Acantharia

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Acantharia are marine planktonic unicellular eukaryotes within the Radiolaria and currently encompass nearly 50 genera and 150 species. They are distributed worldwide from subsurface to deep waters and appear to be most numerous in oligotrophic surface waters. Their main distinctive features are an internal star-shaped skeleton made of strontium sulfate mineral and an amoeboid cell that possesses multiple nuclei, extensive axopods and contractile myonemes. Acantharia feed on a large variety of prey, but some species are mixotrophs through symbiosis with intracellular eukaryotic microalgae, typically the haptophyte *Phaeocystis*. As part of their life cycle, some taxonomic groups form heavy cysts that rapidly sink to deep waters creating a biogeochemically relevant vertical flux of carbon, strontium and barium. Overall, Acantharia remain poorly studied, and our knowledge of their biology and ecology is still in its infancy.

Introduction

Acantharia are holoplanktonic unicellular eukaryotes (protists) that live in marine environments from the subsurface to the mesopelagic zone worldwide. They belong to the Radiolaria, and currently comprise around 50 genera and 150 species (Bernstein *et al*., 1999). The acantharian cell typically measures from tens to several hundred of micrometers and exhibits a characteristic star-shaped mineral skeleton made of strontium sulfate (Odum, 1951; Suzuki and Aita, 2011). Acantharia have different life strategies (e.g. encystment for reproduction and symbiosis with intracellular microalgae), and are important components of oceanic plankton communities, contributing to marine food web and biogeochemical cycles of various elements, such as carbon, strontium and barium. Acantharia were discovered and

described in the mid-eighteenth century, in the Mediterranean Sea, by Johannes Müller, who proposed the first classification based on skeleton morphology (Müller, 1859). Since then, the original and complex acantharian cells drew more attention from cellular biologists in the late twentieth century than from marine ecologists. Despite their worldwide distribution, abundance and biogeochemical significance in surface oceans, Acantharia have been largely overlooked in ecological surveys of marine plankton. This is mainly because of their delicate skeleton that rapidly dissolves upon death and in classical fixatives (e.g. formaldehyde; Beers and Stewart, 1970), the resulting absence of a fossil record in contrast to other radiolarian groups and the lack of success in culturing them. Recent molecular phylogenetic studies have improved the understanding of the evolutionary history and life strategies of Acantharia, and have highlighted several contradictions with the morphology-based taxonomic classification.

Taxonomy and Morphology

Taxonomic classification and molecular phylogeny

The Acantharia is a monophyletic taxon within the radiolarians in the eukaryotic super-group Rhizaria (Krabberød *et al*., 2011; Adl *et al*., 2012). The first classification of Acantharia (originally named Acanthometren) was initiated by Müller (1856, 1859) and completed by his student Haeckel (1887, 1888). This classification initially comprised 372 species, and further studies added around 80 more (Popofsky, 1904; Mielck, 1907). Working on living specimens in the Mediterranean Sea (Naples, Italy) and considering additional criteria of the cell, W.T. Schewiakoff emended this classification in 1926 and erected the main taxonomic framework encompassing a total of 130 species (Schewiakoff, 1926). Minor modifications have since been made to this classification (Reshetnyak, 1981; Bernstein *et al*., 1999; Febvre *et al*., 2000). The order Acantharia currently comprises nearly 50 genera and 150 species, which are grouped into 18 families and distributed in four suborders: Holacanthida, Chaunacanthida, Symphiacanthida and Arthracanthida (**Figure 1**; Bernstein *et al*., 1999; Suzuki and Aita, 2011). **See also**: Haeckel, Ernst Heinrich Philipp August; Protozoa; Radiolaria

