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New data on lower Permian rugose corals from the Southern Karavanke Mountains (Slovenia)

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KEY WORDS - Gregaria corals, Carinthiaphyllum*, Asselian-Sakmarian, Southern Alps.*

ABSTRACT - Studies of upper Palaeozoic corals from the Southern Alps (Karavanke Mountains in Slovenia and Carnic Alps along the Austrian/Italian border) started at the end of the 19th century. Since the mid-20th century, corals of the Karavanke Mountains have been studied in detail by several authors. Recently, several coral type localities and the coral groups occurring therein have been reinvestigated. This paper deals in particular with the study of Carinthiaphyllum *Heritsch, 1936 and all previously known data have been revised within this study. Most specimens of* Carinthiaphyllum *originate from museum collections and from new findings in the Dovžanova Soteska area of northern Slovenia. Additional material is represented by newly found samples from the locality of Mt. Boč in eastern Slovenia. The stratigraphic position and age of the* Carinthiaphyllum *occurrences are determined by fusulinid and conodont assemblages. Two species,* Carinthiaphyllum crasseseptatum *Gräf & Ramovš, 1965 and* C. ramovsi *n. sp., are described herein. New morphological features, including root-like protrusions and connecting stereoplasmic tubes, have been found for the first time in gregaria growth mode. Therefore, these new observations provide evidence of a solitary gregaria growth mode: individuals are invariably separated with contact and reciprocal support only by root-like, sometimes channeled tubes occurring as outgrowths of the archaeothecal wall. An emended diagnosis of* Carinthiaphyllum *is proposed herein. The studied collection is housed in the Museum für Naturkunde (Leibniz-Institut) at the Humboldt University in Berlin.*

INTRODUCTION

Studies of the upper Palaeozoic corals from the Southern Alps (Karavanke Mountains in Slovenia and Carnic Alps along the Austrian/Italian border) started at the end of the 19th century. The lower Permian rugose corals in particular are widespread in different parts of the Southern Karavanke Mountains. They also occur in southern Slovenia, near the town of Ortnek, which belongs to the External Dinarides (Fig. 1). Schellwien (1898a) mentioned three species found in upper Palaeozoic rocks in Dovžanova Soteska gorge (Devil's gorge, Teufelsschlucht in German language literature), Southern Karavanke Mts: *Caninia* aff. *kokscharowi* Stuckenberg, 1895, *Diphyphyllum* sp., and *Cyathaxonella* sp. Since the mid-20th century, corals of the Karavanke Mountains have been studied by several authors. In an historical overview, Heritsch (1933, p. 43) wrote (our translation from Slovenian): "Corals from the Trogkofel Limestone have never been described so far." To fill this gap, he described seven species from Dovžanova Soteska: *Sinophyllum pendulum* Grabau, 1928, *Lopholasma ilitschense* Soshkina, 1928, *Amplexocarinia geyeri* Heritsch, 1933, *Tachylasma aster* Grabau, 1922, *Caninophyllum gortanii* Heritsch, 1933, *Palaeosmilia hammeri* Heritsch, 1933, and *Lonsdaleia yokoyamai* Heritsch, 1933. Later the list of species was supplemented by *Carinthiaphyllum suessi* Heritsch, 1936. Summarizing previous works on Slovenian corals, Gräf & Ramovš (1965) reported twelve species of late Carboniferous to middle Permian age. Some species are identical with taxa described in 1936 by Heritsch from the Carnic Alps, namely: *Amandophyllum carnicum* (Heritsch, 1936), *A. ruedemanni* Heritsch, 1936, *A. smithi* Heritsch, 1936, *Carinthiaphyllum* cf. *suessi*, and *Wentzelophyllum*? *stillei* (Heritsch, 1936). The others were considered similar to Uralian faunas, i.e., *Amplexocarinia irginae* Soshkina, 1928, and *Ufimia exceptata* (Soshkina, 1928). The age of these species was determined as early Permian. From the Vitanje Hills in the eastern part of the Southern Karavanke Mts, Ramovš & Schouppé (1961) reported four species, namely: *Lophophyllidium minimum* (Heritsch, 1936), *Amplexocarinia heimoi* Heritsch, 1936, *Amandophyllum carnicum* (Heritsch, 1936), and *Gshelia* cf. *calophylloides* (Holtedahl, 1913). Recently, small ahermatypic, non-dissepimental corals of the new genus *Sloveniaxon* Kossovaya, Novak & Weyer, 2012 were described from the middle Asselian, uppermost level of the Dovžanova Soteska Formation (Kossovaya et al., 2012), and the large-sized "caninioid" *Preisingerella stegovnikensis* Kossovaya, Novak & Weyer, 2016 from the slope facies of the Asselian-Sakmarian Born Formation in the Stegovnik section (Southern Karavanke Mts) (Kossovaya et al., 2016, fig. 1).

The present revision of the *Carinthiaphyllum* fauna of the Karavanke Mts reveals three species, namely: *C. crasseseptatum* Gräf & Ramovš, 1965, *C. suessi*, and *C. ramovsi* n. sp. All coral localities under consideration, except for Ortnek, are in the Southern Karavanke Mts that belong to the Southern Alps.

The collection of *Carinthiaphyllum* specimens originates from the old samples and new findings in Dovžanova Soteska 3.5 km NNE of the town of Tržič in northern Slovenia. The parallel determination of fusulinid index-fossils is used for precise determination of ages of the main *Carinthiaphyllum* occurrences. A second collection is represented by samples from Mt. Boč

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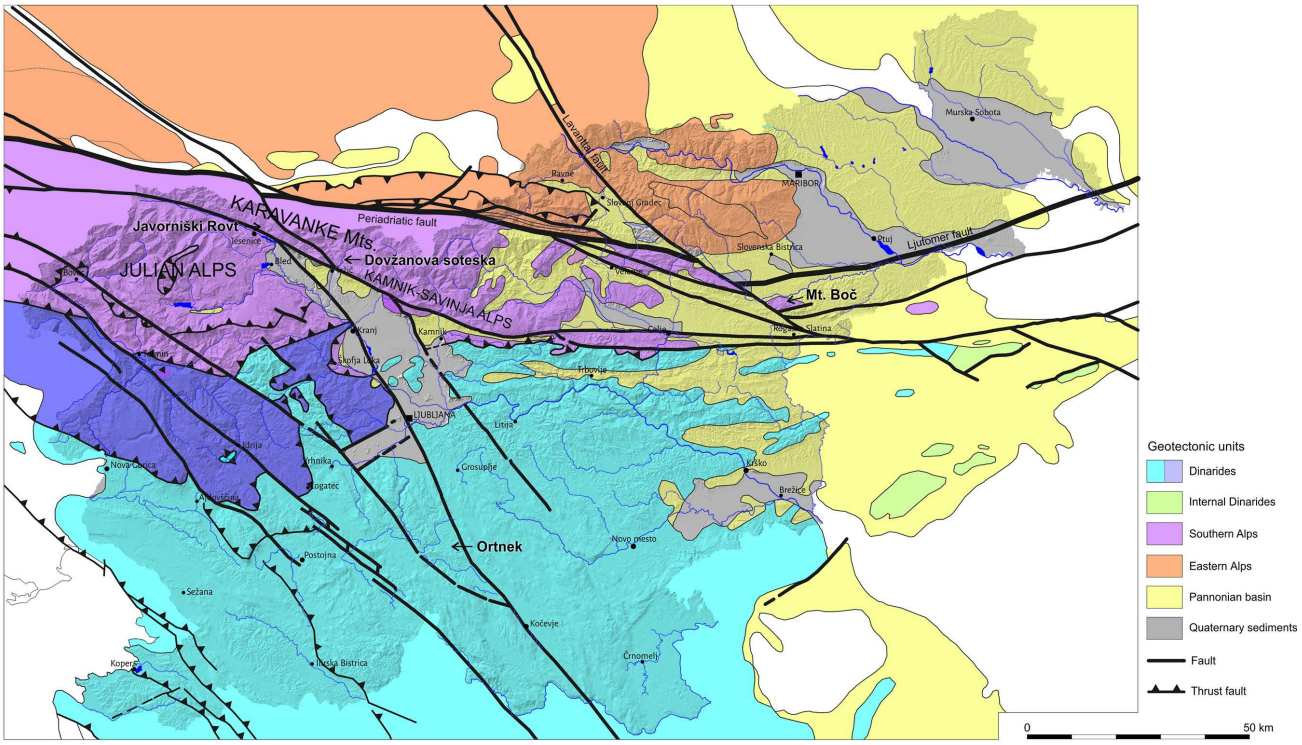


Fig. 1 - (color online) Geotectonic map of Slovenian territory (according to Placer, 2008) with lower Permian coral localities.

(Wotsch-Berg in German language literature) NNW of the town of Rogaška Slatina in eastern Slovenia (Fig. 1).

GEOLOGICAL AND STRATIGRAPHICAL SETTING

Slovenia is located at the junction of the Eastern Alps, Southern Alps, Dinarids, and the Pannonian Basin. The rocks of these geotectonic units belong to the Adriatic Lithospheric Microplate, which detached from the African Plate during the Mesozoic and collided with the Eurasian Plate during the Alpine Orogeny in Neogene times. The Southern Alps in Slovenia are represented by the Southern Karavanke Mts, which are the eastern prolongation of the Carnic Alps (Austria/Italy), where many corals have been described by Heritsch (1936) (Fig. 1).

