Lexicon of Extrazooidal Calcification in Cancellate Cyclostomes

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1. The language of bryozoology

Part of the learning curve when entering a new discipline is understanding and applying jargon, or 'technical vocabulary' (Hayes, 1992). Bryozoology is no exception. Over two and half centuries a rich descriptive lexicon has developed around the morphology of the Bryozoa. The process mirrors the evolution of the organisms being described: new terms evolve and stabilize in meaning, new meanings may be added, and some terms fall into disuse. The ever-changing lexicon is always a work in progress (Boardman and Cheetham, 1983).

In large, fast-moving fields, such as computer or medical science, practitioners pay perfunctory attention to research more than a few decades old. However, in bryozoan taxonomy – a discipline with a long history but a relatively small number of active workers at any one time – it is often necessary to refer to taxonomic descriptions and other works dating back centuries (Winston, 1999, p. 127). Doing so can bring the changing lexicon into sharp relief, as the investigator grapples to understand what was actually meant by a particular usage of language through the filter of contemporary meaning.

As part of an ongoing revision of the Australasian Horneridae (Smith, 2008; Smith *et al*., 2008; Smith *et al*., 2012) our examination of the cyclostome literature highlighted a wide range of technical terms that had evolved in meaning and/or were multi-definitional. Some of these terms could lead to significant confusion: do hornerids really have 'maculae'? Are 'vacuoles' present in the secondarily thickened walls of certain hornerids? Is the hornerid 'epitheca' a thick layer of solid calcification or a thin cuticular covering?

To assess the scale and nature of change we examined a subset of the bryozoan lexicon describing secondary (=extrazooidal) calcification in free-walled cyclostomes. Our purpose was not to redefine or endorse certain terms, but rather to review what these terms mean, and to provide a case study of lexical evolution in a specialized area of biology.

2. Measuring the extent of change in a bryozoan sub-lexicon

Our lexical analysis focuses on 27 current or former morphological terms used in English-language bryozoological literature to describe the extrazooidal structures in free-walled cyclostomes, with the focus on the Cancellata (although many of the terms are applicable to the Bryozoa generally). We recorded the changing context and usage of terms over time, and their meanings were interpreted wherever possible. Many of the source publications were listed by Smith *et al*. (2008) in their Appendix and dealt with the Recent and fossil Horneridae. A range of other cyclostome literature was also examined. Results are consequently applicable to most other free-walled Cyclostomata.

To establish definitions, the context in which a term was used in the publication, contemporaneous works, or accompanying illustrations, was used to infer the intended meaning as far as possible. Bryozoological glossaries and listings of terminological definitions from 1896 to 2015 were also consulted, including Gregory (1895); Gregory (1896); Canu and Bassler (1920); Borg (1926); Bassler (1953); Bock (1982); Boardman and Cheetham (1983); Hayward and Ryland (1985); Boardman and Buttler (2005); and Bock (2015).

We have not attempted to generate an exhaustive lexical bibliography or to list every single usage for each term. Consequently results are conservative in their assessment of change. Current and past definitions, usages, caveats and example citations were compiled for each term. We used this dataset to rate the extent of change and plasticity in the meaning of these descriptors, which was in turn used to generate a 'potential for confusion' index, presented in Table 1 and in Figure 1. It should be noted that, although we have endeavored to be rigorous in our assessment methodology, the value coded for each term is somewhat arbitrary, owing to the relative size and number of caveats, and the range of possible meanings, which affected relative weightings. Results should, therefore, seen as broadly indicative rather than conclusive.

3. Results

The following list contains morphological terms that have been used to describe secondary (extrazooidal) calcification structures in studies of Cancellata and other free-walled cyclostome suborders. Some of these terms have little current taxonomic utility or are now used primarily for Paleozoic free-walled stenolaemates.

Canal
Meaning(s): Early synonym for *cancellus*.

Usage: Used to describe cancellate structures on lateral and obverse walls.

Contextual references: Gregory, 1899; Ross, 1977.

Remarks: Not widely used in the sense of 'cancellus' since Gregory. Ross (1977) also used the term 'canal' to describe longitudinal non-calcified conduits within the cyclostome skeleton (later refuted by Weedon and Taylor, 1996).

Cancellus (pl. cancelli, adjs, cancellate, cancellated)

Meaning(s): Has different meanings depending on cyclostome suborder: In lichenoporid cyclostomes, 'a calcified tube, which may be a kenozooid or extrazooidal'(definition from Bock, 2015). They occupy spaces surrounding autozooids (=alveoli of Borg, 1926). Small spines, often with hooks, are present on the interior of the lichenoporid cancellus wall. 'Secondary calcification may form horizontal laminae closing the cancellus' (Bock, 2015). In hornerids and other cancellates, a tube or cavity in the thick, secondarily calcified skeleton. For cancellates the term corresponds to the 'interstitial tubes' of Smitt (1867) and Waters (1887), and the 'pore ducts' of Borg, 1926. Derived from the Latin noun 'cancellus', meaning 'lattice', 'enclosure' or 'grid'.

Usage: Early uses of the term implied a honeycomb-like network of thin partitions separating autozooids. Gregory (1896) applied the term cancelli primarily to the Lichenoporidae for the structures now referred to as alveoli. Gregory (1899) reassigned the Horneridae and Petaloporidae to the Cancellata, causing the term 'cancelli' to become associated with the pit-like structures typical of these families.

Subsequently Canu and Bassler (1920) used a suite of other terms to describe structures in the Cancellata, and returned the term 'cancelli' to the lichenoporids, which were now in the Rectangulata.

