Phil. Trans. R. Soc. Lond. B. **294**, 413–546 (1981) [413]
Printed in Great Britain

THE FUNCTIONAL MORPHOLOGY OF ATLANTIC DEEP WATER SPECIES OF THE FAMILIES CUSPIDARIIDAE AND POROMYIDAE (BIVALVIA): AN ANALYSIS OF THE EVOLUTION OF THE SEPTIBRANCH CONDITION

By J. A. ALLEN and RHONA E. MORGAN
*University Marine Biological Station, Millport KA*28 0*EG, Isle of Cumbrae, U.K.*

(*Communicated by Sir Maurice Yonge, F.R.S. – Received* 13 *June* 1980)

CONTENTS

The Royal Society is collaborating with JSTOR to digitize, preserve, and extend access to *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences.*
www.jstor.org

Anatomical studies show that three families, Verticordiidae, Poromyidae and Cuspidariidae, have many features in common. All are carnivores, have similar digestive systems, and have a horizontal septum dividing the mantle into infra- and supraseptal cavities. This partition is developed to different degrees in the different families. In the Verticordiidae the reduced gill is connected by a membrane to the body mantle and intersiphonal septum. The species rely mainly on ciliary currents for respiration and water change. In the Cuspidariidae, there is a thick, muscular sheet which in the most specialized species is pierced by only four pairs of pores. Regular pumping movements change the water in the mantle cavities. Because of their obvious relation, the three families are combined within the suborder Septibranchia, of the order Anomalodesmata (Bivalvia).

On the basis of this study the Verticordiidae and Poromyidae are more closely related to one another than either is to the Cuspidariidae. This is demonstrated by the differences in the siphon structure and reproductive systems. The first two families are hermaphrodite, short-siphoned, have a large forward projecting valve at the base of the inhalant siphon, and bear 13 or 15 short tapering tentacles around the siphonal apertures. The Cuspidariidae are dioecious, long-siphoned, the inhalant aperture being sealed internally by a simple vertical sheet pierced by a keyhole slit, and consistently have three dorsal exhalant tentacles and four ventral inhalant tentacles.

In the past, the taxonomy of the family Cuspidariidae has been based solely on hinge characteristics. This study, on the basis of gross morphological differences, identifies three genera: *Cuspidaria*, *Halonympha* and a new genus, *Protocuspidaria*. Subdivisions of these genera continue to be based on hinge characters, there being few anatomical differences.

Protocuspidaria, *Halonympha* and *Cuspidaria* form a series in the development of the septum from a reduced eulamellibranch gill to the typical muscular septum of the genus *Cuspidaria*. This involves a vast increase in musculature with the development of dorsal attachments of these muscles onto the shell. Associated with this development is a decrease in the size of the palps and an increase in the rostral length of the shell.

The septum in both the Poromyidae and Cuspidariidae contains five pairs of muscles; the anterior and posterior septal muscles, the inner and outer longitudinal septal muscles and the lateral septal muscles. These muscles lie between two epithelial layers which are continuous with those of the mantle and the viscera. In the Poromyidae, the septum is already very muscular and pierced by two (*Poromya*) or three (*Cetoconcha*) pairs of grouped branchial apertures. In the Cuspidariidae, while there is a progressive increase in the musculature of the septum, the branchial apertures are always set in a single series on either side of the foot.

Studies on the comparative morphology of the families, particularly of the nervous systems and musculature, show that the septum is developed mainly from the gill. Except for *Cetoconcha*, where a few filaments of the outer demibranch persist posteriorly and form the third posterior group of branchial apertures, the openings in the septum are derived from the descending lamella of the inner demibranch. The musculature is mainly derived from that of the inner demibranch. A reduced gill becomes connected via a membrane, laterally to the mantle, anteriorly to the margin of the mouth, posteriorly to the intersiphonal septum and medially to the foot. The anterior septal muscle of the Poromyidae and Cuspidariidae is homologous with the axial muscle of eulamellibranch bivalves. This enlarges, extends forward and, in all but *Protocuspidaria*, makes an anterior dorsal attachment on the shell. The posterior septal muscle is derived by an increase, fusion and extension of the longitudinal filamentar muscles of several posterior gill filaments of the outer demibranch. This, in all but the more 'primitive' genera (*Protocuspidaria* and *Halonympha*), also makes a posterior dorsal attachment. The increase and modification of the longitudinal filamentar muscles of the inner demibranch gives rise to the bulk of the septum, forming the lateral septal muscles and the pore-closing mechanism. Pallial muscle along the lateral margin of the septum probably gives rise to the outer longitudinal septal muscle. There is also firm evidence that the inner longitudinal muscle, which provides the seal around the foot, is pedally derived.

The Verticordiidae, Poromyidae and Cuspidariidae have a specialized carnivorous habit. In the Verticordiidae food capture is by trapping of passing prey on sticky tentacles, while in the Cuspidariidae feeding involves active use of the muscular pumping septum to suck in the prey detected by the sensory tentacles. In the Poromyidae, however, the seal is incomplete posterior to the foot, and the pumping mechanism is possibly not as efficient as it is in the Cuspidariidae, but neither are the tentacles sticky as they are in the Verticordiidae. It therefore seems likely that they utilize a pumping action that is supplemented by ciliary action for both respiration and drawing in food.

INTRODUCTION

This paper is the second of a study on the deep sea septibranch bivalves of the Atlantic. The first paper concerned the little-known family Verticordiidae and its probable evolution from anomalodesmacean eulamellibranch bivalves (Allen & Turner 1974). Here, we turn to the more modified families Poromyidae and Cuspidariidae.

The highly successful sampling techniques evolved since 1962 by the participants of the Woods Hole Oceanographic Institution deep-sea benthic programme have provided many new species (Allen & Sanders 1973, 1981; Sanders & Allen 1973, 1977; Allen & Turner 1974; Oliver & Allen 1980*a*, *b*; Allen 1978, 1979). The poromyid and cuspidariid collections are no exception, 50 species being present in samples from the abyssal Atlantic, of which 27 are undescribed. This second paper is also concerned with the origin and development of the septum that divides the mantle cavity into upper and lower chambers and which is found only in these two families. Because new genera and species are central to the elucidation of and the evolution of the group it has been found necessary to include descriptive taxonomy. The anatomy of a few key species is described in detail, with the descriptions of other species emphasizing points of difference. New and previously described species remaining in our collections that require further taxonomic study will be the subject of a further paper.

For information on our sampling techniques and overall design of the research programme, see Sanders *et al.* (1965). In addition, this paper includes observations on material gathered by the French and British deep-sea sampling programmes.

HISTORICAL

In 1888, Pelseneer created a new order, the Septibranchia, to accommodate the genera *Poromya*, *Silenia* (=*Cetoconcha*) and *Cuspidaria*. He considered these to be distinct from both the Anatinacea, where Fischer (1880–1887) had placed them, and the Corbulidae, where Jeffreys (1881), Smith (1885) and Sars (1878) had placed them. Later, Pelseneer (1891) raised the Septibranchia to a separate subclass of the Lamellibranchia, although he acknowledged that they were closely related to the Anatinacea (=Anomalodesmacea). Pelseneer (1888*b*) noted that *Poromya* and *Cetoconcha* were more closely related to one another than to *Cuspidaria*, and grouped *Poromya* and *Cetoconcha* together in the family Poromyidae, leaving *Cuspidaria* in its own family, the Cuspidariidae. Although the Poromyidae originally distinguished *Poromya* and *Cetoconcha* from *Cuspidaria*, nomenclatural derivations of the name *Poromya* for higher taxa have been used in rather different ways (table 1). Thus, Ridewood (1903) refers to the suborder Poromyacea in which he included all the septibranchiate bivalves (table 1) as well as genera of the family Verticordiidae. Various authors have followed this taxonomy (e.g.: Thiele 1935; Vokes 1967; Newell 1965; Moore 1969; Knudsen 1970; Allen & Turner 1974), while others (e.g.: Pelseneer 1888*a*, *b*, 1891, 1911; Nicol 1966; Bernard 1974) have separated the Verticordiidae but still include them within the Anomalodesmacea†. It is now generally accepted that the septibranchs are related to the anomalodesmacean eulamellibranchs and the Pandoracea in particular (Yonge & Morton 1980); however, Purchon (1963), from his studies on the bivalve stomach, removed the septibranchs from the Eulamellibranchia and placed them together with the Protobranchia in a new group, the Oligosyringia. More recently Bernard (1969, 1974) has followed this arrangement by placing *Cuspidaria*, *Cetoconcha* and *Poromya* within a group, the Septibranchida, close to the Protobranchia, while retaining the Verticordiidae within the Anomalodesmacea.

The term septibranch has been used in various ways to describe the group of bivalve families possessing a septum, e.g. Septibranchia (Pelseneer 1888*b*; Okutani 1968; Nicol 1966), Septipalliata (Plate 1897), Septibranchoida (Knudsen 1970; Vokes 1967) and Septibranchida (Keen 1963; Bernard 1969). Alternatively, because of the anomalous position of the Verticordiidae, it has been abandoned altogether as a taxonomic division (Thiele 1935; Moore 1969; Allen & Turner 1974).

At a lesser level *Cetoconcha* has been accorded family status (see, for example: Ridewood 1903; Knudsen 1970; Allen & Turner 1974), although more often it has been included as a genus of the family Poromyidae (see, for example: Thiele 1935; Vokes 1967; Moore 1969; Bernard 1974). Here we accord *Cetoconcha* only generic status within the Poromyidae and propose a classification as presented in table 1, in which the three families Cuspidariidae, Poromyidae and Verticordiidae are combined in a suborder Septibranchia, a more descriptive name than any derived from *Poromya*. The Septibranchia we divide into two superfamilies, Poromyoidea and Cuspidaroidea,

---

† For a history of the taxonomy of the Verticordiidae see Allen & Turner (1974).

Table 1. Comparison of the classification of the Septibranchs of various authorities

	Dall 1886	Pelseneer 1891, 1911	Ridewood 1903	Thiele 1935	Purchon 1963	Newell 1965
class	Pelecypoda	Bivalvia	Lamellibranchia	Bivalvia	Bivalvia	Bivalvia
subclass	—	Eulamellibranchia	—	—	—	—
family	—	Verticordiidae	—	—	—	—
subclass	—	Septibranchia	—	—	Oligosyringia	Anomalodesmata
order	—	—	Synaptorrhabda	Eulamellibranchiata	Septibranchia	Poromyoida
suborder	—	—	Poromyacea	Anomalodesmata	—	—
superfamily	—	—	—	—	—	—
family	—	—	—	—	—	—
superfamily	—	—	—	Poromyacea	—	Poromyacea
family	Verticordiidae	—	Verticordiidae	Verticordiidae	—	Verticordiidae
family	Poromyidae	Poromyidae	Poromyidae	Poromyidae	—	Poromyidae
genus	*Poromya*	*Poromya*	*Poromya*	*Poromya*	—	*Poromya*
section	Cetoconcha	—	—	—	—	—
family	—	—	Cetoconchidae	—	—	—
genus	—	*Silenia*	*Cetoconcha*	*Cetoconcha*	—	*Cetoconcha*
superfamily	—	—	—	—	—	—
family	Cuspidariidae	Cuspidariidae	Cuspidariidae	Cuspidariidae	—	Cuspidariidae

	Vokes 1967	Moore 1969	Nordsieck 1969	Knudsen 1970	Bernard 1974	present
class	Bivalvia	Bivalvia	Bivalvia	Bivalvia	Bivalvia	Bivalvia
subclass	—	—	—	—	—	—
family	—	—	—	—	—	—
subclass	Anomalodesmata	Anomalodesmata	—	—	Anomalodesmata	Lamellibranchia
order	Septibranchoidea	Pholadomyoida	Septibranchia	Septibranchoidea	Septibranchida	Anomalodesmata
suborder	—	—	—	—	—	Septibranchia
superfamily	—	—	—	—	Verticordiacea	—
family	—	—	—	—	Verticordiidae	—
superfamily	Poromyacea	Poromyacea	—	—	Poromyacea	Poromyoidea
family	Verticordiidae	Verticordiidae	Verticordiidae	Verticordiidae	—	Verticordiidae
family	Poromyidae	Poromyidae	Poromyidae	Poromyidae	Poromyidae	Poromyidae
genus	*Poromya*	*Poromya*	*Poromya*	*Poromya*	*Poromya*	*Poromya*
section	—	—	—	—	—	—
family	—	—	—	—	—	—
genus	*Cetoconcha*	*Cetoconcha*	*Cetoconcha*	*Cetoconcha*	*Cetoconcha*	*Cetoconcha*
superfamily	—	—	—	—	—	Cuspidaroidea
family	Cuspidariidae	Cuspidariide	Cuspidariidae	Cuspidariidae	Cuspidariidae	Cuspidariidae

to distinguish the markedly different morphology of the Cuspidariidae from the Poromyidae and Verticordiidae.

Taxonomy of the Septibranchia

Suborder Septibranchia Pelseneer, 1888

Gills variously reduced, either one or both demibranchs present, filaments reduced in length and number, or with a few small paired pores present. Filaments or pores set in a septum, which may be very muscular, and which is attached to the mantle, siphons and body. Foot moderately small, with a byssus gland and groove, but few or no threads produced. Carnivorous habit. Wide anterior mouth, reduced palps, ridged muscular oesophagus, oval stomach with a variously developed outer muscle layer, rounded style sac and combined midgut, two digestive ducts anterior to the combined style sac and midgut apertures, simple hindgut that passes posterior to stomach to the mid-dorsal line, through the pericardium and over the posterior adductor to the anus, anterior to exhalant siphon.

Superfamily Poromyoidea

Shell and siphons short, latter with numerous short tapering tentacles. Inhalant valve large and projecting inwards. Lips large and cup-shaped, anterior pair the larger. Gill filaments in a membranous septum, either reduced but recognizable or as two paired groups of short, horizontal filaments (sieve plates or pores), or as three paired groups of filaments, the latter much reduced and forming the lips of pores in a very muscular septum; hermaphrodite.

Family Verticordiidae Stolicza, 1870

See Allen & Turner (1974) for details. Possess a reduced but recognizable eulamellibranch gill set in a non-muscular membranous septum. Radial mantle glands may be present. Tentacles around inhalant aperture, papillate and usually branched.

Family Poromyidae Dall, 1886

Shell surface smooth or with radial lines of granules. Muscular septum, anterior and posterior septal muscles attached to shell; either two paired groups of sieve plates or pores or three paired groups of pores. Common ring of 13 or 15 tapering tentacles around both siphons. No radial mantle glands. Two genera: *Poromya* and *Cetoconcha*.

Genus Poromya Forbes, 1844

(*Embla* Lovén, 1846; *Thetis* H. & A. Adams, 1856; *Ectorisma* Tate, 1892; *Questiomya* Iredale, 1930)

Type species: *P. granulata* (Nyst & Westendorp, 1839) (*P. anatinoides* Forbes, 1844).

Two paired groups of sieve plates or pores in muscular septum, cardinal tooth, which may be much reduced, on right hinge plate.

Although the genus was described by Forbes (1844), it was Dall (1881) who gave the first accurate description. Later Dall (1886) erected the family Poromyidae, synonymizing *Poromya* with *Embla*. *Poromya* was described as having an anterior cardinal tooth in the right valve with a corresponding pit in the left valve, a ligament part internal and part external, short siphons surrounded by a ring of tentacles and a septum with no free branchiae. Pelseneer (1888*a*, *b*, 1891, 1911) investigated the anatomy and added to the description: 15 tentacles around the siphons; a large inwardly projecting inhalant valve internal to the siphon; the genus is hermaphrodite.

Dall (1886) distinguished a section called *Cetoconcha*, in which he included poromyids which, in contradiction with his definition, had a weak cardinal tooth or in which it was absent. Later Dall (1889*a*) realized that he had included in this section species that have two paired groups of apertures, as in typical poromyids, and species that had three paired groups of pores. As a result he placed species with a weak hinge and a *Poromya*-type septum into a subgenus *Cetomya*, and raised *Cetoconcha* to generic status to accommodate those species that lack a tooth, but have three paired groups of pores. Dall (1890*a*) subsequently divided the genus *Poromya* into three subgenera on the basis of their shell characters.

Subgenus *Poromya*: shell surface granular; strong cardinal tooth in right valve.
Subgenus *Cetomya*: shell surface granular; obsolete cardinal tooth in right valve.
Subgenus *Dermatomya*: shell surface smooth; strong cardinal tooth in right valve.

Thiele (1935) confirmed this and noted *Thetis* H. & A. Adams, 1856 as a synonym of *Poromya*.

There is confusion in the literature concerning the validity and status of the generic names *Ectorisma* Tate and *Questiomya* Iredale. The type, *Ectorisma granulata* (Tate), is considered by Hedley (1907) and Dall (1908) to be a species of *Poromya*. Hedley (1907) pointed out that *granulata* was preoccupied but considered that the Tate species was probably identical to *P. laevis* Smith, 1885. Dall (1908) affirms the change of name to *P. laevis* Smith. Iredale (1930) doubted that *Ectorisma* was congeneric with *Poromya* and maintained that *Ectorisma* should be reinstated. He erroneously reported that Hedley (1907) had changed the specific name of the type to *P. illevis* Smith, and considered that Tate's specific name of *E. granulata* should be reinstated. Iredale (1930) also erected another new genus, *Questiomya*, to accommodate the species *P. undosa* Hedley and Pettard, 1906, which he considered was neither a *Poromya* nor an *Ectorisma* species. We have been unable to examine specimens. Because Iredale (1930) did not describe the supposed differences, we synonymize *Thetis*, *Embla*, *Ectorisma* and *Questiomya* with the genus *Poromya*.

Genus Cetoconcha Dall, 1886 (*Silenia* Smith, 1885)

Type species: *C. bulla* (Dall, 1878) (=*Lyonsia bulla* Dall, 1878).

Originally named *Silenia* with *S. sarsi* as the type (Smith 1885); Smith characterized the genus as having an external ligament; lips of unequal size, the anterior being larger; a siphon surrounded by a ring of tentacles and branchial pores in the septum arranged in three paired groups; one pair set transversely posterior to the foot and the other two set longitudinally, lateral and close to the foot. Dall (1886) used *Cetoconcha* for species with these characteristics, but as a section of the genus *Poromya*. It was not until Pelseneer (1888*a*) had studied the anatomy of *Silenia sarsi* that Dall (1889*a*, *b*) acknowledged the synonomy nominating *C.* (*Lyonsia*) *bulla* (Dall, 1878) as the type and raised *Cetoconcha* to generic level.

Occasionally *Cetoconcha* has been given family status (see, for example: Ridewood 1903; Knudsen 1970; Allen & Turner 1974), but more frequently, and we now think more appropriately, it has been given generic status. Although it is generally accepted that *Cetoconcha* has no hinge teeth, on shell characters alone the genus can be confused with *Cetomya* which has a very weak cardinal tooth. The only sure way to distinguish *Cetoconcha* from *Cetomya* is to examine the septum.

Bernard (1974) confused the genus *Cetoconcha* with the subgenus *Cetomya*, naming as subgenera of *Poromya*, *Dermatomya* and *Cetoconcha*, distinguished on the presence or absence of a granular shell surface, and overlooked the fact that *Cetoconcha* has three paired groups of branchial openings, whereas the subgenera *Cetomya*, *Dermatomya* and *Poromya* have two.

Key to the genera and subgenera of the family Poromyidae

1.	No hinge teeth. Three paired groups of branchial pores in the septum.	genus *Cetoconcha*
2.	Hinge teeth present, but may be very weak. Two paired groups of branchial pores or filaments in the septum.	genus *Poromya* 3
3*a*.	Shell surface granular; strong cardinal tooth in right valve.	subgenus *Poromya*
3*b*.	Shell surface smooth; strong cardinal tooth in right valve.	subgenus *Dermatomya*
3*c*.	Shell surface granular; very weak cardinal tooth.	subgenus *Cetomya*

Superfamily Cuspidaroidea

Shell rostrate; cardinal and/or lateral, or no hinge teeth present[†]; resilium and lithodesma present. Well developed siphons with three tentacles dorsal to narrow exhalant siphon, and four ventral tentacles lateral to inhalant siphon. Inhalant valve a vertical partition pierced by a keyhole slit. Palps generally small and reduced, but when developed the posterior pair is the larger. Generally four or five pores (but occasionally eight or more pores or gill filaments) on each side of foot. Muscular septum. Dioecious.

Family Cuspidariidae Dall, 1886

Definition as above.

Genus Cuspidaria Nardo, 1840 (*Neaera* Gray, 1834)

Type species: *Cuspidaria cuspidata* (Olivi, 1792).

Shell variously ornamented, rostrate.

All references from before 1886 refer to *Neaera*, the name then shown to be invalid and preoccupied (Dall 1886). Adams (1864) defined the genus as inequivalve, with a lamellar shell surface and a hinge with a single posterior lateral tooth on the right valve, the latter being the main character on which the genus was originally based. As new species were found other types of hinge were described. Jeffreys (1881), who included *Cuspidaria* in the family Corbulidae, divided the species into groups according to shell ornamentation. Those with a single posterior lateral tooth in the right valve he categorized as either group A (smooth shells) or group *Aulacophora* (concentrically striated shells). Smith (1885) on the basis of the *Challenger* material revised the genus and placed *Cuspidaria* within the subfamily Corbulinae of the family Myidae and divided it into groups lettered A–M according to the type of hinge. Group A combined Jeffreys's group A and *Aulacophora*, and the subgenus *Cuspidaria sensu stricto* as presently known, and was characterized by a single posterior lateral tooth in the right valve and smooth or concentric striations on the shell valves.

Dall (1886) used the Smith classification in his important paper on the *Blake* Mollusca, in which he established the family Cuspidariidae and recognized several subgenera, namely *Cuspidaria*, *Cardiomya*, *Rhinoclama*, *Leiomya*, *Tropidomya* and *Halonympha*, and also a new genus *Myonera*. All were based on variations in shell sculpture and hinge teeth. Since then the group has been divided into 12 Recent taxa, still on the basis of hinge type and sculpture, namely *Cuspidaria*, *Cardiomya*, *Myonera*, *Rhinoclama*, *Luzonia*, *Leiomya*, *Tropidomya*, *Plectodon*, *Pseudoneaera*,

---

[†] Cuspidariid teeth may have been secondarily developed and be analogous to laterals and cardinals of other lamellibranch bivalves (Yonge & Morton 1980).

Table 2. Anatomical characteristics of the Cuspidariidae in collections taken from the Atlantic Ocean

species	ligament		sculpture			septum		pores			lateral septals		palps type			tentacles		gonad type	
	opis.	amph.	sm.	conc.	rad.	thick	thin	4pr	5pr	+	cont.	2 pr	I	II	III	club	frill	I	II
								subgenus *Cuspidaria*											
C. obesa	*	—	*	—	—	*	—	*	—	—	*	—	*	—	—	*	—	—	*
C. parva	*	—	*	—	—	—	*	*	—	—	*	—	*	—	—	*	—	*	—
C. cuspidata	*	—	*	—	—	*	—	—	*	—	—	*	—	*	—	—	*	*	—
C. jeffreysi	*	—	*	—	—	*	—	*	—	—	—	*	—	*	—	—	*	*	—
C. ventricosa	—	*	*	—	—	—	*	*	—	—	—	*	—	*	—	—	*	—	*
C. circinata	*	—	—	*	—	—	*	—	—	8	*	—	*	—	—	*	—	*	—
C. undata	*	—	—	*	—	*	—	*	—	—	*	—	*	—	—	*	—	*	—
C. bernardi	*	—	*	—	—	*	—	*	—	—	—	*	*	—	—	—	*	*	—
C. atlantica	*	—	—	*	—	—	*	*	—	—	*	—	*	—	—	*	—	*	—
								subgenus *Cardiomya*											
C. costellata	—	*	—	—	*	*e.	—	*	—	—	*	—	*	—	—	*	—	*	—
C. curta	—	*	—	—	*	*e.	—	*	—	—	*	—	*	—	—	*	—	*	—
C. knudseni	—	*	—	—	*	*e.	—	*	—	—	*	—	*	—	—	*	—	*	—
C. perrostrata	—	*	—	—	*	*e.	—	*	—	—	*	—	*	—	—	*	—	*	—
								subgenus *Myonera*											
C. (*M.*) *atlantica*	*	—	—	*	—	—	*	*	—	—	*	—	*	—	—	*	—	*	—
C. (*M.*) *octaporosa*	*	—	*	—	—	—	*	—	—	8	*	—	—	—	*	*	—	*	—
C. (*M.*) *paucistriata*	*	—	—	*	*	*	—	—	—	—	*	—	*	—	—	*	—	—	*
C. (*M.*) *demistriata*	—	*	—	*	*	*e.	—	*	—	—	*	—	*	—	—	*	—	*	—
C. (*M.*) *tillamookensis*	—	*	—	*	*	*e.	—	*	—	—	*	—	*	—	—	*	—	*	—
								subgenus *Rhinoclama*											
C. (*R.*) *abrupta*	*	—	*	—	—	*	—	*	—	—	—	*	—	*	—	*	—	*	—
C. (*R.*) *notabilis*	*	—	—	*	—	*	—	*	—	—	*	—	—	*	—	—	*	*	—
C. (*R.*) *halimera*	*	—	—	*	—	—	*	*	—	—	*	—	—	*	—	—	*	*	—
								subgenus *Luzonia*											
C. (*L.*) *simplex*	*	—	*	—	—	*	—	*	—	—	*	—	*	—	—	*	—	*	—
								subgenus *Tropidomya*											
C. (*T.*) *abbreviata*	*	—	—	*	—	*	—	—	*	—	*	—	*	—	—	*	—	—	*
C. (*T.*) *diagonalis*	*	—	—	*	—	*	—	—	*	—	*	—	*	—	—	*	—	—	**b.
								genus *Halonympha*											
H. atlanta	*	—	*	—	—	*	—	—	—	8	*	—	—	—	*	*	—	*	—
H. depressa	*	—	*	—	—	*	—	—	—	16	*	—	—	—	*	*	—	*	—
								genus *Protocuspidaria*											
P. verityi	*	—	*	—	—	—	*	—	—	12	*	—	—	—	*	*	—	*	—
P. simplis	*	—	*	—	—	—	*	—	—	12	*	—	—	—	*	*	—	*	—
P. atlantica	*	—	*	—	—	—	*	—	—	12	*	—	—	—	*	*	—	*	—

Abbreviations used: amph., amphidetic; opis., opisthodetic; e., extra lateral septal muscle insertion; conc., concentric; rad., radial; b., branched digestive gland; cont., continuous; sm., smooth.

Austroneaera, *Vulcanomya* and *Halonympha*. These have been given varying status at different times. For example, Thiele (1935) lists them all as distinct subgenera of the genus *Cuspidaria*, Vokes (1967) lists them all as separate genera and Moore (1969) lists the genus *Cuspidaria* with six subgenera (*Cuspidaria*, *Halonympha*, *Leiomya*, *Pseudoneaera*, *Rhinoclama*, *Tropidomya*), together with four other genera (*Austroneaera*, *Cardiomya*, *Myonera*, *Plectodon*). In the most recent taxonomic paper, Bernard (1974) recognizes four genera from the eastern Pacific, *Cuspidaria*, *Myonera*, *Plectodon* and *Cardiomya*, and places the remaining subgenera as synonyms of *Cuspidaria*.

Differences in hinge teeth and/or sculpture may not be the strongest of characters on which to base the taxonomy of this group of bivalves. We have examined specimens and descriptions of known genera and subgenera and sought conformity between differences in morphological characters and the existing divisions based on the shell (table 2). We find three distinct types of body form involving the degree of development of the septum and palps. With the exception of *Halonympha* and a new genus *Protocuspidaria*, all taxa listed above have a well developed muscular septum with strong anterior and posterior septal muscle attachments.

Although we have been able to examine the anatomy of only three species of *Halonympha*, because they differ in hinge and septal morphology from all other cuspidariids, we believe that they should be regarded as belonging to a separate genus. A new and, as yet, small group of cuspidariids, which we name *Protocuspidaria*, also has distinct hinge and septal characteristics. Of these genera (*Cuspidaria*, *Halonympha* and *Protocuspidaria*) the vast majority of known species belong with *Cuspidaria*. The division is not entirely clear-cut because three species of *Cuspidaria* in the collection (table 2) have a septum of the *Halonympha* type yet do not possess the corresponding hinge characters of this genus. While this may add doubt to the value of the hinge as a taxonomic character we believe that it would be unwise to abandon completely the traditional classification of the group. Hinge characters are of immediate help in identifying a species.

The genus *Cuspidaria* can be divided into ten subgenera: *Cuspidaria*, *Cardiomya*, *Myonera*, *Rhinoclama*, *Luzonia*, *Plectodon*, *Pseudoneaera*, *Vulcanomya*, *Tropidomya* and *Leiomya*.

Subgenus Cuspidaria Dall, 1886

Type species: *Cuspidaria cuspidata* (Olivi, 1792) (*Tellina cuspidata* Olivi).

Posterior lateral tooth in the right valve only, shell surface either smooth or concentrically striated.

Subgenus Myonera Dall & Smith, 1886 (see Dall 1886)

Type species: *Myonera paucistriata* Dall & Bush, 1885 (see Bush 1885).

No teeth in either valve, vertical or posteriorly directed internal ligament, concentric and/or radiating shell sculpture.

First described as a genus by Dall (1886), *Myonera* is equivalent to two sections denoted L and M by Smith (1885), who described section L as having no teeth, concentric sculpture and a short posteriorly directed resilifer, giving as an example *N. angularis* Jeffreys and *N. sulcifera* Jeffreys, and section M as having no teeth, but radial striations and an anteriorly directed resilifer (*N. fragilissima* (Smith)). In fact *N. sulcifera* and *N. fragilissima* were wrongly placed because both are described as having a posterior lateral tooth in the right valve (Jeffreys 1881; Smith 1885), i.e. the former is a species of *Cuspidaria*, and the latter *Cardiomya*. Because we have found no anatomical evidence to differentiate species of *Myonera* from others of the genus *Cuspidaria* we prefer to retain the taxon at subgeneric level.

Subgenus Cardiomya A. Adams, 1864 (*Spathophora* Jeffreys, 1881) (*Kurodamya* Okutani & Sakurai, 1964)

Type species: *Cuspidaria* (*Cardiomya*) *gouldiana* (Hinds, 1843).

Posterior lateral tooth in right valve, radiating shell sculpture.

Jeffreys (1881) either ignored or was ignorant of the description of Adams (1864) of this subgenus in which *C.* (*C.*) *gouldiana* (Hinds) was named as the type, when he placed three species in a group that he called *Spathophora*, naming *C. curta* as the type. Smith (1885) recognized *Spathophora* as synonymous with *Cardiomya*. Both Smith (1885) and Dall (1886) regarded *Cardiomya* as a subgenus. More recently Thiele (1935) referred to it as a section of the subgenus *Cuspidaria*, but Okutani & Sakurai (1964), Moore (1969) and Bernard (1974) elevate it to generic status. Bernard (1974) distinguished the genus on the basis of the radial sculpture, prominent 'fossette' and thinner septum as compared with *Cuspidaria* and briefly describes the anatomy of two (*C. pectinata* (Carpenter) and *C. californica* (Dall)) of the twelve species that he lists. There is no distinct difference between the anatomy of species of *Cardiomya* and that of *Cuspidaria*. Thus, thin septa are not restricted to *Cardiomya*, several species of *Myonera* have one or more radial ribs and several species of *Cuspidaria*, *Luzonia* and *Myonera* have amphidetic ligaments (the 'prominent fossette' of Bernard (1974)). Okutani & Sakurai (1964) separated species that lack radial ribs on the anterior half of the shell, possess a hook-like posterior lateral tooth and have beaded radii on the rostrum in a new subgenus *Kurodamya*†. Species of *Cardiomya* possess the two latter characters and it seems unnecessary to divide the group further on the basis of the lack of radial ribs on half of the shell. We therefore synonymize *Kurodamya* with *Cardiomya*.

