TOWARDS A NEW SYNTHESIS OF EVOLUTIONARY RELATIONSHIPS AND CLASSIFICATION OF SCLERACTINIA

JAROSŁAW STOLARSKI AND EWA RONIEWICZ

Instytut Paleobiologii, Polska Akademia Nauk, Twarda 51/55, 00-818 Warszawa, Poland
<stolacy@twarda.pan.pl>, <eron@twarda.pan.pl>

ABSTRACT—The focus of this paper is to provide an overview of historical and modern accounts of scleractinian evolutionary relationships and classification. Scleractinian evolutionary relationships proposed in the 19th and the beginning of the 20th centuries were based mainly on skeletal data. More in-depth observations of the coral skeleton showed that the gross-morphology could be highly confusing. Profound differences in microstructural and microarchitectural characters of e.g., Mesozoic microsolenine, pachythecaliine, stylophylline, stylinine, and rhipidogyrine corals compared with nominotypic representatives of higher-rank units in which they were classified suggest their separate (?subordinal) taxonomic status. Recent application of molecular techniques resulted in hypotheses of evolutionary relationships that differed from traditional ones. The emergence of new and promising research methods such as high-resolution morphometrics, analysis of biochemical skeletal data, and refined microstructural observations may still increase resolution of the ''skeletal'' approach. Achieving a more reliable and comprehensive scheme of evolutionary relationships and classification framework for the Scleractinia will require close cooperation between coral biologists, ecologists, geologists, geochemists, and paleontologists.

INTRODUCTION

THE FOUNDATION for our understanding of scleractinian evolutionary relationships was established in the 19th and the beginning of the 20th centuries, when numerous papers dealing with anatomy, physiology, behavior, and skeletal macro- and microstructures were published (e.g., Bourne, 1887, 1899; Pratz, 1882; Fowler, 1885, 1886, 1887, 1888, 1890; Duerden, 1902, 1904). A few authors (Duerden, 1902; Matthai, 1914) used anatomical features of coral polyps as key-characters in classification, but the two most advanced 19th century classifications (Milne Edwards and Haime, 1857; Ogilvie, 1897) were established using complex and relatively accessible skeletal characters.

Milne Edwards and Haime's (1857) classification was based mainly on macroscopic skeletal characters and was rooted in the broad zoological and paleontological knowledge of the two authors. Their greatest achievement was providing a uniform terminology for structures and a framework of classification into which any new form could be placed. This scheme, originally bipartite (Aporosa and Perforata) and then tripartite [Duncan (1885) included Fungida of equal rank with the Aporosa and Perforata], survived until Vaughan and Wells's revision (1943). In contrast, Ogilvie's (1897) classification was developed mainly using observations of skeletal microstructures of some representatives of Recent and fossil corals. Special attention was paid to the structure and pattern of the distribution of septal trabeculae. Though acknowledged by contemporary workers, the microstructural observations of Ogilvie (1897) were not implemented in scleractinian studies until Vaughan and Wells's (1943) revision, in which many of Ogilvie's (1897) original drawings were reproduced.

During the 20th century, four main systems of scleractinian classification (Vaughan and Wells, 1943; Wells, 1956; Alloiteau, 1952; Chevalier, 1987) attempted to assimilate new data on the diversity and skeletal structures of Mesozoic and Cenozoic faunas. The authors of these systems contributed significantly to our knowledge of the Scleractinia, and were active in the systematics of both Recent and fossil corals. At this time, because the main taxonomic criteria were skeletal, there was no discrepancy between zoological and paleontological classifications. The agreement between zoological and paleontological classifications is noteworthy, because different classifications existed for many other groups of organisms (e.g., molluscs) depending on the field of the researcher.

The emergence of molecular techniques at the end of 20th century resulted in hypotheses of evolutionary relationships that were independent and different from traditional ones based on the skeletal data (Romano, 1996, 2000; Veron, 1996). New interpretations of coral biomineralization challenged the traditional concept of physiochemical control of skeletal formation (Cuif, 1997, 1998; Gautret, 1997) During the same period, new records and revisions of Recent azooxanthellate (Cairns, 1979, 1982, 1984, 1995, 1998, 1999; Zibrowius, 1980; Stolarski, 2000), zooxanthellate (Hoeksema, 1989; Wallace, 1999; Veron, 2000) and fossil coral faunas (e.g., Beauvais, 1982; Morycowa, 1971; Roniewicz, 1989; Löser 1989, 1994; Baron-Szabo and Steuber, 1996; Baron-Szabo, 1997, 1998, 2000; Lathuilière, 2000a, 2000b) significantly improved understanding of scleractinian morphological and microstructural diversity through time. Last but not least, new hypotheses about the processes underlying scleractinian evolution (e.g., the concept of reticulate evolution by Veron, 1995) and about the integration of spectra of morphological variation into scleractinian classification (e.g, Lathuiliere, 1996) were proposed. All of these new observations and hypotheses concerning Recent and fossil scleractinians have not yet been discussed and summarized in the form of a Treatise on Invertebrate Paleontology or Zoology. However, it has become crucial for today's workers to learn how best to reconcile the increasingly growing discrepancy between molecular vs. morphological systems of scleractinian phylogeny and classification. Will it be possible to maintain the unity of zoological and paleontological classification in the future? Will it be possible to establish the level of macro- and microstructural skeletal observations that will reliably explain relationships between fossil and Recent taxa? Will the observations of Recent forms correspond with those suggested by molecular analyses?

→

FIGURE *1*—Main 20th Century classifications of Scleractinia. *1,* Vaughan and Wells (1943); *2,* Wells (1956); *3,* Alloiteau (1952); *4,* Chevalier and Beauvais (1987). Arrows indicate changes in taxonomic position of some of taxa discussed in the text. Further changes in systematics affected by microstructural observations of asterisked taxa explained in section: Modifications in scleractinian systematics. . . .
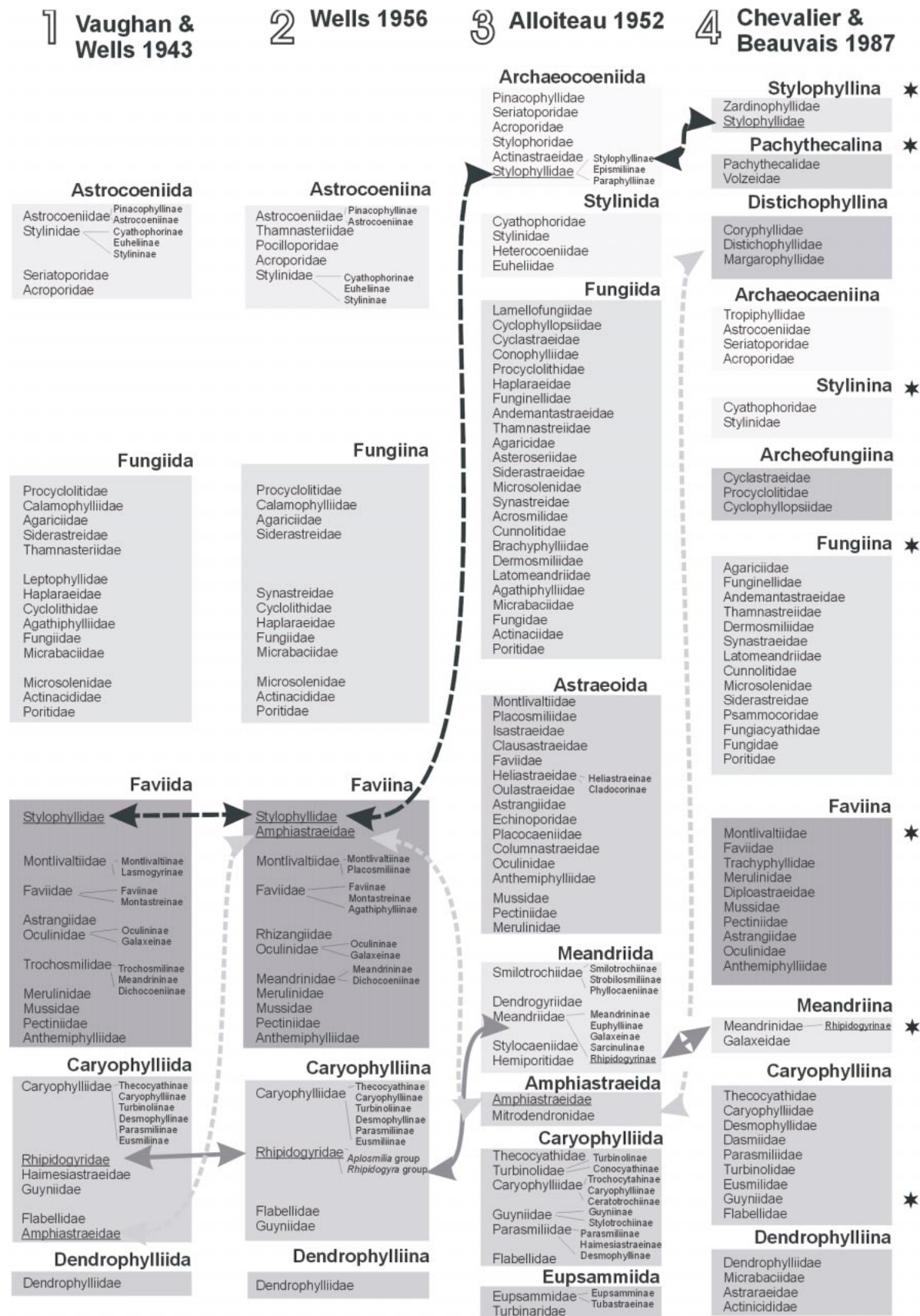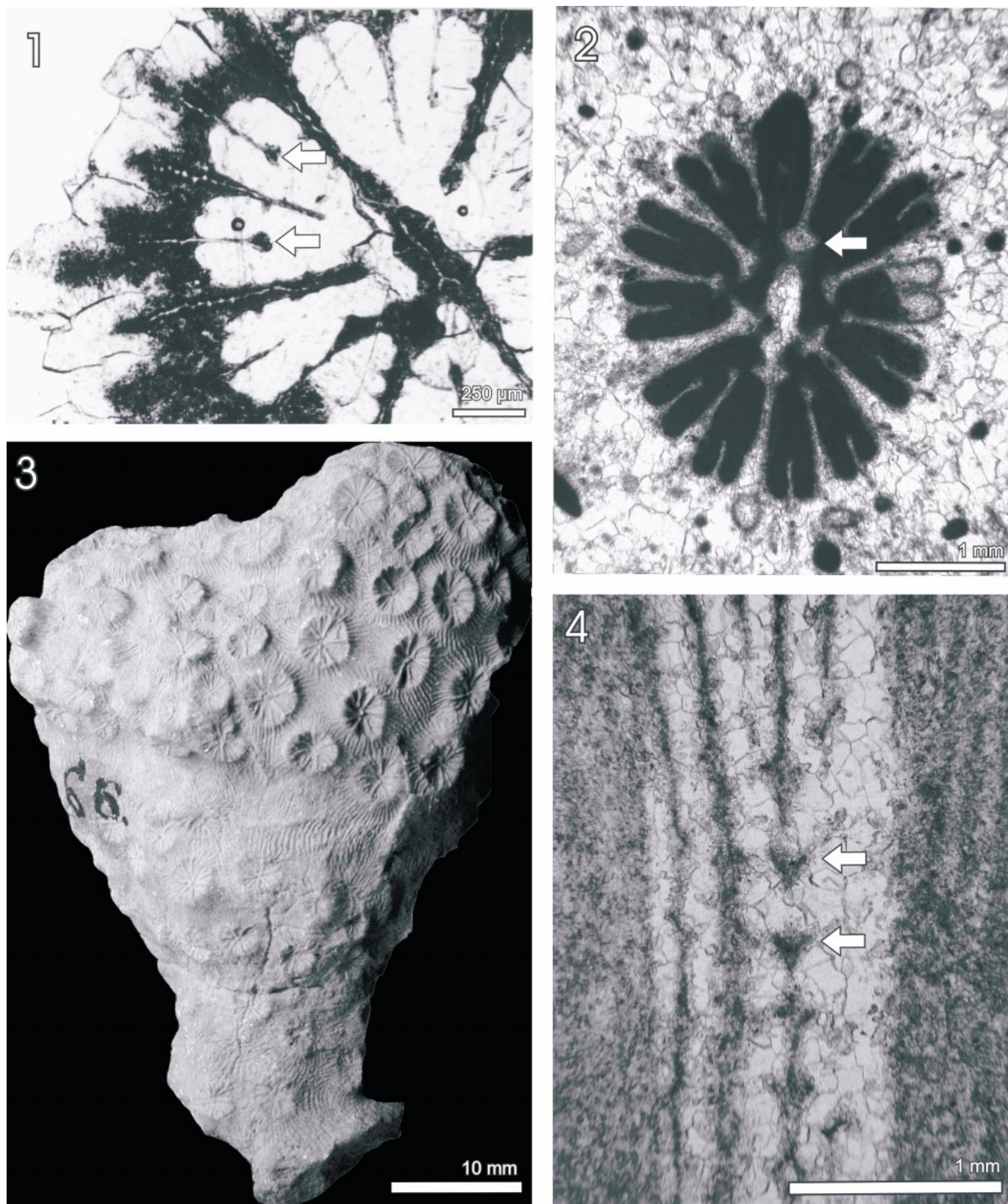
FIGURE 2—1–4, Architecture and microstructure of the stylinid skeleton; 1, Stylina gaulardi Michelin, 1843. MNHN, coll. Michelin, No. 213. Jurassic, Oxfordian. France, unknown locality. Transverse secion. Radial elements of costoseptal type (=trabeculae in divergent system) with thin septal portions with large auriculae at the inner border (arrow). Septal calcification centers separated, small-sized. Lateral trabecular branches form pointed granulations on septal faces. 2, Stylina subornata (d'Orbigny, 1850). ZPAL H.III/1375. Jurassic, Oxfordian. Niziny, Poland. Auriculae in transverse

We strongly believe that it is beneficial to both zoologists and paleontologists to continue the debate about the importance and taxonomic application of skeletal vs. ''soft-tissue'' characters. The potential for in-depth skeletal studies has not yet been exhausted and, in fact, coralla of Recent scleractinians have only been superficially investigated by means of microstructural analysis. To this end, we would like to show herein the panorama of various paleontological and zoological systems of scleractinian classification. In the first section, we recapitulate the main 20th century proposals. In the second and third sections, we present the main modifications of these proposals resulting from microstructural studies. In the fourth section, we discuss the main discrepancies between proposals of evolutionary relationships based on skeletal vs. molecular data, and in the fifth section, we describe the emergence of new and promising methods that can be used to increase the resolution of the ''skeletal'' approach.

