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RESEARCH ARTICLE

An updated classification of growth forms in non-geniculate coralline algae (Corallinophycidae, Rhodophyta)

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Abstract

The current challenge of defining growth forms in the non-geniculate coralline red algae was addressed. Since the 19th century, those who have worked on this large and globally distributed group of algae have tried to summarize and systematically describe their growth forms. This effort resulted in a plethora of terms, which could sometimes be confusing, overlapping, and difficult to apply in the field. We reviewed the past literature to provide a coherent key to the non-geniculate coralline growth forms, incorporating the latest observations. Our revision expands the 10 currently recognized growth forms (*unconsolidated*, *encrusting*, *warty*, *lumpy*, *fruticose*, *discoid*, *layered*, *foliose*, *ribbon-like*, and *arborescent*) by redefining some of them, by reintroducing the *columnar* growth form, and by adding two new growth forms—*convoluted*

Abbreviation: CCA, crustose coralline algae

and *imbricate*—to include recently documented specimens. This updated and refined tool better encompasses the diverse external morphologies of non-geniculate corallines. The goal was to facilitate taxonomic descriptions and to support ecological studies of non-geniculate corallines given the extreme difficulty of identifying species using only external characters.

KEYWORDS
CCA (crustose coralline algae), descriptive keys, encrusting coralline algae, maërl, morphological diversity, rhodolith

INTRODUCTION

Coralline red algae (orders Corallinales, Corallinapetrales, Hapalidiales, Sporolithales; subclass Corallinophycidae, Rhodophyta) are ubiquitous in the photic zone of benthic marine habitats worldwide. They are often the dominant benthic cover (e.g., Lemoine, 1913; Norris & Lebednik, 1970), especially under highly disturbed conditions associated with extreme wave exposure (e.g., Adey, 1978; Gherardi & Bosence, 1999) and intense grazing pressure (e.g., Hind et al., 2019; Moosa et al., 2025; Steneck & Dethier, 1994; Steneck & Paine, 1986), largely due to their cell walls being impregnated with calcium carbonate polymorphs mainly in the form of high-magnesium (high-Mg) calcite (Lebrato et al., 2016; Nash et al., 2019). For convenience, two groups of corallines have traditionally been identified based on external appearances: the geniculate or articulated corallines and the non-geniculate or non-articulated corallines. That there is no phylogenetic basis for this distinction was recognized by Cabioch (1972, 1988) based on morpho-anatomy and later supported by DNA sequencing (e.g., Bailey & Chapman, 1998; Hind et al., 2016, 2018). The ancestral condition was likely non-geniculate based on the fossil record. Phylogenetic analyses showed that the evolution of genicula occurred independently multiple times (e.g., Aguirre et al., 2010; Bailey & Chapman, 1998; Bittner et al., 2011; Kato et al., 2011), and the loss of genicula back to the ancestral (non-geniculate) condition occurred at least three times independently in the subfamily Corallinoideae (e.g., Hind et al., 2016, 2018; Hind & Saunders, 2013). Non-geniculate corallines are often referred to as crustose coralline algae (CCA sensu Adey & Macintyre, 1973) or encrusting coralline algae (e.g., Steneck & Paine, 1986), especially in ecological studies. Geniculate corallines have erect, flexible uprights arising from an encrusting base or rhizome-like holdfasts (Johansen, 1981, p. 2). Their upright axes are flexible due to having uncalcified nodes called genicula (singular = geniculum) that separate larger calcified internodes or intergenicula (singular = intergeniculum). In contrast, non-geniculate corallines are completely calcified, lacking any uncalcified nodes. Both groups may occur attached to a substrate (epigenous) or may be unattached (i.e., free-living). Most recently, Jardim et al. (2025) proposed the term *encrusting nongeniculate coralline algae* for all attached non-geniculate corallines. Free-living geniculate corallines have been referred to as articuliths (Tâmega et al., 2017, 2021). Free-living non-geniculate corallines have variously been called maërl/maerl (e.g., Bosence, 1976; Cabioch, 1969; Crouan & Crouan, 1867), rhodoliths (e.g., Barnes et al., 1970; Bosence, 1983; Toomey, 1975), rhodolites (Bosellini & Ginsburg, 1971), and marl (e.g., Johansen, 1981; see Aguirre et al., 2017; Riosmena-Rodríguez, 2017, p. 9; and Teichert, 2024 for a non-exhaustive list of terms and definitions that have been used for free-living non-geniculate corallines). Of these latter terms, "rhodolith" (meaning rhodophycean or red stone) has received the greatest acceptance (Adey & Macintyre, 1973) and is now more widely used (Rendina et al., 2022) than the others. Maërl/rhodoliths usually occur when protuberances, margins, or other portions of attached and unattached individuals break off and continue to grow as free-living individuals. Maërl/rhodoliths are more polymorphic than articuliths, ranging from entirely solid (non-nucleated) free-living nodules or fragments, to biogenic gravels composed of either a single species (monospecific) or several species (multispecific) that grow concentrically around an inorganic or organic core (nucleated, e.g., a sand grain, small stone, shell, or other calcareous algae; Bosence, 1976, 1983; McCoy & Kamenos, 2015; Tâmega et al., 2024, Teichert, 2024).

In addition to being attached and/or free-living, non-geniculate corallines occur in an astonishing variety of growth forms (i.e., have varying external appearances). In the older literature (e.g., Foslie, 1895, 1900; Heydrich, 1897; Lemoine, 1910, 1913), differences in growth forms were often used for species delimitation, initially accomplished by adding form names after the specific epithet, for example, *Lithothamnion lichenoides* f. *patena* (Foslie, 1898, p. 7, 1900, p. 12). Although growth forms are possibly genetically fixed in some species (e.g., *Porolithon craspedium*; see Jeong et al., 2023), they are often environmentally mediated in other species, due to grazing pressure (e.g., Littler & Littler, 2000, 2003, 2013; Maneveldt & Keats, 2008; Steneck & Adey, 1976) and hydrodynamic conditions (e.g., Aguirre et al., 2017; Carro et al., 2014; Jardim et al., 2022), for example. Nonetheless, growth forms of non-geniculate coralline species continue to be useful for local taxonomic delimitations and species keys, especially when the local ecology and morphological variation are known through DNA sequencing. To overcome the challenge of inconsistencies in the terms used to describe the range of growth forms exhibited by attached and free-living (rhodoliths) non-geniculate corallines, Woelkerling et al. (1993) undertook a comprehensive analysis of all growth form terminologies used at the time. Bosellini and Ginsburg (1971), however, formulated a rudimentary morphological classification system, but this was only for rhodoliths. Bosence (1976, 1983) subsequently formulated a more detailed morphological classification system, but this, too, was only for rhodoliths. Woelkerling et al. (1993) formulated a morphological classification system that included attached and free-living non-geniculate corallines, demonstrating that over 100 different terms had been used to describe the various growth forms but that these could be narrowed to 10 broad growth forms (= focal points, sensu Woelkerling et al., 1993), namely: *unconsolidated*, *encrusting*, *warty*, *lumpy*, *fruticose*, *discoid*, *layered*, *foliose*, *ribbon-like*, and *arborescent*. The intention was to provide a uniform system for describing non-geniculate coralline algal growth forms to make published accounts more comparable. Even though the 10 broad growth forms described by Woelkerling et al. (1993) are still valid today, they required updating, as recent research (e.g., Jeong et al., 2023) highlighted growth forms that cannot be assigned under the Woelkerling et al. (1993) system. Recently, Jardim et al. (2025) proposed a unified terminology for best practice based on an organismal typology of six morphologies to promote a standardized reporting on ecological research and conservation management practices (see additional comments in the Discussion). The aim of this paper was to update the various growth forms and their definitions to better reflect current knowledge as a result of recent research. This paper has provided a tool for understanding and recognizing the diversity of non-geniculate coralline algal growth forms. Alongside a companion paper that addresses the geniculate coralline growth forms (Schwoerbel et al., 2026), this work is intended to facilitate taxonomic descriptions and support ecological studies, especially given the difficulty in identifying species using external characters only (see, e.g., Gabrielson et al., 2018; Puckree-Padua, Gabrielson, et al., 2020; Puckree-Padua, Haywood, et al., 2020; Puckree-Padua et al., 2021, 2022; van der Merwe et al., 2015).

MATERIALS AND METHODS

Non-geniculate corallines from our combined collections and from extensive observations from various localities across the world comprised the basis for this analysis. As in Woelkerling et al. (1993), in order to ensure complete objectivity, analyses were conducted independently of the taxonomic names attached to specimens. Growth form names were assigned based on static observations of field-collected and herbarium specimens, including type specimens, although taxon names did not influence the assigned growth form name.

To assign names to the various growth forms the following aspects were considered:

1. Pseudoparenchymatous versus free filaments

Most non-geniculate corallines have an internal anatomy that is based on the aggregation of branching filaments, each of which is formed through the divisions of its own, single, meristematic cell. This type of thallus anatomy has been referred to as pseudoparenchymatous. Some non-geniculate corallines, however, lack a fully pseudoparenchymatous anatomy and are instead composed partly or entirely of free filaments (see examples in the Discussion) that may be adherent to a certain degree.

2. Presence or absence of outgrowths, here defined as secondary growth that results in either protuberances or lamellate branches

Is a specimen smooth and largely featureless, or does it produce outgrowths?

3. Type of outgrowths

Does a specimen produce protuberances, here defined as cylindrical to compressed or more irregularly shaped outgrowths that usually have a radial internal organization, or lamellate branches, here defined as more or less flattened or curved outgrowths that usually have a dorsiventral or isobilateral internal organization?

4. Protuberance/lamellate branch length/height, diameter/width, orientation, and degree of adherence
5. Method of attachment for those non-geniculate corallines with a fan-shaped morphology

Intergrades have been defined as having an intervening growth form that cannot be placed into either of two discrete growth forms. The extent to which intergrades occur between growth forms was also determined from our combined collections and observations, as well as from those already identified by

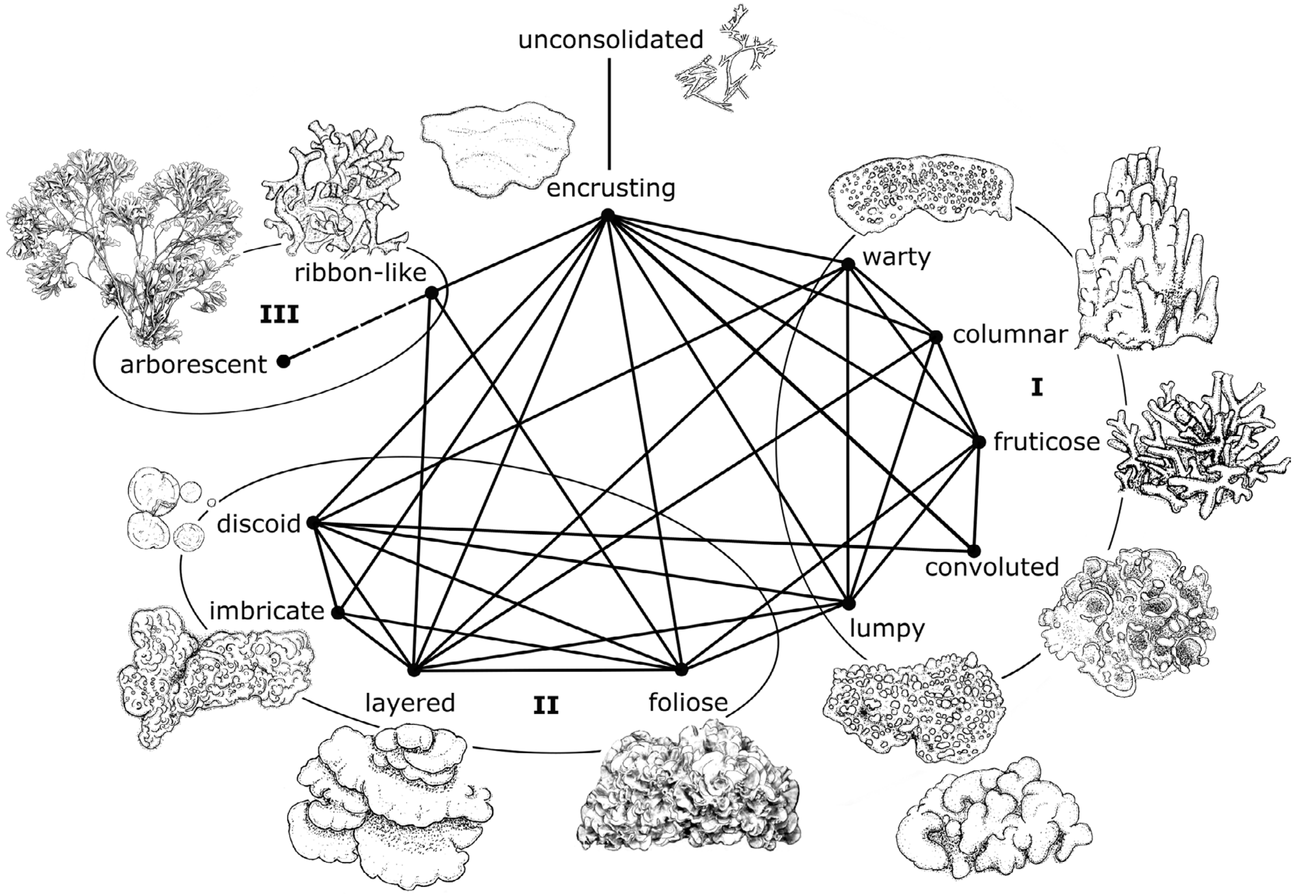

FIGURE 1 Growth forms network with diagrammatic representations (not to scale) of the various growth forms for the non-geniculate coralline algae. Lines between growth points represent known intergrades (solid lines) or closest morphological relations (dashed lines). Ellipses show protuberant (I), lamellate (II), and flabelliform (III) growth forms. Original growth forms network adapted with permission of CSIRO Publishing, from Woelkerling et al. (1993); permission conveyed through Copyright Clearance Center, Inc.

Woelkerling et al. (1993). The growth forms network subsequently produced (Figure 1) was modified from that of Woelkerling et al. (1993) and was based on our additional collective observations. The taxonomy or type status of the examined specimens had no influence on the development of the growth forms or the subsequent growth forms network. Taxon examples provided in the Discussion are of type specimens (both sequenced and not sequenced) and/or of specimens confirmed through DNA sequencing.

