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## First Mesozoic record of the scleractinian *Madrepora* from the Maastrichtian siliceous limestones of Poland

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**Abstract** The objective of the present article is to document the first stratigraphic occurrence of the colonial oculinid *Madrepora*, known from the modern seas as an azooxanthellate taxon that contributes to the formation of deep-water coral reefs. The Upper Cretaceous specimens of *Madrepora* sp. reported herein from Poland were recovered from Upper Maastrichtian (Nasiłów and Bochoznica localities) and Lower Maastrichtian (Bliżów locality) siliceous limestones. The corals are preserved as imprints of the branch fragments and molds of the calices. Despite their moldic preservation, the coral remains exhibit key generic features of the genus *Madrepora*; including (1) sympodial colony growth form with calices arranged in opposite and alternating rows in one plane of the branch, and (2) imprints of the granular coenosteum texture, occasionally showing peculiar reticulate patterns. Some features of the Cretaceous *Madrepora* sp., such as the reticulate coenosteum texture, the range of the corallite diameter (2.8–4 mm), and the arrangement of the septa in three regular cycles resemble the skeletal features of the modern, typically constructional, species *M. oculata* (type species). The lack of any evidence of coral buildups and related debris in the whole Upper Cretaceous/Paleogene sequences from Poland and the sparse occurrence of colony fragments, suggests that the Cretaceous *Madrepora* sp. formed small, isolated colonies.

**Keywords** Scleractinia · *Madrepora* · Cretaceous · Maastrichtian · Siliceous limestone

### Introduction

The last few decades of exploration of Recent deep-water environments cast an entirely new light on the importance of scleractinian corals for the deep-water ecosystems. Deep-water coral reefs (reef sensu Freiwald 1998; Freiwald et al. 2004), whose framework is formed by scleractinian taxa with arborescent growth forms, proved to be the regions of essential habitat, feeding grounds, recruitment and nursery for a great deal of marine organisms. Deep-water coral reef ecosystems are currently a subject of broad multidisciplinary studies (reviews by Freiwald et al. 2004; Roberts et al. 2006). Among the current research topics, traditional skeletal-based and molecular approaches, a baseline for biodiversity assessments, are receiving considerable attention. The results of these studies show that in contrast to the tropical reefs, renowned for the scleractinian diversity, the Recent deep-water coral build-ups are generally formed by only 1 to 3 azooxanthellate scleractinian species. Globally, only six genera (and six species) contribute significantly to the deep-water constructions: the traditional oculinids *Madrepora oculata* Linnaeus (1758), *Oculina varicosa* Lesueur (1821), the caryophyllids *Lophelia pertusa* (Linnaeus 1758), *Goniocorella dumosa* (Alcock 1902), *Solenosmilia variabilis* Duncan (1873), and the dendrophylliid *Enallopsammia profunda* (de Pourtalès 1867). The evolutionary history of the Recent scleractinian taxa contributing to the formation of deep-water coral reefs is still poorly known. Until now, the earliest confirmed records of these genera have been documented for the Cenozoic: (1) *Madrepora sobral* Filkorn (1994) from the Paleocene of Seymour Island, Antarctica (Filkorn 1994; Stolarski 1996); (2) *Oculina becki* (Nielsen 1922) from the Paleocene of Denmark (Floris 1980; Bernecker and Weidlich 1990, 2005). The generic attribution of Campanian *Oculina nordenskjoldi* (Felix 1909) from Antarctica is controversial, see Filkorn 1994; (3) *Enallopsammia laddi*

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Wells 1977 from the Late Eocene of Tonga; (4) *Lophelia defrancei* (Milne Edwards and Haime 1857) from the Middle Miocene of Sardinia (De Angelis d'Ossat and Neviani 1897; see also the overview by Taviani et al. 2005). Two genera have been recognized only from modern seas: (5) *Goniocorella* and (6) *Solenosmilia*.

The goal of this report is to document the earliest, Late Cretaceous occurrence of *Madrepora* (*Madrepora* sp.) that represents also the first colonial scleractinian described from Upper Cretaceous deposits of Poland. Amateur collectors and paleontologists familiar with the Upper Cretaceous deposits of Poland, interviewed by the senior author, acknowledged the possibility of overlooking colonial coral remnants that could be taken for common odd-shaped sponge fragments. We hope that this paper will trigger recognition of dissolved *Madrepora* branches and more data about this potential construction-builder will become available soon.

## Materials and methods

Fossil remains of the scleractinian corals are rare in the Upper Cretaceous deposits of Poland. From the Maastrichtian deposits of the Lublin Upland, only scleractinians with solitary growth forms were described and traditionally all were classified into Caryophylliina (= Turbinolidae in Siemiradzki 1926). Most of the coral finds in siliceous limestones (most common Upper Cretaceous facies in this region) are represented by poorly integrated molds or imprints (as are most of the originally aragonite shells), although body fossils with the original skeleton interpreted as neomorphically altered are also reported (Gautret et al. 2000).

The three colony fragments described in this paper are represented by the imprints of branches and molds of corallites. Typically, the surface of the cavities left by the dissolved skeleton is coated by orange-brown ferrous oxides (Figs. 2, 3). The branch fragments were collected at three localities. The best preserved one (colony removed from the rock in two parts ZPAL H.19/6/B139, and ZPAL H.19/6/B140, respectively) is from the Late Maastrichtian of Nasiłów (Fig. 1). It consists of ca. eight branches and about 25 corallites (Figs. 2A, 3). The other two specimens examined in this study, the first from the Late Maastrichtian of Bochoćnica (ZPAL H.19/8/B160; Fig. 4), the second from the Early Maastrichtian of Bliżów (ZPAL H.19/7/B144; Fig. 2B), consist of one and two branches, respectively, with five corallites preserved on each specimen. Attempts to cast some corallites with resin and to dissolve the ambient rock, proved unsuccessful as many of the post-septal fissures are filled with the calcite cement or marly sediment that prevent either resin penetration or the rock dissolution; the rock itself is too fragile to be sectioned.

As a comparative material we used Recent and Lower Pleistocene specimens of the type species of *Madrepora* (*M. oculata*). The first were collected from the Mediterranean (off-shore Marseille, Capraia Island and Santa

Maria di Leuca) and the second from silty deposits cropping out in southern Italy (Lazzaro, Reggio Calabria).

*Institutional abbreviations* PMC, Museum of Paleontology, University of Catania (Università di Catania, Dipartimento di Scienze Geologiche); ZPAL, Institute of Paleobiology, Polish Academy of Sciences (Instytut Paleobiologii, PAN, Warszawa).

