Early Norian (Triassic) corals from the Northern Calcareous Alps, Austria, and the intra-Norian faunal turnover

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The first description of early Norian coral fauna from the Northern Calcareous Alps (Dachstein Plateau and Gosaukamm), Austria, is presented: 31 scleractinian species from 24 genera (including three corals not formally determined), and three hexanthiniarian species belonging to two genera. The stratigraphical position of the main part of the fauna discovered in the South Dachstein Plateau at the Feisterscharte is determined by means of the conodont *Epigondolella quadrata* (Lacian 1); single finds are from the horizons with *Epigondolella triangularis* and *Norigondolella navicula* (Lacian 3), and one close to the horizon with *Epigondolella* cf. *multidentata* (Alaunian 1). Rare corals from the Gosaukamm are from the Lacian 1 and Alaunian. Five species are described as new: *Retiophyllia vesicularis*, *Retiophyllia aranea*, *Margarosmilia adhios*, *Hydrasmilia laciana*; one new genus and species from the family Coryphylliidae, *Margarogyra hirsuta*; one new genus and species, *Thamnasterites astreoides*, cannot be assigned to a family. Two hexanthiniarian species, *Pachysolenia cylindrica* and *Pachydendron microthallos*, known exclusively from the Tethyan lower Norian, represent stratigraphically valuable species. A regularly porous coral from the family Microsolenidae, *Eocomoseris*, which up to now has only been known from the Jurassic and Cretaceous, is here identified from the Triassic strata (originally described as *Spongiomorpha* [*Hexastylopsis*] *ramosa*). Predominant taxa show solitary and phaceloid (pseudocolonial) growth forms and an epithecal wall; pennules-bearing corals are common. Carnian genera and genera typical of the Lacian and Lacian–early Alaunian prevail; a hydrozoan genus *Cassianastraea* has also been encountered as well as a scleractiamorph coral, *Furcophyllia septafindens*). The faunal composition contrasts with that of well known late Norian–Rhaetian ones, the difference being observed not only at the generic but also at the family level. The post-early Norian change in coral spectrum documents the turnover of the coral fauna preceding that at the Triassic/Jurassic boundary.

Key words: Scleractinia, Hexanthiniaria, corals, taxonomy, faunal turnover, Norian, Triassic, Alps, Dachstein, Tethys.

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Introduction

The early Norian coral fauna of the Northern Calcareous Alps, Austria, belongs to the end-member of the earliest Mesozoic coral fauna that appeared in the middle Anisian. The first, Anisian phase of its development remains very poorly known due to the scarcity of coral finds. However, the high variability of growth forms and colony types (Bechstädt and Brandner 1970; Scholz 1972; Deng and Kong 1984; Qi and Stanley 1984; Morycowa 1989, Senowbari-Daryan et al. 1993), as well as the microstructural diversity (Roniewicz and Morycowa 1989, 1993), make this fauna from its inception greatly diversified taxonomically at generic and suprageneric levels as well as advanced in colony integration. This shows that Anisian scleractinians were a heterogeneous group with a long pre-Triassic and Early Triassic history that remains completely obscure due to their being then presumably devoid of skeletons (Stanley 2003 and references therein). The antiquity of the Scleractinia is documented by molecular data demonstrating that the basic differentiation of the predecessors of extant coral groups took place in the late Palaeozoic (Romano and Palumbi 1996). Mesozoic Scleractinia were associated with Hexanthiniaria, corals differing from the scleractinians in morphology and microstructure, and considered to be a separate cnidarian order (Montanaro-Gallitelli 1975), earlier classified within Scleractinia as the family Zardinophyllidae Montanaro-Gallitelli, 1975 (= Pachythecaliidae Cuif, 1975). In the early Norian, this group was especially diverse and well distributed in the Tethys.

In the Tethyan palaeoprovince, early Norian coral finds are far fewer than late Norian–Rhaetian ones. The first descriptions of early Norian corals from the 1970s were from the Taurus Mountains, Anatolia, Turkey (Cuif 1975a–c; 1976); stratigraphic data date them as Lacian, *Stikinoceras kerri* Ammonoid Zone (Krystyn in Marcoux et al. 1986: 17). A brief report on some corals from the Southeast Pamir

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Table 1. List of the Early Norian cnidarians from the Dachstein Plateau, with indication of their structural features and distribution; in brackets: related or similar taxa and their distribution. Abbreviations: Corallum: *ast,* astraeoid; *cer,* cerioid; *ph,* phaceloid*; s,* solitary; *th,* thamnasterioid. Micromorphology: *g,* granulation; *m,* menianes; *p,* pennules.

Species	Growth form	Micromorphology	Other occurrences
Anthozoa: order Hexanthiniaria			
Pachysolenia cylindrica	ph	–	early Norian, Taurus, Pamirs
Pachysolenia cf. *cylindrica*	ph?	–	
Pachydendron microthallos	ph	–	early Norian, Taurus, Pamirs
Anthozoa: order Scleractinia			
Volzeia sp.	ph	g	
Cuifia marmorea	s	g	
Noriphyllia dachsteinae	s	g	
Margarogyra hirsuta sp. nov.	th	g	
Distichophyllia sp.	s	g	
Retiophyllia aff. *fenestrata*	ph	g	
[*Retiophyllia fenestrata*]			[Rhaetian, NCA]
Retiophyllia sp.	ph	g	
Retiophyllia aff. *tolminensis*	ph	g	
[*Retiophyllia tolminensis*]			[Carnian, Julian Alps]
Retiophyllia aranea sp. nov.			
Retiophyllia vesicularis sp. nov.	ph	g	
Craspedophyllia? sp.	ph	m	
Margarophyllia cf *capitata*	s	g	
[*Margarophyllia capitata*]			[Carnian, Dolomites]
Margarosmilia nova	ph	g	early Norian, Julian Alps
Margarosmilia adhios sp. nov.	ph	g	
Thamnomargarosmilia aff. *prima*	ph	g	
[*Thamnomargarosmilia prima*]			[early Norian, Pamirs]
Ceriostella aff. *variabilis*	cer	g	
[*Ceriostella variabilis*]			[late Ladinian, North America]
Conophyllia cf. *hellenica*	s	?	
[*Conophyllia hellenica*]			[late Canian–early Norian, Hydra Island]
Conophyllia sp.	ph	p	
Rhopalodendron cf. *juliense*	ph	p	
[*Rhopalodendron juliense*]			[early Norian, Julian Alps]
Cuifastraea sp. 1	th	p-m	
Cuifastraea? sp. 2	th	m	
Tropiphyllum ornatum	s	m	early Norian, Taurus
Thamnasteriamorpha aff. *frechi*	th	m	
[*Thamnasteriamorpha frechi*]			[Carnian, Dolomites]
Guembelastraea aff. *guembeli*	cer	m	
[*Guembelastraea guembeli*]			[Carnian, Dolomites]
Eocomoseris aff. *ramosa*	th	m	
[*Eocomoseris ramosa*]			[Rhaetian, NCA]
Parastreomorpha sp.	th	g g	
Hydrasmilia laciana sp. nov.	ph		
Thamnasterites astreoides gen. et sp. nov.	ast	g?	
Forking coral	ph	?	
Solitary "dwarfish" coral	s	?	
Thick walled- pachythecal-like coral	?	sharp granules	
Hydrozoa: order Lemniscaterina			
Cassianastraea reussi			late Ladinian–Carnian, Dolomites, North America

Mountains, Tajikistan (Melnikova 2001) gave their age as late Carnian–early Norian, and the same interval was assumed for corals from Hydra Island, Greece (Turnšek and Senowbari-Daryan 1994). Descriptions of corals from the Julian Alps of Slovenia (Turnšek and Ramovš 1987, Ramovš and Turnšek 1991) defined their age as early Norian. The descriptions presented herein concern corals from the Northern Calcareous Alps (NCA), Austria, from sites in the southern Dachstein Plateau (Table 1).

The differences in faunal composition between the successive phases of faunal transformations observed in Triassic corals (Roniewicz and Morycowa 1989; Roniewicz 2010) concerned not only genera, but also changes in the proportions of families belonging to the microstructurally heterogeneous order Scleractinia Bourne, 1900 and the microstructurally homogeneous order Hexanthiniaria Montanaro-Gallitelli, 1975, as well as the representation of an informal taxonomic unit, the scleractiniamorphs (Stolarski et al. 2004; Melnikova and Roniewicz 2007). Comparison of early Norian and Late Norian/Rhaetian coral faunas shows their taxonomic distinctness at generic and family levels (Table 2), and demonstrates an intra-Norian turnover in coral history (Roniewicz 2010) foreshadowing the much more extensive turnover at the Rhaetian/Hettangian boundary.

Table 2. Distribution of the scleractinian families in the late Carnian–early Norian (LC–EN), and late Norian–Rhaetian (LN–R) time intervals. Legend: ▬ present families; ■ dominant families; □ families not encountered in the late Norian–Rhaetian strata, but re-appearing in the Jurassic.

	Family	LC-EN ca. 50 genera	LN–R ca. 40 genera
1	Zardinophylliidae	▬	▬
2	Amphiastraeidae	▬	□
3	Volzeiidae	■	
4	Protoheterastraeidae	▬	
5	Coryphylliide	▬	▬
6	Reimaniphylliidae	▬	■
7	Distichoflabellidae		▬
8	Margarophylliidae	■	▬
9	Procyclolitidae		▬
10	Alpinophylliidae		▬
11	Actinastraeidae	▬	▬
12	Conophyllidae	■	
13	Cycliphylliidae (ex Cyclophylliidae)	▬	▬
14	Gablonzeridae	▬	▬
15	Curtoseriidae	▬	▬
16	Cuifastraeidae	▬	■
17	Thamnasteriidae	▬	▬
18	Pamiroseriidae	▬	■
19	Tropiastraeidaea	■	
20	Astreomorphidae	▬	■
21	Microsolenidae	▬	▬
22	Stylophyllidae	▬	■
23	Gigantostylidae		▬
24	Unknown family A	*Hydrasmilia*	
25	Unknown family B	*Thamnasterites*	
26	Unknown family C	Forking coral	
27	Unknown family D	solitary “dwarfish” coral	
28	Furcophylliidae (a scleractiniamorph group)	▬	
	Families in total	24	19

Institutional abbreviations.—GBA, Geologische Bundesanstalt Wien, Austria; MIGWr, Geological Institute, University of Wrocław, Poland; IGD, Insitute of Geology, Tajik Academy of Sciences, Dushanbe, Tajikistan; NHMW, Naturhistorisches Museum Wien, Austria; UMIP, the University of Montana, Missoula, USA; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Material

The collection from the Dachstein Plateau, completed by Harald Lobitzer and Gerhard Mandl in the years 1987–1989 is housed at the Geologische Bundesanstalt Wien (GBA). The material consists of more than 30 samples and 200 thin sections (thin sections are marked with the sample number and a letter). Additionally, some early Norian corals from the neighbouring Gosaukamm range collected by Martin Schauer have been taken into consideration. The material from the Gosaukamm was sent to me for examination by the late Helmuth Zapfe; the collection is housed at the Naturhistorisches Museum Wien (NHMW).

The comparative material, i.e., lower Norian corals from the Taurus Mountains, Anatolia, Turkey, originates from the collections of Jean-Pierre Cuif deposited in the Institute of Paleobiology Polish Academy of Sciences (Warsaw, Poland); the lower Norian corals from North America are from the collections of the University of Missoula (Montana, USA); thin sections from Volz’s collection of Carnian corals are from the University of Wrocław (Poland); the Hettangian–Sinemurian corals from the Pamirs are from the collection of the Geological Institute, Tajik Academy of Sciences (Dushanbe, Tajikistan).

Geological setting

The geological setting and preliminary characteristics of the corals from the Dachstein Plateau and remarks on other coral occurrences of similar age were given in Roniewicz et al. (2007).

The corals were collected by G. Mandl and H. Lobitzer in the vicinity of the Feisterscharte pass in the South Dachstein Plateau (Fig. 1), in majority, at a distance of 50–150 m from the Guttenberg-Hause (Roniewicz et al. 2007). They are contained in compact, light-grey wackestones and pack-

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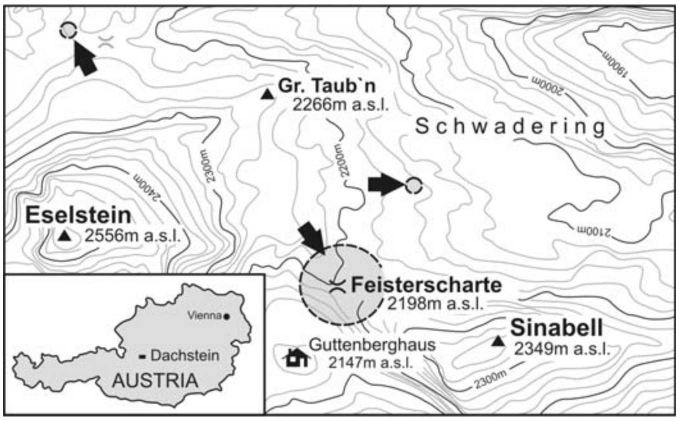

Fig. 1. Southern slopes of the Dachsteinplateau: location of the Feisterscharte pass (N 47°27'10", E 13°41'08") in vicinity of which early Norian corals were sampled. Small circles indicate places of singular finds, and a large circle indicates the area, which yielded the majority of samples.

stones with dissolution voids, and in rudstones/packstones interpreted as reef detritus. Within the rudstones, the corals occur as rounded organodetrital clasts within a detrital matrix; the coral fragments range in size from a few millimetres up to some centimetres. The collection contains large phaceloid coralla with intercorallite space filled with wackestone or fine organodetrital packstone, and complete massive colonies 8–10 cm in diameter. All the skeletons, primarily aragonitic, have been transformed into calcite and deeply recrystallised. Nevertheless, micromorphological features are usually preserved and traces of primary microstructure necessary for taxonomic assignment are sometimes discernible.

Conodont stratigraphy presented by Mandl (in Roniewicz et al. 2007) determined the age of the main part of the fauna as Lacian 1 according to the occurrence of "*Epigondolella primitia*". These conodont specimens have recently been redetermined as *Epigondolella quadrata* Orchard by Krystyn in Krystyn et al. (2009), but the early Lacian age is still valid. Some finds came from the Lacian 3 in the beds above the horizon with *Epigondolella triangularis* and *Norigondolella navicula* (Lacian 2) and one find came from close to the horizon with *E.* cf. *multidentata* (Alaunian 1). The foraminifers examined in thin sections cut from coral samples confirm the early Norian age of the corals (Ebli in Roniewicz et al. 2007). Some Lacian and Alaunian corals are also known from other places in the NCA (Gosaukamm) and some of them have been included herein. The distribution of corals in the lower Norian in the Tethys, among others indicating the stratigraphic value of the Lacian hexanthiniarians (*Pachysolenia cylindrica* Cuif, 1975 and *Pachydendron microthallos* Cuif, 1975), was given in Roniewicz et al. (2007).

Field observations by G. Mandl and H. Lobitzer show that the original coral environment consisted of coral patches in the early Norian of the Dachstein Plateau (Roniewicz et al. 2007), and in the Lacian, coral growth occurred on the margin of the Dachstein platform (Krystyn et al. 2009).

Early Norian corals and their relationships to stratigraphically adjacent faunas

The Norian coral fauna comprises two different assemblages. The early Norian fauna is composed mainly of Carnian genera while, with some exceptions, the middle/late Norian and Norian–Rhaetian faunas lack the Carnian elements. The middle Norian coral fauna has been very poorly documented and in practice remains unrecognisable due to the common lack of a precise stratigraphy of the coral-bearing beds of this age. The only monographic description of early Norian–middle Norian corals concerns the fauna from the Kenkeren Mountain Range in the Koryakia, North East Asia (Melnikova and Byčkov 1986). As far as Alpine and Pamirian coral faunas are concerned, late Norian faunas are similar to the Rhaetian ones exemplified by the Zlambach assemblage (compare Frech 1890, Roniewicz 1989).

Affinity with Carnian fauna

The St. Cassian corals from the Dolomites typify the Carnian coral fauna of the western Tethys (see Volz 1896; Montanaro-Gallitelli 1975; Cuif 1975a–c, 1976, 1977). The most characteristic feature of this fauna is the high proportion of volzeidean corals (*Protoheterastraea* Wells, 1943; *Volzeia* Cuif, 1967; *Margarophyllia* Volz, 1896; *Margarosmilia* Volz, 1896; *Toechastraea* , 1896; *Craspedophyllia*, 1896), other diverse groups of corals with meniane/pennular micromorphology of the septal flanks (*Geumbelastraea* Cuif, 1976; *Stuoresia* Cuif, 1976; *Thamnasteriamorpha* Melnikova, 1996; *Conophyllia* d'Orbigny, 1849 [= *Omphalophyllia* Laube in Volz, 1896]) and others with sharp granulations (*Myriophyllum* Cuif, 1975; *Koilocoenia* Duncan, 1884 (= *Coelocoenia* Volz, 1896); corals determined by Volz (1896) as *Pinacophyllum* Frech, 1890, hexanthiniarian pachythecal corals (*Zardinophyllum* Montanaro-Gallitelli, 1975; *Quenstedtiphyllia* Melnikova, 1975) and rare stylophyllids (*Protostylophyllum* Roniewicz and Michalik, 2002). The assemblages also include the distinctive hydrozoan taxon *Cassianastraea reussi* (Laube, 1865) (see Montanaro-Gallitelli 1980) and *Furcophyllia septafindens* (Volz, 1896) of an unknown systematic affiliation, assigned to an informal scleractiniamorph group of corals (Stolarski et al. 2004). The scleractiniamorphs are a group of corals that are similar to the scleractinian corals, but with features that are alien to Scleractinia. This heterogeneous group has been known up to now from the Palaeozoic (Ezaki 2000 and references therein).

In the Tethys province, the majority of the above-listed Carnian genera have been recorded from the early Norian (Taurus Mountains, Turkey: Cuif 1977 and references therein; Dachstein Plateau, Austria: Table 1 herein; Pamir Mountains, Tajikistan: Melnikova 2001) or from deposits of the late

Carnian–early Norian age (Turnšek and Senowbari-Daryan 1994). So far, only *Koilocoenia*, *Pinacophyllum*, and *Furcophyllia septafindens* were not found, the latter taxon with its inception in the late Ladinian (Melnikova and Roniewicz 2007).

