08

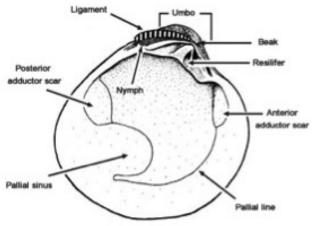
Bivalve classification and taxonomy

V. Venkatesan and K.S. Mohamed

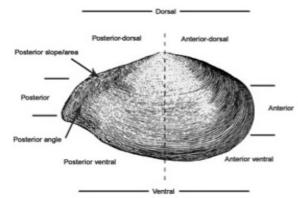
Molluscan Fisheries Division, Central Marine Fisheries Research Institute, Kochi-682 018

Introduction

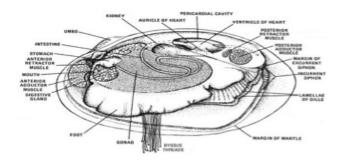
Bivalve is the second most dominant class in the phylum Mollusca. Bivalves are characterized by a laterally compressed body with an external shell of two halves that is hinged dorsally. The valves are united dorsally by elastic, a partially calcified or chitinous external or internal ligament and are held together by one or two adductor muscles. The head is rudimentary and have lost the buccal or radular apparatus. The mantle lobes are either connected or free ventrally. Most of the sensory structures are located in the mantle margin. They are mostly ciliary feeders, with sieving and sorting mechanisms on labial palps and leaf-like ctenidium. The mantle cavity includes a pair of ctenidia suspended laterally. The mouth and anus are located at opposite ends of the body and the gut is typically convoluted. The foot is compressed and adopted for burrowing, except in sedentary forms where it is rudimentary. Most bivalves are marine and there are no terrestrial forms. Fertilization occurs usually external, followed by trochophore and veliger stages larvae and metamorphosis to adult form. A total of 3271 species of molluscs was reported from India in which bivalves formed 33.6% (Appukuttan 1996)



Inner surface of a clam (bivalve) shell



Sections of a bivalve shell



Typical bivalve anatomy

Earlier classification systems of bivalves

Several classification schemes have been existed based on the comparative anatomical studies of extant bivalves. Earlier attempts to classify bivalves provided by Cox (1960) in his review were based on 1) gill structure (b) grades of gill structure 3) ciliation on gill filament. Later works proposed to classify the bivalves were based on other structures such as stomach (Purchon 1968), ctenidial-labial palp associations (Stasek, 1963). Thiele (1929 -1935) proposed a classification

of bivalves which was the first extensively used classification of bivalves. This old classification divided them into three orders: Taxodonta (protobranchiate bivalves), Anisomyaria (pteriomorphian bivalves) and Eulamellibranchiata. The order Eulamellibranchiate was divided into four sub orders: Schizodonta, Heterodonta, Adapedonta and Anomalodesmata.

A classification of bivalves presented by Newell (1965, 1969) based on the shell structure and anatomy was the basis of the modern classification of bivalves with six subclasses: the Palaeotaxodonta (=Nuculoidea and Nuculanoidea), Cryptodonta(=Solemyoidea), Pteriomorphia, Paleoheterodonta, Heterodonta and Anomalodesmata. Although six subclasses presented by Newell (1965) have been kept as such in the modern bivalve classification, later on a new taxonomical—level classification was proposed (Vokes 1980 and Beesley *et al.* 1998). Classification systems of following 5 subclasses are used before phylogenitic analysis carrying out (Giribet and Wheeler, 2002) or in other words, an emergence of modern system of classification.

Subclass Protobranchia

This group is the ancient marine infaunal bivalves which evolve in the Ordovician period. They have an aragonitic shell with nacre or a homogeneous structure. This subclass includes three superfamlies namely Solemyoidea, Nuculoidea and Nuculanoidea.

Subclass Pteriomorphia (=Filibranchia)

This group is marine, epifaunal forms in which most of them bear byssus threads. Pterio morphia contains economically important bivalves such as mussels, arks, oysters and scallops. In this group, five orders are recognized: Mytiloida, Arcoida, Pterioida, Limoida and Ostreoida. Pteriomorphia is characterized by asymmetries, inequilateral shells generally made up of calcite and aragonite, asymmetries in the adductor muscles that develop into heteromyarian or monomyarian, the foot has decreased or lacking in some group.

