The contribution of Dennis P. Gordon to the understanding of New Zealand Bryozoa

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Introduction

Few biologists have had such an impact on the understanding of New Zealand biodiversity as Dr Dennis Preston Gordon (1944 –) (Figure 1). His canon of more than 170 scientific publications covers the full gamut of biodiversity studies, ranging from taxonomy and systematics, ecology, evolution and life history, to large-scale syntheses of regional and global patterns, and the higher order of classification of all living organisms.

In the 1990s, as project leader of the taxonomy programme at NIWA, Dennis became increasingly involved in tackling the overarching challenges facing biodiversity science[1]. His work in this area has informed research and environmental management decision-making in New Zealand and elsewhere. He became an advocate for the organisational infrastructure, networks and databases, required to understand and wisely manage the great menagerie of life on Earth. In this capacity he played many key roles at an international level. Dennis chaired the Species 2000 Asia-Oceania Working Group, and served on the Ocean Biogeographic Information System (OBIS) International Committee and on the Steering Committee of WoRMS, the World Register of Marine Species.

Dennis Gordon's *magnum opus* is the *New Zealand Inventory of Biodiversity* – a momentous, three-volume work[2]. Its brief was to inventory all species known to exist – or to have existed

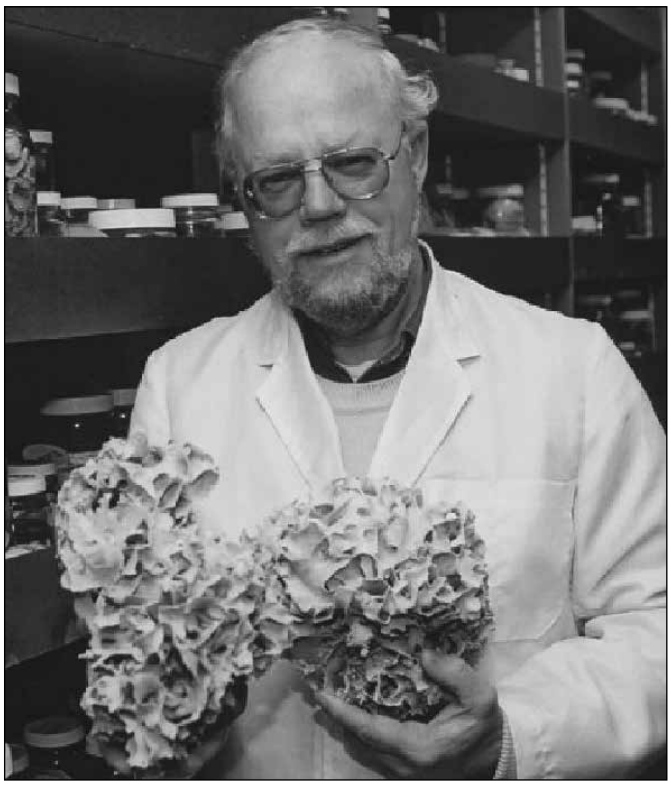

Figure 1. Dr Dennis Gordon holding two very large New Zealand bryozoans.

(Photo by Alan Blacklock.)

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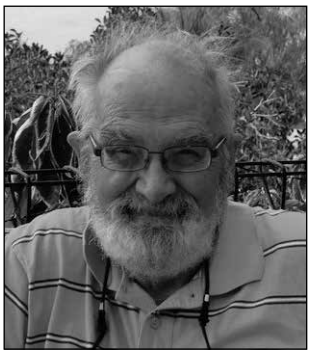

Phil Bock is an Honorary Researcher at Museum Victoria, Melbourne, Australia. In his retirement, he travels, communicates on social media, and maintains the *Bryozoa Home Page*, www.bryozoa.net, a very useful resource for all bryozoologists.

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– in all of New Zealand's terrestrial and aquatic environments over the last half billion years. After a decade of sustained scholarship and organisation (the *Inventory* has 237 authors from 19 countries), it is a resource that the entire nation can take pride in. No other country has produced a similar document.

To a different, smaller and more dispersed community, Dennis wears a different hat. He is one of the world's leading bryozoan biologists and taxonomists. His contribution to understanding of this phylum in New Zealand and beyond has been immense. This article describes the bryozoological legacy (so far) of Dr Dennis Preston Gordon.

