Microstructural diversity of the stylophyllid (Scleractinia) skeleton

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Coralla of the three species of solitary corals described herein from the Sinemurian (Lower Jurassic) of Sicily, i.e., *Haimeicyclus haimei* (Chapuis and Dewalque, 1853), *Stylophyllopsis* sp. cf. *S. rugosa* (Duncan and Wright, 1867), and *Stylophyllopsis* sp. A., conform to the overall stylophyllid morphology. Their septa consist of spines that are increasingly covered with sclerenchyme and low in the calice form compact blades. The pattern of diagenetic alteration of septa is diverse but consistent within particular taxa. It suggests that the spectrum of the original microstructures is wider than traditionally suggested for stylophyllids. In *H. haimei*, the septa are covered with dense granulations and completely recrystallized. Granulations also cover septal faces of S*tylophyllopsis* cf. *rugosa* and have rod-like foundations. In *Stylophyllopsis* sp. A., vestiges of the narrow mid-septal zone (similar to that in minitrabecular corals) occur in the proximal part of larger septa, whereas septal spines which are similar to those in S*tylophyllopsis* cf. *rugosa* occur in their distal parts. Similar diversity of microstructures is reported also in Triassic stylophyllids that have aragonitic coralla. The presence of distinct septal spines along with wide-ranging microstructural diversity of traditional Triassic–Jurassic stylophyllids, casts light on their possible evolutionary relationships, and can be a useful criterion for further revision of the group. For example, Jurassic thecocyathids, considered ancestral to caryophylliinans, share similar spiny/lobate septa with stylophyllids. Also Recent deep-water anthemiphylliids with spiny/lobate septa are strikingly similar to stylophyllids. Although this may be another example of parallel evolution, the separation of anthemiphylliids from other scleractinian clades on a mitochondrial 16S RNA tree topology suggests their ancient roots and enable us to suggest a stylophyllid ancestry. The supposed cyclic pattern of protoseptal insertion in Early Jurassic *H. haimei* supports the hypothesis of scleractinian-like (and not rugosan) ancestory of the stylophyllid evolutionary lineage.

Key words: Scleractinia, Stylophyllina, ontogeny, microstructure, Jurassic, Sinemurian, Sicily.

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Introduction

Stylophyllids are a distinct group of Mesozoic scleractinians with septa composed of spines (or lobes) that are covered with sclerenchymal deposits later in ontogeny. Stylophyllids, formerly classified in suborder Faviina (see Wells 1956) together with the monotypic Gigantostyliidae Frech, 1890, are presently included in Stylophyllina Beauvais, 1982 based on microstructural observations (Cuif 1973; Beauvais 1982; Roniewicz 1989). Accordingly, stylophyllinan septa are considered non-trabecular whereas the five other traditional scleractinian suborders have trabecular septal structure. Moreover, as stated in the emended diagnosis of the suborder by Roniewicz (1989: 115), the whole (not only septal) stylophyllinan skeleton is „built of stereomal tissue, organized in bundles of fibres forming wall, radial elements and dissepiments; bundles of fibres are subcylindric or scale-like in shape" (see also Cuif 1973). These distinctive features of stylophyllinans provide support for the hypothesis of their origin independent from other lineages of early Mesozoic scleractinians (Roniewicz and Morycowa 1993).

Intriguingly, overall morphology of some stylophyllinans resembles some Paleozoic rugosans (Frech 1890 was also impressed by architecture of stylophyllids and originally classified them among rugosans). For example, simple, dissepimental calices with spiniform septa of the Triassic *Stylophyllum* (e.g., *Stylophyllum paradoxum* Frech, 1890) are similar to the Permian endamplexid *Spineria* Schouppé and Stacul, 1959 (compare respectively: Roniewicz 1989: pls. 36–38 and Schouppé and Stacul 1959: pl. 13: 60–65). Though stylophyllinan-endamplexid similarity may be another example of pervasive convergence among corals, no data on early skeletal ontogeny or septal insertion pattern (see Oliver 1980) have been published that would falsify the hypothesis of their evolutionary relationships. The only illustrations of earliest growth stages of Triassic stylophyllids are given by Cuif (1973: figs. 5, 8, 15) and show juvenile or early astogenetic stages. Insertion pattern of the protosepta (in initial coralla), however, remains unknown (noteworthy, the earliest ontogenetic stages have also not been documented in *Spineria*, thus it is not clear how "orthodox" in terms of protoseptal insertion pattern that rugosan genus is).

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This paper documents poorly known details of the skeletal development of the Lower Jurassic stylophyllids based on Sinemurian specimens from Sicily (for preliminary report see Stolarski and Russo 2002). The focus is on microstructures and those aspects of the skeleton that may contribute to the debate on stylophyllinan origin and evolution. Sicilian corals, though diagenetically altered, suggest that original microstructural organization of their skeleton was much more diverse than traditionally proposed for that group. This suggestion is further supported by re-examination of some Triassic stylophyllids from Northern Calcareous Alps with preserved aragonitic coralla.

Materials and methods

Collection of Jurassic solitary stylophyllids from Sicily described herein consists of about 80 specimens of discoidal *Haimeicyclus haimei* (Chapuis and Dewalque, 1853), 11 cylindrico-trochoid *Stylophyllopsis* sp. A, and one trochoid *Stylophyllopsis* sp. cf. *S. rugosa* (Duncan and Wright, 1867). Study of the Jurassic corals has been complemented by comparison with Triassic stylophyllids from Northern Calcareous Alps (Austria), and Recent anthemiphylliids from the French expeditions to the Indo-Pacific (MD08 and VOLSMAR cruises), which are currently under study by Helmut Zibrowius (Marseille). A selection of Early Jurassic corals were examined with the Philips XL20 scanning electron microscope (SEM), cut and used for preparation of thin and polished sections. Microstructural data were acquired from Jurassic and comparative Recent coral skeletons using light etching (0.1% acetic acid; etching time 60 seconds) of the polished surfaces. The elemental composition of some diagenetic alterations of the skeleton was analysed with a EDAX dual-window (UTW/Open) ECON detector integrated with an SEM microscope. Septal fragments of three stylophyllid species (*Haimeicyclus haimei* (Chapuis and Dewalque, 1853), specimen IPUM-Sic.3; *Stylophyllopsis* sp. cf. *S. rugosa* (Duncan and Wright, 1867), specimen IPUM-Sic.5; *Stylophyllopsis* sp. A specimen IPUM-Sic.12) were analyzed for the presence calcite vs. aragonite using X-ray diffraction analysis (XRD).

Institutional abbreviations.—Specimens are housed in the following institutions: Geologische Bundesanstalt, Wien (GBA), Institute of Paleontology, University of Modena, Italy (IPUM), and Institute of Paleobiology, Polish Academy of Sciences, Warsaw (ZPAL).

Other abbreviations.—CD, calicular diameter; GCD, greater calicular diameter; H, height of corallum; LCD, lesser calicular diameter; S, number of septa; Sx, septa of a cycle designated by numerical script.

Geological setting

In the Early Jurassic, carbonate sedimentation prevailed on shelves of the northwest edge of the Tethys. A muddy-bottom
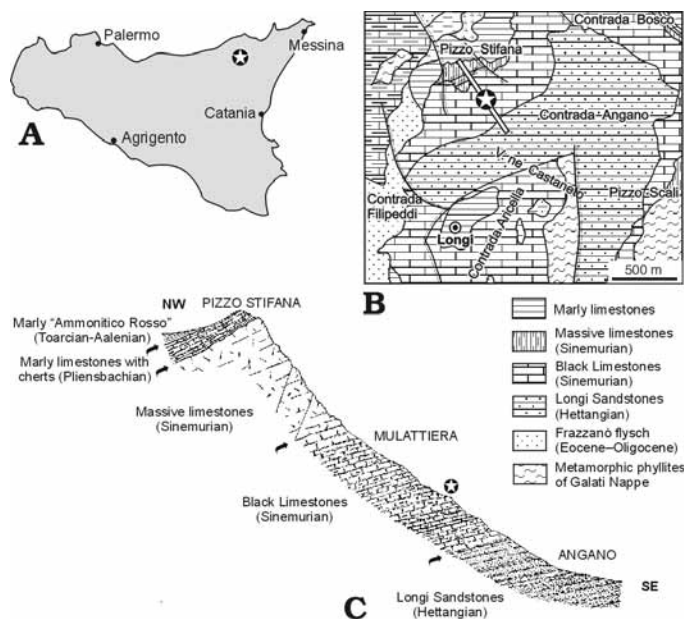

Fig. 1. **A**. Schematic map of Sicily (Italy) showing geographic position of outcrops with Early Jurassic scleractinians (asterisk). **B**. Part of geological map of area near Longi village showing position of Sinemurian Black Limestones (asterisk on white bar that indicates geological section showed on C). **C**. Geological section showing strata sampled for corals (asterisk). B, C after Lentini 1973.

coral fauna is known from the adjacent paleogeographical regions, e.g., from Belgium (Joly 1936), Luxembourg (Chapuis and Dewalque 1853); France (Dumortier 1864; Lejeune 1935; see also Elmi 1990); Great Britain (Duncan 1967, 1868; Straw 1925; see also Beauvais 1976); and North Italy (Airaghi 1907). Early Jurassic carbonate deposits yielding corals described herein occur in northeast Sicily. They are a part of the Longi Nappe sedimentary sequence which consists of a series of marine deposits dated from Lower Jurassic to Eocene (Fig. 1; see also Ogniben 1960). Several sedimentary units have been recognized from the Longi Nappe sequence (see Maugeri 1932; Lentini 1973). The corals have been collected from the marine Sinemurian Black Limestones overlying the Hettangian transgressive, coastal-deltaic Longi Sandstones. The sequence of the Black Limestones consists of three main units (bottom-up order): (1) bedded crinoidal limestones (ca. 75 m thick), rich in ostracods, arenaceous foraminiferans and algae *Thaumatoporella*; (2) marly limestones (ca. 100 m thick), black or blue, including rare lenses of cherts rich in serpulids and solitary corals in the lower part and brachiopods, bivalves and echinoderms in the upper part; (3) alternating grey marls and marly limestones (ca. 60 m thick), including bivalves and rarely brachiopods and solitary corals. Corals come from the second unit (marly limestones) exposed at some distance from the nearest village of Longi, which is hereafter used in the text as a locality name. The Sinemurian age of Black Limestones is supported by occurrence of the ammonites *Arnioceras speciosum* and *Epophioceras carinatum*, which indicate an interval between the *Coroniceras bucklandi* and the *Arietites obtusum* zones.