Subclass Palaeoheterodonta

This group includes two distinct orders viz. Trigonioida and Unionoida. Shells of this group are characterized by an aragonite deposition in the form of prism (prismatonacre). Trigonioida is marine forms of recent bivalves represented by the single genus *Neotrigonia*. Unionoida contains several members of freshwater bivalves such as freshwater mussels, pearl producing mussels etc and are characterized by prismatonacreous shell that are equivalve, equilateral and two adductor muscles with associated pedal retractors (Prezant, 1998a).

Subclass Heterodonta

This group is the largest, most diverse and most widely distributed among the bivalve subclasses (Prezant,

1998b). Most heterodonts are marine forms while few are freshwater forms (eg. Corbulidae, Sphaeriidae etc). Dimyarian heterodonts are siphonate and mostly filterfeeders with large eulamellibranch ctenidia and small palps. Most members have a heterodont dentition. This group includes families viz. Carditidae, Astaridae, Cyprinidae, Dressenidae, Lucinidae, Chamidae, Cardiidae, Tridacnidae, Veneridae, Tellinidae, Amphidesmatidae, Solecurtidae, Donacidae and Mactridae.

Subclass Anomalodesmata

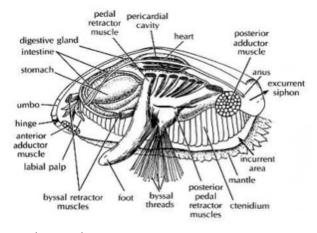
This subclass contains a collection of strange bivalves in which most of them are marine forms, some estuarine. Most species of this group are small and burrowing forms with primatonacreous shells. They have either modified eulamellibranchiate ctenidia or reduced ctenidia to setibranch condition. The setibranch families are characterized by gills in the form of a muscular septum which pumps water through the mantle cavity; mantle edges mostly free; adductor muscles equal; hinge weekly denticulate or edentate; macrophagous feeders contains deep water carnivorous bivalves and the families includes Verticordiidae, Poromyidae, Cuspidariidae etc.

New classification systems of bivalves

Modern classification of bivalves proposed here by Ponder and Lindber (2008) is based mostly on the collective studies of morphology and molecular data by Giribet and Wheeler (2007) but also include results from other works (Campbell 2000; Steiner and Hammer 2000; Dreyer *et al.* 2003; Giribet and Distel 2003; Williams *et al.* 2004; Taylor *et al.* 2005; Bieler and Mikkelsen 2006). This proposed classification is not the final one and is based on cladistic hypotheses in which rank are not given.

Autolamellibranchiata

This group possesses modified or reduced ctenidia for filter feeding and is divided into Pteriomorphia and Heteroconchia. Pteriomorphia includes largely epifaunal bivalves bearing byssal threads like oysters, scallops, mussels and arks.



Mussel: Internal anatomy

Table 1. The New Bivalve Classification

iable	i. iiie i	vew bivaive	Classification	II	
Biva	alvia Linr	naeus, 1758			
1.	Oppor	Opponobranchia or Protobranchia			
	1.1	Nuculoida Dall, 1889			
	1.2	Solemyoida Dall, 1889			
2.	Nucul	Nuculanoida Carter, D.C. Cam pbell and M. R. Campbell, 2000			
3.	Autolamellibranchiata Grobben, 1894				
	3.1 Pteriomorphia Beurten, 1944				
	3.2	Heteroconchia Cox, 1960			
		3.2.1 Palaeoheterodonta Newell, 1965			
			3.2.1.1	Trigonioida Dall, 1889	
			3.2.1.2	Unionoida Stoliczka,1871	
		3.2.2 Heterodonta Neumayr, 1883			
			3.2.2.1	Archiheterodonta new name	
			3.2.2.2	Euheterodonta Giribet and Distel, 2003	
				Anomalodesmata	
				Arcticoidea	
				Cardioidea	
				Chamoidea	
				Cyamioidea	
				Dreissenoidea	
				Galeommatoidea	
				Glossoidea	
				Lucinoidea	
				Mactroidea	
				Myoidea	
				Solenoidea	
				Tellinoidea	
				Veneroidea	

[Source: image taken or modified from Ponder and Lindber (2008) and Beesley et al. (1998)]

Distintive characters of commercially important species

Mussels

The genus *Perna* (family Mytilidae) is characterized by the absence of anterior adductor muscle, occurrence of one or two well developed hinge teeth, partition of the crystalline sac from the mid-gut, broad partition of the two posterior byssal retractors etc. In India, there are two species of commercially important mussels viz. the green mussel *Perna viridis* and the brown mussel *Perna indica* contribute to the fishery.

