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Molecular phylogenetic investigations of the relationships of the echinoderm-parasite family Eulimidae within Hypsogastropoda (Mollusca)

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ABSTRACT

The gastropod family Eulimidae has attracted considerable attention as one of the most diverse groups of parasitic molluscs in terms of number of species and ranges of body plans and parasitic strategies. However, the phylogenetic position of the family has not been established within the Hypsogastropoda and this has hampered the inference of ancestral states in the evolution of the morphology and parasitic strategies. Here we present Bayesian and maximum likelihood phylograms of Hypsogastropoda based on nuclear and mitochondrial loci (18S and 28S rRNA, Histone H3, COI and 16S rRNA) and a better taxonomic sampling than in previous molecular analyses, to determine the position of Eulimidae. The resulting trees suggest Vanikoridae as the sister group of Eulimidae; the two families are collectively placed in the newly redefined superfamily Vanikoroidea, with Truncatelloidea and (potentially paraphyletic) Rissooidea as closest relatives. Vanikorids are protandrous hermaphrodites as are many eulimids and are essentially carnivorous, differing from the mostly gonochoristic and herbivorous/detritivorous Truncatelloidea and Rissooidea. The mode of feeding may have a phylogenetic signal also within Eulimidae, where radula-less species constitute a robust clade. Other new findings include a close affinity of the submarine-cave Pickworthiidae to Cerithioidea and a terminal position of Nystiellidae within the paraphyletic Epitoniidae.

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1. Introduction

1.1. Evolution of parasitism in gastropods

Parasitism has been acquired more than 60 times in the animal kingdom and several parasitic lineages have achieved great diversification over time (Poulin and Morand, 2000; Summers et al., 2003). The class Gastropoda (Mollusca) is one of the most successful animal lineages as parasites and has acquired parasitism at least eight times, fewer only than the numbers in two arthropod classes, Copepoda and Malacostraca (Poulin and Morand, 2000). Parasitic gastropods have been successful also in terms of host diversity, while each lineage of the parasites has a relatively restricted selection of hosts: Eulimidae on echinoderms, Pyramidellidae on molluscs and polychaetes, Epitoniidae, Coralliophilinae and Pediculariinae on anthozoans (Warén, 1984). Utilization of

diverse hosts enables niche differentiation and diversification of parasites (Eichler's rule; see Vas et al., 2012). Indeed, the Eulimidae and Pyramidellidae are among the "Big Five" families of Gastropoda and each occupies approximately 5% diversity of the phylum Mollusca in tropical coastal environments (Bouchet et al., 2002). The two families therefore comprise many thousands of species among the estimated 200,000 living species of molluscs (Ponder and Lindberg, 2008). The multiple acquisitions of parasitism have greatly contributed to the overall diversity of the phylum.

With the great impact on the global evolution of animals and plants, the origins of parasitic lineages and their evolutionary histories of ecological and morphological traits have attracted much attention from phylogenetic systematists (e.g. Whitefield, 1998; Herlyn et al., 2003; Littlewood, 2006). However, while the phylogenetic position of the parasites among non-parasitic taxa is not necessarily well understood, such knowledge is essential for the inference of the ancestral states and evolutionary transition in the parasitic lineage. Among the parasitic groups of Gastropoda, phylogenetic position has been investigated for the Coralliophilinae (Barco et al., 2010), Pediculariinae (Meyer, 2003, 2004; Schiaparelli et al., 2005) and Pyramidellidae (Dinapoli and

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Klussmann-Kolb, 2010; Jörger et al., 2010; Dayrat et al., 2011; Dinapoli et al., 2011). These studies have provided interesting insights that parasitic snails often constitute a clade with carnivorous taxa, which might represent the prerequisite condition for parasitism. Coralliophilinae is one of the terminal subfamilies of the large carnivorous family Muricidae (Barco et al., 2010). This family also includes *Vitularia*, which parasitizes molluscan hosts (Herbert et al., 2009) and represents either the sister clade of Coralliophilinae or another terminal lineage among carnivorous genera (Barco et al., 2010). Pediculariinae belongs to the monophyletic, otherwise carnivorous Ovulidae (Schiapparelli et al., 2005), whose putative sister taxa also comprise predators on sponges and tunicates (Cypraeidae, Velutinidae and Triviidae; Wilson, 1998a,b). Pyramidellidae represents a possible sister clade of Glacidorbidae (Dinapoli and Klussmann-Kolb, 2010; Dinapoli et al., 2011) or Amphiboloidea (Jörger et al., 2010) or Lymnaeioidea (Dayrat et al., 2011). The species of Glacidorbidae feed on the tissue of wounded invertebrates (Ponder, 1986). On the other hand, amphiboloids and lymnaeoids are deposit feeders and omnivores strongly oriented to animal food, respectively (Bovbjerg, 1968; Roach and Lim, 2000).

1.2. Eulimidae and its phylogenetic position

The family Eulimidae represents one of the most diverse groups of parasitic molluscs in terms of not only the number of extant species but also the existence of the widest range of parasitic strategies. These parasites exhibit a large variety of parasitic modes (e.g. endoparasitism, ectoparasitism and gall forming), sexual strategies (hermaphroditic, gonochoristic and environmental sex determination) and shell shapes (slender, conical, globose and capuliform; Warén, 1984). The Eulimidae are exclusive parasites of echinoderm hosts including all five classes, i.e. Echinozoa, Holothurozoa, Asterozoa, Ophiurozoa and Crinozoa (Warén, 1984), while the Late Cretaceous origin of this gastropod family clearly post-dates the Paleozoic divergence of the echinoderm clades (Neumann and Wisshak, 2009).

