

Middle Miocene scleractinian coral assemblages from the Pannonian Basin (Central Paratethys) with description of a new *Trochocyathus* (*Aplocyathus*) species

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Abstract: Two newly collected scleractinian coral assemblages from the lower Badenian (Middle Miocene) deposits of Letkés and Tekerés (Hungary) are documented. The material comprises diverse zooxanthellate and azooxanthellate coral taxa interpreted as representing mixed shallow- and deep-water components. 17 species are recorded for the first time in the region, significantly increasing the known diversity of Badenian corals in the Pannonian Basin. A systematic study of the material enables the description of a new species, *Trochocyathus* (*Aplocyathus*) *zoltani* sp. n., characterized by a small bowl-shaped corallum with distinctive double rows of costal spines. The new data refine the paleobiogeographic distribution and bathymetric interpretation of Middle Miocene scleractinians in the Central Paratethys and suggest that the regional scleractinian coral diversity was considerably higher than previously recognized.

Keywords: Scleractinia, Middle Miocene, Badenian, Central Paratethys, Pannonian Basin

Introduction

Due to the Mid-Miocene Climatic Optimum, the Central Paratethys became a tropical-subtropical archipelagic sea in the early Middle Miocene (early Badenian regional stage = Langhian; 15.98–13.82 Ma; Harzhauser et al. 2024a). As the sea was connected to the Proto-Mediterranean Sea via the Slovenian Strait (Bartol et al. 2014), marine faunal diversity increased significantly compared to the Early Miocene (Harzhauser et al. 2024b). As for scleractinian corals, approximately 130 species of Badenian age have been reported in the literature from the province (Chaix et al. 2018; Kovács 2025a, b).

This contribution presents preliminary results from two newly collected coral assemblages from the early Badenian Pannonian Basin system of the Central Paratethys (Letkés, N Hungary; Tekerés, S Hungary), describing the faunal composition and documenting the extended paleogeographical distributions of several well-known species. In addition, the abundance of this material made it possible to introduce a new solitary coral species: *Trochocyathus* (*Aplocyathus*) *zoltani* sp. n.

Material and methods

The scleractinian coral specimens under study were collected by the author and Zoltán Vicián at Letkés, and by Márton Szabó (HNHM) and Tamás Németh at Tekerés. Part of the Letkés material, the entire Tekerés material, and the types of *Trochocyathus* (*Aplocyathus*) *zoltani* sp. n. are housed in

the Hungarian Natural History Museum, Budapest (HNHM), collection of the Department of Paleontology and Geology. Taxonomy and description terminology follow Cairns & Zibrowius (1997), Cairns & Kitahara (2012), and Hoeksema et al. (2026).

Measurements in mm. Abbreviations: D – calicular diameter, H – corallum height, W – corallum width, C – septal cycle, S – septum.

Localities and geological settings

Letkés is a famous early Badenian site in the W Börzsöny Mts (N Pannonian Basin), fossiliferous localities around the village are known for their rich marine invertebrate assemblages. The Börzsöny Mts belong to the Miocene Inner Carpathian Volcanic Chain of the Central Paratethys and are composed primarily of volcanic formations (Börzsöny Andesite Complex; Karátson 2024). On its margins, however, there are varieties of Badenian sedimentary rocks (limestone, clay, sand) that represent the Pécsszabolcs Member of the Lajta Limestone Formation (Selmeczi et al. 2024). The geological and paleogeographical settings of the Letkés area were discussed by Hámor (2005), reporting both nearshore and offshore marine deposits around the village. Although the maximum sea depth in the Badenian Pannonian Basin is thought to be about 600 m (Báldi et al. 2002), the depth could be approximately 400 m in the W Börzsöny area (Hámor 2005).

Mollusk fossils were described earlier by Csepregy-Meznerics (1956) and Strausz (1966) from different localities in the vicinity, and recently from the Bagoly Hill A locality (that was discovered in 2010) by Dulai (2025) and by the present author with co-authors (see Kovács & Vicián 2023;

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Biskupič & Kovács 2025, and references therein). Regarding scleractinian corals, more than 20 species were reported from the coral assemblage at the Bagoly Hill A locality by Kovács (2025a).

The excavation under study (Bagoly Hill B section) is located 500 m east of the village ($47^{\circ}53'26.8''\text{N}$, $18^{\circ}47'00.6''\text{E}$) and 160 m north of the Bagoly Hill A section, in a trench between the hill and the plough field (Fig. 1). The locality is characterized by approximately 2 m thick, resedimented beds of limonitic clayey sand (Pécsszabolcs Member of the Lajta Limestone Formation). The section yielded highly diverse scleractinian coral, bryozoan, mollusk, brachiopod, crustacean, echinoid, otolith, and fish teeth material; the taphocoenosis contains specimens derived from shallow- to deep-water paleoenvironments (Kovács 2025b).

The geology and stratigraphy of the Orfű–Tekeres area in the Mecsek Mts (S Pannonian Basin) were examined by Chikán (1991) and Báldi et al. (2002). The lower Badenian deposits of the region represent the Pécsszabolcs Member of the Lajta Limestone Formation and the Tekeres Schlier Member of the Baden Formation (Selmecezi et al. 2024). The maximum sea depth was approximately 600 m in the Badenian Mecsek Mts area (Báldi et al. 2002).

The locality under study is located 100 m east of the Herman Ottó Lake coastline at the south-western foot of the Kopasz Hill ($46^{\circ}10'28.2''\text{N}$, $18^{\circ}07'50.3''\text{E}$) (Fig. 1). Clayey silt and sand of 180 cm thickness were excavated by an artificial trench; the deposit belongs to the Tekeres Schlier. The macrofauna is very rich in early Badenian mollusk, coral, and fish fossils (Szabó et al. 2022). The mollusk assemblage is characterized by the dominance of deep-water (circalittoral – upper bathyal) taxa; however, species typical of shallow water are also present with worn or fragmentary shells, indicating that numerous specimens were transported from coastal settings into deeper-water environments (Kovács 2020; Kovács & Stein 2026). An exceptionally diverse chondrichthyan assemblage was described from the locality by Szabó et al. (2022).

Research history of the scleractinian corals of the Miocene Pannonian Basin

Research on the Miocene Scleractinia of the Central Paratethys started in the 1830' (e.g., Pusch 1837). Comprehensive studies were published by Reuss (1848, 1872), including localities in the Pannonian Basin, e.g., Diósjenő and Nagymaros in the Börzsöny Mts. From the late 19th to the early 21st centuries, the Badenian scleractinian corals of the Hungarian fossiliferous sites were mentioned or dealt with in detail by Franzenau (1886), Kopek (1952, 1954), Kühn (1963a,b), Hegedűs (1970), Scholz (1970), Hegedűs & Jankovich (1972), Oosterbaan (1990), Saint Martin et al. (2000), Dulai et al. (2021), Henn (2023), and Kovács (2025a,b). In addition to these works, numerous papers have addressed Miocene Paratethyan corals found in Central European countries (for details, see Chaix et al. 2018 and Kovács 2025a with additional references). Since the present paper focuses primarily on azooxanthellate coral species, I mention here only a few of these studies that specifically dealt with solitary corals of the Paratethys and provide important background information for the analysis of the material under study: Procházka (1888, 1893), Dembińska-Rózkowska (1932), Vašíček (1946), Moenke (1953), Zázvorka (1956), Kojumdgieva (1960), Kühn (1965, 1967), Stolarski (1991, 1992, 1996), Tiță (2000), Rus & Popa (2008), Kleprlíková & Doláková (2016), and Kleprlíková (2018).