In modern works, 'cancellus' appears primarily used for cancellate cyclostomes (and conescharellinid cheilostomes).

Contextual references: Hincks, 1880; Gregory, 1896; Harmer, 1896; Philipps, 1899; Gregory, 1899; Waters, 1904; Canu and Bassler, 1920; Borg, 1926; Borg, 1933; Borg, 1941; McKinney et al., 1993; Taylor and Jones, 1993; Alvarez, 1995; Boardman, 1998; Taylor, 2001; Taylor and Gordon, 2003; Bock, 2004; Bock and Cook 2004; Smith *et al*., 2012; Gordon and Taylor, 2015.

Remarks: Morphogenetic concepts remain ambiguous.

Harmer (1896, Figure 6) described both cancelli and alveoli from the same lichenoporid colony. Borg reclassified the same structures as primary and secondary alveoli.

The distinction between a cyclostome kenozooid and a cancellus is often blurred. Modern publications sometimes synonymise cancelli with kenozooids (using one term followed by the other in parentheses) to describe structures.

Cryptocyst*; *cryptocystal (adj.)

Meaning(s): Interior-walled calcification deposited beneath a hypostegal pseudocoelom during free-walled growth of frontal walls.

Usage: Used for cyclostomes but more often for cheilostomes in modern works. As an

adjective 'cryptocyst' in cyclostomes is now usually supplanted by terms 'free-walled' or 'interior-walled'.

Contextual references: Borg, 1926; Borg, 1941; Borg, 1944; Hayward and Ryland, 1985.

Remarks: Not a useful morphological descriptor for designating cancellate skeletal structures, since almost all zoarial calcification (both autozooidal and extrazooidal) is cryptocystal in this suborder.

Exozone/Endozone

Meaning(s): Endozone: The inner zone of a massive or erect stenolaemate colony, composed of the thin-walled proximal parts of the zooecia typically oriented subparallel to the branch growth direction. Exozone: The outer zone of a massive or erect stenolaemate colony, composed of the thick-walled distal parts of the zooecia typically oriented subperpendicular to the branch growth direction (Pitt and Taylor, 1990).

Usage: Exozone/endozone are most commonly applied to extinct stenolaemate orders, but also widely used for erect cerioporines (e.g., *Heteropora*) and cancellates (e.g., *Hornera*, *Calvetia*).

Contextual references: Boardman and Cheetham, 1969; Pitt and Taylor, 1990; McKinney *et al*., 1993; Boardman, 1998; Taylor and Gordon, 2003; Boardman and Buttler, 2005.

Remarks: In cancellates, the exozone is thickened by expansive extrazooidal calcification rather than thickening of the zooecial walls (cf. definition of Pitt and Taylor, 1990).

Epitheca

Meaning(s): Multiple meanings, including the 'basal lamina from which zooids arise' or the outer chitinous membrane (Bassler, 1953). An attribute of true epitheca is its non-poriferous nature.

Usage: Has been widely used in the paleontological literature on extinct stenolaemates (superorder Paleostomata). Also used in some early works to describe thickened dorsal walls of hornerids (Gregory, 1899; Waters, 1904).

Contextual references: Gregory, 1896; Gregory, 1899; Waters, 1904; Bassler, 1953.

Remarks: Term is effectively redundant for stenolaemates. In modern works the term is often used to describe the exterior cuticular layer of the cheilostome frontal wall.

Extrazooidal (adj., i.e., 'extrazooidal skeleton')

Meaning(s): Calcification outside formed zooecial boundaries. This includes interzooidal structures, secondary wall thickening and development of accessory structures (such as spines and webs).

Usage: For cancellates with massive secondary calcification 'extrazooidal' is now commonly used in place of 'stereom' and 'sclerenchyma', *sensu* Bassler 1953, or 'epitheca', *sensu* Gregory, 1899 and Waters, 1904.

Contextual references: Boardman and Cheetham, 1973; Brood, 1976; Boardman, 1983; Boardman and Cheetham, 1983; Pachut *et al*., 1991; McKinney *et al*., 1993; Boardman, 1998; Taylor and Weedon, 2000; Boardman and Buttler, 2005.

Remarks: This term raises the question of whether secondarily formed structures are homologous with autozooids and heterozooids. If yes, the term 'multizooidal', often used for cheilostomes, might be more appropriate.

Autozooidal wall calcification can apparently be partly 'extrazooidal' in composition in some hornerids (Boardman, 1998, p.14).

'Stereom', often used for extinct stenolaemate orders, could be applied to solid masses of extrazooidal calcification in living stenolaemates.

Hypostegal coelom/pseudocoelom

Meaning(s): Pseudocoelomic cavity between outer membranous wall and carbonate-secreting membrane beneath outer cuticle.

Usage: From Borg (1926). Since Nielsen (1970, Neilsen and Pedersen 1979) the term 'pseudocoelom' has been used, but note Nielsen and Pederson's 1979 caveat that either term does not have embryological connotations when applied to cyclostomes.

Contextual references: Borg, 1926; Borg 1944; Tavener-Smith, 1969; Tavener-Smith and Williams, 1972; Ross, 1977; Nielsen, 1970; Nielsen and Pedersen, 1979; Hayward and Ryland, 1985; Taylor and Weedon, 2000.

Remarks: The hypostegal pseudocoelom and associated epithelia are fundamental structures in determining patterns of wall formation in Cancellata.

Ross (1977) argued against the existence of the hypostegal pseudocoelom, but this was refuted by Weedon and Taylor, 1996.

Kenozooid*

Meaning(s): Structural heterozooid lacking polypide 'usually without orifice or muscles' (Hayward and Ryland, 1985).

