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The systematics of carnivorous sponges ☆

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ABSTRACT

Carnivorous sponges are characterized by their unique method of capturing mesoplanktonic prey coupled with the complete or partial reduction of the aquiferous system characteristic of the phylum Porifera. Current systematics place the vast majority of carnivorous sponges within Cladorhizidae, with certain species assigned to Guitarridae and Esperlopsidae. Morphological characters have not been able to show whether this classification is evolutionary accurate, and whether carnivory has evolved once or in several lineages.

In the present paper we present the first comprehensive molecular phylogeny of the carnivorous sponges, interpret these results in conjunction with morphological characters, and propose a revised classification of the group. Molecular phylogenies were inferred using 18S rDNA and a combined dataset of partial 28S rDNA, COI and ALG11 sequences. The results recovered carnivorous sponges as a clade closely related to the families Mycalidae and Guitarridae, showing family Cladorhizidae to be monophyletic and also including carnivorous species currently placed in other families. The genus *Lycopodina* is resurrected for species currently placed in the paraphyletic subgenus *Asbestopluma* (*Asbestopluma*) featuring forceps spicules and lacking sigmas or sigmancistras. The genera *Chondrocladia* and *Cladorhiza* are found to be monophyletic. However, results indicate that the subgenus *Chondrocladia* is polyphyletic with respect to the subgenera *Meliiderma* and *Symmetrocladia*. *Euchelipluma*, formerly Guitarridae, is retained, but transferred to Cladorhizidae. The four known carnivorous species currently in *Esperiopsis* are transferred to *Abyssocladia*. *Neocladia* is a junior homonym and is here renamed *Koltunicladia*.

Our results provide strong evidence in support of the hypothesis that carnivory in sponges has evolved only once. While spicule characters mostly reflect monophyletic groups at the generic level, differences between genera represent evolution within family Cladorhizidae rather than evolution of carnivory in separate lineages. Conflicting spicule characters can be reinterpreted to support the inclusion of all carnivorous sponges within Cladorhizidae, and a carnivorous habit should thus be considered the main diagnostic character in systematic classification.

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1. Introduction

An aquiferous system used to filter water for particulate matter is generally considered a defining feature of sponges (e.g. Bergquist, 1978). The only known exceptions are the carnivorous sponges

(Demospongiae: Poecilosclerida) which have developed the ability to trap, envelop, and digest prey items, representing a unique evolutionary innovation within the phylum Porifera. Prey capture is dependent on the plastic nature of the sponge and follows an initial entanglement of the prey followed by migration and complete envelopment into the sponge by amoebocytes, which are able to digest the prey over a period of several days (Vacelet and Dupont, 2004). Morphological adaptations to carnivory include an erect body morphology, a complete or partial reduction of the aquiferous system and the presence of filaments or inflatable spheres with an adhesive surface to catch and digest suitable prey. Typical prey items are small crustaceans, but the sponges are not very selective,

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and prey suitability seems to be governed mainly by the prey having appendages that can become entangled in contact with the sponge (Vacelet, 2007; Vacelet and Dupont, 2004).

This carnivorous feeding strategy is generally considered to be an evolutionary adaptation to the oligotrophic conditions of the deep sea, where filter feeding is less viable for obtaining nutrients (e.g. Vacelet, 2007). Carnivorous sponges are thus mainly considered deep-sea sponges, and they constitute a large part of the sponge fauna at bathyal, abyssal and even hadal depths, with a depth record of 8840 m (Koltun, 1970). They are, however, also very much present in shallower habitats on the upper slope and shelf and are not uncommon up to a depth of a couple of hundred meters. Certain species have been reported even shallower (<100 m), and a couple of species are known as shallow as 20 m, mainly, but not exclusively, in cave habitats (Aguilar et al., 2011; Bakran-Petricioli et al., 2007; Chevaldonné et al., 2014; Vacelet, 1996; Vacelet and Boury-Esnault, 1996; van Soest and Baker, 2011). Carnivorous sponges are frequently found in the general enrichment zones around hydrothermal vents and seeps, benefiting from the increased prey availability at these sites (Vacelet, 2006b). Chemoautotrophic symbiotic bacteria have been reported from two species of carnivorous sponges, but the extent of symbiotic relationships is not known (Riesgo et al., 2007; Vacelet and Boury-Esnault, 2002; Vacelet et al., 1995, 1996). However, the symbiotic microbiome could be involved in the digestion process (Dupont et al., 2014, 2013; Vacelet and Dupont, 2004).

