



Intrinsic constraints on budding in the deep-sea coral *Dendrophyllia* cf. *horsti* from the Red Sea

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Abstract

Colonial corals display diverse growth forms shaped by both environmental conditions and intrinsic developmental mechanisms. Understanding these internal morphogenetic rules is critical for accurately modeling coral colony formation. In this study, we investigated the intrinsic budding patterns of *Dendrophyllia* cf. *horsti*, an azooxanthellate deep-sea coral from the Red Sea. Using detailed morphological analyses of colony architecture, we identified consistent intrinsic constraints that govern colony development. Lateral corallites bud at a consistent angle (mean 15.9°) relative to the growth axis, and the orientation of the directive septa in daughter corallites remains stable across generations (mean 19.8°). Budding was consistently restricted to two specific sites per internode located near the lateral primary septa. In most colonies, budding occurred on the same side at successive internodes, although occasional observations suggested variation in the relative position of budding sites. These findings suggest that even in deep-sea, non-photosynthetic species, colony morphology is strongly regulated by intrinsic developmental constraints, as previously demonstrated in congeneric species. The results contribute valuable data for simulating coral growth and highlight the importance of intrinsic constraints in shaping colonial forms across Scleractinia.

Keywords Morphogenesis · Coral growth model · Intrinsic regularities · Deep-sea corals · Coral architecture

Introduction

The wide variety of coral growth forms has prompted a focus on understanding morphogenesis and identifying the rules that regulate coral development (Llabrés et al. 2024).

Defining coral growth rules is fundamental to advance models able to describe modular organisms' morphogenesis using a parsimonious set of parameters (Llabrés et al. 2024), as extensively done for trees and silviculture (Honda 1971; Makowski et al. 2019). Models can be used for heuristic purposes and pragmatic applications, such as guiding restoration and conservation efforts on a large scale (Cresswell et al. 2020; Duarte et al. 2020).

Colonial corals, either zooxanthellate or azooxanthellate, present a modular structure composed of repeated clonal units (polyps) that arise through asexual processes such as budding (Hill 1935). Final morphology depends both on genetically intrinsic traits (e.g., Dauget 1991; Rinkevich 2002; Permata and Hidaka 2005; Shaish and Rinkevich 2009; Guerrini et al. 2021) and environmental factors, such as light availability and water flow (Todd 2008; Filatov et al. 2010). Understanding how budding gives rise to individual corallites and their spatial arrangement is key to deciphering colony morphogenesis (Sentoku and Ezaki 2012b). A possible stringent species-specific “morphometric code”, composed of a set of rules, is used repeatedly

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and in different combinations during colony architecture's construction (Rinkevich 2002).

Intrinsic rules governing coral colony morphology have received little attention (Re et al. 2024), compared to other modular organisms, such as clonal plants and marine seagrasses (Sintes et al. 2005; Du and Jiao 2020). Existing studies have largely focused on shallow-water corals, identifying allometric growth rules for shallow water taxa (Gateño and Rinkevich 2003; Shaish and Rinkevich 2009; Guerrini et al. 2021). Yet, there has been a gap in efforts to measure and understand the growth of deep-water species.

Dendrophylliidae Gray, 1847 is a family of scleractinian corals with a worldwide distribution, except for Antarctica, from shallow reef to deep-water (2165 m), comprising 24 genera and 186 species (Hoeksema and Cairns 2024). The family includes both solitary (i.e., the whole genus *Balanophyllia*) and colonial forms (Hoeksema and Cairns 2024). In the latter, the colony is composed of a primary polyp, most often sexually produced, which gives rise to secondary polyps by lateral extratentacular budding in most of the genera, with only some exceptions of intratentacular budding recorded (Cairns 2001). Several species in the family Dendrophylliidae, are not influenced by light, as the lack of photoreceptor genes (i.e., opsin genes, Gornik et al. 2021) in the genus suggests and they obtain nutrients by capturing plankton and suspended organic matter (Gori et al. 2015).

Colonial dendrophylliids may present a monopodial or sympodial growth (Fig. 1A). In monopodial growth, the axial corallite undergoes continuous elongation, concurrently generating lateral offsets. In contrast, sympodial growth involves the axial corallite producing lateral corallites and subsequently halting its growth. Lateral corallites extend the colony upwards and bud off new lateral offsets.

Corals in the family Dendrophylliidae exhibit a peculiar septal arrangement, known as the Pourtalès plan (Fig. 3A; de Pourtalès 1871; Wells 1956). The calice has an oval shape, with the greater calicular diameter (GCD, *sensu* Cairns 1994) aligned with the region containing the two directive septa (Fig. 3A). The four primary septa, excluding the directive septa, are referred to as lateral primary septa. The lesser calicular diameter (LCD) is perpendicular to the directive septa (Fig. 3A). Despite the high variability in growth forms (Cairns 2001), dendrophylliids bud following strict developmental regularities and subtle differences in defined growth parameters (i.e., orientation of the branching plane φ ; budding interval i , and branching angle θ) explain a wide range of colonial growth forms, as demonstrated in a computer simulation by Ohno et al. (2015) and studies on living specimens, limited to the Japan area (Sentoku and Ezaki 2012a, b, c, d, 2013).

