学位論文　（要約）

Evolution of parasitic strategies and morphological diversification in eulimid and pyramidellid gastropods

（ハナゴウナ科およびトウガタガイ科腹足類における寄生戦略の進化と形態多様化）

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Abstract

Parasitism is one of the commonest and most successful modes of life on Earth. Parasites have played a significant role in the evolution of other, non-parasitic organisms and hence contributed to the overall biodiversity. Furthermore, they can alter the physiology and behavior of the hosts that have a significant role in systems, which in turn modifies community structure. Illuminating current status and evolutionary transitions of host-parasite interaction is therefore crucial to understand the origin and maintenance mechanisms of biodiversity. Diversification processes of parasites have indeed been investigated using molecular methods for various lineages in several phyla including Arthropoda, Nematoda, Platyhelminthes and Acanthocephala. However, quite little is known about the timing of their ecological transitions, morphological evolution and species diversification, making it difficult to reveal a more complete picture of parasite evolution. This scarcity of knowledge is attributable to the extremely rare fossil record for small and soft-bodied parasites.

The class Gastropoda offers an unmatched advantage for studying the evolution of parasites with its abundant fossil record. Among parasitic gastropods, the Eulimidae and Pyramidellidae have achieved significant diversification during their Cenozoic radiation that resulted in thousands of extant species in each family. Interestingly, ecological and morphological traits are quite different between the two groups. Eulimids are exclusive parasites of echinoderms and exhibit rich varieties of parasitic strategies (temporary, ecto- and endoparasitism) and shell shapes (slender, globose and capuliform). Pyramidellids in contrast parasitize on annelids and other mollusks, mostly as temporary parasites with rather uniformly high-spired shells. Despite being such fascinating targets for studies on parasite evolution, their ingroup relationships have been poorly understood due to the lack of comprehensive molecular phylogenies. Here in this dissertation, the evolutionary histories and diversification

patterns are first illuminated and compared between these two largest families of parasites in Gastropoda.

The relationships of the Eulimidae among non-parasitic taxa are not well understood, while such knowledge is essential for the inference of the ancestral states and evolutionary transition in a parasitic lineage. In the Chapter 1 of this thesis, Bayesian and maximum likelihood phylograms are reconstructed to explore the phylogenetic position of Eulimidae within its parent taxon Hypsogastropoda, based on the nucleotide sequences of five genes (nuclear 18S/28S rRNA and Histone H3 and mitochondrial 16S rRNA and COI) from 58 species in 38 hypsogastropod families and from five cerithioideans as the outgroup. The phylogenetic trees suggest Vanikoridae as the sister group of Eulimidae; the two families are collectively placed in the newly redefined superfamily Vanikoroidea, with Truncatelloidea and Rissooidea as its closest relatives. Vanikorids are protandrous hermaphrodites as are many eulimids and are essentially carnivorous, differing from the mostly gonochoristic and herbivorous or detritivorous Truncatelloidea and Rissooidea. The parasitic lifestyle in the Eulimidae was probably derived from carnivorous mode of feeding as in the case of many other parasitic organisms.

The internal phylogeny of the Eulimidae and their evolutionary consequences are examined in the Chapter 2 by molecular phylogenetic reconstruction and morphometric analysis of shells. Phylogenetic trees are inferred from six-gene sequences (a total of 4.7 kb) from 101 eulimid species belonging to over 50 genera as well as three vanikorids for outgroup comparison. Reconstruction of ancestral character states and divergence time estimates based on the tree topology reveal that (1) eulimids exploiting each of the five echinoderm classes belong to two or three phyletic groups, (2) each of the teleoconch and radula has been lost more than once in the evolution of eulimids, and (3) globose to capuliform shells as well as endoparasitism have evolved independently and rapidly in several of the lineages. In addition, the principal component analysis based on seven measurements of eulimid shells reveals a strong correlation between shell morphology and parasitic strategy. These results indicate that the evolution of the Eulimidae involves the process of repeated adaptive radiation. Respective radiations have started from temporary parasitic ancestors bearing a slender shell and ended in permanent ectoparasites and endoparasites with globose to patelliform shells or without a shell. These radiations involving the adhesion and infiltration to the host of a particular echinoderm class thus have a strong deterministic component, as has shown in the replicated adaptive radiation by other organismal lineages on islands and in lakes. Fossil records suggest that the repeated radiation has occurred throughout the evolutionary history of Eulimidae, since well before and more frequently than it can be traced by the ancestral state reconstruction based on phylogenetic relationships among extant species and distribution of their ecological traits.

The Chapter 3 is devoted to illuminate evolutionary relationships and diversification process in the Pyramidellidae. A molecular phylogeny of the family is reconstructed based on six-gene sequences (5.1 kbp); also estimated are the ancestral conditions of the shell shapes and habitats. This phylogenetic analysis includes 59 pyramidellid species in more than 40 genera as well as 14 related taxa for comparison. The resulting trees reject the monophyly of the Pyramidellidae and all of its four subfamilies as currently defined based almost solely on shell morphology. Although many species of the family apparently exhibit low host specificity, which may decrease the diversity of accessible niches for colonization, they probably have achieved the great diversification through frequent shifts among different environments while often retaining dependence to a particular lineage of hosts, ranging from a single species to various taxa in a phylum. The reasons why pyramidelloids have not specialized to give rise endoparasites or why they have achieved a permanent ectoparasitic lifestyle only once are discussed in comparison with the repeated adaptive radiation of the Eulimidae.

Summing up, the diversification processes greatly differ in the two most speciose groups of parasitic gastropods, Eulimidae and Pyramidellidae: Recurrent specialization to the permanent parasitic lifestyle has enhanced the diversification in the former, while frequent habitat shifts among disjunct marine environments have contributed to the species richness of the latter. The present study on eulimid diversification provides perhaps the most complete and dynamic picture of parasite evolution in terms of the large number of parallel specialization events. This study also indicates that the fossil records of the Gastropoda can provide unmatched knowledge on the evolution of host-parasite interaction, particularly if a number of conchological characters are properly evaluated and only truly unique conditions are used to diagnose monophyletic groups. Further investigations on the evolutionary history of parasitic gastropod lineages, each of which exhibits different ecological and morphological conditions but unanimously benefits from the rich fossil record, would elucidate diversification of parasitic organisms in time and space.

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General Introduction

本章については、5年以内に雑誌などで刊行予定のため、非公開。

Chapter 1

Phylogenetic position of the Eulimdiae within Hypsogastropoda

1-1. Introduction

The class Gastropoda 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 & Morand, 2000). 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. Whitfild, 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 & 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 (Schiaparelli et al., 2005), whose putative sister taxa also comprise predators on sponges and tunicates (Cypraeidae, Velutinidae & Triviidae; Wilson, 1998a, 1998b).

Pyramidellidae represents a possible sister clade of Glacidorbidae (Dinapoli & Klussmann-Kolb, 2010; Dinapoli et al., 2011), Amphiboloidea (Jörger et al., 2010) or Lymnaeoidea (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 & Lim, 2000).

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. Echinoidea, Holothuroidea, Asteroidea, Ophiuroidea and Crinoidea (Warén, 1984), while the Late Cretaceous origin of this gastropod family clearly post-dates the Paleozoic divergence of the echinoderm clades (Neumann & 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 & Lindberg, 1997) and therefore treated as an informal group in the working classification by Bouchet & 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 & 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 & Lindberg, 1997; Bouchet & Rocroi 2005; Ponder et al., 2008). Of these, Neogastropoda constitutes a robust clade (Ponder & 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 & 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 & 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 & de Keyzer, 1998a) 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.

1-2. Materials and Methods

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 1-1). 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 & Ponder, 2013). Also included in the analysis was the type species of *Aclis* in the family Aclididae. Bouchet & 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 & 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 1-2). Most live snails were boiled in 70–90 ºC 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 1-1. All shell, operculum, radula and cephalic part of the animal were kept undamaged in most specimens for future taxonomic studies.

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 (Kameda & Kato, 2011). Neogastropoda was also represented by new sequences of *Chauvetia tenuisculpta* (Buccinidae), which is plausibly a parasite on echinoderms (Oliver & Rolan, 2008; Wirtz, 2011).

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; see Appendix 1). 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 (10x), 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 ºC, the reaction solution was run for 35 cycles with the following parameters: denaturation for 30 sec at 94 ºC, annealing for 40 sec at 50 ºC and extension for 60 sec at 72 ºC, followed by the final extension at 72 °C for 4 min; an annealing temperature at 42 ºC was used instead for the COI amplification. If amplification was unsuccessful under these conditions, either or both of the primers were replaced by others listed in Table S1-1. Amplicons were purified by ExoSAP-IT (Affymetrix) following the described protocol. Purified PCR products were sequenced with the amplification and/or internal primers; sequencing reactions were prepared using a Big Dye Terminator Cycle Sequence Kit ver. 3.1 (Applied Biosystems) following the manufacturer's protocol. The reaction mixtures were analyzed on an ABI PRISM 3130xl sequencer after purification with a Big Dye XTerminator Purification Kit (Applied Biosystems).

Phylogenetic analyses

I generated two datasets based on different combinations of genes and OTUs. The first dataset comprised partial sequences of the 28S (spanning domains D1–D5; see Michot et al., 1984) and COI genes representing 60 species and 40 families from the whole Hypsogastropoda and its outgroup taxa. The second, five-gene dataset was made to reconstruct a more detailed phylogeny for Eulimidae and its related taxa, which were illustrated by the two-gene analyses. This dataset consisted of longer 28S fragments (D1–D7b), entire 18S and partial H3, COI and 16S sequences from 30 species and 15 families. For each dataset, the sequences of the three rRNA and one coding (COI) genes were aligned individually by ProAlign 0.5 alpha 1 (Löytynoja & Milinkovitch, 2003) with the band-width set to 1,200; the COI fragments were aligned as deduced amino acid sequences. The H3 sequences had no indels and were aligned by eye in MEGA 5 (Tamura et al., 2011). Each aligned dataset was masked to remove alignment ambiguous sites by ProAlign and Gblocks 0.91b (Castresana, 2000), resulting in four alignments (2gPA, 2gGB, 5gPA and 5gGB). For the 2gPA and 5gPA alignments, regions with posterior probabilities below 50% in the ProAlign analyses were excluded in the succeeding phylogenetic reconstruction. The 2gGB and 5gGB alignments were masked with the default parameters of Gblocks except that the "Minimum number of sequences for a conserved position" was set to 60% of OTUs, "Minimum number of sequences for a flank position" to 80% of OTUs and "Allowed gap positions" to "With half."

Phylogenetic trees were reconstructed from the four alignments using the Bayesian inference and Maximum Likelihood (ML) methods. In the Bayesian analyses performed with MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003), the general time-reversible model was used for all the datasets with invariant site frequency and gamma-shaped parameters estimated from the data (GTR + Γ + I), which was selected as the best-fit model by the Akaike information criterion in MEGA 5. The shape, proportion of invariant sites, state frequency and substitution rate parameters were estimated for each codon position separately in the amino acid coding COI and H3 genes. Each gene was allowed to have different parameters, hence the two-gene and five-gene alignments had four and nine partitions, respectively. Two parallel runs were made for 20,000,000 generations (with a sample frequency of 100), using the default value of four Markov chains. The first 100,000 trees for each run were discarded to make sure the four chains reached stationarity by referring to the average standard deviation of split frequencies (Ronquist & Huelsenbeck, 2003). The consensus tree and posterior probabilities (PP) were computed from the remaining 200,000 trees (100,000 trees, two runs). Posterior probabilities equal to or above 0.95 were considered meaningful support. The ML analyses were performed using the Pthreads version of RAxML v7.2.6 (Stamatakis, 2006) with the same partitions as the Bayesian analyses and the following commands: a rapid bootstrap analysis and search for the best-scoring ML tree in one single program run (-f a) and 1,000 bootstrap replicates (-# 1000) under the GTR + Γ + I substitution model (-m GTRGAMMAI). Bootstrap probabilities (BP) equal to or above 70% were considered meaningful support. Bayesian analyses were also performed for individual genes with 5,000,000 generations and burn-in value setting at 25,000 to compare evolutionary rates and to eliminate possible contamination and erroneous sequences. All trees were edited by FigTree v1.3.1 (http://tree.bio.ed.ac.uk/software/figtree/).

1-3. Results

Sequence data

The numbers of total, excluded, variable, and parsimony-informative sites are shown for the four alignments in Table 1-3. *Stenothyra thermaecola* and *Tubbreva* sp. were found to have extremely high evolutionary rates of the 28S gene and were therefore excluded from the multi-gene alignments; *Aclis minor* was also excluded due to difficulties in amplifying gene fragments except H3. The two-gene dataset had 2,235 sites, of which 309 and 382 were masked in the 2gPA and 2gGB alignments, respectively. The five-gene dataset had 5,616 sites and 610 and 646 were excluded in the respective 5gPA and 5gGB analyses. Gblocks tended to exclude more sites of 18S and 28S than ProAlign did, whereas the 16S alignments showed the opposite pattern. The proportion of variable sites varied from 9.6% in the 18S gene of the 5gGB alignment to 60.6% in the COI of the 2gGB alignment. Parsimony-informative sites varied from 4.8% in the 18S of the 5gGB to 50.2 % in the COI of the 2gPA (Table 1-3). There were two 3-bp deletions in the COI matrix at the positions 95–97 (*Vanikoro helicoidea*) and 296–298 (*Caecum globellum* and *Iravadia sakaguchii*).

Phylogenetic analyses of the combined datasets

Bayesian and likelihood analyses yielded the same results for all four alignments in terms of clades with meaningful support values. I therefore show only Bayesian trees with posterior probabilities and ML bootstrap values on branches (Figs. 1-1, 1-2).

The two-gene dataset recovered the Eulimidae as a robust monophyletic clade in the analyses of both 2gPA and 2gGB alignments (PP = 1.00, BP ≥ 98%; Fig. 1-1, see Appendix 1 for the 2gGB tree). The family consisted of two subclades, reflecting the presence or absence of the radula (1.00, ≥ 89%; Table 1-2). The monophyletic Vanikoridae (*Vanikoro* + *Macromphalus*: 1.00, 100%) constituted a well-supported clade with Eulimidae as the newly redefined superfamily Vanikoroidea (1.00, 100%). *Lyocyclus*, a genus previously assigned to Vanikoridae or its own family Lyocyclidae, was found to be distant from the type genus *Vanikoro* and formed a moderately supported clade with *Macrocypraea* (Cypraeidae) in the 2gGB analysis (0.96, < 50%). The previously suggested affinity of Hipponicidae to Vanikoridae (as a member of Vanikoroidea; e.g. Ponder & Warén 1988; Bouchet & Rocroi 2005) was clearly rejected in all analyses. The superfamily Rissooidea (Rissoidae, Rissoinidae and Barleeiidae) was paraphyletic to the Vanikoroidea albeit with insignificant support values (≤ 0.91, ≤ 68%). The two superfamilies constituted a robust clade with the Truncatelloidea (1.00, 89%). Twenty other suprageneric nodes received meaningful PP and BP values in both analyses: *Niso* + *Pyramidelloides* + *Hemiliostraca* (1.00, ≥ 95%), *Monogamus* + *Vitreolina* + *Stilifer* + *Thyca* (1.00, 100%), *Monogamus* + *Vitreolina* (≥ 0.97, ≥ 83%), *Stilifer* + *Thyca* (1.00, 100%), Rissoidae (1.00, 100%), *Benthonella* + *Lucidestea* (1.00, ≥ 90%), Rissoinidae (1.00, 100%), Rissoinidae + Barleeiidae (1.00, ≥ 92%), Truncatelloidea (1.00, 100%), *Assiminea* + *Truncatella* + *Cecina* + *Falsicingula* + *Potamopyrgus* + *Amphithalamus* (≥ 0.97, ≥ 71%), *Assiminea* + *Truncatella* + *Cecina* + *Falsicingula* (1.00, ≥ 99%), *Teniostoma* + *Iravadia* (≥ 0.99, ≥ 72%), Hipponicidae (1.00, 100%), Epitonioidea (1.00, ≥ 91%), Janthinidae + *Alexania* + *Epitonium* (1.00, 100%), Janthinidae + *Alexania* (≥ 0.95, ≥ 72%), Nystiellidae + *Opalia* (1.00, ≥ 96%), Pterotracheoidea (1.00, ≥ 87%), Neogastropoda (≥ 0.99, ≥ 78%), Cerithioidea + Pickworthiidae (1.00, ≥ 99%), *Pelycidion* + *Microliotia* (≥ 0.99, ≥ 75%). The Tornidae and Epitoniidae *sensu* Bouchet & Rocroi (2005) were recovered as non-monophyletic groups in our analyses. The monophyly of Cerithioidea + Pickworthiidae was confirmed by a separate two-gene analysis with *Campanile symbolicum* (Campaniloidea) and three heterobranch species as outgroup taxa (see Appendix 1).

The five-gene dataset recovered the relationships among and within the Vanikoroidea, Truncatelloidea and Rissooidea with higher posterior and bootstrap values (Figs. 1-2, see Appendix 1 for the 5gGB tree). The sister relationship between the redefined Vanikoroidea and Truncatelloidea was supported in both 5gGB (1.00, 64%) and 5gPA (0.95, 62%) analyses. The superfamily Rissooidea, here represented by Rissoidae and Rissoinidae, was supported in the Bayesian analysis of the 5gGB alignment (0.97; ML: < 50%) but not in the 5gPA analyses (0.88, < 50%). The relationships among eulimid genera in the 5gGB trees were not concordant with those recovered in the two-gene and 5gPA analyses: *Hemiaclis* was the basal-most offshoot of the family in the 5gGB analyses (1.00, 75%) while it constituted a clade with *Niso* + *Pyramidelloides* + *Hemiliostraca* with lower support indices in the 5gPA analyses (0.96, 68%). The two ophiuroid parasites included in the dataset formed a robust clade in both analyses (*Pyramidelloides* + *Hemiliostraca*; 1.00, ≥ 92%). On the other hand, the asteroid parasites *Stilifer* and *Thyca* were distantly related to *Niso*, another group exploiting sea stars (1.00, 100%).

Independent gene analyses

Most of the 13 Bayesian analyses for independent gene sequences resulted in poorly resolved trees (see Appendix 1), while the monophyly of the Eulimidae was unambiguously supported in 28S, COI and 16S trees (PP = 1.00). Other clades with meaningful posterior probabilities (≥ 0.95) include: all four eulimids without the radula (supported by 18S, 28S and COI), Vanikoridae (18S, 28S, H3 and 16S), Vanikoroidea (28S), Rissoidae (18S and 28S), Rissoinidae (18S, 28S and COI), Hipponicidae (28S and COI), Nystiellidae + *Opalia* (28S, H3 and 16S), Epitonioidea (18S and 28S). There were a few contradictory clades with meaningful support values in the independent gene trees, particularly between nuclear rRNA and mitochondrial COI topologies with regard to the positions of Vanikoridae, possibly reflecting excessive evolutionary rates of the latter gene and long-branch attraction.

The shorter fragments of the 28S gene (D1–D5) confirmed the truncatelloid affinity of *Stenothyra thermaecola* (PP = 1.00), while *Tubbreva* sp. of Cingulopsidae appeared in a large, basal polytomy (Appendix 1; see also Criscione & Ponder, 2013). The phylogenetic position of *Aclis minor*, the type of the family Aclididae, could not be resolved with the available H3 sequences. However, this H3 sequence showed the smallest uncorrected distances to *Schwartziella subulata* (5.2%) and *Macromphalus* sp.

(6.2%; Appendix 1), which suggests a position of the family among the Vanikoroidea, Rissooidea and Truncatelloidea, and corroborates with the classification by Fretter & Graham (1982), Bouchet & Rocroi (2005) and Warén (2013).

1-4. Discussion

Phylogenetic position and ancestral states of the Eulimidae

The most significant finding of the present study is the robust sister relationship of the Eulimidae and Vanikoridae (Figs. 1-1, 1-2) and we propose that the two families constitute a newly redefined Vanikoroidea Grey, 1840, which has nomenclatural precedence over Eulimoidea Philippi, 1853. Earlier molecular phylogenies that suggested that the closest relationship of Eulimidae is with Rissoinidae (Colgan et al., 2007; Churchill et al., 2011a; Criscione & Ponder, 2013) did not include vanikorids. The gastropod classification by Bouchet & Rocroi (2005) assigned Vanikoridae along with Hipponicidae and Haloceratidae into Vanikoroidea, and Eulimidae and Aclididae in Eulimoidea, based on shared, but plausibly symplesiomorphic, conditions of the early ontogeny and feeding ecology (see Ponder, 1998). The Hipponicidae and Vanikoridae have been analyzed in a molecular phylogeny that showed their distant relationship (Collin, 2003; see also Ponder et al., 2008), but again Eulimidae was not included.

