

Classification of cheilostome polymorphs

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1. Introduction

It is still debated whether apparent increases in biological complexity are driven by natural selection for greater efficiency¹ or are merely due to ‘diffusive’ processes away from minimum complexity.² The continued existence of simple bacteria and the reduction of complexity in many species (such as eye degeneration in cave fish,³ digit loss in squamate reptiles,^{4,5} and the evolution of lungless salamanders⁶) favor a diffusive explanation over long time scales.^{7,8,9} Evolution does not ensure that the “end point” of a lineage will be more complex than its ancestors. Despite this, backtracking through some grades of complexity appears to be impossible: no multicellular organism has produced

a unicellular lineage, and no eukaryote has generated a prokaryotic line.¹⁰

Perhaps complexity should be selected for because it allows organisms greater efficiency through division of labor (via cell types, organ systems, polymorphs, etc.).¹¹ Evidence for active trends in increasing complexity can be observed through changes in minimum complexity, subclade skewness, and ancestor-descendant comparisons.¹² Indeed, directional selection for increased complexity has been found within clades¹³ (suture structures in ammonoids,¹⁴ limb tagmosis in arthropods,^{15,16} and hinge geometry of brachiopods^{17,18}), though these trends can depend on the measure of complexity used.^{19,20}

There is also an apparent cost to complexity: increases in the number of traits in an organism results in a decrease in the amount of “progress” a single mutation can achieve toward optimal trait values.²¹ Although mutation rate does increase with complexity, it does not do so quickly enough to eliminate the cost.^{22,23} This means that more complex organisms are less adaptable than their simpler counterparts.²⁴ However, the cost of complexity can be alleviated by features that increase adaptive potential. This evolvability can be enhanced either by reducing the lethality of mutations or reducing the number of mutations required to produce a new trait.²⁵ One of the most important ways to do this is through modular construction.²⁶ Modularity (compartmentalization) increases adaptive potential by allowing modules to experience and respond to selection separately.²⁷ This is similar in principal to fire doors in a building: if there is a fire (a deleterious mutation) the damage is contained within a certain area (module). Adaptive potential and decreases in structural interdependence are further enhanced by module redundancy, which allows function to be preserved while new traits and functions arise in the redundant modules.²⁸

It is clear that modularity can facilitate the evolution of complexity by reducing its cost, but both concepts require further study. Evolutionary questions regarding the existence of less-than-maximal modularity and the secondary integration of modules,²⁹ and those conditions that may select for (or against) modular and complex organisms still need to be addressed. Bryozoans, with their rich fossil record and modular colonial construction, are excellent taxa for exploring these questions. Competitive interactions³⁰ and indirect measures of fecundity (ovicells) are also preserved in bryozoan fossils, allowing researchers to determine the relative success of bryozoan body plans through evolutionary timescales. The Cheilostomata are particularly useful for studying the evolution of complexity and modularity because of their polymorphic zooids and derivative or associated units.³¹ These polymorphs (divergent modules that exhibit discontinuous variation) have arisen independently multiple times in cheilostome evolution,^{32,33} providing multiple temporal/environmental settings to examine (potential) selection for increased complexity.

However, cheilostome polymorphs are currently described using ambiguous and broad terminology. To rectify this, we have created an extensive classification system for cheilostome polymorphs. To the best of our knowledge this has not been attempted before, despite being sorely needed. The classification system presented here provides comprehensive and standardized terminology along with illustrations of key terms. In addition to evolutionary studies, this system will also be useful for taxonomists, ecologists, and zoologists investigating the often unknown or debated functions of these polymorphs.

Readers unfamiliar with bryozoan anatomy should examine Figure 1, which provides an overview of the standard anatomical descriptions used in this classification system. Briefly, an autozoid consists of a cystid (body wall) and a polypide (moveable soft body), which includes the tentacle crown, digestive tract, musculature, and parts of the nervous system.^{34,35} There is a variety of frontal wall morphologies present in cheilostomes (membranous, gymnocystal cribrimorph, umbonuloid, lepralioid, and cryptocystal). Although some cheilostome frontal shields were kenozooidal in origin, they are now so derived that they are no longer recognizable as separate modules or polymorphs. In contrast, the cribrimorph shield differs in comprising discrete spines (costae) and does not appear to be as integrated as other frontal shields. Therefore umbonuloid and lepralioid shields are not considered polymorphs and will not be discussed here. The frontal morphology most pertinent to this classification system is the cribrimorph shield, which is composed of costae (modified spines). Anatomical details of polymorphs are discussed in the specific sections on each.

1.1 Standardized terms and system design

Ambiguous terminology is a threat to good science. The presence of synonyms and vague descriptions introduces an unwanted degree of subjectivity and can invalidate comparisons between studies. Moreover, the terms currently used to describe cheilostome polymorphism neglect the full range of morphological variation present in these structures.

The system complements the classification of colony growth forms by providing a zoid-level and cormidium-level view of polymorphism morphology (discussed in section 1.2).³⁶ Following Hageman *et al.* (1998), it is nonhierarchical in form, allowing statistical comparisons to be made at many levels of detail. A non-hierarchical form allows polymorphs to be described even when important characters are missing (useful for fossil bryozoans), and allows the system to be easily updated. A flexible and updatable system is desirable, since many bryozoans — perhaps with highly irregular morphology — remain to be discovered.³⁷ Our classification system is also comprehensive: it encompasses 86 different traits (with 289 levels) and includes numeric, binary, ordinal, and factor data types. Over two-thirds (~70%) of these traits can be observed in fossil specimens, though this relies strongly on good preservation. A comprehensive system provides increased ecological resolution to examine trait-environment relationships,³⁸ and the inclusion of many datatypes facilitates its statistical use.

This classification attempts to preserve the terminology already in use by bryozoan taxonomists, while providing more stringent definitions. When new terminology had to be introduced, particularly for avicularia, it was drawn from the morphological classifications of plants.³⁹ Parts of the classification follow the work of Vieira *et al.*⁴⁰ and Ostrovsky,^{41,42} though much is based on our extensive examination of specimens, Scanning Electron Microscope (SEM) micrographs, and taxonomic literature.^{43,44,45,46} Illustrations for this system were created using Microsoft Paint, Krita, Inkscape, and ImageJ.

Finally, this system creates the groundwork for a database of polymorphism morphology to be created. Such a database, paired with information on colony form, specimen location, and ecological data will, we hope, be of great use to the bryozoology research community.

1.2 Polymorphism

Variation in bryozoan zooids can be divided into three categories; astogenetic, ontogenetic, and polymorphic.⁴⁷ Astogenetic variation encompasses the differences in shape and size between the ancestrula, zooids in the zone of astogenetic change, and zooids within the zone of astogenetic repetition. Ontogenetic variation refers to changes in shape and size that occur as a zooid develops. Both astogenetic and ontogenetic variation are continuous, which means there is transitional gradient between the different shapes and sizes of zooids present within a colony. This is in contrast to polymorphic variation, which is discontinuous and displays abrupt changes in shape, size, and other characteristics (see Table 1).^{48,49} Like autozooids, polymorphs may also exhibit astogenetic and ontogenetic variation. There are two main categories of bryozoan polymorphism— 1) autozooidal polymorphs and 2) heterozooids.⁵⁰

An autozooidal polymorph retains a protrusible tentacle crown, though it may or may not be able to feed. Autozooidal polymorphs include reproductive zooids, appendaged autozooids, and cyclostome nanozooids (not discussed). Reproductive zooids (specialized male and female zooids) can be distinguished by changes to their cystid and/or polypide (see Table 1). These zooids are typically non-feeding, using their tentacle crowns to facilitate reproduction (e.g. male zooids releasing sperm).⁵¹ Although tentacle number and length can be necessary to distinguish autozooids from reproductive morphs (as in *Odontoporella bishopi*)⁵², the primary concern of this paper is the classification of skeletal characteristics for use in neontology and paleontology.

Appendaged autozooids are capable of feeding and are distinguished from feeding autozooids only by the presence of non-zooidal adventitious modules. These modules are projections from the cystid that 1) are not separated from the zooidal coelom by a pore plate, 2) display reduced integration in form/function, and 3) exhibit variation separately from the parent zooid. A non-kenozooidal spine is an example of a non-zooidal adventitious module because it is a projection of the body wall that is clearly separable from the autozooid (via cuticular spine-bases) and can exhibit a variety of forms (cervicorn, antenniform, fused, etc.). Note that an appendaged autozooid may also host zooidal adventitious modules (heterozooids) in addition to its non-zooidal adventitious modules.

Unlike autozooidal polymorphs, heterozooids do not have a protrusible tentacle crown and are unable to feed.^{53,54} Heterozooids include avicularia, kenozooids, and cyclostome gonozooids (not discussed). In avicularia, which possess a highly modified cystid and musculature, the tentacle crown is reduced to a vestige. In kenozooids the polypide is completely absent.^{55,56}

Zooid Type	Zooid Subtype	Cystid Change	Polypide Change	NZAM	ZAM	Example
Ancestrula	kenozooidal	none	absent	no	no	some <i>Hippothoa</i>
	resembling daughter autozooids	none	var. in T#, feeding	yes/no	yes/no	most taxa
Autozooid (feeding, post ancestrular)	standard	no change	no change	yes/no	yes/no	most taxa
	B-zooid	various shape & size	var. in T#, feeding	yes/no	yes/no	many <i>Steginoporella</i>
Reproductive zooid	male	none	var. in T#, non-feeding	no	yes?	<i>Odontoporella bishopi</i>
		reduced	reduced, non-feeding	yes/no	no	many Hippothoidae
	female	none	var. in T#, feeding	yes/no	yes/no	many taxa
		enlarged zooid	var. in T#, non/feeding	yes/no	yes/no	many Adeonidae
		dwarf zooid	vestigial, non-feeding	no	yes	<i>Haplopoma sciaphilum</i>
Avicularium	vicarious	enlarged mandible, distal tapering, etc.	vestigial	yes/no	yes/no	many taxa
	interzooidal		vestigial	yes/no	no	most <i>Micropora</i>
	interzooidal vibracular		vestigial	yes/no	no?	<i>Setosella</i>
	adventitious		vestigial	no	no	<i>Chaperiopsis</i>
	adventitious vibracular		vestigial	yes/no	yes/no	many Candidae
Kenozooid	space filler - determinate	various	absent	yes/no	yes/no	<i>Spiralaria florea</i>
	space filler - indeterminate	stochastic changes	absent	yes/no	yes/no	many taxa
	spiniform	various	absent	yes/no	no	<i>Bellulopora</i>
	rhizoids	various	absent	yes/no	no	many taxa

Table 1. Variation in the cystid and polypide of cheilostome zooids. Astogenetic and ontogenetic variation in shape and size occur in all zooid types except for irregularly budded space-filling kenozooids, so this is not included in the table. **Cystid change** and **Polypide Change** refer to differences between the zooid and a feeding zooid in the zone of astogenetic repetition. Variation in tentacle number is shortened to “var in T#”, and zooids that can either be feeding or non-feeding are marked as “non/feeding”. **NZAM** shows whether a zooid is able to host non-zooidal adventitious modules (“appendages”), while **ZAM** shows whether a zooid can host zooidal adventitious modules (heterozooids); “yes/no” signifies that both states are manifested, depending on taxon.

1.3 Modularity and the cormidium

Modularity relies on the concept of the “primary module”, which is the basic repeated unit within a structure. In monomorphic bryozoans, which have colonies that consist only of autozooids, the primary module is simply an autozooid. In polymorphic taxa, the primary module is expanded to include the autozooid and its associated polymorphs, which repeat together within the colony. This unit of repeating autozooids and polymorphs is referred to as a cormidium (a “colony within a colony”) since it can carry out most functions vital for life.^{57,58} To reduce ambiguity we are introducing two new terms associated with the cormidium: submodule and paramodule. Submodules are the components of a cormidium and can be autozooids, autozooidal polymorphs, non-zooidal adventitious modules (e.g. non-kenozooidal spines on an autozooid), heterozooids, or multi-zooidal complexes (ovicells, see section 2.6 and Figure 2D, E for submodule examples). The fundamental basis of the cormidium is the autozooid (which provides the energy necessary to carry out other life functions), and therefore a cormidium cannot be composed entirely of non-feeding heterozooids in Bryozoa. Repeating heterozooids within colonies that are not associated with autozooids are referred to as paramodules, (e.g. kenozooids making up a kenozooidal stalk). Therefore a colony can consist of base autozooids, cormidia, and paramodules.

Polymorphic taxa are further complicated by the presence of different cormidia. An extreme version of this can be seen in *Corbulipora tubulifera* Hincks, 1881 which has three discrete cormidial phases.⁵⁹ The phases (1-3) are easily discernible because they occur in distinct bands, possess unique combinations of submodules, and even have different frontal shields.⁶⁰ However, clear cormidial differences do not always occur. Cormidial types may be interspersed with each other (or autozooids and paramodules) seemingly at random, and the changes in submodule composition may be minute. This raises the question of what minimum difference should be used to distinguish cormidia. Distinguishing traits should either change those vital functions that the cormidia can perform, or the magnitude of those functions. Submodule composition directly affects the vital functions of a cormidium, while the number of each submodule type should change the magnitude of those functions.⁶¹ Changes in submodule morphology between cormidia may influence both type and magnitude of vital functions. Here, the key word is “may” – to the best of our knowledge, there have been no investigations into how morphological changes (particularly of heterozooids) influence function. It is likely however, that changes in shape or discontinuous jumps in size would influence function. Therefore, all three distinguishing traits (submodule composition, number of each submodule, and submodule morphology) should be used to distinguish cormidial types.

An appendaged autozooid is a single polymorphic zooid that functions like a cormidium owing to the presence of its non-zooidal adventitious modules. Since the non-zooidal adventitious modules change either the number or magnitude of functions an autozooid can fulfil, the non-zooidal adventitious modules and the autozooid are considered as distinct submodules when describing cormidia. This puts appendaged autozooids in a

grey area between being a single zooid and a cormidium. However, a grey area here facilitates comparisons between autozooids with non-zooidal adventitious modules and autozooids with zooidal adventitious modules (e.g. non-kenozooidal vs kenozooidal spines), and should be maintained.