Although there are 43 species of *Cardiomya* described in the literature, comparison of the figures alone suggests some synonymies. For example *C.* (*C.*) *persculpture* (Prashad) may be synonymous with *C.* (*C.*) *alcocki* (Smith); *C.* (*C.*) *isolirata* (Bernard) with *C.* (*C.*) *beringhensis* (Leche), and possibly *C.* (*C.* (*K.*)) *fortisculpture* (Kuroda) with *C.* (*C.*) *semicostata* (Prashad).

Subgenus Rhinoclama Dall & Smith, 1886 (*Rhinomya* Adams, 1864) (*Austroneaera* Powell, 1937)

Type species: *R. adamsi* Morgan & Heppell, 1981.

Anterior and posterior lateral teeth in the right valve only.

This subgenus has caused much confusion in the literature because it has been based on a misidentified type, which is an undescribed species.‡

Adams (1861) described a subgenus *Rhinomya* to accommodate a species *R. rugata* Adams and, what he erroneously considered to be a previously described species, *C. philippinensis* Hinds (1843). The latter he named as the type, the subgenus being characterized by the possession of anterior and posterior lateral hinge teeth in the right valve. Smith (1885), dividing the *Challenger* cuspidariids into lettered sections, overlooked the name *Rhinomya* but recognized that the Adams specimen referred to as *C. philippinensis* was different from *C. philippinensis* Hinds. These he placed in different sections (G and H respectively), the former characterized by the possession of an anterior and posterior lateral tooth in the right valve, the latter by a single cardinal

---

† Okutani & Sakurai (1964) name *Cardiomya* (*Kurodamya*) *fortisculpture* Kuroda as the type.

‡ See appendix. Submitted to the International Commission of Zoological Nomenclature. File reference number ZN(S) 2151.

in the right valve. Instead of describing the Adams specimen and renaming it, Smith (1885) merely changed the authority, i.e. *C. philippinensis* Adams (*nec* Hinds).

Dall (1886) compounded the error by erecting a section *Rhinoclama* of the subgenus *Leiomya*, to encompass *Rhinomya* Adams and sections G and F (Smith 1885), naming *N. philippinensis* (A. Adams) Smith as the type. Later Dall (1890) established another subgenus *Luzonia* characterized by the possession of a single anterior cardinal tooth, rightly using the original species, *C. philippinensis* Hinds, as the type. Thus two subgenera with very different hinge types were listed based on types with the same name but with different authority.

Since then Prashad (1932) has described *Rhinoclama* as a subgenus of *Cuspidaria*, while Johnson (1934) considers it a section of the genus *Leiomya*. Thiele (1935) mistakenly states that the subgenus of *Rhinoclama* has no teeth at all and, to avoid confusion between the types of the two subgenera *Rhinoclama* and *Luzonia*, changes the name *C. philippinensis* Adams (*nec* Hinds) to *C. adamsi* Thiele. Unfortunately this name is invalid because it refers to a *nomen nudum*. Smith (1885) wrongly credits it to Adams. Nordsieck (1969) also perpetuates the error by following Thiele (1935). Moore (1969) follows Thiele's definition of *Rhinoclama* as being edentulous, but reverts to using *C. philippinensis* Hinds as the type.

The type specimen *C. philippinensis* Hinds of the subgenus *Luzonia* (B.M.N.H. (British Museum (Natural History)) no. 1961 122) has an anterior cardinal tooth in the right valve. There is another specimen (B.M.N.H. no. 1.28.416.1878) labelled '*Rhinomya A. A. philippinensis* Hinds; Location Uraga', which is almost certainly the specimen referred to as *R. philippinensis* Hinds by Adams (1864), and that Thiele (1935) renamed *C. adamsi*. It comes from the same location as that which Adams described, and the specimen is part of the Adams collection bought by a Mr Geale, and later given to the British Museum (Natural History). It has a single anterior and posterior lateral tooth in the right valve.

Powell (1937) described a new genus *Austroneaera* to accommodate Australian species with an anterior and posterior lateral tooth in the right valve only. From the description, there appears to be no difference between this and *Rhinoclama*, and we therefore synonymize *Austroneaera* with the subgenus *Rhinoclama*.

Subgenus Luzonia Dall & Smith, 1890 (see Dall 1890)

Type species: *Cuspidaria* (*Luzonia*) *philippinensis* (Hinds, 1843).

Anterior cardinal tooth in right valve only, no lateral teeth present.

The subgenus includes those species listed in section H of Smith (1885).

As discussed above, there has been confusion about the type species *C. philippinensis* Hinds. Re-examination of the type specimen (B.M.N.H. no. 1961 112) confirms that it has a single anterior cardinal tooth in the right valve.

Since Dall (1890) first described and then re-examined the subgenus (Dall 1903), the taxon has been overlooked. Thiele (1935) omits it from his descriptions of the subgenera of *Cuspidaria* and provides no alternative group to accommodate species with this type of hinge. The most recent description by Moore (1969) erroneously states that *Luzonia* is cogeneric with *Rhinoclama* and that the latter has no teeth. Until this study, *Luzonia* included only the type species and *C.* (*L.*) *chilensis* Dall; here it is enlarged by two more species.

Subgenus Tropidomya Dall & Smith, 1886 (see Dall 1886)
(*Tropidophora* Jeffreys, 1881)

Type species: *Cuspidaria* (*Tropidomya*) *abbreviata* (Forbes, 1843).

Single anterior cardinal tooth in each valve.

The type was originally described as having no lateral teeth. Jeffreys (1865, 1869), who included it as *Neaera abbreviata* in his *British conchology*, later (Jeffreys 1881) placed it in a group *Tropidophora* which included species with a keel on the shell. Smith (1885) ignored this name and placed the species in his group 1, characterized by a 'denticle' anterior to the beaks but with no lateral teeth. Because *Tropidophora* was preoccupied, Dall (1886) changed the name to *Tropidomya*, identifying it with group 1, and noted a single anterior cardinal tooth in each valve.

Doubts have been expressed (Tebble 1966) as to whether the pear-shaped swelling beneath the beak is a true cardinal tooth. A tooth is present in specimens of *C.* (*T.*) *abbreviata* examined here, which is distinct from that of any other cuspidariid, and therefore the taxon is retained.

Subgenus Plectodon Carpenter, 1864

Type species: *Plectodon scaber* Carpenter, 1864.

Anterior dorsal shell margins incurved, elongate reflected anterior and posterior lateral teeth in right valve, opisthodetic ligament.

Original studies on *Plectodon scaber* (Carpenter, 1864) accurately described the hinge characters, but the ensuing literature is confused and misleading. Carpenter (1864) described *Plectodon* as a member of the Anatinidae characterized by 'spirally intwisted' dorsal margins beneath the umbones, laminated lateral teeth and a hidden internal resilifer. Examination of the type specimen (U.S.N.M. (United States National Museum) no. 63943) and of a specimen of *Plectodon granulata* Dall (U.S.N.M. no. 94214) shows spiral incurving of the anterior dorsal shell margin of both valves, and elongate, reflected, anterior and posterior lateral teeth in the right valve. There is a unique, posteriorly directed resilifer below the posterior dorsal margin in both valves. The shell surface is usually granulate. Dall (1886) termed the spiral margins 'tooth-like prominences', stated that they bore a minute external ligament, but did not mention either the resilifer or the lateral teeth. He inferred that the latter were present when stating that the hinge was as in *Leiomya* except for the spiral intwisting. Presumably as a result of this, *Plectodon scaber* was included in a section of the subgenus *Leiomya* (Dall, 1886), together with a new species *P. granulata*, and a smooth-surfaced variety *velvetina*. Subsequent authors mention the small external ligament and tooth-like prominence but ignore Carpenter's original description (1864). Johnson (1934) and Bernard (1974) list the taxon as a subgenus of *Leiomya*, and Thiele (1935) as a subgenus of *Cuspidaria*, characterized by having 'a tooth-like thickening of the hinge margin', while Moore (1969) classifies it as a genus possessing a pseudocardinal under an external ligament.

Examination of both *P. scaber* and *P. granulata* emphasizes the need to adhere to the original description and confirms *Plectodon* as a subgenus characterized by a distinct spiral incurving hinge margin, anterior and posterior lateral teeth in the right valve, and 'hidden' internal resilifer in each valve.

Examination of the type of *Cuspidaria brazieri* Smith (B.M.N.H. no. 87.2.9.2528), assigned to the subgenus *Leiomya* by Dall (1886), and of a specimen in the Royal Scottish Museum from Port Jackson shows that this species has a *Plectodon*-type hinge.

Subgenus Leiomya Adams A., 1864

Type species: *Cuspidaria* (*Leiomya*) *adunca* (Gould, 1861).

Anterior bifid cardinal tooth in the right valve, non-bifid cardinal tooth in left valve, anterior and posterior lateral tooth in right valve.

Adams (1864) described *Leiomya* as a subgenus of *Leptomya*, a genus long since removed from the Cuspidariidae (Vokes 1967), naming *C. adunca* Gould as the type. According to Adams (1864) *Leiomya* is characterized by the possession of two anterior 'primary' teeth in the right valve and a single 'primary' tooth in the left valve, plus two strong lateral teeth; but Adams does not say in which valve the latter are found.

Dall (1886) examined Adams's and Gould's material and noted that the two anterior primary teeth in the right valve were in fact a single bifid anterior cardinal and a single non-bifid cardinal tooth in the left valve. Lateral teeth are present in the right valve only. With the removal of *C. brazieri* Smith (see above), the subgenus becomes monospecific. According to Johnson (1934) the type should be in the United States National Museum (U.S.N.M. no. 1296) although Dall (1889*a*, p. 239) reported it as 'not located' and it still remains so, but a specimen labelled '*Leiomya adunca* Gould, A. Adams. Japan.' (U.S.N.M. no. 21156) exactly matches the described hinge. For unknown reasons Johnson (1934) uses *Leiomya* to accommodate the subgenera *Plectodon* and *Halonympha* as well as the section *Rhinoclama*. Bernard (1974) also synonymizes *Rhinoclama* with the genus *Leiomya*. This cannot be upheld.

Subgenus Vulcanomya Dall, 1886

Type species: *Cuspidaria* (*Vulcanomya*) *smithi* Dall, 1886.

Cardinal teeth absent, anterior and posterior lateral tooth in right valve, anterior lateral tooth in left valve.

This subgenus is based on a single species, possibly a single specimen. Dall (1886) considered that Smith (1885) had erroneously assigned the specimen to *C.* (*L.*) *adunca* Gould, which he (Smith) had placed in section I. Dall (1886) states that the specimen differs in having no cardinal teeth, an anterior and a posterior lateral tooth in the right valve, and an anterior lateral tooth in the left valve, and names it *Vulcanomya smithii* and reports it as being housed in the B.M.N.H. There is a specimen in the non-type collection labelled '*N. adunca* Gould = *Vulcanomya smithii* Dall' which we believe is the type. This has been confirmed by the Museum.

The hinge differs from that of *C.* (*L.*) *adunca* Gould, having a short rounded tooth on either side of the resilifer in the right valve and a tiny double notch in the anterior dorsal margin of the left valve.

Nordsieck (1969) lists two species (*Vulcanomya teres* (Jeffreys) and *V. semistrigosa* (Jeffreys)), both of which were previously listed as *Rhinoclama*. We can find no justification for his action; both species have elongate lateral teeth and lack an anterior tooth in the left valve. A single right valve labelled *C.* (*V.*) *cearae* Dall (U.S.N.M. no. 95443) cannot be identified either as a species of *Rhinoclama* or of *Vulcanomya*. It does not correspond to any other known species.

Genus Halonympha Dall & Smith, 1886 (see Dall 1886)

Type species: *H. claviculata* (Dall, 1881).

Halonympha was originally described as a subgenus of *Cuspidaria* to accommodate species with an acute cardinal tooth in the right valve and a posterior 'clavicular' rib in both valves (Dall

1886).† Dall (1886) recognized section K (Smith 1885) as being identical, furthermore found a specimen in the U.S.N.M. labelled '*C. inflata*, Porcupine Station 39' (Jeffreys 1881) to be identical to *H. claviculata.*

The distinctive clavicle or 'buttress' (Dall 1886) is a raised ridge on the inside of the shell that extends along the dorsal edge and, in some specimens, onto the ventral edge of the posterior adductor muscle scar. This rib is much more pronounced in some species than in others.

There are four described species, namely *H. claviculata* Dall, *H. striatella* Verrill & Bush, 1898, *H. aethiopica* Thiele & Jaeckel, 1931 and *C. depressor* (Jeffreys, 1881), here found to be a *Halonympha* species. A further, and as yet undescribed, species is present in the collections of the B.M.N.H., labelled '*C H. ros* Verco' (no. 910. 3. 29. 9594).

Genus Protocuspidaria new genus

Type species: *P.* (*Protocuspidaria*) *verityi.*

Definition

Shell small, rounded outline, posterior dorsal margin straight, rostrum very short and truncate; equivalve, but slightly inequilateral, umbones small and bubble-like; shell surface covered in numerous, crowded, thread-like, concentric striae, oblique rostral ridge not present, but striae irregular and confused posteriorly and extend onto rostrum; resilium small, hinge either lacks teeth, or has an elongate anterior lateral in the right valve only, or has an anterior lateral tooth in both valves. Septum membranous, lacks dorsal attachments to shell and encloses two longitudinal rows of gill filaments, one either side of the foot; posterior palps large and cup-shaped, siphons cuspidariid in form with three dorsal tentacles and four ventral tentacles and a simple vertical partition, pierced by a keyhole slit, the inhalant valve. Dioecious.

Protocuspidaria represents an earlier stage in the evolution of the septum to that shown by *Halonympha* in that it possesses true gill filaments with skeletal rods, reduced in size and set in a membranous septum. Neither anterior nor posterior dorsal septal muscles are attached to the shell. The palps are as in *Halonympha*, and the siphons are cuspidariid and not poromyid in form.

There are relatively few specimens in the collections but, although they all look externally similar, three hinge types are represented. The first has no teeth, resembling the subgenus *Myonera*, while the other two have previously unknown types, one with an anterior lateral tooth in the right valve only, and the other with an anterior lateral tooth in both valves.

Thus, we use anatomical characters to separate three *genera* in the family Cuspidariidae:

Cuspidaria, with a muscular septum pierced by four to ten pairs of highly specialized pores, anterior and posterior septal muscles attached to the shell, and small palps;

Halonympha, with a less muscular septum, pierced by several slits between very reduced gill filaments but which have no skeletal rods, an anterior septal muscle attached to the shell and large posterior palps;

Protocuspidaria, with a membranous septum with little muscle containing typical gill filaments, with a skeletal rod, no septal muscle attachments to the shell and large posterior palps.

These genera can, for convenience of identification, be divided into subgenera on the basis of hinge characters.

---

† Nordsieck (1969) uses these same characters on which to base the genus, yet inexplicably includes *C. nitens* (Locard, 1898) with a posterior lateral tooth in the right valve, and *C. laediformis* (Dautzenberg & Fischer, 1897) without teeth.

Protocuspidaria can be divided further into:

(*Protocuspidaria*) anterior lateral tooth in the right valve only, type species *P.* (*P.*) *verityа*;

(*Bidentaria*) anterior lateral tooth in both valves, type species *P.* (*B.*) *atlantica*;

(*Edentaria*) no teeth in either valve, type species *P.* (*E.*) *simplis*.

There are two species described in the literature whose shells are very similar, but not conspecific, with the present specimens of *Protocuspidaria*. These are *Myonera ruginosa* Jeffreys, 1881, which, like *Edentaria*, has no teeth, and *Cuspidaria colopodes* Dautzenberg & Fischer, 1897, which, like *Bidentaria*, has an anterior lateral tooth in both valves. Since the internal anatomy of these two species has never been described, it is impossible to know if they are species of *Cuspidaria* or *Protocuspidaria*. There is no other known species with a hinge resembling that of a subgenus of *Protocuspidaria*.

Nordsieck (1969) includes *C. colopodes* in a new genus *Jeffreysomya* which is characterized by a flatter and not very obviously rostrate shell. Unfortunately he includes species with several hinge types under this name and does not refer to their anatomy. His definition of the genus is too insubstantial to be accepted.

Key to the Recent genera and subgenera of the family Cuspidariidae

1*a*.	With hinge teeth.	2
1*b*.	Without hinge teeth.	10
2*a*.	Hinge with specialized buttress around the posterior adductor muscle scar, more than five pairs of pores in septum.	genus *Halonympha*
2*b*.	Hinge without buttress.	3
3*a*.	Single anterior lateral tooth in right valve or in both valves.	11
3*b*.	No anterior lateral teeth, or if present always associated with other teeth.	genus *Cuspidaria* 4
4*a*.	Hinge teeth in right valve only.	5
4*b*.	Hinge teeth in both valves.	7
5*a*.	Posterior lateral tooth in right valve only.	6
5*b*.	Anterior and posterior lateral tooth in the right valve only.	subgenus *Rhinoclama*
5*c*.	Anterior cardinal tooth in right valve only.	subgenus *Luzonia*
6*a*.	Shell without radiating sculpture.	subgenus *Cuspidaria*
6*b*.	Shell with radiating sculpture.	subgenus *Cardiomya*
7*a*.	Elongate anterior and posterior lateral teeth in right valve.	8
7*b*.	Short rounded anterior and posterior lateral tooth in right valve, and single cardinal in the left valve.	9
7*c*.	No lateral teeth in either valve, but anterior cardinal in both.	subgenus *Tropidomya*
8*a*.	Single cardinal tooth in left valve, bifid cardinal tooth in right valve, anterior and posterior lateral tooth in right valve.	subgenus *Leiomya*
8*b*.	Spiral incurving of anterior dorsal margin both valves, internal ligament (resilifer) hidden beneath it, and anterior and posterior lateral tooth in right valve.	subgenus *Plectodon*
9*a*.	Double notched, ledge-like cardinal in left valve, short rounded anterior and posterior lateral tooth in right valve.	subgenus *Vulcanomya*
9*b*.	Anterior 'denticle' in left valve, anterior and posterior lateral tooth in right valve.	subgenus *Pseudoneaera*
10*a*.	With a muscular septum pierced by four or five pairs of specialized pores.	subgenus *Myonera*
10*b*.	Flimsy septum, containing numerous modified, reduced gill filaments.	genus *Protocuspidaria* subgenus *Edentaria*
11*a*.	Anterior lateral tooth in right valve, septum containing numerous modified, reduced gill filaments.	genus *Protocuspidaria* subgenus *Protocuspidaria*
11*b*.	Anterior lateral tooth in both valves, septum containing numerous modified, reduced gill filaments.	genus *Protocuspidaria* subgenus *Bidentaria*

DESCRIPTIONS OF REPRESENTATIVE SPECIES IN THE SEPTIBRANCHIA FROM THE DEEP ATLANTIC

Genus Cuspidaria

Subgenus Cuspidaria

Cuspidaria obesa (Lovén, 1846) (figures 1–12)

1846	*Neaera obesa*	Lovén (p. 202)
1878	*Neaera obesa*	Sars (p. 86, pl. 16, figs a–c)
1885	*Neaera obesa*	Smith (p. 43)
1886	*Cuspidaria obesa*	Dall (p. 295)
1897	*Cuspidaria obesa*	Plate (pp. 24–8)
1898	*Cuspidaria obesa*	Verrill & Bush (p. 804, pl. 75, fig. 7)
1898	*Cuspidaria obesa*	Locard (p. 172)
1934	*Cuspidaria obesa*	Johnson (p. 33)
1958	*Cuspidaria obesa*	Ockelmann (p. 160)
1962	*Cuspidaria obesa*	Clarke (p. 72)
1974	*Cuspidaria obesa*	Reid & Reid (pp. 47–56)

Material

ship	date	stn	latitude	longitude	depth/m	number
?	?		60° 07.0′ N	05° 27.0′ E		5
?	11. 07. 1895		66° 35.0′ N	56° 38.0′ W		2
?	18. 04. 1972		60° 11.0′ N	05° 38.0′ W		2
J. Charcot						
(Polygas)	21. 10. 72	DS16	47° 35.2′ N	08° 40.5′ W	2246	125
	22. 10. 72	DS18	47° 32.2′ N	08° 44.9′ W	2138	60
(Biogas II)	19. 04. 73	DS31	47° 32.5′ N	09° 04.2′ W	2813	198
(Biogas III)	26. 08. 73	DS41	47° 28.3′ N	09° 07.2′ W	3548	77
	24. 08. 73	CV22	47° 41.8′ N	08° 18.7′ W	1331	1
(Biogas IV)	23. 02. 74	DS59	47° 31.7′ N	09° 06.2′ W	2775	25
	25. 02. 74	DS61	47° 34.7′ N	08° 38.8′ W	2250	2
	26. 02. 74	DS64	47° 29.2′ N	08° 30.7′ W	2156	1
	20. 10. 74	DS71	47° 34.3′ N	08° 33.8′ W	2194	1

Distribution

Subarctic, boreal, Mediterranean, N Atlantic. (Ockelmann 1958; Clarke 1962.) Depth range: 18(?)–4453 m.

Description

This large, well documented species was selected to give most of the basic information on the morphological characteristics of the genus *Cuspidaria*, and all other species have been compared with it.

Although this species was described by Lovén (1864) and then again by Sars (1878), it was Plate (1897) who first examined the internal anatomy, when he compared it with that of *C. cuspidata* (Olivi). Though based on different evidence, Plate (1897) came to much the same conclusions that are presented here concerning the origin of the septum. More recently, Ockelmann (1958) described its distribution and the probable type of larval development, while Yonge (1928) and Reid & Reid (1974) have observed the septum in live animals.

The shell is oval and has a fairly long, handle-like rostrum. It is slightly inequivalve, the left valve overlapping the right ventrally; it is inequilateral, the anterior half being slightly shorter than the posterior half. The posterior dorsal margin is long, sloping and slightly concave; the anterior dorsal margin is convex but the slope of the umbonal section is continuous with that of the posterior dorsal margin. The umbones are low, rounded and posteriorly inclined. The anterior margin is slightly extended. The ventral margin is sinuate at the base of the rostrum, whose distal margins are parallel. The shell surface is smooth, opaque and covered with very faint concentric growth lines that become more defined but irregular at the base of the rostrum. There is a faint oblique rostral ridge from umbo to posterior ventral margin, with a number of incomplete wavy longitudinal ridges running the length of the rostrum from the distal posterior margin (figure 1).

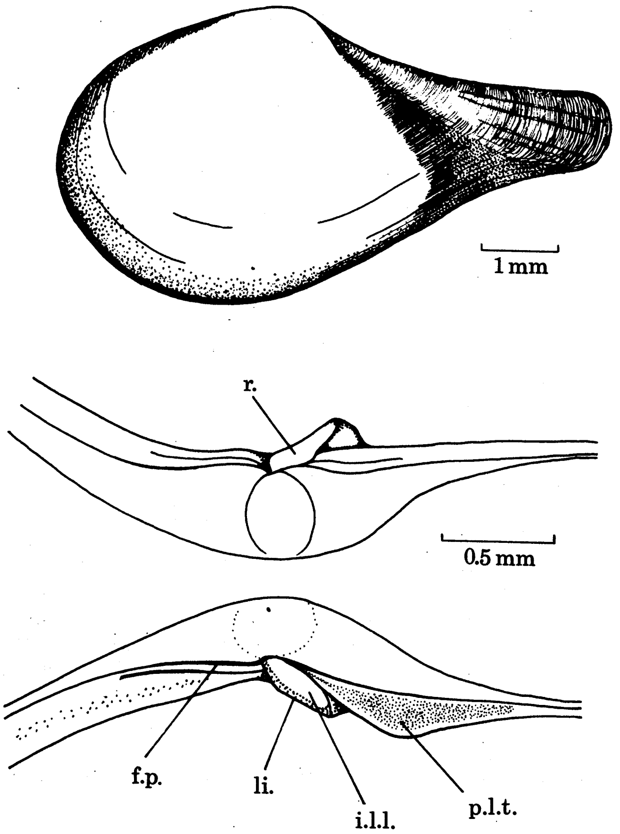


FIGURE 1. *Cuspidaria obesa*. Lateral view of the shell from the left side and a dorsolateral view of the hinge of both valves.

(List of abbreviations used in figures given on pp. 545 and 546)

The resilifer, that portion of the dorsal shell margin to which the resilium is attached, is directed posteriorly and obliquely ventrally with its free edge facing anteriorly. The resilium is roughly triangular in shape (Yonge & Morton 1980).

The hinge in *C. obesa*, as in all species of the subgenera *Cuspidaria* and *Cardiomya*, consists of a single elongate, triangular posterior lateral tooth in the right valve (figure 1). There appears to be no lithodesma in this species, though this is present in other species of the subgenus.

Maximum shell measurements are: length 12.7 mm; height 6.8 mm; width 3.2 mm.

Mantle

As in all the Cuspidariidae, the mantle, except for the margin, is thin and transparent. Apart from a rather large pedal gape occupying the anterior two-thirds of the ventral edge, the margins are fused along their length. Posterior inhalant and exhalant siphons are present. Yonge (1928) states that these are formed by the fusion of all three mantle folds and that the siphonal sheath, which surrounds both the inhalant and exhalant siphons, and which secretes the tubular 'rostrum', is unique among bivalves.

The degree of fusion varies along the length of the margin. Anterior and posterior to the pedal gape the inner folds and inner faces of the middle folds are fused, the pallial muscle being continuous from one mantle lobe to the other. A narrow ventrally projecting ridge separates the two periostracal grooves. Close to the pedal gape less of the inner face of the middle fold is fused with its counterpart and the periostracal grooves here lie further apart. Posteriorly the formation of the siphons involves fusion of part of the outer folds.

The inner mantle epithelium immediately dorsal to the inner mantle fold bears a longitudinal tract of ciliated cells which, in section, appears as a ridge five or six cells wide which extends from the mouth to the base of the siphons. Observations on living *C. cuspidata* have shown this tract to be rejectory. Associated with it is a longitudinal band of gland cells, consisting of numerous large, faintly staining cells (blue in Azan triple stain) aggregated below the ciliated tract. In *C. obesa* there appears to be only one type of gland cell; these stain in Alcian Blue and produce mucus that contributes to the production of pseudofaeces. In other species (e.g. *C. parva*) there is an additional, distinct and densely staining type of gland cell in this position.

Septum

The Cuspidariidae have no recognizable gills but a horizontal muscular septum. *C. obesa* exhibits the most common form of septum and one that is thought to be the most advanced. The origin of the septum has been a subject of controversy since Dall (1886) first described the structure. Although the morphology of *Cuspidaria* has been studied (Yonge 1928; Pelseneer 1888*a*, *b*, 1891, 1911; Grobben 1892; Bernard 1974; Reid & Reid 1974) as yet no one has presented any convincing evidence concerning the origin of the septum.

Dall (1886, 1889*a*, *b*) stated that the septum was not homologous with a normal gill, whereas Pelseneer (1888*a*, *b*, 1891, 1911), who described the anatomy of *C. fragilissima* Smith, *C. curta* Jeffreys, *C. platensis* Smith and *C. rostrata* Spengler, concluded that it was derived from the gill, as did Grobben (1892) from studies on *C. cuspidata*. Both Plate (1897) and Yonge (1928) studied *Cuspidaria obesa*, the former believing that the septum was not derived from the gill, the latter concluding the opposite. Yonge (1928) gives a good description of the septum and names four of the constituent muscles.

In *C. obesa*, the septum is a muscular partition, slung longitudinally in the horizontal plane, that divides the mantle cavity into an infraseptal and a supraseptal cavity (figure 2). The septum is suspended by pairs of retractor muscles, known as the anterior and posterior septal muscles (Dall 1889*a*, *b*; Grobben 1892; Yonge 1928). These muscles are attached to the shell on either side of the midline, close to the respective adductor muscles. The septum is deeply divided anteriorly where the foot passes through it (figure 3). It is fused to the foot, as it is to the mantle, the body close to the mouth and the intersiphonal partition. It would form a complete partition across the mantle cavity if it were not for four pairs of specialized pores that pierce it. These can open and close.

Dall (1889*b*) first described the septum as consisting of several longitudinally arranged bands of muscle. Yonge (1928) identified inner longitudinal septal muscles, anterior and posterior septal muscles and anterior and posterior lateral septal muscles. This study has confirmed these

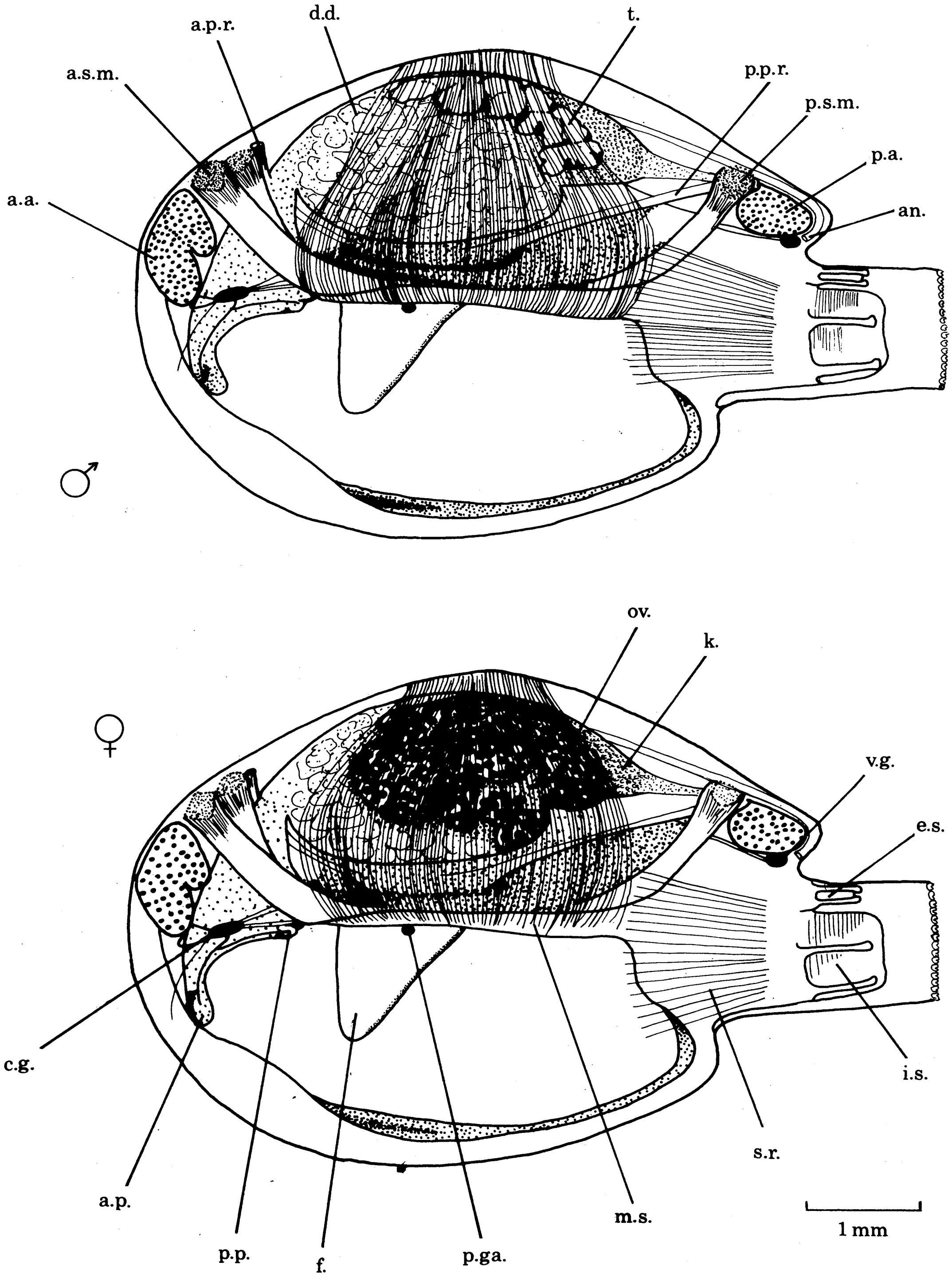


FIGURE 2. *Cuspidaria obesa*. The anatomy of male and female specimens seen from the left side.

and added a further pair. The arrangement in *C. obesa* is typical of most species of the genus *Cuspidaria* with four or five pairs of pores. The muscles are defined as follows (figure 3).

