Calcification in the Cnidaria Through Time: An Overview of Their Skeletal Patterns from Individual to Evolutionary Viewpoints

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Abstract

Compared to the several hundreds of Families recognized among the Cnidaria phylum, the number of taxa in which a biomineralization process has been developed appears rather restricted. However an in-depth understanding of the resulting hard-parts is of major importance with respect to both evolutionary history of some major components of the phylum and contribution to a general model of calcium carbonate mineralization among living organisms. Results of a top-down approach involving recent physical characterization methods are summarized, emphasizing the remarkable and somewhat paradoxical aspects of this biochemically driven crystallization process.

11.1 Calcification in the Cnidaria Compared to Their Overall Evolutionary Tree

Cnidocytes, these sophisticated cellular weapons common to the organisms gathered in the phylum Cnidaria were characterized by cytologists since the nineteenth century (Hatschek coined *Cnidaria* in 1888) but it is only recent molecular investigations that revealed the huge time-gap existing between creation of these specialized cells (i.e. the potential origin of the phylum) and the Ordovician period, the lowest part of the geological column in which sediments contain a noticeable amount of well recognizable fossil coral skeletons (−485 to −443 million years). Actually, notwithstanding the remaining discrepancies among molecular phylogenies and uncertainty regarding calibration of the molecular clock, results converge to indicate that origins of the phylum Cnidaria (as well as occurrence of its main branching phases) are deeply rooted in Precambrian times, i.e. largely older

than the 540 My time-line, the basal Cambrian limit that corresponds to the first development of mineralized skeletons in a wide array of Invertebrate animals. Erwin et al. (2011) suggested that origin of the Cnidaria took place during the Cryogenian, this enigmatic period of time during which most -if not all- of the Earth surface was covered by ice and snow (−850 to −635 million years). Waggoner and Collins (2004), then later Cartwright and Collins (2007) suggested an ancestry of more than 1 billion years. More recent investigations led van Iten et al. (2014) to consider that placing the major diversification of the Cnidaria (sub-phylum and class levels) « in the Ediacarian or even the Cryogenian period » is a « very plausible » working hypothesis. Origin of octocorals for instance, considered either as sister group of Hexacorallia following the Collins' hypothesis (2009) or sister group of the Medusozoa (according to Park et al. 2011) occurred well before the Ediacarian time (formerly Vendian) 635–542 million years ago (Taylor et al. 2013).

Evidence that major evolutionary divergence had already occurred long before the lower limit of the Cambrian is established by the recently discovered middle Cambrian (−505 My) jellyfish fauna from Utah (Cartwright et al. 2007), comprising specimens that exhibit diagnostic characters at the family level. In addition to the surprising fact that such a

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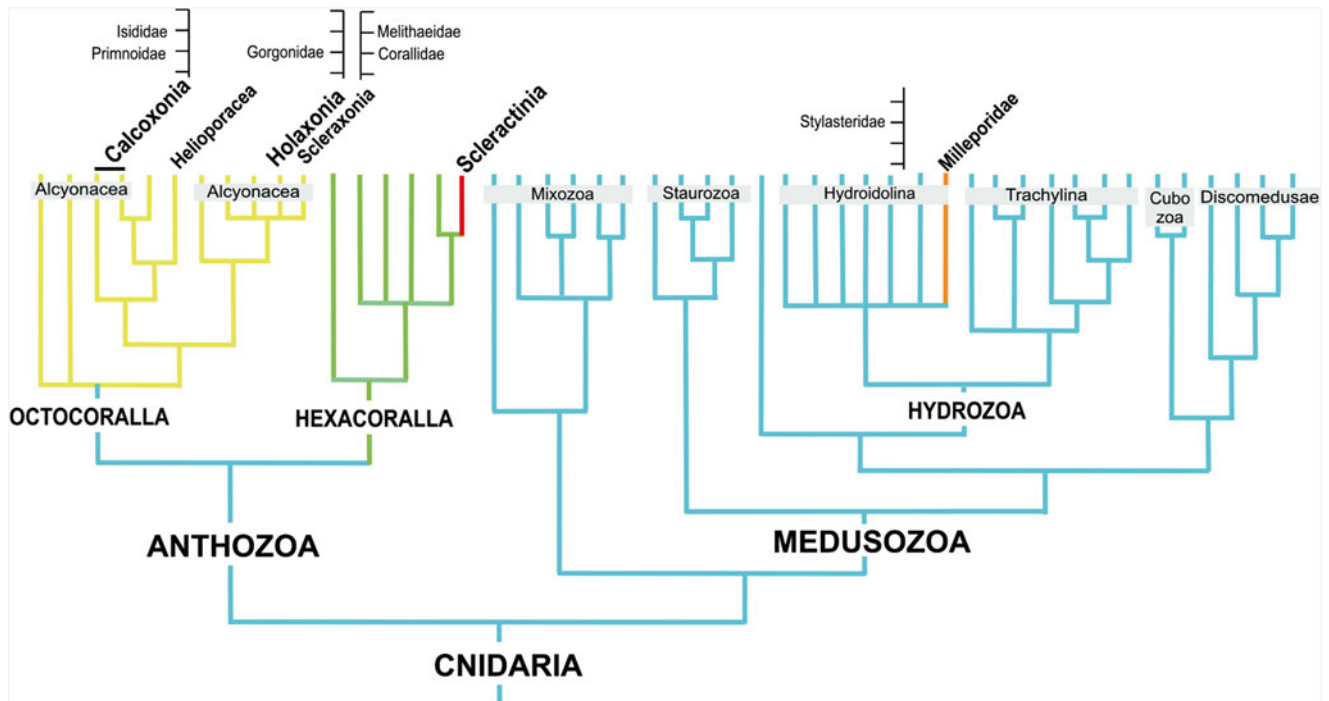
Fig. 11.1 A recent phylogenic arborescence based on molecular data (Collins 2009) on which mention is made of the major calcifying groups among living Cnidaria

significant set of data is provided by non-calcified animals, this also provides a milestone example allowing assessment of a quite advanced status of the evolutionary branching process for the phylum Medusozoa as early as Middle Cambrian times. According to the Marques and Collins' remark (2004) that "Medusozoa is just as basal within Cnidaria as is Anthozoa" an equivalent taxonomical complexity may exist in both groups. Supporting such a statement, the long-term investigation of Jenkins studying the world-wide distributed Ediacarian frond-like fossils (1978–1984) led him to conclude that a "likely presence of spicules" may suggest attribution of some of them to "highly evolved octocorals" (Jenkins 1984, p 100).

When considering calcification, an overview of the distribution of the calcareous skeletons among extant Cnidaria lineages makes obvious that a majority of them do not develop a biomineralization mechanism (Fig. 11.1).

It is remarkable that the prominent role recognized to Cnidaria in marine geology relies essentially on a single lineage, the Scleractinia, due to the unique ability of this group to construct solid calcareous structures distributed from the highly dynamic sea waters of the tropical reef barriers to the dark and cold deep-sea waters. This feature reflects the contrasted morphologies of the mineralized structures that living Cnidaria are able to produce. Animals belonging to the Cnidaria are extremely diverse from a morphological viewpoint and in their large majority have developed a colonial mode of life. What makes specimens of calcifying

Hexacorallia so easily recognized and recorded even in ancient sedimentary rocks is their remarkable ability to produce skeletons in which the radial organization of the polyp body is generally well recognizable (Fig. 11.2a). Considering the whole phylum this is a quite rare property. Although a radial anatomical symmetry of the individual polyp is a general pattern in the phylum Cnidaria, the calcified structures produced by the octocoral colonies are solid ramified constructions whose organization does not reflect the anatomy of the individual polyps (Fig. 11.2b). Even more distant from polyp anatomy is the third form of calcification that is used in the Cnidaria: the calcareous sclerites of octocorals (Figs. 11.2c and 11.3). These are essentially single cell products (or sometimes more or less syncytial), with sometimes a remarkable taxonomic specificities (e.g. Primnoidae).

These images explain why geological investigators are facing major difficulties with respect to taxonomical identification of fossilized remains. Sclerites are dispersed after decay of the animal tissues, forming multispecies postmortem assemblages whereas the calcified axes of colonies are generally unable to provide valuable criteria at the lower taxonomic levels (Bengtson 1981). This also explains the origin of the large under-evaluation of the non-Hexacorallia skeletons as sedimentary contributors.