Coral assemblages

1. Letkés, Bagoly Hill B

The scleractinian coral assemblage of the Bagoly Hill B locality is of special interest, as its alpha-diversity with 42 species is considered the highest in the Badenian Pannonian Basin. Besides the description of a new taxon, 15 species are recorded for the first time in the region.

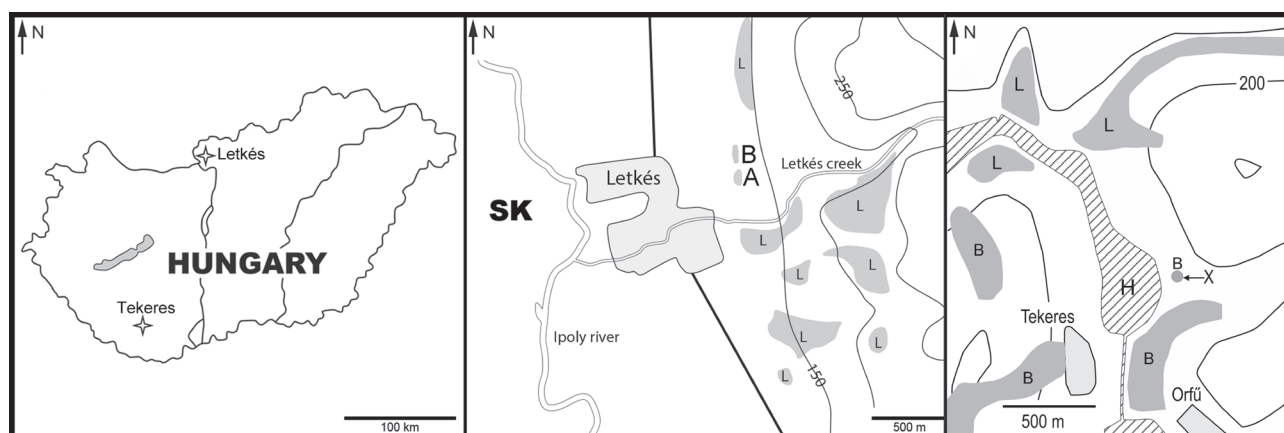


Fig. 1. Locations and lower Badenian marine deposits in the studied areas. Letkés: A – Bagoly Hill A section; B – Bagoly Hill B section; L – Lajta Limestone Formation. Tekeres: H – Herman Ottó Lake; X – Kopasz Hill section; B – Baden Formation; L – Lajta Limestone Formation.

The material consists of both zooxanthellate and azooxanthellate taxa (Table 1). Of the 15 zooxanthellate species, 13 are hermatypic, and 2 are ahermatypic. All of the studied shallow-water species are represented by poorly preserved, fragmentary colonies with a generally worn surface; they are considered an allochthonous part of the material. Four species are abundant: *Porites leptoclada*, *Stylophora subreticulata*, *Tarbellastraea reussiana*, and *Stylocora exilis*. One species is a new record in the Pannonian Basin: *Alveopora meridionalis*, represented by a small colony (see Chevalier 1962a; Chaix et al. 2018).

The azooxanthellate group contains 1094 moderately to well-preserved coral specimens representing 27 species. The most abundant species are *Caryophyllia (A.) verrucosa* (327 specimens) and *Balanophyllia (B.) praelonga* (134 specimens), while *Deltocyathus italicus* (112 specimens), *Ceratotrochus (E.) duodecimcostatus* (100 specimens), and *Trochocyathus (T.) affinitatus* (72 specimens) are common. The relatively large number of *Flabellum* specimens (94) and the high alpha-diversity of the genus (4 species) are unique in the Pannonian Basin. Seven species are new records in the Middle Miocene Central Paratethys: *Balanophyllia (B.) cf. falcifera*, *B. (B.) italica*, *Culicia parasita*, *Paleoastroides cf. dehmi*, *Flabellum cf. extensum*, *Sphenotrochus intermedius*, *Peponocyathus michelottii* (for these taxa see Sismonda 1871; Chevalier 1962a; Kühn 1965; Chaix et al. 1999; Chaix & Cahuzac 2005; Spadini 2020, 2021). Seven species that are known in the Paratethys are recorded for the first time from the Badenian Pannonian Basin: *Dendrophyllia taurinensis*, *Caryophyllia* sp. aff. *depauperata*, *C. inops*, *C. smithii*, *Ceratotrochus (C.) multiserialis*, *Deltocyathus italicus*, and *Tethocyathus microphyllus*.

II. Tekeres, Kopasz Hill

The scleractinian coral assemblage of the Kopasz Hill locality was briefly reported by Henn (2023); a larger sample analyzed herein comprises 15 species (Table 1). The assemblage is also characterized by a mixture of shallow- and deep-water taxa. The poorly diversified, allochthonous zooxanthellate group consists of a few small, fragmentary colonies of *Porites* sp., *Tarbellastraea reussiana*, and *Stylophora subreticulata*. Besides these forms, fragments of *Stylocora exilis* and the ahermatypic *Rhizangia* sp. appear sporadically. The deep-water azooxanthellate group displays higher diversity, 10 species are recorded: *Balanophyllia praelonga*, *Balanophyllia* sp., *Dendrophyllia* sp. (Fig. 4.1), *Flabellum roysianum*, *Caryophyllia (A.) verrucosa*, *Caryophyllia* sp. (Fig. 4.2), *Ceratotrochus (E.) duodecimcostatus*, *Ceratotrochus (C.) granulatus* Dembińska-Rózkowska, 1932 (Fig. 4.3), *Peponocyathus duncani* (Fig. 4.4–5), and *Stephanophyllia elegans* (Bronn, 1837). The solitary corals are characterized by moderate to good preservation; however, many fragmentary specimens are also present, which suggests redeposition. The most abundant form is *Caryophyllia* sp. (210 specimens), while *Caryophyllia (A.) verrucosa* (75 specimens), *Cerato-*

trochus (E.) duodecimcostatus (41 specimens), and *Stephanophyllia elegans* (~30 specimens) are common in the material. *Ceratotrochus (C.) granulatus* with four specimens is recorded for the first time in the Badenian Pannonian Basin. The *Caryophyllia* sp. specimens are closely allied in size and morphology to the *Caryophyllia* material presented by Stolarski (1991: 41, pl. 1, figs. 1–2); they probably represent a new species. The *Peponocyathus duncani* specimen in Fig. 4.4 exhibits features of transverse division, whereas the specimen in Fig. 4.5 still retains an attached anthocyathus, the daughter specimen separating from the parental individual. This process was described in detail by Stolarski (1992). The material figured herein supports the hypothesis that this species reproduced primarily by transverse division.