Specimens illustrated in this paper are housed in the following institutions: The Natural History Museum, London (BM), Geisetal Museum, Halle (GMH), Geologische Bundesanstalt, Wien (GBA), Museum Nationale d'Histoire Naturelle, Paris (MNHN), National Museum of Natural History, Smithsonian Institution (NMNH), Naturhistorisches Museum Wien (NHMW), Institute of Paleobiology, Warsaw (ZPAL), and Institute of Paleontology, University of Modena, Italy (IPUM).

THE MAIN 20TH CENTURY SYSTEMS OF THE SCLERACTINIAN CLASSIFICATION

Vaughan and Wells, 1943 and Wells, 1956.—The authors of these two classification systems summarized the results of over one hundred years of study of extant and fossil corals with an emphasis on the Cenozoic and Cretaceous coral faunas of North and Central America. The classification proposed by Vaughan and Wells (1943) was organized in a conventional taxonomic key. The classification criteria were hierarchically ordered, and the whole scheme was uniform and clear for both extant and fossil corals. The clarity of this proposal was highly appreciated by students of Scleractinia, and the newer revised version of the same system (Wells, 1956) is still widely used.

Vaughan and Wells (1943) and Wells (1956) used the principle that the septal trabeculae are the key to scleractinian evolution, allowing five suborders to be distinguished (Fig. 1.1, 1.2). These suborders were diagnosed by the following features of septa: 1) laminar or as simple spines, composed of few simple or compound trabeculae (suborder Astrocoeniina); 2) fenestrate, formed by numerous simple or compound trabeculae, united by synapticulae (suborder Fungiina); 3) laminar or as isolated spines, formed by one or more fan systems of numerous simple or compound trabeculae (suborder Faviina); 4) laminar, composed of one fan of numerous simple trabeculae (suborder Caryophylliina); and 5) laminar and irregularly perforated, composed of one fan of numerous simple trabeculae, united by synapticulae (suborder Dendrophylliina). In addition to the skeletal characters, Vaughan and Wells (1943) and Wells (1956) also considered the following polypoid features: cycles of tentacles (≤2 cycles in astrocoeniines, and ≥2 in other suborders) and presence of stomodeal ridges (lacking in astrocoeniines, and present in other suborders).

The classification criteria used to distinguish families in the Vaughan and Wells (1943) and Wells (1956) schemes included: wall type, occurrence of endotheca, and type of budding. Vaughan and Wells(1943) and Wells (1956) both distinguished 33 families,

but these are not fully comparable, because they occasionally assigned clusters or individual genera to different families. Wells's (1956) classification encompasses 450 fossil and extant genera. Mesozoic taxa are either assigned to the families with predominantly Recent taxa sharing morphological characters with them, or form entirely extinct families.

Alloiteau, 1952.—Alloiteau was concerned mainly with Tertiary and late Cretaceous corals. His approach to coral systematics was highly structural, and probably influenced by his education in engineering and his work as an architect prior to his paleontological career. Alloiteau's (1952) classification relies in general outline on the Vaughan and Wells (1943) scheme, but includes many more microstructural observations and does not refer to the anatomical characters of the polyp. Alloiteau's innovations consist of observations on the microarchitecture (ornamentation) of the septa and on the types of sclerenchymal tissue, which were at that time poorly recognized.

Alloiteau (1952) distinguished eight suborders and 71 families (including 36 entirely extinct; see Fig. 1.3). Some former families (Stylinidae, Meandrinidae, Amphiastraeidae) have been elevated to the subordinal rank on the basis of microstructural characters. Suborders are diagnosed by the following corallite features: 1–2) synapticulae absent, endotheca developed, radial symmetry and continuous (Stylinida) or discontinuous (Archeocaeniida) septa built of a few trabeculae; 3–4) corallites with the above characteristics but with septa constructed by numerous trabeculae having distal borders with distinct ornamentation (Astraeoida) or nearly lacking ornamentation (Meandriida); 5) synapticulae absent, endotheca developed, strong bilateral symmetry, wall archaeothecal (Amphiastraeida); 6) synapticulae absent, endotheca rare or absent (Caryophylliida); 7–8) synapticulae present, septa perforate with continuous (Fungiida) or discontinuous trabeculae (Eupsammiida).

Alloiteau (1952) raised several of Vaughan and Wells's (1943) subfamilies to family rank and then subdivided these families into subfamilies on the basis of dubious characters (e.g., presence or absence of pali in Caryophylliidae, or presence or absence of septal Pourtale's plan in his Eupsammiida). Unfortunately, taxonomic splitting practices such as these overshadow Alloiteau's innovative use of microstructural characters.

Chevalier and Beauvais, 1987.—Chevalier and Beauvais's (1987) scheme also suggested that microstructural characters were the key to the scleractinian classification. Chevalier had lifelong experience in microstructural observations of Recent and Tertiary corals, and his meticulous drawings in three monographs (Chevalier, 1961, 1971, 1975) are perhaps the most accurate ever made. Beauvais, who took over the project of the *Treatise* after Chevalier's death, worked on Mesozoic (mostly Cretaceous) corals. Chevalier and Beauvais's classification (1987) includes 11 suborders (Fig. 1.4), adding three new suborders to those distinguished by Alloiteau (1952): Stylophyllina L. Beauvais, 1979, Distichophylliina L. Beauvais, 1979, and Archaeofungiina Alloiteau, 1952 [Amphiastraeida, as distinguished by Alloiteau (1952), corresponds with Pachythecaliina Eliasova, 1976 in Chevalier and Beauvais's (1987) scheme]. Suborders were diagnosed using the following features (after Beauvais, 1981): 1) non-trabecular septa without medioseptal plane, radial elements of thecal origin composed of lamellar sclerenchyme (Stylophyllina); 2) non-trabecular septa with medioseptal plane independent of the

section (arrow). *3, Stylina pediculata* Koby, 1904, ZPAL z.p.H.I/4. Jurassic, Oxfordian. Babugan, Crimea, Ukraine. General view of plocoid colony. *4, Heliocoenia variiailis* Etallon, 1859. ZPAL H.III/1606. Jurassic, Oxfordian. Wierzbica, Poland. Auriculae in longitudinal section (arrows).
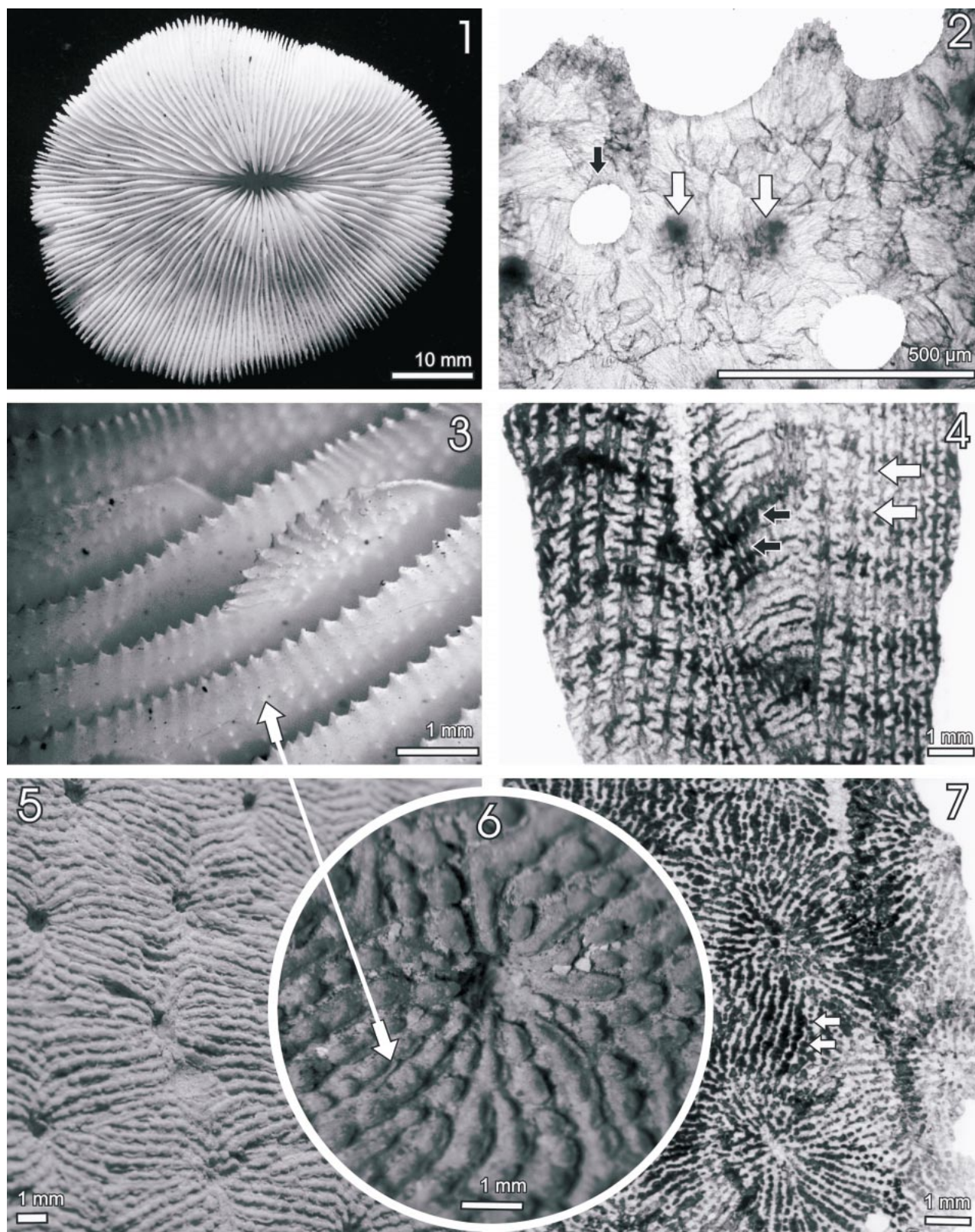
FIGURE *3—1–7,* Architecture and microstructure of the fungiine vs. microsolenine skeleton; *1, 2, 3, Fungia* (*Lobacis*) *scutaria* Lamarck, 1801. ZPAL H.22/1. Pacific region, unknown locality. Distal view (*1*), longitudinal section of the distal part of the septum (*2),* and enlarged distal septal edge (*3*) to show denticulation and lateral pointed granulations. Note: septal denticulation, v_reculae and accidentally distributed pores. 4, 7, *Microsolena* sp. ZPAL H.III/1450. Jurassic, Lower Kimmeridgian. Sulejow n. Pilica, Poland. *4,* Longitudinal section partially through median plane with trabeculae and regular pores (small black arrows), and partially through lateral septal portions with menianes composed of pennulae (larger white arrows). Pennulae are semilunar in cross section, with ends directed upwards. Septal pores develop between neighboring trabeculae and are closed

fibrous theca (Pachythecaliina); 3) non-trabecular septa with medioseptal plane having lateral axes, wall septo- or parathecal (Distichophylliina); 4–5) septa with trabeculae not organized into divergent systems; synapticulae present (Archaeofungiina) or absent (Archaeocoeniina); 6–10) septal trabeculae continuous, organized into divergent systems; septal granulations may (Fungiina) or may not (Stylinina, Faviina, Meandrina, Caryophylliina) connect to form synapticulae; septal trabeculae simple (Stylinina), or simple and compound (Faviina, Meandrina, Caryophylliina); septal distal edge dentate (Faviina) or smooth (Meandrinina, Caryophylliina); endotheca present (Meandrinina) or absent (Caryophylliina); 11) septal trabeculae discontinuous, formed by vertical and horizontal sclerodermites (Dendrophylliina).

The microstructural criteria that Chevalier and Beauvais used to distinguish suborders containing only extinct taxa (i.e., Pachythecaliina, Distichophylliina, Archaeofungiina) are unclear or have not been supported by further research (e.g., Roniewicz, 1989, Roniewicz and Stolarski, 2001). The only exception is the Stylophyllina, a distinct scleractinian group that was precisely characterized by Cuif (1972) prior to Chevalier and Beauvais's work [supplementary data on their unique status were provided by Roniewicz (1989)]. The main paradox of Chevalier and Beauvais's (1986) scheme lies in the classification of excellently preserved and microstructurally well-characterized Triassic taxa with corals of different ages, which have unknown or poorly characterized microstructural features. For example: i) Triassic *Myriophyllum* Cuif, 1975, a genus that has been well described on the basis of excellently preserved coralla, is assigned to Cyclastraeidae, in which the nominative Cretaceous *Cyclastrea* Alloiteau, 1952, is known only from insufficiently characterized fossils; ii) various taxa of the Triassic Volzeiidae with distinct microstructure (Cuif, 1975; see details in the section "Modifications in Scleractinian Systematics") are linked with Jurassic-Cretaceous Agathiphylliinae and Heterocoeniinae that represent corals having different microstructural traits (see Stolarski and Russo, 2000); iii) the Procyclolitidae, in which the nominative *Procyclolites* has non-trabecular septa (Cuif, 1975), contains Liassic *Thecoseris* and *Epiphyllum,* and Cretaceous *Thecoseriopsis,* which have trabecular septal structure. Possibly, for that reason, Chevalier and Beauvais (1987) considered compound trabeculae to be one of the diagnostic characters of the family. Many other taxonomic decisions in Chevalier and Beauvais's *Treatise* are not sufficiently explained [e.g., Zardinophyllidae Montanaro-Gallitelli, 1975, and Pachythecaliidae Cuif, 1975, are assigned to different suborders, although most authors consider them synonymous, because they share the same synapomorphy: see review by Stolarski and Russo (2001)]. In view of these and many other formal shortcomings [e.g., the authorship of Volzeiidae and Distichophylliidae (a junior synonym of Reimaniphylliidae!) is attributed to L. Beauvais, 1981, but in fact belongs to Melnikova, 1974, etc.], one should consider this system difficult to accept, although students of Recent corals (e.g., Veron, 1995, 2000) sometimes use it.

MICROSTRUCTURAL REVOLUTION

Pioneering works by Koch (1882), Bourne (1887), Frech (1890), Volz (1896), and Ogilvie (1897) advocated that coral skeleton, particularly as observed in microscale, is the key to coral classification. Bryan and Hill (1942) emphasized the value of microstructural observations by suggesting that corals initiate skeletal growth by forming calcification centers, whose position is genetically determined, and skeletal parts are formed via purely physico-chemical processes. Diverse patterns of distribution of calcification centers are thus crucial to coral classification (usually, spatial relationships between individual calcification centers were not described but trabeculae were, i.e., rods, as seen in longitudinal section, composed of calcification centers and fibers that grow around them; see Fig. 2). Ideas about coral biomineralization have evolved considerably since then (see section Towards a New Synthesis), but the key-role of calcification centers as carriers of taxonomic information has not been challenged. Improvements in the microstructural approach have developed as new techniques were implemented, e.g., traditional petrographic thin-sections, ultra-thin sections (Lafuste, 1970), the scanning electron microscope.

