

**SIPHONAL STRUCTURE IN THE VENERIDAE (BIVALVIA: HETERODONTA)  
WITH AN ASSESSMENT OF ITS PHYLOGENETIC APPLICATION AND A REVIEW  
OF VENERIDS OF THE GULF OF THAILAND**

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**ABSTRACT.** – A survey of venerid bivalves of the Gulf of Thailand revealed 78 species belonging to 10 of the 14 recognised subfamilies. Included in this survey were 25 species collected during a field workshop held near Chantaburi in the northern Gulf of Thailand during August–September 2005; all species are known previously from that location. Fifteen species belonging to seven subfamilies were observed alive for characters of the siphons, including relative length, degree of union (“fusion”), pigmentation, number, branching pattern and distribution of the tentacles, behaviour during siphoning, and the effects of preservation on these characters. Examination of the marginal mantle folds revealed one outer and three inner folds (i.e., OF, IF-1, IF-2, and IF-3, relative to the periostracal groove) per side. Only the innermost (“fourth” or IF-3) mantle folds are involved in forming the venerid siphons, contrary to most published opinions that also include the second innermost (“third” or IF-2) mantle fold in the process. Siphonal formation in venerids thus most closely resembles Type A of Yonge, rather than Type B as has been interpreted by most authors. Preservation has its most severe effects on separated siphons, which can appear falsely united, either entirely or to an extent different from that observed in living specimens. Subfamily characterisations for eight of the recognised venerid subfamilies are provided based upon these data and previously published reports using living specimens. When mapped on a previously published recent phylogeny, no phylogenetic patterns emerge, suggesting that siphonal characters are highly homoplastic.

**KEYWORDS.** – Siphons, morphology, diversity, characters, phylogenetics, homoplasy.

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## INTRODUCTION

Veneridae Rafinesque, 1815 (collectively called Hoi venus or Hoi sai in Thai), is the most speciose family of living bivalves with approximately 800 extant representatives, many of which are commercially important. They are abundant and extremely successful in shallow marine communities worldwide, except at high latitudes. The majority are infaunal suspension feeders that can move short distances within the substratum using a muscular foot.

In the Gulf of Thailand, venerids are ubiquitous, occurring in a variety of soft substrata. Lyngé (1909) produced the first major summary of marine bivalve diversity in that region, based on the Danish Expedition to the gulf in 1899–1900, listing 52 venerid species (this and others corrected here according to currently accepted synonymies); Lyngé (1909: map) labelled Kungkrabaen Bay (the specific location for this study) as “Tung Kaben,” but his samples were from offshore of the bay. Kurozumi et al. (1989) recorded 11

venerid species (10 of which are here considered valid) along the coast of Sichang and neighbouring islands, in the northern gulf. Scott (1995) reported three members of the family from sediments in the central gulf in depths ranging between 60 and 70 metres. Thirty-eight venerids were found in the southern gulf by Swennen et al. (2001), and 28 in Holocene deposits near Bangkok or in nearby Recent near-shore communities by Robba et al. (2002, 2003; not including species found only in non-Recent sediments). In mangrove communities, two species (both previously recorded) have been found in the upper gulf (C. Printrakoon, unpubl.). In total, the Gulf of Thailand is known from previous accounts to support 78 species of venerids in ten of the 14 subfamilies supported by the recent phylogenetic analysis of Mikkelsen et al. (2006) (Table 1).

Despite their remarkable ecological and economic importance, there is a surprising scarcity of anatomical data on venerid species, with only about 50 having some detailed information published on soft-part morphology (see Bieler et al., 2004, for a brief review). Thus, traditional taxonomic treatment of the family is still largely based on conchological characters that, as suggested by Harte (1992) and others, could have evolved convergently in distantly related species due to similar lifestyles, therefore masking their true phylogenetic affinities. In an extensive morphology- and multiple gene-based phylogeny of the superfamily Veneroidea, including 114 species in five families and all 17 nominal venerid subfamilies, Mikkelsen et al. (2006) found Veneridae and six subfamily groups to be monophyletic. Other subfamily groups and Veneroidea itself were either non-monophyletic or the results remained inconclusive; two former veneroid families (Petricolidae and Turtoniidae) were formally subsumed into Veneridae and ranked as subfamilies. Morphological characters were highly homoplastic and few in number, illustrating the general anatomical uniformity of the family and providing an explanation for its historically controversial taxonomy (Keen, 1969; Boss, 1982). Amongst the organ systems surveyed, the siphons, which not only play important functional roles in nutrition, reproduction, and defence (Zwarts & Wanink, 1989; Jeffrey et al., 1999) but have also been used as traditional taxonomic characters in Veneridae, proved particularly challenging to study and interpret in preserved specimens. Due to their muscular/haemocoelic composition, these structures are liable to varying degrees of contraction upon fixation, leading to artefactual differences in siphonal morphology amongst preserved individuals of any given species. This of course makes comparison across distinct taxa similarly problematic. Nonetheless, the crucial role that the development of siphons has played in the evolution of bivalves by enabling these animals to invade several new ecologic niches as either deep burrowers or borers of hard substrata (Yonge, 1957; Stanley, 1968), combined with their obvious functional importance (Zwarts & Wanink, 1989; Jeffrey et al., 1999), strongly argue for the potential usefulness of siphons as a source of data for phylogenetic reconstruction. In one recent study (Kappner & Bieler, 2006), the degree of siphonal union (= “fusion”) – i.e., having (at least partially) separated incurrent and excurrent siphons versus having completely united siphons – was considered

a distinguishing character between two large monophyletic clades in the Veneridae, the often-confused subfamilies Venerinae and Chioninae.

During the 2005 Second International Marine Bivalve Workshop, an opportunity was taken to compare the siphonal morphology in living specimens of 15 venerid species, belonging to seven nominal subfamilies, and to investigate general trends and the degree of artefactual change due to preservation. The results of this investigation are reported herein.

## MATERIALS AND METHODS

**Collection of specimens.** – Between 22 Aug.2005 and 2 Sep.2005, living specimens of Veneridae were collected by hand or by shovelling and sieving (through a 1–2 mm mesh) in intertidal sediments within and in the vicinity of Kungkraen Bay (Ta Mai District, Chantaburi Province) in the northern Gulf of Thailand. Venerid collecting stations include KKB-02, 03, 04, 05, 06, 11, 12, 15, 16, 21; see Bieler et al. (2008) for full locality data. At KKB-12, a particularly interesting and effective method for collecting large-bodied *Periglypta puerpera* specimens was demonstrated to us by a local fisherman, i.e., visually locating the siphons, inserting a knife or screwdriver into one of the siphons and extracting the clam clamped down upon the blade; this method was subsequently used for some of our material. At KKB-15, living *Meretrix meretrix* specimens were located by retracing the furrows left by a commercial/artesanal clam fisherman using a shallow hoeing device (Fig. 1) that pushed shallow-burrowing individuals to the surface. Living specimens of *Neotapes undulata* were acquired at a regional fish market in the city of Chantaburi.

**Siphonal morphology and behaviour.** – All collected specimens were kept completely immersed in seawater during transport to the laboratories of Burapha University (Chantaburi Campus), where each animal was moved into a



Fig. 1. Commercial fisherman collecting *Meretrix meretrix* at station KKB-15 by cutting shallow furrows in the intertidal sand with a simple rectangular hoe, which forced the shallow-burrowing clams to the surface.

Table 1. Venerids recorded from the Gulf of Thailand.

Taxa	Lyngé, 1909	Kurozumi et al., 1989	Scott, 1995	Swennen et al., 2001	Robba et al., 2002, 2003	Printrakoon, unpubl. data	This study
<b>CHIONINAE</b>							
<i>Anomalocardia squamosa</i> (Linnaeus, 1758)	X			X	X	X	X
<b>CLEMENTINIINAE</b>							
<i>Clementia vatheleti</i> Mabilie, 1901				X			
<b>DOSINIINAE</b>							
<i>Asa dautzenbergi</i> Fischer-Piette & Delmas, 1967					X		
<i>Dosinella angulosa</i> (Philippi, 1847a)	X						
<i>Dosinia brevilunata</i> Fischer-Piette & Delmas, 1967				X			
<i>D. cretacea</i> (Reeve, 1850)	X			X	X		X
<i>D. dilecta</i> A. Adams, 1855	X			X	X		X
<i>D. exasperata</i> (Philippi, 1847a)	X						
<i>D. exilium</i> G. B. Sowerby III, 1909				X			
<i>D. juvenilis</i> (Gmelin, 1791)	X <sup>1</sup>			X			X
<i>D. sanata</i> Fischer-Piette & Delmas, 1967	X			X	X		X
<i>D. traillii</i> A. Adams, 1855				X	X		X
<i>Dosinia</i> sp.					X		
<i>Phacosoma derupta</i> (Römer, 1860)					X		
<i>P. tumida</i> (J. E. Gray, 1838)	X			X	X		
<i>Sinodia trigona</i> (Reeve, 1850)	X			X	X		X
<b>GOULDINIINAE</b>							
<i>Circe lirata</i> (Römer, 1869)	X			X			
<i>C. rivularis</i> (Born, 1778)		X					
<i>C. scripta</i> (Linnaeus, 1758)	X			X			X
<i>Dorisca</i> cf. <i>nana</i> (Melvill, 1898)	X		X				
<i>Gafrarium dispar</i> (Holten, 1802)	X	X			X		X
<i>G. divaricatum</i> (Gmelin, 1791)	X	X		X			X
<i>G. melvilli</i> (Lyngé, 1909)	X				X		
<i>G. pectinatum</i> (Linnaeus, 1758)	X						X
<i>G. tumidum</i> Röding, 1798	X	X		X			X
<i>Rediciree sulcata</i> (J. E. Gray, 1838)	X			X			
<b>MERETRICINAE</b>							
<i>Meretrix lyrata</i> (G. B. Sowerby II, 1851)	X					X	
<i>M. meretrix</i> (Linnaeus, 1758)	X			X	X		X
<i>Meretrix</i> sp.				X			

