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The Biology and Evolution of Calcite and Aragonite Mineralization in Octocorallia

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Octocorallia (class Anthozoa, phylum Cnidaria) is a group of calcifying corals displaying a wide diversity of mineral skeletons. This includes skeletal structures composed of different calcium carbonate polymorphs (aragonite and calcite). This represents a unique feature among anthozoans, as scleractinian corals (subclass Hexacorallia), main reef builders and focus of biomineralization research, are all characterized by an aragonite exoskeleton. From an evolutionary perspective, the presence of aragonitic skeletons in Octocorallia is puzzling as it is observed in very few species and has apparently originated during a Calcite sea (i.e., time interval characterized by calcite-inducing seawater conditions). Despite this, octocorals have been systematically overlooked in biomineralization studies. Here we review what is known about octocoral biomineralization, focusing on the evolutionary and biological processes that underlie calcite and aragonite formation. Although differences in research focus between octocorals and scleractinians are often mentioned, we highlight how strong variability also exists between different octocoral groups. Different main aspects of octocoral biomineralization have been in fact studied in a small set of species, including the (calcitic) gorgonian *Leptogorgia virgulata* and/or the precious coral *Corallium rubrum.* These include descriptions of calcifying cells (scleroblasts), calcium transport and chemistry of the calcification fluids. With the exception of few histological observations, no information on these features is available for aragonitic octocorals. Availability of sequencing data is also heterogeneous between groups, with no transcriptome or genome available, for instance, for the clade Calcaxonia. Although calcite represents by far the most common polymorph deposited by octocorals, we argue that studying aragonite-forming could provide insight on octocoral, and more generally anthozoan, biomineralization. First and foremost it would allow to compare calcification processes between octocoral groups, highlighting homologies and differences. Secondly, similarities (exoskeleton) between *Heliopora* and scleractinian skeletons, would provide further insight on which biomineralization features are driven by skeleton characteristics (shared by scleractinians and aragonitic octocorals) and those driven by taxonomy (shared by octocorals regardless of skeleton polymorph). Including the diversity of anthozoan mineralization strategies into biomineralization studies remains thus essential to comprehensively study how skeletons form and evolved within this ecologically important group of marine animals.

Keywords: octocorallia, biomineralization, aragonite, evolutionary biology, calcite

INTRODUCTION

Biomineralization refers to the process by which organisms produce minerals. The ability to form biomineral structures is taxonomically widespread and has evolved multiple times during the Earth's history, including twenty independent origins within Metazoa and four within plants (Knoll, 2003). Biominerals serve a wide variety of biological functions including, among others, body support, defense against predation, navigation (Frankel et al., 1997) and (in plants) the regulation of photosynthesis and ion concentration (He et al., 2014 for review). Many groups of marine invertebrates (e.g., sponges, molluscs, and echinoderms) produce biominerals and among these, anthozoan coral (Cnidaria: Anthozoa) calcium carbonate biomineralization holds an extreme ecological significance, as it forms the 3D-framework of one of the most biodiverse ecosystems on the planet, coral reefs. Within Anthozoa, calcifying corals are found in two distinctive clades: the order Scleractinia (subclass Hexacorallia) and the subclass Octocorallia (**Figure 1f**). Scleractinian corals currently are the major contributors to reef accretion, and have thus been the focus of biomineralization research over the years (e.g., Tambutté et al., 2011; Falini et al., 2015). On the other hand, calcium carbonate ($CaCO_3$) production in octocorals, commonly referred to as *soft corals,* is often modest and can be of several orders of magnitude lower compared to scleractinians (Smith and Kinsey, 1976; Herrán et al., 2017; Edinger et al., 2019). Despite this, some octocoral species (primarily the order Helioporacea) can significantly contribute to reef formation (Zann and Bolton, 1985) and can become the main reef builders within different habitats (Shaish et al., 2010; Yasuda et al., 2012). Octocorals can also exhibit higher resilience to environmental conditions, enabling them to outperform and replace scleractinians after events such as coral bleaching, pollution and *Acanthaster* outbreaks (Nishishira, 1974; Stobart et al., 2005; Ruzicka et al., 2013). Moreover, from a biomineralogical perspective, octocorals are more diverse than scleractinians, as they have evolved a wide range of different biomineralization strategies. These include the production of skeletal structures composed of different calcium carbonate polymorphs (aragonite and calcite) and of organic components (Gorgonin). On the other hand, all modern scleractinian species are characterized by the production of aragonite skeletons only.

In light of this, octocorals represent an interesting target for biomineralization research. Yet they remain marginally studied. One of the main questions surrounding octocoral calcification is whether the morphological and compositional diversity of their skeletons is related to differences in the cellular and molecular mechanisms employed by them for biomineralization. As in other animal groups, calcification in Octocorallia is a *biologically controlled* process, in which the precipitation mineral is not a byproduct of metabolic processes (*biologically induced mineralization*), but is rather under strict physiologic control (Lowenstam, 1981; Mann, 1983). In general, biological control can be broadly subdivided into two main processes, namely, the regulation of ion (e.g., calcium) transport and concentration at the calcification sites (Kingsley and Watabe, 1985; Watabe and Kingsley, 1992; Bertucci et al., 2013), and the secretion of an organic matrix into the mineral fraction of the skeleton (Weiner et al., 1983). The composition of organic matrix in octocorals is of particular interest, as it has been shown—in other calcifying taxa—that it regulates *in vitro* precipitation of different $CaCO_3$ polymorphs (Goffredo et al., 2011; Laipnik et al., 2019). Despite this, little is known about skeleton formation in octocorals, especially whether these animals have (and how they evolved) the ability to control the formation of different $CaCO_3$ polymorphs. Finally, furthering our knowledge on octocoral calcification would also allow to obtain comparative information on the biomineralization strategies of two different groups of calcifying corals, and better understand how biomineralization evolved within the Anthozoa.

In this review, we examine the research status of calcite and aragonite biomineralization in octocorals. After introducing Octocorallia and highlighting the diversity of their skeletons, we summarize what is known about the evolutionary histories of biomineralization in octocorals, with a focus on polymorph diversity. We then surveyed available information on the cellular and molecular processes responsible for the formation of different skeletons. The aim was to (1) highlight the numerous current knowledge gaps characterizing octocoral biomineralization (especially pertaining to aragonite-forming species), and (2) propose novel potential approaches and/or research avenues to gain insight on the molecular mechanisms underlying such skeleton diversity.

OCTOCORALS: *SOFT* BIOMINERALIZERS

The cnidarian subclass Octocorallia represents a group of marine benthic organisms, currently comprising more than 3,400 described valid species (Williams and Cairns, 2015). They inhabit all marine habitats, but do mostly occur in either shallow tropical or deep sea environments. Around 75% of octocoral species have been described from waters below 50 m and the deepest specimen to date was recorded at 6,400 m depth (Roberts et al., 2009; Zapata Guardiola and López González, 2012). They are globally distributed, albeit very few species are cosmopolitan, with the highest diversity occurring in the Indo-Pacific region (Williams and Cairns, 2013; Pérez et al., 2016). Octocorals represent important marine community members and can increase habitats' spatial complexity (Quattrini et al., 2014). In deep sea environments, for example, octocorals can occur at high densities and sustain biodiverse ecosystems by providing substratum and shelter to other organisms like fishes (Caley and St John, 1996), or nudibranchs, crustaceans, and echinoderms (Krieger and Wing, 2002; Mortensen and Buhl-Mortensen, 2005; De Clippele et al., 2015). As observed in scleractinians, octocoral can also establish symbiotic relationships (obligate or facultative) with photosynthetic microalgae (zooxanthellae) or be non-symbiotic (Fabricius and Alderslade, 2001). This octocoral-algae association is considered mutualistic: the symbiont obtains inorganic nutrients from the coral, while the host receives in turn organic compounds, the products of photosynthesis. Primary productivity is nonetheless usually low, and octocorals often rely also on heterotrophy (e.g., suspension feeding, prey capture) (Sorokin, 1991; Fabricius and Klumpp, 1995; Ribes et al., 1998).

With the sole exception of members of the genus *Taiaroa* (Bayer and Muzik, 1976), octocorals are colonial, and consist of multiple polyps embedded and interconnected by tissue (coenenchyme). Octocoral colonies can be morphologically very distinct and exhibit a wide range of forms from encrusting to arborescent (**Figures 1a–e**). Nevertheless, polyps are always characterized by an eightfold symmetry (i.e., they possess eight tentacles and eight internal mesenteries). This represents the synapomorphy of the group and separates Octocorallia from all remaining anthozoan taxa, in which a sixfold symmetry is present. In octocorals, polyp tentacles are also often characterized by lateral branched structures called pinnulae. This does however not constitute an octocoral synapomorphy as species with smooth tentacles have also been described (Alderslade and McFadden, 2007). Biomineralization is also not shared by all octocorals, and species lacking any mineral structure have been described in different groups (Alderslade and Mcfadden, 2011; Benayahu et al., 2017; Lau and Reimer, 2019b).