Usage: In a cancellate context 'kenozooid' often refers to tubular supporting structures that are partly emergent, or identifiable as constructed tubes rather than cavities (as seen on the hornerid basal disc). In this case, the kenozooids do have a terminal orifice.

Contextual references: Levinson, 1902; Borg, 1926, p. 306; Boardman, 1983;Schäfer, 1991; Taylor and Weedon, 2000; Gordon and Taylor, 2001; Gordon and Taylor, 2015.

Remarks: *although not extrazooidal structures, kenozooids are included here because of their occasional synonymy with cancelli.

Inferred meaning in context of Cancellata is a zooid formed by tube *growth* – i.e., carbonate deposition rather than localized non-deposition. Further work needed.

Cyclostome kenozooids often possess a skeletal orifice overlain by an outer membranous wall (cf. definition at left).

Macula, maculae

Meaning(s): Pre-1900 'maculae' occasionally used as a synonym for 'cancelli' in some descriptions.

In modern usage 'maculae' refers to distinct patches of zooids of a different nature than the surrounding zooids, such as kenozooids, undeveloped autozooidal buds, or areas

of thick skeleton with fewer autozooidal apertures.
Usage: has stabilized to the modern definition.
Contextual references: Gregory, 1895; Gregory, 1899; Bassler, 1953 in Glossary); Boardman and Cheetham, 1973; Boardman, 1983.
Remarks: Confusion may have arisen from multiple meanings of 'macula' in Latin. The term can mean 'spot' or 'blemish' (the most frequent usage in a modern scientific context) or 'meshes of a net', the sense used by Gregory (1895).
Most cancellates lack 'maculae' in the modern sense of the term.

Mesopore
Meaning(s): 'Minute non-tabulate tubes parallel to zooecia which open on the zoarial surface adjacent to zooecial apertures' (Bassler, 1953).
'Zoarial structure between autozooids formed by a colony-wide depositing epidermis' (defined by Boardman and Cheetham, 1969, when referring to a trepostome).
'Space-filling polymorph in exozone between feeding zooecia" (for Paleozoic stenolaemates) (Boardman and Cheetham, 1983).
Usage: Advocated by Canu and Bassler, 1920, for some cancellates (*Polyascocecia* = *Reteporidea*) but term is now mainly used for Paleozoic taxa (e.g., trepostomes, cryptostomes).
Boardman (1983) listed mesopores (=mesozooid) as zooidal structures. Boardman and Buttler (2005) reinterpreted mesopores as extrazooidal parts.
Contextual references: Ulrich, 1890; Gregory, 1899 (but see note); Canu and Bassler, 1920; Bassler, 1953; Boardman and Cheetham, 1969; Schäfer, 1991 ('metaporen'); Boardman, 1983; Boardman and Cheetham, 1983; Boardman and Buttler (2005).
Remarks: Term has a history of confusion: Gregory, 1899 and Canu and Bassler, 1920 used different definitions of 'mesopore', with Gregory 1899 stating their absence was diagnostic of the Cancellata, while 'mesopores' were included as diagnostic for the group by Bassler (1953, p. G58).
It is uncertain whether these are zooidal or extrazooidal parts (may depend on taxon).
Term is now used only for Paleozoic stenolaemates (Palaeostomata).

Mural Cavity, Cavity
Meaning(s): Cancellus. Term has been used to describe hornerid thin sections.
Usage: Synonymous with cancelli in more recent works.
Contextual references: Gregory, 1899 (Mural Cavity); Tavener-Smith and Williams, 1972 (Cavity).
Remarks: 'Cavity' is contextual term for cancelli observed in thin sections.

Nematopore
Meaning(s): Defined as 'inferior and opposite ramifications' of autozooidal tubes (Canu and Bassler, 1920); 'mural tubes' in Tavener-Smith and Williams, 1972.

Usage: Characteristic of abfrontal walls of cytidid cancellates (*Diplodesmopora*).
Contextual references: Canu and Bassler, 1920; Bassler, 1953; Tavener-Smith and Williams, 1972.
Remarks: More likely to be true kenozooidal structures, rather than pits / cancelli in developmental terms.

Nervus (pl. *nervi*)
Meaning(s): Network of secondarily calcified zoarial ridges on outer surface of many cancellates.
Usage: In current use for cancellates, especially for the Horneridae. However, some recent cancellate descriptions (Taylor and Gordon, 2003; Smith *et al*., 2012) have omitted 'nervi', instead using 'striae'. Early works used a wide range of descriptive terms, such as 'fibrillae' (MacGillivray, 1895) and 'striae' (Kirkpatrick, 1888).
Contextual references: Bassler, 1953; Tavener-Smith and Williams, 1972; Mongereau, 1972 [1970 in refs]; McKinney *et al*., 1993; Smith *et al*., 2008; Di Martino and Taylor, 2014.
Remarks: Useful term for a common structure in cancellates. Frontal nervi can be sinuous (as in *Hornera*) or linear (*Clavicavea*).

Non-Modular (adj., i.e., 'non-modular colony regions')
Meaning(s): Areas of a bryozoan colony that are not part of any autozooid or heterozooid. A functional term relating to the role of zooids as modules within a colony.
Usage: Synonym for 'extrazooidal' parts of a colony according to McKinney and Jackson, 1989.
Contextual references: McKinney and Jackson, 1989.
Remarks: Potential for confusion, because some non-modular structures are 'modular' in appearance, such as trepostome mesopores and cyclostome cancelli.

