

## Scleractinia fauna from the Middle Miocene deposits of Letkés (Börzsöny Mts, Hungary)

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### *Scleractinia*-fauna Letkés (Börzsöny hegység) középső miocén rétegeiből

#### Összefoglalás

A tanulmány Letkés (Börzsöny hegység) bagoly-hegyi lelőhelyének gazdag, kora badeni (középső miocén) Scleractinia-faunáját mutatja be. A vizsgált anyagban a sekélytengeri zátonyépítő, a fotoszintetizáló zooxantella algákkal szimbiózisban élő telepes korallok (például az *Echinopora*, *Porites*, *Siderastrea*, *Tarbellastraea* és *Turbinaria* nemzetségek képviselői) mellett a mély vízi afotikus zónára jellemző, ahermatipikus magános korallnemzetségek (például *Balanophyllia*, *Caryophyllia*, *Flabellum*, *Stephanophyllia*) példányai is jelentős számban megjelennek. Az itt leírt és ábrázolt 25 faj a Pannon-medence legmagasabb diverzitással jellemezhető korallgyűjtését képviseli; emellett 12 faj új előfordulás Magyarországon.

*Tárgyszavak:* középső miocén, badeni, Pannon-medence, Börzsöny hegység, Letkés, Scleractinia

#### Abstract

A rich Middle Miocene Scleractinia fauna is described and illustrated from the Badenian (Middle Miocene) deposits of Letkés (Börzsöny Mts, N Pannonian Basin, Hungary). The material consists of both zooxanthellate (e.g., *Echinopora*, *Porites*, *Siderastrea*, *Tarbellastraea*, *Turbinaria*), and azooxanthellate (e.g., *Balanophyllia*, *Caryophyllia*, *Flabellum*, *Stephanophyllia*) taxa. The 25 species represent the most highly diverse coral assemblage of the Pannonian Basin. Twelve species are recorded for the first time in Hungary.

*Keywords:* Middle Miocene, Badenian, Pannonian Basin, Börzsöny Mts, Letkés, Scleractinia

### Introduction

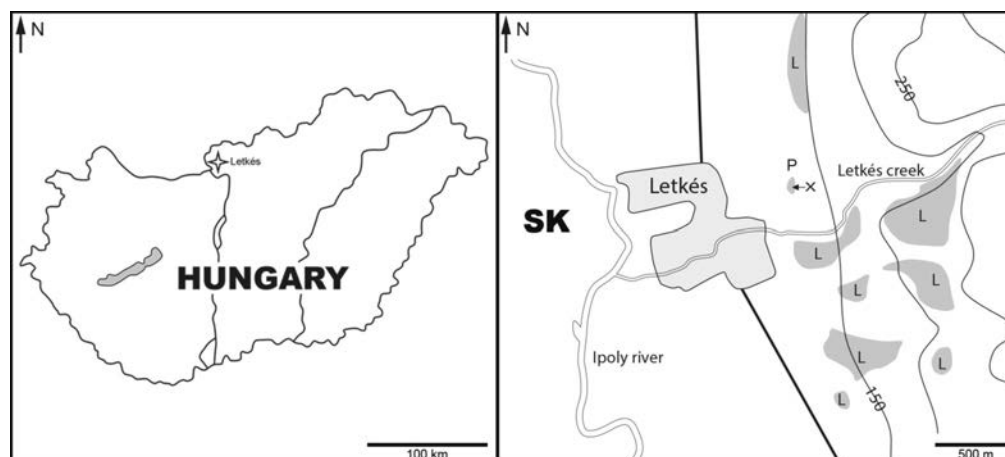
The aim of this paper is to describe the early Badenian (early Langhian, Middle Miocene) Scleractinia fauna of the Bagoly Hill locality at Letkés (northern Pannonian Basin, Börzsöny Mts, Hungary) as a contribution to the knowledge of this order in the Middle Miocene Central Paratethys. Based on new field work at the locality during the past decade, and revision of the collection of the Hungarian Natural History Museum, Budapest, 25 species are recorded herein. This Scleractinia fauna displays the highest alpha diversity in the Badenian Pannonian Basin.

#### Locality

Letkés is a well-known early Badenian fossiliferous site between the River Ipoly and the western hills of the Bör-

zsöny Mts (N Hungary) (Figure 1). The study locality is situated about 400 m eastward from the village of Letkés on the western slope of the Bagoly Hill (N 47.888319°, E 18.784647°). The Börzsöny Mts (N Pannonian Basin) belongs to the Miocene Inner Carpathian Volcanic Chain in the Central Paratethys and consists mainly of andesite of about 1000 m thickness. At the margins the volcanic rocks are overlain by shallow marine sedimentary formations belonging to the Lajta Limestone Formation (limestone, schlier, different clayey, sandy and marly deposits) (SELMECZI 2015: 39; SELMECZI et al. 2024: 84). The study locality consists mainly of resedimented, yellowish-brownish clayey sand beds without clearly visible layers – the sediments represent the lower Badenian Pécsszabolcs Member of the Lajta Limestone Fm.

The subsurface thickness of the section is about 170 cm. The uppermost unit (40–60 cm) is characterized by marly



**Figure 1.** Location of Letkés in Hungary, and the lower Badenian marine deposits east of the village

L - Lajta Limestone Fm., P - Pécsszabolcs Member, X - Bagoly Hill locality

**I. ábra.** Letkés és a falutól K-re található alsó badeni üledékek

L - Lajtai Mésző F., P - Pécsszabolcsi Tagozat, X - A vizsgált bagoly-hegyi feltárás

sand with some bentonite, containing mainly coastal to nearshore mollusc shells. The next, limonitic sandy unit (20–60 cm) contains transported fragmentary colonial coral blocks and rock fragments of different groups of andesite and andesitic tuff but some quartz pebbles also occur – the origin of this assemblage is probably related to earth quakes. The richest macrofauna came from this unit. Well-preserved mollusc shells are frequent in “pockets” among rocks or coral blocks. The presumably resedimented third unit (20–30 cm) is a limonitic clayey sandy facies with similarly rich but poorly to moderately preserved mollusc remains. At the base of the section there is a 10–20-cm-thick autochthonous light gray clay bed, which sporadically contains mollusc shells and solitary corals. This fourth unit is underlain by an unfossiliferous, greenish clay layer.

The macrofauna of the locality is remarkably rich consisting of fossils of mainly rocky intertidal, inner to middle neritic communities containing mostly colonial and solitary corals, bryozoans, serpulids, bivalves, gastropods, scaphopods, polyplacophores, and rarely brachiopods, crustaceans (cirripeds, ostracods, decapods), fragmentary echinoid remains, otoliths and fish teeth. The paleontological research of the macrofauna was mainly focused on molluscs (for research history, see KOVÁCS & VICIÁN 2023 and references therein).

### Research history

Research of Miocene Scleractinia of the Central Paratethys started in the 1830s (e.g., PUSCH 1837). The first comprehensive study was published by REUSS (1848) including a Pannonian Basin locality [Ipolyság (Šahy, Slovakia)] north of the Börzsöny Mts. Later REUSS (1871) in his summary of the Miocene coral assemblages of Austria–Hungary mentioned three localities from the recent Hungary: Diósjenő and Nagymaros (North Hungarian Mountains), Pécsvárad (Mecsek Mts). In the 20<sup>th</sup> century the Badenian scleractinians of the Pannonian Basin were listed or dealt

with in detail by KOPEK (1952, 1954), KÜHN (1963a, b), KOLOSVÁRY (1964), HEGEDŰS (1970), SCHOLZ (1970), BÁLDI & KÓKAY (1970), HEGEDŰS & JANKOVICH (1972), MÜLLER (1984), OOSTERBAAN (1990), SAINT MARTIN et al. (2000), DULAI et al. (2021), HENN (2023). The Scleractinia literature of the Miocene Central Paratethys was summarized by CHAIX et al. (2018).

Miocene corals at Letkés were recorded by FRANZENAU (1886) for the first time who listed three species from unknown localities around the village: *Acanthocyathus transsilvanicus* REUSS, *Astraea crenulata* GOLDFUSS, and *Porites incrustans* DEFRANCE. Later two taxa were mentioned by NOSZKY (1925): *Acanthocyathus transsilvanicus* REUSS, and “*Astraea granulata* GOLDFUSS” (it is probably a misspelling of *A. crenulata*). KOPEK (1954) described six species from “limestone and marl” of Letkés: *Acanthocyathus vindobonensis* REUSS, *Balanophyllia varians* (REUSS), *Flabellum roissyanum* EDWARDS & HAIME, *Orbicella conoidea* (REUSS), *Plesiastraea desmoulini* EDWARDS & HAIME, and *Siderastraea crenulata* (GOLDFUSS). KOLOSVÁRY (1964) mentioned the occurrence of *Stylophora subreticulata* REUSS at the site. Considering the synonymies eight species were reported in the literature, while 25 species are presented in this paper, twelve species are new occurrences in the Hungarian part of the Pannonian Basin.

In a somewhat broader context, it is worth mentioning that the research of the Middle Miocene Paratethyan Scleractinia may also include a lithological issue, the presence of corals in the Leitha/Lajta Limestone (see e.g., PILLER & KLEEMANN 1991; RIEGL & PILLER 2000; REUTER et al. 2012; WIEDL et al. 2012, 2013; PILLER 2022). This rock type is widespread in the studied region of the Börzsöny Mts (e.g., Ipolytölgyes, Nagymaros-Törökmező, Zebegény) (KOPEK 1954, SCHOLZ 1970, MÜLLER 1984, SELMECZI et al. 2024), but neither its coral content of different ages (early–middle–late Badenian), nor the faunal change of Scleractinia between the Miocene Climate Optimum (~17–14 Ma) and the Middle Miocene Climate Transition (~14–13 Ma) have been

investigated in the last few decades in the Hungarian literature. As the hard limestone reported by CSEPREGHY-MEZNERICS (1956) around Letkés village are missing at the studied Bagoly Hill locality, the present work only notes this important problem but does not address it.

## Material and methods

Except for the examined museum specimens (see below), the studied material was collected at the Bagoly Hill locality of Letkés by Zoltán VICIÁN and the author, and was stored in the collection of the Hungarian National Museum Public Collection Centre – Hungarian Natural History Museum, Budapest (HNHM), and in private collections. The assemblage consists mainly of moderately preserved, fragmentary solitary corals and colonies, calices are generally worn.

Taxonomy of the Scleractinia is widely discussed in the literature; the classifications of BARON-SZABO & CAIRNS (2017) and HOEKSEMA & CAIRNS (2024) are accepted herein.

General revision of the Scleractinia in the Miocene Pannonian Basin obviously requires a comprehensive research (DULAI et al. 2021, HENN 2023) with comparisons of the type specimens introduced by MICHELOTTI (1838), SISMONDA (1871), REUSS (1871), CHEVALIER (1962), KÜHN (1963b), etc. and the use of new methods, e.g., landmark techniques (LÓPEZ-PÉREZ 2012). However, this revision is beyond the scope of the present work. The descriptions for fossil material are based on traditional macro- and micromorphological analyses (BUDD et al. 1996, 2012; LÓPEZ-PÉREZ 2012) considering mainly corallite diameter (D), theca thickness, columella characters, septal cycles (complete cycle: SC, incomplete cycle: i), number of septa (SN), septal sculpture, distance between corallites (c-c), features of coenosteum and branching types. Other abbreviations used are Z for zooxanthellate species, and NZ for azooxanthellate species. Measurements are expressed in mm.

## Systematic palaeontology

Class Anthozoa EHRENBERG, 1834  
Subclass Hexacorallia HAECKEL, 1896  
Order Scleractinia BOURNE, 1900  
Suborder Refertina OKUBO, 2016  
Family Dendrophylliidae GRAY, 1847  
Genus *Balanophyllia* WOOD, 1844

*Balanophyllia praelonga* (MICHELOTTI, 1838)  
(Plate I, Figs 1–4, 7–9)

1838 *Turbinolia praelonga* nobis – MICHELOTTI, p. 67.  
1932 *Balanophyllia* aff. *praelonga* MICHELOTTI – DEMBIŃSKA-RÓZKOWSKA, p. 135, pl. 4, fig. 4.  
1953 *Eupsammia irregularis* – MOENKE, p. 243, text-figs 3–5 (*non* SEGUENZA).  
1962 *Balanophyllia* (*Eupsammia*) *praelonga* (MICHELOTTI) – CHEVALIER, p. 464, text-figs 177–178.

1964 *Eupsammia praelonga* (MICHELOTTI) – CHEVALIER, p. 25, text-fig. 13, pl. 2, fig. 5.

1991 *Balanophyllia praelonga* (MICHELOTTI) – STOLARSKI, p. 57, pl. 10, figs 1–4.

2019 *Balanophyllia* (*Eupsammia*) cf. *praelonga* (MICHELOTTI) – SPADINI, p. 86, fig. 28.

*Material* – 7 ceratoid solitary coralla (NZ). HNHM, INV 2024.503. 504., 505., 506., and the author's collection.

	Height	D	SC	SN
Pl. I/1–2	27.5	13×11.8	4+1i	54
Pl. I/3–4	24.6	12.4×11.8	3+?	?
Pl. I/7–8	18	7.7×6.8	3+1i	46
Pl. I/9	12	5×4.5	3+1i	41

*Description* – Trochoid, straight to slightly curved coralla with subcircular cross sections. The septal structure is characterized by the presence of the Pourtalès Plan, it has four complete and a fifth incomplete cycles. Septa have granular septal face, columella is trabecular. Theca bears fine, granular costae. Costae on the specimen figured in *Plate I/7* are covered by epithecal bands.

*Remarks* – *Balanophyllia praelonga* is characterized by moderate morphological variability in the shape of coralla (straight to somewhat curved – see ZUFFARDI-COMERCI 1932, pl. 16, figs 6–7) and its septa is arranged in a Pourtalès Plan. The studied material agrees well with the specimens described from the Korytnica Basin (Poland) (see STOLARSKI 1991, pl. 10, figs 1–4). *Caryophyllia* (*Caryophyllia*) *leptaxis* REUSS, 1871 has similar corallum in size and morphology but it differs by its septal structure (see below), while *C. (C.) attenuata* REUSS, 1871 is distinguishable by its smaller size, more slender corallum, thicker wall, and also septal structure (REUSS 1871, pl. 1, fig. 2; KOPEK 1954, pl. 8, figs 4–5, 8). *Balanophyllia praelonga* is a new record in the Pannonian Basin.

*Distribution* – Middle–Late Miocene: Proto-Mediterranean Sea (Corsica, Italy). Middle Miocene: North Sea Basin (Belgium, Germany), Central Paratethys (Czechia, Hungary, Poland). Late Miocene: Proto-Mediterranean Sea (Morocco).