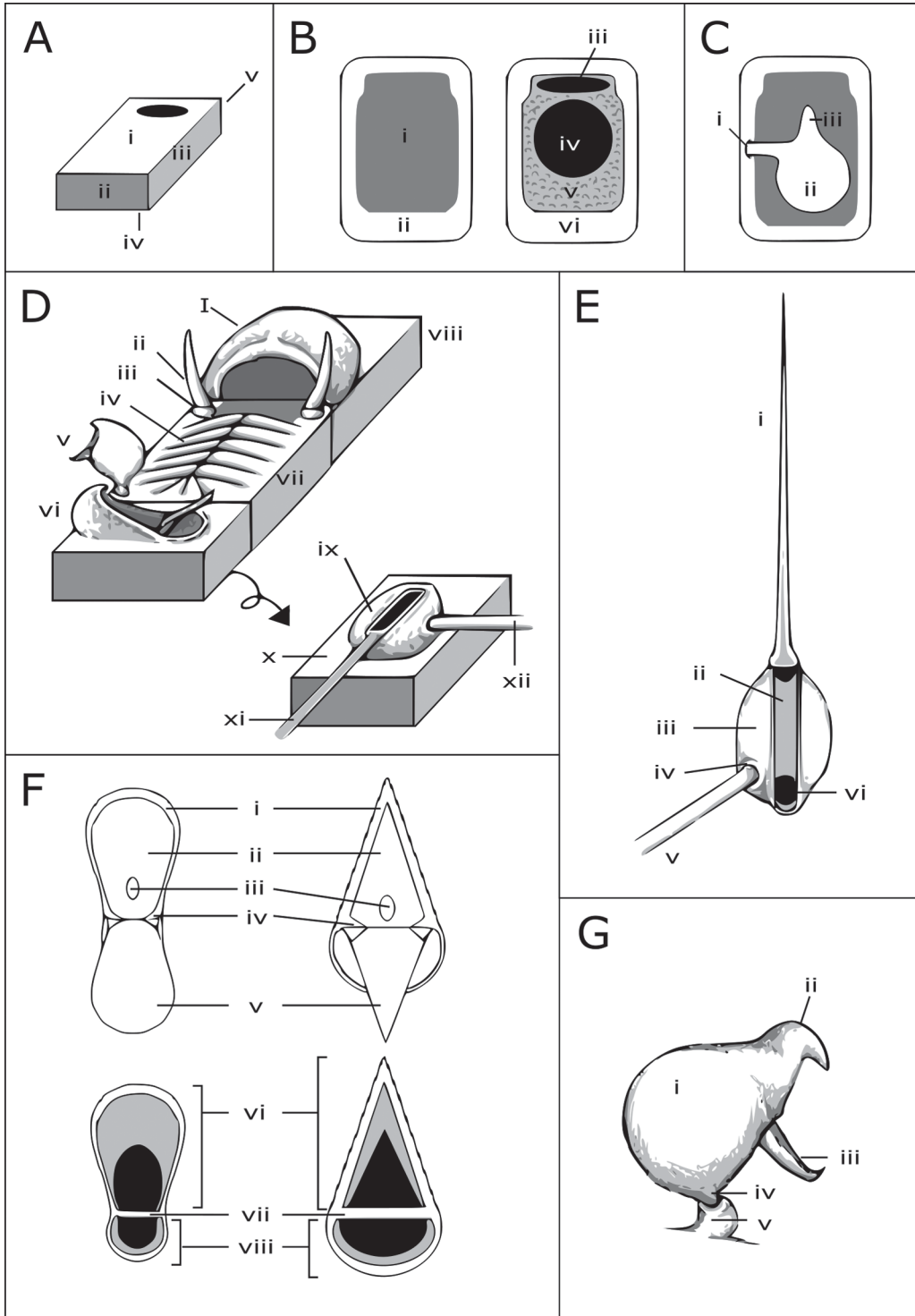
If colonies are monocormidial, then the arrangement of primary modules into higher-level structures is fairly simple (Figure 2D-F). If the colony is nonbranching then the secondary module is the entire colony, while in branching colonies, the secondary modules are branches that repeat within the tertiary structure of the colony.⁶² Colonies with multiple types of cormidia have more complicated secondary structures (Figure 2G-I). In *C. tubulifera*, each cormidial phase can be considered a secondary module that may (phases 2 and 3) or may not (phase 1) repeat within the tertiary structure.⁶³ Other polycormidial colonies have multiple cormidial types interspersed throughout the colony without any visible pattern (e.g. *Chaperiopsis rubida* (Hincks 1881), pers. obs.). The pattern may not be the order of budding, but the relative abundance of each cormidium present in the secondary structure, which may change between branches.

These explorations of definitions may seem overly rigorous, but understanding and defining the modular construction of bryozoans allows us to examine responses to selection pressures at different levels of organization. Selection pressures at the level of the primary module (zooid/cormidium) can be different from those at the level of secondary and tertiary modules (colony level).⁶⁴ A non-modular organism might be caught between two selective pressures, but the modular nature of bryozoans allows them to tailor their zooid-level and colony-level responses separately.⁶⁵ Changing the composition of submodules within cormidia does not restrict the form a colony can take, and vice-versa. This is particularly evident when examining predation. Attacks by zooid-level predators (which damage a single zooid), allow the colony to persist, while attacks by colony-level predators, which damage large parts of the colony or the entire colony, tend to result in colony death.⁶⁶ Although epibionts can be deterred by zooid-level defenses (such as avicularia^{67, 68}, spines⁶⁹ and ovicells⁷⁰) these are not effective against larger predators, which typically consume bryozoans as “bycatch” while pursuing epibionts or the bryozoan’s substratum. Instead, bryozoans avoid large predators through changes in their colony form.⁷¹

1.4 Usage

The classification is organized based on the types of polymorphs present in cheilostomes (avicularia, vibracula, spines, scuta, oecia, and kenozooids including rhizoids). For accessibility, the traits (characters) are organized by the position, shape, size, etc. of those polymorphs. Trait levels (character states) are listed under each trait. If a trait is ordinal or binary then each trait level is listed with a number in parentheses, which is how they should be recorded for statistical analyses. When necessary, the polymorphs, traits and trait-levels are described and illustrated.

To use this classification to its full extent, specimens should be examined under an



SEM. Most characters within the system are minute and may be indistinguishable or unmeasurable by light microscopy (though one character, the internal channels of scuta, does require a light microscope to classify). The user must decide whether to bleach specimens: cuticularly joined structures (spines, mandibles, etc.) will fall off if bleached, but some structures do require bleaching to classify them (lumen pores in spines). Since the system is nonhierarchical, users can handpick those characteristics that are most pertinent to their research. As mentioned previously, this classification system has a wide range of applications: taxonomy; examining complexity and modularity; determining trait-environment relationships; building a database of cheilostome polymorphs; etc.

2. Classification of polymorphs

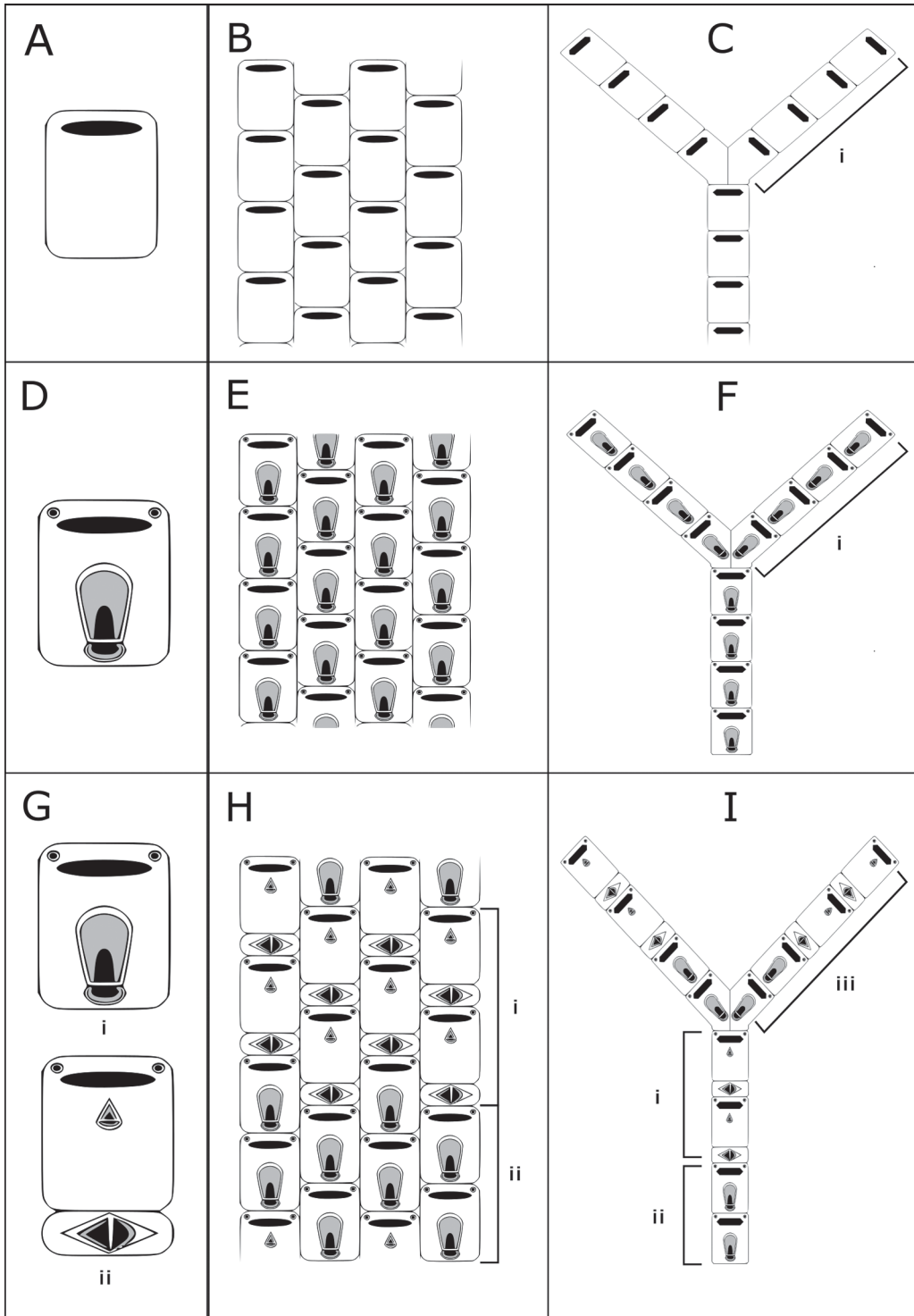
2.1 AVICULARIA

Avicularia are transformed zooids in which the operculum is modified into a mandible and the polypide is reduced to a vestige with a ciliary tuft.^{72,73,74} When the vestige is stimulated, either mechanically or chemically, the mandible is snapped shut against the palatal surface of the rostrum via adductor muscles (see Figure 1F-G for anatomical descriptions).^{75,76}

Type: A general classification of avicularia based on their size and budding pattern (Figure 3A).

- *Vicarious* (0): Distally or distolaterally budded. Generally equal in size to autozooids and replacing them in the budding sequence. May retain functional polypide and gut. May retain functional polypide and gut (as in *Steginoporella*⁷⁷, *Crassimarginatella*⁷⁸, and *Wilbertopora*⁷⁹).
- *Interzooidal* (1): Distally budded. Smaller than autozooids and occur in-between them (i.e., their basal walls touch the substratum in encrusting forms).
- *Adventitious* (2): Budded on frontal, lateral and/or basal walls of autozoid. Smaller than autozooids and occurring upon them (i.e., their basal walls do not touch the substrate in encrusting forms).

Figure 1. Zooid and polymorph anatomy. A. Zooid walls i. frontal, ii. ventral, iii. lateral, iv. basal, v. dorsal; **B. Frontal surface** i. membranous frontal wall, ii. calcified gymnocyst, iii. orifice, iv. opesia, v. cryptocyst, vi. calcified gymnocyst; **C. Scutum anatomy** i. articulated base, ii. proximal lobe, iii. distal lobe; **D. Hypoetheical cormidium** i-vii have the frontal wall facing up, while ix-xii have the basal wall facing up i. oecium of ovicell, ii. spine, iii. spine base, iv. costa of a cribrimorph shield, which lack spine bases, v. adventitious bird's head avicularium, vi. interzooidal sessile avicularium, vii. ovicelled maternal zoid, viii. distal daughter zoid, ix. vibraculum, x. basal wall, xii. vibraculum mandible, xii. rhizoid; **E. Vibracula anatomy** i. mandible, also referred to as a "seta", ii. palatal surface, iii. vibracular chamber, iv. rhizoid pore, v. rhizoid, vi. foramen in palatal surface; **F. Avicularia anatomy** i-v show a relaxed avicularia while vi-viii show skeletonized avicularia, i. rostrum, ii. palatal surface, iii. orifice, where the reduced polypide/ciliary tuft protrudes from, iv. hinge, v. mandible, vi. rostrum, vii. pivot bar, viii. opesia; **G. Bird's head avicularium** i. cystid, ii. rostrum, iii. mandible, iv. peduncle, v. peduncle cushion, which is formed by the autozoid.



Position: The location of the avicularium on its zooid, which is most pertinent for adventitious forms.

- **Zooid Wall:** The budding site of the avicularium, based on the orientation in Mukai *et al.* (1997).⁸⁰ Interzooidal and vicarious avicularia are generally considered dorsally budded.

