MICROSTRUCTURAL EVIDENCE OF THE STYLOPHYLLID AFFINITY OF THE GENUS *CYATHOPHORA* (SCLERACTINIA, MESOZOIC)

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Abstract: The genus *Cyathophora* Michelin, 1843 (Cyathophoridae) is removed from the suborder Stylinina Alloiteau, 1952 and transferred to the Stylophyllina Beauvais, 1980. Morphologically, it differs from stylinine corals in that rudimentary septa are developed in the form of ridges or spines on the wall and may continue onto the endothecal elements as amplexoid septa. Relics of primary aragonite microstructure, preserved in silicified colonies of *Cyathophora steinmanni* Fritzsche, 1924 (Barremian–early Aptian) and in a calcified colony of *C. richardi* Michelin, 1843 (middle Oxfordian), indicate a non-trabecular structure of their skeletons. The sclerenchyme of radial elements is differentiated into fascicles of fibres, and in the form of fascicles or a non-differentiated layer of fibres, it continues as the upper part of endothecal elements and as the incremental layers of the wall. A micro-lamellation of the skeleton corresponds to the accretionary mode of skeleton growth found in Recent corals. A similarity between the septal microstructure of *Cyathophora* and that of the stylophyllid genera, the Triassic *Anthostylis* Roniewicz, 1989 and the Triassic–Early Jurassic *Stylophyllopsis* Frech, 1890, is interpreted as a result of their being phylogenetically related. The microstructure of the Jurassic *Stylina gaulardi* Michelin, 1843 has been considered for purposes of comparison. The systematics of the genus *Cyathophora* is formally revised with *C. richardi* Michelin reinstated as the type species.

Key words: Microstructure, homeomorphy, taxonomy, Cyathophoridae, Stylinidae, Stylophyllidae, Triassic, Jurassic, Cretaceous.

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INTRODUCTION

The authors present new data on the skeleton microstructure of the genus *Cyathophora* Michelin, 1843, observed in silicified skeletons of the Early Cretaceous *C. steinmanni* Fritzsche, 1924 and recognizable also as aragonite relics in the calcitized skeleton of the middle Oxfordian *C. richardi* Michelin, 1843, which serve as the basis for revision of the genus.

Corals of the genus *Cyathophora*, ranging from the Middle Jurassic to the early Late Cretaceous, were most common in the Late Jurassic and Early Cretaceous. A majority of Jurassic–Cretaceous coral genera can be classified within multigeneric families that differ from each other in corallite morphology and skeleton microstructure, e.g., the scleractinian families Stylinidae d'Orbigny, Montlivaltiidae Dietrich, Microsolenidae Koby, Latomeandridae Alloiteau, Haplaraeidae Vaughan and Wells, Rhipidogyridae Koby and hexanthiniarian Amphiastreidae Ogilvie. Within these families, genera differ from one another in corallum growth-form (i.e., solitary, phaceloid, colonial forms) or in the mode of budding, which produces colonies with diverse inter-corallite relations. Surprisingly, no unquestionable counterparts among Jurassic or Cretaceous corals are known which could be classified together with *Cyathophora*. Up to the early 1900s, *Cyathophora* was maintained in the Stylinina Alloiteau (e.g., Löser, 1994), but Morycowa and Masse (1998) did not support this approach to classification and regarded the genus to be of an uncertain systematic position. Pandey *et al.* (2002) assigned it to the Stylinina with a question mark.

The genus *Cyathophora* Michelin was based on the well-documented Oxfordian species *C. richardi* Michelin, 1843; however, Milne Edwards and Haime (1857) considered it to be a junior synonym of *Astrea bourgueti* Defrance, 1826, an unfigured species that was imprecisely diagnosed. The latter name has been applied to many poorly diagnosed

Table 1

List of the specimens examined

Species	Coll. no.	Age	Locality	Figure	Measurements in mm
Cyathophora richardi Michelin, 1843	MNHN MO0071, coll. d'Orbigny	lO	Tonnerre, France	1A, B	**d** 5–6; **c-c** 6–9
Cyathophora richardi Michelin, 1843	ZPAL H.III/230, 610, 1513	mO	Bałtów, Świętokrzyskie Mts., Poland	1E–J	**d** 6.5–8 (9); **c-c** 7–11; **ed** ca. 4/3
Cyathophora claudiensis Etallon, 1859	ZPAL. H.III/827	lO	Niziny, Świętokrzyskie Mts., Poland	1K, L	**d** 6–7; **c-c** 8–9; **ed** 7/3
Cyathophora thurmanni Koby, 1882	MHN, coll. Koby	lO	Soyhières, Jura Mts., Suisse	1C, D	**d** 5–6; **c-c** 7–8 (12)
Cyathophora steinmanni Fritsche, 1924	UJ 4P/10, 60–62, 68, 70	B–eA	Jastrzębia, Trzemesna, Polish Outer Carpathians	2A–L 3A–L	**d** 2–3; **c-c** 2.0–3.5; **ed** 6–8/3
Stylina gaulardi Michelin, 1843	MNHN, no. 213, coll. Michelin	lO	Dun, Meuse, France	4A–C	**d** 2–2.3; **c-c** 2.5–4 (6)
Stylophyllopsis rugosa (Duncan and Wright, in Duncan, 1868)	BM R. 13287	EJ	Honeybourne, east of Evesham, Worcester, England	5A, B, E	**d** 22 × 25; **h** > 30; **s** ca.80
Stylophyllopsis mucronata (Duncan, 1868)	BM R. 13320	EJ	Fenny Compton, south-east of Warwick, England	5C, D	**d** 20; **h** 18
Anthostylis acanthophora (Frech, 1890)	NHMW 1982/57/32	R	Fischerwiese, Northern Calcareous Alps, Austria	5F–H	**d** 2.5–3.0; **c-c** 2.5–3.0; **ed** 6–8/3 (Cuif:1972, p. 281: **d** up to 3–4 mm)

Explanation of abbreviations: **c-c** – distance between corallite centres, **d** – corallite diameters, **ed** – density of endothecal elements (number of elements *per* mm, measured in longitudinal sections), **h** – height of the specimen, **s** – number of septa, A – Aptian, B –Barrermian, J – Jurassic, K – Kimmeridgian, O – Oxfordian, R – Rhaetian, e – early, l – late, m – middle. For other abbreviations see the Introduction.

forms, ranging from the Bajocian to the Cretaceous (Pandey *et al.*, 2002). To date, *Cyathophora richardi* has not been formally revised, although Alloiteau (1948), on the basis of a specimen from the collection of d'Orbigny, presented a well-substantiated criticism of its being a junior synonym of *A. bourgueti.* The lectotype of *Cyathophora richardi*, recognized recently in the collections of the Museum National d'Histoire Naturelle, Paris (cat. no. A32288), figured in Michelin (1843, pl. 26: 1a, b), Lathuilière (2014), and Zaman and Lathuilière (2014, figs 1, 2), enables the present authors to re-establish this species as the type species of *Cyathophora* Michelin.

The specimens of *C. richardi* considered herein come from a rich coral assemblage (about 30 species: Roniewicz, 1966; Table 1, Bałtów 2), in a reefoid limestone of the middle Oxfordian of the Świętokrzyskie Mountains, Central Poland, which was characterized in terms of sedimentology and palaeoenvironment by Roniewicz and Roniewicz (1971). The stratigraphical position of these structures has been established as the *Gregoryceras transversarium* Zone (Kutek in Roniewicz and Roniewicz, 1971; Gutowski, 1998).

The colonies of *C. steinmanni*, considered herein, were collected from conglomerates of Barremian age at Trzemesna (Silesian Unit) and of early Aptian age at Jastrzębia (Subsilesian Unit), the Outer Carpathians, Poland. They belong to a rich, shallow-water coral fauna that was redeposited penecontemporaneously with respect to the aforementioned sediments (Morycowa, 1964). The Barremian age of the coral-bearing sediments at Trzemesna was indicated by foraminifers (Koszarski, 1961) and the early Aptian age at Jastrzębia by the ammonite *Procheloniceras albrechtiaustriae* (Hohenegger in Uhlig, 1883; see Książkiewicz, 1938; Ropolo *et al.*, 2008).

