Annals of Bryozoology 6

Annals of Bryozoology 6: aspects of the history of research on bryozoans

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&
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This volume is dedicated with affection to Alan Cheetham,
inspirational colleague and founder of the International Bryozoology Association

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Cover illustrations

Front: Fritz Braem's 1890 illustration of statoblast germination in *Cristatella mucedo* Cuvier, 1798 (see paper by Martha *et al*., p. 51).

Back: Portion of a plate from Alicide d'Orbigny's *Paléontologie française* (1850–1852) showing the Cretaceous bryozoan *Retepora royana*.

Background: Structure of *Flustra* from Robert Hooke's *Micrographia* (1665).

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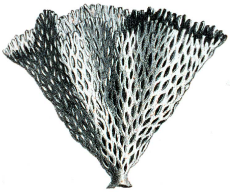

PREFACE

In 2001 the International Bryozoology Association met in Dublin for its 12th International Symposium, and the final day was devoted to a joint meeting with the Society for the History of Natural History during which a number of papers on the history of research into bryozoans were delivered. These were subsequently published as *Annals of Bryozoology* (Dublin, 2002). Such was the enthusiasm for the volume that soon afterwards offers of further papers were received by the editors and a number of historical papers were presented at the next IBA symposium in Chile in 2004. It was then felt that publication of a second volume was justified. The co-editors are hugely gratified that there is continued interest in this subject and that the series has now reached volume 6.

This current volume contains a number of papers presented at the IBA Larwood Meeting held in Orkney, Scotland in 2015 at the International Symposium hosted in Melbourne in April 2016. We are most grateful to the conveners of these meetings Joanne Porter and Jennifer Loxton, and Rolf Schmidt for facilitating these papers.

The eight papers contained in this volume may be subdivided into a number of categories, although they are presented in alphabetical order by first authors as is the series style.

Six of the papers focus on the work and lives of a number of bryozoologists. Juan Cancino and colleagues pay tribute to Roger Hughes and outline his considerable research output. Of particular note is the reminder of his role as a mentor—he supervised thirty-six Ph.D. students and it is evident in the warmth of the paper that Roger was held in very high regard. The detailed morphological studies of the embryologist Fritz Braem is brought to light. He conducted a number of significant studies over a period of six decades, much done after he left academic life. In recent years there has been a welcome return to studies of freshwater bryozoans in Lithuania. The paper by Ingrida Satkuskiene recalls the important freshwater bryozoans studies by Brone Pajiedaite in the early 1930s, and one of her specimens shows a phylactolaemate ovary which the authors remark is seldom seen. In 1945 she was arrested and deported to Siberia where she died. In England during the early 1900s R.M. Brydone and W.D. Lang fell out over their bryozoological research. Paul Taylor and his colleagues outline the reasons for this scientific animosity. Patrick Wyse Jackson and Neil Clark discuss the work of the two John Young who both worked for the same institution in Glasgow during the 1800s. Together in the 1870s they erected a number of fenestrate genera, while later one of them continued research on bryozoans for which he received the acclaim of his peers. Abigail Smith provides a biographical listing of various and numerous naturalists named Smith or variants thereof.

This volume contains two papers that deviate from the historical scope of the others, and are important lexicons of morphological terminology. As such the contribution by Peter Batson and Abigail Smith will help standardise use of terms for extrazooidal calcification in some cyclostomes, while Carolann Schack, Dennis Gordon and Ken Ryan provide a comprehensive classification of cheilostome polymorphs. It is hoped that such papers will act as standard bearers for many decades to come.

It gives us great preasure to dedicate this volume to Alan Cheetham founder of the International Bryozoology Association on his 90th birthday.

Patrick Wyse Jackson (Trinity College, Dublin)
& Mary Spencer Jones (Natural History Museum, London)

4th January 2018

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.

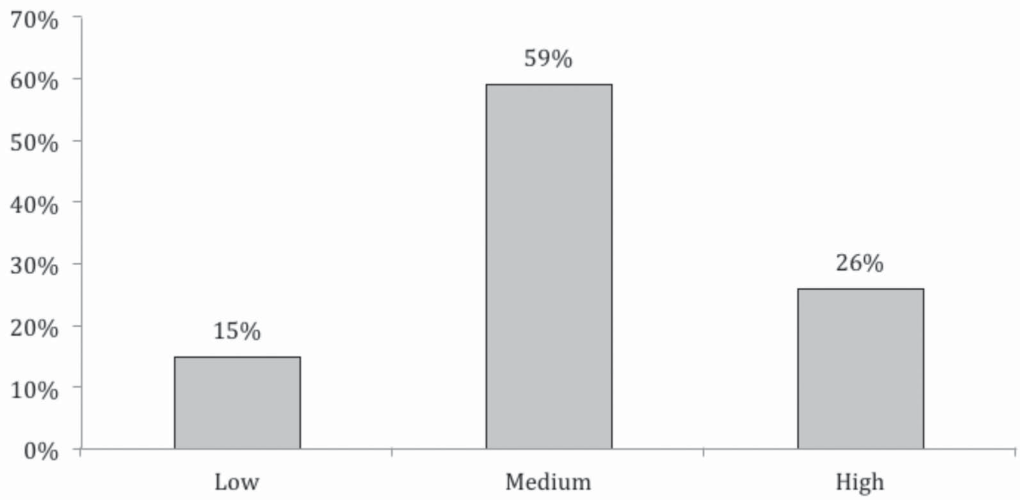

Figure 1. Potential for confusion among 27 current and historic morphological terms applied to extrazooidal calcification of cancellate cyclostomes. Data includes all terms listed above.

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

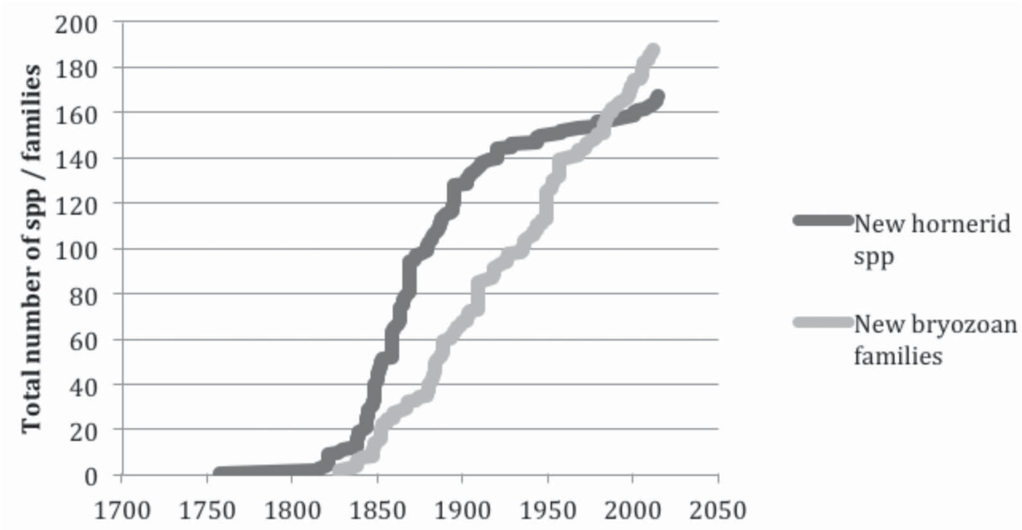

Figure 2. Cumulative curves showing all descriptions of new fossil and living hornerid bryozoans from 1758 to 2016 (data from Smith et al.*, 2008), and currently valid extant bryozoan families (data from Bock and Gordon, 2013)*

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.

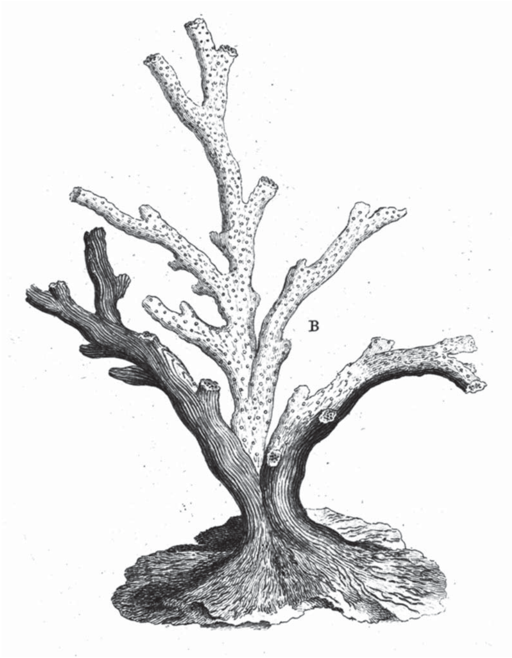

Figure 3. John Ellis' 1755 illustration of the cancellate, Hornera lichenoides.

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 redefinition 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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References

Alvarez, J. A. 1995. New data on the family Lichenoporidae Smitt (Bryozoa: Cyclostomida) from the Mediterranean region. *Journal of Natural History,* 29(4): 1067-1079.

Bassler, R.S. 1953. Part G Bryozoa. *Treatise on Invertebrate Paleontology*. Geological Society of America and The University of Kansas, Lawrence, 253 pp.

Berning B., Tilbrook, K.J., and Ostrovsky, A.N. 2014. What, is anything, is a lyrula? In: Rosso A., Wyse Jackson P.N. and Porter J. (eds.) Proceedings of the 16th International Conference of the International Bryozoology Association. *Studi Trentini di Scienze Naturali,* 94: 21-28.

Boardman, R.S. 1983. General Features of the Class Stenolaemata, pp. 49-137. In: Robison, R.A. (ed.). Part G, Bryozoa Revised, Volume 1. *Treatise on Invertebrate Paleontology*, Geological Society of America and The University of Kansas, Lawrence, 625 pp.

Boardman, R.S. 1998. Reflections on the morphology, anatomy, evolution and classification of the Class Stenolaemata (Bryozoa). *Smithsonian Contributions to Paleobiology,* 86, 59 pp.

Boardman, R.S, and Buttler, C.J. 2005. Zooids and Extrazooidal Skeleton in the Order Trepostomata (Bryozoa). *Journal of Paleontology*, 79 (6): 1088-1104.

Boardman, R.S. and Cheetham, A.H. 1969. Skeletal Growth, Intracolony Variation, and Evolution in Bryozoa; a review. *Journal of Paleontology*, 43: 205-233.

Boardman, R.S. and Cheetham, A.H. 1973. Degrees of Colony Dominance in Stenolaemate and Gymnolaemate Bryozoa, pp. 121-220. In: Boardman, R.S., Cheetham, A.H. and Oliver, Jr., W.A. (eds), *Animal Colonies*. Stroudsburg, Pennsylvania: Dowden, Hutchinson, and Ross.

Boardman, R.S. and Cheetham, A.H. 1983. Glossary of morphological terms, pp. 304-320. In: Robison, R.A. (ed.). Part G, Bryozoa Revised, Volume 1. *Treatise on Invertebrate Paleontology*, Geological Society of America and The University of Kansas, Lawrence, 625 pp.

Bock, P.E. 1982. Bryozoans (Phylum Bryozoa), pp. 319-394. In: Shepherd, S.A. and Thomas, I.M. (eds) *Marine Invertebrates of Southern Australia* Part I. Adelaide, Woolman.

Bock, P.E. 2015. Glossary for the Bryozoa on *bryozoa.net*.

Bock, P.E. and Cook, P.L. 2004. A review of Australian Conescharellinidae (Bryozoa: Cheilostomata). *Memoirs of Museum Victoria,* 61(2): 135-182.

Bock, P.E. and Gordon, D.P. 2013. Phylum Bryozoan Ehrenberg, 1931. In: Zhang, Z.Q. (ed.) Animal Biodiversity: an outline of higher level classification and survey of taxonomic richness (Addenda 2013). *Zootaxa,* 3703: 1-82.

Borg, F. 1926. Studies on Recent cyclostomatous Bryozoa. *Zoologicska Bidrag Från Uppsala*, Band 10, Almqvist and Wiksells, Uppsala, 507 pp.

Borg, F. 1933. On a supposed species of *Heteropora* (Bryozoa). *Journal of Natural History*, 12(72): 583-587.

Borg, F. 1941. On the Structure and Relationships of *Crisina* (Bryozoan, Stenolaemata). *Arkiv fur Zoologi*, 33A (11): 1-44.

Borg, F. 1944. The Stenolaematous Bryozoa. In: Bock, S. (ed) *Further Zoological Results of the Swedish Antarctic Expedition 1901-1903*. Norstedt and Söner, Stockholm, 271 pp.

Brood, K. 1976. Wall structure and evolution in cyclostomate Bryozoa. *Lethaia*, 9: 377-389.

Busk, G. 1859. *A monograph of the fossil Polyzoa of the Crag*. Palaeontographical Society, London, volume XIV, 136 pp.

Busk, G. 1861. Description of new Polyzoa collected by J Y Johnson Esq at Madeira in the years 1859 & 1860. *Quarterly Journal of Microscopical Science*, N.S., 1, 1861, 77-80.

Busk, G. 1875. *Catalogue of the Marine Polyzoa in the collection of the British Museum. Part III Cyclostomata*. Trustees of the British Museum (Natural History), London. 41 pp.

Busk, G. 1886. Report on the Polyzoa collected by the HMS *Challenger* during the years 1873-1876. The Voyage of the HMS *Challenger*, Part L, Zoology, Volume XVII, part II – The Cyclostomata, Ctenostomata, and Pedicellinea. Her Majesty's Stationery Office, London, 47 pp.

Canu, F. and Bassler, R.S. 1920. North American Early Tertiary Bryozoa. *United States National Museum Bulletin* 106, 879 pp.

Canu, F. and Bassler, R.S. 1929. Bryozoa of the Philippine region. *United States National Museum Bulletin* 100, 1-685.

Di Martino, E. and Taylor, P.D. 2014. Miocene Bryozoa from East Kalimantan, Indonesia. Part I: Cyclostomata and 'Anascan' Cheilostomata. *Scripta Geologica,* 146: 17-126.

Gordon, D.P. and Taylor, P.D. 2001. New Zealand Recent Densiporidae and Lichenoporidae (Bryozoa: Cyclostomata). *Species Diversity,* 6: 243-290.

Gordon, D.P. and Taylor, P.D. 2015. Bryozoa of the Early Eocene Tumaio Limestone, Chatham Island, New Zealand. *Journal of Systematic Palaeontology,* 13 (12): 983-1070.

Gregory, J.W. 1895. On the British Palaeogene Bryozoa. *Transactions of the Zoological Society of London*, 13: 219-280.

Gregory, J.W. 1896. *Catalogue of the fossil Bryozoa in the British Museum (Natural History): The Jurassic Bryozoa.* London, Trustees of the British Museum, 239 pp.

Gregory, J.W. 1899. *Catalogue of the fossil Bryozoa in the Department of Geology British Museum (Natural History).* Volume 1. The Cretaceous Bryozoa. London, Trustees of the British Museum (Natural History), London, 457 pp.

Harmer, S.F. 1896. On the Development of *Lichenopora verrucaria* Fabr. *Quarterly Journal of Microscopical Science,* 39: 71-144.

Harmer, S.F. 1915. Polyzoa of the Siboga Expedition. Part 1. Entoprocta, Ctenostomata and Cyclostomata. *Siboga Expedition Reports*, 28a: 1-180.

Hayes, D.P. 1992. The Growing Inaccessibility of Science. *Nature,* 356: 739-740.

Hayward, P.J. and Ryland, J.S. 1985. *Cyclostome Bryozoans.* Synopses of the British Fauna (New Series) No. 34, Linnean Society of London, Brill and Bachuys, London, 147 pp.

Hincks, T. 1880. *A history of the British marine Polyzoa.* London, John Van Voorst, Two volumes, 601 pp.

Hinds, R.W. 1975. Growth Mode and Homeomorphism in Cyclostome Bryozoa. *Journal of Paleontology*, 49(5): 875-910.

Hutton, F.W. 1873. *Catalogue of the marine Mollusca of New Zealand with diagnoses of the species.* Colonial Museum and Geological Survey Department, Wellington, Government Printer, Wellington, New Zealand, 116 pp.

Jullien, J. 1886. Les Costulidées, nouvelle famille de Bryozaires. *Bulletin de la Société zoologique de France,* 11: 601-620.

Kirkpatrick, R. 1888. Polyzoa of Mauritius. *Annals and Magazine of Natural History,* 6(1): 72-85.

Lamouroux, J.V.F. 1821. *Exposition méthodique des genres de l'ordre des polypiers, avec leur description et celles des principales espèces figurées dans 84 planches; les 63 premiers appartenant a l'histoire naturelle des zoophytes d'Ellis et Solander.* Volume 5. Agasse, Paris, pp. 115.

Levinson, G.M.R. 1902. Studies on Bryozoa. *Videnskabelige Meddelelser fra den naturhistoriske Foreningi København*, 54: 1-31.

Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis, Tomus I. Editio Decima, reformata. Homiae, Laurentii Salvii. From Caroli Linnaei, Systema Naturae.* Photographic Facsimile of the First Volume of the Tenth Edition (1939). British Museum (Natural History), London, 824 pp.

MacGillivray, P.H. 1895. A monograph of the Tertiary Polyzoa of Victoria. *Transactions of the Royal Society of Victoria,* IV. Melbourne, Ford and Son, 166 pp.

McKinney, F.K. and Jackson J.B.C. 1989. *Bryozoan evolution.* Allen and Unwin, London, 238 pp.

McKinney, F.K., Taylor, P.D. and Zullo, V.A. 1993. Lyre-shaped Hornerid Bryozoan Colonies: Homeomorphy in Colony Form between Paleozoic Fenestrata and Cenozoic Cyclostomata. *Journal of Paleontology*, 67(3): 343-354.

Mongereau, N. 1972. Le genre *Hornera* Lamouroux, 1821, en Europe (Bryozoa - Cyclostomata). *Annalen des naturhistorischen Museums in Wien* 76: 311-373.

Nielsen, C. 1970. On Metamorphosis and Ancestrula Formation in Cyclostomatous Bryozoans. *Ophelia*, 7: 217-256.

Nielsen, C. and Pedersen, K.G. 1979. Cystid Structure and Protrusion of the Polypide in *Crisia* (Bryozoa, Cyclostomata). *Acta Zoologica,* 60(2): 65-88.

Osburn, R C. 1953. Bryozoa of the Pacific Coast of America, Part 3, Cyclostomata, Ctenostomata, Entoprocta, and Addenda. *Allan Hancock Pacific Expeditions,* 14(3): 613-841.

Pachut, J.F., Cuffey, R.J. and Anstey, R.L. 1991. The concepts of astogeny and ontogeny in stenolaemate bryozoans, and their illustration in colonies of *Tabulipora carbonaria* from the Lower Permian of Kansas. *Journal of Paleontology*, 65: 213-233.

Pergens, E. 1889. Untersuchungen an Seebryozoen. *Zoologischer Anzeiger*, 12: 504-510, 526-533.

Philipps, E.G. 1899. Report on the Polyzoa collected by Dr Willey from the Loyalty Isles, New Guinea and New Britain. *Wiley's Zoological Results*, Part IV, Cambridge University Press, pp. 439-450.

Pitt, L.J. and Taylor, P.D. 1990. Cretaceous Bryozoa from the Faringdon Sponge Gravel (Aptian) of Oxfordshire. *Bulletin of the British Museum (Natural History) Geology,* 4: 61-152.

Ross, J.R.P. 1977. Microarchitecture of body wall of extant cyclostome ectoprocts. *American Zoologist,* 17: 83-105.

Ryland, J.S. and Hayward, P.J. 1991. Marine Flora and Fauna of the Northeastern United States: Erect Bryozoa. *NOAA Technical Report NMFS 99*, US Department of Commerce, 47 pp.

Schäfer, P. 1991. Brutkammern der Stenolaemata (Bryozoa): Konstruktionsmorphologie und phylogenetische bedeutung. *Courier Forschungsinstitut Senckenberg,* 136: 1-147.

Smith, A.M. 2008. Corrections to the global distribution of *Hornera pectinata* (Bryozoa: Horneridae). In: Hageman, S.J., Key, M.M. Jr., and Winston, J.E. (eds), *Bryozoan Studies 2007*, Proceedings of the 14th IBA Conference, Boone, North Carolina, July 1-8, 2007. *Virginia Museum of Natural History Special Publication*, 15: 295-300.

Smith, A.M., Taylor, P.D., and Spencer, H.G. 2008. Resolution of taxonomic issues in the Horneridae (Bryozoa: Cyclostomata), pp. 359-412. In: Wyse Jackson, P.N. and Spencer Jones, M.E. (eds), *Annals of Bryozoology 2, aspects of the history of research on bryozoans. Dublin, Ireland.*

Smith, A.M., Taylor, P.D., and Milne, R. 2012. *Hornera striata* (Milne Edwards, 1838) a British Pliocene cyclostome bryozoan incorrectly recorded from New Zealand with notes on some non-fenestrate *Hornera* from the Coralline Crag. Ernst, A., Schafer, P. and Scholz, J. (eds). *Bryozoan Studies 2010. Lecture Notes in Earth Systems Sciences*, 143, 339-356.

Smitt, F.A. 1867. Kritisk Förteckning öfver Skandinaviens Hafs-Bryozoer. II. *Öfversigt* *af Kongliga Vetenskaps-Akademiens Förhandlingar*, 23: 395-534.

Smitt, F.A. 1872. Floridan Bryozoa collected by Count L. F. de Pourtalès. Part I. Köngl. *Svenska Vetenskaps-Akademiens Handlingar Bandet* 10, No. 11. Stockholm, Norstedt and Söner, pp. 1-20.

Tavener-Smith, R. 1969. Skeletal structure and growth in the Fenestrellidae (Bryozoa). *Paleontology,* 12(2): 281-309.

Tavener-Smith, R. and Williams, A. 1972. The secretion and structure of the skeleton of living and fossil Bryozoa. *Philosophical Transactions of the Royal Society of London,* Ser. B., 264(859): 97-159.

Taylor, P.D. 2001. Preliminary Systematics and Diversity Patterns of Cyclostome Bryozoans from the Neogene of the Central American Isthmus. Morphology and Evolution of the Late Cenozoic Marine Biota of Tropical America. *Journal of Paleontology*, 75(3): 578-589.

Taylor, P.D. and Gordon, D.P. 2003. Endemic new cyclostome bryozoans from Spirits Bay, a New Zealand marine-biodiversity "hotspot." *New Zealand Journal of Marine and Freshwater Research,* 37: 653-669.

Taylor, P.D. and Jones, C.G. 1993. Skeletal ultrastructure in the cyclostome bryozoan *Hornera*. *Acta Zoologica* (Stockholm), 74(2): 135-143.

Taylor, P. D., Lombardi, C. and Cocito, S. 2014. Biomineralization in bryozoans: present, past and future. *Biological Reviews*, DOI 10.1111/brv.12148.

Taylor, P.D. and Weedon, M.J. 2000. Skeletal ultrastructure and phylogeny of cyclostome bryozoans. *Zoological Journal of the Linnean Society,* 128: 337-399.

Ulrich, E.O. 1890. Palaeozoic Bryozoa of Illinois. *Report of the Geological Survey of Illinois*, 8: 285-688.

Waters, A.W. 1887. On Tertiary Cyclostomatous Bryozoa from New Zealand. *Quaternary Journal of the Geological Society*, 43: 337-350.

Waters, A.W. 1888. On some ovicells of Cyclostomatous Bryozoa. *Linnean Society Journal – Zoology,* 20: 275-281.

Waters, A.W. 1904. Zoologie: Bryozoa. *Expedition Antarctique Belge, Resultats du Voyage du S Y Belgica en 1897-1898-1899, Rapports Scientifiques*. Buschmann, Anvers, 114 pp.

Weedon, M.J. and Taylor, P.D. 1995. Calcitic nacreous ultrastructures in bryozoans: implications for comparative biomineralization of lophophorates and molluscs. *Biological Bulletin,* 188: 281-292.

Weedon, M.J. and Taylor, P.D. 1996. Skeletal ultrastructures in some cerioporine cyclostome bryozoans. *Acta Zoologica,* 77: 249-265.

Whitten, R.F. 1979. *Systematics and ecology of northern Hauraki Gulf Bryozoa*. Unpublished PhD thesis (Geology), University of Auckland, New Zealand, 515 pp.

Winston, J. E. 1999. *Describing Species: Practical Taxonomic Procedure for Biologists*. Columbia University Press, New York, 518 pp.

Roger N. Hughes' contribution to Bryozoology

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1. Introduction

"From an early age Roger Hughes (Figure 1) was interested in ponds, streams and woods" wrote his friend Steve Ward in an obituary for *The Guardian*, published on 4 October 2015. Rephrasing such words we can say "From early age Roger, the scientist, was devoted to molluscs, crustaceans, and fish". Clonal organisms, mainly bryozoans, were a later, but a fertile topic. In the present work we aim to review his contribution to bryozoology using as a tool the citation index of ISI Web of Science (WOS from here onwards) and Google Scholar (GS). Although Citation Indexes as tools are too coarse to assess the relevance of a scientific contribution, we have to agree that such approach gives us at least an approximation of the impact a publication produces in the scientific community. A cited paper has been read, thought through, and made relevant to the reader's own research and scientific findings. In that sense Roger Hughes was relevant and profusely quoted, with more than 4600 and 9300 citations in WOS and GS, respectively (as recorded until 6 January 2016).

Figure 1. (a and b) Roger Hughes at Llyn Idwall with María Cristina Orellana, February 2012 (Photograph by J.M. Cancino).

2. Roger's path through science

Roger N. Hughes (1944–2015) studied Zoology at the University College of North Wales, now Bangor University, and obtained a PhD in Marine Ecology in 1968, under Dennis Crisp's Supervision. In 1969, he was awarded a Killam Post-Doctoral Fellowship at Dalhousie University to study benthic ecology and feeding behaviour of marine gastropods. In 1971 he returned to work at the University in Bangor, at which he remained until his retirement in 2011. However as a Professor Emeritus he stayed on at Bangor University, until his final illness, acting as an editor for prestigious journals dealing with marine biology and marine ecology.

Roger became well established as an invertebrate zoologist during the 1970s with his work on gastropod ecology, leading later to his book *A functional biology of marine gastropods* (Hughes 1986; GS 184 citations). While we here deal with his contribution to bryozoology, it should be realized that, throughout his career, he continued to study the ecology and eco-physiology not only of molluscs (both bivalves and gastropods), but also crustaceans and fish. Among the gastropod taxa he studied were vermetids: sessile, filter-feeding prosobranchs with partially uncoiled shells that form dense aggregations on certain warm water shores (Hughes 1979; GS 32 citations). Such aggregations, the result of larval settlement patterns, are of course not colonies but led Roger to discuss them at the influential Durham symposium on *Biology and systematics of colonial organisms* (Larwood and Rosen 1979).

Roger Hughes wrote 3 books and 207 papers. Over 77% of these publications were written with one or more co-authors, from which is clear that one of Roger's talents was his willingness to work in partnership, giving support, and being open to new ideas. In total he supervised 36 Ph.D. and 27 M.Sc. students and at least 6 postdoctoral fellows.

In his GS site (https://scholar.google.cl/citations?user=hlLlDAMAAAAJ&hl=es), by January 2016 he included 209 publications, with 9300 citations. Since at the time of death part of his work was in press, by 1 October 2016 the number of entries in GS had increased to 230, and the citations to 9,835.

Table 1. Roger Hughes. Number of publications classified by taxa and subjects. (Source of data Google Scholar, 6 January 2016)

	Mollusca	Crustacea	Fish	Clonal organisms and Bryozoa	Other Taxa General topics	Total
Optimal Foraging and Ecological energetics	28	21	18	0	17	**84**
Autecology and distribution patterns	24	8	7	6	11	**56**
Life history and reproductive biology	10	1	0	24	4	**39**
Taxonomy and morphology	3	0	0	3	2	**8**
Genetic bar-coding and genotype-environment interactions	6	0	1	13	0	**20**
Total	**71**	**30**	**26**	**46**	**34**	**207**

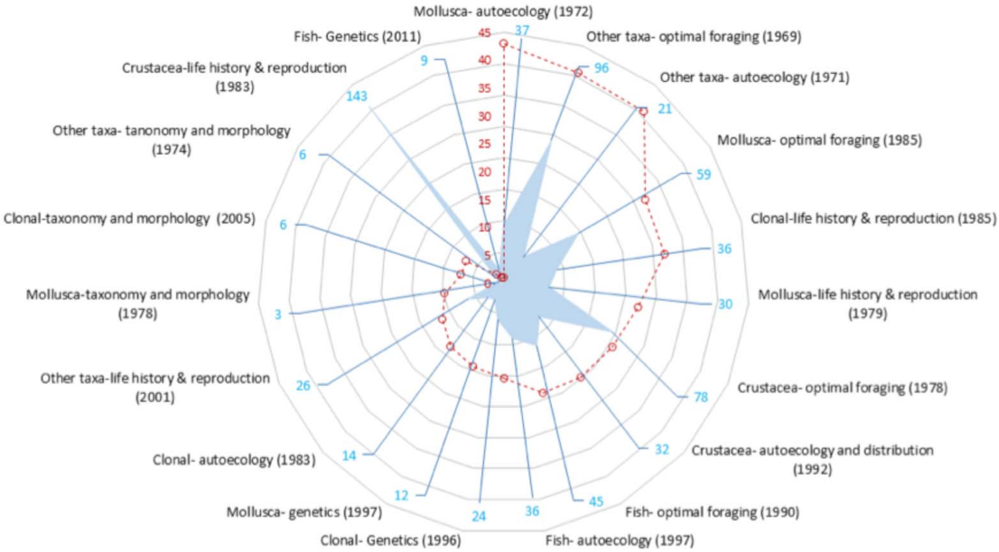

Figure 2. Research topics of R.N. Hughes, with year of first paper published (in brackets). Number of years the topics were pursued are indicated by open circles and dotted line, in a scale from zero at the centre and 45 years in the outer circle. Note that duration decreases clockwise, from year 43 to year 1. Average GS citations of the papers by topic, as classified in Table 1, are indicated by the stared filled area and the numbers at the outer circle.

Using the data base available in January 2016, his publications can be classified as shown in Table 1. Regarding taxa, molluscs and clonal organisms (bryozoans included) were the two principal groups of interest, followed by crustaceans, general topics (multi-taxa, models and books) and fish (Table 1).

The main subjects of interest included optimal foraging and ecological energetics; followed by distribution patterns and autecology; reproductive biology and life history; genetic-barcoding-genotype – environment interactions; and lastly taxonomy and morphology (Table 1).

Molluscan autecology and distribution patterns were pursued by Roger for 43 years (first paper published in 1972, last in 2015), with 17 papers published (Table 1, and an average of 37.1 citations (Figure 2). His first scientific publication (Hughes, 1969; cited 202, and 141 times, according to, GA, and WOS, respectively) deals with the feeding behaviour of *Scrobicularia plana*, an intertidal mud-flat bivalve mollusc. Energetics and distribution patterns, mostly in molluscs, were the subjects of his first 9 years of research, in Wales, Barbados, Canada and Aldabra in the Indian Ocean. With Bob Elner as a first author, Roger published his most cited paper (Elner and Hughes 1978; cited 372 times (WOS) and 482 (GA)), dealing with energetics in the crab *Carcinus maenas*. From there onwards, crustaceans became one of his main topics, without leaving the molluscs, his first group of interest. Later topics included clonal organisms and fish.

Total WOS citations per year increased through time, reaching a maximum of 212 in 2008 (Figure 3). Note that at the time data were obtained, WOS did not include any information of publications before 1977, molluscs therefore, are not seen here as the first group of interest.

Most citations refer to foraging behaviour and energetics (Figure. 3). Reproductive biology, distribution patterns and taxonomy (not shown in Figure 3) were themes that Roger kept active all through his scientific life. From the early 1990s DNA fingerprinting and barcoding was included as a tool of his work, becoming by 2012 the second most cited subject among his publications (Figure 3).

3. From clonal organisms to Bryozoa

Early in his scientific life Roger worked with corals and, as mentioned before, larval settlement patterns of vermetids, the latter leading him to the Durham Symposium on Biology and Systematics of Colonial Organisms (Hughes 1979). By that time he was showing an increasing interest in clonal organisms. In Bangor he was an active member of a multidisciplinary discussion group on this subject, which included botanists and zoologists: John L. Harper, colleagues and students from Plant Biology, plus colleagues and students from Zoology and Applied Zoology, the former Departments of today’s School of Biological Sciences.

His interest in genuinely clonal organisms led to his contribution on reef associated organisms to a Darwin anniversary symposium in 1982 (Hughes, 1983), which concentrated mainly on corals. That neo-Darwinian evolutionary theory, based essentially on the life

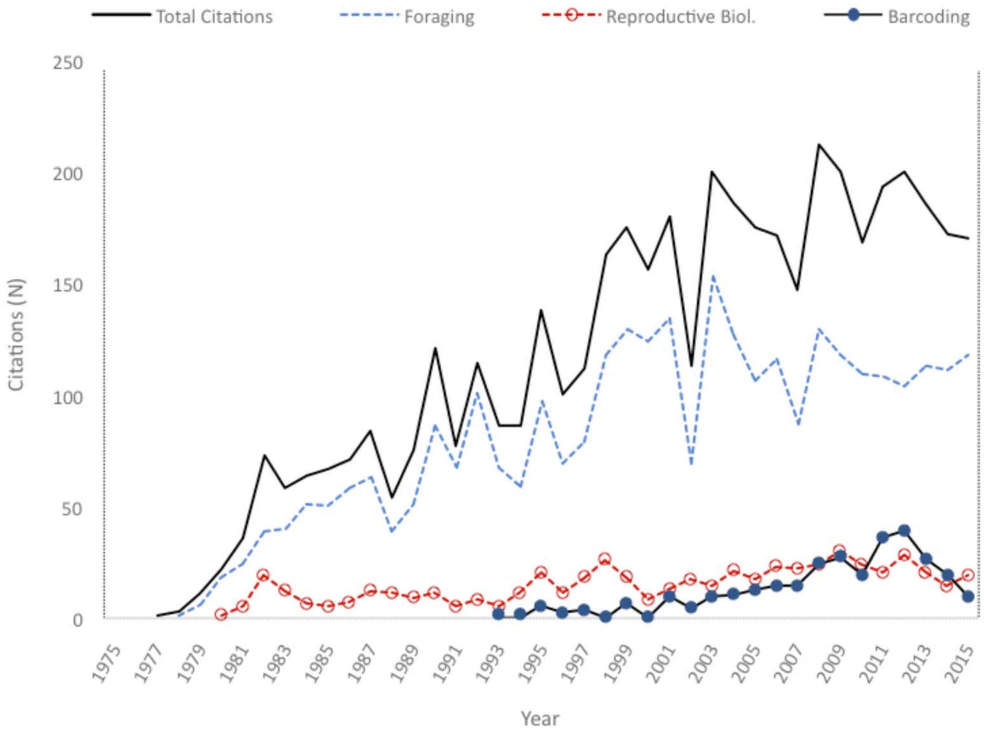

Figure 3. Roger N. Hughes. Total citation per year classified by research topic (source of data WOS, 6 January 2016). Note that database does not include any information of publications before 1977.

histories of unitary (or non-colonial) organisms, had largely ignored clonal (and colonial) organisms, was becoming widely appreciated at around this time (e.g. Harper 1977, Bell 1982). Also in February 1982, at a symposium on clonal organisms, held at Yale University, Roger gave a paper reviewing cloning in the Metazoa, though the resulting volume containing expanded versions of the contributions was published much later (Hughes and Cancino 1985, with more than 100 citations in GS). Undoubtedly, the participants and presentations at these symposia stimulated Roger's interest in Bryozoa and other genuinely colonial invertebrates. His book, the wide-ranging *A functional biology of clonal animals,* followed in 1989, (with over 300 citations, and his fifth most cited contribution in GS). To read the acknowledgements in this book is very instructive, giving an idea of the variety of scientists and specialists that Roger kept in contact with to produce such a far reaching book covering all clonal animals.

4. Bryozoa

In 1979, Juan M. Cancino arrived from Chile, with the idea of working on Optimal

Foraging, but Roger advised him to think of a totally different subject, clonal organisms, and gave him the freedom to choose the taxa and the subject for his Ph.D. thesis. Roger took him to the outflow stream from Llyn Idwal in Snowdonia, as he did with John Ryland in 1984, and with many visitors (Figure 1) to see over-wintering gemmules of the freshwater sponge *Spongilla lacustris*, which, like the sessoblasts of *Fredericella sultana*, and the hibernacula of the diffuse colonies of the freshwater ctenostome *Paludicella articulata,* also present in that lake, are asexually produced, non-dispersive propagules. These organisms were considered as study subjects for Cancino's thesis, as well as marine Bryozoa, common organisms in the Menai Strait and on Anglesey shores easily accessible from Bangor. Information on their occurrence and some aspects of their ecology was readily available from John Ryland's studies at Menai Bridge in the late 1950s. After reading Ryland's papers (1959, 1962)**,** *Celleporella hyalina* (L.) was the species selected (Cancino, 1983, 1986). At that time Gary Carvalho was working, with Roger's supervision, on another cloning organism the crustacean, *Daphnia magna* (Carvalho and Hughes, 1983, 143 GS citations).

The decision to study *Celleporella hyalina* was inspired, as important advantages of the species for experimental work soon became apparent. The non-feeding larvae are easily released and settled rapidly in the laboratory, and colonies were found to grow and reproduce well in small culture vessels, both in the field and in the laboratory (Cancino 1983). Initial topics were naturally in the realm of eco-physiology (e.g. Hughes and Hughes 1986) and life-histories (Cancino 1983, Cancino and Hughes 1987, 1988), as had characterized his work on gastropods. Studies with Juan Cancino (Cancino and Hughes 1987, 1988, Cancino *et al*. 1991, 1994) and David Hughes (Hughes and Hughes 1986a, D.J. Hughes 1987, 1992) provided valuable understanding of the species and its requirements and initiated consideration of the effects of genotype on environmental responses.

Although bryozoans had been maintained in the laboratory before, especially by Jebram (e.g., 1975), the development of reliable mass culture methods for suitable phytoflagellate food was a landmark achievement that paved the way for ground-breaking studies on the growth and reproduction of *Celleporella hyalina*. Using protocols developed with Ewan Hunter (Hunter and Hughes 1993a, b) and perfected with Patricio Manríquez (1999) well-grown colonies could then be reared and physically divided to produce a set of independent clonal (sub-) colonies. This allowed variation between genotypes to be assessed experimentally, with each genotype represented in each experimental treatment. Colonies in laboratory culture could be kept in reproductive isolation from other genotypes until contact was deliberately instigated by moving genotypes into the same container, giving the opportunity for mating (Figure 4). The presence, unusual in a bryozoan, of three morphologically distinct zooids – feeding, female and male – in *C. hyalina* enabled the assessment of *in vivo* reproductive investment and relative allocation to the two genders from simple counts of the three zooid morphs. Brooded embryos were visible and easy to count (Cancino and Hughes 1987, 1988). *C. hyalina* also proved amenable to molecular approaches, starting with the development of a suite of microsatellite markers with Kathryn Hoare in the late 1990s (Hoare *et al*. 1998).

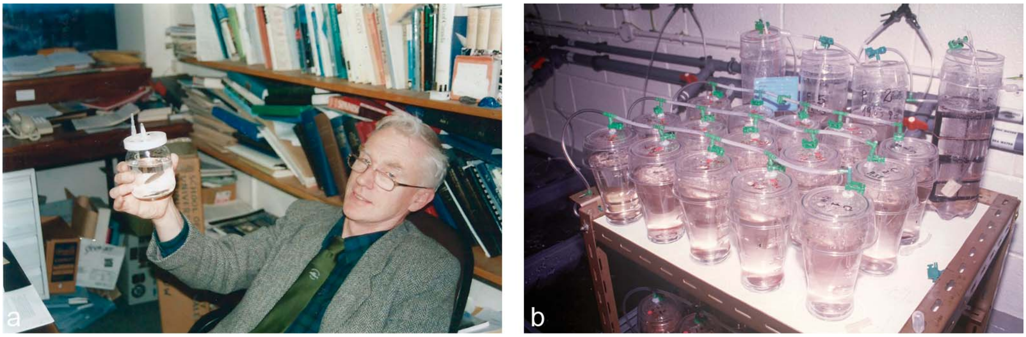

Figure 4. (a) Roger handling an experimental jar for growing isolated colonies of Celleporella hyalina*; (b) experimental setting as designed by P.H. Manríquez (Photographs by P.H. Manríquez and J.M. Cancino respectively 1998).*

Exploiting these advantages, Roger and his co-workers used *C. hyalina* to explore several basic questions in bryozoan biology concerning life-history strategy and the factors influencing reproductive investment, as well as characterizing the mating system and the physical means of mating in this sessile hermaphrodite. Studies based on cultured stocks originating from wild populations in North Wales, augmented by molecular paternity analysis where appropriate, established that reproductively isolated colonies brooded at a much-reduced rate, if at all, and selfing resulted in marked inbreeding depression (Hunter and Hughes 1993b; Hoare *et al*. 1998). The production of female zooids was low in reproductive isolation but was increased by even brief exposure to allosperm, particularly from an unrelated clone (Bishop *et al*. 2000, Hughes *et al*. 2002) – an example of restrained investment in female function in the absence of an opportunity to outcross. Hughes *et al*. (2002) also documented the uptake and storage of sperm by very small, immature colonies and the transfer of sperm from feeding zooids to female zooids budded after the period of allosperm availability; the mechanism of this transfer remains to be elucidated. Sperm released into in the water were shown to be relatively long-lived despite their dilution (Manríquez *et al*. 2001), and recipient colonies could take up and use sperm from relatively very dilute suspension (Pemberton *et al*. 2003). These results suggested that limitation of zygotic output by insufficient sperm availability ('sperm limitation') was unlikely in natural settings, but rather that sperm competition (with the added potential for female choice to influence paternity), was likely to predominate during the remote mating process. This mechanism was likely to be shared by many bryozoans and several other sessile aquatic groups which release sperm but retain eggs for fertilization and generally brood the resulting embryos. Broadly similar conclusions from a different evidence base were reached by Hughes *et al*. (2009) from a study of self-compatible genets of *C. hyalina s.l.* from other parts of the geographical range (see below).

Molecular analysis was also used to investigate the population-genetic consequences of the species' mating system and of developmental mode in natural populations, in comparison with the cyphonautes-producing species *Electra pilosa* (Goldson *et al*. 2001;

see also Seed and Hughes 1992 for comparisons including these two species). In parallel, molecular analysis of samples from widely geographically spaced locations was also applied to document cryptic speciation in *C. hyalina* and its relatives, and to detect multiple distinct lineages within *C. hyalina* in the NE Atlantic (Hoare *et al*. 2001, Gomez *et al*. 2007a, b, Hughes *et al*. 2008, Waeschenbach *et al*. 2012). This molecular phylogeography was paralleled by laboratory-based testing of reproduction by the sampled genotypes in reproductive isolation and when paired with colonies from the same and from different localities, to assess between-population reproductive compatibility. In addition to elucidating species boundaries, this work resulted in the discovery of lineages that routinely selfed, in contrast to the original cultures obtained from natural populations in North Wales and Devon. This provided the opportunity to compare routinely selfing and non-selfing lineages in laboratory culture, to test theoretical predictions concerning the relative strength of inbreeding depression, and the allocation to female function in the absence of a source of allosperm (i.e. in reproductive isolation) (Hughes *et al*. 2009); this work involved molecular paternity analysis. The basic approach of manipulative experiments on cultured and cloned colonies of *Celleporella hyalina,* discussed above, was also used to demonstrate the influence of relatedness on fusion of colonies (Hughes *et al*. 2004a), and to demonstrate an effect of temperature, but not food supply, on zooid size (Hunter and Hughes 1994), this effect being confirmed while investigating the influence of temperature and oxygen supply on the number and size of structures from cellular to colony level (Atkinson *et al*. 2006).

Another important topic investigated was the role of light in initiating the release of *Celleporella* larvae and their subsequent behaviour (Cancino *et al*. 1991, 1993, 1994, see Figure 5). Most bryozoans release their larvae as a direct response to increasing irradiance levels in early morning, the effect declining during the day. Roger and co-authors carefully controlled and quantified results also showed how the response was affected by the tidal cycle: high tide, especially in turbid waters, substantially reducing the amount of light

Figure 5. (a) with the larval collecting machine and collaborators in Chile, January 1990 (clockwise, Roger, P.H. Manríquez, M.H. Muñoz, and J.M. Cancino); (b) collecting fronds of Laminaria saccharina *with* Celleporella hyalina, *to study larval liberation pattern, with Claudio Ramírez in Wales August 1990 (Photographs by J.M. Cancino).*

reaching the attached algae on which the bryozoans live. They also related the patterns of release to the behaviour of larvae during their free-swimming period, comparing these in the species pair *Alcyonidium hirsutum* and *A. gelatinosum*, which cohabit *Fucus serratus* in the Menai Strait. In the former, light is the trigger for larval release, and the larvae initially display positive phototaxis; in the latter, larval release is largely at night and the larvae do not respond to directional illumination. The question on how long the non-feeding lecithotrophic larva are able to swim for, without losing the ability to settle and metamorphose was also addressed, and for the first time in bryozoan consequences of larval behaviour on the future performance of the colonies they generate were demonstrated (Orellana and Cancino 1991, Orellana *et al*. 1996, Hunter and Fusetani 1996, Cancino and Gallardo 2004).

A different strand of Roger's work on bryozoans investigated the occurrence of polyembryony (the production of multiple clonal progeny from a single sexually-produced zygote) throughout the bryozoan order Cyclostomata. This reproductive mode is widespread thoughout the living world but relatively uncommon, and is regarded as an evolutionary puzzle, involving paying the cost of sexual reproduction while apparently forsaking the perceived benefits, and thus has broad interest as potentially offering insight into a major evolutionary enigma, the persistence of sex. The occurrence of prolific polyembryony throughout an entire order (or almost so) of Metazoa is unique to the Bryozoa and requires explanation, but this topic had received relatively little attention for some decades and was ripe for the exploitation of new technologies. Roger's work with various collaborators confirmed the basic occurrence of polyembryony in cyclostomes by molecular means (Hughes *et al*. 2004b). The distribution of genetic diversity in natural populations was investigated in one species (Pemberton *et al*. 2007), and the results suggested that one of the published hypotheses for the adaptive value of polyembryony in the group could be discounted. Helen Jenkins' recent Ph.D. study, a collaboration between the University of Bangor, The Natural History Museum in London, and the Marine Biological Association of the UK, brought two species of cyclostome into culture for experiments with cloned colonies, and developed molecular markers for paternity analysis and the recognition of clonal genotypes. The data published so far (Jenkins *et al*. 2015) extend the evidence of restrained female investment in reproductive isolation, shown previously for routinely outcrossing *Celleporella hyalina*, to the two species of cyclostome (one outcrossing, but the other self-fertilizing to an appreciable degree in reproductive isolation). As with the cheilostome *C. hyalina*, production of female zooids in the cyclostomes is promoted by exposure to allosperm, but differences of detail between the bryozoan species studied so far suggest that the mechanism by which this effect operates might have a complex evolutionary history within the phylum.

Roger provided elegant reviews of the biology of modular animal colonies in Hughes, (2005, GS 35 citations), and in the final chapter of the 1989 book on clonality in animals (Hughes 1989). Here, as previously in Hughes and Cancino (1985), he repeatedly emphasized the parallels, as sessile modular entities, between these colonies and land plants. Consequences of colonial encrusting body form on metabolic rate was also explored as a general topic of interest (Hughes and Hughes 1986b). However, dealing with clonal organisms the most ambitious endeavor he achieved was his 1989 book, nicely reviewed by Richard K. Grosberg (1989) and in which Roger set to explain "how clonal reproduction arises, whether it is responsive to natural selection, why many clones also reproduce sexually, and whether clonal reproduction has new implications for life history theory" (Hughes 1987).

In total 53 of Roger's publications dealt with clonal organisms (listed in chronological order below), 42 of them with bryozoans, which led Roger, in his most recent CV to describe his current research as: "*Gametic recognition and mate choice in marine colonial invertebrates. Use of clonal animals to partition genetic and environmental control of resource allocation in the investigation of life-history evolution. Molecular phylogenetics and phylogeography of hippothoid bryozoans*".

5. Roger N. Hughes' service to science and to the scientific community around the world.

Roger obtained all his degrees from the University of Wales (B.Sc. Hons Zoology class I in 1965; Ph.D. Marine Ecology 1968; D.Sc. 1982) and all his academic life was linked to the same University, starting as a Lecturer in Zoology in 1971; Senior Lecturer 1984, Reader 1984, Personal Chair 1988, The Lloyd Roberts Chair of Zoology 2000, to his final nomination as a Professor Emeritus in 2012. However from early in his scientific life he had the world on mind. In April–July 1968 he was a Member of the Royal Society Expedition to Aldabra Atoll, in the Indian Ocean. The following year he was awarded a Killam Post-Doctoral Fellowship that allowed him to move to Dalhousie University, Halifax, Nova Scotia, Canada, for two years 1969–1970.

Financed by the Royal Society Travel Grants for Marine Biological Research he visited: Jeddah**,** Saudi Arabia 1973; Cape Town 1975; Barbados 1980; Panama 1982; Hong Kong 1983; Trinidad 1984; Cape Town 1985; Panama 1988; Japan 1990; Perth Australia 1991; Italy 1992; USA 1993; Chile, 1995 and 2004.

He was a Visiting Lecturer at University of Cape Town July-December 1975, and July-December 1985; visiting Scientist under British Council Links Scheme at Universidad Católica de Chile, Santiago November-December 1986, and January 1989. Universidad Católica de la Santísima Concepción, Concepción in 1993, and 1995, and financed by CONICYT in April–July 2014 (his very last international trip).

As a good international ambassador he received at Bangor many visiting fellows, in his last CV, he mentions: Dr A.J. Underwood 1982 (Biology, University of Sydney); Dr C.L. Griffiths 1986-87 (Zoology, University of Cape Town); Dr R.L. Vadas 1989 (Botany and Plant Pathology, University of Maine, Orono); Dr J.M. Cancino 1990 (Ecologia, Pontificia Universidad Católica de Chile, Santiago); Dr M.D. Subosky 1991 (Psychology, Queen's University, Kingston, Ontario); Professor C.D. McQuaid 1991–1992 (Zoology, Rhodes University, S. Africa); Dr K. Warburton 1992 and 1995 (Zoology, University of Queensland, Brisbane); Dr J. Blay 1994–95 (Zoology, University of Cape Coast, Ghana); Dr J.-G. J.

Godin 1994 (Biology, Mount Allison University, Canada); Professor H.U. Riisgård 1996–7 (Biology, Odense University, Denmark); Dr C. Nielsen, 1997 (Zoology Museum, University of Copenhagen); Dr M.H. Son, 1997–8 (University of South Korea, KRF scholarship); Dr S. Craig, 1998-9 (University of California, NATO / NSF scholarship). It is most likely there were many more not in the list (including bryozoologists such as Dr Andrey N. Ostrovsky, for example, in 2002).

He served science with a prolific editorial output being a member of the Editorial board of the *Journal of Animal Ecology*, 1991–1996; Contributing Editor, *Marine Ecology Progress Series* 1984–2015; Managing Editor, *Journal of Experimental Marine Biology and Ecology* 2005–2015; Managing Editor *Oceanography and Marine Biology: an Annual Review* 2010–2015. Volume 53 of the *Annual Review* was published in 2015 with Roger as the chief Editor for the final time (Hughes *et al*. 2015).

He acted as a Referee for 65 journals: *Advances in Marine Biology, Acta Ecologica, African Journal of Ecology, American Naturalist, Animal Behaviour, Animal Cognition, Aquatic Sciences, Archiv für Hydrobiologie, Asian Marine Biology, Australian Journal of Marine and Freshwater Research, Basic and Applied Ecology, Behaviour, Behavioural Ecology, Behavioural Ecology and Sociobiology, Biodiversity and Conservation, Bollettino Malacologico, Canadian Journal of Zoology, Current Biology, Ecology, Ecology Letters, Ecological Monographs, Ecological Applications, Ecosphere, Estuaries, Ethology, Ecology and Evolution, Evolution, Experientia, Functional Ecology, Hydrobiologia, Human Reproduction, Israel Journal of Zoology, Journal of African Zoology, Journal of Animal Ecology, Journal of Comparative Psychology, Journal of Crustacean Biology, Journal of Estuarine and Coastal Research, Journal of Experimental Marine Biology and Ecology, Journal of Fish Biology, Journal of the Marine Biological Association, U.K., Journal of Molecular Evolution, Journal of Molluscan Studies, Journal of Natural History, Journal of Shellfish Research, Journal of Theoretical Biology, Malacologia, Marine Behaviour and Physiology, Marine Biology, Marine Ecology, Molecular Ecology, Molecular Phylogenetics and Evolution, Nature, Oikos, Philosophical Transactions of the Royal Society, London, Physiological and Biochemical Zoology, Polar Biology, Proceedings of the National Academy of Sciences, USA, Proceedings of the Royal Irish Academy, Proceedings of the Royal Society, London, Revista Chilena de Historia Natural, Scientia Marina, South African Journal of Marine Ecology, South African Journal of Marine Science, South African Journal of Zoology, Trends in Ecology and Evolution* and *Vie et Milieu*.

He also acted as a referee for research councils such as NERC, BBSRC, NSF, Italian Ministry for University and Research, UGC Hong Kong, New Zealand, Israel, South Africa, Netherlands Organisation for Scientific Research (NWO, the Dutch Research Council).

He obtained 18 Grants from the Natural Environmental Research Council, 1 from Leverhulme; and 6 from the European Union, jointly with scientists from the UK and overseas including G. Carvalho, (Swansea, and Bangor); B. Bayne, (Plymouth Marine Laboratory); R. Seed (Menai Bridge); S.J Hawkins; T.A. Norton, and D. Atkinson

(Liverpool), M. Burrows and R. Batty (Dunstaffnage); J.D.D. Bishop, (MBA Plymouth); A.R. Cossins and C.V. Howard (Liverpool), B. Howell (Conwy); S.F. Craig, (Bangor); D.H. Lunt (Hull); J.M. Cancino and H.I. Moyano (Concepción, Chile); G. Chelazzi, (project coordinator, Florence), M. Valero, Lille); K. Johannesson, (project coordinator, Gothenburg). Most likely many others are missing, since among bryozoologists, for example, A. Waeschenbach, from the Natural History Museum, London and J.S. Porter, from Edinburgh, coauthored Roger's papers.

Many of the 36 Ph.D. students he supervised kept in contact with him for life, and as he mentions in his last CV "*many secured posts in biological research, notably at the University of Aberdeen, University of Wales, Bangor, University of York and the Catholic University of Chile, Santiago, Catholic University in Concepción, Chile; and research posts at The Water Research Laboratory, Marlow; the State University of New York at Stony Brook; The Institute of Fisheries and Oceans, Canada; The Smithsonian Tropical Research Institute, Panama; Dunstaffnage Marine Laboratory, Scotland; Ministry of Agriculture, Fisheries and Food, Conwy*". Post-doctoral Fellows included: Isabelle Colson, Peter Wright, Simon Morley, Mike Burrows, Kei Kawai, Kathryn Hoare.

He also acted as an External Examiner for 51 Ph.D. and 7 M.Sc. theses in the UK, Italy, Spain, Australia, South Africa, India, Canada, and the USA.

Several of his former students, colleagues and friends from different Universities assembled in Bangor to honor Roger at his retirement (Figure 6) and left to posterity the special issue of *Marine Ecology Progress Series* entitled "Evolution and ecology of marine biodiversity: mechanisms and dynamics" edited by Michel J. Kaiser, Michael T. Burrows, and Helen Hughes (*MEPS* **430**, 98–288, 2011).

Figure 7. (a) with Juan Carlos Castilla at Bangor University on 14 July 2008 (photograph by Elena Rho); (b) with Helen, beside the Andean mountains, near Santiago, in Roger's second trip to Chile, January 1990 (photograph by J.M. Cancino); (c) with P.H. Manríquez (front), Helen and friends near La Serena, Chile, May 2014 (photograph by P.H. Manríquez).

6. Roger and Chile

The disposition to work with others is clear from above and from the long list of coauthors in Roger's scientific publications. However another and most appreciated feature of Roger (and Helen as well), was the talent for establishing long lasting friendly relations. One example we know well is that of Roger's relationship with people in Chile, which dates back to 1967–1968. In those years, he and Juan Carlos Castilla as Ph.D. students at the University of Wales shared the same supervisor, Professor Dennis J. Crisp. Since then Roger, Juan Carlos and their respective wives Helen and Elena became good friends (Figure 7a). Years later, in 1979 Juan M. Cancino, a former student of Castilla, followed a similar route and as described above, became Roger's Ph.D. student. His friendship with Juan Carlos and Juan paved the way for 6 visits to Chile; the first in 1986 and the last one in 2014 (Figures 7b, c). During his visits to Chile Roger conducted short studies using local bryozoans as biological models and he taught short courses on topics as optimal foraging, reproductive biology (Figure 8a) and biology of clonal organisms from which many Chilean marine and terrestrial biologists benefited across the country.

Figure 6 opposite. Former students, colleagues and friends that attended the Symposium to honor Roger at his retirement, beside the Menai Strait, on 20 March 2010. Three of the authors of the present paper are in the picture (Helen Hughes, Ryland and Bishop). Juan C. Castilla also attended from Chile (second from the right, front line). J.M. Cancino, being the President (Rector) of his university, could not attend due to the 8.8 Chilean earthquake, on 27 February. (Photograph distributed by the organizers of the Symposium, photographer unknown).