Pit
Meaning(s): An early synonym for hornerid cancelli (e.g. Busk, 1886), later proposed by Borg as a formal term to replace 'cancelli' in the Cancellata.
Usage: Principally used in Victorian-era research and in the works of Borg. The term was not included in any of the bryozoological glossaries published after Borg's studies.
Contextual references: Busk, 1859; Busk, 1886; Waters, 1888; Waters, 1904; Borg, 1926; Borg, 1941; Borg, 1944.
Remarks: In the 20th Century the term 'pit' may have been regarded as too generic to function as technical vocabulary.

Pore, pore duct, pore tube, interstitial pore
Meaning(s): 'Pore' was a common early synonym for cancelli in early hornerid descriptions, and still used in this context until the 1990s.
Borg (1941) used 'pore ducts' or 'pits' in preference to cancelli.

Usage: Usages variable and sometimes unclear. Cancelli typically have pores at their base, so the term 'pore duct' is informative.

Contextual references: Lamouroux, 1821; Smitt, 1867; Smitt, 1872; Hutton, 1873; Busk, 1875; Waters; 1888; Waters, 1904; Borg, 1926; Borg, 1941; Busk, 1859; Busk, 1875; Harmer, 1915; Whitten 1979; Schäfer, 1991; Ryland and Hayward, 1991.

Remarks: Can cause confusion with mural pores.

Apart from portions of gonozooids in some families (e.g., Stegohorneridae), there are no pseudopores in Cancellata as skeletal growth is interior walled.

Pseudopuncta

Meaning(s): 'Pseudopunctae' are dome-shaped discontinuities in bryozoan laminae (Tavener-Smith and Williams, 1972).

Usage: Pseudopuncta are similar to stylets/styles in Paleozoic stenolaemates (*sensu* Taylor and Jones, 1993) and Recent *Densipora* (Boardman, 1983).

Contextual references: Tavener-Smith and Williams, 1972; Boardman, 1983 ('styles', 'stylets').

Remarks: In hornerids raised surface features (pustules) have been termed 'typical pseudopuncta' by Tavener-Smith and Williams, 1972.

***Puncta*, punctations, punctures** (adj. punctate)

Meaning(s): In some early hornerid descriptions, 'puncta' was a synonym for a mural pore (Busk, 1859) but has also been used to describe cancelli, and more recently has been used to describe 'canals' [pseudopores] opening onto the external shell surface' in taxa like *Berenicia* (Tavener-Smith and Williams, 1972).

Usage: The adjective 'punctate' was defined by Gregory (1896) as 'large' pores in the zooecial wall, with smaller pores being described as 'punctulate'.

Contextual references: Busk, 1859; Busk, 1875; Gregory, 1895; Gregory, 1896; Waters, 1904; Tavener-Smith and Williams, 1972.

Remarks: Multiple meanings of 'puncta' and its derivations mean care must be taken in interpretation of early works.

Pustule

Meaning(s): Raised projections on the outer skeletal walls of many cancellates, that are the surface expression of pseudopunctae.

Usage: Pustules are usually <10 micrometers in diameter in hornerids and possess distinctive 'triple spikes' in some taxa (Taylor and Jones, 1993).

Contextual references: Taylor and Jones, 1993; Taylor *et al*., 2014.

Remarks: Pustules 'abundant on the topologically outer skeletal walls of *Hornera*' (Taylor and Jones, 1993).

Sclerenchyma

Meaning(s): Thick, secondarily formed calcification on branches of fenestrate cyclostomes.

Usage: Term not used for modern cyclostomes (?).
Contextual references: Ulrich, 1890; discussed by Boardman and Cheetham, 1973.
Remarks: Not in use.

Stereom
Meaning(s): 'Extrazooidal deposits … solid skeletal masses between zooids generally occurring in exozones' (Boardman and Buttler, 2005).
Usage: Principally used in the paleontological literature for extinct stenolaemate orders.
Contextual references: Bassler, 1953; Pachut *et al*., 1991; Boardman and Buttler, 2005.
Remarks: Because it does not have other meanings (cf. 'epitheca') 'stereom' is a potentially useful term for massive secondary calcification in modern cancellates, but has not been used in this context, possibly because in most species cancelli interrupt the solidity of the structure.

Sulcus (pl. *sulci*)
Meaning(s): *Two definitions* depending on context: For bryozoans in general 'sulci' refers to the grooves delineating zooids. For cancellates it usually refers to the grooves delineating nervi / striae, which usually do not conform closely to zooid boundaries (e.g., Mongereau, 1972).
Usage: Long-established term in current use for many bryozoan groups.
Contextual references: Busk, 1859; Hutton, 1873; Busk, 1875; Busk, 1886; MacGillivray, 1895; Waters, 1904; Canu and Bassler, 1920; Osburn, 1953;
Tavener-Smith and Williams, 1972; Mongereau, 1972; Hayward and Ryland (1985);
McKinney *et al*., 1993; Di Martino and Taylor, 2014.
Remarks: Although the meaning of sulcus is quite simple ('groove'), there is potential for confusion owing to contradictory definitions in glossaries, and different contexts in which they apply (e.g, adjacent zooidal and extrazooidal structures in the same branch).

Tergopore
Meaning(s): Dorsal cancelli (kenozooids?) 'as wide as polypide tubes but with polygonal aperture' Bassler (1953).
Usage: Coined by Canu and Bassler, 1920 to describe dorsal cavities in *Pleuronea* and crisinids (e.g., *Mesonea*).
Contextual references: Canu and Bassler, 1920; Borg, 1941; Bassler, 1953; Hinds, 1975; Boardman and Cheetham, 1973; Brood, 1976; Boardman, 1983.
Remarks: In the context of the crisinid *Mesonea* the term 'tergopore' was retracted by Canu and Bassler, 1929, but has been used occasionally since then, including by Bassler (1953). Borg (1944) regards tergopores as cancelli. Boardman and Cheetham (1973) discussed crisinid tergopores (without using the term), indicating they were large enough to be zooidal in nature. More recently, Boardman (1983) listed tergopores as zooidal polymorphs rather than extrazooidal parts. Further work needed.