- *Frontal:* Zooid wall containing orifice (ventral wall)
- *Lateral:* Transverse wall perpendicular to the direction of growth and the frontal wall
- *Distal:* Transverse wall facing the direction of growth
- *Proximal:* Transverse wall facing away from the direction of growth
- *Basal:* Zooid wall opposite frontal wall (dorsal wall)

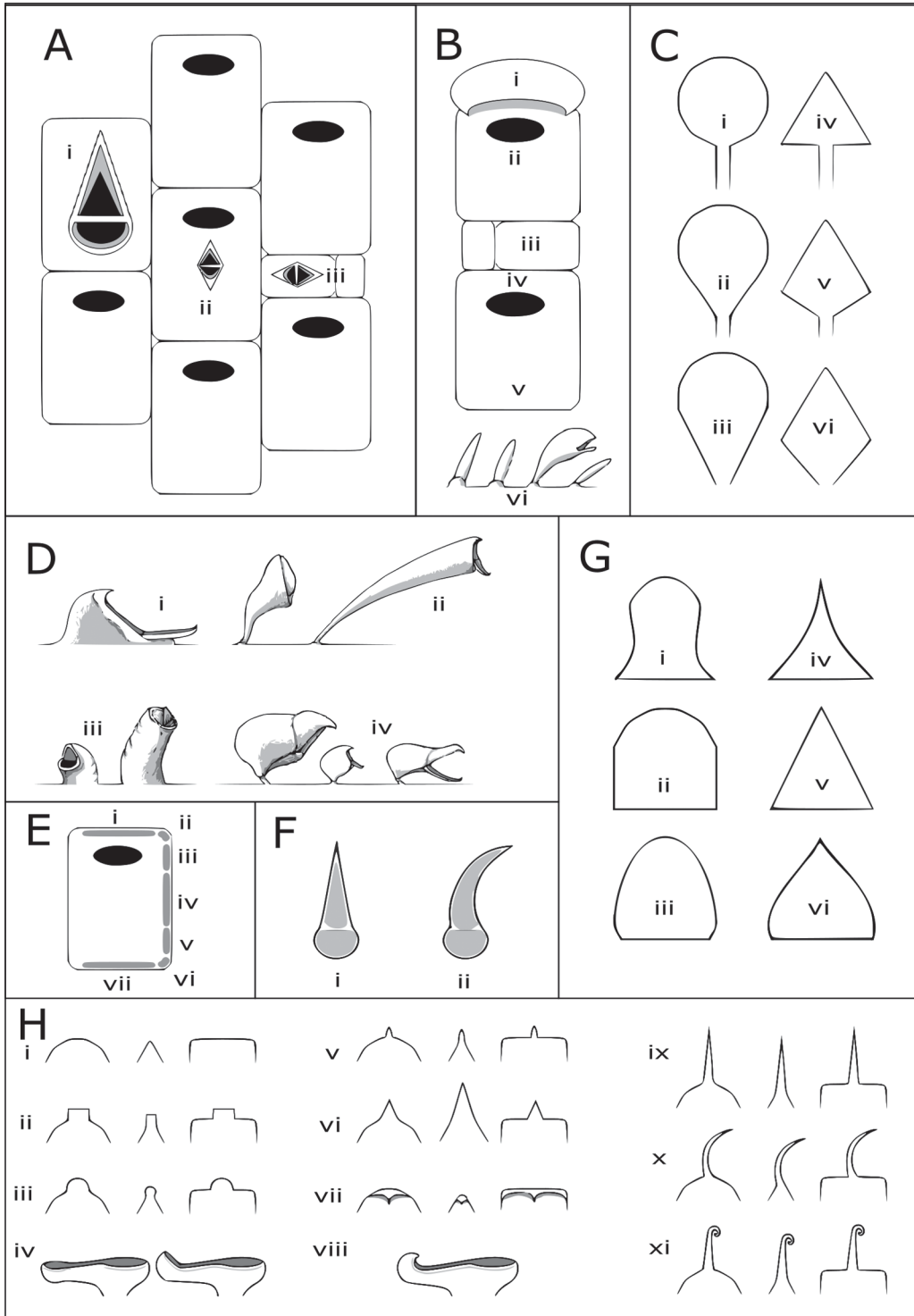
- **Relative Location:** Location relative to other morphological features of the parent autozooid (Figure 3B).

- *Hyper-oral:* Located next to orifice, distally
- *Sub-oral:* Located next to orifice, proximally
- *Spine substitute:* Replaces spine in series
- *Ovicell:* Associated with the oecium of the ovicell
- *Gymnocyst:* Located on gymnocyst, but not near any distinctive morphological features
- *Between zooids:* For vicarious and interzooidal avicularia.

- **Distal-proximal location:** Location on a modified distal-proximal axis (Figure 3E).

- *Mid-distal (0):* Located at distal end of zooid, on or close to its vertical midline (hyper-oral)
- *Distal Corner (1):* Located on one distal corner of zooid (typically hyper-oral)
- *Distolateral (2):* Located below (proximal to) distal corners of zooid (typically in-line with or below orifice)

Figure 2. Modularity and cormidial examples. A-C are monomorphic bryozoans, D-F show polymorphic, monocormidial bryozoans, and H-G are polymorphic, polycormidial bryozoans. A. The primary module of a monomorphic bryozoan that consists of a single autozooid. B. A nonbranching monomorphic colony: here the entire colony is a secondary module. C. A branching monomorphic colony: here each branch is a secondary module (i), and the entire colony is a tertiary module. D. The primary module of a monocormidial bryozoan: a cormidium. The cormidium in this case possesses four submodules; an autozooid, two spines, and an adventitious avicularium. E. A nonbranching monocormidial colony: here the entire colony is a secondary module. F. A branching monocormidial colony: here a branch is a secondary module (i) and the entire colony is a tertiary module. G. The primary modules of a polycormidial colony: two cormidia (i and ii). Cormidium i. is the same as in D above and cormidium ii. has five submodules; an autozooid, two spines, an adventitious avicularium, and an interzooidal avicularium. H. A nonbranching polycormidial colony: here each cormidial band (i and ii) is a separate secondary module, while the entire colony is a tertiary module. I. A branching polycormidial colony: each cormidial band (i and ii) is a secondary module, each branch (iii) is a tertiary module, and the whole colony is a fourth-level module.



- *Mid-Lateral (3)*: Located near horizontal midline of zooid. Also used for vicarious and interzooidal avicularia which are located in the center of their own zooids.
- *Proximolateral (4)*: Located between horizontal midline and proximal end of zooid.
- *Proximal Corner (5)*: Located on one proximal corner of zooid
- *Mid-Proximal (6)*: Located at proximal end of zooid, on or close to its vertical midline

Rostral Direction: The direction the tip of the rostrum is pointing along the parent zooid's distal-proximal axis. This is the direction in which the mandible closes. If the direction is variable, then select the direction most rostra are facing in respect to their own zooids.

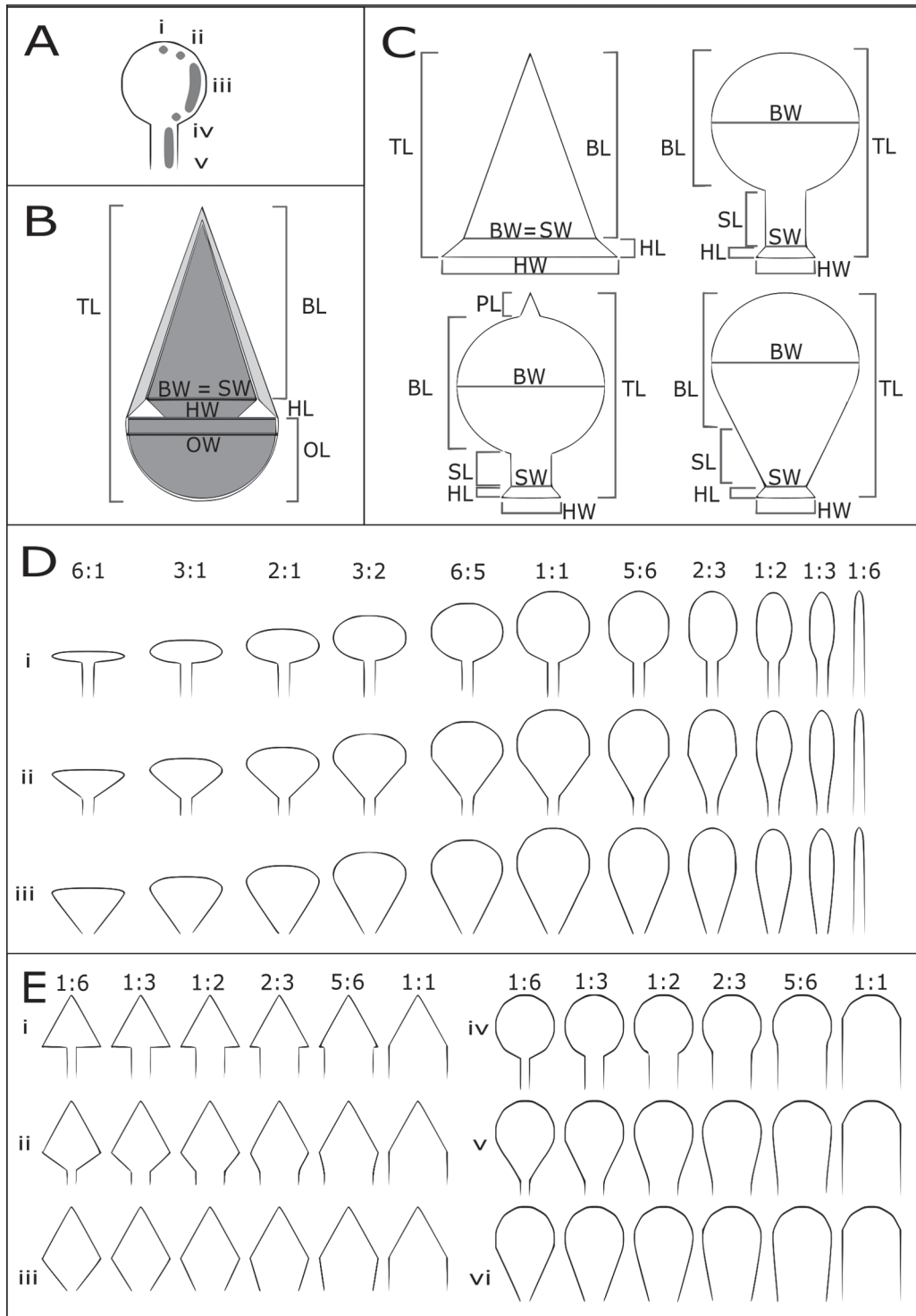
- Distal (0)
- Distolateral (1)
- Lateral (2)
- Proximolateral (3)
- Proximal (4)

Variable Direction: The variability of direction of the rostrum in relation to the zooid's distal-proximal axis.

- *Non-variable (0)*: Direction of the rostrum is constant in relation to the zooid's distal-proximal axis for all aviculiferous zooids within the colony.
- *Variable (1)*: Direction of the rostrum is unconstrained and can face in a variety of directions within the colony.

Attachment: The form of the cystid and manner of attachment of the adventitious avicularium to its parent zooid (Figure 3D). Vicarious and interzooidal avicularia are sessile, but adventitious avicularia have a greater diversity of attachment types. The peduncular cushion, which is formed by the parent zooid,⁸¹ is an important distinguishing

Figure 3. Avicularium classification. Where appropriate, historical morphological terms are given in brackets and quotes alongside those present in this classification system. A. Avicularia types i. vicarious, ii. adventitious, iii. interzooidal; B. Relative location i. ovicell, ii. sub-oral, iii. between zooids, iv. hyper-oral, v. gymnocyst; C. Tapering i. rounded, abrupt tapering ("spathulate"), ii. rounded, partial tapering ("spathulate"), iii. rounded, full tapering ("spathulate"), iv. pointed, abrupt tapering ("deltoid" or "triangular"), v. pointed, partial tapering ("trullate"), vi. pointed, full tapering ("rhomboid"); D. Attachments i. sessile, ii. tubular, iii. columnar, iv. bird's-head; E. Location i. mid-distal, ii. distal corner, iii. distolateral, iv. lateral, v. proximolateral, vi. proximal corner, vii. mid-proximal; F. Curvature i. straight, ii. curved; G. Concavity i. rounded, concave ("spathulate"), ii. rounded, straight ("linguiform"), iii. rounded, convex ("ovate"), iv. pointed, concave, v. pointed, straight ("deltoid" or "triangular"), vi. pointed, convex; H. Projections i. none, ii. oblong, iii. auriculate, iv. auriculate rostrum side view, v. mucronate, vi. cuspidate, vii. hooked, viii. hooked rostrum side view, ix. aristate, x. falcate, xi. cirrhose.



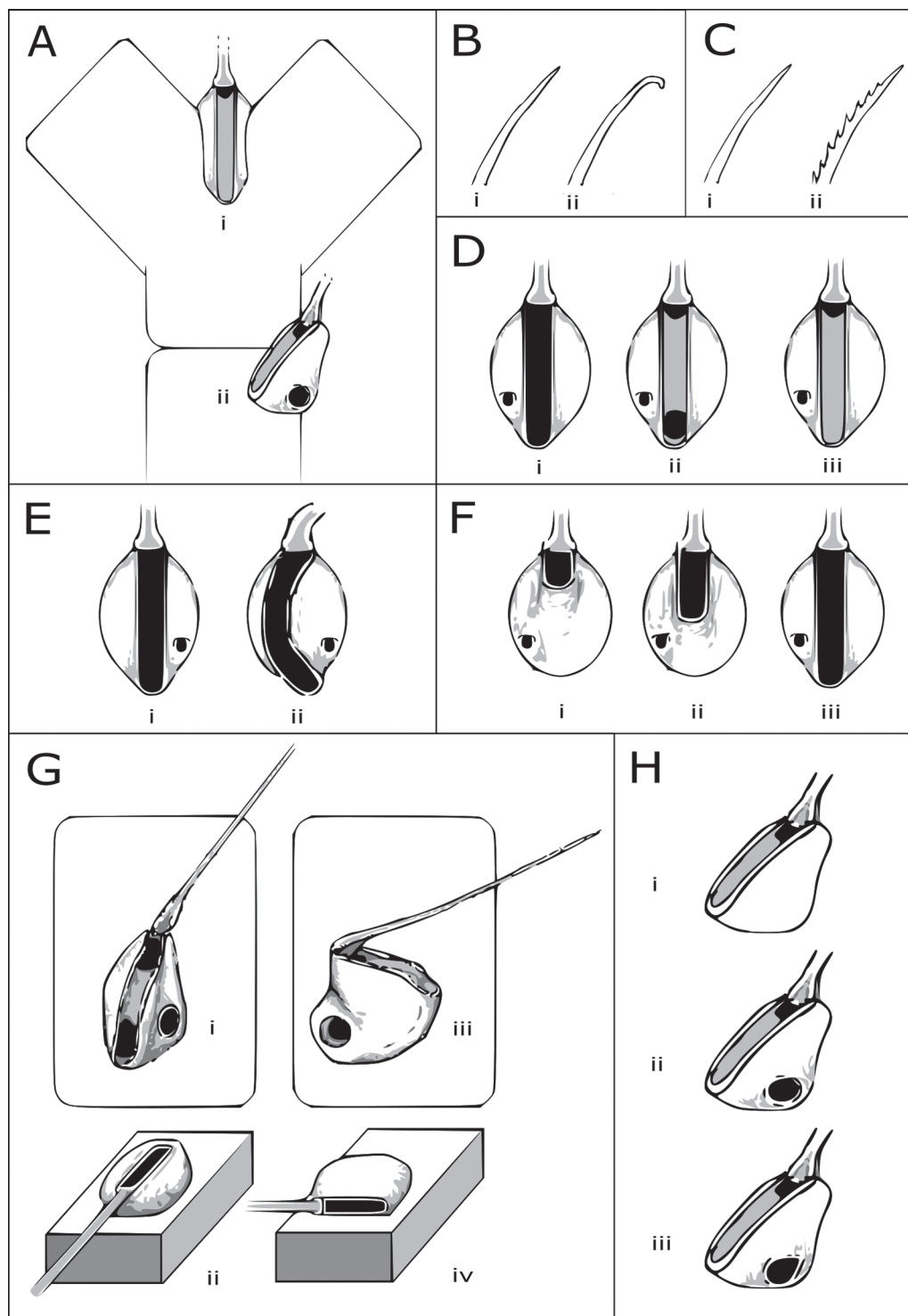
characteristic.

