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PHYLOGENETIC ANALYSIS OF THE PERI-HYDROTHERMAL VENT BIVALVE *BATHYPECTEN VULCANI* BASED ON 18S rRNA

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ABSTRACT

The species *Bathypecten vulcani* (Schein-Fatton, 1985), found at the periphery of hydrothermal vents at the East Pacific Rise, possesses primitive shell microstructures, which have led to its characterization as a living fossil. The shell-based classification of *B. vulcani* within the Pectinoidea has been difficult, the species bearing similarities to both the Pectinidae and the Propeamussiidae; as a result, interpretations of the anatomy and biology of the species in an evolutionary and taxonomic context have been hindered. Here, an 18S rRNA-based molecular phylogeny is used to compare *B. vulcani* with other pectinoids. The molecular trees group *B. vulcani* with the propeamussiid *Parvamussium undisonum*, in a clade distinct from all pectinids. These results support the inclusion of *B. vulcani* within the propeamussiid clade, making it the most well-studied representative of this poorly known group.

Key words: *Bathypecten vulcani*, Propeamussiidae, phylogeny, 18S, hydrothermal.

INTRODUCTION

Several faunal species believed to be endemic to hydrothermal vents possess anatomical characters described as primitive or archaic (Newman, 1985). Among these is the bivalve *Bathypecten vulcani*, which has been found at the periphery of hydrothermal vents at the East Pacific Rise, at 9°N and 13°N. In its original description, *B. vulcani* was classified as a pectinid, having shell structural and ultrastructural characters reminiscent of Paleozoic pectinoids (Schein-Fatton, 1985). Based on these shell characters, the species was deemed a living fossil.

An examination of the gill of *Bathypecten vulcani* revealed a simple, homorhabdic organization, which is primitive in comparison to the heterorhabdic gills of all other described pectinids (Le Pennec et al., 1988), including *Hemipecten forbesianus*: the specimens originally described by Yonge (1981) as having homorhabdic gills were recently found to have heterorhabdic gills (Beninger, pers. obs). Structural similarities between the gills of *B. vulcani* and those of early developmental stages of pectinids suggested that an evolutionary transition from homorhabdic to heterorhabdic gills had occurred within the Pectinidae (Beninger et al., 1994).

Schein-Fatton (1988) re-evaluated the phylogenetic position of *Bathypecten vulcani*, as well as that of its newly renamed congener, *B. eucymatus* (Dall, 1898), collected at abyssal depths from the Bay of Biscay. A reexamination of the shell microstructure of both *Bathypecten* species showed differences between the two species, with *B. vulcani* having more archaic features, and characters that could not be reconciled with either the Pectinidae or the Propeamussiidae. According to Waller (1972, 1984), the major character allowing distinction between both groups is the ctenolium: it is present, at least in early stages, in all pectinids, but absent in propeamussiids. In *B. vulcani*, the ctenolium is lacking (Schein-Fatton, 1988).

The genus *Bathypecten* was eventually placed within the Pectinidae, in the subfamily Propeamussiinae (Schein, 1989, from the family-group name Propeamussiidae Abbott, 1954), a sister-group to the subfamily Pectininae. Diagnostic characters for the subfamily Propeamussiinae are the same as those for the family Propeamussiidae, *sensu* Waller (1978). It is important to note that in the classification of Schein (1989), as in other classi-

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fications (e.g., Waller, 1978, 1984), both groups are considered to be sister taxa. In this paper, we will refer to these taxa by their family names, Pectinidae and Propeamussiidae, according to common usage, and to avoid confusion; this does not imply familial rather than subfamilial status.

More recently, it was found that the ultrastructure of the spermatozoa of *Bathypecten vulcani* differed significantly from that of pectinids, given that it could not be classified into either of the pectinid structural categories of Le Pennec et al. (2002). Unfortunately, due to the absence of information on spermatozoan ultrastructure in propeamussiids (Healy et al., 2000), it is unknown whether the spermatozoa of *B. vulcani* resemble those of propeamussiids. Similarly, a more detailed analysis of the anatomy, ciliation, and mucocyte types and distribution of the gill in *B. vulcani* has shown that it is substantially different from that of adult pectinids; however, it shows a number of similarities with the limited information available for propeamussiid gills (Beninger et al., 2003).

