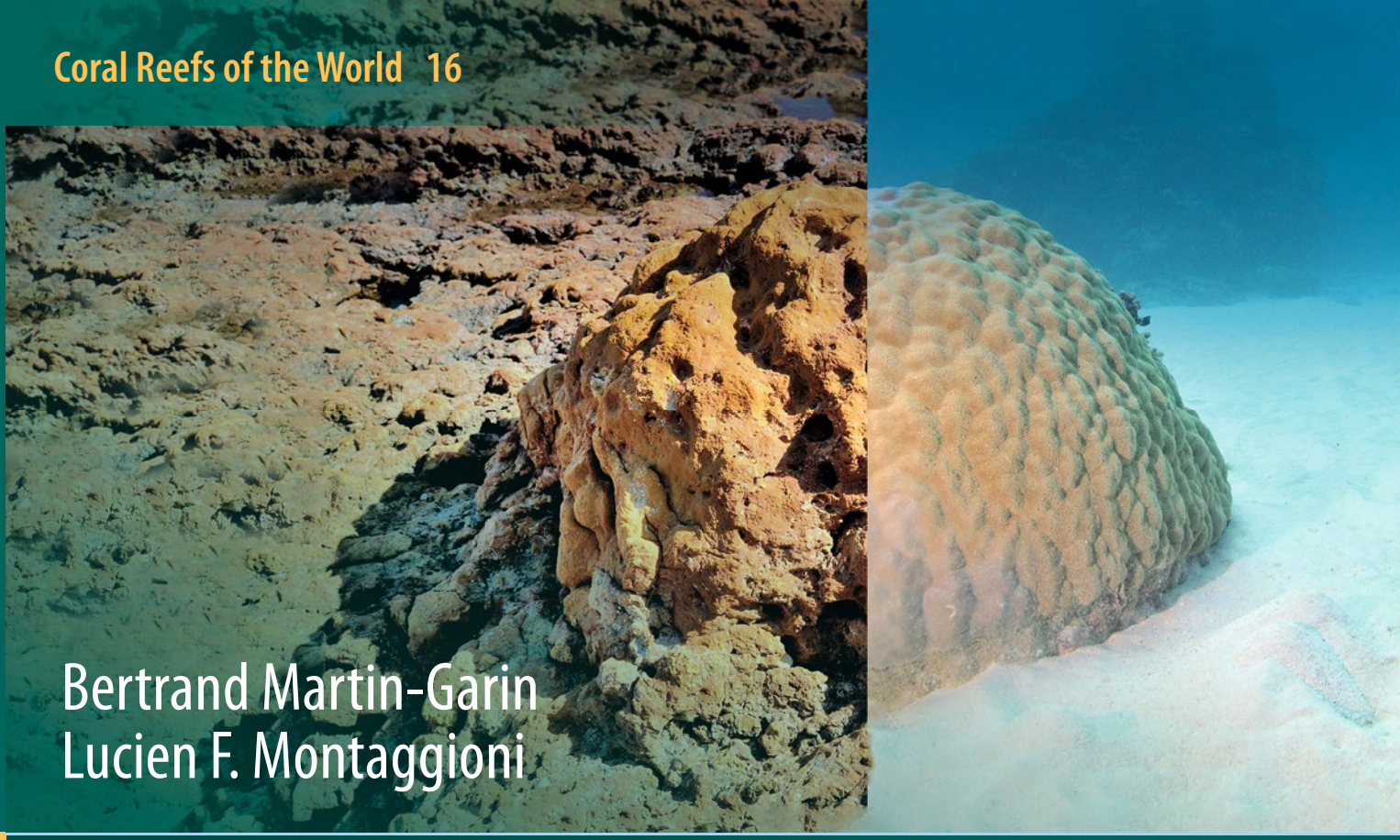
Coral Reefs of the World 16



Bertrand Martin-Garin
Lucien F. Montaggioni

Corals and Reefs

From the Beginning to an Uncertain Future

Springer

Coral Reefs of the World

Volume 16

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Cover illustration: Massive colony of a scleractinian coral of the genus *Porites*. Left: fossil *Porites* from the Miocene (−23 Ma) of the Côte-Bleue (France). Right: recent *Porites* from Lizard Island (Australia). Photography and editing by B. Martin-Garin