- *Sessile*: Avicularium is broad-based on parental zooid, and secondary calcification may result in an opesia flush with the frontal wall. Rostrum may be flush with the frontal wall or tilted upwards.
- *Columnar*: Opesia and rostrum are elevated from the frontal wall of its zooid. Avicularium is supported on a thick stalk that does not have a peduncular pad/cushion. The stalk may be tapered toward the point of attachment.
- *Tubular*: Opesia and rostrum are elevated from the frontal or frontolateral wall of the zooid. The avicularium is supported on a stalk that tapers from rostrum and opesia toward the peduncular pad/cushion.
- *Bird's head*: Opesia and rostrum are elevated from the frontal wall of its zooid. The bulbous body of the avicularium is supported on a thin stalk with a peduncular pad/cushion. This form allows the avicularium to “nod”.

Additional information on the avicularian cystid is given with three descriptors:

- **Spikes**: Spine-like protrusions (spikes) on the avicularian cystid. This typically occurs on columnar avicularia.
 - *None*: No spikes are present on cystid of the avicularium
 - *Simple*: Spikes are unbranched
 - *Branching*: Spikes are branched
 - *Mixed*: Unbranched and branching spikes are present on cystid of the avicularium
- **Spike Abundance**: The number of spikes on the cystid of the avicularium.
- **Elevation**: The distance between surface of the opesia and the frontal surface of the zooid. If the avicularium is crowning an ovicell, then the elevation is measured from the surface of the ovicell to the end of the avicularium.
 - *None (0)*: Face of the avicularium is flush with the zooid's frontal surface (embedded by secondary calcification).
 - *Short (1)*: Elevation is less than or equal to $\frac{1}{4}$ the length of the gymnocyst, but not flush with the frontal surface ($0 < x \leq \frac{1}{4}$)
 - *Intermediate (2)*: Elevation is between $\frac{1}{4}$ and $\frac{1}{2}$ the length of the gymnocyst ($\frac{1}{4} < x \leq \frac{1}{2}$)

Figure 4. Avicularium classification continued. A. Projection locations i. mid-disal, ii. distal corner, iii. lateral, iv. bulb-stem, v. stem; B. Rostrum measurements TL. total length, HL. hinge length, HW. hinge width, SL. stem length, SW. stem width, BL. bulb length, BW. bulb width, PL. projection length, OL. opesia length, OW. opesia width; C. Mandible measurements; D. Bulb width: bulb height i. abrupt tapering, ii. partial tapering, iii. full tapering. E. Stem width: bulb width i. pointed, abrupt tapering, ii. pointed, partial tapering, iii. pointed, full tapering, iv. rounded, abrupt tapering, v. rounded, partial tapering, vi. rounded, full tapering. D and E both show a range of potential mandible and rostral morphologies, which may not all be realized in nature.



- *Long (3)*: Elevation is between $\frac{1}{2}$ and 1x the length of the gymnocyst. ($\frac{1}{2} < x \leq 1$)
- *Very Long (4)*: Elevation is greater than 1x the length of the gymnocyst. ($1 < x$)

Mandible and Rostral Shape: The shape of the rostrum and the mandible. These should be described separately since the rostrum shape does not always match the shape of the mandible.

- **Overall Shape:** The general shape of the mandible/rostrum including the stem, bulb, and all projections.

- *Pointed (0)*: Mandible /rostrum narrows to a point or multiple points
- *Rounded (1)*: Mandible /rostrum widens and is blunt

- **Curvature:** Bending of the overall shape of the mandible/rostrum in the horizontal plane (x-y axis) (Figure 1F).

- *Straight (0)*: Mandible/rostrum is not bent
- *Curved (1)*: Mandible/rostrum is bent laterally

- **Proximal Tapering:** The transition between the stem and the bulb (Figure 3C)

- *No stem (0)*
- *Abrupt (1)*: There is a sharp change from the stem to the bulb
- *Partial (2)*: The transition from the bulb to the stem is smoother, but the lower part of the stem is still straight and distinct (parallel edges)
- *Full (3)*: The stem widens at the base and is difficult to distinguish from the base.

- **Bulb Outline:** The roundness of the mandible/rostrum edges relative to each other in the horizontal (x-y) plane, not including the hinge (Figure 3G).

- *Concave (0)*: The edges curve inwards
- *Straight (1)*: The edges are straight.
- *Convex (2)*: The edges curve outwards

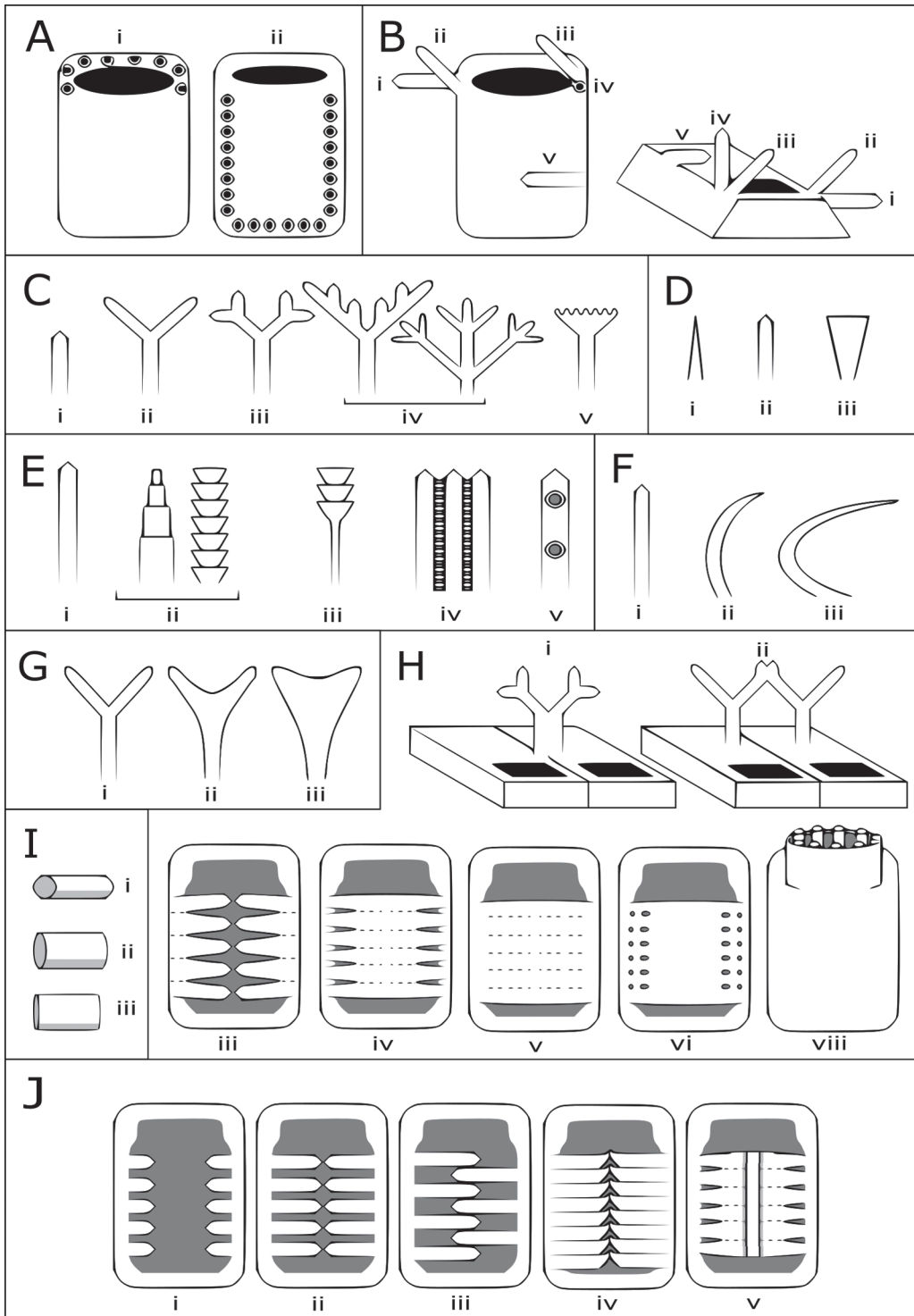
- **Bulb Shape:** The shape of the bulb (the main part of the mandible/rostrum, sometimes separated from the hinge by a stem), ignoring any projections.

- *Pointed*: Bulb is widest at base and narrows to a point
- *Rounded*: Bulb is widest at midpoint and rounds towards tip

- **Bulb Tip:** The shape of the tip of the bulb (not including projections). This usually matches the bulb shape, but cases occur where the tip is different from the overall bulb shape.

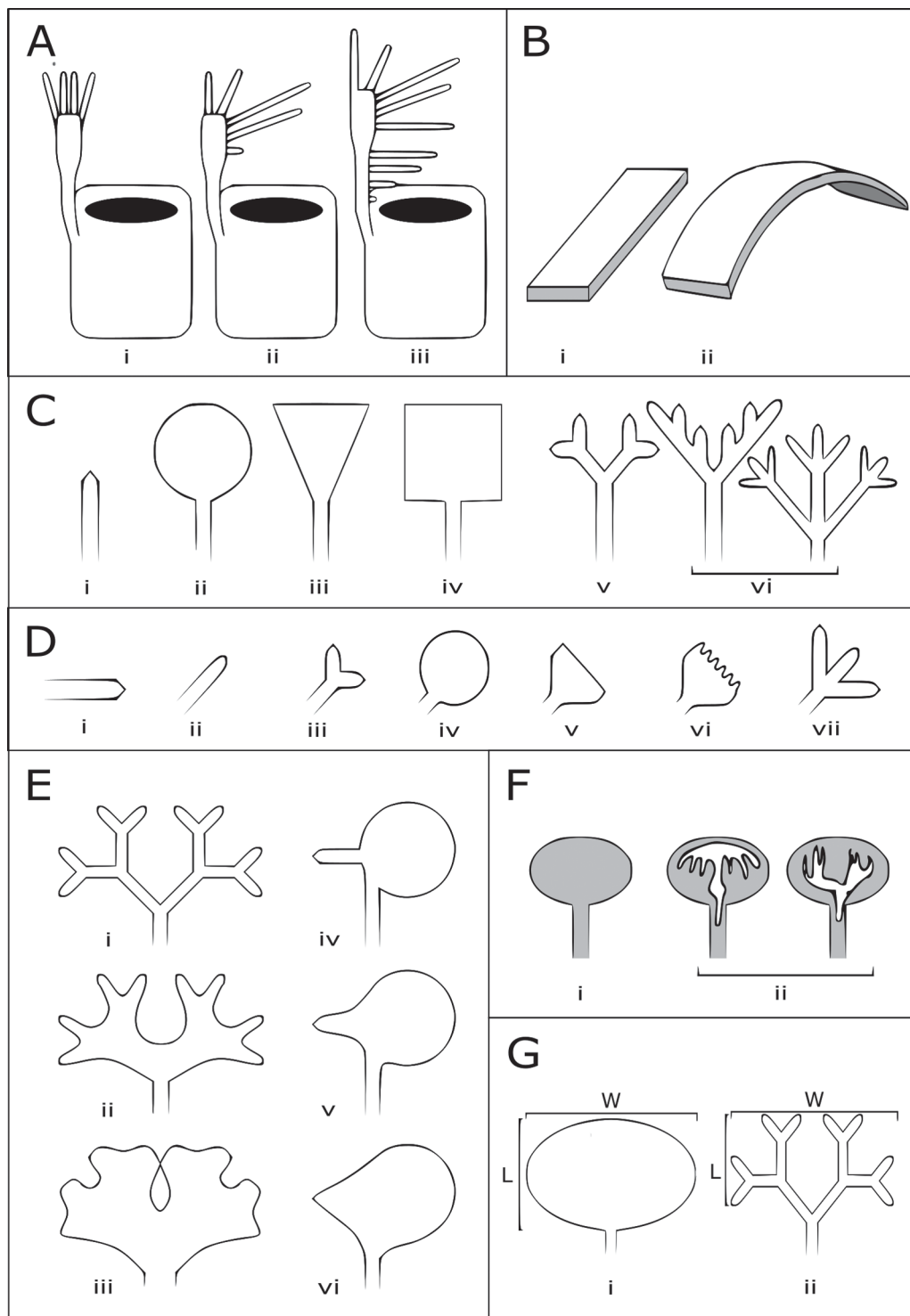
- *Pointed*: Tip narrows to a sharp point
- *Rounded*: Tip is smooth and rounded off
- *Truncated*: Tip is flat

Figure 5. Vibraculum classification. A. Vibraculum position i. axial, ii. non-axial; B. Vibraculum mandible tip i. straight, ii. hooked; C. Vibraculum mandible surface i. smooth, ii. barbate; D. Palatal surface i. absent, ii. present, with foramen, iii. present, no foramen; E. Setal groove curvature i. straight, ii. curved; F. Setal groove length i. short, ii. intermediate, iii. long; G. Setal groove location i. oblique, basal view of zooid, ii. oblique, isometric view of zooid, iii. transverse, basal view of zooid, iv. transverse, isometric view of zooid; H. Rhizoid pore i. absent, ii. circular, iii. ovate.