With respect to animal anatomy the mineralized hardparts of the Cnidaria are always ectodermal in origin but can be produced through two modes of biomineralization:
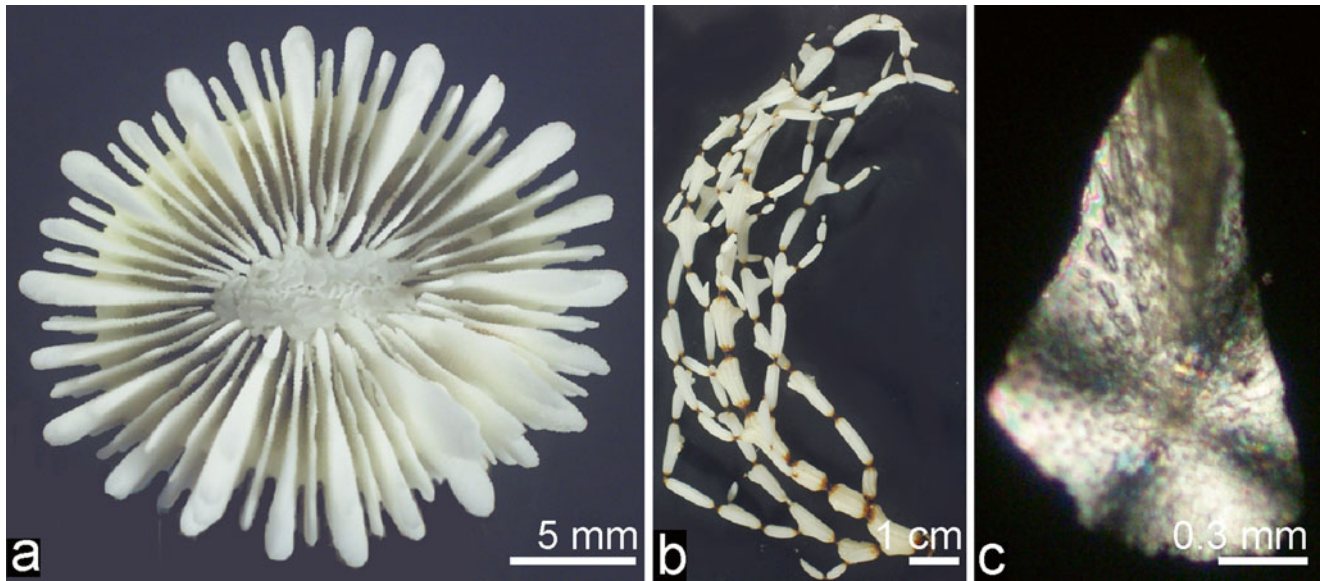
Fig. 11.2 Contrasting morphologies of calcified structures produced by Cnidaria. (**a**) A perfectly radial skeleton built by a Scleractinia (*Cynarina*); (**b**) An arborescent support built by *Isidella* (Octocorallia, Gorgonacea); (**c**) One of the numerous types of sclerites surrounding the animal body from a Primnoidae colony (Octocorallia, Gorgonacea; polarized light, crossed nicols)

intracellular and extracellular (i.e. epithelial) calcification. The former results in small and discrete mineral units (called sclerites or spicules) dispersed into the ectodermal tissues and mesoglea (the gel-like substance located between the ectodermal and endodermal cell layers). Conversely the epithelial mode of mineralization results in macroscopic individual specimens the dimension of which may be up to the meter range in colonial species (e.g. *Porites* colonies).

Regarding skeleton mineralogy extant Cnidaria exclusively use calcium carbonate although Bayer and McIntyre (2001) have detected carbonate hydroxy-apatite as minor component of the axis of many gorgonians. In addition, a strong biological control is exerted on selection of the Ca-carbonate polymorph: calcite or aragonite. Scleractinian corals for instance produce aragonite skeletons even when living on deep-sea floors (e.g. *Lophelia*) where at such temperatures, depths and pCO$_2$ aragonite particles descending from sea surface are dissolved before reaching sea floor. However calcite was used by the Paleozoic predecessors of the present reef builders. Contrastingly the Octocorallia use calcite with the remarkable exception of *Heliopora* (the Blue Coral) whose skeletal fibers are composed of aragonite. Such exceptions raise questions about the mode of selection of the skeletal Ca-carbonate polymorph and the continuity of this mineralogical character through time (see also below Tabulate corals). It is noteworthy that no example has been found of simultaneous production of calcite and aragonite in distinct areas of the skeleton, as occurs regularly in some Pelecypods for instance (e.g. blue mussel or pearl oysters).

11.2 Skeletal Calcification: Evidence of a Stepping Biological Process Acting at the Micrometer Scale

Interestingly intracellular and epithelial modes of calcification can be employed simultaneously in Cnidaria skeletogenesis, as exemplified by the *Corallium rubrum* whose intensely red colored solid axes contributed to the myth of Medusa as they were interpreted as "the blood which continued to drip from Medusa's severed head » (Ovid, Metamorphoses). These branching axes which were used since antiquity as source of handcrafted jewels are only a part of the mineralized structures produced by this species. At the periphery of the axis a cortical structure consisting of sclerites densely distributed into the mesoglea (but always individually distinct) contributes to protection of the polyps (Figs. 11.3 and 11.4).

Each species produces a set of morphologically specific sclerites, providing evidence of the biological control exerted during the biomineralization process. Overall, each sclerite epitomizes the still unsolved paradox of Ca-carbonate skeletal units. It has long been known from optical observations that whatever their morphological complexity each sclerite exhibits a crystal-like behavior, i.e. displaying optical extinction when rotated between crossed-nicols (Fig. 11.3g, h). On the other hand Floquet and Vielzeuf (2012) have established by careful back-scattered electron diffraction measurements that the mineral components of the sclerites were arranged in conformity with axial orientations of a calcite lattice. In contrast to these crystallographic patterns, back scattered electron
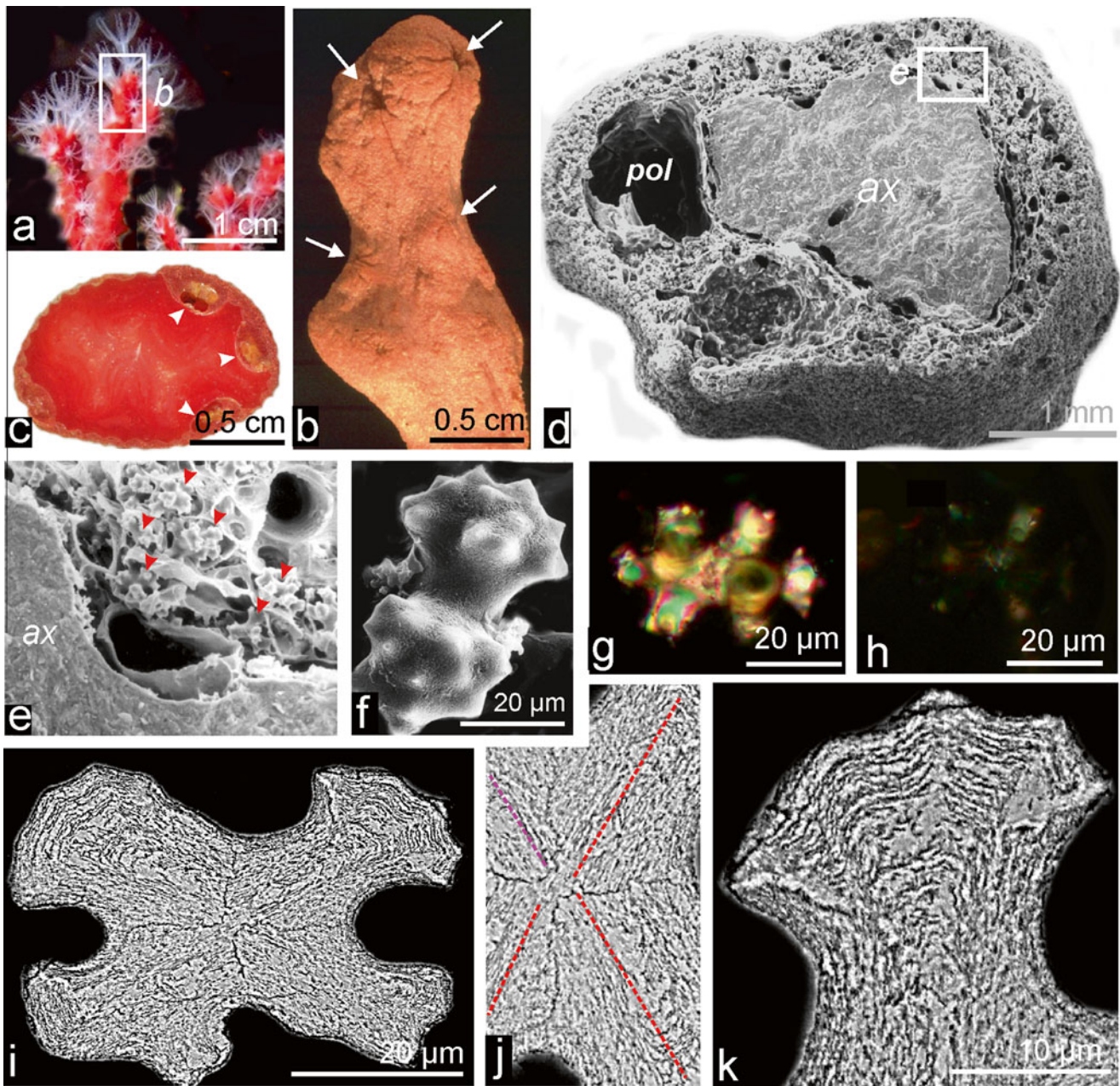
Fig. 11.3 Cortical skeleton made of sclerites in *Corallium rubrum*. (**a–c**) The extended polyps (**a**) can be retracted within chambers covered by the peripheral cortex (**b**: *arrows* external view) and section (**c**); (**d**, **e**) SEM view of a section perpendicular to growth direction of the skeletal axis (*ax*), *red arrows*: sclerites. (**f**) Typical view of an isolated sclerite; (**g**, **h**) Crystal-like behavior of a sclerite observed in polarized light (crossed nicols): rotation changes from brightly colored (**g**) to extinct appearance (**h**) of the whole sclerite; **i–k** Evidence of the layered growth mode of the sclerite obtained on a polished surface observed with electron microscope in the back-scattered mode. With this observational mode the contrast is due to the proportion of back-scattered electrons that depends on the physical properties of substrates: typically organic and mineral areas are delineated. Note the distinctly growing branches (**j**), each of them with its own growth direction. Detailed observation of a branch (**k**) shows the progressive shape modification of the superposed growth layers resulting in the species-specific morphology of the sclerite