The Vanikoridae are globose to conical, small- to medium-sized, non-parasitic snails living in shallow intertidal waters as well as at subtidal, shelf and bathyal depths (Warén & Bouchet, 1988; Ponder, 1998). There seems to be no clear synapomorphy among described conchological or anatomical conditions to support the monophyletic group comprising Eulimidae and Vanikoridae. However, limited anatomical information available for vanikorids has been obtained mainly from the large, possibly autapomorphic genus *Vanikoro* (e.g. Simone, 2002) and little is known for the various genera from deeper waters; one of the few shared anatomical features of the family is the presence of the epipodial flap on each side of the foot, which is lacking in Eulimidae (Warén & Bouchet, 1988).

Interestingly, the two families share some reproductive and ecological conditions. Most hypsogastropod species are dioecious (Heller, 1993), while many eulimids are sequential hermaphrodites (Warén, 1984; Bouchet & Warén, 1986) as are vanikorids (Ponder, 1998). In addition, Goto et al. (2011) have found a vanikorid, *Macromphalus tornatilis*, in the burrows of echiuran worms and suggested a certain association between them. Although the feeding ecology of the Vanikoridae has not been adequately studied, sponge spicules, foraminifers and diatoms have been found in the stomach contents of *Vanikoro cancellata* (Golding et al., 2009). Indeed, species of *Vanikoro* are almost always found attached on/near sponges on the underside of deep-buried coral rubble (Y. Kano, personal observation; Appendix 1), suggesting omnivorous or carnivorous feeding habits for the family. If this is the case, the common ancestor of Eulimidae and Vanikoridae might have depended on animal flesh for its nutrient requirement and differentiated from the detritivorous modes in the Rissooidea and Truncatelloidea, which represent possible sister clades of Vanikoroidea (Fig. 1-1). The parasitic mode of life in eulimids has therefore likely originated from a predatory ancestor as in the cases of some other gastropod (Schiaparelli et al., 2005; Barco et al., 2010).

Vanikoroidea potentially includes two other extant families, namely Aclididae and Haloceratidae. Aclidids are small animals imperfectly known both in morphology and way of life, because of their rarity and sublittoral habitats. The species of the type genus *Aclis* are almost certainly carnivores, which have an acrembolic proboscis and small ptenoglossan radula (Fretter & Graham, 1982). They most closely resemble the Eulimidae among the polyphyletic ptenoglossan families in that they share similar anatomical conditions and protoconch morphology, although the tumid teleoconch whorls and the lack of a penis differentiate the former from the latter (Fretter & Graham, 1982; Bouchet & Rocroi, 2005). The presence of a large epipodial fold on each side of the foot in *Aclis* (Bouchet and Warén, 1986; Gofas et al., 2011) and vanikorids (Warén & Bouchet, 1988; Ponder 1998) may further suggest the affinity of Aclididae to Vanikoroidea. The available specimen of the type species (*A. minor*) yielded only a H3 sequence that did not clearly show a phylogenetic position in the Bayesian analysis for this gene, while the comparison of genetic distances supported the vanikoroid affinity but not a relationship to the Epitoniidae, another possible candidate as the closest relative of Aclididae (Bouchet & Warén, 1986). A previous molecular phylogeny transferred Aclididae to the superorder Heterobranchia based on sequences from *Larochella* (Dinapoli & Klussmann-Kolb, 2010; see also Warén, 2013). However, so-called aclidids contain many polyphyletic genera with small and slender shells but with a fundamentally different anatomy, and *Larochella* actually belongs to an unrelated heterobranch family, Graphididae (Warén, 2013), or its possible senior synonym Tofanellidae (Gründel & Nützel, 2013). A future analysis with a better-preserved specimen of *A. minor* is needed to determine the precise phylogenetic position of Aclididae.

The deep-sea family Haloceratidae represents another rare and poorly studied group with an uncertain affinity in Hypsogastropoda. Warén & Bouchet (1991) noted in the description of the family that haloceratids are probably sedentary carnivorous animals with sequential hermaphroditism (see also Warén, 1993). These characteristics may suggest their close affinity to the Vanikoridae (Ponder 1998) as well as to the Eulimidae and the predatory mode of life as the ancestral condition for the latter family. Haloceratids are also similar to vanikorids in sharing a characteristic foot that is divided into two functionally different parts, although other morphological conditions instead suggest their affinity to either the Capulidae (Capuloidea) or the Laubierinidae (Tonnoidea; Warén & Bouchet 1991). The Haloceratidae may represent another important group in future phylogenies to shed light on the evolution of the parasitic mode of life in Vanikoroidea.

Convergent evolution and superficial resemblance to Vanikoroidea

The present study reveals that some taxa that have been included in Vanikoroidea or assigned close to or within Vanikoridae are distantly related and have independently acquired morphological resemblance. Simone (2002, 2011) showed that the Vanikoridae have certain similarities to the Hipponicidae, Calyptraeidae and Capulidae in conchological and anatomical characters. Of these, Hipponicidae has been considered a member of Vanikoroidea, while each of Calyptraeidae and Capulidae represents an independent superfamily in many of the current classifications (e.g. Bouchet & Rocroi, 2005). All four families have been included in a molecular phylogenetic analysis (Collin, 2003) that showed distant relationships among the Hipponicidae, Vanikoridae and Calyptraeidae + Capulidae. Based on the present and previous molecular phylogenies, Hipponicidae is provisionally transferred from Vanikoroidea to its own monotypic superfamily Hipponicoidea Troschel, 1861. Convergence is also apparent within the Vanikoridae. There are little-known genera from the deep sea, for example *Lyocyclus*, which have been classified into this family based on similarities in external anatomy and radular morphology, regardless of their rather unusual shell shapes (Warén & Bouchet, 1988; Warén, 1989). *Lyocyclus* is found to be very distant from *Vanikoro* + *Macromphalus* and represents its independent family Lyocyclidae Thiele, 1925 (Fig. 1-1). There might be more heterogeneous taxa in Vanikoridae that deserve independent familial status or belong to other hypsogastropod families.

Polyphyly of the informal group Ptenoglossa was reaffirmed (see Bouchet & Rocroi, 2005; Colgan et al., 2007; Churchill et al., 2011a). Ptenoglossate radulae have been acquired independently in Vanikoroidea, Epitonioidea and Triphoroidea as well as in many other, totally distant gastropod groups, e.g. some of Trochaclididae, Pseudococculinidae (both Vetigastropoda) and Architectonicidae (Heterobranchia), probably to serve similar feeding ecologies (Warén, 1984; Warén & Gofas, 1996). Also, parasitism on echinoderms has probably evolved more than once in Hypsogastropoda. *Chauvetia tenuisculpta* apparently parasitize echinoids and asteroids (Oliver & Rolan, 2008; Wirtz, 2011), while the present trees confirm its position within Neogastropoda (Buccinidae) and distant from Eulimidae (Fig. 1-1).

Ecological radiation and morphological differentiation in the Eulimidae

The present phylogeny demonstrates that the family Eulimidae constitutes a robust clade (Figs. 1-1, 1-2), although the nine genera included in the analysis have considerably different morphologies, hosts and parasitic strategies (Table 1-2). Adams and Adams (1853) established a separate family Styliferidae for *Stilifer* that bears a broader and more globose shell than that of *Eulima*, the type genus of Eulimidae. Succeeding authors had placed several other eulimid genera with similarly broad shells in Styliferidae (e.g. Laseron, 1955). These conchological differences, however, have been shown to be specializations connected with the degree of parasitism; the inflated shells are presumably apomorphic and acquired in multiple genera where parasites permanently attach to their hosts (Warén, 1984). The distant relationship between *Stilifer* and another globose genus *Monogamus* in the present molecular trees verifies the plasticity of the shell shape in the evolution of the Eulimidae. Further support of this plasticity is indicated by the terminal position of the limpet-shaped genus *Thyca*, which shows an even more derived condition from *Stilifer*. This apparently represents morphological adaptation for stronger attachment to the host with a larger sole of the foot, as suggested for multiple lineages of rocky-shore limpets to substrates (Vermeij, 1993).

The Eulimidae are exclusive parasites of echinoderms including all five classes. Warén (1984) noted that each class of the host seemed to be infected by a single lineage of eulimids, with a possible exception by the genus *Vitreolina* that includes ophiuroid and echinoid parasites. However, the present phylogeny demonstrates at least one more exceptional case where a host class is parasitized by multiple eulimid clades. The asteroid parasites *Stilifer* and *Thyca* are distantly related to *Niso*, another group exploiting sea stars (Warén, 1984). Regardless, the evolutionary history of host associations cannot be dealt with precisely without including additional taxa. There are more than 1,250 described species and over 90 genera in the family which has a global distribution from the equator to the poles and occupy a wide range of depths, from intertidal to abyssal waters (Warén, 1984; Bouchet & Warén, 1986). The polarity of evolutionary transitions among sexual (gonochoristic and protandric/simultaneous hermaphroditic) strategies is even more difficult to evaluate due to the rarity of properly preserved specimens that represent various ontogenetic stages.

One of the few morphological or ecological characters that accord well with our tree topology is the presence or absence of the radula. Radula-less species always constitute a robust monophyletic clade, while snails with the radula (*Hemiaclis*, *Niso*, *Pyramidelloides* and *Hemiliostraca*) were either monophyletic or paraphyletic in the two-gene and five-gene reconstructions, respectively (Figs. 1-1, 1-2; Table 1-2). The Eulimidae have acquired the ptenoglossate radula in parallel to those of Epitonioidea and Triphoroidea (see above) and one of the ancestral lineages of the family has apparently lost this digestive apparatus, which may have a limited use in their blood-sucking mode of feeding (Warén, 1984). A more detailed ingroup phylogeny would provide further insights on the loss of the radula and transitions of other morphological and ecological traits.

Rissooidea and Truncatelloidea

Relationships among Vanikoroidea, Rissooidea and Truncatelloidea were not clearly resolved in our trees. The sister relationship between Vanikoroidea and Truncatelloidea was supported by the highest Bayesian posterior probability but insignificant ML bootstrap values in the 5gPA tree (Fig. 1-2, see also Appendix 1). This topology differs from that of a previously published phylogeny (Criscione & Ponder, 2013), which places a eulimid species within the Rissooidea with high posterior and bootstrap support (PP = 1.00, BP = 93%) based on two of the five markers used in the present analyses (28S and 16S, a total of *ca*. 2.2 kbp). Possible explanations for the incongruence include differences in the numbers of markers and OTUs and the method of sequence alignment (see also Fig. 1-1). On the other hand, Barleeiidae and Rissoinidae consistently form a robust clade within Rissooidea, both in the present and previous (Criscione & Ponder, 2013) phylogenies. These two families share a pegged operculum, which is lacking in the type family Rissoidae (Ponder, 1985).

Our phylogenetic reconstruction reveals more insights on the internal relationship of the Truncatelloidea. The analyzed ten families belong to one of two major clades: Anabathridae + Hydrobiidae + Assimineidae + Truncatellidae + Pomatiopsidae + Falsicingulidae, and Elachisinidae + Caecidae + Iravadiidae + Tornidae (Figs. 1-1, 1-2). The former clade comprises all marine, freshwater and terrestrial taxa, while the species of the latter clade inhabit only the marine environment including brackish estuaries and mangrove swamps (see Ponder & de Keyzer, 1998a). A subclade of the former clade (Hydrobiidae + Assimineidae + Truncatellidae + Pomatiopsidae + Falsicingulidae) has already been recovered with the highest PP value in Criscione & Ponder (2013), while its sister relationship to Anabathridae is first resolved here (Fig. 1-2). The monophyletic nature of the Tornidae (= Vitrinellidae; Bouchet & Rocroi, 2005) is clearly rejected by the sister relationship between *Vitrinella* and *Iravadia*, confirming the previous suspicion that this family comprises heterogeneous groups (Ponder & de Keyzer, 1998a).

Other hypsogastropod clades

The present phylogeny provides further information on the suprageneric classification of Hypsogastropoda and other caenogastropod taxa. Nystiellidae of the superfamily Epitonioidea (*Opaliopsis* sp.) is included for the first time in a molecular analysis and is found to occupy a terminal position within the Epitoniidae. Nystiellidae was originally established as a subfamily of Epitoniidae (Bouchet & Warén, 1986) and later given a distinct familial status based almost solely on the presence of dense axial ribs in the protoconch (Nützel, 1998; Bouchet & Rocroi, 2005). However, nystiellids have general shell shapes that are very similar to those of some typical epitoniids with a smooth protoconch (e.g. *Opalia*; Bouchet & Warén, 1986). The present tree indeed shows a close relationship between *Opalia* and *Opaliopsis* (Fig. 1-1); the protoconch ornamentation has possibly been acquired as an apomorphy in the latter lineage. The neustonic Janthinidae represents another terminal clade within the Epitoniidae as has already been discussed by Churchill et al. (2011a). Interestingly, *Alexania* represents the closest benthic relative of Janthinidae in our trees with meaningful nodal support values (Fig. 1-1). The broad, smooth and brown shell of *Alexania* differs noticeably from the tall, ribbed white shells of other epitoniids and closely resembles that of the plesiomorphic janthinid genus *Recluzia* (Robertson & Habe, 1965; Churchill et al., 2011a, b). Unfortunately, our knowledge of their anatomy is insufficient to verify their close kinship and to infer morphological differentiation and adaptation that have accompanied the radical habitat transition from the benthic to neustonic mode of life.

A further, significant finding concerns the position of the little-known, mainly cavernicolous family Pickworthiidae. Only a few snails of the family have been collected alive from submarine caves and similar cryptic voids in the shallow subtidal waters of the tropics and subtropics (Table 1-1; Bouchet & Le Renard, 1998; Kase, 1998). The Pickworthiidae have been tentatively assigned to Littorinoidea based on protoconch morphology alone (Bouchet & Le Renard, 1998; Bouchet & Rocroi, 2005), while the same morphological character also implies a relationship to Cerithioidea, a possible sister clade of Hypsogastropoda (Ponder & Lindberg, 1997; Colgan et al., 2007; Ponder et al., 2008). Our molecular data recover three pickworthiid genera as the sister clade of, or paraphyletic to, the Cerithioidea (Fig. 1-1). The genera *Pelycidion* and *Microliotia* are clustered with high support values, whereas the former has been classified in an independent family (Pelycidiidae) with a unique combination of the tall, minute shell and rhipidoglossate-like radula (Ponder & Hall, 1983; Bouchet & Le Renard, 1998) or later a subfamily of Pickworthiidae (Bouchet & Rocroi, 2005). The paraphyletic nature of Pickworthiinae (here represented by *Microliotia* and *Mareleptopoma*), however, suggests that the morphologies unique to *Pelycidion* are apomorphic, derived conditions within the family. Cerithioid anatomy has been examined in detail (e.g. Houbrick, 1988; Strong et al., 2011), but the Pickworthiidae are neglected due to the inaccessibility of live animals (Bouchet and Le Renard, 1998; Kase, 1998). In summary, integrated molecular, morphological and ecological investigations, covering taxa from the deep sea and other inaccessible habitats, are essential to reveal hypsogastropod relationships and evolution of various life history strategies including parasitism.

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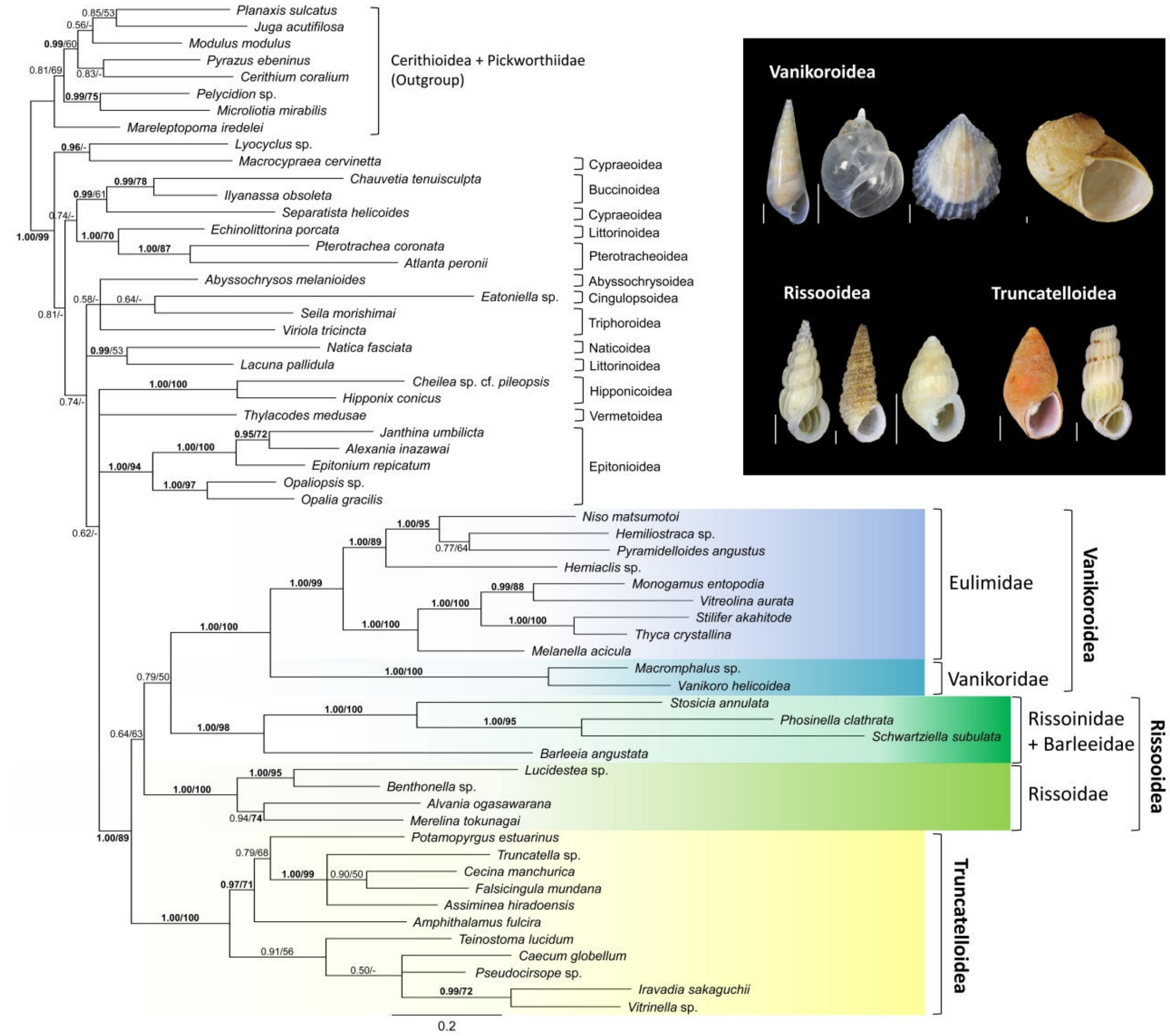

Figure 1-1. Bayesian phylogeny of Hypsogastropoda inferred from 2gGB alignment of 28S (D1–D5) and COI genes (1,853 sites in total). Numerals on branches denote posterior probabilities (PP, left) and likelihood-based bootstrap values shown as percentages (BS, right); significant support in bold (PP ≥ 95%, BS ≥ 70%). Shells from upper left to lower right: *N. matsumotoi*, *M. acicula*, *M. entopodia*, *T. crystallina*, *V. helicoidea*, *S. subulata*, *R. clathrata*, *M. tokunagai*, *A. ogasawarana*, *I. sakaguchii*, *Truncatella* sp. and *C. globella* (scale bars: 1 mm).

