

Yakhtashian (Artinskian–Early Kungurian) cyanobacteria and calcareous algae from the Carnic Alps (Austria/Italy)

Karl Krainer, Daniel Vachard, and Maria Schaffhauser

ABSTRACT

The Lower Permian calcareous algae are revised in the Zweikofel, Zottachkopf and Trogkofel formations of the Carnic Alps (Austria–Italy border). The cyanobacteria and red algae are *Nostocites*, *Archaeolithoporella*, *Renalcis*, *Gahkumella*, *Koivaella*, *Girvanella*, *Mitcheleania*, *Clinertonella*, *Garwoodia*, *Parachaetetes*, and *Archaeolithophyllum lamellosum* Wray. Among the possible Bryopsidales, *Homannisiphon* is emphasized, and the phylloid algae are formally assigned to the family Anchicodiaceae emend. with the tribe Anchicodiae nomen translatum synonymized with Ivanoviae, and the genera *Anchicodium*, *Kansaphyllum*, *Iranophyllum*, *Ivanovia*, *Eugonophyllum*, *Calcipatera*, and *Neoanchicodium*. The new and emended species of phylloid algae are *Eugonophyllum magnum* (Endo) emend. (synonymous with *Succodium duisbergi* Homann), and *Calcipatera schoenlaubi* n. sp. Among the Dasycladales, the tribe Anthracoporellae n. trib. is described; the epimastoporaceans are revised; and *Gyroporella*, *Macroporella*, *Mizzia* and *Connexia* are mentioned. Among the Epimastopora-ceae, the genera *Epimastopora*, *Epimastoporella*, *Globuliferoporella* and *Pseudoepimastopora* are emended and re-described as *Epimastopora* emend., *Epimastopora* n. gen., *Pseudoepimastopora* emend., and *Globuliferoporella* emend. *Epimastopora japonica* Endo is formally designated as the type species of *Epimastopora* emend.; *E. likana* Kochansky and Herak and *E. cf. izawaikensis* Endo are other regional representatives of *Epimastopora* emend.; *Globuliferoporella piai* (Kordé) n. comb. emend. is proposed as type species in replacement of *G. symmetrica* sensu Chuvashov non Johnson; and *Atractyliopsis carnica* Flügel is re-assigned to *Pseudoepimastopora* emend. Among the Algospongia, the genera *Claracrusta*, *Ungdarella* and *Efluegelia* are analyzed. Flügel's "Algen Sporen" are interpreted as desmae of sponges. Pseudovermiporellids, tubiphytids and ellesmerellids, considered here as foraminifers, are described in a second paper.

Karl Krainer. Institute of Geology, University of Innsbruck, Innrain 52, A-6020 Innsbruck, Austria. Karl.Krainer@uibk.ac.at

Daniel Vachard. Collegial and International Research Centre of Active Seniors (CIRCAS), 1 rue desTilleuls, 59152 Gruson, France. Daniel.Vachard@free.fr

Maria Schaffhauser, Tiroler Landesmuseum, Fachbereich Erdwissenschaften, Krajnc Straße 1, 6060 Hall, Austria. M.Schaffhauser@tiroler-landesmuseen.at

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INTRODUCTION

Algae from the Carnic Alps and Karawanken Mountains (Austria, Italy and Slovenia) have been described, for more than one century, by Gortani (1906); Pia (1937); Kochansky-Devidé (1970a, 1979); Homann (1972); Flügel (1979, 1980, 1981); Flügel and Flügel-Kahler (1980); Flügel et al. (1997); Krainer (1991, 1993, 1995a); Samankassou (1997a, 1997b); Krainer et al. (2003b); Forke and Samankassou (2000); Vachard and Krainer (2001a, 2001b); and Schönlaub and Forke (2007). However, these authors described calcareous algae only from parts of the lower Permian succession of the Carnic Alps or presented a brief overview. For example, calcareous algae from the Trogkofel Formation were mostly described from samples which were not collected at the type locality or type section. A type section of the Trogkofel Formation was first defined and described by Schaffhauser (2013) and Schaffhauser et al. (2015). The large number of samples (and thin sections) from the lower Permian succession, particularly from the type sections of the Zweikofel, Zottachkopf and Trogkofel formations, which were taken for microfacies and micropaleontological

investigations (e.g., Krainer et al., 2009; Krainer and Schaffhauser, 2012; Schaffhauser, 2013; Schaffhauser et al., 2015), allowed us to study the algal assemblages in much more detail. We already described the latest Pennsylvanian and earliest Permian algae of the Auernig and Rattendorf groups (Vachard and Krainer 2001a, 2001b). In this paper, we present a comprehensive description of calcareous algae of the upper Cisuralian Zweikofel, Zottachkopf and Trogkofel formations in the Carnic Alps along the Austrian/Italian border (Figures 1 and 2).

LOCATION AND METHODS

The Zweikofel Formation was studied at the type section at Zweikofel (sections ZK, ZKO), Garnitzenbach (section GB, including the uppermost part of the underlying Grenzland Formation) and the Zottachkopf Formation at several sections in the Trogkofel–Zottachkopf massif where the formation underlies the massive Trogkofel Limestone. The Zottachkopf Formation was studied on the northern side (sections TNA, TNB, TNC, Z, and ZT), the southern side (section TKS) and southwestern side (section TKW) of the Trogkofel mas-

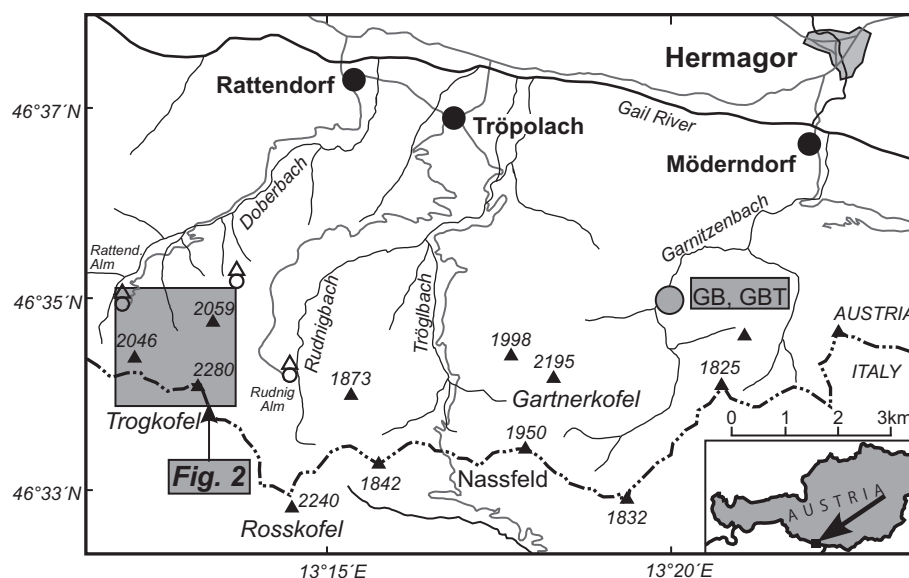


FIGURE 1. Map of the Trogkofel area in the Carnic Alps (southern Austria). GB: section Garnitzenbach of the uppermost part of the Grenzland Formation and Zweikofel Formation, GBT: Section Garnitzenbach of the Trogkofel Formation.

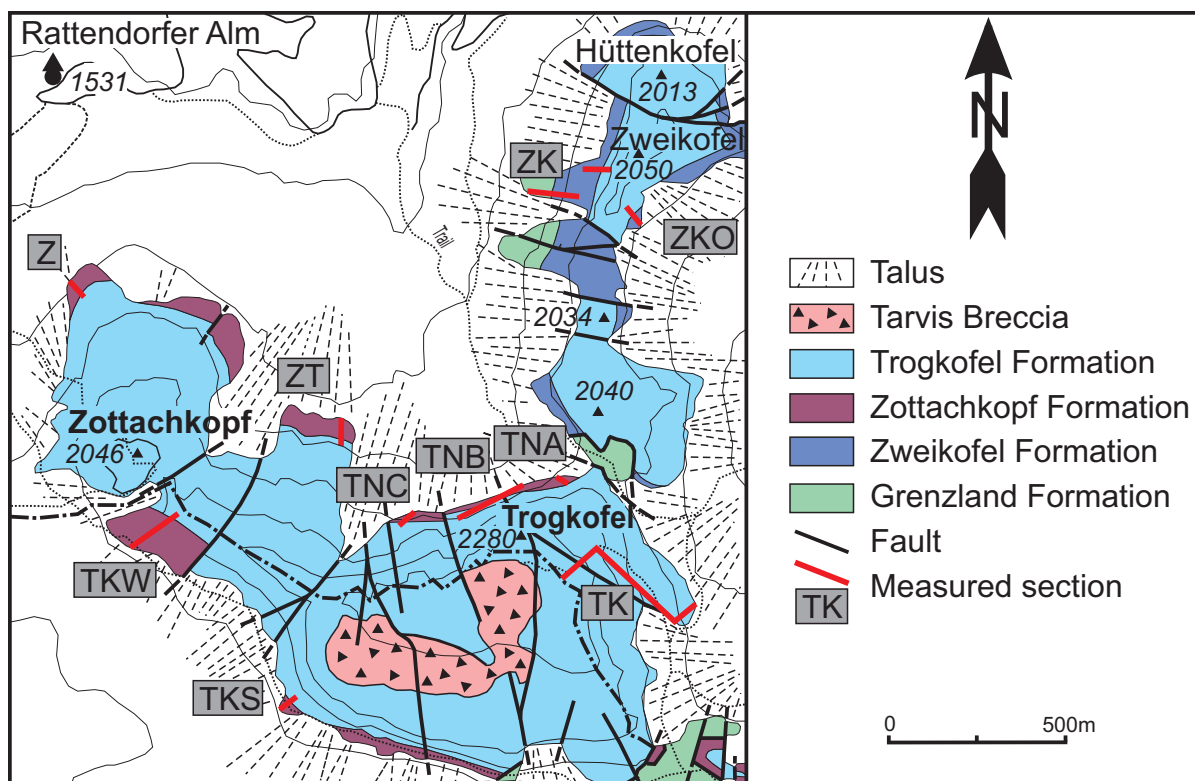


FIGURE 2. Detailed geologic map of the Trogkofel area. ZK: type section of the Zweikofel Fm, ZKO: section through the uppermost part of the Zweikofel Fm at Zweikofel East, TNA, TNB and TNC: sections of the Zottachkopf Fm on the northern side of the Trogkofel Massif, ZT: section through the upper part of the Zottachkopf Fm and basal part of the Trogkofel Fm, Z: section on the northern side of Zottachkopf through the upper part of the Zottachkopf Fm and basal Trogkofel Fm, TKW: section Trogkofel West through the uppermost part of the Zottachkopf Fm and basal part of the Trogkofel Fm, TKS: section Trogkofel South including the uppermost part of the Zottachkopf Fm and basal Trogkofel Fm; TK: type section of the Trogkofel Fm.

sif. Most of these sections include the Zottachkopf Formation and the lowermost part of the Trogkofel Formation.

The Trogkofel Formation was studied at the type section (section TK), which is exposed on the northeastern side of the Trogkofel massif. One section through part of the Trogkofel Formation was studied at Garnitzenbach (section GBT), about 10 km east of the Trogkofel massif (Figure 1). The basal Trogkofel Formation was studied at several sections in the Trogkofel and Zottachkopf massif. The locations of the studied sections are shown on Figures 1 and 2.

From all sections, samples were collected from which thin sections were prepared for microfacies analysis and determination of fossils, particularly calcareous algae and foraminifers. In order to complete our biostratigraphical and taxonomical documents, we have also revisited and re-studied the sections of the Artinskian Zweikofel Formation (sections ZK and GB, Figures 1 and 2), already mentioned in Vachard and Krainer (2001b). We

analyzed more than 675 thin sections in terms of microfacies and microfossils. Microfossils were described, photographed and documented in 20 plates of calcareous microflora (this work), and 47 plates of microfauna (Krainer et al., submitted).

Taxonomic descriptions and systematics follow the schemes of algal taxonomy proposed by Bassoullet et al. (1979), Bucur (1994), Granier and Grgasović (2000), and Vachard and Cózar (2010). The material is housed at Innsbruck University, Austria (collection numbers GB1–175, GBT1–11, TK 1–70, TKS1–19, TKW1–18, TM1–9, TNA1–30, TNB1–23, TNC1–11, Z1–19, ZK1–215, ZKO1–47, and ZT1–18).

HISTORICAL BACKGROUND

Upper Paleozoic sediments and fossils of the Carnic Alps have been studied by Austrian, Italian and German scientists, starting with the work of Frech, Geyer, Gortani, Schellwien, Stache, Taramelli, Vinassa de Regny and others, at the end of

the nineteenth century, and continued between the two World Wars by Heritsch, Kahler and Selli, who established the basic stratigraphic scheme summarized in Heritsch (1943). After World War II, paleontological and biostratigraphical studies as well as mapping were intensified, resulting in geological maps of the Naßfeld-Pramollo area (Kahler and Prey, 1963; Selli, 1963; Schönlaub, 1987; Venturini, 1990b; Schönlaub and Forke, 2007), refined biostratigraphical subdivisions, especially those of the Late Carboniferous and Early Permian, based on fusulinids (Kahler, 1985, 1986), as well as microfacies and facies models describing depositional patterns of reef and non-reefal shelf sediments such as those of Flügel (1971a, 1974, 1980, 1981, 1987); Buggisch et al. (1976); Buttersack and Boeckelmann (1984); Venturini, (1990a, 1991); Massari and Venturini (1990); Massari et al. (1991); Krainer (1991, 1992, 1995a, 2007); Flügel et al. (1997); Forke et al. (1998); Samankassou (1998, 1999, 2002, 2003); Krainer et al. (2003b); Sanders and Krainer (2005); Krainer and Schaffhauser (2012); Schaffhauser (2013); Schaffhauser et al. (2015). Most studies involved 1) fusulinids summarized in Kahler (1985, 1986); and completed in Forke (1995, 2000, 2002); Forke et al. (1998); Forke and Samankassou (2000); Kahler and Krainer (1993); Krainer and Davydov (1998); Davydov and Krainer (1999); and Davydov et al. (2013); 2) calcareous algae in Homann (1972); Flügel and Flügel-Kahler (1980); 3) conodonts in Forke (2002); and 4) smaller foraminifers in Vachard and Krainer (2001a, 2001b). Boersma and Fritz studied fossil plants summarized in Fritz and Krainer (2006, 2007). Forke et al. (2006) and Schönlaub et al. (2007) provided a summary of the Upper Paleozoic succession of the Carnic Alps.

GEOLOGIC SETTING

In the Carnic Alps, the Variscan Orogenic Phase culminated during the middle Westphalian and was followed by block- and wrench-faulting resulting in the formation of discrete sedimentary basins (Venturini, 1982, 1990a, 1991). These basins were filled with deltaic to shallow marine sediments of the Late Carboniferous Bombaso Formation and Auernig Group, and the Late Carboniferous/Early Permian Rattendorf and Trogkofel groups (Figures 3–5). This approximately 2000 m thick, sedimentary succession of dominantly shallow marine siliciclastic and carbonate rocks unconformably overlies the folded Variscan basement. The succession is of Middle Pennsylvanian (latest Moscovian) to Early Permian (Kungurian) age and was deposited in sedimentary basins that formed by block faulting

during the Westphalian. The succession is divided into the Bombaso Formation (= Collendiaul Formation and Malinfier Formation, according to Schönlaub and Forke, 2007), Auernig Group (or Auernig Formation according to Schönlaub and Forke, 2007), Rattendorf Group and Trogkofel Group; summaries of which were given in Schönlaub and Forke (2007).

The Auernig and Rattendorf groups are composed of mixed siliciclastic-carbonate shelf deposits forming well-developed cycles. Thanks to the rich fusulinid fauna, the Auernig Group is dated as Kasimovian and Gzhelian (Kahler, 1983a, 1985, 1986, 1989; Krainer and Davydov, 1998). Plant fossils, which are known from many localities and different stratigraphic levels throughout the succession, indicate a Stephanian age (Fritz et al., 1990; Fritz and Krainer, 1993, 1994, 1995, 2006, 2007).

The Auernig Group is conformably overlain by the Rattendorf Group, which is divided into the Schulterkofel Formation (Lower *Pseudoschwagerina* Limestone: abbreviated into LPL, LP or UPK), Grenzland Formation and Zweikofel Formation (Upper *Pseudoschwagerina* Limestone: abbreviated into UP, UPL or OPK). Recently, Schaffhauser et al. (2010) introduced the Zottachkopf Formation, which underlies the Trogkofel Formation in the Trogkofel massif, differs in facies and is probably younger than the Zweikofel Formation. The Zweikofel and Zottachkopf formations are overlain by the Trogkofel Formation.

CISURALIAN RATTENDORF GROUP AND TROGKOFEL FORMATION

Rattendorf Group

The Rattendorf Group consists of shallow marine carbonate and siliciclastic sediments of nearshore, inner shelf and outer shelf environments. The succession is divided into the Schulterkofel, Grenzland, Zweikofel and Zottachkopf formations.

Schulterkofel Formation

At the type section, the Schulterkofel Formation is approximately 137 m thick and composed of three depositional cycles consisting of shallow marine limestones and thin siliciclastic intervals (mostly sandstone), which form the bases of the depositional sequences and were deposited during relative sea-level lowstands. During transgression, well-bedded fossiliferous limestones and massive algal mounds accumulated (Krainer et al., 2003b). Bedded cherty limestones with marl intercalations

SUB-SYSTEMS	SUBCOMMISSION ON PERMIAN STRATIGRAPHY		UNITED STATES OF AMERICA		RUSSIA (URALS)	CENTRAL TETHYS	CHINA
LATE	Lopingian	Changhsingian				Dorashamian	Changhsingian
		Wuchiapingian				Dzhulfian	Wuchiapingian
			Ochoian				
MIDDLE	Guadalupian	Capitanian	Capitanian		Tatarian	Midian	Maokouian
		Wordian	Wordian		Kazanian		
						Murghabian	
		Roadian	Roadian		Ufimian	Kubergandian	
EARLY	Cisuralian	Kungurian	Leonardian	Cathedralian	Kungurian	Bolorian	Chihsian
		Artinskian		Hessian	Artinskian	Yakhtashian	
		Sakmarian	Wolfcampian	Lenoxian	Sakmarian	Sakmarian	Mapingian
		Asselian		Nealian	Asselian	Asselian	

FIGURE 3. Correlation of Permian stages.

are interpreted to have been deposited during relative sea-level highstands with water depths of some tens of meters. Fusulinid-rich limestone beds are present at different stratigraphic levels, particularly at the base and on top of the siliciclastic intervals. Fusulinids of these beds are considered as parautochthonous assemblages, accumulated during periods of low sediment input (Buggisch et al., 1976, Flügel, 1974, 1977; Forke et al., 1998; Homann, 1969; Samankassou, 1997a, 1999).

Grenzland Formation

The Lower Permian (Asselian–Sakmarian) Grenzland Formation of the Rattendorf Group, is exposed along the Austrian/Italian border. The Grenzland Formation is more than 300 m thick, and is composed of siliciclastic sediments and intercalated fossiliferous limestone. A complete section is not exposed; data are derived from several sub-sections. There is no overlap between the individual subsections.

The lower part (50–100 m), which conformably rests on fossiliferous limestone of the Schul-

terkofel Formation, is non-cyclic, entirely siliciclastic and composed of siltstone, sandstone and rare fine-grained conglomerate. Siltstone locally contains brachiopods, crinoid fragments and abundant trace fossils (mainly *Zoophycos*), and sandstone commonly displays hummocky cross-bedding.

The middle (~175 m) and upper parts (~105 m) are a cyclic succession of quartz-rich conglomerate and crossbedded sandstone of a nearshore facies, hummocky crossbedded sandstone of the lower shoreface, offshore siltstone and shale and fossiliferous limestone forming well-developed parasequences. The upper part is conformably overlain by the Zweikofel Formation. In the middle and upper parts, at least 15 cycles (parasequences) are recognized, and the thickness of these parasequences ranges from approximately 10 to 30 m. A cyclic sequence is predominantly composed of shallow marine siliciclastic sediments (quartz-rich conglomerates, sandstones and siltstones) and intercalated, thin, fossiliferous limestone intervals (Buttersack and Boeckelmann,

TETHYS		GLOBAL STAGES	URALS	CHINA	CARNIC ALPS	TEXAS		NEW MEXICO
KUB.	<i>Cancellina</i>	ROADIAN	?UFIMIAN	XIANGBOAN	TARVIS BRECCIA	CUTOFF FORMATION (part.)		?
	<i>Armenina</i>	272.3						
BOLORIAN	<i>Misellina parvicostata</i>	KUNGURIAN	IRENIAN	(part.)		LEONARDIAN	CATHEDRALIAN (LATE LEONARDIAN)	SAN ANDRES FORMATION
	<i>Brevaxina dyhrenfurthi</i>							
	<i>Pamirina darvasica</i>		FILIPOVIAN		GOGGAU MEMBER			GLORIETA SST.
YAKHTASHIAN	<i>Robustoschwagerina tumida</i> <i>Chalaroschwagerina vulgaris</i> <i>Darvasella</i> spp.		279.3	SARANIAN	LUODIANIAN		TROGKOFEL FORMATION	
	<i>Darvasites contractus</i> <i>Chalaroschwagerina solita</i>	ARTINSKIAN	SARGINIAN	ZOTTACHKOPF FM.		LENOXIAN (part.) (LATE WOLFCAMPIAN)	APACHE DAM FORMATION	
	?		IRGINIAN	ZWEIKOFEL FORMATION			ROBLEDO MOUNTAINS FORMATION	
	<i>Zellia colanii</i> <i>Minojapanella</i> sp.		BURTSEVIAN				COMMUNITY PIT FORAMTION (uppermost part)	
		290.1						

FIGURE 4. Correlation of Yakhtashian and Bolorian regional stages.

1984; Boeckelmann, 1985). In the upper part a thin interval of nonmarine fine-grained red beds with an intercalated pedogenic limestone is present. A caliche horizon and a red shale horizon with scattered angular quartz grains in the upper part of the sequence point to subaerial exposure. Plant fossils have been described from a thin shale intercalation by Fritz and Boersma (1984) and Fritz and Krainer (2004). Based on fusulinids, the middle and upper parts are of Sakmarian age. Zircons from an ash layer near the top of the lower part yielded a U/Pb radiometric age of 296.46 ± 0.11 Ma (latest Asselian). The cycles coincide therefore with the maximum extent of the Gondwana glaciation in the Southern Hemisphere, which occurred during the Asselian–early Sakmarian, and are interpreted to be caused by glacio-eustatic sea-level fluctuations (Krainer, 2012).

Zweikofel Formation

This formation is represented by a cyclic sequence composed predominantly of dark gray, thin-bedded fossiliferous limestones and intercalated thin intervals of silt- and sandstones and fine-grained, well-rounded and well-sorted quartz-rich conglomerates. Limestones contain abundant fossils, particularly calcareous algae (Homann, 1972),

small foraminifers (Flügel, 1971b), fusulinids, corals, bryozoans, brachiopods, gastropods, bivalves and echinoderm fragments. Microfacies have been described by Flügel (1968), Buttersack and Boeckelmann (1984), and Sanders and Krainer (2005). Small algal mounds occur in the lower part (Forke, 1995; Samankassou, 2003). Cycles indicate repeated shifting from nearshore to offshore environments in an open marine shelf lagoon with normal water circulation (Flügel, 1981). Compared to the Schulterkofel and Grenzland formations, the limestones are characterized by more diverse fossil assemblages and microfacies types (Flügel, 1971a, 1981; Flügel et al., 1971).

According to Krainer and Schaffhauser (2012), the mixed siliciclastic-carbonate Zweikofel Formation at the type section (Zweikofel) and at Garnitzenbach is 94–106 m thick and consists of a cyclic succession of thin- to thick-bedded fossiliferous limestone and five intercalated, thin intervals of siltstone, sandstone and fine-grained, quartz-rich conglomerate. Fossils indicate deposition in a shallow-marine nearshore environment. The carbonate facies is characterized by moderate- to high-energy facies types (bioclastic, oolitic and oncolitic grainstone to packstone) and low- to moderate-energy facies types (bioclastic and oolitic

Ma	GUAD.	Roadian	Kahler 1986		Schönlaub & Forke 2007		Davydov et al. 2013 this study		
		272,3							
		Kungurian					Goggau Limestone	<i>Pamirina darvasica</i>	
280							Trogkofel Limestone	<i>Robustoschw. tumida</i> <i>Chalaroschwagerina globularis</i> <i>Darvasella</i> spp.	
		283,5					Zottachkopf Fm.	<i>Chalaroschw. solita floccosa</i> <i>Perigondwania forkii</i> <i>Robustoschw. nucleolata</i> <i>Sakmarella lubenbachensis</i> <i>Sakmarella fluegeli</i> <i>Zellia colanii</i>	
		Artinskian	TROGKOFEL GROUP	Goggauer Kalk	<i>Pamirina Pseudofusulina vulgaris</i>	Trogkofel Limestone	<i>Robustoschwagerina spatiosa</i>	Zweikofel Formation	
				Treßdorfer Kalk	<i>Praeparafusulina lutugini</i>				
290		290,1		Seikofelkalk	<i>Pseudofusulina tschernyschewi</i>	Zweikofel Formation	<i>Robustoschw. geyeri</i> <i>Zellia heritschi</i> <i>Paraschw. s.l. nitida</i>		
		Sakmarian		Trogkofelkalk Rotkalk des Trogkofelkalkes	<i>Pseudoschw. lata</i> <i>Robustoschw. schellwieni</i> <i>Robustoschw. geyeri</i>				
		295,0	RATTENDORF GROUP	Oberer Pseudo- schwagerinenkalk	<i>Pseudoschw. pulchra</i> <i>Zellia heritschi</i>	Grenzland Formation	<i>Zellia praeheritschi</i> <i>Paraschw. s.l. pseudomira</i> <i>Sphaeroschw. asiatica</i> <i>Sphaeroschw. carniolica</i> <i>Pseudoschw. extensa</i>	Grenzland Formation	
		Asselian		Grenzlandbänke	<i>Pseudoschw. carniolica</i> <i>Pseudoschw. aequalis + confinii</i>				
				Unterer Pseudo- schwagerinenkalk	<i>Occidentoschw. alpina</i> <i>Rugosofusulina praevia</i>		Schulterkofel Formation		<i>Schwagerina versabilis</i> <i>Daixina postgallowayi</i>
300		298,9					Schulterkofel Formation	<i>Schwagerina versabile</i> <i>Ultradaixina postsokensis</i> <i>Daixina sokensis</i>	
		Gzhelian	AUERNIG GROUP		<i>Pseudofusulinoides</i> <i>Pseudofusulina Dutkevitchia</i>	Auernig Formation	<i>Daixina communis</i> <i>Daixina alpina</i> <i>Dutkevitchia multiseptata</i>	Auernig Group	
		303,7							
		Kasimovian			Auernig Schichtgruppe				
		307,0							
		Moscovian							
310									

FIGURE 5. Pennsylvanian and Cisuralian series in the Carnic Alps.

wackestone to packstone, floatstone and rare cyanobacterial bindstone). A diverse faunal and algal assemblage indicates deposition in a shallow neritic, normal-salinity, low- to high-energy environment (Krainer and Schaffhauser, 2012).

The Zweikofel Formation is composed of six depositional sequences, which are interpreted as high-frequency cycles caused by glacio-eustatic sea-level fluctuations of the Gondwana glaciation (Krainer and Schaffhauser, 2012).

Within the Zweikofel Formation, five fusulinid assemblages are distinguished at Zweikofel, indicating approximately an Artinskian age, and the regional subdivisions, late Hermagorian to Yakhtashian (Krainer and Schaffhauser, 2012; Davydov et al., 2013).

Zottachkopf Formation

Detailed sedimentological studies of the Lower Permian succession at Zweikofel, Trogkofel and Zottachkopf showed that the bedded facies,

which underlies the massive Trogkofel Limestone at Trogkofel and Zottachkopf differs significantly from the Zweikofel Formation at Zweikofel and Garnitzenbach (as defined by Krainer, 1995b).

The Zweikofel Formation with its type section at Zweikofel (Krainer, 1995b; Krainer and Schaffhauser, 2012) is a mixed siliciclastic-carbonate, cyclic succession of thin- to thick-bedded fossiliferous limestone and five intercalated thin intervals of siliciclastic sediments that allow a subdivision of the Zweikofel Formation into six depositional sequences. These depositional sequences can be further subdivided into parasequences, which are interpreted as high-frequency cycles caused by glacio-eustatic sea-level fluctuations of the Gondwana glaciation (Krainer and Schaffhauser, 2012).

This bedded facies is absent at Zweikofel where the boundary between the Zweikofel Formation and overlying Trogkofel Formation is a surface of erosion, documented by a truncation surface and locally by up to more than 15 m thick, coarse

carbonate breccia composed of reworked limestone clasts displaying a facies similar to the Zweikofel Formation (Krainer et al., 2009). Obviously, the bedded facies (Zottachkopf Formation) has been eroded at Zweikofel.

The bedded facies, originally termed “Oberer Schwagerinenkalk” (Upper *Schwagerina* Limestone; Kahler and Kahler, 1937), is characterized by dark gray, thin bedded limestone containing abundant small oncoids. In the lower part siliciclastic sediments and reddish limestones rich in crinoid fragments occur. Locally, algal mounds are developed, particularly south of Zottachkopf. This bedded succession at Trogkofel and Zottachkopf was assigned to the “Upper *Schwagerina* Limestone” (= Zweikofel Formation) by Heritsch et al. (1934), Kahler and Kahler (1937), Flügel (1968, 1971a, 1975), Homann (1972) and Kahler (1986).

As this bedded facies is not an equivalent of the Zweikofel Formation, but is probably younger and differs in age and facies, Schaffhauser et al. (2010) proposed the term Zottachkopf Formation and included it in the Rattendorf Group.

The type section of the Zottachkopf Formation is located at the base of the steep northern slope of the Trogkofel (sections TNA—lower part, TNB—main part, and TNC—upper part). Reference sections are located on the southern and southwestern side of Trogkofel (TKS, TKW) where the upper part of the Zottachkopf Formation and basal part of the overlying Trogkofel Formation are well exposed. We also studied the Zottachkopf Formation at the sections Trogkar and Zottachkopf (Figure 2).

The Zottachkopf Formation is approximately 120 m thick and comprises thin- to medium-bedded fossiliferous limestones, reef mounds and a succession of red colored limestones with siliciclastic intervals. The carbonate facies is characterized by bioclastic pack/grain/rudstones and oncoidal floatstones, packstones to grainstones. Other common facies include fusulinid packstones, floatstones and echinoderm limestones. Fossils indicate deposition in a shallow marine environment. Compared to the sediments of the Zweikofel Formation, the deposits of the Zottachkopf Formation do not show this well-developed cyclicity, do not contain oolitic grainstones and algal floatstones, and contain only small-sized oncoids. The limestones are characterized by low terrigenous input in the lower part, display an algal assemblage that is dominated by phylloid algae (*Neoanchicodium*) and contain algal mounds up to several meters thick on the southern side of the Zottachkopf. Oncoidal floatstones, fusulinid float-

stones and algal limestones indicate a shallow marine, low-energy environment on the southern side of the Trogkofel in contrast to stronger agitated conditions on the northern side and at Zottachkopf. A position closer to the shelf-edge is assumed. The Zottachkopf Formation is sharply overlain by the Trogkofel Limestone.

The upper part of the Zottachkopf Formation is exposed on the southern side of the Trogkofel massif and is composed of thin-bedded limestones (oncoidal floatstone, fusulinid floatstone, and bioclastic wackestone) with wavy bedding surfaces intercalated with algal mounds that consist of phylloid algal limestone and tubiphytid-algal boundstone. The section on the northern side of Trogkofel is characterized by alternating thin- to thick-bedded limestones, locally displaying poorly preserved cross-bedding. Five small, laterally arranged mounds with thin-bedded intermound facies are intercalated. Oncoidal floatstones are overlain by bioclastic packstones to grainstones and oncoidal packstones. The thickness of this succession reaches 90 m on the northern and about 40 m on the southern side of the Trogkofel massif. Locally, a few single rugose corals and small coral colonies are present in dark gray thin-bedded limestone.

On the north-facing Trogkofel cliff, a well-bedded and red-colored succession of limestone and calcareous siltstone is exposed at the base of the Zottachkopf Formation (section TNA; Figure 2). The succession starts with reddish to gray limestone. Up-section two intervals of siliciclastic sediments (calcareous siltstone) are intercalated. Sedimentary features like small channel deposits, ripple cross-bedding, cross-bedding and horizontal lamination with interspersed quartz grains up to 2 cm in size are more common in the lower interval. These intervals are overlain by wavy to well-bedded limestone composed of bioclastic packstones to rudstones rich in echinoderms, fusulinids and/or oncoids. Thick-bedded limestone of oncoidal packstones and wackestones represent the top of this section. A fault separates this succession from the overlying Trogkofel Formation.

Preliminary biostratigraphic data from fusulinids of the north-facing Trogkofel cliff indicate a late Artinskian age for the Zottachkopf Formation.

Based on a detailed microfacies analysis, Flügel (1971a) interpreted the bedded limestone facies of the Zottachkopf section as deposits of a shallow marine environment with water depths of 10–20 m, normal salinity, mainly on hard bottoms formed by biodebris and algal fragments

cemented by encrusting foraminifers. He proposed a shelf lagoon of an inner shelf region without noticeable influence of coastal sedimentation as depositional setting.

Summing up, the facies of the Zottachkopf Formation is similar to the limestone facies of the Zweikofel Formation, although in detail some differences exist. The Zottachkopf Formation differs from the Zweikofel Formation in the following points: 1) the Zottachkopf Formation does not show the high-frequency cycles and the distinct siliciclastic horizons present in the Zweikofel Formation (Krainer and Schaffhauser, 2012); 2) fusulinids indicate a slightly younger age for the Zottachkopf Formation compared to the Zweikofel Formation; 3) in the Zweikofel massif, the Zweikofel Formation is erosively overlain by a coarse-grained limestone breccia indicating that the Zottachkopf Formation has been completely eroded there.

Trogkofel Formation

The Rattendorf Group is overlain by the dominantly massive Trogkofel Limestone, composed of *Tubiphytes*–*Archaeolithoporella* buildups that Flügel (1980, 1981) interpreted as shelf-edge carbonates.

Recently, Schaffhauser (2013) and Schaffhauser et al. (2015) studied the Trogkofel Formation at the type section. There, the Trogkofel Formation is up to 500 m thick and composed of massive to indistinctly bedded limestone. Locally, the limestone is dolomitized. At the base of this massif, bedded shelf limestones (Zottachkopf Formation) are sharply overlain by the dominantly massive Trogkofel Formation. Farther north, at the Zweikofel massif, the boundary between the Zweikofel Formation and the overlying, clino-bedded Trogkofel Formation is a disconformity. Deposition of the Trogkofel Formation started after a backstep from shelf deposition (Zottachkopf and Zweikofel formations) to a carbonate shelf-margin setting with buildups. The backstep was associated with syndimentary tectonics.

The lower to middle part of the Trogkofel Formation at the type section is characterized by patch buildups that formed in a foreslope to upper slope setting. The main buildup facies include *Tubiphytes*–bryozoan–algal–cement boundstones, botryoidal-fibrous cementstones with *Archaeolithoporella*, and phylloid-algal bafflestones. The reef complex was capped by shelf margin sand shoal deposits and intertidal stromatolites. The build-ups alternate with bioclastic limestone intervals up to 10–15 m thick. The upper ~100 m of the

type section are composed primarily of bioclastic grainstones rich in fusulinids and fragments of calcareous green algae; the bioclastic grainstone intervals episodically aggraded at least to near sea-level. The upper part of the section probably resulted from a shoaling because of moderate progradation-aggradation of the platform, or because of eustatic or tectonic sea-level lowering and/or changed patterns of off bank sediment dispersal.

Syn depositional deformation, and the uplift that terminated deposition of the Trogkofel Formation, may be related to the “Saalian tectonic movements.” The truncation surface that caps the Trogkofel Formation is overlapped by carbonate-lithic breccias (Tarvis Breccia) (Schaffhauser et al., 2015). The nonmarine Tarvis Breccia is composed almost entirely of reworked Trogkofel limestone clasts, indicating that the upper part of the Trogkofel Formation was subaerially exposed and eroded.

RATTENDORF GROUP AND TROGKOFEL FORMATION BIOSTRATIGRAPHY

Kahler (1980, 1986) studied the fusulinids of the upper Paleozoic succession (including the Trogkofel Limestone) in the Carnic Alps over decades and proposed a biostratigraphic chart. For a long time, the stratigraphy in the Carnic Alps remained a lithostratigraphy, in groups and formations, due to the difficulties of the regional correlation with the Permian chronostratigraphy essentially established in the former USSR (Miklukho-Maklay, 1958; Leven, 1975). The Permian lithostratigraphy in the Carnic Alps includes the following formations in ascending order: Schulterkofel Fm, Grenzland Fm, Zweikofel Fm, Zottachkopf Fm, Trogkofel Fm, Goggau Fm, Tarvis Breccia, Val Gardena Fm, and Bellerophon Fm.

Schulterkofel Formation

Based on fusulinids, most of the Schulterkofel Formation is of latest Carboniferous age (*Schwagerina robusta*–*Bosbytauella* (= sic: *Ultradaixina*) *bosbytauensis* Zone), and the uppermost part (highstand systems tract of sequence 3) is dated as early Asselian due to the occurrence of “*Schellwienia*” *bornemanni*, “*Zigarella*” *panjiensis* and “*Likharevites*” *inglorius* (Krainer and Davydov, 1998), even if the validity of these three genera is currently under discussion (see also Kahler and Krainer, 1993; Davydov and Krainer, 1999; Forke, 2002). According to Schönlaub and Forke (2007), the Carboniferous/Permian (C/P) boundary probably lies within the uppermost limestone beds of the

Schulterkofel Formation. They proposed to place the C/P boundary at the base of the Grenzland Formation.

Grenzland Formation

Limestones of the Grenzland Formation contain fusulinids indicating a middle–late Asselian age (Kahler, 1985, 1986; Forke, 1995; Krainer and Davydov, 1998). From the upper part of the Grenzland Formation, Forke (2002) described a fusulinid fauna containing *Alpinoschwagerina* (sic: *Paraschwagerina*) ex gr. *nitida* and early representatives of *Zellia* and *Robustoschwagerina* which indicate an early Sakmarian age (Schönlaub and Forke, 2007).

Zweikofel Formation

Forke (1995) dated the Zweikofel Formation as Sakmarian (*Robustoschwagerina geyeri* Zone and *Zellia heritschi* Zone). Conodonts indicate that the Zweikofel Formation extends into the early Artinskian (Schönlaub and Forke, 2007). The occurrence of some species of the conodont *Neostreptognathodus* and fusulinid *Robustoschwagerina*, in the basal facies in the lower part of the Trogkofel Limestone induced Schönlaub and Forke (2007) to propose a late Artinskian age for the Trogkofel Limestone.

Kahler and subsequent workers included the Zottachkopf Formation in the “Upper *Pseudoschwagerina* Limestone,” which was renamed by Krainer (1995b) as the Zweikofel Formation. According to Heritsch et al. (1934), the type section of the Upper *Pseudoschwagerina* Limestone is at Zottachkopf (section Zottachkopf of this study). Krainer (1995b) defined the section at Zweikofel as the type section of the Upper *Pseudoschwagerina* Limestone (Zweikofel Formation). The type section was studied in detail by Krainer et al. (2009) and Krainer and Schaffhauser (2012).

Kahler (1986) dated the “Upper *Pseudoschwagerina* Limestone” (Zweikofel Formation) as late Asselian based on the occurrence of *Pseudoschwagerina pulchra* and *Zellia heritschi*. Forke (1994, 2002) restudied the fusulinid and conodont fauna of the Zweikofel Formation which he dated as upper Sakmarian to Artinskian due to the occurrence of *Robustoschwagerina geyeri*, *Zellia heritschi* and *Alpinoschwagerina* (sic: *Paraschwagerina*) sensu lato *nitida* (Schönlaub and Forke, 2007).

The fusulinid fauna of the type section at Zweikofel was intensively studied by Davydov et al.

(2013) who determined five fusulinid zones, from bottom to top:

- 1) *Sakmarella moelleri*–*Alpites* (sic: *Darvasites*) *deminuatis* Zone;
- 2) *Sakmarella fluegeli*–*Zellia colaniae* (sic: *colanii*) Zone;
- 3) *Sakmarella lubenbachensis*–*Robustoschwagerina nucleolata* Zone;
- 4) *Leeina pseudodivulgata*–*Chalaroschwagerina incomparabilis* Zone; and
- 5) *Chalaroschwagerina solita floccosa* Zone.

Davydov et al. (2013) proposed the new regional Hermagorian stage as an equivalent of the entire Sakmarian and lower Artinskian of the Global Scale. Fusulinid Zone 1 which occurs in the basal 2 m of the Zweikofel Formation is similar to that of the underlying Grenzland Formation and is assigned to the Sakmarian. Fusulinid zones 2 and 3 indicate an age younger than Sakmarian but older than Yakhtashian. These fusulinid zones are assigned to the late Hermagorian. Fusulinid zones 4 and 5 correspond to the lower Yakhtashian. Therefore, the fusulinid fauna of the Zweikofel Formation at the type section indicates a late Hermagorian to early Yakhtashian age (approximately corresponding to the Artinskian) (Krainer and Schaffhauser, 2012; Davydov et al., 2013).

Zottachkopf Formation and Trogkofel Formation

According to Kahler (1980, 1986), the Rotkalk des Trogkofels, Trogkofelkalk and Seikofelkalk are Sakmarian in age, whereas the Treßdorfer Kalk and Goggauer Kalk are Artinskian, and the Tarviser Breccie is of “Cisjanskian” age. The biostratigraphic age of the Trogkofelkalk is mainly based on fusulinids from Forni Avoltri, as, according to Kahler (1980), the Trogkofel Limestone at the type locality contains only few fusulinids that are not determinable due to dolomitization.

Forke (1995) noted the problem of dating the Trogkofel Limestone as hitherto no fusulinid fauna has been described from the Trogkofel Limestone at Trogkofel; in his discussion he refers to the fusulinids of the Trogkofelkalk of Forni Avoltri. Further confusion produced the misinterpretation of the stratigraphic position of the fusulinid-bearing Red Limestone (Rotkalk der Höhe 2004). The red limestones from locality “Höhe 2004” yielded a fusulinid fauna including *Robustoschwagerina geyeri*, first recognized as a “*Pseudoschwagerina*” by Kahler and Kahler (1938), indicating a younger age than that of the Upper *Pseudoschwagerina* Limestone. Kahler (1983a, 1986, 1992) dated these red

limestones as Sakmarian and therefore ascribed them to the Trogkofel Limestone. Forke (1995) placed the red limestone into the Upper *Pseudoschwagerina* Limestone (= Zweikofel Formation), and dated the entire Zweikofel Formation as Sakmarian. Schönlaub and Forke (2007) dated the Zweikofel Formation as late Sakmarian to early Artinskian.

Detailed field studies at Zweikofel, Trogkofel and Zottachkopf showed that the red limestone and associated bedded facies that underlies the massive Trogkofel Limestone at Trogkofel and Zottachkopf differs significantly from the Zweikofel Formation at Zweikofel and Garnitzenbach. Outcrops at the base of the steep cliff at the northern side of Trogkofel showed that these red limestones occur near the base of a succession composed mainly of thin-bedded limestone approximately 120 m thick. For this succession which differs from the Zweikofel Formation, Schaffhauser et al. (2010) proposed the term Zottachkopf Formation (see Krainer and Schaffhauser, 2012). Davydov et al. (2013) studied the fusulinid fauna of this red limestone of Höhe 2004. The fauna includes fusulinids that are characteristic of the fusulinid Zone 5 at the top of the Zweikofel Formation (Artinskian). Additionally, the assemblage contains abundant *Darvasella*, including *D. praecox* Leven in Leven, Leonova and Dmitriev, 1992, and *Laxifusulina*, as well as advanced *Robustoschwagerina* species, which in Darvas are characteristic of the upper Yakhtashian and Bolorian and thus pointing to a slightly younger age compared to the Zweikofel Formation (Davydov et al., 2013).

The basal Trogkofel Limestone at Trogkar contains fusulinids that are typical of the upper Yakhtashian in Darvas (Davydov et al., 2013), including *Quasifusulina magnifica* Leven in Leven, Leonova and Dmitriev, 1992, *Chalaroschwagerina globularis* Skinner and Wilde, 1966, *Robustoschwagerina tumida* (Likharev, 1939), *Perigondwania? sera* (Leven in Leven, Leonova and Dmitriev, 1992), *P. oingaronica* (Leven in Leven, Leonova and Dmitriev, 1992), and *Praeskinnerella pseudogruperensis* Leven in Leven, Leonova and Dmitriev, 1992. According to Davydov et al. (2013), the Trogkofel Limestone is of late Artinskian to early Kungurian (upper Yakhtashian) age, but it should be considered that fusulinids from the middle and upper part of the Trogkofel Limestone have not yet been studied.

Summing up, fusulinids of the red limestone at the base of the Zottachkopf Formation indicate a slightly younger age (late Artinskian) than the

Zweikofel Formation. The overlying lower part of the Trogkofel Formation is dated as late Artinskian to early Kungurian.

SYSTEMATIC PALEONTOLOGY

(by D. Vachard)

The studied groups are: Cyanobacteria, Rhodophyta, Bryopsidales (including phylloid algae and gymnocodiaceans), Dasycladales and Algospongia (Figure 6). Their supposed phylogenies, based on numerous observations of the algal and pseudoalgal Paleozoic groups are summarized here in four figures (Figures 7-10). The taxa mentioned in this study are listed in a table (Table 1). Taxonomic descriptions and systematics follow the schemes of algal taxonomy proposed by Bassoulet et al. (1979), Bucur (1994), Granier and Grgasović (2000), and Vachard and Cózar (2010). The material is housed at Innsbruck University, Austria (collection numbers GB1–175, GBT1–11, TK 1–70, TKS1–19, TKW1–18, TM1–9, TNA1–30, TNB1–23, TNC1–11, Z1–19, ZK1–215, ZKO1–47 and ZT1–18).

Figures 9-30

Abbreviations: Throughout the text, we used the following abbreviations: L = length; D = outer diameter; d = inner diameter; s = thickness of thallus; p = diameter of pores (= diameter of laterals, siphons, or utricles); and ip = distance between two pores (i.e., between two laterals, two siphons, or two utricles).

Phylum CYANOBACTERIA (ex Stanier, 1974)
Cavalier-Smith, 2002

Description. Microbial structures represented by isolated, coccoid or tubular filaments (eventually with pseudoramifications, or true bifurcations), bioconstructions of types of stromatolite, oncoids, microbialites or dendrolites, or nodular colonies composed of single to bifurcated spans of filaments. Wall dark microgranular; rarely recrystallized.

Remarks. Cyanobacteria (or cyanoprokaryotes, or formerly blue-green algae, cyanophyceae, myxophyceae and calcimicrobes) were always particularly hard to be classified, and recently the whole classification was restructured and revised based on molecular sequence data (Komárek et al., 2014). Due to the possible morphological complexity of the cyanobacteria from coccoid individuals to hemispherical colonies of bifurcated filaments, we speculate here that a possible phylogeny at the ordinal hierarchical levels are represented (Figure

CLASSES		FAMILIES AND RELATED GROUPS
INCERTAE SEDIS	ALGOSPONGIA	STACHEIACEAE
		UNGDARELLACEAE
		CLARACRUSTACEAE
CHLOROPHYTA	DASYCLADALES	„ALGAL SPORES“
		LULIPOREAE
		MIZZIEAE
		GYROPORELLEAE
		MACROPORELLEAE
		EPIMASTOPOREAE
		ANTHRACOPORELLEAE
	BRYOPSIDALES	GYMNOCODIACEAE?
		ANCHICODIACEAE
		FAMILY INDET.
	RHODOPHYTA	CORALLINACEAE
	CYANOBACTERIA	ELIANELLACEAE
		GARWOODIACEAE
		GIRVANELLACEAE
		CHABAKOVIACEAE
		APHRALYSIACEAE
		STROMATOLITIC STRUCTURES
		CHROOCOCCALES

FIGURE 6. Algal classification adopted here.

9) by 1) coccoid thalli (incerti ordinis 1; probably Chroococcales Geitler, 1925); 2) filamentous and/or coccoid, stromatolitic and microbialitic taxa (incerti ordinis 2: stromatolites sensu lato); 3) carbonate stromatolitic textures (incerti ordinis 3; family Aphralysiaceae Vachard in Vachard, Hauser, Martini, Zaninetti, Matter and Peters, 2001a); 4) colonial coccoid? textures (incerti ordinis 4; family Chabakoviaceae Kordé, 1973); 5) tubular, single filaments (?order Proauloporaes Luchinina, 1975 or Oscillatoriales Elenkin, 1934; family Girvanellaceae Luchinina, 1975); 6) colonial groups of filaments (?order Proauloporaes or Oscillatoriales; family Garwoodiaceae Shuysky, 1973).

Class CYANOPHYCEAE Sachs, 1874
Order ?CHROOCOCCALES Geitler, 1925
Genus NOSTOCITES Maslov, 1929

Type Species. *Nostocites vesiculosa* Maslov, 1929, by subsequent designation by Maslov, 1956b.

Description. Flattened thallus composed of a sheet of loosely packed, globular or dolioliform cells; one cell-thick; each cell emplacement is

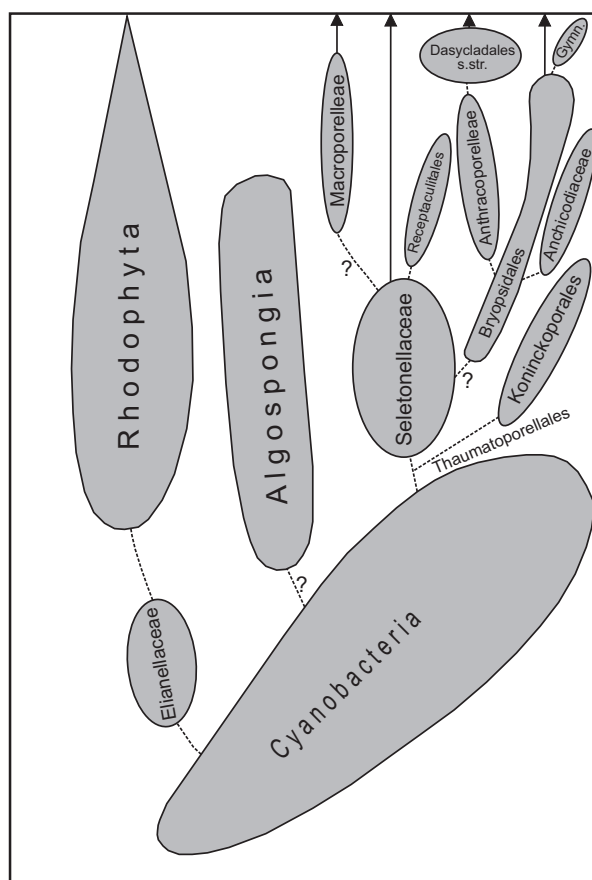


FIGURE 7. Hypothetical algal phylogeny proposed in this paper, mainly at the level of the classes.

entirely recrystallized in yellowish, hyaline calcite often with a dark inclusion in its center.