From the 1950s to the 1980s, research on coral microstructures that focused on evolutionary and classification aspects was concentrated in the Institute of Paleontology at the National Museum of Natural History in Paris. Works by Alloiteau (1952, 1957) showed that traditional morphological approaches were one-sided and that comparison of macro- and microstructural data revealed numerous convergences (homeomorphies) between Recent and fossil corals. It became clear that without the confirmations provided by more in-depth microstructural studies (see section "Modification in Scleractinian Systematics"), the gross-morphology of the coral skeleton could be highly confusing. Numerous French researchers followed the microstructural approach: J. Lafuste and P. Semenoff-Tian-Chanski worked with Paleozoic corals, whereas J. P. Chevalier, G. A. Gill, and J. P. Cuif were experts on scleractinians. The papers of Chevalier (1961, 1971, 1975) are an excellent iconographic archive of the various skeletal microstructures of Cenozoic scleractinians. Dealing mainly with species-level taxonomy, Chevalier showed also that microstructure is consistent at the family level, and that closely related families (e.g., Faviidae, Mussidae, and Pectinidae) possessed transitions between microstructural types (Chevalier, 1961, 1971, 1975). Gill (1967, 1970, 1980a) focused on the skeletal microarchitecture of Cenozoic and Mesozoic scleractinians and introduced several new suprageneric taxonomic criteria (e.g., presence of pennulae, auriculae, futurae). The taxonomic revisions of Cuif (1973, 1975a, 1975b, 1976, 1977) are milestones in the understanding of microstructural and microarchitectural diversity of Triassic (Carnian and Norian) scleractinians. Cuif's studies were based on excellently preserved fossils, and thus obtain almost the same level of accuracy as studies of extant scleractinians. Microstructural features were used to cluster genera into families.

The Parisian microstructural school influenced researchers of Mesozoic and Cenozoic corals outside of France, encouraging them to use a similar methodology [e.g., Montanaro Gallitelli (1975), Gill (1973, 1980a) and Russo (1979) in Italy, and Morycowa (1971) and Roniewicz (1976, 1982, 1989) in Poland]. In English-speaking countries, access to SEM techniques triggered a renaissance of 19th century interests in the structure and formation of the basic elements of the scleractinian skeleton. The most influential papers were by Wells (1969) on dissepiments, Barnes (1972) on epitheca, Jell (1974), Sorauf (1970, 1972, 1974) and Sorauf and Jell (1977a, 1977b) on septa, wall, and many other minute skeletal structures. The aftermath of this "microstructural revolution" was the appearance of new theories of scleractinian classification.

←

from above and below by succeeding generations of fused pennulae. *7,* Transverse section showing regular, structural porosity of septa (arrows). 5, 6, *Microsolena* sp. ZPAL z.p. H.IV/1. Jurassic, Callovian. Moscow region, Russia. Large-sized trabeculae and pennular microarchitecture (arrow: compare with fungiine granulations on *3*).
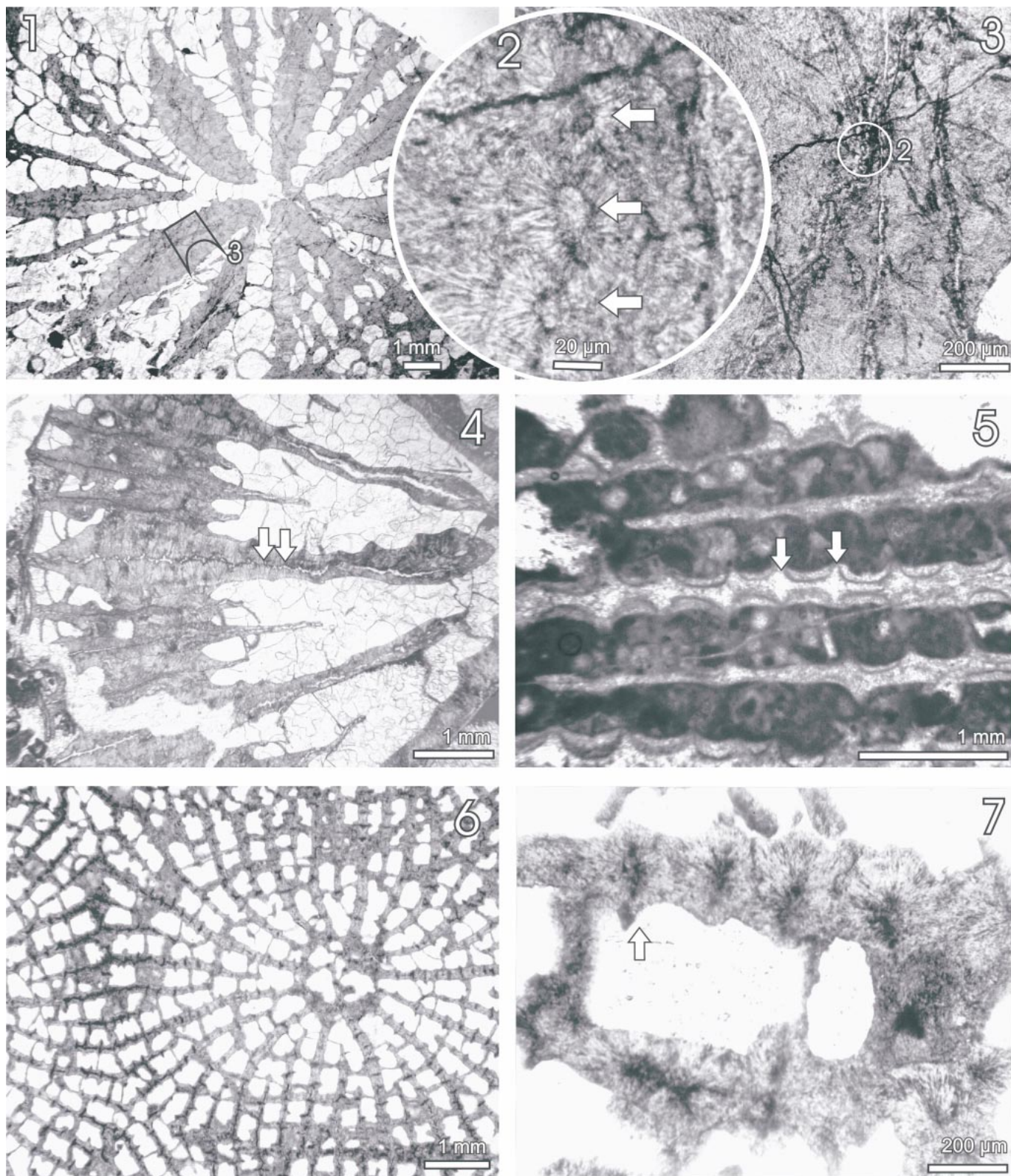
FIGURE 4—1–7, Architecture and microstructure of the montlivaltiid vs. volzeiine skeleton. 1, 2, 3, *Palaeastraea grandissima* (Frech, 1890). GBA 1982/12/283. Triassic, Rhaetian. Fischerwiese, Northern Calcareous Alps, Austria; 1, Transverse section of the colony showing septa with thin zigzag midline and thick lateral stereome (3—enlargement); 2, Detail of the zigzag mid-septal zone showing small-sized calcification centres (''minitrabeculae''—arrows); 4, *Retiophyllia norica* (Frech, 1890). GBA 1982/12/113. Triassic, Rhaetian. Fischerwiese, Northern Calcareous Alps, Austria. Small-sized calcification centers of the zigzag mid-septal zone (arrows) and lateral thick stereome in transversely sectioned septum; 5, *Montlivaltia* sp. ZPAL H.III/792. Jurassic, Oxfordian. Minostowice, Poland. Typical rhomboidal pattern of diagenetic alteration of montlivaltiid

The most significant revisions of scleractinian classification resulted from studies of Mesozoic faunas. Numerous families and genera of Recent and Teriary corals are very similar, and no discrepancy is observed in their microstructural characteristics (e.g., Chevalier, 1961); however, microstructure of older corals differs more, the further they are below the Cenozoic/Cretaceous boundary. Unfortunately, geologically older skeletons are often diagenetically altered and their original microstructure is not preserved. However, exceptionally preserved Mesozoic coral faunas provide satisfactory insight into the history of diversification of scleractinian microstructure. Coralla showing original, aragonitic mineralogy are known from a number of localities. Among the most famous of these are: Dolomites, Italy (Late Triassic: Volz, 1896; Montanaro Gallitelli, 1975; Cuif, 1973, 1975a, 1975b, 1976); Alakir Çay, Turkey (Late Triassic: Cuif, 1975, 1976); Zlambach Beds in Northern Calcareous Alps, Austria (Late Triassic: Roniewicz, 1989); Ostromice, Poland (Late Jurassic: Roniewicz, 1982, 1984); Rarău, Romanian Eastern Carpathians (Early Cretaceous: Morycowa, 1971); and Gosau, Austria (Late Cretaceous: M. Beauvais, 1982). Thanks to these unusual findings, a large spectrum of Mesozoic scleractinian microstructures and microarchitectures became recognized during the 1980s. This significant increase in new taxonomic data on Mesozoic scleractinians made the existing classifications of Vaughan and Wells (1943) and Wells (1965) outdated. Some modifications were already introduced by Alloiteau (1952) and Chevalier and Beauvais (1987), or outlined by Roniewicz and Morycowa (1993). Others await inclusion in a new revision of scleractinian classification. We reiterate the most important suggestions for modification of the still widely used Wells (1956) classification below. For the sake of clarity, we retain the framework of the traditional Wells' suborders.

ASTROCOENIINA

Stylinina (=Stylinida) Alloiteau, 1952.—Jurassic-Cretaceous stylinids have been classified by Vaughan and Wells (1943) as one of the four families of Astrocoeniida. However, as openly stated by these authors, "finer skeletal structures (. . .) so far as they are known they are not like other astrocoeniids" (Vaughan and Wells, 1943, p. 108). Stylinids resemble other corals originally assigned to astrocoeniids in small corallite dimensions and having tabular endotheca, but differ in microarchitectural and microstructural features. Combinations of characters diagnostic of this suborder include (Figs. 1.1–1.4, 9.1–9.2): 1) occurrence of spoon-like outgrowths ("auriculae"—see Gill, 1976) developed on the axial septal edge (the revision of the Cyathophoridae that do not have auriculae is pending); 2) distal septal edge denticulated, lateral faces with spiniform ornamentation; 3) septal calcification centers separated, small-sized, distributed along the distal edge and on the lateral face of the distal edge; and 4) septal trabeculae diverging or (?) arranged in series, simple with lateral axes having the same diameter as the main trabeculae.

Originally four families were included in the stylinines (Alloiteau, 1952, see also Fig. 1), i.e., Cyathophoridae, Stylinidae, Heterocoeniidae, and Euhelliidae. Subsequently, Heterocoeniidae have been transferred to Amphiastraeina (Kołodziej, 1995; compare also Stolarski and Russo, 2001), whereas Morycowa and

Roniewicz (1990) erected the Cladophylliidae as a new stylinine family.

FUNGIINA

Microsolenina Morycowa and Roniewicz, 1995.—Jell's (1974) and Gill's (1980a) studies on fungiine corals provided a number of microstructural and microarchitectural observations of *Fungia* (nominotypic genus of the suborder) that were important in revising the fungiines (Fig. 3.1–3.3). In particular, Jell (1974) showed that the trabeculae in various species of *Fungia* are composed of calcification centers that formed repeatedly to produce the main axis and, occasionally, of numerous additional centers that produce lateral trabecular axes (vepreculae sensu Jell, 1974); see Figure 3.2. Gill (1980) demonstrated that septal interconnections in *Fungia,* traditionally called "synapticulae," are formed parallel to the septal plane and should be called "futurae" (whereas typical, simple synapticulae are formed perpendicularly to the septal plane).

Jurassic-Cretaceous scleractinians with porous septa, pennular ornamentation, and thin-walled dissepiments (i.e., Microsolenidae, Latomeandridae, Synastreidae, and Cunnolitidae) were assigned traditionally to the Fungiina [Alloiteau (1952), Chevalier and Beauvais (1987), Vaughan and Wells (1943), and Wells (1956) distinguished only the Microsolenidae—see Fig. 1]. In contrast to *Fungia* and closely related taxa, their septal trabeculae (main trabecular body) are large and polycentric (i.e., have no structurally delimited axis and are composed of fascicles of fibers originating from calcification centers that are more or less irregularly distributed—see Morycowa and Roniewicz, 1995). Small secondary trabeculae diverge laterally and fuse into characteristic balcony-like stuctures ("pennulae") that may merge into lath-like "menianae" (see Gill, 1967; also Figs. 3.4–3.7, 9.19). Septa in the four mentioned groups are connected via typical "simple" synapticulae. Microstructural and microarchitectural characters distinguish these Jurassic-Cretaceous corals well from Cenozoic *Fungia*-like forms. Morycowa and Roniewicz (1995) formalized this hypothesis by erecting the new suborder Microsolenina for Microsolenidae, Latomeandridae, Synastreidae, and Cunnolitidae. The Fungiina are thus restricted to the Fungiidae and, possibly, the Funginellidae Alloiteau, 1952.

FAVIINA

Montlivaltiidae Dietrich, 1926.—Gill's (1967) description of septal microstructure of Jurassic-Cretaceous *Montlivaltia* and closely related taxa resulted in revision of Montlivaltiidae and in significant modifications to the taxonomic content and stratigraphic range of this family [according to Vaughan and Wells (1943), Wells (1956), and Alloiteau (1952), the representatives of this family appeared in the Triassic and lasted till the end of Mesozoic era].