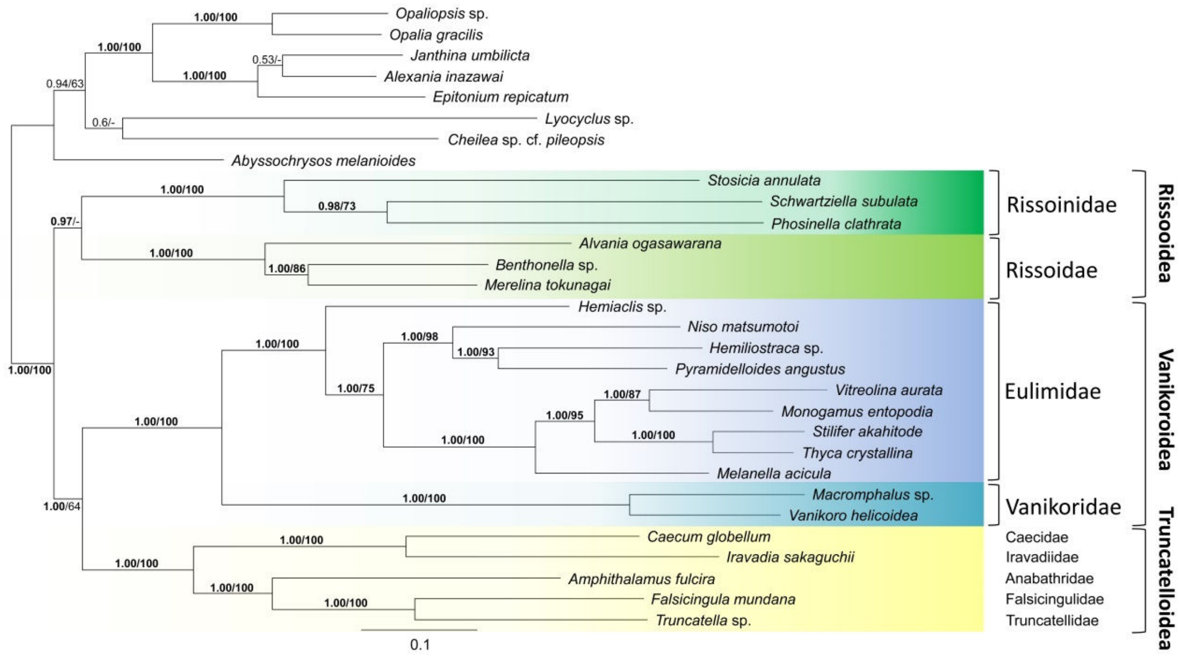

Figure 1-2. Bayesian phylogeny of Vanikoroidea, Truncatelloidea and Rissooidea inferred from 5gGB alignment of 28S (D1–D7b), 18S, H3, 16S and COI genes (4,969 sites in total). Numerals on branches denote posterior probabilities (PP, left) and likelihood-based bootstrap values shown as percentages (BS, right); significant support in bold (PP ≥ 95%, BS ≥ 70%).

Table 1-1. Species used in present analyses with DDBJ/EMBL/GenBank accession numbers and collection sites and habitats of specimens. Accession numbers of newly obtained sequences are given in bold. Suprageneric classification reflects topology of new trees.

Classification	Species	28S D1–5	28S D6–7b	18S	H3	16S	COI	DNA/Voucher	Coordinates	Locality; habitat and depth
Vanikoroidea[*1]										
Eulimidae	*Hemiaclis* sp.	**AB930331**	**AB930331**	**AB930382**	**AB930436**	**AB930409**	**AB930465**	YK#1580	31°07’N, 131°39’E	KT-11-12 (T-10-2), off Cape Toi, Miyazaki, Japan; 1063–1082 m
	Hemiliostraca sp.	**AB930332**	**AB930332**	**AB930383**	**AB930437**	**AB930410**	**AB930466**	YK#1584	31°44’N, 131°28’E	Nojima, Miyazaki, Japan; intertidal rocky shore
	Melanella acicula	**AB930330**	**AB930330**	**AB930381**	**AB930435**	**AB930408**	**AB930464**	YK#1571	28°09’N, 129°21’E	Isu, Amami Is., Japan; intertidal, on *Stichopus chloronotus*
	Monogamus entopodia	**AB930324**	**AB930324**	**AB930375**	**AB930429**	**AB930402**	**AB930458**	YK#1481	28°07’N, 129°21’E	Yadorihama, Amami Is., Japan; intertidal, on *Echinometra mathaei*
	Niso matsumotoi	**AB930335**	-	**AB930385**	**AB930440**	**AB930413**	**AB930469**	YK#1594	34°26’N, 136°55’E	Off Toba, Mie, Japan; 10–25 m
	Pyramidelloides angustus	**AB930336**	**AB930336**	**AB930386**	**AB930441**	**AB930414**	**AB930470**	YK#1601	26°52’N, 128°16’E	Cape Hedo, Okinawa Is., Japan; intertidal, on *Ophiocoma scolopendrina*
	Stilifer akahitode	**AB930327**	**AB930327**	**AB930378**	**AB930432**	**AB930405**	**AB930461**	YK#1541	32°33’N, 130°06’E	Tsuji Is., Amakusa, Japan; intertidal, in *Certonardoa semiregularis*
	Thyca crystallina	**AB930326**	**AB930326**	**AB930377**	**AB930431**	**AB930404**	**AB930460**	YK#1519	09°49’N, 123°22’E	Moalboal, Cebu Is., Philippines; on *Linckia laevigata*
	Vitreolina aurata	**AB930323**	**AB930323**	**AB930374**	**AB930428**	**AB930401**	**AB930457**	YK#1475	34°40’N, 138°59’E	Shimoda, Izu, Japan; intertidal, on *Hemicentrotus pulcherrimus*
Vanikoridae	*Macromphalus* sp.	**AB930369**	**AB930369**	**AB930399**	**AB930453**	**AB930425**	-	YK#1655	09°29’N, 123°41’E	Off Panglao Is., Bohol, Philippines; ca. 300 m, on sunken wood
	Vanikoro helicoidea	**AB930359**	**AB930359**	**AB930395**	**AB930450**	**AB930421**	**AB930487**	YK#1643	24°27’N, 124°08’E	Kabira, Ishigaki Is., Japan; tidal flat
Rissooidea										
Barleeiidae	*Barleeia angustata*	**AB930348**	-	-	-	-	**AB930479**	YK#1630	34°40’N, 138°59’E	Shimoda, Izu, Japan; intertidal rocky shore
Rissoidae	*Alvania ogasawarana*	**AB930358**	**AB930358**	**AB930394**	**AB930449**	-	**AB930486**	YK#1642	24°29’N, 124°17’E	Tamatorizaki, Ishigaki Is., Japan; intertidal rocky shore
	Benthonella sp.	**AB930363**	**AB930363**	**AB930396**	-	**AB930422**	**AB930489**	YK#1647	31°07’N, 131°39’E	KT-11-12 (T-10-2), off Cape Toi, Miyazaki, Japan; 1063–1082 m
	Lucidestea sp.	**AB930347**	-	-	-	-	-	YK#1628	34°40’N, 138°59’E	Shimoda, Izu, Japan; intertidal rocky shore
	Merelina tokunagai	**AB930344**	**AB930344**	**AB930389**	**AB930443**	**AB930416**	**AB930476**	YK#1623	34°40’N, 138°59’E	Shimoda, Izu, Japan; intertidal rocky shore
Rissoinidae	*Phosinella clathrata*	**AB930351**	**AB930351**	**AB930392**	**AB930446**	**AB930419**	-	YK#1633	24°21’N, 123°45’E	Shirahama, Iriomote Is., Japan; tidal flat
	Schwartziella subulata	**AB930341**	**AB930341**	**AB930388**	**AB930442**	-	**AB930474**	YK#1618	31°24’N, 130°11’E	Koura, Kagoshima, Japan; intertidal rocky shore
	Stosicia annulata	**AB930349**	**AB930349**	**AB930391**	**AB930445**	**AB930418**	**AB930480**	YK#1631	32°30’N, 131°43’E	Nobeoka, Miyazaki, Japan; intertidal rocky shore
Truncatelloidea										
Anabathridae	*Amphithalamus fulcira*	**AB930345**	**AB930345**	**AB930390**	**AB930444**	**AB930417**	**AB930477**	YK#1624	34°40’N, 138°59’E	Shimoda, Izu, Japan; intertidal rocky shore
Assimineidae	*Assiminea hiradoensis*	AB611805	-	-	-	-	AB611807			
Caecidae	*Caecum globellum*	**AB930352**	**AB930352**	**AB930393**	**AB930447**	-	**AB930481**	YK#1634	34°40’N, 138°59’E	Shimoda, Izu, Japan; intertidal rocky shore
Elachisinidae	*Pseudocirsope* sp.	**AB930360**	-	-	-	-	-	YK#1644	30°16’N, 130°25’E	Kurio, Yakushima Is., Japan; intertidal rocky shore
Falsicingulidae	*Falsicingula mundana*	**AB930366**	**AB930366**	**AB930398**	**AB930452**	**AB930424**	**AB930492**	YK#1651	35°42’N, 135°03’E	Kotobikihama, Kyoto, Japan; intertidal rocky shore
Hydrobiidae	*Potamopyrgus estuarinus*	**AB930357**	-	-	-	-	**AB930485**	YK#1640	36°34’S, 174°41’E	Orewa, N of Auckland, New Zealand; estuary

Iravadiidae	*Iravadia sakaguchii*	**AB930339**	-	**AB930387**	-	**AB930415**	**AB930473**	YK#1616	31°25’N, 131°15’E	Honjo R., Kushima, Miyazaki, Japan; estuary
Pomatiopsidae	*Cecina manchurica*	AB611741	-	-	-	-	AB611743			
Stenothyridae	*Stenothyra thermaecola*	**AB930355**	-	-	-	-	-	YK#1638	33°16’N, 131°22’E	Yufuin, Oita, Japan; hot spring
Tornidae	*Teinostoma lucidum*	**AB930343**	-	-	-	-	-	YK#1621	35°15’N, 139°35’E	Hayama, Kanagawa, Japan; intertidal rocky shore
	Vitrinella sp.	**AB930362**	-	-	-	-	-	YK#1646	35°15’N, 139°35’E	Hayama, Kanagawa, Japan; intertidal rocky shore
Truncatellidae	*Truncatella* sp.	**AB930353**	**AB930353**	-	**AB930448**	**AB930420**	**AB930482**	YK#1635	24°47’N, 125°16’E	Hisamatsu, Miyako Is., Japan; stream mouth
Cingulopsoidea										
Cingulopsidae	*Tubbreva* sp.	**AB930370**	-	-	-	-	-	YK#1656	32°33’N, 130°06’E	Tsuji Is., Amakusa, Japan; intertidal rocky shore
Eatoniellidae	*Eatoniella* sp.	**AB930346**	-	-	-	-	**AB930478**	YK#1626	34°40’N, 138°59’E	Shimoda, Izu, Japan; intertidal rocky shore
Hipponicoidea[*1]										
Hipponicidae	*Cheilea* sp. cf. *pileopsis*	**AB930365**	-	**AB930397**	**AB930451**	**AB930423**	**AB930491**	YK#1650	24°28’N, 123°49’E	Hatoma Is., Okinawa, Japan; tidal flat
	Hipponix conicus	**AB930364**	-	-	-	-	**AB930490**	YK#1649	31°44’N, 131°28’E	Nojima, Miyazaki, Japan; intertidal rocky shore
Epitonioidea										
Epitoniidae	*Alexania inazawai*	**AB930329**	**AB930329**	**AB930380**	**AB930434**	**AB930407**	**AB930463**	YK#1552	28°26’N, 129°40’E	Tekebu, Amami Is., Japan; tidal flat
	Epitonium replicatum	**AB930328**	**AB930328**	**AB930379**	**AB930433**	**AB930406**	**AB930462**	YK#1551	32°29’N, 131°41’E	Kadokawa, Miyazaki, Japan; intertidal seagrass bed
	Opalia gracilis	**AB930334**	**AB930334**	**AB930384**	**AB930439**	**AB930412**	**AB930468**	YK#1591	17°29’S, 149°50’W	Phaena, Moorea Is., French Polynesia; intertidal seagrass bed
Janthinidae	*Janthina umbilicata*	**AB930333**	**AB930333**	-	**AB930438**	**AB930411**	**AB930467**	YK#1590	36°50’S, 174°26’E	Muriwai, W of Auckland, New Zealand; beach drift
Nystiellidae	*Opaliopsis* sp.	**AB930373**	-	-	**AB930456**	**AB930427**	-	YK#1775[*2]	18°33’S, 164°20’E	Récif Pétrie, New Caledonia; 580–703m
Capuloidea										
Capulidae	*Separatista helicoides*	**AB930338**	-	-	-	-	**AB930472**	YK#1615	31°18’N, 130°12’E	Marukihama, Kagoshima, Japan; intertidal, on *Sabellastarte* tube
Vermetoidea										
Vermetidae	*Thylacodes medusae*	**AB930337**	-	-	-	-	**AB930471**	YK#1614	35°09’N, 139°35’E	Off Misaki, Kanagawa, Japan; 80 m
Cypraeoidea										
Cypraeidae	*Macrocypraea cervinetta*	FM999134	-	-	-	-	DQ207132			
Naticoidea										
Naticidae	*Natica fasciata*	**AB930361**	-	-	-	-	**AB930488**	YK#1645	24°27’N, 124°08’E	Kabira, Ishigaki Is., Japan; tidal flat
Pterotracheoidea										
Atlantidae	*Atlanta peronii*	**AB930340**	-	-	-	-	-	YK#1617	32°15’N, 129°29’E	N295 (B), SW of Nagasaki, Japan
Pterotracheidae	*Pterotrachea coronata*	**AB930356**	-	-	-	-	**AB930484**	YK#1639	32°12’N, 128°58’E	N295 (O), off Fukue Is., Nagasaki, Japan
Triphoroidea										
Cerithiopsidae	*Seila morishimai*	**AB930354**	-	-	-	-	**AB930483**	YK#1637	32°35’N, 130°23’E	Nogama Is., Amakusa, Japan; intertidal rocky shore
Triphoridae	*Viriola tricincta*	**AB930342**	-	-	-	-	**AB930475**	YK#1620	31°14’N, 130°39’E	Ibusuki, Kagoshima, Japan; tidal flat

Abyssochrysoidea										
Abyssochrysidae	*Abyssochrysos melanioides*	**AB930325**	**AB930325**	**AB930376**	**AB930430**	**AB930403**	**AB930459**	YK#1482	32º07'N, 133º42'E	KT-11-12 (K), SE of Cape Ashizuri, Kochi, Japan; 2107–2168 m
Littorinoidea										
Lacunidae	*Lacuna pallidula*	AJ488645	-	-	-	-	AJ488604			
Littorinidae	*Echinolittorina porcata*	AJ623186	-	-	-	-	AJ622969			
Buccinoidea										
Buccinidae	*Chauvetia tenuisculpta*	**AB930371**	-	-	-	-	-	YK#1730[*3]	14º45'N, 17º30'W	Cape Verde, Dakar, Senegal; 16 m, on *Paracentrotus lividus*
Nassariidae	*Ilyanassa obsoleta*	AY145411	-	-	-	-	DQ238598			
Superfamily unknown										
Aclididae	*Aclis minor*	-	-	-	**AB930455**	-	-	YK#1734[*4]	58º52'N, 11º05'E	Kostergrund, Bohuslän, Sweden, Skagerrak; fine silt, 20–40 m
Lyocyclidae	*Lyocyclus* sp.	**AB930372**	**AB930372**	**AB930400**	**AB930454**	**AB930426**	-	YK#1732[*5]	22º54'S, 169º27'E	Banc Ellet, New Caledonia; 159–756 m
(Outgroup taxa)										
Cerithioidea										
Cerithiidae	*Cerithium coralium*	AM932695	-	-	-	-	AM932754			
Modulidae	*Modulus modulus*	FJ606987	-	-	-	-	AM932757			
Planaxidae	*Planaxis sulcatus*	FJ606988	-	-	-	-	HQ834106			
Pleuroceridae	*Juga acutifilosa*	DQ256748	-	-	-	-	EF586920			
Potamididae	*Pyrazus ebeninus*	FJ606989	-	-	-	-	AM932752			
Superfamily unknown										
Pickworthiidae	*Pelycidion* sp.	**AB930350**	-	-	-	-	-	YK#1632	34º40'N, 138º59'E	Shimoda, Izu, Japan; intertidal rocky shore
	Mareleptopoma iredalei	**AB930367**	-	-	-	-	-	YK#1652	26º43'N, 127º50'E	Daidokutsu, Ie Is., Okinawa, Japan; submarine cave, 20 m
	Microliotia mirabilis	**AB930368**	-	-	-	-	**AB930493**	YK#1654	10º28'S, 105º36'E	Thunder Dome, Christmas Is., Australia; submarine cave, 8–10 m

[*1] Redefined superfamilies. [*2] Muséum National d'Histoire Naturelle, Paris (MNHN) IM-2009-24069; [*3] Swedish Museum of Natural History (SMNH) 109316; [*4] SMNH-123661; [*5] MNHN IM-2009-24193.

Table 1-2. Ecological and morphological characteristics of eulimid species included in the present phylogeny. Specimens of *Niso matsumotoi* and *Hemiliostraca* sp. were collected as free-living while the two genera are known to parasitize Asteroidea and Ophiuroidea, respectively (Warén, 1984); no information available for *Hemiaclis*. Morphological conditions after Warén (1984) and Bouchet and Warén (1986).

Species	Host class	Mode of life	Shell shape	Radula
Hemiaclis sp.	unknown	Temp	conical	present
Hemiliostraca sp.	Ophiuroidea	Temp	slender	present
Melanella acicula	Holothuroidea	Temp	slender	absent
Monogamus entopodia	Echinoidea	Ecto	globose	absent
Niso matsumotoi	Asteroidea	Temp	conical	present
Pyramidelloides angusta	Ophiuroidea	Temp	slender	present
Stilifer akahitode	Asteroidea	Endo	globose	absent
Vitreolina auratus	Echinoidea	Temp	slender	absent

Table 1-3. Summary of four sequence alignments.

	Alignment length	Excluded sites	Variable sites	Parsimony informative
2gGB				
28S D1–D5	1,605	382	331	224
COI	630	0	382	316
Total	2,235	382	713	540
2gPA				
28S D1–D5	1,605	306	384	268
COI	630	3	380	315
Total	2,235	309	764	583
5gGB				
28S D1–D7b	2,352	397	375	274
18S	1,795	60	167	83
H3	314	0	110	90
16S	525	189	205	173
COI	630	0	375	303
Total	5,616	646	1,232	923
5gPA				
28S D1–D7b	2,352	337	399	287
18S	1,795	50	174	84
H3	314	0	110	90
16S	525	220	172	141
COI	630	3	373	302
Total	5,616	610	1,228	904

Chapter 2

Elucidating the evolutionary history of parasitism in eulimid gastropods: gradual specialization to permanent endoparasites or repeated adaptive radiation?

本章については、5年以内に雑誌などで刊行予定のため、非公開。

Chapter 3

Evolutionary relationships and diversification pattern in Pyramidellidae

本章については、5年以内に雑誌などで刊行予定のため、非公開。

General Discussion

本章については、5 年以内に雑誌などで刊行予定のため、非公開。

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References

Adams, H., Adams, A., 1853. From Eulimidae to Styliferidae. *In*: *The Genera of Recent Mollusca; Arranged According to Their Organization, Vol. 1*. van Voorst, London, pp. 235–239.

Altnöder, A., Bohn, J.M., Rückert, I.-M., Schwabe, E., 2007. The presumed shelled juvenile of the parasitic gastropod *Entocolax schiemenzii* Voigt, 1901 and its holothurian host *Chiridota pisanii* Ludwig, 1886. *Spixiana* 30: 187–199.

Anton, R.F., Schrödl, M., 2013. The gastropod-crustacean connection: towards the phylogeny and evolution of the parasitic copepod family Splanchnotrophidae. *Zoological Journal of the Linnean Society* **167**: 501–530.

Baer, J.D., 1952. *Ecology of Animal Parasites*. University of Illinois Press, Urbana.

De Baets, K., Littlewood, D.T.J., 2015. The importance of fossils in understanding the evolution of parasites and their vectors. *Advances in Parasitology* **90**: 1–49.

Barco, A., Claremont, M., Reid, D.G., Houart, R., Bouchet, P., Williams, S.T., Cruaud, C., Couloux, A., Oliverio, M., 2010. A molecular phylogenetic framework for the Muricidae, a diverse family of carnivorous gastropods. *Molecular Phylogenetics and Evolution* **56**: 1025–1039.

Bieler, R., 1988. Phylogenetic relationships in the gastropod family Architectonicidae, with notes on the family Mathildidae (Allogastropoda). *Malacological Review, Supplement* **4**: 205–240.