Table 1. Cont'd

Taxa	Lyngé, 1909	Kurozumi et al., 1989	Scott, 1995	Swennen et al., 2001	Robba et al., 2002, 2003	Printrakoon, unpubl. data	This study
<b>PETRICOLINAE</b>							
<i>Petricola divergens</i> (Gmelin, 1791)				X			X
<i>P. lapicida</i> (Gmelin, 1791)	X						
<b>PITARINAE</b>							
<i>Callocardia guttata</i> A. Adams, 1864	X				X		
<i>Costacallista erycina</i> (Linnaeus, 1758)					X		
<i>Costellipitar manillae</i> (G. B. Sowerby II, 1851)					X		
<i>Hyphantosoma nancyae</i> Lamprell & Whitehead, 1990				X			
<i>Lioconcha fastigiata</i> (G. B. Sowerby II, 1851)		X					
<i>L. ornata</i> (Dillwyn, 1817)	X						X
<i>L. polita</i> (Röding, 1798)	X			X			
<i>Pitar deshayesi</i> (Pfeiffer, 1869)	X						
<i>P. gouldii</i> (Reeve, 1864)				X			
<i>P. yerburyi</i> (E. A. Smith, 1891)	X						
<i>Pitar</i> sp.		X		X			
<i>Pitarina affinis</i> (Gmelin, 1791)	X						
<i>P. hebraea</i> (Lamarck, 1818)	X						
<i>P. minuta</i> (Koch in Philippi, 1845)	X						
<i>P. striata</i> (J. E. Gray, 1838)	X				X		X
<i>Sulcilioconcha trimaculata</i> (Lamarck, 1818)	X						
<b>SUNETTINAE</b>							
<i>Sunetta contempta</i> E. A. Smith, 1891				X (as cf.)	X		
<i>S. effossa</i> (Hanley, 1843)				X			
<b>TAPETINAE</b>							
<i>Gomphina radiata</i> (G. B. Sowerby I, 1835)	X						
<i>Irus macrophyllus</i> (Deshayes, 1853)	X			X			
<i>Marcia hianina</i> (Lamarck, 1818)	X			X		X	X
<i>M. japonica</i> (Gmelin, 1791)				X			
<i>M. marmorata</i> (Lamarck, 1818)				X			
<i>Neotapes undulata</i> (Born, 1778)	X			X			X
<i>Paphia exarata</i> (Philippi, 1846)				X			
<i>P. obscurata</i> (Deshayes, 1853)	X			X			

Table 1. Cont'd

Taxa	Lyngé, 1909	Kurozumi et al., 1989	Scott, 1995	Swennen et al., 2001	Robba et al., 2002, 2003	Printrakoon, unpubl. data	This study
<i>P. rotundata</i> (Linnaeus, 1758)	X						
<i>P. semirugata</i> (Philippi, 1847b)	X			X			
<i>P. vernicosa</i> (A. A. Gould, 1861)		X					
<i>Protapes gallus</i> (Gmelin, 1791)	X			X	X		
<i>Ruditapes philippinarum</i> (A. Adams & Reeve, 1850)	X						X
<i>R. variegatus</i> (G. B. Sowerby II, 1852)	X			X			X
<i>Tapes sericeus</i> Matsukuma, 1986		X					
<b>VENERINAE</b>							
<i>Antigona lamellaris</i> Schumacher, 1817	X			X			
<i>Globivenus toreuma</i> (A. A. Gould, 1851)	X						
<i>Periglypta chemnitzii</i> (Hanley, 1845)				X			
<i>P. puerpera</i> (Linnaeus, 1758)		X			X		X
<i>P. reticulata</i> (Linnaeus, 1758)	X						
<i>Timoclea<sup>2</sup> arakana</i> (G. Nevill & H. Nevill, 1871)			X				
<i>T. imbricata</i> (G. B. Sowerby II, 1853)	X						
<i>T. lionota</i> (E. A. Smith, 1885)	X				X		
<i>T. marica</i> (Linnaeus, 1758)	X						
<i>T. scabra</i> (Hanley, 1845)	X		X	X	X		X
<i>T. siamensis</i> (Lyngé, 1909)	X				X		
<i>T. subnodulosa</i> (Hanley, 1845)	X <sup>1</sup>			X	X		X
<b>SUBFAMILY INCERTAE SEDIS<sup>2</sup></b>							
<i>Placamen calophyllum</i> (Philippi, 1836)	X			X	X		X
<i>P. chloroticum</i> (Philippi, 1849)	X			X			X

<sup>1</sup> Collecting localities include "off Tung Kaben, 6 fathoms, mud mixed with sand" (Lyngé, 1909: 243, 248).<sup>2</sup> A recent molecular phylogenetic analysis of members of Chioninae and Venerinae (Kappner & Bieler, 2006) changed the subfamilial allocation of some genera and found others to lie outside of both subfamilies; on this basis, *Timoclea* appears here in Venerinae, whereas *Placamen* is placed in subfamily incertae sedis based on molecular evidence (I. Kappner, unpubl.).

beaker (or other container) containing gravel and seawater and positioned with the anterior margin of the shell partially buried in the gravel (Fig. 2A). The specimen was left undisturbed under a dissecting microscope until its siphons were extended, protruding from the posterior margin of the shell. Morphological and behavioural observations were undertaken and the results recorded by photomicrographs and drawings. Caution was used in selecting specimens of *Periglypta* for observations, avoiding those that had been damaged by the collecting efforts.

The effects of preservation on gross siphonal morphology were assessed by fixing some of the analysed specimens either directly in 70% ethanol or in 5% formalin after being relaxed in isotonic magnesium sulphate and/or chilling in a laboratory refrigerator for 2–6 hours. Animals fixed in formalin were transferred to 70% ethanol after three days. Siphonal morphology of all preserved specimens was analysed six months after preservation and the results compared with observations made in vivo. The degree of pallial fusion involved in the formation of siphons (Yonge's 1982 Types) was investigated in preserved specimens only.

Lengths of the shell (sl; anterior to posterior shell margin) and pallial sinus (ps; posterior shell margin to anteriormost point of the sinus) were measured to the nearest 0.1 mm using callipers or a stereomicroscope equipped with an ocular micrometer. The ratio ps:sl was used as an expression of the relative size of the pallial sinus. Diameter of the siphonal apertures and lengths of the excurrent and incurrent siphons, excurrent valvular membrane, and terminal tentacles of both siphons (Fig. 3) were measured in living specimens to the nearest 1 mm using graph paper whilst avoiding contact with the animal to prevent withdrawal of the organs.

To facilitate comparison amongst the examined taxa, the relative lengths of the valvular membrane and tentacles are given as a proportion of the radius of the respective siphonal aperture. Thus, long tentacles/membrane are structures whose length equals or exceeds the radius, medium-sized tentacles/membrane are shorter than the radius but reach at least half of that distance, and short tentacles/membrane are shorter than half the radius (Fig. 3). Similarly, species whose siphonal length was found to exceed the combined diameter of their apertures during in vivo observations are described herein as possessing long siphons, whereas all other species are considered to bear short siphons.

Cited repositories are: FMNH, Field Museum of Natural History, Chicago; MZSP, Museu de Zoologia da Universidade de São Paulo.

## SYSTEMATIC DESCRIPTIONS

### CHIONINAE

#### *Anomalocardia squamosa* (Linnaeus, 1758)

(Figs. 4A, 5A)

**Material examined.** – In vivo: 1 juv. ex. (FMNH 312152), KKB-02; 1 ex. (FMNH 309788), KKB-03; 1 ex. (FMNH 309791), KKB-16; preserved: 4 ex. (MZSP 81671), KKB-03.

**Observations.** – Siphons short, ps:sl 0.34, separated, with black pigment dots along base of tentacles and forming a few radial lines along external walls; white pigment distributed as scattered spots throughout internal and external walls, tentacles, and long valvular membrane. Incurrent aperture fringed by 40–42 long, simple tentacles, eight of which are slightly longer and marked by semicircular black pigment band around inner face of base. Excurrent siphon with 31 or 32 long, simple tentacles, equidistantly distributed along base of valvular membrane.

During siphoning, the eight slightly longer tentacles of the incurrent siphon are held over the aperture, whereas the remaining tentacles of both the incurrent and excurrent siphons point either parallel to the direction of water flow or angled slightly away from the aperture.

### DOSINIINAE

#### *Dosinia cretacea* (Reeve, 1850)

(Figs. 2B–C, 4B, 5B)

**Material examined.** – In vivo: 1 ex. (FMNH 309751), KKB-03.

**Observations.** – Siphons long, ps:sl 0.69, united to distal tips, with uniform light brown collar around each distal aperture and scattered white pigment dots distributed on walls, fading towards basal region. Incurrent aperture fringed by seven short, simple, papilla-like tentacles. Excurrent siphon devoid of tentacles, with short valvular membrane.

Due to the small size of the tentacles, the position during siphoning did not vary.

#### *Dosinia juvenilis* (Gmelin, 1791)

(Figs. 4C, 5C)

**Material examined.** – In vivo: 1 ex. (FMNH 309752), KKB-03.

**Observations.** – Siphons long, ps:sl 0.67, united to distal tips, with dark brown collar around incurrent aperture, and discontinuous radial stripes of white pigment throughout walls and tentacles. Incurrent aperture crowned by 16 short, simple tentacles. Excurrent siphon devoid of tentacles, with short valvular membrane.

