



New insights into diversity and evolution of deep-sea Mytilidae (Mollusca: Bivalvia)

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ABSTRACT

Bathymodiolinae mussels have been used as a biological model to better understand the evolutionary origin of faunas associated with deep-sea hydrothermal vents and cold seeps. Most studies to date, however, have sampled with a strong bias towards vent and seep species, mainly because of a lack of knowledge of closely related species from organic falls. Here we reassess the species diversity of deep-sea mussels using two genes and a large taxon sample from the South-Western Pacific. This new taxonomic framework serves as a basis for a phylogenetic investigation of their evolutionary history. We first highlight an unexpected allopatric pattern and suggest that mussels usually reported from organic falls are in fact poorly specialized with regard to their environment. This challenges the adaptive scenarios proposed to explain the diversification of the group. Second, we confirm that deep-sea mussels arose from organic falls and then colonized hydrothermal vents and cold seeps in multiple events. Overall, this study constitutes a new basis for further phylogenetic investigations and a global systematic revision of deep-sea mussels.

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1. Introduction

Phylogenetic studies based on sampling that does not reflect the breadth of species diversity across ecosystems may lead to biased conclusions about their evolutionary history. However, prior knowledge regarding the possible relationships among ecosystems and the species diversity that should be sampled to properly address evolutionary issues are not always available. Evolutionary studies focusing on evolutionary relationships among organisms from deep-sea ecosystems often suffer from this problem (Samadi et al., 2006; McClain, 2007; O'Hara, 2007; Vrijenhoek, 2009).

In this regard, the case of hydrothermal vent and cold seep faunas is striking. Being the first discovered of chemosynthesis-based ecosystems, vents and seeps are one of the most amazing findings in oceans in the last 40 years (Cavanaugh et al., 2006; Dubilier et al., 2008; Lonsdale, 1977). As a consequence, both environments have been extensively studied and much data are now available regarding vent and seep ecology, as well as the physiological features of organisms living there (Hourdez and Lallier, 2006; Sibuet and Olu, 1998; Van Dover, 2000). But in contrast, their evolutionary origins are less well documented. Distel et al. (2000) neverthe-

less showed the close relationship between symbiont-bearing mussels of the genera *Bathymodiolus* Kenk and Wilson 1985 and *Tamu* Gustafson, Turner, Lutz and Vrijenhoek 1998 (Mytilidae: Bathymodiolinae), endemic to vents and seeps, and the small-sized mussels of the genera *Idas* Jeffreys 1876, *Adipicola* Dautzenberg 1927 and *Benthomodiolus* Dell 1987 (Mytilidae: Modiolinae), usually associated with shallower and more poorly known organic fall ecosystems. These mainly consist in sunken wood and vegetal debris but also include vertebrate bones. While decomposing at the deep-sea floor, organic falls produce sulfide that is used by mussels through chemosynthetic symbionts similar to those of vent and seep mussels (Duperron et al., 2009).

Distel et al. (2000) therefore clarified an important issue: understanding of the evolutionary history of vent and seep mussels requires knowledge of their relationships with relatives from organic falls. They additionally proposed the "wooden-step" hypothesis, which suggests that the mussels from vents and seeps evolved recently from ancestors associated with organic falls. Other data confirmed that many vent faunas are much younger than previously thought (Little and Vrijenhoek, 2003), and challenged previous hypotheses that suggested that hydrothermal vents had experienced "a long and continuing evolutionary history" (Newman, 1985). However, the "wooden-step" hypothesis proposed by Distel et al. (2000) relies more on ecological and

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paleontological data (Kiel and Goedert, 2006a; Smith and Baco, 2003) than on a reliable phylogenetic reconstruction. Indeed the 18S rRNA-based tree provided in their study was poorly resolved. More recent studies investigating the evolutionary origin of vent and seep mussels used more rapidly evolving genes and/or more taxa (Jones et al., 2006; Samadi et al., 2007; Lorion et al., 2009; Fujita et al., 2009). But at most 6 species from organic falls were used in these studies, out of at least 20 reported in the taxonomic literature (Dell, 1987; Warén and Carrozza, 1990). This is because most species were described long time ago: their soft tissues are lacking or not very suitable (formalin-fixed) for extensive molecular studies. New samples are thus strongly needed. As organic falls are unevenly distributed at the deep-sea floor and often thinly dispersed, sampling strategies different from those used for the exploration of vents and seeps are also required.

Once solved, the issue of sampling leads to other difficulties related to the poor taxonomic knowledge of mussels associated with organic falls. Indeed, many species were described on the basis of a few shell characters, providing few diagnosable characters (see however Dell, 1987 and Gustafson et al., 1998). The species descriptions were often based on a few specimens and thus generally without description of life stages, levels of environmental plasticity and any other details of polymorphism that characterize species. As a consequence, some species descriptions are ambiguous and the distinction between the genera *Idas* and *Adipicola* is debated (Gustafson et al., 1998; Warén, 1993). Therefore, the methods for species delimitation and the potential extent of diversity in mussels from organic falls would greatly benefit from a complete reassessment. This task is made difficult by several issues related to the evolutionary significance of shell characters classically used for alpha-taxonomy in molluscs (Knowlton, 2000; Vrijenhoek, 2009). Indeed, shell morphology in molluscs is subject to crypticism (Won et al., 2003b; Lee and Foighil, 2004; Johnson et al., 2009), environmental plasticity (Yeap et al., 2001; Wulfschleger and Jokela, 2002; Baker et al., 2003; Hollander et al., 2006; Pfenninger et al., 2006) and growth allometry (Horikoshi and Tsuchida, 1984). By contrast, using anatomical characters is often more useful in species delimitations (e.g. Cosel, 2008). However, especially when specimens are small (mussels from organic falls are usually less than 1 cm length), it is difficult and time consuming to analyze anatomical characters for many specimens. Moreover anatomy may not solve the problem of cryptic species.