Taxonomically, Octocorallia is currently divided into three orders: Helioporacea, Pennatulacea, and Alcyonacea (Bayer, 1981b). The first two are grouped based on well-defined characters: the presence of an aragonite skeleton (Helioporacea) and the oozoid, a differentiated polyp that ensures attachment to the substratum (Pennatulacea). Order Alcyonacea is subsequently divided into six sub-ordinal groups based on their skeleton characteristics: Alcyoniina, Holaxonia, Stolonifera, Calcaxonia, Scleraxonia, and Protoalcyonacea (Grasshoff, 1999; Fabricius and Alderslade, 2001). Molecular phylogenetic studies of Octocorallia, however, have repeatedly shown that these groups are artificial and should be abandoned. For example, the analysis McFadden et al. (2006) found the suborders Stolonifera, Alcyoniina, and Scleraxonia polyphyletic. Polyphyly for Scleraxonia was also observed in Sánchez et al. (2003a), while Alcyoniina and Calcaxonia appeared paraphyletic.

DIVERSITY AND COMPOSITION OF OCTOCORAL SKELETONS

Compared to modern scleractinians, which all produce massive aragonitic exoskeletons, octocorals have evolved a diverse array of skeletal structures. In the vast majority of species, the skeletal elements consist of multiple micro- or millimetric calcareous structures called sclerites, which occur embedded within the animal tissues. The overall sclerite morphology (e.g., spicule, spindle, rod, plate) (Devictor and Morton, 2010) and the different types of ornamentations can differ sensibly between species (**Figure 2**) and have been thus used extensively for species delimitation (Bayer, 1981a; Fabricius and Alderslade, 2001; Tentori and van Ofwegen, 2011). Molecular phylogenies have confirmed the taxonomic value of sclerite morphology to some extent, despite also highlighting instances of homoplasy (Sánchez et al., 2003b; Vargas et al., 2010c, 2014; Ament-Velásquez et al., 2016; Poliseno et al., 2017). Morphological plasticity linked to environmental conditions (Prada et al., 2008) and predation (West, 1997) has also been reported. Intraspecific variability is also present and different sclerite types and abundance can be observed within single individuals (Van Alstyne et al., 1992; Vargas et al., 2010a,b). In some species, different sclerite morphologies appear to correlate with their different localization (e.g., polyp, base) within the animal body (Williams, 1986, 1992; Alderslade, 2000; Tentori and van Ofwegen, 2011). Sclerites are found embedded within the mesoglea—a collagen-like substance between the ectodermal and endodermal layers (Barzansky and Lenhoff, 1974)—of the coenenchyme (tissue connecting the polyps) and/or the polyp (Fabricius and Alderslade, 2001).

Mineralogy: Octocoral sclerites are all composed of $CaCO_3$ in the form of high-magnesium calcite. More detailed compositional analyses have been obtained for the sclerites of Mediterranean gorgonians and precious corals. In the former, magnesium concentrations ranged between 1.4 and 2.2% (Weinbauer and Vellmirov, 1995). Slightly higher values (2.1–3.0%) have been found in *C. rubrum* (Family Corallidae), although variability in magnesium content both within single sclerites, individuals and between colonies was reported (Weinbauer et al., 2000). Strontium is another common component of octocoral sclerites and its concentration values in gogonians can range between 0.1 and 0.2% (Weinbauer and Vellmirov, 1995). Incorporated amounts of magnesium and strontium have been extensively used to reconstruct paleoclimatic conditions. For example, the concentration of magnesium in octocoral sclerites is positively correlated with seawater temperature (Weinbauer and Vellmirov, 1995; Yoshimura et al., 2011), although in *C. rubrum* this correlation appears not to hold when colonies are exposed to large temperature fluctuations (Vielzeuf et al., 2013). Finally, several trace elements have been detected in the sclerites of *C. rubrum* including lithium, iron, zinc and barium (Vielzeuf et al., 2013, 2018).

In some octocoral groups a mineral axial skeleton is deposited alongside sclerites. The axis provides support to the colony and can be entirely composed of biogenic calcite or be a combination of scleroproteins (collectively referred

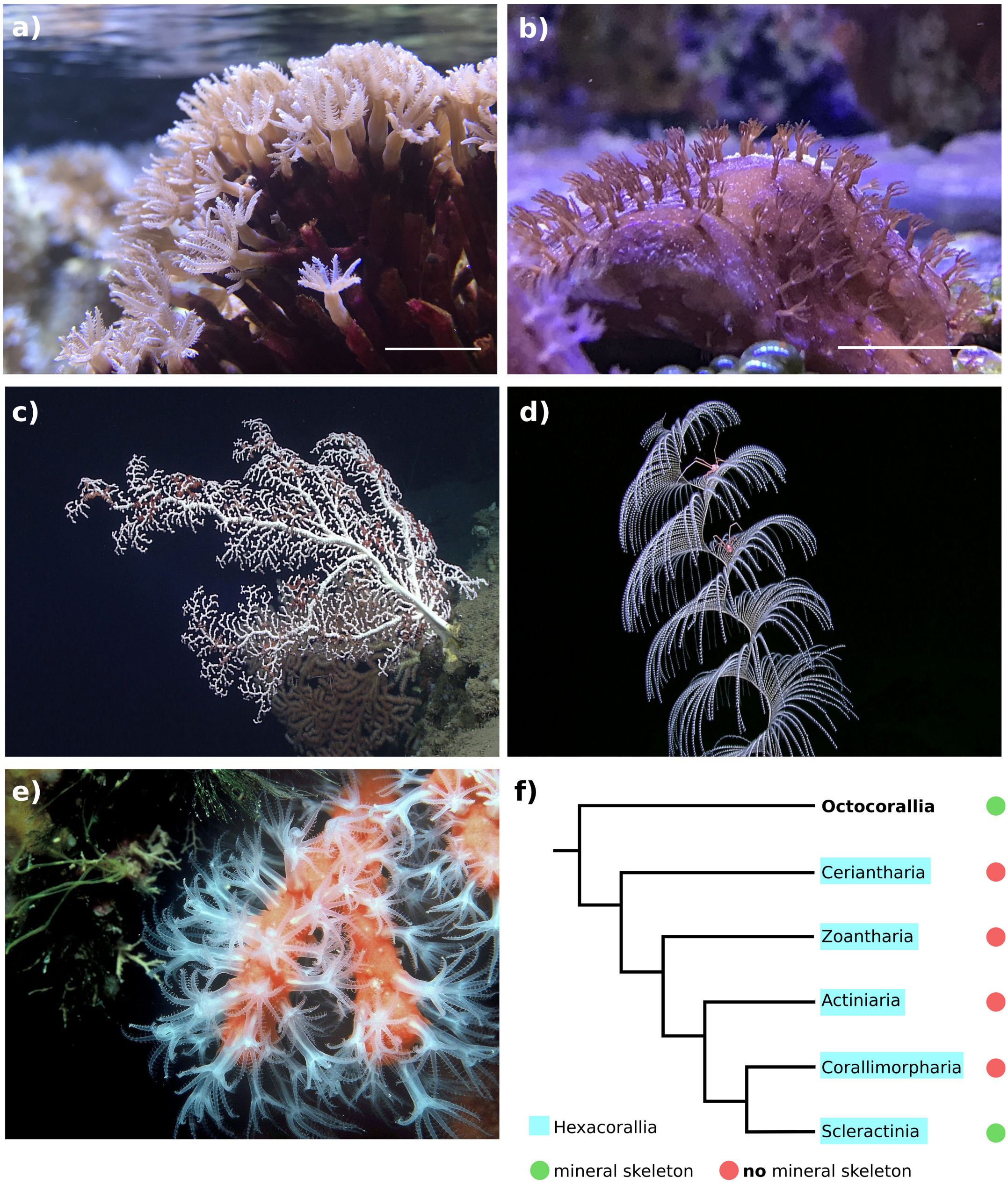

FIGURE 1 | (a) *Tubipora musica* (order Stolonifera) (scale bar: 1 cm). **(b)** *Heliopora coerulea* (order Helioporacea) (scale bar: 1 cm). **(c)** *Paragorgia* sp. (order Alcyonacea). **(d)** *Iridogorgia* sp. (order Alcyonacea). **(e)** *Corallium rubrum* (order Alcyonacea). **(f)** Phylogenetic tree of class Anthozoa highlighting presence-absence patterns of mineral skeletons. We based the Anthozoa phylogenetic tree on Kayal et al. (2018). Here, Ceriantharia was found as sister taxon to other members of Hexacorallia. This has been recently corroborated in a phylogenomic analysis by McFadden et al. (2021). However, an alternative tree topology puts Ceriantharia as sister to remaining Anthozoa (Stampar et al., 2014). Pictures credit: **(a,b)** Department of Earth and Environmental Science, Ludwig-Maximilians-Universität München, **(c)** NOAA Office of Ocean Exploration and Research, Deep Connections 2019, and **(d)** NOAA Okeanos Explorer Program, Gulf of Mexico 2012 Expedition.