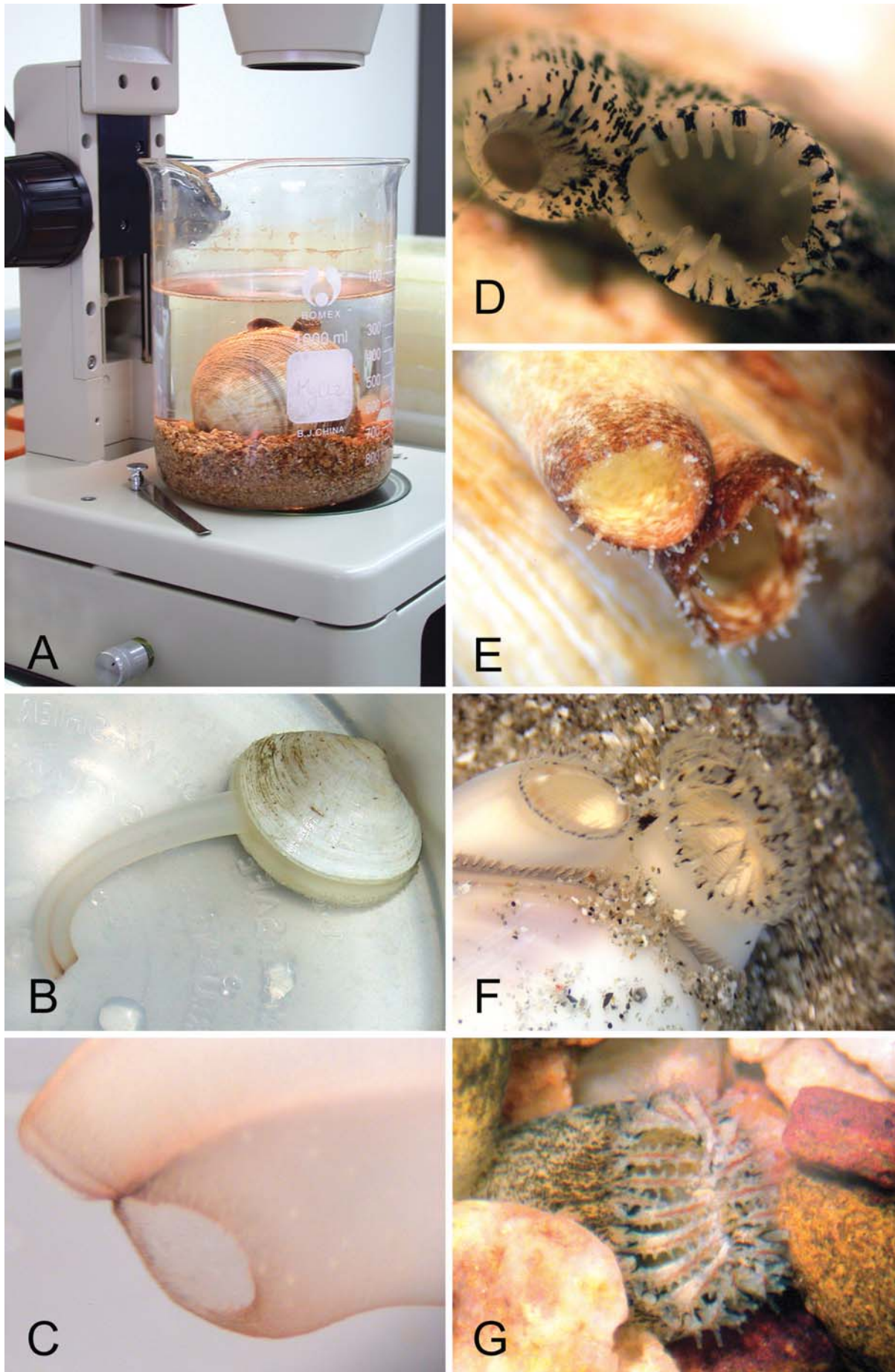


Fig. 2. Laboratory images of live veneroid siphons: A, *Periglypta puerpera* in laboratory set-up; B–C, *Dosinia cretacea*, KKB-03; D, *Placamen chloroticum*, KKB-02; E, *Pitarina striata*, KKB-03; F, *Meretrix meretrix*, KKB-15; G, *Ruditapes variegatus*, KKB-05.

During siphoning, the siphonal tentacles of *D. juvenilis* are held parallel to the direction of water flow.

**GOULDIINAE**

***Circe scripta* (Linnaeus, 1758)**  
(Figs. 4D, 5D)

**Material examined.** – In vivo: 1 juv. ex. (FMNH 312149), KKB-03.

**Observations.** – Siphons short, ps:sl 0.26, separated, with scattered black pigment dots on terminal margin and along dorsal and ventral walls of each siphon. Incurrent siphon slightly shorter than excurrent. Incurrent aperture crowned by 25 long, simple tentacles. Excurrent aperture with long valvular membrane surrounded at its base by 15 simple, medium-sized tentacles.

During siphoning, the tentacles of the incurrent siphon are held slightly angled towards the centre of the aperture; those of the excurrent siphon point either parallel to the direction of the water flow or angled slightly away from the aperture.

***Gafrarium dispar* (Holten, 1802)**  
(Figs. 4E, 5E)

**Material examined.**– In vivo: 1 ex. (FMNH 309782), KKB-21; preserved: 1 ex. (MZSP 81672), KKB-21.

**Observations.**– Siphons short, ps:sl 0.23, separated, with orange pigment dots scattered throughout external walls of both siphons, stronger on distal ends and fading towards basal regions; pigmentation also present on tentacles of incurrent siphon. Incurrent aperture fringed by 20–25 long, simple tentacles, interspersed with 20–30 short, simple tentacles. Excurrent aperture with long valvular membrane, surrounded at its base by 45 medium-sized tentacles interspersed with a few short, simple ones. Tentacles of the excurrent siphon not uniformly distributed around base of valvular membrane but clustering on dorsal and ventral borders of the latter.

The position of the tentacles during siphoning was not recorded in this species.

***Gafrarium divaricatum* (Gmelin, 1791)**  
(Figs. 4F, 5F)

**Material examined.** – In vivo: 2 ex. (FMNH 309786), KKB-05; preserved: 4 ex. (MZSP 81673), KKB-05.

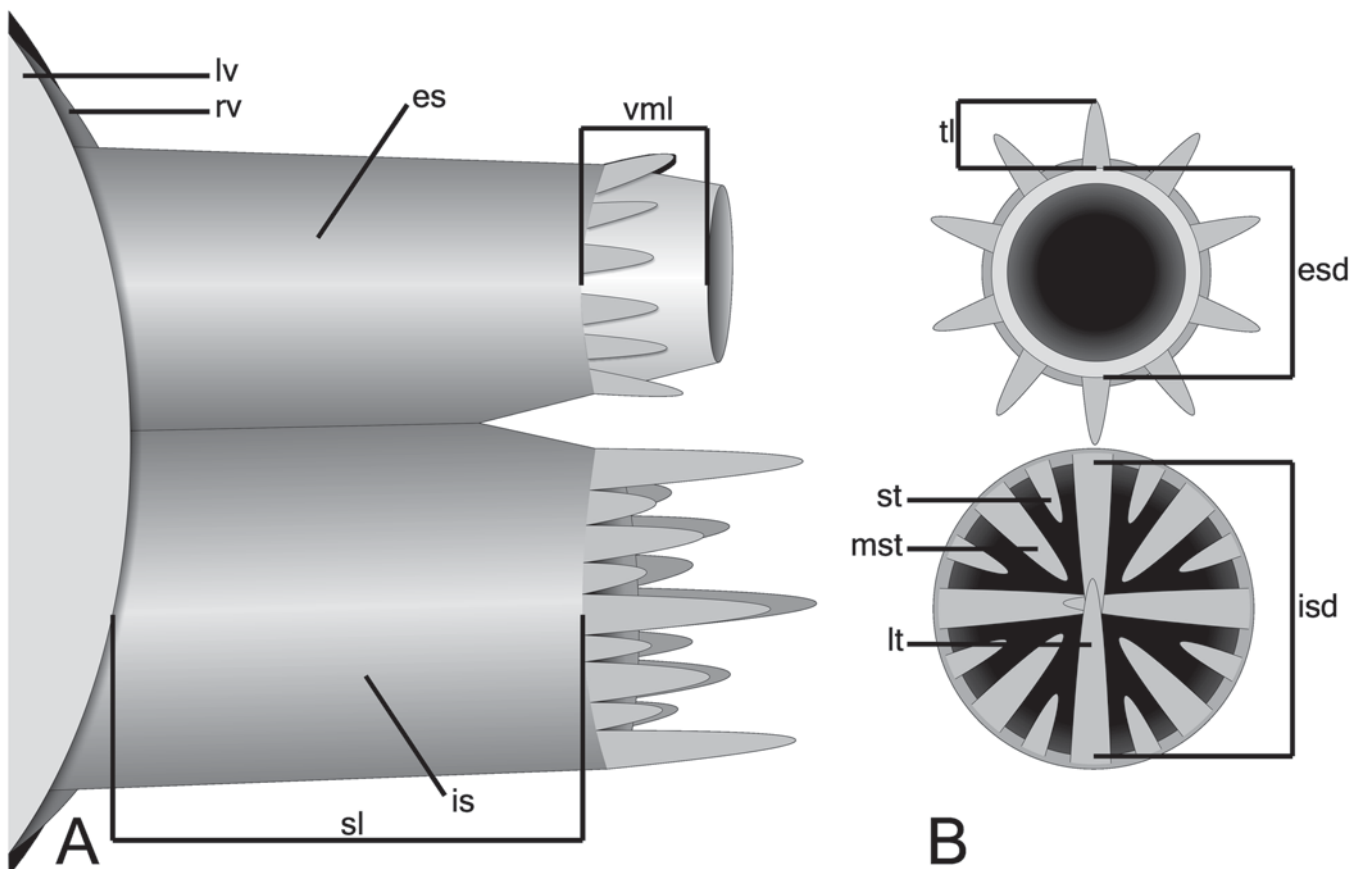


Fig. 3. Diagrammatic lateral (A) and apertural (B) representations of the siphons of a hypothetical venerid, showing the placement of siphonal measurements and examples of short, medium-sized, and long tentacles. Abbreviations used: es, excurrent siphon; esd, diameter of the excurrent siphonal aperture, taken at the base of the valvular membrane; is, incurrent siphon; isd, diameter of the incurrent siphonal aperture; lt, long tentacle; lv, left valve; mst, medium-sized tentacle; rv, right valve; sl, siphonal length; st, short tentacle; tl, tentacle length; vml, valvular membrane length.





Fig. 4. Shells of the venerid species examined by this study: A, *Anomalocardia squamosa* (KKB-03/04, FMNH 309733, length 27.9 mm); B, *Dosinia cretacea* (KKB-03/04, FMNH 309751, length 19.6 mm); C, *D. juvenilis* (KKB-11, FMNH 309750, length 21.9 mm); D, *Circe scripta* (KKB-06, FMNH 309728, length 46.3 mm); E, *Gafrarium dispar* (KKB-21, FMNH 309782, length 17.2 mm); F, *G. divaricatum* (KKB-05, FMNH 309743, length 26.8 mm); G, *G. pectinatum* (KKB-21, FMNH 309776, length 30.6 mm); H, *G. tumidum* (KKB-16, FMNH 309777, length 32.0 mm); I, *Meretrix meretrix* (KKB-16, FMNH 309781, length 53.3 mm); J, *Pitarina striata* (KKB-03/04, FMNH 309735, length 38.6 mm); K, *Marcia hiantina* (KKB-03/04, FMNH 309747, length 42.0 mm); L, *Neotapes undulatus* (Chantaburi Market, FMNH 309778, length 30.4 mm); M, *Ruditapes variegatus* (KKB-21, FMNH 309779, length 35.0 mm); N, *Periglypta puerpera* (KKB-12, FMNH 309783, length 75.5 mm); O, *Placamen chloroticum* (KKB-03/04, FMNH 309780, length 36.5 mm).