(i) *The outer longitudinal septal muscles* extend along the outer lateral edges of the septum and have posterior and anterior muscle attachments to the shell.

(ii) *The posterior septal muscles* extend anteriorly from the posterior muscle attachment and lie internal to the posterior part of the outer longitudinal muscles. These, initially vertically orientated suspensory muscles, fan out in the horizontal plane of the septum; the fibres from the left and right sides curve towards each other, and cross behind the foot.

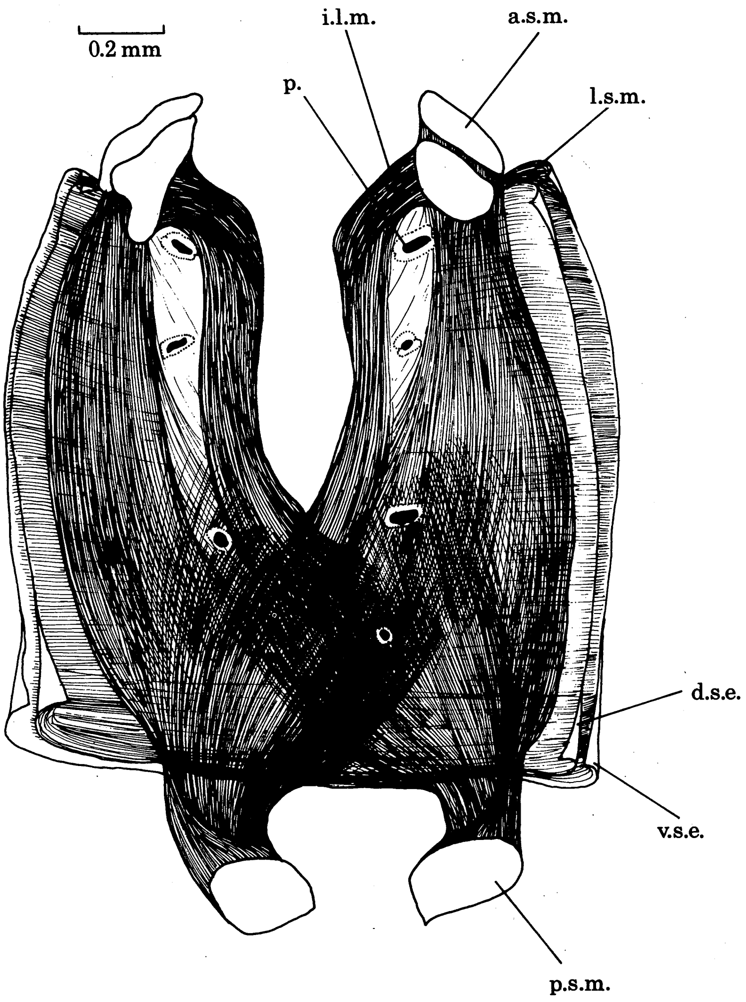


FIGURE 3. *Cuspidaria obesa*. Dorsal view of the septum.

(iii) *The anterior septal muscles* are longer and narrower than the posterior septal muscles and extend from the anterior attachment posteriorly and internal to the anterior part of the outer longitudinal muscle. Behind the foot they merge with each other and the posterior septal muscles.

(iv) *The inner longitudinal muscles* are narrow bands of muscle that extend from the anterior attachment, lateral to the anterior septal muscles and the pores at the inner margin of the septum close to the foot. Posterior to the foot they merge with the other muscles.

As Grobben (1892) noted, the anterior muscle attachment is double and divided into a main part involving the anterior septal and the outer longitudinal muscles, and a smaller, slightly more posterior, attachment of the inner longitudinal muscle together with a few fibres from the anterior septal muscle. It is probable that the inner longitudinal muscle has a different function from the other muscles and is important in maintaining the tissue seal around the foot (figure 3).

The four septal muscles described above are composed of flattened, transversely striated fibres which Yonge (1928) considered to be unique, if not in the animal kingdom then certainly in the Bivalvia.

(v) *The lateral septal muscles* take the form of fine bands of fibres lying beneath the dorsal septal epithelium which extend into the mantle dorsal to the septum. Posterior to the foot they traverse left to right across the septum, whereas anteriorly they merge with the inner longitudinal muscle. The majority of cuspidariids, including *C. obesa*, have a continuous series of lateral septal muscles between the anterior and posterior limits of the septum. In a small proportion of the species they are divided into two groups and exceptionally, in *C. fragilissima* (Yonge 1928), there are four such groups. The lateral septal muscles are unstriated†, as are the small sphincter muscles around each pore.

The muscles of the septum lie between thin dorsal and ventral septal pavement epithelia (Grobben 1892). The dorsal septal epithelium is continuous with that covering the viscera and lining the supraseptal cavity, while the ventral epithelium is continuous with that covering the foot and palps, and lining the infraseptal mantle cavity. A horizontal seal is thus formed. Although the epithelia around the foot possess elastic qualities, because the connection between the foot and septum is intimate, the two must move in concert to some extent, otherwise extension of the foot would be largely confined to that portion ventral to the septum.

Pores

The septal pores are arranged on either side of the foot, more or less equally spaced. In *C. obesa*, as in most cuspidariids, there are four pairs of pores, but, as Grobben (1892), Pelseneer (1911) and Yonge (1928) noted, some species have five pairs. The present collections show that a few species have more than five pairs of pores, the number of pairs ranging from eight to twenty. These species have proved important in determining the probable evolution of the septibranch septum.

Typical pores, such as those seen in *C. obesa*, are tubular and oval in cross section. The long axis is approximately transverse to the septum, that is, in the same plane as the lateral septal muscles. The epithelium lining the pore is thicker than that of the dorsal and ventral septal epithelia. Peripheral to the pore the dorsal epithelium is depressed ventrally but with the margins of the pore raised to form a dorsal lip (figure 4). In *C. obesa* the lips of the pore extend almost to the level of the dorsal surface of the septum; in other species, e.g. *C. parva*, they appear to extend to half the thickness of the septum, though this may be the result of preservation. The lips form a valve allowing water to pass in one direction only: from infra- to supraseptal cavity.

As Grobben (1892) and Yonge (1928) noted the pores bear two rings of cilia. The dorsal ring is four or five cells broad bearing numerous long cilia, while the ventral ring at the ventral edge of the pore is somewhat broader with much shorter cilia. Bands of unstriated muscle lie beneath the bands of cilia on either side of the long axis of the pore. These come together at the lateral limits of the pore and follow the path of the lateral septal muscles. Observations in live

---

† Bernard (1974) claims that the siphonal retractors are also striated. We have found no evidence to support this.

specimens of *C. cuspidata* show that the pore closes along the longitudinal axis by the contraction of the muscles moving from an arched to a straight course and opens on relaxation of the muscles.

Digestive system

The digestive system in the Cuspidariidae is remarkably constant in form and structure, and is similar to that of the Verticordiidae (Allen & Turner 1974).

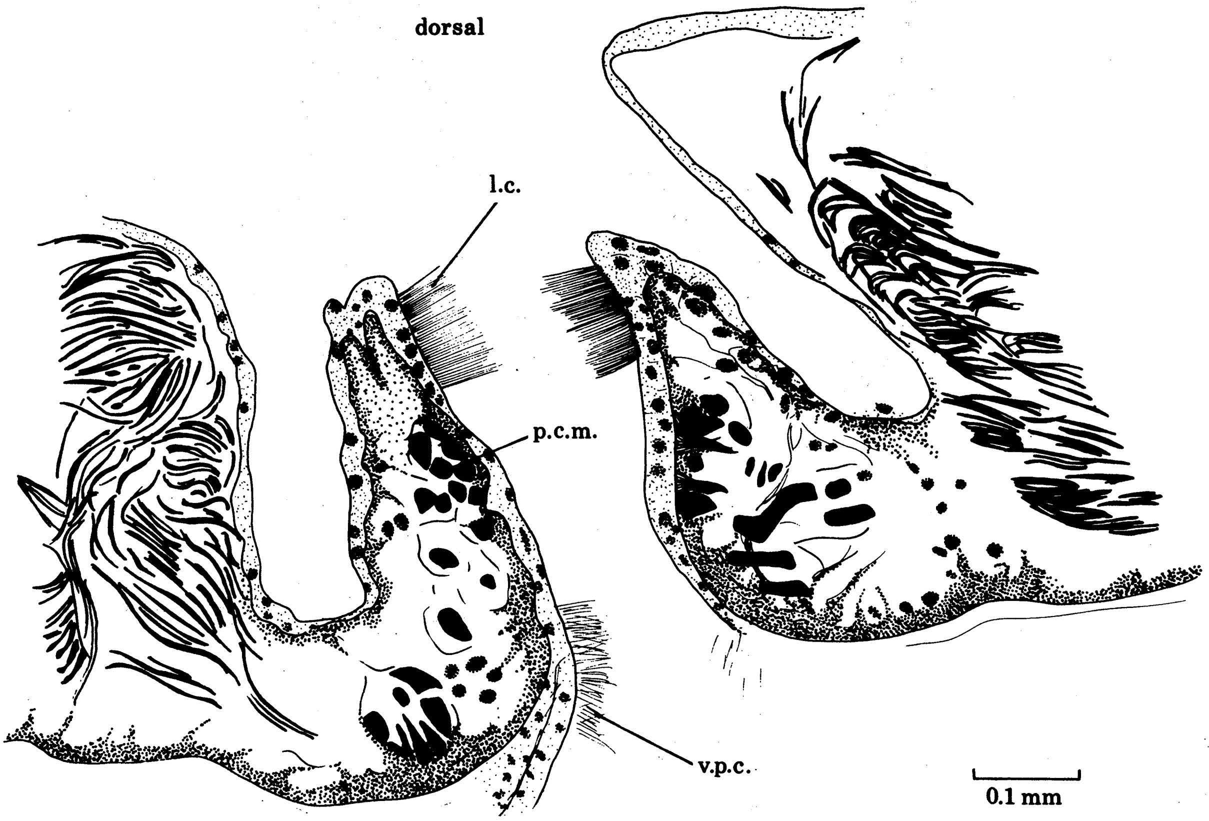


FIGURE 4. *Cuspidaria obesa*. Vertical section through a septal pore.

Anteriorly the wide ventrally directed mouth tapers dorsally to an extremely muscular oesophagus, which curves posteriorly between the anterior septal muscles to the stomach. The epithelial lining of the oesophagus is thrown into approximately 15 irregular longitudinal folds surrounded by a thick layer of circular muscle, with numerous radial fibres peripheral to it, and with an outer layer of longitudinal muscle. The narrow opening of the oesophagus into the anterior end of the stomach is guarded by a sphincter. The stomach is a simple, oval sac that lies posteroventrally within the body. The combined style sac and midgut open from the anterior, right, ventral side of the stomach floor (figure 5). Except dorsally the anterior half of the stomach is covered by digestive gland, while the posterior end is covered by gonad. The stomach wall is thrown into several low longitudinal ridges similar to those described in the Verticordiidae (Allen & Turner 1974). Yonge (1928) and Bernard (1974) both consider the cuspidariid stomach to be highly muscular, but in all the species examined here there is little muscle in comparison with that surrounding the oesophagus. We distinguish two stomach muscle layers, neither very thick. The outer longitudinal muscle of the oesophagus extends posteriorly over the

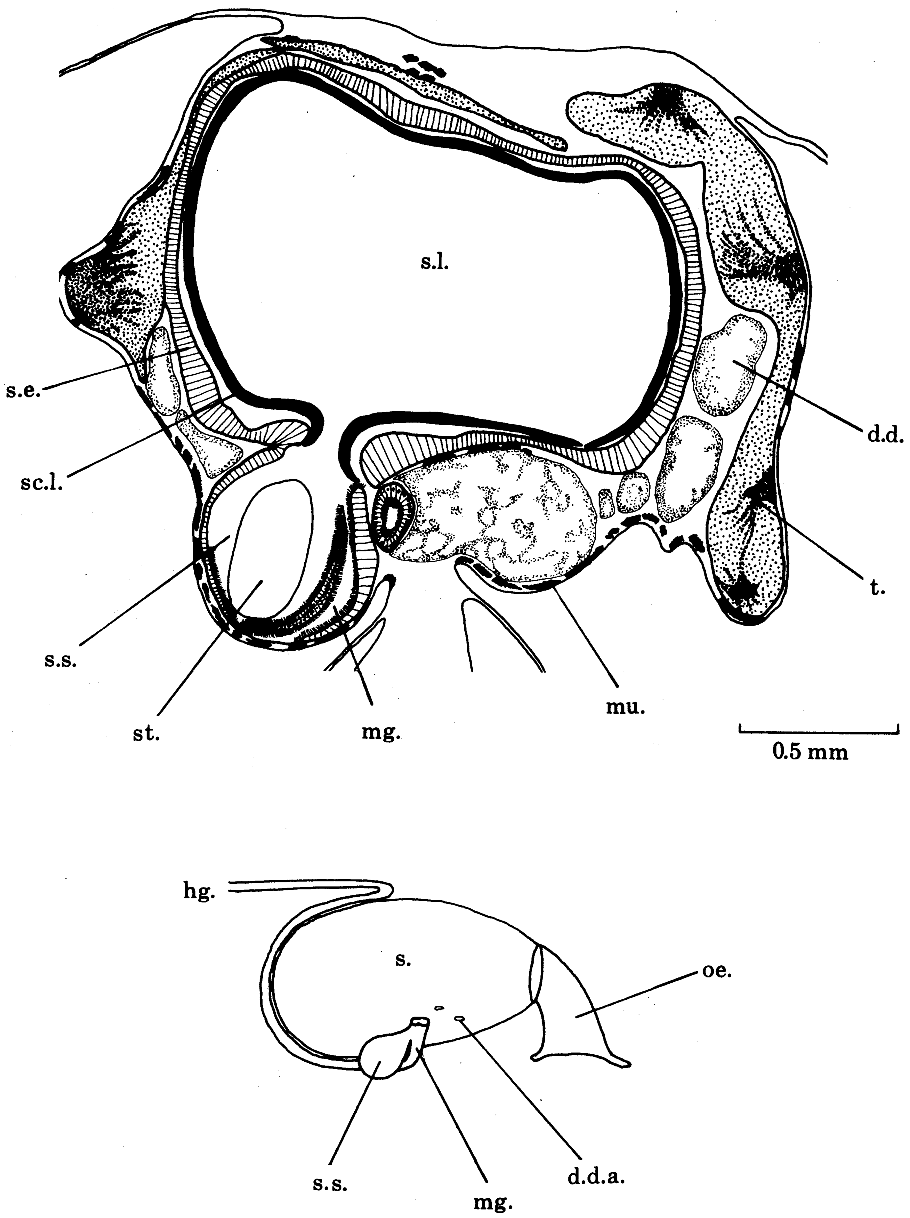


Figure 5. *Cuspidaria obesa*. Transverse section of the body through the stomach with (inset) a diagram of the general course of the gut.

anterior dorsal surface of the stomach but, more posteriorly, these rise from the stomach wall and lie above the gonad. Also, over the posterior wall of the stomach, muscle extends from the ventral side dorsally. This latter is part of a set of muscles that are lateral extensions of the foot musculature. The anterior and posterior pedal retractors run as a sheet beneath, and in part lateral to, the sides of the stomach. For a short distance anteriorly the fibres lie close to the stomach wall before passing below the digestive gland close to the visceral epithelium. Two branches of this ventral muscle run transversely through the digestive gland close to the short ducts to the digestive gland. The ducts open to the ventral floor of the stomach, anterior to the style sac aperture (figures 5, 6). It would seem that the anterior muscles only can act directly on the stomach; any posterior muscle contraction will affect also the digestive gland and gonad.

The stomach is lined with a transparent gastric shield secreted by epithelial columnar cells filled with granules. Granules are also present between the cells and the shield proper and presumably will be added to the scleroprotein layer. Except for a restricted region around and between the digestive ducts, the midgut opening and a narrow ridged tract on the stomach floor leading from the oesophagus to the openings, the gastric shield lines the stomach completely. The shield-free region is the only ciliated area of the stomach. The right digestive duct is slightly anterior to the left. The ducts are as short as they are wide (0.04 mm × 0.04 mm) and approximately a quarter of the diameter of the style sac–midgut aperture. The style sac is small and cytologically similar to that of other bivalves. The small globular style does not extend above the floor of the stomach (figure 5). The midgut is anterior to the style sac. The hindgut passes along the ventral side of the stomach and then dorsally and posterior to the stomach before turning along the mid-dorsal line to pass through the pericardium to the anus. The rectal region, between heart and posterior adductor muscle, as in the Verticordiidae, is expanded slightly.

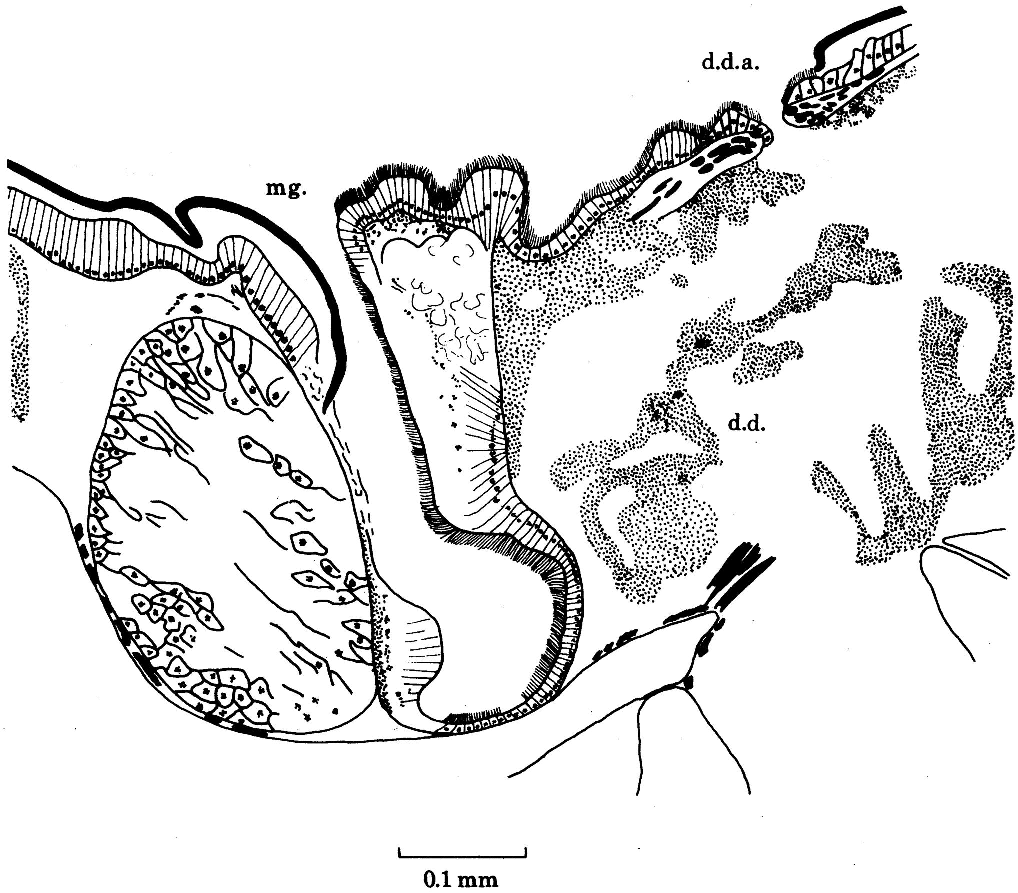


FIGURE 6. *Cuspidaria obesa.* Transverse section of the floor of the stomach to show the style sac, midgut and aperture of the left digestive duct.

The structure of the digestive diverticula is similar in all the Cuspidariidae. They consist of a mass of thin-walled, interconnecting tubules without secondary ducts, that extend around the oesophagus, and lateral to, and beneath the stomach.

Palps

The palps in the Cuspidariidae are generally small and reduced. There appear to be three types, here termed I, II and III. The distinction is based on the extent of their development (figure 7).

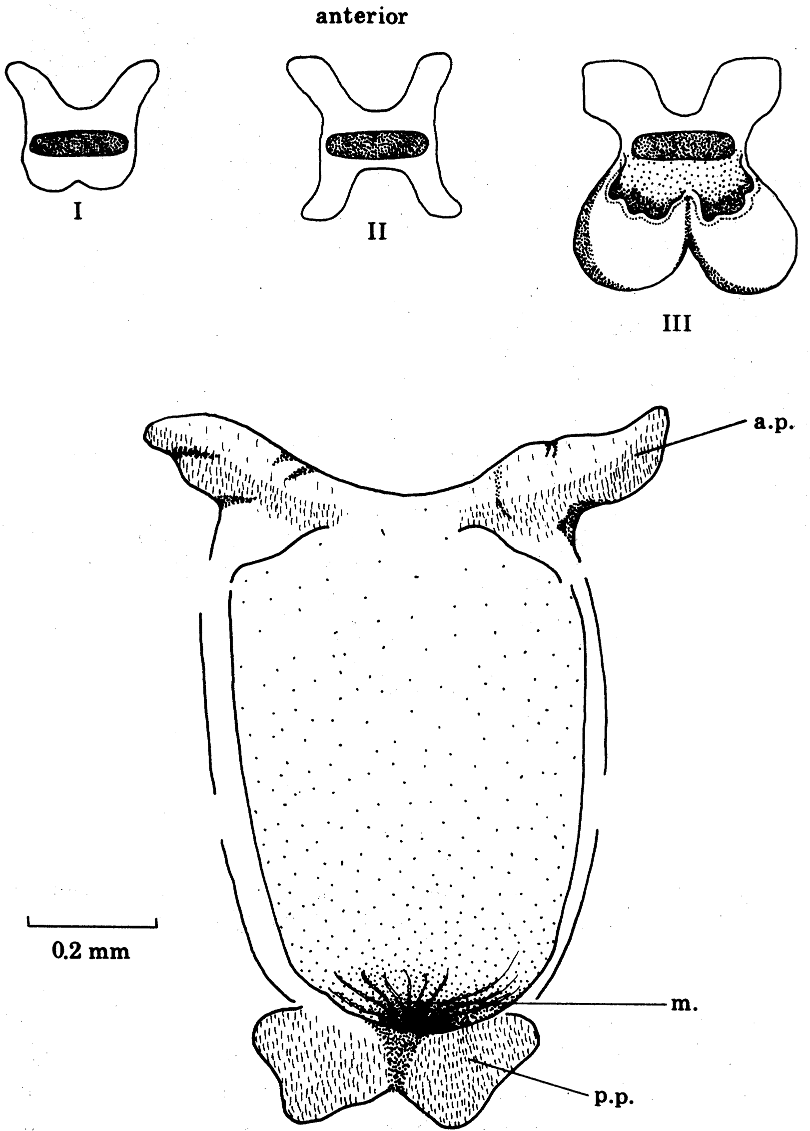


Figure 7. Diagram to show the three types of palps found in the family Cuspidariidae, and an oral view of those found in *Cuspidaria obesa*.

Type I. These are the most common and the smallest and are confined to the Cuspidariidae. They are found in *C. obesa*. They consist of narrow horn-shaped anterior palps, with the posterior palps reduced to thickened pads at the posterolateral margin of the mouth. The cells of the outer epithelium are apparently unciliated and squamous, whereas those of the inner are ciliated and regular cuboid. There are more muscle fibres within the posterior palps than in the anterior despite their reduced size. As Yonge (1928) noted, the ciliated inner surfaces of the palps may be wrinkled, but not ridged. The posterior palps are evenly ciliated, while the anterior palps have a broad dense band of cilia running the length of the outer edge of their inner surface. Of the species examined 24 have palps of type I, and belong to various subgenera. Those described by Dall (1889*a*, *b*), Grobben (1892), Yonge (1928) and Bernard (1974) generally conform to type I.

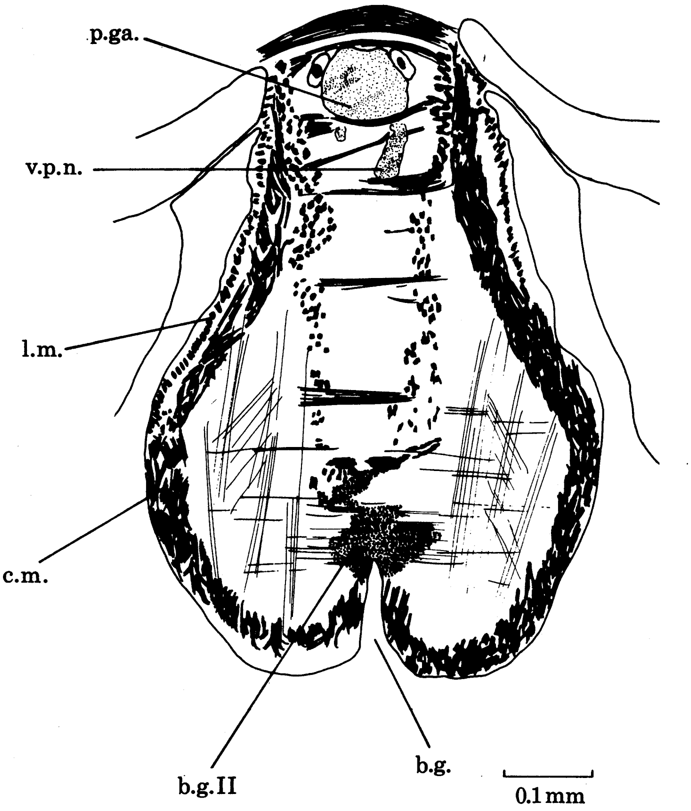


FIGURE 8. *Cuspidaria obesa*. Transverse section of the foot.

Type II. This has not been distinguished before. Larger than type I, the posterior palps are long, narrow, horn-shaped and similar to the anterior palps. This type is also confined to the genus *Cuspidaria*.

Type III. This differs from types I and II in being much larger. Type III palps are found in species with more than five pairs of septal pores. Here the anterior palps are flap-shaped and the posterior palps are cup-shaped. The bowl of the cup faces anteriorly. This type of palp is reminiscent of those seen in some species of the Verticordiidae such as *Lyonsiella abyssicola*, except that there it is the anterior palps that are large and cup-shaped, not the posterior.

The study of living *C. cuspidata*, a species with type II palps, shows that though reduced, these palps play a part in sorting small particles before they enter the mouth. Rejected particles travel the length of the inner face of the palp and fall off the tip onto the mantle rejectory tract.

Foot and byssus

In *C. obesa*, as in all cuspidariids, the foot is narrow, tapering and more or less round in cross section (figures 2, 8). The foot is suspended from the shell by a long, posterior pedal retractor that bifurcates immediately before its attachment to the shell anterior to the posterior adductor, and a pair of shorter anterior pedal retractors that run below the ventral edge of the viscera to attach on the shell close to the anterior adductor muscle (figure 2).

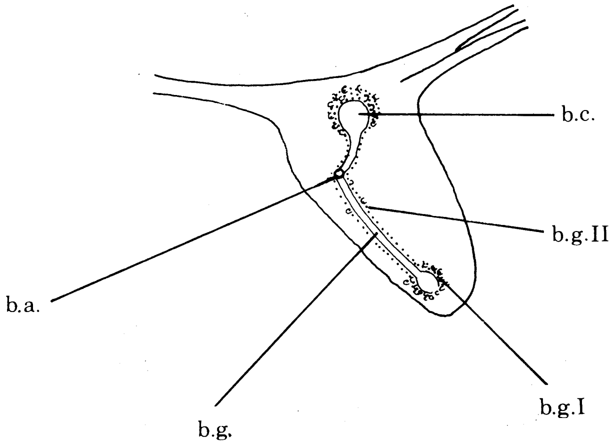


FIGURE 9. *Cuspidaria obesa*. Diagram to show the various components of the byssus apparatus.

The foot musculature comprises an inner layer of circular muscle, an outer layer of longitudinal muscle and several bands of transverse muscle from left to right across the foot. Two large fused pedal ganglia are situated in the base of the foot and are joined by a pair of pedal connectives from the cerebropleural ganglia and give rise to a pair of ventral pedal nerves supplying the foot (figure 8). On the posteroventral face of the foot a byssal groove extends from the aperture of the byssal duct to a small depression close to the tip. Both the groove and the posterior surface of the foot are heavily ciliated and well supplied with mucous cells. The byssus apparatus consists of an inverted pear-shaped, ciliated byssogenous cavity in the base of the foot that connects by a narrow, ciliated byssal duct, to the byssal groove (figure 9). The cavity is surrounded by several posteriorly directed byssal retractor muscle fibres. Two types of gland cell are associated with the byssus, both around the byssogenous cavity and duct, and alongside the groove and the terminal depression. The predominant gland cells are large subephithelial thin-walled cells full of small granules, that stain pale blue in Azan triple stain. Overlying these cells, but less numerous, is a second distinctive gland cell that stains a greenish colour in Azan triple stain. This type contains small groups of large irregularly shaped granules. Alcian Blue and Neutral Red stains indicate that both types of gland cell produce a substance different from that of the numerous ordinary epithelial mucous cells of the foot. Although all species of the genus *Cuspidaria* examined have this type of byssal apparatus it is not certain that all produce byssus threads. Threads have been seen in only two species.