The pattern of distribution of calcification centers proved to be a useful character in the revision of the Montlivaltiidae. Jurassic-Cretaceous *Montlivaltia* (type: *Montlivaltia caryophyllata* Lamouroux, 1821, Bathonian of Calvados) have large-sized and well-separated calcification centers that also form on lateral outgrowths. The resulting septal trabeculae are thick with regularly produced lateral branches (Figs. 4.5, see also 4.6–4.7 and 9.9–9.10). These lateral branches are manifested on the septal face as spines distributed along the trabecular ridge, forming so-called "carenae" (Gill, 1967; Gill and Lafuste, 1968). By contrast, in

←

large-sized trabeculae (arrows) with lateral branches in transverse section of the septum; *6, 7, Isastraea* cf. *bernensis* Etallon, 1864. ZPAL H.IV/303. Jurassic, Oxfordian. Erratic boulders. Ostromice, Poland. Montlivaltiid type of septal microstructure with large trabeculae and short lateral projections that form septal granulations (arrow). Transverse section.
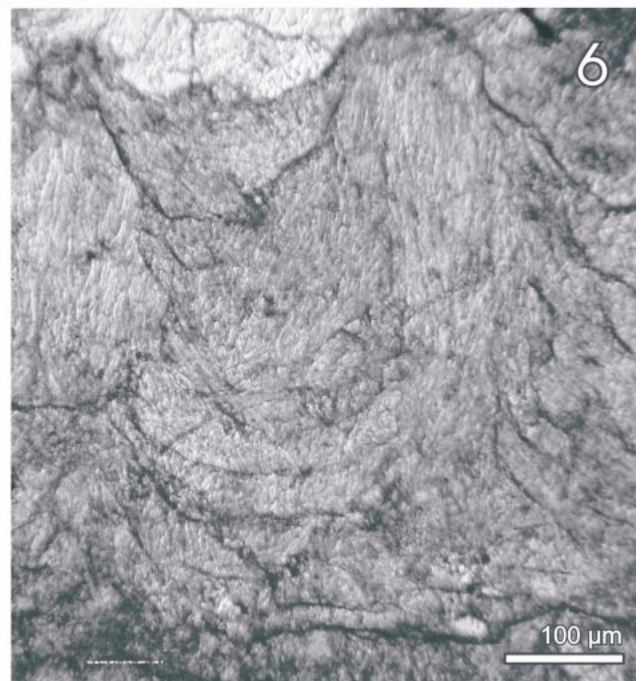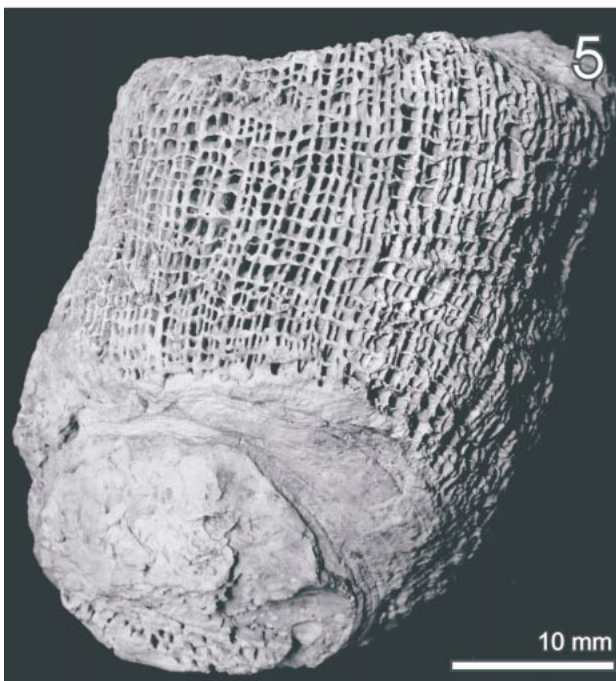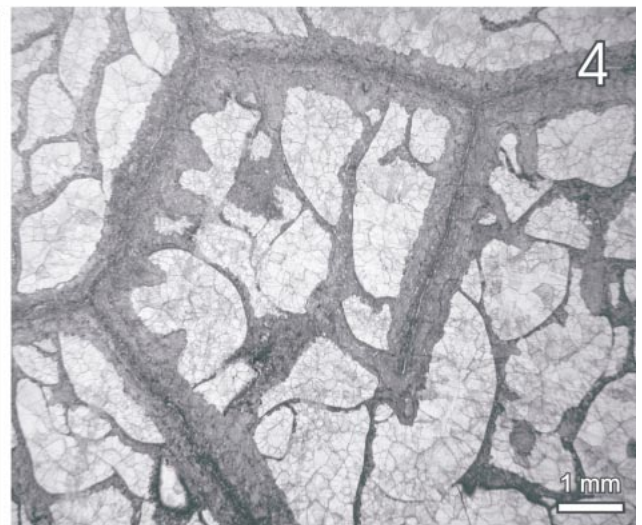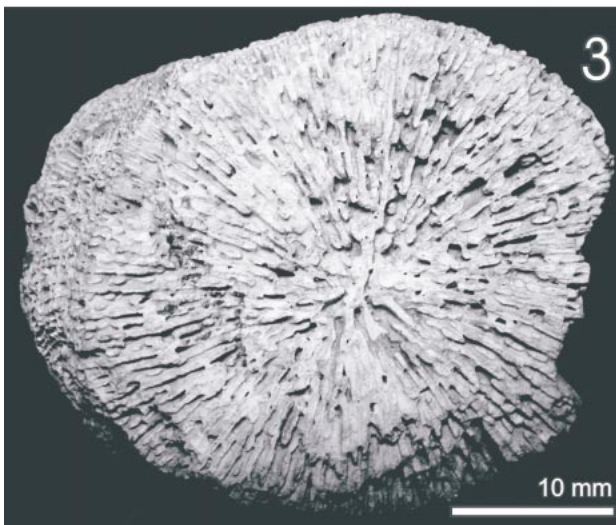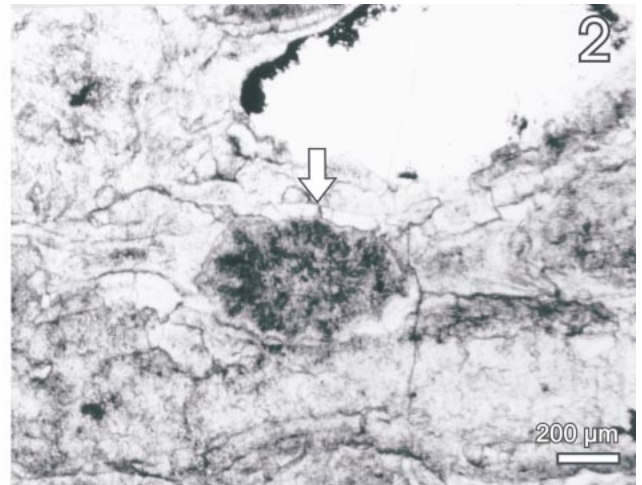
Triassic *Thecosmilia* (species assigned recently to *Retiophyllia* Cuif, 1968 and *Volzeia* Cuif, 1968—see Cuif, 1975) and *Montlivaltia* (species assigned recently to *Distichophyllia* Cuif, 1975; *Cuifia* Melnikova, 1975), septal calcification centers are small-sized and closely spaced. The resulting septal trabeculae are very small sized and, in older septal portions, are covered on both sides with thick sclerenchymal layers (Figs. 4.4, 9.11–9.12, compare also Fig. 4.1–4.3). Thick sclerenchyme may consist of 1) more or less homogenous layers of fibers (diagnostic to Volzeiidae) or 2) fibers arranged around large-sized lateral calcification centers (diagnostic to Reimaniphylliidae). Because septal microstructures of Triassic volzeiids and reimaniphylliids are strikingly similar to that of caryophylliines, Roniewicz (1984, 1989) postulated evolutionary relationships between these corals [see also Roniewicz and Morycowa (1993)].

Stylophyllina L. Beauvais, 1981.—Stylophyllidae Frech, 1890 were assigned to the Faviina and the Archeocoeniida (Vaughan and Wells, 1943; Wells, 1956, and Alloiteau, 1952, respectively) and hence to corals with well-developed septal trabeculae. Cuif (1973) showed that the skeletons of various species (including types) of *Stylophyllum* Reuss and *Stylophyllopsis* Frech differ from other scleractinians in their "non-trabecular structure" i.e., that all of their parts (septa, dissepiments, and intercallicular part of the wall) are formed by the same type of periodically rhythmically deposited fibrous tissue (Fig. 9.7–9.8). L. Beauvais (1981) considered this feature diagnostic at the subordinal level. Studies on excellently preserved Late Triassic stylophyllids from the Zlambach Beds (Roniewicz, 1989) revealed that their skeletal tissue consists of scale-like, fibrous elements appearing as characteristic "coarse" texture on the surface of skeletal elements (Fig. 5.3–5.6, see also Fig. 5.1–5.2). Most likely, the growth process of the stylophyllid skeleton differed from that of other scleractinians: typical Scleractinia have well-defined calcification centers [even in the peculiar extant *Guynia* calcification centers are highly visible, though not separated (Stolarski, 2000)], whereas in stylophyllines the calcification centers are absent or not clearly delineated.

Pachythecaliina Eliasova, 1976.—Pachythecalliines are perhaps the most unusual Mesozoic corals because of their strongly bilateral mode of septal insertion in initial coralla and, usually, their very thick corallite wall (Figs. 6.1–6.6, 9.20–9.21). In a strict sense, the suborder contains the Zardinophyllidae Montanaro-Galitelli, 1975 (=Pachythecaliidae Cuif, 1975) and the Amphiastreidae Ogilvie, 1897, but various Mesozoic corals e.g., carolastraeids, donacosmiliids, intersmiliids, and heterocoeniids, have been linked with the pachythecalliines (see review in Stolarski and Russo, 2001). Because the Zardinophyllidae were diagnosed quite recently (1975), only Chevalier and Beauvais's (1987) classification deals with both main pachythecaliine groups. In former classifications, only the status of the amphiastraeids was considered, but it was subjected to very divergent views: Vaughan and Wells (1943) classified them among the caryophylliids, Wells (1956) assigned them to the Faviina, Alloiteau (1952) erected the new suborder Amphiastraeida, and Chevalier and Beauvais (1987) did not mention them at all [though L. Beauvais (1981) classified them among her Distichophylliina]. Moreover, because of obscure classification criteria adopted by Chevalier and Beauvais (1987), zardinophyllids (restricted to *Zardinophyllum*) and Pachythecaliidae (Pachythecaliidae

sensu Cuif, 1975) were assigned to different suborders [Stylophylliina(!) and Pachythecaliina, respectively (Fig. 1)].

According to Alloiteau (1952), the Amphiastraeida have an "archeothecal" wall (i.e., of mixed septo-dissepimental origin), strong bilateral symmetry, and numerous small-sized septal trabeculae, and they reproduce asexually via intra- and extracalicular budding. Recent studies on amphiastraeids (Melnikova and Roniewicz, 1976; Roniewicz and Stolarski, 2001) showed that the corallite wall (pachytheca) consists of large, horizontally arranged trabeculae ("modules" of Roniewicz and Stolarski, 1999) and Alloiteau's "archeothecal" wall should not be considered a valid term (see also Stolarski, 1995). Amphiastraeid budding is invariably intracalicular, and because new buds show the unique feature of enlarging at the expense of calicular space in the parental corallite (so-called pocket budding or "Taschenknospung"), this type of budding is considered an amphiastraeid synapomorphy. The strong bilateral symmetry of the initial ontogenetic stages of amphiastraeids and zardinophyllids is an argument for linking these two groups together. This argument is supported by the occurrence of pachytheca only in these corals (a pachythecaliine synapomorphy). Montanaro-Gallitelli (1975) postulated that the zardinophyllids belonged to the separate order Hexantiniaria.
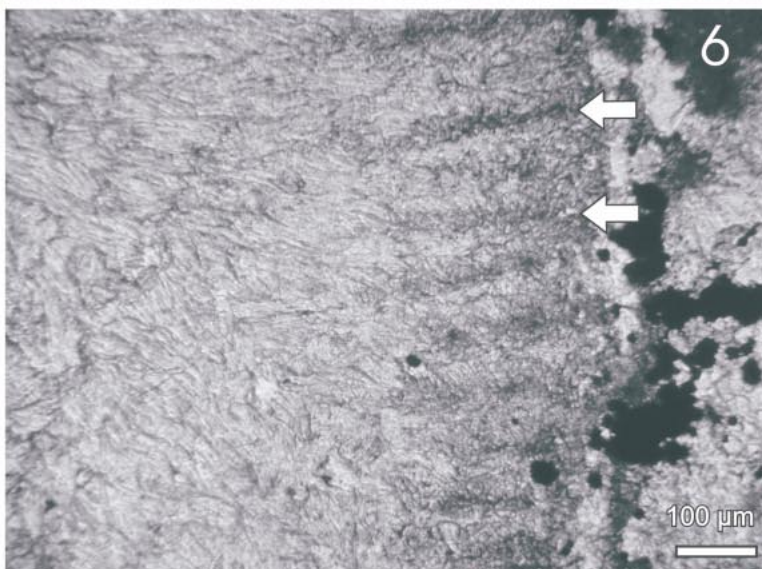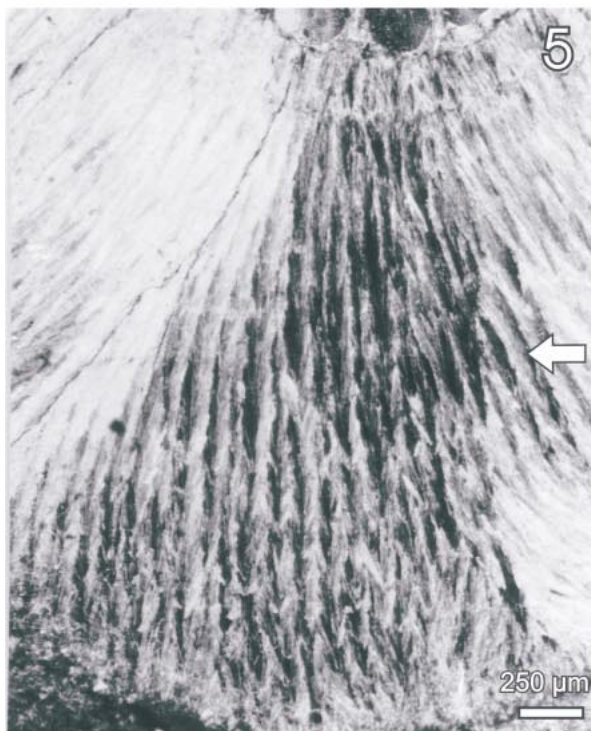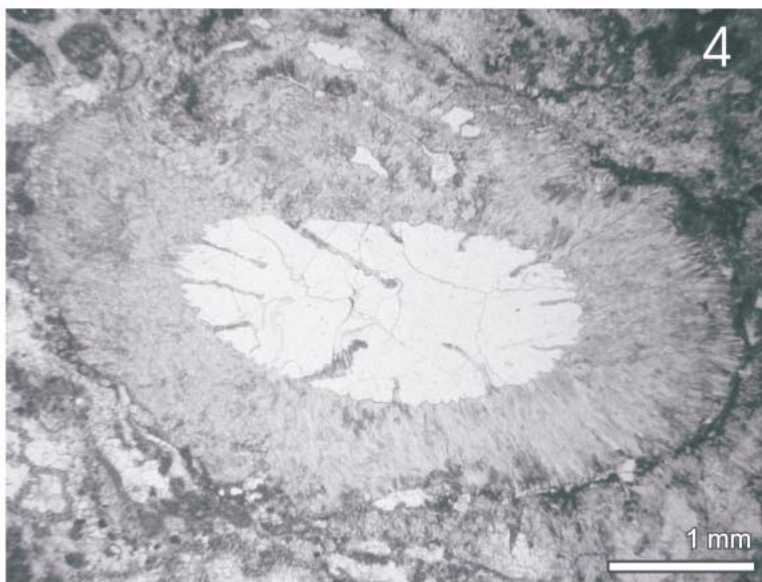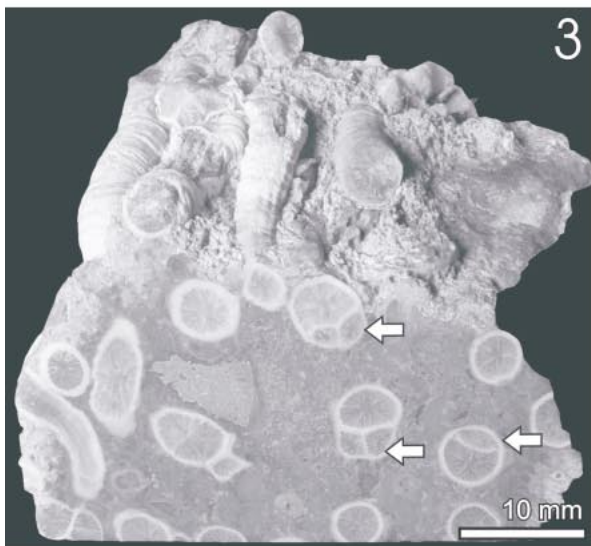
CARYOPHYLLIINA

Rhipidogyrina Roniewicz, 1976.—In the Vaughan and Wells (1943) and Wells (1956) classifications, the Rhipidogyridae Koby, 1904, were assigned to the suborder Caryophylliina; whereas Alloiteau (1952) considered them to be a subfamily of Meandrinidae (suborder Meandriida); see Figure 1.