Morphological identification and classification of uncultured protists such as Acantharia remains a highly challenging task. In Acantharia, there are relatively few diagnostic characters, which
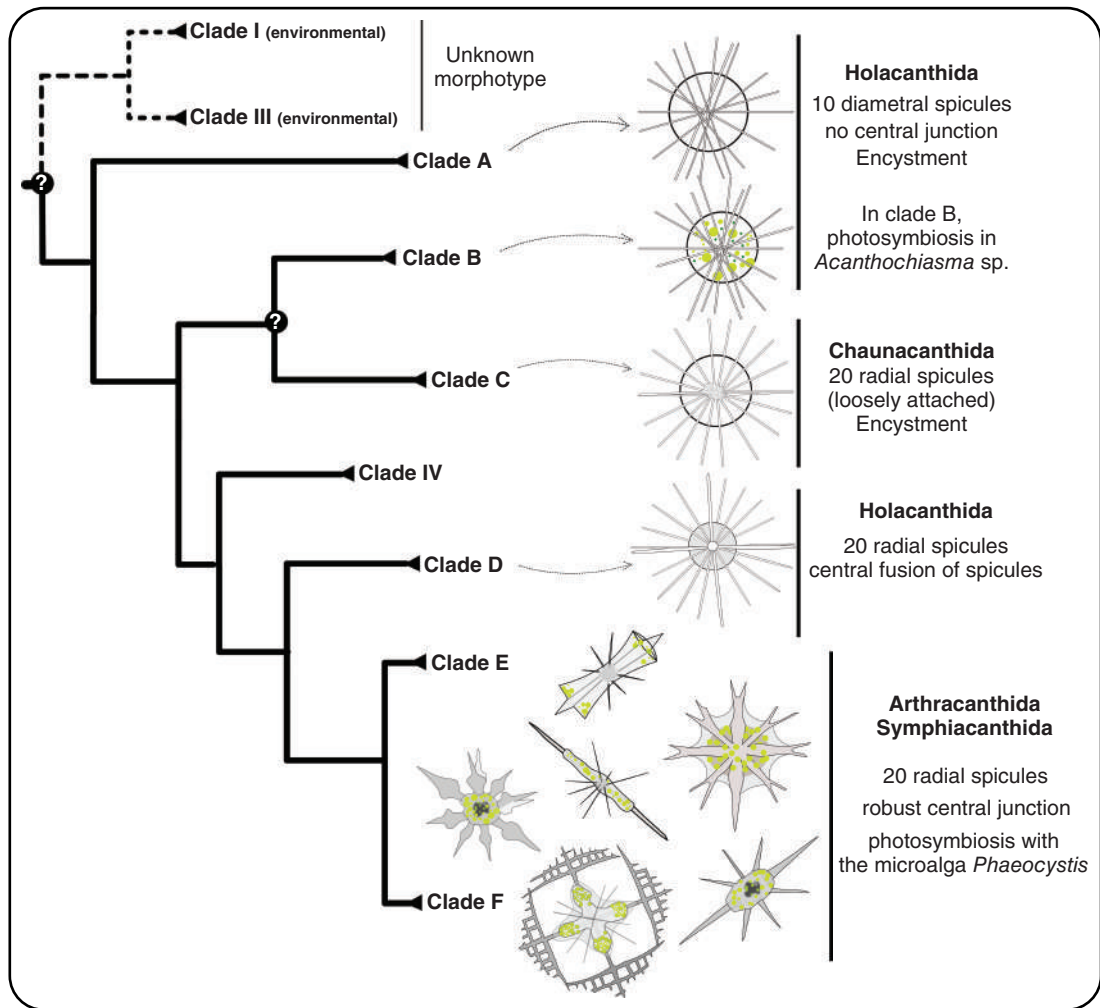
Figure 1 Schematic phylogenetic tree of Acantharia based on ribosomal genes (18S and 28S rRNA) from Decelle *et al.* (2012a, 2013), showing the match between molecular clades, morphological features of the skeleton (i.e. central junction, presence of symbionts) and the four taxonomic suborders (Holacanthida, Chaunacanthida, Symphiacanthida and Arthracanthida). Note that the central junction of clade IV is not reported here as it is not visible due to dense endoplasm. Morphology of acantharians from clades I and III is unknown as all ribosomal sequences come from environmental plankton community samples. Nonsupported nodes are reported by a surrounded question mark.

can sometimes require delicate preparation and manipulation to be observed. Moreover, some of these characters can be altered during sampling and can significantly evolve during the ontogeny of the cell. Recently, phylogenetic analyses based on the ribosomal 18S and 28S rRNA genes from single morphologically identified acantharian cells revealed the existence of nine main clades (A–F, and I, III and IV) and several subclades (**Figure 1**; Decelle *et al.*, 2012a, 2013). At the suborder level, Chaunacanthida are monophyletic as all representatives fall in clade C, contrary to Holacanthida that are polyphyletic, being distributed across clades A, B and D. Arthracanthida correspond to the most recently diverged monophyletic group, comprising clades E and F, in which several subclades were identified. As in a previous study (Hollande *et al.*, 1965), the existence of Symphiacanthida has been questioned as species of this suborder are distributed across clades E and F and share several morphological

characters with Arthracanthida. In addition to these molecular clades for which cells have been isolated and morphologically identified, there are two environmental clades (I and III) for which no sequences of isolated specimens are available. Despite several conflicts with the traditional classification (i.e. several families and genera are polyphyletic), the molecular phylogenies revealed the evolutionary history of the mineral skeleton and highlighted the taxonomic relevance of specific morphological criteria (Decelle *et al.*, 2012a). **See also**: **Protist Evolution and Phylogeny**; **Protist Systematics**

