Bryozoa—not a minor phylum

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Introduction

At the one-day symposium to mark the first author's formal retirement, he gave a presentation titled 'A life in bryozoology', noting that he began publishing on Bryozoa in the late 1960s, with a taxonomic article in a student journal (Gordon 1967) followed by a paper in *Nature* (Gordon 1968). Of the 174 peer-reviewed papers published since then, 137 have focused on some aspect of bryozoology (e.g. ecology, conservation, growth, anatomy, ultrastructure, form and function, systematics, paleontology, phylogeny, marine fouling and invasive species, marine natural products). During the past 50 years of his research, perceptions of phylum Bryozoa in the scientific community have changed markedly from what was historically the case. The purpose of this short paper is to highlight what has changed.

A 1930s–1960s view of Bryozoa

A few years before his formal research on Bryozoa began at university, the first author became acquainted with Bryozoa at Mt Albert Grammar, Auckland, thanks to teacher-prescribed textbooks in the form of a two-volume paperback—*Animals Without Backbones* (Buchsbaum 1958). The text of the volumes was unchanged from the first (1938) edition, in which Bryozoa was included as a 'minor phylum' in a short chapter called 'Lesser lights', which also included Rotifera, Gastrotricha, Brachiopoda, Phoronida and Chaetognatha. Buchsbaum's criteria for assembling these disparate groups in the one chapter was that 'they have a small number of species or of individuals; the members are of small size; they constitute no important source of food or disease for man; and they illustrate no principle of theoretical interest that is not as well shown by other phyla' (Buchsbaum 1958, p. 188). This was still the prevailing view in the 1960s, although Bryozoa did actually rate an entire lecture in the mid-sixties invertebrate course in the then Zoology Department at Auckland University. For Bryozoa today, Buchsbaum's criteria no longer apply.

A 21st century view of Bryozoa

First, consider the numbers. Bryozoa now constitutes a phylum of ~21,300 described species, of which >6000 are living (Figure 1) and ~15,000 are fossil—up from about 15,040 species (~12,000 fossil) in the 1920s (Marcus 1930). Data from

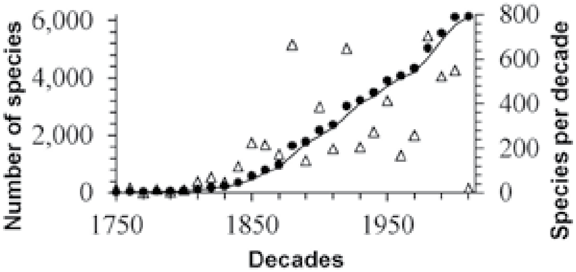

Figure 1. Number of Recent bryozoan species (i.e. species living today or within the last 12,000 years) described per decade (empty triangles), and cumulative number of species (black circles). The curve shows a near-linear rate of description since the early 19th century, with peak decades of discovery in the 1880s, 1920s and 1980s. The 1960s–1970s have relatively few species described, as well as the 1910s and 1930s–1940s owing to the impacts of world wars. From Bock, P. (2014). Bryozoa. Accessed 7 October 2016 through the World Register of Marine Species at http://www.marinespecies.org/aphia.php?p=taxdetails&id=146142

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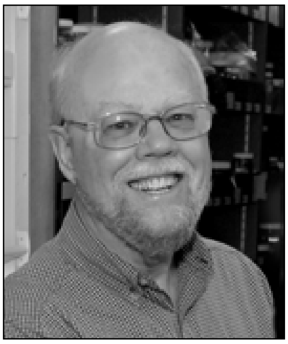
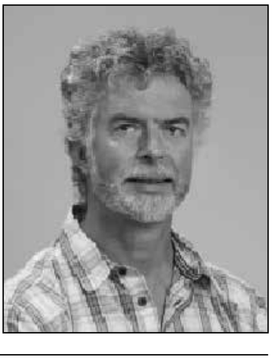


Dennis Gordon is an Emeritus Researcher at NIWA, where he worked for 36 years (13 of those years as a DSIR scientist) prior to official retirement in October 2015. During that period he was part of the biological oceanography group before leading a programme in marine taxonomy and later overseeing the marine biodiversity group as a Principal Scientist. Beyond his specialised research on the systematics, biology and phylogeny of living and fossil Bryozoa, Dr Gordon has a broad interest in all of life and served on the international teams that coordinate the production of the Catalogue of Life and the World Register of Marine Species. In 2005 he received the New Zealand Marine Sciences Society Award for his contribution to the advancement of marine science in New Zealand. He also coordinated, edited and part-authored the 2009–12 trilogy of volumes, *New Zealand Inventory of Biodiversity*, for which he received the 2012 NIWA Research Excellence award. Dr Gordon is a past council member of the New Zealand Association of Scientists.