to as gorgonin; Bayer, 1981b) and calcite. Axial skeletons can arise from different calcification mechanisms that often entail the fusion of sclerites. In the precious coral *Corallium rubrum,* for example, sclerites at the tips of colony branches fuse to form the core of the axis, which is secondarily thickened by subsequent deposition of mineral layers (Allemand, 1993; Debreuil et al., 2012). In *C. johnsoni* however, the axial skeleton appears to be devoid of scleritic material (Lawniczak, 1987). In Octocorallia, different biomineralization strategies could have thus evolved within genera. In the family Ellisellidae, sclerites forming the axial core are often markedly different from those found in the coenenchyme (Devictor and Morton, 2010). Alternatively, sclerites can also assemble into reticulate structures (e.g., *Melithaea*) (Cuif, 2016). In octocorals

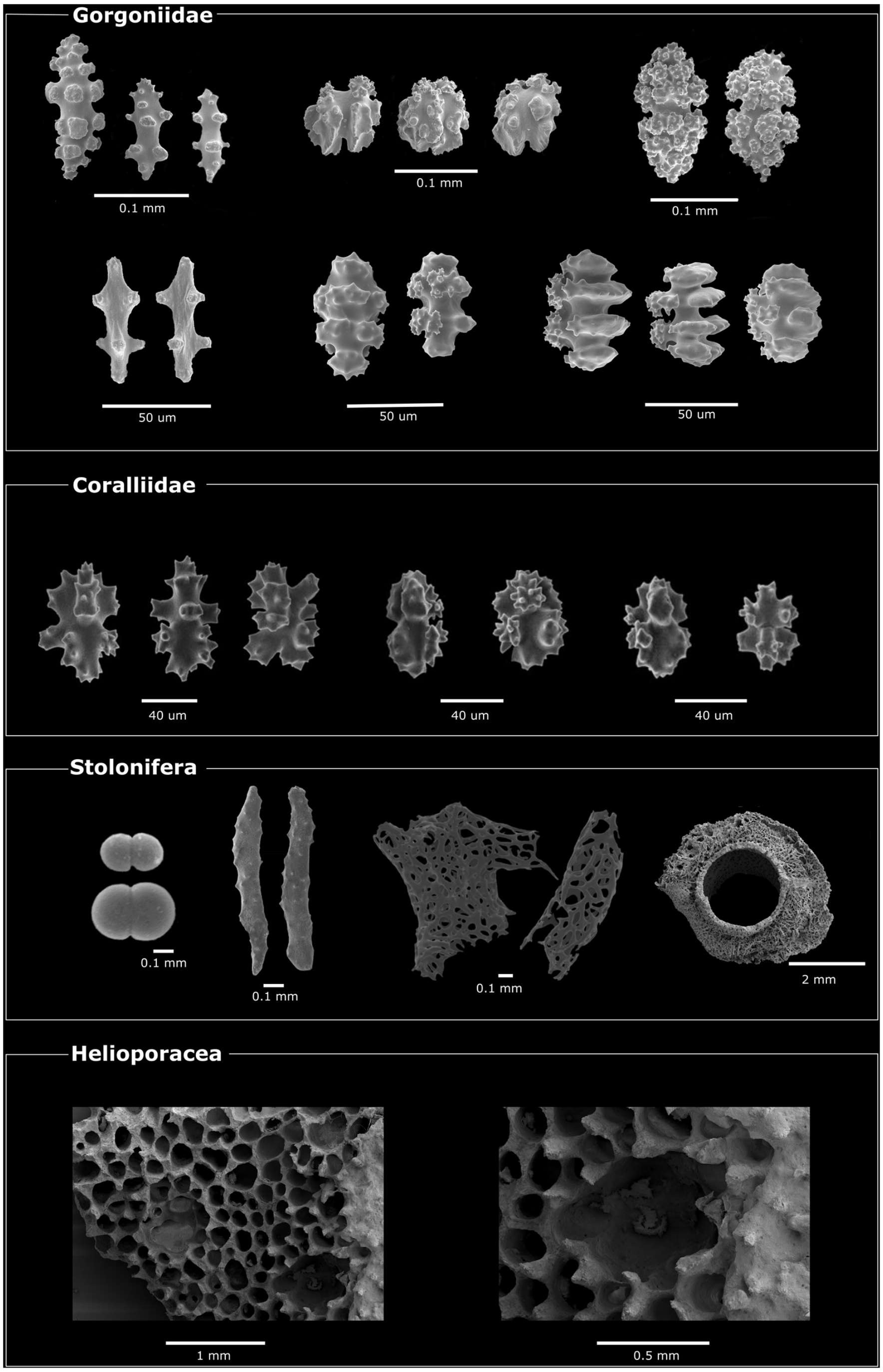

FIGURE 2 | Overview of skeletal structures present in different octocoral clades. Images acquired by scanning electron microscopy (SEM). Images sources: Gorgoniidae from Horvath (2019), Corallidae from Simpson and Watling (2011) (Cambridge Press©, reproduced with permission of copyright holder), Stolonifera from Lau et al. (2019) and personal image, Helioporacea (personal images). Image from Conci (2020).

producing proteinaceous skeletons, the axis can be reinforced with endogenous/biogenic (high magnesium calcite) or non-endogenous (calcite, aragonite, or amorphous $CaCO_3$) minerals (Lewis et al., 1992). Amounts and origin of the axis mineral fraction can differ between groups. In Calcaxonia, large amounts of non-scleritic or scleritic calcite are present, while members of the suborder Holaxonia are characterized by small quantities of embedded calcium carbonate (Bayer and Macintyre, 2001). In bamboo corals (Family Isididae), the proteinaceous and mineral fractions of the axial skeleton are arranged to form an alternation of flexible joints and rigid mineral internodes (Noé and Dullo, 2006).

Exceptions to the "*calcite rule*" are members of Order Helioporacea, in which a trabecular skeleton of fibrous aragonite is present (Hill, 1960). In the genus *Heliopora* and *Nanipora*, only aragonite is observed, while in the genus *Epiphaxum* calcite sclerites are formed alongside the aragonitic skeleton (Lozouet and Molodtsova, 2008; Miyazaki and Reimer, 2015). However, compared to the high-magnesium calcite of sclerites, the magnesium content found in *Heliopora's* aragonite skeleton is lower (ca. 0.5 mol%) (Velimirov, 1980).

Finally, hydroxyapatite ($Ca_{10}(PO_4)6(OH)_2$) has also been detected in some gorgonians and currently represent the only possible instance of likely biologically produced calcium phosphate in cnidarians (Macintyre et al., 2000).

EVOLUTIONARY HISTORY OF OCTOCORAL BIOMINERALIZATION

The origin of Octocorallia and the evolutionary relationships between different skeletal structures, notably between aragonite skeletons and calcite structures (sclerites and axis), remain largely elusive. This is in part caused by the poor preservation (Cope, 2005) and challenging identification (Deflandre-Rigaud, 1957; Kocurko and Kocurko, 1992) of octocoral skeletal elements in the fossil record, and the current lack of robust phylogenetic analyses for Octocorallia (but see Quattrini et al., 2020).

The earliest putative octocoral fossils currently date back to the Ediacaran (Glaessner, 1985). A putative Cambrian bryozoan fossil (genus *Pywackia*) (Landing et al., 2010) was later re-classified as an octocoral (Ausich and Babcock, 1998; Taylor et al., 2013), although this claim has been questioned (Landing et al., 2015). Earliest undisputed specimens of the group currently date back to the Ordovician, and belong to the gorgonian genus *Petilavenula* (Cope, 2005). Paleozoic (Silurian) octocoral fossils also include examples of a spiculite, a type of calcareous rock composed of cemented sclerites (Bengtson, 1981). Other octocoral groups appeared in the fossil record during the Cretaceous period (**Figure 3**). These include sea pens (order Pennatulacea) (Reich and Kutscher, 2011) and precious corals (family Coralliidae) (Schlagintweit and Gawlick, 2009). The oldest fossil specimens of aragonitic *Heliopora* and *Epiphaxum* species also date back to the Createaceous (Eguchi, 1948; Colgan, 1984; Lozouet and Molodtsova, 2008). A recent time-calibrated molecular phylogenetic analysis has corroborated the hypothesis of a Cretaceous origin for helioporaceans, while the proposed origin of pennatulaceans was pushed back to the Carboniferous (Quattrini et al., 2020).