In comparison with the Carnian, the hexanthiniarian corals diversified significantly in the early Norian (*Pachythecalis* Cuif, 1975; *Pachysolenia* Cuif, 1975; *Pachydendron* Cuif, 1975; *Sichuanophyllia* Kong and Zhang, 1985). The newly appeared scleractinian genera *Coryphyllia* Cuif, 1975 and *Thamnomargarosmilia* Melnikova, 1996 are known from the early Norian (Cuif 1975a; Melnikova 2001), and the genus *Hydrasmilia* Turnšek, 1994 ranges from the latest Carnian to the earliest Norian (Turnšek and Senowbari-Daryan 1994) to the early Alaunian. In addition to coral genera known from the Carnian, the hydrozoan *Cassianastraea reussi* (Laube, 1865) has been found (Fig. 8D), a taxon originally described as a Carnian scleractinian coral from the Dolomites (Laube 1865). Recent data extend its stratigraphical and geographical ranges from the late Ladinian of North America (Roniewicz and Stanley 1998) up to the early Norian in the Dachstein Plateau and Taurus Mountains in Turkey (undescribed material, ZPAL collection). It was Montanaro-Gallitelli (1980) who questioned its assignment to the Scleractinia and placed the genus in the newly erected hydrozoan order Lemniscaterina.

The above early Norian faunal pattern is valid for the Dachstein Plateau and Taurus Mountains (compare Cuif 1975a, 1976). It is noteworthy that the coral fauna from the Taurus Mountains was originally considered to be Carnian on the basis of its taxonomic content and occurrence in agglomerations of a Cipit-boulder type (Marcoux and Poisson 1972; Cuif 1975a).

Early Norian versus late Norian–Rhaetian and Early Jurassic corals

In the Tethys and in the Pacific province, late Norian– Rhaetian coral faunas are composed chiefly of extremely diversified Reimaniphylliidae, followed by Procyclolitidae, Pamiroseriidae, Cuifastraeidae, Astraeomorphidae, and Actinastraeidae, associated in the Rhaetian with diverse stylophyllinan corals, i.e., Gigantostyliidae and Stylophyllidae (for comparison, see Melnikova 1975; Stanley 1979; Montanaro-Gallitelli et al. 1979; Roniewicz 1989, 1996). In the Stylophyllidae, intensive radiation resulted in the development of nine mono- and polyspecific genera, compared to only one monospecific genus, *Protostylophyllum*, in the Carnian.

In the Tethyan province, the fauna of the late Norian–Rhaetian differs from that of the early Norian, first in lacking such typical Carnian corals as volzeiids, conophylliids, *Toechastraea* and *Guembelastraea*, and in the reduction of pachythecal corals to a rare relict form (*Zardinophyllum carpathicum* Roniewicz and Michalik, 1998, Rhaetian, Male Karpaty Mountains, Slovakia). In contrast, in the literature concerning North American terranes such a sharp difference is not observed, and the spectrum of early Norian genera seems to be highly "Norian" in character (as observed by Montanaro-Gallitelli et al. 1979: 134). Corals have not been reported from the Carnian of the North American terranes in the eastern Panthalassa Ocean, whereas they are present on the western borders in the Far East (Russia, Sikhote Alin Highlands: Moiseev 1951; Japan Kyushiu and Shikoku Islands: Kanmera 1964 and Okuda et al. 2005, respectively). However all of these sites are tectonically displaced terranes so their exact palaeogeography is unclear.

A surprising discovery in the Triassic faunas, hidden among a heterogeneous group of the Spongiomorphidae, was that of regularly porous corals of the genus *Eocomoseris* Melnikova et al. 1993, identified originally in the Hettangian–Sinemurian of the South East Pamirs, Tajikistan. In the Triassic, beside the considered herein occurrence in the lower Norian of the Dachsteinplateau, this genus was described by Frech (1890) as *Spongiomorpha* (*Heptastylopsis*) from the Rhaetian of the Northern Calcareous Alps.

Corals and extinction events within the LateTriassic

The family-level analyses of marine and terrestial organisms (Sepkoski 1986) show two Late Triassic drops in diversity, the first in the Carnian and the second at the end of the Triassic. The Carnian diversity loss has been interpreted either as an artifact or a real phenomenon (Benton 1986). Palaeontological data show that, beginning with the middle of the Carnian, many groups of marine organisms (ammonites, echinoderms, bivalves, bryozoans, reef organisms, and marine tetrapods), as well as terrestrial plants and vertebrates decreased in diversity or even disappeared (compare Hallam and Wignall 1997). However, the exact timing of the Carnian extinction events has not been accurately determined because of stratigraphic problems and unresolved boundaries.

So far, no indisputable evidence of the intra-Norian extinctions has been reported in the literature. An exception may be that of Ladinian–Carnian bivalve survivors that persisted in lower Norian strata of the Wallowa Terrane in North America (Oregon) and probably disappeared after the early Norian. This highly diversified bivalve fauna was described by Newton et al. (1987). These authors admitted the possibility of intra-Norian extinction, while they neglected the significance of any decrease in bivalve taxa in the Carnian, concluding instead that the Carnian extinction was an artifact caused by disparities in preservation and their bias in the diversity records.

It is intriguing that the early Norian coral fauna in the Wallowa Terrane shows no Carnian taxa known from the

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Tethys (although *Stuoresia*, *Margarastraea* were cited in Stanley and Whalen 1989), and the same applies to other early Norian North American coral faunas (Stanley 1979: *Elysastrea*, *Margarastraea*; Montanaro-Gallitealli et al. 1979: *Thamnasteriamorpha*, *Margarosmilia*, *Margarastraea*, *Guembelastraea*). The illustrations accompanying the descriptions do not show features typical of those genera; the determinations seem to be biased by common coral homeomorphy, or a very poor preservation of silicified specimens. In fact, Montanaro-Gallitelli et al. (1979: 134) admitted, that determinations with the names of Carnian taxa were used provisionally. Recent research on corals from the North American craton (Zonneveld et al. 2007) in late Carnian rocks (*Epigondolella nodosa* Conodont Zone; northeastern British Columbia, Canada) will be helpful in determining the specificity of the coral fauna from East Panthalassa and taxonomical differences between this and Tethyan faunas.

Tethyan corals provide important arguments in the discussion concerning intra-Norian faunal turnover. Late Carnian corals (e.g., those from the Dolomites and Pamirs), together with early Norian ones, mark the first late Triassic diversity peak, biased by the exceptionally well preserved Carnian St. Cassian fauna from the Dolomites. Early Norian diversity was based on many Carnian genera that continued into the Norian. The late Carnian–early Norian peak was markedly augmented by early Norian radiation of the hexanthiniarian and coryphylliid corals and by the beginning of the development of the reimaniphylliids. Taking into account the small number of coral sites, the early Norian shows relatively high diversification of the coral fauna at the generic and suprageneric level. In the most diverse assemblages, the relationship of the number of genera to families was as follows: in the Dachstein Plateau 26 genera from at least 12 families (including unknown genera and unknown families; Tables 1 and 2), and in the Taurus Mountains approximately 24 genera from 10 families. In both regions, volzeioidean corals are the most diverse, being represented by 22 genera from five families. Hexanthiniarian corals are represented by four genera belonging to two families; stylophyllinan corals (present in the Carnian and abundant in the Rhaetian), have not been found in early Norian faunas so far, supposedly for scarce representation in the fauna of this age. The total number of late Carnian–early Norian coral genera exceeds 50.

Within a short period, this fauna was replaced by another of a different composition. This turnover, taking place some time before the late Norian, and was first documented by the disappearance of the Carnian families Volzeiidae and Conophylliidae and a spectacular reduction in the hexanthiniarian corals; secondly, by a burst of radiation in families that were of no importance in the earlier fauna (Reimaniphylliidae, Cuifastraeidae, Pamiroseriidae, Stylophyllidae). The coral radiation in the late Norian–Rhaetian interval marks the second Late Triassic peak, with about 40 coral genera tabulated (Table 2).

A question arises concerning the ecological character of the coral fauna described in this paper: is it of a shallow-water character comparable to that of Recent reef corals, or a fauna from below normal wave base? The fauna is represented by coral fragments of various sizes and degrees of fragmentation embedded in organodetrital limestone (see microfacies descriptions by Mandle in Roniewicz et al. 2007). Its composition of 24 epithecate species of a solitary and subcolonial, phaceloid growth form and only 9 compact, colonial ones (Table 1) precludes provenance from a very shallow water biotope, because this type of skeletal structure is supposed to be non-resistant to highly agitated water (Roniewicz and Stolarski 1999). Extant corals of similar structure are known from depths below the depth range of the shallow-water reefs. A majority of the taxa (Table 1) show septal micromorphology in the form of granulations; only seven, mostly colonial, taxa show plate-like pennules merging into menianes (i.e., flanges on the septal sides, paralleling the distal septal border; both terms: pennules and menianes, introduced by Gill 1967). In the Recent, the former type of micromorphology is known in corals of nearly all shallow-water and deep-water environments, while the latter type (represented by agariciid corals) is confined to the depths from a few tens of meters on the deep slopes of reefs (Chevalier 1987) to below 100 m on the sea floor (Schlichter 1992).

Conclusions

- Early Norian coral faunas of the Tethys (the Northern Calcareous Alps, Hydra Island, Taurus Mountains, Pamir Mountains), contain numerous Carnian genera which can be locally dominant. Similarly, a prolonged duration of Carnian bivalve taxa into the early Norian (*Mojsicovicsites kerri* Zone in Newton et al. 1987; the stratigraphy specified with conodonts as the *Epigondolella primitia* and *Metapolygnathus communisti* zones in Nützel et al. 2003) is observed in the fauna from the North American Wallowa terrane.
- The first Late Triassic diversity drop of coral fauna in post-Kerri time gave the succeeding, largely spread Norian–Rhaetian fauna its specific character, marked by the elimination of Carnian genera and families and the development of families having only a minor importance in Carnian or lower Norian sequences (Table 2). The Hexanthiniaria, non-scleractinian corals typical of the Tethyan early Norian especially, also became reduced, and then, only found in traces in the Rhaetian fauna (Roniewicz and Michalik 1991, 1998). The above mentioned North American bivalve fauna, which crossed the Carnian/Norian boundary, were eliminated during the intra-Norian environmental changes as well.
- The post-Kerri turnover in coral fauna was incomparably less radical than that at the end of the Triassic (Roniewicz and Morycowa 1989, 1993; Roniewicz 2010). The changes observed on the familial level signal a dramatic turnover in this fauna (Table 2), but the losses and recoveries on the generic level cannot be presented in exact numbers until a revision of Late Triassic coral fauna is more advanced.

- Thanks to the wide geographical distribution and a stratigraphic range restricted to the early Norian Lacian, two readily determinable hexanthiniarian corals, pachythecal *Pachysolenia cylindrica* and *Pachydendron microthallos,* might be chosen as guide fossils for the early Norian. From the formal point of view, these taxa do not satisfy the requirements of classic index fossils, as the upper limit of their occurrence, marking a faunal crisis of unknown palaeogeographical range, can be fixed either at the early/middle Norian boundary, or within the middle Norian, while the lower boundary may be biased by insufficient sampling caused by the scarcity of coral finds in the late Carnian. In any case, they both can serve as rare examples of well identifiable guide fossils for the Lacian within the coral facies in the Tethys (see also herein remarks on *Pachydendron microthallos*).
- Carnian corals are known from the western boundary of the Panthalassa Ocean in the Far East of Asia and in Japan, while they are absent from the North American terranes. However, on the North American craton, in northeastern British Columbia, Canada, a diversified late Carnian fauna has been recorded (Zonneveld et al. 2007).
- The faunas of late Norian–Rhaetian type from the Tethyan Province and that of the early Norian–Rhaetian of the Pacific Province, both devoid of Carnian genera, have some common elements (compare Stanley 1979; Montanaro-Gallitelli et al. 1979), although not so numerous as might appear from simple comparisons of faunal lists. This will provide the basis for a renewed discussion on Late Triassic coral migrations initiated in the 1980s (e.g., Stanley 1988; Stanley and Whalen 1989), suggested tectonic movement of terranes as a medium of coral dispersion versus long distance dispersal. However, before new discussions are initiated, taxonomic revisions are needed, especially of early Norian Triassic corals.
- The corals studied constitute, in general, a shallow water fauna, albeit one that developed below normal wave base. In the growth forms represented, this fauna is not comparable with Recent reefal corals from highly agitated water. The term "reefal" can be applied here only in a very broad sense in that the Dachstein corals, on the basis of the demonstrable zooxanthellate nature of Late Triassic corals in general (Stanley and Swart 1995), are inferred to have lived in the photic zone. Meniane-bearing thamnasterioid taxa, mixed with much more numerous corals having septa covered with granulations may also be indicative of considerable depths similar to those occupied by extant *Agaricia* from the deep reef slopes.

Systematic palaeontology

Abbreviations.—c-c, distance between calicular axes; d, corallum diameter; D, colony diameter; dl, diameter of calicular lumen; dtr, diameter of trabecula mesured in radial direction; ed, density of endotheca, number of dissepiments per mm; f, length of calicular fossa; lt, lateral thorns per mm; md, density of menianes, number of menianes counted in longitudinal section; s, number of septa; S1 ... Sn, septa of succeeding size orders; sd, septal density (number of septa per mm, measured directly at the calicular rim); td, density of tabular endotheca, number of tabulae per mm.

Class Anthozoa Ehrenberg, 1834

Order Hexanthiniaria Montanaro-Gallitelli, 1975

Family Zardinophyllidae Montanaro-Gallitelli, 1975

Genus *Pachysolenia* Cuif, 1975

Type species: *Pachysolenia cylindrica* Cuif, 1975, early Norian, Taurus Mountains, Turkey.

Pachysolenia cylindrica Cuif, 1975

Fig. 2A.

1975 *Pachysolenia cylindrica* sp. nov.; Cuif 1975b: 174, text-figs. 8, 9, pl. 14: 4, 5.

1986 *Pachysolenia cylindrica* Cuif, 1975; Melnikova 1986: 87, pl. 20: 2, pl. 21: 2.

2007 *Pachysolenia cylindrica* Cuif, 1975; Roniewicz et al. 2007: 588, pl. 3: 1, 2.

Material.—GBA 2007/152/1, a fragment of a dense, phaceloid corallum; isolated corralites in thin sections from the specimens GBA 2009/019/4, 2009/019/3.

Measurements (in mm):

GBA	d	dl	s in calices filled with calcite	ed/3	Remarks
2007/152/1	7–9	3–4	12 (6S1+6S1) not observable due to recrystallization	3	adult
2009/019/3	4.5–5	2.5–3		–	early stage
2009/019/4	3.5–4	2.5		–	early stage

Remarks.—In the corallites from the above three samples, all with lumen filled with blocky calcite, only the longest septa (S1 and S2) may be observed, the others being destroyed. In contrast to the image suggesting a thick-septal skeleton presented in Fig. $2A_3$, the S1 and S2 septa were originally very thin, and only secondarily became covered during diagenesis by a film of calcite crystals of small size that partially enhanced their shape. The calices are tube-like, and devoid of septa. In the calices filled with sediment, the internal surface shows sharp tips of the modules producing the pachythecal wall (compare Roniewicz and Stolarski 1999).

Stratigraphic and geographic range.—Austria: Northern Calcareous Alps, Dachstein Plateau, 50 m north of Feisterscharte, lower Norian, *Epigondolella quadrata* Conodont Zone. Turkey: Taurus Mountains, Alakir Çay Valley, *Stikinoceras kerri* Ammonoid Zone. Tajikistan: SE Pamirs, Djilgakochusu Valley, Shaimak svite, upper Carnian–lower Norian.

Pachysolenia cf. *cylindrica* Cuif, 1975

Fig. 2B.

2007 *Pachysolenia* cf. *cylindrica* Cuif, 1975; Roniewicz et al. 2007: pl. 5: 1.

Material.—A fragment of corallite in organodetrital limestone GBA 2007/152/3, with thin section.

doi:10.4202/app.2009.0092

Measurements (in mm):

d	dl	s	Remarks
8×10	4×5	8S1+8S2+16S3	adult

Remarks.—Multiseptal coral that may represent either an aberrant form of *P. cylindrica* or a separate multiseptal taxon.

Stratigraphic and geographic range.—Austria: Northern Calcareous Alps, Dachstein Plateau, 50 m north of Feisterscharte, lower Norian, *Epigondolella quadrata* Conodont Zone.

Genus *Pachydendron* Cuif, 1975

Type species: *Pachydendron microthallos* Cuif, 1975, early Norian, Taurus Mountains, Turkey.

Pachydendron microthallos Cuif, 1975

Fig. 2C, D.

1975 *Pachydendron microthallos* Cuif, 1975; Cuif 1975b: 169, text-figs 5–7, pl. 14: 2.
1986 *Pachydendron microthallos* Cuif, 1975; Melnikova 1986: 88, pl. 20: 3, 4.
1987 *Pachydendron microthallos* Cuif, 1975; Turnšek and Ramovš 1987: 37, pl. 7: 3, 4.
2007 *Pachydendron microthallos* Cuif, 1975; Roniewicz et al. 2007: 590, pl. 4: 1.

Material.—Two fragments of large phaceloid coralla with numerous corallites: GBA 2007/152/2 and 2009/019/1, single corallites in thin sections from the specimens GBA 2009/019/2, 2009/019/3, 2009/019/4, and 2009/019/5.

Measurements (in mm):

d	dl	s	td/2.5	Remarks
0.8-1.3	–	6S1	–	early stage
2.0–3.0	1.0–1.25	6S1+6S2+nS3/4	6	adult stage

Remarks.—The indication of the Upper Norian/Rhaetian as the stratigraphical position of this species in the Northern Julian Alps (Turnšek and Ramovš 1987) needs verification, because none of the well identified early Norian species are known in the late Norian; early Norian genera related to *Pachydendron* (*Pachythecalis*, *Pachysolenia*) are restricted to the early Norian.

Stratigraphic and geographic range.—Austria: Northern Calcareous Alps, Dachstein Plateau, north of Feisterscharte, lower Norian, *Epigondolella quadrata* Conodont Zone. Turkey: Taurus Mts, Alakir Çay: *Stikinoceras kerri* Ammonoid Zone. Tajikistan: SE Pamirs, Shindy Say Valley and Djilgakochusu Valley, Shaimak svite, upper Carnian–lower Norian. Slovenia: Northern Julian Alps: upper Norian/Rhaetian.