Tubercle

Meaning(s): Used variously to describe pustules, or larger raised surface structures (20–120m) in many taxa.

Usage: Often referring to surface expressions of styles or pseudopunctae in Paleozooic stenolaemates.

Contextual references: McGillivray, 1895; Tavener-Smith and Williams, 1972; Taylor *et al*., 2014.

Remarks: Seen in late-stage secondary calcification of some hornerids (unpublished data).

Tube, tubule, *tubuli*

Meaning(s): Early synonyms of autozooids, kenozooids and/or cancelli depending on context.

Usage: Rarely used now, other than as modifiers, e.g., 'tubular kenozooids'.

Contextual references: Busk, 1861; Busk, 1875; Gregory, 1899; Canu and Bassler, 1920; Bassler, 1953.

Remarks: Note multiple uses, especially in older works. Additional potential for confusion with 'tubula' in cheilostomes.

Vacuole

Meaning(s): 'Slender tube (kenozooecium) approximately normal to front or back zoarial surface, separated from neighbouring similar tubes by stereom.'
Bassler (1953). 'Orifice faisant communiquer la cavité du zoïde avec l'extérieur' (Mongereau, 1972).

Usage: Synonymous with cancelli in some works (e.g., Mongereau, 1972).

Contextual references: Waters, 1904; Canu and Bassler, 1920; Borg, 1941; Mongereau, 1972; Hinds, 1975; Boardman, 1998.

Remarks: Borg (1941) argued this usage of 'vacuole' does not align well with other uses of the term (cf. cell biology) and implies a fully enclosed space rather than a tube (this descriptor reflects the way cancelli often appear in thin section).

Potential for Lexical Confusion

Only 15% of the terms examined were ranked with a low confusion potential; 59% were medium, and 26% were ranked with high confusion potential (Figure 1). The mean confusion index score for all terms was 2.1 (1 = low and 3 = high).

Examples of terms with in the 'low' category were those such as 'endozone', 'nervus' and 'pustule'; they were categorized by being single-meaning terms easily assignable to the relevant morphology based on a relatively brief definition.

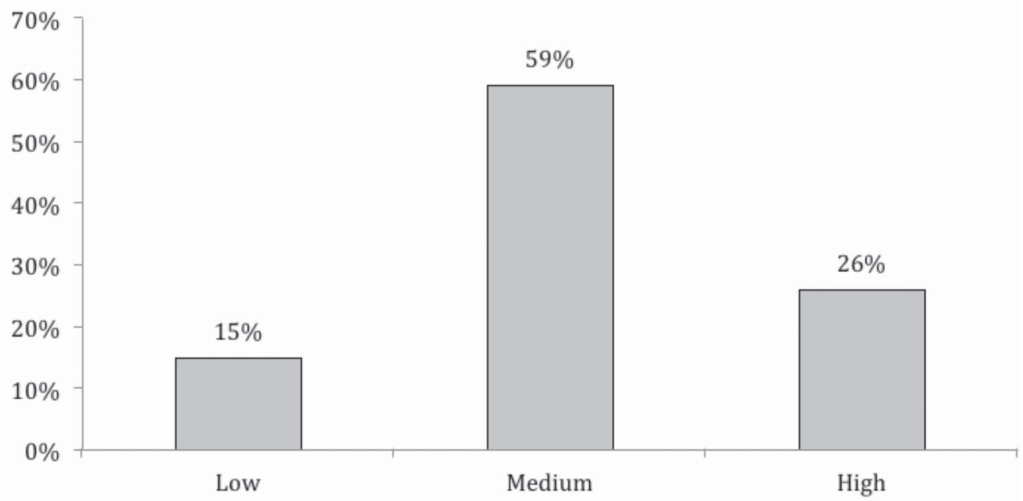

Figure 1. Potential for confusion among 27 current and historic morphological terms applied to extrazooidal calcification of cancellate cyclostomes. Data includes all terms listed above.

Terms with a 'medium' or 'high' confusion rating usually included one or more of the following traits:

(1) multiple meanings, or a more nuanced meaning when applied specifically to cancellates (e.g., 'sulci', 'cancelli');

(2) significantly changed in meaning over time (e.g., 'puncta', 'epitheca' or 'macula');

(3) associated with dynamic or incompletely defined morphological concepts ('extrazooidal', 'kenozooids', 'cancelli');

(4) are used only for a specific taxonomic group (e.g., cytidid nematopores) despite being potentially used for other groups.

4. General lexical trends through time

The following discussion focuses on the evolving lexicon of extrazooidal calcification terminology applied to the suborder Cancellata. To provide taxonomic context, Figure 2 shows description rates through time for the largest cancellate family, the Horneridae, beginning with *Hornera lichenoides* (Linnaeus, 1758, originally described as *Millepora lichenoides*; Figure 3) as well as the description rate of new families of extant bryozoan. Most of the Cancellata were described by 1900, whereas the higher level taxonomy (as represented by description of new families) has proceeded at a more steady rate over the last two centuries (Figure 2).