Deep-sea corals in the Red Sea were first documented in 1906 (Marenzeller 1906). However, only recent expeditions (Roder et al. 2013; Qurban et al. 2014, 2020; Chimienti et al. 2022; Maggioni et al. 2022; Terraneo et al. 2023; Macrina et al. 2024; Vicario et al. 2024; Nolan et al. 2024) allowed for distribution, biological and morphological traits investigation of these hardly accessible organisms. The physical deep-sea environment in the Red Sea shows a warm but stable water temperature around 21.5 °C, salinity above 40 and low dissolved oxygen (1–2 mgL⁻¹) below the thermocline (>200 m) (Roder et al. 2013), producing unique conditions for the growth of deep-sea corals.

Here, we examine for the first time regularities in the asexual budding mode of the scleractinian coral *Dendrophyllia* cf. *horsti* from the Red Sea and compare the species architecture with the growth pattern of other Dendrophylliidae

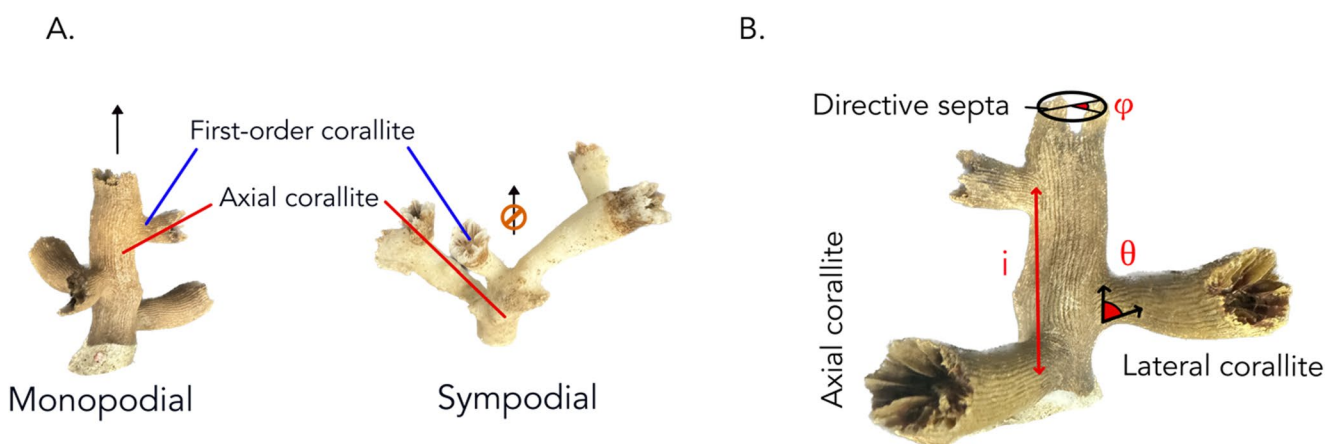


Fig. 1 (A) Schematic of monopodial (sample NTN0160-sample10) versus sympodial growth (sample CHR0262-BIO2); (B) Schematic diagram of the three main growth parameters (sample NTN0160-

sample10), orientation of the branching plane (φ); budding interval (i), and branching angle (θ), playing a fundamental role in defining colony form. This illustration was created in Procreate®

species from previously published accounts. We aim to define the location of budding, orientation, and inclination of the lateral corallites to understand the nature of developmental constraints in the formation of the colony. Although previous studies on shallow water corals, namely *Stylophora pistillata* and *Dipsastraea favus*, suggest the emergence of distinct morphometric landscapes and allometric rules governing polyp budding (Gateño and Rinkevich 2003; Guerini et al. 2021), further studies on the intrinsic regularities of scleractinian corals are still lacking. Addressing this gap is important to implement growth models (e.g. Llabrés et al. 2024), which can be used for exploring morphological variations, predict theoretical growth forms (Eble 2000; McGhee 2006) and guide restoration projects (Cresswell et al. 2020). Insights from deep-sea corals growth patterns could also inform researchers on the genetic constraints driving coral morphogenesis.

Materials and methods

Dendrophylliidae coral specimens ($n=16$) were collected during three research expeditions on board the vessel R/V OceanXplorer: (i) the Deep Blue Expedition, which took place from October to November 2020, (ii) the Red Sea Decade Expedition (RSDE), that explored the Saudi

Arabian Eastern Red Sea coastline (to the limit of the Economic Exclusion Zone) from February 2022 to June 2022, and (iii) the OceanX Relationships Cultivation expedition in June 2022. Corals were collected from the Gulf of Aqaba to the south Red Sea mesophotic and deep coral assemblages at depths from 156 to 344 m (Tab.S3, Fig.S3) using Remote Operated Vehicles (Argus Mariner XL108 ROV, CHR codes) and Triton 3300/3 Submersible (NDR and NTN codes) operations (Tab.S3, Fig. 2A).

After collection, the samples were labelled, photographed (Fig. 2B), subsampled for molecular analyses and dried for subsequent morphological measurements. Samples were identified based on morphological and molecular data (see Supplementary material for the full methodology). Moreover, on a selected sample, Micro Computed Tomography scan was conducted (See Supplementary material).

