

Sponges from the Middle Triassic reef limestone of the Aggtelek Karst (NE Hungary)

BABA SENOWBARI-DARYAN¹, †SÁNDOR KOVÁCS and FELICITÁSZ VELLEDEITS²

This work is dedicated to our late colleague Dr. Sándor Kovács, who unfortunately died before the work was finished. He collected the majority of the sponge samples described in this paper and the main result of the stratigraphy of the reef carbonates is his contribution.

¹Geozentrum Nordbayern, Department of Paleontology, University of Erlangen-Nürnberg, Loewenichstrasse 28, 91054 Erlangen, Germany; basendar@pal.uni-erlangen.de

²Limestone Bt., Andrassy Gy. u. 6., 2120 Dunakeszi, Hungary; fvelledits@freemail.hu

(Manuscript received January 19, 2011; accepted in revised form March 17, 2011)

Abstract: The hypercalcified sponge fauna of the Middle Triassic (Anisian–Ladinian) reef limestone exposed between Aggtelek–Jósvafő–Égerszög (northern Hungary) is described. Almost all the identified species are chambered sponges (“sphinctozoa”). Only two fragments of a not determinable species of non-chambered species (“inozoa”) were identified. Hexactinellid sponges are not found. The majority of the Middle Anisian “sphinctozoans” are absolutely different genera, not known from the Permian reefs. The sponge fauna of the Triassic pioneer reefs in the Aggtelek Karst are distinctly small-scaled occurring in “*Tubiphytes*”-dominated carbonates. The following taxa are described: *Amblysiphonella* sp., *Celyphia zoldana* Ott, Pisa & Farabegoli, *Colospongia catenulata catenulata* Ott, *C. catenulata macrocatenulata* Scholz, *Follicatena cautica* Ott, *Kovacsia baloghi* (Kovács), *Solenolmia manon manon* (Münster), *S. radiata* Senowbari-Daryan & Riedel, *Olangocoelia otti* Bechstädt & Brandner, *Thaumastocoelia dolomitica* Senowbari-Daryan, Zühlke, Bechstädt & Flügel, *Thaumastocoelia* cf., *Th. cassiana* Steinmann.

Key words: Anisian–Ladinian, NE Hungary, Aggtelek, reef, sponges, “sphinctozoans”.

Introduction

The number and abundance of hypercalcified sponge taxa — particularly those of chambered construction, the “sphinctozoa”, described in this paper — occurring in Permian reefs and reefal deposits decreased considerably after the dramatic mass extinction crises at the end of the Paleozoic. Almost all species of “sphinctozoans” disappeared and holdovers of this group are not known from the Early Triassic (Scythian) and from the Middle Triassic pioneer reefs. The absence of Permian “sphinctozoa” genera in the Middle Triassic also exhibits the disappearance of this group at the generic level. Morphologically identical or similar “sphinctozoans” appear first in Norian reefs.

The pioneer Triassic reefs, and consequently the “sphinctozoans”, appeared first in the Middle Anisian and became more abundant during the Ladinian to Late Triassic. The majority of Middle Anisian “sphinctozoans” are absolutely different genera, not known from the Permian reefs. Anisian reefs and reef builders are known from several localities in the world (Flügel & Senowbari-Daryan 2001), but the most information about the paleontological contents of Anisian reefs comes from the Dolomites of northern Italy (Gaetani et al. 1981; Fois & Gaetani 1984; Scheuber 1990; Senowbari-Daryan et al. 1993), Austria (Schafhauser 1997), China (Enos et al. 1997; Lehrmann et al. 1998) and Hungary (Scholz 1972; Senowbari-Daryan & Velledits 2007a,b). The known “sphinctozoa” taxa of the Middle Triassic and those described in this paper are morphologically small-sized,

while those of the Late Triassic (especially of the Norian–Rhaetian) are large-scale representatives. “Sphinctozoans” appear first in the Middle Anisian and become more abundant during the Ladinian to Late Triassic.

It was Scholz (1972) who first gave detailed information on the fauna and flora of the Aggtelek reef, but his age determination (Pelsonian–middle Illyrian) was not correct, because he considered the reef limestone heteropic with the Steinalm Limestone. His dating was based on dasycladales, and foraminifera originated from the Pelsonian Steinalm Limestone. The latest detailed (1:10,000) geological mapping (Velledits et al. 2011) has revealed, that the Steinalm Limestone was not heteropic with the Aggtelek reef. The Steinalm Limestone is overlain by a deep-water limestone (Jenei Limestone, see Figs. 1a,b, 2 and 3).

This deep-water intercalation constitutes the underlying unit of the Aggtelek reef. Scholz’s inaccurate age determination was cited in the literature many times e.g. Kovács (1978a), Flügel (1982, 2002), Senowbari-Daryan et al. (1993), Payne et al. (2006).

Sponges of the Hungarian Ladinian–Carnian Wetterstein Limestone were described by Balogh & Kovács (1976), Kovács (1978a,b), and Flügel et al. (1991/1992).

The studied “sphinctozoans” originate from the Aggtelek reef. It is exposed on the Aggtelek Karst, between Aggtelek–Jósvafő–Égerszög (Fig. 1a) and in the Baradla Cave between Aggtelek and Jósvafő (Fig. 1b). It forms a belt, which extends 7 km long in a NW–SE direction and its width varies between 1–3 km (Fig. 1a).

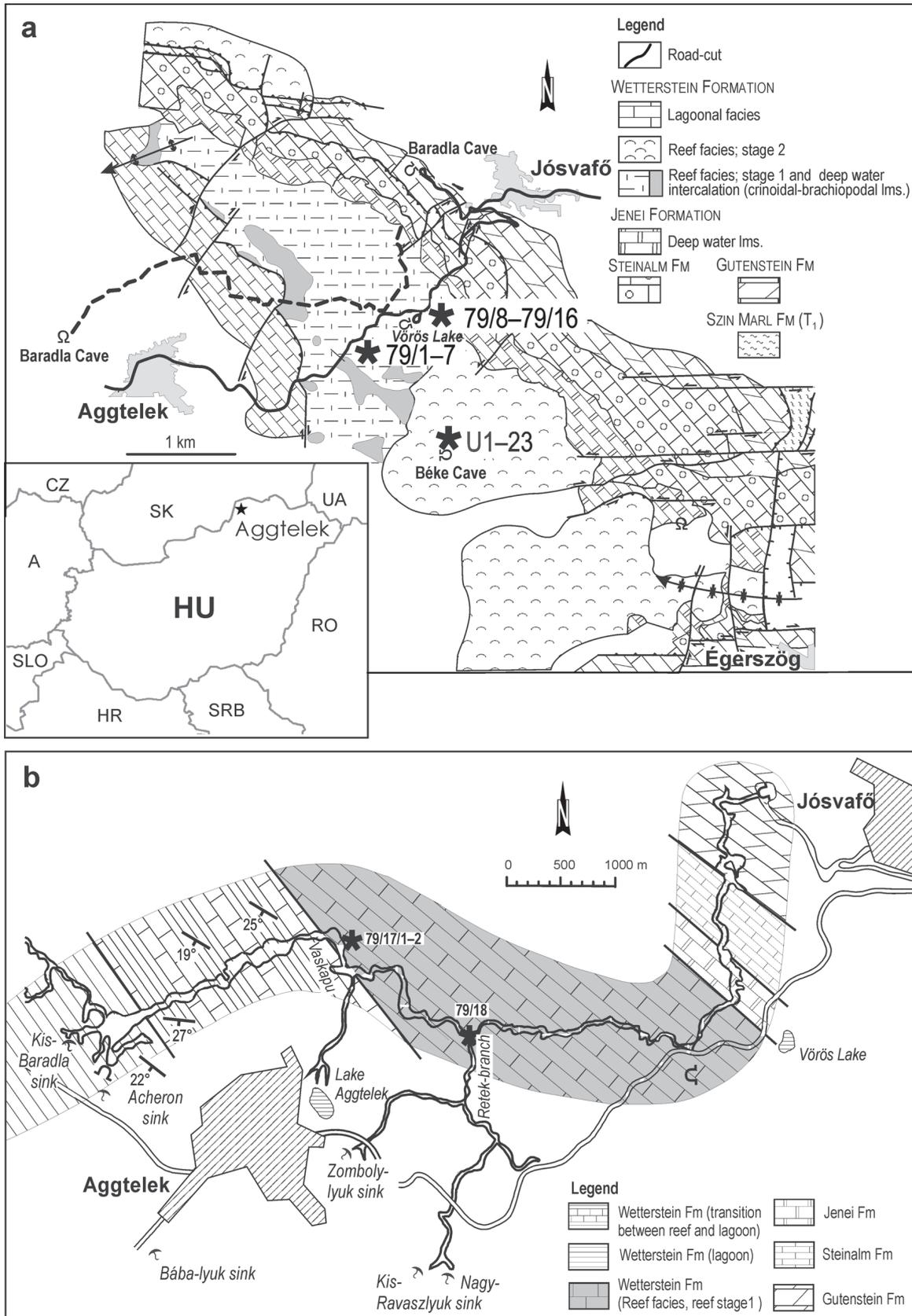


Fig. 1. a — Geological map of the Aggtelek-Jósvafő area (Velledits et al. 2011) and the sampling points (asterisks). *Dashed line* depicts the vertical projection of the Baradla Cave. *Asterisks* — locations of the samples from surface exposures. **b** — Middle Triassic formations revealed by the Baradla Cave with the location of the sampling points.

Geologic-stratigraphic setting

The Triassic formations building up the Aggtelek Karst belong to the Silica Nappe which is the uppermost nappe of the Inner Western Carpathians (Kozur & Mock 1973; Mello et al. 1997). According to its lithostratigraphic succession the Silica Nappe corresponds to the “Juvavicum” of the Northern Calcareous Alps (NCA) (Lein 1987; Tollmann 1987; Kozur 1991), recently considered to be the “Hallstatt mélange” (Gawlick et al. 1999). In the Middle-Late Triassic both the Western Carpathians and the Northern Calcareous Alps were situated on the northern shelf of the north-western end of the opening Neotethys (Tollmann 1987; Kovács 1997; Haas et al. 2001; Schmid et al. 2008). The Triassic rifting had a profound influence on the evolution of the Silica Nappe and thus also on the evolution of the area under study.

According to Kovács (1989) three units (Aggtelek, Szőlösardó and Bódva) of the Silica Nappe formed a fairly uniform ramp from the Early Triassic until the late Pelsonian. The ramp was dissected due to rifting (Fig. 2). From that time onward the evolution of the three units was different. The major part of the Aggtelek Unit survived as a platform up to the Tuvalian, while the Szőlösardó Unit

represented the shelf-slope and the periplatform environment and the Bódva Unit corresponded to the pelagic basin bordering the opening ocean.

In the Aggtelek Unit in the late Pelsonian (Binodosus Subzone, Velledits et al. 2011) the uniform Steinalm Platform was drowned and dissected. Basins and highs were formed. In the NW part of the studied area the lower-middle? Illyrian basinal carbonates were overlain by a platform margin reef (reef stage 1) developed on a morphological high. According to our present knowledge this is the oldest known Triassic platform margin reef within the Alpine-Carpathian region. The reef association is dominated by sphinctozoans and microproblematicas. The fossils are characteristic of the Wetterstein-type reef communities (Velledits et al. 2011).

Differently from this in the SE part of the studied region a basin existed from the late Pelsonian until the end of the Illyrian (Fig. 1a). During the late Illyrian–Early Ladinian the reef prograded to the SE, where reef stage 2 was established. Meanwhile, on the NW part of the platform a lagoon was formed behind reef stage 2.