RESULTS

In addition to Woelkerling et al.'s (1993) 10 broad growth forms (*unconsolidated*, *encrusting*, *warty*, *lumpy*, *fruticose*, *discoid*, *layered*, *foliose*, *ribbon-like*, *arborescent*), we propose the reinclusion of a previously reported growth form, namely *columnar* (see Bosence, 1983), as well as the addition of two new growth forms, *convoluted* and *imbricate*, to include more recently documented specimens. These and the other preestablished growth forms (see Woelkerling et al., 1993) may be separated into five very broad categories: unconsolidated, encrusting, protuberant (bearing cylindrical to compressed or more irregularly shaped outgrowths that usually have a radial internal organization; sensu Woelkerling et al., 1993), lamellate (lamella-like; bearing roughly flattened or curved outgrowths that usually have a dorsiventral, sensu Woelkerling et al., 1993, or isobilateral internal organization, Table 1), and flabelliform (Figure 1, Table 2). These categories coincide with the network and ellipses of broad growth forms in Woelkerling et al. (1993, figure 1). Specific terms for these growth forms are in bold below as well as in italics throughout the text.

Unconsolidated (Figure 2)

Individuals composed partly or entirely of free filaments that may be adherent to varying degrees. This growth form is the only one in which individuals are not fully pseudoparenchymatous. It is mainly restricted to thin (unistratose to bistratose) epiphytic (Figure 2a–d), endophytic (Figure 2e,f), and parasitic

TABLE 1 Glossary of relevant terms and their definitions.

Anatomy/Anatomical	Concerned with the internal structure (of cells, filaments, etc.) and their organization/arrangement
Dorsiventral organization	Having dissimilar upper (dorsal) and lower (ventral) surfaces
Intergrade	Having an intervening growth form (external appearance) that cannot be placed into either of two discrete growth forms
Isobilateral organization	Having identical parts on each side of a central axis
Lamellate branch[a]	More or less flattened or curved outgrowth that usually has a dorsiventral or isobilateral internal organization
Morphology/ Morphological	Concerned with the overall form and external features (color, pattern, shape, size, etc.)
Outgrowth	Secondary growth that results in either protuberances or lamellate branches
Protuberance[a]	Cylindrical to flattened or more irregularly shaped outgrowth that usually has a radial internal organization
Pseudoparenchymatous	Having an internal anatomy that is based on the aggregation of branching filaments, each of which is formed through the divisions of its own, single, terminal, or intercalary meristematic cell (or subepithallial initial)
Radial organization	Diverging in lines from a common center

[a]Modified after Woelkerling et al. (1993).

species. Except for their reproductive structures and exposed filaments, endophytic filaments of *unconsolidated* individuals are uncalcified. *Unconsolidated* individuals may also exhibit, in part, the *encrusting* growth form (Figure 2a).

Encrusting (Figure 3)

Individuals are essentially smooth, lacking protuberances and lamellate branches, and largely or entirely adherent to a substrate (Figure 3a–f). Individuals sometimes appear protuberant because they are growing over an uneven surface (Figure 3d); this appearance is not, however, an inherent morphological trait. Intergrades are common between *encrusting*, *warty*, and *lumpy* growth forms (Figure S1a) but may also occur between *encrusting*, *fruticose*, *discoid*, *imbricate*, *layered*, *foliose*, *convoluted*, *columnar*, and *ribbon-like* growth forms (Figures S1e, S2a,c,e).

Protuberant

The following five growth forms are broadly categorized as protuberant. A protuberance is here defined as a cylindrical to compressed or more irregularly shaped outgrowth that usually has a radial internal organization (sensu Woelkerling et al., 1993).

Protuberant—**Warty** (Figure 4)

Individuals with protuberances that are mostly as long as they are wide, and usually less than 3 mm in length and diameter. Protuberances mostly do not abut and are unbranched (Figure 4a–f). Intergrades are common between *warty*, *lumpy*, and *fruticose* growth forms (Figure S1c), but may also occur between *warty*, *discoid*, *layered*, and *columnar* growth forms (Figure S2d,e).

Protuberant—**Lumpy** (Figure 5)

Individuals with swollen, often crowded protuberances that are usually less than 6 mm in length but more than 3 mm in diameter. Protuberances often abut and are rarely branched (Figure 5a–f). Intergrades may also occur between *lumpy*, *discoid*, *layered*, *foliose*, *fruticose*, and *columnar* growth forms (Figure S1c,d).

Protuberant—**Fruticose** (Figure 6)

Individuals with slender, terete (cylindrical) to compressed protuberances that are usually more than 6 mm in length and less than 5 mm in diameter but generally much longer than wide (Figure 6a–f). Protuberances, often branching, may be free from one another but may also fuse laterally to varying degrees. Intergrades may also occur between *fruticose*, *convoluted*, *columnar*, and *foliose* growth forms (Figure S1f).

Protuberant—**Columnar** (Figure 7)

Individuals with robust, vertically elaborate, column-like protuberances 8–200 mm in height and width, generally longer than wide, producing some of the

TABLE 2 Key references to non-geniculate coralline algal growth forms, their broader categories and their corresponding terminologies, compared with our revised system.

Harvey (1849)	Johansen (1981)	Bosence (1983) – For rhodoliths	Woelkerling and Irvine (1988)	Woelkerling and Campbell (1992)	Woelkerling et al. (1993): Broad growth form categories	Woelkerling et al. (1993): Growth forms	This study: Broad growth form categories	This study: Growth forms
–	Parasitic corallines	–	Unconsolidated	–	Unconsolidated	Unconsolidated	Unconsolidated	Unconsolidated
Flat incrustaceans	Thin crusts, Epiphytic corallines	–	Crustose	Encrusting	Encrusting	Encrusting	Encrusting	Encrusting
Stony branches	Thick crusts, Unattached corallines	Branching	Protuberant	Warty	Protuberant	Warty	Protuberant	Warty
				Lumpy		Lumpy		Lumpy
				Protuberant		Fruticose		Fruticose
		Columnar		–		–		Columnar
		–		–		–		Convoluted
Leafy lobes		Laminar		–	Lamellae/ Lamellate	Discoid	Lamellate	Discoid
	Thin crusts			–		–		Imbricate
				Layered		Layered		Layered
				Coalescent		Foliose		Foliose
–	Ribbon corallines	–	Taeniform	–	Ribbon-like (taeniform)	Ribbon-like	Flabelliform (fan-like)	Ribbon-like
–		–		–	Arborescent (tree-like)	Arborescent		Arborescent

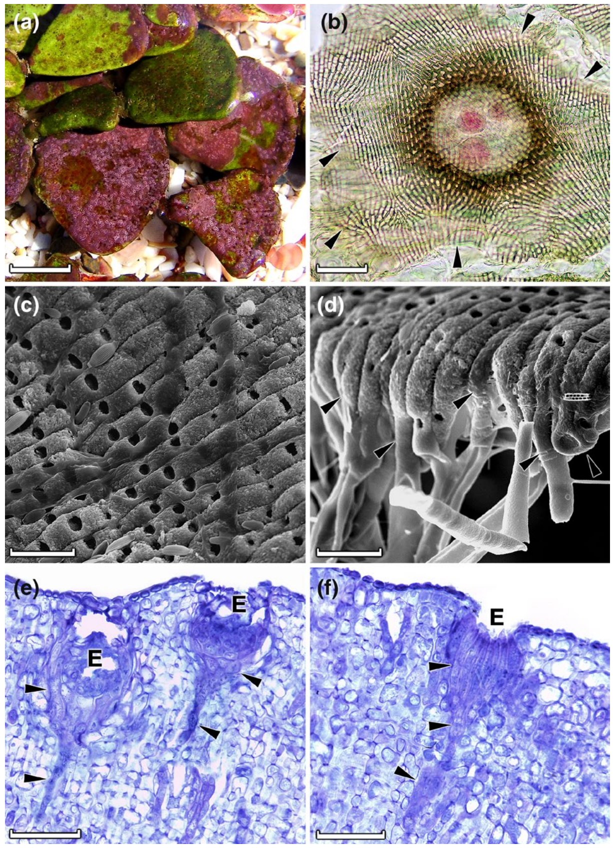

FIGURE 2 Examples of specimens/species that represent the *unconsolidated* growth form. (a) Macro view of typical specimens epiphytic on *Halimeda* sp. (b) Magnified view of several epiphytic specimens showing extensive, compact creeping filaments [arrowheads]. (c, d) Magnified SEM views of compact creeping filaments showing free ends [arrowheads]. (e, f) Vertical sections through a host alga showing endophytic [E] unconsolidated [arrowheads] thalli. Scale bars: (a) = 10 mm; (b) = 500 µm; (c, d) = 20 µm; (e, f) = 50 µm. Photographs: (a, e, f) by G.W. Maneveldt; (b–d) by I. Bárbara & V. Peña.

largest known non-geniculate individuals (Figure 7a–f). Protuberances are often clavate (club-shaped; Figure 7b,c) and form early in development. The individual is comprised largely of protuberances, sometimes with a little evidence of an *encrusting* base. Protuberances may fuse to form broader vertical expanses but generally do not branch laterally. *Columnar* individuals have, thus far, only been reported as attached to a substrate and may be highly polymorphic (Figure 7a–f). Intergrades may also occur between *columnar* and *layered* growth forms (Figure S2f).

Protuberant—**Convoluted (Figure 8)**

Individuals with robust, often flattened protuberances of varying heights and widths, arranged in a three-dimensional (3-D), branched, cavitied form in which upright lobes are produced (Figure 8a–f). The growth

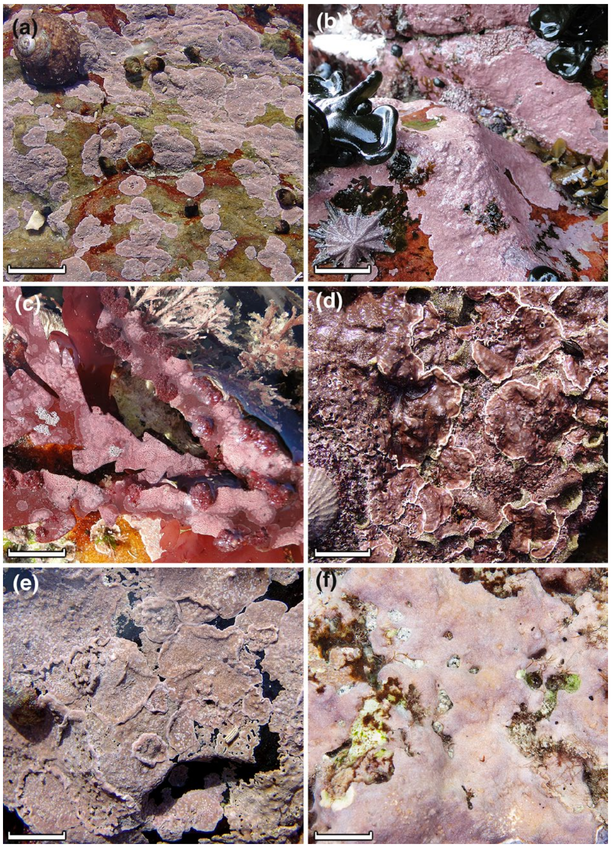

FIGURE 3 Examples of specimens/species that represent the *encrusting* growth form. (a) *Chamberlainium agulhense* from South Africa. (b) *Phymatolithopsis roseola* from South Africa. (c) Crusts epiphytic on a *Laurencia* sp. from South Africa. (d) *Phragmope* sp. from South Africa. Individuals may sometimes appear warty to lumpy, but this is often due to the substrate over which they are growing. (e) *Chamberlainium tenue* from South Africa. (f) Subtidal specimen(s) from Guam. Scale bars: (a, e) = 10 mm; (b) = 30 µm; (c) = 5 mm; (d) = 25 mm; (f) = 20 mm. Photographs: (a–e) by G.W. Maneveldt; (f) by T. Schils.

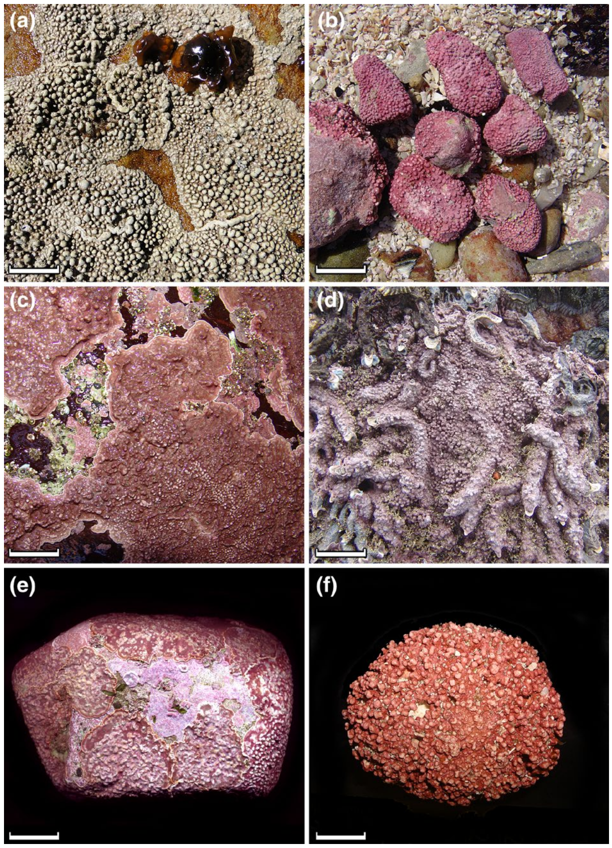

FIGURE 4 Examples of specimens/species that represent the *warty* growth form. (a) *Chamberlainium occidentale* from South Africa. (b) *Heydrichia cerasina* from South Africa. (c) An as yet unidentified Hapalidiales species from South Africa. (d) *Synarthrophyton papillatum* from South Africa. (e) *Synarthrophyton robbenense* from South Africa. (f) Subtidal rhodolith from Brazil. Scale bars: (a–d) = 10 mm; (e) = 20 mm; (f) = 15 mm. Photographs: (a–e) by G.W. Maneveldt; (f) by R. da Gama Bahia.

form is similar to the *foliose* growth form but differs in that corallines displaying the latter growth form produce outgrowths in several different planes (see below). In rhodoliths, these protuberances extend more or less radially from the core of the coralline (Figure 8e,f). This form has been reported to occur in response to grazing (e.g., Littler & Littler, 2000, 2003, 2013; Maneveldt & Keats, 2014). Intergrades are known to exist between *convoluted*, *encrusting*, *discoid*, and *fruticose* growth forms (see, e.g., Littler & Littler, 2000 p. 23; 2003, p. 19; Figures S1f, S2b).