Systematic paleontology

Suborder Stylophyllina Beauvais, 1982
Family Stylophyllidae Frech, 1890

Frech (1890) distinguished three Triassic genera within the Stylophyllidae: *Stylophyllum*, *Stylophyllopsis* and *Meandrostylis* (as a subgenus of *Stylophyllum*). Roniewicz (1989), in a comprehensive revision of stylophyllid taxa, listed the following Triassic and Jurassic stylophyllid genera (stratigraphic ranges in brackets): *Stylophyllum* Reuss, 1854 (Norian–Rhetian); *Stylophyllopsis* Frech, 1890 (Anisian–Pliensbachian); *Meandrostylis* Frech, 1890 (Rhetian); *Coccophyllum* Reuss, 1864 (Norian–Rhetian); *Pinacophyllum* Frech, 1890 (Norian–Rhetian); *Anthostylis* Roniewicz, 1989 (Rhetian); ?*Oppelismilia* Duncan, 1867 (Hettangian–Sinnemurian); ?*Leptophyllia* Duncan, 1868 (Hettangian–Sinemurian); and *Heterastraea* Tomes, 1888 (Hettangian–Sinnemurian). Roniewicz and Morycowa (1989) also listed among stylophyllids *Discocoenia* Tomes, 1884 (Hettangian), *Discocoeniopsis* Beauvais, 1976 (Hettangian–Sinemurian) and *Phacelepismilia* Beauvais, 1976 (Hettangian–Sinemurian), and possibly three following Sinemurian–Plinsbachian taxa described by Turnsek et al. (1975): "*Pinacophyllum*", "*Isastraea*", and "*Paraphyllogyra*". Generic taxonomic criteria include mode of growth, colony type, type of septal ornamentation, wall structure, and type of columella.

Many taxa that are currently classified among stylophyllids, originally were assigned in the "catch-all" genus *Montlivaltia* Lamouroux, 1821. Also Chapuis and Dewalque (1853) included in this genus solitary, discoidal *M. haimei*, a species recognized herein among coral collection from Longi. Alloiteau (1957: 105), aware of the confused status of *Montlivaltia*, designated *M. haimei* a type species of *Haimeicyclus*. Eight specimens of *M. haimei* from Villers-sur-Semoy (Belgium) examined by Alloiteau (1957) have been described as lacking endotheca and synapticulae. Photographs of two of these specimens housed at Museum National d'Histoire Naturelle, Paris (out of three specimens and one thin transverse section) kindly provided to me by Dr. Bernard Lathuiliere (Nancy), demonstrate the accuracy of Alloiteau's description. On the contrary, apparently the same coralla used by Beauvais (1986) to propose erroneously *Haimeicyclus* as a new generic name for *M. haimei* have been characterized as possessing endotheca composed of thin dissepiments, sparse synapticulae, and septa with short menianae, features not recognized in Alloiteau's description. Clearly, from these two different descriptions of apparently the same coral samples, only Alloiteau's (1957) correspond to the original Chapuis and Dewalque's (1853) description of *M. haimei*. Though taxa with discoidal coralla already have been included to stylophyllids (i.e., *Discocoenia* Tomes, 1884 and *Discocoeniopsis* Beauvais, 1976), *Haimeicyclus* seems to be a valid genus. Type species of *Discocoenia* (*D. bononiensis* Tomes, 1884), *D. ruperti* Duncan, 1867, and *D. radiata* Duncan, 1867 were included in the genus by Beauvais (1976), and have only a slightly crenulated distal septal margin. Though, dense granulations on septal faces (Beauvais 1970: fig. 1; Beauvais 1976: figs. 31, 32) are shared with stylophyllids, however, lack of septal spines make a stylophyllid affiliation of the genus questionable. On the other hand, type species of *Discocoeniopsis*, *D. nummiformis* (Duncan, 1867) from the Sinemurian of England, has stylophyllid-like spines on septal distal margin (Beauvais 1976: 51). However, prominent costosepta and epitheca extending only partially on the flat corallum basis, point toward a relationship with the skeletal elements in the thecocyathid genus *Discocyathus* Milne Edwards and Haime, 1848 than those in stylophyllids (see e.g., Roniewicz and Stolarski 1999: fig. 12B, C). Clearly, *D. nummiformis*, which lacks pali and a lamellar columella, is not congeneric with *Discocyathus*, though differences in development of skeletal elements make its position very distinct among stylophyllids.

Genus *Haimeicyclus* Alloiteau, 1957

Type species: *Montlivaltia haimei* Chapuis and Dewalque, 1853, by original designation.

Species assigned: *Haimeicyclus haimei* Chapuis and Dewalque, 1853; *H. guettardi* de Blainville, 1830; *H. papillatus* Duncan, 1867; *H. hibernicus* Duncan, 1867.

Diagnosis (emended).—Solitary, discoidal to slightly cylindrical stylophyllid. Septal spines embedded in stereome and form compact septa. Epitheca developed on the entire corallum basis.

Haimeicyclus haimei (Chapuis and Dewalque, 1853)
Figs. 2–5.

Montlivaltia haimei sp. nov.; Chapuis and Dewalque 1853: 263–264, pl. 38: 5.
Montlivaltia haimei Chapuis and Dewalque; Duncan 1867: 35, pl. 10: 24–32.
Montlivaltia haimei Chapuis and Dewalque; Quenstedt 1881: 576, pl. 164: 32.
Montlivaltia haimei Chapuis and Dewalque; Lejeune 1935: pl. 1: 3, 9, 17, pl. 2: 4,
Montlivaltia haimei Chapuis and Dewalque; Joly 1936: 166, pl. 3: 1–7.
Montlivaltia haimei var. *alta* Chapuis and Dewalque; Joly 1936: 166–167, pl. 3: 8–10.
Haimeicyclus haimei Chapuis and Dewalque; Alloiteau 1957: 105.
Montlivaltia haimei Chapuis and Dewalque; Beauvais 1976: 72, pl. 16: 5.
?*Haimeicyclus haimei* Chapuis and Dewalque; Beauvais 1986: 54.

Material.—81 specimens representing various ontogenetic stages, ranging from early juveniles ca. 0.5 mm in diameter having twelve septa to adults ca. 30 mm in diameter with six incomplete septal cycles (IPUM-Sic.3, 14–93); see Fig. 3.

Description.—Corallum discoidal, circular, free in adult stage. Proximal side of adult coralla may bear no traces of substrate but often various bivalve shell fragments or flat, often washed away substrate can be observed (Fig. 2E$_2$). Juveniles can also be attached to the adult coralla (Fig. 4B$_1$, B$_2$, D$_2$–D$_4$). Initial portions of adult coralla, exposed by light etching (Fig. 4C) and initial or early juvenile specimens attached to adult coralla (Fig. 4B$_1$, B$_2$) are twelve-septate and
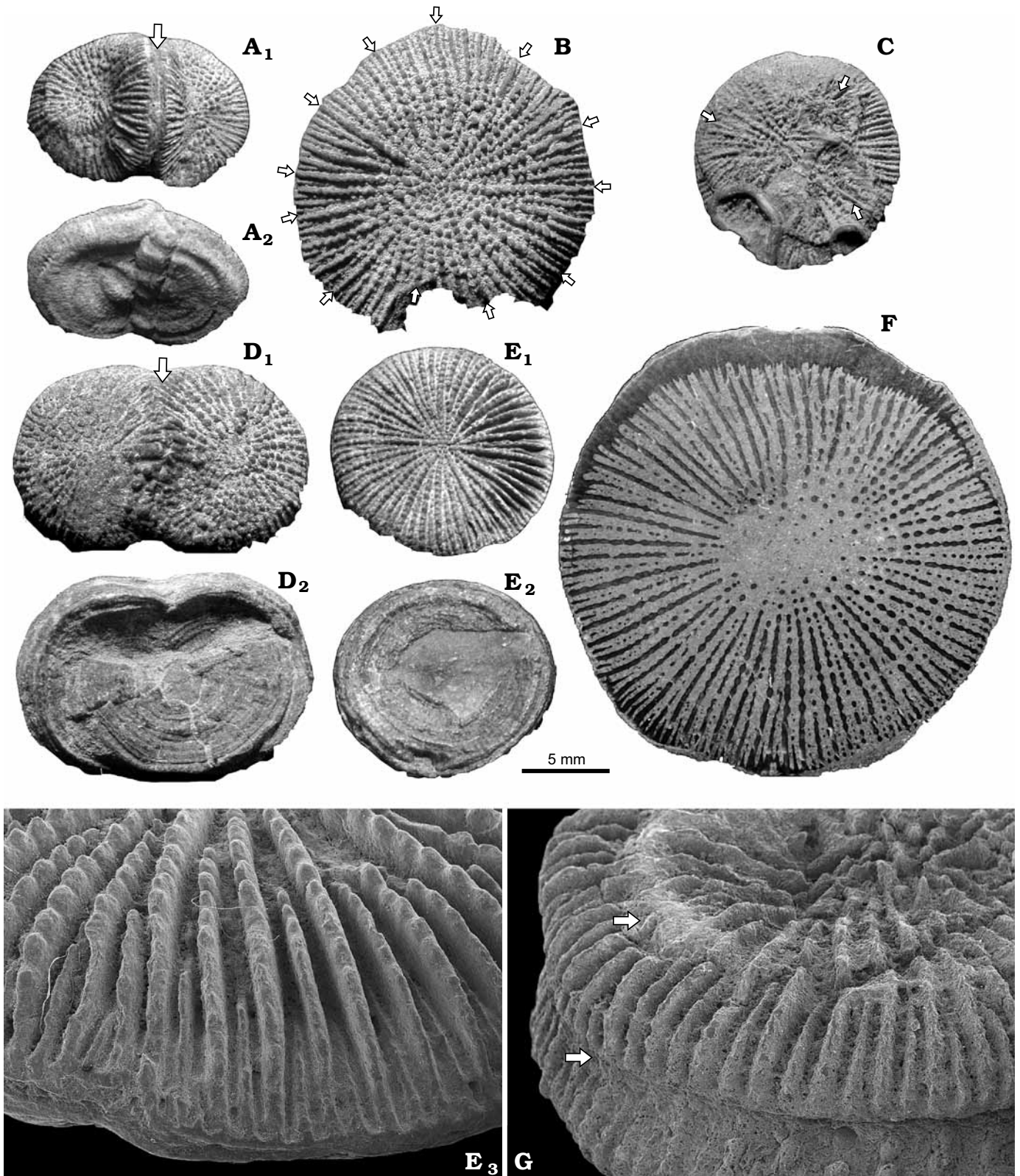
Fig. 2. *Haimeicyclus haimei* (Chapuis and Dewalque, 1853). **A**. IPUM-Sic.92a, b with two calices in distal (A_1) and proximal-lateral (A_2) views. Calices are separated by epithecal walls (arrow in A_1) and resulted from growth of two juveniles attached to common substrate. **B**. Distal view of IPUM-Sic.82. Twelve S1–2 arrowed. **C**. Distal view of IPUM-Sic.40 with uppermost part of calice disintegrated into 3 (arrows) independent calicular regions ("rejuvenescence"), and overgrown by serpulid tubes (lower part of picture). **D**. IPUM-Sic.80 with two calices (D_1, distal view) resulted from regeneration of parental calice (D_2, basal view). In contrast to IPUM-Sic.92a, b (A_1, A_2), higher cycle septa in contact zone between calices of IPUM-Sic.80 are common for both calices. **E**. IPUM-Sic.89 in distal (E_1), and proximal views (E_2, note rhomboidal shape of imprinted substatum); E_3, enlargement of corallum edge. **F**. The largest specimen IPUM-Sic.75. **G**. Corallum IPUM-Sic.45 with two distinct "rejuvenescence" constrictions (arrows). All from Sinemurian Black Limestones, Longi, Sicily.
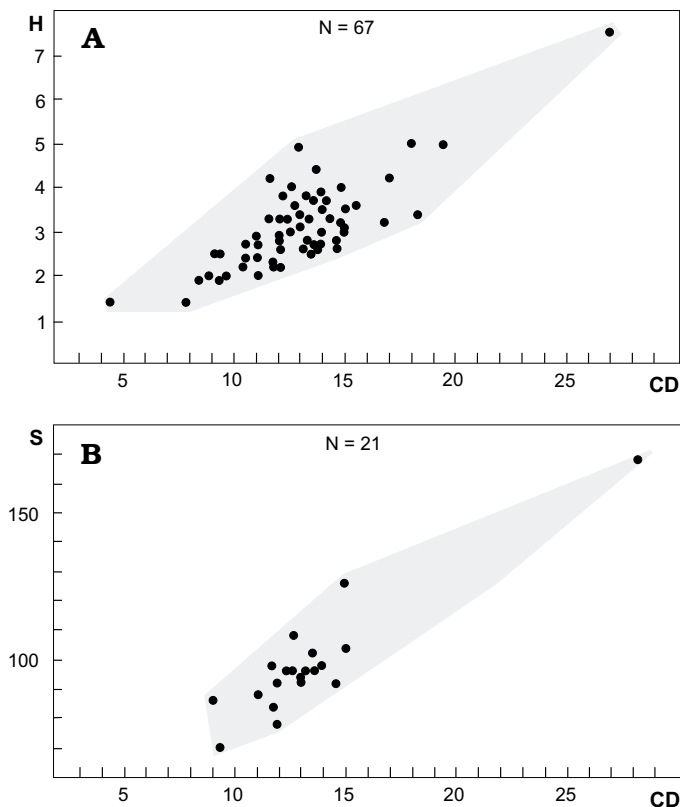
Fig. 3. *Haimeicyclus haimei* (Chapuis and Dewalque, 1853). **A**. Bivariate biometric plot of calicular diameter (CD) *versus* corallum height (H). **B**. Bivariate biometric plot of calicular diameter (CD) *versus* septal number (S).