Blaxter, M.L., de Ley, P., Garey, J.R., Liu, L.X., Scheldeman, P., Vierstraete, A., Vanfleteren, J.R., Mackey, L.Y., Dorris, M., Frisse, L.M., Vida, J.T., Thomas, W.K., 1998. A molecular evolutionary framework for the phylum Nematoda. *Nature* **392**: 71–75.

Bouchet, P., Warén, A., 1986. Revision of the northeast Atlantic bathyal and abyssal Aclididae, Eulimidae, Epitoniidae (Mollusca, Gastropoda). *Bollettino Malacologico, Supplement* **2**: 299–576.

Bouchet, P., Le Renard, J., 1998. Family Pickworthiidae, *In*: Beesley, P.L., Ross, G.J.B., Wells, A. (Eds.), *Fauna of Australia, Vol. 5, Mollusca: The Southern Synthesis*. CSIRO Publishing, Melbourne, pp. 739–741.

Bouchet, P., Lozouet, P., Maestrati, P., Héros, V., 2002. Assessing the magnitude of species richness in tropical marine environments: exceptionally high numbers of molluscs at a New Caledonia site. *Biological Journal of the Linnean Society* **75**: 421–436.

Bouchet, P., Rocroi, J.P., 2005. Classification and nomenclator of Gastropod families. *Malacologia* **47**: 1–397.

Bovbjerg, R.V., 1968. Responses to food in lymnaeid snails. *Physiological Zoology* **41**: 412–423.

Brooks, D.R., Ó Grady R.T., Glen, D.R., 1985. Phylogenetic analysis of the Digenea (Platyhelminthes: Cercomeria) with comments on their adaptive radiation. *Canadian Journal of Zoology* **63**: 411–443.

Bucklin, A., Frost, B.W., Bradford-Grieve, J., Allen, L.D., Copley, N.J., 2003. Molecular systematic and phylogenetic assessment of 34 calanoid copepod species of the Calanidae and Clausocalanidae. *Marine Biology* **142**: 333–343.

Buckling, A., Rainey, P.B., 2002. The role of parasites in sympatric and allopatric host diversification. *Nature* **420**: 496–499.

Byers, J.E., 2008. Including parasites in food webs. *Trends in Parasitology* **25**: 55–57

Carpentieri, P., Serpetti, N., Colloca, F., Criscoli, A., Ardizzone, G., 2015. Food preferences and rhythms of feeding activity of two co-existing demersal fish, the longspine snipefish, *Macroramphosus scolopax* (Linnaeus, 1758) and the boarfish

Capros aper (Linnaeus, 1758), on the Medditerranean deep shelf. *Marine Ecology* **2015**: 1–13.

Carroll, J.M., Finelli, C.M., 2015. Impacts of the ectoparasitic snail *Boonea impressa* on growth of postset juvenile oysters. *Journal of Molluscan Studies* **81**: 161–163.

Castresana, J., 2000. Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution* **17**: 540–552.

Chapman, A.D., 2009. *Numbers of Living Species in Australia and the World, 2nd edition*. Australian Biological Resource Study, Canberra.

Chiba, S., 2004. Ecological and morphological patterns in communities of land snails of the genus *Mandarina* from the Bonin Islands. *Journal of Evolutionary Biology* **17**: 131–143.

Churchill, C.K.C., Ó Foighil, D., Strong, E.E., Gittenberger, A., 2011a. Females floated first in bubble-rafting snails. *Current Biology* **21**: 802–803.

Churchill, C.K.C., Strong, E.E., Ó Foighil, D., 2011b. Hitchhiking juveniles in the rare neustonic gastropod *Recluzia* cf. *jehennei* (Janthinidae). *Journal of Molluscan Studies* **77**: 441–444.

Colgan, D.J., Ponder, W.F., Eggler, P.E., 2000. Gastropod evolutionary rates and phylogenetic relationships assessed using partial 28S rDNA and histone H3 sequences. *Zoologica Scripta* **29**: 29–63.

Colgan, D.J., Ponder, W.F., Beacham, E., Macaranas, J., 2007. Molecular phylogenetics of Caenogastropoda (Gastropoda: Mollusca). *Molecular Phylogenetics and Evolution* **42**: 717–737.

Combes, C., 2005. *The Art of Being a Parasite*. The University of Chicago Press, Chicago and London.

Collin, R., 2003. Phylogenetic relationships among calyptraeid gastropods and their implications for the biogeography of marine speciation. *Systematic Biology* **52**: 618–640.

Cossmann, M., Pissarro, G., 1904–06. *Iconographie Complète des Coquilles Fossiles de l'Éocène des Environs de Paris.* H. Bouillant, Paris.

Cossmann, M., Peyrot, A., 1917–18. Conchologie néogénique de l'Aquitanie. *Actes de la Société Linnéenne de Bordeaux* **70**: 1–491.

Coyne, J.A., Orr, H.A., 2004. *Speciation.* Sinaure Associates, Sunderland.

Criscione, F., Ponder, W.F., 2013. A phylogenetic analysis of rissooidean and cingulopsoidean families (Gastropoda: Caenogastropoda). *Molecular Phylogenetics and Evolution* **66**: 1075–1082.

Cumming, R.L., 1993. Reproduction and variable larval development of an ectoparasitic snail, *Turbonilla* sp. (Pyramidellidae, Opisthobranchia), on cultured giant clams. *Bulletin of Marine Science* **52**: 760–771.

Cumming, R.L., Alford, R.A., 1994. Population dynamics of *Turbonilla* sp. (Pyramidellidae, Opisthobranchia), an ectoparasite of giant clams in mariculture. *Journal of Experimental Marine Biology and Ecology* **183**: 91–111.

Darriba, D., Taboada, G.L., Doallo, R., Posada, D., 2012. jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* **9**: 772.

Dayrat, B., Tillier, A., Lecointre, G., Tillier, S., 2001. New clades of euthyneuran gastropods (Mollusca) from 28S rRNA sequences. *Molecular Phylogenetics and Evolution* **19**: 225–235.

Dayrat, B., Conrad, M., Balayan, S., White, T.R., Albrecht, C., Golding, R., Gomes, S.R., Harasewych, M.G., de Frias Martins, A.M., 2011. Phylogenetic relationships and evolution of pulmonate gastropods (Mollusca): new insights from increased taxon sampling. *Molecular Phylogenetics and Evolution* **59**: 425–437.

Dgebuadze, P.Y., Fedosov, A.E., Kantor Y.I., 2012. Host specificity of parasitic gastropods of the genus *Annulobalcis* Habe, 1965 (Mollusca, Gastropoda, Eulimidae) from crinoids in Vietnam, with descriptions of four new species. *Zoosystema* **34**: 139–155.

Dinapoli, A., Klussmann-Kolb, A., 2010. The long way to diversity – phylogeny and evolution of Heterobranchia (Mollusca: Gastropoda). *Molecular Phylogenetics and Evolution* **55**: 60–76.

Dinapoli, A., Zinssmeister, C., Klussmann-Kolb, A., 2011. New insights into the phylogeny of the Pyramidellidae (Gastropoda). *Journal of Molluscan Studies* **77**, 1–7.

Dreyer, H., Wägele, J.W., 2001. Parasites of crustaceans (Isopoda: Bopyridae) evolved from fish parasites: molecular and morphological evidence. *Zoology* **103**: 157–178.

Drummond, A.J., Suchard, M.A., Xie, D., Rambaut, A., 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution* **29**: 1969–1973.

Dunne, J.A., Lafferty, K.D., Dobson, A.P., Hechinger, R.F., Kuris, A.M., Martinez, N.D., McLaughlin, J.P., Mouritsen, K.N., Poulin, R., Reise, K., Stouffer, D.B., Thieltges, D.W., Williams, R.J., Zander, C.D., 2013. Parasites affect food web structure primarily through increased diversity and complexity. *PLoS Biology* **11**: e1001579.

Emelianov, I., 2007. How adaptive is parasite species diversity? *International Journal of Parasitology* **37**: 851–860.

Euzet L., Combes, C., 1998. The selection of habitats among the monogenean. *International Journal for Parasitology* **28**: 1645–1652.

Folmer, O., Black, M., Hoeh, W., Luts, R., Vrijenhoek, R., 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* **3**: 294–299.

Frédérich, B., Sorenson, L., Santini, F., Slater, G.J., Alfaro, M.E., 2013. Iterative ecological radiation and convergence during the evolutionary history of damselfishes (Pomacentridae). *American Naturalist* **181**: 94–113.

Fretter, V., Graham, A., 1982. The prosobranch molluscs of Britain and Denmark, Part 7. ‘Heterogastropoda’. *Journal of Molluscan Studies, Supplement* **11**: 363–434.

Fretter, V., Graham, A., 1994. *Britich Prosobranch Molluscs. Their Functional Anatomy and Ecology, Revised and Updated Edition.* The Ray Society, London.

Futuyma, D.J., Moreno, G., 1988. The evolution of ecological specialization. *Annual Review of Ecology and Systematics* **19**: 207–233.

Gage, J.D., Tyler, P.A., 1991. *Deep-Sea Biology: A natural history of organisms at the deep-sea floor*. Cambridge University Press, Cambridge.

Gillespie, R., 2004. Community assembly through adaptive radiation in Hawaiian spiders. *Science* **303**: 356–359.

Givnish, T.J., 1997. Adaptive radiation and molecular systematics: issues and approaches, *In*: Givnish, T.J., Sytsma, K.J. (Eds.), *Molecular Evolution and Adaptive Radiation*. Cambridge University Press, Cambridge, pp. 1–54.

Glasby, C.J., Hutchings, P.A., Fauchald, K., Paxton, H., Rouse, G.W., Russell, C.W., Wilson, R.S., 2000. Class Polychaeta, *In*: Beesley, P.L., Ross, G.J.B., Glasby, C.J. (Eds.), *Fauna of Australia, Vol. 4A, Polychaetes & Allies: The Southern Synthesis*. CSIRO Publishing, Melbourne, pp. 1–296.

Glenner, H., Hebsgaard, M.B., 2006. Phylogeny and evolution of life history strategies of the parasitic barnacles (Crustacea, Cirripedia, Rhizocephala). *Molecular Phylogenetics and Evolution* **41**: 528–538.

Gofas, S., Moreno, D., Salas, C., 2011. *Moluscos marinos de Andalcía. Vol. I.* Servicio de Publicaciones e Intercambio Científico, Universidad de Málaga, Málaga.

Gould, S.J., 1989. Wonderful life: the Burgess Shale and the nature of history. Norton, New York.

Golding, R.E., Ponder, W.F., Byrne, M., 2007. Taxonomy and anatomy of Amphiboloidea (Gastropoda: Heterobranchia: Archaeopulmonata). *Zootaxa* **1476**: 1–50.

Golding, R.E., Ponder, W.F., Byrne, M., 2009. The evolutionary and biomechanical implications of snout and proboscis morphology in Caenogastropoda (Mollusca: Gastropoda). *Journal of Natural History* **43**: 2723–2763.

Goto, R., Hamamura, Y., Kato, M., 2011. Morphological and ecological adaptation of *Basterotia* bivalves (Galeommatoidea: Sportellidae) to symbiotic association with burrowing echiuran worms. *Zoological Science* **28**: 225–234.

Goto, R., Kawakita, A., Ishikawa, H., Hamamura, Y., Kato, M., 2012. Molecular phylogeny of the bivalve superfamily Galeommatoidea (Heterodonta, Veneroida) reveals dynamic evolution of symbiotic lifestyle and interphylum host switching. *BMC Evolutionary Biology* **12**: 172.

Gougerot, L., Le Renard, J., 1977. Nouvelles espèces de petits gastéropodes marins de l'Éocène des Bassins de Paris, de Nantes et du Cotentin. *Bulletin d'Information des Geologues du Bassin de Paris* **14**: 3–33.

Grande, C., Templado, J., Cervera, J.L., Zardoya, R., 2002. The complete mitochondrial genome of the nudibranch *Roboastra europaea* (Mollusca: Gastropoda) supports the monophyly of opisthobranchs. *Molecular Biology and Evolution* **19**: 1672–1685.

Grande, C., Templado, J., Cervera, J.L., Zardoya, R., 2004. Molecular phylogeny of Euthyneura (Mollusca: Gastropoda). *Molecular Biology and Evolution* **21**: 303–313.

Gray, J.E., 1853. On the division of ctenobranchous gasteropodous Mollusca into larger groups and families. *Proceedings of the Zoological Society of London* **21**: 32–44.

Guindon, S., Gascuel, O., 2003. A simple, fast and accurate method to estimate large phylogenies by maximum-likelihood. *Systematic Biology* **52**: 696–704.

Habe, T., 1952. Parasitic gastropods found in echinoderms from Japan. *Publications of the Seto Marine Biological Laboratory* **2**: 73–85.

Habe, T., 1965. Description of *Annulobalcis shimazui* n. gen. et sp. (Eulimidae). *Venus* **24**: 106–107.

Habe, T., 1976. Parasitic gastropods from echinoderms of Japan. *Bulletin of the Natural Science Museum, ser. A, Zoology* **2**: 157–168.

Haines, C.M.C., Edmunds, M., Pewsey, A.R., 1994. The pea crab, *Pinnotheres pisum* (Linnaeus, 1767), and its association with the common mussel, *Mytilus edulis* (Linnaeus, 1758), in the Solent (UK). *Journal of Shellfish Research* **13**: 5–10.

Hasegawa, K., 1997. Sunken wood-associated gastropods collected from Suruga Bay, Pacific side of the Central Honshu, Japan, with descriptions of 12 new species. *National Science Museum Monographs* **12**: 59–123.

Haszprunar, G., 1985. The Heterobranchia—a new concept of the phylogeny of the higher Gastropoda. *Zeitschrift für Zoologie, Systematik und Evolutionsforschung* **23**: 15–37.

Hatcher, M.J., Dunn, A.M., 2011. *Parasites in Ecological Communities: From Interactions to Ecosystems.* Cambridge University Press, Cambridge.

Healy, J.M., 1988. Sperm morphology and its systematic importance in the Gastropoda. *Malacological Review, Supplement* **4**: 251–266.

Heding, S.G., Mandahl-Barth, G., 1938. Investigations on the anatomy and systematic position of the parasitic snail *Entocolax* Voigt. *Meddelelser om Grønland* **108**: 1–40.

Heller, J., 1993. Hermaphroditism in molluscs. *Biological Journal of the Linnean Society* **48**: 19–42.

Herbert, G.S., Dietl, G.P., Fortunato, H., Simone, L.R.L., Sliko, J., 2009. Extremely slow feeding in a tropical drilling ectoparasite, *Vitularia salebrosa* (King and Broderip, 1832) (Gastropoda: Muricidae), on molluscan hosts from Pacific Panama. *Nautilus* **123**: 121–136.

Héritier, L., Badets, M., du Preez, L.H., Aisien, M.S.O., Lixian, F., Combes, C., Verneau, O., 2015. Evolutionary processes involved in the diversification of chelonian and mammal polystomatid parasites (Platyhelminthes, Monogenea, Polystomatidae) revealed by palaeoecology of their hosts. *Molecular Phylogenetics and Evolution* **92**: 1–10.

Herlyn, H., Piskurek, O., Schmitz, J., Ehlers, U., Zischler, H., 2003. The syndermatan phylogeny and the evolution of acanthocephalan endoparasitism as inferred from 18S rDNA sequences. *Molecular Phylogenetics and Evolution* **26**: 155–164.

Høisæter, T., 2014. The Pyramidellidae (Gastropoda, Heterobranchia) of Norway and adjacent waters. A taxonomic review. *Fauna norvegica* **34**: 7–78.

Hori, S., 2000a. Familiy Eulimidae, *In*: Okutani, T. (Ed.), *Marine Mollusks in Japan*. Tokai University Press, Tokyo, pp. 344–363.

Hori, S., 2000b. Familiy Pyramidellidae, *In*: Okutani, T. (Ed.), *Marine Mollusks in Japan*. Tokai University Press, Tokyo, pp. 702–731.

Hori, S., Tsuchida, E., 1995. A revision of systematic position of genus *Leucotina* (Gastropoda: Heterobranchia). *Venus* **54**: 279–293.

Houbrick, R.S., 1988. Cerithioidean phylogeny. *Malacological Review, Supplement* **4**: 88–128.

Hutchings, P., 1998. Biodiversity and functioning of polychaetes in benthic sediments. *Biodiversity and Conservation* **7**: 1133–1145.

Huys, R., Llewellyn-Hughes, J., Olson, P.D., Nagasawa, K., 2006. Small subunit rDNA and Bayesian inference reveal *Pectenophilus ornatus* (Copepoda *incertar sedis*) as highly transformed Mytilicolidae, and support assignment of Chondracanthidae and Xarifiidae to Lichomolgidae (Cyclopioda). *Biological Journal of the Linnean Society* **87**: 403–425.

Huys, R., Llewellyn-Hughes, J., Conroy-Dalton, S., Olson, P.D., Spinks, J.N., Johnston, D.A., 2007. Extraordinary host switching in siphonostomatoid copepods and the demise of the Monstrilloida: integrating molecular data, ontogeny and antennulary morphology. *Molecular Phylogenetics and Evolution* **43**: 368–378.

Huyse, T., Poulin, R., Théron, A., 2005. Speciation in parasites: a population genetics approach. *Trends in Parasitology* **21**: 469–475.

Ingram, T., Kai, Y., 2014. The geography of morphological convergence in the radiations of Pacific *Sebastes* rockfishes. *American Naturalist* **184**: E115–E131.

Jangoux, M., 1987. Diseases of Echinodermata. II. Agents metazoans (Mesozoa to Bryozoa). *Diseases of Aquatic Organisms* **2**: 205–234.

Janzen, D., 1968. Host plants as islands in evolutionary and contemporary time. *American Naturalist* **102**: 592–595.

Jeyaprakash, A., Hoy, M.A., 2009. First divergence time estimate of spiders, scorpions, mites and ticks (subphylum: Chelicerata) inferred from mitochondrial phylogeny. *Experimental and Applied Acarology* **47**: 1–18.

Johnson, K.P., Shreve, S.M., Smith, V.S., 2012. Repeated adaptive divergence of microhabitat specialization in avian feather lice. *BMC Biology* **10**: 52.

Jörger, K.M., Stöger, I., Kano, Y., Fukuda, H., Knebelsberger, T., Schrödl, M., 2010. On the origin of Acochlidia and other enigmatic euthyneurian gastropods, with implications for the systematics of Heterobranchia. *BMC Evolutionary Biology* **10**: 323.

Kameda, Y., Kato, M., 2011. Terrestrial invasion of pomatiopsid gastropods in the heavy-snow region of the Japanese Archipelago. *BMC Evolutionary Biology* **11**: 118.

Kano, Y., 2008. Vetigastropod phylogeny and a new concept of Seguenzioidea: independent evolution of copulatory organs in the deep-sea habitats. *Zoologica Scripta* **37**: 1–21.

Kano, Y., Chiba, S., Kase, T., 2002. Major adaptive radiation in neritopsine gastropods estimated from 28S rRNA sequences and fossil records. *Proceedings of the Royal Society B* **269**: 2457–2465.

Kano, Y., Chikyu, E., Warén, A., 2009. Morphological, ecological and molecular characterization of the enigmatic planispiral snail genus *Adeuomphalus* (Vetigastropoda: Seguenzioidea). *Journal of Molluscan Studies* **75**: 397–418.

Kase, T. 1998. The family Pickworthiidae (Gastropoda : Caenogastropoda) from tropical Pacific submarine caves : four new species of *Sansonia*. *Venus* **57**: 161–172.

Kat, P.W., 1984. Parasitism and the Unionacea (Bivalvia). *Biological Reviews* **59**: 189–207.

Katoh, K., Standley, D.M., 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* **30**: 772–780.

Kawai, T., Nagasawa, K., 2006. Host body size, prevalence and breeding season of the microparasitic snail *Pelseneeria castanea* on the sea urchin *Strongylocentrotus nudus* in castal waters of the Sea of Japan off Western Hokkaido, Japan. *Japanese Journal of Benthology* **61**: 16–20.

Kemp, P., Bertness, M.D., 1984. Snail shape and growth rates: evidence for plastic shell allometry in *Littorina littorea*. *Proceedings of the National Academy of Sciences* **81**: 811–813.