Comprehensive summaries of the upper Palaeozoic lithostratigraphic units of the post-Variscan sequence are available in several publications (e.g., Venturini, 2006; Schönlaub & Forke, 2007; Novak & Skaberne, 2009; Schönlaub, 2014; Novak et al., 2019). With respect to previous publications on the lower Permian corals in Slovenia, it is important to note that for decades all coral-bearing limestones have been regarded to represent the Trogkofel Limestone of the Carnic Alps (Heritsch, 1938). This is the case with all localities: Dovžanova Soteska, Mt. Boč, and Ortnek. Recently found conodonts *Streptognathodus bellus* Chernykh & Ritter, 1997, *S.* aff. *nodulinearis* Reshetkova & Chernykh, 1986, *S.* aff. *isolatus* Chernykh, Ritter & Wardlaw, 1997, *Hindeodus minutus* (Ellison, 1941), and *Diplognathodus* together with the fusulinid species *Dutkevitchia complicata* (Schellwien, 1898b), *Rugosofusulina latispiralis* Forke, 2002, *Pseudoschwagerina* aff. *uddeni* (Beede & Kniker, 1924) in the Dovžanova Soteska gorge indicate an early to middle Asselian age for the Dovžanova Soteska Formation limestones (Buser & Forke, 1996; Forke, 2002; Novak, 2007). The overlying Born Formation has been first assigned by Kahler & Kahler (1937), Heritsch (1941), and Ramovš (1956) to the Upper *Pseudoschwagerina* Limestone (former name of the Zweikofel Formation) of the Carnic Alps, based on lithological similarities and the lower Permian fusulinids. The detailed mapping showed that this unit overlies the Dovžanova Soteska Limestone, which at that time was regarded as the Trogkofel Limestone and that therefore cannot be older. The problem has been solved by Buser (1974, 1980) with application of the concept of Clastic Trogkofel Beds with reworked fusulinid fauna, introduced by Ramovš (1968), as a lateral development of the Trogkofel Limestone. This concept proved to be misleading in all re-studied sections in the Karavanke Mts (Forke, 2002; Novak & Forke, 2005). The fusulinid assemblage of *Sphaeroschwagerina carniolica* (Kahler & Kahler, 1937), *Rugosofusulina* cf. *likana* Kochansky-Devidé, 1959, *Paraschwagerina mukhamedjarovica* Rauzer-Chernousova, 1949, and *Darvasites eocontractus* Leven & Scherbovich, 1980 indicates a late Asselian-Sakmarian age. Both formations probably represent a time-equivalent to predominantly clastic and fossil-barren beds of the Grenzland Formation in the Carnic Alps (Forke, 2002) (Fig. 2). Fusulinid assemblages of the Dovžanova Soteska and Born formations correspond to faunas of the *Sphaeroschwagerina moelleri-Schwagerina fecunda* fusulinid Zone and to the lower part of the *Sphaeroschwagerina sphaerica-Schwagerina firma* fusulinid Zone, which represent the middle and late Asselian age in the Southern Urals.

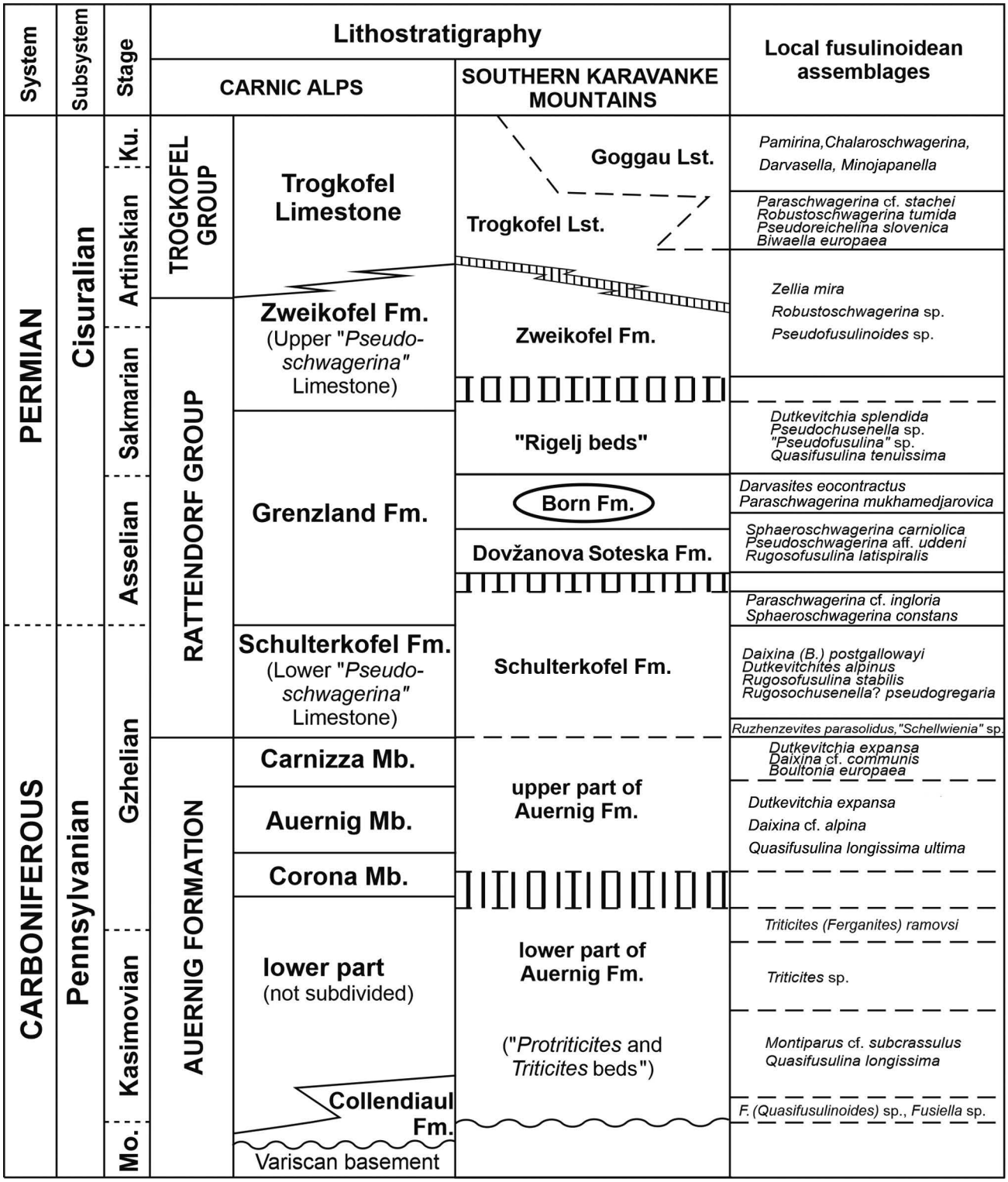


Fig. 2 - Pennsylvanian-lower Permian lithostratigraphic units in the Southern Karavanke Mts with local fusulinoidean assemblages and correlation with the Carnic Alps. All Slovenian corals discussed in this paper belong to the marked Born Formation. Mo., Moscovian; Ku., Kungurian.

Dovžanova Soteska section

Dovžanova Soteska (Devil's gorge) is known as a fossil-rich upper Carboniferous to lower Permian classical locality since Schellwien (1898a, b, 1900). Two levels with corals were recently studied at Dovžanova Soteska (Figs 3-5). The first level occurs in the uppermost part of the Dovžanova Soteska Formation within an 80 cm thick horizon of thin-bedded brownish-grey calcareous siltstone and marly limestone. They were deposited in the deepening phase of a reef facies formation (Novak, 2007). This deep water and slope facies is rich in small, non-dissepimental ahermatypic corals of *Sloveniaxon*

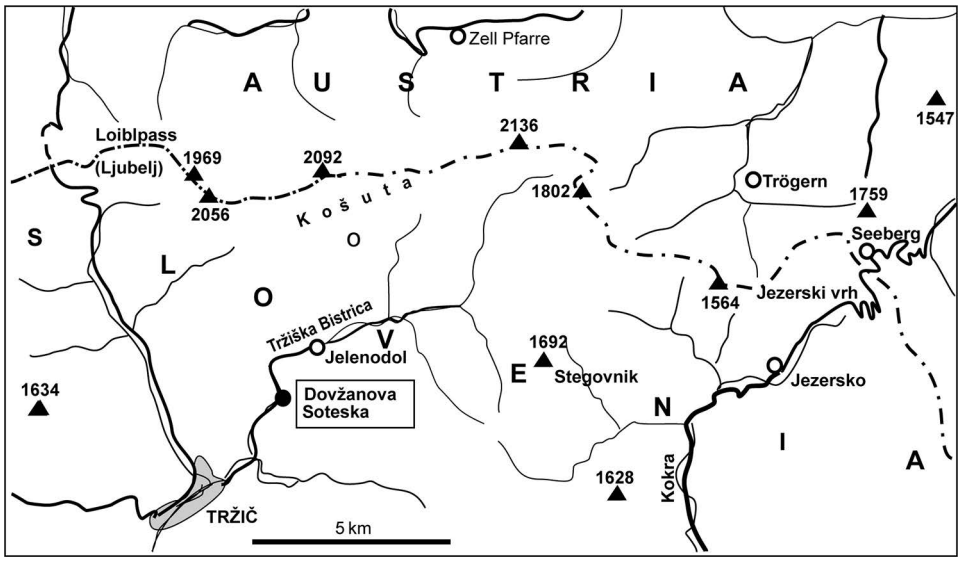


Fig. 3 - Locality map of Dovžanova Soteska gorge.

Kossovaya, Novak & Weyer, 2012. The early-middle Asselian age of the Dovžanova Soteska Formation is established by conodonts (Buser & Forke, 1996) and by the fusulinid assemblage of the *Pseudoschwagerina* aff. *uddeni-Rugosofusulina latispiralis* Zone (Forke, 2002; Novak, 2007).

The second horizon with corals occurs in the middle part of the overlying Born Formation, represented predominantly by dark-grey bedded limestones deposited in the open-marine inner platform. Corals occur in a patch reef facies on top of one of the rocky pyramids. It is built of massive, light grey boundstone, mostly composed of bioclasts (crinoid fragments and echinoid spines, bryozoans, fusulinid and smaller foraminifera), bound by *Tubiphytes* in partly dolomitized dismicritic matrix (Fig. 6a-b). It includes accumulations of "gregaria" corals, assigned here to *C. crasseseptatum* Gräf & Ramovš, 1965, and some small massive colonies.

Mt. Boč occurrence

The second new collection came from Mt. Boč, the tectonically dislocated part of the Southern Karavanke Mts north of Rogaška Slatina in eastern Slovenia. Along Labot (Lavanttal) and Donat faults, Boč and Plešivec massifs represent eastern prolongations of the Southern Karavanke geotectonic unit. Southeastern Karavanke shear zone is displaced along the dextral Labot (Lavanttal) fault for 10-18 km (Fodor et al., 1998; Vrabec & Fodor, 2006; Placer, 2008). One hundred to two hundred meters wide and several hundred meters long lenses of Permian-Mesozoic carbonates are incorporated within the shear zone and can be interpreted as strike-slip duplexes (Márton et al., 2002). The upper Palaeozoic rocks occur on the northern and southern slopes of the Boč anticline and as isolated elongate, strongly deformed tectonic lenses in the core of the Donat fault zone north of the town of Rogaška Slatina and eastwards to Žetale (Ramovš, 1959) (Fig. 5).

The lower Permian light-grey, thick-bedded to massive bioclastic limestone (wackestone to boundstone) (Fig. 6c-d) is only exposed in bands or scattered outcrops as a result of strong overprint by the Alpine tectonics and thick cover of weathering residue. Therefore, no lithostratigraphic succession can be traced in this area. The fusulinid assemblage is similar to that in the Born Formation in the stratotype section in the Dovžanova Soteska gorge, indicating the same age of the unit at Boč.