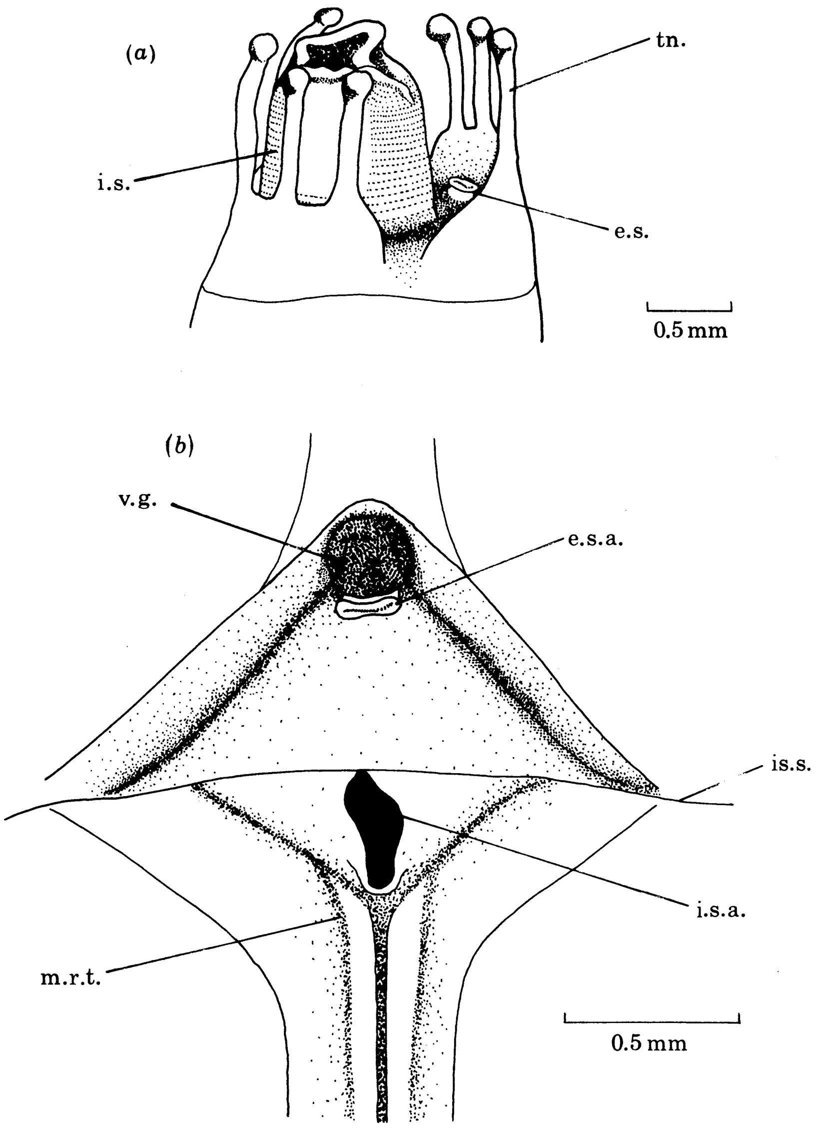


FIGURE 10. *Cuspidaria obesa*. (*a*) Lateral view of the siphons with the common sheath removed. (*b*) View of the base of the siphons from the inside of the mantle cavity.

Siphons

In *C. obesa*, typical of the species of *Cuspidaria*, there is a broad, ventral inhalant and a narrow, dorsal exhalant siphon that is usually inverted within the supraseptal cavity (figures 10, 11). The siphons are encased in a tubular posterior extension of the mantle, the common siphonal sheath, which extends from the posterior end of the septum and, in its turn, is encased by the posterior extension of the shell, the rostrum. Siphon formation in *Cuspidaria* involves the fusion, to some extent, of all three mantle folds (Yonge 1957). The outer mantle fold is not involved in the formation of the siphons themselves and the inner fold is not involved in the formation of the common siphonal sheath (figure 11). The inner lobes and inner face of the middle folds of the posterior ventral mantle margin are fused, i.e. the periostracal grooves are separated by the fused middle fold. Posterior to the septum the dorsal and ventral septal epithelia form the intersiphonal septum. The common siphonal sheath contains a longitudinal sheath of muscles, the siphonal retractor muscles, which extend posteriorly as far as the base of the enclosed siphons. At a point level with the base of the rostrum the inner mantle layer extends inwards across the inhalant aperture to form a vertical partition pierced by a keyhole slit. The slit, ringed by muscle, can be closed. The inner mantle fold together with the middle fold forms the siphon. The outer fold and middle fold form the common siphonal sheath around the siphons (figure 11). In life this sheath extends just beyond the end of the rostrum and a ring of papillae on the inside rim lie flush with the sediment surface. The periostracum originates to the outside of these papillae, indicating that the papillae are derived from the sensory middle fold.

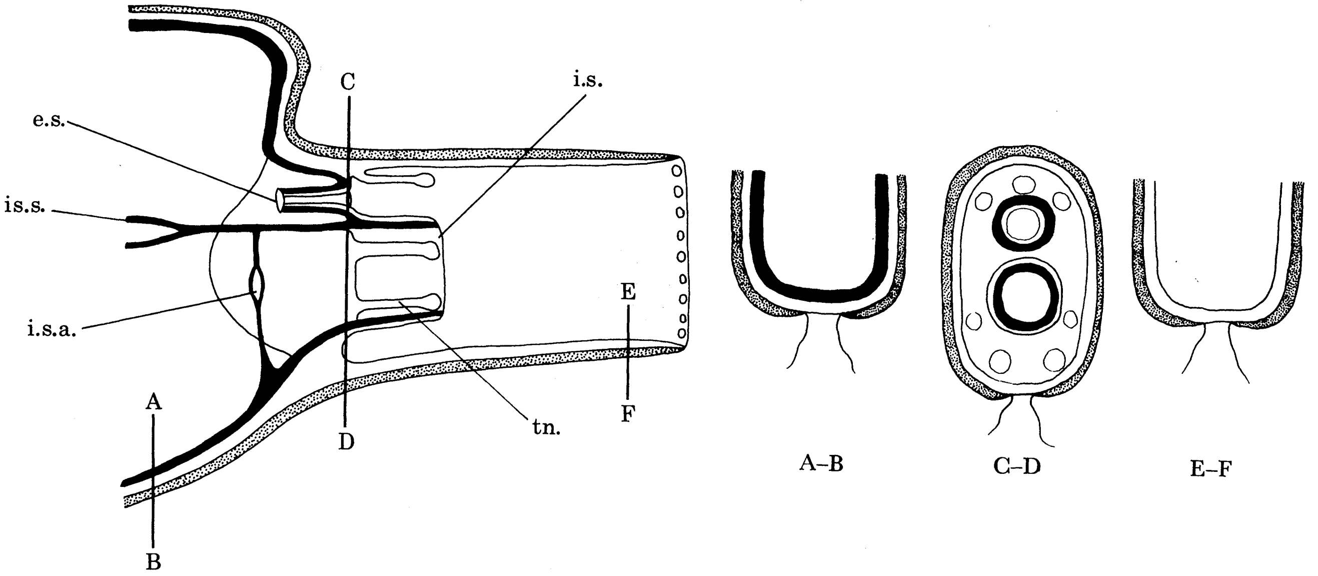


Figure 11. *Cuspidaria obesa.* Diagrammatic views of a sagittal section of the siphons and transverse sections at A–B, C–D and E–F. ■, Inner mantle fold; □, middle mantle fold; ▦, outer mantle fold.

The inhalant siphon has two layers of longitudinal muscle derived from the inner mantle fold, arranged in bundles within the circumference. The longitudinal muscles terminate short of the rim. There is a single ring of circular muscle around the rim, and at the base of the inhalant siphon there are two layers of circular muscle bounding the inner and outer surfaces. The exhalant siphon is narrow and contains only a single layer of circular and longitudinal muscle. There is no inner valve in the exhalant siphon, but it can be inverted, and contraction of the circular muscles can seal the aperture at the base of the siphon (figure 11).

In all species of *Cuspidaria* there are seven tentacles, four ventral around the inhalant siphon and three dorsal around the exhalant siphon. The tentacles are derived from the sensory middle mantle fold. There are two types within the family, most, like those of *C. obesa*, are club-ended, i.e. slightly domed at the tip, while a few, e.g. *C. cuspidata* and *C. rostrata* (Reid & Reid 1974), are 'frilled' with sucker-like discs at the tip (table 2).

The musculature of the tentacles is difficult to distinguish, but it is reported (Reid & Reid 1974) that they work on the principle of longitudinal muscles acting against haemocoelic pressure. Most species have an irregular central core of longitudinal muscle but in *C. obesa* peripheral longitudinal muscle is arranged in four strands, with four separate haemocoels between.†

In *C. obesa* the three dorsal tentacles are joined at their bases and to the exhalant siphon, forming a low peripheral wall from which the tentacles extend. This wall contains muscle fibres that cross the base of the tentacles. In *C. obesa* the margin of the wall is smooth, but in some species (e.g. *C.* (*Myonera*) *mexicana* (Knudsen 1970)), the web between the dorsal tentacles bears irregular projections. The bases of the inhalant tentacles do not form an obvious wall and never have projections. The tentacles extend to the level of the siphons. Studies on *C. cuspidata* indicate that the tentacles have a sensory perception function but do not assist in the physical capture of the prey and its transfer into the mantle cavity as is the case in the Verticordiidae (Allen & Turner 1974).

The rim of the siphonal sheath bears a row of papillae. It is in-turned in preserved specimens, but in live specimens it is out-turned, so that the papillae lie exposed and level with the surface of the substrate. Knudsen (1970), in figures, refers to them as 'inhalant' papillae and distinguishes several types, which he terms: bilobed; U-shaped; cylindrical; rectangular; and multiple. He considers them to be species-specific. *C. obesa* has approximately 10–20 equidistant U-shaped papillae on a slightly thickened rim. In other species the papillae are mostly U-shaped or rounded and we do not believe they can be used as specific characters.

Reproductive system

Few observations have been made on this system and there is disagreement as to whether species are hermaphrodite or unisexual. Pelseneer (1891) originally said that they were hermaphrodite, but later changed his mind and agreed with Grobben (1892) that cusparidiids are dioecious. Dall (1886, 1889*a*, *b*, 1890, 1903), though he wrote much on the family, barely touched on their anatomy. Yonge (1928), reported that they are hermaphrodite and Odhner (1960) gives a figure of *C. nybelini* supposedly with both testes and ovary. Knudsen (1970) assumes they are hermaphrodite although he was unable to demonstrate mature gonads in any of his specimens. The most recent reference by Bernard (1974), who supposedly examined numerous species of *Cuspidaria*, states that cuspidariids are hermaphrodite, and describes the gonad of *M. tillamookensis* and *C. parapodema.*

Examination of 50 species of *Cuspidaria* has shown that not one is hermaphrodite. The observations of Bernard (1974) on *C. parapodema* and Odhner (1960) on *C. nybelina* prevent us from making a categorical statement but it seems that the vast majority are dioecious (figure 2). It could be that some are protandric hermaphrodites, but we have no evidence of this. Species of *Poromya* and *Cetoconcha* are hermaphrodite and the anatomy of the reproductive system is very different from that of the Cuspidariidae, where in general paired ovaries or testes lie dorsal to the posterolateral and dorsal walls of the stomach. The gonads converge behind the stomach as a pair of ducts that open one each side into the supraseptal chamber close to the posterior adductor muscle.

In *C. obesa* the testes are atypical in that they differ in shape from the majority of other cuspidariids. Ockelmann (1958) suggested that this could distinguish *C. obesa* from similar species such as *C. glacialis* and *C. subtorta*. Here, termed type II, each testis consists of approximately 20

---

† Observations on living *C. cuspidata* confirm those of Reid & Reid (1974). The tentacles are capable of rapid withdrawal by contraction of the longitudinal muscles followed by slower extension by relaxation of the muscles and movement of fluid into the sinuses. The tentacles have sensory receptors, and both *C. rostrata* and *C. cuspidata* with 'frilled' tentacles have groups of peripheral bristles.

irregular, deeply divided, angular to oval lobes over the dorsal and posterior surface of the stomach. The ducts pass between the bifid posterior pedal retractor muscle and open into the supraseptal chamber.

In *C. obesa* the ovaries, like the testes, differ from those of most other cuspidariids. Each bears several short projecting lobes bound by a thin transparent wall through which the eggs are clearly visible. There are 20–30 eggs per lobe (figure 2).

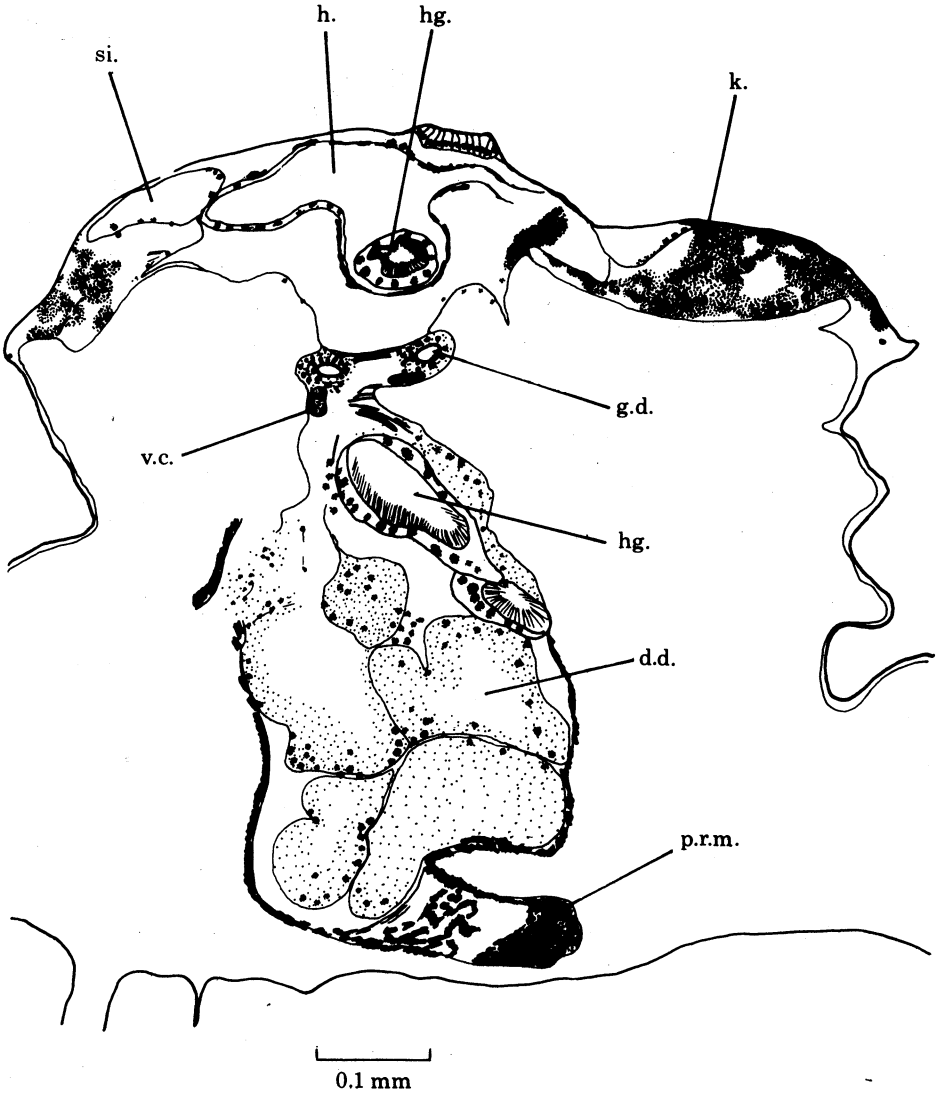


FIGURE 12. *Cuspidaria obesa*. Transverse section through the posterior part of the body to show the heart, sinuses and kidney.

Heart and sinuses

In *C. obesa*, as in all septibranchs, the heart is mid-dorsal and connects with a sinus system that ramifies through the mantle, septum and siphons. This system is best observed in larger animals such as *Poromya* and *Cetoconcha*. Reid & Reid (1974) give a figure showing sinus tissue in *Cuspidaria rostrata* identical to that seen in *Poromya*, *Cetoconcha* and the cuspidariids described here.

The heart lies above the posterior end of the stomach between the paired gonad. Typically, it consists of a narrow tubular muscular-walled ventricle into which a pair of thin-walled auricles discharge laterally, the whole being enclosed by a thin-walled pericardium (figure 12). The gut passes through the ventricle. The sinuses open into the auricles and extend over the gonads and kidneys and within the mantle, septum and siphons. They are divided by numerous membranes and penetrate between the muscle blocks of the siphonal retractors and the muscle blocks of the dorsal side of the septum into the septum. The septal sinuses communicate with a pair of large rostral sinuses, one along each edge of the intersiphonal septum, which in turn connect with three main siphonal sinuses and with interconnecting smaller sinuses that pass into the tentacles (Reid & Reid 1974). The sinuses of the exhalant siphon are separated from those of the intersiphonal septum, the rostrum and the inhalant siphon by connective tissue, this allowing independent movement of the siphons.

Kidney

The kidneys consist of a pair of thin-walled lobulate sacs situated dorsally between the posterior wall of the gonad and the posterior adductor muscle. They lie ventral to the hindgut but above the posterior pedal retractor, and thus are wedge-shaped. The sacs are joined together over a small area below the gut posterior to the gonad. The kidneys extend laterally and dorsally on either side of the hindgut and beneath the sinuses within the mantle close to the septum. The cells of the kidney wall are small and irregular, and appear to secrete particulate material into the lumen. The kidney empties into the posterior supraseptal cavity by two ducts, one on either side of the hindgut, close to where the latter passes between the insertions of the posterior septal muscles.

Lacuna system

Allen & Turner (1974) described this system in the Verticordiidae as large cells associated with the kidneys, gonads, and sinuses that are either empty or filled with darkly staining, homogenous material. These cells also occur in the families Cuspidariidae and Poromyidae, but there is still little indication of their function. Their extent and relative position in the different genera provides some further evidence about the evolution of the septum.

In the genus *Cuspidaria* the number of lacunal cells is greatly reduced in comparison with the genera *Halonympha*, *Protocuspidaria*, *Poromya*, *Cetoconcha* and *Verticordia* and it has not been possible to demonstrate them in every species. When visible, they are restricted to small groups in connective tissue surrounding the visceral ganglia, anus and dorsal side of the base of the exhalant siphon. In *C. obesa* only one or two cells are discernable. Here we have found only cells filled with densely staining material and it is possible that in *Verticordia* small sinuses were mistaken for empty lacunal cells.

Nervous system

The nervous system is typical of that found in all cuspidariids, which have a septum pierced by four or five pairs of pores.

There are three pairs of ganglia, the cerebropleural, pedal and visceral. We find no separate siphonal ganglion such as is reported by Reid & Reid (1974).

The cerebropleural ganglia are discrete elongate bodies lying one on either side of the buccal funnel, slightly dorsal to the margin of the mouth, and are connected to one another by a commissure, which passes around the front of the buccal funnel. Seven nerves connect with each ganglion. The three anterior nerves are:

(i) a pallial nerve, which runs forward into the mantle edge, and along this, to join the visceral ganglion posteriorly;

(ii) a palp nerve, which runs obliquely forward into the anterior palp, where it gives off a long branch that doubles back to supply the posterior palp;

(iii) an anterior adductor nerve (the most anterior of the three), which passes to the muscle. The four posterior nerves are:

(i) a visceral connective, which passes from the cerebropleural ganglion beneath the epithelium covering the gonad and digestive gland, to the visceral ganglion, behind the stomach the left and right connectives come together in the midline;

(ii) a septal nerve, which originates in the visceral ganglion and passes anteriorly beneath the dorsal surface of the outer longitudinal muscle of the septum to the cerebral ganglion;

(iii) a pedal connective, which passes directly from the cerebropleural to the pedal ganglion;

(iv) an inner septal nerve, which passes from the cerebropleural ganglion to the pedal ganglion via the inner longitudinal muscle of the septum.

The visceral ganglia are situated beneath, and slightly in front of, the posterior adductor muscle, relatively close to the anus and the base of the exhalant siphon. Pelseneer (1888, 1891, 1911), Grobben (1892), and Yonge (1928) report a pair of additional 'siphonal' ganglia. These take the form of two large nerves, which pass from the visceral ganglia to the siphons. In *C. obesa* large nerve trunks supply the intersiphonal septum, the siphons and the tentacles. Reid & Reid (1974) reported a visceral ganglion at the entrance of the exhalant siphon, and a 'siphonal' ganglion at the base of the tentacles. We confirm that in contracted specimens the visceral ganglia are situated close to the entrance of the exhalant siphon and we believe that when the siphons extend it is the visceral ganglia that are carried posteriorly for a short distance to the position identified by Reid & Reid (1974) as being occupied by the 'siphonal' ganglion.

Pelseneer (1891) and Grobben (1892) described the nervous systems of *C. rostrata* and *C. cuspidata* respectively, but although they acknowledge that the septum is innervated by a nerve of visceral origin, they did not trace this nerve forward to the cerebropleural ganglion, nor did they see the inner septal nerve. However, Plate (1897), who examined *C. obesa*, describes the septal innervation as wholly cerebral. He saw both septal connectives with the cerebropleural ganglion, but considered the outer septal nerve to be a branch of the anterior end of the visceral nerve. Bernard (1974) also reports that in the Cuspidariidae and Poromyidae the septum is cerebrally innervated. We believe that the opposite is predominantly true. Only the inner septal nerve, which in *C. obesa* passes to the pedal ganglion, originates in the cerebropleural ganglion. As will be shown in *Poromya* and *Cetoconcha*, the main outer septal nerve originates in the visceral ganglion just as does the ctenidial nerve in the Verticordiidae.

The nervous system in *C. obesa* is thus similar to that in most bivalves in the arrangement of the ganglia. There is complete separation of visceral and septal nerves. As in the gills of other bivalves septal innervation is predominantly via a nerve from the visceral ganglion, and there is little doubt that the septal nerve is homologous with the ctenidial nerve. As for the inner longitudinal septal muscle, the inner septal nerve is probably not ctenidial in origin (figure 96).

Cuspidaria parva Verrill & Bush, 1898 (figures 13–18)

1898	*Cuspidaria parva*	Verrill & Bush (p. 801, pl. 74 fig. 9, pl. 77 fig. 7)
1934	*Cuspidaria parva*	Johnson (p. 33)
1962	*Cuspidaria parva*	Clarke (p. 72)

Material

ship	date	stn	latitude	longitude	depth/m	number
Atlantis II	21. 08. 64	62	39° 26.0′ N	70° 33.0′ W	2496	1
	25. 08. 64	73	39° 46.5′ N	70° 43.3′ W	1470	57
Chain	06. 07. 65	87	39° 48.7′ N	70° 40.8′ W	1102	121
	04. 05. 66	103	39° 43.6′ N	70° 37.4′ W	2022	95
	05. 05. 66	105b	39° 56.6′ N	71° 00.6′ W	530	51
Atlantis II	08. 12. 66	131	39° 38.5′ N	70° 36.5′ W	2178	20
	05. 02. 67	142	10° 30.0′ N	17° 51.5′ W	1624–1796	40
	05. 02. 67	144	10° 36.0′ N	17° 49.0′ W	2051–2357	4
	06. 02. 67	145	10° 36.0′ N	17° 49.0′ W	2185	1
	14. 02. 67	156	00° 46.0′ S	29° 28.0′ W	3459	2
	20. 02. 67	167	10° 58.0′ S	34° 17.0′ W	943–1007	4
Sarsia	19. 07. 67	56s	43° 43.0′ N	03° 47.8′ W	641	1
	25. 07. 67	65s	46° 15.0′ N	04° 50.0′ W	1922	2
Discovery	16. 03. 68	6701	27° 45.2′ N	14° 13.0′ W	1934	1
	18. 03. 68	6709	27° 29.8′ N	15° 20.1′ W	2351	4
Atlantis II	23. 05. 68	201	09° 25.0′ S	11° 35.0′ E	1964–2031	16
	26. 03. 71	259	37° 13.3′ S	52° 45.0′ E	3305–3317	1
Challenger	05. 06. 73	4	56° 52.0′ N	10° 01.0′ W	1993	numerous
La Perle						
(Biogas I)	09. 08. 73	DS13	47° 33.7′ N	08° 39.9′ W	2165	3
(Polygas)	21. 10. 72	DS15	47° 35.2′ N	08° 40.1′ W	2246	25
	21. 10. 72	DS16	47° 36.1′ N	08° 40.5′ W	2325	105
	22. 10. 72	DS17	47° 32.0′ N	08° 45.5′ W	2103	13
	24. 10. 72	DS20	47° 33.0′ N	09° 03.5′ W	4226	3
	24. 10. 72	DS21	47° 31.5′ N	09° 40.7′ W	4190	12
	01. 11. 72	DS25	44° 08.2′ N	04° 15.7′ W	2096	5
	01. 11. 72	DS26	44° 08.2′ N	04° 15.0′ W	2076	5
J. Charcot						
(Biogas II)	19. 04. 73	DS32	47° 32.2′ N	08° 05.3′ W	2138	11
	20. 04. 73	DS33	47° 39.7′ N	08° 05.5′ W	2338	2
(Biogas III)	24. 08. 73	DS35	47° 34.4′ N	08° 40.7′ W	2226	9
	24. 08. 73	DS37	47° 31.8′ N	08° 34.6′ W	2110	4
	01. 09. 73	DS49	44° 05.9′ N	04° 15.6′ W	1845	1
	01. 09. 73	DS50	44° 08.9′ N	04° 15.9′ W	2124	2
(Biogas IV)	18. 02. 74	DS51	44° 11.3′ N	04° 15.4′ W	2430	21
	18. 02. 74	DS52	44° 06.3′ N	04° 22.4′ W	2006	33
	19. 02. 74	DS53	44° 30.4′ N	04° 56.3′ W	4425	1
	21. 02. 74	DS54	46° 31.1′ N	10° 29.2′ W	4659	1
	23. 02. 74	DS57	47° 30.8′ N	09° 07.6′ W	2906	3
	23. 02. 74	DS58	47° 34.1′ N	09° 08.2′ W	2775	2
	24. 02. 74	DS60	49° 26.8′ N	09° 07.2′ W	3742	2
	25. 02. 74	DS61	47° 34.7′ N	08° 38.8′ W	2250	14
	26. 02. 74	DS62	47° 32.8′ N	08° 40.0′ W	2175	8
	26. 02. 74	DS63	47° 32.8′ N	08° 35.0′ W	2126	31
(Biogas V)	15. 06. 74	DS65	47° 36.1′ N	08° 40.5′ W	2360	58
	17. 06. 74	DS67	47° 31.0′ N	09° 35.0′ W	4150	3
(Biogas IV)	25. 02. 74	CP01	47° 34.6′ N	08° 34.0′ W	2119	5
(Biogas VI)	20. 10. 74	CP09	47° 33.0′ N	08° 44.1′ W	2171	23
	23. 10. 74	CP13	47° 34.4′ N	08° 38.0′ W	4134	1
	31. 10. 74	CP23	44° 04.6′ N	04° 21.4′ W	1980	2
(Biogas IV)	24. 02. 74	CV38	47° 30.9′ N	08° 59.5′ W	2695	3
	31. 10. 74	CP24	44° 08.1′ N	04° 16.2′ W	1995	1
(Biogas VI)	20. 10. 74	DS71	47° 34.3′ N	08° 33.8′ W	2194	5
	20. 10. 74	DS73	47° 32.1′ N	09° 06.0′ W	2805	3
	21. 10. 74	DS74	47° 33.0′ N	09° 07.8′ W	2777	27
(Biogas VI)	24. 10. 74	DS77	47° 31.8′ N	09° 34.6′ W	4240	7
	31. 10. 74	DS86	44° 04.8′ N	04° 18.7′ W	1950	58
	01. 11. 74	DS87	44° 05.2′ N	04° 19.4′ W	1913	42
	01. 11. 74	DS88	44° 05.2′ N	04° 15.7′ W	1894	1
Thalassa	22. 10. 73	Z397	47° 33.8′ N	07° 05.7′ W	850	1
	22. 10. 73	Z400	47° 33.4′ N	07° 19.0′ W	1175	1
	27. 10. 73	Z443	48° 56.0′ N	11° 02.0′ W	660	1
	27. 10. 73	Z449	48° 41.3′ N	10° 33.8′ W	730	4

Reference material

U.S.N.M. no. 35569 *Cuspidaria parva* Verrill & Bush, stn 2115, Hatteras.

U.S.N.M. no. 78483 *Cuspidaria parva* Verrill & Bush, stn 2710, SE Nantucket.

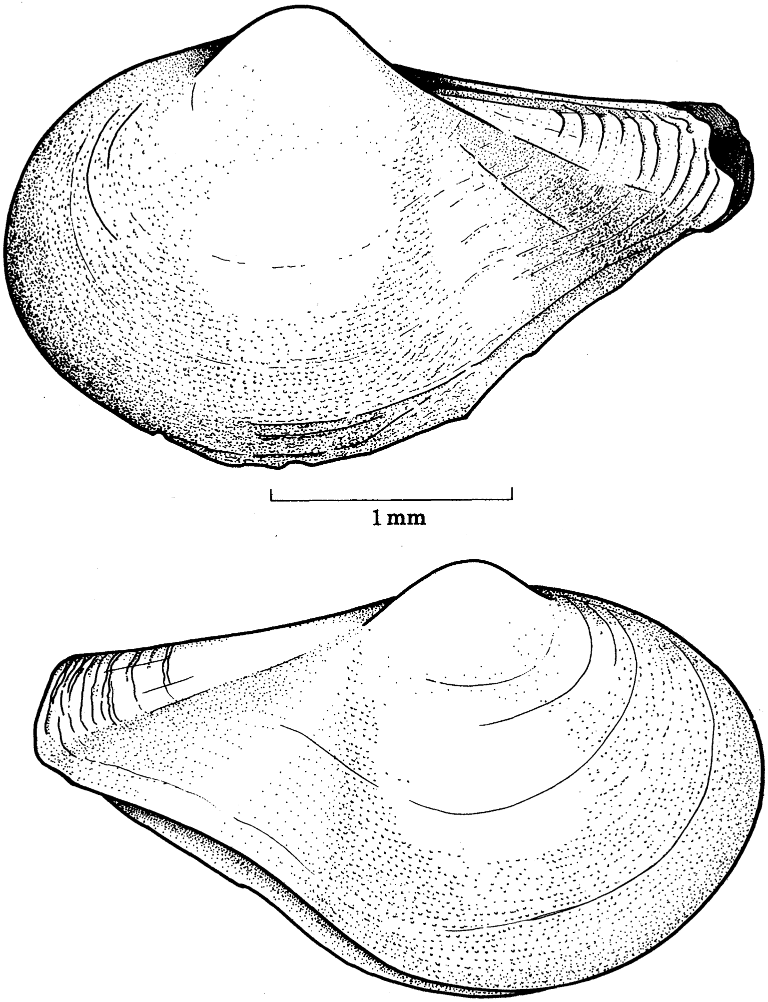


FIGURE 13. *Cuspidaria parva*. Lateral view of the shell from the right and left sides.

Distribution

Previous records. North America Basin, Cape Cod and south east of Nantucket.

New records. Bermuda transect (North America), west of Scotland, Biscay, Canaries, Atlantic adjacent to São Paulo and Ascension Islands, west Africa off Senegal, off east coast of Uruguay. Depth range: 257–3317 m.

Description

Verrill & Bush (1898) described the shell characters of *C. parva*; subsequently it has been merely mentioned in species lists and no account of its anatomy has been given.

As Verrill & Bush (1898) state, the most important distinguishing feature of this species is that it is inequivalve (figure 13). The ventral margin of the left valve at the base of the rostrum is less sinuous than that of the right and thus overlaps it. In addition the right dorsal valve overlaps the left along the posterior dorsal margin. The dorsal margin is straight or slightly concave, the anterior dorsal margin being evenly rounded and not produced as it is in *C. obesa*; the rostrum is relatively long, the distal margins being parallel. There is considerable variation in outline with age and size (figure 14). The shell surface is fairly smooth, with only faint concentric growth lines. The slight granular appearance is due to numerous tiny pits in the shell surface. An oblique rostral ridge runs from umbo to posterior ventral margin. Here the sculpture is more coarse and less regular. Two or three faint and incomplete longitudinal lines may be present extending towards the umbo from the distal end of the rostrum.