MATERIAL

The material considered consists of colonies of *Cyathophora* Michelin collected in Poland and specimens of *Stylina* Lamarck, *Stylophyllopsis* Frech and *Anthostylis* Roniewicz from other coral collections elsewhere in Europe (Table 1). The morphology and microstructure of the skeleton were examined in transverse and longitudinal sections of *Cyathophora richardi* Michelin (three specimens), *C. claudiensis* Etallon (one specimen) and *C. steinmanni* Fritsche (above five specimens). The specimens of *C. richardi* considered herein, housed at the collections of the Institute of Paleobiology, Polish Academy of Sciences, Warszawa (ZPAL H. III/230, 610, 1513), showed specific features on the colony surface with large, crowded calices. *C. claudiensis* (ZPAL H. III/827) exhibited a colony structure in thin sections that could be compared with that in *C. richardi*.

Usually, only gross morphology is preserved in colonies of *Cyathophora*, but the calcified skeleton of *C. richardi* (ZPAL H.III/230) revealed traces of the original microstructure in both transverse and longitudinal thin sections, while in some silicified skeletons of *C. steinmanni*, well-preserved microstructural elements of septa were observed, some with fine growth lamellae. The examination of

C. steinmanni was based on five complete colonies and several fragmentary colonies, housed at the Museum of the Institute of Geological Sciences, Jagiellonian University in Kraków (UJ 4P/10, 60, 62, 68, 70). The specimen UJ 4P/60 was preserved in transparent silica, which allowed the authors to observe the primary morphology of rows of "denticles" (the tips of fascicles of fibres) on the inner surface of the wall and on the calicular floor of the corallites. Additionally, specimen UJ 4P/68 showed the microstructural features of the skeleton, including the accretionary lines in the radial elements, wall and endotheca.

One of the specimens of *Cyathophora richardi* from the Michelin collection of the Muséum National d'Histoire Naturelle in Paris, no. MO0071, Oxfordian, Tonnerre, SE of the Paris Basin, that are discussed and figured in the present paper, and a close species, *C. thurmanni* Koby from the collection of the Muséum d'Histoire Naturelle in Genève (coll. Koby, Jura Bernois, Soyhières), provided information on the morphology of the calicular colony surface.

The microstructural characteristics of the stylophyllid skeleton presented here were based on the specimens of *Stylophyllopsis rugosa* (Duncan and Wright in Duncan, 1868), BM R. 13287, from the Hettangian (Early Jurassic), and *Anthostylis acanthophora* (Frech, 1890), NHMW 1982/57/32, from the Late Triassic (Rhaetian). The stylinid coral, *Stylina gaulardi* Michelin, 1843, from the Late Jurassic (MNHN collection Michelin, original number 213), allowed comparison with the microstructural characteristics of *Cyathophora*.

Institutional acronyms: BM British Museum, London; MNHN Muséum National d'Histoire Naturelle, Paris; MHN Muséum d'Histoire Naturelle, Genève; NHM Naturhistorisches Museum Wien; UJ 4P Museum of the Institute of Geological Sciences, Jagiellonian University, Kraków; ZPAL Institute of Paleobiology, Polish Academy of Sciences, Warszawa.

MICROSTRUCTURE OF THE CORAL SKELETON AND TERMINOLOGY OF THE SKELETAL STRUCTURE

The present authors review the microstructural patterns and terminology that were originally described in earlier literature. They urge that the microstructural terminology that is not used in the present account, but applied in earlier papers, should be abandoned. In this paper, the authors present the structural terminology concerning septal microstructure (after Roniewicz, 1989; Roniewicz and Morycowa, 1989; Morycowa and Roniewicz, 1995a), followed by terminology related to growth of the coral skeleton (Stolarski, 2003; Budd and Stolarski, 2011).

Terminology of skeletal structure. The term microstructure corresponds to an arrangement of aragonitic crystals, termed fibres or fibrocrystals, observable in aragonitic skeletons. The fibres are arranged in a different manner in different parts of the skeleton. The most simple, palisade arrangement of fibres, is typical of the upper dissepimental layer, while a fan-like arrangement is typical of the lower dissepimental layer (Wells, 1969). Septa show a trabecular,

or non-trabecular (fascicular) microstructure. In some corals, the septa are lined with a sclerenchymal deposit, which is in continuation with the palisaded dissepimental layer.

The most general taxonomical differentiation of Mesozoic scleractinian groups corresponds to their trabecular or non-trabecular septal microstructure, which is described below.

Trabecular microstructure – fibres are organized into rod-like, axiferous trabeculae built of fibres, arranged radially in relation to the trabecular axis. In some corals, e.g., in Stylinidae, the septa are exclusively trabecular. The separate trabeculae (with diameters from about 50 to 100 μm or more), when observed in transverse section show more or less wide centres, encircled by radially arranged fibro-crystals; in longitudinal sections, a trabecula shows a central axis. In other corals, the septa show a well-defined midseptal zone, composed of a single row of small and tightly crowded axes (ca. 20–50 μm in diameter; in the descriptive terms named earlier, minitrabeculae, e.g, in Caryophylliide, compare Roniewicz, 1989; Roniewicz and Morycowa, 1989), in some corals coalesced into a continuous mid-septal line. The mid-septal line is parallelled on both sides by lateral sclerenchyme.

In the longitudinal radial section of a septum, the course of the trabecula is clearly indicated by its axis, its limits being more or less distinct. The trabecula (Jell, 1969, primary trabecula; Morycowa and Roniewicz, 1995a, main trabecular body) sets off secondary trabeculae (Jell, 1969), or lateral offsets (Morycowa and Roniewicz, 1995a) toward its sides to produce lateral septal granulations.

Non-trabecular or fascicular microstructure – the skeleton is built of the sclerenchyme deposited in portions, i.e., showing fibrocrystals arranged into fascicles of fibres (named also fibre bundles) or scales that form the skeleton (e.g., Stylophyllidae, see Roniewicz, 1989; Roniewicz and Morycowa, 1989, 1993; Morycowa and Roniewicz, 1995a; Stolarski and Russo, 2002).

Micromorphology of septa (= ornamentation, microarchitecture) concerns the details observed on septal margins (denticulation) and lateral surface (differently shaped granules and pennules), expressing the internal septal microstructure.

Terminology of skeleton growth. An accretionary model of skeletal formation claims that the variability of coral microstructure reflects a combination of location and shape of the skeletal accretion zones and their different development in mineral *vs.* organic phases of secretion (Stolarski, 2003). A minute striation, corresponding to the elemental accretional portions, can be observed in the skeleton (Stolarski, 2003, fig. 2B, E). With the initiation of this new paradigm of coral skeletal formation, terms such as spherulite retain only historical meaning (see Bryan and Hill, 1941), while centre of calcification, which is still in use as a descriptive term, depicts septa with distinctive trabecular axes observed in transverse sections.

New terms involving the accretionary model (after Stolarski, 2003 and some after Stolarski in Budd and Stolarski, 2011) are discussed below:

– rapid accretion deposit (RAD; Budd and Stolarski, 2011) corresponds to a deposit taking place during intense growth, the tip of a denticle on the distal septal edge (or lat-

eral granulations); the deposit is enriched in the organic phase and surrounded by more slowly growing TD (see below); defined in Stolarski (2003) as deposits of centres of rapid accretion (dCRA);

– Rapid Accretion Front (RAF), a zone built of multiple separate RAD's, or the homogeneous midseptal zone; the RAF is parallelled on two sides by two zones of the TD;

– thickening deposit (TD), the skeleton deposited close to the RAD or RAF in the area of growth, where the mineral phase prevails over the organic one.

A question arises as to how this terminology of growth relates to a structural one. Let us look at a well-preserved skeleton in oriented sections. When the septum is cut transversely, the RAD together with the surrounding field of TD show a structure that is known as a trabecula and the trabecula has an axis ("centre of calcification" encircled by an area of radially arranged fibres). This arrangement represents the RAD with its fibrocrystals rapidly growing upward and rich in organics, surrounded by laterally and more slowly growing fibrocrystals of the TD, poor in organics (see Stolarski, 2003, fig. 17). Usually, the more widely spaced the neighbouring RAD, the larger the fields of TD; the more crowded the RAD, the smaller the fields of TD. The RAF is a zone built of multiple, separate RADs (corresponding to a row of well defined axes, when observed in longitudinal section, i.e., minitrabeculae in Roniewicz, 1989, p. 8), or of a homogeneous midseptal zone. In structural terms, the septum of such a structure is trabecular.