Order Scleractinia Bourne, 1900

Family Volzeiidae Melnikova, 1974

Genus *Volzeia* Cuif, 1967

Type species: *Thecosmilia badiotica* Volz, 1896, Carnian, Dolomites, Italy.

Volzeia sp.

Fig. 3G.

Material.—GBA 1995/2/1/2 and 2009/019/6, with thin sections.

Measurements (in mm):

GBA	d	s	sd/1	ed/3
2009/019/6	6.0×7.0	38 (9S1+9S2+16S3+4S4)	3	5–6
	6.0×9.0	e.40		
	7.0×10.0	32 (8S1+8S2+16S3)		
	10.0	e.47		
1995/2/1/2	7×9	e.45	3 (4)	–
	7	e.48		

Description.—Wedge-like septa firmly fused with the wall, differentiated into four size orders. The S1 septa reaching the axis, S4 septa rare, short and thin. Lateral septal granules scattered, protruding. Dissepiments numerous and large, inclined axialward. Wall thin and firm (never abraded in the material examined). Division subequal.

Remarks.—*Volzeia* sp. resembles the coral described as *V. badiotica* (Volz, 1896) from the Carnian of Slovenia (Turnšek et al. 1982: pl. 3: 4, 5; Ramovš and Turnšek 1984: pl. 8: 1). Both forms differ from the late Carnian *V. badiotica* in the low number of septa and insignificant septal ornamentation. In the collection (organodetritic sample GBA 2009/019/29), another poorly identifiable phaceloid coral is present which has been determined as *Volzeia*? sp. for the traces of microstructure in the form of a wavy or straight midseptal line.

Stratigraphic and geographic range.—Austria: Northern Calcareous Alps, Dachstein Plateau, north of Feisterscharte, lower Norian *Epigondolella quadrata* Conodont Zone.

Family Coryphylliidae Beauvais, 1981 emended by Roniewicz and Stanley, 2009

Supplementary to the original diagnosis.—Septal stereome composed of thin fibre bundles with tips manifested on the septal surface as sharp and dense granules, thinner and much denser than lateral granules of the Margarophylliidae and Reimaniphylliidae; wall of a complex septal-epithecal structure.

Remarks on the family Coryphylliidae.—In the family Coryphylliidae, the adaptive radiation resulted in development of a number of genera with a solitary corallum (*Coryphyllia*, *Noriphyllia*, *Cuifia*, *Coryphyllina*). The family is based on their simple septal microstructure, i.e., thin, straight midseptal zone associated with thick lateral stereome; the differences in relations between septa and epithecal wall appear taxonomically significant (Roniewicz and Stanley 2009: fig. 2a–g, comparison of the wall structure). The fourth solitary coral, *Coryphyllina* Roniewicz, 1996, has a position aside the above enumerated core taxa, due to partitioning of the midseptal zone which resulted in decomposing the septal blade at the internal septal border into projections producing a papillar columella (Roniewicz 1996: pl. 5: 1d). Speciation in this group of genera produced one to three species per genus. The most spectacular species are known for their large and tall, columnar coralla which attained diameters of up to 100 mm and over 100 mm

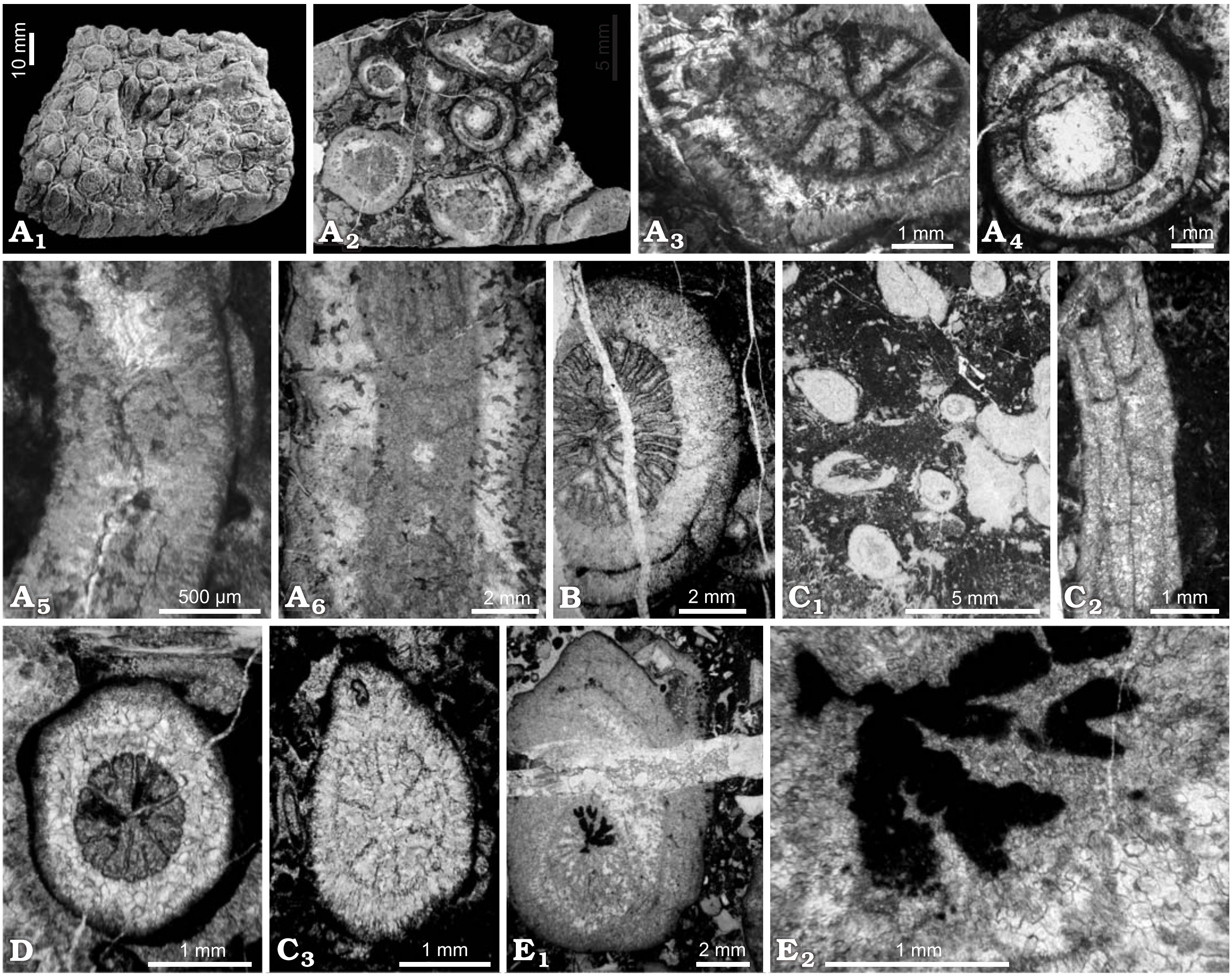

Fig. 2. Hexanthiniarian corals from vicinity of Feisterscharte, Austria, early Norian, Triassic. **A**. *Pachysolenia cylindrica* Cuif, 1975; GBA 2007/152/1. A fragment of phaceloid corallum in upper view (A_1); transverse section (A_2); a corallite with septa thickened by a cover of fine crystals (A_3); a tube-like, distal part of the calice with a thick pachythecal wall (A_4); a magnified fragment showing modular structure of the pachythecal wall with internal wall surface longitudinally sculptured with minute ridges at left (A_5); a corallite in longitudinal section showing a thick wall and thin, rare tabulae (A_6). **B**. *Pachysolenia* cf. *cylindrica* Cuif, 1975; GBA 2007/152/3. Transverse section of the corallite with abundant septa. **C**, **D**. *Pachydendron microthallos* Cuif, 1975. **C**. GBA 2007/152/2. Corallum in transverse section (C_1); corallite with rare tabulae in longitudinal section (C_2); and a corallite (C_3) with traces of microstructure in the wall with lumen filled by coarse calcite crystals. **D**. GBA 2009/019/3. Corallite with recrystallised wall, transverse section. **E**. Indetermined solitary hexanthiniarian coral?; GBA 2009/019/12. Thick-walled pachythecal-like coral in transverse section (E_1), and its fragment (E_2) showing septa with sharp ornamentation.

in height (e.g., Rhaetian *Cuifia gigantella* Melnikova, 1975, Norian *Cuifia marmorea* (Frech, 1890).

Early Jurassic genus *Axotrochus* Beauvais, 1986 was included to the family Coryphylliidae, but a solid, lense-like columella and a very thick wall of a non-precised microstructure, preclude this assignement.

Genera included.—Solitary *Coryphyllia* Cuif, 1975, *Cuifia* Melnikova, 1975, *Coryphyllina* Roniewicz, 1996, *Noriphyllia* Roniewicz and Stanley, 2009; phaceloid *Paracuifia* Melnikova, 2001; astraeoid *Palaeastraea* Kühn, 1936; kuhnastreoid *Kuhnastraea* Cuif, 1976; thamnasterioid *Margarogyra* gen. nov. and *Alakiria* Cuif, 1976.

Genus *Cuifia* Melnikova, 1975

Type species: *Cuifia gigantella* Melnikova, 1975, Norian–Rhaetian, SE Pamirs, Tajikistan.

Cuifia marmorea (Frech, 1890)

Fig. 3F.

1890 *Montlivaltia marmorea* sp. nov.; Frech 1890: 41, pl. 11: 6, 6a.

1996 *Cuifia marmorea* (Frech, 1890); Roniewicz 1996: 15, pl. 1: 1–3; pl. 2: 1–3; pl. 4: 3.

Material.—Fragmentary corallum GBA 1995/2/1/1, and fragments in organodetritic limestone GBA 2009/019/4, thin sections.

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Measurements (in mm):

GBA	d	s
1995/2/1/1	40–50 (shorter diameter)	e. 150 (S1–S5)

Remarks.—In organodetritic limestone GBA 2009/019/5, a corallum with diameter of ca. 10×16 mm and a wall structure typical of genus *Cuifia* is present which may represent a juvenile stage of an unidentified species of this genus.

Stratigraphic and geographic range.—Austria: Northern Calcareous Alps, Dachstein Plateau, north of Feisterscharte: lower Norian, *Epigondolella quadrata* Conodont Zone; vicinity of Altaussee: Volz 1896 indicates the *Pinacoceras–Arcestes* Ammonoid Zone; Gosaukamm: Sevatian/Lower Rhaetian? (found in the scree).

Genus *Noriphyllia* Roniewicz and Stanley, 2009

Type species: *Noriphyllia anatoliensis* Roniewicz and Stanley, 2009, early Norian, Taurus Mountains, Turkey.

Noriphyllia dachsteinae Roniewicz and Stanley, 2009

Fig. 3A.

2009 *Noriphyllia dachsteinae*; Roniewicz and Stanley 2009: 474, pl. 1: G, H.

Material: Fragmentary coralla GBA 2009/019/12 and 2009/019/7, with thin sections.

Measurements (in mm):

GBA	d	s	sd/3
2009/019/12	18×20	ca. 100 (16S1+16S2+3S31+n S4/5)	6

Remarks.—The most typical features of this coral are: solitary growth form; narrow calicular pit; septa of lower three orders subequal in thickness; dense granulation of septal faces composed of small, pointed granules; abundant dissepiments; thick wall of epithecal-septal structure.

Stratigraphic and geographic range.—Austria: Northern Calcareous Alps, Dachstein Plateau, north of Feisterscharte, lower Norian, *Epigondolella quadrata* Conodont Zone.

Genus *Margarogyra* nov.

Type species: *Margarogyra hirsuta* sp. nov., type and only species; see below.

Diagnosis.—Thamnasterioid coral with circumoral budding. Septa built of long, well delimited fibre portions that emerge on septal faces as densely packed, sharply-ended granules. The highest order septa are vertically discontinuous. Dissepiments vesicular, abundant.

Comparisons.—In its septal microstructure based on thin trabecular elements observable at the internal border of the S4 septa, and in the densely packed thin stereomal fascicles that form the majority of the septal blades, the genus thus resembles the solitary *Noriphyllia* (compare Roniewicz and Stanley 2009).

In thamnasterioid relationships of corallites and in corallite dimensions the new genus is similar to the genus *Campesteria* Caruthers and Stanley, 2008. However, the distal borders of the S1 septa of *Campesteria prolixia* bear thick granulations that are especially clearly seen in the specimen UMIP 26953 in Carruthers and Stanley (2008: fig. 6: 1, at lower right corner). This micromorphological feature, indicating a thick-trabecular and not a thin-trabecular, coryphylliid microstructure, has not been observed in *Margarogyra hirsuta* nor in any coryphylliid coral.

Margarogyra hirsuta sp. nov.

Fig. 3B–D.

Etymology: From Latin *hirsuta,* hairy, rough; from the rough surface of the septa.

Type series: Holotype: GBA 2009/019/9, with thin sections; paratypes: 2009/019/3, 8–10, with thin sections.

Type locality: Austria, Northern Calcareous Alps, southern Dachstein Plateau, site ca. 50 m north-west of Feisterscharte.

Type horizon: Norian, Lacian 1, *Epigondolella quadrata* Conodont Zone; light-grey organodetritic limestones.

Diagnosis.—Coryphylliid with circumoral budding. Central corallite large, with up to 90 septa, encircled by smaller corallites with up to 40 septa. Septa thin adaxially, moderately enlarged peripherally; the S1–S2 septa distally thick, with distal border rounded.

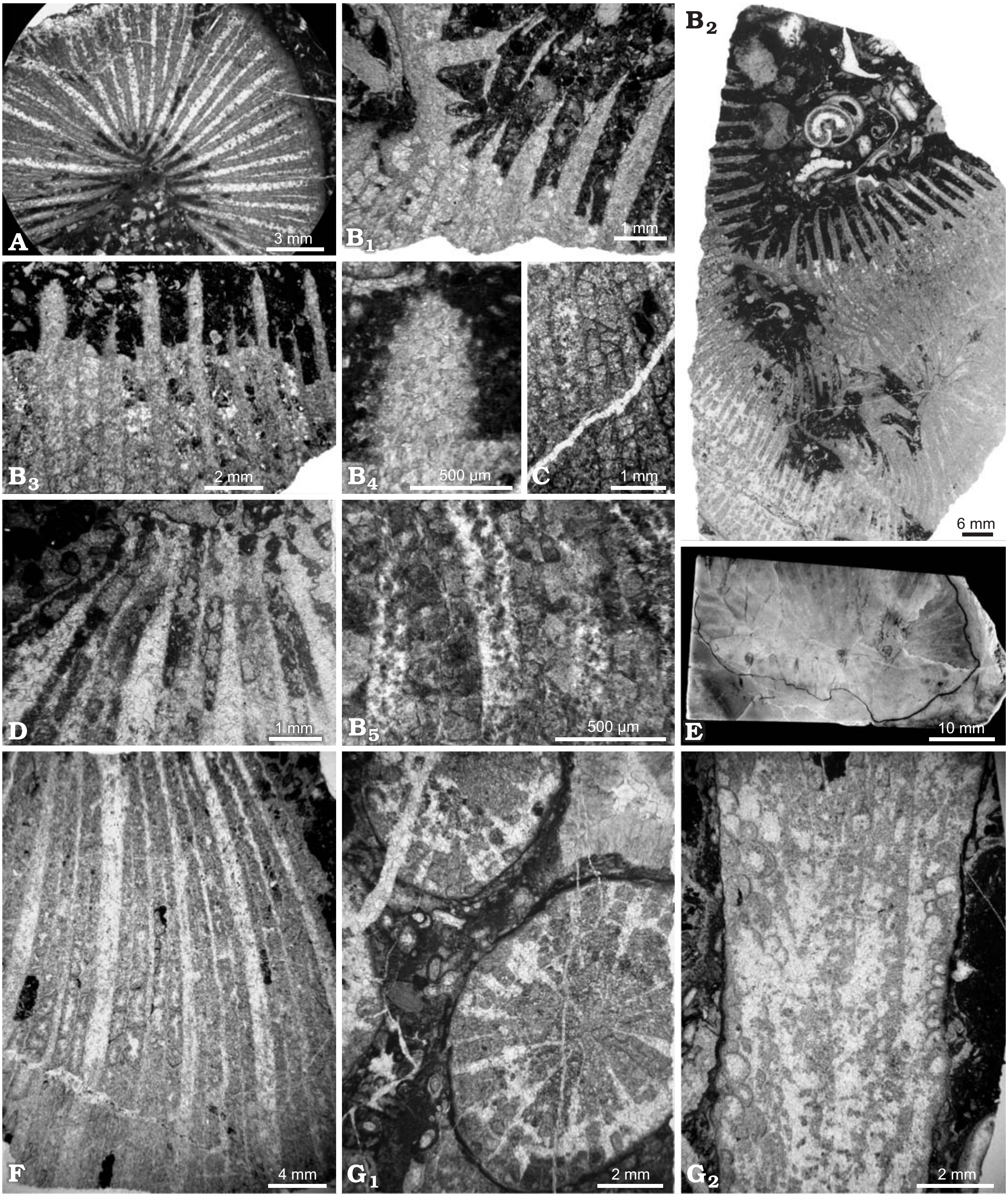
Material.—The type series (see above) and fragments in detritic limestone GBA 2009/019/4, 5, and 17, all with thin sections.

