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Molecular Phylogenetics and Evolution 44 (2007) 685–698
MOLECULAR PHYLOGENETICS AND EVOLUTION
www.elsevier.com/locate/ympev

A molecular phylogeny of the marine mussel genus *Perna* (Bivalvia: Mytilidae) based on nuclear (ITS1&2) and mitochondrial (COI) DNA sequences

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Received 1 September 2006; revised 17 December 2006; accepted 20 December 2006
Available online 31 December 2006

Abstract

A molecular phylogeny is presented for marine mussels of the genus *Perna*, based on nuclear (ITS1, ITS2) and mitochondrial (COI) DNA sequence data. The three generally recognised species (*Perna viridis*, *Perna perna* and *Perna canaliculus*) and one putative species (*Perna picta*) were each sampled from several locations within their known geographic distributions. A range of phylogenetic analyses was used to investigate the current taxonomic assignments, evolutionary relationships and the biogeographical history of the genus. The different analyses produced similar, well supported topologies and verified the monophyly of the genus with respect to five mytilid outgroup species. *P. perna* (Atlantic), *P. viridis* (Indo-West Pacific), and *P. canaliculus* (New Zealand) each formed distinct clades, confirming their specific status. Putative *P. picta* from North Africa clustered within the *P. perna* clade and is not regarded as a separate species. *P. perna* and *P. canaliculus* were the most closely related of the three species. Possible biogeographic explanations for the present species distributions are evaluated.

Keywords: *Perna*; Bivalves; Mussels; Internal transcribed spacer; ITS; Ribosomal RNA; COI

1. Introduction

Mussels of the genus *Perna* Philipsson 1788 belong to the Mytilidae or true mussels (Mollusca; Bivalvia; Lamellibranchia; Mytiloida; Mytilidae). This genus contains green and brown mussels from tropical, subtropical, warm temperate and cold temperate regions, mostly from the southern hemisphere, but also from northern Africa and the northern coasts of South America (Gosling, 2003; Siddall, 1980). Depending on the species in question, they exist in intertidal and shallow subtidal habitats, including estuaries, mangroves and open rocky shores (Gosling, 2003; Hicks, 2001; Siddall, 1980). These mussels are both ecologically and economically important throughout their ranges, and have long constituted an important source of human food (e.g., Griffiths and Branch, 1997; Nichol, 1986; Parkington, 1976; Swadling, 1977; Tomalin and Kyle, 1998). *Perna* species are cultured and/or harvested from wild populations in countries such as India, the Philippines, Thailand, China, Venezuela and New Zealand (Appukuttan and Nair, 1980; Hickman, 1991; Jeffs et al., 1999; Narasimham, 1980; Parulekar et al., 1982; Vakily, 1989).

As with other mytilid mussels, the genus *Perna* has a somewhat confused taxonomic history (Siddall, 1980; Vakily, 1989). The taxonomy, synonymies and geographical distribution of extant *Perna* species were reviewed by Siddall (1980). In addition to the *Perna* Philipsson 1788 genus under consideration here, the name *Perna* has also been used to describe the genera *Modiolus* H & A Adams 1858,

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doi:10.1016/j.ympev.2006.12.019

Isognomon Bruguiere 1792 and *Pinna* Linnaeus 1758 (Siddall, 1980; Vakily, 1989). A search of the Paleobiology database (http://paleodb.org/—url accessed 24 August 2006) revealed 17 records for fossil *Perna* Philipsson 1788 dating back to the Jurassic period, although the database and references therein indicate that the generic assignment of the earlier (Jurassic—Cretaceous) records is uncertain. Further examination of the specimens would be necessary to confirm or refute their assignment to *Perna* Philipsson 1788, but this is beyond the scope of the present study. The Treatise on Invertebrate Paleontology (Moore, 1969) indicates that the genus *Perna* Retzius 1788 (= *Perna* Philipsson 1788, ICZN Opinion 495) extends back to the Eocene (max. 60 Ma). A single fossil specimen from the late Eocene (37.2–40.4 Ma) of Seymour Island, Antarctic Peninsula was tentatively assigned to *Perna* Philipsson 1788 by Stilwell and Zinsmeister (1992) on the basis of its overall shape and similarity to *Perna canaliculus* from New Zealand, although the Antarctic specimen is somewhat larger (length 45 cm, width 15 cm) than current *Perna* individuals, which typically reach 10–15 cm shell length. In South America, fossil *Perna* are recorded from the late Oligocene/early Miocene of Argentina (del Rio, 2004) and Peru (DeVries, 1998). The only known record of fossil *Perna* in South Africa is from the late Miocene/early Pliocene, 3.5–7 Ma (the Paleobiology database http://paleodb.org/; Rich, 1980). In New Zealand, the earliest known occurrence is a record of *Perna tetleyi* in the early Miocene, approximately 20 Ma (Beu, 2004; Powell and Bartrum, 1929). The genus has been classified as part of the Malayo-Pacific biota which arrived in New Zealand from tropical and subtropical regions to the north during the Eocene—Miocene (Fleming, 1979). Many of these Malayo-Pacific immigrants to New Zealand died out in the late Miocene and the Pliocene (Fleming, 1979). The next record of *Perna* in New Zealand is in the early Pliocene (approximately 5 Ma) and is assigned to an extant species, *P. canaliculus* (Beu, 2004; Fleming, 1966). Beu (2004) noted that *Perna* also appeared briefly in southern Australia early in the Pliocene and suggested that this record may refer to the ancestor of *P. canaliculus*, which later became extinct in Australia. The present day *P. canaliculus* in New Zealand may have descended from the early Miocene *P. tetleyi* or, given the large gap in the fossil record, may be the result of a separate early Pliocene dispersal to New Zealand, possibly via southern Australia (Beu, 2004). To our knowledge, there are no records of fossil *Perna* from Asia or the Indo-West Pacific.