OCCURRENCES OF *CARINTHIAPHYLLUM* SPECIES IN SLOVENIA

Some specimens found in the Dovžanova Soteska gorge by previous investigations were considered as *Carinthiaphyllum kahleri* Heritsch, 1936 (Holzer & Ramovš, 1979). According to the primary description of Heritsch (1936), who studied the collection from the Carnic Alps, the maximum diameter in this species is 12.5 mm with 23 major septa (Tab. 1). In the specimens from Dovžanova Soteska described by Holzer & Ramovš (1979) the maximum diameter is 10 mm. The figure 1 in plate 2 of Holzer & Ramovš (1979) shows a trabecular septal microstructure and a specific thickening of the peripheral part of septa similar to "naotic" structures. Some septa come to the thick pseudocolumella (morphological term of Milne-Edwards & Haime, 1848, p. 78, revised by Berkowski & Weyer, 2012, p. 246). Corals assigned to *Carinthiaphyllum kahleri* by Holzer & Ramovš (1979) differ from the type specimens (Heritsch, 1936) by a lack of lonsdaleioid dissepiments, smaller diameter and reduced number of septa (Fig. 7).

Carinthiaphyllum suessi was described at first from Dovžanova Soteska. The main morphological features are the wide diameter (19-20 mm) and the high number of septa (27 × 2) (Heritsch, 1936) (Fig. 7). Specimens determined in open nomenclature as *C.* cf. *suessi* were found at Javorniški Rovt (Gräf & Ramovš, 1965). A comparison with the holotype of *C. suessi* showed that specimens of Gräf & Ramovš have a smaller diameter and a higher number of septa (11 mm-62 septa). The pseudocolumella in the calice is similar to that of the new species, described herein (Gräf & Ramovš, 1965, pl. 6,

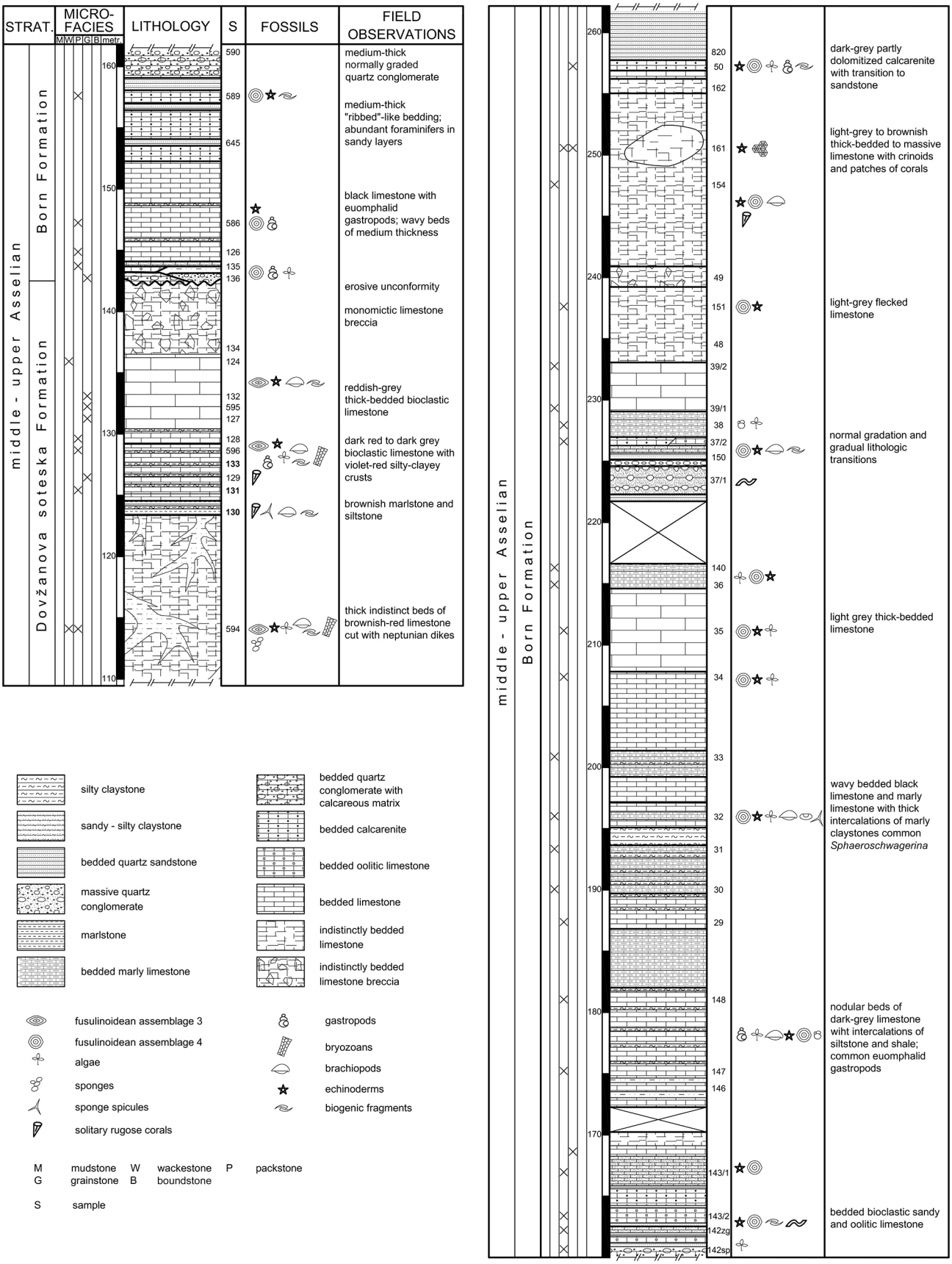


Fig. 4 - Lithostratigraphic section of Dovžanova Soteska gorge with two coral horizons.

fig. 2). Another occurrence was mentioned from Mt. Boč (Heritsch, 1941).

Carinthiaphyllum crasseseptatum Gräf & Ramovš, 1965 was found in an isolated limestone block at the

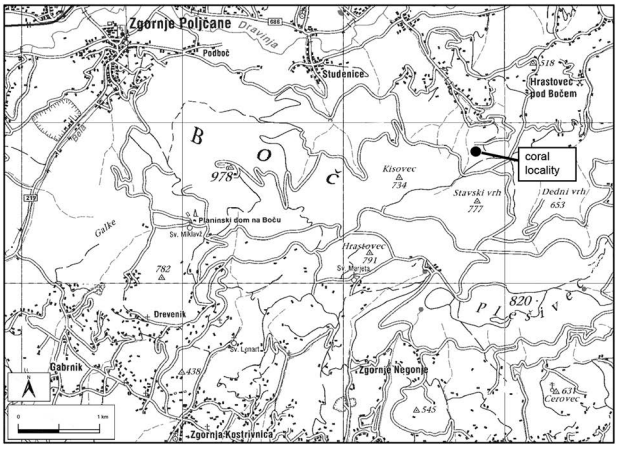


Fig. 5 - Locality map of Mt. Boč coral occurrence.

Ortnek locality. A few more typical morphological features are: a pseudocolumella of various thickness and structure with developed radial lamellae, numerous septa (27 + 27) at a diameter of 9 mm. Several major septa join the pseudocolumella (Fig. 7).

Thus, according to the reinvestigation of published and new collections, three species are established in the Karavanke Mountains. In addition to all already mentioned species, the association in the Carnic Alps includes two more species: *Carinthiaphyllum kahleri* Heritsch, 1936 and *Carinthiaphyllum carnicum* Heritsch, 1936 (Heritsch, 1941; Homann, 1971). *Carinthiaphyllum suessi* was also found in Greece (Schouppé, 1961).

TAXONOMIC REMARKS

The higher taxonomical position of the genus has changed since the first reference to Clisiophyllidae Nicholson, 1889 (in Nicholson & Lydekker, 1889) by Heritsch (1936), at first to Neockoninckophyllidae Fomichev, 1953 (Fomichev, 1953), and now to Geyerophyllidae Minato, 1955 (Minato, 1955; Minato & Kato, 1967, 1975; Cocke, 1970; Hill, 1981; Rodriguez, 1985; Rodriguez & Bamber, 2012). A few main features such as clinotabulae and connection of pseudocolumella with cardinal septum are typical for the genera included in this family. The detailed study of young stages was demonstrated for *Geyerophyllum* Heritsch, 1936 (Cocke & Cocke, 1968), *Darwasophyllum* Pyzhyanov, 1964, *Carinthiaphyllum* (Minato & Kato, 1967 and herein), and for *Amygdalophylloides* Dobrolyubova & Kabakovich, 1948. Most of the genera included in this family have a solitary growth mode, and some demonstrated gregaria

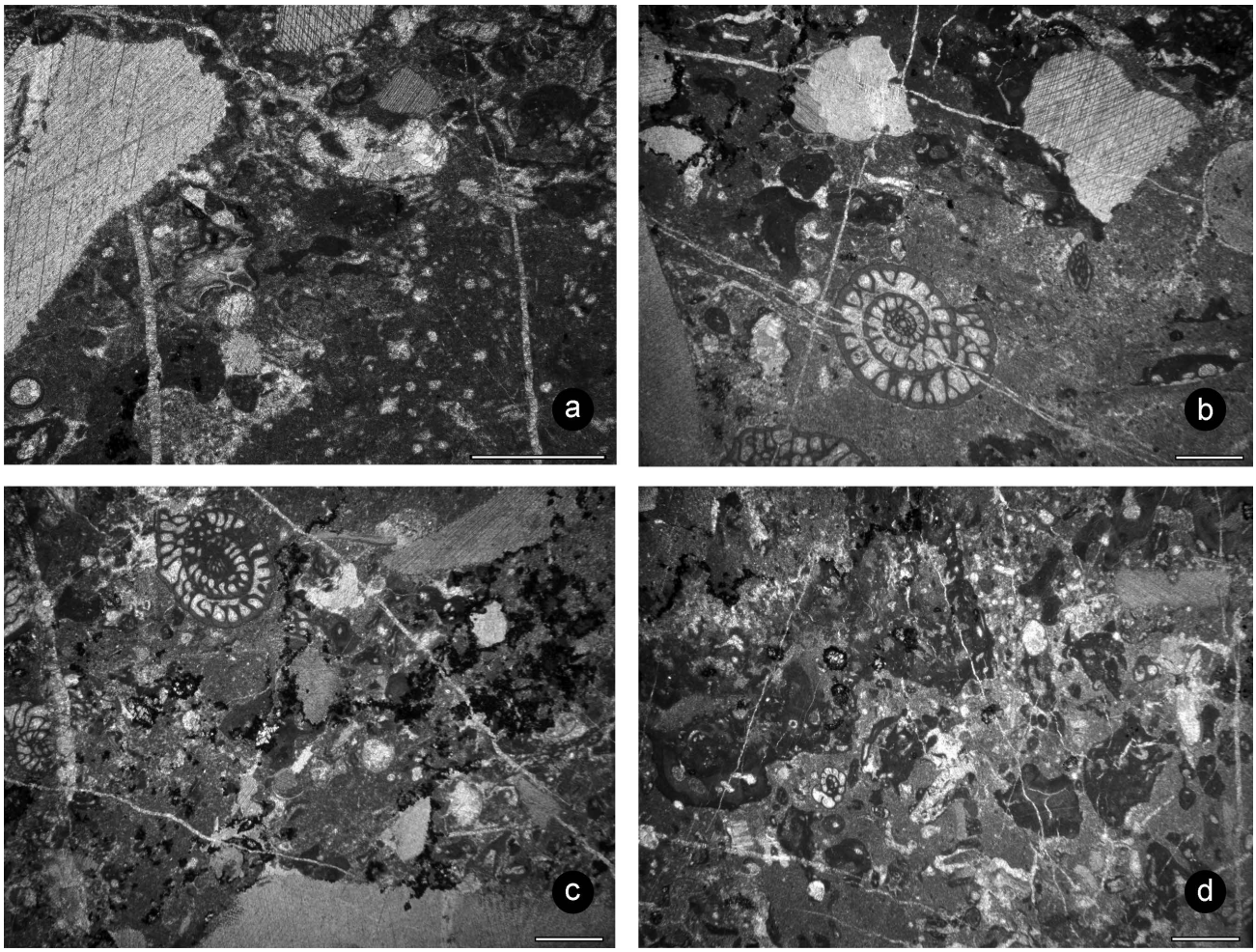


Fig. 6 - Microfacies types of coral-bearing limestones within Born Formation from Dovžanova Soteska (a-b) and from Mt. Boč (c-d). Scale bars = 1 mm.