Figure 8. (a) in a field trip near Concepción with a class attending a Marine invertebrate reproduction course given by Roger, on the left, and colleagues from Bangor University (Raymond Seed, standing beside Roger, and Chris Richardson, far right) on January 1998, at Universidad Católica de la Santísima Concepción (UCSC). Staff member from the latter on the picture: Ricardo Otaíza, on the back behind R. Seed, and J.M. Cancino, beside C. Richardson, photograph by J.M. Cancino); (b) at Pan de Azúcar, National Park, northern Chile, January 2004 (photograph by J.M. Cancino); (c) in Antofagasta with John Ryland, waiting to see Chilean bryozoans, as part of the Pre-conference Trip, January, 2004 (photograph by Hans Arne Nakrem); (d) bryozoologists attending the IBA Post-conference trip at Punta Arenas Main Square, beside Magellan and the Magellan strait native people sculpture, January 2004 (photograph by Hans Arne Nakrem)

*Figure 9 opposite. (a) a conference on Clonal Organisms to UCSC Science faculty members and students, 14 April 2014 (photograph UCSC); (b) after a conference on penguins to students of 3 English High Schools in Concepción, 18 May 2014 (photograph USCS); (c and d) the last trip to the Andes, (c) with Helen and a millenarian monkey puzzle tree (*Araucaria araucana*); (d) with Helen, M.C. Orellana, and the Lonquimay Volcano on the background (19 April 2014, photographs by J.M. Cancino).*


a
UCSC
b
c
d

In two of those courses a former student of Juan M. Cancino and Juan Carlos Castilla's research assistant, Patricio Manríquez, met Roger. Few years later, in 1996 Patricio with the strong support of Roger started his Ph.D. with him as supervisor, using *C. hyalina* to investigate different aspects of reproductive ecology.

In 2004 Roger and Helen attended the 13th IBA Conference held in Concepción, and as part of the Pre- and Post-Conference field trips had the opportunity to travel from the desert in the far North to the Magellan Strait (Figures 8b-d)

During 2014, Roger and Helen visited Chile for the last time. As usual he managed to visit his Chilean friends; Juan M. Cancino, Maria Cristina Orellana and Antonio Brante in Concepción, Juan Carlos Castilla and Elena in Las Cruces, and Patricio Manríquez in Coquimbo. During this long-term scientific-human connection with Chile Roger always showed the most generous attitude, sacrificing invaluable family time, to cooperate with us. Roger's support included both improving the edition of our manuscripts as well as inspiring, encouraging and stimulating improvements of some un-tackled aspects of our own research. To prove our gratitude his name was commonly present in the acknowledgement section of many of our manuscripts, and for this he will surely stay forever in our minds.

Roger also received at Bangor undergraduate students of UCSC (a new University created in 1991 from a former Campus of the Pontificia Universidad Católica de Chile), including Dr Antonio Brante, (Head of the Ecology Department at UCSC at the time this paper is written). Brante and Hughes, (2001) resulted from trusting in an unknown undergraduate student from a faraway, small University, (recommended by Roger's former student: Juan Cancino, Dean of Science). After retirement Roger accepted Antonio's invitation to visit UCSC for 2 months under a financial scheme of the Chilean CONICYT, supported as well by UCSC (Figures 9a-d). Solas *et al.* (2015) is the result of this last stay at UCSC. Illness struck Roger soon after his return from Chile. This was his 6th and final trip to Chile and perhaps his most clear tribute to friendship across 4 Chilean academic-generations (from Castilla, to Cancino to Manríquez and Brante to Maribel Solas, Antonio's student). The photos included in this publication are here for us to remember him by.

Another version of this same history, written by Juan Carlos Castilla and Roger, while in Chile in 2014, can be read following link (Chilean News at page 23):

https://www.bangor.ac.uk/oceansciences/alumni_newsletters/the_bridge_2014.pdf

7. Roger N. Hughes' publications on Clonal organisms and Bryozoa

1. Hughes, R.N. 1983. Evolutionary ecology of colonial reef organisms, with particular reference to corals. *Biological Journal of the Linnean Society* **20**(1), 39–58.
2. Carvalho, G.R. and Hughes, R.N. 1983. The effect of food availability, female culture density and photoperiod on ephippia production in *Daphnia magna* Straus (Crustacea, Cladocera). *Freshwater Biology* **13**(1), 37–46.
3. Hughes, R.N. and Cancino, J.M. 1985. An ecological overview of cloning in Metazoa.

In Jackson J.B.C., Buss L.W. and Cook R.E. (eds.), *Population Biology and Evolution of Clonal Organisms*, Yale Univ. Press, New Haven, pp. 153–186.

4. Hughes, D.J. and Hughes, R.N. 1986a. Life-history variation in *Celleporella hyalina* (Bryozoa). *Proceedings of the Royal Society of London Series B-biological Sciences* **228**(1251), 127–132.
5. Hughes, D.J. and Hughes, R.N. 1986b. Metabolic implications of modularity: studies on the respiration and growth of *Electra pilosa*. *Philosophical Transactions of the Royal Society of London Series B-biological Sciences* **313**(1159), 23–29.
6. Hughes, R. N. 1987: *The functional ecology of clonal animals*. Functional Ecology 1(1), 63–69.
7. Cancino, J.M. and Hughes, R.N. 1987. The effect of water flow on growth and reproduction of *Celleporella hyalina* (L.) (Bryozoa, Cheilostomata). *Journal of Experimental Marine Biology and Ecology* **112**(2), 109–130.
8. Hughes, R.N. 1987a. The functional ecology of clonal animals. *Functional Ecology* **1**, 63–69.
9. Hughes, R.N. 1987b. Conditions favouring mictic and amictic reproduction. *Functional Ecology* **1,** 163–165.
10. Cancino, J.M. and Hughes, R.N. 1988. The zooidal polymorphism and astogeny of *Celleporella hyalina* (Bryozoa, Cheilostomata). *Journal of Zoology* **215**, 167–181.
11. Hughes, R.N. 1989. *A Functional Biology of Clonal Animals*. Chapman and Hall, London 331 pp.
12. Hunter, E. and Hughes, R.N. 1991. Growth of laboratory cultured colonies of *Celleporella hyalina* (L.). *In*: F.P. Bigey (ed), *Bryozoaires actuelles et fossiles: Bryozoa living and fossil. Bulletin de la Société des Sciences Naturelles de l'Ouest de la France Mem. HS 1 Nantes (France)* pp. 187–191.
13. Cancino, J.M., Hughes, R.N. and Ramirez, C. 1991. Environmental cues and the phasing of larval release in the bryozoan *Celleporella hyalina* (L.). *Proceedings of the Royal Society of London Series B-biological Sciences* **246**(1315), 39–45.
14. Hauser, L., Carvalho, G.R., Hughes, R.N. and Carter, R.E. 1992. Clonal structure of the introduced freshwater snail *Potamopyrgus antipodarum* (Prosobranchia: Hydrobiidae), as revealed by DNA fingerprinting, *Proceedings of the Royal Society of London Series B-biological Sciences* **249**(1324), 19–25.
15. Seed, R. and Hughes, R.N. 1992. Reproductive strategies of epialgal bryozoans. *Invertebrate Reproduction and Development* **22**(1–3), 291–300.
16. Hunter, E. and Hughes, R.N., 1993c. The effect of cell concentration on colony growth and feeding in the bryozoan *Celleporella hyalina*. *Journal of the Marine Biological Association of the United Kingdom* **73**(2), 321–331.
17. Hunter, E. and Hughes, R.N. 1993a. Effects of diet on life-history parameters of the marine bryozoan, *Celleporella hyalina* (L.). *Journal of Experimental Marine Biology and Ecology* **167**(2), 163–177.
18. Hunter, E. and Hughes, R.N., 1993b. Self-fertilization in *Celleporella hyalina*. *Marine Biology* **115**(3), 495–500.

19. Cancino, J.M., Orellana, M.C., Muñoz, M.R. and Hughes, R.N. 1993. Ciclo diario de liberación larval en dos especies de briozoos. *Revista de Biología Marina (Valparaíso)* **27,** 213–223.

20. Hunter, E. and Hughes, R.N. 1994. The influence of temperature, food ration and genotype on zooid size in *Celleporella hyalina* (L.). In: Hayward, P.J., Ryland, J.S. and Taylor, P.D. (eds). *Biology and Palaeobiology of bryozoans. Proceedings of the 9th International Bryozoology Conference*, Swansea, (1992). Olsen and Olsen, Fredensborg. pp. 83–86.

21. Cancino, J.M., Hughes, R.N. and Orellana, M.C. 1994. A comparative study of larval release in bryozoans. *In*: Hayward, P.J., Ryland, J.S. and Taylor, P.D. (eds). *Biology and Palaeobiology of bryozoans*. Proceedings of the 9th International Bryozoology Conference, Swansea, (1992). Olsen and Olsen, Fredensborg. pp. 41–46.

22. Hunter, E. and Hughes, R.N. 1995. Environmental and genetic components of variation in sexual allocation by an epialgal bryozoan. *Marine Ecology Progress Series* **120**(1–3), 193–201.

23. Whitehead, J. W., Seed, R. and Hughes, R.N. 1996. Factors controlling spinocity in the epialgal bryozoan *Flustrellidra hispida* (Fabricius). *In*: Gordon, D.P., Smith, A.M. and Grant-Mackie, J.A. (eds) *Bryozoans in space and time*. National Institute of Water and Atmospheric Research, Wellington, New Zealand. pp. 367–375.

24. Orellana, M.C., Cancino, J.M. and Hughes, R.N. 1996. Is settlement in lecithotrophic bryozoan larvae constrained by energy reserves? *In* Gordon, D.P., Smith, A.M. and Grant-Mackie, J.A. (eds) *Bryozoans in space and time*. National Institute of Water and Atmospheric Research, Wellington, New Zealand. pp. 221–226.

25. Hunter, E., Hughes, R.N. and Goldson, A. 1996. Environmental and genetic control of somatic and sexual performance in *Celleporella hyalina* (L.) *In* Gordon, D.P., Smith, A.M. and Grant-Mackie, J.A. (eds) *Bryozoans in space and time*. National Institute of Water and Atmospheric Research, Wellington, New Zealand. pp. 149–156.

26. Hughes, R.N. 1996. Evolutionary ecology of parthenogenetic strains of the prosobranch snail, *Potamopyrgus antipodarum* (Gray) (= *P. jenkinsi* (Smith). *Malacological Review, Suppl*. **6**, 101–113.

27. Hoare, K., Hughes, R.N. and Gliddon, C.J., 1998. Polymorphic microsatellite markers isolated from the bryozoan *Celleporella hyalina* (L.), *Molecular Ecology* **7**(3), 355–356.

28. Hoare, K., Hughes, R.N. and Goldson, A.J. 1999. Molecular genetic evidence for the prevalence of outcrossing in the hermaphroditic brooding bryozoan *Celleporella hyalina*. *Marine Ecology Progress Series* **188**, 73–79.

29. Bishop, J.D.D., Manríquez, P.H. and Hughes, R.N. 2000. Water-borne sperm trigger vitellogenic egg growth in two sessile marine invertebrates, *Proceedings of the Royal Society of London Series B-Biological Sciences* **267**(1449), 1165–1169.

30. Manríquez, P.H., Hughes, R.N. and Bishop, J.D.D. 2001. Age-dependent loss of fertility in water-borne sperm of the bryozoan *Celleporella hyalina*. *Marine Ecology Progress Series* **224**, 87–92.

31. Hoare, K. and Hughes, R.N. 2001. Inbreeding and hermaphroditism in the sessile brooding bryozoan *Celleporella hyalina*. *Marine Biology* **139**(1), 147–162.

32. Hoare, K., Goldson, A.J., Giannasi, N. and Hughes, R.N. 2001. Molecular phylogeography of the cosmopolitan bryozoan *Celleporella hyalina*: Cryptic speciation? *Molecular Phylogenetics and Evolution* **18**(3), 488–492,

33. Goldson, A.J., Hughes, R.N. and Gliddon, C.J. 2001. Population genetic consequences of larval dispersal mode and hydrography: a case study with bryozoans. *Marine Biology* **138**(5), 1037–1042.

34. Craig, S.F., D'Amato, M.E., Harley, M., Bishop, M., Bishop, J., Hughes, R.N. and Carvalho, G.R. 2001. Isolation and characterization of microsatellites in the bryozoan *Crisia denticulata*. *Molecular Ecology Notes* **1**(4), 281–282.

35. Wright, P. and Hughes, R.N. 2002. A comparison of the early astogeny and life history of *Celleporella carolinensis* and *Celleporella hyalina*. *In* Wyse Jackson, P.N., Buttler, C.J. and Spencer Jones, M.E. (eds). *Bryozoan Studies 2001*. Swets and Zeitlinger, Lisse. pp. 353–357.

36. Hughes, R.N., Wright, P. Manríquez, P.H. and Bishop, J.D.D. 2002. Predominance of obligate outbreeding in the simultaneous hermaphrodite *Celleporella hyalina* sensu lato. *In* Wyse Jackson, P.N., Buttler, C.J. and Spencer Jones, M.E. (eds). *Bryozoan Studies 2001*. Swets and Zeitlinger, Lisse. pp. 159–161

37. Hughes, R.N., Manríquez, P.H. and Bishop, J.D.D. 2002. Female investment is retarded pending reception of allosperm in a hermaphroditic colonial invertebrate. *Proceedings of the National Academy of Science USA* **99**, 14884–14886.

38. Pemberton, A.J., Hughes, R.N., Manríquez, P.H. and Bishop, J.D.D. 2003. Efficient utilization of very dilute aquatic sperm: sperm competition may be more likely than sperm limitation when eggs are retained. *Proceedings of the Royal Society of London Series B-biological Sciences* **270**, 223–226.

39. Hughes, R.N., Manríquez, P.H., Bishop, J.D.D. and Burrows, M.T. 2003. Stress promotes maleness in hermaphroditic modular animals. *Proceedings of the National Academy of Sciences of the United States of America* **100**(18), 10326–10330.

40. Hughes, R.N., Manríquez, P.H., Morley, S., Craig, S.F. and Bishop, J.D.D. 2004a. Kin or self-recognition? Colonial fusibility in *Celleporella hyalina*. *Evolutionary Development* **6**, 431–437.

41. Hughes, R.N., D'Amato, M.E., Bishop, J.D.D., Carvalho, G.R., Craig, S.F. Hansson, L.J., Harley, M.A. and Pemberton, A.J. 2004b. Paradoxical polyembryony? Embryonic cloning in an ancient order of marine bryozoans. *Biology Letters* **1**, 178–80.

42. Hughes, R.N. 2005. Lessons in modularity: the evolutionary ecology of colonial invertebrates. *Scientia Marina* **69**, (Suppl. 1) 169–179.

43. Atkinson, D., Morley, S.A. and Hughes, R.N. 2006. From cells to colonies: at what levels of body organization does the 'temperature-size rule' apply? *Evolution and Development* **8**, 202–214.

44. Wright, P., Hayward, P.J. and Hughes, R.N. 2007. New species of *Antarctothoa*

(Cheilostomata: Hippothoidae) from the Falkland Isles, South Shetland Isles and the Magellan Strait. *Journal of the Marine Biology Association UK* **87**, 1133–1140.

45. Pemberton, A.J., Hansson, L.J., Craig, S.F., Hughes, R.N. and Bishop, J.D.D. 2007. Microscale genetic differentiation in a sessile invertebrate with cloned larvae: investigating the role of polyembryony. *Marine Biology* **153**, 71–82.
46. Gómez, A., Wright, P., Lunt, D.H., Cancino, J.M., Carvalho, G.R. and Hughes, R.N. 2007. Mating trials validate the use of DNA barcoding to reveal cryptic speciation of a marine bryozoan taxon. *Proceedings of the Royal Society London B* **274**, 199–207.
47. Gómez, A., Hughes, R.N., Wright, P., Carvalho, G.R. and Lunt, D.H. 2007. Mitochondrial DNA phylogeography and mating compatibility reveal marked genetic structuring and speciation in the NE Atlantic bryozoan *Celleporella hyalina*. *Molecular Ecology* **16**, 2173–2188.
48. Hughes, R.N., Gómez, A., Wright, P., Moyano, H.I., Cancino, J.M., Carvalho, G.R. and Lunt, D.H. 2008. Molecular phylogeny supports division of the 'cosmopolitan' taxon *Celleporella* (Bryozoa; Cheilostomata) into four major clades. *Molecular Phylogenetics and Evolution* **46**, 369–374.
49. Hughes, R.N., Wright, P., Carvalho, G.R. and Hutchinson, W.F. 2009. Patterns of self-compatibility, inbreeding depression, outcrossing, and sex allocation in a marine bryozoan suggest the predominating influence of sperm competition. *Biological Journal of the Linnean Society* **98**, 519–531.
50. Waeschenbach, A., Porter, J.S. and Hughes, R.N. 2012. Molecular variability in the *Celleporella hyalina* (Bryozoa; Cheilostomata) species complex: evidence for cryptic speciation from complete mitochondrial genomes. *Molecular Biology Reports* **39**, 8601–8614.
51. Broom, M., Hughes, R.N., Burrows, M.Y. and Ruxton, G.D. 2012. Evolutionary stable sex allocation by both stressed and unstressed potentially simultaneous hermaphrodites within the same population. *Journal Theoretical Biology* **30**, 96–102.
52. Hughes, R.N. and Wright, P.J. 2014. Self-fertilization in the *Celleporella angusta* clade and a description of *Celleporella osiani* sp. nov. *In* Rosso, A. Wyse Jackson, P.N. and Porter, J. (eds) *Bryozoan Studies 2013*. *Studi Trentini Scienze Naturali* **94**, 119–124.
53. Jenkins, H.L., Bishop, J.D.D. and Hughes, R.N. 2015. Prudent female allocation by modular hermaphrodites: female investment is promoted by the opportunity to outcross in cyclostome bryozoans. *Biological Journal of the Linnean Society* **116**, 593–602.

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References (other than those listed in the previous section

Bell, G. 1982. *The masterpiece of Nature. The evolution and genetics of sexuality*. Croom Helm, London & Canberra, 635 pp.

Cancino, J.M. 1983. *Demography of animal modular colonies*. Ph.D. thesis, University of Wales, Bangor.

Cancino, J.M. 1986. Marine macroalgae as a substratum for sessile invertebrates: a study of *Celleporella hyalina* (Bryozoa) on fronds of *Laminaria saccharina* (Phaeophyta). *Monografías Biol*ógicas **4**, 279–308.

Cancino J.M. and Gallardo J.A. 2004. Efectos del retardo del asentamiento en las expectativas de vida del briozoo *Bugula flabellata* (Bryozoa: Gymnolaemata) *Revista Chilena de Historia Natural* **77**, 227–234.

Elner R.W. and Hughes, R.N. 1978. Energy maximization in the diet of the shore crab, *Carcinus maenas*. *Journal of Animal Ecology* **47** (1), 103–116.

Grosberg R.K. 1992. Asexual Obsessions. *Evolution* **46** (6), 1976–1979.

Harper, J.L. 1977. *Population Biology of plants*. Academic Press, London, 892 pp.

Hughes, D.J., 1987. Gametogenesis and embryonic brooding in the cheilostome bryozoan *Celleporella hyalina*. *Journal of Zoology (London)* **212**, 691–712.

Hughes, D., 1992. Genotype-environment interactions and relative clonal fitness in a marine bryozoan. *Journal of Animal Ecology* **61**, 291–306.

Hughes, R.N. 1968. *The population ecology and energetics of Scrobicularia plana da Costa*. Ph.D. thesis, University College of North Wales, Bangor.

Hughes, R.N. 1969. A study of feeding in *Scrobicularia plana*. *Journal of the Marine Biological Association of the United Kingdom* **49**, 805–823.

Hughes, R.N. 1970. Population Dynamics of the Bivalve *Scrobicularia plana* (Da Costa) on an Intertidal Mud-Flat in North Wales. *Journal of Animal Ecology* **39**(2), 333–356.

Hughes, R.N. 1970. An Energy Budget for a Tidal-Flat Population of the Bivalve *Scrobicularia plana* (Da Costa). *Journal of Animal Ecology* **39**(2), 357–381.

Hughes, R.N. 1979. Coloniality in Vermetidae (Gastropoda). pp. 243–253 in Larwood, G. & Rosen, B.R. *Biology and Systematics of Colonial Organisms*. Systematic Association Special. London, Academic Press. Vol.11.

Hughes, R.N., Hughes D.J., Smith, I.P. and Dale, A.C. (eds). 2015. *Oceanography and Marine Biology: An Annual Review* **53**, 1–358.

Hunter E. and Fusetani N. 1996. Studies on the effects of larval swimming time on settlement, metamorphosis and post-larval development of *Bugula neritina* (Cheilostomatida). In: Gordon D.P., Smith, A.M. and Grant-Mackie J.A. (eds) *Bryozoans in Space and Time*: 139–148. National Institute of Water and Atmospheric Research Ltd, Wellington, New Zealand.

Kaiser, M.J., Burrows, M.T and Hughes H. (eds) 2011. Evolution and ecology of marine biodiversity: mechanisms and dynamics. *Marine Ecology Progress Series* **430**, 98–288.

Manríquez, P.H. 1999. *Mate choice and reproductive investment in the cheilostome* *bryozoan Celleporella hyalina* (L.). Ph.D. thesis, University of Wales Bangor.

Orellana M.C. and Cancino, J.M. 1991. Effects of delaying settlement on metamorphosis and early colonial growth in *Celleporella hyalina* (Bryozoa:Cheilostomata). In: Bigey F.P. (ed) Bryozoariesactuels et fossiles: bryozoa living and fossil: 309–316. *Bulletin de la Société des Sciences Naturelles de l'Ouest de la France*, Nantes, France.

Ryland, J.S. 1959. Experiments on the selection of algal substrates by polyzoan larvae. *Journal of Experimental Biology* **36**(2), 613–631.

Ryland, J.S. 1962. The association between Polyzoa and algal substrata. *Journal of Animal Ecology* **31**(2), 331–338.

Solas M.R., Hughes R.N., Márquez F. and Brante A. 2015. Early plastic responses in the shell morphology of *Acanthina monodon* (Mollusca, Gastropoda) under predation risk and water turbulence. *Marine Ecology Progress Series* **527**, 133–142.

"Variation of the tentacles in *Paludicella*": the unfinished work of the German bryozoologist and embryologist Fritz Braem

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1. Introduction

During a visit to the *Zoologische Staatssammlung München* (ZSM; Zoological State Collections Munich) in November 2015, Bernhard Ruthensteiner (section leader Evertebrata varia) handed over to one of us (JS) two envelopes with documents from two German

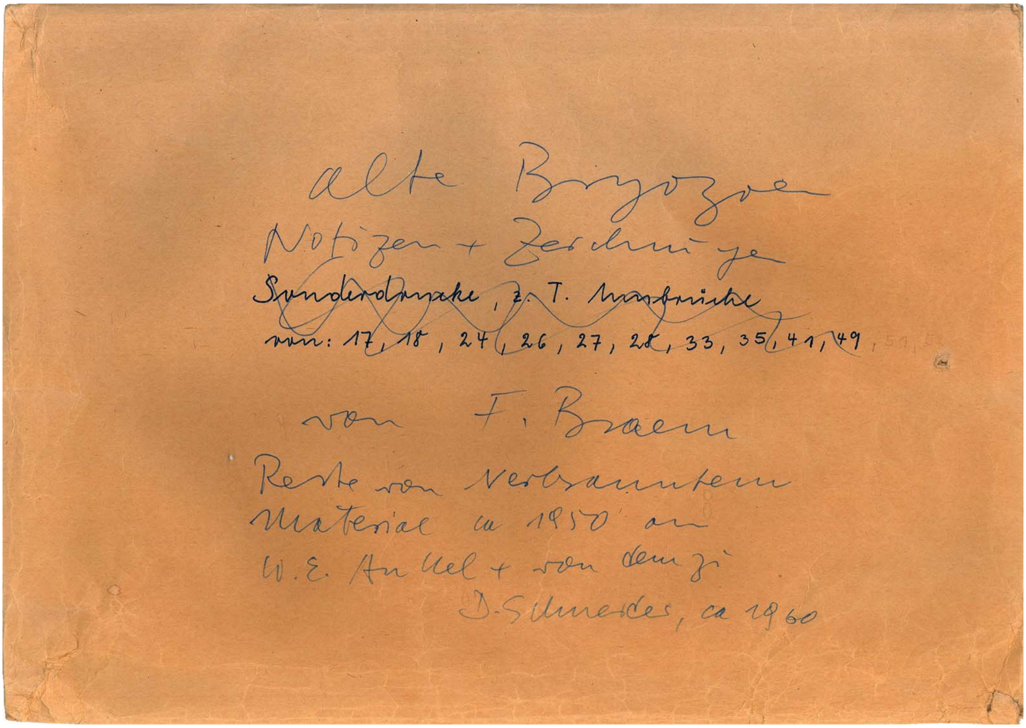
We dedicate our contribution to the memory of Michael Türkay (1948–2015), who had always been fond of science history research, and who once suggested a study on Fritz Braem, the least known member of the German *Valdivia* Deep Sea Expedition (1888/89).

In memoriam Michael Türkay (1948–2015), head of the Department of Invertebrate Zoology (presently Marine Zoology) at the Senckenberg Research Institute from 1989–2014.

bryozoologists that he donated to the archive of the Senckenberg Gesellschaft für Naturforschung (SGN; Senckenberg Society for Natural Sciences) in Frankfurt am Main, Germany. While one of the envelopes included drawings, film strips, letters and other documents by Dietrich Schneider (1919–2008), the other envelope contained drawings and a letter by Fritz Braem (1862–?). A handwritten note on the cover of the letter comprising the Braem material (Figure 1) confirmed that these documents were handed over by Braem *ca*. 1950 to Wulf Emmo Ankel (1897–1983) and in *ca*. 1960, Ankel passed along Braem's documents to Schneider. Schneider donated the material and his own material to the ZSM thereafter.

Dietrich Schneider worked on marine bryozoans (especially *Bugula* Oken, 1815 and phototropism in Bryozoa) during the 1950s to 1960s (e.g. Schneider 1959; Schneider & Kaissling 1964). Accordingly, Schneider's documents include correspondence letters with several leading bryozoologists of this period including Diethardt Jebram (1937–2004), Ehrhard Voigt (1905–2004) and Claus Nielsen (born 1938). The documents also confirm that Schneider attended the 1983 IBA Conference in Vienna, and visited Voigt in Hamburg. In our article, however, we shall focus on the contents of the second envelope, which is the legacy of Fritz Braem.

Fritz Braem was a bryozoologist and embryologist from Germany, who published for over 63 years on freshwater and brackish bryozoans. He is considered as being one of the pioneers in the study of the anatomy and the embryology of ctenostome and phylactolaemate bryozoans. Still, almost nothing is known about Fritz Braem. This may be due to the fact that Braem's works were not so well received by the scientific community when he was



alte Bryozoen
Notizen + Zeichnungen
~~Sonderdrucke, z. T. Manuskripte~~
~~von: 17, 18, 24, 26, 27, 28, 33, 35, 41, 49~~
von F. Braem
Reste von verbranntem
Material ca 1950 an
W.E. Ankel + von dem zu
D. Schneider, ca 1960

*Figure 1. Envelope containing the recovered documents of Fritz Braem. The handwriting on the cover of the envelope reads „*alte Bryozoen Notizen *(sic)* + Zeichnungen von F. Braem. Reste von verbranntem Material ca. 1950 an W.E. Ankel + von dem zu D. Schneider, ca. 1960 *(“old bryozoan notes + drawings by F. Braem. Remains of burnt material ca. 1950 [handed] to W.E. Ankel + then [handed] to D. Schneider, ca. 1960)”.*

still alive and he had many scientific disputes with other bryozoologists including Charles Benedict Davenport (1866–1944), Karl Kraepelin (1848–1915) and Asajiro Oka (1866–1944). Despite the want of appreciation by the scientific community and despite having abandoned a science career in 1899, Braem continued his studies on freshwater and brackish bryozoans and continued publishing his results. The recovered material shows that Braem had at least one unfinished project, most of the material and results of which, however, were burnt during World War II.

The recovered material includes a handwritten letter by Fritz Braem, in which he describes, what he remembers from a long-term study on the variation of the tentacles of *Paludicella articulata* (Ehrenberg, 1831). The study included of about 14,000 tentacle measurements on *P. articulata* from rivers and creeks near Berlin, Breslau and Königsberg. Braem observed a large variation in the number of tentacles (5 to 20 tentacles per zooid)[1] and an increase in the number of tentacles in *Paludicella* from the same locality over the year with a peak in October to November. He also found a positive relationship between the length of the tentacles and the amount of tentacles per zooid. A translation of the full letter is provided in Section 4.

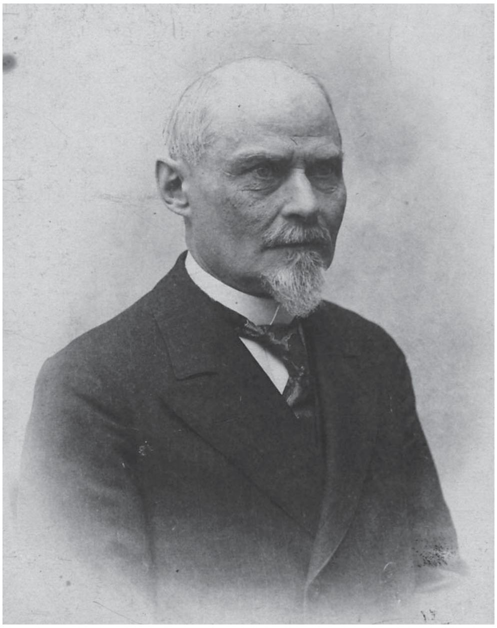


Figure 2. Fritz Braem (1862–?) in 1921. Photograph courtesy of the Staatsblibliothek zu Berlin (State Library of Berlin).

The documents, both of Fritz Braem and of Dietrich Schneider, are now stored in the archive of the SGN (V 176 Nr. 6626 at the Institut für Stadtgeschichte Frankfurt am Main; repository of the archive of the SGN) as suggested by Bernhard Ruthensteiner. The drawings were scanned and are available, as well as PDFs of Fritz Braem's publications, from the authors of this article.

2. Biography of Fritz Braem

Not much is known about the life of Fritz Braem (Figure 2). Most information of his early life is available from the curriculum vitae in his Ph.D. thesis (Braem 1890a), while some insight into his later life was recorded in the yearbooks of the German librarians (*Jahrbuch der Deutschen Bibliothekare*), where Braem is listed from 1902 to 1931. Virtually nothing was found on the private life of Braem. Thus, it remains unclear, whether he ever married and whether he had children, brothers or sisters.

Fritz Braem was born on 1 November 1862 to Minna Braem, née Schmidt, and Heinrich Braem on the estate of his parents in Prilacken, 20 km NW of Königsberg, Prussia (now Kaliningrad, Russian Federation). He attended the Altstädtisches Gymnasium in Königsberg from 1871 and graduated in 1881. The same year, he started to study philology (study of languages) at the Albertus-University of Königsberg, a decision that he regretted later on.[2] In early 1885, he shifted his attention towards the study of natural sciences.

Carl Chun (1852–1914), Professor of Zoology at the Albertus-University of Königsberg at that time, advised Braem to focus his studies on freshwater bryozoans, which Braem started in the summer of 1886.[3] In June 1888, he graduated from the University of Königsberg after passing a state examination and continued his studies as a Ph.D. student of Chun. Braem completed his Ph.D. thesis on the systematics and biogenesis of Prussian freshwater bryozoans on 16 July 1890. He continued to work for Chun as a research fellow and followed him to the Schlesische Friedrich-Wilhelms University in Breslau (now Wroclaw, Poland) in April 1891. He gained a further qualification (habilitation) in June 1893 working on swifts (Braem 1893a) for zoology and comparative anatomy and continued working at the University of Breslau as an associate professor (*Privatdozent*). Fritz Braem belonged to the scientific staff of the first German deep-sea cruise, the *Valdivia* expedition from July 1898 to April 1899 (Figure 3) that was organized by Chun. The scientific career of Braem ended directly after the return of the SS *Valdivia*. The reasons for this turning point in Braem's life have not been made public. We assume that it was not Braem's free choice taking into account his continued scientific ambitions. Braem stayed in correspondence with Chun, but they never saw each other again.[4] Chun edited one of Braem's later publications (Braem 1908a) and Braem contributed with an article to a 'Festschrift' on the occasion of Chun's 60th birthday (Braem 1913).

Figure 3. The participants of the Valdivia *expedition (1898–1899), which was organised by Carl Chun (white circle). Braem (black circle) belonged to the scientific staff of the deep-sea expedition. Photograph courtesy of the Senckenberg archive (Institut für Stadtgeschichte Frankfurt am Main; V 176 Nr. 3219).*

Braem seems to have returned to his hometown Königsberg in 1899 and begun a traineeship at the University Library of Königsberg in 1901. He then started to work as a volunteer at the University Library of Berlin on 15 April 1902 and shortly afterwards at the *Deutsches Bureau der Internationalen Bibliographie der Naturwissenschaften* ("German Bureau for the International Bibliography of Natural Sciences"). Braem received the title Professor on 15 March 1912. He returned from the Bureau to the University Library of Berlin in December 1915, but started to work as an assistant at the State Library of Berlin in November 1916. Braem finally was appointed as *Bibliotheksrat* ('senior librarian officer') in July 1918 and worked at the State Library until he retired on 31 March 1928.

Braem lived in Uhlandstrasse 88 in Berlin-Wilmersdorf, this address being attested for the last time in the address register of Berlin for the year 1943. He died after July 1950, but it was not possible to find any other evidence, neither in the genealogy records of FamilySearch, the world's largest genealogy organization, nor in the register of deaths for Berlin-Wilmersdorf housed in the state archive of Berlin. The last signs of his life are actually the newly discovered letter dated June and July 1950 and his last publication of a manuscript completed much earlier in August 1943 (Braem 1951). Braem handed over his unpublished drawings, a letter and the manuscript for his last publication to Wulf Emmo Ankel, who edited this publication for *Zoologica* in late 1950.

3. Fritz Braem's publications on bryozoans

Braem made 25 scientific contributions to bryozoology that were published over a range of 63 years. His publications can be subdivided into three phases. The first publications appeared during his early scientific career, when he belonged to the scientific staff of Carl Chun at the Universities of Königsberg and Breslau. This phase includes twelve works on bryozoans from 1888 to 1897. His first publications (Braem 1888a, b, 1889a, b) are preliminary results of his Ph.D. thesis. In these publications he referred several times to the first part of Karl Kraepelin's work on German freshwater bryozoans (Kraepelin 1887). It is interesting that Braem accused Kraepelin of having included findings that Braem had communicated to him in his work[5], and he attacked and corrected Kraepelin in his preliminary results several times, making his point also in his later publications. It must be considered very risky by Braem, since he was a student at that time and Kraepelin a professor. Braem finished his Ph.D. thesis on the systematics of freshwater bryozoans in Prussia in 1890 (Braem 1890a), and published a more comprehensive monograph dealing with the anatomy, germination, embryology, sexual reproduction, statoblast formation (Figure 4) and funiculus formation of phylactolaemates and the ctenostome *Paludicella ehrenbergii* van Beneden, 1848 [= *P. articulata* Ehrenberg, 1831] (Braem 1890b). Braem continued thereafter to study the germ layers of freshwater bryozoans (Braem 1892, 1895) and worked on the sexual reproduction of the ctenostome *P. ehrenbergii* [= *P. articulata*] (Braem 1897) and the phylactolaemate *Plumatella fungosa* (Pallas, 1768) (Braem 1896). In a short note, Braem confirmed the finding of

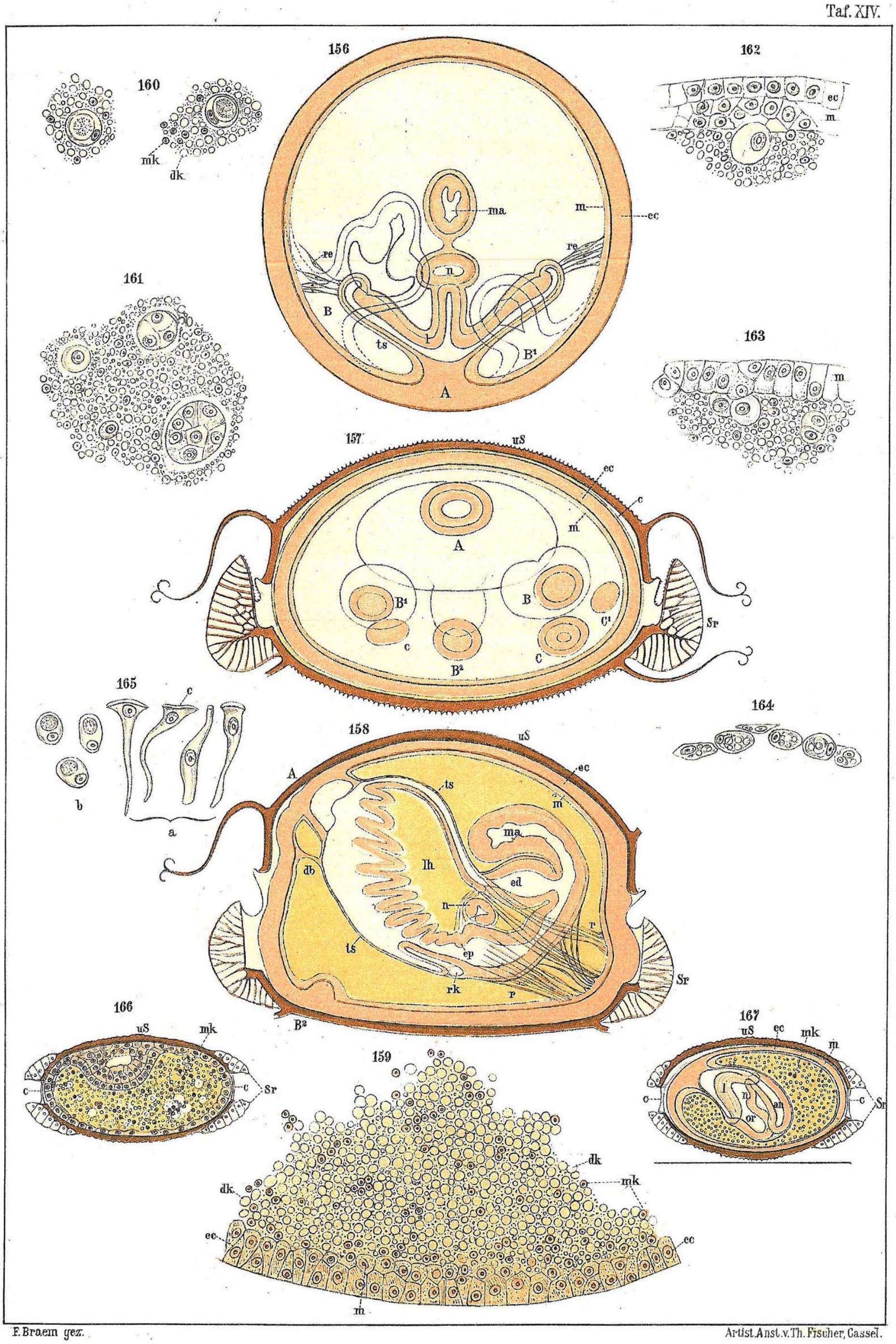


Figure 4. Braem's colour plate (1890b, pl. XIV) showing the germination of statoblasts in Cristatella mucedo *Cuvier, 1798.*

Cristatella mucedo Cuvier, 1798 in Kamchatka, the statoblasts of which were collected by the Polish zoologist Benedykt Dybowski (1833–1930), and he also reported a parasite found in *Cristatella* from Prussia (Braem 1893b). After Kraepelin published the second part of his work on German freshwater bryozoans (Kraepelin 1892) and criticized many of Braem's previous findings, Braem responded by accusing Kraepelin of claiming credits for the work of others and making false statements due to the lack of scientific results (Braem 1893c).[6]

Braem stopped publishing on bryozoans a couple of years prior to the start of the *Valdivia* expedition, but he returned to his studies while working at the German Bureau for the International Bibliography of Natural Sciences in the 1900s. Between 1908 and 1914, he published ten additional studies on bryozoans. In 1908 alone, four publications appeared in which he studied the sexual reproduction of *Fredericella sultana* (Blumenbach, 1779) (Braem 1908a), the spermatozoa of freshwater phylactolaemates (Braem 1908c) and ctenostomes (Braem 1908b) and the ovum of *P. fungosa* (Braem 1908d). Braem later received material from the Issyk-Kul in Kyrgyzstan collected by the Russian zoologist Dmitry D. Pedashenko (1868–1927) and described the fauna consisting of one phylactolaemate and one ctenostome bryozoan and studied the parasites found in the former (Braem 1911a). He continued his work by comparing the larvae of cheilostome bryozoans and pterobranchs (Braem 1911c) and studying the variation in the statoblasts of *Pectinatella magnifica* (Leidy, 1851) (Braem 1911b, 1912), and the germination of statoblasts in *C. mucedo* and *P. magnifica* (Braem 1913). Braem's last work from the second phase of publications was on the budding in *Paludicella* (Braem 1914b).

Braem stopped publishing on bryozoans in 1914, the reason being probably that Braem changed his position twice and was promoted to a senior librarian officer at the State Library of Berlin in 1918. It may be safe to speculate that Braem did not have enough time and opportunities anymore to maintain his scientific research especially during WWI. However, subsequently he continued his research on bryozoans in his own free time and using his own resources, since most of the fieldwork for his final contribution (Braem 1951) was done in 1921–1929. During the 1930s, he mainly worked on the variations of the tentacles of *Paludicella*, the results of which are summarized in his letter (Section 4 below), but in the late 1930s to early 1940s, Braem would complete another four publications. Braem corresponded with Sidney Harmer (1862–1950) in 1926[7] and started a revision of material from the *Siboga* expedition of *Victorella sibogae* Harmer, 1915, which was the only species assigned to *Victorella* Saville Kent, 1870 from a marine environment. He found that the species belonged to a yet undescribed genus and family (Braem 1939). In Braem (1940a), he revised material of *Pottsiella erecta* (Potts, 1884) from Pennsylvania and erected a new family for this ctenostome bryozoan. In another publication, he compared the intestines of cheilostome and ctenostome gymnolaemate bryozoans (Braem 1940b). Braem's last manuscript was written by August 1943, but would not be published until 1951. Braem (1951) described the brackish bryozoan fauna of the River Ryck near Greifswald and the results of a long-term study started in 1911 and completed in 1941.

4. Variation of the tentacles in *Paludicella*

A translation of Braem's letter (Figures 5–9) reads as follows:

> Among my burnt [during WWII] materials, there were also charts with approximately 14,000 (fourteen thousand) absolutely definite tentacle counts of *Paludicella*. The animals were mostly derived from the area around Königsberg in Prussia, Breslau and Berlin, most of them from the Woltersdorfer Fließ near Berlin. Origin, date, and when appropriate the kind of individual (whether dietallae, intercalary or regenerative bud or individual larvae) were noted down for all. Extreme cases (of significantly high or low numbers) were documented by a series of sections.
>
> The amount of variation in *Paludicella* is extremely high, it reaches from five to 20 tentacles. Five tentacles build an exception as they were found only once. I do not recall whether it was a dietalla, intercalary or regenerative bud. The animal was developed normally in all parts. Six tentacles did not occur which might also be a coincidence. From seven to 20 tentacles, the series was complete and all numbers were represented, while seven, eight and 20 tentacles were of smaller numbers; maybe below ten. Eight tentacles were not more frequent than seven, but were even short of seven which is most likely coincidence; in any case this shows that (*Pal.* bares no closer relation to the eight tentacle forms [crossed out]) number eight in *Pal.* in no way dominates, which could be expected since this number is the predominant one in relatives of *Pal.* and also the case in *Victorella*. Nine tentacles are already significantly more frequent and frequency increases now with growing numbers until it reaches its peak with 16 or 17 tentacles. In one case of animals that were collected in June 1929 at the Lauther Mühlenfließ near Königsberg (under the Chausseebridge), the count (more than one hundred individuals) even showed 18 as the most frequent number. After a slow rise to the peak, frequency decreases rapidly: 19 tentacles are considerably rarer than 18, and 20, the highest number that I have encountered, is a very infrequent case.
>
> The result of the average value of numbers of tentacles determined for the Woltersdorf specimens for the respective months was a slow increase in the course of the year so that they were highest in October and November. I cannot say for sure what this resulted from.
>
> [Crossed out section] *The length of tentacles increases (by a multiple* [crossed out]) *according to their number. On average ten tentacles are longer than nine tentacles, eleven longer than ten and so on. In general, this is the case, but of course there are single cases of deviation. The shortest tentacles were not those of the animal with five t.* [tentacles]*, but of one with a number of seven t., the longest not those of one with 20, (but with 18 t.* [crossed out]*, I (also do not think with 19 t., but one with 18 or 17 t.)* [replaced here] *since the lengths also vary when the number of tentacles is identical, thus reaching into areas of higher or lower numbers of tentacles.*
>
> The length of tent. increases significantly according to their number. On average ten are longer than nine, eleven longer than ten and so on. In general this is the case but

of course there are single cases of deviation since the lengths also vary when the number of tentacles is identical, thus reaching into areas of higher or lower numbers of tentacles. I remember for instance that the shortest of all tentacles were not those of an animal with five, but with seven t., the longest not those of one with 20, I also do not think with 19 t., but one with 18 or 17 t. I cannot give exact measures. The longest tentacles remain below 1 mm, the shortest may have measured 1/10 or fewer.

The increase of length according to the number of tentacles stands in opposition to the behaviour of the phylactolamates' statoblasts' spines, whose size decreases with growing number. This is due to that as essential organs the tentacles stand in approximately determined relation to the size of the whole body, which in *Pal.* varies to the same amount as the size and number of the tent. In comparison to the biggest, the smallest individuals of *Pal.* are true midgets, and could neither produce nor operate such an immense tentacle apparatus as the former could. In the statoblasts that are of approximately the same size, the number of cells available for the formation of spines is equivalent, and where many spines evolve, their size inevitably needs to be smaller than where only few of them are present.

This is what I kept from the charts. They are raw material that was awaiting subtler attention, which I could not give them.

June 1950

The following data on the tentacles of ancestrulae that evolved from larvae between the years 1935–37 is not based on memories, but on notes that were saved. The colonies covered with eggs were placed into glasses of water stuffed with microscope slides and collodium lamellae at which the hatched larvae could find the opportunity to settle. In order to examine the growth, the microscope slides etc. were removed and investigated under the microscope in flat small bowls. The entire material originated from the old Havel at Birkenwerder.

In the following collocation, the number of ancestrulae observed with their number of tentacles is indicated below the year dates.

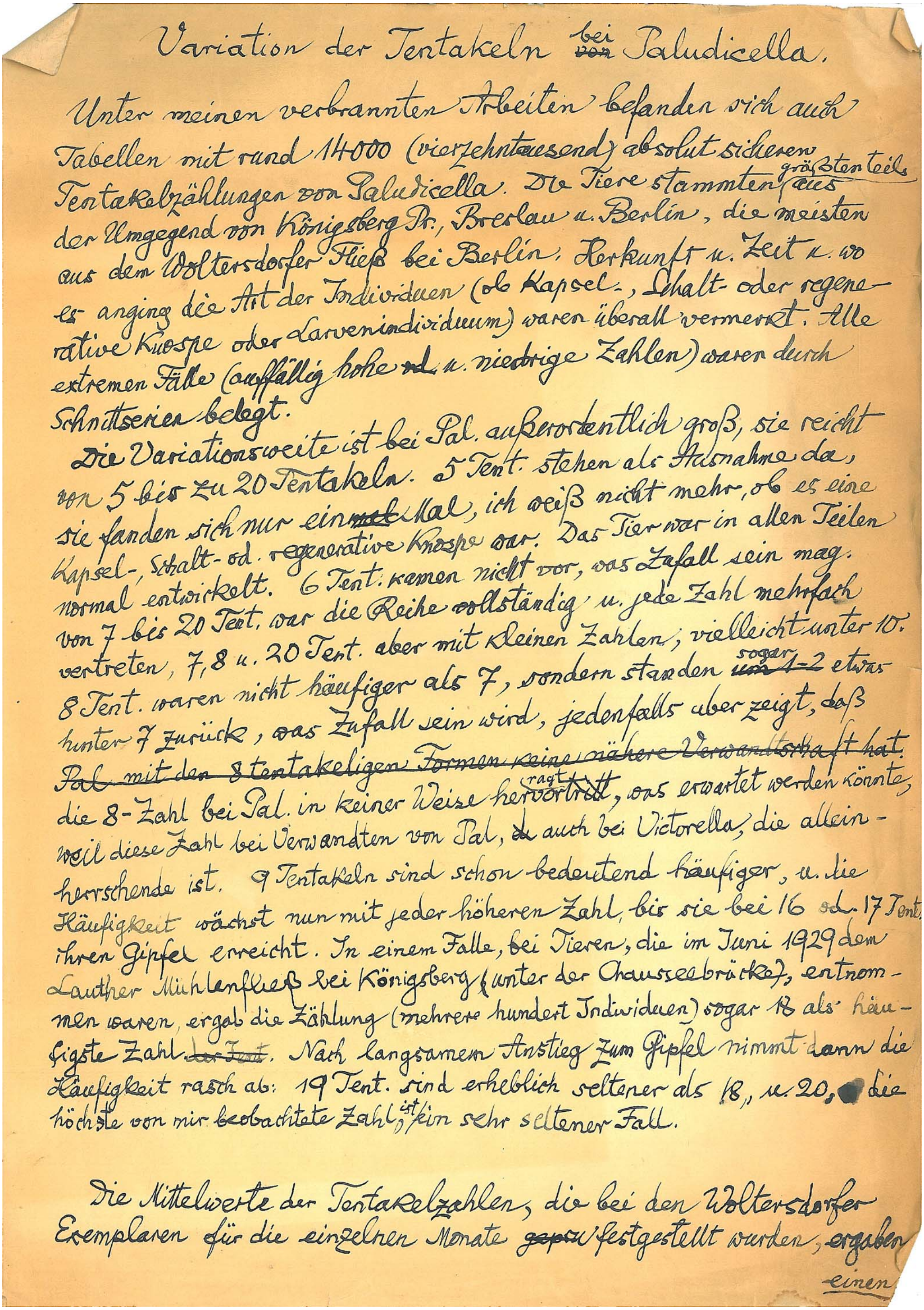
	1935	**1936**	**1937**	**1935–37**
mother colonies	from July and Aug.	f. June a. July	f. July a. Aug.	f. June–Aug.
9 tent.		1	1	2
10 –	5	17	4	26
11 –	20	48	11	29
12 –	1	8	2	11
	26	74	18	118

One can observe that in all three years with 60 % of all cases eleven tentacles were most frequent, followed by ten tent., then 12 and finally nine. This may also be the case

> for other years of which the records are lost, however, I remember also having found 13 tent. Within the 118 pieces, one finding I made in October 1935 at a time I had presumed the sexual development as long completed, is not being measured. Up to then the latest date, I had found *Paludicella* become sexually mature was August 30, 1935. Due to sickness during September that year, I could not visit the site. When I came back there on 3 October, I stumbled upon a stick covered with eggs. This also remained the latest date in the following years for me to discover such. At home, 13 larvae from these eggs developed into young small colonies with protrudable ancestrulae, [with] eight a. nine tent., [in] each one colony, ten tent. [in] nine [colonies] a. eleven tent. [in] two colonies. Here, in contrast to the summer animals, the scale of tentacles went down one level, twelve tent. are entirely missing and eight add, while ten tent., instead of eleven tent. in summer, presents the dominant number. This can only be an effect of the lower temperatures in my rooms that ranged between 16 and 18°C back then. The feeding can only be a factor after protrusibility[8] since the larva up to then lives on the yolk accumulated inside and the degenerating larval organs of which remnants can often be even found in the rectum even when protrusibility has been reached. The longer duration of development of these autumnal individuals can also be led back to the influence of temperature. The 118 summer specimens needed at least four, mostly five, and sometimes six days from settlement to protrusibility of the primary polypide. The same took the 13 autumn specimens once seven, mostly eight, once nine a. once eleven days. When in one incident after 19 days no protrusibility had occurred. I conserved the animal and determined the number of tentacles by section (nine tent.).
>
> Measuring the tentacles of the primary animals shortly after first becoming protrusible showed the following results: nine tent. 0.1 mm, 10 t. 0.12–0.17 mm, 11 t. 0.13–0.22 mm, 12 t. 0.16–0.23 mm.

The letter is accompanied by a short note (Figure 10).

> Everything else, meaning the largest part, is burnt.
>
> F. Braem
>
> July 1950



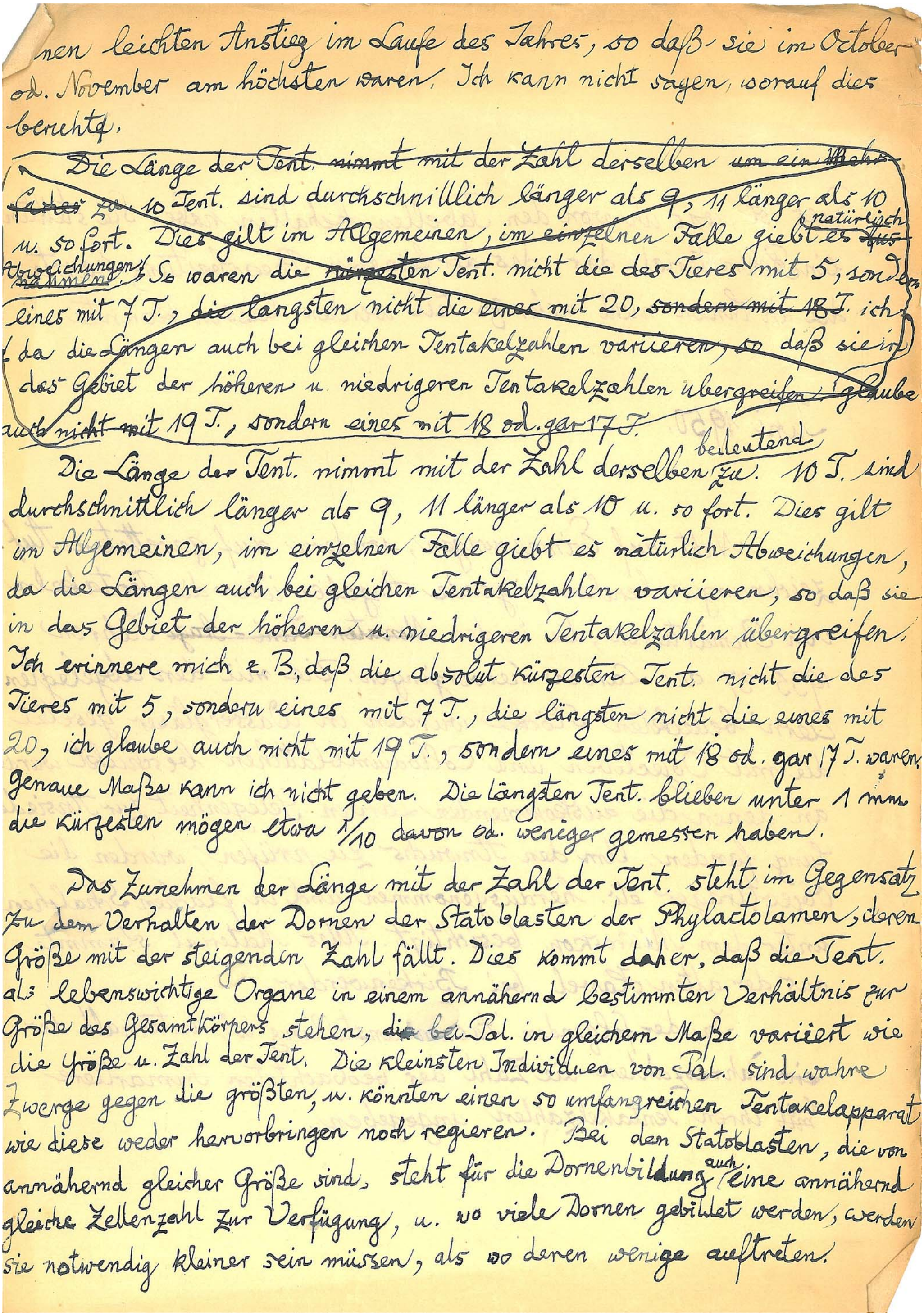
Variation der Tentakeln ~~von~~ bei Paludicella.

Unter meinen verbrannten Arbeiten befanden sich auch Tabellen mit rund 14000 (vierzehntausend) absolut sicheren Tentakelzählungen von Paludicella. Die Tiere stammten größtenteils aus der Umgegend von Königsberg Pr., Breslau u. Berlin, die meisten aus dem Woltersdorfer Fließ bei Berlin. Herkunft u. Zeit u. wo es anging die Art der Individuen (ob Kapsel-, Schalt- oder regenerative Knospe oder Larvenindividuum) waren überall vermerkt. Alle extremen Fälle (auffällig hohe ~~od.~~ u. niedrige Zahlen) waren durch Schnittserien belegt.

Die Variationsweite ist bei Pal. außerordentlich groß, sie reicht von 5 bis zu 20 Tentakeln. 5 Tent. stehen als Ausnahme da, sie fanden sich nur ein~~mal~~ Mal, ich weiß nicht mehr, ob es eine Kapsel-, Schalt- od. regenerative Knospe war. Das Tier war in allen Teilen normal entwickelt. 6 Tent. kamen nicht vor, was Zufall sein mag. Von 7 bis 20 Tent. war die Reihe vollständig u. jede Zahl mehrfach vertreten, 7, 8 u. 20 Tent. aber mit kleinen Zahlen, vielleicht unter 10. 8 Tent. waren nicht häufiger als 7, sondern standen ~~um 1-2~~ sogar etwas hinter 7 zurück, was Zufall sein wird, jedenfalls aber zeigt, daß ~~Pal. mit den 8 tentakeligen Formen keine nähere Verwandtschaft hat.~~ die 8-Zahl bei Pal. in keiner Weise hervor~~tritt~~ragt, was erwartet werden könnte, weil diese Zahl bei Verwandten von Pal., ~~da~~ auch bei Victorella, die alleinherrschende ist. 9 Tentakeln sind schon bedeutend häufiger, u. die Häufigkeit wächst nun mit jeder höheren Zahl, bis sie bei 16 od. 17 Tent. ihren Gipfel erreicht. In einem Falle, bei Tieren, die im Juni 1929 dem Lauther Mühlenfließ bei Königsberg (unter der Chausseebrücke), entnommen waren, ergab die Zählung (mehrere hundert Individuen) sogar 18 als häufigste Zahl ~~der Tent~~. Nach langsamem Anstieg zum Gipfel nimmt dann die Häufigkeit rasch ab: 19 Tent. sind erheblich seltener als 18, u. 20, die höchste von mir beobachtete Zahl, ist ein sehr seltener Fall.