The phylogenetic position of the family has not been established within the Gastropoda. Eulimids had been placed in Ptenoglossa, which originally included a number of families that share a comb-like or “ptenoglossate” radula (Gray, 1853). Ptenoglossa was later confined to Eulimoidea, Epitonioidea and Triphoroidea based on the common presence of an acrembolic proboscis and two pairs of salivary glands in the three superfamilies (see Ponder et al., 2008). However, this group was found to be paraphyletic or polyphyletic in a cladistic analysis using morphological characters (Ponder and Lindberg, 1997) and therefore treated as an informal group in the working classification by Bouchet and Rocroi (2005). In particular, eulimids differ from other ptenoglossans in lacking the distinctive parasperm (Healy, 1988). Molecular phylogenetic studies also support the polyphyly of the Ptenoglossa among the Hypsogastropoda (Colgan et al., 2000, 2007; Churchill et al., 2011a; Criscione and Ponder, 2013).

Hypsogastropoda represents the largest clade among the superorder Caenogastropoda with Cerithioidea as a possible sister taxon and consists of three provisional subgroups, i.e. Littorinimorpha, Neogastropoda and Ptenoglossa (Ponder and Lindberg, 1997; Bouchet and Rocroi, 2005; Ponder et al., 2008). Of these, Neogastropoda constitutes a robust clade (Ponder and Lindberg, 1997; Zou et al., 2011) that is only remotely related to eulimids (Colgan et al., 2007). Previous phylogenetic studies have identified the Rissoinidae of the Littorinimorpha as the sister clade of Eulimidae (Colgan et al., 2007; Churchill et al., 2011a; Criscione and Ponder, 2013). However, this relationship remains inconclusive due to insufficient taxon sampling. Littorinimorpha and Ptenoglossa comprise a total of 65 families in 18 superfamilies (Bouchet and Rocroi,

2005), only less than half of which were included in those phylogenies, and the closest relative of Eulimidae may be found among other neglected taxa. Also the microalgal and bacterial feeding of rissoinids (Ponder and de Keyser, 1998) is at variance with the generally suggested position of parasitic lineages among carnivorous relatives.

In this study, 58 species from 38 hypsogastropod families were analyzed along with five outgroup species from Cerithioidea, with a special emphasis on littorinimorph and ptenoglossan taxa. Our goals are to determine the phylogenetic position of Eulimidae and to verify the monophyletic nature of the family in order to unravel the ancestral states from which parasitic life has derived.

2. Materials and methods

2.1. Taxonomic sampling

Fifty-two littorinimorph and ptenoglossan species belonging to 32 families were collected and selected for the present molecular analysis to increase the total phylogenetic diversity of operational taxonomic units (OTUs; Table 1). Special emphasis was placed on Rissooidea and Truncatelloidea, which have been identified as possible close relatives of Eulimidae in previous studies (Colgan et al., 2007; Criscione and Ponder, 2013). Also included in the analysis was the type species of *Aclis* in the family Aclididae. Bouchet and Rocroi (2005) remarked that the Aclididae share certain morphological conditions with the Eulimidae and classified the two families as the exclusive members of Eulimoidea. However, a molecular phylogeny transferred the family to the superorder Heterobranchia based on sequences from *Larochella*, but not from the type genus *Aclis* (Dinapoli and Klussmann-Kolb, 2010; see also Warén, 2013). Nine eulimid species were also included in our phylogenetic reconstruction to cover the widest ranges of morphology and host diversity of the family as possible (Table 2). Most live snails were boiled in 70–90 °C water for 0.1–1 min and the animals were extracted from the shells and preserved in pure ethanol. Voucher material has been deposited at Atmosphere and Ocean Research Institute, The University of Tokyo, unless otherwise noted in Table 1. All shell, operculum, radula and cephalic part of the animal were kept undamaged in most specimens for future taxonomic studies. Photographs of shells are available from the authors on request.

For outgroup comparisons, published cerithioid sequences were retrieved from the DDBJ/EMBL/Genbank (e.g. Zou et al., 2011), along with other sequences from five littorinimorph and one neogastropod species (e.g. Kameda and Kato, 2011). Neogastropoda was also represented by new sequences of *Chauvetia tenuisculpta* (Buccinidae), which is plausibly a parasite on echinoderms (Oliver and Rolan, 2008; Wirtz, 2011).

2.2. DNA extraction, PCR amplification and sequencing

Total DNA was extracted from the foot tissue using DNeasy Blood and Tissue Kit (Qiagen) and purified by GeneReleaser (Bioventures) following the manufacturer's recommendations. Portions of the mitochondrial and nuclear genes were amplified using the primer sets LCO1490-HCO2198 (for mitochondrial cytochrome c oxidase subunit 1, COI), 16SarL-16SbrH (16S rRNA), LSU5-LSU1600R and 1100F-na2 (nuclear 28S rRNA), 18A1-1800r (18S rRNA) and H3MF-H3MR (Histone H3; Table 3). PCR reactions were conducted in a total volume ca. 25 µl: 17.5 µl DDW, 0.13 µl TaKaRa Ex Taq Hot Start Version (TaKaRa Bio Inc.), 2.5 µl Ex Taq Buffer (10×), 2.0 µl dNTP mixture (2.5 mM each), 0.3 µl forward and reverse primers (20 µM each) and 2.5 µl genomic DNA. After an initial denaturation for 2 min at 94 °C, the reaction solution was run for 35 cycles with the following parameters: denaturation for

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