*Balanophyllia* sp.  
(Plate I, Figs 5–6)

*Material* – 2 fragmentary dendroid colonies (NZ). HNHM, INV 2024.507., and the author's collection.

Height	D	SC	SN
18.5	15.2×12.8	4	48

*Description* – The figured specimen is a fragmentary juvenile form having only four complete cycles, the septal structure is characterized by the presence of the Pourtalès Plan. The costae are equal in breadth. Neither the base, nor the calice are well-preserved, so important diagnostic features cannot be analyzed.

*Remarks* – Although the studied specimens are close in morphology to that illustrated by KOPEK (1954) as *Balanophyllia varians* REUSS, 1860 from Letkés, the genus and

species level arrangements are uncertain because in case of fragmentary dendrophyllid coralla as e.g., fragments of detached branches of *Dendrophyllia* may look like *Balano-phyllia* with polycyclic bases (STOLARSKI 1991).

*Distribution* – Late Oligocene–Middle Miocene: NE Atlantic (France). Early Miocene: North Sea Basin (Germany). Middle Miocene: Proto-Mediterranean Sea (Italy), Central Paratethys (Bosnia, Czechia, Hungary, Poland, Romania). Late Miocene: Proto-Mediterranean Sea (Greece, Morocco). Pliocene: NE Atlantic (France), Mediterranean Sea (Greece).

Genus *Turbinaria* OKEN, 1815

*Turbinaria cyathiformis* (BLAINVILLE, 1830)  
(Plate I, Figs 10–11)

1830 *Gemmpora cyathiformis* – BLAINVILLE, p. 353.

1954 *Turbinaria cyathiformis* (BLAINVILLE) – KOPEK, p. 28, pl. 10, figs 7, 9–12, pl. 11, figs 1, 5.

1960 *Turbinaria cyathiformis* (BLAINVILLE) – KOJUMDGIEVA, p. 25, pl. 8, fig. 3.

1984 *Turbinaria cyathiformis* (BLAINVILLE) – BOREL BEST, pl. 4, figs 1–5.

1990 *Turbinaria cyathiformis* (BLAINVILLE) – OOSTERBAAN, p. 14.

2021 *Turbinaria cyathiformis* (BLAINVILLE) – SAINT MARTIN et al., p. 17, fig. 12F.

*Material* – 3 fragmentary massive, laminate colonies (Z). HNHM, INV 2024.508., and the author's collection.

Colony	D	SC	SN	c-c
33×24×10	1,5–2	2+1i	20	1–6

*Description* – Flat, laminate colonies. Corallites are irregularly spaced, they are curved in the coenosteum, and calices are at an angle to the surface. Coenosteum is spongy with granular surface. The species is characterized by two complete and one incomplete cycles (KOPEK 1954, SAINT MARTIN et al. 2021), the highest number of septa of the studied specimens is 20.

*Remarks* – *Turbinaria cyathiformis* is rare at the study locality but abundant in the coral reef facies around Márk-háza (Cserhát Hills) (KOPEK 1954; HEGEDŰS & JANKOVICH 1972; own data). The species is typical of clear, oxygen-rich, shallow-water (5–30 m) environments (OOSTERBAAN 1988).

*Distribution* – Late Oligocene: Tethys (Malta). Late Oligocene–Middle Miocene: NE Atlantic (France), Proto-Mediterranean Sea (Italy). Middle Miocene: Central Paratethys (Austria, Bulgaria, Hungary).

Family Flabellidae BOURNE, 1905

Genus *Flabellum* LESSON, 1831

(*Flabellum* species of the Miocene Paratethys are not assigned to subfamilies in HOEKSEMA & CAIRNS 2024.)

*Flabellum roissyanum* MILNE EDWARDS & HAIME, 1848  
(Figure 2/A–B)

1848 *Flabellum roissyanum* – MILNE EDWARDS & HAIME, p. 268, pl. 8, fig. 1.

1954 *Flabellum roissyanum* MILNE EDWARDS et HAIME – KOPEK, p. 22, pl. 8, figs 6–7 (only).

1960 *Flabellum roissyanum* EDWARDS et HAIME – KOJUMDGIEVA, p. 22, pl. 6, fig. 10.

1962 *Flabellum avicula* (Michelotti) var. *roissyana* MILNE EDWARDS et HAIME – CHEVALIER, p. 387, text-fig. 135h, pl. 14, figs 12–13.

1963b *Flabellum roissyanum* MILNE EDWARDS & HAIME – KÜHN, p. 86, pl. 17, figs 1–2.

1991 *Flabellum roissyanum* MILNE EDWARDS & HAIME – STOLARSKI, p. 55, pl. 9, figs 1–5, pl. 12, fig. 1.

2016 *Flabellum roissyanum* MILNE EDWARDS & HAIME – KLEPRLÍKOVÁ & DOLÁKOVÁ, p. 83, fig. 6.2.

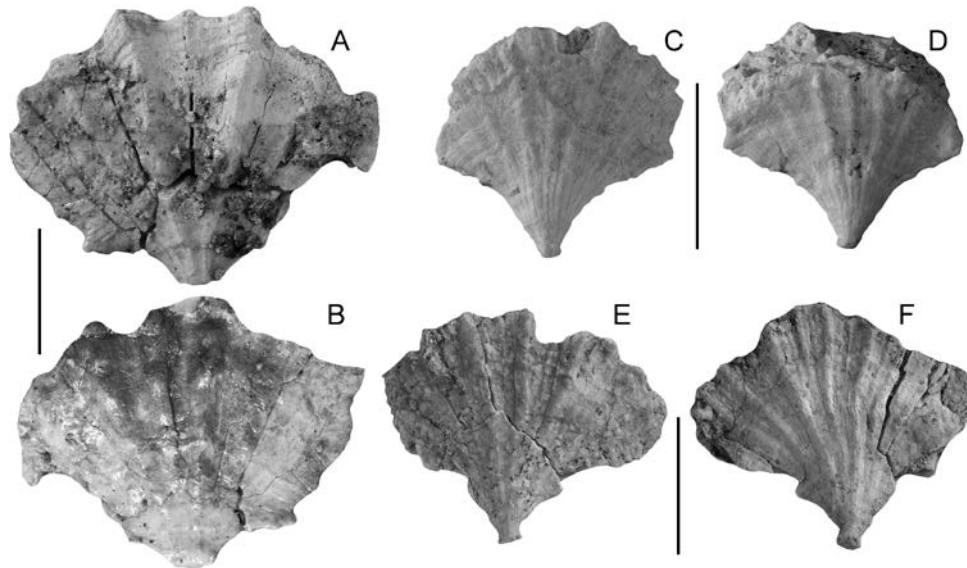
*Material* – 1 fragmentary flabellate solitary corallum (NZ), Letkés, unknown locality. HNHM, M.59.824.

Height	Width	Thickness
22.4	29.4	14

*Description* – The specimen figured herein was in andesite tuffite matrix (similar deposits occur at the Bagoly Hill locality as well), so details of septa cannot be traced. Cross section of the corallum is oval with a shallow mid-lateral concavity. From the seven costae the third and fifth are the strongest, and they bear three moderately developed spines.

*Remarks* – The studied specimen is a donation to the Hungarian Natural History Museum, it came from an unknown locality around Letkés. *Flabellum roissyanum* MILNE EDWARDS & HAIME was interpreted as a variety of *Flabellum avicula* (MICHELOTTI, 1838) by CHEVALIER (1962). This arrangement was discussed in the literature (see STOLARSKI 1991, CHAIX et al. 2018, SPADINI & PIZZOLATO 2021), in this paper the classification of STOLARSKI (1991) and KLEPRLÍKOVÁ & DOLÁKOVÁ (2016) is accepted. Although the *Flabellum* species are characterized by remarkable intraspecific variability (STOLARSKI 1991, SCHNEIDER et al. 2019), *F. roissyanum* and *F. avicula* are distinguishable in morphology: the holotype of *F. roissyanum* is a more compressed corallum with a lateral concavity and it bears much coarser primary ribs (see CHEVALIER 1962, pl. 14, figs 12–13; KÜHN 1963b, pl. 17, fig. 1) (for *F. avicula* see MICHELOTTI 1838, pl. 3, fig. 2; CHEVALIER 1962: 386–390, pl. 22, figs 6–7).

Revising the Miocene *Flabellum* species, KÜHN (1963b) introduced a new taxon, *F. krejci*, and among its synonymies the N Hungarian *F. roissyanum* material of KOPEK (1954) was listed. However, the specimens illustrated by KOPEK (l.c.) differ from each other in morphology and represent different taxa: 1) The specimen on plate 8, figs 6–7 corresponds to the holotype of *Flabellum roissyanum*. 2) The large specimen on plate 8, figs 9–10 is a representative of *Flabellum kopeki* KOJUMDGIEVA (see KOJUMDGIEVA 1960: 23, pl. 7, fig. 1). 3) The specimens on plate 9, figs 1–6 are representatives of *Flabellum krejci* KÜHN. *Flabellum roissyanum* is frequent in the lower Badenian clayey deposits of Szokolya (Börzsöny Mts) (KOPEK 1954; own data). The species does not occur in the studied assemblage of the Bagoly Hill locality.



**Figure 2.** A–B. *Flabellum roissyanum* MILNE EDWARDS & HAIME, 1848. HNHM, M.59.824. (covered by lacquer), lateral views, Letkés, unknown locality. C–D. *Flabellum cf. suessi* REUSS, 1871. NÁDAI Collection, lateral views, Bagoly Hill, Letkés. E–F. *Flabellum cf. suessi* REUSS, 1871. VICIÁN Collection, lateral views, Bagoly Hill, Letkés. Scale bars 10 mm.

**2. ábra.** A–B. *Flabellum roissyanum* MILNE EDWARDS & HAIME, 1848. HNHM, M.59.824. (lakkal bevonva), laterális nézetek, Letkés, ismeretlen lelőhely. C–D. *Flabellum cf. suessi* REUSS, 1871. NÁDAI László gyűjteménye, laterális nézetek, Bagoly-hegy, Letkés. E–F. *Flabellum cf. suessi* REUSS, 1871. VICIÁN Zoltán gyűjteménye, laterális nézetek, Bagoly-hegy, Letkés. Méretvonalak: 10 mm.

Genus *Flabellum* is typical of deep water sea (circalittoral–uppermost bathyal, aphotic zones, 150–1000 m) (SQUIRES 1961, CAIRNS 2004).

**Distribution** – Middle–Late Miocene: Proto-Mediterranean Sea (Italy). Middle Miocene: Central Paratethys (Austria, Bulgaria, Czechia, Hungary, Poland, Romania, Slovakia). Pliocene: Mediterranean Sea (Greece, Italy).

*Flabellum cf. suessi* REUSS, 1871  
(Figure 2/C–F)

- 1871 *Flabellum suessi* nov. sp. – REUSS, p. 227, pl. 4, fig. 8.  
1962 *Flabellum suessi* REUSS – CHEVALIER, p. 397 (*partim*).  
1963b *Flabellum suessi* REUSS – KÜHN, pl. 17, fig. 2.  
2016 *Flabellum suessi* REUSS – KLEPRLÍKOVÁ & DOLÁKOVÁ, p. 83, fig. 6.3.  
2023 *Flabellum cf. suessi* REUSS – HENN, conference presentation.

**Material** – 2 fragmentary flabellate solitary coralla (NZ). Private collections of László NÁDAI and Zoltán VICIÁN.

	Height	Width	Thickness
Fig. 2/E–F	17	20	10.6
Fig. 2/C–D	13.7	15	8.6

**Description** – Cross sections of the calices are narrow pointed oval in shape, lateral faces are covered by weakly developed costae and growth lines. The five primary costae are of similar breadth, finer secondary costae are present in interspaces. As calices are filled with sediments, the septal structure cannot be analyzed. The angle of lateral edges is 120°. Pedicels are small and relatively long.

**Remarks** – Size and external morphology of the studied specimens are close to the holotype of *Flabellum suessi* REUSS (see KÜHN 1963b, pl. 17, fig. 2) but ornamentation of

the specimen in Figure 2/E–F somewhat differs by slightly flexuous ribs. The species is distinguished from the more common *Flabellum roissyanum* MILNE EDWARDS & HAIME and from *F. multicoatum* REUSS, 1871 by its smaller size, pointed oval calice and much weaker sculpture; from *F. austriacum* PROCHÁZKA, 1893 by its shorter and more compressed corallum; from *F. krejci* KÜHN by its smaller size and much narrower calice, and from *F. laevissimum* KÜHN, 1963 by its oval shape calice.

*Flabellum suessi* was recorded from Karpatian (= Helvetian) deposits at Mogyoród (Gödöllő Hills, Hungary) by HORUSITZKY (1926: 164). This record is verified herein based on the collection of the Hungarian National History Museum where a *Flabellum suessi* specimen is stored from the vicinity of Mogyoród (HNHM M.61.6495.). The species was recorded by HENN (2023) from the Badenian deposits of Tekeres (Mecsek Mts, southern Pannonian Basin).

**Distribution** – Central Paratethys. Early–Middle Miocene: Hungary. Middle Miocene: Czechia, Poland.

Poritidae GRAY, 1840  
*Porites* LINK, 1807

*Porites vindobonarum prima* KÜHN, 1927  
(Plate I, Figs 12–14)

- 1927 *Porites vindobonarum prima* KÜHN – KÜHN in FELIX, p. 473.  
1932 *Porites vindobonarum prima* KÜHN – DEMBIŃSKA-RÓZKOWSKA, p. 154, pl. 6, fig. 10.  
1954 *Porites vindobonarum prima* KÜHN – KOPEK, p. 29, pl. 11, figs 7, 9.  
1991 *Porites vindobonarum prima* KÜHN in FELIX – RONIEWICZ & STOLARSKI, p. 77, pl. 4, fig. 3.  
2008 *Porites vindobonarum prima* KÜHN – RUS & POPA, p. 331, pl. 4, fig. 3.

2018 *Porites vindobonarum prima* KÜHN in FELIX – GÓRKA, p. 250, fig. 6.

2018b *Porites vindobonarum prima* KÜHN – KLEPRLÍKOVÁ, p. 63, figs 1.5–6, 2.1.

**Material** – Massive, cerioid colonies (Z). HNHM, M.61.4376 (1 specimen, Letkés, unknown locality), INV 2024.509. 510., 511.1–3., and numerous specimens from the Bagoly Hill in the author's collection.

Colonies width	D	SC	SN
50–300	1.2–1.4	2	12

**Description** – Corallites are small, closely spaced, two complete cycles are recognized. The septal arrangement agrees with that illustrated by DEMBIŃSKA-RÓZKOWSKA (1932: 155, text-fig. 2).