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Preface

Life emerged on our planet about 3.8 billion years ago. However, it had to wait more than 3 billion years for the earliest pluricellular animals to start secreting a mineralised exoskeleton, more frequently, composed of calcium carbonate. Appearing about 600 million years ago, these organisms were millimetre- to centimetre-sized. Some, taxonomically linked to the *Cnidaria* phylum, were likely ancestors of earlier corals. Although small-sized, it seems that these were able to build decimetre- to metre-thick reliefs on sea floors. True framework reefs, probably not, true buildups, undoubtedly. Over the Paleozoic times, shallow, warm-water environments were dominated, from about 500 million years ago, by two primitive coral groups (Tabulata and Rugosa) which ended up disappearing about 252 million years ago. The first scleractinian species, which are the reef-building coral forms today, appeared presumably −300 million years ago. Already suspected in primitive coral forms, photosymbiosis between corals and microalgae, regarded as a major physiological innovation, will greatly contribute to the expansion and success of scleractinians in all warm seas worldwide, mainly from about −240 million years.

However, the history of coral evolution was not as just going on and on. Life has been hit by numerous crises and suffered the effects of weapons of mass destruction at various dates, extraterrestrial (bolide fall) or terrestrial (volcanism, mainly). Whilst a great number of groups of organisms have since been eradicated, scleractinian corals have always managed to avoid the worst and to survive owing to their particularly efficient adaptive capacities. Current global warming and its serious harms to the environment and biodiversity are offering a real challenge to reef-building corals. Will corals be able to face up to this new crisis, although environmental changes do not operate currently at rates of the order of a few million years, but of human lifespan?

It is this long history of corals and reef phenomenon that we attempt to reconstruct in this book, the history of emblematic biota throughout the evolution of Earth over the last 600 million years.

The book includes a short introductory chapter, in which the term *corals* is defined and the concepts of *reef* and *coral reef* are addressed, five descriptive chapters, a list of references, and one index.

Chapter 2 is devoted to coral taxonomy and the biology—reproduction, biomineralisation processes—anatomy, structure, and ecophysiology—symbiosis, trophic regime—of scleractinian corals.

Chapter 3 aims at describing all attributes of modern coral reefs and their history over the Quaternary era. The chapter presents the different reef morphotypes and relevant biozonations, major controls of coral and reef growth, of geographical distribution patterns, and of internal reef structure, nature, and distribution, and sedimentary biofacies. Then, the reef growth throughout the Pleistocene and, especially, since the last deglaciation is summarised. The chapter ends with a short description of methods used to reconstruct paleoclimatic and paleoenvironmental parameters based on biometric and biochemical analyses from individual coral colonies to reef scale.

Chapter 4 addresses the questions about physicochemical conditions that would have driven the emergence of life on Earth. The chapter then addresses how and when biomineralisation, early calcifying organisms, early cnidarians, early corals, and early scleractinians appeared and how and when coral–algal photosymbiosis was acquired. Finally, the history of builders and relevant buildups and *reefs* throughout the Phanerozoic times is told, step by step, from the lower Cambrian to the Pliocene end.

Chapter 5 examines the biological crises and mass extinctions suffered by floral and faunal organisms since the beginning of the Phanerozoic and, more specifically, corals and other reef-dwelling organisms. The respective role and compared effects of terrestrial and extraterrestrial killing agents are addressed as well as responses of corals and reefs to resulting environmental disturbances. Finally, the major crises regarded as responsible for coral disappearance and reef demise and episodes of reef recovery are reviewed.

Chapter 6 explores the question of the future of coming coral generations and coral reefs in today's context of climate change. The different factors that are controlling climate and environmental changes are described, and their effects on oceans and coral ecosystems are explained. Special attention is given to the response of low-lying coral islands—atolls, especially—to ongoing and future climatic disturbances including a rapid rise in sea level and increasing storm energy.