imaging of *C. rubrum* spicules reveals that morphology of the superposed growth layers which progressively built the sclerites (Fig. 11.3i–k) is completely independent of the growth surfaces of the virtual crystal that can be reconstructed through the series of back-scattered electron diffractions. Varying during growth, the curved profiles of the micrometer-thick growth layers of the sclerites (Fig. 11.3k) clearly show that, if viewed as crystal-like skeletal units, the sclerites do not grow in agreement with the classical rules of crystal growth (formation of plane surfaces forming regular angles between them).
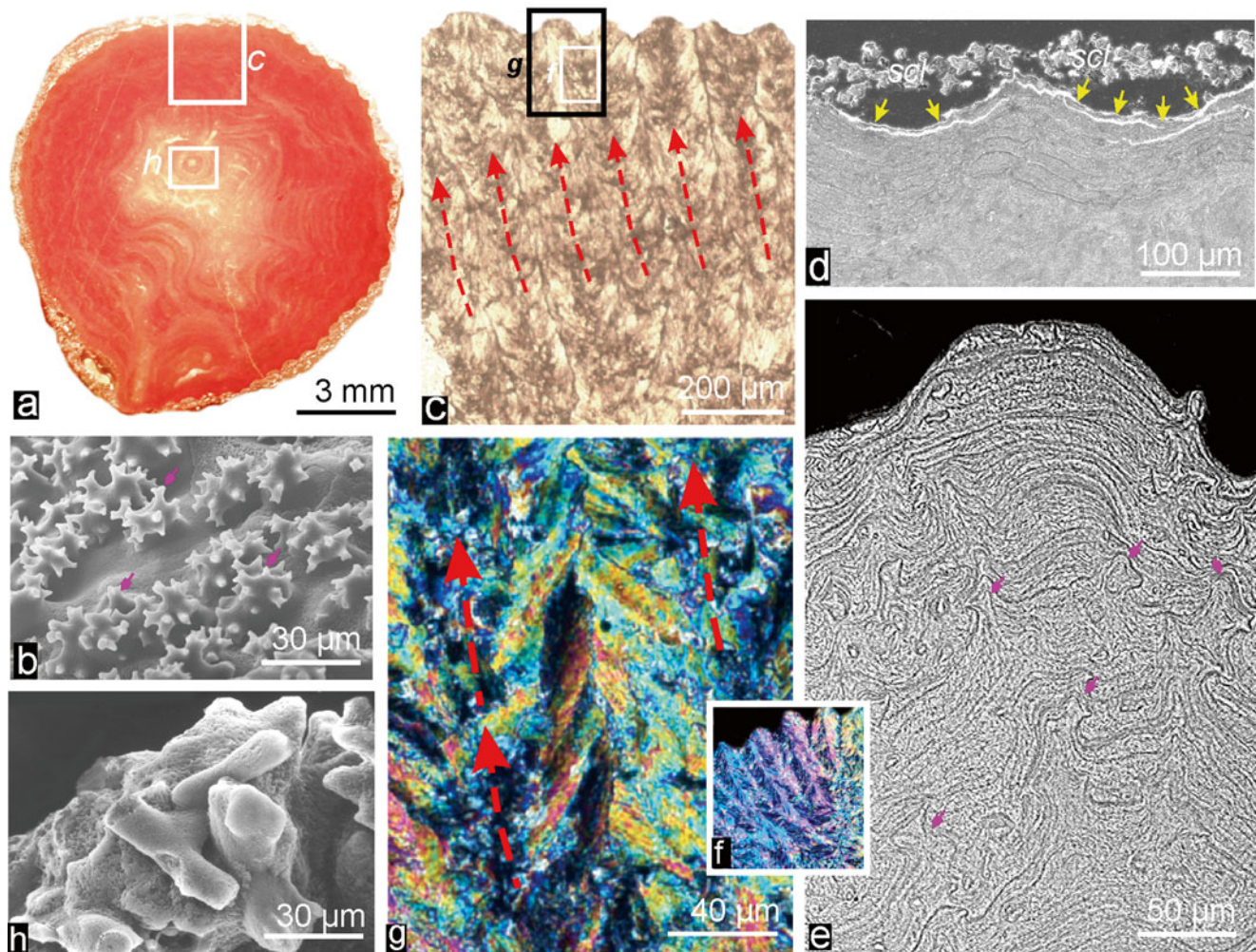
Fig. 11.4 Microstructure of the skeletal axis of *Corallium rubrum*. (**a**) Overall section; (**b**) Spinose expansions on axis surface; (**c**) Microscopic thin section (natural light) showing the arrangement of fibers into radial fascicles (*arrows*); (**d**) Thin cortex of sclerites covering the axis surface marked by longitudinal groves (*arrows*); (**e**) Enlarged view of a fibrous fascicle showing the distorted profile of the micrometer thick growth layers (*arrows*); (**f**, **g**) Microscopic ultra-thin section (approximately 4–5 μm thick) showing the diverging arrangement of fibers; (**h**) Young immature sclerites visible at the distal ends of the axes, in which they are eventually incorporated

Of importance is that each sclerite grows inside the biological envelope formed by one or several associated cells. Formation of species-specific morphologies for this few tens of micrometers sized unit is obtained through repeated deposition of mineralized growth layers whose thickness and shape locally vary through time, providing typical illustration of a layered growth and crystallization process (Cuif et al. 2011). Formation of species-specific morphologies implies that the involved cell (or group of cells) develops a sequential mineralization process in which the layered deposition of calcium carbonate is controlled not only with respect to selection of the used polymorph (e.g. calcite in octocoral sclerites) but, much more fundamentally, through a genetically driven crystallization program which precisely modulates the secretion activity of the mineralizing areas.

The microstructure of the solid skeletal axis, which is by far the most familiar structure of the *C. rubrum*, provides additional evidence of this layered biomineralization process. A detailed description of the skeletal axis of *C. rubrum* was made by Lacaze-Duthiers (1864). Taking into account the spinose expansions covering the axis surface (Fig. 11.4a, b) his interpretation was that the whole axis was constructed of cemented sclerites. However, observation of polished surface and microscopic thin sections disproves but also explains this interpretation, by establishing the layered growth mode of the whole axis. Figure 11.4e–g provide a new example of the paradoxical crystallization mode previously observed in the sclerites. Here at the surface of the branching axis the ectodermal epithelium produces continuous layers of mineralized materials. Instead of a regular

concentric arrangement these micrometer thick layers display strong distortions (Fig. 11.4e), producing the spinose expansions visible on the outer surface of the axis (Fig. 11.4b), that were long considered as spicules partly emerging from the bulk.

At the very top of the axis (Fig. 11.4h) corresponding to the central part of axis section (4a) young and not fully developed sclerites may be incorporated into the axis (note their morphological difference with fully developed sclerites (Fig. 11.3f). However below the axis tip the whole structure is constructed through a layered mineralization process (Fig. 11.4e). From a petrographic view point the *Corallium* axes are built by calcite crystals (high magnesium content calcite) arranged into fascicular units (Fig. 11.4f, g). However, as in the sclerite case, traces of the growth layering observed within the axis (Fig. 11.4e) reveal the stepping growth mode of the crystal-like fibers, formed by superposition of variously contorted mineralization layers. Once again microstructure and crystallography of the axis offer contradictory patterns, as previously observed in the sclerites, allowing assessment of a biological control exerted on mineral deposition by the ectodermal cell layer.

From an historical view-point these superposed growth lines establishing the existence of a stepping growth mode for the *Corallium rubrum* skeleton components (both sclerites and axes) were first reported by microscopic observation made by Kölliker (1864) not on the *C. rubrum* but on a Scleractinia corallite identified as *Astrea*. The first diagrams of such growth lines were given by Ogilvie (1896) in her extensive structural analysis of the coral skeletons. Since these milestone studies the concept of a layered growth mode of skeletons fell into disfavor and prevalence was given to the more apparent crystalline patterns. The formal statement marking this conceptual change is found in the Bryan and Hill's paper (1941) in which the coral fiber is described as "a single crystal of orthorhombic aragonite". Over several decades this concept of a crystalline coral fiber was considered definitive, thereby providing the foundation for the interpretation of isotopic or chemical measurements in the geochemical investigations using corals as environmental archives. A series of microstructural observations completed by physical characterizations (see below Figs. 11.7 and 11.8) have re-established the primary importance of the layered growth and crystallization as the basic calcification mechanism. Figures 11.3 and 11.4 have shown that both the sclerites and axes of the *Corallium rubrum* were also built by such a mode of growth.

11.3   Skeletal Diversity Among Octocorallia

Corallium rubrum, whose skeleton comprises both sclerites and solid axes, exemplifies a type of dual calcification largely represented among corals belonging to the subclass Alcyonaria (=Octocorallia). Apart from species in which sclerites remain essentially isolated as in the "soft corals" (e.g. *Dendronephthya*, Fig. 11.5a), an important difference exists among octocoral species producing axes regarding the origin and structure of this supporting organ. In contrast to the *Corallium rubrum*, in which the massive but layered structure of the axes has been recognized (once disproved the initial interpretation), three-dimensional associations of sclerites have been developed as for example in *Melithaea* resulting in complex axial architectures (Fig. 11.5b–g). In this species, the large and densely packed sclerites form thick laminae associated into a reticulated structure, very solid although not massive. Calcified sclerites exhibit a readily visible fibrous structure that is actually the microstructural organization of the whole colony.

Thus, the entire supporting skeleton is built by densely packed sclerites. Such a fundamentally fibrous organization with its variously oriented building units explains the remarkable mechanical properties of this type of supporting structure. It allows *Melithaea* and comparable species to create large colonies, erect but remaining flexible (contrasting with the massive axis of the red coral) and able to accommodate relatively intense water movements.

Other types of dual supporting structure are exploited by members of the Gorgonids, with two distinct organizations of the axes. In the typical form the axial structure is essentially constructed by superposed horny layers. In aging individuals, calcification of the horny layers may occur (Fig. 11.6b, arrows) mostly at the basis of the axis (Esford and Lewis 1990; Bayer and MacIntyre 2001). In addition, as in *Eunicella* for instance, the horny axis is covered by a cortex composed of closely joined balloon-club sclerites supported by a more internal layer of spindle sclerites (Fig. 11.6c, d).