Remarks. *Nostocites* is an easily identifiable taxon, despite its disputable botanical assignment (Maslov, 1929; Pia, 1937; Vachard et al., 2001a). An assignment to the globochaetaceans (Vachard, 1980; Vachard and Beckary, 1991; Perret et al., 1994; Skompski, 1996; Vachard et al., 2001a; Mamet, 2006) and/or other groups of the marine bacterioplankton seems to be most logical.

Occurrence. Early Viséan–late Capitanian (Vachard et al., 2001a); probably cosmopolitan.

Nostocites vesiculosa Maslov, 1929

Figure 11.1-2

- *1929 *Nostocites vesiculosa* Maslov, p. 1538, text-figs. 1–3, 7, pl. 70, figs. 2, 7, 9–10.
- 1937 *Nostocites vesiculosa*; Pia, p. 807–808 (no illustration).
- 1963 *Nostocites vesiculosa*; Maslov et al. in Orlov, p. 46, fig. 29.
- vp. 1977a *Globochaete* sp.; Vachard, p. 374, table 1 (part.: only the late Viséan specimens; no illustration).

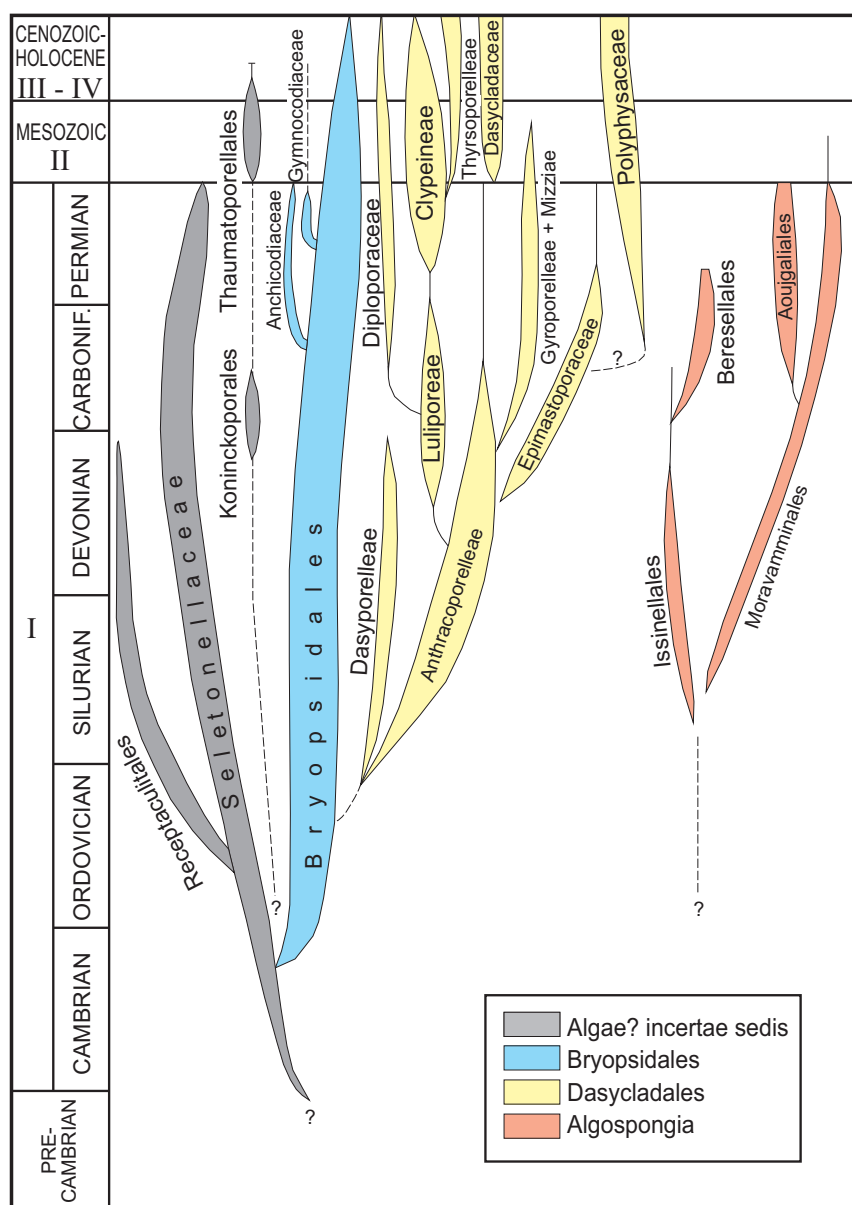


FIGURE 8. Hypothetical algal phylogeny, mainly at the level of orders and families.

- | | | | |
|---------|---|---------|---|
| 1978 | <i>Litostroma</i> sp.; Jansa et al., p. 1436, pl. 1, figs. 10, 11. | 1985 | <i>Nostocites vesiculosa</i> ; Mamet and Pinard, pl. 1, fig. 19. |
| 1978 | <i>Nostocites vesiculosa</i> ; Mamet and Roux, p. 80, pl. 6, fig. 2 only (non figs. 1, 3 = ornamented ostracods) (with three references in synonymy). | 1986 | <i>Nostocites</i> sp.; Groves, p. 490, figs. 8, 9. |
| | | ? 1987 | <i>Nostocites vesiculosa</i> ; Mamet et al., p. 58, pl. 30, figs. 1, 2 (with synonymy). |
| 1981 | <i>Nostocites vesiculosa</i> ; Mamet and Martínez, pl. 3, fig. 8. | v. 1990 | <i>Nostocites vesiculosa</i> ; Vachard, p. 94 (no illustration). |
| 1983 | <i>Nostocites</i> cf. <i>N. vesiculosa</i> ; Groves, p. 31–32, pl. 7, figs. 7, 10–12 (with synonymy). | v. 1991 | <i>Nostocites</i> ex gr. <i>vesiculosa</i> ; Vachard and Beckary, p. 322_323, pl. 2, fig. 10 (with synonymy). |
| p. 1983 | <i>Nostocites vesiculosa</i> ; Mamet and Roux, p. 98, pl. 10, figs. 9–11 (non figs. 12, 13 = ostracods) (with synonymy). | v. 1991 | <i>Nostocites vesiculosa</i> ; Vachard et al., p. 677, pl. 1, fig. 7. |
| | | 1992 | <i>Nostocites vesiculosa</i> ; Mamet and Préat, p. 60, pl. 1, fig. 6. |

TABLE 1. List of the algal main groups and their species and taxa described in this paper.

Algal main groups	Species or taxa	Illustrations in this study
ALGOSPONGIA	<i>Efluegelia</i> ex gr. <i>johnsoni</i> (Flügel 1966)	Figure 27.10 - 27.12, Figure 29.1 - 29.9, 29.12, Figure 30.1, 30.2, 30.5, 30.8 - 30.11
	<i>Efluegelia johnsoni</i> (Flügel, 1966) emend. Vachard in Massa and Vachard, 1979	Figure 29.10, 29.11, Figure 30.3, 30.4, 30.6, 30.7
	<i>Ungdarella uralica</i> Maslov, 1956a non 1956b nec 1950	Figure 27.13 - 27.15, Figure 28.1 - 28.9
	<i>Claracrusta catenoides</i> (Homann, 1972) emend. Vachard in Vachard and Montenat, 1981	Figure 20.1, Figure 26.5 - 26.8
	"Algen-Sporen" (algal spores)	Figure 21.7, 21.9, 21.11, Figure 22.11, 22.12, Figure 23.16, Figure 24.3, Figure 25.3, 25.4, 25.10, Figure 27.13 - 27.15, Figure 28.8, 28.9, Figure 30.11
	<i>Salopekiella?</i> sp.	Figure 27.5
	<i>Connexia slovenica</i> Kochansky-Devidé, 1979	Figure 26.1 - 26.4, Figure 27.9
	<i>Mizzia cornuta</i> Kochansky-Devidé and Herak, 1960	Figure 22.7, 22.8, Figure 23.3, 23.5, 23.6, 23.8, 23.13, 23.18
	<i>Mizzia yabei</i> (Karpinsky, 1909) emend. Pia, 1920	Figure 22.12?, 22.13?, Figure 23.4, 23.15 - 23.17, Figure 25.1, 25.2, 25.5, 25.7, 25.8, 25.9 (bottom), 25.10
	<i>Mizzia velebitana</i> Schubert, 1908	Figure 22.9 - 22.11, Figure 23.7, 23.9 - 23.12, 23.14? Figure 25.3, 25.4, 25.5, 25.9 (top), 25.11 - 25.13, 25.14?
	<i>Pseudoepimastopora carnica</i> (Flügel, 1966 n. comb., emend herein)	Figure 25.1 - 25.12, Figure 27.3, 27.6
	<i>Gyroporella</i> sp.	Figure 25.9?, Figure 27.1
	<i>Macroporella</i> cf. <i>siamensis</i> Endo, 1969	Figure 23.1, 23.2
	<i>Globuliferoporella?</i> sp.	Figure 25.13
	<i>Globuliferoporella angulata</i> Chuvashov, 1974	Figure 21.2 - 21.5, 21.6?
DASYCLADALES	<i>Globuliferoporella piai</i> (Kordé, 1951) n. comb.	Figure 19.12, 19.13, 19.15, Figure 21.1, 21.7?, 21.8 - 21.11
	<i>Epiastopora fluegeli</i> (Kulik, 1978) n. gen. n. comb.	Figure 19.10
	<i>Epiastopora alpina</i> (Kochansky-Devidé and Herak, 1960) n. gen. n. comb.	Figure 19.5, 19.10, Figure 20.5, Figure 21.8, Figure 22.2, 22.5
	<i>Epimastopora</i> cf. <i>izawaikensis</i> Endo, 1953a	Figure 19.14, Figure 20.6
	<i>Epimastopora likana</i> Kochansky-Devidé and Herak, 1960 emend. herein	Figure 18.8, 18.10, 18.11, Figure 19.3, 19.4, 19.12 (bottom, center), Figure 20.3, Figure 22.3, 22.6?, Figure 27.2?, 27.5
	<i>Epimastopora japonica</i> Endo, 1951 emend Mamet, Roux and Nassichuk, 1987	Figure 18.6, 18.7, 18.9, Figure 19.1, 19.2, 19.6 - 19.9, 19.12 (left)
	<i>Paraepimastopora kanumai</i> (Endo in Endo and Kanuma, 1954)	Figure 18.4, 18.5?
	<i>Anthracoporella vicina</i> Kochansky-Devidé and Herak, 1960	Figure 18.2, 18.3, Figure 20.2
	<i>Anthracoporella spectabilis</i> Pia, 1920 emend De Castro, 2002	Figure 18.1, Figure 22.1
	<i>Nanjinophycus?</i> sp.	Figure 17.7, Figure 22.4?
	<i>Calcipatera schoenlaubi</i> n. sp.	Figure 17.5, 17.6, 17.8 - 17.11, Figure 20.1
	<i>Neoanchicodium catenoides</i> (Endo in Endo and Kanuma, 1954)	Figure 16.4 - 16.9, Figure 17.7, 17.8, Figure 18.6
	<i>Eugonophyllum?</i> <i>konishi</i> Kulik, 1978	Figure 17.1, 17.2
	<i>Eugonophyllum magnum</i> (Endo, 1951)	Figure 11.4, Figure 14.11, 14.12, Figure 15.1 - 15.12,

TABLE 1 (continued).

Algal main groups	Species or taxa	Illustrations in this study
	emend. Konishi and Wray, 1961	Figure 16.1 - 16.3, 16.10 - 16.13, Figure 17.3 - 17.4 Figure 20.4, Figure 26.16, Figure 29.9, Figure 30.11
	<i>Ivanovia tenuissima</i> Khvorova, 1946	Figure 14.6 - 14.8
	<i>Anchicodium japonicum</i> Endo, 1953a	Figure 14.9, 14.10
	<i>Homannisiphon morikawai</i> (Endo, 1954)	Figure 13.6 - 13.16, Figure 14.1 - 14.5
	<i>Archaeolithophyllum lamellosum</i> Wray, 1964	Figure 13.2
RED ALGAE	<i>Parachaetetes ortonelloides</i> (Endo, 1961c) n. comb.	Figure 13.1, 13.3 - 13.5
	<i>Garwoodia</i> sp.	Figure 12.5
	<i>Clinortonella</i> cf. <i>goggauensis</i> (Flügel and Flügel-Kahler, 1980)	Figure 12.2, 12.12?
	<i>Koivaella</i> ex gr. <i>permiensis</i> Chuvashov, 1974	Figure 12.3, 12.4, 12.6 - 12.10
	<i>Mitcheldeania</i> sp.	Figure 11.5
	<i>Girvanella</i> sp.	Figure 11.4
CYANOBACTERIA	<i>Gahkumella</i> sp.	Figure 11.3
	<i>Renalcis</i> cf. <i>granosus</i> Vologdin, 1932	Figure 12.1, Figure 27.4
	<i>Archaeolithoporella hidensis</i> Endo, 1961a	Figure 11.7 - 11.10, Figure 12.11
	<i>Stromatolites</i> indet.	Figure 11.6
	<i>Nostocites vesiculosa</i> Maslov, 1929	Figure 11.1, 11.2

non 1996	<i>Nostocites vesiculosa</i> ; Sebbar and Mamet, text-fig. 5.31, pl. 3, fig. 3 (= hinge of ostracod).	v.2005	<i>Nostocites vesiculosus</i> (sic); Saïd, p. 178, fig. X.1.12.
v. 1996	<i>Nostocites vesiculosa</i> ; Vachard and Maslo, text-fig. 2 p. 361.	2006	<i>Nostocites vesiculosa</i> ; Mamet, p. 346, 348, pl. 7, figs. 20–23 (with 25 references in synonymy, even if many of them rather concern <i>Globochaete</i>).
1996	<i>Globochaetes</i> (sic); Jones and Somerville, fig. 4h.	2007	<i>Nostocites vesiculosa</i> ; Cózar et al., text-fig. 3 p. 101.
1996	<i>Globochaete alpina</i> (Lombard); Skompski, pl. 16, fig. 4.	v2008	<i>Nostocites vesiculosa</i> ; Pille, p. 55–56, pl. 17, fig. 6.
?1999	<i>Nostocites vesicula</i> (sic); Sebbar and Mamet, text-fig. 3.53 (no illustration).	2010	<i>Nostocites vesiculosa</i> ; Mamet and Préat, p. 32, pl. 9, figs. 7, 8.
2000	<i>Nostocites vesiculosa</i> (= <i>Globochaete</i> auct.); Mamet and Stemmerik, fig. 9G.	v2014	<i>Nostocites vesiculosa</i> ; Vachard et al., fig. S3(12).
v.2001a	<i>Nostocites</i> sp.; Vachard and Krainer, p. 151 (no illustration).	Description. Only two sections were measured: thallus diameter = 250–500 µm; cell diameter = 30–50 µm; central inclusion diameter = 7 (rarely 10) µm. Remarks. <i>Nostocites vesiculosa</i> is generally the unique species of the genus (Mamet and Roux, 1978); some other specific taxa remain in open nomenclature (Vachard and Krainer, 2001a). Some atypical recrystallizations of dolomite rhomboedra can be confused with <i>Nostocites</i> (for example, <i>Nostocites?</i> of Krainer et al., 2017b, figure 27H), as well as, and more paradoxically, some hinges of	
v2001a	<i>Nostocites vesiculosa</i> ; Vachard in Vachard et al., p. 390, 392–393, text-fig. 6 p. 379, fig. 18.1 (with seven references in synonymy).		
v2003a	<i>Nostocites vesiculosa</i> ; Krainer et al., p. 18, 19, table 1 p. 18, pl. 3, fig. 13, pl. 5, fig. 3.		
2003	<i>Nostocites vesiculosa</i> ; Khodjanyazova and Mamet, pl. 5, fig. 14.		
?2004	<i>Nostocites vesiculosa</i> ; Cózar, text-fig. 3 p. 371, text-fig. 4 p. 372 (no illustration).		
?2004	<i>Nostocites vesiculosa</i> ; Cózar and Somerville, text-fig. 3, text-fig. 9 (no illustration).		

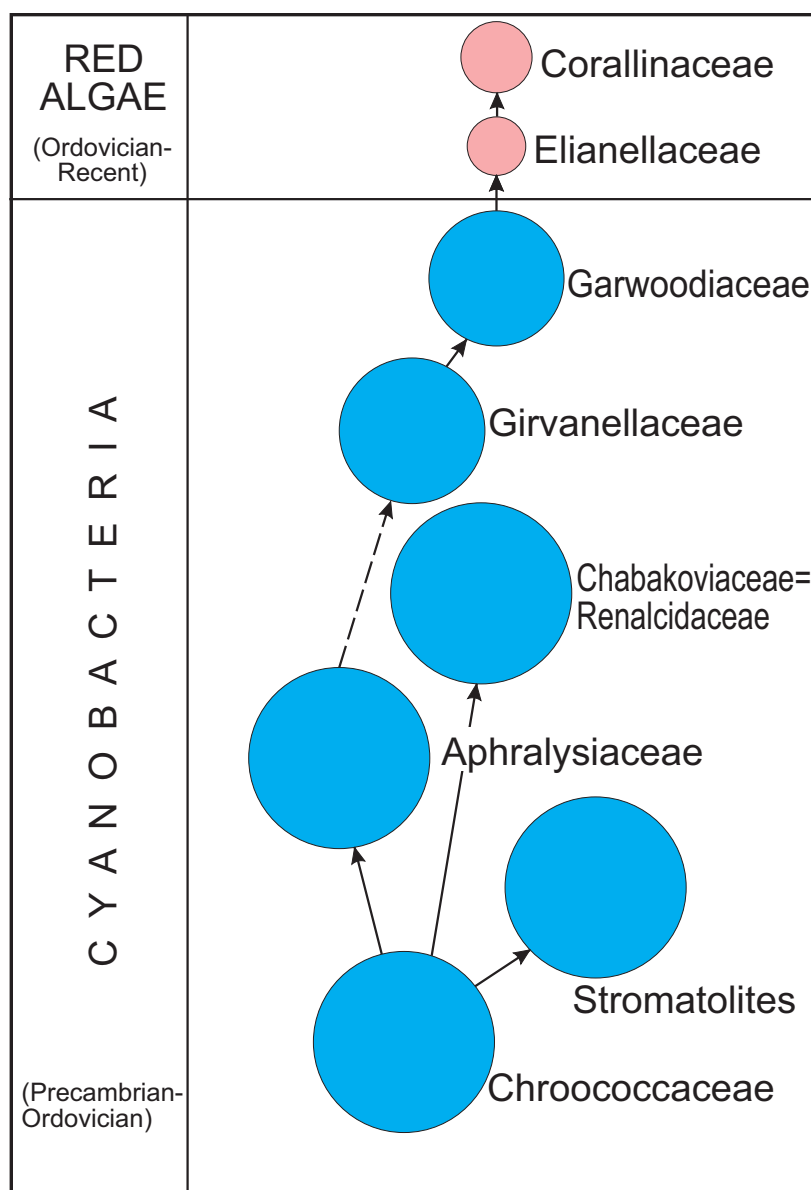


FIGURE 9. Possible phylogeny of cyanobacterial groups mentioned in this study.

ostracods (Mamet and Roux, 1978, 1983; Mamet et al., 1987; Sebbar and Mamet, 1996; as indicated by Krainer et al., 2003a, plate 6, figure 8).

Occurrence. Early Viséan–late Capitanian (Vachard et al., 2001a); probably cosmopolitan. In the Carnic Alps: Auernig Fm (Vachard and Krainer, 2001a). This study: Zweikofel Fm (sample ZK203_3) and Trogkofel Fm (sample TK26_3).

Incerti ordinis
Stromatolites indet.
Figure 11.6

1968 Stromatolithen Typ LLH–S/LL–H–C; Flügel, p. 56 (no illustration).

1968 Stromatolithen Typ SS–C/LLH–C; Flügel, p. 56 (no illustration).

Description. This term is used here for designating microbialites with a laminar, plane, distinct stratification, with entirely calcareous material.

Remarks. Within the Trogkofel Formation, crudely laminated bindstones composed of cyanobacteria, probably *Girvanella* and other micritic-walled tubes form stromatolites up to 10 cm thick, which may be termed skeletal stromatolites according to Riding (1991) (Schaffhauser, 2013; Schaffhauser et al., 2015). In reef cavities millimeter-sized laminated sediments occur, which are composed of peloidal grainstone laminae and cement crusts (Schaffhauser, 2013). These crusts may be termed hybrid

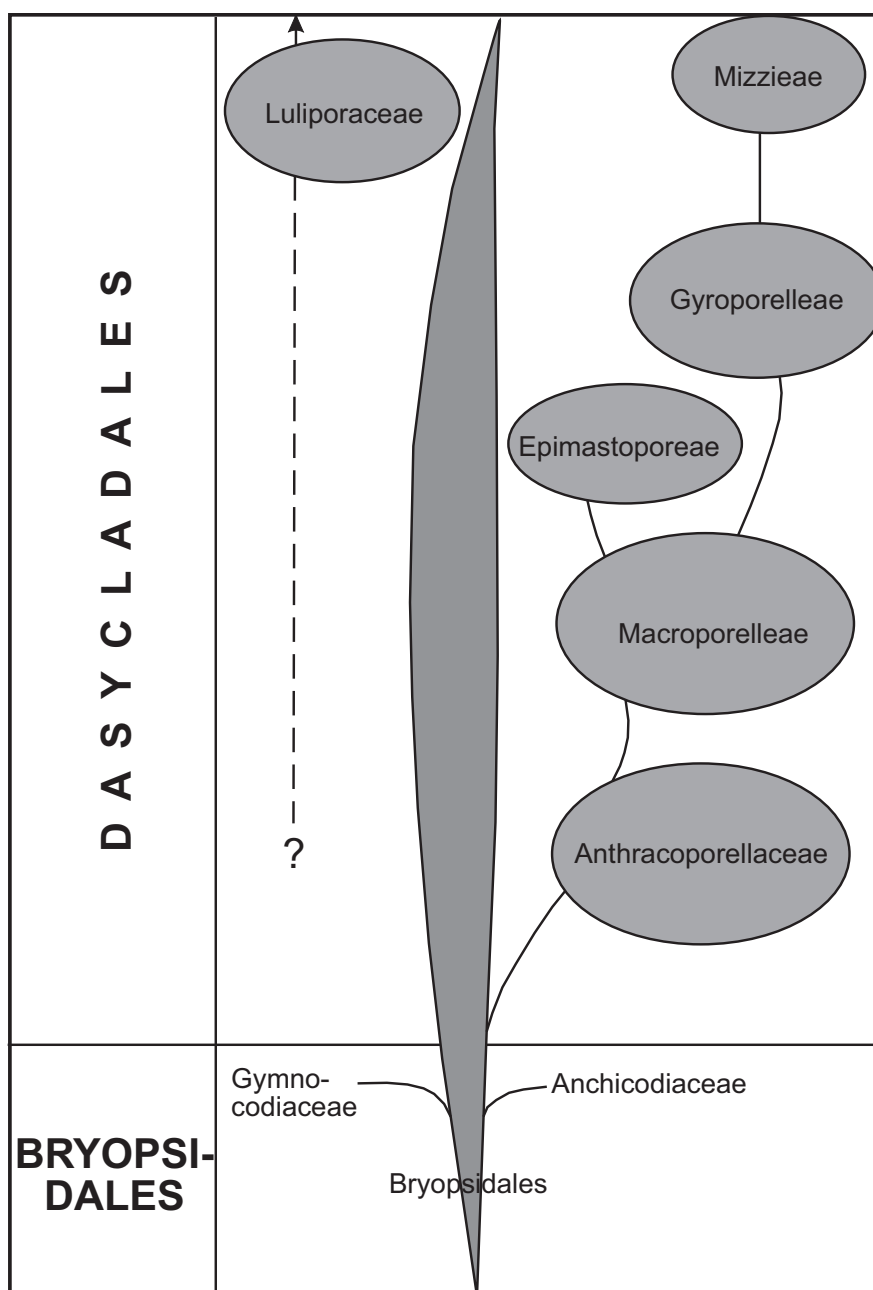


FIGURE 10. Another possible phylogeny of the Bryopsidales and Dasycladales mentioned in this study, mainly at the level of families and tribes.

crusts according to Riding (2008). In the reef cavities the laminites are associated with reef cements and micropeloidal pack- and wackestone (Schaffhauser, 2013). Stromatolites are not known from the Zweikofel and Zottachkopf formations, but they are relatively common in the Trogkofel Fm (Flügel, 1968).

Occurrence. In our material of the Carnic Alps, only one specimen (sample TKW2_1) was studied from the Zottachkopf Fm.

Incerti ordinis
Family APHRALYSIACEAE Vachard
in Vachard, Hauser, Martini, Zaninetti, Matter and Peters, 2001a
Genus *ARCHAEOLITHOPORELLA* Endo, 1961a
Type species. *Archaeolithoporella hidensis* Endo, 1961a, by original designation.
Description. Large flattened crusts or oncoids (tebagites) constituted by laminar layers alternatively dark and clear, interpretable as superposed

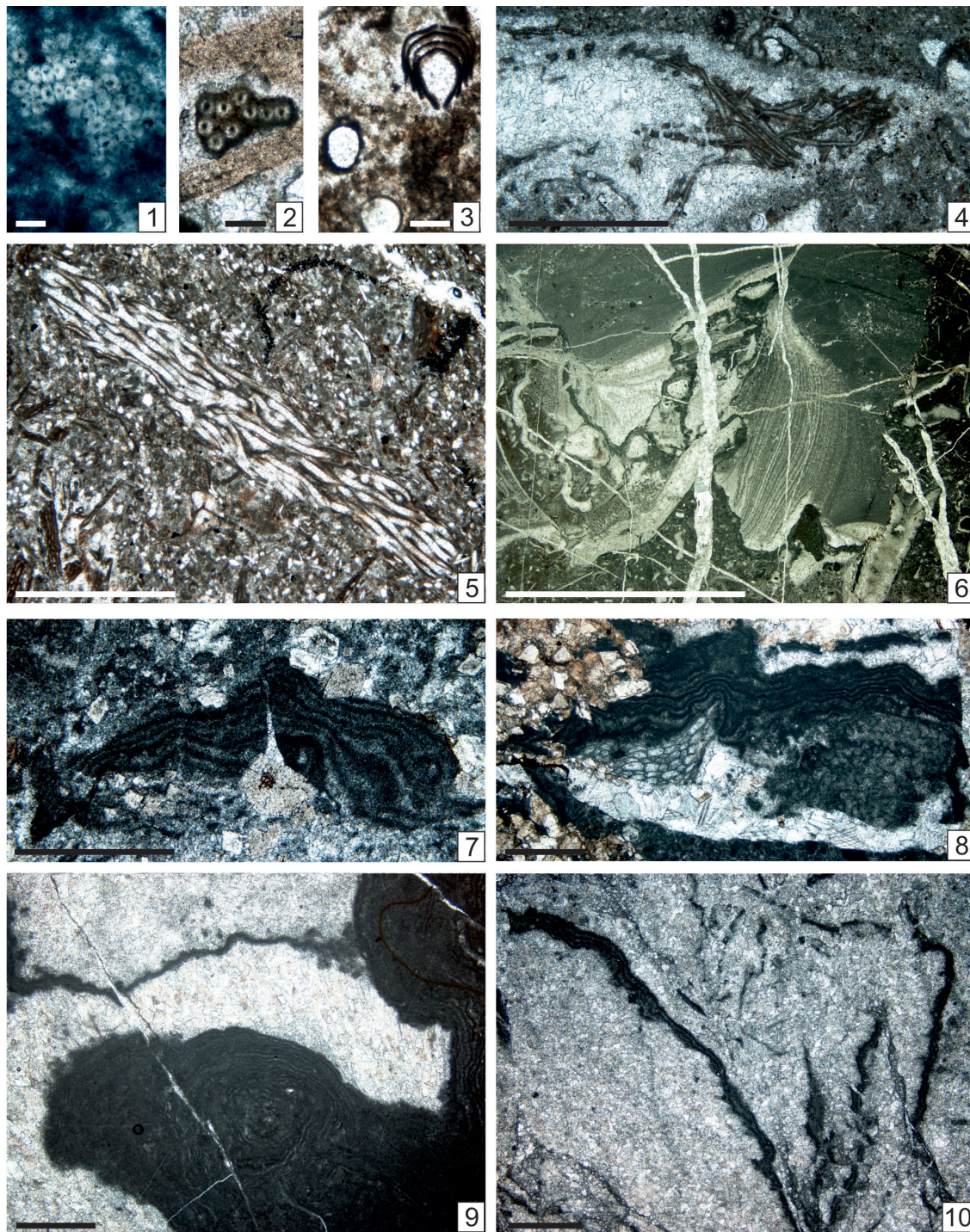


FIGURE 11. 1, 2. *Nostocites vesiculosa* Maslov, 1929. 1. Random section. Sample TK26_3/00011. 2. Random section. Sample ZK203_3. 3. *Gahkumella* sp. Two transverse sections (bottom, left) and an axial section (top, right). Sample GB 157_13. 4. *Girvanella* sp. Longitudinal and transverse sections perhaps boring an *Eugonophyllum magnum* (Endo, 1951) emend. Konishi and Wray, 1961 encrusted by a tuberitinid (bottom) and palaeonubeculariid (top). Sample GB35_4. 5. *Mitcheldeania* sp. Longitudinal section showing the large filaments and their bifurcations. Sample GB17_2b. 6. Stromatolite. Axial sections. Sample TKW2_1. 7–10. *Archaeolithoporella hidensis* Endo, 1961a. 7. Longitudinal section attached on a tubiphytid. Sample GBT4_1. 8. Longitudinal section attached on tubiphytid and a bryozoa. Sample GBT11_2. 9. Large colony, in transverse section, subrounded by botryoidal cement. Sample TK68_1. 10. Thin colonies encrusting large botryoidal cement. Sample TK60_AP. Scale bars: 0.1 μ m (Figures 11.1–11.3) and 1 μ m (Figures 11.4–11.10).

sheets of cylindrical trichomes without pseudoramicifications forming stromatolitic structures. Wall dark microgranular.

Occurrence. Rare in Asselian–Sakmarian of the Urals; Artinskian–Changhsingian, cosmopolitan.

Archaeolithoporella hidensis Endo, 1961a
Figure 11.7–10, Figure 12.11

- *1961a *Archaeolithoporella hidensis* Endo, p. 182, pl. 39, figs. 3–5.
- 1961b *Archaeolithoporella hidensis*; Endo, p. 41, pl. 16, fig. 4.
- 1961c *Archaeolithoporella hidensis*; Endo, p. 84, pl. 2, figs. 1, 2.
- 1963 *Archaeolithoporella hidensis*; Johnson, p. 98, pl. 48, fig. 1 (not 2, as indicated in the text).
- .1964 Algues encroûtantes; Glintzboeckel and Rabaté, pl. 59, figs. 1, 2, pl. 105, figs. 1, 2.
- .1966 Stromatolithen-Typ LLH–S/LLH–C; Flügel, p. 52–53, pl. 9, figs. 2, 3.
- .1970a Stromatoliti/Stromatolithen; Kochansky-Dev-
idé, p. 210, 238, pl. 20, figs. 1, 2.
- .1972 Stromatolithen-Typus LLH–C/LLH–C;
Homann, p. 250–251, pl. 9, fig. 67.
- 1975 an irregular lamina of possible algal origin;
Wilson, pl. 25, fig. B.
- 1976 *Archaeolithoporella hidensis*; Emberger p.
100 (no illustration) (with three references in
synonymy).
- 1977 Stromatolites-lined cavities; Flügel, p. 325, pl.
2, fig. 3.
- .1977 *A. hidensis* (sic); Lemoine, p. 1322 (no illus-
tration).
- .1979 *Archaeolithoporella* laminae; Babcock, pl. 1,
fig. 6.
- .1979 *Archaeolithoporella* sp.; Flügel, p. 572, pl. 1,
fig. 3.
- .1979 Stromatolithes; Nguyen Duc Tien, pl. 27, figs.
8, 9.
- 1980 *Archaeolithoporella hidensis*; Flügel, pl. 13,
figs. 2, 4, 6, 7.
- 1980 *Archaeolithoporella hidensis*; Flügel and Flü-
gel-Kahler, p. 160–161, pl. 10, figs. 2, 4, 7
(with five references in synonymy).
- .1981 *Archaeolithoporella*; Flügel, text-fig. 4a–e,
5b, d, e, 6d, 9a, b.
- v1981 Stromatolithes (...) (*Archaeolithoporella*);
Vachard in Vachard and Montenat, p. 32–33,
pl. 15, fig. 1.
- .1983 *Archaeolithoporella*; Mazzullo and Cys, figs.
2A, B, 3A–C.
- 1984 *Archaeolithoporella*; Flügel, Kochansky-Dev-
idé and Ramovš, p. 180, 183, 186–193, 196,
209–212, pl. 24, figs. 4, 6, pl. 25, figs. 2, 3, 5–
8, pl. 26, figs. 5, 6, 8, pl. 27, figs. 2, 3, 5, pl.
28, fig. 4, pl. 31, figs. 1, 7, 10, 12, pl. 36, fig.
3, pl. 38, fig. 5.
- .1986a Stromatolithes; Nguyen Duc Tien, pl. 8, fig.
11 only (non fig. 9 = ?*Clinortonella*; nec fig.
10 = *Girvanella*).
- .1988 *Archaeolithoporella*; Senowbari-Daryan and
Di Stefano, pl. 8, fig. 1.
- v.1988 *Archaeolithoporella*; Vachard and Razgallah,
fig. 1.
- .1989 *Archaeolithoporella*; Flügel and Reinhardt, p.
507–509, 511–515, fig. 7b.
- v1990 *Archaeolithoporella hidensis*; Vachard and
Miconnet, p. 301, pl. 1, fig. 13.
- 1990 *Archaeolithoporella*; Fan et al., pl. 4, fig. 4, pl.
8, figs. 1, 3, 4, 6, pl. 10, fig. 3.
- v1991 *Archaeolithoporella hidensis*; Razgallah and
Vachard, p. 192–197, pl. 3, figs. 2–7, pl. 4,
figs. 1–6, pl. 5, figs. 1–8, pl. 6, figs. 1–8 (with
42 references in synonymy).
- 1991 *Archaeolithoporella hidensis*; Wu, p. 755, pl.
2, fig. 5, pl. 3, fig. 5.
- .1991 *Archaeolithoporella*; Flügel et al., pl. 42, fig.
9, pl. 48, figs. 6–10.
- .1991 *Archaeolithoporella*; Riding and Guo, figs.
15, 16.
- .1991 *Archaeolithoporella*; Toomey, p. 213, text-fig.
3 p. 214, pl. 31, figs. 1, 2, pl. 33, fig. 5, pl. 34,
fig. 9.
- ? .1993 stromatolith crusts; Chuvashov et al., pl. 4,
figs. 3, 4.
- v1993a *Archaeolithoporella hidensis*; Vachard et al.,
pl. 2, fig. 3.
- .v1993 *Archaeolithoporella*; Dawson, p. 9, 12, 16, 31
(no illustration).
- .1994 *Archaeolithoporella*; Wang et al., p. 725–731,
figs. 2, 3, 4.1–9, 5, 6.
- 1994 Stromatolite; Fontaine et al., pl. 30, fig. 4.
- .1995 *Archaeolithoporella*; Pratt, p. 80, 82, 83, 84,
87?, 103, text-figs. 38, 39A, 39B p. 84.
- 1995 *Archaeolithoporella/Shamovella* (sic) bound-
stone; Le Mone, p. 141 (no illustration).
- 1995 *Archaeolithoporella* sp.; Forke, p. 240, fig.
17.8.
- .1998 *Archaeolithoporella*; Kirkland et al., figs. 7A–
D, 8B, 18.
- 1999 *Archaeolithoporella hidensis*; Fagerstrom
and Weidlich, p. 132, 136, 140, 145, 146,
148, 150, 151, 152, 153, text-fig. 2 p. 133,
tabl. 1 p. 134, 132, 136, 140, 145, 146, 148,
150, 151, 152, 153, pl. 14, figs. 1, 2, 4, pl. 15,
fig. 4, pl. 16, fig. 4, tabl. 3 p. 142, text-fig. 7 p.
151.
- .2001 *Archaeolithoporella*; Moore, fig. 5.15A, B.
- v.2001a *Archaeolithoporella*; Vachard in Vachard et
al., p. 382, figs. 12.6, 14.9.

- v.2001b *Archaeolithoporella hidensis*; Vachard in Vachard et al., pl. 3, fig. 7.
- .2001 *Archaeolithoporella*; Shen and Kawamura, pl. 23, fig. 3, pl. 24, figs. 2, 4, 5, pl. 25, figs. 1, 2.
- 2002 *Archaeolithoporella hidensis*; Weidlich, p. 339, 341, 357, text-figs. 5.D.3, 7.C.3, 13.D.1, 13.D.2, 13.F.1.
- v2003a *Archaeolithoporella*; Krainer et al., p. 8, 17 (no illustration).
- .2003 *Archaeolithoporella*; Noé, pl. 4, fig. 8, pl. 9, figs. 2–4, pl. 13, fig. 5, pl. 15, figs. 5–7, pl. 21, figs. 1, 6–8.
- 2003 *Archaeolithoporella hidensis*; Noé, pl. 13, figs. 3, 4.
- 2003 *Archaeolithoporella*; Chen et al., p. 121, 124, 126, 128, 131, 132, pl. 16, figs. 2, 6, 7, pl. 17, figs. 1–3, 6, 7, pl. 18, fig. 1.
- .2004 *Archaeolithoporella* sp.; Flügel, fig. 7.14B, pl. 42 (full page), fig. 10.59, pl. 98, figs. 5, 8, pl. 145, fig. 1.
- . ?2005 *Archaeolithoporella hidensis*; Fagerstrom and Weidlich, p. 508, 509, 511, 512 (no illustration).
- 2007 *Archaeolithoporella*; Bensing, fig. 1.1 p. 6.
- .2007b *Archaeolithoporella*; Krainer and Vachard, p. 291, 294, figs. 24–26.
- v2011 *Archaeolithoporella* sp.; Vachard and Moix, p. 152 (no illustration).
- v2011 *Archaeolithoporella hidensis*; Moix et al., p. 68, 75, pl. 1, figs. 17, 18, pl. 4, fig. 15b.
- v2013 *Archaeolithoporella hidensis*; Moix et al., p. 408 (no illustration).
- v2013 *Archaeolithoporella*; Kossovaya et al., p. 351, 353, fig. 5a(A) (no illustration).
- 2013 *Archaeolithoporella*; Wahlman and Tasker, p. 305, 311 (no illustration).
- 2013 *Archaeolithoporella*; Wahlman et al., p. 1895, 1903, 1905, 1908, 1912, 1916, tabl. 1, figs. 15C, 15D, 17C.
- v2015 *Archaeolithoporella hidensis*; Angiolini et al., table 2a.
- v2016 *Archaeolithoporella hidensis*; Angiolini et al., fig. 11.A.

Description. Millimeter- to centimeter-sized bioconstructions. Thickness of laminae = 35–50 µm. Thickness of dark layers (“walls”) = 10–35 µm; thickness of clear layers (trichomes?) = 20–30 µm. Commonly, these colonies are associated with botryoid cements in the Carnic Alps, Jebel Tebaga, Darvas, El Capitan and South China (Flügel, 1980, 1981; Flügel et al., 1984, 1991; Razgallah and Vachard, 1991; Kirkland et al., 1998; Moore, 2001; Noé, 2003; Flügel, 2004; Angiolini et al., 2016; and this study).

Remarks. We adopt here the description and interpretation of Vachard et al. (2001a) for *Archaeolithoporella*. Biosedimentologically, the largest mounds of the Carnic Alps occur in the Trogkofel limestone, and are composed of *Tubiphytes*–*Archaeolithoporella* boundstone, which shows some similarities to the “*Tubiphytes* thickets” of stage 2 of the massive Capitan Reef Complex of the Guadalupe Mountains of New Mexico/West Texas (Krainer, 2007).

Occurrence. Possibly present as early as the Asselian in the Urals (Chuvashov et al., 1993), the species as a double acme in the western Paleotethys; first in the Artinskian–Kungurian (e.g., in the Carnic Alps and Darvas: Flügel and Flügel-Kahler, 1980 and Angiolini et al., 2016), then in the Capitanian (e.g., Apennines, Italy; Vachard and Miconnet, 1990); Jebel Tebaga, Tunisia (Razgallah and Vachard, 1991); western Sicily (Italy; early Guadalupian re-dated here; Flügel et al., 1991); Turkey (Vachard and Moix, 2011; Moix et al., 2011); El Capitan Reef (New Mexico, USA; Babcock, 1979; Noé, 2003; Flügel, 2004); South China (Shen and Kawamura, 2001); Late Permian of Greece (Vachard et al., 1993a); up to the Changhsingian of South China (e.g., Riding and Guo, 1991; Flügel, 2004). In the Carnic Alps, the *Archaeolithoporella* crusts were known in OPK (Homann, 1972); Upper *Pseudoschwagerina* Limestone Member and Trogkofel Group (Flügel, 1979; Vachard and Krainer, 2001b); Trogkofel (Flügel, 1966; Krainer, 2007); Tarviser Brekzie (Flügel, 1980); in Seikofel, Forni Avoltri, Straniger Alm, Treßdorfer Alm, and Tarvis-Goggau (Flügel and Flügel-Kahler, 1980); and numerous other localities (Flügel and Flügel-Kahler, 1980). In this study, the best specimens come from the Trogkofel Fm (samples GTB4_1; GTB11_1; GTB11_2; TK60_1; TK60_AP; and TK68_1).

Incerti ordinis

Family CHABAKOVIACEAE Kordé, 1973

Synonym. Renalcidae Riding and Brasier, 1975; Renalcidae nomen transl. Vachard and Beckary, 1991 emend. Vachard, 1993.

Description. Globose trichomes, hemispherical to reniform, entirely calcified or hollow, arranged in uniseriate, ramified series. Wall microgranular, dark or grayish.

Remarks. The family Renalcidae was interpreted by Riding and Brasier (1975) as composed of the “oldest foraminifers in the world”. It is now unanimously admitted as a group of cyanobacteria (calcibionta or calcimicrobes; Luchina, 2009). Whatever the reciprocal interpretations of *Renalcis*

and *Chabakovia* Vologdin, 1932, the priority name for the family is Chabakoviaceae, even if Renalcidae is most commonly used in the literature.

Occurrence. The family is principally Early Cambrian in age, but the genus *Renalcis* displays other later acmes (Frasnian, Viséan and Bashkirian) and may extend up to the Permian (see below). Its appearance is possibly situated in the latest Precambrian (Late Vendian; Luchinina and Terleev, 2004).

Genus RENALCIS Vologdin, 1932 emend.
Luchinina, 2009

Type species. *Renalcis granosus* Vologdin, 1932, by original designation.

Synonyms. See Mamet and Roux (1983), Mamet (1991), Vachard (1993) and Luchinina (2009).

Diagnosis. Chabakoviaceans with hollow, inflated, hemispherical to reniform trichomes, arranged in numerous ramified series. Wall dark microgranular, relatively thick and with small cracks at the base. The hollow parts of trichomes and small cracks in walls are filled with white microsparite.

Occurrence. Neoproterozoic–Frasnian; probably cosmopolitan (Roux, 1985; Vachard, 1993; Stephens and Sumner, 2002). Late Viséan–Bashkirian in Paleotethys and Urals shelves (Vachard, 1977a, 1977b; Saltovskaya, 1984a). Early Moscovian of Japan (Mamet, 2002) and Spain (Samankassou et al., 2013). Very rare in Early Permian of the Carnic Alps (Vachard and Krainer, 2001b; and this work) and Middle Permian of southernmost Tunisia (Vachard and Razgallah, 1988).

Renalcis cf. *granosus* Vologdin, 1932
Figure 12.1, Figure 27.4

- * 1932 *Renalcis granosus* Vologdin, p. 15, fig. 9.
- 1955 *Izhella nubiformis* Antropov, p. 47, pl. 1, figs. 4–6.
- 1959 *Renalcis granosus*; Reitlinger, p. 12, pl. 2, fig. 7.
- p1983 *Renalcis granosus*; Mamet and Roux, p. 92–95, pl. 12, figs. 1–10, pl. 13, figs. 1–9, pl. 14, fig. 1–10 (with synonymy).
- v1987 *Renalcis* sp.; Delvolvé and Perret, pl. 2, fig. 3.
- v.1988 Quatre “cloques” de *Renalcis*; Vachard and Razgallah, fig. 1.
- v.1989b *Renalcis* ex gr. *nubiformis*; Vachard et al., p. 701, pl. 1, fig. 7 (with two references in synonymy).
- v1991 *Renalcis* ex gr. *nubiformis*; Vachard and Beckary, p. 321, pl. 1, figs. 1, 2.

- ?2001 *Izhella*; Chuvashov and Anfimov, fig. 6a (most probably *Palaeonubecularia*).
- v.2001b *Renalcis*; Vachard and Krainer, p. 178, pl. 3, figs. 5, 6.
- 2002 “*Renalcis granosus*”; Mamet, pl. 1, fig. 6.
- 2004 *Renalcis*; Shen and Webb, fig. 4B.
- 2009 *Renalcis granosus*; Luchinina, pl. 13, fig. 1.
- 2013 *Renalcis*; Samankassou et al., fig. 5.1.

Description. Length of thalli = up to 500 µm; width of thalli = 550 µm; average diameter of a chamber/cell = 200x100 µm; “wall” thickness = 60 µm.

Remarks. This identification of other Permian *Renalcis* confirms the report of Vachard and Razgallah (1988) of late Middle Permian *Renalcis* in Jebel Tebaga (Tunisia) questioned by Riding and Guo (1991). On the other hand, this paper of Vachard and Razgallah (1988) illustrated excellent Mid-Permian epiphytaceans *Tharama* Wray, 1967, however ignored by Săsăran et al. (2014, p. 8) in their review of the post-Late Devonian to pre-Late Jurassic epiphytaceans.

Occurrence. As for the genus. In the Carnic Alps, only two specimens were found by Vachard and Krainer (2001b, plate 3, figures 5, 6; sample ZKO20), and two specimens were found during this study in the Trogkofel Fm (samples GBT11_2 and TK20_1_1).

Genus GAHKUMELLA Zaninetti, 1978

Type species. *Gahkumella huberi* Zaninetti, 1978, by original designation.

Diagnosis. Colonies of uniseriate, hollow, crescentic cells. Wall dark microgranular.

Occurrence. Late Permian of Iran (Zaninetti, 1978). Roadian of Turkey (Moix et al., 2013; Vachard and Moix, 2013). Late Jurassic of Saudi Arabia (Hughes, 2010, 2013) and Spain (Granier, 1986). The Cretaceous genus *Cretaciclodus* Luperto Sinni, 1979 (see Săsăran et al., 2014 with references therein) is probably related to *Gahkumella*.

Gahkumella sp.
Figure 11.3

Description. Height of thalli = 200 µm; diameter of thallus = 100–200 µm; thickness of lamellae = 5–7 µm; thickness of interlamellae = 7–10 µm; diameter of central cavity = 70–100 µm.

Occurrence. As for the genus. In the Carnic Alps, in this study, only one specimen was found in the Zweikofel Fm (sample GB 157_13).

Order OSCILLATORIALES Elenkin, 1934 or
PROAULOPORALES Luchinina, 1975
Family GIRVANELLACEAE Luchinina, 1975

Description. Cylindrical trichomes with no, rare or frequent pseudoramifications. Wall dark microgranular.

Occurrence. Neoproterozoic–Cretaceous, cosmopolitan.

Genus GIRVANELLA Nicholson and Etheridge, 1878

Type species. *Girvanella problematica* Nicholson and Etheridge, 1878, by original designation.

Description. Cylindrical trichomes without pseudoramifications. Wall dark microgranular.

Remarks. See the details on the calcification of the trichomes of cyanobacteria in e.g., Pentecost and Riding (1986) and Merz (1992).

Occurrence. Neoproterozoic–Early Cretaceous (Johnson and Konishi, 1956; Flügel, 2004) or Late Cretaceous (Camoin, 1989), cosmopolitan and eurytope. Modern equivalents were described by Riding (1975).

Girvanella sp.
Figure 11.4

Description. Free and well-preserved *Girvanella* are rare in our material, but they appear generally completely micritized and only present within cyanobacterial crusts. These latter are generally associated with *Claracrusta* in complex biopisoliths of *Otonosia*-type (sensu Vachard, 1980 = *Osagia*-type sensu Mamet et al., 1987 or sensu Mamet, 1991). This type of grain and microecosystem is common during the Permian; however, it appears in the early Serpukhovian of Spain (Cózar et al., 2003) and even in the latest Visean of Morocco; i.e., since the concomitant FAD (first appearance datum) of *Claracrusta* (Vachard and Cózar, 2010, and see below). Outer diameter = 50 µm; inner diameter = 25 µm; wall thickness = 10–13 µm.

Remarks. The following taxa of *Girvanella* have been traditionally mentioned in the region: *Girvanella* cf. *ducii* Wethered, 1890 (by Flügel, 1979, 1980); *G.* cf. *magna* Johnson, 1946; *G.* cf. *texana* Johnson, 1950 (by Flügel, 1968, 1979); *G. kordeae* Güvenç, 1975; *G.* sp. A; and *G.* sp. B (by Kochansky-Devidé, 1970a); *Girvanellen* (by Flügel, 1980); and “Algen-Kruste”; Flügel and Flügel-Kahler, 1980; from LP (Lower *Pseudoschwagerina* Limestone Member, currently Schulterkofel Formation; late Gzhelian to earliest Asselian in age) to TK (Troglkofel Group; middle Artinskian–early Kungurian) by Flügel (1979, plate 1, figure 4). In reality, 1) no *Girvanella ducii* were observed in our material; 2) *G. kordeae* and *G. texana* are poorly defined species; 3) *G.* cf. *kordeae* was renamed *Ortonella myrae* Rácz by Flügel and Flügel-Kahler (1980,

plate 11, figures 9 and 12), 4) *Girvanella kordeae* and *G.* sp. B belong probably to the ellesmerellids (see the second part of this study).

Occurrence. Permian girvanellaceans are cosmopolitan. In the Carnic Alps, they were especially described from Forni Avoltri. Our main fossiliferous samples are located in the Grenzland Fm (sample GB19_1b); Zweikofel Fm (samples GB35_4; GB60_1_2; GB60_5; ZK97_13; ZK201_10); Zottachkopf Fm (samples TKS3_2; TKS12_4; TKW4_4; TKW 4_1a; TKW6B_3; TKW9_1; TKW9_2; TKW10_2b; TKW10_4; TKW13B_4; TNA16_2_1; TNA16_2_4a; TNA18_1; TNA18_2_2; TNA18_2_3; TNA1_1_4; TNC5_2; TNC5_3_2; Z6B_1; Z6B_3a; Z6B_3b); and Troglkofel Fm (sample TKS14_1a).

Genus MITCHELDEANIA Wethered, 1886
emend. Mamet and Roux, 1975a non Wood, 1941

Type species. *Mitcheldeania nicholsoni* Wethered, 1886 emend. Mamet and Roux, 1975a, by original designation.

Description. Relatively large cylindrical trichomes with pseudoramifications. Wall dark microgranular.

Remarks. In our knowledge, this genus was not yet mentioned in Permian beds.

Occurrence. Ordovician–Mississippian, cosmopolitan (Roux, 1985; Mamet, 1991; Mamet et al., 1992); Pennsylvanian of Greenland and Japan (Mamet and Stemmerik, 2000; Mamet, 2002).