Roniewicz (1975) recognized the neorhipidacanth microstructure of rhipidogyrid septa, which resembles rhipidacanth microstructure of Paleozoic Phillipsastraeidae (Rugosa; see Jell, 1969). The most remarkable feature of neorhipidacanth microstructure is the occurrence of small-sized trabeculae producing numerous lateral branches that constitute the whole body of the septum (Figs. 7.4–7.7, 9.4). In slightly oblique sections, septal trabeculae have a "brush-like" appearance. This microstructural pattern, differs essentially from the caryophylliines, whose small-sized trabeculae are restricted to the mid-septal zone (except for septal ornamentation that may have trabecular foundations; Figs. 7.6, 7.8, 9.5–9.6). Also, septa of the meandrinids differ from the rhipidogyrid pattern because they lack lateral branches and have stereomaltype thickening of septa (see Alloiteau 1952: fig. 95). Because of these differences in septal microstructures, Roniewicz (1975) proposed elevation of the rhipidogyrids to subordinal rank. Apart from these important microstructural differences, rhipidogyrines and caryophylliines share the basic pattern of sclerenchymal (tectura) deposition, which thicken the external corallite surface (see Stolarski, 1995; Roniewicz and Stolarski, 1999). One may speculate that the ability to form an extensive tectura to serve as protective and reinforcing structure was a key innovation allowing for rapid expansion of the rhipidogyrines in the latest-Jurassic and Cretaceous and the caryophylliines in Cenozoic. The evolutionary relationships of the rhipidogyrines are not yet fully understood (Roniewicz and Morycowa (1993) suggested their connections with the stylinids) and it is commonly assumed that they became extinct at the end of the Mesozoic era.

←

FIGURE 5—1–7, Architecture and microstructure of stylophylline skeleton. *1, 2, Stylophyllopsis rugosa* (Duncan, 1868). BM R.13287. Jurassic, Sinemurian. Honeybourne, Worcester, Great Britain; *1,* Distal-lateral view of corallum showing septal spines with "coarse" texture; *2,* Septum in transverse section with spine (arrow) built of fibre bunches. *3, 5, Stylophyllopsis polyactis* Frech, 1890. NHMW (sample without number). Triassic, Rhaetian. Kesselwand-Rohrmoos, Northern Calcareous Alps, Austria. Note septa firmed of isolated spines; *4, 6, Stylophyllum vesiculatum* Roniewicz, 1989, NHMW 1982/56/34. Triassic, Rhaetian. Kesselwand-Rohrmoos. Septa and wall formed by fibrous tissue.

Guyniidae.—This small family of mainly extant and deep-water corals with characteristic ''thecal pores'' has remained in the suborder Caryophylliina until recent studies of their skeleton (Stolarski, 2000). Microstructural features of two main skeletal elements—the septa and wall—vary considerably in representatives of traditional guyniids, and were used to divide this group into following families: 1) Guyniidae sensu stricto (restricted to monotypic *Guynia*), which has a wall (epitheca) and septa with nonseparated calcification centers (a unique combination of features among Recent Scleractinia; Figs. 8.1, 8.4, 9.13–9.14); 2) Schizocyathidae Stolarski, 2000, which has an epithecate wall and septa composed of clearly separated calcification centers (Figs. 8.5, 9.15–9.16; and 3) Stenocyathidae Stolarski, 2000, which has a wall (marginotheca) and septa composed of well separated calcificatioin centers (Figs. 8.2–8.3, 9.17–9.18). Significant differences in the basic architecture of the skeleton of Guyniidae, Schizocyathidae, and Stenocytahidae support hypothesis of their evolutionary relationships with different lineages of caryophylliines (i.e., Schizocyathidae with Gardineriidae Stolarski, 1996, and Stenocyathidae with Flabellidae Bourne, 1905) or, in the case of *Guynia*, with some early Mesozoic groups (?zardinophylliids,?stylophylliines). ''Thecal pores'' could develop independently in these lineages (see arguments in Stolarski, 2000, p. 32). On the other hand, since all traditional guyniids have specialized thecal pores, one might argue that different types of microstructures developed in corals of the same clade. There are no clearcut arguments that would support one of these hypotheses; however, the traditional paradigm that microstructures are the most conservative and thus the most useful characters in higher-rank classification supports the hypothesis of a polyphyletic origin of traditional guyniids. Because most of the traditional guyniids are living taxa, molecular studies or other biologically oriented approaches could provide new input to this debate.

MOLECULAR REVOLUTION

The introduction of PCR (Polymerase Chain Reaction) techniques was a breakthrough in molecular systematics, triggering molecular studies of corals. Results of these studies cast new light on various aspects of the population and evolutionary biology of Scleractinia, including relationships between and within extant families, and provided support for evolutionary hypotheses about extant corals that are based on the fossil record (see also Veron et al., 1996, p. 2). This last aspect is particularly relevant to the issues discussed in the present paper and was addressed in the following, more up-to-date papers:

1) Romano and Palumbi (1996) analyzed sequences of mitochondrial 16S ribosomal RNA in 34 species of mostly reef-building taxa belonging to 24 genera and 14 families. Phylogenetic analysis based on the molecular data supports clustering the species into traditional morphologically-based families; however, it does not support their grouping into traditional suborders. For example, clusters [*Pavona, Leptoseris*], [*Fungiacyathus*], and [*Cycloseris, Fungia, Zoopilus, Coscinaraea, Psammocora*] consisting of genera grouped by Wells (1956) in Fungiina, are placed on opposite ends of the molecular tree topology. At the same time,

genera belonging to different traditional suborders are placed on the same branch of the tree, e.g., *Euphyllia* and *Cataphyllia* (traditional Caryophylliina *in* Wells, 1956) are clustered with *Merulina, Hydnophora, Echinopora, Caulastrea, Cyphastrea, Leptoria, Pectinia,* and *Lobophyllia* (Faviina *in* Wells, 1956); *Turbinaria* and *Tubastraea* (Dendrophylliina/Eupsammiida in traditional classifications) are grouped with *Porites, Goniopora,* and *Fungiacyathus* (traditional Fungiina). One of the most interesting results of Romano and Palumbi's (1996) study is the recognition of two major clades of Recent Scleractinia that diverged from a common stock in the Paleozoic before the appearance of scleractinian skeleton. There are no clear-cut morphologic criteria allowing discrimination between these clades; however, representatives of the first, ''robust corals'' clade (e.g., *Euphyllia, Lobophyllia*) often form a relatively solid, heavily calcified skeleton and reproduce asexually via intratentacular budding, whereas representatives of the second ''complex corals'' clade (e.g., *Acropora, Fungiacyathus*) often have a less heavily calcified skeleton and reproduce asexually via extratentacular budding.

2) Veron et al. (1996) analyzed sequences of different gene segments (5′ end of the nuclear 28S ribosomal RNA) of 15 species (different from those used by Romano and Palumbi, 1996) belonging to 14 genera (six genera included also in Romano and Palumbi, 1996) and 10 families. In general, Veron et al. (1996) agreed with Romano and Palumbi's (1996) conclusion that molecular analysis supports clustering of genera in traditional families but found their grouping into suborders to be debatable. In particular, as also suggested by Romano and Palumbi (1996), the Poritidae (*Porites, Gonipora*) [traditionally grouped in the suborders Fungiina] and Dendrophylliidae (*Turbinaria* and *Tubastraea*) [the nominative family of the suborder] are more closely related to each other than they are to other scleractinians. On the other hand, genera that clustered in various faviine families remain a coherent group although *Leptastrea* was not included in the study [*Leptastrea* was the only faviine taxon in Romano and Palumbi's (1996) study that clustered not with other faviines but with the (*Psammocora, Coscinaraea, Zoopilus, Fungia, Cycloseris*) group]. Veron et al. (1996) also implied that the Scleractinia are monophyletic, i.e., that extant families have ''a common ancestor at a point in time subsequent to their derivation from anemone-like or corallimorph-like ancestors'' (Veron et al., 1996, p. 8) but are divided into two major groups (thus confirming Romano and Palumbi's, 1996 results).

3) Romano and Cairns's (2000) molecular analysis is the most comprehensive published thus far; 88 species representing 71 genera and 20 families were sampled of both reef-building and nonreef-building taxa, among which 68 species were sampled for mitochondrial 16S ribosomal RNA sequences and 45 species for nuclear 28S ribosomal RNA sequences (the data set includes sequences previously used by Romano and Palumbi, 1996, and Veron et al., 1996). Basically, the resulting phylogenetic hypothesis based on mitochondrial 16S rRNA supports the bipartite division of Scleractinia into two major clades of ''robust'' and ''complex'' corals. However, it also detects two additional clades [*Odontocyathus, Vaughanella,* and *Ceratotrochus* (''*C.*'' *magnaghii*), traditionally in

←

FIGURE 6—*1–7,* Architecture and microstructure of the pachythecaliine skeleton. *1, Pachythecalis major* Cuif, 1975. ZPAL H.XXI/5. Triassic, Lower Norian. Alakir Çay, Turkey. Pachythecal wall consisting of several generations of stereomal deposits (arrows); *2, Zardinophyllum zardinii* Montanaro-Gallitelli, 1975. IPUM11. Triassic, Middle Carnian, San Cassiano Beds. Alpe di Specie, Italy. Smooth growing septal edge and finely ribbed surface of inner side of wall. *3, Quenstedtiphyllia fritschi* (Volz, 1896), GMH. holotype. Triassic, Middle Carnian, San Cassiano Beds. Precise locality unknown. Taschenknospung budding (arrows); *4, Pachydendron microthallos* Cuif, 1975, ZPAL H.XXI/1. Triassic, Lower Norian. Alakir Çay, Turkey. Pachythecal modules expressed as fine ribs on wall internal surface; *5, 6, Pachysolenia cylindrica* Cuif, 1975, ZPAL H.XXI/6 and ZPAL H.XXI/7, respectively. Triassic, Lower Norian. Alakir Çay,Turkey. Long pachythecal modules (5) and calcification centers in axis of pachythecal modules (arrows on 6).
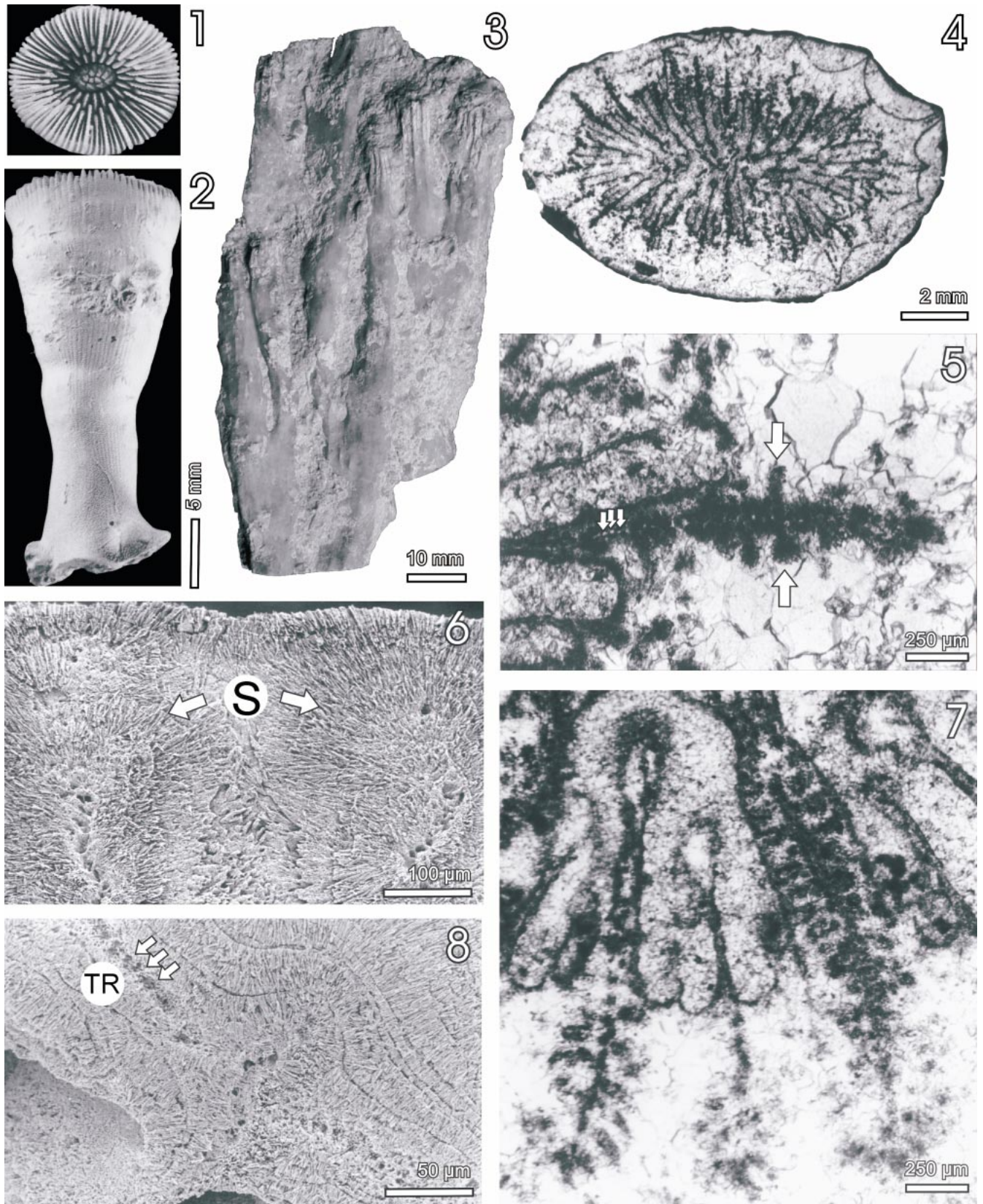
FIGURE 7—1–7, Architecture and microstructure of the rhipidogyrine vs. caryophylliine skeleton. *1, 2, 6, 8, Caryophyllia cyatus* (Ellis & Solander, 1786), ZPAL H.XV/1 in distal (*1*) and lateral (*2*) views. 6, Septothecal wall (S) in adult part of the corallum formed by costal parts of two neighboring septa (arrows); *8,* trabeculothecal wall (TR) in juvenile part of the corallum has own calcification centers (arrows). Note that septal and trabeculothecal calcification centers are small-sized and closely-spaced; *3, Aplosmilia semisulcata* Michelin, 1843, MNHN M00267 (neotype),