In the evolution of the Aggtelek reef two different stages can be distinguished. (1) Reef stage 1 of Illyrian age. It crops out only in the NW part of the studied area. Reef stage 1 can

be followed on the edge of the platform in the neighbourhood of a basin over a distance of 3.5 km (Fig. 1a). Consequently we can conclude that it was a platform margin reef.

In the Early Ladinian (Curionii Zone or somewhat later) the reef (stage 1) prograded into the SE situated basin, where (2) reef stage 2 came into existence. Its age is late Illyrian–Early Ladinian.

Because reef-building organisms do not allow exact biostratigraphic age determination, the age of reef stage 1 was determined by the age determination of the underlying and intercalating deep-water limestone, and with the overlying lagoonal unit. The conodonts

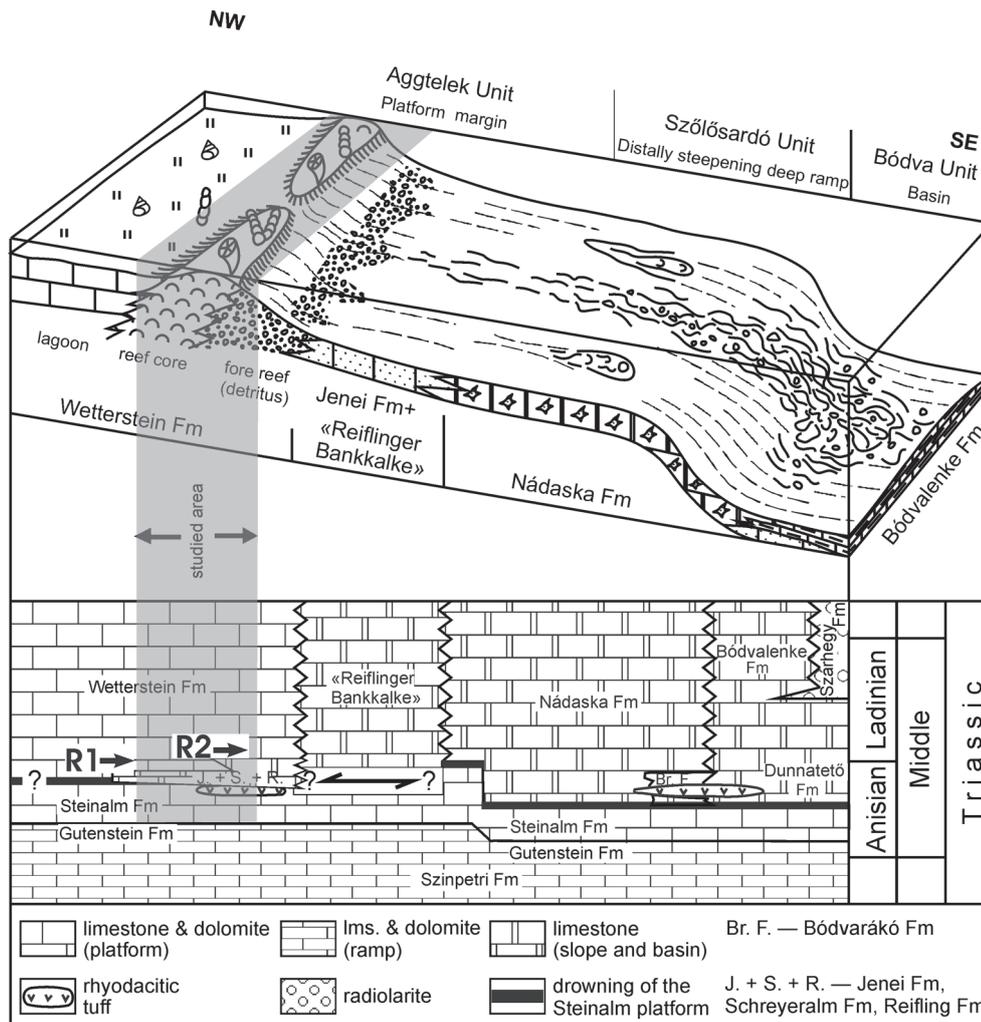


Fig. 2. Middle Triassic depositional model and Triassic lithostratigraphy of the Aggtelek and neighbouring units. (Modified after Kovács 1997.) Light grey shading indicates the studied area. **R1** — Wetterstein Formation reef facies, stage 1. **R2** — Wetterstein Formation reef facies, stage 2.

(*Gondolella liebermani*, *G. szaboi*, *Gladigondolella budurovi* det. by S. Kovács) and radiolaria (*Pararuesticyrtium* (?) cf. *illyricum*, *Eptingium* cf. *ramovsi*, *Pseudostylosphaera japonica* det. P. Dumitrica) from the underlying basal carbonates of reef stage 1 refer to middle Illyrian (Trinodosus Zone up to the greater part of the Reitzi Zone). The deep-water intercalation in the upper part of reef stage 1 contains conodonts (*Gondolella fuelepei*, *G. trammeri* det. S. Kovács) referring to Avisianum Subzone or younger age (Fig. 3). In the overlying lagoonal

limestone *Diplopora annulata* appears in large quantity, indicating a late Illyrian–Fassanian age.

The age of reef stage 2 was determined with the help of conodonts from the underlying strata. *G. trammeri*, *G. transitita*, *G. transitita/pseudolonga* and much younger forms *Gondolella* gr. “*Bakalovi*” (*sensu* Kovács 1994) indicating late Illyrian to Fassanian (upper Secedensis to Curionii Zones) age. The cessation time of reef stage 2 is not known because the overlying strata is tectonically sheared.

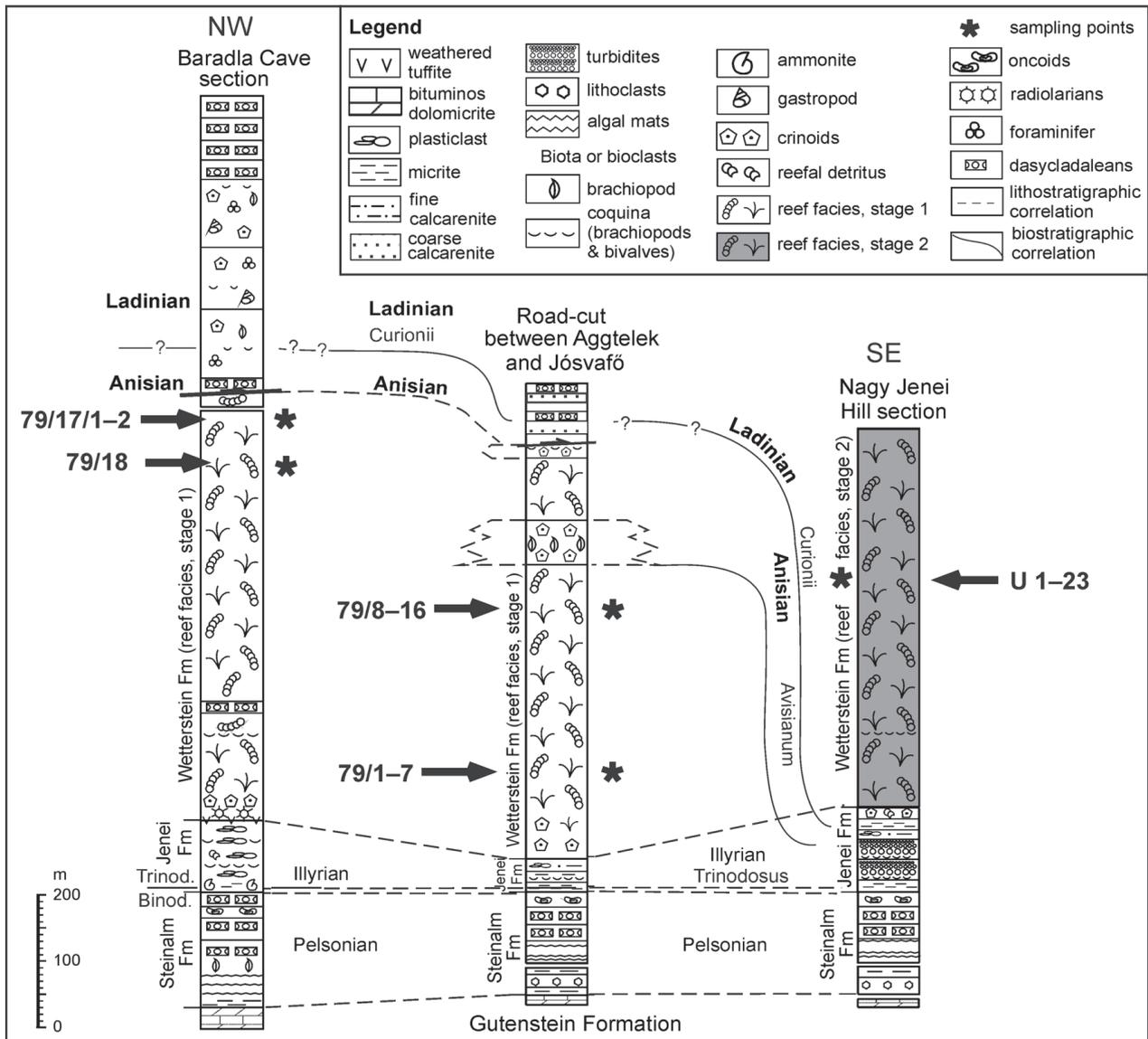


Fig. 3. Stratigraphical positions of the samples.

Fig. 4. “Sphinctozoans” from the Anisian-Ladinian Aggtelek reef limestones, NE part of Hungary. Scale in A–F and K = 2 mm, in G–J = 5 mm. **A** — *Follicatena cautica* Ott. Longitudinal section through a specimen composed of several spherical to barrel-shaped chambers. The chambers communicate with others and with the outside by single openings. Chamber interiors are filled with vesiculae. 79/1/4b. **B** — *Colospongia catenulata catenulata* Ott. Longitudinal section through five chambers. Some vesiculae are secreted in one chamber interior. U9b. **C** — *Colospongia catenulata macrocatenulata* Scholz. Magnification of two chambers from a specimen shows the pronounced and even perforation of the chamber walls. 79/9d. **D** — 1 — Longitudinal section through two chambers of *Solenolmia radiata* Senowbari-Daryan & Riedel and 2 — *Colospongia catenulata catenulata* Ott. Note the alternating growth stages of both sponges: the wall of the early three chambers of ...