Locality	Co-occurring species	Age
Dovžanova Soteska	*Carinthiaphyllum crasseseptatum* Gräf & Ramovš, 1965 new collection, *Carinthiaphyllum suessi* Heritsch, 1936	upper Asselian
Mt. Boč	*Carinthiaphyllum ramovsi* n. sp. new collection, *C. suessi* Heritsch (1941)	upper Asselian
Javorniški Rovt	*Carinthiaphyllum ramovsi* n. sp. (re-definition of *C.* cf. *suessi* Heritsch, illustrated in Gräf & Ramovš, 1965)	upper Asselian - lower Sakmarian
Ortnek	*Carinthiaphyllum crasseseptatum* Gräf & Ramovš, 1965	upper Asselian-Sakmarian

Tab. 1 - Stratigraphic distribution and occurrences of *Carinthiaphyllum* species in Slovenia.

growth, for example *Darwasophyllum* Pyzhyanov, 1964 (Rodriguez & Bamber, 2012). Cocke (1970) accepted a double growth mode (both solitary and colonial) for *Geyerophyllum* Heritsch, 1936, depending on different environmental conditions. Interpretation of the growth mode of *Carinthiaphyllum* changed a few times from solitary (Heritsch, 1936), to fasciculate (Minato & Kato, 1967; Rodriguez, 1985), fasciculate or solitary (Hill, 1981), fasciculate or solitary/gregaria (Rodriguez & Bamber, 2012). The first to proclaim a gregaria growth mode for *Carinthiaphyllum* was Fedorowski (1980); he showed the *Carinthiaphyllum* corals growing one on another. Accumulations of corals in transverse sections give an impression similar to fasciculate colony (Fedorowski, 1980, pl. 26, fig. 2); he and other authors estimated the gregaria growth mode as of generic value.

The growth mode of *Carinthiaphyllum yezoense* Minato & Rowett, 1967 from the Lower Pennsylvanian of Hokkaido is unclear; in spite of lack of budding, it was considered as a fasciculate colony. The species has many morphological differences from the type species and is to be referred to *Carinthiaphyllum* with question. Distant co-occurrences of "corallites" and their probable parallel growth is considered as fasciculate growth mode and hypothesized as a case of asexual reproduction (Minato & Rowett, 1967a, b).

The new material of *Carinthiaphyllum* from the Karavanke Mountains demonstrates the distinct gregaria growth mode (see later) for the genus with some additional morphological features.

DESCRIPTION OF SPECIES

Family Geyerophyllidae Minato, 1955

Genus *Carinthiaphyllum* Heritsch, 1936
Type species *Carinthiaphyllum kahleri* Heritsch, 1936.

Species included - *Carinthiaphyllum kahleri* Heritsch, 1936 (Carnic Alps, lower Permian, Homann, 1971), *C. carnicum* Heritsch, 1936 (lower Permian, Carnic Alps, Minato & Kato, 1967; Homann, 1971), *C. suessi* (Karavanke Mts, lower Permian, Heritsch, 1941; Greece, Schouppé, 1961), *C. crasseseptatum* Gräf & Ramovš, 1965 (Karavanke Mts, lower Permian), *C. ramovsi* n. sp. (Karavanke Mts, lower Permian), *C.* sp. (Texas, USA, lower Permian, Fedorowski, 1980), *C. heritschi* Pyzhyanov, 1966 (Zaalai Range, Kyzyl Su River, Tadzhikistan, lower Permian), *C. maklayi* Pyzhyanov, 1966 (Darvaz Range, Obi-Hungou River, Tadzhikistan, lower Permian), *C.*? *elegans* Wu & Zhao, 1989 (Weining Formation, Lower Pennsylvanian), *C.*? sp. (Fomichev, 1953, Donets Basin, upper Gzhelian), *C.*? *exquisitum* Wu & Zhao, 1974 (Bashkirian, China), *C.*? *yezoense* Minato & Rowett, 1967 (Moscovian, Japan), *C. bayanbulagense* Guo, 1983 (Pennsylvanian, China), *C. subdenroides* Guo, 1983 (Pennsylvanian, China), *C. xiangchengense* Wu & Zhang, 1985 (Carboniferous, China), *C. provectum* Yu Xueguang, 1991 (Carboniferous, China), *C. eostrotionideum*

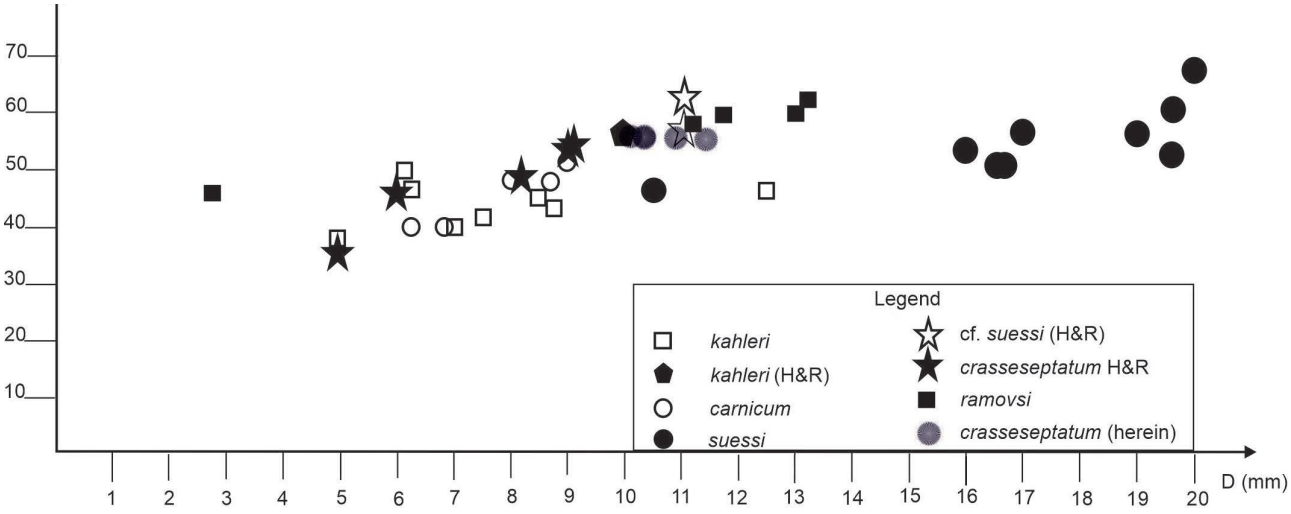


Fig. 7 - Correlation between septal number and diameter for *Carinthiaphyllum* found in the Mediterranean Province: *C. kahleri*, *C. carnicum*, *C. suessi*, *C. crasseseptatum*, *C. ramovsi*. (H & R): measurements were done from the publication of Holzer & Ramovz (1979).

Zhu & Zhao, 1992 (uppermost Carboniferous - lowermost Permian, China), *C. igoi* Niikawa, 1981 (Moscovian, Japan).

Non *Carinthiaphyllum multicystatum* Kossovaya, 1986 (upper Kasimovian-Gzhelian, Samarskaya Luka, Russian Platform). In the opinion of one of the authors (Kossovaya) this species belongs to *Geyeronaotia* Rodriguez, 1984.

Discussion - The original diagnosis of Heritsch (1936) included: 1) the columella (continuation of counter septum) with a thin, mostly irregularly curved median plate. Surrounded cuts of thin plates followed orientation of septa, but they are never connected with them. Isolated tangential cuts are interpreted as tabellae. The columella is thickened by stereoplasm attached to the plates (=radial lamellae), giving the impression of a lophophylloid columella; 2) the middle region of septa may be free of dissepiments, or these reach up to the ends of major septa. Sections near to the calice show a free space between columella and the septal ends; 3) the peripheral zone has compact dissepiments in several rows. Sometimes locally at the margin there are big tangential vesicles (lonsdaleioid dissepiments), which are never constantly developed.

The connection of the pseudocolumella to the cardinal septum was mentioned by Fomichev (1953, p. 399). A further diagnosis of the genus *Carinthiaphyllum* was proposed by Pyzhyanov (1966), before the clinotabulae were accepted as a diagnostic feature of the genus (Minato & Kato, 1967). His main ideas can be summarized as follows: solitary corals with three-zonal structure. The central zone is occupied by a thick pseudocolumella connected at young stages with cardinal and counter septa and later with cardinal only. The pseudocolumella consists of central and radial lamellae. The inner part of the tabularium is occupied by split tabulae inclined to columella (= clinotabulae). Just near the columella, tabulae can be graded or sometimes rise to pseudocolumella. At the periphery of the coral, there are a few rows of interseptal dissepiments. The inner wall is rare and thin.