In contrast a strongly calcified axial skeleton is observed in many other species in which flexibility is maintained by regularly spaced non-mineralized nodes (Fig. 11.1b: *Isidella*). These are the "bamboo corals" that are currently intensively studied owing to their potential as environmental archives for the reconstruction of chemical or physical changes that may have occurred in deep sea-waters. Slow growing, heavily calcified and widely distributed with respect to depths of living areas, these bamboo corals complement scleractinian deep-sea corals in the study of oceanic circulations. Calcified structures among these species are weakly diversified: many of them display regular deposition of calcite layers associated to organic components, the latter made visible by Orange acridine staining (Fig. 11.6f–h). As a result, skeletal microstructures consist of superposed simple calcite layers (Fig. 11.5i, j) whose detailed mineralization patterns do not enable formation of detailed taxonomic criteria (Noe and Dullo 2006). Conversely such a simple growth layering is advantageous with respect to chemical or isotopic measurements: a simple radial sampling provides a reliable access to time.
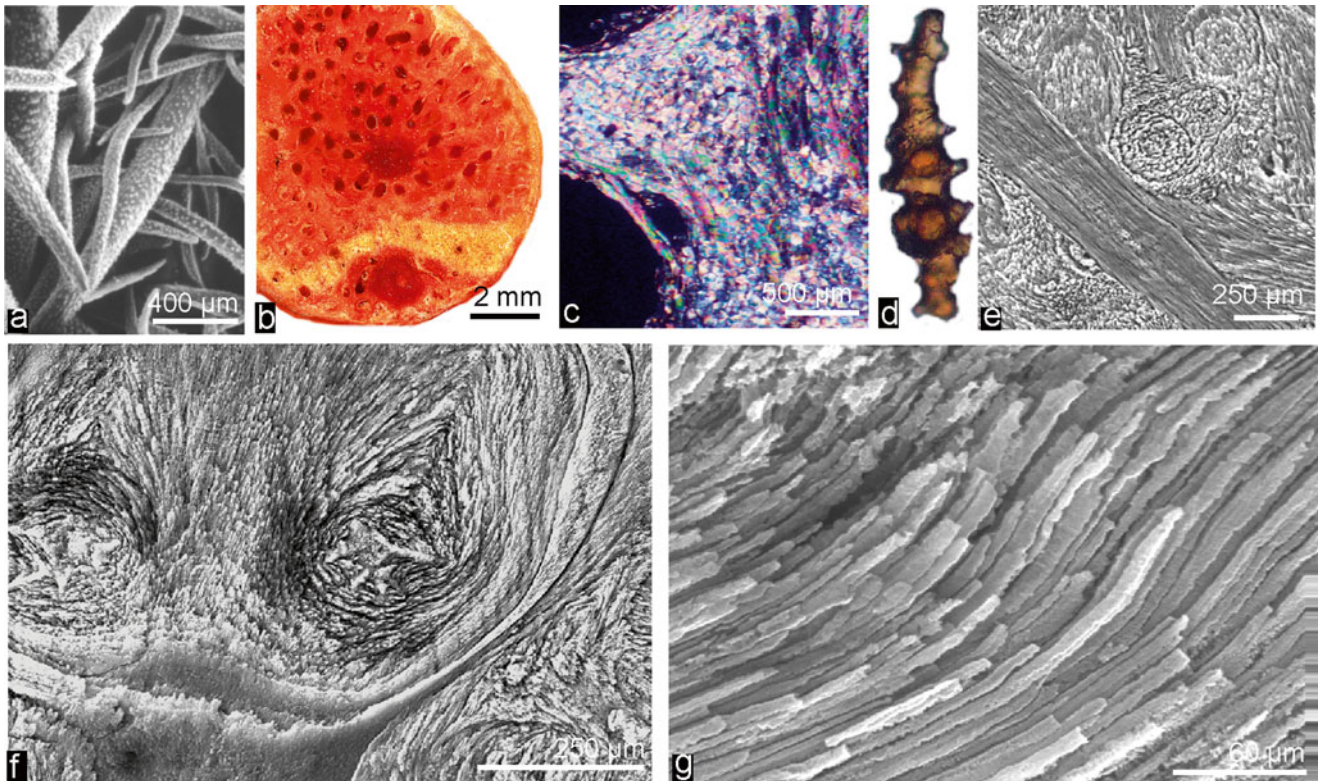
Fig. 11.5 Two spatial arrangements of sclerites. (**a**) Variously sized isolated sclerites (*Dendronephthya*); (**b–g**) Complex axial supporting architectures built by reticulated thick laminae made of densely packed elongated sclerites in *Melithea*: (**b**) section of the supporting axis; (**c**) optical view (polarized light); (**d**) isolated sclerite; (**e**) SEM image (medium enlargement) of the axial spicules; (**f, g**) fibrous structure of the densely packed sclerites

However, some members of the group Isididae (e.g. *Isidella*, Fig. 11.6k–o) exhibit structural indications of a more diversified control on calcification. Microstructural units result from deposition of areas enriched in organic components whose regular variation during growth (Fig. 11.6k, l) creates apparently incurved structures. Within the resulting sectors, however, the layered growth mode (Fig. 11.6m) and orientation of fiber fascicles conform throughout to a radial mode of growth as shown by polarized light (Fig. 11.6n, o).

11.4 Innovative Calcification in the Hexacorallia: Access to Long Term Evolution Through Microstructural Analysis

In spite of obvious morphological differences the calcareous structures of Octocorallia examined so far (sclerites or axes) have in common a low degree of microstructural differentiation. In the mineralizing Hexacorallia, in addition to the fact that the skeleton secreting epithelium includes the basal ectodermal layer of the polyps themselves (explaining why radial organization is visible in the Scleractinia skeletons;

see Fig. 11.1), this calicoblastic ectoderm exhibits a remarkable histological specificity regarding organization of the microstructural units, a property whose elucidation was achieved through a century long controversy.

It is noteworthy that up to the last decades of the nineteenth century (including the influential Milne-Edwards and Haime's studies from 1848 up to 1860) only morphological approaches were used to classify the Scleractinia skeletons. The transition to structural analysis at the micrometer scale is due to Ogilvie who established the taxonomic value of the microstructural patterns (three dimensional arrangements of fibers) and coined the term "center of calcification" as a key point in formation of the Scleractinia septa (1896). However at that time the 10-year old controversy between von Heider (1886) and von Koch (1886) (based on their opposing views regarding the role of the ectodermal cell layer in the mineralization process) was still continuing. It is only after Bournes' careful histological studies of the basal cell layer of the polyp (1899) that the extracellular calcification of the skeleton was conceded, disproving the von Heider's opinion that coral skeletons were constructed by calcification of the epithelial cells themselves. Unfortunately this later view was supported by Ogilvie, thereby casting doubt on her own results. This paved the way to the chemical concept of a spherulitic
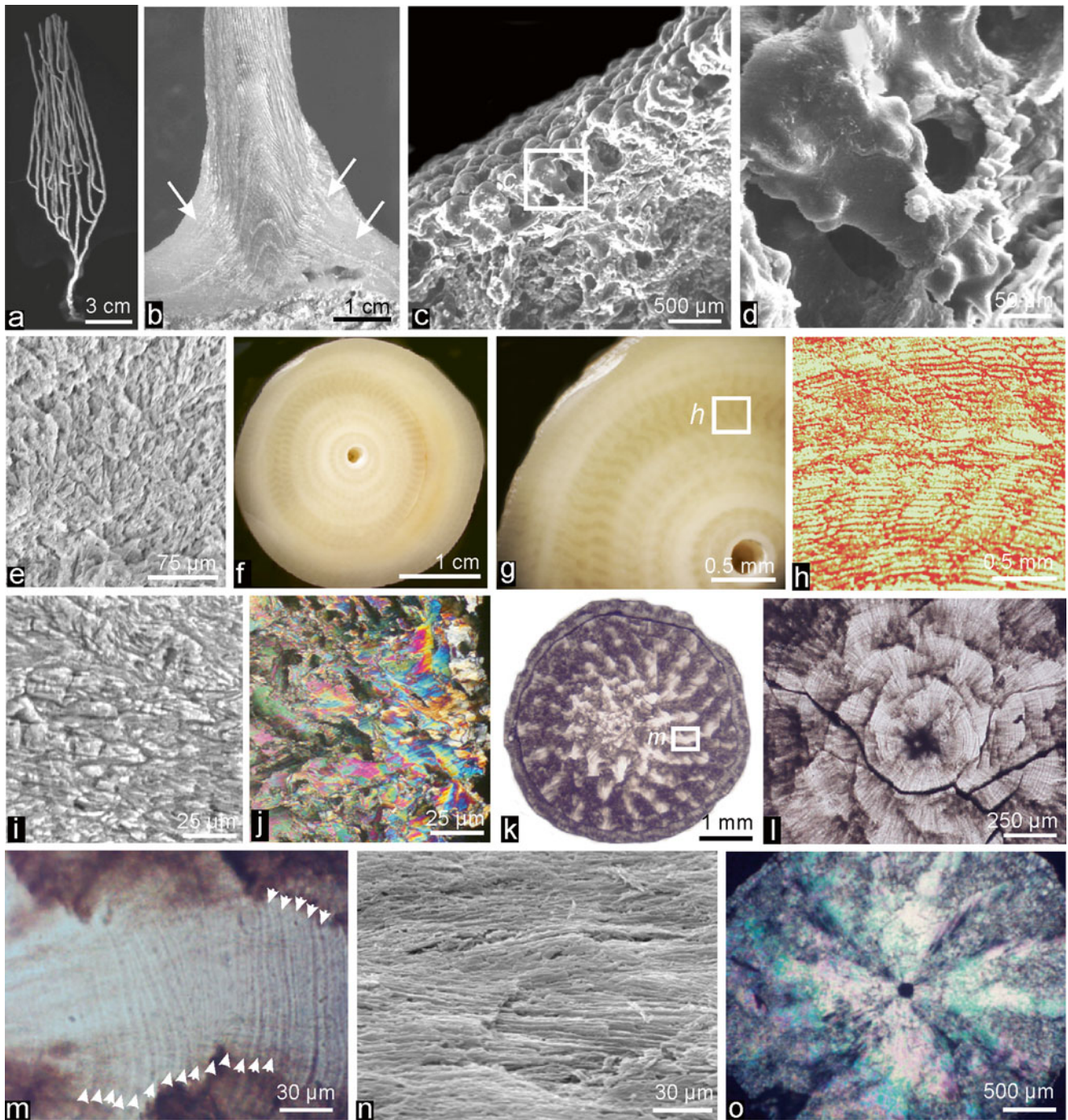
Fig. 11.6 Calcification in gorgonian corals. (**a–c**) In *Eunicella* the closely assembled sclerites form a protective cortex; (**d, e**) Calcification limited to the basal layers basis of the axis (**d**) exhibits weakly organized calcareous units (**e**); (**f–j**) A remarkable regular layering of calcification in the axis of a Isididae coral. Orange acridine staining (**h**), SEM view of the mineral phase (**i**) and microscopic thin section (**j**, crossed-nicols) show that no long range crystallinity can be observed; (**k–o**) A weak coordination between mineralizing areas (**k–m**) results in some consistency between crystallization of successive layers (**m, n**) and an overall structural organization of the axis (**o**)