In the end, the conclusions stemming from observations of *Bathypecten vulcani* anatomy (e.g., the gill of *B. vulcani* represents the ancestral pectinid condition – Beninger et al., 1994) could not be confidently interpreted in a taxonomic and evolutionary context, due to the uncertain phylogeny of this species based on shell characters alone. In order to better classify *B. vulcani* within the Pectinoidea, the 18S rRNA sequence is here obtained and compared with that of other pectinids and propeamussiids.

MATERIALS AND METHODS

Sample Collection

Two specimens of *Bathypecten vulcani* were collected in May 2000 from the periphery of hydrothermal vents at 9°N along the East Pacific Rise, at the sites Tubeworm Pillar (9°49.6'N, 104°17.38'W, depth: 2,540 m) and Marker 141 (9°49.8'N, 104°17.4'W, depth: 2,530 m). At Tubeworm Pillar, the bivalves were within about 10 m from active smokers; at Marker 141, they were about 350 m from the closest smokers, which were at Tubeworm Pillar. Upon arrival at the surface, the bivalves were immediately fixed in absolute ethanol.

Ethanol-preserved specimens of *Parvamussium undisonum* (Dijkstraw, 1995) were obtained from the Muséum National d'Histoire Naturelle, Paris (Norfolk 1 expedition, station DW 1699, coll. M. Boisselier).

DNA Extraction and Amplification

The ethanol-preserved animals were washed in distilled water prior to DNA extraction. Genomic DNA was extracted from the adductor muscle and gills with the "DNeasy Tissue Kit"® (Qiagen). The near-complete 18S rRNA gene was amplified using the primers 18A1 (5'- CCT ACC TGG TTG ATC CTG CCA G - 3') and 1800r (5'- ATG ATC CTT CCG CAG GTT CAC C - 3'). The PCR-reactions were made on a Robocycler 96 (Stratagene) in a 30 µl reaction mix (1.5 mM $MgCl_2$, each dNTP at 250µM, each primer at 0.5 µM, 0.6 units Biotaq Red polymerase [Bioline] and the supplied reaction buffer at 1 x concentration). The PCR cycle conditions were: initial denaturation step of 2 min at 94°C, 36 cycles of 30 sec denaturation at 94°C, 45 sec annealing at 50°C, and 2 min primer extension at a 72°C, followed by a final primer extension step of 10 min at 72°C. PCR products were purified with the Concert Rapid PCR Purification System (Life Technologies) and sequenced with a range of primers (Steiner & Dreyer, 2003) on an ABI 3700 at VBC-Genomics Bioscience Research GmbH, Vienna.

Choice of Taxa, Alignment and Phylogenetic Analysis

The 18S rRNA sequences of *Bathypecten vulcani* and *Parvamussium undisonum* were aligned with those of all available species of Pectinidae, Spondylidae, Limidae (excluding the species of *Limatula* because of their divergent sequences), Anomiidae, and Plicatulidae (Table 1). According to Steiner & Hammer (2000), Giribet & Wheeler (2002), and Matsumoto (2003), the latter three family-groups comprise the closest relatives to the Pectinoidea. Additional outgroup taxa were selected from the Pinnidae and Arcoidea (Table 1). The computer-aided alignment of these 34 sequences produced by CLUSTAL X 1.8 (Thompson et al., 1997) using default parameters and subsequent manual corrections is available from the authors (GS).