Lamellate

The following four growth forms are broadly categorized as lamellate (lamella-like). A lamella is here defined as a more or less flattened or curved outgrowth that usually has a dorsiventral (sensu Woelkerling et al., 1993) or isobilateral internal organization. Here, we have expanded on the Woelkerling et al.'s (1993) definition of lamella to include individuals that have an isobilateral internal organization (e.g., *Tenarea tortuosa*, Woelkerling et al., 1985, p. 323, figuress 7–11).

Lamellate—**Discoid (Figure 9)**

Discoid corallines are fundamentally *encrusting*, but here individuals are each comprised of unbranched, smooth, more or less circular, thin to thick (generally > five cells) thalli of varying sizes, or secondarily (through secondary, intercalary meristematic activity) produce attached, smooth, more or less circular thalli of varying sizes (Figure 9a–f). Primary (resulting from primary, terminal meristematic activity) and secondary (resulting from secondary, intercalary meristematic activity over primary thalli) discs are held in place through cell adhesion and may be applanate (horizontally expanded and flattened) or curved to varying degrees (Figure 9c,e). *Discoid* individuals may be attached to various substrates. This growth form is reminiscent of ontogenetic

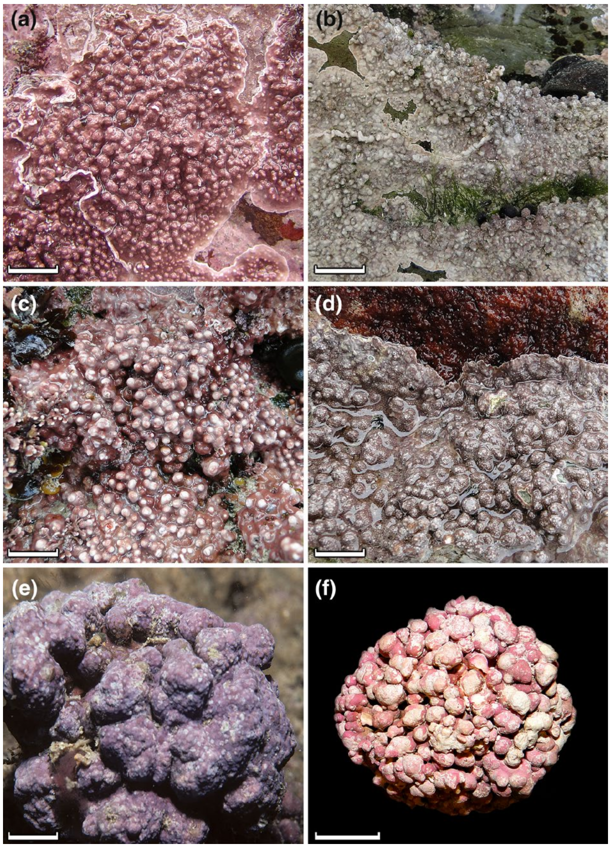

FIGURE 5 Examples of specimens/species that represent the *lumpy* growth form. (a) An as yet unidentified Hapalidiales species from South Africa. This specimen also shows intergrading with the warty growth form (bottom right). (b) *Chamberlainium glebosum* from South Africa. (c) *Roseolithon superpositum* from South Africa. (d) *Chamberlainium capense* from South Africa. (e) An as yet unidentified Corallinales species from Fiji. (f) *Sporolithon indopacificum* from Tanzania. Scale bars: (a, b) = 20 mm; (c) = 15 mm; (d, f) = 10 mm; (e) = 5 mm. Photographs: (a–d), (f) by G.W. Maneveldt; (e) by D.W. Keats.

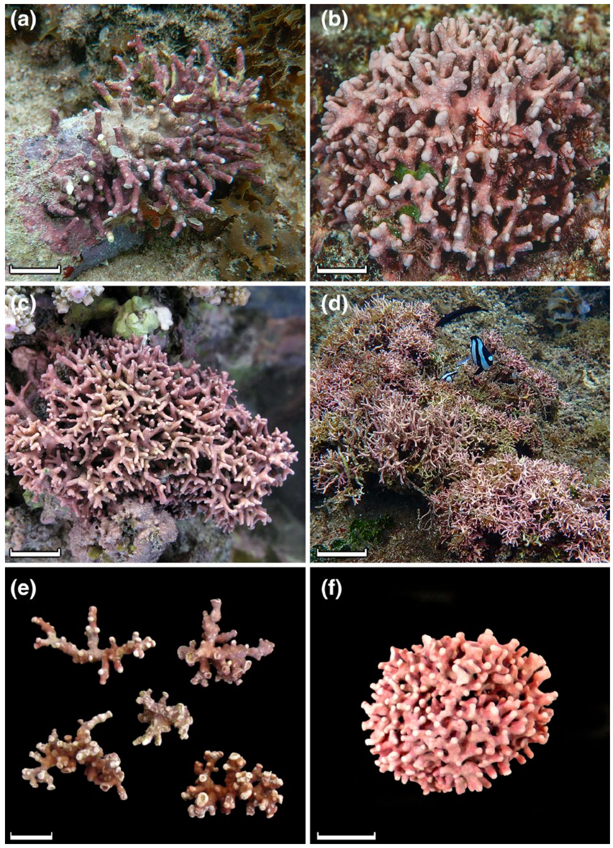

FIGURE 6 Examples of specimens/species that represent the *fruticose* growth form. (a) An as yet unidentified Corallinales species from Japan. (b) An as yet unidentified Corallinales species from Guam. (c) Attached form of *Lithophyllum longense* from Australia. (d) An as yet unidentified Corallinales species from Guam. (e) Rhodolith fragments from Brest, France. (f) Rhodolith form of *Lithophyllum longense* from Tanzania. Scale bars: (a, b, e, f) = 10 mm; (c) = 20 mm; (d) = 50 mm. Photographs: (a) by A. Kato; (b, d) by T. Schils; (c) by J. Huisman; (e) by F. Tâmega; (f) by G.W. Maneveldt.

development in non-geniculate corallines in which primary, terminal meristematic activity initially produces more or less circular thalli. Intergrades may also exist between *discoid*, *imbricate*, and *foliose* growth forms.

Lamellate—**Imbricate (Figure 10)**

Imbricate corallines are also fundamentally *encrusting* and also undergo secondary growth (through secondary, intercalary meristematic activity) to produce several to many flattened, often parallel running, overlapping, tightly adherent, applanate, layered lamellate branches arranged horizontally (Figure 10a–f). However, unlike *discoid* corallines that produce thin to thick (generally > five cells), discrete circular lamellate branches, *imbricate* corallines produce thin (generally < five cells), often extensively running, parallel, overlapping lamellate branches that are rarely circular. Lamellate branches give the coralline a distinctly scaly appearance in surface view. Intergrades exist between *imbricate*, *encrusting*, *discoid*, *layered*, and *foliose* growth forms (Figures S1b, S2c).

Lamellate—**Layered (Figure 11)**

Individuals consisting of several to many flattened, loosely adherent to mostly free (as opposed to tightly adherent in *imbricate* forms), overlapping, complanate, thin to thick (generally > five cells) layered lamellate branches arranged horizontally (Figure 11a–f). Lamellate branches often give the coralline a terraced appearance in surface view. Intergrades may also exist between *layered*, *foliose*, and *ribbon-like* growth forms (Figures S1b, S2a).

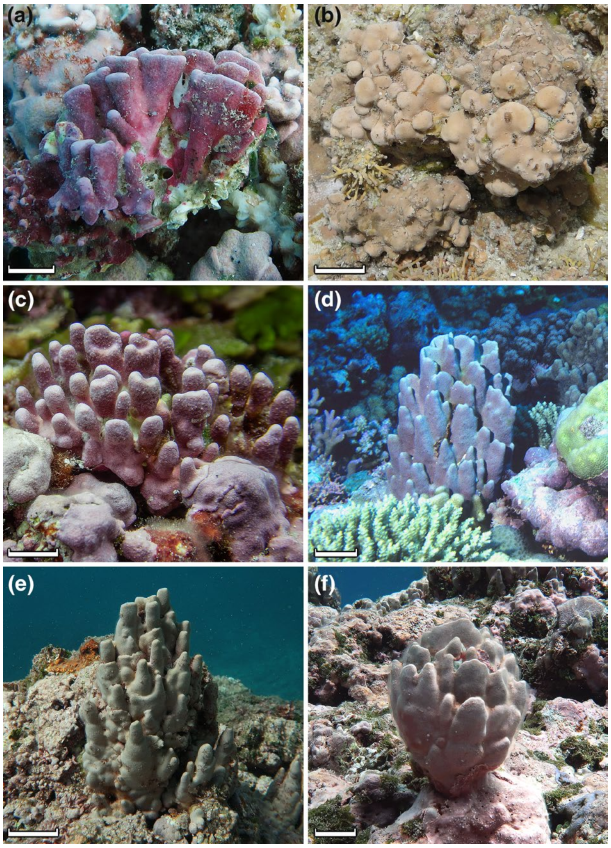

FIGURE 7 Examples of specimens/species that represent the *columnar* growth form. (a) *Porolithon lobulatum* from Australia. (b) *Phymatolithon ferox* from South Africa. (c) An as yet unidentified *Porolithon* species from Guam. (d) An as yet unidentified *Porolithon* species from Fiji. (e, f) *Porolithon pinnaculum* from Australia. Scale bars: (a, c) = 5 mm; (b) = 10 mm; (d, e) = 50 mm; (f) = 30 mm. Photographs: (a, e, f) by G. Diaz-Pulido; (b) by G.W. Maneveldt; (c) by T. Schils; (d) by D.W. Keats.

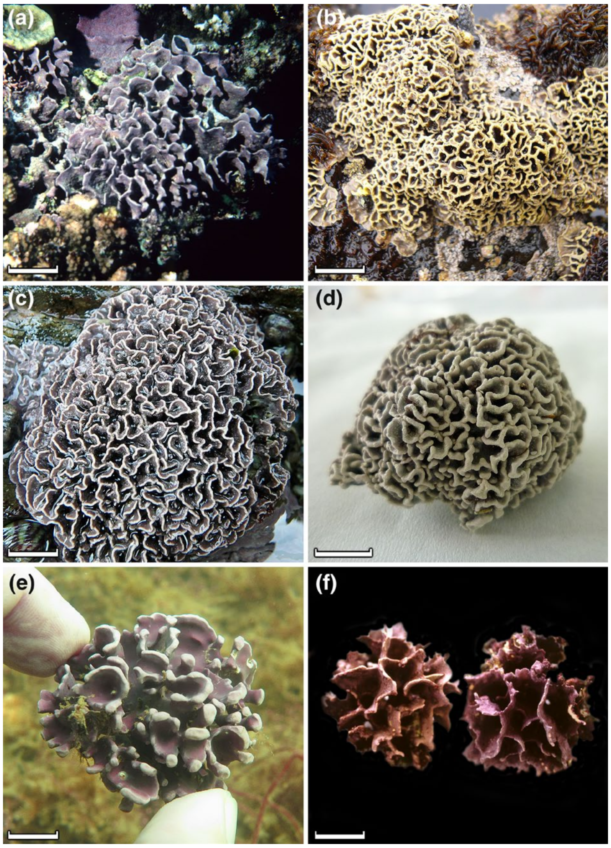

FIGURE 8 Examples of specimens/species that represent the *convoluted* growth form. (a) An as yet unidentified *Porolithon* species from Fiji. (b) An as yet unconfirmed *Lithophyllum* species from Japan. (c) An as yet unconfirmed *Lithophyllum* species from the Atlantic Iberian Peninsula. (d) An as yet unidentified Corallinales species from the Mediterranean. (e) An as yet unidentified rhodolith from Brest, France. (f) As yet unidentified rhodoliths from Fiji. Scale bars: (a) = 30 mm; (b, c, e) = 10 mm; (d), (f) = 20 mm. Photographs: (a, f) by D.W. Keats; (b) by M. Baba; (c) by I. Bárbara; (d) by L. Pezzolesi; (e) by F. Tâmega.

Lamellate—**Foliose (Figure 12)**

Individuals consisting of several to many flattened branched, thin to thick (generally > five cells) layered lamellate branches arranged at various angles to one another and in various planes (Figure 12a–e). Lamellate branches may be free from one another or interwoven and fused to varying degrees. *Foliose* corallines appear similar to *convoluted* corallines as both growth forms exhibit a 3-D, branched, cavitied form but differ in that the latter growth form produces flattened protuberances that are abutting and upright, as opposed to producing lamellate branches that are arranged at various angles to one another. Intergrades are also known to exist between *foliose* and *ribbon-like* growth forms.

Flabelliform

The remaining two growth forms are broadly categorized as flabelliform. Individual thalli are characteristically fan-shaped, often with flat, ribbon-like branches that are weakly calcified. Thalli are upright but can appear prostrate, which depends on the size of the alga, with larger and heavier individuals often appearing prostrate.

Flabelliform—**Ribbon-like (Figure 13)**

Individuals flabellate (fan-shaped), lacking a distinct holdfast and stipe, and bearing flat, taeniform (ribbon-like), lamellate branches that are weakly calcified; generally attached to a substrate through cell adhesion or locally by rhizoids. Individuals may appear fruticose, but here branches are flattened (Figure 13a–f).

Flabelliform—**Arborescent (Figure 14)**

Individuals flabellate (fan-shaped) and tree-like, composed of a distinct holdfast and stipe, and bearing flat,

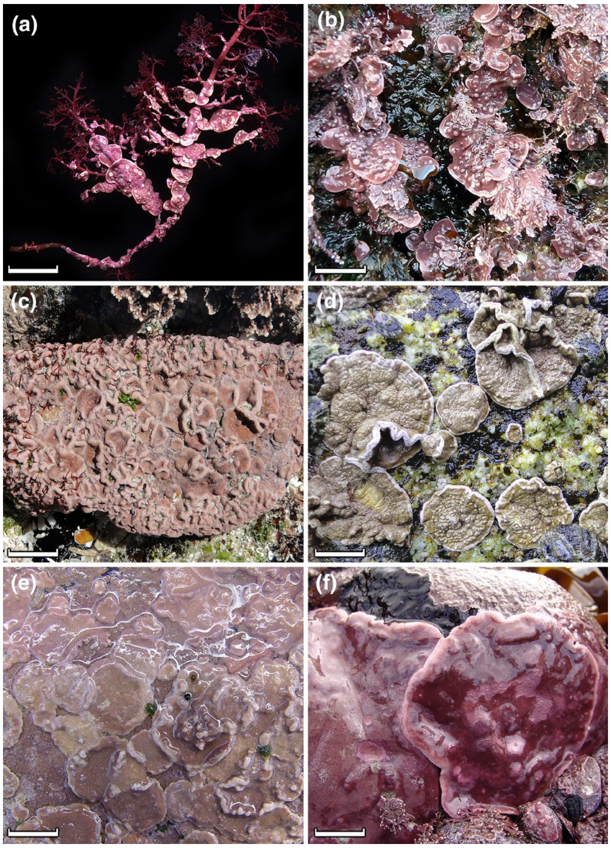

FIGURE 9 Examples of specimens/species that represent the *discoid* growth form. (a) Individuals of an as yet unconfirmed *Amphithallia* species from South Africa. (b) Individuals of an as yet unconfirmed *Mesophyllum* species from the Atlantic Iberian Peninsula. (c) Individuals of an as yet unconfirmed *Hydrolithon* species from South Africa. (d) *Chamberlainium impar* from South Africa. This species sometimes also has a *warty* appearance. (e) *Pneophyllum marlothii* from South Africa. (f) *Heydrichia woelkerlingii* from South Africa. Scale bars: (a, d) = 5 mm; (b, c, f) = 10 mm; (e) = 15 mm. Photographs: (a, c–f) by G.W. Maneveldt; (b) by I. Bárbara.

taeniform (ribbon-like) to flabellate, branched lamellate branches that are weakly calcified (Figure 14a–f). The presence of a holdfast and stipe distinguishes the *arborescent* growth form from the *ribbon-like* growth form (Figure 14a,c).