1750–1880: The Age of Adjectives

By 1880 more than 100 species of hornerid bryozoan had been described, representing ~63 % of all descriptions of this family to date (Figure 2). By necessity, these early

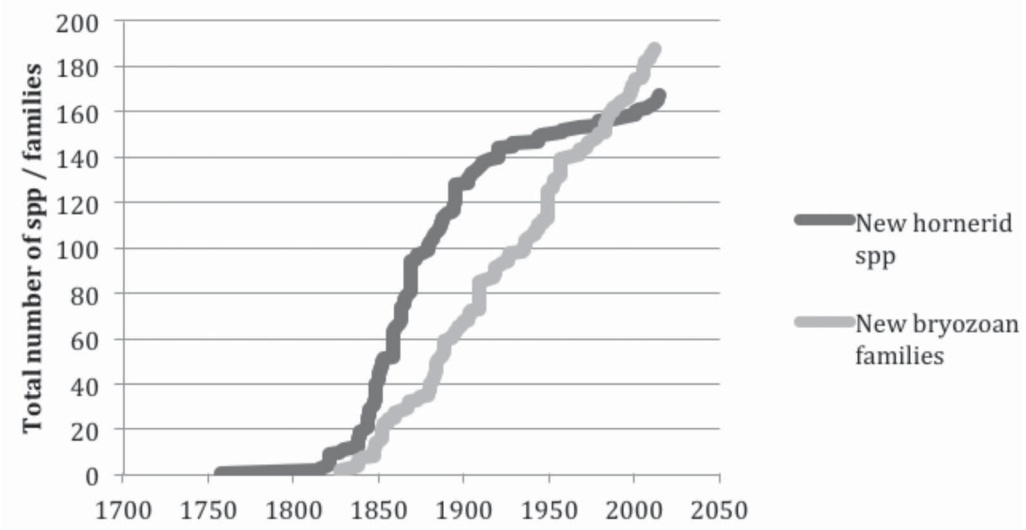

Figure 2. Cumulative curves showing all descriptions of new fossil and living hornerid bryozoans from 1758 to 2016 (data from Smith et al.*, 2008), and currently valid extant bryozoan families (data from Bock and Gordon, 2013)*

accounts relied heavily on descriptive language because an extensive technical vocabulary had not yet developed for the Bryozoa. For example, Lamouroux's 1821 description of the genus *Hornera* (translated from French) begins with: 'Colony is stony, tree-like, fragile, twisted and turning irregularly; stalk and branches covered with pores on the external surface, little pores quite well spaced... .'

Longer species accounts from this era (e.g., Busk, 1859) are often surprisingly clear in meaning because of the abundance of adjectives and other descriptive language. However, terms like 'pore', 'pit' and 'puncta' were not fixed to a particular structure or spatial scale, and tended to be qualified to establish meaning – e.g., 'small rounded pores' or 'minute puncta' (Busk, 1859). Few early taxonomists presented measurements of small structures with their descriptions, and examination of illustrations is often necessary to determine the structure being discussed.

Early taxonomic descriptions highlight the brevity enabled by modern technical vocabulary: For example, Hincks (1880) wrote of the frontal surface of *Hornera* 'the zooecia are covered in front by a calcareous crust, which takes the form of wavy longitudinal ridges, often anastomosing, which wind round and inclose the orifices of the cells, and give a fibrous appearance to the surface of the zoarium.' To describe the same structure today, a taxonomist might simply write, 'well-developed frontal nervi present'. The difference between the two approaches is that the latter relies upon the reader having a preconceived idea of what 'nervi' are, or at least the inclusion of well-labelled figures.

1880–1930: A Developing Lexicon

During this period several factors influenced the cyclostome extrazooidal calcification lexicon: (1) the dawning understanding of modes of skeletal wall formation, and (2) the increasing stabilization of the higher taxonomy of the Cyclostomata.

Many common usages of already-established terms date from this time, while newer terms such as 'hypostegal coelom', 'cryptocyst' and 'kenozooid' were applied in a more developmentally directed sense by Borg (1926) and others. Around this time, Canu and Bassler (1920) introduced a detailed scheme for classifying different types of non-autozooidal tubes found in cyclostomes, often linking the terms to specific taxonomic groups. Included in their classification were definitions of new terms and redefinitions of existing terms: these included 'nematopores', 'tergopores', 'cancelli', 'vacuoles', and 'mesopores' (a term first introduced by Ulrich in 1890).

Term	Meaning changed?	Multiple meanings in modern context?	No longer used in original sense?	Taxon-specific usage?	Exceptions or caveats relative to usual definition?	'Potential for Confusion' (1=low 3=high)
Canal			Y			2
Cancellus	Y	Y	Y		Y	3
Cryptocyst					Y	1
Endozone					Y	1
Epitheca	Y	Y	Y			2
Exozone					Y	2
Extrazooidal					Y	2
Hypostegal pseudocoelom					Y	2
Kenozooid					Y	3
Macula	Y		Y			3
Mesopore				Y	Y	3
Mural cavity			Y			2
Nematopore				Y		2
Nervus				Y		1
Non-modular					Y	2
Pit			Y			2
Pore / pore duct			Y	Y		2
Pseudopuncta					Y	2
Puncta / punctation	Y	Y	Y		Y	3
Pustule						1
Sclerenchyma			Y	Y		2
Stereom				Y	Y	2
Sulcus		Y			Y	2
Tergopore				Y		2
Tubercle						2
Tubule, tubuli	Y		Y			3
Vacuole		Y	Y	Y	Y	3
% of Terms	**19**	**19**	**41**	**30**	**48**	**Avg: 2.1**

Table 1. Evolution of the English-language lexicon of extrazooidal calcification in free-walled cyclostomes. Contributing factors to the 'potential for confusion index' include: (a) term has changed meaning over time, (b) term has different meanings, e.g., when applied to different taxa, (c) term has fallen into disuse in the formerly used context, (d) restriction of a term to a specific taxon (e) presence of caveats or exceptions.