Ketmaier, V., Joyce, D.A., Horton, T., Mariani, S., 2008. A molecular phylogenetic framework for the evolution of parasitic strategies in cymothoid isopods (Crustacea). *Journal of Zoological Systematics and Evolutionary Research* **46**: 19–23.

Kiel, S., Bandel, K., 2001. About Heterostropha (Gastropoda) of the Campanian of Torallola, Spain. *Journal of the Czech Geological Society* **46**: 319–334.

Knapp, J., Nakao, M., Yanagida, T., Okamoto, M., Saarma, U., Lavikainen, A., Ito, A., 2011. Phylogenetic relationships within *Echinococcus* and *Taenia* tapeworms (Cestoda: Taeniidae): an inference from nuclear protein-coding genes. *Molecular Phylogenetics and Evolution* **61**: 628–638.

Kocot, K.M., Cannon, J.T., Todt, C., Citarella, M.R., Kohn, A.B., Meyer, A., Santos, S.R., Schander, C., Moroz, L.L., Lieb, B., Halanych, K.M., 2011. Phylogenomics reveals deep molluscan relationships. *Nature* **477**: 452–456.

Kozak, K.H., Mendyk, R.W., Wiens, J.J., 2009. Can parallel diversification occur in sympatry? Repeated patterns of body-size evolution in coexisting clades of North American salamanders. *Evolution* **63**: 1769–1784.

Kunz, W., 2002. When is a parasite species a species? *Trends in Parasitology* **18**: 121–124.

Kuris, A.M., Blaustein, A.R., Javeir Alió, J., 1980. Hosts as islands. *American Naturalist* **116**: 570–586.

Lafferty, K.D., 2013. Parasites in marine food webs. *Bulletin of Marine Science* **89**: 123–134.

Lafferty, K.D., Allesina, S., Arim, M., Briggs, C.J., Leo, G.D., Dobson, A.P., Dunne, J.A., Johnson, P.T.J., Kuris, A.M., Marcogliese, D.J., Martinez, N.D., Memmott, J., Marquet, P.A., McLaughlin, J.P., Mordecai, E.A., Pascual, M., Poulin, R., Thieltges, D.W., 2008. Parasites in food webs: the ultimate missing links. *Ecology Letters* **11**: 533–546.

Lanterbecq, D., Rouse, G.W., Milinkovitch, M.C., Eeckhaut, I., 2006. Molecular phylogenetic analyses indicate multiple independent emergences of parasitism in Myzostomida (Protostomia). *Systematic Biology* **55**: 208–227.

Laseron, C.F. 1955. Revision of the New South Wales eulimoid shells. *Australian Zoologist* **12**: 83–107.

Laseron, C.F., 1959. The family Pyramidellidae (Mollusca) from Northern Australia. *Marine & Freshwater Research* **10**: 177–268.

Lauridsen, B.W., Schnetler, K.I., 2014. A catalogue of Danian gastropods from the Baunekule facies, Faxe Formation, Denmark. *Geological Survey of Denmark and Greenland Bulletin* **32**: 1–117.

Lester, R.J.G., Sewell, K.B., 1989. Checklist of parasites from Heron Island, Great Barrier Reef. *Australian Journal of Zoology* **37**: 101–128.

Leung, T.L.F., in press. Fossil of parasites: what can the fossil record tell us about the evolution of parasitism? *Biological Reviews.*

Littlewood, D.T.J., 2006. The evolution of parasitism in flatworms, *In*: Maule, A.G., Marks, N.J. (Eds.), *Parasitic Flatworms: Molecular Biology, Biochemistry, Immunology and Phylogeny*. CABI, Wallingford, pp. 1–36.

Littlewood, D.T.J., Rohde, K., Bray, R.A., Herniou, E.A., 1999. Phylogeny of the Platyhelminthes and the evolution of parasitism. *Biological Journal of the Linnean Society* **68**: 257–287.

Littlewood, D.T.J., Curini-Galletti, M., Herniou, A., 2000. The interrelationships of Proseriata (Platyhelminthes: Seriata) tested with molecules and morphology. *Molecular Phylogenetics and Evolution* 16: 449–466.

Lockyer, A.E., Olson, P.D., Østergaard, P., Rollinson, D., Johnston, D.A., Attwood, S.W., Southgate, V.R., Horak, P., Snyder, S.D., Le, T.H., Agatsuma, T., McManus, D.P., Carmichael, A.C., Naem, S., Littlewood, D.T.J., 2003. The phylogeny of the Schistosomatidae based on three genes with emphasis on the interrelationships of *Schistosoma* Weinland, 1858. *Parasitology* **126**: 203–224.

Lorentz, F., 2005. Mollusca (molluscs), *In*: Rohde, K. (Ed.), *Marine Parasitology*. CABI Publishing, Wallingford, pp. 240–245.

Löytynoja, A., Milinkovitch, M.C., 2003. A hidden Markov model for progressive multiple alignment. *Bioinformatics* **19**: 1505–1513.

Losos, J.B., 2010. Adaptive radiation, ecological opportunity, and evolutionary determinism. *American Naturalist* **175**: 623–639.

Losos, J.B., Jackman, T.R., Larson, A., de Queiroz, K, Rodrígues-Schettino, L., 1998. Contingency and determinism in replicated adaptive radiations of island lizards. *Science* **279**: 2115–2118.

Lozouet, P., 1999. New species of gastropods (Mollusca: Gastropoda) from Oligocene and Lower Miocene of Aquitaine (Southwestern France). Part 2. *Cossmanniana* **6**: 1–68.

Lozouet, P., Dockery, D.T., 2001. First fossil record of the genus *Pyramidelloides* (Mollusca, Gastropoda, Eulimidae) discovered in the Eocene deposits of Alabama. *Comptes Rendus de l'Académie des Sciences, ser. IIA, Earth and Planetary Science* **333**: 351–356.

Lützen, J., 1968. Unisexuality in the parasitic family Entoconchidae (Gastropoda: Prosobranchia). *Malacologia* **7**: 7–15.

Lützen, J., 1976. On a new genus and two new species of Prosobranchia (Mollusca), parasitic on the tropical sea urchin *Echinometra mathaei*. *Israel Journal of Zoology* **25**: 38–51.

Maddison, W.P., Maddison, D.R., 2015. *Mesquite: a modular system for evolutionary analysis, version 3.04.* Available at http://mesquiteproject.org

Matsuda, H., Hamano, T., Nagasawa, K., 2013. Growth and reproductive cycle of *Hypermastus tokunagai* (Caenogastropoda: Eulimidae), an ectoparasite of the sand dollar *Scaphechinus mirabilis* (Clypeasteroida: Scutellidae) in the Seto Inland Sea, Japan. *Journal of the Marine Biological Association of the United Kingdom* **93**: 1041–1051.

Melville, J., Harmon, L.J., Losos, J.B., 2006. Intercontinental community convergence of ecology and morphology in desert lizards. *Proceedings of the Royal Society B* **273**: 557–563.

Mendlová, M., Šimková, A., 2014. Evolution of host specificity in monogeneans parasitizing African cichlid fish. *Parasites & Vectors* **7**: 69.

Meyer, C.P., 2003. Molecular systematics of cowries (Gastropoda: Cypraeidae) and diversification patterns in the tropics. *Biological Journal of the Linnean Society* **79**: 401–459.

Meyer, A., Kocher, T.D., Basasibawaki, P., Wilson, A.C., 1990. Monophyletic origin of Lake Victoria cichlid fishes. *Nature* 347: 550–553.

Meyer, C.P., 2004. Toward comprehensiveness: increased molecular sampling within Cypraeidae and its phylogenetic implications. *Malacologia* **46**: 127–156.

Michot, B., Hassouna, N., Bachellerie, J.P., 1984. Secondary structure of mouse 28S rRNA and general model for the folding of the large rRNA in eukaryotes. *Nucleic Acids Research* **10**: 4259–4279.

Mladineo, I., Bott, N.J., Nowak, B.F., Block, B.A., 2010. Multilocus phylogenetic analyses reveal that habitat selection drives the speciation of Didymozoidae (Digenea) parasitizing Pacific and Atlantic bluefin tunas. *Parasitology* **137**: 1013–1025.

Moran, A.L., 1999. Size and performance of juvenile marine invertebrates: potential contrasts between intertidal and subtidal benthic habitats. *American Zoologist* **39**: 304–312.

Morris, S.C., 1981. Parasites and the fossil record. *Parasitology* **82**: 489–509.

Morris, S.C., Crompton, D.W.T., 1982. The origins and evolution of the Acanthocephala. *Biological Reviews* **57**: 85–115.

Morton, B., 1979. The population dynamics and expression of sexuality in *Balcis shaplandi* and *Mucronalia fulvescens* (Mollusca: Gastropoda: Aglossa) parasitic upon *Archaster typicus* (Echinodermata: Asteroidea). *Malacologia* **18**: 327–346.

Murphy, N., Banks, J.C., Whitfield, J.B., Austin, A.D., 2008. Phylogeny of the parasitic microgastroid subfamilies (Hymenoptera: Braconidae) based on sequence data from seven genes, with an improved time estimate of the origin of the lineage. *Molecular Phylogenetics and Evolution* **47**: 378–395.

Musashi, T., Habe, T., 1991. Notes on the distribution and host of *Pelseneeria castanea* (Dall, 1925), a parasitic snail. *Chiribotan* **22**: 69–71.

Nakamura, K., Kano, Y., Suzuki, N., Namatame, T., Kosaku, A., 2007. 18S rRNA phylogeny of sea spiders with emphasis on the position of Rhynchothoracidae. *Marine Biology* **153**: 213–223.

Neumann, C., Wisshak, M., 2009. Gastropod parasitism on late Cretaceous to early Paleocene holasteroid echinoids—evidence from *Oichnus* isp. n. *Palaeogeography, Palaeoclimatology, Palaeoecology* **284**: 115–119.

Nützel, A., 1998. Über die stammesgeschichte der Ptenoglossa (Gastropoda). *Berliner Geowissenschaftliche Abhandlungen, ser. E* **26**: 1–229.

Okutani, T. (Ed.), 2000a. *Marine Mollusks in Japan*. Tokai University Press, Tokyo.

Okutani, T., 2000b. Familiy Calyptraeidae, *In*: Okutani, T. (Ed.), *Marine Mollusks in Japan*. Tokai University Press, Tokyo, pp. 200–201.

Oliver, J.D., Rolan, E., 2008. Las especies del género *Chauvetia* del área de Dakar, Senegal, África occidental, con la descripción de diez especies nuevas. *Iberus* **26**: 133–175.

Palumbi, S., Martin, A., Romano, S., McMillan, W.O., Stice, L., Grabowski, G., 1991. *The Simple Fool's Guide to PCR, Version 2.0*. Department of Zoology and Kewalo Marine Laboratory, University of Hawaii, Honolulu.

Park, J.K., Kim, K.H., Kang, S., Kim, W., Eom, K.S., Littlewood, D.T.J., 2007. A common origin of complex life cycles in parasitic flatworms: evidence from the complete mitochondrial genome of *Microcotyle sebastis* (Monogenea: Platyhelminthes). *BMC Evolutionary Biology* **7**: 11.

Peñas, A., Rolán, E., 2010. Deep water Pyramidelloidea of the Tropical South Pacific: *Turbonilla* and related genera. *Mémoires du Muséum national d'Histoire naturelle* **200**: 1–436.

Perkins, E.M., Donnellan, S.C., Bertozzi, T., Chisholm, L.A., Whittington, I.D., 2009. Looks can deceive: molecular phylogeny of a family of flatworm ectoparasites (Monogenea: Capsalidae) does not reflect current morphological classification. *Molecular Phylogenetics and Evolution* 52: 705–714.

Poinar, G., Kerp, H., Hass, H., 2008. *Palaeonema phyticum* gen. n., sp. n. (Nematoda: Palaeonematidae fam. n.), a Devonian nematode associated with early land plants. *Nematology* **10**: 9–14.

Ponder, W.F., 1985. A review of the genera of the Rissoidae (Mollusca: Mesogastropoda: Rissoacea). *Records of the Australian Museum, Supplement* **4**: 1–221.

Ponder, W.F., 1986. Glacidorbidae (Glacidorbacea: Basommatophora), a new family and superfamily of operculate freshwater gastropods. *Zoological Journal of the Linnean Society* **87**: 53–83.

Ponder, W.F., 1987. The anatomy and relationships of the pyramidellacean limpet *Amathina tricarinata* (Mollusca: Gastropoda). *Asian Marine Biology* **4**: 1–34.

Ponder, W.F., 1998. Superfamily Vanikoroidea, *In*: Beesley, P.L., Ross, G.J.B., Wells, A. (Eds.), *Fauna of Australia, Vol. 5, Mollusca: The Southern Synthesis.* CSIRO Publishing, Melbourne, pp. 769–772.

Ponder, W.F., Gooding, R.U., 1978. Four new eulimid gastropods associated with shallow-water diadematid echinoids in the Western Pacific. *Pacific Science* **32**: 157–181.

Ponder, W.F., Hall, S.J., 1983. Pelycidiidae, a new family of Archaeogastropod molluscs. *Nautilus* **97**: 30–35.

Ponder, W.F., Warén, A., 1988. Classification of the Caenogastropoda and Heterostropha—a list of the family-group names and higher taxa. *Malacological Review, Supplement* **4**: 288–326.

Ponder, W.F., Lindberg, D.R., 1997. Towards a phylogeny of gastropod molluscs—an analysis using morphological characters. *Zoological Journal of the Linnean Society* **19**: 83–265.

Ponder, W.F., de Keyzer, R.G., 1998a. Superfamily Rissooidea, *In*: Beesley, P.L., Ross, G.J.B., Wells, A. (Eds.), *Fauna of Australia, Vol. 5, Mollusca: The Southern Synthesis.* CSIRO Publishing, Melbourne, pp. 745–766.

Ponder, W.F., de Keyzer, R.G., 1998b. Superfamily Pyramidelloidea, *In*: Beesley, P.L., Ross, G.J.B., Wells, A. (Eds.), *Fauna of Australia, Vol. 5, Mollusca: The Southern Synthesis.* CSIRO Publishing, Melbourne, pp. 865–869.

Ponder, W.F., Colgan, D.J., Healy, J.M., Nützel, A., Simone, L.R.L., Strong, E.E., 2008. Caenogastropoda, *In*: Ponder, W.F., Lindberg, D.R. (Eds.), *Phylogeny and Evolution of the Mollusca.* University of California Press, Berkeley, pp. 331–383.

Ponder, W.F., Lindberg, D.R., 2008. Molluscan evolution and phylogeny, *In*: Ponder, W.F., Lindberg, D.R. (Eds.), *Phylogeny and Evolution of the Mollusca.* University of California Press, Berkeley, pp. 1–17.

Poppe, G.T., 2008. *Philippine Marine Mollusks. Vol. 1, Gastropoda-Part 1.* ConchBooks, Hackenheim.

Poulin, R., 2007. *Evolutionary Ecology of Parasites, 2nd edition.* Princeton University Press, Princeton and Oxford.

Poulin, R., Morand, S., 2000. The diversity of parasites. *The Quarterly Review of Biology* **75**: 277–293.

Poulin, R., Morand, S., 2004. *Parasite Biodiversity.* Smithsonian Institution Press, Washington, D.C.

Pras, S., 2013. Correct type designation for two mollusc genera: *Polygireulima* Sacco 1892 (Gastropoda: Eulimidae) and *Coripia* de Gregorio 1885 (Bivalvia: Carditidae). *Cossmanniana* **15**: 99–103.

Rascalou, G., Gourbière, S., 2014. Competition, virulence, host body mass and the diversification of macro-parasites. *Journal of the Royal Society Interface* **11**: 20131108.

R Core Team, 2015. *R: A language and environment for statistical computing, version 3.2.2.* R Foundation for Statistical Computing, Vienna, Austria. Available at http://www.r-project.org/

Rees, D.J., Noever, C., Høeg, J.T., Ommundsen, A., Glenner, H., 2014. On the origin of a novel parasitic-feeding mode within suspension-feeding barnacles. *Current Biology* **24**: 1429–1434.

Ricklefs, R.E., Schluter, D. (Eds.), 1993. *Species Diversity in Ecological Communities: Historical and Geographical Perspective.* University of Chicago Press, Chicago.

Roach, A.C., Lim, R.P., 2000. Variation in the population dynamics of the intertidal pulmonate gastropod *Salinator solida* Martens (Gastropoda: Amphibolidae) at Towra Point, NSW, Australia. *Wetlands Ecology and Management* **8**: 53–69.

Robertson, R., Habe, T., 1965. *Alexania* replaces *Habea* (Epitoniidae). *Nautilus* **78**: 140–141.

Rohde, K., 2005. Definitions, and adaptations to a parasitic way of life, *In*: Rohde, K. (Ed.), *Marine Parasitology*. CABI Publishing, Wallingford, pp. 1–6.

Ronquist, F., Huelsenbeck, J.P., 2003. MrBayes3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* **19**: 1572–1574.

Rundell, R.J., Price, T.D., 2009. Adaptive radiation, nonadaptive radiation, ecological speciation and nonecological speciation. *Trends in Ecology and Evolution* **24**: 394–399.

Schander, C., van Aartsen, J.J., Corgan, J.X., 1999a. Families and genera of the Pyramidelloidea (Mollusca: Gastropoda). *Bollettino Malacologico* 34: 145–166.

Schander, C., Hori, S., Lundberg, J., 1999b. Anatomy, phylogeny and biology of *Odostomella* and *Herviera*, with the description of a new species of *Odostomella*. *Ophelia* **51**: 39–76.

Schander, C., Halanych, K.M., Dahlgren, T., Sundberg, P., 2003. Test of the monophyly of Odostomiinae and Turbonilliinae (Gastropoda, Heterobranchia, Pyramidellidae) based on 16S mtDNA sequences. *Zoologica Scripta* **32**: 243–254.

Schiaparelli, S., Barucca, M., Olmo, E., Boyer, M., Canapa, A., 2005. Phylogenetic relationships within Ovulidae (Gastropoda: Cypraeoidea) based on molecular data from the 16S rRNA gene. *Marine Biology* **147**: 411–420.

Schluter, D., 2000. *The Ecology of Adaptive Radiation.* Oxford University Press, Oxford.

Schluter, D., 2009. Evidence for ecological speciation and its alternative. *Science* **323**: 737–741.

Schulte, R.D., Makus, C., Hasert, B., Michiels, N.K., Schulenburg, H., 2010. Multiple reciprocal adaptations and rapid genetic change upon experimental coevolution of an animal host and its microbial parasite. *Proceedings of the National Academy of Sciences* **107**: 7359–7364.

Severns, M., 2011. *Shells of the Hawaiian Islands*. IKAN Unterwasser-Archiv, Frankfurt.

Šimková, A., Morand, S., Jobet, E., Gelnar, M., Verneau, O., 2004. Molecular phylogeny of congeneric monogenean parasites (*Dactylogyrus*): a case of intrahost speciation. *Evolution* **58**: 1001–1018.

Šimková, A., Verneau, O., Gelnar, M., Morand, S., 2006. Specificity and specialization of congeneric monogeneans parasitizing cyprinid fish. *Evolution* **60**: 1023–1037.

Simone, L.R.L., 2002. Comparative morphological study and phylogeny of representatives of the superfamily Calyptraeoidea (including Hipponicoidea) (Mollusca, Caenogastropoda). *Biota Neotropica* **2(2)**: 1–137.

Simone, L.R.L., 2011. Phylogeny of the Caenogastropoda (Mollusca), based on comparative morphology. *Arquivos de Zoologia* **42**: 83–323.

Smith, S.A., Wilson, N.G., Goetz, F.E., Feehery, C., Andrade, S.C.S, Rouse, G.W., Giribet, G., Dunn, C.W., 2011. Resolving the evolutionary relationships of molluscs with phylogenomic tools. *Nature* **480**: 364–367.

Sohl, N.F., 1964. Neogastropoda, Opisthobranchia and Basommatophora from the Ripley, Owl Creek and Praire Bluff Formations. *Professional Papers of the U.S. Geological Survey* **331B**: 153–344.

Song, Y., Wang, G.T., Yao, W.J., Gao, Q., Nie, P., 2008. Phylogeny of freshwater parasitic copepods in the Ergasilidae (Copepoda: Poecilostomatoida) based on 18S and 28S rDNA sequences. *Parasitology Research* **102**: 299–306.