To assess the regularity in budding, selected features were measured following Sentoku and Ezaki (2012a): (a) greater calicular diameter (GCD); (b) lesser calicular diameter (LCD); (c) total height of the axial corallite (TH); and (d) length of the lateral corallites (LH) with an electronic caliper (Fig. 3A, B). Moreover, (e) budding sites; (f) orientation of the directive septa; and (g) inclination of budding (Fig. 3C) were determined through detailed photographs (Olympus Tough TG-6 camera) using ImageJ/Fiji. Budding sites are defined by their location on the parental corallite

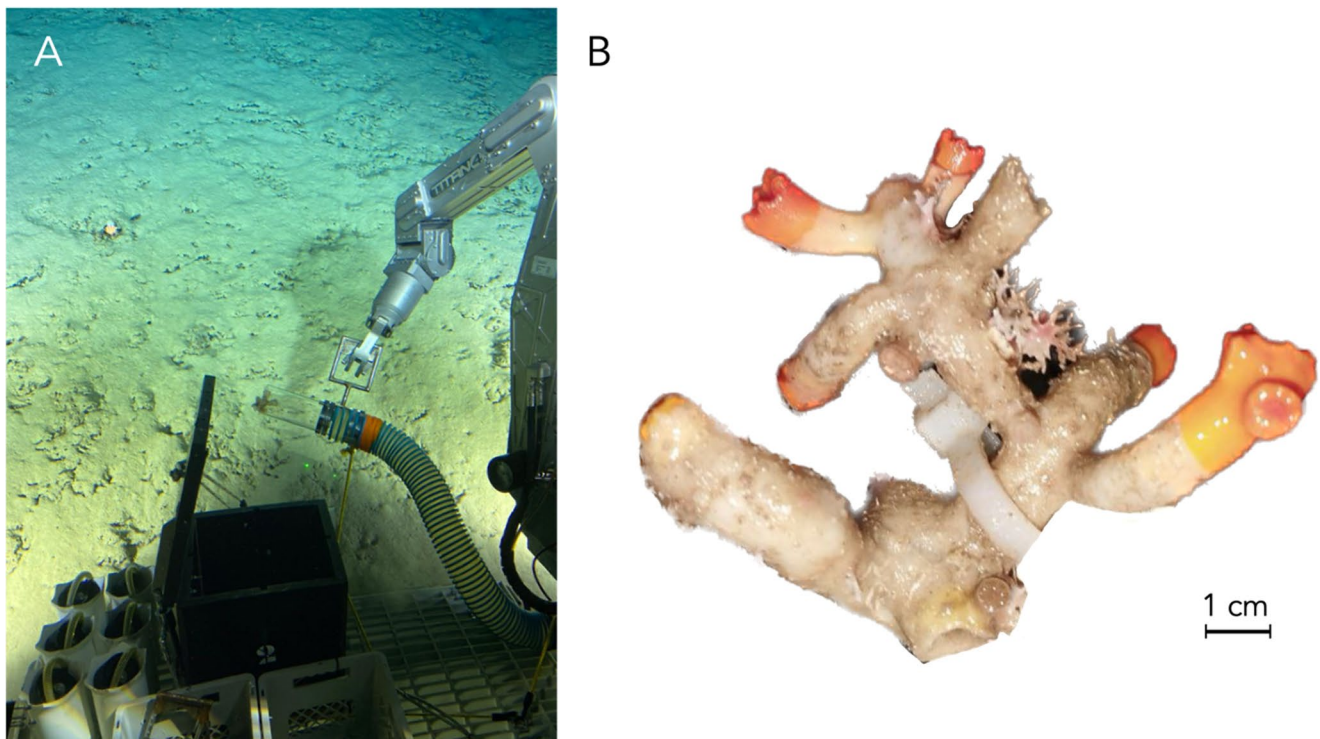


Fig. 2 Sampling operations on board the vessel R/V OceanXplorer with the use of the mechanical arm and suction sampler of the Remote Operated vehicle (ROV) dive CHR279. The green laser was used for

objects measurement (distance 10 cm). **B**) *Dendrophyllia* sp. sample NTN151-BIO22 photographed after collection with an Olympus TG6 camera. This illustration was created in Procreate®

