A model for furcate septal increase in a Triassic scleractiniamorph

JAROSŁAW STOLARSKI, EWA RONIEWICZ, and TOMASZ GRYCUK

Triassic corals with septa that branch repeatedly and centripetally are here assigned to a new genus *Furcophyllia*. Septa of *F. septafindens* (Volz, 1896), re-described from the Italian Dolomites, are composed of 3–10 blades ("septal brooms"). Distances between adjacent septa and their branches are equal, and the thickness of all blades is approximately the same throughout ontogeny. However, none of the septal brooms show the same branching pattern. Proposed herein is a simple computer model that reproduces septal pattern, similar to that of *Furcophyllia*, based on a minimal set of rules: (i) uniform coverage of intra-calicular space; (ii) regular bifurcations following some probability; (iii) keeping some minimal distance between septal branches. The elaborate septal pattern of *Furcophyllia* suggests a distinct organization of the polyp's soft tissue, especially mesenteries whose appearance in modern corals is associated with insertion of sclerosepta. Hypothesis 1 suggests that mesenterial pairs flanked only "septal brooms" and that septal branches functionally corresponded with septal microarchitecture. Hypothesis 2 suggests that mesenterial pairs developed between all septal branches that functionally correspond with conventional septa. Delicate menianae, which developed on *Furcophyllia* septal faces (and many other Triassic corals) resemble similar septal microarchitecture of the Recent agariciid *Leptoseris fragilis* and may be closely related to the suspension feeding strategy of this coral. The furcate septal arrangement in *Furcophyllia* is unique among Triassic corals, and generally, among Mesozoic and Cenozoic corals. The only analogous corals are Cretaceous aulastraeoporids (e.g., *Preverastrea*, *Paronastraea*), *Trochoidomeandra*, and some Jurassic rhipidogyrids having secondary (apophysal) septal branches. In some Recent caryophylliids (*Trochocyathus rhombocolumna*, *Phacelocyathus flos*) primary septa may also split dichotomously and centripetally.

Key words: Scleractinia, septal growth, computer model, Triassic, Dolomites, Italy.

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Introduction

In most scleractinians, septa contribute most to corallum structure (although, for example, in pachythecaliinans, the wall is the dominating skeletal element; see Cuif and Stolarski 1999; Stolarski and Russo 2001). Septal microstructures, as well as the direct relationship of the septal system with the internal organization of the polyp, offer a possible perspective on the pathways of evolution of Scleractinia and their taxonomy. The textbook examples of septal increase in Recent and fossil Scleractinia usually show simple and straight septa that appear in skeletal ontogeny as consecutive cycles. The spectrum of variability in septal morphology is actually much greater. Septa can be nearly completely straight, smooth, and solid as in many traditional caryophylliinans (e.g., *Desmophyllum*), or undulating, porous, and covered with elaborate granulations (e.g., in Microsolenina). In some corals, septa are reduced to spines as in stylophyllids or pocilloporids. Septa may reach the corallum center or be restricted to the peripheral zone; their edges can be free or merged with other septa or the columella to form a complex axial structure.

In this paper, based on new material from Italian Dolomites, we re-describe a Triassic coral, which has a septal increase pattern that is significantly different from the examples mentioned above. Lower-order septa of the coral examined branch repeatedly and dichotomously in the upper part of the calice, and form sets composed of numerous branches (here called, based on their shape in cross-sections, septal brooms), see Fig. 1. The branching pattern is different for each septal broom. Nonetheless, distances between all septa and their branches as well as their thickness remain approximately constant throughout corallum ontogeny (Fig. 1). To elucidate this phenomenon, we utilize a computer model that reproduces septal pattern similar to that of *Furcophyllia* using a minimal set of rules. We also discuss various constructional and functional aspects of septal organization possible in *Furcophyllia* and other corals with similar skeletal characters.

Institutional abbreviations.—Specimens are housed in the following institutions: Dipartimento del Museo di Paleobiologia e dell'Orto Botanico, Università di Modena e Reggio Emilia, Modena, Italia (IPUM), Instytut Nauk Geologicznych Uni-

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wersytetu Jagiellońskiego, Kraków, Poland (UJ), Museum National d'Histoire Naturelle, Paris, Institut de Paléontologie, France (MNHN), Muzeum Geologiczne Uniwersytetu Wrocławskiego, Wrocław, Poland (MGUWr), National Museum of Natural History, Washington D.C., USA (USNM), and Instytut Paleobiologii PAN, Warsaw, Poland (ZPAL).

Other abbreviations.—CD, calicular diameter; dCRA, deposits of Centers of Rapid Accretion; GCD, greatest calicular diameter; H, height of corallum; LCD, least calicular diameter; RAF, rapid accretion front; Sd, septal density; Sx, septa of a cycle designated by numerical script.

Triassic coral

In his monograph on the celebrated St. Cassian Triassic scleractinians from the Italian Dolomites, Volz (1896: 44) described the unusual new coral *Montlivaltia septafindens* (Latin *findo* = split, divide), which has septa that repeatedly split into descendant branches. Volz (1896) assigned this species to the 19th century catch-all genus *Montlivaltia*, i.e., to the first (*M. obliqua* Münster, 1841) of four species groups of the genus, characterized by the occurrence of "*Urseptum*" (= narrow RAF, see Stolarski 2003) and "*echter Theca*" (wall with its own "calcification centers": see concepts of wall structures in Stolarski 1995). Since Volz' time, the genus *Montlivaltia* has been revised and currently comprises species with large-sized, well-separated dCRA, which have lateral septal outgrowths (see Gill 1967, 1970; Stolarski and Roniewicz 2001). These microstructural characters are expressed in the microarchitecture of *Montlivaltia* by dentate septal margins and lateral septal "carinae". Although coralla of *M. septafindens* are often diagenetically altered, their microarchitectural characters i.e., non-dentate and narrow septal edges, support the new generic (*Furcophyllia*) assignment of the coral. Evidence that no Triassic and in general, no scleractinians have such unusual septal increase, supports keeping the newly described taxon in an informal group of scleractiniamorphs.

Volz' (1896) three syntypes of *F. septafindens*, were lost during WW II. The only exception is a longitudinal section (Volz 1896: pl. 3: 25) recovered from the Geological Museum of the Wrocław University (MGUWr). This section, however, provides limited insight into species diagnostic characters, e.g., it does not record the branching septal pattern and, in fact, may represent a different species (see Remarks section). The new specimen described herein is thus the only one that shows the species-diagnostic septal branching and that can be re-examined comprehensively. It includes an ontogenetically later part of the corallum in comparison to Volz' specimens, and therefore, the species description is significantly enhanced.

Scleractiniamorpha
Genus *Furcophyllia* nov.

Type species: *Montlivaltia septafindens* Volz, 1896.

Derivation of the name: From Latin *furca* = a pitchfork, corresponding to the shape of the longest septa; and Greek *phyllon* = a leaf, a conventional ending for coral taxa, intentionally changed into *phyllia*; feminine.

Diagnosis.—Solitary, ceratoid coral differing from all known scleractinians by multiple, centripetal and usually alternating bifurcations of lower-order septa in later ontogeny.

Remarks.—The coral has been assigned to an informal category of scleractiniamorphs because of its similarity with conventional scleractinians (e.g, corallum shape, type of septal microarchitecture) but it strikingly differs from all known scleractinians by its septal formation.

Septal symmetry is not resolved into an hexameral pattern typical of Scleractinia (and scleractiniamorphs), however, insertions of additional septa in ontogeny of conventional scleractinians may significantly alter the original hexameral arrangement (e.g., Mori 1987). For these reasons, lack of a distinct hexameral symmetry, does not preclude its presence in initial/early juvenile stages, and this assumption was used to construct a computer model (see section Computer modeling of branching septa).

Furcophyllia septafindens (Volz, 1896)
Figs. 1, 2.

Montlivaltia septafindens Volz, 1896: 44, pl. 3: 22–25.

Neotype: IPUM-DOL/610; proximal part not preserved.

Type locality: St. Cassian Beds, Forcella di Sett Sass (descriptions in Ogilvie 1893: fig. 3).

Material.—The neotype (IPUM-DOL/610), thin-sectioned (IPUM-DOL/610-str, 610-slon) and with a series of peels (ZPAL H.24/1-peels/1–13). Also examined was Volz's original longitudinal thin section (MGUWr 137sz), however, it may not represent the taxon here described (see Remarks).

Table 1. Measurements (in mm; calicular dimensions measured for distalmost part of preserved corallum).

	H	GCD	LCD	Sd (mm)	F(ossa)
Volz (1896: 44)	20–35	30–40	19	7–8/1	20
IPUM-DOL/610	> 30	30	27	5/1	17

Description.—Corallum ceratoid, laterally flattened. Calicular rim narrow, axial fossa long, radial elements thin and abundant. Proximal part obliquely broken: lower half of the section records earlier, whereas upper half records later phases of corallum ontogeny. Septa originate as single blades at the calicular perimeter.