Bryozoans: a fascinating phylum

It was as a zoology student at the University of Auckland in the mid-1960s that Gordon began his studies on bryozoans. This was during the John Morton era of 'form and function' biology, and was a formative time for the budding researcher. Gordon honed his skills in observation, taxonomy, natural history and scientific writing, and published an article on the bryozoans of Auckland shores in *Tane*, the journal of the Auckland University Field Club, later becoming its co-editor for a time[3]. In 1968, while still an MSc student, his international publishing career began promisingly with an article in *Nature* on sexual dimorphism in *Hippopodinella adpressa*[4]. A year later Gordon departed to Halifax, Canada, to commence his PhD at Dalhousie University, studying the biology of the intertidal species, *Cryptosula pallasiana*[5,6]. By the end of his studies he was well and truly hooked on bryozoans.

Bryozoa are beguiling and abundant aquatic animals, if not well known outside of marine biology. With >20,000 living and fossil species, they are not at all a minor phylum. They are often among the most speciose macrofaunal groups in samples taken from parts of New Zealand's continental shelf [7]. Some of the larger, coral-like species play a keystone role in benthic communities, locally providing habitat for a myriad of other organisms, and producing much of the seafloor sediment over large tracts of the New Zealand continental margin[8].

Like corals, bryozoans are colonial organisms consisting of interconnected individuals (zooids). Each zooid is typically smaller than a millimeter and most bear a crown of ciliated tentacles that capture phytoplankton. Viewed together, the zooids of a bryozoan colony look intricately tessellated, like a miniature M.C. Escher lithograph. The zooids collectively grow into a wide range of shapes, from flat crusts and amorphous lumps to branching and lattice-like forms. In texture, colonies range from soft and flexible to rigid and thickly calcified, and they come in all the colours of the rainbow (Figure 2). The phylum has a reputation of being taxonomically challenging, and the group's relative obscurity may stem in part from their micro-modular nature. Identification is based largely on features of the individual zooids, not the colony as a whole, so even a football-sized colony may require a microscope to accurately determine its species.

Following completion of his PhD in 1973, Dennis commenced a post-doctoral position at the University of Wales, Swansea, followed by a research fellowship at Leigh Marine Laboratory, University of Auckland. During this time he published on bryozoan biology and ecophysiology, including his discovery of a gizzard in cheilostomes[9], studies on the enigmatic 'brown bodies' produced by bryozoans[5], and a review on bryo-