The skeleton

One of the main characteristics of Acantharia is their mineral skeleton made of strontium sulfate ($SrSO_4$, also called celestite), covered by a cell membrane and composed of spicules crossing
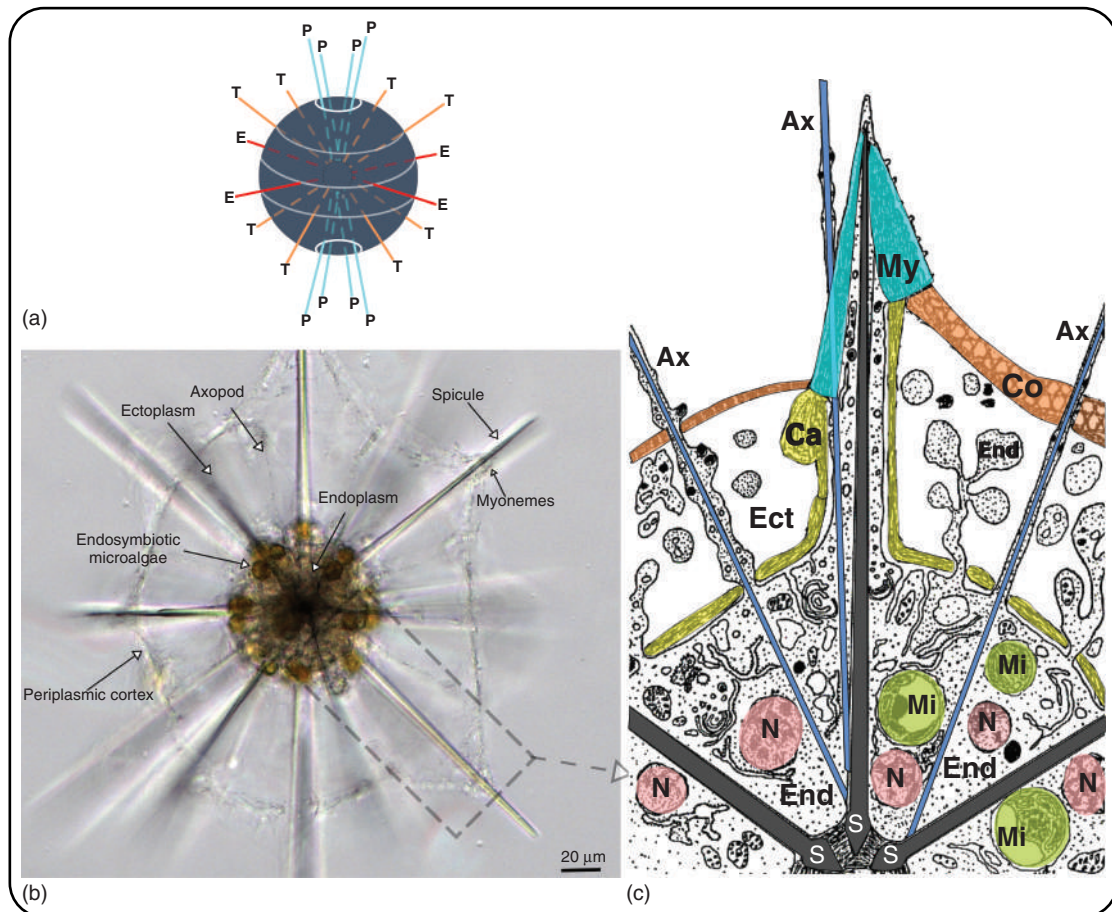
Figure 2 General organisation of the acantharian cell and its endoskeleton. (a) Geometric arrangement of the spicules following Müller's law: two quartets of polar spicules (P) alternate with two quartets of tropical spicules (T) and one quartet of equatorial spicules (E). (b) Light microscopy photograph of an acantharian cell (Arthracanthida) hosting endosymbiotic microalgae (small round brown/yellow cells) within the endoplasm. (c) Zoom of a cell portion showing the general ultrastructure: the endoplasm (End) is limited by the capsular wall (Ca), and the ectoplasm (Ect) is covered by the periplasmic cortex (Co). Several nuclei (N) and endosymbiotic microalgae (Mi), which are only present in clades E and F, and in a single species of clade B, are located in the endoplasm. Myonemes (My) are linked to the periplasmic cortex and to the apex of the spicules (S). Thin radiating axopods (Ax) can extend several microns into the surrounding water for prey capture.

the cell. While other radiolarians use silica for building their skeletons, Acantharia are the only known organisms in the marine environment able to biomineralise strontium sulfate as the principal component of the skeleton. As seawater is highly undersaturated with respect to strontium, skeletons dissolve rapidly after cell death and, as a consequence, no fossil record of Acantharia has been found in marine sediments (Beers and Stewart, 1970). Although the mechanisms of celestite biomineralisation remain enigmatic, it has been demonstrated that each spicule is a single rhombic monocrystal that grows by celestite precipitation within a perispicular vacuole (Wilcock *et al.*, 1988). The acantharian skeleton can also coprecipitate significant amounts of barium, influencing the formation of barite ($BaSO_4$) in the oceans (Bernstein *et al.*, 1992). The skeleton consists of either 10 diametral or 20 radial spicules that are spatially organised according to Müller's law (Müller, 1859; Haeckel, 1862): two quartets of 'polar' tips alternate with two quartets of 'tropical' tips and one quartet of 'equatorial' tips (**Figure 2a**). Depending on the

species but also within an individual cell, spicules can have different lengths, widths and forms (**Figure 3**). Spicules can harbour spines, serrations, wing-like extensions and single or branched apophyses, which can form lattice or perforated plates. In some cases, the plates are connected with one another laterally, forming a lattice shell around the cell (**Figure 3J, l**).