In the more proximal part of corallum, internal borders of septa lying on the opposite sides of the calice meet along the fossa. The axial borders of the longest septa are clavate, whereas the borders of the shorter septa are sharp (Fig. 1D). In the more distal part of the corallum, septa differentiate into branching septal sets separated by non-branching septa (Fig. 1A, G). Branching septa bifurcate centripetally, repeatedly, and usually alternately; they form sets of numerous branches herein called septal brooms. Branching affects at least 52 septa that are composed of 3–10 blades (Fig. 1B). Each septal
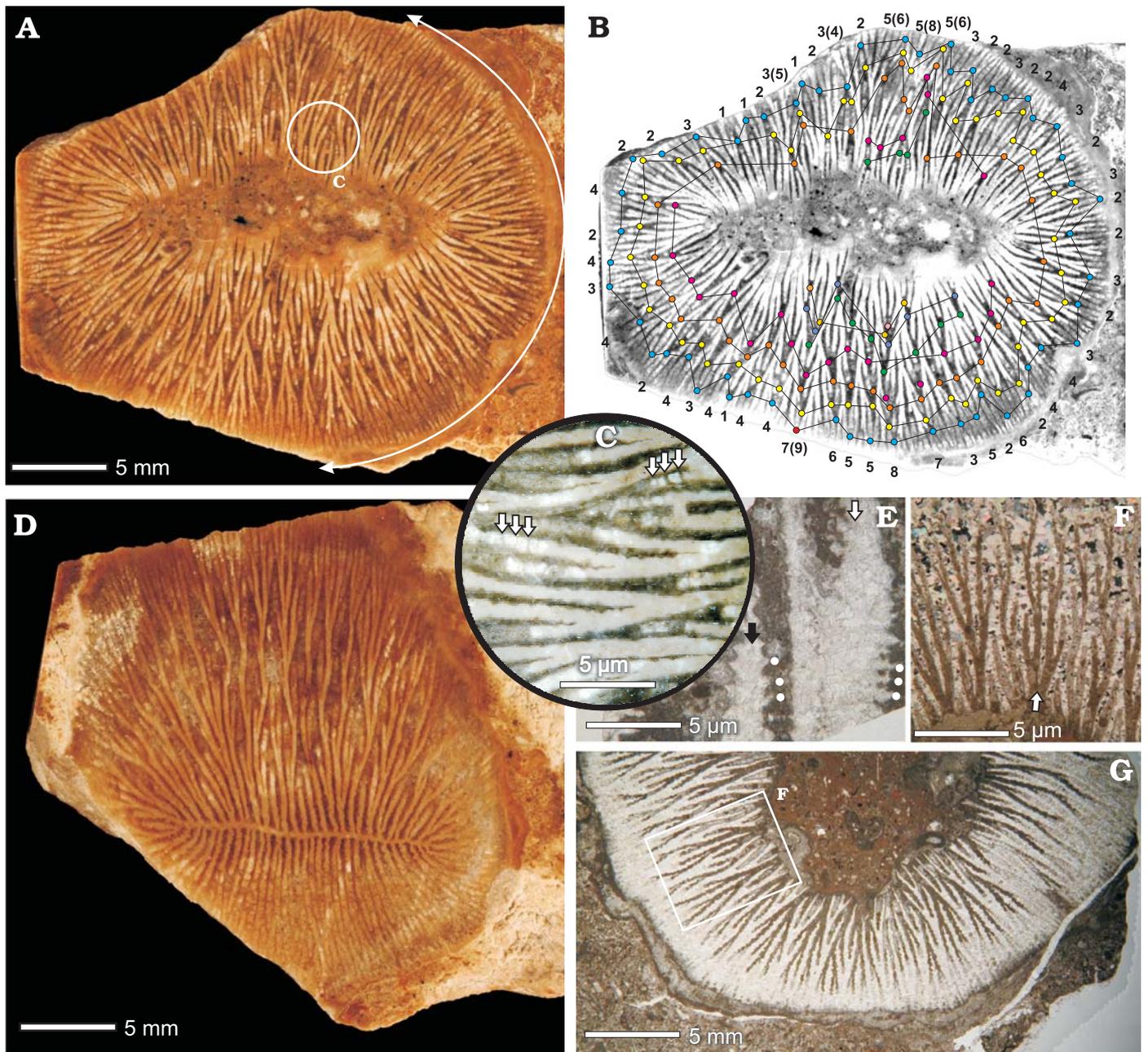
Fig. 1. *Furcophyllia septafindens* (Volz, 1896). IPUM-DOL/610 (thin-section figured in 1F, 1G is IPUM-DOL/610-str, and in 1E is IPUM-DOL/610-slon). Triassic (Middle Carnian), St. Cassian Beds, Forcella di Sett Sass, Dolomites (Italy). **A**, **B**. Transverse polished section through distal part of corallum (see Fig. 2A); with the brightness and contrast of picture; **B** adjusted. Septa of principal orders (52) branch repeatedly and centripetally and form septal brooms composed of 3–10 blades. Branching nodes of individual septal brooms are indicated as small circles in B and their total number are summed at the septal base (if given: number in bracket is the total number of nodes, the first number indicates branch generations of septal broom); nodes of the same generation (identically colored) connected with thin lines between brooms. About 110 septa of all orders were counted in a well preserved part of the corallum (white line with arrows); the estimated septal number for the section is ca. 300. **C**. Thin and dense dissepiments, easily visible, particularly in septal branching nodes (arrows). **D**. Transverse-oblique polished section in a more proximal part of corallum (see Fig. 2A); the upper half of the section is cut through a higher part of corallum and shows branching septa, whereas in the lower half of the section (and corallum) septa branch only rarely. Slightly expanded ends of the longest septa/branches (ca. 60) meet along a narrow and long axial fissure. **E**. Section with septa cut obliquely-longitudinally (white arrow) or perpendicularly (black arrow); note minute and dense menianae (white dots). **F**. Enlarged region of transverse thin section (**G**) in crossed polarized light (XPL) to accentuate shape of sediment-infilled spaces (dark) between recrystallized septa (light). **G**. Transverse thin section of the uppermost part of preserved corallum (note the wide sediment-infilled fossa).

broom has a unique branching pattern however, in which further generations appear successively in a manner resembling sympodial growth of branches. Remarkably, distances between adjacent branches and septa are equal; interseptal spaces are very narrow, 0.2–0.3 mm across (Fig. 1F). The number and size of the septa that separate the branching sets
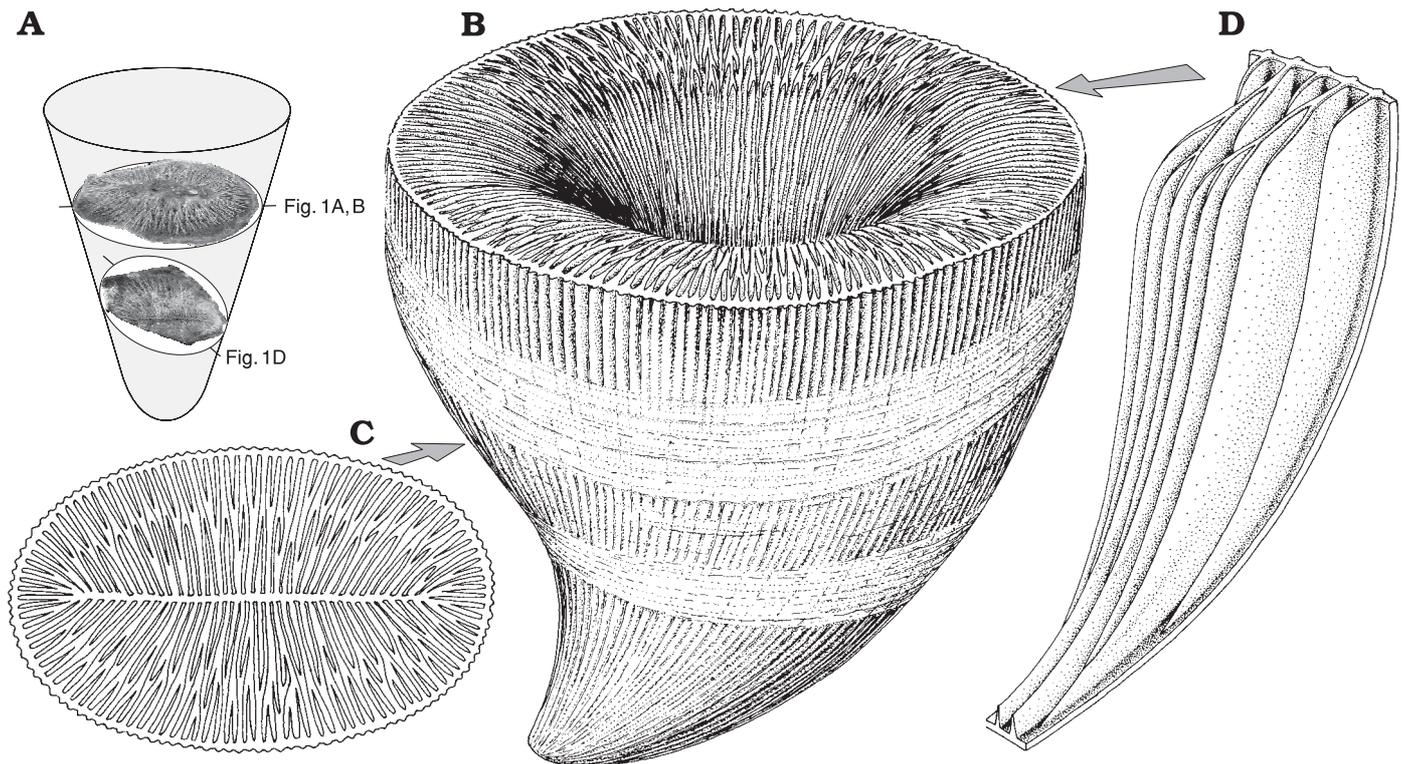
A