have a similar diameter. Juvenile coralla attached to the same small-sized substratum may adhere to themselves (Fig. 2A$_1$, A$_2$). Such double calices possess independent epithecate walls in their contact zone (arrow in Fig. 2A$_1$). Seemingly similar coralla with two calices may develop from a single but regenerated calice (Fig. 2D$_1$, D$_2$). In contrast to the "adhering" specimens, two "regenerated" calices share some skeletal elements, e.g., septa of higher cycles (arrow in Fig. 2D$_4$) and do not develop an epithecate wall in the contact zone between calices. Calices disintegrated into several, not clearly defined zones (Fig. 2C), showing asymmetrical constriction (Fig. 5A, B), or constricted repeatedly two or more times (Fig. 2G) have also been observed.

In adults, septa hexamerally arranged in 6 incomplete cycles according to the formula S1–2≥S3>S4>S5>S6. Septa S1–3 reach calicular center; S4 extend to ca. 3/4 of the calicular radius; S5 to the half of the calicular radius, and S6 are developed only at calice periphery. All septa consist of spines that lower in fossa are covered with sclerenchyme and form a compact septum. In lower cycle septa (S1–3), individual spines are recognizable only on their distal edge whereas septa of higher cycles, especially of ultimate or penultimate cycles, composed of spines individualized in distal and proximal parts of calice (Fig. 5B, C). Surface of spines covered with dense granulations ca. 40–50 μm in diameter. Lower in calice, septal faces covered with thicker layers of sclerenchyme and

become smoother, except for places with septal spines still projecting through sclerenchymal deposits. Skeleton completely recrystallized, calcitic (confirmed by X-ray diffraction). Epithecate wall spread on entire proximal side and in larger specimens slightly more cylindrical, bending upwards.

Remarks.— In most Scleractinia the length of the septa correlates with the order of their appearance. Septa of the first cycle, inserted at the beginning of the coral skeletogenesis are usually much longer and thicker in comparison to the septa of higher cycles inserted later in ontogeny (however, one of the exceptions is *Schizocyathus fissilis* Pourtalès, 1874 with S2<S3 in adult coralla. S2 in *S. fissilis* degenerate during corallum growth, most likely because of functional involvement in corallum longitudinal division; see Stolarski 2000). On the other hand, in *Zardinophyllum zardinii* Montanaro-Gallitelli, 1975 (representative of pachythecaliines—supposed rugosan descendants), the first 6 initial septa are not inserted simultaneously and this is reflected in their unequal length and thickness (Stolarski 1996, 1999). Because the first twelve septa of initial and early juvenile coralla of *H. haimei* (Fig. 4B$_1$, B$_2$, C) have similar length and thickness, one may infer that they were inserted simultaneously and thus the early ontogeny follows a cyclic pattern recognized in typical scleractinians.

Juvenile coralla (but also serpulid tubes) are occasionally found attached to both sides of adult coralla (e.g., Fig. 4D$_1$, D$_2$). Such coralla do not show any defensive reaction against incrustation (e.g., constrictions of the corallum diameter as in Fig. 2C) and it is clear that juveniles could not grow on the proximal side of adult coralla without inverting position of the latter. Thus, most likely, adult coralla were incrusted while dead, and incrustations on both sides were possible because of occasional rolling on such skeletons. On the other hand, the situation when juveniles are attached only to the substrate that also serves adults (Fig. 4B$_4$) suggests that only the substrate was rolled and not the adult corallum. Judging by the transitional spectrum of morphologies of incrusting initials and juveniles, and by comparisons with initial and juvenile portions of adult coralla, all juveniles incrusting adult coralla belong to the same species. Attachment of juveniles to the adult coralla of the same species were observed in extant (Gerodette 1981; Fadlallah and Pearse 1982) and fossil corals (Stolarski 1995). In modern seas, corals that produce such settling larvae are brooders releasing large, benthic crawling planulae. Initial coralla that develop after metamorphosis of such large, benthic planulae often exceed 2 mm in diameter (see Squires 1962; Gerodette 1981; Fadlallah and Pearse 1982). The occurrence of numerous juveniles attached to adults in *H. haimei* may suggest similar benthic behavior, however, much smaller size (ca. 1 mm in diameter) favors a scenario in which local hydrological conditions forces part of the coral "spat" to settle on available hard substrates, i.e., the adult coralla.

The skeleton of *H. haimei* is competely recrystallized (calcitic), however, dense and homogenous granulation on septal spines conform to a "coarse" texture observed on septa
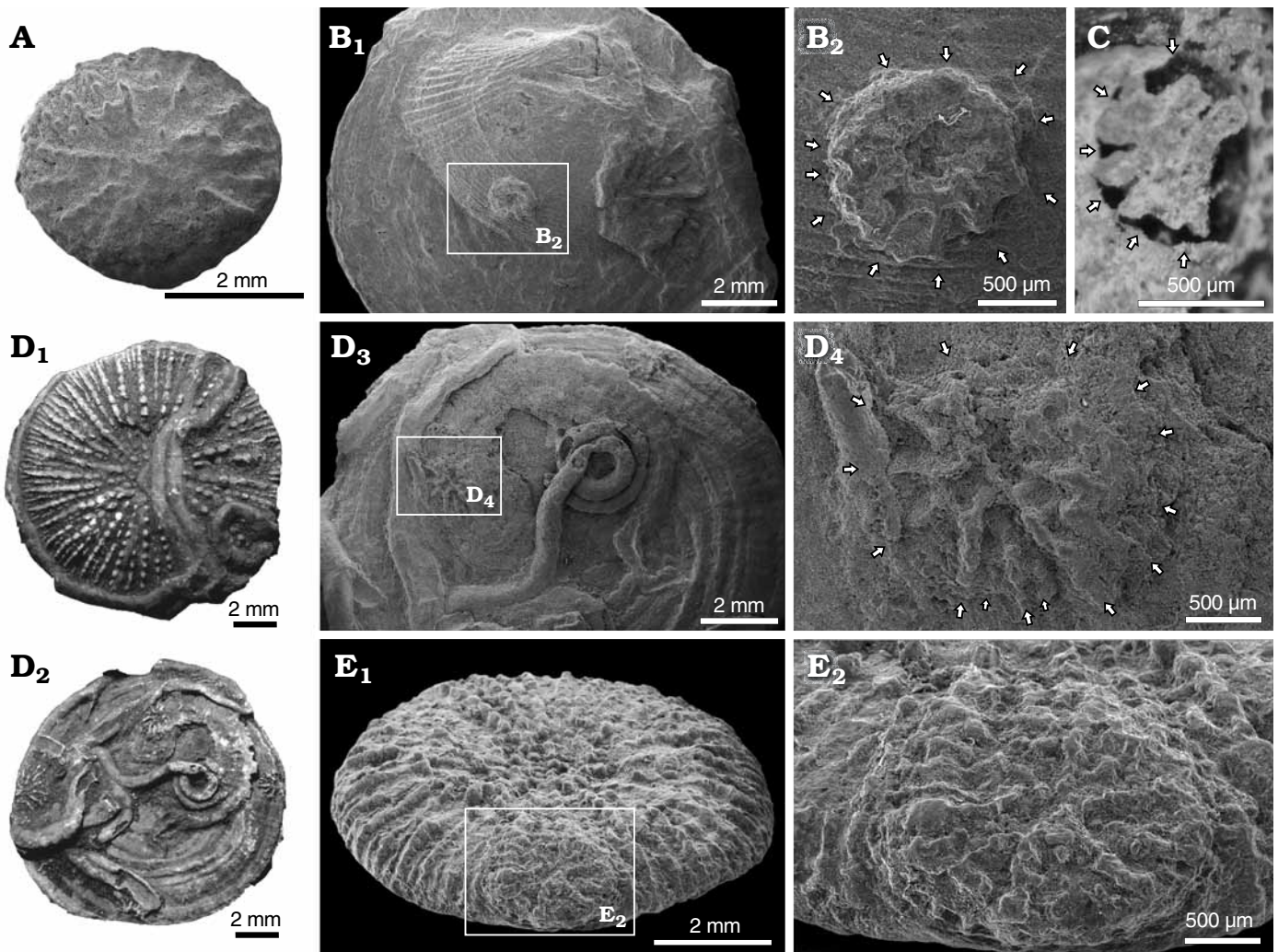
Fig. 4. *Haimeicyclus haimei* (Chapuis and Dewalque, 1853). **A**. Juvenile specimen IPUM-Sic.93 with 48 septa on polished base (herein in distal view). **B**. Proximal view of IPUM-Sic.94 attached to the bivalve shell incrusted by juvenile specimen IPUM-Sic.94a with 12 septa (arrows). **C**. Etched, initial portion of the corallum IPUM-Sic.68 with voids corresponding to position of protosepta (arrows mark position of six septa on half of corallum). **D**. IPUM-Sic.88 incrusted by serpulid tubes and juvenile scleractinians, in distal (D_1) and proximal (D_2) views in conventional photographs, and on SEM micrographs (proximal views D_3, D_4) showing enlargement of twelve septate juvenile (two septa of additional cycle marked with smaller arrows). **E**. IPUM-Sic.9191 in oblique view (E_1) with juvenile (?bud) attached laterally (E_2, enlargement). All from Sinemurian Black Limestones, Longi, Sicily.

of the below described *Stylophyllopsis* cf. *rugosa* and thus implies similar microstructure (see Discussion).