The distinction between the four acantharian suborders is mainly based on the way the spicules cross the cytoplasm (**Figure**s **1** and **4**). In Holacanthida (mainly represented by the earliest diverging clades A and B), which was considered by Schewiakoff to be the most basal group, the 10 diametral needle-shaped spicules loosely cross the centre of the cell. Chaunacanthida (clade C) have 20 radial spicules (sometimes denticulated) that are more or less joined at the cell centre by contractile fibrils and can fold like an umbrella (**Figures 3g** and **4a**, **b**), whereas Symphiacanthida and Arthracanthida (clades E and F) have 20 solid radial spicules that cannot be dissociated, and their fusion forms a central body at the cell centre (**Figure**
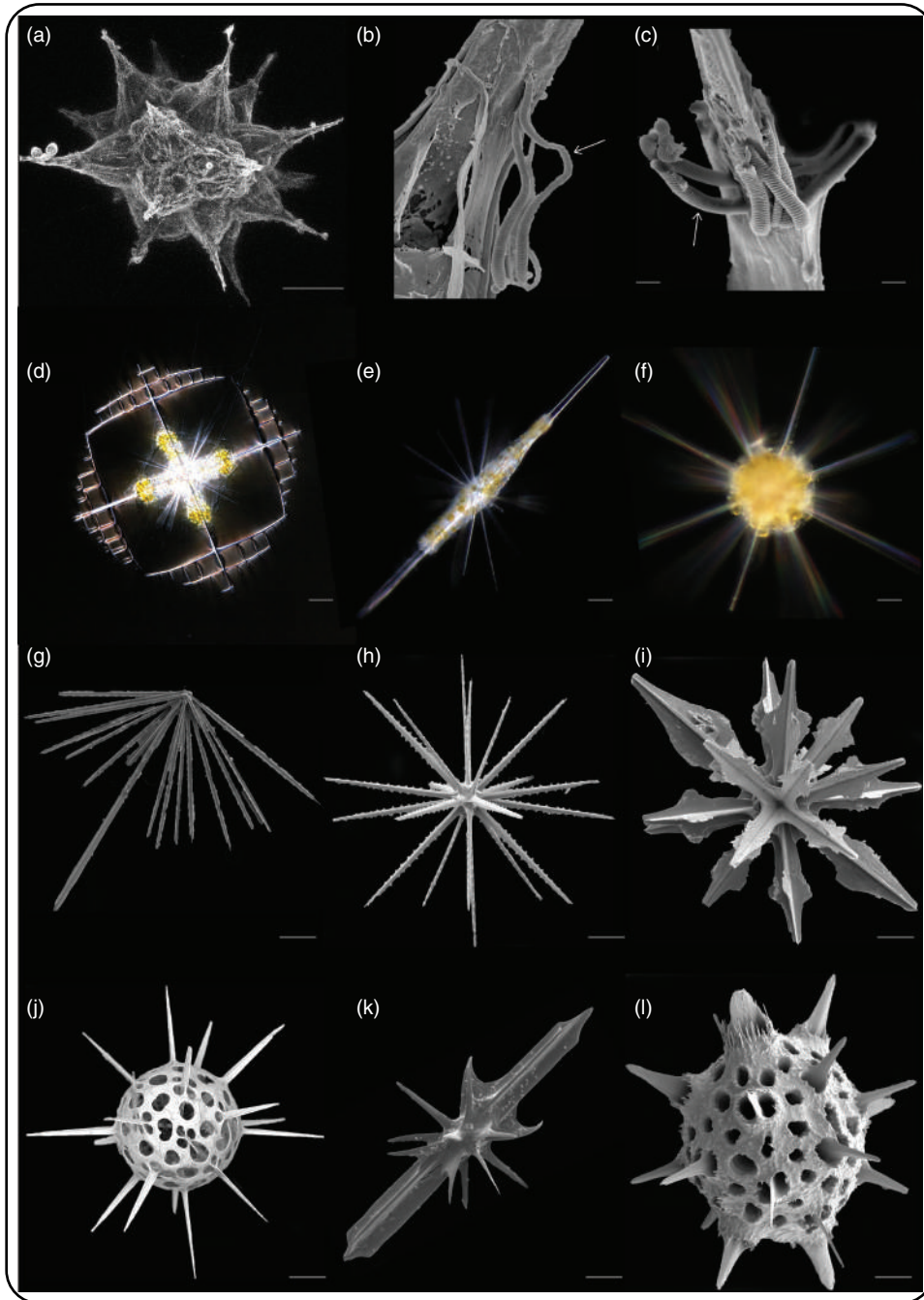
Figure 3 A panel of acantharian cells and their various cytoplasmic and skeletal features imaged by light (LM), confocal and scanning electron microscopy (SEM). (a) External view of a living acantharian cell with its periplasmic cortex attached to each spicule of the skeleton; scale bar = 50 μm (Image courtesy of Sébastien Colin; confocal microscopy). (b, c) SEM images of myonemes (indicated by arrows) located at the extremity of a spicule; scale bars = 1 μm. (d–f) LM images of symbiotic acantharians from clade F (Arthracanthida) with intracellular microalgae (yellow cells) belonging to the Haptophyceae genus *Phaeocystis*; scale bars = 20 μm. (g–l) SEM pictures of different acantharian celestite skeletons from the Chaunacanthida of clade C (g), and the Arthracanthida of clades F (h, i) and E (j–l); scale bars = 30 μm.
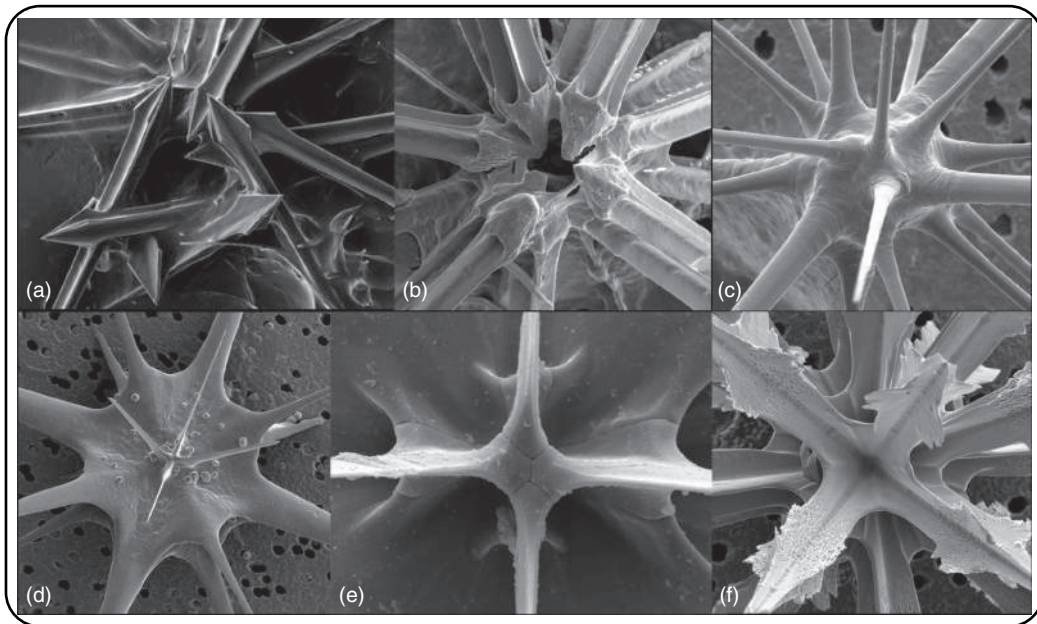
Figure 4 Scanning electron microscopy (SEM) images of acantharian skeletons showing the evolution of the central junction (the way the spicules cross the cell) across molecular clades: (a, b) central junction can be loose in clade C, (c) tight with fused spicules in clade D or (d–f) tight and well developed, forming a large central body in most species of clades E and F. Note that acantharians from clades A and B have no central junction (their 10 spicules simply cross the cell), and specimens are therefore very fragile and difficult to observe in SEM.

