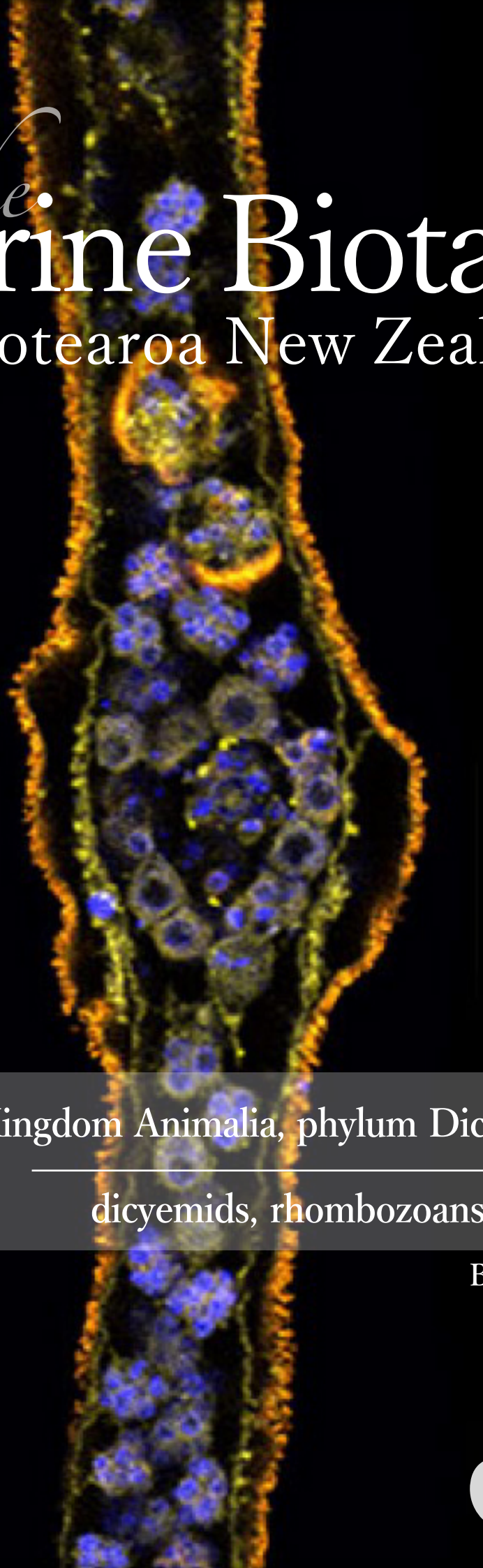
the Marine Biota of Aotearoa New Zealand



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Kingdom Animalia, phylum Dicyemida

dicyemids, rhombozoans

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CHAPTER 9

NIWA Biodiversity Memoir 136 2023

NIWA Taihoro Nukurangi

To cite this article: Presswell, B. (2023) Chapter 9. Kingdom Animalia, phylum Dicyemida (dicyemids & rhombozoans). Pp. 182–184 *in*: Kelly, M., Mills, S., Terezow, M., Sim-Smith, C., Nelson, W. (Eds) The Marine Biota of Aotearoa New Zealand. Updating our marine biodiversity inventory. *NIWA Biodiversity Memoir* 136, 494 pp. https://docs.niwa.co.nz/library/public/NIWAbm136-ch09.zip

9 Kingdom Animalia, phylum Dicyemida (dicyemids & rhombozoans)

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Summary

The Aotearoa New Zealand Dicyemida fauna is effectively unknown (Table 9.1; Fig. 9.1). The total number of recorded taxa from the New Zealand region is six species in two genera, a total that has remained unchanged since the previous review by Hochberg (2009). The only change made here is to update the name given in Hochberg (2009) as *Dicyemennea rostratum* Short & Hochberg, 1969, to *D. rostrata*. A checklist of extant marine New Zealand Dicyemida is provided.