Stamatakis, A., 2006. RAxML-VI-HPC: maximum likelihood phylogenetic analysis with thousands of taxa and mixed models. *Bioinformatics* **22**: 2688–2690.

Steiner, G., Dreyer, H., 2003. Molecular phylogeny of Scaphopoda (Mollusca) inferred from 18S rRNA sequences—support for a Scaphopoda–Cephalopoda clade. *Zoologica Scripta* **32**: 343–356.

Strong, E.E., Gargominy, O., Ponder, W.F., Bouchet, P., 2008. Global diversity of gastropods (Gastropoda; Mollusca) in fleshwater. *Hydrobiologia* **595**: 149–166.

Strong, E.E., Colgan, D.J., Healy, J.M., Lydeard, C., Ponder, W.F., Glaubrecht, M., 2011. Phylogeny of the gastropod superfamily Cerithioidea using morphology and molecules. *Zoological Journal of the Linnean Society* **162**: 43–89.

Suárez-Morales, E., Harris, L.H., Ferrari, F.D., Gasca, R., 2014. Late postnaupliar development of *Monstrilla* sp. (Copepoda: Monstrilloida), a protelean endoparasite of benthic polychaetes. *Invertebrate Reproduction & Development* **58**: 60–73.

Summers, K., McKeon, S., Sellars, J., Keusenkothen, M., Morris, J., Gloeckner, D., Pressley, C., Price, B., Snow, H., 2003. Parasitic exploitation as an engine of diversity. *Biological Reviews* **78**: 639–675.

Summers, M.M., Rouse, G.W., 2014. Phylogeny of Myzostomida (Annelida) and their relationships with echinoderm hosts. *BMC Evolutionary Biology* **14**: 170.

Takano, T., Kano, Y., 2014. Molecular phylogenetic investigations of the relationships of the echinoderm-parasite family Eulimidae within Hypsogastropoda (Mollusca). *Molecular Phylogenetics and Evolution* **79**: 258–269.

Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M., Kumar, S., 2011. MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molecular Biology and Evolution* **28**: 2731–2739.

Telford, M.J., Lowe, C.J., Cameron, C.B., Ortega-Martinez, O., Aronowicz, J., Oliveri, P., Copley, R.R., 2014. Phylogenomic analysis of echinoderm class relationships supports Asterozoa. *Proceedings of the Royal Society B* **281**: 20140479.

Thompson, J.N., 1994. *The coevolutionary process.* University of Chicago Press, Chicago.

Tompkins, D., Dunn, A.M., Smith, M.J., Telfer, S., 2011. Wildlife diseases: from individuals to ecosystems. *Journal of Animal Ecology* **80**: 19–38.

Tsuchiya, K., 2000. Family Muricidae, *In*: Okutani, T. (Ed.), *Marine Mollusks in Japan*. Tokai University Press, Tokyo, pp. 364–421.

Vas, Z., Csorba, G., Rózsa L., 2012. Evolutionary co-variation of host and parasite diversity—the first test of Eichler's rule using parasitic lice (Insecta: Phthiraptera). *Parasitology Research* **111**: 393–401.

Vermeij, D.J., 1993. *A Natural History of Shells*. Princeton Univ. Press, Princeton.

Verneau, O., Bentz, S., Sinnappah, N.D., du Preez, L., Whittington, I., Combes, C., 2002. A view of early vertebrate evolution inferred from the phylogeny of polystome parasites (Monogenea: Polystomatidae). *Proceedings of the Royal Society B* **269**: 535–543.

De Vlas, J., 1979. Annual food intake by plaice and flounder in a tidal flat area in the Dutch Wadden Sea, with special reference to consumption of regenerating part of microbenthic prey. *Netherlands Journal of Sea Research* **13**: 117–153.

Vonnemann, V., Schrödl, M., Klussmann-Kolb, A., Wägele, H., 2005. Reconstruction of the phylogeny of the Opisthobranchia (Mollusca: Gastropoda) by means of 18S and 28S rRNA gene sequences. *Journal of Molluscan Studies* **71**: 113–125.

Wada, S., Kameda, Y., Chiba, S., 2013. Long-term stasis and short-term divergence in the phenotypes of microsnails on oceanic islands. *Molecular Ecology* **22**: 4801–4810.

Warén, A., 1980a. Revision of the genera *Thyca*, *Stilifer*, *Scalenostoma*, *Mucronalia* and *Echineulima* (Mollusca, Prosobranchia, Eulimidae). *Zoologica Scripta* **9**: 187–210.

Warén, A., 1980b. Descriptions of new taxa of Eulimidae (Mollusca, Prosobranchia), with notes on some previously described genera. *Zoologica Scripta* **9**: 283–306.

Warén, A., 1981a. Revision of the genera *Apicalia* A. Adams and *Stilapex* lredale and description of two new genera (Mollusca, Prosobranchia, Eulimidae). *Zoologica Scripta* **10**: 133–154.

Warén, A., 1981b. Eulimid gastropods parasitic on echinoderms in the New Zealand region. *New Zealand Journal of Zoology* **8**: 313–324.

Warén, A., 1983. An anatomical description of *Eulima bilineata* Alder with remarks on and a revision of *Pyramidelloides* Nevill (Mollusca, Prosobranchia, Eulimidae). *Zoologica Scripta* **12**: 273–294.

Warén, A., 1984. A generic revision of the family Eulimidae (Gastropoda, Prosobranchia). *Journal of Molluscan Studies, Supplement* **13**: 1–96.

Warén, A., 1989. New and little known Mollusca from Iceland. *Sarsia* **74**: 1–28.

Warén, A. 1991. New and little known Mollusca from Iceland and Scandinavia. Sarsia 76: 53–124.

Warén, A., 1993. New and little known Mollusca from Iceland and Scandinavia. Part 2. *Sarsia* **78**: 159–201.

Warén, A. 2011. Molluscs on biogenic substrates, *In*: Bouchet, P., Le Guyader, H., Pascal, O. (Eds.), *The Natural History of Santo*. Muséum national d'Histoire naturelle, Paris; IRD Marseille; Pro-Natura international, Paris, pp. 438–448.

Warén, A., 2013. Murchisonellidae: who are they, where are they and what are they doing? (Gastropoda, lowermost Heterobranchia). *Vita Malacologica* **11**: 1–14.

Warén, A., Sibuet, M., 1981. *Ophieulima* (Mollusca, Prosobranchia), a new genus of ophiuroid parasites. *Sarsia* **66**: 103–107.

Warén, A., Bouchet, P., 1988. A new species of Vanikoridae from the western Mediterranean, with remarks on the northeast Atlantic species of the family. *Bollettino Malacologico* **24**: 73–100.

Warén, A., Bouchet, P., 1991. Mollusca Gastropoda: systematic position and revision of *Haloceras* Dall, 1889 (Caenogastropoda, Haloceratidae fam. nov.). *Mémoires du Muséum National d'Histoire Naturelle, Paris, Ser. A* **150**: 111–161.

Warén, A., Gittenberger, E., 1993. *Turbo politus* Linnaeus, 1758 (currently *Melanella polita*; Mollusca, Gastropoda): proposed conservation of usage of the specific name, so conserving the specific name of *Buccinum acicula* Müller, 1774 (currently *Cecilioides acicula*). *Bulletin of Zoological Nomenclature* **50**: 107–110.

Warén, A., Gofas, S., 1996. *Kaiparapelta askewi* McLean & Harasewych, 1995 (Gastropoda: Pseudococculinidae): a spongivorous cocculiniform limpet and a case of remarkable convergence in radular morphology. *Haliotis* **25**: 107–116.

Webster, B.L., Southgate, V.R., Littlewood, D.T.J., 2006. A revision of the interrelationships of *Schistosoma* including the recently described *Schistosoma guineensis*. *International Journal for Parasitology* **36**: 947–955.

Westwood, J.H., Yoder, J.I., Timko, M.P., dePamphilis C.W., 2010. The evolution of parasitism in plants. *Trends in Plant Science* **15**: 227–235.

White, T.J., Bruns, T., Lee, S., Taylor, J.W., 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics, *In*: Innis, M.A., Gelfand, D.H., Sninsky, J.J., White, T.J. (Eds.), *PCR Protocols: a Guide to Methods and Applications.* Academic Press, New York, pp. 315–322.

Whitfield, J.B., 1998. Phylogeny and evolution of host-parasitoid interactions in Hymenoptera. *Annual Review of Entomology* **43**: 129–151.

Whitfield, J.B., 2002. Estimating the age of the polydnavirus/braconid wasp symbiosis. *Proceedings of the National Academy of Sciences* **99**: 7508–7513.

Wiens, J.A., 1989. *The Ecology of Bird Communities*. Cambridge University Press, Cambridge.

Williams, S.T., Reid, D.G., Littlewood, D.T.J., 2003. A molecular phylogeny of the Littorininae (Gastropoda: Littorinidae): unequal evolutionary rates, morphological parallelism, and biogeography of the southern ocean. *Molecular Phylogenetics and Evolution* **28**: 60–86.

Williams, S.T., Ozawa, T., 2006. Molecular phylogeny suggests polyphyly of both the turban shells (family Turbinidae) and the superfamily Trochoidea (Mollusca: Vetigastropoda). *Molecular Phylogenetics and Evolution* **39**: 33–51.

Wilson, B., 1998a. Superfamily Cypraeoidea, *In*: Beesley, P.L., Ross, G.J.B., Wells, A. (Eds.), *Fauna of Australia, Vol. 5, Mollusca: The Southern Synthesis.* CSIRO Publishing, Melbourne, pp. 780–786.

Wilson, B., 1998b. Superfamily Velutinoidea, *In*: Beesley, P.L., Ross, G.J.B., Wells, A. (Eds.), *Fauna of Australia, Vol. 5, Mollusca: The Southern Synthesis.* CSIRO Publishing, Melbourne, pp. 786–790.

Windsor, D.A., 1998. Most of the species on Earth are parasites. *International Journal for Parasitology* **28**: 1939–1941.

Wirtz, P., 2011. New records of marine invertebrates from the coast of Senegal. *Arquipelago - Life and Marine Sciences* **28**: 7–9.

Wise, J.B., 1996. Morphology and phylogenetic relationships of certain pyramidellid taxa (Heterobranchia). *Malacologia* **37**: 443–511.

Witman, J.D., Sebens, K.P., 1992. Regional variation in fish predation intensity: a historical perspective in the Gulf of Maine. *Oecologia* **90**: 305–315.

Wood, C.L., Byers, J.E., Cottingham, K.L., Altman, I., Donahue, M.J., Blakeslee, A.M.H., 2007. Parasites alter community structure. *Proceedings of the National Academy of Sciences* **104**: 9335–9339.

Wrigley, A., 1944. English Eocene Eulimidae with notes on the torsion of *Eulima* and on Charlesworth's illustrations. *Journal of Molluscan Studies* **26**: 47–62.

Yang, Z., Wafula, E.K., Honaas, L.A., Zhang, H., Das, M., Fernandez-Aparicio, M., Huang, K., Bandaranayake, P.C.G., Wu, B., Der, J.P., Clarke, C.R., Ralph, P.E., Landherr, L., Altman, N.S., Timko, M.P., Yoder, J.I., Westwood, J.H., dePamphilis, C.W., 2015. Comparative transcriptome analyses reveal core parasitism genes and suggest gene duplication and repurposing as sources of structural novelty. *Molecular Biology and Evolution* **32**: 767–790.

Yokoyama, M. 1922. Fossils from the Upper Musashino of Kazusa and Shimosa. *Journal of the Collage of Science, Tokyo Imperial University* **44**: 1–200.

Zapata, F., Wilson, N.G., Howison, M., Andrade, S.C.S., Jörger, K.M., Schrödl, M., Goetz, F.E., Giribet, G., Dunn, C.W., 2014. Phylogenetic analyses of deep gastropod relationships reject Orthogastropoda. *Proceedings of the Royal Society B* **281**: 20141739.

Zietara, M.S., Lumme, J., 2002. Speciation by host switch and adaptive radiation in a fish parasite genus *Gyrodactylus* (Monogenea, Gyrodactylidae). *Evolution* **56**: 2445–2458.

Zou, S., Li, Q., Kong, L., 2011. Additional gene data and increased sampling give new insights into the phylogenetic relationships of Neogastropoda, within the caenogastropod phylogenetic framework. *Molecular Phylogenetics and Evolution* **61**: 425–435.

Appendix 1.

Supplementary data for Chapter 1

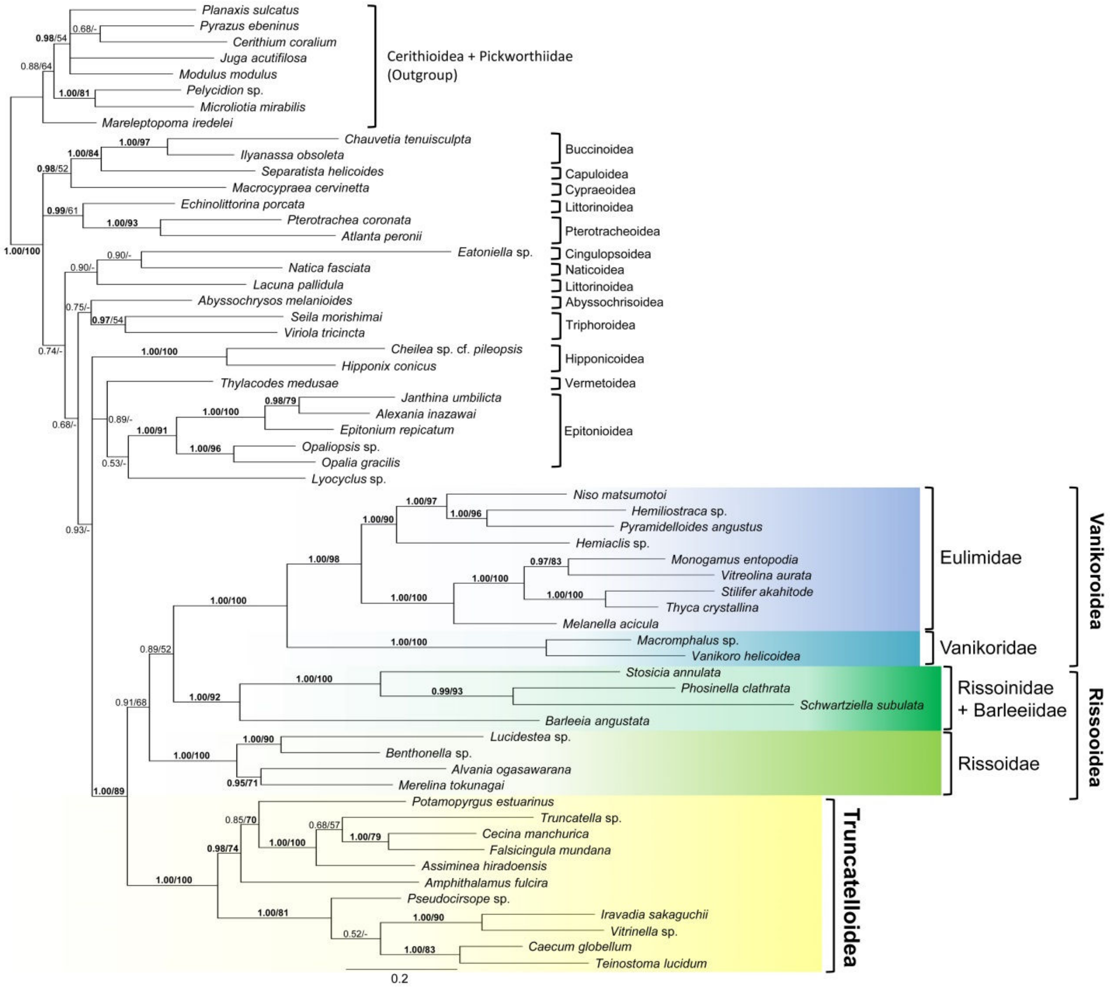


Figure S1-1. Bayesian phylogeny of Hypsogastropoda inferred from 2gPA alignment of 28S (D1–D5) and COI genes (1,926 sites in total). Numerals on branches denote posterior probabilities (PP, left) and likelihood-based bootstrap values shown as percentages (BS, right); significant support in bold (PP ≥ 0.95, BS ≥ 70%).

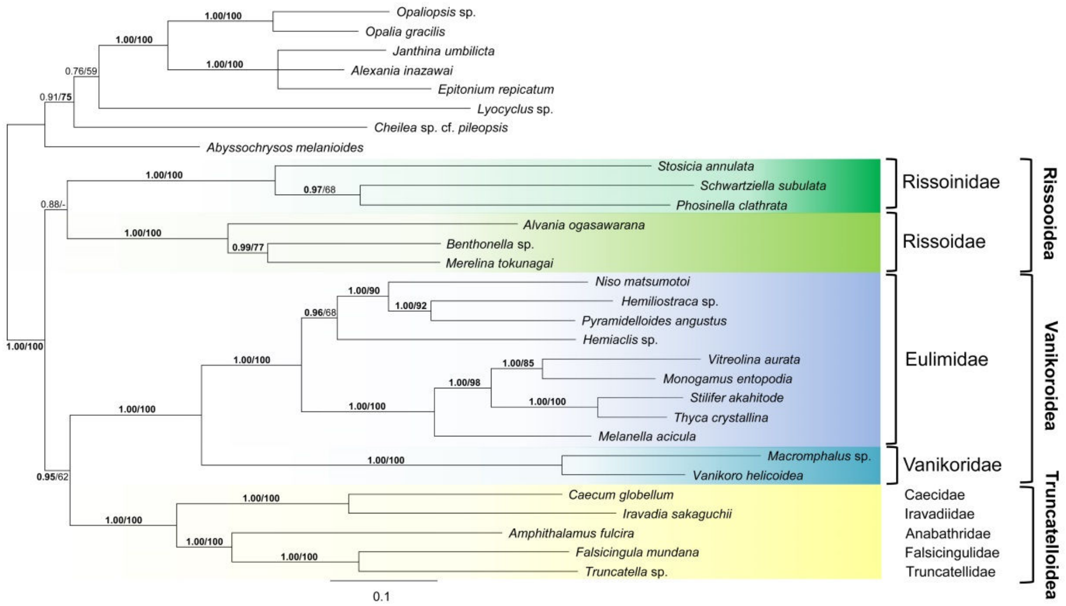


Figure S1-2. Bayesian phylogeny of Vanikoroidea, Truncatelloidea and Rissooidea inferred from 5gPA alignment of 28S (D1–D7b), 18S, H3, 16S and COI genes (5,006 sites in total). Numerals on branches denote posterior probabilities (PP, left) and likelihood-based bootstrap values shown as percentages (BS, right); significant support in bold (PP ≥ 0.95, BS ≥ 70%).

