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ScienceDirect
Molecular Phylogenetics and Evolution 41 (2006) 436–444
MOLECULAR PHYLOGENETICS AND EVOLUTION
www.elsevier.com/locate/ympev

A molecular phylogenetic analysis of strombid gastropod morphological diversity

Jared M. Latiolais [a], Michael S. Taylor [a,b], Kaustuv Roy [c,1], Michael E. Hellberg [a,*,1]

[a] Department of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803, USA
[b] Department of Biological Sciences, Univ of Notre Dame, Notre Dame, IN 46556-0369, USA
[c] Section of Ecology, Behavior and Evolution, Division of Biological Sciences, University of California, San Diego, 9500 Gilman Drive, La Jolla, CA 92093-0116, USA

Received 9 February 2006; revised 19 May 2006; accepted 24 May 2006

Abstract

The shells of strombid gastropods show a wide variety of forms, ranging from small and fusiform to large and elaborately ornamented with a strongly flared outer lip. Here, we present the first species-level molecular phylogeny for strombids and use the resulting phylogenetic framework to explore relationships between species richness and morphological diversity. We use portions of one nuclear (325 bp of histone H3) and one mitochondrial (640 bp of cytochrome oxidase I, COI) gene to infer relationships within the two most species-rich genera in the Strombidae: *Strombus* and *Lambis*. We include 32 species of *Strombus*, representing 10 of 11 extant subgenera, and 3 of the 9 species of *Lambis*, representing 2 of 3 extant subgenera. Maximum likelihood and Bayesian analyses of COI and of H3 and COI combined suggest *Lambis* is nested within a paraphyletic *Strombus*. Eastern Pacific and western Atlantic species of *Strombus* form a relatively recent monophyletic radiation within an older, paraphyletic Indo-West Pacific grade. Morphological diversity of subclades scales positively with species richness but does not show evidence of strong phylogenetic constraints.

Keywords: Morphospace; Shell shape; Cytochrome oxidase I; Histone H3; *Strombus*; *Lambis*

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1. Introduction

Biological diversity can be measured in ways ranging from simple counts of species or higher taxa to quantitative measures of morphological, functional or phylogenetic diversity (Harper and Hawksworth, 1994; Purvis and Hector, 2000), but the relationships between various measures of biodiversity remain poorly known. Morphological diversity is one of the more intuitive measures of biodiversity (Williams et al., 1994), but richness of species or higher taxa can be a poor predictor of morphological diversity, both for living biota as well as for extinct taxa (Foote, 1995, 1997; Roy and Foote, 1997; Roy et al., 2001; McClain et al., 2004). To date, studies of morphological diversity patterns in a phylogenetic framework have focused on vertebrates (Hulsey and Wainwright, 2002; Harmon et al., 2003; Ricklefs, 2004, 2005), freshwater mollusks (Wilson et al., 2004) or fossil taxa (e.g., Wagner, 1995, 1996); such analyses are lacking for living marine invertebrates.

The morphological variation seen within the marine gastropod family Strombidae (conchs and their kin) make them fine candidates for examining how morphological diversity scales with species richness. All strombids exhibit determinate shell growth (Abbott, 1960; Vermeij and Signor, 1992), providing an unambiguous gauge of adult size and shape. The two most species-rich of traditionally defined strombid genera are *Lambis* Röding 1798 and *Strombus* Linné 1758 (Abbott, 1960, 1961). Species in both of these genera are herbivores associated with shallow-water reefs and grass beds. Both possess similar soft tissue

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[*] Corresponding author. Fax: +1 225 578 2597.
E-mail address: mhellbe@lsu.edu (M.E. Hellberg).
[1] These authors contributed equally to this work.

1055-7903/$ - see front matter © 2006 Elsevier Inc. All rights reserved.
doi:10.1016/j.ympev.2006.05.027

anatomies, egg masses, and radulae (Abbott, 1961), which led Kronenberg (1998) to suggest that *Lambis* and *Strombus* belong together in a group within the Strombidae, even though their shells show striking morphological differences (Fig. 1). In a previous study, Roy et al. (2001) examined the relationship between spatial patterns of morphological diversity and species richness in *Strombus* and *Lambis* but, because of the lack of a well-supported phylogeny, could not examine how species richness of individual clades of strombid gastropods related to their morphological diversity.