**Remarks** – The studied colonies agree well in form and size with the material presented by GÓRKA (2018) from the Polish-Ukrainian Fore-Carpathian Basin (Ukraine). At the Bagoly Hill locality both encrusting and massive colonies occur. *Porites leptoclada* REUSS is distinguishable by its dendroid-type corallum and variable-sized corallites (see REUSS 1871, pl. 17, figs 3–4), while *P. maigensis* KÜHN, 1925 has wider corallites (D 1.5–2 mm). *Porites manciensis* CHEVALIER differs by its smaller corallites (D 0.8–1 mm), and presence of a third incomplete cycle (CHEVALIER 1962, CHAIX et al. 2018). Corallites of *Porites collegniana* MICHELIN, 1842 (= *P. incrustans* MILNE EDWARDS & HAIME, 1851) are wider and possess well-developed walls (see CHEVALIER 1962, pl. 26, figs 1, 3; and the syntype: MNHN.F.M00730\*). Remains of *Lithophaga lithophaga* (LINNAEUS, 1758) shells and commensal cirripedes are frequent within the massive colonies (Plate I, Fig. 14).

The studied hermatypic coral assemblage is dominated by *Echinopora oligophylla* (REUSS, 1871), *Tarbellastraea reussiana* (MILNE EDWARDS & HAIME, 1850) and *Porites vindobonarum prima*. The latter species was recorded from Grund (Austria), Sámsonháza (Hungary), the Korytnica Basin (Poland), Lăpugiu de Sus (Romania) and the Medobory Hills (Ukraine), these localities indicate shallow-water (5–30 m) to upper mesophotic (30–50 m) habitats. Miocene paleobathymetric data by PERRIN (2000) suggest shallow-water distribution (1–13 m) for *Porites* cf. *collegniana* associated with *Montastraea* and *Tarbellastraea* species. The Recent *Porites* species occur in shallow-water to upper mesophotic environments.

**Distribution** – Middle Miocene: Central Paratethys (Austria, Bulgaria, Hungary, Poland, Romania, Ukraine).

\*<https://science.mnhn.fr/institution/mnhn/collection/fl/item/m00730> (accessed: 10.11.2023)

Family Rhizangiidae D'ORBIGNY, 1851

Genus *Siderastrea* BLAINVILLE, 1830

*Siderastrea felixi* DEMBIŃSKA-RÓZKOWSKA, 1932  
(Plate I, Figs 15–16)

1932 *Siderastraea felixi* n. sp. – DEMBIŃSKA-RÓZKOWSKA, p. 131, pl. 3, figs 2–2a, pl. 7, fig. 3.

1954 *Siderastraea crenulata* – KOPEK, p. 15, pl. 4, fig. 6, pl. 6, fig. 1 (non GOLDFUSS).

2008 *Siderastraea felixi* ROSZKOWSKA [sic] – CHAIX & SAINT MARTIN, p. 197, fig. 4E.

**Material** – 4 cerioid colonies (Z). HNHM INV 2024.512., and private collections of Tamás NÉMETH and the author.

	Colony	D	SC	SN
Pl. I/15–16	33×25×19	3–4	3+1i	24–33
	30×24×12	3–4	3+1i	24–31

**Description** – Small, pebble form colonies. Calices are shallow and polygonal, corallites are closely spaced, walls cannot be seen on the surface. Septa could be confluent or not with adjacent corallites, septal margins and faces are finely granular. The species is characterized by three complete and a fourth incomplete cycles. Septa of the first two cycles reach the weakly developed columella.

**Remarks** – *Siderastrea felixi* is somewhat similar to *S. crenulata* (GOLDFUSS, 1826) in its granular surface and very weakly developed wall but is distinguished by its much smaller corallites (D max. 4 mm as opposed to 6–7 mm on *crenulata*). The other *Siderastrea* species described from the Badenian Central Paratethys [*S. froehlichiana* (REUSS, 1847), *S. miocenica italica* (DEFRANCE, 1826), *S. lomnickii* DEMBIŃSKA-RÓZKOWSKA, 1932, *S. radians* (PALLAS, 1766)] differ in morphology by possessing considerably wider calices and well-developed walls which appear on the surface. *Siderastrea felixi* was suggested as a potential synonym of *S. miocenica* OSASCO var. *regularis* D'ORBIGNY, 1852 by CHEVALIER (1962: 427). This variety is really similar to *Siderastrea felixi* in its small calices (D 2–4 mm) but also has well-developed walls (CHEVALIER l.c., pl. 25, fig. 4). The specimen illustrated by RUS & POPA (2008, pl. 3, fig. 8) from Lăpugiu de Sus (Romania) under the name *Siderastrea froehlichiana* differs from REUSS' species by its small calices (D 2–3 mm as opposed to D 4.5–5 on *S. froehlichiana*). This material was revised by CHAIX et al. (2018: 330) regarding it as *Siderastrea felixi* but based on the wall structure it seems closer to *S. miocenica regularis*. The specimens described by KOPEK (1954) as *Siderastrea crenulata* differ from GOLDFUSS' taxon by their much smaller corallites (D 3–4 mm), they are recognized herein as representatives of *S. felixi*. Outside the Central Paratethys the species is known in the Miocene NE Atlantic (France; CAHUZAC & CHAIX 1996) and the Proto-Mediterranean Sea (Algeria, Morocco, Italy; CHAIX & SAINT MARTIN 2008). In Hungary *Siderastrea* cf. *felixi* was recorded by KÓKAY (1985) from the Late Badenian Pannonian Basin.

Fossil *Siderastrea* species display a wide bathymetric range. Miocene Central Paratethyan representatives were recorded from shallow-water to upper mesophotic habitats (see localities in REUSS 1871; KOPEK 1954; KOJUMDIEVA 1960; HEGEDŰS 1970, RONIEWICZ & STOLARSKI 1991; CHAIX et al. 2018). A Mio-Pliocene Caribbean *Siderastrea* assemblage was described from shallow-water environments (FOSTER 1981), the Recent *Siderastrea* species are also typical of shallow reef habitats.

*Distribution* – Middle Miocene: NE Atlantic (France), Central Paratethys (Hungary, Poland). Late Miocene: Proto-Mediterranean Sea (Algeria, Italy, Morocco).

*Siderastrea radians* (PALLAS, 1766)  
(Plate I, Figs 17–18)

1766 *Madrepora radians* – PALLAS, 322.

2008 *Siderastrea radians* (PALLAS) – CHAIX & SAINT MARTIN, p. 194, fig. 4C.

2018 *Siderastrea radians* (PALLAS) – CHAIX et al., p. 330, fig. 5B.

*Material* – 3 cerioid colonies (Z). Private collections of László NÁDAI and the author.

	Colony	D	SC	SN
Pl. I/17–18	26×24×16.4	3.5–4.5	3+1i	29–38
	20×20×11	3.5–4.5	3+1i	29–41

*Description* – Small, subhemispherical colony. Calices are shallow and polygonal, corallites are closely spaced, thin walls can be seen on the surface. Septa could be confluent or not with adjacent corallites, septal margins and faces are strongly granular. The species is characterized by three complete and a fourth incomplete cycles. Septa of the first two cycles reach the weakly developed columella,  $S_3$  are irregularly fused with  $S_2$ .

*Remarks* – *Siderastrea radians* was frequently confused with *S. crenulata* (GOLDFUSS, 1826) in the Paratethyan literature (CHAIX et al. 2018) which is a Late Miocene–Early Pliocene species and endemic to Italy (CHAIX et al. 2008), and it has wider corallites (D 6–7 mm). *Siderastrea miocenica italica* (DEFRANCE) also has wider corallites (D 5 mm), the septal margins are less granular, columella is more developed and projected, and more synaptical rings are present. *Siderastrea radians* is a new record in the Miocene Pannonian Basin.

The colony figured herein is of particular interest for a phenomenon that can rarely be studied on fossil *Siderastrea* specimens. Juvenile corallites appear on the colony as a probable consequence of an environmental stress that occurred previously. The polyps almost died but they started to form regenerated corallites by parvicidal budding in the middle of the former corallites (Jaroslav STOLARSKI pers. com.; and see DUERDEN 1904; NEVES et al. 2010).

*Distribution* – Late Oligocene–Recent. Late Oligocene–Middle Miocene: NE Atlantic (France). Middle Miocene: Proto-Mediterranean Sea (Greece), Central Paratethys (Hungary, Romania). Late Miocene: Proto-Mediterranean Sea (Algeria, Greece, Italy, Morocco, Spain, Tunisia).

Suborder Vacatina OKUBO, 2016

Family Caryophylliidae DANA, 1846

Genus *Caryophyllia* LAMARCK, 1801

Subgenus *Caryophyllia* (*Acanthocyathus*) MILNE EDWARDS & HAIME, 1848

*Caryophyllia* (*Acanthocyathus*) *verrucosa*  
(MILNE EDWARDS & HAIME, 1848)  
(Plate II, Figs 1–7)

1848 *Trochocyathus verrucosus* – MILNE EDWARDS & HAIME, p. 311.

1888 *Acanthocyathus vindobonensis* REUSS – PROCHÁZKA, p. 318–320, pl. 2, fig. 7, pl. 3, figs 1–10.

1953 *Acanthocyathus verrucosus* (MILNE EDWARDS & HAIME) – KÜHN, p. 218.

1954 *Acanthocyathus vindobonensis* REUSS – KOPEK, p. 25, pl. 9, figs 12–20.

1960 *Caryophyllia* (*Acanthocyathus*) *vindobonensis* (REUSS) – KOJUMDIEVA, p. 21, pl. 6, figs 6–7.

2000 *Acanthocyathus transsilvanicus* REUSS – TIŢĂ, p. 374, figs 1–4.

2008 *Caryophyllia* (*Acanthocyathus*) *transilvanicus* [sic] (REUSS) – RUS & POPA, p. 329, pl. 3, figs 3–5.

2018a *Caryophyllia* (*Acanthocyathus*) *vindobonensis* (REUSS) – KLEPRLÍKOVÁ, p. 40, fig. 1.

*Material* – Trochoid solitary coralla (NZ). HNHM, M.61.4378. (collected by Ilona CSEPREGHY-MEZNERICS from the clay bed of the “Ruined chapel” locality at Letkés), INV 2024.513. 514, 515., 516.1–10., and more than 250 fragmentary specimens from the Bagoly Hill in private collections of László NÁDAI, Tamás NÉMETH and the author (NZ).

	Height	D
Pl. II/1–2	31	14.4×12.3
Pl. II/3–4	25	18.4×11.6
Pl. II/5–6	20.3	11.7×9.3
Pl. II/7	31	14×10.9

*Description* – Trochoid coralla with different width, sub-circular to oval cross sections, trabecular columella, and septa with granular septal face. The species is characterized by four complete and a fifth incomplete cycles. Theca bears 6 rows of lateral spines.

*Remarks* – The species is characterized by moderate morphological variability in cross section of corallites (wide to narrow oval), numbers of septa (in the studied material SN 52–64) and strength of the ribs and lateral spines (KOPEK 1954). REUSS (1871) introduced two species with closely allied morphology: *Acanthocyathus vindobonensis* and *A. transsilvanicus*. Pannonian Basin representatives of these taxa were compared by KOPEK (1954) and considering the high number of transitional forms – following the revision of PROCHÁZKA (1888) – only one species was recognized as available (based on priority): *Acanthocyathus vindobonensis*. This arrangement was accepted by KOJUMDIEVA (1960). Earlier this taxon had been interpreted as a synonym of *Acanthocyathus verrucosus* (MILNE EDWARDS & HAIME) by KÜHN (1953) and *A. transsilvanicus* was treated as a subspecies (*A. verrucosus transsilvanicus* REUSS) by KÜHN (1963b). CHEVALIER (1962: 348) also separated *transsilvanicus* from *verrucosus*. However, subspecies of *Caryophyllia* (*Acanthocyathus*) *verrucosa* are not accepted in the recent literature (CHAIX et al. 2018, HOEKSEMA & CAIRNS 2024). The specimen in *Plate II, Figure 7* is a slender corallum, bearing strong, sharp ribs without projected spines, it represents the *transsilvanica* morphotype (see REUSS 1871, pl. 10, fig. 4; KÜHN 1963b, pl. 17, fig. 8).

The subgenus is typical of deep water sea (circalittoral to uppermost bathyal, aphotic zones). In the Australian region four Recent *Caryophyllia* (*Acanthocyathus*) species were recorded by CAIRNS (2004) with average bathymetrical range of 152–307 m.

*Distribution* – Late Oligocene–Middle Miocene: Proto-Mediterranean Sea (Italy). Middle Miocene: Central Paratethys (Austria, Bulgaria, Czechia, Hungary, Poland, Romania, Slovakia). Miocene: Proto-Mediterranean Sea (Türkiye?).

Subgenus *Caryophyllia* (*Caryophyllia*) LAMARCK, 1801

*Caryophyllia* (*Caryophyllia*) cf. *leptaxis* REUSS, 1871  
(Plate II, Figs 8–9)

1871 *Caryophyllia leptaxis* nov. sp. – REUSS, p. 207, pl. 1, fig. 8

1900 *Caryophyllia leptaxis* REUSS – PROCHÁZKA, p. 146.

1952 *Caryophyllia* cf. *leptaxis* REUSS – KOPEK, p. 78, pl. 14, fig. 4.

1962 *Caryophyllia* cf. *leptaxis* REUSS – CHEVALIER, p. 337.

*Material* – 1 fragmentary trochoid solitary corallum (NZ). HNHM, INV 2024.517.

Height	D	SC	SN
15.8	9.3×8.2	4+1i	52

*Description* – Small, straight and broad corallum with oval cross section, trabecular columella, and septa with granular septal face. The species is characterized by four complete and a fifth incomplete cycles (REUSS 1871: 207). Theca is costate with fine, granular costae of equal breadth.

*Remarks* – The species differs from *Caryophyllia* (*Acanthocyathus*) *verrucosa* in smaller size and in morphology by its broader monocyclic base and straight corallum without any spiny sculpture. The rare *Caryophyllia* (*Caryophyllia*) *leptaxis* is a new record in the Pannonian Basin.

The subgenus is typical of deep seawater (upper bathyal, aphotic zone). In the Australian region 14 Recent *Caryophyllia* (s.s.) species were recorded by CAIRNS (2004), their average bathymetrical range is 215–828 m.

*Distribution* – Middle Miocene: Central Paratethys (Czechia, Hungary, Slovakia).