KEY TO GROWTH FORMS

1a.	Individuals not pseudoparenchymatous, composed partly or entirely of free filaments, usually either parasitic on or endophytic in other corallines, or occurring as thin, unistratose to bistratose crusts	**Unconsolidated**
1b.	Individuals fully pseudoparenchymatous	2
2a.	Individuals featureless, consisting of smooth crusts devoid of apparent outgrowths	3
2b.	Individuals not featureless, producing outgrowths of varying lengths/heights and diameters/widths	4
3a.	Mature individuals not circular, but of varying shapes	**Encrusting**
3b.	Mature individuals more or less circular	**Discoid**
4a.	(2) Individuals bearing protuberances that are without furrows or ridges and with a mostly radial (filaments diverging in lines from a common center) internal organization	5
4b.	Individuals bearing lamellate branches in furrows or ridges with a dorsiventral (having dissimilar upper [dorsal] and lower [ventral] surfaces) or isobilateral (having identical parts on each side of a central axis) internal organization	9
5a.	Individuals bearing short (< 6 mm in length) and swollen, to slender (> 6 mm in length) to compressed protuberances	6
5b.	Individuals with long (up to 20 cm in height), vertically elaborate protuberances	8
6a.	Individuals with protuberances that are less than 3 mm in length and diameter, are not abutting, and are unbranched	**Warty**
6b.	Individuals with swollen, slender to compressed protuberances that are more than 3 mm in length and diameter, are free from one another, are often abutting, or are laterally fused to varying degrees	7
7a.	Individuals with protuberances that are usually less than 6 mm in length, swollen and often abutting	**Lumpy**
7b.	Individuals with protuberances that are usually more than 6 mm in length, slender, terete to compressed, often taper, free from one another, abutting or laterally fused to varying degrees	**Fruticose**
8a.	(5) Individuals with column-like protuberances that may be clavate, abutting, or fused	**Columnar**
8b.	Individuals with flattened protuberances arranged in a 3D cavitied form	**Convoluted**

9a.	(4) Individuals with layered lamellate branches	10
9b.	Individuals with fan-shaped lamellate branches	12
10a.	Individuals in a 3D cavitied form, with lamellate branches arranged at various angles to one another	**Foliose**
10b.	Individuals crustose, with lamellate branches arranged horizontally to one another	11
11a.	Individuals scaly in appearance, with tightly adherent lamellate branches	**Imbricate**
11b.	Individuals terraced in appearance, with loosely adherent to free lamellate branches	**Layered**
12a.	(9) Individuals not stipitate, attached to a substrate by cell adhesion or locally by rhizoids	**Ribbon-like**
12b.	Individuals stipitate, attached to a substrate by a distinct holdfast	**Arborescent**

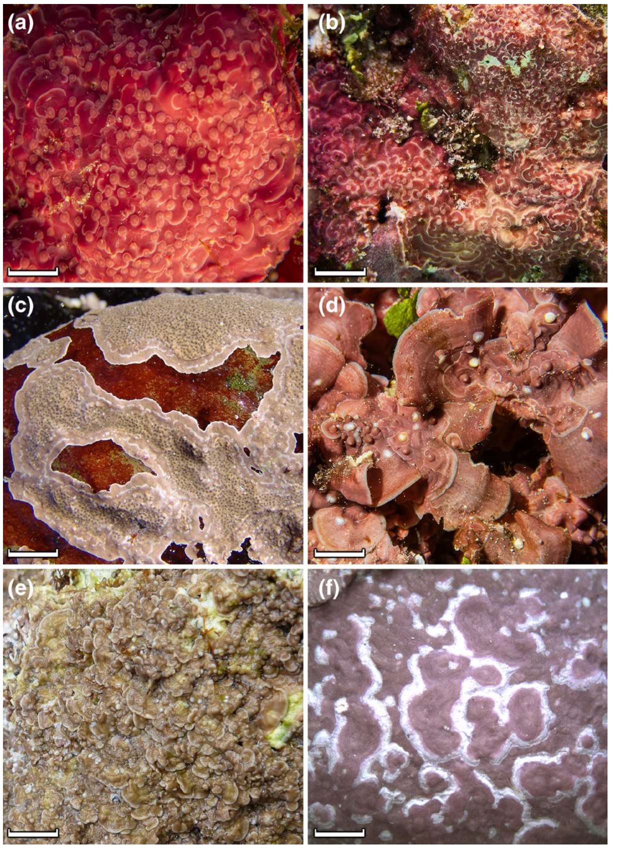

FIGURE 10 Examples of specimens/species that represent the *imbricate* growth form. (a), (b) An as yet unconfirmed *Titanoderma* species from Guam. (c) *Phymatolithon foveatum* from South Africa. (d) An as yet unconfirmed *Mastophora* species from Guam. Under the previous system, this specimen would be an example of a *layered* coralline because it has free primary thalli. However, since the specimen has secondary lamellate branches that are tightly adherent and overlapping, it is regarded as being *imbricate* under the new system. (e) An as yet unconfirmed *Neogoniolithon* species from Japan. (f) Magnified view of marginal scrolls (lamellate branches) from an as yet identified Hapalidiales species from South Africa. Under the previous system figures, (c) and (f) would have been classified as encrusting. However, these specimens produce secondary applanate, thin, overlapping layered lamellate branches (white swirls), which we consider represent the *imbricate* growth form in our new system. Scale bars: (a, c, e) = 10 mm; (b) = 20 mm; (d) = 25 mm; (f) = 2 mm. Photographs: (a, b, d) by T. Schils; (c, f) by G.W. Maneveldt; (e) by A. Kato.

DISCUSSION

The morphological classification system proposed here constitutes a refinement and update of those growth forms recognized in recent research on non-geniculate corallines. Like Woelkerling et al. (1993), we opted to differentiate the growth forms based on anatomical organization; presence or absence of outgrowths; the type, shape, length/height, diameter/width, orientation and degree of adherence of these outgrowths; and the method of attachment to a substrate, all of which represent different degrees of complexity (Figure 1). The growth forms for geniculate corallines are covered in a separate paper (Schwoerbel et al., 2026).

Although having a rich, but somewhat convoluted taxonomic history dating back to the first century AD (Irvine et al., 1994, p. 11; see also Leão et al., 2024 for the chronology of important milestones in the history of non-geniculate coralline algal taxonomy), non-geniculate corallines only received a formal application of a morphological classification system in the early 1970s (see below). Prior to this, early coralline algal researchers (e.g., in roughly chronological order: Ellis, Lamarck, Lamouroux, Philippi, Kützing, Decaisne, Harvey, Foslie, Kjellman, Heydrich, Yendo, Lemoine, Cabioch) described coralline algal morphologies subjectively, without any reference to a standardized terminology and without giving a clear definition of the terms used (e.g., Kützing, 1841, 1843, 1849; Lemoine, 1913). Harvey (1849), however, loosely categorized the non-geniculate corallines into "flat incrustaceans" (= *encrusting* here), "stony branches" (= protuberances here), and "leafy lobes" (= lamellate branches here). Foslie (1895, 1898, 1900) "described some 428 species and infraspecific taxa of non-geniculate corallinales during the period 1891-1909, based many of his taxa on slight differences in growth-form" (Woelkerling et al., 1993, p. 277) and only used such generalized terms as *crust like expanses* or *crustaceous species*, *branched*, and *vigorously developed* for more broader characterizations. In many of Foslie's descriptions, the concept of the *typical form* (type specimen) was applied, with specimens deviating from the typical form given form names. Several subsequent authors (e.g.,

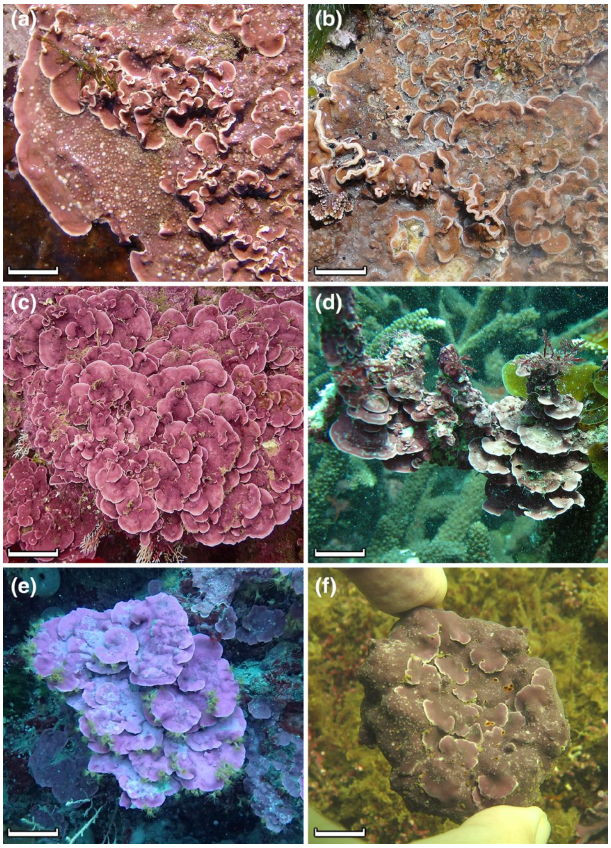

FIGURE 11 Examples of specimens/species that represent the *layered* growth form. (a), (b) An as yet unidentified Hapalidiales species from South Africa. (c) An as yet unconfirmed *Mastophora* species from Guam. (d) Individuals from an as yet unidentified species from Australia. Note that individual lamellate branches are also *imbricate*. Under the previous system, this specimen may even have been classified as *discoid*. (e) An as yet unidentified species from the Mediterranean. (f) An as yet unidentified rhodolith from Brest, France. Scale bars: (a, b, d–f) = 10 mm; (c) = 30 mm. Photographs: (a, b) by G.W. Maneveldt; (c) by T. Schils; (d) by G. Diaz-Pulido; (e) by L. Le Gall; (f) by F. Tâmega.

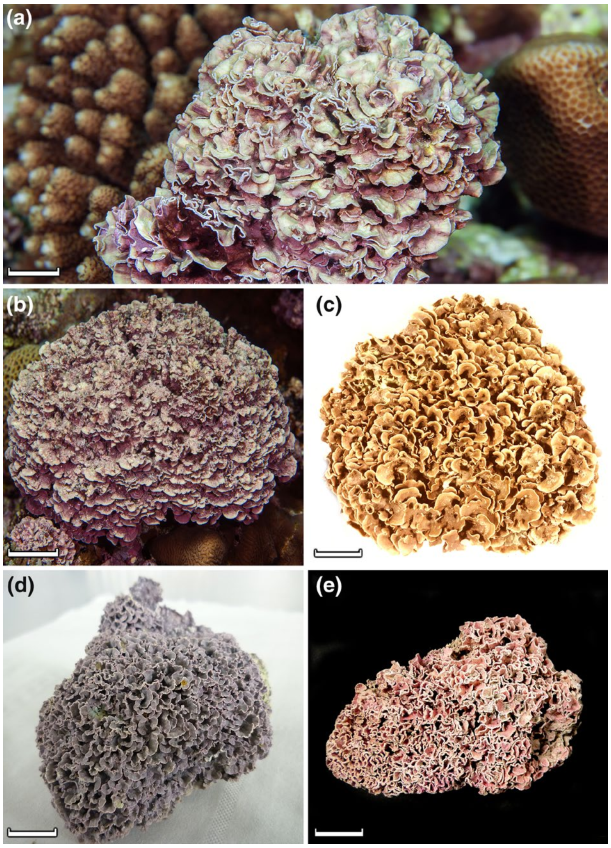

FIGURE 12 Examples of specimens/species that represent the *foliose* growth form. (a), (b) An as yet unconfirmed *Mastophora* species from Guam. (c) An as yet unconfirmed *Mesophyllum* species from Japan. (d) *Lithophyllum byssoides* from the Mediterranean. (e) An as yet unidentified rhodolith from Tanzania. Scale bars: (a, d, e) = 10 mm; (b) = 30 mm; (c) = 20 mm. Photographs: (a, b) by T. Schils; (c) by M. Baba; (d) by F. Rindi; (e) by G.W. Maneveldt.

Heydrich, 1897; Lemoine, 1910, 1913; Masaki, 1968; Suneson, 1943) followed this practice.

The Woelkerling et al. (1993) system of 10 growth forms (as focal points) was a refinement of those originally proposed by Bosellini and Ginsburg (1971), Johansen (1981), Bosence (1976, 1983), Woelkerling and Irvine (1988), and Woelkerling and Campbell (1992). Based on rhodolith morphology, Bosellini and Ginsburg (1971, p. 674) assigned rhodolith specimens on a rudimentary morphological classification to five shape classes (spheroidal, elliptical, amoeboidal, discoidal, and flat), including several secondary subclasses (oval, elongated, biconvex, flat-top, and equant). These growth forms were, however, based on a water-energy gradient, which was later established to be unfounded (Adey & Macintyre, 1973; Bosence, 1976). Johansen (1981, p. 4) used a combination of morphological and ecological (habit and substrate) attributes, which often led to confusion. Additionally, some of the Johansen (1981, pp. 4, 44–55) growth forms were considered too broad, especially his separation of thin and thick crusts into different growth forms, suggesting that thin and thick crusts could not look similar. Woelkerling and Irvine (1988, pp. 5–7), although recognizing four morphological growth forms (unconsolidated, crustose, protuberant, and taeniform), placed their growth forms into three groups (semi-endophytic, epigenous, and unattached) based on morphological and ecological (habit and substrate) attributes, which similarly limited the use of their system.