Systematic paleontology

Class Anthozoa Ehrenberg, 1834
 Subclass Hexacorallia Haeckel, 1896
 Order Scleractinia Bourne, 1900
 Suborder Vacatina Okubo, 2016
 Family Caryophylliidae Dana, 1846
 Genus *Trochocyathus* Milne Edwards & Haime, 1848
 Subgenus *Aplocyathus* d'Orbigny, 1850

Trochocyathus (Aplocyathus) zoltani sp. n.
 (Figs. 5–6.1–4)

Holotype: HNHM PAL 2026.23.1., H: 12.1 mm, D: 20.0×18.7 mm (Fig. 5).

Paratype 1: HNHM PAL 2026.24.1., H: 9.8 mm, D: 16.5×15.4 mm (Fig. 6.1).

Paratype 2: HNHM PAL 2026.25.1., H: 8.2 mm, D: 17.6×16.6 mm (Fig. 6.2).

Type strata: Lower Badenian clayey sand (Pécsszabolcs Member of the Lajta Limestone Formation).

Type locality: Letkés, Bagoly Hill B section, Hungary.

Derivation of name: In honor of Zoltán Vicián, Hungarian fossil shell collector.

Additional material: 3 specimens in private collections (Fig. 6.3–4).

Diagnosis: Small, bowl-shaped corallum, slightly elliptical calice, low, convex base, papillose columella. C₁ costae bearing two short costal spines (1 basal, 1 lateral). Septal structure of four complete and one incomplete cycles with 60–68 septa, inner edges of S₁–S₂ septa bordered by pali.

Description of holotype: Moderately preserved, bowl-shaped corallum with slightly elliptical calice. Costae are narrow, rounded, granular, and moderately developed only near the calice; they are very weak below, except for the broad, rounded C₁–C₂ costae. The six C₁ costae bear spiny tubercles at base (height of tubercles is 1.3 mm), while four C₁ costae have slightly curved, more prominent secondary (lateral) spines above the basal tubercles with a length of max. 2.3 mm. The base is low and convex with an imprint of the original

Table 1: Scleractinian coral species at the Bagoly Hill A (BHA) (Kovács 2025a), the Bagoly Hill B (BHB) (Letkés, Börzsöny Mts) and the Kopasz Hill (KH) (Tekeres, Mecsek Mts) localities (Hungary).

Species	BHA	BHB	KH	Illustration
Zooxanthellate, hermatypic				
<i>Turbinaria cyathiformis</i> (Blainville, 1830)	*	*	—	
<i>Alveopora meridionalis</i> Chevalier, 1962	—	*	—	Fig. 2.1
<i>Porites leptoclada</i> Reuss, 1872	—	*	—	Fig. 2.2
<i>Porites vindobonarum prima</i> Kühn, 1927	*	*	—	
<i>Porites</i> sp.	—	—	*	
<i>Cladangia conferta</i> (Reuss, 1848)	—	*	—	
<i>Rhizangia</i> sp.	—	—	*	
<i>Siderastrea felixi</i> Dembińska-Rózkowska, 1932	*	—	—	
<i>Siderastrea italica</i> (Defrance, 1826)	—	*	—	
<i>Siderastrea radians</i> (Pallas, 1766)	*	—	—	
<i>Favia gotschevi</i> Kojumdgieva, 1960	*	cf.	—	Fig. 2.3
<i>Mussismilia vindobonensis</i> Chevalier, 1962	*	*	—	
<i>Stylocora exilis</i> Reuss, 1872	*	*	*	Fig. 2.4
<i>Echinopora oligophylla</i> (Reuss, 1872)	*	—	—	
<i>Echinopora tchihatcheffi</i> (Chevalier, 1962)	*	—	—	
<i>Thegioastraea incerta</i> (Osasco, 1897)	—	*	—	Fig. 2.5
<i>Tarbellastraea ellisiana</i> (Defrance, 1826)	*	—	—	
<i>Tarbellastraea reussiana</i> (Milne Edwards & Haime, 1850)	*	*	*	Fig. 2.6
<i>Montastraea</i> sp.	*	—	—	
<i>Stylophora subreticulata</i> Reuss, 1872	*	*	*	
<i>Solenastrea inaequalis</i> (Chevalier, 1962)	*	—	—	
<i>Solenastrea desmoulinsi</i> (Milne Edwards & Haime, 1851)	*	*	—	
Zooxanthellate, ahermatypic				
<i>Oulangia?</i> sp.	—	*	—	
<i>Syzygophyllia brevis</i> Reuss, 1860	*	*	—	
Azooxanthellate				
<i>Culicia parasita</i> (Michelin, 1847)	—	*	—	Fig. 2.7
<i>Balanophyllia</i> (<i>Balanophyllia</i>) cf. <i>falcifera</i> Sisonda, 1871	—	*	—	Fig. 3.1
<i>Balanophyllia</i> (<i>B.</i>) <i>italica</i> (Michelin, 1841)	—	*	—	Fig. 3.2
<i>Balanophyllia</i> (<i>B.</i>) <i>praelonga</i> (Michelotti, 1838)	*	*	*	Fig. 3.3
<i>Balanophyllia</i> sp.	*	—	*	
<i>Dendrophyllia taurinensis</i> Milne Edwards & Haime, 1848	—	*	—	
<i>Dendrophyllia</i> sp.	—	*	*	Fig. 4.1
<i>Paleoastroroides</i> cf. <i>dehmi</i> Kühn, 1965	—	*	—	Fig. 3.4
<i>Coenocyathus</i> sp.	—	*	—	
<i>Flabellum</i> cf. <i>extensum</i> Michelin, 1842	—	*	—	Fig. 3.5
<i>Flabellum krejci</i> Kühn, 1963	—	*	—	
<i>Flabellum roissyanum</i> Milne Edwards & Haime, 1848	—	*	*	
<i>Flabellum</i> cf. <i>suessi</i> Reuss, 1872	*	*	—	
<i>Caryophyllia</i> (<i>C.</i>) <i>smithii</i> Stokes & Broderip, 1828 morph. <i>clavus</i> Scacchi, 1835	—	*	—	Fig. 3.6
<i>Caryophyllia</i> (<i>Acanthocyathus</i>) <i>verrucosa</i> (Milne Edwards & Haime, 1848)	*	*	*	
<i>Caryophyllia</i> sp. aff. <i>depauperata</i> Reuss, 1872	—	*	—	
<i>Caryophyllia inops</i> Reuss, 1872	—	*	—	
<i>Caryophyllia leptaxis</i> Reuss, 1872	*	*	—	
<i>Caryophyllia</i> sp.	—	—	*	Fig. 4.2
<i>Ceratrotrochus</i> (<i>Ceratrotrochus</i>) <i>granulatus</i> Dembińska-Rózkowska, 1932	—	—	*	Fig. 4.3
<i>Ceratrotrochus</i> (<i>Ceratrotrochus</i>) <i>multiserialis</i> (Michelotti, 1838)	—	*	—	Fig. 3.7
<i>Ceratrotrochus</i> (<i>Edwardsotrochus</i>) <i>duodecimcostatus</i> (Goldfuss, 1826)	*	*	*	
<i>Deltocyathus italicus</i> (Michelotti, 1838)	—	*	—	Fig. 3.8
<i>Peponocyathus duncani</i> (Reuss, 1872)	—	*	*	Fig. 4.4–5
<i>Peponocyathus michelottii</i> (Milne Edwards & Haime, 1857)	—	*	—	Fig. 3.9
<i>Sphenotrochus intermedius</i> (Goldfuss, 1826)	—	*	—	Fig. 3.10
<i>Stephanophyllia elegans</i> (Bronn, 1837)	—	—	*	
<i>Stephanophyllia nystii</i> Milne Edwards & Haime, 1850	*	*	—	
<i>Tethocyathus microphyllus</i> (Reuss, 1872)	—	*	—	Fig. 3.11
<i>Trochocyathus</i> (<i>Trochocyathus</i>) <i>affinitatus</i> Strand, 1928	—	*	—	Fig. 3.12
<i>Trochocyathus</i> (<i>Aplocyathus</i>) <i>zoltani</i> sp. n.	—	*	—	Figs. 5, 6