Genus *Ceratotrochus* MILNE EDWARDS & HAIME, 1848

Subgenus *Ceratotrochus* (*Edwardsotrochus*) CHEVALIER, 1962

*Ceratotrochus* (*Edwardsotrochus*) *duodecimcostatus*  
(GOLDFUSS, 1826)  
(Plate II, Figs 10–13)

1826 *Turbinolia duodecimcostata* nobis – GOLDFUSS, p. 52, pl. 15, fig. 6.

1954 *Ceratotrochus duodecimcostatus* (GOLDFUSS) – KOPEK, p. 20, pl. 7, figs 7–11, pl. 8, figs 1–3.

1991 *Ceratotrochus* (*Edwardsotrochus*) *duodecimcostatus* (GOLDFUSS) – STOLARSKI, p. 53, text-fig. 7, pl. 5, figs 1, 4, 6.

2019 *Ceratotrochus* (*Edwardsotrochus*) *duodecimcostatus* (GOLDFUSS) – SPADINI, p. 81, figs 11–12.

*Material* – 90 fragmentary trochoid solitary coralla (NZ). HNHM, INV 2024.518., 519.1–3., and private collections of László NÁDAI, Tamás NÉMETH and the author.

	Height	D	SC
Pl. II/10–11	37	17×15.3	5
Pl. II/12–13	43.7	22×15.4	5

*Description* – Coralla are high, robust, slightly curved,

their cross section is wide oval, calice is deep, external wall is granular, spiny sculpture is absent or limited to the external lateral ridge. The species is characterized by five cycles, the 12 septa of the first two cycles are more developed, they rise above the calical rim; septal face is granular. The corresponding 12 primary costae are also stronger than the secondaries.

*Remarks* – The constrictions of theca on both *Caryophyllia* (*Acanthocyathus*) *verrucosa*, and *Ceratotrochus* (*Edwardsotrochus*) *duodecimcostatus* specimens correspond to growth cycles.

*Distribution* – Early Miocene: Proto-Mediterranean Sea (Switzerland). Early Miocene–Pliocene: Proto-Mediterranean Sea (Italy). Middle Miocene: Central Paratethys (Austria, Bosnia, Bulgaria, Czechia, Hungary, Poland). Miocene: North Sea Basin (Germany). Pliocene: Mediterranean Sea (Algeria, France, Morocco, Spain, Tunisia).

Family Faviidae MILNE EDWARDS & HAIME, 1857

Subfamily Faviinae MILNE EDWARDS & HAIME, 1857

Genus *Favia* BLAINVILLE, 1820

*Favia* cf. *melitae* CHEVALIER, 1962  
(Plate II, Figs 14–15)

1962 *Favia melitae* nov. sp. – CHEVALIER, p. 134, pl. 9, fig. 8.

1997 *Favia* cf. *melitae* CHEVALIER – BARON-SZABO, p. 101, pl. 1, figs A–B, D, pl. 2, fig. B.

*Material* – 1 fragmentary plocoid colony (Z). HNHM, INV 2024.520.

Colony	D	SC	SN	c-c
28×24×21	4–6	3+1i	24–27	1–2

*Description* – Rounded colony with a convex base. Coralites are subcircular to oval in shape, and irregularly spaced. Calices are deep with shape of truncated cone, theca is thick and costate, costae are not confluent. Coenosteum is covered by costae. The specimen has three complete and the fourth incomplete cycles, septa of the first two cycles reach the columella, paliform lobes are present, septal face is granular.

*Remarks* – The most closely allied form in size and macromorphological features is the Miocene *Favia melitae* CHEVALIER described from the Proto-Mediterranean Sea (Malta) and also recorded from the Badenian Central Paratethys (Slovenia) by BARON-SZABO (1997). The species differs from most congeners in its smaller size.

It is worth comparing the studied specimen to the other *Favia* species recorded from the Miocene Central Paratethys. *Favia magnifica* REUSS differs by its much larger size and sharp calical rims (REUSS 1871: 238, pl. 11, figs 1–3) (*F. magnifica* was recorded from the N Pannonian Basin by KOPEK 1954 and SCHOLZ 1970). The calices of *Favia corollaris* REUSS (originally described from Nagymaros, Börzsöny Mts) are lower, and more closely spaced (REUSS 1871: 238, pl. 12, fig. 3); *F. friedbergi* DEMBIŃSKA-RÓZKOWSKA differs by its larger corallites with higher number of septa



(DEMBIŃSKA-RÓZKOWSKA 1932: 158, pl. 3, fig. 1); *F. gotschevi* KOJUMDGIEVA is characterized by its much larger corallites (KOJUMDGIEVA 1960, pl. 2, figs 1–2). *Favia somaliensis* GREGORY, 1900 was reported from the Badenian of Romania by CHAIX et al. (2018: 344). This species is typical of the Middle Eocene–Oligocene of East Africa and the specimens illustrated by GREGORY (1900, pl. 1, fig. 4; 1921, pl. 6, fig. 4) seem different in size and morphology from the material referred to by CHAIX et al. (l.c.: RUS & POPA 2008, pl. 1, fig. 3) – the occurrence of *Favia somaliensis* in the Badenian Central Paratethys needs verification. *Favia cf. melitae* is a new record in the Hungarian part of the Pannonian Basin.

**Distribution** – Middle Miocene: Proto-Mediterranean Sea (Malta), Central Paratethys (Hungary, Slovenia).

Genus *Mussismilia* ORTMANN, 1890

*Mussismilia vindobonensis* CHEVALIER, 1962  
(Plate II, Figs 16–21)

- 1962 *Mussismilia vindobonensis* nov. sp. – CHEVALIER, p. 285, text-fig. 103, pl. 14, figs 4, 14, pl. 15, fig. 1.  
1970 *Mussismilia vindobonensis* CHEVALIER – SCHOLZ, p. 198, pl. 5, figs 1–5.  
1990 *Mussismilia vindobonensis* CHEVALIER – OOSTERBAAN, p. 11, pl. 2, figs 3–4.  
1997 *Mussismilia vindoboniensis* [sic] CHEVALIER – BARON-SZABO, p. 103, pl. 3, figs C–E.

**Material** – 22 fragmentary phaceloid colonies (Z). HNHM, INV 2024.521., 522., 523.1–3., and private collections of László NÁDAI, Tamás NÉMETH and the author.

	Height	D	SC	SN
Pl. II/20–21	61	Da 23×18	4+1i	>48
Pl. II/16–17	37	22×12	4+1i	55
Pl. II/18–19	40	26×20	4+1i	62

**Description** – Large coralla with 1–4 parallel columns, shallow, oval calices, septal face is strongly granular, margin is strongly serrate, wall is septo- to parathecal. The species is characterized by four complete and a fifth incomplete cycles, septa of the first three cycles reach the large, trabecular columella.

**Remarks** – The studied specimens agree well in size and morphology with the Pannonian Basin material presented in the literature (SCHOLZ 1970, OOSTERBAAN 1990). Intratentacular branching is typical of the genus, so the *Mussismilia vindobonensis* specimens generally appear as 1–4 parallel columns of corallites (see SCHOLZ 1970, pl. 5; BARON-SZABO 1997, pl. 3, fig. C).

**Distribution** – Middle Miocene: Proto-Mediterranean Sea (France, Spain), Central Paratethys (Hungary, Slovenia).

Subfamily Mussinae ORTMANN, 1890

Genus *Syzygophyllia* REUSS, 1860

*Syzygophyllia brevis* REUSS, 1860  
(Plate II, Figs 22–25)

1860 *Syzygophyllia brevis* m. n. sp. – REUSS, p. 217, pl. 1, figs 10–12, pl. 2, fig. 10.

1906 *Syzygophyllia brevis* REUSS – MACOVEI, p. 129, pl. 7, fig. 3.  
1960 *Syzygophyllia brevis* REUSS – KOJUMDGIEVA, p. 19, pl. 5, figs 3–5.

1970 *Syzygophyllia brevis* REUSS – SCHOLZ, p. 198, pl. 4, fig. 3.

1991 *Syzygophyllia brevis* REUSS – RONIEWICZ & STOLARSKI, p. 76, pl. 1, fig. 2.

2008 *Syzygophyllia brevis* REUSS – RUS & POPA, p. 328, pl. 2, figs 6–7.

2008 *Acanthophyllia ampla* – RUS & POPA, pl. 2, figs 8–9.

**Material** – 11 fragmentary turbinate solitary coralla (Z). HNHM, INV 2024.524., 525., and private collections of László NÁDAI and the author.

	Height	D	SC	SN
Pl. II/22–23	28.5	23×21	?	?
Pl. II/24–25	21	28×25	5+1i	104

**Description** – Coralla are septocostate, epitheca is weakly developed consisting of thin, irregular, undulating bands. Septa of the first and second cycles reach the spongy columella, septal margins are denticulate, septal face is finely granular,  $S_4$  are irregularly fused with  $S_3$ ,  $S_5$  are regularly fused with  $S_4$ . The species is characterized by five complete and one incomplete cycles. The exact number of septa of the specimen in *Plate II, Figs 22–23* cannot be traced for poor preservation. The species displays moderate morphological variability in height of the corallum and shape of the cross section (subcircular to suboval).

**Remarks** – One of the specific features of *Syzygophyllia brevis* is the cyclic rejuvenation by intratentacular budding (RUS & POPA 2008), and as a consequence a few specimens display irregular shapes during their growth (REUSS 1860, pl. 1, fig. 10; KOJUMDGIEVA 1960, pl. 5, fig. 4; RUS & POPA 2008, pl. 2, figs 6–7; *Plate II, Figs 22–23*). *Syzygophyllia brevis* was listed among the zooxanthellate species by CHAIX et al. (2018, table I). This interpretation is accepted herein on the basis of its occurrence in shallow-water habitats and co-occurrence with colonial corals. In the Pannonian Basin *Syzygophyllia brevis* is the only solitary coral which appears in the Badenian shallow-water invertebrate fauna of Márk-háza (own data, not recorded by HEGEDŰS & JANKOVICH 1972) and it is the most abundant solitary coral species in the Badenian shallow patch-reef paleoenvironment at Bánd (own data, not recorded by HEGEDŰS 1970). Recent solitary zooxanthellate corals [e.g., genus *Scolymia*, or *Balanophyllia europaea* (RISSE, 1826)] represent a small group within the Scleractinia.

**Distribution** – Middle Miocene: Central Paratethys (Bulgaria, Czechia, Hungary, Poland, Romania).

Genus *Stylocora* REUSS, 1871 (not assigned to subfamily in HOEKSEMA & CAIRNS 2024)

*Stylocora exilis* REUSS, 1871  
(Plate III, Figs 1–5)

1871 *Stylocora exilis* nov. sp. – REUSS, p. 235, pl. 8, figs 4–7.

1932 *Stylocora exilis* REUSS – DEMBIŃSKA-RÓZKOWSKA, p. 130, pl. 4, fig. 2.

1991 *Stylocora exilis* REUSS – PILLER & KLEEMANN, fig. I6c.

1991 *Stylocora exilis* REUSS – RONIEWICZ & STOLARSKI, p. 74, pl. 3, figs 1–6.

2016 *Stylocora exilis* REUSS – KLEPRLÍKOVÁ, p. 46, pl. 9, fig. 3.

**Material** – More than 150 fragmentary subdendroid colonies (Z). HNHM, INV 2024.526., 527., 529., 530.1–12., and the author's collection.

	Length	D	SC	SN
Pl. III/1–2	15.7	3	3	24
Pl. III/4	14.3	3	3	24
Pl. III/5	13	3.1	3	24

**Description** – Theca of the small, tube-shaped corallites (width: 2.5–3 mm) is thick, granular, and – mainly close to the calices – costate. The species is characterized by three complete cycles. Septa of the first cycle reach the weakly developed columella, and rise above the calical rim, septal face is strongly granular. Extratentacular branching is typical of the species, 1–3 juvenile corallites can appear at the same level, usually with 90° branching angle (RONIEWICZ & STOLARSKI 1991: 74), different development is rare (KLEPRLÍKOVÁ 2016, pl. 9, fig. 3). Intraspecific variability appears in strength of costae.

**Remarks** – Three specimens in the *Stylocora exilis* material deserve attention. Their morphology slightly differs from the others by bearing longer branches, and showing dendroid type development (Plate III, Fig. 5). *Stylocora exilis* is a new record in the Pannonian Basin.

*Stylocora exilis* was characterized by wide bathymetrical distribution. Its occurrence at Grund and Niederleis (Austria) (REUSS 1871) indicates shallow-water environments but the Baden Fm. at Lysice (Lissitz, Czechia) suggests circalittoral range.

**Distribution** – Middle Miocene: Central Paratethys (Austria, Czechia, Hungary, Poland).

Merulinidae MILNE EDWARDS & HAIME, 1857

Genus *Echinopora* LAMARCK, 1816

*Echinopora oligophylla* (REUSS, 1871)  
(Plate III, Figs 6–12, Plate IV, Figs 1–2)

1871 *Heliastrea oligophylla* nov. sp. – REUSS, 241, pl. 13, fig. 1.

1954 *Orbicella oligophylla* (REUSS) – KOPEK, p. 9, pl. 2, figs 1–2.

1962 *Heliastrea oligophylla* REUSS – CHEVALIER, p. 170, pl. 6, fig. 11, pl. 7, fig. 5, pl. 9, fig. 2.

1962 *Heliastrea oligophylla* REUSS var. *major* nov. var. – CHEVALIER, p. 171, pl. 5, fig. 22, pl. 7, fig. 6.

1970 *Heliastrea oligophylla major* CHEVALIER – HEGEDŰS, p. 186, pl. 1, fig. 2.

1972 *Heliastrea oligophylla* REUSS – HEGEDŰS & JANKOVICH, pl. 3, figs 1–2.

2005 *Heliastrea oligophylla* REUSS – TSAPARAS & MARCOPOULOU-DIACANTONI, p. 631, pl. 1, figs 3–4.

**Material** – Numerous fragmentary plocoid colonies (Z). HNHM, INV 2024.532., 533., 534., 535., 536., 537., 538., and private collections of Tamás NÉMETH and the author.

Largest colony	D	SC	SN	c-c
200×160×120	5–6	2+1i	17–21	1.5–2.5
Pl. IV/1–2	5.5	3+1i	24	1.5–2.5

**Description** – Corallites are long, generally circular or rarely oval in shape, and closely spaced, calices rise approx. 1.8 mm above the coenosteum, calical rims are sharp, septal face is granular, coenosteum are covered by costae, endothecal and exothecal dissepiments are vesicular. The species is characterized by two complete and one incomplete cycles, the number of septa of the studied corallites (17–21) is slightly higher than in KOPEK (1954) (16–19). Corallites of one colony (Plate IV, Figs 1–2) display three complete and a fourth incomplete cycles.