The Woelkerling and Campbell (1992, pp. 3–4) system, based solely on morphology, comprised six growth forms (encrusting, layered, warty, protuberant, lumpy, coalescent) but was limited to describing only southern Australian species of *Lithophyllum* so did not recognize the range of external appearances in other non-geniculate corallines studied to date. Examining over 5000 populations of non-geniculate corallines from across the world, Woelkerling et al. (1993, p. 280) expanded the Woelkerling and Campbell (1992)

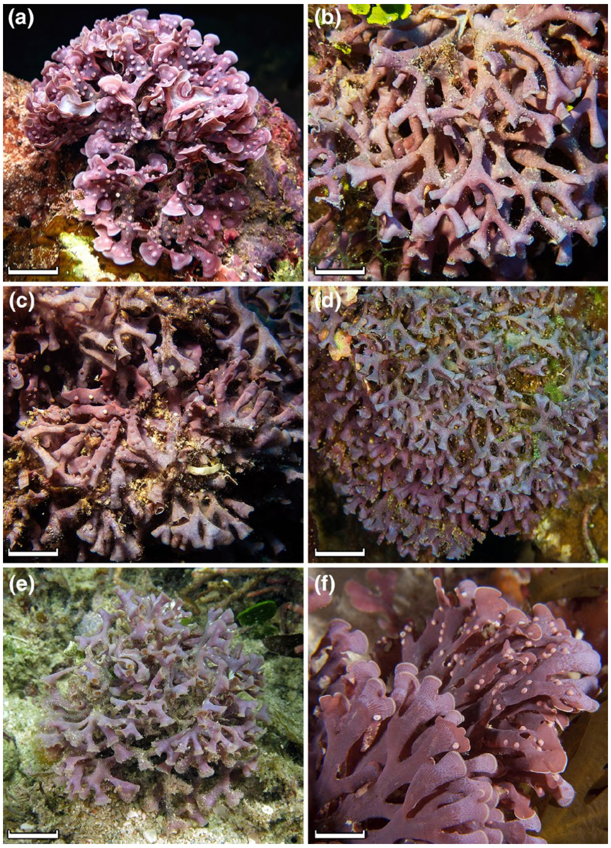

FIGURE 13 Examples of specimens/species that represent the *ribbon-like* growth form. (a) *Mastophora rosea* from the Philippines. (b–d) *Mastophora rosea* from Guam. (e, f) As yet unconfirmed *Mastophora* species from Australia. Scale bars: (a, e) = 20 mm; (b, d) = 10 mm; (c) = 15 mm; (f) = 5 mm. Photographs: (a–d) by T. Schils; (e–f) by J. Huisman.

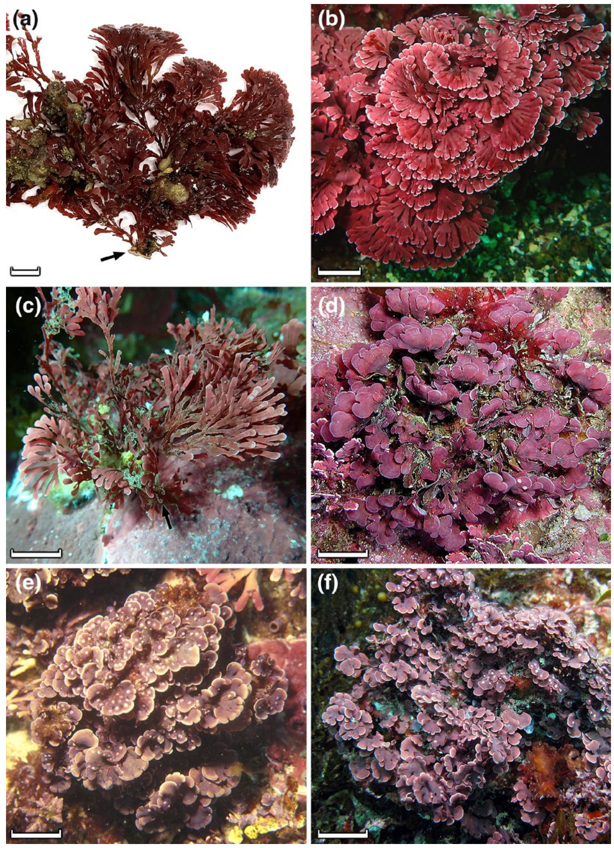

FIGURE 14 Examples of specimens/species that represent the *arborescent* growth form. (a, b) *Metamastophora flabellata* from Tasmania, Australia; herbarium (a) and field specimens (b) Note the holdfast [arrow] in the herbarium specimen. (c) An as yet unconfirmed *Metamastophora* species from Tasmania, Australia. Note the approximate position of the holdfast [arrow]. (d) An as yet unconfirmed species from South Africa. (e, f) As yet unconfirmed *Metamastophora* species from Australia. Scale bars: (a, d, e) = 10 mm; (b) = 15 mm; (c, f) = 20 mm. Photographs: (a) by J. Schwoerbel; (b) by M. Rose; (c) by H. Forbes; (d) by T. Schils, (e, f) by J. Huisman.

system to 10 growth form focal points (*unconsolidated*, *encrusting*, *warty*, *lumpy*, *fruticose*, *discoid*, *layered*, *foliose*, *ribbon-like*, and *arborescent*). This revised system was compatible with that previously devised by Bosence (1976, p. 380) of spheroidal, ellipsoidal, and discoidal for rhodoliths, based independently on specimen shape and branching density and later expanded on by Bosence (1983, p 220; laminar, branching, columnar), but still only for rhodoliths. In this latter system, laminar specimens comprised simple (unbranched, featureless) crusts that may form a leafy habit, branching specimens that produced protuberances of varying densities apically or laterally beset with very dense intergrowing protuberances with flattened ends, and columnar specimens that produced short, stocky, protuberances that are almost as wide as they are high. Woelkerling et al. (1993, p. 284) argued that their system "has the advantage of being applicable to attached as well as unattached plants and thus is better suited for use in taxonomic and floristic studies," although they acknowledged that the combined Bosence (1976, 1983) system "is potentially more useful in ecological studies of unattached plants." Additionally, the Bosence (1976, 1983) system can be used to describe multispecific rhodoliths, whereas the Woelkerling et al. (1993, p. 284) system "is designed for describing individual plants or species," which is how taxonomic descriptions are presented.

To promote consistency in the reporting of ecological research and conservation management practices, Jardim et al. (2025; see also figure, 3) proposed an organismal typology based on six very broad morphologies: attached geniculate corallines; free-living geniculate corallines; encrusting non-geniculate corallines (which lumps smooth, featureless crusts with those that have outgrowths); free-living fragmented non-geniculate corallines; free-living nodular, nucleated non-geniculate corallines; and free-living nodular, non-nucleated non-geniculate corallines. Under this system, free-living geniculate (articuliths) and free-living non-geniculate (maërl, rhodoliths) corallines were collectively referred to as *coralline algal beds*. The proposed Jardim et al. (2025) morphological classification system was meant to promote a unified approach to describing broad-scale ecological research and for inferring best practices for conservation management. Although this morphological classification system is a valuable high-level approach, it is less appropriate to the finer scale descriptions proposed here.

In addition to the 10 growth forms (focal points) described by Woelkerling et al. (1993), we propose the reinclusion of a previous growth form, namely *columnar*, in line with Bosence (1983), but also including large specimens often up to 20 cm in height and width, with robust, vertically elaborate protuberances of varying heights and widths in that growth form. Furthermore, we added two new growth forms, *convoluted* and *imbricate*, to include more recently documented specimens. These and the other 10 preestablished growth forms may be separated into five very broad categories: unconsolidated, encrusting, protuberant, lamellate, and flabelliform (Figure 1).

The *unconsolidated* growth form remains the only one that is not based on a fully pseudoparenchymatous construction but rather on partly to entirely free filaments. This growth form is still largely restricted to endophytic (e.g., *Austrolithon intumescens*, Harvey & Woelkerling, 1995, p. 363, figures 5–10; *Choreonema thuretii*, Woelkerling, 1987, p. 115, figures 4, 5; *Lesueuria minderiana*, Woelkerling & Ducker, 1987, p., 197, figures 7–9), parasitic (e.g., *Epulo multipedes*, Townsend & Huisman, 2004, p. 290, figures 4, 6–8), and very thin epiphytic species (e.g., *Pneophyllum confervicola*, Chamberlain, 1994, p. 139, figure 62A).

Encrusting corallines are fundamentally crustose, lacking protuberances and lamellate branches. Corallines encompassing this growth form are generally smooth and featureless. *Encrusting* is a common growth form of many non-geniculate corallines and exists in all orders. In Corallinales, this form includes, for example, all *Crusticorallina* species (Hind et al., 2016, p. 932); many *Lithophyllum* species, including the generitype *L. incrustans* (Hernandez-Kantun et al., 2015, figure 4a; Woelkerling, 1983, p. 315, figure 15) and *L. atlanticum* (Vieira-Pinto et al., 2014, p. 362); many *Chamberlainium* species: *C. agulhensis*, *C. cochleare*, *C. decipiens*, *C. natalense*, and *C. tenue*, for example (Puckree-Padua, Haywood, et al., 2020, pp. 471, 480; 2022, p. 180; van der Merwe et al., 2015, pp. 473, 475; this study, Figure 3a,e); and *Porolithon onkodes* and those species passing under that name, many still undescribed (Gabrielson et al., 2018). In Corallinapetrales, the generitype *Corrallinapetra novaezelandiae* is *encrusting* (Nelson et al., 2015, p. 459, figure 2a), whereas *Co. gabrielii* (Jeong et al., 2021, p. 852, figure 3a), the only other species currently in the genus, may also be *encrusting*. In Hapalidiales, this form includes, for example, some *Clathromorphum* species, including the generitype *Cl. compactum* (Printz, 1929, pl. 41, figure 1); several *Lithothamnion* species, including its generitype *Lithothamnion muelleri* (Wilks & Woelkerling, 1995, p. 555); and all currently known *Phymatolithopsis* species (Jeong et al., 2022, pp. 165, 169, figures 3a,b, 6b; Maneveldt et al., 2024, pp. 9, 16, figures 3, 4, 40–42; van der Merwe & Maneveldt, 2014, pp. 178, 182, figure 75; this study, Figure 3b). In Sporolithales, *Heydrichia groeneri* (Keats & Chamberlain, 1995, p. 52, figure 1) is entirely *encrusting*, whereas several species of *Sporolithon* may be *encrusting*, including, for example, *S. crypticum*, *S. immotum*, *S. nodosum* (Gabrielson et al., 2023, p. 7, 8, 10), and *S. tenue* (Bahia et al., 2014, p. 46). Geniculate corallines, however, that form extensive crusts with few to no upright axes can also appear *encrusting* (e.g., Brodie et al., 2013; Irvine et al., 1994; Schwoerbel et al., 2026). Geniculate species such as *Chiharaea americana* and *Ch. bodegensis* form extensive crusts that can often be confused with *encrusting* non-geniculate species (Martone et al., 2012). Rather than being an intermediate growth form between geniculate and non-geniculate corallines, such species represent a geniculate coralline algal lineage with a reduced number of upright axes (Martone et al., 2012) or a lineage in which upright axes are absent because of environmental stresses (Guy-Haim et al., 2016). In many ecological studies from tropical and subtropical regions (e.g., Smith et al., 2016, 2020), *encrusting* corallines are usually referred to as CCA.

Protuberant corallines comprise by far the largest category, including thalli that are *warty*, *lumpy*, *fruticose*, *columnar*, and *convoluted*. The first three growth forms are consistent with Woelkerling et al. (1993). We consider the broad classification of protuberant to be when a thallus surface has irregularities resulting from secondary growth to produce outgrowths that usually have a radial internal organization. The various protuberant growth forms are distinguished by the length, width, and appearance of the protuberances. Uniformly *warty* corallines include *Heydrichia cerasina* (Maneveldt & van der Merwe, 2012, p. 13, figures 1–3; this study, Figure 4b), *Roseolithon littorale* (Min-Khant-Kyaw et al., 2024, p. 526, figure 4), and the lectotype of *Boreolithothamnion sonderi* (Gabrielson et al., 2023, figure S1, see also Printz, 1929, pl. 4, figure 6, as *Lithothamnion sonderi*). Uniformly *lumpy* corallines include *Roseolithon purii* (Coutinho et al., 2022, p. 242, figure 62), *Roseolithon superpositum* (Gabrielson et al., 2023; see also Keats et al., 2000, figures 1, 2, as *Lithothamnion superpositum*; Printz, 1929, pl. 12, figure 6, as *Lithothamnion superpositum*), and *Sporolithon indopacificum* (Maneveldt et al., 2017, p. 119, figure 3; this study, Figure 4f). *Fruticose* corallines are common, especially in the genus *Lithophyllum*, and include the widely distributed *L. kaiseri* (Hernandez-Kantun et al., 2016, p. 625) and *L. longense* (Maneveldt et al., 2019, p. 159; this study, Figure 6c) and several other species thus far only reported to be *fruticose*, for example, *L. affine* (Basso et al., 2015, p. 186), *L. kotschyanum* (Basso et al., 2014, p. 712), *L. subplicatum* (Basso et al., 2015, p. 190), and *L. subreduncum* (Basso et al., 2015, p. 192).

Woelkerling et al. (1993, table 1) provided a non-exhaustive list of terms used to describe growth forms of non-geniculate corallines, including the term *columnar*. *Columnar*, however, never was proposed as a distinct growth form; the reason remains unclear especially since Bosence (1983) provided a clear characterization of that concept, albeit only considering the inclusion of specimens that produce short stocky protuberances that are almost as wide as they are high. *Columnar* specimens are here considered to include those specimens that are robust with vertical protuberances that are several millimeters to 20 cm in height and width and that are often clavate (club-shaped). Here, we further expand on the Bosence (1983) concept of *columnar* to include the massive, mountain-like thalli observed in several tropical species that bear broad individual to fused vertical columns at maturity and that are usually common in remote, oceanic reef atolls (Jeong et al., 2023; Maneveldt & Keats, 2016). The *columnar* growth form appears to be genetically predetermined (e.g., *Porolithon craspedium*, see Printz, 1929, pl. 69, as *Lithophyllum craspedium*) albeit not unique to any one species (Jeong et al., 2023; Richards et al., 2021). In contrast, several species representing the *convoluted* growth form (e.g., *Neogoniolithon acropetum*, see Printz, 1929, pl. 51, as *Goniolithon acropetum*; *Porolithon antillarum*, see Maneveldt & Keats, 2014, figures 25, 26; Printz, 1929, pl. 68, as *Lithophyllum antillarum*; *Porolithon sandvicense*, see Printz, 1929, pl. 70, as *Lithophyllum sandvicense*) are possibly grazer-mediated (see e.g., Littler et al., 1995; Littler & Littler, 1999, 2000, 2003, 2013; Maneveldt & Keats, 2014). This morphology has been reported in tropical waters across the Caribbean and South Pacific oceans (Littler et al., 1995; Littler & Littler, 2000, 2003, 2013; Maneveldt & Keats, 2014; Printz, 1929) and may possibly be more widespread. Additionally, most specimens of *Lithophyllum byssoides* typically exhibit the *convoluted* growth form (Pezzolesi et al., 2017, figures 4–5) but whether the growth form is environmentally mediated is unclear.