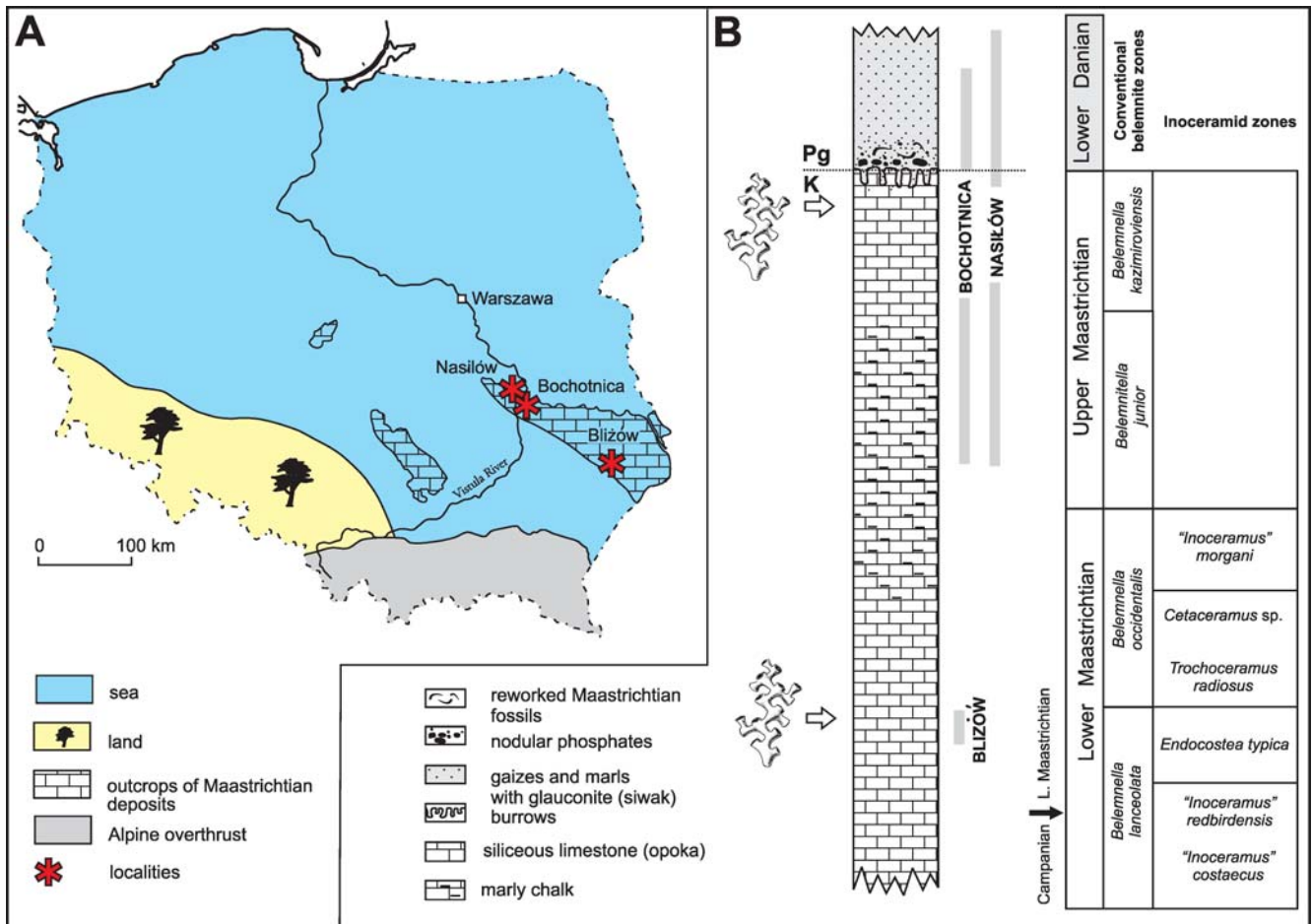
## Geologic setting and palaeoenvironmental remarks

### *Maastrichtian deposits in the Lublin Upland*

The studied samples with the colony fragments of *Madrepora* sp. are from the Maastrichtian deposits exposed in three outcrops on the Lublin Upland: Nasiłów (1) and Bochoćnica (2) located on the Vistula river banks ("Vistula section" further in the text), and (3) Bliżów located in the central part of the Lublin Upland (Fig. 1). The Late Cretaceous succession in Lublin Upland is predominantly marly-calcareous, locally with siliciclastic input, and composed of siliceous limestones (local term: opoka), marlstones, and marly limestones; white chalk appears in the eastern part of the region (Pozaryski 1956; Krassowska 1997; Hakenberg and Świdrowska 2001).

The Maastrichtian in Poland is traditionally subdivided into four belemnite zones: Lower Maastrichtian *Belemnella lanceolata* and *Belemnella occidentalis* zones and Upper Maastrichtian *Belemnella junior* and *Belemnella kazimiroviensis* zones (Cieśliński and Wyrwicka 1970; Błaszkiwicz 1980; Abdel-Gawad 1986). According to a new basal Maastrichtian boundary definition (Odin and Laumerelle 2002), most of the *B. lanceolata* Zone should, however, be retained in the Campanian (e.g., Niebuhr 2003; Walaszczyk 2004; see also Fig. 1B). The Lower Maastrichtian may additionally be subdivided based on inoceramids, as recently proposed by Walaszczyk et al. (2002). The tentative correlation of the inoceramid and belemnite zonations is presented in Fig. 1 (see also Machalski 2005).

In the Vistula section, at the western margin of the Lublin Upland, the Maastrichtian (*B. lanceolata* Zone) starts with opoka. The facies changes in the upper part of the *B. occidentalis* zone. Somewhere at this level a more marly (with chalk intercalations) succession appears, which ranges up to the base of the *B. kazimiroviensis* zone, where it turns again into siliceous limestone (Błaszkiwicz 1980). These upper siliceous limestones crop out in two quarries of Nasiłów and Bochoćnica, which yield the fragments of *Madrepora* sp. described herein. The facies change from the siliceous limestones to marls and chalk in the Vistula section may possibly be a record of a mid-Maastrichtian deepening of the basin. A shallowing trend is observed towards the top of the Maastrichtian, which is capped by the greensand horizon of Danian age (Machalski and Walaszczyk 1987; Machalski 1998). Abdel-Gawad (1986: Table 10), based on analysis of benthic mollusk assemblages, suggested relatively shallow continental shelf settings for the Late Maastrichtian deposits: ca. 100–150 m depths for the *B. lanceolata*, *B. occidentalis*, and *B. junior* zones, and 20–



**Fig. 1** Paleogeography of Poland in Maastrichtian (after Świdrowska and Hakenberg 1999) and location of *Madrepora*-bearing sites (A). B Stratigraphic position and simplified lithological profiles of *Madrepora*-bearing sites. Extend of Paleogene (Pg) and Cretaceous (K) deposits (gray bars) in three sampled quarries, i.e., Bochotnica, Blizów, and Nasilów and approximate position (white arrows) of *Madrepore* finds. Stage stratigraphy according to tradi-

tional Boreal subdivisions; black arrow marks proposed new position of the base of the Maastrichtian (Odin and Lamaurelle 2001). Conventional belemnite zonation after Jeletzky (1951); Birkelund (1957); Błaszkiwicz (1980) modified; inoceramid zonation after Ireneusz Walaszczyk personal communication (2006), see also Machalski (2005)