In the sclerenchyme of the Stylophyllina, the fascicles of fibres correspond in size to the RAD of a caryophylliid coral, but they do not have a distinct internal structure. Such a skeleton is described as fascicular and non-trabecular (Roniewicz, 1989: fascicles of fibers or bundles of fibers: pls 42, 43); this structure is analogous to that termed as penicillate structure used by Cuif and Gautret (1993).

The above review shows that the terminology used to describe coral growth parallels the structural one. In the descriptions that follow the authors use a simple structural terminology, in some cases introducing useful terms for skeletal growth. The term "centre" signifies a centre of trabecula or an axis within the midseptal zone, and corresponds to the RAD.

POSITION OF THE GENUS *CYATHOPHORA* IN SYSTEMATICS

The earliest appearance of the genus *Cyathophora* Michelin was in the Early Jurassic of South America (Gerth, 1928). However, this occurrence has never been confirmed (Pandey *et al.*, 2002). The earliest well-documented *Cyathophora* was described from the Bajocian of India (Pandey *et al.*, 2002), the latest is from the Cenomanian of Europe (Löser, 1989; Eliášová, 1992, 1997), with the acme of cyathophoran development in the Late Jurassic. Up to now, more than 60 nominal species of the genus have been described, with the majority from the Late Jurassic (Lathuilière, 1989; Pandey *et al.*, 2002).

Currently, *Cyathophora* is considered to be a stylininan genus, because it has a plocoid colony and corallites with

septa not abundant and a subtabular endotheca. However, its typical set of features, i.e., rudimentary, amplexoid septa developed on the internal wall surface and descending upon the surface of subtabular elements of endotheca (Alloiteau, 1948, text-fig. 7; Morycowa, 1971, pl. 5; Pandey *et al.*, 2002, fig. 8; herein Fig. 1I, J), differentiate it from Jurassic-Cretaceous corals, with the exception of *Prodonacosmilia* Melnikova in Melnikova and Roniewicz, 1976. The latter genus, known from the Early Jurassic of the Pamirs and the Tithonian of the Carpathians (Melnikova and Roniewicz, 1976), is represented by phaceloid coralla with amplexoid septa. Its relationship with *Cyathophora* could be either proven or rejected by a microstructural test of new material, because the specimens currently available do not retain traces of primary microstructure.

Originally, Michelin (1843) did not specify the systematic position of the genus *Cyathophora*. Milne Edwards and Haime (1857) classified it among the Stylinaceae in the family Astreidae. De Fromentel (1858, p. 198) considered it to be a representative of the 'Polypiers Tabuleés', owing to tabuloid endotheca and underdeveloped septa, and classified it originally into the Thécostégitiniens (De Fromentel, 1858, p. 278), the family situated in his system close to the pocillopores. Later, this author considered all species of the genus *Cyathophora*, except for *Cyathophora richardi* Michelin, to be close to *Stylina* Lamarck (de Fromentel, 1883). Because of tabuloid endotheca, Koby (1882, 1889) included *Cyathophora* together with the genera *Cryptocoenia* d'Orbigny and *Convexastrea* d'Orbigny in the family Stylinidae, in the sub-group of genera lacking a columella. Vaughan and Wells (1943), in considering cyathophoran endotheca to be purely tabular and different from that in other stylinid genera, created a new subfamily Cyathophorinae, raised by Alloiteau (1952) to the family rank in the suborder Stylinina Alloiteau.

Recent microstructural studies, in addition to the commonly known morphological similarity of the stylophyllid corals to *Cyathophora*, revealed a surprising similarity in micromorphology and microstructure. Microstructure and micromorphology appear to be most useful in bringing the palaeontological results of coral examination nearer to those obtained in neontological studies, based on molecular analysis [compare family Faviidae in Chevalier (1975) and Romano and Cairns (2000), or the results of Benzoni *et al.* (2007) in defining relations among genera within the families Siderastraeidae and Fungiidae, or Budd and Stolarski (2009, 2011) concerning Atlantic mussiid and faviid corals]. Encouraged by positive results in the application of micromorphology and microstructure for discrimination of suprageneric taxa of Mesozoic corals (Gill, 1967, 1970, 1977; Roniewicz, 1976, 1989; Cuif, 1977; Morycowa and Roniewicz, 1995b; Roniewicz and Stolarski, 2001; Stolarski and Roniewicz, 2001), the present authors have undertaken a microstructural examination of *Cyathophora* in the hope that this approach helps them in re-defining its possible relationships, indicating Stylophyllidae as possibly the closest, phylogenetically related group.

STRUCTURAL PATTERN IN THE FAMILY CYATHOPHORIDAE VAUGHAN AND WELLS, 1943, EMEND. ALLOITEAU, 1952

Structure of the skeleton in *Cyathophora richardi* Michelin, 1843

Cyathophora richardi was described from the Oxfordian of France (Michelin, 1843; Alloiteau, 1948; Zaman and Lathuilière, 2014) and from Poland (Roniewicz, 1966). There is also a description in Beauvais (1964), unfortunately with an erroneous presentation of a specimen of *Stylina* as the type of *Cyathophora richardi.*

The species, originally well illustrated, is characteristic of its corallite and colony features. The specimen in the d'Orbigny collection (MNHN 4567), was used by Alloiteau (1948) in his description and discussion of the peculiarity of the skeleton structure in this genus.

Morphology of colony and corallite. The specimens of *C. richardi* (the type material and Polish specimens) represent colonies subglobular in shape, subcerioid, with extremely reduced peritheca and exclusively extracalicular budding. In the corals examined here, the colony structure corresponds exactly to that observed in the type specimen, illustrated in the Michelin collection (1843, pl. 26, fig. 1a, b). The calices are large (Table 1), widely open, shallow, and with a slightly elevated calicular border. Radial elements are of the costo-septal type. The costae are thick and short, and non- and subconfluent. The septa are developed as ridges on the inner side of the wall and in the form of amplexoid septa and are extended on the upper side of tabulae. This feature is one of the most characteristic of the genus, as indicated by Alloiteau (1948, pp. 717–718, fig. 7). In the material considered here, prolongations of the amplexoid septa are observable on the surface of tabulae, present also in longitudinal thin sections (Fig. 1I, J). This characteristic, exemplified by *C. bourgueti* from the Bajocian of India, was included also in the scheme by Pandey *et al.* (2002, fig. 8), but it cannot be observed in *C. claudiensis* (Figs. 1K, L) or in some large-corallite cyathophoran corals, described from Bulgaria (Roniewicz, 2008, fig. 16B, F, I). In transverse sections, the septa show sharply pointed inner margins. In another close species, *C. thurmanni* Koby, distal margins show the distal ends of thick septal spines (Fig. 1C). The endotheca is composed of tabulae, extended tabuloid dissepiments and rare vesicular dissepiments (ZPAL H.III/230). In *C. richardi*, the density of peritheca is similar to that of the endotheca, but in other species (e.g., *C. claudiensis*, Fig. 1K, L) the endotheca may be denser in structure.

Microstructure of the skeleton. The skeleton is calcified, with rare traces of the primary aragonite microstructure, observable in the specimen ZPAL H.III/230. Thick and short costo-septa are made of a number of thick septal spines with multifascicular structure observable in transverse section (Fig. 1H). The fascicles of fibres are preserved as numerous, opaque elements, circular in section, 60–80 µm in diameter, corresponding in dimensions to the fascicles of fibres in the septa of *C. steinmanni* (compare Fig. 3K, L). In longitudinal section, traces of microstructure are seen, as well, but individual fascicles cannot be observed (Fig. 1 I, J).

The compound structure of septa, made of numerous multifascicular spines, in *C. richardi* differs from the simpler structure of the septa, observed in *C. steinmanni.*

Structure of the skeleton in *Cyathophora steinmanni* Fritzsche, 1924

Cyathophora steinmanni belongs to a group of species with small diameters of corallites (Table 1). *C. steinmanni* was described by Fritzsche (1924, p. 316, pl. 3, fig. 8, pl. 4, fig. 3) from the Lower Cretaceous of South America, from Chile, and was redescribed by Morycowa on the basis of material from the Polish Outer Carpathians (1964, p. 24, pl. 3, fig. 2a b, pl. 5, fig. 3). The latter material for the first time enabled microstructural observations in the genus.