Die Mittelwerte der Tentakelzahlen, die bei den Woltersdorfer Exemplaren für die einzelnen Monate ~~gegen~~ festgestellt wurden, ~~ergaben~~ einen

Figure 5. First page of Braem's letter on the variation of the tentacles in Paludicella articulata. *(Institut für Stadtgeschichte Frankfurt am Main; V 176 Nr. 6626)*



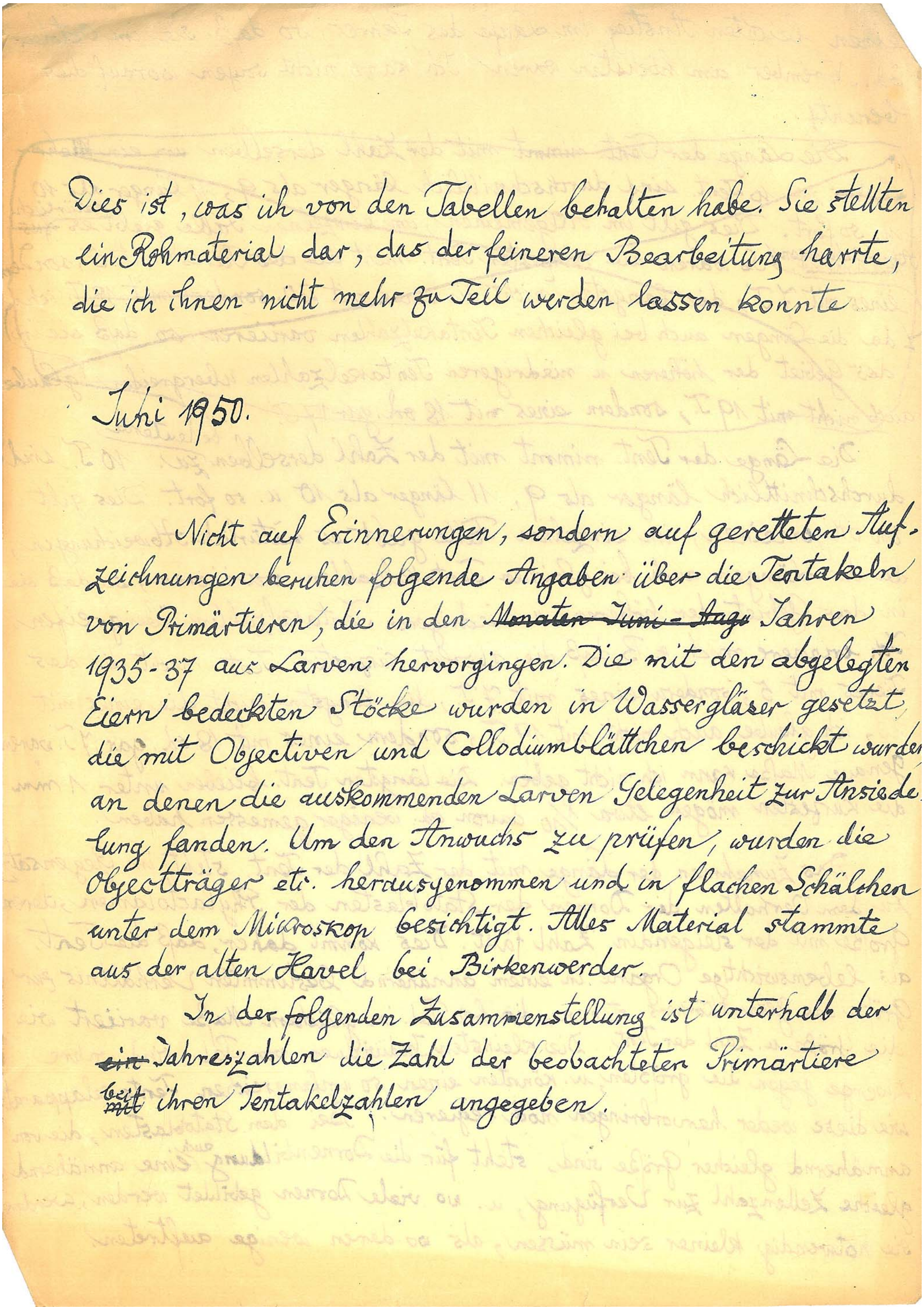
nen leichten Anstieg im Laufe des Jahres, so daß sie im October od. November am höchsten waren. Ich kann nicht sagen, worauf dies beruhte.

~~Die Länge der Tent. nimmt mit der Zahl derselben um ein Mehrfaches zu. 10 Tent. sind durchschnillich länger als 9, 11 länger als 10 u. so fort. Dies gilt im Algemeinen, im einzelnen Falle giebt es natürlich Ausnahmen Abweichungen, So waren die kürzesten Tent. nicht die des Tieres mit 5, sondern eines mit 7 T., die langsten nicht die eines mit 20, sondern mit 18 T. ich (da die Längen auch bei gleichen Tentakelzahlen variieren, so daß sie in das Gebiet der höheren u. niedrigeren Tentakelzahlen übergreifen) glaube auch nicht mit 19 T., sondern eines mit 18 od. gar 17 T.~~

Die Länge der Tent. nimmt mit der Zahl derselben bedeutend zu. 10 T. sind durchschnittlich länger als 9, 11 länger als 10 u. so fort. Dies gilt im Algemeinen, im einzelnen Falle giebt es natürlich Abweichungen, da die Längen auch bei gleichen Tentakelzahlen variieren, so daß sie in das Gebiet der höheren u. niedrigeren Tentakelzahlen übergreifen. Ich erinnere mich z. B., daß die absolut kürzesten Tent. nicht die des Tieres mit 5, sondern eines mit 7 T., die längsten nicht die eines mit 20, ich glaube auch nicht mit 19 T., sondern eines mit 18 od. gar 17 T. waren. Genaue Maße kann ich nicht geben. Die längsten Tent. blieben unter 1 mm, die kürzesten mögen etwa 1/10 davon od. weniger gemessen haben.

Das Zunehmen der Länge mit der Zahl der Tent. steht im Gegensatz zu dem Verhalten der Dornen der Statoblasten der Phylactolamen, deren Größe mit der steigenden Zahl fällt. Dies kommt daher, daß die Tent. als lebenswichtige Organe in einem annähernd bestimmten Verhältnis zur Größe des Gesamtkörpers stehen, die bei Pal. in gleichem Maße variiert wie die Größe u. Zahl der Tent. Die kleinsten Individuen von Pal. sind wahre Zwerge gegen die größten, u. könnten einen so umfangreichen Tentakelapparat wie diese weder hervorbringen noch regieren. Bei den Statoblasten, die von annähernd gleicher Größe sind, steht für die Dornenbildung auch eine annähernd gleiche Zellenzahl zur Verfügung, u. wo viele Dornen gebildet werden, werden sie notwendig kleiner sein müssen, als wo deren wenige auftreten.

Figure 6. Second page of Braem's letter on the variation of the tentacles in P. articulata.



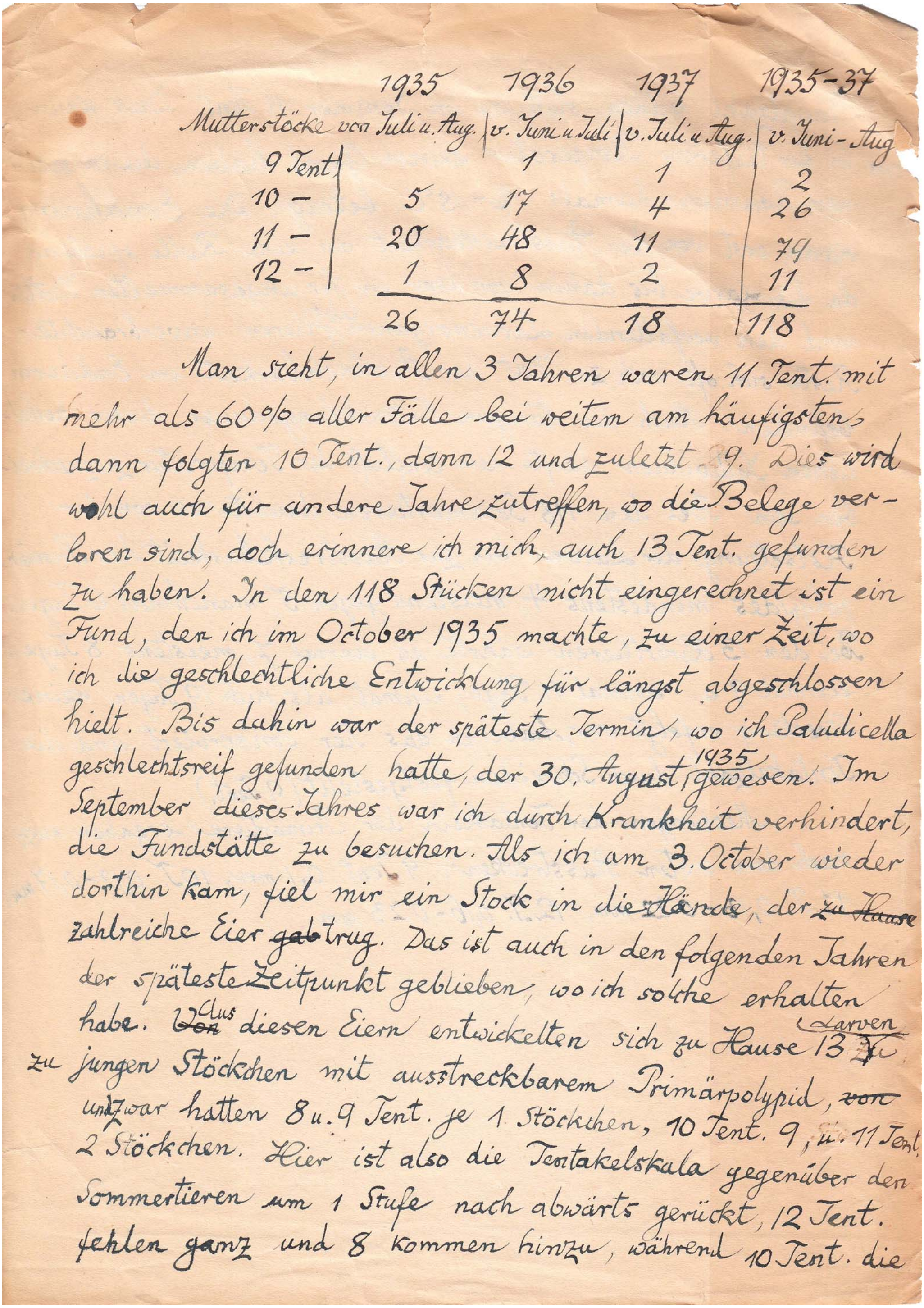
Dies ist, was ih von den Tabellen behalten habe. Sie stellten ein Rohmaterial dar, das der feineren Bearbeitung harrte, die ich ihnen nicht mehr zu Teil werden lassen konnte

Juni 1950.

Nicht auf Erinnerungen, sondern auf geretteten Aufzeichnungen beruhen folgende Angaben über die Tentakeln von Primärtieren, die in den ~~Monaten Juni - Aug.~~ Jahren 1935-37 aus Larven hervorgingen. Die mit den abgelegten Eiern bedeckten Stöcke wurden in Wassergläser gesetzt, die mit Objectiven und Collodiumblättchen beschickt wurden an denen die auskommenden Larven Gelegenheit zur Ansiedelung fanden. Um den Anwuchs zu prüfen, wurden die Objectträger etc. herausgenommen und in flachen Schälchen unter dem Mikroskop besichtigt. Alles Material stammte aus der alten Havel bei Birkenwerder.

In der folgenden Zusammenstellung ist unterhalb der ~~ein~~ Jahreszahlen die Zahl der beobachteten Primärtiere ~~mit~~ bei ihren Tentakelzahlen angegeben.

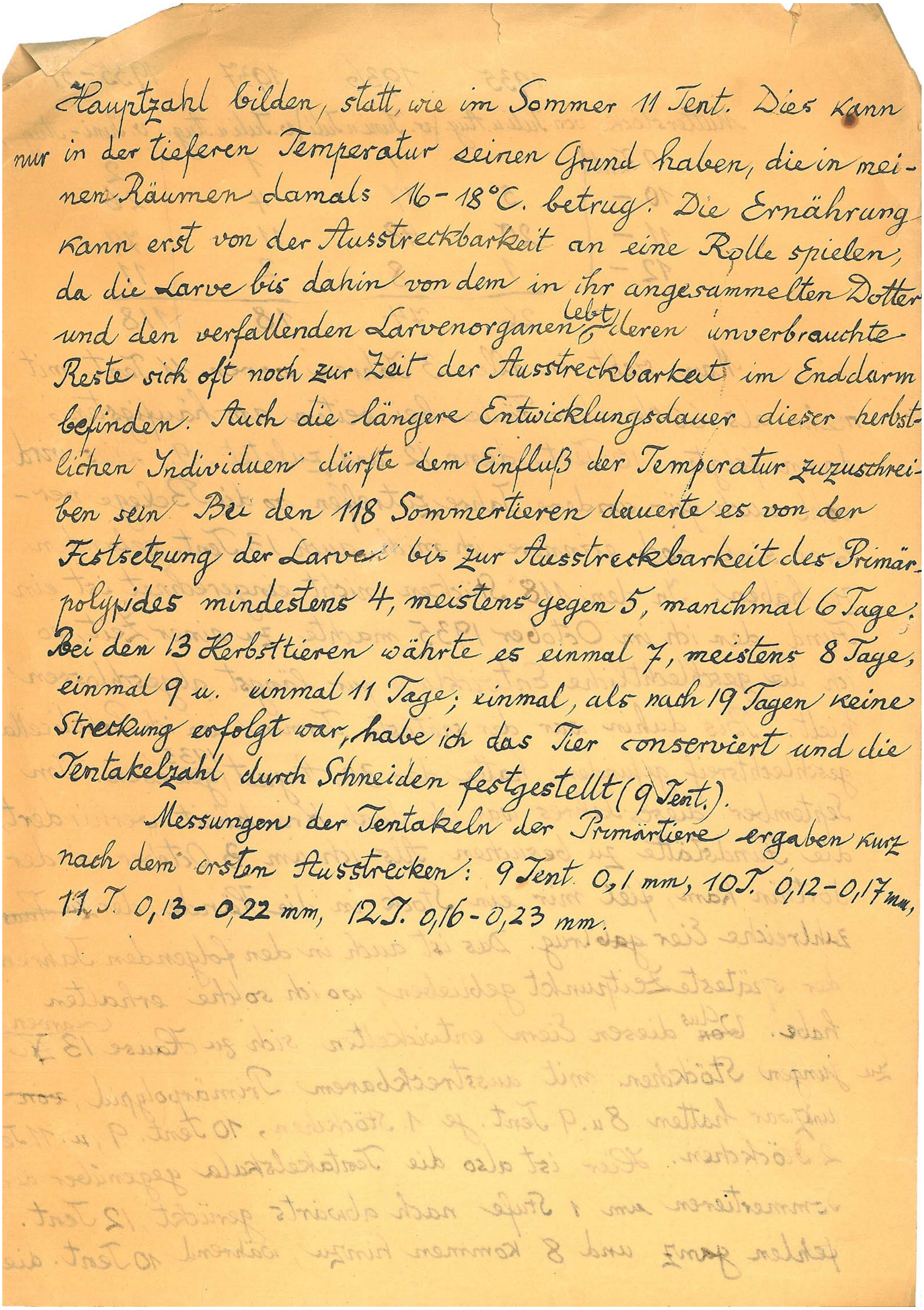
Figure 7. Third page of Braem's letter on the variation of the tentacles in P. articulata.



	1935	1936	1937	1935-37
Mutterstöcke	von Juli u. Aug.	v. Juni u. Juli	v. Juli u. Aug.	v. Juni - Aug.
9 Tent		1	1	2
10 –	5	17	4	26
11 –	20	48	11	79
12 –	1	8	2	11
	26	74	18	118

Man sieht, in allen 3 Jahren waren 11 Tent. mit mehr als 60% aller Fälle bei weitem am häufigsten, dann folgten 10 Tent., dann 12 und zuletzt 9. Dies wird wohl auch für andere Jahre zutreffen, wo die Belege verloren sind, doch erinnere ich mich, auch 13 Tent. gefunden zu haben. In den 118 Stücken nicht eingerechnet ist ein Fund, der ich im October 1935 machte, zu einer Zeit, wo ich die geschlechtliche Entwicklung für längst abgeschlossen hielt. Bis dahin war der späteste Termin, wo ich Paludicella geschlechtsreif gefunden hatte, der 30. August 1935 gewesen. Im September dieses Jahres war ich durch Krankheit verhindert, die Fundstätte zu besuchen. Als ich am 3. October wieder dorthin kam, fiel mir ein Stock in die Hände, der ~~zu Hause~~ zahlreiche Eier ~~gab~~ trug. Das ist auch in den folgenden Jahren der späteste Zeitpunkt geblieben, wo ich solche erhalten habe. ~~Von~~ Aus diesen Eiern entwickelten sich zu Hause 13 Larven ~~Ti~~ zu jungen Stöckchen mit ausstreckbarem Primärpolypid, ~~von~~ und zwar hatten 8 u. 9 Tent. je 1 Stöckchen, 10 Tent. 9, u. 11 Tent. 2 Stöckchen. Hier ist also die Tentakelskala gegenüber den Sommertieren um 1 Stufe nach abwärts gerückt, 12 Tent. fehlen ganz und 8 kommen hinzu, während 10 Tent. die

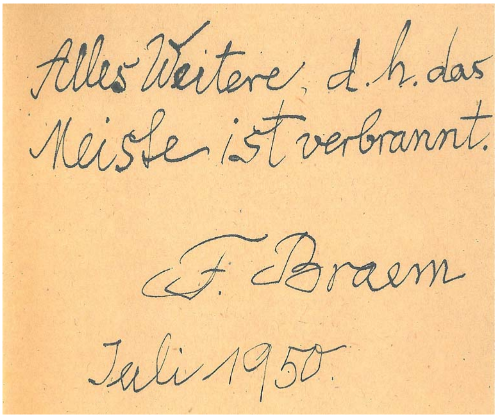
Figure 8. Fourth page of Braem's letter on the variation of the tentacles in P. articulata.



Hauptzahl bilden, statt, wie im Sommer 11 Tent. Dies kann nur in der tieferen Temperatur seinen Grund haben, die in meinen Räumen damals 16–18°C. betrug. Die Ernährung kann erst von der Ausstreckbarkeit an eine Rolle spielen, da die Larve bis dahin von dem in ihr angesammelten Dotter und den verfallenden Larvenorganen lebt, deren unverbrauchte Reste sich oft noch zur Zeit der Ausstreckbarkeit im Enddarm befinden. Auch die längere Entwicklungsdauer dieser herbstlichen Individuen dürfte dem Einfluß der Temperatur zuzuschreiben sein. Bei den 118 Sommertieren dauerte es von der Festsetzung der Larven bis zur Ausstreckbarkeit des Primärpolypides mindestens 4, meistens gegen 5, manchmal 6 Tage; Bei den 13 Herbsttieren währte es einmal 7, meistens 8 Tage, einmal 9 u. einmal 11 Tage; einmal, als nach 19 Tagen keine Streckung erfolgt war, habe ich das Tier conserviert und die Tentakelzahl durch Schneiden festgestellt (9 Tent.).

Messungen der Tentakeln der Primärtiere ergaben kurz nach dem ersten Ausstrecken: 9 Tent. 0,1 mm, 10 T. 0,12–0,17 mm, 11 T. 0,13–0,22 mm, 12 T. 0,16–0,23 mm.

Figure 9. Fifth page of Braem's letter on the variation of the tentacles in P. articulata.


Alles Weitere, d.h. das
Meiste ist verbrannt.

F. Braem

Juli 1950.

Figure 10. Note accompanying the recovered material of Fritz Braem.

5. New taxa erected by Fritz Braem

Fritz Braem was no taxonomist but an anatomist. Nevertheless, in his later publications, he suggested some new taxa, the first of which was a freshwater ctenostome that he found in bryozoan material from the Issyk-Kul (Braem 1911a). Overall, Braem erected six new bryozoan taxa, all of which are ctenostomes (Table 1). Among these are two new species, three new genera and one new family; *Bulbella* Braem, 1951 (type species *B. abscondita* Braem, 1951), Pottsiellidae (type genus *Pottsiella* Kraepelin, 1887), *Sundanella* Braem, 1939 (type species *Victorella sibogae* Harmer, 1915), *Tanganella* Braem, 1951 (type species *Paludicella muelleri* Kraepelin, 1887) and *Victorella continentalis* Braem, 1911a.

In his revision of *Victorella sibogae* Harmer, 1915, Braem (1939) found that the species is quite distinctive from any *Victorella* species and created the new, monospecific genus *Sundanella*. He also found that the species was so distinctive from any other ctenostome that he proposed a new family for it. Although the proposed family included only one genus, which would be the stem for the family-group name, he did not clearly use the name

Table 1. Bryozoan taxa erected by Fritz Braem. All taxa are Ctenostomata.

Taxon	**First description**	**Occurrence**	**Habitat**
Bulbella	Braem, 1951	Ryck, Germany	Brackish
Bulbella abscondita	Braem, 1951	Ryck, Germany	Brackish
Pottsiellidae	Braem, 1940a	Tacony Creek, USA	Freshwater
Sundanella	Braem, 1939	Java Sea, Indonesia	Marine
Tanganella	Braem, 1951	Ryck, Germany	Brackish
Victorella continentalis	Braem, 1911a	Issyk-Kul, Kyrgyzstan	Freshwater

to refer to the new family.[9] This is a violation of Article 11.7 of the *International Code of Zoological Nomenclature* (ICZN 1999) and the family name Sundanellidae is attributed to Jebram (1973), who was the first to use it as a scientific name.[10] The name Pottsiellidae was also proposed in Jebram (1986), Braem (1940a) not being cited by Jebram (1986). Since the use of Pottsiellidae in Braem (1940a) is in accordance with the *International Code of Zoological Nomenclature*, the family name proposed in Jebram (1986) is a homonym and the oldest available name, i.e. Pottsiellidae Braem, 1940a, has to be considered the valid name for the taxon (ICZN 1999, Article 23.1).

6. Braem's drawings

The recovered documents contain approximately 350 sheets with drawings and explanatory notes of Fritz Braem. The drawings are usually made on the reverse sides of advertisements, wedding invitations and others. Part of the drawings were also produced on papers from the *Valdivia* expedition. From the dates indicated on some of the reverse sides, we can say that Braem conducted his studies in the 1920s to 1930s. Braem's drawings are very diverse and very detailed. Most show different aspects in the embryonic development of *Paludicella articulata* (Ehrenberg, 1831). However, there are also some drawings of other freshwater and marine ctenostomes including *Amathia pustulosa* (Ellis & Solander, 1786), *Buskia socialis* Hincks, 1887 and *Pottsiella erecta* (Potts, 1884) that show different aspects in the morphology of these species.

Out of the material, we selected to depict three drawings, all of which show new information that have not been previously published to our knowledge. Figure 11 shows the early cleavage in *P. articulata* including also polar bodies, which are extremely difficult to observe and mitotic spindles. Braem also has tracked the fate of early blastomeres, which is a remarkable achievement. In Figure 12, the early embryonic development, the gastrulation, of *P. articulata* is depicted and in Figure 13, Braem showed a fully developed larva of this species. Its embryonic development and the full larva itself are shown in more detail than previously available. Note that no scale is provided, nor are all the drawings prepared by Braem to the same scale.

7. Braem's work on bryozoan anatomy and reproductive biology

Several of Braem's achievements are still unsurpassed today. Our knowledge on the embryonic development of Phylactolaemata largely results from his works (Braem 1890b, 1897, 1908a). There were several contributions to this field from other authors (e.g. Reinhard 1881, Kraepelin 1892, Marcus 1934, Mukai 1982), but none are as detailed and beautifully illustrated as those of Braem. Studying particularly the early embryonic development is extremely difficult since early brooding sacs resemble asexually produced buds and thus are difficult to discriminate. Likewise, Braem was one of the first to recognize the placental nourishment of the embryos in this group (summarized in Ostrovsky *et al*. 2016) as well as the first to describe and illustrate larval metamorphosis

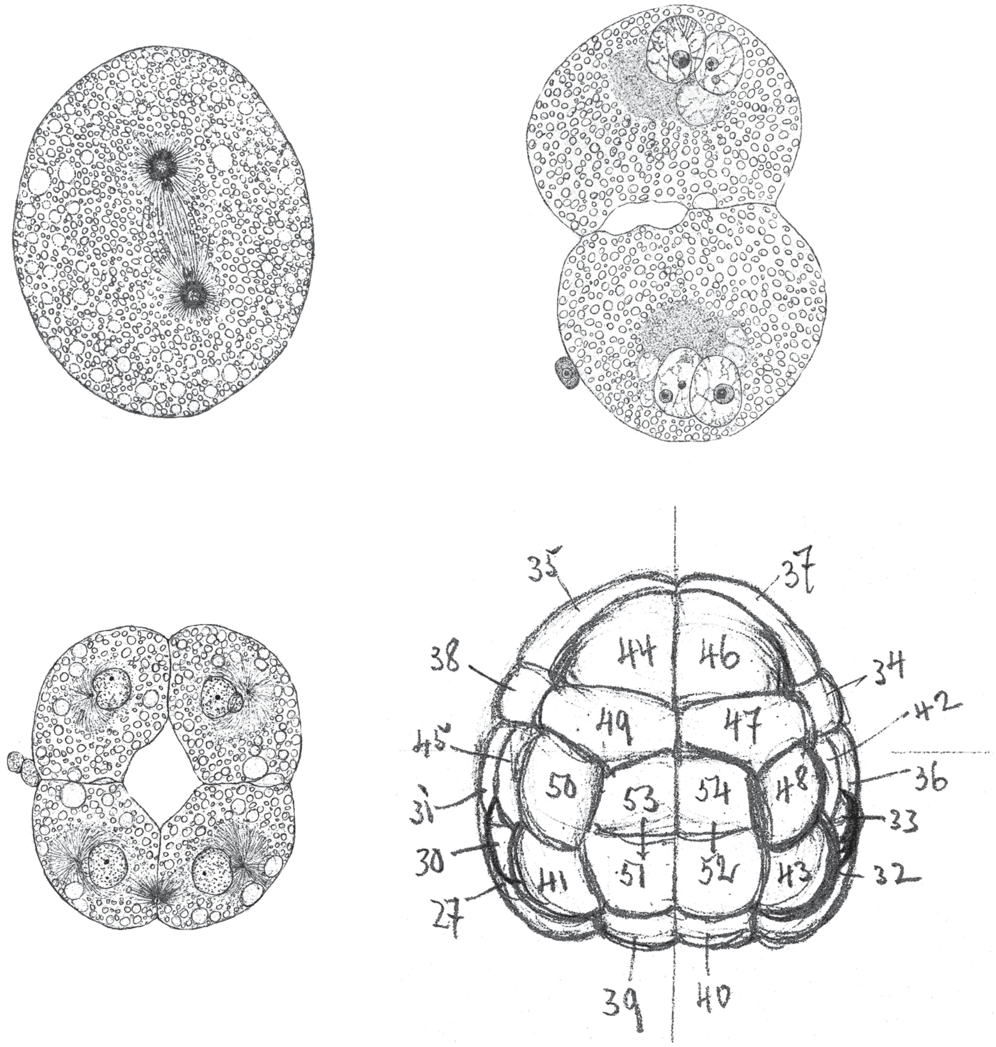


Figure 11. Early cleavage in Paludicella articulata *(Ehrenberg, 1831), showing polar bodies, mitotic spindles, and tracking the ancestry of blastomeres.*

in Phylactolaemata.

Statoblasts are phylactolaemate specific dormant buds that are mainly used for overwintering and dispersal. The germination of these dormant stages is triggered by different environmental cues (e.g. Brown 1933, Oda 1959, Mukai 1982). Braem (1890b) was the first to experimentally test different factors, such as temperature on the germination of statoblasts. Likewise, he was one of few investigators studying the germination process on a histological level (Braem 1890b, 1913). In fact, his observations giving details on the organization of the early epithelium, formation of the internal bud and organogenesis during the germination process provide the original data on these matters. There are

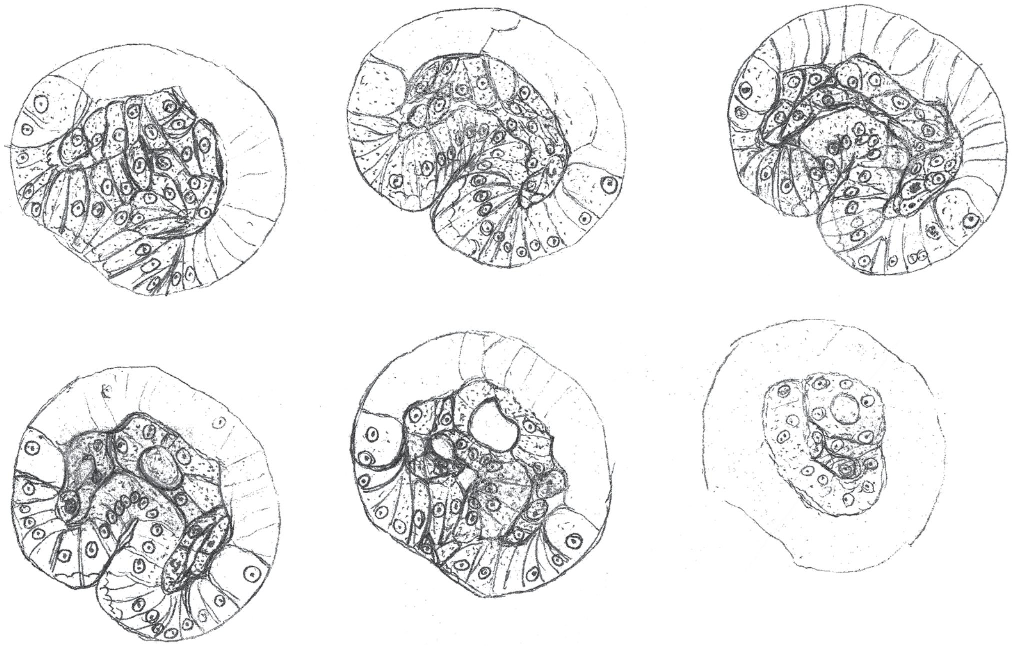


Figure 12. Early embryonic development in Paludicella articulata *(Ehrenberg, 1831) showing gastrulation.*

Figure 13. Fully developed larva of Paludicella articulata *(Ehrenberg, 1831).*

several difficulties beset with such a study: first, early germination stages develop with the statoblast valves closed and when the latter open, the polypide bud is already quite advanced (see also Handschuh *et al.* 2008). Thus, the analysis of these early stages is quite time consuming and needs a large amount of material. Second, histological preparation of the closed statoblasts requires a lot of technical skill. This comprises of mechanical cutting of the statoblast to ensure proper infiltration of chemical media including embedding media, as well as sectioning hard substances, such as statoblast valves, in the relatively soft paraffin. This shows that Braem was a very patient and accurate morphologist, which is reflected in the precision of his descriptions as well as his accurate drawings – particularly in his early period when he was still an active scientist. Interestingly his works, after his scientific career was over, were never as beautiful as in his early years – presumably due to lack of time.

Braem's second most important contribution in bryozoology was the study of primarily victorellid ctenostomes. His work from 1951 is still the largest and most thorough investigation on victorellid morphology. This does not just include the morphology of adults, but also developmental aspects like budding as well as sexual development. His observations on brooding were the first in victorellid ctenostomes and only a few other researchers have investigated this group in this respect (Smith *et al.* 2003, Vieira *et al.* 2014). As mentioned above, he described some new victorellid species and was the first to describe their larval structure and metamorphosis (in *Bulbella abscondita* and *Tanganella muelleri*). In this context, Braem was the first to recognize soft-body morphological features, such as the cardiac sphincter for species discrimination. Based on his work on ctenostomes, a particular interesting feature which Braem published on in 1940 was the cross-striation of the pharynx in gymnolaemaetes which represent myoepithelial muscle fibres (Braem 1940b, Mukai *et al.* 1997). As he mentioned himself, he was not the first to describe this feature, but he comparatively discussed its importance for the suction feeding in non-phylactolaemates. It is noteworthy that he also studied sectioned material of cyclostome bryozoans (*Crisia eburnea*) (Braem 1940b). Additionally, Fritz Braem was the first to describe and illustrate the presence of the placental nourishment in Ctenostomata when describing the embryonic growth and development in *Sundanella sibogae* (Braem 1939). It is clear from reading this paper that Braem did not understand the process.

In regard to the lost manuscript mentioned above, it should also be mentioned that Braem was the first, and has been the only one, to observe embryos and larvae of *Paludicella articulata*, probably the sole genus of the ctenostome superfamily Paludicelloidea (Braem 1896, unpublished observations from above). While gonads had been previously observed (Allman 1856, Kraepelin 1887), it is even more surprising that nobody has been able to observe larvae – or even gonads – subsequently in this species, despite its cosmopolitan distribution and high abundance. Consequently, Braem's contributions also are the only ones for the Paludicelloidea.

Conclusively, Fritz Braem was one of the most accurate bryozoan anatomists ever and a very careful observer and descriptor. His scientific legacy comprises his significant research output that provides the most reliable information and forms the foundation of our knowledge on phylactolaemate and ctenostome internal morphology, as well as embryology. His data is still actively used nowadays and, thus, this great researcher is not forgotten.

8. The *Valdivia* bryozoans

The *Valdivia* expedition was the first German expedition to explore the deep sea and it was organized by Carl Chun. The focus of the *Valdivia* expedition was the Indian Ocean, since the British *Challenger* expedition (1872–1876) had only passed through the southern Indian Ocean. A steam ship, the SS *Valdivia*, was selected in early 1898 for the expedition and was rebuilt in order to meet the criteria of a deep-sea research vessel. The expedition that was named after the vessel started in Hamburg on 31 July 1898 and took altogether nine months (Figure 14). The *Valdivia* explored the eastern Atlantic Ocean from the Faroe Islands to the Bouvet Island, and then passed through the Southern Ocean during the winter. The SS *Valdivia* sailed via the Kerguelen into the Indian Ocean. The expedition officially ended on 5 April 1899, when the vessel reached Aden. The SS *Valdivia* returned via the Red Sea, the Suez Canal, the Mediterranean Sea and the

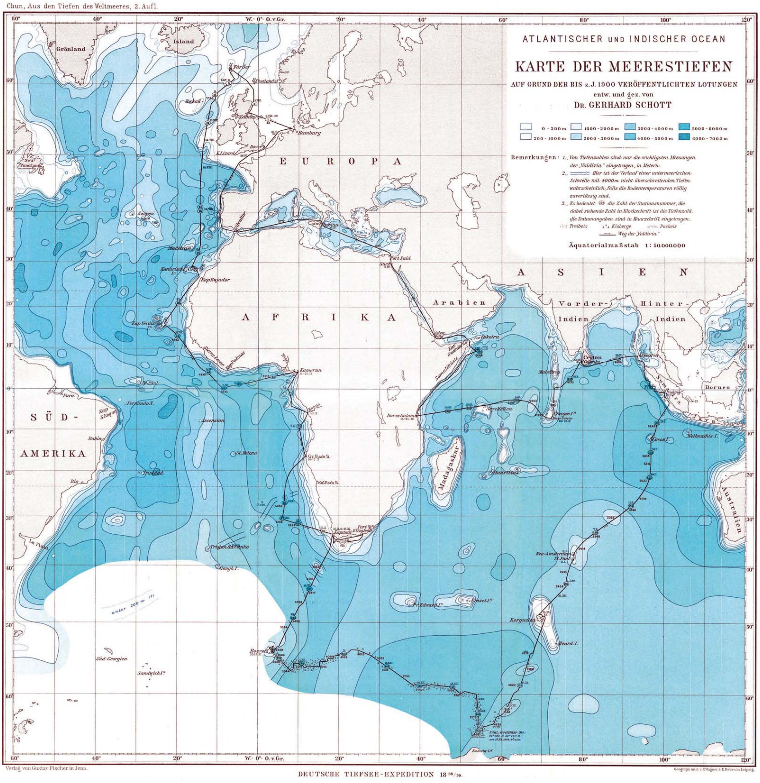


Figure 14. The Valdivia *expedition started in Hamburg and led first to the Faroe Islands. From there, the* Valdivia *crossed the northeastern Atlantic Ocean and navigated along the African coast into the Southern Ocean. The* Valdivia *then crossed the Indian Ocean and returned via the Red Sea and the Mediterranean Sea into the northeastern Atlantic Ocean and back to Hamburg. Photograph from Chun (1905).*

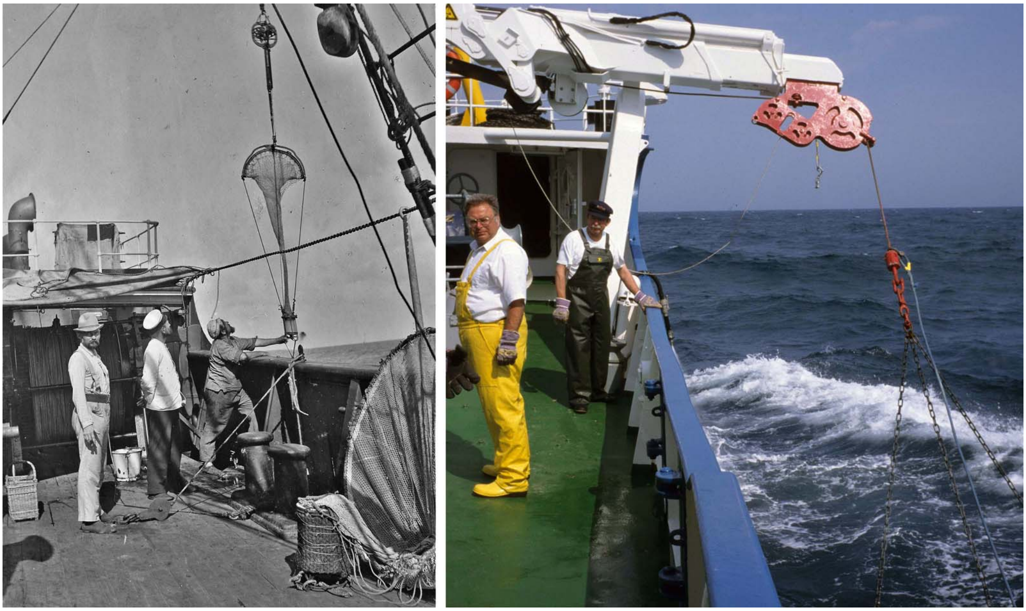


Figure 15. Then and now: Fritz Braem (1862–?) on deck of SS Valdivia *in 1898/9 (left) and Michael Türkay (1948–2015) on deck of FK* Senckenberg *in 1999 (right). Photographs courtesy of the Senckenberg archive (Institut für Stadtgeschichte Frankfurt am Main; V 176 Nr. 3219) and Dieter Fiege.*

northeastern Atlantic Ocean to Hamburg, where the vessel arrived on 1 May 1899.

The expedition was a huge scientific success. The Bouvet Island was rediscovered and its geographical position was fixed. Furthermore, it was verified that the whole water column is populated by organisms, while many researchers at that time believed that only the surface water and the sea floor would be populated. The scientific results of the *Valdivia* expedition were published in 24 volumes between 1902 and 1940. A huge focus was taxonomical work. However, bryozoans are among the least concerned phyla, despite bryozoans having been reported to be very numerous among the collected material.[11] In the first editions of the scientific results, Braem (Figure 15) was listed by Chun to work on the bryozoan material, but he never accomplished this task and Braem also had no other contributions to the scientific results of the *Valdivia* expedition. Carl Apstein (1862–1950), another participant of the *Valdivia* expedition, who edited the last volumes of the scientific results, passed over the *Valdivia* bryozoans to Wilhelm Hasenbank, who conducted a Ph.D. thesis on the material in the early 1930s. However, the Ph.D. thesis remained unfinished and it is unknown what happened to Hasenbank. Still, a part of Hasenbank's work was published in the scientific results (Hasenbank 1932). In this work, Hasenbank described and illustrated 45 species of anascan cheilostomes that were collected in the Atlantic, the Southern and the Indian Oceans. Among these are 14 new (sub) species and two new genera (Table 2). All the bryozoan material of the *Valdivia* expedition, including also Hasenbank's type material, is now lodged at the *Museum für Naturkunde* in Berlin and still awaits proper revision.

Table 2. New cheilostome bryozoan taxa proposed in Hasenbank (1932) for material from the Valdivia expedition. Some of the species have been referred to other genera by subsequent authors. However, since no proper revision of the material occurred, the original classification is used in this list.

Taxon	**Station(s)**	**Locality**	**Bathymetry**
Bugula apsteini	210	SW of Great Nicobar Island, India	752 m
Bugula hessei	211	SW of Katchal Island, India	805 m
Bugula leontodon cornuta	250	SE of Kaambooni, Somalia	1668 m
Cabereopsis			
Cabereopsis elongata	211	SW of Katchal Island, India	805 m
Carbasea macropora	96	S of Cape Agulhas, South Africa	80 m
Eupaxia			
Eupaxia incarnata	250	SE of Kaambooni, Somalia	1668 m
Flustra albida	211	SW of Katchal Island, India	805 m
Flustra gracilenta	28	NW of Cape Bojador, W. Sahara	146 m
Gemellaria loricata aurita	3, 6, 7	NE of Scotland, United Kingdom	79 m
Levinsenella tecta	211	SW of Katchal Island, India	805 m
Menipea klugei nom. nov.	127	SE of Bouvet Island, Norway	567 m
Menipea obtusa	131	SE of Bouvet Island, Norway	457 m
Menipea undulata	250	SE of Kaambooni, Somalia	1668 m
Scruparia spiralis	100	St Francis Bay, South Africa	50 m
Spiralaria denticulata brevimandibulata	100	St Francis Bay, South Africa	50 m

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References

Allman, G.J. 1856. *A monograph of the freshwater Polyzoa, including all the known species, both British and Foreign*. Ray Society, London, 119 pp.

van Beneden, P.-J. 1848. Recherches sur les bryozoaires fluviatiles de Belgique. *Mémoires de l'Académie Royale des Sciences, des Lettres et des Beaux-arts de Belgique* **21**, 1–33.

Blumenbach, J.F., 1779. *Handbuch der Naturgeschichte*. Johann Christian Dieterich, Göttingen, 448 pp.

Braem, F. 1888a. Untersuchungen über die Bryozoen des süßen Wassers. (Vorläufige Mittheilung.). *Zoologischer Anzeiger* **11** (289), 533–539.

Braem, F. 1888b. Untersuchungen über die Bryozoen des süßen Wassers. (Vorläufige Mittheilung.). *Zoologischer Anzeiger* **11** (288), 503–509.

Braem, F. 1889a. Über die Statoblastenbildung bei *Plumatella*. *Zoologischer Anzeiger* **12** (299), 64–65.

Braem, F. 1889b. Die Entwicklung der Bryozoencolonie im keimenden Statoblasten. (Vorläufige Mittheilung.). *Zoologischer Anzeiger* **12** (324), 675–679.

Braem, F. 1890a. *Zur Systematik und Entwicklungsgeschichte der Süsswasser-Bryozoen*. PhD thesis, Albertus-Universität zu Königsberg i. Pr., Königsberg i. Pr., 34 pp. (unpubl.)

Braem, F. 1890b. *Untersuchungen über die Bryozoen des süssen Wassers*. Theodor Fischer, Cassel, 134 pp.

Braem, F. 1892. Die Keimblätter der Bryozoenknospe. *Zoologischer Anzeiger* **15** (387), 113–115.

Braem, F. 1893a. *Bemerkungen über die Gattung* Apus. W. Engelmann, Leipzig, 24 pp.

Braem, F. 1893b. Notiz über *Cristatella*. *Zoologischer Anzeiger* **16** (413), 65–66.

Braem, F. 1893c. *Ein Wort über Herrn Prof. Karl Kraepelin und seinen neuesten Beitrag zur Bryozoenkunde*. Theodor Fischer, Cassel, 14 pp.

Braem, F. 1895. Was ist ein Keimblatt? *Biologisches Centralblatt* **15** (11, 12, 13), 427–443, 466–476, 491–506.

Braem, F. 1896. Die geschlechtliche Entwicklung von *Paludicella ehrenbergii*. *Zoologischer Anzeiger* **19** (493), 54–57.

Braem, F. 1897. Die geschlechtliche Entwickelung von *Plumatella fungosa*. *Zoologica* **10** (23), 1–96.

Braem, F. 1908a. Die geschlechtliche Entwicklung von *Fredericella sultana* nebst Beobachtungen über die weitere Lebensgeschichte der Kolonien. *Zoologica* **20** (52), 1–38.

Braem, F. 1908b. Die Spermatozoen von *Paludicella* und *Triticella*. *Zoologischer Anzeiger* **33** (11), 380–381.

Braem, F. 1908c. Die Spermatozoen der Süßwasser-Bryozoen. *Zoologischer Anzeiger* **32** (23), 671–673.

Braem, F. 1908d. Über die Umwandlung plasmatischer Granula zu halbmondförmign Körpern. *Anatomischer Anzeiger* **33** (13–14), 360–364.

Braem, F. 1911a. Beiträge zur Kenntnis der Fauna Turkestans auf Grund des von D.D. Pedaschenko gesammelten Materials. VII. Bryozoen und deren Parasiten. *Travaux de la Société Impériale des Naturalistes de St-Pétersbourg, Section de Zoologie et*

Physiologie **42**, 3–35.

Braem, F. 1911b. Die Variation bei den Statoblasten von *Pectinatella magnifica*. *Archiv für Entwicklungsmechanik der Organismen* **32** (2), 314–348.

Braem, F. 1911c. Pterobranchier und Bryozoen. *Zoologischer Anzeiger* **38** (24), 546–551.

Braem, F. 1912. Nachträgliches über die Variation der Statoblasten von *Pectinatella*. *Archiv für Entwicklungsmechanik der Organismen* **35** (1), 46–55.

Braem, F. 1913. Die Keimung der Statoblasten von *Pectinatella* und *Cristatella*. *Zoologica* **26** (2), 35–64.

Braem, F. 1914a. Professor Carl Chun, geb. den 1. Oktober 1852, gest. den 11. April 1914. Worte der Erinnerung. *Internationale Revue der gesamten Hydrobiologie und Hydrographie* **7** (1), 91–101.

Braem, F. 1914b. Die Knospung von *Paludicella*. Vorläufige Mitteilung. *Archiv für Hydrobiologie* **9**, 527–549.

Braem, F. 1939. *Victorella sibogae* Harmer. *Zeitschrift für Morphologie und Ökologie der Tiere* **36** (2), 267–278.

Braem, F. 1940a. Über *Pottsiella erecta* (Potts). *Archiv für Hydrobiologie* **36**, 306–318.

Braem, F. 1940b. Über die Querstreifung im Pharynx der gymnolämen Bryozoen und über den Bau des Munddarms. *Zeitschrift für Morphologie und Ökologie der Tiere* **36** (4), 668–676.

Braem, F. 1951. Über *Victorella* und einige ihrer nächsten Verwandten, sowie über die Bryozoenfauna des Ryck bei Greifswald. *Zoologica* **37** (3), 1–59.

Brown, C.J.D. 1933. A limnological study of certain fresh-water Polyzoa with special reference to their statoblasts. *Transactions of the American Microscopical Society* **52** (4), 271–316.

Chun, C. 1905. *Aus den Tiefen des Weltmeeres*. Gustav Fischer, Jena, 592 pp.

Cuvier, G. 1798. *Tableau elementaire de l'histoire naturelle des animaux*. Baudouin, Paris, 710 pp.

Ehrenberg, C.G. 1831. *Symbolæ physicæ, seu icones et descriptiones animalium evertebratorum, sepositis insectis, quae ex itineribus per Libyam, Ægyptum, Nubiam, Dongalam, Syriam, Arabiam et Habessiniam publico institutis sumptu Friderici Guilelmi Hemprich et Christiano Godofredi Ehrenberg medicinae et chirurgiae doctorum, studio annis MDCCCXX–MDCCCXXV redierunt*. G. Reimeri, Berlin, 128 pp.

Ellis, J. and Solander, D. 1786. *The natural history of many curious and uncommon zoophytes, collected from various parts of the globe*. White & Elmsly, London, 206 pp.

Handschuh, S. Schwaha, T. Neszi, N.Z. Walzl, M.G. and Wöss, E.R. 2008. Advantages of 3D reconstruction in bryozoan development research: Tissue formation in germinating statoblasts of *Plumatella fungosa* (Pallas, 1768) (Plumatellidae, Phylactolaemata), pp. 49–55. In: Hageman, S.J., Key, M.M. and Winston, J.E. (eds.) *Bryozoan studies 2007. Proceedings of the 14th International Bryozoology Association Conference, Boone, North Carolina, July 1–8, 2007*. Virginia Museum of Natural History, Martinsville, Va.

Harmer, S.F. 1915. The Polyzoa of the Siboga Expedition. Part I. Entoprocta, Ctenostomata and Cyclostomata. *Siboga-Expeditie* **28a**, 1–180.

Hasenbank, W. 1932. Bryozoen der deutschen Tiefsee-Expedition (I. Teil). *Wissenschaftliche Ergebnisse der deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898–1899* **21**, 319–380.

Hincks, T. 1887. The Polyzoa of the Adriatic: a supplement to Prof. Heller's "Die Bryozoen des adriatischen Meeres", 1867. [Concluded from vol. xvii. p. 271.]. *Journal of Natural History, Series 5* **19** (112), 302–316.

ICZN, 1999. *International Code of Zoological Nomenclature*; 4th ed. International Trust for Zoological Nomenclature, London, 306 pp.

Jebram, D. 1973. Stolonen-Entwicklung und Systematik bei den Bryozoa Ctenostomata. *Journal of Zoological Systematics and Evolutionary Research* **11** (1), 1–48.

Jebram, D. 1986. The ontogenetical and supposed phylogenetical fate of the parietal muscles in the Ctenostomata (Bryozoa). *Journal of Zoological Systematics and Evolutionary Research* **24** (1), 58–82.

Kraepelin, K. 1887. Die deutschen Süßwasser-Bryozoen. I. Anatomisch-systematischer Teil. *Abhandlungen aus dem Gebiete der Naturwissenschaften* **10** (9), 1–168.

Kraepelin, K. 1892. Die deutschen Süsswasser-Bryozoen. II. Entwickelungsgeschichtlicher Teil. *Abhandlungen aus dem Gebiete der Naturwissenschaften* **12** (1–2), 1–67.

Leidy, J. 1851. On some American fresh-water Polyzoa. *Proceedings of the Academy of Natural Sciences of Philadelphia* **5**, 320–322.

Marcus, E. 1934. Über *Lophopus crystallinus* (Pall.). *Zoologische Jahrbücher. Abteilung für Anatomie und Ontogenie der Tiere* **58**, 501–606.

Mukai, H. 1982. Development of freshwater bryozoans (Phylactolaemata), pp. 535–576. In: Harrison, F.W. and Cowden, R.R. (eds.) *Developmental biology of freshwater invertebrates*. Liss, New York.

Mukai, H., Terakado, K. and Reed, C.G., 1997. Bryozoa, pp. 45–206. In: Harrison, F.W. and Woollacott, R.M. (eds.) *Microscopic anatomy of invertebrates. Lophophorates, Entoprocta and Cycliophora*. Wiley-Liss, New York, NY.

Oda, S. 1959. Germination of the statoblasts in freshwater Bryozoa. *Science Reports of the Tokyo Kyoiku Daigaku, Section B* **9**, 90–132.

Oken, L. 1815. *Lehrbuch der Naturgeschichte. Dritter Theil. Zoologie. Erste Abteilung. Fleischlose Thiere*. Reclam, Leipzig, 842 pp.

Ostrovsky, A.N. Lidgard, S. Gordon, D.P. Schwaha, T. Genikhovich, G. and Ereskovsky, A.V. 2016. Matrotrophy and placentation in invertebrates: a new paradigm. *Biological Reviews* **91** (3), 673–711.

Pallas, P.S. 1768. Descriptio *Tubulariae fungosae* prope Wolodimerum mense Iulio 1768 observatae. *Novi commentarii Academiae Scientiarum Imperialis Petropolitanae* **12**, 565–572.

Potts, E. 1884. On *Paludicella erecta*. *Proceedings of the Academy of Natural Sciences of Philadelphia* **36**, 213–214.

Reinhard, V.V. 1881. Outline of the structure and development of freshwater bryozoans.

Proceedings of the Society of Naturalists at the Imperial Kharkov University **15**, 207–301. [In Russian]

Saville Kent, W. 1870. On a new polyzoan, '*Victorella pavida*' from the Victoria Docks. *Quarterly Journal of Microscopical Science* **10**, 34–39.

Schneider, D. 1959. Über den Mechanismus des phototropischen Knospenwachstums bei marinen Bryozoen. *Verhandlungen der Deutschen Zoologischen Gesellschaft* 239–247.

Schneider, D. and Kaissling, K.-E. 1964. Wachstum und Phototropismus bei Moostieren. *Die Naturwissenschaften* **51** (6), 127–134.

Smith, D.G. Werle, S.F. and Klekowski, E. 2003. The anatomy and brooding biology of *Pottsiella erecta* (Potts, 1884) (Ectoprocta: Gymnolaemata: Ctenostomata), with an expanded diagnosis of the Pottsiellidae. *Hydrobiologia* **490** (1), 135–145.

Vieira, L.M. Migotto, A.E. and Winston, J.E. 2014. Ctenostomatous Bryozoa from São Paulo, Brazil, with descriptions of twelve new species. *Zootaxa* **3889** (4), 485–524.

Notes

1 To our knowledge such a low number of tentacles for *Paludicella ariculata* has never been reported by anyone else. One of us (TS), who studied *P. articulata* from March till September in Austria never noticed any large tentacle variation, the average number of tentacles being 15–16. However, during these studies, gonads could not be observed and possibly the low tentacle numbers reported by Braem might be from ancestrulae.

2 Braem (Braem 1890b, p. 134) wrote "*Als ich vor 5$^1/_2$ Jahren einen Irrweg verliess und voll heisser Liebe, aber voll Zweifel an meiner Kraft, an das allgewaltige Werk der Natur trat, war er* [Carl Chun] *es, dessen entgegenkommende Güte meine Schritte gefördert und auf ihrer Bahn gefestigt hat*." ("When I left a wrong track five and a half years ago and came full of hot love, but full of doubt in my power to the all-powerful work of nature, he [Carl Chun] was it, who, with his amiable goodness, promoted my steps and strengthened them in their track.").

3 Braem (1888b, p. 503f) wrote "*Im Sommer 1886 begann ich auf Anregung meines verehrten Lehrers, Herrn Prof. Carl Chun, unsern heimischen Süßwasserbryozoen ein einstellendes Studium zuzuwenden,* [...]" ("In summer 1886, I started a thorough study of our native freshwater bryozoans at the suggestion of my revered teacher, Mr Prof. Carl Chun, [...]").

4 In an obituary for Carl Chun, Braem (1914a) stated: "*Nach der Expedition, also während des größten Teiles der Leipziger Zeit, habe ich nur noch brieflich mit ihm verkehrt*." ("After the expedition, thus for most of the Leipzig Period, I only communicated by letter with him.")

5 Braem (1888b, p. 504) wrote "*Da nun mittlerweile die Ergebnisse meiner Bemühungen in der jüngst erschienenen Arbeit von Herrn Prof. Kraepelin der Hauptsache nach bereits mitgetheilt sind, so beschränke ich mich hier auf die Angabe der Funde, über*

welche an jener Stelle noch nicht berichtet werden konnte." ("Now that the results of my efforts have mainly been communicated in the recently published work of Mr Prof Kraepelin, I restrict myself here to report the findings that have not been mentioned there."). In Braem (1890b, p. 5), he added: "*Neuerdings ist in Folge meiner Mittheilungen an Prof. Kraepelin in Hamburg der grösste Theil meiner Funde bekannt geworden, und ich selbst habe in einem im Zoolog. Anzeiger v. J. 1888 Nr. 288 veröffentlichten Bericht das noch Fehlende nachgetragen*." ("Lately, as a result of my messages to Prof. Kraepelin in Hamburg, most of my findings have become known, and I myself have added the remainder in a published report to the Zoolog. Anzeiger anno 1888 nr. 288.").

6 Braem (1893c, p. 14) concludes: "*Die Polemik Kraepelins zu charakterisiren, ihren Werth, ihre Tragweite zu ermessen, das war der Zweck dieser Zeilen. Die Polemik Kraepelins in ihrer wissenschaftlichen Hinfälligkeit zu beleuchten, das war ich der Sache, das war ich denjenigen schuldig, die meiner Arbeit die Wege geebnet haben. Ich selbst sehe dem Urtheil der Zukunft mit vieler Ruhe entgegen*. [...] *Und eben dies bürgt dafür, dass der Kampf ums Dasein, der in der Wissenschaft so gut wie im praktischen Leben gekämpft wird, doch wohl am Ende ein Kampf um die Wahrheit bleibt*." ("To characterize the polemics of Kraepelin, their value, to balance their consequences, this was the purpose of these lines. Illuminating Kraepelin's polemics in their scientific weakness, this I owed to the subject, this I owed those who paved the way for my work. I myself look with much tranquillity forward to the future judgement. [...] And it is this, what guarantees that the struggle for existence, which is fought in science as good as in the daily life, remains a struggle for the truth after all.").