The emergence of aragonitic skeletons during the Cretaceous is of evolutionary interest, as it lies in apparent disagreement with the calcite-inducing conditions (i.e., low magnesium-calcium molar ratio, or mMg:mCa) experienced by marine calcifiers during that time (Hardie, 1996; Lowenstein et al., 2001). The mMg:mCa of seawater has been hypothesized to represent one of the main drivers of selective inorganic precipitation of $CaCO_3$ polymorphs, with lower (<2) and higher (>2) values promoting the formation of calcite and aragonite, respectively (Morse et al., 1997; Balthasar and Cusack, 2015). Variations in mMg:mCa during the last 500 Mya have created an alternation between aragonite and calcite-favoring environments (referred to as the so-called "Aragonite-" and "Calcite Seas"), and have been shown to correlate with shifts in the skeleton polymorph produced by major calcificiers (Hardie, 1996; Stanley and Hardie, 1998; Knoll, 2003).

Aragonitic scleractinian corals, for example, represent the main reef framework-builders today (mMg:mCa ca. 5.2) and were responsible for reef formation during the Triassic Aragonite Sea (Stanley, 1981). They were, however, replaced by calcitic rudists (class Bivalvia, phylum Mollusca) during the Cretaceous, when Calcite Sea conditions prevailed (Scott, 1988). In addition to driving shifts in the composition of reef building communities, the seawater mMg:mCa appears to have also influenced the polymorph initially adopted by different organisms (Porter, 2010).

Aragonitic octocorals represent one of the very few exceptions to these patterns, as they appear to have evolved the ability to deposit aragonite skeletons during a Calcite Sea interval (Porter, 2010). On one hand, this could be explained by a currently incomplete fossil record. Aragonite-forming octocorals might have appeared earlier during aragonite-favoring conditions. This would, however, imply an extensive gap in the fossil record. On the other hand, precipitation of aragonite could have been promoted by other environmental variables. During the Cretaceous, several seawater properties differed compared to today's conditions. These include higher seawater temperatures (above 32°C at low latitudes) in shallow marine habitats (Schouten et al., 2003; Bice et al., 2006), lower pH (Zeebe, 2001) and lower sulfate ($SO_4{}^{2-}$) concentrations (Algeo et al., 2015). Among these, higher seawater temperatures have been shown to promote the co-precipitation of aragonite, alongside calcite, even at mMg:mCa < 1 (Balthasar and Cusack, 2015). The warm surface temperature characterizing the shallow environments inhabited by *H. coerulea* during the Cretaceous (Zann and Bolton, 1985), might thus have enabled this species to deposit its aragonitic skeleton. A similar scenario has also been proposed to explain the appearance of aragonitic brachiopod shells in the Silurian and Ordovician (Balthasar et al., 2011; Balthasar and Cusack, 2015).

Inferences on the evolution of octocoral biomineralization are furthermore hampered by the current lack of robust phylogenies for Octocorallia. The most comprehensive analysis, published by McFadden et al. (2006), identified two major clades (Holaxonia + Alcyoniina and Pennatulacea + Calcaxonia) plus a third clade consisting of genus *Anthomastus* and the precious coral *Corallium ducale*. The blue coral *H. coeruela* formed a clade with sea pens and calcaxonians. The hypothesis of a close evolutionary relationship between aragonitic octocorals (genera *Heliopora* and *Nanipora*) was later corroborated by Miyazaki and Reimer (2015) using different molecular markers. In another phylogeny, based on mitochondrial protein-coding genes, *H. coerulea* was, however, retrieved as sister to the rest of Octocorallia (Kayal et al., 2013). Nonetheless, the latter study aimed at resolving evolutionary relationships between Cnidaria major clades, and included a smaller taxon sampling of octocorals. In any case, no mitochondrial or nuclear

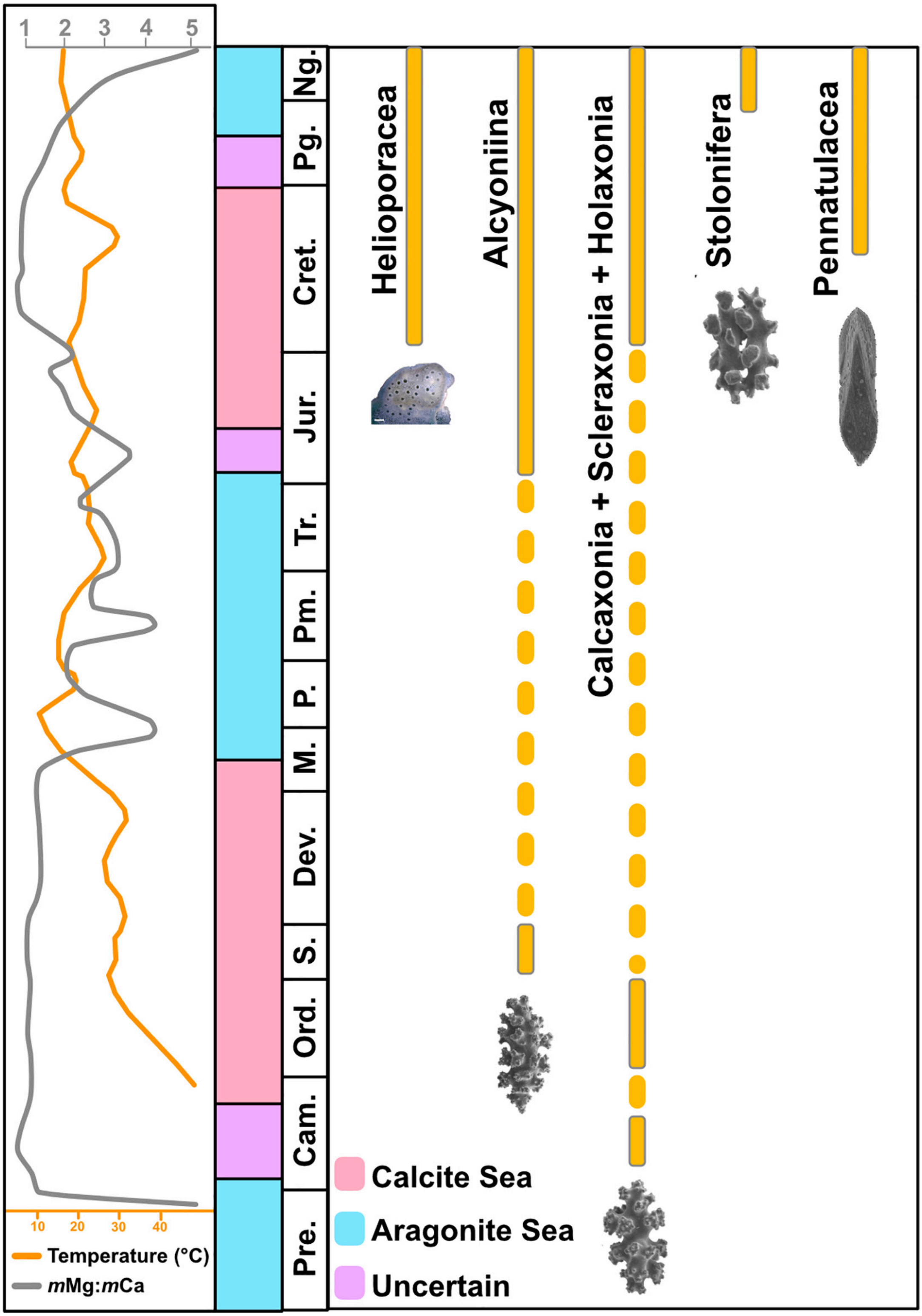

FIGURE 3 | Current fossil record of different octocoral taxa and concurrent environmental conditions (magnesium-calcium molar ratio, *m*Mg:*m*Ca, and sea surface water temperature) during the last 500 Mya. Fossil record based on Reich (2009). Seawater surface temperature and *m*Mg:*m*Ca based on Song et al. (2019) and Hardie (1996), respectively. Skeleton images: Helioporacea (Gert Wörheide), Alcyoniina (McFadden and Ofwegen, 2017) (Magnolia Press© reproduced with permission of copyright holder), Holaxonia (Dautova, 2019), Stolonifera (Lau et al., 2018) and Pennatulacea (Williams, 2015). Pre, Precambrian; Cam, Cambrian; Ord, Ordovician; S, Silurian; Dev, Devonian; M, Mississippian; P, Pennsylvanian; Pm, Permian; Tr, Triassic; Jur, Jurassic; Cret, Cretaceous; Pg, Plaeogene; Ng, Neogene.

marker have proved effective in resolving deep phylogenetic relationships between octocoral clades to date. This suggests that octocorals might have undergone a rapid radiation. Because phylogenomic analyses with larger taxon sampling to reconstruct the evolutionary history between octocoral groups are currently lacking, there clearly is the need for increased transcriptome and genome sequencing efforts to fill this knowledge gap (Rokas et al., 2005; McFadden et al., 2010). Nonetheless, some sequencing data is already available for some species and octocorals have been included in broader phylogenomic and phylotranscriptomic analyses to assess evolutionary relationships between cnidarian (Zapata et al., 2015; Kayal et al., 2018) or metazoan (Simion et al., 2017) groups. Several octocoral transcriptomes have been sequenced in the last few years and three genomes were released in the last 2 years (**Table 1**).