Macro- and microstructure of the skeleton were examined in transverse and longitudinal thin sections (Figs 2, 3). The skeletons have been silicified with different preservation in whole colonies and their parts. In many colonies, only the gross morphology is preserved and no traces of fibrous skeleton structure are detectable, while in others, either skeletal fibre distribution is excellently traceable, or portions of skeleton growth (accretion) are affected by a specific mode of preservation. Additionally, in a specimen perfectly preserved in transparent silica, vertical rows of isolated "denticles" (i.e., fascicles of fibres) are observed inside the calice: on the wall and on the calicular floor (Fig. 2D–F).

Morphology of colony and corallite. The colonies are plocoid-subcerioid with very narrow peritheca, in places completely reduced (Fig. 2A–C). Budding is perithecal. Radial elements are costo-septal in type. The septa are developed as ridges on the inner surface of the wall and are provided with equal spiny denticulation (Fig. 2D, E). Amplexoid septa extend from the wall onto the surface of the tabula (Figs 2D, E, 3D, G) and occasionally form a central protuberace (Fig. 3C, G). In transverse section, the septa show a pointed inner edge (Fig. 2E). The costal parts are thick and nonconfluent. The distal margin of the costo-septum is covered with rare, sharp spines (Fig. 2H–L), which correspond to the distal ends of the fascicles of fibres (see below). The endotheca is formed of horizontal or convex tabulae and tabuloid dissepiments with the addition of vesicular dissepiments (Fig. 3A–E, G); accretion marks of the basal plate in the endothecal elements can be observed on the lower side of tabula (Fig. 2G). The exotheca and endotheca are similar in density (Fig. 3B). The wall is septo-parathecal.

Microstructure of skeleton. Radial elements are built of a number of straight elements of a simple structure, the *fascicles of fibres*, most frequently 60–80 µm in diameter (with observed extreme values from 45 µm to 100 µm). The septa, in the form of rows of fascicles connected with each other, descend from the wall onto the surface of tabulae (Figs 2D–F, 3D, G), where they may decompose in a disorderly manner into individual fascicles (Fig. 2D–F). In the septa, the fascicles lying at the mid-line are arranged fan-like and are separated from each other (Figs 2I–L, 3L). The axis of divergence in the fan is vertical and follows the fascicle, situated in the wall. As a rule, this fascicle is associated on both sides with one or two others, lying in the plane of the wall (Fig. 2H–L). The septal inner border is
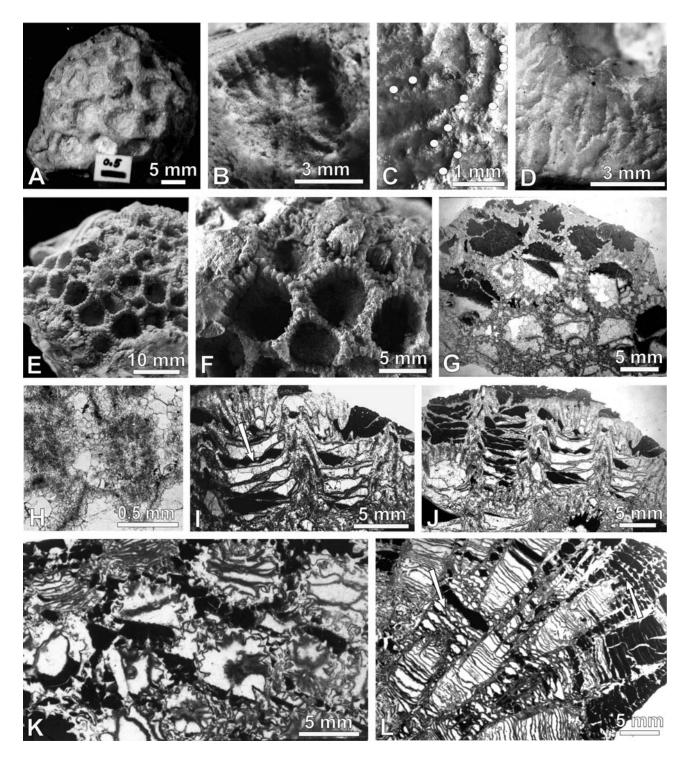
Fig. 1. Corals of the genus *Cyatophora* Michelin, 1843. **A, B, E–J.** *Cyathophora richardi* Michelin, 1843; A, B. Colony from the Michelin type collection; A. Subcerioid colony in lateral view; B. Calice with amplexoid septa descending from the wall onto the surface of the endothecal element; Tonnerre, France, Oxfordian (MNHN, coll. Michelin, MO0071); E–J. Colony from the ZPAL collection; E. Subglobular colony in lateral view; F. Fragment showing thick costo-septa and lack of a perithecal space; G. Transverse thin section showing densely arranged corallites and rarely with narrow peritheca; H. Two septal spines in transverse thin section with traces of the fascicles of fibres; I, J. Longitudinal thin sections showing endotheca with sections of amplexoid septa situated on the upper surface of tabuloid elements (arrow); peritheca reduced; Bałtów, Świętokrzyskie Mountains, Poland, Oxfordian (ZPAL H.III/230). **C, D.** *Cyatophora thurmanni* Koby, 1881; C. Intercalicular space with costae showing tips of thick septal spines (marked with circles); D. Costae of neighbouring calices meeting in the intercalicular space; Soyhières, Suisse, Oxfordian (MHN Genève, Koby coll.). **K, L.** *Cyathophora claudiensis* Etallon, 1859; K. Transverse section of subcerioid-plocoid colony showing corallites divided by a narrow peritheca; L. Longitudinal section showing corallites with densely arranged tabulae lacking prolongation of septa, and well-developed peritheca built of tabuloid and dissepimental elements bearing amplexoid costae (arrows); Niziny, Świętokrzyskie Mountains, Poland, Oxfordian (ZPAL. H.III/827).
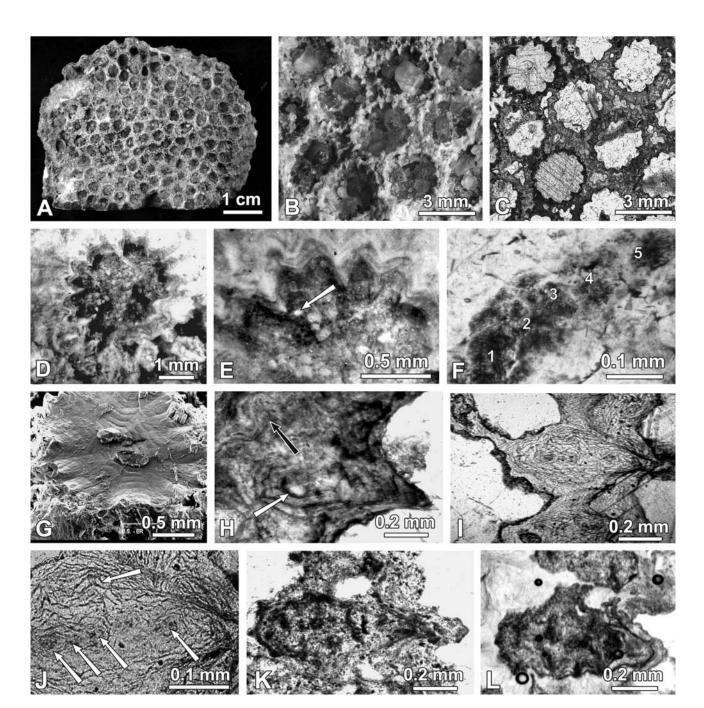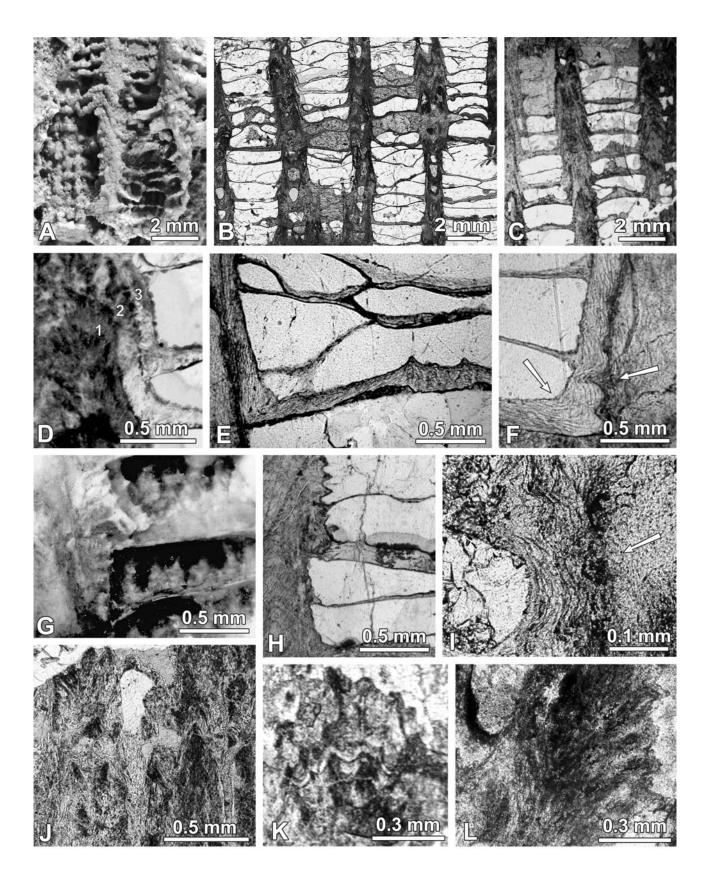
Fig. 2. Corals of the species *Cyathophora steinmanni* Fritzsche, 1924. **A–C, F, H.** Colony structure and traces of skeleton microstructure; A. Colony in calicular view; B. A fragment displaying plocoid to subcerioid arrangement of calices; note deep calices with elevated wall. C. Corallites divided by a narrow perithecal space fading in places, transverse thin section; F. Transverse section of the endothecal element covered with multiple fascicles of fibres (dark, roundish fields – 1–5); H. Enlarged septum S1 with accretion lines and traces of a vertical fascicle (white arrow at the centre) and two diverging lateral fascicles (dark arrow – upper left); Jastrzębia near Lanckorona, Polish Outer Carpathians, early Aptian (colony: UJ 4P 10; thin section: UJ 4P 10a). **D, E, G.** Colony with primary characteristics of the skeleton preserved in transparent silica; D. Fragment of partly abraded surface of colony showing a single calice with amplexoid septa, the septa continue as isolated fascicles of fibres on the surface of tabula, disorderly growing fascicles are developed as well; E. Detail showing rudimentary septa and well-defined septal spines (arrow); G. Succeeding growth lines of the basal plate of the tabula observed on its lower side; Jastrzębia near Lanckorona, Polish Outer Carpathians, early Aptian (UJ 4P 60); I, J. Skeleton presenting traces of primary microstructure. I. Costo-septum in transverse section showing lines of accretion of the skeleton; dark points represent fascicles of fibres preserved in traces, concentric arrangement of the accretion lines show the position of more or less completely recrystallized fascicles of fibres; J. Enlarged detail from Fig. 2I: lower arrows indicating vertical fascicles of fibres and an upper arrow showing completely recrystallized lateral fascicle; Trzemesna, Polish Outer Carpathians, late Barremian (UJ 4P 68a); K, L. Radial elements showing traces of septal microarchitecture and microstructure; costo-septa are composed of single rows of fascicles of fibres at the septal part, with additional, laterally inclined fascicles in the wall and in the costal part; Jastrzębia near Lanckorona, Polish Outer Carpathians, early Aptian (UJ 4P 70a).