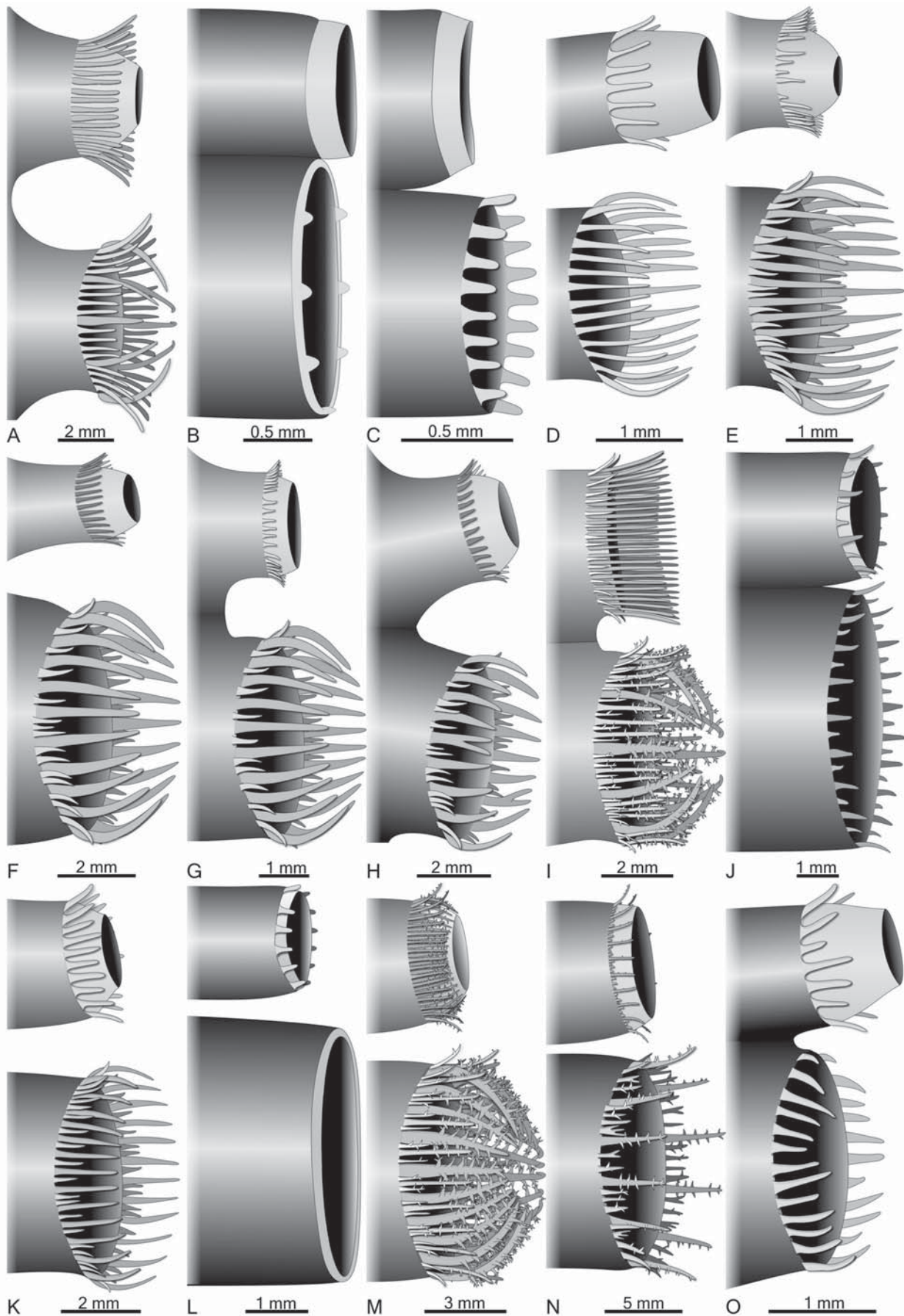


Fig. 5. Left lateral view of the siphonal tips of the venerid species examined by this study: A, *Anomalocardia squamosa*; B, *Dosinia cretacea*; C, *D. juvenilis*; D, *Circe scripta*; E, *Gafrarium dispar*; F, *G. Divaricatum*; G, *G. Pectinatum*; H, *G. Tumidum*; I, *Meretrix meretrix*; J, *Pitarina striata*; K, *Marcia hiantina*; L, *Neotapes undulata*; M, *Ruditapes variegatus*; N, *Periglypta puerpera*; O, *Placamen chloroticum*.

**Observations.** – Siphons short, ps:sl 0.24, separated, with black and orange pigment dots scattered throughout external walls of both siphons, stronger on distal ends and fading towards basal regions; pigmentation also present on tentacles of incurrent siphon; internal walls of both siphons covered by white pigment dots. Incurrent aperture fringed by ca. 50 simple tentacles, organised in two rows. Innermost row comprising ca. 20 long tentacles, interspersed with groups of 1–3 short tentacles of second row, the latter inserted slightly farther from aperture. Excurrent aperture with long valvular membrane, surrounded at its base by 26–32 medium-sized, simple tentacles.

During siphoning, the innermost row of incurrent siphonal tentacles is usually held pointing towards the centre of the aperture. The second row of incurrent tentacles, as well as the excurrent siphonal tentacles, point either in the direction of water flow or angled slightly away from the aperture.

***Gafrarium pectinatum* (Linnaeus, 1758)**  
(Figs. 4G, 5G, 7B)

**Material examined.** – In vivo: 1 ex. (FMNH 309776), KKB-21; preserved: 1 ex. (MZSP 81674), KKB-21.

**Observations.** – Siphons short, ps:sl 0.23, separated, with uniformly-distributed orange pigment and scattered black pigment dots surrounding both apertures, fading towards basal regions; pigmentation also present on tentacles of incurrent siphon. Incurrent aperture bordered by ca. 42 simple tentacles, with long tentacles interspersed with short ones. Excurrent aperture with short valvular membrane, surrounded by ca. 42 short, simple tentacles that are not uniformly distributed around base of valvular membrane but cluster on dorsal and ventral border of the latter.

The position of the tentacles during siphoning was not recorded in this species.

***Gafrarium tumidum* Röding, 1798**  
(Figs. 4H, 5H)

**Material examined.** – In vivo: 1 ex. (FMNH 312150), KKB-02; preserved: 3 ex. (MZSP 81675), KKB-03.

**Observations.** – Siphons short, ps:sl 0.24, separated, with black pigment dots scattered throughout walls of both siphons, stronger on distal ends and fading towards basal region; pigmentation also present on tentacles of incurrent siphon; densely distributed white pigment dots on internal walls of both siphons. Incurrent aperture fringed by ca. 42 simple tentacles, organised in two rows. Innermost row comprising ca. 16 medium-sized tentacles, interspersed with groups of 1–3 short tentacles of second row, the latter inserted slightly farther from aperture. Excurrent aperture with medium-sized valvular membrane, surrounded at its base by 27 short, simple tentacles.

During siphoning, the innermost row of incurrent siphonal tentacles is usually held pointing towards the centre of the aperture. The second row of incurrent tentacles and all of the excurrent tentacles point either in the direction of water flow or angled slightly away from the aperture.

**MERETRICINAE**

***Meretrix meretrix* (Linnaeus, 1758)**  
(Figs. 2F, 4I, 5I, 6B)

**Material examined.** – In vivo: 2 ex. (FMNH 309790), KKB-15; preserved: 3 ex. (MZSP 81676), KKB-15.

**Observations.** – Siphons long, ps:sl 0.45, united to the distal tips, with black pigment dots bordering insertion of each tentacle and also forming stripe extending from dorsal border of incurrent to ventral border of excurrent aperture. With ca. 80 bipinnate tentacles bordering incurrent aperture, arranged in three rows. Innermost row comprising ca. 10 long tentacles, each subdivided into 9–11 secondary branches that, in turn, give rise to 2 or 3 tertiary branches. Second row formed by ca. 30 medium-sized tentacles that intersperse with those of inner row in groups of three. Outermost row formed by ca. 40 short tentacles, interspersed with tentacles of first and second rows. Excurrent aperture with short valvular membrane, surrounded at its base by ca. 50 long tentacles interspersed with 30–40 short ones, most of which are simple, rarely bifid, or pinnate with few papilla-like secondary branches.

During siphoning, the innermost row of incurrent siphonal tentacles is usually bent over the aperture, forming a finely meshed sieve. The second and outermost rows of incurrent tentacles, as well as all of the excurrent siphonal tentacles, point parallel to the direction of water flow or sometimes slightly away from the aperture.

**PITARINAE**

***Pitarina striata* (Gray, 1838)**  
(Figs. 2E, 4J, 5J)

**Material examined.** – In vivo: 2 ex. (FMNH 39749), 312151, KKB-03; preserved: 1 ex. (MZSP 81677), KKB-03.

**Observations.** – Siphons long, ps:sl 0.47, united to distal tips, with more or less conspicuous spots of orange pigment distributed throughout walls and dark collar of black pigment around and between each distal aperture but fading towards basal regions; internally with uniformly distributed white pigment dots. Incurrent aperture crowned by 34 or 35 short, simple tentacles, half of them slightly longer (but still “short” by present criteria) than remaining tentacles. Excurrent aperture with short valvular membrane, surrounded at its base by 20–22 short, simple tentacles, half of them slightly longer (but still “short” by present criteria) than remaining tentacles.