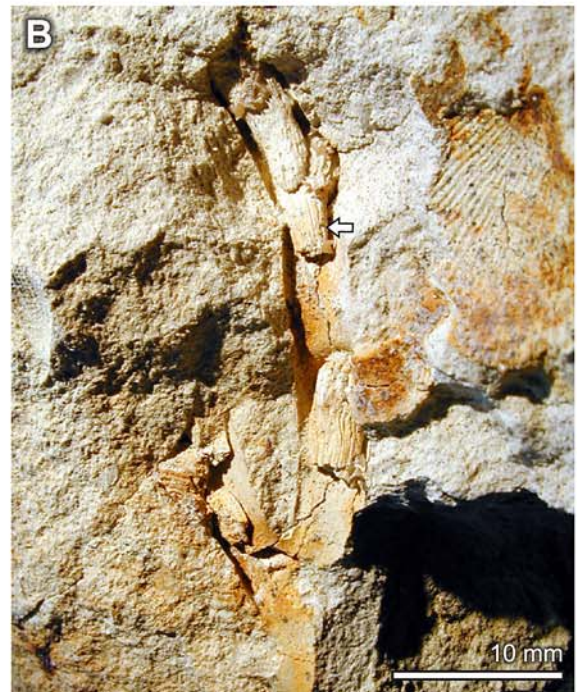
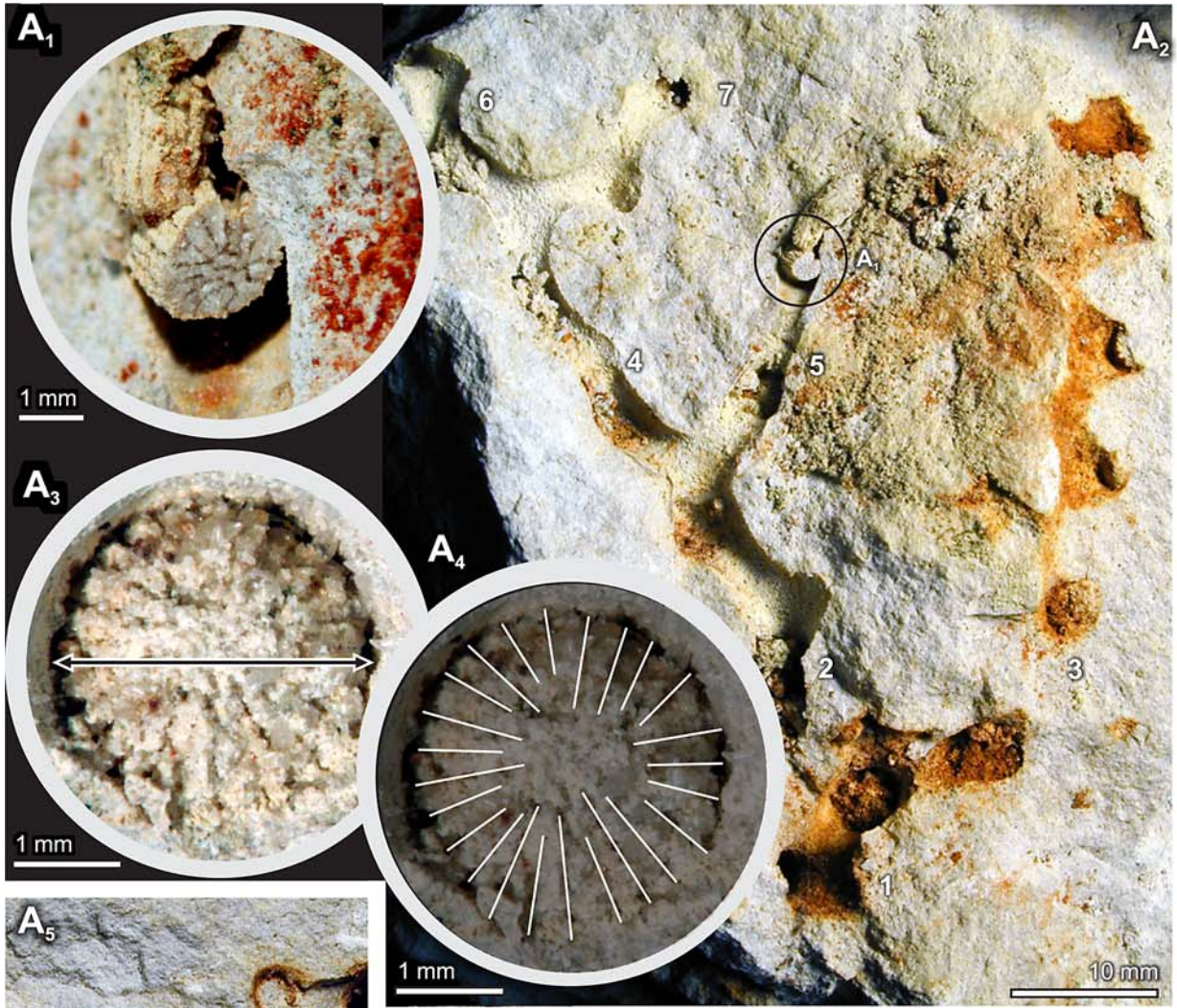
80 m for the upper *B. kazimiroviensis* zone, respectively (see also Machalski 1998).

A similar trend in the evolution of the sedimentary environment may also be suggested for the central part of the Lublin Upland. As in the Vistula section, the pattern with siliceous limestone (occasionally with terrigenous siliclastic admixture) in the Lower Maastrichtian, an increase in the marly content in the Mid-Maastrichtian, and return to the opoka facies in the Upper Maastrichtian, is reported (see Cieśliński and Rzechowski 1993). At this level of generalization, a uniform palaeoenvironmental scenario for the whole area may be assumed.

#### Localities

**Nasilów and Bochotnica:** The siliceous limestone Upper Maastrichtian succession exposed in the Nasilów quarry is ca. 14 m thick, and is capped by ca. 12-m-thick Danian deposits. In the Bochotnica quarry, the exposed Upper Maas-

trichtian sequence is ca. 3 m thick and is covered by few meter thick Danian deposits. The specimens of *Madrepore* sp. were collected in both quarries from the topmost part of the Upper Maastrichtian sequence: in Nasilów, from ca. 1 m thick, post-depositionally cemented limestone layer (“hard-ground” of earlier authors; see Machalski 1998), in Bochotnica from the siliceous limestone right below the hard limestone layer. Traditionally, the topmost Upper Maastrichtian sediments in the Vistula section are interpreted as shallow water, and part of a regressive sequence (Abdel-Gawad 1986; Radwański 1996; Machalski 2005). Macrofossils that most frequently occur in the uppermost siliceous limestones are diverse gastropods, bivalves, sponges, and ammonites (Abdel-Gawad 1986; Machalski 2005). Molds of solitary corals are occasionally present (undescribed ZPAL collection of the senior author). Occurrence of articulated shells of the scallop *Dhondtichlamys acuteplicata* and terbratulid brachiopod *Neoliothyryna* sp. and preservation of articulated large bivalves in life position, i.e., *Pholadomya*, *Pinna* (umbones down), *Pycnodonte* (convex shell down)



suggest *in situ* occurrence of the fauna (Machalski 2006, pers. comm.). On the other hand, on some bedding surfaces one may observe accumulations of fragmentarily preserved fossils, including disarticulated bivalve shells, that suggest influence of storms or/and activity of shell-crushing predators (Radwański 1996). Noteworthy, these fragmentary preserved fossils represent the same taxa as known from the undisturbed parts of the sequence. The only evidently exotic elements mixed occasionally with autochthonous and parautochthonous fauna in Nasiłów and Bochothnica are wood fragments and short branches of coniferous plants (Malicki et al. 1967).