**Remarks** – The species was originally described from Lăpugiu de Sus (Romania) and from the North Hungarian Mountains (REUSS 1871: 242). The studied specimens correspond to the type (REUSS l.c., pl. 13, fig. 1) and the illustrated material in the literature. As genus *Heliastrea* MILNE EDWARDS & HAIME, 1848 is a non-available taxon, species described in the literature under this genus were revised by HOEKSEMA & CAIRNS (2024) and *H. oligophylla* REUSS and *H. tchihatcheffi* CHEVALIER were assigned to genus *Echinopora* LAMARCK, 1816.

*Echinopora mellahica* (GREGORY) is a similar form but the type specimens differ in smaller (D 4–5 mm), more widely spaced corallites and the presence of three complete (and occasionally a fourth incomplete) cycles (GREGORY 1906: 52, pl. 6, figs 3–4). This taxon was recorded from the Pannonian Basin by SCHOLZ (1970) and OOSTERBAAN (1990); however, both authors used a rather wide species concept: they agreed in the presence of at least three cycles but disagreed in the morphological interpretations (e.g., D 5–10 mm in SCHOLZ, while 1.8–7 mm in OOSTERBAAN). *Echinopora mellahica* was synonymized under *Heliastrea brevis* (DUNCAN, 1864) by CHAIX et al. (2018), while both are available taxa in HOEKSEMA & CAIRNS (2024) (for morphology and paleogeographical distribution of *Montastraea brevis* see BUDD 1991). *Echinopora oligophylla* – together with *Tarbellastrea reussiana* – is among the most abundant colonial coralla at Letkés.

Fragments of worm tubes and remains of *Lithophaga lithophaga* shells are common in the studied colonies of *Echinopora oligophylla*. Three coralla retained shells of the endoparasite gastropod *Leptoconchus jaegeri* ROLLE, 1863 (Muricidae, Coralliophilinae) (Plate III, Fig. 6; and see KOVÁCS & VICIÁN 2024, fig. 42), while fragments of the cirripede *Ceratoconcha* cf. *santacruzensis* (BAŁUK & RADWAŃSKI, 1967) occur in a few colonies (Plate III, Figs 11–12).

The evaluation of paleobathymetric range of fossil colonial corals faces at least two problems: i) the lack of consensus of genus level classifications makes the comparison with Recent genera uncertain; ii) the paleobathymetric distribution of corals depends on local environmental conditions (PERRIN 2000). Nevertheless, the Recent *Echinopora* species are known from shallow-water (3–30 m) habitat.

**Distribution** – Early Miocene: Proto-Mediterranean Sea (Algeria). Middle Miocene: Central Paratethys (Bosnia, France, Hungary, Romania, Spain), Proto-Mediterranean Sea (Syria), Late Miocene: Proto-Mediterranean Sea (Greece).

*Echinopora tchihatcheffi* (CHEVALIER, 1962)  
(Plate III, Fig. 13, Plate IV, Figs 3–5)

- ? 1871 *Heliastreaa defrancei* MILNE EDWARDS et HAIME – REUSS, p. 239, pl. 9, fig. 3, pl. 10, fig. 1.  
1962 *Heliastreaa tchihatcheffi* nov. nom. – CHEVALIER, p. 174, tabl. 4, text-fig. 57, pl. 6, fig. 12.  
1972 *Heliastreaa oligophylla major* – HEGEDŰS & JANKOVICH, pl. 2, figs 1, 4 (non CHEVALIER).  
2002 *Montastreaa tchihatcheffi* (CHEVALIER) – SCHUSTER, p. 63, pl. 4, figs 1–2.  
2008 *Montastreaa tchihatcheffi* (CHEVALIER) – RUS & POPA, p. 327, pl. 2, fig. 2.  
2008 *Montastreaa* sp. – RUS & POPA, p. 327, pl. 2, fig. 3.

*Material* – 1 fragmentary plocoid colony (Z). HNHM, INV 2024.539.

Colony	D	SC	SN	c-c
130×98×76	9–10	3+1i	28–36	1.5–3

*Description* – Corallites are long and circular in shape; coenosteum bears large granules, and is covered by costae. The specimen has three complete and a fourth incomplete cycles, paliform lobes are present, septal face is granular. Columella is trabecular with ~3 mm length. Endothecal and exothecal dissepiments are tabular to vesicular.

*Remarks* – Based on size and morphological features the most closely allied form is the Early–Middle Miocene *Echinopora tchihatcheffi* (CHEVALIER), although the corallites of the holotype are somewhat more widely spaced and columellas are slightly larger (3.5–4 mm) (CHEVALIER 1962, tabl. 4, pl. 6, fig. 12). The *Heliastreaa defrancei* MILNE EDWARDS & HAIME material in REUSS (1871, pl. 9, fig. 3, pl. 10, fig. 1) was synonymized by CHEVALIER (l.c.), these specimens, however, are characterized by four cycles, and their c-c is larger. (*Heliastreaa defrancei* specimens with small D of 4–6 mm were frequently recorded in the Paratethyan literature – KOPEK 1954, KOJUMDIEVA 1960, GÓRKA 2018 – these records need to be revised.) *Echinopora tchihatcheffi* was described by RUS & POPA (2008, pl. 2, fig. 2) from Lăpugiu de Sus (Romania) and their *Montastreaa* sp. (l.c., pl. 2, fig. 3) is also considered herein as a representative of the species. In the Hungarian literature a very similar corallum was presented by HEGEDŰS & JANKOVICH (1972, pl. 2, figs 1, 4). The colony from Márkháza (Cserhát Hills) under the name *Heliastreaa oligophylla major* has corallites of the same size and identical septum structure as that of the specimen figured herein. The D of corallites of *Heliastreaa (Heliastreaa) oligophylla* var. *major* CHEVALIER is not significantly larger than that of *Echinopora oligophylla* (REUSS) (see CHEVALIER 1962: 170, tabl. 4, pl. 7, fig. 6); and the taxon is recognized as a synonym of *E. oligophylla* by HOEKSEMA & CAIRNS (2024). *Echinopora tchihatcheffi* is a new record in the Pannonian Basin.

*Distribution* – Early Miocene: Proto-Mediterranean Sea (Egypt). Middle Miocene: Central Paratethys (Austria?, Hungary, Romania), Proto-Mediterranean Sea (Italy, Türkiye), NE Atlantic (France).

Genus *Tarbellastraea* ALLOITEAU, 1952

*Tarbellastraea ellisiana* (DEFRANCE, 1826)  
(Plate IV, Figs 6–9)

- 1826 *Astrea ellisiana* – DEFRANCE, p. 382.  
1984 *Tarbellastraea ellisiana* (DEFRANCE) – BOREL BEST, pl. 5, figs 1–4.  
1996 *Tarbellastraea ellisiana* (DEFRANCE) – BUDD et al., p. 546, text-fig. 1/C, pl. 3, fig. 2.  
2008 *Tarbellastraea ellisiana* (DEFRANCE) – CHAIX & SAINT MARTIN, p. 188, fig. 2D.  
2018 *Tarbellastraea ellisiana* (DEFRANCE) – CHAIX et al., p. 334, fig. 6G.

*Material* – 8 fragmentary plocoid colonies (Z). HNHM, INV 2024.540., 541., 542., and the author's collection.

Largest colony	D	SC	SN	c-c
110×75×50	2.5–4.5	3+1i	28	1–5

*Description* – Colonies of irregular shape and surface. Calices appear as vertical or slant truncated cones above the coenosteum with 1.5–3 mm height. Corallites are circular in shape, diameter is variable (generally 2.5–4.5 mm) but D of one corallite reaches 5 mm. Calical rim is rounded, wall is costate, coenosteum is granular, exotheca is vesicular. Distances of corallites are variable (1–5 mm). Extratentacular branching is common. The species is characterized by three complete and a fourth incomplete cycles, septal face is granular.

*Remarks* – The variability of the species was emphasized by CHEVALIER (1962: 194). The most closely allied specimen to the studied material in size and morphology is the *Tarbellastraea ellisiana* colony from the Badenian deposits of Lăpugiu de Sus (Romania) presented by CHAIX et al. (2018, fig. 6G). Diameters of corallites of this corallum are 2.5–4 mm, they are irregularly spaced, and the specimen has three complete and a fourth incomplete cycles (l.c. 334). *Tarbellastraea ellisiana* is a new record in the Pannonian Basin.

*Distribution* – Early Miocene: NE Atlantic (Portugal). Early–Middle Miocene: NE Atlantic (France). Middle Miocene: Central Paratethys (Hungary, Romania), Proto-Mediterranean Sea (Italy). Late Miocene: Proto-Mediterranean Sea (Algeria, Greece).

*Tarbellastraea reussiana*  
(MILNE EDWARDS & HAIME, 1850)  
(Plate V, Figs 1–2)

- 1850a *Astrea reussiana* – MILNE EDWARDS & HAIME, p. 110.  
1952 *Orbicella reussiana* (MILNE EDWARDS et HAIME) – KOPEK, p. 72, pl. 12, figs 1–2, pl. 13, figs 1, 3.  
1954 *Orbicella reussiana* (MILNE EDWARDS et HAIME) – KOPEK, p. 9, pl. 1, figs 9–12.  
1970 *Tarbellastraea reussiana* (MILNE EDWARDS et HAIME) – HEGEDŰS, p. 187, pl. 1, fig. 4.  
1970 *Tarbellastraea reussiana* (MILNE EDWARDS & HAIME) – SCHOLZ, p. 195.  
non 1990 *Tarbellastraea reussiana* (MILNE EDWARDS & HAIME) – OOSTERBAAN, p. 9, pl. 1, fig. 3.

- 1998 *Tarbellastraea reussiana* (MILNE EDWARDS & HAIME) – SCHULTZ, pl. 19, figs 3–4.  
 2018 *Tarbellastraea reussiana* (MILNE EDWARDS & HAIME) – CHAIX et al., p. 334, fig. 6H.  
 2018b *Tarbellastraea reussiana* (MILNE EDWARDS & HAIME) – KLEPRLÍKOVÁ, p. 63, fig. 2.2–3.  
 2021 *Tarbellastraea reussiana* (MILNE EDWARDS & HAIME) – DULAI et al., fig. 1A.

**Material** – Plocoid colonies (Z). HNHM, M.59.2862 (2 colonies, Letkés, unknown locality), INV 2024.543., 544., 545.1-3., and numerous fragmentary colonies in private collections of László NÁDAI, Tamás NÉMETH and the author.

Colonies size	D	SC	SN	c-c
50–300	2–2.5	3	24	0.5

**Description** – Corallites are long, generally circular, rarely oval in shape and closely spaced. Calical rim is sharp, coenosteum is covered by costae, endothecal and exothecal dissepiments are vesicular.

**Remarks** – The species is characterized by moderate morphological variability – the taxonomical revision of the literature was arranged by CHAIX et al. (2018). According to OOSTERBAAN (1990), *Heliastrea conoidea* REUSS, 1871 is a synonym of *Tarbellastraea reussiana*, although D of *H. conoidea* corallites is usually 3 mm, and the distance between them is approx. 3 mm. On the other hand *Heliastrea conoidea* was recognized as a synonym of *Tarbellastraea ellisiana* (DEFRANCE) by CHAIX et al. (2018). The specimen presented by OOSTERBAAN (1990, pl. 1, fig. 3) from Bánd (Bakony Mts, Hungary) – which has widely spaced corallites with higher calices and stronger costae – markedly differs from the colonies illustrated by REUSS (1871, pl. 8, fig. 2) and CHAIX et al. (2018, fig. 6H), as well as from the *Tarbellastraea reussiana* material of Letkés; it is more closely allied in morphology to *Tarbellastraea ellisiana* (DEFRANCE). *Tarbellastraea reussiana* is the most frequently reported representative of the genus in the Miocene Proto-Mediterranean Sea and the Central Paratethys (CHAIX et al. 2018, KLEPRLÍKOVÁ 2018b). Based on these records the species was typical of shallow-water paleoenvironments.

*Lithophaga lithophaga* shells or internal molds are common in the studied *Tarbellastraea reussiana* colonies. Occurrence of another boring bivalve, *Jouannetia semicaudata* DESMOULINS, 1828 is also reported herein. According to BAŁUK & RADWAŃSKI (1984), commensal cirripedes are frequent in *Tarbellastraea reussiana* coralla in the Korytnica Basin assemblage. Although the species is abundant at Letkés, only a few colonies contain remains of small cirripede specimens.

**Distribution** – Miocene. NE Atlantic and Proto-Mediterranean Sea (Algeria, Egypt, France, Greece, Italy, Libya, Malta, Morocco, Spain, Türkiye). Central Paratethys (Austria, Bulgaria, Czechia, Hungary, Moldova, Poland, Romania, Slovakia, Ukraine).

- Family Micrabaciidae VAUGHAN, 1905  
 Genus *Stephanophyllia* MICHELIN, 1841

*Stephanophyllia nystii* MILNE EDWARDS & HAIME, 1850  
 (Figure 3/A–F)

- 1850b *Stephanophyllia nystii* nob. – MILNE EDWARDS & HAIME, p. 35.  
 1871 *Stephanophyllia nystii* MILNE EDWARDS & HAIME – REUSS, p. 256 *partim*, pl. 21, fig. 10.  
 1964 *Stephanophyllia nystii* MILNE EDWARDS & HAIME – CHEVALIER, p. 19, text-figs 8–12, pl. 2, fig. 1.  
 2017 *Stephanophyllia nystii* MILNE EDWARDS & HAIME – BARON-SZABO & CAIRNS, fig. 5.2a–2c.