The book ends with conclusive remarks, focused on the major role played by corals, mainly symbiotic scleractinian corals, in tropical marine ecology over the Phanerozoic, their great resilience to mass extinctions, and thus the dominant role of *reef features* in the Earth's history.

The authors are particularly grateful to personalities and colleagues who, in varying capacities, have allowed this book to be written and published. Firstly, many thanks are offered to colleagues who, in our respective careers, have been able to create conditions to our professional growth. Bertrand Martin-Garin acknowledges the help given early by Bernard Lathuillière, Professor at the université de Lorraine (Nancy, France), and Jörn Geister, Privat-Docent at Universität Bern (Switzerland). Lucien Montaggioni owes a debt to Bernard Salvat, Professor Emeritus and former Director of the Institute for Coral Reef Studies in French Polynesia, and late Guy Cabioch, formerly Research Director at the French Institute for Development. We would also like to thank Perle Abbrugiati, Chief Editor, and Jean-Claude Bertrand and Ivan Dekeyser, Co-Editors of Science Series at Aix-Marseille université (France) Press for granting authorisation to publish an English version of the book. Thanks are due to André Strasser, Professor Emeritus at the université de Fribourg (Switzerland), and Julien Denayer, Assistant Professor at the université de Liège (Belgium), for their comments and reviews of an early version of the manuscript.

Marseille, France

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Lucien F. Montaggioni

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Introduction: The Reef Phenomenon

1

> "Corals are the noblest plants in the Ocean, they are the roses of the capricious sea goddess, as rich in forms and colors as the whims of these same goddesses" *in* Joseph Roth, *the Merchant of Corals*, *The Leviathan* (1938).

Though they have a mineral *skeleton*, corals have been classified amongst invertebrates—animals without a spinal column and bone structures—a term without taxonomic value created by Jean-Baptiste de la Lamarck at the beginning of the nineteenth century. Corals are eumetazoans (higher metazoans), meaning pluricellular animals with more advanced cellular differentiation. However, it was not until the mid-eighteenth century that corals were recognised as animals. Since ancient Greece, corals and especially the Mediterranean red coral were considered as *flowering plants,* the *flowers* corresponding to the polyps spread out on the surface of the *stony* mass, therefore considered as *stone plants*: *Lithodendron*—in Greek.

In this case, coral polyps possess a calcareous skeleton and have the capacity to develop more or less bushy encrustations, such as the species *Corallium rubrum*—Mediterranean red coral—living at depths going down to −200 m, or even deeper, to construct edifices of meter to pluridecameter thickness as do species belonging to the order *Scleractinia* (*hard corals*).

Amongst scleractinians, the distinction between those able to build wave-resistant buildups, referred to as *hermatypic*—herms: reef, buildup, in the Greek language—and those not able to produce reefs and buildups, referred to as ahermatypic, is classically used (Wells 1933). The former are predominantly found in warm, shallow waters. The latter are regarded to be more adapted to colder and deeper waters, at depths—to many thousands of metres—but capable of producing edifices at least as high and wide as those created by tropical corals. Hermatypic forms are concentrated within the photic zone, i.e. the bathymetric range receiving a luminous flux high enough to allow for photosynthesis to occur, as they are living in association with symbiotic microalgae (zooxanthellae). Ahermatypic forms, usually regarded as lacking symbiotic algae, do not have such light-related constraints.

However, the classic distinction between hermatypic, reef-building and ahermatypic, non-reef-building forms appears to be arbitrary and confusing (Schuhmacher and Zibrowius 1985). Hermatypic forms can possess symbiotic algae (zooxanthellate) or be devoid of algal symbionts (azooxanthellate). All zooxanthellate hermatypic forms are constructional. Amongst zooxanthellate ahermatypic species, some can be constructional, and others are non-constructional. Some azooxanthelle hermatypic forms can be constructional. Amongst azooxanthellate ahermatypic corals, some can be constructional or non-constructional.