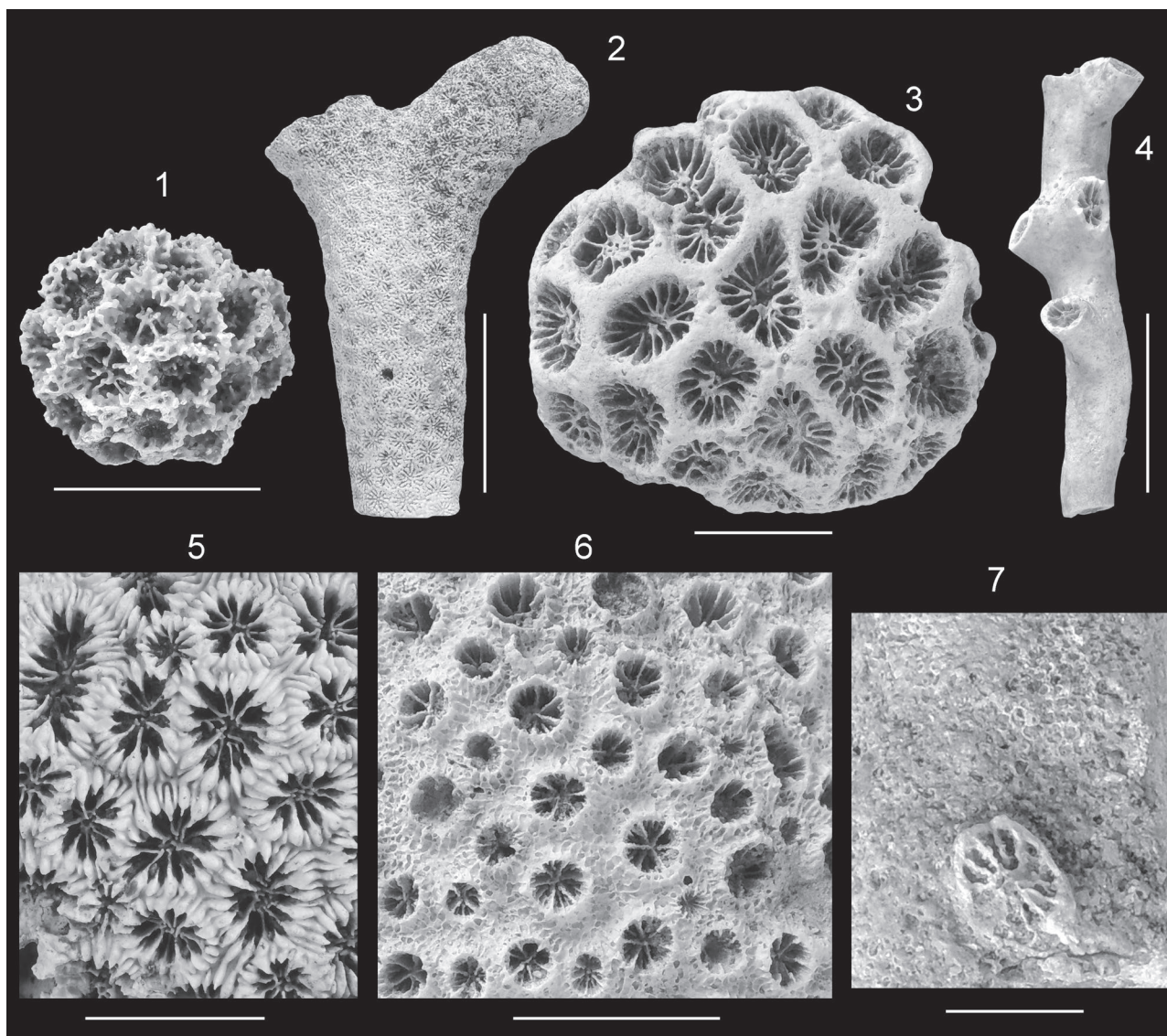


Fig. 2. Early Badenian zooxanthellate and azooxanthellate corals from the Bagoly Hill B section at Letkés (Hungary). 1 – *Alveopora meridionalis* Chevalier, 1962 (W 12.8, H 7.9, D 3). 2 – *Porites leptoclada* Reuss, 1872, HNHM INV 2026.19. (H 27, D 1.5). 3 – *Favia* cf. *gotschevi* Kojumdgieva, 1960 (W 34, H 17, D 6–8). 4 – *Stylocora exilis* Reuss, 1872, HNHM INV 2026.20. (H 26, D 2.5–3). 5 – *Thegioastraea incerta* (Osasco, 1897) (D 4–7). 6 – *Tarbellastraea reussiana* (Milne Edwards & Haime, 1850), HNHM INV 2026.21. (max. D 2.5). 7 – *Culicia parasita* (Michelin, 1847) (D 3×2.4) associated with a bryozoan *Celleporaria* sp. colony. Scale bars 10 mm for figs. 1–6; 5 mm for fig. 7.

substratum attachment. The specimen has four complete (S_1 – S_4) and one incomplete (S_5) septal cycles; the number of septa is 60. S_1 – S_2 septa are broader than others; their upper margin is rounded; all septa are granular laterally. S_1 – S_2 septa are ~5.5 mm wide inward and exsert 5 mm above the wall; the exsertness of S_3 – S_4 septa is 3 mm; S_5 is short. Inner edges of S_1 – S_2 septa are bordered by well-defined pali; the pali of S_3 – S_4 cannot be traced due to the poor preservation of septa. Columella is deep and papillose, but only 2–3 pillars can be seen because of the sediment filling that could not be removed.