Measurements (in mm):

GBA	D (colony)	d		s		sd/5
		central calice	other calices	central calice	other calices	
2009/019/9	60–80	ca. 40		90		11–13
			20		38, 40	11–12
			6		15	

Description.—Colonies fungiform, with flat upper surface and a short, monocalicular trunk (GBA 2009/019/17). Circumoral budding with lamellar linkages; central corallite (or 2–3 corallites) large, other corallites far smaller, unequal in diameter, more or less parallelling the colony margin. New individuals initiated by division of calices, or through interruption of septa of adult corallites. Central corallite oval, multiseptal (GBA 2009/ 019/9); other corallites regularly radial, with a small number of septa. Axial pits circular and small. The distance between the central and the nearest corallites 12 to 23 mm (GBA 2009/019/3); the distance between the corallites outside the central one is

Fig. 3. Coryphyllid, reimaniphylliid, and volzeiid scleractinian corals from vicinity of Feisterscharte, Austria, early Norian, Triassic. **A**. *Noriphyllia dachsteinae* Roniewicz and Stanley, 2009; GBA 2009/019/12. Distal part of the calice, holotype corallum in transverse section. **B–D**. *Margarogyra hirsuta* gen. et sp. nov. **B**. Holotype GBA 2009/019/9. A colony in transverse section showing a fragment with budding corallite (B$_1$) on the peripheral part of the central corallite (B$_2$); distal part of colony in longitudinal section showing different height of septa of different size orders (B$_3$) and granulation of the distal →



septal border (B_4); traces of septal microstructure in transverse section (B_5). **C**. GBA 2009/019/3 f. Transverse section of colony with numerous thin-walled dissepiments in the interseptal space. **D**. GBA 2009/019/10 b. Fragment of calice in transverse section near to the axial part showing irregular granulation of septal sides. **E**. *Distichophyllia* sp.; GBA 2009/019/7. Polished section of a damaged specimen. **F**. *Cuifia marmorea* (Frech,1890); GBA 2009/019/4e. Fragment of corallum in transverse section showing septa strongly differentiated in size orders. **G**. *Volzeia* sp.; GBA 2009/019/6 a and 6 e, respectively. Phaceloid corallum in transverse (G_1) and longitudinal (G_2) sections. Note thin, but resistant wall and abundant dissepiments.

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from 10 to15 mm. Septal apparatus composed of septa from two to four size orders: (i) in large corallites, the S1septa are thick (up to 1 mm) and approaching the axis, the S2 septa thinner adaxially and shorter than the S1septa, the S3 septa very thin and short, the S4 septa extremely thin (50–75 μm), low, and appearing irregularly; (ii) in small, regular corallites, only thick and long S1 septa and short S2 septa are observed; (iii) in calices at the colony rim, the S4 septa are developed in some systems. The S3 septa and S4 septa are zigzag and very thin in comparison with the S1 septa. Distally, the S1–S2 septa, subequal in height, have thick, rounded margins; the S3 septa and S4 septa are of a conspicuously smaller height. The adaxial part of the septa is thin, zigzag, and covered with sharp, rather rare granulations; more peripherally the blades become thick and their faces are covered with densely crowded, uniform, sharp granules (5–6 per 1 mm in transverse section). Endotheca built of small vesiculae.

Microstructure. The thinnest parts of the S3 septa and S4 septa show well individualised and thin fibre portions diverging from the septal plane. Their nature, either thin-trabecular or only fascicular, could not be recognised, but such an arrangement closely resembles that observed in some margarophylliid septa where the lateral offsets of thin trabeculae diverge from the midseptal plane. The diverging elements of 50–75 μm are thinner than those in margarophylliid septa. The original structure of the fibre portions has not been examined due to recrystallisation; however, in the related *Noriphyllia anatoliensis*, a relatively well preserved skeleton (Roniewicz and Stanley 2009; Fig. 3A–C) shows fascicular fibre portions, some with a faintly marked axis of fibre orientation.

Stratigraphic and geographic range.—As for the type specimens.

Family Reimaniphyllidae Melnikova, 1974

Genus *Distichophyllia* Cuif, 1975

Type species: *Montlivaltia norica* Frech, 1890, Rhaetian, Northern Calcareous, Alps, Austria.

Distichophyllia sp.

Fig. 3E.

Material.—Polished corallum GBA 2009/019/7.

Measurements (in mm):

d	f
e. 40×50	ca. 13

Remarks.—Corallum oval in transverse section, with a long and narrow axial fissure. Septa fusiform with a zigzag midline typical of *Distichophyllia*. The corallum is strongly damaged.

Stratigraphic and geographic range.—Austria: Northern Calcareous Alps, Dachstein Plateau, north of Feisterscharte, lower Norian, *Epigondolella quadrata* Conodont Zone.

Genus *Retiophyllia* Cuif, 1967

Type species: *Retiophyllia frechi* nom. nov. Roniewicz, 1989 (*Thecosmilia fenestrata* sensu Frech, 1890 non Reuss, 1854) Rhaetian, Northern Calcareous, Alps, Austria.

Remarks.—The species assigned herein to *Retiophyllia* represent a wide spectrum of septal and endothecal morphologies. Four of them resemble Rhaetian corals from the *fenestrata*-, *norica*-, and *multiramis*-groups. The fifth species, *R. vesicularis* sp. nov., differs from all other species in having a small number of septa and convex axial dissepiments.

Retiophyllia aff. *fenestrata* (Reuss, 1854)

Fig. 4C.

Material.—A fragment of phaceloid corallum GBA 2009/019/11, with thin sections.

Measurements (in mm):

d	s	sd/1	ed/3
6	36 (9S1+9S2+18S3)	3–4	4

Remarks.—This early Norian coral is similar to the Rhaetian *Calamophyllia fenestrata* Reuss (1854: 105, pl. 5: 20 non 21), which was revised and assigned to the genus *Retiophyllia* Cuif by Roniewicz (1989: 59, pl. 9: 6; pl. 10: 1; pl. 13: 1, see also for synonymy). It has the corallite dimensions of adult *R. fenestrata* but shows septa differentiated into three orders only as seen in juvenile specimens of the species from Fischerwiese and the vicinity of the Gosaukamm (Kesselwand).

Stratigraphic and geographic range.—Austria: Northern Calcareous Alps, Dachstein Plateau, north of Feisterscharte, lower Norian, *Epigondolella quadrata* Conodont Zone.

Retiophyllia sp.

Fig. 4A.

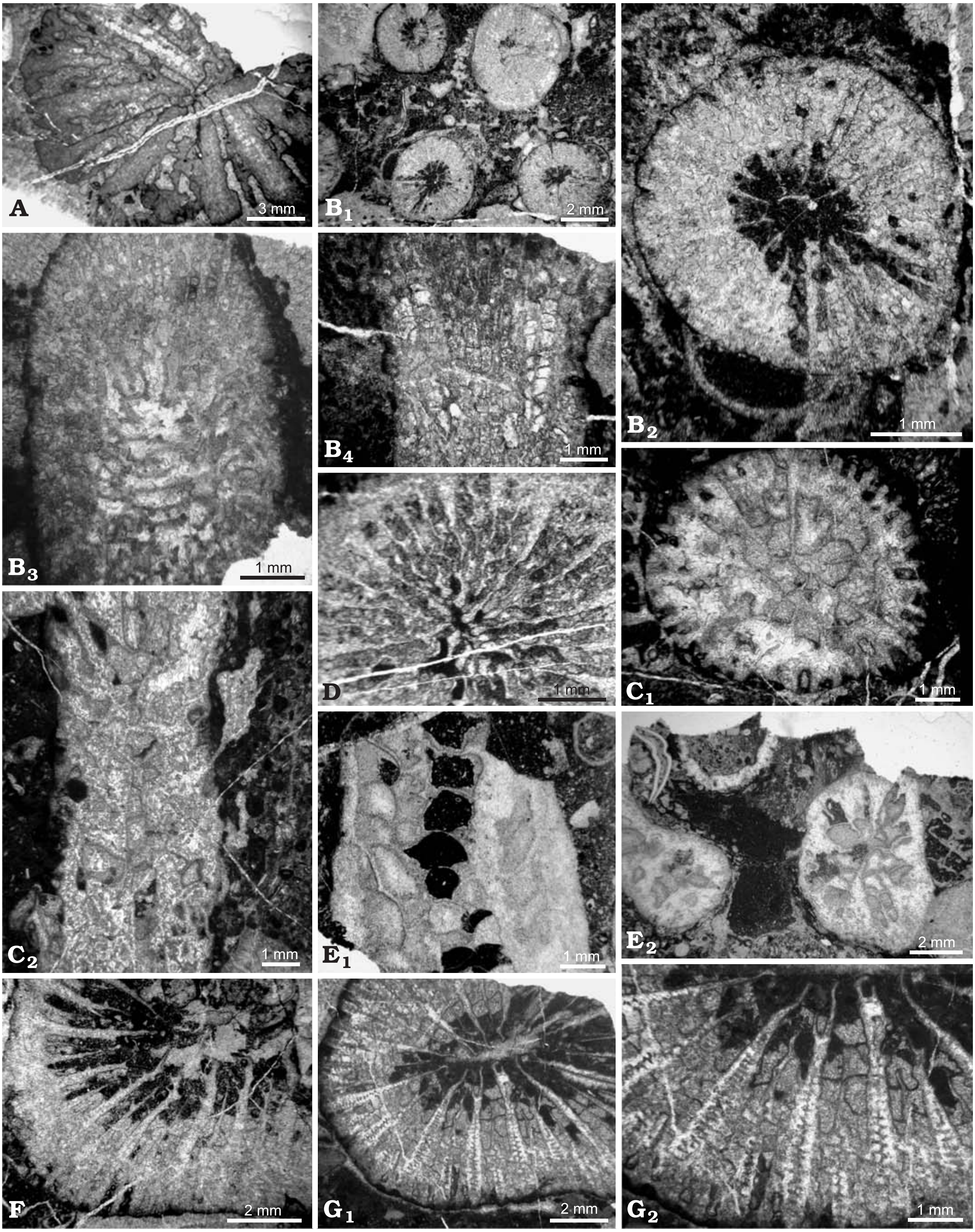
Material.—GBA 2009/019/4, a corallum fragment in organodetrital limestone, with thin section.

Measurements (in mm):

d	s
e.20	ca.35

Remarks.—The coral resembles *Retiophyllia robusta* Ronie-

Fig. 4. Reimaniphylliid corals from vicinity of Feisterscharte, Austria, early Norian, Triassic. **A**. *Retiophyllia* sp.; GBA 2009/019/4g. Septal apparatus with thick S1 septa, transverse section. **B**. *Retiophyllia aranea* sp. nov.; GBA 2009/019/14. corallites circular in section (B_1) with a large axial space (B_2); longitudinal/oblique section (B_3) showing sub-horizontal, large dissepiments in the axial space, and longitudinal section of distal part of the corallite (B_4) showing convex dissepiments at the periphery. **C**. *Retiophyllia* aff. *fenestrata* (Reuss, 1854); GBA 2009/019/11a, b. Corallites in transverse (C_1) and longitudinal (C_2) sections showing small number of septa and large dissepiments. **D**. *Retiophyllia* aff. *tolminensis* Turnšek, 1987; GBA 2007/152/3f. Corallite in transverse section showing zigzag septa. **E**. *Retiophyllia vesicularis* sp. nov.; GBA 2009/019/12g, c. Corallites in longitudinal (E_1) and transverse (E_2) sections; note large and convex dissepiments and irregular shape of septa. **F–G**. *Craspedophyllia*? sp. **F**. GBA 2009/019/16b; transverse sections with corallites showing rare, obliquely directed menianes. **G**. Zigzag traces of septal microstructure; GBA 2009/019/17a (G_1), GBA 2009/019/17b (G_2). →



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wicz, 1989 from the Rhaetian Zlambach Beds in its elongated calicular fossa, and robust septa of four size orders. Twelve thick septa reach the fossa, with the six S1 septa thicker than the S2 septa. The zigzag midline is well marked. Dissepiments are rare.

Stratigraphic and geographic range.—Austria: Northern Calcareous Alps, Dachstein Plateau: north of Feisterscharte, lower Norian, *Epigondolella quadrata* Conodont Zone.

Retiophyllia aff. *tolminensis* Turnšek, 1987

Fig. 4D.

Material.—GBA 2009/019/3, a fragment of corallite in detrital limestone, with thin section.

Measurements (in mm):

d	s
6	<40 (8S1+S2+S3+S4)

Description.—Calices with a narrow, elongated axial fossa. Radial elements thin, differentiated into four size orders. Costal parts coalesced into a stereozonal wall of an obscure structure. The S1 septa approaching the fossa, the S2 septa shorter or subequal to the S1 septa, the S3 septa ca. three-fifths of the S1 septa in length, the S4 septa variable in length or lacking. In transverse sections, the course of the radial elements is zigzag, and granulations are located at the protruding points of the zigzag line of septa.

Remarks.—The coral has a distinctive shape and septal ornamentation. It is close to the late Carnian–early Norian *R. tolminensis* Turnšek, 1987 from Perbla, Slovenia (Turnšek et al. 1987: 44, pl. 2: 1–4, pl. 3: 1, 2, without synonymy). The Dachstein taxon and *R. tolminensis* are related to each other; their conspecificity, however, cannot be proven from the limited Dachstein material available.

Stratigraphic and geographic range.—Austria: Northern Calcareous Alps, Dachstein Plateau, north of Feisterscharte, lower Norian, *Epigondolella quadrata* Conodont Zone.

Retiophyllia aranea sp. nov.

Fig. 4B.

Etymology: From Latin *aranea*, spider; referring to the thin plot of the skeletal elements.

Holotype: GBA 2009/019/14 with thin sections.

Type locality: Austria, Northern Calcareous Alps, southern Dachstein Plateau, site ca. 50 m north-west of Feisterscharte.

Type horizon: Norian, Lacian 1, *Epigondolella quadrata* Conodont Zone; light-grey Dachstein limestones.

Diagnosis.—*Retiophyllia* with about 50 septa at a diameter of 4 mm, flat calicular floor, and relatively large peripheral dissepiments.

Comparison.—The species differs from the congeneric species in thin, numerous septa at a small corallite diameter, and in zonation of the endotheca, with a ring of large dissepiments encircling the axial cavity with a calicular floor made of flat, tabuloid dissepiments. From the coral most similar in measurable features, *R. paraclathrata* Roniewicz in Turnšek (1997: 183, figs. A–H; with synonymy), the new species differs, beside the endotheca of a structure described above, in possessing finer septa. The corallites fork at an acute angle. It cannot be determined if apophyseal intercorallite connections are present.

Material.—The holotype and specimen GBA 2009/019/15, with thin sections.

Measurements (in mm):

GBA	d	s	sd/1	ed/3	Remarks
2009/019/14	4.0–4.5	41–47	4–5	10–14	adults
2009/019/15	4.0–4.5	40–60	4–5	–	

Description.—Septa thin, differentiated into four size orders, arranged in adult forms into 9–10 systems. The S1 septa and S2 septa fusiform and exsert, the S1 septa reaching the axis, the S2 septa conspicuously shorter, the S3 septa of about half the length of the S1 septa. The S4 septa very short and variably developed: rare in the holotype colony but regularly distributed in the corallites of GBA 2009/019/15. In transverse sections, the septal flanks show rare, protruding granules. Endotheca abundant. At the zone of maximum thickness of fusiform septa, the endotheca is composed of a ring of convex, relatively large dissepiments; smaller dissepiments develop externally to that ring; horizontal, tabuloid dissepiments form a large and flat calicular floor. Wall thin. Corallum increasing by equivalent division of corallites, lacking constriction at the early stage of division, and with long-lasting connection between new corallites.

Stratigraphic and geographic range.—Austria: Northern Calcareous Alps, Dachstein Plateau, north of Feisterscharte, lower Norian, *Epigondolella quadrata* Conodont Zone. Slovenia: Northern Julian Alps, Lacian.

Retiophyllia vesicularis sp. nov.

Fig. 4E.

Etymology: From Latin *vesicularis*, vesicular; in reference to the structure of the endotheca.

Type material: Holotype: GBA 2009/019/12, with thin sections; paratype: GBA2009/019/13.1.

Type locality: Austria, Northern Calcareous Alps, southern Dachstein Plateau, site ca. 50 m north-west of Feisterscharte.

Type horizon: Norian, Lacian 1, *Epigondolella quadrata* Conodont Zone, light grey organodetritic limestone.

Diagnosis.—Maximum diameter of ca. 5–7 mm; axial cavity empty and wide. Septal apparatus of unstable symmetry, chiefly sixfold. Septa of three size orders, short; the S1 septa very thick. Dissepiments large, vesicular.

Comparison.—From other species it differs in large, convex dissepiments and S1 septa dominating in size over the remaining ones. The external wall surface shows longitudinal furrows associated with the S1 septa, a feature not encountered in other species of the genus.

Material.—The holotype (see above) with thin sections, and GBA 2009/019/13.

Measurements (in mm):

GBA	d	s	ed/5	Remarks
2009/019/12	5–7	24 (6S1+6S2+12S3)	7–8	adult stage
	3.5			early stage

Description.—Adult corallites circular in section, with exsert S1 septa. A tendency to petaloid shape of corallite in transverse section is observed, with furrows in the position of the S1 septa. Free axial space wide. Septal apparatus composed of very few septa arranged into six (rarely five) regular systems,. The S1 septa, ending at some distance from the axis, are very thick, fusiform, with large, irregular lateral granules. The S2 septa are about half the radius in length, the S3 septa subequal in thickness to the S2 septa, attaining one-fourth the radius. Adaxial septal parts thin, zigzag. Endotheca composed of large, equal vesiculae which are arranged in a single peripheral circle and an axial series traversing the lumen. Axial dissepiments are convex. Wall thick. ?Colony increase by the equivalent division of corallites.

Microstructure.—A straight row of small-trabecular centres may be discerned in the midline.

Stratigraphic and geographic range.—Austria: Northern Calcareous Alps, Dachstein Plateau, north and south of Feisterscharte, lower Norian, *Epigondolella quadrata* Conodont Zone.

Genus *Craspedophyllia* Volz, 1896

Type species: *Axosmilia alpina* Loretz, 1875, Carnian, Dolomites, Italy.

Remarks.—Genus *Craspedophyllia* was originally assigned to the family Procyclolitidae Vaughan and Wells 1943, then moved to the Alpinophylliidae Roniewicz, 1989 (Roniewicz et al. 2005), and herein to the family Reimaniphylliidae. The reason for this inconsistency lies in the lack of well preserved septal microstructure, the diagnostic feature for taxa of suprageneric rank. The traces of the microstructure observed in the material under study (see below) allow for the assignment of *Craspedophyllia*, together with *Distichophyllia* and *Retiophyllia*, to the family Reimaniphylliidae.

The taxon described herein belongs to a phaceloid group of species included to *Craspedophyllia*. This morphpology is especially common among diverse thin-septal and columella-bearing corals from a wide border belt between the Tethys and Panthalassa, described from Timor (Roniewicz et al. 2005) and Japan (Okuda et al. 2005).

Craspedophyllia? sp.

Fig. 4F, G.

Material.—GBA 2009/019/16 and 2009/019/17, fragments of corallites in organodetrital limestones, with thin sections.