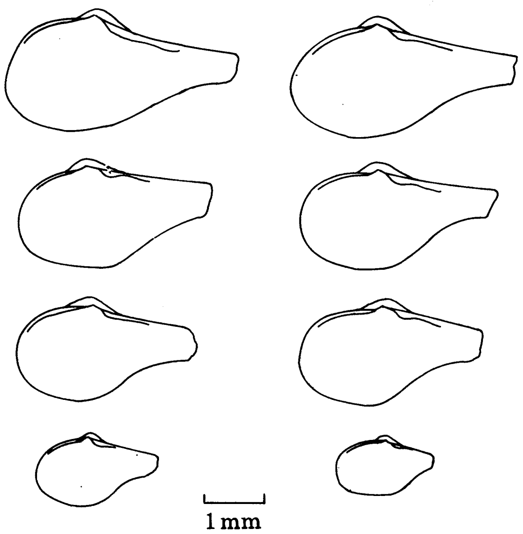


Figure 14. *Cuspidaria parva*. Variations in the outline of the shell.

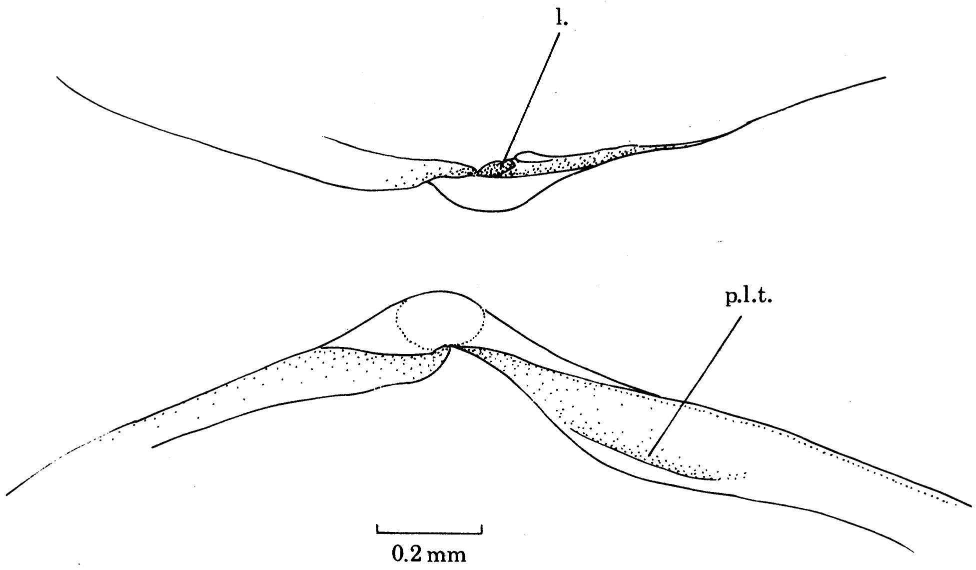


Figure 15. *Cuspidaria parva*. Lateral view of the hinges of the right and left valves.

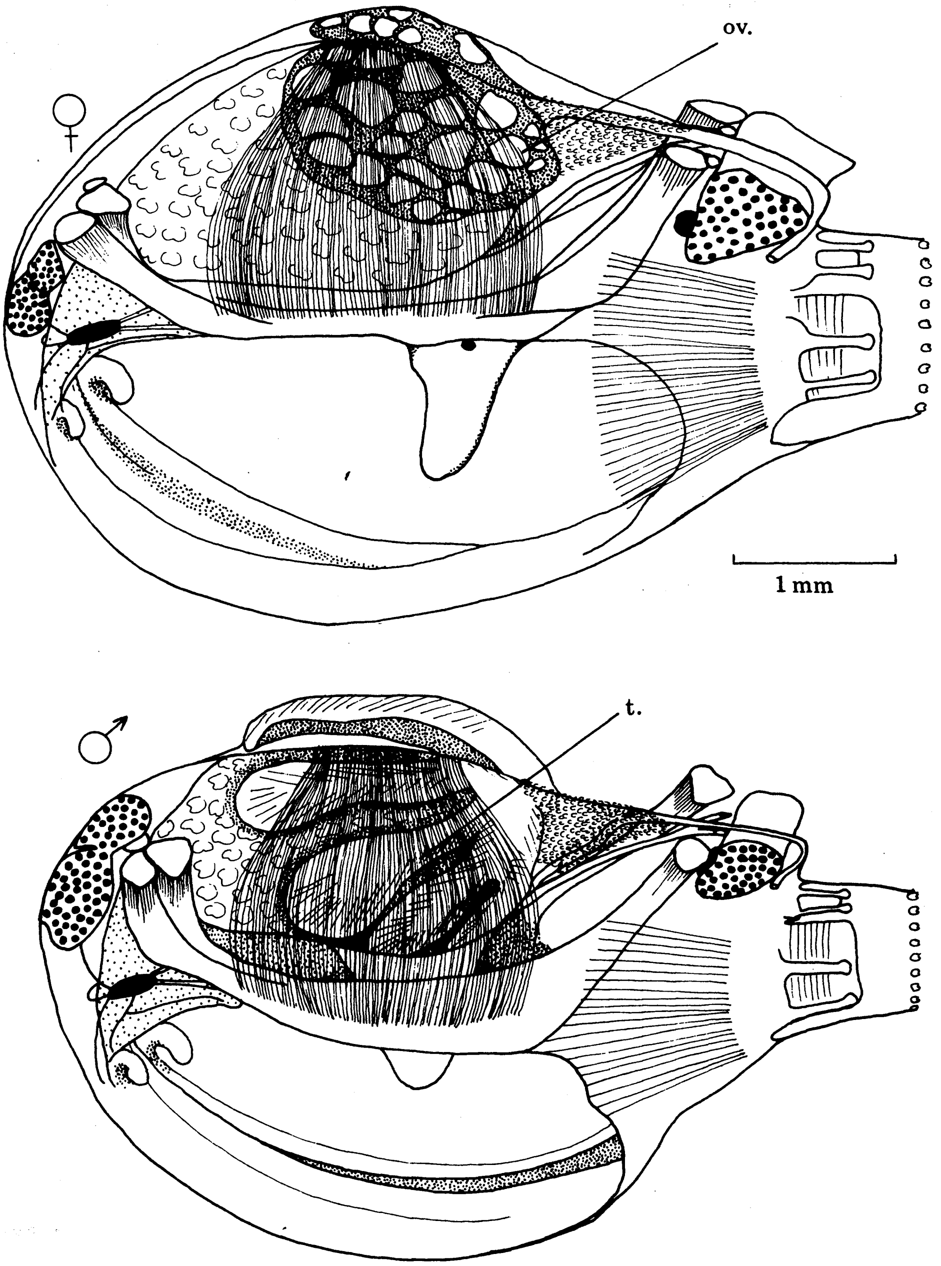


Figure 16. *Cuspidaria parva*. The anatomy of male and female specimens as seen from the left side (cf. figure 2).

This species may be confused with other North Atlantic cuspidariids such as *C. obesa* Lovén and *C. glacialis* Sars.

Maximum shell measurements recorded are: length 3.5 mm; height 2.1 mm; width 1.8 mm. Our largest specimen is smaller than the specimen described by Verrill & Bush (1898), which is 4.5 mm long. Two samples taken in successive years at different, but close, stations on the Woods Hole to Bermuda traverse are infected with an as yet unidentified marine ascarid nematode that lies curled on top of the viscera, obliterating the gonad; 4 % of a sample of 104 individuals from station 87 taken on 6. 7. 65, and 56% of a sample of 78 individuals from station 103 on 4. 5. 66 were infected.

Much of the anatomy is similar to that of *C. obesa* (figure 16). However, mention should be made of some points of difference. In contrast to *C. obesa*, *C. parva* has a 'thin' septum, though the constituent septal muscles are identical. In *C. parva* the lips of the pores only extend to half the thickness of the septum (figure 17).

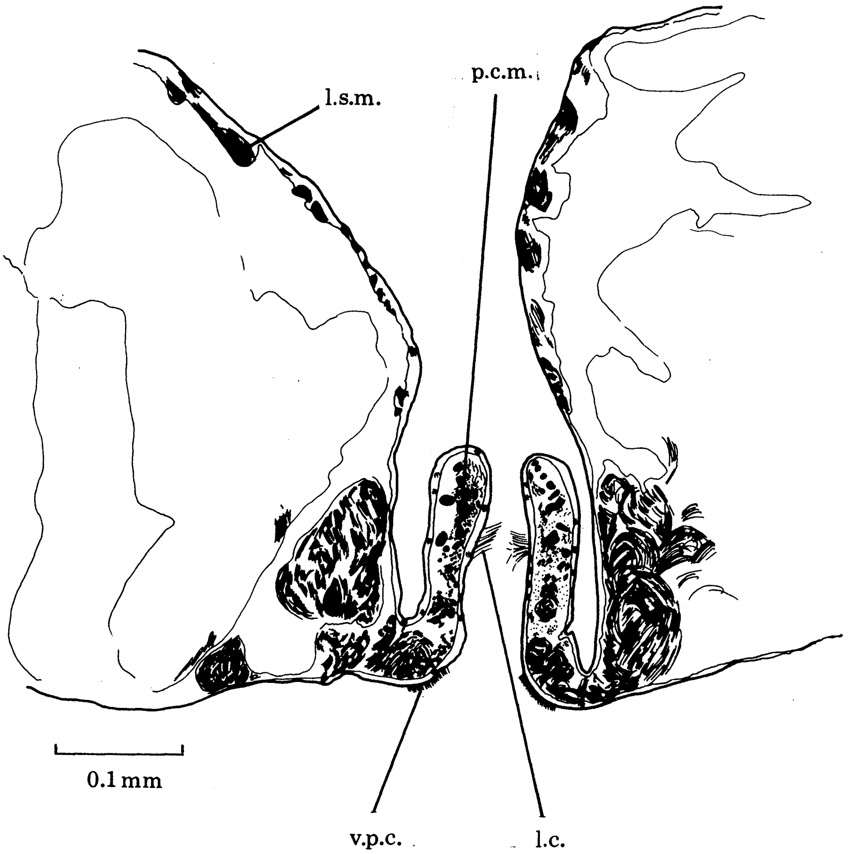


FIGURE 17. *Cuspidaria parva*. Longitudinal section through a septal pore.

The testis of *C. parva* is more typical of cuspidariids than that of *C. obesa* and consists of 4–8 finger-like projections which extend forward around the stomach (here designated as type I). The significance of this difference is not evident; the internal arrangement of a central mass of spermatogonia and ripe rod-shaped spermatozoa radiating to the outer surface is essentially the same in both species. The ovaries lie in a similar position to the testis and are simple thin-walled compartmented sacs, not externally lobed. The eggs proliferate from the ovary wall as stalked oocytes which are then released into the lumen. The eggs are not all at the same stage of development, there being approximately 200 in a specimen measuring 3.4 mm × 1.8 mm. The largest eggs measure approximately 89 μm × 78 μm in preserved specimens.

The lacuna system is particularly distinct and consists of groups of large densely staining cells (red in Azan triple stain), close to the visceral ganglia, with a further scatter close to the anus and in the walls of the supraseptal cavity (figure 18).

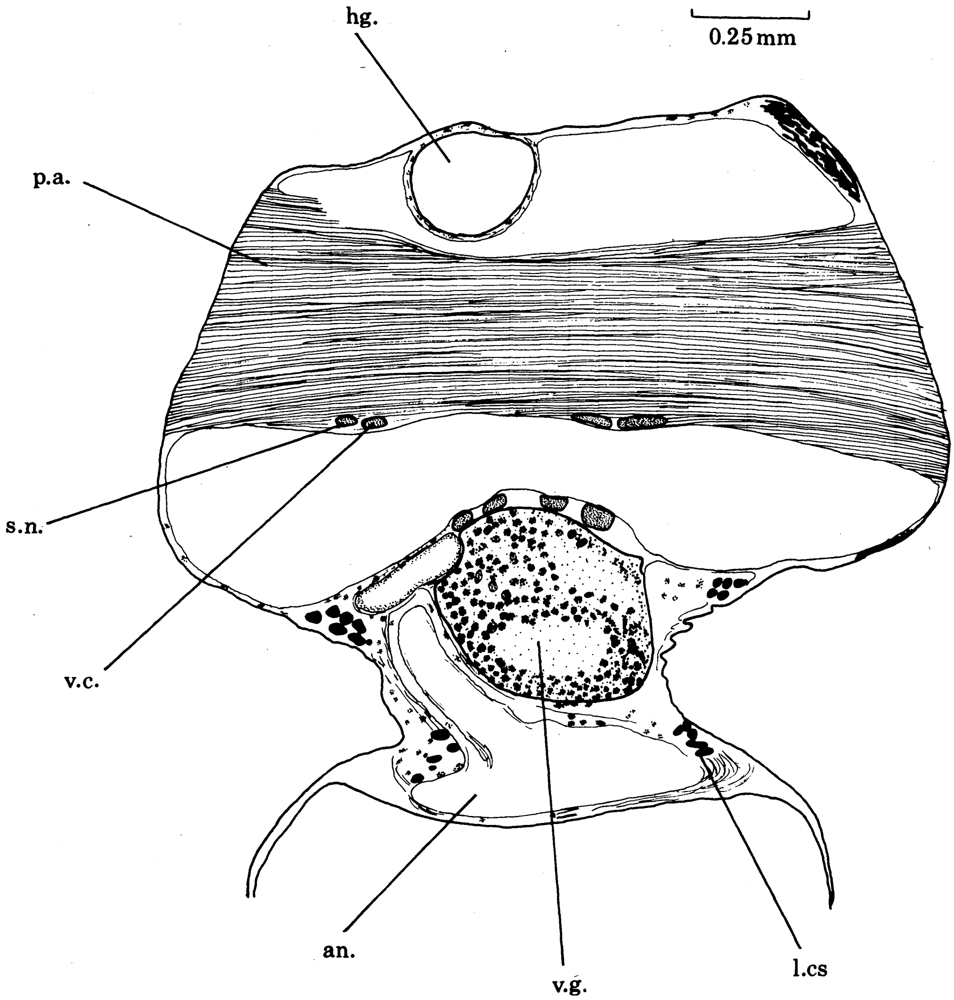


FIGURE 18. *Cuspidaria parva*. Transverse section of the body in the region of the posterior adductor, to show the position of the lacunal cells.

Cuspidaria cuspidata (Olivi, 1792)

1792	*Tellina cuspidata*	Olivi (p. 101, pl. iv, fig. 3)
1826	*Erycina cuspidata*	Risso (p. 366)
1836	*Corbula cuspidata*	Philippi (p. 17, pl. I, fig. 19)
1840	*Cuspidaria cuspidata*	Nardo (p. 175)
1844	*Thracia brevirostrata*	Brown (p. 110)
1846	*Neaera brevirostris*	Lovén (p. 48)
1848	*Corbula cuspidata*	Forbes & Hanley (p. 195)
1858	*Neaera cuspidata*	Adams & Adams (p. 369)
1859	*Neaera cuspidata*	Sowerby (pl. 1, fig. 27)
1865	*Neaera cuspidata*	Jeffreys (p. 53)
1869	*Neaera cuspidata*	Jeffreys (p. 191, pl. xlix, fig. 5)
1875	*Neaera cuspidata*	Mörch (p. 131)
1878	*Neaera cuspidata*	Sars (p. 86)
1881	*Neaera cuspidata*	Jeffreys (p. 938)
1885	*Neaera cuspidata*	Smith (p. 35)
1887	*Cuspidaria cuspidata*	Fischer (fig. 879)
1891	*Cuspidaria cuspidata*	Dautzenberg (p. 612)
1892	*Cuspidaria cuspidata*	Grobben (p. 101)
1898	*Cuspidaria cuspidata*	Locard (p. 173)

1899	*Cuspidaria cuspidata*	Locard (p. 125)
1911	*Cuspidaria cuspidata*	Pelseneer (p. 80)
1927	*Cuspidaria cuspidata*	Dautzenberg (p. 335)
1928	*Cuspidaria cuspidata*	Yonge (p. 221)
1935	*Cuspidaria cuspidata*	Thiele (p. 947)
1962	*Cuspidaria cuspidata*	Clarke (p. 71)
1969	*Cuspidaria cuspidata*	Moore (p. N854)
1969	*Cuspidaria cuspidata*	Nordsieck (p. 174)

For other records see Dautzenberg (1927).

Distribution

Eastern Atlantic, Norwegian Sea to south of Equator. Depth range 20–1850 m.

Because it has a wide distribution in shallow European waters this is probably the best known species of the genus *Cuspidaria*. Grobben (1892) gave the first overall account of its biology, and since then it has been mentioned many times in the literature (see above). Specimens from off the Northumberland coast were used to observe the functioning of the septum.

Description

C. cuspidata differs little from *C. obesa* except that there are five, and not four, pairs of pores in the septum, the tentacles are frilled, and the palps are of type II (table 2, figure 7).

Cuspidaria jeffreysi (Dall, 1881) (figures 19, 20)

1881	*Neaera jeffreysi*	Dall (p. 111)
1886	*Cuspidaria jeffreysi*	Dall (p. 295, pl. 3, fig. 2)
1962	*Cuspidaria jeffreysi*	Clarke (p. 72)

Material

ship	date	stn	latitude	longitude	depth/m	number
Chain	04.05.66	103	39° 43.6′ N	70° 37.4′ W	2022	1
Discovery	15.03.68	6696	28° 06.0′ N	13° 28.0′ W	1780	1
Walda		DS10	18° 40.0′ S	10° 56.3′ W	1432	1

Distribution

Previous records. Gulf of Mexico and Caribbean Basin.

New records. North America Basin, Canaries Basin and Angola Basin. Depth range: 849–2022 m.

Description

The type was concisely described and figured by Dall (1881, 1886) and the present specimens are similar except that the rostrum is slightly shorter than that figured by Dall (1886) (figure 19). The species is distinctive; the curvature of the posterior dorsal margin of the shell and hinge line is shallow in lateral view as is the sinuation ventral to the rostrum. The anterior shell margin is smoothly rounded and the anterior dorsal margin immediately anterior to the umbo is characteristically raised (figure 19). The anterior half of the shell is swollen and large umbones are inclined slightly anteriorly. The left valve is slightly larger than the right, the outer surface of the shell, except for concentric lines of growth, is without sculpture. There is a moderately developed triangular posterior lateral tooth in the right valve.

The anatomy is similar to *C. obesa* and needs little additional description.

C. jeffreysi is unusual in that there is a well developed ridge of gland cells beneath the inner

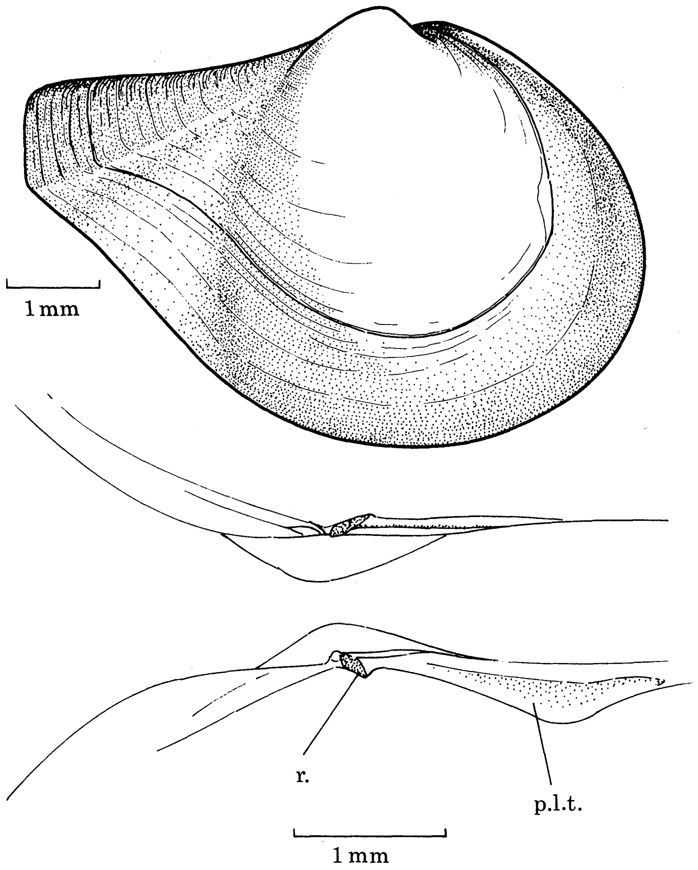


FIGURE 19. *Cuspidaria jeffreysi.* Lateral view of shell from the right side and lateral view of the hinge of both valves.

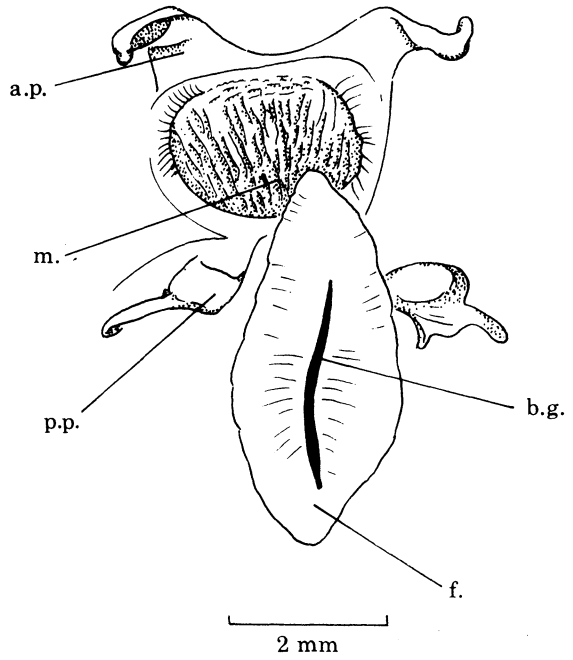


FIGURE 20. *Cuspidaria jeffreysi.* Oral view to show the form and position of the palps.

muscular lobe of the ventral edge of the mantle. The gland cells are of two types, similar to those of other bivalves (Allen 1968). Other species of *Cuspidaria* have few gland cells in this position and it must be assumed that in *C. jeffreysi* it is related to the quantity of sediment entering the mantle cavity.

The siphonal tentacles are 'frilled'. Sections show a central strand of longitudinal muscle and closely packed epithelial cells lining the distal end. The siphonal sheath bears a row of bifurcate papillae. The septum is thick and muscular with four pairs of pores. The paired lateral septal muscles are particularly well developed. The posterior palps are unusually long with a distal horned extension while the anterior palps are short and stumpy (figure 20). The gonads are not branched.

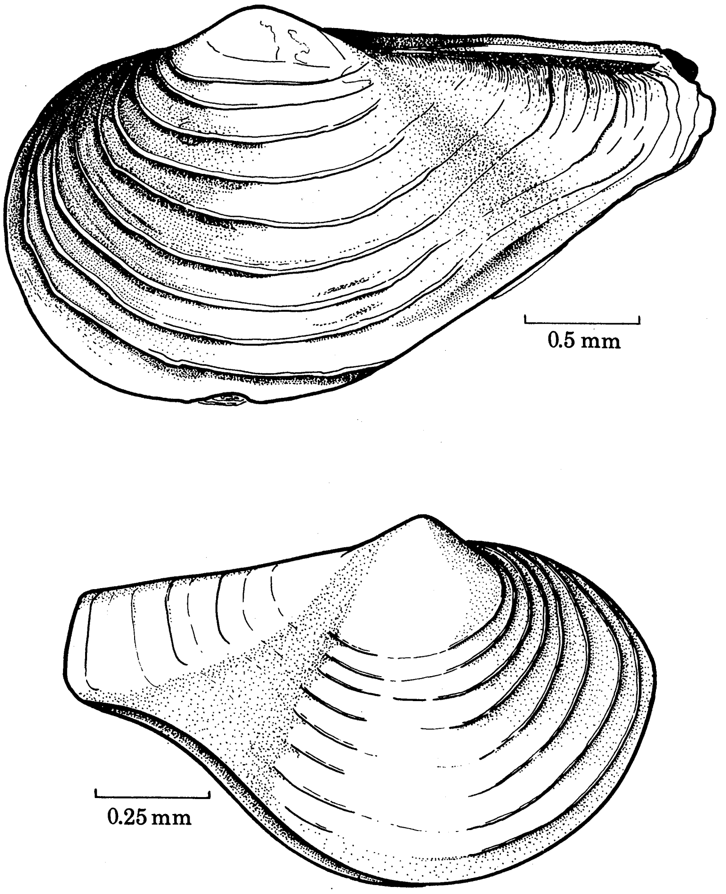


FIGURE 21. *Cuspidaria atlantica*. Lateral views to show variation in the form of the rostrum.

Cuspidaria atlantica new species (figures 21–23)

Holotype: Atlantis II, station 189, 23° 0.0′ S 12° 45.0′ E in 1007–1014 m (Museum of Comparative Zoology, Harvard).

Material

ship	date	stn	latitude	longitude	depth/m	number
Chain	05. 05. 66	105	39° 56.6′ N	71° 03.6′ W	530	1
Atlantis II	16. 05. 68	189	23° 00.0′ S	12° 45.0′ E	1007–1014	23
	17. 05. 68	191	23° 05.0′ S	12° 31.5′ E	1546–1559	10
	17. 05. 68	192	23° 02.0′ S	12° 19.0′ E	2117–2154	1
Walda		DS10	18° 40.0′ S	10° 56.3′ E	1432	3
Discovery	15. 03. 68	6696A	28° 06.0′ N	13° 28.0′ W	1780	1

Distribution

North America Basin, Angola Basin, Canaries Basin. Depth range: 530–2154 m.

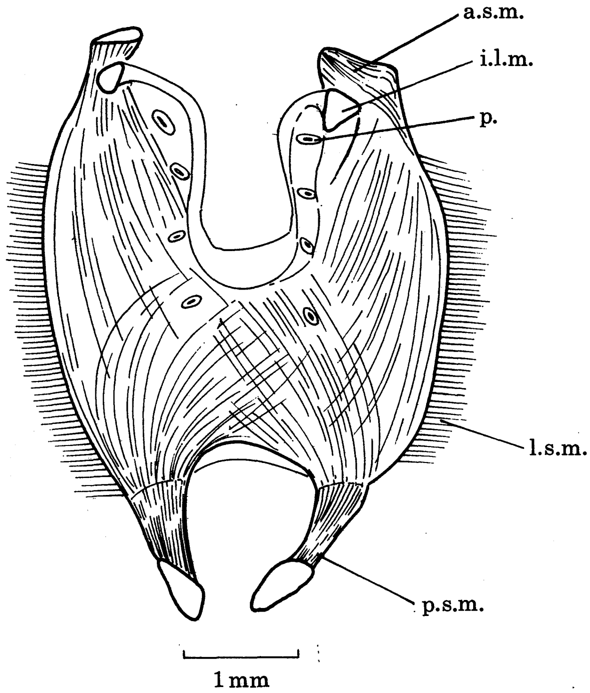


FIGURE 22. *Cuspidaria atlantica*. Dorsal view of the septum.

Description

Shell small, fragile, largest specimen 3.1 mm in length; moderately inflated, rostrum moderately long and tapering, inequivalve, ventral margin of left valve overlapping right; umbo moderately large; posterior dorsal margin almost straight, anterior margin evenly rounded, merging evenly with anterior ventral margin, posterior ventral margin widely and shallowly sinuate, posterior margin of rostrum rounded; shell, white, ornamented with up to 11 strong ledge-like and widely separate concentric lamellae, successively more distinct and apart from four on the umbonal region, more or less evenly spaced, concentric lamellae at base of rostrum less pronounced and merge with finer growth lines at an oblique ventral rostral ridge; two faint striae dorsal to and parallel to ventral rostral ridge, rounded dorsal oblique ridge close to the posterior dorsal shell margin; hinge, right valve with strong triangular posterior lateral tooth, slightly reflected at outer edge, small central resilifer below beak, oblique and encroaches anterior outer edge of tooth, left valve without teeth but resilifer encroaches anterior limit of the thickened posterior dorsal margin of valve.

The present specimens (figure 21) correspond with specimens U.S.N.M. no. 151906 *M. lamellifera* Dall. These latter do not match *Myonera lamellifera* Dall, 1881 U.S.N.M. no. 448492.

There is a single row of bifurcate papillae on the siphonal sheath and the tentacles are 'club headed'. The septum is thin but with the constituent muscles clearly defined. The first of four pairs of pores penetrates a thick membrane between the inner longitudinal muscle and the main anterior septal muscle (figure 22). The lateral septal muscles are continuous along the outer edges of the septum. The anterior palps are horn-shaped and the posterior are reduced to bulges of the thickened lip of the mouth (type I) (figure 23). Some specimens were mature, the ovary occupying much of the body space and the ova of the most mature specimen have a maximum length of 0.09 mm.

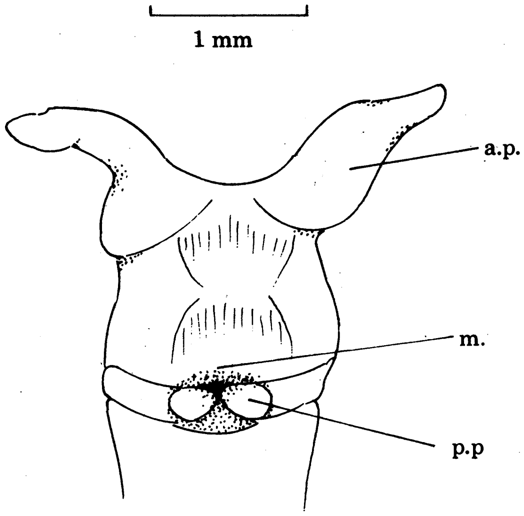


FIGURE 23. *Cuspidaria atlantica*. Oral view to show form and position of the palps.

Cuspidaria barnardi Knudsen, 1970 (figure 24)

1970 *Cuspidaria barnardi* Knudsen (pp. 139–141, figs 96 and 97)

Material

ship	date	stn	latitude	longitude	depth/m	number
Atlantis II	18. 12. 66	131	39° 31.5′ N	70° 36.5′ W	2178	2
	07. 02. 67	148	10° 37.0′ N	18° 14.0′ W	3814–3828	1
	14. 03. 71	245	36° 55.0′ S	53° 01.4′ W	2707	1

Distribution

Previous records. Cape Basin.

New records. North America Basin, Argentine Basin and Sierra Leone Basin. Depth range: 2707–3828 m.

Description

The original description of the shell is detailed (Knudsen 1970) and requires little addition except that the shell is equivalve and that there is a well developed and acute posterior lateral tooth on the right valve.

The anatomy is briefly described by Knudsen (1970). The septum is thick with four pairs of pores present. There are two pairs of lateral septal muscles, the anterior and outer longitudinal septal muscles are separate and relatively narrow (figure 24). The anterior palps are small flaps and the posterior palps are flattened posteriorly directed extensions of the rim of the lip. The siphonal papillae are bifurcate.