- **Projection Shapes:** Irregularities or projections on the mandible/rostrum that complicate its shape (Figure 3H).
 - *None:* No projections present
 - *Oblong:* Small rectangular projection
 - *Auriculate:* Small rounded projection. If a mandible is hooked, the rostrum may have an auriculate projection to sheath the hooked portion of the mandible
 - *Mucronate:* Abrupt, short point
 - *Cuspidate:* Slightly tapered, short point
 - *Hooked:* Pointed projection curving inwards. If a mandible is hooked, the rostrum may have a larger, hollow, hooked projection to hold the hook of the mandible.
 - *Aristate:* Long, thin, and pointed projection
 - *Falcate:* Long, thin, and curved projection ending in a point
 - *Cirrhose:* Long, thin projection that ends in spiral
- **Projection Location(s):** The location of the projection on the mandible/rostrum (Figure 4A). This should influence function – a hook at the tip of a mandible/rostrum should be more effective than a lateral one.
 - *None:* Mandible/rostrum does not possess projections
 - *Bulb (Mid-distal):* Located on tip of bulb
 - *Bulb (Distal corner):* Located on distal corner of bulb
 - *Bulb (Lateral):* Located on the side of bulb
 - *Bulb-Stem:* Located at the transition between bulb and stem
 - *Stem:* The projection is located on the stem
- **Teeth:** Very small, short, spine-like projections that are repeated along the edges of the mandible/rostrum.
 - *None:* No teeth present
 - *Sharp:* Teeth strongly pointed
 - *Blunt:* Teeth resemble scalloped edges and can be round or slightly pointed.
- **Teeth Location:** The location of teeth on the mandible/rostrum
 - *None:* The mandible/rostrum does not possess teeth
 - Teeth are present on the
 - *Bulb*
 - *Bulb-stem:* Bulb-stem transition

Figure 6. **Spine classification** **A. Spine locations** *i. oral, ii. opesial, see Figure 1e for other locations: circles represent the location of spine bases; B. Angle* *i. flat (outer), ii. obtuse, iii. acute, iv. erect, v. flat (inner); C. Branching* *i. unbranched, ii. forked, iii. bifid, iv. cervicorn, v. tines; D. Spine thickness* *i. tapering, ii. consistent, iii. flaring; E. Spine construction* *i. simple, ii. antenniform, iii. stalked antenniform, iv. pinnate, v. lumen pores; F. Spine curvature* *i. none, ii. slight, iii. strong; G. Spine distinctness* *i. distinct, ii. intermediate, iii. indistinct; H. Spine fusion* *i. lateral neighbors, ii. medial neighbors, iii. lateral, iv. medial, v. complete, vi. lacunae, vii. peristome; I. Spine compression* *1. cylindrical, ii. somewhat flattened, iii. flattened; J. Midline interaction* *i. separate, ii. meet, iii. interdigitate, iv. push, v. carina*



- *Stem*
- *Rachis*: Central ridge of avicularium
- *Projection*
- *Entire*: Whole perimeter of the mandible/rostrum has teeth

Shape Measurements: Much of the variation in shape can be explained with simple ratios, particularly bulb width: bulb length, and stem width: bulb width (Figure 4B-E).

- **Total Length:** From the base of the mandible/rostrum to the tip, including any projections
- **Hinge Length:** Distance from the mandible/rostrum's base until the slope changes
- **Hinge Width:** The widest part of the mandible/rostrum's base
- **Stem Length:** Distance from the change in slope to the bottom of the bulb
- **Stem Width:** width after a change in slope of the mandible/rostrum
- **Bulb Length:** The length of the bulb, not including projections. If the mandible/rostrum is rounded and possesses a strongly tapered stem, measure from the midpoint of the bulb to its tip and multiply this value by 2 to get the total length.
- **Bulb Width:** The maximum width of the bulb
- **Projection Length:** Only measured for projections at the tip of the bulb
- **Opesia Length:** The maximum length of the opesia
- **Opesia Width:** The maximum width of the opesia

2.2 VIBRACULA

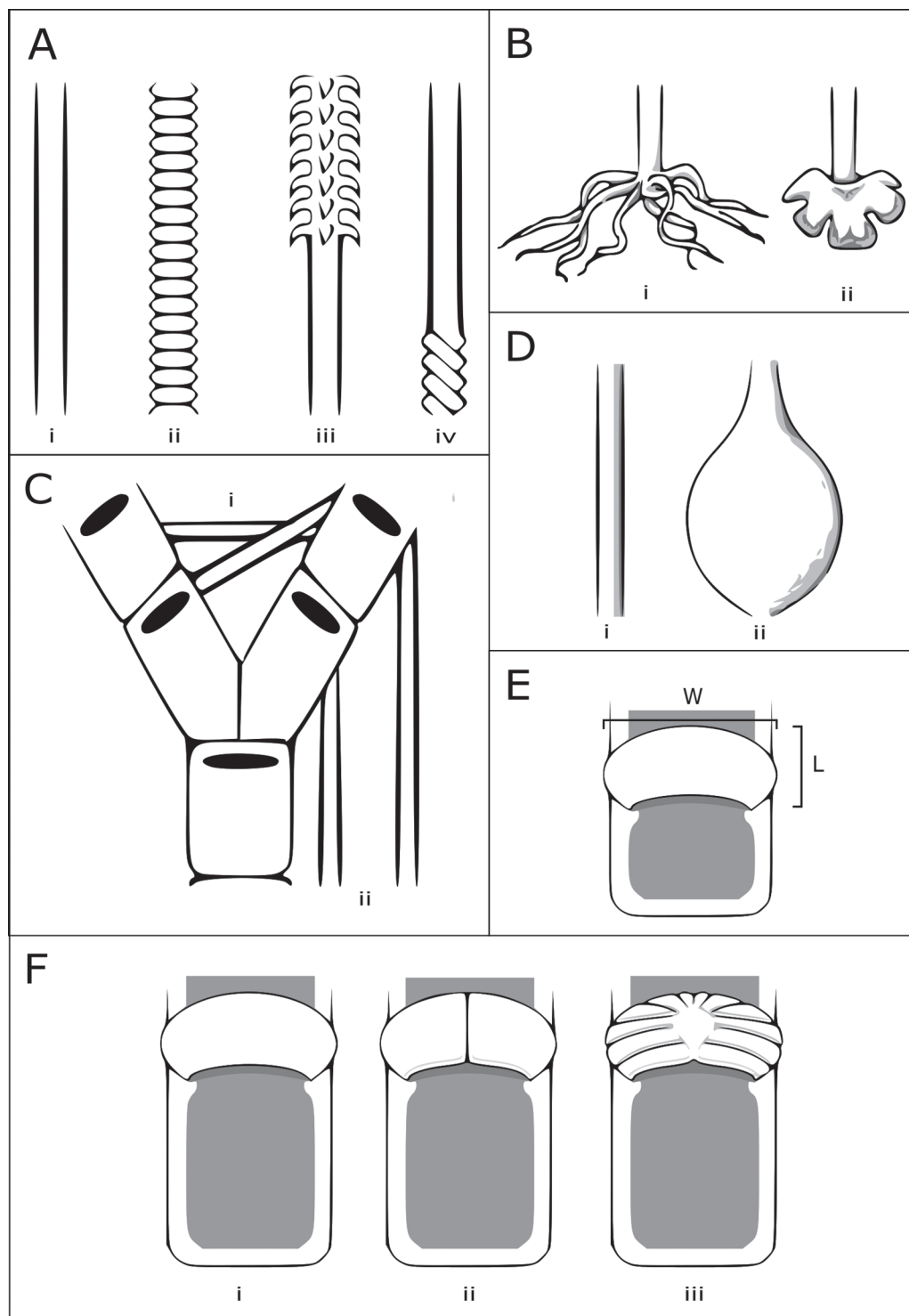
Vibracula are adventitious avicularia with extreme morphology. The mandible/rostrum is very long, and their hinge structure allows the mandible/rostrum to rotate over the surface of the colony (unlike avicularia which can only swing in one plane^{82,83}). (Figure 1E for anatomical descriptions.)

Location:

- *Zooid Wall*:

- Frontal
- Lateral
- Distal

Figure 7. Spine and scutum classification **A. Spiniferous process** *i. bulb tip, ii. bulb only, iii. entire*; **B. Scutum cross-section** *i. flat, ii. curved*; **C. Scutum overall shape** *i. spike, ii. round, iii. fan, iv. oblong, v. bifid, vi. cervicorn*; **D. Scutum lobe types** *i. spike (h), ii. spike (a), iii. forked, iv. round, v. truncated, vi. tines, vii. trifid*; **E. Scutum distinctness** *i. branching, distinct, ii. branching, intermediate, iii. branching, indistinct, iv. mixed lobes, distinct, v. mixed lobes, intermediate, vi. mixed lobes, indistinct*; **F. Scutum internal channels** *i. absent, ii. present*; **G) Scutum measurements** *i. length (L). and width (W). of an unbranching scutum, ii. length and width of a branching scutum.*



- Proximal
- Basal
- **Direction:** The direction the vibraculum faces in relation to the distal-proximal axis of the zooid
 - Distal (0)
 - Distolateral (1)
 - Lateral (2)
 - Proximolateral (3)
 - Proximal (4)
- **Position:** (Figure 5A)
 - *Non-axial (0):* Vibraculum does not occur at a branch node
 - *Axial (1):* Vibraculum occurs at a branch node

Mandible structure: Unlike avicularia, vibracula have much less variation in their mandible structure (also referred to as setae).

- **Mandible Length:**
 - *Short (0):* Mandible shorter than the gymnocyst length of an autozooid
 - *Intermediate (1):* Mandible between 1 and 2 zooids long
 - *Long (2):* Mandible longer than 2 zooids
- **Mandible Tip:** (Figure 5B).
 - *Straight (0):* Mandible tip is uncurved
 - *Hooked (1):* Mandible tip curls into a hook
- **Mandible Surface:** (Figure 5C).
 - *Smooth (0):* Mandible surface entire
 - *Barbate (1):* Mandible surface covered in small, pointed protrusions

General Structure:

- **Palatal Surface:** The palate is the surface where the mandible rests in the rostrum and is contained in the setal groove (Figure 5D).
 - *Absent (0):* No palatal surface present
 - *Present, with foramen (1):* Palatal surface present with a small hole (foramen) near the distal end
 - *Present, no foramen (2):* Palatal surface present and lacks a hole at the distal end
- **Setal Groove Curvature:** (Figure 5E).
 - *Straight (0)*
 - *Curved (1)*
- **Setal Groove Length:** Length of setal groove relative to body of vibraculum (Figure 3F). Regardless of setal groove length, the mandible will always be longer.

Figure 8. **Rhizoid and ovicell classification.** **A. Rhizoid surface** *i. smooth, ii. ringed, iii. hooked, iv. coiled at origin;* **B. Rhizoid tip** *i. fimbriate, ii. holdfast;* **C. Connections** *i. branches, ii. substratum;* **D. Rhizoid thickness** *i. consistent, ii. dilated;* **E. Ovicell measurements** *l. length, w. width;* **f. Ooecium structure** *i. entire, ii. bilobed, iii. multilobed.*

- *Short (0)*: Groove length less than $\frac{1}{4}$ the length of vibraculum
- *Intermediate (1)*: Groove length between $\frac{1}{4}$ and $\frac{1}{2}$ the length of vibraculum
- *Long (2)*: Groove length is between $\frac{1}{2}$ and 1x the length of vibraculum
- **Setal Groove Location:** (Figure 5G).
 - *Transverse (0)*: Setal groove/palatal surface is perpendicular to the zooid wall
 - *Oblique (1)*: Setal groove/palatal surface is parallel to the zooid wall
- **Rhizoid Pore:** Vibracula often have pores that rhizoids bud from (Figure 5H).
 - *Absent (0)*: No rhizoid pore present
 - *Circular (1)*: Rhizoid pore circular in shape
 - *Ovate (2)*: Rhizoid pore egg-shaped

2.3 SPINES

“Spine” is a non-technical term that is used here to refer to both derived kenozooids (= “spinozooids” of Silén⁸⁴) and body-wall projections from the parent zooid (spiniform non-zooidal adventitious modules).^{85,86} Both structures are typically hollow, have varying degrees of calcification, and possess an inner lining of epithelial cells.^{87,88,89} With one exception, (spinozooids in *Belluopora*) the lumen of both spine types is confluent with the zooidal coelom and lacks a pore-cell complex.^{90,91,92} It is important to note that not all spines may be homologous, and it may not be valid to compare spines in different locations (i.e. spines that lack “topographical correspondence” as described in Vieira *et al.* 2014).⁹³ (Figure 1E for anatomical descriptions).