Occurrence.—Sinemurian of Sicily, Early Jurassic (Hettangian–Sinemurian) of Belgium, Germany, Luxembourg, England.

Genus *Stylophyllopsis* Frech, 1890

Diagnosis (emended).—Solitary or phaceloid stylophyllid with cylindrical or trochoid coralla. Septal spines embedded in stereome and form compact septa; spines on septal axial edge dissociated.

Remarks.—Frech (1890) suggested that many species of *Montlivaltia* and *Thecosmilia* from the English Lias (= Early Jurassic) should be included in the genus *Stylophyllopsis* based on septal structure, and other less important features (see also Straw 1925). Roniewicz (1989: 123) included in *Stylophyllopsis* the following Early Jurassic species: *S. brevis*

(Duncan, 1867); *S. mucronata* (Duncan, 1867); *S. murchisoni* (Duncan, 1867); *S. patula* (Duncan, 1867); *S. rugosa* (Duncan and Wright, 1867); *S. victoriae* (Duncan, 1867); *S. walliae* (Duncan, 1867); *S. elchabirensis* Beauvais, 1986; *Stylophyllopsis* in Turnsek et al. 1975. Actually, the number of Early Jurassic species may be higher, as one may guess morphologies of various *Montlivaltia* from yet unrevised Early Jurassic coral collections (e.g., Airaghi 1907; Dulai 1995).

Stylophyllopsis sp. cf. *S. rugosa* (Duncan and Wright, 1867)

Figs. 7, 8.

Material.—1 specimen (IPUM-Sic.5).

Description.—Corallum trochoid, GCD = 17 mm, LCD = 15 mm, H = 20 mm (juvenile corallum portion is not preserved); corallum surface worn (Fig. 7D), only occasionally
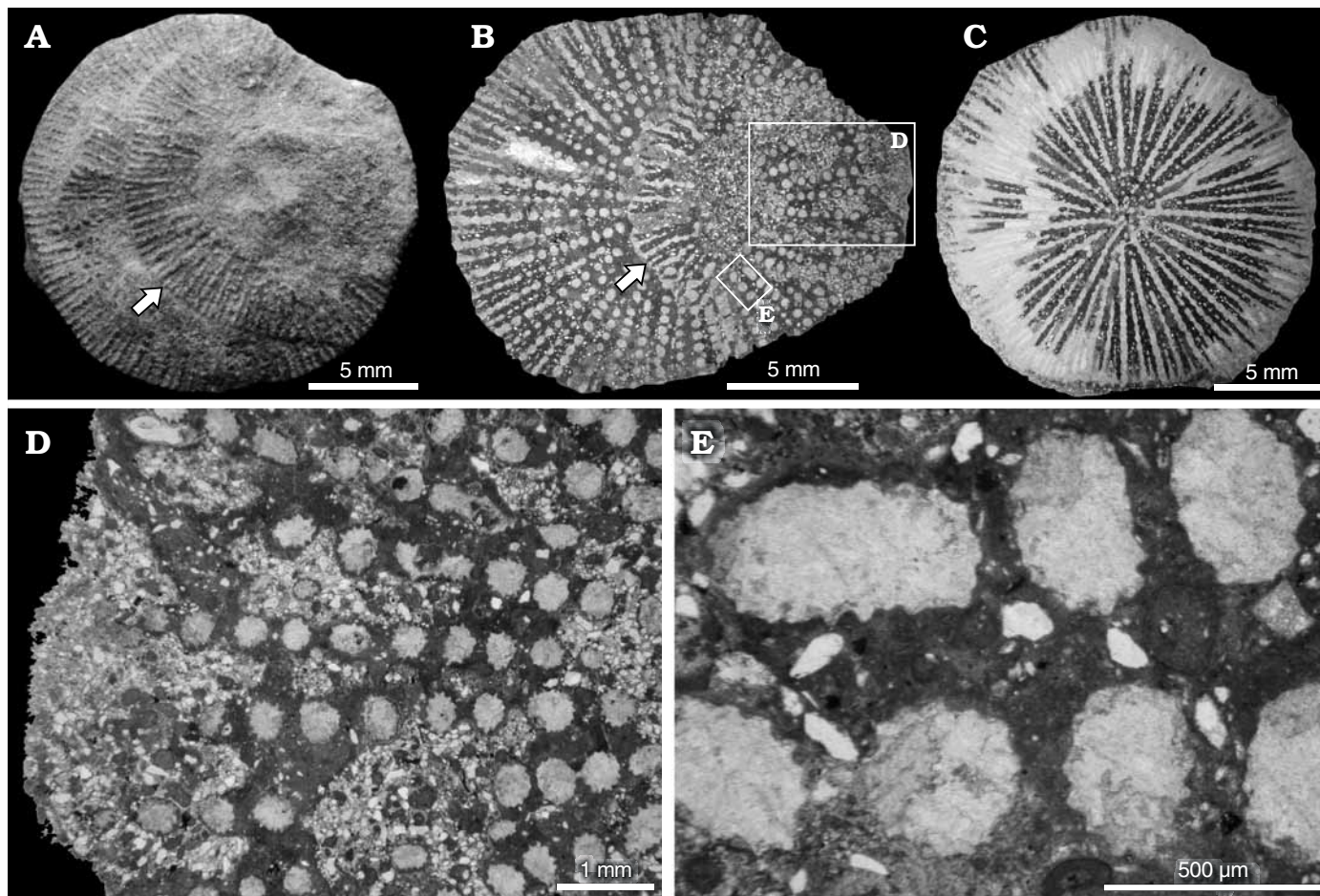
Fig. 5. *Haimeicyclus haimei* (Chapuis and Dewalque, 1853), IPUM-Sic.3. **A**. Distal view with narrowed, "rejuvenated", calice (arrows on **A** and **B**). **B**. Transverse sections of distal part of calice. **C**. Proximal part of the calice. **D**, **E**. Enlargements of section B). Note "shaggy" surface of transversely sectioned spines (**D**, **E**) and spines of first septal cycles embedded in stereome in lower part of corallum (**C**). Specimen from Sinemurian Black Limestones, Longi, Sicily.

some remnants of the epithecal wall are preserved. Septa hexamerally arranged in five full cycles and some rudimentary S6 according to the formula S1–2>S3>S4>S5>S6 (see also changes in septal number in corallum ontogeny in Fig. 6). All septa consist of spines that lower in fossa are embedded in sclerenchyme (in available transverse sections of calice, septal spines of S1–2 are already covered with sclerenchymal deposits). S1–2 reach the calicular center, S3 extend nearly to the center, S4 to ca. 3/4 of the calicular radius, whereas S5 may reach half of the calicular radius but often are developed as isolated spines protruding from the wall, similarly as rudimentary S6. Sharp and dense granulations occur on septal spines (Fig. 7B, E) which, if not completely covered with sclerenchyme, may partly protrude from the septum giving its surface a spiny appearance. Axial septal edges, particularly of higher septal cycles, are dissociated into septal spines (Fig. 7A, B). Endotheca composed of oblique and arched dissepiments.

Though the skeleton is diagenetically altered (it has entirely calcitic mineralogy as proven by X-ray diffraction), transverse sections of spines show a distinct, star-shape pattern in organization of internal rod-shape structures. In optical microscope, rod-shape structures are dark-grey and form the core of granulations on septal spines surface. EDS mapping does not indicate enrichment of "dark rods" by Mn, Fe
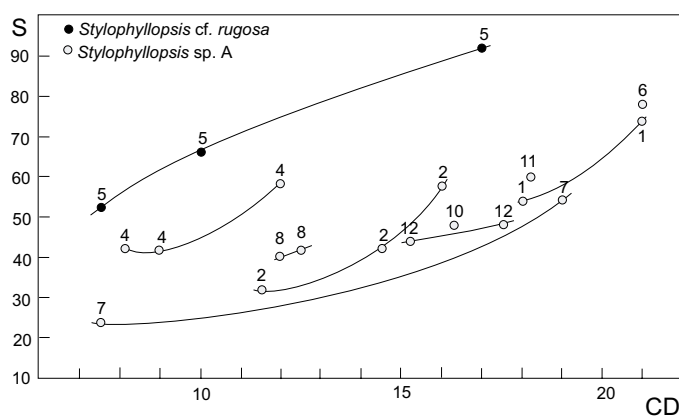