4d–f). Arthracanthida and Symphiacanthida that were suggested to represent the most derived forms of Acantharia (Schewiakoff, 1926) exhibit the most complex and diverse skeleton morphologies, having thick and robust spicules of different form and shapes, as well as shells formed by apophyses or plate connections (**Figure 3h–l**).

The cell

The internal skeleton of Acantharia supports an amoeboid cell that is divided in two main compartments: the inner (endoplasm) and outer (ectoplasm) cytoplasm (**Figure 2b**, **c**). The endoplasm contains the main organelles, such as several nuclei, mitochondria and Golgi bodies (Febvre *et al*., 2000; Suzuki and Aita, 2011; Suzuki *et al*., 2009). The endoplasm, which can vary in colour (e.g. yellow, brown, black and red), is delimited by the capsular wall consisting of a 20–30 nm thick porous fibrillar meshwork. The ectoplasm corresponds to very flexible cytoplasmic extensions protruding through pores of the capsular wall, and is mainly involved in prey capture and digestion in food vacuoles. The ectoplasm is surrounded by the periplasmic cortex, which is a thin fibrillar meshwork of 20 large polygonal pieces, each centred on each spicule, and connected to each other by elastic junctions. Around each spicule, the periplasmic cortex turns down like a collar and links with the capsular wall. The cortex is also attached to the tip of each spicule by 2–80 contractile ribbons of 8–60 µm in length, called myonemes (**Figures 2** and **3b**, **c**; Febvre, 1981; Febvre *et al*., 2000). Also present in the radiolarians Taxopodia (Cachon *et al*., 1977) and the ciliate genus *Vorticella* (Buhse *et al*., 2011), the myoneme is a dense bundle of thin, twisted and nonactin contractile filaments that can contract and relax (Febvre and Febvre-Chevalier, 1989). Myoneme contraction–relaxation in Acantharia is considered to control buoyancy in the water column. Myonemes can produce three kinds of movement: (1) rapid contraction triggered by calcium influx, causing transient inflation of the cell volume; (2) relaxation, causing the cortex to return to its initial form and (3) slow undulating movement accompanied by progressive contraction (Febvre and Febvre-Chevalier, 1989). Compared to some species of Holacanthida that do not possess (or at least are not visible) myonemes, Arthracanthida tend to have more myonemes per spicule (Schewiakoff, 1926). Acantharia are also known to possess long and thin assemblages of microtubules called axopods (a type of pseudopodia with a rigid axoneme bundle), which radiate from the cell surface in all directions (**Figure 2**; Febvre-Chevalier and Febvre, 1993). Also present in Heliozoa and other Radiolaria, their number and position are species-specific in Acantharia. Although not very dynamic, axopods are mainly used for prey capture, as well as bidirectional transport of organelles and vesicles through the ectoplasm and the endoplasm. **See also**: **Heliozoa**; *Vorticella*; **Protozoan Organelles of Locomotion**