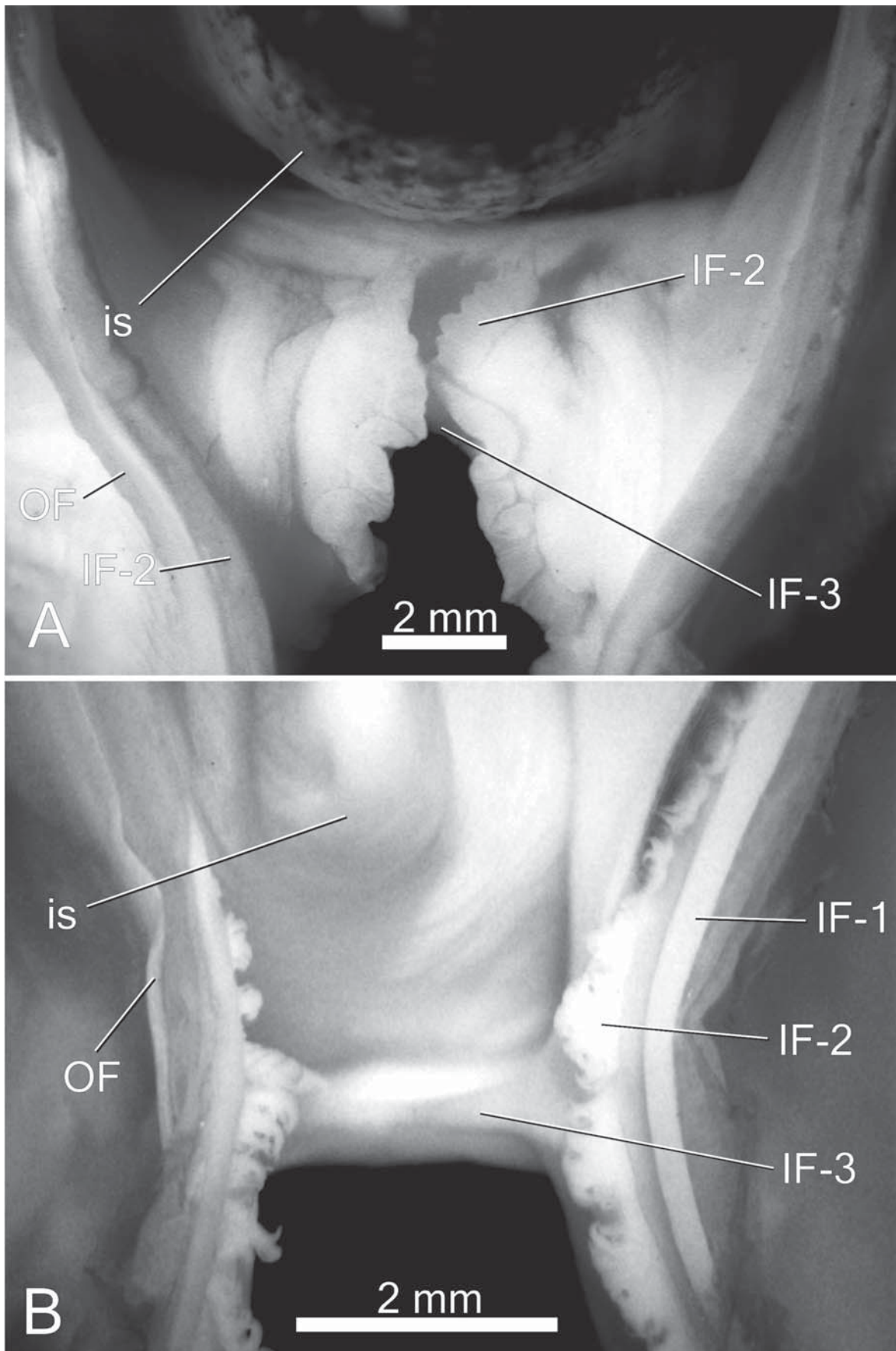


Fig. 6. Posterior view of the mantle margins of *Periglypta puerpera* (A) and *Meretrix meretrix* (B) after the removal of the shell, showing the point of fusion of the innermost pair of mantle folds (IF-3) near the ventral wall of the inhalant siphon and the path taken by the remaining three pairs of mantle folds. The two outermost pairs of folds (OF and IF-1) extend dorsally, nearing the posterior border of the mantle isthmus. The second innermost pair of folds (IF-2) end, unfused, near the ventral margin of the incurrent siphon (is) in *P. puerpera* (A) but in *M. meretrix* (B), they also extend farther, nearing the mantle isthmus.

During siphoning, all siphonal tentacles point either parallel to the direction of water flow or angled slightly away from the aperture. The incurrent aperture frequently flares distally.

#### TAPETINAE

##### *Marcia hiantina* (Lamarck, 1818)

(Figs. 4K, 5K)

**Material examined.** – In vivo: 1 ex. (FMNH 309747), KKB-03; preserved: 2 ex. (MZSP 81678), KKB-03.

**Observations.** – Siphons long, ps:sl 0.45, united half-way, with radial stripes of black pigment fading towards basal region, stronger along dorsal and ventral walls of each siphon; internally with uniformly distributed white pigment dots. Approximately 62 tentacles inserted on border of incurrent aperture, arranged in two rows. Inner row comprising 25 medium-sized, simple tentacles; outer row formed by 37 short, simple tentacles, inserted in slightly external position. Excurrent aperture with medium-sized valvular membrane, surrounded at its base by 20 medium-sized, simple tentacles.

During siphoning, the tentacles of the inner row on the incurrent siphon are held directed towards the centre of the aperture. The remaining tentacles of both siphons point either parallel to the direction of water flow or angled slightly away from the aperture.

##### *Neotapes undulata* (Born, 1778)

(Figs. 4L, 5L)

**Material examined.** – In vivo: 1 ex. (FMNH 312148), Chantaburi Market; preserved: 4 ex. (MZSP 81679), Chantaburi Market.

**Observations.** – Siphons long, ps:sl 0.44, separated, with a collar of orange pigment externally surrounding each distal aperture. Incurrent aperture lacking tentacles. Excurrent aperture with short valvular membrane, surrounded at its base by 12 short, simple, sometimes papilla-like tentacles.

Due to the small size of the tentacles, the position during siphoning did not vary.

##### *Ruditapes variegatus* (G. B. Sowerby II, 1852)

(Figs. 2G, 4M, 5M, 7A)

**Material examined.** – In vivo: 1 ex. (FMNH 309785), KKB-05; preserved: 1 ex. (MZSP 81680), KKB-05.

**Observations.** – Siphons long, ps:sl 0.41, separated, with black pigment dots loosely arranged in radial stripes, strong on distal tips and fading towards basal region; each incurrent siphonal tentacle with conspicuous stripe of orange pigment on outward face and ring of black pigment around insertion. Approximately 75–80 tentacles on border of incurrent aperture, arranged in three rows. The

innermost row comprising ca. 20 long bipinnate tentacles, each divided into 8–14 secondary branches that are further divided into 2–7 tertiary branches. Second row formed by ca. 20 medium-sized, bipinnate tentacles (divided into 6–8 secondary branches) that intersperse with those of innermost row. Outermost row composed of ca. 40 short, pinnate or simple tentacles, inserted in slightly more external position and interspersed with tentacles of first and second rows. Excurrent aperture with medium-sized valvular membrane, surrounded at its base by 80–85 medium-sized, pinnate tentacles, each bearing 8–10 secondary branches.

During siphoning, the innermost row of incurrent siphonal tentacles is usually held bent over the aperture, forming a finely meshed sieve with its network of fine branches. The second and outermost rows of incurrent tentacles, as well as all of the excurrent siphonal tentacles, point parallel to the direction of water flow or slightly away from the aperture.

#### VENERINAE

##### *Periglypta puerpera* (Linnaeus, 1758)

(Figs. 2A, 4N, 5N, 6A)

**Material examined.** – In vivo: 2 ex. (FMNH 309787), KKB-12; preserved: 1 ex. (MZSP 81681), KKB-12.

**Observations.** – Siphons long, ps:sl 0.53, separated, with densely distributed black pigment extending from distal tips and covering ca. two thirds of total length; scattered white pigment dots uniformly covering inner walls. Each siphon with many tentacles; ca. 43 and 75 tentacles fringing incurrent and excurrent apertures, respectively. Tentacles on border of incurrent aperture arranged in two rows; inner row comprising 10 medium-sized, pinnate tentacles, each divided into 9–11 short secondary branches. Outer row formed by short, simple or pinnate tentacles, inserted in slightly external position and interspersed in groups of 2–4 with tentacles of first row. Excurrent aperture with short valvular membrane, surrounded at its base by crown of 18–22 short pinnate tentacles, interspersed with groups of 2–4 shorter simple tentacles. Pinnate tentacles of excurrent siphon each with 3 or 4 papilla-like secondary branches.

During siphoning, the inner row of incurrent siphonal tentacles is usually held bent over the aperture, forming a finely meshed sieve with its network of fine branches. The outer row of incurrent tentacles, as well as all of the excurrent siphonal tentacles, point parallel to the direction of water flow or slightly away from the aperture.

#### SUBFAMILY INCERTAE SEDIS

##### *Placamen chloroticum* (Philippi, 1849)

(Figs. 2D, 4O, 5O)

**Material examined.** – In vivo: 1 ex. (FMNH 309748), KKB-02; 2 ex. (FMNH 309789), KKB-16; preserved: 1 ex. (MZSP 81682), KKB-02.

**Observations.** – Siphons short, ps:sl 0.40, united to distal tips, with adjacent black pigment dots aligned radially, forming fine stripes throughout entire length of external walls, fading on long valvular membrane of excurrent aperture. Incurrent aperture fringed by 23–25 short to medium-sized tentacles, most simple (two of the three observed living specimens had 1 or 2 bifid tentacles on incurrent siphon). Excurrent siphon bearing 7–14 short to medium-sized, simple tentacles inserted along base of valvular membrane.

During siphoning, the incurrent siphonal tentacles are usually held leaning towards the centre of the aperture or sometimes parallel to the water flow. Those on the excurrent siphon are held either parallel to the water flow or pointing away from the aperture.

## RESULTS

**Venerid diversity in the Gulf of Thailand.** – Twenty-five species of Veneridae were collected during this study from the northern Gulf of Thailand (Table 1), all of which have been previously recorded from the gulf. Fifteen species were obtained alive and observed for siphonal morphology and behaviour (Fig. 4).

**Siphonal morphology.** – In all species, the excurrent aperture terminates in a translucent, dome-shaped membrane (e.g., “valvular membrane” of Yonge, 1957; “conical valve” of Jones, 1979; “siphonal membrane” of Narchi & Dario, 2002), considerably thinner than the proximal siphonal wall. The valvular membrane directs the water current; it is always free and never involved in siphonal union. Upon withdrawal, it inverts into the siphon’s lumen, re-everting as soon as siphoning resumes. When present, tentacles of the excurrent siphon arise from the base of the membrane and during siphoning are held pointing either parallel to the direction of water flow or outward away from the opening.