**Material** – 3 fragmentary discoidal solitary coralla (NZ). Private collections of Tamás NÉMETH and the author.

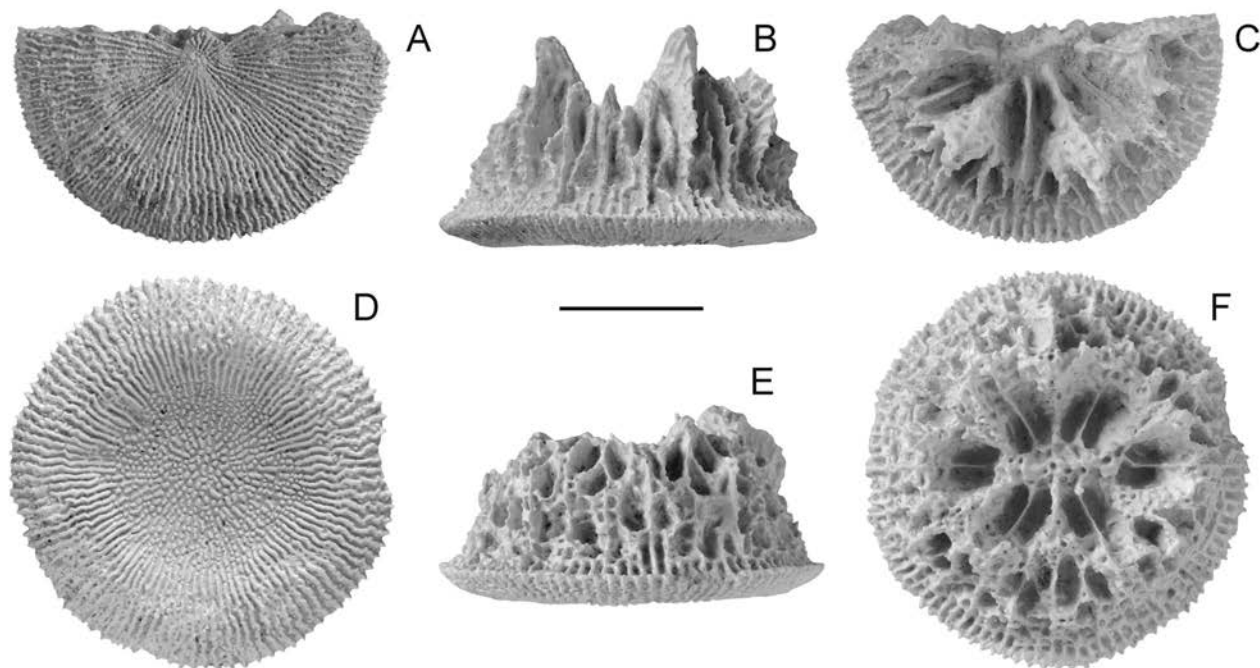
	Height	D	SC
–	15.8	28	5
Fig. 4/A-C	14.6	25.7	5
Fig. 4/D-F	13.5	26.4	5

**Description** – Discoidal, cupulate and synapticulothecate corallum with slightly concave basis covered by radial, thin, irregularly developed and granular costae. Septa are high, porous, lacinate, septal face is strongly granular, columella is spongy. The species is characterized by five cycles.

**Remarks** – Specimens of *Stephanophyllia elegans* (BRONN, 1831), *S. imperialis* MICHELIN, 1841 and *S. nystii* MILNE EDWARDS & HAIME, 1850 display moderate variability in size and morphology, so the number of available Neogene species was discussed in the literature. *Stephanophyllia elegans* clearly differs from the Miocene congeners by its small size (max. D 18 mm; STOLARSKI 1991) and lower septa (see the type specimen in BRONN 1838, pl. 36, fig. 7); however, the morphological features of *S. imperialis* and *S. nystii* are remarkably similar (STOLARSKI 1991, SPADINI 2019). Nevertheless, all three species are available in BARON-SZABO & CAIRNS (2017) and HOEKSEMA & CAIRNS (2024). Based on their large size, porous septa and broader, spongy columella (which is lamellar on *S. imperialis*), the studied specimens are assigned to *Stephanophyllia nystii* (for comparison of *S. imperialis* and *S. nystii* see BARON-SZABO & CAIRNS 2017, fig. 5.2a–e).

Although *Stephanophyllia nystii* is recorded for the first time in the Pannonian Basin, the genus is known in Hungary: *Stephanophyllia* cf. *elegans* was described from the Egerian (Late Oligocene–Early Miocene) by HEGEDŰS (1959), *S. imperialis* was listed by NÉMETH (2005) from the Badenian of Devecser (Bakony Mts) (the specimen actually represents *S. nystii*), while both *S. elegans* and *S. imperialis* were mentioned by HENN (2023) from the Badenian deposits of Tekeres (Mecsek Mts).

The occurrences of *Stephanophyllia imperialis* in the Baden Fm. in the Vienna Basin (Austria: Baden, Bad Vöslau, Möllersdorf) (REUSS 1871, KÜHN 1967) indicate circalittoral to upper bathyal environments. Recent *Stephanophyllia* species are typical of deep water sea (upper bathyal zone): the Pleistocene–Recent *S. complicata* MOSE-



**Figure 3.** *Stephanophyllia nystii* MILNE EDWARDS & HAIME, 1850; Bagoly Hill, Letkés. A-C. Basal, lateral and calical views (author's coll.). D-F. Basal, lateral and calical views (NÉMETH Collection). Scale bar 10 mm.

**3. ábra.** *Stephanophyllia nystii* MILNE EDWARDS & HAIME, 1850; Bagoly-hegy, Letkés. A-C. Bazális, laterális és kehelynézet (szerző gyűjteménye). D-F. Bazális, laterális és kehelynézet (NÉMETH Tamás gyűjteménye). Méretvonal: 10 mm.

LEY, 1876 occurs in average depth of 260–518 m, while the Recent *S. neglecta* BOSCHMA, 1923 in depth of 246–351 m (CAIRNS 1999, 2004). The specimens recorded herein were found in the lowermost grey clay layer at the base of the studied section.

**Taxonomical notes** – 1) The year of designation of *Stephanophyllia elegans* (= *Fungia elegans* n. sp.) is 1831 and not 1838 (ICZN Articles 10–12; BRONN 1831: 133–134; KÜHN 1967: 6). 2) Use of the name of the species as *nystii* instead of *nystii* is an unjustified emendation (see ICZN Article 33.4).

**Distribution** – Middle Miocene: North Sea Basin (Germany, Netherlands), Central Paratethys (Hungary). Pliocene: North Sea Basin (Belgium).

Family Montastraeidae YABE & SUGIYAMA, 1941  
Genus *Montastraea* BLAINVILLE, 1830

*Montastraea* sp.  
(Plate V, Fig. 3)

**Material** – 1 fragmentary plocoid colony (Z). HNHM, INV 2024.546.

Colony	D	SC	SN	c-c
50×33×16	5	3	24	2–4

**Description** – Corallites are circular in shape, calices rise 1 mm high above the coenosteum bearing fine, granular costae which cover the coenosteum, theca is septothecate. Endothecal and exothecal dissepiments are vesicular. The species is characterized by three complete cycles, septa of the first two cycles reach the relatively poorly developed columella, septal face is granular.

**Remarks** – Based on morphological features (BUDD 1991, HUANG et al. 2014), the corallum figured herein is assigned to genus *Montastraea*. It somewhat resembles the Miocene *Montastraea piveteaui* (CHEVALIER, 1954). Corallites of this species are similarly spaced and the coenosteum is also covered by granular costae, but the corallites are wider (D 6–7 mm), costae are slightly broader, and the columella is much more developed (see CHEVALIER 1954: 139–142, pl. 3, figs 2–3, pl. 4, fig. 2, pl. 5, fig. 1). Corallum of similar morphology has not been recorded from the Miocene Pannonian Basin.

**Distribution of *Aquitanastraea piveteaui*** CHAVELIER, 1954: Early Miocene: NE Atlantic (France). Middle Miocene: Proto-Mediterranean Sea (Italy, Türkiye).

Pocilloporidae GRAY, 1840  
*Stylophora* SCHWEIGGER, 1820

*Stylophora subreticulata* REUSS, 1871  
(Plate V, Figs 4–6)

1871 *Stylophora subreticulata* nov. sp. – REUSS, p. 250, pl. 5, fig. 10, pl. 7, fig. 1, pl. 13, fig. 5.

1954 *Stylophora subreticulata* REUSS – KOPEK, p. 28, pl. 10, figs 1–6, 8.

1960 *Stylophora subreticulata* REUSS – KOJUMDZIEVA, p. 14, pl. 1, fig. 3.

1962b *Stylophora subreticulata* REUSS – CHEVALIER, p. 23, pl. 1, fig. 1.

1970 *Stylophora subreticulata* REUSS – HEGEDŰS, p. 186, pl. 1, fig. 1.

? 2008 *Stylophora subreticulata* REUSS – RUS & POPA, p. 325, pl. 1, fig. 2.

*Material* – 24 fragmentary subdendroid colonies (Z). HNHM, INV 2024.547., 548., 549.1-4., and private collections of László NÁDAI and the author.

	Colonies size	D	SC	SN	c-c
Pl. V/6	40×33	0.7–1	1	6	0.5–2
Pl. VI/4–5	20.5×11.3×8.3	0.7–1	1	6	0.5–2

*Description* – Irregularly shaped subcylindrical, tuber-shaped or branching colonies. Corallites are small, circular in shape and deep. Septa are fine, calices rise slightly above the coenosteum, and are irregularly spaced, coenosteum is finely granular. The polygonal nets around the corallites on the coenosteum mentioned by REUSS (1871: 250, pl. 5, fig. 10) are present on a few specimens. Endothelial dissepiments are tabular, exotheca is compact. The specimens are generally characterized by one complete cycle. In the studied material a few corallites reach D 1.5 mm which was described as characteristic diameter by REUSS (l.c.), and the second, incomplete cycle appears sporadically.

*Remarks* – The material illustrated by KOPEK (1954) was synonymized under *Stylophora reussiana* MONTANARO-GALLITELLI & TACOLI, 1951 by OOSTERBAAN (1990). This species differs from KOPEK's specimens in its much thicker peripheral part of the septa and two complete and a third incomplete cycles (RONIEWICZ & STOLARSKI 1991). *Stylophora calcinata* (MAYER) is also a similar form with its small corallites (D 1 mm) and granular surface, but it differs by its two complete cycles (MAYER 1864, CHAIX et al. 2018); this species was recorded from the southern Pannonian Basin (N Bosnia) by JOVANOVIĆ et al. (2021).

*Distribution* – Middle Miocene: Central Paratethys (Austria, Bulgaria, Hungary, Romania). Late Miocene: Proto-Mediterranean Sea (Morocco).

*Stylophora* sp.  
(Figure 4)

*Material* – 1 fragmentary plocoid colony (Z). Private collection of László NÁDAI.

Colony	D	SC	SN	c-c
19×13×10	0.9–1.1	1	6	0–0.5

*Description* – Irregularly shaped colony. Corallites are small, subcircular in shape and deep. Septa are well-developed, calices are closely spaced, walls are thick. Calices are generally characterized by one complete cycle; however, one finer septum of the second cycle appears in a few calices.

*Remarks* – The specimen differs from the Miocene *Stylophora* species described in the literature by its remarkably closely spaced calices. Moreover, *Stylophora subreticulata* has much finer septa, while septa of *S. reussiana* have much thicker peripheral part. The corallites of the *Stylophora* specimen illustrated by JOVANOVIĆ et al. (2021, fig. 7.3–4) as *S. depauperata* REUSS are closer to each other than on *S. calcinata*, *S. subreticulata* or *S. reussiana*, but the specimen in question is distinguishable from the material studied herein by its strongly granular surface.

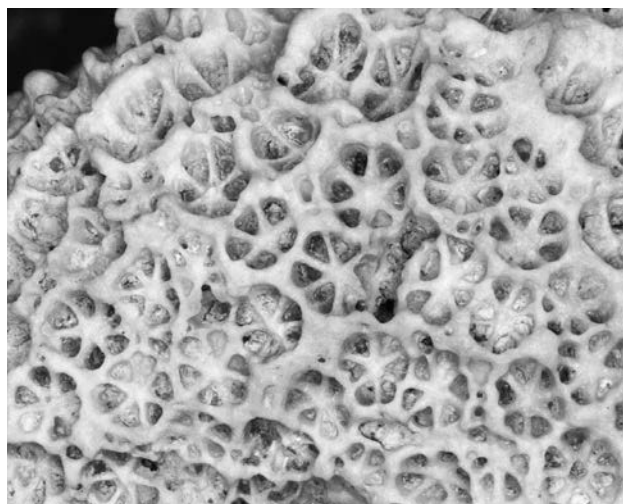


Figure 4. *Stylophora* sp. Calical surface (width of illustrated part 7.5 mm), NÁDAI Collection.

4. ábra. *Stylophora* sp. Kehelyfelszín (az ábrázolt részlet szélessége 7,5 mm), NÁDAI László gyűjteménye.

*Scleractinia incertae sedis*

*Solenastrea* MILNE EDWARDS & HAIME, 1848

*Solenastrea inaequalis* (CHEVALIER, 1962)  
(Plate V, Figs 7–8)

1962 *Palaeoplesiastraea inaequalis* nov. sp. – CHEVALIER, p. 268, pl. 21, fig. 1, pl. 24, fig. 1.

1991 *Paleoplesiastraea inaequalis* CHEVALIER – RONIEWICZ & STOLARSKI, p. 75, pl. 2, fig. 5.

*Material* – 1 fragmentary plocoid colony (Z). HNHM, INV 2024.550.

Colony	D	SC	SN	c-c
39×26×16	2–2.5	3	24	0.3–1

*Description* – Small corallites of different shapes (circular, oval, triangular, rectangular), with three complete cycles, septa are strongly granular. Calices rise slightly above the coenosteum, closely spaced, coenosteum is not covered by costae, endothelial dissepiments are tabular to slightly vesicular, exotheca consists of thick tabulae.

*Remarks* – The corallum agrees well in size and morphology with the holotype of *Solenastrea inaequalis* (CHEVALIER) (MNHN.F.R10560) which is available online as well\*. The species is a new record in the Pannonian Basin.

*Distribution* – Middle Miocene: Proto-Mediterranean Sea (Italy), Central Paratethys (Hungary, Poland).

\*<https://science.mnhn.fr/institution/mnhn/collection/fl/item/r10560> (accessed: 11.11.2023)

*Solenastrea* ? sp.  
(Plate V, Figs 9–11)

*Material* – 2 fragmentary plocoid colonies (Z). HNHM, INV 2024.551., and the author's collection.

Colony	D	SC	SN	c-c
80×60×35	1.5–2.5	3	24	0.5–1.5

**Description** – Tuber-shaped colonies with irregular surface. Corallites are long, circular in shape, closely spaced, with variable distances (0.5–1.5 mm). Thin walls of calices rise slightly above the spongy coenosteum, costae missing, exotheca is vesicular. The specimens are characterized by three complete cycles,  $S_1$  and  $S_2$  septa reach the weakly developed columella, septal face is strongly granular.

**Remarks** – The corallum figured herein displays some resemblance to the Late Oligocene–Miocene *Solenastrea desmoulinsi* (MILNE EDWARDS & HAIME, 1851) in its overall appearance and presence of three complete cycles. The latter species, however, is distinguished by its wider corallites (D 3–4 mm in MILNE EDWARDS & HAIME 1851: 100; 2–4 mm in CHEVALIER 1962: 266; 4–5 mm in CHAIX et al. 2018: 337) and costate calices (CHEVALIER 1962, pl. 13, fig. 4., pl. 24, fig. 5; CHAIX et al. 2018, fig. 7B). The *Solenastrea hyades* (DANA, 1846) colonies recorded by BARON-SZABO (1997) from the Badenian of Slovenia also differ by their larger corallites (D 2–3.5 mm) and septothecal wall.