The term *reef* is derived from the word *arrecife* in Spanish, its roots originating from the Arabian word *ar-raṣīf*, name given to a causeway or a key. According to the Dictionary, the word *reef* refers to a rock or group of rocks, a shoal located on the water's edge of coastal areas. In addition, a coral reef corresponds to a rocky outcropping mass, a topographic anomaly built by corals in warm and clear waters, capable of resisting the action of storm waves. Unfortunately, the term *reef* has been overused. It has also been erroneously used to describe coral constructions from cold and deep waters, so qualified as *deep-water coral reefs*, and also often used by a number of authors to define organic edifices in the geological record, which are actually an assemblage of organisms with a mineralised skeleton that possess a variable construction power, or yet, to define muddy masses produced by microbes with strong power of retention, whilst all these structures have developed at depth, often far from the sea surface. In fact, the terms *bioconstructions (buildups)* or bio*accumulations* would be more appropriate to describe the last two cases than the word *reef*. Although it is true that in the geological record, it is often difficult to differentiate the structures that developed near the sea surface from those that flourished several meters deeper. The word *reef* will be applied here to any structure resulting from the direct

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or indirect activity of living organisms, whether it is a real built structure or a simple accumulation.

Owing to their large variety of forms and compositions, *bioconstructions* and *bioaccumulations* are classified in many ways, the most used being that of Riding (2002). It is based on the spatial arrangement and composition of *reef* structures. The structures result from the action of diverse processes put into play—construction, sedimentation and cementation—processes which ultimately determine the composition of sediment, or the respective proportions of each of the principal constituents: (1) in-place or reworked skeletons of building, (2) bioclastic sediments (matrices), a product of skeleton breakdown, filling inter- and intra-skeletal spaces, cavities, pores, and residual spaces, and (3) inter- and intra-skeletal cements that ensure structure consolidation. According to Riding, organic reefs can be described on the basis of a triangular diagram, of which the peaks correspond respectively to the following three major components: S (skeletons essentially in growth position), M (matrix fillings), and C (cavities and cements)—(Fig. 1.1).

In this context, organic reefs are identified amongst three categories: (1) *matrix-supported reefs* that include *agglutinated microbial reefs*, *cluster reefs,* and *segment reefs*, (2) *skeleton-supported reefs* or *framework reefs*, and (3) *cement reefs*.

Microbial reefs are composed of stacked micro-laminae or clotted and granular masses that result from trapping of particles by a mucilage (mucus) and precipitation of calcium carbonate; these are controlled by microbial activity. Skeletons in growth position and inter- and intra-skeletal primary cavities are rare or even absent. Early marine cementation favours the consolidation and maintenance of the structure, the latter generally forming reliefs, which can attain many metres high depending on sediment supply by marine currents.

Cluster reefs consist of skeletal organisms in growth position, but scattered throughout the structure. Inter-skeletal areas are occupied generally by bioclastic matrices. The amount of early cements outside of intra-skeletal cavities remains limited. The absence of coalescing framework limits both the vertical and lateral expansion of edifices, thus producing low-lying topography in the surrounding environment.

Segment reefs are structures in which in-place skeletons can be relatively dense, even in close contact, but most often are reworked and partly removed. Matrix deposits form the main parts of the buildup volumes, but are weakly affected by early cementation. The resulting reliefs remain poorly developed.

Framework reefs are characterised by the predominant building role of skeletons. These skeletons are in contact or coalescent, consisting of a continuous and rigid framework, capable of forming topographic anomalies of great amplitude