B

C

D

Fig. 1A, B

Fig. 1D

Fig. 2. Reconstruction of *Furcophyllia septafindens* (Volz, 1896). **A**. Presumable position of polished sections (Fig. 1A, D) indicated on a simplified outline of the corallum. **B**. Distal-lateral view of a cornute corallum (see Volz 1896: fig. 22); septa very dense, probably not very exsert, fossa deep (IPUM-DOL/610), costae covered with bands of thin epitheca (speculation based on common occurrence of epitheca in Triassic scleractinians). **C**. Postulated section in the region indicated by the arrow: septa bifurcate rarely and extend to a narrow axial fissure (see Volz 1896: fig. 23, and herein Fig. 1D). **D**. Enlarged portion of the distal corallum showing centripetal septal bifurcations (septal flank menianae are omitted). Reconstructions based on sections of IPUM-DOL/610, and specimens of *Montlivaltia septafindens* illustrated by Volz (1896: pl. 3: 22–25).

are variable. In places there are only 2–3 separating septa, in other places there are as many as 7 septa (Fig. 1A). The longest septum reaches half the distance to the fossa; the next order septa are considerably shorter. The shortest septa are thin and regularly distributed. All septa and septal branches have approximately the same thickness in cross-section (usually ca. 0.2 mm in the thickest part). Remarkably thinner septa (ca. 0.08 mm thick) are ontogenetically younger i.e., their axial margins and the incipient septa inserted at the wall region. About 110 septa of all orders (including also incipient septa, only 0.5 mm in length) were counted in the thecal zone of the well preserved part of the calice (white line with arrows in Fig. 1A). The estimated septal number in the thecal zone for the distal part of the corallum is ca. 300. The septa in transverse section show regular thickenings, ca. 250 μm in diameter. Short symmetrical and asymmetrical offsets form regularly distributed lateral septal granulations. The granulations are free or fuse into ridges (menianae), parallel to the distal septal border (Fig. 1E).

Endotheca dense, constructed of abundant, small or flat and extended dissepiments. Dissepiments are steeply inclined in an axial direction. The wall is constructed by peripheral borders of thin and densely crowded septa and, occasional dissepiments. In places, there are possible traces of thin epitheca.

Remarks.—Volz (1896: 45, pl. 3: 24) documented a narrow mid-septal zone (RAF *sensu* Stolarski 2003) in the species, the "*Urseptum*"; the character is common in traditional caryophylliinans (clearly polyphyletic in molecular studies: Romano and Cairns 2000). Though the original microstructure of the newly acquired specimen is diagenetically altered, Volz' observations are supported by the very thin axial borders of septa.

The species is very rare, as already noted by Volz (1896: 45), until now recognized only at the Forcella di Sett Sass locality. Of the two figured specimens (Volz 1896: pl. 3: 22–25), one is presented in lateral view (pl. 3: 22) and in transverse sections (pl. 3: 23 and 24); the second is in longitudinal (pl. 3: 25) section. One of the transverse sections (pl. 3: 24) shows abundant, small dissepiments, whereas the longitudinal section shows vesicular, large and scanty dissepiments. The specimen investigated here, IPUM-DOL/610, with diagnostic branching septa, has endotheca corresponding to the first of the Volz' illustrations (Volz 1896: pl. 3: 24). It is thus very likely that the second illustration of Volz (pl. 3: 25) does not represent the same taxon.

Various aspects of the unique septal branching of *Furcophyllia* are discussed in the following sections. Here we focus on another distinct character of *Furcophyllia*, its very long and narrow calicular fossa. This feature correlates with

lateral corallum compression and the lack of an axial structure. This is a relatively rare architectural combination in Recent (occurs e.g, in *Flabellum*) and fossil corals. Among contemporaneous Triassic corals, calices with comparably long fossae occur in the Triassic coral *Cuifia* Melnikova, 1975. For example, in a specimen of *C. marmorea* (Frech, 1890) described by Roniewicz (1996) the GCD reaches 110 mm, and the fossa is 30 mm long.

Occurrence.—Carnian, St. Cassian Beds, Forcella di Sett Sass, Dolomites, Italy.

Computer modeling of branching septa

The intriguing pattern of septal arrangement in *Furcophyllia septafindens* (Volz, 1896) provides the stimulus for examining their geometrical relationships using a simple computer model. The term "simulation" used further in the text, refers to visualization of the septal pattern using some geometrical rules defined in the study and does not pretend to illustrate biochemically- or anatomically-driven septal morphogenesis.

An example using *F. septafindens* shows that the septal branching is generally regular and "deterministic", demonstrated by the almost uniform partitioning of calicular space and the approximately equal distance between septal branches. This suggests the existence of some general rules governing the process of septal growth. It was interesting to find a minimal set of rules, which can be used to generate the main features of the septal pattern. Uniform partitioning of corallite space seems to be the overriding rule, valid for most corals, and this rule serves as the basis of our model. Some additional rules, especially related to the process of branching, are discussed in this section.

Minimal model

In our simple geometrical model of septal branching, a simulation was performed for a two-dimensional slice of circular corallite. All septa are initialized at the theca. During the simulation, the septa expand together toward the center according to the following rules: (i) septa tend to be uniformly distributed in the space; (ii) septa are able to bifurcate with some probability; (iii) some minimal distance exists between septal branches. These general rules are uniquely expressed in our model.

Parameters of the model.—Two basic parameters are defined at the beginning: maximal septum order, n_{max}, and mean number, q, of bifurcations per radius of coral cross-section. In a fully symmetric model, an initial number of septa, k_{ini}, at the corallite border is expressed by n_{max} as follows:

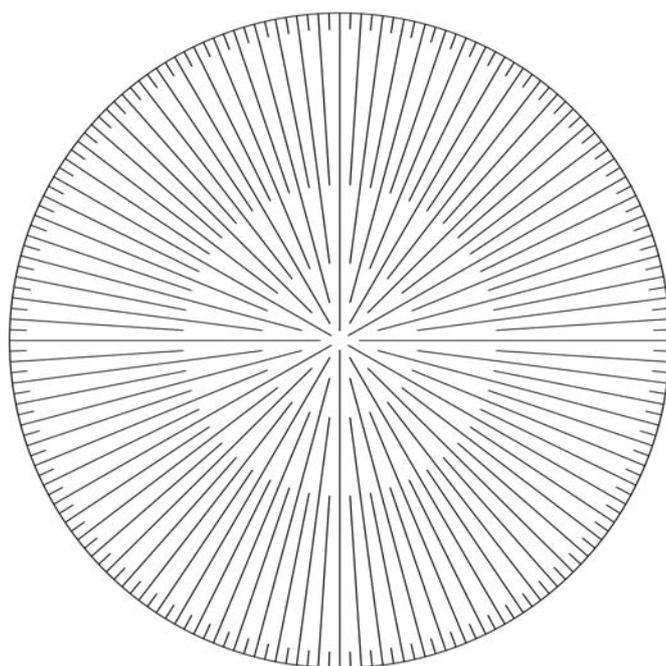$$k_{ini} = 6 \cdot 2^{n_{max}-1}.$$

Fig. 3. Symmetric septal pattern with suppressed bifurcations for $\alpha = 0.9$. All septa of higher orders stop their growth when the minimal distance d_0 to the nearest neighbor is achieved.