**Bliżów:** The ca. 10-m-thick Lower Maastrichtian succession, accessible in the quarry in Bliżów (the locality where the third specimen of *Madrepora* sp. was found), is represented by siliceous limestones of the upper *Endocostea typica* inoceramid zone, a possible equivalent of an upper *B. lanceolata*. Occurrence of articulated bivalves (in this locality represented also by inoceramids) on some bedding planes and, on the other hand, local accumulations of fragmentarily preserved fossils, disarticulated bivalves in other rock samples, strikingly resemble depositional setting suggested for the uppermost Maastrichtian deposits exposed in Nasiłów and Bochothnica quarries. Also in Bliżów, the only evidently exotic elements are flora fragments represented mostly by deciduous plant leaves (Machalski 2006, pers. comm.).

### Systematic paleontology

Genus: *Madrepora* Linnaeus, 1758

Diagnosis: Colonial, extratentacular budding, usually alternate and in one plane, forming dendroid colonies. Coenosteum dense; costae absent. Corallites often filled internally by stereome. Pali typically absent. Columella absent or spongy (compare Linnaeus 1758: 793; Verrill 1901: 113; Cairns 1979: 39; Filkorn 1994: 72).

Type species: *Madrepora oculata* Linnaeus, 1758, by subsequent designation (Verrill 1901)

*Remarks* Attribution of the Cretaceous coral to the oculinid (see Discussion) genus *Madrepora* is based on recogni-

tion on the mold of the following diagnostic generic features: occurrence of zigzag alternate budding, no evidence of costae on the coenosteum imprints, traces of spongy columella, and evidences (lack of sediment infilling of branches) that some corallites could have been filled by stereome. Occurrence of paliform lobes cannot be ascertained. Some characters of the herein described *Madrepora* are typical of the type species of *Madrepora* (*M. oculata*), i.e., size and shape of calices, pattern and number of septa, reticulate texture of coenosteum. This strengthens the generic attribution.

Four traditional oculinid genera have been acknowledged recently by Baron-Szabo (2002) from the Upper Cretaceous: *Diblasus* Lonsdale (1850), *Archohelia* Vaughan (1919), *Palaeohelia* Alloiteau (1958), and *Bantamia* Yabe and Eguchi (1943). They differ from *Madrepora* in: irregular basal budding (*Diblasus*), tendency of spiral arrangement of corallites around the branches (*Archohelia*, *Bantamia*), and corallites deeply embedded in a dense and strongly costatae coenosteum (*Palaeohelia*). There are records of other oculinid Cretaceous corals (see Vaughan and Wells 1943; Alloiteau 1952) but none of these shows combination of diagnostic *Madrepora* characters.

The zigzag growth pattern of *Madrepora* is shared also by some dendrophylliids (*Enallopsammia*, some species of *Dendrophyllia*; see Cairns 2001), some traditional oculinids, and exclusively Mesozoic scleractinians attributed to styliniids (e.g., Late Jurassic *Enallhelia* Milne Edwards and Haime, 1849) or rhipidogyrids (*Tiaradendron* Quenstedt, 1858); see Lauxmann (1991). Attribution of the Cretaceous coral studied herein to dendrophylliids can be excluded as they typically have septa arranged according to the Pourtalès pattern and synapticulothecal wall. These features can be easily recognized even in corallum molds but none of them were recognized in herein described specimens. Furthermore, none of the traditional gross morphology characters used in diagnosis of rhipidogyrid and stylinid corals (very thick stereomal deposits, lamellar columella and presence of distinct styliform columella, respectively) can be recognized in the examined Cretaceous corals from Poland.

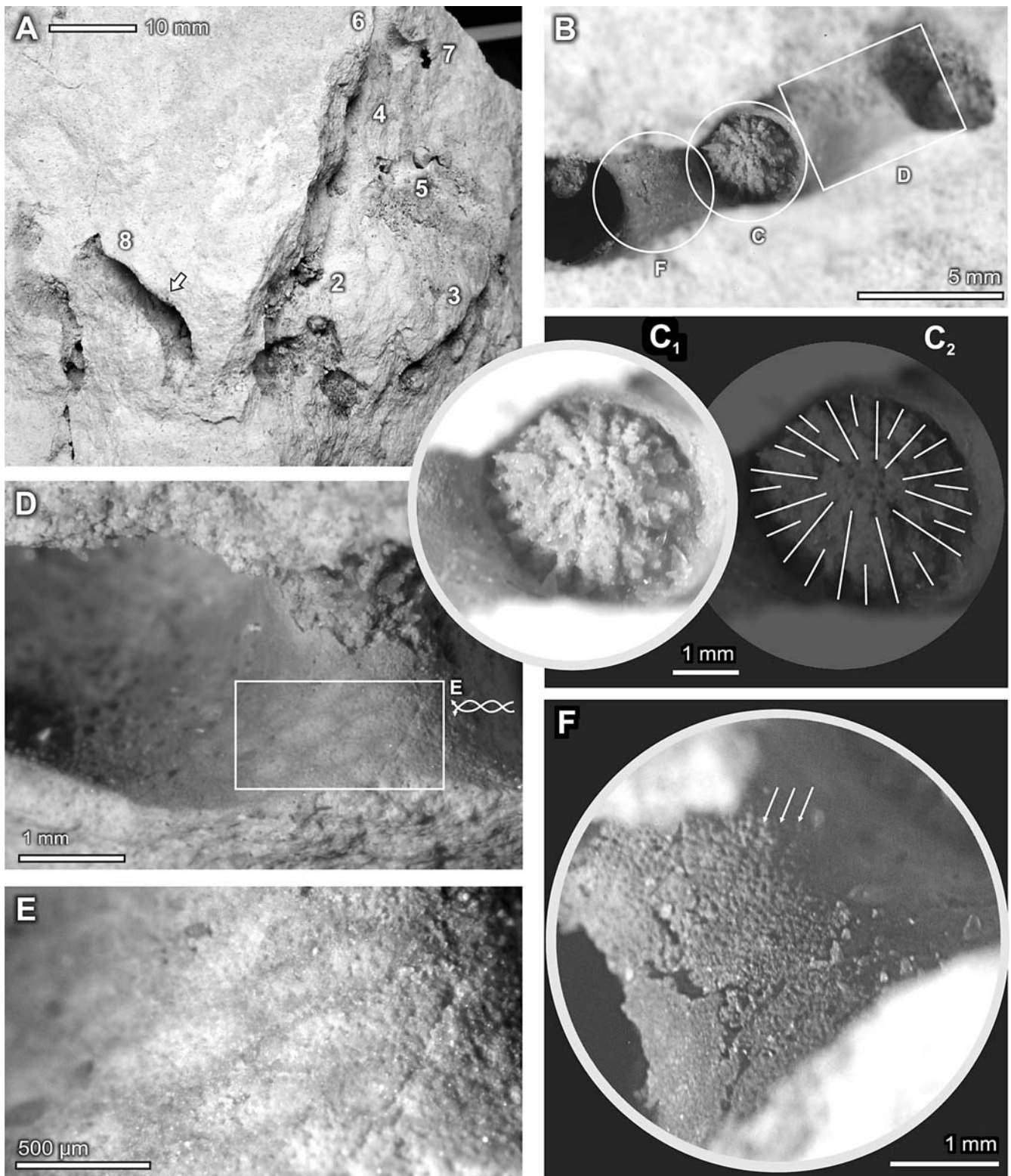
*Madrepora* sp. (Figs. 2–4)

*Material* Three fragmentary colonies: (1) colony fragment in two parts (ZPAL H.19/6/B139, and ZPAL H.19/6/B140) from the Late Maastrichtian of Nasiłów, (2) colony branch fragment from the Late Maastrichtian of Bochothnica (ZPAL H.19/8/B160), (3) colony branch fragment from the Early Maastrichtian of Bliżów (ZPAL H.19/7/B144; Fig. 2B).