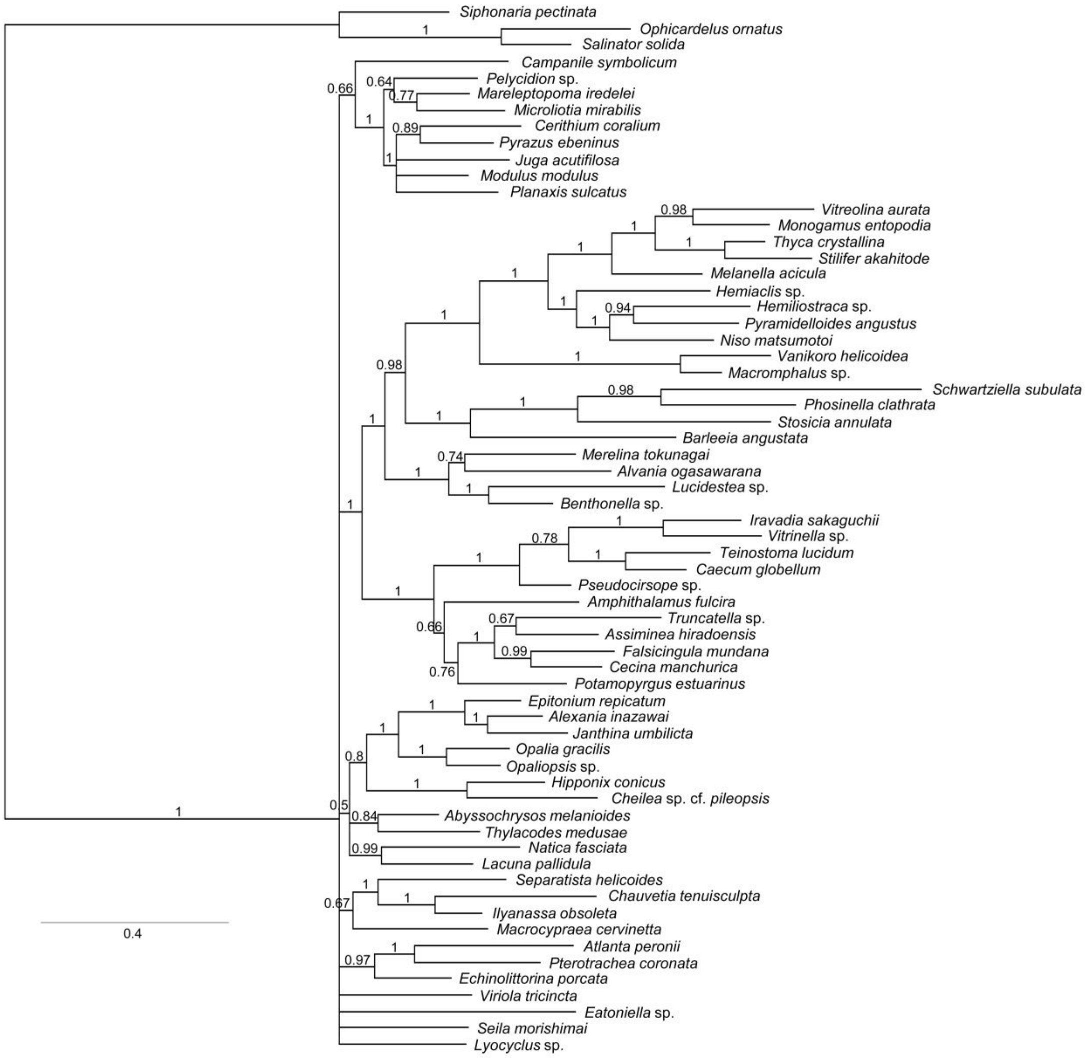
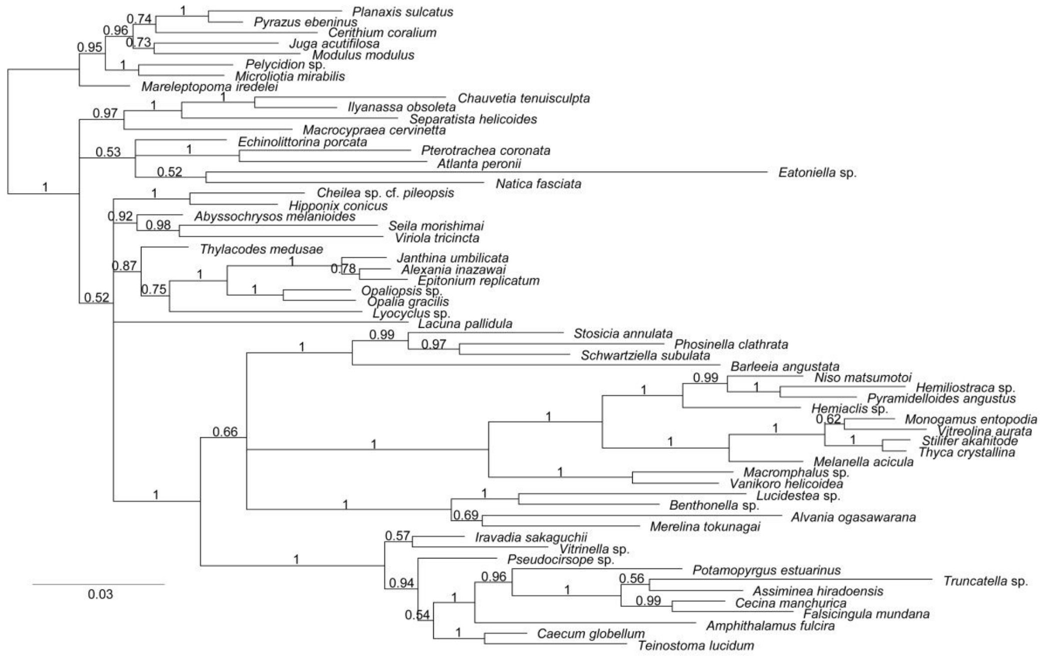


Figure S1-3. Bayesian tree inferred from 28S D1–D5 and COI sequences with *Ophicardelus ornatus*, *Salinator solida*, *Siphonaria pectinata* (Heterobranchia) and *Campanile symbolicum* (Campaniloidea) as outgroup taxa.

2gPA alignment



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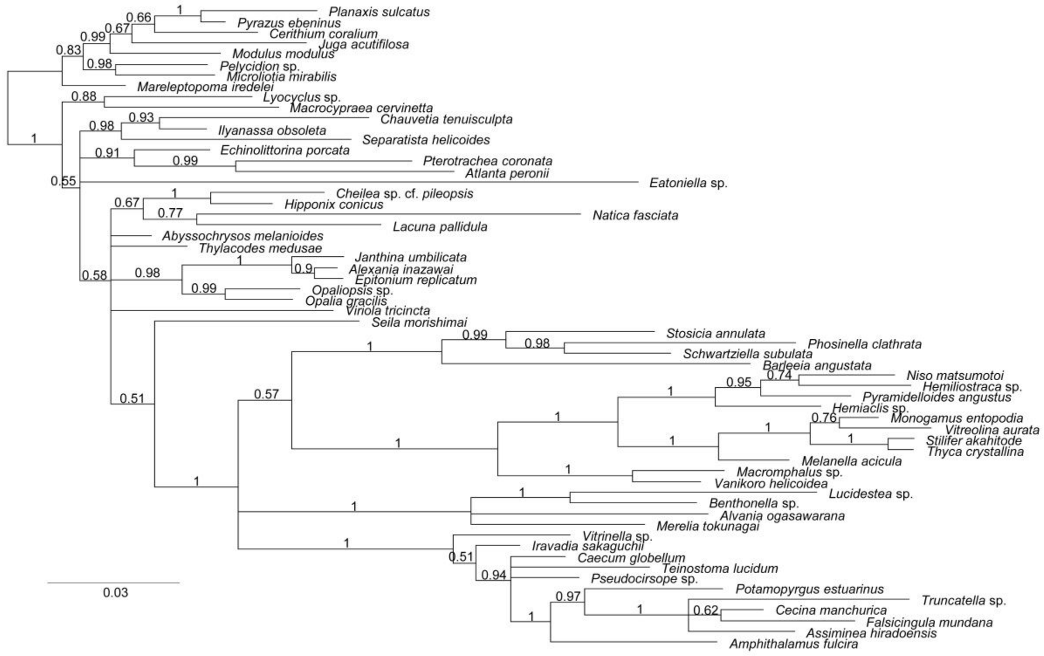
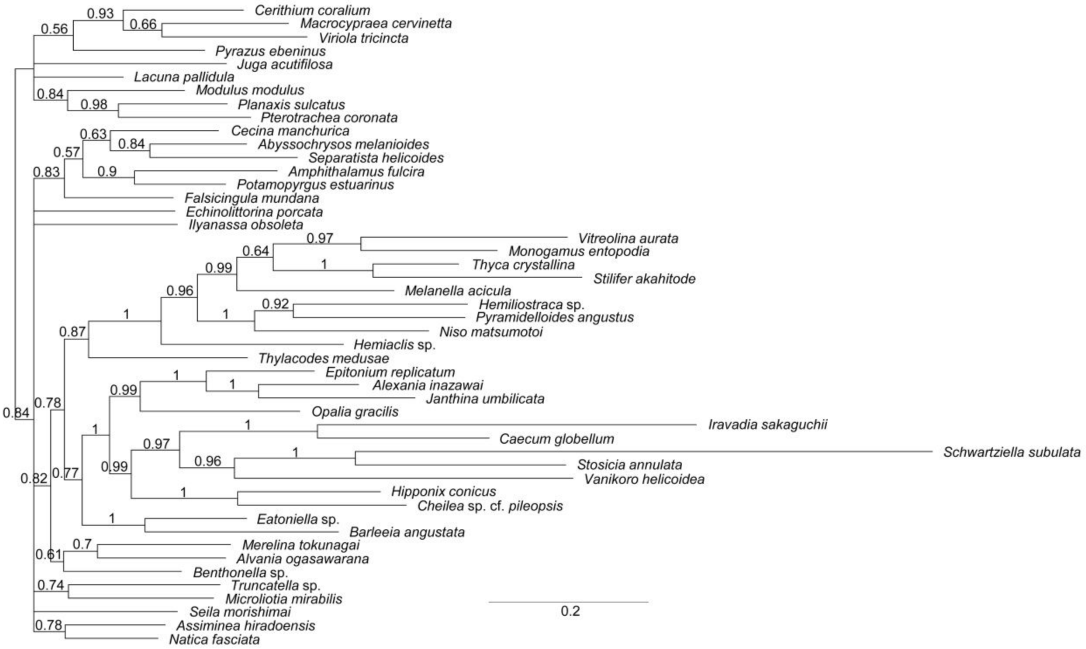


Figure S1-4. Bayesian trees inferred from 28S (D1–D5) gene sequences for two-gene dataset.

2gPA alignment



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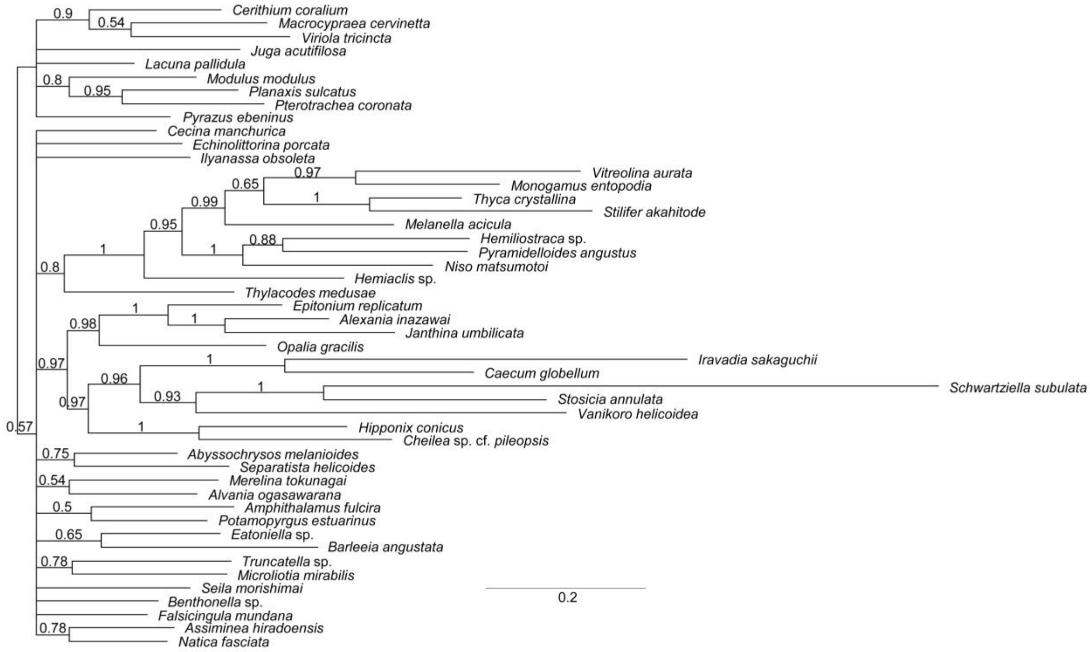
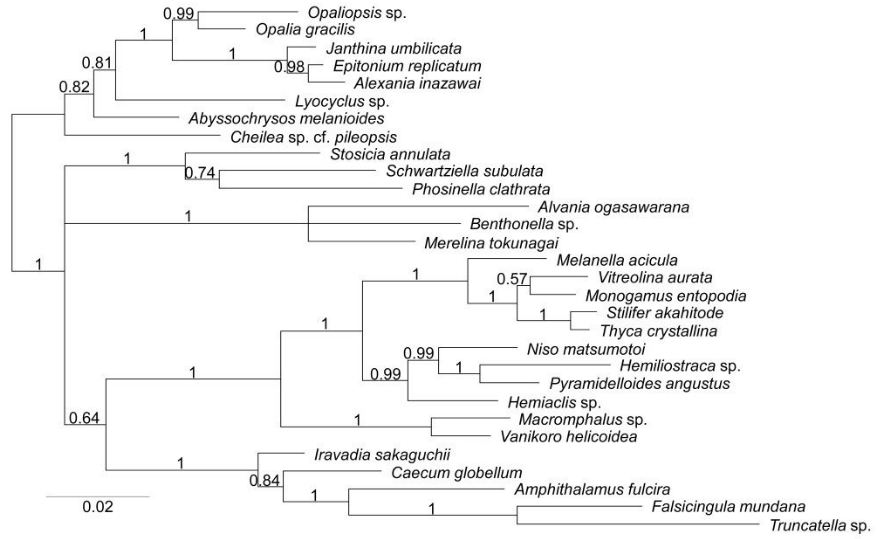


Figure S1-5. Bayesian trees inferred from COI gene sequences for two-gene dataset.

5gPA alignment



5gGB alignment

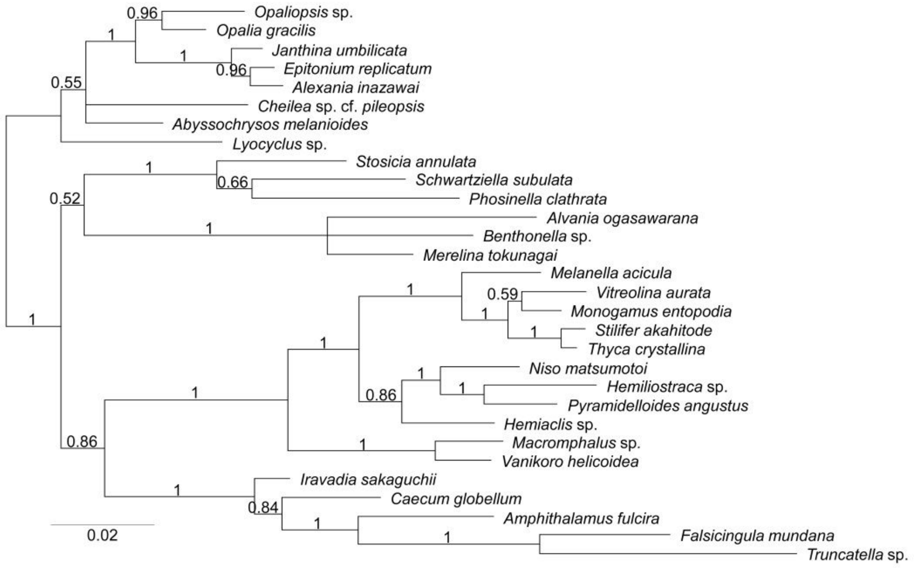
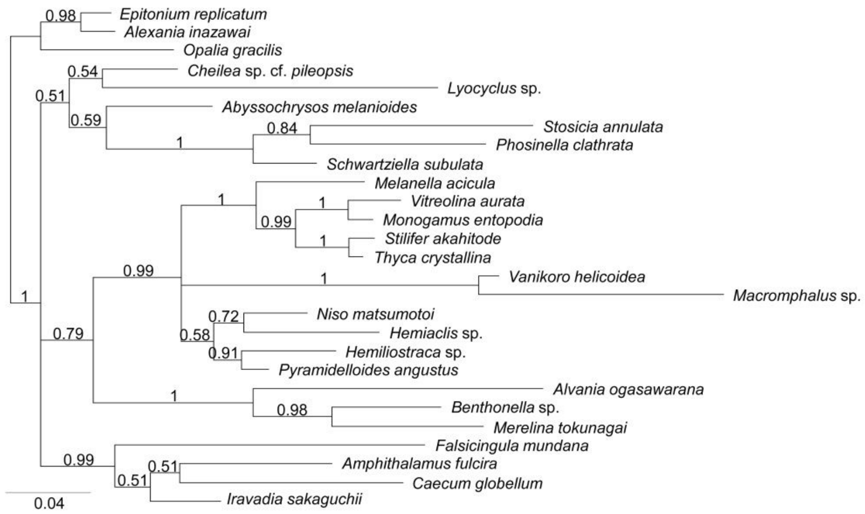


Figure S1-6. Bayesian trees inferred from 28S (D1–D7b) gene sequences for five-gene dataset.

5gPA alignment



5gGB alignment

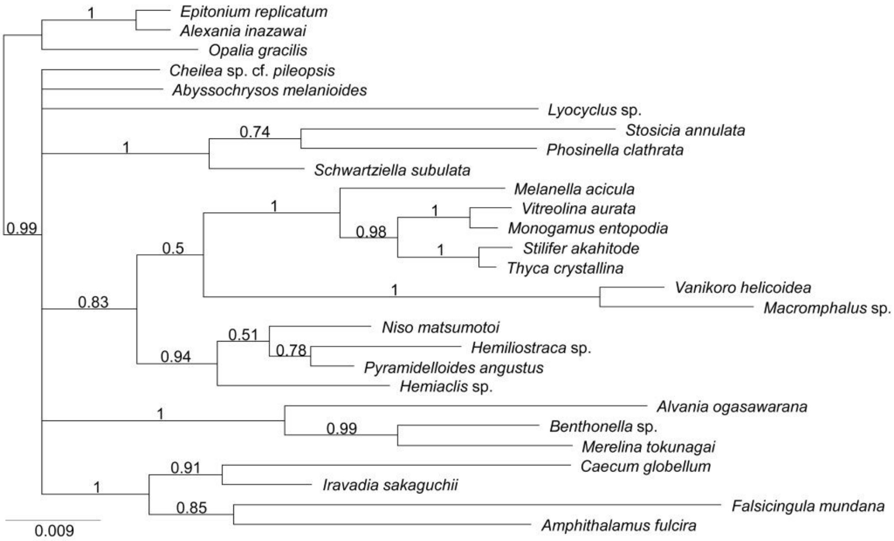
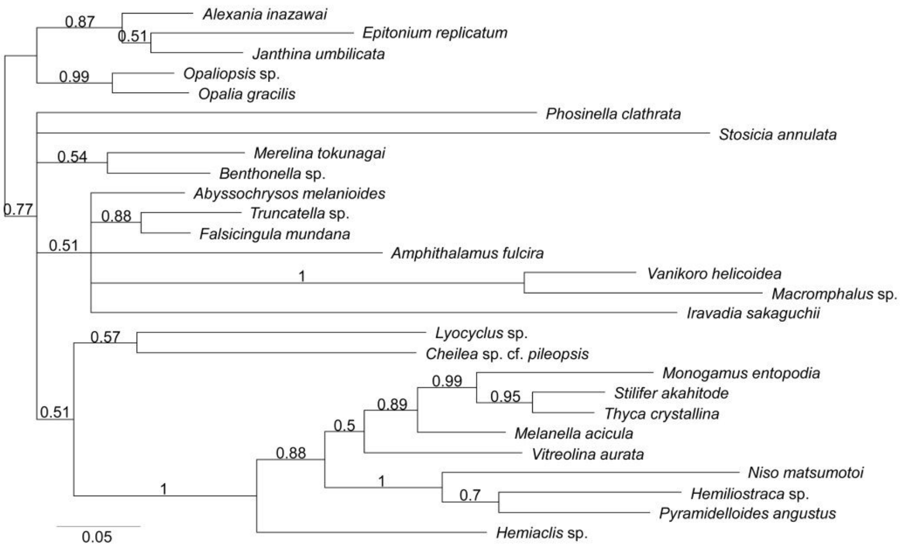


Figure S1-7. Bayesian trees inferred from 18S gene sequences for five-gene dataset.