Minato & Kato (1967) re-described *Carinthiaphyllum carnicum* Heritsch, 1936 (based on the Heritsch collection, housed at the University of Graz, Austria, and on their own small collection from the type region), and proposed the main changes in the diagnosis of *Carinthiaphyllum*. The first detailed study of the early stages demonstrated the connection of the pseudocolumella with the cardinal septum, not with the counter septum. The generic diagnosis by Minato & Kato (1967, p. 11) is as follows: "Fasciculate corals with a long cardinal septum, the axial end of which usually is expanded to form a prominent, solid columella in neanic to ephebic stages. The columella may be, however, somewhat modified to form an axial structure with a median plate, a few septal lamellae, and some irregular axial tabellae-like structures in the latest ontogenetic stage. Septa are of two orders, pinnately arranged, especially in the early ontogenetic stage, but tend to show more or less radial symmetry in the mature stage. The fine structure of septa is fibro-normal to diffuso-trabecular. Dissepiments are concentrically disposed between septa in transverse sections. Lonsdaleoid dissepiments occur only rarely in late stages. Tabulae are mostly inclined axially and include steeply or gently inclined clinotabulae." The presence of clinotabulae was also mentioned for the first time.

The most disputable feature considered in this diagnosis is the fasciculate mode of coral growth. In the first description of Heritsch (1936) the growth form was interpreted as solitary. The controversy started with Minato & Kato (1967, 1975), who declared that the close position of "corallites" in spite of lack of visible budding can be considered as proof of a fasciculate colony.

Microstructure - The morphological term trabicula was revised by Weyer (2014, p. 116) selecting for Rugosa as "morpho-terminological type" the species *Palaeocyclus porpita* (Linné, 1767), going back to the original spelling of Milne-Edwards & Haime (1848: trabiculina; 1850: trabicula). The version "trabecula" was introduced by Pratz (1882, without any discussion on this change in spelling), and later he was often cited (incorrectly) as the author of the term. In the Latin language, both variants are correct: trabicula and trabecula as diminutive of "traps, trapis".

The morphological term diffuso-trabecular (in German: "diffus-trabekulär") was proposed by Schindewolf (1942, p. 25), mentioning and illustrating only Scleractinia as examples. It is unclear if these are real trabicular spines (minitrabiculae sensu Roniewicz, 1984) or half-moon shaped growth segments (German "Stirnzonen": Schouppé & Stacul, 1955, 1959, revised in Weyer, 2014 as typical lamellar = fibronormal septal microstructure).

There are quite a few publications recording a diffuso-trabecular microstructure, e.g., in such unrelated genera as *Euryphyllum* (Kato, 1976), *Carcinophyllum* (Niikawa, 1979), *Yamatophyllum* (Ezaki & Kato, 2014). In spite of differences in the septal microstructure of all these genera, there is a row of trabiculae.

According to Holzer & Ramovš (1979, p. 7), the septal microstructure of "*Carinthiaphyllum kahleri* Heritsch, 1936" (= *C. suessi* in our identification) is a trabicular construction with lateral lamellar stereoplasmic thickening (terminology of Schouppé & Stacul, 1962, fig. 3). The microstructure in mature stages of our studied species of *Carinthiaphyllum* shows several rows of trabiculae, clearly visible in the peripheral zone near the archaeothecal wall - corresponding to the term multitrabicular (as "multitrabecular") of Kato (1963). This term is better defined than "diffusotrabicular". Weyer (1981, 1984) called the multi-spinous septal margins at the uppermost calicular rim (with broad septal sockets) multitrabicular, changing deeper in the calice to a coarse monacanth microstructure typical for Neaxoninae Hill, 1981 = Petraiidae Koninck, 1872.

Revised diagnosis - After our present revision, the main features of *Carinthiaphyllum* Heritsch are: solitary or gregaria growth mode, pseudocolumella connected with the cardinal septum, pseudocolumella of compact structure or with well-developed axial lamellae, trabicular/multitrabicular septal microstructure of septa, sometimes lonsdaleioid dissepiments or "naotic structure" of septa at periphery of the calice. Clinotabulae present.

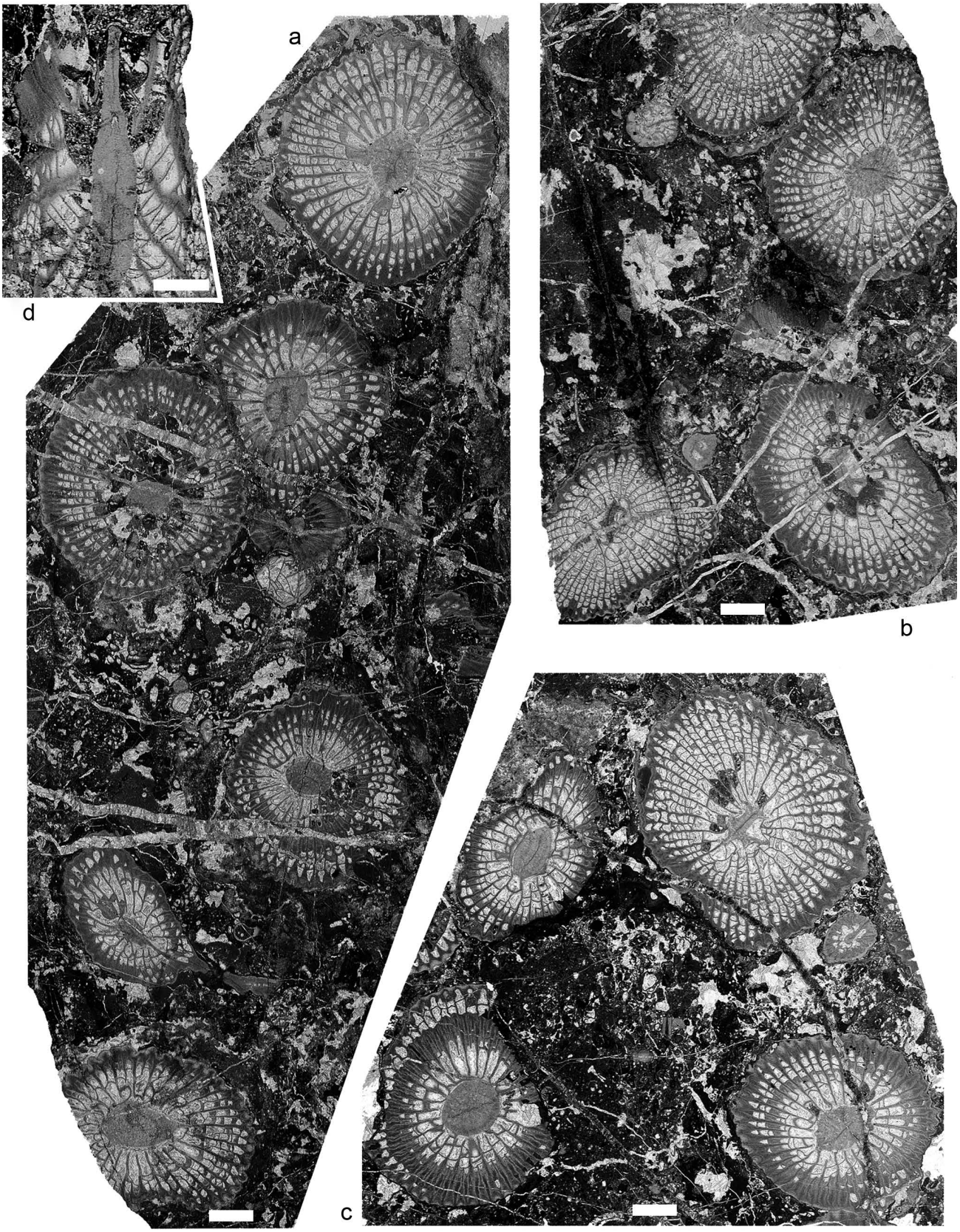


Fig. 8 - *Carinthiaphyllum crasseseptatum* Gräf & Ramovš, 1965, upper Asselian (middle Born Formation), locality Dovžanova Soteska NNE of Tržič. a-c) Transverse sections of gregaria, nrs MB.K.8073.-1., 8072.-3., 8071.-3. d) Longitudinal section, nr. MB.K.8074.-2. All scale bars = 2 mm.

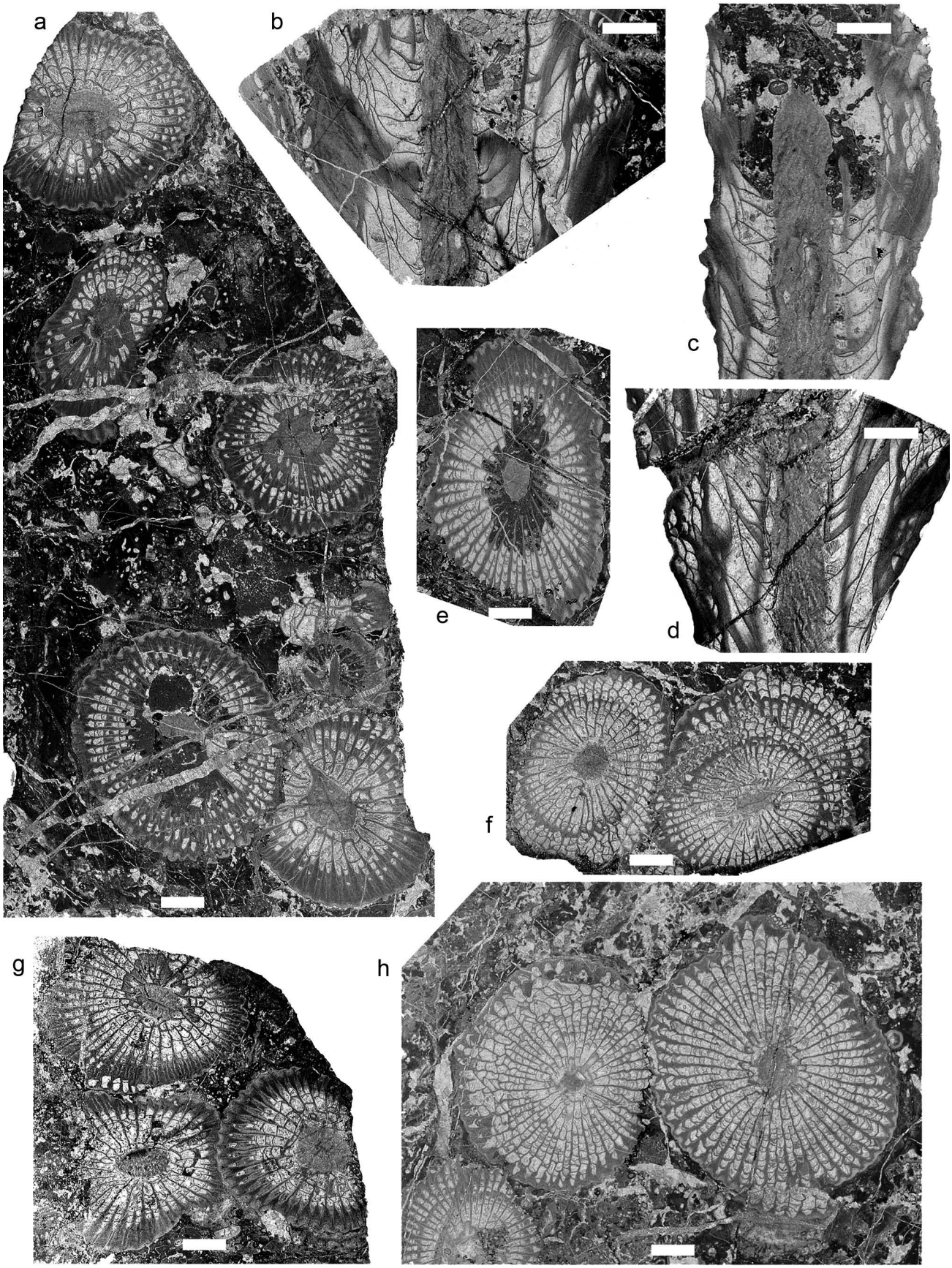


Fig. 9 - *Carinthiaphyllum crasseseptatum* Gräf & Ramovš, 1965, upper Asselian (middle Born Formation), locality Dovžanova Soteska NNE of Tržič. a) Transverse sections of a gregarium, nr. MB.K.8073.-2. b-d) Longitudinal sections, nrs MB.K.8075.-1., 8073.-3., 8077. e-h) Transverse sections, nrs MB.K.8072.-1., 8071.-1., 8076.-1., 8072.-5. All scale bars = 2 mm.