In all investigated species the incurrent siphon is larger in diameter than the excurrent one, especially near the terminus. In most of the examined species (*Anomalocardia squamosa*, *Gafrarium dispar*, *G. divaricatum*, *G. pectinatum*, *G. tumidum*, *Meretrix meretrix*, *Marcia hiantina*, *Ruditapes variegatus*, *Periglypta puerpera*, and *Placamen chloroticum*), the incurrent aperture is terminally fringed by tentacles of different sizes, the largest usually inserted most internally. During siphoning, tentacles of the incurrent siphon are held at various angles. As a general rule, however, the largest tentacles are held bent over the aperture, forming a sieve, whereas the remaining (smaller) ones usually point either parallel to the direction of water flow or slightly away from the aperture, presumably complementing the sieving function of the largest tentacles.

The size of the pallial sinus correlates, as expected, with the length of the siphons. In species with long siphons, the pallial sinus is longer/deeper than 40% of total shell length (ps:sl > 0.40).

The mantle of all species examined here for degree of pallial fusion involved in the formation of siphons (*Anomalocardia squamosa*, *Gafrarium dispar*, *G. divaricatum*, *G. pectinatum*, *G. tumidum*, *Meretrix meretrix*, *Pitarina striata*, *Marcia hiantina*, *Neotapes undulata*, *Ruditapes variegatus*, *Periglypta puerpera*, and *Placamen chloroticum*) bears one outer and three inner folds (i.e., OF, IF-1, IF-2, and IF-3, relative to the periostracal groove) per side. Only the innermost (“fourth” or IF-3) mantle folds are involved in forming the siphons; the second innermost folds (IF-2) of the left and right mantle lobes extend from the dorsal border of the anterior adductor muscle to the ventral limit of the incurrent siphon where they end abruptly, not fusing in the midline (Fig. 6A). The exception is *Meretrix meretrix* (Fig. 6B), in which the second innermost folds (IF-2) are tinged with brown pigment at this point (ventral limit of the incurrent siphon) but extend farther, hanging free throughout the entire siphonal embayment and nearing the posterior border of the mantle isthmus.

**The effects of preservation.** – With retraction upon preservation, short separated siphons, such as those of *Anomalocardia squamosa* and the four studied species of *Gafrarium*, appear fully united in virtually all of the preserved material. Species with long siphons were not as susceptible to artefactual misinterpretation; long separated siphons continued to appear fully separated whereas in *Marcia hiantina*, the only studied species with long siphons united half-way, preserved siphons appeared separated at their terminal quarter only. In all investigated taxa, pigmentation was still retained after six months in preservative, although the black pigment readily abraded from the surface when rubbed with a pair of forceps or other dissecting instrument. Short simple tentacles and short branches of complex tentacles become inconspicuous in most preserved specimens and can be easily overlooked. The valvular membrane is usually inverted into the lumen of the excurrent siphon and frequently becomes indistinguishable from the rest of the siphonal wall, especially in species that lack tentacles inserted along the base of the membrane, such as *Neotapes undulata*, *Dosinia cretacea* and *Dosinia juvenilis*.

Regardless of the species concerned, the amount of morphological information that can be retrieved from the siphonal tips of preserved specimens is highly dependent on the degree of retraction of the apertural region. Thus, the most reliable specimens are those in which the aperture has remained open after preservation (Fig. 7A) as opposed to those in which the siphonal tips have inverted into the lumen of the organ, closing the distal aperture by apposition of its margins (Fig. 7B). In the former specimens, the approximate number, arrangement, and relative sizes of the tentacles around the siphonal apertures can often be correctly assessed, whereas in the latter, such tasks are much more difficult, requiring not only dissection of the specimen but also interpretation of highly retracted and imbricated structures.

## DISCUSSION

**Traditional veneroid siphonal morphology.** – Traditional veneroid taxonomy and species descriptions typically include three siphonal features: relative length, degree of union of the incurrent and excurrent siphons, and the presence or absence of distal tentacles. Nearly 90 species can be characterised in these respects either from written descriptions or images in the literature. Reliability of these data vary from indistinct and undescribed gross-anatomical drawings or photographs (e.g. M. E. Gray, 1857), to brief and unillustrated descriptions (e.g., “siphons rather long”; Pelseneer, 1911), to meticulously detailed drawings of the siphons and tentacles derived from observations of living animals (e.g., Lam, 1980; Narchi, 1980).

Relative length seems to be the most problematic traditional character. Although some authors provide a context for siphonal length [e.g. “when fully extended, may exceed the shell length by a few millimetres”; Lam, 1980: 18, for *Ruditapes philippinarum* (A. Adams & Reeve, 1850)], most fail to provide any point of reference, stating merely “long” or “short.” Variability (or conflicting data) is also evident; for example, *Costacallista erycina* (Linnaeus, 1758) (syn. *florida* Lamarck, 1818), is cited as having long (M. E. Gray, 1857) or very short (Fishelson, 2000) siphons. At least part of this inconsistency could be due to preservation artefact in soft-tissue organs that can extensively extend and retract. Relative length can also vary ontogenetically, as is well-known in *Mercenaria mercenaria* (Linnaeus, 1758), in which the juveniles have longer siphons (Carriker, 1961), and in

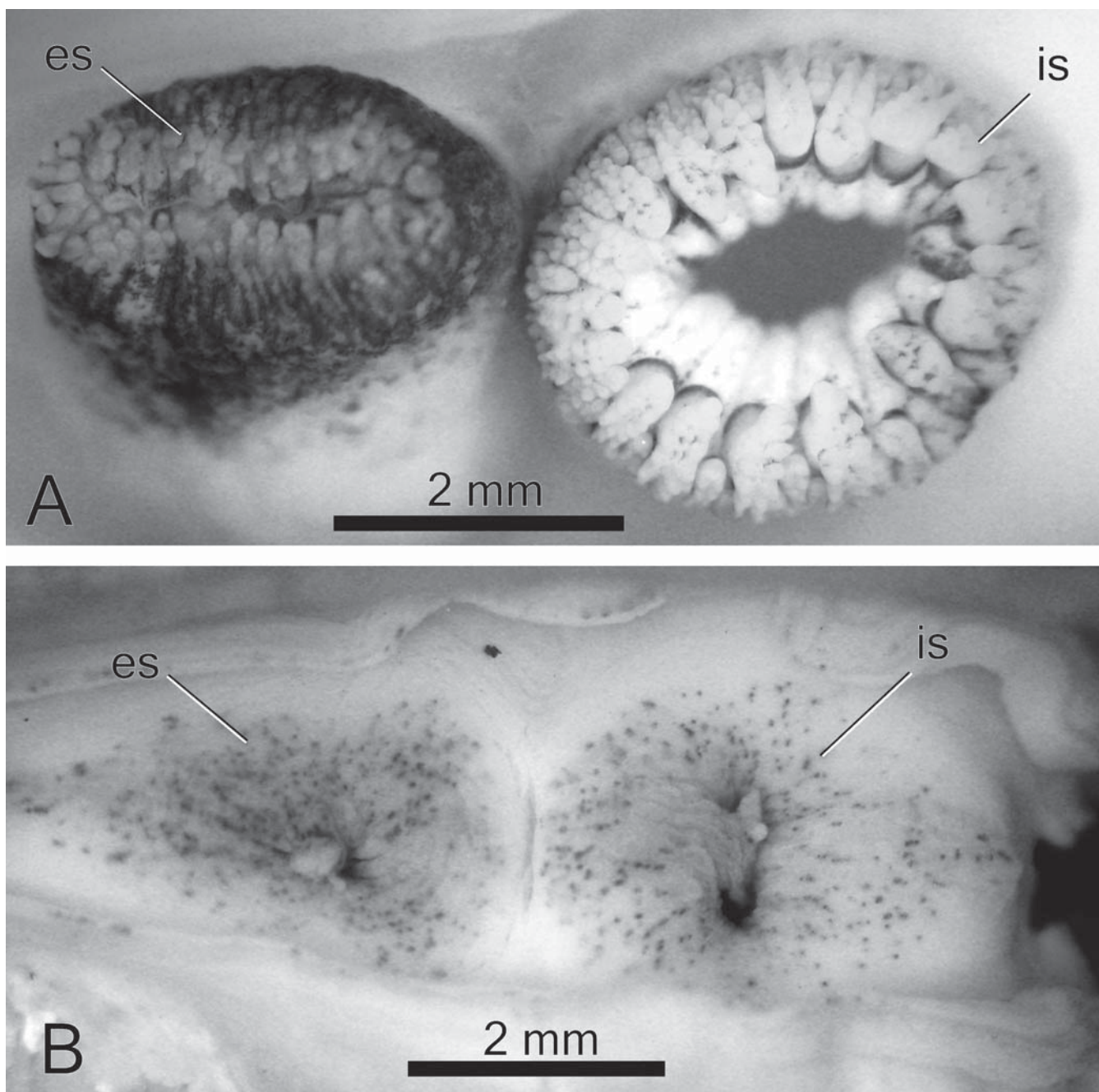


Fig. 7. The siphons of preserved specimens of *Ruditapes variegatus* (A) and *Gafrarium pectinatum* (B). In *R. variegatus*, the siphonal apertures remained open after preservation and much of their morphology is still visible. In *G. pectinatum*, the tips inverted into the lumen of the siphons, hiding the tentacles and other features. Abbreviations used: is, incurrent siphon; es, excurrent siphon.

*Petricolaria pholadiformis* (Lamarck, 1818), in which the juveniles have shorter siphons (Morse, 1919).

Although traditional features continue to contribute to the definition of taxa at all levels, all of these characteristics have been previously correlated with habitat and lifestyle. Ansell (1961: 512) provided a “phylogenetic” diagram of Veneroidea, in which the plesiomorphic state is short united siphons associated with shallow burrowing, close to the sediment surface; *Gafrarium* and *Callista* in this system are “least specialized,” retaining the plesiomorphic state. “Only slightly more specialized” are some species of *Venus* with longer siphons. Long siphons are present in two lineages loosely associated with specialised habits: (1) deep-burrowing *Dosinia* and *Glaucanome*, with long united siphons; and (2) rock-boring or burrowing *Petricola* and *Mysia*, respectively, with long separated siphons. Owen (1959) noted that long united siphons have evolved independently by convergence in veneroids (e.g., *Glaucanome*) and several unrelated groups of deep-burrowing bivalves (e.g., *Mya*, *Panopea*).