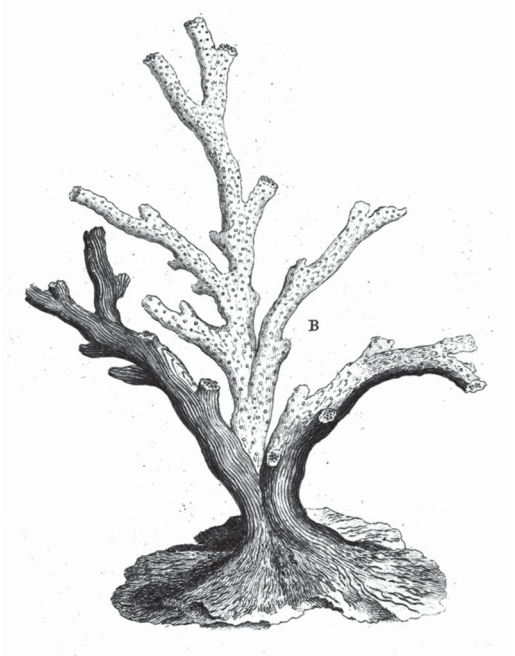

Figure 3. John Ellis' 1755 illustration of the cancellate, Hornera lichenoides.

Cultural interchange and cross-fertilisation of terminological concepts were prevalent in this era of multi-lingual science publishing, even though translations of the terms themselves were often used. Scientists were expected to be proficient in all major European languages, or at least make regular use of a translator. Thus it was business-as-usual when Gregory (1895) wrote in English that he concurred with Pergens' (1889) paper (published in German) disagreeing with Jullien's (1886) paper (published in French) on the morphogenesis of cancellate 'maculae' (a Latin-derived term, see above).

Enduring lexical complications have arisen because of changes in high-level taxonomic classification. The history of the morphological term 'cancellus' provides a striking example. When Gregory (1896) established the cyclostome suborder Cancellata in his catalogue of Jurassic Bryozoa, he did not include any taxa currently regarded as cancellates in it. Gregory's early Cancellata was instead equivalent to the modern Rectangulata, while he placed the hornerids in the suborder Tubulata. This arrangement made sense at the time because the thin-walled, honeycomb-like interzooidal structures then referred to as 'cancelli' (as seen in *Lichenopora*) typified the bryozoans we now call rectangulates. In 1899, however, Gregory revised the higher taxonomy of the Cyclostomata in his Cretaceous catalogue, removing the lichenoporids from the Cancellata and replacing them with the Horneridae and Petaloporidae. For consistency, he then referred to the secondarily calcified walls of these 'new' cancellates as 'cancellate', essentially redefining the term, as was pointed out by Waters (1904). Later workers accepted Gregory's taxonomic revision of the Cancellata, but were reluctant to adopt the re-

definition of the term that described the accompanying wall type. So for many years afterwards the term 'cancelli' continued to be applied to rectangulate extrazooidal structures (e.g., lichenoporid alveoli), while the analogous, but quite different, structures that exemplify the Cancellata as currently conceived were called anything *but* cancelli (e.g., Canu and Bassler, 1920; Borg, 1941). Borg's influential 1926 dissertation strongly endorsed Harmer's (1896) term 'alveoli' for lichenoporids, in the process freeing up 'cancelli' for the equivalent structures in cancellates.

The works of Borg (1926, 1941, 1944) were instrumental in elucidating the underlying growth mechanisms that unite the modern Cancellata. He erected the suborder Pachystega to contain them. Perhaps partly for this reason, Borg eschewed the use of 'cancelli' and other cancellate-specific terminology such as the scheme proposed by Canu and Bassler (1920). He felt the slew of taxon-specific terms 'hardly necessary' (Borg, 1944, p.178) and preferred blunter, more explanatory terms: e.g., 'pore', 'pore ducts' and 'pore pits'. However, 'cancelli' for 'pore pits' in the Cancellata is now widely used in the English-language literature.

The 1930s onwards: the Lexicon 'settles'

By 1930, 87% of living and fossil hornerid taxa had been described (Figure 2), and they were established as part of the Cancellata (Pachystega). Only a few new morphological terms describing secondary calcification have entered widespread use since this time. Most of these are more conceptual or over-arching than previous morphological terms: they include 'endozone', 'exozone', 'extrazooidal', 'multizooidal' and 'non-modular'. In addition, 'hypostegal pseudocoelom' – an alteration of Borg's 'hypostegal coelom', was proposed by Nielsen and Pedersen (1979). A few additional terms relating to extrazooidal calcification at the ultrastructural scale (not covered in our analysis) came into widespread use following the adoption of SEM: they included 'crystallite', 'semi-nacreous' and 'screw dislocation'. Many of these ultrastructural terms were imported terminology developed for ultrastructure in other phyla, such as brachiopods and molluscs (Weedon and Taylor, 1995).

During this period usages of some terms drifted further away from their former uses: 'epitheca' is now used primarily for cheilostomes, 'maculae' in the sense of 'cancelli' is no longer used, and 'vacuole' has largely been left for the cell biologists. The suite of taxon-specific terms for different 'tubes' advocated by Canu and Bassler (1920) still appear from time to time, but usually in an explanatory context: e.g., 'referred to as X by Canu and Bassler'. In the Cancellata, probably the largest present-day terminological issues relate to uncertainty around the morphogenetic distinctions between zooidal and extrazooidal structures, such as cancelli and co-occurring kenozooids within the same colony. This question requires a more detailed treatment, and will be discussed in a later paper.