The parameter q is strictly associated with the probability of bifurcation. If Δr is a step in a radial direction and a is the radius of a coral cross-section, the probability of bifurcation per simulation step is given by:

$$p = q \frac{\Delta r}{a}.$$

An important parameter connected with the maximal septum order, n_{max}, is the minimal distance, d_0, between neighboring septa. The distance between septa at a coral margin is proportional to the radius, a, of the cone shell. If this distance approaches the doubled value of the minimal distance, d_0, new septa of a higher order appear. Thus the ratio $2\pi a/(d_0 k_{ini})$ varies in range from 1 to 2. These two extreme values correspond to the situation when new septa of succeeding orders appear. To describe transition cases between these two, well defined states, the scaling factor $a \in [0.5,1]$ is introduced. Finally, the minimal distance, d_0, is determined as follows:

$$d_0 = \alpha \frac{2\pi a}{k_{ini}}. \qquad (1)$$

Some details of our simulation.—In this simulation, septa are generated in subsequent steps. All septa start at positions corresponding to the symmetric arrangement that may vary slightly with a random angle displacement. An amplitude of this displacement is less than $0.005\delta\varphi_n$, where $\delta\varphi_n = 2\pi/(6 \cdot 2^{n-1})$ is the angular distance of a septum of the n-th order to the neighboring septum of a lower order. In each step, the
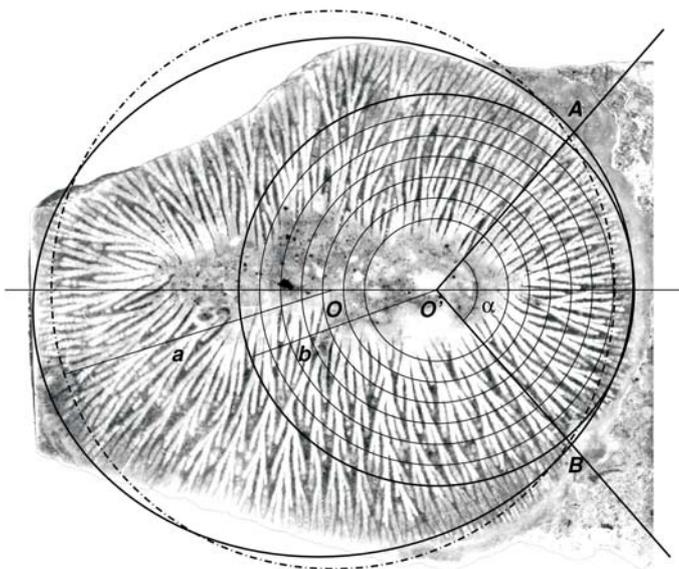
Fig. 4. Mean distance between neighboring septa estimated by number of septa in a centrosymmetric corallum section (*AOB'*). Measurements were repeated at distances from the center of symmetry *O'* (set of concentric circles) and rescaled by factor $2\pi/\alpha$ to the full angle. The resulting values, corresponding to circle *O'* of radius *b*, were multiplied by factor *a/b* to obtain results for an elliptical calicular outline. Parameter α is the "effective" radius of an ellipse, i.e., radius of circle *O* (dot-dashed line) with circumference equal to that of the ellipse.

following possibilities of septal position need to be assessed: (a) every septum bifurcates with the probability *p*, provided that sufficient space is available; (b) each septum is extended toward the corallum axis, being controlled by the rule of uniform septal distribution; and (c) each septum terminates if the rule of minimal distance between neighboring septa is not maintained.

The position of the next portion of a septum is specified using polar coordinates, as they are most adequate to describe objects with radial symmetry. In the polar coordinates a vector of displacement has two components, radial and angular. The radial displacement, Δr, was maintained as constant at each step of the simulation, whereas magnitude and direction of angular displacement, $\Delta\varphi$, were steered by the rules defined at the beginning of this Section. To realize the rule of a uniform distribution, the angular (lateral) displacement of the *i*-th septum was proportional to the following term:

$$\Delta\varphi \approx (\varphi_{i+1} - \varphi_i) - (\varphi_{i-1} - \varphi_i),$$

where $\varphi_x (x = i, i - 1, i + 1)$ are the angular coordinates of the *i*-th septum and its nearest neighbors. If the expressions in both parentheses (representing the angular distances of the *i*-th septum to the neighboring septa) are equal, the rule of uniform distribution is locally fulfilled and there is no angular displacement of the *i*-th septum.

In our simulation, differences in septal length (septal order) resulting from ontogenetic timing are also considered.

To model this, each septum is given a survival parameter *s*. This parameter is initially defined as a negative septal order (the septal order with a minus sign). At each step in the simulation, if the distance between neighboring septa is less than the minimal distance, d_0, survival parameters of both septa are compared and one of them, that with the smaller *s*, halts its growth. After each bifurcation, the survival parameter is decreased by 0.5. In this way, initial predominance of the preexisting (older) septa diminishes as they approach the axis. A new septum then will assume the survival parameter of the fertile septal branch, decreased by 1.

Total length of septa.—One of the interesting parameters of a septal pattern is the total length of all septa. For a fully-symmetric coral with suppressed bifurcations (see Fig. 3) each septum of the *n*-th order has the same length:

$$L_n = a - d_0 / \delta\varphi_n.$$

The total length, L_s, is then given by:

$$L_s = \sum_{n=1}^{n_{max}} k_n(a - d_0 / \delta\varphi_n) = a \sum_{n=1}^{n_{max}} k_n\left(1 - \alpha \frac{2\pi}{k_{ini}\delta\varphi_n}\right).$$

Substituting $\delta\varphi_n = 2\pi/(6 \cdot 2^{n-1})$ in the above equation yields:

$$L_s = a \sum_{n=1}^{n_{max}} k_n\left(1 - \alpha \frac{6 \cdot 2^{n-1}}{k_{ini}}\right).$$

Introducing a new parameter, $\beta \equiv 6\alpha / k_{ini} = \alpha / 2^{n_{max}-1}$, and using the formula for a number of septa of the *n*-th order given by:

$$k_n = \begin{cases} 6 & , \quad \text{if } n = 1 \\ 6 \cdot 2^{n-2}, & \text{if } n > 1 \end{cases}, \tag{2}$$

we finally find:

$$L_s = 6a\left((1 - \beta) + \sum_{n=2}^{n_{max}} 2^{n-2}(1 - 2\beta 2^{n-2})\right)$$

$$= 6a\left((1 - \beta) + \sum_{n=0}^{n_{max}-2}(2^n - 2\beta 4^n)\right)$$

$$= 6a\left((1 - \beta) + (2^{n_{max}-1} - 1) - \frac{2}{3}\beta(4^{n_{max}-1} - 1)\right) \tag{3}$$

$$= 6a\left(2^{n_{max}-1} - \frac{1}{3}\beta(2^{2n_{max}-1} + 1)\right)$$

$$= k_{ini}a\left(1 - \frac{2}{3}\alpha\left(1 - \frac{1}{2^{2n_{max}-1}}\right)\right).$$

For a large n_{max} the above formula simplifies, taking the form:

$$L_s \approx k_{ini}a\left(1 - \frac{2}{3}\alpha\right) \tag{4}$$
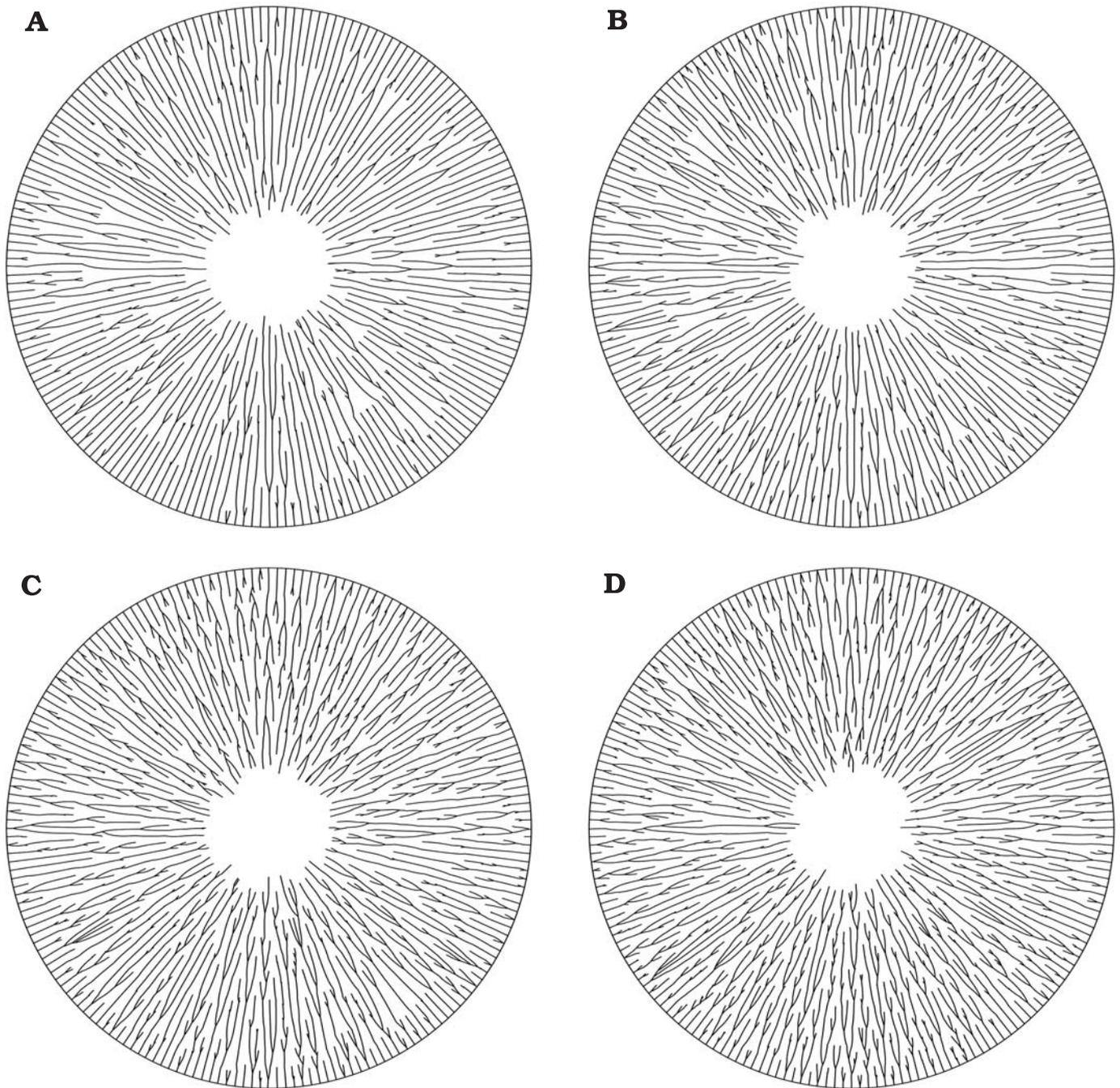
A

B

C

D

Fig. 5. Examples of septal patterns (**A–D**) generated from a minimal set of rules for maximal septum order $n_{max} = 6$. Mean numbers, q, of bifurcations for the corallum radius are 3, 6, 9, and 12 for **A**, **B** (closest to studied specimen), **C** and **D**, respectively. Short "unsuccessful branches" on septal faces result from very simple rules of the geometrical model and in more fine-tuned model can be easily eliminated.

and the maximal length of septa (for $\alpha = 0.5$) is as follows:

$$L_s = \frac{2}{3} k_{ini} a = 2^{2n_{max}+1} a. \tag{5}$$

In practice, Eq. (4) can be used just for $n_{max} = 5$ for which $1/(2^{2n_{max}-1}) \approx 0.002$, and the above approximation gives the correct value with an error less than 0.4%. In the case of branching, the total length of septa depends on the probability of bifurcation. This problem is discussed in the next section.

Results and comments

To verify the model, some parameters of the simulated pattern were compared with measured values for *Furcophyllia*. Number of septa and mean distance between neighboring septa were estimated using measurements made in a section *AO'B*, located at the centrosymmetric region of the coral (Fig. 4). The measurements were repeated at distances r from the point *O'*, and then rescaled by the factor $2\pi/\alpha$, where α is

the opening angle in section $AO'B$, to obtain values for the full angle.

The above recipe yields the parameters of septal pattern for a circular coral of radius b. However, the studied specimen of *Furcophyllia* has an elliptical symmetry, so we must additionally recalculate the obtained values. The perimeter, p, of an ellipse can be approximately expressed by the semiminor and semimajor axes, a_1 and a_2, as follows:

$$p \approx 2\pi \underbrace{\sqrt{(a_1^2 + a_2^2)}}_{a} , \qquad (6)$$

where a is an "effective" radius of an ellipse, i.e. the radius of a circle with a circumference equal to that of an ellipse (Fig. 4). To estimate the number of septa at the border of an elliptical shell, we multiply the value found for circle O' by the factor $a/b = 1.424$. The final results are listed in Table 2.

Table 2. Number of septa k_{ini} and mean distance, $<d>$, between neighboring septa estimated using measurements made in a centrosymmetric portion of *Furcophyllia*. Parameter r defines the radial distance from the center of coral (in units of radius a of coral). Number of septa for $r = 1$ is higher than theoretical value $k_{ini} = 192$, corresponding to maximal septum order $n_{max} = 6$. This disagreement may result from inconsistent insertion of septal cycles later in ontogeny (common to many corals), which results from more local morphogenetic control of their formation. The mean distance between neighboring septa, $d_0 = 0.029$, determined for the centrosymmetric model lies within the range determined by measurement.

r	k_{ini}	$<d>$
1.00	240	0.0261
0.89	209	0.0268
0.79	183	0.0270
0.68	156	0.0273
0.58	125	0.0288
0.47	94	0.0313
0.36	62	0.0364

The second parameter studied here was the mean distance, $<d>$, between neighboring septa. Taking $a = 1$ (in some arbitrary units of length) we determine a minimal distance $d_0 \in [0.0164, 0.0327]$ depending on the value of parameter $a \in [0.5,1]$. The measured values of $<d>$ are in a range predicted by theory.

Four examples of a septal pattern generated for different probabilities of bifurcation, are presented in Fig. 5. Note that the efficiency of filling a space is higher for a large probability of bifurcation. This remarkable finding is strictly related to an issue discussed below.

An interesting quantity, which is connected with the general question about the underlying ground rules of septal branching, is the total length, L, of all septa. In the case of a symmetric pattern, assuming $n_{max} = 6$, $\alpha = 0.5$, and $a = 1$, according to Eq. (5), we find $L_s = 128$. This is a limiting value of total length in our model. Fig. 6 shows the dependence of the total length of septa, L/L_s relative to the limiting value L_s
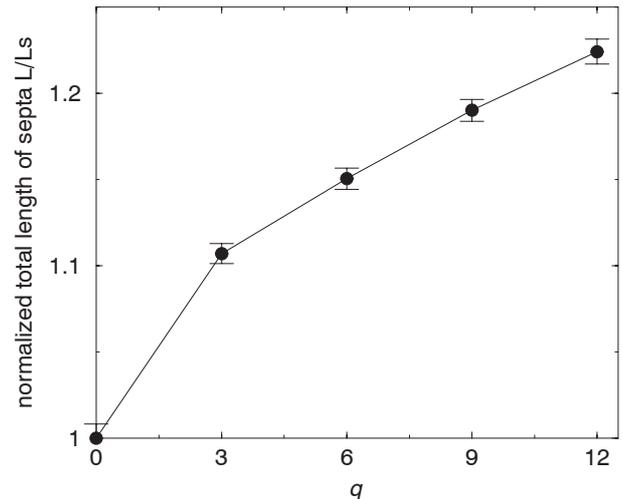

Fig. 6. Dependence L/L_s of normalized total length of septa on the number of bifurcations per corallite radius. Branching leads to an increase in total length of septa.

on the number, q, of bifurcations for a corallite radius. As would be expected, this parameter increases with q. Possible functional aspects of polyp's structures associated with septa, thus possible adaptive significance of large total lenght of septa, are presented in the Discussion section.

Based on the qualitative agreement of the properties of a modeled coral with the real one, we conclude that just the minimal model defined herein is enough to illustrate the overall character of septal growth.

Discussion

The computer model presented suggests that the distinct septal growth pattern in *Furcophyllia* may result from a combination of growth rules acting in concert: (A) keeping equal distances between neighboring septa and septal branches, (B) insertion of numerous septa that retain approximately equal thickness throughout the ontogeny; and (C) centripetal bifurcation of lower-cycle septa. Septa following "A" and "B" rules are common in various fossil and extant corals. A complex system of septal bifurcations is unique to *Furcophyllia*, nevertheless, septa with more or less regular branching do occur in Scleractinia and in other skeletonized anthozoans. This suggests that the peculiar septal pattern in *Furcophyllia* is an extreme, but otherwise it is one of the septal patterns available to scleractinians/anthozoans. Some constructional and functional aspects of septal architectures are discussed below.