Fig. 6. Bivariate biometric plot of calicular diameter (CD) *versus* number of septa (S) for *Stylophyllopsis* sp. cf. *S. rugosa* (Duncan and Wright, 1867), and *Stylophyllopsis* sp. A. Note different shapes of ontogenetic trajectories of both species.
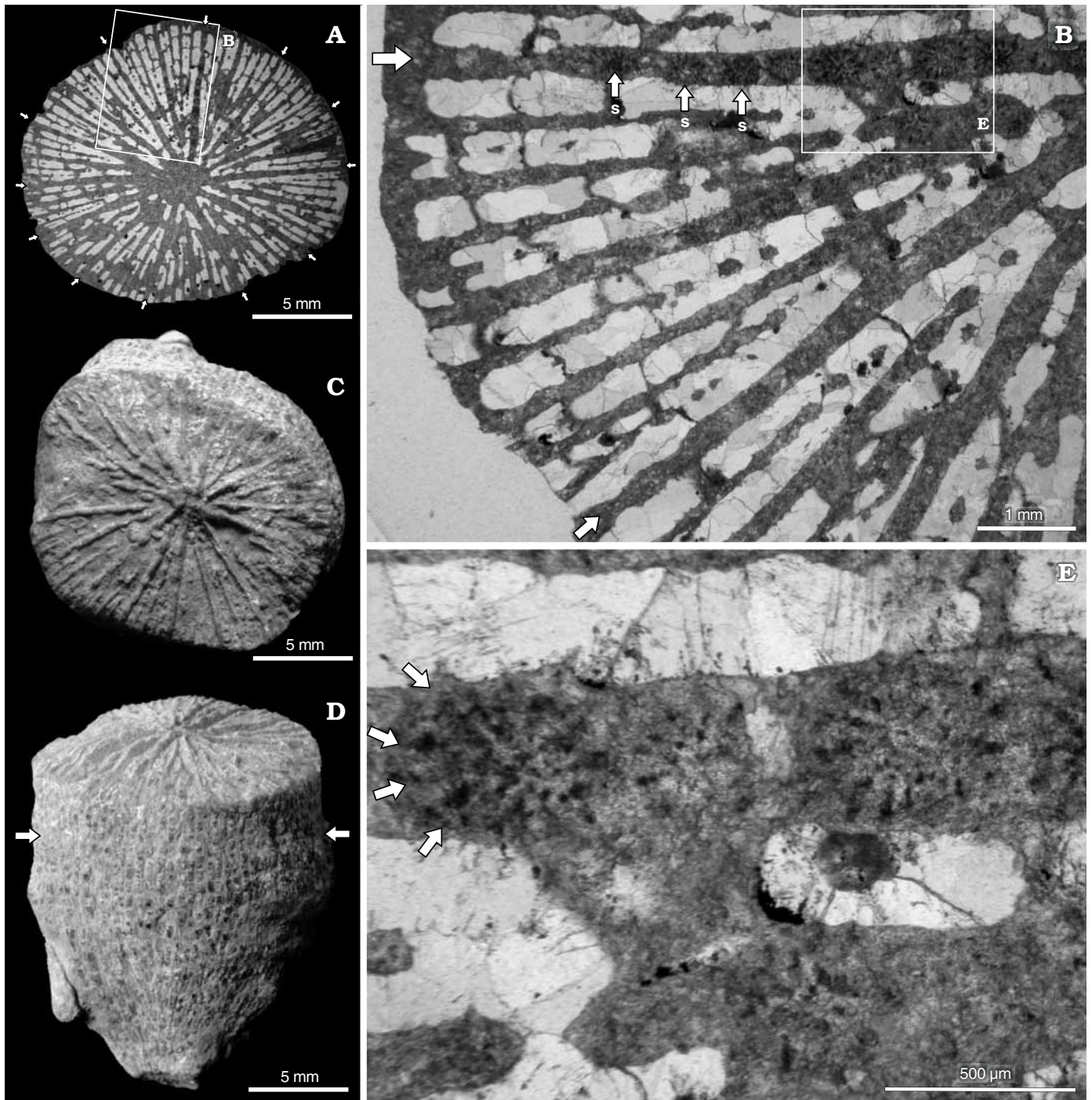
Fig. 7. *Stylophyllopsis* sp. cf. *S. rugosa* (Duncan and Wright, 1867), IPUM-Sic.5 with abraded surface (epitheca not preserved). **A**. Transverse section (enlarged part on B, E) **C**, **D**. Distal (**C**) and lateral (**D**) views of corallum (arrows mark sectioned region). **B**, **E**. Transverse section. Note septal spines (s) with radiating darker structures (arrows on **E**). Specimen from Sinemurian Black Limestones, Longi, Sicily.

or Si, elements typical of diagenetic minerals. On the other hand, SEM observations of lightly etched polished sections of septa, show differences in relief between areas of "dark rods" (as seen in optical microscope) and adjacent parts of septal spines (Fig. 8A–D). Neomorphic crystals in regions of "dark rods" show very distinct, fine-porous pattern of etching (pockmarked surface), in contrast to much less porous texture of etched crystals outside the "dark rods" zone.

Remarks.—*Stylophyllopsis rugosa* Duncan and Wright, 1867 was originally described from the Late Sinemurian (*Echinoceras raricostatum* Zone) of Honeybourne (England). The Sicilian specimen described herein differs from the lectotype (illustrated by Duncan 1867: pl. 15: 16, and by Beauvais 1976: pl. 11: 6) in having a shorter corallum and a higher number of septa at a given calicular diameter, i.e., 80 septa at 25 mm diameter *versus* ca. 92 septa at 17 mm diameter (see also Fig. 6).
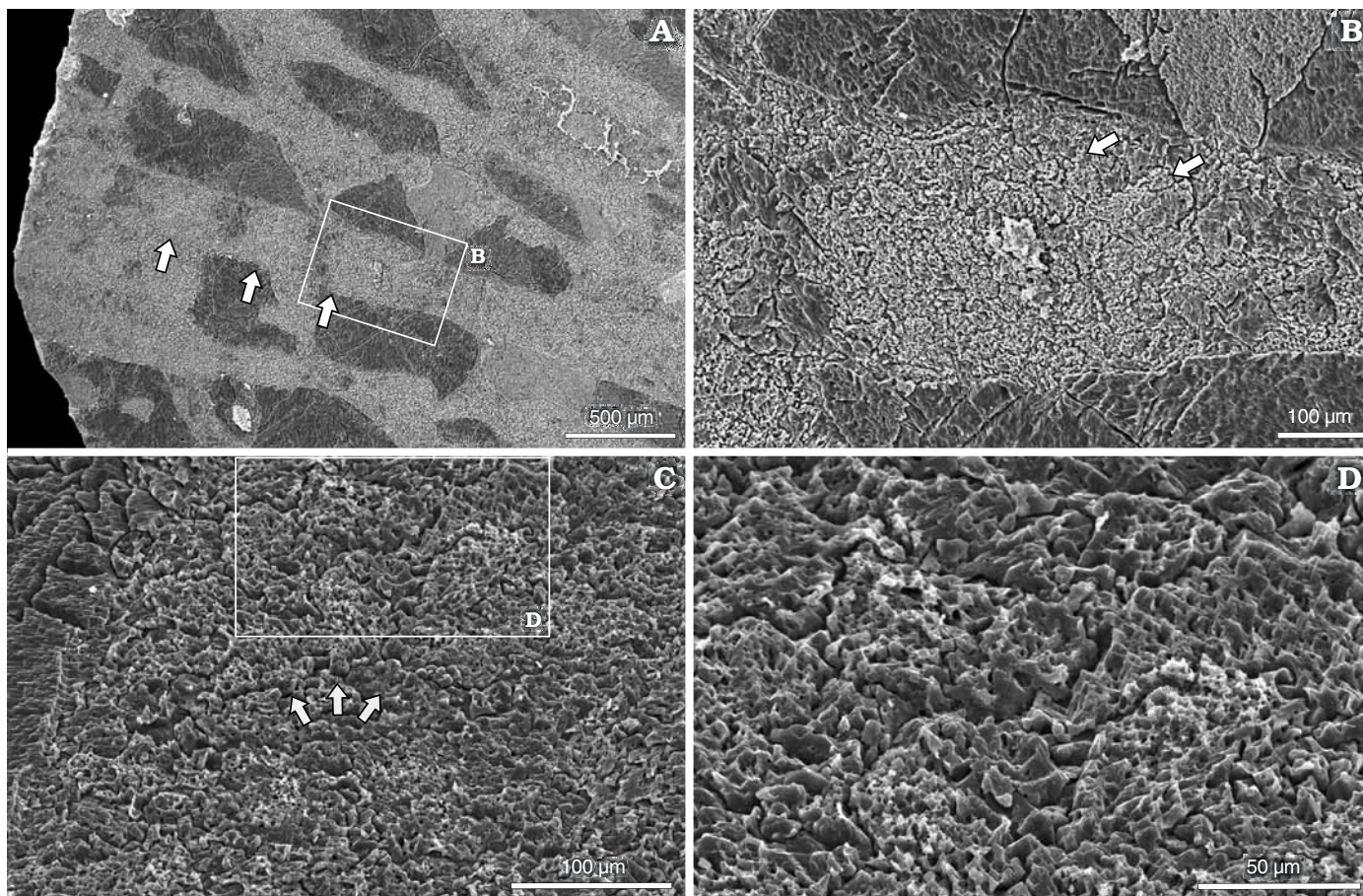
Fig. 8. *Stylophyllopsis* sp. cf. *S. rugosa* (Duncan and Wright, 1867), IPUM-Sic.5. SEM micrographs of transverse, polished and etched corallum surfaces. **A**. Corallum fragment with septal spines (arrows); rectangle indicate position of enlargement on B. **B–D**. Dark, radiating structures shown in Fig. 7E are composed of crystals with pockmarked surfaces (arrows in **B**, **C**). Specimen from Sinemurian Black Limestones, Longi, Sicily.

However, according to the Duncan's description (1867: 58), coralla of this species are quite variable (including forms with five full septal cycles and rudimentary septa of higher cycles) and the Sicilian specimen fits within this range of variability. Nevertheless, because of the worn surface of the Sicilian specimen, its specific attribution is given with caution.

The pockmarked surface of etched polished skeletal surfaces suggests occurrence of mineral or organic inclusion that undergo preferential etching. A similar etching pattern was observed in diagenetically altered coralla of the Cretaceous *Aulosmilia* (see Sorauf and Cuif 2001: fig. 5); in skeleton neomorphised to calcite, the mid-septal zone have abundant inclusions whereas septal flank areas are composed of massive calcite without inclusions (Sorauf and Cuif 2001: 161). The mid-septal zone corresponds to the position of calcification centers in skeletons of extant corals, whereas the flank areas to the zone have longer aragonite fibers. Calcification centers, which originated during the first phase of septal formation, are composed of minute aragonite crystals and are rich in organic components, whereas zones with fibers, originated during the next, successive phases of septal growth, contain a smaller amount of organic components. As stated by Sorauf and Cuif (2001: 161): "primary septal area

with greater content of organic matrix underwent diagenesis separately, and possibly earlier than the secondary skeleton, with diagenesis of primary septum preserving more inclusions". One may thus suggest that densely pockmarked crystals arranged in star-like patterns in septal spines of Sicilian *Stylophyllopsis* sp. cf. *S. rugosa* are remnants of calcification centers developed in axes of radially arranged ?trabeculae.

Occurrence.—Early Jurassic (Sinemurian), Sicily.

Stylophyllopsis sp. A.
Figs. 9, 10A, B.

Material.—11 specimens (IPUM-Sic.1, 2, 4, 6–13).