Lamellate corallines comprise the next largest category and include those individuals that are *discoid*, *imbricate*, *layered*, and *foliose*. Unlike protuberances that usually have a radial internal organization, lamellate individuals produce secondary thalli that have a dorsiventral or isobilateral internal organization like that of their primary thallus organization. Although our definition of *foliose* matches that of Woelkerling et al. (1993), our concepts of *discoid* and *layered* differ slightly. Woelkerling et al. (1993, p. 280) defined *discoid* as "plants each consisting of an unbranched and largely unattached disc-like lamella of varying shape." A species thus far characteristic of this growth form is *Synarthrophyton patena* (see Printz, 1929, pl. 10, figure 1, as *Lithothamnion patena*). However, here we also include species with firmly attached primary thalli that are more or less circular, such as *Chamberlainium impar*, which can sometimes also appear *warty* (Puckree-Padua, Haywood, et al., 2020, figure 6; this study, Figure 9d), *Heydrichia woelkerlingii* (Townsend et al., 1994; this study, Figure 9f) and *Lithophyllum hibernicum* (V. Peña, pers. obs.). During our investigations, we also encountered species (e.g., *Pneophyllum marlothii*, Puckree-Padua, Gabrielson, et al., 2020, figure 3; this study, Figure 9e; *Pneophyllum discoideum*, Chamberlain, 1994, fig. 26, as *Spongites discoideus*; Puckree-Padua, Gabrielson, et al., 2020) that are primarily *encrusting* but that secondarily produce thick *discoid* thalli, which often may even produce abutting, swollen protuberances (equivalent to the *lumpy* growth form). Such species demonstrate the high degree of morphological variability even within a single specimen (see e.g., Gomes et al., 2024; Hernandez-Kantun et al., 2016; Kato et al., 2022; Kim et al., 2024; Pezzolesi et al., 2017, 2019). The *discoid* growth form is reminiscent of ontogenetic development in non-geniculate corallines in which primary, terminal meristematic activity results in more or less circular thalli.

Woelkerling et al. (1993, p. 280) defined *layered* as "plants consisting of several to many flattened, lamellate branches arranged in horizontally oriented layers. Such lamellate branches often give the plant a terraced appearance in surface view." Although we have retained much of this definition for *layered* in the currently proposed system, here we also have made a distinction between the level of adherence of the secondary thalli. In the *imbricate* growth form, secondary overlapping thalli are tightly adherent giving the coralline a scaly appearance in surface view; whereas in our concept of *layered*, the overlapping secondary thalli are loosely adherent to free, giving the coralline a terraced appearance in surface view. *Phymatolithon foveatum* (Chamberlain & Keats, 1994, p. 116, as *Leptophytum foveatum*) and *Phymatolithon nantuckensis* (Adey et al., 2018, p. 41) have an *imbricate* growth form. Specimens of *Titanoderma* frequently show the *imbricate* growth form (e.g., Chamberlain & Irvine, 1994, pp. 99, 102, 108; Jesionek et al., 2016, figure 5a; this study, Figure 10a,b), including *Titanoderma tessellatum* (Lemoine, 1929, p. 69, pl. 1, figure 6, as *Lithophyllum* [*Dermatolithon*] *tessellatum*). *Phymatolithon squamulosum* can be both *imbricate* and *layered* (Adey et al., 2018, p. 42), the latter growth form commonly observed in some *Lithophyllum* species, including Mediterranean *L. stictiforme* (Pezzolesi et al., 2019, figure 2) and Atlantic Iberian Peninsula *L. artabricum* (Peña & Torres, 2021, figure 1). The type specimens of several other little-studied non-geniculate corallines also are *layered*, including *Lithothamnion simulans* f. *crispescens* (Printz, 1929, pl. 8, figure 17), *Lithothamnion neglectum* (Printz, 1929, pl. 9, figure 4), and *Lithothamnion mesomorphum* (Printz, 1929, pl. 9, figures 7, 8), currently regarded as synonyms of *Mesophyllum crispescens*, *Synarthrophyton neglectum*, and *Mesophyllum mesomorphum*, respectively. *Imbricate* and *discoid* corallines are also similar. Both are fundamentally *encrusting* and both can undergo secondary growth to produce lamellate branches. However, unlike *discoid* corallines that are featureless and produce thin to thick (generally > five cells), discrete circular lamellate branches, *imbricate* corallines are scaly in appearance due to their producing thin (generally < five cells), often extensively running, parallel, overlapping lamellate branches that are rarely circular.

Foliose corallines are similar to *convoluted* corallines as both growth forms exhibit a 3-D, branched, cavitied form but differ from the latter in that lamellate branches are thin, simple or branched (at various angles to one another, and in various planes), variously curved, but may also be free from one another or interwoven and fused to varying degrees, as opposed to protuberances that are extensively branched, abutting with upright lobes, and with protuberances extending more or less radially from the core in rhodoliths. *Tenarea tortuosa* (Woelkerling et al., 1985, figures 1–2) is *foliose*. The widely distributed and morphologically variable *Lithophyllum kaiseri* can also be *foliose* (Hernandez-Kantun et al., 2016, figure 3). Many specimens that would be classified as *foliose* under the Woelkerling et al. (1993) system are instead *convoluted* in our system (e.g., *Lithophyllum byssoides*, Pezzolesi et al., 2017, figures 4–5).

Flabelliform individuals may be *ribbon-like* or *arborescent*. The presence of a holdfast and stipe in the *arborescent* growth form is what distinguishes it from the *ribbon-like* growth form, which is instead attached to a substrate through cell adhesion or by rhizoids. Both growth forms comprise entire individuals and/or their lamellate branches that are fundamentally fan-shaped (flabellate, a 1-dimentional structure) and closely resemble geniculate corallines in appearance (but lacking the uncalcified nodes—genicula). In the arborescent growth form, fan-like branches are arranged at various angles to one another, giving the coralline a multidimensional, tree-like appearance. *Ribbon-like* non-geniculate corallines can also appear arborescent (tree-like), but this is because they often comprise several thalli interwoven to give the multidimensional, tree-like appearance. The genera *Mastophora* and *Tenarea* include examples of the *ribbon-like* growth form, whereas the currently regarded monospecific genera *Metamastophora* and *Mastophoropsis* are the only known examples of the *arborescent* growth form (Woelkerling et al., 1993).

It is important to note that within and between these broad growth form categories individual specimens and species may display more than one discrete growth habit. For example, *Porolithon gardineri* (Richards et al., 2021, figure 10), *Porolithon lobulatum* (Jeong et al., 2023, figure 4c–h), and *Porolithon pinnaculum* (Jeong et al., 2023, figure 8) show large morphological variability within the *columnar* growth form. Similarly, *Lithophyllum stictiforme* from the Mediterranean shows large morphological variability within the *layered* growth form (Pezzolesi et al., 2019, figure 2). Additionally, intergrades among the different growth forms are common, which often makes it difficult to assign a specimen to a discrete growth form category (Figures S1, S2). For example, *Lithophyllum incrustans* rhodoliths from Ireland represent intergrades between the *encrusting* and *lumpy* growth forms (Hernandez-Kantun et al., 2015, figure 4b,c) and between the *convoluted* and *fruticose* growth forms (Hernandez-Kantun et al., 2015, figure 4d).

CONCLUSIONS

Recent research necessitated the refinement of the Woelkerling et al. (1993) growth forms classification system to synthesize previously reported and additional growth forms that are increasingly encountered, including those that cannot be easily assigned under any of the previous growth forms classification systems. Most importantly, there is clear evidence that individual coralline species frequently show changes in their morphology through natural ontogenetic processes (e.g., Bosellini & Ginsburg, 1971; Bosence, 1983; Johansen, 1969) and also due to various environmental factors (e.g., Carro et al., 2014; Jardim et al., 2022; Johansen, 1981; Maneveldt & Keats, 2008; Steneck & Adey, 1976), often resulting in more than one growth form, even in the same individual. Additionally, intergrades exist between many of the growth forms, often making it difficult to categorize certain morphologies perfectly into any one of the growth forms in the classification system here proposed; with time, even this system will require refinement. Other classification schemes for macroalgae using anatomical, morphology, and physiological traits (e.g., Littler et al., 1983; Steneck & Dethier, 1994) have proved very useful for gaining a better understanding of the ecological functioning of benthic marine ecosystems, although the link between form and function in coralline algae still needs to be critically evaluated (e.g., see Mauffrey et al., 2020, for a critique of form-based grouping schemes). We hope that this paper will facilitate not only taxonomic descriptions of non-geniculate corallines, but also support ecological studies given the difficulty in identifying species using external characters only. It is important to note, however, that these classification systems reveal the (human) need to compensate for human cognitive limitations (Jardim et al., 2025) but in no way represent the full diversity of developmental and environmentally driven possibilities that exist naturally in the coralline algae.

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REFERENCES

Adey, W. H. (1978). Coral reef morphogenesis: A multidimensional model: New data from coring and carbon-14 dating provide keys for unraveling some classical enigmas. *Science*, *202*, 831–837.

Adey, W. H., Hernandez-Kantun, J. J., Gabrielson, P. W., Nash, W. C., & Hayek, L.-C. C. (2018). *Phymatolithon* (Melobesioideae, Hapalidiales) in the boreal–subarctic transition zone of the North Atlantic: A correlation of plastid DNA markers with morpho-anatomy, ecology, and biogeography. *Smithsonian Contributions to the Marine Sciences*, *41*, 1–90.

Adey, W. H., & Macintyre, I. G. (1973). Crustose coralline algae: A re-evaluation in the geological sciences. *Geological Society of America Bulletin*, *84*, 883–904.

Aguirre, J., Braga, J. C., & Bassi, D. (2017). Rhodoliths and rhodolith beds in the rock record. In R. Riosmena-Rodríguez, W. Nelson, & J. Aguirre (Eds.), *Rhodolith/Maërl beds: A global perspective* (pp. 105–138). Springer.

Aguirre, J., Perfectti, F., & Braga, J. C. (2010). Integrating phylogeny, molecular clocks, and the fossil record in the evolution of coralline algae (Corallinales and Sporolithales, Rhodophyta). *Paleobiology*, *36*, 519–533.

Bahia, R. G., Amado-Filho, G. M., Maneveldt, G. W., Adey, W. H., Johnson, G., Marins, B. V., & Longo, L. L. (2014). *Sporolithon tenue* sp. nov. (Sporolithales, Corallinophycidae, Rhodophyta): A new rhodolith-forming species from the tropical southwestern Atlantic. *Phycological Research*, *62*, 44–54.

Bailey, J. C., & Chapman, R. L. (1998). A phylogenetic study of the Corallinales (Rhodophyta) based on nuclear small-subunit rRNA gene sequences. *Journal of Phycology*, *34*, 692–705.

Barnes, J., Bellamy, D. J., Jones, D. J., Whitton, B. A., Drew, E., & Lythgoe, J. (1970). Sublittoral reef phenomena of Aldabra. *Nature*, *225*, 268–269.

Basso, D., Caragnano, A., Le Gall, L., & Rodondi, G. (2015). The genus *Lithophyllum* in the north-western Indian Ocean, with description of *L. yemenense* sp. nov., *L. socotraense* sp. nov., *L. subplicatum* comb. et stat. nov., and the resumed *L. affine*, *L. kaiseri* and *L. subreduncum* (Rhodophyta, Corallinales). *Phytotaxa*, *208*, 183–200.

Basso, D., Caragnano, A., & Rodondi, G. (2014). Trichocytes in *Lithophyllum kotschyanum* and *Lithophyllum* spp. (Corallinales, Rhodophyta) from the NW Indian Ocean. *Journal of Phycology*, *50*, 711–717.

Bittner, L., Payri, C. E., Maneveldt, G. W., Couloux, A., Cruaud, C., de Reviers, B., & Le Gall, L. (2011). Evolutionary history of the Corallinales (Corallinophycidae, Rhodophyta) inferred from nuclear, plastidial and mitochondrial genomes. *Molecular Phylogenetics and Evolution*, *61*, 697–713.

Bosellini, A., & Ginsburg, R. N. (1971). Form and internal structure of recent algal nodules (rhodolites) from Bermuda. *Journal of Geology*, *79*, 669–682.

Bosence, D. W. J. (1976). Ecological studies on two unattached coralline algae from western Ireland. *Palaeontology*, *19*, 365–395.

Bosence, D. W. J. (1983). Description and classification of rhodoliths (rhodoids, rhodolites). In T. M. Peryt (Ed.), *Coated grains* (pp. 217–224). Springer.

Brodie, J., Walker, R. H., Williamson, C., & Irvine, L. M. (2013). Epitypification and redescription of *Corallina officinalis* L., the type of the genus, and *C. elongata* Ellis et Solander (Corallinales, Rhodophyta). *Cryptogamie Algologie*, *34*, 49–56.

Cabioch, J. (1969). Les fonds de maerl de la baie de Morlaix et leur peuplement végétal. *Cahiers de Biologie Marine*, *10*, 139–161.

Cabioch, J. (1972). Étude sur les Corallinacées. II. La morphogenèse; conséquences systématiques et phylogénétiques. *Cahiers de Biologie Marine*, *13*, 137–288.

Cabioch, J. (1988). Morphogenesis and generic concepts in coralline algae – a reappraisal. *Helgoländer Wissenschaftliche Meeresuntersuchungen*, *42*, 493–509.

Carro, B., Lopez, L., Peña, V., Bárbara, I., & Barreiro, R. (2014). DNA barcoding allows the accurate assessment of European maerl diversity: A proof-of-concept study. *Phytotaxa*, *190*, 176–189.

Chamberlain, Y. M. (1994). Mastophoroideae Setchell. In L. M. Irvine & Y. M. Chamberlain (Eds.), *Seaweeds of the British Isles: Volume 1. Rhodophyta. Part 2B. Corallinales. Hildenbrandiales* (pp. 113–158). HMSO.