Fossil and Recent analogues

Equal interseptal spaces and septal density.—*Furcophyllia* is a densely-septate coral with ca. 35 septa per 10 mm at the calicular perimeter. Interseptal loculi (including loculi between septal branches) are narrow, ca. 0.3–0.4 mm;
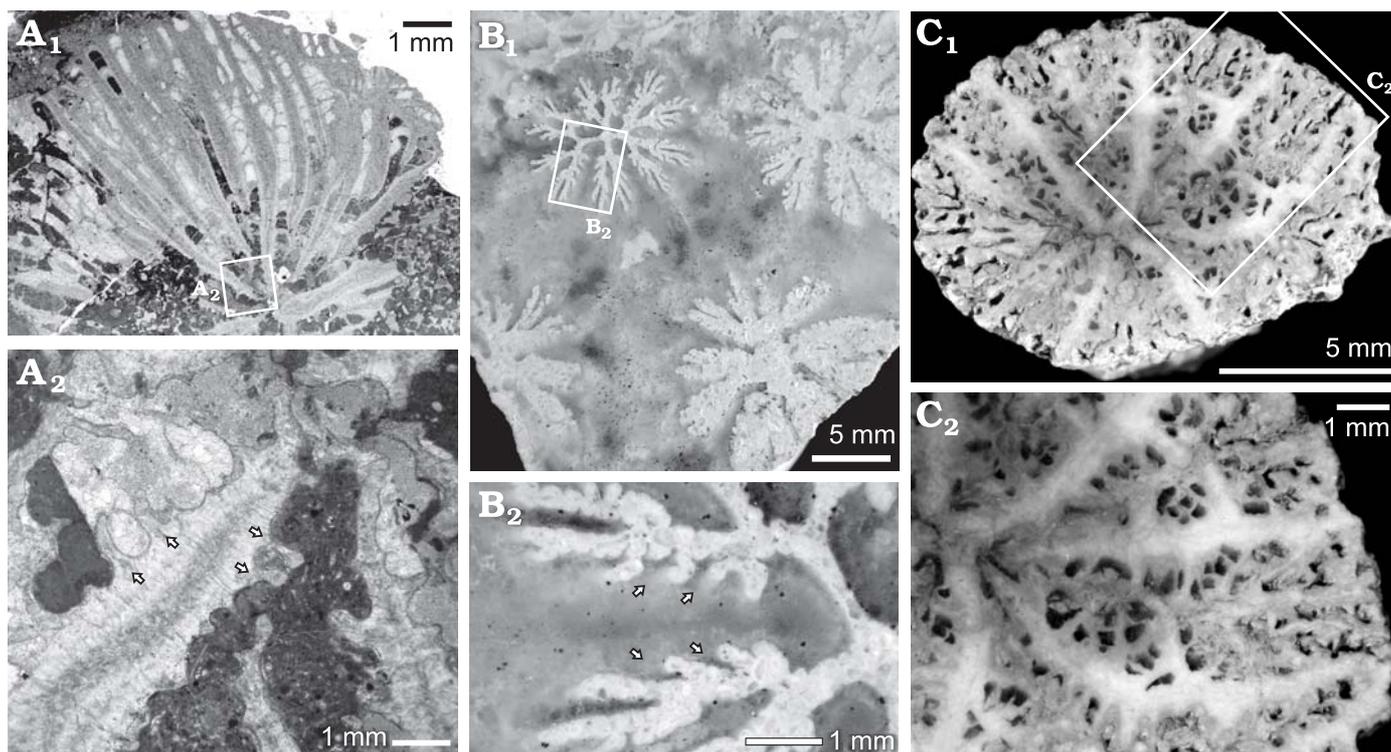
Fig. 7. Examples of fossil corals with secondary septal outgrowths. **A**. Transverse thin section of *Preverastrea robusta* Morycowa 2002. Cretaceous (Albian), Agrostylia, Parnassus (Central Greece), UJ158P31a. Generally thick and smooth septa (A_1, overall view) develop several secondary outgrowths towards the axial zone (A_2, enlargement of area enclosed by rectangle in A_1). **B**. *Paronastraea*? sp., Cretaceous of France (MNHN, no number, Michelin collection); B_1, transverse polished section; B_2, enlarged area outlined in B_1, showing thick and well-developed primary septal-like protrusions (arrows), tiny spines may also occur. **C**. Transverse polished section of *Trochoidomeandra problematica* Morycowa, 1971, Cretaceous (Lower Aptian), Valea Izvorul Alb (Romania), UJ 190. Calice lumen filled with dense and thick dissepiments and long septal protrusions (secondary septa); C_2 is enlarged area of C_1.

distances between septa are kept approximately constant throughout corallum ontogeny. It is a general rule for anthozoans to keep equal distances between neighboring septa that appear to be a natural outcome of a radial (and hexameral in scleractinians) polyp symmetry. Even in corals with septa thickened during ontogeny by skeletal deposits, interseptal spaces shrink evenly between all septa. However, distances between septa may differ significantly between scleractinian taxa. The narrowest interseptal loculi are possessed by corals with numerous and very thin septa. Triassic *Myriophyllia badiotica* Loretz, 1875, is an example of coral with extremely thin and numerous septa i.e., 5–7 septa per millimeter, each 0.05–0.15 mm thick (measured on IPUM-DOL/510 specimen from Alpe di Specie, Italian Dolomites; see also Volz 1896: fig. 41). Among Recent corals, fungiids as well as some agariciids and pectiniids have thin, numerous and dense septa (e.g., the agariciid *Leptoseris* sp. (USNM 90215) has ca. 8 septa per millimeter at the calicular perimeter). Most likely, the minimal distance between septa is constrained by the thickness of mesenterial tissues. On the other hand, some caryophylliinans have low septal densities and wide interseptal loculi (e.g., in *Stephanocyathus* or *Gardineria* septa are usually spaced about one per millimeter, whereas in the eusmiliid *Nemenzophyllia* sp. (USNM 86922) only 5 septa occur per 10 mm at the calicular perimeter).

Interestingly, equal distances are kept not only between septa, but generally, between various regularly added skeletal structures. For example, spoon-like structures called pennulae develop on the septal faces of many Mesozoic corals. They are distributed at equal distances and occur alternately on septal faces of neighboring septa. Lathuilière and Gill (1995: fig. 2) showed that after insertion of a new septum between two older ones, pennulae on neighboring septa become spatially adjusted by the development of phase-shifted "mini-pennulae". After a short period of disturbance, pennulae become again homogenously distributed.

Equal thickness of septa in ontogeny.—In corals with numerous and crowded septa, the septa are, by default, thin. However, even in these corals, the septa often only remain thin in the distal part of the corallum. In the more proximal part (i.e., later in ontogeny), they may be covered by thickening deposits. These deposits are particularly conspicuous in corals that do not develop tabulae, vescicular dissepiments, or other interseptal structures, which restrict the calicular lumen, e.g., in some caryophylliinans. Being in direct and long contact with the skeletogenic epithelium, the septa of these corals may constantly increase in thickness. Conversely, the presence of thin septa throughout corallum ontogeny usually corresponds with the rapid withdrawal of tissue from the

lower portion of the skeleton; direct contact of skeletogenic epithelium with older septa is blocked by tabulae or/and dissepiments. These were exactly the conditions that were responsible for growth of thin septa in *Furcophyllia*. One may reconstruct the calice of *Furcophyllia* as relatively deep (as suggested by a dozen millimeters deep fossa; Fig. 1A, G), but with interseptal loculi filled with numerous, thin dissepiments. Thus, the polyp's tissue does not penetrate interseptal regions more than fewer than 12 millimeters. Thin septa that were "enclosed" in inter-dissepimental compartments remained thin throughout ontogeny.

Septal bifurcations.—Survey of taxa indexed in the *Treatise on Invertebrate Palaeontology* (Wells 1956) and in newer coral literature, indicates clearly that although the bifurcating pattern of septal increase is unique to *Furcophyllia* gen. nov., some analogies do exist among other Cenozoic, Mesozoic and, to some extent, in certain Paleozoic corals.

Septa of Cretaceous aulastraeoporids (e.g., *Preverastrea*, *Paronastraea*) develop secondary outgrowths (see Fig. 7A, B). These secondary outgrowths bear various names in the literature: lateral outgrowths or thorns (Turnšek and Michajlovič 1981), "*apophysale Septen*" (Baron-Szabo and Steuber 1996, see also Kołodziej 2003), septal apophyses (Löser 1998), or lateral trabecular projections (Morycowa and Marcopoulou-Diacantoni 2002). Similar apophysal septa occur also in Jurassic rhipidogyrids: in *Rhipidogyra* and related genera (Eliášová 1973: figs. 9, 10) one or two pairs of thin, often long septa develop on both sides of very thick first- and second- order septa. Secondary septal outgrowths may develop granulations on their faces (Fig. 7A$_2$), which suggests a continuum of developmental processes governing formation of both "normal" and secondary septa. Transformation of septal outgrowths into functionally "normal" septa of newly differentiated corallites was actually documented in the poly-stomodeal/colonial Cretaceous *Trochoidomeandra problematica* Morycowa, 1971 (see Fig. 7C). The main difference between septa in *Furcophyllia* and the corals mentioned above lies in the distinct size hierarchy between "normal" and secondary septal outgrowths [but see, *Preverastrea aptiana* (Turnšek, 1981) in Baron-Szabo and Steuber 1996: pl. 9: 4]. There also is a lack of a bifurcate and alternating branching pattern in aulastraeoporids and rhipidogyrids *versus* the equal-rank, bifurcate, and alternate septal branching pattern in *Furcophyllia*.