Measurements (in mm):

GBA	d	s	sd/2	lt/1
2009/019/16	9×12	83 (13S1+13S2+26S3+31S4)	5	6
2009/019/17	13	e. 72	5	6–8

Description.—Corallum phaceloid. Calices deepened at the center. Septa fusiform, differentiated into four size orders: the S1 to S3 septa regularly distributed, with the S1 and S2 septa the thickest of all. The S1 septa approaching the axis, the S2 septa conspicuously shorter, the S3 septa of about half the radius, the S4 septa from about a quarter to one-third the radius in length. Menianes wide and rare, in transverse section resembling long, thorny septal outgrowths strongly inclined to the axis. Endotheca abundant. Wall pellicular.

Microstructure.—The midseptal line in the S1to S3 septa is in the form of a dense zigzag line, and the lateral stereome is differentiated into regular trabecular portions with symmetrically or asymmetrically developed lateral axes.

Remarks.—This form differs in robust and sparse septa from branching species of *Craspedophyllia* (e.g., *C. ramosa* Roniewicz et al. 2005, or determined to be *Craspedosmilia graeca* Turnšek and Senowbari-Daryan, 1994 in Okuda et al. 2005). Its microstructure of septa and menianes are typical of the genus, but, unlike other species, it has calices deepened centrally and lacking reliable evidence of columella.

Stratigraphic and geographic range.—Austria: Northern Calcareous Alps, Dachstein Plateau, north of Feisterscharte, lower Norian, *Epigondolella quadrata* Conodont Zone.

Family Margarophyliidae Volz, 1896

Genus *Margarophyllia* Volz, 1896

Type species: *Margarophyllia capitata* Münster, 1841, Carnian, Dolomites, Italy.

Margarophyllia cf. *capitata (*Münster, 1841)

Fig. 5E.

Material.—GBA 2009/019/2, a fragment of corallum in organodetrital limestone, with thin sections.

Measurements (in mm):

d	s	f
10×13	90 (12+12+24+42)	2.0

Remarks.—In its diameter, the coral resembles *M. capitata* (Münster, 1841) described by Volz (1896: 46, pl. 3: 1–4). In contrast to the Carnian species, it has numerous septa (in *M. capitata* the index s:d is 6, while in the Norian taxon it is ca. 9), and a rudimentary columella formed by the axial borders of the longest septa.

Stratigraphic and geographic range.—Austria: Northern Calcareous Alps, Dachstein Plateau, north of Feisterscharte, lower Norian, *Epigondolella quadrata* Conodont Zone.

Genus *Margarosmilia* Volz, 1896

Type species: *Montlivaltia zieteni* Klipstein, 1843, Carnian, Dolomites, Italy.

Margarosmilia nova Turnšek, 1991

Fig. 5D.

1991 *Margarosmilia nova* Turnšek 1991; Ramovš and Turnšek 1991: 184, pl. 6: 1–3.

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Material.—GBA 2009/019/4, single corallite in organodetrital limestone, with thin sections.

Measurements (in mm):

d	s
18.0×22.0	ca. 100 (12+12+24+21+22S5 or more)

Remarks.—The fragment of phaceloid corallum in the form of a single corallite corresponds to the Slovenian species *M. nova* Turnšek in its diameters and number of septa and is very similar to the corals from the Carnian (Julian and Tuvalian) described from Slovenia as *Margarophyllia capitata* (Turnšek et al. 1982, 1987).

Stratigraphic and geographic range.—Austria: Northern Calcareous Alps, Dachstein Plateau, north of Feisterscharte, lower Norian, *Epigondolella quadrata* Conodont Zone. Slovenia: Northern Julian Alps, Lacian.

Margarosmilia adhios sp. nov.

Fig. 5G, H.

Etymology: From Greek *adhios,* empty; in reference to the empty axial space.

Type series: Holotype GBA 2009/019/19 and paratype 2009/019/18.

Type locality: Austria, Northern Calcareous Alps, southern Dachstein Plateau, site ca. 50 m north-west of Feisterscharte.

Type horizon: Norian, Lacian 1, *Epigondolella quadrata* Conodont Zone; light grey Dachsteinkalk.

Diagnosis.—*Margarosmilia* of ca. 50 septa at a corallite diameter of 6 mm, well developed septa of first three size orders, rare S4 septa, and a large axial pit. Endotheca differentiated into axial extended, flat dissepiments and peripheral small, vesicular ones.

Comparison.—The species differs from the congeneric species in small corallite diameters and in zonation of the endotheca.

Material.—The type series and GBA 2009/019/16, all with thin sections.

Measurements (in mm):

GBA	d	s	sd/1	ed/3
2009/019/18	6	ca. 50	3	8–10 at centre >10 at periphery
2009/019/19	6	ca. 50 (10+10+20+nS4)	3	8–10 at centre

Description.—Axial pit relatively large and empty. The S1 to S3 septa fusiform, wavy adaxially and very thick peripherally. The S2 septa are shorter than the S1septa, the S3 septa reach about half the length of the S1septa, the S4 septa rudimentary, developed in the form of thin blades. Endotheca peripherally built of high vesiculae, smaller at the circumference than at the zone of maximum thickening of the septa; the axial area built of flat dissepiments delineating a subhorizontal calicular floor. Wall epithecal, very thin, rarely preserved.

Microstructure.—In the peripheral, fusiform septal portion, the zigzag midline is preserved with clearly defined lateral trabeculae.

Stratigraphic and geographic range.—As for the type material.

Genus *Thamnomargarosmilia* Melnikova, 1996

Type species: *Thamnomargarosmilia prima* Melnikova, 1996, Rhaetian, SE Pamirs, Tajikistan.

Thamnomargarosmilia aff. *prima* Melnikova, 1996

Fig. 5F.

Material.—GBA 1995/2/1/2, a fragment of corallum of. *T.* aff. *prima* in organodetrital limestone, with thin sections.

Measurements (in mm):

d	s	Remarks
6.5	50	
7.0	56(9+9+18+20)	
8.0	65(9+9+17+30)	
T. prima Melnikova, 1996: p. 12, pl. 2:1		
5–7	32–36	early stage
8–9	45–50	adult
12	>60	adult

Description.—Corallum phaceloid. Corallites circular in section with small, circular and empty axial pit. Septa uniform in thickness, differentiated into four size orders: the S2 septa slightly shorter than the S1 septa, the S3 septa attaining ca. three-quarters the length of the S1 septa, the S4 septa variable in length. Dissepiments small and homogeneous. Epithecal wall very thin, pellicular, mostly damaged. Increase through intracalicular budding, with the centre of a new corallite initiated as an interruption of some two to three septa of the adult. Bi- and tri-centric states of corallites are observed with temporary lamellar connections between the centres. The new corallite diverge from the parent at nearly right angles.

Remarks.—The Alpine coral has smaller corallite diameters and more numerous septa than the example from the Pamirs *T. prima* Melnikova, 1996 (Melnikova 1996: 12, pl. 2: 1). The Pamirian form, represented by the holotype only, shows a bushy morphology composed of phaceloid-thamnasterioid embranchments.

In addition to the fragmentary corallum of *T.* aff. *T. prima*, the sample contains fragments of solitary *Cuifia marmorea* (see above) and a solitary coral described below as "solitary dwarfish coral gen. indet."

Stratigraphic and geographic range.—Austria: Northern Calcareous Alps, Dachstein Plateau, north of Feisterscharte, lower Norian, *Epigondolella quadrata* Conodont Zone. The Pamir species comes from the upper Carnian–lower Norian, Shaimak Svite, SE Pamirs, Djilgakochusu Valley, Tajikistan.

Genus *Ceriostella* Roniewicz and Stanley, 1998

Type species: *Ceriostella variabilis* Roniewicz and Stanley, 1998, Ladinian, Nevada, USA.

Remarks.—Genus *Ceriostella,* with *C. variabilis* as the type species, was initially recognised in North America in the up-

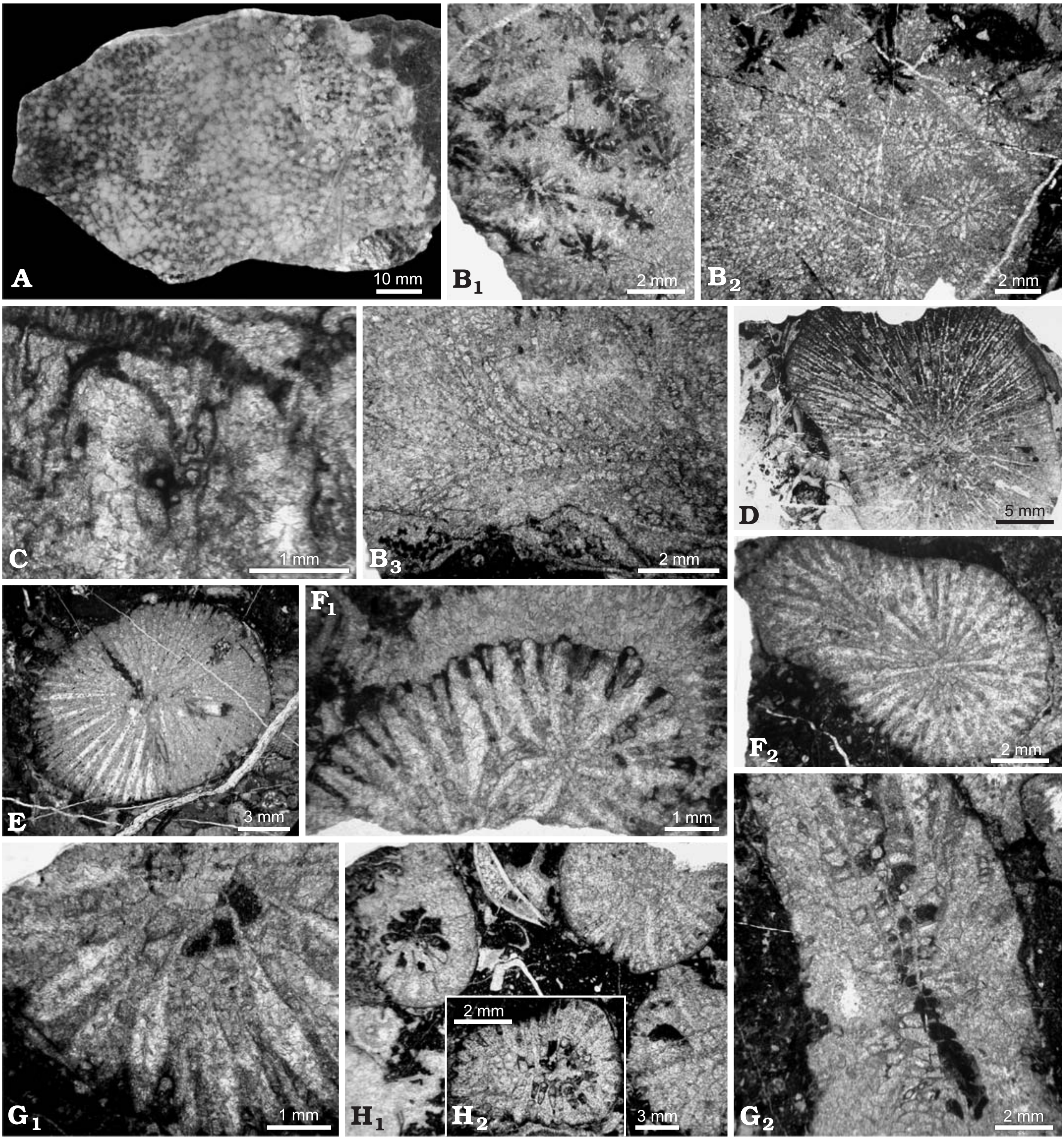

Fig. 5. Margarosmiliid corals from vicinity of Feisterscharte, Austria, early Norian, Triassic. **A**–**C**. *Ceriostella* aff. *variabilis* Roniewicz and Stanley, 1998. **A**. GBA 2009/019/20; a colony in polished section. **B**. GBA 2009/019/22; transverse thin sections (B_1, B_2), note cerioid colony and a lack of columella; longitudinal section (B_3) showing mode of growth of corallites at the periphery of lamellar colony. **C**. GBA 2009/019/23a; calice in longitudinal/oblique section showing rare granules on the septal side and internal border micromorphology (at the middle). **D**. *Magarosmilia nova* Turnšek, 1991; GBA 2009/019/4 i; transverse section. **E**. *Margarophyllia* cf. *capitata* (Münster, 1841); GBA 2009/019/2c; transverse section. **F**. *Thamnomargarosmilia* aff. *prima* Melnikova, 1996; GBA 1995/2/1/2f, c; transverse sections showing budding with lamellar linkages between centres (F_1), and a typical circular shape of adult corallite (F_2) with a new one growing laterally. **G**, **H**. *Margarosmilia adhios* sp. nov. **G**. GBA 2009/019/18a; a fragment of transverse section (G_1) of a corallite with traces of microstructure; longitudinal section (G_2) of corallite showing small dissepiments. **H**. GBA 2009/019/19a, c; transverse section of phaceloid corallum (H_1); a section of the corallite at a preliminary stage of sub-symmetric division (H_2).

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per Ladinian of the New Pass Range, central Nevada, below the beds containing the ammonoid *Protrachyceras* (*P. sutherlandi* Ammonoid Zone).

The genus is characterised by cerioid colonies composed of small corallites with radially arranged septa of three size orders, lacking columella, increasing by peripheral budding.

Ceriostella sp.

Fig. 5A–C.

Material.—Nearly complete colonies GBA 2009/019/20 and 2009/019/22, and fragments of colonies GBA 2009/019/3, 2009/019/5, 2009/019/7 and 2009/019/23, with thin sections. The skeletons are deeply recrystallised.

Material and measurements (in mm) made on thin sections:

GBA	d	c-c	s in regularly developed calices
2009/019/3 2009/019/22	2.5–3.0	2.5–3.5	24 (6S1+6S2+12S3) – 32 (8+8+16)
2009/019/5 2009/019/20 2009/019/23	1.5–2.0	1.5–2.0	12 (5S1+5S2+2S1), 16 (4S1+4S1+8S1) – 20 (5S1+5S2+e.10S3)

Description.—Colonies from lamellar to massive, more than 100 mm in height. Corallites densely packed, polygonal. Radial elements differentiated into three size orders, with the S1septa the thickest and approaching the centre, the S2 septa shorter and much thinner than the S1 septa, and the S3 septa very thin and short. The irregular number of the S1 septa from four to eight results in a variable symmetry of the septal apparatus, allowing for a provisional discrimination of the two groups of specimens indicated above. Because of the extremely limited observations it is impossible to establish whether or not this variability has any diagnostic value. Septal distal border very thin; septal sides with sharp granules. Endotheca dissepimental, vesicular.

Remarks.—The Alpine taxon is close to the North American upper Ladinian species, *Ceriostella variabilis* Roniewicz and Stanley, 1998, but its state of preservation precludes any detailed examination of structures or comparison with similar taxa.

Stratigraphic and geographic range.—Austria: Northern Calcareous Alps, Dachstein Plateau, north of Feisterscharte, lower Norian, *Epigondolella quadrata* Conodont Zone.

Family Conophylliidae Alloiteau, 1952

Genus *Conophyllia* d'Orbigny, 1849

Type species: *Montlivaltia granulosa* Münster, 1841, Carnian, Dolomites, Italy.

Conophyllia cf. *hellenica* Turnšek and Senowbari-Daryan, 1994

Fig. 6E.

2007 *Procyclolites*; Roniewicz et al. 2007: 582, Table 1.

Material.—Fragments of large, solitary corals in organodetrital limestone, samples GBA 2009/019/5, 7, and 12, with thin sections.

Measurements (in mm):

GBA	d	f	sd/5
2009/019/12	e.30	e.200	12

Remarks.—The solitary growth form, thin and straight septa with faces covered by pennules or menianes, small-dissepimental endotheca, and the synapticulae enable assignment of this form to *Conophyllia*. In its large diameter and numerous septa, it is similar to *Conophyllia hellenica* Turnšek and Senowbari-Daryan (1994: 484, pl. 10: 1–4) described from Hydra Island, Greece, but the Alpine form differs from the latter in strongly protruding pennules.

Stratigraphic and geographic range.—Austria: Northern Calcareous Alps, Dachstein Plateau north of Feisterscharte, lower Norian, *Epigondolella quadrata* Conodont Zone. *Conophyllia hellenica* is known from the Pantokrator Limestone of Hydra Island, Greece, Carnian–lowermost Norian.

Conophyllia sp.

Fig. 6B, C.

Material.—A fragment of corallum GBA 2009/019/25 and fragmentary corallites in detrital limestone GBA 2009/019/3, with thin sections.