### Conclusion

In this paper 25 scleractinian species are recorded from the lower Badenian deposits of the Bagoly Hill locality at Letkés (Börzsöny Mts, Hungary) – the fauna appears to be the richest one in the Miocene Pannonian Basin. Twelve species are new occurrences in the Hungarian part of the Pannonian Basin: *Balanophyllia praelonga* (MICHELOTTI, 1838), *Caryophyllia* (s.s.) cf. *leptaxis* REUSS, 1871, *Echinopora tchihatcheffi* (CHEVALIER, 1962), *Favia* cf. *melitae* CHEVALIER, 1962, *Montastraea* sp., *Siderastrea radians* (PALLAS, 1766), *Solenastrea inaequalis* (CHEVALIER, 1962), *Solenastrea* ? sp., *Stephanophyllia nystii* MILNE EDWARDS & HAIME, 1850, *Stylocora exilis* REUSS, 1871, *Stylophora* sp., and *Tarbellastraea ellisiana* (DEFRANCE, 1826). The assemblage consists of both zooxanthellate and azooxanthellate taxa. In the first group three colonial species are the most abundant: *Echinopora oligophylla*, *Porites vindobonorum prima* and *Tarbellastraea reussiana*. These hermatypic corals indicate shallow marine (*Echinopora* and *Tarbellastraea*) and upper mesophotic (*Porites*) paleoenvironments, which is also verified by the high diversity of coastal and nearshore molluscs. However, formations of reef in the study area cannot be traced. Fringing reef facies of the Lajta Limestone Fm. are known around the Börzsöny Mts in the vicinity of Ipolytölgyes, Nagymaros (Törökmező) and Zebegény. From these localities, Törökmező is the richest (~10

scleractinian species) containing almost exclusively reef-building taxa (KOPEK 1954; own data).

On the other hand, the presence of azooxanthellate species of genera *Balanophyllia*, *Caryophyllia* (s.s.), *Ceratrotrochus*, *Flabellum* and *Stephanophyllia* with dominance of *Caryophyllia* (*Acanthocyathus*) *verrucosa* proves deeper, cold-water (aphotic) habitats, and this fact corresponds to the occurrence of rich offshore gastropod assemblages. The Scleractinia material of the Bagoly Hill locality – similarly to that of the molluscs – shows a mixture of taxa derived from different biotopes.

The coral assemblage resembles that of Lăpugiu de Sus (Romania), however, it is less diversified. The latter site is characterized by a very rich Badenian Scleractinia fauna containing more than 60 species (RUS & POPA 2008, CHAIX et al. 2018). The abundance and high biodiversity of corals at Letkés and Lăpugiu de Sus indicate tropical climatic conditions, which – on the other hand – was also verified by comprehensive research of the mollusc fauna of the Middle Miocene Central Paratethys (see papers on gastropods by HARZHAUSER & LANDAU 2016, 2023; KOVÁCS et al. 2018; KOVÁCS & VICIÁN 2023). Comparing it to the late Early Miocene Karpatian age (17.30–15.97 Ma), the abundance of thermophilic species in the marine invertebrate and vertebrate assemblages is typical of the early–middle Badenian (15.97–13.82 Ma) as the result of the Miocene Climate Optimum (HARZHAUSER & PILLER 2007, METHNER et al. 2020, GEBHARDT et al. 2023, HARZHAUSER et al. 2024).

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**Plate I – I. tábla**

- Figs 1–2.** *Balanophyllia praelonga* (MICHELOTTI, 1838). HNHM, INV 2024.503. Calical and lateral views. *Kehely és laterális nézet.*
- Figs 3–4.** *Balanophyllia praelonga* (MICHELOTTI, 1838). HNHM, INV 2024.504. Calical and lateral views. *Kehely és laterális nézet.*
- Figs 5–6.** *Balanophyllia* sp. HNHM, INV 2024.507. Transverse section and lateral view. *Keresztmetszet és laterális nézet.*
- Figs 7–8.** *Balanophyllia praelonga* (MICHELOTTI, 1838). HNHM, INV 2024.505. Lateral view and transverse section. *Laterális nézet és keresztmetszet.*
- Fig. 9.** *Balanophyllia praelonga* (MICHELOTTI, 1838). HNHM, INV 2024.506. Lateral view. *Laterális nézet.*
- Figs 10–11.** *Turbinaria cyathiformis* (BLAINVILLE, 1830). HNHM, INV 2024.508. Colony surface and longitudinal break. *Telepfelszín és hosszmetset.*
- Figs 12–13.** *Porites vindobonarum prima* KÜHN, 1927. HNHM, INV 2024.509. Colony surface and calical view. *Telepfelszín és kehelynézet.*
- Fig. 14.** *Porites vindobonarum prima* KÜHN, 1927. HNHM, INV 2024.510. Colony surface with remains of cirripede specimens. *Telepfelszín kacslábú rákok maradványaival.*
- Figs 15–16.** *Siderastrea felixi* DEMBIŃSKA-RÓZKOWSKA, 1932. HNHM, INV 2024.512. Colony surface and calical view. *Telepfelszín és kehelynézet.*
- Figs 17–18.** *Siderastrea radians* (PALLAS, 1766). NÁDAI Collection, colony surface and calical view. *Telepfelszín és kehelynézet, NÁDAI László gyűjteménye.*
- Letkés, Bagoly Hill/Bagoly-hegy. Scale bars/méretvonalak: 10 mm for Figs 1–7, 10–12, 14; 5 mm for Figs 16–18, 2 mm for Figs 8–9, 1 mm for Figs 13, 15.

**Plate II – II. tábla**

- Figs 1–2.** *Caryophyllia (Acanthocyathus) verrucosa* (MILNE EDWARDS & HAIME, 1848). HNHM, INV 2024.513. Calical and lateral views. *Kehely- és laterális nézet.*
- Figs 3–4.** *Caryophyllia (Acanthocyathus) verrucosa* (MILNE EDWARDS & HAIME, 1848). HNHM, INV 2024.514. Calical and lateral views. *Kehely- és laterális nézet.*
- Figs 5–6.** *Caryophyllia (Acanthocyathus) verrucosa* (MILNE EDWARDS & HAIME, 1848). HNHM, INV 2024.515. Lateral views. *Laterális nézetek.*
- Fig. 7.** *Caryophyllia (Acanthocyathus) verrucosa* (MILNE EDWARDS & HAIME, 1848). NÁDAI Collection, lateral view. *Laterális nézet, NÁDAI László gyűjteménye.*
- Figs 8–9.** *Caryophyllia (Caryophyllia) cf. leptaxis* REUSS, 1871. HNHM, INV 2024.517. Calical and lateral views. *Kehely- és laterális nézet.*
- Figs 10–11.** *Ceratotrochus (Edwardsotrochus) duodecimcostatus* (GOLDFUSS, 1826). HNHM, INV 2024.518. Calical and lateral views. *Kehely- és laterális nézet.*
- Figs 12–13.** *Ceratotrochus (Edwardsotrochus) duodecimcostatus* (GOLDFUSS, 1826). NÉMETH Collection, calical and lateral views. *Kehely- és laterális nézet, NÉMETH Tamás gyűjteménye.*
- Figs 14–15.** *Favia cf. melitae* CHEVALIER, 1962. HNHM, INV 2024.520. Colony surface and basal view. *Telepfelszín és bazális nézet.*
- Figs 16–17.** *Mussismilia vindobonensis* CHEVALIER, 1962. HNHM, INV 2024.521. Transverse section and lateral view. *Keresztmetszet és laterális nézet.*
- Figs 18–19.** *Mussismilia vindobonensis* CHEVALIER, 1962. NÉMETH Collection, calical and lateral views. *Kehely- és laterális nézet, NÉMETH Tamás gyűjteménye.*
- Figs 20–21.** *Mussismilia vindobonensis* CHEVALIER, 1962. HNHM, INV 2024.522. Calical and lateral views. *Kehely- és laterális nézet.*
- Figs 22–23.** *Syzygophyllia brevis* REUSS, 1860. HNHM, INV 2024.524. Calical and lateral views. *Kehely- és laterális nézet.*
- Figs 24–25.** *Syzygophyllia brevis* REUSS, 1860. HNHM, INV 2024.525. Calical and lateral views. *Kehely- és laterális nézet.*
- Letkés, Bagoly Hill/Bagoly-hegy. Scale bars/méretvonalak: 10 mm for Figs 1–7, 10–11, 13–25; 5 mm for Figs 8–9, 12.

**Plate III – III. tábla**

- Figs 1–2.** *Stylocora exilis* REUSS, 1871. HNHM, INV 2024.526. Upper calices and lateral view. *Felső kelyhek és laterális nézet.*
- Fig. 3.** *Stylocora exilis* REUSS, 1871. HNHM, INV 2024.527. Transverse section. *Keresztmetszet.* D 2.5 mm.
- Fig. 4.** *Stylocora exilis* REUSS, 1871. HNHM, INV 2024.528. Lateral view. *Laterális nézet.*
- Fig. 5.** *Stylocora exilis* REUSS, 1871. HNHM, INV 2024.529. Lateral view. *Laterális nézet.*
- Fig. 6.** *Echinopora oligophylla* (REUSS, 1871). HNHM, INV 2024.532. Lateral view with a muricid gastropod *Leptoconchus jaegeri* ROLLE, 1863 specimen of 15.8 mm shell length (HNHM, INV 2024.531.). *Laterális nézet egy Muricidae-családdhoz (Gastropoda) tartozó Leptoconchus jaegeri ROLLE, 1863 példánnyal (hossza: 15,8 mm).*
- Figs 7–8.** *Echinopora oligophylla* (REUSS, 1871). HNHM, INV 2024.533. Calical surface and longitudinal section. *Kehelyfelszín és hosszszelvény.*
- Fig. 9.** *Echinopora oligophylla* (REUSS, 1871). HNHM, INV 2024.534. Transverse section with different stages of intratentacular branching. *Keresztmetszet különböző kehelyosztódási fázisokkal.*
- Fig. 10.** *Echinopora oligophylla* (REUSS, 1871). HNHM, INV 2024.535. Lateral view. *Laterális nézet.*
- Fig. 11.** Detail of the specimen in Fig. 10. Longitudinal section with remains of a cirripede specimen. *A 10. ábrán ábrázolt példány részlete. Hosszszelvény egy kacslábúrák-példány maradványával.*
- Fig. 12.** *Echinopora oligophylla* (REUSS, 1871). HNHM, INV 2024.537. Transverse section with remains of cirripede specimens. *Keresztmetszet kacslábú rákok maradványaival.*
- Fig. 13.** *Echinopora tchihatcheffi* (CHEVALIER, 1962). HNHM, INV 2024.539. Lateral view. *Laterális nézet.*
- Letskés, Bagoly Hill/Bagoly-hegy. Scale bars/méretvonalak: 2 mm for Figs 1–5; 10 mm for Figs 6–13.

**Plate IV – IV. tábla**

- Figs 1–2.** *Echinopora oligophylla* (REUSS, 1871). HNHM, INV 2024.538. Transverse section and lateral view. *Keresztmetszet és laterális nézet.*
- Figs 3–5.** *Echinopora tchihatcheffi* (CHEVALIER, 1962). HNHM, INV 2024.539. The specimen on Plate IV, Fig. 13. Calical surface, calical view and transverse section. *A IV. tábla 13. ábráján látható telep kehelyfelszíne, kehelynézete és keresztmetszete.*
- Figs 6–7.** *Tarbellastraea ellisiana* (DEFRANCE, 1826). HNHM, INV 2024.540. Calical surface and longitudinal section. *Kehelyfelszín és hosszszelvény.*
- Fig. 8.** *Tarbellastraea ellisiana* (DEFRANCE, 1826). HNHM, INV 2024.541. Colony surface. *Kehelyfelszín.*
- Fig. 9.** *Tarbellastraea ellisiana* (DEFRANCE, 1826). HNHM, INV 2024.542. Colony surface. *Kehelyfelszín.*
- Letskés, Bagoly Hill/Bagoly-hegy. Scale bars/méretvonalak: 10 mm for Figs 1–3, 6–9; 5 mm for Figs 4–5.

**Plate V – V. tábla**

- Fig. 1.** *Tarbellastraea reussiana* (MILNE EDWARDS & HAIME, 1850). HNHM, INV 2024.543. Calical surface. *Kehelyfelszín.*
- Fig. 2.** *Tarbellastraea reussiana* (MILNE EDWARDS & HAIME, 1850). HNHM, INV 2024.544. Colony surface. *Telepfelszín.*
- Fig. 3.** *Montastraea* sp. HNHM, INV 2024.546. Calical surface. *Kehelyfelszín.*
- Figs 4–5.** *Stylophora subreticulata* REUSS, 1871. HNHM, INV 2024.547. Colony surface and longitudinal section. *Telepfelszín és hosszszelvény.*
- Fig. 6.** *Stylophora subreticulata* REUSS, 1871. HNHM, INV 2024.548. Colony surface. *Telepfelszín.*
- Figs 7–8.** *Solenastrea inaequalis* (CHEVALIER, 1962). HNHM, INV 2024.550. Calical surface and longitudinal section. *Kehelyfelszín és hosszszelvény.*
- Figs 9–11.** *Solenastrea* ? sp. HNHM, INV 2024.551. Colony surface, calical surface and longitudinal section. *Telep- és kehelyfelszín, hosszszelvény.*
- Letskés, Bagoly Hill/Bagoly-hegy. Scale bars/méretvonalak: 10 mm.