Caryophylliina, and *Anthemiphyllia,* traditionally in Faviina] that do not group with the two major clades but form a basal polytomy together with them and with the corallimorpharian *Corynactis.* The more slowly, or more rapidly, evolving gene region (depending on the time period when these lineages diverged from each other) is necessary to resolve the relationships between these basal clades. Romano and Cairns's (2000) analysis supports the conclusion of previous molecular studies that many coherent families do not cluster into traditional suborders. In addition, genera traditionally grouped into large families may cluster in different clades. The most striking example of this are the traditional caryophylliids, which are situated in different parts of the tree topology [*Odontocyathus, Vaughanella, Ceratotrochus*]. These taxa form an independant clade—[*Thalamophyllia*] clusters with the agariciids in "complex corals," but [*Euphyllia, Cataphyllia*] clusters with the merulinids, which belong to the "robust corals." [*Cladocora, Polycyathus, Paracyathus*] is grouped with [*Rhizosmilia, Phyllangia*], and together with the meandrinids forms a larger subset of the "robust corals" clade, and [*Caryophyllia, Crispatotrochus*] form a more independent branch within "robust corals" clade. Also traditional oculinids are grouped with "complex" [*Acrhelia, Galaxea*], or with "robust" [*Oculina*] corals. Romano and Cairns (2000) argued that nuclear 28S rRNA sequences are less useful in resolving relationships among scleractinian families than mitochondrial 16S rRNA sequences (fewer number of variable characters). Even if 28S and 16S tree topologies are generally similar, groupings in 28S topology have no or very low support in bootstrap analysis (see Romano and Cairns, 2000: fig. 1).

Molecular studies of the evolutionary relationships of the Scleractinia have drawn several main conclusions that differ from traditional hypotheses: 1) poritiids (Poritiina of Veron, 1995) do not cluster with traditional Fungiina but do group with the dendrophylliids (Dendrophylliina) in the "robust corals" clade; 2) the agariciids and fungiacyathids (traditional Fungiina) cluster as independent clades in the "complex coral" clade, whereas the Fungiidae (the nominative of the traditional suborder) and the Siderastraeidae (Fungiina) form a group within the "robust corals" clade; 3) pocilloporids and acroporids (traditionally clustered in Astrocoeniina) are distantly located on the molecular tree ("robust" vs. "complex" corals, respectively, in Romano and Cairns's (2000) analysis); 4) anthemiphylliids, traditionally grouped with faviines, form a clade distinct from all other scleractinians; and 5) traditional caryophylliids are polyphyletic and their various groups are dispersed along the tree topology.

One would expect that the results of molecular studies and those inferred from more in-depth microstructural observations of some Recent taxa (Roniewicz and Morycowa, 1993) would be more complementary, but they are not. In particular, two main groups of extant scleractinians indicated by microstructural studies (i.e., representatives of "minitrabecular" and "thick-trabecular" corals) consist of mixture of families grouped either in "complex" or in "robust" coral clades in the molecular topology. However, some suggestions derived from microstructural studies agree with those resulting from molecular analysis, e.g., "*Fungia* group" is independent from other "fungiids" (see also section "Modification in Scleractinian Taxonomy") and clusters with faviids, pectiniids, and mussids (Morycowa and Roniewicz, 1995). We assume that the lack of congruence between molecular and morphological hypotheses at the family level results from: 1) the small number of extant taxa, whose skeletal microstructural and detailed macroscopic characters were studied with sufficient resolution; 2) an overly simplified scheme of traditional microstructural analysis (in many cases, microstructural characteristics were limited to simple descriptions of trabeculae, e.g., "small" and "large," whereas significant difference can be detected at a much smaller scale (see section "Towards a new synthesis"). Also, potentially some other segments of mitochondrial/nuclear DNA sequences may demonstrate better resolution in comparison with those used so far.

TOWARDS A NEW SYNTHESIS

Achieving a more reliable and comprehensive scheme of evolutionary relationships and classification framework for the Scleractinia will require close cooperation between coral biologists, ecologists, geologists, geochemists, and paleontologists. Great progress in analytical methods in all these fields has created a fertile environment for interdisciplinary discussion to occur on a more profound level than was previously possible. Interdisciplinary research at the frontiers of population genetics, in-depth morphometric and molecular studies, and in-depth morphological and biochemical studies have the greatest potential for changing current classification systems. Many additional approaches, e.g., anatomical studies of coral gametes (Harrison and Jamieson, 1997) or cnidae (Pires and Pitombo, 1992; Pires, 1997), will complement this research.

Population genetics vs. morphometric studies.—The low-resolution of the traditional morphological approach is the main reason for inaccuracy in species recognition, especially in paleontology (frequently influenced by author's splitter vs. lumper tendency). For example, in many fossil collections (including those made by most influencial coral workers) species have been designated based on almost "untouched" material (including forms with calices completely covered with sediment where virtually nothing can be said about actual septal pattern). On the other hand, diagnoses of many species are based only on characters visible on a single section (serial sectioning is the most appropriate technique in the case of rock-embedded specimens, which allows for 3D reconstruction of the corallum). It is thus not surprising that estimates of species diversity obtained from such studies are incompatible with those resulting from more in-depth, biologically-based approaches (for review of various biologically-based approaches see Lang, 1984). New light has been cast on the species concept in corals by chromosomal and genetic studies. From a theoretical standpoint, the common type of scleractinian sexual reproduction, i.e., by synchronous mass spawning that results in the mixing of gametes from a wide range of species, creates an opportunity for hybridization. Indeed, as shown by Kenyon (1997), Odorico and Miller (1997), Hatta et al. (1999), and Van Oppen et al. (2000), morphologically different species of *Acropora* hybridize during multispecies spawning events. Currently there are insufficient data to assess the range of hybridization in living corals; however its occurrence undoubtedly complicates our ability to distinguish inter- vs. intraspecific relationships. If hybridization is a common process in corals, then the main external factor driving coral evolution is most likely surface circulation currents and thus vicariance (Veron, 1995). Surface

←

coll. Michelin. Jurassic, Oxfordian. St. Mihiel, France; *4, 5, Aplosmilia* sp. ZPAL H.XVII/21. Jurassic, Middle Oxfordian. Pagny-sur-Meuse, France. Transverse section showing neorhipidacanth septal microstructure with thin, densely crowded main trabeculae (small arrows) and long lateral trabeculae (larger arrows); *7, Ironella rutimeyeri* (Koby, 1889). MHN Geneve (specimen without number, originaly labeled as *Heliastraea langi* Koby). Jurassic, Oxfordian. Gilley (Jura), Switzerland. Transverse section showing neorhipidacanth microstructure of septum: main trabeculae in mid-septal zone associated with a row of lateral, secondary trabeculae. In the costal part long secondary trabeculae.
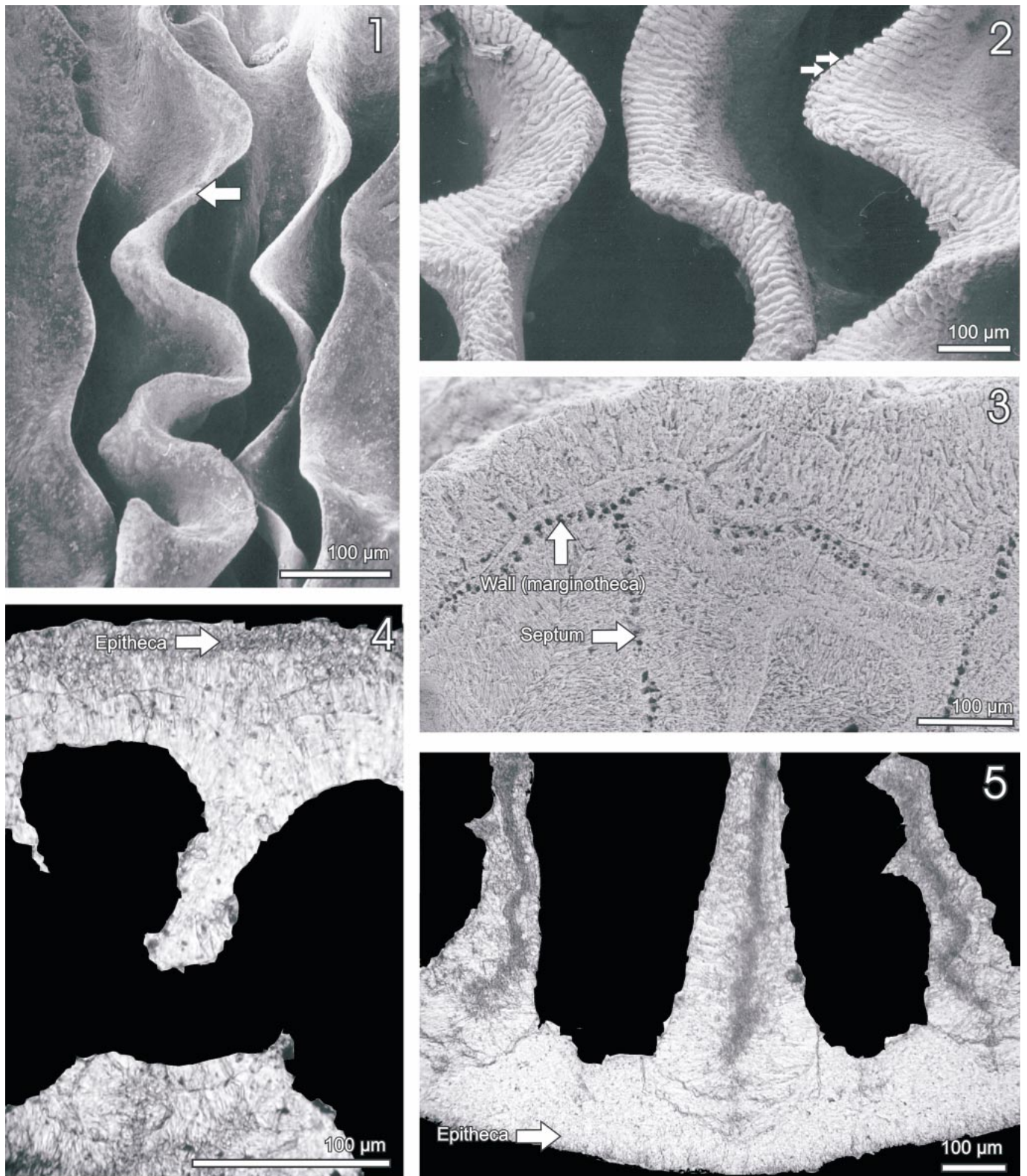
FIGURE 8—*1–7*, Architecture and microstructure of guyniid, schizocyathid, and stenocyathid skeleton; 1, 4, *Guynia annulata* Duncan, 1872; *1,* ZPAL H. XIV/22, Recent, Indian Ocean, JAGO-Coelacanthe, 4.12.1989, Sta.??, 11°51.40′S/43°19.20′E, 196 m. Smooth and undulated growing septal edge (arrow); *4,* ZPAL H. XIV/23, Recent, Mediterranean, Marseille, submarine caves, few meters depth. Epithecal calcification centers (arrow); *2, Truncatoguynia irregularis* Cairns, 1989. ZPAL H.XIV/11, Recent; New Zealand, 3,9 km off Nugent and Raoul Islands, 146–165 m. Undulated septal edge with trabecular dentitions (arrows); *3, Stenocyathus vermiformis* Pourtalès, 1868, ZPAL H.XIV/15, MARION DUFRESNE, MD50, Sta. 21(DC99), 38°47.81′S/77°34.61′E, 320–450 m. Small-sized and separated wall and septal calcification centers (arrows); *5, Schizocyathus fissilis* Pourtalès, 1874, NMNH 61728/1, Recent, Atlantic Ocean, Caribbean Sea, EXPLORER, 16°35.4′N/82°47.2′W, 183–335 m. Epithecal wall (arrow) incorporating septa.
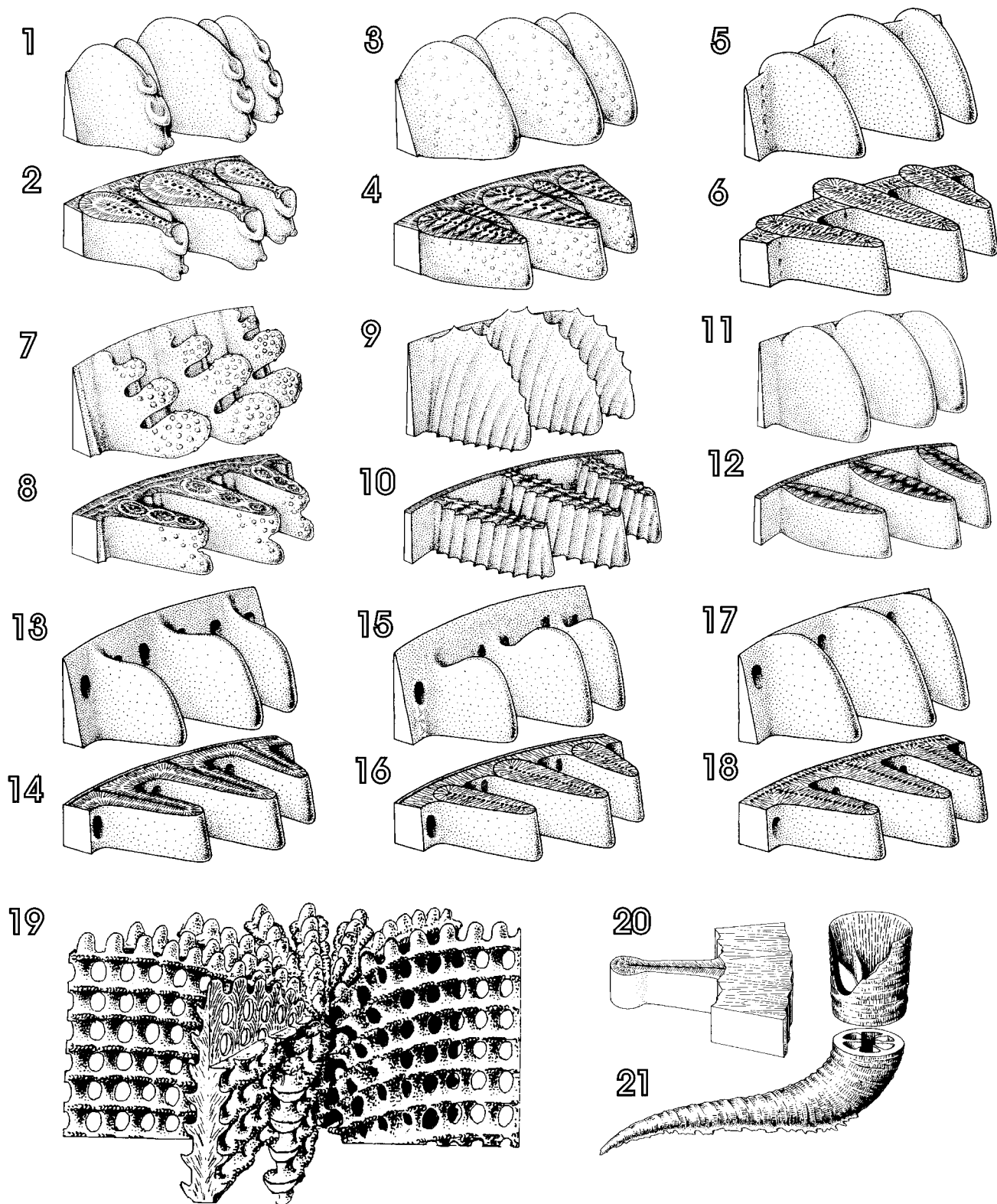
FIGURE *9*—Macro- and microstructural characters of some major taxonomic units discussed in the text. Models not to scale. *1, 2,* Stylinina—auriculae (arrows); *3, 4,* Rhipidogyrina—neorhipidacanth septal microstructure with numerous lateral trabecular branches (arrows); *5, 6,* Caryophylliina—calicfication centers limited to mid-septal zone (arrows); *7, 8,* Stylophyllina—septal spines composed of packages of fibers (arrows); *9, 10,* Montlivaltiidae—large-sized septal trabeculae with lateral branches manifested on septal faces as "carenae" (arrows); *11, 12,* Reimaniphylliidae—small-sized septal calcification centers in zigzag mid-septal zone; *13, 14,* Guyniidae sensu stricto (*Guynia*)—septa and wall (epitheca) with non-separated calcification centers; *15, 16,* Schizocythidae—wall with non-separated calcification centers (epitheca), septa with separated calcification centers; *17, 18,* Stenocyathidae—wall and septa with separated calcification centers; *19,* Microsolenina—porous septa with pennular ornamentation (arrows); *20, 21,* Pachythecaliina—scolecoid corallum of *Zardinophyllum* (*21*) and its pachythecal wall (*20*-arrow). *19* after Morycowa and Roniewicz (1995).