Mitcheldeania sp.
Figure 11.5

Description. Although rare, the observed specimens display all the genus criteria with the dichotomous filaments and the following measurements: Outer diameter = 40–50 µm; inner diameter = 30–35 µm; wall thickness = 5–7 µm.

Occurrence. This study: Grenzland Fm (sample GB17_2b).

Genus KOIVAELLA Chuvashov, 1974

Type species. *Koivaella permianensis* Chuvashov, 1974, by original designation.

Description. Cylindrical trichomes with distal, oblique pseudoramifications. Wall dark microgranular.

Remarks. Several tubular undivided microfossils with a dark microgranular wall are difficult to discriminate during the Permian and the Triassic. There are 1) primitive tubular foraminifers *Earlandia* Plummer, 1930, and/or *Hyperammina* Brady, 1878, and/or *Aeolisaccus* Elliott, 1958, of the authors (see Glintzboeckel and Rabaté, 1964; Berczi-Makk, 1987; Vachard et al., 2010; Krainer

and Vachard, 2011; Nestell et al., 2015; Vachard, 2016a, 2016b; and the second paper of this study); 2) uncoiled parts of calcivertellid foraminifers (see, e.g., Homann, 1972, plate 9, figures 69, 70); 3) tubular (initial?) parts of tubiphytids; 4) a last group of dark tubules might correspond to *Koivaella* devoid of ramifications; especially, *Aeolisaccus gracilis* Pantić, 1972 (see also Flügel, 1966, plate 10, figure 3); 5) tubular cyanobacteria similar to *Girvanella* or *Microcoleus* Desmazières, 1830, ex Gomont, 1892 (e.g., Bignot, 1972; Golubić, 1973; Colin and Vachard, 1977).

Occurrence. Late Pennsylvanian–Late Triassic of the Urals, Carnic Alps, Sicily, Slovenia, Greece, Tunisia, southern Turkey (Hazro), Iran (Alborz, Zagros), Afghanistan, Thailand, Sumatra, Malaysia and New Mexico (USA) (compiled in this study).

Koivaella ex gr. *permiensis* Chuvashov, 1974
Figure 12.3, 12.4, 12.6–10

- | | | | |
|--------|--|---------|--|
| 1964 | Hyperamminidae; Glintzboeckel and Rabaté, pl. 58, figs. 1, 2. | v1990 | <i>Koivaella</i> ; Caridroit et al., p. 346 (no illustration). |
| *1974 | <i>Koivaella permiensis</i> Chuvashov, p. 35, pl. 22, figs. 1–11. | v1991 | <i>Koivaella</i> ; Razgallah and Vachard, p. 197, pl. 3, figs. 5, 6. |
| v1980 | <i>Koivaella permiensis</i> ; Vachard, p. 336–337, pl. 22, figs. 6, 8, 14, 15, pl. 24, fig. 14. | 1993 | <i>Koivaella permiensis</i> ; Chuvashov et al., pl. 14, fig. 1. |
| 1980 | <i>Koivaella permiensis</i> ; Flügel, p. 87 (no illustration). | v1993a | <i>Koivaella permiensis</i> ; Vachard et al., pl. 1, fig. 8, pl. 3, fig. 5, 6?, pl. 4, fig. 10. |
| 1980 | Gegabelte Röhrchen, vergleichbar mit <i>Koivaella permiensis</i> ; Flügel and Flügel-Kahler, pl. 11, fig. 10. | 1993 | <i>Koivaella</i> ; Senowbari-Daryan and Flügel, pl. 9, fig. 1–6. |
| v1981 | <i>Koivaella permiensis</i> ; Vachard in Vachard and Montenat, p. 29, pl. 2, figs. 1, 4–6, pl. 4, figs. 9, 12, pl. 5, fig. 12, pl. 12, fig. 8 (with two references in synonymy). | 1994 | <i>Koivaella permiensis</i> ; Fontaine et al., pl. 45, fig. 2. |
| 1983 | <i>Koivaella permiensis</i> ; Jenny-Deshusses, p. 161, pl. 17, fig. 7 (with two references in synonymy). | v.1997 | <i>Koivaella</i> ; Fontaine et al., tabl. 2, p. 144 (no illustration). |
| p.1984 | Tube-like microfossils; Flügel et al., pl. 42, figs. 1–8 (neither pl. 42, figs. 9–11, nor pl. 29, fig. 1). | ?1999 | unnamed tubules; Fagerstrom and Weidlich, tabl. 3 p. 142 (no illustration). |
| 1984 | <i>Koivaella permiensis</i> ; Senowbari-Daryan, p. 13–15, pl. 1, fig. 5, pl. 2, figs. 1–8, pl. 3, fig. 8, pl. 4, figs. 6, 7, pl. 6, fig. 5, pl. 10, fig. 1 (with five references in synonymy). | v2001b | <i>Koivaella permica</i> (sic); Vachard and Krainer, pl. 3, fig. 7. |
| v1984 | <i>Koivaella permiensis</i> ; Fontaine and Vachard, p. 51 (no illustration). | v2001b | <i>Koivaella permica</i> (sic); Vachard et al., pl. 3, figs. 1, 5. |
| v1986 | <i>Koivaella permiensis</i> ; Fontaine and Vachard, p. 113 (no illustration). | 2003 | <i>Koivaella permiensis</i> ; Noé, pl. 17, fig. 3, pl. 18, fig. 1. |
| ?1986 | <i>Parathurammia</i> sp.; Nguyen Duc Tien, pl. 1, fig. 15 (apparently similar to the bases of groups of trichomes illustrated by Vachard, 1980). | 2003 | Large branched tubes; Noé, pl. 18, fig. 2. |
| v1988 | <i>Koivaella permiensis</i> ; Fontaine et al., p. 66, fig. 3: 2. | 2003 | Cluster of thin-walled non-branched micritic tubules; Noé, pl. 18, fig. 3. |
| | | 2003 | Non-branched thin tubules; Noé, pl. 18, fig. 4. |
| | | 2004 | <i>Koivaella</i> ; Flügel, pl. 98, fig. 3. |
| | | v2009 | <i>Koivaella permiensis</i> ; Krainer et al., pl. 3, figs. 8, 9, 12. |
| | | v2011 | <i>Koivaella permiensis</i> ; Moix et al., p. 68, 75 (no illustration). |
| | | v2011 | <i>Koivaella</i> sp.; Vachard and Moix, p. 152 (no illustration). |
| | | 2013 | <i>Koivaella</i> ; Senowbari-Daryan, p. 103, 105, fig. 15d–15f (non fig. 15g = <i>Earlandia</i>). |
| | | v.?2015 | <i>Koivaella permiensis</i> ; Krainer et al., p. 24, figs. 22.15, 23.4. |
| | | v?2017a | <i>Koivaella</i> ; Krainer et al., p. 20 (no illustration). |

Description. Although rare, the observed specimens display all the specific criteria with the following measurements: Outer diameter = 70–115 µm, inner diameter = 10–15 µm, wall thickness = 20–40 µm, angle of pseudoramification = 30–40°.

Occurrence. As for the genus, worldwide. In the Carnic Aps, the species-group is known from Forni Avoltri (Flügel, 2004) and Zweikofel Fm (Vachard and Krainer, 2001b: sample ZK215x). This study: Zottachkopf Fm (samples TNB3_1_6; TNB13_4; TNC5_1); and Trogkofel Fm (samples TK9_1; TK 50_1_4; TK 50_1_5; TK_50_1_7_10).

Family GARWOODIACEAE Shuysky, 1973

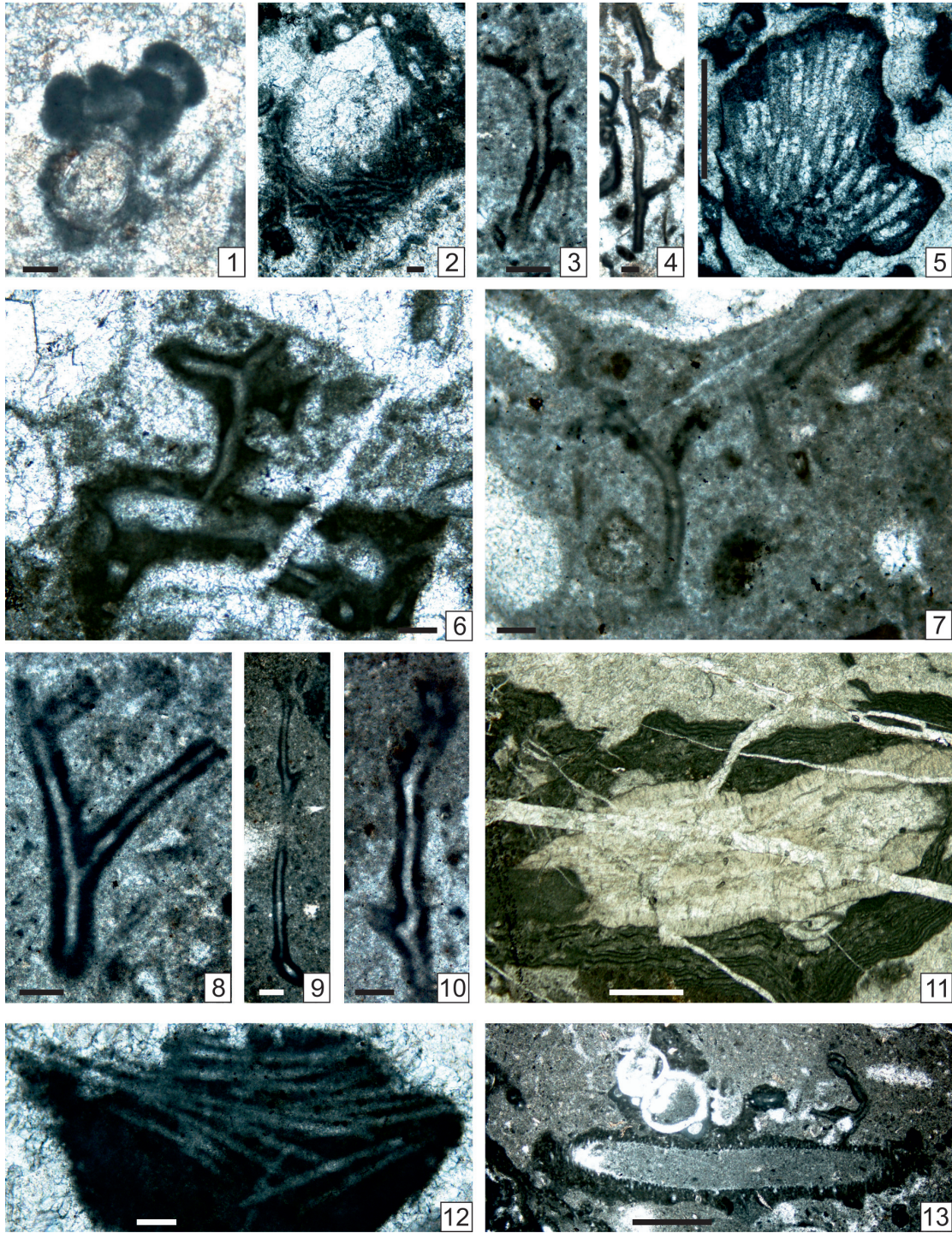


FIGURE 12. 1. *Renalcis* cf. *granosus* Vologdin, 1932. Longitudinal section. Sample TK20_1_1. 2, 12? *Clinortonella* cf. *goggauensis* (Flügel and Flügel-Kahler, 1980). 2. Axial section with typical filaments. Sample TK6_4. 12. Axial section with trichomes or sponge microscleeres. Sample TNA_4_2. 3–4, 6–10. *Koivaella* ex gr. *permiensis* Chuvashov, 1974. 3. Bifurcated filament. Sample TK9_1. 4. Another type of bifurcated filament. Sample TNB.13_4. 6. A bifurcated filament preceded by a basal part more or less similar to a tubiphytid. Sample TNB3_1_6. 7. Several filaments. Sample TNB8_1_7. 8. Bifurcated filament. Sample TK50_1_7. 9. Another typical filament. Sample TK50_1_5. 10. Another bifurcated filament. Sample TK50_1_4. 5. *Garwoodia* sp. Longitudinal section showing the typical bifurcation (right). Sample TK5_3. 11. *Archaeolithoporella hidensis* Endo, 1961a attached on a coral? Sample TK60_1. 13. *Terebella* sp. Longitudinal tube. Sample TNC5_1. Scale bars: 0.1 μ m (Figures 12.1–12.4, 12.6–12.10, 12.12) and 1 μ m (Figures 12.5, 12.11, 12.13).

Description. Colonies of cylindrical trichomes with frequent ramifications displaying various angles and types of bifurcation. Wall dark microgranular.

Remarks. Prior to the translation of Shuysky (1973), the subfamily was first named by Endo (1961b, p. 24), but was also attributed to Johnson (1964, p. 99) by Emberger (1976).

Occurrence. ?Cambrian–Ordovician–Permian, cosmopolitan (Mamet, 1991). Modern equivalents possibly exist (Riding, 1975); therefore, this morphogenus would be known during the whole fossiliferous times.

Genus CLINORTONELLA Vachard and Moix, 2013

Type species. *Ortonella goggauensis* Flügel and Flügel-Kahler, 1980, by original designation.

Synonym. *Ortonella* sensu Flügel and Flügel-Kahler (1980) (part.) (non sensu Garwood, 1914); ?stromatolites (part.).

Description. Hemispherical colonies composed of numerous, cylindrical, radiating and ramified trichomes. The ramification is always at acute angle, and occasionally in-diapason. Wall dark microgranular.

Occurrence. Goggau Limestone (Kungurian) of the Carnic Alps; questionable in the Capitanian of Cambodia; Artinskian–early Wordian of the Lycian Nappes (SW Turkey; Vachard and Moix, 2013).

Clinortonella cf. *goggauensis* (Flügel and Flügel-Kahler, 1980)

Figure 12.2, 12.12?

- ?1979 *Girvanella permica* Pia; Nguyen Duc Tien, pl. 27, fig. 14.
- 1980 *Ortonella goggauensis* Flügel and Flügel-Kahler; Flügel, pl. 4, figs. 1, 5, 6 (nom. nud.).
- *1980 *Ortonella goggauensis* Flügel and Flügel-Kahler, p. 168, 170, 172, pl. 11, figs. 3?, 5–8.
- ?1986a Stromatolithes; Nguyen Duc Tien, pl. 8, fig. 9 only (non fig. 10 = *Girvanella*; nec fig. 11 = *Archaeolithoporella*).
- ?1986b *Girvanella permica* Pia; Nguyen Duc Tien, pl. 8, fig. 9.
- 2013 *Clinortonella goggauensis* n. gen. n. comb.; Vachard and Moix, p. 15, fig. 9.5–9.7.

Description. Outer diameter = 1250 x 600 µm, inner diameter = 10–15 µm, angle of pseudoramification = 20–30°.

Occurrence. Early Permian of the Carnic Alps and Turkey, and perhaps Middle Permian of Cambodia (compiled in this study). In the Carnic Alps, Trogkofel Limestone of Sexten and Forni Avoltri (Flügel, 1980; Flügel and Flügel-Kahler, 1980). This study: basal Zweikofel Fm (sample GB35_4?);

Zottachkopf Fm (sample TNA4_2); and Trogkofel Fm (sample TK6_4).

Genus GARWOODIA Wood, 1941

Type species. *Mitcheldeania gregaria* (Nicholson, 1888) emend. Wood, 1941, by original designation.

Description. Cylindrical trichomes with frequent ramifications, with the second branch re-becoming rapidly parallel with the first branch. Wall dark microgranular.

Occurrence. Ordovician–Permian (Roux, 1985; Vachard et al., 1989b) or Devonian–Cretaceous (Flügel, 2004), probably cosmopolitan despite rarely cited.

Garwoodia sp.

Figure 12.5

- ?1979 *Garwoodia gregaria* (Nicholson); Flügel, p. 572 (no illustration).
- 1980 *Garwoodia* sp.; Flügel and Flügel-Kahler, p. 166, pl. 9, figs. 6, 8.

Description. Outer diameter of colonies = 2000 x 2100 µm; inner diameter of trichomes = 75–100 µm; thickness of calcification between trichomes = 10–15 µm.

Remarks. The genus was mentioned but not illustrated from the Upper *Pseudoschwagerina* Limestone (Zweikofel Formation; early Artinskian in age) by Flügel (1979, p. 572).

Occurrence. In the Carnic Alps: Trogkofel-Kalk of Forni Avoltri and Goggau Limestone near Goggau-Tarvis (Flügel and Flügel-Kahler, 1980). This study: Trogkofel Fm (sample TK5_3).

Phylum RHODOPHYTA Wettstein, 1901

Class and order undetermined

Family ELIANELLACEAE Granier in Granier and Dias-Brito, 2016

Genus PARACHAETETES Deninger, 1906

Type species. *Parachaetetes tornquisti* Deninger, 1906, by original designation.

Description. Thalli large, fan-shaped, with numerous cellular files whose vertical and horizontal walls are well preserved, well calcified, and regularly arranged. Wall dark microgranular. Walls and/or thalli are often recrystallized taphonomically into whitish neosparite. Secondary algal borings affecting these neosparitized thalli cannot be confused with algal filaments.

Remarks. Some identifications of *Parachaetetes* are disputable. For example, Cretaceous and Paleocene species of this genus, such as *Parachaetetes asvapatii* “Pia in Rao and Pia, 1936” illustrated by Johnson and Kaska (1965), and re-illustrated by Granier et al. (2017), belong to

Elianella elegans Pfender and Basse, 1948. In contrast, some “*Solenomeris* sp.” of Johnson and Kaska (1965) belong to *Parachaetetes* sp. (Granier et al., 2017). *Parachaetetes* and other elianellaceans can present a diagenesis which mimics that of some Bryopsidales (Vachard et al., 1989a; Flügel et al., 1992; Senowbari-Daryan and Zamparelli, 2005; Senowbari-Daryan et al., 2008), especially the morphogenus *Poncetellina* Mamet and Roux, 1984 (for *Poncetella* Mamet and Roux, 1983 pre-occupied), described as *Codiale* but with a type species originally, and very probably correctly, called *Solenopora erecta* Poncet, 1971. Similarly, there is a species described as *Pycnoporidium ortonelloides*, redescribed here after, which recombine the genus and species names evoking both groups.

Occurrence. The genus *Parachaetetes* is relatively abundant in the latest Devonian and Tournaisian (Pia, 1937; Berchenko, 1982; Mamet and Rudloff, 1972; Mamet and Roux, 1983; Ivanova and Bogush, 1992; Shen and Webb, 2004). It is relatively rare from Viséan to the Wordian. In turn, they are relatively abundant in the late Capitanian of Jebel Tebaga, Tunisia (Vachard et al., 1989a), and the Capitanian of the southern USA with “*Solenopora*” *texana* (see Johnson, 1950; Noé, 2003) is also present in the late Changhsingian of South China (Flügel and Reinhardt, 1989; Fan et al., 1990). They are well known from Late Triassic to Eocene (Peterhans, 1929; Flügel, 1975; Aguirre and Barattolo, 2001).

Parachaetetes ortonelloides (Endo, 1961c) n. comb.

Figure 13.1, 13.3–5

- *1961c *Pycnoporidium ortonelloides* Endo, p. 83, pl. 1, pl. 2, pl. 3, fig. 1.
- 1961d *Pycnoporidium ortonelloides*; Endo, p. 122, pl. 7, fig. 5.
- ?1968 *Solenopora* cf. *texana* Johnson; Flügel, p. 55 (no illustration).
- 1976 *Pycnoporidium ortonelloides*; Emberger, p. 104 (no illustration) (with three references).
- ?1979 *Solenopora centurionis* Pia; Flügel, p. 572 (no illustration).
- ?1979 *Solenopora texana* Johnson; Flügel, p. 572 (no illustration).
- 1980 *Pycnoporidium ortonelloides*; Flügel and Flügel-Kahler, pl. 9, figs. 1, 2.
- ?1980 *Solenopora* cf. *centurionis* Pia; Flügel and Flügel-Kahler, pl. 9, figs. 3, 5.
- 1980 *Ortonella densa* Nguyen Lan Tu; Flügel and Flügel-Kahler, p. 167, pl. 9, fig. 7.
- ?2003 *Parachaetetes* sp.; Noé, pl. 14, fig. 3.

v?2013 *Parachaetetes* sp.; Kossovaya et al., p. 358, 359, table 2, fig. 8m, 8p.

Description. Length of fragments = 2,800–6,300 x 700–3,300 µm; width (rarely 700)–1,000–2,000 µm; width of cellular files = 40 µm. This taxon could be a taphotaxon related to *Parachaetetes lamellatus* Konishi, 1954b, which was illustrated from the Trogkofel Fm by Riding and Guo (1991, figure 18, as “*Solenopora*”), as that was suggested by Vachard et al. (1989a).

Occurrence. Permian of Tethys, Japan and the Urals. In the Carnic Alps: Schulterkofel and Zweikofel formations (Flügel, 1979). Forni Avoltri (Flügel and Flügel-Kahler, 1980). Very rare in our material of the Zweikofel Fm (samples GB136_1; GB159_2; GB168_3; ZK99_B; ZK99a_5); and Zotachkopf Fm (sample Z9B_1).

Class FLORIDEOPHYCEAE Cavalier-Smith, 1998
Order ARCHAEOLITHOPHYLLALES Vachard and Kabanov, 2007

Remarks. The traditional idea that no genera are known between the Pennsylvanian-Permian range of *Archaeolithophyllum* and the first acme of the corallinaceans during the Early Cretaceous (e.g., Lemoine, 1977; Bucur et al., 2004) led Vachard and Kabanov (2007) to introduce an order Archaeolithophyllales, as distinct of the order Corallinales Silva and Johansen, 1986. However, due to the presence of relatively similar hypothalli and perithalli, both orders belong probably to the same class. Furthermore, a representative of the order Corallinales was unquestionably found in the Late Triassic: *Norithamnium* Senowbari-Daryan, Keupp, Abate and Vartis-Matarangas, 2002. However, the phylogeny suggested by these latter authors, with *Archaeolithophyllum* passing to *Norithamnium* by the intermediary of *Archaeolithoporella* is erroneous, because this latter genus belongs most probably to the cyanobacteria (see earlier).

Family ARCHAEOLITHOPHYLLACEAE

Chuvashov in Chuvashov, Luchinina, Shuysky, Shaikin, Berchenko, Ishchenko, Saltovskaya and Shirshova, 1987

Genus ARCHAEOLITHOPHYLLUM Johnson, 1956 emend. Wray, 1964

Synonyms. *Kasimophyllum* Mamet and Villa, 2004.

Type species. *Archaeolithophyllum missouriense* (sic: *missouriensum*) Johnson, 1956; by original designation.

Description. Phylloid thallus, occasionally bifurcated, which occurs as isolated blades or foliate

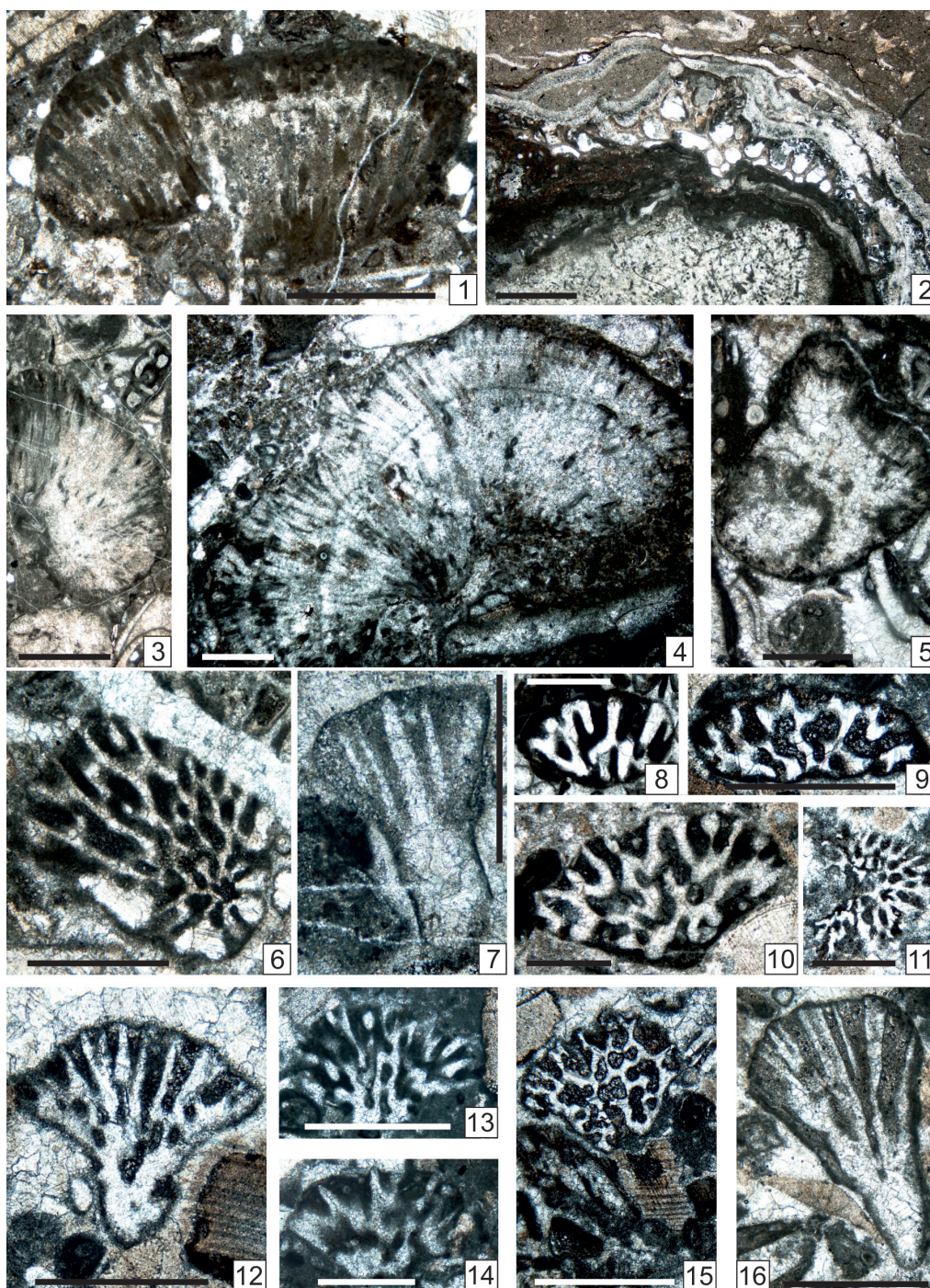


FIGURE 13. 1, 3, 4, 5. *Parachaetetes ortonelloides* (Endo, 1961c) n. comb. 1. Poorly preserved axial section with relatively broad recrystallized cellular files. Sample GB168_3. 3. Recrystallized axial section. Sample GB136_1. 4. Less recrystallized axial section. Sample Z9B_1. 5. Poorly preserved section resembling *Ivanovia*. Sample GB159_2. 2. *Archaeolithophyllum lamellosum* Wray, 1964. Several encrusting thalli, in axial section, attached on bryozoan, cyanobacterial crust and phylloid alga. Sample GB77_A2. 6–16. *Homannisiphon morikawai* (Endo, 1954). Several oblique sections. 6. Sample GB51_1 (previously published by Vachard and Krainer, 2001b, plate 13, figure 15). 7. Sample GB52_2. 8. Sample ZK99_5. 9. Sample Z1_4c. 10. Sample GB5_8. 4. 11. Sample Z1_5. 12. Sample Z1_2. 13. Sample TNA2_1_2. 14. Sample TNA2_1_1. 15. Transverse oblique section. Sample Z1_3_4. 5. 16. Sample GB50_1 (previously published by Vachard and Krainer, 2001b, plate 13, figure 14). Scale bars: 0.2 μm (Figures 13.1, 13.2, 13.3); 0.5 μm (Figures 13.8, 13.11, 13.14); and 1 μm (Figures 13.4–13.9, 3.10, 12, 13.13, 13.15, 13.16).

and encrusting multilayered masses; internal tissue differentiated into a thick hypothallus, with arcuate rows of wide polygonal cells, and a thinner perithallus, with small cells; knobby and spinose protuberances present on the upper and basal surface; conceptacles ovoid to highly arched, irregularly distributed over the upper surface of the thallus, with a single atypical aperture; cell fusions occasionally present. Cellular walls currently composed of low-Mg calcite with low Sr concentrations (according to Corrochano et al., 2013).

Occurrence. Early Serpukhovian (Vachard et al., 1989b, 2016; Cózar et al., 2003, 2005, 2010; Cózar, 2005) to late Capitanian; cosmopolitan. In the mounds of the Auernig Formation (Orenburgian = Newwellian), in the Carnic Alps, *Archaeolithophyllum missouriense* is still relatively common (Krainer, 2007); after that, very rare *A. lamellosum* constitute the last representatives of the genus in this region (this paper).

Archaeolithophyllum lamellosum Wray, 1964
Figure 13.2

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|---|--|
| <p>*1964 <i>Archaeolithophyllum lamellosum</i> Wray, p. 8–9, pl. 2, figs. 1, 3–5?, 7.</p> <p>?1968 <i>Archaeolithophyllum</i> sp.; Flügel, p. 56 (no illustration).</p> <p>1976 <i>Archaeolithophyllum lamellosum</i>; Emberger, p. 99 (no illustration) (with two references).</p> <p>?1979 <i>Archaeolithophyllum lamellosum</i>; Flügel, p. 572 (no illustration).</p> <p>1980 <i>Archaeolithophyllum lamellosum</i>; Flügel, p. 53, p. 63, pl. 12, figs. 2, 4.</p> <p>1980 <i>Archaeolithophyllum</i> sp.; Flügel, pl. 13, fig. 6.</p> <p>1980 <i>Archaeolithophyllum delicatium</i> Johnson; Flügel and Flügel-Kahler, p. 157, pl. 8, fig. 5 (with two references).</p> <p>1980 <i>Archaeolithophyllum lamellosum</i>; Flügel and Flügel-Kahler, p. 157–158, 160, pl. 8, fig. 6, pl. 9, fig. 1 (with three references).</p> <p>1983a <i>Archaeolithophyllum</i> cf. <i>A. lamellosum</i>; Toomey, pl. 21, fig. 10.</p> <p>1983b <i>Archaeolithophyllum lamellosum</i>; Toomey, figs. 4b–4f, 5a–5h.</p> <p>v1992 <i>Archaeolithophyllum lamellosum</i>; Krainer, pl. 5, fig. 3.</p> <p>1995a <i>Archaeolithophyllum lamellosum</i>; Krainer, p. 200, 208, 210, 211, 212 (no illustration).</p> <p>1996 <i>Archaeolithophyllum lamellosum</i>; Skompski, p. 224–225, pl. 14, figs. 3–6.</p> <p>1998 <i>Archaeolithophyllum lamellosum</i>; Forke et al., pl. 3, fig. 7.</p> <p>v2001a “<i>Archaeolithophyllum</i>” <i>lamellosum</i>; Vachard and Krainer, p. 151 (no illustration).</p> | <p>v2001b “<i>Archaeolithophyllum</i>” <i>lamellosum</i>; Vachard and Krainer, p. 172 (no illustration).</p> <p>v2003a <i>Archaeolithophyllum lamellosum</i>; Krainer et al., p. 8, 14, pl. 1, fig. 6.</p> <p>2003 <i>Archaeolithophyllum lamellosum</i>; Samankassou and West, p. 219, 225, 227, 235 (no illustration).</p> <p>2003 <i>Archaeolithophyllum lamellosum</i>; Cózar et al., pl. 4, fig. 12.</p> <p>2004 <i>Archaeolithophyllum</i>; Flügel, pl. 56, figs. 1, 2.</p> <p>2005 <i>Archaeolithophyllum lamellosum</i>; Cózar, text-fig. 3, p. 408, text-fig. 4, p. 409, fig. 70.10–11.</p> <p>2005b <i>Archaeolithophyllum lamellosum</i>; Cózar and Somerville, p. 90, pl. 2, fig. 3.</p> <p>2005 <i>Archaeolithophyllum lamellosum</i>; Cózar et al., p. 14, 16, tabl. 2, fig. 4A–D.</p> <p>v2008 <i>Archaeolithophyllum lamellosum</i>; Pille, p. 59, pl. 19, figs. 12–14.</p> <p>v 2009 <i>Archaeolithophyllum lamellosum</i>; Krainer et al., p. 10, 12, 13, pl. 2, figs. 1–6.</p> <p>2010 <i>Archaeolithophyllum lamellosum</i>; Cózar et al., fig. 4t.</p> <p>2013 laminar red algae; Wahlman and Tasker, fig. 17F.</p> <p>v.?2015 <i>Archaeolithophyllum lamellosum</i>; Krainer et al., figs. 21.23, 21.24.</p> <p>v.2015 <i>Archaeolithophyllum lamellosum</i>; Lucas et al., fig. 9B.</p> <p>v2016 <i>Archaeolithophyllum lamellosum</i>; Vachard et al., fig. 4B.</p> <p>v.?2017 <i>Archaeolithophyllum lamellosum</i>; Lucas et al., p. 15 (no illustration).</p> <p>v.2017a <i>Archaeolithophyllum lamellosum</i>; Krainer et al., p. 20, 31, pl. 30, fig. 12.</p> |
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Description. Encrusting thalli measuring: Length = 6,000 µm; width = 200 µm.

Occurrence. As for the genus. In the Carnic Alps: Pizzul Fm (late Kasimovian/early Gzhelian) (Krainer, 1992; Vachard and Krainer, 2001a); Schulterkofel Fm to Trogkofel Fm (Flügel, 1979; Krainer, 2007). Forni Avoltri; Seikofel (Flügel, 1980); Goggau (Flügel and Flügel-Kahler, 1980). This study: Zweikofel Fm (sample GB77A_2).

Phylum CHLOROPHYTA Pascher, 1914

Class BRYOPSIDOPHYCEAE Bessey, 1907

Order BRYOPSIDALES Schaffner, 1922

Incertae familiae

Genus HOMANNISIPHON Vachard and Krainer, 2001b

Type species. *Ortonella morikawai* Endo, 1954; by original designation.

Description. Thallus cordiform (= heart-shaped). Sparitized skeleton formerly aragonitic. Radiate siphons beginning at the base of the thallus and

diverging toward the apex, dichotomously branching several times. Tube cylindrical with some swollen parts. Deltoid extremities of siphons. Conceptacles not obvious.

Other species. *Salopekiella*? sp. sensu Mu, 1982; *Anchicodium maximum* Senowbari-Daryan and Rashidi, 2010.

Occurrence. Late Pennsylvanian (late Kasimovian–early Gzhelian) of Japan (Endo, 1954). Sakmarian of the Urals (Chuvashov, 1974; Kulik, 1978). Early Sakmarian (= Upper *Pseudoschwagerina* Limestone = Zweikofel Formation) of the Carnic Alps and the Karawanken Mountains (Kochansky-Devidé, 1970a; Homann, 1972; Vachard and Krainer, 2001b). Early Permian of Tibet (Mu, 1982) and Iran (Senowbari-Daryan and Rashidi, 2010).

Homannisiphon morikawai (Endo, 1954)

Figure 13.6–16, Figure 14.1–5

- *1954 *Ortonella morikawai* Endo, p. 219–220, pl. 19, figs. 8, 9.
- 1957 *Ortonella morikawai*; Endo, p. 296, pl. 43, figs. 4, 5.
- 1963 *Ortonella morikawai*; Johnson, p. 131, pl. 16, figs. 6, 7, pl. 76, figs. 5–8.
- 1970a *Ortonella morikawai*; Kochansky-Devidé, p. 212, 240, pl. 22, figs. 1, 2, pl. 24, figs. 1, 2.
- .1972 *Salopekiella* cf. *S. velebitana* Milanović; Homann, p. 230–231, pl. 7, figs. 56–58.
- .1974 *Thaiporella uralica* Chuvashov, p. 19–20, pl. 5, figs. 1, 2 (non fig. 3 which is the holotype of this species and was re-illustrated by Chuvashov et al., 1993, pl. 14, fig. 14).
- 1976 *Ortonella morikawai*; Emberger, p. 92 (with four references in synonymy).
- 1977 *Ortonella morikawai*; Flügel, p. 318 (no illustration).
- 1978 *Ortonella* cf. *morikawai*; Kulik, p. 190–191, pl. 3, fig. 2.
- 1979 *Ortonella morikawai*; Flügel, p. 572 (no illustration).
- .?1982 *Salopekiella*? sp.; Mu, p. 230, pl. 4, fig. 7 (or another species of *Homannisiphon*).
- .1988 *Epimastopora*?; Fontaine et al., pl. 13, fig. 1.
- non 1996 *Ortonella morikawai*; Sano and Kanmera, pl. 59, fig. 10.
- 2001b *Homannisiphon morikawai*; Vachard and Krainer, p. 182, 184, pl. 3, figs. 13–16.
- v2013 *Homannisiphon morikawai*; Moix et al., p. 411, pl. 6, figs. 14, 17.

Description. Length of fragments: (rarely 500)–2,300–4,500 µm; width of fragments = (rarely 700)–1,000–2,000 µm; siphon diameter = 50–100 µm; intersiphon width = 20–50 µm.

Occurrence. Late Carboniferous of Japan (Endo, 1954, 1957); Sakmarian of the Urals (Chuvashov, 1974; Kulik, 1978), West Thailand (Fontaine et al., 1988), and Turkey (Moix et al., 2013). In the Carnic Alps: Upper *Pseudoschwagerina* Limestone = Zweikofel Formation (Homann, 1972; Vachard and Krainer, 2001b: GB50, GB51, ZK77, and ZK88); Trogkofel Group of the Carnic Alps (Flügel, 1979) and Slovenia (Kochansky-Devidé, 1970a). In this study: Zweikofel Fm (samples GB50_1; GB51_1; GB52_2; GB58_4; ZK99_5); Zottachkopf Fm (samples TNB10_4; TNA2_1_1; TNA2_1_2; TNA3_3; Z1_2; Z1_3; Z1_4a; Z1_4b; Z1_4c; Z1_5); and Trogkofel Fm (sample TK18_4).

Family ANCHICODIACEAE Shuysky in Chuvashov, Luchinina, Shuysky, Shaikin, Berchenko, Ishchenko, Saltovskaya and Shirshova, 1987 emend. herein

Emended diagnosis. The thalli are foliate or ribbon-shaped, straight or curved, rarely undulated, sinuous, or ramified. The medullar siphons are numerous, thin, and sinuous, but rarely preserved; the cortical siphons are more rectilinear near the lower and/or outer surfaces, cylindrical or more globular (utricles), rarely bifurcated. The calcification, initially aragonitic, becomes neomicrosparitic and may occlude many parts of the thalli, especially the central zone. Conceptacles are unknown except for the genus *Eugonophyllum* and some species of *Ivanovia*.

Composition. Anchicodiaceae Shuysky in Chuvashov, Luchinina, Shuysky, Shaikin, Berchenko, Ishchenko, Saltovskaya and Shirshova, 1987 nom. transl. herein (= Ivanoviae Shuysky in Chuvashov, Luchinina, Shuysky, Shaikin, Berchenko, Ishchenko, Saltovskaya and Shirshova, 1987; because of the priority imposed by the family name).

Remarks. As the informal group of “phylloid algae” named by Pray and Wray (1963) is often rejected because of various paleobotanical inconsistencies, we prefer to use here the name Anchicodiaceae as already advised by Skompski (1996, p. 216), but which is still rarely used in the literature. Nevertheless, even if Shuysky in Chuvashov et al. (1987) has created the family Anchicodiaceae, he assigned, in the same publication, the genus *Anchicodium* to the tribe Ivanoviae, and did not create the tribe Anchicodiaceae; in consequence, both taxonomic units Anchicodiaceae and Anchicodiaceae are formally revised in this paper. This algal group was diversely interpreted (Pray and Wray, 1963; Wray, 1968; Roux, 1985; Chuvashov et al., 1987; Wahlman, 1988; Vachard et al., 1989a, 2001a,

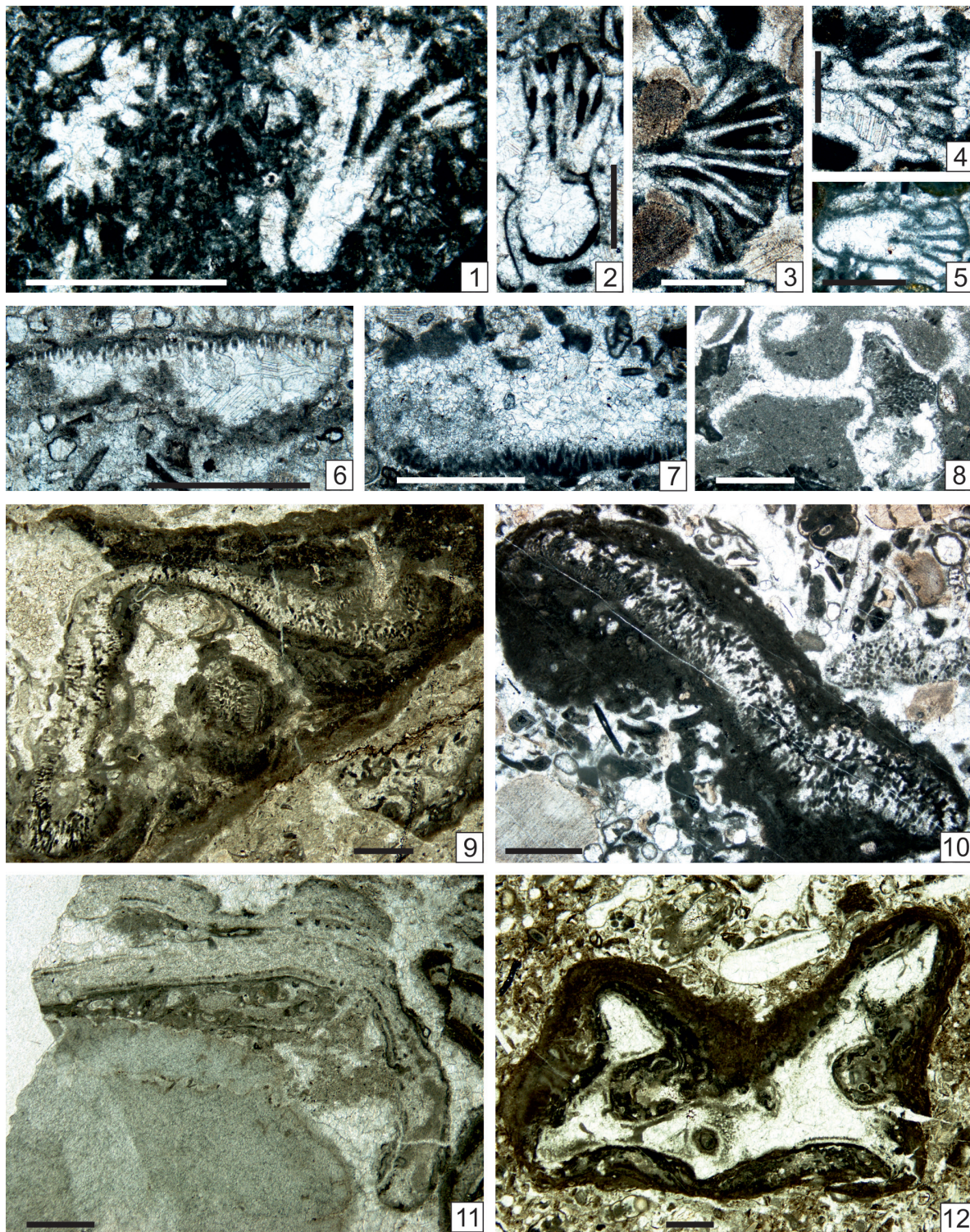


FIGURE 14. 1–5. *Homannisiphon morikawai* (Endo, 1954). Several oblique sections. 1. Sample TK18_4. 2. Sample TNB10_4. 3. Sample Z1_4a. 4. Sample Z1_4b. 5. Sample TNA3_3. 6–8. *Ivanovia tenuissima* Khorova, 1946. 6. Longitudinal section. Sample GB_76_3. 7. Longitudinal section. Sample TNA2_1_4c. 8. Tangential section. Sample TNC5_2. 9, 10. *Anchicodium japonicum* Endo, 1953a. 9. Longitudinal section. Sample TKS3_1. 10. Longitudinal section. Sample ZK67_A. 11, 12. *Eugonophyllum magnum* (Endo, 1951) emend. Konishi and Wray, 1961. 11. Longitudinal section. Sample Z2_1. 12. Longitudinal section. Sample Z7_1_width 9.5 μm . Scale bars: 0.1 μm (Figure 14.6), 0.5 μm (Figures 14.1–14.5), and 1 μm (Figures 14.7–14.11).

2015; Kirkland et al., 1991, 1993; Baars and Torres, 1991; Riding and Guo, 1991; Dawson, 1992; Moshier and Kirkland, 1993, 1994; Pintigore, 1994; Forsythe et al., 2002; Forsythe, 2003; Schlagintweit, 2010; Granier, 2012; Corrochano et al., 2013), but it is generally considered as a group of green algae more or less similar to *Halimeda* (Rauzer-Chernousova and Korolyuk, 1981; Baars, 1992; Torres et al., 1992; Kirkland et al., 1993; Torres, 1995). However, some structures, similar to the conceptacles of the red algae *Archaeolithophyllum*, are occasionally obvious on many species of *Eugonophyllum* (Konishi and Wray, 1961, plate 75, figures 12, 16; Toomey and Windland, 1973, figures 8F, 8G; Toomey, 1983a, plate 21, figure 12; Vachard et al., 1989b, plate 3, figures 2–5; 1993b, plate 1, figures 1, 2); Kirkland et al., 1993, text-figure 5 p. 114; Krainer et al., 2003a, plate 7, figure 12, plate 8, figure 19), as well as in *Ivanovia triasica* Torres, 2003. Several morphogenera or and/or taphotaxa have been distinguished, and based, for a long time, on the characters summarized by Konishi and Wray, 1961, text-figure 1; Wray, 1964; Tillman, 1971; Chuvashov et al., 1987; and Toomey, 1991). These morphogenera are principally *Anchicodium* Johnson, 1946; *Eugonophyllum* Konishi and Wray, 1961; *Ivanovia* Khvorova, 1946; *Neoanchicodium* Endo in Endo and Kanuma, 1954 (non sensu Mamet et al., 1987); and several genera described more recently but which are probably junior synonyms, such as *Kansaphyllum* Baars, 1992 and *Iranicodium* Senowbari-Daryan and Rashidi, 2010. The preserved parts of the siphons, in form of utricles, generally constitute a peripheral belt, but their inner ramifications (thinner and more zigzagging) occasionally attain the center of the recrystallized thalli; this latter stage of preservation is conspicuous in *Kansaphyllum*, *Anchicodium* sensu Torres and Baars, 1992, and even, in *Halimeda soltanensis* Poncet, 1989, which was considered as the maximal stage of modification of *Ivanovia tebagaensis* Vachard, Gargouri-Razgallah and Chaouachi, 1989a (Vachard et al., 1989a), but which is most probably a species of *Calcipatera* (see later).

A huge literature is devoted to the phylloid-algal-buildups (Peterson and Hite, 1969; Toomey and Winland, 1973; Wilson, 1975; Cys and Mazullo, 1977; Toomey et al., 1977; Heckel and Cocke, 1979; Mazullo and Cys, 1979; Toomey, 1980, 1991; Choquette, 1983; Chuvashov and Riding, 1984; Bowsher, 1986; Dawson and Carozzi, 1986; Fagerstrom, 1987; West, 1988; Vachard et al., 1989a; Roylance, 1990; James and Bourque,

1992; Soreghan and Giles, 1999; Wahlman, 2002; Samankassou and West, 2002, 2003; Flügel, 2004; Krainer et al., 2007; Enpu et al., 2007; Gong et al., 2009). In contrast, mounds constructed by non-phylloid algae (i.e., other bryopsidales and dasycladales) are rare (e.g., Mississippian of Nova Scotia, Arctic Archipelago of Canada: Davies et al., 1989; Carnic Alps of Austria/Italy: Flügel, 1987; Flügel et al., 1997; Krainer, 1995a, 2007; Krainer and Vachard, 2007a; Krainer et al., 2003b; Samankassou, 1999, 2003). It is noteworthy that, in the Carnic Alps, phylloid green algal mounds often occur above or below *Anthracoporella* mounds (Samankassou, 2003).

Occurrence. Middle Pennsylvanian–Middle Permian, cosmopolitan. Rare in the Late Permian. Triassic representatives are disputable and possibly Permian in age.

Tribe ANCHICODIAE nomen transl. herein
pro family Anchicodiaceae

Synonym. *Ivanoviae* Shuysky in Chuvashov, Luchinina, Shuysky, Shaikin, Berchenko, Ishchenko, Saltovskaya and Shirshova, 1987.

Diagnosis. Thalli foliate or ribbon-shaped, straight or curved, and rarely undulated. The medullar and cortical siphons are numerous, aspondyl, short, and sinuous, and all irregularly arranged. Conceptacles unknown.

Remarks. Ancestral, pre-Bashkirian Anchicodiae are generally poorly known and unnamed; they correspond partly to *Mellporella* Rácz, 1966a and perhaps *Mellporellopsis* Vachard in Vachard, Hauser, Martini, Zaninetti, Matter and Peters, 2001a, which are two typical Bryopsidales. The most remote ancestor could be *Vignella* Mamet and Prétat, 2005, because of the shape of the cortical siphons of this Givetian alga. According to Torres and Baars (1992), true *Anchicodium* are possibly cylindrical and branched, whereas *Kansaphyllum* and *Iranophyllum* could be phylloid equivalents, but this suggestion is irrelevant with the shape of the type species of *Anchicodium*, which, as well as *Anchicodium* sensu Konishi and Wray (1961, text-figure 1), is more similar to *Iranocodium* and *Kansaphyllum* than to *Anchicodium* sensu Torres and Baars, 1992. Hence, we prefer to admit here that *Anchicodium* (at least by its type species), *Kansaphyllum* and *Iranocodium*, are phylloid and therefore three synonyms; the non-phylloid “*Anchicodium*” sensu Torres and Baars, 1992, being to be re-named.

Occurrence. ?Latest Mississippian of Algeria. Early Pennsylvanian–Early Permian, probably cosmopolitan.

Genus ANCHICODIUM Johnson, 1946

Synonyms. ?*Kansaphyllum*, ?*Iranophyllum*.

Type species. *Anchicodium funile* Johnson, 1946; by original designation.

Description. The thalli are foliate or ribbon-shaped, straight or curved, rarely sinuous. The siphons are numerous, aspondyl and sinuous, becoming more rectilinear near the outer surface; except for this difference, the limits of the medullar and cortical zones are generally inconspicuous. Conceptacles are unknown.

Other species. *Anchicodium gracile* Johnson, 1946; *A. undulatum* Johnson, 1946; *A. nodosum* Johnson, 1946; *A. plumosum* Johnson, 1946; *A. permianum* Johnson, 1946; *A. japonicum* Endo, 1953a; *A. fukujiense* Endo and Horiguchi, 1957; *A. ankarensis* Bilgütay, 1960; *A. densum* Endo, 1961d; *A. sindbadi* Elliott, 1970a; *A. robustum* Mu, 1982; *A. zhongbaensis* Mu, 1982; *Kansaphyllum rezakii* Baars, 1992; *Anchicodium iranikum* Senowbari-Daryan and Rashidi, 2010; *A. maximum* Senowbari-Daryan and Rashidi, 2010; *Iranophyllum asymmetricum* Senowbari-Daryan and Rashidi, 2010; non *Anchicodium magnum* Endo, 1951 (= *Eugonophyllum* fide Konishi and Wray, 1961 and see later); non *A. flexosum* Endo, 1961c (= *Neoanchicodium*); non *A. fascicularis* Chuvashov, 1974 (= *Richella* Mamet and Roux in Mamet et al., 1987); non *A. wensuensis* Mu, 1985 (*Calcipatera*; see later); non *A. expressum* Wu, 1991 (= *Ivanovia*).