7 Braem (1939, p. 267).

8 Zooids are able to protrude their lophophore.

9 Braem (1939, p. 278) wrote "*Ich sehe in* Victorella Sibogae *Harmer nicht nur den Vertreter einer neuen Gattung, sondern auch den einer neuen Familie, die in die Nähe der Cylindroeciiden zu stellen sein dürfte. Für die Gattung schlage ich den Namen Sundanella vor*." ("I see in *Victorella Sibogae* Harmer not only the representative of a new genus, but also of a new family, which might be closely related to the Cylindroeciidae. For the genus, I suggest the name *Sundanella*.").

10 Jebram (1973, p. 39).

11 Hasenbank (1932, 319).

An overview on freshwater bryozoan research in Lithuania

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1. Introduction

Freshwater bryozoans are among the most fascinating invertebrate animals, although many aspects of their ecology, physiology and development are still poorly understood (Wood 2005). The most recent published inventory shows 21 species of freshwater bryozoans in Europe (Woss, 2013), with a number of these species being recorded in countries bordering Lithuania (Latvia, Estonia, Poland, and Belarus). From Lithuania what little is known about bryozoans comes mostly from field work conducted during 1931–1933 by Brone Pajiedaite. This work culminated in a Master's thesis in which 7 freshwater bryozoan species were described (Pajiedaite 1933). Since that time no further studies in Lithuania have been conducted on this animal group.

This review article has two aims: (1) to collect and review all available information related to the Lithuanian bryozoans, emphasizing the importance of the bryozoans in ecosystems and human life; and (2) to declare that bryozoan research Lithuania has restarted.

Figure 1. Brone Pajedaite and Veronika Zvironaite (Photograph courtesy of the Jewish Museum in Vilnius, Lithuania).

2. Biography of Brone Pajiedaite

Born in 1910, Brone Pajiedaite studied biology and dentistry in two faculties of Vytautas Magnus University. In addition to her work with freshwater bryozoans, she also prepared for a career in dentistry. Friends described her as a dynamic woman with a strong personality. During the WWII Brone Pajedaite, together with other members of Lithuanian academic community Petronele Lastiene and Veronica Zvironaie, participated in the rescue of Jewish children (Kultura, 2011) (Figure 1). In 1945 they were arrested by the Soviets, being part of a group of Lithuanian activists who had signed a petition for Lithuanian independence. Petronele and Veronika were deported to Siberia. Brone Pajedaite was imprisoned and is reported to have died there after about a year. On July 30, 2000, Yad Vashem recognized Brone Pajedaite, Petronele Lastiene and Veronika Zvironaite as "Righteous Among the Nations" (http://www3.lrs.lt/docs2/WPSGXTXP.PDF).

3. Review of Brone Pajiedaite's Masters Research

Brone Pajiedaite studied freshwater bryozoans in Lithuania during 1931–1933. What prompted her to undertake this work is not known. References in the thesis include several popular works on freshwater biology, and these may have inspired her to seek out bryozoans. She also acknowledges support from her thesis advisor, Tadas Ivanauskas, the most prominent zoologist in Lithuania, although his broad interests were more focused on vertebrates (eg. Ivanauskas 1957).

In any case, Brone Pajiedaite collected freshwater bryozoans from widely scattered locations in Lithuania, including lakes, ponds, and rivers (Figure 2). She worked along shorelines as well as swimming from a boat. Some sites were revisited during the second year and any changes were noted. In 1931, for example, she found *Paludicella reticulata* growing on leaves of the yellow water lily (*Nuphar lutea*) and water lilies (*Nymphaea alba*), but the bryozoan had disappeared by 1932. Pajiedaite concluded that the cause may be related to changing environmental conditions.

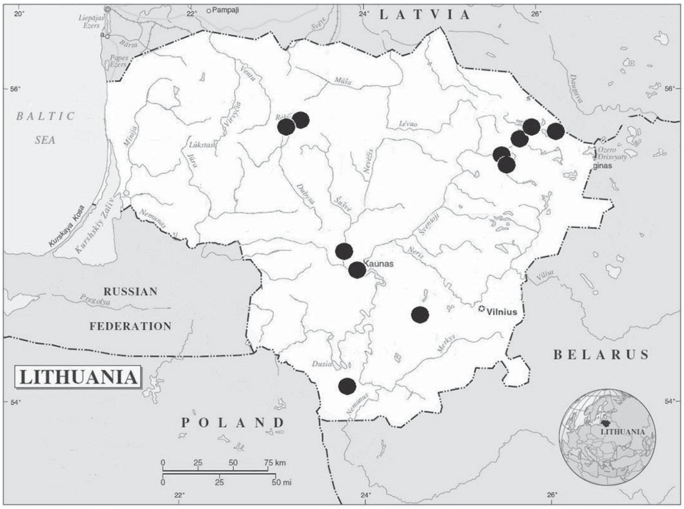

Figure 2. Bryozoan collection sites in Lithuania visited by Brone Pajiedate (1931–1933).

Figure 3. Photo from a representative slide in the Pajiedaite collection showing two plumatellid zooids with developing sperm on the funiculi and an ovary (circled). To our knowledge this is the first and only photograph of a phylactolaemate ovary, which is transitory and seldom seen.

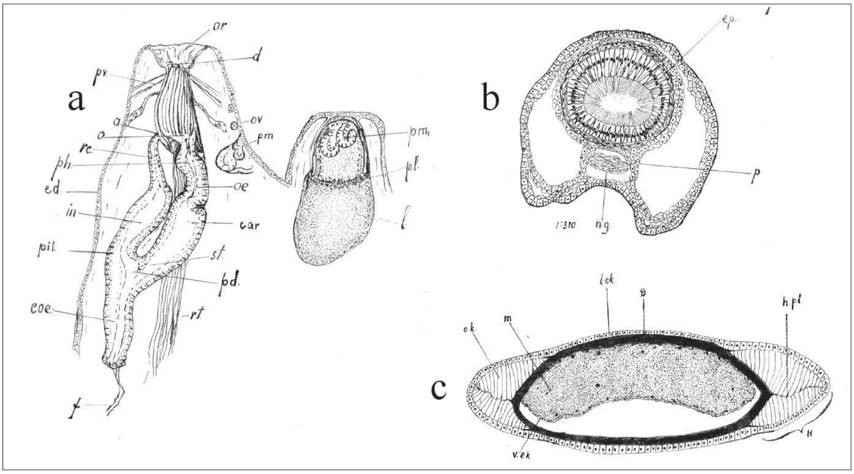

Figure 4. Composite of representative drawings made from sectioned material collected by Brone Pajiedaite. (a) Gut anatomy and developing larva in Plumatella fungosa*; (b) cross section of a plumatellid zooid just below the lophophore showing esophagus and neural ganglion; (c) lateral section of a plumatellid statoblast. (Modified from Pajiedaite, 1933).*

Field specimens were anaesthetized with cocaine and fixed in formalin or alcohol. Back in the laboratory, Pajiedaite recorded observations of living material from an aquarium. She also made permanent microscope mounts of sectioned bryozoan specimens stained with fuchsine, rubin S., haemotoxylin, eosin or haematoxylin- eosin (Figures 3-4).

Altogether Brone Pajiedaite identified seven freshwater bryozoan species, including almost all the species known in Europe at that time. She realized, however, that her collection was still too limited for a thorough assessment of the Lithuanian freshwater bryozoan fauna. After two years of her survey, she had still not found *Fredericella sultana* or *Lophopus crystallinus*, which were known to occur in neighbouring countries.

Good sources of information were apparently not easily accessible. Brone seemed to rely heavily on the broad overviews by Braem (1914) and Marcus (1925). She also referenced an obscure Kraepelin (1902) work, but not Loppens, Borg, or Abricosov, who were publishing at that time, nor any of the classic works of the 19th Century, eg. Kraepelin (1887). Exactly at the time of Pajiedaite's work in Lithuania, Mary Rogick was just learning about bryozoans on Lake Erie in the USA. Adriana Vorstman's studies of Indonesian phylactolaemates had been published several years earlier but were unknown to Pajiedaite.

Listed below are the species that were collected and described by Brone Pajiedaite. Most of these were, in her words, "monitored live through a microscope to make characteristic drawings ", some of which are presented here (Figure 5). Brone provided descriptions of all species, including morphological variations, drawings of statoblasts (Figure 6). She also characterized the substrates on which the colonies were most commonly found and provided locality data.

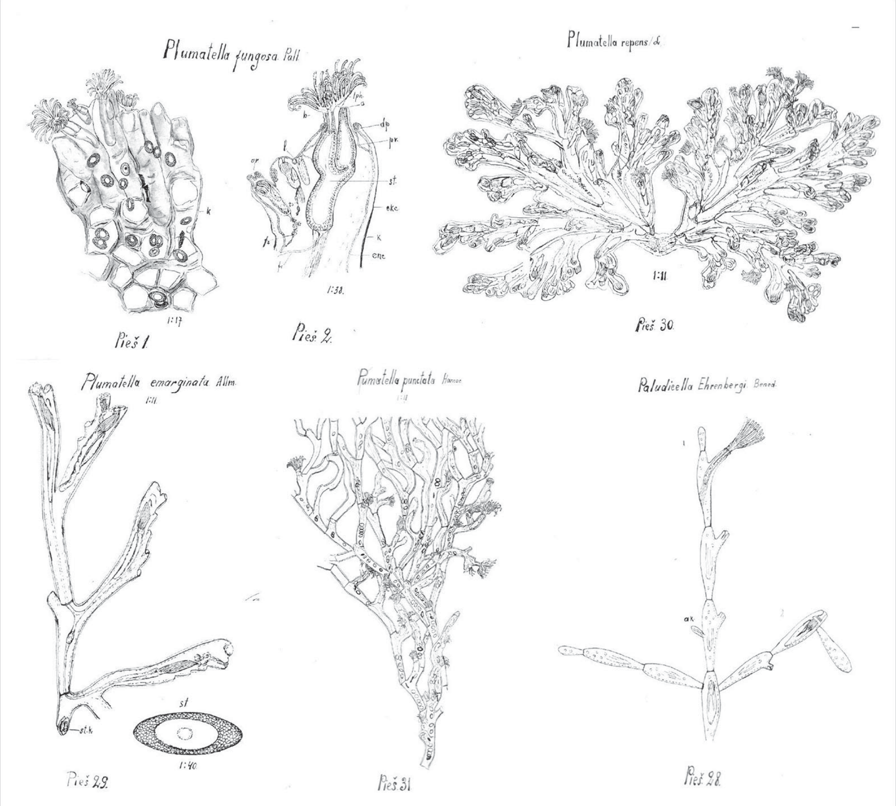

Figure 5. Composite of line drawings made by Brone Pajiedaite from her specimens collected in Lithuania. (Modified from Pajiedaite, 1933).

Cristatella mucedo Cuvier, 1798

This species was found in Aukatadvaris Lake and Veravos Bogs (Kaunas district) and was also quite common in southern Lithuania. In 1931, it was found abundantly in the Satarecius Pond. Pajiedaite stated that colonies had only immature statoblasts during June and July, but mature statoblasts could be seen in August and September. Pajiedaite noted that statoblasts of this species varied significantly in size among different habitats.

Plumatella fungosa (Pallas, 1768)

According to Pajiedaite this species is common in Lithuania (Figure 4). It was found in Utenos district (Lake Kunigiakiai) and Kaunas district (port Kaunas city and Nevezis River near Raudondvaris). Pajiedaite found that *P. fungosa* prefers standing water and shallow areas, where the water is often not very clean and clear. For example, she noted *P. fungosa* colonies in the old port of Kaunas, where the water was contaminated with steamship oil. Colonies could be found on a variety of submerged substrates, including tree branches (*Alnus; Salex*), roots, reeds (*Juncus*), cattails (*Phragmites*), shells (*Anadonta, Dreissena*), and stones.

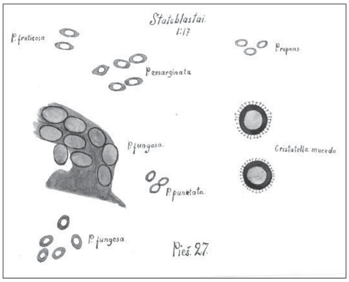

Figure 6. Drawings of statoblasts collected in Lithuania by Brone Pajiedaite (from Pajiedaite, 1933.)

Plumatella repens (Linnaeus, 1758)

Pajiedaite referred to *P. repens* as one of the most common bryozoan species (Figure 5) in Lithuania, occurring in lakes, rivers, small streams, ponds, and hollows. In contrast to *P. fungosa, P. repens* preferred cleaner and more flowing water. Colonies seemed to occur mostly on submerged macrophytes.

Plumatella emarginata Allman, 1844

This species (Figure 4) was reported in Utena District (Lake Paatis, Satarecius Pond), Kaunas District, Sauliai District (Dubysa River), and Lazdijai District (Lake Snaigynas). Colonies of *P. emarginata* were found growing on submerged logs, stones, and mollusc shells (*Viviparus, Dreissena*). The study described statoblasts of this species. Colonies of *P. emarginata* were compared with the very similar *P. repens*, highlighting the differences. In Pajiedaite's mind, however, there may have been some confusion regarding this species. Her drawing labelled as *P. emarginata* (Figure 5) appears instead to be *Plumatella fruticosa*, with characteristic stumps on a free branch where fragments have broken off.

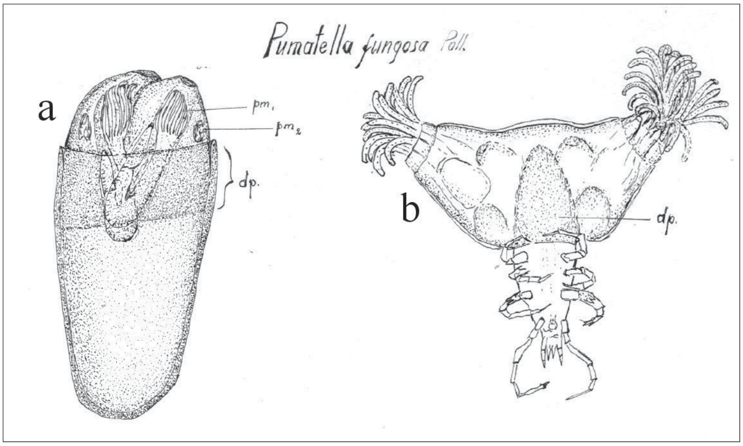

Figure 7. Larvae of Plumatella fungosa. *(a) Early stage of settlement with mantle starting to pull back from the zooids; (b) Larva having settled on the abdomen of a water mite. (Modified from Pajiedaite, 1933).*

Plumatella fruticosa Allman 1844

This species was found in only two locations: River Dubysa (Siauliai district.) and pond Satarecius (Utena district).

Hyalinella punctata (Hancock, 1850)

Brone Pajiedaite referred to this species by its original name, *Plumatella punctata*. She discovered it in Jatkuniskio lakes (Zarasai district) and the River Dubysa (Siauliai district) on the leaves of yellow water-lily (*Numphar lutea*).

While conducting her survey of freshwater bryozoans, Brone Pajiedaite noted how bryozoan distribution may be influenced by water temperature, cleanliness, and vegetation. For example, she realized that in Central Lithuania (around Kaunas) the temperature was a few degrees higher than in the eastern part of the country (around Dusetos). Possibly as a result, *Paludicella* was found only in the eastern and northern parts of Lithuania; *Cristatella mucedo* occurred only in the central and southern part of Lithuania, while species of the genus *Plumatella* were prevalent everywhere.

Brone Pajiedaite made notes on bryozoan associations with other organisms, such as sponges, molluscs, and rotifers. She often found bryozoans colonies gnawed by snails (*Planorbis, Lymnea*), and she mentioned that larvae can easily settle on other organisms. One of her illustrations shows a young larval colony of *P. fungosa* growing on a water mite (Figure 7).

In the course of her studies, Brone Pajiedaite prepared at least 70 microscope slides (Figure 3) and an unknown number of whole specimens. Unfortunately, the whole specimens were apparently destroyed during World War II (1941–1945).

4. Bryozoan research in Lithuania after 82 years

No bryozoan research has occurred in Lithuania since 1933, and for nearly 82 years there has been no information about them! In 2007, scientists from the Vytautas Magnus University (Prof. Vida Mildaziene and Sarunas Asmantas) made a popular science video about bryozoans (https://vimeo.com/25460026). So far, based on unpublished data from various expeditions in Lithuania, we found several species of bryozoans: *Cristatella mucedo* (in lakes Plateliai, Peraokanas, Snaigynas), *Plumatella repens* and *Plumatella fungosa* (in ponds in surrounding of Kaunas) mentioned in Brone Pajiedaite's study (Figure 8). It should be noted that the authors of this paper will begin to systematically investigate bryozoans from Lithuania, and the first step is to carry out a revision of freshwater bryozoan species in those localities studied by Brone Pajiedaite during 1931–1933.

5. Bryozoan expected to occur in Lithuania

Bryozoan species found in countries neighboring Lithuania are characteristic of

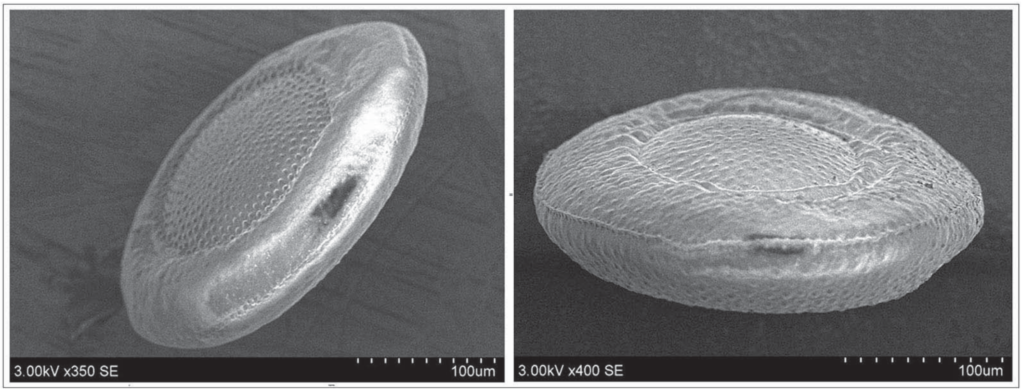

Figure 8. SEM micrographs of the free statoblasts of Plumatella repens *(left) and* Plumatella fungosa *(right) from recent collections in Lithuania. (Photos by Simona Tuckute).*

Europe, but of course the total number of species is now much higher than those recorded by Brone Pajiedaite in 1931–1933. For example, although Pajiedaite did not find *Fredericella sultana* in Lithuania, it has been reported from both Latvia and Estonia (Wöss, 2013). Other species have been discovered or introduced to eastern Europe since 1933, including *Plumatella bombayensis* Annandale, 1908 in Belarus (Wood & Okamura 2005), *Internectella bulgarica* Gruncharova, 1971 in Bulgaria (Gruncharova 1971), *Pectinatella magnifica* (Leidy, 1851) in Poland, Romania, Czech Republic and elsewhere (Balounová *et al*. 2013), and *Plumatella casmiana* Oka, 1907 in Poland, Austria, and Bulgaria (Massard & Geimer 1995). Other species likely to be found in Lithuania are listed by Wood & Okamura (2005), including *Lophopus crystallinus* (Pallas, 1768), *Plumatella geimermassardi* Wood & Okamura, 2004, and possibly even *Plumatella rugosa* Wood *et al*. 1998, *Plumatella reticulata* Wood, 1988, and *Fredericella indica* Annandale, 1909. So it is clear that the Lithuania bryozoan species list is likely to expand and that much future research remains to be done.

Acknowledgments

The authors are grateful to the Dr Andrius Petruskevicius of Vilnius University, for providing the historical document – B. Pajiedaite Master's thesis and to Professors Vaiva and Vita Lesauskaites of Lithuanian University of Health Sciences for the biographical information about her aunt, Brone Pajiedaite.

References

Balounová, Z., Pechousková, E., Rajchard, J., Joza, V. and Sinko, J. 2013. World-wide distribution of the Bryozoan *Pectinatella magnifica* (Leidy 1851). *European Journal of Environmental Sciences* **3**(2), 96–100.

Braem, F. 1914. Die Knospung von *Paludicella*. *Archiv für Hydrobiologie und Planktonkunde*, Stuttgart, n.s., **8**, 527–549.

Ivanauskas, T. 1957. Lietuvos pauksciai. Vilnius, Valstybine politines ir mokslines literatukros leidykla.

Gruncharova, T. 1971. *Internectella bulgarica* nov. gen. nov. sp. a new bryozoan species (Bryozoa, Phylactolaemata). *Comptes rendus de l'Académie bulgare des Sciences* **24**(3), 361–364.

Kraepelin, K. 1887. Die Deutschen Süßwasserbryozoen. I. Anatomisch-systematischer Teil. *Abhandlungen aus dem Gebiet der Naturwissenschaft hrsg. vom Naturwissenschaft Verein, Hamburg* **10**, 1–168.

Kraepelin, K. 1902. *Naturstudien in Wald und Feld: Spaziergangs-Plaudereien. Ein Buch für d. Jugend. Mit Zeichnungen von O. Schwindrazheim*. Teubner.

Kultura [Culture: Art Science Literature] (2011). Nr. **47**, (158) (in Lithuanian)

Marcus, E. 1925. Bryozoa. In: P. Schulze (ed.): *Biologie der Tiere Deutschlands*, Lieferung 14, Berlin, 1–46.

Massard, J.A., and Geimer, G. 1995. On the distribution of *Plumatella casmiana* in the European and Mediterranean parts of the Palaearctic region (Bryozoa, Phylactolaemata). *Bulletin de la Societe des naturalistes Luxembourgeois* **96**, 157-–165.

Pajiedaite, B. 1933. Indelis ir Lietuvos geluju vandenu samangyviu (Bryozoa) tyrinejima [Contribution to the Research of Freshwater Bryozoa in Lithuania]. Master's Thesis, Vytautus Magnus University, Kaunas, Lithuania, 77 pp.

Wood, T. and B. Okamura. 2005. *A new key to the freshwater bryozoans of Britain, Ireland, and Continental Europe, with notes on their ecology*. Freshwater Biological Association **63**, Ambleside, UK.

Wöss, E. 2013. Bryozoa. Fauna European. Version 2.6, http://www.faunaeur.org

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 efficiency[1] 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 salamanders[6]) 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 clades[13] (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 interactions[30] 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 autozooid 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 fontal 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 zooid-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 *Hippothoa*
	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 *Steginoporella*
Reproductive zooid	male	none	var. in T#, non-feeding	no	yes?	*Odontoporella bishopi*
		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	*Haplopoma sciaphilum*
Avicularium	vicarious	enlarged mandible, distal tapering, etc.	vestigial	yes/no	yes/no	many taxa
	interzooidal		vestigial	yes/no	no	most *Micropora*
	interzooidal vibracular		vestigial	yes/no	no?	*Setosella*
	adventitious		vestigial	no	no	*Chaperiopsis*
	adventitious vibracular		vestigial	yes/no	yes/no	many Candidae
Kenozooid	space filler - determinate	various	absent	yes/no	yes/no	*Spiralaria florea*
	space filler - indeterminate	stochastic changes	absent	yes/no	yes/no	many taxa
	spiniform	various	absent	yes/no	no	*Bellulopora*
	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.

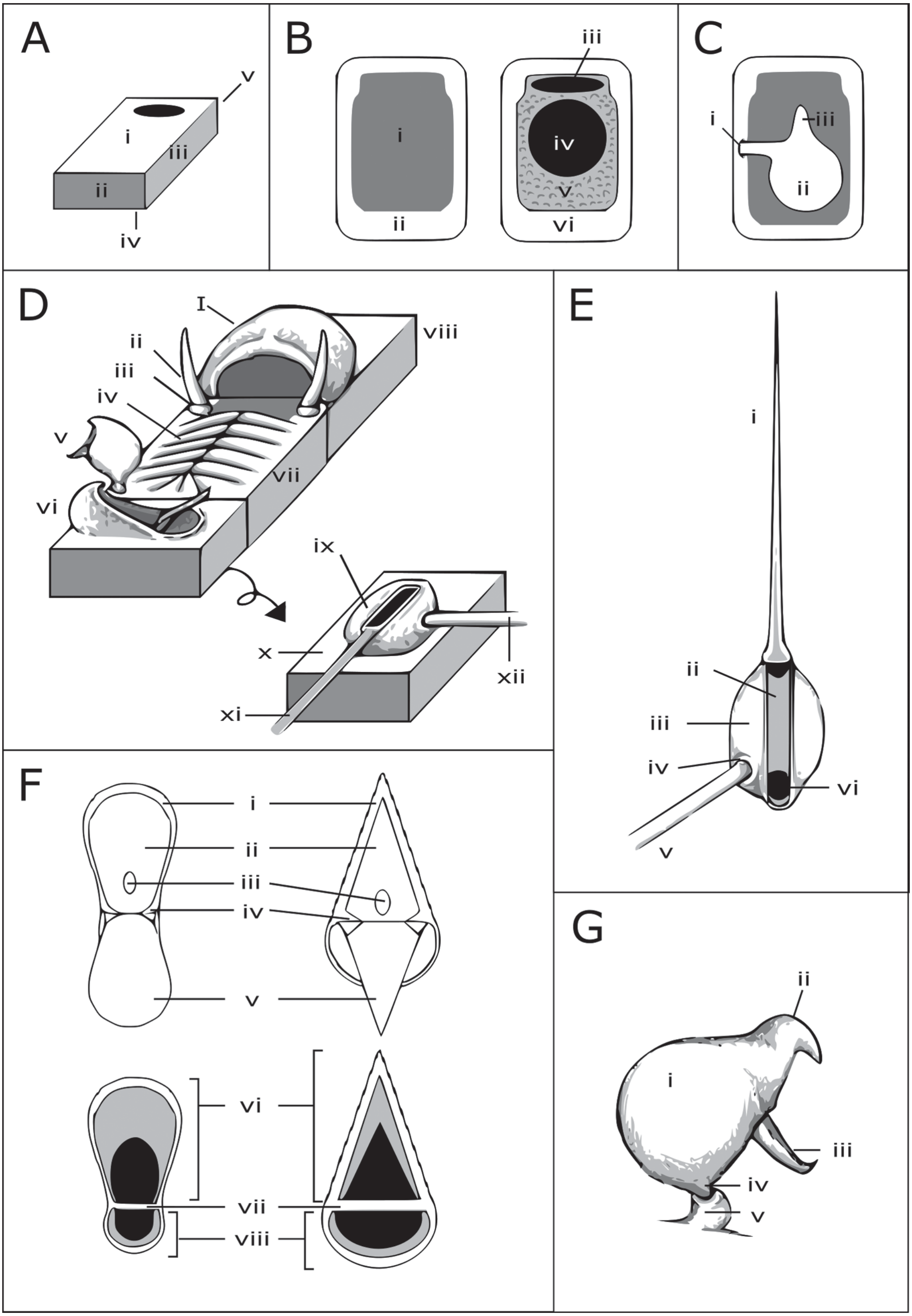
If colonies are monocormidial, then the arrangement of primary modules into higher-level structures is fairly simple (Figure 2D-F). If the colony is nonbranching then the secondary module is the entire colony, while in branching colonies, the secondary modules are branches that repeat within the tertiary 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], spines[69] and ovicells[70]) 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, ooecia, 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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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

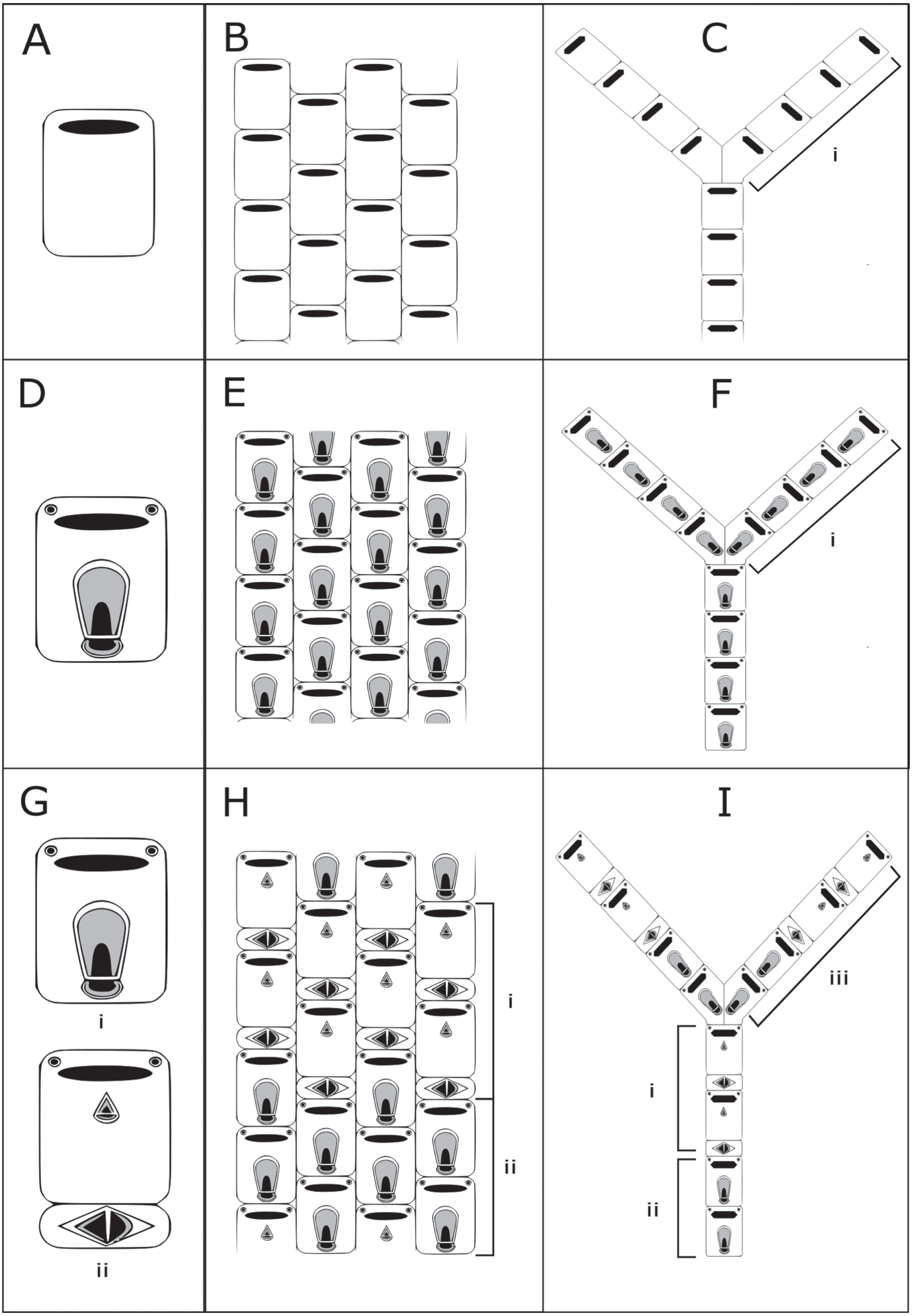
2.1 AVICULARIA

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 autozooid. 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. Frontral surface** *i. membranous frontal wall, ii. calcifed 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. ooecium 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 zooid, viii. distal daughter zooid, 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 skeleterized 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 autozooid.*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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)

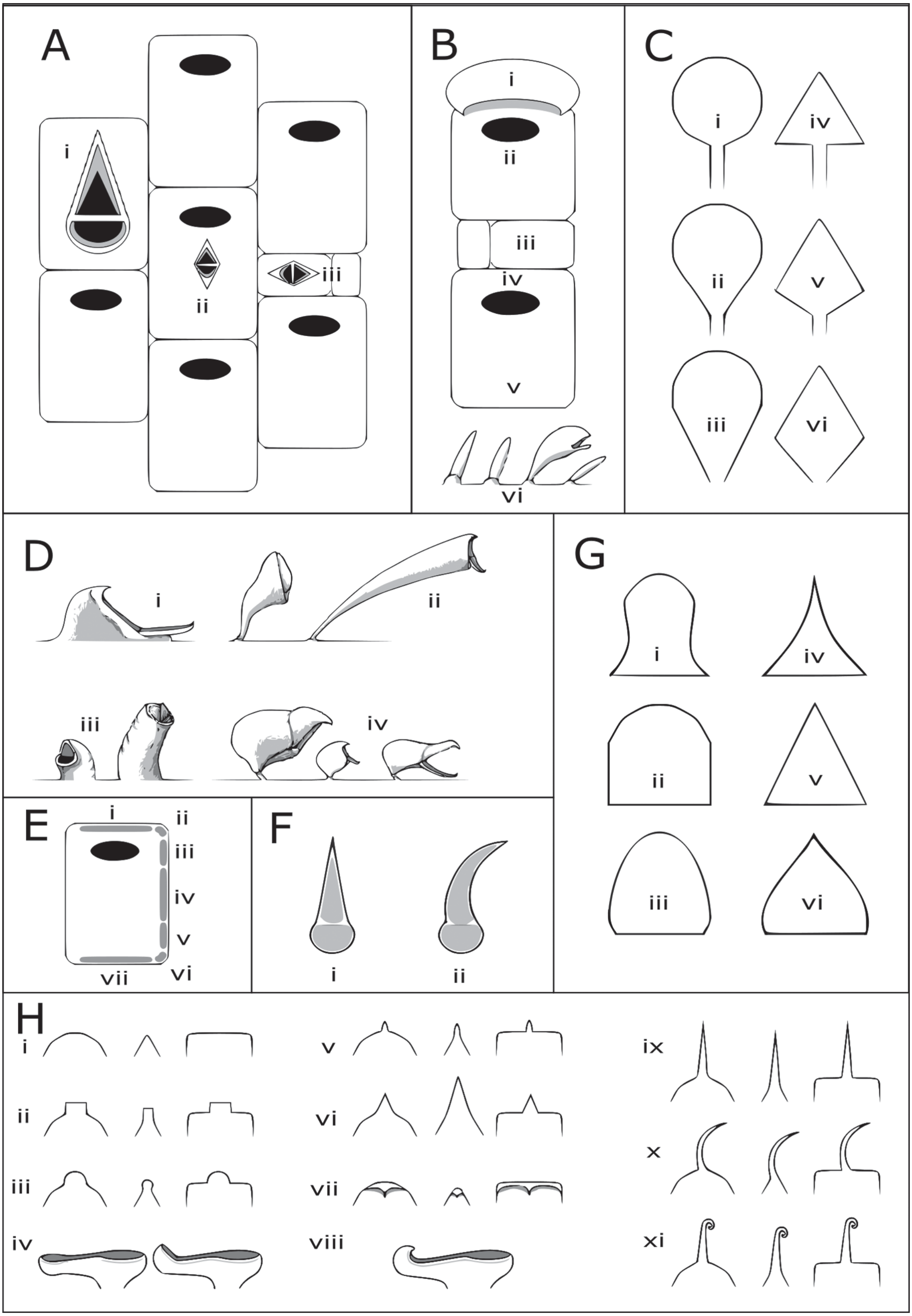
- *Relative Location*: Location relative to other morphological features of the parent autozooid (Figure 3B).

- *Hyper-oral:* Located next to orifice, distally
- *Sub-oral:* Located next to orifice, proximally
- *Spine substitute:* Replaces spine in series
- *Ovicell:* Associated with the ooecium 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 posesses 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.*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- *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.

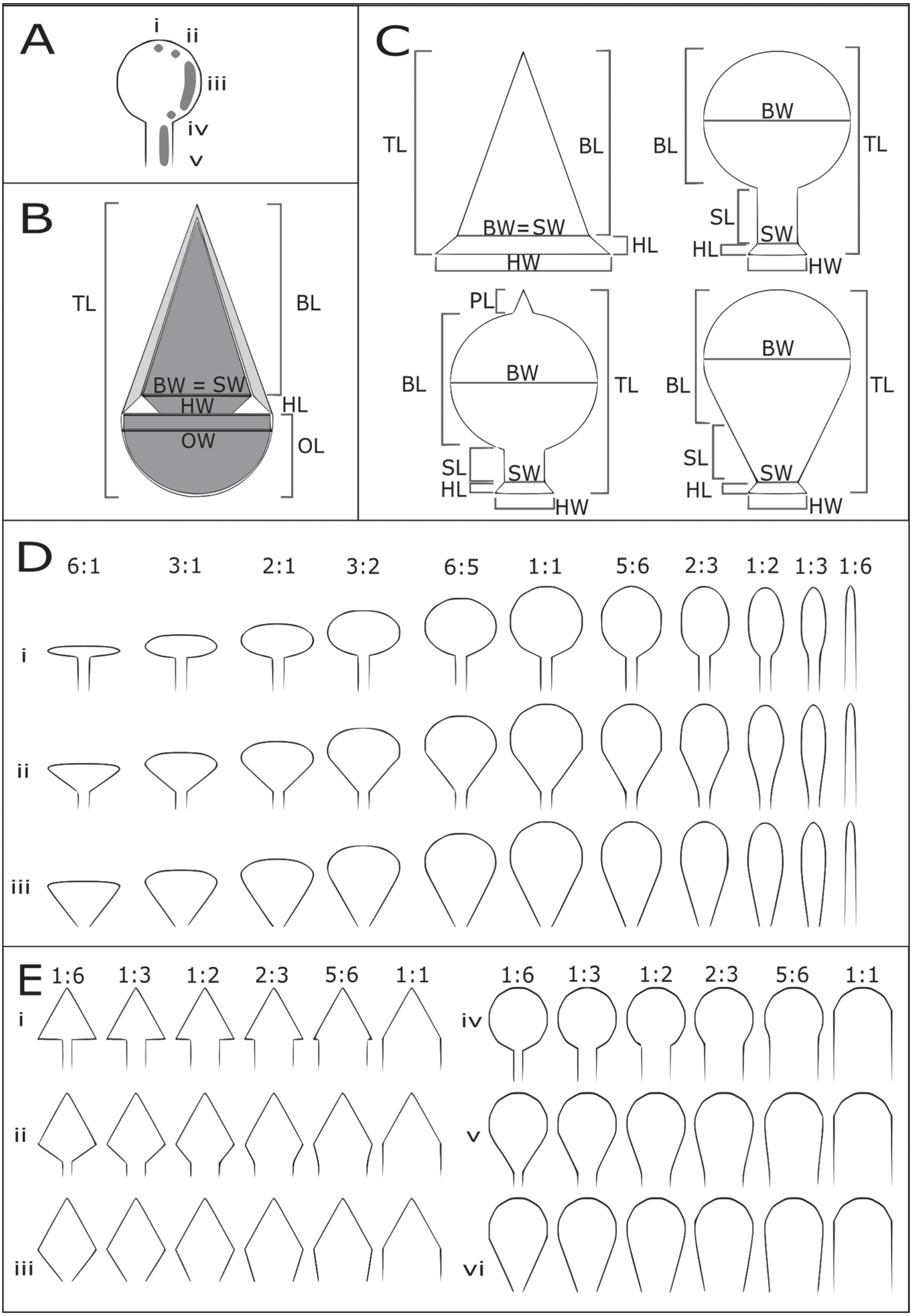
- Distal (0)
- Distolateral (1)
- Lateral (2)
- Proximolateral (3)
- Proximal (4)

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.*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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.

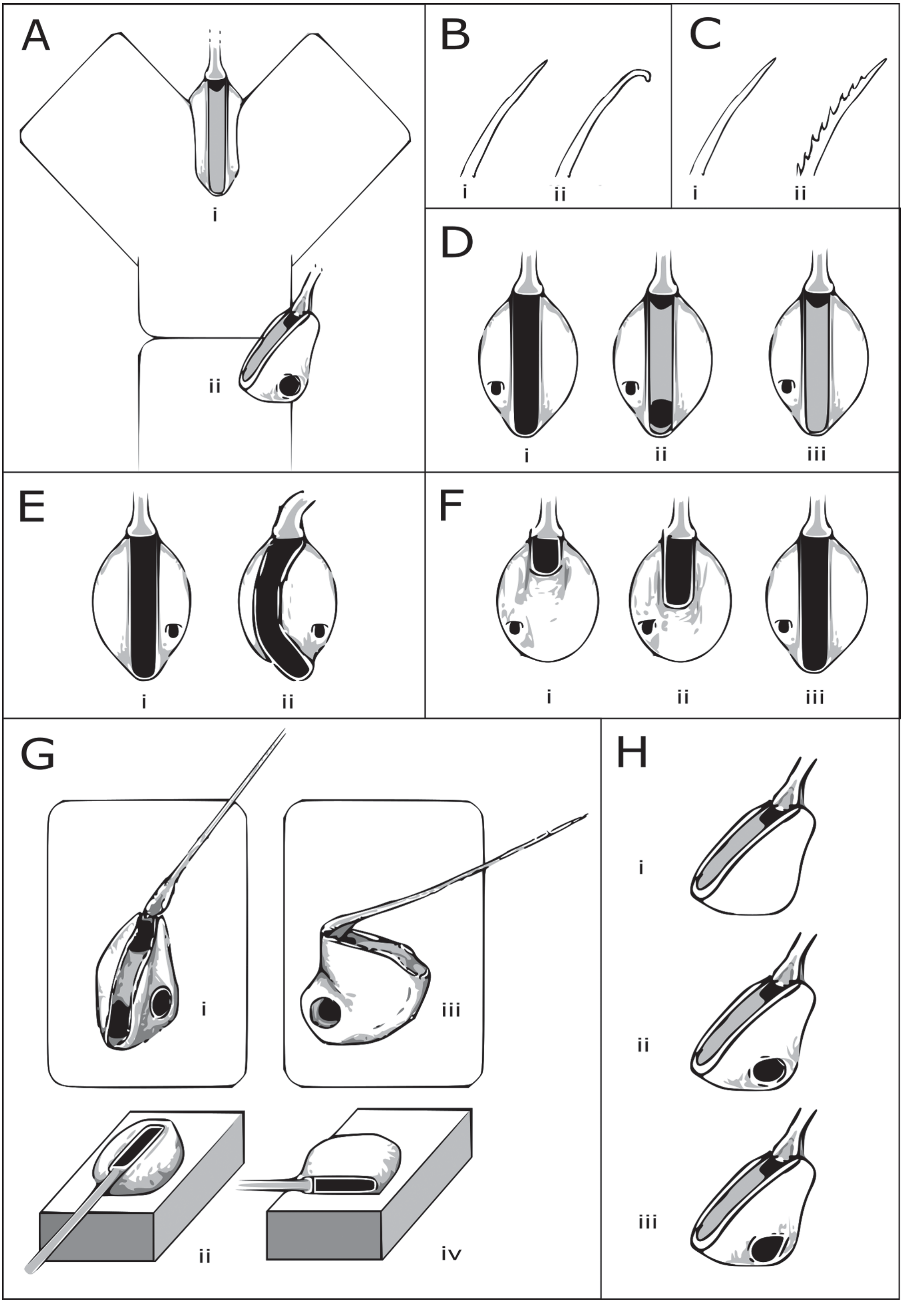
- *None:* No spikes are present on cystid of the avicularium
- *Simple:* Spikes are unbranched
- *Branching:* Spikes are branched
- *Mixed:* Unbranched and branching spikes are present on cystid of the avicularium

- *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 $^1/_4$ the length of the gymnocyst, but not flush with the frontal surface ($0 < x \leq {}^1/_4$)
- *Intermediate (2):* Elevation is between $^1/_4$ and $^1/_2$ the length of the gymnocyst ($^1/_4 < x \leq {}^1/_2$)

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.*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- *Long (3):* Elevation is between $^1/_2$ and 1x the length of the gymnocyst. ($^1/_2 < x \leq 1$)
- *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

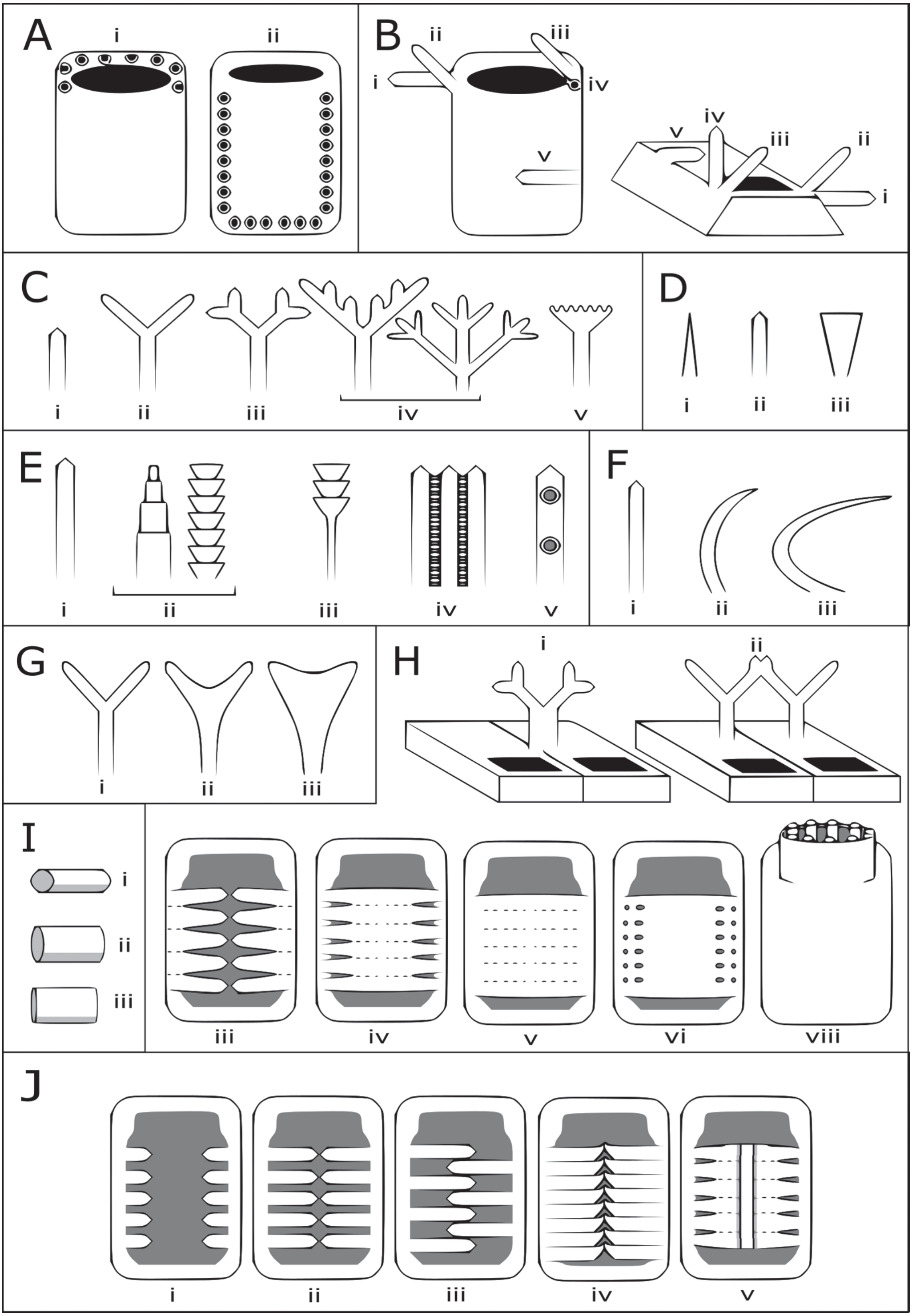
- Bulb Shape: The shape of the bulb (the main part of the mandible/rostrum, sometimes separated from the hinge by a stem), ignoring any projections.

- *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.*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- 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

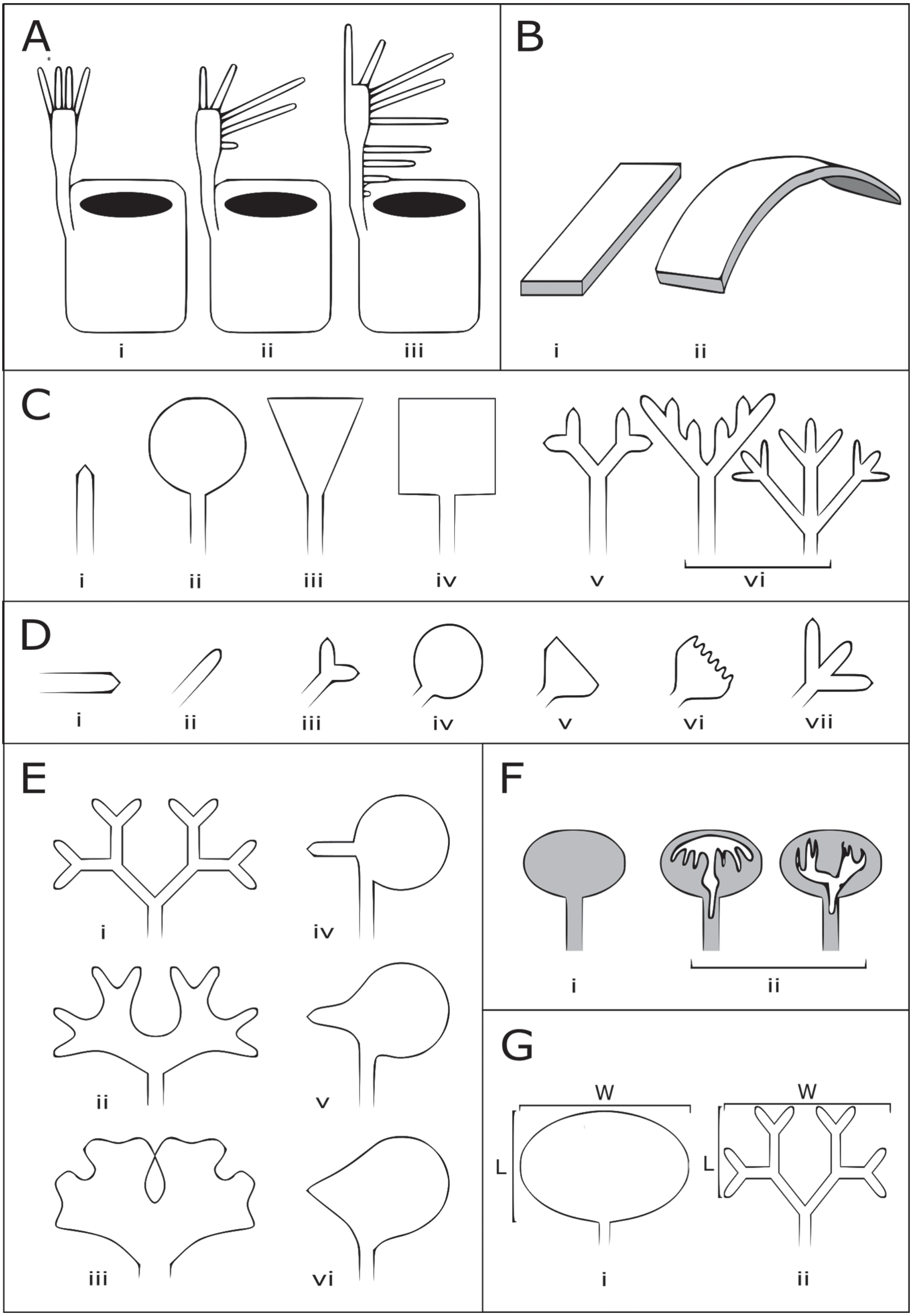
- Teeth**:** Very small, short, spine-like projections that are repeated along the edges of the mandible/rostrum.

- *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*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  - *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

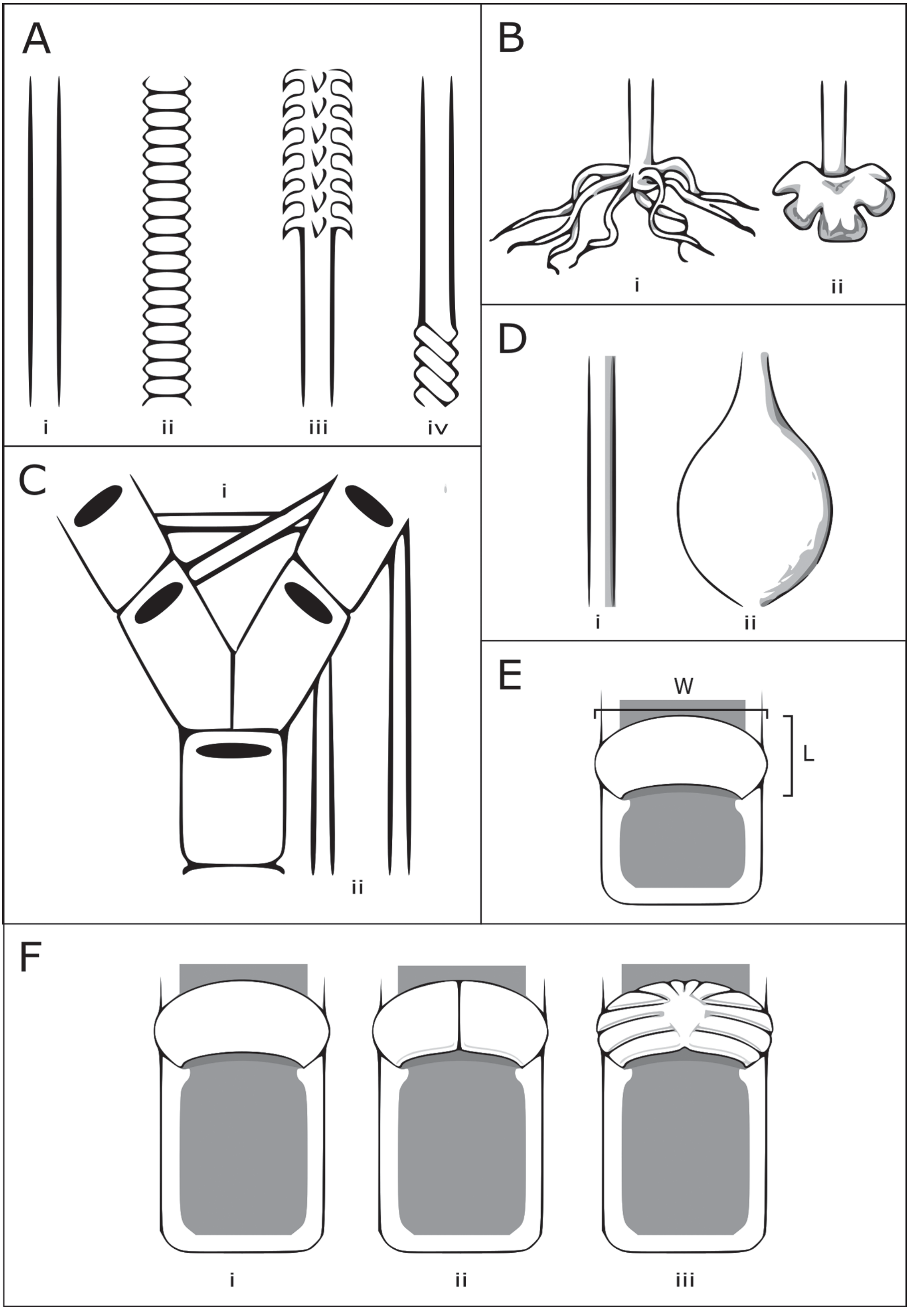
Vibracula are adventitious avicularia with extreme morphology. The mandible/ rostrum is very long, and their hinge structure allows the mandible/rostrum to rotate over the surface of the colony (unlike avicularia which can only swing in one plane[82,83]). (Figure 1E for anatomical descriptions.)

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.*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- 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 1/4 the length of vibraculum
- *Intermediate (1):* Groove length between 1/4 and 1/2 the length of vibraculum
- *Long (2):* Groove length is between 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 Silén[84]) 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

- Opesial: 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°), pointing towards midline
- *Erect (2)*: Spine perpendicular to frontal surface of the zooid
- *Obtuse (3)*: Spine angled above frontal surface of the zooid (>90°), 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 ≈ minor axis)
- *Somewhat flattened (1):* Spine cross-section is elliptical (major axis > minor axis)
- *Flattened (2):* Spine cross-section narrowly elliptical (major axis >> 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 $^1/_4$ the length of the gymnocyst
- *Intermediate (1):* Spine length is between $^1/_4$ and $^1/_2$ the length of the gymnocyst
- *Long (2):* Spine length is between $^1/_2$ 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 $^1/_8$ the width of the gymnocyst
- *Intermediate (1):* Base width of the spine base is about $^1/_8$ the width of the gymnocyst
- *Thick (2):* Base width is about $^1/_5$ the width
- *Very thick (3):* Base width is greater than $^1/_5$ 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 can 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 1/8 the width of the gymnocyst
- *Intermediate (1):* Base width is about 1/8 the width of the gymnocyst
- *Thick (2):* Base width about 1/5 the width of the gymnocyst
- *Very thick (3):* Base width greater than 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 rhizozooids, 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 ooecium enclosing a brooding cavity. The ooecium is a body-wall outgrowth formed from the distal daughter zooid in most cases.[96,97] Spines provided by the distal daughter evolved into ooecia 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 ooecium 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 (ooecial vesicle) or autozooidal operculum, or both.

In some cheilostomes (Tendridae, Scrupariidae, Thalamoporellidae, Alysidiidae, and Belluloporidae), the skeletal parts of independently evolved ooecia-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 ooecium-contributing distal daughter makes ovicells difficult to describe in cormidial terms. This if 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.