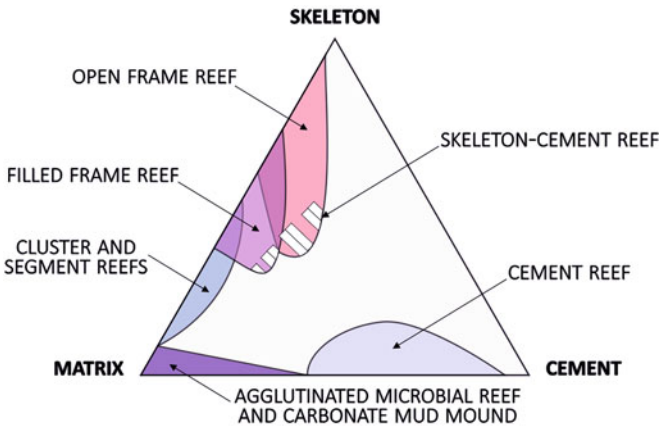

Fig. 1.1 Ternary classification of different reef types based on their major components—in-place skeletons, sedimentary (detrital) matrices, and cavities—cements. At the apices, the amount of the components is 100%, whilst it regularly decreases towards the opposite sides along the lines perpendicularly running from the apices. Accordingly, at each side, the amount of the relevant component is zero. For instance, the open-framework reef type contains 50–90% of in-place skeletal products, 10% of detrital matrices, and 0–30% of cements. Frame reefs, cluster reefs, and segment reef have relatively similar compositional patterns; cluster reefs have lower percentages of in-place skeletal products, but higher amounts of detrital material. By contrast, there is no overlap between microbial reefs, mud mounds, and cement reefs. Modified from Riding (2002)

over the surrounding environments, regardless of the rate of particulate sedimentation and cementation. Intra-skeletal spaces are occupied by fine-grained sediments and early marine cements, and inter-skeletal spaces as well, but partly. Two types of *framework reefs* can be distinguished, those with open cavities (*open-framework reefs*) and those with sealed cavities (*filled framework reefs*). In the former, the cavities remain open during the first stages of reef building, in turn allowing cryptic and sciaphilic organisms to colonise them, and are eventually filled with matrices and cements. In the latter, infilling of inter-skeletal space occurs coevally with skeletal growth.

Cement reefs result from cementation of skeletal organisms, dominantly in growth position. These cements are an important part of the structure; their forms are often derived from those of skeletal growth.

It is important to note that microbial, cluster, and segment reefs are structurally simple, consisting of low-amplitude reliefs (decimetric to metric scale), usually stratified. Framework and cement reefs possess a more complex and massive internal structure, due to the absence of stratifications, and create reliefs of greater amplitude (plurimetric to decametric scale).

To this list of reef structures must be added *carbonate mud mounds*, which can create structures of great amplitude, without any skeletal elements. They generally result from biochemical processes controlled by the activity of microbial

communities, which are capable of calcifying or precipitating cements to their surroundings.

The majority of modern organic reefs—coral and algal reefs, mollusc- and tubeworm-built structures—are rigid structures that sometimes emerge at low tides and are resistant to wave energy. Except for structures created by worms which arise from bioaccumulation, modern reefs can be generally classified amongst framework reefs, even though, in the case of coral reefs, due to the fact that the amount of coral detritus is often much higher than that of in situ corals, the term "detritus reefs" can be applied.

When comparing recent reefs (modern and Quaternary) and Pre-Neogene reefs—more than 23 million years; Fig. 1.2—it appears that these have morphological and structural dissimilarity. Indeed, beyond the nature and type of testaceous organisms implicated in their formation, one of the main causes responsible for disparity between recent and older reefs is to be sought in the very marked cyclicity of climate change. It began in the Miocene—about 15 million years ago—then greatly amplified during the Quaternary—from 2.5 million years ago. Glaciation and deglaciation have driven sea level fluctuations of great amplitude, which have favoured the development of vast and thick reef systems with great structural complexity. The majority of modern coral reefs have developed during the last deglacial sea level rise, starting approximately 19,000 years ago and ending less than 6000 years ago. Reef drilling indicates that reef settlement has been initiated at around 10,000–8000 years ago (see Montaggioni 2005). However, a number of bioconstructions and bioaccumulations of the Paleozoic, Mesozoic, and part of the Cenozoic have been able to develop over periods of a few tens to hundreds of thousands of years, often encompassing several biostratigraphic zones. Consequently, modern and Quaternary coral reefs cannot serve as a robust baseline for interpretating the palaeoecological reef record, if not for brief periods during the Phanerozoic—last 541 million years; Fig. 1.2.