Septal increase in micrabaciids (Cretaceous–Recent) has been interpreted as truly bifurcating (Cairns 1989). These corals have completely everted calices with septa growing centrifugally, with higher order septal-cycles appearing in the peripheral zone of the corallum as successive bifurcations of lower-cycle septa. The difference between septal branching in micrabaciids and *Furcophyllia* lies in the centrifugal vs. centripetal direction of this process, respectively. Furthermore, in micrabaciids, higher-order septa develop via peripheral branching of lower-order septa but six, primary septa remain free and not divided. Conversely, in *Furco-*

phyllia, septa of higher orders are inserted at the wall perimeter as independent blades, whereas lower-order septa bifurcate extensively. To elucidate the septal bifurcation mechanism in micrabaciids, further studies that focus on the ontogeny of septa traced in juvenile forms are required (recent interpretations are based on adult coralla).

Duerden (1904) documented septal bifurcations in the peripheral corallum zone of *Siderastrea* and *Caryophyllia*. Septa that bifurcate are always exosepta (i.e., those formed in space between neighboring mesenterial couples). After bifurcation, two branches of exoseptum detach from each other and become independent (if a fragment of original exoseptum is left in axial part of corallum, it may transform into a palus). Space between two exosepta is later filled with new entoseptum that lies in the plane of the original, non-bifurcated exoseptum (see details in Duerden 1904, also Vaughan and Wells 1943). The difference between splitting of exosepta and septal bifurcations of *Furcophyllia* lies in the centrifugal *versus* centripetal, respectively, direction of the process.

For the first time, we here demonstrate centripetal septal branching in two specimens of the Recent Indo-Pacific caryophylliid *Trochocyathus rhombocolumna* Alcock, 1902 (Fig. 8). Dichotomous branching occurs only in distal and axial parts of primary septa. The suggestion that splitting could occur in the ontogeny of some lower-cycle septa, implied by the "herring-bone" arrangement of some costae (Fig. 8B$_2$), has not been supported by serial sectioning of the corallum. Only two specimens with branching of primary septa were found in the large (a few dozen specimens) collection of *T. rhombocolumna* currently being studied by Dr. Helmut Zibrowius (Marseille). This may suggest a teratological stimulus involved in this unusual septal development. However, typical traces of coral intruders have not been detected. Incipient branching of primary septa has also been illustrated in the Caribbean *Phacelocyathus flos* (Pourtalès, 1878) by Cairns (1979: pl. 27.2). Occurrence of primary septa bifurcations in different taxa suggests common, although unknown, underlying mechanism. An argument against teratological hypothesis is that significant changes in septal development may occur in the ontogeny of apparently "healthy" morphotypes of *Madrepora oculata* Linnaeus, 1758, in which normal septal blades traced in early ontogenetic stages transform into chaotically distributed small rods later in ontogeny (Cairns 1998: fig. 1f–h). This indicates a whole spectrum of septal modifications. Since only coralla of *T. rhombocolumna* with bifurcating septa are preserved, only further sampling focused on finding soft tissue will shed light on the actual biological meaning of this skeletal modification. Additional anatomical studies of more readily accessible colonies of *Madrepora oculata* Linnaeus, 1758 are pending.

Bifurcating septa are characteristic of Dividocorallia, the oldest (Devonian–Carboniferous) and most bizarre corals with bifurcating septa (see Fedorowski 1991). Ontogeny of the dividocoral's septa starts with bifurcation of an initial single oblique septum and is followed by peripheral dichoto-
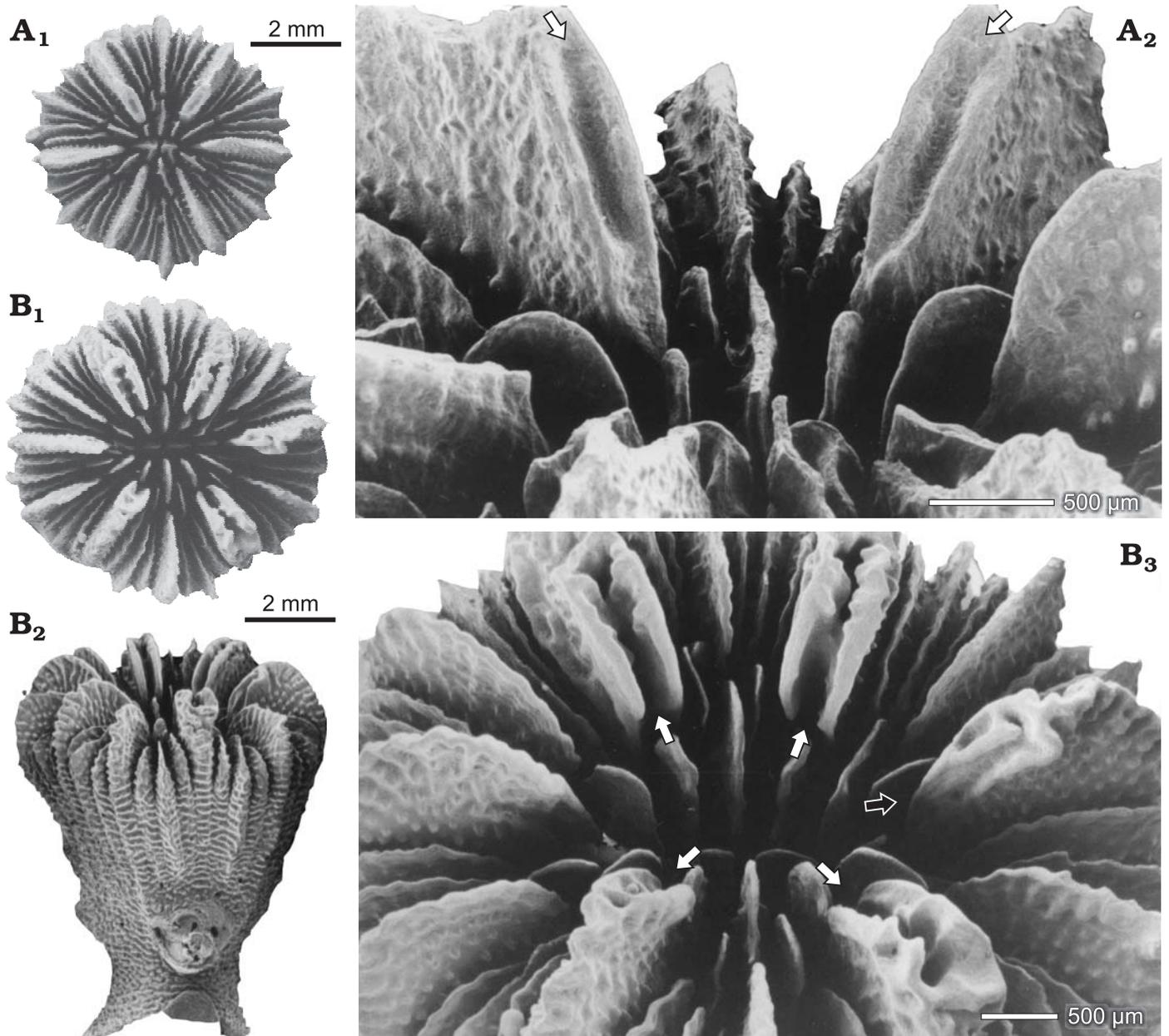
Fig. 8. Septal bifurcation in *Trochocyathus rhombocolumna* Alcock, 1902, BIOCAL, St. DW 08, 12.08.1985, 20˚34.35’S/166˚53.90’E, 435 m. ZPAL H.25/2-Car (**A**) and ZPAL H.25/3-Car (**B**) in distal (A_1, B_1) and lateral-oblique (A_2, B_2, B_3) views . Primary septa split dichotomously in the axial region. In the axial region 2 of 6 primary septa of smaller corallum (**A**) develop shallow groves (arrows in A_2); in larger specimen (**B**) 5 of 6 primary septa split and develop 2 independent branches (white arrows). Septum on the right (black arrow) shows a malformation in development of bifurcation. Pali develop in front of S_1 (bifurcating) and S_2 septa (A_1, B_1); note also the wrinkled texture of the external part of the corallum wall (B_2).

mous division of parental septa. According to Fedorowski (1991: 28), the dichotomous branching pattern develops through "insertion of a new fork from the axially-lateral part of the creative septum" , which thus differs from "true division" i.e., the "simultaneous appearance of two equal forks". However, this accurate interpretation does not differ from the fact that the division results in the final appearance of two equivalent septa. In heterocorals (the best known dividocoral order), dichotomous septal division is centrifugal (this generally applies to dividocorals), and occurs on the surface of the

corallum, which is distally convex and lacks a calice (a distinct difference with *Furcophyllia*). Fedorowski (1991: 46) proposed a hypothetical reconstruction of the mesentherial arrangement in heterocorals (e.g., dichotomous division of "mesentherium" or their pairs) and explained their possible function as structures facilitating effective water and nutrient circulation within the polyp.