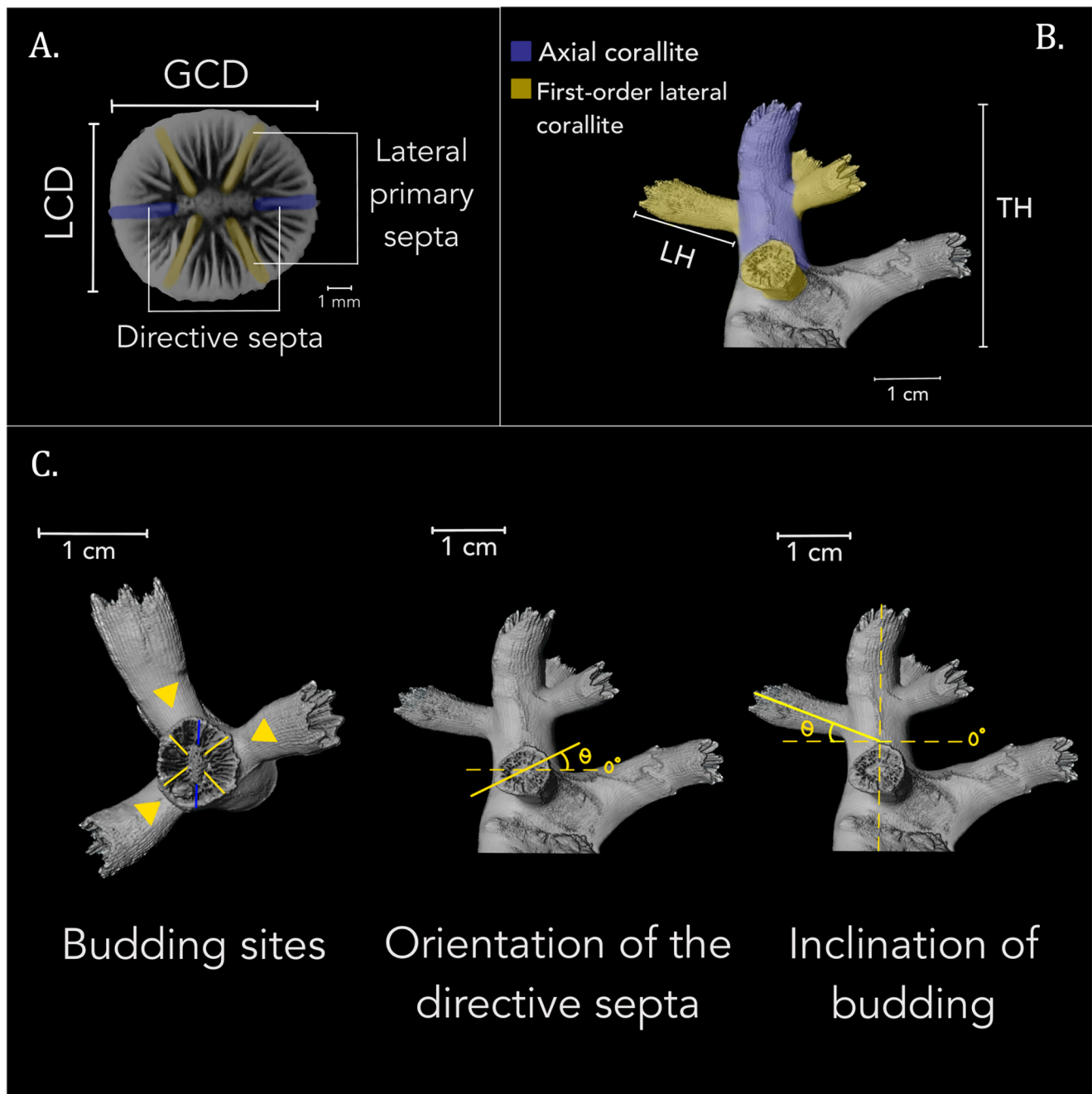


Fig. 3 Micro CT scan images of a dendrophylliid sample. **(A)** Horizontal section of the axial corallite, showing the typical Pourtales plan organization of dendrophylliids corals. Highlighted are the directive septa (in blue), the lateral primary septa (in yellow) and the greater and lesser calicular diameter (GCD and LCD). **(B)** the volume rendering of the coral sample, showing the total height of the corallum (TH) and the length of the lateral corallite (LH). In light blue is shown the axial corallite, and in yellow the first-order lateral corallite. **(C)** From left to right, a schematic view of the measurements conducted on the

samples. Budding sites are the locations on the parental corallite where the new offsets bud. Orientation of the directive septa represent the angle between a line connecting the two directive septa (solid line) and a horizontal line (dotted). Lastly, inclination of budding shows the angle between the direction of the lateral corallites (solid line) and a horizontal line (dotted) oriented perpendicular to the growth direction of the corallite axis (depicted by a yellow dotted line). This illustration was created in Procreate

in respect to the lateral primary septa, where new offsets bud. The orientation of the directive septa in the lateral corallites is measured as the inclination of the directive septa axis relative to the horizontal plane. Finally, the inclination of budding refers to the deviation of the lateral offset from the horizontal line perpendicular to the orientation of the parental corallite.

The average value of GCD, LCD ($\pm$ SD) have been calculated on 74 corallites (axial $n=15$; first-order=41; second-order=18) (Tab.S5, Tab.S6). LH was measured on 96 corallites (first-order=49; second-order=39; third-order=8) (Tab.S7). The greater calicular diameter (GCD) and lesser calicular diameter (LCD) were measured only for integral corallites with distinguished hierarchy in the colony, resulting in a difference in sample size. Inclination of budding were measured on $n=102$ (first-order=54; second-order=43; third-order=4) (Tab.S9) and orientation of the directive septa on $n=50$ corallites (Tab.S8).

For budding sites, orientation of the directive septa and inclination of budding, the data were plotted on rose diagrams with 10° bins and the average, minimum and maximum values calculated. Kruskal-Wallis test has been used for each parameter to test significant differences among the different types of corallites. In case of p -value < 0.05 , a post-hoc Dunn test was run to determine which groups were significantly different. A linear regression between each variable measured, and depth of collection was used to test for the effect of depth.

Results

Samples were identified morphologically and molecularly as *Dendrophyllia cf. horsti* (see Supplementary material). They exhibited a monopodial dendroid growth form, with a growing axial corallite generating lateral offsets. Among the

16 colonies analyzed, the average height was 6.2 ± 3.93 cm ($n=16$), ranging from smaller colonies of 1.4 cm with fewer corallites, to complex colonies of 16 cm in height, without any depth correlation (Tab.S4; Fig.S4). Partial colony mortality often left behind calcium carbonate skeleton, complicating the detection of the primary axial corallite as the living portion continued to grow. The average greater calicular diameter (GCD) dimension was 7.2 ± 0.6 mm ($n=74$) (Table 1, Tab.S5) and 6.21 ± 0.56 mm ($n=74$) for the lesser calicular diameter (LCD) (Tab.S6). However, axial corallites showed significant results in both morphometric measurements compared to second order corallites (GCD: H2 7.02; p -value 0.03; LCD: H2 11.11; p -value 0.004; Tab. S4). No differences were found in corallite size at different depths (Fig.S4). The lateral length of offset corallites (LH) averaged $24.88 \text{ mm} \pm 16.1$ mm ($n=96$) (Tab.S7). Significant differences were found between first and second-order corallites (H2 11.01; p -value 0.004) and LH showed a significant increase with depth ($R^2 = 0.052$; $F1 = 4.077$; p -value = 0.028; Tab.S4, Fig. S4).