The evolutionary history of corals and coral reefs would have started at the beginning of the Ordovician period (Fig. 1.2), around 470 million years ago. It has known a number of highs and lows from the beginning. Perhaps, the present times are merely another challenge for these great architects to overcome.

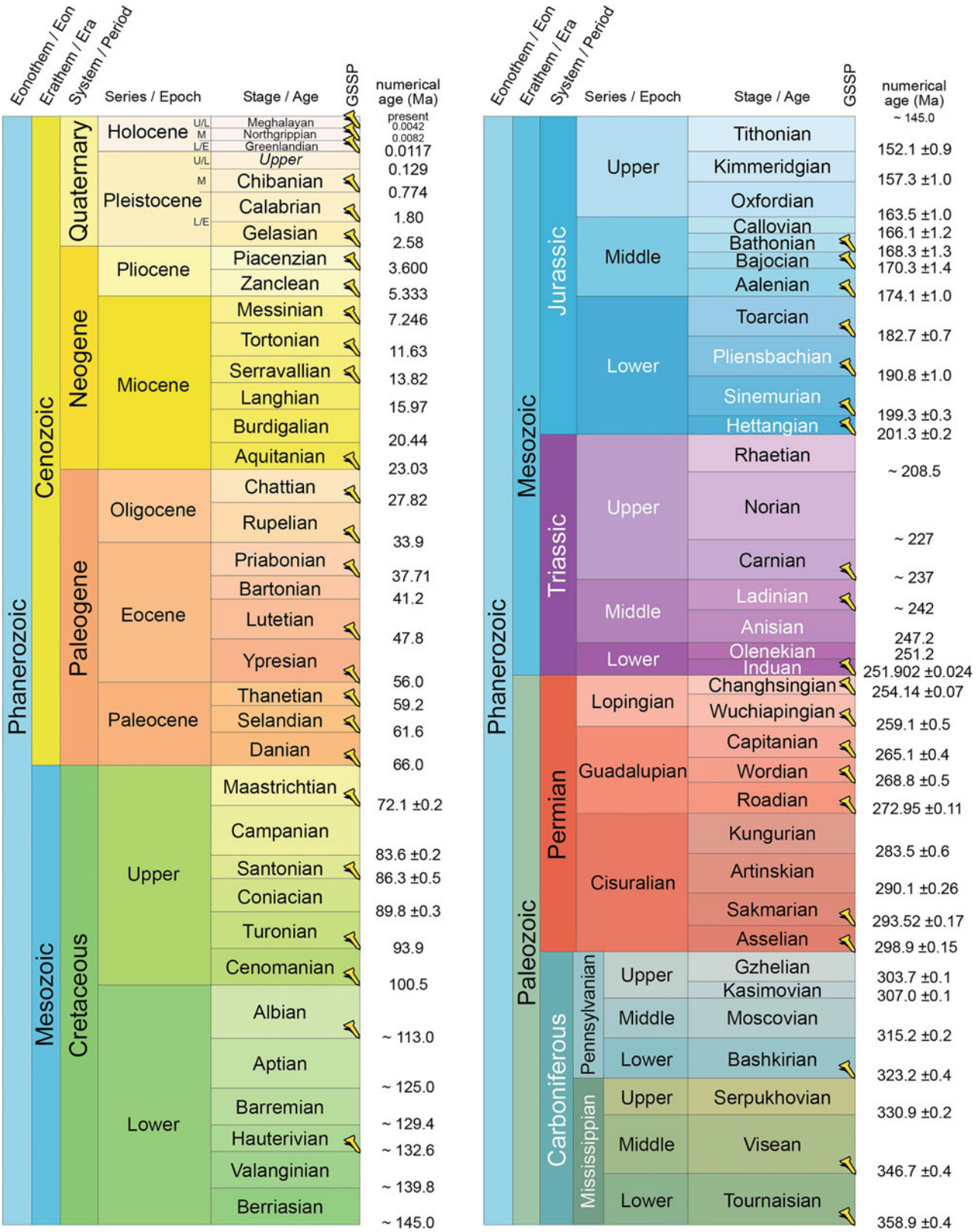

Fig. 1.2 International Stratigraphic Chart published by the International Commission on Stratigraphy and used in this book. The chart provides two distinct time scales in which the history of the Earth is inscribed: the relative, chronostratigraphic scale and the absolute, chronometric scale expressed in million years. From Cohen et al. (2013)

