Phylogenetic studies of the marine bivalve subfamily Venerinae (Bivalvia: Veneridae)

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Goal of present studies
How did morphological diversity evolve over time in the marine bivalve subfamily Venerinae?
• Investigate evolutionary relationships using mitochondrial and nuclear gene sequences
• Provide a robust phylogenetic framework for understanding venerine morphological character evolution
• Test traditional systematic hypotheses

Taxonomic controversy
Venerine shells are morphologically very similar to those of the subfamily Chioninae and can only be distinguished from each other by the presence or absence of an anterior lateral tooth. Taxonomists have been arguing for over 150 years about the significance of this minute anterior lateral tooth and have been arguing for over 150 years about the taxonomy of this group remains controversial.

Fischer-Piette (1975) carried out the last major revision of the Venerinae. He separated the two subfamilies and revised the Venerinae as a one-genus subfamily (Venus). In the most recent study dealing with this subject, Chionin and Venerinae were synonymized based on phylogenetic features Coan and Scott (1997). Venerinae currently comprises 41 extant genera (10 former Venerinae and 31 former Chionin) with over 180 species.

Methods
We performed a phylogenetic analysis of our 3-genome dataset based on partial sequences of the mitochondrial 16S gene (602 bp), COI gene (569 bp) and nuclear Histone 3 gene (328 bp) including 55 species of 37 genera of Venerinae s.l. as well as 18 outgroup taxa of other venerine subfamilies.

Alignments were computed with the PAUP* program. The model BAPEWSS (Brown, 1980) was used to determine the “burn in”. Maximum parsimony analysis was carried out with 100 random sequence additions per replicate. TBR branch swapping was used to determine the acceptance of the new tree. The phylogenetic analysis was repeated 20 times, and the average proportion of compatible trees were measured.

Morphological Trait Mapping
Altogether 75 conchological characters as well as six characters of internal anatomy were investigated (data not presented here). The morphological characters were mapped onto the molecular topology of the concatenated analysis and three informative characters were found:
(1) Presence or absence of crenulations in interior shell margin (Fig. 3B)
(2) Presence (Fig. 3C1) or absence (Fig. 3C2) of anterior lateral tooth in left valve
(3) Degree of siphon fusion; partially to completely separated (Fig. 3D1) vs. completely fused (Fig. 3D2)

Results & Discussion
The two tested traditional systematic hypotheses (Keen, 1969) was not present in the resulting 50% majority rule consensus tree.

• Several genera (Charinella, Clausineillia, Tawere, Timochea) were probably mis-classified in the past due to homoplasy in morphological features.

Monophyly of Venerinae s.l. or Venerinae s.s. (Keen, 1969) was not present in the resulting 50% majority rule consensus tree.

• The two tested traditional systematic hypotheses are rejected with p<0.001 in the constraint analysis and outside the 95% confidence set in ELT tree.

A combination of morphological characters can be used to distinguish the two subfamilies (Fig. 3):
Venerinae have separated siphons and most taxa in this group have an anterior lateral tooth
Chioninae have fused siphons and lack an anterior lateral tooth.

Within the Venerinae the monophyletic generic groupings have been identified.

Problems with sequencing COI
• 14 of the 56 sampled taxa did not deliver any results for the partial COI gene
• Museum material often in unknown fixatives can cause difficulties in amplifying longer sequences

“Barcoding” will likely be successful with fresh material, but could be very labor and time intensive with older museum material.

Literature cited


Acknowledgements
Thanks to the curators and staff of following museums for loan of specimens and tissue: MNHN, Paris; IRSNB, Brussels; MNNU, Wellington, New Zealand; FLHMN, Gainesville; LACM, Los Angeles; BMNH, London.

For assistance during field collections we thank: Katja Delfner-Janssen (Berlin, Germany), Sona Marino (Instituto Nacional de Desenvolvimento das Pescas - Mindelo, Cabo Verde); Elise Delgado and crew (Mindelo, Cape Verde Islands), Eunis Barnes and crew (São, Cabo Verde), Patrice Petit De Voize (Fédération Française d’Etudes et de Sports Sous-Marine - Commission nationale de Biologie, France), Haidar el Ali (Oceana, Dakar, Senegal), Lisa Kerkendale (FLHMN), Emily Glover and John Taylor (BMNH), Fred Wells (Western Australian Museum, Perth), and Rachel Colm (Smithsonian Tropical Research Institute, Panama).

We are grateful to the following people for help in obtaining additional specimens: Claude Berthout (Centre ORSTOM de Nouméa, New Caledonia), Alan G. Bea (University of Geological and Nuclear Sciences, Lower Hutt, New Zealand), Rachel Colm (Smithsonian Tropical Research Institute, Panama), Louise Crowley (American Museum of Natural History, New York), Brian Dyer (University of Canterbury), F.C. Kappner (Bochum, Germany), Alan J. Kohn (University of Washington, Seattle), Taiwo-Kuma (Wageningen University, Wageningen, The Netherlands), and M. Pea-Pevironmental (University of Zagreb, Croatia).

Additional funds were provided by UEC's Provost Award for Graduate Research, PRIMN Zoology Department's Marshall Field Fund, and the Conchologists of America.

Figure 1. Divergent systematic hypotheses (a) after Keen (1969) and (b) after Coan and Scott (1997) author’s interpretation.

Figure 2. Molecular phylogeny of Veneridae: 50% majority rule consensus tree based on a Bayesian analysis of the concatenated dataset (16S, COI and ITS). Posterior probabilities are indicated above branches, and from bootstrap replicates below branches. Morphological trait mapping onto the molecular phylogeny of venerine bivalves: Character 2 (crenulations in interior margins), black boxes = presence, white boxes = absence; Character 2 (antenal lateral tooth of Type I), black boxes = presence, white boxes = absence; Character 3 (siphons), black boxes = separated, white boxes = fused.

Figure 3. Morphological features that were found to be useful for classification and that were utilized for mapping on the molecular tree. A. Presence of internal siphon; b. Crenulations of the interior shell margin; c. Presence of an anterior lateral tooth of Type I (C1) and absence of anterior lateral tooth of Type II (D1) on the left valve; d. Presence of internal lateral teeth of Type II (D2) on the right valve.