Number of Spines: the level of spination a colony possesses

- **Total Number of spines:** The total number of spines on the zooid
- **Number of spines:** The number of spines of a specific type. This can be used to separate groups of spines with that exhibit different traits.
- **Paired:** Symmetry in spine number and position location across the midline of the bryozoan. Spines are typically paired, though irregularities can occur.
 - No (0)
 - Yes (1)
- **Location:** the general location of spines on the zooid’s distal-proximal axis (Figure 3E, and Figure 6A).
 - Mid-distal
 - Distal corner
 - Distolateral
 - Orificial: Spines surrounding the orifice (not including sub-oral spines)
 - Sub-oral
 - Lateral
 - Proximolateral
 - Proximal corners
 - Mid-proximal

- Opesia: spines surrounding the opesia (not including sub-oral spines)
- Distal Wall
- Outer distal corner: Edge between the dorsal and lateral wall
- Distal (Lateral wall): Distal end of a lateral wall
- Lateral (Lateral wall): Near middle of a lateral wall
- Proximal (Lateral wall): Proximal end of a lateral wall
- Proximal Wall
- **Direction:** The direction a spine is pointing along its zooid's distal-proximal axis.
 - *Abfrontal:* Spine perpendicular to the frontal surface, its tip facing directly upwards
 - Distal
 - Distolateral
 - Lateral
 - Proximolateral
 - Proximal
- **Angle:** The angle of the spine in relation to the zooid surface (Figure 6B).
 - *Flat (inner) (0):* Spine parallel to frontal surface of the zooid, its tip facing midline
 - *Acute (1):* Spine angled above frontal surface ($<90^\circ$), pointing towards midline
 - *Erect (2):* Spine perpendicular to frontal surface of the zooid
 - *Obtuse (3):* Spine angled above frontal surface of the zooid ($>90^\circ$), pointing away from midline
 - *Flat (outer) (4):* Spine parallel to the frontal surface of the zooid, its tip facing away from midline

Structure: The shape, size, and growth patterns of spines.

- **Branching:** The growth/division pattern of spine tips (Figure 6C).
 - *Unbranched:* Simple spine with single tip
 - *Forked:* Spine branches into two sections
 - *Bifid:* Each branch bifurcates into two sections that are similar in length, capable of further bifurcation
 - *Cervicorn:* Irregular branching, with branches either undergoing trifurcation or antler-like growth
 - *Tines:* Spine widens and possesses multiple small tips in a single row
- **Branch Distinctness:** The clarity of a spine's branching structure, or the sharpness of the division between spines (Figure 6G).
 - *Distinct (0):* Each branch node clearly visible and terminal branch ends have similar width to earlier ones
 - *Intermediate (1):* Branch tips clear, but branch thickness obscures earlier nodes
 - *Indistinct (2):* Branching structure strongly obscured by branch thickness, branch tips hard to distinguish

- **Curvature:** The extent of curvature in a spine (Figure 6F).
 - *None (0):* Spines are completely straight
 - *Slight (1):* Spines are slightly curved
 - *Strong (2):* Spines are strongly curved
- **Compression:** The difference between the major and minor axes of the spine cross-section (Figure 6I).
 - *Cylindrical (0):* Spine cross-section is close to circular (major axis \approx minor axis)
 - *Somewhat flattened (1):* Spine cross-section is elliptical (major axis $>$ minor axis)
 - *Flattened (2):* Spine cross-section narrowly elliptical (major axis \gg minor axis)
- **Proximity:** The amount of space between neighboring spine bases.
 - *Sparse (0):* Spines spaced more than two spine bases apart
 - *Intermediate (1):* Spines spaced one spine base apart
 - *Appressed (2):* Spine bases touch their neighbors
- **Construction:** The growth structure of the spine (Figure 6E).
 - *Simple:* Spines relatively smooth with continuous structure
 - *Antenniform:* Spine made of regularly repeating segments, either of similar size or decreasing in size towards the tip. A simple spine can be mistaken for an antenniform one due to regeneration after breakage, which produces a similar looking structure. However, regenerated spines do not repeat regularly and the breaks between their segments typically appear ragged.
 - *Stalked Antenniform:* Antenniform structure on a thin, simple stalk
 - *Pinnate:* Spine connected to its neighbors via short, thin, lateral “struts”
 - *Lumen pores:* Holes in the spine calcification sealed by a cuticular plug, only seen after bleaching. The hole is in the spine itself, unlike lacunae, which are holes between spines. Also called pelmata or pelmatidia
- **Spine Tip:** The structure of the spine’s terminal end.
 - *Pointed:* Spine ends in a sharp point and is calcified
 - *Rounded:* Spine tip is rounded and is calcified
 - *Truncated:* Spine tip is flat and calcified
 - *Membrane:* Spine tip is flat, covered by a small membrane
- **Basal Joint:** The point of attachment between a spine and the zooidal surface.
 - *Absent (0):* Base unjointed or calcified
 - *Present (1):* Base has cuticular articulation
- **Thickness:**
 - *Tapering (0):* Spine tapers to a thinner width
 - *Consistent (1):* Spine width stays relatively constant along its length
 - *Flaring (2):* Spine increases in width along its length
- **Length:**
 - *Short (0):* Spine length less than $\frac{1}{4}$ the length of the gymnocyst
 - *Intermediate (1):* Spine length is between $\frac{1}{4}$ and $\frac{1}{2}$ the length of the gymnocyst
 - *Long (2):* Spine length is between $\frac{1}{2}$ and $1x$ the length of the gymnocyst
 - *Very long (3):* Spine length greater than the length of the gymnocyst

- Base Width:

- *Thin (0)*: Base width is less than $\frac{1}{8}$ the width of the gymnocyst
- *Intermediate (1)*: Base width of the spine base is about $\frac{1}{8}$ the width of the gymnocyst
- *Thick (2)*: Base width is about $\frac{1}{5}$ the width
- *Very thick (3)*: Base width is greater than $\frac{1}{5}$ the width

Fusion: Spines often calcify together, either with spines on the same zooid or neighboring ones.

- Fusion: (Figure 6H)

- *None*: No fusion between spines
- *Lateral*: Spines fuse with their adjacent neighbors along their sides
- *Medial*: Spines fuse at their tips with the spines across from them
- *Lateral neighbors*: Spines of one zooid fuse laterally with those of a neighboring zooid
- *Medial neighbors*: Spines of one zooid fuse medially with those of a neighboring zooid
- *Complete*: Spines fuse with their adjacent neighbors and the spines across from them, forming a continuous surface
- *Lacunae*: Spines fuse to form a complete structure, except for small holes between spines
- *Peristome*: Spines laterally fuse with their neighbors around the orifice

- Midline Interaction: Spines situated opposite each other may interact at the midline of the zooid. This can also be applied to spines medially fused with their neighbors (Figure 6J).

- *Separate*: Opposite spines do not approach each other
- *Meet*: The tips of opposite spines touch each other on the midline
- *Interdigitate*: Opposite spines mesh with each other
- *Push*: The tips of opposite spines grow into each other, pushing their tips upward
- *Carina*: When spines are medially fused, additional raised calcification occurs over the spine tips

Spiniferous Process: Occasionally, spines are borne away from the zooid itself on a long extension, which can host multiple spines (Figure 7A).

- *None (0)*: No spiniferous process present
- *Bulb tip (1)*: Spines only present on the tip of spiniferous process
- *Bulb only (2)*: Spines only present on the bulbous end of process but not along the thinner extending “arm”
- *Entire process (3)*: Spines present along the length of process

Zooid: The number and type of spines can change depending on what kind of zooid they originate from, with the ancestrula typically more spinose and armored than later zooids.

- Autozooid
- Ancestrula
- Ovicelled zooid

2.4 SCUTA

Scuta are modified spines that are large, shield-like, and lie flat over the opesia. They are unpaired and do not exist within a spine-series. See Figure 1C for anatomical descriptions.

Scutum Shape:

- **Overall Shape:** The entire shape of the scutum, regardless of its individual lobe shapes (Figure 7C).

- *Spike:* Scutum thin and spine-like
- *Round:* Scutum terminates in a large rounded structure
- *Fan:* Scutum widest at the tip
- *Oblong:* Scutum terminates in a rectangular structure
- *Bifid:* Scutum branches, undergoing roughly equal bifurcation at each node
- *Cervicorn:* Scutum branches, undergoing trifurcation or antler-like growth

- **Lobe Types:** This trait is applied to the distal, central and proximal lobes of the scutum (Figure 7D). The default is two lobes (distal and proximal), though there may be cases where all 3 are present, or where only the central lobe is present. To prevent differences in classification, the simplest lobe type should be used. For example, instead of describing a scutum as having 1 central lobe that is trifid, the scutum should be described as having 3 lobes, each with a spike.

- *None:* No lobe present
- *Spike (H):* Horizontal (perpendicular to the stem of the scutum), thin, spine-like lobe
- *Spike (A):* Angled, thin, spine-like lobe
- *Forked:* Bifurcated spine-like lobe
- *Round:* Circular lobe
- *Truncated:* Fan-like lobe that terminates in a blunt edge
- *Tines:* Fan-like lobe that terminates in a row of small spikes
- *Trifid:* Trifurcated spine-like lobe

- **Relative Lobe Size:** A comparison of the relative sizes of the proximal and distal lobes.

- *Reduced (0):* Proximal lobe is smaller than distal lobe
- *Symmetrical (1):* Proximal and distal lobes are roughly equal in size, or both are absent
- *Enlarged (2):* Proximal lobe is larger than distal lobe

Structure:

- **Distinctness:** This provides a measure of the permeability of the scutum, and the degree of lobe fusion (Figure 7E).

- *Distinct (0):* In branching scuta each branch node is clearly visible and the terminal branch ends have a similar width to earlier ones. In non-branching scuta, lobes are clearly defined and the transition between them is abrupt.
- *Intermediate (1):* In branching scuta branch tips are clear, but branch thickness obscures earlier nodes. In non-branching scuta the transition between lobes is gentle, but lobes can be distinguished.
- *Indistinct (2):* In branching scuta branching structure is strongly obscured by branch thickness, branch tips are hard to distinguish. In non-branching scuta lobes are difficult to distinguish and nearly appear as a single shape.

- **Cross-section:** (Figure 7B).

- *Flat (0):* Scutum uncurved and may be parallel with the opesia.
- *Curved (1):* Scutum arched over the opesia.

- **Internal Channels:** Some scuta possess internal channels, which are only visible under a light microscope (Figure 7F).

- Absent (0)
- Present (1)

Base: The scutum is a modified articulated spine, and it possesses a spine base.

- **Base Location:**

- Distal (0)
- Distolateral (1)
- Lateral (2)
- Proximolateral (3)
- Proximal (4)

- **Base Width:**

- *Thin (0):* Base width less than $\frac{1}{8}$ the width of the gymnocyst
- *Intermediate (1):* Base width is about $\frac{1}{8}$ the width of the gymnocyst
- *Thick (2):* Base width about $\frac{1}{5}$ the width of the gymnocyst
- *Very thick (3):* Base width greater than $\frac{1}{5}$ the width of the gymnocyst

Measurement: The size of the scutum (Figure 7G).

- *Length:* Maximum length of the scutum, not counting the stem

- *Width:* maximum width of the scutum

- *Percent cover of the opesia:* This measurement takes into account the holes present in branching structures and irregular lobe shapes. The part of the stem that covers the opesia is included in the measurement.

2.5 RHIZOIDS

Rhizoids, also referred to as rhizozoids, rootlets, and radicle fibers, are elongated kenozooids that extend to the substratum or other areas of the colony. They provide attachment to the substrate and colony support, and are common in flexible erect colonies (Silén, 1977).

Form: Some structures are similar in appearance and function to rhizoids, and these are distinguished here.

Prop (0): Extensions of the basal calcified wall. Colony supported on the substrate by several short, cylindrical structures that lack holdfasts or fimbriated structures (see rhizoid tip).

- *Rhizoid (1):* Colony anchored to the substrate or other branches by long, hollow, cylindrical kenozooids that may terminate in a holdfast or a fimbriated structure. Variable calcification.

Origin: It is common for rhizoids to originate from the basal wall or a vibracular chamber. They rarely arise from a frontal wall.

- Lateral wall
- Basal wall
- Dorsal wall
- Ventral wall
- Frontal wall
- *Vibracular chamber:* The rhizoid emerges from a pore in a vibraculum

Rhizoid Surface: (Figure 8A).

- *Smooth:* Rhizoid surface is unblemished
- *Ringed:* Rhizoid resembles a string of close-set, short cylindrical beads of similar lengths.
- *Hooked:* Parts of rhizoid surface covered in backwards-facing hooks
- *Coiled (base):* Rhizoid is coiled at the origin

Rhizoid Tip: The terminal end of the rhizoid anchors the bryozoan, and different types may be found on different substrates (Figure 8B).

- *Single:* Rhizoid ends abruptly or tapers.
- *Fimbriate:* Rhizoid tip splits into many thin hair-like ends
- *Holdfast:* Rhizoid ends in a thicker, sometimes spikey structure

Connections: Rhizoids can either anchor the colony to the substrate or can connect branches to each other (Figure 8C).

- *Substrate (0)*

- Branches (1)

Thickness: Rhizoids are typically slender, but some can be swollen into a bulbous structure (Figure 8D).

- *Consistent (0)*: Rhizoid has a continuous thickness
- *Dilated (1)*: Rhizoid possesses are swollen sections

2.6 SKELETAL CHAMBERS FOR EMBRYONIC INCUBATION

This part of the classification system follows that of Ostrovsky *et al.* (2009)⁹⁴ and Ostrovsky (2013).⁹⁵ Although it includes all brood chambers present in cheilostomes, the focus here is on the skeletal ones. The commonest type are exterior ovicells that consist of a calcified double-walled oecium enclosing a brooding cavity. The oecium is a body-wall outgrowth formed from the distal daughter zooid in most cases.^{96,97} Spines provided by the distal daughter evolved into oecia through fusion or reduction in the number of spines, their flattening, loss of basal articulation, relocation of spine bases, in addition to other trends.⁹⁸ Since the oecium originated evolutionarily from spines, it could be considered kenozooidal in nature. The maternal (egg-producing) zooid transfers the egg to the ovicell and closes it with a body-wall plug (oecial vesicle) or autozooidal operculum, or both.

In some cheilostomes (Tendridae, Scrupariidae, Thalamoporellidae, Alysidiidae, and Belluloporidae), the skeletal parts of independently evolved oecia-like structures do not rely on a distal daughter. Instead, they form from plate-like kenozooids, kenozooidal spines, or outgrowths of the maternal body-wall.

The variable presence of an oecium-contributing distal daughter makes ovicells difficult to describe in cormidial terms. This is further complicated by the ability of the distal daughter to act as a maternal zooid to *its own* distal daughter. To simplify, only the maternal zooid will be considered as possessing an ovicell. Although this is an artificial cut-off, it is necessary to prevent cormidial overlap/ the double-counting of submodules, which would present difficulties in statistical analysis. The distal daughter zooid should only be included in the cormidium if it is a kenozooid or avicularium. Thus, a maternal zooid would be in a cormidium that consists of two submodules (autozooid + ovicell), while the distal daughter would be considered as a standard autozooid unless it possessed other polymorphs. If the distal daughter is not an autozooid, the cormidium would consist of three submodules (autozooid + ovicell + kenozooid/avicularium).