formed of monolinearly arranged fascicle tips, marked as sharp denticles (6–10 and more in 1 mm), while the rest of the costo-septal blade, multifascicular in structure, is made of a small number of fascicles lying in the plane of the septum and others, diverging to the sides (Fig. 2K, L). When compared with large-corallite species, the costo-septum in *C. steinmanni* is made of a single morphological element, homologous to the individual septal spine of *C. richardi*.

In specimen UJ P 68 of *Cyathophora steinmanni*, besides massive incremental layers of the whole skeletal fabrics, a uniform micro-lamellation can be observed (Figs 2I, J, 3E–I). In each skeletal element, there are discernible

Fig. 3.   Corals of the species *Cyathophora steinmanni* Fritzsche, 1924. **A.** Corallite in longitudinal broken section showing tabular endothecal elements and septal spines on the wall; Jastrzębia near Lanckorona, Polish Outer Carpathians, early Aptian (UJ 4P 62). **B, D.** Longitudinal thin sections; B. Tabuloid endotheca and narrow peritheca; D. Wall showing fascicular microstructure and succeeding growth phases (1-3), each with formation of a tabular element of the endotheca; Jastrzębia near Lanckorona, Polish Outer Carpathians, early Aptian (UJ 4P 10b). **C, J, K.** Longitudinal thin sections; C. Tabuloid endotheca, at right, thick stereomal deposits discernible on the tabula; J. The section parallel to the wall cutting costal parts of radial elements, which are built of diverging fascicles of fibres. K. Longitudinal section of the septum built of well-defined fascicles of fibres arranged in fan-like form, with well-marked skeletal growth lines (UJ 4P 70b); Jastrzębia near Lanckorona, Polish Outer Carpathians, early Aptian. **E, F, I.** Longitudinal thin sections; E. Fascicles of fibres developed on the upper surface of the tabula; F. Wall region showing two phases of primary growth position of the septum with fascicles of fibres, the ends of which form denticulation on the septal border (right arrow), overgrown with new portion of the skeleton with well-marked succeeding growth lines (left arrow); I. Fascicles of fibres of the inner septal border (arrow) overgrown by new portion of the skeleton; Trzemesna, Polish Outer Carpathians, late Barremian (UJ 4P 68b). **G, H, L.** Longitudinal sections; G. Polished section showing succeeding tabulae and amplexoid septa formed of fascicles of fibres. **H.** Longitudinal thin section showing wall, tabulae and a fragment of inner septal border with denticulation; L. Longitudinal thin section of septum with fascicles of fibres, the ends of which form denticulation on the septal inner border, growth lines are not discernible; Jastrzębia near Lanckorona, Polish Outer Carpathians, early Aptian (UJ 4P 60b).

superposing micro-lamellae, sub-parallel to the skeletal surface. The micro-lamellae are irregular in shape, about 10–15 μm thick, somewhat scaly in nature, when observed in thin sections. Skeletal elements are in structural continuity. In longitudinal sections of the wall, the lamellation observed in massive incremental layers of the sclerenchyme (the latter about 600 to 1600 μm in thickness), reveals a continuity with the lamellation of the upper dissepimental layer. The micro-lamellae of the tabula (or dissepiment) continue into the layers lining the wall (Fig. 3F). At this state of preservation, the primarily fibrous fascicles are perceived as simple spines without traces of fibrous structure. A solitary spine developed on the tabula, when observed in longitudinal section, shows a micro-lamellation continuing into that of the tabula (Fig. 3E).

The micro-lamellation observed in the cyathophoran skeleton corresponds to primary skeleton lamellation, resulting from the accretionary mode of formation of successive mineral- or organics-rich elementary portions, as is observed in extant and fossil corals (Stolarski, 2003, figs 8C, 12A, 15B2).

The corallite morphology and microstructure of septa presented here allow differentiation of the genus *Cyathophora* from the genus *Stylina* as well as differentiation from other genera of the suborder Stylinina Alloiteau, 1952.

STRUCTURAL PATTERN IN THE FAMILY STYLINIDAE D'ORBIGNY, 1851

In the family Stylinidae, the radial elements are well-developed, composed of trabeculae and ending on the inner border with auriculae (Gill, 1977). The endotheca is predominantly tabuloid, while the exotheca is mostly vesicular. In some genera, a columella is present.