Mark Costello is an ecologist, particularly interested in global patterns of marine biodiversity and biogeography, and in marine conservation. He led the startup of the *World Register of Marine Species* and *Ocean Biogeographic Information System* (as part of the Census of Marine Life). Originally from Ireland, he has worked in Britain and Canada, and been teaching on marine ecology, biogeography, biodiversity informatics and marine reserves in the University of Auckland since 2004.



the World Register of Marine Species (WoRMS) (Figure 1) show the rate of description of Recent species from 1758 (the starting point of zoological names in the tenth edition of Carl Linnaeus's *Systema Naturae*) to the present day. There is no upper asymptote and it is likely that an additional 5000+ species could be added (Appeltans *et al*. 2012). In New Zealand seas alone there are more than 1000 living species, of which about 340 remain to be described. Bryozoans are abundant in some biotopes, where they form biogenic habitat for numerous other organisms (Wood *et al*. 2012). Their skeletal remains constitute the single most abundant component of carbonate sediments on New Zealand's continental shelves (Nelson *et al*. 1988), reflected in equivalent taxonomic and numerical abundances of bryozoans in New Zealand's Cenozoic limestone rocks (e.g. Gordon & Taylor 2015). Living taxa constitute the taxonomically most speciose macrofaunal invertebrate group in the Spirits Bay area, New Zealand's marine-biodiversity hotspot, where there are about 300 species of bryozoans, almost as many as in the combined Exclusive Economic Zones of Britain and Ireland (Cryer *et al*. 2000; Taylor & Gordon 2003). Studies of tropical coral reefs during the 2000–2010 Census of Marine Life revealed that bryozoan diversity is very high and significantly understudied and that there could be as many as 1000 species in the Great Barrier Reef alone (Gordon & Bock 2008). Recent studies on seamounts and in the deep sea also show that bryozoan diversity can be locally very high, as on New Zealand's Cavalli Seamounts (e.g. Rowden *et al*. 2004), with high levels of generic diversity (e.g. Gordon 2014).

What about size? All bryozoans are colonial (Figures 2, 3), even those few that technically comprise only a single feeding zooid (the bryozoan individual) with attached diminutive polymorphs or zooid buds, and, while it is true that most zooids are around half a millimeter in length (the largest achieve 10 mm), colonies in some parts of the world can be a metre across. Intermediate sizes, from robust fist-shaped clumps as hard as coral, to cabbage-like brittle growths of alien species on shaded wharf piles, are not uncommon. As mentioned above, the larger forms can form biogenic habitat for myriad other organisms, as was once the case off Abel Tasman National Park prior to bottom trawling (Bradstock & Gordon 1983) and is still the case around many parts of our coastline. Bryozoan micro-reefs attract juveniles of commercial fish such as snapper, terakihi and John Dory, which shelter and feed there.

It is true that bryozoans constitute no important source of food or disease for humankind, though they do provide a food source for a documented 399 predator species (Lidgard 2008). There are cases of fishers in Britain's North Sea getting contact dermatitis from handling bryozoan bycatch (Carle & Christopherson 1982) but this is in the nature of an allergic reaction rather than a malady. More significantly, bryozoans are turning out to have an interesting variety of secondary metabolites that continue to be investigated for marine natural products, which potentially include cytotoxic, antibiotic, antiviral, anticancer, neutriceutical, radioprotection and even antifouling (e.g. Blackman & Walls 1995; Rinehart *et al*. 1996; Kawamata *et al*. 2006; Andersen 2012; Pejin *et al*. 2013, 2014). The most promising are macrocytic lactone bryostatin-1, an antitumour metabolite with significant biological activities (Sima & Vetvicka 2011) including immunomodulation, down-regulation of multi drug-resistance gene expression, anticancer activity and enhancement of the activity of chemotherapeutics. Bryostatins are already in clinical use (Blackhall *et al*. 2001; El-Rayes *et al*. 2006; Peterson *et al*. 2006). Alkaloid pterocellins were isolated from a bryozoan found in New Zealand (Prinsep *et al*. 2004) and they possess cytotoxic activities against murine leukemia, human melanoma and breast cancer cell lines. Additionally, and remarkably, bryostatin-1 appears to have potential for treating memory disorders (e.g. Sun & Alkon 2005, 2006). Initially promising studies using rats are currently being followed up by a more-intensive clinical study on human Alzheimer's patients (Staken & Payne 2015; ClinicalTrials.gov 2015).