Description.— Corallum trochoid to subcylindrical, variable in shape and size up to 23 × 20 mm in calicular diameter and 45 mm in height; juvenile portions are not preserved (see Fig. 9). Septa hexamerally arranged in 4 full cycles, and some S5 in larger specimens; septal formula S1–2>S3>S4>S5. S1–2 extend nearly to calicular center and may be a part of loose axial structure (Fig. 9B). S3 extend to ca. 3/4 of the calicular radius, S4 may reach half of the calicular radius (then often occur short S5) but can be much shorter (then S5 are not developed). Septal spines may dissociate from the lower cycle septa
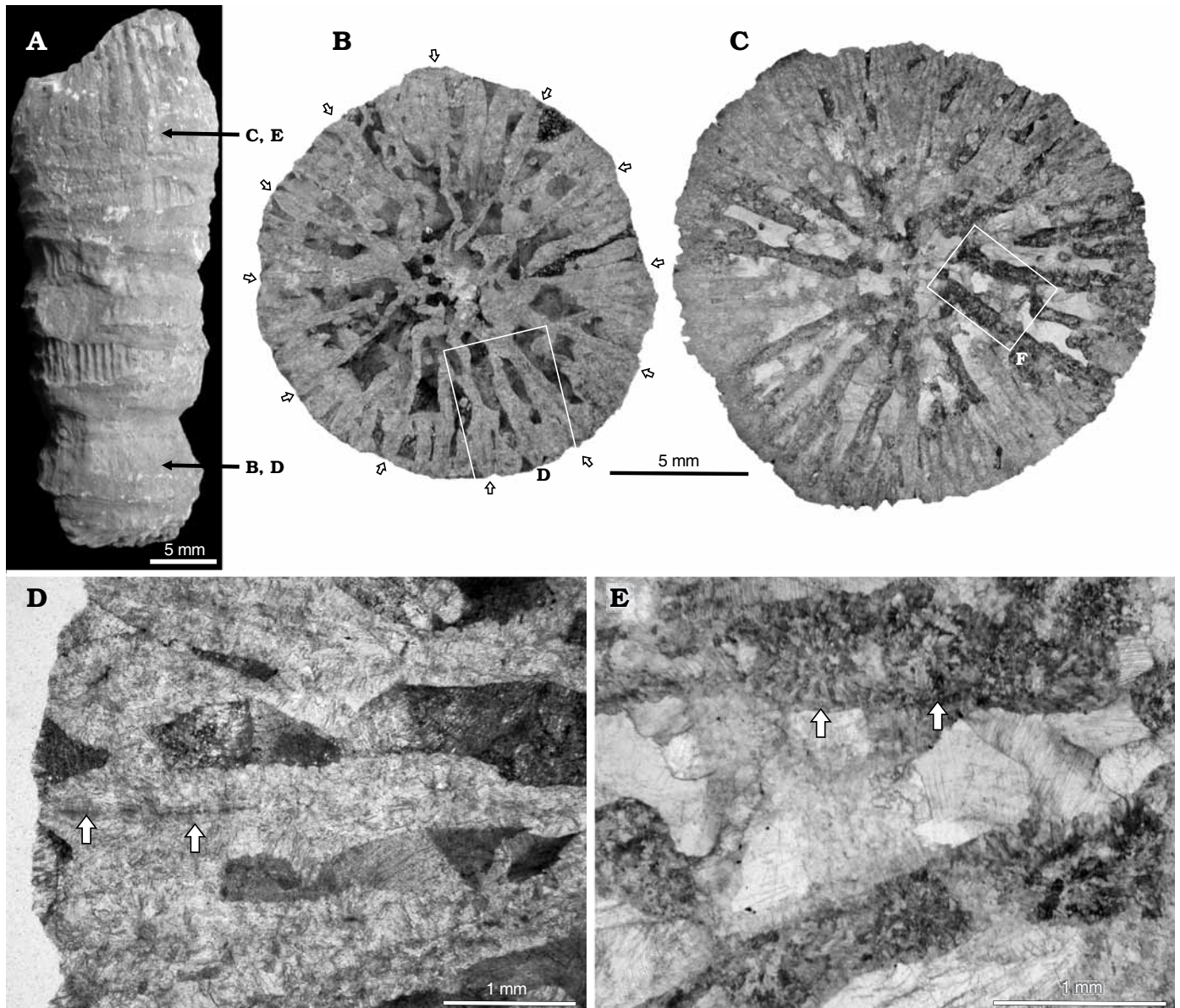
Fig. 9. *Stylophyllopsis* sp. A, IPUM-Sic.12. **A**. Lateral view showing position of B and C sections (arrows). **B**, **D**. Transverse thin section of proximal portions of corallum (arrows point to S_{1-2} on **B**). Enlarged fragment of septum (**D**) shows narrow "mid-septal" zone (arrow). **C**, **E**. Transverse thin sections of distal portion of corallum. Enlarged septal fragment (**E**) shows embedded septal spines (arrow). Specimen from Sinemurian Black Limestones, Longi, Sicily.

($S1$–3) in axial region, but in coralla with damaged uppermost parts, septal spines are distinguishable in sections by bulbous axial septal portions. Septal faces are smooth or, occasionally, covered with minute granulations. In transverse section, septa are spindle-shaped with a well-developed costal part that is covered with pellicular epitheca (e.g., Fig. $10A_1$, A_2). Endotheca consists of sparse, arched dissepiments.

The skeleton is diagenetically altered (entirely calcitic as proven by X-ray diffraction). As in *Stylophyllopsis* sp. cf. *S. rugosa*, darker and lighter coloration of some distinct structures can be distinguished. Often, in transverse sections of proximal portions of corallum, a distinct mid-septal zone is visible (Figs. 9B, D, $10A_2$). This narrow and often dark zone occurs as a semi-continuous "line" in costal parts of septa but

in axial septal portions it dissociates into modules, often restricted to the bulbous septal portions (Fig. $10A_2$). Commonly, several smaller units may be seen within a mid-septal zone; these are much smaller bodies of about 80μm in diameter of dark (Fig. 9D) but also light (Fig. $10A_2$) coloration. In more distal portions of the same coralla (e.g., Fig. 9C, E), the mid-septal zone may still occur in costal portions of septa, but oval structures with diagenetic pattern similar to that in septal spines of *Stylophyllopsis* sp. cf. *S. rugosa* (see Fig. 7E) often occur there.

Remarks.—Sections of nine Sicilian specimens (IPUM-Sic.1, 2, 4, 6–8, 10–12) show a consistent pattern of skeletal diagenetic alteration. A narrow, mid-septa zone, often composed of row of about 80 μm bodies, can be seen in transverse sec-
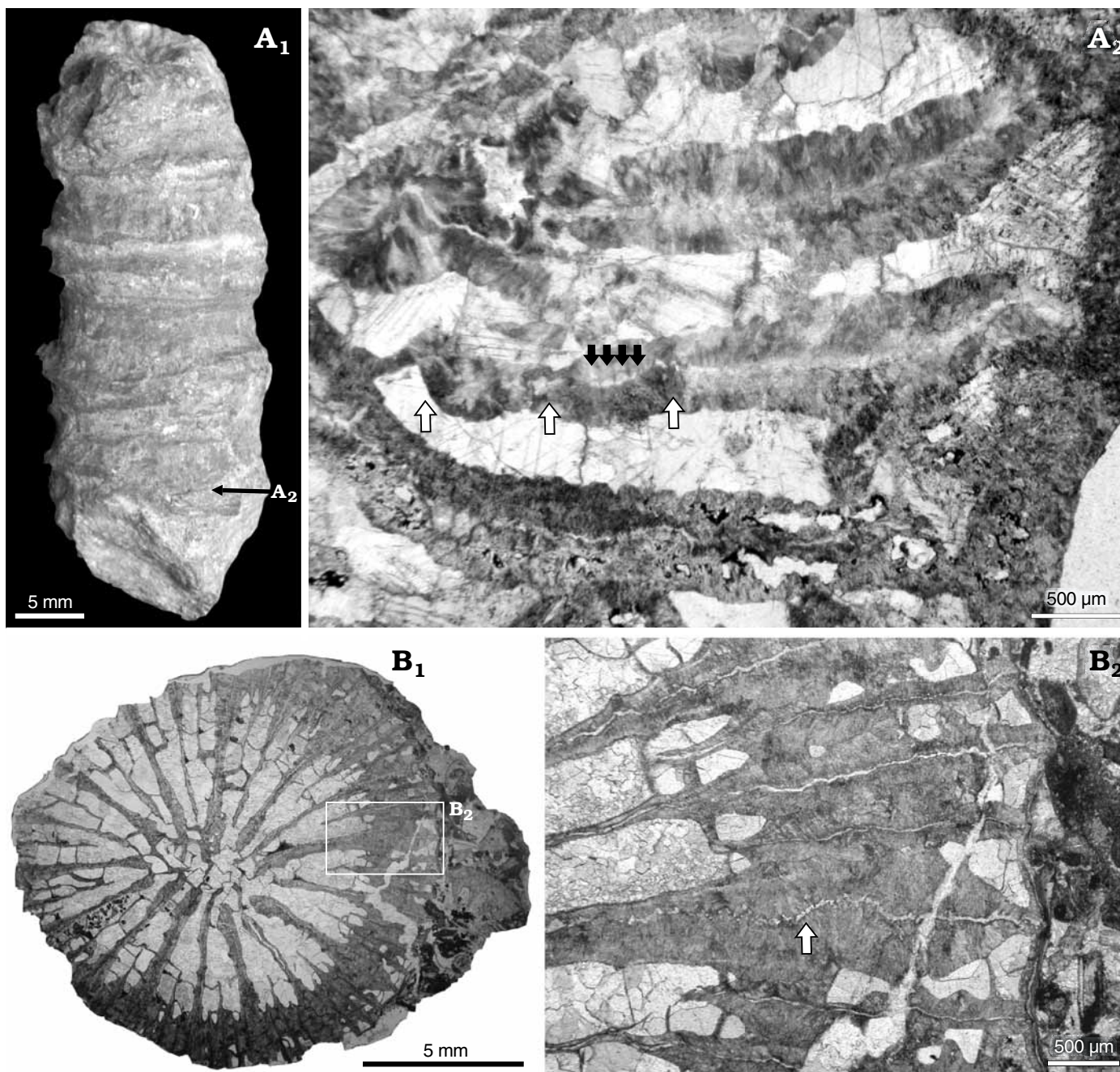
Fig. 10. **A**. *Stylophyllopsis* sp. A, lateral view of IPUM-Sic.8 (A₁), and transverse thin section (A₂) showing septal spine (structure beween two, white arrows) with numerous, small-sized structures "calcification centers" (black arrows). Sinemurian Black Limestones, Longi, Sicily. **B**. *Retiophyllia norica* (Frech, 1890), GBA 1982/12/113 in transverse thin section (B₁); B₂, small-sized calcification centers of zigzag mid-septal zone (arrow) and lateral thick stereome in enlarged part of septum. Triassic, Rhaetian. Fischerwiese, Northern Calcareous Alps, Austria.

tions of septa, particularly from the proximal corallum parts. Small-sized bodies represent, most likely, vestiges of calcification centers. In this respect, *Stylophyllopsis* sp. A. resembles "minitrabecular" corals (= Caryophylliina *sensu* Roniewicz 1989), in which the mid-septal zone consists of numerous, small-sized calcification centers aligned in a row or zig-zag line (Fig. 10B₁, B₂; see also Roniewicz 1984; Roniewicz and Morycowa 1993). Also spindle-like shapes of transversely sectioned septa strengthen similarity with "mini-

trabecular" corals (compare Fig. 10A₂ and 10B₁, B₂). However, spines that dissociate from adaxial regions of some septa or are distinguished in sections as series of bulbous septal swellings with individual mid-septal zones (Fig. 10A₂), suggest transitional minitrabecular-stylophylline skeletal architecture of that species. Diagenetic structures of such spines also resemble those observed e.g., in *Stylophyllopsis* sp. cf. *S. rugosa* (Fig. 7B, E).

The Sicilian *Stylophyllopsis* sp. A. may represent a new

species, but it is described under open nomenclature pending revision of various Early Jurassic stylophyllid corals described as "*Montlivaltia*".

Occurrence.—Early Jurassic (Sinemurian), Sicily.

Discussion

Stylophyllinan skeleton.—The skeleton of stylophyllinan corals was considered non-trabecular (Cuif 1973; Beauvais 1982; Roniewicz 1989) in contrast to coralla of the other five traditional suborders that have, at least, trabecular septa (see Roniewicz and Morycowa 1993). This implies that the stylophyllinan skeleton is built of fibrous sclerenchyme, and individual fibers that are not organized into "continuously growing rods formed by fibers [...], provided with an axis" (definition of trabecula in Glossary of Roniewicz and Stolarski 1999). According to the modern concept of scleractinian biomineralization, the trabecula, as defined above, encompasses structures formed in two successive calcification phases, i.e., calcification centers and fibers (see Cuif and Sorauf 2001 for summary). Dimensions, growth patterns and biochemical composition of calcification centers and fibers may differ significantly, providing characters for phylogenetic analysis.