Remarks. *Anchicodium*, *Kansaphyllum*, and *Iranocodium* are probably synonymous due to the great variability of the arrangements of the filaments in *Anchicodium*. On the other hand, *Anchicodium* is the oldest mound-building Pennsylvanian–Early Permian organism, for example, in New Mexico (Krainer et al., 2009 with references therein).

Occurrence. Rare and questionable in the Serpukhovian of Algeria (Lemosquet and Poncet, 1977; Sebbar and Lys, 1989; Sebbar and Mamet, 1996); Bashkirian of Spain and northern Africa (Vachard and Beckary, 1991; Sebbar and Mamet, 1996; with references therein). Relatively common and cosmopolitan (Tethys, Tibet, Japan and USA) from Moscovian to Early Permian. Rare up to the Guadalupian of Tunisia (Vachard et al., 1989a). Very rare in the Capitanian/Late Permian (e.g., with “*Eugonophyllum*” sp. sensu Vachard et al., 1993a, plate 2, figure 1, emended herein; and probably *Anchicodium sindbadi*; although this taxon is reworked in the Cretaceous according to Elliott (1970), and its real age poorly established).

Anchicodium japonicum Endo, 1953a

Figure 14.9, 14.10

- *1953a *Anchicodium japonicum* Endo, p. 123–124, pl. 11, fig. 5, pl. 12, figs. 5–7.
- 1961d *Anchicodium japonicum*; Endo, p. 133, pl. 12, figs. 5–7.
- ?1968 *Anchicodium magnum* Endo; Flügel, p. 56 (no illustration).
- ?1968 *Anchicodium plumosum* Johnson; Flügel, p. 56 (no illustration).
- 1976 *Anchicodium japonicum*; Emberger, p. 79 (no illustration).
- ?1979 *Anchicodium fukujiense* Endo and Horiguchi; Flügel, p. 572 (no illustration).
- 1980 *Anchicodium japonicum*; Flügel and Flügel-Kahler, p. 116–117, pl. 1, figs. 2, 3.
- ?1980 *Eugonophyllum mulderi* (Rácz); Flügel, p. 120–121, pl. 1, fig. 8.
- ?1995 *Eugonophyllum* sp.; Forke, p. 240, pl. 15/1.
- ?2004 *Eugonophyllum mulderi*; Flügel, pl. 58, fig. 5.
- ?2010 *Anchicodium iranikum* Senowbari-Daryan and Rashidi, p. 1011, pl. 1, figs. B, C, E–G, pl. 2, figs. A–D, pl. 4, figs. B, C, E, text-figs. 4–6.
- v.2015 *Calcipatera* sp.; Lucas et al., fig. 21.18.

Description. *Anchicodium* with well-differentiated cortex and medulla (by this character, it differs from the coeval species *A. sindbadi*). The dimensions given by Flügel and Flügel-Kahler (1980) are the following: Thallus length = 1,100–7,800 µm; thallus width = 400–800 µm; cortical zone thickness = 140–200 µm; diameter of siphons = 30–40 µm.

Occurrence. Early Permian of Japan (Endo, 1953a, 1961d) and perhaps central Iran (as *Anchicodium iranikum* Senowbari-Daryan and Rashidi, 2010). In the Carnic Alps: Lower and Upper *Pseudoschwagerina* Limestone (Schulterkofel and Zweikofel formations), Grenzland Formation, Trogkofel Formation (Flügel, 1979); Forni Avoltri (Flügel, 1980); Seikofel (Flügel and Flügel-Kahler, 1980). This study: rare in the Zweikofel Fm (sample ZK67_A) and Zottachkopf Fm (samples TNA18_2_3; TKS 3_1_width 8 µm).

Genus IVANOVIA Khvorova, 1946

Type species. *Ivanovia tenuissima* Khvorova, 1946; by original designation.

Synonyms. ?*Bolivianella* Mamet, 1996.

Description. The recrystallized thalli are straight or curved, rarely sinuous or cupuliform, and composed of whitish, moderately to coarsely grained sparite. The shape of the preserved siphons is cylindrical to triangular, perpendicular to the wall and communicating with the external part of the thalli. They are uniform and homogeneous in

shape and distance between them; hence, the microperforated zone appears very regular in thickness. The dark, micritic cement filling of the siphons is optically homogeneous.

Remarks. *Ivanovia* is principally a Middle–Late Pennsylvanian genus; it is interpreted as an important builder in the Paradox Basin and New Mexico, USA (Baars and Torres, 1991; Krainer et al., 2009). In the Permian, the best known species of *Ivanovia* is *I. tebagaensis* Vachard, Gargouri-Razgallah and Chaouachi, 1989a. Despite of several interpretations (Torres, 1995, 1999; Torres et al., 2003) of this species as coenocytic, cyathiform, and with an asexual reproduction, *I. tebagaensis* is most probably a junior synonym of *I. triassica* Torres, 2003. Furthermore, all the so-called Triassic *Ivanovia* described by Reid (1986) and Torres (2003) from Yukon Territory (Canada) could proceed from Permian olistolites which are relatively common in all the North Cordilleran areas (e.g., Skinner and Wilde, 1966; Rigaud, 2012). Finally, *Ivanovia tebagaensis* and *I. triassica* possibly correspond to a new taxon because they differ from true *Ivanovia* by the presence of hemispherical conceptacles only known in *Eugonophyllum*.

Furthermore, it is probable that *Bolivianella* is in reality represented by partly broken and/or dissolved thalli of *Ivanovia* and does not correspond to the reconstruction of Mamet (1996, text-figure 3A, 3B).

Occurrence. Late Moscovian–Early Permian, cosmopolitan (Mamet et al., 1987; Mamet, 1991). Middle Permian (late Capitanian) of Tunisia (Vachard et al., 1989a). Triassic *Ivanovia* are questionable (see earlier).

Ivanovia tenuissima Khvorova, 1946
Figure 14.6–8

- 1946 *Ivanovia tenuissima* Khvorova, p. 737–739, figs. 1, 2.
- 1963 *Ivanovia tenuissima*; Johnson, p. 24, pl. 20, figs. 1, 2.
- 1966b *Ivanovia tenuissima*; Rácz, p. 258–259, pl. 7, figs. 35–39.
- .1964 *Ivanovia tenuissima*; Kochansky-Devidé, p. 513 (no illustration).
- 1976 *Ivanovia tenuissima*; Emberger, p. 84 (no illustration) (with four references).
- ?1980 *Ivanovia* cf. *tenuissima*; Flügel, pl. 2, fig. 8.
- .1980 *Ivanovia* cf. *tenuissima*; Flügel and Flügel-Kahler, p. 121, pl. 1, fig. 1.
- 1987 *Ivanovia tenuissima*; Mamet et al., p. 19–20, pl. 7, figs. 1–6, pl. 8, figs. 1–5 (with eight references in synonymy).
- ?1991 *Ivanovia* sp.; Flügel et al., pl. 47, fig. 13.

- ?1991 *Pseudoepimastopora* aff. *ampullacea* Elliott; Flügel et al., pl. 47, fig. 5.
- .1996 *Ivanovia* cf. *tenuissima*; Mamet, pl. 1, fig. 8.
- ?2004 *Ivanovia*; Flügel, pl. 58, fig. 4 (= *I. tebagaensis*).
- 2004 *Ivanovia tenuissima*; Mamet and Villa, tabl. 3 p. 157, p. 166, fig. 12a, j–n (with six additional references to Mamet et al., 1987).
- v2012 *Ivanovia tenuissima*; Vachard et al., p. 235, 237, pl. 1, fig. 1.
- v2013 *Ivanovia tenuissima*; Vachard et al., p. 7 (no illustration).

Description. The morphology and the dimensions are typical. Length of remain = several millimeters; width of remain = 500–1,000 µm; length of siphons (= “thickness of cortex” of the authors) = 50–150 µm; width of siphons = 10–30 µm; interval between siphons = 10–20 µm.

Remarks. *Ivanovia tenuissima* is generally well identified in the literature; nevertheless, it was designated as *Permocalculus tenellus* by Homann (1972, plate 1, figure 3, plate 3, figure 17a–c) and as *Eugonophyllum* by Kabanov et al., 2006 (plate 1, figure 7).

Occurrence. Probably cosmopolitan from the Middle Pennsylvanian to the Late Cisuralian. In the Carnic Alps: Forni Avoltri (Flügel, 1979; Flügel and Flügel-Kahler, 1980); Upper *Pseudoschwagerina* Limestone (= Zweikofel and Zottachkopf formations) (Flügel, 1979); this study: Zweikofel Fm (samples GB49_2; GB76_3); Zottachkopf Fm (samples TNA2_1; TNC5_2); and Trogkofel Fm (sample TK26_2).

Genus EUGONOPHYLLUM Konishi and Wray,
1961

Type Species. *Eugonophyllum johnsonii* Konishi and Wray, 1961; by original designation.

Synonyms. *Anchicodium* (part.); *Succodium* (part.)

Description. Phylloid thallus with a peripheral layer of U-shaped subcortical siphons and neomicrosparitized cortical and medullar zones. Presence of more or less prominent, spherical, apical and lateral conceptacles.

Remarks. Concerning the putative synonymy of *Eugonophyllum* with *Paradella* Maslov, 1956a suggested, for example, by Kochansky-Devidé (1970b), Roux (1985) and Mamet et al. (1987), it is evident that, by its morphology and measurements, a specimen of *Paradella adunca* Maslov, 1956a (plate 84, figure 1; thin section n° 304-5a at the Institute of Geological Sciences of the Russian Academy of Sciences) is similar to *Eugonophyllum johnsonii*. The conceptacles of *Eugonophyllum-*

type are implicitly described (as conceptacles 2) and illustrated by Maslov (1956a) in *P. adunca*. On the other hand, *P. arcuata* Maslov, 1956a, could be another synonym; moreover, it comes from the same thin section n° 304-5a. However, *Paradella* is probably an invalid genus, because no holotype was designated by Maslov (1956a); moreover, it was never re-described in the Devonian.

Occurrence. Possible primitive forms in the Bashkirian (Vachard et al., 1989b, plate 3, figures 1–5, 7, plate 4, figure 1b; erroneously interpreted as recrystallized *Archaeolithophyllum*). Moscovian (Kashirian)–Capitanian, cosmopolitan: USA (New Mexico, Texas, Kansas, Oklahoma, Alabama, Colorado, Idaho), Canadian Arctic, Mexico (Sonora, Chiapas), Croatia, Serbia, Carnic Alps (Austria, Italy), northern Spain, Tunisia, Greece, Russia (Urals, Bashkortostan), Turkey, Tien Shan, Thailand, Vietnam and Japan.

Eugonophyllum magnum (Endo, 1951) emend.
Konishi and Wray, 1961

Figure 11.4, Figure 14.11–12, Figure 15.1–12,

Figure 16.1–3, 16.10–13,

Figure 17.3–4, Figure 20.4, Figure 26.16, Figure 29.9, Figure 30.11

- *1951 *Anchicodium magnum* Endo, p. 125–126, pl. 11, figs. 3–5.
- 1954 *Anchicodium magnum*; Endo, p. 218, pl. 19, fig. 4.
- 1957 *Anchicodium magnum*; Endo, p. 292–293, pl. 41, fig. 4, pl. 42, fig. 2.
- 1957 *Anchicodium magnum*; Endo in Endo and Horiguchi, p. 175–176, pl. 15, fig. 3.
- 1961b *Anchicodium magnum*; Endo, pl. 11, fig. 5.
- 1961d *Anchicodium magnum*; Endo, p. 134–135, pl. 6, figs. 4–6.
- 1961 *Eugonophyllum magnum*; Konishi and Wray, p. 663, pl. 75, fig. 6 (with five references).
- 1963 *Eugonophyllum magnum*; Johnson, p. 127, pl. 18, fig. 7, pl. 74, fig. 3.
- 1964 *Eugonophyllum*?; Kochansky-Devidé, pl. 1, fig. 1.
- 1965 *Neoanchicodium catenoides* Endo; Ramovš and Kochansky-Devidé, p. 28–29 (= 346–347), pl. 8, fig. 4.
- .1966 *Permocalculus* cf. *P. tenellus* (Pia); Flügel, p. 16–17, pl. 1, fig. 3.
- 1966 *Eugonophyllum johnsoni* Konishi and Wray; Flügel, p. 20–21, pl. 3, figs. 3, 4.
- ?1968 *Eugonophyllum johnsoni*; Flügel, p. 55, 56 (no illustration).
- ?1968 *Anchicodium magnum* Endo; Flügel, p. 56 (no illustration).

- 1969 *Eugonophyllum magnum*; Güvenç, p. 448–449, pl. 10, figs. 1–4.
- p1970a *Eugonophyllum magnum*; Kochansky-Devidé, p. 210–211, 238–239, pl. 20, figs. 3, 5, 6 (non fig. 4 = *E. ? konishi*; see later).
- ?1970a *Anchicodium fukuyiense* Endo and Horiguchi; Kochansky-Devidé, p. 211, 239, pl. 21, figs. 1, 2, 3?
- 1972 *Anchicodium magnum*; Homann, p. 175–177, pl. 2, fig. 13.
- 1972 *Eugonophyllum johnsoni*; Homann, p. 177–178, pl. 2, fig. 14.
- 1972 *Succodium duisbergi* Homann, p. 185–186, tabl. 19 p. 187, pl. 3, fig. 17.
- p1972 *Neoanchicodium catenoides*; Homann, p. 183–184, pl. 3, figs. 20, 21 (non fig. 22 = true *Neoanchicodium catenoides*).
- .1972 *Permocalculus* cf. *P. tenellus* (Pia) Elliott; Homann, p. 161–163, pl. 1, fig. 3 (with 11 references in synonymy).
- 1976 *Anchicodium magnum*; Emberger, p. 80 (no illustration) (with five references).
- 1977 *Eugonophyllum johnsoni*; Flügel, tabl. 2 p. 320, pl. 1, fig. 4.
- non 1977 *Anchicodium magnum*; Lemosquet and Poncet, p. 337, pl. 8, figs. 1–6, pl. 9, fig. 1 (= another species of *Anchicodium*).
- ?1978 *Eugonophyllum johnsoni*; Kulik, p. 184–185, pl. 1, figs. 1–3.
- ?1978 *Eugonophyllum johnsoni*; Kochansky-Devidé and Ramovš, p. 237 (no illustration).
- ?1979 *Anchicodium magnum* Endo; Flügel, p. 572 (no illustration).
- ?1979 *Succodium duisbergi*; Flügel, p. 572 (no illustration).
- 1980 *Eugonophyllum johnsoni*; Flügel, pl. 7, figs. 4, 5, pl. 12, fig. 5.
- p1980 *Eugonophyllum*; Flügel, pl. 8, fig. 1 (bottom), pl. 9, figs. 1, 4 (non pl. 10, fig. 1 = *Neoanchicodium catenoides*).
- 1980 *Archaeolithophyllum* sp.; Flügel and Flügel-Kahler, pl. 10, figs. 2, 7, pl. 13, fig. 6.
- 1980 *Eugonophyllum johnsoni*; Flügel, pl. 7, fig. 5, pl. 8, fig. 1, pl. 9, figs. 1, 4, pl. 10, fig. 1, pl. 12, fig. 5.
- 1980 *Eugonophyllum johnsoni*; Flügel and Flügel-Kahler, p. 117–118, 120, pl. 1, figs. 4–6.
- 1982 *Atractyliopsis* sp.; Mu, p. 219, pl. 5, fig. 1.
- 1983 *Succodium duisbergi*; Bassoullet et al., p. 571–572, pl. 15, fig. 8–10.
- 1985 *Eugonophyllum magnum*; Mu, pl. 15, figs. 2–4, 8.
- .1987 Phylloid algae; Flügel, pl. 9, fig. 3.
- 1989 *Neoanchicodium catenoides*; Vachard in Fontaine and Gafoer, pl. 56, figs. 1–3, 5.

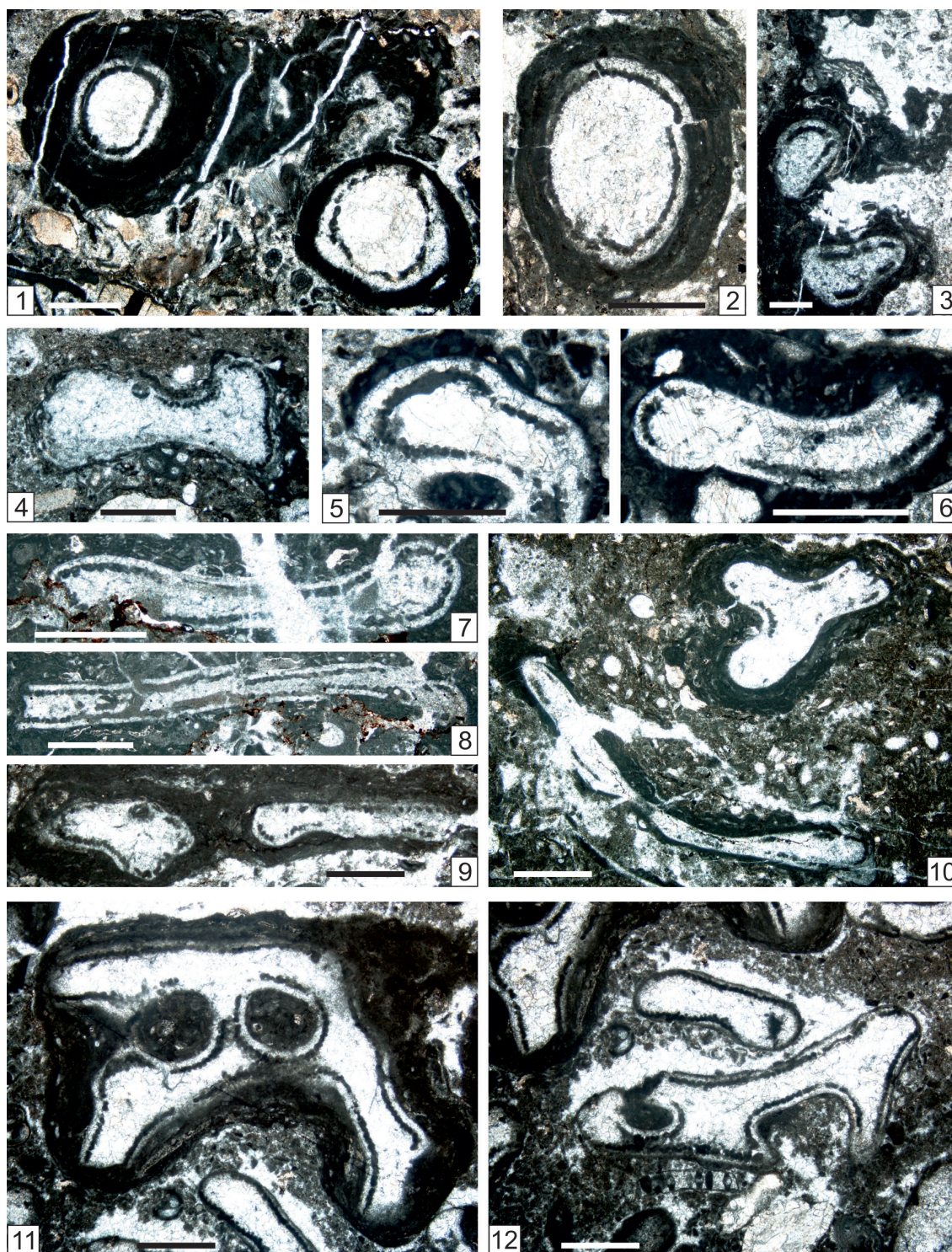


FIGURE 15. 1–12. *Eugonophyllum magnum* (Endo, 1951) emend. Konishi and Wray, 1961. 1. Two transverse sections as nuclei of oncoids. Sample TKS1_1b. 2. Transverse section as nucleus of an oncoid. Sample TKS3_2. 3. Two oblique sections with a *Tetrataxis* sp. Sample Z12B_3. 4. Longitudinal section showing a conceptacle. Sample TKS6_1. 5. Longitudinal section with a loop. Sample TKS13_2. 6. Longitudinal section as nucleus of an oncoid. Sample TKS13_3. 7. Longitudinal section. Sample TKS14_1a. 8. Longitudinal section. Sample TSK14_1b. 9. Two longitudinal sections (one with a conceptacle). Sample Z6B_1. 10. Two longitudinal sections (one with a bifurcation of the thallus). Sample TKW6_1b. 11. Typical longitudinal section (with two loops). Sample Z6B_3a. 12. One typical section (center) with four other ones. Sample Z6B_3b. Scale bars: 0.5 μ m (Figure 15.3); all others = 1 μ m.

- non 1989 *Anchicodium magnum*; Sebbar and Lys, pl. 1, fig. 3 (= another species of *Anchicodium*).
 .1991 *Neoanchicodium*; Riding and Guo, fig. 13.
 .1991 *Eugonophyllum*; Riding and Guo, fig. 14.
 ?1991 *Pseudoepimastopora* aff. *ampullacea* Elliott; Flügel et al., pl. 47, fig. 5 (or *Eugonophyllum*?).
 1995 *Neoanchicodium* sp.; Forke, p. 240, pl. 15, fig. 2.
 .2004 *Eugonophyllum*; Flügel, pl. 58, fig. 3.
 ?2007 *Eugonophyllum* sp.; Schönlaub and Forke, figs. 23.3, 23.4, 149.3, 149.4.

Description. Network of blades loosely anastomosed and fragments partly ramified. Utricles well described by Homann (1972). L = 2,200–5,000 µm; w = 360–1,700–(2,200) µm; thickness of cortical layer = 50–130 µm; utricle diameter = (7)–10–20–(50) µm; diameter of conceptacles = 300 µm; thallus loop diameter = 600–1,150 µm.

Remarks. Our material suggests that a morphological (and perhaps phylogenetic) transition exists between *Eugonophyllum* and *Neoanchicodium*, by a coalescence of the blades forming the thalli, and a deepening within the thallus of the utricular cortical zone (see e.g., the material present in the interval from TKS11 to TKS14 or in Z9_2/Z9_3).

Occurrence. Early–Middle Permian of Japan (Endo, 1961d); Artinskian of Sumatra (Vachard in Fontaine and Gafoer, 1989); Xizang (Mu, 1982); Xinjiang (Mu, 1985); Artinskian of Slovenia (Kochansky-Devidé, 1970a). In the Carnic Alps and Velebit in Croatia: Upper *Pseudoschwagerina* Limestone (Zottachkopf Fm) of Zottach-Kopf (Homann, 1972); Forni Avoltri (Flügel, 1980); lithoclasts of the Tarviser Brekzie (Flügel and Flügel-Kahler, 1980); and in this study: Grenzland Fm (sample GB19_1b); Zweikofel Fm (samples GB132_3; GB136_2; GB154_6; ZK95a_7; ZK99a_A; ZK187_F; ZK188_1_A; ZK200_1; ZK201_A; ZK204_A); Zottachkopf Fm (TKS1_1b; TKS2_5; TKS3_2; TKS4_2; TKS4_3; TKS6_1; TKS11_2; TKS13_2; TKS13_3; TKS14_1a; TKS14_1b; TKW2_1; TKW5_2a; TKW5_2b; TKW6_1a; TKW6_1b; TKW6B_3; TKW10_4; Z2_1; Z6B_1; Z6B_3a; Z6B_3b; Z7_1; Z9_2; Z9B_2; Z12B_3); basal Trogkofel Fm (samples TKS11_2; TKS 14_1a; TKS 14_1b; TKS 16_1; TM7_3); and Trogkofel Fm (samples TK47_1; TK48_2; TK51A_2; TK52_1).

Eugonophyllum? *konishi* Kulik, 1978
 Figure 17.1, 17.2

- *1978 *Eugonophyllum konishi* Kulik, p. 186, pl. 2, figs. 1–3.

- p1970a *Eugonophyllum magnum* (Endo); Kochansky-Devidé, p. 210, 238–239, pl. 20, fig. 3 (only, non figs. 1, 5, 6 = true *Eugonophyllum magnum*).
 1995 *Eugonophyllum* sp.; Forke, pl. 15, fig. 1.
 ? 2011 *Eugonophyllum* sp.; Vachard and Moix, pl. 3 fig. 14.

Description. Phylloid thallus with a unilateral, peripheral layer of acrophore, bifurcated, rarely trifurcated cortical siphons, perpendicular to the outer surfaces, and with a neomicrosparitized, narrow medullar zone. Conceptacles of *Eugonophyllum johnsoni*-type. L = 2,300–4,400 µm; w = 420–700 µm; thickness of cortical layer = 150–200 µm; utricle diameter = 50–60 µm; diameter of conceptacles = 300–500 µm.

Remarks. Either this species corresponds to exceptionally, well-preserved cortical siphons, or it corresponds to a different, unpublished genus.

Occurrence. ?Late Pennsylvanian of Turkey (Vachard and Moix, 2011). Early Permian of the Urals (Kulik, 1978). Artinskian of Slovenia (Kochansky-Devidé, 1970a). In the Carnic Alps (this study): basal Trogkofel Fm (sample TM6A_1); and Trogkofel Fm (sample TK49_2).

Genus NEOANCHICODIUM Endo in Endo and Kanuma, 1954

Type species. *Neoanchicodium catenoides* Endo in Endo and Kanuma, 1954; by original designation.

Description. Thallus composed of several anastomosed blades forming various loops. Cortical and medullar zone sparitized. Medullar zone neosparitized generally inconspicuous. Subcortical zone with large connected utricles forming a peripheric to central, round catena in transverse section. Conceptacles unknown.

Other species. ?*Anchicodium flexosum* Endo, 1961c (see above). *Neoanchicodium paradoxa* Kulik, 1978; *N. pseudoarticulatum* Kulik, 1978; *N. shichanense* Kulik, 1978.

Occurrence. Kasimovian–Sakmarian (Chuvashov et al., 1993). Asselian–Artinskian of Japan (Smegai Formation), New Mexico, Canadian Arctic, Austria (Auernig Fm–Trogkofel Fm), Slovenia, Montenegro, Bashkortostan (Russia) and Turkey (Roux, 1985). Late Sakmarian of Sumatra (Fontaine and Vachard, 1984, re-dated here). Kubergandian of Thailand.

Neoanchicodium catenoides Endo in Endo and Kanuma, 1954

Figure 16.4–9, Figure 18.6, Figure 27.7–8

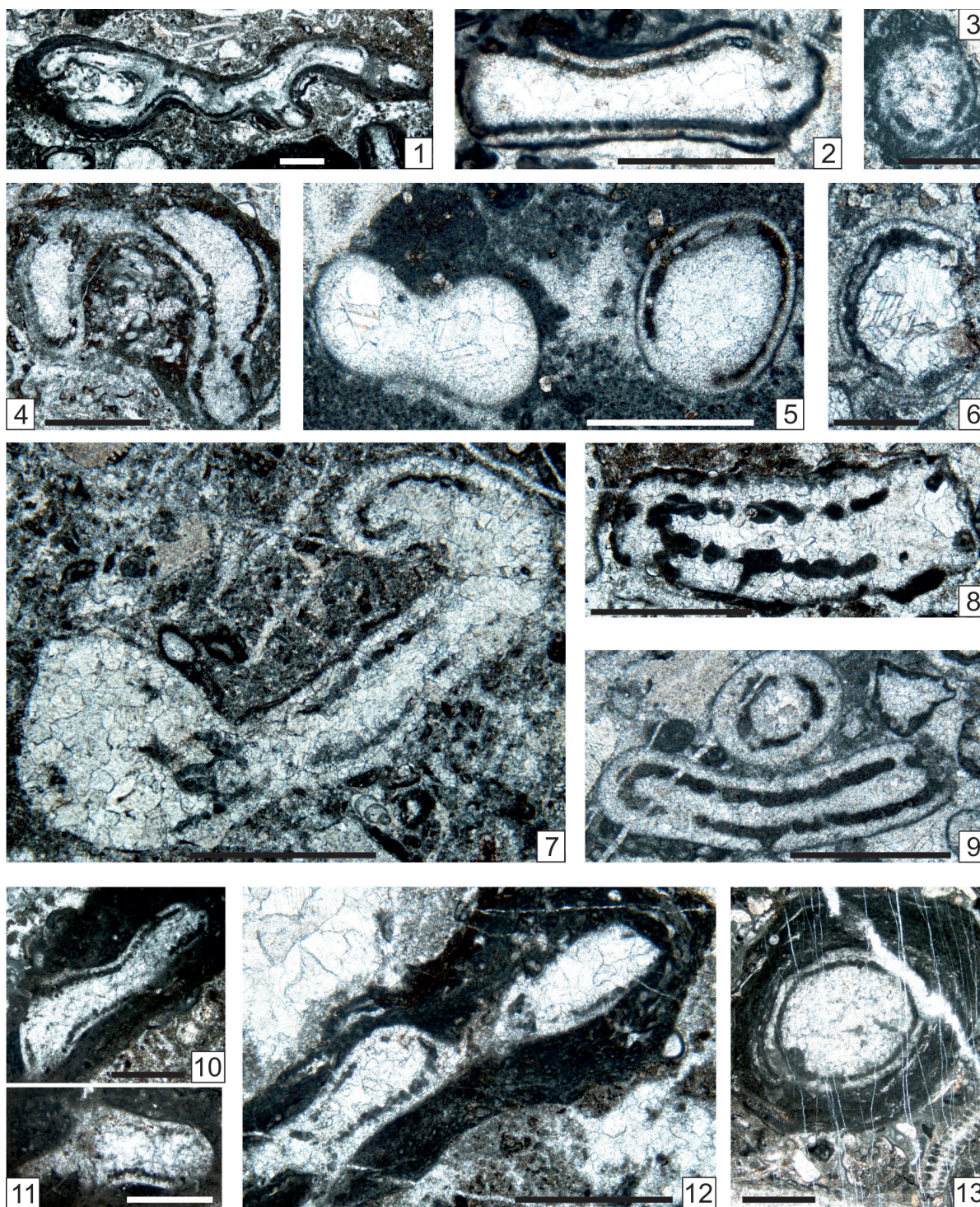


FIGURE 16. 1–3, 10–13. *Eugonophyllum magnum* (Endo, 1951) emend. Konishi and Wray, 1961. 1. Typical, ramified axial section. Sample. Z9B_2a. 2. Longitudinal section. Sample TK51A_2. 3. Transverse section. Sample GBT3_1. 10. Longitudinal section. Sample Z9_2. 11. Longitudinal section. Sample Z9_2. 12. Longitudinal section encrusted with girvanellaceans and a tuberitinid (center, right). Sample TKW10_4. 13. Transverse section with *Globuliferoporella* sp. (bottom, right). Sample TKS4_3. 4–9. *Neoanchicodium catenoides* Endo in Endo and Kanuma, 1954. 4. Longitudinal section. Sample TKW9_2. 5. Neomicrosparitized transverse section (left) and more typical transverse section (right). Sample TK_64_2. 6. Transverse section. Sample GBT4_3. 7. Longitudinal section. Sample TKW9_5. 8. Longitudinal section. Sample TKW9B_2. 9. Transverse section (top, center) and longitudinal section (bottom). Sample TNC2_4. Scale bars: 0.5 μ m (Figures 16.4, 16.6); all others = 1 μ m.

- *1954 *Neoanchicodium catenoides* Endo in Endo and Kanuma, p. 202–203, pl. 15, figs. 7–10.
- 1961b *Neoanchicodium catenoides* Endo, p. 30, pl. 11, fig. 10.
- 1961d *Neoanchicodium catenoides* Endo, p. 108, pl. 18, fig. 4, pl. 19, figs. 1, 2.
- 1962 *Neoanchicodium catenoides*; Kochansky-Devidé and Milanović, p. 219, pl. 8, figs. 3, 4.
- 1963 *Neoanchicodium catenoides*; Johnson, p. 130, pl. 71, fig. 9.
- 1965 *Neoanchicodium catenoides*; Herak, p. 210, 214 (no illustration).
- 1966 *Neoanchicodium catenoides*; Flügel, p. 21–22, pl. 3, figs. 1, 2.
- 1968 *Neoanchicodium catenoides*; Flügel p. 55, 56 (no illustration).
- 1969 *Neoanchicodium catenoides*; Endo, p. 44, pl. 11, figs. 1–5.
- 1970a *Neoanchicodium catenoides*; Kochansky-Devidé, p. 211–212, 239–240, pl. 21, figs. 4–6 (with three references in synonymy).
- p1972 *Neoanchicodium catenoides*; Homann, p. 183–184, pl. 3, fig. 22 (non figs. 20, 21 = *Eugonophyllum magnum*).
- 1978 *Neoanchicodium catenoides*; Kulik, p. 187–188, pl. 2, fig. 6.
- 1979 *Neoanchicodium catenoides*; Flügel, p. 572, pl. 1, fig. 9.
- p1980 *Eugonophyllum*; Flügel, pl. 10, fig. 1 (non pl. 8, fig. 1, nec pl. 9, figs. 1, 4 = *Eugonophyllum magnum*).
- 1980 *Neoanchicodium catenoides*; Flügel and Flügel-Kahler, p. 122–123, pl. 1, fig. 7 (with 11 references in synonymy).
- 1982 *Neoanchicodium catenoides*; Mu, p. 217–218, pl. 3, figs. 5, 8.
- 1985 *Neoanchicodium catenoides*; Roux, pl. 2, fig. 10.
- 1987 *Neoanchicodium catenoides*; Mamet et al., p. 18–19, pl. 6, figs. 9–15, pl. 7, figs. 7, 8.
- non 1989 *Neoanchicodium catenoides*; Vachard in Fontaine and Gafoer, pl. 56, figs. 1–3, 5 (see earlier: *Eugonophyllum magnum*).
- v2003a *Neoanchicodium catenoides*; Krainer et al., table 1 p. 18, p. 19, pl. 6, fig. 31, pl. 7, fig. 12, pl. 8, fig. 19.
- 2004 *Neoanchicodium*; Flügel, pl. 58, fig. 2, pl. 100, figs. 1, 2.
- v2011 *Neoanchicodium catenoides*; Vachard and Moix, p. 157 (no illustration).
- v?.2015 *Neoanchicodium cf. catenoides*; Lucas et al., fig. 40.1.
- v.2017a *Neoanchicodium catenoides*; Krainer et al., p. 20, pl. 43, figs. 10, 11, pl. 44, figs. 5, 7, pl. 47, figs. 2, 4.

Description. Dimensions of thalli = 2,000–5,000 x 1,000–3,200 µm; utricle diameter = 10–20 (30) µm; distance utricles–periphery = 150–400 µm.

Occurrence. Early Permian of Japan (Endo and Kanuma, 1954), Montenegro (Kochansky-Devidé and Milanović, 1962); Dinarides (Herak, 1965: Sakmarian-Kungurian); southwestern Turkey (Vachard and Moix, 2011: Sakmarian/early Artinskian); Tibet (Mu, 1982); Canadian Arctic (Roux, 1985; Mamet et al., 1987), and New Mexico (Lucas et al., 2015; Krainer et al., 2017a). In the Carnic Alps, FO (first occurrence) in the Orenburgian of Kronalpe (Vachard and Krainer, 2001a), and present in the whole Rattendorf Group and Trogkofel Formation (Flügel, 1968, 1979; Vachard and Krainer, 2001b); Seikofel, Forni Avoltri, and Gog-gauer-Kalk (Flügel and Flügel-Kahler, 1980; Flügel, 2004). This study: Zweikofel Fm (samples ZK198_A; ZK199_A; ZK201_10); Zottachkopf Fm (samples TKS1_1a; TKS2_1; TKS4_3; TKS12_1; TKW9_2; TKW9_5; TKW9_4a; TKW9B_2; TNC2_4; Z6_3; Z9_2; Z9B_2a; Z9B_3; Z11_2; Z12_2; Z12B_3; Z14_1); and Trogkofel Fm (samples GBT3_1; GBT4_2; GBT4_3; TK51A_2; TK64_2).

Genus *Calcipatera* Torres, West and Sawin, 1992 emend. herein

Type species. *Calcipatera cottonwoodensis* Torres, West and Sawin, 1992; by original designation.

Synonyms. *Anchicodium* sensu Laporte (1962) (see Torres and Baars, 1992) and *Anchicodium* sensu Mu (1985); *Halimeda* sensu Poncet (1989).

Emended diagnosis. Phylloid thallus with a bilateral, peripheral layer of acrophore, trifurcated cortical siphons (S1, S2, S3), perpendicular to the outer surfaces and with a neomicrospartized, narrow medullar zone. Conceptacles not observed.

Remarks. Late Capitanian *Halimeda soltanensis* Poncet, 1989 of Bir Soltane (Tunisia) does not belong to *Halimeda*, but are probably part of *Calcipatera*, due to the trifurcated utricles of the cortical zone. Similarly, *Anchicodium wensuensis* Mu, 1985 does not belong to *Anchicodium* but to *Calcipatera*.

Occurrence. Late Pennsylvanian of the USA (Torres et al., 1992 with references therein). Early Permian of South China (Mu, 1985). Late Cisuralian of the Carnic Alps (this study). ?Kubergandian of Oman (Vachard et al., 2001a). Late Capitanian of Tunisia (Poncet, 1989; re-interpreted here).

Calcipatera schoenlaubi n. sp.
Figure 17.5–6, 17.8–11, Figure 20.1

?1980 *Epimastopora* cf. *kanumai* Endo; Flügel and Flügel-Kahler, p. 149, pl. 6, fig. 7.

?v 2001a *Kansaphyllum* or “*Halimeda*”; Vachard et al., fig. 14.10.

?v.2015 *Calcipatera* sp.; Lucas et al., fig. 21.18.

Etymology. Dedicated to Hans-Peter Schönlaub, for his work in the Carnic Alps.

Holotype. Institute of Geology, University of Innsbruck, Cat. Nrs. TNA16 (thin section); Figure 17.8; sample TNA16_1_1.

Paratypes. Institute of Geology, University of Innsbruck, Cat. Nrs. TNA 16, TNA 18, TM 7, TK 16 and TK 53 (thin sections); Figures 17.5, 17.6, 17.9–11 and 20.1.

Type locality. Trogkofel Massif.

Type level. Zottachkopf Fm.

Diagnosis. A species of *Calcipatera* characterized by three orders of thin cortical siphons, and short, poorly preserved medullar siphons. No conceptacles are known.

Description. Thallus length = 2,600–7,000 µm; thallus width = (370)–500–830 µm; cortical zone thickness = 250–400 µm; diameter of cortical siphons (S1, S2 and S3, from medulla to periphery): S1 = 50–70 µm; S2 = 30–40 µm; and S3 = 15–25 µm.

Material. 10 specimens.

Repository of the types. Institute of Geology, University of Innsbruck (Austria).

Comparison. The new species differs from *C. wensuensis*, which is similar, by a little larger test and different dimensions of the three orders of cortical siphons: S1, S2 and S3 (in *C. wensuensis*: S1= 60–100 µm; S2 = 40–80 µm; S3 = 20–50 µm). It differs from *C. cottonwoodensis* by thinner and more elongate cortical siphons and shorter medullar siphons, and from *C. soltanensis* by less numerous cortical siphons and poorly preserved medullar siphons.

Occurrence. ?Kubergandian of Oman (Vachard et al., 2001a); ?Permian of New Mexico (Lucas et al., 2015). In the Carnic Alps: perhaps in Forni Avoltri (Flügel and Flügel-Kahler, 1980; and this study: Zweikofel Fm (samples ZK67_A; ZK85_A); Zottachkopf Fm (TNA16_1_1; TNA16_2_2; TNA16_2; TNA16_2_4a; TNA16_2_5; TNA18_2_3); basal Trogkofel Fm (samples TM7_3; TK_16_2); Trogkofel Fm (sample TK53_1).

?Family GYMNOCODIACEAE Elliott, 1955

Remarks. The gymnocodiaceans are relatively well-known algae, based on the work of Pia (1937); Elliott (1955); Kochansky-Devidé and Slišković (1969); Termier et al. (1977); Vachard (1980); Roux (1985); Roux and Deloffre (1990); Bucur (1994);

and Vachard et al. (2015). The saga of the genus *Gymnocodium* (Pia, 1920) Elliott, 1955 is well known (Elliott, 1955; Roux and Deloffre, 1990), and mainly punctuated by the successive interpretations of Pia (1912, 1920, 1927 and 1937). Finally, this alga was assigned by this latter author to the chaetangiacean red algae and compared with the extant genus *Galaxaura* Lamouroux, 1812. For a long time considered as red algae (Pia, 1937; Elliott, 1955; Termier et al., 1977), the Gymnocodiaceae are currently assigned to the green algae (Chuvashov et al., 1987; Bucur, 1994; Vachard et al., 2015).

Composition. After the work of Pia, Elliott (1955) created the extinct family Gymnocodiaceae with *Gymnocodium* to *Permocalculus* Elliott, 1955. More recently, these algae were revised by Güvenç (1966); Kochansky-Devidé and Slišković (1969); Roux and Deloffre (1990), Roux (1991) and Deloffre (1992). In Roux and Deloffre (1990) and Roux (1991), the Gymnocodiaceae encompassed six genera and subgenera: *Gymnocodium*; *Permocalculus* (*Permocalculus*); *Permocalculus* (*Pyruclites*) Mu, 1981; *Abatea* Senowbari-Daryan and Schäfer, 1980; *Nanjinophycus* Mu and Riding, 1983; and *Oligoplagia* (Herak, 1944) Flügel, 1971b. The genera *Dzhulfanella* Kordé, 1965; *Tauridium* Güvenç, 1966, *Aphroditicodium* Elliott, 1970a; and *Asterocalculus* Sokač and Grgasović, 1998 could also belong to the Gymnocodiaceae. *Dzhulfanella* is a morphotype of *Permocalculus*, according to Roux (1991), as such as *Tauridium*. Furthermore, *Thailandoporella* Endo, 1969, and *Siamporidium* Endo, 1969, are probably other taphotaxa corresponding to *Permocalculus* (Vachard et al., 2005). On the other hand, *Succodium* Konishi, 1954b, presents many similarities with *Permocalculus*, but also with *Nanjinophycus* Mu and Riding, 1983. This interpretation of *Succodium* and *Nanjinophycus*, as two stages and not two genera, might explain that they are infrequently mentioned in the literature because its identification depends on their stages of preservation. The main species of *Permocalculus* are: *P. gracilis* (Pia, 1937); *P. plumosus* Elliott, 1955; *P. digitatus* Elliott, 1955; *P. solidus* (Pia, 1937); and *P. tenellus* (Pia, 1937). It is likely that the other species described by Pia, Elliott, Johnson and Kordé are synonymous (Roux, 1991). Despite the Lopin-gian crisis of the carbonates (Weidlich, 2002), *Permocalculus* and *Gymnocodium* still constitute many thick bioaccumulations during the Late Permian. Then, *Gymnocodium* disappears at the PTB (Permian-Triassic Boundary), whereas *Permocal-*

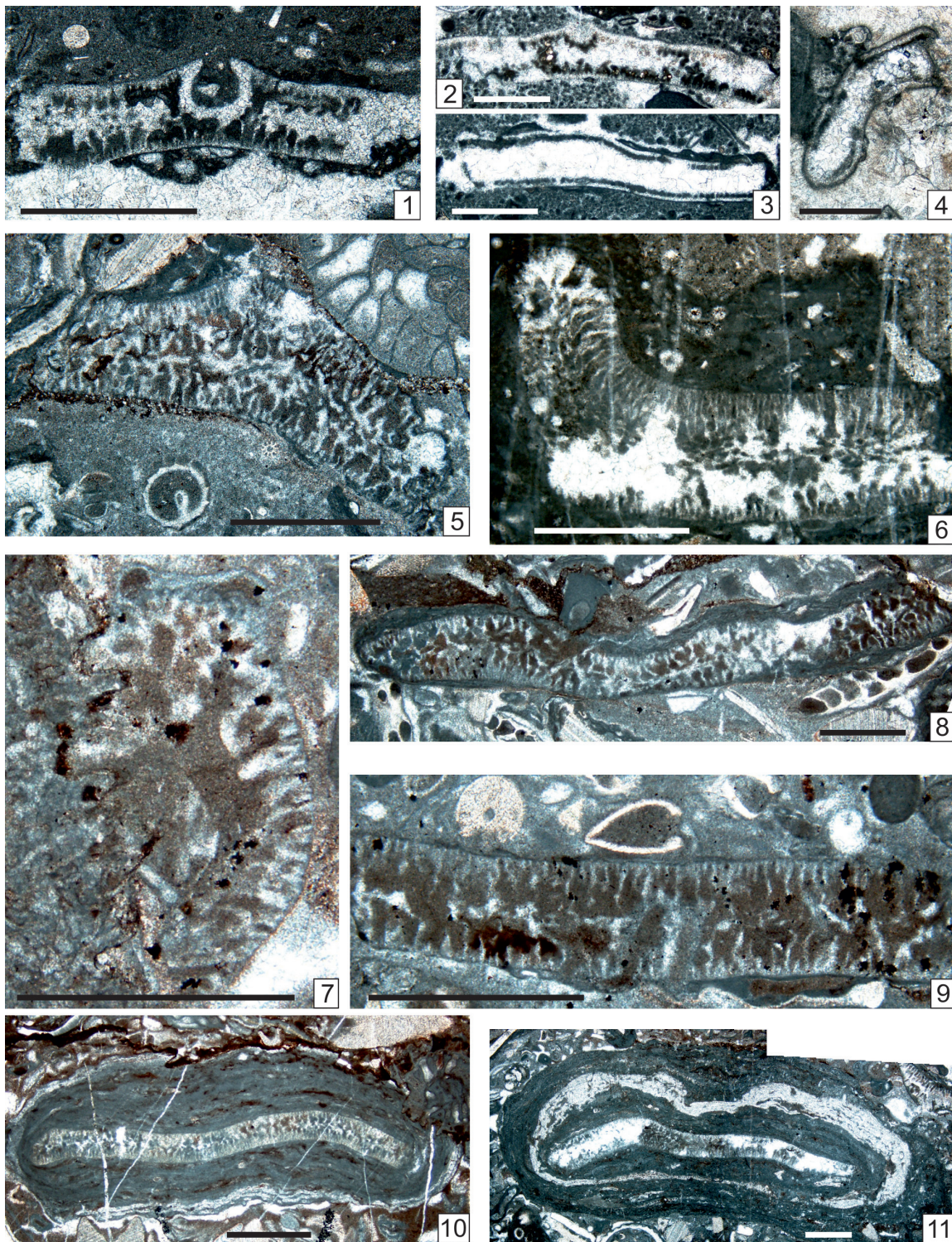


FIGURE 17. 1, 2. *Eugonophyllum? konishi* Kulik, 1978. Two fertile longitudinal sections. 1. Sample TM6A_1. 2. Sample TK49_2. 3, 4. *Eugonophyllum magnum* (Endo, 1951) emend. Konishi and Wray, 1961. Two longitudinal sections. 3. Sample TK47_1. 4. Sample TK52_1. 5, 6, 8–11. *Calcipatera schoenlaubi* n. sp. Six subaxial sections. 8. Holotype. Sample TNA16_1_1. 6. Paratype. Sample ZK85A. 9. Paratype. Sample TK16_2_2. 10. As nucleus of an girvanellacean oncoïd. Paratype. Sample TNA18_2_3. 11. As nucleus of an oncoïd with girvanellacean and claracrustacean. Paratype. Sample TNA16_2_4. 7. *Nanjinophycus?* sp. Broken longitudinal section. Sample TNA16_2_1. Scale bar 1 µm.

culus is still encountered in the Mesozoic (Elliott, 1955; Granier et al., 2017).

Occurrence. ?Late Pennsylvanian. Cisuralian–Triassic. Lazarus effect in the Cretaceous.

Genus NANJINOPHYCUS Mu and Riding, 1983

Synonyms. *Succodium* (part.).

Type species. *Nanjinophycus ovatus* Mu and Riding, 1983; by original designation.

Description. Thalli segmented. The segments are spherical, ovoid or barrel-like. Some specimens with well-preserved calcified medullar zone are known. The distal parts of the cortical filaments are vesiculifer, and connected to the surface with two to four terminal branchlets. Fertile specimens are unknown.

Occurrence. Early Permian of South China; Permian of Viet Nam (Mu and Riding, 1983); ?Capitanian of Cambodia (Nguyen Duc Tien, 1986a, pl. 9, figs. 1, 2). Questionably present in the Artinskian of the Carnic Alps (this study).

Nanjinophycus? sp.

Figure 17.7, Figure 22.4?

- ?1970a *Permocalculus* aff. *kanmerai* (Konishi); Kochansky-Devidé, p. 219, 243–244, pl. 26, figs. 1, 2.
- 1972 *Gymnocodium* cf. *gracile* Kordé; Homann, p. 160–161, pl. 1, fig. 8.
- ?1979 *Gymnocodium* cf. *bellerophontis* Rothpletz; Flügel, p. 572 (no illustration).
- ?1979 *Permocalculus* sp.; Flügel, p. 572 (no illustration).
- ?1989 *Permocalculus tenellus* Pia; Vachard in Fontaine and Gafoer, pl. 8, figs. 4, 5, pl. 9, fig. 2.
- 2004 *Permocalculus*; Flügel, pl. 57, fig. 7.

Description. L = 1,400–2,000 µm; w = approximately 1,000–1,500 µm; diameter of laterals L1 = 20–50 µm; diameter of laterals L2 and L3 = 10–20 µm.

Occurrence. LP, UP, TK; i.e., Zweikofel and Zottachkopf formations (Flügel, 1979). In this study: Zweikofel Fm (sample GB76_3); and Zottachkopf Fm (samples TNA16_1_2; TNA_16_2_1; TNA16_1_2; TNA16_2_1).

Class CHLOROPHYCEAE Kützing, 1843

Order DASYCLADALES Pascher, 1931

Family SELETONELLACEAE Kordé, 1950 nom. transl. Kordé, 1973 emend.

Bassoullet, Bernier, Deloffre, Génot, Jaffrezo and Vachard, 1979

Description. Aspondyl Dasycladales.

Occurrence. This family corresponds to the aspondyl (i.e., random and without verticils)

arrangements of the laterals of dasycladales (Bassoullet et al., 1979; Roux, 1985; Deloffre, 1987, 1988); its representatives are common from the Ordovician to the Triassic (and were mentioned from the Cambrian to the Early Cretaceous; see Deloffre, 1988, table 3).

Tribe ANTHRACOPORELLEAE n. trib.

Diagnosis. Aspondyl Dasycladales rarely bifurcated, with simple or bifurcated laterals, and a thin calcified, perforate cortex covering the extremities of the laterals.

Composition. *Anthracoporella* Pia, 1920; *Zaporella* Rácz, 1966a; *Givetianella* Mamet and Prétat, 1982; *Couvinianella* Mamet and Prétat, 1992 (which probably corresponds to the Devonian *Anthracoporella* of the literature) (Shuysky, 1973; Saltovskaya, 1984b; Shuysky and Patrunov, 1991; Mamet and Prétat, 1992); *Favoporella* Wu, 1991; *?Iskanderkulia* Saltovskaya, 1984b; *?Mellporella* Rácz, 1966a.