Polyp anatomy.—Although not testable in Paleozoic heterocorals, the association of septal and mesenterial develop-
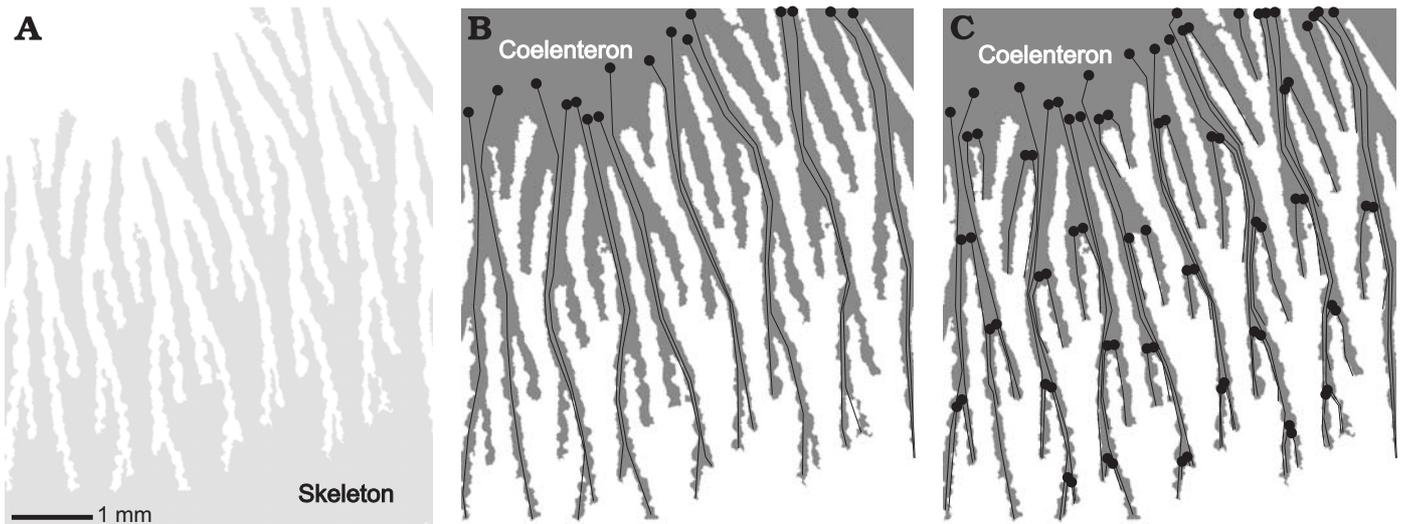
Fig. 9. Interpretation of skeleton (**A**, light grey) and soft-tissue (**B**, **C**, dark grey) relationships in *Furcophyllia septafindens* (Volz, 1896): mesenteries (lines with bulbous endings) could develop only between septal brooms (**B**), or between all septal branches (**C**). Thickness of mesenteries not to scale.

ments is supported by observations on the appearance of mesenteries in living corals. They develop before entosepta or the insertion of exosepta, but always as tissues flanking the septa (see overview in Vaughan and Wells 1943). Attention devoted to the reconstruction of mesenterial arrangement is understandable given the biological importance of these structures. Mesenteries are crucial to cnidarian biology because they are sites for digestion and absorption of food and development of gametes; they also bear longitudinally arranged muscles necessary for defensive reactions (Schick 1991). Changes in mesenterial arrangement may thus have direct influence on the fitness of the organism. Lastly, the development of tentacles, the most important tactile, prehensile and food transporting organs of the polyp in most corals, is associated with intra-mesenterial chambers (it is noteworthy that not all corals develop tentacles; e.g., Schlichter 1992; Schlichter and Brendelberger 1998; Goldberg 2002). The elaborate septal pattern of *Furcophyllia* suggests a distinct organization of the polyp's soft tissue. Two hypotheses for mesenterial arrangement of the polyp are proposed:

(1) The first hypothesis assumes that mesenterial pairs flanked the entire septal broom and non- branched higher-order septa (Fig. 9B). The septal broom would thus be homologous with a single, non-branched septum, whereas its septal branches would be homologous to structures developed on septal faces in most corals, e.g., granulations, menianae.

(2) According to the second hypothesis, mesenterial pairs flanked not only the entire septal broom (parental septum) but also all secondary septal branches. Septal branches would thus be homologous with conventional septa (Fig. 9C).

Because the number of mesenteries envisaged in the second hypothesis can be many times higher than in the model of *Furcophyllia* polyp suggested by the first hypothesis, one

may speculate about the multiplication of structures associated with mesenteria: loci of gonad development and, possibly, tentacles. Feeding and reproductive performance of the polyp could benefit from such anatomical modifications. However, the alleged functional advantage is not supported by the evolutionary history of Mesozoic corals. If actually advantageous, one would expect a significant increase in the role of *Furcophyllia*-like septal patterns in the evolution of various coral lineages, but this is not the case. Until new anatomical evidence is obtained regarding mesenterial arrangement in living corals with bifurcate septa (e.g., *T. rhombocolumna*), neither of the above two hypotheses is strongly supported.

Some septal modifications may point to polyp functions that are not related to the function of mesenteries. For example, Goffredo and Telò (1998) suggested that large skeletal chambers that develop between septa of dendrophylliid *Balanophyllia europaea* (Risso, 1826) may facilitate incubation of great number of embryos until advanced stages (specialized brooding mode of this coral). *Furcophyllia* interseptal spaces are not widened to support a similar strategy. However, the septa of *Furcophyllia* bear very delicate, horizontal outgrowths, i.e., menianae (Fig. 1E), which suggests another functional interpretation of the polyp. Similar, but more distinct menianae in the modern agariciid *Leptoseris fragilis* (Milne Edwards and Haime, 1849) delineate gastric ducts of the coelenteron (Schlichter 1991). The gastrovascular system of *Leptoseris* is adapted to a unique suspension feeding strategy: gastric ducts perforated by microscopic pores act as sieves that let water out and keep organic particles in the coelenteron. Menianae-bearing corals are common in the Triassic and later in the Mesozoic (but extremely rare in Cenozoic) and their morphological similarity to *Leptoseris* has led some researchers to suggest a suspension feeding strategy for these fossil corals (Lathuilière and Gill 1995; Mory-

cowa and Roniewicz 1995). Given similar menianae in the microarchitecture of septa of *Furcophyllia*, it is tempting to speculate about a system of gastric ducts additionally complicated by septal bifurcations and a possible suspension feeding strategy for this coral. However, support for the hypothesis depends on examination of other, rare menianeabearing Recent scleractinians (e.g., *Dactylotrochus cervicornis* Moseley, 1881).

Conclusions

- Lower-order septa of Triassic *Furcophyllia septafindens* (Volz, 1896), re-described herein from the Italian Dolomites, branch repeatedly and centripetally. Septa are composed of 3–10 blades ("septal brooms") and do not all show the same branching pattern. On the other hand, distances between adjacent septa and their branches are equal, and the thickness of all blades is approximately the same throughout ontogeny.
- The furcate septal arrangement in *Furcophyllia* is unique among Triassic corals, and generally among Mesozoic and Cenozoic corals. One analogy involves Cretaceous aulastraeoporids, *Trochoidomeandra*, and Jurassic rhipidogyrids with respect to secondary (apophysal) septal branches and some Recent caryophylliids (*Trochocyathus rhombocolumna*, *Phacelocyathus flos*). In the latter, primary septa split dichotomously and centripetally.
- The proposed simple computer model simulates septal branching, similar to that of *Furcophyllia*; and follows a minimal set of rules: (i) uniform coverage of intra-calicular space; (ii) bifurcations with some probability; (iii) keeping some minimal distance between septal branches.
- The elaborate septal pattern of *Furcophyllia* suggests a distinct organization of the polyp's soft tissue, especially mesenteries. Mesenterial pairs could flank only "septal brooms". Septal branches would thus correspond functionally with septal microarchitecture (hypothesis 1), or mesenterial pairs could have developed between all septal branches that functionally correspond with conventional septa (hypothesis 2).
- Delicate menianae that developed on septal faces of *Furcophyllia* (and numerous coeval corals) resemble a similar septal microarchitecture in the Recent agariciid *Leptoseris fragilis* and may be related to the suspension feeding strategy of this coral.

Acknowledgements

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