In this context, it seems relevant to first use molecular characters for species delimitation (Blaxter, 2003; Blaxter, 2004; Vogler and Monaghan, 2007). From a given set of specimens, primary hypotheses of species delimitation can be drawn, for instance, using a criterion of similarity based on genetic distances. In an integrative framework (De Queiroz, 2007; Samadi and Barberousse, 2009), these primary hypotheses can be refined using the alternative criterion of monophyly (Meier and Willman, 2000; Sites and Marshall, 2004; Wheeler and Meier, 2000) and/or additional unlinked markers. The analysis of unlinked markers moreover allows evaluating the occurrence of gene flow between putative species, and thus to use the additional criterion of reproductive isolation (Taylor et al., 2000). Interestingly, recent methodological developments, rooted in the methodological framework of the coalescent theory, offer reliable opportunities to use simultaneously several of these criteria (Nielsen et al., 2001; Pons et al., 2006). Finally, the molecular hypotheses of species delimitation should be discussed using ecological and morphological data (Will and Rubinoff, 2004; Will et al., 2005).

To fulfill the sampling needs required to document the evolutionary history of deep-sea mussels, specimens associated to organic falls were collected throughout the South-West Pacific, one of the most species-rich area of the marine environments. Here, an integrative approach to taxonomy based on the analysis of

two unlinked gene fragments is used to overcome the poor evolutionary significance of shell characters. Both the sampling effort and the integrative approach provide a new taxonomic framework for the mussels associated to organic falls. This then serves as a basis for investigation of the diversification processes of mussels in the deep-sea. Hypotheses regarding the speciation patterns in mussels from organic falls are formulated and constitute first insights regarding biogeography in these environments. Relationships among mussels from organic falls with mussels from vent and seep allow discussion of various aspects of the “wooden-step” hypothesis such as the connectivity among habitats and the relative roles of adaptive and stochastic processes in the species diversification. Finally, implications of our results for further investigations of the systematics of deep-sea mussels are evaluated.

2. Material and methods

2.1. Sampling

Most of the new material studied herein was collected during cruises of the Tropical Deep-sea Benthos program from 1999 to 2006 (Bouchet et al., 2008). Samples from these cruises include 212 mussels collected off the Philippines (137 specimens), Vanuatu (58 specimens), Solomon Islands (9 specimens), Chesterfields Islands (4 specimens), and Fiji (4 specimens) (Fig. 1). These new samples represent a total of 18 localities and 59 stations trawled at depth ranging from 103 m to 1392 m (Supplementary data 1 and 2). Moreover two colonization modules were deployed off Noumea (New Caledonia) in October 2003 and September 2005

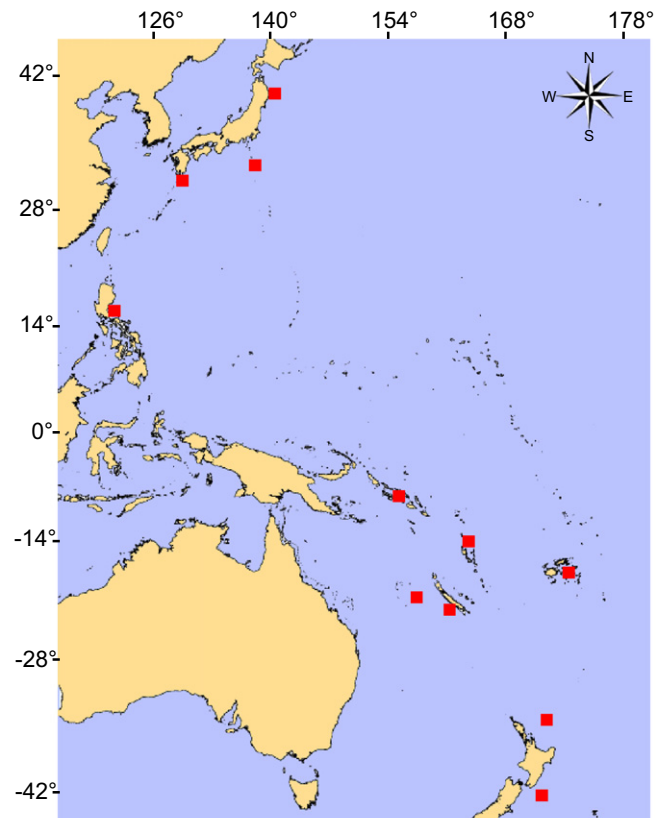


Fig. 1. Western Pacific map showing the distribution of localities (squares) from which mussels associated with organic falls were available for this study, taking into account new samples and data from Genbank.

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