Carinthiaphyllum crasseseptatum Gräf & Ramovš, 1965
(Figs 8-11)

1965 *Carinthiaphyllum crasseseptatum* n. sp. Gräf & Ramovš, p. 169-170, Pls 8-10.
1972 *Carinthiaphyllum crasseseptatum* - Ramovš, Pl. 3, fig. 2.
1979 *Carinthiaphyllum kahleri* Heritsch - Holzer & Ramovš, Pl. 25.

Holotype - Specimen shown by Gräf & Ramovš (1965, pl. 8), housed in the Geological and Palaeontological department of Ljubljana University, locality Ortnek, Slovenia.

Description - Solitary (gregaria) with small corals. Septa of two orders. Major septa are long, some of them are connected with the pseudocolumella (Fig. 9a, f, h). Cardinal septum is long, connected with pseudocolumella (Figs 8a, 10d). Counter septum is equal in length with the other major septa. The peripheral part of major septa near the outer wall is thickened and has a triangular shape (Figs 8-9, 10a-b, 11). The length of minor septa changes from 1/2 to 2/3 of major septa according to the growth of corals (compare Fig. 9a, c). Pseudocolumella is very variable; its shape either oval compact (Figs 8, 9a) with tightly arranged radial lamellae (Fig. 9d), or consists of several radial lamellae and a median lamella (Figs 9b-c, 10f). This median lamella is well visible in all corals. Lonsdaleioid dissepiments are rare and occur in the mature stage (Fig. 9g). Interseptal dissepiments are rather numerous. The peripheral parts of septa show growth lines resembling "naotic structures" (Figs 8c, 9h, 10a-b, 11). The clinotabulae are deeply inclined (Fig. 9b, d). Tabulae situated between clinotabulae and pseudocolumella are flat. Microstructure multitrabicular at the upper margin of calice (visible in the broad triangular septal bases forming the archaeothecal wall), but monacanth in the interior thinner septa (Fig. 10a-c).

Measurements - Diameter 9 mm - 24 major septa; 10.2 mm - 30 major septa; 12 mm - 29 major septa. The original description of Gräf & Ramovš (1965) shows diameter 9 mm - 27 major septa (Fig. 7).

Discussion - Corals assigned to *C. kahleri* by Holzer & Ramovš (1979) are included in the synonymy of *C. crasseseptatum.* They have maximum diameter 10 mm, with total septal number 56. Size and septal numbers, the peripheral parts of septa and the microstructure as shown by Holzer & Ramovš (1979) are identical with our material. The same "naotic-like" structures of the peripheral parts of septa are typical for *C. crasseseptatum*

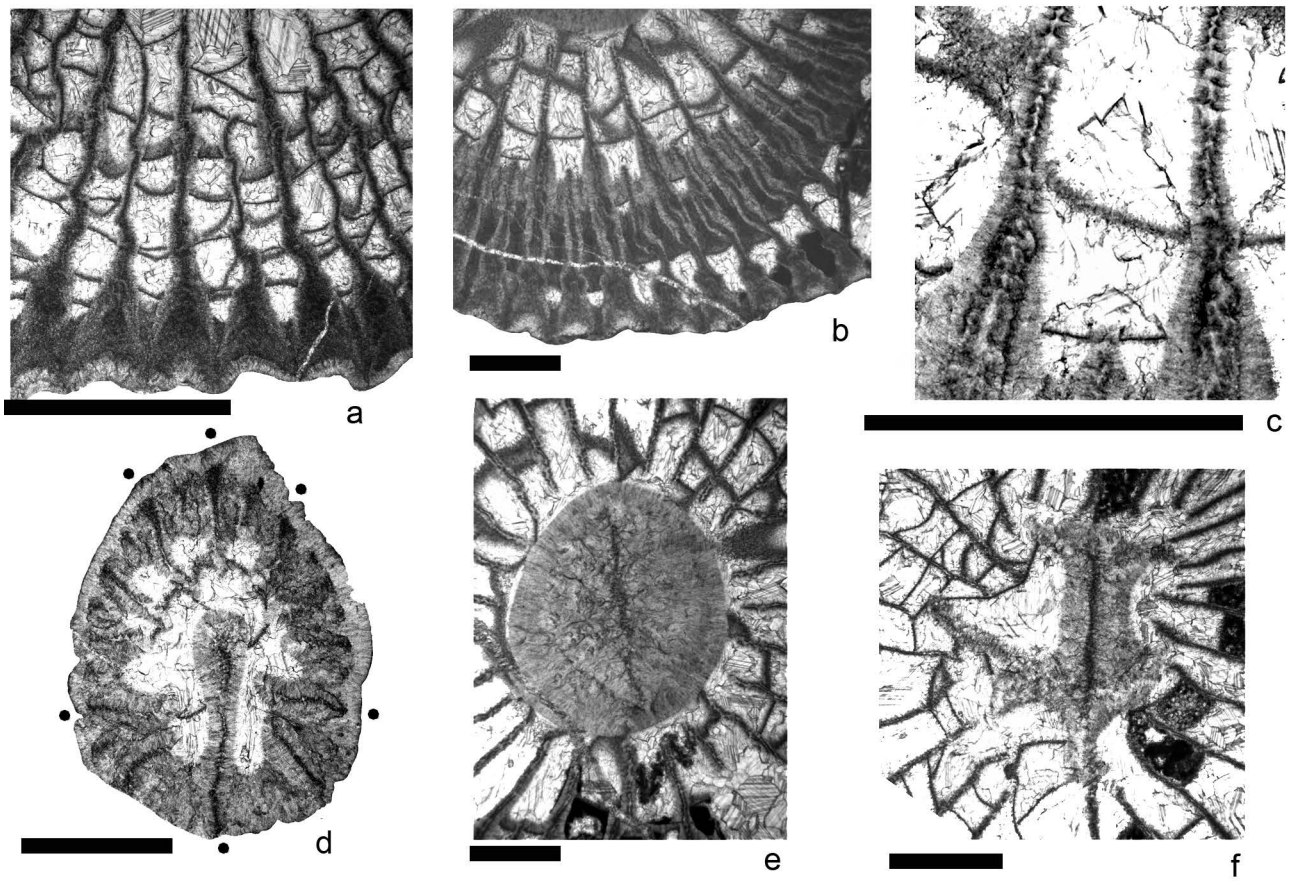


Fig. 10 - *Carinthiaphyllum crasseseptatum* Gräf & Ramovš, 1965, middle/upper Asselian (middle Born Formation), locality Dovžanova Soteska NNE of Tržič. nr. MB.K.8071.3. (see also Fig. 8a). a-c) Trabicular septal microstructures, often overprinted by growth lines ("Stirnzonen"), multitrabicular in the peripheral broader septal sockets, monacanth in the interior thinner septal parts. d) Juvenile transverse section (joined cardinal septum and pseudocolumella). e) Compact oval adult pseudocolumella (bordered by an axial tabula). f) Smaller adult pseudocolumella with longer free-ending septal lamellae. All scale bars = 1 mm.

Fig. 11 - *Carinthiaphyllum crasseseptatum* Gräf & Ramovš, 1965, middle/upper Asselian (middle Born Formation), locality Dovžanova Soteska NNE of Tržič. Transverse sections of eight corals in a gregarium, nr. MB.K.8072. Scale bar = 2 mm.

and were mentioned in the original text (Gräf & Ramovš, 1965, pl. 8, p. 169). The topotype specimens of *C. kahleri* differ by a larger number of septa, slightly larger diameter (12.5-11.0 mm - 23 [x2] septa, and 13.0-11.5 mm - 23 [x2] septa according to Heritsch, 1936).

Material - Several samples include numerous corals with cross sections clearly visible on weathered surfaces. Samples were collected from the top of the middle "rocky pyramids" (named Kušpegarjevi turni = Kušpegar towers) at the locality Dovžanova Soteska, NNE of Tržič, Slovenia, in the reef facies, upper Asselian. The collection is housed in Berlin (Museum für Naturkunde, nrs MB.K.8071.-8078., 62 thin sections).

Carinthiaphyllum ramovsi n. sp. (Figs 12-14)

1965 *Carinthiaphyllum* cf. *suessi* Heritsch - Gräf & Ramovš, Pl. 5, fig. 2.

Holotype - Specimen MB.K.8067a., (five transverse and five longitudinal sections - in four sections also containing the paratype nr. MB.K.8067b.). Locality Mount Boč north of Rogaška Slatina, Karavanke Mts, Fig. 12a-e, upper Asselian.

Derivation of the name - In memory of Anton Ramovš (1924-2011), famous geologist in Ljubljana, for his stratigraphic and palaeontological studies of the Palaeozoic of Slovenia.

Diagnosis - Small gregaria corals possessing major and minor septa, which are thinner than the wider interseptal spaces (Fig. 12). Broad septal sockets at the wall are extremely short; major septa are thin in the dissepimentarium, slightly thickened in the tabularium. Cardinal septum is connected with pseudocolumella (Figs 12-14). Thick pseudocolumella consists of numerous radial lamellae and median lamella (Fig. 12e). Axial tabula is developed and connected with radial lamellae. Their peripheral ends enter the tabularium (Fig. 14c-d). Clinotabulae present (Fig. 13c-d). Dissepiments are interseptal and lonsdaleioid (rare) (Fig. 12a, d, f). Root-like structures and archaeothecal protrusions are common (Fig. 12f).