*Description* Fragments of all three examined colonies have sympodial (uniserial erect) growth form that results in zigzag arrangement of calices (their occurrence in opposite and alternating rows). This feature is particularly well visible in Fig. 2A<sub>2,5</sub> but the same pattern can also be inferred for the other colony branches.

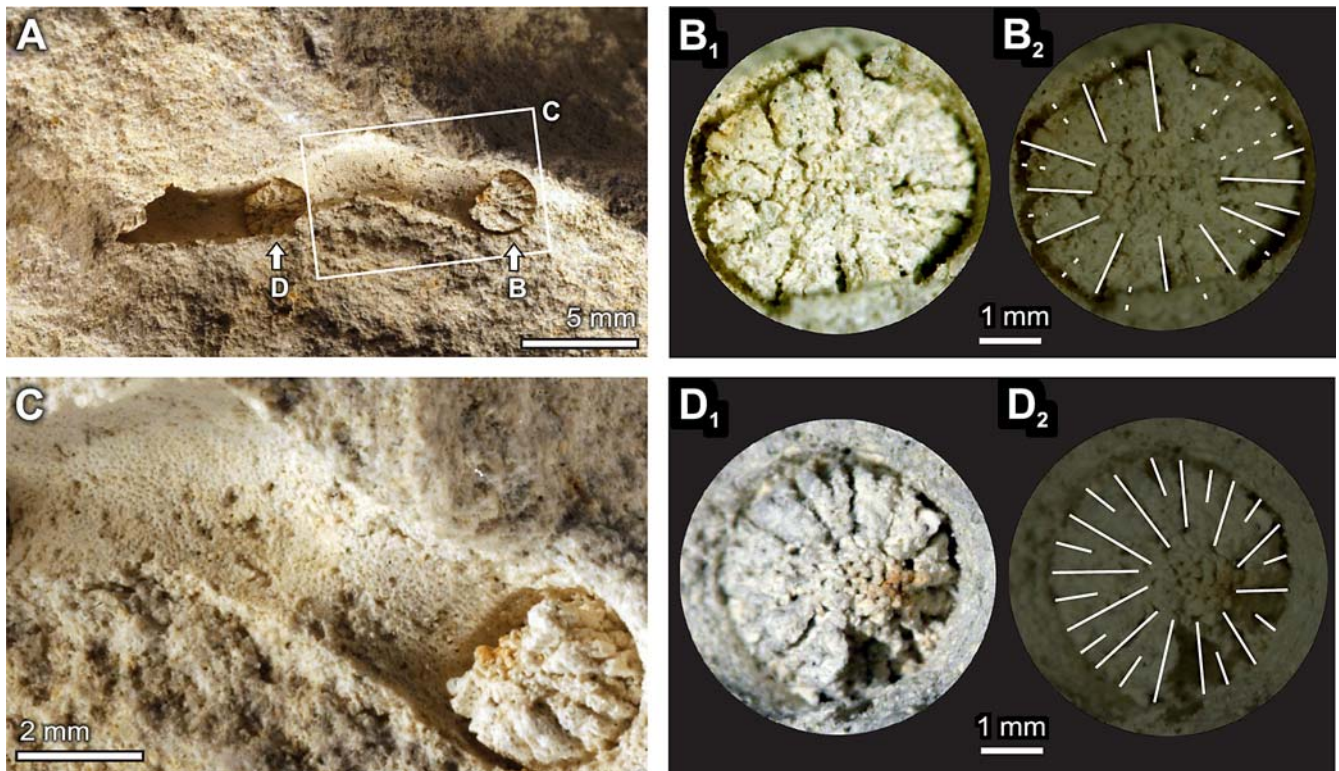
The best preserved colony fragment from Nasiłów (ZPAL H.19/6/B139, B140), is ca. 50 mm in length and consists of imprints of eight branches that include molds of ca. 25

◀ **Fig. 2** Preservation and colony/corallite morphology of Late Cretaceous *Madrepora* sp.: **A** Fragment of the colony (two parts: ZPAL H.19/6/B139 and ZPAL H.19/6/B140, figured in **A**<sub>1–4</sub> and **A**<sub>5</sub>, respectively) from the Upper Maastrichtian (*Belemnella kazimiroviensis* Zone) siliceous limestone of Nasiłów near Kazimierz Dolny (central Poland); **A**<sub>1</sub> close-up of the mold of the branch fragment right below the calicular region; **A**<sub>2</sub> part of the largest colony with 3 branching nodes (individual branches numbered from 1 to 7) and ca. 18 calices. Corallum typically preserved as mold, rarely septal regions are infilled (recrystallized?) with calcite (enlarged in **A**<sub>1</sub>); Close-up of the calicular mold (**A**<sub>3</sub>, bottom-up view, calicular diameter marked with arrow) and interpretation of septal arrangement (**A**<sub>4</sub>); **A**<sub>5</sub>. Counterpart of the largest colony fragment (corresponding branches in **A**<sub>2</sub> and **A**<sub>5</sub> bear the same numbers) with three branching nodes and ca. 17 calices (sympodially arranged). Encircled is branch region enlarged in **A**<sub>3</sub>, **A**<sub>4</sub>. **B** ZPAL H.19/7/B144, Lower Maastrichtian (*Belemnella lanceolata* Zone) siliceous limestone of Bliżów near Krasnobród (eastern Poland); fragmentarily preserved colony with one branching node and ca. 3–4 calices (some inter-corallite regions preserved as casts, arrow)



**Fig. 3** Preservation, colony/corallite morphology and coenosteum texture of Late Cretaceous *Madrepora* sp. **A** Side view of the slab with colony (ZPAL H.19/6/B139; see Fig. 2A) with another 8th colony branch (*arrow*) preserving imprints of original thecal texture **B** Mold of 8th branch with calicular and inter-calicular regions enlarged in subsequent (C, E, respectively) views. **C** Close-up of calicular mold

(**C**<sub>1</sub>, bottom-up view) and interpretation of septal arrangement (**C**<sub>2</sub>). **D**, **E** Imprints of reticulate texture of coenosteum (intertwining arrows) in inter-calicular region (**E**, close-up). **F** Imprint of coenosteum granulation showing some linear arrangement (*arrows*). Upper Maastrichtian, *Belemnella kazimiroviensis* zone, siliceous limestone of Nasitów near Kazimierz Dolny, central Poland



**Fig. 4** Preservation, colony/corallite morphology and coenosteum texture of Late Cretaceous *Madrepora* sp. (ZPAL H.19/8/B160). **A** Mold of branch fragment with three corallites (two of them enlarged in **B** and **D**, arrows). **B** Close-up of calicular mold (**B**<sub>1</sub>, bottom-up view) and interpretation of septal arrangement (**B**<sub>2</sub>, dim septal position marked with dashed lines). **C** Close-up of imprint of evenly

distributed coenosteum granulations. **D** Close-up of another calicular mold (**D**<sub>1</sub>, bottom-up view) and interpretation of septal arrangement (**D**<sub>2</sub>). Upper Maastrichtian, *Belemnella kazimiroviensis* Zone, siliceous limestone of Bochothnica near Kazimierz Dolny, central Poland

calices. The most externally located branches of this colony fragment (numbered 3 and 6 in Figs. 2A<sub>2</sub>, 3A) extend from each other for about 55 mm. The consecutive branches diverge at ca. 50–70° angles. The branch diameter ranges from ca. 3–5 mm (distal and proximal parts, respectively).