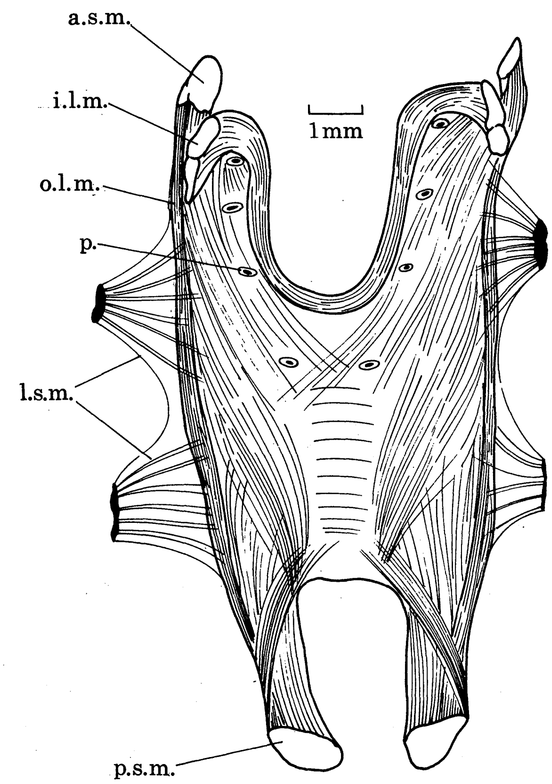


FIGURE 24. *Cuspidaria barnardi*. Dorsal view of the septum.

Cuspidaria undata (Verrill, 1884)

1884	*Neaera undata*	Verrill (p. 223)
1885	*Neaera undata*	Verrill (p. 57)
1886	*Myonera undata*	Dall (p. 304)
1886	*Cuspidaria lucifuga*	Fischer (p. 1155)
1889	*Myonera undata*	Dall (p. 68)
1898	*Cuspidaria undata*	Verrill & Bush (p. 789; p. 72, fig. 1, pl. 78, figs 3 and 4)
1898	*Cuspidaria lucifuga*	Locard (p. 184, pl. 7, figs 46–51)
1907	*Cuspidaria brucei*	Melville & Standen (p. 122, pl. 1, fig. 19)
1960	*Cuspidaria nybelini*	Odhner (p. 381, pl. 1, figs 6 and 7, text figs 7–10)
1962	*Cuspidaria brucei*	Clarke (p. 71)
1962	*Cuspidaria lucifuga*	Clarke (p. 72)
1962	*Myonera undata*	Clarke (p. 72)
1970	*Myonera undata*	Knudsen (p. 136, figs 93 and 94)

Material

ship	date	stn	latitude	longitude	depth/m	number
Chain	04. 07. 65	84	36° 24.4′ N	67° 56.0′ W	4749	1
J. Charcot	25. 10. 74	CP16	46° 32.2′ N	10° 28.5′ W	4825	5

Distribution

Throughout the Atlantic and Indian oceans. Depth range: 4000 m and below.

Description

This is a large well known species. Knudsen (1970) discusses it in some detail and little needs to be added to his account. We confirm that there is an elongate, posterior lateral tooth present in the right valve. Knudsen (1970) refers to a small anterior hinge tooth in the right valve, but this is not shown in his figure (94A) and neither is there an anterior tooth in the present specimens. We believe that Knudsen is referring to the thickened anterior rim of the resilium and that therefore this species belongs to the subgenus *Cuspidaria*.

Cuspidaria circinata (Jeffreys, 1876) (figure 25)

1876	*Neaera circinata*	Jeffreys (p. 497)
1881	*Neaera circinata*	Jeffreys (p. 942, pl. 71, fig. 6)
1885	*Neaera circinata*	Smith (p. 42, pl. 10, figs 4, 4b)
1889	*Cuspidaria circinata*	Dautzenberg (p. 87)
1898	*Cuspidaria circinata*	Locard (p. 185)
1927	*Cuspidaria circinata*	Dautzenberg (p. 338)
1962	*Cuspidaria circinata*	Clarke (p. 71)

Material

ship	date	stn	latitude	longitude	depth/m	number
Atlantis II	19. 02. 67	162	08° 02.0′ S	34° 03.0′ W	1493	1
	13. 03. 71	242	38° 16.9′ S	51° 56.1′ W	4382	3
	14. 03. 71	245	36° 55.7′ S	53° 01.4′ W	2707	1
La Perle	22. 10. 72	DS17	47° 32.0′ N	08° 45.5′ W	2103	1
J. Charcot	25. 02. 74	CP01	47° 34.6′ N	08° 38.8′ W	2245	1 s†
	21. 06. 74	CP07	44° 09.8′ N	04° 16.4′ W	2170	1

† The symbol s denotes empty shell.

Distribution

Throughout eastern Atlantic. Depth range: 565–4382 m.

Description

Shell rounded; posterior dorsal margin straight, posterior ventral margin sinuate, anterior dorsal, anterior and ventral margins continuously curved; rostrum, relatively short, deep and posteriorly truncate with oblique ridge to ventral corner, second rostral ridge close and almost parallel to dorsal margin; numerous distinct concentric striae, somewhat more closely spaced at umbo, extend to rostral sinuation, fine concentric growth lines on rostrum; umbo prominent, inclined obliquely anterior; hinge narrow, elongate posterior lateral tooth in right valve (figure 25).

The specimens correspond to the various and inadequate descriptions listed in the synonymy. The type was not examined but the specimens are identical to those taken by the Challenger Expedition (B.M.N.H.). They are also similar to *Cuspidaria munieri* described by Dautzenberg & Fischer (1897) and Dautzenberg (1927), the type of which also proved to be unobtainable.

The present specimens show that the anatomy is similar to that described for *C. obesa* except that there are eight pairs of pores in a thin septum. The lateral septal muscles are a continuous series and the posterior septals are directed dorsally. The ends of the tentacles are club-shaped. Both the anterior and the posterior palps are small and horn-shaped.

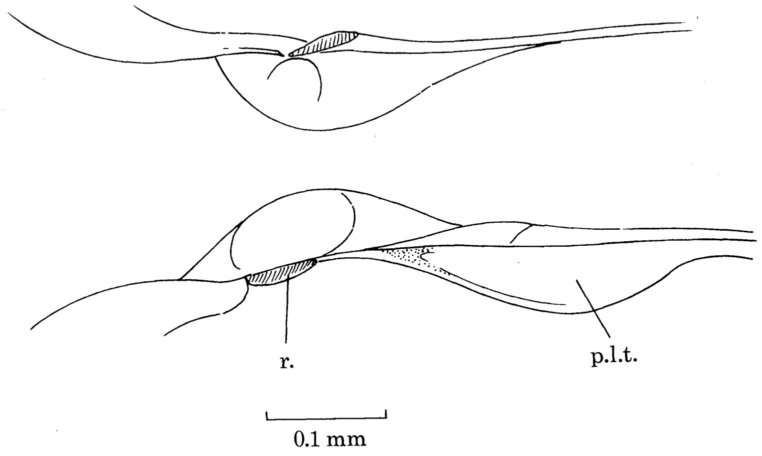


FIGURE 25. *Cuspidaria circinata.* Dorsolateral view of the hinge of both valves.

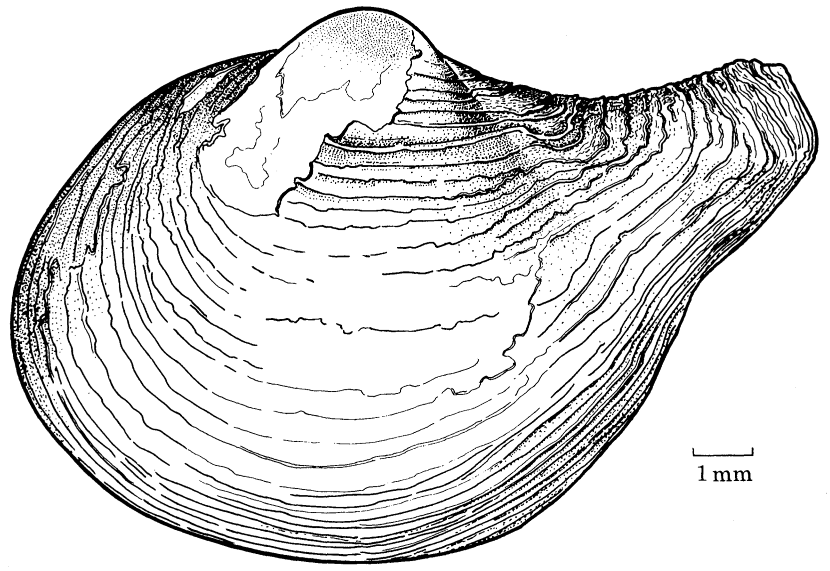


FIGURE 26. *Cuspidaria ventricosa.* Lateral view of the shell from the left side.

Cuspidaria ventricosa Verrill & Bush, 1898 (figure 26)

1898 *Cuspidaria ventricosa* Verrill & Bush (p. 802, pl. 72 fig. 5, pl. 76 fig. 6)

Material

ship	date	stn	latitude	longitude	depth/m	number
Walda	??. 07. 71	CY13	12° 03.7′ S	12° 22.3′ E	2044	1 s
Challenger	22. 09. 73	16	56° 45.0′ N	09° 28.0′ W	1632	1 lv †

† The symbol lv denotes left valve.

Distribution

North America Basin, Angola Basin, west European Basin. Depth range: 349–2044 m.

Description

The original and only description by Verrill & Bush (1898) is based on two live specimens and four valves at depths ranging from 349 to 1769 m between 40° 29.0′ N and 66° 4.0′ W and 38° 27.5′ N and 70° 54.5′ W. They do not figure a specimen in external view, but examination of the type confirmed our identification. Significant shell characters include coarse, crowded concentric growth lines, upturned rostrum with single dorsal rostral ridge (figure 26). Internally the shell has an oblique posterior rib, probably opposite the posterior limit of the siphon, and numerous very fine radiating striae on a nacrous surface.

Subgenus Cardiomya

The four *Cardiomya* species in our collections differ from *Cuspidaria* species in that they possess a central triangular resilium and a very small extra lateral septal muscle insertion. Although not common, these variations are not restricted to the subgenus *Cardiomya*. In other details the anatomy of the *Cardiomya* species conforms with that of *Cuspidaria*.

Cardiomya perrostrata (Dall, 1881) (figures 27, 28)

1881	*Neaera ornatissima* var. *perrostrata*	Dall (p. 110)
1882	*Neaera perrostrata*	Verrill (p. 561)
1884	*Neaera perrostrata*	Verrill (p. 277)
1886	*Cuspidaria (Cardiomya) perrostrata*	Dall (p. 296, pl. 2, fig. 3a, b)
1884	*Neaera perrostrata*	Verrill (p. 277)
1886	*Cuspidaria (Cardiomya) perrostrata*	Dall (p. 296, pl. 2, fig. 3a, b)
1898	*Cardiomya perrostrata*	Verrill & Bush (p. 809, pl. 73, fig. 2, pl. 74, fig. 3)
1898	*Cardiomya abyssicola*	Verrill & Bush (pl. 74, fig. 1)
1934	*Cardiomya perrostrata*	Johnson (p. 33)

Material

ship	date	stn	latitude	longitude	depth/m	number
Atlantis II	28. 08. 62	Sl. 2	40° 01.8′ N	70° 42.0′ W	200	2
	27. 11. 67	172	40° 12.3′ N	70° 44.7′ W	119	2
	28. 11. 67	173	40° 10.8′ N	70° 43.6′ W	112	2
D.M.L.†		351	off N Carolina		?	3
		3417	off N Carolina		?	8

† Duke Marine Laboratory.

Distribution

East coast of North America, south from Martha's Vineyard to the West Indies. Depth range: 112–200 m.

Description

The shell is globose with a long narrow rostrum. The surface has many faint concentric growth lines and bears 15–30 strong flat-topped curved radial ribs, which extend from or close to the umbo to the ventral margin; consequently the latter is crenellate (figure 27). The radial ribs are interspersed with occasional intercalary ribs, extending to the ventral margin; the ribs are closer together anteriorly. The sculpture of the rostrum is rough, with numerous crowded concentric growth lines and three or four fine longitudinal lines. Other distinguishing features are the evenly rounded anterodorsal margin, the straight, or slightly concave, posterior dorsal margin, and the slight sinuation at the base of the rostrum. The hinge bears a single posterior lateral tooth in the right valve only; the resilifer is central and triangular (figure 28).

The shell is similar to several other *Cardiomya* species in having a straight posterior dorsal margin, a rounded anterior margin, many radial ribs and a narrow rostrum. For example, *C. pectinata* Carpenter has fewer radial ribs and is without longitudinal lines on the rostrum; *C. californica* Dall has longitudinal rostral lines but is heavier and less globose, with a distinct angle on the anterior dorsal margin; *C. abyssicola* Verrill & Bush and *C. nipponnica* Okutani are also angulate.

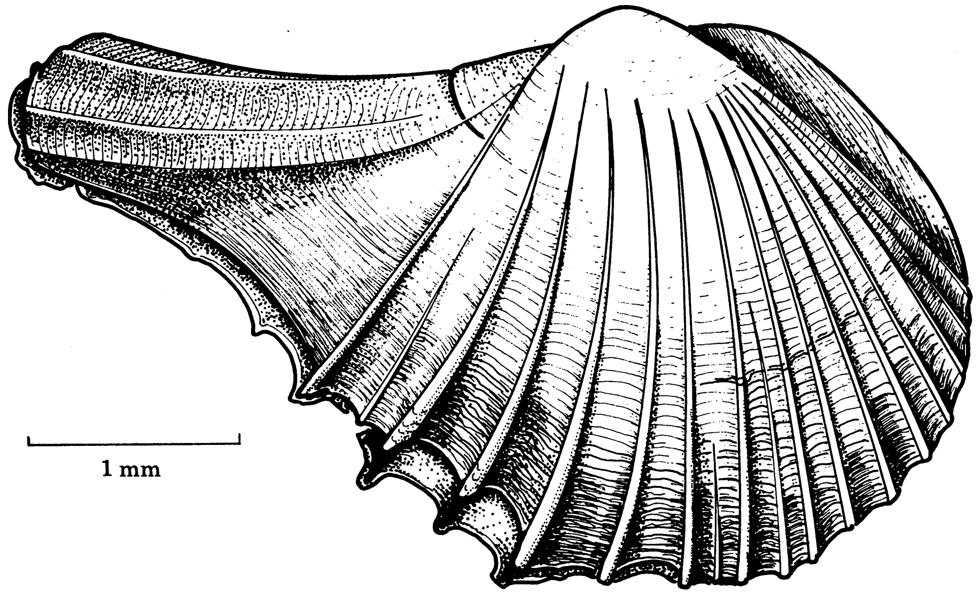


FIGURE 27. *Cardiomya perrostrata*. Lateral view of the shell from the right side.

Specimens from stations Sl. 2, 172 and 173 are identical but those from other stations show some variation. Thus, those from stations 351 and 3417 have a slight angle at the anterior dorsal margin and have a slightly more concave posterior dorsal margin with straighter radii. At present we retain them as specimens of *Cardiomya perrostrata*, reflecting differences in widely spaced populations.

Shell measurements are as follows.

	length/mm	height/mm	width/mm
Atlantis II	3.63	2.24	1.68
	4.70	2.90	—
Duke Marine Laboratory	3.63	2.09	1.43
	5.90	3.19	2.42

Most cuspidariids have an oblique resilifer; in *C. perrostrata* it is triangular, extending more or less equally on both sides of the umbo.

The ligaments of a number of anomalodesmacean bivalves have been described, e.g. *Cochlodesma praetenue* (Allen 1960), *Laternula truncata* (Morton 1973), *Entodesma saxicola* (Yonge 1952, 1976; Morgan & Allen 1976) and *Mytilimeria* (Yonge 1952). All have a lithodesma. Similarly Allen & Turner (1974), who consider the family Verticordiidae to be closely related both to the Lyonsiidae and the Poromyidae and Cuspidariidae, describe *Lyonsiella abyssicola* as having ligaments and a lithodesma similar to that described here for *C. perrostrata* and other species. In the Lyonsiidae (*Lyonsia, Entodesma, Mytilimeria*), Yonge (1976) has shown that the primary ligament, consisting of inner with anterior and posterior outer layers, is displaced ventrally. Fused periostracum from the two ends unites above it to form a dorsal secondary ligament. In these endentulous Anomalodesmacea this aligns the valves, the primary ligament being solely concerned with producing the opening moment. The ventral displacement of the primary ligament involves its widening, with a consequent loss of efficiency were it not for the presence of a centrally running calcareous lithodesma within the inner layer, i.e. secreted by the mantle isthmus. Further work (Yonge & Morton 1980) has revealed precisely the same conditions in the related families Pandoridae, Cleidothaeridae and Myochamidae but *not* in the Thraciidae and related families which they propose removing from the Pandoracea into a new superfamily. In the Poromyacea this lyonsiid ligament is present in the Verticordiidae and the Cuspidariidae (as Yonge & Morton illustrate) but *not* in the Poromyidae, where the primary ligament is opisthodetic and external and there is neither secondary ligament (only secondary periostracal

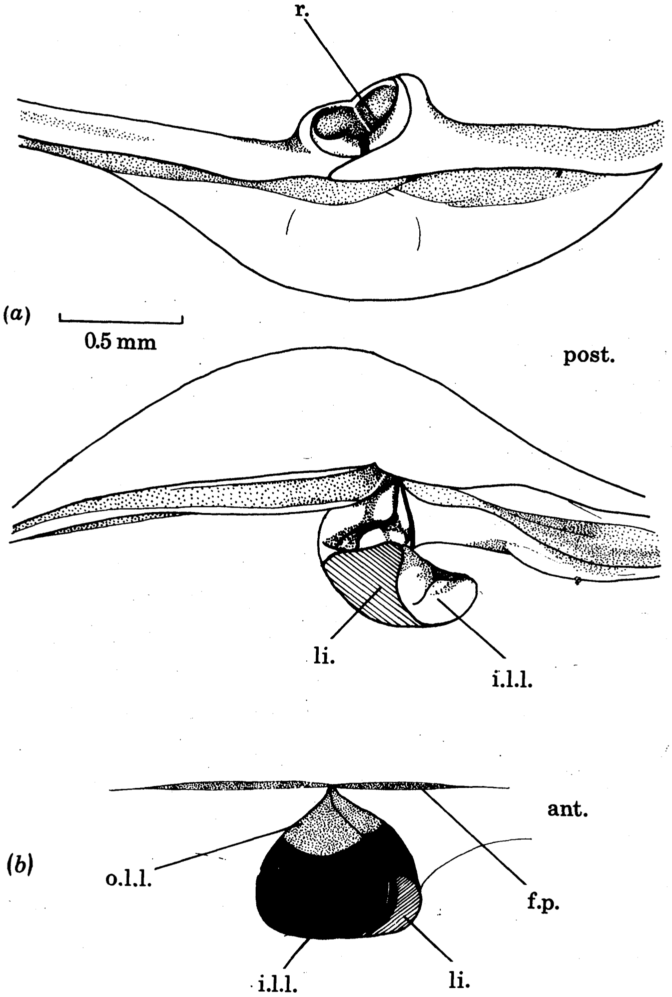


FIGURE 28. *Cardiomya perrostrata.* (*a*) Dorsolateral view of the hinge of both valves. (*b*) Posterolateral view of the ligament.

extensions at each end) nor lithodesma. Yonge & Morton recommend retention of the Poromyacea (Septibranchia) although they regard the Verticordiidae and Cuspidariidae as more closely related than either is to the Poromyidae, which is not the conclusion reached in this paper.

In *C. perrostrata* the resilium consists of two triangular lateral halves, united dorsally at their apex (figure 28*b*). Each fits into a concave triangular resilifer. Between the halves there is a ventral tongue-shaped lithodesma (figures 28*a*, *b*), which is short, wide and tapers a little posteriorly. In larger specimens the posterior dorsal limit of the lithodesma curls back on itself. The resilium is extended externally, anteriorly and posteriorly along the mid-dorsal by fused periostracum.

An extra lateral septal attachment is present. This is a relatively uncommon feature in the family Cuspidariidae, occurring in only seven of fifty species examined. The extra attachment is formed from a narrow band of muscle fibres of the outer longitudinal muscle orientated tangentially and posteriorly to insert on the shell, lateral to the septum, close to the anterior end of the siphonal retractor muscles (figure 34).

It is not clear why the extra attachment is present in some species and not in others, but its presence may be connected with the total amount of muscle in the septum. All of those species with the extra attachment have a thick septum. Unfortunately, by no means all species with thick septa have the extra attachments.

The specimens are identical to that from the type locality figured by Verrill & Bush (1898), pl. 74, fig. 1) and labelled *C. abyssicola*. Knudsen (1970) considers this latter specimen to be different from the type specimen of *C. abyssicola* (U.S.N.M. no. 78896), from the same station and figured in the same paper (Verrill & Bush 1898, pl. 77, fig. 9), and in this we agree. Knudsen (1970) also described two left valves taken by the *Galathea* Expedition as conspecific with that type. The present specimens differ from these valves in having longer, straight posterior dorsal margins, more rounded anterior dorsal margins and several less radial ribs.

Cardiomya costellata (Deshayes, 1830) (figure 29)

†1830	*Corbula costellata*	Deshayes (p. 86, pl. 7, figs 1–3)
1843	*Neaera costellata*	Hinds (p. 77)
1846	*Neaera sulcata*	Lovén (p. 48)
1865	*Neaera costellata*	Jeffreys (vol. 3, p. 49; vol. 5, p. 191, pl. 49, fig. 3)
1881	*Neaera costellata*	Jeffreys (p. 944)
1886	*Cardiomya costellata*	Dall (p. 297)
1898	*Cuspidaria costellata*	Locard (p. 193)
1901	*Cuspidaria costellata*	Friele & Grieg (p. 34)
1962	*Cardiomya costellata*	Clarke (p. 71)

Material

ship	date	stn	latitude	longitude	depth/m	number
Sarsia	12. 07. 67	29	47° 40.0′ N	05° 00.0′ W	119	1
	15. 07. 67	40	43° 35.6′ N	03° 24.8′ W	860	1
	19. 07. 67	56	43° 43.0′ N	03° 47.8′ W	641	2
	24. 07. 67	63	46° 17.5′ N	04° 45.2′ W	1336	2
Thalassa	1973	Z398	47° 36.0′ N	07° 16.8′ W	330	1
	1973	Z415	48° 07.2′ N	08° 26.2′ W	380	4
	1973	Z417	48° 12.0′ N	09° 09.5′ W	865	1
	1973	Z444	48° 58.2′ N	10° 58.5′ W	380	1
	1973	Z458	48° 37.3′ N	09° 53.0′ W	350	1
Challenger	22. 09. 73	17	56° 42.3′ N	09° 22.9′ W	1434	1

† An abbreviated synonymy, see Dautzenberg (1927) for a complete listing.

Distribution

North Atlantic, particularly European margin, extending from continental shelf to the lower part of the continental slope. Depth range: *ca.* 5–2000 m.

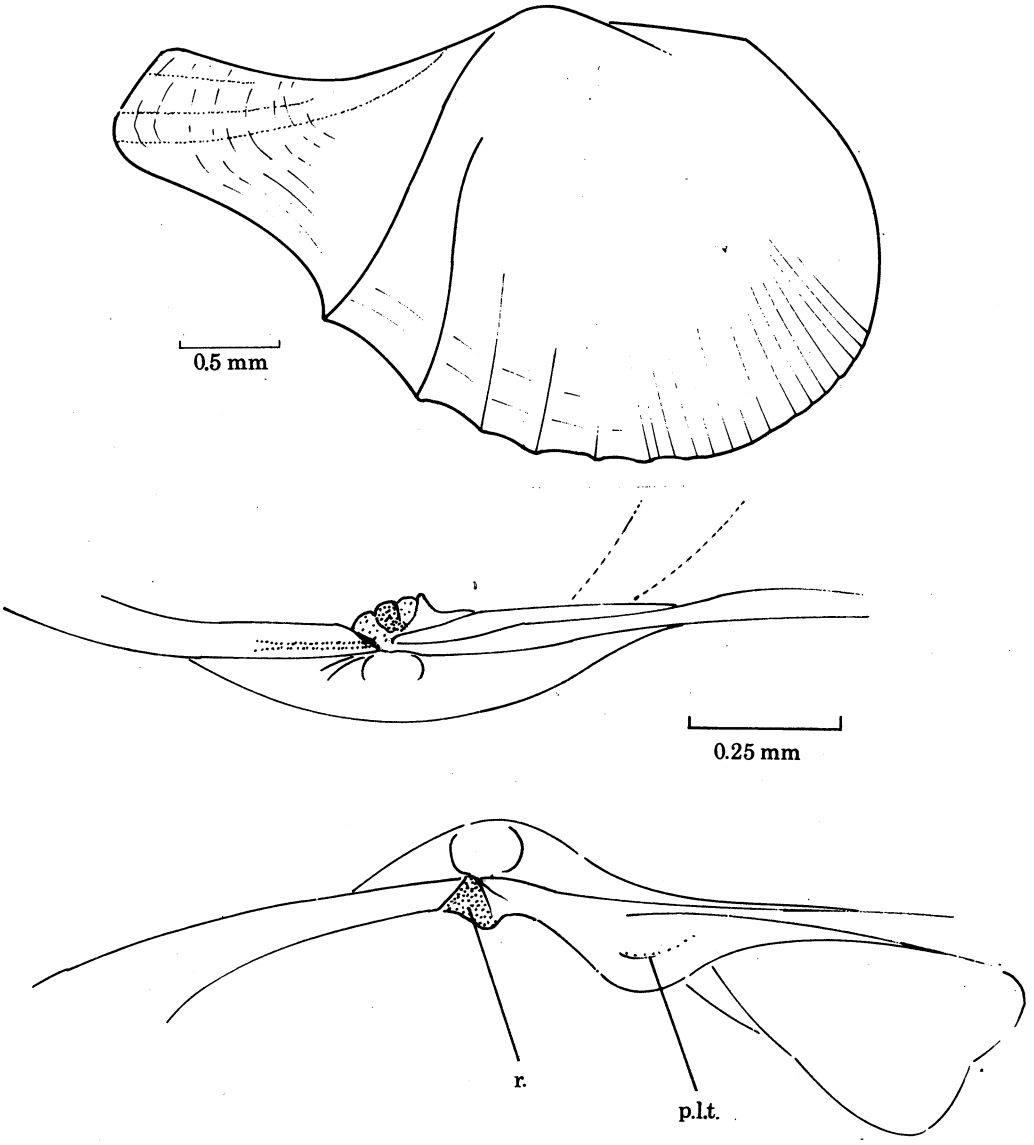


FIGURE 29. *Cardiomya costellata.* Lateral view of the shell from the right side and lateral view of the hinge of both valves.

Description

Cardiomya costellata, like *Cuspidaria cuspidata*, is one of the better known species of the family Cuspidariidae, being found in sparse numbers in relatively shallow depths over a wide area. As for many species of this family the shells are rather variable in shape. This is due partly to inherent variation and partly to the damage and repair of a very fragile shell. The species is well described by the earlier authors listed in the synonymy.

The shell is ornamented with two or three radial ribs on the posterior part of the shell, of which the most posterior is the strongest and extends closest to the dorsal part of the shell. Anteriorly there are numerous fainter radial striae. The concentric growth lines are more marked close to the ventral margin. The posterior dorsal margin is concave and the anterior dorsal margin is raised and angled at the point where it joins the rounded anterior margin. The ventral margin is minutely scalloped anteriorly, with a few larger scallops, the number being dependent on the number of ribs. The rostrum is upturned and relatively narrow, with parallel dorsal and ventral margins and two or three oblique ridges, of which the ventral is the strongest (figure 29). The right valve bears a distinct triangular posterior lateral tooth and a central triangular resilium. Some shells have a thickened dorsal edge to the posterior adductor scar which merges with the inner margin of the hinge plate.

The anatomy does not differ from *C. perrostrata*.

Cardiomya knudseni new species (figures 30–32)

Holotype: *Atlantis II*, station 262, 38° 46.0′ N, 52° 17.9′ W in 2440 m (Museum of Comparative Zoology, Harvard).

1898 *Cardiomya abyssicola* Verrill & Bush (p. 807 (in part), pl. 74, fig. 1; not pl. 73, fig. 4, and pl. 77, fig. 9)

Material

ship	date	stn	latitude	longitude	depth/m	number
Atlantis II	21. 08. 64	64	38° 46.0′ N	70° 06.0′ W	2886	3
	24. 08. 64	72	38° 00.0′ N	71° 47.0′ W	2864	3
	24. 08. 66	126	39° 37.0′ N	66° 47.0′ W	3806	1
	11. 03. 71	239	36° 49.0′ S	53° 15.4′ W	1661	1
	27. 03. 71	262	36° 05.2′ S	52° 17.9′ W	2440	7
J. Charcot (Polygas)	21. 10. 72	DS15	47° 35.2′ N	08° 40.1′ W	2246	1
	22. 10. 72	DS17	47° 32.0′ N	08° 45.5′ W	2103	1
	22. 10. 72	DS18	47° 32.2′ N	08° 44.9′ W	2138	2
	01. 11. 72	DS25	44° 08.2′ N	04° 15.7′ W	2096	1 s
	19. 04. 73	DS31	47° 32.5′ N	09° 33.9′ W	2813	1 s
	18. 02. 74	DS51	44° 11.3′ N	04° 15.4′ W	2430	2

Distribution

North America Basin, Argentine Basin, west European Basin. Depth range: 1661–2886 m.

Description

Shell, white, nacrous internally, fragile, somewhat inflated, up to 30 radial, rounded ribs, spaced more or less equidistant from anterior ventral margin to posterior ventral margin close to base of rostrum, most prominent midventrally, at most one or two faint anterior dorsal ribs with occasional secondary ribs central to primary ribs; posterior dorsal margin straight, anterior dorsal margin short and raised, anterior margin obliquely angled and flattened, ventral margin with a distinct rostral sinuation; rostrum moderately long, broad, well defined, with three or four fine raised oblique striae; no teeth on left hinge, posterior lateral tooth on right hinge, resilifer triangular. Maximum length 8.1 mm.

Knudsen (1970) found that Verrill & Bush (1898) had included two species in their description and figures of *Cardiomya abyssicola*. The present specimens (figures 30, 31) agree with the description by Verrill & Bush of two small live specimens from Albatross station 2723, one of which they figure (pl. 74, fig. 1) and which differs from the figure of the type specimen (now broken) (pl. 77, fig. 9). *Cardiomya abyssicola* differs from *C. knudseni* in having many more sharp ribs which extend to the anterior dorsal limit of the shell while the posterior dorsal margin curves upwards.

The septum is thin with four pairs of pores and a musculature similar to that of *Cuspidaria obesa*. The anterior palps are long and narrow and the posterior are reflected. Except that the anterior part of the inner stomach wall bears 13 longitudinal ridges which gradually fade behind the level of the style sac – midgut aperture, the gut is also similar to the latter species. There are two ducts leading to the digestive diverticula that lie close together, the right slightly more anterior than the left. The style sac lies ventral and far anterior with the hindgut running along the ventral surface of the posteriorly extended stomach. Laterally there are three bands of muscular tissue (figure 32). The digestive gland surrounds the oesophagus and anterior part of the stomach and extends ventrally and, in part, laterally along the stomach and is not lobulate.