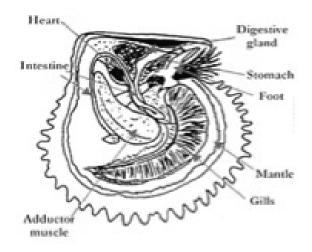
Perna indica

The outer surfaces of the shell valve and mantle margin are respectively dark brown and brown in colour. Anterior end of the shell is pointed and straight. Ventral shell margin is more or less straight. Middle dorsal margin has a distinct angle/

lump while posterior margin is broadly rounded. One large hinge teeth on the left valve and a corresponding depression on the right valve; foot is tongue shaped with byssal threads.

Perna viridis

The outer shell surfaces and mantle margin are respectively green and yellowish green in colour. Shell is large, elongate sub-trigonal. Anterior end of the shell is pointed with the beak turned down. Ventral shell margin is slightly concave. Middle dorsal margin is angularly convex while posterior margin is broadly rounded. Two small hinge teeth on the left valve and one on the right valve; foot is tongue shaped with byssal threads



Pearl oyster: internal anatomy

Pearl oysters

Taxonomy

The pearl oyster belongs to the family Pteriidae. This group is characterized by a straight hinge with 1-2 small tooth-like thickening, a cavity below the anterior angle for the byssus and usually a scaly surface of the outer shell valves. The family comprises two commercially important genus viz. *Pinctada* spp and *Pteria* spp.

In *Pteria* spp the shell width is much longer than the height and the hinge angle is prominent and pronounced. In *Pinctada* spp the hinge is rather long and straight, the long axis of the shell is not at right angle at the hinge, the left valve is usually deeper than the right and there is a byssal notch on each valve at the base of the anterior lobe. The colouration of periostracum is changeable and is often brownish with radial markings.

In Indian waters, six species of pearl oysters viz. *Pinctada fucata* (Gould), *P. margaritifera* (Linnaeus), *P. chemnitzii* (Philippi), *P. sugillata* (Reeve), *P. anomioides* (Reeve) and

P. atropurpurea (Dunken) have been reported.

Pinctada fucata (Gould)

The hinge is nearly as wide as the width of the shell, left valve is deeper than the right, byssal notch slit-like, left valve greatly convex, posterior ear well developed with fairly developed sinus, anterior margin of shell just far in advance in front of anterior ear. Hinge teeth are present in both valves, one each at the anterior and posterior ends of the ligament. The anterior ear is larger than the other species. The posterior ear is fairly well developed. The outer surface of the shell valves with 6 - 8 radial bands of reddish brown on a pale yellow background. The nacreous layer is thick and has a bright golden, pink or ivory colour with metallic lustre. The non-nacreous margin on the inner surface of valves has reddish or brownish patches.

Pinctada margaritifera (Linnaeus)

The anterior margin of the shell extends in front of the anterior lobe. The anterior ear is well developed whereas the posterior ear and sinus are absent. The byssal notch is broad. The hinge is shorter than the width of the shell and is devoid of teeth. Left valves are moderately convex. The posterior end of the shell meets the hinge almost at a right angle. The outer shell is dark graying-brown with greenish tinge and radially distributed white spots. The nacreous layer is iridescent with a silvery sheen colour and the non-nacreous margin is black colour. Due to the dark marginal colouration of the shell, this pearl oyster is also known as the "Black-lip pearl oyster".

Pinctada chemnitzii (Philippi)

The shell is very comparable to that of *P. fucata* with the exception of very less convexity of valves and better developed of posterior ear. The hinge is almost as long as the anteroposterior measurement of the valves. The anterior ear is well developed and the byssal notch is slit-like. Hinge teeth of the anterior and posterior are present; the former is minute and rounded and the latter prominent and ridge-like commencing a little in advance of the posterior area of the hinge ligament. The posterior ear and the posterior sinus are well developed. The outer shells are yellowish externally with about four or more light brownish radial markings. The growth lines of the shell are broad. The nacreous layer is bright and lustrous and the non-nacreous layer is brownish.