In the colonies examined, two lateral corallites typically formed at each internode near the lateral primary septa (Figs. 4 and 5A). In most cases, budding occurred on the same side at successive internodes (Fig. 4B). In a few instances, the relative position of budding sites differed between consecutive internodes, producing an apparent alternation of lateral offsets (Fig. 4A). However, in all specimens budding remained restricted to the same two sites near the lateral primary septa. This observation indicates that the primary developmental constraint lies in the localization of budding sites, while variation in their relative position may occur between internodes. Given the limited number of specimens analyzed with micro-CT, this spatial variation cannot yet be interpreted as a distinct budding rule. The internode length was on average 13.9 ± 4.2 mm, suggesting a relatively consistent spacing in corallite formation.

The orientation of the directive septa in 50 lateral corallites revealed a preferential angle of 10° to 30° (80%) relative to the horizontal plane, with an average angle of $19.8 \pm 7.7^\circ$ ($n=50$) and a maximum of 46.5° (Tab.S8, Fig. 5B). This orientation was maintained across generations, indicating a stable pattern in the alignment of corallites. A significant increase of the angle with the depth was visible in the linear regression ($R^2 = 0.09$; $F1 = 4.64$; p -value = 0.036; Fig. S4B).

Finally, the inclination of budding ranged from 0° to 47° , with an average value of $15.98 \pm 10.55^\circ$ ($n=102$; Tab.S9; Fig. 5C). A majority (62%) of the 102 corallites measured had an inclination between 0° and 20° , suggesting that lateral corallites, regardless of generation, tend to grow almost perpendicular to the parental corallite. About 35% of the lateral corallites budded at angles between 20° and 40° , with only a small percentage (2%) exceeding 40° .

Table 1 GCD, LCD and LH average value (mm) $\pm$ SD measured over different corallite types (axial $n=15$, first $n=41$ and second order $n=18$). LH average (mm) $\pm$ SD measured over different corallite types

Measurement	Corallite type	Average (mm)	SD (mm)	n
Greater Calicular Diameter	Axial	7.86	1.01	15
	First-order	7.18	1.22	41
	Second-order	6.6	1.06	18
	Total	7.19	1.21	74
Lesser Calicular Diameter	Axial	6.78	0.80	15
	First-order	6.17	0.94	41
	Second-order	5.67	0.89	18
	Total	6.17	0.97	74
Length of lateral corallite	First-order	28.64	15.88	49
	Second-order	20.15	16.40	39
	Third-order	24.85	8.23	8
	Total	24.88	16.02	96

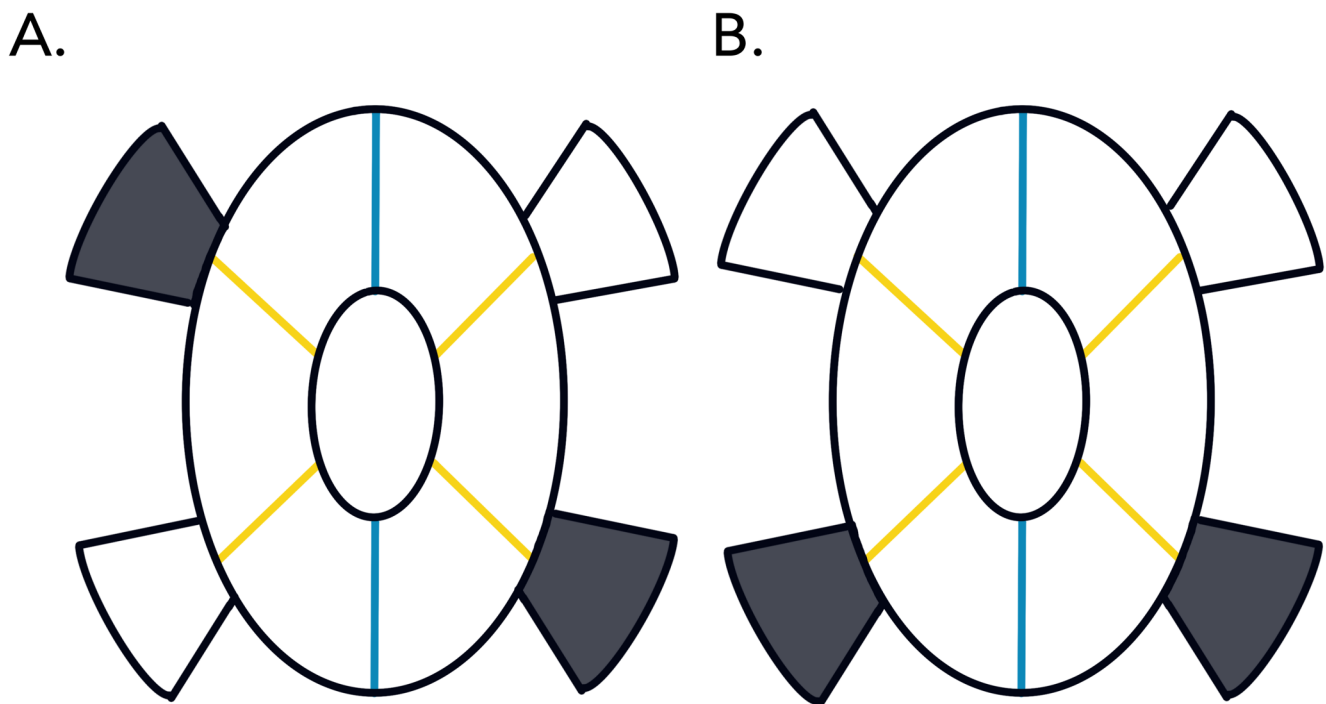


Fig. 4 Schematic representation of the budding sites on the parental corallite (top view of the corallite). The blue lines denote the directive septa, while the yellow lines indicate the primary septa of the parental corallite. Lateral corallites are shown in white for the most recent internode and in dark gray for the previous internode. **(A)** Budding sites

alternate between opposite sides of the axial corallite at consecutive internodes. **(B)** Budding sites occur on the same side of the axial corallite at subsequent internodes. This budding pattern suggests bilateral symmetry along the directive septa. This illustration was created in Procreate®