Continues on the next page

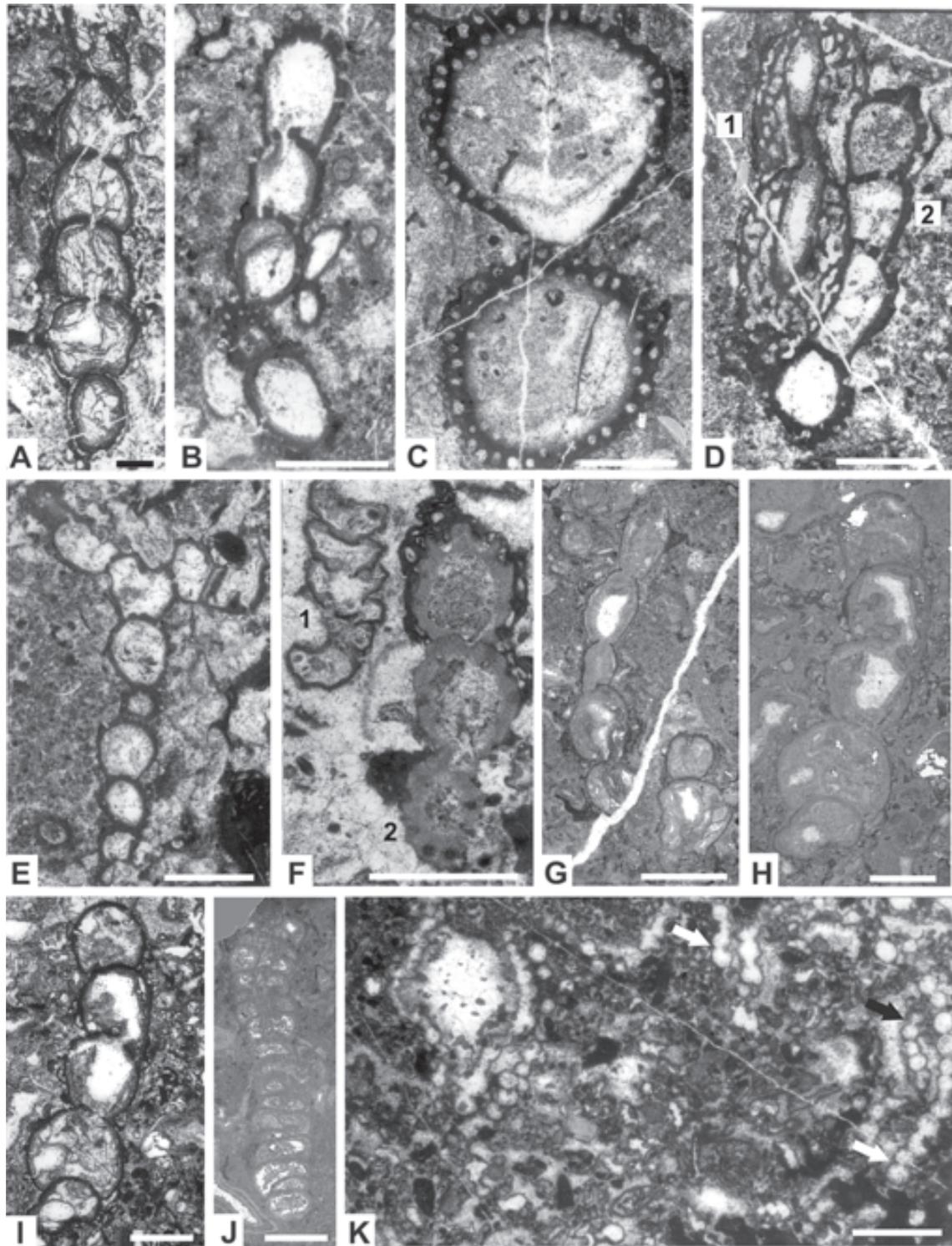


Fig. 4. Text continues from the previous page. ... *Colospongia* is missing and the three chambers are lying on the first chamber wall of *Solenolmia*. Despite this the wall of the fourth chamber of *Colospongia* is well developed and here *Solenolmia* has no wall. **E** — *Colospongia catenulata catenulata* Ott. Longitudinal section through a branched specimen shows the uneven perforation of the chamber walls (Fig. 7). 79/4/1. **F** — 1 — Chambered sponge? or foraminifer? gen. et sp. indet. and 2 — *Colospongia catenulata catenulata* Ott. 79/2a. **G** — *Follicatena cautica* Ott. Sections through two specimens show similar characteristics as Fig. A. 79/3b. **H** — *Follicatena cautica* Ott. Longitudinal section similar to Fig. A. 79/2/2a. **I** — *Follicatena cautica* Ott. Longitudinal section similar to Fig. A. 79/2/2a. **J** — *Amblysiphonella* sp. Longitudinal section through numerous low rectangular to crescent-shaped chambers. In the upper part of the sponge the spongocoels are cut. 79/17/1b. **K** — *Olangocoelia otti* Bechstäd & Brandner. Section through numerous small spherical chambers arranged in rows. Chambers are connected either directly or by a short and narrow tube (arrows). 79/51.

Samples 79/1–18 originate from reef stage 1 (Illyrian), whereas samples U1–23 come from reef stage 2 (upper Illyrian–Lower Ladinian).

Systematic paleontology

Remarks: The systematic classification of Fink & Rigby (2004) with minor modifications is used to describe the sponges in this paper.

Phylum: **Porifera** Grant, 1836

Class: **Demospongia** Sollas, 1875

Order: **Vaceletida** Finks & Rigby, 2004

Family: **Colospongiidae** Senowbari-Daryan, 1990

Synonymy: **Colospongiidae** Boiko & Belyaeva (in Boiko et al. 1991); **Parauvanelliidae** Wu, 1991; **Imbricatocoeliidae** Wu, 1991 (see Finks & Rigby 2004: p. 697)

Subfamily: **Colospongiinae** Senowbari-Daryan, 1990

Genus: *Colospongia* Laube, 1864

Type species: *Manon dubium* Münster, 1841.

Further species: All specimens of *Colospongia* with stratigraphic range and geographic distribution are listed by Senowbari-Daryan & Garcia Bellido (2002).

Remarks: Two subspecies of *Colospongia* are known: the type species *C. catenulata catenulata* from the Wetterstein Limestone (Ladinian–Carnian) described by Ott (1967) and *C. catenulata macrocatenulata* described by Scholz (1972) from the Illyrian part (reef stage 1) of the Aggtelek reef, about 2 km northeast of Aggtelek. According to Scholz this subspecies differs from *C. catenulata catenulata* Ott (1967) by the large chamber diameters (in *C. catenulata catenulata*: 1.3–6.0 mm; in *C. catenulata macrocatenulata* up to 9 mm). In fact, we also found in the investigated material two different-sized *Colospongia*. The first one (as illustrated in Fig. 4B,E) is small and reaches a maximum

chamber diameter of 2.3 mm with a maximum chamber height of 2.5 mm (Fig. 5). The second species (as in Fig. 4C; Fig. 6H–I) is a large one with a maximum diameter of 8.5 mm and height of 9 mm (Fig. 5). Data for the thickness of chamber walls and pore diameters of both species are almost identical.

The dimensions of the first species of investigated material are smaller than the average data reported of *Colospongia catenulata catenulata* by Ott (1967) (see above). The dimensions of the large species correspond to the data given for *Colospongia catenulata macrocatenulata* by Scholz (1972). Based on chamber dimensions we describe both subspecies separately.

Colospongia catenulata catenulata Ott, 1967

(Fig. 4B,D/2–E; Fig. 7; Fig. 8B)

- 1967 *Colospongia catenulata* n. sp. — Ott; p. 32, pl. 7, fig. 3–4, pl. 8, fig. 1–5
 1972 *Colospongia catenulata* Ott — Ott; pl. 1, fig. 1
 1974 *Colospongia catenulata* Ott — Jablonsky; p. 194, pl. 68, fig. 1
 1976 *Colospongia catenulata* Ott — Balogh & Kovács; p. 300, pl. 1, fig. 5
 1983 *Colospongia catenulata catenulata* Ott — Senowbari-Daryan & Schäfer; p. 181, pl. 2, fig. 3, 6
 1986 *Colospongia catenulata catenulata* Ott — Senowbari-Daryan & Abate; p. 63, pl. 1, fig. 7, pl. 2, fig. 1–2
 1989 *Colospongia catenulata catenulata* Ott — Mastandrea & Rettori; p. 17, pl. 1, fig. a–c; pl. 3, fig. 1
 1990 *Colospongia catenulata* — Ciarapica et al.; Fig. 2/A (left: the same specimen illustrated in Mastandrea & Rettori 1989)
 1997 *Colospongia catenulata catenulata* Ott — Ruffer & Zamparelli; pl. 28, fig. 3
 2005 *Colospongia catenulata catenulata* Ott — Emmerich, Zamparelli, Bechstädt & Zühlke; fig. 11/7, 10
 2005 ?*Colospongia* sp. — Emmerich, Zamparelli, Bechstädt & Zühlke; fig. 10/7–8
 2006 *Colospongia catenulata* Ott — Nittel; pl. 7, fig. 1
 ? 2006 *Colospongia catenulata* Ott — Nittel; pl. 7, fig. 2

Material: In numerous thin sections (for the illustrated specimens see plate explanations).

Description: *Colospongia catenulata catenulata* is one of the most beautiful “sphinctozoan” sponges and easy for determination. The straight or slightly curved sponge is composed of numerous spherical to barrel-shaped chambers arranged one above another like a chain. The chamber size is almost constant in the whole sponge stem. Chamber walls are pierced with evenly sized pores, but occasionally with an uneven distribution (Fig. 7). The diameter of the pores increases moderately to the outside of the chamber walls. Chamber interiors are usually hollow, with vesiculae rarely observed in some chambers. The ratios of chamber heights/chamber widths of *C. catenulata catenulata* are shown in Fig. 5.

Occurrence and stratigraphical range: *Colospongia* is a long lasting sponge genus occurring from the Carboniferous to the Late Triassic. *C. catenulata catenulata* is known from several Ladinian–Carnian reef localities in the former Tethyan realm (Austria, Greece, Italy, Slovakia). The species is described from the Anisian reef limestones of Latemar (Dolomites, Italy) by Emmerich et al. (2005). *C. catenulata catenulata* was described in Hungary for the first time from the Ladinian–Carnian Wetterstein Limestone of the Alsóhegy Karstplateau, northern Hungary by Balogh &

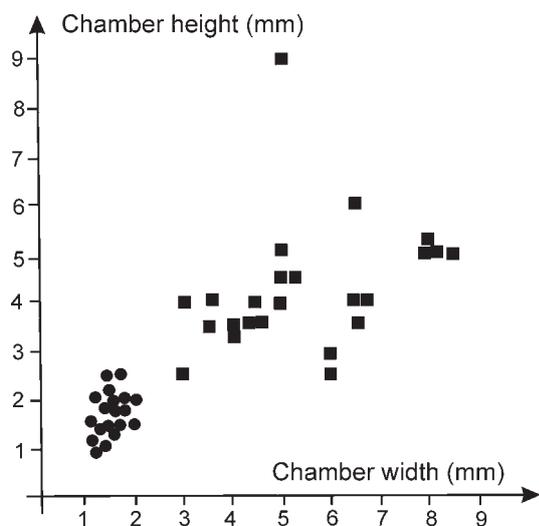


Fig. 5. Ratio of chamber height/chamber width in *Colospongia catenulata catenulata* Ott (dots, 19 measurements) and *Colospongia catenulata macrocatenulata* Scholz (rectangle, 24 measurements).