Remarks. True Dasycladales appear in Middle Ordovician. The previous, Cambrian forms (including Seletonellaceae sensu stricto) are very disputable, as well as the vermiporellaceans (which were also assigned to the Ulotrichales by Kozłowski and Kazmierczak, 1968; Vachard et al., 1989b; and Pille, 2008). *Anthracoporella*, which for a long time was admitted as a paragon of the Paleozoic Dasycladales (Pia, 1920; Emberger, 1976; Mamet, 1991; De Castro, 1997; Vachard et al., 2001a), even if it was previously compared to *Vermiporella* (Pia, 1920; Endo 1961b), is currently considered as a disputable dasyclad (De Castro, 2002; Granier, 2012). The discovery of endospores, morphologically similar to those of evolved dasycladales (e.g., some *Diplopore* illustrated by Pia, 1920, Elliott, 1972, Flügel, 2004; *Triploporella* described by Barattolo, 1982, 1983 and De Castro, 1982; and *Acicularia?* of De Castro and Sirna, 1996), in our opinion, might allow to confirm the assignment of *Anthracoporella* to the dasycladales.

Occurrence. Middle Devonian–Middle Permian; the genera of this tribe are either cosmopolitan or only present in the Tethyan–Uralian realm.

Genus ANTHRACOPORELLA Pia, 1920

Type species. *Anthracoporella spectabilis* Pia, 1920; by original designation.

Synonyms. *Epimastopora* (part.); *Anchicodium* (part.); *Paraepimastopora* (part.) (see Vachard et al., 2001a).

Description. Thallus large, cylindrical, ramified. Laterals numerous, aspondyl, acrophore, simple, rarely bifurcated. An outermost, thin calcified cuti-

cle covers the pores of the laterals; this cuticle is finely perforated. Fertile endospore specimens have been discovered in this study.

Other species. See Vachard in Vachard and Montenat (1981, p. 34–35); Saltovskaya (1984b, p. 142) and Vachard in Vachard et al. (2001a, p. 384).

Remarks. Many references to *A. spectabilis* are in reality assignable to *A. vicina* or to another unpublished species of *Anthracoporella*, following the references listed herein (see later).

Occurrence. Questionable in the late Bashkirian of Spain (Rácz, 1966a), early Moscovian of Croatia (Kochansky-Devidé, 1970b) and France (Delvolvé et al., 1987), late Moscovian of Spain (Rácz, 1966b), and latest Moscovian of New Mexico (Lucas et al., 2015, figure 21.D, 21.F; for a taxon that most probably belongs to *Paraepimastopora*). The acme period, and probably cosmopolitan distribution, is likely Kasimovian (Vachard and Moix, 2013) to Artinskian (this study), rather than early Moscovian–Sakmarian according to Chuvashov et al. (1993). Rare in the Capitanian of Croatia, Slovenia, Afghanistan, Oman, Malaysia (Vachard et al., 2001) and South China (Lai et al., 2008). In the Carnic Alps: in the Rattendorf Group and Troglkofel Formation (Flügel, 1979); Forni Avoltri (reworked); Hüttenkofel, Gzhelian (Flügel, 2004); Karawanken Mountains (Pia, 1920; Flügel and Flügel-Kahler, 1980).

Anthracoporella spectabilis Pia, 1920 emend. De Castro, 2002
Figure 18.1, Figure 22.1

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| <p>*1920 <i>Anthracoporella spectabilis</i> Pia, p. 15–18, text-fig. 3 p. 16, pl. 1, figs. 7–11.</p> <p>1937 <i>Anthracoporella spectabilis</i> Pia, p. 809–810 (no illustration).</p> <p>1954a <i>Macroporella</i> (?) sp., gen. et sp. nov. indet. (sic); Konishi, p. 6–7, pl. 2, fig. 18 (sic fig. 16 in the text).</p> <p>1960 <i>Anthracoporella spectabilis</i>; Kochansky and Herak, p. 66–69, pl. 1, fig. 6, pl. 2, figs. 1–6 (with six references in synonymy).</p> <p>1962 <i>Anthracoporella spectabilis</i>; Kochansky-Devidé and Milanović, p. 216, pl. 6, fig. 1.</p> <p>p1963 <i>Anthracoporella spectabilis</i>; Johnson, pl. 8, figs. 1–3, pl. 9, fig. 3 (non figs. 1, 2 = <i>A. vicina</i>), pl. 49, figs. 1–6.</p> <p>p1963 <i>Anthracoporella spectabilis</i>; Maslov et al., text-fig. 20a, 20b (non pl. 15, figs. 1, 2 = <i>A. vicina</i>).</p> <p>1964 <i>Anthracoporella spectabilis</i>; Bebout and Coogan, p. 1094, pl. 169, figs. 1–4.</p> <p>1964 <i>Anthracoporella spectabilis</i>; Kochansky-Devidé, p. 515, 516 (no illustration).</p> | <p>?1966a <i>Anthracoporella spectabilis</i>; Rácz, p. 92–93, pl. 5, figs. 4–7 (with six references; another species and/or another genus?).</p> <p>1966 <i>Anthracoporella spectabilis</i>; Chanton, tabl. 1 p. 404 (no illustration).</p> <p>?1968b <i>Epimastopora malaysiana</i> Elliott, p. 491–493, pl. 93, figs. 3, 4.</p> <p>1970a <i>Anthracoporella spectabilis</i>; Kochansky-Devidé, p. 212, pl. 22, fig. 3.</p> <p>1974 <i>Anthracoporella spectabilis</i>; Chuvashov, p. 20–21, pl. 6, figs. 1–6.</p> <p>1976 <i>Anthracoporella spectabilis</i>; Emberger, p. 19, 21 (no illustration) (with 46 references).</p> <p>?1982 <i>Zaporella baxoensis</i> Mu, p. 230–231, pl. 9, figs. 1–5.</p> <p>non 1985 <i>Anthracoporella spectabilis</i>; Mu, pl. 14, figs. 7, 8 (7 = <i>Anthracoporella</i>? sp.; 8 = <i>A. vicina</i>).</p> <p>?1985 <i>Epimastopora tomurica</i> Mu, p. 145, pl. 15, fig. 9.</p> <p>?1987 <i>Anthracoporella spectabilis</i>; Delvolvé et al., p. 544, 545, pl. 1, fig. 5 (perhaps another species).</p> <p>1997 <i>Anthracoporella spectabilis</i>; De Castro, pl. 1, figs. 1, 2, pl. 2, figs. 1–12, pl. 3, figs. 1–5.</p> <p>1997a <i>Anthracoporella</i>; Samankassou, fig. 7.3.</p> <p>1997 <i>Anthracoporella spectabilis</i>; Sokač et al., p. 145 (no illustration).</p> <p>1998 <i>Anthracoporella</i>; Samankassou, figs. 5, 6.</p> <p>1998 <i>Anthracoporella</i>; Forke et al., pl. 1, figs. 5–7, pl. 2, fig. 4, pl. 3, figs. 1, 2.</p> <p>1999 <i>Anthracoporella spectabilis</i>; Fagerstrom and Weidlich, p. 145 (no illustration).</p> <p>2000 <i>Anthracoporella spectabilis</i>; Granier and Grgasović, p. 11–15 (no illustration, with 85 references).</p> <p>?2000 <i>Zaporella baxoensis</i>; Granier and Grgasović, p. 163 (no illustration, with one reference).</p> <p>v.2001a <i>Anthracoporella spectabilis</i>; Vachard and Krainer, p. 149, 150, 151 (no illustration).</p> <p>2002 <i>Anthracoporella spectabilis</i>; De Castro, p. 6, 8, 10, 11, pl. 1, figs. 1, 2, pl. 2, figs. 1–12, pl. 3, figs. 1–5.</p> <p>non 2002 <i>Anthracoporella spectabilis</i>; Mamet, pl. 3, figs. 1, 2 (probably a <i>Paraepimastopora</i>).</p> <p>2003 <i>Anthracoporella</i>; Samankassou, p. 201, 205, 208, 209, 212, 214, 215, text-figs. 8A, 12A, 12B, 13A, 13B, 19.3.</p> <p>v.2003a <i>Anthracoporella spectabilis</i>; Krainer et al., table 1, p. 18, p. 19, pl. 3, fig. 28.</p> <p>v.2003b <i>Anthracoporella</i>; Krainer et al., pl. 57, figs. 3–7, pl. 58, figs. 4–5.</p> <p>2004 <i>Anthracoporella spectabilis</i>; Mamet and Villa, p. 159–160, fig. 7a–7d (reference is made to the 85 references of synonymy lists of</p> |
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- Homann (1972) and Granier and Grgasović (2000); and 12 references are added).
- 2004 *Anthracoporella* sp.; Flügel, pl. 3, figs. 3, 4.
- 2004 *Anthracoporella spectabilis*; Flügel, pl. 59, fig. 6.
- 2005 *Anthracoporella* sp.; Fohrer and Samankassou, p. 317, 318, 321, 325, 327, 328, text-fig. 4a–4c.
- 2005 *Anthracoporella spectabilis*; Fagerstrom and Weidlich, p. 511 (no illustration).
- 2007a *Anthracoporella*; Krainer and Vachard, p. 283–284, figs. 6–8, 11.
- 2007 *Anthracoporella*; Schönlaub and Forke, figs. 11.3, 11.4, 22.2, 23.5, 23.6, 149.5, 149.6, 152.3, 152.4.
- v2007 *Anthracoporella spectabilis*; Krainer, p. 633–638, figs. 9, 10, 16, 17.
- v2011 *Anthracoporella spectabilis*; Vachard and Moix, p. 154 (no illustration).
- v2013 *Anthracoporella spectabilis*; Parvizi et al., p. 154, text-fig. 5, fig. 6a.
- v?p2017a *Anthracoporella* sp.; Krainer et al., pl. 37, fig. 1 (non pl. 43, fig. 5).

Description. Very rare, deformed specimens; perhaps reworked from older deposits. Length = 4,000 µm; wall thickness = 300 µm; diameter of laterals (pores) = 50 µm.

Remarks. In the Carnic Alps, *Anthracoporella spectabilis* is the dominant mound-forming organism in the Auernig Fm (Orenburgian = Newwellian) (Krainer et al., 2003b; Krainer, 2007). In the mounds of the Schulterkofel Fm, a few calcisponges and phylloid algae occur locally at the base and on top of some *Anthracoporella* mounds (Flügel, 1987; Flügel et al., 1997; Krainer, 1995a, 2007; Krainer et al., 2003b; Samankassou, 1999, 2003).

Occurrence. Rare in the Moscovian; probably cosmopolitan during the Kasimovian–Sakmarian; rare in the Artinskian (Slovenia, Kochansky and Herak, 1960; Kochansky-Devidé, 1970a; Xizang/Tibet, Mu, 1982; Thailand, Endo, 1969). Possible Lazarus effect in the Capitanian (Slovenia, Oman, Iran, Perigondwanan Afghanistan, Sumatra, Vietnam, Laos, Cambodia, and Japan). In the Carnic Alps: Gailtal (Pia, 1920); Schulterkofel, Tröpolach, Auernig, Gartnerkofel, Krone, Zirkel (Pia, 1937); uppermost Schulterkofel Fm–Zweikofel Fm (Flügel, 1966; Homann, 1972); UP (Flügel, 1968, 1979); Forni Avoltri (Flügel and Flügel-Kahler, 1980); Auernig Fm of Kronalpe, Garnitzenberg (Krainer, 1991, 1992, 1995a); Schulterkofel (Kahler and Krainer, 1993; Krainer et al., 2003b); Auernig Fm (Vachard and Krainer, 2001b). This study: Zottachkopf Fm (samples TNA2_1_4a and Z3_2).

Anthracoporella vicina Kochansky and Herak, 1960

Figure 18.2, 18.3, Figure 20.2

- 1956b *Anthracoporella spectabilis*; Maslov, p. 9, pl. 12, figs. 1–3 (with six references in synonymy).
- 1960 *Anthracoporella* (sic) *spectabilis*; Bilgütay, p. 53–54, pl. 1, figs. 3, 4.
- *1960 *Anthracoporella vicina* Kochansky and Herak, p. 69–70, pl. 1, figs. 1–5.
- 1963 *Anthracoporella spectabilis*; Maslov et al., pl. 15, figs. 1, 2.
- p1963 *Anthracoporella spectabilis*; Johnson, pl. 9, figs. 1, 2 (non pl. 8, figs. 1–3, nec pl. 49, figs. 1–6 = true *A. spectabilis*).
- ?1965 *Anthracoporella spectabilis*; Herak, p. 214 (no illustration; most probably *Paraepimas-topora*).
- 1965 *Anthracoporella spectabilis*; Ramovš and Kochansky-Devidé, p. 343–344 (= 25–26), pl. 8, fig. 5.
- 1966 *Anthracoporella spectabilis*; Flügel, p. 23–24, pl. 6, fig. 1 (with 19 references in synonymy).
- ?1966b *Anthracoporella spectabilis*; Rácz, pl. 5, fig. 27.
- 1968a *Anthracoporella spectabilis* Pia; Elliott, p. 21, pl. 2, figs. 1, 2.
- 1968 *Anthracoporella spectabilis*; Flügel, p. 46, 49, 55, 56 (no illustration).
- ?1969 *Anthracoporella spectabilis*; Endo, p. 46, pl. 9, figs. 1, 2 (with five references) (very questionable specimens).
- ?1970 *Anthracoporella spectabilis*; Nguyen Lan Tu, p. 21–22, pl. 5, figs. 1–5, pl. 6, figs. 1, 2 (with 16 references) (perhaps another species).
- 1970a *Anthracoporella vicina*; Kochansky-Devidé, p. 212, p. 240, pl. 22, fig. 4.
- ?1970b *Anthracoporella spectabilis*; Kochansky-Devidé, p. 12, pl. 4, fig. 1.
- 1971 A *Anthracoporella spectabilis*; Ramovš, pl. 2, fig. 1.
- 1972 *Anthracoporella spectabilis*; Homann, p. 189–191, pl. 3, fig. 23 (with 38 references in synonymy).
- 1974 *Anthracoporella spectabilis*; Chuvashov, p. 20–21, pl. 6, figs. 1–6.
- 1976 *Anthracoporella vicina*; Emberger, p. 21 (no illustration) (with eight references).
- ?1977 *Anthracoporella spectabilis*; Vachard in Montenat et al., pl. 9, fig. 2.
- 1978 *Anthracoporella spectabilis*; Kulik, p. 191–193, pl. 4, figs. 1–6.
- 1979 *Anthracoporella spectabilis*; Flügel, p. 572 (no illustration).

- 1979 *Anthracoporella vicina*; Flügel, p. 572 (no illustration).
- ?v1980 *Anthracoporella spectabilis*; Vachard, p. 347–348, pl. 5, figs. 2–4, pl. 23, figs. 6–8 (= another species).
- 1980 *Anthracoporella spectabilis*; Flügel and Flügel-Kahler, p. 123–124, pl. 7, fig. 7 (with 14 references in synonymy).
- v1981 *Anthracoporella spectabilis*; Vachard in Vachard and Montenat, p. 35, pl. 3, fig. 1 (with 16 references).
- v1981 *Anthracoporella vicina*; Vachard in Vachard and Montenat, p. 34 (no illustration).
- 1981 *Anthracoporella spectabilis*; Ramovš and Kochansky-Devidé, pl. 1, fig. 5.
- 1982 *Anthracoporella spectabilis*; Mu, p. 219–220, pl. 5, fig. 7.
- 1982 *Anthracoporella spectabilis*; Milanović, pl. 10, fig. 3.
- ?1984 *Anthracoporella spectabilis*; Flügel, Kochansky-Devidé and Ramovš, p. 194, pl. 29, fig. 3.
- 1984b *Anthracoporella spectabilis*; Saltovskaya, pl. 31, figs. 1–3.
- 1985 *Anthracoporella*; Roux, pl. 4, fig. 2.
- p1985 *Anthracoporella spectabilis*; Mu, pl. 14, fig. 8 (non fig. 7 = *Anthracoporella*? sp.).
- 1986a *Anthracoporella spectabilis*; Nguyen Duc Tien, pl. 9, fig. 1B, pl. 10, fig. 2.
- ?1986b *Vermiporella nipponica*; Nguyen Duc Tien, pl. 15, fig. 9 (probably another genus).
- 1986b *Vermiporella nipponica*; Nguyen Duc Tien, pl. 15, fig. 1.
- 1987 *Anthracoporella spectabilis*; Flügel, pl. 7, figs. 1–6, pl. 8, figs. 1–8.
- ?1987 *Anthracoporella spectabilis*; Delvolvé et al., p. 544, 545, pl. 1, fig. 5 (perhaps another species).
- 1988 *Anthracoporella spectabilis*; Sartorio and Venturini, p. 36 (not numbered illustration).
- 1988 *Anthracoporella spectabilis*; Nguyen Duc Tien in Fontaine et al., pl. 2, figs. 14, 15.
- non 1991 *Anthracoporella*; Riding and Guo, fig. 7 (another genus).
- 1991 *Anthracoporella spectabilis*; Krainer, fig. 4.
- 1991 *Anthracoporella*; Krainer, fig. 2.
- 1991 *Anthracoporella spectabilis*; Wu, p. 756–757, pl. 1, fig. 3, pl. 2, fig. 4.
- 1992 *Anthracoporella spectabilis*; Krainer, pl. 6, fig. 4.
- 1992 *Anthracoporella*; Krainer, fig. 31, pl. 36, fig. 3.
- 1993 *Anthracoporella*; Krainer, text-fig. 19.
- 1993 *Anthracoporella spectabilis*; Kahler and Krainer, pl. 67, fig. 3.
- 1995 *Anthracoporella spectabilis*; Pajić and Filipović, pl. 49, figs. 1–4, 6, pl. 51, figs. 1–6.
- 1995 *Anthracoporella spectabilis*; Forke, p. 240, pl. 15/3.
- 1995a *Anthracoporella*; Krainer, pl. 38, figs. 4, 5, pl. 39, fig. 6, pl. 41, fig. 1.
- 1995a *Anthracoporella spectabilis*; Krainer, pl. 40, figs. 5, 6, pl. 41, figs. 5, 6.
- ?2001a *Anthracoporella spectabilis*; Vachard et al., p. 385, 387, fig. 12.1–12.10 (= another species?).

Description. Outer diameter = 1,500–1,825(–3,600) µm; inner diameter = 450–600(–800–2,000) µm; wall thickness = 500–600(–750) µm; lateral diameter = 20–50 µm; lateral diameter (pores) = 15–20 µm; interpores = 7–10 µm; diameter of endospores = 20–30 µm; number of endospores: 25; diameter of pores in endospores = 3–5 µm.

Remarks. *Anthracoporella spectabilis* and *A. vicina* having the same distribution, Upper Pennsylvanian to Lower Permian, and being often associated, they represent possibly two stages or two morphologies of the same species. Traditionally, they are considered as two species.

Occurrence. Late Pennsylvanian–Early Permian of Croatia, Slovenia, the Urals (Russia), Turkey (compiled in this work). This study: Zweikofel Fm (sample GB58_6); Zottachkopf Fm (samples TNA2_1_4a; TNA2_1_5; TNA2_2_1); basal Trogkofel Fm (sample TM_3a); and Trogkofel Fm (samples TK46_2; TK 50_2_1).

Tribe EPIMASTOPOREAE Vachard, Krainer and Lucas, 2012

Description. See the descriptions of the subtribe Epimastoporellinae Cózar and Vachard, 2004, and tribe Epimastoporeae Vachard, Krainer and Lucas, 2012. Large fragments of cylindrical, club-shaped or most commonly subspherical dasycladales. Broad central cavity and relatively thin walls. Lateral simple, numerous, aspondyl but almost euspondyl and having some shapes relatively uncommon among the dasycladales; i.e., prismatic, “clepsydral” (Barattolo et al., 1993), ellipsoidal, sometimes very inflated in the centre, dumbbell-like, etc. (perhaps in relation with an unknown mode of reproduction). They communicate with the exterior by a small pore or apparently have no preserved connections (*Globuliferoporella*). Outer and inner surfaces generally smooth but intusannulations exist in *Paraepimastopora*.

Composition. *Epimastopora* (Pia, 1922) Elliott, 1956 emend. herein (= *Epimastoporella* Roux, 1979 nom. superfl. = “*Embergerella*” Güvenç, 1972

pre-occupied, see Granier and Deloffre, 1994 p. 50); *Epiastopora* n. gen.; *Palaepimastoporella* Cózar and Vachard, 2004; *Paraepimastopora* Roux, 1979 emend. Krainer and Vachard, 2002; *Globuliferoporella* Chuvashov, 1974; ?*Borisovella* Ivanova, 1988; ?*Sphenoporella* Chuvashov in Chuvashov and Anfimov, 1988 (see discussion in Cózar and Vachard, 2004).

Remarks. The group of the Epimastoporeae, homogenous and sufficiently distinct of the Gyroporelleae by the shapes of laterals and thalli, has been only relatively recently considered as constituting a tribe (Vachard et al., 2012). The members of this tribe were before emplaced in the tribe Mastoporeae (Deloffre, 1988, p. 170).

Occurrence. Late Viséan to Late Permian; cosmopolitan in the Late Pennsylvanian–Early Permian, or, otherwise, Paleotethyan.

Genus *PARAEPIMASTOPORA* Roux, 1979
emend. Krainer and Vachard, 2002

Synonyms. *Epimastopora* (part.); *Anthracoporella* (part.), *Anchicodium* (part.).

Type species. *Epimastopora kansasensis* Johnson, 1946; by original designation.

Diagnosis. Thallus probably cylindrical or club-shaped with regular intusannulations, poorly calcified and often broken. Skeleton perforated by numerous, thin, acrophore laterals, closely spaced, and with relatively thickly calcified interpores.

Other species. *Epimastopora jewetti* Johnson, 1946; *E. kanumai* Endo in Endo and Kanuma, 1954; *E. lateinterporosa* Endo, 1961a; *E. longituba* Endo, 1957; *E. regularis* Johnson, 1946; *E. urtazymensis* Chuvashov and Anfimov, 1988; *E. sp. 1* sensu Chuvashov, 1974; *Paraepimastopora noetschensis* Krainer and Vachard, 2002; *P. somervillei* Vachard and Cózar in Vachard, Cózar, Aretz and Izart, 2016.

Remarks. Contrary to Granier and Deloffre (1994), we think that *Paraepimastopora* and *Tauridium* Güvenç, 1966, are not synonymous; *Tauridium*, as well as *Dzhulfanella* or *Pyrulites*, most probably represent different stages of preservation of *Permocalculus* (Vachard et al., 2005).

Occurrence. Rare in the late Viséan–Serpukhovian of the Paleotethys (Vachard et al., 2012, 2016); common in the Middle–Late Pennsylvanian and probably cosmopolitan (Vachard et al., 2012); rare in Early–Middle Permian (Parvizi et al., 2013).

Paraepimastopora kanumai (Endo in Endo and Kanuma, 1954)
Figure 18.4, 18.5?

- *1954 *Epimastopora kanumai* Endo in Endo and Kanuma, p. 195, pl. 13, figs. 8–10.
- 1957 *Epimastopora kanumai*; Endo, p. 285, pl. 37, figs. 9, 10, pl. 38, fig. 1.
- 1957 *Epimastopora kanumai*; Endo and Horiguchi, p. 171–172, pl. 13, fig. 5, pl. 14, figs. 1, 2 (with two references in synonymy).
- 1961a *Epimastopora kanumai*; Endo, p. 184–185, pl. 30, fig. 5 (with three references in synonymy).
- 1961c *Epimastopora kanumai*; Endo, p. 126–127, pl. 1, figs. 1–3, pl. 2, fig. 2 (with five references in synonymy).
- 1963 *Epimastopora kanumai*; Johnson, p. 110–111, pl. 57, figs. 3–9.
- 1966 *Anthracoporella spectabilis* Pia; Flügel, p. 23–24, pl. 6, fig. 1.
- 1968 *Epimastopora kanumai*; Flügel, p. 56 (no illustration).
- 1969 *Epimastopora kanumai*; Endo, p. 80, pl. 41, figs. 2, 3 (with six references in synonymy).
- 1972 *Epimastopora kanumai*; Homann, p. 199–201, pl. 4, fig. 26 (with 14 references in synonymy).
- ?1973 *Orthriosiphon*; Maslov, pl. 11, fig. 6 (another aspect of a not perforated intusannulation).
- 1974 *Anchicodium sindbadi* Elliott; Chuvashov, p. 16, pl. 1, figs. 1–4 (erroneously synonymized with *Anthracoporella spectabilis* by Granier and Grgasović, 2000).
- 1976 *Epimastopora kanumai*; Emberger, p. 40 (no illustration).
- ?1979 *Epimastopora kansaensis* (sic) Johnson; Flügel, p. 572 (no illustration).
- 1979 *Epimastopora kanumai*; Flügel, p. 572 (no illustration).
- ?1980 *Epimastopora seleukensis* Kulik; Flügel and Flügel-Kahler, p. 152–153, pl. 6, fig. 3 (right).
- ?1980 *Epimastopora camasobresensis*; Flügel and Flügel-Kahler, p. 148–149, pl. 6, fig. 5.
- ?1980 *Epimastopora kansasensis*; Flügel and Flügel-Kahler, p. 148–149, pl. 6, fig. 6.
- non1980 *Epimastopora* cf. *kanumai*; Flügel and Flügel-Kahler, p. 149, pl. 6, fig. 7 (probably *Calcipatera*; see later).
- v1981 “*Epimastopora*” *kanumai*; Vachard in Vachard and Montenat, pl. 3, fig. 3.
- ?1981 *Epimastopora* sp. C; Mu, p. 45, pl. 4, fig. 4.
- 1982 *Epimastopora kanumai*; Mu, p. 225, pl. 5, fig. 6.
- ?1985 *Epimastopora kansasensis*; Mu, pl. 14, fig. 1.
- 1987 *Epimastopora kanumai*; Mamet et al., p. 35 (attributed to *Paraepimastopora*) (no illustration).

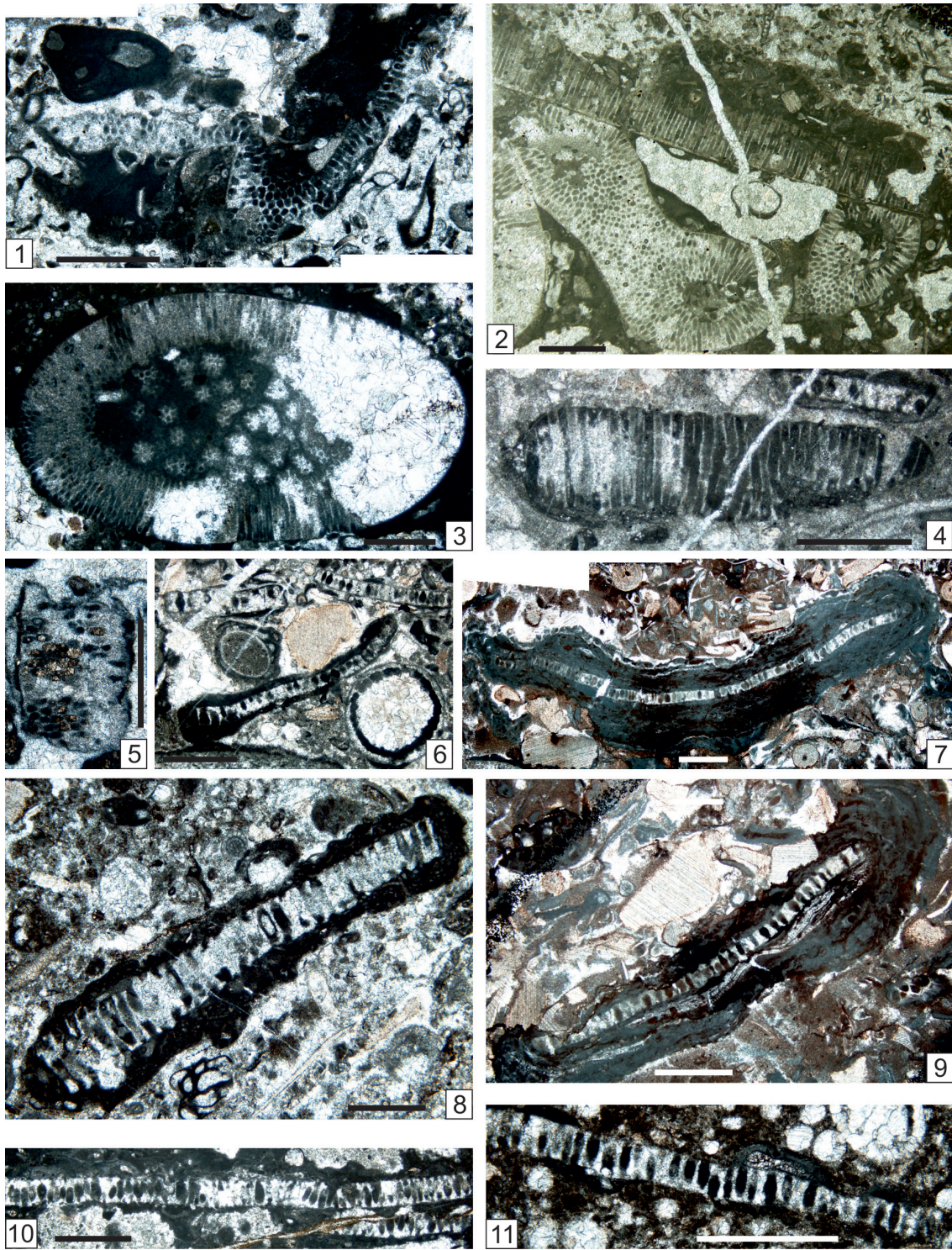


FIGURE 18. 1. *Anthracoporella spectabilis* Pia, 1920. Deformed, longitudinal section. Sample TNA2_1_4a. 2, 3. *Anthracoporella vicina* Kochansky and Herak, 1960. 2. Several sections in different planes. Sample TNA2_1_5. 3. Fertile specimen with endospores. Sample TNA2_2_1. 4, 5? *Paraepimastopora kanumai* (Endo in Endo and Kanuma, 1954). 4. Fragment of thallus in longitudinal section. Sample GB58_6. 5. Fragment of thallus in tangential section. Sample TK46_2. 6, 7, 9. *Epimastopora japonica* Endo, 1951 emend. Mamet, Roux and Nassichuk, 1987. Different longitudinal sections. 6. Sample TKS2_1. 7. Sample TNA18_2_1a. 9. Sample TNA18_2. 8, 10, 11. *Epimastopora likana* Kochansky and Herak, 1960 emend. herein. Two longitudinal sections. 8. Sample TKW9B_3. 10. Sample TNC5_4. 11. Sample ZK199_A. Scale bar = 1 µm.

- v1993b *Epimastopora kanumai*; Vachard et al., pl. 1, fig. 4.
- 1994 *Paraepimastopora kanumai*; Granier and Deloffre, p. 70 (no illustration).
- 2000 *Epimastopora kanumai* [cf. *Paraepimastopora kanumai*]; Granier and Grgasović, p. 56 (no illustration).
- 2000 *Paraepimastopora kanumai* [= *Epimastopora kanumai*]; Granier and Grgasović, p. 118–119 (no illustration) (with 17 references in synonymy).
- v2015 *Paraepimastopora kanumai*; Krainer et al., fig. 17.3, 17.4.

Description. A species with relatively wide laterals, round pores, thick wall and intusannulations rarely preserved (only illustrated by Homann, 1972). The interpore width is half to equal to the lateral diameter. Length of thallus = 3,500–7,000 µm; thickness of the thallus = 600–850 µm; lateral diameters (pores) = 60–90 µm; width of interpores = 50–105 µm.

Remarks. The similar species *P. urtazymensis* is less thick, and with less numerous laterals. Although coeval with *P. urtazymensis* (from Podolskian of the Urals), our material is more similar to *P. kanumai*.

Occurrence. Late Pennsylvanian–Middle Permian of the Urals, Carnic Alps (Austria; Italy), Serbia, Greece, Afghanistan, Xinjiang and Xizang (China), Thailand, Japan and New Mexico (compiled in this study). In the Carnic Alps: Schuterkofel and Zweikofel formations (Flügel, 1968, 1979); Forni Avoltri (Flügel and Flügel-Kahler, 1980). This study: Zweikofel Fm (samples GB58_6; ZK65_1_C) and Trogkofel Fm (samples GBT3_3; TK46_2).

Genus EPIMASTOPORA Pia, 1922 emend. herein

Synonyms. *Epimastoporella* Roux, 1979; *Pseudoepimastopora* (in the sense of Homann, 1972); “*Embergerella*” Güvenç, 1972 pre-occupied.

Type species. *Epimastopora japonica* Endo, 1951 emend. Mamet et al., 1987, subsequently designated herein.

Emended diagnosis. Large fragments of sub-spherical epimastoporeae. Lateral simple, numerous, aspondyl but almost euspondyl, inflated and ellipsoidal in the central part, thin and cylindrical in the distal and proximal extremities.

Other species. *Succodium ambiguum* Kordé, 1965; *Embergerella anatoliana* Güvenç, 1972; *Pseudoepimastopora croatica* Homann, 1972 (sic: *kroatica*; nomen correctum by Kulik, 1978); *Epimastopora hunrazensis* Zanin Buri, 1965 (part.: holotype pl. 8, fig. 6; but the majority of the illustrated specimens belong to *Epiastopora*; see later);

E. iwaizakiensis Endo, 1953a; *E. ketini* Bilgütay, 1960; *E. kosakiensis* Konishi, 1954a; ?*E. minima* sensu Homann, 1972 (non Elliott, 1956 = a gymnocodiacean).

Excluded species. *Epimastopora alpha* Elliott, 1956 (nomen incorrectum); *E. beta* Elliott, 1956 (nomen incorrectum); *E. bashkirica* Kulik, 1978 (= ?*Gyroporella*); *E. cekici* sensu Chuvashov et al., 1987; *E. ? crassithea* Chuvashov and Anfimov, 1988 (= *Pseudoepimastopora* or *Atractyliopsis* auctorum); *E. densipora* Endo, 1969 (= *Paraepimastopora*); *E. digitula* Chuvashov and Anfimov, 1988 (gyroporellacean?); *E. faveolata* Shuysky and Patrunov, 1991 (mastoporellacean?); *E. jewetti* Johnson, 1946 (= *Paraepimastopora*); *E. kansaensis* Johnson, 1946 (= *Paraepimastopora*); *E. kanumai* Endo, 1954 (= *Paraepimastopora*); *E. lateinterporosa* Endo, 1961d (= *Paraepimastopora*); *E. longituba* Endo, 1956; *E. macropora* sensu Perret and Vachard, 1977 (*Borisovella*?); *E. minima* Elliott, 1956 (a gymnocodiacean); *E. oblonga* Shuysky and Patrunov, 1991 (= a Devonian selectionellacean); *E. regularis* Johnson, 1946 (= *Paraepimastopora*); *E. urtazymensis* Chuvashov and Anfimov, 1988 (= *Paraepimastopora*); *E. ? tenuis* Berchenko, 1982 (invalid because not described; moreover, the illustrations correspond to a kirkbyid ostracod); *E. ? sphaenopora* Chuvashov, 1974 (= *Sphaenoporella* Chuvashov and Anfimov, 1988). On the other hand, *Epimastopora malaysiana* Elliott, 1968b, and *E. tomurica* Mu, 1985 are most probably two species of *Anthracooporella*; see earlier).

Remarks. Despite its cosmopolitan distribution and its huge productivity, the genus *Epimastopora* remained taxonomically disputed. Recently, Parvizi et al. (2013, p. 154–155) discussed the nomenclatural proposals of Elliott (1956), Kochansky-Devidé and Herak (1960), Roux (1979), and Granier and Deloffre (1995). Parvizi et al. (2013) suggested that 1) the genus *Epimastoporella* Roux, 1979, cannot be distinguished from *Epimastopora* (Pia, 1922) ex Kochansky and Herak, 1960; 2) *Epimastopora* sensu Roux, 1979 is evidently preoccupied by *Globuliferoporella* Chuvashov, 1974.

Before that, Homann (1972) considered two different groups of epimastoporeans; he called *Epimastopora* the taxa with prismatic/clepsydral laterals, and *Pseudoepimastopora* the taxa with ellipsoidal laterals. Nevertheless, Homann has given a misinterpretation of the so-called *Pseudoepimastopora*, which was not consistent with that of its type species: *Pseudoepimastopora pertunda* Endo, 1960 (see later). On the other hand, the

reconstruction of *Epimastoporella* as a cylindrical alga (Roux, 1979) is another misinterpretation, because the different species of this taxon and especially the type species *Epimastopora japonica* Endo, 1951 selected by Roux (1979) himself, have a spherical thallus. In contrast, Roux's reconstruction is more consistent with the primitive Viséan genus *Palaepimastoporella*.

Although described before the revision of Kochansky and Herak (1960), the "*Epimastopora*" species of Johnson (1946), Kordé (1951) and Endo (1951) cannot be used as type species for this genus, because: 1) they were described very remote from the type areas in the Carnic Alps; 2) they did not correspond to the intentions of Pia (1922), who worked only with European material (see, in this regard, the Recommendations 9A.3 and 10.5 of the International Code of Botanical Nomenclature); 3) two of these species belong nowadays to distinct, valid genera because the taxon of Kordé (1951) "*E.*" *piai*, has been re-assigned to *Globuliferoporella* (see later), and that of Johnson (1946), "*E.*" *kansasensis*, to *Paraepimastopora*. Another nomenclatural problem discussed by Parvizi et al. (2013) was the possible designation, as type species of *Epimastopora*, of either *Epimastopora beta* Elliott, 1956 (precisely created as a synonym of *Gyroporella*? n. f. indet. in the sense of Gortani, 1906, plate 1, figure 2) or *Epimastopora alpina* Kochansky and Herak, 1960 (= *Epimastopora* sp. in the sense of Pia, 1937, plate 97, figure 4). After this study and our new revision of the literature, it is undisputable that: 1) the emendation of Elliott (1956) was inconsistent with the Botanical Code in force at that time (see Granier and Grgasović, 2000 and Parvizi et al., 2013); 2) similarly, *Epimastopora beta* was invalid, and therefore cannot be the type species of *Epimastopora*; 3) in contrast *Epimastopora japonica* Endo 1951, as emendated by Mamet et al., 1987, is present in our material and probably synonymous of *Gyroporella* n.f. indet. sensu Gortani (see later) and can be admitted as type species of *Epimastopora*. On the other hand, morphological differences can be characterized with the group "*Epimastopora*" *alpina* that is designated in this paper as the type species of *Epiastopora* n. gen.

Occurrence. Moscovian–late Middle Permian, cosmopolitan (even if Pia, 1937, p. 829, indicated initially, that *Epimastopora* "was only known in the Troglkofel Limestone of the Carnic Alps and Karawanken").

Epimastopora japonica Endo, 1951 emend.
Mamet, Roux and Nassichuk, 1987

Figure 18.6–9, Figure 19.1–2, 19.6–9, 19.12 (left)

- p1906 ?*Gyroporella* n. f. ind. Gortani, p. 7, pl. 1, fig. 1.
- p1937 *Epimastopora* nov. sp.; Pia, pl. 97, fig. 4 (both large specimens; right).
- *1951 *Epimastopora japonica* Endo, p. 124–125, pl. 11, figs. 1, 2.
- 1953b *Epimastopora japonica*; Endo, p. 99–100, pl. 9, figs. 1–4.
- 1956 *Epimastopora alpha* Elliott, p. 327 (invalid new name proposed for the Gortani's taxon).
- 1960 *Pseudoepimastopora japonica*; Endo, p. 269–270, pl. 44, fig. 1.
- 1961a *Epimastopora japonica*; Endo, p. 203–204, pl. 38, figs. 16–18.
- 1963 *Epimastopora japonica*; Johnson, p. 111 (no illustration).
- 1963 *Pseudoepimastopora japonica*; Johnson, p. 120, pl. 69, fig. 1.
- 1969 *Pseudoepimastopora japonica*; Endo, p. 49, pl. 46, figs. 5–7.
- 1972 *Pseudoepimastopora japonica*; Homann, p. 225–226, pl. 5, fig. 34 (with 10 references in synonymy).
- .1976 *Epimastopora japonica*; Emberger, p. 40 (no illustration).
- .1976 *Pseudoepimastopora japonica*; Emberger, p. 69 (no illustration) (with eight references).
- 1979 *Epimastoporella japonica*; Roux, p. 809 (no illustration).
- 1987 *Epimastoporella japonica*; Mamet et al., p. 34–35, pl. 15, figs. 6–12, pl. 16, figs. 1–3 (with 17 references in synonymy).
- ?1995 *Epimastopora japonica*; Pajić and Filipović, pl. 48, figs. 6, 8.
- 2000 *Epimastopora alpha*; Granier and Grgasović, p. 59 (no illustration).
- 2000 *Epimastoporella japonica*; Granier and Grgasović, p. 62–64 (with 45 references in synonymy and no illustration).
- v2013 *Epimastoporella japonica*; Parvizi et al., p. 155, 157, fig. 6g.
- v2015 *Epimastopora japonica*; Lucas et al., fig. 40.24.

Description. The relatively irregular arrangement of the elongate fusiform laterals is characteristic. Length of remains = 3,300–7,500 µm; width of remains = 200–400 µm; diameter of pores (= laterals) = 80–100 µm; interpore width = 25–40 µm.

Occurrence. Early Permian of Turkey, Austria, Italy, Slovenia, Urals, Sumatra, Tibet, ?New Mexico. ?Guadalupian of Slovenia and Iran. In the Car-

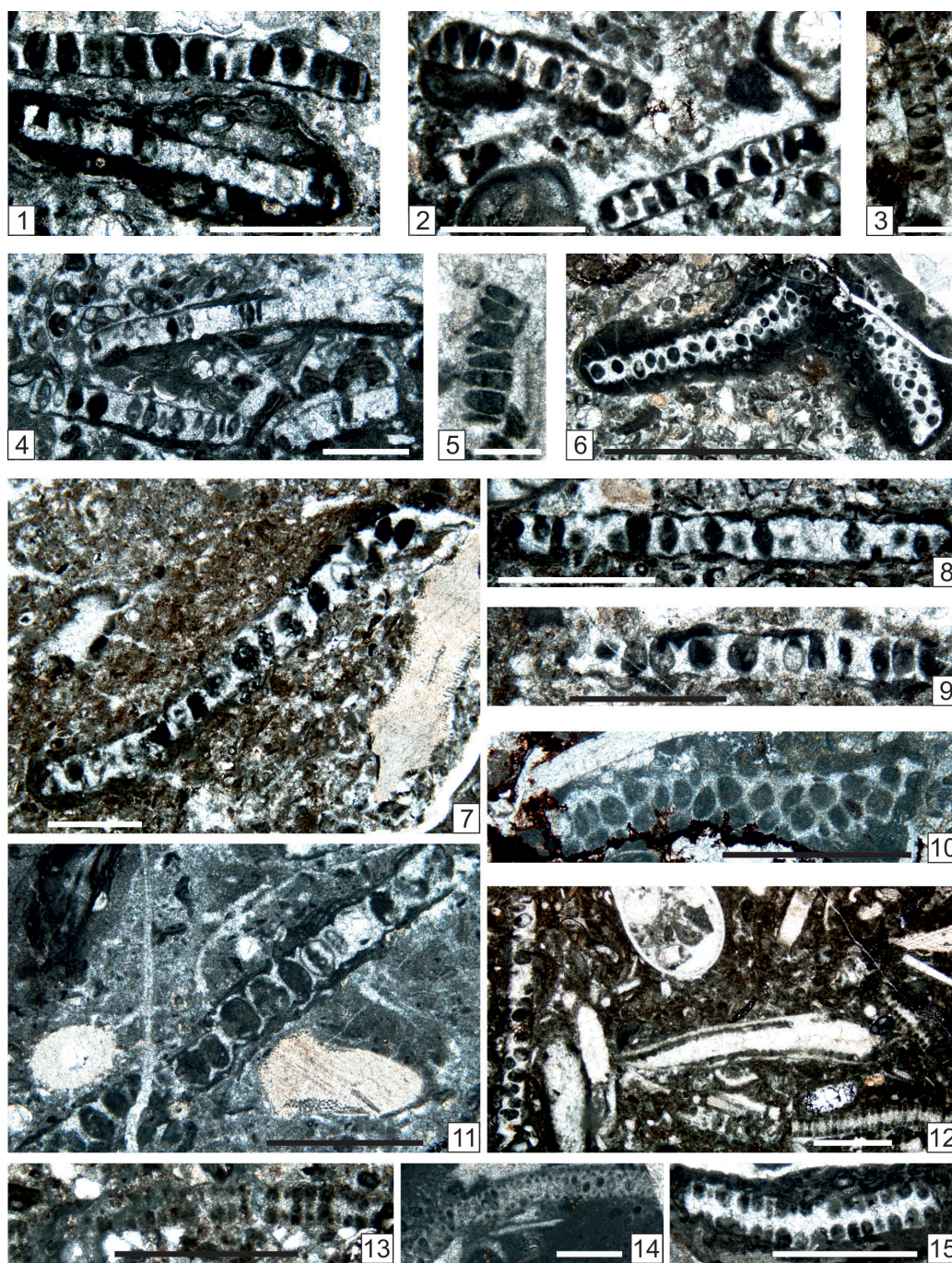


FIGURE 19. 1, 2, 6–9, 12 (left). *Epimastopora japonica* Endo, 1951 emend. Mamet, Roux and Nassichuk, 1987. Several longitudinal and oblique sections. 1. Sample TNC7_1. 2. Sample Z6_3. 3. Sample ZK98_18. 4. Sample ZT1_3. 6. Sample TKW5B_4b. 7. Sample TKW12_2a. 8. Sample TKW5B_3. 9. Sample Z5_1. 12. Sample ZK188_1_A. 3, 4. *Epimastopora likana* Kochansky and Herak, 1960 emend. herein. Several longitudinal sections. 3. Sample ZK98_18. 4. Sample ZT1_3. 5, 10. *Epiastopora alpina* (Kochansky and Herak, 1960) n. gen. n. comb. 5. Longitudinal section. Sample GB60_8. 10. Transverse section. Sample TNA1_2_2. 11. *Epiastopora fluegeli* (Kulik, 1978) n. comb. Longitudinal section. Sample TKW13B_8. 12, 13, 15. *Globuliferoporella piai* (Kordé, 1951). Several longitudinal sections. 12. (right: bottom and center) with *Epimastopora japonica* Endo, 1951 emend. Mamet, Roux and Nassichuk, 1987 (left), *E. likana* Kochansky and Herak, 1960 emend. herein (bottom center) and *Eugonophyllum magnum* (Endo, 1951) emend. Konishi and Wray, 1961 (center). Sample ZK188_1_A. 13. Sample ZK184_1. 15. Sample TKW10_2B. 14. *Epimastopora* cf. *izawaikensis* Endo, 1953a. Sample TK55_1. Scale bars: 0.5 μ m (Figures 19.3, 19.5); all others = 1 μ m.

nic Alps: Schulterkofel Fm to Trogkofel Fm (Flügel, 1968, 1979; Vachard and Krainer, 2001b); Tröpolacher Alm, Seikofel, Forni Avoltri, Trogkofel, Repwand, Goggauer Kalk, Treßdorfer Kalk (Flügel and Flügel-Kahler, 1980); this study: Zweikofel Fm (samples GB60_8; ZK98_18; ZK188_1_A); Zottachkopf (samples TKS2_1; TKW5B_3; TKW5B_4b; TKW12_2a; TKW13B_8; TNA1_2_2; TNA18_2_1a; TNA18_2; TNC7_1; Z5_1; Z6_3; ZT1_3); and basal Trogkofel Fm (sample TM7_1a).

Epimastopora likana Kochansky and Herak, 1960 emend. herein

Figure 18.8, 18.10–11, Figure 19.3–4, 19.12 (bottom, center), Figure 20.3, Figure 22.3, 22.6?, Figure 27.2?, 27.5

- p1906 ?*Gyroporella* n. f. ind. Gortani, p. 7, pl. 1, fig. 2 (non fig. 1 = *E. japonica*).
- 1956 *Epimastopora beta* Elliott, p. 327 (invalid nom. nov. for the previous taxon).
- *1960 *Epimastopora likana* Kochansky and Herak, p. 78–79, pl. 4, figs. 5–10 (valid name for the figure 2 of Gortani).
- 1962 *Epimastopora likana*; Kochansky-Devidé and Milanović, p. 216–217, pl. 6, fig. 3.
- 1963 *Pseudoepimastopora likana*; H. Flügel, p. 87–88, pl. 1, fig. 5.
- 1965 *Epimastopora likana*; Herak, p. 214 (no illustration).
- 1966 *Pseudoepimastopora likana*; E. Flügel, p. 42–43, pl. 7, figs. 3, 4 (with five references in synonymy).
- 1968 *Pseudoepimastopora likana*; E. Flügel, p. 56 (no illustration).
- ?1968 *Epimastopora japonica*; E. Flügel, p. 55, 56 (no illustration).
- 1970a *Epimastopora likana*; Kochansky-Devidé, p. 214, 241, pl. 23, fig. 9.
- 1972 *Pseudoepimastopora likana*; Homann, p. 228–230, pl. 4, fig. 33, pl. 5, fig. 37 (with 13 references in synonymy).
- ?1972 *Embergerella anatoliana* Güvenç, p. 22–24, figs. 1–3.
- 1974 *Pseudoepimastopora likana*; Chuvashov, p. 25–26, pl. 11, figs. 1–8.
- 1976 *Epimastopora likana*; Emberger, p. 41 (no illustration).
- 1976 *Pseudoepimastopora likana*; Emberger, p. 71 (no illustration) (with 15 references).
- non 1978 *Pseudoepimastopora likana*; Kulik, p. 201–203, pl. 6, figs. 3–4 (probably *Epiastopora*).
- 1978 *Pseudoepimastopora likana*; Lys et al., pl. 5, fig. 2a, 2b.
- .1979 *Pseudoepimastopora izawaikensis* (Endo); Flügel, p. 572 (no illustration).
- ?1979 *Pseudoepimastopora japonica*; Flügel, p. 572 (no illustration).
- ?1979 *Pseudoepimastopora kroatica* Homann; Flügel, p. 572 (no illustration).
- 1979 *Pseudoepimastopora likana*; Flügel, p. 572 (no illustration).
- non 1979 *Pseudoepimastopora likana*; Zagorodnyuk, p. 7, pl. 1, fig. 5 (= *Globuliferella piai*).
- p1980 *Epimastopora alpina* Pia; Flügel, pl. 6, figs. 1, 2 (only a true *E. alpina* is visible in the top center of fig. 2).
- 1980 *Epimastopora piaie* Bilgütay; Flügel, pl. 6, figs. 3, 4.
- p.1980 *Epimastopora*; Flügel, pl. 8, fig. 1 (center only; other figures (top) are *E. ex gr. alpina*).
- p1980 *Epimastopora alpina*; Flügel and Flügel-Kahler, p. 142–144, pl. 2, figs. 1, 2, pl. 7, fig. 9 (non pl. 5, figs. 3–5 = *Epiastopora alpina*; non pl. 5, fig. 6, 7 = other genera).
- 1980 *Epimastopora? likana*; Flügel and Flügel-Kahler, p. 149–151, pl. 1, fig. 6, pl. 6, fig. 6, pl. 7, figs. 4–6, 8 (with 5 references in synonymy).
- ?1980 “*Epimastopora*” *likana*; Vachard, pl. 23, figs. 3, 9 (probably another species).
- ?1981 “*Epimastopora*” *likana*; Vachard in Vachard and Montenat, p. 36, pl. 3, figs. 4?, 6.
- ?1982 *Epimastopora iwaizakensis*; Mu, p. 229, pl. 6, figs. 3, 4.
- ?1985 *Epimastopora piaie*; Mu, pl. 3, figs. 3, 4.
- ?1990 *Pseudoepimastopora likana*; Flügel, pl. 2, fig. 1 (an atypical oblique section).
- 1991 *Epimastoporella*; Riding and Guo, fig. 8.
- 1993b *Pseudoepimastopora likana*; Vachard et al., pl. 1, fig. 6.
- 1997 *Pseudoepimastopora likana*; Vachard et al., fig. 12.15.
- 1997 *Epimastopora likana*; Sokač et al., p. 145 (no illustration).
- 2000 *Epimastoporella japonica*; Granier and Grgasović, p. 57, 62–64, 65, figs. 12, 13 (with 45 references in synonymy).
- 2007 *Epimastopora* sp.; Schönlaub and Forke, figs. 23.1, 23.2, 149.1, 149.2.
- v2009 *Epimastopora ex gr. likana*; Krainer et al., p. 13, pl. 4, fig. 16.
- v2011 *Epimastopora likana*; Vachard and Moix, p. 154, 156 (no illustration).
- v2012 *Epimastopora likana*; Kolodka et al., p. 138, 139, fig. 8a–8b.
- v2012 *Epimastopora ex gr. likana*; Vachard et al., p. 235, 239–240, pl. 1, fig. 4.
- v2013a *Epimastopora ex gr. likana*; Vachard et al., p. 7 (no illustration).