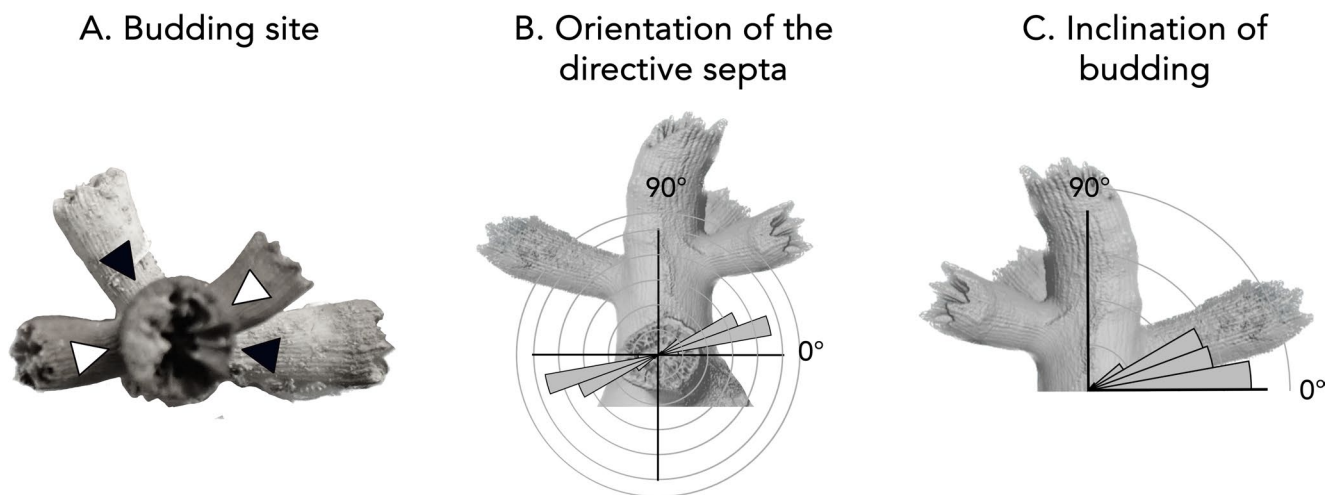


Fig. 5 **(A)** A visual representation of the budding sites on the coral skeleton. **(B)** Rose diagram illustrating the orientation of directive septa in lateral offsets ($n=50$), categorized into 10° bin intervals. The frequency of each range is represented by concentric gray circles

($n=5, 10, 15, 20, 25, 30$). **(C)** Rose diagram showing the inclination angles of lateral budding ($n=102$), also grouped in 10° intervals, with the frequency of each range depicted by gray circles ($n=10, 20, 30, 50$). This illustration was created in Procreate®

The authors acknowledge that the overall sample size is limited, which may constrain the detection of rare or atypical budding patterns. However, given the consistency of the observed regularities across multiple generations and colonies, and considering that these specimens originate from an understudied deep-water region of the Red Sea, we believe the findings provide valuable first insights into the developmental constraints shaping colony morphology in *Dendrophyllia* cf. *horsti*.

Discussion

Our results on the growth pattern of the Red Sea species *Dendrophyllia* cf. *horsti* align with previous findings on other Dendrophylliidae (Table 2), showing strong species-specific intrinsic regularities maintained across generations (Sentoku and Ezaki 2012 a, b, c, 2013; Sentoku et al. 2015a, b). Moreover, a distinct polarity was noted in the parental corallite, determining the budding sites, as previously found in *Dendrophyllia ehrenbergiana*, *D. boshmai* van der Horst, 1926 and *D. cribrosa* Milne Edwards & Haime, 1851 (Sentoku and Ezaki 2012c, 2013). It is important to note that the specimens described by Sentoku and Ezaki (2012c)

as *Dendrophyllia ehrenbergiana* have since been synonymized with *Tubastraea coccinea*. However, it is likely that the specimens analyzed in their study do not belong to the modern genus *Tubastraea*. To maintain alignment with the original source, we refer to the taxon as *D. ehrenbergiana* throughout this manuscript, while acknowledging the taxonomic ambiguity.

These results highlight the significant role of intrinsic genetic forces in shaping colony morphology, regardless of growth mode (monopodial vs. sympodial) or structural form (e.g., dendroid, massive etc.). A computational model used to simulate morphogenesis in dendrophylliids coral showed that subtle modifications in three parameters (inclination of budding, budding orientation and interval of budding) can explain the shift from dendroid to massive forms (Ohno et al. 2015).