In addition to the presence or absence of terminal tentacles on one or both siphons, the nature of those tentacles (whether simple or elaborated in some fashion) has also been linked to habitat. Ansell (1961) found that *Circumphalus*, *Timoclea*, *Clausinella*, *Venerupis* and *Gafrarium*, all of which live in gravely or rocky sediments, have branched (“digitate”) tentacles, whereas *Chamelea* and *Dosinia*, which live in cleaner sand or gravel bottoms, have simple tentacles. The implication is that more complex tentacles have evolved to prevent particles from entering the mantle cavity in habitats where suspended sediment is heavy. Exceptions do however occur; Bieler et al. (2004) noted that *Periglypta listeri* (J. E. Gray, 1838) has digitate tentacles but lives in a relatively clean gravel/sand habitat.

Some siphonal characters have been used in previous phylogenetic analyses of bivalves. Boss (1978) split the Pandoroidea (sensu Newell, 1965) into two clades based on, amongst other characters, the relative length of the siphons. The phylogeny of Cardiidae by Schneider (1998) coded four siphonal characters, but none of these were the traditional characters of length, unification, or presence/absence of tentacles. Instead, Schneider’s (1998) characters concerned the location and distribution pattern of the tentacles, presence/absence of a valvule on the interior of the siphonal apparatus, and whether or not the incurrent siphon is separated from the pedal aperture; all were informative to some extent (some for major divisions) in the final cladogram. Giribet & Wheeler (2002) also coded four siphonal characters in their combined morphological and molecular phylogeny of bivalves, taking into account the presence/absence of siphons, degree of pallial fusion involved in siphonal formation, and the traditional character of unification; how informative these siphonal characters were in the resultant cladograms was unfortunately not discussed. In another application, Fishelson (2000: 497) identified ultrastructural characters that “can be used as markers for ecological as well as phylogenetic considerations” (although Fishelson did not use them in a phylogeny); three types of sensory organs on or within the

siphons were shown to differ in distribution and relative quantity amongst taxa. Despite these works, the traditional characters of length, degree of union, and tentacle complexity remain problematic, and the higher taxa defined (in part) by these characters remain suspect.

**Degree of pallial fusion involved in the formation of siphons.** – The mantle margins of bivalves are typically split into three folds, the outer, middle and inner (Yonge, 1957) or OF, IF-1, and IF-2 in the terminology of Waller (1978; i.e., one outer fold and two inner folds relative to the periostracal groove). In the Veneridae, however, there are four folds (OF, IF-1, IF-2 and IF-3; Ansell, 1961; Hillman & Shuster, 1966; Jones, 1979), although the origin of the extra inner fold is contentious (see Hillman & Shuster, 1966, for a review). It is generally agreed in the literature that venerid siphons are formed by fusion of the two innermost folds (IF-2 and IF-3) from one side with those of the other. This condition has been variously interpreted depending upon the perceived homologies of these four folds with those of the “typical bivalve mantle margin.” Type A of Yonge (1982) has been suggested by authors who consider IF-2 and IF-3 to both be components of the inner mantle fold (e.g., Morton, 1985; Morton & Knapp, 2004), whereas Type B of Yonge (1982) is used by authors (e.g., Yonge, 1957; Ansell, 1961; Narchi, 1972, 1980; Narchi & Gabrieli, 1980; Guéron & Narchi, 2000; Narchi & Dario, 2002; Bieler et al., 2004) who regard IF-2 and IF-3 to represent parts of the middle and inner folds, respectively.

However, in all species studied herein for degree of pallial fusion involved in the formation of siphons, only the innermost mantle folds (IF-3) are involved in the formation of the siphonal tubes. The second innermost folds (IF-2) hang free for the entire extension of the siphonal embayment in *Meretrix meretrix*, whereas in the remaining taxa examined, they end abruptly, and separately, within the siphonal embayment ventral to the inhalant siphon. In no case are they fused in the midline with one another. Siphons formed solely by fusion of IF-3 folds (Type A of Yonge, 1982) might be the correct assumption for all venerids because the IF-2 folds terminating near the inhalant siphon can give the false appearance of fusion that, it is suggested here, lead to the historical misinterpretation of siphonal formation in this family.

**General characterisation.** – Apart from the degree of pallial fusion involved in their formation, the only other siphonal features that showed no variation in the taxa examined herein were: (1) the relative diameter of the siphonal distal apertures, always larger in the incurrent siphon; and (2) presence of a valvular membrane at the distal tip of the excurrent siphon. The latter is widespread in the family, being found in representatives of all subfamilies hitherto studied, i.e., Chioninae (M. E. Gray, 1857; Morse, 1919; Ansell, 1961; Narchi, 1972; Jones, 1979; Narchi & Gabrieli, 1980; Guéron & Narchi, 2000; Morton & Knapp, 2004), Dosiniinae (Ansell, 1961), Gemminae (Morse, 1919; Sellmer, 1967; Narchi, 1971), Gouldiinae (Ansell, 1961), Meretricinae (Narchi, 1970, 1972; S. Gray 1982; Narchi & Dario, 2002),



Pitarinae (M. E. Gray, 1857; Morse, 1919; Narchi, 1971; S. Gray, 1982; but see note about *Callocardia hungerfordi* (G. B. Sowerby II, 1888), below), Tapetinae (G. B. Sowerby II, 1854; M. E. Gray, 1857; Ansell, 1961; Nielsen, 1963; Lam, 1980; Morton, 1985; Bieler et al., 2005) and Venerinae (M. E. Gray, 1857; Narchi, 1980; Bieler et al., 2004).

**Subfamily characterisations.** – Detailed descriptions and illustrations of chionine siphons have been published for *Anomalocardia brasiliana* (Gmelin, 1791) by Narchi (1972), *Veremolpa scabra* (Hanley, 1845) by Narchi (1980), *Protothaca subrostrata* (Lamarck, 1818) by Narchi & Gabrieli (1980), *P. pectorina* (Lamarck, 1818) by Guéron & Narchi (2000), and *Chione elevata* (Say, 1822) by Morton & Knapp (2004); *A. squamosa* has been added by this study. [Note: Although numerous other published and unpublished siphonal descriptions/illustrations are known to the authors, only those clearly based on observations of living specimens are discussed in this section.] The pattern of pigmentation is similar for all of these species, each possessing radial lines of black pigment along the external wall, rings of black pigment around the base of the tentacles, or both. The incurrent aperture is always fringed by many simple tentacles of two different sizes interspersed, the longer ones being held over the aperture during siphoning. The excurrent siphon bears many simple tentacles, all of which are similar in length. Based in part on data obtained from preserved specimens (and thus preservation artefacts), Kappner & Bieler (2006) suggested that all Chioninae have fused siphons. However, this is not supported by our results or previous studies based on observation of living specimens: partially or fully separated siphons occur in *A. squamosa*, *A. brasiliana*, *P. subrostrata*, and *C. elevata*, whereas in *V. scabra* and *L. pectorina*, they are united to the tips.

Members of the subfamily Dosininae have not been as extensively studied as those of Chioninae, there being only one species, *Asa lupinus* (Linnaeus, 1758), in which siphonal morphology was previously described for living specimens (Jeffreys, 1863 [as *Venus lincta* Pulteney, 1799]; Ansell, 1961). Siphons of the two species described herein, *D. cretacea* and *D. juvenilis*, are in most aspects very similar to those of *A. lupinus*. All three taxa possess long, completely united siphons with relatively few, very short, simple tentacles fringing the incurrent aperture. Excurrent siphonal tentacles are absent in *D. cretacea* and *D. juvenilis* but occur in *A. lupinus* (fide Jeffreys, 1863; Ansell, 1961), *Pectunculus exoleta* (Linnaeus, 1758) (M. E. Gray, 1857; Jeffreys, 1863), and in *D. excisa* (Schroeter, 1788) and *D. victoriae* Gatliff & Gabriel, 1914 (both P. M. Mikkelsen, unpubl. data).

*Gouldia minima* (Montagu, 1803) is the only member of Gouldiinae to have its siphons previously described and illustrated in detail (Ansell, 1961). The present study considerably expands the data available for this subfamily by providing detailed descriptions of *Circe scripta*, *Gafrarium dispar*, *G. divaricatum*, *G. pectinatum*, and *G. tumidum*. All studied species herein are similar to *G. minima* in bearing short, separated siphons with many simple tentacles fringing

both the incurrent and excurrent apertures. Tentacles of the incurrent siphon are evenly distributed around the aperture; those of the excurrent siphon cluster on the dorsal and ventral proximal border of the valvular membrane in *G. dispar* and *G. pectinatum* but are evenly distributed in the remaining species.

Narchi (1972) and Narchi & Dario (2002) described and illustrated in detail the siphons of the meretricines *Tivela mactroides* (Born, 1778) and *T. ventricosa* (J. E. Gray, 1838), respectively. The incurrent siphon of each is similar to that of *Meretrix meretrix* (this study) in bearing many bipinnate tentacles arranged in successive rows, with the longest tentacles occupying the innermost row. The excurrent siphon is also similar in possessing only simple tentacles and a short valvular membrane. The siphons of *M. meretrix* are long and united to the tips, whereas in *T. mactroides* and *T. ventricosa*, they are short and separated.

In Pitarinae, siphonal morphology has been previously studied in detail in *Pitar morrhuanus* (Dall, 1902) (Morse, 1919 [as *Venus mercenaria*]), *Nutricola tantilla* (A. A. Gould, 1853) (Narchi, 1971; S. Gray, 1982), *N. confusa* (S. Gray, 1982) (see S. Gray, 1982) and *Callocardia hungerfordi* (see Morton, 2000); *Pitarina striata* has been added by this study. *C. hungerfordi* is either an exception amongst venerids in lacking a valvular membrane (Morton, 2000), or the structure might be lost during ontogeny, as suggested for *P. morrhuanus* by Morse (1919). Adults of all studied species except *P. morrhuanus* and *N. tantilla* bear long siphons. Juvenile *P. morrhuanus* also bear long and narrow siphons but, according to Morse (1919), they become very short in adults; in *N. tantilla*, siphons were shown to be shorter than their combined diameter by Narchi (1971), but longer by Gray (1982). *N. tantilla* is also exceptional for being the only studied pitarine in which the siphons are united half-way instead of fully united (Narchi, 1971; Gray, 1982). Short, uniformly distributed, simple tentacles fringe the siphonal tips of all the investigated species.