Embryo Incubation Chamber:

- External membranous sac (0)
- *Skeletal chamber (1)*: Includes ovicells and brood chambers formed by spines. These can external or internal
- Non-calcified internal brood sac (2)

- *Intracoelomic incubation (3)*: Occurs in specialized female zooids

Skeletal Chamber:

- *None (0)*
- *Acanthostegous (1)*: Adjacent mural spines (spines near the edge of the frontal wall) overarch an incubational space above the frontal wall (including frontal membrane).
- *Ooecia (2)*: Consists of a calcified double wall (ooecium) enclosing a brooding cavity that is plugged by a non-calcified portion of the maternal zooid's distal wall. The ooecium is phyletically derived from one or more spines of the distal daughter zooid.

Ovicell Immersion: This examines how much the brood cavity is sunken below the surface of the zooid. There is a trend in Recent bryozoa towards the immersion of the brood cavity in the frontal surface.^{99,100} Note that this refers to the brood cavity and not the ooecium itself, which is always an external structure.

- *Immersed (0)*: Brood cavity entirely below the surface of the zooid
- *Sub-immersed (1)*: Less than half of the brood cavity above the surface of the zooid
- *Prominent (2)*: More than half of the brood cavity above the surface of the zooid.

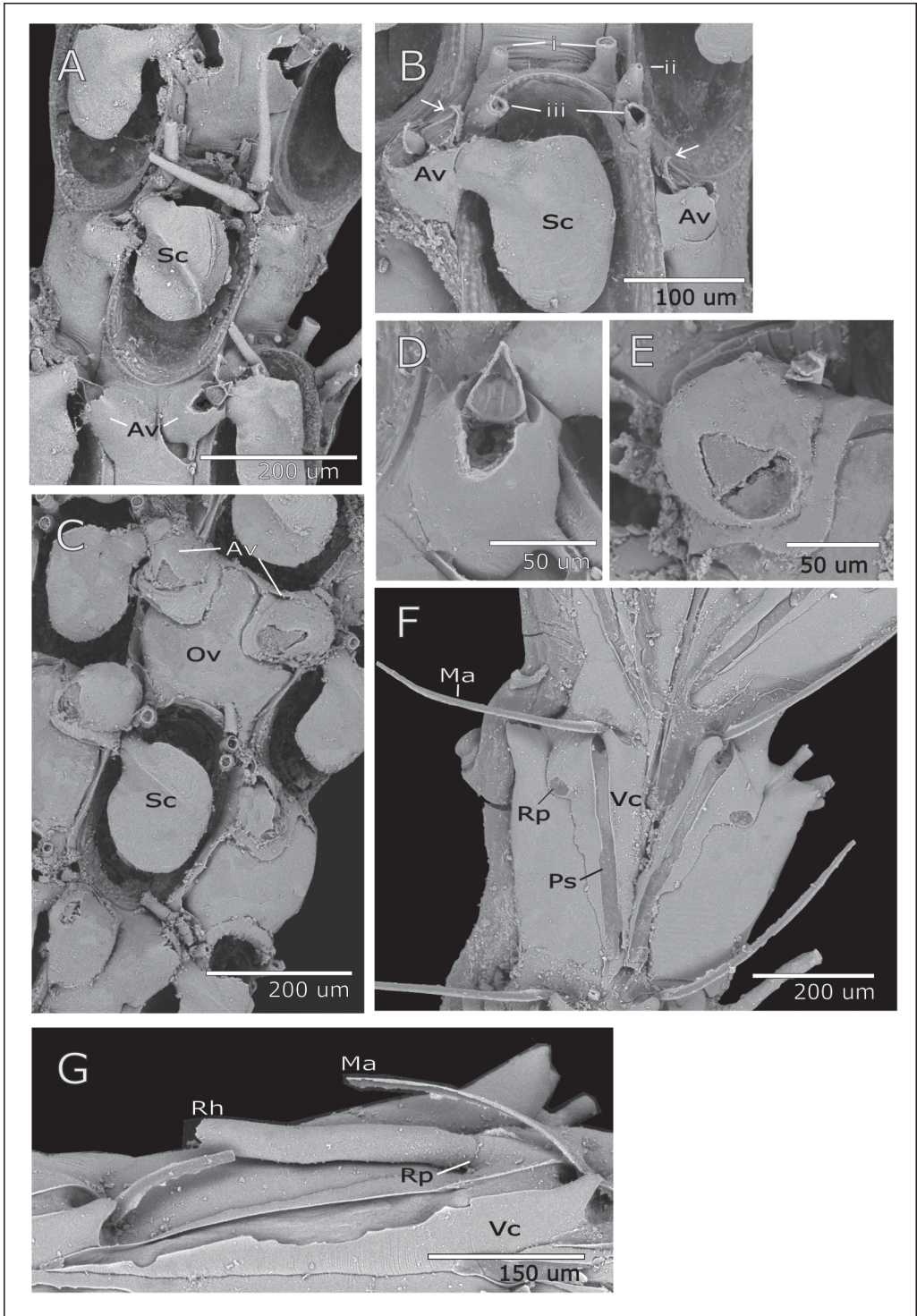
Ooecium Structure: This examines the number of parts that constitute the ooecium (Figure 8F). Note that this is not based on the number of parts that the ooecium was derived from evolutionarily, but the appearance of the derived structure.

- *Entire (0)*: Ooecium appears whole
- *Bilobed (1)*: Ooecium appears to be constructed from two parts/components, which are fused in the middle
- *Multilobed (2)*: Ooecium appears to be constructed from more than two parts/components

Daughter Zooid: The type of distal daughter zooid from which the ooecium originates.

- Autozooid (0)
- Avicularium (1)
- Kenozooid (2)

Figure 9. SEM images of Amastigia puysegurensis. These images have been digitally modified to remove fouling debris. "Sc" = Scutum, "Av" = Avicularium, "Ov" = Ovicell, "Ma" = mandible, "Ps" = Palatal surface / setal groove, "Vc" = Vibracular chamber, "Rp" = Rhizoid pore "Rh" = rhizoid **A.** Frontal view of non-ovicelled autozooids, showing some intact spines, scuta, and avicularia; **B.** Close-up of a non-ovicelled autozooid, showing three kinds of spines (i-iii, all broken off), a scutum, and two avicularia. The hooked projection on the avicularian mandibles can clearly be seen (arrows); **C.** Frontal view of ovicelled autozooids, showing scuta and avicularia; **D.** The gymnocystal avicularium of an autozooid; **E.** An avicularium crowning an ovicell; **F.** Basal side of a branch, showing paired vibracula. **G.** Vibraculum with a rhizoid emerging from the rhizoid pore.



Measurement: The shape of the ovicell is roughly described through length and width ratios (Figure 8E).

- *Length:* Maximum length of ovicell along distal-proximal axis
- *Width:* Maximum width of ovicell

3. Example Classification:

The scope of this classification may seem daunting to potential users, especially from a data organization viewpoint. To alleviate this, and to reduce any confusion about the use of the classification system itself, we have provided a full example. *Amastigia puysegurensis* Gordon, 1986 (Candidae) is a useful model species because it possesses each kind of polymorphism described in this classification. A specimen of *A. puysegurensis* from the NIWA Invertebrate Collection¹⁰¹ was imaged with a SEM (Figure 9).¹⁰² The classification is presented below (Table 2-7), with each trait in bold. In a normal data table each trait should be in a separate column, but the layout is condensed here to save space. Note that when multiple kinds of a certain polymorphism were present (e.g. avicularia, spines) each kind received its own classification.

Avicularium	Type	Zooid Wall	Relative Location	Location	Rostral Direction
<i>Avi</i>	2	Frontal	Gymnocyst	4	3
<i>Avi (ovi)</i>	2	Frontal	Ovicell	1	1
Avicularium	Variable Direction	Attachment	Spikes	Spike Abundance	Elevation
<i>Avi</i>	0	Columnar	None	0	1
<i>Avi (ovi)</i>	0	Columnar	None	0	1
Avicularium	Overall Shape (Rostrum)	Bulb Shape (Rostrum)	Curvature (Rostrum)	Tapering (Rostrum)	Bulb Outline (Rostrum)
<i>Avi</i>	0	0	0	0	1
<i>Avi (ovi)</i>	0	0	0	0	1
Avicularium	Bulb Tip (Rostrum)	Projection Shapes (Rostrum)	Projection Location(s) (Rostrum)	Teeth (Rostrum)	Teeth Location (Rostrum)
<i>Avi</i>	Pointed	None	None	None	None
<i>Avi (ovi)</i>	Rounded	None	None	None	None
Avicularium	Overall Shape (Mandible)	Bulb Shape (Mandible)	Curvature (Mandible)	Tapering (Mandible)	Bulb Outline (Mandible)
<i>Avi</i>	0	0	0	0	1
<i>Avi (ovi)</i>	0	0	0	0	1
Avicularium	Bulb Tip (Mandible)	Projection Shapes (Mandible)	Projection Location(s) (Mandible)	Teeth (Mandible)	Teeth Location (Mandible)
<i>Avi</i>	Pointed	Hooked	Bulb (mid-distal)	None	None
<i>Avi (ovi)</i>	Rounded	None	None	None	None

Table 2. Avicularium classification of *A. puysegurensis*, which has two kinds of avicularia. The first form (“*Avi*”, Figure 9A, B, and D) is present on the gymnocyst of autozooids and ovicelled zooids, either singly or as a pair. The second form (“*Avi (ovi)*”) crowns the oecium and is present in pairs (Figure 9C and E).

Vibraculum	Zooid Wall	Direction	Position	Mandible Length	Mandible Tip	Mandible Surface
-	Basal	4	0	1	NA	0
Vibraculum	Palatal Surface	Setal Groove Curvature	Setal Groove Length	Setal Groove Location	Rhizoid Pore	
-	2	0	2	1	1	

Table 3. Vibraculum classification of *A. puysegurensis* (Figure 9F). Vibraculae on adjacent zooids are paired with each other.

Spines	Total Num.	Num. Spines	Paired	Location	Angle	Direction
Spine I	5	2	1	Distal corner	3	Distal
Spine II	5	1	0	Distolateral	3	Distal
Spine III	5	2	1	Distolateral	3	Distal
Spines	Branching	Branch distinctness	Curvature	Compression	Proximity	Construction
Spine I	unbranched	0	0	0	2	Simple
Spine II	unbranched	0	0	0	2	Simple
Spine III	unbranched	0	0	0	2	Simple
Spines	Spine Tip	Basal Joint	Thickness	Length	Base width	Fusion
Spine I	NA	1	0	NA	1	None
Spine II	NA	1	0	2	2	None
Spine III	NA	1	0	2	2	None
Spines	Midline Interaction	Spiniferous Process	Zooid			
Spine I	None	None	autozooid			
Spine II	None	None	autozooid			
Spine III	None	None	autozooid			

Table 4. Spine classification of *A. puysegurensis*. Spine numbers vary depending on whether the zooid is marginal, central or ovicelled. Here, the spines of a central, non-ovicelled zooid are examined. Since spines cannot safely be considered homologous without topographical correspondence,¹⁰³ the three spine positions (i, ii, iii in Figure 9B) are examined separately.

Scuta	Overall Shape	Distal Lobe Type	Central Lobe Type	Proximal Lobe Type	Relative Lobe Size
-	Round	Truncated	None	Round	2
Scuta	Distinctness	Cross Section	Internal Channels	Base Location	Base Thickness
-	2	0	NA	1	2

Table 5. Scutum classification of *A. puysegurensis* (Figure 9A-C). The side (left or right) the scutum arises from is variable.

Rhizoids	Form	Origin	Surface	Tip	Connects	Thickness
-	1	Vibracular chamber	Smooth	NA	0	0

Table 6. Rhizoid classification of *A. puysegurensis* (Figure 9G).

Skeletal Chambers for Embryonic Incubation	Embryo Incubation Chamber	Skeletal Chamber	Immersion	Distal Zooid	Ooecium Structure
-	1	2	2	autozooid	0

Table 7. Embryo incubation classification *A. puysegurensis* (Figure 9B).

4. Discussion

The cheilostome polymorphism classification system presented here provides comprehensive and standardized morphological terminology. This classification system is robust, and is capable of describing a vast range of forms in fossil and recent cheilostomes. For example, $\sim 8 \times 10^9$ possible avicularia can be described qualitatively by this classification, not counting avicularia that possess multiple projections or those with divergent mandible and rostral morphologies. The nonhierarchical structure facilitates statistical comparisons at different levels of detail and allows it to be used even when some traits are missing. This classification system is well suited for use in morphological studies, several of which are discussed below.

It is important to identify those aspects of complexity that can be measured by this classification in cheilostome bryozoans. Complexity, as defined by McShea (1996)¹⁰⁴, can be divided into four categories:

1. Nonhierarchical object complexity: The number of different parts at a specific spatial or temporal scale
2. Nonhierarchical process complexity: The number of different interactions at a specific spatial or temporal scale
3. Hierarchical object complexity: The number of levels of organization
4. Hierarchical process complexity: The number of levels in a causal hierarchy¹⁰⁵

Since this classification system is focused on morphology, it facilitates the investigation of hierarchical and nonhierarchical object complexity. In bryozoans, nonhierarchical object complexity can be examined at the scale of the submodule (the number of different projections on an avicularian mandible), the cormidium (the number of different submodules), or colony form (the number of different cormidia and paramodules).¹⁰⁶ These levels are fairly independent of each other: a colony may be monocormidial (low complexity), but the one cormidium it possesses could have many submodules (high complexity). Hierarchical object complexity considers all levels of modular organization together, independent of their internal complexity. By this metric, monomorphic nonbranching colonies are the least complex (two levels: zooid, colony; see Figure 2B), while polymorphic branching colonies are the most complex (four levels: submodule, cormidium, branch, colony; see Figure 2I).¹⁰⁷ The appropriateness of each measure of complexity depends on the questions being asked. However, general questions about whether complexity has increased in cheilostomes should consider hierarchical and nonhierarchical object complexity at all levels of modular organization to produce a more nuanced picture of complexity in evolution. These measures of complexity can then be used in conjunction with tests for active selection described in McShea (1994).¹⁰⁸

This classification system also provides a framework for comparing bryozoan polymorphism morphology, which would be highly useful in a trait-environment analysis. Although relationships between bryozoan polymorphism and the environment have been investigated before, these studies only considered the number of different polymorph types (polymorphism diversity) and found no relationship with environmental

gradients.^{109,110} Although Schopf (1973) described a latitudinal trend in avicularian mandible shape, where pointed mandibles were commoner in the tropics, this was not tested statistically.¹¹¹ This highlights a gap in the literature that should be addressed. Since the classification system presented here is comprehensive in nature, it provides a high level of morphological (and thus ecological) resolution, which is necessary when teasing apart potential trait-environment relationships. The statistical methods then used would depend on the level of analysis: average, community-level trends could be investigated using canonical correspondence analysis (CCA), while RLQ analysis could be used for species-level trends.¹¹² Once these trends are identified, they can be used to predict bryozoan species/community responses to environmental shifts (e.g. climate change), or to reconstruct the paleoenvironment from fossil traits.