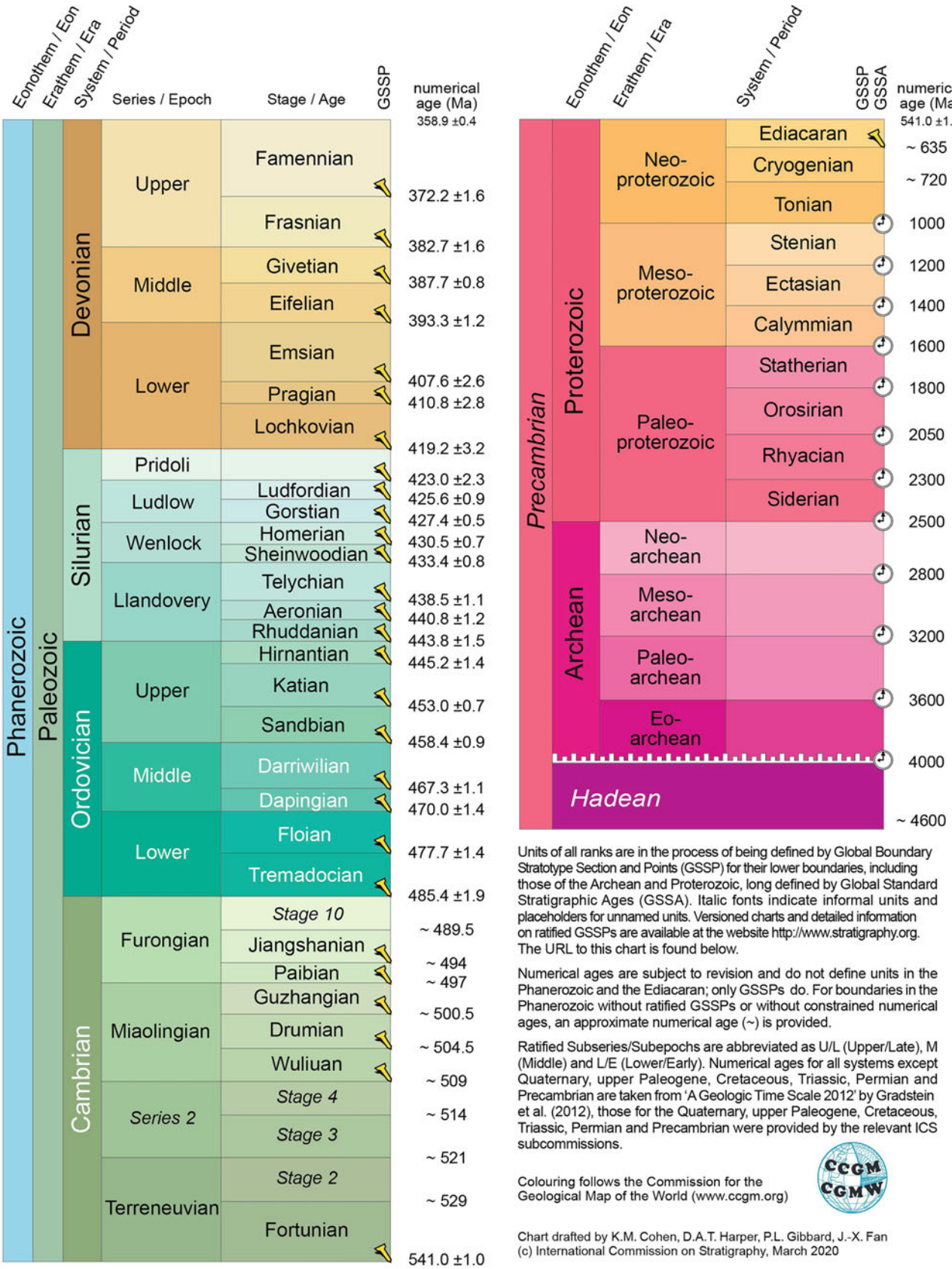

Fig. 1.2 (continued)