Pinctada sugillata (Reeve)

The hinge is noticeably shorter than the anterio-posterior axis of the shell. The antero-posterior measurement is approximately equal to the dorso-ventral measurement. The anterior ear is small and the byssal notch is a fairly wide slit-like. The anterior ears are somewhat bent towards the right. The posterior ear and sinus are poorly developed. The

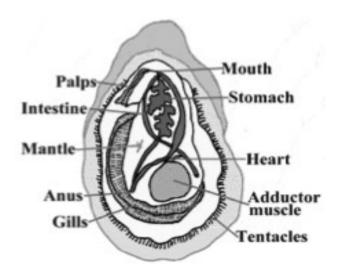
convexity of the valves is not prominent, especially that of the right valve. The anterior hinge teeth are small and roundish and the posterior one is slightly elongated. The shell valves are dark grey with a tinge of brown with six yellowish radial markings. The lower or posterior regions of valves are light yellow and gray.

Pinctada anomioides (Reeve)

The hinge is shorter than the width of the widest region of the antero-posterior axis of the shell. The hinge and dorso-ventral axis have a ratio of 1:1.4. Hinge teeth are absent or poorly developed. The anterior ear is moderately developed and the byssal notch at its base is deep. The posterior ear and sinus are absent. The outer shell valves are yellowish or grayish with faint radial markings. The nacreous layer is well developed.

Pinctada atropurpurea (Dunker)

The shell is roundish with its hinge narrow. The valves are thin, translucent and moderately convex. The nacreous layer is thin and the byssal notch is deep. A poorly developed anterior hinge tooth may be present in some oysters. Externally, the shell valves are copper coloured.



General anatomy of edible oyster

Edible oysters

Edible oysters belonging to the family Ostreidae and are found in hard substratum in the bays and creeks near coastal waters. They are attached permanently to the substratum.

Taxonomy

In Indian waters, six species of edible oysters are reported. They are the Indian backwater oyster *Crassostrea madrasensis* (Preston), Chinese oyster *C. rivularis* (Gould), West coast oyster *C. gryphoides* (Schlotheim), Indian rock oyster *Saccostrea*

cucullata (Born), Bombay oyster Saxostrea cucullata (Awati and Rai) and the giant oyster Hyostissa hyotis (Linnaeus).

Crassostrea madrasensis (Preston)

Shell valves are irregular in shape usually straight/elongate. Shell valves are covered by numerous foliaceous laminae. Left valve is deep while right one slightly concave. Hinge is narrow and elongated. Adductor muscle scar is kidney-shaped and sub central; dark purple in colour. Inner surface of valve is white, glossy and smooth with purplish black colouration on the inner margin.

C. gryphoides (Schlotheim)

Shell valves are elongate and thick. Shell is oblong, narrow in the anterior margin and broader in the posterior margin, laminated, lower valve very thick, especially in the anterior region below the ligamental area. Adductor muscle scar is broad, more or less oblong or heart shaped and pearly white with striations on the scar are absent or unclear. Upper valve thin flat and opercular, no denticles on the margin. Left valve is cup-like. Hinge region is well developed and has a deep median groove with lateral elevations.

C. rivularis (Gould)

Shell valves large, roughly round, flat, thick and with a shallow shell cavity. Left valve is thick and slightly concave and the right one is about the same size or slightly larger. Adductor muscle scar is oblong and white or smoky white in colour.

Saccostrea cucullata (Born)

Shell more or less trigonal, sometimes oblong, extremely hard and pear-shaped. The margins of the valves have well developed angular folds sculptured with laminae. Small tubercles present along the inner margin of the right valve and there are corresponding pits in the left valve. Adductor muscle scar is kidney shaped.

Clam

In Indian waters, a number of species coming under the families viz. Veneridae, Arcidae, Tridacnidae, Corbiculidae, Solenidae, Mesodesmatidae, Donacidae and Tellinidae are exploited from the time immemorial. The cultivable species by and large fit in to the first four aforementioned families.

Arcidae

Commercially important species under this family is represented by single species, *Anadara granosa*. It is found all along the Indian coast in soft muddy substratum and forms a fishery of some magnitude in the Kakinada Bay.

Anadara granosa

Shell valves are thick, inflated and dark brown. This species varies from other clams in having taxodont dentition and about 20 prominent ribs with rectangular nodules.

Veneridae

This family is characterized by the hinge with three cardinal teeth, a single anterior tooth on the left valve and a corresponding depression on the right valve, slightly unequal sized adductor muscle scars (= 2 Nos). This group contains three importance genera viz. Paphia, Meretrix and Marcia.

Paphia malabarica

Shell is slightly inflated, triangularly ovate and surface is concentrically grooved. The anterior and posterior margins are narrowly rounded. Hinge area is short with narrowly diverging teeth. Pallial sinus is 'U' shaped and very deep. Lunule is relatively short. Shell length is only one and one third times longer than height. The outer shell valves are yellowish brown in colour indistinctly rayed with greyish brown bands or blotched with brownish angular markings.