Description - Small gregaria corals possessing major and minor septa. Major septa are long; some of them are connected with pseudocolumella. No fossula is visible. The counter septum is equal or slightly shorter than the other major septa (compare Fig. 13a and 13b). In Fig. 12d the counter septum is much shorter than most other major septa. The minor septa length is 2/3 of major septa. The thickness of all septa is rather equal along the length of septa (in transverse section). The outer wall has wavy inner margin and a well-visible trabicular structure in the broad septal sockets (Fig. 13f). In the early ontogenetic stages, the inner part of the cardinal septum is connected with the pseudocolumella (Fig. 14). In the mature stage major septa are joined with concentric axial tabulae surrounding the pseudocolumella (Fig. 13). The latter consists of numerous, rather densely packed radial lamellae and the median lamella (Figs 12a, d, 13b, e). The number of radial lamellae corresponds to the number of major septa. Some outer parts of the radial lamellae go out of the outer margin of the pseudocolumella and are clearly visible in transverse and longitudinal sections (Fig. 13); in the latter, they join the axial tabula or sometimes even reach beyond it into the tabularium. The dissepimentarium consists of six rows of nearly vertical small interseptal, slightly convex dissepiments. Lonsdaleioid dissepiments appear at late mature stages. Clinotabulae are deeply inclined. Tabulae are concave and occur rather rarely. Septa and axial lamellae have a trabicular microstructure.

Measurements - Maximum diameter of coral reached 13.3 mm with 62 septa (Tab. 2).

Ontogenesis - The earliest observed stage demonstrates the connection of cardinal and counter septa; both lateral septa are also present (Fig. 14a). The cardinal septum is extremely thick. Next two sections show the thickening of the inner end of the cardinal septum and the beginning of the pseudocolumellar growth (Fig. 14b); they have 21 and 23 major septa (Fig. 14b-c), and the counter septum lost the connection with the pseudocolumella.

Discussion - The new species differs from the type species *Carinthiaphyllum kahleri* Heritsch, 1936 by the complex axial structure and a larger diameter with higher numbers of septa. *C. suessi* is distinctly larger (Fig. 7). The lack of strongly thickened peripheral septal sockets with "naotic-like" structures and the presence of a more complex axial structure distinguish the new species from *Carinthiaphyllum crasseseptatum*.

Reproduction - *Carinthiaphyllum ramovsi* n. sp. has a gregaria growth mode with juvenile corals settling on the outer wall of a nearly mature coral (sometimes with root-like protrusions) (Figs 13b, 14e-f). The septa of the "substrate" corals do not connect with those of juvenile corals; there is never a wall interrupted by any connecting pores. In mature stage, neighbouring corals may touch each other some time for support, when growing upwards nearby. Special outgrowth root-like structures were observed only in this species. The additional stereoplasmic protrusion was segregated by the archaeotheca of the "substrate" coral for a connection with the juvenile neighbors. The protrusion exists temporarily and was not observed between mature stages.

Material - One small limestone sample with 12 transverse coral thin sections; nr. MB.K.8067.-8068. is housed in the Museum für Naturkunde in Berlin.

GREGARIA MODE OF CORAL GROWTH

The term gregaria growth form of solitary corals was proposed by Fedorowski (1980) for the case of accumulated corals, appearing like a fasciculate colony, but with no visible features of buddings. According to this author "two facts are striking: 1) only larvae of the same species settled together, 2) specimens are differentiated

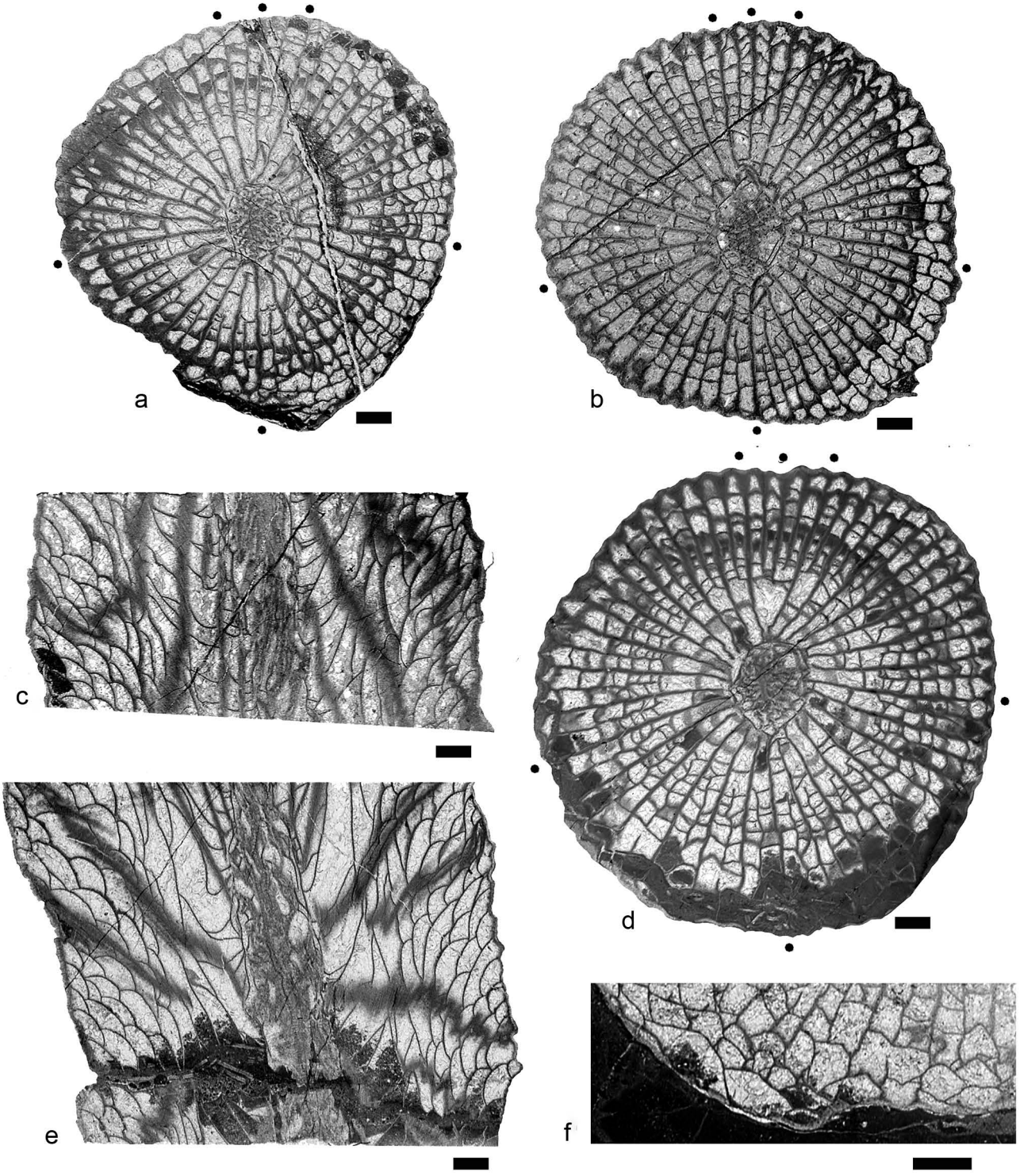
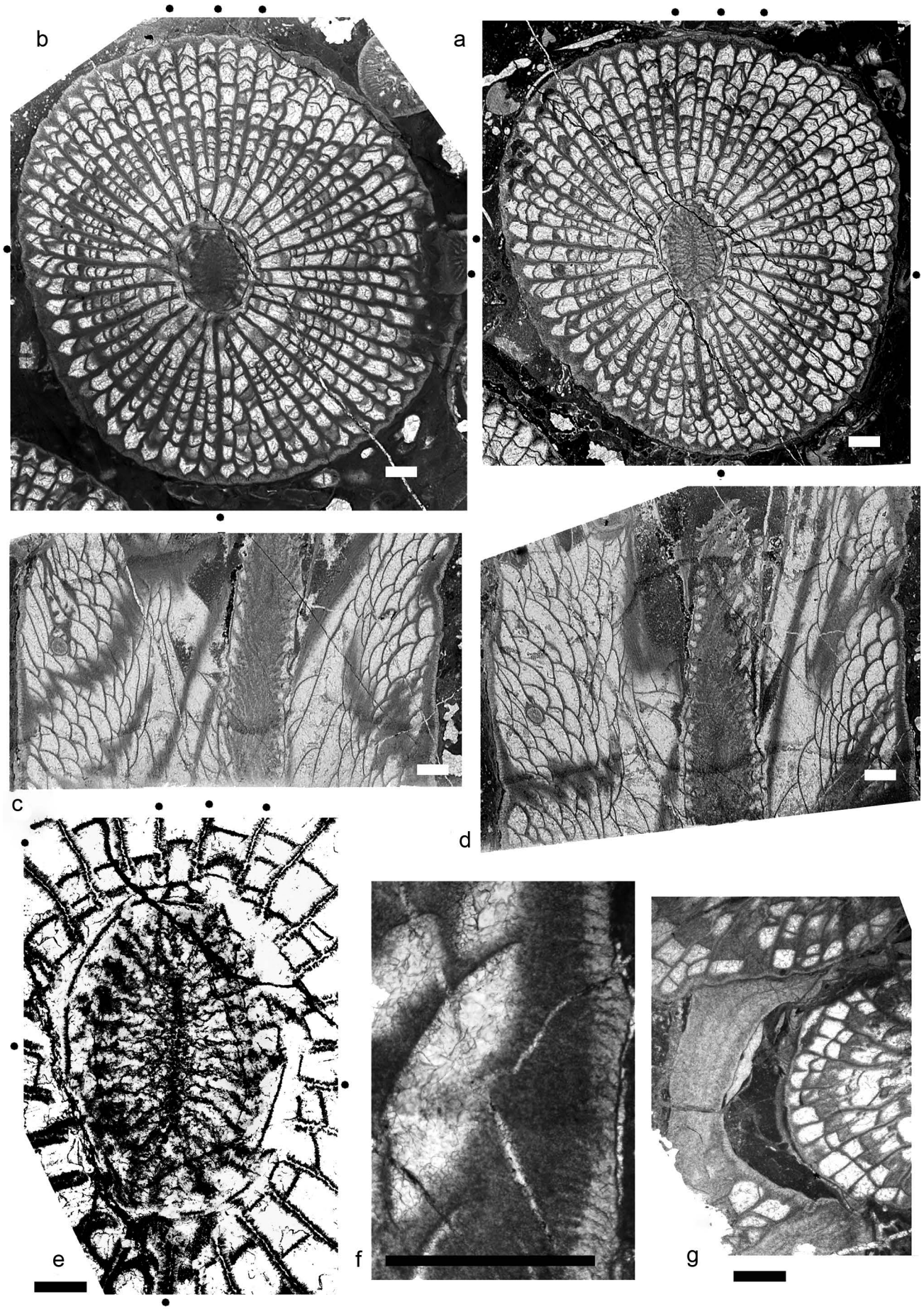


Fig. 12 - *Carinthiaphyllum ramovsi* n. sp., upper Asselian, locality Mount Boč north of Rogaška Slatina. Abbreviations (for all figures) - N: number of all septa; n: number of major septa; D: diameter; C: cardinal septum; c: counter septum; L: lateral septum; numbers are the major septa in four quadrants. Sequence of transverse and longitudinal (parallel to the cardinal-counter plane) subtabular sections (six protosepta marked). a-d) Holotype nr. MB.K.8067; septal formula for transverse section (a) (from left to right): C-6-L-9-c-8-L-6 (n-33; N-59; D-11, 2); septal formula for transverse sections (b) and (d): C-6-L-9-c-8-L-7 (n-34, N-60, D-11, 7-13 mm). c-e) Longitudinal sections. f) Specimen nr. MB.K.8068 with normal and occasional lonsdaleioid dissepiments. All scale bars = 1 mm.