Life Strategies: Nutrition and Reproduction

Predation

Although quantitative data on feeding behaviour and nutritional physiology are presently lacking, Acantharia are known to graze

on diverse prey using their extensive axopods and digest them in the ectoplasm. By gently collecting acantharian cells by scuba diving in the North Atlantic Ocean, a study investigated the prey composition in cytoplasmic food vacuoles based on microscopy observations (Swanberg and Caron, 1991). Although 60% of collected Acantharia had no detectable prey, the identifiable prey were mostly ciliate tintinnids (corroborated with the observations of Schewiakoff in Naples, 1926), while copepods, mollusc larvae and phytoplankton (diatoms and dinoflagellates) were also found to a lesser extent. Bacteria have also been observed in food vacuoles with appropriate staining techniques (Bernstein *et al.*, 1999). Acantharia maintained in the laboratory upon collection can be fed with microalgae and crustacean larvae (Amaral-Zettler *et al.*, 1997 and personal observations). Therefore, Acantharia seem to have a generalist diet, taking advantage of available prey in their surrounding environment. **See also**: **Protozoan Nutrition and Metabolism**

Photosymbiosis with microalgae

In addition to their heterotrophic behaviour, all acantharian species from the Arthracanthida and Symphiacanthida (clades E and F) live in symbiosis with ten to hundreds of intracellular eukaryotic microalgae (photosymbiosis) (**Figure 3d–f**). These symbiotic acantharians have a more complex and robust skeleton, as well as more myonemes and axopods compared to their non-symbiotic relatives (Schewiakoff, 1926; Decelle *et al.*, 2012b). Contrary to other symbiotic radiolarians (e.g. Spumellaria and Collodaria), where symbionts tend to be maintained in peripheral cytoplasmic regions, Acantharia hold their microalgae in the endoplasm, likely representing a higher degree of integration (**Figure 2**). The number of symbionts increases during the growth of the host (Michaels, 1991), but it is unclear whether the microalga is able to divide internally and/or if the host continuously acquires new symbionts from the environment during its development.

Ultrastructural observations from three acantharian species (*Lithoptera muelleri*, *Acanthometra pellucida* and *Amphilonche elongata*) described the symbiotic microalgae as belonging to the phytoplankton lineage Haptophyta (Febvre and Febvre-Chevalier, 1979). Ribosomal and plastidial genetic markers obtained from several single acantharian cells collected in different oceanic regions worldwide confirmed and further identified the symbionts as belonging to the haptophyte genus *Phaeocystis* (Decelle *et al.*, 2012b), an ubiquitous microalga well known for forming extensive nuisance blooms in coastal areas (Schoemann *et al.*, 2005). Specificity of the symbiosis is mainly dependent on geography whereby all acantharian host species live with the local species of *Phaeocystis* in a given oceanic region (e.g. *P. cordata* and *P. antarctica* in the Mediterranean Sea and Antarctic, respectively; Decelle *et al.*, 2012b). Molecular clock analyses suggest that the onset of the Acantharia–*Phaeocystis* symbiosis occurred in the middle Mesozoic, between 175 and 93 Mya, corresponding to a period where surface waters were highly oligotrophic (Decelle *et al.*, 2012b).

Other microalgal cells have also been reported in close relationship with another acantharian host species, *Acanthochiasma* sp. (Holacanthida), belonging to the early diverging clade B

(**Figure 1**; Schewiakoff, 1926; Decelle *et al.*, 2012c). Several host cells were isolated from one location in the Mediterranean Sea for two consecutive years and multiple algal partners, including distantly related dinoflagellates (*Heterocapsa* sp., *Pelagodinium* sp., *Azadinium* sp. and *Scrippsiella* sp.) as well as a haptophyte (*Chrysochromulina* sp.), were detected based on ribosomal gene sequencing. This original association where multiple microalgal partners can be present within the same host cell simultaneously raises questions about the specificity and functioning of the relationship. **See also**: **Endosymbionts**; **Protozoan Symbioses**; **Algal Symbioses**

In addition to mutualistic symbioses, some parasitic interactions have also been identified. The dinoflagellates *Amoebophrya* and *Oodinium* have been described as parasites of Acantharia in the Mediterranean Sea (Cachon and Cachon, 1987), but no recent studies have investigated such interactions and their impact on the life cycle and ecology of Acantharia. **See also**: **Parasitism: The Variety of Parasites**

Reproduction and life cycle

Knowledge of the life cycle of uncultivable protists such as Acantharia remains very limited. It is not clear whether asexual reproduction really exists in Acantharia, although it has been reported in one family of Holacanthida (Acanthochiasmidae; Schewiakoff, 1926). Processes associated with sexual reproduction have been more frequently observed and are known to occur through two distinct mechanisms: (1) either directly from the adult or 'vegetative' stage (**Figure 5a–f**), (2) or after encystment of the cell (**Figure 5g, h**) (Hollande and Enjumet, 1957; Hollande *et al.*, 1965; Massera Bottazzi, 1973). In both cases, the cell undergoes gametogenesis where multiple nuclear divisions occur within the nuclear envelope, and each nucleus becomes an individual biflagellated 'swarmer' of less than 5 μm in size (**Figure 5i**; Schewiakoff, 1926; Decelle *et al.*, 2012b). At maturity, when the endoplasm turns whitish, thousands of these swimming swarmers are released to the environment from the vegetative cell, or through pores or upon rupture of the cyst wall (**Figure 5a–f**). These swarmers likely correspond to sexual gametes although neither the ploidy nor a putative fusion has ever been demonstrated. Cyst-forming acantharians essentially belong to the early diverging clades A, B and C (Holacanthida and Chaunacanthida) that do not exhibit robust fusion of the spicules (**Figure 4a, b**). By contrast, direct gametogenesis from the vegetative stage generally occurs in other clades of Arthracanthida and Symphiacanthida that have a rigid skeleton due to tightly joined spicules (**Figure 4d–f**; Febvre *et al.*, 2000; Decelle *et al.*, 2013). These acantharians that are in symbiosis with the microalga *Phaeocystis* digest and/or release their symbionts just before gametogenesis, and their swarmers lack symbionts (Decelle *et al.*, 2012b). This leads to an obligate *de novo* acquisition of new symbionts from the environment during the early life stages (i.e. horizontal transmission).