The majority of sequencing datasets is derived from octocorals of the suborder Holaxonia, while for other groups the number of species with a sequenced transcriptome/genome is extremely limited. To date, to the best of our knowledge, no data is available for Calcaxonia. Despite the recent increase in availability of octocoral *omic* resources, dozens of genera remain to be sequenced before phylogenomic (or phylotranscriptomic) analyses, with taxon samplings equivalent to previous studies (e.g., 103 species included in McFadden et al., 2006), can be conducted. In this light, research efforts aimed at resolving the origin and evolution of octocorals should (1) focus on filling the gap in terms of availability of data for calcaxonian octocorals and (2) examine existing phylogenies to prioritize the sequencing of taxa belonging to unresolved clades.

SCLEROBLASTS: THE OCTOCORAL CALCIFYING CELLS

Biological control over biomineralization often entails specialized cell types carrying out skeleton formation. For example, cells forming the scleractinian aboral ectoderm (or calicoblastic layer) or the outer epithelium of the molluscan mantle are, respectively, responsible for the deposition of skeletons or shells, respectively (Saleuddin, 1977; Johnston, 1980; Jolly et al., 2004). In octocorals, sclerites are produced by calcifying cells called scleroblasts. These cells likely originate in the ectodermal layer (Hickson, 1895; Woodland, 1905; Bayer and Owre, 1967; Watabe and Kingsley, 1992) and from there migrate into the mesoglea. Scleroblasts can exhibit varying morphological states, which appear to be correlated with different developmental stages of sclerite formation (Watabe and Kingsley, 1992). Based on histological and electron microscopy observations, a two step growth model for sclerite development has been proposed, involving an intracellular and a possible extracellular formation phase (see Watabe and Kingsley, 1992, for a review). Several authors provided a description of scleroblasts associated with different maturation stages in different octocorals, for example *Leptogorgia virgulata* (Kingsley and Watabe, 1982), *Sinularia* (Jeng et al., 2011), pennatulaceans (Dunkelberger and Watabe, 1974), and the precious coral *C. rubrum* (Grillo et al., 1993). An entirely intracellular growth model was initially proposed for the sea pen *Renilla reniformis* (Dunkelberger and Watabe, 1974), but later observations revealed the presence of an additional extracellular growth phase also in this octocoral species (Watabe, 1981).

TABLE 1 | Number of octocoral genomes and transcriptome publicly available.

Taxon	Genome	Transcriptome	Species in McFadden et al. (2006)
Alcyoniina	2	3	37
Calcaxonia			12
Helioporacea		1	1
Holaxonia	1	8	29
Pennatulacea	1	2	10
Scleraxonia		2	7
Stolonifera		3	7

Number indicates number of species with at least one transcriptome and/or genome sequenced. Numbers are compared to taxon sampling in McFadden et al. (2006). Numbers based on NCBI Sequence Read Archive (SRA), NCBI Transcriptome Shotgun Assembly (TSA) Database and the Cnidarian Blast Database available at http://data.centrescientifique.mc (Karako-Lampert et al., 2014). Assignment of species to subordinal groups based on the World Register of Marine Species. All databases last accessed on 21.08.2020.

Sclerite deposition appears to initially occur within a series of vacuoles present in the cytoplasm of scleroblasts (Watabe and Kingsley, 1992). Secretion of an organic matrix (discussed in the following section) into these vacuoles precedes mineral deposition and continues throughout sclerite formation (Kingsley and Watabe, 1982). The function of these organic matrices apparently is to provide a scaffold for mineral deposition (Lowenstam and Weiner, 1989). During the *intracellular* phase, scleroblasts are characterized by a prominent nucleus and their cytoplasm is rich in vesicles and mitochondria (Kingsley and Watabe, 1982; Grillo et al., 1993; **Figure 4.1a**). At this stage, scleroblasts are not solitary in the mesoglea but they instead form cell aggregates (Grillo et al., 1993). As sclerites grow, vacuoles occupy an increasingly larger space within the scleroblast, while the nucleus and cytoplasm are now restricted to the periphery of the cell (Watabe and Kingsley, 1992; **Figure 4.1b**). These changes are followed by the extrusion of the sclerite into the mesoglea (**Figure 4.1c**). A detailed description of the transition between the intracellular and extracellular phase has been provided for *L. virgulata* by Kinglsey and Watanabe (1982). These authors have shown that the extrusion of sclerites involves the fusion of the cell plasma membrane with the vacuole containing the sclerite. The maturation stage at which the sclerites become extracellular appears to vary between species. In *L. virgulata*, for example, the emergence of sclerites from the scleroblasts occurs at a late growth stage, and sclerites already exhibit their characteristic wart-like branching structures (Kingsley et al., 1987). In the gorgonian *Pseudoplexaura flagellosa,* on the other hand, crystals are extruded and they eventually aggregate into sclerites extracellularly (Goldberg and Benayahu, 1987). Once extracellular, sclerites can be enveloped by different scleroblasts, which are in contact by means of pseudopod-like extensions (Grillo et al., 1993). In *C. rubrum* for instance, two scleroblasts joined by septate junctions surround growing sclerites in the mesoglea (Le Goff et al., 2017; **Figure 4.2**). One or more scleroblasts associated with

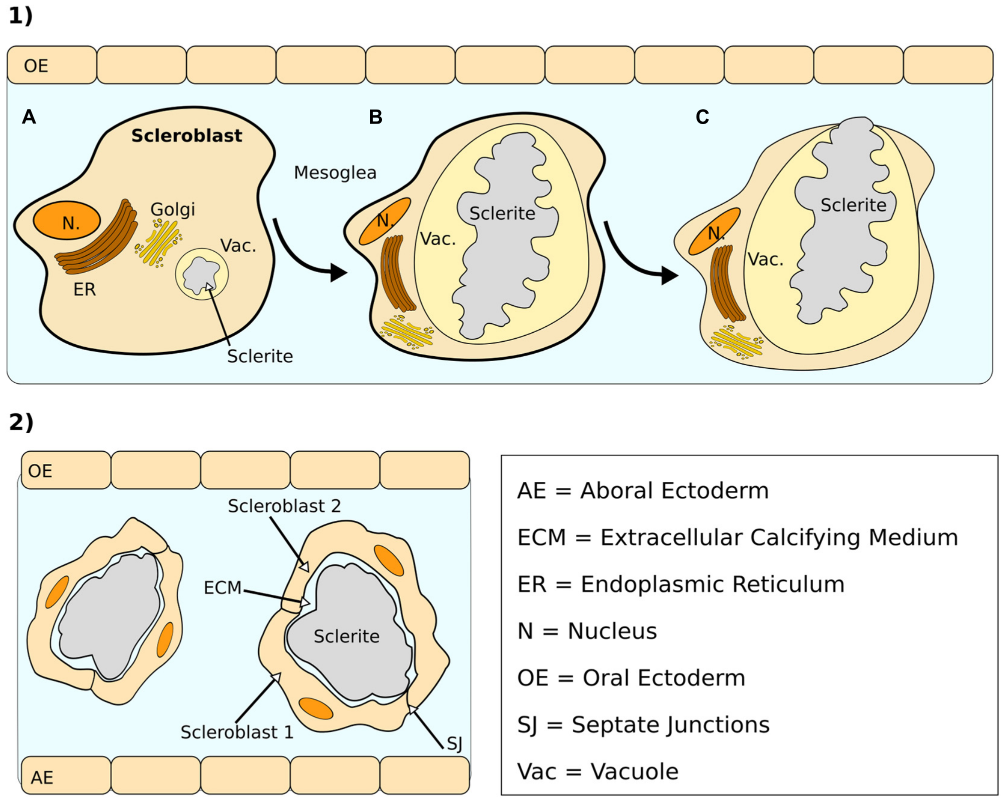

FIGURE 4 | (1) Different sclerite growth phases in *Leptogorgia virgulata*: (a) early intracellular deposition in a vacuole, (b) latest stage of intracellular deposition, and (c) transition between intracellular and extracellular stage by expulsion from vacuole/cell into the mesogloea. During the latter, vacuole and cell membrane fuse together and the sclerite is extruded from the scleroblasts (based on Watabe and Kingsley, 1992). **(2)** Extracellular growth of a sclerite in *Corallium rubrum*. Two scleroblasts—connected by septate junctions (SJ) envelop a single sclerite, surrounded by an extracellular calcifying medium (based on Le Goff et al., 2017).

single sclerites have also been observed in *Swiftia exserta* (Menzel et al., 2015).