The specimen from Bochothnica (ZPAL H.19/8/B160) represents an imprint of a single branch, ca. 50 mm long that includes molds of five calices (three relatively well-exposed calices are illustrated in Fig. 4A).

The specimen from Bliżów (ZPAL H.19/7/B144) is an imprint of dichotomously branching colony fragment, ca. 40 mm long with ca. four calices. In contrast to the specimens from Nasilów and Bochothnica, intercalicular molds in ZPAL H.19/7/B144 extend deeper into the branch (Fig. 2B). Although septal fissures are recognizable, the infilling is compressed and reconstruction of the septal pattern cannot be performed accurately; nonetheless ca. 12 septal fissures occur on the half of the calice mold (Fig. 2B; estimated 24 for the whole calice).

On some branch imprints, coenosteal texture is preserved (ZPAL H.19/6/B139, B140) showing linear (Fig. 3F) and reticulate intercostal striae (Fig. 3D, E). Lens-shaped areas delineated by the reticulate network are ca. 0.5 × 0.25 mm in size. In ZPAL H.19/8/B160, this texture is finely granulated (finely pitted on mold, Fig. 4A, C) whereas in ZPAL H.19/7/B144 the surface of the branch imprint is smooth (Fig. 2B).

Calicular diameters, estimated by a distance between two opposite edges of the mold (Fig. 2A<sub>3</sub>), in all three examined specimens range from 2.8 up to ca. 4 mm; in more distal parts of the colony ZPAL H.19/6/B139, B140 calices have smaller diameters (2.8–3.5), whereas their largest diameters are in more proximal colony part. Size and arrangement pattern of fissures after dissolved septa allow the following interpretation of their original formula  $S1 = S2 > S3$  (Figs. 2A<sub>3,4</sub>, 3C<sub>1,2</sub>). The inner edges of the S1-2 septal fissures reach the center of circular calicular mold (ca. 1 mm in diameter) that contains traces of spongy axial structure (Figs. 2A<sub>3</sub>, 3C<sub>1</sub>, 4B<sub>1</sub>, D<sub>1</sub>). The corallum is typically preserved as mold, rarely septal regions are infilled (recrystallized?) with the calcite.

None of the delicate intra-calicular structures known from the coralla of modern *Madrepora* (paliform lobes, septal granulation) can be reliably traced in the examined fossil specimens, however the occurrence of interconnected pits in the center of calicular mold suggests presence of spongy/papillar axial structure (Figs. 3C, 4B, D).

*Remarks* Characters that are traditionally considered in taxonomy of *Madrepora* include number of septal cycles, type of columella and paliform development, and pattern of the coenosteal texture. For modern seas, six *Madrepora* species are considered valid (Cairns et al. 1999; Cairns 1999). The type species of the genus, *Madrepora oculata* Linnaeus

(1758) is supposed to have a broad range of morphological variability and a worldwide distribution, whereas other five species are considered to have more restricted geographic distribution: from the western Atlantic is reported *M. carolina* (de Pourtalès 1871) and from the western and central Pacific *M. arbuscula* (Moseley 1881), *M. kauaiensis* Vaughan 1907, *M. minutiseptum* Cairns and Zibrowius 1997, and *M. porcellana* (Moseley 1881).

However, the currently adopted taxonomy of *Madrepora* is based on gross morphology characters, and not supported by the intracolony and intra- and inter-specific studies of morphological variability of characters. Thus it remains unknown what is the taxonomic status of various morphotypes of *M. oculata* considered as a one worldwide species. For example, Cairns (1991: 9; 1998: 374; 1999: 61) considering different calicular diameters, mode of columella and paliform development, distinguished two extreme morphotypes: (1) “*tenuis*” (“*beta*” of Cairns 1991, ?*M. kauaiensis* Vaughan, 1907): large colonies with non-anastomosing branches; calices 3–3.5 mm in diameter with deep fossa, rudimentary columella, and S2 with lacinate paliform lobes; and (2) “*formosa*” (“*alpha*” of Cairns 1991): smaller colonies with anastomosing branches; calices 2.2–2.5 mm in diameter with shallow fossa, well developed columella, and S2 with prominent paliform lobes). As suggested by Filkorn (1994: 72), the above-mentioned features may actually vary in colony astogeny and in Paleocene *Madrepora sobral*, the fossa depths, are variable and inversely proportional to calicular diameter and “generally shallowest on larger corallites and deepest on smaller corallites”. Furthermore, as showed in Recent (Zibrowius 1980: 36) and Lower Pleistocene specimens of *Madrepora oculata* (Vertino 2003:123), the fossa depth, the shape and size of the columella and the septal granulations can remarkably vary within the same colony. Generally, the distal-most (and consequently youngest) corallites show deeper fossa, less developed columella and septal granulations than the more proximal corallites. Re-assessment of the existing *Madrepora* taxonomy will also come from combined skeletal-molecular studies that already appeared to be a powerful tool in resolving generic- and species-level phylogenetic relationships in Scleractinia (Cuif et al. 2003; Fukami et al. 2004).

Lack of reliable morphologic criteria in taxonomy of Recent *Madrepora* implies that also taxonomic attribution of at least thirty nominal Cenozoic species of *Madrepora* (estimates by Wells 1977) is pending. Some of these nominal taxa have been recently revised. For example, Vertino (2003) attributed six Seguenza’s (1864) fossil species of *Madrepora* (originally described as: *Amphihelia miocenica* Seguenza (1864), *A. sculpta*, Seguenza (1864), *Diplohelia reflexa* Milne Edwards and Haime (1857), *D. meneghiniana* Seguenza (1864), *D. doderleiniana* Seguenza (1864), *D. sismondiana* Seguenza (1864) to *Madrepora oculata* referring to the wide intra-specific morphological variability of the Recent species (see Zibrowius 1980).