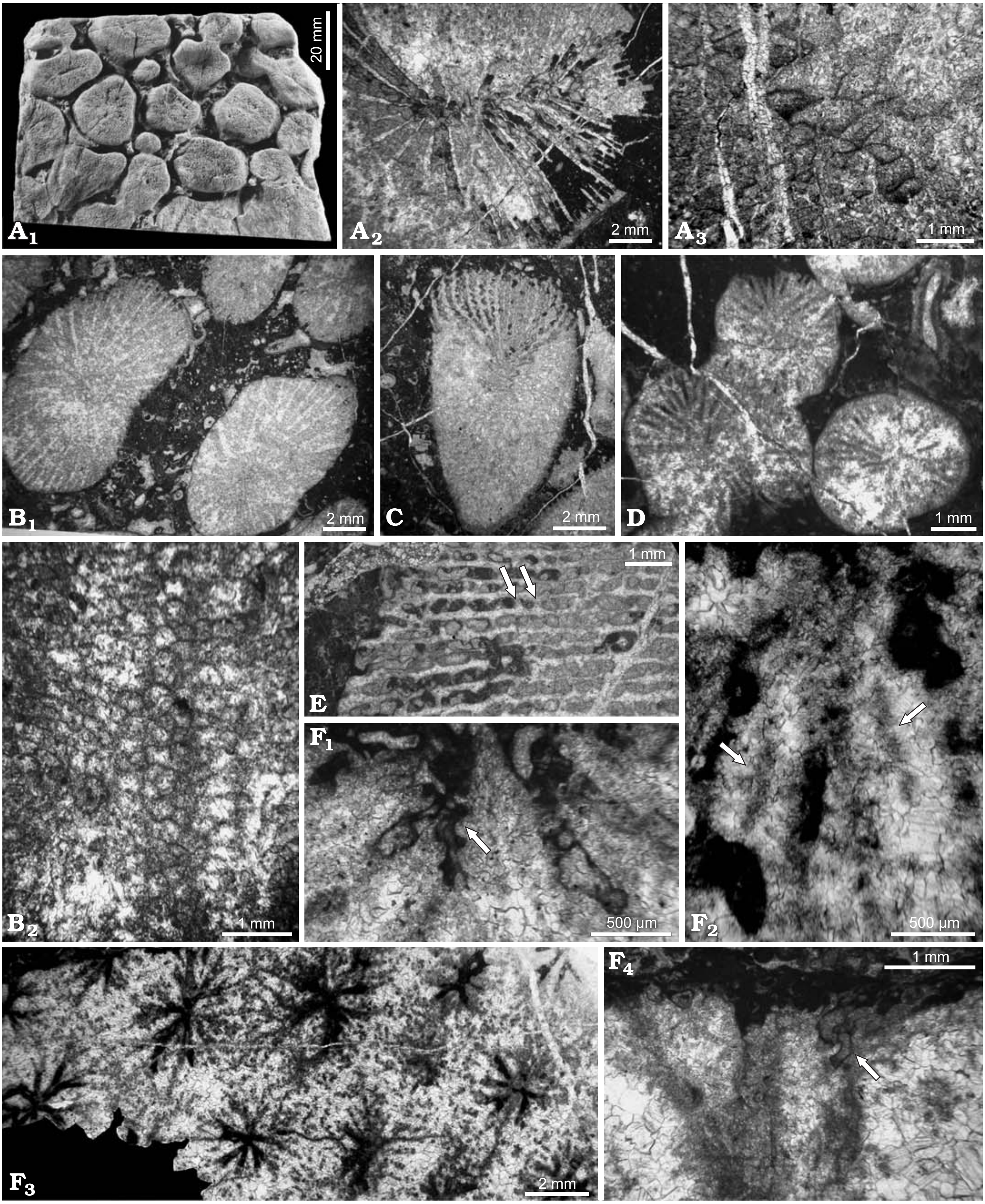
Measurements (in mm):

GBA	d	s	sd/1	ed/3
2009/019/25	5–7	45–49(12S1)	4	13
2009/019/3	6.5	e..58	3–4	

Description.—Corallum phaceloid. Septa thin, covered with pennules, and differentiated in length into four size orders. In completely developed systems, the septa are arranged into descending series. The fine-structural, spongy columella is made of projections of the S1 septa. Dissepiments abundant, small, thin-walled. Budding intracalicular, asymmetrical, initiated by formation of lateral elongation of the calice.

Remarks.—The very fragmentary and poor state of preservation of the skeleton precludes any detailed comparisons with corals of known species. In its septal structure the coral fits the diagnosis of *Conophyllia*, but differs from it in the growth form. It is similar to *Craspedosmilia* Turnšek and Senow-

Fig. 6. Conophylliid corals and corals of unknown families from vicinity of Feisterscharte, Austria, early Norian, Triassic. **A**. *Hydrasmilia laciana* sp. nov.; GBA 2009/019/28b, f. A fragment of phaceloid corallum in calicular view (A_1); transverse thin section of corallite (A_2) to show thin, abundant septa, and longitudinal radial section (A_3) with small dissepiments of the peripheral corallite part. **B**, **C**. *Conophyllia* sp. **B**. GBA 2009/019/25b, c. A fragment of phaceloid corallum in transverse (B_1) and longitudinal (B_2) sections showing small-dissepimental endotheca. **C**. GBA 2009/019/3p. Longitudinal/oblique section of the calice showing pennular micromorphology of the septa. **D**. *Rhopalodendron* cf. *juliense* Turnšek, 1989; GBA 2009/019/26a. Corallites with anastomosing septa and a poor columellar structure, transverse thin section. **E**. *Conophyllia* cf. *hellenica* Turnšek and Senowbari-Daryan, 1994; GBA 2009/019/12i. A fragment in transverse section, note pennular micromorphology and synapticulae (arrows). **F**. *Thamnasterites astraeoides* gen. et sp. nov. →



GBA 2009/019/4t–w. Transverse section (F_1), adaxial corallite part with wedge-like internal septal borders and lateral septal micromorphology in the form of pennular strucures (arrow); traces of microstructure in the form of a thick mid-septal line (F_2) (arrows); transverse section (F_3); note the lack of a structurally delimited wall; longitudinal section cutting the calice (F_4), thick pennular structures at the centre (arrow).

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bari-Daryan, 1994 in growth form, but it differs in the structure of the columella (in that genus developed as a solid, large structure).

Stratigraphic and geographic range.—Austria: Northern Calcareous Alps, Dachstein Plateau, north of Feisterscharte, lower Norian, *Epigondolella quadrata* Conodont Zone.

Genus *Rhopalodendron* Turnšek, 1989

Type species: *Rhopalodendron juliense* Turnšek, 1989, Pokljuka Mountain, Slovenia.

Rhopalodendron cf. *juliense* Turnšek, 1989 (ex *juliensis*)

Fig. 6D.

Material.—Fragmentary corallaGBA 2009/019/26 and 2009/019/27, thin sections.

Measurements (in mm) of the Alpine and Slovenian corals:

Specimen	d	s
GBA 2009/019/26 GBA 2009/019/27	2.5–3.0 (4.0)	>40
Rhopalodendron juliense Turnšek, 1989:		
1989 from the Cordevolian	2.5–3.5 (4.0)	40–50
1991 from the Lacian	2–3	30–48

Remarks.—The coral from the Dachstein Plateau (GBA 2009/019/26) shows septa in descending series, typical of the conophylliids, and frequent intracalicular budding. However, it is so poorly preserved that no details of septal structure are observable. Generally, with its thin corallites, numerous, thin septa, and thin columella it corresponds to the corals described as *Rhopalodendron juliense* from diverse localities (Pokljuka Mts, Hydra Island, Julian Alps), ranging from the lower Carnian (Cordevolian) to the lower Norian (Lacian) (compare Turnšek and Buser 1989: 87, pl. 8: 1–6; Ramovš and Turnšek 1991: 186, pl. 8: 1–3; Turnšek and Senowbari-Daryan 1994: 483, pl. 6: 5, 6).

Stratigraphic and geographic range.—Austria: Northern Calcareous Alps, Dachstein Plateau, north of Feisterscharte, lower Norian, *Epigondolella quadrata* Conodont Zone.

Family Cuifastraeidae Melnikova, 1983

Genus *Cuifastraea* Melnikova, 1983

Type species: *Cuifastraea granulata* Melnikova, 1983, Norian, SE Pamirs, Tajikistan.

Cuifastraea? sp. 1 and sp. 2

Fig. 7C, D.

Material.—Two small fragments of colonies from organodetrital limestone GBA 2009/019/4 and 2009/019/13, with thin sections.

Measurements (in mm):

GBA	d	c-c	s	md	dtr	endo-theca	columella
Cuifastraea? sp. 1							
2009/019/4 Fig. 7C	11		ca. 40	7/3 mm	125 µm	vesicular	lacking
Cuifastraea? sp. 2							
2009/019/13 Fig. 7D	3.5; 4.5	3.5–6	24–28	3/500 µm		vesicular	a few trabecular offsets

Remarks.—The material consists of two small fragments of different colonies displaying thamnasterioid relationships between the corallites, thick-trabecular, compact septa covered laterally with eminent structures, the longitudinal sections of which resemble pennules or menianes. They differ from known Sevatian and Rhaetian species in the following features: *Cuifastraea*? sp. 1 (Fig. 7C) has very thick septa, not encountered earlier in the genus; *Cuifastraea*? sp. 2 (Fig. 7D) has pennules. The coalescence of of these pennules into menianes is unknown.

Stratigraphic and geographic range.—Austria: Northern Calcareous Alps, Dachstein Plateau, north of Feisterscharte, lower Norian, *Epigondolella quadrata* conodont Zone.

Genus *Tropiphyllum* Cuif, 1975

Type species: *Tropiphyllum ornatum* Cuif, 1975, early Norian, Taurus Mountains, Turkey.

Tropiphyllum ornatum Cuif, 1975

Fig. 7E.

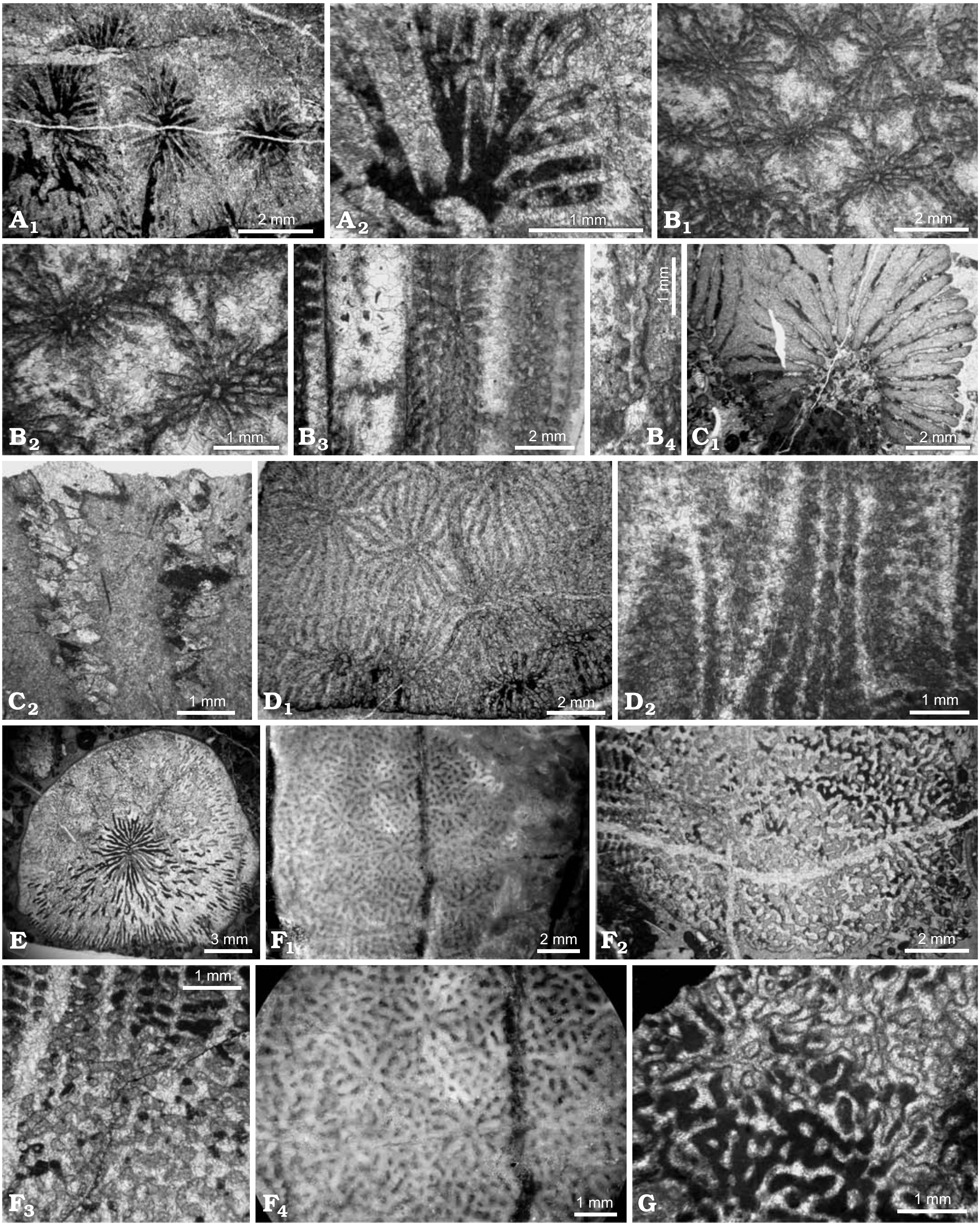
1975 *Tropiphyllum ornatum* Cuif, 1975; Cuif 1975c: 92, text-fig. 12, pl. 11: 1–3.

Material.—Specimen GBA 2009/019/10, with thin section.

Measurements (in mm):

GBA	d	s	sd/5	f
2009/019/10	16	e.130 (22S1)	17–19	1.2
Specimen from the Taurus Mountains				
Cuif 1975: pl. 11: 1–3	up to 25	e. 180		

Fig. 7. Tropiastraeid, cuifastraeid, and microsolenid corals. **A**–**F**. Vicinity of Feisterscharte, Austria, early Norian, Triassic. **A**. Early/middle Norian. **B**–**F**. Early Norian. **G**. South-East Pamirs; Early Jurassic, Hettangian–Sinemurian. **A**. *Guembelastraea* aff. *guembeli* (Laube, 1865); GBA 2009/019/24a. Transverse sections showing cerioid coral (A_1), and its thin septa (A_2) with long, oblique menianes. **B**. *Thamnasteriamorpha* aff. *frechi* (Volz, 1896); GBA 2009/019/21b, f. Transverse sections (B_1, B_2) showing thin-septal, thamnasterioid corallites with thin, styliform columella; longitidinal sections showing thick menianes (B_3) with margins directed upwards (B_4). **C**. *Cuifastraea*? sp. 1; GBA 2009/019/4o, p. Transverse (C_1) and longitudinal (C_2) section of thick-septal coral. **D**. *Cuifastraea*? sp. 2; GBA 2009/019/13c, d. Thamnasterioid colony in transverse (D_1) and (D_2) longitudinal sections; menianes of an unknown length are present (D_2). **E**. *Tropiphyllum ornatum* Cuif, 1975; GBA 2009/019/10c. Corallum in transverse section showing abundant, thin septa of wavy shape and a rudimentary papillar columella. **F**. *Eocomoseris* aff. *ramosa* (Frech, 1890); GBA 2009/019/3. Transverse polished section of a colony (F_1) embranchment and its magnification (F_4) showing porous skeleton, six-fold septal symmetry and monotrabecular columella; thin section (F_2) and its fragment with longitudinal section of meniane-bearing septa (F_3). **G**. *Eocomoseris lamellata* Melnikova, 1993; IGD/1e-Zch. Transverse section with porous septa and monotrabecular columella. →



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Description.—Radial elements wavy, densely packed, differentiated into four size orders. The S1 septa approaching the axis, the S2 septa up to four-fifths the length of the S1 septa, the S3 septa markedly shorter, the S4 septa very thin, and variable in length. The internal septal borders set off rare trabecular processes that form a small papillar columella. Dissepiments numerous. Menianes subhorizontal, with alternating position on septal faces.

Remarks.—This coral probably represents an earlier ontogenetic stage than that of the type from the Taurus Mountains in Turkey (Cuif 1975c). Smaller numbers of septa at a larger diameter differentiate this taxon from the phaceloid *Gillastraea delicata* Melnikova, 1983 (adults 7–11 mm with 140–150 septa; corallites at early stages 2.4–4.0 mm, with 40 septa) with which it might be misidentified.

Stratigraphic and geographic range.—Austria: Northern Calcareous Alps, Dachstein Plateau: north of Feisterscharte, lower Norian, *Epigondolella quadrata* conodont Zone. Turkey: Taurus Mountains.

Family Tropiastraeidae Cuif, 1977

Genus *Thamnasteriamorph*a Melnikova, 1971

Type species: *Thamnastraea frechi* Volz, 1896, Carnian, Dolomites, Italy.

Thamnasteriamopha aff. *frechi* (Volz, 1896)

Fig. 7B.

Material.—A fragment of colony GBA 2009/019/21, with thin sections.

Measurements (in mm):

GBA	d	c-c	s	md/2	ed/3
2009/019/21	2.5–3	(2.5) 3.0–3.2	ca. 25	4	12
Thamnastraea frechi Volz, 1896: 59, pl. 6: 1–10					
Holotype MIGWr 79sz	2.5–3.5	2.5–3.5	16–25	6–7	

Description.—Colony lamellar. Radial elements (biseptal plates) not numerous, thin, confluent, differentiated into three size orders. Systems irregular. Menianes regularly spaced, symmetrical or alternating, thick, wide, their edges bent upwards and smooth. Internal septal edges thin. Columella styliform, thin. Endotheca of rare, thin, extended dissepiments. In the wall region, synapticulae can be observed. Increase by intercalicular budding, or through corallite division.

Microstructure.—Traces of the microstructure are observable in the septal blades.

Remarks.—The number of septa, and diameters of calices of the Norian form are close to those of the holotype (MGUWr 79sz) of the Carnian *Thamnastraea frechi* Volz, 1896 (type species of *Thamnasteriamorpha*). However, the coral from the Dachstein differs from the type in possessing a thin columella and menianes that are not densely arranged (compare the Measurements above). The state of preservation does not allow for a more detailed description of the characters of the Norian coral.

Stratigraphic and geographic range.—Austria: Northern Calcareous Alps, Dachstein Plateau, north of Feisterscharte, lower Norian, *Epigondolella quadrata* conodont Zone.

Genus *Guembelastraea* Cuif, 1976

Type species: *Isastrea Gümbeli* Laube, 1865, Carnian, Dolomites, Italy.

Guembelastraea aff. *guembeli* (Laube, 1865)

Fig. 7A.

Material.—Fragments of colonies GBA 2009/019/5 and 24, with thin sections.

Measurements (in mm):

c-c	s
2.5–4.0	40–50 (and more)

Remarks.—Colony cerioid, massive; corallites polygonal, lacking any columella. Septa thin, with rare pennules. The coral greatly resembles Carnian *Guembelastraea guembeli* (Laube, 1865) from St. Cassian (Laube 1865: 263, pl. 7: 2). From the early Norian *Guembelastraea pamphyliensis* Cuif, 1976 from the Taurus Mountains, Turkey, the taxon examined differs in two taxonomically important features: a weak development of septal pennules (in *G. pamphylliensis* densely covering the septal flanks) and, judging from the illustrations (Cuif 1976: pl. 9: 2–4), in smaller corallite diameters.

Stratigraphic and geographic range.—Austria: Northern Calcareous Alps, Dachstein Plateau, north of Feisterscharte, early or middle Norian, deposits close to the horizon with *Epigondolella* cf. *E. multidentata* (Alaunian 1).

Family Microsolenidae Koby, 1889

Genus *Eocomoseris* Melnikova, Roniewicz, and Loeser, 1993

Type species: *Eocomoseris gurumdyensis* nom. nov. (= *Eocomoseris ramosa* Melnikova, 1993), Hettangian–Sinemurian, SE Pamirs, Tajikistan.