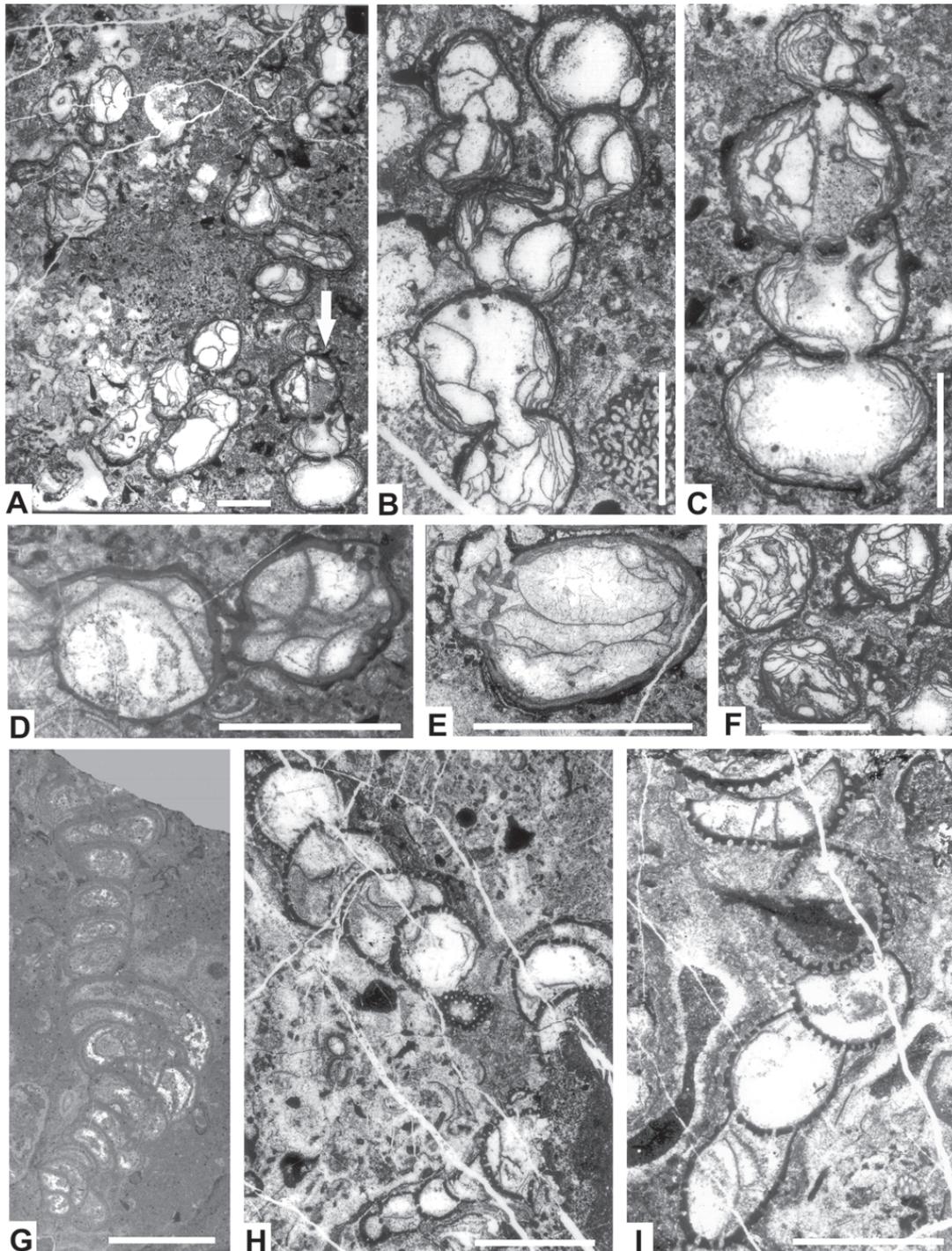


Fig. 6. “Sphinctozoans” from the Anisian-Ladian Aggtelek reef limestones, NE part of Hungary. Scale in all figs. 5 mm. **A–F** — *Follicatena cautica* Ott. **A** — Several longitudinal, oblique and cross-sections showing the abundance of sponges in the investigated material. For magnification of the specimen indicated with an arrow see Fig. C. 79/3c. **B** — Section through a branched specimen showing the single openings or sieve-plates in the chamber walls and the vesiculae within the chamber interiors. U3a. **C** — The magnification from Fig. A (white arrow) shows four chambers with thin walls, the perforation pattern of chamber walls and the abundance of concentric vesiculae within the chambers. 79/3c. **D** — Section through two chambers showing the vesiculae within the chamber interiors and the sieve-plates in the chamber walls. U16. **E** — Similar to Fig. D. The sieve-plate with several openings is clearly visible. U8c. **F** — Cross-sections through three chambers showing the abundant vesiculae within the chamber interiors. 79/3b. **G** — *Amblysiphonella* sp. The specimen seems to be branched in the middle part or the ‘normal’ growth has been interrupted. 79/17/1a. **H** — *Colospongia catenulata macrocatenulata* Scholz. Section through two specimens (or a branched specimen?) with numerous spherical chambers. Chamber walls are pierced by evenly distributed pores. Some vesiculae are within the chamber interiors. 79/9a. **I** — *Colospongia catenulata macrocatenulata* Scholz. Section through a specimen showing similar characteristics to the sponge in Fig. H. 79/9b.

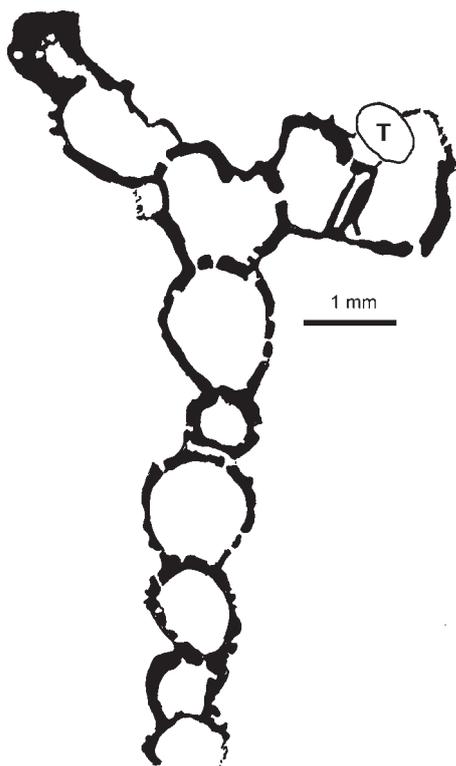


Fig. 7. A branched specimen of *Colospongia catenulata catenulata* Ott shows the unevenly distributed pores of the chamber walls. T — A specimen of a “*Tubiphytes*”-like organism embedded in the chamber of the sponge (drawn from Fig. 4E).

Kovács (1976). It was also described from the Carnian reef of the Bükk Mountains (NE Hungary) by Flügel et al. (1991/92) and now in this paper; both from reef stage 1 and reef stage 2.

Colospongia catenulata macrocatenulata Scholz, 1972
(Fig. 4C; Fig. 6H-I)

1972 *Colospongia catenulata* Ott, 1967 ssp. *macrocatenulata* nov. ssp.
— Scholz; p. 344, pl. 4, fig. 4, pl. 5, fig. 3-6

Material: At least 5 specimens.

Description: The characteristics of the sponge skeleton of *C. catenulata macrocatenulata* correspond to *C. catenulata catenulata*, described above. The only difference between the subspecies is their chamber sizes. For comparison of the chamber sizes of both species the ratios of chamber heights/ chamber widths are shown in Fig. 5.

Occurrence and stratigraphical range: *C. catenulata macrocatenulata* is known from the Illyrian-Lower Ladinian reef limestones between Aggtelek and Jósvalfő; both from reef stage 1 and reef stage 2 (see Fig. 1a-b). Scholz (1972) misdetermined the age of the reef as Pelsonian (see chapter: Introduction, above).

Family: **Sebargasiidae** de Laubenfels, 1955
Genus: *Amblysiphonella* Steinmann, 1882

Type species: *Amblysiphonella barroisi* Steinmann, 1882.

Amblysiphonella sp.
(Fig. 4J; Fig. 8C)

Material: Two specimens.

Description: The specimens of this sponge are poorly preserved and therefore all characteristics are not recognizable. The diameter of both specimens, illustrated in Fig. 4J and Fig. 8C is about 8 mm and they are composed of low rectangular to crescent-shaped chambers with heights of about 3 mm. Some chambers are not well developed. The sponge seems to have two or more axial spongocoels, which are not clearly recognizable. Also due to the recrystallization of the skeleton only indications of the wall perforation can be detected. Rarely vesiculae seem to be present in some chambers.

Family: **Solenolmiidae** Engeser, 1986

Synonymy: **Deningeriidae** Boiko (in Boiko et al. 1991)

Subfamily: **Solenolmiinae** Senowbari-Daryan, 1990

Genus: *Solenolmia* Pomel, 1872

Synonymy: *Dictyocoelia* Ott, 1967

Type species: *Scyphia? manon* Münster, 1841.

Further species: See Senowbari-Daryan & Garcia-Bellido (2002: p. 1530).

Solenolmia manon manon (Münster), 1841
(Fig. 9A-D)

1841 *Scyphia? manon* n. sp. — Münster; p. 29, pl. 1, fig. 15

1987 *Solenolmia manon manon* (Münster) — Senowbari-Daryan & Riedel; p. 7, pl. 1, fig. 1-2, pl. 2, fig. 1, 3-4, pl. 3, fig. 7-8

1989 *Solenolmia manon manon* (Münster) — Mastandrea & Rettori; p. 22, pl. 3, fig. 2

1990 *Solenolmia manon manon* (Münster) — Senowbari-Daryan; p. 89, pl. 29, fig. 1-2 (cum syn.)

1991/92 *Solenolmia manon manon* (Münster) — Flügel et al.; pl. 1, fig. 9

1997 *Solenolmia manon manon* (Münster) — Ruffer & Zamparelli; pl. 27, fig. 4, pl. 28, 5

2005 *Solenolmia manon manon* (Münster) — Emmerich, Zamparelli, Bechstädt & Zühlke; fig. 11/3-5, 11

2006 *Solenolmia manon manon* Nittel; pl. 5, fig. 2 (magnification in pl. 7, fig. 6)

Material: Numerous specimens (for the investigated material see the plate explanations).

Description: Specimens of this sponge are composed of several spherical, hemispherical or barrel-shaped chambers in a moniliform arrangement one after the other. The chamber height is variable (2.0–6.5 mm) but their diameter in the whole stem is almost constant (4–5.5 mm). Chamber interiors are filled with a fine reticulate skeleton. Chamber walls are thin and coarsely perforated, appearing as dark lines in transmitted light. Compared with the sponge diameter, a relatively narrow spongocoel of about 0.5–1 mm in diameter (with spongocoel wall up to 1.5 mm) passes internally through the whole sponge. The spongocoel wall is thick and exhibits a fine vertically oriented lamellar structure.