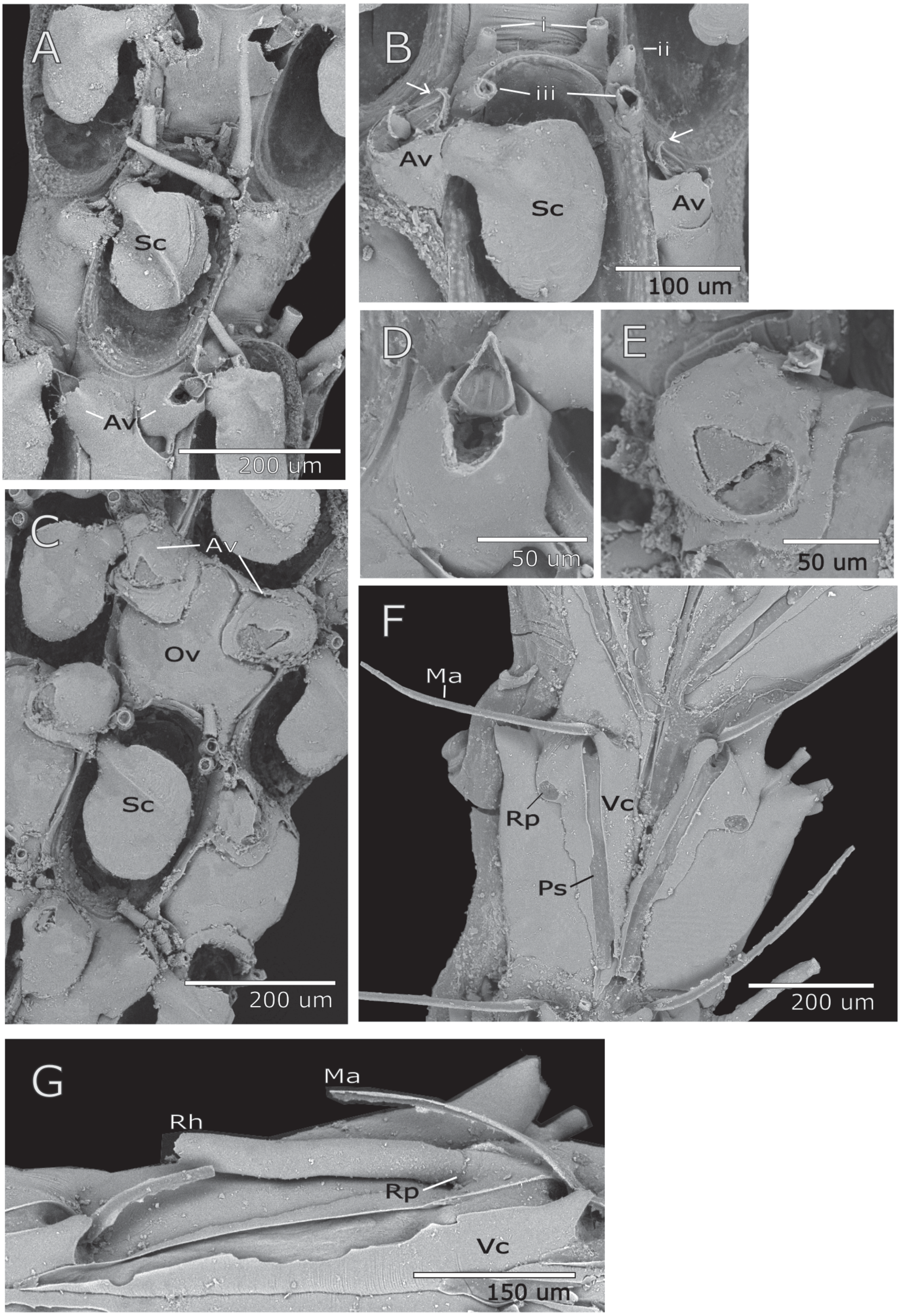
Ooecium Structure: This examines the number of parts that constitute the ooecium (Figure 8F). Note that this is not based on the number of parts that the ooecium was derived from evolutionarily, but the appearance of the derived structure.

- *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.*


A
Sc
Av
200 um
B
i
ii
iii
Av
Sc
Av
100 um
D
50 um
E
50 um
C
Av
Ov
Sc
200 um
F
Ma
Rp
Vc
Ps
200 um
G
Ma
Rh
Rp
Vc
150 um

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 Collection[101] 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**
Avi	2	Frontal	Gymnocyst	4	3
Avi (ovi)	2	Frontal	Ovicell	1	1
Avicularium	**Variable Direction**	**Attachment**	**Spikes**	**Spike Abundance**	**Elevation**
Avi	0	Columnar	None	0	1
Avi (ovi)	0	Columnar	None	0	1
Avicularium	**Overall Shape (Rostrum)**	**Bulb Shape (Rostrum)**	**Curvature (Rostrum)**	**Tapering (Rostrum)**	**Bulb Outline (Rostrum)**
Avi	0	0	0	0	1
Avi (ovi)	0	0	0	0	1
Avicularium	**Bulb Tip (Rostrum)**	**Projection Shapes (Rostrum)**	**Projection Location(s) (Rostrum)**	**Teeth (Rostrum)**	**Teeth Location (Rostrum)**
Avi	Pointed	None	None	None	None
Avi (ovi)	Rounded	None	None	None	None
Avicularium	**Overall Shape (Mandible)**	**Bulb Shape (Mandible)**	**Curvature (Mandible)**	**Tapering (Mandible)**	**Bulb Outline (Mandible)**
Avi	0	0	0	0	1
Avi (ovi)	0	0	0	0	1
Avicularium	**Bulb Tip (Mandible)**	**Projection Shapes (Mandible)**	**Projection Location(s) (Mandible)**	**Teeth (Mandible)**	**Teeth Location (Mandible)**
Avi	Pointed	Hooked	Bulb (mid-distal)	None	None
Avi (ovi)	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 ooecium 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, ~8 x10^9 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 hierarchy [105]

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 concurrently[116], 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

1 De Duve 1995 in Knoll and Bambach note 7, and Wagner 1996 in Caroll, note 8.

2 Gould 1996 in Knoll and Bambach note 7, and Gould 1998 in Caroll, note 8.

3 W.R. Jeffery, A.G. Strickler, and Y. Yamamoto. "To see or not to see: Evolution of eye degeneration in Mexican blind cavefish." *Integrative and Comparative Biology* 43 (2003): 531–41.

4 J.J. Wiens, M.C. Brandley, and T.W. Reeder. "Why does a trait evolve multiple times within a clade? Repeated evolution of snakelike body form in squamate reptiles." *Evolution* 60 (2006): 123–41.

5 R.L. Young, V. Caputo, M. Giovannotti, T. Kohlsdorf, A.O. Vargas, G.E. May, and G.P. Wagner. "Evolution of digit identity in the three-toed Italian skink *Chalcides chalcides*: A new case of digit identity frame shift." *Evolution & Development* 11 (2009): 647–58. doi:10.1111/j.1525-142X.2009.00372.x.

6 Z.R. Lewis, and J. Hanken. "Convergent evolutionary reduction of atrial septation in lungless salamanders." *Journal of Anatomy* 230 (2017): 16–29. doi:10.1111/joa.12535.

7 A.H. Knoll and R.K. Bambach. "Directionality in the history of life: Diffusion from the left wall or repeated scaling of the right?" *Paleobiology* 26 (2000): 1–14.

8 Carroll, S. B. "Chance and Necessity: The Evolution of Morphological Complexity and Diversity." *Nature* 409 (2001): 1102–9. doi:10.1038/35059227.

9 Changes to the complexity in one structure within the body require concurrent changes to another. In squamate reptiles, species with reduced limbs and digit numbers have accompanying increases in the number of vertebrae (Young *et al*., note 5). These changes facilitate burrowing and locomotion in dense vegetation, and could be considered an example of a net-zero change in complexity (Wiens *et al*. note 4; Young *et al*., note 5). A similar 'neutral complexity' change occurs in cave fish: while the eyes are degenerated, other sensory organs in the head (e.g. taste buds) are enhanced (Jeffery *et al*., note 3). Of course, 'neutral complexity' does not always occur: due to the interconnectivity of the circulatory and pulmonary systems, lungless salamanders undergo a reduction in their atrial septa to prevent disastrous blood pressure differentials within their hearts (Lewis and Hanken, note 6).

10 Knoll and Bambach, note 7.

11 Rensch 1960 and Bonner 1988 in McShea, note 12.

12 D.W. McShea. "Mechanisms of large-scale evolutionary trends." *Evolution* 48 (1994): 1747–63. doi:10.2307/2410505.

13 See synthesis in Caroll, note 8.

14 E.G. Allen. "New perspectives on a classic macroevolutionary trend: Complexity, extinction selectivity, and the evolution of Paleozoic ammonoid suture morphology." Ph.D., The University of Chicago, 2005. http://search.proquest.com.helicon.vuw.ac.nz/docview/

305416684/abstract/88B0B2037704186PQ/1.

15 J.L. Cisne. "Evolution of the world fauna of aquatic free-living arthropods." *Evolution* 28 (1974): 337–66.

16 Although there appears to be directional selection for increased limb specialization, there has been very little increase in limb tagmosis since the Permian, suggesting a natural limit that prevents maximum tagmosis (i.e. every limb pair specialized for a separate function). See Cisne, note 15.

17 S.J. Carlson. "Evolutionary trends in the articulate brachiopod hinge mechanism." *Paleobiology* 18 (1992): 344–66.

18 Although the overall trend in hinge geometry for brachiopods is best explained by 'diffusive' evolution, there is directional selection within the deltiodonts (which have noninterlocking hinges) for increased mechanical advantage, allowing a gape to be maintained in potentially adverse conditions (e.g. sediment and epibionts on valves). See Carlson, note 17.

19 D.W. McShea. "Complexity and evolution: What everybody knows." *Biology and Philosophy* 6 (1991): 303–24.

20 Conflicting results between Saunders *et al.* (who found evidence for an active trend in ammonoid suture structure; 1999) and Boyajian and Lutz (who found a passive trend; 1992) are due in part to different correlations between complexity measures used and morphology. The suture complexity index of Saunders *et al.* (1999) corresponded more closely with morphology than the fractal dimenson used by Boyajian and Lutz (1992). Allen, note 14.

21 Orr 2000, Welch and Waxman 2003, in Haygood, note 22.

22 R. Haygood. "Mutation rate and the cost of complexity." *Molecular Biology and Evolution* 23 (2006): 957–63. doi:10.1093/molbev/msj104.

23 Mutations, of course, may also result in reduced complexity

24 This is in contrast to acclimatization. More complex organisms may be less adaptable, but increased complexity may allow species to increase their success via behavioral changes (e.g. humans and the use of clothing and fire to invade colder habitats).

25 M. Kirschner and J. Gerhart. "Evolvability." *Proceedings of the National Academy of Sciences of the United States of America* 95 (1998): 8420–27.

26 Carroll, note 8

27 Kirschner and Gerhart, note 25

28 Kirschner and Gerhart, note 25

29 U. Krohs. "The cost of modularity." In *Vienna Series in Theoretical Biology/: Functions in Biological and Artificial Worlds/: Comparative Philosophical Perspectives*, edited by Ulrich Krohs and Peter Kroes. Cambridge, US: The MIT Press, 2009. http://site.ebrary.com/lib/alltitles/docDetail.action?docID=10277587.

30 L.H. Liow, E. Martino, K.L. Voje, S. Rust, and P.D. Taylor. "Interspecific interactions through 2 million years: Are competitive outcomes predictable?" *Proceedings of the Royal Society B: Biological Sciences* 283 (2016).

31 D.J. Hughes and B.C. Jackson. "Do constant environments promote complexity of form?: The distribution of bryozoan polymorphism as a test of hypotheses." *Evolution* 44 (1990): 889–905.

32 A.H. Cheetham, J. Sanner, P.D. Taylor, and A.N. Ostrovsky. "Morphological differentiation of avicularia and the proliferation of species in Mid-Cretaceous *Wilbertopora* (Bryozoa: Cheilostomata)." *Journal of Paleontology* 80 (2006): 49–71.

33 S. Lidgard, M.C. Carter, M.H. Dick, D.P. Gordon, and A.N. Ostrovsky. "Division of labor and

recurrent evolution of polymorphs in a group of colonial animals." *Evolutionary Ecology* 26 (2012): 233–57.

34 H. Mukai, T. Kiyoshi, and C.G. Reed. "Chapter 3: Bryozoa." In *Microscopic anatomy of invertebrates: Lophophorates, Entoprocta, and Cycliphora*, edited by F.W. Harrison and R.M. Woollacott, 13:45–206, 1997.

35 F.K. McKinney and J.B.C. Jackson. *Bryozoan Evolution*. Review Copy. Special Topics in Palaeontology. Boston: Unwin Hyman, 1989.

36 S.J. Hageman, P.E. Bock, Y. Bone, and B. McGowran. "Bryozoan growth habits: Classification and analysis." *Journal of Paleontology* 72 (1998): 418–36.

37 Estimated 2800–5200 undescribed and undiscovered species; see Gordon, D.P. & Bock, P.E., Supplemental information Table S2, Bryozoa *in* Appeltans, W., *et al*. 'The magnitude of global marine species diversity.' *Current Biology* 22 (2012): 1–14.

38 Hageman *et al*., 1998 note 36

39 A.E. Radford, W. Dickison, J.R. Massey, and C.R. Bell. "Chapter 6." In *Vascular Plant Systematics*, Online. New York: Harper and Row, 1998. http://www.ibiblio.org/botnet/glossary/

40 L.M. Vieira, M.E. Spencer Jones, J.E. Winston, A.E. Migotto, and A.C. Marques. "Evidence for polyphyly of the genus *Scrupocellaria* (Bryozoa: Candidae) based on a phylogenetic analysis of morphological characters." *PLOS ONE* 9 (2014): e95296. doi:10.1371/journal.pone.0095296.

41 A.N. Ostrovsky, C. Nielsen, N. Vavra, and E. Yagunova. "Diversity of brood chambers in calloporid bryozoans (Gymnolaemata, Cheilostomata): comparative anatomy and evolutionary trends." *Zoomorphology* 128 (2009): 13–35. doi:10.1007/s00435-008-0070-8.

42 A.N Ostrovsky. "Cheilostome brood chambers: Structure, formation, evolution." In *Evolution of Sexual Reproduction in Marine Invertebrates: Example of gymnolaemate bryozoans*, by A. Ostrovsky, 115–228. Dordrecht: Springer Netherlands, 2013. http://link.springer.com/10.1007/978-94-007-7146-8_2.

43 S.F. Harmer. *Polyzoa of the Siboga Expedition Part II, Cheilostomata Anasca*. Siboga-Expedite 28. Leiden, the Netherlands: E. J. Brill, 1957.

44 D.P. Gordon. "The marine fauna of New Zealand: Bryozoa: Gymnolaemata from the Kermadec Ridge." *New Zealand Oceanographic Institute Memoir* 91, (1984): 1-198.

45 D.P. Gordon. "The marine fauna of New Zealand: Bryozoa: Gymnolaemata (Ctenostomata and Cheilostomata Anasca) from the western South Island continental shelf and slope." *New Zealand Oceanographic Institute Memoir* 95 (1986): 1-121.

46 D.P. Gordon. "The Marine Fauna of New Zealand: Bryozoa: Gymnolaemata (Cheilostomata Ascophorina) from the Western South Island Continental Shelf and Slope." *New Zealand Oceanographic Institute Memoir* 97 (1989): 1-158.

47 R.S. Boardman, A. H. Cheetham, and P.L. Cook. "Intracolony Variation and the Genus Concept in Bryozoa." *In Proceedings of the North American Paleontological Convention*, Part C:294–320. USA, 1969.

48 Boardman *et al*., note 47

49 C.D. Harvell. "The Evolution of Polymorphism in Colonial Invertebrates and Social Insects." *The Quarterly Review of Biology* 69 (1994): 155–85.

50 L. Silén. "Chapter 6: Polymorphism." In *Biology of Bryozoans*, edited by R.M. Woollacott and R.L. Zimmer, 183–231. New York: Academic Press, 1977.

51 J.S. Ryland. "Physiology and Ecology of Marine Bryozoans." *Advances in Marine Biology* 14

(1976): 285–443.

52 D.P. Gordon. “Zooidal Dimorphism in the Polyzoan *Hippopodinella adpressa* (Busk).” *Nature* 219 (1968): 633–34.

53 Mukai *et al*. note 34

54 M.C. Carter, D.P. Gordon, and J.P.A. Gardner. “Preliminary Analysis of Avicularian Morphology.” In *Proceedings of the 14th International Bryozoology Association Conference*, edited by S.J. Hageman, M.M. Key, and J.E. Winston, 19–30. Boone, North Carolina, United States, 2008.

55 Mukai *et al*. note 34

56 Carter *et al.,* note 54

57 W.N. Beklemishev. *Principles of Comparative Anatomy of Invertebrates*. Translated by J.M MacLennan and Z Kabata. Vol. 1 Promorphology. Edinburgh: Oliver & Boyd, 1969.

58 J.S. Ryland, “Bryozoan coloniality- structure and physiology.” In Biology and systematics of colonial organisms: Proceedings of an international symposium held at the University of Durham, [April 1976], edited by G.P. Larwood and B.R. Rosen, 211–42. Academic Press, 1979.

59 P.E. Bock and P.L. Cook. “Occurrence of three phases of growth with taxonomically distinct zooid morphologies.” In *Biology and Palaeobiology of Bryozoans*, edited by P.J. Hayward, J.S. Ryland, and P.D. Taylor, 33–36. School of Biological Sciences, University of Wales, Swansea: Olsen & Olsen, 1994.

60 Bock and Cook, note 59. The first phase of *Corbulipora tubulifera* has autozooids with cribrimorph shields and rhizoids, and buds a kenozooidal stalk. The second phase has autozooids with exposed frontal walls, ovicells, and avicularia. The third phase reverts to the cribrimorph shield but retains avicularia. The second and third phase alternate in distinct bands.

61 It makes intuitive sense that having more of submodule “A” would result in a cormidium that performs function “A” to a greater degree than a cormidium with fewer “A” submodules. The extent of change will likely depend on submodule type. However, studies have not been undertaken to determine the effect of the number of submodules on their function.

62 S.J. Hageman. “Complexity Generated by Iteration of Hierarchical Modules in Bryozoa.” *Integrative and Comparative Biology* 43 (2003): 87–98.

63 Bock and Cook note 59.

64 Hageman, 2003 note 62.

65 Hageman, 2003 note 62.

66 S. Lidgard. “Predation on marine bryozoan colonies: Taxa, traits and trophic groups.” *Marine Ecology Progress Series* 359 (2008): 117–31. doi:10.3354/meps07322.

67 K.W. Kaufmann, “The form and functions of the avicularia of bugula (phylum Ectoprocta).” *Postilla* 151 (1971): 1–26.

68 J.E. Winstson. “Victims of avicularia.” Marine Ecology 7 (1986): 193–99.

69 C.D. Harvell. “Predator-induced defense in a marine bryozoan.” *Science* 224 (1984): 1357–59.

70 McKinney *et al*. (2003) in Lidgard 2008, note 56.

71 Lidgard 2008, note 66.

72 McKinney and Jackson, note 35.

73 Mukai *et al*. note 34.

74 Carter *et al*. 2008, note 54.

75 Kaufmann, note 67.
76 Mukai *et al.,* note 34.
77 Silén, note 50.
78 P.L. Cook, "Polyzoa from West Africa. The Malacostega. Part 1." *Bulletin of The British Museum (Natural History) Zoology* 16 (1968): 115–60.
79 Cheetham *et al.*, note 32
80 Mukai *et al.,* note 34.
81 Kaufmann, note 67.
82 McKinney & Jackson, note 35.
83 Carter *et al.* 2008, note 54.
84 Silén, note 50.
85 Ryland, 1979 see note 58
86 A.H. Cheetham, and P.L. Cook. "General features of the class Gymnolaemata." In *Treatise on Invertebrate Paleontology: Part G Bryozoa Revised*, 1: Introduction, Order Cystoporata, Order Cryptostomata: 138–207. Geological Society of America, 1983.
87 Silén, note 50.
88 Ostrovsky, A.N. "Comparative studies of ovicell anatomy and reproductive patterns in *Cribrilina annulata* and *Celleporella hyalina* (Bryozoa: Cheilostomatida)." *Acta Zoologica* 79 (1998): 287–318.
89 Lidgard *et al.*, 2012 note 33.
90 Silén, note 50.
91 Cheetham and Cook 1983, note 76.
92 A.N. Ostrovsky, personal communication, Nov. 1, 2016.
93 Vieira *et al.*, note 40.
94 Ostrovsky *et al.*, note 41
95 Ostrovsky, 2013, see note 42.
96 A.N. Ostrovsky and P.D. Taylor. "Ovicell development in the Early Calloporid *Wilbertopora* Cheetham,1954 (bryozoa: Cheilostomata) from the Mid-Cretaceous of the USA." *Bryozoan Studies*, 2004, 223–30.
97 A.N. Ostrovsky and P.D. Taylor. "Brood chambers constructed from spines in fossil and Recent cheilostome bryozoans." *Zoological Journal of the Linnean Society* 144 (2005): 317–61.
98 Ostrovsky and Taylor, note 96
99 A.N. Ostrovsky, M.H. Dick, and S.F. Mawatari. "The internal-brooding apparatus in the bryozoan genus *Cauloramphus* (Cheilostomata: Calloporidae) and its inferred homology to ovicells." *Zoological Science* 24 (2007): 1187–96.
100 Ostrovsky *et al.* 2009, note 41.
101 NIWA Specimen #98339, collected on 10/23/1967 at station E821 (Latitude: -46.725°, Longitude: 165.774°, Depth: 549 m) with a medium Agassiz trawl.
102 Air-dried specimens were sputter coated with gold-palladium before photographing with a Hitachi TM3000 Benchtop SEM.
103 Vieira *et al.*, note 40.
104 D.W. McShea. "Perspective: Metazoan complexity and evolution: Is there a trend?" *Evolution* 50 (1996): 477–92.
105 McShea note 104.

106 This classification system was designed to measure cormidia near the growing edge of a colony, in the zone of astogenetic repetition. However, one could use it to examine astogenetic or ontogenetic changes in cormidial complexity, which would change the temporal scale being examined.

107 It is possible for polymorphic branching colonies to become even more complicated if their cormidia are organized in a particular pattern within each branch.

108 McShea, note 12.

109 Hughes and Jackson, note 31.

110 C. Simpson, J.B.C. Jackson, and A. Herrera-Cubilla. "Evolutionary determinants of morphological polymorphism in colonial animals." *bioRxiv* Preprint (2016): 46409. doi:10.1101/046409.

111 T. Schopf. "Ergonomics of polymorphism: its relation to the colony as the unit of natural selection in species of the phylum ectoprocta." In *Animal Colonies*, edited by R.S. Boardman, A.H. Cheetham, and W.A. Oliver, 247–93. Dowden, Hutchinson and Ross, Inc, 1973.

112 M. Kleyer, S. Dray, F. de Bello, J. L ps, R.J. Pakeman, B. Strauss, W. Thuiller, and S. Lavorel. "Assessing species and community functional responses to environmental gradients: Which multivariate methods?" *Journal of Vegetation Science* 23 (2012): 805–21. doi:10.1111/j.1654-1103.2012.01402.x.

113 Kaufmann, note 67.

114 J.E. Winston, "Why bryozoans have avicularia- A review of the evidence." *American Museum Novitates* 2789 (1984): 1–26.

115 Silén, note 50.

116 Though genome complexity and morphological complexity do not always correspond. See McShea, note 12.

117 W. Thuiller, D.M. Richardson, M. Rouget, S. Proches, and J.R.U. Wilson. "Interactions between environment, species traits, and human uses describe patterns of plant invasions." Ecology 87 (2006): 1755–69.

118 T.A. Henry. "GLS-corrected RLQ analysis: A new multivariate method for incorporating spatial and phylogenetic information into trait-environment analyses." Masters, The University of Guelph, 2016. https://atrium.lib.uoguelph.ca/xmlui/bitstream/handle/10214/9726/Henry_Thomas_201605_MSc.pdf?sequence=3.

119 C. Guisande, R.P. Vari, J. Heine, E. Garcia-Rosello, J. Gonzalez-Dacosta, B.J.G. Perez-Schofield, L. Gonzalez-Vilas, and P. Pelayo-Villamil. "VARSEDIG: An algorithm for morphometric characters selection and statistical validation in morphological taxonomy." *Zootaxa* 4126 (2016): 571–80.

Appendix 1. Selected Definitions

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

Autozooidal polymorph: A zooid that retains a protrusible tentacle crown but differs from an autozooid 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.

Heterozooid: 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 autozooid or a heterozooid.

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 autozooid (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				

‘Smiths’ in Bryozoology

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1. Introduction

A search through the extensive reference lists of the Bryozoa Home Page (Bock 2014) and earlier compendia (such as Nickles and Bassler 1900) finds more than 75 papers that have at least one author or editor identified as Smith, Schmidt, Smitt, Smythe, or a hyphenated name with Smith in it. A survey of IBA publications to date reveals that no other name is as common (though there are a number of replicated names such as Brown, Moore, Morris, Turner, and Yang). There are at least 15 Smith and Smith-variant authors published in the bryozoological literature, of whom five have published on bryozoans over several years or more. How can bryozoologists keep track of all these Smiths? Even in the age of Google Scholar, name-confusion is common, as anyone with a common surname who tries to keep track of their own citations can attest. Here we identify and describe each bryozoologist Smith and review his/her publications for ease of reference and to avoid future confusion.

2. Smithian contributions to bryozoology

A number of Smiths *s.l.* have had only a tangential relation to bryozoans, but in the interests of clarify and completeness, they are listed here in alphabetical order. In most cases all the information in each paragraph is a matter of public record and available on the internet.

Percy William Bassett-Smith (1861-1927) was a surgeon in the British Royal Navy who sailed on the *HMS Rambler* to the China Sea and collected bryozoans. They were identified, figured and described by Kirkpatrick (1890). Bassett-Smith was later knighted.

It is said that he preferred advancing science in the navy than service at sea.

Brigitta M. Schmid attended the IBA meeting in Paris (1989), and published a paper in the proceedings outlining a fauna from the Miocene of Nußdorf, Austria (Schmid 1991). At that time she was based at the Institut für Paläontologie in Vienna, and published on other fossil groups such as urchins.

Ferdinand Schmidt published a paper in 1885 or 1886 (reports vary) on freshwater bryozoans of Livonia, a region in modern-day Latvia and Estonia (F Schmidt 1885).

Carl Friedrich Schmidt (1832-1908) was a geologist from St Petersburg, Russia who studied and worked there and later in Tartu, Estonia. He led many expeditions in the 1850s and 1860s, concentrating on lower Paleozoic fossils of Africa. He is remembered for setting up the overall stratigraphic scheme for the Cambrian, Devonian and Silurian Periods (Kaljo 1958). His 1858 paper on the Silurian of the Baltic mentioned several bryozoans (CF Schmidt 1858).

Daniela N. Schmidt attended the University of Bremen, Germany and then received her PhD from ETH Zurich, Switzerland. She is now Professor of Palaeobiology at the University of Bristol, specialising in the effects of climate change and ocean acidification on ecology and evolution of marine organisms. Bryozoans are among the taxa she uses to identify such effects (Raggazola *et al*. 2014).

Oscar Schmidt published two papers (the later one of which was translated into English) in which he discussed and described some species of the solitary Entoproct *Loxosoma* (Schmidt 1876, 1879).

Rolf Schmidt (b. 1972) (Figure 1) was born in Freiburg, Germany, and later emigrated to Australia. He completed his BSc (Hons) and PhD in Geology at the University of Adelaide, Australia in 2003. He has been employed as Collection Manager of Invertebrate Palaeontology at Museum Victoria from 2002 to the present.

Schmidt's publications on Australian bryozoans include ecological adaptations (Brown *et al*. 2002) paleoenvironments and assemblages (Schmidt and Bone 2002, 2003, 2004, 2005, 2007, Schmidt and Gallagher 2014). His most cited paper (Google Scholar) is that in which he and Yvonne Bone described the new genus *Nudicella* (Schmidt and Bone 2004). In addition to attending IBA meetings from 2001 onwards, and many southern hemisphere Australarwood meetings, Schmidt has served on council and as 'webmaster' to the association. He was the main host of the 17th IBA Conference in Melbourne in 2016.

Abigail Marion Smith (b. 1961) (Figure 2) comes from Massachusetts. She studied geology and biology at Colby College in Maine, graduating in 1982, then Earth Science at the Massachusetts Institute of Technology (1984), and finally achieved her doctorate

Figure 1. Rolf Schmidt

Figure 2. Abigail M. Smith

at the University of Waikato, Hamilton, New Zealand in 1992. She has worked at the University of Otago (Dunedin, New Zealand) since 1993 and has served as the Head of Department of Marine Science and Professor there.

Smith's primary interest is in skeletal composition (Smith and Nelson 1993, AM Smith *et al*. 1998, 2004, 2006, Smith and Key 2004, Smith and Garden 2012), but she has also published on growth and calcification rates in bryozoans (Smith and Nelson 1994a, AM Smith et al 2001), on taphonomic processes and paleoenvironmental interpretation in bryozoan sediments (AM Smith *et al*. 1992, Smith and Nelson 1994b, 1996, AM Smith 1995,) and on wider sea-water chemistry implications (Key and Smith 2003; AM Smith 2014). She has also dabbled in taxonomy (AM Smith 2008a, AM Smith *et al*. 2008, AM Smith *et al*. 2012), control of freshwater bryozoan infestations (AM Smith *et al*. 2005), and historical studies (AM Smith 2008b; AM Smith *et al*. 2014). She has published several bryozoan papers jointly with her research students (e.g., Steger and Smith 2005, Wejnert and Smith 2008, Wood *et al*. 2012, Enke *et al*. 2014).

Smith has been a member of the IBA since 1990, served on the organizing committee for the 10th IBA Conference in Wellington, New Zealand held in 1995, and she co-edited that conference volume (Gordon *et al*. 1996). Since 2001 she has served as the Treasurer of the Association and is now in her fifth term of office. She was the Conference Secretary for the 17th IBA Conference in Melbourne, 2016.

C. Smith was a co-author on a paper describing the bryozoan-rich Sulphur Well member, of the Lexington Limestone (Middle Ordovician) from central Kentucky (Ettensohn *et al*. 1986). In that paper he is identified as coming from the Department of

Geology, University of Kentucky.

Charles A.F. Smith III was a geophysicist at the University of Chicago who worked on large-scale models in marine ecology including bryozoans (e.g., Schopf *et al*. 1978) and paleobiology (CAF Smith 1977). His work was well-regarded at the time; he received a 1978 grant from the Henry-Marsh Fund, National Academy of Sciences for his work on variations in Ordovician fossils.

Damon Stanwell-Smith (b. 1970) is a UK-based marine biologist, with a BSc in Marine Biology from Swansea. His main (perhaps only) bryozoology paper (Stanwell-Smith and Barnes 1997) dates from his time at British Antarctic Survey (BAS) at Cambridge; he received his PhD from the BAS in the same year. An experienced commercial diver, he has also directed a consultancy company specialising in long-term monitoring, managed biodiversity research in East Africa and Southeast Asia, and led expeditions of icebreaker *MV Polar Star*. He is currently Senior Programme Officer, Ecosystem Assessment and Acting Head, Marine Assessment and Decision Support Programme, United Nations Environmental Programme, World Conservation Monitoring Centre.

Denys B. Smith (1929-2007) wrote more than 60 books and papers on Permian geology (e.g. DB Smith 1992), especially of the British Isles, while employed by the British Geological Survey. He was also President of the Leeds Geological Association and later the Yorkshire Geological Society (Cooper 2008). His study of the bryozoan-algal patch reefs of the upper Permian of northeast England remains the most comprehensive assessment of these geological features (DB Smith 1981).

Douglas G. Smith (b. 1955) grew up in Massachusetts, USA, graduating with a Bachelor's degree in 1977 from University of Massachusetts, Amherst. He became a lecturer and curator of Invertebrates in the Department of Biology, University Massachusetts at Amherst. Although now retired he remains active, continuing his research at Amherst.

Smith published extensively on freshwater bryozoans from North America between 1985 and 2003. He described new species (DG Smith 1992), distributions (DG Smith 1985, 1988, 1993) and morphology (DG Smith 1995, DG Smith *et al*. 2003). DG Smith and Wood's (1995) review of *Plumatella javanica* is his most highly cited bryozoan article (Google Scholar). He is also known for his five volumes of keys to the freshwater invertebrates of Massachusetts (with bryozoans appearing in DG Smith 1989) and his 4th Edition of *Pennak's Freshwater Invertebrates of the United States, Porifera to Crustacea* (DG Smith 2001), which included freshwater bryozoans in Chapter 12.

Franz Smith (b. 1970) studied for his BSc in the Virgin Islands, then received his PhD at Otago University in 1999, for a study on sessile invertebrates in Fiordland, New Zealand. His subsequent work has been in Chile, Australia, and around Antarctica. His interest in bryozoans led to collaboration with Dennis Gordon at NIWA (F Smith and Gordon 2003). His most recent work is on classification systems for marine communities at CSIRO, Brisbane, Australia.

James Perrin Smith recorded bryozoan fossils from the Coal Measures at Poteau Mountain, "Indian Territory", and in northeastern Arkansas (Smith, 1896). He is the only Smith recorded in Nickles and Bassler's (1900) review of American fossil bryozoans.

L.W. Smith who was a student at the University of Swansea presented a paper on the ultrastructure of the tentacles of *Flustrellidra hispida* (LW Smith 1973) at the second IBA meeting in Durham, 1971.

Ralph Ingram Smith (1916-1993) was best-known as one of the editors of *Light's manual: intertidal invertebrates of the central California coast*. This "bible" □of the Pacific intertidal first appeared in 1941 (Light 1941) and was extensively expanded in a second edition published in 1954 (Light and Smith 1954). It is now known as the "Light and Smith Manual" to honour his contribution (Carlton 2007). He also produced a guide to invertebrates on the east coast of the USA (RI Smith 1964) that contained contributions on bryozoans authored by Mary Rogick (Rogick 1964a, b, Winston 2014). Another Smith from Massachusetts, Ralph received his degrees from Harvard, the PhD in 1942. He taught invertebrate zoology at University of California at Berkeley from 1946 until his retirement in 1987 (Carlton 2007). Each of the four editions of *Light's manual* has contained a chapter on Ectoprocta or Bryozoa, mostly the work of Dorothy and John Soule (Soule *et al*. 1975), alongside Penny (*née* Pinter) Morris and, more lately, Henry Chaney (Soule *et al*. 2007)

Stanley Smith (1883-1955) published on fossil corals from around the world in the 1910s-1940s. He studied at Newcastle upon Tyne, then worked at universities around the UK and Canada before finishing up at the University of Bristol, where he worked from 1922 until his retirement in 1948 (Thomas 1955). His study of Valentian corals from Shropshire and Montgomeryshire (S Smith 1930) included reference to associated bryozoans in the faunas he described.

Stephen V. Smith studied carbonate production off southern California (SV Smith, 1972), including a section on bryozoan growth and calcification. His BA in Geology was from the University of Texas, followed by an MS in 1966 from Northwestern University and a PhD in 1970 at the University of Hawaii, where he is now an Emeritus Professor. His most-cited publications are in the area of marine nutrient fluxes and balances.

Fredrik Adam Smitt (sometimes 'Fritz', e.g., Nickles and Bassler, 1900, p. 544) (1839-1904) (Figure 3) was born in Halmstad, Sweden. Educated at Lund University and later Uppsala University in Sweden, he graduated from Uppsala in 1859, after which he

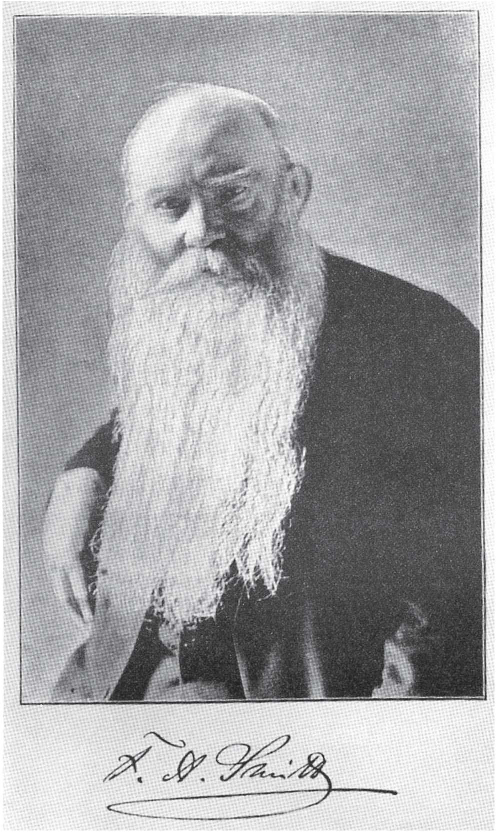

Figure 3. ***Fredrik Adam Smitt***

took charge of zoological collections there. He received a PhD from Uppsala University in 1863 on the topic of development of marine bryozoans (Schopf and Bassett 1973). Appointed Professor of Vertebrates at Naturhistoriska Riskmuseum in Stockholm, he worked there for the rest of his life. He was the naturalist on the *Magdalena* expedition to Spitsbergen in 1861, and later on the *Josephine*, well known for his energy and toughness in these difficult environments.

"Smitt was the first Swedish naturalist to accept and apply Darwin's theory of evolution" (Schopf and Bassett 1973). His research concentrated on evolutionary relationships among groups of organisms, with Bryozoa taking a central role in his publications and exploration. His work on Swedish (Smitt 1865, 1867, 1868a, b, 1872b, 1876, 1899) and Floridan (Smitt 1872a, 1873) bryozoans, as well as on the overall classification of bryozoans (Smitt 1868c, 1879 a, b) was thoroughly researched and beautifully illustrated, with the innovation, still followed today, of concentrating on zooid-level characters for diagnosis (Schopf and Bassett 1973). The most-cited of these (112 citations according to Google Scholar) is his monograph on Floridan bryozoans (Smitt 1872); this material has been recently re-evaluated and re-described (Winston

2005). Smitt was the scientist who coined the term “zooecium”, and was the first to recognise evolutionary lineages in his “Bryozoa Marina” (Smitt 1868c). Later in life he published on fishes and whales, as well as writing for a more general scientific audience (Smitt 1896).

Louis Bouvier Smyth (1883-1952), Professor of Geology at Trinity College, Dublin was an expert on corals from the Carboniferous. In a short paper published in 1922, however, he described the trepostome bryozoan *Stenophragmidium serrata* from the Carboniferous of County Antrim, Ireland (Smyth 1922).

Thomas Smyth, a Masters student at Trinity College, Dublin published a useful listing of the distribution of freshwater bryozoans in Ireland (Smyth 1994) and also examined the survival ability of statoblasts in a lake in western Ireland (Smyth and Reynolds 1995).

Thomas Cavalier-Smith (b. 1942) is a British biologist who is one of the most famous of those whose interest in bryozoans was occasional (e.g., Cavalier-Smith 1993, 1998, 2002). While Professor of Evolutionary Biology (now Emeritus) at the University of Oxford, he was presented with the International Prize for Biology in 2004, the Linnean Medal in 2007, and other awards (en.wikipedia.org/wiki/Thomas_Cavalier-Smith). He co-authored a paper on lophophorate phylogeny in *Science* (Conway Morris *et al*. 1996).

Robert L. Foster-Smith, known as Bob, co-authored with Peter Hayward the bryozoan section of the *Directory of the British Marine Fauna and Flora* produced by the British Marine Conservation Society (Hayward and Foster-Smith, 1987). He also produced a series of habitat maps and biological surveys of sublittoral habitats around the British coastline (e.g., Foster-Smith and Foster-Smith 1987), and developed classification systems for marine biotopes (Connor *et al*. 1995). He is now the chief consultant for Envision Mapping in the UK.

Anthony (Tony) Nelson-Smith collaborated with Peter Hayward on non-bryozoan subjects and he published with John Ryland a paper on the bryozoans of the west of Ireland (Ryland and Nelson-Smith 1975).

Ronald A. Tavener-Smith. The first Smith known to attend IBA meetings was Ronald A. Tavener-Smith (b. 1933). Born in North Wales, he attended University College of Wales, Aberystwyth, graduating in 1952. After serving in the British Army and on the Geological Survey of Northern Rhodesia, he took an academic position at Queen’s University, Belfast (1958-1972) and then at University of Natal, Durban (1972-1995). He is now an Emeritus Professor at the University of KwaZulu-Natal, South Africa.

Tavener-Smith published on bryozoans from 1965 into the 1980s, including papers in IBA volumes from 1968 Milan and 1971 Durham conferences. Though he was primarily a paleontologist, Tavener-Smith’s papers focus on structure and skeletal organisation in both fossil and living bryozoans (Tavener-Smith 1968, 1969a, b, 1973b, Tavener-Smith and Williams 1970, 1972). He also published some general (Larwood *et al*. 1967), descriptive (Tavener-Smith 1965a, 1966a, b, 1971, 1973a, 1974) and taxonomic (Tavener-Smith 1965b, 1975, 1981) studies. The most highly-cited paper among his bryozoan publications is Tavener-Smith and Williams (1972) on the secretion and structure of living and fossil bryozoan skeletons (73 according to Google Scholar). In the late 1980s he left bryozoans behind and instigated research on coal and the geology of Natal.

3. Bryozoan taxa named for Smiths

A number of bryozoan taxa have been either named for F. A. Smitt, beginning with *Smittia* Hincks, 1879, or are taxa based upon his name erected due to distinctions from earlier-named similar taxa (i.e. *Alismittina* Soule and Soule 1954, *Parasmittina* Osburn, 1952, *Smittoidea* Osburn, 1952). The most speciose genera are *Smittina* Norman, 1903 (165 species) and *Parasmittina* Osburn, 1952 (138 species). Levinsen (1909) erected the family Smittinidae and Superfamily Smittinoidea.

In 2015, Gordon and Taylor (2015) named *Exochella abigailae* for Abigail M. Smith.

4. Conclusions

Smiths *et similis* have been key participants in bryozoology as far back as 1865. Soon after the IBA was founded a century later in 1965 Tavener-Smith participated in early meetings. After a brief Smith-hiatus, AM Smith and R Schmidt have supported the IBA at conferences, in proceedings volumes, and in its governance. Meanwhile many other Smiths have played roles as co-authors, editors, and occasional participants in the science of bryozoology, roles commemorated in the names of bryozoan taxa such as *Smittina* and *Smittoidea*.

It could be argued that a collection of profiles such as this, based only on a surname, is close to random and thus less than 'scientific'. Nevertheless, the opportunity to gather together a subset of the bryozoan literature for analysis is a real one, just as is a study of Polish bryozoologists, or of bryozoologists of the 1920s. It is perhaps justifiable solely on the basis that a conscientious scientist must know at all times to which Smith he or she is referring.

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References

Anonymous. 1905. Fredrik Adam Smitt. *Kungliga Svenska Vetenskaps-Akademiens Arsbok for ar 1903* **1905,** 225–240.

Bock, P. 2014. The Bryozoa Home Page. http://bryozoa.net/index.html, visited June, 2014.

Brown, K.M., Schmidt, R. and Bone, Y. 2002. Observations on ecological adaptations of *Lanceopora smeatoni* (MacGillivray), from West Island, South Australia, pp. 61–65. In: P.N. Wyse Jackson, C.J. Buttler and M.E. Spencer Jones (eds) *Bryozoan Studies 2001*. A.A. Balkema Publishers, Lisse, Abingdon, Exton, Tokyo.

Carlton, J.T. (ed.) 2007. *The Light and Smith Manual: Intertidal Invertebrates from Central California to Oregon*. Fourth Edition, revised and expanded.

Cavalier-Smith, T. 1993. Kingdom Protozoa and its 18 phyla. *Microbiological Reviews* **57**, 953–994.

Cavalier-Smith, T. 1998. A revised six-kingdom system of life. *Biological Reviews* **73,** 203–266.

Cavalier-Smith, T. 2002. The phagotrophic origin of eukaryotes and phylogenetic classification of Protozoa. *International Journal of Systematic and Evolutionary Microbiology* **52**, 297–354.

Connor, D.W., Hiscock, K., Foster-Smith R.L., Covey, R. 1995. Classification system for benthic marine biotopes, pp. 155–166. In: *Biology and Ecology of Shallow Coastal Waters*, Olsen and Olsen, Fredesnborg.

Conway Morris, S., Cohen, B.L., Gawthrop, A.B., Cavalier-Smith, T., Winnepenninckx, B. 1996. Lophophorate phylogeny. *Science* **272**, 282.

Cooper, A. H. 2008. Denys Smith Memorial Trip: The Geology of Knaresborough Gorge ☐ YGS 1 June 2008. *British Geological Survey Open Report* OR/08/044. 18pp.

Enke, S., Smith, A.M. and Hageman, S.J. 2014. Bryozoan settlement substrates and implications for carbonate sediment production. In: A. Rosso, P.N. Wyse Jackson and J.S. Porter (eds). *Bryozoan Studies 2013, Proceedings of the 16th International Bryozoology Association Conferenc*e, Catania Italy, September 2013. *Studi Trentini di Scienze Naturali* **94**, 95–99.

Ettensohn, F.R., Amig, B.C., Pashin, J.C., Greb, S.F., Harris, M.Q., Black, J.C., Cantrell, D.J., Smith, C.A. and McMahan, T.M. 1986. Paleoecology and paleoenvironments of the bryozoan-rich Sulphur Well Member, Lexington Limestone (Middle Ordovician), central Kentucky. *Southeastern Geology* **26**, 199–219.

Foster-Smith R.L. and Foster-Smith J.L. 1987. *A marine biological survey of Beadnell to Dunstanburgh Castle, Northumberland: a contribution to the Marine Nature Conservation Review (MNCR).* Nature Conservancy Council, UK, 164 pp.

Gordon, D.P., Smith, A.M. and Grant-Mackie, J.A. (eds). 1996. *Bryozoans in Space and Time*. NIWA, Wellington. 442 pp.

Gordon, D.P. and Taylor, P.D. 2015. Bryozoa of the early Eocene Tumaio limestone, Chatham Island, New Zealand. *Journal of Systematic Palaeontology* **13** (12), 983–

1070.

Hayward, P. J. and Foster-Smith, R., 1987. Bryozoa, pp. 280–294. In: Howson, C.M. (ed.) *Directory of the British marine fauna and flora. A coded checklist of the marine fauna and flora of the British Isles and its surrounding seas*. Marine Conservation Society, Ross-on-Wye.

Kaljo, D. 1958. Fr Schmidt – Eesti geoloogia aluste rajaja (Fr. Schmidt – the founder of Geology bases). *Eesti Loodus (Estonian Naturalists)* **4**, 193–196.

Key, M.M., Jr. and Smith A.M. 2003. From plate tectonics to bryozoan evolution. *Boletin de la Sociedad de Biologia de Concepcion* **74**, 75.

Kirkpatrick, R. 1890. Report up on the Hydrozoa and Polyzoa collected by P.W. Bassett-Smith, Esq., surgeon RN, during the survey of the Tizard and Macclesfield banks, in the China Sea, by *H.M.S. Rambler*, Commander W.U. Moore. *Annals and Magazine of Natural History*, Series 6, **5**, 11–24.

Larwood, G.P., Medd, A.W., Owen, D.E. and Tavener-Smith R. 1967. Bryozoa, Chapter 11, pp. 379 □395. In: *The Fossil Record*. Geological Society of London.

Nickles, J.M. and Bassler, R.S. 1900. Synopsis of American fossil Bryozoa. *United States Geological Survey Professional Paper* **173**, 663 pp.

Ragazzola, F., Taylor, P.D., Bazzicalupo, P., Okamura, B. and Schmidt, D.N. 2014. A new species of the cheilostome bryozoan *Chiastosella* in the Southern Ocean, past and present. *Polar Biology* **37**, 773–779.

Rogick, M.D. 1964a. Phylum Entoprocta, pp. 165–166. In: R.I. Smith (ed.). *Keys to Marine Invertebrates of the Woods Hole Region*. Woods Hole, Massachusetts, Systematics-Ecology Program, Marine Biological Laboratory.

Rogick, M.D. 1964a. Phylum Ectoprocta, pp. 167–187. In: R.I. Smith (ed.). *Keys to Marine Invertebrates of the Woods Hole Region*. Woods Hole, Massachusetts, Systematics-Ecology Program, Marine Biological Laboratory.

Ryland, J.S. and Nelson-Smith, A. 1975. Littoral and Benthic Investigations on the West Coast of Ireland: IV (Section A: Faunistic and Ecological Studies.) Some Shores in Counties Clare and Galway. *Proceedings of the Royal Irish Academy* **75B**, 245–266.

Schmid, B.M. 1991. Recent bryozoan species from the Miocene of Nußdorf (Vienna) and their use for ecological interpretation. In: Bigey, F.P and d'Hondt, J.-L. (eds). *Bryozoaires Actuels et Fossiles: Bryozoa Living and Fossil. Bulletin de la Socit des Sciences Naturelles de l'Ouest de la France, Mmoire HS* **1**, 399–408.

Schmidt, C.F. 1858. Untersuchungen ber die silurische Formation von Estland, Nord-Livland und Oesel. *Archiv fur die Naturkund Liv-, Est- und Kurlands* **Bd. ii,**. 1–247, 467–474.

Schmidt, F. 1885. Die Süsswasserbryozoen Livlands. *Sitzungsberichte der Naturforscher-Gesellschaft zu Dorpat* VII. **2**, 350–359.

Schmidt, O. 1876. Die Gattung *Loxosoma*. *Archiv für Mikroskopische Anatomie* **12**(1), 1–14.

Schmidt, O. 1879. XLIV.—Remarks upon the memoirs on *Loxosoma*. *Annals and Magazine of Natural History Ser 5* **3**, 393–404. (Translated by W.S. Dallas from a 1878 article in *Zeitschrift für Wissenschaftliche Zoologie* **11**, 68)

Schmidt, R. and Bone, Y. 2002. Eocene Bryozoan Assemblages of the St Vincent Basin, South Australia, pp. 293–298. In: P.N. Wyse Jackson, C.J. Buttler and M.E. Spencer Jones (eds.) *Bryozoan Studies 2001*. A.A. Balkema Publishers, Lisse, Abingdon, Exton, Tokyo.

Schmidt, R. and Bone, Y., 2003. Biogeography of Eocene bryozoans from the St Vincent Basin, South Australia. *Lethaia* **36**, 345–356.

Schmidt, R. and Bone, Y. 2004. Australian Cainozoic Bryozoa, *Nudicella* gen. nov. (Onychocellidae, Cheilostomata) with palaeoenvironments and biogeography. *Alcheringa* **28**, 185–203.

Schmidt, R. and Bone, Y. 2005. Palaeoenvironments of Eocene Bryozoa, St Vincent Basin, South Australia, pp. 281–291. In: H.I. Moyano G., J.M. Cancino and P.N. Wyse Jackson (eds) *Bryozoan Studies 2004*. A.A. Balkema Publishers, Leiden, London, New York, Philadelphia, Singapore.

Schmidt, R. and Bone, Y. 2007. Australian Cainozoic Bryozoa, 2: Free-living Cheilostomata of the Eocene St Vincent Basin, S.A., including *Bonellina* gen nov. *Alcheringa* **31**, 67–84.

Schmidt, R. and Gallagher, S.J., 2014. Front Row Seats to the Ice Age: Oligocene Bryozoa from a core on the south-eastern Australian Shelf. In: A. Rosso, P.N. Wyse Jackson and J.S. Porter (eds). *Bryozoan Studies 2013, Proceedings of the 16th International Bryozoology Association Conferenc*e, Catania Italy, September 2013. *Studi Trentini di Scienze Naturali* **94**, 223–227.

Schopf, T.J.M. and Bassett, E.L. 1973. F.A. Smitt, Marine Bryozoa, and the Introduction of Darwin into Sweden. *Transactions of the American Philosophical Society*, New Series **63**, 1–30.

Schopf, T.J.M., Fisher, J.B. and Smith, C.A.F., III. 1978. Is the marine latitudinal diversity gradient merely another example of the species area curve?, pp. 365–386. In: B. Battaglia and J.A. Beardmore (eds) Marine organisms: genetics, ecology and evolution. Plenum Press, New York.

Smith, A.M. 1995. Palaeoenvironmental interpretation using bryozoans: a review. *Geological Society of London Special Publication*, **83**, 231–243.

Smith, A.M. 2008a. Corrections to the global distribution of *Hornera pectinata* (Bryozoa: Horneridae), pp. 295–300. In: S.J. Hageman, M.M. Key, J. and J.E. Winston (eds). *Bryozoan Studies 2007. Proceedings of the 14th International Bryozoology Association Conference, Boone, North Carolina, July 1-8, 2007*. Virginia Museum of Natural History, Martinsville.

Smith, A.M. 2008b. Women in the International Bryozoology Association, 1965 to 2001, pp. 347–358. In: P.N. Wyse Jackson and M.E. Spencer Jones (eds). *Annals of Bryozoology 2*. International Bryozoology Association, Dublin.

Smith, A.M. 2014. Growth and Calcification of Marine Bryozoans in a Changing Ocean. *Biological Bulletin* **226**, 203–210.

Smith, A.M., Brunton, M.A. and Batson, P.B. 2005. Infestation of a temperate reservoir by freshwater bryozoans - an integrated research programme, 293–301. In: H.I. Moyano G., J.M. Cancino and P.N. Wyse Jackson (eds) *Bryozoan Studies 2004*. A.A. Balkema Publishers, Leiden, London, New York, Philadelphia, Singapore.

Smith, A.M. and Garden, C. J. 2012. Being a Bimineralic Bryozoan in an Acidifying Ocean, pp. 327–337. In: A. Ernst, P. and J. Scholz (eds). *Bryozoan Studies 2010*. Springer, Heidelberg.

Smith, A.M. and Key, M.M., Jr. 2004. Controls, variation, and a record of climate change in detailed stable isotope record in a single bryozoan skeleton. *Quaternary Research* **61**, 123–133.

Smith, A.M., Key, M.M., Jr. and Gordon, D.P. 2006. Skeletal mineralogy of bryozoans: Taxonomic and temporal patterns. *Earth-Science Reviews* **78**, 287–306.

Smith, A.M. and Nelson, C.S., 1993. Mineralogical, carbonate geochemical, and diagenetic data for modern New Zealand bryozoans. *Occasional Report, Department of Earth Sciences, University of Waikato* **17**, 1–71.

Smith, A.M, and Nelson, C.S. 1994a. Calcification rates of rapidly colonising bryozoans in Hauraki Gulf, northern New Zealand. *N.Z. Journal of Marine and Freshwater Research* **28**, 227–234.

Smith, A.M. and Nelson, C.S. 1994b. Selectivity in sea-floor processes: taphonomy of bryozoans, pp. 177–180. In: P.J. Hayward, J.S. Ryland and P.D. Taylor (eds). *Biology and Palaeobiology of Bryozoans*. Olsen and Olsen, Fredensborg.

Smith, A. M. and Nelson, C.S. 1996. Differential abrasion of bryozoan skeletons: taphonomic implications for paleoenvironmental interpretation, pp. 305–313. In: D.P. Gordon, A.M. Smith and J.A. Grant-Mackie, J.A., (eds). *Bryozoans in Space and Time*. NIWA, Wellington.

Smith, A.M., Nelson, C.S. and Danaher, P.J. 1992. Dissolution behaviour of bryozoan sediments: taphonomic implications for nontropical shelf carbonates. *Palaeogeography Palaeoclimatology Palaeoecology* **93**, 213–226.

Smith, A.M., Nelson, C.S., Key, M.M., Jr. and Patterson, W.P. 2004. Stable isotope values in modern bryozoan carbonate from New Zealand and implications for paleoenvironmental interpretation. *New Zealand Journal of Geology and Geophysics* **47**, 809–821.

Smith, A.M., Nelson, C.S., and Spencer, H.G. 1998. Skeletal carbonate mineralogy of New Zealand bryozoans. *Marine Geology*, **151,** 27–46.

Smith, A.M., Spencer Jones, M.E. and Wyse Jackson, P.N. 2014. Bryozoans of the Krusenstern Expedition (1803-1806), pp. 183–194. In: P.N. Wyse Jackson and M.E. Spencer Jones (eds). *Annals of Bryozoology 4*. International Bryozoology Association, Dublin.

Smith, A.M., Stewart, B., Key, M.M., Jr and Jamet, C.M., 2001. Growth and carbonate production by *Adeonellopsis* (Bryozoa: Cheilostomata) in: Doubtful Sound, New Zealand. *Palaeogeography Palaeoclimatology Palaeoecology* **175**, 201–210.

Smith, A.M., Taylor, P.D. and Milne, R. 2012. *Hornera striata* (Milne Edwards, 1838), a British Pliocene Cyclostome Bryozoan Incorrectly Recorded from New Zealand, with Notes on Some Non-fenestrate *Hornera* from the Coralline Crag, pp. 339–356. In: A. Ernst, P. and J. Scholz (eds). *Bryozoan Studies 2010*. Springer, Heidelberg.

Smith, A. M., Taylor, P. D. and Spencer, H. G., 2008. Resolution of taxonomic issues in the Horneridae (Bryozoa: Cyclostomata), pp. 359–411. In: P.N. Wyse Jackson and M.E. Spencer Jones (eds). *Annals of Bryozoology 2*. International Bryozoology Association, Dublin.

Smith, C.A.F. 1977. Diversity associations as stochastic variables. *Paleobiology* **3**, 41–48.

Smith, D.B. 1981. Bryozoan-algal patch-reefs in the Upper Permian Lower Magnesian Limestone of Yorkshire, Northeast England. *Society of Economic Paleontologists and Mineralogists Special Publication* **30**, 187–202.

Smith, D.B. and Taylor, J.C.M. 1992. Permian. *Geological Society, London, Memoirs* **13**, 87–96.

Smith, D.G. 1985. *Lophopodella carteri* (Hyatt), *Pottsiella erecta* (Potts) and other freshwater Ectoprocta in the Connecticut River (New England, USA). *Ohio Journal of Science* **85**, 67–70.

Smith, D.G. 1988. *Stephanella hina* (Ectoprocta: Phylactolaemata) in North America, with notes on its morphology and systematics. *Journal of the North American Benthological Society* **7**, 253–259.

Smith, D.G. 1989. *Keys to the freshwater macroinvertebrates of Massachusetts 4: Benthic Colonial Phyla*. Massachusetts Department of Environmental Quality Engineering, Division of Water Pollution Control, Westborough, MA., 48 pp.