- v.2013 *Epimastoporella likana*; Parvizi et al., p. 157, fig. 6b–6d.
- ?v.2015 *Epimastopora* ex gr. *E. japonica*; Krainer et al., fig. 20.5.
- v.2017 *Epimastopora likana*; Lucas et al., p. 15 (no illustration).
- v.2017a *Epimastopora likana*; Krainer et al., p. 20, pl. 24, fig. 7, pl. 35, figs. 10?, 14?
- v.2017a *Epimastopora* cf. *japonica*; Krainer et al., p. 20 (no illustration).

Description. The elongate fusiform shape of the laterals is characteristic. Length of remains = 1,000–3,500 µm; width of remains = 200–300 µm; diameter of pores (= laterals) = 60–100 µm; interpore width = 30–60 µm.

Occurrence. Late Pennsylvanian–Late Permian; cosmopolitan (Italy, Croatia, Slovenia, Austria, Greece, Urals, Turkey, Iran, Afghanistan, Guatemala, New Mexico). Middle Permian specimens of Turkey were probably described as *Embergerella anatoliana* Güvenç, 1972. In the Carnic Alps: Schülterkofel Fm (questionable) and Zweikofel Fm (Flügel, 1968, 1979); Forni Avoltri, Tarviser Brekzie (Flügel and Flügel-Kahler, 1980). This study: Zweikofel Fm (samples GB156_8; ZK97_19; ZK98_18; ZK99_A; ZK188_1_A; ZK188_3; ZK199_A); Zottachkopf Fm (samples TKS2_1; TKS2_2; TKW5B_3; TKW5B_4a; TKW5B_4b; TKW9B_3; TKW12_2a; TNA18_2_2; TNC5_4; TNC7_1; Z5_1; Z6_3; ZT1_3); and basal Trogkofel Fm (sample TM7_1a).

Epimastopora cf. *izawaikensis* Endo, 1953a

Figure 19.14, Figure 20.6

- *1953a *Epimastopora izawaikensis* Endo, p. 120–121, pl. 11, figs. 7–9.
- 1972 *Pseudoepimastopora izawaikensis*; Homann, p. 223–224, pl. 5, fig. 36.
- 1976 *Epimastopora izawaikensis*; Emberger, p. 41 (no illustration).
- 1976 *Pseudoepimastopora izawaikensis*; Emberger, p. 69 (no illustration) (with four references).
- 1979 *Epimastopora izawaikensis*; Mamet et al., pl. 3, figs. 4, 5.
- 1982 *Epimastopora izawaikensis*; Mu, p. 229, pl. 6, figs. 3, 4.
- 1984 *Pseudoepimastopora izawaikensis*; Flügel et al., p. 195, pl. 30, fig. 4.
- ?1987 *Epimastoporella izawaikensis*; Mamet et al., p. 33–34, pl. 16, figs. 4–13.
- 1991 *Pseudoepimastopora izawaikensis*; Flügel et al., pl. 47, fig. 7.
- ?1991 *Epimastopora*; Riding and Guo, fig. 5.

Description. Length of remains = 1,650–5,500 µm; width of remains = 250–310 µm; diameter of pores (= laterals) = 75–100 µm; interpore width = 100–150 µm.

Occurrence. Moscovian–Permian of Japan, Turkey, Canadian Arctic (Mamet et al., 1987), Sicily, China, Croatia (this compilation). In the Carnic Alps (this study): Zweikofel Fm (sample GB136_2); basal Trogkofel Fm (samples TM5_2; TM7_1b); and Trogkofel Fm (sample TK55_1).

Genus EPIASTOPORA n. gen.

Synonyms. *Epimastopora* (part.); ?*Epimastoporella* (part.), ?*Pseudoepimastopora* (part.)

Type species. *Epimastopora alpina* Kochansky and Herak, 1960; by original designation, herein.

Diagnosis. Thallus probably spherical and with a large central cavity. Laterals simple, aspondyl to almost euspondyl, prismatic in shape (Homann, 1972, plate 4, figure 25, plate 5, figure 39; Chuvashov, 1974, plate 11, figures 3–6; Kulik, 1978, plate 5, figure 3; Milanović, 1982, plate 10, figure 2; Krainer, 1991, text-figure 1) or clepsydral (according to Barattolo et al., 1993).

Other species. *Epimastopora bodoniensis* Rácz, 1966a; *E. camasobresensis* Rácz, 1966b; *E. fluegeli* Kulik, 1978; *E. grandis* Chuvashov et Anfimov, 1988; *E. hunrazensis* Zanin Buri, 1965 (part.); *E. rolloensis* Rácz, 1966a; *E. seleukensis* Kulik, 1978; ?*Epimastoporella* sp. sensu Sebbar and Mamet, 1999; ?*Pseudoepimastopora likana* sensu Kulik, 1978; *P. shatchtauensis* Kulik, 1978.

Remarks. Although poorly known in the Early–Middle Pennsylvanian (Rácz, 1966b; Chuvashov and Anfimov, 1988), *Epiastopora* may derive from the late Viséan–Serpukhovian taxon *Palaepimastoporella*, as early as in the early Bashkirian, with a transitional form more or less similar to *Epimastoporella* sp. sensu Sebbar and Mamet, 1999 (plate 1, figures 7, 9).

Occurrence. Rare in the Pennsylvanian (see earlier). Common and probably cosmopolitan in the Cisuralian (this study). Rare in the Middle and Late Permian (Zanin Buri, 1965; Mohtat Aghai and Vachard, 2005).

Epiastopora alpina (Kochansky and Herak, 1960)
n. gen. n. comb.

Figure 19.5, 19.10, Figure 20.5, Figure 21.8,
Figure 22.2, 22.5

- p. 1937 *Epimastopora* nov. sp. Pia, p. 828, pl. 97, fig. 4 (large specimen, left).
- * 1960 *Epimastopora alpina* Kochansky and Herak, p. 78, pl. 4, figs. 1–4.

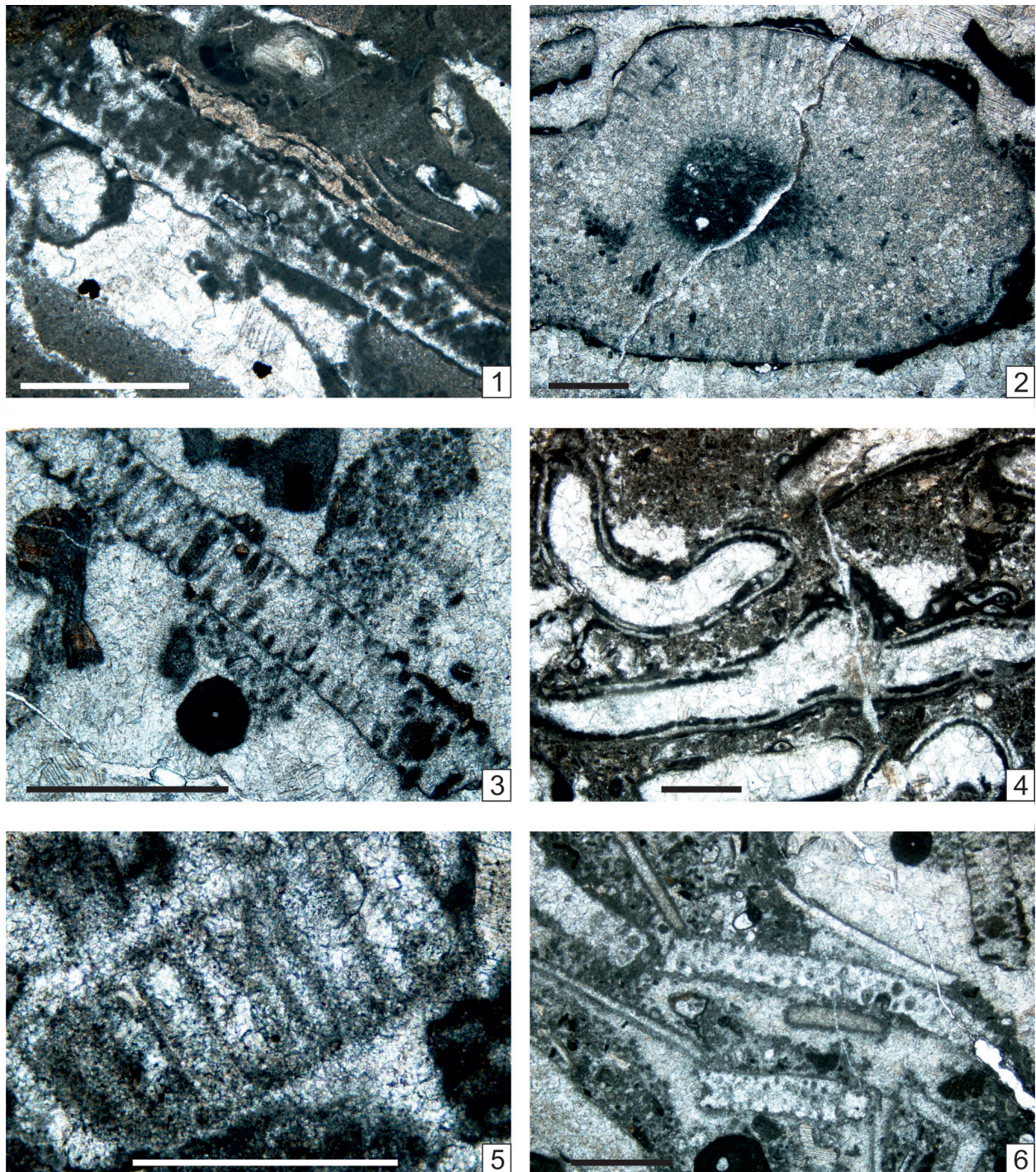


FIGURE 20. 1. *Calcipatera schoenlaubi* n. sp. Paratype encrusted by *Claracrusta catenoides* (Homann, 1972) emend. Vachard in Vachard and Montenat, 1981. Sample TM8_1. 2. *Anthracoporella spectabilis* Pia, 1920. Sample TM7_4. 3. *Epimastopora likana* Kochansky and Herak, 1960 emend. herein. Sample TM7_1a. 4. *Eugonophyllum magnum* (Endo, 1951) emend. Konishi and Wray, 1961. Sample ZK201_A. 5. *Epiastopora alpina* (Kochansky and Herak, 1960) n. gen. n. comb. Fragment of longitudinal section. Sample GB54_7. 6. *Epimastopora* cf. *iwaizensis* Endo, 1953a. Sample TM7_1b. Scale bars: 0.5 μ m (Figure 20.5); all others = 1 μ m.

- 1965 *Epimastopora alpina*; Herak, p. 214 (no illustration).
- non 1965 *Epimastopora alpina*; Kordé, pl. 55, figs. 1, 2 (possible gymnocodiaceans).
- 1966 *Epimastopora alpina*; Flügel, p. 35–37, pl. 6, figs. 4, 5 (with five references in synonymy).
- .1968 *Epimastopora alpina*; Flügel, p. 55, 56 (no illustration).
- 1970a *Epimastopora alpina*; Kochansky-Devidé, p. 214, 241, pl. 23, figs. 7, 8, 11.
- ?1972 *Epimastopora alpina*; Homann, p. 193–197, pl. 4, fig. 25, pl. 5, fig. 39.
- 1976 *Epimastopora alpina*; Emberger, p. 38 (no illustration with 16 references).
- 1978 *Epimastopora alpina*; Kulik, p. 195–197, pl. 5, figs. 1–3 (with seven references).
- .1979 *Epimastopora* (sic) *alpina*; Flügel, p. 572, pl. 1, fig. 6 (= *E. spp.*).
- p1980 *Epimastopora*; Flügel, pl. 8, fig. 1 (top only; other ones, in center, are *E. ex gr. likana*).
- p.1980 *Epimastopora alpina* Pia; Flügel, pl. 6, figs. 3, 4, (non pl. 8, fig. 3 = *Epimastopora* and *Globuliferoporella*; nec pl. 10, fig. 5 = *Epiastopora fluegeli*).
- p1980 *Epimastopora alpina*; Flügel and Flügel-Kahler, p. 142–144, pl. 5, figs. 3–5, pl. 7, fig. 9 (non figs. 1, 2 = *Epimastopora likana*, nec figs. 6, 7 = other genera; pl. 7, fig. 9 = *Epimastopora likana*) (with six references).
- 1980 *Epimastopora bodoniensis* Rácz; Flügel and Flügel-Kahler, p. 146, pl. 6, fig. 1 (with three references in synonymy).
- ?1980 *Epimastopora camasobresensis* Rácz; Flügel and Flügel-Kahler, p. 146, pl. 6, fig. 5 (with one reference in synonymy).
- 1980 “*Epimastopora*” *alpina*; Vachard, pl. 23, fig. 1.
- ?1982 *Epimastopora alpina*; Mu, p. 224, pl. 5, fig. 10.
- 1985 *Epimastopora alpina*; Mu, p. 224, pl. 15, figs. 5, 6.
- ?1991 *Paraepimastopora*; Riding and Guo, fig. 5.
- ?1995 *Epimastopora* sp.; Forke, p. 240, pl. 15, fig. 4.
- ?1996 *Epimastoporella japonica* (Endo); Mamet, pl. 1, figs. 9–12.
- 1997 *Epimastopora alpina* Pia; Sokač et al., p. 145 (no illustration).
- 2000 *Epimastoporella alpina* Kochansky et Herak ex Roux (sic); Granier and Grgasović, p. 59–60 (no illustration, with 27 references in synonymy).
- v.2001a *Epimastopora alpina*; Vachard and Krainer, p. 151 (no illustration).
- v.2001b *Epimastopora alpina*; Vachard and Krainer, p. 172 (no illustration).
- v. 2003a *Epimastopora alpina*; Krainer et al., p. 10, 19, table 1 p. 18, pl. 5, figs. 7, 8, 10, 17, 19.
- ?2004 *Epimastopora* grainstone; Flügel, pl. 60, fig. 4, pl. 105, fig. 2.
- v2009 *Epimastopora alpina*; Krainer et al., p. 13, pl. 4, fig. 14.
- v2012 *Epimastopora alpina*; Kolodka et al., p. 138, fig. 8a.
- v2012 *Epimastopora ex gr. alpina*; Vachard et al., p. 235, 239, pl. 1, fig. 3.
- v2013a *Epimastopora ex gr. alpina*; Vachard et al., p. 7 (no illustration).
- ?v.2015 *Epimastopora ex gr. E. alpina*; Krainer et al., figs. 19.10, 20.10.
- v.2015 *Epimastopora ex gr. E. alpina*; Lucas et al., figs. 12.3?, 21.16, 40.9, 40.25.
- v2017a *Epimastopora alpina*; Krainer et al., p. 20 (no illustration).
- Description.** The rectangular longitudinal section of the laterals is characteristic. Length of remains = 850–8,000 µm; width of remains = 200–410 µm; diameter of pores (= laterals) = 80–250 µm; interpore width = 20–85 µm. These dimensions are rather small for an *E. alpina* (compare with those indicated by Kulik, 1978).
- Occurrence.** Kasimovian–Artinskian, cosmopolitan. Rare in the early Capitanian of Iran (Mohtat-Aghai and Vachard, 2005; Kolodka et al., 2012). In the Carnic Alps: Auernig Fm (Vachard and Krainer, 2001a); Rattendorf Group and Trogkofel Formation; Forni Avoltri (Flügel, 1968, 1979, 1980; Vachard and Krainer, 2001b). This study: Zweikofel Fm (samples GB38_6; GB54_7; GB58_6; GB60_8; GB60_9; ZK99c_11; ZK188_1_A); Zottachkopf Fm (samples TKW13_2b; TKW13B_8; TNA1_2_2; TNC5_3_2; TNC7_2; Z5_1; Z6B_5).
- Epiastopora fluegeli* (Kulik, 1978)
Figure 19.11
- *1978 *Epimastopora fluegeli* Kulik, p. 198, pl. 5, figs. 4–6 (with one reference in synonymy).
- p.1980 *Epimastopora alpina* Pia; Flügel, pl. 10, fig. 5 (non pl. 6, figs. 1, 2 = rare *Epimastopora* and rare *Epimastopora likana*; nec pl. 8, fig. 3 = *Epimastopora* and *Globuliferoporella*).
- 1980 *Epimastopora fluegeli*; Flügel and Flügel-Kahler, p. 146, pl. 6, fig. 2 (with one reference in synonymy).
- 2000 *Epimastopora fluegeli*; Granier and Grgasović, p. 56 (no illustration, with two references in synonymy).
- v2009 *Epimastopora fluegeli*; Krainer et al., pl. 4, fig. 18.
- non v2013 *Gyroporella* aff. *fluegeli*; Parvizi et al., p. 157, fig. 7i.

v2017a *Epimastopora fluegeli*; Krainer et al., p. 20 (no illustration).

Description. *Epimastopora fluegeli* differs from *E. alpina* by more regularly arranged and broader laterals (= pores) and thinner interpores. Length of remains = 2,000–8,000 µm; width of remains = 200–400 µm; diameter of pores (= laterals) = 80–200 µm; interpore width = 10–40 µm.

Occurrence. Early Permian of Russia, Italy, and New Mexico. In this study: Zweikofel Fm (sample GB38_6) and Zottachkopf Fm (samples TKW13B_8 and TNA18_2_1a).

Genus GLOBULIFEROPORELLA Chuvashov, 1974 emend. herein

Synonyms. *Epimastopora* sensu Kordé, 1951 and sensu Roux, 1979 (see discussion earlier); *Gyroporella* (part.).

Emended type species. *Globuliferoporella piai* (Kordé, 1951) nom. nov. (= *Epimastopora piai* Kordé, 1951 = *Globuliferoporella symmetrica* (Johnson) sensu Chuvashov, 1974 non *Gyroporella symmetrica* Johnson, 1946); by subsequent designation herein.

Emended diagnosis. Epimastoporellacean with dumb-bell-shaped laterals, perpendicular to both surfaces of the thallus.

Occurrence. Late Kasimovian–Gzhelian Bashkortostan (Zagorodnyuk, 1979; Chuvashov and Anfimov, 1988). ?Gzhelian of northern Spain (Mamet and Villa, 2004). Cisuralian of Greece, Slovenia, Tibet, South China, Sumatra, Urals, Canadian Arctic, Bolivia (compiled here). Orenburgian–Artinskian of the Carnic Alps (Vachard and Krainer, 2001a, and this work). ?Murgabian of Turkey (Flügel, 1990). Permian of Western Sicily (Flügel et al., 1991).

Globuliferoporella piai (Kordé, 1951) n. comb.
Figure 19.12–13, 19.15, Figure 21.1, 21.7?, 21.8–11

- *1951 *Epimastopora piai* Kordé, p. 177, pl. 1, figs. 1–3.
- 1963 *Epimastopora piai*; Maslov et al., pl. 17, fig. 6.
- 1966 *Globuliferoporella symmetrica* (sic; the correct Latin spelling is *symmetrica*) Johnson; Flügel, p. 39–41, pl. 7, figs. 1, 2.
- 1968 *Globuliferoporella symmetrica* (sic); Flügel, p. 55, 56 (no illustration).
- ?1970a *Epimastopora piai*; Kochansky-Devidé, p. 214, 241, pl. 23, fig. 10 (or *E. piae*)
- ?1972 *Globuliferoporella symmetrica* (sic); Homann, p. 207–210, pl. 6, fig. 43.

- non.1973 *Epimastopora piai*; Kitaev, pl. 4, fig. 6 (an *Epiastopora*).
- 1974 *Globuliferoporella symmetrica* (sic); Chuvashov p. 27, pl. 12, figs. 1–7 (sic 1–8).
- 1978 *Globuliferoporella symmetrica* (sic); Kulik, p. 205, pl. 7, figs. 3–6.
- 1979 *Globuliferoporella symmetrica* (sic); Flügel, p. 572, pl. 1, fig. 6.
- 1979 *Pseudoepimastopora likana* (Kochansky (sic) et Herak); Zagorodnyuk, p. 7, pl. 1, fig. 5.
- 1979 *Epimastopora symmetrica* (sic); Mamet et al., pl. 3, fig. 8.
- non 1979 *Globuliferoporella symmetrica* (sic); Zagorodnyuk, p. 7–8, pl. 1, fig. 7, pl. 2, fig. 1 (= *G. angulata*).
- v non1980 *Gyroporella symmetrica*; Vachard, p. 351, 352, 353 (= a true *Gyroporella*).
- ?1980 *Globuliferoporella symmetrica* (sic); Flügel, pl. 9, fig. 1.
- non 1980 *Epimastopora piae* Bilgütay; Flügel, pl. 6, figs. 3, 4 (an *Epimastopora*).
- p1980 *Globuliferoporella symmetrica* (sic); Flügel and Flügel-Kahler, p. 153–154, pl. 7, figs. 1, 3 (non fig. 2 = *Globuliferoporella angulata*).
- 1985 *Globuliferoporella symmetrica* (sic); Mu, p. 145, pl. 13, figs. 1a, 1b, 2, 7, 8.
- p1987 *Epimastopora symmetrica* (sic); Mamet et al., p. 36–37, pl. 7, figs. 8–11, pl. 18, fig. 1, 5–16 (non figs. 2–4 = tangential section of *Epiastopora*).
- 1988 *Epimastopora symmetrica* (sic); Chuvashov and Anfimov, p. 64, pl. 26, figs. 5, 6.
- 1990 *Globuliferoporella symmetrica* (sic); Flügel, pl. 2, fig. 2.
- ?1991 *Epimastopora*; Riding and Guo, fig. 5.
- 1993 *Globuliferoporella symmetrica* (sic); Chuvashov et al., pl. 14, figs. 8–9.
- ?1996 *Epimastopora* sp.; Mamet, p. 121, pl. 1, fig. 12.
- 2000 *Epimastopora piai* Kordé; Granier and Grgasović, p. 57 (no illustration, with four references in synonymy).
- 2000 *Epimastopora symmetrica* (sic) (Johnson); Granier and Grgasović, p. 58–59, 67 (no illustration, with 24 references in synonymy).
- v 2001b *Globuliferella piai* Kordé; Vachard and Krainer, pl. 3, fig. 8.
- ?2004 *Epimastopora symmetrica* (sic); Mamet and Villa, p. 62, fig. 8p (with two additional references in synonymy to those of Granier and Grgasović, 2000).

Description. Thallus length = 800–1,700 µm; thallus width = 150–200 µm; maximal diameters of laterals = 30–60–(75) µm; central diameter of laterals = 10–20–(30) µm; interpores = 10–25 µm.

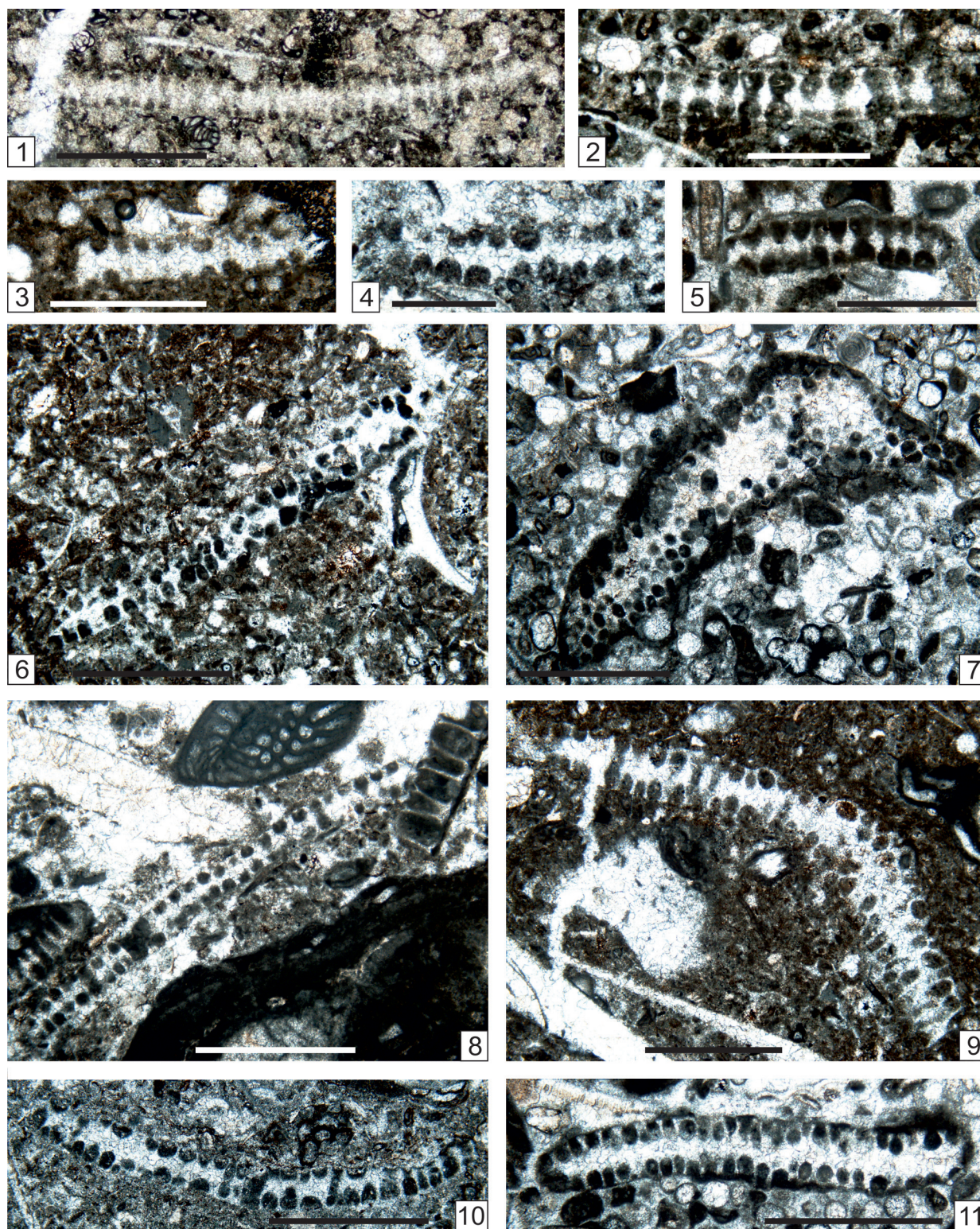


FIGURE 21. 1, 7?, 8–11. *Globuliferoporella piai* (Kordé, 1951). 1. Longitudinal section. Sample GB67_7a. 7? Tangential section. Sample Z10B_2. 8. Longitudinal section with *Epiastopora alpina* (Kochansky and Herak, 1960) n. gen. n. comb. (top right). Sample Z6B_5. 9. Oblique section. Sample TKW12B_2. 10. Longitudinal section. Sample TKW9_1. 11. Longitudinal section. Sample Z10_1. 2–5, 6? *Globuliferoporella angulata* Chuvashov, 1974. Three oblique longitudinal sections. 2. Sample GB153_A. 3. Sample ZK96_3. 4. Sample TKW9B_1. 5. Sample ZK187_2. 6. Sample TKW12_2b. Scale bars: 0.5 μ m.

Remarks. In reality, *Gyroporella symmetrica* is a true *Gyroporella* and is Capitanian in age (see Parvizi et al., 2013, figure 6f). *Globuliferoporella* is a well-defined genus, even if it was confused with *Epimastopora* by Roux (1979), Granier and Grgasović (2000) and Mamet and Villa (2004). Consequently, a type species must be defined for *Globuliferoporella*. The oldest described species presenting the characters of *Globuliferoporella* is *Epimastopora piai*, subsequently designed as type species here.

Occurrence. ?Gzhelian of northern Spain (Mamet and Villa, 2004). Cisuralian of Urals, Canadian Arctic, South China, Carnic Alps, Slovenia, Bolivia (compiled here). ?Murgabian of Turkey (Flügel, 1990). Schulterkofel and Zweikofel formations (Flügel, 1968, 1979); Trogkofelkalk of Karawanken Mountains and Forni Avoltri (Flügel, 1966); Garnitzenbach, Grenzland Fm (Vachard and Krainer, 2001b; sample GB5). This study: Zweikofel Fm (samples GB67_7a, GB136_2?; GB153_A; ZK96_3; ZK97_19; ZK184_1; ZK187_2; ZK188_1_A; ZK191a_12; ZK201_A); Zottachkopf Fm (samples TKS2_1_4; TKS4_3; TKW9_1; TKW9B_1; TKW10_2B; TKW10_2c; TKW12_2b; TKW12B_2; Z6B_5; Z10_1; Z10B_1; Z10B_2?; ZT1_4); and Trogkofel Fm (sample TK55_1).

Globuliferoporella angulata Chuvashov, 1974
Figure 21.2–5, 21.6?

- *1974 *Globuliferoporella angulata* Chuvashov, p. 27–28, pl. 12, figs. 8, 9, pl. 13, figs. 1–8 (sic: 7; in the text).
- .1979 *Globuliferoporella symetrica* (sic) (Johnson); Zagorodnyuk, p. 7–8, pl. 1, fig. 7, pl. 2, fig. 1.
- 1979 *Epimastopora* (= *Globuliferoporella*); Mamet et al., pl. 3, fig. 7 (part.: right; non fig. 6 left; nec fig. 7 = *Epiastopora*).
- p.1980 *Globuliferoporella angulata*; Flügel and Flügel-Kahler, p. 153–154, pl. 7, fig. 2 (non figs. 1, 3 = *Globuliferoporella piai*).
- ?.1982 *Globuliferoporella angulata*; Mu, p. 226, pl. 9, fig. 10.
- 1989 *Globuliferoporella angulata*; Vachard in Fontaine and Gafoer, pl. 6, figs. 10, 11, pl. 9, fig. 2.
- 1989 *Globuliferoporella angulata*; Nguyen Duc Tien, pl. 18, figs. 5, 6–8.
- v1993b *Globuliferoporella angulata*; Vachard et al., pl. 1, fig. 3.
- v?1993b *Pseudoepimastopora shachtauensis* Kulik; Vachard et al., pl. 1, fig. 5.
- ?1996 *Epimastopora symetrica* (sic); Mamet, p. 121, pl. 1, figs. 13, 14.

- 2000 *Epimastopora angulata* (Chuvashov) Roux; Granier and Grgasović, p. 55, 67 (no illustration, with five references in synonymy).

Description. Length = 800–1600 µm; width = 150–330 µm; pores = 40–150 µm; interpores = 20–30–(50) µm.

Occurrence. Late Pennsylvanian of Bashkortostan; Cisuralian of the Urals, Carnic Alps, Greece, Tibet, Sumatra and Bolivia. In the Carnic Alps: Forni Avoltri and Trogkofel (Flügel and Flügel-Kahler, 1980) and this study: Zweikofel and Zottachkopf formations (samples GB67_7a, GB153_A; TKW9B_1; TKW12_2b; ZK96_3; and ZK187_2).

Globuliferoporella? sp.
Figure 24.13

- 1991 *Epimastopora* sp.; Riding and Guo, pl. 1, fig. 5.

Description. A unique specimen could correspond to an apex or a base of *Globuliferoporella* due to its circular transverse section of thallus and the form of its laterals, but an assignment to another, probably unpublished genus, is possible. Thallus width = 1,050 µm; cortical zone thickness = 300 µm; maximal diameter of laterals: 70 µm.

Occurrence. Basal Trogkofel Formation (sample Z19_3).

Tribe MACROPORELLAE Pia, 1920 emend.
Bassoullet, Bernier, Deloffre,
Génot, Jaffrezo and Vachard, 1979
Genus MACROPORELLA Pia, 1912

Type species. *Macroporella dinarica* Pia, 1912; by original designation.

Description. Thallus aspondyl, cylindrical not ramified. Laterals simple, acrophore.

Remarks. Nice specimens have been illustrated from Trogkofel limestone by Riding and Guo (1991); our material is less well preserved and cannot be specifically determined.

Occurrence. Late Moscovian (with the group *Macroporella ginkeli* Rácz, 1966a) of Spain and the Urals (Russia); Early Permian of Montenegro (Kochansky-Devidé and Milanović, 1962); Middle Permian (with the *M. apachena* Johnson, 1951, *M. maxima* Endo, 1952, and *M. siamensis* Endo, 1969-groups); USA (Johnson, 1951); Japan (Endo, 1952); Thailand (Endo, 1969); South China, at the base of the Maokouan regional stage (Lai et al., 2008); Armenia (Kordé, 1965); Carnic Alps (Flügel and Flügel-Kahler, 1980; Riding and Guo, 1991; this study); Tunisia (H. Termier et al., 1977); Philippines (Kiessling and Flügel, 2000); Turkey (Angiolini et al., 2007); Thailand (Endo, 1969; Vachard et

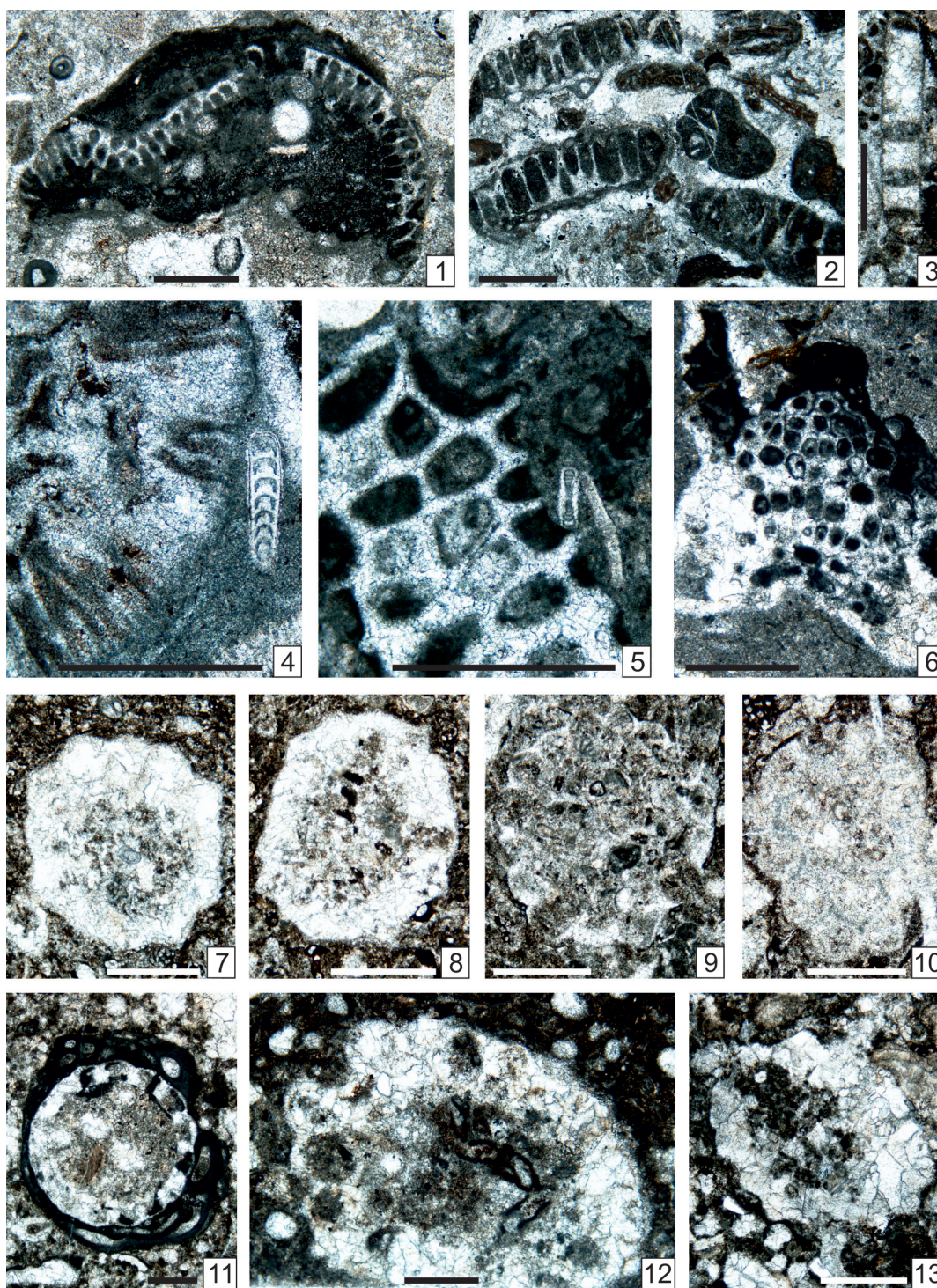


FIGURE 22. 1. *Anthracoporella spectabilis* Pia, 1920 emend. De Castro, 2002. Deformed longitudinal section. Sample Z3_2. 2, 5. *Epiastopora alpina* (Kochansky and Herak, 1960). 2. Several sections. Sample GB38_6. 5. Transverse section with *Pseudovidalina* sp. Sample TKW13_2b. 3, 6? *Epimastopora likana* Kochansky and Herak, 1960 emend. herein. 3. Broken longitudinal section. Sample ZK97_19. 6? Tangential section. Sample TNC5_3. 4. *Nanjinophycus*? sp. Transverse section with numerous, bifurcated, acrophore to phloiophore laterals. Sample TNA16_1_2. 7, 8. *Mizzia cornuta* Kochansky and Herak, 1960. Two recrystallized transverse sections. 7. Sample GB130_1. 8. Sample GB130_3. 9–11. *Mizzia velebitana* Schubert, 1908. Three transverse sections. 9. Sample GB129_3. 10. Sample GB67_10. 11. Encrusted by *Palaeonubecularia* sp. Sample ZK207_7. 12?, 13? *Mizzia yabei* (Karpinsky, 1909) emend. Pia, 1920. Two oblique sections. 12. Sample ZK96_11. 13. Sample GB163_5. Scale bars: 0.5 μ m.

al., 1992). Late Permian of Greece (Vachard et al., 1993a, 2003). Middle–Late Triassic with typical *Macroporella* ex gr. *alpina* (e.g., Bucur and Enos, 2001).

Macroporella cf. *siamensis* Endo, 1969

Figure 23.1–2

To compare with:

- *1969 *Macroporella siamensis* Endo, p. 53, pl. 12, figs. 6–11.
- 1976 *Macroporella siamensis*; Emberger, p. 56 (no illustration).
- 1980 *Macroporella*; Flügel, pl. 14, fig. 3 (poorly visible).
- ?1980 *Macroporella* aff. *tenuimarginata* Endo; Flügel and Flügel-Kahler, p. 136, pl. 4, figs. 1, 6.
- ?1981 *Macroporella* sp.; Mu, p. 45, pl. 4, fig. 1.
- ?1991 *Macroporella* sp.; Riding and Guo, fig. 4 (or another species).

Description. Our rare specimens have the same proportions as *M. siamensis* but are smaller. Length = 4,000 µm; outer diameter = 1,740–3,470 µm; inner diameter = 960–1,900 µm; pores = 50–70 µm interpores = 100–160 µm.

Occurrence. Kungurian/Roadian of Thailand (Endo, 1969). In the Carnic Alps, in the Trogkofel limestone. Flügel (1980), Flügel and Flügel-Kahler (1980) and Riding and Guo (1991) have published some illustrations of other species of *Macroporella*; our rare specimens were found in the Trogkofel Fm (samples GBT3_3 and GBT3_4).

Tribe GYROPORELLEAE Pal, 1976 nom. transl.
Bassoullet, Bernier, Deloffre, Génot, Jaffrezo, and Vachard, 1979, emend. herein

Emended diagnosis. Thallus cylindrical to club-shaped. Aspondyl, almost euspondyl. Laterals numerous, closely arranged, vesiculifer with a form varying from drumstick (i.e., with two parts: one cylindrical and the distal spherical) to Scottischardon-shaped (i.e., with three parts: the innermost short cylindrical, acrophore; the central second one spherical and inflated; the outermost conical truncated). The pores are circular. The central stem is relatively frequently individually calcified.

Occurrence. Middle Pennsylvanian–Jurassic, probably cosmopolitan.

Genus GYROPORELLA Gumbel, 1872, emend.
Kochansky-Devidé, 1970b

Type species. *Gyroporella vesiculifera* Gumbel, 1872.

Synonyms. *Permoperplexella* Elliott, 1968a; *Pseudogyroporella* Endo, 1961a; *Thailando-*

porella Endo, 1969; *Mizzia?* sp. sensu Wilson, 1975; *Atractyliopsis* sensu Riding and Guo, 1991; *Physoporella* part. (sensu Endo, 1961a); *Epimastopora* (part.); *Globuliferoporella* (part.).

Description. Thallus aspondyl, cylindrical not ramified. Laterals simple, cladophore.

Remarks. The variability of the species in the Permian contributed to the creation of diverse “genera” as *Permoperplexella* or *Pseudogyroporella*. Kashirian species are yet relatively diversified, and the origin is probably located in the Bashkirian. The reconstructions of Pia (1920), Roux (1985, text-figure 17) and Mamet (1991, figure Xq) showing an euspondyl thallus are misinterpreted.

Although attributed to different families, *Gyroporella* and *Mizzia* belong probably to the same lineage (Ghazzay-Souli et al., 2015). Transitional forms are *Gyroporella dissecta* Chuvashov, 1974 and *Mizzia longiporosa* Endo, 1961d sensu Mu, 1982.

Occurrence. Kashirian of Croatia. Late Desmoinesian of New Mexico. Late Moscovian of southern Urals and northern Spain. Late Pennsylvanian–Permian of the Urals, northern Spain, Croatia, Montenegro, Greece, Carnic Alps, Turkey, Iraqi Kurdistan, Iran, Kazakhstan, Afghanistan, Thailand, Malaysia, South China, Vietnam, Cambodia, Sumatra, Japan, Russia (Urals), USA (Texas, New Mexico, Washington); Guatemala, and Canada (British Columbia, Canadian Arctic) (compiled in this study). Triassic of the Carnic Alps. Questionable in the late Moscovian of Thailand (Fontaine et al., 1997). LAD in the earliest Jurassic (Deloffre, 1988).

Gyroporella sp.

Figure 25.9?, Figure 27.1

Description. Even if many species of *Gyroporella* have been mentioned in the Carnic Alps (Austria/Italy) and adjacent areas of Slovenia and Croatia (see the next paragraph), our material contains very rare representatives of this genus, which are, at a consequence, remained in open nomenclature. Only two sections could belong to this genus (Figure 25.9 (bottom right); which is possibly also a *Mizzia yabei*; see later) and a transverse section (Figure 27.1), the measurements of which are: D = 1,500 µm; d = 750 µm; initial diameter of laterals = 100 µm; distal part of laterals: 200 µm; interpores = 100 µm.

Remarks. The species of *Gyroporella*, mentioned in the Carnic Alps (Austria/Italy) and adjacent areas of Slovenia and Croatia, were:

- 1) *Gyroporella* cf. *G. nipponica* Endo and Horiguchi by Flügel, 1968, p. 56 (no illustration),

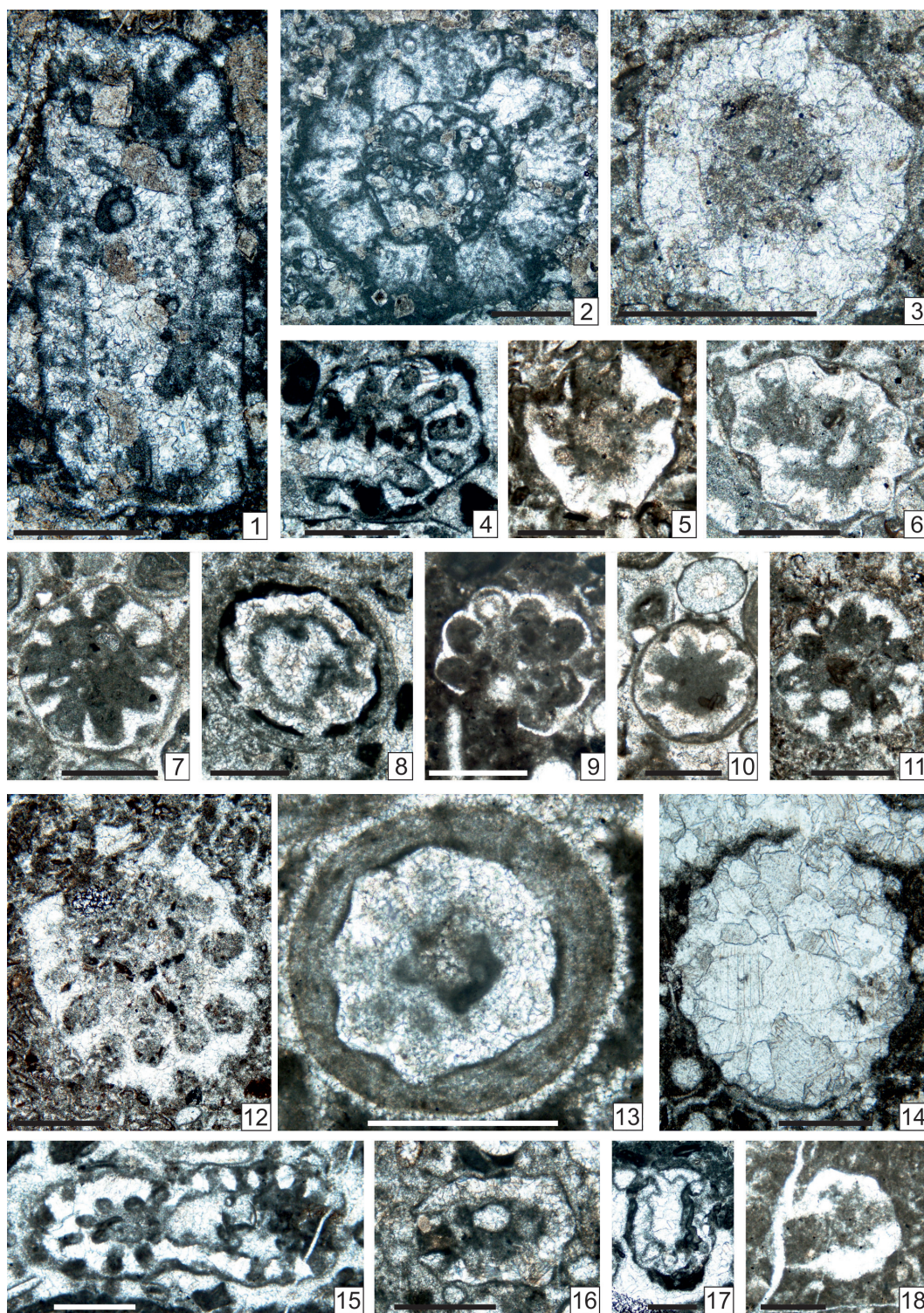


FIGURE 23. 1, 2. *Macroporella* cf. *siamensis* Endo, 1969. Longitudinal section. Sample GBT3_3. 2. Transverse section. Sample GBT3_4. 3, 5, 6, 8, 13, 18. *Mizzia cornuta* Kochansky and Herak, 1960. Several oblique transverse sections. 3. Sample GB40_5. 5. Sample GB40_6. 6. Sample GB70s_3. 7. Sample GB72_3. 8. Sample GB105_5. 13. Sample GB106_A. 18. Sample GBT1_4. 7, 9–12, 14? *Mizzia velebitana* Schubert, 1908. Several oblique transverse sections. 9. Sample GB109_2. 10. Sample GB111_4. 11. Sample GB129_6. 12. Sample GB66_11. 14? Sample GB156_9. 4, 15–17. *Mizzia yabei* (Karpinsky, 1909) emend. Pia, 1920. Several oblique sections. 4. Sample GB43_5. 15. Sample TK12_4. 16. Sample ZK202_6. 17. Sample Z14_1_2. Scale bars: Figures 23.1–23.3 = 1 μ m; all others = 0.5 μ m.

- 1979 p. 572 (no illustration); Kochansky-Devidé, 1970a, p. 216, 242, plate 24, figures 1–6 (which are in reality probably several genera including *Mizzia* and *Pseudoepimastopora* emend.); Flügel and Flügel-Kahler, 1980, p. 134–135, plate 4, figures 2, 4, 9; Vachard and Krainer, 2001a, p. 151 (no illustration) and 2001b, p. 172, plate 1, figure 1.
- 2) *Gyroporella microporosa* Endo, by Kochansky-Devidé, 1970a, p. 217, 242, plate 7, figure 7; Flügel, 1979, p. 572 (no illustration).
 - 3) *Gyroporella? tenuimarginata* Kochansky-Devidé, by Kochansky-Devidé, 1970a, p. 217, 242, plate 7, figure 8; Flügel, 1979, p. 572 (no illustration).
 - 4) *Gyroporella intusannulata* Kochansky-Devidé; Kochansky-Devidé, 1970a, p. 217–218, 242, plate 25, figures 1–9; Flügel, 1979, p. 572 (no illustration).
 - 5) *Gyroporella igoi* Endo; Flügel, 1979, p. 572 (no illustration).
 - 6) *Gyroporella longithalla* Endo; Flügel, 1979, plate 1, figure 7; Flügel and Flügel-Kahler, 1980, p. 132, 134, plate 4, figure 5.
 - 7) *Gyroporella* cf. *likana* Kochansky-Devidé; Flügel and Flügel-Kahler, 1980, p. 131–132 plate 4, figure 8.
 - 8) *Gyroporella dissecta* Chuvashov; Vachard and Krainer, 2001a, p. 151 (no illustration).
 - 9) *Gyroporella* sp., by Kochansky-Devidé, 1970a, p. 218–219, plate 7, figure 9; Riding and Guo, 1991, figure 10; Flügel, 2004, plate 101 (full page).
 - 10) *Atractyliopsis* sp.; Riding and Guo, 1991, plate 1, figure 3.

Occurrence. In the Carnic Alps: Auernig Fm (Vachard and Krainer, 2001a); Schulterkofel Fm; Zweikofel Fm; Trogkofel Fm, Forni Avoltri (Flügel, 1968, 1979; Vachard and Krainer, 2001b). Seikofel, Sexten, Dolomites, Italy (Flügel, 2004). In this study: Zweikofel Fm (sample ZK204_A?) and Zottachkopf Fm (sample ZT1_6).