Data presented herein suggest that skeleton of the stylophyllids (major group of stylophyllians), were much more microstructurally diversified than is traditionally proposed. Firstly, this is suggested by the diverse pattern of diagenetic alteration of the skeleton which is consistent within the three previously described Early Jurassic species. Diagenetic style depends strongly on microstructural and compositional properties of the skeleton (see summary by Sorauf and Cuif 2001) thus, conversely, diagenetic patterns may serve as a proxy of original microstructures. A second argument is provided by Triassic stylophyllids from Zlambach Beds (Northern Calcareous Alps, Austria) with preserved aragonitic coralla. In their septa, the following four microstructural patterns were observed: (1) septa composed of fibrous sclerenchyme without clearly delineated calcification centers (in *Stylophyllum polyacanthum* Reuss, 1854, *Stylophyllum vesiculatum* Roniewicz, 1989, see Fig. 11A$_1$, A$_2$)[1]; (2) septal spines with a "mid-septal zone" composed of minute calcification centers in *Stylophyllopsis rudis* (Emmrich, 1853), similar to that in *Stylophyllopsis* sp. A described herein (Fig. 11D$_1$, D$_2$, see also Roniewicz 1989: pl. 42: 7); (3) septal spines with single and large calicification centers in *Stylophyllum paradoxum* Frech, 1890 or some specimens assigned by Roniewicz (1989) to *Stylophyllopsis lindstroemi* Frech, 1890; Fig. 11C$_1$, C$_2$; and (4)

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[1] This microstructure is observed also in *Gigantostylis epigonus* Frech, 1890 monotypic member of Gigantostyliidae Frech, 1890, the second stylophyllinan family. In *Gigantostylis* compact septa are built of scale-like units and are not composed of fused septal spines (see Roniewicz 1989: 138; Stolarski 2000: 32).

[2] Noteworthy, original diagnosis of the family was purely morphological, according to which stylophyllids have distinct septal spines, see Frech 1890: 42.

septal spines with star-like pattern of ?diagenetic alteration in *Stylophyllopsis lindstroemi* Frech, 1890 (Fig. 11B$_1$, B$_2$) similar to that in described herein *Stylophyllopsis* sp. cf. *S. rugosa* (Fig. 7B, E) or *Stylophyllopsis* sp. A (Fig. 9E). These observations showing microstructural diversity raise questions about the monophyly of traditional stylophyllinans: Do different sizes and distribution patterns of calcification centers in various stylophyllid coralla argue about their affinity with mini- and, respectively, some thick trabecular corals? Or, conversely, do they indicate great variability within a monophyletic group? Are there any additional data that may argue for either mono- or polyphyletic status of stylophyllids?
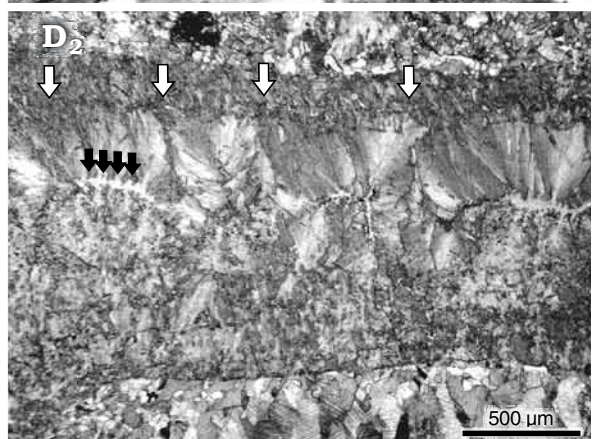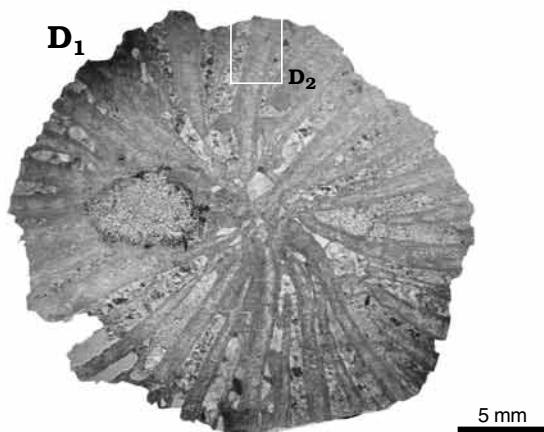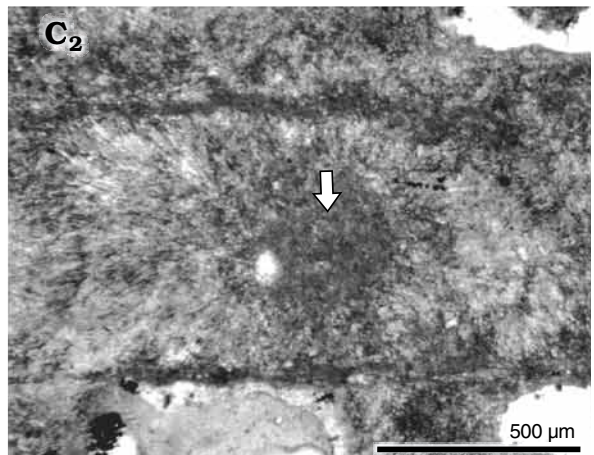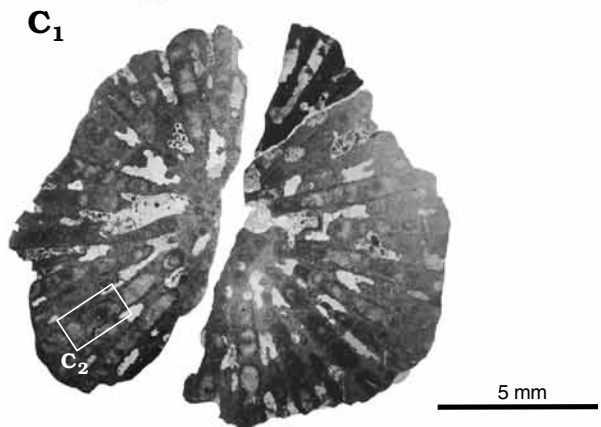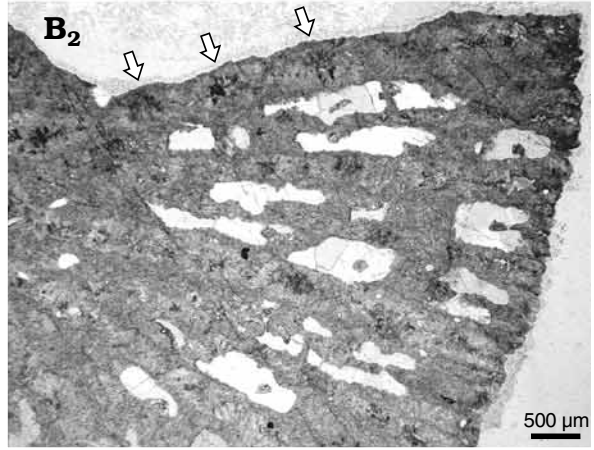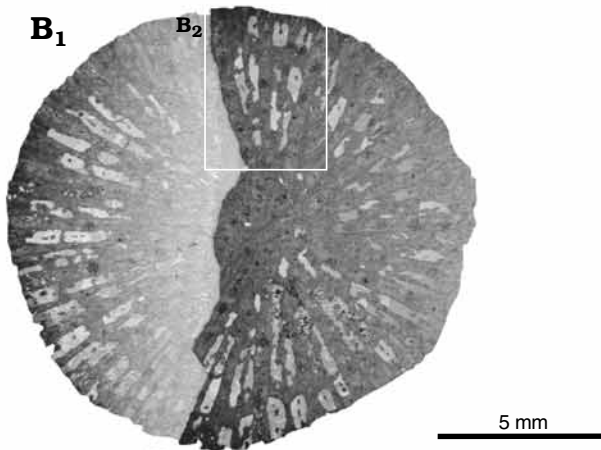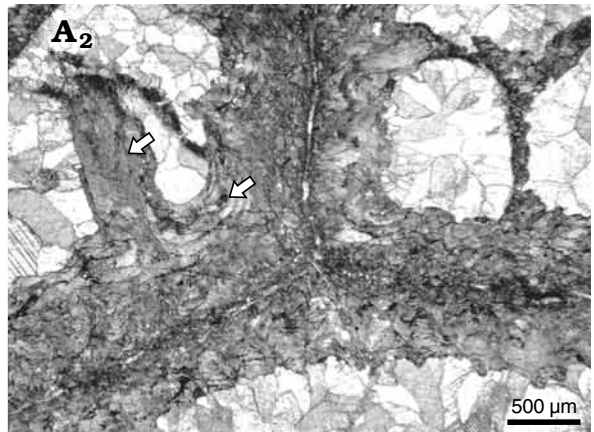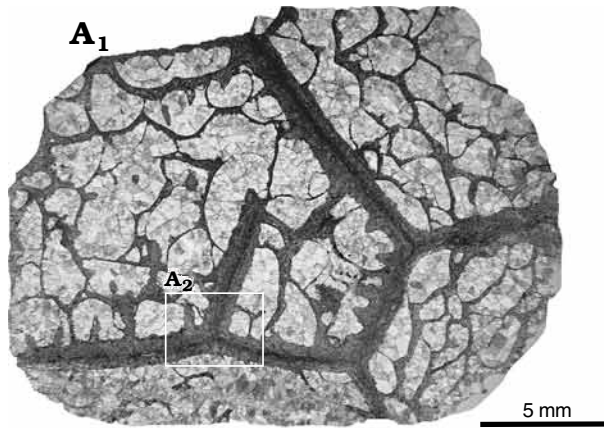
Aligned and small-sized calcification centers in septal spines of the Triassic *Stylophyllopsis rudis* (Emmrich, 1853), or their vestiges in Sinemurian *Stylophyllopsis* sp. A, are very similar to those in minitrabecular corals. However, a distinct "border layer" between centers and fibers that occurs around calcification centers in minitrabecular corals (Roniewicz 1996: fig. 1: 9, 11; Stolarski and Roniewicz 2001: fig. 4: 2) has not been recognized. The "border layer" around calcification centers in minitrabecular corals is composed of aragonite fibers (10–20 µm length), and results in a clear separation of calcification center from adjacent fibrous parts of skeleton, whereas in the investigated stylophyllids this separation is not so distinct. The same observations apply to calcification centers of the Triassic *Stylophyllum paradoxum* Frech, 1890 or specimen labelled herein *Stylophyllopsis lindstroemi* (Fig. 11C$_1$, C$_2$) that, though of similar size to those of some thick-trabecular corals, differ from them in lacking a distinct "border layer". Further research, extended also to extant mini- and thick-trabecular corals, is needed to corroborate universal nature of the "border layer". Individual calcification centers have not been traced in *Stylophyllum polyacanthum* Reuss, 1854, or *Stylophyllum vesiculatum* Roniewicz, 1989, and a scale-like pattern of fiber deposition suggests yet another pattern of biocalcification in these species.