Variability: The new species displays moderate morphological variability in the number of septa and the development of lateral spines. Paratype 1 has a somewhat distorted base, six

basal and two lateral spines, and 64 septa (Fig. 6.1). Paratype 2 has 68 septa and columella with approximately 16 visible pillars, it bears five basal spines, the sixth spine is replaced by a weakly developed node, and it bears only one lateral spine (Fig. 6.2). Three coralla (two of them illustrated in Fig. 6.3–4) agree well in almost all morphological features with the type specimens but they are shorter, their walls are lower and the lateral spines did not develop – they somewhat resemble *Trochocyathus* (*Aplocyathus*) *sexspinae* (Chevalier, 1962) from the N Italian Miocene. Still, this species is characterized by a different morphology (see below).

Remarks: Although the columella cannot be analyzed in all details, other morphological features of the study specimens

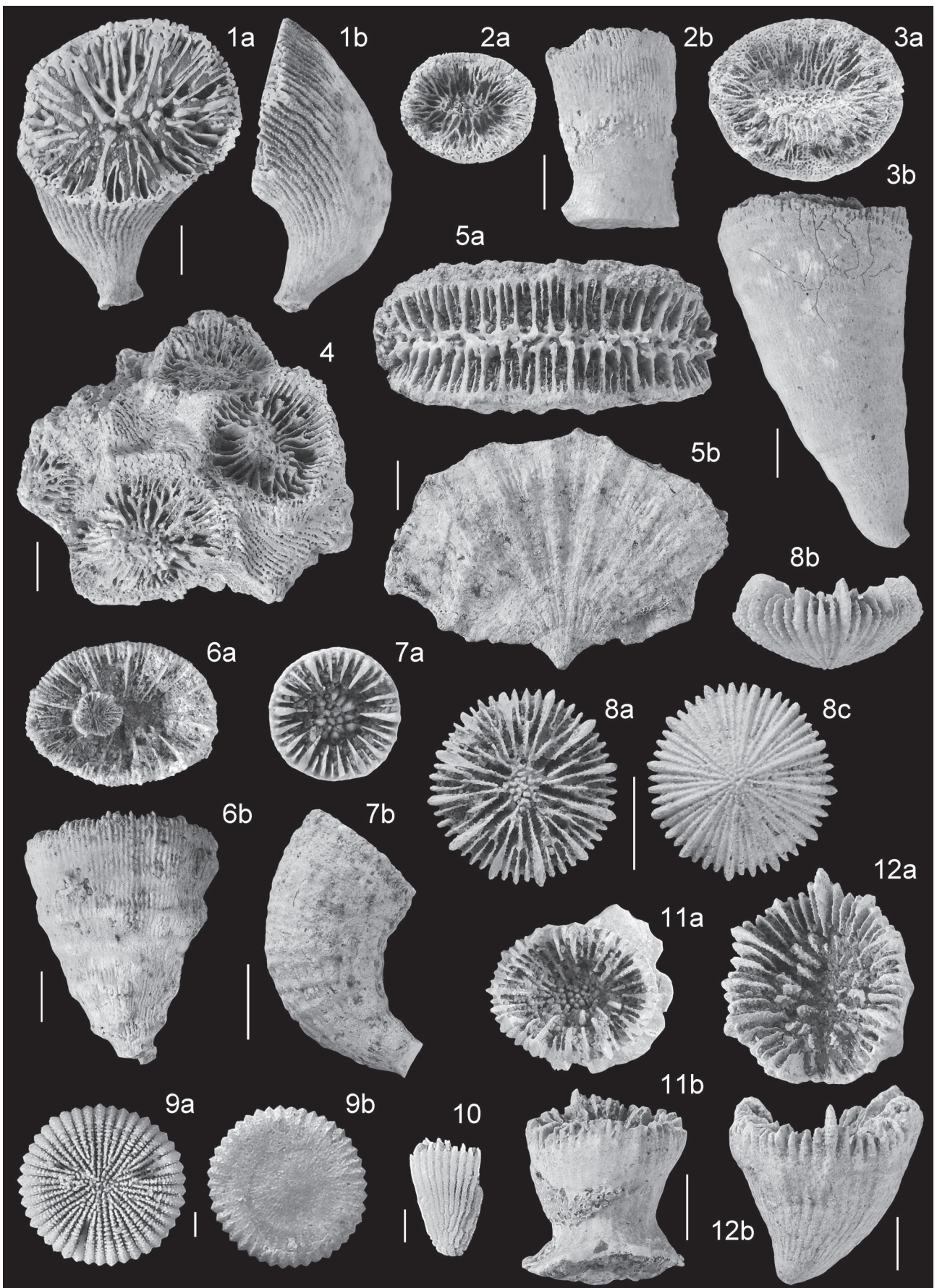


Fig. 3. Early Badenian azooxanthellate corals from the Bagoly Hill B section at Letkés (Hungary). 1 – *Balanophyllia* (*B.*) cf. *falcifera* Sismonda, 1871, HNHM INV 2026.22. (H 30, D 22×18). 2 – *B. (B.) italica* (Michelin, 1841) (H 18.4, D 11.5×10.1). 3 – *B. (B.) praelonga* (Michelotti, 1838), HNHM INV 2026.23. (H 37, D 20×16). 4 – *Paleoastroides* cf. *dehmi* Kühn, 1965 (W 35, D 13-14). 5 – *Flabellum* cf. *extensum* Michelin, 1842 (H 24, D 35×14). 6 – *Caryophyllia* (*C.*) *smithii* Stokes & Broderip, 1828 morph. *clavus* Scacchi, 1835, HNHM INV 2026.24. (H 25, D 19×14.5). 7 – *Ceratotrochus* (*C.*) *multiserialis* (Michelotti, 1838), HNHM INV 2026.25. (H 17, D 8.8). 8 – *Deltocyathus italicus* (Michelotti, 1838), HNHM INV 2026.26. (H 4.4, D 8.6). 9 – *Peponocyathus michelottii* (Milne Edwards & Haime, 1857) (H 1.8, D 6.7). 10 – *Sphenotrochus intermedius* (Goldfuss, 1826), HNHM INV 2026.27. (H 3.6, D 2.4×1.5). 11 – *Tethocyathus microphyllus* (Reuss, 1872) (H 12.0, D 9.6×7.9). 12 – *Trochocyathus* (*T.*) *affinitatus* Strand, 1928, HNHM INV 2026.28. (H 14.8, D 20×16). Scale bars 5 mm for figs. 1–8, 11, 12; 1 mm for figs. 9, 10.