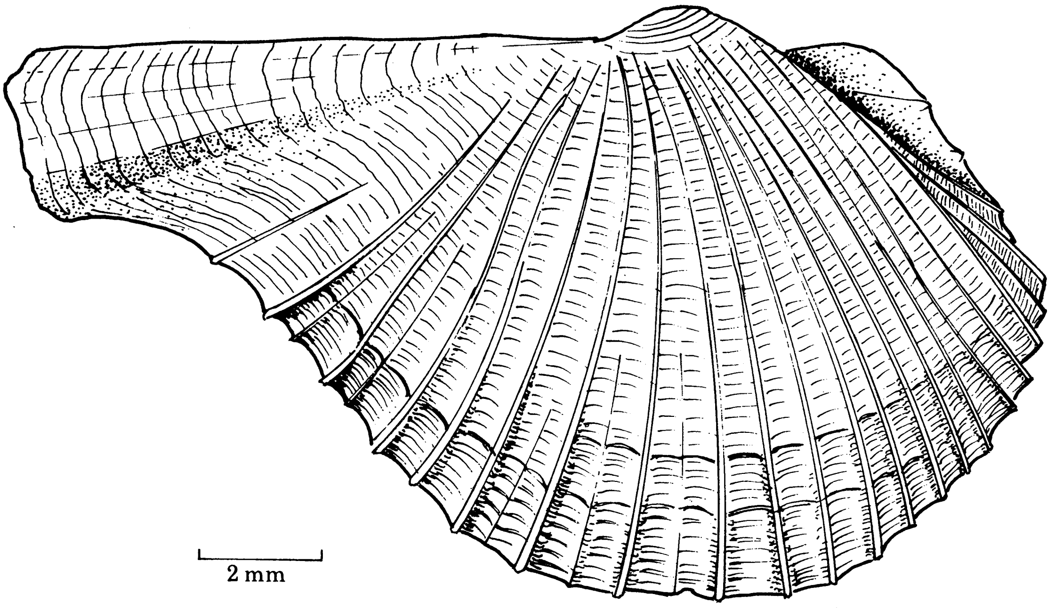


FIGURE 30. *Cardiomya knudseni*. Lateral view of the shell from the right side.

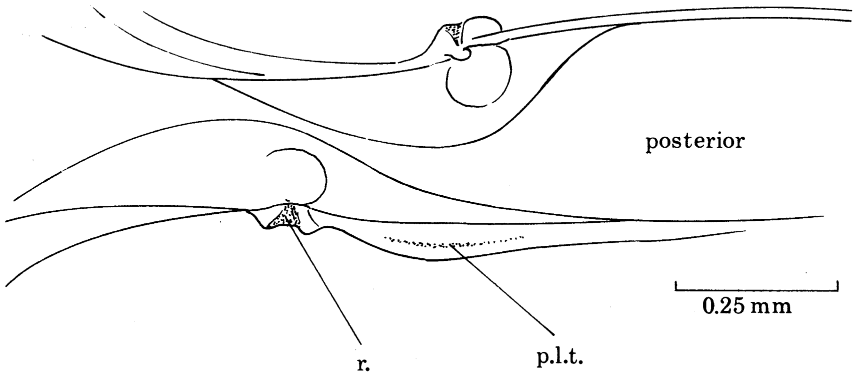


FIGURE 31. *Cardiomya knudseni*. Dorsolateral view of the hinge of both valves.

In other respects the anatomy resembles that of *Cuspidaria obesa*.

Cardiomya curta (Jeffreys, 1876)

1876	*Neaera curta*	Jeffreys (p. 495)
1881	*Neaera curta*	Jeffreys (p. 943, pl. 71, fig. 10)
1885	*Neaera curta*	Smith (p. 49)
1889	*Cuspidaria curta*	Dautzenberg (p. 88)
1898	*Cuspidaria curta*	Locard (p. 192, pl. 9, figs 24–28)

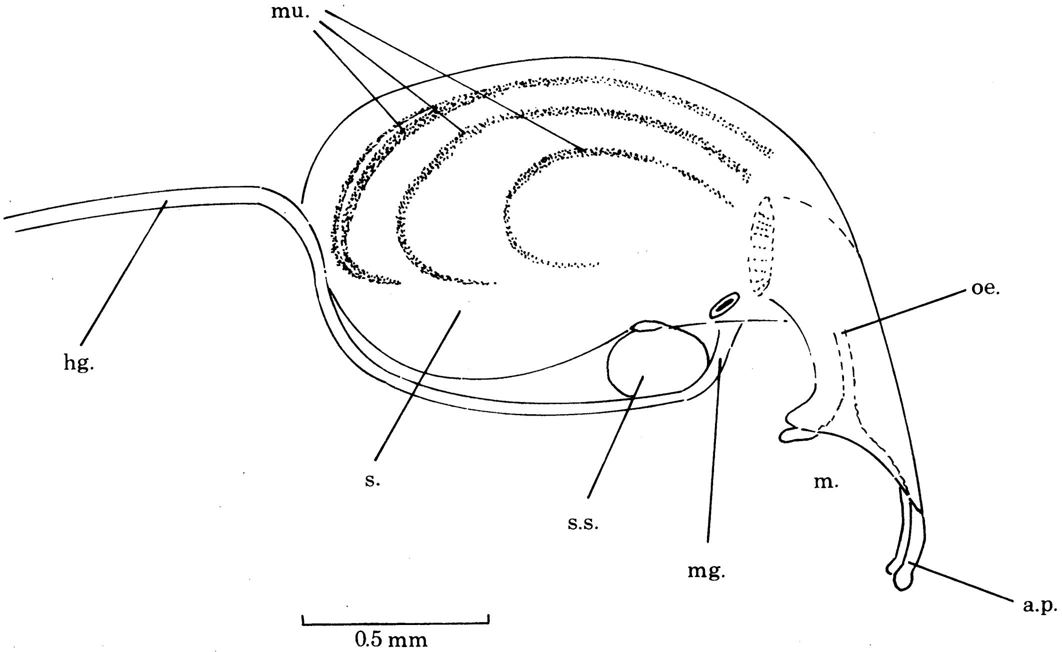


FIGURE 32. *Cardiomya knudseni*. Semidiagrammatic view of the gut from the right side.

Material

ship	date	stn	latitude	longitude	depth/m	number
Atlantis II	18. 08. 66	118	39° 19.4′ N	64° 38.9′ W	1153	1 s 1 d †
J. Charcot (Biogas II)	20. 04. 73	DS33	47° 39.7′ N	08° 05.5′ W	2338	2
Challenger	22. 09. 73	7	56° 37.5′ N	09° 09.0′ W	800	1 s
Thalassa	27. 10. 73	Z447	48° 47.3′ N	11° 12.0′ W	1430	3

† The symbol d denotes badly damaged.

Distribution

West European Basin, Canaries Basin and North America Basin. Depth range: 35–2078 m.

Description

Nothing needs to be added to the description of Jeffreys (1878, 1881) and Locard (1898). The anatomy is similar to that of *C. knudseni*.

Subgenus Myonera

Of 15 species of *Myonera* examined, 13 have similar morphologies to *Cuspidaria*. Two other species while appearing to conform to *Myonera* on the basis of hinge characters have more than five pairs of pores in the septum. Unfortunately the specimens of these two species are in poor condition, the shell of one being in fragments while all the specimens of the other species are damaged in the hinge region.

Of the 13 species most have smooth shells, though some are concentrically striated or have distinct radial keels. When the latter are present they are fewer in number than in species of *Cardiomya*. All have continuous lateral septal muscles and three species also have an extra lateral attachment to the shell. Approximately half the species examined have type II, as opposed to type I palps, and half have 'frilled' as opposed to club-ended tentacles.

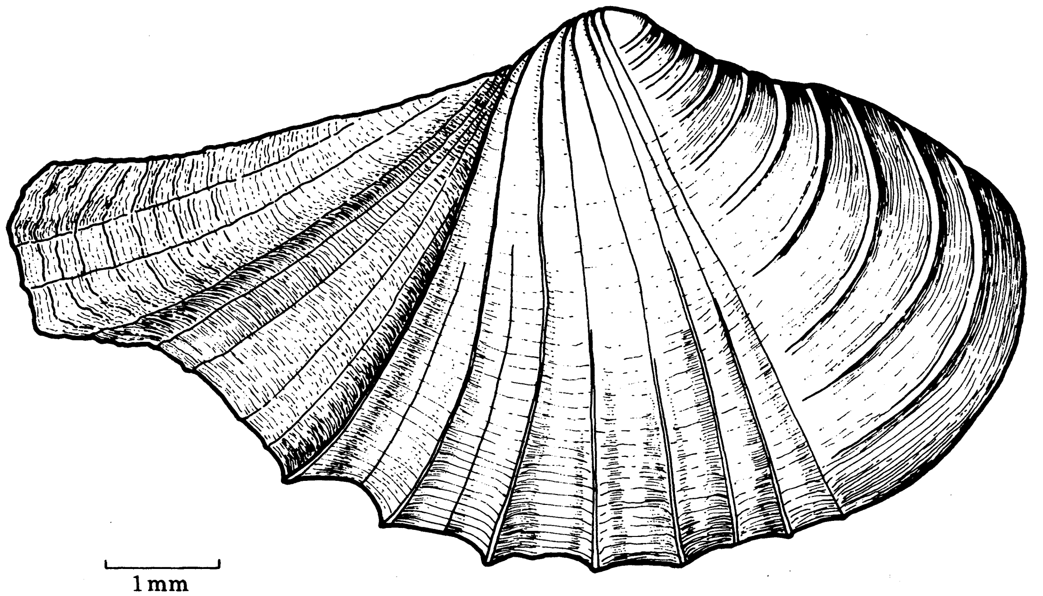


FIGURE 33. *Myonera demistriata*. Lateral view of the shell from the right side.

Myonera demistriata new species (figures 33, 34)

Holotype: *Atlantis II*, station 256, 37° 40.9′ S, 52° 19.3′ W in 3906 m (Museum of Comparative Zoology, Harvard).

Material

ship	date	stn	latitude	longitude	depth/m	number
Atlantis II	21. 08. 64	62	39° 26.0′ N	70° 33.0′ W	2496	1
	21. 08. 64	64	38° 46.0′ N	70° 06.0′ W	2886	14
	18. 08. 66	118	32° 19.0′ N	64° 34.8′ W	1135–1153	1
	24. 03. 71	256	37° 40.9′ S	52° 19.3′ W	3906–3917	8

Distribution

Northwest Atlantic off the east coast of North America. Depth range: 1135–3917 m.

Description

Shell elongate, 12 or 13 radial ribs present anterior to rostrum on posterior region of shell extending from umbo to ventral margin, each rib is sharp and terminates in a point at ventral margin; seven or eight form main ribs with five faint radial ribs present posterior to main ribs, the most posterior forms ventral limit of the rostrum; oblique rostrum traversed by numerous concentric growth lines and one or two incomplete, longitudinal striae; 11–15 low, rounded concentric undulations present anterior to main ribs; no hinge teeth present; resilifer almost central, slightly elongate posteriorly; resilium triangular.

M. demistriata (figure 33) is similar to *M. tillamookensis* Dall (1916) (figure 39) in that it has anterior concentric sculpture, and several posterior radial striae. It differs in that *M. tillamookensis* has no longitudinal striae on the rostrum, the latter being wide, rounded and triangular.

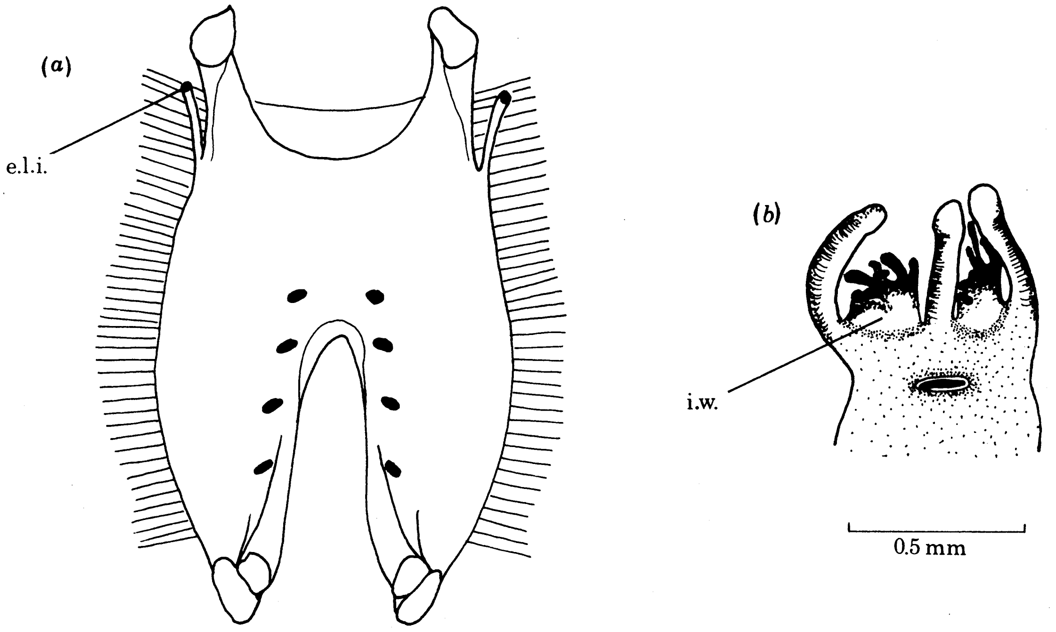


FIGURE 34. *Myonera demistriata.* (*a*) Dorsal view of the septum to show the extra lateral septal insertion. (*b*) Exhalant tentacles with the intertentacular tuberculous web.

The ventral margin is more sinuous than in *M. tillamookensis*. *M. demistriata* also resembles *C. hadalis* Knudsen except that the latter has more numerous, smaller, radial striae and much fainter concentric striae. *C. hadalis* is much less swollen, with no sinuation at the base of the rostrum.

Maximum shell measurements are: length, 9.1 mm; height, 5.3 mm.

The only significant variation in the anatomy, in comparison with the subgenus *Cuspidaria*, is the presence of an extra lateral septal insertion similar to that of *Cardiomya perrostrata*. A web is present between the three dorsal exhalant tentacles and bears small irregular tubercles on its free edge (figure 34). *M. mexicana* is the only species in which this latter feature has been previously reported (Knudsen 1970). The tentacles are club-ended. Palps are of type 1. Lateral septal muscles are continuous along the edge of the septum, the latter being pierced by five pairs of pores. The gonad is of type 1.

Myonera atlantica new species (figures 35, 36)

Holotype: U.S.N.M. no. 151906 labelled *M. lamellifera*.

Material

ship	date	stn	latitude	longitude	depth/m	number
Atlantis II	23. 08. 64	70	36° 23.0′ N	67° 58.0′ W	4680	1
	05. 02. 67	142	10° 30.0′ W	17° 51.0′ W	1624–1796	6
Sarsia	05. 07. 67	65	46° 15.0′ N	04° 50.0′ W	1922	2
Discovery	15. 03. 68	6696	26° 06.0′ N	13° 28.0′ W	1780	1
Atlantis II	23. 05. 68	202B	08° 56.0′ S	12° 15.0′ E	1427–1643	1
	27. 03. 71	262	36° 05.2′ S	52° 17.9′ W	2240–2480	
Challenger	05. 06. 73	4	56° 52.0′ N	10° 01.0′ W	1993	1
J. Charcot						
(Polygas)	24. 10. 72	DS20	47° 33.0′ N	09° 36.7′ W	4226	26
	24. 10. 72	DS21	47° 31.5′ N	09° 40.7′ W	4190	29
	25. 10. 72	DS22	47° 34.1′ N	09° 38.4′ W	4144	9
(Biogas II)	18. 04. 73	DS30	47° 38.3′ N	09° 33.9′ W	4106	2
	19. 04. 73	DS31	47° 32.5′ N	09° 04.2′ W	2813	5
(Biogas III)	24. 08. 73	DS37	47° 31.8′ N	08° 34.6′ W	2110	1
	26. 08. 73	DS41	47° 28.3′ N	09° 07.2′ W	3548	45
	27. 08. 73	DS45	47° 33.9′ N	09° 38.4′ W	4260	1
(Biogas IV)	18. 02. 74	DS52	44° 06.3′ N	04° 22.4′ W	2006	1
	22. 02. 74	DS55	44° 34.9′ N	09° 40.9′ W	4125	30
	23. 02. 74	DS56	47° 32.7′ N	09° 28.2′ W	4050	3
	23. 02. 74	DS57	47° 30.8′ N	09° 07.6′ W	2906	3
	23. 02. 74	DS58	47° 34.1′ N	09° 08.2′ W	2775	6
	24. 02. 74	DS60	47° 26.8′ N	09° 07.2′ W	3742	17
(Biogas V)	16. 06. 74	DS66	47° 28.2′ N	09° 00.0′ W	3480	2
	17. 06. 74	DS67	47° 31.0′ N	09° 35.0′ W	4150	31
	20. 10. 74	DS71	47° 34.3′ N	08° 33.8′ W	2194	1
	22. 10. 74	DS75	47° 28.1′ N	09° 07.8′ W	3250	1
	23. 10. 74	DS76	47° 34.8′ N	09° 33.3′ W	4228	58
	24. 10. 74	DS77	47° 31.8′ N	09° 34.6′ W	4240	21
	31. 10. 74	DS86	44° 04.8′ N	04° 18.7′ W	1950	3
	01. 11. 74	DS87	44° 05.2′ N	04° 19.4′ W	1913	1
	01. 11. 74	DS88	44° 05.2′ N	04° 15.7′ W	1894	1

Distribution

Off the east coast of America, Bay of Biscay and off northwest Scotland. Depth range: 1427–4680 m.

The specimens are conspecific with U.S.N.M. no. 151906, wrongly identified as *M. lamellifera* Dall, 1886.

Description

Shell oblong; wide, ill defined rostrum; posterior ventral margin with angular concavity, posterior dorsal margin straight and slightly sloping, anterior dorsal margin oblique, without shoulder, ventral margin shallow; the posteroventral angle accentuating oblong outline of shell; up to ten sharp, ledge-like, evenly spaced, concentric lamellae parallel to ventral margin, terminating at oblique rostral ridge; rostrum traversed by numerous, crowded, dorsally directed striae, one or two incomplete, longitudinal striae similar to rostral ridge; hinge edentulous; resilifer narrow, extending obliquely backwards; resilium oblique.

Maximum shell measurements are: length, 5.08 mm; height, 3.57 mm; width, 2.55 mm.

M. atlantica differs from the type specimen of *M. lamellifera* Dall (U.S.N.M. no. 448492) in being less oblique anteriorly, in having a straighter posterior dorsal margin and in having fewer concentric lamellae that terminate at a distinct oblique rostral ridge. Both species have an angular concavity at the base of the rostrum which, at first sight, gives them a similar appearance (figure 35).

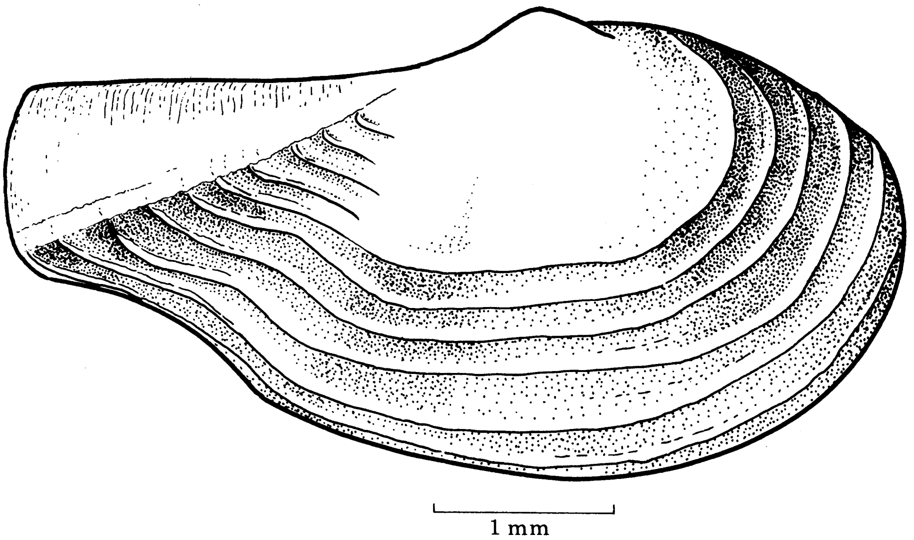


FIGURE 35. *Myonera atlantica*. Lateral view of the shell from the right side.

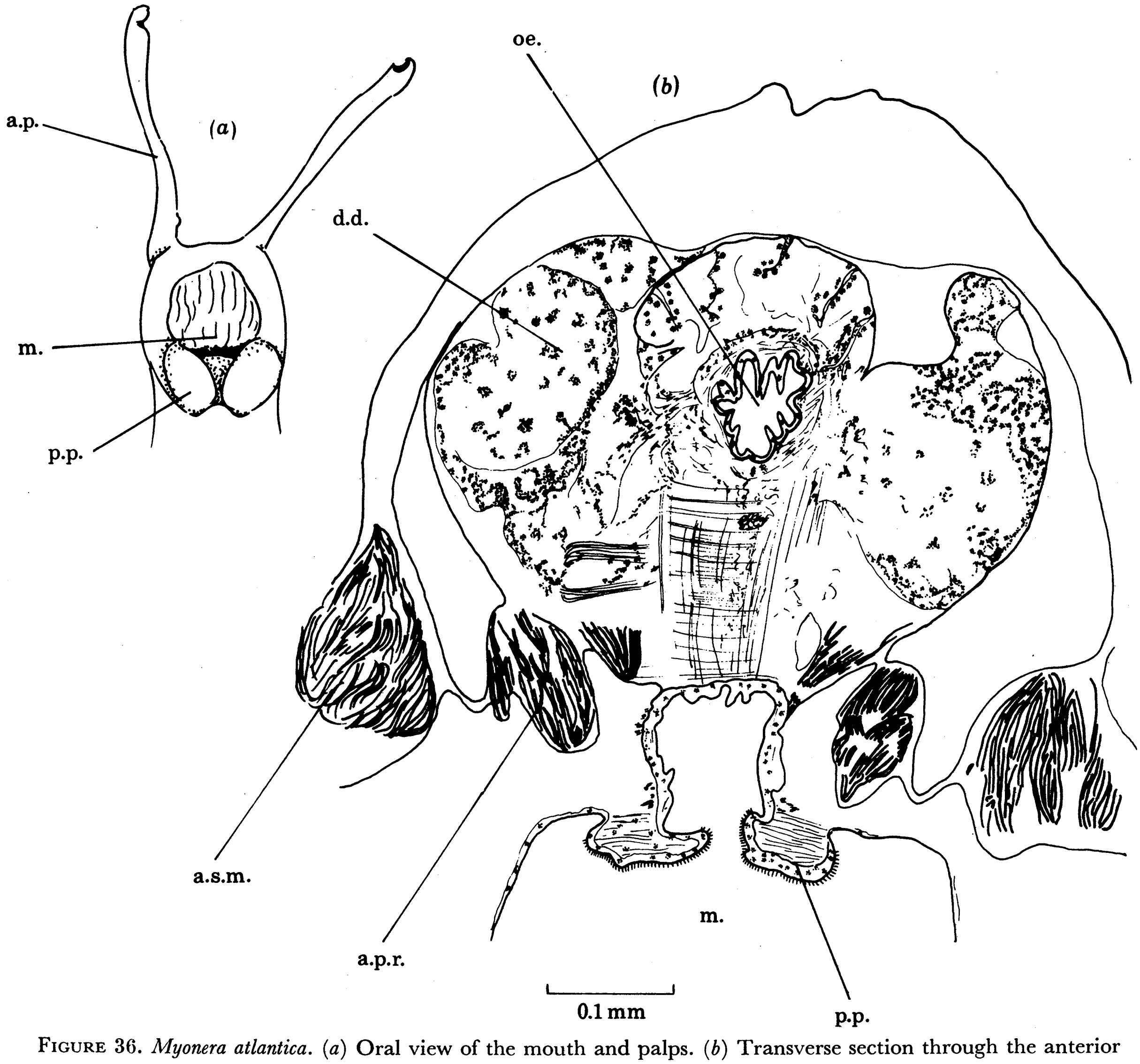


FIGURE 36. *Myonera atlantica*. (*a*) Oral view of the mouth and palps. (*b*) Transverse section through the anterior part of the body and posterior palps.

The general morphology of this species is similar to that of *C. obesa*. The posterior palps, although of type I, are somewhat extended in *M. atlantica*, but are not as long as in type II (figure 36). The digestive gland is more anterior than in most other cuspidariids, and does not extend posterior to the style sac. The stomach wall is thinner than in *C. obesa* and, if anything, there is less muscle present. There are four pairs of septal pores.

It must be emphasized that there is no anatomical feature different enough to distinguish *Myonera* from *Cuspidaria*.

Myonera paucistriata Dall, 1886 (figures 37, 38)

1885	*Neaera paucistriata*	Bush (p. 473 (*n.n.*))
1886	*Myonera paucistriata*	Dall (p. 302)
1890	*Myonera paucistriata*	Dall (p. 283, pl. 13, fig. 12)
1896	*Myonera bicarinata*	Smith (p. 374)
1911	*Cuspidaria paucistriata*	Pelseneer (p. 80)
1934	*Myonera paucistriata*	Johnson (p. 33)
1938	*Myonera dispar*	Dall *et al.* (p. 225, pl. 58, figs 5–7)
1962	*Myonera dispar*	Okutani (p. 35)
1970	*Myonera bicarinata*	Knudsen (p. 136)
1970	*Myonera dispar*	Knudsen (p. 136)

Material

ship	date	stn	latitude	longitude	depth/m	number
Atlantis II	19. 08. 66	119	32° 15.8′ N	66° 31.6′ W	2095–2223	1
	24. 08. 66	126	39° 37.0′ N	66° 47.0′ W	3806	1
Sarsia	25. 07. 67	65	46° 15.0′ N	04° 50.0′ W	1922	4
Atlantis II	26. 03. 71	259	37° 13.3′ S	52° 45.0′ W	3305–3317	1
(Bermuda Slope)	22. 04. 60	—	32° 16.6′ N	64° 36.3′ W	1700	1
D.M.L.		351	off N Carolina		?	1
La Perle	08. 08. 72	DS11	47° 35.5′ N	08° 33.7′ W	2205	2
J. Charcot (Polygas)	22. 10. 72	DS17	47° 32.0′ N	08° 45.5′ W	2103	1
	22. 10. 72	DS18	47° 32.2′ N	08° 44.9′ W	2138	1
	01. 11. 72	DS26	44° 08.2′ N	04° 15.0′ W	2076	1
	23. 10. 72	CV11	47° 29.1′ N	08° 16.1′ W	2141	1
(Biogas IV)	18. 02. 74	DS52	44° 06.3′ N	04° 22.4′ W	2006	2
	25. 02. 74	DS61	47° 34.7′ N	08° 38.8′ W	2250	5
	26. 02. 74	DS62	47° 32.8′ N	08° 40.0′ W	2175	1
	26. 02. 74	CP02	47° 33.2′ N	08° 41.4′ W	2177	2
(Biogas V)	14. 06. 74	CV39	47° 33.5′ N	08° 45.0′ W	2350	2
	20. 10. 74	CP09	47° 33.0′ N	08° 44.1′ W	2171	2

There are three species described in the literature from different localities that appear identical: *M. paucistriata* Dall, 1886, *M. bicarinata* Smith, 1896 and *M. dispar* Dall, Bartsch and Rehder, 1938.

We have been able to examine the type specimen of *M. dispar* (U.S.N.M. no. 110752), taken off the Hawaiian Islands in 1000 m, which is identical to specimens of *M. paucistriata* (U.S.N.M. nos 193041 and 63197). Both specimens of this latter species are from off the Tortugas (678 m), the former being described and figured by Dall (1886). Unfortunately the type specimen of *M. bicarinata* Smith was not seen, It is represented in the B.M.N.H. collection by a figure and note by Smith to say that the specimen is in the Museum of Calcutta, India. The figure in no way differs from *M. paucistriata* and *M. dispar*, and although the three come from different oceans we suggest that they be synonymized.

Distribution

Previous records. Pacific (Hawaiian Islands), northwest Atlantic, west coast of Malabar.

New records. Northwest Atlantic, Bay of Biscay. Depth range: 678–3806 m.

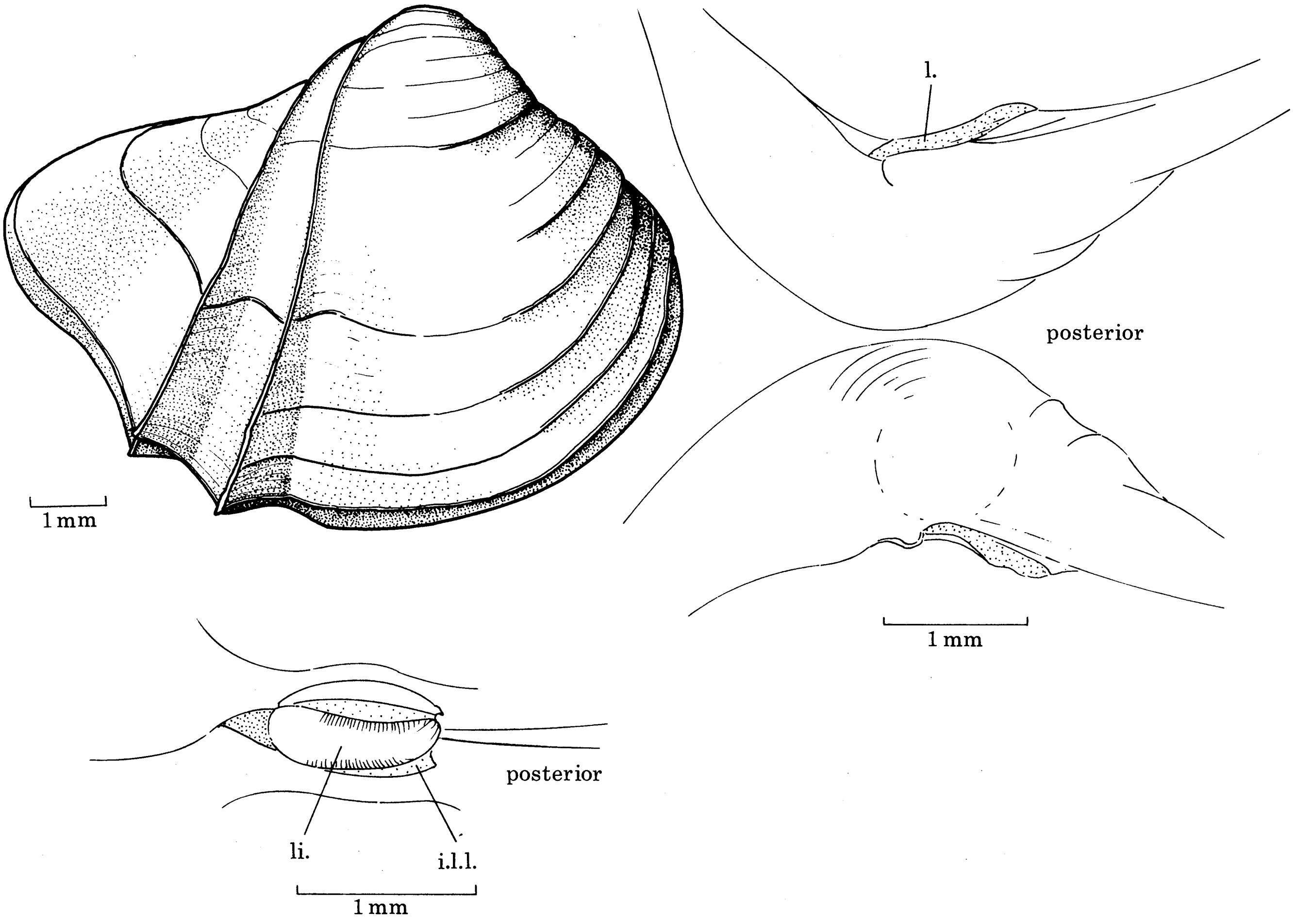


FIGURE 37. *Myonera paucistriata*. Lateral view of the shell from the right side and dorsolateral and ventral views of the hinge of both valves.