In *Sinularia* species, an additional cementation phase takes place at the base of the colony, where mature sclerites are fused together by amorphous calcium carbonate (Jeng et al., 2011). Sclerite fusion is also observed among different stoloniferous octocoral species (Lau and Reimer, 2019a).

Less is known about the cells responsible for the growth of axial skeletons. A description of the epithelial cells responsible for the axis annular growth in *C. rubrum* has, however, been provided by Grillo et al. (1993). These authors did not report any observable differences between the cells enveloping the axial skeleton and the scleroblasts found in the mesoglea. Based on this, they proposed that these cells constitute actual scleroblasts and that sclerite-forming cells might be the result of calcifying epithelium fragmentation.

Information about calcifying cells in aragonite-forming octocorals is extremely limited but the presence of a calcifying epithelium in *H. coerulea* was already reported in an early observation (Moseley, 1876). Calcifying cells in *H. coerulea* were originally defined as "mesodermic" (Moseley, 1876), but were later described as of ectodermal origin (Bourne and Lankester, 1895). The latter authors also reported an increase in size and granule content during the diversification of calcifying (calicoblastic) cells from epithelial cells. The calcifying epithelium of *H. coerulea* was later further characterized by Le Tissier (1991), who noted the presence of vesicles in the cytoplasm of calicoblastic cells found in areas of active skeleton deposition. However, whether these cells can be classified as "scleroblasts" (homologous to those characterizing calcitic species) is not currently known. In fact, although it appears that both aragonite and calcite skeletons in Octocorallia are deposited by specialized ectodermal calcifying cells, possible differences in cytological characteristics and gene expression patterns between "calcite-forming scleroblasts" and aragonite-forming cells have not been investigated.

Biological Control I: Skeleton Organic Matrix

Octocoral sclerites and skeletons are biocomposite materials formed by a mineral ($CaCO_3$) and an organic fraction. The latter is also referred to as the *skeleton organic matrix* (SkOM). In scleractinian corals, SkOM quantities can range between 0.3 and 2% of the total dried skeleton weight (Constantz and Weiner, 1988; Allemand et al., 1994; Cuif et al., 2004; Goffredo et al., 2011; Ramos-Silva et al., 2013). Higher amounts have been reported in Octocorallia. In gorgonians, the SkOM represents between 1 and 5% of the skeleton weight (Silberberg et al., 1972; Kingsley and Watabe, 1983). However, a sensibly lower value (ca. 0.04%) was later obtained for the octocoral *Sinularia* sp. (Rahman et al., 2013). Precisely quantifying organic materials occluded within coral skeletal structures is, however, a challenging task. Following skeleton/sclerites decalcification, SkOM isolation requires a series of washing steps that can contribute to loss of low-molecular weight components from the sample, which in turn can lead to underestimations of SkOM amounts (Puverel et al., 2007; Allemand et al., 2011). Compositionally, the SkOM consists of a diverse mixture of different macromolecules. Major components of both octocoral and scleractinian matrices include proteins (Fukuda et al., 2003; Ramos-Silva et al., 2013), both mono- and polysaccharides (Goldberg, 2001; Naggi et al., 2018; Takeuchi et al., 2018) and lipids (Farre et al., 2010; Reggi et al., 2016). In the gorgonian *Eugorgia ampla*, lipids can represent ca. 60% of the SkOM and are followed in abundance by proteins (Fox et al., 1969). In *Corallium* species, for example, proteins constitute ca. 0.01% of the total skeleton weight (Debreuil et al., 2011). Among carbohydrates, glucose, galactose, galactosamine, and mannose were the most represented in the sclerites of *Pseudoplexaura* (Goldberg, 1988). Additional studies have also focused on the pigments responsible for the coloration of skeletal elements in gorgonians (carotenoids) (Leverette et al., 2008), *H. coerulea* (biliverdin IXa) (Rüdiger et al., 1968; Hongo et al., 2017) and precious corals (canthaxanthin) (Merlin and Delé-Dubois, 1986; Cvejic et al., 2007; Bracco et al., 2016).

One property of the octocoral SOM, shared by many different calcifying organisms (Puverel et al., 2005; Marin and Luquet, 2007; Mann et al., 2010), is the abundance of proteins highly enriched in acidic (isoelectric point < 4.5) amino acids, primarily aspartic acid (Watabe and Kingsley, 1992; Rahman and Oomori, 2009). One possible biological reason being the proposed interaction of carboxylic groups, found in the side chain of aspartic acid, interacting with calcium ions (Weiner and Hood, 1975). The mechanisms underlying SkOM regulation over coral calcification remain, however, elusive, and no functional information is currently available. The first octocoral skeletal protein to be characterized was extracted from the sclerites of *C. rubrum*, and named scleritin (Debreuil et al., 2012). This occurred almost a decade after the isolation of the first skeletal protein (galaxin) from a scleractinian skeleton (Fukuda et al., 2003). Scleritin does not possess any known protein domain and appears solely expressed by scleroblasts found in the mesoglea, but not by the cells in calcifying epithelium forming the axial skeleton (Debreuil et al., 2012). As previously mentioned, the latter have been classified as composed of scleroblasts, due to the absence of morphological differences with the mesogleal sclerite-producing cells (Grillo et al., 1993). However, the expression pattern of scleritin suggests that cells involved in these two calcification processes (i.e., sclerite formation and axial skeleton deposition) employ different proteins and are thus characterized by different gene expression profiles. Another extracellular protein (ECMP-67), with the ability to regulate $CaCO_3$ polymorphism *in vitro,* was also isolated from the sclerites of *Lobophytum crassum* (Rahman et al., 2011).

Over the years, different coral SkOM components - including proteins, polysaccharides and lipids—have been in fact shown to promote the formation of different calcium carbonate polymorphs *in vitro* (Rahman and Oomori, 2009; Reggi et al., 2016; Naggi et al., 2018; Laipnik et al., 2019). However, whether these molecules possess the same properties *in vivo* remains to be determined. More recently, the advent of mass spectroscopy coupled with transcriptomics has enabled researchers to shift from the analysis of single proteins to the characterization of whole skeletal proteomes. This allowed to describe the "skeletogenic proteins" (Jackson et al., 2007), "skeletome" (Ramos-Silva et al., 2013) or "biomineralization toolkits" (Drake et al., 2013) in different calcifying organisms. This approach was recently applied to obtain the first proteomes found in octocoral skeletons and sclerites and provide a comparative analysis of octocorals producing aragonite (*H. coerulea*) and calcite (*Tubipora musica* and *S.* cf. *cruciata*) (Conci et al., 2020). An extremely low overlap was reported between aragonite and calcite-producing species, pointing to different protein repertoires being used by species forming different polymorphs. The only instance of a shared protein was a carbonic anhydrase homolog to CruCA-4. This protein was originally described, alongside other five carbonic anhydrases, in *C. rubrum* and found overexpressed in tissues enriched in calcifying cells (Le Goff et al., 2016). Carbonic anhydrases (CAs) are a superfamily of enzymes responsible for catalyzing the interconversion between carbon dioxide (CO_2) and bicarbonate ($HCO_3{}^-$) (Supuran, 2008), and are commonly found in different animal skeletons, including scleractinian corals (Miyamoto et al., 1996; Mann et al., 2008; Ramos-Silva et al., 2013; Mann, 2015). In anthozoan corals, CAs can regulate the concentration of $HCO_3{}^-$ in calcification spaces (see Bertucci et al., 2013 for a review). Scleritin was identified in the organic matrix of both *T. musica* and *S.* cf. *cruciata*, but not in the aragonitic *H. coerulea (Conci et al., 2020)*, consistent with the hypothesis of its involvement in sclerite formation. Nonetheless, despite not being secreted into the skeleton, scleritin homologs are actively being expressed in *H. coerulea* (Conci et al., 2019). This could point on one hand to *H. coerulea* scleritin playing a different role (not requiring secretion into the skeleton) in calcification. Alternatively, the protein could hold an unrelated function and could have been recruited for biomineralization by octocorals producing calcite sclerites. In this light, comparison of the characteristics and function of calcification-related proteins in both aragonite and calcite-forming octocorals could highlight differences between groups and detect co-option events of proteins for biomineralization.

