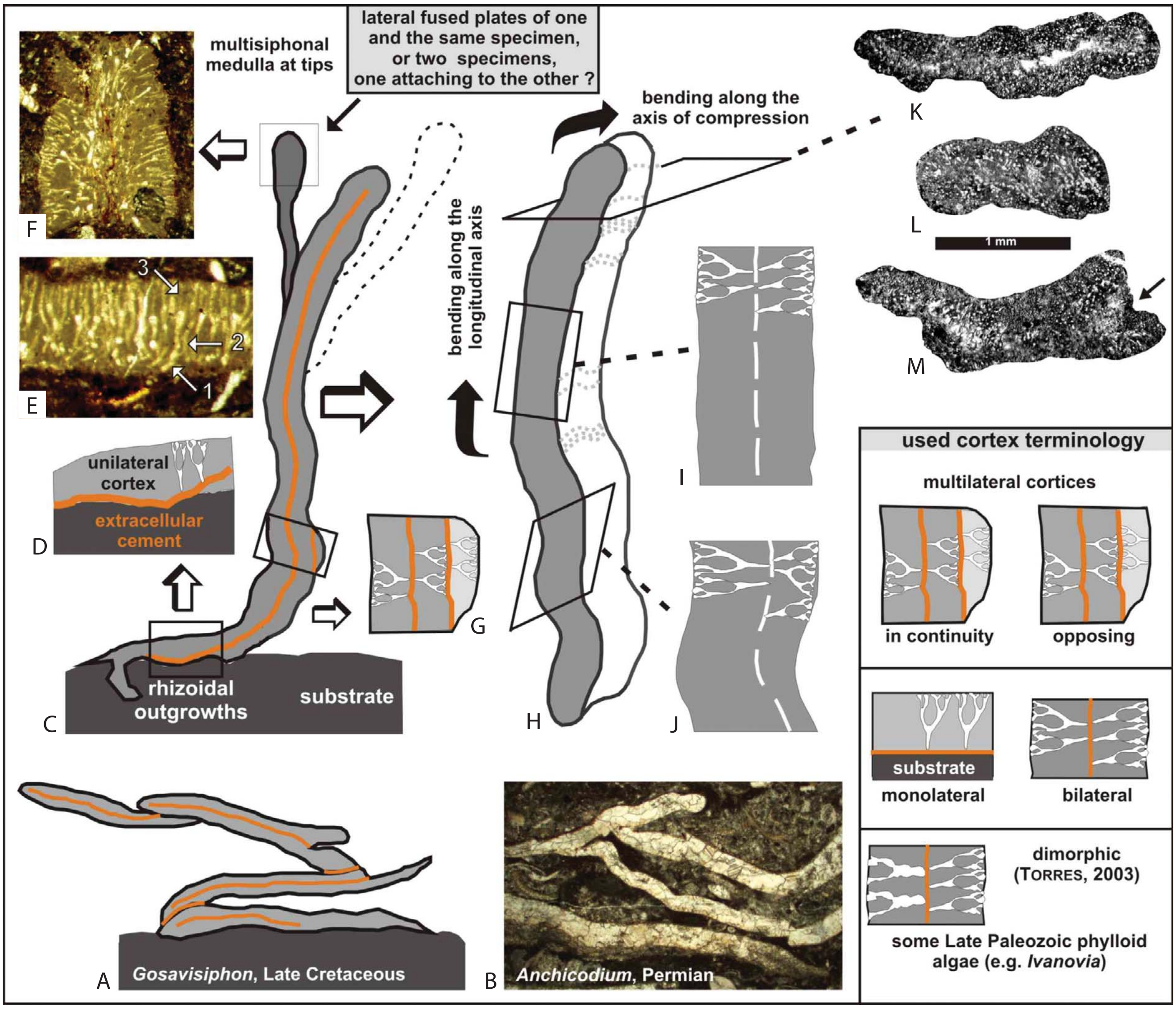

Figure 14: Hypothetical reconstruction, thin-section interpretation of *Gosavisiphon paucimedullaris* (SCHLAGINTWEIT & EBLI) (A, C–M), used cortex nomenclature compared to the Permian *Anchicodium* (B) (explanation in the text). A, C–D, G–J Reconstructions; E) Thin-section showing several series (1–3) of branching filaments in the cortex. F) tip of a plate. K–M Transverse sections of plate, M) with lateral fusion.