Chamberlain, Y. M., & Irvine, L. M. (1994). Lithophylloideae Setchell. In L. M. Irvine & Y. M. Chamberlain (Eds.), *Seaweeds of the British Isles: Volume 1. Rhodophyta. Part 2B. Corallinales. Hildenbrandiales* (pp. 58–112). HMSO.

Chamberlain, Y. M., & Keats, D. W. (1994). Three melobesioid crustose coralline red algae from South Africa: *Leptophytum acervatum* (Foslie) comb. nov., *L. foveatum* sp. nov. and *L. ferox* (Foslie) comb. nov. *Phycologia*, *33*, 111–133.

Coutinho, L. M., Gomes, F. P., Sissini, M. N., Vieira-Pinto, T., de Oliveira Henriques, M. C. M., Oliveira, M. C., Horta, P. A., & de Barros Barreto, M. B. B. (2022). Cryptic diversity in non-geniculate coralline algae: A new genus *Roseolithon* (Hapalidiales, Rhodophyta) and seven new species from the Western Atlantic. *European Journal of Phycology*, *57*, 227–250.

Crouan, H. M., & Crouan, P. L. (1867). *Florule du Finistère*. F. Klincksieck.

Foslie, M. (1895). The Norwegian forms of *Lithothamnion*. *Det Kongelige Norske Videnskabers Selskabs Skrifter*, *1894*, 29–208.

Foslie, M. (1898). List of species of the lithothamnia. *Det Kongelige Norske Videnskabers Selskabs Skrifter*, *1898*(3), 1–11.

Foslie, M. (1900). New or critical calcareous algae. *Det Kongelige Norske Videnskabers Selskabs Skrifter*, *1899*(5), 1–34.

Gabrielson, P. W., Hughey, J. R., & Diaz-Pulido, G. (2018). Genomics reveals abundant speciation in the coral reef building alga *Porolithon onkodes* (Corallinales, Rhodophyta). *Journal of Phycology*, *54*, 429–434.

Gabrielson, P. W., Maneveldt, G. W., Hughey, J. R., & Peña, V. (2023). Taxonomic contributions to Hapalidiales (Corallinophycidae, Rhodophyta): *Boreolithothamnion* gen. nov., *Lithothamnion* redefined and with three new species and *Roseolithon* with new combinations. *Journal of Phycology*, *59*, 751–774.

Gherardi, D. F., & Bosence, D. W. (1999). Modeling of the ecological succession of encrusting organisms in recent coralline-algal frameworks from Atol das Rocas, Brazil. *PALAIOS*, *14*, 145–158.

Gomes, F. P., Lyra, M. D. B., Vieira-Pinto, T., Jesionek, M. B., Coutinho, L. M., Henriques, M. C. M. D. O., Bahia, R. D. G., Salgado, L. T., Oliveira, M. C., & Barros-Barreto, M. B.

B. D. (2024). Survey of non-geniculate coralline red algae from Brazil and the identification of four new species of *Lithophyllum* (Corallinales, Corallinophycidae). *Phycologia*, *63*, 339–359.

Guy-Haim, T., Silverman, J., Raddatz, S., Wahl, M., Israel, A., & Rilov, G. (2016). The carbon turnover response to thermal stress of a dominant coralline alga on the fast warming Levant coast. *Limnology and Oceanography*, *61*, 1120–1133.

Harvey, A. S., & Woelkerling, W. J. (1995). An account of *Austrolithon intumescens* gen. et sp. nov. and *Boreolithon van-heurckii* (Heydrich) gen. et comb. nov. (Austrolithoideae subfam. nov., Corallinaceae, Rhodophyta). *Phycologia*, *34*, 362–382.

Harvey, W. H. (1849). *Nereis Australis, or algae of the Southern Ocean. Part II*. Reeve.

Hernandez-Kantun, J. J., Gabrielson, P. W., Hughey, J. R., Pezzolesi, L., Rindi, F., Robinson, N. M., Peña, V., Riosmena-Rodriguez, R., Le Gall, L., & Adey, W. (2016). Reassessment of the branched *Lithophyllum* spp. (Corallinales, Rhodophyta) in the Caribbean Sea with global implications. *Phycologia*, *55*, 619–639.

Hernandez-Kantun, J. J., Rindi, F., Adey, W. H., Heesch, S., Peña, V., Le Gall, L., & Gabrielson, P. W. (2015). Sequencing type material resolves the identity and distribution of the generitype *Lithophyllum incrustans*, and related European species *L. hibernicum* and *L. bathyporum* (Corallinales, Rhodophyta). *Journal of Phycology*, *51*, 791–807.

Heydrich, F. (1897). Melobesieae. *Berichte der Deutschen Botanischen Gesellschaft*, *15*, 403–420.

Hind, K. R., Gabrielson, P. W., Jensen, C. P., & Martone, P. T. (2016). *Crusticorallina* gen. nov., a nongeniculate genus in the subfamily Corallinoideae (Corallinales, Rhodophyta). *Journal of Phycology*, *52*, 929–941.

Hind, K. R., Gabrielson, P. W., Jensen, C. P., & Martone, P. T. (2018). Evolutionary reversals in *Bossiella* (Corallinales, Rhodophyta): First report of a coralline genus with both geniculate and non-geniculate species. *Journal of Phycology*, *54*, 788–798.

Hind, K. R., & Saunders, G. W. (2013). A molecular phylogenetic study of the tribe Corallineae (Corallinales, Rhodophyta) with an assessment of genus-level taxonomic features and descriptions of novel genera. *Journal of Phycology*, *49*, 103–114.

Hind, K. R., Starko, S., Burt, J., Lemay, M., Salomon, A., & Martone, P. T. (2019). Trophic control of cryptic coralline algal diversity. *Proceedings of the National Academy of Sciences*, *116*, 15080–15085.

Irvine, L. M., Chamberlain, Y. M., & Johansen, H. W. (1994). Introduction. In L. M. Irvine & Y. M. Chamberlain (Eds.), *Seaweeds of the British Isles Volume 1. Rhodophyta. Part 2B. Corallinales. Hildenbrandiales* (pp. 1–30). HMSO.

Jardim, V. L., Gauthier, O., Toumi, C., & Grall, J. (2022). Quantifying maerl (rhodolith) habitat complexity along an environmental gradient at regional scale in the Northeast Atlantic. *Marine Environmental Research*, *181*, 105768.

Jardim, V. L., Grall, J., Barros-Barreto, M. B., Bizien, A., Benoit, J., Braga, J. C., Brodie, J., Burel, T., Cabrito, A., Diaz-Pulido, G., Gagnon, P., Hall-Spencer, J. M., Helias, M., Horta, P. A., Joshi, S., Kamenos, N. A., Kolzenburg, R., Krieger, E. C., Legrand, E., … Burdett, H. L. (2025). A common terminology to unify research and conservation of coralline algae and the ecosystems they create. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *35*, e70121.

Jeong, S. Y., Diaz-Pulido, G., Maneveldt, G. W., Gabrielson, P. W., Nelson, W. A., Won, B. Y., & Cho, T. O. (2022). *Phymatolithopsis* gen. nov. (Hapalidiales, Corallinophycidae, Rhodophyta) based on molecular and morpho-anatomical evidence. *Journal of Phycology*, *58*, 161–178.

Jeong, S. Y., Gabrielson, P. W., Hughey, J. R., Hoey, A. S., Cho, T. O., Abdul Wahab, M. A., & Diaz-Pulido, G. (2023). New branched *Porolithon* species (Corallinales, Rhodophyta) from the Great Barrier Reef, Coral Sea, and Lord Howe Island. *Journal of Phycology*, *59*, 1179–1201.

Jeong, S. Y., Nelson, W. A., Sutherland, J. E., Peña, V., Le Gall, L., Diaz-Pulido, G., Won, B. Y., & Cho, T. O. (2021). Corallinapetrales and Corallinapetraceae: A new order and family of coralline red algae including *Corallinapetra gabrielii* comb. nov. *Journal of Phycology*, *57*, 849–862.

Jesionek, M. B., Bahia, R. G., Hernández-Kantún, J. J., Adey, W. H., Yoneshigue-Valentin, Y., Longo, L. L., & Amado-Filho, G. M. (2016). A taxonomic account of non-geniculate coralline algae (Corallinophycidae, Rhodophyta) from shallow reefs of the Abrolhos Bank, Brazil. *Algae*, *31*, 317–340.

Johansen, H. W. (1969). Morphology and systematics of coralline algae with special reference to Calliarthron. *University of California Publications in Botany*, *49*, 1–78.

Johansen, H. W. (1981). *Coralline algae, a first synthesis*. CRC Press.

Kato, A., Baba, M., & Suda, S. (2011). Revision of the Mastophoroideae (Corallinales, Rhodophyta) and polyphyly in nongeniculate species widely distributed on Pacific coral reefs. *Journal of Phycology*, *47*, 662–672.

Kato, A., Basso, D., Caragnano, A., Rodondi, G., Le Gall, L., Peña, V., Hall-Spencer, J. M., & Baba, M. (2022). Morphological and molecular assessment of *Lithophyllum okamurae* with the description of *L. neo-okamurae* sp. nov. (Corallinales, Rhodophyta). *Phycologia*, *61*, 117–131.

Keats, D. W., Maneveldt, G., & Chamberlain, Y. M. (2000). *Lithothamnion superpositum* Foslie: A common crustose red alga (Corallinaceae) in South Africa. *Cryptogamie Algologie*, *21*, 381–400.

Kim, G. W., Jeong, S. Y., Won, B. Y., & Cho, T. O. (2024). Distribution pattern of a new record crustose red alga, *Lithophyllum neo-okamurae* (Corallinales, Rhodophyta), in Korea. *Environmental Biology Research*, *42*, 258–266.

Kützing, F. T. (1841). Ueber die "Polypieres calcifères" des Lamouroux. In K. C. F. Fischer (Ed.), *Zu der öffentlichen Prüfung sämmtlicher Classen der Realschule zu Nordhausen 1841* (pp. 3–34). Realschule.

Kützing, F. T. (1843). *Phycologia generalis*. F. A. Brockhaus.

Kützing, F. T. (1849). *Species algarum*. F. A. Brockhaus.

Leão, L. A., Bahia, R. D. G., Karez, C. S., Salgado, L. T., & Pereira, R. C. (2024). Revisiting the evolution of non-geniculate coralline algae taxonomy: History and perspectives. *Aquatic Botany*, *194*, 103788.

Lebrato, M., Andersson, A. J., Ries, J. B., Aronson, R. B., Lamare, M. D., Koeve, W., Oschlies, A., Iglesias-Rodriguez, M. D., Thatje, S., Amsler, M., Vos, S. C., Jones, D. O. B., Ruhl, H. A., Gates, A. R., & McClintock, J. B. (2016). Benthic marine calcifiers coexist with $CaCO_3$-undersaturated seawater worldwide. *Global Biogeochemical Cycles*, *30*, 1038–1053.

Lemoine, M. (1910). Répartition et mode de vie du maërl (*Lithothamnium calcareum*) aux environs de Concarneau (Finistère). *Annales de L'institut Océanographique, Monaco*, *1*, 1–28.

Lemoine, M. (1913). Mélobésiées. Revision des Mélobésiées antarctiques. In Anon (Ed.), *Deuxième Expédition Antarctique Française (1908–1910) Commandée par le Dr. Jean Charcot. Sciences Naturelles, Documents Scientifiques, Botanique* (Vol. *1*, pp. 1–67, pls 1–2). Masson et Cie.

Lemoine, M. P. (1929). Les Corallinacées de l'Archipel des Galapagos et du Golfe de Panama. *Archives du Muséum National D'Historie Naturelle*, *6*, 37–88.

Littler, D. S., & Littler, M. M. (2000). *Caribbean reef plants*. OffShore Graphics.

Littler, D. S., & Littler, M. M. (2003). *South Pacific reef plants*. OffShore Graphics.

Littler, M. M., & Littler, D. S. (1999). Castles built by a chiton from the great Astrolobe reef, Fiji. *Coral Reefs*, *18*, 158.

Littler, M. M., & Littler, D. S. (2013). The nature of crustose coralline algae and their interactions on reefs. *Smithsonian Contributions to the Marine Sciences*, *39*, 199–212.

Littler, M. M., Littler, D. S., & Taylor, P. R. (1983). Evolutionary strategies in a tropical barrier reef system: Functional-form groups of marine macroalgae. *Journal of Phycology*, *19*, 229–237.

Littler, M. M., Littler, D. S., & Taylor, P. R. (1995). Selective herbivore increases biomass of its prey: A chiton-coralline reef-building association. *Ecology*, *76*, 1666–1681.

Maneveldt, G. W., Gabrielson, P. W., & Kangwe, J. (2017). *Sporolithon indopacificum* sp. nov. (Sporolithales, Rhodophyta) from tropical western Indian and western Pacific oceans: First report, confirmed by DNA sequence data, of a widely distributed species of *Sporolithon*. *Phytotaxa*, *326*, 115–128.

Maneveldt, G. W., Gabrielson, P. W., Townsend, R. A., & Kangwe, J. (2019). *Lithophyllum longense* (Corallinales, Rhodophyta): A species with a widespread Indian Ocean distribution. *Phytotaxa*, *419*, 149–168.

Maneveldt, G. W., Jeong, S. Y., Hughey, J. R., & Gabrielson, P. W. (2024). *Phymatolithopsis acervata* comb. nov., and *P. roseola* sp. nov. (Hapalidiales, Rhodophyta) from South Africa with a comment on infraordinal classification. *Botanica Marina*, *67*, 249–275.

Maneveldt, G. W., & Keats, D. W. (2008). Effects of herbivore grazing on the physiognomy of the coralline alga *Spongites yendoi* and on associated competitive interactions. *African Journal of Marine Science*, *30*, 581–593.

Maneveldt, G. W., & Keats, D. W. (2014). Taxonomic review based on new data of the reef-building alga *Porolithon onkodes* (Corallinaceae, Corallinales, Rhodophyta) along with other taxa found to be conspecific. *Phytotaxa*, *190*, 216–249.

Maneveldt, G. W., & Keats, D. W. (2016). Taxonomic review based on new morpho-anatomical data of the algae *Porolithon craspedium* and *P. gardineri* (Corallinaceae, Corallinales, Rhodophyta), and comments on other taxa ascribed to the genus. *Phytotaxa*, *289*, 1–35.

Maneveldt, G. W., & van der Merwe, E. (2012). *Heydrichia cerasina* sp. nov. (Sporolithales, Corallinophycidae, Rhodophyta) from the southern-most tip of Africa. *Phycologia*, *51*, 11–21.