The analyses described above would not be possible with a purely phylogenetic study. Phylogenetics would not be able to separate forms arising from the high phenotypic plasticity in bryozoans, or provide comparisons between convergently evolved morphologies. Descriptions of form are particularly important for polymorphism, since many have unknown or debated functions (especially avicularia^{113,114}).¹¹⁵ Although this classification system does not explore function, the breadth of morphologies described here may facilitate analysis of form and function. Even within a single type of polymorphism, the range of forms suggests specialization for several different functions - though whether this holds true remains to be seen. However, analyses of complexity and trait-environment relationships would both benefit from the inclusion of genetic data. Genome and morphological complexity could be examined concurrently¹¹⁶, and phylogenetic effects could be controlled for in trait-environment analysis.^{117,118} Using this classification system in tandem with phylogenetics should contribute to a fuller understanding of cheilostome evolution and ecology.

Finally, this classification system should be of use to taxonomists. Although describing polymorphs and cormidia with this system is less concise than typical taxonomic descriptions (e.g. “spatulate mandible” vs “rounded overall shape, bulb, and tip; abrupt tapering; not curved; convex; no projections; no teeth”) the terminology is less ambiguous and captures a greater morphological resolution. Taxonomists may also wish to focus on species-discriminating traits, which can be picked from this classification system using the VARSEDIG algorithm.¹¹⁹

Throughout all the potential analyses mentioned, the standardized terminology provided here will allow clear, valid comparisons to be drawn between different studies. This will, we hope, encourage and enhance future research on bryozoan polymorphism.

5. Author contributions

CRS examined specimens, wrote, illustrated, and tested the classification system. DPG and KGR supervised the project. DPG provided guidance on terminology and definitions, the scope of the classification, and bryozoan anatomy. KGR assisted in fine-tuning definitions and increased the clarity of the classification system.

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Notes

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Appendix 1. Selected Definitions

Appendaged autozoid: An autozoid that possesses non-zooidal adventitious modules.

Autozooidal polymorph: A zooid that retains a protrusible tentacle crown but differs from an autozoid in the form of its cystid, polypide, or both. This includes reproductive zooids, appendaged autozooids, and nanozooids.

Cormidial arrangement: The pattern of cormidia within a colony so as to comprise secondary or higher-level modules.

Cormidium: A “colony within a colony” that consists of a feeding zooid and associated polymorphs. The cormidium is capable of performing most functions vital for life. Multiple types of cormidia may be present within a colony.

Heterozoid: Zooids that lack a feeding polypide and are separated from the autozooidal coelom by a pore plate (e.g. avicularia, some reproductive zooids).

Module: Any unit within a colony, the components of which are more integrated with each other than those of other units.

Monocormidial: A bryozoan colony that only possesses one type of cormidium.

Monomorphic: A structure that is made of only one kind of unit. In bryozoans, it refers to a colony that consists only of autozooids.

Non-zooidal adventitious module: A projection of the zooidal body wall that is not separated from the coelom by a pore plate, but displays reduced integration and exhibits variation separate from the parent zooid. These are typically spines, such as the spinules of *Membranipora membranacea* Linnaeus, 1767 or the spines of *Electra pilosa* Linnaeus, 1767. The parent zooid hosting a non-zooidal adventitious module may be an autozoid or a heterozoid.

Paramodule: Heterozooids that exist and repeat outside of cormidia (e.g. kenozooids in an anchoring kenozooidal stalk).

Polycormidial: A bryozoan colony that possesses multiple types of cormidia

Polymorph: A zooid or adventitious module that exhibits discontinuous variation (separating them from astogenetic and ontogenetic zooidal changes).

Polymorphic: Pertaining to the discontinuous variation that is exhibited by *any* modular structure in a bryozoan colony, including autozooids, etc.

Primary module: The basic repeating unit of a modular structure. In bryozoans, the primary module is either the autozoid (in monomorphic colonies) or the cormidium (in polymorphic colonies).

Secondary module: A structure formed through the repetition of primary modules, e.g. a branch composed of repeating cormidia. In terms of modular organization, this term is synonymous with “secondary structure”.

Submodule: The component parts (autozooids, autozooidal polymorphs, and heterozooids) of a cormidium.

Tertiary module: A structure formed through the repetition of secondary modules. In terms of modular organization, this term is synonymous with “tertiary structure”.

Appendix 2

Avicularia	Trait	Levels	# Levels	Data Type	Preserved in Fossils?
General	Type	Vicarious (0) Interzooidal (1) Adventitious (2)	3	Ordinal	Yes
Position	Zooid Wall	Frontal Lateral Distal Proximal Basal	5	Factor	Yes
	Relative Location	Hyper-oral Sub-oral Spine substitute Ovicell Gymnocyst Between zooids	6	Factor	Yes
	Distal-Proximal Location	Mid-Distal (0) Distal Corner (1) Distolateral (2) Lateral (3) Proximolateral (4) Proximal Corner (5) Mid-Proximal (6)	7	Ordinal	Yes
Direction	Rostral Direction	Distal (0) Distolateral (1) Lateral (2) Proximolateral (3) Proximal (4)	5	Ordinal	Yes
	Variable Direction	Non-variable (0) Variable (1)	2	Binary	Yes
Attachment	Attachment	Sessile Columnar Tubular Bird's head	4	Factor	Yes
	Spikes	None Simple Branching Mixed	4	Factor	Sometimes
	Spike Abundance	NA	NA	Numeric	Uncertain
	Elevation	None (0) Short (1) Intermediate (2) Long (3) Very long (4)	5	Ordinal	Yes
Mandible/Rostral shape	Overall Shape	Pointed (0) Rounded (1)	2	Binary	Only Rostra
	Curvature	Straight (0) Curved (1)	2	Binary	Only Rostra
	Tapering	No stem (0) Abrupt (1) Partial (2) Full (3)	4	Ordinal	Only Rostra
	Bulb Outline	Concave (0) Straight (1) Convex (2)	3	Ordinal	Only Rostra
	Bulb Shape	Pointed (0) Rounded (1)	2	Binary	Only Rostra
	Bulb Tip	Pointed Rounded	3	Factor	Only Rostra

		Truncated			
	Projection Shapes	None Mucronate Cuspidate Aristate Falcate Cirrhose Hooked Auriculate Oblong	9	Factor	Only Rostra
	Projection Location(S)	None Bulb (mid-distal) Bulb (distal corner) Bulb (lateral) Bulb-stem Stem	6	Factor	Only Rostra
	Teeth	None Sharp Blunt	3	Factor	Only Rostra
	Teeth Location	None Bulb Bulb-stem Stem Rachis Projection Entire	7	Factor	Only Rostra
Shape Measurements	Total Length	NA	NA	Numeric	Only Rostra
	Hinge Length				
	Hinge Width				
	Stem Length				
	Stem Width				
	Bulb Length				
	Bulb Width				
	Projection Length				
	Opesia Length				
Opesia Width					

Vibracula	Trait	Levels	# Levels	Data Type	Preserved in Fossils?
Location	Zooid Wall	Frontal Lateral Distal Proximal Basal	5	Factor	Yes
	Direction	Distal (0) Distolateral (1) Lateral (2) Proximolateral (3) Proximal (4)	5	Ordinal	Yes
	Position	Non-axial (0) Axial (1)	2	Binary	Yes
Mandible Structure	Mandible Length	Shorter (0) Intermediate (1) Long (2)	3	Ordinal	No
	Mandible Tip	Straight (0) Hooked (1)	2	Binary	No
	Mandible Surface	Smooth (0) Barbate (1)	2	Binary	No
General Structure	Palatal Surface	Absent (0) Present, with foramen (1)	3	Ordinal	Uncertain

		Present, no foramen (2)			
	Setal Groove Curvature	Straight (0) Curved (1)	2	Binary	Uncertain
	Setal Groove Length	Short (0) Intermediate (1) Long (2)	3	Ordinal	Uncertain
	Setal Groove Location	Transverse (0) Oblique (1)	2	Binary	Uncertain
	Rhizoid Pore	Absent (0) Circular (1) Ovate (2)	3	Ordinal	Uncertain

Spines	Trait	Levels	# Levels	Data Type	Preserved in Fossils?
Number of spines	Total Number of Spines	NA	NA	Numeric	Yes
	Number of Spines	NA	NA	Numeric	Yes
	Paired	No (0) Yes (1)	2	Binary	Yes
Location	Location	Mid-Distal Distal Corner Distolateral Orificial Sub-Oral Lateral Proximolateral Proximal Corners Mid-Proximal Opesial Distal Wall Outer Distal Corner Distal (Lateral wall) Lateral (Lateral Wall) Proximal (Lateral Wall) Proximal Wall	16	Factor	Yes
	Angle	Flat (inner) (0) Acute (1) Erect (2) Obtuse (3) Flat (Outer) (4)	5	Ordinal	Only costae
	Direction	Abfrontal Distal Distolateral Lateral Proximolateral Proximal	6	Factor	Only costae
Structure	Branching	Unbranched Forked Bifid Cervicorn Tines	5	Factor	Rarely
	Branch Distinctness	Distinct (0) Intermediate (1) Indistinct (2)	3	Ordinal	Rarely
	Curvature	None (0) Slight (1) Strong (2)	3	Ordinal	Rarely
	Compression	Cylindrical (0) Somewhat flattened (1)	3	Ordinal	Rarely

		Flattened (2)			
	Proximity	Sparse (0) Intermediate (1) Appressed (2)	3	Ordinal	Yes
	Construction	Simple Antenniform Stalked Antenniform Pinnate Lumen Pores	5	Factor	Rarely
	Spine Tip	Pointed Rounded Truncated Membrane	3	Factor	Rarely
	Basal Joint	Present (1) Absent (0)	2	Binary	Yes
	Thickness	Tapering (0) Consistent (1) Flaring (2)	3	Ordinal	Rarely
	Length	Short (0) Intermediate (1) Long (2) Very long (3)	4	Ordinal	Rarely
	Base width	Thin (0) Intermediate (1) Thick (2) Very thick (3)	4	Ordinal	Yes
Fusion	Fusion	None Lateral Medial Lateral neighbors Medial neighbors Complete Lacunae Peristome	8	Factor	For costae, potentially for other spines
	Midline Interaction	Separate Meet Interdigitate Push Carina	5	Factor	For costae, potentially for other spines
Other	Spiniferous Process	None (0) Bulb tip (1) Bulb Only (2) Entire Process (3)	4	Ordinal	Uncertain
Zooid	Zooid	Autozooid Ancestrula Ovicelled zooid	3	Factor	Yes

Scuta	Trait	Levels	# Levels	Data Type	Preserved in Fossils?
Shape	Overall Shape	Spike Round Fan Oblong Bifid Cervicorn	6	Factor	Uncertain
	Lobe Types	None Spike (H) Spike (A) Forked Round Truncated Tines	8	Factor	Uncertain

		Trifid			
	Relative Lobe Size	Reduced (0) Symmetrical (1) Enlarged (2)	3	Ordinal	Uncertain
Structure	Distinctness	Distinct (0) Intermediate (1) Indistinct (2)	3	Ordinal	Uncertain
	Cross-section	Flat (0) Curved (1)	2	Binary	Uncertain
	Internal Channels	Absent (0) Present (1)	2	Binary	No
Base	Base Location	Distal (0) Distolateral (1) Lateral (2) Proximolateral (3) Proximal (4)	5	Ordinal	Yes
	Base Thickness	Thin (0) Intermediate (1) Thick (2) Very Thick (3)	4	Ordinal	Yes
Measurement	Height	NA	NA	Numeric	Uncertain
	Width				
	Percent Cover				

Rhizoids	Trait	Levels	# Levels	Data Type	Preserved in Fossils?
General	Form	Prop (0) Rhizoid (1)	2	Binary	Uncertain
	Origin	Lateral wall Basal wall Dorsal wall Ventral wall Vibracular chamber	5	Factor	Uncertain
	Surface	Smooth Ringed Hooked Coiled (base)	4	Factor	Uncertain
	Tip	Single Fimbriate Hold-fast	3	Factor	Uncertain
	Connects	Substrate (0) Branches (1)	2	Binary	Uncertain
	Thickness	Consistent (0) Dilated (1)	3	Ordinal	Uncertain

Skeletal Chambers for Embryonic Incubation	Trait	Levels	# Levels	Data Type	Preserved in Fossils?
General	Embryo Incubation Chamber	External membranous sac (0) Skeletal chamber (1) Non-calcified internal brood sac (2) Intracoelomic incubation (3)	4	Ordinal	For skeletal chambers

	Skeletal Chamber	None (0) Acanthostegous (1) Ooecia (2)	3	Ordinal	Yes
	Immersion	Immersed (0) Sub immersed (1) Prominent (2)	3	Ordinal	Yes
	Distal zooid	Autozooid Kenozooid Vicarious avicularium	3	Factor	Yes
	Ooecia Structure	Entire (0) Bilobed (1) Multilobed (2)	3	Ordinal	Yes
Measurement	Length	NA	NA	Numeric	Yes
	Width				

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