Biological Control II: Ion Transport and Regulation

For $CaCO_3$ precipitation to occur, different physio-chemical conditions have to be reached within the calcification spaces. One critical parameter is the saturation state (Ω) of the solution with respect to a certain $CaCO_3$ polymorph ($\Omega_{\text{Aragonite}}$ or Ω_{Calcite}). This value is calculated as the ratio of Ca^{2+} and $CO_3{}^{2-}$ ion activity products to the stoichiometric solubility product of aragonite or calcite (Morse and Mackenzie, 1990). At Ω = 1 solid mineral and seawater are in equilibrium, while at $\Omega > 1$ and $\Omega < 1$ precipitation and dissolution, respectively, occur. The saturation state is also intimately linked to the pH of the solution as this can influence the availability of $CO_3{}^{2-}$ ions. It has been suggested that corals might be able to modulate the composition of their calcifying fluids, with respect to seawater, to promote $CaCO_3$ precipitation and enhance calcification. In scleractinian corals for example, Ω_{Ar} of calcifying fluids can be on average around 12 (DeCarlo et al., 2017) and display diurnal cyclic variability (DeCarlo et al., 2019). This value is sensibly higher compared to seawater in reef environments (Ω_{Ar} ca. 3) (Mongin et al., 2016).

Several chemical parameters of the calcifying fluids have been studied in scleractinian corals (Cai et al., 2016; Comeau et al., 2017; Sevilgen et al., 2019), while information on octocorals is very limited. This is partly due to the presence of additional tissue layers preventing direct access to the calcification space (Le Goff et al., 2017). Information on the pH of calcifying fluids (pH_{cf}) in both coral groups is however available. In scleractinian corals, pH_{cf} is higher compared to the pH_{sw}, but increases in seawater acidity appear to cause declines in the pH of calcifying fluids (Venn et al., 2013; Holcomb et al., 2014). Contrarily, early analyses in *C. rubrum* (based on boron isotopic analysis) did not detect the presence of significant pH upregulation between seawater and the pH_{cf} of the axial skeleton (McCulloch et al., 2012). This was later corroborated by pH-sensitive dye-based measurements showing that sclerites and axis growth occur at a pH of 7.97 ± 0.15 and 7.89 ± 0.09, respectively (Le Goff et al., 2017). In the same study however, pH_{cf} was found more alkaline compared to the cytoplasm of calcifying cells, which implies—as in scleractinians (Zoccola et al., 2004)—the active proton removal from calcification spaces, possibly operated by a Ca^{2+}-ATPase (Le Goff et al., 2017). Measurements for sclerites were obtained during the extracellular phase (i.e., sclerites enveloped by two scleroblasts), while no information is currently available for pH of the calcifying medium within scleroblasts vacuoles (i.e., intracellular stage).

Analysis was then conducted at normal pH_{sw} values. Whether *C. rubrum* is able to maintain pH homeostasis under seawater acidification conditions has not been determined. Differences in pH regulation between scleractinian skeletons and octocoral sclerites could be related to the different localization or composition (aragonite vs. calcite) of the skeletal structures. For example, the cells and/or mesoglea surrounding octocoral sclerites could buffer the effects of seawater chemistry. Surrounding tissues have, for instance, been proposed to act as a protective barrier against the effects of ocean acidification (OA) in octocorals (discussed in the next section; Gabay et al., 2014). However, the multi-step (intracellular and extracellular) growth model of octocoral sclerites previously described, opens to the possibility that sclerites could experience different environments—in terms of calcifying fluids chemistry and their interaction with seawater—during their formation.

Ocean acidification also appears to impact $CaCO_3$ polymorphs differently, with calcite being apparently less affected (although depending on magnesium content) (Ries et al., 2009). A possible approach to further elucidate pH_{cf} regulation mechanisms in octocorals could be the characterization of calcifying fluids pH in *H. coerulea,* for which no information is currently available. Such analysis could determine, on one hand, whether the absence of pH_{cf} regulation is indeed a common trait among Octocorallia, independently of the characteristics of the mineral structures (calcite sclerites/axis vs. aragonite skeleton). Alternatively, aragonitic octocorals could exhibit pH_{cf} increases as observed in scleractinian, pointing to pH upregulation representing a required feature for aragonite deposition in both coral groups.

Within the calcification space, calcium concentration in scleractinians is not necessarily higher compared to seawater, but some species can modulate calcium levels in response to decreases in seawater pH (DeCarlo et al., 2018). For octocorals, to the best of our knowledge, no information has been obtained. Calcium transport to calcification sites has been studied in *Leptogorgia virgulata* and a general model of calcium transfer has nonetheless been provided by Watabe and Kingsley (1992). Transport of Ca^{2+} during the intracellular growth of sclerites in octocorals represents a multi-step process (**Figure 5**). To reach the calcification space, calcium first diffuses from seawater into the outer epithelial cells and is actively extruded into the mesoglea. Studies involving specific transporters inhibitors have highlighted the action of Ca^{2+}-ATPases during this step, while Na^{+}-K^{+} exchangers don't appear to be involved (Kingsley and Watabe, 1984). Once in the mesoglea, the majority of calcium ions reach the axis epithelium and are incorporated into the axial skeleton, while others diffuse into the scleroblasts. Inside calcifying cells, calcium is transported inside electron-dense bodies (Kingsley and Watabe, 1985) to the calcifying vacuoles where sclerites form (Kingsley and Watabe, 1982). Both the membrane of scleroblasts and calcium-transporting vesicles exhibit signs of Ca^{2+}-ATPases activity (Kingsley and Watabe, 1984).

The origin and transport of carbon (CO_2 and $HCO_3{}^{-}$) has also been investigated in *L. virgulata* (Lucas and Knapp, 1997). In this species, carbonic anhydrase represented the major carbon source followed by bicarbonate. Inhibition of carbonic anhydrases caused significant declines in incorporation rates of both dissolved and metabolically produced CO_2, pointing to an important role of these enzymes in the regulation of carbon availability. Carbonic anhydrases, for example, have been proposed to operate on the membrane of calcifying vacuoles and electron-dense bodies (Kingsley and Watabe, 1987; Lucas and Knapp, 1996) and the aforementioned presence of CruCA-4 homologs inside octocoral skeletons confirms the presence of these enzymes within the calcifying medium (Conci et al., 2020).

ANTHROPOGENIC THREATS TO OCTOCORAL BIOMINERALIZATION

The effects of anthropic stressors on the ability of marine organisms to calcify have been the topic of a number of studies. In corals, for example, changes in calcification rates and growth have been studied in relation to different stressors, such as seawater temperature (Howe and Marshall, 2002;

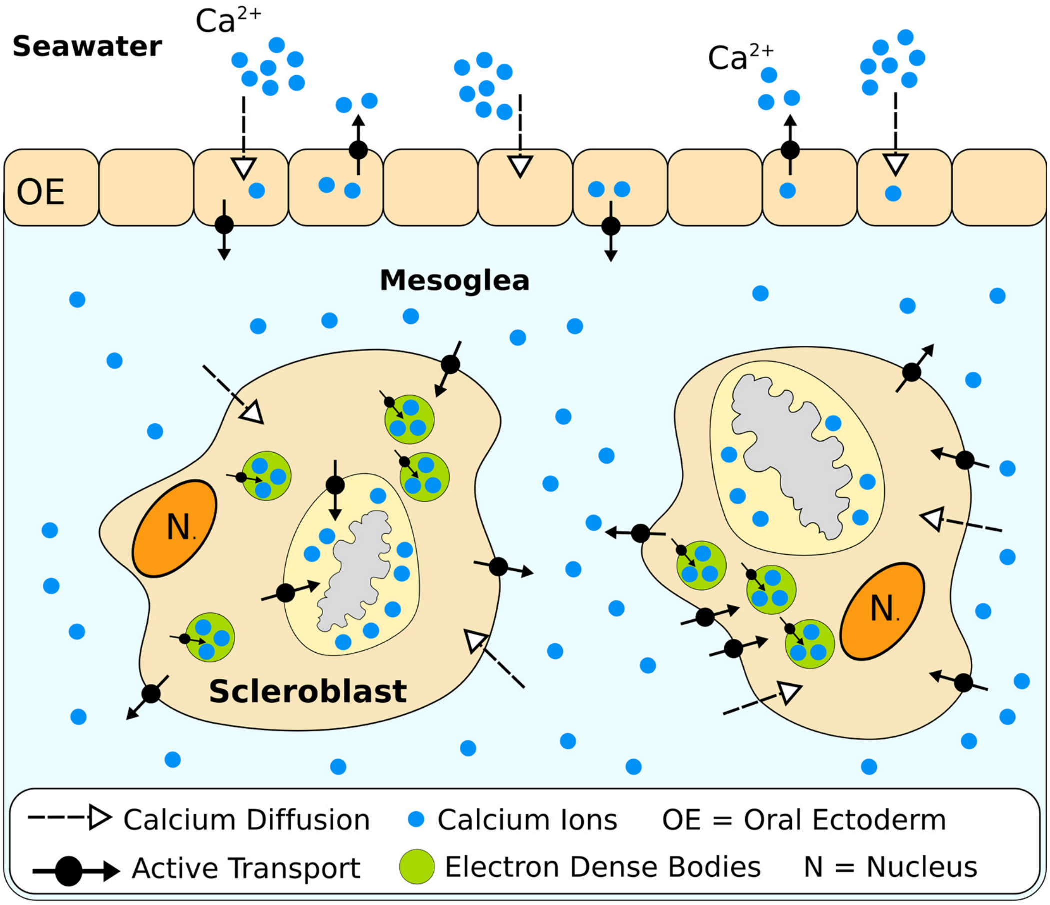

FIGURE 5 | Proposed model of calcium transport from seawater to growing sclerites in *Leptogorgia virgulata* (based on Watabe and Kingsley, 1992).