During encystment, the acantharian cell drastically changes its morphology: spicules of the skeleton are generally released or broken, the main cellular components (e.g. myonemes, axopods and ectoplasm) resorbed, and adjacent plaques are secreted and joined to one another, forming a large and robust seed-like cyst
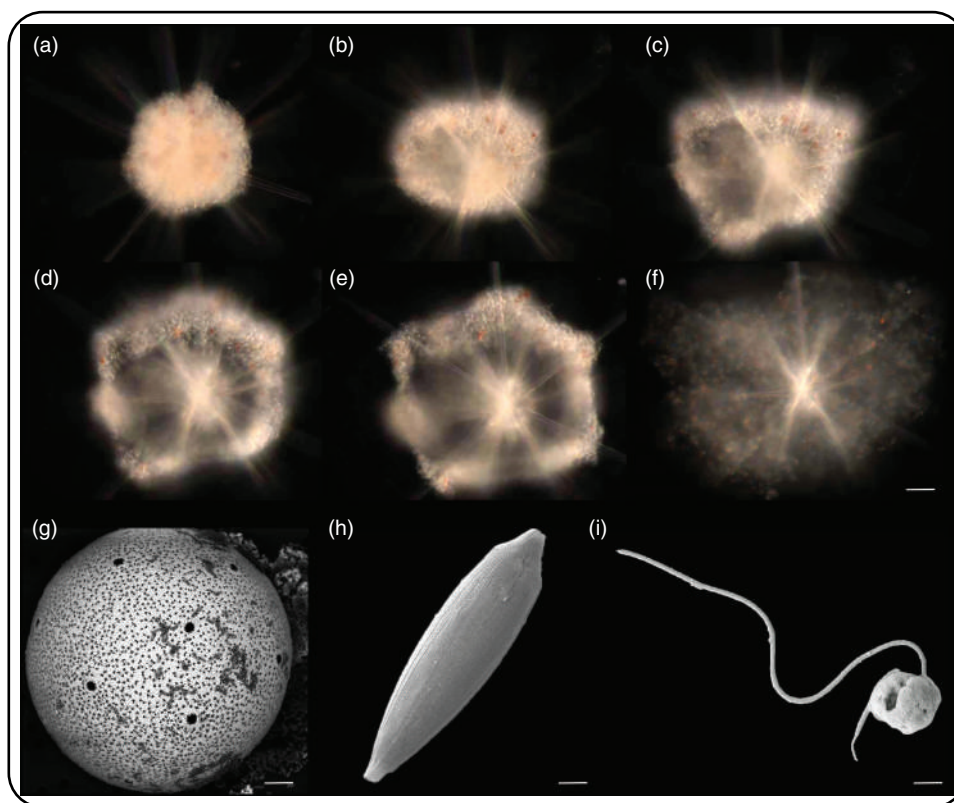
Figure 5 Reproduction in Acantharia occurs either directly from the adult stage (a–f), or after encystment of the cell (g, h). (a–f) Light microscopy images showing a time lapse of an acantharian cell at the end of a gametogenesis when thousands of swarmers produced within the endoplasm are released in the environment within few minutes; scale bar = 20 μm. (g) Round and (f) elongated acantharian cysts photographed by scanning electron microscopy; scale bars = 20 and 100 μm, respectively. (i) Scanning electron microscopy photograph of an acantharian swarmer with its two flagella; scale bar = 1 μm.

of up to 1 mm in size (**Figure 5g, h**). Depending on the families and species, cysts exhibit a large variety of shapes and forms: oval, round, elongated, with or without mineral plates and pores (Spindler and Beyer, 1990; Bernstein *et al*., 1999; Decelle *et al*., 2013). Encystment is not considered to be a dormancy strategy to face unfavourable environmental conditions as often usually observed in other marine protists (Von Dassow and Montresor, 2011), but is rather part of the reproductive process of Acantharia (Schewiakoff, 1926; Hollande *et al*., 1965; Massera Bottazzi, 1973). Strontium sulfate is the densest known oceanic biomineral ($SrSO_4$ density = 3.96 g cm^{-3}), twice as dense as calcium carbonate. The ballasted cyst therefore sinks rapidly at a speed that can reach 200–500 m per day, and presumably releases swarmers at depth in the mesopelagic and bathypelagic zones (Antia *et al.*, 1993; Martin *et al.*, 2010; Decelle *et al.*, 2013). Corroborating this hypothesis, a study in the Atlantic Ocean found that the highest abundance of juveniles was between 500 and 900 m depth (Massera Bottazzi and Andreoli, 1982). Collected by plankton nets and sediment traps, cysts were observed in different oceanic regions worldwide (e.g. Weddel and Mediterranean Seas, Iceland Basin, Atlantic and Indian Oceans) down to 2000 m at densities up to 32 cysts m^{-3}. Cyst sedimentation tends to show a temporal pattern in regions with high seasonality, particularly preceding phytoplankton blooms (Massera Bottazzi, 1973; Spindler and Beyer, 1990; Martin *et al*., 2010; Decelle *et al*., 2013). It has been hypothesised that releasing swarmers in deep layers of the water column could allow swarmers and juveniles to escape predation and access higher nutrient and organic matter concentrations (Martin *et al*., 2010). **See also**: **Protozoan Cysts and Spores**