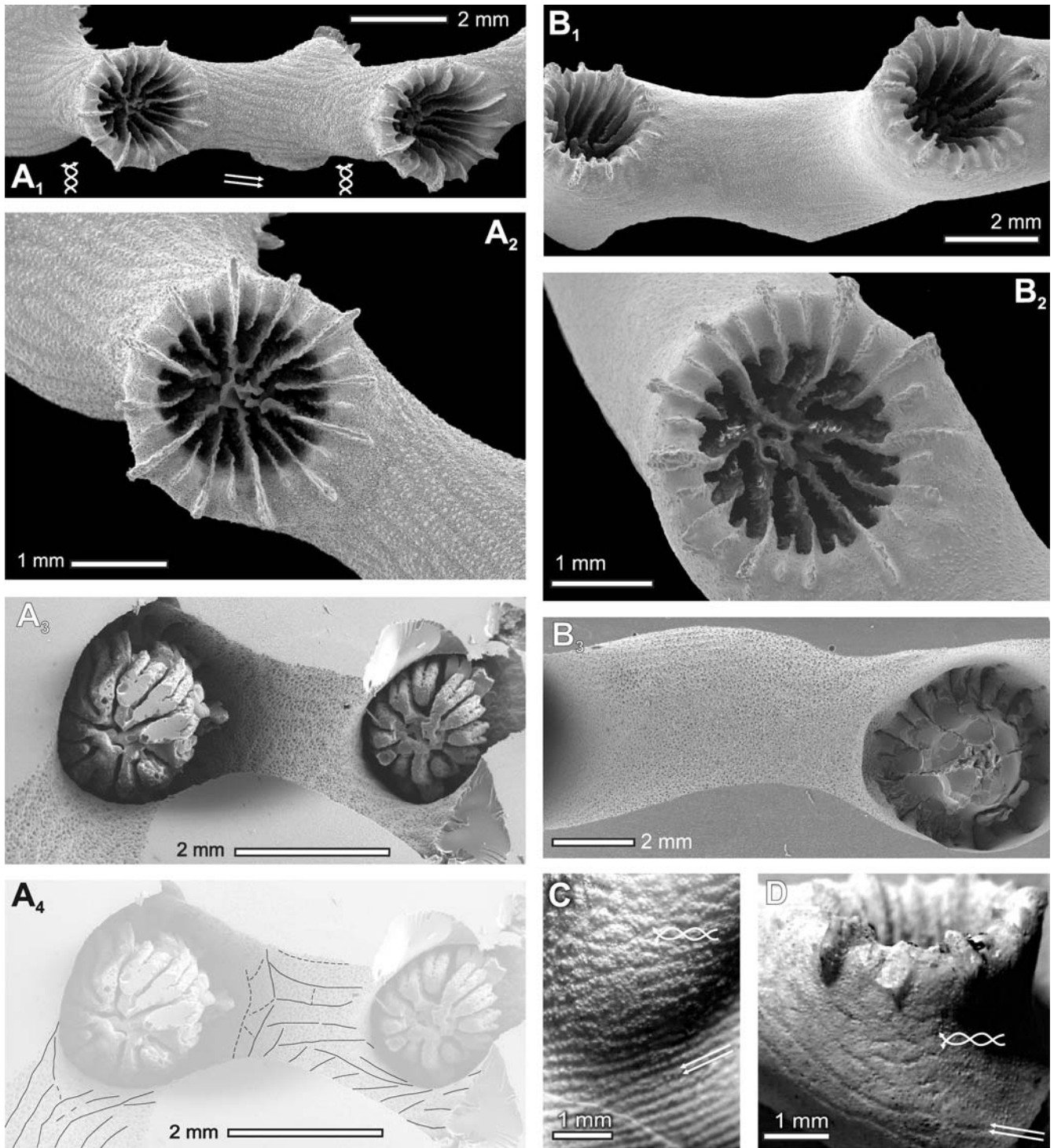
The fragmentary colonies of the Cretaceous *Madrepora* described herein do not provide sufficient details on calicular morphology (paliform lobes, septal granulation) to

classify them at species level; the taxon is thus described in open nomenclature. The specimen from Bliżów (ZPAL H.19/7/B144) shares with the specimens from Nasilów (ZPAL H.19/6/B139, 140) and Bochoznica (ZPAL H.19/7/B160) similar branch and calicular diameters and alternating branching mode but differs in smooth imprint of the coenosteum and possibly in having deeper calices, as can be assessed from the sediment infilling of the intracalicular space (occasionally, we observed that in distal branches of Recent *Madrepora*, stereome may not completely infill the intracalicular space). Among the oldest representatives of *Madrepora* six nominal species are known from the Eocene (compare Wells 1977) and one from the Paleocene (*M. sobral* Filkorn, 1994). *Madrepora* sp. described herein has calices of comparable diameter with Paleocene *Madrepora sobral* Filkorn, 1994 (2.8–4 mm vs. 2–(3–5)–7 mm, respectively). *Madrepora* sp. and *M. sobral* also have in common 24 hexamerally arranged septa (S1 > = S2 > S3). Lack of reticulate corallite wall texture in all examined specimens of *M. sobral* (see Stolarski 1996) hints on some differences between these two compared species (but see remarks on occurrence of reticulate texture in Recent *M. oculata*, below). Three other Paleogene (Eocene) *Madrepora* species, i.e., *M. granulata* (Tenison-Woods 1880) from the lowest Eocene-lower middle Oligocene of New Zealand (Squires 1958), *M. natchitochensis* (Vaughan 1900) from the Eocene of Louisiana and Texas, and *Madrepora* sp. from the Eocene of Tonga (Wells 1977) have also 24-septate corallites that differ from our *Madrepora* sp. by smaller calicular diameters (1–3), (1.3–2), and 2 mm in diameter, respectively. Noteworthy corallites of *Madrepora* sp. from the Eocene of Tonga (Wells 1977: pl.2:2) display clearly reticulate wall texture, although this aspect has not been mentioned in the original description.

The range of variability of corallite diameter and the presence of the reticulate coenosteum texture in the specimen from Nasilów (ZPAL H.19/6/B139, ZPAL H.19/6/B140; Fig. 3D, E) is most similar to *M. oculata* (compare reticulate texture in Fig. 5:A, C, D; corallite diameters of Recent forms: 2.3–3.0 mm Cairns and Zibrowius 1997; 3.0–3.5 mm Cairns 1999; 3.6–4.0 mm Cairns 1991). The plastic casts of two branches of modern *Madrepora oculata* (Fig. 5) show that, the wall textures (reticulate vs. delicate longitudinal striae patterns) and calicular casts resemble those ones preserved in the Cretaceous *Madrepora* sp. Relatively homogenous granular corallite wall/coenosteum texture in specimen from Bochoznica (ZPAL H.19/8/B160), without reticulate pattern, fits within the range of morphological variability of *M. oculata* (Fig. 5B1–3).

