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Molecular Phylogeny and Morphological Evolution of the Acantharia (Radiolaria)

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Acantharia are ubiquitous and abundant rhizarian protists in the world ocean. The skeleton made of strontium sulphate and the fact that certain harbour microalgal endosymbionts make them key planktonic players for the ecology of marine ecosystems. Based on morphological criteria, the current taxonomy of Acantharia was established by W.T. Schewiakoff in 1926, since when no major revision has been undertaken. Here, we established the first comprehensive molecular phylogeny from single morphologically-identified acantharian cells, isolated from various oceans. Our phylogenetic analyses based on 78 18S rDNA and 107 partial 28S rDNA revealed the existence of 6 main clades, sub-divided into 13 sub-clades. The polyphyletic nature of acantharian families and genera demonstrates the need for revision of the current taxonomy. This molecular phylogeny, which highlights the taxonomic relevance of specific morphological criteria, such as the presence of a shell and the organisation of the central junction, provides a robust phylogenetic framework for future taxonomic emendation. Finally, mapping all the existing environmental sequences available to date from different marine ecosystems onto our reference phylogeny unveiled another 3 clades and improved the understanding of the biogeography and ecology of Acantharia.

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Key words: Acantharia; strontium sulfate; molecular phylogeny; Radiolaria; Rhizaria; single-cells.

Introduction

Acantharia are marine protists taxonomically affiliated to the super-group Rhizaria, the phylum Retaria and to the first rank taxon Radiolaria (Adl et al. 2005; Moreira et al. 2007). Their characteristic star-shaped morphology consists of a skeleton of 10 or 20 spicules made of celestite (strontium sulphate; Odum 1951; Suzuki and Aita, 2011), arranged according to the geometric law of Müller (1859). The skeleton supports a typical rhizarian amoeboid cell whose shape and motility are controlled by-characteristic axopods and myonemes (Febvre, 1981). The Acantharia are the only known organisms able to biomineralize strontium sulfate as the principal component of the skeleton.

In surface waters of marine ecosystems, Acantharia consistently outnumber their rhizarian counterparts, such as Foraminifera and Polycystinea (Caron and Swanberg 1990; Michaels et al. 1995; Stoecker et al. 2009). Their abundance tends to increase in oligotrophic waters from equatorial to subtropical latitudes (Massera Bottazzi and

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Andreoli 1982), and they can form blooms at certain periods of the year, reaching densities up to 500 000 individuals.m^{-2} (Massera Bottazzi and Andreoli 1978, 1981). Acantharian cells have also been found hundreds and even thousands of meters deep in the water column (Antia et al. 1993; Bernstein et al. 1987; Martin et al. 2010). Within the marine food web, the Acantharia are active predators (Swanberg and Caron 1991), and they significantly contribute to carbon flux and biogeochemical cycles of strontium and barium in the oceans (Bernstein et al., 1987; Martin et al. 2010). Furthermore, they indirectly contribute to primary production through endosymbiotic relationships with tens to hundreds of microalgae per cell (Michaels 1988, 1991). Despite holding a key position in marine ecosystems, the Acantharia have been largely overlooked in ecological studies, essentially due to dissolution of the skeleton in classical fixatives (Beers and Stewart 1970) and the lack of success in culturing them. Our knowledge of their biology and diversity is therefore still in its infancy.

The first classification of Acantharia was initiated by Johannes Müller (1856, 1859), and completed by his student Ernst Haeckel (1887, 1888). This classification initially comprised 372 species, and further studies added around 80 more (Mielck 1907; Popofsky 1904a, b, 1906). All of the diagnostic characters used by these authors were exclusively based on the morphology of the skeleton, such as the length, form and central junction of the spicules. Working on living specimens, W.T. Schewiakoff emended this classification in 1926 by taking into account various features of the cell body (e.g. structure and colour of the cytoplasm, absence or presence of the central capsule, myonemes). In his remarkable monograph based on accurate observations of 500 living cells, he confirmed a total of 130 species, and erected the main taxonomic framework for the Acantharia (Schewiakoff 1926). Minor modifications have since been made to this classification (Bernstein et al. 1999; Febvre et al. 2000; Reshetnyak 1981; Tan 1998; Trégouboff 1953). The class Acantharia currently comprises around 50 genera and 150 species, which are grouped into 18 families distributed in 4 orders: Holacanthida, Chaunacanthida, Symphiacanthida and Arthracanthida (Bernstein et al. 1999). The distinction between the four orders is mainly based on the way the spicules cross the cytoplasm. In the Holacanthida, which was considered by Schewiakoff to be the most basal order, 10 diametral spicules loosely cross the centre of the cell, where they tangle to form a central body (Acanthocollidae) or do not join at all (Acantochiasmidae and Acanthoplegmidae). The Chaunacanthida are characterized by having 20 spicules that are more or less joined at the cell centre and that can be easily dissociated. The Symphiacanthida and the Arthracanthida have 20 tightly joined spicules. The spicules in the Symphiacanthida are attached to each other at the centre by their basal parts, forming a uniform central body. The Arthracanthida, which are characterized by the presence of a thick central capsule, were suggested to represent the most derived forms of Acantharia (Schewiakoff 1926), and are divided into two suborders, the Sphaenacantha and the Phyllacantha.

Hitherto, there has been little effort to validate this morphology-based acantharian taxonomy using molecular phylogenetics. Because of the elusive nature of Acantharia and the difficulty to perform accurate morphological identification on living specimens, very few cells have been isolated, morphologically identified and sequenced (about 20 18S rDNA sequences are publicly available to date). For instance, only 4 of the 30 genera of Arthracanthida are represented in GenBank from isolated specimens (Gilg et al. 2009; Oka et al. 2005; Zettler et al. 1997). Molecular phylogenies including these sequences have nevertheless highlighted inconsistencies within the existing morphological classification. The orders Symphiacanthida and Arthracanthida are mixed, the Chaunacanthida includes specimens identified as Symphiacanthida, and the Holacanthida is simply missing in these analyses (Gilg et al. 2009; Oka et al. 2005). Yet, together with more recent investigations (Krabberød et al. 2011), these studies demonstrated the monophyly of the Acantharia among the Radiolaria.

In addition to sequences from isolates, numerous sequences assigned to Acantharia have been retrieved from environmental surveys of genetic diversity in various environments, including coastal (Marie et al. 2010), deep (Not et al. 2007; Quaiser et al. 2010), Antarctic and Arctic (López-García et al. 2001 and Lovejoy et al. 2006 respectively), and anoxic (Alexander et al. 2009; Stoeck et al. 2003) waters, as well as, sediments from the mid-Atlantic ridge and the southern Guaymas vent field (López-García et al. 2003 and Edgcomb et al. 2002 respectively). This considerable diversity of environmental 18S rDNA sequences from Acantharia has no associated morphological information. This phenomenon will undoubtedly be further amplified with the advent of environmental surveys using high-throughput DNA sequencing technologies. As for many protist groups, reference sequences (from

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