Remarks.—The genus *Eocomoseris* was first identified in the Jurassic and Cretaceous (Melnikova et al. 1993); its species, among others, were earlier classified with the spongiomorphids. Ezzoubair and Gautret (1993) showed that there were essential microstructural differences between the Triassic *Spongiomorpha* (*Hexastylopsis*) *ramosa* Frech, 1890 and the remaining spongiomorphids, and stated that the former had a skeleton of scleratinian type.

The coral species included to the genus were discussed in Melnikova et al. 1993, and beside the species described in that paper (Early Jurassic *E. lamellata* Melnikova, 1993, *E. ramosa* Melnikova, 1993) renamed herein (see below) into *E. gurumdyensis* nom. nov., both from the Pamirs, and Cenomanian *E. raueni* Loeser, 1993 from Germany), the list of coral taxa from the literature, which could be identified with *Eocomoseris*, is as follows: Early Jurassic *Microsolena fromenteli* Terquem and Piette, 1868 from France, and *Actinaraea bevoayensis* (Alloiteau, 1958) in Turnšek et

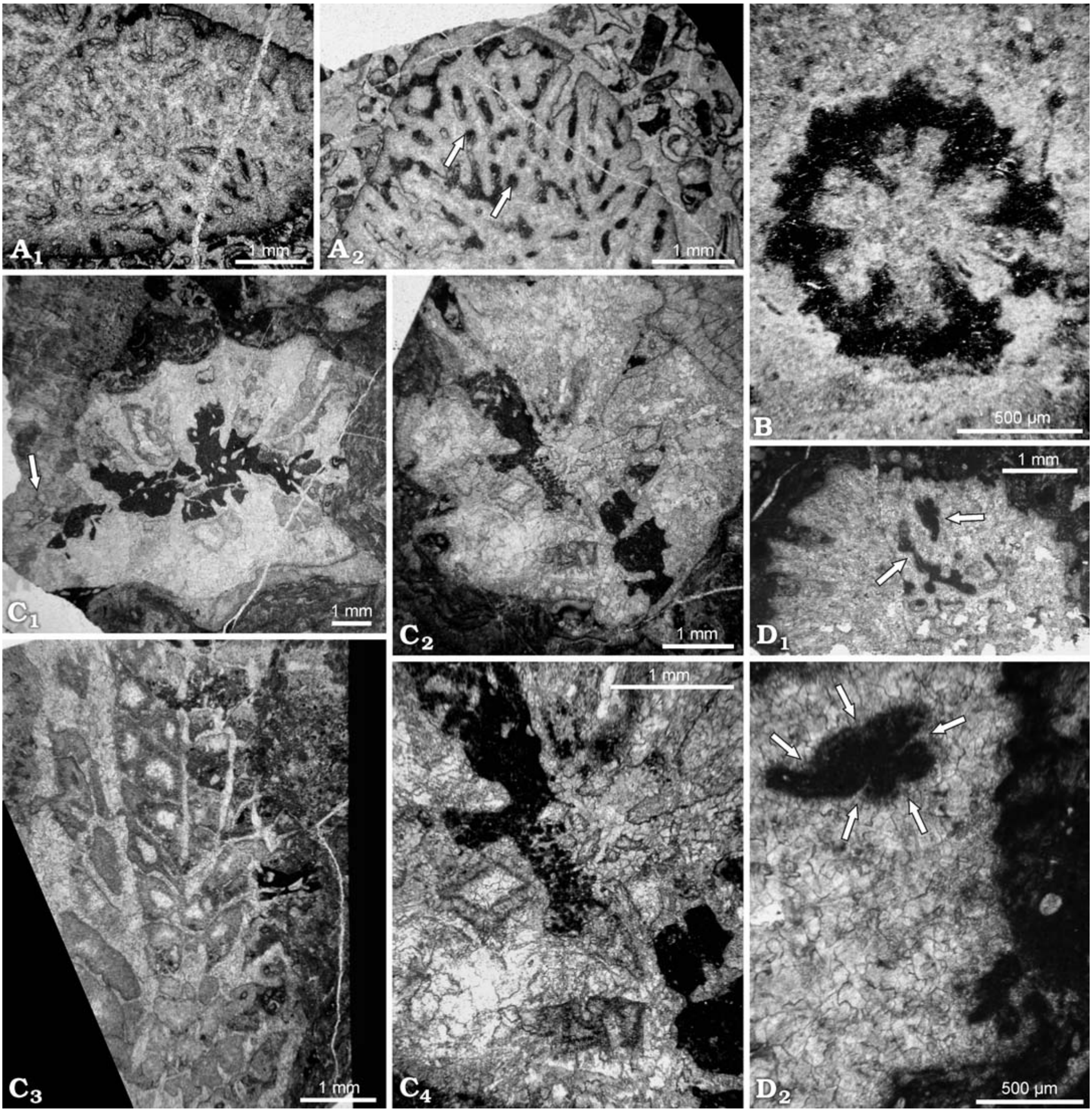

Fig. 8. Astraeomorphid coral and some undetermined coral taxa, and the hydrozoan *Cassianastraea reussi* (Laube, 1865). Vicinity of Feisterscharte, Austria, early Norian, Triassic. **A**. *Parastraeomorpha* sp.; GBA 2009/019/3c. A colony fragment in transverse section (A_1), and the same in oblique section (A_2) showing synapticulae (arrows). **B**. A solitary coral of the smallest fossil scleractinian corals described so far; GBA 1995/2/1/2h. Note the external corallite surface micromorphology. **C**. Forking thick-septal coral; GBA 2007/152/3b–d. Transverse section of the distal corallite part (C_1); a new centre indicated by an arrow; proximal corallite part with papillar columella (C_2), and its details magnified (C_4); longitudinal section (C_3) showing tabuloid dissepiments. **D**. *Cassianastraea reussi* (Laube, 1865); GBA 1995/2/1/2f. Transverse section of a branch (D_1), with a calice (upper arrow) and canals (lower arrow); a fragment of the same section (D_2) to show a calice with five septa (marked with arrows).

al. 1975 from Spain, and Kimmeridgian/Tithonian *Thamnasteria vereschagini* Krasnov, 1983 from Sakhalin. In addition, the following taxa having been classified in the Spongiomorphidae: the Early Jurassic *Spongiomorpha crassa* LeMaitre, 1935 (LeMaitre 1935: 29, pl. 1: 4, not figs. 1–3) and *S.* (*Heptastylopsis*) *asiatica* LeMaitre, 1935 (LeMaitre 1935: 33, pl. 3: 1, 3, 4), both from Morocco, and the Late Jurassic taxon from Spain attributed to *Spongio-*

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morpha globosa Yabe and Sugiyama, 1931 by Flügel and Hötzl (1966: pl. 18: 1–5).

The genus ranges from the Late Triassic to early Late Cretaceous.

Eocomoseris aff. *ramosa* (Frech, 1890)

Fig. 7F.

Material.—Small fragments of colonies in detrital limestone, GBA 2009/019/3 and 2009/019/4.

Measurements (in mm if not stated otherwise):

Specimen	c-c	s	md/ 40 µm	d tr µm
GBA 2009/019/3	1.5–2	12, 14	3	200 (peripheral trabecula)
E. gurumdyensis nom. nov. (= *E. ramosa* Melnikova, 1993), Hettangian-Sinemurian, Pamirs				
Collective measurements of the specimens: IGD/2-Zch, 8-Zch, 13-Zch, 14-Zch, 3411, 3632, 3633	0.9–1.2	13–16	3–3.5	60–100
E. lamellata Melnikova, 1993, Hettangian–Sinemurian, Pamirs				
Collective measurements of the specimens IGD/1-Zch, 18-Zch, 25-Zch, 3629, 3663, 5083	1.8–3.0	16–22	2–3	120–160

Description.—Colonies thin-branched (fragments of 13 mm in diameter), thamnasterioid, formed by small, densely crowded corallites. Septa short, regularly perforated, built of 3–4 trabeculae, pores of the diameter similar to the diameter of trabeculae. Columella monotrabecular. Menianes are continuous, regularly distributed.

Remarks.—This early Norian Alpine taxon is here considered to be related to the Rhaetian *E. ramosa* (Frech, 1890). Unfortunately, the original description of the Rhaetian *Spongiomorpha* (*Hexastylopsis*) *ramosa* Frech (1890: 76, text-figs. a–e) gives only the most general information on the ramous habit of colonies and the horizontal flanges on the septa, without providing any species-specific features. It points to a resemblance of the septal flanges to those in *Astraeomorpha*.

This Alpine coral resembles two Early Jurassic species from the South-East Pamirs in Tajikistan: *Eocomoseris lamellata* Melnikova, 1993 (shown herein for comparison with the Alpine species in Fig. 7G), and *E. gurumdyensis* nom. nov. (see the Nomenclatorial note below, and the Measurements above).

Stratigraphic and geographic range.—Austria: Northern Calcareous Alps, Dachstein Plateau, north of Feisterscharte, lower Norian, *Epigondolella quadrata* Conodont Zone.

Nomenclatorial note.—*E. gurumdyensis* nom. nov.: holotype housed at the Institute of Geology, Dushanbe, IGD/8-Zch; type locality: Zurchiertsek Valley, SE Pamirs, type horizon: Hettangian/Sinemurian bed, the lowermost sequence of the Gurumdy Svite in the Zurchiertsek Valley.

Eocomoseris gurumdyensis is a new name introduced herein to replace *E. ramosa* Melnikova, 1993, a junior subjective homonym of *Spongiomorpha* (*Heptastylopsis*) *ramosa* Frech, 1890, which is herein assigned to *Eocomoseris*.

Family Astraeomorphidae Frech, 1890

Genus *Parastraeomorpha* Roniewicz, 1989

Type species: *Parastraeomorpha minuscula* Roniewicz, 1989, Rhaetian, Northern Calcareous Alps, Austria.

Parastraeomorpha sp.

Fig. 8A.

Material.—Fragments of colonies in sample GBA 2009/019/3.

Remarks.—Small fragments of thamnasterioid colonies with skeleton structure typical of *Parastraeomorpha*. Calicular centres 1.5–2.5 mm apart. Septa compact, synapticulae numerous. The fragments are preserved in detrital limestone, together with fragments of *Pachysolenia cylindrica* and other skeletal detritus.

Stratigraphic and geographic range.—Austria: Northern Calcareous Alps, Dachstein Plateau north of Feisterscharte, lower Norian, *Epigondolella quadrata* Conodont Zone.

Genera of uncertain families

Family A

Genus *Hydrasmilia* Turnšek and Senowbari-Daryan, 1994

Type species: *Hydrasmilia rhytmica* Turnšek and Senowbari-Daryan, 1994, Carnian–early Norian, Hydra Island, Greece.

Remarks.—A lack of menianes makes the original classification of this genus into the Procyclolitidae hardly acceptable. Because of the poor preservation of the skeleton, the family-diagnostic features of the genus cannot be determined.

Hydrasmilia laciana sp. nov.

Fig. 6A.

Etymology: From the name of the substage Lacian.

Holotype: A fragment of phaceloid corallum GBA 2009/019/28.

Type locality: Austria, Northern Calcareous Alps, southern Dachstein Plateau, north-east of Feisterscharte.

Type horizon: Norian, Lacian 3, massive limestone above horizon with the *Epigondolella triangularis* and *Norigondolella navicula* assemblage.

Diagnosis.—*Hydrasmilia* with corallites of ca. 15 mm in diameter and more than 100 septa differentiated into four size orders.

Material.—Dachstein Plateau: the holotype specimen represents a 70×100×50 mm fragment of a very large corallum. Gosaukamm: NHMW, field nos. 1991/5, 1991/16, 1991/21 from the Lacian; NHMW 1991/37 from the Alaunian; all with thin sections.

Measurements (in mm):

GBA	d	s	sd/3	ed/1	f	Remarks
2009/019/28	14×17	> 110		4–4.5	2.5	
	12×15	e.95(16+16 +32+e30)	8			
	13×16					
	9×11					connected after budding
NHMW 1991/5	11×24					prepared to budding
	11×19					bicentric
	13					

Description.—Corallum phaceloid. Corallites parallel, densely crowded, with rhythmically expanding and contracting diameters, in contact where diameters are enlarged. Axial fossa very narrow. Septal apparatus composed of numerous thin septa, zigzag adaxially, differentiated into four size orders: the S1 septa reaching the axial fossa, the S2 septa slightly shorter than the former, the S3 septa ca. four-fifths the length of the S1 septa, the S4 septa developed in the majority of systems, variable in length up to one-third that of the S1 septa. Septal sides with abundant, small and obtuse granules. Internal borders of the longest septa can produce a parietal columella. Endotheca dense, built of low, horizontally expanding dissepiments axially, and vesicular peripherally. Wall originally thin, pellicular, secondarily slightly thickened from the internal side by a sclerenchymal deposit. Monocentric subcircular and oval corallites are typical, but prolonged detachment of the corallites after budding produced clusters of two to three and even four individuals. Increase by intracalicular budding gave subequivalent and unequivalent corallites (ratio of new to adult corallite diameters is about 1:6). In some corallites creation of a new centre took place by an interruption of two to three septa. In others, new corallites resulted through simple elongation of the adult and separation of an elongated part. The corallites became isolated from each other by a thin dividing wall and detached in developing deep and narrow invaginations of the external wall. Division took place after formation of a wall.

Remarks.—Three species were described from Hydra Island, Greece (Turnšek and Senowbari-Daryan 1994): *H. rhythmica*, *H. fossulata*, and *H. ornamenta*, differing slightly in number of septa and ornamentation, and in diameters. In corallite dimensions, the Alpine form is closest to *H. fossulata*, but it differs from all of them in a much lower density of septa (*H. fossulata:* 7–8 in 2 mm, *H. ornamenta*: 11–12 in 2 mm).

Three specimens from the Gosaukamm were collected by Martin Schauer in the 1980s: two close to the Lacian exposures in the Armkar, and one specimen from the Alaunian exposure in the Oberes Armkar (locality details after Schauer in Roniewicz 1996: fig. 1).

Stratigraphic and geographic range.—Austria: Northern Calcareous Alps, Dachstein Plateau, north of Feisterscharte, massive ”reef” facies of the Lacian 3, above the conodont-bearing horizon with the association of *Epigondolella triangularis* and *Norigondolella navicula*; Gosaukamm Armkar, Lacian, and Oberes Armkar, Alaunian.

Family B

Remarks.—The set of morphological and microstructural features (preserved in traces), seemingly unique for *Thamnasterites* gen. nov., do not allow for unambiguous familial classification of this genus.

Genus *Thamnasterites* nov.

Etymology: Resembling genus *Thamnasteria* in the shape and small size of corallites and pennula-like septal micromorphology, although differing from it in the astreoid, not thamnasterioid type of colony, and in thin elements of the microstructure.

Type species: *Thamnasterites astraeoides* sp. nov., by monotypy; see below.

Diagnosis.—Colony astraeoid. Costosepta nonconfluent, fusiform. Septa with flat pennular structures. Endotheca vesicular. Axial cavity empty. Budding intercalicular.

Remarks.—Monotypic genus, distinguished by its small corallites with fusiform, thick costosepta, septa with pennular structures, and a lack of wall and peritheca (astraeoid colony). There are no comparable forms among Triassic corals described so far.

Thamnasterites astraeoides sp. nov.

Fig. 6F.

Etymology: From Latin *astraea*, star.

Holotype: An incomplete colony GBA 2009/019/4.

Type locality: Austria, Northern Calcareous Alps, southern Dachstein Plateau, north of Feisterscharte.

Type horizon: Norian, Lacian 1, massive, organodetrital limestone at the horizon with the *Epigondolella quadrata* Conodont Zone.

Diagnosis.—Adult corallites about 4 mm in diameter. Radial elements thick, ca. 20 in number.

Material.—The holotype with thin sections.

Measurements (in mm):

d adults	c-c	s	eh
4	3–5	12–22 (6+6+S3)	0.2–0.25

Description.—Colony lamellate, corallites astraeoid arranged homogeneously, their radial elements nonconfluent. Costosepta fusiform and very thick with the exception of the internal edge. The fusiform morphology shows that the costosepta were exsert, so the neighbouring calices were probably separated by a depression. Septa differentiated into three size orders subequal in thickness: the S1 septa approaching near the center, the S2 septa considerably shorter, the S3 septa very short. Septal surface covered with rare large, flat pennula-like micromorphology. Wall lacking. Dissepiments vesicular. Budding intercalicular.

The traces of the microstructure are preserved as a dark line (dots in linear arrangement?) in the septal mid-line, and as more or less dispersed dots in the remaining parts of septa. The above traces, peculiar for the small-corallite coral, are

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uncomparable to microstructural remains in other Triassic corals recognised so far.

Stratigraphic and geographic range.—Like the holotype.

Undeterminable corals

These corals, most probably representing new genera, but not determined further due to the scarcity of the material, are included here in order to show the diversity of the fauna considered. All the material originates from the vicinity of Guttenberg–Hause, north of Feisterscharte.

Material and measurements (in mm):

Coll. No. GBA	Taxon	d	s	ed	Remarks
1995/2/1/2 (thin section) Fig. 8B	solitary "dwarfish", coral	1	24 septa (6+6+12); 24 costae		wall septothecal, sculptured
2007/152/3 (thin sections) Fig. 8C	forking coral	6×10	>24 (12+12+S3 +S4)	tabuloid dissepiments 6/5mm	columella papillar; budding intracalicular
2009/019/12/3 (thin section) Fig. 2E	solitary? pachythecal-like coral	lumen 3; corallite 7	e.24 (6+6+e.12); sharp septal micro-morphology		thick wall, septa ornamented

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References

Alloiteau, J. 1952. Madréporaires post-paléozoïques. *In*: J. Piveteau (ed.), *Traité de Paléontologie 1*, 539–684. Masson et C^{ie}, Paris.

Alloiteau, J. 1958. Monographie des Madréporaires fossiles de Madagascar. *Annales Géologiques de Madagascar* 25: 1–218.

Beauvais, L. 1981. Sur la taxinomie des Madréporaires mésozoiques. *Acta Palaeontologica Polonica* 25: 345–360.

Beauvais, L. 1986. Monographie des Madréporaires du Jurassique inférieur du Maroc. *Palaeontographica A* 194: 1–68.