Plate I – I. tábla

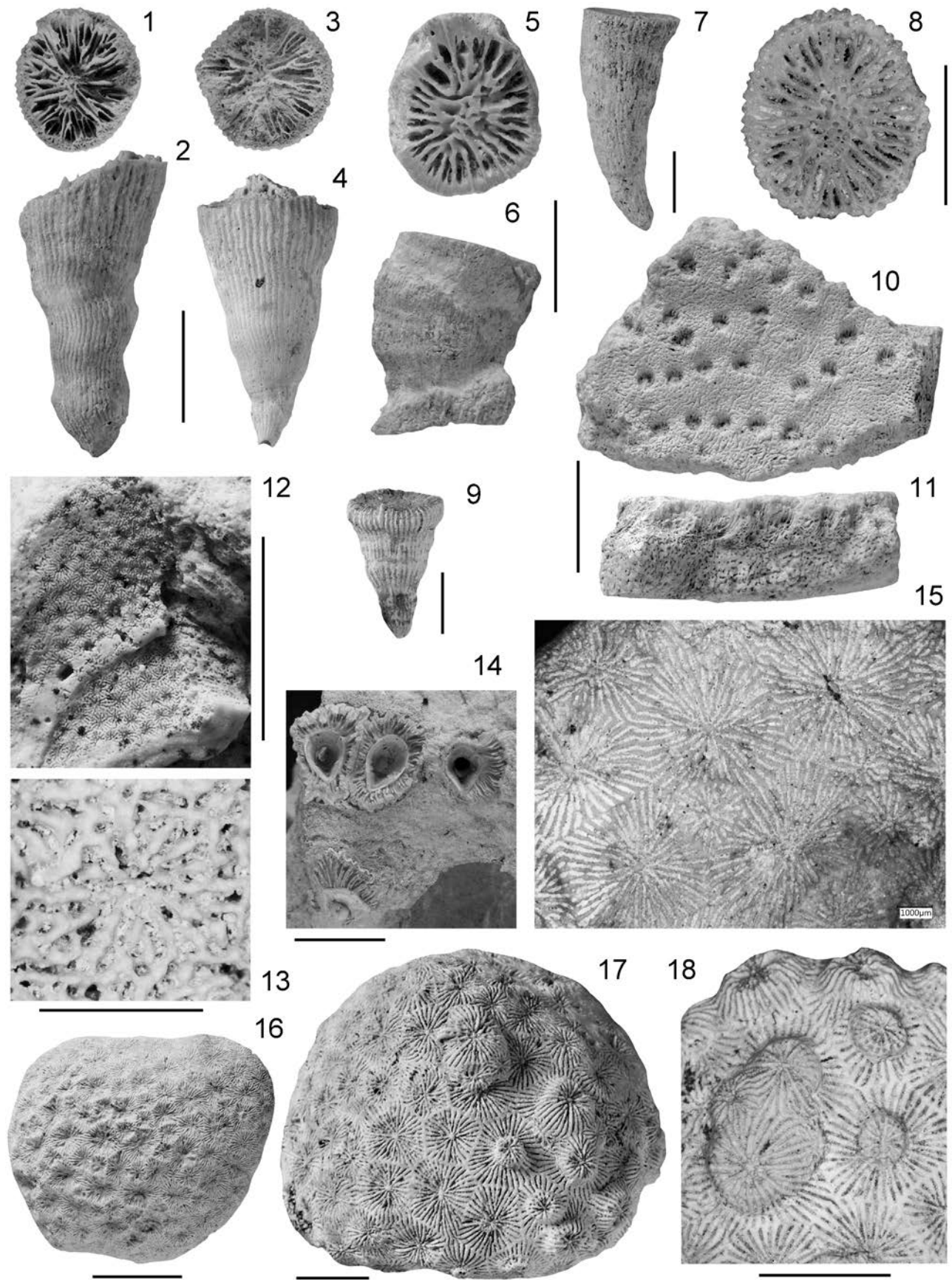


Plate II – II. tábla

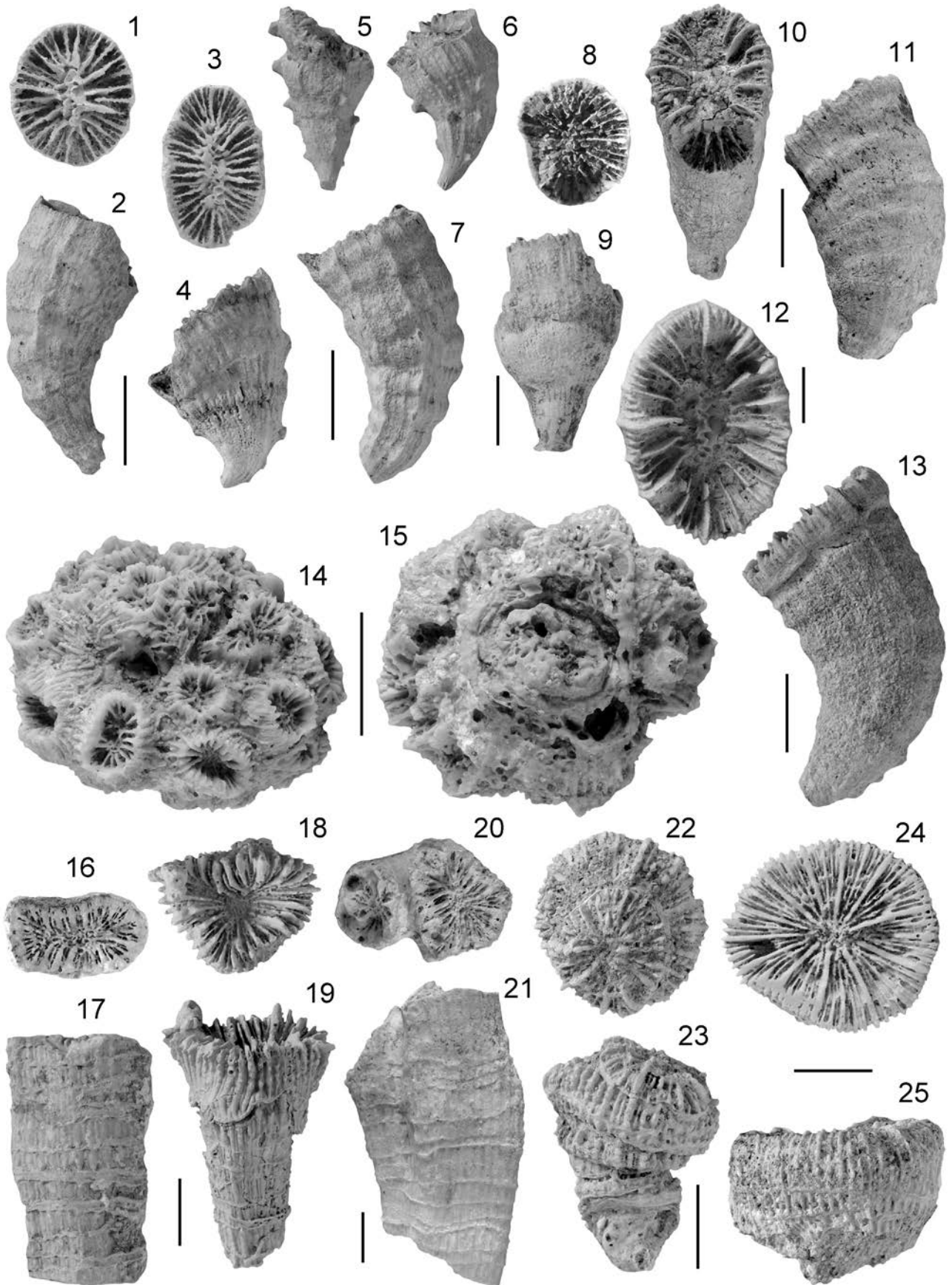




Plate III – III. tábla

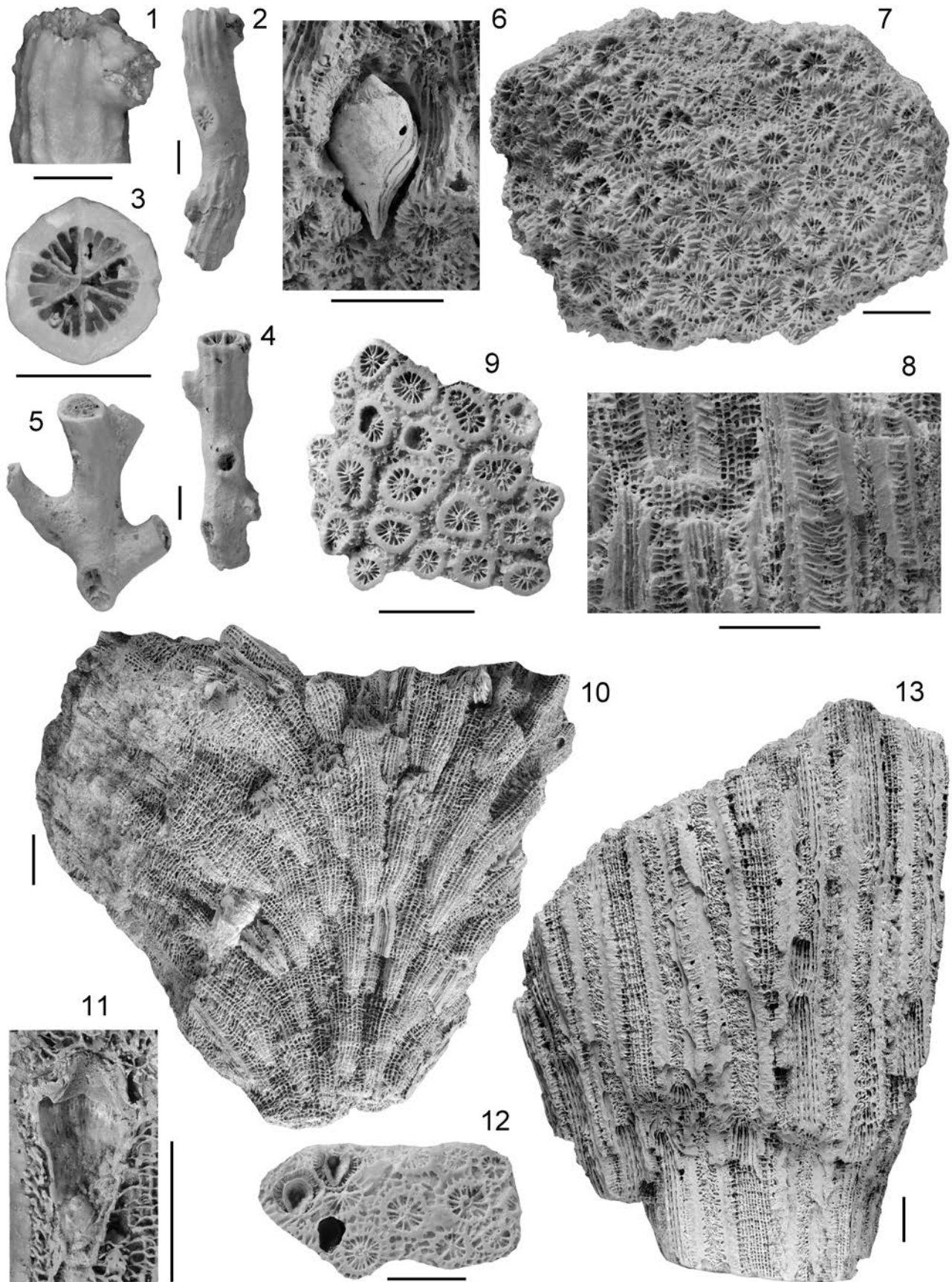




Plate IV – IV. tábla

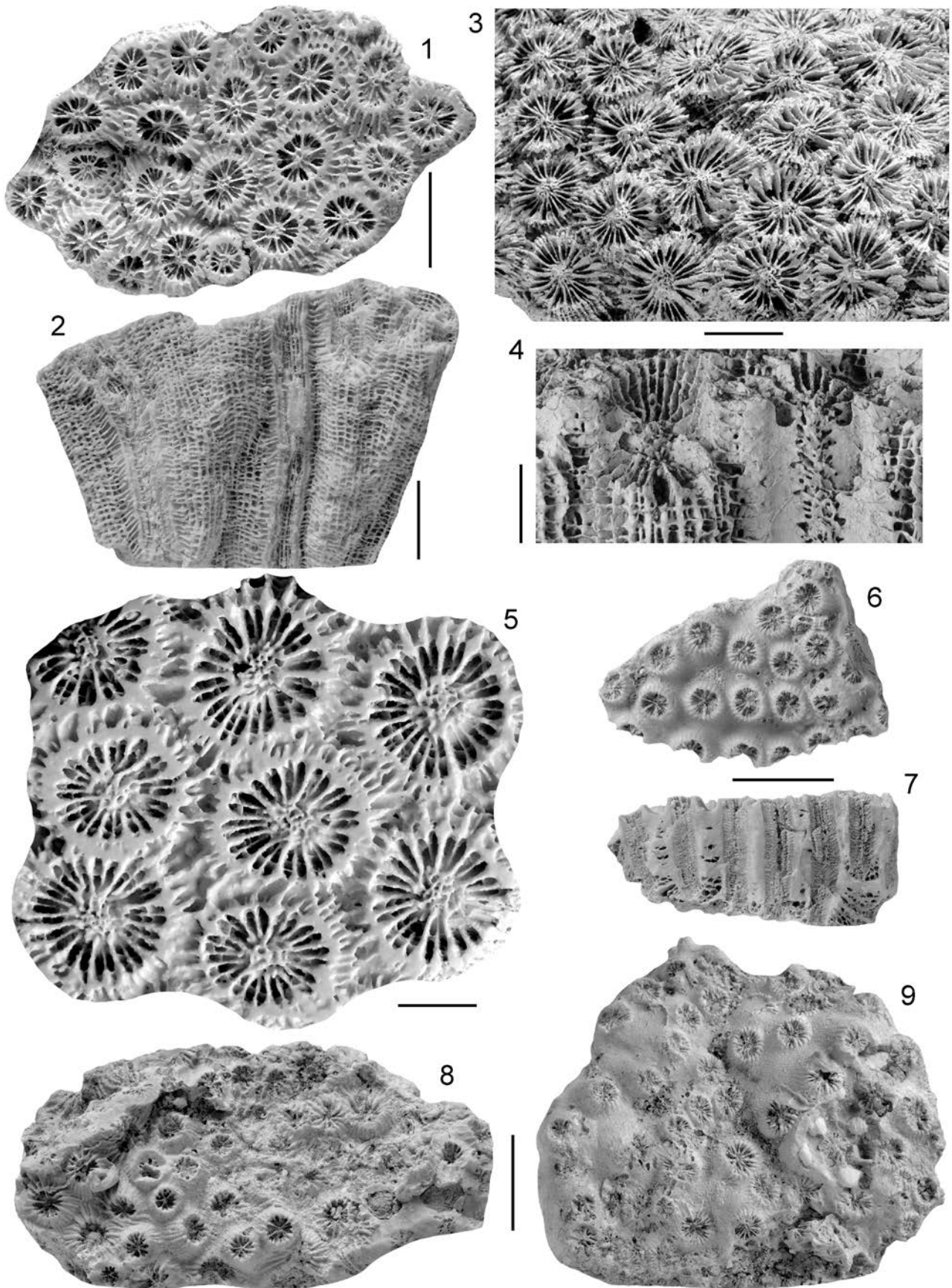


Plate V – V. tábla