Comparison with previous studies confirmed that no budding occurs near the directive septa of the parental corallite in colonial Dendrophylliidae (Sentoku and Ezaki 2012a) and highlights the potential role of lateral primary septa as growth axes. This suggests a genetically predetermined developmental constraint governing the overall colony architecture. In *D. cf. horsti*, budding was consistently constrained to two lateral sites per internode. In most colonies,

Table 2 Summary of the regularities in budding of deep-sea corals. The average value is reported in bold and the maximum and minimum values in brackets. All the species are azooxanthellate except †. *Duncanopsammia peltata* is known to assume a variety of growth forms but in the in the reported study a cup form was used*. § obsolete and possible misidentification in the referenced work - we retain the original name for consistency

Species	Growth form	Budding site	Orientation of directive septa	Inclination of budding	Budding interval	Reference
<i>Dendrophyllia arbuscula</i> van der Horst, 1922	Monopodial Dendroid	Budding occurs near the four lateral primary septa, forming a cross shape.	1.05° (0–20°)	25° (10–40°)	15 mm	Sentoku and Ezaki (2012a)
<i>Tubastraea coccinea</i> Lesson, 1830	Monopodial Massive	Budding occurs near the four lateral primary septa.	5.71° (0–20°)	61° (45–75°)	No vacant space is left	Sentoku and Ezaki (2012b)
<i>Dendrophyllia ehrenbergiana</i> §	Monopodial Bushy	Budding occurs near the two lateral primary septa on a convex side of the parental corallite (bilateral symmetry).	5.89° (0–20°)	42.3° (30–60°)	When space is available	Sentoku and Ezaki (2012c)
<i>Cyathelia axillaris</i> (Ellis & Solander, 1786) (Oculinidae)	Sympodial Bushy	Budding occurs near the two second-order septa.	93° (80–100°)	49° (40–50°)	not reported	Sentoku and Ezaki (2012d)
<i>Duncanopsammia peltata</i> (Esper, 1790) before <i>Turbinaria peltata</i> †	Monopodial Cup form*	Budding occurs near one and/or two lateral primary septa, only on one side (bilateral symmetry).	56° (45–75°)	34° (15–45°)	not reported	Sentoku et al. (2015a)
<i>Dendrophyllia boshmai</i> van der Horst, 1926	Sympodial Dendroid	Budding occurs alternatively at one of the two lateral primary septa on one side only (zig-zag fashion, bilateral symmetry)	7.5° (0–10°)	57.4° (45–60°)	not reported	Sentoku and Ezaki (2013)
<i>Dendrophyllia cribrosa</i> Milne Edwards & Haime, 1851	Sympodial Dendroid	Budding occurs at a specific site at the two lateral primary septa on one side only (helix fashion, bilateral symmetry and specific helix polarity)	5.7° (0–10°)	28.7° (30–45°)	not reported	Sentoku and Ezaki (2013) Sentoku et al. (2015b)
<i>Dendrophyllia</i> cf. <i>horsti</i> Red Sea	Monopodial Dendroid	Budding occurs at a specific site at the two lateral primary septa on one side only	19.8° (5.5–46°)	15.98° (0–47°)	13.9 mm	This work

budding occurred on the same side at successive internodes, although occasional variation in the relative position of budding sites produced an apparent alternation of offsets. Given the limited number of specimens analyzed with micro-CT, this variation cannot yet be interpreted as a distinct budding rule. This pattern may suggest the emergence of bilateral symmetry with a defined polarity in the parental corallite, as previously found in the monopodial species *Dendrophyllia ehrenbergiana* and the two sympodial species *D. boschmai* and *D. cribrosa* (Table 1). However, in *Dendrophyllia ehrenbergiana*, the polarity of the axial corallites is more pronounced, presenting a visible convex and concave side in the axial corallite (Sentoku and Ezaki 2012c). In contrast, *Dendrophyllia cf. horsti* shows no such curvature on the parental corallite. In some colonies, budding appears to alternate between the two lateral primary septa at successive internodes (Fig. 5), although this configuration was not consistently observed across all specimens.

Despite cnidarians are being traditionally characterized by radial symmetry in their bauplan, internal asymmetries and deviations from the stereotyped radially are found in many groups of cnidarians (Gershwin 1999). Matus et al. (2006) demonstrated the asymmetrical expression of regulatory genes during the embryogenesis of sea anemones, suggesting the genetic basis for bilaterality in early cnidarian ancestors. Solitary corals belonging to the order Ceriantharia typically present a bilateral symmetry in their anatomical organization (Malakhov 2016). Recent studies further confirmed the work of Matus and colleagues, indicating the presence of key signaling pathways, essential for body axis development in Bilateria in cnidarians (Holstein 2022). However, little is known on the bilateral symmetry during the asexual budding and whole-body regeneration of scleractinian corals (Luz et al. 2021). The emergence of bilateral symmetry in sessile cnidarians has been postulated as a way to improve internal circulation (i.e., cilia arrangement) and filter feeding efficacy (Finnerty 2005). In *D. ehrenbergiana*, the polarity of individual corallites is reflected in the overall colony architecture and number of offsets in each side of the axial corallite (Sentoku and Ezaki 2012c). Similarly, budding sites in *Dendrophyllia cf. horsti* suggest the emergence of bilateral symmetry in the polyp structure, where intrinsic developmental constraints govern the localization of budding sites at each internode. These findings provide insights for the understanding of ‘shape-making mechanism’ of modular organisms.