Unweighted heuristic parsimony (MP) searches were made with PAUP* 4.0b10 (Swofford, 1998) on a PC with 50 random addition sequences and TBR branch swapping. Bootstrap support (BP) was assessed by 1,000 replicates, each with three random sequence additions. The program MODELTEST 3.06 (Posada & Crandall, 1998) determined the GTR+I+Ã model as most suitable for maximum-likelihood analyses (ML). The param-

eters estimated from the data were set for a ML search submitting the parsimony strict consensus tree to SPR branch swapping with rearrangements limited to cross four branches in PAUP*. We tested the phylogenetic signal and the robustness of the ML tree with the quartet-puzzling program TREE-PUZZLE 5.0 (Schmidt et al., 2002) under the same model as the ML analysis and parameters estimated by the program and with 100,000 puzzling steps. In addition, we analyzed phylogenetic relationships with Bayesian inference implemented in MRBAYES 3.0b4 (Huelsenbeck & Ronquist, 2001). We ran six chains through 200,000 generations under the GTR+I+Ã model starting with random trees. The first 300 trees were discarded as burn-in for the calculation of posterior probabilities.

TABLE 1. Systematic list of species used in the phylogenetic analysis, with the GenBank accession number of the 18S rRNA sequences.

Systematic position	Species	Accession Number
Arcoidea		
Arcidae	*Arca noae* (Linné, 1758)	X90960
	Acar plicata (Dillwyn, 1817)	AJ389630
	Barbatia virescens (Reeve, 1844)	X9197
Noetiidae	*Striarca lactea* (Linné, 1758)	AF120531
Glycymerididae	*Glycymeris pedunculus* (Linné, 1758)	AJ389631
	Glycymeris sp.	X91978
Pinnoidea		
Pinnidae	*Pinna muricata* (Linné, 1758)	AJ389636
	Atrina pectinata (Linné, 1767)	X90961
Anomioidea		
Anomiidae	*Anomia ephippium* (Linné, 1758)	AJ389661
	Pododesmus caelata (Reeve, 1859)	AJ389650
	Pododesmus macrochisma (Deshayes, 1839)	
Plicatuloidea		
Plicatulidae	*Plicatula plicata* (Linné, 1767)	AJ389651
	Plicatula australis (Lamarck, 1819)	AF229626
Limoidea		
Limidae	*Lima lima* (Linné, 1758)	AJ389652
	Limaria hians (Gmelin, 1791)	AF120534
	Ctenoides annulatus (Lamarck, 1819)	AJ389653
Pectinoidea		
Spondylidae	*Spondylus crassisquamatus* (Lamarck,1819)	AJ389646
	Spondylus hystrix (Röding, 1798)	AJ389647
	Spondylus sinensis (Schreibers, 1793)	AF229629
Propeamussiidae	*Bathypecten vulcani* (Schein-Fatton, 1985)	AY557608
	Parvamussium undisonum (Dijkstra, 1995)	AY557607*
Pectinidae	*Pecten maximus* (Linné, 1758)	L49053
	Placopecten magellanicus (Gmelin, 1791)	X53899
	Adamussium colbecki (E. A. Smith, 1902)	AJ242534
	Flexopecten glaber (Linné, 1758)	AJ389662
	Argopecten irradians (Lamarck, 1819)	L11265
	Argopecten gibbus (Linné, 1758)	AF074389
	Chlamys islandica (Müller O. F., 1776)	L11232
	Chlamys hastata (Sowerby, 1843)	L49049
	Mimachlamys varia (Linné, 1758)	L49051
	Crassadoma gigantea (Gray, 1825)	L49050
	Exellichlamys spectabilis (Reeve, 1853)	AJ389648
	Pedum spondyloideum (Gmelin, 1791)	AJ389649

*The partial 28S sequence of *Parvamussium undisonum* is deposited under the accession number AY557609.