Ecology and Biogeography

Abundance and distribution in the oceans

In surface oceanic waters, Acantharia are ubiquitous and typically outnumber their rhizarian counterparts, such as Foraminifera, Spumellaria and Nassellaria (Swanberg and Caron, 1991; Michaels *et al*., 1995). Their abundance varies between 3 and 40 cells per liter and tends to increase in oligotrophic waters from equatorial to subtropical latitudes (Massera Bottazzi and Andreoli, 1982). Most acantharians are concentrated near the surface, particularly during calm and sunny periods, and their number rapidly declines below 20–50 m (Michaels, 1988). Acantharian cells are fragile, and measured densities can vary

depending on the sampling method. Plankton net tows typically underestimate acantharian cell abundance by an order of magnitude compared to more gentle methods, such as Niskin bottles and scuba divers (Michaels, 1988). Although very little information is available in the literature, contrasted patterns of seasonality of Acantharia in surface waters have been reported between different oceanic regions. In the Atlantic Ocean at tropical and subtropical latitudes, acantharian cells tend to be more abundant during winter and spring, whereas in the Mediterranean Sea and the North Pacific Ocean, highest abundances occur during the summer and fall (Massera Bottazzi and Andreoli, 1982; Michaels, 1991). At certain periods of the year, Acantharia can form 'blooms', reaching densities up to 500 000 individuals m^{-2} at the subsurface (Massera Bottazzi and Andreoli, 1981; and personal observations in spring in the Gulf of Naples, Mediterranean Sea). These blooms are mainly formed by acantharians from Arthracanthida and Symphiacanthida (clades E and F) that live in photosymbiosis with the microalga *Phaeocystis* and typically represent 80% of the total acantharian biomass at the surface (Stoecker *et al.*, 1996). This ecological success is very likely due to their mixotrophic capacity, enhancing nutrient acquisition in an otherwise oligotrophic environment. Acantharia–*Phaeocystis* symbiosis is not only found in low-nutrient pelagic waters but also in coastal and productive areas, such as the English Channel and the Southern Ocean (Decelle *et al.*, 2012b). During iron fertilisation experiments in the Southern Ocean, the relative contribution of acantharians to protozooplankton (heterotrophic protist) biomass doubled from 22% to 44% inside the iron patch, outcompeting ciliates and dinoflagellates (Assmy *et al.*, 2014).

Acantharian adult cells, more particularly species affiliated to Holacanthida and Chaunacanthida that do not establish a symbiosis with photosynthetic partners, have been found hundreds and even thousands of meters deep in the water column, generally harbouring large lipid reserves and numerous food vacuoles (Schewiakoff, 1926; Bernstein *et al.*, 1987; Antia *et al.*, 1993). Environmental molecular surveys (i.e. metabarcoding and clone library studies) that sequenced the 18S rRNA gene also found numerous acantharian sequences at depth (e.g. 1000, 2000 and 3000 m; Countway *et al.*, 2007; Gilg *et al.*, 2009; Not *et al.*, 2007). Corroborating past microscopy observations, most of these ribosomal sequences not only belong to clades A (Holacanthida) and C (Chaunacanthida) but also to the morphologically uncharacterised clades I and III (**Figure 1**; Decelle *et al.*, 2012a, 2013). The vertical distribution of Acantharia can also vary depending on the hour of the day. At the surface, adult and juveniles tend to be more numerous during the day than at night, and this is the opposite in deep layers (e.g. 300–400 m; Massera Bottazzi and Andreoli, 1982). **See also**: **Protozoan Ecology**

Biogeochemical impact

The relatively high abundance, mixotrophic behaviour and original life cycle of Acantharia make them key components of pelagic ecosystems. With their microtubule-stiffened axopods that can capture a large diversity of prey, from bacteria to metazoans, Acantharia act as grazers within marine food webs. In addition, symbiotic acantharians can account for up to 20% of the total primary production through photosynthesis of their symbiotic microalgae in oligotrophic surface waters, and up to 41% during bloom-like events of acantharian hosts (Michaels, 1988, 1991). Overall, they significantly contribute to biogeochemical cycles of carbon, strontium and barium in the oceans, mainly through cyst formation that creates a significant vertical flux of these elements to the mesopelagic and bathypelagic zones (Bernstein *et al.*, 1987, 1992; Antia *et al.*, 1993; Michaels *et al.*, 1995; Martin *et al.*, 2010). For instance, during a 2-week sampling period in the Iceland Basin, acantharian cysts contributed up to 48% and 59% of the particulate organic carbon and nitrogen flux, respectively, into the bathypelagic zone (Martin *et al.*, 2010). By precipitating celestite and barium for building their skeletons and cysts, Acantharia can reduce strontium concentrations by up to 5% and significantly affect barium concentrations in surface waters (Bernstein *et al.*, 1992; De Villiers, 1999; De Deckker, 2004).

Acknowledgements

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