In the Recent *Madrepora* species the shape and branch diameter differ significantly between distal and basal parts of the colony. The calices of the distal-most branches are well individualized, exsert and zigzag arranged whereas those ones from the thick basal parts are generally recessed in the coenosteum (Cairns 1979; Zibrowius 1980). Due to the relatively exsert calices and their zigzag arrangement in the Cretaceous *Madrepora* sp. fragments, we assume that they represent distal parts of large colonies (the largest Re-





**Fig. 5** Colony/corallite morphology and coenosteum texture of Neogene *Madrepora oculata* Linnaeus, 1758. **A** Sympodially arranged corallites (**A<sub>1</sub>**) showing longitudinal in inter-corallite (*parallel arrows*) and reticulate textures in near-corallite regions (*intertwining arrows*); distal close-up of 24-septate corallite (**A<sub>2</sub>**); plastic mold of the colony branch (corallum dissolved; **A<sub>3</sub>**) with outlined imprints of parallel vs. reticulate coenosteum texture (**A<sub>4</sub>**); ZPAL H.25/4-Car, Recent, off-shore Marseille, Canyon of Cassidaigne, north-west Mediterranean, depth 260 m. **B** Sympodially arranged corallites (**B<sub>1</sub>**) showing longitudinal striae and homogenous granulations (**B<sub>2</sub>**, close-

up distal view of 24-septate corallite); **B<sub>3</sub>** Plastic mold of the colony branch (corallum dissolved); ZPAL H.25/5-Car, Recent, Tyrrhenian Sea, near Capraia Island, depth 450 m (Station 1756/26.6.1961, Calypso). **C, D** Longitudinal (*parallel arrows*) vs. reticulate (*intertwining arrows*) coenosteum texture in branch and calicular regions of Recent (PMC.V/I/H.C2, Ionian Sea, off-shore Santa Maria di Leuca, Station 10, 39°33.1'N, 18°32.09'E, depth 785 m) and Lower Pleistocene (PMC.V/I/Pl.C1, Lazzaro, Reggio Calabria, southern Italy) specimens (**C** and **D**, respectively)

cent *Madrepora* colonies may reach over 50 cm in height) or fragments of small colonies.

## Discussion

Cretaceous *Madrepora* in scleractinian higher level taxonomy

Results of recent molecular analyses challenge traditional notions of scleractinian evolution based primarily on macromorphologic characters. Most of the traditional supra-family groups (Romano and Palumbi 1996; Romano and Cairns 2000), but recently also families and genera (Cuif et al. 2003; Fukami et al. 2004) do not represent clades (monophyletic units) and thus cannot be kept in a phylogeny-reflecting taxonomic framework. Also Oculinidae, the family *Madrepora* was traditionally attributed to, appears polyphyletic: (1) *Madrepora* (*M. oculata*) represents a single sub-clade on molecular tree topology (Le Goff-Vitry et al. 2004, “Oculinidae 1” sensu Kerr 2005), whereas (2) “*Oculina patagonica*” (“Oculinidae 2” sensu Kerr 2005) together with some traditional Caryophylliidae, Faviidae, Meandrinidae, and Rhizangiidae integrates into larger clade Placoida, and still another clade is constituted by *Galaxea* spp. (“Oculinidae 3” sensu Kerr 2005). Noteworthy, “Oculinidae 3” are assigned to Complexa (“complex corals” by Romano and Palumbi 1996), whereas Placoida and “Oculinidae 1” (*Madrepora*) to Robusta (“robust corals” by Romano and Palumbi 1996), two major clades that differ by 29.4% in their 16S ribosomal DNA sequences (Romano and Palumbi 1996). At the moment we cannot point out any clear-cut skeletal synapomorphy that would support differentiation of the “madreporid” clade from the adjacent robustan ones. However, we may hint on the value of the thecal structures that, although underestimated in traditional “septo-centric” scleractinian taxonomy, recently appeared to be valuable characters supporting some molecular clades (e.g., Fukami et al. 2004). Based on morphological similarity between *Madrepora oculata* (“Oculinidae 1”) and the herein described *Madrepora* sp. (including unique reticulate wall texture in both taxa), we suggest that they belong to the same scleractinian sub-clades: “Robusta” (Romano and Palumbi 1996; name by Kerr 2005) and “Oculinidae 1” (Le Goff-Vitry et al. 2004; name by Kerr 2005). The Late Cretaceous occurrence of *Madrepora* species similar to the Recent *M. oculata* supports the basal phylogenetic position of this last species within the robust coral clade (Le Goff-Vitry 2004). Recently, Medina et al. (2006) suggested that the divergence date of the short/robust scleractinian clade was ca. 70 Ma (earliest fossil appearance of *Astrangia*), the calibration now supported by our findings.

Cretaceous *Madrepora* from Poland – was it a deep-water and/or construction builder?

Because of striking morphological similarity of the Cretaceous specimens described herein and the Recent species

*Madrepora oculata* it is tempting to inquire about the original environmental conditions and life mode of the Cretaceous species from Poland. Scleractinians are traditionally referred as good environmental indicators. Indeed, many aspects of the corallum morphology emerge by interaction of genetic and environmental factors (see overview by Kaandorp and Kübler 2001). Development of scleractinian polyps can be constrained by various factors like nutrient and substrate availability, water temperature, and oxygen content. Obligate symbiosis of many shallow-water taxa with photosynthetic protists (zooxanthellae) constrains their distribution to the photic zone. Unlike the tropical shallow-water zooxanthellate species, the distribution of azooxanthellate corals is entirely independent from the light, and consequently, the bathymetry may not be a key factor constraining their distribution. For example, the Recent *Madrepora oculata*, that together with *Lophelia pertusa* is the main North-Atlantic deep-sea frame-building coral and typically occurs between 400 and 1,000 m, has recently been collected at the unusual shallow depth of 55 m off Brazil (Freiwald et al. 2004). Nonetheless, it is well known that the distribution of azooxanthellate coral reefs is limited and influenced by the following factors: (1) elevated hard substrates or coarse rubble (“self-sustaining” coral structures) where the coral larvae can settle on; (2) strong currents providing suspended food to the filter-feeding corals and “sweeping” both substrate and coral polyps (3) temperature and salinity, generally ranging within 4–13°C and 32–38 ppt, respectively (Cairns and Stanley 1981; Freiwald 2002; Freiwald et al. 2004; Roberts et al. 2006).

The available palaeoenvironmental reconstructions for the uppermost Maastrichtian (Nasiłów, Bochotnica sites) suggest relatively shallow-water settings, most likely above the storm wave base (ca. 20–80 m, see Abdel-Gawad 1986). Although Recent *Madrepora* is abundant in deep, non-shelfal environments, more shallow-water settings may occasionally be, as noted above, within the depth range of its occurrence. The lack of any evidence of coral buildups/debris over a large area in the Upper Cretaceous/Paleogene sequences from Poland, the limited number of the colony fragments recovered, their relatively small diameter and the general fragile structure of the original corallum (no features suggesting strong mechanical resistance of the corallum as often observed in Recent forms: thick coenosteum, anastomosing branches) suggest that the Cretaceous *Madrepora* specimens described herein represented rather small, isolated colonies than fragments of larger reefal structures. Probably, these small *Madrepora* colonies settled on small hard substrata as commonly do Recent *Madrepora oculata* patchily distributed on soft-bottom environments (e.g., Mediterranean, junior author 2006 personal observation; Rockall Bank, Atlantic, Wilson 1979). Under optimal conditions, such small colonies may eventually enlarge considerably, forming patches, thickets, etc. (Wilson 1979). Although, there is no evidence of *Madrepora* reefs in the Maastrichtian from the Lublin Upland, the frame-building potential of the Cretaceous species cannot be excluded. Indeed, this potential came out already

right after the Cretaceous/Paleogene boundary. *Madrepora* buildups have been recognized from the Paleocene of the Seymour Island (Filkmorn 1993, 1994).

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