crystallization formulated by Bryan and Hill (1941): "the coral fiber is a single crystal of orthorhombic aragonite" and the long standing view of a "biologically induced" origin of the coral fibers (up to Veis 2005). Simultaneously nature and role of the "centers of calcification" were questioned. This was still the case in the two main treatises on Scleractinia published in the middle of the twentieth century. The concept of centers of calcification was used "for practical purposes" by Vaughan and Wells (1943, p. 32), in association with the neighboring fiber fascicle to form the sclerodermites viewed as the actual skeletal units whereas "center of calcification" was always written with quotation marks in the Wells' chapter "Scleractinia" (1956: R.C. Moore, Treatise on Invertebrate Paleontology part F, p. 337, Fig. 231). At that time, and subsequently for a long period, no evidence was available to support the concept of a biological control of crystallization by the secreted mineralizing matrices outside the ectodermal cell layer.

A key result towards a better understanding of corallite ontogenesis was obtained by Vandermeulen and Watabe (1973) who established that formation of septa and walls was a two-step process. The early mineralization stage consists in deposition of small granular crystals forming the very first wall and radial septa, later reinforced (step 2) by deposition of fibrous layers on both sides of the initial micro-granular structures. Remarkably, all along corallite or colony life, the superposed micrometer thick growth layers produced by the basal cell layer of the polyps replicate the same dual secretion process.

The controversial points that, over several decades, had queried the existence of the "centers of calcification" and the biochemical control of mineral deposition were explained by converging data from scanning electron microscopy, atomic force imaging and synchrotron-based characterizations (Fig. 11.7). These observations showed that distinct areas of the calicoblastic ectoderm were dedicated to production of specific organic compounds generating the microgranular structures typical for early (=distal) calcification whereas lateral areas are producing the fiber growth layers (Cuif and Dauphin 1998, 2005; Cuif et al. 2003a, 2012).

Here lies the structural innovation that makes the calcification process of Hexacorallia lineages distinct from those of Octocorallia. Not only is the radial organization of the polyp reflected in the calcareous skeleton but also the spatial arrangement of the distal mineralization area have demonstrated an exceptional evolutionary potential, as established by fossil data distributed from Ordovician to recent. Surprisingly this major influential role was first highlighted by Volz (1896) using fossil specimens, taking advantage of the exceptional preservation status of the coral fauna in the Triassic Saint-Cassian strata from Süd-Tyrol (then Dolomites). In most of these fossils a specific spatial arrangement of the initial calcification stages was emphasized by differential fossilization. Volz coined the term "urseptum" (= primitive septum, 1896, p. 9 Fig. 4) hypothesizing that these

figures could reflect the initial step in formation of the septa. It is noteworthy that the biological and physical characterizations that fully supported this view were only obtained about a century later. Origin of this full biological control on formation of the granular "urseptum" and fibrous skeletal structures was made more understandable through atomic force microscopy in the phase-contrast mode, showing that both skeletal areas (distal and lateral) forming a growth layer were built by mineral granules of 75–100 nm in mean diameter surrounded by an irregular organic cortex (Fig. 11.7j). Obviously, far from a simple spherulitic crystallization, the cyclic mechanism forming the corallite growth-layers involves precisely distributed organic compounds in a controlled crystallization process which is not fully explained yet at molecular scale.

Importance of the Volz concept cannot be overestimated. Not only can diversity of septal structures between genera and families be accurately established (e.g. Figs. 11.8 and 11.9 in this paper) but also through a careful reconstruction of changes in the microstructural patterns during coral ontogenesis does a detailed knowledge of the species specific septal developments become accessible. By so doing a comprehensive understanding of the skeletal ontogenic program that drives mineral deposition by the calicoblastic ectoderm can be obtained. Well preserved fossils (e.g. the Triassic *Distichophyllia norica* Fig. 11.9a–f) exemplify the possibility of reconstructing skeletal ontogenesis from very ancient samples. That microstructural ontogenesis has a strong evolutionary potential was assessed by a comparative study involving molecular based phylogeny from polyp tissues and in parallel, analysis of septal microstructures in the corresponding corallites (Cuif et al. 2003a, b). By this method inadequacy of the classical and long authoritative supra-generic taxonomy and phylogenetic arborescence of families from the Triassic to recent Scleractinia (as suggested by Wells 1956, p. F363) was established long before occurrence of molecular studies.

Creating a common evolutionary scheme encompassing skeleton-producing Hexacorallia is a long standing project, first attempted by investigators at the end of the nineteenth century (e.g. Frech 1890; Ogilvie 1896) who admitted continuity between corals distributed from Paleozoic to recent. In contrast, the mid-twentieth century Treatises (Vaughan and Wells 1943; Wells 1956 and recent revisions) integrated the Haeckel suggestion (1896) that Paleozoic and post-Paleozoic corals were fully distinct lineages, the later having been produced by "newly calcifying anemones".