Introduction

Dicyemid 'mesozoans' are microscopic (0.25–10 mm long), highly specialised organisms that are all endoparasites or endosymbionts, occurring in high densities in the renal appendages of benthic cephalopod molluscs. The body consists of a single, elongate, axial cell, surrounded by a fixed number of ciliated cells (8–40 depending on the species), which is the smallest complement of cells in any multicellular organism. The anterior end is modified into a calotte, or head-like organ, that is covered with short, stiff, thigmotactic cilia that facilitate attachment to the renal tissue of the host. There is no internal body cavity or organs, and embryos develop inside the cytoplasm of the axial cell (Catalano 2012).

The name Dicyemida, meaning 'two embryos', refers to the two distinct types of embryos that are produced in the life cycle. There are two stages of development (vermiform and infusoriform stages) and two modes of reproduction (sexual and asexual). The vermiform stages (vermiform embryo, nematogen and rhombogen) form asexually from a single agamete and remain in the renal appendages, deriving nutrients from the host's urine. At some point, probably as a result of severe overcrowding, the rhombogen stage produces male and female gametes and a somatic gonadal founder cell, which together constitute a hermaphroditic gonad (Czaker 2011; Furuya *et al.* 2003a). The subsequent self-fertilised infusoriform larva is released into the host's urine, from which it passes into the seawater. The method of host infection is not known.

The extreme secondary simplicity of the body plan, probably a result of their parasitic lifestyle, is mirrored in their genetic profile. Many genes that are highly conserved in other bilaterian taxa are absent in the genomes of Dicyemida, and the loss of genes related to the basement membrane, neuronal and muscular systems, amongst others, relate to their extraordinary simplicity. The genome is further distinguished by the mitochondrial genes, which are not located on a single long DNA molecule as in most animals but partitioned into smaller circular molecules. Another unique feature is the presence of thousands of non-coding circular DNA sequences (Zverkov *et al.* 2019). Although their uniquely modified genomes make them difficult to place securely in a phylogeny, genomic sequencing and transcriptomic data suggest that the dicyemids form a separate clade, proposed as sister to the assemblage of Platyhelminthes, Gastrotricha, Entoprocta, and Cycliophora (Zverkov *et al.* 2019). Dicyemida was historically placed along with Orthonectida (another clade of highly derived organisms) in the phylum Mesozoa. However, molecular studies showed Mesozoa to be paraphyletic (Zverkov *et al.* 2019) and these two taxa are now accepted as separate phyla.

The phylum is globally distributed and currently contains three families: Dicyemidae, Conocyemidae and Kantharellidae, although the validity of the Kantharellidae is disputed as it contains a single, inadequately described species (Catalano 2012). The three families include 122 accepted species in nine genera (World Register of Marine Species; WoRMS; https://www.marinespecies.org/), although confusion surrounds the validity of 20% of taxa at all levels, due to incomplete descriptions, loss of type specimens, errors in taxonomy, and conceptual differences (Catalano 2012). Genera are determined by the number and orientation of cells in each tier of the calotte, presence or absence of abortive axial cells, and the presence or absence of syncytial stages (Hochberg 1982, 1983). Species delineation is based on the size of the adult stages, the number of body cells, the shape of the calotte, the anterior extension of the axial cell, the presence or absence of verruciform cells, and the structure of the infusoriform larvae (Hochberg 1982, 1983).

In New Zealand, the dicyemid fauna remains largely unknown. New Zealand waters are home to 35 octopus

Table 9.1. Summary of Dicyemida diversity in the Aotearoa New Zealand region expressed as total numbers and percentage change. Data for 2000 are derived from Hochberg (2009: p. 132). OTU = Operational Taxonomic Unit.

	Dicyemida		% change
	2000	2023	
Total species diversity	6	6	0
Described extant species	5	5	0
Undescribed extant species (OTU)	1	1	0
Described endemic extant genera	0	0	0
Described endemic extant species	6	6	0

(Octopoda) species and seven squid (Sepiolida) species, with benthic or epibenthic habits, but only two species of shallow-water octopus have been examined for dicyemids. The five nominal species in two genera that have been recorded from these two hosts were all described in two papers (Short & Hochberg 1969; Short 1971), with a sixth, undescribed, species added by Furuya *et al.* (2003b). All are endemic to New Zealand, and no new collections have been reported in the literature since these accounts (Table 9.1).