Smith, D.G. 1992. A new freshwater moss animal in the genus *Plumatella* (Ectoprocta: Phylactolaemata: Plumatellidae). *Canadian Journal of Zoology* **70**, 2192–2201.

Smith, D.G. 1993. On a freshwater moss-animal (Ectoprocta) from St John, US Virgin Islands. *Caribbean Journal of Science* **29**, 214–219.

Smith, D.G. 2001. *Pennak's freshwater invertebrates of the United States - Porifera to Crustacea* Fourth Edition. John Wiley and Sons, New York, 638 pp.

Smith, D.G., Werle, S.F. and Klekowski, E. 2003. The anatomy and brooding biology of *Pottsiella erecta* (Potts, 1884) (Ectoprocta: Gymnolaemata: Ctenostomata), with an expanded diagnosis of the Pottsiellidae. *Hydrobiologia* **490**, 135–145.

Smith, D.G. and Wood, T.S. 1995. A review of *Plumatella javanica* Kraepelin 1906 (Ectoprocta) with a reassessment of statoblast morphology. *Tropical Zoology* **8**, 361–366.

Smith, F. and Gordon, D.P. 2003. Sessile invertebrates, pp. 80–91. In: N. Andrew and M.P. Francis (eds). *The Living Reef: The Ecology of New Zealand's Rocky Reefs*. Craig Potton Publishing, Nelson.

Smith, J.P. 1896. Marine fossils from the Coal Measures of Arkansas. *Proceedings of the American Philosophical Society* **35**, 213–285.

Smith, L.W. 1973. Ultrastructure of the tentacles of *Flustrellidra hispida* (Fabricius), pp. 335–342. In: G.P. Larwood (ed.). *Living and Fossil Bryozoa*. Academic Press, London.

Smith, R.I. 1964. *Keys to Marine Invertebrates of the Woods Hole Region: a manual for* *the identification of the more common marine invertebrates*. Contribution No. 11, Systematics-Ecology Program, Marine Biological Laboratory, Woods Hole.

Smith, S., 1930. Some Valentian corals from Shropshire and Montgomeryshire, with a note on a new stromatoporoid. *Quarterly Journal of the Geological Society (London)* **82**, 291–326.

Smith, S.V. 1972. Production of calcium carbonate on the mainland shelf of southern California. *Limnology and Oceanography* **17**, 28–41.

Smitt, F.A. 1865. Kritisk förteckning öfver Skandinaviens Hafs-Bryozoer: Pt I. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar* **22**, 115–149.

Smitt, F.A. 1867. Kritisk förteckning öfver Skandinaviens Hafs-Bryozoer. II. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar* **23**, 395–534.

Smitt, F.A. 1868a. Kritisk förteckning öfver Skandinaviens Hafs-Bryozoer: Pt III. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar* **24**, 279–429.

Smitt, F.A. 1868b. Kritisk förteckning öfver Skandinaviens Hafs-Bryozoer. IV. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar* **25**, 3–230.

Smitt, F.A. 1868c. Bryozoa marina in regionibus arcticis et borealibus viventia recensuit. *fversigt af Kongliga Vetenskaps-Akademiens Förhandlingar* **24**, 443–487.

Smitt, F.A. 1872a. Floridan Bryozoa collected by Count L.F. de Pourtales, Part 1. *Kongliga Svenska Vetenskaps-Akademiens Handlingar* **10**, 1–20.

Smitt, F.A. 1872b. Kritisk förteckning fver Skandinaviens Hafs-Bryozoer, Part V. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar* **28**, 1115–1134.

Smitt, F.A. 1873. Floridan Bryozoa collected by Count L.F. de Pourtales, Part 2. *Kongliga Svenska Vetenskaps-Akademiens Handlingar* **11**, 1–83.

Smitt, F.A. 1876. Kritisk förteckning öfver Skandinaviens Hafs-Bryozoer. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar* **24**, 3–230.

Smitt, F.A., 1879a. Recensio systematica animalium Bryozoorum, quae in iterinibus, annis 1875 et 1876 ad insulas Novaja Semlja. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar* **35**, 11–26.

Smitt, F.A. 1879b. Recensio animalium Bryozoorume e mari arctico, quae ad paeninsulam Kola, in itinerare anno 1877. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar* **35**, 19–32.

Smitt, F.A. 1896. *La filiation des Espces d'Animaux*. pp. 235–238. In *CR des seances 3-me Congrès Intern Zool Leyde* 1895.

Smitt, F.A. 1899. Preliminary notes on the arrangement of the genus *Gobius*, with an enumeration of its European species. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar* **56**, 543–555.

Smyth, T.J. 1994. The distribution of freshwater Bryozoa in Ireland. *Bulletin of the Irish Biogeographical Society* **17**, 9–22.

Smyth, T.J. and Reynolds, J.D. 1995. Survival ability of statoblasts of freshwater Bryozoa found in Renvyle Lough, County Galway. *Biology and Environment* **95B**, 65–68.

Soule, J.D., Soule, D.F. and Pinter, P.A. 1975. Phylum Ectoprocta (Bryozoa), pp. 579–608. In: R.I. Smith and J.T. Carlton (eds). *Light's manual: intertidal invertebrates of* *the central California coast*. 3rd edition. University of California Press, Berkeley, Los Angeles.

Stanwell-Smith, D. and Barnes, D.K.A. 1997. Benthic community development in Antarctica: recruitment and growth on settlement panels at Signy Island. *Journal of Experimental Marine Biology and Ecology* **212**, 61–79.

Steger, K.K. and Smith, A.M. 2005. Carbonate mineralogy of free-living bryozoans (Bryozoa: Otionellidae), Otago shelf, southern New Zealand. *Palaeogeography, Palaeoclimatology, Palaeoecology* **218**, 195–203.

Tavener-Smith, R. 1965a. A new fenestrate bryozoan from the Lower Carboniferous of County Fermanagh. *Palaeontology* **8**, 478–491.

Tavener-Smith, R. 1965b. A revision of *Retepora nodulosa* Phillips, 1836. *Geological Magazine* **102**, 135–142.

Tavener-Smith, R. 1966a. The micrometric formula and the classification of fenestrate cryptostomes. *Palaeontology* **9**, 413–425.

Tavener-Smith, R 1966b. Ovicells in fenestrate cryptostomes of Visean age. *Journal of Paleontology* **40**, 190–198.

Tavener-Smith, R. 1968. Skeletal structure and growth in the Fenestellidae (Bryozoa) (Preliminary Report). *Atti della Società Italiana di scienze naturali, e del Museo civico di storia naturale. Milano* **108**, 85–92.

Tavener-Smith, R. 1969a. Wall structure and acanthopores in the bryozoan *Leioclema asperum. Lethaia* **4**, 89–97.

Tavener-Smith, R. 1969b. Skeletal structure and growth in the Fenestellidae (Bryozoa). *Palaeontology* **12**, 281–309.

Tavener-Smith, R. 1971. *Polypora stenostoma*, a Carboniferous bryozoan with cheilostomatous features. *Palaeontology* **14**, 178–187.

Tavener-Smith, R. 1973a. Fenestrate Bryozoa from the Visean of County Fermanagh, Ireland. *Bulletin of the British Museum (Natural History) (Geology)* **23**, 391–493.

Tavener-Smith, R. 1973b. Some aspects of skeletal organization in Bryozoa, pp. 349–359. In: G.P. Larwood (ed.). *Living and Fossil Bryozoa*. Academic Press, London.

Tavener-Smith, R. 1974. Early growth stages in rhabdomesoid bryozoans from the Lower Carboniferous of Hook Head, Ireland. *Palaeontology* **17**, 149–164.

Tavener-Smith, R. 1975. The phylogenetic affinities of fenestelloid bryozoans. *Palaeontology* **18**, 1–17.

Tavener-Smith, R. 1981. The neotype of *Retepora nodulosa* Phillips, 1836. *Geological Magazine*, **118**, 565.

Tavener-Smith, R. and Williams, A. 1970. Structure of the compensation sac in two ascophoran bryozoans. *Proceedings of the Royal Society London Series B* **175**, 235–254.

Tavener-Smith, R. and Williams, A. 1972. The secretion and structure of the skeleton of living and fossil Bryozoa. *Philosophical Transactions of the Royal Society of London* **264**, 97–159.

Thomas, H.D. 1955. Obituary: Dr. Stanley Smith. *Nature* **176**, 377.

Wejnert, K.E. and Smith, A.M. 2008. Within-colony variation in skeletal mineralogy of *Adeonellopsis* sp. (Cheilostomata: Bryozoa) from New Zealand. *New Zealand Journal of Marine and Freshwater Research* **42b** 389–395.

Winston, J.E., 2005. *Re-description and revision of Smitt's "Floridan Bryozoa" in the collection of the Museum of Comparative Zoology, Harvard University*. Virginia Museum of Natural History Memoir **14**, 1–148.

Winston, J.E. 2014. Mary Dora Rogick: Mid-Century Nexus of Bryozoology, pp. 195–229. In P.N. Wyse Jackson and M.E. Spencer Jones (eds). *Annals of Bryozoology 4*. International Bryozoology Association, Dublin.

Wood, A.C.L., Probert, P.K., Rowden, A.A. and Smith, A.M. 2012. Complex habitat generated by marine bryozoans: a review of its distribution, structure, diversity, threats and conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems* **22**, 547–563.

Reginald Marr Brydone (1873–1943) and his scientific animosity with William Dickson Lang (1878–1966)

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1. Introduction

With so few practitioners and so much to study, bryozoology is seldom a contentious branch of science. But in the early years of the 20th century an animosity developed between two palaeobryozoologists – R. M. Brydone and W. D. Lang – who were both studying cheilostome bryozoans from the Late Cretaceous Chalk of England. The dispute between Brydone and Lang must be viewed in the context of differences in their backgrounds, as well as contrasting approaches to the description and illustration of fossil bryozoans. A peak of acrimony was reached in the privately published monograph of Brydone (1929), which was highly critical of Lang's research, referring to him in derogatory terms as a "salaried public servant" (ibid, p. 9).

Whereas the life and works of Lang are reasonably well known, those of Brydone have been scarcely documented. The objectives of this paper are to provide a first biography of Brydone, based on the scant source material that is available, and to discuss the history and likely reasons for his conflict with Lang. On a more general level, the discord between these two bryozoologists epitomises the resentments and tensions that sometimes develop between non-vocational ('amateur') palaeontologists who undertake their work as an unpaid hobby, and vocational ('professional') palaeontologists paid to study fossils.

2. W. D. Lang

As a Fellow of the Royal Society, William Dickson Lang was accorded a posthumous memoir containing a comprehensive account of his life and work (White 1966). In addition, Taylor (2002) and Sendino (2014) have also summarized his ideas about orthogenesis (see below) and the conservation of his material, respectively. Therefore, only a brief biography is given here.

Lang was born in 1878 in the Punjab, India, where his father was an engineer. A year after William's birth, the worsening health of his father forced the family to return to Britain where they made their home in Harrow, NW London. One year later, Lang's father died. Lang's secondary education was received at the famous Harrow School from where he was admitted to Pembroke College, Cambridge University in 1898, reading the Natural Sciences Tripos with Zoology and gaining a Second Class degree in 1902 and an M.A. in 1903. On the first day of October 1902 he entered the employment of the British Museum (Natural History) in South Kensington, London, where he was to spend the rest of his working life. He became Deputy Keeper of Geology in 1927 and Keeper the following year, retiring in 1938 and moving from London to a home he had built for his family in Charmouth, Dorset, apparently never to reappear at the BM(NH). Lang died in Dorset on March 3rd 1966, aged 89. He was survived by his wife Georgiana Catherine Dixon, who he had married in 1908, and their son Geoffrey and daughter Brenda.

Lang developed an interest in the geology and fossils of Dorset as early as 1898 when he was still a Cambridge student. Indeed, outside bryozoology he is best known for his publications on the stratigraphy of the Lias (Early Jurassic) rocks around Lyme Regis. At the BM(NH) he was put in charge of fossil protozoans, sponges, corals, bryozoans and miscellaneous smaller groups. The huge number of bryozoan specimens personally registered into the BM(NH) collections by Lang testify to his hard work and energy as a curator. Despite producing a few publications on Jurassic cyclostomes, his main research focus was on Cretaceous bryozoans, particularly cribrimorph cheilostomes, culminating in a two-part monograph in the guise of a catalogue of cribrimorphs in the BM(NH) collections (Lang 1921, 1922).

Lang was a leading advocate of the theory of orthogenesis, the notion that evolution occurred along predetermined pathways initiated at the start of a lineage, which at least in their later stages were non-adaptive and eventually led to the extinction of the lineage. In the case of cribrimorphs, Lang identified multiple lineages he considered to have independently undergone increasing calcification of the frontal shield through the Late Cretaceous, culminating in extinction through self-entombment of their zooids (Taylor 2002). Lang supposed that over-calcification occurred after the removal of inhibitions that had prevented it from happening in the early representatives of the lineages. Lang's application of orthogenesis to cribrimorphs represented one of the most complete for any group of fossils (Bowler 1983). However, the tide had turned against the once popular theory of orthogenesis by the time of Lang's work and his ideas were severely criticised by other palaeontologists, Brydone included (see below).

3. R. M. Brydone

Very little has been written about the life of Brydone. The biography below was put together mostly from his obituaries (Ellis 1944; Lang 1944), information provided by his school (Suzanne Foster, pers comm., 6 September 2016), his Oxford college (Jennifer Thorp, pers comm., 9 February 2016), a file of the correspondence he and his widow had with the Sedgwick Museum, and miscellaneous directories. We know of no portrait of Brydone as an adult but he can be seen as a youth in a couple of photographs of Winchester College scholars, one of which is reproduced here (Figure 1).

Reginald Marr Brydone was born on 27th July 1873 in Petworth, a small town in West Sussex, England. His mother was Amy Elizabeth Turner. His father Henry Gray Brydone was one of the four children of James Marr Brydone (1779–1866), a Scottish surgeon with the Royal Navy who was famous for being the first person to sight the Franco-Spanish fleet

Figure 1. Winchester College Scholars photographed in 1889. Brydone, who would have been 15 or 16 years old at the time, is indicated by the white rectangle. Photograph courtesy of the Warden and Scholars of Winchester College.

at the Battle of Trafalgar in 1805. After serving as a Surgeon Superintendent on an Australia-bound convict ship, J. M. Brydone worked for George Wyndham, the son of the 3rd Earl of Egremont of Petworth House, and the Brydone family established its roots in Petworth, Sussex. Reginald's father, H. G. Brydone, became a lawyer. In 1867, he was listed in Kelly's Post Office Directory as solicitor and steward of the honor and manor of Petworth, as well as steward to Lord Leconfield. On his death in 1901 the estate of H. G. Brydone was left to Reginald. This amounted to the not inconsiderable sum of £12,002 1s, which is equivalent to over £1,330,000 in today's money.

In September 1886, R. M. Brydone became a pupil at Winchester College, a prestigious public school in Hampshire established in 1382, initially as a fee paying 'Commoner' but from September 1887 as a scholar, which allowed him the privilege of living in one of the original buildings of the College. Information kindly provided by the Winchester College archivist shows that Brydone was a keen sportsman, playing 'Winchester Fives' (a rare variety of handball), cricket and football, the latter continuing after he had left Winchester when he played for the Old Wykehamist XI. He was also a rower and a gymnast. While at Winchester College he developed an interest in geology through Charles Griffith, an Assistant Master at Winchester between 1859 and 1902. Ellis (1944) recorded that the young Brydone undertook geological fieldwork with Griffith, and the 25th November 1942 edition of the Winchester College journal *The Wykehamist* stated (p. 377): "Together they tramped the greater part of the countryside of Hampshire and the neighbouring counties, searching for specimens". These collecting trips were evidently not in vain as Brydone was awarded a prize for the best collection of fossils at a meeting of the Natural History Society of the College on 25th July 1891. He had previously won a prize for science in 1889 and was subsequently awarded a 'leaving exhibition' on departing the College.

Brydone was admitted to New College, Oxford University in 1892, matriculating with a First in Classics Moderations in 1894. The following year he was elected to a Burdett-Coutts Scholarship, a university award for the study of geology with an annual value at the time of £115. In 1896 he graduated from Oxford with a First in Natural Sciences (Geology). Despite his success in geology, Brydone's subsequent career was as a solicitor, following in the footsteps of his father. Little is known about this side of Brydone's life, although a register of former pupils at Winchester College (Wainewright 1907, p. 457) states that he achieved 1st Class Honours as a solicitor in 1900, was awarded the New Inn Prize and the Mellersh Prize, and at that time was practising his profession at 16 South Audley Street, which is in the exclusive Mayfair district of London. This is consistent with evidence from a census, telephone directories and correspondence showing that Brydone lived in London during the early years of the 20th century: in 1904 he was renting rooms at 152 Cambridge Street, Hanover Square; by 1911 he had moved to Twyford Mansions, Marylebone; and in 1927 to Maybury Mansions, Paddington. The obituary of Brydone in the 20th October 1943 edition of *The Wykemist* (p. 438) notes in addition that he served for many years as Secretary to the Trustees of the Stock Exchange in London.

Brydone acquired a house in Mundesley, Norfolk, to which he retired in 1918 after the onset of periostitis of the femur, a debilitating illness that he was to endure for the rest of his life. Despite his illness, Brydone wrote a letter dated 4th August 1939 to A. G. Brighton of the Sedgwick Museum, Cambridge reporting that he was able to revisit some localities after about 1923 when he "became able to ride a bicycle after a fashion".

After spending the first sixty years of his life as a bachelor, he married Edith Eleanor Lawford in 1933 (*Cryptostoma eleanorae* Brydone, 1936 was dedicated to his wife). Brydone died ten years later, on 6th August 1943, aged 70, following a few weeks of illness. In his will he left effects to the value of £12,997 15s 5d (equivalent to about £550,000 in today's money) to his widow who remained at Ivy Farm House, Mundesley, with her daughter after Reginald's death.

4. Brydone's publications

Brydone published his first paper privately in 1900. This described the geology and fossils of the Chalk at Trimingham in Norfolk, based on visits he had made there between 1896 and 1900. The style of writing is mature and authoritative, and the young Brydone does not hold back in contesting the work of Clement Reid (1853–1916), a distinguished geologist with the Geological Survey. Thirty-six species of bryozoans are included in a faunal list, many of which were originally described from Rügen in Germany. Brydone (1900, p. 13) noted: "The Polyzoa are so significant that I thought it well to indicate the reported occurrences of the more peculiar forms." The seeds of his future interest and his prolific output as a bryozoan taxonomist can perhaps be found in this statement.

Between 1906 and 1942, Brydone published a further 55 papers: 21 of these concerned the Chalk and its stratigraphy (Brydone 1906a, b, c, d, e, 1908, 1913e, 1914d, e, f, g, 1915, 1917d, 1918c, 1920, 1930a, b, 1931, 1932a, b, c), and one focused on bryozoan nomenclature (Brydone 1941). However, the majority of Brydone's publications comprised descriptions of 'new or imperfectly known' Chalk bryozoans, 30 published in the *Geological Magazine* (1909a, b, 1910a, b, c, d, e, f, 1911, 1912a, b, c, d, 1913a, b, c, d, 1914a, b, c, 1916a, b, c, d, 1917a, b, c, 1918a, b, 1942) and three published privately (Brydone 1929, 1930b, 1936).

Brydone's first taxonomic descriptions of bryozoans appeared in a paper published in 1906 (Brydone 1906e). He introduced 13 new species from the Chalk of Trimingham, Norfolk and elsewhere, one of which – *Membranipora griffithi* – was dedicated to his friend from Winchester, Charles Griffith, who had introduced him to geology. The accompanying figures are tiny and somewhat crude drawings showing small groups of zooids (Figure 2). These figures had apparently been shown to Lang before publication of the paper (see below). To his credit, Brydone paid attention to ovicells and avicularia whenever they were present. On the other hand, the localities of his new species are not always stated, nor are all of the new taxa compared with existing species. This paper sets out the principles Brydone applied to bryozoan taxonomy. In particular, he considered that: "... the rigid application to Cretaceous forms of canons of classification derived from the study of Tertiary and recent forms is very undesirable." (Brydone 1906e, p. 290). He also doubted the wisdom of the then common practise of assigning Cretaceous bryozoans

Fig. 1. Fig. 4. Fig. 8. Fig. 13.

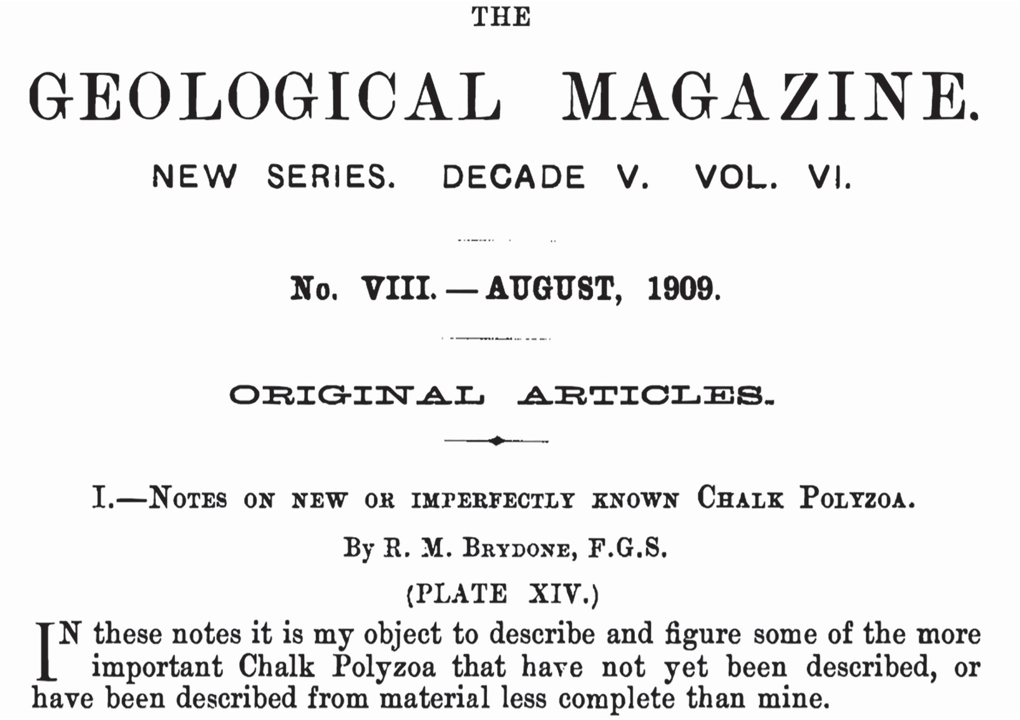
Figure 2. Reproductions of some of the tiny drawings from Brydone's first paper to describe bryozoans (Brydone 1906e). It was these drawings, or their forerunners, that Lang referred to as 'diagrams', much to the displeasure of Brydone. The species illustrated are new, all from the Cretaceous Chalk of Trimingham, Norfolk. They are: Membranipora griffithi *(fig. 1), named for his friend and former master at Winchester College Charles Griffith who introduced him to geology;* Semieschara mundesleiensis *(fig. 4), showing four autozooids, an ovicell (bottom left) and two avicularia (top right);* Cribrilina dibleyi *(fig. 8), a cribrimorph subsequently assigned to* Castanopora *by Lang (1916a); and* Cribrilina gregoryi *(fig. 13), a cribrimorph placed by Lang (1916a) in* Pelmatopora.

to modern species, and on the taxonomic significance of colony-form.

In 1909 the first of the series *Notes on new or imperfectly known Chalk Polyzoa* was published in the *Geological Magazine* (Brydone 1909a) (Figure 3). This and subsequent papers were only a few pages in length and were illustrated by plates comprising typically retouched photographs of bryozoans and occasional line drawings. Among these papers, Brydone (1917a) is particularly interesting in the present context as it contains the first criticisms of Lang's newly published revisions of Cretaceous cribrimorphs (Lang 1916a, b). While agreeing with Lang's opinion that the characters distinguishing between the two extant genera previously used for Cretaceous cribrimorphs – *Cribrilina* and *Membraniporella* – are not of generic significance, he was understandably sceptical of Lang's creation of more than 50 new Cretaceous genera to replace them. Brydone bemoaned the complete lack of figures and the brevity of the generic and specific descriptions in Lang's papers. The impossibility of recognizing Lang's genera is clear from Brydone's next two papers (Brydone 1917b, c) in which he continued to place new Cretaceous cribrimorph species into the Recent genera *Cribrilina* and *Membraniporella* rather than attempting to use Lang's new Cretaceous genera.

When he had recovered sufficiently from his illness, Brydone resumed publishing on Chalk bryozoans. The fruits of his labours were the three-part *Further notes on new or imperfectly known Chalk Polyzoa* (Brydone 1929, 1930b, 1936), published privately and printed by Dulau & Co. Ltd. of 32 Old Bond Street, London. Yet more new species were introduced, especially of the ubiquitous '*Membranipora*', and some of his previously published species were revised (as Medd 1965 has pointed out, all of the species assigned by Brydone to *Membranipora* must be transferred to other genera). The monograph features 42 plates of retouched photographs.

The Appendix to the current paper lists all of the 452 bryozoan species and varieties introduced by Brydone.



THE

GEOLOGICAL MAGAZINE.

NEW SERIES. DECADE V. VOL. VI.

No. VIII.—AUGUST, 1909.

ORIGINAL ARTICLES.

I.—NOTES ON NEW OR IMPERFECTLY KNOWN CHALK POLYZOA.

By R. M. BRYDONE, F.G.S.

(PLATE XIV.)

IN these notes it is my object to describe and figure some of the more important Chalk Polyzoa that have not yet been described, or have been described from material less complete than mine.

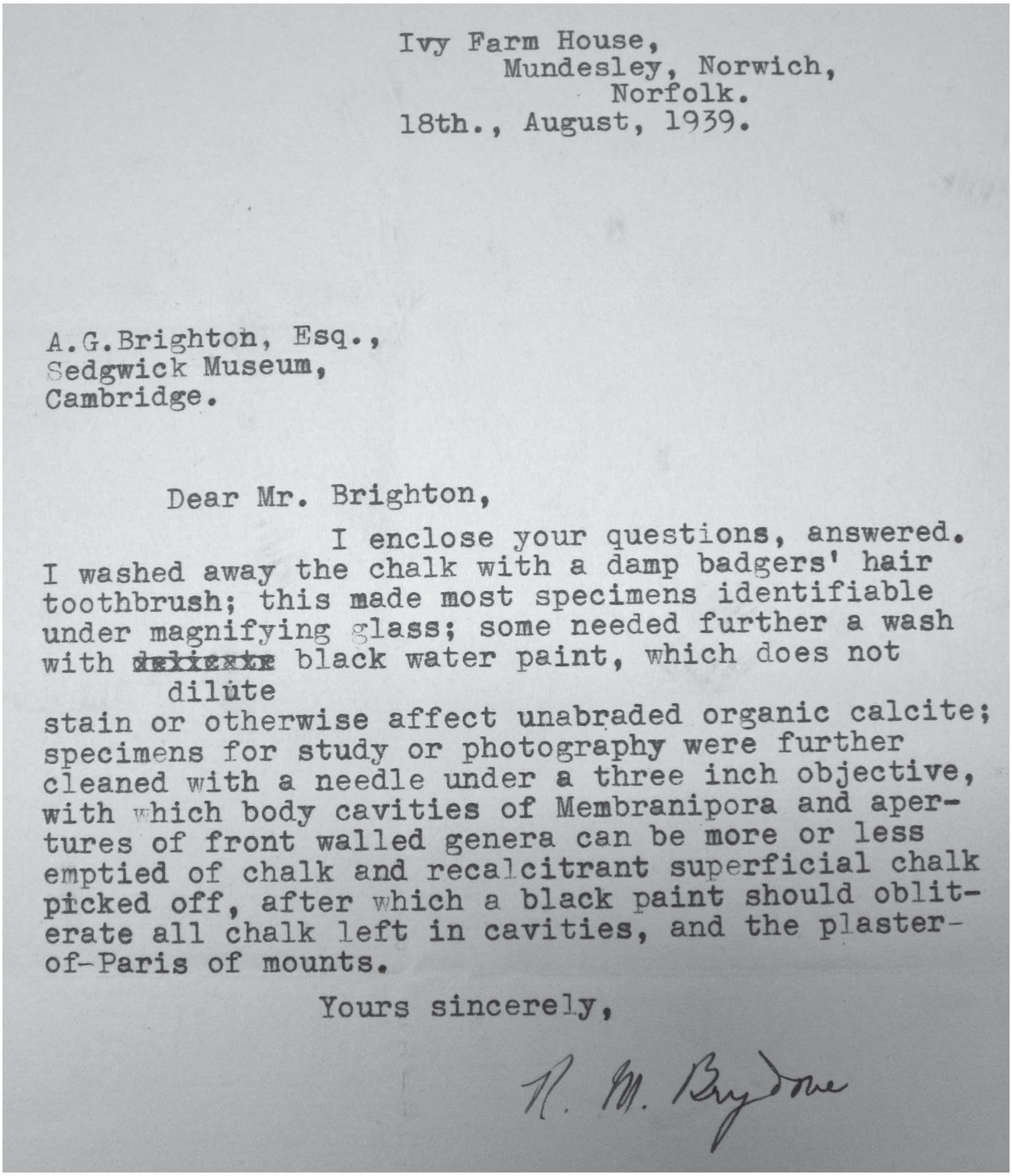
Figure 3. Title and opening paragraph of Brydone (1909a), the first of the long series of papers published in the Geological Magazine *describing Chalk bryozoans.*

5. The conflict between Brydone and Lang

Brydone's self-published monograph

While Lang's view of his conflict with Brydone must be understood from the contents of his letter to Edwards (see below), Brydone's side is made explicit from the Introduction to his three-part, privately published monograph (Brydone 1929, 1930b, 1936) (a letter in the Sedgwick Museum archive written by Brydone to A.G. Brighton and dated 18th July 1942 mentions that he was preparing a fourth part). Brydone devoted no fewer than seven pages to criticising Lang in this work. The areas of criticism were: (1) orthogenesis; (2) introduction of new taxa without figures; (3) usefulness of brief diagnoses; (4) interpretation of colony-forms; (5) intraspecific variability; (6) observation of minute features; and (7) use of staining.

(1) Orthogenesis. Lang's elaborate view of orthogenesis has been detailed elsewhere (Taylor 2002). Without mentioning Lang's name, Brydone is scornful in his criticism of Lang's interpretation of bryozoan evolution in terms of orthogenesis and the progressive removal of inhibitions to over-calcification:



Ivy Farm House,
Mundesley, Norwich,
Norfolk.
18th., August, 1939.

A.G.Brighton, Esq.,
Sedgwick Museum,
Cambridge.

Dear Mr. Brighton,

I enclose your questions, answered. I washed away the chalk with a damp badgers' hair toothbrush; this made most specimens identifiable under magnifying glass; some needed further a wash with ~~delicate~~ dilute black water paint, which does not stain or otherwise affect unabraded organic calcite; specimens for study or photography were further cleaned with a needle under a three inch objective, with which body cavities of Membranipora and apertures of front walled genera can be more or less emptied of chalk and recalcitrant superficial chalk picked off, after which a black paint should obliterate all chalk left in cavities, and the plaster-of-Paris of mounts.

Yours sincerely,

R. M. Brydone

Figure 4. Signed letter from R. M. Brydone to A. G. ('Bertie') Brighton of the Sedgwick Museum, Cambridge, offering advice about the cleaning and staining of Chalk bryozoans.

"A theory of this kind is almost as elusive as a Christian Science argument. It starts by assuming a general tendency to secrete a hard skeleton. That assumption may be described as plausible on the ground that many animals succeed in doing it. It may also be described as improbable on the ground that many animals do not do so or only do so to a neglibible extent. The theory then proceeds to assume the existence of an inhibition. Here we at once part company with reality. An inhibition being wholly negative is incapable of demonstration: it is purely imagined

> and extremely vague. How, for instance, is the inhibition imposed, and by what power?" (Brydone 1929, p. 6).

The ridicule continues:

> "Hard skeletons become a menace instead of a strength or protection….Life is really gradual suicide. The jelly-fish and the slug take rank in the highest moral class as either being free from all desire for suicide or having got the desire under very effective control." (Brydone 1929, p. 7).

(2) Introduction of new taxa without figures. Brydone (1929) repeated his earlier criticism (Brydone 1917) of Lang (1916a, b) in which new taxa were introduced without illustration. Accompanied by nothing more than a very brief description, this rendered Lang's new species unidentifiable. An unfortunate consequence of Lang's inadequate descriptions was that a couple of species created by Brydone – *Membraniporella altonensis* Brydone, 1918a and *M. pyramidalis* Brydone, 1917b – turned out to have been described already by Lang (1916a, b) as *Thoracopora costata* Lang, 1916b and *Tricephalopora obducta* Lang, 1916a, respectively, if the synonymies given by Lang (1921, 1922) are to be accepted. Brydone (1929, p. 8) went on to assert: "… there is ample justification for refusing to recognise any recent description of a Polyzoon unaccompanied by a figure.." With some justification, Brydone objected to the habit of Lang, and J. W. Gregory before him, of publishing 'pre-emptive' short descriptions of new species in journal papers before providing more comprehensive and illustrated descriptions of the same species in their catalogues of bryozoans in the British Museum (Natural History): "The procedure is perhaps least commendable when it is adopted by salaried public servants, and the cream of the work they have been paid to do is not enjoyed by their employers but is skimmed for the private advantage of some publisher." (Brydone 1929, p. 9). In fact, Lang's (1916a, b) 'descriptions' take the form of a series of hierarchically arranged 'Tabular Diagnoses', from subfamilies to genera to species. Unaccompanied by figures, they are of little use for identifying cribrimorph species.

(3) Usefulness of brief diagnoses. Brydone (1929, p. 8) was scathing in his criticism of Lang's brief taxonomic diagnoses, stating: "It is not indeed possible for these diagnoises to constitute definitions of any species: they do not contain a single word referring to an individual character, much less any word describing any individual character; and a species without any individual character is obviously no species. It is no exaggeration to say that dozens of different species might fall within every word of any of these "diagnoses"….If Lang's "diagnoses" are to be accepted as valid descriptions of species we must regard precision and thoroughness as unscientific and foolish."

(4) Interpretation of colony-forms. Brydone took issue with Lang who created different species for otherwise identical bryozoans if they are found encrusting a hard substrate or are unattached, as well as his use of the term 'erect' as a synonym of 'free'. With regard

to the former, he pointed out that colonies of the commonest Chalk cribrimorph, *Cribrilina* [*Pelmatopora*] *gregoryi*, could be found either encrusting or free.

(5) Intraspecific variability. In Brydone's opinion, Lang used minor differences of no taxonomic value to differentiate between some of the species he published in 1916 (Lang 1916a, b). Small differences in zooidal length, for example, were not significant as this character could be observed to vary within a single colony. "We do not make separate species of men or brachiopods or corals for every difference in their length" (Brydone 1929, p. 10). Likewise, Brydone considered Lang's taxonomic use of differences in numbers of spines and sizes of avicularia to be unjustifiable.

(6) Observation of minute features. Brydone was troubled by Lang's observation and use of minute pores – pelmata – in the costae for his family Pelmatoporidae: "I am unable to concur at all in his observations of the presence of conspicuous or very regular pelmata.." (Brydone 1929, p. 12). Even if pelmata are present, Brydone believed that because they are invisible under a 'pocket magnifier', they are 'disqualified' for use in making distinctions between species. Of course with the benefit of modern microscopy including SEM, it is now clear that pelmata are indeed present in many Cretaceous cribrimorphs and should not be neglected.

(7) Use of staining. Brydone believed that Lang's habit of permanently staining specimens may have introduced artefacts, explaining not only the existence of pelmata but also of some of the apparent avicularia described by Lang. What appear to be cavities could be simply unevenly stained patches. For Brydone (1929, p. 13) staining ".. is a practice which I must deprecate. Anyone who has experimented on the application of stains to organic calcite–as, for instance, in marking (or trying to mark) fossils with their localities in ink–knows how erratically the stain behaves, and how unreliable, therefore, must any theories be which are based on appearances resulting from the application of stains to calcite. It must be obvious that a specimen which has been artificially stained cannot be a type of any species intended–as presumable fossil species are intended–for the reception of fossils in their natural state. You might almost as well stain a bluebell black and call it a typical bluebell."

It seems somewhat contradictory of Brydone to write a letter to A. G. Brighton dated 18th August 1939 with the advice that Chalk bryozoans should be washed and subsequently stained with black water-colour paint (Figure 4). Perhaps in the ten years between his adverse comments about staining and the writing of this letter he had a change of opinion?

Lang's letter to Edwards about Brydone

The clearest insight into dispute between Brydone and Lang, at least from Lang's standpoint, can be obtained from a letter written by Lang in 1944 to his successor as Keeper of Geology at the British Museum (Natural History), Wilford Norman Edwards

(1890–1956), concerning a draft obituary of Brydone (Lang 1944). This letter was formerly taped to the inside of the museum library's bound copy of Brydone's three privately published papers but now resides in the archives (Figure 5). Because of the importance of the letter in understanding the relationship between Brydone and Lang, an entire transcript is given below.

Lias Lea
Charmouth
Bridport
3. xi. 1944

Dear Edwards,

I enclose a draft of an obituary of Brydone, in which I have incorporated the information you have so kindly collected for me and sent with your letter this morning.

Would you mind looking this through, and if you approve of it, perhaps it would be as well not to wait for the date of B[rydone]'s birth (which only matters for the sake of future researchers, who would turn to an obituary in a scientific journal first of all if they wished to find this out), and if the Geol. Soc. [Geological Society of London] are in a hurry, could you send it to them?

If you have comments to make, will you return the draft to me with your criticisms, that I may consider them?

It has long been on my conscience that, probably by lack of perception and tact, I alienated Brydone's material from the museum; and on having to write this obituary, I have been trying to remember exactly all my dealings with him. I can only recall that I met him twice. On the first occasion (when of course I did not know how sensitive he was) I caused him considerable annoyance by calling his drawings 'diagrams'. It was his drawings for the figures on pp. 293–300 of the Geol. Mag. 1906, dec 5, vol iii, which Dr Henry [Woodward] sent round to Gertrude W. [Woodward] to touch up, and Brydone brought to me (I suppose at Dr H's request) for my comment. This was (as far as I remember) that the diagrams seemed rather woolly and would be better if the detail could be brought out. Probably B[rydone] had drawn them under a camera lucida with great care, and since they were meant to represent the actual appearance of the specimen, my careless expression 'diagram' offended him. It was a bad beginning, but too trivial for the consequences, if it led to the Museum losing B[rydones]'s stuff! He told me then (or about then, possibly by letter) that he would give the museum types or at least named material of his new species, and he did so with the earliest new species he described.

I feel more culpable for probably having been the cause of Dr Henry's discontinuing B[rydone]'s articles on new Chalk Polyzoa, in the Geol. Mag. (but see post-script. Could it have been Rastall? but I think not). After several of these had appeared, Dr H[enry Woodward] asked me if I thought he had better continue them. Of course I did not advise him one way or the other, but tried to give him as disinterested a view of their value as I could – which was not easy since I was the immediate victim of the disadvantages arising, as I thought, from the articles. They were these: undoubtedly it was desirable to monograph the Chalk Cheilostomes so that the new British forms should have names for reference. But Brydone was not monographing in the full sense, [he] merely named, describing, figuring what he considered new forms, and only to some extent comparing them with previously described species. This looked like giving the succeeding monographer a deal of trouble in addition to having to do what Brydone has left undone. Also

I considered that for this thorough work B[rydone]'s descriptions and figures were inadequate, as without supplementary diagrams, the photographs did not show sufficient detail (e.g. the presence or absence and number of spines surrounding the apertures). Had I been more experience in monographs and monographers, I might have thought less of their troubles and more of the convenience of Chalk-workers who needed names of Chalk fossils for me during their life-times, more than scholarly monographs next century perhaps. All I know is that Dr H[enry Woodward] did discontinue the series as a sequel to his conversation with me, and it is natural that (if Brydone could have known that Dr Henry asked my advice) he should have concluded that I dissuaded Dr H, and felt justified in his arrogance. As you know, he continued his publication on his own.

The other time I met him was when he happened to be in the museum, and must have had something to say or show to me, because in conversation he mentioned that he had a lot of material of a new form I had just described – *Semimultelea dixoni*. I asked him to give the museum some. In a few days he sent it but it turned out to be an already described form (which we were very glad to have) quite different form that I described. That interview was quite smooth, as far as I remember.

Once again, I wrote to him acknowledging a copy of his map and paper on the Hampshire Chalk, telling him how much I admired the work, but suggesting that it might be improved by colouring the zones so as to correspond with Rowe's maps. I suppose I consciously trod on a corn, for it brought a snappy and tart reply. You will say that it was tactless to mention Rowe – but how was I to know?

I can't remember corresponding with him besides, only writing to thank him for sending me his "Further Notes of new… Chalk Polyzoa, Part I." I did not comment on his prefatory remarks except to say that we did not seem to agree altogether in our conclusions. I hoped someday to discuss them. This correspondence was unilateral.

I imagine Brydone's bark was much worse that his bite, and his letters less polished (like Jukes Browne's) than his conversation.

He may, too, have had that feeling, which I am sure Buckman suffered from, that the amateur is at a disadvantage compared with a man whose position is assured by the office he holds. It is true that Buckman's bread and butter depended to some extent on his reputation, while Brydone's did not. But Brydone's reference to the 'salaried public servant' in his damnatory preface shows I think that he felt this disadvantage. Undoubtedly having one's position assured does (though it shouldn't) make it easier to express one's opinions freely in scientific papers.

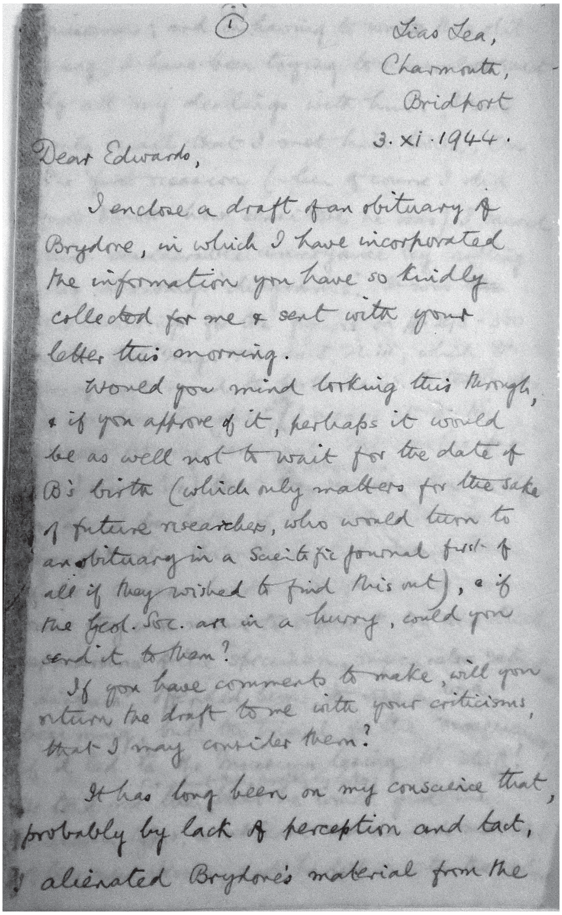
Of course I have often considered answering Brydone's criticisms; but on reading over his introduction have quailed at the magnitude of the task. My work – more, my whole outlook, is one huge fallacy (as Spath remarked of Hyatt's 'Genesis of the Anatidae'). Once one began a defence, it would never end, like even a small controversy. I has hoped that by now some other worker would have gone over the ground and pronounced on how far Brydone's criticisms are justified. For if one takes the trouble to sift out what is merely querulous (like the "salaried public servant"), what is trivial, what is technical (the use of 'type-specimen'), what is due to misunderstanding, and, then is a residuum of criticism which should be taken seriously, but could only be appreciate and appraised by specialists working over the same ground. I had expected and intended Thomas to carry on my work; but he dissipated himself in immediate matters and miscellaneous correspondence; and a specialist cannot be a driven horse.

I am afraid that what began as a post-script, or at the most a excursus, upon the loss to the B.M. of Brydone's collections, has become elongated into an 'apologia pro vita sua in rebus

Brydoneis'. I hope you don't mind acting as my confessor, and if I have sinned in giving Brydone just cause of offence, you will put it down to my inexperience and lack of tact, not to malice, and absolve me –

Yours sincerely
W. D. Lang,

P.S. I can't make my memory about H. H. Woodward and Brydone's publications tally with the dates. Brydone's papers in the Geol. Mag left off in 1918 (when he was ill). His (undated) damnatory publication was acknowledged by me in 1930. He says then that a change in editorship broke his series in the Geol. Mag. When did Dr H. die?



①

Lias Lea,
Charmouth,
Bridport
3. xi. 1944.

Dear Edwards,

I enclose a draft of an obituary of Brydone, in which I have incorporated the information you have so kindly collected for me & sent with your letter this morning.

Would you mind looking this through, & if you approve of it, perhaps it would be as well not to wait for the date of B's birth (which only matters for the sake of future researches, who would turn to an obituary in a Scientific journal first of all if they wished to find this out), & if the Geol. Soc. are in a hurry, could you send it to them?

If you have comments to make, will you return the draft to me with your criticisms, that I may consider them?

It has long been on my conscience that, probably by lack of perception and tact, I alienated Brydone's material from the

Figure 5. First page of the crucial letter written by Lang to W. N. Edwards, Keeper of Geology at the British Museum (Natural History), about the recently deceased Brydone. The letter explained his fraught relationship with Brydone and the reason why Brydone's fossil collections went to the Sedgwick Museum rather than the BM(NH). NHM Library and Archives, Palaeontology collection MSS LAN.

While Lang's main motive for writing this letter was to obtain Edward's permission to submit for publication his obituary of Brydone, it also served as a vehicle for Lang to describe his poor relationship with Brydone. Their adversity was doubtless the reason why Brydone's large important fossil collection, including numerous type bryozoans, was donated in the late 1930s to the Sedgwick Museum in Cambridge rather than to the British Museum (Natural History). For example, judging by correspondence in the Sedgwick Museum the first batch of specimens described by Brydone in his 1916–8 *Geological Magazine* papers was collected by a private car dispatched from Cambridge sometime soon after 8th July 1938. The label accompanying a small display of fossils donated by Brydone states that his donation of 37,659 fossils represents the largest number of fossils originating from a single collector in the Sedgwick Museum. Brydone also donated material to the British Geological Survey, and to museums in Norwich and Ipswich.

The letter not only provides the only significant statement of Lang's side of his dispute with Brydone, but also contains the only documentation of face-to-face meetings between the two. According to Lang, albeit with the possibility of some memory lapse, the two protagonists met only twice. Their first meeting occurred at some unspecified date in the first years of the 20th century, presumably in about 1905, when Brydone visited Lang to obtain his comments on some illustrations of bryozoans that were eventually published in 1906 (Brydone 1906e). Unfortunately, Lang referred to these illustrations as 'diagrams', implying that they were stylistic representations when in fact they were probably accurate drawings made using a camera lucida. The sensitive Brydone evidently took umbrage to this faux pas. Nevertheless, Lang's account of his second meeting with Brydone, again on an unknown date but probably on or very soon after 1906 to judge by the fact that it occurred just after Lang had described the eleid cyclostome *Semimultelea dixoni* Lang, 1906 (now *Reptomultelea dixoni*, see Taylor 1994), seems to have passed off without any animosity. Indeed, in 1910 Brydone dedicated a new species – *Membranipora langi* Brydone, 1910c – to Lang, suggesting that the two meetings did not seriously dent Brydone's regard for Lang.

During the early years of the 20th century when politeness and good manners were held in high esteem, it is unlikely that face-to-face meetings between scientists such as Lang and Brydone would have become incendiary. Nor is it likely that Lang's correspondence with Brydone was sufficient to cause the rift, even though it is clear that Lang's comments may not have been well-received by Brydone, notably his suggestion to use the same zonal colouring scheme as that employed by Rowe in his geological maps. Instead, a more important contributory factor to the problems between the two bryozoologists may be found in Lang's account of the discontinuation of Brydone's publications in the *Geological Magazine*. Although Lang claimed not to have beeen responsible for this action, Brydone apparently believed that Lang's advice to the editor, Henry Woodward, had led to him to decline publication of further submissions from Brydone. According to Lang, when consulted by Woodward he offered no opinion on whether or not to discontinue the series. However, Lang's letter does imply that he might have told Woodward of his dislike of Brydone's approach to species description. The termination of Brydone's publications in the *Geological Magazine* more or less coincided with a period of serious illness in 1918, which must have left him feeling particularly aggrieved and all too willing to seek a scapegoat. Interestingly, Brydone's own explanation (Brydone 1929, p. 5) for the discontinuation of his series in the *Geological Magazine* was that between 1918 and 1920 when he was able to resume his work the editorship of the journal had changed and there was ".. no space available in it." (Brydone 1929, p. 5). Henry Woodward (1832–1921) was the sole editor of the *Geological Magazine* until the end of 1918 (Anon. [Obituary] 1921) when he was joined in this role by R. H. Rastall (1871–1950; see obituary written by Bulman 1950). Perhaps significantly, whereas Woodward was a palaeontologist, Rastall was an economic geologist and petrologist with a "distaste" for palaeontology (Bulman 1950, p. 75). Also worth noting is the fact that, according to Bulman (1950), *Geological Magazine* narrowly escaped extinction in 1918, which might have led to a changed publication policy and greater stringency on what kinds of articles were accepted.

Contrasting approaches to bryozoan research

Whatever factors led to the animosity between Brydone and Lang, one thing is clear – they had very different approaches to the descriptive taxonomy of bryozoans. The contrast is manifested in several ways: mode of acquiring material, illustration, creation of supraspecific taxa, scope of study, and attention to the published literature.

Lang's major and later works on bryozoans all concerned Late Cretaceous cribrimorphs from Britain and elsewhere in Europe; his earlier publications from the period before 1916 were more taxonomically adventurous, covering anascan cheilostomes as well as a few cyclostomes, mostly of Late Cretaceous age but with some descriptions of Jurassic and Early Cretaceous species. In contrast, Brydone focused almost entirely on Late Cretaceous cheilostomes from Britain. Lang had the large international collections of the British Museum (Natural History) at his disposal and there is little indication that he undertook any significant collecting of his own of cribrimorphs. In particular, he made use of continental European material purchased from, or donated by, F. Canu (France), A. Fric (Bohemia) and A. Laur (Germany), as well as various collectors of English Chalk fossils, such as A. W. Rowe (1858–1926), C. T. A. Gaster (1887–1963), F. J. Möckler and the grocer and prison warder William Gamble who sold the BM(NH) large quantities of bryozoans collected from the area around Chatham in Kent (see Lang 1921, pp. lxxii–lxxv). In contrast, Brydone seems to have relied entirely on specimens he collected personally, which explains why the majority of the bryozoans he described are from the English Chalk from the counties where he lived, initially Hampshire and subsequently Norfolk.

Regarding illustration, Brydone's early papers featured small drawings of bryozoan zooids (Figure 2). These are the drawings that Lang unwisely called 'diagrams' in conversation with Brydone. However, the majority of Brydone's papers contain photographs of specimens which he apparently took himself. For their time, these are of excellent quality, although there are clear indications of retouching of opesia, spine bases and

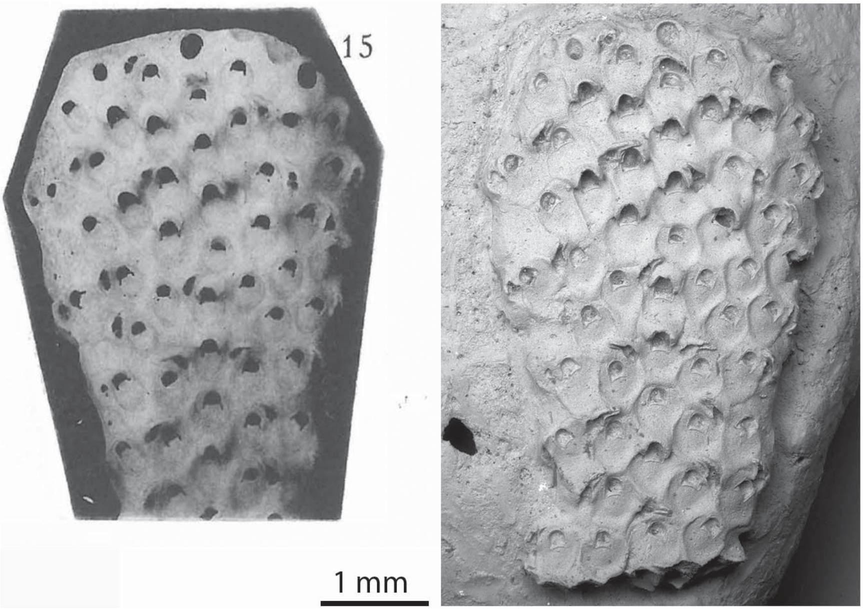


Figure 6. Rhagasostoma gibbosum *(Marsson) as figured by Brydone (1930, pl. 26, fig. 15) compared with a recent SEM image of the same specimen (Sedgwick Museum B36679; Upper Cretaceous,* lunata *Chalk, Trimingham, Norfolk). Note the retouching of Brydone's figure including removal of the background and, importantly, blackening of apertures and opesiules that are filled with white chalk in the specimen itself.*

backgrounds using black ink (Figures 6–7), a practise employed at the same time by the well-known collaborators Canu and Bassler in their papers on bryozoans. Lang never used photographs to illustrate the bryozoans he described. Instead he relied on a combination of ink wash drawings of groups of zooids, executed by Miss Gertrude M. Woodward, and highly stylized diagrams of single zooids that he himself drew (Figure 7). The latter formed a crucial element in his definitions of cribrimorph taxa. Moreover, Brydone (1917a, 1929, p. 8) was also highly critical of Lang's introduction of many taxa without figures (Lang 1916a, b) before figuring the same taxa four years later (Lang 1920).

Although Brydone named a large number of new species – including 'varieties', 472 in total – he refrained from introducing new supraspecific taxa with the exception of three new genera: *Pseudostega* Brydone, 1910d (the replacement name *Pseudostege* Brydone 1918b, proposed because of homonymy with the suprafamilial taxon Pseudostega, is unnecessary), *Rotoporina* Brydone, 1930 and *Volviflustrellaria* Brydone, 1936. In contrast, Lang named a considerable number of new genera, subfamilies and families. A significant proportion of Lang's genera were monospecific when created, and many of his families were monogeneric. It is clear from Brydone's failure to adopt Lang's higher taxa that he did not agree with this taxonomic profligacy.

Reflecting Brydone's own collecting activities, his publications were essentially faunal studies describing the new cheilostome species he found in the Chalk localities that

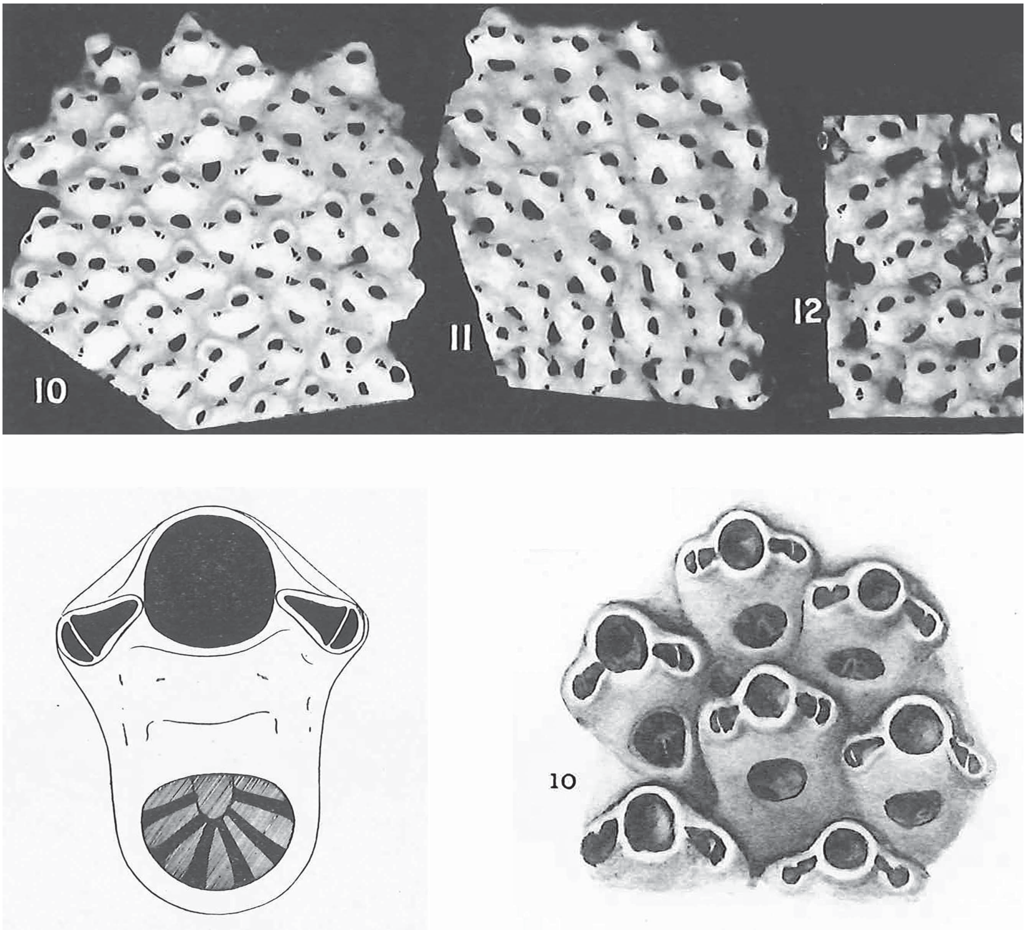


Figure 7. The contrasting styles of illustration employed by Brydone and Lang, exemplified by their figures of Tricephalopora obducta *Lang, 1916a, which was considered by Lang (1922) to be a senior synonym of* Membraniporella pyramidalis *Brydone, 1917b. At the top are three of Brydone's retouched photographs (Brydone 1917b, pl. 9, figs 10–12). Lower left is a typical Lang stylised diagram (Lang 1922, fig. 26), and lower right is one of his ink wash figures drawn by Gertrude M. Woodward (Lang 1922, pl. 1, fig. 10).*

he had personally sampled. There was no attempt at monography in the sense of describing all species from a chosen taxonomic group, although this is not to say that his papers represented random selections of taxa. Indeed, Brydone's three-part monograph dealt successively with species he assigned to specific genera, beginning with the simple yet diverse species of '*Membranipora*' and progressing to species of ascophorans and anascans with well-developed cryptocysts. Brydone's lack of access to significant material from continental Europe (note that he did describe a few species from France; see Appendix) would have made monography impossible. To be comprehensive Brydone would have needed to revise the countless species described by, for example, d'Orbigny from the French Upper Cretaceous. Here is where Lang had a distinct advantage over Brydone: the BM(NH) collections contained ample topotypic and other bryozoans from localities in continental Europe, including not only France but also The Netherlands, Belgium, Germany, Denmark and Bohemia. It was thus possible for Lang to revise his favoured group, the cribrimorphs, comprehensively. Therefore, the scope Brydone's and Lang's studies of Upper Cretaceous cheilostomes differed greatly. Doubtless Brydone felt his way of working was superior as he had better local knowledge of the stratigraphical and geological contexts of the species described, whereas Lang could claim that his approach was more inclusive and international in scope.