Approximately 130 species with a morphology suggesting carnivory have been described to date. Due to the poor sampling of most of the world's oceans this number probably represents only a portion of the total amount of carnivorous sponges, and new species are continually being described (Kelly and Vacelet, 2011). The vast majority of carnivorous sponges are presently placed within Cladorhizidae Dendy, 1922 (Porifera: Demospongiae: Poecilosclerida). This family currently contains seven genera and five subgenera accepted by the World Porifera Database (van Soest et al., 2015): *Abyssocladia* Lévi, 1964; *Asbestopluma* (*Asbestopluma*) Topsent, 1901; *Asbestopluma* (*Helophloeina*) Topsent, 1929; *Cercicladia* Ríos, Kelly & Vacelet, 2011; *Chondrocladia* (*Chondrocladia*) Thomson, 1873; *Chondrocladia* (*Meliiderma*) Ridley and Dendy, 1887; *Chondrocladia* (*Symmetrocladia*) Lee et al., 2012; *Cladorhiza* Sars, 1872; *Lolliopocladia* Vacelet, 2008 and *Neocladia*, Koltun, 1970. Morphological adaptations suggesting a carnivorous feeding strategy (erect morphology, filaments, lack of aquiferous system, observations of partially digested prey) are also present in certain other taxa such as *Euchelipluma* spp. Topsent, 1909 (Guitarridae Dendy, 1924) and some species currently placed within *Esperiopsis* Carter, 1882 (Esperiopsidae Hentschel, 1923).

Carnivorous sponges belong to order Poecilosclerida, which forms part of the clade Heteroscleromorpha Cárdenas, Pérez & Boury-Esnault, 2012 in molecular analyses (Borchiellini et al., 2004; Cárdenas et al., 2012; Erpenbeck and Wörheide, 2007; Lavrov et al., 2008; Morrow et al., 2012; Redmond et al., 2013). Chela microscleres are unique to the order Poecilosclerida, and a clade containing chela-bearing poecilosclerids is usually recovered in molecular analyses close to several polyphyletic assemblages of mostly hadromerid sponges (Erpenbeck et al., 2007a; Erpenbeck and Wörheide, 2007; Lavrov et al., 2008; Morrow et al., 2012; Redmond et al., 2013; Thacker et al., 2013). Within the order, chela morphology was previously one of the major characters forming the basis of the subordinal classification, comprising Microcionina, Latrunculina, Myxillina and Mycalina (Hajdu et al., 1994; Hooper and van Soest, 2002; Kelly and Samaai, 2002). Molecular evidence shows that this classification does not describe the true evolutionary relationships of the order (Erpenbeck and Wörheide, 2007; Hajdu et al., 2013) and it is no longer considered valid in a newly

proposed classification of the Demospongiae (Morrow and Cárdenas, 2015).

The systematics of the carnivorous sponges is currently based primarily on spicule characters, with a special emphasis on chela type at the generic level (Hajdu and Vacelet, 2002). While the current cladorhizid genera are quite well characterized, they collectively contain a large range of chela morphologies, including both palmate and anchorate forms of both iso- and anisochelae as well as more particular forms such as abyssochelae, cleistochelae and cercichelae. This has caused several authors to question the monophyly of family Cladorhizidae (Lopes et al., 2011; Vacelet, 2006a). Thus morphological characters alone have not been able to answer the question of whether carnivory has evolved multiple times within the Poecilosclerida, or whether the carnivorous sponges represent a monophyletic group with a wide range of spicule assemblages (see Kelly and Vacelet, 2011). Only a few molecular sequences are available for carnivorous sponges (Borchiellini et al., 2004; Chevaldonné et al., 2014; Riesgo et al., 2014; Vargas et al., 2013) and there has been no comprehensive attempt to establish the phylogenetic relationships of the group and their relationship to other poecilosclerids.

Accordingly, we investigated (1) whether carnivory in sponges has evolved once or several times, i.e. whether the carnivorous sponges constitute a monophyletic group, (2) the systematic position of carnivorous sponges in relation to other poecilosclerids, (3) the accuracy of the current intra-family systematics of family Cladorhizidae as well as (4) the systematics of carnivorous species currently assigned to other families. In this study, our overall aim has been to construct the first comprehensive phylogeny of the carnivorous sponges using molecular data, and relate the molecular findings to morphological characters. Based on our findings, we propose a revision of the current systematics of the carnivorous sponges and provide an overview of and key to identification of carnivorous genera and subgenera.

2. Materials and methods

2.1. Collection, preservation and identification

Specimens from the North Atlantic and Arctic were collected on board the Norwegian Institute of Marine Research and University of Bergen research vessels RV "G.O. Sars" and RV "Hans Brattström", and the German GEOMAR research vessel RV "Poseidon". Specimens from the New Zealand EEZ were collected on board the National Institute of Water & Atmospheric Research (NIWA) research vessel RV "Tangaroa". SW Atlantic specimens were collected on board the RV "Miguel Oliver" as part of the ATLANTIS project mapping the continental margin off Argentina. SW Indian Ocean specimens were collected on board the RV "Vizconde de Eza" in April 2009 during the MAINBAZA cruise to study benthic biodiversity of the continental margin off Mozambique, and the RV "James Cook" cruise no. 66 to the Southwest Indian Ocean Ridge (SWIOR) in 2011. Additional specimens were obtained from the collections at the Naturalis Biodiversity Center (Leiden) as well as single specimens from several sources (Table 1).

Most of the material was preserved in 96% ethanol. Some material originally preserved in 70% ethanol was also successfully sequenced, though in many cases only partially. All samples used for the phylogenetic analyses, as well as additional specimens used for morphological comparison, were examined and identified to species level. Species yet to be formally described have been assigned alphabetical characters to distinguish different species. Taxonomic descriptions of these species will be presented in forthcoming papers.

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