Villorita cyprinoides

Shell is thick, ovately triangular with strong concentric ridges. Hinge border is very short and thick, always with three oblique cardinal teeth; the anterior in the right valve and posterior in the left valve are less developed. Ridges are more strongly developed in the anterior half. Umbones are prominent and well elevated. Pallial sinus is small. Lunule is narrow and ligament is large. Shell is dark olive brown to blackish brown in colour.

Meretrix casta

Shell is thick, moderately large with a brown horny periostracum. Shell is also smooth and triangularly ovate with devoid of any sculpture. Outer surface of the valves is very fainted rayed with greyish radial lines or pale yellowish brown tinted with dark grey posteriorly.

Meretrix meretrix

Shell varies from *M. casta* in having less elongated lateral tooth, more ovate shell and larger size. Periostracum is thin and of grey or straw colour. Postero-dorsal margin of the outer shell is greyish blue or bluish brown band

Marcia opima

Shell is thick, inflated, smooth and triangularly ovate. Pallial line is deeply sinuate. Tip of the pallial sinus is bluntly angular.

Lunule is distinct, flattened and rather broad. Area behind the umbones is clear, flattened and deeply elongated reaching almost upto the hind margin of the shell. Outer surface of shell is pale yellowish brown or straw coloured variously blotched and rayed with purplish grey markings. The inner surface of the valve is white.

Gafrarium tumidum

Shell is thick, strongly inflated and sculptured with thick, nodular radial ribs which tend to bifurcate towards the ventral margin. The interstitial spaces between some of the main ribs, there are secondary rows of nodules. The pallial line is full and well developed. The outer surface is white with irregular dark spots posteriorly and near the umbo.

Tridacnidae

The tridacnid clams are characterized by large massive shells with broad radial ribs, sometimes having large fluted scales. Border of valves is usually scalloped.

Tridacna crocea

Shell is large, thick, and triangularly ovate with large byssal opening. Shell valves contain 6-10 broad flattened ribs with concentric ridges. Outer shell valves are greyish white flushed with yellow or pinkish orange.

T. maxima

Shell is strongly inequilateral. The shell is similar to that of *T. crocea* except that the 6-12 broad radial ribs have better developed concentric scales. Large byssal gape with distinct plicae is at edges. Ventral border of the valve often deeply scalloped. Shell is greyish white, sometimes tinged with yellow or pinkish orange.

T. squamosa

Shell is large, thick and strongly inflated with small or medium sized byssal gape. Shell valves posses 4-12 strongly convex ribs with riblets in interspaces. Broad, sometime long fluted scales on ribs which may project beyond ventral margin noticeably. Shell is greyish white, sometimes tinged with yellow.

Donacidae

Donax cuneatus

Shell is trigonal, inequilateral. Shell possesses a curved keel extending from the umbo to the postero-ventral corner; there are sharp concentric and fine radiating ones which are conspicuous in the anterior and posterior regions only. The anterior end is broad and rounded while the posterior end is

narrow and rounded. Pallial sinus is deep. The outer surface of shell is white covered with pale violet especially towards umbo and the posterior region is darker. The inner surface is of deep violet colour.

Mesodesmatidae

Mesodesma glabratum

Shell is thick, inequilateral and roughly trigonal. The outer surface of shell has well developed concentric striae. The umbo is small. Hinge has two cardinal teeth and there is an anterior lateral tooth. The pallial sinus is small and angular.

Solenidae

Solen kempi

Shell is small, about six times as long as high. Anterior region is obliquely truncate while posterior region rounded. Cardinal tooth is in right valve with a shallow groove all over its breadth. Dorsal margin of soft body is somewhat concave in the anterior region and convex in the posterior region. Siphon is long and segmented. Foot is long flattened and about half the length of body. Periostracum is yellowish brown and glossy.

