Zootaxa 3479: 1–32 (2012)
www.mapress.com/zootaxa/

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

Article

urn:lsid:zoobank.org:pub:8EECE188-8369-4B4A-BBB7-04E5ABDA2CB5

A review of the families, genera and species of Dicyemida Van Beneden, 1876

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Abstract

The classification of the species in the phylum Dicyemida Van Beneden, 1876, a group of small organisms which parasitise the renal appendages of benthic cephalopods, is reviewed. While dicyemid parasites have simple multicellular morphology, their lifecycle is complex and it is uncertain whether their affinities are with the protozoans or metazoans. Hence they are commonly given an intermediate 'mesozoan' status. Although 112 species are described, confusion exists for 20% of the taxa over the validity of certain families, genera and species, which has been attributed to incomplete and information-poor descriptions, loss of type specimens, errors in taxonomy and conceptual differences. The history of dicyemids dating from the first known reference by Filippo Calvolini of Italy in 1787 is presented, along with the characteristics which are commonly used to classify genera and species. All species described to date are listed with reference to the original published records and the validity of ambiguous records is explored. A way forward using alternative technologies such as molecular genetic methods based on next generation sequencing platforms is suggested, which may help to address unresolved systematic and life history questions surrounding this parasite group. This review aims to assist taxonomists to help unravel the confusion surrounding the poorly studied and little understood Dicyemida.

Key words: classification, taxonomy, Mesozoa, parasite, Mollusca, Cephalopoda, kidneys

Introduction

Dicyemid mesozoans, small microscopic, worm-like organisms, are the most common and characteristic parasites in the renal appendages (synonyms with kidneys, renal sacs and renal organs) of benthic cephalopods, occurring in densities of thousands of animals per cm^3 (Furuya & Tsuneki 2003; Furuya *et al*. 2004; Finn *et al*. 2005). Their body organisation is simple, comprising only eight to 40 cells, with neither body cavities nor differentiated organs (Suzuki *et al*. 2010). Specifically, dicyemids are characterised by having one long cylindrical axial cell (from where developing embryos are derived) which is surrounded by ciliated peripheral cells (Awata *et al*. 2006). At the anterior region, the peripheral cells are modified to form a calotte which is the parasites' foothold into the convoluted surface of the host renal appendage (Furuya *et al*. 2003a, 2007). The arrangement of cells in the calotte traditionally determines the familial and generic placement of species. Typically, differences occur both in the number and arrangement of the two most anterior tiers of calotte cells: metapolar and propolar cells (see Fig. 1).

In contrast to their simple morphology, dicyemid parasites have a complex lifecycle with two stages of development (vermiform and infusoriform stages) and two modes of reproduction (asexual and sexual) (Fig. 2). The vermiform stages (vermiform embryo, nematogen and rhombogen) are formed asexually from an agamete and spend all of their lifecycle attached to the host's renal appendages where they derive metabolic requirements from dissolved nutrients in the host's urine (Hochberg 1982; Furuya *et al*. 2001; Finn *et al*. 2005) (Fig. 2). The infusoriform stage (infusoriform embryo) develops from a fertilised egg cell produced around a hermaphroditic gonad called the infusorigen. The infusoriform embryo represents the dispersal stage, which escapes from the host via the urine into the sea to infect a new host individual (McConnaughey 1951; Furuya *et al*. 2003b) (Fig. 2). A

Accepted by N. Dronen: 4 Jul. 2012; published: 12 Sept. 2012