Previous detailed accounts of tapetine siphonal morphology have been made for numerous species: *Venerupis senegalensis* (Gmelin, 1791) [as *V. pullastra* (Montagu, 1803)], *Tapes aureus* and *Ruditapes decussatus* (Lamarck, 1818), all by Ansell (1961), *Irus macrophyllus* (Deshayes, 1853) [as *I. irus* (Linnaeus, 1758)] by Morton (1985), *Marcia japonica* (Gmelin, 1791), *M. marmorata* (Lamarck, 1818), *T. dorsatus* (Lamarck, 1818), and *R. philippinarum*, all by Lam (1980), *Katylisia rhytiphora* (Lamy, 1935) by Nielsen (1963), and *Venerupis galactites* (Linnaeus, 1758) by Bieler et al. (2005). These descriptions plus comparison of the siphons of *M. hiantina*, *Neotapes undulata* and *R. variegatus* (this study) with previous accounts by Lam (1980) reveal that siphonal morphology in the Tapetinae is remarkably variable. Most possess long siphons that are either partially or fully separated; those of *M. japonica*, *M. marmorata*, and *T. dorsatus* are short, and those of *V. senegalensis* are united for the entire siphonal length. The incurrent aperture is usually fringed by many long, branched (pinnate or bipinnate) tentacles. However, medium-sized, simple tentacles occur in *M. hiantina* and *N.*

Table 2. Siphonal characters for eight venerid subfamilies as inferred from this study and detailed published accounts (see text for references).

Subfamily	Siphonal length	Degree of union	Pigmentation	Incurrent tentacles	Excurrent tentacles	Valvular membrane	Tentacle sieve
Chioninae	variable, ps:sl 0.29–0.48	variable	black radial lines and/or black pigment rings around tentacle bases	numerous (~20–48), simple, two sizes	numerous (~20–36), simple, single size	medium-sized to long	yes
Dosiniinae	long, ps:sl 0.67–0.69	fully united	collar of pigment around incurrent or both apertures	few (7–16) very short, simple	absent or very short, simple	short	no
Gemminae	short (?), ps:sl 0.31	contentious	patches and streaks of reddish brown pigment near the tip; white patches on the inner surfaces	few (8–12), simple, two sizes	absent	long	yes
Gouldiinae	short, ps:sl 0.23–0.26	separated	scattered pigment dots on terminal margins and incurrent tentacles, usually also extending and fading towards the basal regions	numerous (25–55), simple	numerous (15–42), simple	variable	yes
Meretricinae	variable, ps:sl 0.40–0.45	variable	black pigment around the base of the tentacles	numerous (50–200), branched, at least three sizes	numerous (20–90), simple	short to medium-sized	yes
Pitarinae	usually long, ps:sl 0.29–0.48	usually fully united	tips pigmented	few to numerous (8–35), short, simple	numerous (18–25), short, simple	variable	usually not
Tapetinae	usually long, ps:sl 0.32–0.55	usually separated or partially united	tips and incurrent tentacles pigmented; often with pigment spots or stripes fading towards base	usually numerous (0–80), long, branched	usually numerous (12–85) simple, length variable	variable	usually yes
Venerinae	long, ps:sl 0.49–0.53	separated	tips pigmented; tentacles devoid of pigment	numerous (40–43), medium-sized, branched	numerous (30–75), branched	short	yes

*undulata* completely lacks tentacles on the incurrent siphon. Tentacles of the excurrent siphons are simple in all species except *R. variegata*, and vary from very short in *N. undulata* to long in *V. galactites*. Length of the valvular membrane is similarly variable, being short and incomplete in *V. galactites*, and rather long in *I. macrophylla*.

The siphons of the venerine *Periglypta puerpura* (this study) are very similar to those of *P. listeri* described by Bieler et al. (2004). In both species the incurrent and excurrent siphons are separated, densely pigmented at the tips, and fringed by many pinnate tentacles, those of the incurrent siphon medium-sized and with more secondary branches.

Amongst the subfamilies of Veneridae not represented in the present study, detailed published data on siphonal morphology in Gemminae is only available for *Gemma gemma* (Totten, 1834) (Morse, 1919; Sellmer, 1967; Narchi, 1971). Length of the siphons is somewhat uncertain; siphons were shown to be shorter than their combined diameter by Narchi (1971: fig. 4b), but longer by Morse (1919: fig. 32); however, the ps:sl ratio of 0.31, measured from an illustration of the interior of the right valve (Narchi, 1971: fig. 2), indicates short siphons. Degree of union of the incurrent and excurrent siphons is contentious; Morse (1919) and Sellmer (1967) described them as united to the tips, whereas Narchi (1971) regarded the siphons as separated along the distal half. The incurrent aperture is fringed by 8–12 simple tentacles of two sizes interspersed. The excurrent siphon lacks tentacles and bears a long valvular membrane; this last observation is also true for *Parastarte triquetra* (Conrad, 1846) (P. M. Mikkelsen, unpubl. data, based on preserved material).

**The effects of preservation.** – As shown herein, the effects of preservation on siphonal morphology are variable and unpredictable; often two individuals of the same species, preserved by the same method, imply different morphologies. The problem can be minimized by analyzing multiple specimens and placing greater confidence on those in which the siphonal apertures have remained open after preservation. Likewise, coding siphonal characters from published anatomical descriptions or illustrations is generally jeopardised by the (often unspecified) condition of the specimens used by the authors. In studies requiring comparison of siphonal morphology between taxa (including phylogenetic analyses), observations of living specimens are preferred if not essential.

**Phylogenetic application.** – Of the morphological features described for the siphons of the 15 species surveyed during this investigation (i.e. relative siphonal length, degree of union, pigmentation, relative length of the valvular membrane, and number, branching pattern, relative length, and distribution of tentacles) only two, degree of union and relative siphonal length (the latter expressed as size of pallial sinus), have been used in phylogenetic analyses of the family (Mikkelsen et al., 2006). This was a direct result of the unavailability of living specimens and the uncertainties of scoring siphonal characters based on preserved specimens or literature accounts. One of the goals of the present study

was to suggest codeable phylogenetic characters derived from venerid siphons in living condition. However, when the summarised results of this study (Table 2) are mapped onto the latest phylogeny (Mikkelsen et al., 2006: fig. 12B), no patterns emerge for any of the potential characters. That tree shows two major clades: (1) comprising Dosiniinae, Chioninae + Venerinae (combined), and Tapetinae; and (2) Gemminae, Callistinae, Turtoniinae, Pitarinae sensu stricto, Petricolinae and most members of Gouldiinae (although not monophyletic). When mapped at the subfamilial level, each clade contains members showing long or short siphons, united or separated siphons and simple or branched tentacles that either do or do not form a sieve during siphoning. It is therefore evident that siphonal characters have been heavily influenced by habitat, masking phylogenetic signal at least at the subfamilial level.

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## THAI ABSTRACT

การสำรวจชนิดของหอยสองฝาวงศ์เวเนอริดีจากอ่าวไทยพบว่ามีหอยทั้งสิ้น 78 ชนิดที่เป็นสมาชิกของ 10 จาก 14 วงศ์ย่อยที่เป็นที่ยอมรับในปัจจุบัน รายงานครั้งนี้รวมถึงหอยเวเนอริดี 25 ชนิด ที่เก็บจากบริเวณอ่าวคุ้งกระเบนในประเทศไทยระหว่างเดือนสิงหาคม ถึง กันยายน พุทธศักราช 2548 หอยทั้งหมดที่ค้นพบบริเวณอ่าวคุ้งกระเบน เป็นหอยที่เคยมีการรายงานแล้ว ทั้งนี้หอยเวเนอริดี 15 ชนิดจาก 7 วงศ์ย่อยเป็นหอยที่ได้มีการศึกษาขณะยังมีชีวิตอยู่ โดยมีการพิจารณาลักษณะของท่อน้ำในด้านความยาวและลักษณะการเชื่อมกัน ลักษณะเมือคัส จำนวนการแตกแขนงและการกระจายของหนวดบริเวณปลายท่อน้ำรวมทั้งพฤติกรรมระหว่างที่มีการดูดและพ่นน้ำ รวมทั้งผลของการใช้น้ำยาคงสภาพร่วมกับการพิจารณาเนื้อเยื่อบริเวณขอบแมนเทิลซึ่งพบว่าเนื้อเยื่อพันนอก 1

ส่วน และเนื้อเยื่อพับในอีก 3 พับ (OF, IF-1, IF-2, และ IF-3) โดยเทียบจาก periostracal groove การสร้างท่อน้ำของหอยเวเนอริคใช้เพียงแผ่นแมนเทิลส่วน IF-3 เท่านั้น ซึ่งแตกต่างจากรายงานว่าสร้างจากแผ่น IF-2 ด้วย ดังนั้นการพัฒนาท่อน้ำของหอยเวเนอริคจึงคล้ายกับแบบ A (Type A) ของ Yonge มากกว่าแบบ B (Type B) ที่มีการตีความไว้โดยนักวิจัยส่วนมาก การใช้น้ำยาคงสภาพมีผลอย่างมากกับท่อน้ำชนิดที่มีลักษณะแยกกันตลอดแนวความยาว ทำให้ท่อน้ำมีลักษณะเสมือนเชื่อมกัน บางส่วนหรือทั้งหมด ซึ่งเป็นสภาพที่แตกต่างจากหอยขณะยังมีชีวิตอยู่มาก ผู้วิจัยให้รายละเอียดลักษณะวงศ์ย่อยของเวเนอริค 8 วงศ์ย่อยโดยใช้ลักษณะของหอยขณะยังมีชีวิต เมื่อเทียบกับลักษณะทาง phylogeny ที่ได้เคยมีการตีพิมพ์ไว้แล้ว และไม่พบรูปแบบทาง phylogenetic แต่อย่างใด แสดงให้เห็นว่าลักษณะเฉพาะของท่อน้ำมีลักษณะที่เป็นแบบ homoplastic อย่างสูง

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