An in-depth reexamination of this concept (authoritative throughout the whole twentieth century) is currently ongoing mostly through molecular investigations. Several studies have converged to consider that scleractinian lineages (the "modern corals") are more or less deeply rooted within the Paleozoic period (e.g. Medina et al. 2006), a result that clearly disproves the Haeckel concept that was based
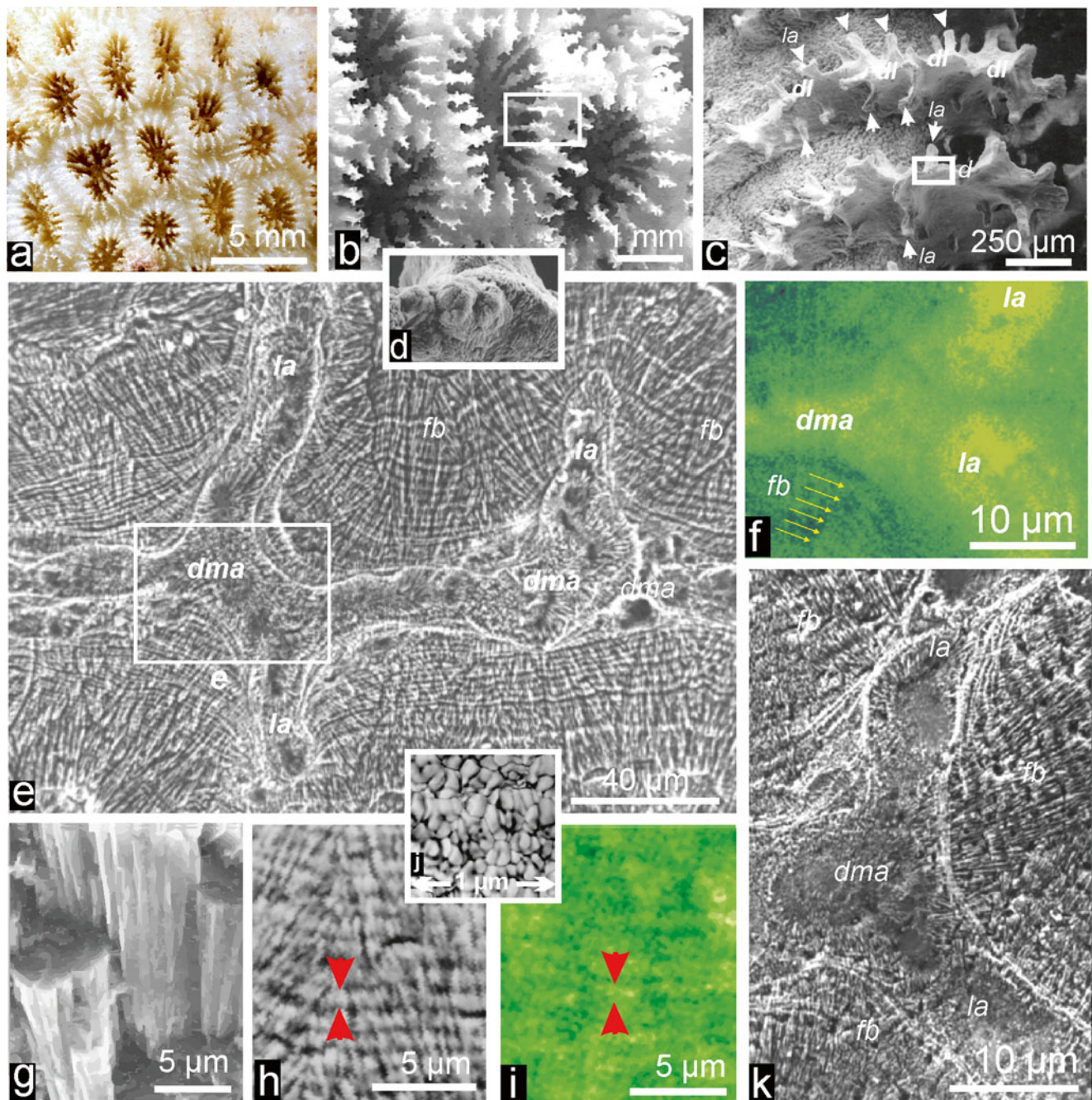
Fig. 11.7 Distal (or early) mineralization areas followed by stepping deposition of fibers exemplified by *Favia stelligera* skeleton. (**a–d**) Close examination of septa reveals the distal mineralization area (*dma* = Volz "Urseptum") with its distinctive mode of microcrystalline mineralization (**d**). This area comprises the distal line (*dl*), variously designed depending upon species) and the lateral axes (*la*) whose spatial arrangement will generate the genus/species specific septal microstructure; (**e**) Distal line and lateral axes can be made visible through appropriate sections of the septa (polished and etched surfaces), opening possibility of reconstructing septal development through time; (**f**) Synchrotron-based mapping of sulfated polysaccharides emphasizes the biochemical contribution to both initial and secondary steps of septum construction: distal line made of more or less fused spots with higher polysaccharide concentration than in the calcified layers forming fibers; (**g–i**) The usual SEM view of fibers as elongated compact aragonite crystals strongly contrasts with pictures obtained from polished sections (**i**) (mapping of polysaccharides) and (**h**) (stepping growth visible after etching); (**j**) Atomic Force Microscopy (phase contrast imaging) reveals the granular organo-mineral structure forming the skeletal growth layer. Note the 1 μm wide field view; (**k**) Superimposed deposition of fibrous layers units onto the initial septal framework the Volz' Urseptum)
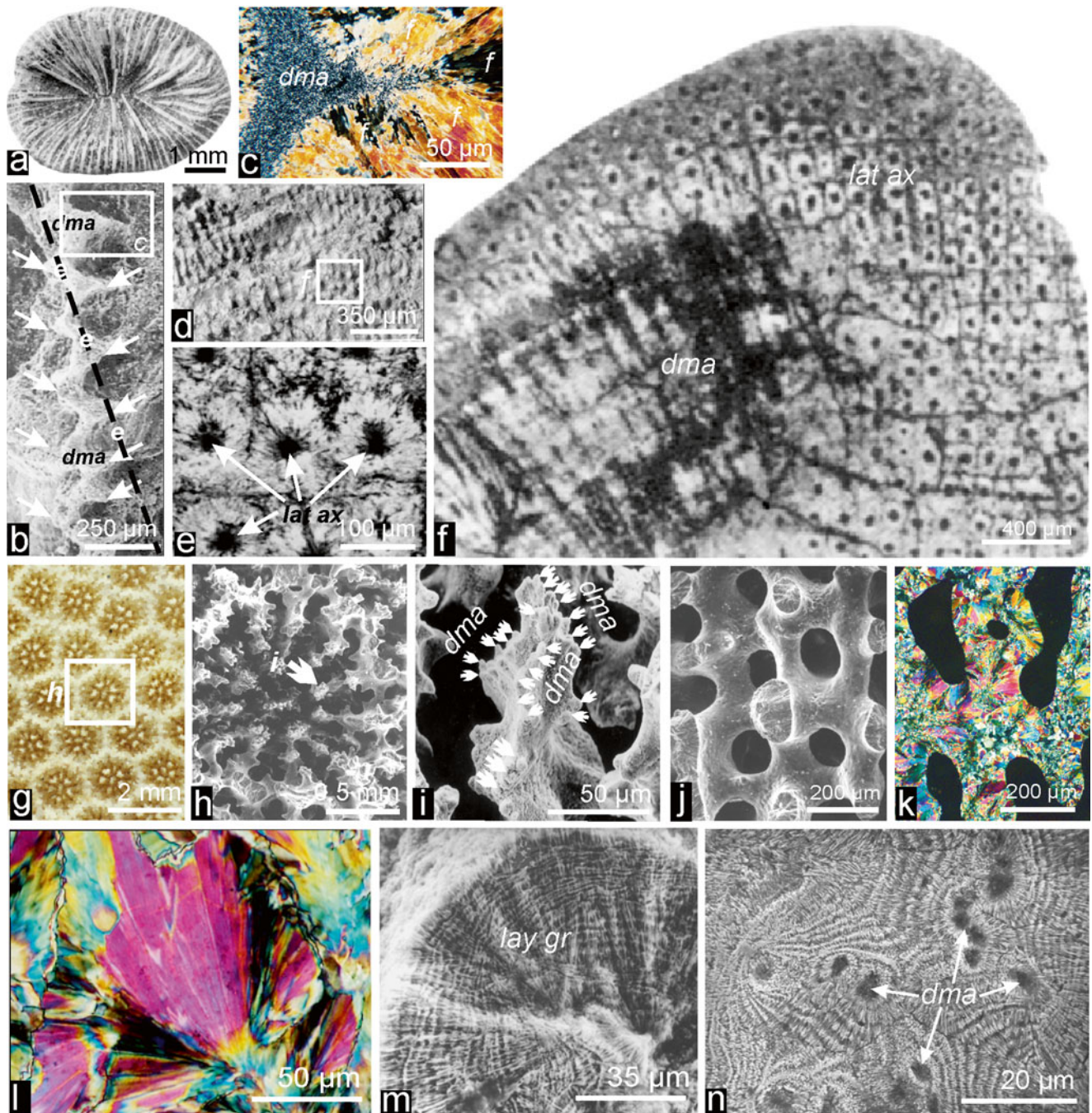
Fig. 11.8 Two distinct types of spatial distribution of the distal (or early) mineralizing areas (*dma* = "centers of calcification" = Volz' "urseptum") viewed from upper surface of the septa (the distal growth line) and from inside septal structures. (**a**) Overall morphology of *Distichophyllia*, Triassic species from the Austrian Zlambach schichten; (**b**) Zig-zag morphology of the distal mineralization upper line; (**c**) fibrous fascicles inserted onto one of the lateral axes expanding from the distal-zig-zag line (note the granular microstructure of the axis); (**d**, **e**) Granules visible on the lateral surfaces of the septa (**d**) are caused by growth of the lateral axes surrounded by fibers as shown by micro-scopic thin sections (**e**); (**f**) Overall view of a microscopic thin section in a septum of *Distichophyllia* slightly oblique to the median plan of the septum: growth patterns of the two distinct microstructural areas can be observed. (**g**, **h**) Morphology of a *Porites* corallite; (**i**) morphology of the upper part of a skeletal rod: note the distribution of the distal mineralizing areas as small and distinct spherical units; (**j–l**) Morphology and microstructure of the skeletal rods in SEM view (**j**), crossed nicols microscopic thins sections (**k**, **l**); (**m**, **n**) Layered growth (lay gr) of the skeletal rods (**m**) and dispersed distribution of the distal mineralizing areas surrounded by the layered growth of fibers (**n**)
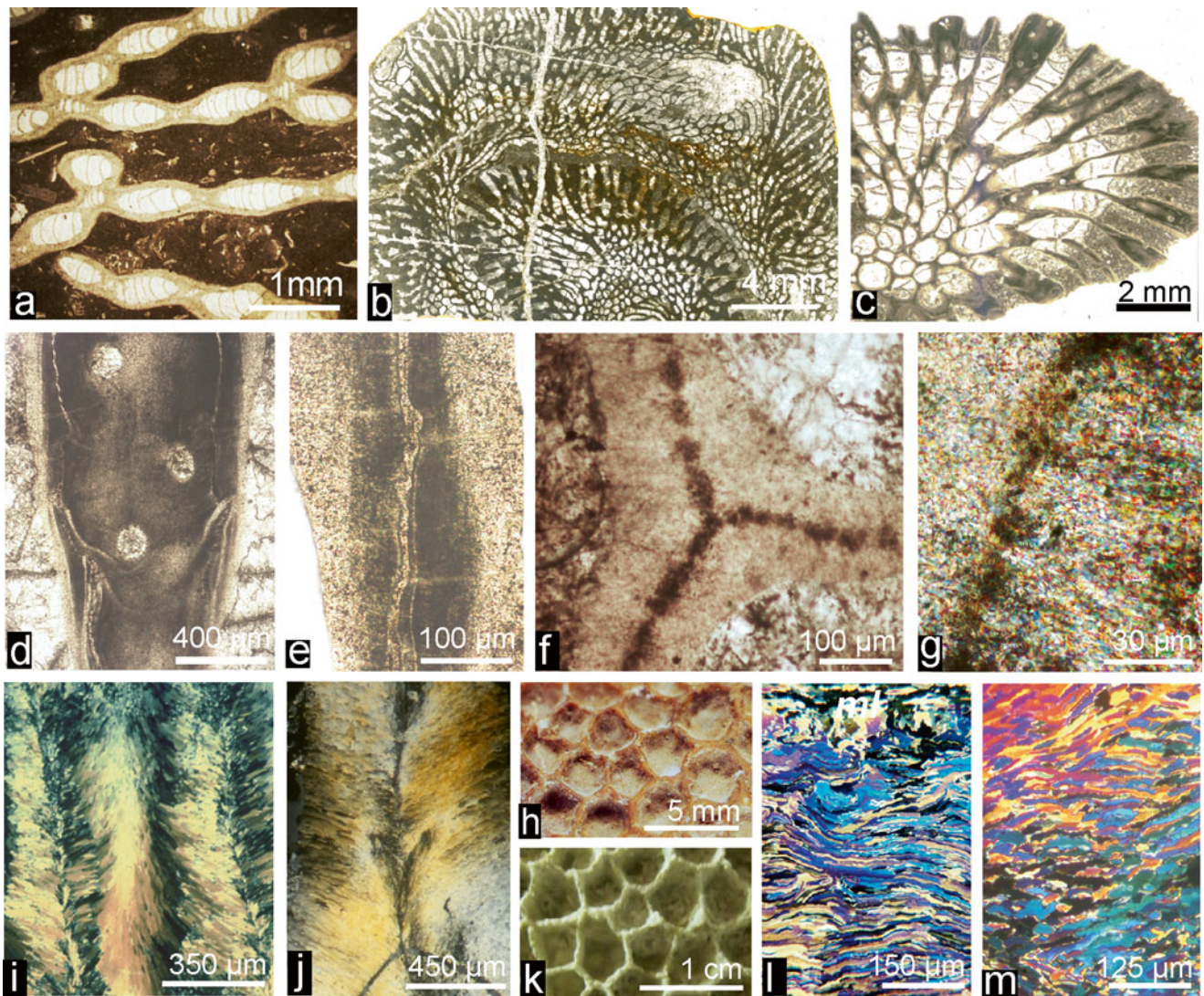
Fig. 11.9 Morphological and histological patterns of some Tabulate corals. (**a–c**) Section in colonies of *Halysites* (**a**), *Alveolites* (**b**), *Thamnopora* (**c**); (**d, e**) Pores in the wall of *Thamnopora* and section perpendicular to the wall; (**f–h**) Fibrous microstructure of the wall of *Favosites* (**f, g**), and morphology of the corallites (**h**). Note the distinct spots forming the median line; (**i, j**) Other examples of fibrous microstructures: *Thamnopora* (**i**), *Trachypsammia* (**j**) both from Plusquellec coll. (University of Brest); (**k–m**) Morphology of the calices (**k**) and wall microstructures (**l, m**) in *Michelinia*, examples of lamellar microstructure (Lafuste coll., MNHN Paris) *ml* median line between calices