Four dicyemid species were found in the octopus *Robsonella huttoni* Benham, 1943, which was originally identified as *Robsonella australis* (Hoyle, 1885) in the early papers by Short & Hochberg (1969) and Short (1971). The identity of the host was confirmed by O'Shea (1999) who examined the vouchers of the host material collected by Short, identifying them as *R. huttoni*. The host species is referred to in some works as *Octopus huttoni* (Benham, 1943), but was returned to its original combination on the strength of molecular analyses that placed it in a clade with other species of *Robsonella* (Ibáñez *et al.* 2020). Three dicyemid species have been found in *Pinnoctopus cordiformis* (Quoy & Gaimard, 1832) [= *Octopus maorum* Hutton, 1880 in O'Shea (1999), = *Macroctopus maorum* (Hutton, 1880) in Norman & Hochberg 2005]. In the case of both hosts, up to three species of dicyemid may co-occur in the same host individual. One unique feature is found in three of the New Zealand species: infusoriform larvae are described as having 23 different types of cell, variations of which are observed in different species, yet the three species of Dicyemidae, *Dicyema knoxi* Short,

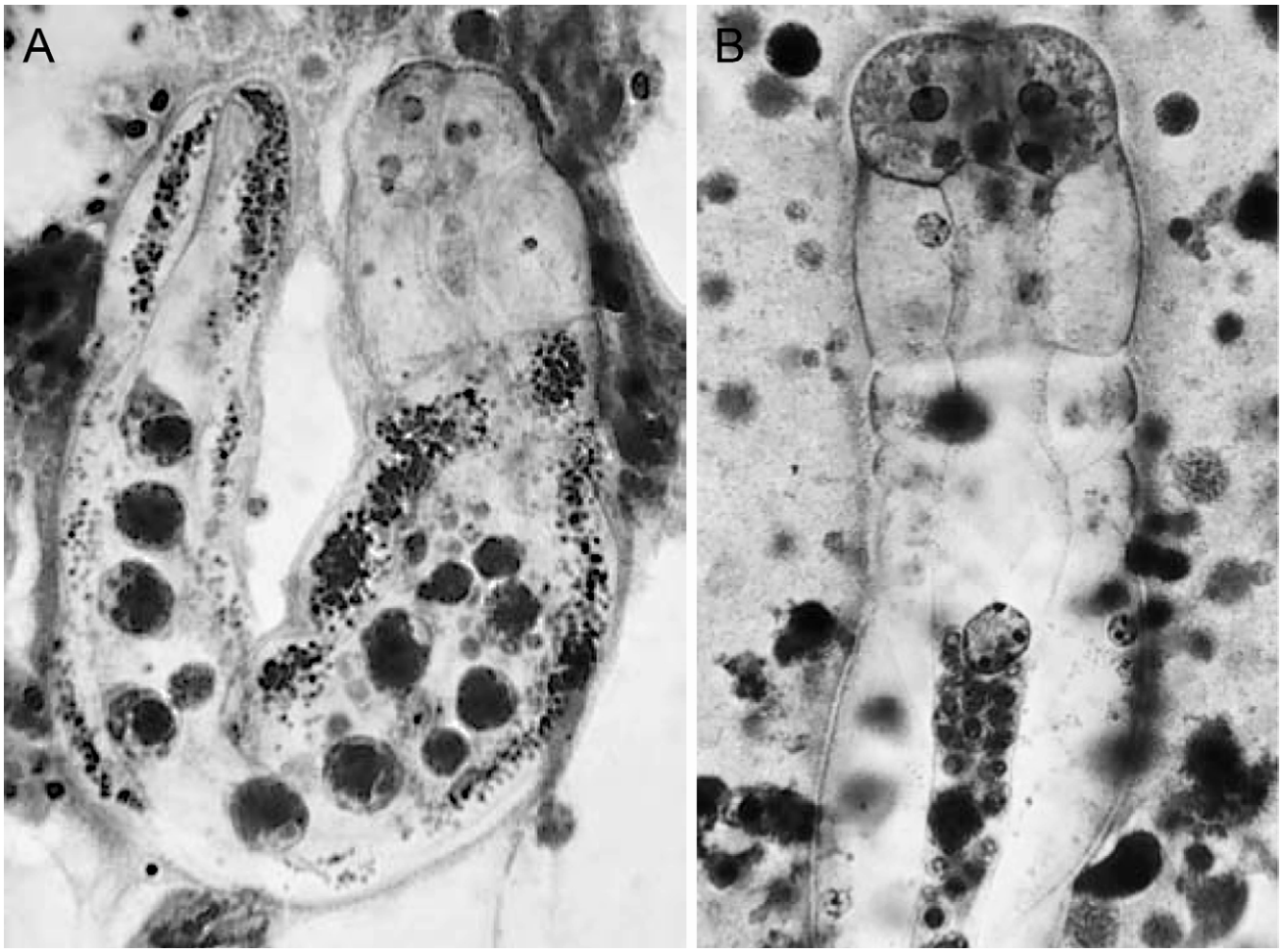

Figure 9.1. Phylum Dicyemida: **A.** Stained individual of *Dicyemennea kaikouriensis* Short & Hochberg, 1969, in the kidney of octopus *Pinnoctopus cordiformis* (Quoy & Gaimard, 1832); **B.** Anterior end of stained individual of *Dicyema robsonellae* Short, 1971, in the kidney of octopus *Robsonella huttoni* Benham, 1943. Reproduced from Hochberg (2009), with permission from editor D.P. Gordon, and Canterbury University Press.

1971, *D. maorum* Short, 1971, and *D. robsonellae* Short, 1971, possess a pair of 'postcapsular' cells which have only been found in these New Zealand species (Furuya *et al*. 2004) (Fig. 9.1).

Knowledge gaps, research progress and future priorities