Lang was critical of Brydone for introducing so many new species without sufficient attention to the existing literature. It may be that Brydone did not have easy access to this literature; in any case, even today the descriptions and illustrations of species introduced by d'Orbigny and others are often not easy to use when attempting to identify bryozoans without topotypical material to hand.

6. Conclusions

Brydone does seem to have possessed an abrasive personality and was fond of resorting to sarcasm when criticising the work of others. For example, he was deeply unconvinced of the taxonomic weight placed by Canu and Bassler on characters of the ovicells, stating (Brydone 1936, p. 67): "I strongly suspect that this doctrine of the pre-eminence of the ovicell is really based not on reasoning, but on sentiment, by crediting the very imperfectly conscious Polyzoa (by a sort of pathetic fallacy) with the same sense of modesty as the very self-conscious human race has developed for itself, and equating the ovicell with the loin-cloth." Canu and Bassler were not the only ones to be criticized by Brydone. As is made explicit in the letter of Lang's to Edwards, Brydone also found fault in the work of A. W. Rowe on Chalk stratigraphy (Brydone 1906d, 1914e, 1915).

Brydone's final publication in the 1942 volume of the *Geological Magazine* offers particular clues about his personality. This short paper comprises comments on some of the species he had introduced in part 3 of his privately published monograph (Brydone 1936) and was prompted by a letter he had received – and replied to – from "… a Continental fellow-author of works on fossil Polyzoa, especially Cretaceous." (Brydone 1942, p. 62). Brydone agreed to clarify the identities of his new species "… on the understanding that the inquirer accepted as valid any answers which he could not dispute." For whatever reason the fellow author was not named but there can be little doubt that it was Ehrhard Voigt (1905–2004). Brydone's final sentence (ibid, p. 64) states: "I heard from my inquirer in March, 1937, that he could not go into my answers promptly as he was called out for military training, and I have not since heard anything from him." The tone of the second of these three quotations is inappropriately dictatorial, while the third suggests a personal annoyance with Voigt that is hard to justify given the political situation at the time with Europe in the throes of World War 2.

While Brydone may not have been correct in all of his opinions of Lang, he did offer useful criticisms of Lang's work, especially with regard to Lang's bizarre theories of orthogenesis in cribrimorphs, and the problems caused by naming new species without illustration. By the time Brydone had published his damning comments on Lang's work in 1930, Lang had ceased his research on bryozoans and was probably disinclined to respond. He did, however, pen an obituary of Brydone containing criticisms not generally voiced on such occasions. For instance, Lang contended that more detail was required than is evident in Brydone's photographs for his species to be compared with those already established, and berated Brydone for not supplementing his photographs with diagrams showing further details (Lang 1944). He was also critical of Brydone for not using the same colour scheme as Rowe for the zones in his geological maps of the Chalk, remarking that "… some found him a difficult collaborator. Possibly it made for better understanding in the end that one who held opinions so strongly should publish them categorically and without compromise, rather than discuss them unprofitably with other workers in the same field." (Lang 1944, p. lxvi).

Brydone the Oxford-educated, non-vocational palaeontologist and Lang the Cambridge-educated, vocational palaeontologist engaged in acrimonius disputes over almost all of the areas of Chalk bryozoology where they overlapped. Each had his own way of conducting research, both were strong-willed and there was little room for compromise. While Brydone's work would have been considerably more valuable if it had taken into account the studies of 19th century continental European bryozoologists and had been consolidated into a few more comprehensive taxonomic monographs, Lang's would have benefited by more complete illustrations and a simpler taxonomy not driven by his ideas of orthogenesis.

7. Acknowledgements

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References

Anon. 1921. Obituary. Henry Woodward. *Geological Magazine*, **58**, 481–484.

Bowler, P.J. 1983. *The Eclipse of Darwinism*. Johns Hopkins University Press, Baltimore.

Brydone, R.M. 1900, *The Stratigraphy and Fauna of the Trimmingham [sic] Chalk*. Published privately, London, 16 pp.

Brydone, R.M. 1906a. Correspondence – The Trimmingham Chalk. *Geological Magazine*, Decade 5, **3**, 527–528.

Brydone, R.M. 1906b. Further Notes on the Stratigraphy and Fauna of the Trimmingham Chalk, *Geological Magazine*, Decade 5, **3,** 13–22.

Brydone, R.M. 1906c. Further Notes on the Stratigraphy and Fauna of the Trimmingham Chalk, *Geological Magazine*, Decade 5, **3,** 72–78.

Brydone, R.M. 1906d. Further Notes on the Stratigraphy and Fauna of the Trimmingham Chalk, *Geological Magazine*, Decade 5, **3,** 124–131.

Brydone, R.M. 1906e. Further Notes on the Stratigraphy and Fauna of the Trimmingham Chalk. *Geological Magazine*, Decade 5, **3**, 289–300.

Brydone, R.M. 1908. Subdivisions of the Chalk of Trimmingham. *Quarterly Journal of the Geological Society* **64**, 401–411.

Brydone, R.M. 1909a. Notes on New or Imperfectly Known Chalk Bryozoa (Polyzoa). *Geological Magazine*, Decade 5, **6,** 337–339.

Brydone, R.M. 1909b. Notes on New or Imperfectly Known Chalk Bryozoa (Polyzoa). *Geological Magazine*, Decade 5, **6,** 398–401.

Brydone, R.M. 1910a. Notes on New or Imperfectly Known Chalk Polyzoa. *Geological Magazine*, Decade 5, **7,** 4–5.

Brydone, R.M. 1910b. Notes on New or Imperfectly Known Chalk Polyzoa. *Geological Magazine*, Decade 5, **7,** 76–77.

Brydone, R.M. 1910c. Notes on New or Imperfectly Known Chalk Polyzoa. *Geological Magazine*, Decade 5, **7,** 145–147.

Brydone, R.M. 1910d. Notes on New or Imperfectly Known Chalk Polyzoa. *Geological Magazine*, Decade 5, **7,** 258–260.

Brydone, R.M. 1910e. Notes on New or Imperfectly Known Chalk Polyzoa. *Geological Magazine*, Decade 5, **7,** 390–392.

Brydone, R.M. 1910f. Notes on New or Imperfectly Known Chalk Polyzoa. *Geological Magazine*, Decade 5, **7,** 481–483.

Brydone, R.M. 1911. Notes on New or Imperfectly Known Chalk Polyzoa. *Geological Magazine*, Decade 5, **8,** 153–156.

Brydone, R.M. 1912a. Notes on New or Imperfectly Known Chalk Polyzoa. *Geological Magazine*, Decade 5, **9**, 7–8.

Brydone, R.M. 1912b. Notes on New or Imperfectly Known Chalk Polyzoa. *Geological Magazine*, Decade 5, **9**, 145–147.

Brydone, R.M. 1912c. Notes on New or Imperfectly Known Chalk Polyzoa. *Geological Magazine*, Decade 5, **9**, 294–296.

Brydone, R.M. 1912d. Notes on New or Imperfectly Known Chalk Polyzoa. *Geological Magazine*, Decade 5, **9**, 433–435.

Brydone, R.M. 1913a. Notes on New or Imperfectly Known Chalk Polyzoa. *Geological Magazine*, Decade V, **10**, 97–99.

Brydone, R.M. 1913b. Notes on New or Imperfectly Known Chalk Polyzoa. *Geological Magazine*, Decade 5, **10**, 196–199.

Brydone, R.M. 1913c. Notes on New or Imperfectly Known Chalk Polyzoa. *Geological Magazine*, Decade 5, **10**, 248–250.

Brydone, R.M. 1913d. Notes on New or Imperfectly Known Chalk Polyzoa, *Geological Magazine*, Decade 5, **10**, 436–438.

Brydone, R.M. 1913e. The Proposed Recognition of Two Stages in the Upper Chalk. *Geological Magazine*, Decade 5, **10**, 56–62.

Brydone, R.M. 1914a. Notes on New or Imperfectly Known Chalk Polyzoa. *Geological Magazine*, Decade 6, **1**, 97–99.

Brydone, R.M. 1914b. Notes on New or Imperfectly Known Chalk Polyzoa. *Geological Magazine*, Decade 6, **1,** 345–347.

Brydone, R.M. 1914c. Notes on New or Imperfectly Known Chalk Polyzoa. *Geological Magazine*, Decade 6, **1,** 481–483.

Brydone, R.M. 1914d. The Zone of Offaster Pilula in the South English Chalk. *Geological Magazine*, Decade 6, **1**, 359–369.

Brydone, R.M. 1914e. The Zone of Offaster Pilula in the South English Chalk. *Geological Magazine*, Decade 6, **1,** 405–411.

Brydone, R.M. 1914f. The Zone of Offaster Pilula in the South English Chalk. *Geological Magazine*, Decade 6, **1,** 449–457.

Brydone, R.M. 1914g. The Zone of Offaster Pilula in the South English Chalk. *Geological Magazine*, Decade 6, **1,** 509–513.

Brydone, R.M. 1915. Marsupites Chalk of Brighton. *Geological Magazine*, Decade 6, **2,** 12–15.

Brydone, R.M. 1916a. Notes on New or Imperfectly Known Chalk Polyzoa. *Geological Magazine*, Decade 6, **3,** 97–100.

Brydone, R.M. 1916b. Notes on New or Imperfectly Known Chalk Polyzoa. *Geological Magazine*, Decade 6, **3,** 241–243.

Brydone, R.M. 1916c. Notes on New or Imperfectly Known Chalk Polyzoa. *Geological Magazine*, Decade 6, **3,** 337–339.

Brydone, R.M. 1916d. Notes on New or Imperfectly Known Chalk Polyzoa. *Geological Magazine*, Decade 6, **3,** 433–435.

Brydone, R.M. 1917a. Notes on New or Imperfectly Known Chalk Polyzoa. *Geological Magazine*, Decade 6, **4,** 49–53.

Brydone, R.M. 1917b. Notes on New or Imperfectly Known Chalk Polyzoa. *Geological Magazine*, Decade 6, **4**, 145–148.

Brydone, R.M. 1917c. Notes on New or Imperfectly Known Chalk Polyzoa. *Geological Magazine*, Decade 6, **4**, 492–496.

Brydone, R.M. 1917d. The Base of the Chalk Zone of Holaster planus in the Isle of Wight, *Geological Magazine*, Decade 6, **4,** 245–249.

Brydone, R.M. 1918a. Notes on New or Imperfectly Known Chalk Polyzoa. *Geological Magazine*, Decade 6, **5**, 1–4.

Brydone, R.M. 1918b. Notes on New or Imperfectly Known Chalk Polyzoa. *Geological Magazine*, Decade 6, **5**, 97–100.

Brydone, R.M. 1918c. The Thickness of the Zone of *Belemnitella mucronata* in the Isle of Wight. *Geological Magazine*, Decade 6, **5**, 350–354.

Brydone, R.M. 1920. The Origin of Flint. *Geological Magazine*, **57**, 401–404.

Brydone, R.M. 1929. *Further notes on new or imperfectly known Chalk Polyzoa*. Part I (pp. 1–38). Privately published, London.

Brydone, R.M. 1930a. The Norwich Chalk. *Transactions of the Norfolk and Norwich Naturalists' Society* **13**, 47–49.

Brydone, R.M. 1930b. *Further notes on new or imperfectly known Chalk Polyzoa*,. Part 2 (pp. 39–60). Privately published, London.

Brydone, R.M. 1931. The Course of Marsupites and Uintacrinus across Norfolk. *Transactions of the Norfolk and Norwich Naturalists' Society* **13**, 115–118.

Brydone, R.M. 1932a. The Zone of granulated Actinocamax in East Anglia. *Transactions of the Norfolk and Norwich Naturalists' Society* **13**, 285–293.

Brydone, R.M. 1932b. The Lower Beds of Chalk near Ipswich. *Journal of the Ipswich and District Natural History Society* **1** (3), 1–5.

Brydone, R.M. 1932c. *Uintacrinus* in North Suffolk. *Journal of the Ipswich and District Natural History Society* **2** (3), 1–4.

Brydone, R.M. 1936. *Further notes on new or imperfectly known Chalk Polyzoa*. Part 3 (pp. 61–90). Privately published, London.

Brydone, R.M. 1941. A Problem in Polyzoan Nomenclature. *Geological Magazine* **78**, 236–238.

Brydone, R.M. 1942. On Some Recently Described Cretaceous Cheilostomatous Polyzoa. *Geological Magazine* **79**. 62–64.

Bulman, O.M.B. 1950. Obituary. R.H. Rastall, 1871–1950. *Geological Magazine* **87**, 72–76.

Ellis, E.A. 1944. [Obituary.] Reginald Marr Brydone, FGS. *Transactions of the Norfolk and Norwich Naturalists' Society* **15**(5) [for 1943], 444–445.

Lang, W.D. 1906. The reptant eleid Polyzoa. *Geological Magazine*, Decade 5, **3**, 60–69.

Lang, W.D. 1916a. A revision of the 'Cribrimorph' Cretaceous Polyzoa. *Annals and Magazine of Natural History*, Series 8, **18**, 81–112.

Lang, W.D. 1916b. A revision of the 'Cribrimorph' Cretaceous Polyzoa. *Annals and Magazine of Natural History*, Series 8, **18**, 381–410.

Lang, W.D. 1921. *Catalogue of the fossil Bryozoa (Polyzoa) in the Department of Geology, British Museum (Natural History). The Cretaceous Bryozoa (Polyzoa). Volume 3. The cribrimorphs. – Part 1*. British Museum (Natural History), London, cx + 269 pp.

Lang, W.D. 1922. *Catalogue of the fossil Bryozoa (Polyzoa) in the Department of Geology, British Museum (Natural History). The Cretaceous Bryozoa (Polyzoa). Volume 4. The cribrimorphs. – Part 2*. British Museum (Natural History), London, 404 pp.

Lang, W.D. 1944. [Obituary Notices]. Reginald Marr Brydone. *Proceedings of the Geological Society of London* **1944**, lxv–lxvi.

Medd, A.W. 1965. *Dionella* gen. nov. (Superfamily Membraniporacea) from the Upper Cretaceous of Europe. *Palaeontology* **8**, 492–517.

Sendino, C. 2014. Cleaning and conservation of fossil bryozoan cavity slides of the William Dickson Lang Collection at the Natural History Museum, London, pp. 169–

181. In: P.N. Wyse Jackson and M.E. Spencer Jones (eds). *Annals of Bryozoology 4: aspects of the history of research on bryozoans*. International Bryozoology Association, Dublin.

Taylor, P.D. 2002. W.D. Lang, orthogenesis and the evolution of Cretaceous cribrimorph Bryozoa. In: P.N. Wyse Jackson and M.E. Spencer Jones (eds), pp. 275–298. *Annals of Bryozoology: aspects of the history of research on bryozoans*. International Bryozoology Association, Dublin.

Wainewright, J.B. 1907. *Winchester College 1836–1906. A Register*. Wells, Winchester, 676 pp.

White, E.I. 1966. William Dickson Lang. *Biographical Memoirs of the Fellows of the Royal Society* **12**, 367–386.

Appendix. Bryozoan species from the Upper Cretaceous named by R. M. Brydone in order of their date of publication.

	Species and Brydone's stratigraphical comments	**Locality**
1.	*Membranipora griffithi* Brydone, 1906b	Trimingham, Norfolk
2.	*Membranipora trimminghamensis* Brydone, 1906b	Trimingham, Norfolk
3.	*Membranipora britannica* Brydone, 1906b Recognisable in *Micraster coranguinum* zone; rare below *Belemnitella mucronata* zone	Trimingham, Norfolk
4.	*Semieschara mundesleiensis* Brydone, 1906b	Trimingham, Norfolk
5.	*Semieschara canui* Brydone, 1906b	Trimingham, Norfolk
6.	*Eschara rowei* Brydone, 1906b	Trimingham, Norfolk
7.	*Cribrilina sherborni* Brydone, 1906b	Trimingham, Norfolk
8.	*Cribrilina dibleyi* Brydone, 1906b	Trimingham, Norfolk
9.	*Cribrilina jukes-brownei* Brydone, 1906b	Trimingham, Norfolk
10.	*Mucronella batheri* Brydone, 1906b	Trimingham, Norfolk
11.	*Semieschara woodsi* Brydone, 1906b Senonian. *Marsupites* zone; mostly base of *Belemnitella mucronata* zone	Trimingham, Norfolk
12.	*Semieschara pergensi* Brydone, 1906b Senonian. Upper *Belemnitella quadrata* zone	Trimingham, Norfolk
13.	*Cribrilina gregoryi* Brydone, 1906b Senonian.*Belemnitella quadrata* zone; appears in *Micraster cortestudinarium* comparatively rare above *Belemnitella mucronata*	Seaford Trimingham, Norfolk
14.	*Homalostega anglica* Brydone, 1909a	Trimingham, Norwich and Sheringham, Norfolk
15.	*Homalostega biconvexa* Brydone, 1909a	Trimingham, Norfolk
16.	*Homalostega cuniformis* Brydone, 1909a	Trimingham, Norfolk
17.	*Membraniporella monastica* Brydone, 1909b	Trimingham, Norfolk
18.	*Membraniporella castrum* Brydone, 1909b	Trimingham, Norfolk
19.	*Cribrilina ostreicola* Brydone, 1909b	Trimingham, Norfolk
20.	*Cribrilina subvitrea* Brydone, 1909b	Trimingham, Norfolk
21.	*Homalostega cuniformis* Brydone, 1909a	Trimingham, Norfolk
22.	*Membranipora humiliata* Brydone, 1910a	Trimingham, Norfolk
23.	*Membranipora anterides* Brydone, 1910a	Trimingham, Norfolk

24. *Membranipora invigilata* Brydone, 1910b	
Micraster coranguinum zone	Gravesend
Possibly *Actinocamax quadratus* zone	Trimingham, Norfolk
25. *Membranipora britannica* var. *præcursor* Brydone, 1910b	Trimingham, Norfolk; Winchester
26. *Membranipora sagittaria* Brydone, 1910c	
Micraster coranguinum zone	Gravesend
Actinocamax quadratus zone	Hampshire
Belemnitella mucronata zone	Isle of Wight
27. *Membranipora dolium* Brydone, 1910c	
Actinocamax quadratus zone	Hampshire
Belemnitella mucronata zone	Bramford, Suffolk; Cromer, Norfolk
28. *Membranipora anguiformis* Brydone, 1910c	Trimingham, Norfolk;
29. *Membranipora langi* Brydone, 1910c	Cromer and Trimingham.
Actinocamax quadratus zone	Hampshire
30. *Membranipora woodwardi* Brydone, 1910d	
Micraster coranguinum zone; *Marsupites* zone; *Actinocamax quadratus* zone	Hampshire
Micraster coranguinum zone	Gravesend, Kent
31. *Membranipora coralliformis* Brydone, 1910d	
Micraster coranguinum zone	Gravesend, Kent; Hampshire
32. *Pseudostega cantiana* Brydone, 1910d	
Micraster coranguinum zone (rare)	Gravesend, Kent Chislehurst, Kent
33. *Rhagasostoma novaki* Brydone, 1910e	
[nom. nov. for *Membranipora depressa* Novak non v.Hagenow]	Trimingham, Norfolk
34. *Rhagasostoma novaki* var. *anglica* Brydone, 1910e	
Belemnitella mucronata zone	Trimingham, Norfolk; Isle of Wight
35. *Cribrilina claviceps* Brydone, 1910e	
Micraster coranguinum zone	Gravesend; Hampshire
Marsupites zone	Hampshire
36. *Cribrilina furcifera* Brydone, 1910e	
Micraster coranguinum zone	Kent
Marsupites zone	Hampshire
Actinocamax quadratus zone	Hampshire; Sussex
Belemnitella mucronata zone	Hampshire
37. *Cribrilina filliozati* Brydone, 1910e	
Actinocamax quadratus zone	Hampshire
38. *Steginopora denticulata* Brydone, 1910f	
Micraster coranguinum zone (rare)	Gravesend, Kent Broadstairs, Kent Kingsgate Bay, Kent Leaves Green (near Bromley), Kent
39. *Steginopora gravensis* Brydone, 1910f	
Micraster coranguinum zone (very rare)	Gravesend
40. *Membraniporella fallax* Brydone, 1910f	
Micraster coranguinum zone	Gravesend
Marsupites zone (dwarf form)	Hampshire

41. *Membraniporella pustulosa* Brydone, 1910f	
All zones from *Micraster coranguinum* to *Belemnitella mucronata*.	
42. *Pavolunulites scandens* Brydone, 1911	
Upper *Micraster cortestudinarium* zone	Sussex
43. *Pavolunulites declivis* Brydone, 1911	Trimingham, Norfolk
Actinocamax quadratus zone	Hampshire; Isle of Wight
44. *Pavolunulites subquadrata* Brydone, 1911	
Upper *Micraster cortestudinarium* zone	Sussex; Isle of Wight; Hampshire
45. *Lunulites marsonni* Brydone, 1911	
[nom. nov. for *L. crassa* (Beissel) non Tenison-Woods]	Trimingham, Norfolk
46. *Discoflustrellaria trimensis* Brydone, 1912a	Trimingham, Norfolk (very rare)
47. *Lateroflustrellaria robusta* Brydone, 1912a	Trimingham, Norfolk
48. *Rhagasostoma sussexiense* Brydone, 1912b	
Upper *Micraster cortestudinarium* zone	Seaford, Sussex Beachy Head, Sussex
49. *Rhagasostoma palpigerum* Brydone, 1912b	
Offaster pilula sub-zone	
Uintacrinus band	Hampshire; Kent
Marsupites band	Hampshire
50. *Semieschara proteus* Brydone, 1912c	
Upper *Actinocamax quadratus; Micraster cortestudinarium; Micraster coranguinum; Holaster planus*	
51. *Membranipora pyrigera* Brydone, 1912d	
Actinocamax quadratus zone; Lower *Belemnitella mucronata* zone; *Micraster coranguinum* zone; *Marsupites* zone	
52. *Membranipora tenebrosa* Brydone, 1912d	
Actinocamax quadratus zone	
53. *Membranipora pellicula* Brydone, 1912d	
Rare in *Offaster pilula* (not below)*; Actinocamax quadratus* subzone; Lower *Belemnitella. mucronata* zone	
54. *Membranipora withersi* Brydone, 1912d	
Actinocamax quadratus subzone	
55. *Mucronella (?) spenceri* Brydone, 1913a	
Offaster pilula zone; *Actinocamax quadratus* zone	
56. *Homalostega cavernosa* Brydone, 1913a	Trimingham, Norfolk
57. *Homalostega vulcani* Brydone, 1913a	Trimingham, Norfolk
58. *Membranipora gravensis* Brydone, 1913b	
Micraster coranguinum zone	Gravesend
59. *Membranipora sparksi* Brydone, 1913b	
Actinocamax quadratus	Sparks' Pit, near Cosham, Hampshire
60. *Membranipora cervicornis* Brydone, 1913b	
Belemnitella mucronata	Portsdown
61. *Membranipora plicatella* Brydone, 1913b	Trimingham, Norfolk
62. *Membranipora aedificata* Brydone, 1913b	Trimingham, Norfolk
63. *Semieschara labiatula* Brydone, 1913c	
Offaster pilula zone (rare)*; Actinocamax quadratus* zone (fairly common)	Trimingham, Norfolk
64. *Semieschara occlusa* Brydone, 1913c	Trimingham, Norfolk

65. *Cribrilina suffulta* Brydone, 1913d	
Micraster coranguinum zone*Uintacrinus* band	Gravesend
66. *Cribrilina cacus* Brydone, 1913d	Trimingham, Norfolk
67. *Cribrilina cicatricifera* Brydone, 1914a	
Micraster coranguinum	Weybourne, Norfolk Gravesend, Kent
68. *Cribrilina vulnerata* Brydone, 1914a	Trimingham and Weybourne, Norfolk
69. *Mollia laminaria* Brydone, 1914a	Weybourne, Norfolk
70. *Homalostega marginula* Brydone, 1914a	
Micraster cortestudinarium	Seaford, Sussex; Dover, Kent
71. *Homalostega nitescens* Brydone, 1914a	Trimingham and Weybourne, Norfolk
72. *Homalostega antecedens* Brydone, 1914a	
Actinocamax quadratus	Shawford, Hampshire; Sussex
. *Offaster pilula*	Sussex
73. *Membranipora simulacrum* Brydone, 1914b	
Micraster coranguinum zone	Kent
Uintacrinus band	Hampshire
74. *Membranipora suffragista* Brydone, 1914b	
Micraster coranguinum zone	Kent; Hampshire
Uintacrinus band; *Marsupites* zone	Hampshire
75. *Membranipora boletiformis* Brydone, 1914b	
Actinocamax quadratus	Shawford, Hampshire
Offaster pilula	Seaford, Sussex
76. *Membranipora cuculligera* Brydone, 1914c	
Micraster coranguinum zone	Hampshire; Kent; Gravesend
77. *Membranipora vestigialis* Brydone, 1914c	
Micraster coranguinum zone	Hampshire; Kent; Gravesend
Offaster pilula	Sussex
78. *Membranipora præcipua* Brydone, 1914c	Trimingham, Norfolk
79. *Membranipora sacerdotalis* Brydone, 1914c	Trimingham, Norfolk
80. *Membranipora subacuminata* Brydone, 1916a	
Belemnitella mucronata	Portsdown
81. *Membranipora studlandensis* Brydone, 1916a	
Belemnitella mucronata	Studland, Dorset
82. *Membranipora demissa* Brydone, 1916a	
Belemnitella mucronata	Studland, Dorset
Micraster cortestudinarium	
83. *Membranipora woodwardi* Brydone, 1910d var. *pinguescens* Brydone, 1916a	
Micraster cortestudinarium	Trimingham, Norfolk
Offaster pilula	Seaford, Sussex
Actinocamax quadratus	
84. *Membraniporella pontifera* Brydone, 1916a	
Micraster cortestudinarium	Hampshire
Micraster coranguinum	Gravesend, Kent
85. *Membraniporella obscurata* Brydone, 1916a	
Micraster cortestudinarium	Seaford, Sussex Hampshire; Kent

86. *Membranipora missilis* Brydone, 1916b	
Marsupites	Well, Hampshire
Offaster pilula	Sussex
Actinocamax quadratus	Brighton
87. *Membranipora fannia* Brydone, 1916b	
Actinocamax quadratus	Shawford, Hampshire
88. *Membranipora cupolata* Brydone, 1916b	Trimingham and Weybourne, Norfolk
89. *Membranipora vectensis* Brydone, 1916b	
Holaster planus	Isle of Wight
90. *Membranipora fascelis* Brydone, 1916c	
Micraster coranguinum	Gravesend, Kent
Marsupites	Hampshire; Kent
91. *Membranipora faustina* Brydone, 1916c	
Micraster cortestudinarium	Basing, Hampshire
92. *Membranipora feronia* Brydone, 1916c	
Actinocamax quadratus	Shawford, Hampshire
Belemnitella mucronata	
93. *Membranipora flacilla* Brydone, 1916c	
Belemnitella mucronata	Weybourne, Norfolk
94. *Membranipora flammia* Brydone, 1916c	
Actinocamax quadratus	Shawford, Hampshire
95. *Membranipora flora* Brydone, 1916c	
Micraster cortestudinarium	Seaford, Sussex
96. *Membranipora fluonia* Brydone, 1916d	
Belemnitella mucronata	Weybourne, Norfolk
97. *Membranipora fonteia* Brydone, 1916d	
Belemnitella mucronata	Weybourne, Norfolk
98. *Membranipora cubitalis* Brydone, 1916d	
Belemnitella mucronata	Weybourne, Norfolk
99. *Membranipora fulgora* Brydone, 1916d	
Belemnitella mucronata	Weybourne, Norfolk
100. *Membranipora furina* Brydone, 1916d	
Belemnitella mucronata	Weybourne, Norfolk
101. *Membranipora crateroides* Brydone, 1917a	
Belemnitella mucronata	Weybourne and Norwich, Norfolk
102. *Membraniporella tæniata* Brydone, 1917a	
Actinocamax quadratus	East Dean and Shawford, Hampshire
103. *Membraniporella bitubularis* Brydone, 1917a	
Micraster cortestudinarium	Seaford, Sussex; Green, Kent
104. *Cribrilina tumuliformis* Brydone, 1917a	
Micraster coranguinumUintacrinus band	Leaves and Gravesend, Kent
105. *Cribrilina seafordensis* Brydone, 1917a	
Micraster cortestudinarium	Seaford, Sussex
106. *Membraniporella thoraciformis* Brydone, 1917b	
Actinocamax quadratus	Shawford and Portsdown, Hampshire
107. *Membraniporella manonia* Brydone, 1917b	
Belemnitella mucronata	Portsdown, Hampshire

108.	*Membraniporella transligata* Brydone, 1917b	Coltishall, Trimingham and Weybourne, Norfolk
109.	*Membraniporella pyramidalis* Brydone, 1917b	Trimingham, Norfolk
110.	*Cribrilina transita* Brydone, 1917c	
	Uintacrinus band	Brighton, Sussex; Broughton, Hampshire
111.	*Cribrilina t-formis* Brydone, 1917c	
	Offaster pilula	Rottingdean, Sussex
	Echinocorys scutatus var. *depressus*	
112.	*Cribrilina bramfordensis* Brydone, 1917c	
	Actinocamax quadratus	Bramford, Suffolk
113.	*Membraniporella subcastrum* Brydone, 1917c	
	Echinocorys. scutatus var. *depressus*	Rottingdean, Sussex
114.	*Membraniporella gabina* Brydone, 1917c	
	Actinocamax quadratus	Freshwater, Isle of Wight
115.	*Cribrilina repleta* nom. nov. (Renames *Cribrilina suffulta*, Brydone, 1913d)	
	Micraster coranguinum	Soberton, Hampshire
116.	*Cribrilina galanthis* Brydone, 1917c	
	[nom. nov. for *Cribrilina gregoryi* Brydone, 1913d]	
117.	*Membraniporella altonensis* Brydone, 1918a	
	Holaster planus	Alton, Hampshire
118.	*Membraniporella shawfordensis* Brydone, 1918a	
	Actinocamax quadratus	Shawford, Hampshire
119.	*Membraniporella bedhamptonensis* Brydone, 1918a	
	Belemnitella mucronata	Bedhampton, Hampshire, Isle of Wight
120.	*Membraniporella trimensis* Brydone, 1918a	
	Belemnitella mucronata	Trimingham, Norfolk
121.	*Pseudostege concursa* Brydone, 1918b	
	Actinocamax quadratus Belemnitella mucronata	Shawford and Portsdown, Hampshire
122.	*Cellepora (?) diastoides* Brydone, 1918b	Trimingham, Norwich and Weybourne, Norfolk
123.	*Membranipora seafordensis* Brydone, 1918b	
	Micraster cortestudinarium	Seaford, Sussex
124.	*Membranipora multifissa* Brydone, 1918b	
	Micraster coranguinum	Gravesend, Kent
125.	*Membranipora sevingtonensis* Brydone, 1918b	
	Micraster coranguinum	Sevington, Hampshire
126.	*Membranipora sandalina* Brydone, 1918b	
	Micraster coranguinum	Gravesend, Kent
127.	*Membranipora hebens* Brydone, 1929	
	Actinocamax quadratus	Hampshire
128.	*Membranipora eastonensis* Brydone, 1929	
	Actinocamax quadratus	Isle of Wight
129.	*Membranipora repetita*	Trimingham, Norfolk
130.	*Membranipora pudica* Brydone, 1929	
	E. scutatus var. depressus	Sussex
131.	*Membranipora verecunda* Brydone, 1929	
	Actinocamax quadratus	Portsdown, Hampshire
132.	*Membranipora thanetiana* Brydone, 1929	
	Marsupites	Margate, Kent

133. *Membranipora walthamensis* Brydone, 1929	
Actinocamax quadratus	Hampshire
134. *Membranipora tactimargo* Brydone, 1929	
Actinocamax quadratus	Hampshire
135. *Membranipora arcana* Brydone, 1929	
Belemnitella mucronata	Isle of Wight
136. *Membranipora conficiens* Brydone, 1929	Trimingham, Norfolk
137. *Membranipora initialis* Brydone, 1929	
Offaster pilula (cinctus band*)*	Sussex
138. *Membranipora clairensis* Brydone, 1929	
"Upper" *Actinocamax quadratus*	Droxford, Hampshire
139. *Membranipora exhauriens* Brydone, 1929	
Belemnitella mucronata	Hampshire, Isle of Wight
140. *Membranipora exhauriens* var. *sheringensis* Brydone, 1929	Weybourne, Norfolk
141. *Membranipora exhauriens* var. *apotheca* Brydone, 1929	
"Upper" *Belemnitella mucronata* basal	Weybourne, Norfolk
Belemnitella mucronata	Hampshire, Isle of Wight, Meudon (France)
142. *Membranipora flaminia* Brydone, 1929	
Porosphaera beds	Trimingham, Norfolk
143. *Membranipora flavia* Brydone, 1929	
Micraster coranguinum	Trimingham, Norfolk
quadratus	
144. *Membranipora fornax* Brydone, 1929	
Micraster cortestudinarium	Sussex
145. *Membranipora alrensis* Brydone, 1929	
Marsupites	Hampshire, Sussex
Micraster coranguinum	Isle of Wight
146. *Membranipora bightonensis* Brydone, 1929	
Offaster pilula	Hampshire
147. *Membranipora doliola* Brydone, 1929	
Belemnitella mucronata	Hampshire
148. *Membranipora capedo* Brydone, 1929	
basal *Belemnitella mucronata*	Hampshire
149. *Membranipora nanula* Brydone, 1929	
Porosphaera beds	Trimingham, Norfolk
150. *Membranipora fastigii* Brydone, 1929	
Micraster coranguinum	Isle of Wight
151. *Membranipora manorialis* Brydone, 1929	
Higher *Micraster coranguinum*	Hampshire
152. *Membranipora rupensis* Brydone, 1929	
Marsupites	Black Rock, Brighton, Sussex
153. *Membranipora portus* Brydone, 1929	
Offaster pilula	Newhaven, Sussex
154. *Membranipora arretonensis* Brydone, 1929	
Actinocamax quadratus	Arreton, Isle of Wight
155. *Membranipora farringensis* Brydone, 1929	
Actinocamax quadratus	Isle of Wight
156. *Membranipora acuum* Brydone, 1929	
basal *Belemnitella mucronata*	Hampshire
157. *Membranipora meudonia* Brydone, 1929	Meudon, France

158. *Membranipora gimensis* Brydone, 1929	
Porosphaera beds	Trimingham, Norfolk
159. *Membranipora sussexiensis* Brydone, 1929	
Micraster cortestudinarium	Sussex
160. *Membranipora michelensis* Brydone, 1929	
Micraster coranguinum	Micheldever, Hampshire
161. *Membranipora adunca* Brydone, 1929	
Marsupites	Alresford, Hampshire
162. *Membranipora inhospita* Brydone, 1929	
Marsupites	Sussex
163. *Membranipora brightonensis* Brydone, 1929	
Marsupites	Sussex
164. *Membranipora pererrans* Brydone, 1929	
Marsupites	SussexKent
165. *Membranipora roedeanensis* Brydone, 1929	
Echinocorys scutatus var. depressus	Roedean, Sussex
166. *Membranipora dunensis* Brydone, 1929	
Actinocamax quadratus	Downend, Isle of Wight
167. *Membranipora twyfordensis* Brydone, 1929	
Actinocamax quadratus	
168. *Membranipora palpebra* Brydone, 1929	Trimingham, Norfolk
169. *Membranipora palpebra* var. *nuntians* Brydone, 1929	Weybourne, Norfolk
170. *Membranipora mundesia* Brydone, 1929	
Porosphaera beds	Trimingham, Norfolk
Sponge beds	
171. *Membranipora cuckmerensis* Brydone, 1929	
Micraster cortestudinarium	Sussex
172. *Membranipora ossuaria* Brydone, 1929	
Micraster cortestudinarium	Sussex
173. *Membranipora chyngtonensis* Brydone, 1929	
Micraster cortestudinarium	Chyngton, Sussex
174. *Membranipora foslia* Brydone, 1929	
Micraster cortestudinarium	Sussex
175. *Membranipora hopensis* Brydone, 1929	
Micraster cortestudinarium	Sussex
176. *Membranipora comes* Brydone, 1929	Fécamp, France
177. *Membranipora sevingensis* Brydone, 1929	
Micraster coranguinum	Hampshire
178. *Membranipora walleriana* Brydone, 1929	
Micraster coranguinum	Hampshire
179. *Membranipora lutriana* Brydone, 1929	
Actinocamax quadratus	Hampshire
180. *Membranipora albida* Brydone, 1929	
Belemnitella mucronata	Whitecliff Bay, Isle of Wight
181. *Membranipora bramensis* Brydone, 1929	
Actinocamax quadratus	Bramford, Suffolk
Belemnitella mucronata	
182. *Membranipora putamen* Brydone, 1929	Trimingham, Norfolk
183. *Membranipora caminus* Brydone, 1929	Trimingham, Norfolk
184. *Membranipora perspicata* Brydone, 1929	Trimingham, Norfolk

185. *Membranipora transaviculata* Brydone, 1929	*Marsupites*	Hampshire; Kent
186. *Membranipora transpinosa* Brydone, 1929	*Offaster pilula*	Sussex
187. *Membranipora fufla* Brydone, 1929	*Offaster pilula*	Sussex
188. *Membranipora exsanguis* Brydone, 1929	*Micraster cortestudinarium*	Sussex Hampshire
189. *Membranipora index* Brydone, 1929	*Micraster cortestudinarium*	Sussex Hampshire
190. *Membranipora torpedo* Brydone, 1929	Coniacian	Fécamp, France
191. *Membranipora cantiana* Brydone, 1929	*Marsupites*	Margate, Kent
192. *Membranipora scotneiensis* Brydone, 1929	*Echinocorys scutatus var. depressus*	Sutton Scotney, Hampshire
193. *Membranipora pertenera* Brydone, 1929	*Offaster pilula*	Sussex
194. *Membranipora hursleiensis* Brydone, 1929	*Actinocamax quadratus*	Hursley, Hampshire
195. *Membranipora prætermissa* Brydone, 1929		
196. *Membranipora procurrens* Brydone, 1929		
197. *Membranipora taenialis* Brydone, 1929	basal *Belemnitella mucronata*	Hampshire
198. *Membranipora benensis* Brydone, 1929	basal *Belemnitella mucronata*	Bembridge Down, Isle of Wight
199. *Membranipora pyriporina* Brydone, 1929	*Belemnitella mucronata*	Isle of Wight
200. *Membranipora fulcra* Brydone, 1929	*Micraster cortestudinarium*	Sussex
201. *Membranipora riensis* Brydone, 1929	*Marsupites*	Rye Common, Hampshire
202. *Membranipora margatensis* Brydone, 1929	*Marsupites*	Margate, Kent
203. *Membranipora bradingensis* Brydone, 1929	"lower" *Belemnitella mucronata*	Brading, Isle of Wight
204. *Membranipora retrorsa* Brydone, 1929	Sponge beds	Trimingham, Norfolk
205. *Membranipora surculus* Brydone, 1929		Trimingham, Norfolk
206. *Membranipora middletonensis* Brydone, 1929	"lower" *Belemnitella mucronata*	Isle of Wight
207. *Membranipora protensa* Brydone, 1929	"lower" *Belemnitella mucronata*	Isle of Wight
208. *Membranipora aftonia* Brydone, 1929	*Belemnitella mucronata*	Isle of Wight
209. *Membranipora retusa* Brydone, 1929	*Actinocamax quadratus*	Bramford, Suffolk

210.	*Membranipora wintonensis* Brydone, 1929	
	Holaster planus	Winchester
211.	*Membranipora secutrix* Brydone, 1929	
	Offaster pilula	Sussex
212.	*Membranipora gabinia* Brydone, 1929	
	Offaster pilula	Sussex
213.	*Membranipora formicaria* Brydone, 1929	
	"lower" *Belemnitella mucronata*	Isle of Wight
214.	*Membranipora calva* Brydone, 1929	
	Sponge beds	Trimingham, Norfolk
215.	*Membranipora branscombensis* Brydone, 1929	
	Rhynchonella cuvieri	Branscombe, Devon
216.	*Membranipora berriensis* Brydone, 1929	
	Rhynchonella curieri	Branscombe, Devon
217.	*Membranipora comptonensis* Brydone, 1929	
	Holaster planus	Compton Bay, Isle of Wight Hampshire
218.	*Membranipora pecoris* Brydone, 1929	
	Micraster cortestudinarium	Stockbridge, Hampshire
219.	*Membranipora follis* Brydone, 1929	
	Micraster cortestudinarium	Sussex
220.	*Membranipora intricata* (Lonsdale, 1850) var. *bellica* Brydone, 1929	
	Micraster cortestudinarium	Sussex
221.	*Membranipora alveolus* Brydone, 1929	
	Micraster cortestudinarium	Sussex
222.	*Membranipora fécampensis* Brydone, 1929	
	Micraster cortestudinarium	Sussex Fécamp, France
223.	*Membranipora trulla* Brydone, 1929	
	Coniacian	Fécamp, France
224.	*Membranipora galatea* Brydone, 1929	
	Offaster pilula	Sussex
225.	*Membranipora dolina* Brydone, 1929	
	Offaster pilula	Sussex
226.	*Membranipora passerina* Brydone, 1929	
	Actinocamax quadratus	Hants
227.	*Membranipora octavia* Brydone, 1929	
	Actinocamax quadratus	Hants
228.	*Membranipora aftonensis* Brydone, 1929	
	Belemnitella mucronata	Isle of Wight
229.	*Membranipora paucimutata* Brydone, 1929	Trimingham, Norfolk
230.	*Membranipora famelica* Brydone, 1929	Trimingham, Norfolk
231.	*Membranipora subfulgora* Brydone, 1929	
	"lower" *Belemnitella mucronata*	Isle of Wight
232.	*Membranipora alumensis* Brydone, 1929	
	"lower" *Belemnitella mucronata*	Alum Bay, Isle of Wight
233.	*Membranipora scalprum* Brydone, 1929	
	Belemnitella mucronata	Weybourne, Norfolk
234.	*Membranipora fluonia* var. *galba* Brydone, 1929	
	Porosphaera beds	Trimingham, Norfolk

235.	*Membranipora plebicola* Brydone, 1929	
	Porosphaera beds	Trimingham, Norfolk
236.	*Membranipora galeria* Brydone, 1929	Trimingham, Norfolk
237.	*Membranipora faviola* Brydone, 1929	Trimingham, Norfolk
238.	*Membranipora pollex* Brydone, 1929	Trimingham, Norfolk
239.	*Membranipora galvia* Brydone, 1929	Trimingham, Norfolk
240.	*Membranipora repugnans* Brydone, 1929	Trimingham, Norfolk
241.	*Membranipora gerana* Brydone, 1929	Trimingham, Norfolk
242.	*Membranipora catinus* Brydone, 1929	Trimingham, Norfolk
243.	*Membranipora gegania* Brydone, 1929	
	Porosphaera beds	Trimingham, Norfolk
244.	*Membranipora vittata* Brydone, 1929	Trimingham, Norfolk
245.	*Membranipora vittata* var. *gemina* Brydone, 1929	
	Porosphaera beds	Trimingham, Norfolk
246.	*Biflustra transposita* Brydone, 1929	
	Offaster pilula	Hampshire
	Echinocorys scutatus var. depressus	Sussex
247.	*Biflustra transgemmata* Brydone, 1929	
	Actinocamax quadratus	Isle of Wight Hampshire
248.	*Biflustra filicosa* Brydone, 1929	
	basal *Belemnitella mucronata*	Isle of Wight
249.	*Biflustra genucia* Brydone, 1929	Meudon, France
250.	*Biflustra roborata* Brydone, 1929	Trimingham, Norfolk
251.	*Biflustra infundibulum* Brydone, 1929	Trimingham, Norfolk
252.	*Discoflustrellaria senonensis* Brydone, 1929	
	Echinocorys scutatus var. depressus to basal *Belemnitella mucronata*	
253.	*Discoflustrellaria senonensis* var. *vaccina* Brydone, 1929	
	basal *Belemnitella mucronata*	Isle of Wight
254.	*Discoflustrellaria senonensis* var. *nodensis* Brydone, 1929	
	"lower" *Belemnitella mucronata*	Nodewell, Isle of Wight
255.	*Lunulites tenax* Brydone, 1929	
	basal *Belemnitella mucronata*	Hampshire
	"upper" *Actinocamax quadratus*	
256.	*Lunulites tenebrosa* Brydone, 1929	
	Actinocamax quadratus	Hampshire
257.	*Lunulites incumbens* Brydone, 1929	
258.	*Membranipora devonica* Brydone, 1930	
	Rhynchonella cuvieri	Branscombe, Devon
259.	*Membranipora insultans* Brydone, 1930	Weybourne, Norfolk
260.	*Membranipora cubitalis* (Brydone, 1916d) var. *bicavata* Brydone, 1930	
261.	*Membranipora taverensis* Brydone, 1930	
	Belemnitella mucronata	Taverham Drayton Cringleford, Norfolk
262.	*Vincularia glycera* Brydone, 1930	
	Micraster cortestudinarium	Sussex
263.	*Vincularia glycera* var. *gorgo* Brydone, 1930	
264.	*Vincularia glycera* var. *gracilla* Brydone, 1930	

265. *Vincularia vertebralis* Brydone, 1930	
“upper” *Actinocamax quadratus*	Isle of Wight
“lower” *Belemnitella mucronata*	
266. *Vincularia weybournensis* Brydone, 1930	Weybourne, Norfolk
267. *Vincularia weybournensis* var. *sussexiensis* Brydone, 1930	
Micraster cortestudinarium	Sussex
268. *Vincularia anguina* Brydone, 1930	
Micraster coranguinum	Isle of Wight
269. *Vincularia henstingensis* Brydone, 1930	
Actinocamax quadratus	Hampshire
270. *Vincularia candyana* Brydone, 1930	
Actinocamax quadratus	Hampshire
271. *Vincularia glaphyra* Brydone, 1930	Trimingham, Norfolk
272. *Vincularia glaucia* Brydone, 1930	Trimingham, Norfolk
273. *Vincularia præcursor* Brydone, 1930	
Holaster planus	Hampshire
274. *Vincularia grania* Brydone, 1930	Weybourne
275. *Vincularia inconspicua* Brydone, 1930	
Porosphaera beds	Trimingham, Norfolk
276. *Vincularia tegminula* Brydone, 1930	
Porosphaera beds	Trimingham, Norfolk
277. *Vincularia tegmen* Brydone, 1930	
“Lower” *Belemnitella mucronata*	Isle of Wight
278. *Vincularia gygæa* Brydone, 1930	
Holaster planus (the *Vectensis* bed)	Isle of Wight
279. *Vincularia harmonia* Brydone, 1930	
Echinocorys scutatus var. *depressus*	Sussex
280. *Vincularia supercilium* Brydone, 1930	
basal *Belemnitella mucronata*	Sussex
Offaster pilula	Isle of Wight
281. *Vincularia allas* Brydone, 1930	
Porosphœra beds	Trimingham, Norfolk
282. *Vincularia brightonensis* Brydone, 1930	
Marsupites	Sussex
283. *Vincularia hecuba* Brydone, 1930	
“Lower” *Belemnitella mucronata*	Isle of Wight
284. *Vincularia hecate* Brydone, 1930	Meudon, France
285. *Vincularia hecamede* Brydone, 1930	
Actinocamax quadratus	Isle of Wight
286. *Vincularia lesueurina* Brydone, 1930	
basal *Belemnitella mucronata*	West Hampshire
287. *Vincularia caveina* Brydone, 1930	
“Lower” *Belemnitella mucronata*	Isle of Wight
288. *Vincularia hedyle* Brydone, 1930	Meudon, France
289. *Vincularia helena* Brydone, 1930	Weybourne, Norfolk
290. *Vincularia hegemone*	Weybourne, Norfolk
291. *Vincularia helice* Brydone, 1930	Trimingham, Norfolk
292. *Vincularia foricula* Brydone, 1930	Trimingham, Norfolk
293. *Onychocella disparilis* var. *hellotis* Brydone, 1930	Weybourne, Norfolk
294. *Onychocella disparilis* var. *helvia* Brydone, 1930	
Porosphaera beds	Trimingham, Norfolk

295.	*Onychocella substrumulosa* Brydone, 1930	Weybourne, Norfolk
296.	*Onychocella heraclea* Brydone, 1930	Weybourne, Norfolk
297.	*Onychocella herennia* Brydone, 1930	Trimingham, Norfolk
298.	*Onychocella hercyna* Brydone, 1930	
	Porosphaera beds	Trimingham, Norfolk
299.	*Onychocella altonensis* Brydone, 1930	
	Holaster planus	Alton, Hampshire
300.	*Onychocella hersilia* Brydone, 1930	
	Micraster cortestudinarium	Sussex
301.	*Onychocella hermione* Brydone, 1930	
	Micraster cortestudinarium	Sussex
	Micraster coranguinum	Isle of Wight
302.	*Onychocella hermione* var. *protendens* Brydone, 1930	
	Micraster cortestudinarium	
303.	*Onychocella hesione* Brydone, 1930	
	Micraster coranguinum	Hampshire
304.	*Onychocella hestia* Brydone, 1930	
	Micraster coranguinum	Hampshire
	Offaster pilula	Isle of Wight
	Actinocamax quadratus	
305.	*Rhagasostoma intelegans* var. *incarcerata* Brydone, 1930	Weybourne, Norfolk
306.	*Rhagasostoma intelegans* var. *testudinaria* Brydone, 1930	
	Micraster cortestudinarium	Sussex
307.	*Rhagasostoma subgibbosum* Brydone, 1930	
	basal *Belemnitella mucronata*	Hampshire Isle of Wight
308.	*Rhagasostoma gibbosum* (Marsson) var. *weybournensis* Brydone, 1930	Trimingham, Norfolk
309.	*Rhagasostoma sheringense* Brydone, 1930	Weybourne, Norfolk
310.	*Rhagasostoma trimense* Brydone, 1930	Trimingham, Norfolk
311.	*Rhagasostoma trulla* Brydone, 1930	Trimingham, Norfolk
312.	*Onychocella mimosa* Brydone, 1930	
	Porosphaera beds	Trimingham, Norfolk
313.	*Onychocella miscens* Brydone, 1930	Trimingham, Norfolk
314.	*Latereschara hantonensis* Brydone, 1930	
	Holaster planus	Alton, Hampshire
315.	*Latereschara cuckmerensis* Brydone, 1930	
	Micraster cortestudinarium * (Rowe's lower fourth of the *Micraster coranguinum* zone)	Sussex
316.	*Latereschara proboscidea* Brydone, 1930	
	Basal *Belemnitella mucronata*	Hampshire, Isle of Wight
317.	*Latereschara ovigera* Brydone, 1930	Trimingham, Norfolk
318.	*Latereschara saltans* Brydone, 1930	Trimingham, Norfolk
319.	*Rotiporina culveriana* Brydone, 1930	
	Holaster planus	Isle of Wight
320.	*Rotiporina altonensis* Brydone, 1930	
	Holaster planus	Hampshire
321.	*Rotiporina altonensis* var. *sublævis* Brydone, 1930	
	Micraster cortestudinarium	
322.	*Rotiporina roborata* Brydone, 1930	
	Uintacrinus chalk	Hampshire, Kent, Sussex
	Offaster pilula	
	Actinocamax quadratus	

323. *Rotiporina decorata* Brydone, 1930	
Echinocorys scutatus var. *depressus*	Sussex
324. *Rotiporina subangulata* Brydone, 1930	
Actinocamax quadratus	
basal *Belemnitella mucronata*	
“Lower” *Belemnitella mucronata*	
325. *Rotiporina antrifera* Brydone, 1930	
Basal and “lower” *Belemnitella mucronata*	Hampshire Isle of Wight
326. *Rotiporina shidensis* Brydone, 1930	
“lower” *Belemnitella mucronata*	Isle of Wight
327. *Rotiporina trimensis* Brydone, 1930	Trimingham, Norfolk
328. *Porina goldfussi* Brydone, 1930	Meudon, France
329. *Porina goldfussi* var. *meudonensis* Brydone, 1930	
Not below “Lower” *Belemnitella mucronata*	
330. *Porina hipparchia* Brydone, 1930	
Junction of *Actinocamax quadratus* and *Belemnitella mucronata*	
331. *Porina portuosa* Brydone, 1930	
Echinocorys scutatus var. *depressus*	Hampshire
332. *Porina aftonensis* Brydone, 1930	
Actinocamax quadratus	Hampshire Isle of Wight
basal *Belemnitella mucronata*	
333. *Porina francorum* Brydone, 1930	Meudon, France
334. *Porina craterica* Brydone, 1930	Meudon, France
335. *Porina hippolyte* Brydone, 1930	Meudon, France
336. *Porina diversa* Brydone, 1930	Weybourne, Norfolk
337. *Porina hortensia* Brydone, 1930	Trimingham, Norfolk
338. *Porina historis* Brydone, 1930	Trimingham, Norfolk
339. *Porina horatia* Brydone, 1930	Trimingham, Norfolk
340. *Porina vesicosa* Brydone, 1930	Trimingham, Norfolk
341. *Porina hostilia* Brydone, 1930	Trimingham, Norfolk
342. *Porina acutimargo* Brydone, 1930	Trimingham, Norfolk
343. *Porina acutimargo* var. *laminata* Brydone, 1930	
Porosphaera beds	Trimingham, Norfolk
344. *Porina sussexiensis* Brydone, 1930	Brighton, Sussex
345. *Porina allantica* Brydone, 1930	Trimingham, Norfolk
346. *Porina socia* Brydone, 1930	
“Lower” *Belemnitella micronata*	Isle of Wight
347. *Porina tenuimuralis* Brydone, 1930	
“Middle” *Belemnitella mucronata*	Studland and Lulworth, Dorset
348. *Porina subvalligera* Brydone, 1930	Meudon, France
349. *Porina scoriacea* Brydone, 1930	
“Lower” *Belemnitella mucronata*	Isle of Wight
350. *Porina nodensis* Brydone, 1930	
“Lower” *Belemnitella mucronata*	Isle of Wight
351. *Porina secreta* Brydone, 1930	
Echinocorys scutatus var. *depressus*	Sussex
352. *Porina secreta* var. *ovingensis* Brydone, 1930	
353. *Porina lapidosa* Brydone, 1930	Trimingham, Norfolk
354. *Porina maculata* Brydone, 1930	
“Lower” *Belemnitella mucronata*	Isle of Wight

355.	*Porina lata* Brydone, 1930	
	Porosphaera beds	Trimingham, Norfolk
356.	*Porina subfragilis* Brydone, 1930	
	"Lower" *Belemnitella mucronata*	Isle of Wight
357.	*Porina impendens* Brydone, 1930	Meudon, France
358.	*Porina offa* Brydone, 1930	
	"Lower" *Belemnitella mucronata*	Isle of Wight
	"Middle" *Belemnitella mucronata*	Studland, Dorset
359.	*Porina subarticulata* Brydone, 1930	Trimingham, Norfolk
360.	*Systenostoma asperulum* (Marsson) var. *præcox* Brydone, 1930	
	Belemnitella mucronata	
361.	*Systenostoma asperulum* (Marsson) var. *parisiensis* Brydone, 1930	Meudon, France
362.	*Membranipora eleanoræ* Brydone, 1936	Eaton and Taverham, Norfolk
363.	*Membranipora suffolcia* Brydone, 1936	
	Top of zone of granulated *Actinocamax quadratus*	Bramford, Suffolk
364.	*Membranipora shavensis* Brydone, 1936	
	Actinocamax quadratus	Hampshire
365.	*Membranipora perincerta* Brydone, 1936	
	Micraster cortestudinarium	Sussex
366.	*Latereschara proboscidea* Brydone, 1930 var. *expansa* Brydone, 1936	
367.	*Onychocella devoniensis* Brydone, 1936	
	Cidaris beds of *Rhynchonella cuvieri*	Branscombe, Devon
368.	*Onychocella introversa* Brydone, 1936	
	Belemnitella mucronata	
	Micraster cortestudinarium	
	Micraster coranguinum	
	Marsupites	
369.	*Onychocella testudinaria* Brydone, 1936	
	Micraster cortestudinarium	Sussex
		Kent
		Hampshire
370.	*Onychocella hantoniensis* Brydone, 1936	
	E. scutatus var. *depressus*	Sussex
	Basal *Belemnitella mucronata*	Isle of Wight
	Actinocamax quadratus	Hants
	Actinocamax quadratus-Belemnitella mucronata junction	Bramford, Suffolk
371.	*Onychocella norfolcia* Brydone, 1936	
	"Middle" *Belemnitella mucronata*	Catton, Weybourne and
	Porosphaera beds	Trimingham, Norfolk
	Basal *Belemnitella mucronata*	
372.	*Onychocella quadraticola* Brydone, 1936	
	Actinocamax quadratus	Hampshire
373.	*Onychocella alticollis* Brydone, 1936	
	Micraster coranguinum	Isle of Wight
374.	*Onychocella eleanoræ* Brydone, 1936	Trimingham, Norfolk
375.	*Onychocella bassleri* Brydone, 1936	
	Micraster cortestudinarium	Sussex
376.	*Onychocella quadraticola brightoniensis* Brydone, 1936	
	Uintacrinus chalk to lower *Echinocorys scutatus* var. *depressus*	
	Mainly *Marsupites*	