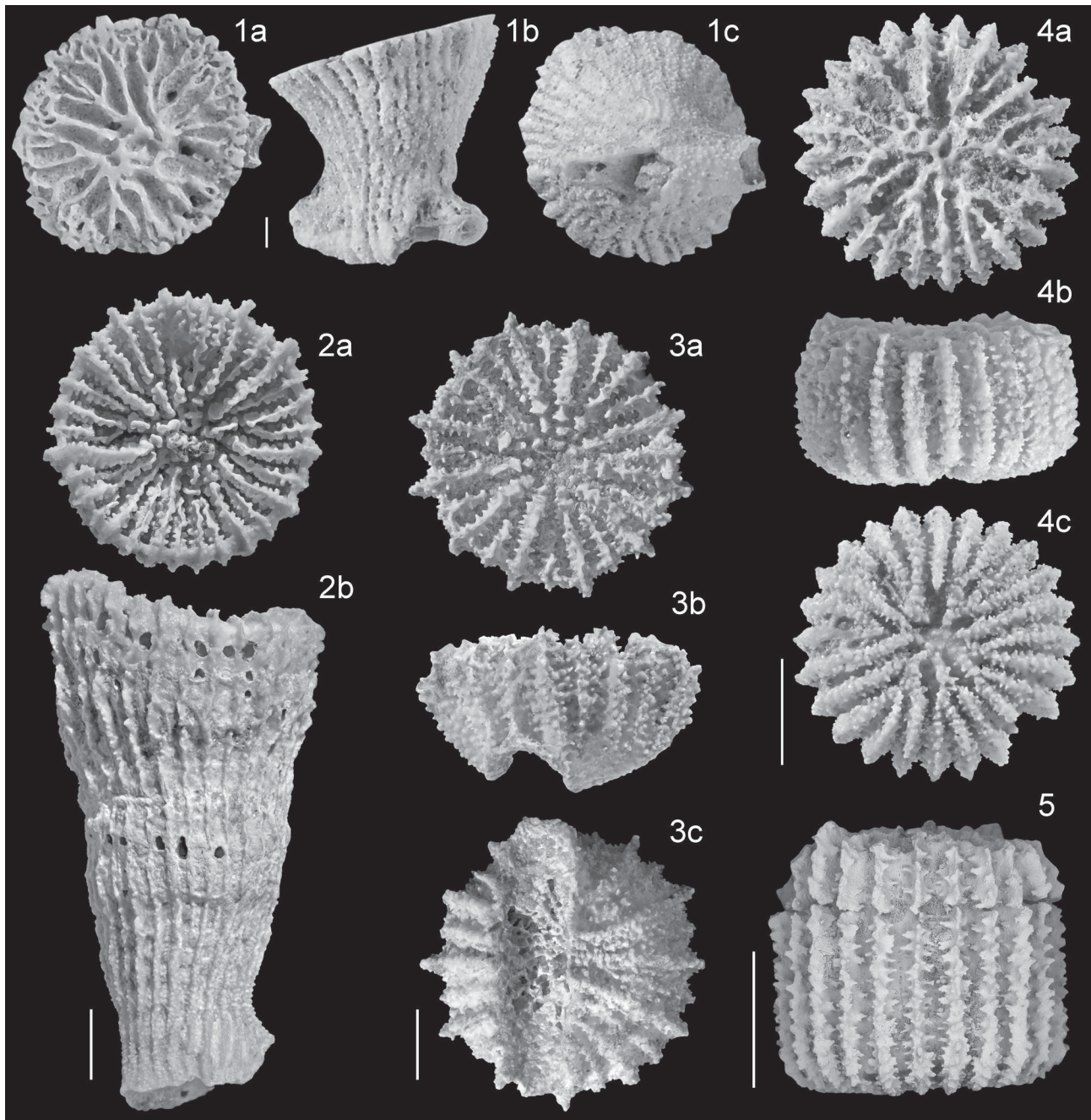


Fig. 4. Early Badenian azooxanthellate corals from the Kopasz Hill section at Tekeres (Hungary). 1 – *Dendrophyllia* sp., HNHM INV 2026.29. (H 8.3, D 8.2×7.4). 2 – *Caryophyllia* sp., HNHM INV 2026.32. (H 7.8, D 4.3). 3 – *Ceratotrochus granulatus* Dembińska-Rózkowska, 1932, HNHM INV 2026.30. (H 2.1, D 4). (4, 5) *Peponocyathus duncani* (Reuss, 1872): 4 – HNHM INV 2026.31.A. (H 1.5, D 2.7), 5 – HNHM INV 2026.31.B. (D 2.1, H 2). Scale bars 1 mm. (figs. 2–4: photo by G. Stein)