Morphology and microstructure of skeleton in *Stylina* Lamarck

The genus *Stylina*, with the type species, *S. echinulata* Lamarck, 1816, like many other genera introduced in the XIX century, still awaits formal revision. The characteristic features of *Stylina* are as follows: colony plocoid, peritheca dissepimental, endotheca mostly tabuloid, columella styliform, auricular morphology of the inner septal margin, and trabecular microstructure of septa. The last three features are absent in *Cyathophora.*

The microstructure characteristics of the genus, observed in *Stylina gaulardi* Michelin, 1843 (Fig. 4A–C, Table 1, presented also in Stolarski and Roniewicz, 2001, fig. 2.1), are as follows: the septa are built of a single row of typically developed *trabeculae* having centres with transparent axial fields of RAD, surrounded by thickening deposits TD (Fig. 4B, C; see above heading, Terminology of Skeletal Structure). The trabeculae have lateral offsets (Jell, 1969: secondary trabeculae), which form lateral granules distributed asymmetrically on both septal sides; the diameter of the lateral offset does not equal that of the main trabecular body (terminology after Morycowa and Roniewicz, 1995a). In this Jurassic species, the diameters of the main trabecular body measured in a radial direction are approximately 50 μm. In other Cretaceous species, similar diameters attaining 45–65 μm are observed in *S. parvistella* Volz (Morycowa, 1971, p. 46) and larger diameters from 64 to 100 (120) μm, in *S. regularis* de Fromentel (Morycowa, 1971, p. 47, fig. 6D). Also other Cretaceous corals *Heliocoenia carpathica* Morycowa (Morycowa, 1964, pl. 8, fig. 1c) and *H. rarauensis* Morycowa (Morycowa, 1971, pl. 8, fig. 1b–d), exhibit recrystallized, nontransparent trabeculae in the septa (40–60 μm) and thicker trabeculae in the costal part (110–200 μm in diameter).

A comparison of the two architectural and microstructural patterns in stylinids and cyathophorids proves that *Cyathophora* should not be classified near the stylinids. The microstructural features of the cyathophoran skeleton are similar to those of the Stylophyllidae, suborder Stylophyllina Beauvais, 1980.

STRUCTURAL PATTERN IN THE FAMILY STYLOPHYLLIDAE FRECH, 1890

Morphology and microstructure of skeleton in some Triassic and Jurassic stylophyllids

In the Stylophyllidae, the septa are composed of *septal spines,* the endotheca is mostly tabuloid, and all skeletal parts (i.e., septal spines, endotheca and wall) are in structural continuity. The septal spines either coalesce to form septal blades, or remain free.

The morphology of corallites and the microstructural characteristics of diverse Triassic stylophyllid genera were described by Cuif (1972) and Roniewicz (1989), while Early Jurassic examples were described by Stolarski and Dieni (2002), and Stolarski and Russo (2002).

In approximately 10 examined species of common Rhaetian genera *Stylophyllum* Reuss, *Stylophyllopsis* Frech, *Pinacophyllum* Frech, *Coccophyllum* Reuss and *Anthostylis* Roniewicz, the skeleton fibres are arranged in fascicles or in scales (Roniewicz, 1989, pl. 42). The *fascicles of fibres* (named also *fibre boundles* by Roniewicz, 1989) form with their tips a sharp and dense micro-ornamentation of the skeleton surface (compare Roniewicz 1989, pl. 42, fig. 4a–c, pl. 43, fig. 2a). Similar micro-ornamentation covers the septal spines in the stylophyllinan Sinemurian corals *Stylophyllopsis, Haimeicyclus* and others (Stolarski and Roniewicz, 2001, fig. 4.2; Stolarski and Russo, 2002, figs 5, 7; herein Fig. 5 A–E): the diameters of the fascicles considered are ca. 40 µm. In addition to the above, typical stylophyllid characters of morphology and microstructure are to be observed in a large-corallite, branching coral from the Middle Jurassic, described under the name of *Epistreptophyllum* from the Callovian of Israel (Gill, 1982).

In the majority of stylophyllid genera, the septal spines are thick and compound in structure, built of multiple, elongated, crowded fascicles, strikingly similar to those observed in the costo-septa of *Cyathophora richardi,* while the structure of *Anthostylis,* represented by one species, *A. acanthophora* (Frech, 1890), resembles that in *C. steinmanni* (Fig. 5F–H, compare to Fig. 2D, E).

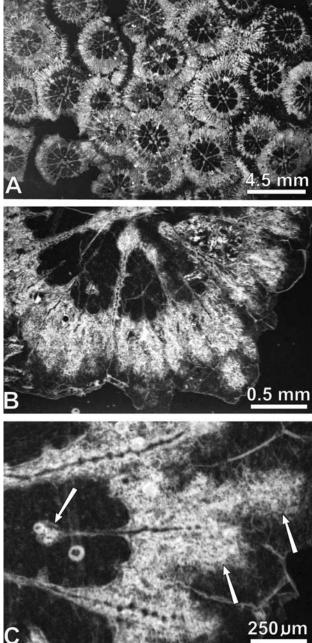### Morphology and microstructure of skeleton in *Anthostylis acanthophora* (Frech, 1890)

Morphology. The colony of the type of *Anthostylis acanthophora* is massive and cerioid, radial elements are sub- and non-confluent, and in the peripheral part of each septum a large vertical, trabecula-like mural spine is present. The endotheca is formed of flat or convex tabulae and tabuloid or rare vesicular dissepiments; a central protuberance is frequently developed on the upper surface of the endothecal elements, formed of fibrous sclerenchyme. Gross growth layers of the sclerenchyme may be observed.

Microstructure. The septa are formed of single rows of fascicles of fibres measuring 80–100 µm in diameter (Fig. 5F–H), which are similar to those from the most simply structured cyathophoran septa exemplified by *Cyathophora steinmanni.* Mural spines, attaining diameters of 250–350 µm, show a structure analogous to trabeculae, with radial fibres and a distinctive axis (compare *Coccophyllm acanthophorum* Frech in Cuif (1972, fig. 31; herein Fig. 5G, H).

Fig. 4. Corals of the species *Stylina gaulardi* Michelin, 1843. **A.** Colony in transverse sections. **B.** Radial apparatus showing typical stylinid features: costo-septa with well-developed costal part, septa with sharp lateral granulations and auriculae on the inner septal borders, at the upper part, a fragment of columella; trabeculae well-marked. **C.** Septum adaxially ending with auricula (left arrow) and septa made of single rows of well-defined trabeculae (observable at the mid-line of the septum); granulations prominent and rare; arrows (at right) show large costal parts; Dun, Meuse, France, Oxfordian (MNHN, coll. Michelin, no. 213).

Although similar to each other in general morphology, the Triassic *Anthostylis* and Cretaceous species of *Cyathophora steinmanni* differ in the type of radial elements (septa in the former and costo-septa in the latter) and in wall elements; in *Anthostylis* these are represented by mural spines,
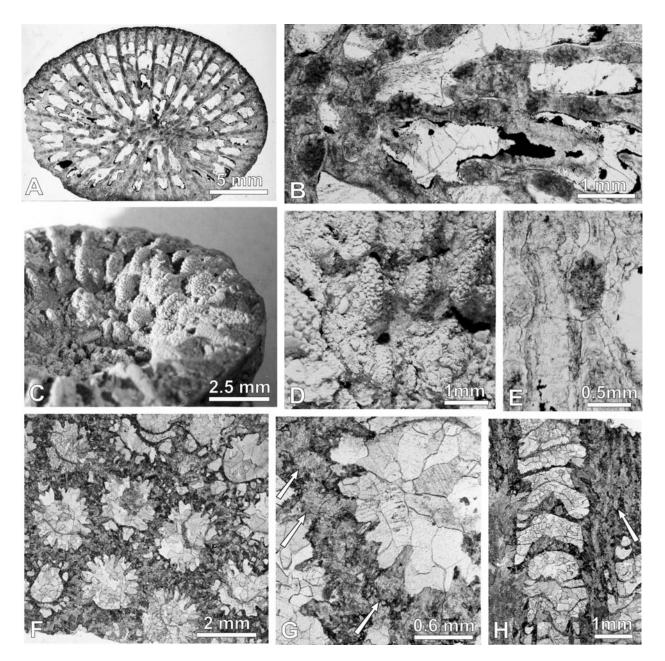
Fig. 5. Corals of the genera *Stylophyllopsis* Frech, 1890 and *Anthostylis* Roniewicz, 1989. **A, B, E.** *Stylophyllopsis rugosa (*Duncan and Wright, in Duncan 1868); A. Corallum in transverse section showing well-defined septal spines in the septa; B, E. Septa built of septal spines showing fascicles of fibers; Honeybourne, East of Evesham, Worcester, England, Charmutian, Early Jurassic (BM R. 13287). **C, D.** *Stylophyllopsis mucronata* (Duncan, 1868); C. Calice with thick septal spines covered with minute granulation; D. Surface of septal spines with ornamentation by tips of fascicles of fibres; Fenny Compton, south-east of Warwick, England, Early Jurassic (BM R. 13320). **F–H.** *Anthostylis acanthophora* (Frech, 1890); F, G. Transverse sections showing corallites with short septa and large elements of endotheca, arrows show thick, trabecula-like elements of the wall; H. Longitudinal section with tabular endotheca showing stereomal deposit at the middle of the corallite and the wall made of thick trabecula-like, vertical elements (arrow). Northern Calcareous Alps, Rhaetian, Late Triassic (NHMW 1982/57/32).

while in *C. steinmanni* they are composed of diverging fascicles of fibres (Fig. 3J–K).