Genus PSEUDOEPIMASTOPORA Endo, 1960
emend. herein

Type species. *Pseudoepimastopora pertunda* Endo, 1960 emend. herein.

Emended diagnosis. Thallus ellipsoidal to ovoid. Laterals simple, almost euspondyl, perpendicular to the central cavity, with a perpendicular shape: with a complex form defined here as Scottishchardon, i. e., with three parts; the innermost is short, cylindrical, acrophore; the central second one is spherical and inflated; the outermost is conical truncated.

Remarks. We do not agree with Granier and Deloffre (1994, p. 58, 72) who considered *Pseudoepimastopora* as a nomen nudum. It is poorly defined, but perfectly valid, and consequently was to be revised. The principal taxonomic problem is that, erroneously, Endo (1960) and Johnson (1963) have described the shape of the laterals as similar to those of *Epimastopora japonica*; i.e., as to those of the genus *Epimastopora* emend. herein. This real shape of the laterals was correctly described in *P. impera* Ràcz, 1966a in a taxon considered therefore as a questionable *Pseudoepimastopora* (sensu Endo or Johnson). Here, we valid the species *P. pertunda* by designation of the figure 5 as unique holotype (Endo designated initially two “holotypes”: figures 3 and 5), and consequently, we valid definitively the genus *Pseudoepimastopora*. As already indicated by Granier and Deloffre (1994, p. 58), the consequence of such an emendation leads to consider *Epimastoporella* as a senior synonym of *Pseudoepimastopora*, and to discard definitively *Epimastoporella* from the literature. We re-established *Epimastopora* Pia, 1922, emend. Kochansky and Herak, 196, as the name for many “*Epimastoporella*”. In consequence, *Globuliferoporella* corresponds currently to its original definition. In contrast, as, contrary to Granier and Deloffre (1994), we consider *Tauridium* as a possible senior synonym of *Permocalculus*, the genus *Paraepimastopora* Roux, 1979, becomes again perfectly valid (see earlier). *Pseudoepimastopora* in the sense of Homann (1972) is misinterpreted, and encompasses in reality *Epimastopora* species; similarly, *Pseudoepimastopora* sensu Flügel et al. (1991) is either *Epimastoporella* (plate 47, figure 7) or a phylloid alga *Ivanovia* or *Eugonophyllum* (plate 47, figure 5).

Pseudoepimastopora primaeva Chuvashov and Anfimov, 1988 (re-illustrated in Chuvashov et al., 1993, plate 3, figure 2), from the late Moscovian of the eastern slope of the western Urals, is possibly a transitional form between *Gyroporella* and *Pseudoepimastopora* emend. herein.

There are, in the literature, four interpretations for the groups of small spheres more or less linked by a microsparitic cement, which are generally assigned to the dasycladales: 1) the sporangia of acetabulariaceans (including the Mesozoic to Recent aciculariaceans or polyphysaceans, and perhaps *Atractyliopsis* Pia, 1937, emend. Accordi, 1956, sensu stricto and *Atractyliopsis?* sensu Cózar et al., 2014); 2) entire calcification of the central cavity of endospore genera (e.g., *Aciculella* Pia, 1930 non 1927 emend. Elliott, 1971; “*Atractyli-*

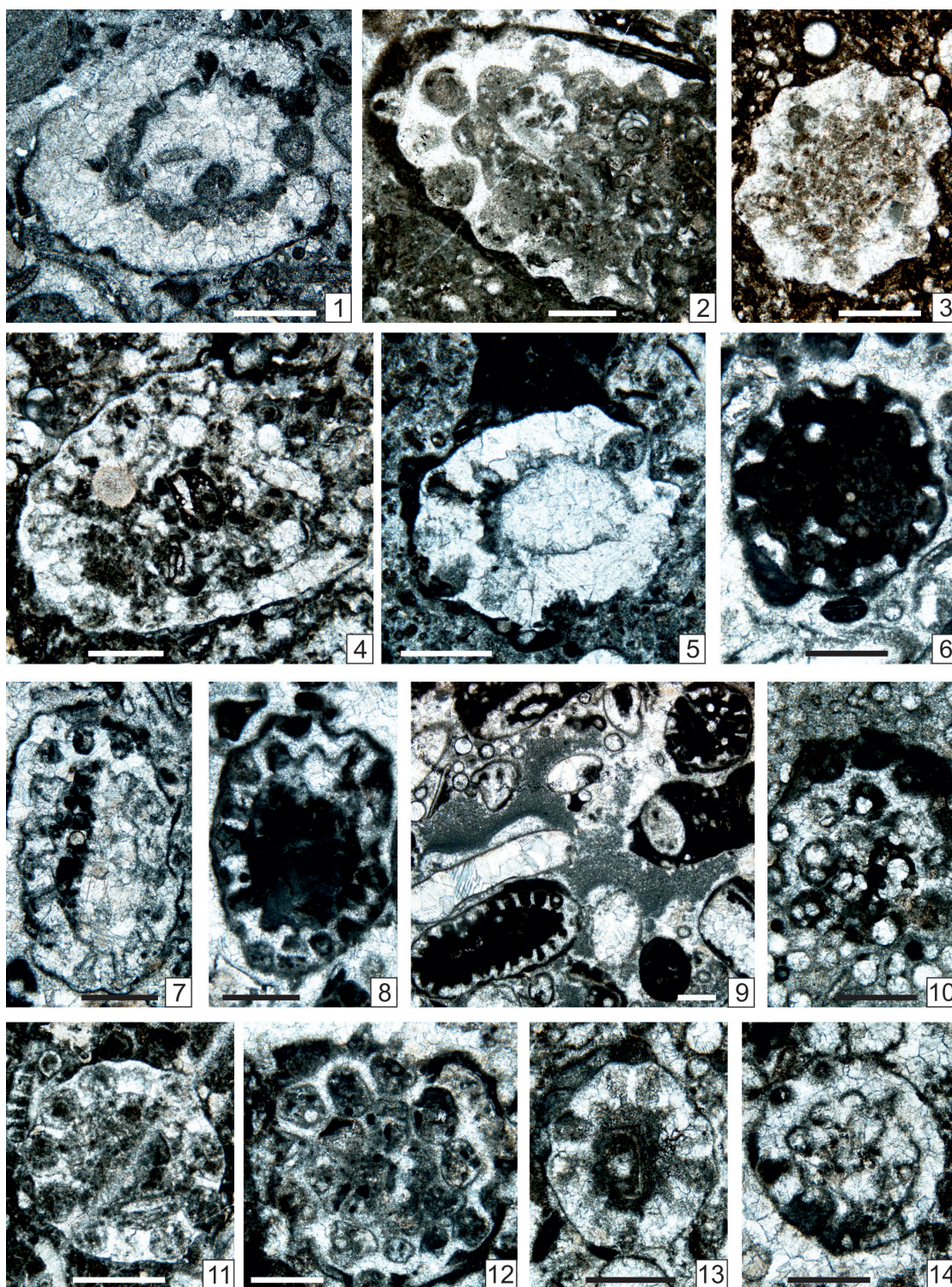


FIGURE 24. 1, 2, 5, 7, 8, 9 (bottom), 10. *Mizzia yabei* (Karpinsky, 1909) emend. Pia, 1920. 1. Oblique section. Sample GB43_5. 2. Oblique section. Sample GB71_1_1. 5. Oblique section. Sample Z13B_4. 7. Transverse section. Sample TSK12_2. 8. Transverse section. Sample TKS 12_3a. 9. Subaxial section (bottom, left). Sample ZK204_A. 10. Abraded tangential section. Sample ZK203_2. 3, 4, 6, 9 (top), 11–13, 14? *Mizzia velebitana* Schubert, 1908. 3. Transverse section. Sample GB146_2. 4. Oblique section. Sample GB163_10. 6. Transverse section superficially abraded. Sample TKS13_5. 9. Transverse section (top, right). Sample ZK204_A. 11. Transverse section. Sample GB175_11. 12. Tangential section showing the aspect of surface. Sample ZK94_5_4. 13. Transverse section. Sample ZK200_5. 14. Transverse section showing different stages of diagenesis. Sample ZK200_6. Scale bars: 0.5 μ m.

opsis" sensu Rich 1974, Mamet and Roux 1975b, 1978, and Devuyst 2006, non Pia 1937; and "*Pseudoepimastopora*" sensu Elliott, 1968a) whereas isolated spores can be visible in situ in not recrystallized central cavities (see *Diplopore* in Pia, 1920, Elliott, 1971, and Mu, 1982; and here *Anthracoporella* (Figure 8.3), and see later "Algen Sporen"; 3) thalli of dasycladales with vesiculifer laterals with large distal part and short proximal part (e.g., *Coelosporella* Wood, 1940; *Holosporella* Pia, 1930; and *Pseudoepimastopora* emend. herein); 4) undeterminate groups of spherical bodies having often a dark microgranular wall (e.g., *Ningbingellina* Mamet, 1998; *Ningbingellina* sensu Devuyst, 2006; *Floritheca* Gaillot and Vachard, 2007; *Aphanocapsites* Maslov sensu Mamet and Pr  at, 2013; and *Neoradiosphaeroporella* C  zar and Vachard in Vachard et al., 2016).

Occurrence. Late Virgilian of New Mexico (Krainer et al., 2017a). Asselian–Artinskian of the northwestern margin of the Paleotethys (Montenegro, Turkey, Carnic Alps, Italy, Croatia, Serbia, Texas and New Mexico).

Pseudoepimastopora carnica (Fl  gel, 1966) n. comb., emend. herein

Figure 25.1–12, Figure 27.3, 27.6

- *1966 *Atractyliopsis carnica* Fl  gel, p. 24, pl. 4, figs. 1–3, pl. 5, figs. 1–4.
- 1968 *Atractyliopsis carnica*; Fl  gel, p. 56 (no illustration).
- 1972 *Atractyliopsis carnica*; Homann, p. 192, p. 24, pl. 3, fig. 19, pl. 5, fig. 41.
- 1976 *Atractyliopsis carnica*; Emberger, p. 22 (no illustration) (with five references).
- 1979 *Atractyliopsis carnica*; Zagorodnyuk, p. 8, pl. 1, fig. 6.
- 1979 *Atractyliopsis* (sic) *carnica*; Fl  gel, p. 572.
- 1979 *Atractyliopsis* (sic) *carnica*; Fl  gel, pl. 1, fig. 5.
- ? 1979 *Pseudogyroporella mizziaeformis* Endo; Fl  gel, p. 572 (no illustration).
- 1980 *Atractyliopsis carnica*; Fl  gel, pl. 5, figs. 1–5.
- 1980 *Atractyliopsis* sp.; Fl  gel, pl. 7, fig. 4, pl. 10, fig. 6.
- 1980 *Atractyliopsis carnica*; Fl  gel and Fl  gel-Kahler, p. 124–126, 128, pl. 2, figs. 1–8 (with three references in synonymy).
- 1981 *Gyroporella nipponica* Endo and Horiguchi; Ramov   and Kochansky-Devid  , pl. 1, fig. 4.
- ? 1985 *Poikiloporella* sp.; Mu, pl. 15, fig. 1.
- ? 1991 *Atractyliopsis*; Riding and Guo, fig. 3.
- 2000 *Atractyliopsis carnica*; Granier and Grgasovi  , p. 16–17 (no illustration, with 18 references).

- v. 2001b *Atractyliopsis carnica*; Vachard and Krainer, pl. 3, fig. 11.
- 2004 *Atractyliopsis carnica*; Fl  gel, pl. 60, fig. 7.
- 2013 dasyclad algal fragments; Wahlman and Tasker, fig. 11E.
- v. 2017 "*Atractyliopsis*" *carnica*; Lucas et al., p. 15 (no illustration).
- v. 2017a "*Atractyliopsis*" *carnica* Fl  gel; Krainer et al., p. 20, 39, 40, pl. 25, fig. 2, pl. 27, fig. 4, pl. 37, figs. 2–5, pl. 41, figs. 5, 6, 15–17, pl. 43, figs. 3, 8, 9, 12, 13, pl. 44, figs. 2, 3, 6, 8, pl. 52, fig. 4.

Description. Length: up to 5,000 μm ; outer diameter = 750–1,500 μm ; inner diameter = 450–1,200 μm ; wall thickness = 150–250 μm ; maximal width of pores = 170–250 μm ; minimal width of pores = 40–60 μm ; interpores = 30–40 μm . It differs from *P. pertunda* Endo, 1960 by the shape of the laterals.

Occurrence. Kasimovian of Bashkortostan (Zagorodnyuk, 1979). Late Virgilian of New Mexico (Krainer et al., 2017a). Asselian–Artinskian of the northwestern margin of the Paleotethys (Montenegro, Turkey, Carnic Alps, Italy, Croatia, Serbia and New Mexico). In the Carnic Alps: Forni Avoltri; Zweikofel, Zottachkopf, Trogkofel, Tre  dorfer Kalk, Goggau Kalk (Fl  gel, 1968, 1979; Fl  gel and Fl  gel-Kahler, 1980; Vachard and Krainer, 2001b, sample ZKO10); represents a fertile stage of a dasyclad alga (Fl  gel, 2004). This study: Zweikofel Fm (samples GB36_4; GB60_2_2; GB61_4; GB72_1b; GB119_3; ZK94_7_4; ZK99a_10; ZK99c_9; ZK99c_13); Zottachkopf Fm (samples Z5_2; Z5_3; Z5B_3; Z7_2; Z7_3; Z9_1b; ZT1_5); and Trogkofel Fm (sample TK5_A).

Family DASYCLADACEAE K  tzing, 1843

Tribe MIZZIEAE Vachard, Vandelli and Moix, 2013

Subtribe MIZZIINAE Bassoullet, Bernier, Deloffre, G  not, Jaffrezo and Vachard, 1979

Genus MIZZIA Schubert, 1907

Type species. *Mizzia velebitana* Schubert, 1908.

Description. Thallus moniliform, euspondyl. Laterals vesiculifer more or less wide. Broad internal cavity. Outer surface with perforate cortex and partly prominences.

Remarks. The genus *Mizzia* was remarkably described and interpreted by Pia (1920) and Kochansky-Devid   and Gusi   (1971). However, Chuvashov (2001) separated the three main species *M. velebitana*, *M. yabei* and *M. cornuta* into three different monospecific genera: *Mizzia*, *Yabeites* Chuvashov, 2001, and *Cornutella* Chuvashov, 2001. This proposal is not followed here, because it is inconsistent with our microfacies observations and the general difficulty in order to attribute

numerous specimens to the different species, *M. velebitana*, *M. yabei* or *M. cornuta*. These three latter species are therefore considered here as three species of the same genus.

As indicated by Vachard et al. (2005, 2013), the name “*Mizzia* Schubert, 1909 [or 1907] (...) emend. Rezak, 1959” adopted by Pratulon (1963); Emberger (1976); and Granier and Grgasović (2000), is inappropriate because the unique species described by Rezak (1959), *Mizzia brankampi* Rezak, 1959, is probably an *Eogoniolina* similar to *E. johnsoni* Endo, 1953b; i.e., a representative of another genus. Other misinterpreted *Eogoniolina* include *Mizzia yabei* of the authors and *Permoplexella* Elliott, 1968a. Furthermore, it is yet difficult to determinate the exact number of species of *Mizzia*, and, as a consequence, the “genera” of Chuvashov (2001): *Yabeites* and *Cornutella*, as well as many mizziacean genera created in the studies of Endo, are probably unfounded. Similarly, the limit with *Gyroporella* and its numerous taphotaxa is difficult to be established. As we have never observed relationships between Coniporelleae and *Mizzia*, due to the absence of Triassic transitional taxa, we consider the mizziean forms as a distinct tribe.

Surprisingly, because these taxa have nothing in common, some *Pseudovermiporella* were interpreted as *Mizzia velebitana* (sic) (e.g., Angiolini et al., 2010, figure 4.33).

Occurrence. Early–Late Permian; cosmopolitan; but the precise FAD (first appearance datum) and LAD (last appearance datum) are poorly known; the LAD is apparently Wuchiapingian (Zhao et al., 1981; Vachard et al., 2005; Vachard and Isozaki, unpublished data); even if Changhsingian *Mizzia* have been mentioned by Flügel and Reinhardt (1989), Sha et al. (1992) and Kolodka et al. (2012), all these latter seem to be misinterpreted *Eogoniolina*.

Mizzia velebitana Schubert, 1908

Figure 22.9–11, Figure 23.7, 23.9–12, 23.14?,
Figure 25.3, 25.4, 25.6, 25.9 (top), 25.11–13,
25.14?

- * 1908 *Mizzia velebitana* Schubert, p. 382, pl. 16, figs. 8–12.
- 1920 *Mizzia velebitana*; Pia, p. 19–23, text-fig. 4 p. 21, pl. 1, figs. 12–23.
- 1937 *Mizzia velebitana*; Pia, p. 822–828, text-figs. 1, 2, pl. 9, fig. 3.
- 1942 *Mizzia velebitana*; Johnson, p. 203–205, text-fig. 2 p. 204, pl. 2, figs. 1–4, pl. 3, figs. 1–4.
- ?p1951 *Mizzia velebitana*; Johnson, pl. 7, figs. 1–3 (non pl. 7, fig. 4 = *Eogoniolina*).

- 1960 *Mizzia velebitana*; Kochansky-Devidé and Herak, p. 81, pl. 5, figs. 1–6, 9–12.
- 1963 *Mizzia velebitana*; H. Flügel, p. 87, pl. 1, fig. 3 (with seven references in synonymy).
- 1963 *Mizzia velebitana*; Maslov et al., text-fig. 26.
- non 1963 *Mizzia velebitana*; Pratulon, p. 130–131, pl. 5, figs. 1–7 (with six references in synonymy; for a taxon which belongs, in reality, to *Eogoniolina*).
- 1965 *Mizzia velebitana*; Herak, p. 214 (no illustration).
- 1968 *Mizzia velebitana*; Flügel, p. 46, 49, 56, 57 (no illustration).
- ?1970 *Mizzia velebitana*; Pantić, pl. 2, figs. 1–3.
- 1976 *Mizzia velebitana*; Emberger, p. 59–61 (no illustration) (with 107 references).
- ?p.1978 *Mizzia velebitana*; Zaninetti et al., pl. 84, figs. 1?, 3?, 9? (non fig. 2 = *Salopekiella* sp.; nec figs. 4–6, 11–14 = *Mizzia yabei*; nec fig. 7 = *Gyroporella*? sp.).
- v1980 *Mizzia velebitana*; Vachard, p. 360–362, pl. 4, figs. 4–6, pl. 23, fig. 12, pl. 24, fig. 1 (with 27 references).
- ?1981 *Gyroporella nipponica* Endo and Huzimoto; Bérczi-Makk and Kochansky-Devidé, pl. 3, fig. 7.
- ?1981 *Mizzia velebitana*; Mu, p. 45, pl. 4, fig. 10, 11 (another species or genus?).
- 1979 *Mizzia velebitana*; Flügel, p. 572 (no illustration).
- 1982 *Mizzia velebitana*; Mu, p. 228, pl. 8, figs. 3–5.
- v1985 *Mizzia velebitana*; Vachard, p. 272, pl. 1, figs. 3, 10, pl. 3, figs. 3, 4.
- ?1986a *Mizzia velebitana*; Nguyen Duc Tien, pl. 9, figs. 3, 4 (perhaps *M. yabei*).
- v1986 *Mizzia velebitana*; Fontaine et al., pl. 24, figs. 1–4.
- v1989 *Mizzia cornuta* Kochansky and Herak; Vachard in Fontaine and Gafoer, pl. 7, fig. 2, pl. 9, fig. 4.
- 1989 *Mizzia velebitana*; Köylüoğlu and Altiner, pl. 2, fig. 5.
- v1989 *Mizzia velebitana*; Vachard in Fontaine and Gafoer, pl. 7, fig. 2, pl. 9, fig. 4.
- 1990 *Mizzia velebitana*; Flügel, pl. 1, figs. 1–3.
- 1991 *Mizzia velebitana*; Flügel et al., pl. 47, fig. 2.
- v1992 *Mizzia velebitana*; Vachard et al., pl. 3, fig. 3.
- v1992 *Mizzia velebitana*; Okla, pl. 45, figs 7–10.
- non 1992 *Mizzia velebitana*; Sha et al., pl. 1, fig. 2 (= *M. yabei*).
- 2000 *Mizzia velebitana*; Granier and Grgasović, p. 102–107 (no illustration, with 134 references).
- 2004 *Mizzia velebitana*; Flügel, pl. 59, fig. 4.

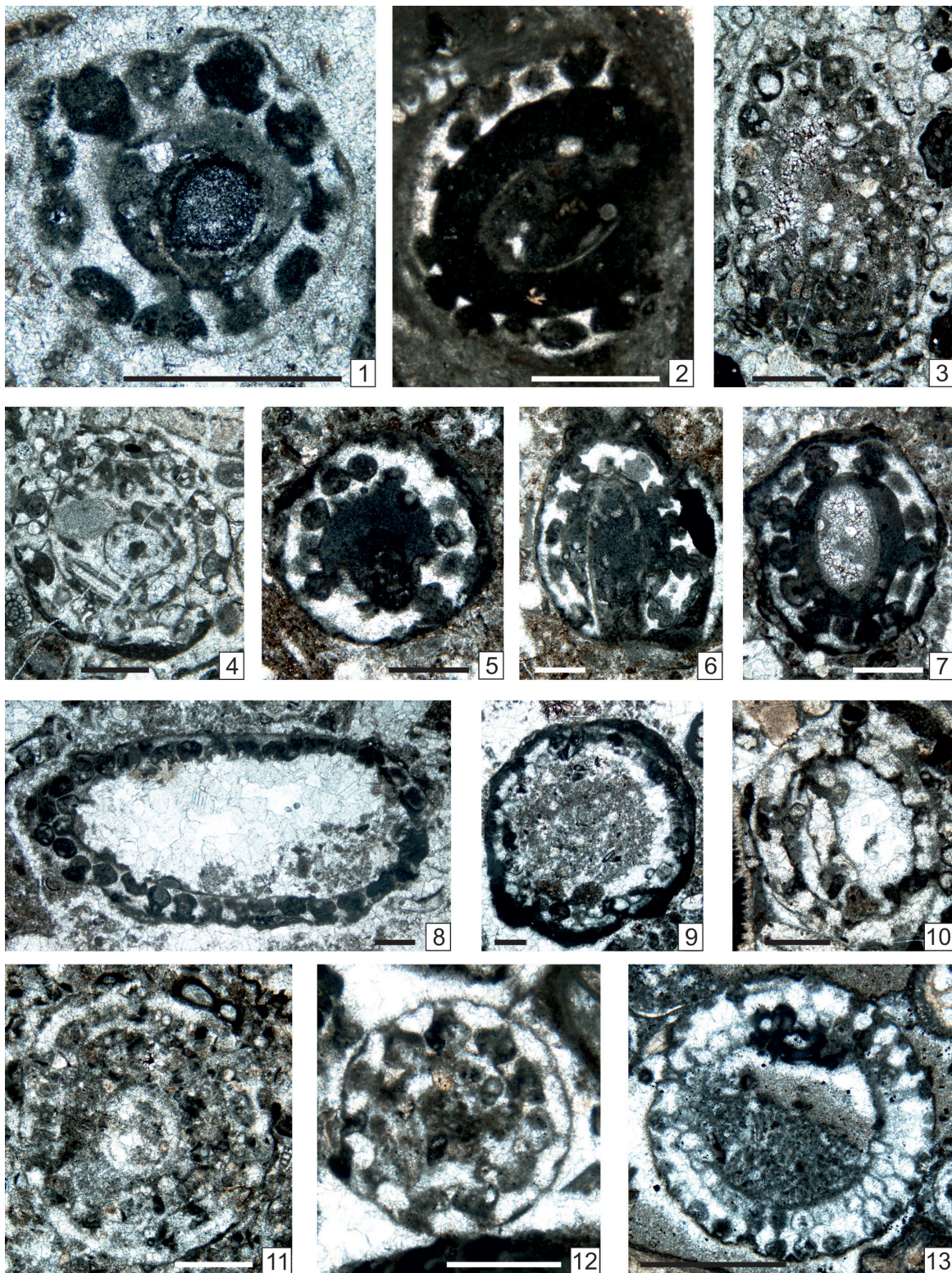


FIGURE 25. 1–12. *Pseudoepimastopora carnica* (Flügel, 1966) emend. herein, n. comb. 1. Transverse section. Sample GB36_4. 2. Oblique transverse section. Sample GB60_2_2. 3. Oblique section. Sample GB61_4. 4. Transverse section. Sample GB72_1b. 5. Transverse section. Sample Z5_2. 6. Oblique section. Sample Z5_3. 7. Transverse section. Sample Z7_2. 8. Longitudinal section. Sample Z7_3. 9. Transverse section. Sample Z9_1b. 10. Transverse section. Sample ZK99c_13. 11. Transverse section. Sample ZK94_7_4. 12. Transverse section. Sample ZK99a_10. 13. *Globuliferoporella?* sp. Transverse section. Sample Z19_3. Scale bars: 0.5 μm.

- p2004 *Mizzia wackestone*; Flügel, pl. 60, fig. 6 (non pl. 59, fig. 5 = *Gyroporella* sp.).
- non 2005 *Mizzia velebitana*; Hughes, pl. 1, figs. 21–23 (= *M. yabei*), pl. 2, fig. 1 (= *Macroporella*? or *Gyroporella*?).
- v2006 *Mizzia velebitana*; Insalaco et al., pl. 1, fig. 4.
- p2009 ? *Mizzia* sp.; Bucur et al., figs. 8.4, 8.5 (non fig. 8.6 = *Gyroporella*).
- . 2010 *Mizzia velebetiana* (sic); Angiolini et al., fig. 4.33.
- v2011 *Mizzia velebitana*; Vachard and Moix, p. 152, pl. 2, fig. 15.
- v2012 *Mizzia velebitana*; Kolodka et al., p. 138, 139 (no illustration).
- v2017 *Mizzia velebitana*; Granier et al., fig. 3A.
- Description.** Large species with subspherical segments and laterals relatively large. The perforate cortex is well visible in this species (Vachard, 1985, plate 3, figure 10). Outer diameter = 800–1,700 µm; inner diameter = 500–900 µm; pore diameter = 100–200 µm; interpores = 20–40 µm.
- Occurrence.** Permian. Japan, Italy (Sicily, ?Dolomites), Slovenia, Croatia, Montenegro, Hungary, Carnic Alps, Greece, Tunisia, Turkey (Hazro, Lycian nappes), Iran (Alborz, Zagros), Saudi Arabia, Afghanistan, Pakistan, South China, Thailand, Malaysia, Sumatra, Philippines, Japan, Guatemala and southeastern USA. In the Carnic Alps: Schülterkofel and Zweikofel formations (Flügel, 1968, 1979). This study: Zweikofel Fm (samples GB123_1; GB123_1_6; GB67_10; GB67_11; GB72_3; GB109_2; GB129_3; GB129_6; GB146_2; ZK203_2); and Zottachkopf Fm (samples TKS 10_2; TKS 13_5).
- Mizzia yabei* (Karpinsky, 1909) emend. Pia, 1920
Figure 22.12?, 22.13?, Figure 23.4, 23.15–17,
Figure 25.1, 25.2, 25.5, 25.7, 25.8, 25.9 (bottom),
25.10
- *1909 *Stolleyella yabei* Karpinsky, p. 268, 269.
- 1920 *Mizzia yabei*; Pia, p. 23–24, text-fig. 5 p. 24, pl. 1, figs. 4–6.
- 1937 *Mizzia yabei*; Pia, p. 828 (no illustration).
- 1942 *Mizzia yabei*; Johnson, p. 207–208, text-fig. 3 p. 204, pl. 3, figs. 4–6, pl. 7, fig. 2.
- 1962 *Mizzia*? cf. *yabei*; Kochansky-Devidé and Milanović, p. 217–218, pl. 7, figs. 1–3.
- ?1963 *Mizzia velebitana*; Pratulon, p. 130–131, pl. 5, figs. 1–7.
- 1965 *Mizzia yabei*; Herak, p. 214 (no illustration).
- 1968 *Mizzia cornuta* Kochansky and Herak; Flügel, p. 57 (no illustration).
- 1970a *Mizzia yabei*; Kochansky-Devidé, p. 213, 240, pl. 23, figs. 5, 6.
- 1973 *Mizzia* sp.; Bozorgnia, pl. 48, fig. 12.
- 1976 *Mizzia yabei*; Emberger, p. 61–62 (no illustration) (with 29 references).
- p.1978 *Mizzia velebitana* Schubert; Zaninetti et al., pl. 84, figs. 4–6, 11–14 (non fig. 2 = *Salopekiella* sp., nec fig. 7 = *Gyroporella*? sp.).
- 1979 *Mizzia yabei*; Flügel, p. 572 (no illustration).
- 1981 *Mizzia yabei*; Ramovš and Kochansky-Devidé, p. 97, pl. 1, fig. 1.
- 1982 *Pseudogyroporella mizziaformis* Endo; Mu, p. 230, pl. 7, figs. 1–3.
- non v1985 *Mizzia yabei*; Vachard, p. 272, pl. 1, fig. 1 (= *Eogoniolina*).
- ?1985 *Pseudogyroporella mizziaformis*; Mu, pl. 14, fig. 4.
- ?1985 *Gyroporella mizziaformis*; Mu, pl. 15, fig. 7.
- ?1986a *Mizzia velebitana*; Nguyen Duc Tien, pl. 9, figs. 3, 4.
- 1990 *Mizzia yabei*; Flügel, pl. 4, fig. 6.
- 1991 *Mizzia cornuta*; Flügel et al., pl. 47, fig. 1.
- ?1991 *Atractyliopsis*; Riding and Guo, fig. 3.
- v. 1992 *Mizzia yabei*; Vachard et al., pl. 3, fig. 5.
- 1992 *Mizzia velebitana*; Sha et al., pl. 1, fig. 2.
- v. 1993a *Mizzia yabei*; Vachard et al., pl. 1, fig. 3, pl. 2, fig. 6.
- 1997 *Mizzia yabei*; Wendt, p. 361, 362, 363, text-fig. 2 p. 362, text-fig. 3 p. 363, text-fig. 4 p. 364, text-fig. 5 p. 365, text-fig. 6 p. 366.
- 2000 *Mizzia yabei* (Karpinsky) Pia; Granier and Grgasović, p. 107–109 (no illustration, with 47 references in synonymy).
- 2000 *Mizzia*; Kiessling and Flügel, pl. 10, fig. 2.
- 2004 *Mizzia*; Flügel, pl. 101 (full page).
- 2005 *Mizzia velebitana*; Hughes, pl. 1, figs. 21–23.
- 2008 *Mizzia velebitana*; Lai et al., text-fig. 3 p. 82
- v2011 *Mizzia yabei*; Vachard and Moix, p. 152 (no illustration).
- v2012 *Mizzia yabei*; Kolodka et al., p. 138, 139, fig. 8l.
- v2013 *Mizzia yabei*; Parvizi et al., p. 161, fig. 7a–7c, 7d?, 7e, 7g?
- v2016 *Mizzia* sp.; Angiolini et al., fig. 11.B, 11C.
- Description.** Segments ovoid; laterals relatively narrow. Outer diameter = 1,300–6,000 µm; wall thickness = 160–240 µm; pore diameter = 80–160 µm.
- Remarks.** *Mizzia yabei* is characterized by club-shaped articles and the drum-stick form of the laterals. *Mizzia velebitana* differs by the wider spherical articles and *M. cornuta* Kochansky and Herak, 1960, by horny protuberances at the extremities of the laterals.
- Occurrence.** Permian. Japan, ?Italy (?Dolomites, ?Sicily), Slovenia, Croatia, Montenegro, Hungary, Carnic Alps, Greece, Tunisia, Turkey (Hazro,

Lycian nappes), Iran (Alborz, Zagros), Saudi Arabia, Afghanistan, Darvas, Pakistan, South China, Thailand, Malaysia, Philippines, Guatemala, south-western USA. In the Carnic Alps: Seikofel, Sexten, Dolomites, Italy (Flügel, 2004); Karawanken Mountains (Ramovš and Kochansky-Devidé, 1981); this study: Zweikofel Fm (samples GB43_5; GB66_11; GB67_10; GB71_1_1; GB71_1_2?; GB72_6; GB127_19; GB146_2; GB163_5; GB163_10; GB174_4; GB175_3; GB175_11; ZK94_5_4; ZK96_11; ZK199_8; ZK200_5; ZK200_6; ZK200_7; ZK202_6; ZK203_2; ZK204_A; ZK207_7); Zottachkopf Fm (samples TKS12_2; TKS12_3a; TKS12_3b; TKS12_4; TKS13_5; Z13B_4; Z14_1_2); and Trogkofel Fm (samples GBT_1_4; TK36_3).

Mizzia cornuta Kochansky and Herak, 1960
Figure 22.7–8, Figure 23.3, 23.5–6, 23.8, 23.13, 23.18

- *1960 *Mizzia cornuta* Kochansky and Herak, p. 83–86, text-fig 4 p. 84, pl. 7, figs. 1–14.
- 1962 *Mizzia cornuta*; Kochansky-Devidé and Milanović, p. 217, pl. 6, figs. 4–5.
- non.1964 *Mizzia cf. cornuta*; Kochansky-Devidé, p. 513, 516 (no illustration; but probable tectonic mélange).
- 1965 *Mizzia cornuta*; Herak, p. 210, 214 (no illustration).
- 1968 *Mizzia cornuta*; Flügel, p. 46, 55, 56, 57 (no illustration).
- 1970a *Mizzia cornuta*; Kochansky-Devidé, p. 213, 240, pl. 23, figs. 1–4.
- ?1970 *Mizzia cornuta*; Pantić, pl. 1, figs. 2, 3 (or abraded *M. yabei*?).
- 1979 *Mizzia cornuta*; Emberger, p. 57 (no illustration) (with 18 references).
- 1979 *Mizzia cornuta*; Flügel, p. 572 (no illustration).
- 1980 *Mizzia cornuta*; Flügel and Flügel-Kahler, p. 137–138, pl. 2, figs. 9, 10 (with 11 references).
- 1982 *Mizzia cornuta*; Mu, p. 227–228, pl. 8, fig. 6.
- v1989 *Mizzia cornuta*; Vachard in Fontaine and Gafoer, pl. 7, fig. 1.
- ?1991 *Mizzia cornuta*; Flügel et al., pl. 47, fig. 1 (most probably *M. yabei*).
- v. 1992 *Mizzia cornuta*; Vachard et al., pl. 3, fig. 8.
- v1993a *Mizzia cornuta*; Vachard et al., pl. 1, fig. 4, pl. 7, fig. 14.
- 1997 *Mizzia cornuta*; Sokač et al., p. 145 (no illustration).
- 2000 *Mizzia cornuta*; Granier and Grgasović, p. 99–101, figs. 16, 17 (with 27 references).

- v.2001a *Mizzia cornuta*; Vachard and Krainer, p. 151 (no illustration).
- 2001 *Cornutella cornuta*; Chuvashov, p. 102, fig. 2g.
- v.2003a *Mizzia cf. cornuta*; Krainer et al., table 1 p. 18, p. 19, pl. 7, fig. 10.
- 2007 *Mizzia cornuta*; Sremač, pl. 2, fig. 3.
- 2007 *Mizzia cornuta*; Grgasović and Sokač, pl. 2, fig. 4.
- v2011 *Mizzia cornuta*; Vachard and Moix, p. 152 (no illustration).
- v2013 *Mizzia cornuta*; Vachard et al., p. 530, fig. 7.1.
- v2016 *Mizzia cf. cornuta*; Angiolini et al., fig. 12B.
- v.2017a *Mizzia cf. cornuta*; Krainer et al., p. 20 (no illustration).

Description. Thallus length = 1,000–1,100 µm; thallus outer diameter = 790–1,500 µm; thallus inner diameter = 370–600 µm; wall thickness = 250–400 µm; diameter of laterals (= pores) = 90–150 µm; interpore = 45–55 µm. As indicated in its diagnosis, *M. cornuta* is smaller than *M. velebitana*, and classically the laterals are prolonged by “limy horns”.

Occurrence. The species is distributed in the entire Permian, from Asselian to Changhsingian. Early Permian of western Tethys. Late Kungurian of southern Crete (Vachard et al., 2013). ?Early Guadalupian of western Sicily (Flügel et al., 1991). Acme in the Middle Permian of Croatia, Slovenia, Montenegro, Serbia, Chios Island, Carnic Alps, Tunisia, Turkey (western Taurus), Urals, Iran (Alborz), Tibet, Thailand, Sumatra, New Mexico (USA). Late Permian of Greece (Vachard et al., 1993a). Late Midian–Changhsingian of southern Turkey (Hazro), Zagros, Fars and Abu Dhabi. In the Carnic Alps: Auernig Fm (Vachard and Krainer, 2001a); Schulterkofel Fm, Zweikofel Fm and Trogkofel Fm (Flügel, 1968, 1979). This study: Zweikofel Fm (samples GB40_6; GB 40_6a; GB43_5; GB66_11; GB70s_3; GB72_3; GB105_5; GB106_A; GB109_2; GB111_4; GB128_1; GB128_4; GB129_3; GB129_6; GB130_1; GB130_3; GB152_13; GB156_4?, GB156_9; GB163_5; GB163_16; GB165_8; GB171_11; GB173_2; GB173_18; GB174_1; ZK94_54?); Zottachkopf Fm (samples Z13B_4; Z14_1); and Trogkofel Fm (sample GBT1_1).

Family DIPLOPORACEAE Pia, 1920 nom. transl.
Shuysky, 1987 and/or Deloffre, 1987
Tribe LULIPOREAE Shuysky in Chuvashov, Luchinina, Shuysky, Shaikin, Berchenko, Ishchenko, Saltovskaya and Shirshova, 1987,

emend. Vachard, Hauser, Martini, Zaninetti, Matter and Peters, 2001a

Remarks. The Luliporeae are metaspondyl Dasycladales with one to several verticils of simple laterals L1 (rarely L2 and L3) with an individualized calcification. The Diploporeae are metaspondyl dasyclads, which lack vestibules (although some confusions are possible when the L1 are very short), contrary to the Velebitelleae, which are metaspondyl dasyclads with vestibules. The Clypeinae have simpler verticils (Vachard et al., 2001a).

Occurrence. Early Devonian (Emsian)–Middle Permian (Capitanian); Tethyan and Uralian shelves as well as the Americas from Guatemala to New Mexico (USA).

Genus CONNEXIA Kochansky-Devidé, 1970b

Type species. *Connexia fragilis* Kochansky-Devidé, 1970b

Description. Thallus with distant verticils. Cylindrical central cavity. Each verticil displays a first generation of acrophore, cylindrical laterals, followed by a tuft of secondary laterals, metaspondyl, elongate piriform. The axial cell and each lateral possesses its proper calcification.

Occurrence. Only Asselian according to Chuvashov et al. (1993), although given as present in the early Moscovian (Kochansky-Devidé, 1970b). Most probably Kasimovian (Vachard and Moix, 2011) to Kungurian (Angiolini et al., 2016): Tunisia, Tibet, Sumatra, Carnic Alps, Croatia, Guatemala (Vachard et al., 1997).

Connexia slovenica Kochansky-Devidé, 1979
Figure 26.1–4, Figure 27.9

- 1970a *Teutloporella* n. sp.; Kochansky-Devidé, p. 214, 416, 241–242, pl. 22, figs. 5, 6.
- 1972 *Likanella?* cf. *L. spinosa* Milanović; Homann, p. 210, pl. 6, fig. 44.
- ?1979 *Salopekiella* sp.; Flügel, p. 572 (no illustration).
- *1979 *Connexia slovenica* Kochansky-Devidé, p. 6–7, pl. 1, figs. 16, pl. 2, figs. 1–3 (with five references in synonymy).
- 1980 *Connexia carniapulchra* Flügel and Flügel-Kahler; Flügel, pl. 8, fig. 4 (nom. nud.)
- 1980 *Connexia carniapulchra* Flügel and Flügel-Kahler, p. 128, 130–131, pl. 2, fig. 9, pl. 3, figs. 1–8.
- 1982 Dasycladaceae gen. et sp. indet.; Mu, p. 231, pl. 6, figs. 11–13.
- v1989 *Connexia slovenica*; Vachard in Fontaine and Gafoer, pl. 7, figs. 3–6, pl. 9, figs. 2, 3.
- 1991 *Connexia* sp.; Flügel et al., pl. 47, fig. 4.

- 2000 *Connexia slovenica*; Granier and Grgasović, p. 30–31 (no illustration, with 13 references).
- v2001a *Connexia slovenica*; Vachard and Krainer, p. 151, pl. 5, figs. 2, 3.
- v2001b *Connexia slovenica*; Vachard and Krainer, p. 172, pl. 3, figs. 9, 10.
- v?2001a *Likanella?* sp.; Vachard et al., fig. 14.5.
- 2004 *Connexia*; Flügel, pl. 101 (full page).
- v2011 *Connexia* sp.; Vachard and Moix, p. 152, 154, pl. 2, fig. 17, pl. 3, figs. 18, 26?
- v2015 *Connexia slovenica*; Ghazzay-Souli et al., p. 253 (no illustration).
- v.2017 *Connexia* cf. *fragilis* Kochansky-Devidé; Lucas et al., p. 15 (no illustration).
- v.2017a *Connexia* cf. *fragilis*; Krainer et al., p. 20, 40, pl. 30, fig. 2, pl. 35, fig. 4.
- v.2017a *Connexia* ex gr. *fragilis*; Krainer et al., p. 20, 40, pl. 43, fig. 16.

Description. Outer diameter = 3,100 µm; inner diameter = 1,700 µm; length of laterals = 1,250–1,700 µm; diameter of laterals = 150–280 µm; interpores = 50–100 µm; number of tufts per verticil: 10. *C. slovenica* differs only from *C. fragilis* by more numerous tufts in the verticils (10–11 versus 5–6).

Occurrence. Late Pennsylvanian (Vachard and Krainer, 2001a; Vachard and Moix, 2011)–Early Permian of the Carnic Alps, Slovenia and Tibet; Asselian of Tunisia and New Mexico; Artinskian of Guatemala; Sakmarian of Sumatra (see compilation in Granier and Grgasović, 2000); ?Kubergandian of Oman (Vachard et al., 2001a); ?Capitanian of western Sicily (Flügel et al., 1991) and Texas (Flügel, 2004, plate 145, figure 4). In the Carnic Alps: Pizzul Fm (Vachard and Krainer, 2001a); Zottachkopf (Homann, 1972); Zweikofel Fm (Flügel, 1979; Vachard and Krainer, 2001b; sample ZKO32); Trogkofelkalk of Slovenia (Kochansky-Devidé, 1979); Forni Avoltri (Flügel, 1980; Flügel and Flügel-Kahler, 1980); Zweikofel; Trogkofel; Traverser Brekzie (Flügel, 2004). In this study, very rarely found in the Zweikofel Fm (sample GB40_2); Zottachkopf Fm (samples GBT3_2; Z9B_7; ZK199_4?; ZT1_5); and Trogkofel Fm (samples GBT3_4?; GBT4_2; GBT4_2).

Genus *Salopekiella* Milanović, 1965

Type species. *Salopekiella velebitana* Milanović, 1965.

Description. Thallus with pile of conical segments. Cylindrical central cavity. Each segment bears a pair of verticils of primary laterals, euspondyl, oblique and phloioophore.

Occurrence. Middle Permian of Croatia, Afghanistan, Thailand, Turkey and Tunisia (compiled

herein). Perhaps present in the Artinskian of the Carnic Alps (this study).

Salopekiella? sp.

Figure 27.5

Description. A unique section shows prominent verticils and a cylindrical axial cell similar to those of *Salopekiella*; however, this latter genus appears in the Middle Permian. Length = 2,100 µm (with four verticils); outer diameter = 950 µm, inner diameter = 610 µm, wall thickness = 180 µm; width of laterals = 150 µm.

Occurrence. Very rare and questionable in the basal Troglkofel Fm (sample TM5_2).

“Algen Sporen”

Figure 21.7, 21.9, 21.11, Figure 22.11–2, Figure 23.16, Figure 24.3, Figure 25.3, 25.4, 25.10, Figure 27.13–15, Figure 28.8–9, Figure 30.11

Remarks. In our material, the Algen Sporen of Flügel (see e.g., Flügel, 1979, plate 1, figure 5; 1980, plate 5, figures 1, 4, 5, plate 2, figure 10) are relatively common. They have also been designated as *Penella pongaensis* Mamet and Villa, 2004 (p. 176, figure 15b–15k). Cózar et al. (2018) discuss a green algal origin of these “algal spores” in late Viséan to early Bashkirian shallow-marine limestones of the Cantabrian Mountains (Spain). In our opinion, both taxa are most probably abraded desmes of Geodiidae sponges (rhaxes, rhaxasters) or other neosparitized, siliceous sponge spicules such as the selenasters of *Placospongia* (MacIntyre, 1977; Lukowiak et al., 2018).

Occurrence. Late Pennsylvanian to Holocene, probably cosmopolitan.

Class ALGOSPONGIA G. Termier, Termier and Vachard, 1977, emend. Vachard and Cózar, 2010

Remarks. Two groups of incertae sedis algae were encompassed in the incertae sedis class Algospongia by G. Termier et al. (1977): Moravammiales and Aoujgaliales. They were hardly discussed (Mamet, 1991), and often separated in two groups by the authors, the former being considered as green algae and the latter as red algae. We use here the revision of Vachard and Cózar (2010) for the description of the two groups and we admit the reality of the class Algospongia.

Occurrence. Ordovician–Permian (rare but unquestionable taxa in the Jurassic–Cretaceous). Ordovician with Wetheredellaceae and some *Moravammia*? Late Silurian/ Early Devonian–Late Permian for the other families. Rare Lazarus effects in the Mesozoic (*Kamaena khuraisensis* Adams and Al-Zahrani, 2000; *Koskinobullina*

socialis Cherchi and Schroeder, 1979; and *Hensonella dinarica* Elliott, 1960).

Order MORAVAMMINALES Pokorný, 1951, emend. Vachard in Termier, Termier and Vachard, 1975

Family CLARACRUSTACEAE Vachard in Vachard, Hauser, Martini, Zaninetti, Matter and Peters, 2001a, emend. Vachard and Cózar, 2010

Genus CLARACRUSTA Vachard in Vachard and Montenat, 1981

Type species. *Girvanella catenoides* Homann, 1972.

Synonyms. *Girvanella* (part.); *Berestovia* Berchenko, 1982 (non sensu Mamet and Villa, 2004).

Description. Thallus encrusting, formed by a superposition of continuous rows of highly calcified hemispherical to ellipsoidal cells, flattened at the base. Wall hyaline, yellowish.

Remarks. *Claracrusta* associated with *Girvanella* and/or other cyanobacterial crusts constitute the assemblages of “*Otonosia*”-type, very numerous during the Permian, but yet present since the Brigantian (Vachard and Cózar, 2010). The *Otonosia* biopisoids, composed of cyanobacteria and *Claracrusta*, in the Late Pennsylvanian and Early Permian (e.g., Homann, 1972; Vachard, 1980) are probably paleoecologically comparable with the modern macroids with *Acervulina* (i.e., biopisoids growing in relatively deep, 60–70 m deep fore-reef, or cryptic habits) (Hottinger, 1983; Perrin, 1992).

Occurrence. Late Viséan to Late Permian, cosmopolitan (Vachard and Cózar, 2010 with references therein).

Claracrusta catenoides (Homann, 1972) emend.

Vachard in Vachard and Montenat, 1981

Figure 20.1, Figure 26.5–8

- p1919 *Otonosia laminata* Twenhofel, p. 348–350, text-fig. 3.
- p.1963 *Otonosia laminata*; Johnson, p. 134–135, pl. 80, fig. 1 (only; figs. 2–5 are uninterpretable outer view of oncooids)
- p. 1967 *Otonosia laminata*; Fournié, pl. 1, fig. 1 (only; figs. 2–4 are uninterpretable outer view of oncooids).
- *1972 *Girvanella catenoides* Homann, p. 239–241, pl. 8, figs. 59 a–c.
- .1972 “*Stacheoides*” *spissa* Petryk and Mamet, p. 28–29, pl. 8, figs. 1–4.
- 1974 *Donezella intertexta* Chuvashov, p. 33–34, pl. 20, figs. 5–9.
- 1979 *Donezella intertexta* Zagorodnyuk, p. 12, pl. 3, fig. 6 (sic; in reality, fig. 5).

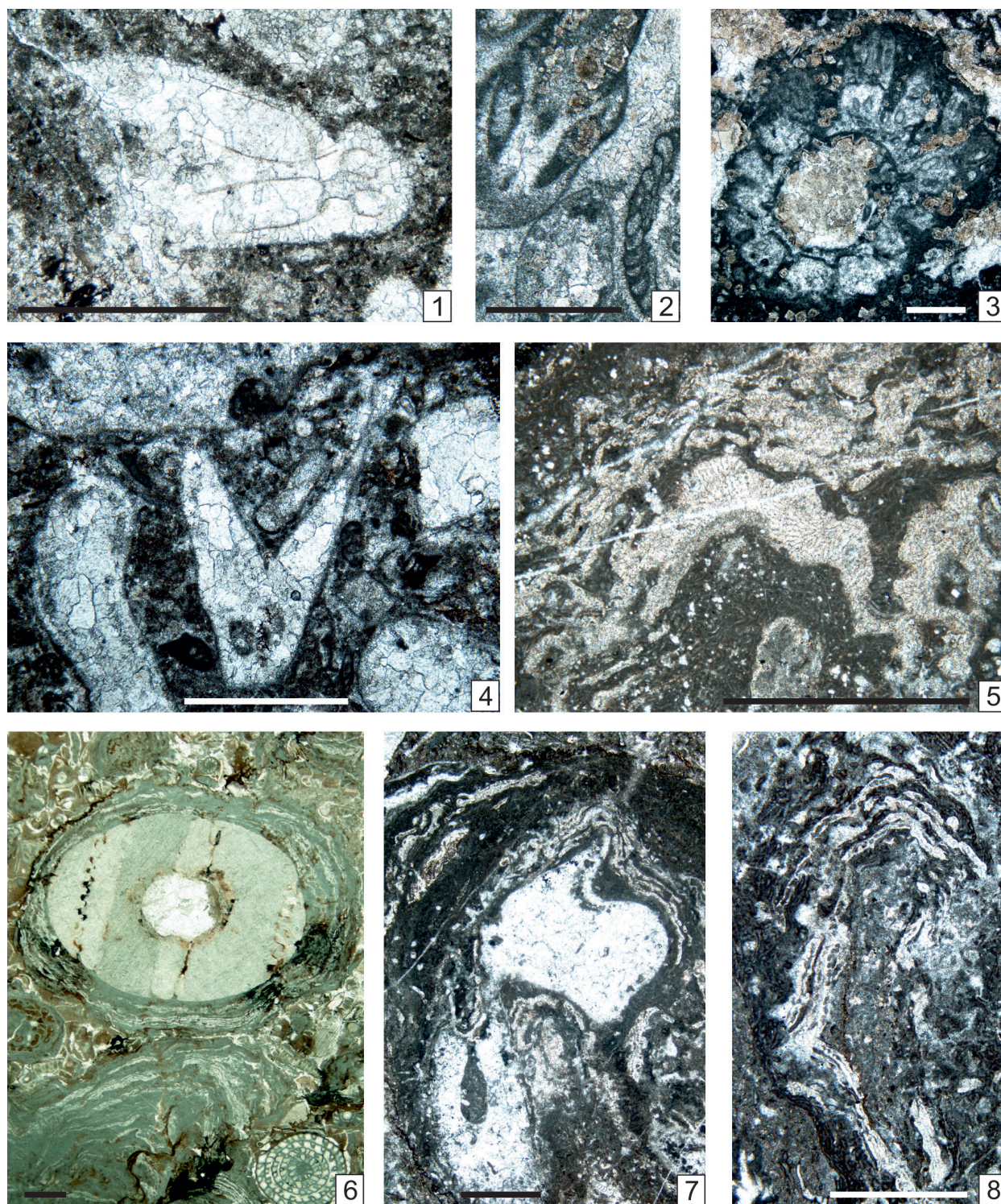


FIGURE 26. 1, 2, 4. *Connexia slovenica* Kochansky-Devidé, 1979. 1. Oblique section of two laterals. Sample GB40_2. 2. Fragment of longitudinal section. Sample GBT4_2. 4. Two laterals. Sample Z9B_7. 3. *Connexia?* sp. Sample GBT3_2. 5–8. *Claracrusta catenoides* (Homann, 1972) emend. Vachard in Vachard and Montenat, 1981. Longitudinal section with a tangential section in Figure 26.5. 5. Sample GB36_5. 6. Sample TNA18_1_2. 7. Sample TKW6B_3. 8. Sample TKW4_1. Scale bars: 1 µm.