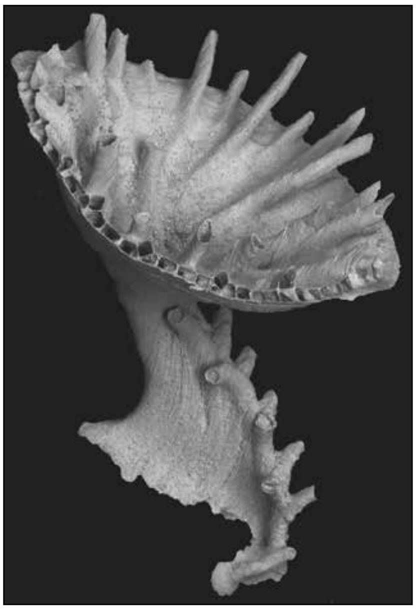


Figure 2. *Discantenna tumba* **Gordon & Taylor, 2010, an endemic genus and species of cyclostome bryozoan (class Stenolaemata) from the Graveyard Seamount complex on the Chatham Rise.**

When it comes to matters of theoretical interest, bryozoans have proven to be ideal for investigating significant evolutionary questions at micro to macro scales (e.g. Jackson & Cheetham 1990, 1999; McKinney 1995a,b; McKinney *et al*. 1998; Barnes & Dick 2000; Taylor 2016). For example, how much of the variation within living and fossil bryozoan colonies and individual zooids is inherited? What is the significance of morphological stasis, i.e. the unchanged appearance of certain skeletal characters over long periods of millions of years? Is the hypothesis of punctuated equilibrium (the hypothesis that evolutionary development is marked by isolated episodes of rapid speciation between long periods of little or no change) real? [Bryozoans give some of the best evidence of the phenomenon.] When and how in the geological record did key morphological novelties

Figure 3. *Foveolaria* **n. sp., an undescribed species of cheilostome bryozoan (class Gymnolaemata) collected from the New Zealand deep sea from fishing bycatch through the Scientific Observer Programme.**

originate? How does varied competitive ability among different evolutionary branches of bryozoans work out over geological time, inasmuch as some clades were displaced? The reasons why bryozoans are so useful in addressing these and related questions include their fossilisable skeletons and their modular nature—individual bryozoan colonies are made up of parts and subparts, including zooids that feed, are non-feeding and modified for defence, attachment, or reproduction, and also parts of zooids, like spines and cuticular structures, that can be modified. Tracing adaptive changes in those modules and submodules that are preserved in the fossil record has proven to be very fruitful in elucidating evolutionary trajectories because life-history, phylogenetic, environmental and biotic-interaction data for both extant and fossil populations are easily collected for comparative study. Because so much information is preserved in the fossil remains, paleo-ecological studies can be made on such features as boundary interactions between spatially competing encrusting colonies, certain types of predation (evidenced by boreholes) and seasonal growth (reflected in varying zooid size). The rich fossil record of bryozoans is very fine-grained in some parts of the world and adaptive changes, if present, can be tracked through specific periods of time. A current example is an ongoing study of bryozoan competitive ability in the Plio-Pleistocene of the Wanganui Basin (Liow *et al*. 2016).

Modularity has been a significant factor in the evolutionary success and radiation of bryozoans, especially in the largest order, Cheilostomata, which originated in the late Jurassic about 150 million years ago. In the Cretaceous, especially starting around 110 million years ago, the evolution of novel complex structures from simpler pre-existing modules (zooids and spines, for example) is well-shown by the fossil record (e.g. Gordon & Voigt 1996; Jablonski *et al*. 1997; Ostrovsky & Taylor 2005). Some feeding zooids evolved into non-feeding defensive zooids (avicularia)—in these, the lid-like opercula that protect the retracted feeding apparatus became modified as jaw-like mandibles; in turn, some avicularian mandibles became narrow and bristle-like, as in the ambulatory zooids of free-living colonies that can 'walk' on the seafloor. Some spines evolved into reproductive incubatory chambers (ooecia); some small, interzooidally budded non-feeding zooids evolved into a variety of frontal body walls. Bryozoan modularity also has implications for theoretical studies of resource partitioning, since defensive and other zooidal morphs cannot feed and are therefore energetically expensive to produce (e.g. Harvell 1986). There are other surprising features about bryozoans, too, that have only recently merited attention but which are worthy of further study, such as the remarkably common occurrence of matrotrophy, i.e. maternal provisioning of developing embryos, including via placental structures (Ostrovsky *et al*. 2009), as well as the existence of the seemingly paradoxical prevalence of polyembryony (embryo cloning) in an entire class of Bryozoa—Stenolaemata (e.g. Hughes *et al*. 2005). Concerning the future of bryozoan studies, one can only say, 'Watch this space. The bryozoan star is in the ascendancy!'

Acknowledgment

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