The last major taxonomic revisions of *Strombus* and *Lambis* were undertaken almost half a century ago (Abbott, 1960, 1961). Since then, some subspecies have been elevated to species status (e.g., Mienis, 1971; Kronenberg and Vermeij, 2002), subgenera have been raised to genera (e.g., Kronenberg, 1998), putative species have been revealed as hybrids (Kronenberg, 1993, 1999), and species have been carved from existing genera to create new monotypic genera (e.g., *Mirabilistrombus*, Kronenberg, 1998; *Tridentarius*, Kronenberg and Vermeij, 2002). Few studies, however, have addressed relationships among subgenera (sensu Abbott). Stone (2001) explored relationships among nine species of *Lambis* and three *Strombus* outgroups using morphological characters. One *Lambis* species (*L. crocata*) fell among the outgroups, suggesting that *Lambis* was paraphyletic and *Strombus* was polyphyletic, although bootstrap support values for all relationships were too low (<40%) for any robust conclusions. At a higher taxonomic level, Kronenberg and Vermeij (2002) recognized a shell character (glazing of the outer lip) shared by all Neotropical species as well as some Indo-Pacific (sub)genera, including *Euprotomus* and *Tridentatus*. Kronenberg and Vermeij (2002) also agreed with Stone (2001) that *Lambis* and *Strombus sensu lato* (*s.l.*) were polyphyletic or paraphyletic.

Here, we use DNA sequences from two protein-coding gene regions, one mitochondrial (cytochrome oxidase subunit I, COI) and one nuclear (histone subunit 3, H3), to infer molecular phylogenetic relationships among species and superspecific taxa within *Lambis* and *Strombus*. We then use this molecular phylogeny in conjunction with quantitative measures of shell shape to examine the relationship between taxonomic and morphological diversity within this group. We also assess whether the strombids of the New World are a monophyletic radiation, or a polyphyletic assemblage of species collected from a more ancient and species-rich Indo-West Pacific fauna.

2. Materials and methods

2.1. Selection of taxa

This study includes 31 species of *Strombus*, representing 10 of the 11 extant subgenera of Abbott (1960), and 3 of the 9 species of *Lambis* representing 2 of the 3 extant subgenera (Supplementary material Table 1). Our taxon sampling is nearly complete for the Eastern Pacific and Western Atlantic regions (lacking only the Brazilian *S. goliath* of 12 species in total), but less so for the Indo-Pacific. Like most other invertebrate groups, the total number of Indo-Pacific species belonging to Strombidae is currently unknown but our sample of 23 species represents about a third of the 72 named species and subspecies of Abbott (1960, 1961). However, because our study includes representatives from nearly all traditionally defined subgenera (sensu Abbott, 1960, 1961) of *Strombus* and *Lambis*, the resulting phylogeny should reflect the relationships among the main lineages within Strombidae.

2.2. DNA extraction, amplification, and sequencing

Genomic DNA was extracted using protocols that varied with the quality and age of samples (see Supplementary material Table 1 for collection information). For well preserved museum samples and for fresh tissue, we used a modified cetyltrimethylammonium bromide (CTAB) extraction, followed by phenol/chloroform extraction and alcohol precipitation protocol (Toonen, 1997). When this approach failed (usually for older museum samples), a modified version (Chase et al., 1998) of the QIAmp DNA

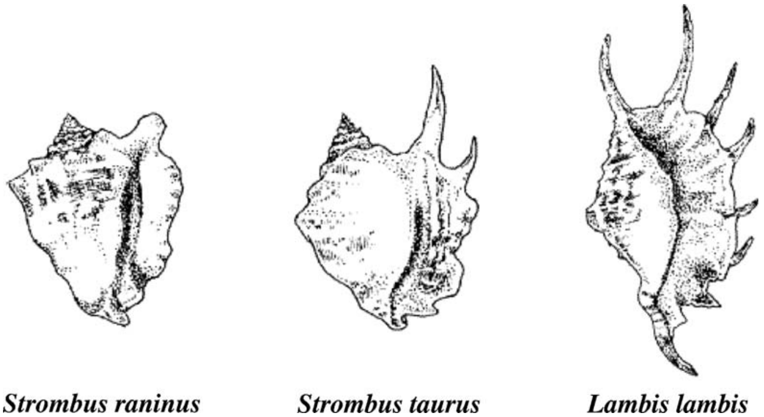

Fig. 1. Shell morphologies for three strombid species. *Strombus raninus* is a Caribbean species placed by Abbott (1960) in the subgenus *Tricornis*. *Strombus taurus*, also in *Tricornis*, is found in the Marshall and Marianas Islands of the central Pacific. *Lambis lambis* ranges from eastern Africa to the central Pacific. Illustrations by Ben Anders.