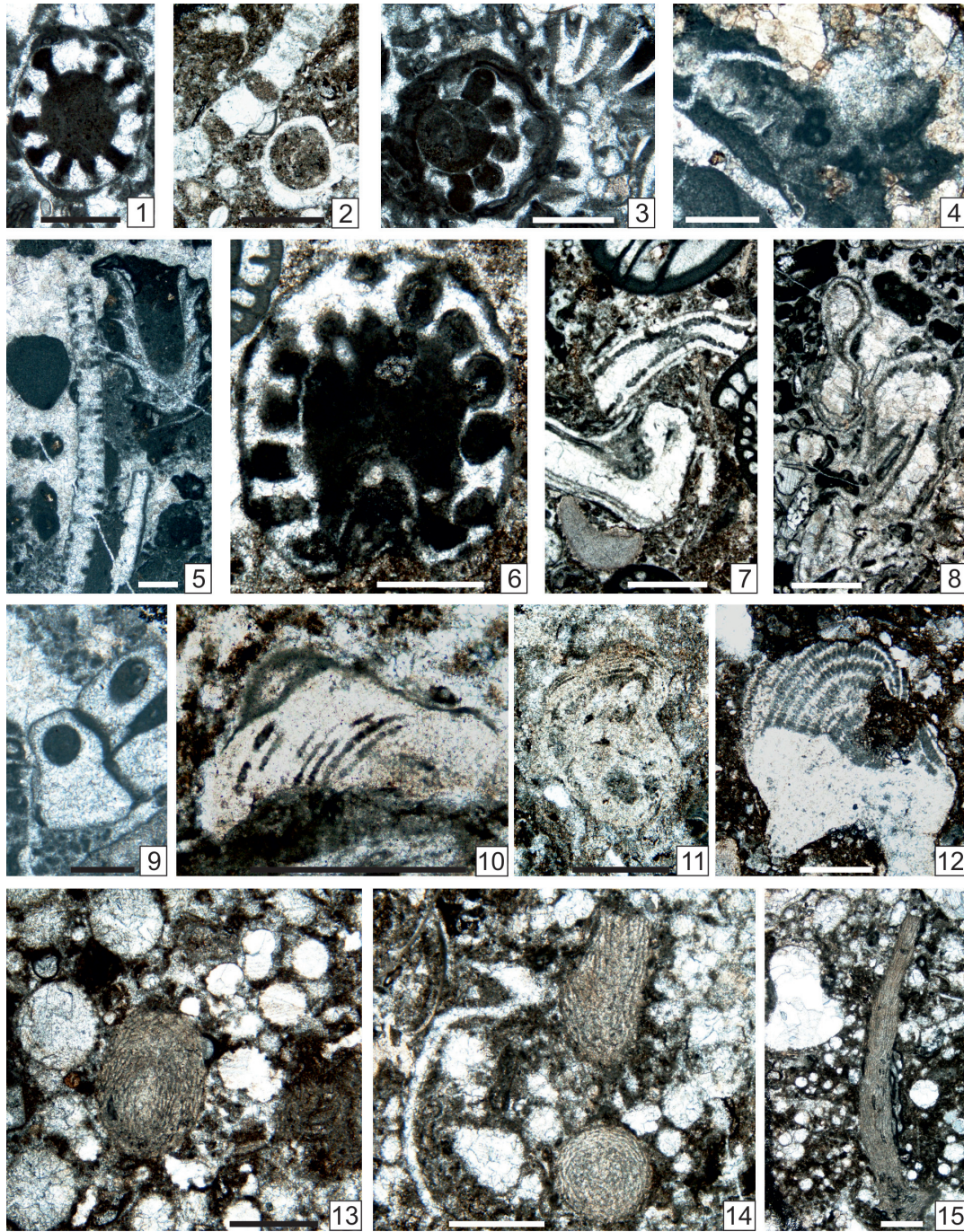


FIGURE 27. 1. *Gyroporella* sp. Transverse section. Sample ZT1_6. 2. *Epimastopora likana* Kochansky and Herak, 1960 emend. herein. Longitudinal section. Sample GB156_8. 3, 6. *Pseudoepimastopora carnica* n. comb., emend. herein. 3. Transverse section with *Connexia slovenica* Kochansky-Devidé, 1979 (top, right) in axial section. Sample ZT1_5. 6. Oblique transverse section. Sample Z5B_3. 4. *Renalcis* cf. *granosus* Vologdin, 1932. A colony associated with *Tubiphytes carinthiacus* (Flügel). Sample GBT11_2. 5. *Epimastopora* cf. *izawaikensis* Endo, 1953a. Longitudinal section (left) with *Salopekiella*? sp. (top right) in axial section. Sample TM5_2. 7, 8. *Neoanchicodium catenoides* Endo in Endo and Kanuma, 1954. Numerous sections. 7. Sample Z9B_3. 8. Sample TKS12_1_2. 9. *Connexia slovenica* Kochansky-Devidé, 1979. Small fragment with two laterals, in transverse and oblique sections. Sample TK32. 10–12. *Efluegelia* ex gr. *johnsoni* (Flügel, 1966). Three longitudinal sections more or less recrystallized. 10. Sample GB157_10. 11. Sample GB162_1. 12. Sample Z17B_1. 13–15. *Ungdarella uralica* Maslov, 1956. Several sections with “Algen Sporen”. 13. Sample ZK198_9. 14. Sample ZK200_2. 15. Sample ZK200_9. Scale bars: Figure 27.8 = 1 μ m, Figure 27.11 = 0.25 μ m, all others = 0.5 μ m.

- v1980 *Claracrusta catenoides*; Vachard, p. 392–393, pl. 3, fig. 1, pl. 7, fig. 5, pl. 25, fig. 1, pl. 26, figs. 1–3.
- 1980 *Girvanella catenoides*; Flügel, pl. 9, figs. 2, 5.
- v1981 *Claracrusta catenoides*; Vachard in Vachard and Montenat, p. 57–58, pl. 1, fig. 1, pl. 8, figs. 8, 10, 12, pl. 9, fig. 1, pl. 12, fig. 10 (with synonymy).
- 1982 *Berestovia filaris* Berchenko, p. 53, pl. 12, figs. 1–4.
- 1983 *Berestovia filaris*; Berchenko in Aizenverg et al., p. 128, pl. 84, fig. 2, pl. 86, figs. 5, 6, pl. 87, fig. 1.
- p. 1983 *Donezella delicata*; Berchenko in Aizenverg et al., p. 126, pl. 86, figs. 2, 3 (non pl. 85, figs. 5–9, true *D. delicata*).
- v1984 *Claracrusta catenoides*; Fontaine and Vachard, p. 51 (no illustration).
- 1985 *Rothpletzella?* sp., Mu, pl. 12, figs. 4–6.
- 1986 *Claracrusta catenoides*; Poncet, p. 192, pl. 3, fig. 5.
- 1988 *Claracrusta catenoides*; Ivanova, p. 7 (no illustration).
- 1989 *Claracrusta* sp.; Sebbar and Lys, pl. 1, fig. 6.
- v1989 *Claracrusta catenoides*; Vachard in Fontaine and Gafoer, pl. 8, fig. 6.
- 1990 *Claracrusta catenoides*; Flügel, pl. 1, fig. 4.
- 1990 *Claracrusta catenoides*; Bogush et al., p. 84–85, tabl. 1 p. 9, pl. 5, fig. 10 (with synonymy).
- vp. 1992 no legend (encrusting the *Coeloporella*); Vachard et al., pl. 3, fig. 11.
- v1993b *Claracrusta catenoides*; Vachard et al., pl. 2, fig. 5.
- 1995 *Claracrusta catenoides*; Forke, p. 241, pl. 17, figs. 5, 7.
- 1996 *Claracrusta catenoides*; Mamet, pl. 2, figs. 8–14, pl. 3, figs. 6, 7.
- 1996 *Claracrusta catenoides*; Sebbar and Mamet, pl. 1, figs. 4, 5.
- v1996 *Claracrusta catenoides*; Proust et al., p. 346 (no illustration).
- v1996 *Claracrusta catenoides*; Vachard and Maslo, p. 369–370, text-fig. 2 p. 360–365, pl. 1, figs. 1, 2 (with synonymy).
- 1997 *Berestovia filaris* Berchenko; Harris et al., fig. 9.12.
- v.1997 *Claracrusta catenoides*; Fontaine et al., p. 7 (no illustration).
- 1999 *Berestovia?* ou *Iberiaella?*; Sebbar and Mamet, text-fig. 3.100.
- 1999 *Claracrusta catenoides*; Sebbar and Mamet, text-fig. 3.99.
- 2000 *Claracrusta* sp.; Sebbar, pl. 1, fig. 10.
- 2000 *Claracrusta catenoides*; Mamet and Stemmerik, fig. 9 E, 9F.
- v2001a *Claracrusta* ex gr. *catenoides*; Vachard and Krainer, pl. 5, fig. 8.
- 2002 *Claracrusta catenoides*; Mamet, p. 502, pl. 7, fig. 3 (with synonymy).
- 2003 *Claracrusta catenoides*; Khodjanyazova and Mamet, pl. 5, figs. 8, 9.
- 2003 *Claracrusta catenoides*; Cózar et al., pl. 5, fig. 1.
- v2003a *Claracrusta catenoides*; Krainer et al., table 1 p. 18, p. 19, pl. 3, fig. 32.
- 2003 Red algae-like organisms (R); Igawa, p. 74, pl. 12, fig. 10, pl. 13, fig. 3?, pl. 14, fig. 8.
- ? 2004 *Claracrusta* spp. (mostly *C. catenoides* (Homman) (sic) emend. Vachard); Cózar, p. 373, text-fig. 3 p. 371 (no illustration).
- 2004 *Claracrusta catenoides*; Cózar and Rodríguez, fig. 9.17.
- 2004 *Claracrusta catenoides*; Cózar and Somerville, text-fig. 5 p. 46, text-fig. 8 p. 48, text-fig. 9 p. 49, fig. 13. 6, 10, fig. 14.25.
- 2004 *Claracrusta catenoides* (= *Berestovia filaris* Berchenko, 1982; see Mamet, 2002); Brenckle, pl. 6, fig. 10.
- 2004 *Berestovia filaris* Berchenko; see Mamet 2002 (sic); Mamet and Villa, p. 172, pl. 6, fig. 14n, 14o (with four references in synonymy).
- 2004 *Claracrusta catenoides* (Homann); see Mamet 2002 (sic); Mamet and Villa, p. 172, pl. 6, fig. 10 (with 19 references in synonymy).
- 2005 *Claracrusta catenoides*; Mamet and Zhu, fig. 5I, 6D.
- 2005a *Claracrusta catenoides*; Cózar and Somerville, text-fig. 16 p. 25, fig. 14.6.
- 2005b *Claracrusta catenoides*; Cózar and Somerville, pl. 2, fig. 5.
- 2006 *Claracrusta* based-oncoid; Kabanov et al., pl. 1, fig. 16.
- 2008 *Claracrusta* ex gr. *catenoides*; Pille, p. 77–78, pl. 25, figs. 9–15.
- v2009 *Claracrusta catenoides*; Krainer et al., p. 13, 15, pl. 3, fig. 4.
- v2010 *Claracrusta catenoides*; Vachard and Cózar, p. 183, pl. 6, figs. 2–5.
- 2010 *Claracrusta catenoides*; Mamet and Pr  at, p. 16, pl. 4, figs. 1–4.
- v2011 *Claracrusta catenoides*; Vachard and Moix, p. 152, 154, 156 (no illustration).
- v2012 *Claracrusta catenoides*; Kolodka et al., fig. 8h.
- v2013 *Claracrusta catenoides*; Moix et al., p. 411.
- v.2015 *Claracrusta*; Krainer et al., figs. 19.2, 20.6, 20.7.
- v2017 *Claracrusta* ex gr. *catenoides*; Lucas et al., p. 15 (no illustration).

- v2017a *Claracrusta catenoides*; Krainer et al., p. 20, 39, pl. 19, fig. 12, pl. 27, figs. 6, 7, pl. 34, fig. 8, pl. 37, fig. 9.
- v2017b *Claracrusta* sp.; Krainer et al., fig. 28A?, B, F?.

Description. See Vachard (1980, p. 393) and Pille (2008, p. 78). Diameter of cells = 30–50 µm; height of cells = 40–70 µm; wall thickness = 7–10 µm.

Occurrence. As for the genus. In the Carnic Alps: Orenburgian (Vachard and Krainer, 2001a); this study: Zottachkopf Fm (samples TKW 4_4; TKW 4_1; TKW6B_3; TNA16_2_4a; TNA18_1_2; TNA1_1_4; Z6B_3a; Z6B_3b); basal Trogkofel Fm (samples GB36_5; TM7_3).

Order AOIJGALIALES Termier, Termier and Vachard, 1975, emend.

Vachard and Cózar, 2010

Family UNGDARELLACEAE Maslov, 1956b

Description. Aoujgaliales arborescent, cylindrical, branched, and embracing growth of the chamber rows. In some of the specimens, there is an initial stage, attached, followed by an erect stage. The endoskeleton is composed of conical to paraboloid concentric laminae growing upward continuous rows of chambers, and perforated pillars, transverse, perpendicular to each lamina, acting as communications between the chambers. Wall calcitic, yellowish and hyaline.

Occurrence. Late Viséan (late Asbian) to latest Permian (Changhsingian). Cosmopolitan up to the Early Permian; after that, Paleotethyan and Neotethyan.

Genus UNGDARELLA Maslov (1950) 1956a

Type species. *Ungdarella uralica* Maslov (1950) 1956a.

Description. Thallus cylindrical and branched. In some of the specimens, there is an initial stage, attached, followed by an erected stage. The endoskeleton is composed by conical to paraboloid concentric laminae growing upward and perforated pillars perpendicular to each lamina. A medium perforation within the pillar acts as communication between the chamberlets ("cells" of the authors). Wall calcitic, yellowish, hyaline.

Remarks. For the year of description of this genus see Vachard and Cózar (2010; with references therein). *Ungdarella* is generally interpreted as a red alga, with a hypothallus and a perithallus (Mamet, 1991; Flügel, 2004, plate 108, figures 7, 8), but this explanation is irrelevant (Vachard and Cózar, 2010). The skeletal network of *Ungdarella* is generally sharply recrystallized, but when it is well preserved, it appears as perforated and partly filled

with micrite and differs from the completely close cells of red algae always occupied by a precipitated microsparite. Due to this strong and variable recrystallization, the four morphogenera created by Ivanova (1999) and Chuvashov and Anfimov (2007) are most probably several diagenetic stages of true *Ungdarella* (Vachard and Cózar, 2010). On the other hand, some systems of attachment, totally unknown among the red algae, have been illustrated (Vachard and Cózar, 2010; with references therein).

Occurrence. Late Asbian (late Viséan) to Changhsingian (latest Permian). The FAD is probably the best marker at the base of the late Asbian (upper part of MFZ 14 biozone = Cfm6, Cf6Y2 or upper V3bY: Vachard, 1988; Gallagher and Somerville, 1997; Gallagher, 1998; Cózar and Somerville, 2004; Poty et al., 2006; Hance et al., 2011). Common in the Tethyan and Uralian shelves up to the Early Permian; absent from Siberia (Ivanova and Bogush, 1992) and Japan (Mamet, 2002); rare in the North American Craton (where the most common ungdarellaceans belong to *Komia* Kordé, 1951; Krainer et al., 2017a, 2017b). During the Middle–Late Permian, *Ungdarella* is only Paleotethyan and Neotethyan.

Ungdarella uralica Maslov, 1956a, non 1956b, nec 1950

Figure 27.13–15, Figure 28.1–9

- 1950 *Ungdarella uralica* Maslov, p. 75–78, fig. 1.
- *1956a *Ungdarella uralica*; Maslov, p. 73, pl. 21, text-figs. 18, 19, figs. 2, 3, pl. 23, figs. 1–4.
- 1956b *Ungdarella uralica*; Maslov, p. 151–152, fig. 1.
- 1963 *Ungdarella uralica*; Johnson, p. 6, pl. 1, figs. 1–3.
- 1963 *Ungdarella uralica*; Maslov et al., p. 29, text-figs. 17a–17e, pl. 20, figs. 1, 2.
- 1966 *Ungdarella uralica*; Chanton, p. 407–408, text-fig. 1A, C, pl. 8, fig. 3.
- 1966 *Ungdarella uralica*; Flügel, p. 14–16, pl. 1, figs. 1, 2.
- 1968 *Ungdarella uralica*; Flügel, p. 55 (no illustration).
- 1970b *Ungdarella uralica*; Elliott, p. 448, pl. 83, fig. 6.
- 1972 *Ungdarella uralica*; Chanton-Güvenç, pl. 4, fig. 4.
- 1972 *Ungdarella uralica*; Homann, p. 155–156, 158, pl. 1, fig. 4.
- 1972 *Ungdarella uralica*; Mamet and Rudloff, p. 91, pl. 9, figs. 1–5.
- 1973 *Ungdarella uralica*; Kitaev, pl. 1, fig. 8.

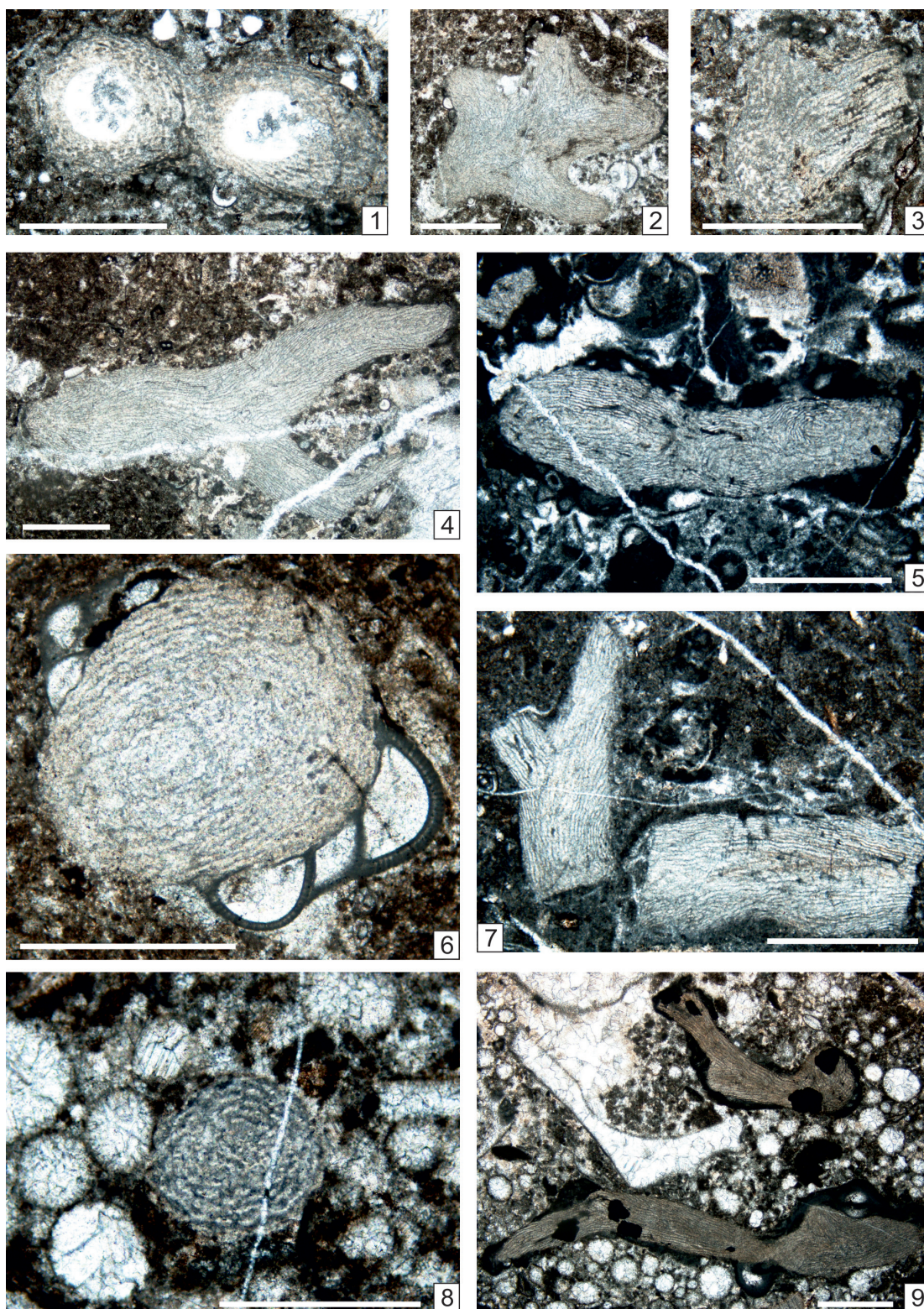


FIGURE 28. 1–9. *Ungdarella uralica* Maslov, 1956. Several oblique sections more or less recrystallized and one transverse section relatively well-preserved (Figure 28.8). 1. Central parts of both branches are chertified. Sample GB123_2a. 2. Sample GB125_2. 3. Sample GB 123_26. 4. Sample GB126_1. 5. Sample TNB15_1_1. 6. With *Mendipsia conili* (Nguyen Duc Tien, 1980). Sample GB130_5a. 7. Sample GBT13. 8. Sample ZK199_1. 9. Sample ZK200_10. Scale bars: Figure 28.7 = 1 μm ; all others = 0.5 μm .

- 1976 *Ungdarella uralica*; Emberger, p. 119 (no illustration) (with 21 references).
- 1977 *Ungdarella uralica*; Perret and Vachard, p. 120–121, pl. 5, fig. 4 (with 26 references in synonymy).
- v1977a *Ungdarella uralica*; Vachard, p. 374, tabl. 1 p. 375 (no illustration).
- 1979 *Ungdarella uralica*; Flügel, p. 572 (no illustration).
- 1979 *Ungdarella uralica*; Zagorodnyuk, p. 11, pl. 3, fig. 3.
- 1979 Boundstone à *Ungdarella uralica*; Mamet et al., pl. 2, fig. 7.
- v1980 *Ungdarella* ex gr. *uralica*; Vachard, p. 405–407, pl. 27, figs. 11–13, pl. 28, figs. 1, 2, 7, 9.
- 1980 *Ungdarella uralica* Maslov; Flügel and Flügel-Kahler, p. 161–162, pl. 8, fig. 4 (with six references in synonymy).
- 1980 *Ungdarella uralica*; Flügel and Flügel-Kahler, p. 161–162, pl. 8, fig. 4.
- v1981 *Ungdarella* ex gr. *uralica*; Vachard in Vachard and Montenat, p. 65–66, pl. 11, figs. 1, 13.
- 1981 *Ungdarella uralica*; Mamet and Martínez, pl. 3, fig. 3.
- 1983 *Ungdarella uralica*; Mamet and Roux, p. 85–86, pl. 8, figs. 7–10.
- 1986a *Ungdarella uralica*; Nguyen Duc Tien, pl. 10, fig. 1.
- 1986b *Ungdarella uralica*; Nguyen Duc Tien, pl. 14, fig. 1B, pl. 15, figs. 7, 8.
- 1986 *Ungdarella uralica*; Poncet, p. 189–190, pl. 2, figs. 4–6.
- 1987 *Ungdarella uralica*; Mamet et al., p. 52, pl. 25, figs. 6–14, pl. 26, figs. 8–10, pl. 27, figs. 1, 9–11 (with 20 references).
- 1987 *Ungdarella uralica*; Chuvashov et al., pl. 21, fig. 1.
- 1987 *Komia*; Chuvashov et al., pl. 21, fig. 4.
- 1989 *Ungdarella uralica*; Sebbar and Lys, pl. 1, fig. 2.
- 1989 *Ungdarella uralica*; Nguyen Duc Tien, pl. 34, figs. 4, 5.
- 1989 *Ungdarella* ex gr. *uralica*; Köylüoğlu and Altiner, pl. 1, fig. 10.
- v1990 *Ungdarella uralica*; Vachard and Miconnet, pl. 4, fig. 11.
- 1990 *Ungdarella uralica*; Flügel, pl. 3, fig. 5.
- 1996 *Ungdarella*; Madi et al., pl. 22, figs. 2, 5.
- v.1998 *Ungdarella uralica*; Fontaine et al., p. 13 (no illustration).
- v2001 *Ungdarella uralica*; Berkli et al., p. 557, 558, 563, 565, text-fig. 6; fig. 5.9
- v2001a *Ungdarella* ex gr. *uralica*; Vachard and Krainer, pl. 5, fig. 7.
- 2004 *Ungdarella uralica*; Mamet and Villa, tabl. 3 p. 157, p. 169–170, fig. 14j (with 24 references in synonymy).
- 2004 *Ungdarella* sp.; Flügel, pl. 56, fig. 6.
- 2006 *Ungdarella uralica*; Mamet, p. 343, pl. 5, figs. 6–18 (with 24 references, including a mention of 20 other references in Mamet et al., 1987).
- 2007 *Ungdarella uralica*; Chuvashov and Anfimov, pl. 11, figs. 1, 2.
- 2008 *Ungdarella uralica*; Pille, p. 92–93, pl. 29, figs. 1–15.
- v2010 *Ungdarella uralica*; Vachard and Cózar, p. 200, text-figs 5.4, 6.1–6.9, pl. 11, figs. 12, 13?, 14–20, pl. 12, figs. 1–5.
- v.2011 *Ungdarella* sp.; Moix et al., p. 75, pl. 4, fig. 16c.
- v.2011 *Ungdarella uralica*; Vachard and Moix, p. 157 (no illustration).
- v2012 *Ungdarella uralica*; Kolodka et al., p. 138, 139, fig. 8i.
- v2013 *Ungdarella uralica*; Parvizi et al., p. 167, figs. 9c, j, k, m (with six references in synonymy).
- v2017 *Ungdarella* ex gr. *uralica*; Lucas et al., p. 15 (no illustration).
- v2017a *Ungdarella uralica*; Krainer et al., p. 20, pl. 24, figs. 2, 3, pl. 28, figs. 6, 7, pl. 30, fig. 11, pl. 36, fig. 11.

Description. Length of fragments up to 6,000 µm; Diameter = 445–1,000 µm; weight of cells? = 5 µm; height of cells? = 3 µm; thickness of cells? = 10 µm.

Occurrence. As for the genus. In the Carnic Alps, Auernig Fm (Vachard and Krainer, 2001a); Zweikofel Fm (Flügel, 1968); Trogkofel Kalk of Forni Avoltri (Flügel and Flügel-Kahler, 1980); this study: Zweikofel Fm (samples GB123_2a; GB123_2b; GB125_2; GB126_1; GB130_5a; GB130_13b; ZK198_9; ZK199_1; ZK199_9; ZK200_2; ZK200_9; ZK200_10; ZK205_6); Zottachkopf Fm (samples TNB15_1_1; TNC7A_2); and Trogkofel Fm (sample GBT1_3).

Family STACHEIACEAE Loeblich and Tappan, 1961
emend. Vachard and Cózar, 2010, nom. correct.
herein

Description. Aoujgaliales attached, showing many rows of quadratic cells or chamberlets with a uniseriate, partly overlapping growth. Chamberlets square or higher than wide with distal and proximal, curved sides and lateral sides rectilinear.

Occurrence. Late Viséan–Late Permian, probably cosmopolitan.

Genus *EFLUEGELIA* Vachard in Massa and Vachard, 1979, emend. herein

Type species. *Cuneiphycus johnsoni* Flügel, 1966.

Description. Test attached, elongate, with large uniseriate growth of chamber rows and asymmetrical growth. Chambers quadratic with curved roofs and triangular pillars.

Remarks. Vachard and Cózar (2010) have synonymized *Fourstonella* and *Efluegelia* because, according to Groves (1986); Mamet and Villa (2004); and Cózar and Rodríguez (2004), the FAD of *Efluegelia* might be in the late Viséan. However, these latter Viséan specimens are most probably atypical specimens of *Fourstonella* (see the distinctive criteria of Vachard et al., 1989b: text-figure 3). Anyway, they differ from the type species *Efluegelia johnsoni* which is principally present and abundant in the Early Permian beds; i.e., long time after the LAD of the true *Fourstonella* in the Moscovian (Kabanov et al., 2006, plate 1, figure 9). This replacement occurs in identical microfacies and paleoecologic conditions. Hence, *Fourstonella* and *Efluegelia* are interpreted as two different genera, even if, of course, *Fourstonella* is the direct ancestor of *Efluegelia*.

Occurrence. Late Viséan–Late Permian with an acme in the Late Pennsylvanian and Early Permian; cosmopolitan.

Efluegelia johnsoni (Flügel, 1966) emend. Vachard in Massa and Vachard, 1979

Figure 29.10–11, Figure 30.3–4, 30.6–7

- *1966 *Cuneiphycus johnsoni* Flügel, p. 17–19, pl. 2, figs. 1–5.
- 1968 *Cuneiphycus johnsoni*; Flügel p. 49, 55, 56 (no illustration).
- 1972 *Cuneiphycus johnsoni*; Homann, p. 167–169, pl. 2, fig. 12 (with five references).
- 1976 *Cuneiphycus johnsoni*; Emberger, p. 120 (bis) (no illustration; with six references).
- ?1978 *Cuneiphycus johnsoni*; Mamet and Roux, p. 83, pl. 7, figs. 11, 12 (probably another genus).
- ?1979 *Efluegelia johnsoni*; Flügel, p. 572 (no illustration).
- 1979 *Cuneiphycus johnsoni*; Zagorodnyuk, p. 12, pl. 3, fig. 5 (sic; in reality, fig. 6).
- v*1979 *Efluegelia johnsoni*; Massa and Vachard, p. 34.
- 1980 *Efluegelia johnsoni*; Flügel, pl. 7, fig. 6, pl. 9, fig. 1.
- 1980 *Efluegelia johnsoni*; Flügel and Flügel-Kahler, p. 163–164, pl. 8, figs. 9, 10 (with eight references in synonymy).

- v1980 *Efluegelia johnsoni*; Vachard, p. 396–397, pl. 5, fig. 2, pl. 23, fig. 8, pl. 25, fig. 1, pl. 27, figs. 1–5, 7, 8, pl. 34, fig. 9 (with 18 references in synonymy).
- vp1981 *Efluegelia johnsoni*; Vachard in Vachard and Montenat, p. 60, pl. 9, fig. 1, pl. 10, figs. 1–3, 5, 6, pl. 13, fig. 2 (non pl. 12, fig. 10 = *E. ex gr. johnsoni*).
- 1981 *Efluegelia johnsoni*; Ramovš and Kochansky-Devidé, p. 97–98, pl. 1, fig. 2.
- 1982 *Efluegelia johnsoni*; Milanović, p. 24–25, pl. 7, fig. 7, pl. 10, fig. 3.
- non 1982 *Cuneiphycus cf. johnsoni* (sic); Mu, p. 216, pl. 1, fig. 1 (= *E. ex gr. johnsoni*).
- 1983a *Cuneiphycus johnsoni*; Toomey, pl. 21, fig. 2.
- v1984 *Efluegelia johnsoni*; Fontaine and Vachard, p. 51 (no illustration).
- 1985 *Cuneiphycus johnsoni*; Mu, p. 144–145, pl. 14, fig. 5.
- 1987 *Cuneiphycus johnsoni*; Mamet et al., p. 55–56, pl. 28, figs. 5–10.
- v1989 *Efluegelia johnsoni* Flügel (sic, without parentheses and umlaut); Vachard in Fontaine and Gafoer, pl. 8, fig. 7.
- v1989b *Efluegelia johnsoni*; Vachard et al., p. 707–708, pl. 2, fig. 3 (with 15 references in synonymy).
- non 1993 *Eflügelia* (sic) *johnsoni*; Chuvashov et al., pl. 13, fig. 11 (another species).
- v1993b *Efluegelia johnsoni*; Vachard et al., pl. 2, figs. 6–8.
- 1995 *Efluegelia johnsoni*; Forke, p. 240, pl. 15, fig. 8.
- v.1998 *Efluegelia johnsoni*; Fontaine et al., p. 13 (no illustration).
- v2001a *Efluegelia johnsoni*; Vachard and Krainer, p. 151 (no illustration).
- v2001b *Efluegelia johnsoni*; Vachard and Krainer, pl. 3, fig. 12.
- v2003a *Efluegelia johnsoni*; Krainer et al., p. 18, 19, table 1 p. 18, pl. 3, figs. 9, 17, 37, pl. 5, figs. 20, 23–25, pl. 6, fig. 13, pl. 7, fig. 17.
- v2003b *Efluegelia johnsoni*; Krainer et al., pl. 60, fig. 6.
- 2004 *Fourstonella? johnsoni*; Mamet and Villa, tabl. 3 p. 157, p. 166–167, fig. 14f (with 28 references).
- 2004 *Efluegelia* Vachard; Flügel, pl. 56, fig. 5.
- ?2004 *Efluegelia johnsoni*; Cózar and Rodríguez, fig. 9.16 (most probably a broken *Fourstonella*).
- 2005 *Fourstonella? johnsoni*; Mamet and Zhu, fig. 5L.
- v2009 *Efluegelia johnsoni*; Krainer et al., p. 13, 15, pl. 3, fig. 10.

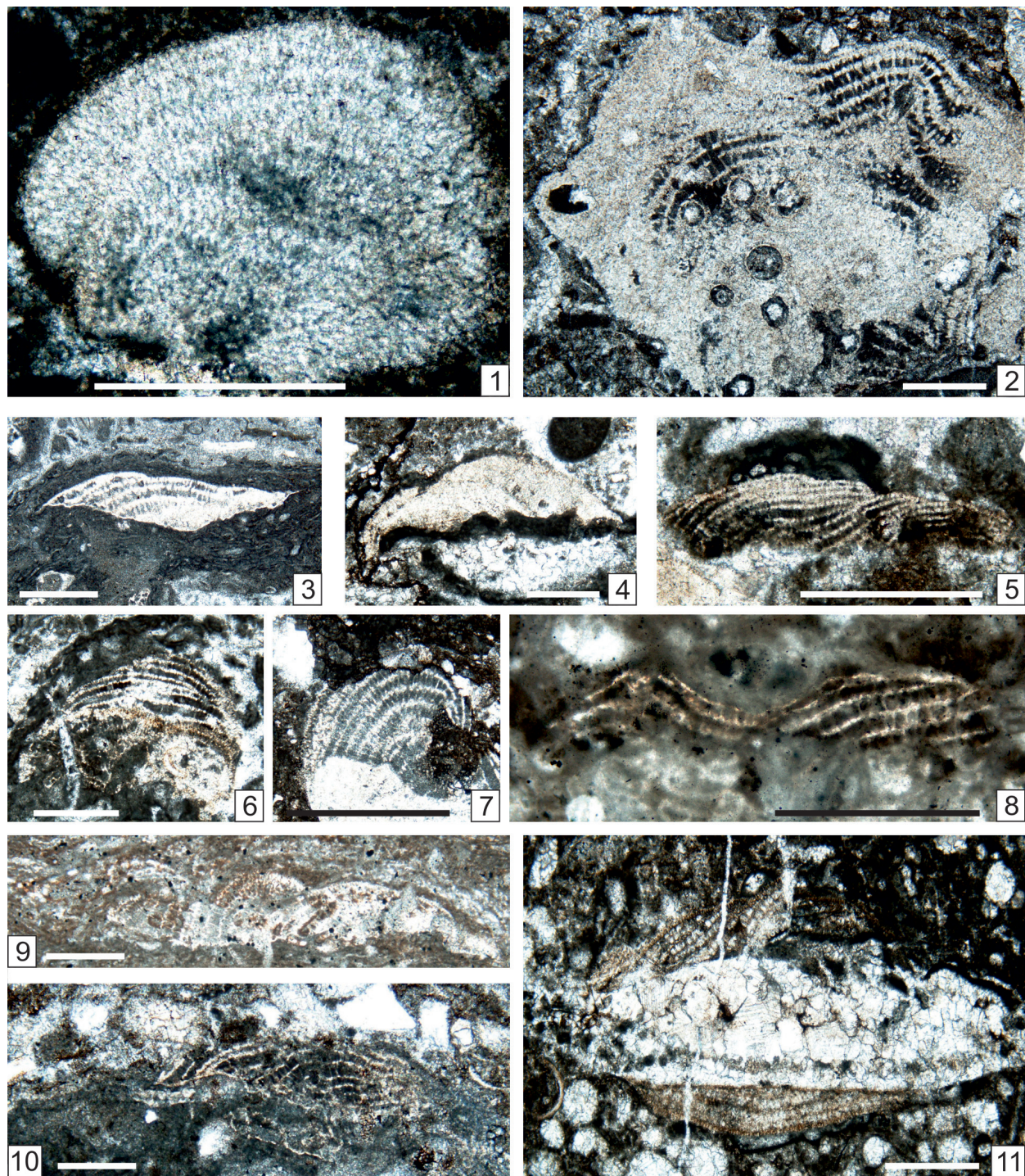


FIGURE 29. 1–9, 12. *Efluegelia* ex gr. *johnsoni* (Flügel, 1966). Various longitudinal and tangential sections. 1. Sample GB03_8. 2. Sample GB49_3. 3. Sample GB 56_2. 4. Sample GB_60_1_4. 5. Sample GB60_7a. 6. Sample GB60_4. 7. Sample GB68_6. 8. Sample TNB15_2_6. 9. Sample TK52_5. 12. Sample GB126_4. 10, 11. *Efluegelia johnsoni* (Flügel, 1966). 10. Sample GB109_4. 11. Sample GB117_1. Scale bars: Figures 29.6, 29.8 = 0.5 μ m, all others = 1 μ m.

- v2010 *Fourstonella* (= *Efluegelia*) *johnsoni*; Vachard and Cózar, p. 208, pl. 13, figs. 12, 16, 17, 20, 23, 27.
- 2010 *Fourstonella johnsoni*; Mamet and Préat, p. 22, pl. 6, figs. 7–14.
- v2012 *Efluegelia* sp.; Kolodka et al., p. 138 (no illustration).
- v2012 *Fourstonella*? (= *Efluegelia*) *johnsoni*; Vachard et al., p. 233, 235, 242–243, pl. 1, fig. 2, pl. 2, fig. 2.
- v2013 *Fourstonella* (= *Efluegelia*) *johnsoni*; Vachard et al., p. 5, 7 (no illustration).
- v2013 *Fourstonella* (= *Efluegelia*) *johnsoni*; Parvizi et al., p. 167, figs. 9d, 9g.
- vp2015 *Efluegelia johnsoni*; Krainer et al., fig. 16.2 (only non figs. 22.20, 23.12 = *E. ex gr. johnsoni*).
- v.2015 *Efluegelia johnsoni*; Lucas et al., figs. 12.14, 23.12.
- v2015 *Efluegelia johnsoni*; Angiolini et al., table 2a.
- v.2017a *Fourstonella* (*Efluegelia*) *johnsonii*; Krainer et al., p. 20, pl. 52, fig. 6.

Description. This taxon is well known in the USA (Toomey and Winland, 1973; Toomey, 1983a; Groves, 1983, 1986; Mamet et al., 1987; Krainer et al., 2003a, 2009; Vachard et al., 2012; Lucas et al., 2015). The dimensions of our specimens are consistent with Flügel's diagnosis: Length of remain = (420–600)–1,000–1,800 µm; width of remain = (100–175)–330–1,000 µm; intervals between pillars ("cell width") = 20–25 µm; intervals between laminae ("cell height") = 15–20 µm; thickness of pillars and laminae = 5–7 µm; number of laminae: up to 10.

Occurrence. As for the genus. In the Carnic Alps: Rattendorf Group and Trogkofel Formation (Flügel, 1968); Forni Avoltri Goggau; Tarviser Brekzie (Flügel, 1979, 1980; Flügel-Kahler, 1980; Vachard and Krainer, 2001b: ZKO10); this study: Zweikofel Fm (samples GB49_3; GB60_1_3; GB60_1_4; GB72_6; GB60_4; GB60_7a; GB109_4; ZK95a_7; ZK99c_11; ZK179_1); Zottachkopf Fm (sample TKW13B_4); and Trogkofel Fm (sample GBT1_2).

Efluegelia ex gr. johnsoni

Figure 27.10–12, Figure 29.1–9, Figure 30.1–2, 30.5, 30.8–11

- ?1974 *Cuneiphyucus johnsoni* Flügel; Chuvashov, p. 34, pl. 21, figs. 1–8.
- 1980 No legend; Flügel, pl. 9, fig. 1.
- vp1981 *Efluegelia johnsoni*; Vachard in Vachard and Montenat, p. 60, pl. 12, fig. 10 (only; non pl. 9, fig. 1, pl. 10, figs. 1–3, 5, 6, pl. 13, fig. 2 = *E. johnsoni*).

- 1982 *Cuneiphyucus cf. Johnsoni* (sic) E. Flügel; Mu, p. 216, pl. 1, fig. 1.
- 1985 *Cuneiphyucus cf. johnsoni*; Mu, p. 144–145, pl. 14, fig. 6.
- vp2015 *Efluegelia johnsoni*; Krainer et al., figs. 22.20, 23.12 (only; non fig. 16.2 = *E. johnsoni*).
- v2015 *Efluegelia johnsoni*; Lucas et al., figs. 12.14, 23.12.

Description. Thalli? encrusting flat or nearly flat objects. Numerous laminar layers of quadratic cells. L = 950–3,000 µm; H = 500–2,160 µm; inter-laminar height (= height of cells) = 30–100 µm; inter-pillar distance (= width of cells) = 20–60 µm; number of laminae: up to 20–25.

Comparison. *Efluegelia ex gr. johnsoni* differs from typical *E. johnsoni* by a higher number of laminae, and parameters that are all larger.

Occurrence. ?Asselian of the Urals (Chuvashov, 1974). Early Permian of South China (Mu, 1982, 1985) and Afghanistan (Vachard and Montenat, 1981). In the Carnic Alps (this study): uppermost Grenzland Fm (samples GB03_8; GB19_1b); Zweikofel Fm (samples GB49_3; GB56_2; GB_60_1_4. 5; GB60_7a; GB60_4; GB68_6; GB73_A; GB117_1; GB126_4; GB157_10; GB162_1; GB174_5; GB174_11); Zottachkopf Fm (samples TKW9_6; Z6_1; Z15_3; Z17B_1; ZK95_gross_3; ZK95a_7; ZK96_3; ZK187_5; ZK199. 11; ZK200_1; ZKa_5); basal Trogkofel Fm (sample GBT1_2); and Trogkofel Fm (samples TNB15.2.6; TK11_2_2; TK52_5).

CONCLUSIONS

- 1) A local, morphological classification of the cyanobacteria is attempted, from coccoid individuals to hemispherical colonies of bifurcated filaments, with the possible order: 1) coccoid thalli (incerti ordinis 1; probably Chroococcales); 2) filamentous and/or coccoid, stromatolitic and microbialitic taxa (incerti ordinis 2: stromatolites sensu lato); 3) carbonate stromatolitic textures (incerti ordinis 3; family Aphralysiaceae); 4) colonial coccoid? textures (incerti ordinis 4; family Chabakoviaceae); 5) tubular, single filaments (order Proauloporales or Oscillatoriales?; family Girvanellaceae); 6) colonial groups of filaments (order Proauloporales or Oscillatoriales; family Garwoodiaceae).
- 2) Some taxa are rare or not mentioned in the Lower Permian deposits: *Nostocites*, *Renalcis*, *Gahkumella*, *Mitcheldeania* and *Garwoodia*. Others are better known: *Archaeolithoporella*, *Girvanella*, and *Koivaella*.
- 3) The rare red algae are recrystallized *Parachaetetes* and *Archaeolithophyllum lamellosum*, that are probably reaching their LAD.

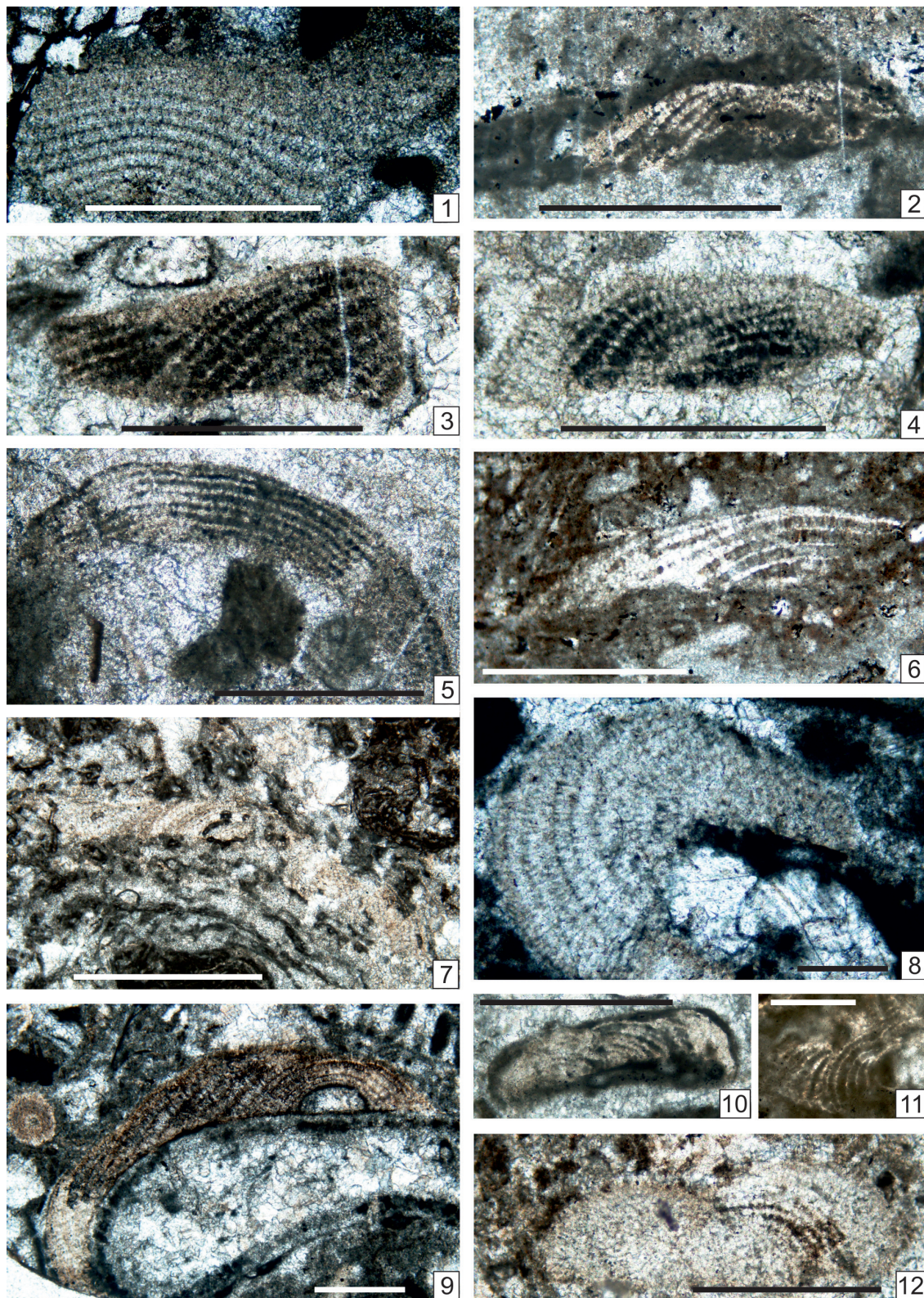


FIGURE 30. 1, 2, 5, 8–11. *Efluegelia* ex gr. *johnsoni* (Flügel, 1966). Various longitudinal and tangential sections 1. Sample GBT1_2. 2. Sample TKW9_6. 5. Sample ZK187_5. 8. Sample ZK95_gross_3. 9. Sample ZKa_5. 10. Sample ZK199. 11. Sample ZK200_1. 3, 4, 6, 7. *Efluegelia johnsoni* (Flügel, 1966). 3. Sample TKW138_4. 4. Sample Z6_1. 6. Sample Z15_3_4. 7. Sample GB174_5. Scale bars: Figures 30.8, 30.9, 30.10 = 0.2 μm , all others = 0.5 μm .

- 4) The descriptions of *Homannisiphon morikawai* are confirmed. This alga is not entirely endemic (it exists probably in Iran), but is rare outside of the Carnic Alps.
- 5) The phylloid algae are taxonomically revised. They constitute the family Anchicodiaceae emend. with the unique tribe Anchicodiae n. trib. (replacing Ivanoviae nom. vanum). The taxa of the Carnic Alps are: *Anchicodium japonicum*; *Ivanovia tenuissima*; *Eugonophyllum magnum*; *E.? konishi*; *Calcipatera schoenlaubi* n. sp., and *Neoanchicodium catenoides*. The other phylloid algae mentioned in the Carnic Alps were not re-found during this study.
- 6) The tribe Anthracoporellae n. trib. is described herein. *Anthracoporella* is discussed, with *A. spectabilis*, rare in our material, and *A. vicina* more common.
- 7) Other aspondyl dasycladales are rare *Macroporella* sp.
- 8) An accurate taxonomic revision of the epimastoporacean dasycladales is also undertaken in this paper. *Parapimastopora* is rare; *Epimastopora* is emended with *Epimastopora japonica* Endo subsequently designated as type species. Other "*Epimastopora*" are assigned to a new genus: *Epiastopora*, with *Epimastopora alpina* as type species. The type species of *Globuliferoporella* is re-designated with *E. piai*, because *G. symmetrica* originally designated as type species is actually a *Gyroporella*.
- 9) In contrast to the previous studies, the genus *Gyroporella* is rare in our material.
- 10) The genus *Pseudoepimastopora*, revised in relation to our studies of the epimastoporaceans, is revised and, unexpectedly is discovered to be the genus corresponding to the disputed "*Atractyliopsis*" *carnica* Flügel.
- 11) Some data are provided on the three species of *Mizzia*: *M. velebitana*, *M. yabei* and *M. cornuta*.
- 12) The unique complex dasycladale is *Connexia slovenica*, which corresponds exactly to the previous descriptions.
- 13) Among the Algospongia (incertae sedis algae), classical taxa have been found: *Claracrusta* ex gr. *catenoides*; *Ungdarella* ex gr. *uralica*; and *Efluegelia johnsoni*.

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