377.	*Onychocella cuckmeriensis* Brydone, 1936	
	Micraster cotestudinarium zone	
	*(Rowe's lower fourth of the *Micraster coranguinum* zone)	Sussex
378.	*Onychocella alrensis* Brydone, 1936	
	Micraster coranguinum	Hampshire
379.	*Onychocella longæva* Brydone, 1936	
	Actinocamax quadratus	Hampshire Isle of Wight
	Belemnitella mucronata	Mendon, France
380.	*Onychocella incrustata* Brydone, 1936	
	"Lower" *Belemnitella mucronata*	Isle of Wight
381.	*Onychocella trimensis* Brydone, 1936	Trimingham, Norfolk
382.	*Onychocella punctula* Brydone, 1936	Trimingham, Norfolk
383.	*Onychocella parallela* Brydone, 1936	Trimingham, Norfolk
384.	*Onychocella sheringensis* Brydone, 1936	Weybourne, Norfolk
385.	*Onychocella advena* Brydone, 1936	Meudon, France
386.	*Onychocella roborata* Brydone, 1936	Trimingham, Norfolk
387.	*Rhagasostoma inelegans* (Lonsdale) var. *angliæ* Brydone, 1936	
	Belemnitella mucronata	Trimingham and Norwich,
	Marsupites	Norfolk
	Porosphaera beds	Bramford, Suffolk
388.	*Rhagasostoma gravense* Brydone, 1936	
	Micraster coranguinum	Gravesend, Kent
389.	*Rhagasostoma gibbosulum* Brydone, 1936	
	"Lower" *Belemnitella mucronata*	Isle of Wight
390.	*Rhagasostoma vectense* Brydone, 1936	
	"Lower" *Belemnitella Belemnitella mucronata*	Isle of Wight
391.	*Rhagasostoma precursor* Brydone, 1936	
	Porosphaera beds	Trimingham, Norfolk
392.	*Rhagasostoma calceolum* Brydone, 1936	
	'Probably *Porosphaera* beds'	Trimingham, Norfolk
393.	*Rhagasostoma calceolum* Brydone, 1936 var. *attoneanum* Brydone, 1936	
394.	*Rhagasostoma gimense* Brydone, 1936	
	Porosphaera beds Sponge beds	Trimingham, Norfolk
395.	*Rhagasostoma procurrens* Brydone, 1936	
	Micraster cortestudinarium	Sussex
396.	*Rhagasostoma marsupitium* Brydone, 1936	
	Marsupites	Sussex
	Uintacrinus chalk	
	Actinocamax quadratus	
	Belemnitella mucronata	Isle of Wight
397.	*Rhagasostoma irrostratum* Brydone, 1936	
	Belemnitella mucronata	Weybourne, Norfolk
398.	*Rhagasostoma pendens* Brydone, 1936	
399.	*Rhagasostoma anglicum* Brydone, 1936	
400.	*Semieschara tridentula* Brydone, 1936	
	Upper *Actinocamax quadratus*	
401.	*Semieschara rottingensis* Brydone, 1936	
402.	*Semieschara acuum* Brydone, 1936	
	"Lower" *Belemnitella mucronata*	Alum Bay, Isle of Wight
403.	*Semieschara clausula* Brydone, 1936	
	Micraster cortestudinarium	Sussex
		Devon
	Micraster coranguinum	Hampshire
404.	*Semieschara quadriconvexa* Brydone, 1936	Trimingham, Norfolk
405.	*Semieschara cattoniana* Brydone, 1936	

406. *Semieschara cattoniana* Brydone, 1936 var. *gimense* Brydone, 1936	
Belemnitella mucronata	
407. *Semieschara norvicia* Brydone, 1936	Hartford and Catton, Norfolk Portsdown, Hampshire
Basal *Belemnitella mucronata*	Alum Bay, Isle of Wight
"Lower" *Belemnitella mucronata*	
408. *Semieschara norvicia* Brydone, 1936 var. *carisiana* Brydone, 1936	
409. *Semieschara latepatens* Brydone, 1936	
"Lower" *Belemnitella mucronata*	Isle of Wight
410. *Semieschara manicosa* Brydone, 1936	
Porosphaera beds	Trimingham, Norfolk
411. *Semieschara scopulorum* Brydone, 1936	
Basal *Belemnitella mucronata*	Isle of Wight
412. *Semieschara hartfordensis* Brydone, 1936	
"Lower" *Belemnitella mucronata*	Hartford, Catton and Cley, Norfolk
413. *Semieschara glavensis* Brydone, 1936	
Belemnitella mucronata	Cley, Norfolk
414. *Semieschara accrescens* Brydone, 1936	
Porosphaera beds	Trimingham, Norfolk
415. *Semieschara globator* Brydone, 1936	
Sponge beds	Trimingham, Norfolk
416. *Semieschara œquipartita* Brydone, 1936	Trimingham, Norfolk
417. *Semieschara inclinata* Brydone, 1936	Weybourne and Catton, Norfolk
418. *Semieschara arrensis* Brydone, 1936	
Actinocamax quadratus	Isle of Wight
419. *Semieschara tumefacta* Brydone, 1936	
420. *Semieschara tertia* Brydone, 1936	
Holaster planus	Hampshire
421. *Semieschara tuftonensis* Brydone, 1936	
Micraster coranguinum	Hampshire
422. *Semieschara walthamensis* Brydone, 1936	
Actinocamax quadratus	Bishop's Waltham and Portsdown, Hampshire
423. *Semieschara alumensis* Brydone, 1936	
"Lower" *Belemnitella mucronata*	Isle of Wight
424. *Semieschara henrici* Brydone, 1936	Studland, Dorset
425. *Semieschara subpunctulata* Brydone, 1936	
Belemnitella mucronata	Hartford and Catton, Norwich
426. *Semieschara peropaca* Brydone, 1936	Trimingham, Norfolk
427. *Tylopora lorea* (Lang) *hantoniensis* Brydone, 1936	
Holaster planus	Hampshire
428. *Semieschara microporina* Brydone, 1936	
"Lower" *Belemnitella mucronata*	Isle of Wight
429. *Micropora bedensis* Brydone, 1936	
basal *Belemnitella mucronata*	Hampshire
430. *Micropora multicrescens* Brydone, 1936	
Porosphaera beds	Trimingham, Norfolk
431. *Micropora monticula* Brydone, 1936	Trimingham, Norfolk

432.	*Puncturiella norviciensis* Brydone, 1936	Trimingham, Norfolk
433.	*Puncturiella norviciensis* var. *ordinata* Brydone, 1936	
434.	*Puncturiella norviciensis* var. *spinulata* Brydone, 1936	
435.	*Puncturiella superba* Brydone, 1936	Trimingham, Norfolk
436.	*Homalostega hartfordensis* Brydone, 1936	Hartford, Norwich
437.	*Homalostega punctilla* Brydone, 1936	Hartford, Catton and Trimingham, Norwich
438.	*Homalostega sussexiensis* Brydone, 1936	
	Micraster cortestudinarium	Sussex
439.	*Cryptostoma wollianum* Brydone, 1936	
440.	*Cryptostoma sub-batheri* Brydone, 1936	Weybourne, Eaton, Hartford and Catton, Norfolk
441.	*Cryptostoma compactum* Brydone, 1936	
	Porosphaera beds	Trimingham, Norfolk
442.	*Cryptostoma corallinum* Brydone, 1936	
	Lower and middle *Belemnitella mucronata* chalk	Norfolk
443.	*Cryptostoma globidecus* Brydone, 1936	
	Lower and middle *Belemnitella mucronata* chalk	Norfolk incl. Trimingham
	Porosphaera beds	Norfolk,
444.	*Cryptostoma sheringense* Brydone, 1936	Weybourne, Norfolk
445.	*Cryptostoma lagenale* Brydone, 1936	Weybourne and Overstrand (erratics), Norfolk
446.	*Cryptostoma aviculigerum* Brydone, 1936	Weybourne, Norfolk
447.	*Cryptostoma eleanoræ* Brydone, 1936	Trimingham, Norfolk
448.	*Cryptostoma* (?) *bifrons* Brydone, 1936	Meudon, France
449.	*Cryptostoma* (?) *carinatum* Brydone, 1936	Meudon, France
450.	*Cellepora accumulate* (Hagenow) var. *bellicosa* Brydone, 1936	
	Porosphaera beds	Trimingham, Norfolk
451.	*Terebripora robusta* Brydone, 1936	Trimingham, Norfolk
452.	*Herpetopora comptoniensis* Brydone, 1936	Chloritic Marl

Young^2: the palaeobryozoological work of John Young and John Young of Glasgow

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1. Introduction

During the mid-Victorian period Glasgow rapidly developed as a major industrial and cultural centre, the latter activity based largely around the university and various scientific societies. The University of Glasgow houses the significant collections of William Hunter (d. 1783) in the Hunterian Museum, now known as 'The Hunterian' (Brock 1980) and for a period in the nineteenth century these were under the collective care of two scientists, both called John Young (Clark 2008). Both men were active members of the Natural History Society of Glasgow and the Geological Society of Glasgow and served on both councils or as officers, and much of their research was published in their respective journals.

2. Mr (later Dr) John Young

The older John Young (1823–1900) (Figure 1, left) was a geologist and museum

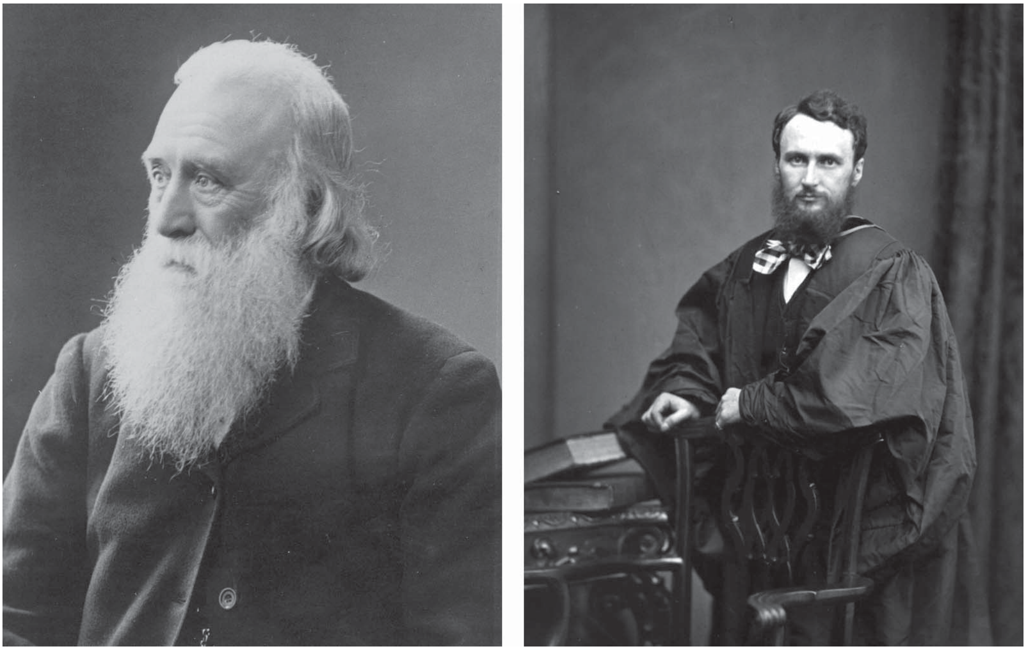


Figure 1. Mr/Dr John Young (left); Prof. John Young (right),

curator who made a significant contribution to the study of fossil bryozoans in the late nineteenth century. Born in Campsie, Stirlingshire, Scotland, he first was employed as a messenger-boy in a textile printing mill and later as an apprentice block cutter in a print works in Lennoxtown (Macnair and Mort 1908) where he remained for twenty-six years. At the age of twenty-four he married Margaret Stirling and the couple had seven children, three daughters and four sons (http://www.hmag.gla.ac.uk/neil/Young/fam003.html).

Young, who in this paper is referred to with the appellation 'Mr' or 'Dr', first came to the attention of the scientific community when he joined the Natural History Society of Glasgow in 1852 (he was later elected a Life Member, and a Vice President in 1877). In 1855 he was employed to arrange a fossil collection for the visit to the city of the British Association for the Advancement of Science. Four years later he was appointed as Assistant Keeper in the Hunterian (Figure 2), and during his career which lasted until his retirement in 1899, he did much to enhance the collections, and published several catalogues and listings of Scottish fossils including that coauthored with James Armstrong (1871). This provided the basis of the comprehensive *Catalogue of Western Scottish Fossils* co-authored with Armstrong and David Robertson that contains detailed lists of taxa and locality data and which was published to coincide with the visit of the British Association for the Advancement of Science to Glasgow in 1876 (Armstrong *et al.* 1876) (Figure 3). Professor John Young (1835–1902) (Figure 1, right) penned an account of the geology and palaeontology of the area, and the volume also contains four plates of graptolites from Moffat drawn and lithographed by Charles Lapworth.

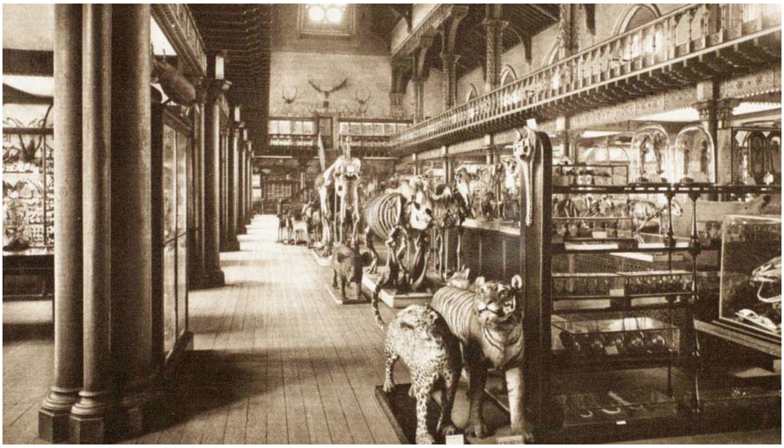
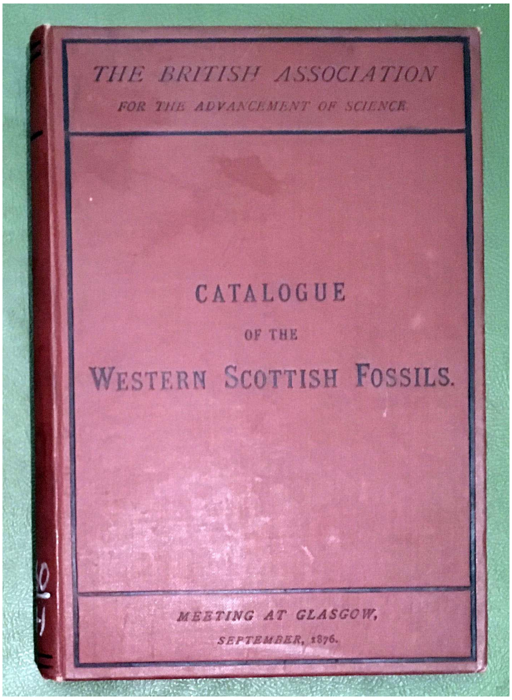


Figure 2. Interior of the Hunterian c. *1890.*

While this paper is primarily concerned with the bryozoological researches of these two Scottish naturalists, it should be remarked that Mr John Young produced a significant volume of papers that demonstrated his interest and abilities in groups besides bryozoans or 'Polyzoa' as he called them. In an early communication he erected the fossil fish *Rhizodopsis* in 1866.

Young was very closely associated with the activities of the Geological Society of Glasgow, quickly becoming deeply immersed following his election as an Honorary Associate in 1859 and Vice-President on 6 October of the same year. In addition to chairing meetings in the absence of the President, he frequently exhibited fascinating specimens, led field excursions, and ran an evening lecture course from 1874 until 1882. His status and standing was summarised in 1908 in a description that referred to him with reference to the understanding of the geological structure of western Scotland, as it having "no greater living authority than Mr. John Young" (Macnair and Mort 1908, p. 52). He was also an Associate Member of the Edinburgh Geological Society in whose journal he also published.

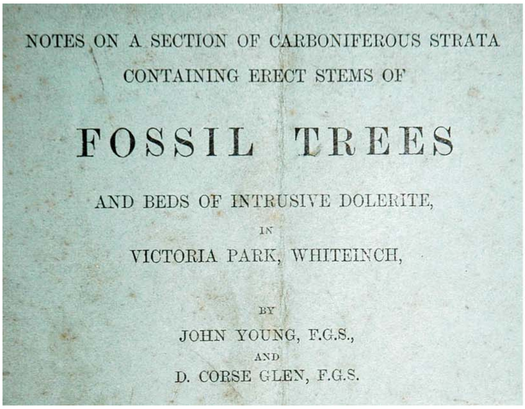


THE BRITISH ASSOCIATION
FOR THE ADVANCEMENT OF SCIENCE

CATALOGUE
OF THE
WESTERN SCOTTISH FOSSILS.

MEETING AT GLASGOW,
SEPTEMBER, 1876.

Figure 3. Cover of the handbook Catalogue of the Western Scottish Fossils *produced for the British Association for the Advancement of Science meeting in Glasgow in 1876.*



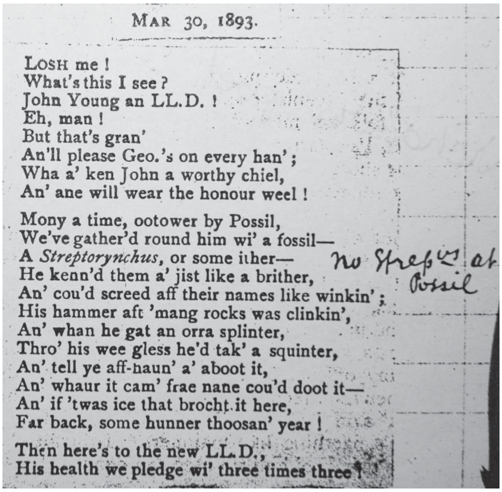
NOTES ON A SECTION OF CARBONIFEROUS STRATA
CONTAINING ERECT STEMS OF
FOSSIL TREES
AND BEDS OF INTRUSIVE DOLERITE,
IN
VICTORIA PARK, WHITEINCH,
BY
JOHN YOUNG, F.G.S.,
AND
D. CORSE GLEN, F.G.S.

Figure 4. Cover page of pamphlet by John Young and David Corse Glen on the geology and palaeobotany of Victoria Park, Glasgow (1888) (left); View of the aptly named Fossil Grove, Victoria Park, Glasgow prior to the erection in 1890 of the pavilion that now projects the site (right).

In 1887 a group of unemployed shipbuilders were provided with work clearing out an old quarry in Victoria Park, and they came across a number of bases of *Lepidodendron* trees *in situ* (Figure 4, right). This find and its geological setting and palaeobotanical significance was described in two papers the following year, one by Young and Corse Glen (1888) (Figure 4, left) and the other by the eminent palaeobotanist Robert Kidston (Gunning 1995, Kidston 1888, www.hmag.gla.ac.uk/neil/FossilGrove/). Fossil Grove is most likely the earliest geoconservation site in the world.

Towards the end of his life he was conferred LL.D. by the University of Glasgow and this was greeted with great acclaim by his associates one of whom published a short poem to mark the event (Figure 5). His new title also later helped others distinguish him from his younger namesake. In publications he is often referred to as "Mr John Young" and was known locally as "John Young, the Good" on account of his careful scientific work. He was reputed to be a good teacher and always willing to help students and fellow naturalists particularly in the field, and was generous in the distribution of materials that he had collected.

He died on 13 March 1900 at Troon, Ayrshire.



MAR 30, 1893.

LOSH me!
What's this I see?
John Young an LL.D.!
Eh, man!
But that's gran'
An'll please Geo.'s on every han';
Wha a' ken John a worthy chiel,
An' ane will wear the honour weel!

Mony a time, ootower by Possil,
We've gather'd round him wi' a fossil—
A *Streptorynchus*, or some ither—
He kenn'd them a' jist like a brither,
An' cou'd screed aff their names like winkin';
His hammer aft 'mang rocks was clinkin',
An' whan he gat an orra splinter,
Thro' his wee gless he'd tak' a squinter,
An' tell ye aff-haun' a' aboot it,
An' whaur it cam' frae nane cou'd doot it—
An' if 'twas ice that brocht it here,
Far back, some hunner thoosan' year!

Then here's to the new LL.D.,
His health we pledge wi' three times three!

no Streps at Possil

Figure 5. Poem published in 1893 celebrating the conferring of the degree of LL.D. on Mr John Young. A hand-written note on the right remarks that the fossil brachiopod Streptorynchus *is not actually found at Possil which is a district in north Glasgow.*

3. Professor John Young

The younger John Young (1835–1902) (Figure 1, right) was educated at the University of Edinburgh where he qualified with a medical degree. Following a short medical career at the Royal Edinburgh Asylum, he jointed the Geological Survey in Scotland and served as a geologist between 1861 and 1866. While on fieldwork he broke his kneecap which left him slightly lame for the rest of his life (Macnair and Mort 1908, p. 211)

In 1866 Young was appointed Professor of Natural History in the University of Glasgow in succession to the American geologist Henry Darwin Rogers and took up the concurrent position of Keeper of the Hunterian. As a lecturer he was never dull and was memorable for being irrational and blessed with a sardonic wit, and was widely known for his unconventional behaviour (Macnair and Mort 1908, Cleevely 1983). He promoted the educational value of the museum, but came into conflict with some of his colleagues when he suggested that the collection of coins be sold as they were not used for teaching.

Given his academic position it is not surprising that he was elected President Geological Society of Glasgow, 7 March 1867 and served until 1872. He was also President of the Natural History Society of Glasgow from 1869 to 1882.

Aside from his scientific research in palaeontology and glacial geology he also published a catalogue of the artworks in the University (1880) and his *Essays and Addresses* were published posthumously in 1904 (Llowlees 1904)

He was distinguished from his namesake by the title “Prof.”, letters “M.D.” or the less complimentary “John Young, the Bad”. The latter may have to do with his unconventional and eccentric behaviour, or simply because it was opposite to the older John Young.

4. Bryozoan research

In a four-year period from 1874 to 1877 John Young and John Young jointly published a series of eight short papers on Scottish Carboniferous Bryozoa (Appendix 1).

Much of this material was collected at various localities in the west of Scotland: Capelrig, Boghead - Hamilton, Gillfoot, Hairmyres, High Blantyre, and Trearne. Of these, Hairmyres yielded exquisitely preserved bryozoans, most of which comprised delicate zoaria such as in the genera *Penniretepora* and *Diploporaria* (Figure 6). The locality, adjacent to the East Kilbride Railway line, had been known to the Scottish naturalist and cleric David Ure (1749–1798) (Clark and Keen 1996, Clark 2015).

Young and Young named several new cryptostome and fenestrate genera: *Rhabdomeson* and *Actinostoma* in 1874, *Diplopora* [now *Diploporaria* Nickles & Bassler, 1900] and *Acanthopora* [now *Penniretepora* d’Orbigny, 1849] in 1875, and a suite of *Penniretepora* species among others (Table 1).

Their papers provided detailed treatments for the time of bryozoan taxonomy and are notable in that attention was paid to aspects of minute skeletal morphology, and for the use of thin sections. They erected the cryptostome genus *Rhabdomeson* on the basis of its distinctive central tubular axis (Figure 7). Although their descriptions are based on

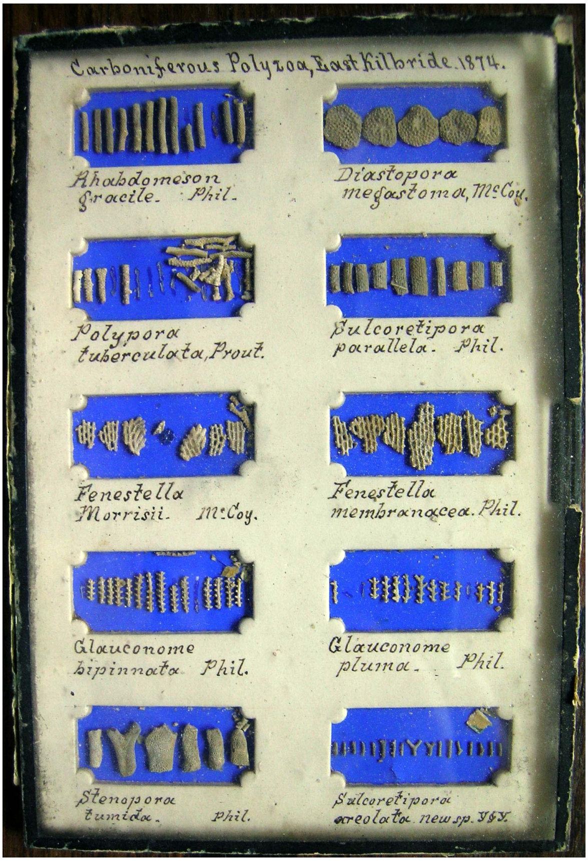


Figure 6. Various Mississippian bryozoans from the Lower Limestone Group, Hairmyres, East Kilbride, Scotland collected, mounted and labelled by John Young in 1874 and presented to David Sanderson. All taxa have since been reassigned. GLAHM 163005, Hunterian Collection.

specimens they collected from Hairmyres in East Kilbride and Trearne in Ayrshire, they perversely selected the species *Millepora gracilis* Phillips, 1841 from the Devonian of north Devon as the type species. During a subsequent revision of the genus, the type specimen of the type species described by Phillips (1841) was found to lack the central axis and so did not belong to *Rhabdomenson* (Wyse Jackson and Bancroft 1995). It was replaced as type species by *Rhabdomeson progracile* Wyse Jackson and Bancroft, 1995 (ICZN 1996) which had been erected and described in detail on the basis of Young and Young's material and other specimens collected throughout Britain and Ireland (Wyse Jackson and Bancroft 1995).

Diplopora was distinguished on account of an accessory pore located just proximally of the autozooecial aperture (Young and Young 1875a) and was first regarded by them as a subgenus; it was later elevated to generic status by Nickles and Bassler (1900) and named *Diploporaria* on account of *Diplopora* being preoccupied. Recognising such a tiny morphological feature (the accessory pore) without the aid of a Scanning Electron

Table 1. New bryozoan taxa described by Young and Young or by Mr John Young

Genera:

- *Actinostoma* Young and Young, 1874
- *Acanthopora* Young and Young, 1875
  - = *Penniretepora* D'Orbigny, 1849
- *Diplopora* Young and Young, 1875
  - = *Diploporaria* Nickles and Bassler, 1900
- *Rhabdomeson* Young and Young, 1874 (Figure 7)
- *Tabulipora* Young, 1882

Species:

- *Actinostoma fenestratum* Young and Young, 1874
- *Glauconome aspera* Young and Young, 1876
  - = *Penniretepora pluma* (Phillips, 1836)
- *Glauconome elegans* Young and Young, 1876 (Figure 8)
  - = *Penniretepora elegans* (Young and Young, 1876)
- *Glauconome flexicarinata* Young and Young, 1876
  - = *Penniretepora pluma* (Phillips, 1836)
- *Glauconome laxa* Young and Young, 1876
- *Glauconome* (*Diplopora*) *marginalis* Young and Young, 1875
  - = *Diploporaria marginalis* (Young and Young, 1875)
- *Glauconome retroflexa* Young and Young, 1876
  - = *Penniretepora pulcherrima* (M'Coy, 1844)
- *Glauconome recticarinata* Young, 1881
  - = *Penniretepora recticarinata* (Young, 1881)
- *Glauconome robusta* Young and Young, 1876
  - = *Penniretepora pulcherrima* (M'Coy, 1844)
- *Glauconome stellipora* Young and Young, 1874
  - = *Penniretepora pluma* (Phillips, 1836)
- *Glauconome* (*Acanthopora*) *stellipora* var. *spinosa* Young and Young, 1875
  - = *Penniretepora recticarinata* (Young, 1881)
- ?*Sulcoretepora robertsoni* Young and Young, 1877
  - = probably *Hyphasmopora* sp.
- *Synocladia* (?) *fenestelliformis* Young, 1881 (Figure 9)
  - = *Polyfenestella fenestelliformis* (Young, 1881)
- *Synocladia*? *scotica* Young and Young, 1878
  - = *Septopora scotica* (Young and Young, 1878)
- *Thamniscus*? *rankini* Young and Young, 1875

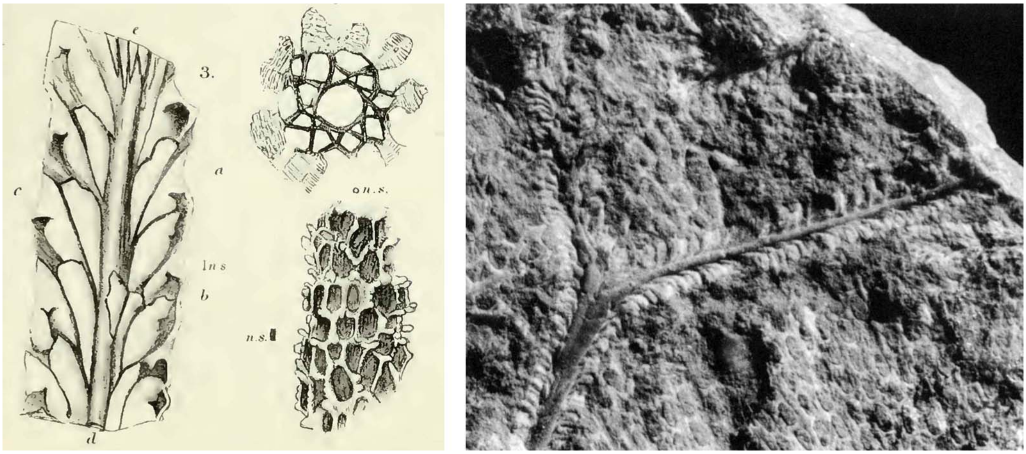


Figure 7. Morphology of Rhabdomeson *showing longitudinal and transverse sections and external features (from Young and Young, 1874) (left);* Rhabdomeson progracile *Wyse Jackson & Bancroft, 1995; GLAHM D.101; from the Mississippian limestone of Laigh Baidland, Dalry, Ayrshire, Scotland. The colony has been split at the depth of the central cylindrical tube to reveal the autozooecial chambers budded away from it (right).*

Microscope is a testament to the careful and meticulous work of the Glaswegian bryozoologists.

A number of new species of *Glauconome* (now *Penniretepora*) (Figure 8) were described in several papers and a comparative table listing the morphological characteristics of them and other *Glauconome* species appeared in Young and Young (1875a).

They were the first researchers to describe and illustrate apertural stylets in fossil bryozoans (Young and Young 1874a). These produce a stellate autozooecial opening in some fenestrate species such as *Actinostoma fenestratum* Young and Young, 1874 (see McKinney and Wyse Jackson 2015, figure 32). These apertural stylets demonstrate that the polypide possessed only eight tentacles in its lophophore.

In 1869 Duncan and Fletcher erected the genus *Palaeocoryne* for what they believed to be hydroids found preserved attached to Carboniferous fenestellid colonies. On closer examination Young and Young (1874d) were able to demonstrate that these were skeletal outgrowths of the bryozoans and not epiphytes, a conclusion subsequently confirmed by later authors (Tavener-Smith 1973, Bancroft 1988, see McKinney and Wyse Jackson 2015, pp. 29–30, fig. 19.6–19.9). At the meeting in London where the paper was delivered Duncan objected to the conclusions stating that he held to his opinion that the outgrowths were parasitical and such skeletal extensions were unknown in modern bryozoans. The extensions probably provided structural support for colonies that enabled them to remain upright in strong water currents.

After 1877 the Youngs, it would appear, didn’t publish again collaboratively, and this could be considered surprising for two reasons: firstly, they produced a number of excellent papers prior to 1877, and secondly Mr John Young continued his interest in

Figure 8. Penniretepora elegans *Young and Young, 1875, reverse surface showing pinnate growth habit comprising a main stem from which secondary lateral stems develop, some of which bear tertiary pinnae, GAGM 01-53wg; Brigantian, Viséan, Mississippian; Dykehead Pit, High Blantyre, Scotland.*

bryozoans and other microorganisms and published until shortly before his death (Appendix 2 and 3). Why might this have been? One can only speculate, but the hierarchy in the Hunterian might have played a part. Perhaps Mr John Young was largely responsible for the joint papers but felt Prof. Young should be credited as the lead author as he was the Keeper of the Hunterian; perhaps Prof. John Young's interest in palaeontology fell away at the time (and this is backed up by examination of the *Royal Society Lists of Scientific Papers* for 1902); or maybe they had a serious falling out. Certainly there is no disputing their hierarchy: in the forward to Prof. Young's 1880 catalogue of the College artworks he asks that readers direct any errors not to himself but to Mr John Young who was charged with compiling these errors for rectification in any future edition of the catalogue. This suggests that the author considered such editorial matters beneath his status in the University.

Whatever the ongoing relationship between the two Hunterian colleagues, between 1874 and 1888 Mr John Young also published at least fifteen bryozoological papers on his own account (Appendix 2). In 1877 he devised a clever preparation method that allowed for the study of the obverse surfaces of fenestrates preserved in shales (Figure 9A). This involved painting a layer of hot asphalt on the exposed reverse surface of the colony and them sticking down brown paper on top. Once cooled the paper could be ripped away and often the hidden obverse surface would be released from the surrounding matrix.

There is no doubt that Mr John Young was a very careful observer and recorder of detail. In his paper of 1882a he observed hemisepta, delicate intrachamber skeletal structures in some taxa (Young 1882a). In the same paper he also described 'cell-pores [autozooecial apertures]...covered by a thin calcareous disc or diaphragm pierced in the centre by a very minute pore...' in four species in three genera. The latter are now known to be Secondary Nanozooecia (see Bancroft 1986b).

In 1882 he erected the trepostome subgenus *Tabulipora* and selected as the species *Cellepora urii* Fleming, 1828 named in honour of David Ure. *Tabulipora* Young, 1882 is now considered to have full generic status and is characterised by the development of ring septae in the exozone (see Wyse Jackson 1996 for description of the type species and two others from Britain and Ireland).

This research provided information on the taxonomy, stratigraphic ranges and geographical distribution of over fifty species in at seventeen genera from the Carboniferous sequences in Scotland (see Armstrong *et al*. 1876, pp. 46–48 for a list of these taxa).

Since the 1970s many of Young and Young's taxa have been subject to restudy. Graham (1975) revised the pinnate *Penniretepora* species, and Bancroft (1984) carried out an extensive reappraisal of Scottish stenolaemate bryozoans as part of a Ph.D. study. He subsequently published a revision of *Synocladia* (Bancroft 1987) and erected the new genus *Polyfenestella* based on the type suite of *Synocladia* (?) *fenestelliformis* Young, 1881 (Bancroft 1986a) (Figure 9). Later Wyse Jackson and McKinney (2013) carried out

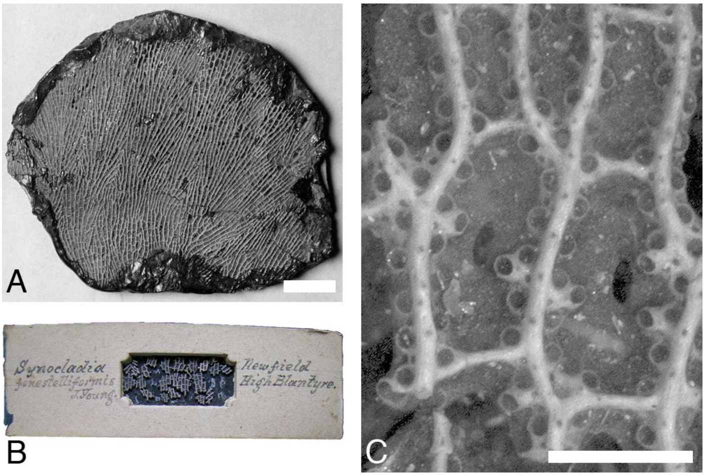


Figure 9. Polyfenestella fenestelliformis *(Young, 1881); (A) GAGM 01-53xl, lectotype; Brigantian, Viséan, Mississippian; Dykehead Pit, High Blantyre, Scotland. Zoarium showing reticulate meshwork composed of thin dichotomising branches. The obverse surface was revealed by John Young using his asphalt methodology of preparation. Image ©CSG CIC Glasgow Museums Collection; (B-C) GAGM 01-53xj, paralectotype; Brigantian, Viséan, Mississippian; Newfield, High Blantyre, Scotland, (B) Cavity slide containing numerous fragments. This is labelled in the distinctive handwriting of Mr John Young, (C) Obverse surface showing bifurcating branches with strong keel, regular keel nodes, triangular to rectangular fenestrules and thin dissepiments. Scale bars: A = 10mm, C = 1mm (Modified from Wyse Jackson and McKinney 2013, figure 1).*

CT microtomography on Young's material and were able to clarify the nature of the polymorphs originally identified as "irregular supplementary cells" by Young (1881, p. 33) and defined as of one of the two distinctive types by Bancroft (1986a).

Synocladia? *scotica* described by Young and Young in 1878 has gone through a turbulent taxonomic history. Graham (1975, p. 10) placed it in synonomy with *Lanarkopora carbonaria* (Etheridge jr., 1873), but Bancroft (1987, 1989) disagreed with the reasoning for the erection of the genus *Lanarkopora* Graham, 1975 (which Graham 1989 refuted), and showed that *scotica* was a junior synonym of *Synocladia carbonaria* Etheridge jr., 1873 but that the species belonged in the genus *Septopora* Prout, 1859.

John Young's final bryozoan paper is a discussion of rare ctenostome bryozoans from the Carboniferous of Scotland. This paper followed his exhibiting the material at a meeting of the Geological Society of Glasgow in May 1894 (Young 1894).

5. Recognition

Within the local scientific and geological community both Professor and Mr John Young made major contributions both in terms of scientific output but also in providing service. As is noted earlier both served on the Council of the Geological Society of Glasgow culminating in terms as President or Vice President.

When Mr John Young was appointed a Lecturer in the Glasgow Mechanics' Institution in 1874 (a position he held concurrently with his post in the Hunterian) his peers presented him with a life membership of the Geological Society of London and a purse of sovereigns (Macnair and Mort 1908). This no doubt would have been of great value to him in his continued research and lecturing career; membership of the London organisation was often beyond all but those with considerable means.

Nine years later he was honoured by the Geological Society of London in being selected the recipient of the Murchison Geological Fund. This is a secondary award after the Murchison Medal funded from a bequest by the Scottish Geologist and Director of the Geological Survey of Great Britain Sir Roderick Impey Murchison (1792–1871). The citation makes clear John Young's achievements: "the value of his long-continued researches on the fossil Polyzoa, especially those of the western part of Scotland, and of his investigations into the structure of the shells of the Carboniferous brachiopods." Young was not in attendance to receive the award from the President of the society, John Whitaker Hulke, but it was later passed onto him. On Young's behalf Professor John Morris read a letter by way of a response to the President and this clearly demonstrates Young's humility but satisfaction at the unexpected award (Young in Hulke 1883, pp. 32–33). He highlighted his microscopic investigations of fossils and remarked that they are better preserved than many other researchers had otherwise suggested. This painstaking study allowed him to be "fortunate in discovering some new forms, and also in finding some new points of structure in others already known and described."

Aside from his own research, which Morris noted had resulted in nearly fifty papers, John Young wrote that he had gained "sufficient reward" in helping eminent palaeontologists in their researches through providing specimens of brachiopods, foraminifera, molluscs, sponges, ostracods and from Scotland. No doubt he was referring among others to Thomas Davidson who named the brachiopods *Productus youngianus* and *Rhynchopora youngii* and to Rupert Jones who named the ostracod *Esteria youngii* all in his honour (*Estheria youngii* was revised by Wilson (1958) as the bivalve *Sanguinolites* cf. *clavatus* which also synonymised Kobayashi's *Lioestheria youngi*). Other taxa named for him included the gastropod *Pleurotomaria youngiana* Armstrong, 1868, the shark *Gyracanthus youngii* Traquair, 1883, and a species of the ctenostome bryozoan *Ascodictyon* named by George Robert Vine in 1891 from the Hairmyres Limestone. It is more than probable that Young sent him the material, as he later sent more specimens just before Vine's death in 1892 (Young 1894, p. 145). That he shared his bryozoan material with a colleague publishing on the same group demonstrates his generosity of spirit and keenness to advance scientific knowledge.

6. The Youngs' bryozoan collection

The bryozoan collections are now housed largely in the Hunterian and in the Glasgow Art Gallery and Museum, Kelvingrove, while a small number are located in the Natural History Museum, London. Beautifully mounted in cavity slides, their provenance is easily verified on account of the distinctive handwriting of Mr John Young (Figures 6 and 9B) who was probably responsible for the curation of the material on which the two men researched. Cleevely (1983, p. 321) remarks that "Young's specimens are notable for their meticulous labels, giving details of horizon, locality and even the date of collection."

In April 1870 Professor John Young exhibited a model of the anatomy of a bryozoan to a meeting of the Natural History Society of Glasgow. This had been made for the Hunterian by a Mr Fenwick.

The Hunterian contains a considerable collection of Carboniferous fossils from Glasgow and adjacent districts collected by Young between 1863 and 1894 (Cleevely 1983). This is not unusual as they were probably collected while engaged in museum and university business. However, given his curatorial position it is odd that his collections are split between two Glasgow institutions. This came about because following his death Mr/Dr John Young's considerable personal collection was acquired by James T. Tullis of Rutherglen, and it was donated by him to the Glasgow Art Gallery and Museum in 1901 (Doughty 1981, Stace *et al*. 1987). Other Young material came via donation by Young himself and John R.S. Hunter-Selkirk (1835–1898), and by Arthur Pratt (1817–1881) and by purchase in 1896 from the estate of David Corse Glen (1824–1892). The collection comprised bryozoans, ostracods, small molluscs, sponge spicules, thin sections of shell microstructure and brachiopods (Cleevely 1983). Stace *et al*. (1987, p. 371) commented that: "Young's collection is the most important collection in the Museum. It formed the basis of the 'Catalogue of Western Scottish Fossils'...".

Professor John Young donated Carboniferous fossils from Glasgow and Australia to the Hunterian (Stace *et al*. 1987), ostracods to the Natural History Museum, London in

1862 and followed this up with specimens of specimens of *Rhabdomeson gracile* in 1874 (Cleevely 1983) shortly after the publication of this taxon. That he distributed specimens beyond Glasgow suggests that he must have considered this bryozoan to have significant scientific importance. Other Young and Young specimens found their way into the collections of the Natural History Museum in London via George Robert Vine (Buttler *et al*. 2002, Wyse Jackson *et al*. 2003).

7. Conclusion

During the late nineteenth century in Great Britain a number of researchers made significant contributions to the naming and undertanding of the morphology of fossil bryozoans. Foremost amongst these was Mr (later Dr) John Young who with Professor John Young worked in the Hunterian of the University of Glasgow. Either collaboratively or alone they described over a dozen new species and five genera from the Carboniferous of Scotland.

References

Bancroft, A.J. 1984. *Studies in Carboniferous Bryozoa*. Unpublished Ph.D. thesis, University of Durham.

Bancroft, A.J. 1986a. A new Carboniferous fenestrate bryozoan genus. *Scottish Journal of Geology* **22**, 99–106.

Bancroft, A.J. 1986b. Secondary nanozooecia in some Upper Palaeozoic fenestrate Bryozoa. *Palaeontology* **29**, 207–212.

Bancroft, A.J. 1987. The fenestrate bryozoan *Septopora carbonaria* (Etheridge Jun, 1873a) from the Carboniferous of Great Britain. *Geological Journal* **22**, 1–10.

Bancroft, A.J. 1988. Palaeocorynid-type appendages in Upper Palaeozoic fenestrate Bryozoa. *Palaeontology* **31**, 665–675.

Bancroft, A.J. 1989. A reply to D.K. Graham regarding the validity of the Carboniferous fenestrate bryozoan genus *Lanarkopora* Graham (1975). *Geological Journal* **24**, 67–68.

Brock, C.H. 1980. Dr William Hunter's Museum, Glasgow University. *Journal of the Society for the Bibliography of Natural History* **9**, 403–412.

Buttler, C.J., Wyse Jackson, P.N. and Sharpe, T. 2002. George Robert Vine (1825–1893): stay maker, bryozoologist and fossil dealer, pp. 1–29. *In* Wyse Jackson, P.N. and Spencer Jones, M.E. (eds) *Annals of Bryozoology: aspects of the history of research on bryozoans*. International Bryozoology Association, Dublin.

Clark, N.D.L. 2008. Working with fossils at the Hunterian Museum: a glimpse into the lives of John Young, John Young and Ethel Currie. *In* 150th Anniversary of the Geological Society of Glasgow, 23rd Feb 2008, Glasgow, UK. http://eprints.gla.ac.uk/89196/ [Accessed 20 October 2017]

Clark, N.D.L. 2015. David Ure (1749-1798): the enlightened fossil collector. Chapter 22, pp. 361–370. *In* Hancock, E.G., Pearce, N. and Campbell, M. (eds) *William Hunter's World: The Art and Science of Eighteenth-Century Collecting*. Ashgate Publishing.

Clark, N.D.L. and Keen, M.C. 1996. David Ure and his Carboniferous ostracods from East Kilbride, Scotland, pp. 1–4. *In* Keen, M.C. (ed.) *Proceedings of the 2nd European Ostracodologists meeting, Glasgow 1993*. British Micropalaeontological Society, London.

Cleevely, R.J. 1983. *World Palaeontological Collections*. British Museum (Natural History and Mansell Publishing Limited, London, 365 pp.

Doughty, P.S. 1981. The state and status of Geology in U.K. Museums. *Geological Society, London, Miscellaneous Paper* **13**, 1–118.

Duncan, P.M. and Fletcher, H.M. 1869. On *Palaeocoryne*, a genus of tubularine Hydrozoa from the Carboniferous Formation. *Philosophical Transactions of the Royal Society of London* **159**, 693–699.

Graham, D.K. 1975. A review of Scottish Carboniferous acanthocladiid Bryozoa. *Bulletin of the Geological Survey of Great Britain* **49**, 1–21.

Graham, D.K. 1989. Note on the Carboniferous bryozoan taxon *Lanarkopora carbonaria* (Etheridge jun.) *Geological Journal* **24**, 69.

Gunning, A. 1995. *The Fossil Grove*. Glasgow Museums, 24 pp.

Hulke, J.W. 1883. Award of the Murchison Geological Fund. *Proceedings of the Geological Society* in *Quarterly Journal of the Geological Society* **33**, 31–33.

International Commission on Zoological Nomenclature 1996. *Rhabdomeson* Young & Young, 1874 (Bryozoa): *Rhabdomeson progracile* Wyse Jackson & Bancroft, 1995 designated as the type species. *Bulletin of Zoological Nomenclature* **53**, 222.

Kidston, R. 1888. Note on the nature of the fossil trees found at Whiteinch. *Transactions of the Geological Society of Glasgow* **8**, 235–236.

Llowlees, D. 1904. *Essays and Addresses by the late John Young, M D, Regius Professor of Natural History in the University of Glasgow. With a memoir*. James Maclehose, Glasgow.

McKinney, F.K. and Wyse Jackson, P.N. 2015. Part G, Revised, Volume 2, Chapter 8A: Order Fenestrata: Morphology and Growth. *Treatise Online* **66**, 1–91.

Macnair, P. and Mort, F. 1908. *History of the Geological Society of Glasgow, 1858-1908, with Biographical Notices of the more prominent members*. Geological Society of Glasgow, Glasgow, pp. 303.

Nickles, J.M. and Bassler, R.S. 1900. A Synopsis of American Fossil Bryozoa including bibliography and synonymy. *United States Geological Survey Bulletin* **173**, 1–663.

Phillips, J. 1841. *Figures and description of the Palaeozoic fossils of Cornwall, Devon, and West Somerset*. Longman, Brown, Green, and Longmans, London, pp. xx+231.

Stace, H.E., Pettitt, C.W.A. and Waterston, C.D. 1987. *Natural Science collections in Scotland*. National Museums of Scotland, Edinburgh, pp. xxvii+373.

Tavener-Smith, R. 1973. Fenestrate Bryozoa from the Viséan of County Fermanagh, Ireland. *Bulletin of the British Museum (Natural History) Geology* **23**, 391–493.

Wilson, R.B. 1958. A revision of the Carboniferous lamellibranchs *Edmondia punctatella* (Jones) and '*Estheria*' *youngii* Jones. *Bulletin of the Geological Survey of Great Britain* **15**, 21–28.

Wyse Jackson, P.N. 1996. Bryozoa from the Lower Carboniferous (Viséan) of County Fermanagh, Ireland. *Bulletin of the British Museum (Natural History) Geology* **52**, 119–171.

Wyse Jackson, P.N. and Bancroft, A.J. 1995. Generic revision of the cryptostome bryozoan *Rhabdomeson* Young and Young, 1874, with descriptions of two species from the Lower Carboniferous of the British Isles. *Journal of Paleontology* **69**, 28–45.

Wyse Jackson, P.N., Buttler, C.J. and Sharpe, T. 2003. Bryozoans and corsetry: the palaeontological work of George Robert Vine (1825–1893) of Sheffield. *Proceedings of the Geologists' Association* **114**, 339–344.

Wyse Jackson, P.N. and McKinney, F.K. 2013. A micro-computed tomography and Scanning Electron Microscopy investigation of the structure of *Polyfenestella* Bancroft, 1986 (Bryozoa: Fenestrata) from the Mississippian of Scotland: revealing the nature of its heteromorphs. *Irish Journal of Earth Sciences* **31**, 19–24.

Young, J. (Prof.) 1880. *Catalogue of pictures, sculptures and other works of art in the University of Glasgow*. James Maclehose, Glasgow, pp. x+22.

Young, J. (Mr) and Corse Glen, D. 1888. Notes on a section of Carboniferous strata, containing erect stems of fossil trees and beds of intrusive dolerite, in the old whinstone Quarry, Victoria Park, Lower Balshagray, near Whiteinch and Partick. *Transactions of the Geological Society of Glasgow* **8**, 227–235.

Obituaries and biographical sources

Mr/Dr John Young (1823–1900)

Anon. 1901. Obituary - John Young, LL.D., F.G.S. Born 1823, died 13th March 1900. *Geologistical Magazine* New Series **7**, 382–384.

Teall, J.J.H. 1901. Obituary - John Young, LL.D. [In Anniversary Address.]. *Proceedings of the Geological Society* in *Quarterly Journal of the Geological Society* **57** p.lxi.

Macnair, P. and Mort, F. 1908. *History of the Geological Society of Glasgow, 1858-1908*, pp. 183–188; 210–212.

Clark, N.D.L. 'John Young (1823-1900) of Campsie, Stirlingshire, Scotland': http://www.hmag.gla.ac.uk/Neil/Young/fam003.html

Clark, N.D.L. 'John Young\Margaret Stirling': http://www.hmag.gla.ac.uk/Neil/Young/fam003.html [accessed 30.3.2015]

Professor John Young (1835–1903)

Anon. 1903. *Nature* **67**, 249.

Anon. 1904. *Nature* **69**, 612–613.

Anon. 1906. *Nature* **73**, 556–557.

Macnair, P. and Mort, F. 1908. *History of the Geological Society of Glasgow, 1858-1908*, pp. 210–212.

George, T.N. 1975. *College Courant, Glasgow*. 8 pp.

Appendix 1. Publications on bryozoans by Professor John Young and Mr (later Dr) John Young

Young, J. and Young, J. 1874a. New Carboniferous Polyzoa. *Quarterly Journal of the Geological Society of London* **30**, 681–683.

Young, J. and Young, J. 1874b. On a new Genus of Carboniferous Polyzoa. *Annals and Magazine of Natural History* Series 4 **13**, 335–339.

Young, J. and Young, J. 1874c. On *Palaeocoryne* and other polyzoal appendages. *Quarterly Journal of the Geological Society of London* **30**, 684–688.

Young, J. and Young, J. 1874d. Note on the occurrence of *Polypora tuberculata* Prout in Scotland. *Geological Magazine,* n.s. Decade 2, **1**, 258–259.

Young, J. and Young, J. 1875a. New species of *Glauconome* from Carboniferous Limestone strata of the West of Scotland. *Proceedings of the Natural History Society of Glasgow* **2**, 325–335.

Young, J. and Young, J. 1875b. On new Carboniferous Polyzoa. *Annals and Magazine of Natural History* Series 4 **14**, 333–336.

Young, J. and Young, J. 1877b. On a new species of *Sulcoretepora*. *Proceedings of the Natural History Society of Glasgow* **3**, 166–168.

Young, J. and Young, J. 1877b. On two new species of Carboniferous Polyzoa. *Proceedings of the Natural History Society of Glasgow* **3**, 354–356.

Appendix 2. Publications on bryozoans and other topics by Mr (later Dr) John Young

Young, J. 1874. Notes accompanying Two Slides of Carboniferous Polyzoa from the Fossiliferous Shales at Hairmyres, near East Kilbride, Lanarkshire. *Transactions of the Edinburgh Geological Society* **2**, 400–402.

Young, J. 1876. On a fresh-water Polyzoon belonging to the genus *Alcyonella*, discovered in the Germain's Loch, near Maryhill, in August, 1869. *Proceedings of the Natural History Society of Glasgow* **2**, 2–3.

Young, J. 1877. Notes on a new method of fixing fronds of Carboniferous Polyzoa on a layer of asphalt, to show the celluliferous face. *Proceedings of the Natural History Society of Glasgow* **3**, 207–210.

Young, J. 1880. Notes on a Carboniferous species of *Glauconome*. *Proceedings of the Natural History Society of Glasgow* **4**, 257–259.

Young, J. 1881. Remarks on the genus *Synocladia* and other allied forms, with description of a new species. *Proceedings of the Natural History Society of Glasgow*

5, 30–35.

Young, J. 1882a. Notes on the perfect pondition of the cell-pores and other points of structure in pertain species of Carboniferous Polyzoa from Western Scotland. *Transactions of the Geological Society of Glasgow* **6**, 211–217.

Young, J. 1882b. On the Identity of *Ceramopora (Berenicea) megastoma*, M'Coy, with *Fistulipora minor*, M'Coy. *Annals and Magazine of Natural History* Series 5 **10**, 427–431.

Young, J. 1882c. Remarks on the external characters which distinguish *Fenestella plebeia* of M'Coy from those of *F. tuberculocarinata* of Etheridge, jun. *Transactions of the Geological Society of Glasgow* **7**, 182–188.

Young, J. 1882d. Notes on Ure's "Millepore", *Tabulipora Urii*, J. Young (*Cellepora Urii,* Flem.). *Annals and Magazine of Natural History* (Series 5) **10**, 427–431.

Young, J. 1883a. On Ure's "Millepore," *Tabulipora (Cellepora) Urii*, Flem. *Annals and Magazine of Natural History* **12**, 154–158.

Young, J. 1883b. Notes on Ure's "Millepore," *Tabulipora Urii,* J. Young *(Cellepora Urii*, Flem.) *Transactions of the Geological Society of Glasgow* **7**, 264-272. [Reprint of 1882b paper].

Young, J. 1884. Notes on the genus *Synocladia* and other allied forms, with description of new species. *Proceedings of the Natural History Society of Glasgow* **5**, 30–35.

Young, J. 1885a. On the Identity of *Ceramopora (Berenicea) megastoma*, M'Coy, with *Fistulipora minor*, M'Coy. *Transactions of the Geological Society of Glasgow* **7**, 244–250.

Young, J. 1885b. Note on *Favosites*(?) *(Calamopora) Dentifera*, Phillips. *Transactions of the Geological Society of Glasgow* **7**, 369–370.

Young, J. 1887. Note on a new family of the Polyzoa Cystodictyonidae (E.O. Ulrich)—with notice of three Carboniferous species. *Transactions of the Edinburgh Geological Society* **5**, 461–466.

Young, J. 1888. On the Structure of *Fistulipora incrustans,* Phill. (*F. minor,* M'Coy). *Annals and Magazine of Natural History* Series 6 **1**, 237–247.

Young, J. 1894. Notes on the occurrence of ctenostomatous Polyzoa in the Carboniferous limestone of western Scotland.. *Transactions of the Geological Society of Glasgow* **10**, 142–147.

Appendix 3. Publications on bryozoans by Mr John Young and co-authors other than Professor John Young

Young, J. and Armstrong, J. 1871. *On the Carboniferous fossils of the West of Scotland; their vertical range and distribution* (J. Young); *With a general catalogue of the fossils and their mode of occurrence, and an index to the principal localities* (J. Armstrong). Glasgow, pp. 103. (Reprinted 1871 as a supplement to *Transactions of the Geological Society of Glasgow* **3**).

Young, J. and Armstrong, J. 1875. The fossils of the Carboniferous Strata of the west of Scotland. *Transactions of the Geological Society of Glasgow* **4**, 267-282.

Armstrong, J., Young, J. and Robertson, D. 1876. *Catalogue of the Western Scottish Fossils*. Blackie & Son, Glasgow, pp. v+164.

Young, J. and Robertson, D. 1877. Note on the Polyzoa of the Hairmyres Limestone Shale, East Kilbride. *Transactions of the Geological Society of Glasgow* **5**, 173–175.