Despite this microstructural diversity, stylophyllids share several unique characters that easily differentiate them from other Triassic–Jurassic scleractinians: their septa are composed of isolated or sclerenchyme embedded spines[2], which are covered with dense granulations. Microstructural diversity of stylophyllids stands thus in opposition to the architectural coherence of the group (similar paradox is observed among traditional Guyniidae, compare Stolarski 2000).

Fig. 11. Triassic (Rhaetian) stylophyllids from Northern Calcareous Alps, Austria with coralla still preserving aragonitic mineralogy. Transverse sections. **A**. *Stylophyllum vesiculatum* Roniewicz, 1989, NHMW 1982/56/34. Septa and wall (arrows in A$_2$) composed of fibrous sclerenchyme without clearly delineated calcification centers. **B**. *Stylophyllopsis lindstroemi* Frech, 1890, NHMW 1959/364/13(1). Septal spines (arrows in B$_2$) with star-like pattern of ?diagenetic alteration. **C**. Specimen assigned by Roniewicz (1989: 129) to *Stylophyllopsis lindstroemi* Frech, 1890, NHMW 1982/57/89. Septal spines show large calicification centers (arrow in C$_2$). **D**. *Stylophylopsis rudis* (Emmrich, 1853), NHMW 1982/56/32(2). Septal spines (white arrows in D$_2$) with "mid-septal zone" composed of minute calcification centers (black arrows in D$_2$). **A**, **D** from Kesselwand-Rohrmoos locality; **B**, **C** from Fischerwiese locality.
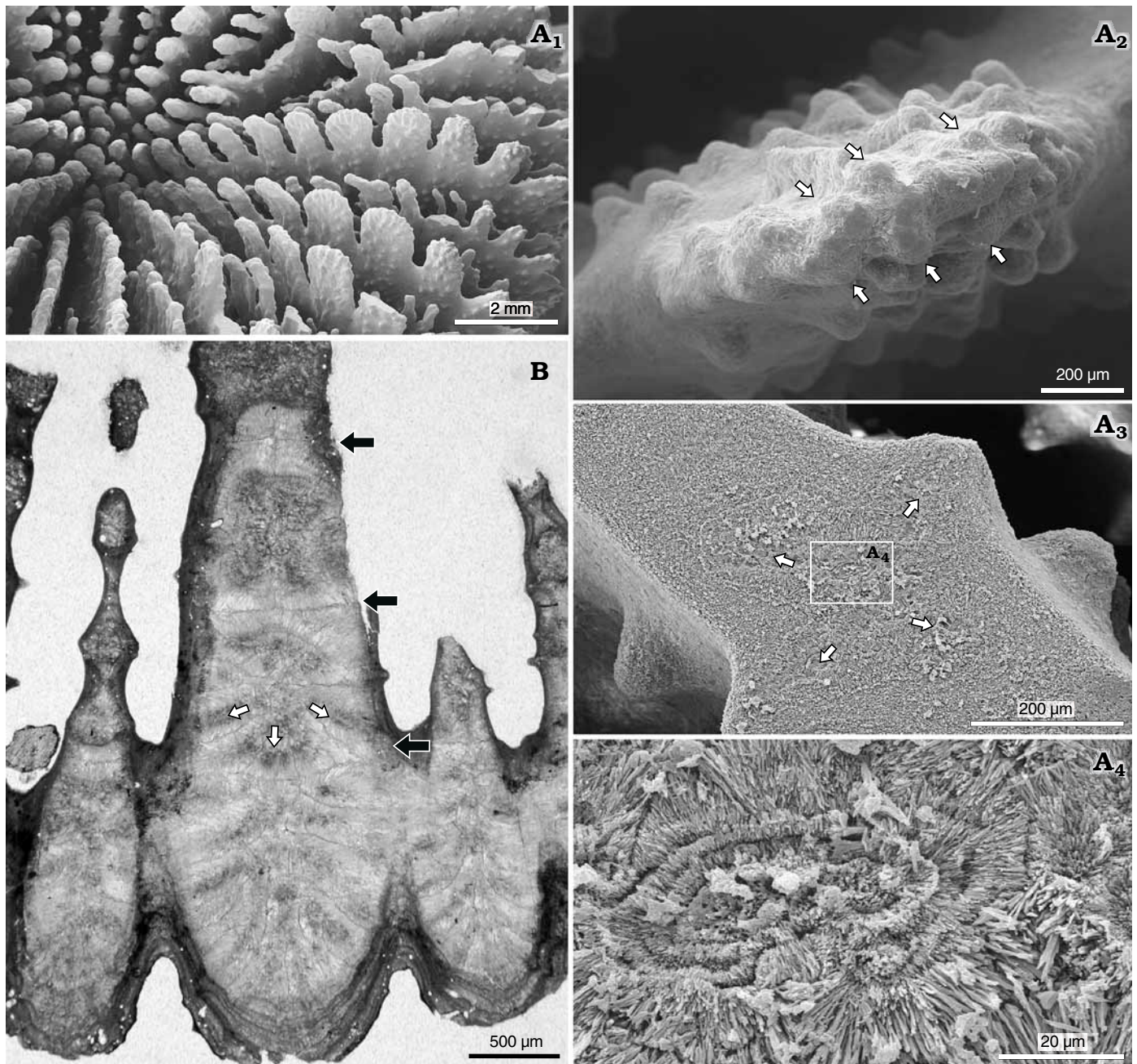
Fig. 12. *Anthemiphyllia dentata* Alcock, 1902. **A**. ZPAL 22/1, Recent, MD08 cruise, Stat. 7, 36˚48.9'S, 52˚07.7'E, 380 m. Lobate septa in distal-oblique view (A₁). Septal lobe in distal view (A₂); lateral ridges marked with white arrows. Polished and etched transverse section of septum in lobe region; trabecular axes formed by calcification centers radiate in four directions (white arrows in A₃), middle calcification center in transverse section (enlarged in A₄). **B**. ZPAL 22/2, Recent, VOLSMAR cruise, Stat. DW 5, 22˚25.9'S, 171˚46.5'E, 620–700 m. Septum in transverse thin section. Sutures delineate borders between individual septal lobes (black arrows) that show radiate pattern of trabeculae distribution (white arrows).

However, because arguments referring to purely morphological data (spines, granulations) can be strengthened by preliminary data about microstructural distinctness of stylophyllids (lack of "border layer" around calcification centers), we favor the hypothesis of the monophyly of traditional stylophyllids which, however, would include microstructurally diverse lineages. These lineages could give rise to various lineages of post-Triassic scleractinians, which are discussed below.

Speculations on stylophyllid evolutionary relationships.— In the quest for understanding stylophyllid evolutionary relationships, attention should be drawn to the coral lineages that are contemporaneous with stylophyllids, and that share with them some of the supposed synapomorphies, i.e., distinct septal spines/lobes and dense granulations covering uniformly the septa. One such coral group, whose roots remain unknown (Wells 1956), are solitary Thecocyathidae. Their first representatives appeared in Toarcian of Europe (*Thecocyathus tintina-*

bulum Goldfuss, 1826), during a time and within a geographic area of stylophyllid evolutionary prosperity. Septa in the first representatives of this family have multiple distinct lobes/spines on the distal margin. The Late Jurassic representatives (see Stolarski and Dieni 2002) have septa covered with dense granulations (microstructural features are unavailable). Traditionally, thecocyathids have been considered ancestral to caryophylliinans, most likely because many of the latter also show various septal projections (lobes, pali). However, microstructural data suggest that caryophylliinan roots may extend down to the Triassic (Roniewicz 1984). Other Jurassic corals of possible stylophyllid affinity are the epismilids (see Roniewicz and Morycowa 1989) and Oxfordian *Palaeomussa* Alloiteau, 1952, which also have lobate septa covered with dense granulations (see Alloiteau 1957: fig. 64a, b).

However, extant, deep-water anthemiphylliids provide an entirely new perspective in the quest for interpreting stylophylliid-related groups. These corals, having mostly a Pacific Ocean[3] distribution, are strikingly similar to solitary stylophyllids in having septa composed of septal spines (lobes), that form a compact blade lower in the calice. The corallum of *Anthemiphyllia dentata* Alcock, 1902, illustrated herein (Fig. 12), shows the main features of that similarity. The surface of the lobate septa is covered with dense, blunt granulations, and occasionally minute ridges (Fig. 12A$_1$, A$_2$). Lightly etched transverse sections of septa show groups of calcification centers radiating from the central region of the lobe and directed towards tips of sectioned granulae (Fig. 12A$_3$, A$_4$). Calcification centers are surrounded by several narrow (about 5–10 µm thick) concentric layers of fibers, greatly resembling transversely sectioned septal spines of some stylophyllids (see Roniewicz 1989: pl. 42: 9). A similar picture, composed of radially arranged darker rods of superimposed calcification centers in septal spines/lobes, can be seen also in transverse sections (Fig. 12B). Clearly, the presence of similar septal spines/lobes on anthemiphylliid and stylophyllid septa is not a strong argument in support of the hypothesis on their evolutionary relationships. Septal spines, as well as some other characters of scleractinian coralla, are "common themes" that repeatedly made their appearance in anthozoan history, suggesting that some ancient developmental mechanisms underlie their formation. A broad stratigraphic gap between extinction of stylophyllids (in Jurassic) and appearance of anthemiphylliids (the earliest known anthemiphylliid is *Anthemiphyllia catinata* Wells, 1907 from the Eocene of Tonga), which exists in conventional scleractinian evolutionary trees, also cannot be disregarded (e.g., Vaughan and Wells 1943). This argument, however, is weakened if the thecocyathids are considered stylophyllid descendants. Another argument that enables speculation about possible Mesozoic anthemiphylliid ancestors is their distinct position on the molecular tree topology.

Anthemiphyllids (i.e., *A. spinifera*) form a basal clade in mitochondrial 16S rRNA analysis (in nuclear 28S rRNA analysis by Romano and Cairns 2001, *A. spinifera* also form a clade that includes coral however *Odontocyathus* (*O. weberianus*; N. Caledonia), *Vaughanella* (*V.* sp.; Vanuatu), and *Ceratotrochus* ("*C*". *magnaghii*; Mediterranean). Microstructural revision of anthemiphyllids and stylophyllids with emphasis laid on nature of septal calcification centers, especially on taxonomic significance of the calcification center "border layer" (in preparation by the senior author), as well as molecular studies on additional anthemiphyllid DNA sequences, are necessary to test hypothesis on their evolutionary relationships.

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[3] Only *Anthemiphyllia patera patera* De Pourtalès, 1878 is known from the western Atlantic (Carribean region) whereas other 7 species and subspecies have western and central Pacific distribution, and *Anthemiphyllia dentata* (Alcock, 1902) is known also from Indian Ocean (see Cairns et al. 1999).

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