circulation, dynamically changing in space and time, controls larval dispersal; hence gene flow across the ocean, and on a global scale, depends on the configuration of continental blocks (driven, in turn, by plate tectonics). One may speculate, if surface circulation vicariance drives the reticulate pattern of evolution; the classical concepts of biological species (based on reproductive isolation) and phylogenetic species (based on phylogenetic relationships determined by monophyly) may not apply (see also Medina et al. (1999). These fascinating, far-reaching perspectives of connections between coral evolution and global tectonics/oceanic currents can only be validated if we develop the tools and procedures to access actual species diversity. During the last two decades, the application of various morphometric methods has significantly increased the resolution of morphospecies distinction (Foster, 1979a, 1979b; Budd, 1991; Budd et al., 1994). Soon it will be shown how estimates about extant species boundaries based on various landmark and non-landmark-based techniques are consistent with those obtained from molecular studies. If this sounds overly optimistic, consider that morphospecies distinguished in collections of Caribbean *Porites* using a landmark-based protocol are in 90 percent agreement with the classification of the same animals using allozyme electrophoresis (Potts et al., 1993; Budd et al. (1994)).

Molecular biology vs. studies on the skeleton.—The next few decades will undoubtedly be a period of rapid growth in the knowledge of genetic diversity of extant Scleractinia. More DNA samples of shallow-water, zooxanthellate reef forms [ca. 665 species, as estimated by Cairns et al. (1999)] and deep-water, azooxanthellate species [according to estimates by Cairns et al. (1999), azooxanthellates are even richer in species (i.e., 669) than the former group] will be sequenced. The results of molecular and in-depth anatomical studies will provide a good point of comparison for those with differing in-depth morphological approaches on extant corals. Better cross-validation approaches will be developed, and better feedback from fossil data is expected. And again, with better feedback between data on extant and fossil scleractinians, a better understanding of evolution and classification of entirely extinct cnidarian groups (e.g., Rugosa) is expected.

In order to increase the resolution of traditional microstructural approach and to properly determine homology between minute structures, an accurate model of scleractinian biomineralization (extant material) and skeletal diagenesis (fossil data) is required. For many decades in the paleontological literature the pattern of distribution of calcification centers (or the pattern of distribution of trabeculae) was the main source of taxonomic information. It was believed that calcification centers are the main skeletal spots where the coral extends direct formation control. Biological control is less strict on the rest of the skeleton, and aragonite fibers are identical with those formed abiotically (Constantz, 1990, 1986a, 1986b). However, as with other invertebrates, the growth of the entire skeleton is mediated by organic matrices and is formed as the result of an interplay between mineral and organic growth phases [(this model was only recently applied to paleontological studies by Cuif et al. (1997, 1999), Cuif and Dauphin (1998), and Gautret et al. (2000)]. Calcification centers consist of isodiametric aragonitic microcrystals (ca. 1 micron in diameter), embedded in an organic component; fibers that form the main part of the skeleton are enveloped by organic coating (Johnston, 1980), and individual fibers consist of mineral (aragonite) components repeatedly sandwiched between organic components. Analyses of the organic phase (mainly glyco-proteic components) extracted from calcification centers and fibers indicate significant differences in composition between centers and fibers and in turn between these two among various species. Preliminary analyses concerning the organic components of a few species of reef corals (Cuif et al., 1997) cluster some genera in a different way than

suggested by traditional schemes or by molecular studies [e.g., *Leptoseris, Cyphastraea, Leptastraea* group together in phylograms based on amino-acid as well as glucid component data, whereas in Romano and Cairns's (2000) tree, *Leptoseris* is among "complex corals," and *Cyphastraea* and *Leptastraea* are in different branches of "robust corals"]. Obviously, there is no reason that these different sources of information should fully overlap; however, one should point out that methodological problems hampering the use of both intra-skeletal organic components and DNA may partly be responsible for this discrepancy. Proper analysis of biochemical data requires a model for biochemical decomposition of organic components after formation. An additional interpretative dimension is the fact that the composition of organic components is also influenced by the type of coral metabolism, which is in turn determined by the presence or lack of endosymbiotic zooxanthellae (Gautret et al., 1997; Cuif et al., 1999). Lastly, in contrast to molecular analyses where it is relatively easy to detect contamination by foreign DNA, only highly accurate sampling avoids contamination by organic components of almost ubiquitous microorganisms (e.g., boring algae or fungi). At present it is difficult to settle the question of the taxonomic usefulness of this approach, but undoubtedly it will provide a new dimension for skeletal studies. Despite the fact that this new area of research wrestles with very basic interpretative problems, one hopes that a new generation of molecular paleobiologists will solve most of these initial difficulties and will provide reliable cross-checking tools, independent of typical biological-based and purely geometrical microstructural approaches.

REFERENCES

ALLOITEAU, J. 1952. Madréporaires post-paléozoïques, p. 539–684. *In* J. Piveteau (ed.), Traité de paléontologie, 1. Paris, Masson.

ALLOITEAU, J. 1957. Contribution a la systématique des madréporaires fossiles. C.N.R.S., Paris. I, p. 426 pp.

BARNES, D. 1972. The structure and formation of growth-ridges in scleractinian coral skeletons. Proceedings of the Royal Society of London B, 182:331–350.

BARON-SZABO, R. C. 1997. Die Korallenfazies der ostalpinen Kreide (Helvetikum: Allgäuer Schrattenkalk; Nördliche Kalkalpen: Branderberger Gosau) Taxonomie. Palökologie. Zitteliana, 21:3–97.

BARON-SZABO, R. C. 1998. A new coral fauna from the Campanian of Northern Spain (Torallola Village, Prov. Lleida). Geologisch-paläontologische Mitteilungen, Innsbruck, 23:127–191.

BARON-SZABO, R. C. 2000. Late Campanian-Maastrichtian corals from the United Arab Emirates-Oman border region. Bulletin of The Natural History Museum, Geology Series, 56:91–131.

BARON-SZABO, R. C., AND T. STEUBER. 1996. Korallen und Rudisten aus dem Apt im tertiären Flysch des Parnass-Gebirges bei Delphi-Arachowa. Berliner Geowissenschaftliche Abhandlungen E, 18:3–75.

BEAUVAIS, L. 1981. Sur la taxinomie des Madréporaires mésozoiques. Acta Palaeontologica Polonica, 25:345–360.

BEAUVAIS, M. 1982. Revision systématique des Madréporaires des couches de Gosau.-Travaux du Laboratoire de Paléontologie des Invertébrés, Université Pierre et Marie Curie 2, 277 p.

BOURNE, G. C. 1887. On the anatomy of *Mussa* and *Euphyllia,* and the morphology of the madreporarian skeleton. Quarterly Journal of Microscopical Science, London, 28:21–52.

BOURNE, G. C. 1899. Studies on the structure and formation of the calcareous skeleton of the Anthozoa. Quarterly Journal of Microscopical Science, London, 41:499–547.

BUDD, A. F. 1991. Neogene paleontology in the northern Dominican Republic. 11. The family Faviidae (Anthozoa: Scleractinia). Pt. I. The

genera *Montastraea* and *Solenastrea.* Bulletin of America Paleontology, 101:1–83.

BUDD, A. F., K. G. JOHNSON, AND D. C. POTTS. 1994. Recognizing morphospecies in colonial reef corals: I. Landmark-based methods. Paleobiology, 20:484–505.

BRYAN, W. H., AND D. HILL. 1942. Spherulitic crystallization as a mechanism of skeletal growth in the Hexacorals. Proceedings of the Royal Society of Queensland, 52:78–91.

CAIRNS, S. D. 1979. The deep-water Scleractinia of the Caribbean Sea and adjacent waters. Studies on the Fauna of Curaçao and Other Caribbean Islands, LVII:1–341.

CAIRNS, S. D. 1982. Antarctic and Subantarctic Scleractinia. Antarctic Research Series, 34:1–74.

CAIRNS, S. D. 1984. New records of ahermatypic corals (Scleractinia) from the Hawaiian and Line Islands. Occasional Papers of Bernice Pauahi Bishop Museum, Honolulu, 25:1–30.

CAIRNS, S. D. 1995. New records of azooxanthellate stony corals (Cnidaria: Scleractinia and Stylasteridae) from the Neogene of Panama and Costa Rica. Proceedings of the Biological Society of Washington, 108: 533–550.

CAIRNS, S. D. 1998. Azooxanthellate Scleractinia (Cnidaria: Anthozoa) of Western Australia. Records of the Western Australian Museum, 18: 361–417.

CAIRNS, S. D. 1999. Cnidaria Anthozoa: deep-water azooxanthellate Scleractinia from Vanuatu, and Wallis and Futuna Islands. *In* A. Crosnier (ed.), Résultats des Campagnes MUSORSTOM. Volume 20. Mémoires du Muséum national d'Histoire naturelle 180:31–167.

CAIRNS, S. D., B. W. HOEKSEMA, AND J. VAN DER LAND. 1999. Appendix: List of Extant Stony Corals. Atoll Research Bulletin, 459:13–46.

CHEVALIER, J. P. 1961. Recherches sur les Madréporaires et les formations récifales miocènes de la Mediterranée occidentale.: Mémoires de la Société Géologique de France, 93:1–562.

CHEVALIER, J. P. 1971. Les Scléractiniaires de la Mélanésie Française (Nouvelle-Calédonie, Iles Chesterfield, Iles Loyauté, Nouvelles Hébrides). Expédition Francaise sur les Récifs Coralliens de la Nouvelle-Calédonie, 1re Partie, 5:1–307.

CHEVALIER, J. P. 1975. Les Scléractiniaires de la Mélanésie Française (Nouvelle-Calédonie, Iles Chesterfield, Iles Loyauté, Nouvelles Hébrides). Expédition Francaise sur les Récifs Coralliens de la Nouvelle-Calédonie, Deuxieme Partie, 7:1–307.

CHEVALIER, J. P., AND L. BEAUVAIS. 1987. Ordre des Scléractiniaires, p. 403–764. *In* P. P. Grasse (ed.), Traité de Zoologie, Cnidaires, Anthozoaires. Masson, Paris.

CONSTANTZ, B. R. 1986a. Coral skeleton construction: a physiochemically dominated process. Palaios, 1:152–157.

CONSTANTZ, B. R. 1986b. The primary surface area of corals and variations in their susceptibility to diagenesis. *In* J. H. Schroeder and B. H. Purser (eds.), Reef Diagenesis. Springer Verlag Berlin, Heidelberg.

CONSTANTZ, B. R., AND A. MEIKE. 1990. Calcite centers of calcification in *Mussa angulosa* (Scleractinia), p. 201–207. *In* R. E. Crick (ed.), Origin, Evolution, and Modern Aspects of Biomineralization in Plants and Animals. Plenum Press, New York.

CUIF, J. P. 1972. Recherches sur les Madréporaires du Trias. I. Famille des Stylophyllidae. Bulletin du Muséum National d'Histoire Naturelle, 17:211–291.

CUIF, J. P. 1975. Caracteres morphologiques, microstructuraux et systématiques des Pachythecalidae nouvelle famille de Madréporaires Triassiques. Géobios, 8:157–180.

CUIF, J. P., AND Y. DAUPHIN. 1998. Microstructural and physico-chemical characterization of ''centers of calcification'' in septa of some Recent scleractinian corals. Paläontologische Zeitschrift, 72:257–270.

CUIF, J. P., AND C. PERRIN. 1999. Micromorphology and microstructure as expressions of scleractinian skeletogenesis in *Favia fragum* (Esper, 1795) (Faviidae, Scleractinia). Zoosystema, 21:137–156.

CUIF, J. P., Y. DAUPHIN, AND P. GAUTRET. 1997. Biomineralization features in scleractinian coral skeletons: source of new taxonomic criteria. Boletín de la Real Sociedad Española de Historia Natural (Sección Geológica), 92:129–141.

CUIF, J. P., Y. DAUPHIN, AND P. GAUTRET. 1999. Compositional diversity of soluble mineralizing matrices in some recent coral skeletons compared to fine-scale growth structures of fibers: discussion of consequences for biomineralization and diagenesis. International Journal of Earth Sciences, 88:582–592.

CUIF, J. P., Y. DAUPHIN, A. FREIWALD, P. GAUTRET, AND H. ZIBROWIUS.