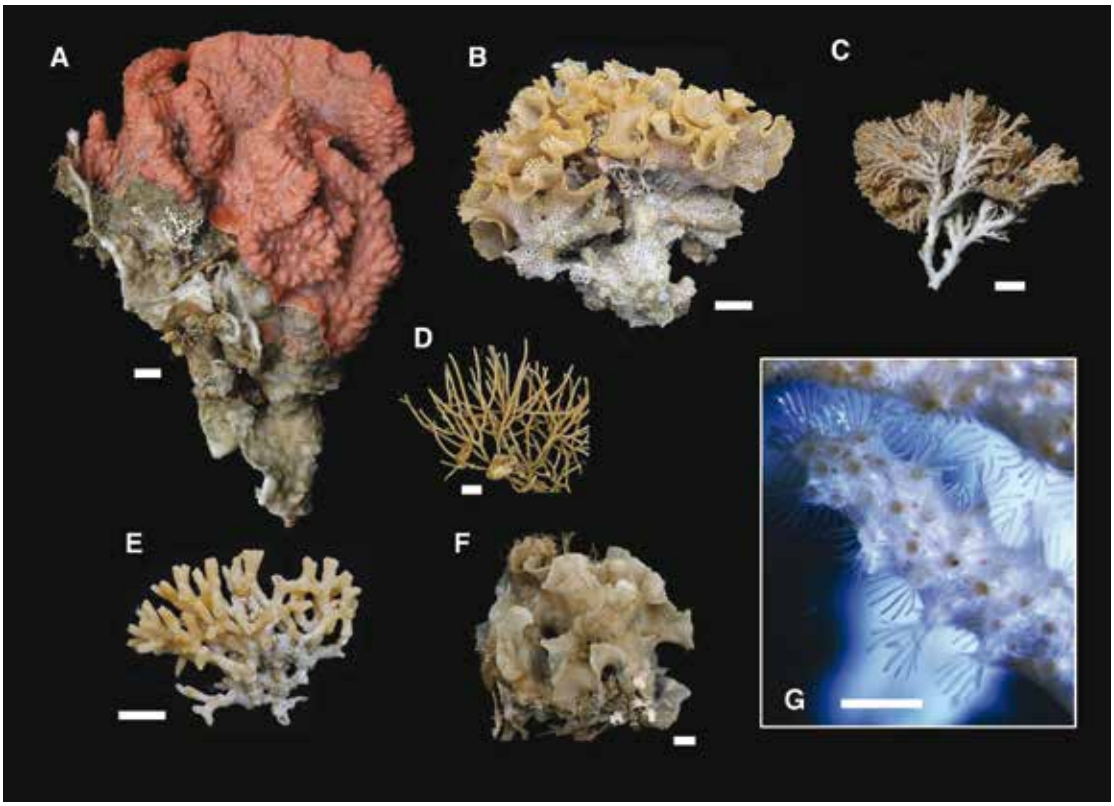

Figure 2: Diversity of colony form among large, conspicuous New Zealand bryozoans: A, ***Celleporaria agglutinans*****, a massive encrusting species; B,** ***Hornera foliacea*****, a reticulate (lace-like) form; C,** ***Hornera robusta*****, an erect branching species; D,** ***Cellaria immersa*****, rigid branches articulated at flexible nodes; E,** ***Heteropora*** **sp., with robust cylindrical branches; F,** ***Hippomenella vellicata*****, a foliose form; G (inset), a micrograph of a living bryozoan colony with the ciliated tentacle crowns of the individual zooids extended. Scale bar: A – F = ~1 cm; G = 0.5 mm. (Photos: Peter Batson)**

zoan aging processes[10]. He also co-wrote, with Leigh's Bill Ballantine, a paper reporting the establishment of New Zealand's first marine reserve to the scientific community[11].

At the end of the 1970s Dennis joined the New Zealand Oceanographic Institute, then part of DSIR and moved to its Wellington campus at Greta Point in Evans Bay, now part of NIWA. With this change came a re-focusing on taxonomic questions. New Zealand had recently declared a 200-nautical-mile Exclusive Economic Zone (EEZ) and there was elevated awareness of the need to document New Zealand's marine biological and geological resources. With access to large historic and rapidly expanding new collections of material from the New Zealand region, Dennis began a sustained period of describing and monographing bryozoan diversity from the region. His previous training and natural ability in pattern recognition would come to the fore in this vocation. Everywhere Dennis looked he saw a treasure trove of unrecognised forms – an alluring, if daunting, challenge for New Zealand's sole 1980s-era bryozoologist.

Bryozoan colonies have a curious tendency to look like other things – seaweeds, corals, hydroids – even dinosaur vertebrae[2] – and so are often misidentified as such. Dennis once described a distinctive deepwater genus, *Discantenna*: no prizes for guessing what it looks like[12]. Some bryozoans have departed far from the norm: New Zealand's seven otionellid species are roughly the size and shape of lentils and have a fringe of bristle-like 'legs'. Rather than gluing themselves to the seafloor like their kin, they clamber over the sandy bottoms on which they live. Others overgrow snails and continue the spiral of the shell beyond the reach of the original occupant.

In 1978 the New Zealand region's known bryozoan biodiversity was 378 species. By 2009, thanks largely to Dennis' efforts, this number had increased to 953 species[2]. These descriptions were published in three large and well-illustrated NZOI memoirs[13, 14, 15] and numerous taxonomic papers, and their impact extended far beyond these shores. Partly this was because of the sheer number of species involved, but also because Dennis had to establish much higher-level taxonomy (new genera and families) to accommodate the many disparate species he encountered. Thus his monograph on the cheilostome bryozoans of the Kermadec Ridge, a work one might assume to have a rather specialised audience, has been cited more than 300 times [13].

Bryozoan colonies often produce beautiful geometric structures, but it takes a microscopic view of their individual zooids to appreciate their true beauty and complexity (Figure 3). At that scale their carbonate skeletons look like spun glass, ornately sculpted, and rich with quantifiable characters. This trait, along with their excellent fossil record, has made them invaluable models for testing evolutionary hypotheses, such as punctuated equilibrium theory [16]. Yet the phylum scarcely rates a mention in most biology textbooks. In his 2003 *New Zealand Geographic* article dedicated to the Bryozoa[7], Dennis suggested that the common names long affixed to the phylum – 'moss animals' and 'sea mats' were not helpful – and he suggested 'lace corals' as a more appealing alternative, and indeed this recommendation has been mostly taken up among marine scientists.