Bechstädt, T. and Brandner, R. 1970. Das Anis zwischen St. Vigil und dem Höhleintal (Pragser- und Olanger Dolomites, Südtirol). *Festband des Geologisches Institut, 300-Jahr-Feier Universität Innsbruck. Dezember 1970*, 9–103. Universität Innsbruck, Innsbruck.

Benton, M.J. 1986. More than one event in the late Triassic mass extinction. *Nature* 321: 857–861.

Bourne, G.C. 1900. The Anthozoa. *In*: E.R. Lankester (ed.), *A Treatise on Zoology, Pt. 2, The Porifera and Coelenterata*,1–84. A. and C. Black, London.

Carruthers, A.H and Stanley, G.D. Jr. 2008. Systematic analysis of Upper Triassic silicified sclaractinan corals from Wrangellia and the Alexander terrane, Alaska and British Columbia. *Journal of Paleontology* 83: 470–491.

Chevalier, J.P. 1987. Ordre des Scléractiniaires. *In*: P.P. Grassé (ed.), *Traité de Zoologie. Anatomie, Systématique, Biologie III, 3, Cnidaires, Anthozoaires*, 403–679. Masson, Paris.

Cuif, J.P. 1967. Structure de quelques polypiers phacéloïdes triasiques. *Bulletin de la Société Geologique de France* (sér. 7) 8: 125–132.

Cuif, J.P. 1975a. Recherches sur les Madréporaires du Trias. II. Astraeoidea. Revision des genres *Montlivaltia* et *Thecosmilia*. Etude de quelques types structuraux de Trias de Turquie. *Bulletin du Muséum National d'Histoire Naturelle* (sér. 3) 275 (novembre–decembre 1974), *Sciences de la Terre* 40: 293–400.

Cuif, J.P. 1975b. Caractères morphologiques, microstructuraux et systématiques des Pachythecalidae nouvelle famille de Madrépoires triasiques. *Geobios* 8: 157–180.

Cuif, J.P. 1975c. Recherches sur les Madréporaires du Trias. III. Etudes des structures pennulaires chez les Madréporaires triasiques. *Bulletin du Muséum National d'Histoire Naturelle* (sér. 3) 310, *Sciences de la Terre* 44: 45–127.

Cuif, J.P. 1976. Recherches sur les Madréporaires du Trias. IV. Formes cério-méandroïdes et thamnastérioides du Trias des Alpes et du Taurus sud-analotien. *Bulletin du Muséum National d'Histoire Naturelle* (sér. 3) 381, *Sciences de la Terre* 53: 68–194.

Cuif, J.P. 1977. Arguments pour une relation phylétique entre les Madréporaires paléozoïques et ceux du Trias. Implications systématiques et l'analyse microstructurale des Madréporaires triasiques. *Mémoires de la Société Géologique de France n.s.* 56 (129): 1–54.

Deng, Z. and Kong, L. 1984. Middle Triassic corals and sponges from Southern and Eastern Yunnan [in Chinese with English summary]. *Acta Palaeontologica Sinica* 23: 489–504.

Deng, Z. and Zhang, Y. 1984. Supplemental notes on Mesozoic Scleractinia from Mts. Hengduan, Southwest China. *Bulletin of the Nanjing Institute of Geology and Palaeontology, Academia Sinica* 9: 285–307.

Ezaki, Y. 2000. Palaeoecological and phylogenetic implications of a new scleractiamorph genus from Permian sponge reefs, South China. *Palaeontology* 43: 199–217.

Ezzoubair, F. and Gautret, P. 1993. Recherches sur les affinités des Spongiomorphidae Frech, 1890. 2. Révision des caractéristiques microstructurales des espèces initialement attribuées aux Spongiomorphidae. *Geobios* 26: 279–290.

Flügel, E. and Hötzl, H. 1966. Hydrozoen aus Ober-Jura der Hesperischen Ketten (Ost Spanien). *Neues Jahrbuch der Geologie u. Paläontologie, Abhandlungen* 124: 103–117.

Frech, F. 1890. Die Korallenfauna der Trias. Die Korallen der juvavischen Triasprovinz. *Palaeontographica* 37: 1–116.

Gill, G.A. 1967. Quelques précisions sur les septes perforés des polypiers mésozoïques. *Mémoires de la Société Géologique de France n.s.* 46 (106): 55–81.

Hallam, A. and Wignall, P.B. 1997. *Mass Extinctions and their Aftermath*. viii + 320 pp. Oxford University Press, Oxford.

Kanmera, K. 1964. Triassic coral Faunas from Konosé Group in Kyushu.

Memoirs of the Faculty of Science, Kyushu University (D) Geology 15: 117–147.

Koby, F. 1889. Monographie des polypiers jurassiques de la Suisse. *Mémoires de la Société Paléontologique Suisse* 16: 457–582.

Krasnov, E.V. 1983. *Korally v rifovyh faciah mezozoâ SSSR*. 160 pp. Nauka, Moskva.

Krystyn, L., Mandl, G.W., and Schauer, M. 2009. Growth and termination of the Upper Triassic platform margin of the Dachstein area (Northern Calcareous Alps, Austria). *Austrian Journal of Earth Sciences* 102: 23–33.

Laube, G.C. 1865. Die Fauna der Schichten von St. Cassian. I. Abteilung. Spongitarien, Corallen, Echiniden und Crinoiden. *Akademie der Wissenschaften, Denkschriften* 24: 223–266.

LeMaitre, D. 1935. Etude paléontologique sur le Lias du Maroc: Description des Spongiomorphides et des Algues. *Notes et Mémoires du Service des Mines du Maroc* 34: 19–59.

Marcoux, J. and Poisson, A. 1972. Une nouvelle unité structurale majeure dans les nappes d'Anatolya: la nappe inférieure et ses séries mésozoïques radiolaritiques (Taurides occidentales, Turquie). *Comptes Rendus hebdomadaires des séances de l'Académie des Sciences D* 275: 655–658.

Marcoux, J., Baud, A., Krystyn, L., and Monod, O. 1986. Late Permian and Triassic in Western Turkey. *Field Workshop 1986, Guide Book Part 2*, 4–17. Subcommission on Triassic stratigraphy, Instanbul Technical University, Istanbul.

Melnikova, G.K. 1971. New data on morphology, microstructure and systematics of the Late Triassic Thamnasterioidea [in Russian]. *Paleontologičeskij žurnal* 2: 21–35.

Melnikova, G.K. 1974. The peculiarities of histological structures and microstructures of the septal apparatus in the Late Triassic Scleractinia [in Russian with English abstract]. *Transactions of Institute of Geology and Geophysics, Sibirian Branch Academy of Sciences USSR* 201: 220–224.

Melnikova, G.K. 1975. *Pozdnetriasovye Scleractinii ûgo-vostočnogo Pamira*. 235 pp. Donish, Dušanbe.

Melnikova, G.K. 1983. New Late Triassic Scleractinia of the Pamirs [in Russian]. *Paleontologičeskij žurnal* 1: 45–53.

Melnikova, G.K. 1986. New data on the systematics and phylogeny of the pachythecaliids (scleractinians) [in Russian]. *In*: B.S. Sokolov (ed.), *Fanerozojskie rify i korally SSSR. Trudy V Vsesoûznogo Simpozûma po korallam. Dušanbe, 1983*, 83–89. Dušanbe.

Melnikova, G.K. 1996. New triassic colonial scleractinians of the southeastern Pamirs [in Russian]. *Paleontologičeskij žurnal* 2: 8–33.

Melnikova, G.K. 2001. Type Coelenterata [in Russian]. *In*: A.Û Rozanov, and R.V. Ševerev, (eds.), Atlas triasovyh bespozvonočnyh Pamira, 30–80. Nauka, Moskva.

Melnikova, G.K. and Byčkov,Y. M. 1986. Late Triassic scleractinians of the Kenkeren Mountain Range [in Russian)]. *In*: Û.D. Zaharov and Û.I. Onoprienko (eds.), *Korrelaciâ permo-triasovyh otloženij Vostoka SSSR*, 63–116. Akademiâ Nauk SSSR. Dalnevostočnyj Naučnyj Centre, Biologo-počvennyj Institut, Vladivostok.

Melnikova, G.K. and Roniewicz, E. 2007. The Middle Triassic scleractinia-like coral *Furcophyllia* from the Pamir Mountains. *Acta Palaeontologica Polonica* 52: 401–406.

Melnikova, G.K., Roniewicz, E., and Loeser, H. 1993. New microsolenid genus *Eocomoseris* (Scleractinia, Early Lias–Cenomanian). *Annales Societatis Geologorum Poloniae* 63: 3–12.

Moiseev, A.S. 1951. On corals and other organisms from limestones of the Primorie district (Tetiukhe river basin) [in Russian]. *Trudy Leningradskogo Obŝestva Estestvoisopytatelej* 68: 208–237.

Montanaro-Gallitelli, E. 1975. Hexanthiniaria, a new ordo of Zoantharia (Anthozoa, Coelenterata). *Bolletino della Società Paleontologica Italiana* 141: 21–25.

Montanaro-Gallitelli, E. 1980. Lemniscaterina, a new order, related to Hydrozoa (Coelenterata). *Memoire della Accademia Nazionale di Scienze Lettre e Arti di Modena* 6: 5–79.

Montanaro-Gallitelli, E., Russo, A., and Ferrari, P. 1979. Upper Triassic coelenterates of western North America *Bolletino della Società Paleontologica Italiana* 18: 133–156.

Morycowa, E. 1989. Middle Triassic Scleractinia from the Cracow-Silesia region, Poland. *Acta Palaeontologica Polonica* 33: 91–121.

Münster, G.G. and Braun, F. 1841. *Beiträge zur Petrefacten-Kunde*, 25–39. Commission der Buchnerschen Buchhandlung, Bayreuth.

Newton, C.R., Whalen, M.T., Thompson, J.B., Prins, N., and Delalla, D. 1987. Systematics and paleoecology of Norian (Late Triassic) bivalves from a tropical island arc: Wallowa Terrane, Oregon. *Journal of Paleontology 4, Supplement 61, Memoir* 22: 1–83.

Nützel, A., Blodgett, R.B., and Stanley, G.D. Jr. 2003. Late Triassic gastropods from the Martin Bridge Formation (Wallowa Terrane) of northeastern Oregon and their paleogeographic significance. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 228: 83–100.

Okuda, H., Ezaki, Y., and Yao, A. 2005. Geological complexes of Sabosan area and limestones containing Triassic scleractinian corals in Kochi Prefecture, southwestern Japan. *Earth Science* 59: 371–382.

Orbigny, A. d' 1849. *Note sur des polypiers fossiles*. 12 pp. Victor Masson, Paris.

Qi, W. and Stanley, G.D. 1989. New Anisian corals from Qingyan, Guiyang, South China [in Chinese with English summary]. *Lithospheric Geoscience* 1989: 11–18, Beijing.

Ramovš, A. and Turnšek, D. 1984. Lower Carnian reef buildups in the Northern Julian Alps (Slovenia, NW Yugoslavia). *Razprave IV Razreda SAZU* 25 (4): 163–200.

Ramovš, A. and Turnšek, D. 1991. The Lower Norian (Latian) development with coral fauna on Razor and Planja in the northern Julian Alps (Slovenia). *Razprave IV Razreda SAZU* 32 (6): 175–213.

Reuss, A.E. 1854. Beiträge zur Charakteristik der Kreideschichten in den Ostaalpen, besonders in Gosauthale und am Wolfgangsee. *Denkschriften der Kaiserlichen Akademie der Wissenschaften, mathematisch-physikalische Classe* 7: 1–157.

Romano, S.L. and Palumbi, S.R. 1996. Evolution of scleractinian corals inferred from molecular systematics. *Science* 271: 640–642.

Roniewicz, E. 1989. Triassic scleractinian corals of the Zlambach Beds, Northern Calcareous Alps, Austria. *Denkschriften der Österreichische Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Klasse* 126: 5–152.

Roniewicz, E. 1996. Upper Triassic solitary corals from the Gosaukamm and other North Alpine regions. *Sitzungsberichte. Abteilung I* 202: 4–41.

Roniewicz, E. 2010. Uniform habit spectrum versus taxonomical discrepancy between earlier and later Triassic corals of the Tethys. X International Congress on Fossil Cnidaria and Porifera, St Petersburg, 2007. *Palaeoworld* (online). doi: 10.1016/j.palwor.2010.08.004

Roniewicz, E. and Michalik, J. 1991. *Zardinophyllum* (Scleractinia) from the Upper Triassic of the central Western Carpathians (Czecho-Slovakia). *Geologica Carpathica* 42, 361–363.

Roniewicz, E. and Michalik, J. 1998. Rhaetian scleractinian corals in the Western Carpathians. *Geologica Carpathica* 49: 391–399.

Roniewicz, E. and Morycowa, E. 1989. Triassic Scleractinia and the Triassic/Liassic boundary. *Memoirs of the Association of the Australasian Palaeontologists* 8: 347–354.

Roniewicz, E. and Morycowa, E. 1993. Evolution of the Scleractinia in the light of microstructural data. *Courier Forschungsinstitut Senckenberg* 164: 233–240.

Roniewicz, E. and Stanley, G.D. Jr. 1998. Middle Triassic cnidarians from the New Pass Range, Central Nevada. *Journal of Paleontology* 72: 246–256.

Roniewicz, E. and Stanley, G.D. Jr. 2009. *Noriphyllia*, a new Tethyan Late Triassic coral genus. *Paläontologische Zeitschrift* 83: 467–478.

Roniewicz, E. and Stolarski, J. 1999. Evolutionary trends in the epithecate scleractinian corals. *Acta Palaeontologica Polonica* 44: 131–166.

Roniewicz, E., Mandl, G.W., Ebli, O., and Lobitzer, H. 2007. Early Norian scleractinian corals and microfacies data on the Dachstein Limestone of Feisterscharte, Southern Dachstein Plateau (Northern Calcareous Alps, Austria). *Jahrbuch der Geologischen Bundesanstalt* 147: 577–594.

Roniewicz, E., Stanley, G.D. Jr., Da Costa Monteiro, F., and Grant-Mackie, J.A. 2005. Late Triassic (Carnian) corals from Timor-Leste (East Timor): their identity, setting, and biogeography. *Alcheringa* 29: 287–303.

Schlichter, D. 1992. A perforated gastrovascular cavity in the symbiotic

doi:10.4202/app.2009.0092

deep-water coral *Leptoseris fragilis*: a new strategy to optimize heterotrophic nutrition. *Helgolander Meeresuntersuchungen* 45: 423–443.

Scholz, G. 1972. An Anisian Wetterstein Limestone reef in North Hungary. *Acta Universitatis Szegediensis, Acta Mineralogica, Petrographica* 22: 337–362.

Senowbari-Daryan, B., Zühlke, R., Bechstädt, T., and Flügel, E. 1993. Anisian (Middle Triassic) buildups of the Northern Dolomites (Italy): the recovery of reef communities after the Permian/Triassic crisis. *Facies* 28: 181–256.

Sepkoski, J.J. Jr. 1986. Phanerozoic Overview of Mass Extinction. *In*: D.M. Raup and D. Jablonski (eds.), *Patterns and Processes in the History of Life*, 277–295. Springer-Verlag, Berlin.

Stanley, G.D. Jr. 1979. Paleoecology, structure, and distribution of Triassic coral buildups in Western North America. *University Kansas Paleontological Contributions* 65: 1–58.

Stanley, G.D. Jr. 1988. The history of Early Mesozoic reef communities: a three-step process. *Palaios* 3: 170–183.

Stanley, G.D. Jr. 2003. The evolution of modern corals and their early history. *Earth Science Reviews* 60: 195–225.

Stanley G.D. Jr. and Swart, P.L. 1995. Evolution of the coral-zooxanthellate symbiosis during the Triassic: a geochemical approach. *Paleobiology* 21: 179–199.

Stanley, G.D. Jr. and Whalen, M.T. 1989. Triassic corals and spongiomorphs from Hells Canyon, Wallowa Terrane, Oregon. *Journal of Paleontology* 63: 800–819.

Stolarski, J., Roniewicz, E., and Grycuk, T. 2004. A model for furcate septal increase in a Triassic scleractiniamorph. *Acta Palaeontologica Polonica* 49: 529–542.

Terquem, O. and Piette, E. 1865. Le Lias inférieur de l'Est de la France: *Mémoire de la Société Géologique de France* 8: 1–175.

Turnšek, D. and Buser, S. 1989. The Carnian reef complex on the Pokljuka (NW Yugoslavia). *Razprave IV Razreda SAZU* 30 (3): 75–127.

Turnšek, D. and Ramovš, A. 1987. Upper Triassic (Norian-Rhaetian) reef buildups in the northern Julian Alps (NW Yugoslavia). *Razprave IV Razreda SAZU* 28 (2): 27–67.

Turnšek, D. and Senowbari-Daryan, B. 1994. Upper Triassic (Carnian–Lowermost Norian) corals from the Pantokrator Limestone of Hydra (Greece). *Abhandlungen der Geologischen Bundesanstalt* 50: 477–507.

Turnšek, D., Buser, S., and Ogorelec, B. 1982. Carnian coral-sponge reefs in the Amphiclina beds between Hudajuzna and Zakriz (western Slovenia). *Razprave IV Razreda SAZU* 24 (2): 53–48.

Turnšek, D., Buser, S., and Ogorelec, B. 1987. Upper Carnian reef limestone in clastic beds at Perbla near Tolmin (NW Yugoslavia). *Razprave IV Razreda SAZU* 27 (3): 37–64.

Turnšek, D., Seyfried, H., and Geyer, O.F. 1975. Geologische und Palaeontologische Untersuchungen an einem Korallenvorkommen in Subbetischen Unterjura von Murcia (Süd-Spanien). *Slovenska Akademija Znanosti in Umetnosti, Razred za Prirodoslovne Vede Razprave* 18 (5): 3–35.

Volz, W. 1896. Die Korallen der Schichten von St. Cassian in Sued Tirol. *Palaeontographica* 43 (1–2): 1–124.

Yabe, H and Sugiyama, T. 1931. On some spomdiomorphid corals from the Jurassic of Japan. *Science Reports of the Tohoku Imperial University ser. 2*, 14: 103–105.

Zonneveld, J.P., Henderson, C.M., Stanley, G.D. Jr., Orchard, M.J., and Gingras, M.K. 2007. Oldest scleractinian coral reefs on the North American craton: Upper Triassic (Carnian), northeastern British Columbia, Canada. *Palaeogeography, Palaeoclimatology, Palaeoecology* 243: 421–450.