5gPA alignment



5gGB alignment

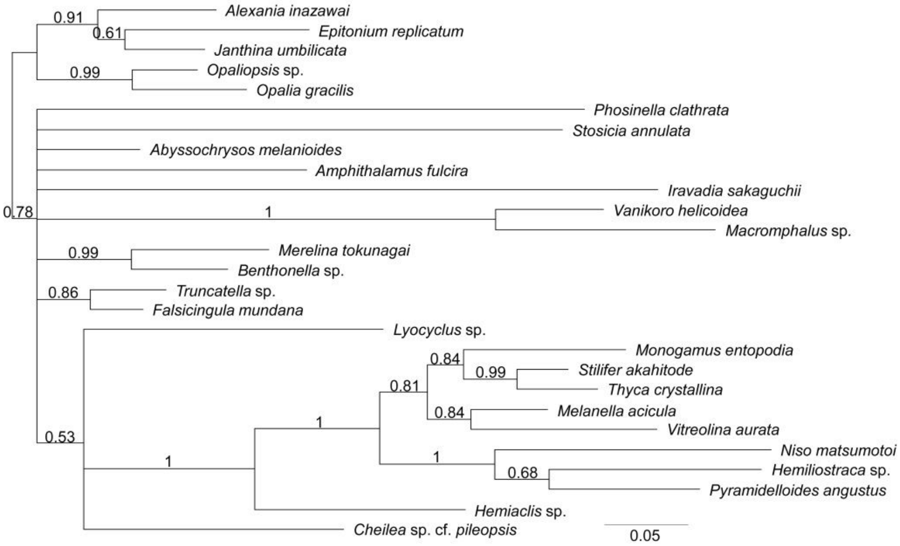
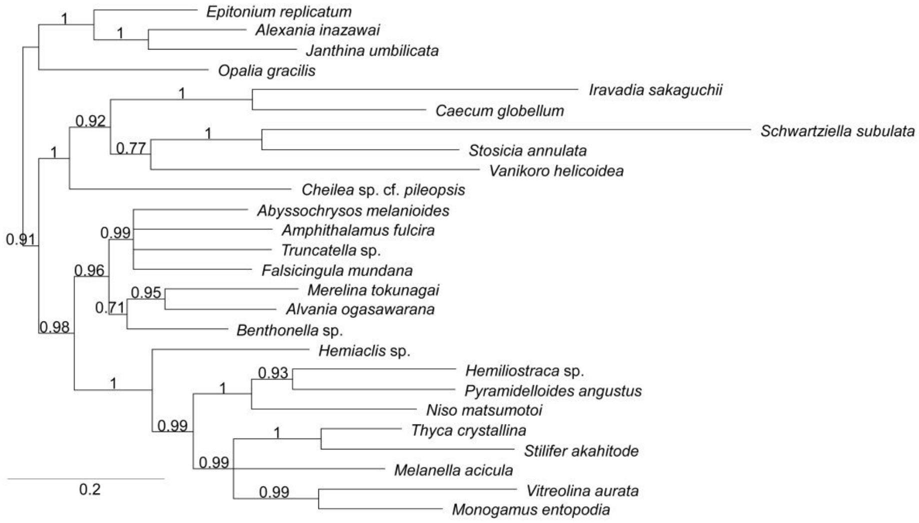


Figure S1-8. Bayesian trees inferred from 16S gene sequences for five-gene dataset.

5gPA alignment



5gGB alignment

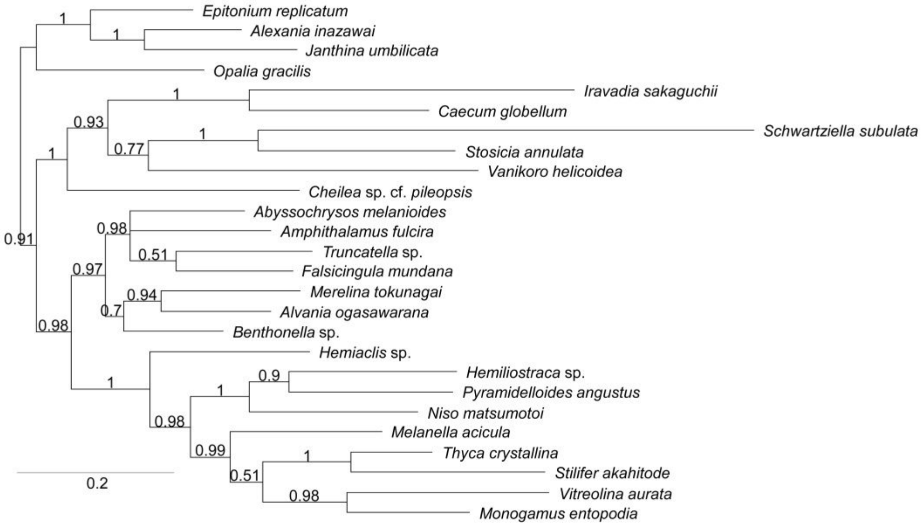


Figure S1-9. Bayesian trees inferred from COI gene sequences for five-gene dataset.

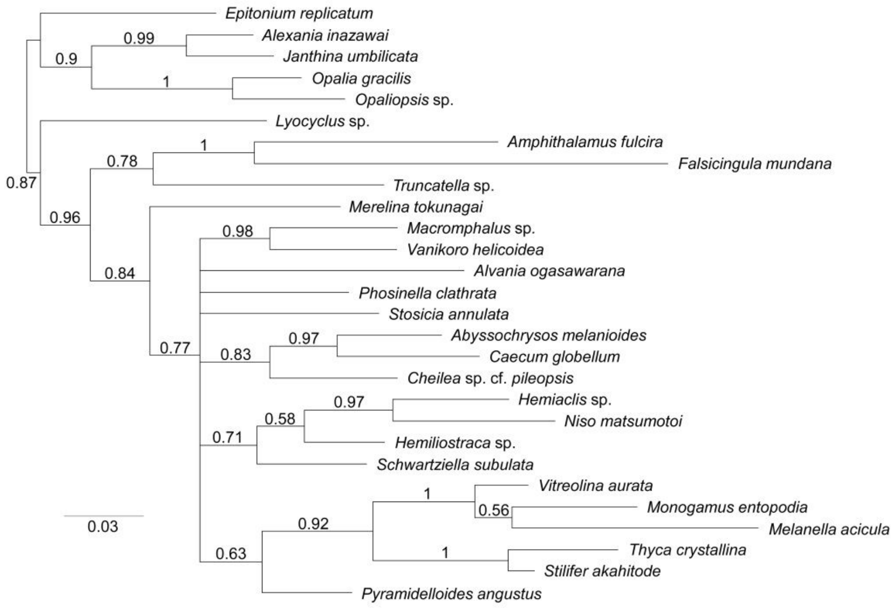


Figure S1-10. Bayesian tree inferred from H3 gene sequences for five-gene dataset.

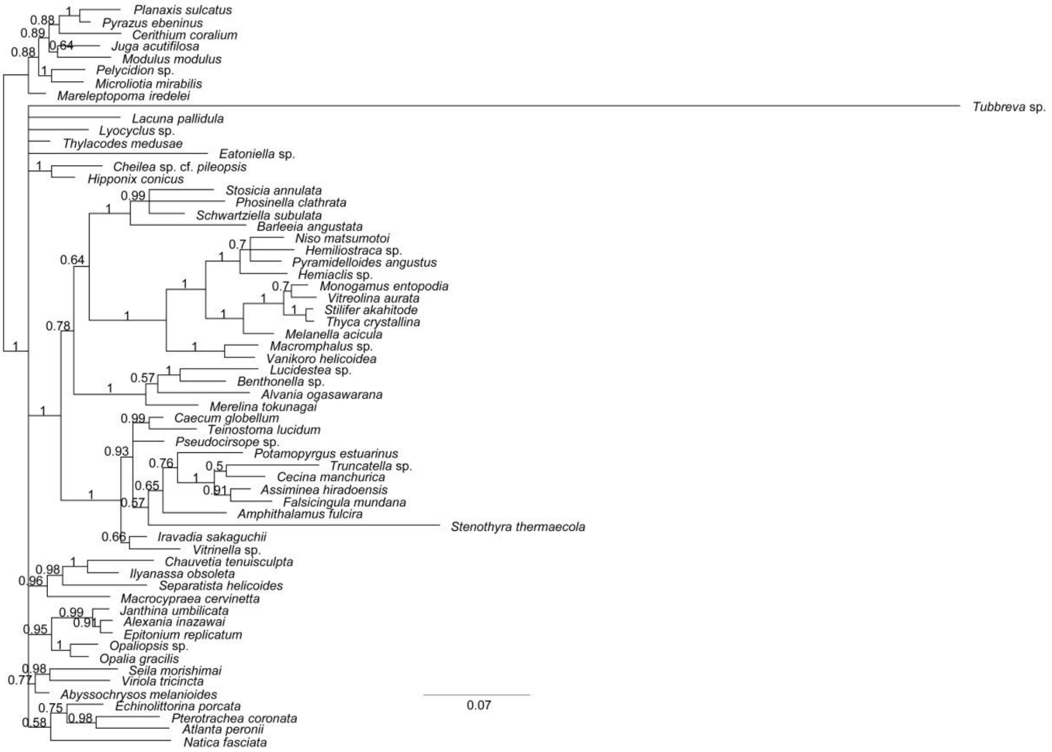


Figure S1-11. Bayesian tree inferred from 28S (D1–D5) gene sequences with *Tubbreva* sp. and *Stenothyra thermaecola*.

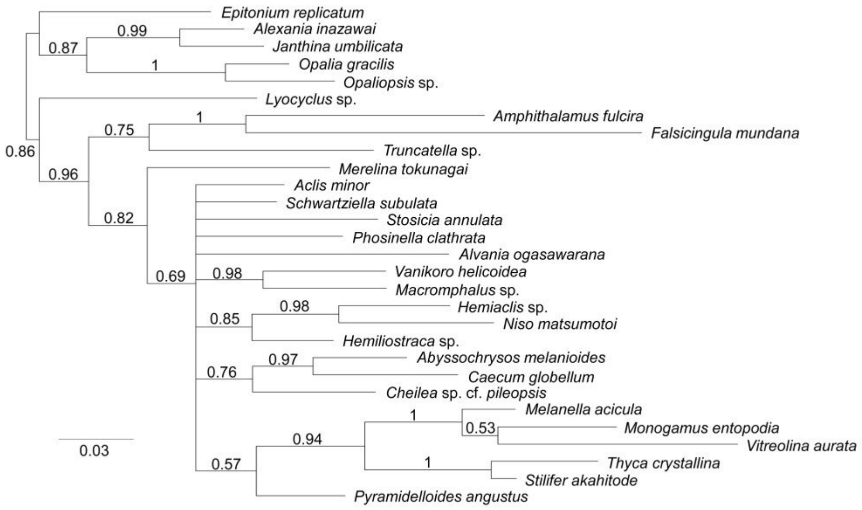


Figure S1-12. Bayesian tree inferred from H3 gene sequences with *Aclis minor*.

Figure S1-13. Live-taken photographs of *Vanikoro* snails, which are almost always found attached on/near sponges on the underside of deep-buried coral rubble. Left: *Vanikoro helicoidea* in Kakeroma Island, Amami, Japan, courtesy of R. Goto. Right: *Vanikoro* sp. cf. *plicata* in Aore Island, Santo, Vanuatu. Note that the shape and arrangement of the greenish egg capsules differ between the two species.

Table S1-1. Nucleotide sequences of primers. Circles represent primers used in each chapter.

Locus	Primer	Sequence	Direction	Chapter 1	Chapter 2	Chapter 3	Reference
28S	28SC1	ACCCGCTGAATTTAAGCAT	Forward			○	Dayrat et al. (2001)
	LSU5	TAGGTCGACCCGCTGAAYTTAAGCA	Forward	○	○	○	Littlewood et al. (2000)
	het3	CCCCAGTAACGGCGAGTGAAGC	Forward			○	Kano et al. (in prep)
	28S_400F	ACTCCATCTAAGGCTA	Forward			○	Kano et al. (in prep)
	28S_500R	CGGTTTCACGTACTCT	Reverse			○	Kano et al. (in prep)
	900F	CCGTCTTGAAACACGGACCAAG	Forward	○	○		Lockyer et al. (2003)
	ECD2S	CTTGGTCCGTGTTTCAAGACGG	Reverse	○	○	○	Williams & Ozawa (2006)
	1100F	GGACCCGAAAGATGGTGAACTATGC	Forward	○	○		Takano & Kano (2014)
	D3m	GACGATCGATTTGCACGTCAGAAT	Reverse	○	○	○	Takano & Kano (2014)
	28SD3	GACGATCGATTTGCACGTCA	Reverse			○	Vonnemann et al. (2005)
	LSU1600R	AGCGCCATCCATTTTCAGG	Reverse	○	○		Williams et al. (2003)
	FL	AAGTGGAGAAGGGTTCCATGT	Forward	○			Takano & Kano (2014)
	hetR	TATCTCCGGGCAAGCCGATTC	Reverse	○			Takano & Kano (2014)
	na2	AGCCAATCCTTATCCCGAAG	Reverse	○			Kano et al. (2002)
18S	18A1	CCTACCTGGTTGATCCTGCCAG	Forward	○	○	○	Steiner & Dreyer (2003)
	NS2	GGCTGCTGGCACCAGACTTGC	Reverse		○	○	White et al. (1990)
	188f	GGATCTATTGGAGGGCAAGT	Forward	○	○	○	Nakamura et al. (2007)
	NS4	CTTCCGTCAATTCCTTTAAG	Reverse		○		White et al. (1990)
	189r	TCGGAATTAACCAGACAAATC	Reverse	○	○	○	Nakamura et al. (2007)
	NS5	AACTTAAAGGAATTGACGGAAG	Forward	○	○	○	White et al. (1990)
	1800r	ATGATCCTTCCGCAGGTTCACC	Reverse	○	○	○	Steiner & Dreyer (2003)

H3	H3MF	ATGGCTCGTACCAAGCAGACTGC	Forward	○	○	○	Kano (2008)
	H3MRI	GGCATGATTGTTACACGCTTGGCGTG	Reverse	○	○	○	Kano et al. (2009)
	H3MR	TGGATGTCCTTGGGCATGATTGTTAC	Reverse	○	○	○	Kano (2008)
16S	Opis A-Rm	ACCCTTATACAARAGG	Reverse			○	This study, modified from Grande et al. (2004)
	16Sar-L	CGCCTGTTTATCAAAAACAT	Forward	○	○	○	Palumbi et al. (1991)
	16Sar-veti	GCCTGTTTAGCAAAAACA	Forward	○	○	○	Kano et al. (2009)
	Opis 1-R	ATTAYGCTACCTTAGCACRGTCA	Reverse			○	Grande et al. (2002)
	16Sab-veti	GATCACGTAAGATTTTAATGGTCG	Reverse	○	○	○	Kano et al. (2009)
	16Sbr-H	CCGGTCTGAACTCAGATCACGT	Reverse	○	○	○	Palumbi et al. (1991)
12S	12S1	GTGCCAGCAGTCGCGGTTAXA	Forward		○		Kano et al. (in prep)
	12S2v	CGAGAGYGACGGGCGA	Reverse		○		Kano et al. (in prep)
	12S2	TACCCCTACTATGTTACGACT	Reverse		○		Kano et al. (in prep)
COI	LCO1490	GGTCAACAAATCATAAAGATATTGG	Forward	○	○	○	Folmer et al. (1994)
	Opis A-Fm	GGRGCARTTAATTTTATTAC	Forward			○	This study, modified from Grande et al. (2004)
	LCOmod	TCTACTAATCATAAGGAYATYGGNAC	Forward	○	○		Kano (2008)
	HCOmod	ACTTCTGGGTGTCCRAARAAYCARAA	Reverse	○	○		Kano (2008)
	HCO2198	TAAACTTCAGGGTGACCAAAAAATCA	Reverse	○	○	○	Folmer et al. (1994)
	Opis COI-Fm	ACTTTTTTTCCTCAACATTTYTT	Forward			○	Kano et al. (in prep), modified from Grande et al. (2004)

Table S1-2: Pairwise p-distance matrix of H3 sequences. *S. subulata* and *Macromphalus* sp. show the lowest distances for *A. minor* (red-letters).

Aclis minor																												
Vanikoro helicoidea	0.088																											
Macromphalus sp.	**0.062**	0.075																										
Vitreolina auratus	0.104	0.091	0.094																									
Monogamus sp.	0.097	0.107	0.081	0.055																								
Thyca cristallina	0.097	0.101	0.110	0.101	0.081																							
Stilifer akahitode	0.091	0.097	0.097	0.084	0.071	0.042																						
Melanella acicula	0.110	0.097	0.097	0.088	0.088	0.130	0.123																					
Hemiaclis sp.	0.094	0.107	0.104	0.114	0.123	0.127	0.120	0.127																				
Hemiliostraca sp.	0.071	0.081	0.075	0.101	0.104	0.123	0.107	0.110	0.071																			
Niso matsumotoi	0.081	0.104	0.084	0.110	0.107	0.127	0.120	0.101	0.071	0.078																		
Pyramidelloides angusta	0.071	0.094	0.071	0.091	0.101	0.101	0.091	0.104	0.091	0.068	0.075																	
Epitonium replicatum	0.146	0.140	0.130	0.149	0.166	0.162	0.166	0.159	0.127	0.136	0.133	0.117																
Alexania inazawai	0.088	0.110	0.104	0.123	0.127	0.133	0.123	0.136	0.075	0.084	0.088	0.084	0.101															
Opalia gracilis	0.114	0.143	0.149	0.156	0.175	0.156	0.140	0.175	0.133	0.143	0.146	0.127	0.120	0.094														
Janthina umbricata	0.084	0.114	0.097	0.107	0.123	0.127	0.120	0.133	0.078	0.091	0.101	0.088	0.107	0.042	0.104													
Abyssochrysos melanoides	0.075	0.088	0.094	0.110	0.101	0.114	0.114	0.117	0.094	0.075	0.097	0.094	0.143	0.104	0.146	0.097												
Schwartziella subulata	**0.052**	0.097	0.081	0.104	0.110	0.117	0.117	0.107	0.068	0.062	0.088	0.084	0.136	0.091	0.123	0.071	0.075											
Manzonia tokunagai	0.088	0.107	0.084	0.120	0.114	0.127	0.117	0.117	0.078	0.088	0.084	0.097	0.127	0.088	0.130	0.084	0.101	0.091										
Amphithalamus fulcira	0.149	0.143	0.153	0.182	0.188	0.156	0.162	0.188	0.127	0.140	0.149	0.136	0.159	0.133	0.153	0.149	0.143	0.143	0.149									
Stosicia annulata	0.078	0.101	0.081	0.114	0.114	0.123	0.101	0.123	0.104	0.101	0.097	0.097	0.143	0.107	0.127	0.110	0.097	0.094	0.107	0.136								
Rissoina clathrata	0.084	0.088	0.088	0.097	0.101	0.127	0.104	0.101	0.107	0.094	0.104	0.091	0.133	0.110	0.133	0.104	0.110	0.081	0.097	0.169	0.088							
Caecum globella	0.088	0.101	0.107	0.110	0.130	0.104	0.104	0.133	0.101	0.094	0.107	0.091	0.136	0.091	0.130	0.081	0.065	0.084	0.114	0.156	0.091	0.123						
Truncatella sp.	0.114	0.114	0.110	0.146	0.146	0.153	0.143	0.143	0.101	0.107	0.110	0.097	0.127	0.084	0.136	0.101	0.123	0.107	0.114	0.127	0.123	0.143	0.127					
Alvania ogasawarana	0.114	0.097	0.088	0.127	0.120	0.136	0.127	0.136	0.104	0.114	0.117	0.104	0.143	0.114	0.166	0.110	0.123	0.114	0.107	0.156	0.104	0.104	0.123	0.117				
Cheilea cf. *pileopsis*	0.071	0.104	0.088	0.127	0.110	0.117	0.120	0.136	0.107	0.084	0.104	0.101	0.130	0.084	0.120	0.088	0.068	0.081	0.104	0.143	0.091	0.097	0.091	0.107	0.104			
Falsicingula mundana	0.136	0.175	0.159	0.198	0.198	0.205	0.195	0.211	0.153	0.140	0.172	0.146	0.172	0.162	0.166	0.172	0.172	0.159	0.156	0.159	0.146	0.146	0.159	0.159	0.153	0.162		
cf. *Opaliopsis* sp.	0.107	0.130	0.130	0.143	0.159	0.140	0.130	0.172	0.117	0.127	0.120	0.120	0.123	0.091	0.058	0.088	0.133	0.120	0.127	0.153	0.130	0.130	0.130	0.127	0.133	0.110	0.162	
Lyocyclus sp.	0.149	0.159	0.162	0.166	0.179	0.153	0.172	0.195	0.127	0.146	0.149	0.130	0.123	0.114	0.140	0.117	0.149	0.136	0.136	0.156	0.159	0.149	0.130	0.140	0.156	0.133	0.169	0.143

Appendix 2.

5年以内に雑誌などで刊行予定のため、非公開。

Appendix 3.

5年以内に雑誌などで刊行予定のため、非公開。