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Into the Intimacy of Corals, Builders of the Sea

2

> "It's in this last that precious coral belongs, an unusual substance that, at different times, has been classified in the mineral, vegetable, and animal kingdoms [. . .] A coral is a unit of tiny animals assembled over a polypary that's brittle and stony in nature. These polyps have a unique generating mechanism that reproduces them via the budding process, and they have an individual existence while also participating in a communal life" *in* Jules Verne, Twenty thousand leagues under the sea (1869–1870).

The phylum *Cnidaria* is particularly diversified, including organisms such as medusas, sea anemones and corals, and also lesser-known organisms such as alcyonarians, zoanthids, siphonophores, or even myxozoans. There are no less than 11,000 species today (Brusca and Brusca 2003; Zapata et al. 2015) that belong to the phylum of cnidarians the name of which refers to the urticant characteristics of some of their cells: *knidē* (*κνίδη)* meaning *stinging nettle* in ancient Greek.

2.1 Taxonomic Affiliation

2.1.1 Systematic Classification of Cnidarians

Cnidaria is a phylum of the *Metazoa* kingdom (Metazoan, animal) composed of two groups: *Anthozoan* and *Medusozoan*—(Zapata et al. 2015); Fig. 2.1. These clades are well identified today from phylogenetic analyses of molecular data (Bridge et al. 1992; Berntson et al. 1999; Collins et al. 2006; Kitahara et al. 2010; Zapata et al. 2015) and are typified by highly specific morphological characteristics (Bridge et al. 1995; Marques and Collins 2004; Collins et al. 2006; Zapata et al. 2015). However, for a long time, the understanding of the main relationships between *Anthozoa* and *Medusozoa* have proved difficult (McFadden et al. 2006; Rodríguez et al. 2014) partly due to divergences in form and structure between some fossil groups of the Cambrian—geological period between—541 million years ago (Ma) and—485.4 Ma—within the phylum *Cnidaria* (Cartwright and Collins 2007). As a result, a number of hypotheses have been proposed regarding the relationships between the different taxa.

- The clade *Medusozoa*—often considered as a subphylum—would include the classes *Hydrozoa*, *Scyphozoa, Staurozoa* and *Cubozoa* (Fig. 2.1). Hydrozoans are the "false jellyfish" rhythmed by ontogenesis with a polyp and medusa stages, and comprising hydras and siphonophores, with free-floating and drifting colonial forms. Scyphozoans are free and swimming "true jellyfish"—with or without a polyp stage. Stauromedusae never have a polyp stage and remain blocked at the medusa stage, but they are fixed to their substrate throughout their entire life. Meanwhile, Cubomedusae, called "sea wasps", with a more or less cubic form, are particularly urticant and dangerous, even deadly.
- Studies using ribosomal DNA (France et al. 1996; Odorico and Miller 1997; Song and Won 1997; Berntson et al. 1999; Zapata et al. 2015) have revealed the monophyly of the *Anthozoa* clade—considered to be a class. It includes approximately 7500 existing species that have been described (Daly et al. 2007) and is composed of two main sub-classes: *Hexacorallia* and *Octocorallia* (Fig. 2.1). Octocorallians include soft corals (alcyonarians), gorgonians and sea pens (*Pennatulacea*). Hexacorallians comprise six orders currently: cerianthids (*Ceriantharia*), zoanthids (*Zoanthidea*), black corals (*Antipatharia*), sea anemones (*Actinaria*), corallimorphs (*Corallimorpharia*) and hard corals—*Scleractinia* (Fig. 2.1).

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