Marshall and Clode, 2004), pollution (Spencer Davies, 1990; Biscéré et al., 2015) and turbidity (Kendall et al., 1985; Browne, 2012).

However, particular focus has been dedicated to study the effects of the so-called "ocean acidification" (OA), i.e., the decrease in sea surface water pH caused by the increase in the atmospheric carbon dioxide (CO_2) concentration (Hoegh-Guldberg et al., 2007; Solomon et al., 2007). Ocean acidification linked detrimental effects on biomineralization have been reported for multiple marine groups including calcifying algae (Kuffner et al., 2008), scleractinian corals (Marubini et al., 2003; Hoegh-Guldberg et al., 2007; Mollica et al., 2018) and molluscs (Comeau et al., 2009; Gazeau et al., 2013). Research has however also highlighted several instances of resilience to ocean acidification, highlighting species-specific responses to low pH (Cross et al., 2015a,b; González-Pech et al., 2017; Lenz and Edmunds, 2017).

Octocorals appear to exhibit varying responses to ocean acidification. An inverse correlation between calcification rates and $p\mathrm{CO}_2$ have been reported for *Eunicea flexuosa* when exposed to a pH range of 8.1 and 7.1 (Gómez et al., 2015). Contrarily, in another study no changes in branch extension and sclerite structure could be observed in the same species at pH 7.75 compared to control values (pH 8.1) (Enochs et al., 2016). Lower pH (7.6 and 7.3) had no effects on polyp weight and protein content in different octocorals nor in chlorophyll abundance ordensity of its symbiotic algae (Gabay et al., 2013). One possible explanation behind octocoral resilience could be the location inside the mesoglea of their sclerites with the surrounding tissues acting as a protective barrier (Gabay et al., 2014). A similar scenario has also been proposed for the organic layers protecting mollusc shells against dissolution (Rodolfo-Metalpa et al., 2011). From an ecological perspective, different tolerance to changing environmental conditions is of importance as it can determine which species will thrive or decline under future conditions, and cause profound changes in marine communities composition (Fabricius et al., 2011). And shifts from stony (more vulnerable) to soft coral (more resistant)-dominated environments have already been observed (Inoue et al., 2013).

DISCUSSION

Octocorals (Cnidaria: Anthozoa) represent a group of benthic marine organisms that have evolved a wide variety of biomineralization strategies. The composite biomaterials produced by these organisms include structures composed of different calcium carbonate ($CaCO_3$) polymorphs (aragonite and calcite). From an evolutionary perspective, the presence of aragonite skeletons in Octocorallia is puzzling as it is observed in an extremely low number of species in a single clade, the Helioporacea. Apparently, this occurrence represents one of the very few instances of aragonite formation originating during a Calcite Sea interval (Porter, 2010). Despite the diversity of their skeletal elements, octocorals have only been marginally studied for biomineralization research. This has been partially caused by their low contribution to $CaCO_3$ production and reef formation (Smith and Kinsey, 1976; Herrán et al., 2017; Edinger et al., 2019) compared to scleractinian corals, the other group of calcifying anthozoans and main reef builders in today's oceans. Additionally, octocoral species often inhabit deeper marine habitats compared to scleractinians (Roberts et al., 2009), which can hinder field observation and the collection of specimens for follow-up studies. With the aim to identify current knowledge gaps and propose possible future research approaches, here we reviewed the research status of octocoral biomineralization. We focused and compared what is known about the evolutionary, cellular and molecular processes underlying different octocoral skeletons, with a focus on $CaCO_3$ polymorph (i.e., aragonite and calcite) diversity.

Although differences in research output between scleractinian and octocoral calcification are often mentioned, we highlighted how differences—both in terms of data availability and scientific knowledge—exist with respect to the process of biomineralization between different octocoral groups. Several mechanisms and features of octocoral biomineralization, such as the characteristics of the calcifying cells (e.g., scleroblasts) or Ca^{2+} transport, have mostly been investigated in species depositing calcite. Although calcite represents by far the most commonly deposited polymorph in octocorals, studying aragonite formation provides the opportunity to further our understanding on multiple aspects of the origin and evolution of octocoral and scleractinian biomineralization. Firstly, differences between aragonite and calcite formation are not necessarily limited to skeleton polymorphism. In fact, calcite and aragonite-forming species also differ in terms of other calcification-related properties, such as the composition of the organic matrix proteome (Conci et al., 2020) and possibly the type and characteristics of calcifying cells and epithelia. With the exception of early descriptions from the late nineteenth century (e.g., Bourne and Lankester (1895), no study has in fact focused on the calcifying cells of aragonitic octocorals. In addition, the different localization of calcitic and aragonitic structures (i.e., surrounded by tissue or not) could also entail the different regulation of the chemistry and pH of the calcification fluids, as observed between scleractinians (Venn et al., 2013; Holcomb et al., 2014) and *Corallium rubrum* (Le Goff et al., 2017). In fact, the scleractinian-like characteristics of helioporacean skeletons (i.e., aragonite exoskeleton), provide the unique opportunity to compare aragonite formation between Octocorallia and Scleractinia, and in turn determine which biomineralization features are driven by phylogeny (i.e., properties shared by octocorals producing different polymorphs) and which are instead related to the characteristics of the skeleton (i.e., properties shared by aragonitic octocorals and scleractinians). So far, this research avenue has not been fully explored, but at present the data at hand suggest that the aragonitic *Heliopora coerulea* employs a different biomineralization strategy compared to both calcitic octocorals and scleractinians. The only aspect for which information is currently available for all three groups concerns the composition of the skeleton proteomes. Their analyses have shown that very few proteins found in the skeleton of *Heliopora coerulea* are also found in other calcifying corals, irrespective of whether those are of calcite or aragonite (Ramos-Silva et al., 2013; Conci et al., 2020).

Difference in research focus and information availability are not limited to calcite vs. aragonite species, but can also be observed within the former. The majority of information for calcite-forming octocorals has been obtained from a small set of species, including the gorgonian *Leptogorgia virgulata* and the precious coral *Corallium rubrum*. This includes (1) the current knowledge on ion sources and transport needed for calcification, (2) detailed description of scleroblasts, and (3) both mechanisms of intracellular and extracellular formation of sclerites. Although extremely informative, a research approach focusing on very few "model species" may lead to an underestimation of the diversity of biomineralization strategies exhibited by different octocoral groups. The possible presence of substantial differences in sclerites and/or skeleton formation that can also occur even within a single genus (e.g., *Corallium*) (Lawniczak, 1987), requires extensive comparative analyses instead.

In the light of this, a possible step could be to taxonomically widen the generation of—*omic* resources, optimized to encompass a broad diversity of octocoral skeletal structures. The simultaneous presence, within Octocorallia, of calcite, aragonite and aragonite + calcite skeletons represents an ideal scenario to compare gene repertories across species producing different polymorphs, and compare those with scleractinian corals. Moreover, in addition to the aforementioned need for DNA sequencing data from the Calcaxonia, sequencing projects for skeleton-lacking octocorals (e.g., genus *Phenganax*) (Alderslade and Mcfadden, 2011) would also be beneficial, as they would allow to detect differences in the molecular mechanisms of biomineralization between calcifying and non-calcifying octocorals. The increase in the availability of octocoral genomes and transcriptomes would then in turn allow to progressively conduct more taxonomically comprehensive phylogenetic analysis, and resolve deep evolutionary relationships between clades, and ultimately how biomineralization in Octocorallia evolved.

AUTHOR CONTRIBUTIONS

NC wrote the manuscript. SV and GW edited the manuscript. All authors contributed to the discussion.

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