essentially on skeleton morphology. During the two most recent decades the exclusive use of molecular data as phylogenic tools produced a number of diverging phylogenetic arborescences (e.g. Chen et al. 1995; Veron et al. 1996; Romano and Palumbi 1996; Romano and Cairns 2000) up to present (Fukami et al. 2008; Budd et al. 2010; Stolarski et al. 2011). As pointed out by Budd et al. (2010) confusion as a "hall-mark of scleractinian classification… reemerged in the late 20th century when molecular techniques began to be applied to scleractinian systematics".

From a methodological view-point microstructural investigation based on the concept of evolving microstructures through both individual skeletal ontogenesis and long-term evolution offers a unique opportunity to take advantage of the large fossil data-base collected during two centuries of paleontological studies. As the permanent biological control of the corallite calcareous structures is now well established, collaborating investigations involving gene expression and molecular mechanisms of skeletogenesis coupled to microstructural analysis of the resulting structures could contribute to creating a more consistent evolutionary framework.

It is remarkable that among the many research studies that aim at deciphering the biomineralization mechanisms, a growing number is studying influence of natural organic components extracted from calcified biominerals (e.g. Reggi et al. 2014) in place of organic chemicals as it was initially done (e.g. Kitano and Hood 1965). Further steps consist in using mineralizing molecules produced by molecular clon-

ing and gene expression (Mass et al. 2013). Deciphering the sequence of genomic events (the mineralization program) that control the spatial organization of the mineral particles successively generating the initial septal framework (the Volz' "urseptum") followed by stepping deposition of the layered fibrous tissue may reduce the gap between morphological and molecular phylogenies.

11.5 How Do Extinct Lineages May Contribute to Our Representation of Long Term Evolution of the Calcifying Cnidaria

Molecular phylogeny (e.g. Fig. 11.1) yields models in which the distances between groups (i.e. potential evolutionary affinities) result in series of generally bifurcating branches. Such overall schemes obviously suggest that evolution of the phylum consists in a progressive differentiation through time, more or less similar to the classical Darwinian scheme. Taking into account the fossil data leads to a completely different view.

An overall survey of fossils identified as Cnidaria in the first part of the fossiliferous period (Paleozoic) shows that during about 250 million years Cnidaria diversity is higher than in any later period. In addition to the presence of a complex series of genera and families having produced undoubtedly Hexacorallia coral looking samples (comprising septa, walls and endothecal structures), a number of various colonial forms exhibit such distinct patterns that they were identified as a major taxon as early as 1850: the Tabulata Milne-Edwards and Haime. Tabulata (Tabulate corals) formed colonies whose tubular units, freely growing or associated into massive constructions lack radial internal subdivision. In contrast, the tube internal space is subdivided by calcified layers (tabulae) typically perpendicular to growth axis of the corallites (Fig. 11.9). Septa are lacking, but regularly distributed spines may exist, as well as communication pores between neighbor corallites.

The order Tabulata encompasses at least six distinct taxonomic units whose consistency was recently challenged by the biological evidence that some Demosponges (Sponges with siliceous spicules) were able to built additional calcareous skeletons made of densely packed tubes whose internal space was transversally subdivided by typical tabulae. *Acanthochaetetes* for instance, admittedly related to the Paleozoic Chatetetid group was accepted as a fossil coral up to the discovery of a living species *A. wellsi* (Hartmann and Goreau 1975) whose soft tissues demonstrated that it belongs to Sponges. Among the remaining Tabulate corals important microstructural differences are observable. Many of them are built by fibrous tissues, and in some cases skeletal patterns suggest possible "centers of calcification" (Fig. 11.9f, g).

A remarkable contrast exists between these fibers, more or less perpendicular to the common wall between neighbor corallites and the skeletal lamellae that are basically parallel to the corallite walls. Figures of the fibrous walls in the Tabulate corals *Thamnopora* and *Trachypsammia* (Fig. 11.9i, j) and the lamellar *Michelinia* (Fig. 11.9l, m) epitomize this difference in the biomineralization processes: both taxa gather colonies that are composed of polygonal units (Fig. 11.9h–k). Some criticisms have been presented against the use of microstructural patterns in Tabulate studies due to potential influence of diagenetic processes (e.g. Oekentorp 2007). Interestingly, a series of recent isotopic measurements (Zapalski 2014) suggests that in some cases (as it may also occur for skeletons of Scleractinia) the influence of these post-mortem changes might have been less than suspected. Additionally, remarkable improvements have been brought to histological studies during last decades. Ultra-thin sections (thickness 4–5 μm) observed between crossed nicols (Lafuste 1963) enable examination of individual skeleton units as exemplified by Fig. 11.9h, i, l, m.

Recent publications (e.g. Zaika 2010) have supported the use of investigations based on the concept of biomineralization. Considering what has occurred to the morphology-based evolutionary scheme of the Scleractinia (e.g. Wells 1956) when it was confronted to microstructural analysis and then molecular studies, working hypothesis can reasonably be made that precise histological characterizations of Tabulate corals may determine an in-depth modification of the classical figure of lineages diverging from a single ancestor (e.g. Scrutton 1983, p. 113).

11.6 Genomic Control Versus Environmental Influences on Cnidaria Calcification

In addition to evolutionary processes, another type of influence may affect, and indeed may be recorded within Cnidaria skeletons. From early Ordovician times to present the mechanisms of calcification in the Cnidaria have been submitted to the continuous changes that have occurred in sea-water composition. In addition to these slow running changes much more abrupt variations may have been influential on the biomineralization process. Since the landmark paper by Raup and Sepkowski (1982) the origin of the "big five" evolutionary crises has triggered a number of investigations in which magma floods linked to plate tectonics and asteroid collisions with Earth are associated. Variations in chemical composition of sedimentary carbonates through the geological column led Sandberg (1983) to construct an oscillating curve summarizing the dominance of calcite or aragonite precipitation in the Paleozoic and post-Paleozoic times respectively. This result has been tentatively correlated to the

catalogue of Ca-carbonate polymorphs used by living organisms through time (Stanley and Hardie 1998; Ries et al. 2006). Distribution of calcite versus aragonite in the Cnidaria skeletons that have been examined through the whole geological column can be summarized as a general agreement marked by noticeable exceptions. Most of the Paleozoic Cnidaria were using calcite as skeletal mineral but in the Tabulate family Tetradiidae skeletons were recognized aragonitic (Wendt 1989). Post-Paleozoic Cnidaria offer a contrasted view. Among the numerous and diversified Octocorallia calcite is quite dominant (in contrast to the Sandberg's aragonite sea) with the exception of the Blue Coral (*Heliopora coerulea*) that constructs its skeleton with aragonitic fibers. Scleractinia have produced aragonite skeletons since the Triassic period but during Cretaceous some examples have convincingly established evidence of shift to calcitic skeletons (Stolarski et al. 2007). Interestingly some aragonite corals were found in the upper Permian (Wendt 1990) whereas other representatives of the Paleozoic corals still have their calcite skeletons. Some remarkable Triassic corals produced aragonite skeletons although having preserved the typical "bauplan" (or "skeletogenesis program") of a typical Permian calcitic family (Cuif 2013). This complex result suggests that instead of being submitted to a simple chemical control, determination of the used polymorph and its possible variation through time should be examined from a biomineralization viewpoint.