The directive septa of the lateral corallites are consistently oriented with an angle comprised between 10–30° with an average value of 19.8° (Fig. 5B). Compared with similar monopodial dendroid Dendrophylliidae, the directive septa of *Dendrophyllia cf. horsti* result more tilted compared to the sub-perpendicular position in *D. arbuscula* van

der Horst, 1922 (Table 1). The orientation of the directive septa of daughter corallites influences colony architecture by defining the position of the next generation of corallites. In *D. arbuscula*, overcrowding often results from the four budding sites at each internode, limiting the colony’s development beyond four corallite generations due to space constraints. By contrast, *Dendrophyllia cf. horsti* produces only two lateral offsets per internode, providing more space for colony growth and daughter corallites addition. We found a significant increase of the angle in corals collected from deeper sites. This orientation could allow the colony to optimize the extension through lateral offsets.

Inclination of budding of the new corallites remained consistently at an average angle of 15.98°, the smallest inclination found in the dendrophylliids species studied (Table 1). However, dendroid colonies generally present a sub-perpendicular inclination of the lateral offsets, as *D. arbuscula* and *D. cribrosa*. A more diagonally upward lateral inclination is visible in species showing a massive or bushy form, to avoid corallites overcrowding and optimize space occupation (Sentoku and Ezaki 2012b).

Azooxanthellate deep-sea corals’ growth is generally less influenced by light, even if they can colonize shallow and mesophotic environments, compared to the phototropic growth of shallow-water colonies (Kaniewska et al. 2009). Although zooxanthellate, the massive species *Duncanopsammia pelatata* Esper, 1790 maintains the same regularities in budding mode despite the need to optimize light acquisition (Sentoku et al. 2015a). Moreover, growth forms of corals have often been interpreted as also shaped by their interaction with the turbulent flow they grow in (Hossain and Staples 2020). Nevertheless, comparing the growth mode of the dendrophylliids species studied and the environment they inhabit, it can be noted that slight changes in these strict intrinsic parameters have enabled different species to occupy several ecological niches (Sentoku and Ezaki 2013), optimize the resources available (Sentoku et al. 2015a) or reduce physical disturbance (Sentoku and Ezaki 2012b). Sympodial forms have been found to be able to grow larger colonies, leading to more effective utilization of resources. However, due to their denser architecture and the higher number of actively growing polyps, these colonies exhibit slower growth rates than monopodial forms and require more abundant food to meet their greater cumulative metabolic demands. As a result, the distributional ranges of sympodial colonies are more restricted compared to monopodial ones (Sentoku and Ezaki 2013).

The overall colony architecture of *Dendrophyllia cf. horsti* (Fig. 6) presents a dendroid structure similar to *D. arbuscula*, however less crowded due to the presence of two offsets per internode. This pattern results in a looser structure, able to grow taller colonies (up to 16 cm) compared



Fig. 6 Corallum of *Dendrophyllia* sp. (sample NDR925_4). This illustration was created in Procreate®

to *D. arbuscula* (5 cm). In this regard, the spatial corallites distribution in the studied species resemble the strategy of sympodial dendrophylliids forms, which efficiently utilize resources by spreading the colony structure (Sentoku and Ezaki 2013). The Red Sea is known for its higher temperature through the entire water column (around 21.5 °C below the thermocline) compared to other ocean basins and low oxygen concentration at depth (Roder et al. 2013; Rasul et al. 2015; Naqvi 2021). Previous studies on the metabolic rates of Red Sea deep-sea corals, including *Dendrophyllia* sp., showed low metabolic and calcification rates compared to deep-sea cold-water corals (Roder et al. 2013). Given the unresolved species-level taxonomy within the genus in Roder et al. (2013), we cannot confirm whether the samples belong to the same species as the ones analyzed in this study. Morphological modifications, such as the reduced tissue area, confined only to the polyp, in the Red Sea deep sea corals have been previously considered an adaptation to minimize the metabolic demand (Roder et al. 2013). Similarly, living tissue limited only around the polyps was observed in the colonies collected for this study (Fig. 2B). A recent study has further highlighted that genes related

to cilia motion and mitochondrial hypometabolism are expressed in Red Sea deep corals, potentially to cope with oligotrophic conditions and low oxygen (Yum et al. 2017). The architectural structure of *Dendrophyllia* cf. *horsti* in the Red Sea is the results of subtle modifications in few morphometric parameters compared to other dendrophylliids species. A more open structure, allowing for a better colony expansion, could increase the colony area in contact with the water, optimizing resource acquisition in an oligotrophic basin, as found in *Desmophyllum pertusum* Linnaeus, 1758 (De Clippele et al. 2018).

Few parameters affect the overall colonial growth form, including budding interval, branch length, corallite size, and the inclination of lateral corallites. Such parameters are maintained constant within species and across generations, suggesting the presence of a species-specific “morphometric code” used repeatedly during growth (Rinkevich 2002). While most parameters appeared conserved, our observation of positional alternation in budding sites should be interpreted cautiously, as further analyses are required to confirm this as a species-specific feature. Future studies including a larger number of micro-CT scans across multiple

colonies will be necessary to fully evaluate the range of spatial configurations of budding in this species. These factors should be considered when assessing whether the growth patterns observed in Dendrophylliidae apply more broadly across other taxa. Even the more complex dendroid colonies are generated according to specific universal rules that govern all generations of corallites. Understanding these regularities not only deepens our insights into the construction of colonial metazoans but also offers important clues for improving predictive coral growth models, which will prove fundamental for testing specific biological questions and inform policy makers in conservation and restoration efforts.

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Data availability The datasets generated and analysed during the current study are available in the Supplementary section.

Declarations

Competing Interests The authors have no relevant financial or non-financial interests to disclose.

Ethics Approval Samples collection has been conducted following in-

stitutional guidelines under Saudi Arabia Royal decree approval.

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