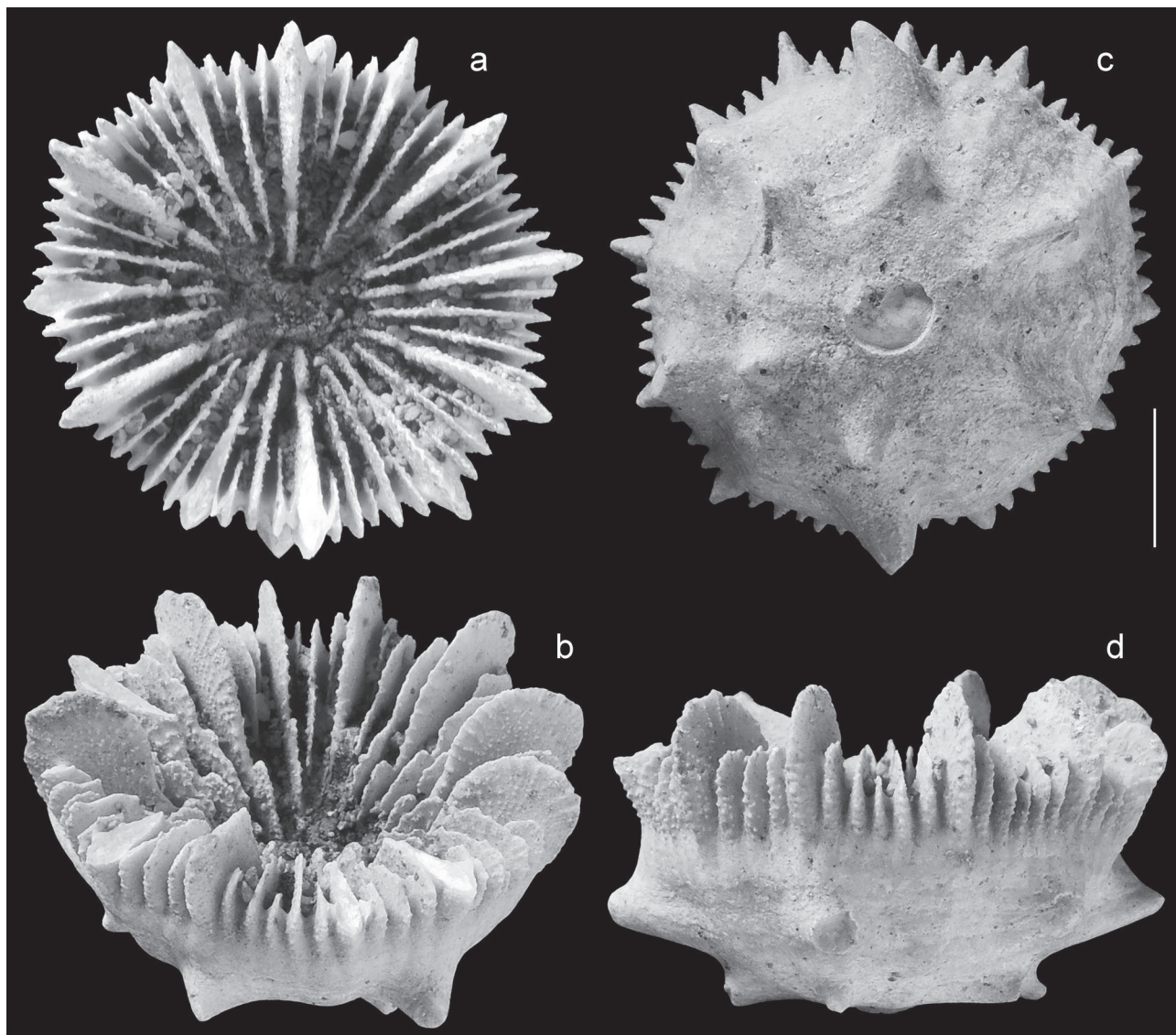


Fig. 5. *Trochocyathus (Aplocyathus) zoltani* sp. n. Holotype, HNHM PAL 2026.23.1: a, b – calical views, c – basal view, d – lateral view. Lower Badenian clayey sand (Pécszabolcs Member of the Lajta Limestone Formation), Bagoly Hill B, Letkés (Hungary). Scale bar 5 mm.

(shape, septal structure, presence of basal spines) correspond to those of *Aplocyathus* (see Chevalier 1962a: 315), so the new species is assigned to this subgenus.

Trochocyathus (Aplocyathus) zoltani sp. n. is a distinctive form bearing two rows of costal spines; it differs from all known Miocene congeners. Four fossil species were attributed to *Trochocyathus (Aplocyathus)* by Chevalier (1962a). The type species, *Trochocyathus (Aplocyathus) armatus* (Michelotti, 1838) has a smaller, cylindrical corallum with five long basal spines (Michelotti 1838, pl. 1, fig. 9; Oppenheim 1922, pl. 1, fig. 6; Vertino et al. 2014, fig. 14.5.a–b). This species is known from Egerian (Late Oligocene–Early Miocene: Chattian–Aquitania) and Karpatian (late Early Miocene) deposits in Hungary (Hegedűs 1962; Kókay 1972). *Trochocyathus (Aplocyathus) pyramidatus* (Michelotti, 1838) is characterized by a strongly conical form (Michelotti 1838, pl. 2, fig. 4; Osasco 1897,

fig. 33; Chevalier 1962b, pl. 4, fig. 6), while *T. (A.) planulatus* Osasco, 1897 is a broad, cylindrical corallum with a different septal structure, and it bears weakly developed tubercles instead of spines (Osasco 1897, figs. 34–35; Chevalier 1962a: 319). The most closely allied species in morphology to *Trochocyathus (Aplocyathus) zoltani* sp. n. is *T. (A.) sexspinae* (Chevalier, 1962) from the Middle Miocene of the Torino Hills (N Italy). The holotype of the latter species is identical in size (H 12, D 20) to the holotype of *Trochocyathus (Aplocyathus) zoltani* sp. n., and it has 68 septa and six basal spines (Chevalier 1962a: 317, text-fig. 106e, table 16, pl. 1, figs. 7–8). However, its basal spines are clearly stronger and more projected, and although it has a relatively high wall, it lacks lateral spines (see the holotype online: <http://coldb.mnhn.fr/catalognumber/mnhn/f/a70313>).

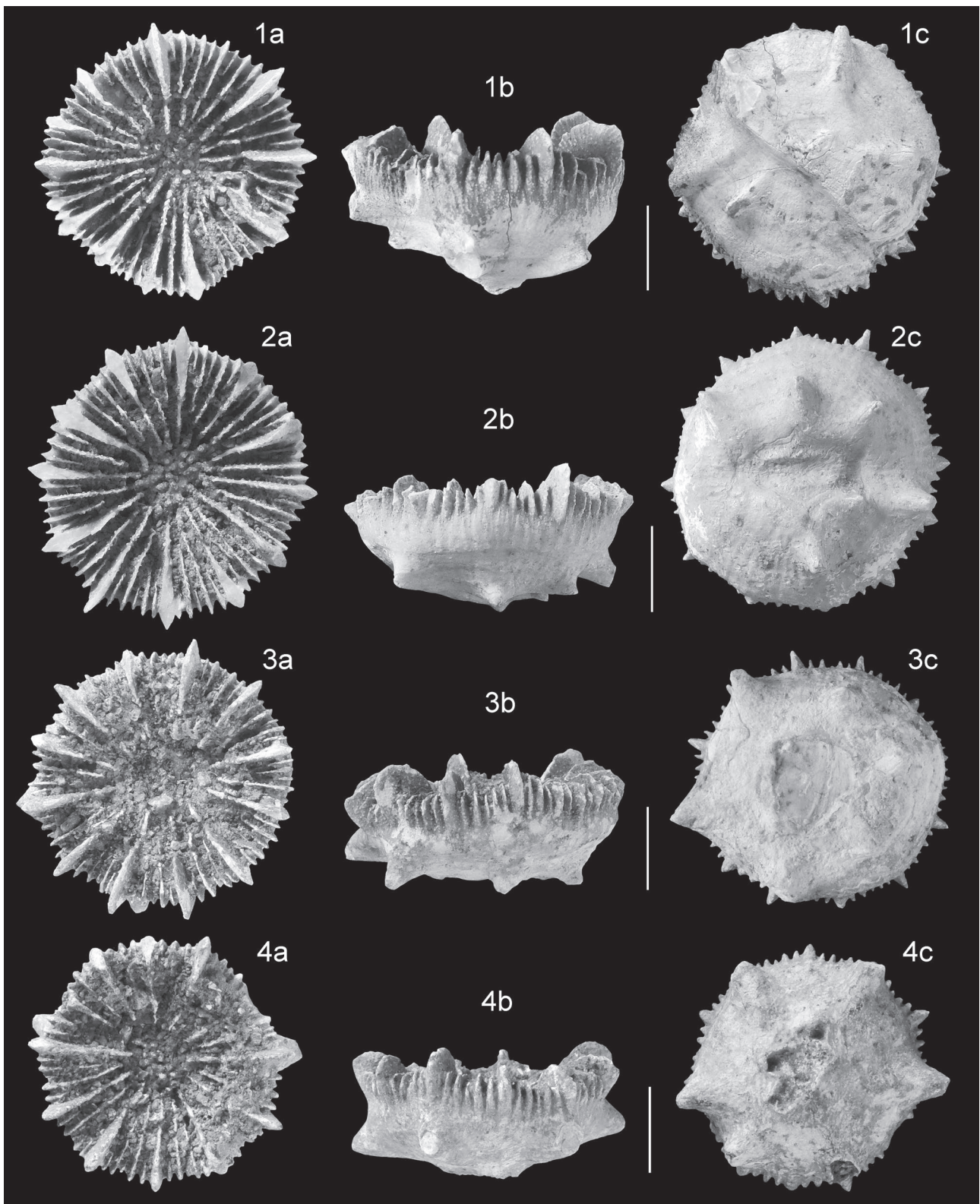


Fig. 6. (1–4) *Trochocyathus (Aplocyathus) zoltani* sp. n.: 1 – Paratype 1, HNHM PAL 2026.24.1., calical, lateral, and basal views. 2 – Paratype 2, HNHM PAL 2026.25.1., calical, lateral and basal views. 3 – Vicián Collection, calical, lateral, and basal views (H 8.6, D 17.7×16.8). 4 – Author's Collection, calical, lateral, and basal views (H 7.7, D 15.6). Lower Badenian clayey sand (Pécsszabolcs Member of the Lajta Limestone Formation), Bagoly Hill B, Letkés (Hungary). Scale bars 5 mm.

