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Research paper

Molecular phylogeny of Elphidiidae (foraminifera)

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ABSTRACT

The Elphidiidae represent one of the most abundant and diversified foraminiferal family in shallow water habitats worldwide. Playing crucial roles in diverse ecosystems, they occur since the Eocene to present and are widely used for paleoenvironmental reconstructions. However, the lack of a clear taxonomic consensus led to a vast confusion concerning the relation of Elphidiidae with other rotaliids, in particular Nonionidae (*Haynesina*) and Rotaliidae (*Ammonia*). Moreover, high morphological plasticity of the test prevented the establishment of a clear definition for many species and genera of this family. Here, 66 new sequences of the SSU rRNA gene were obtained and used to build an extensive dataset including 94 complete or partial sequences of the SSU rDNA of 17 different morphospecies of Elphidiidae, *Haynesina* and *Ammonia*. Phylogenetic analyses of this dataset allowed identifying six strongly supported clades. Comparison of these molecular clades with the morphological characters of the analyzed individuals showed major discrepancies with the current taxonomic system. The relations between the six clades depended on the selection of the outgroup to the Elphidiidae. For biological and morphological reasons, we privileged here the choice of *Ammonia*, prompting the inclusion of *Haynesina* to the family Elphidiidae. However, this does not necessarily imply a monophyletic origin of all these taxa. In fact, we cannot exclude that Elphidiidae as they are defined here are paraphyletic and that *Ammonia* as well as some other rotaliids are branching within them.

1. Introduction

Members of the family Elphidiidae (Galloway, 1933) represent one of the most important component of recent benthic foraminiferal assemblages in inner shelf environments worldwide (Murray, 1991a). Mostly grazing on diatom microalgae (Lee, 1980), many elphidiids have the capacity to retain chloroplasts from their algal preys (kleptoplastidy) and perform photosynthesis (Lopez, 1979; Cedhagen, 1991; Pillet et al., 2011). Consequently, they mainly live in the photic zone, where they can be remarkably abundant. Depending on the season and food availability, they can be found at densities reaching up to several hundred individuals per square centimeter (Murray, 1991b).

Taxonomic classification of elphidiids is notoriously complex for several reasons. First, the group is extraordinarily species rich, with more than 120 morphospecies and subspecies (Hayward and Gross, 2012) only for the genus *Elphidium* (de Montfort, 1808). Distinction between *Elphidium* and close relative genera is sometimes questionable (Haynes, 1973) and, consequently, taxonomic descriptions of the same morphospecies by different authors are often inconsistent. Furthermore, important morphological variation can be observed among different individuals of the same species, depending on physico-chemical environmental parameters (Poag, 1978; Miller et al., 1982). The presence of these morphological variants, referred to as 'ecophenotypes', represents an additional difficulty to correctly set the limits between different morphospecies. Considering that members of genus *Elphidium* and relative genera have been described for more than 250 years by geographically isolated authors, it is not surprising that the taxonomy of the group is extremely confusing. At least 17 synonyms of *Elphidium* are recognized at generic level (Loeblich and Tappan, 1988) and most morphospecies belonging today to that genus were assigned once or several times to different genera.

The evolutionary history of the family Elphidiidae is closely related to that of the family Nonionidae (Schultze, 1854). Earliest fossils of genus *Nonion* are found in Jurassic material, but the family became abundant and divers only in the Eocene (Cushman, 1939). The genus *Elphidium* hypothetically derived from the morphologically similar genus *Nonion* in the early Eocene, where the first fossils are found (Cushman, 1939). Most of early *Elphidium* species, from Eocene to Oligocene, show a rudimentary development of the morphological key characters that are specific to Elphidiidae. In fact, septal bridges and sutural openings were developed progressively and therefore *Elphidium* represents a good fossil index for the Tertiary period (Cushman, 1939).

The main morphological characters that are used to describe Elphidiidae are summarized in Table 1 and Supplementary Fig. S1. Because of some morphological similarities, members of the genus *Elphidium* were originally placed within the family Nonionidae (Schultze, 1854). In 1933, Galloway suggested to split the family

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Table 1
Summary of the morphological characters for each molecular clade of elphidiids and relatives.

	Clade A	Clade B	Clade C	Clade D[a]		Clade E	Clade F
				Elphidium asklundi	*Haynesina nivea*		
Chamber arrangement	Involute	Involute	Involute or slightly evolute	Involute	Involute	Involute or slightly evolute	Involute
Shape (cross section)	Strongly compressed to convex	Convex (lenticular)	Strongly compressed to convex	Slightly compressed	Moderately compressed	Moderately to strongly compressed	Moderately compressed
Peripheral outline	Circular to slightly lobate	circular	Circular to slightly lobate	Lobate	Slightly lobate	Slightly lobate	Slightly lobate
Peripheral angle	Rounded to acute	Acute	Rounded to subacute	Broadly rounded	Rounded	Broadly rounded to rounded	Rounded
Keel	+[b]	+	−	−	−	−	−
Chambers	Slightly inflated	Flat	Slightly inflated or almost flat	Inflated	Inflated	Slightly inflated	Slightly inflated or inflated
Umbilical area	Slightly depressed to convex	Convex	Depressed	Slightly depressed	Depressed	Depressed or slightly depressed	Depressed to almost flat
Intraseptal interlocular spaces[c]	Long, deep	(Intraseptal channels)	Moderate length, shallow to moderate depth	Long, deep	Short to moderate length, shallow	Long, variable depth	Moderate length to long, variable depth
Septal bridges	+	−	−	+	−	+	+
Primary apertures	Multiple interio-marginal	Multiple interio-marginal, irregular slits	Single or multiple (rarely) interio-marginal, slit-like	Multiple interio-marginal, subcircular	Multiple interio-marginal, slit-like or subcircular, peristomal rims present	Single or multiple interio-marginal, slit-like	Multiple interio-marginal, peristomal rims present
Areal supplementary apertures	+/−	−	−	−	−	+/−	−
Ornamentation							
Umbilical area	Moderate to high	−	Poor	High	Moderate	High	Moderate
Margins	High	Intraseptal canal vents	Moderate	High	Poor	High	Moderate to high
Apertural region	High	High	Moderate	Moderate	Poor to moderate	High	Moderate

[a] As morphology highly differs between members of clade D, this molecular clade was separated into two sub-clades.
[b] With the exception of *Elphidium williamsoni*, which has no keel.
[c] Only intraseptal interlocular spaces between 2 and 3 youngest chambers are considered, as older ones undergo infilling by secondary calcite and their length is reduced. The depth measure refers to the proximal (umbilical) part of intraseptal interlocular space only.