It is now established that the biological calcification process involves several tens (or hundreds) molecules whose genomic approaches have revealed the diversity and taxonomy-linked specificity. Secreted outside the mineralizing organ (e.g. the basal ectoderm of the Cnidaria) these complex molecular assemblages control every aspect of skeletal deposition. Which part of these secreted compounds determines the used calcium carbonate polymorph is still unknown, as is the sensitivity of this mineralogy driving molecular assemblage to environmental conditions. What underlines the paleontological data is that a mineralogical shift may occur without changing the microstructure of the skeletons. These recent data have important taxonomic implications as they clearly suggest that skeletal mineralogy as a taxonomic character must be subordinated to the much more complex genomic mechanism that drives the three-dimensional assemblage of the skeletal units. Among the present Cnidaria the Stylasteridae (skeleton producing Hydrozoa) offers the most demonstrative example that mineralogy cannot be considered as major criteria because if the majority of them produce aragonite skeletons a significant part use the calcite polymorph without significant correlation to taxonomy (Cairns and Macintyre 1992).

What has been revealed about histological diversity of the Tabulate corals during the last decades suggests that distinct branches are deeply rooted in the Precambrian, and should be

considered as illustrations of the huge gap between formation of the phylum and separated emergences of calcification.

Undoubtedly overall evolutionary process of the Cnidaria during the Paleozoic (as seen from calcifying forms) appears more comparable to what can be seen in other phyla. The 510 million year old fossils of Burgess (middle Cambrian) bring punctual evidence for a proliferating branching pattern inherited from early stages of Arthropod diversification. This is also well demonstrated by the phylum Echinodermata in which about 15 major subdivisions in the Class range were recognized during the Paleozoic era (and sometimes more e.g. Paul and Smith 1988). Of these 15 Classes, only five survived the mass extinction that marks the end of the Paleozoic era. Diversity of the Tabulata corals through Paleozoic offers a strikingly comparable panorama, the last family becoming extinct during the Permian. From a methodological viewpoint evaluating biological diversity by taking into account low level taxa obviously favors the recent periods of time, neglecting the more deeply original lineages which deserve higher taxonomic ranking but have become extinct during geological history.

11.7 Enigmatic Specimens from the Cambrian Period and Earliest Indication of a Cnidarian Type Calcification

Below the Lower Ordovician, fossil records do not provide unambiguous information about Cnidaria. Data illustrating at best this uncertainty are the numerous imprints first found by Reginald Sprigg (1947) in the Ediacara site (an about 635–542 million years old outcrop of the Flinders Range, South Australia) and subsequently discovered in many other places always older than the Cambrian period (i.e. the occurrence of animals bearing mineralized structures). This led to the concept of an Ediacarian age predating the "Cambrian biological explosion". There is a wealth of literature (Pratt et al. 2001) dedicated to these fossils since the Glaessner's paper "Precambrian animals" (1961). Exemplifying how uncertain interpretation of these documents can be, the long standing attribution to marine jellyfishes of many of the samples known from the Ediacara outcrops have been challenged during recent years by a series of new observations. The familiar figures of *Dickinsonia*, *Cyclomedusa* etc. long viewed as primitive Cnidaria were more probably fossil remains of "lichens or microbial consortia developed in paleosols formed onto emerged sandy sea shores" (Retallack 2013).

Many small and morphologically diverse calcareous structures have been discovered in sediments of the Cambrian period. Reviewing these fossils, Jell (1984) made a rather skeptical statement regarding our ability to decide on morphological basis only whether they actually belong to the phylum

Fig. 11.10 *Flindersipora* morphological and microstructural patterns. (**a**, **b**) Section perpendicular to growth axis: possible wall and radial components of the skeleton; (**c**, **d**) Fibrous microstructure viewed on natural light (**c**); crossed-nicols polarized light show that fibers have undergone a slight diagenetic process restricted to crystallographic coalescence of the neighbor fibrous units (**d**)
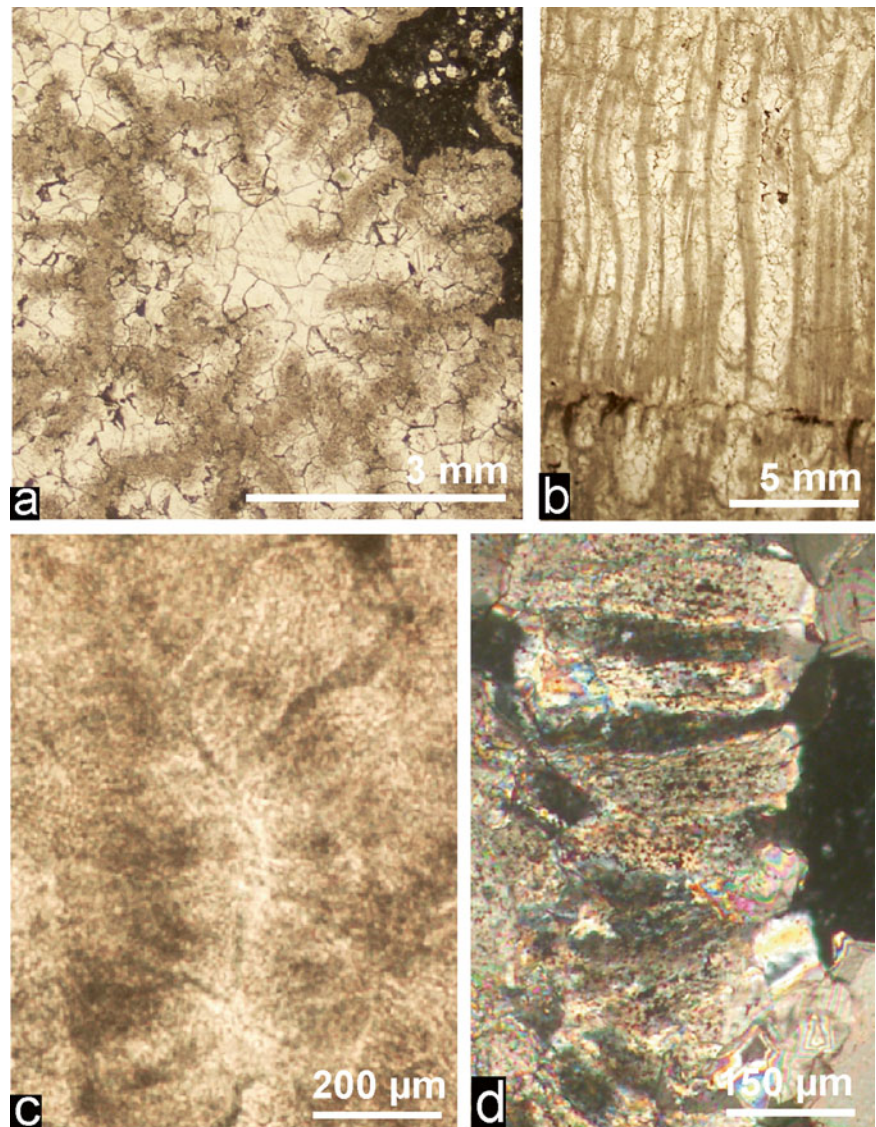
Cnidaria or not. A recent example is given by some Middle Cambrian (−509 to −493 My) conically shaped calcareous structures possessing height symmetrically arranged internal radial lamellae (*Cambroctoconus* Park et al. 2011). Compared to these small and localized fossils the enigmatic Conularids appear much more important. However, as a recent episode of the 150 year old controversy regarding their biological placement, the Babcock (1991) versus Van Iten (1991) confrontation could not permit a firmly based opinion to be established. Ranging from middle Cambrian to Triassic (Moore and Harrington 1956) these organisms were producing phosphatic pyramidal shells reminding that Bayer and McIntyre (2001) have detected carbonate hydroxy-apatite in skeleton of some Gorgonians. Fourfold symmetry (a pattern known from some Medusozoa) and exceptional soft-part preservation revealing soft protruding tentacles support Cnidarian interpretation as a definitely marginal sub-phylum. Recent re-interpretation of the Cambrian bryozoa *Pywackia* as an octocoral (Taylor et al.

2013) provides an example of these calcareous structures reinforcing the evidence that not only were the major branches of the Cnidaria well established far below the basal Cambrian but also indicate that the complex metabolic pathway leading to production of mineralized structures has been undergone by a variety of lineages.

Among them *Flindersipora* (Lafuste et al. 1988, 1991) appears as a remarkable exception. This colonial skeleton is dated from the Lower Cambrian of Australia through its association with Botomian Archaeocyathids. The thick skeletal layers are made of vertical laminae frequently radially arranged (Fig. 11.10a), a structure suggesting a colonial organization laterally expanding. Noticeably, each component of the calcified structure exhibits a double-sided fibrous microstructure with a continuous median line between the fibrous layers (Fig. 11.10c, d).

What makes *Flindersipora* an interesting case-study in the search for earliest corallian organization is the similarity

between the microstructural patterns observable in these basal Cambrian specimens (Fig. 11.10) and equivalent pattern in more recent specimens. Architecture of the *Flindersipora* is presently unique among the morphological diversity of the numerous Cambrian enigma (Babcock 1991) and cannot be definitely placed in any of the present higher taxa. But its histological features indicate that the sequential coordination of gene activity required to produce a bilateral fibrous biocalcification was well established at the lowest Cambrian times, providing the earliest support to prevalence of microstructural characteristics over morphological and architectural patterns.

Consistency of the structural and biochemical data obtained by applying physical methods to recent and fossil Cnidaria skeletons offers a renewed perspective in the project of an integrated taxonomic approach enabling a more reliable evolutionary scheme to be progressively constructed.

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