Hochberg (2009) estimated that 25–50 further species remained to be discovered in New Zealand. With no expert in the country and relatively few worldwide, it is unlikely that this diversity will be uncovered soon. There is a single review of the classification of the Dicyemida (Catalano 2012), which is the most comprehensive and helpful text to date, and an updated list of accepted dicyemid taxa may be found in WoRMS.

Acknowledgements

Thanks to Kathrin Bolstad, Auckland University of Technology, for the most current information on cephalopods, and to Professor Robert Poulin, University of Otago, Dunedin, for his review of this chapter.

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References to the taxonomic authorities and dates for Dicyemida taxa in this chapter and in the associated checklist can be located in the World Register of Marine Species (WoRMS) (https://www.marinespecies.org/).

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Checklist of extant Dicyemida known from the New Zealand EEZ

The checklist is arranged according to the currently accepted systematics and classificatory scheme employed by the World Register of Marine Species, Dicyemida (https://www.marinespecies.org/aphia.php?p=taxdetails&id=14221). Taxa assumed to be endemic taxa are indicated by 'E'. Host species are provided, but we have not included the host taxonomic authorities, which are available in WoRMS (https://www.marinespecies.org).

Phylum DICYEMIDA			
Class RHOMBOZOA			
Family DICYEMIDAE			
Dicyemennea kaikouriensis	Short & Hochberg, 1969	E	host *Pinnoctopus cordiformis*
Dicyemennea rostrata	Short & Hochberg, 1969	E	host *Robsonella huttoni*
Dicyema robsonellae	Short, 1971	E	host *Robsonella huttoni*
Dicyema knoxi	Short, 1971	E	host *Pinnoctopus cordiformis*, *Robsonella huttoni*
Dicyema maorum	Short, 1971	E	host *Pinnoctopus cordiformis*
Dicyema sp. E	Furuya, Hochberg & Tsuneki 2003	E	host *Robsonella huttoni*

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ISSN 1174-0043; 136
ISBN 978–1–99–117447–5 (digital edition)
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