RESULTS AND DISCUSSION

18S Sequence and Molecular Phylogeny

The alignment resulted in a data matrix with 1,973 characters, of which 215 are parsimony-informative. The parsimony search yielded 112 shortest trees of 517 steps (CI = 0.594, RC = 0.478). The topology of the resulting strict consensus tree (Fig. 1) differs only slightly from the single maximum-likelihood tree (-lnL = 6386.38877) (Fig. 2). All analyses firmly support the taxa Propeamussiidae (*Parvamussium* + *Bathypecten*), Pectinidae, and the Spondylidae. The monophyly of the Pectinoidea is always recovered, albeit with varying branch support. The Propeamussiidae and Pectinidae always appear as sister taxa with low support. This distinction is corroborated by the analysis of the mitochondrial gene, cytochrome-oxidase-I (Matsumoto, 2003), which supports pectinoid monophyly but yields a sister group relationship of Propeamussiidae to the clade (Spondylidae + Pectinidae). The two propeamussid species have similar and highly divergent sequences and, accordingly, an extremely long common branch. Although the limid species have similarly long branches, there is no indication of a long-branch attraction effect.

The molecular information is therefore consistent with the inclusion of *Bathypecten vulcani* in the propeamussiid group, rather than with the pectinid group.

Soft Anatomical and Spermatozoan Characters

Comparisons of new and published data concerning anatomical and spermatozoan characteristics of *Bathypecten vulcani*, pectinids, propeamussiids, and spondylids reveals that *B. vulcani* shares more affinities with the Propeamussiidae. Some of these anatomical characters may be apomorphies of propeamussiids, others are likely to be plesiomorphies, as discussed below.

The gill structure of *Bathypecten vulcani* is much simpler than that of pectinids (Beninger

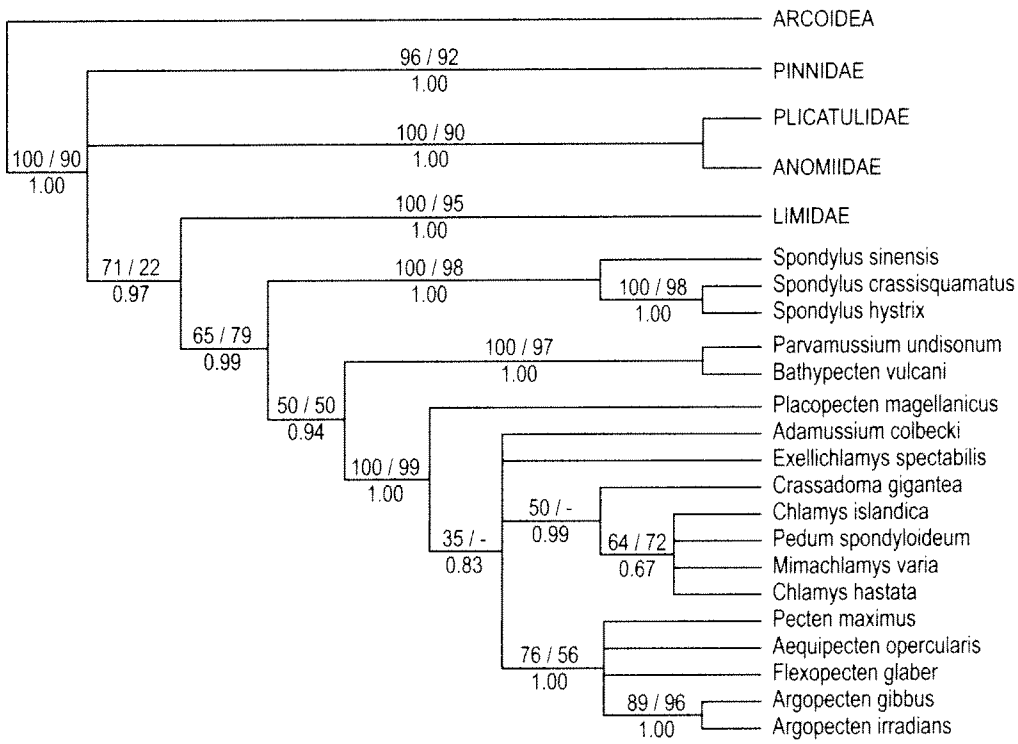

FIG. 1. Strict consensus of 112 most parsimonious trees. Bootstrap and ML-puzzling supports are above, posterior probabilities below branches.