5. Discussion

This contribution has duel functions: first, it is a resource to assist interpretation of several centuries of published works describing extrazooidal calcification in free-walled cyclostomes. Secondly, it provides a case study of the extent of plasticity and change in a sub-lexicon of bryozoology.

Is the changing Lexicon a problem?

Lexical change introduces an additional layer of complexity into language, requiring a more nuanced understanding of each term's use in a particular context. This comes only from experience. We framed our analysis in terms of 'potential for confusion', a value-loaded term that reflected our interest at the time. We could just as easily have described our index as 'lexical plasticity and complexity'. It was interesting to see just how much variability existed in our small subsample of the bryozoological lexicon, with only 15% of terms having a 'low' potential for confusion, and 85% of terms being either somewhat or very potentially confusing. This result might reflect an overly sensitive definition of what constitutes *potential* for confusion.

Nearly half of terms had a caveat of some sort, ranging from minor to major, and 41% of terms were no longer used in the original sense (Figure 1). In daily life we accept multi-definitional words without thinking because of our life-long exposure to them. Similarly, most experienced taxonomists have had time form their own understanding of the technical language, and lexical plasticity is generally not a problem for them. It is, however, easy to become confused early on in the 'learning curve'. It can be particularly daunting when contextually relevant definitions or illustrations are lacking or hard to find.

The question of whether a technical lexicon is 'fit for purpose' is a perennial one that has occupied practitioners of many different disciplines. Common concerns about jargon include its role in making it difficult to enter a subject area, and decreasing the accessibility of a subject to non-specialists such as policy makers (e.g., Hayes, 1992). It was beyond our scope to address this lively topic in our analysis. However, in bryozoology, concerns have been raised that specific terms are over-specialised (e.g., Borg, 1941), redundant (e.g., Bassler, 1953), or poorly defined (e.g., Berning *et al*., 2014). Innumerable taxonomic papers include remarks on specific terminology along these lines, and this tradition can be expected to continue. For example, many current morphological terms describe analogous structures that may have arisen multiple times across different clades. As knowledge of bryozoan phylogeny and morphogenesis improves, it is likely that many new terms will arise as strictly homologous structures become more recognizable (Paul Taylor, pers. comm.).

Occasionally there have been calls for a more systematic 'clean up' of the entire lexicon. In the introduction to the glossary of bryozoan morphology in the *Treatise of Invertebrate Paleontology*, Part G, Bassler (1953) wrote that 'literature on Recent and fossil Bryozoa is encumbered by a multiplicity of morphological terms to such extent that

understanding of these animals by non-specialists is impeded greatly and unnecessarily.' In the accompanying glossary, Bassler italicized morphological terms he considered suitable for removal from the bryozoological lexicon. These included 'funiculus', 'pseudopore' and 'nanozooid' – seemingly indispensible terms in a modern context.

Boardman and Cheetham (1983) took a different view from Bassler (1953) when they updated the *Treatise*, stating: 'We do not believe that terms or their definitions should be fixed. Morphologic concepts are progressive approximations of full biologic understanding. Therefore, definitions should be constantly revised as knowledge of biologic relationships increases... .' Viewed from Boardman and Cheetham's perspective, the extrazooidal calcification lexicon described in this article shows a healthy amount of change over time. Although this review focused on English-language literature, we speculate that the bryozoological lexicon in other languages is likely to exhibit a similar pattern.

What of total lexicon size – are bryozoan taxonomists drowning in unnecessary jargon as Bassler suggested? Relative to sub-disciplines within medical science, social science and engineering, the lexicon of bryozoan morphology seems very modest. Practitioners of those disciplines require thick dictionaries of packed with technical vocabulary. The current edition of *The Meriam-Webster's Medical Dictionary* contains 38,000 entries, and the most recent edition of *Mosby's Medical Dictionary* contains 56,000 entries, and runs to almost 2,000 pages. By comparison, Bassler's morphological glossary was ten pages long, including the terms he thought could be discarded, while that of Boardman and Cheetham (1983) is seventeen pages long. At the time of writing, the online bryozoological glossary provided at *bryozoa.net* (Bock, 2015) is 6261 words long – approximately the length of this paper. (Of course it does not include the thousands of general biological and geological terms that bryozoologists must also be familiar with.) Factors that may contribute to the small lexicon include the relative simplicity of the organisms, their highly conserved bryozoan *bauplan*, and the small size of the research community studying the phylum.

6. Summary and Conclusions

We have described change in the sub-lexicon of bryozoology concerned with cyclostome extrazooidal calcification. Most of the terms we reviewed showed at least some plasticity in meaning, and therefore some potential for confusion. This is most evident when older works are read in the light of modern definitions that have changed over time. The high level of plasticity in the meaning of most technical terms, which *by definition* are intended to be highly concise and constrained, is perhaps surprising. However it is an inevitable consequence of an advancing, evolving field.

New terms and definitions arise and change in bryozoology in an organic way, principally through the medium of publishing. A particular term's success is determined by its uptake and ongoing usage. This reflects the relevance and utility of the term, so the process is self-governing. Relative to other disciplines the total size of the bryozoological lexicon does not appear oversized or over-specialised, and is in fact relatively small. The

commonest potential sources of confusion in the terms we examined were those that are no longer used in their original sense, and those with multiple or significant caveats or exceptions. Terms with several, sometimes contrary, meanings or with taxon-specific uses were also common in the lexicon.

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