On the basis of morphological and chromosomal analyses the genus is thought to comprise three extant species (Siddall, 1980), although this has never been tested using molecular approaches. Until about 20 years ago the taxa had maintained separate geographic distributions (see Fig. 1) and were therefore easy to differentiate. *Perna perna* Linnaeus 1758, the brown or rock mussel, is found in Africa (throughout South Africa; on the Atlantic coasts of Namibia and Angola; the Cape Verde Islands and from Mauritania northwards; on the Indian Ocean coast of Mozambique, and on the west coast of Madagascar; extending through the Gulf of Aden into the Red Sea) and along the Atlantic coast of South America (from Rio de la Plata, Argentina, to Recife, Brazil; and then again on the Caribbean shores of Venezuela). The green mussel, *Perna viridis* Linnaeus 1758, has an extensive Indo-Pacific distribution from the Persian Gulf, through India and SE Asia, as far north (approximately 40°N) as Japan, Korea and southern China (Cheung, 1993; Huang et al., 1983; Monirith et al., 2003), and as far east as Papua New Guinea (Morton, 1987). Interestingly, both *P. perna* and *P. viridis*

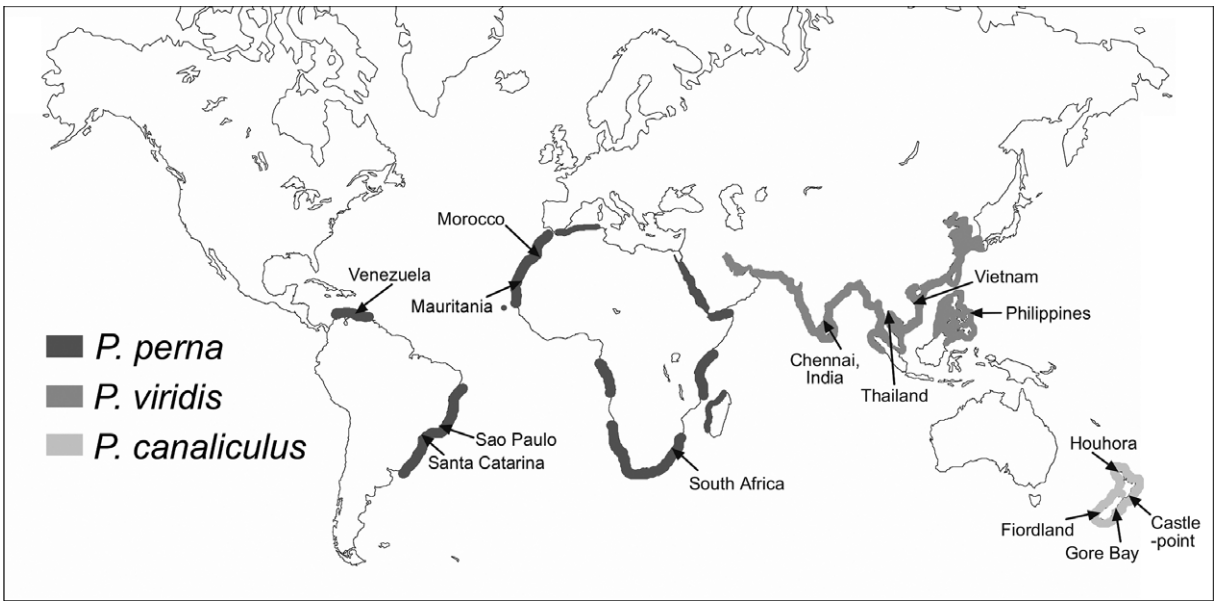

Fig. 1. Geographical distribution of the three *Perna* species until about 20 years ago. Recent introductions mentioned in text are not marked. Arrows indicate sampling locations.