meda sp., *Neomeris mokragorensis* RADOIČIĆ & SCHLAGINTWEIT, *Dissocladella? pyriformis* SCHLAGINTWEIT, *Terquemella*? *intermedia* PIA, *Terquemella*? n. sp., *Oroseina pletzachensis* SCHLAGINTWEIT & EBLI, *Thyrsoporella eisenbachensis* SCHLAGINTWEIT & LOBITZER (only at the Eisenbach locality) and benthic foraminifera *Vidalina hispanica* SCHLUMBERGER, quinqueloculinids, cuneolinids, *Tetrataxiella*? *floriformis* SCHLAGINTWEIT & SANDERS, gastropods, ostracods and remains of land plants. Within this facies, fine grains of pyrite may be present within chambers of benthic foraminifera or algal pores. *Gosavisiphon* also occurs in floatstones with debris of rudistids and stromatoporoids (Noth-Klamm, Gams locality). The monotypic assemblage from the tempestite beds within the Santonian Hofergraben Marls, are high-energy accumulations where the plates of *Gosavisiphon* may show parallel arrangement/orientation (Fig. 9A). These tempestites most obviously accumulated some distance from the original low energy habitat of the alga. It is noteworthy, that epibionts or encrustations were never observed on the algal plates of *Gosavisiphon*. The microfacies and the accompanying microfauna and flora account for a sheltered, terrestrially influenced lagoonal setting of presumably nutrient-rich waters, where rudistid biostromes occur in lateral association. The strata containing *Gosavisiphon paucimedullaris* generally follow the basal clastics (conglomerates, breccias, sandstones) of the transgressive Lower Gosau Subgroup.

5. CONCLUSIONS

Halimeda paucimedullaris SCHLAGINTWEIT & EBLI, being a non-segmented platy siphonous green alga, represents the type-species of the so far monospecific new genus *Gosavisiphon*. It represents a pluricentrimetric Cretaceous seaweed (macroalga) that is so far only known from the Upper Cretaceous of the Northern Calcareous Alps. It flourished in soft-bottom, terrigeneous influenced lagoonal environments, attached to biogenic hard substrates. The known stratigraphic range is Middle/Upper Cenomanian to Santonian. For reasons of pragmatism and taxonomic simplification *Gosavisiphon* is tentatively placed in the family Udoteaceae and can be excluded as a candidate for the Halimedaceae. With its membraneous architecture it can generally be compared with the non-systematic 'phylloid algae' with their discontinuous appearance in the Late Palaeozoic (Late Carboniferous–Early, p.p. Late Permian) and Late Triassic (Norian) reefal platform margin deposits. In contrast to Late Palaeozoic aragonitic phylloid algae that were in most cases strongly altered by diagenesis, the specimens of *Gosavisiphon* exhibit many clearly discernible internal features. With these new findings and interpretation, the stratigraphic record of phylloid algae with siphonous internal structures becomes much broader, again witnessing a huge gap in the Jurassic–Lower Cretaceous interval. This offers further possibilites for future discussions, for instance about the phylogeny of the calcareous green algae as some Late Palaeozoic phylloid algae were already compared with a few extant taxa of the Udoteaceae by some palaeontologists.

The findings of ovoid flattened segments of *Halimeda* sp. in the Middle/Late Turonian of the Lower Gosau Subgroup are the oldest records of this morphological type allowing direct comparisons with extant representatives of the genus. So far, comparable segments were not known prior to the Early Tertiary with *Halimeda eocaenica* MORELLET & MORELLET. Middle/Upper Triassic to Early Cretaceous representatives referred to *Halimeda* show cylindrical segments with circular cross sections and can, in my opinion, not be directly compared with extant species of *Halimeda*. This interpretation is completely different from previous assumptions, not accepted by all subsequent workers, that the first appearance of the genus is from the Late Permian. Based on the segment morphology as one of the main important features of fossil representatives, the first *Halimeda* s. str. seems to appear around the Lower/Upper Cretaceous boundary, substantiated by the Turonian findings.

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