1999. Biochemical markers of zooxanthellae symbiosis in soluble matrices of skeleton of 24 Scleractinia species. Comparative Biochemistry and Physiology A, 123:269–278.

DUERDEN, J. E. 1902. West Indian madreporarian polyps. National Academy of Sciences (Washington), Memoir, 7:399–648.

DUERDEN, J. E. 1904. The coral *Siderastrea radians* and its postlarval development. Carnegie Institute of Washington Publications, 20:1–130.

DUNCAN, P. M. 1885. A revision of the families and genera of the Sclerodermic Zoantharia, Ed. & H., or Madreporaria (M. Rugosa excepted). Journal of the Linnean Society, Zoology, 18:1–204.

FOWLER, G. H. 1885. The anatomy of the Madreporaria: I. Quarterly Journal of Microscopical Science, 25:577–597.

FOWLER, G. H. 1886. The anatomy of the Madreporaria: II. Quarterly Journal of Microscopical Science, 27:1–16.

FOWLER, G. H. 1887. The anatomy of the Madreporaria: III. Quarterly Journal of Microscopical Science, 28:1–19.

FOWLER, G. H. 1888. The anatomy of the Madreporaria: IV. Quarterly Journal of Microscopical Science, 28:415–430.

FOWLER, G. H. 1890. The anatomy of the Madreporaria: V. Quarterly Journal of Microscopical Science, 30:405–422.

FOSTER, A. B. 1979a. Phenotypicplasticity in the reef corals Montastraea annularis (Ellis & Solander) and Siderastrea siderea (Ellis & Solander). Journal of Experimental Marine Biology and Ecology, 39:25–54.

FOSTER, A. B. 1979b. Environmental variation in a fossil scleractinian coral. Lethaia, 12:245–264.

FRECH, F. 1890. Die Korallenfauna der Trias. Die Korallen der juvavischen Triasprovinz. Palaeontographica, 37:1–116.

GAUTRET, P., J. P. CUIF, AND A. FREIWALD. 1997. Composition of soluble mineralizing matrices in zooxanthellate and non-zooxanthellate scleractinian corals: biochemical assessment of photosynthetic metabolism through the study of a skeletal feature. Facies, 36:189–194.

GAUTRET, P., J. P. CUIF, AND J. STOLARSKI. 2000. Organic components of the skeleton of scleractinian corals—evidence from in situ acridine orange staining. Acta Palaeontologica Polonica, 45:107–118.

GILL, G. A. 1967. Quelques précisions sur les septes perforés des Polypiers mésozoïques. Mémoires de la Société Géologique de France (n.s.), 46:58–81.

GILL, G. A. 1970. La structure et la microstructure septale de *Montlivaltia* Lmx.: crit res nouveaux pour la systématique des Hexacoralliaires. Comptes Rendus Hébdomadaires des Séances de l'Académie des Sciences, D 270:294–297.

GILL, G. A. 1980a. The futurae (''compound synapticulae''), their structure and reconsideration of their systematic value. Acta Palaeontologica Polonica, 25:301–310.

GILL, G. A. 1980b. Recognition of pennular structures typical of Mesozoic corals in *Discotrochus orbignyanus* from the Eocene of the Gulf States. Journal of Paleontology, 54:1108–1112.

GILL, G. A., AND A. RUSSO. 1973. Présence d'une structure septale de type ''Montlivaltide'' chez *Trochosmilia* Madréporaire Éocène. Annales de Paléontologie, Invertebrates, 59:37–61.

GOREAU, T. F. 1959. The physiology of skeleton formation in corals. I. A method for measuring the rate of calcium deposition by corals under different conditions. Biological Bulletin, 116:59–75.

HARRISON, P. L., AND B. G. M. JAMIESON. 1997. Cnidaria and Ctenophora. *In* B. G. M. Jamieson (ed.), Reproductive Biology of Inbertebrates 8:21–95. Oxford & IBH Publishing Co. Pty Ltd, New Delhi.

HATTA, M., H. FUKAMI, W. Q. WANG, M. OMORI, K. SHIMOIKE, T. HAYASHIBARA, Y. INA, AND T. SUGIYAMA. 1999. Reproductive and genetic evidence for a reticulate evolutionary history of mass-spawning corals. Molecular Biology and Evolution, 16:1607–1613.

HOEKSEMA, B. W. 1989. Taxonomy, phylogeny and biogeography of mushroom corals (Scleractinia: Fungiidae). Zoologische Verhandelingen Leiden, 254:1–295.

JELL, J. S. 1969. Septal microstructure and classification of the Philipsastraeidae, p. 50–73. *In* K. S. W. Campbell (ed.), Stratigraphy and Palaeontology—Essays in Honour of Dorothy Hill. Australian National University Press, Canberra.

JELL, J. S. 1974. The microstructure of some scleractinian corals. Proceedingsof the 2nd International Coral Reef Symposium, Brisbane, 2: 301–320.

JELL, J. S., AND D. HILL. 1974. The microstructure of corals, p. 8–14. *In* B. S. Sokolov (ed.), Ancient Cnidaria. Volume 1. Publishing House 'Nauka,' Novosibirsk.

JOHNSTON, I. S. 1976. The tissue-skeleton interface in newly-settled polyps of the reef coral *Pocillopora damicornis,* p. 249–260. *In* N. Watabe

and K. M. Wilbur (eds.), The Mechanisms of Mineralization in the Invertebrates and Plants. University of South Caroline Press, Columbia.

JOHNSTON, I. S. 1980. The ultrastructure of skeletogenesis in hermatypic corals.: International Review of Cytology, 67:171–214.

KOCH, G. VON. 1882. Über die Entwicklung des Kalkskeletes von *Asteroides calycularis* und dessen morphologische Bedeutung. Mittheilungen aus der Zoologischen Station zu Neapel, 3:284–292.

LANG, J. C. 1984. Whatever works: The variable importance of skeletal and of non-skeletal characters in scleractinian taxonomy. Paleontographica Americana, 54:18–44.

LAFUSTE, J. 1970. Lames ultra-minces a faces polies. Procede et application a la microstructure des Madreporaires fossiles. Comptes rendus hebdomadaires des seances de l'Academie des Sciences Paris, 270: 679–681.

LATHUILIÈRE, B. 1996. Is morphology a good way to understand the evolution of corals? Paleontological Society Papers, 1:81–105.

LATHUILIÈRE, B. 2000a. Coraux constructeurs de Bajocien inférieur de France. 1ère Partie. Geobios, 33:51–72.

LATHUILIÈRE, B. 2000b. Coraux constructeurs de Bajocien inférieur de France. 2ème Partie. Geobios, 33:153–181.

LÖSER, H. 1989. Die Korallen der sachsischen Oberkreide. Abhandlungen des Staatlichen Museums für Mineralogie und Geologie zu Dresden, 36:88–154.

LÖSER, H. 1994. La fauna corallienne du mont Kassenberg è Muelheim-sur-la-Ruhr (Bassin crétacé de Westphalie, Nord Ouest de l'Allemagne). Coral Research Bulletin, 3:1–93.

MATTHAI, G. 1914. A revision of the Recent colonial Astraeidae possessing distinct corallites.: Transactions of the Linnean Society of London, Ser. 2 (Zoology), 17:1–140.

MEDINA, M., E. WEIL, AND A. M. SZMANT. 1999. Examination of the *Montastraea annularis* species compex (Cnidaria: Scleractinia) using ITS and COI sequences. Marine Biotechnology, 1:89–97.

MILNE EDWARDS, H., AND J. HAIME. 1857. Histoire naturelle des Coralliaires ou polypes proprement dits. Tome second: classification et description des Zoanthaires sclérodermés de la section des Madréporaires apores, 633 p.

MONTANARO GALLITELLI, E. 1975. Hexanthiniaria a new ordo of Zoantharia (Anthozoa, Coelenterata). Bolletino della Società Paleontologica Italiana, 14:21–25.

MORYCOWA, E. 1971. Hexacorallia et Octocorallia du Crétacé inférieur de Rarǎu (Carpathes orientales roumaines). Acta Paleontologica Polonica, 16:1–149.

MORYCOWA, E., AND E. RONIEWICZ. 1990. Revision of the genus *Cladophyllia* and description of *Apocladophyllia* gen. n. (Cladophylliidae fam., Scleractinia). Acta Paleontologica Polonica, 29:165–187.

MORYCOWA, E., AND E. RONIEWICZ. 1995. Microstructural disparity between Recent fungiine and Mesozoic microsolenine scleractinians. Acta Paleontologica Polonica, 40:361–385.

ODORICO, D. M., AND D. J. MILLER. 1997. Variation in the ribosomal internal transcribed spacers and 5.8S rDNA among five species of *Acropora* (Cnidaria; Scleractinia): patterns of variation consistent with reticulate evolution. Molecular Biology and Evolution, 14:465–473.

OGILVIE, M. M. 1897. Korallen der Stramberger Schichten. Palaeontographica, Supplement 2:73–282.

PIRES, D. O. 1997. Cnidae of Scleractinia. Proceedings of the Biological Society of Washington, 110:167–185.

PIRES, D. O., AND F. B. PITOMBO. 1992. Cnidae of the Brazilian Mussidae (Cnidaria: Scleractinia) and their value in taxonomy. Bulletin of Marine Science, 51:231–244.

POTTS, D. C., A. F. BUDD, AND R. L. GARTHWAITE. 1993. Soft tissue vs. skeletal approaches to species recognition and phylogeny reconstruction in corals. Courier Forschungs-Institute Senckenberg, 164:221–231.

PRATZ, E. 1882. Ueber die verwandtschazftlichen Beziehungen einiger Korallengattungen mit hauptsächlicher Berücksichtigung ihrer Septalstructur. Palaeontographica, 29:81–122.

ROMANO, S. L., AND S. D. CAIRNS. 2000. Molecular phylogenetic hypotheses for the evolution of scleractinian corals. Bulletin of Marine Science, 67:1043–1068.

ROMANO, S. L., AND S. R. PALUMBI. 1996. Evolution of scleractinian corals inferred from molecular systematics. Science, 271:640–642.

RONIEWICZ, E. 1976. Les Scléractiniaires du Jurassique supérieur de la Dobrogea Centrale, Roumanie. Palaeontologia Polonica, 34:17–118.

RONIEWICZ, E. 1982. Pennular and non-pennular Jurassic scleractinians—some examples. Acta Paleontologica Polonica, 27:157–193.

RONIEWICZ, E. 1984. Microstructural evidence of the distichophylliid affinity of the Caryophylliina (Scleractinia). Palaeontographica Americana, 54:515–518.

RONIEWICZ, E. 1989. Triassic scleractinian corals of the Zlambach Beds, Northern Calcareous Alps, Austria. Oesterreichische Akademie Der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse Denkschriften, 126:1–152.

RONIEWICZ, E., AND E. MORYCOWA. 1993. Evolution of the Scleractinia in the light of microstructural data. Courier Forschunginstitut Senckenberg, 164:233–240.

RONIEWICZ, E., AND J. STOLARSKI. 1999. Evolutionary trends in the epithecate scleractinian corals. Acta Paleontologica Polonica, 44:131–166.

RONIEWICZ, E., AND J. STOLARSKI. 2001. Triassic roots of the amphiastraeid scleractinian corals. Journal of Paleontology, 75:34–45.

RUSSO, A. 1979. Studio monografico sui Coralli dell'Eocene di Possagno (Treviso, Italia). Atti e Memorie della Accademia Nazionale di Scienze, Lettere e Arti Di Modena, 21:1–87.

SORAUF, J. E. 1970. Microstructure and formation of dissepiments in the skeleton of the recent Scleractinia (hexacorals). Biomineralization Research Reports, 2:1–22.

SORAUF, J. E. 1972. Skeletal microstructure and microarchitecture in Scleractinia (Coelenterata). Palaeontology, 15:88–107.

SORAUF, J. E. 1974. Observations on microstructure and biocrystallization in Coelenterates. Biomineralization Research Reports, 7:37–55.

SORAUF, J. E. 1999. Skeletal microstructure, geochemistry and organic remnants in Cretaceous scleractinian corals: Santonian Gosau Beds of Gosau, Austria. Journal of Paleontology, 73:1029–1041.

SORAUF, J. E., AND J. S. JELL. 1977a. Structure and incremental growth in the ahermatypic coral Desmophyllum cristagalli from the North Atlantic. Palaeontology, 20:1–19.

SORAUF, J. E., AND N. PODOFF. 1977b. Skeletal structure in deep water ahermatypic corals. Mémoires du Bureau de recherches géologiques et minières, 89:2–11.

STOLARSKI, J. 1995. Ontogenetic development of the thecal structures in caryophylliine scleractinian corals. Acta Paleontologica Polonica, 40: 19–44.

STOLARSKI, J. 2000. Origin and phylogeny of Guyniidae (Scleractinia) in the light of microstructural data. Lethaia, 33:13–38.

STOLARSKI, J., AND A. RUSSO. 2001. Evolution of the post-Triassic pachythecaliine corals. Proceedings of the Biological Society of Washington, 114:???–???.

VAN OPPEN, M. J. H., B. L. WILLIS, H. W. J. A. VAN VUGT AND D. J. MILLER. 2000. Examination of species boundaries in the *Acropora cervicornis* group (Scleractinia, Cnidaria) using nuclear DNA sequence analyses. Molecular Ecology, 9:1363–1373.

VAUGHAN, T. W., AND J. W. WELLS. 1943. Revision of the suborders, families, and genera of the Scleractinia. Geological Society of America Special Papers, 44:1–363.

VERON, J. E. N. 1995. Corals in space and time: biogeography and evolution of the Scleractinia. Cornell University Press, Ithaca, N.Y., 321 p.

VERON, J. E. N. 2000. Corals of the world. Australian Institute of Marine Science, Townsville MC, 1382 p.

VERON, J. E. N., D. M. ODORICO, C. A. CHEN, AND D. J. MILLER. 1996. Reassessing evolutionary relationships of scleractinian corals. Coral Reefs, 15:1–9.

VOLZ, W. 1896. Die Korallenfauna der Trias. II. Die Korallen der Schichten von St. Cassian in Süd Tirol. Palaeontographica, 43:1–124.

WALLACE, C. 1999. Staghorn Corals of the World: A Revision of the Genus *Acropora*. Commonwealth Scientific and Industrial Research Organisation (CSIRO) Publishing, Collingwood Victoria, 438 p.

WELLS, J. W. 1956. Scleractinia, p. F328–F444. *In* R. C. Moore (ed.), Treatise on Invertebrate Paleontology. Pt. F (Coelenterata). The University of Kansas Press, Lawrence, Kansas.

WELLS, J. W. 1969. The formation of dissepiments in zoantharian corals, p. 17–26. *In* Stratigraphy and Palaeontology—essays in Honour of Dorothy Hill. Australian National University Press, Canberra.

ZIBROWIUS, H. 1980. Les scléractiniaires de la Méditerranée et de l'Atlantique nord-oriental. Mémoires de l'Institut Océanographique, Monaco, 11:1–284.