Discussion

Comparison of the Bagoly Hill A and Bagoly Hill B coral assemblages

The scleractinian coral assemblage of the Bagoly Hill A locality was described by Kovács (2025a), with 25 species recorded. Comparing the two materials (Table 1), we can note differences not only in diversity but also in faunal composition. The zooxanthellate groups display similar alpha-diversity (Bagoly Hill A: 16 spp., B: 15 spp.), but only 9 species occur in both assemblages. It is interesting that *Echinopora oligophylla* (Reuss, 1872) – one of the dominant species in the A assemblage – is missing in the study material. On the other hand, *Thegioastraea incerta*, which is not rare in the B assemblage, has so far been known only from the patch reef paleoenvironment of the Bánd area (Bakony Mts) in the Pannonian Basin (Oosterbaan 1990). Three common species are abundant at both localities: *Stylocora exilis*, *Stylophora subreticulata*, and *Tarbellastraea reussiana*. There are also differences in the preservation. Among the hermatypic corals, the *Porites*, *Echinopora*, and *Tarbellastraea* species generally occur with large (W ~30 cm) and well-preserved colonies at the A locality, while in the study assemblage, the colonial corals are represented by small, fragmentary specimens with mainly worn calical surface. [Note: two species recorded by Kovács (2025a) from the Bagoly Hill A assemblage are revised herein: *Favia* cf. *melitae* is regarded as *F. gotschevi* Kojumdjieva, 1960; *Solenastrea?* sp. actually represents *Solenastrea desmoulinsi* (Milne Edwards & Haime, 1851)].

In contrast to the previous group, the diversity of the azooxanthellate corals is much higher at the B locality (26 spp.); only seven species occur in the A assemblage. Six species are common; the most abundant is *Caryophyllia (A.) verrucosa* at both localities. The preservation of the solitary forms is generally better in the B assemblage, which can be explained by the fact that, despite sediment redeposition, the deeper-water fossils represent the autochthonous part of the assemblage from this excavation.

Bathymetric interpretation of the azooxanthellate material

Most of the studied azooxanthellate species are thought to be deep-water corals, occurring in circalittoral to upper bathyal habitats. The exact bathymetric range of extinct forms, however, cannot be determined with absolute certainty. Based on morphological analogies between fossil and Recent forms, it is possible to infer the paleoenvironments of some species (Stolarski 1991; Cairns 2003). Nevertheless, this method should be applied with due caution, taking into account the geological data about the sediments in question. Considering the same coral taxa found in the Korytnica Basin (Poland) and the Letkés localities presented herein, bathymetric ranges of the following species can be assumed: *Balanophyllia (B.) praelonga* (~90–500 m), *Caryophyllia (A.) verrucosa* (~40–490 m), *Tethocyathus microphyllus* (~190–800 m), *Pepono-*

cyathus duncani (~50–990 m), *Flabellum roissyanum* (~220–270 m) (Stolarski 1991). *Flabellum roissyanum* is frequent in the lower Badenian clay deposits of the neighboring Szokolya village (Börzsöny Mts) (Kopek 1954). For this species, the bathymetric range depth of 150–200 m was given by Báldi (1961). *Flabellum krejci* is typical of the upper bathyal Baden Formation. Both *Stephanophyllia elegans* (see Stolarski 1991) and the closely allied *S. nystii* could occur between ~230–400 m. Recent coralla of *Caryophyllia (C.) smithii* morphotype *smithii* (sub-cylindrical form) occur in shallow-water habitats. Still, morphotype *clavus* (deep-water, conical form) was recorded by Best (1968) below 60 m and by Quigley et al. (2017) between 20–1440 m, with frequent occurrence below 70 m. *Sphenotrochus intermedius* was probably a circalittoral species; most Recent representatives of the genus occur at depths of less than 100 m (Cairns 2003). Recent *Deltocyathus italicus* ranges between 400–2600 m; based on Badenian deposits, however, the species could have occurred in deep circalittoral–upper bathyal paleoenvironments in the Miocene Central Paratethys. *Trochocyathus (T.) affinitatus* was also described from the Baden Formation (Reuss 1872). Finally, the bathymetric range of Recent *Trochocyathus (Aplocyathus)* species is known from 240–760 m (Cairns 2017).

Conclusion

Two newly collected Middle Miocene scleractinian coral assemblages are presented from the Bagoly Hill B locality at Letkés (Börzsöny Mts, N Hungary) and the Kopasz Hill locality at Tekeres (Mecsek Mts, S Hungary). The zooxanthellate material of the Bagoly Hill B assemblage consists of 15 shallow-water species, most of which are widespread in the Badenian Central Paratethys, and one species is a new record for the Pannonian Basin. The azooxanthellate group contains 27 species, of which 14 are recorded for the first time in the region. The rich material enabled the introduction of a new species, *Trochocyathus (Aplocyathus) zoltani* sp. n. The coral assemblage of the Kopasz Hill locality contains a poor zooxanthellate fauna and a more diversified azooxanthellate material with 10 species; two solitary coral species are new records in the Pannonian Basin.

The coral assemblages described herein significantly expand our knowledge of the early Badenian marine fauna of the Pannonian Basin system. Considering only the azooxanthellate group, 28 species have been known in the region to date (Kopek 1954; Kovács 2025a, b), but based on the new data of this study and the taxonomic review of the literature, it is clear that the alpha-diversity of this group is significantly higher: occurrence of at least 44 species can be confirmed at the Badenian localities of Hungary. The presence of species characteristic of the N Italian Miocene [e.g., *Balanophyllia (B.)* cf. *falcifera*, *B. (B.) italica*, *Flabellum* cf. *extensum*, *Ceratotrochus (C.) multiserialis*, *Deltocyathus italicus*, *Peponocyathus michelottii*] or widespread in the Miocene Proto-Mediterranean Sea (*Culicia parasita*) – which are recorded

herein for the first time in the Pannonian Basin – suggests that, during the Mid-Miocene Climatic Optimum period, the Mediterranean influence on the early Badenian marine fauna of the Central Paratethys was probably stronger than previously thought (see e.g., Kopek 1954, Chaix et al. 2018).

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