& Le Pennec, 1991), spondylids, and limids (Ridewood, 1903; Dakin, 1928): it is non-plicate, homorhabdic, has a non-reflected outer demibranch, and lacks latero-frontal cilia, inter-filamentar junctions, and interlamellar junctions (Beninger et al., 2003). The relatively poorly known propeamussiid gills have many similar features. The organization of *Bathypecten vulcani* gill filaments does not correspond to the inverted arrangement reported for *Propeamussium lucidum*, in which the frontal ciliary tracts were deemed to be located in the suprabranchial chamber (Morton & Thurston, 1989). However, this atypical organization could easily have been misinterpreted, given that filaments without junctions are easily disorganized and entangled during fixation (Morton & Thurston, 1989).

Further examinations of propeamussiid gills would be needed to determine how the *B. vulcani* gill organization compares to other members of this family. If other propeamussiids are found to share the simple gill structure of *B. vulcani*, then some character-states (homorhabdy, lack of plicae, and lack of filamentar and lamellar junctions) are likely to be plesiomorphic for the Propeamussiidae; similar character-states are found in anomiids, plicatulids, and arcids, with some variation in the extent of interfilamentar and interlamellar junctions (Ridewood, 1903; Yonge, 1973). In addition, the small labial palps and non-arborescent lips observed in *B. vulcani* (Beninger et al., 2003), and described in some propeamussiids (Yonge, 1981), may be plesimorphies for the Propeamussiidae (as compared to the condition in the Pectinidae and Spondylidae – Dakin, 1928; Yonge, 1973; Beninger & Le Pennec, 1991). The lack of laterofrontal cilia, as described in *B. vulcani* (Beninger et al., 2003) and in *Propeamussium lucidum* (Morton & Thurston, 1989), is likely to be apomorphic for propeamussiids, as it has been described for no other pteriomorph to date. Also, the unique spermatozoan type described for *B. vulcani* (Le Pennec et al., 2002) may be