Fig. 13 - *Carinthiaphyllum ramovsi* n. sp., upper Asselian, locality Mount Boč north of Rogaška Slatina. a-b) Subtabular transverse sections of paratype nr. MB.K.8067; septal formula for section (a) C-7-L-8-c-8-L-7 (n-34, N-61, D-12, 7 mm); septal formula for section (b) C-7-L-8-c-8-L-8 (n-35, N-62, D-13.3 mm). c-d) Longitudinal sections of paratype nr. MB.K.8067 near the calicular base (at right angle to the cardinal-counter plane) with well-developed clinotabulae. e) Pseudocolumella magnified fragment of the figure (b) with regularly arranged septal lamellae in paratype nr. MB.K.8067. f) Multitrabicular septal microstructure within archaeotheca in paratype nr. MB.K.8067, magnified detail of the figure (d). g) Nr. MB.K.6087c; transverse section with archaeothecal tube-like outgrowth touching two neighbouring corals of the gregarium. All scale bars = 1 mm.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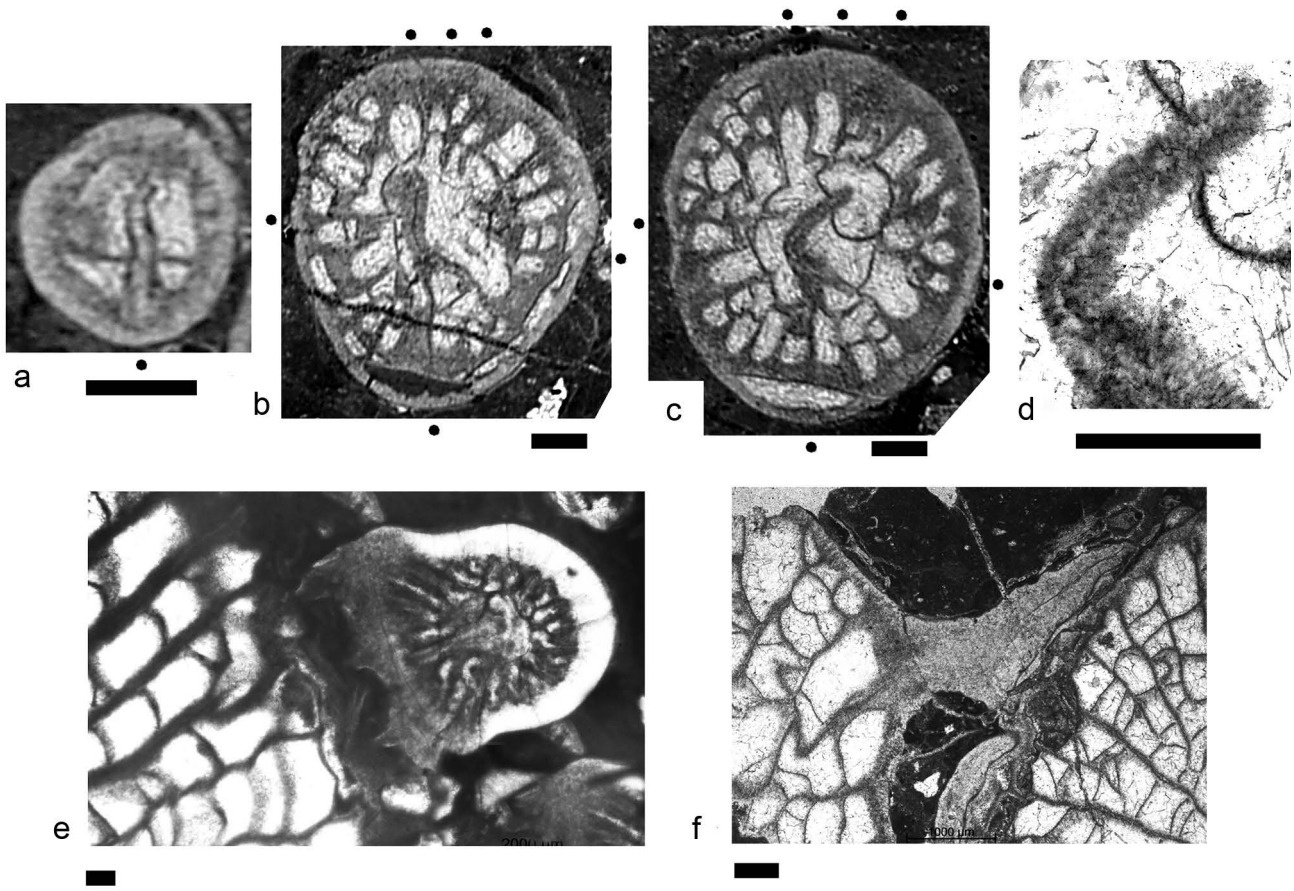

Fig. 14 - *Carinthiaphyllum ramovsi* n. sp., upper Asselian, locality Mount Boč north of Rogaška Slatina. a) Extreme juvenile transverse section nr. MB.K.8068.2a (D 1.05 mm) with prominent cardinal septum only. b-c) Succeeding subtabular transverse sections nr. MB.K.8068.2 with initial pseudocolumella, originating from the cardinal septum, still without further septal lamellae; septal formula for section (c) C-6-L-6-c-6-L-5 (n 27, N 46, D 2.8 mm). d) Section nr. MB.K.8068.2c; pseudocolumella of thin with nearly vertically arranged trabiculae. e) Section nr. MB.K.8068.2; juvenile coral, attached to an adult one, using three archaeothecal outgrowths. f) Section nr. MB.K.8068.2; left coral with tube-like outgrowth, attached to the adult right specimen. All scale bars = 0.5 mm.

in ontogenetic development (which) makes clear that gregaria were acting as comparatively long-lasting larvae settlements" (Fedorowski, 1980, p. 435).

Earlier this phenomenon was interpreted in most cases as fasciculate colonies without observed budding. The consideration of the growth form of corals used as a generic feature demands a detailed look in every case. A first feature of probable gregaria mode is the occurrence of many juvenile stages (just with wall and still very few septa), which did not develop into mature stages. Second feature: no budding is visible. Third criterion can be the appearance of the additional root-like outgrowths or other modification of supporting protrusions. In some cases, such tubes are channeled, but without any fusion of soft parts between the neighboring corals. In our material only one *C. crasseseptatum* specimen had a protrusion, where a channel was seen. Also, in the numerous protrusions of *Carinthiaphyllum ramovsi* n. sp. real fusion was not observed.

The origination of rhizoids is not a unique phenomenon. A good example was shown for solitary corals, surrounded by tabulate *Halysites* colonies. The development of rhizoid strategy is used by *Cystiphyllum visbyense* Wedekind, 1927 for support, using both living and dead parts of *Halysites* colonies. In this case (Ireviken cliff on Gotland Island, upper Llandovery), the rhizoids are constructed by tubes with an empty channel (Berkowski & Zapalski, 2018).

The gregaria growth form was studied in *Darwasophyllum* Pyzhyanov, 1964 (Rodriguez & Bamber, 2012), showing extremely similar features observed here in *Carinthiaphyllum*. The high number of juvenile forms of the same species points to some restrictions for planula distribution, probably some barrier or current. *Lytvophyllum*? *hongi* (Wilson, 1982) is not a pseudocolony (as suggested by Stevens, 2008), but has to be assigned to gregaria. Gregaria accumulation is distributed rather widely in late Palaeozoic times, and in future many corals considered as fasciculate could be revised as gregaria.

The meaning of gregaria is quite close to "pseudocolonial" according to the definition of pseudocolony "as a cluster of individual corallites of the same species that grow close to one another, giving the impression of being produced by offsetting" (Fedorowski, 1978). Spassky & Kravtsov (1974) used pseudocolony in a different sense for cases of intracalicular circumperipheral budding, resulting in many juvenile buds around the big parent coral (like the lectotype of the upper Silurian

Figure	Diameter (mm)	N	n	Ns- number of minor septa
13a	11.2	59	33	26
13b	13.3	62	35	31
12b	11.7	60	34	26
12d	13.0	60	34	26
14b	2.7	46	27	19
14c	2.8	48	28	20

Tab. 2 - Measurements of *Carinthiaphyllum ramovsi* n. sp. (septa are counted morphogenetically as major septa (= protosepta, metasepta) and minor septa (= catasepta). Abbreviations: N - number of all septa; n - number of major septa.

Entelophyllum prosperum (Počta, 1902), refigured in Prantl, 1940, pl. 1, fig. 6). However, the term pseudocolony had another definition earlier, being commonly used among Scleractinia corals - dominating for phaceloid colonies derived from one planula, but lacking later integration of soft parts (Roniewicz & Stolarski, 1999). Thus, Scleractinian pseudocolonies are formed via asexual budding - that is the basic difference against gregaria with their only sexual type of reproduction.

CONCLUSIONS

The revision of *Carinthiaphyllum*, distributed in the lower Permian of the Karavanke Mountains and the Dinarides (Slovenia), is based on new and previously obtained material. It allowed the generic diagnosis to be emended, to more clearly define the species and to separate the new species *Carinthiaphyllum ramovsi* n. sp. The gregaria mode of reproduction was documented for *C. ramovsi* n. sp. and, probably, is one of the typical features for the genus *Carinthiaphyllum* Heritsch, 1936 and family Geyerophyllidae Minato 1955.

The ages of the three species under consideration were determined according to new results on fusulinids and conodonts. Thus, the interval of distribution of *Carinthiaphyllum suessi* and *C. ramovsi* is considered as upper Asselian - lower Sakmarian, and the age of *C. crasseseptatum* is late Asselian - Sakmarian. The brief analysis of the geographical distribution shows that Carboniferous *Carinthiaphyllum* species were characteristic for the eastern part of the Palaeotethys, but Permian ones are typical for the western part of the Palaeotethys Ocean. This supports the assumptions about some isolation of the western Palaeotethys in the Permian.

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