Martone, P. T., Lindstrom, S. C., Miller, K. A., & Gabrielson, P. W. (2012). *Chiharaea* and *Yamadaia* (Corallinales, Rhodophyta) represent reduced and recently derived articulated coralline morphologies. *Journal of Phycology*, *48*, 859–868.

Masaki, T. (1968). Studies on the Melobesioideae of Japan. *Memoirs of the Faculty of Fisheries Hokkaido University*, *16*, 1–80.

Mauffrey, A. R. L., Cappelatti, L., & Griffin, J. N. (2020). Seaweed functional diversity revisited: Confronting traditional groups with quantitative traits. *Journal of Ecology*, *108*, 2390–2405.

McCoy, S. J., & Kamenos, N. A. (2015). Coralline algae (Rhodophyta) in a changing world: Integrating ecological, physiological, and geochemical responses to global change. *Journal of Phycology*, *51*, 6–24.

Min-Khant-Kyaw, Kato, A., Adachi, K., Iryu, Y., & Baba, M. (2024). Coralline red algal species diversity at a shallow rhodolith bed in warm-temperate Japan, including two new species of *Roseolithon* (Hapalidiales, Corallinophycidae). *Phycologia*, *63*, 520–533.

Moosa, W., Phillips, J., & Maneveldt, G. W. (2025). The grazer *Cymbula oculus* (Patellogastropoda: Patellidae) serves as an important settlement substrate for several of its macroalgal prey. *African Journal of Marine Science*, *47*, 1–11.

Nash, M. C., Diaz-Pulido, G., Harvey, A. S., & Adey, W. H. (2019). Coralline algal calcification: A morphological and process-based understanding. *PLoS One*, *14*, e0221396.

Nelson, W. A., Sutherland, J. E., Farr, T. J., Hart, D. R., Neill, K. F., Kim, H. J., & Yoon, H. S. (2015). Multi-gene phylogenetic analyses of New Zealand coralline algae: *Corallinapetra novaezelandiae* gen. et sp. nov. and recognition of the Hapalidiales ord. nov. *Journal of Phycology*, *51*, 454–468.

Norris, R. E., & Lebednik, P. A. (1970). *Aleutian coralline project* (Report to the National Science Foundation) .

Peña, V., & Torres, T. R. D. G. (2021). *Lithophyllum artabricum* V.Peña, sp. nov. (Corallinales, Rhodophyta): A cryptic species in the Atlantic Iberian Peninsula hitherto assigned to *Lithophyllum stictiforme* (Areschoug) hauck. *Cryptogamie Algologie*, *42*, 153–172.

Pezzolesi, L., Falace, A., Kaleb, S., Hernandez-Kantun, J. J., Cerrano, C., & Rindi, F. (2017). Genetic and morphological variation in an ecosystem engineer, *Lithophyllum byssoides*, (Corallinales, Rhodophyta). *Journal of Phycology*, *53*, 146–160.

Pezzolesi, L., Peña, V., Le Gall, L., Gabrielson, P. W., Kaleb, S., Hughey, J. R., Rodondi, G., Hernandez-Kantun, J. J., Falace, A., Basso, D., Cerrano, C., & Rindi, F. (2019). Mediterranean *Lithophyllum stictiforme* is a genetically diverse species complex: Implications for species circumscription, biogeography and conservation of coralligenous habitats. *Journal of Phycology*, *55*, 473–492.

Printz, H. (1929). *M. Foslie – contributions to a monograph of the Lithothamnia*. Det Kongelige Norske Videnskabers Selskab Museet.

Puckree-Padua, C. A., Gabrielson, P. W., Hughey, J. R., & Maneveldt, G. W. (2020). DNA sequencing of type material reveals *Pneophyllum marlothii* comb. nov. from South Africa and *P. discoideum* comb. nov. (Chamberlainoideae, Corallinales, Rhodophyta) from Argentina. *Journal of Phycology*, *56*, 1625–1641.

Puckree-Padua, C. A., Gabrielson, P. W., & Maneveldt, G. W. (2021). DNA sequencing reveals three new species of *Chamberlainium* (Corallinales, Rhodophyta) from South Africa, all formerly passing under *Spongites yendoi*. *Botanica Marina*, *64*, 19–40.

Puckree-Padua, C. A., Gabrielson, P. W., & Maneveldt, G. W. (2022). *Chamberlainium* (Corallinales, Rhodophyta) in South Africa, an exemplar for the study of coralline algae, description of *C. tenue* sp. nov., biogeography of the genus, and species keys. *South African Journal of Botany*, *150*, 178–193.

Puckree-Padua, C. A., Haywood, A., Gabrielson, P. W., & Maneveldt, G. W. (2020). Reassignment of some south African species to *Chamberlainium*, with a comment about the recognition of families of Corallinales (Rhodophyta). *Phycologia*, *59*, 464–496.

Rendina, F., Buonocore, E., di Montanara, A. C., & Russo, G. F. (2022). The scientific research on rhodolith beds: A review through bibliometric network analysis. *Ecological Informatics*, *70*, 101738.

Richards, J. L., Saunders, G. W., Hughey, J. R., & Gabrielson, P. W. (2021). Reinstatement of Indian Ocean *Porolithon coarctatum* and *P. gardineri* based on sequencing type specimens, and *P. epiphyticum* sp. nov. (Corallinales, Rhodophyta), with comments on subfamilies Hydrolithoideae and Metagoniolithoideae. *Botanica Marina*, *64*, 363–377.

Riosmena-Rodríguez, R. (2017). Natural history of rhodolith/maërl beds: Their role in near-shore biodiversity and management. In R. Riosmena-Rodríguez, W. Nelson, & J. Aguirre (Eds.), *Rhodolith/maërl beds: A global perspective* (pp. 3–26). Springer.

Schwoerbel, J., Brodie, J., Calderon, M. S., Gabrielson, P. W., Kato, A., Gall, L., Maneveldt, G. W., Maridakis, C., Martone, P. T., Moro, I., Mrowicki, R. J., Nelson, W. A., Peña, V., Rindi, F., Rousseau, F., Schils, T., Tâmega, F. T. S., & Trentin, R. (2026). Adapting the growth form concept to geniculate coralline algae. *Journal of Phycology*, *62*.

Smith, J. E., Brainard, R., Carter, A., Grillo, S., Edwards, C., Harris, J., Lewis, L., Obura, D., Rohwer, F., Sala, E., Vroom, P. S., & Sandin, S. (2016). Re-evaluating the health of coral reef communities: Baselines and evidence for human impacts across the central Pacific. *Proceedings of the Royal Society B: Biological Sciences*, *283*, 20151985.

Smith, J. N., Mongin, M., Thompson, A., Jonker, M. J., De'ath, G., & Fabricius, K. E. (2020). Shifts in coralline algae, macroalgae, and coral juveniles in the great barrier reef associated with present-day ocean acidification. *Global Change Biology*, *26*, 2149–2160.

Steneck, R. S., & Adey, W. H. (1976). The role of environment in control of morphology in *Lithophyllum congestum*, a Caribbean algal ridge builder. *Botanica Marina*, *19*, 197–215.

Steneck, R. S., & Dethier, M. N. (1994). A functional group approach to the structure of algal-dominated communities. *Oikos*, *69*, 476–498.

Steneck, R. S., & Paine, R. T. (1986). Ecological and taxonomic studies of shallow-water encrusting Corallinaceae (Rhodophyta) of the boreal northeastern Pacific. *Phycologia*, *25*, 221–240.

Suneson, S. (1943). The structure, life-history and taxonomy of the Swedish corallinaceae. *Lunds Universitets Ärsskrift N. F*, *39*, 3–63.

Tâmega, F. T., Torrano-Silva, B. N., Oliveira, M. C., Spotorno-Oliveira, P., Calazans, S. H., Rosas-Alquicira, E. F., Coutinho, R., & Peña, V. (2021). Identification of 'articuliths' in a unique algal bed formation from Brazil and description of *Jania cabista* sp. nov. (Corallinales, Rhodophyta). *Phycologia*, *60*, 283–302.

Tâmega, F. T. D. S., Perna, G. H. H., Spotorno-Oliveira, P., Riosmena-Rodríguez, R., & Gonçalves, J. E. D. A. (2017). A unique free-living geniculate coralline algal bed formation. *Marine Biodiversity*, *47*, 373–374.

Tâmega, F. T. S., Grimaldi, G., Macedo, A., Barbosa, S. O., Anderson, A. B., Bastos, E., Freire, V., Moreira, A., Fernandes, C., Figueiredo, M. A. O., Carneiro, P. B., Gouvêa, L. P., & Horta, P. A. (2024). Biodiversity associated with rhodolith beds in Brazil. In P. A. Horta & M. N. Sissini (Eds.), *Brazilian Rhodolith beds. Brazilian marine biodiversity* (pp. 67–103). Springer.

Teichert, S. (2024). Attached and free-living crustose coralline algae and their functional traits in the geological record and today. *Facies*, *70*, 8.

Toomey, D. (1975). Rhodoliths from the upper Palaeozoic of Kansas and the recent – a comparison. *Neues Jahrbuch für Mineralogie, Geologie Und Paläontologie*, *4*, 242–255.

Townsend, R. A., Chamberlain, Y. M., & Keats, D. W. (1994). *Heydrichia woelkerlingii* gen. & sp. nov., a newly discovered non-geniculate red alga (Corallinales, Rhodophyta) from Cape Province, South Africa. *Phycologia*, *33*, 177–186.

Townsend, R. A., & Huisman, J. M. (2004). *Epulo multipedes* gen. et sp. nov. (Corallinaceae, Rhodophyta), a coralline parasite from Australia. *Phycologia*, *43*, 288–295.

van der Merwe, E., & Maneveldt, G. W. (2014). The genus *Phymatolithon* (Hapalidiaceae, Corallinales, Rhodophyta) in South Africa, including species previously ascribed to *Leptophytum*. *South African Journal of Botany*, *90*, 170–192.

van der Merwe, E. V., Miklasz, K., Channing, A., Maneveldt, G. W., & Gabrielson, P. W. (2015). DNA sequencing resolves species of *Spongites* (Corallinales, Rhodophyta) in the Northeast Pacific and South Africa, including *S. agulhensis* sp. nov. *Phycologia*, *54*, 471–490.

Vieira-Pinto, T., Oliveira, M. C., Bouzon, J., Sissini, M., Richards, J. L., Riosmena-Rodríguez, R., & Horta, P. A. (2014). *Lithophyllum* species from Brazilian coast: Range extension of *Lithophyllum margaritae* and description of *Lithophyllum atlanticum* sp. nov. (Corallinales, Corallinophycidae, Rhodophyta). *Phytotaxa*, *190*, 355–369.

Wilks, K. M., & Woelkerling, W. J. (1995). An account of southern Australian species of *Lithothamnion* (Corallinaceae, Rhodophyta). *Australian Systematic Botany*, *8*, 549–583.

Woelkerling, W. J. (1983). A taxonomic reassessment of *Lithophyllum* (Corallinaceae, Rhodophyta) based on studies of R.A. Philippi's original collections. *British Phycological Journal*, *18*, 299–328.

Woelkerling, W. J. (1987). The genus *Choreonema* in southern Australia and its subfamilial classification within the Corallinaceae (Rhodophyta). *Phycologia*, *26*, 111–127.

Woelkerling, W. J., & Campbell, S. J. (1992). An account of southern Australian species of *Lithophyllum* (Corallinaceae, Rhodophyta). *Bulletin of the British Museum (Natural History), Botany Series*, *22*, 1–107.

Woelkerling, W. J., Chamberlain, Y. M., & Silva, P. C. (1985). A taxonomic and nomenclatural reassessment of *Tenarea*, *Titanoderma* and *Dermatolithon* (Corallinaceae, Rhodophyta) based on studies of type and other critical specimens. *Phycologia*, *24*, 317–337.

Woelkerling, W. J., & Ducker, S. C. (1987). *Lesueuria minderiana* gen. et sp. nov. (Corallinaceae, Rhodophyta) from southern and western Australia. *Phycologia*, *26*, 192–204.

Woelkerling, W. J., & Irvine, L. M. (1988). General characteristics of nongeniculate Corallinaceae. In W. J. Woelkerling (Ed.), *The coralline red algae: An analysis of the genera and subfamilies of nongeniculate Corallinaceae* (pp. 4–28). British Museum (Natural History) and Oxford University Press.

Woelkerling, W. J., Irvine, L. M., & Harvey, A. S. (1993). Growth-forms in non-geniculate coralline red algae (Corallinales, Rhodophyta). *Australian Systematic Botany*, *6*, 277–293.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Examples of specimens/species that demonstrate intergrading growth forms. (a) Heydrichia woelkerlingii thalli from South Africa displaying intergrades between encrusting, warty and lumpy growth forms. (b) An as yet unconfirmed Neogoniolithon species from Japan displaying intergrades between imbricate, layered, and foliose growth forms. (c) *Lithophyllum okamurae* rhodoliths from Japan displaying intergrades between warty, lumpy, and fruticose growth forms. (d) *Phymatolithopsis prolixa* from South Africa displaying intergrades between warty, lumpy, and columnar growth forms. (e) An unconfirmed species of Lithothamnion from Australia, similar to *Lithothamnion proliferum*, displaying an intergrade between encrusting and columnar growth forms. (f) An as yet unidentified rhodolith from Brest, France displaying an intergrade between fruticose and convoluted growth forms. Scale bars: (a) = 50 mm; (b)–(f) = 20 mm. Photographs: (a), (d) by G.W. Maneveldt; (b) by A. Kato; (c) by M. Baba; (e) by J. Huisman; (f) by F. Tâmega.

Figure S2. Examples of specimens/species that demonstrate intergrading growth forms. (a) An as yet unidentified Hapalidiales species from South Africa displaying intergrades between encrusting, layered, and foliose growth forms. (b) An as yet unconfirmed Lithophyllum species from Japan displaying an intergrade between discoid and convoluted growth forms. (c) An as yet unidentified coralline from Peru displaying intergrades between encrusting, imbricate, and layered growth forms. (d) *Pneophyllum marlothii* from South Africa displaying intergrades between discoid and warty growth forms. (e) *Chamberlainium impar* from South Africa displaying intergrades between encrusting, warty, and columnar growth forms. (f) *Porolithon lobulatum* specimens from Australia displaying a layered columnar growth form. Scale bars: (a) = 10 mm; (b), (d), (e) = 15 mm; (c) = 40 mm; (f) = 75 mm. Photographs: (a), (d), (e) by G.W. Maneveldt; (b) by M. Baba. (c) by M. Calderon; (f) by G. Diaz-Pulido.

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