DISCUSSION AND CONCLUSIONS

The inclusion of an organic phase in the fibrocrystal structure and the taxonomical specificity of its biochemical composition are evidence of an organic control over the process of skeletogenesis and the complex, mineral-organic nature of the fibrocrystals (Chevalier, 1971; Cuif *et al.*, 1997, 1999; Gautret *et al.*, 2000; Stolarski, 2003). It supports the view that the microstructural similarities are due to biological relationships. As in Recent corals, the general expression of relationships among the fossil corals was their capacity to build skeletons of a definite microstructural

Comparison of taxonomic features of corals from the suborders Stylophyllina Beauvais and Stylinina Alloiteau

Suborder	Family	Growth form	Radial elements	Columella	Septal microstructure
Stylophyllina Beauvais	Stylophyllidae Frech	solitary, phaceloid (= pseudocolonial), colonial: cerioid, meandroid	septa	papillar: made of septal spines, or lacking	fascicles of fibres: single or composing multifascicular septal spines
	Cyathophoridae Vaughan and Wells	colonial: plocoid	costo-septa	lacking	
Stylinina Alloiteau	Stylinidae Alloiteau	phaceloid (= pseudocolonial), colonial: plocoid, dendroid	costo-septa	trabecular, styliform (circular or flattened in cross section), or lacking	trabeculae

type: either non-trabecular, fascicular, or trabecular ones, and their variations. Observations of Recent coral microstructures show that well-defined septal microstructures are effective for the diagnosis of families (compare Chevalier, 1971, 1975; Pacific representatives of the Faviidae, Mussidae, Caryophylliidae), and that families, defined only by their morphology, should be redefined (Benzoni *et al.*, 2007). The "core" genera in the above families are verified by molecular tests, confirming their close phylogenetic relationships (compare Romano and Cairns, 2000; Benzoni *et al.*, 2007; Budd *et al.*, 2012).

The vestiges of multifascicular septal microstructure observed in *C. richardi* (Fig. 1) correspond to those observed in the septal, thick spines of the Rhaetian *Stylophyllum paradoxum* Frech (Roniewicz, 1989, pl. 42, fig. 9) and the Sinemurian *Stylophyllopsis rugosa (*Duncan and Wright in Duncan, 1868; see Stolarski and Roniewicz, 2001, fig. 5.2; herein Fig. 5A, B, E), *Stylophyllopsis* sp. and *Stylophyllopsis* cf. *rugosa* (Duncan and Wright, in Duncan, 1868; Stolarski and Russo, 2002, figs 5, 7), *Stylophyllopsis mucronata* Duncan (Fig. 5C, D), and *Haimeicyclus* (compare Stolarski and Russo, 2002). The small-coralited *C. steinmanni* has radial elements with the septal part built of a single row of a few fascicles of fibres and a multifascicular costal part (Fig. 2H, K, L). This type of structure is similar to that observed in the septal spines of *Anthostylis,* where the peripheral parts resemble single, thick trabeculae (Fig. 5G, H).

The principal difference between *Cyathophora* and the stylinids lies in the different microstructural types of their skeletons, which are non-trabecular in the former *vs.* trabecular in the latter. Thus, the apparent morphological resemblances between *Cyathophora* and other corals, not parallelled by the microstructural ones, are an example of homeomorphy.

The authors interpret the similarity of the skeleton microstructure of *Cyathophora* and the stylophyllid genus *Stylophyllopsis* as due to their being phylogenetically related. It allows reclassification of the Cyathophoridae, with the only genus *Cyathophora*, from the suborder Stylinina into the Stylophyllina. In this Mesozoic group of corals, the non-trabecular fabrics make a substantial part of the skeleton, including septa, and this microstructure exhibits a considerable range of variations (e.g., *Haimeicyclus* and *Stylophyllopsis* in Stolarski and Russo, 2002, and *Thecocyathus* in Stolarski and Dieni, 2002).

TAXONOMY

Suborder Stylophyllina Beauvais, 1980 emended by Roniewicz, 1989

Macrostructural and microstructural characteristics: Corals from solitary and phaceloid to diverse colonial forms: cerioid, meandroid and plocoid. Radial elements, non-trabecular in structure, composed of septal spines made of single or multiple fascicles of fibres more or less coalesced to form septal blades. Columella papillar, if developed. Sclerenchyme highly uniform in the whole skeleton, continuing from the septa and wall into endotheca and organized either in fascicles of fibres named also bundles of fibres, or into scales.

Families included: Stylophyllidae Frech, 1890, Middle Triassic (middle Anisian)–Middle Jurassic (Callovian); Gigantostyliidae Frech, 1890, Upper Triassic (Rhaetian); *pars* Thecocyathidae Vaughan and Wells, 1943: *Thecocyathus,* Lower Jurassic (Toarcian) – Upper Jurassic (Oxfordian); Cyathophoridae Vaughan and Wells, 1943, Early Jurassic (in Gerth 1928), Middle Jurassic (Bajocian) – Upper Cretaceous (Cenomanian).

The above differentiation into families is based on the structure of the wall and septa. The Gigantostyliidae were discussed in Cuif (1972, 1977, 2010) and Roniewicz (1989); the Stylophyllidae in Cuif (1972), Roniewicz (1989) and Stolarski and Russo (2002); discussion on systematic position of Thecocyathidae with indication of their place within the Stylophyllina was initiated by Stolarski and Dieni (2002) and Stolarski and Russo (2002); Cyathophoridae are discussed herein.

Structural differences between the suborders Stylophyllina Beauvais, 1980 and Stylinina Alloiteau, 1952 (Table 2): The Stylophyllina embrace a large spectrum of growth forms (see above), while Stylinina display a spectrum confined to phaceloid, plocoid and dendroid forms (= uniserial erect in Coates and Jackson, 1987). Corals of the both suborders, similar in their corallite morphology with the exception of styliform columella specific of majority of the Stylinina, differ essentially in the microstructural features (Table 2).

A non-trabecular microstructure of the Stylophyllina displays a broad range of variability, observed in the following genera: *Gigantostylis* Frech from the family Gigantostyliidae, *Pinacophyllum* Frech, *Stylophyllum* Reuss, *Stylophyllopsis* Frech and *Anthostylis* Roniewicz (the latter two see Fig. 5; the remaining see Roniewicz, 1989) from the Stylophyllidae, and *Cyathophora* Michelin (see Figs 1, 3) from the Cyathophoridae. In the stylophyllid group of corals, the most characteristic feature of septal micromorphology is a dense and uniform, minute granulation, made of crowded tips of fascicles of fibres (Fig. 5B, E).

Up to now, the diagnostic features of the Stylinina (families Stylinidae d'Orbigny, Euhelliidae Vaughan and Wells, Cladophyl-

liidae Morycowa and Roniewicz), beside the morphology, have been confined to the micromorphology of septa, i.e., the auriculae on the inner septal borders (Gill, 1977; Morycowa and Roniewicz, 1990) and to their sharp lateral granulations. The trabecular costo-septa of *Stylina gaulardi* Michelin (Fig. 4B, C) presented here allow completion of the list of diagnostic features with trabeculae of small diameters of their *main trabecular body* and lateral *secondary trabeculae,* the latter manifested on septal sides as rare, prominent and sharp granulations. A similar microstructure has been noted in other stylinids.

Stratigraphic range: The Stylophyllina, beginning in the middle Anisian with the Stylophyllidae, continued in the form of Cyathophoridae up to the Cenomanian.

Family CYATHOPHORIDAE Vaughan and Wells, 1943, emended Alloiteau, 1952

The emendation proposed here concerns the microstructural characteristics and the family content.

Emended diagnosis: Radial elements costo-septal. Septa in the form of ridges or spines on the inner-wall surface and, frequently, amplexoid. Endotheca and exotheca tabuloid with the addition of dissepiments. Wall septothecal or septo-parathecal. Sclerenchyme of the wall and radial elements continuing into the upper layer of endothecal elements. Fibrous microstructure of skeleton; the spines (called septal spines) are composed of fibres organized into fascicles.