Occurrence: *Solenolmia manon manon* is known from numerous Anisian-Carnian localities in the west Tethyan realm (see Senowbari-Daryan & Garcia-Bellido 2002: p. 1530;

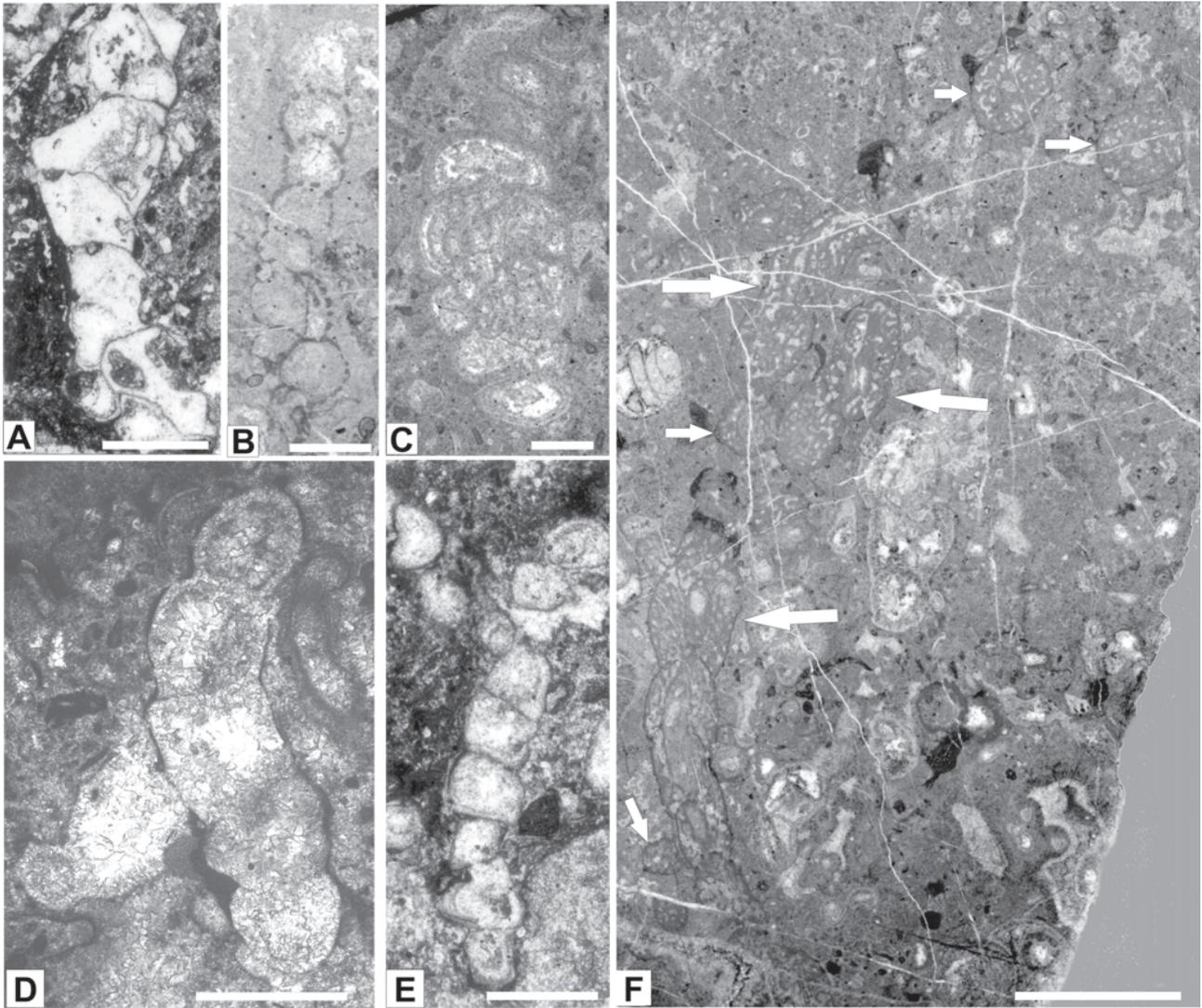


Fig. 8. “Sphinctozoans” from the Anisian-Ladian Aggtelek reef limestones, NE part of Hungary. Scale in all figs. 5 mm. **A** — *Celyphia?* sp. Longitudinal section through several irregularly arranged chambers with thin chamber walls. 79/51. **B** — *Colospongia catenulata catenulata* Ott. Longitudinal section through numerous spherical chambers with evenly perforated chamber walls. 79/3b/2. **C** — *Amblysiphonella* sp. Longitudinal section through several rectangular chambers. The section exhibits in the middle part the existence of one (or several?) spongocoel(s). 79/17/1a. **D** — *Celyphia zoldana* Ott, Pisa & Farabegoli. Section through several circular to rectangular chambers. U8c. **E** — *Celyphia zoldana* Ott, Pisa & Farabegoli. Similar to Fig. D. 79/17/2b. **F** — *Solenolmia radiata* Senowbari-Daryan & Riedel. Cross (small arrows) and longitudinal sections (large arrows) through several specimens. U9c.

synonymy list). Like the preceding species *S. manon manon* was described from Hungary for the first time by Balogh & Kovács (1976).

Solenolmia radiata Senowbari-Daryan & Riedel, 1987
(Fig. 4D/1; Fig. 8F)

1987 *Dictyocoelia* cf. *D. manon minor* — Dullo et al.; p. 532, pl. 3, fig. 2-5
1987 *Solenolmia radiata* n. sp. — Senowbari-Daryan & Riedel; p. 12,
pl. 3, fig. 1-6, pl. 4, fig. 1-4

Material: Several specimens in thin section U9c.

Description: The specimens of this species are composed of several barrel-like chambers with a diameter of 2.5–3 mm.

Chamber heights (2.5–4 mm) are distinctly higher than chamber diameters. An axial spongocoel of 0.3–0.8 mm (measured with the spongocoel wall) or approximately 0.4 mm (without the spongocoel wall) passes internally through the sponge. Chamber walls are thin and appear as dark lines in transmitted light. Chamber interiors are filled with a moderately coarse reticulate fibre skeleton, which appears arranged radially in cross-sections.

Occurrence and stratigraphical range: *Solenolmia radiata* is known from the Carnian Wetterstein Limestone of Austria (Dullo et al. 1987; Senowbari-Daryan & Riedel 1987) and from the upper Illyrian-Lower Ladinian part of the reef (stage 2) east of Aggtelek (Fig. 1a: U1-23), northern Hungary (this paper).

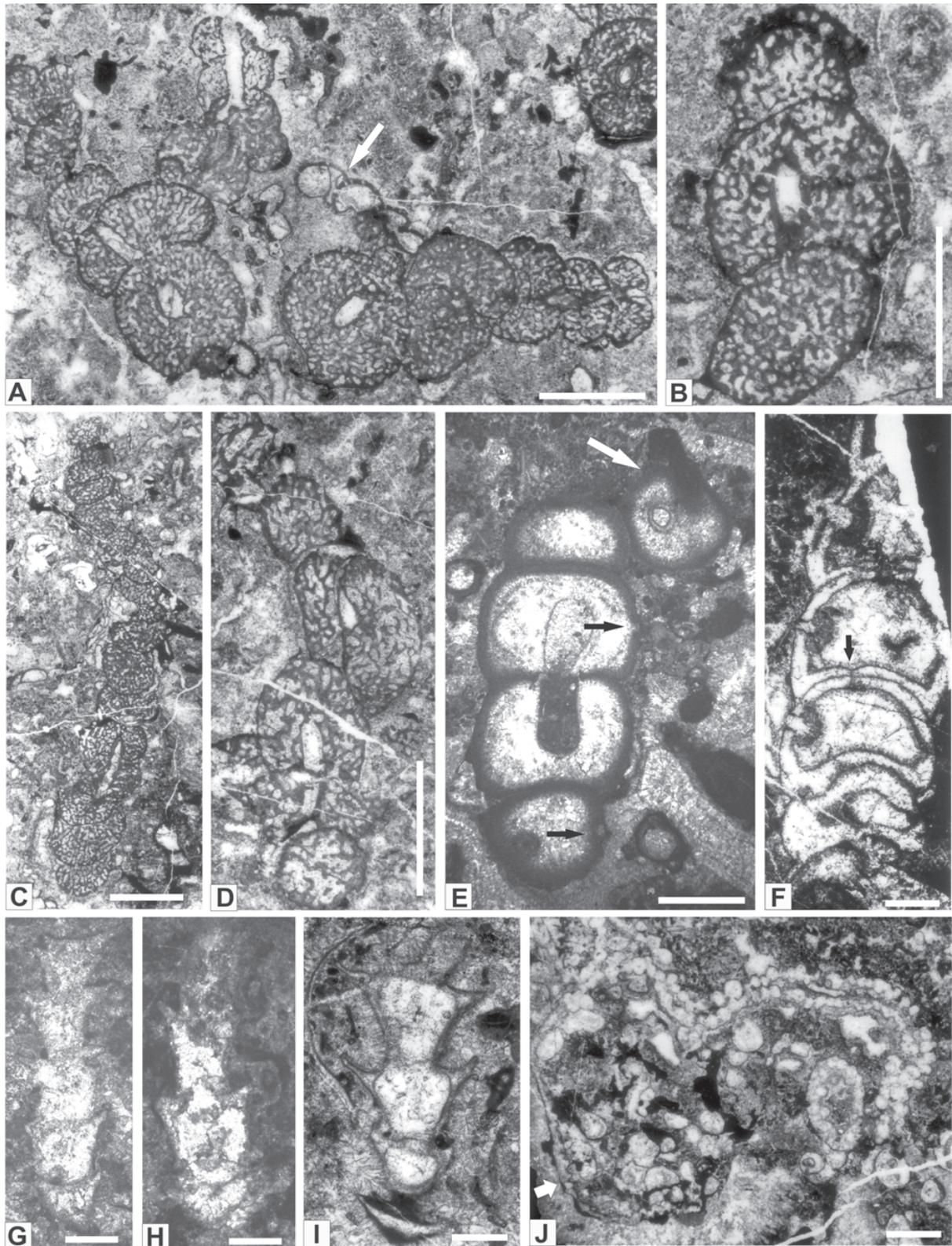


Fig. 9. “Spongiozoans” from the Anisian-Ladian Aggtelek reef limestones, NE part of Hungary. Scale in A–D = 5 mm, in E–F and J = 2 mm, in G–I = 1 mm. **A–D** — *Solenolmia manon manon* (Münster). **A** — Longitudinal and oblique sections through several specimens showing the spherical to hemispherical chambers with thin chamber walls and reticulate filling skeleton within the chamber interiors. The axial spongocoel is about 1/5 of the whole sponge diameter. The arrow indicates a specimen of *Colospongia catenulata catenulata* Ott. 79/14b. **B** — Oblique section through three chambers clearly exhibiting the reticulate filling skeleton and the thin chamber walls. 79/14a. **C** — Marginally...
Continues on the next page

Family: **Celyphiidae** de Laubenfels, 1955
Genus: *Celyphia* Pomel, 1872

Type species: *Manon submarginatum* Münster, 1841.

Further species: See Senowbari-Daryan & Garcia-Bellido (2002: p. 1524).

Celyphia zoldana Ott, Pisa & Farabegoli, 1980
(Fig. 8D–E)

- 1980 *Celyphia zoldana* n. sp. — Ott, Pisa & Farabegoli; p. 833, pl. 62, fig. 1–4
1993 *Celyphia zoldana* Ott, Pisa & Farabegoli — Senowbari-Daryan, Zühlke, Bechstädt & Flügel; p. 208, pl. 43, fig. 1–7, pl. 45, fig. 5–6, pl. 47, fig. 1–2, pl. 48, fig. 1, 3–5, pl. 49, fig. 4–5, 9 (cum syn.)
1997 *Celyphia zoldana* Ott, Pisa & Farabegoli — Schafhauser; p. 107–108, pl. 12, fig. 5
2005 *Celyphia zoldana* Ott, Pisa & Farabegoli — Emmerich, Zamparelli, Bechstädt & Zühlke; fig. 9/1–7

Material: At least two specimens. Both are illustrated in Fig. 8D–E.

Description: The small specimens of this sponge are composed of circular to rectangular chambers with moniliform or occasionally glomerate arrangements. The spherical to barrel-shape (in thin section circular to rectangular) chambers are small and usually less than 2 mm in diameter. The imperforate chamber walls are thick (0.2 mm) and pierced by one or two ostia in each chamber with upraised edges. Chamber interiors are without vesiculae. Specimens are usually attached to the substratum.

Occurrence and stratigraphic range: *Celyphia zoldana* is known from the Anisian of the Dolomites, Italy (Ott et al. 1980; Senowbari-Daryan et al. 1993 and further references; Emmerich et al. 2005), Karawanken, Austria (Schafhauser 1997), and from the reef of Aggtelek; both from reef stage 1 and reef stage 2 (this paper).