During the 1980s and 90s, Dennis published widely on New Zealand Bryozoa, spanning intertidal to deep-sea environments, and began work on regional 'bryofaunas' elsewhere in the Pacific, such as Australia, New Caledonia, and Western Samoa[17, 18, 19]. He also co-authored an atlas on the alien bryozoan

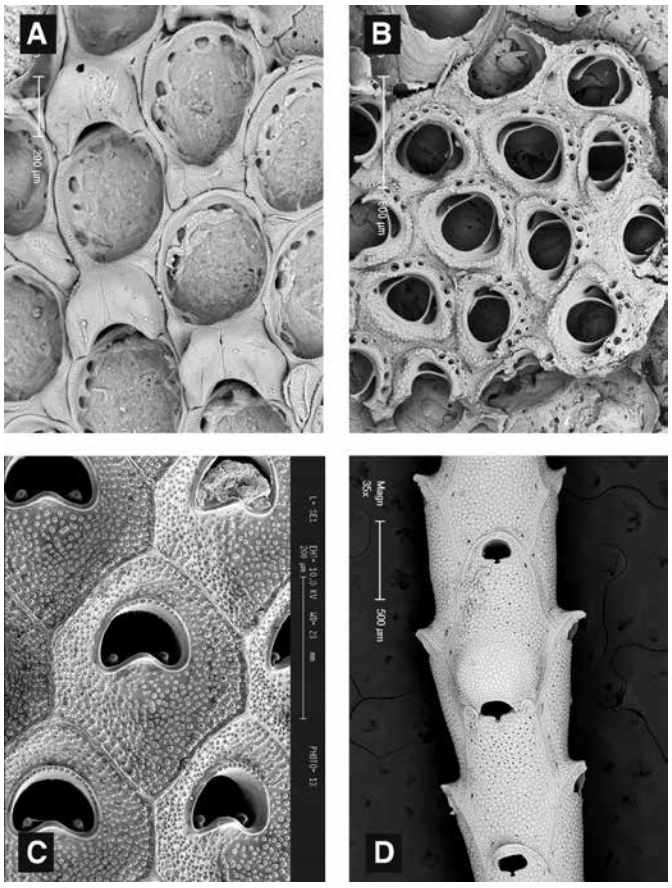

Figure 3: Scanning electron micrographs of some of the cheilostome bryozoans described by Dennis Gordon: A, *Aplousina anxiosa* **Gordon 1986; B,** *Chaperia multispinosa* **Gordon, 1984; C,** *Cellaria* **sp. (Gordon described ten species belonging to this genus, both living and fossil); D,** *Taylorius* **sp. (Gordon recently described three New Zealand species within this genus).**

species invading New Zealand ports and harbours courtesy of international shipping[20]. Among them was his old friend *Cryptosula pallasiana*, the cheilostome he studied in Canada for his doctorate. Collectively these studies no doubt focused his awareness of the challenges facing taxonomy and biodiversity researchers, especially when integrating datasets across biogeographic regions and changing ecosystems. Concurrently Dennis continued to expand his body of work on cheilostome bryozoan systematics, often based on the comparative anatomy of skeletal wall structure[21]. He also authored or coauthored studies of fossil bryozoan assemblages[22], reviewed bryozoan energetics[23], and produced a much-cited paper with Mike Bradstock on the environmental protection of Tasman Bay bryozoans to protect a commercial fish stocks, a world first[24].

Until the mid-1990s, Dennis's bryozoological research focused on the most diverse group: the cheilostomes, which had stormed onto the bryozoan scene in the Cretaceous. This modern clade had several key innovations: box-shaped zooids fitted with hinged jack-in-the-box lids that sealed away the vulnerable soft parts when the tentacles were retracted. However, Dennis did not focus on them entirely. Over the years he had carefully collected and catalogued bryozoans from other living clades, including the freshwater phylactolaemates, soft-bodied ctenostomes, and the archaic cyclostomes whose generally smaller, tubular zooids had changed little since the Paleozoic. Working in collaboration with Paul Taylor of the Natural History Museum, London, and Abby Smith at the University of Otago, Dennis started the process of

describing New Zealand's cyclostomes more thoroughly[25, 26]. By 2010, it had become evident that New Zealand was the global diversity hotspot for these archaic bryozoans, with at least 124 species in our EEZ waters, many of them living on seamounts and offshore ridges[26].