The family is known exclusively for the subcerioid-plocoid type of colony growth form.

Remarks on the systematics: The above diagnosis demonstrates that the Cyathophoridae cannot be maintained among the Stylinina, owing to the different skeleton microstructure. The structure of radial elements allows the discrimination of cyathophorids as a distinct group among Mesozoic corals and the inclusion of them with the Stylophyllina.

Because of limited observations as a result of diagenesis, the cyathophorid microstructure is less known than that of the stylophyllinan corals. Thus, precise delimitation of the microstructural cyathophoran type within a diversified spectrum of stylophyllinan patterns is unfeasible at present.

Generic content of the family: *Cyathophora* Michelin, 1843 and, with reservations, *Confusaforma* Löser, 1987 and *Columellophora* Eliášová, 1989.

Discussion of the former scope of the family: Primarily, Vaughan and Wells, 1943 included to the family (then subfamily) the following genera: *Cyathophora* Michelin, 1843; *Holocysis* Lonsdale, 1849; *Heterocoenia* Milne Edwards and Haime, 1848; *Cassianastraea* Volz, 1896; *Ewaldocoenia* Oppenheim, 1921; *Procyathophora* Weissermel, 1928; *Miyakosmilia* Eguchi, 1936.

The above list of genera is reduced to only one genus, *Cyathophora,* because *Holocystis* belongs to the Stylinidae, while *Heterocoenia,* known under the synonymous names *Miyakosmilia* and *Ewaldocoenia,* represents the family Heterocoenidae on the basis of microstructural data. The Triassic genera *Cassianastraea* and *Procyathophora* have a non-scleractinian type of the skeleton structure; *Cassianastraea* was placed in a new hydrozoan order Lemniscasterina by Montanaro-Gallitelli (1980), with the suggestion that *Procyathophora* by analogy should also be reclassified.

Later, the family content was augmented, among others, with *Cyathophoropsis* Alloiteau, 1947 and *Miophora* Chevalier, 1963. The Early Cretaceous *Cyathophoropsis* Alloiteau is poorly diagnosed and its status as a cyathophorid genus hardly can be maintained. The Miocene genus *Miophora* cannot be maintained in the family because of its specific microstructure of septa and the structural porosity of the wall. Pandey *et al.* (2002) considered the Barremian-Aptian genus *Nowakocoenia* Kołodziej and Gedl, 2000 to be close to *Cyathophora.* However, this genus shows a para-

septotheca built of thin endothecal elements and rare, vertical, continuous wall elements of radial structure (up to 160 µm in diameter), extending into lamellar septa (Kołodziej and Gedl, 2000, figs. 8, 9); this set of features excludes it from C*yathophora.*

There remain two Late Cretaceous genera, Cenomanian *Confusaforma* Löser,1987 and the late Cenomanian-early Turonian *Columellophora* Eliášová, 1989, which, in general, share morphological features with *Cyathophora,* but their microstructural features are unknown.

Genus *Cyathophora* Michelin 1843, emended diagnosis

Synonym: *Amphiphora* Alloiteau and Bernier, 1969
Type species: *Cyathophora richardi* Michelin, 1843

Diagnosis: Plocoid to subcerioid. Radial elements nonconfluent and subconfluent, costo-septa vertically discontinuous. Septa amplexoid, in the form of ridges on the inner surface of the wall with a tendency to extend onto the surface of endothecal elements. Endotheca formed of horizontal or convex tabulae and vesiculous dissepiments. Exotheca of similar structure to endotheca. Wall septothecal or septo-parathecal. Increase by perithecal budding. Microstructure fascicular.

Remarks on diagnostic features: Michelin (1843, p. 104, pl. 26, fig. 1a, b) diagnosed the genus as follows: *"Cyathophora* tuberous, spherical, [built of] aggregated tubes; tubes polygonal, elongated, centrifugal and divided by diaphragms, externally terminating by stars, stars deep, subpolygonal, indistinctly radiate; borders thick".

Despite this general and rather vague diagnosis, the taxon is easily identifiable, thanks to the illustration of the type specimen. It shows the typical structure of the colony, which allows it to be distinguished from other Jurassic corals (see Lathuilière, 2014; Zaman and Lathuilière, 2014, figs 1, 2).

Koby (1882, p. 98) was the first to draw attention to the following characteristics of the septal apparatus in *Cyathophora:* septa barely protruding, nearly rudimentary, represented by striations that descend along the internal side of wall, and to their anastomosis on the tabulae through filiform prolongations.

The Jurassic genus *Amphiphora* Alloiteau and Bernier, 1969 with *A. serannensis* from the late Jurassic of France as the type species (1969, pl. 28, figs 1, 3), represents all morphological features of the genus *Cyathophora* and specific characteristics close to those of *C. richardi* and *C. claudiensis.*

Discussion on the type species: The status of *C. richardi* Michelin, 1843 as the type species of the genus *Cyathophora* Michelin, 1843 was questioned by Milne Edwards and Haime (1857, t. 2, p. 271).These authors included it to the synonymy of *Astrea bourgueti* Defrance, 1826. This choice, although never documented, was commonly accepted. In the literature, diverse species have been synonymized with *Cyathophora bourgueti* on the basis of large corallite diameters, even if their stratigraphic positions are very distant (e.g., Bajocian and Kimmeridgian, Pandey *et al.,* 2002). Other features were not identified, because of the extensive recrystallization of the skeletons.

The choice by Milne Edwards and Haime was questioned by Alloiteau (1948). This author discussed a peculiarity of the skeleton structure in *Cyathophora richardi* Michelin, on the basis of the specimen MNHN no. 4567 from the collection d'Orbigny. Lathuilière (2014) and Zaman and Lathuilière (2014) have presented the lectotype of *Cyathophora richardi* from the Michelin collection, No. MNHN A32288, and stated its consistency with Michelin's original description and figures. These authors follow Milne Edwards and Haime (1857, t. 2, p. 271) in regarding *Astrea bourgueti* Defrance, 1826 as a senior synonym of *C. richardi* Michelin, 1843.

In discussing a commonly supposed identity of *C. richardi* and *A. bourgueti,* Alloiteau (1948) pointed to the fact that Defrance

(1826) and Michelin (1843) identified their species with different taxa, described and illustrated in earlier literature, belonging to the collection no longer in existence. Defrance identified the species with *Heliolithe irregulier* Guettard (1770, pl. 53, fig. 4) as showing widely spaced calices with 24 large and 24 smaller septa, while Michelin identified his species with *Astroites globulaire comprime* Guettard (1770, pl. 55, fig. 3) having crowded pentagonal and hexagonal calices and numerous septa.

The present authors follow Alloiteau in considering *C. richardi* as a valuable, originally well-illustrated species represented by the type specimen still available (MNHN no. A32288), while *A. bourgueti* Defrance, 1826 as a *nomen dubium*, originally not figured, but related to the 18th-century illustration of a coral different from the Michelin specimen and not preserved in any collection.

Remarks on the species included: Owing to homeomorphy, true cyathophoras may be hidden among the species described under the generic names of *Pseudocoenia, Cryptocoenia* and *Adelocoenia*; a list of species described as *Cyathophora* should also be revised. The present authors do not have the possibility to make such a revision and for this reason uphold their opinion on the species content. Lathuilière (1989) in his *Répertoire* listed more than 60 nominal species of *Cyathophora,* among them about 40 Jurassic taxa.

Characteristics for species differentiation, as in the case of all plocoid corals, include the following: diameters of corallites, distance between corallite centres, number of septa, and endothecal density. However, the changeable development of septal blades, resulting in an unstable number of septa and changeable width of peritheca, leads to the imprecise delimitation of taxa. It is supposed that many nominal species are synonyms.

Stratigraphic range: The earliest report on the Early Jurassic *Cyathophora* in South America by Gerth (1928) remains unconfirmed. An unquestionable *Cyathophora*, determined as *C. bourgueti* Defrance, is known from the Bajocian of India (Pandey *et al.*, 2002). The latest *Cyathophora* occurrence is dated as late Cenomanian (*C. fontserei* Battaler, late Cenomanian: Löser, 1989; *C. regularis* de Fromentel, late Cenomanian – early Turonian: Eliášová, 1992, 1997).

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