Celyphia? sp.
(Fig. 8A)

Material: One specimen only.

Description: The only specimen of this sponge is about 17.5 mm long and is composed of several irregularly arranged chambers of about 6 mm in diameter. The sponge seems to be broken in a longitudinal direction, because the chamber walls are straight on one side and cannot be seen on the other side.

The chamber walls of about 0.1 mm thick are imperforate and pierced by rare ostia of 0.1–0.2 mm in diameter.

Remarks: Because of the imperforate chamber walls with some ostia the attribution of this sponge to the genus *Celyphia* is possible, but not certain.

Family: **Thaumastocoeliidae** Ott, 1967

Subfamily: **Thaumastocoeliinae** Senowbari-Daryan, 1990
Genus: *Thaumastocoelia* Steinmann, 1882

Type species: *Thaumastocoelia cassiana* Steinmann, 1882.

Thaumastocoelia dolomitica Senowbari-Daryan, Zühlke, Bechstädt & Flügel, 1993
(Fig. 9G–I)

- 1993 *Thaumastocoelia dolomitica* n. sp. — Senowbari-Daryan, Zühlke, Bechstädt, Flügel; p. 210, pl. 54, fig. 1–4
2005 *Thaumastocoelia dolomitica* Senowbari-Daryan, Zühlke, Bechstädt & Flügel — Emmerich, Zamparelli, Bechstädt & Zühlke; fig. 11/6

Material: Three specimens.

Description: The tiny and moniliform stems of this sponge are composed of cup-like or funnel-shaped chambers with a distinctly collar-like edge on the upper part of the chambers. The diameter of the upper part of the chambers (collar) varies between 1.2 mm and 2.24 mm in different specimens. There is no spongocoel, but the chamber roofs are pierced by several small pores. The chamber walls are thin, like the roofs. Some ostia seem to be located in the exowall (Fig. 10). The biometrical data of *Th. dolomitica* are summarized in Table 1 and a reconstruction is given by Senowbari-Daryan et al. (1993).

Table 1: Biometrical data of *Thaumastocoelia dolomitica* Senowbari-Daryan, Zühlke, Bechstädt & Flügel. **L** — length of sponge, **NC** — number of chambers, **CH** — chamber height, **CDB** — chamber diameter at the base, **DC** — chamber diameter at the top (collar), **TW** — thickness of exowall. All dimensions in mm.

Thin section	L	NC	CH	CDB	DC	TW
U16	4	4	0.8–1.3	0.7	2–2.4	0.1
U21	5.5	5.5	1–1.5	0.7–1.0	1.7–1.9	0.1
U21	3.5	3	1.1–1.3	0.7	1.2–1.3	0.6

Fig. 9. Text continues from the previous page. ... longitudinal section through numerous chambers showing similar characteristics of the sponge to Fig. A. 79/12b. **D** — Section through four chambers showing similar characteristics to Fig. A. 79/14/d. **E** — *Kovacsia baloghi* (Kovács). Marginally longitudinal section through four chambers exhibiting the imperforate chamber walls with only two ostia (arrows). The thin, dark line appearing within the chamber interiors indicates the spongocoel wall, which is filled with micritic sediment or cement in part. The white arrow indicates another specimen cut in cross-section. 79/17/1e. **F** — *Thaumastocoelia* cf. *Th. cassiana* Steinmann. Longitudinal section through several chambers filled with spary calcite cement. Chamber exowalls are pierced with ostia. The arrow indicates the double-layered interwall with an osculum, cut marginally. The ostia of the exowalls show internally a dark line, which is interpreted as vesiculae, closing the ostium. U13. **G–I** — *Thaumastocoelia dolomitica* Senowbari-Daryan, Zühlke, Bechstädt & Flügel. **G** — Section through a poorly preserved specimen with six cup-like or funnel-shaped chambers. The youngest chamber is incompletely formed. U21. **H** — Similar section to Fig. G. U21. **I** — Section through five funnel-shaped chambers. The first chamber is cut only on the collar and the youngest chamber is incomplete. The upraised collar-like edge of the chambers is clearly visible. U16. **J** — *Olangocoelia otti* Bechstädt & Brandner. Section through numerous small spherical chambers arranged in rows, partly in two rows. Some chambers are incompletely formed (see arrow). 79/26.

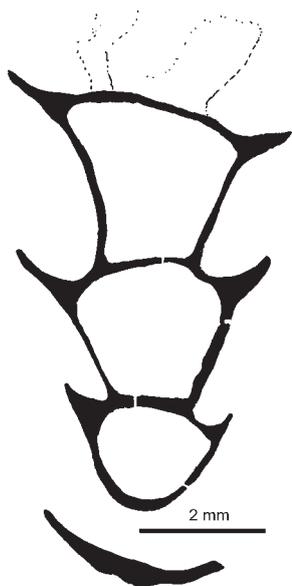


Fig. 10. *Thaumastocoelia dolomitica* Senowbari-Daryan, Zühlke, Bechstädt & Flügel. The section shows the upraised edges of the funnel-shaped chambers and some openings in the chamber exowalls and interwalls (drawn from Fig. 9I).

Remarks: *Thaumastocoelia dolomitica* is one of the smallest “sphinctozoan” sponges. The dimensions of sponge, chambers and chamber elements of the Hungarian specimens correspond to the dimensions of the type material from the Anisian of the Italian Dolomites. The only differences between the specimens of the type material and specimens from Hungary are the distinctly developed collars at the upper edge of the chambers in the Hungarian specimens. The specimen illustrated from the Anisian reef limestones of Latemar (Dolomites, Italy) by Emmerich et al. (2005) also shows well developed collars like the Hungarian specimens.

Occurrence and stratigraphic range: *Thaumastocoelia dolomitica* is known from the Anisian of the type locality (Reflugio Berti/Comelico, Dolomites, Italy) and from the Anisian reef limestones of Latemar (Dolomites, Italy). The third locality where *Th. dolomitica* occurs is the upper part of the Aggtelek reef (upper Illyrian–Lower Ladinian: reef stage 2). In all three localities it is a rare sponge species.

Thaumastocoelia cf. *Th. cassiana* Steinmann, 1882
(Fig. 9F)

Material: One specimen only.

Description: The one specimen of this sponge reaches a length of 25 mm and is composed of six hemispherical chambers in which the oldest and youngest chambers are broken. The chamber diameter is more or less constant in the whole sponge, reaching about 6 mm. Each chamber roof is double-layered and pierced by one opening (or perhaps occasionally by more, as they are not situated in the middle of the roofs). Chamber exowalls are pierced by ostia of up to 1 mm in diameter. Thickness of the chamber walls is about 0.4–0.5 mm. The chamber interiors have no filling skeleton or vesiculae.

Remarks: The asiphonate construction of the sponge, the double-layered chamber roofs and the ostia in the exowall are similar to *Thaumastocoelia cassiana*. The chamber roofs of *Th. cassiana* are pierced by several openings which could not be proven for certain in this sponge. In addition *Th. cassiana* is known only from the Carnian time interval; the present species is from the upper Illyrian–Lower Ladinian part (reef stage 2) of the reef.

Genus: *Follicatena* Ott, 1967

Type species: *Follicatena cautica* Ott, 1967.

Further species: See Senowbari-Daryan & Garcia-Bellido (2002).

Follicatena cautica Ott, 1967
(Fig. 4A,G–I; Fig. 6A–F)

- 1967 *Follicatena cautica* n. sp. — Ott; p. 22, pl. 1, fig. 1–7
 1978b *Follicatena cautica* Ott — Kovács; p. 301, pl. 4, fig. 5
 1978b *Follicatena* cf. *cautica* Ott — Kovács; p. 302, pl. 4, fig. 2
 1989 *Follicatena cautica* Ott — Mastandrea & Rettori; p. 20, pl. 2, fig. a–c
 1990 *Follicatena cautica* — Ciarapica et al.; Fig. 2/A (right)
 1990 *Follicatena cautica* Ott — Senowbari-Daryan; p. 116, pl. 41, fig. 4 (cum syn.)
 1997 *Follicatena cautica* Ott — Ruffer & Zamparelli; pl. 28, fig. 3
 2005 *Follicatena cautica* Ott — Emmerich, Zamparelli, Bechstädt & Zühlke; fig. 11/7, 12–13

Material: Numerous specimens.

Description: *Follicatena cautica* is — along with *Solenolmia manon manon* and *Colospongia catenulata* — the most abundant sponge species in the investigated reef limestones. To show the variable morphology of the sponge, several specimens are illustrated. The chamber arrangement of the single or branched sponge is either moniliform (Fig. 4A,G–I) or occasionally glomerate (Fig. 6A). Diameter of the chambers varies between 3 mm and 8 mm. The chambers communicate with each other and with the outside either by a single opening (Fig. 4A,G,I) or by sieve-plates (Fig. 6E). Chamber walls are thin, but they can appear thicker, if the concentrically multilayered vesiculae are secreted within the chamber interior. Vesiculae are also abundant within the chamber interiors (Fig. 6A–F). The wall between two chambers may be single or double-layered.

Occurrence and stratigraphical range: *Follicatena cautica* is known from the Ladinian–Carnian of several localities in the Alpine–Mediterranean region (see Senowbari-Daryan & Garcia-Bellido 2002 and synonymy list). Boiko (1986) described it from the Carnian of the Pamir Mountains. It occurred in the Aggtelek reef both in reef stage 1 and in reef stage 2.

Genus: *Kovacsia* nov. gen.

Derivatio nominis: This genus name is dedicated to our late colleague Sándor Kovács, who described the sponge in question as *Sollasia* for the first time.

Description: An imperforate chambered sponge with spherical to barrel-shaped chambers arranged one above the

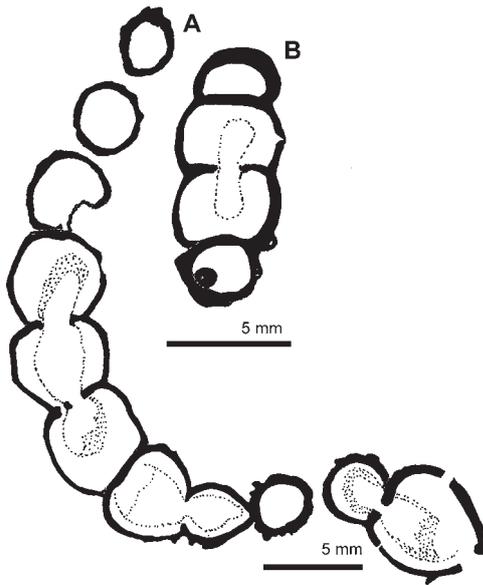


Fig. 11. *Kovacsia baloghi* (Kovács). **A** — The holotype of the species drawn from Kovács (1978a: fig. 6C) and **B** — from Fig. 9E (this paper). Both species show the thin spongocoel wall followed the chamber exowalls. The holotype shows two openings in one chamber roof and only one opening in three chamber roofs. Rarely ostia are cut in the chamber exowalls of both specimens.

other. Chamber size is more or less constant in the whole stem. Ostia are seldom found in the chamber exowalls. There is an axial spongocoel following the exowalls with an extremely thin wall and not everywhere the same diameter.

Type species: *Sollasia? baloghi* Kovács, 1978a.

Kovacsia baloghi (Kovács, 1978a) nov. comb.
(Fig. 9E, Fig. 11)

1978a ?*Sollasia baloghi* n. sp. — Kovács; p. 686; fig. 5B, 6C

Material: One specimen only.