A bryo-legacy

Alone or in collaboration with others, Dennis has described 692 new taxa to date, which include at least 1 superfamily, 22 families and 133 genera of Bryozoa. There are at least 434 Recent (living) species and 105 fossil species named by Dennis Gordon and his colleagues (Appendix 1, published only on the New Zealand Association of Scientists website, www.scientists.org.nz/files/journal/2016-73/).

In the last decade, Dennis has continued to publish widely on bryozoans, as well as broader synthetic works on biological classification and biodiversity[27, 28, 29]. His recent taxonomic papers have ranged far and wide – including species descriptions of living and fossil European, South American, Australian, Asian and Antarctic Bryozoa. Among the more intriguing contributions was a co-authored description of the first truly amphibious bryozoan in this otherwise strictly aquatic phylum. It inhabits the leaves of mangrove trees in Australia's Northern Territory[30].

One of the hallmarks of Dennis's career is his willingness and ability to collaborate, leading to a multidisciplinary and highly collaborative career. He first attended a meeting of the International Bryozoology Association (IBA) in 1971 and has missed only two meetings since. His commitment over the years reached its peak in 1995, when he hosted (almost single-handedly) their triennial meeting, including leading long pre- and post-conference field trips. The 10th International Bryozoology Conference in Wellington, New Zealand, included 73 delegates from 19 countries, and was the first time that the IBA met in the Southern Hemisphere.

The esteem in which Dennis is held by his peers could not be better demonstrated than by the many bryozoans named for him (Table 1). Among them are the genera *Dengordonia* Soule, Soule & Chaney, 1995, *Gordoniella* Zágorsek, 2001 and *Dennisia*, Hara 2001, as well species such as *Klugerella gordoni* Moyano, 1991, *Leptinatella gordoni* Cook & Bock, 2000, *Trochosodon gordoni*, Bock & Cook, 2004, *Caberoides gordoni* Di Martino & Taylor, 2015, and *Reniporella gordoni* Guha & Gopikrishna, 2004.

Over the years Dennis has supported and encouraged many students of the Bryozoa, some of whom have gone on to forge their own careers in this specialised field (in New Zealand, students whom he has supported and mentored include the authors of this paper, Abby Smith and Peter Batson, and also Seaborne Rust, Anna Wood, and Michelle Carter – see full list of publications). It is easy to see, both in person and through his published work, Dennis's unflagging sense of wonder at the natural world.

In addition to his busy working life, Dennis has been married since 1977 to Brenda Raewyn Gordon. The couple are well known in the world-wide bryozoan science community as exceptional and enthusiastic hosts and guides. They have three sons: Timothy, Caleb, and Adrian, and (at present) one grandson. Dennis is a member of the pastoral team in his church, and is a keen photographer, especially of rare and beautiful plants. He retired in 2016, although continuing to work as an Emeritus Researcher at NIWA, and often comments that now he can really give more time to his beloved bryozoans.

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Note: A comprehensive bibliography of the published bryozoological works of Dennis P. Gordon is available at the following link: http://bryozoa.net/gordon_refs.html

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Table 1. Bryozoans named after Dennis Gordon.

Genus	Authorship	Family	Type Species	Authorship
Dengordonia	Soule, Soule & Chaney 1995	SMITTINIDAE	*Dengordonia uniporosa*	Soule, Soule & Chaney 1995
Dennisia	Hara, 2001	LEPRALIELLIDAE	*Dennisia eocenica*	Hara, 2001
Gordoniella	Zágorsek, 2001	CRIBRILINIDAE	*Gordoniella diporica*	Zágorsek, 2001

Species	Authorship	Family
Caberoides gordoni	Di Martino & Taylor, 2015	CATENICELLIDAE
Gordoniella budai	Zágoršek, 2001	CRIBRILINIDAE
Gordoniella diporica	Zágoršek, 2001	CRIBRILINIDAE
Gordoniella longituda	Zágoršek, 2003	CRIBRILINIDAE
Klugerella gordoni	Moyano, 1991	CRIBRILINIDAE
Leptinatella gordoni	Cook & Bock, 2000	CALLOPORIDAE
Reniporella gordoni	Guha & Gopikrishna, 2004	STEGINOPORELLIDAE
Trochosodon gordoni	Bock & Cook, 2004	CONESCHARELLINIDAE
Disporella gordoni (now *D. pristis)*	Taylor, Schembri & Cook, 1989	LICHENOPORIDAE

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