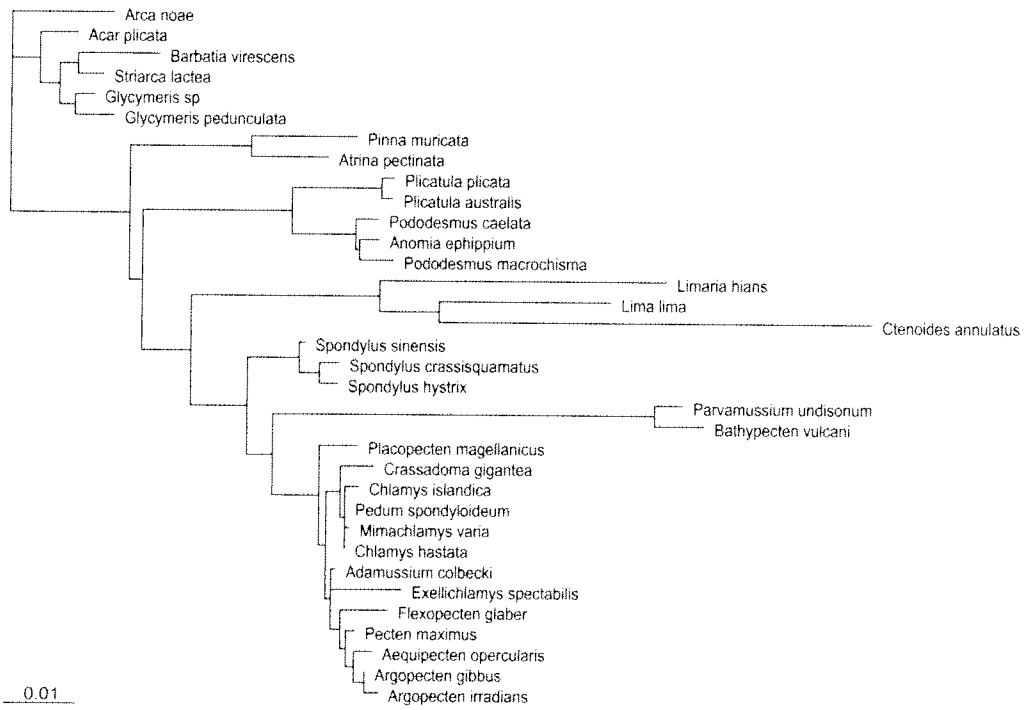

FIG. 2. Maximum likelihood tree (-ln L = 6386.38877) found under the GTR+I+Γ model. Model parameters estimated by MODELTEST: substitution rate matrix A-C = 2.2511, A-G = 2.9955, A-T = 1.6583, C-G = 1.3161, C-T = 4.9707, G-T = 1.00); nucleotide frequencies A = 0.2472, C = 0.2213, G = 0.2724, T = 0.2591; assumed proportion of invariable sites, pinvar = 0.5835; gamma distribution of rates at variable sites in four categories with shape parameter, alpha = 0.6141.

apomorphic for propeamussiids, if a similar structure was found in this group. Further anatomical observations are required to confirm the evolutionary status of these characters.

The presence of prismatic calcite on the left valve, such as found in *Bathypecten vulcani*, is only known from a group of Paleozoic fossils ancestral to the Propeamussiidae, the Pterinopectinidae and the Aviculopectinidae (Newell, 1938). *Bathypecten vulcani* may therefore have retained primitive characters, either by early phyletic divergence from other propeamussiids, or by paedomorphosis.

Propeamussiid Anatomy and Habitat

Several of the anatomical characters of *Bathypecten vulcani* and of other propeamussiids are likely to be related to their deep-sea habitat. As described by Allen (1981), deep-sea bivalves are commonly small in size, and have reduced gills; this miniaturization is thought to be associated with the small amounts of available food at great depths. Most propeamussiids are found at depths greater than 150 m, and were probably deep-sea inhabitants in the Mesozoic and Cenozoic (Waller, 1972).

One of the possible consequences of the deep-sea habitat of propeamussiids, and a possible outcome of their small body size, is the simplification of the gill. At the present state of knowledge, all propeamussiids have homorhabdic gills, with, at least in *Bathypecten vulcani*, few filaments. Due to the size restriction, it might not be possible for a gill with only approximately 50 filaments to become plicate, and by extension, heterorhabdic. Although the gills of developing postlarvae of pectinids are known to develop principal filaments at about 4 mm body size, and plication at about 7 mm (Beninger et al., 1994; Veniot et al., 2003), these growing pectinids contain at least three times as many filaments of the same diameter per gill as *B. vulcani* (Veniot et al., 2003). Although a bivalve the size of a typical propeamussiid can thus have a gill with enough filaments to become plicate and heterorhabdic, this may not be the most efficient organization for an adult bivalve, given the space limitation.

To date, *Bathypecten vulcani* has only been found in the proximity of hydrothermal vents; however, no particular effort has been made to collect this species at other sites. *Bathypecten vulcani* may not be restricted to vent environments, given its feeding regime, which is largely dependent on particulate food originating from surface waters (Le Pennec et al., 2003). Other *Bathypecten* species have been collected from bathyal and abyssal sediments in the Bay of Biscay and in the western Pacific (Schein, 1989), and do not appear to be found at vents. The discovery of *B. vulcani* in environments outside hydrothermal vent sites would confirm that its presence at vents is largely opportunistic; *B. vulcani* may simply be taking advantage of the relatively high amounts of particulate matter that are available at vents (Enright et al., 1981; Gage & Tyler, 1991).

CONCLUSIONS

The results of the present molecular phylogenetic analysis are consistent with *Bathypecten vulcani* being a member of the family Propeamussiidae. This placement is in concordance with the classification of *B. vulcani* based the absence of a ctenolium, this being the major criterion used to distinguish pectinids from propeamussiids (Waller, 1984). Interpretations of the biology of *B. vulcani* should thus be recast in the light of its propeamussiid status, rather than with reference to the pectinids (Beninger et al., 2003; Le Pennec et al., 1988, 2002). Although far from complete, this body of work thus represents the most considerable amount of knowledge concerning any propeamussiid to date.

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