References

- Appukuttan, K.K. 1996. Marine molluscs and their conservation. In *Marine Biodiversity Conservation and Management*. Central Marine Fisheries Institute, Cochin, eds. N.G.Menon and C.S.G. Pillai.
- Beesley, PL, Ross GJB, and Wells, A. 1998. Mollusca: The Southern Synthesis. CSIRO Publishing, Melbourne. 1-1234 pp.
- Bieler, R. and Mikkelsen, P.M. 2006. Bivalvia a look at the branches. *Zool. J. Linn. Soc.*, 148, 223–235.
- Campbell, D. C. 2000. Molecular evidence on the evolution of the Bivalvia. In: *The Evolutionary Biology of the Bivalvia*, Edited by Harper, E. M., Taylor, J. D., and Crame, J. A., London: Geological Society of London Special Publications, Vol. 177, pp. 31–46.
- Cox, LR, 1960. Thoughts on the classification of the Bivalvia. *Proc. Malac. Soc.* Lond. 34: 60 80.
- Dreyer, H., Steiner, G., Harper, E.M., 2003. Molecular phylogeny of Anomalodesmata (Mollusca: Bivalvia) inferred from 18S rRNA sequences. *Zool. J. Linn. Soc.* 139, 229 -246.
- Giribet, G. and Distel, D.L., 2003. Bivalve phylogeny and molecular data. In: Lydeard, C., Lindberg, D.R. (Eds.), Molecular Systematics and Phylogeography of Mollusks. Smithsonian Books, Washington, pp. 45–90.
- Giribet, G., and Wheeler, W.C., 2002. On bivalve phylogeny: a high-level analysis of the Bivalvia (Mollusca) based on combined morphology and DNA sequence data. *Invertebr. Biol.*, 121.
- Giribet, G, and Wheeler W.C. 2007. The case for sensitivity: a response to Grant and Kluge.Cladistics 23:294-296.
- Newell, ND. 1965. Classification of the Bivalvia. Amer. Museum Novit. 2206: 1-25.
- Newell, ND. 1969. Classification of the Bivalvia. In: Treatise on Invertebrate Paleontology, Part N, Mollusca 6, Vol. 1. Bivalvia. Moore R, ed., pp. N205-N244. Geological Society of America and University of Kansas, Boulder-Lawrence.
- Prezant, R.S. 1998a. Subclass Palaeoheterodonta Introduction. In Mollusca: *The Southern Synthesis, Fauna of Australia*, Vol. 5. Edited by P.L. Beesley, G.J.B. Ross, and A.Wells. Melbourne: CSIRO Publishing, pp. 289 294.
- Prezant, R.S. 1998b. Subclass Heterodonta Introduction. In Mollusca: The Southern Synthesis, Fauna of Australia, Vol. 5. Edited by P.L. Beesley, G.J.B. Ross, and A.Wells. Melbourne: CSIRO Publishing, pp. 301 – 306.
- Ponder, W. and D. Lindberg. 2008. Molluscan evolution and phylogeny: An introduction. In: W. F. Ponder and D. R. Lindberg, eds., *Phylogeny and Evolution of the Mollusca*. University of California Press, Berkeley and Los Angeles, California. Pp. 1–17.

Bivalve classification and taxonomy

- Purchon, R.D. 1968. The Biology of the Mollusca. Pergamon Press, Oxford. 560 pp.
- Stasek, CR. 1963. Synopsis and discussion of the association of ctenidia and labial palps in the bivalve Mollusca. Veliger 6: 91 97.
- Steiner, G. and Hammer, S. (2000). Molecular phylogeny of Bivalvia (Mollusca) inferred from, 18S. r D. N. A. sequences with particular reference to the Pteriomorphia. In: *The Evolutionary Biology of the Bivalvia*. Edited by E. M. Harper, J. D. Taylor and J. A. Crame London: Geological Society of London Special Publications, pp. 11–29.
- Taylor, J.D., Glover, E.A. and Williams, S.T., 2005. Another bloody bivalve: anatomy and relationships of *Eucrassatella donacina* from South Western Australia (Mollusca: Bivalvia: Crassatellidae). In: Wells, F.E., Walker, D.I., Kendrick, G.A. (Eds.), The Marine Flora and Fauna of Esperance, Western
- Australia. Western Australian Museum, Perth, pp. 261-288.
- Thiele, J., 1929-1935. *Handbuch der Systematischen Weichtierkunde* (4 volumes). Jena, Germany: Gustav Fischer Verlag.
- Vokes, H.E. 1980. Genera of the Bivalvia: A systematic and bibliographic catalogue revised and updated. Ithaca, NY: Paleontological Research Institution.
- Williams, S.T., Taylor, J.D., and Glover, E.A. 2004. Molecular phylogeny of the Lucinoidea (Bivalvia): Non-monophyly and separate acquisition of bacterial chemosymbiosis. *J. Moll. Stud.* 70: 187–202.