Description: This sponge species is documented by three specimens only. The holotype, illustrated in Kovács (1978a: fig. 6C; redrawn in Fig. 11) is a curved specimen and is composed of eleven spherical chambers. Kovács gives the diameter of the chambers as 2.5–2.7 mm and their height 2.0–2.6 mm.

The specimen in our collection is composed of four chambers with a maximum diameter of 4 mm and is moderately larger than the holotype described originally by Kovács (1978a). The axial canal of approximately 1 mm in diameter is cut in the two middle chambers. The holotype described by Kovács exhibits only one in three chamber roofs but there are two small openings in one chamber roof (see Fig. 11A). The chamber walls are imperforate, but in two chambers large ostia are cut marginally (Fig. 11B). The most characteristic feature of the sponge is the thin spongocoel wall, which is widened in the middle of the chambers (clearly seen in the holotype, see Fig. 11A), more or less following the chamber exowalls. As in the holotype the chamber interiors of our specimen are filled with calcite cement, but the interior

of the spongocoel has a different filling. Such a widening spongocoel in the middle of the chambers is not known from the other “sphinctozoan” genera, either from the Paleozoic or from the Triassic. For this character the new genus *Kovacsia* is introduced (see also remarks).

The white arrow in Fig. 9E points to the second specimen cut in a transversal section. This specimen exhibits the spongocoel appearing as a circle within the chamber.

An aporate chambered sponge with an axial cylindrical spongocoel is characteristic for e.g. the Permian genera *Girtyocoelia* Cossmann (1909), or *Shotorithalamia* Senowbari-Daryan et al. (2006) but the annulated spongocoel wall following the chamber exowalls is known only in the new genus *Kovacsia*.

Remarks: The chamber walls of *Kovacsia baloghi* were characterized by “two layers” according to Kovács (1978a). In his description he wrote (p. 687): “The imperforate wall consists of an inner, dark, micritic layer 0.06–0.18 mm in thickness and an outer, light, recrystallized layer, which is of 0.35 mm maximum thickness and is missing on several parts”. The “outer, light and recrystallized” layer, mentioned by Kovács is an incrustation and is not secreted by the sponge. Consequently the chamber wall consists only of a single micritic layer appearing as a dark micritic layer in transmitted light. This is clearly recognizable in our specimen illustrated in Fig. 9E.

Occurrence and stratigraphical range: *Kovacsia baloghi* is known only from the Anisian (Illyrian; reef stage 1) part of the reef limestone of the Aggtelek reefs, northeast Hungary (Kovács 1978a; and this paper).

Order uncertain

Family: **Olangocoeliidae** Bechstädt & Brandner, 1970

Genus: *Olangocoelia* Bechstädt & Brandner, 1970

Type species: *Olangocoelia otti* Bechstädt & Brandner, 1970.

Olangocoelia otti Bechstädt & Brandner, 1970

(Fig. 4K; Fig. 9J)

1970 *Olangocoelia otti* n. sp. — Bechstädt & Brandner; p. 68, pl. 14, fig. 1–2, pl. 15, fig. 1–4

1990 *Olangocoelia otti* Bechstädt & Brandner — Senowbari-Daryan; pl. 45, fig. 9–10; pl. 46, fig. 1–2 (cum syn.)

1990 *Olangocoelia otti* Bechstädt & Brandner — Scheuber; p. 72, pl. 11, fig. 6

1993 *Olangocoelia otti* Bechstädt & Brandner — Senowbari-Daryan, Zühlke, Bechstädt & Flügel; p. 218, pl. 40, fig. 1–5, pl. 41, fig. 1–4; pl. 42, Fig. 1–2, pl. 45, fig. 7, text-fig. 10

1997 *Olangocoelia otti* Bechstädt & Brandner — Schafhauser; p. 109, pl. 12, fig. 7

2004 *Olangocoelia otti* Bechstädt & Brandner — Finks & Rigby; p. 681, fig. 5a–b

2005 *Olangocoelia otti* Bechstädt & Brandner — Emmerich, Zamparelli, Bechstädt & Zühlke; Fig. 11/1–2

Material: Several “colonies”.

Description: The “colonies” of this sponge are composed of numerous circular to oval chambers arranged in irregularly

curved lines. The chambers are arranged on one layered lines, but occasionally also on two-layered lines. The chains of *Olangocoelia* surround the small irregular cavities, which are usually filled with cement or, rarely, with micritic sediment. The interior of the chambers was hollow and later they became filled with calcite cement. Ostia are rare within the chamber walls. The connection of individual chambers is established either directly or by a small tube. Vesiculae do not occur, either in our material or in the material described by Senowbari-Daryan et al. (1993), but according to Bechstädt & Brandner (1970: p. 69) they occur within some chambers. Senowbari-Daryan et al. (1993: p. 220) observed “dichotomously branched tubes which stretch out from the chambers into the sediments, but never into the cavity surrounded by the chambers” (see Senowbari-Daryan 1993: text-fig. 10). The detailed description of such tubes and also *Olangocoelia otti* is undertaken by Bechstädt & Brandner (1970) and by Senowbari-Daryan et al. (1993).

The systematic position of *Olangocoelia* as a “sphinctozoan” sponge or foraminifer is uncertain (Senowbari-Daryan et al. 1993).

Occurrence: *Olangocoelia otti* is known from several Anisian-Ladinian localities in the Dolomites, northern Italy (Bechstädt & Brandner 1970; Zorn 1971, 1972; Blendinger 1983; Fois & Gaetani 1984; Senowbari-Daryan et al. 1993; Emmerich et al. 2005), Karawanken (Schafhauser 1997), Hungary (this paper) and Carnic Alps (Pfeiffer 1988). It is known both from reef stage 1 and reef stage 2 of the Aggtelek reef.

Discussion

The “sphinctozoan” fauna of the Illyrian-Lower Ladinian Aggtelek reef was previously described by Scholz (1972) and the present paper. The “sphinctozoans” of the Ladinian-Carnian Wetterstein Limestone of Alsóhegy Karstplateau, in northern Hungary (20 km north-east of the Aggtelek reef) were described by Balogh & Kovács (1976) and Kovács (1978a,b). Several taxa, including the genera *Vesicocaulis*, *Uvanella*, *Cryptocoelia*, *Stylothalamia*, *Paravesicocaulis* and “*Verticillites*” described by these authors were not found in the investigated material of the Aggtelek reef limestones. These genera are also not known from other Anisian localities in the world and are “typically” sponges of Wetterstein reef limestone (Ladinian-Carnian).

Some general notes are thought necessary concerning some sponge taxa of the Ladinian-Carnian Wetterstein limestones described by the above mentioned authors from the Alsóhegy Karstplateau: the Species, described as *?Cystothalamia* sp. and illustrated in pl. 3, fig. 1 by Balogh & Kovács (1976) is most probably “*Cystothalamia*” *bavarica*, attributed now to the genus *Alpinothalamia* Senowbari-Daryan (1990). “*Verticillites*” *triassicus* Kovács (1978a) is attributed as type species to the genus *Senowbaridaryana* by Engeser & Neumann (1986). All these genera are typically “sphinctozoans” of the Carnian, but may also occur rarely in the Ladinian time interval.

Acknowledgments: The investigations were carried out by Felicitasz Velledits during a short stay in Germany supported

by the “Deutscher Akademischer Austauschdienst”. The authors thank the journal referees for their valuable comments.

References

- Balogh K. & Kovács S. 1976: Sphinctozoa from the reef facies of the Wetterstein Limestone of Alsóhegy-Mount (South Gemericum, West Carpathian, Northern Hungary). *Acta Mineral. Petrogr. Szeged* 22, 2, 297–310.
- Bechstädt T. & Brandner R. 1970: Das Anis zwischen St. Vigil und dem Höhlensteintal (Pragser und Olinger Dolomiten, Südtirol). *Festband Geol. Inst., 300-Jahr-Feier, Univ. Innsbruck*, 9–103.
- Blendinger W. 1983: Anisian sedimentation and tectonics of the M. Pore-M. Cerneria area (Dolomites). *Riv. Ital. Paleont. Stratigr.* 69, 2, 175–208.
- Boiko E.V. 1986: ‘Sphinctozoans’ from the Late Triassic Reefs from the SE Pamir. In: Sokolov B.S. (Ed.): Phanerozoic reefs and corals of the USSR. *Acad. Nauk USSR, Moscow*, 3–11 (in Russian).
- Boiko E.V., Belyaeva G.V. & Zhuravleva I.T. 1991: Sphinctozoa fanerozoya territorii SSSR. [Phanerozoic ‘sphinctozoans’ from the Territory of USSR.] *Nauka, Moscow*, 1–23 (in Russian).
- Ciarapica G., Cirilli S., Martini R., Rettori R., Zaninetti L. & Salvini-Bonnard G. 1990: Carbonate buildups and associated facies in the Monte Facito Formation (Southern Apennines). *Boll. Soc. Geol. Ital.* 109/1, 151–164.
- Cossmann M. 1909: Rectification de nomenclature. *Rev. Critique Paléontologie* 13, 67.
- de Laubenfels M.W. 1955: Porifera. In: Moore R.C. (Ed.): Treatise on invertebrate palaeontology. Part E: Archaeocyatha and Porifera. *Geol. Soc. Amer., Univ. Kansas Press, New York & Lawrence*, 21–112.
- Dullo W.-Ch., Flügel E., Lein R., Riedel P. & Senowbari-Daryan B. 1987: Algen, Kalkschwämme und Mikroproblematika aus unterkarnischen Riffkalken des Bosruck-Gipfels (Nördliche Kalkalpen, Österreich). *Jb. Geol. B.-A* 129 (3+4), 525–543.
- Emmerich A., Zamparelli V., Bechstädt T. & Zühlke R. 2005: The reefal margin and slope of a Middle Triassic carbonate platform: The Latemar (Dolomites, Italy). *Facies* 50, 573–614.
- Engeser T. 1986: Nomenklatorische Notiz zur Gattung *Dictyocoelia* Ott 1967 (“Sphinctozoa”, Porifera). *Neu. Jb. Geol. Paläont., Mh.* 1986 (10), 587–590.
- Engeser T. & Neumann H.H. 1986: Ein neuer verticillidider “Sphinctozoe” (Demospongiae, Porifera) aus dem Campan der Krappfeld-Gosau (Kärnten, Österreich). *Mitt. Geol. Paläont. Inst. Univ. Hamburg* 61, 149–159.
- Enos P., Jiayoung W. & Yangii Y. 1997: Facies distribution and retreat of Middle Triassic platform margin, Guizhou Province, south China. *Sedimentology* 44, 563–584.
- Finks R.M. & Rigby J.K. 2004: Hypercalcified sponges. In: Kaesler R.L. (Ed.): Treatise on invertebrate paleontology. Part E: Porifera (revised). Vol. 3. *Geol. Soc. Amer., Univ. Kansas, Boulder, Kansas*, 585–764.
- Flügel E. 1982: Evolution of Triassic reefs: Current concepts and problems. *Entwicklung der trias-Riffe: Kenntnisstand und Probleme. Facies*, 297–327.
- Flügel E. 2002: Triassic Reef patterns. In: Kiessling W., Flügel E. & Golonka J. (Eds.): Phanerozoic reef patterns. *SEPM Spec. Publ.*, Tulsa 72, 391–463.
- Flügel E. & Senowbari-Daryan B. 2001: Triassic reefs of the Tethys. In: Stanley G.D. (Ed.): The history and sedimentology of ancient reef systems. *Plenum Press, New York*, 217–249.
- Flügel E., Velledits F., Senowbari-Daryan B. & Riedel P. 1991/1992:

- Rifforganismen aus "Wettersteinkalken" (Karn?) des Bükk-Gebirges, Ungarn. *Geol. Paläont. Mitt. Innsbruck* 18, 35–62.
- Fois E. & Gaetani M. 1984: The recovery of reef-building communities and the role of cnidarians in carbonate sequences of the Middle Triassic (Anisian) in the Italian Dolomites. *Palaeontograph. Amer.* 54, 191–200.
- Gaetani M., Foies E., Jadoul F. & Nicora A. 1981: Nature and evolution of Middle Triassic build-ups in the Dolomites (Italy). *Mar. Geol.* 44, 25–57.
- Gawlick H.J., Frisch W., Vecsei A., Steiger T. & Böhm F. 1999: The change from the rifting to thrusting in the Northern Calcareous Alps as recorded in Jurassic sediments. *Geol. Rundsch.* 87, 644–657.
- Grant R.E. 1836: Animal kingdom. In: Todd R.B. (Ed.): The Cyclopaedia of anatomy and physiology. Vol. 1. *Sherwood, Gilbert & Piper*, London, 107–118.
- Haas J., Hámor G., Jámor Á., Kovács S., Nagymarosy A. & Szederkényi T. 2001: Geology of Hungary. *Eötvös University Press*, Budapest, 1–317.
- Jablonský E. 1974: Segmentierte Kalkschwämme (Sphinctozoa) aus Wettersteinkalken einiger Gebirge der Westkarpaten. *Acta Geol. Geogr. Univ. Comeniana, Geol.* 26, 189–202.
- Kovács S. 1978a: New "sphinctozoan" sponges from the North Hungarian Triassic. *Neu. Jb. Geol. Paläont., Mh.* 1978 (11), 685–697.
- Kovács S. 1978b: Newer Calcareous sponges from the Wetterstein Reef limestone of Alsóhegy Karstplateau (Silica Nappe, Western Carpathians, North Hungary). *Acta Mineral. Petrogr. Szeged* 23, 2, 299–317.
- Kovács S. 1989: Geology of North Hungary: Paleozoic and Mesozoic terranes. In: Kecskeméti T. (Ed.): 21st Europ. Micropaleont. Colloq. Guidebook. *Hung. Geol. Soc.*, Budapest, 15–36.
- Kovács S. 1997: Middle Triassic rifting and facies differentiation in Northeast Hungary. In: Sinha A.K. (Ed.): Geodynamic domains in the Alpine-Himalayan Tethys. *IBH Publishing Co. Pvt. Ltd.*, Oxford, New Delhi, Calcutta, 375–397.
- Kozur H. 1991: The evolution of the Meliata-Hallstatt ocean and its significance for the early evolution of the Eastern Alps and Western Carpathians. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 87, 109–135.
- Kozur H. & Mock R. 1973: Die Bedeutung der Trias-Conodonten für die Stratigraphie und Tektonik der Trias in den Westkarpaten. *Geol. Paläont. Mitt. Innsbruck* 3, 2, 1–14.
- Laube G.C. 1864: Bemerkungen über die Münster'schen Arten von St. Cassian in der Münchner Paläontologischen Sammlung. *Jb. Geol. Reichsanst.* 14, 402–412.
- Lehrmann D.J., Wei J. & Enos P. 1998: Controls on facies architecture of a large Triassic carbonate platform: the great bank of Guizhou, Nanpanjiang Basin, South China. *J. Sed. Res.* B68, 311–326.
- Lein R. 1987: Evolution of the Northern Calcareous Alps during Triassic times. In: Flügel H.W. & Faupl P. (Eds.): Geodynamics of the Eastern Alps. *Deutick*, Wien, 85–102.
- Mastandrea A. & Rettori R. 1989: On the occurrence of a sphinctozoan (Porifera) assemblage in the carbonatic bodies of Monte Facito Formation (Southern Apennines). *Atti Soc. Nat. Modena* 120 (1989), 15–26 (in Italian).
- Mello J., Elečko M., Pristaš J., Reichwalder P., Snopko L., Vass D., Vozárová A., Gaál L., Hanzel V., Hók J., Kováč P., Slavkay M. & Steiner A. 1997: Explanations to the geological map of the Slovak Karst, 1:50,000. *Vyd. D. Štúra*, Bratislava, 1–255 (in Slovak).
- Münster G.F. 1841: Beiträge zur Geognosie und Petrefakten-Kunde des südöstlichen Tirols, vorzüglich der Schichten von St. Cassian. *Bayreuth*, 1–152.
- Nittel P. 2006: Beiträge zur Stratigraphie und Mikropaläontologie der Mitteltrias der Innsbrucker Nordkette (Nördlicher Kalkalpen, Austria). *Geo. Alp.* 3, 93–145.
- Ott E. 1967: Segmentierte Kalkschwämme (Sphinctozoa) aus der alpinen Mitteltrias und ihre Bedeutung als Riffbildner im Wettersteinkalk. *Bayer. Akad. Wiss. Math.-Naturwiss. Kl., Abh., N.F.* 131, 1–96.
- Ott E. 1972: Mitteltriadische Riffe der Nördlichen Kalkalpen und altergleiche Bildungen aus Karaburun und Chios (Ägäis). *Mitt. Gesell. Geol. Bergbaustud.* 21, 251–276.
- Ott E., Pisa G. & Farabegoli E. 1980: *Celyphia zoldana* sp. n., a reef building "sphinctozoan" sponge in Anisian limestones of the Southern Dolomites. *Riv. Ital. Paleont.* 85, 829–842.
- Payne J.L., Lehrmann D.J., Christensen S., Wei J. & Knoll A. 2006: Environmental and biological controls on the initiation and growth of a Middle Triassic (Anisian) reef complex on the Great Bank of Guizhou, Guizhou province, China. *Palaios* 21, 325–343.
- Pfeiffer J. 1988: Paleontology and microfacies of platform margin in the Carnic Alps (Austria, Middle Triassic). *Facies* 19, 33–60.
- Pomel A. 1872: Paléontologie ou description des animaux fossils de la province d'Oran. 5. *Spongiaires*, Oran, 1–256.
- Rüffer T. & Zamparelli V. 1997: Facies and biota of Anisian to Carnian Carbonate platforms in the Northern Calcareous Alps (Tyrol and Bavaria). *Facies* 37, 115–136.
- Schafhauser M. 1997: Stratigraphie und Fazies in der Mitteltrias der Südkarawanken (Kärnten/Österreich) im Vergleich zur lithostratigraphischen Entwicklung des angrenzenden Südalpins. *Unpubl. Ph.D. Thesis, Technische Universität Berlin*, Berlin, 1–161.
- Scheuber M. 1990: Der Spitzkalk von Recoaro (Vicentinische Alpen, Norditalien): Sedimentologie, Paläontologie und Paläogeographie eines mitteltriassischen Sedimentationsraumes. *Facies* 23, 57–96.
- Schmid S.M., Bernoulli D., Fügenschuh B., Matenco L., Schefer S., Schuster R., Tischler M. & Ustaszewski K. 2008: The Alpine-Carpathian-Dinaridic orogenic system: correlation and evolution of tectonic units. *Swiss. J. Geosci.* 101, 139–183. Doi: 10.1007/s00015-008-1247-3
- Scholz G. 1972: An Anisian Wetterstein Limestone Reef in North Hungary. *Acta Mineral. Petrogr. Szeged* 20, 2, 337–362.
- Senowbari-Daryan B. 1990: Die systematische Stellung der thalaminiden Schwämme und ihre Bedeutung in der Erdgeschichte. *Münchner Geowiss. Abh., Reihe A (Geologie und Palaeont.)* 21, 1–325.
- Senowbari-Daryan B. & Abate B. 1986: Zur Paläontologie, Fazies und Stratigraphie der Karbonate innerhalb der "Formazione Mufara" (Obertrias, Sizilien). *Natur. Sicil., Ser. IV* 10 (1–4), 50–104.
- Senowbari-Daryan B. & Garcia-Bellido D.C. 2002: "Sphinctozoa": Chambered sponges (Polyphyletic). In: Hooper J.N.A. & Van Soest R.W.M. (Eds.): System Porifera. A guide to the classification of sponges. *Kluwer Acad./Plenum Publ.*, New York, 1511–1533.
- Senowbari-Daryan B. & Riedel P. 1987: Revision der triadischen Arten von *Solenomia* Pomel 1872 (*Dictyocoelia* Ott 1967) ("Sphinctozoa", Porifera) aus den alpin-mediterranen Raum. *Mitt. Bayer. Staatssamml. Paläont. Hist. Geol.* 27, 5–20.
- Senowbari-Daryan B. & Schäfer P. 1983: Zur Sphinctozoen-Fauna der obertriadischen Riffkalke ("Pantokratorkalke") von Hydra, Griechenland. *Geologica et Palaeont.* 17, 179–205.
- Senowbari-Daryan B. & Velledits F. 2007a: *Axopora aggtelekensis* Scholz 1972, originally described as Hydrozoa, is attributed to the new genus *Anisophytes* n. gen. (Cyanophyta). *Riv. Paleont. Stratigr. Ital.* 113, 3, 357–368.
- Senowbari-Daryan B. & Velledits F. 2007b: *Aggtecella*, a new genus of Corallinales (Rhodophyta) from the Anisian of the Aggtelek-Rudabánya Mountains, NE Hungary. *Facies* 53, 401–407.
- Senowbari-Daryan B., Zühlke R., Bechstädt Th. & Flügel E. 1993:

- Anisian (Middle Triassic) Buildups of the Northern Dolomites (Italy): The recovery of reef communities after the Permian/Triassic Crisis. *Facies* 28, 181–256.
- Senowbari-Daryan B., Rashidi K. & Hamedani A. 2006: Two Permian “sphinctozoan” sponges from the Shotori Mountains (eastern Iran). *Geol. Carpathica* 57, 6, 427–432.
- Sollas W.J. 1875: Sponges. In: *Encyclopedia Britannica*. 9th edition. *Encyclopedia Britannica, Inc.*, London, 1–451.
- Steinmann G. 1882: Pharetronen-Studien. *Neu. Jb. Miner., Geol. Paläont.* 2, 139–191.
- Tollmann A. 1987: Neue Wege in der Ostalpengeologie und die Beziehungen zum Ostmediterrän. (New directions on the Geology of the Eastern Alps and their connection to the Eastern Mediterranean). *Mitt. Österr. Geol. Gesell.* 80, 47–113.
- Velledits F., Péro Cs., Blau J., Senowbari-Daryan B., †Kovács S., Piros O., Pocsai T., Szügyi-Simon H., Dumitrică P. & Pálffy J. 2011: The oldest Triassic platform margin reef from the Alpine-Carpathian Region (Aggtelek, NE Hungary): platform evolution, reefal biota and biostratigraphic framework. *Riv. Paleont. Stratigr. Ital.* 117, 221–268.
- Wu Y.-Sh. 1991: Organisms and communities of Permian Reef of Xiangbo, China. *Int. Acad. Publ.*, Beijing, 1–192.
- Zorn H. 1971: Paläontologische, stratigraphische und sedimentologische Untersuchungen des Salvatoredolomits (Mitteltrias) der Tessiner Kalkalpen. *Schweiz. Paläont. Abh.* 91, 1–90.
- Zorn H. 1972: Mikrofazielle Analyse eines mitteltriadischen Riffkomplexes in den Tessiner Kalkalpen. *Mitt. Gesell. Geol. Bergbaustud.* 21, 123–142.