Description

Shell relatively large, inequivalve, left valve overlaps right along ventral margin, inequilateral; anterior margin rounded; two prominent radial keels extend from umbo to ventral margin; shell surface between keels and posterior to them smooth with only faint growth lines, anterior to keels shell sculpture with up to 15 low concentric undulations, closer to each other dorsally than ventrally; umbones high-pointed, with anterior and posterior dorsal margins sloping evenly to give triangular outline; rostrum short; hinge simple, without teeth; resilifer posteriorly directed, almost parallel to the dorsal margin, resilium oblique (figure 37).

The anatomy is similar to that described for *C. obesa*. There are four pairs of septal pores in a ery thick septum (figure 38).

Maximum shell measurements are: length, 9 mm; height, 6.9 mm.

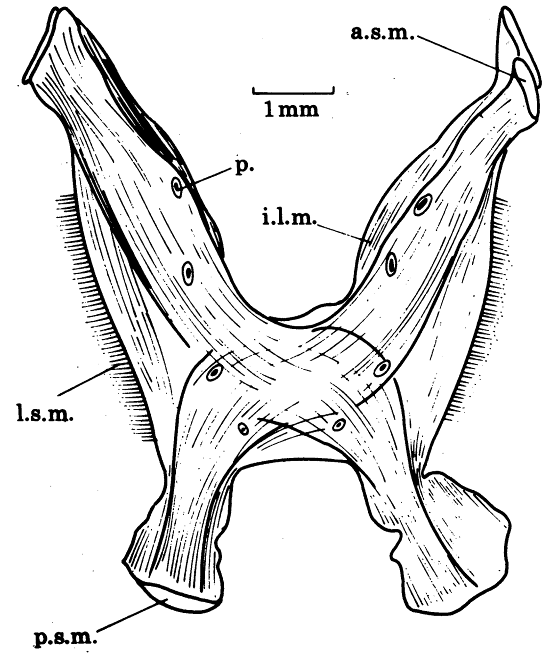


FIGURE 38. *Myonera paucistriata*. Dorsal view of the septum.

Myonera tillamookensis Dall, 1916 (figure 39)

1916 *Myonera tillamookensis* Dall (p. 407)

Material

ship	date	stn	latitude	longitude	depth/m	number
Atlantis I	16.05.68	186	22° 57.0′ S	13° 05.0′ E	439	1
	16.05.68	188	23° 00.0′ S	12° 58.0′ E	619	5

Distribution

Previous records. Off Tillamook Bay, Oregon, U.S.F.C. station 3346.

New records. Angola Basin. Depth range: 439–619 m.

Description

Shell ovate, laterally compressed; ornamented with four prominent radial ribs, most anterior rib lies approximately at centre of shell, most posterior rib immediately anterior to rostrum; two or three radial striae present anterior and posterior to ribs and between ribs, anterior to ribs are concentric undulations, very fine concentric growth lines extend over entire shell; rostrum wedge-shaped without ornamentation; ventral margin not sinuate, posterior dorsal margin almost straight, anterior margin slightly keeled; hinge edentulous, internal ligament in shallow resilifer.

The shape of the shell (figure 39) is similar to *Myonera hadalis* (Knudsen 1970) but differs in the number and position of the radial striae. The two species are recorded from greatly differing depths, *M. hadalis* from greater than 6000 m and *M. tillamookensis* from less than 619 m.

The anatomy does not differ from other species of *Myonera* described here.

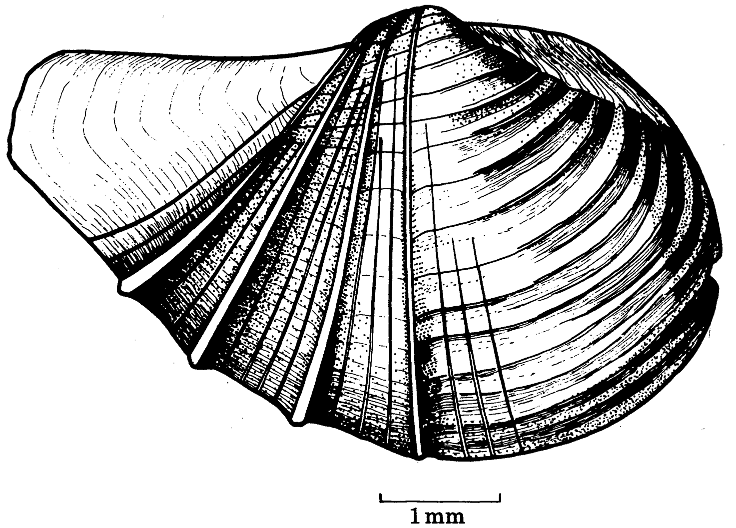


FIGURE 39. *Myonera tillamookensis*. Lateral view of the shell from the right side.

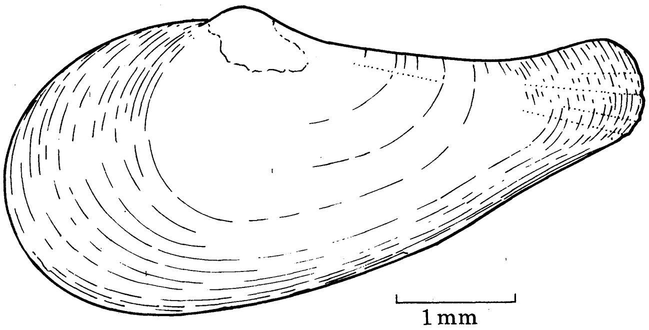


FIGURE 40. *Myonera octaporosa*. Lateral view of the shell from the left side.

Myonera octaporosa new species (figures 40, 41)

Holotype: *Atlantis II*, station 92, 36° 20.0′ N, 67° 56.0′ W in 4800 m (Museum of Comparative Zoology, Harvard).

Material

ship	date	stn	latitude	longitude	depth/m	number
Atlantis II	23. 08. 64	70	36° 23.0′ N	67° 58.0′ W	4680	3
Chain	03. 07. 65	83	34° 46.5′ N	66° 30.0′ W	5000	2
	05. 07. 65	84	36° 25.0′ N	67° 56.0′ W	4749	17
	05. 07. 65	85	37° 59.2′ N	69° 26.2′ W	3834	11
Atlantis II	13. 12. 65	92	36° 20.0′ N	67° 56.0′ W	4694	2
	21. 08. 66	121	35° 50.0′ N	65° 11.0′ W	4800	3
	21. 08. 66	122	35° 50.0′ N	64° 57.5′ W	4833	1
	23. 08. 66	125	37° 24.0′ N	65° 54.0′ W	4825	1
	24. 08. 66	126	39° 37.0′ N	66° 44.0′ W	3806	2
	14. 02. 67	156	00° 46.0′ S	29° 28.0′ W	3459	1

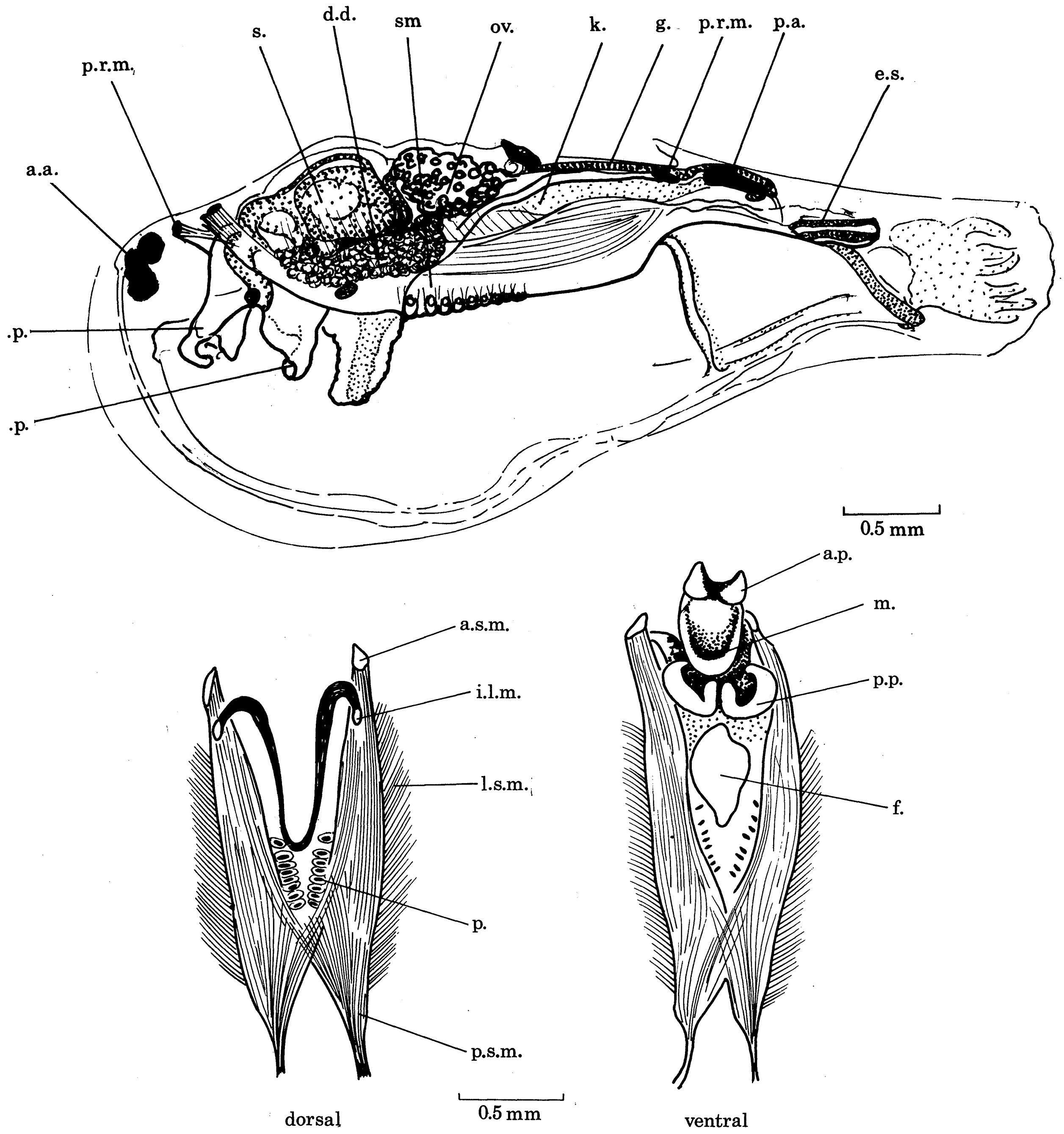


FIGURE 41. *Myonera octaporosa.* Anatomy of specimen from the left side and ventral and dorsal views of the septum.

Description

Shell elongate, narrow; umbos central, low; posterior dorsal margin slightly concave, anterior dorsal margin arched almost level with umbo, anterior margin regularly rounded, ventral margin gently curved with shallow sinuation to form a broad, moderately elongate, rostrum; shell ornamented with up to six ill defined concentric ridges, best formed anteriorly, becoming progressively fainter posteriorly where five irregular growth lines are well marked; oblique, ill defined rostral ridge; two or three faint rostral striae; hinge without teeth (figure 40).

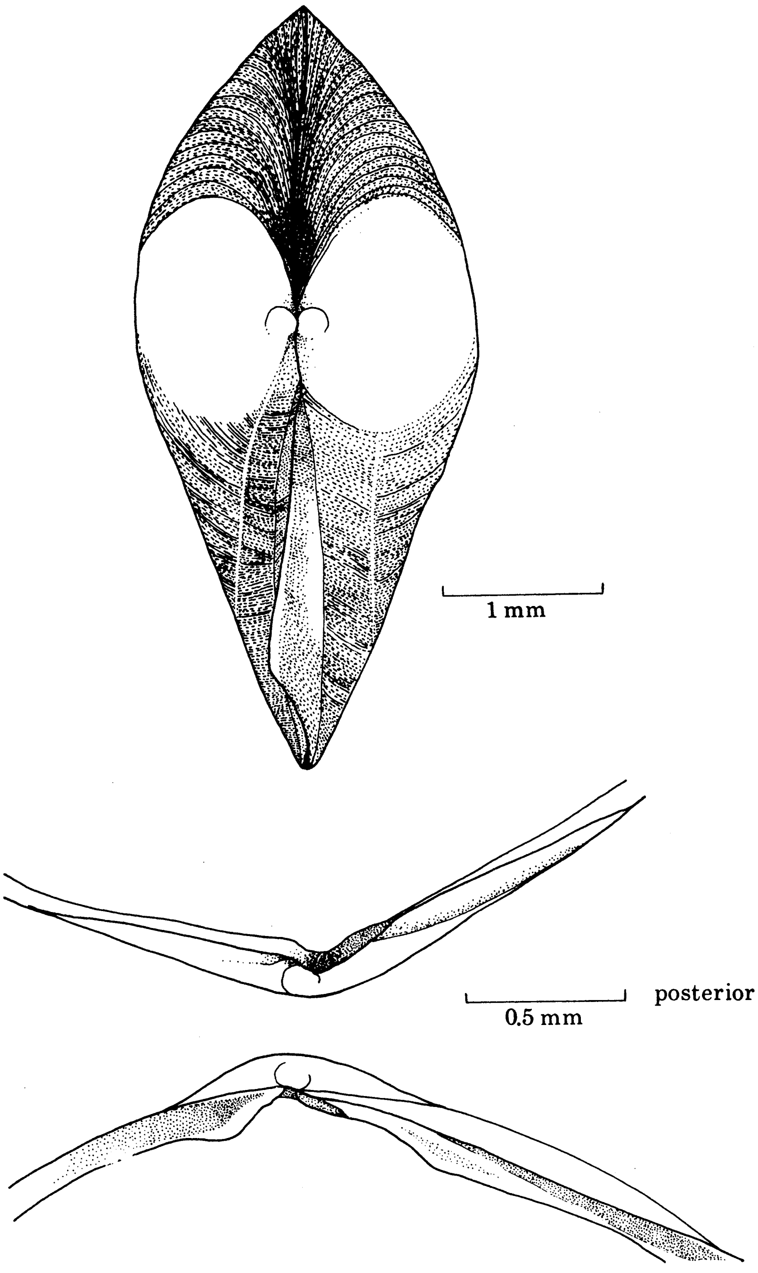


FIGURE 42. *Rhinoclama abrupta.* (*a*) Dorsal view of the shell to show overlapping dorsal margin of the right valve. (*b*) Lateral view of the hinge of both valves.

The septum is thin and has eight paired pores arranged in a V-formation with the apex posterior to the foot (figure 41). There are few posterior dorsal muscle attachments onto the shell, but there is a horizontal connection with the intersiphonal septum. The posterior septal muscles are weak. The lateral septal muscles are continuous. The anterior septal attachment to the shell is double, with well developed inner longitudinal muscles that cross posterior to the foot. The anterior and posterior mid-septal muscles run together and are more straight than those of *C. obesa.* The pores do not have the dorsally directed inner flanged lips but form a straight hole through the tissue with two distinct bands of peripheral cilia.

The posterior palps are well developed and cup-shaped. The anterior palps are more or less triangular. The tentacles are club-ended.

The siphons and other features of the anatomy are as for *Cuspidaria obesa*.

Maximum shell length is 5.3 mm.

Subgenus Rhinoclama

The study of *Rhinoclama* shows no substantial difference between the anatomy of it and the subgenus *Cuspidaria*. *Rhinoclama* is given subgeneric status on the basis of hinge characters alone.

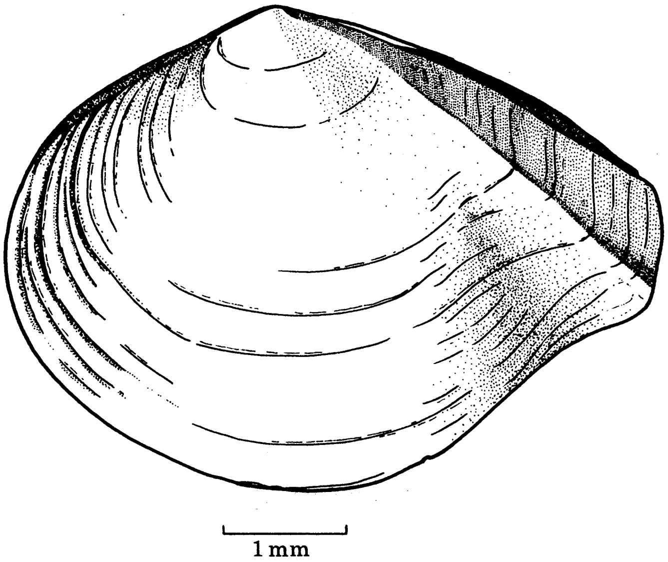


FIGURE 43. *Rhinoclama abrupta*. Lateral view of the shell from the left side.

Rhinoclama abrupta new species (figures 42–45)

Holotype: *Atlantis II*, station 188, 23° 0.0′ S, 12° 58.0′ E, in 619–622 m (Museum of Comparative Zoology, Harvard).

Material

ship	date	stn	latitude	longitude	depth/m	number
Atlantis II	16. 05. 68	188	23° 00.0′ S	12° 58.0′ E	619–622	340
	16. 05. 68	189	23° 00.0′ S	12° 45.0′ E	1007–1014	1

Distribution

Limited to two stations off the coast of Namibia. Depth range: 619–1014 m.

Description

Shell small, rounded, posterior end short, chisel-shaped, distinctive bevelled extension of right valve overlaps dorsal margin of left valve; umbo small, pointed, with dorsal margins sloping equally on either side; rostrum continuous with long sloping posterior dorsal margin, ventral rostral margin short, slightly sinuated, anterior and ventral margins rounded; shell relatively thicker than those of most other small cuspidariids; innumerable fine concentric striae, angulate at ventral rostral ridge; ventral rostral ridge extends from umbo to ventral posterior corner of rostrum, dorsal rostral ridge runs approximately parallel and close to posterior dorsal margin of left valve, but more distant in overlapping right valve; elongate, triangular, anterior and posterior lateral hinge teeth of right valve correspond with grooves in left valve; resilifer small, extends posteriorly; resilium oblique (figures 42, 43).

Maximum shell measurements are: length, 5.5 mm; height, 4.4 mm.

Rhinoclama abrupta differs in a few small respects from other described species of the subgenus. A second type of gland cell is present that has not been recorded previously. Thus, in addition to the large familiar subepithelial gland cells filled with small pale granules, there are a series of very large (30 mm in length) flask-shaped cells (figure 44, g.c.), filled with large granules that stain yellow or bluish in Azan triple stain, of a similar appearance to lacunal cells. These are interspersed among the subepithelial gland cells and are present in the mantle edge from the anterior adductor to the siphons. Each cell opens onto the inner surface of the inner mantle fold by a single duct. While the subepithelial gland cells secrete an acid polysaccharide the flask-shaped cells do not stain with Alcian Blue and presumably secrete basic or neutral material. Their function is not clear.

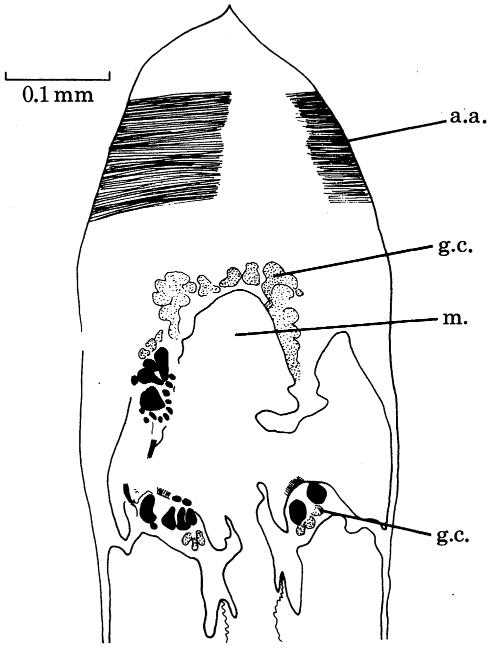


FIGURE 44. *Rhinoclama abrupta*. Transverse section of the anterior region of the body to show the position of the gland cells.

The septum is similar to that in other cuspidariids except that lateral septal muscles are arranged in two separate pairs on either side of the septum between the anterior and posterior septal attachments. The septum is particularly thick and is pierced by four pairs of pores. There are no extra lateral septal attachments (figure 45).

Anterior and posterior septal muscles are not continuous with one another (as Yonge (1928) had originally thought) but distinct with their own points of attachment, although the muscles become contiguous some distance from the attachments. The muscle lying between the posterior two pairs of pores is a branch of the posterior septal muscle while that between the anterior two pairs of pores is a branch of the anterior septal muscle.

Both pairs of palps are well developed and are of type II. The gonad is of type II and, like *C. obesa*, comprises many small lobules rather than a simple pair of compartmented sacs. The tentacles are club-shaped. The lacunal cells are particularly distinct around the edge of the intersiphonal septum, in the wall surrounding the inhalant and exhalant apertures, and around the anus and hindgut. The inner septal nerve passes between the foot and the inner longitudinal muscle of the septum rather than within the latter. The gut is similar to that previously described. In a number of the specimens remains of copepods were found within the stomach.

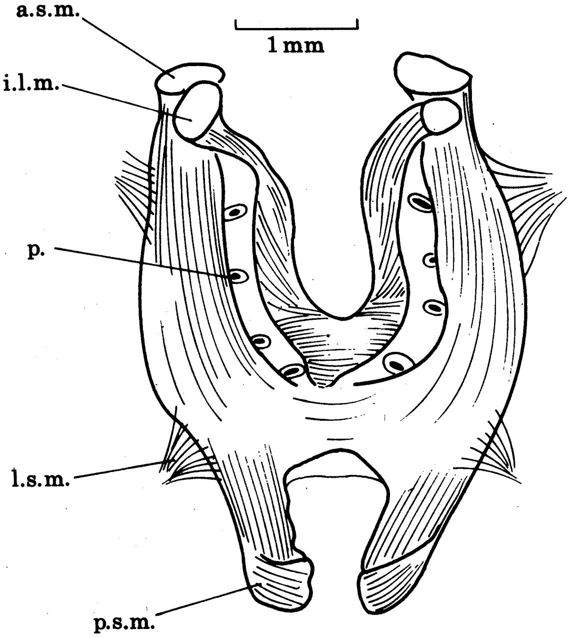


FIGURE 45. *Rhinoclama abrupta*. Dorsal view of the septum.

Rhinoclama notabilis (Jeffreys, 1876) (figures 46–48)

1876	*Neaera notabilis*[†]	Jeffreys (p. 497)
1885	*Neaera filocarinata*[‡]	Smith (p. 44)
1886	*Leiomya* (*Rhinoclama*) *notabilis*	Dall (p. 300)
1898	*Cuspidaria filocarinata*	Locard (p. 117)
1962	*Cuspidaria filocarinata*	Clarke (p. 71)
1970	*Cuspidaria testai*	Knudsen (p. 154)

[†] *Neaera notabilis*: holotype B.M.N.H. no. 11. 28. 53, *Valorous* station 12, in 1450 fathoms (*ca.* 2650 m); U.S.N.M. no. 63962, *Valorous* station 12, in 1450 fathoms (*ca.* 2650 m).

[‡] *Neaera filocarinata*: holotype B.M.N.H. no. 2.9.2415, *Challenger* station 98, in 1750 fathoms (*ca.* 3200 m).

Material

ship	date	stn	latitude	longitude	depth/m	number
Chain 50	14. 02. 67	156	00° 46.0′ S	29° 28.0′ W	3459	1
La Perle (Biogas I)	05. 08. 72	CW03	47° 36.6′ N	08° 17.5′ W	1100	1
J. Charcot (Polygas)	26. 10. 72	DS23	46° 32.8′ N	10° 21.0′ W	4734	1
(Biogas II)	18. 04. 78	DS30	47° 38.3′ N	09° 33.9′ W	4106	2
(Biogas III)	26. 08. 73	DS41	47° 28.3′ N	09° 07.2′ W	3548	2
	27. 08. 73	DS45	47° 33.9′ N	09° 38.4′ W	4260	1
	25. 08. 73	CV23	47° 32.7′ N	08° 34.2′ W	2034	2
	25. 08. 73	CV27	47° 34.2′ N	09° 32.4′ W	4023	4
(Biogas IV)	22. 02. 74	DS55	47° 34.9′ N	09° 40.9′ W	4125	25
	23. 02. 74	DS56	47° 32.7′ N	09° 28.2′ W	4050	2
	23. 02. 74	DS57	47° 30.8′ N	09° 07.6′ W	2906	1
	24. 02. 74	DS60	47° 26.8′ N	09° 07.2′ W	3742	8
Cryos (Biogas V)	16. 06. 74	DS66	47° 28.2′ N	09° 00.0′ W	3480	8
	16. 06. 74	CV41	47° 27.0′ N	09° 01.0′ W	3800	2
J. Charcot (Biogas VI)	22. 10. 74	DS75	47° 28.1′ N	09° 07.8′ W	3250	3
	23. 10. 74	DS76	47° 34.8′ N	09° 33.3′ W	4228	26
	20. 10. 74	CP09	47° 33.0′ N	08° 44.1′ W	2171	1
	23. 10. 74	CP14	47° 32.0′ N	09° 35.9′ W	4237	6

Distribution

Previous records. Western Europe, Canaries, Sierra Leone, St Paul's Isles, mid-Atlantic.

Present records. West European Basin, Cape Verde Basin. Depth range: 1100–4260 m.

Description

This species was originally described by Jeffreys (1876) from a specimen taken by the *Valorous* Expedition; since then, although mentioned in the literature, it has not been further described. Smith (1885) described *Neaera filocarinata* from *Challenger* material, the description corresponding closely to that of *N. notabilis* (Jeffreys, 1876) although he placed *N. notabilis* in a section E, but *N. filocarinata* in section A together with species of *Cuspidaria sensu stricto*. Both are ornamented with 30–40 regular, equidistant, concentric striae. There are two ridges on the rostrum, the dorsal ridge is almost parallel to the dorsal margin and the ventral ridge runs obliquely from the umbo to the posterior limit of the ventral margin (figure 46). The right hinge bears a posterior and an anterior lateral tooth but none in the left valve (figure 47). The present specimen is identical to the holotype of *C. filocarinata* (B.M.N.H. no. 2.9.2415), the damaged type specimen of *C. notabilis* (B.M.N.H. no. 11.28.53) as well as a specimen of *N. notabilis* (U.S.N.M. no. 63962). We consider that the two species should be synonymized under the earlier name *C. notabilis* Jeffreys, and placed in the subgenus *Rhinoclama*.

The specimens are also similar to *C. testai* (Knudsen 1970). This species has a rhinoclamid hinge with distinct close-set concentric striae and a prominent oblique rostral ridge with the suggestion of a fainter dorsal ridge more or less parallel to the posterior dorsal margin. It may be that this is conspecific with the other two species but we have been unable to examine the type.

The anatomy of *R. notabilis* is similar to that of *R. abrupta* except that the tentacles are 'frilled' rather than 'club'-shaped (figure 48).

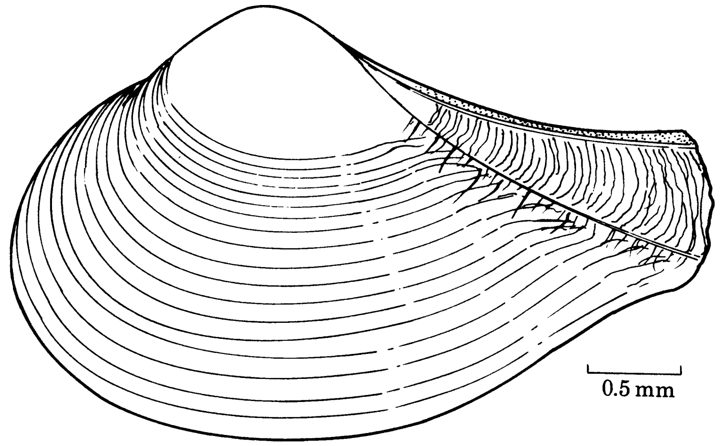


FIGURE 46. *Rhinoclama notabilis*. Lateral view of the shell from the left side.

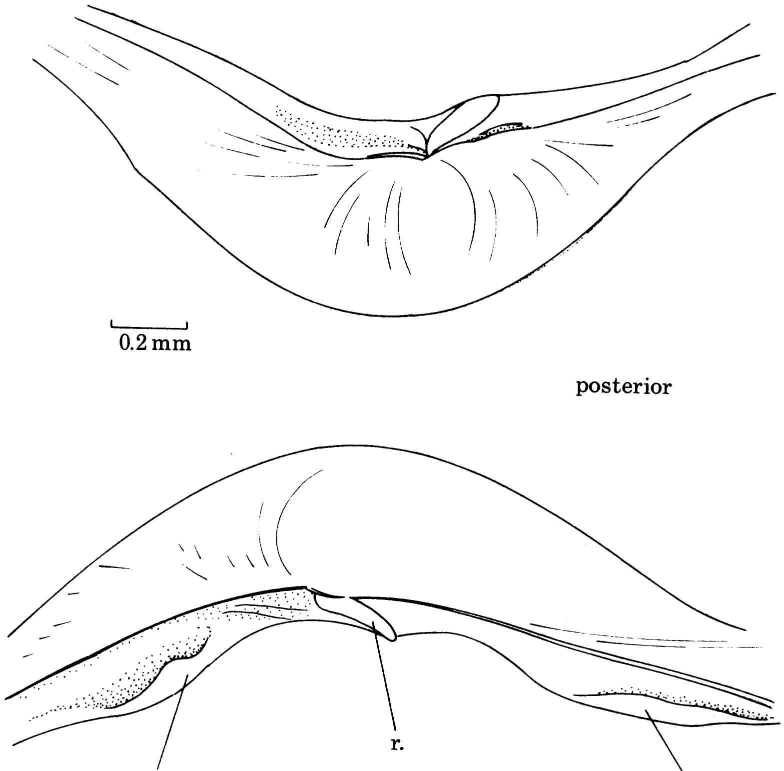


FIGURE 47. *Rhinoclama notabilis*. Dorsolateral view of the hinge of both valves.

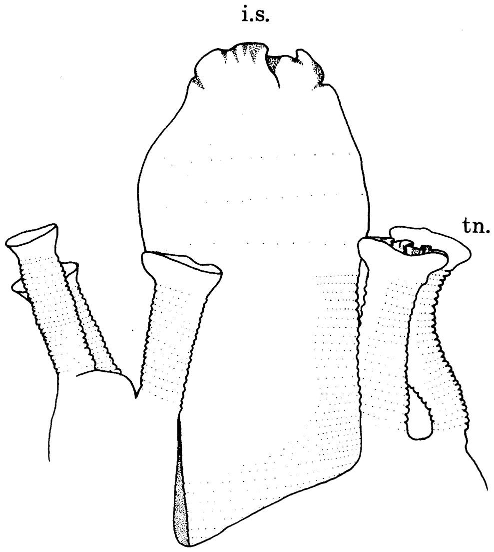


FIGURE 48. *Rhinoclama notabilis*. Tentacles with the inhalant siphon extended.

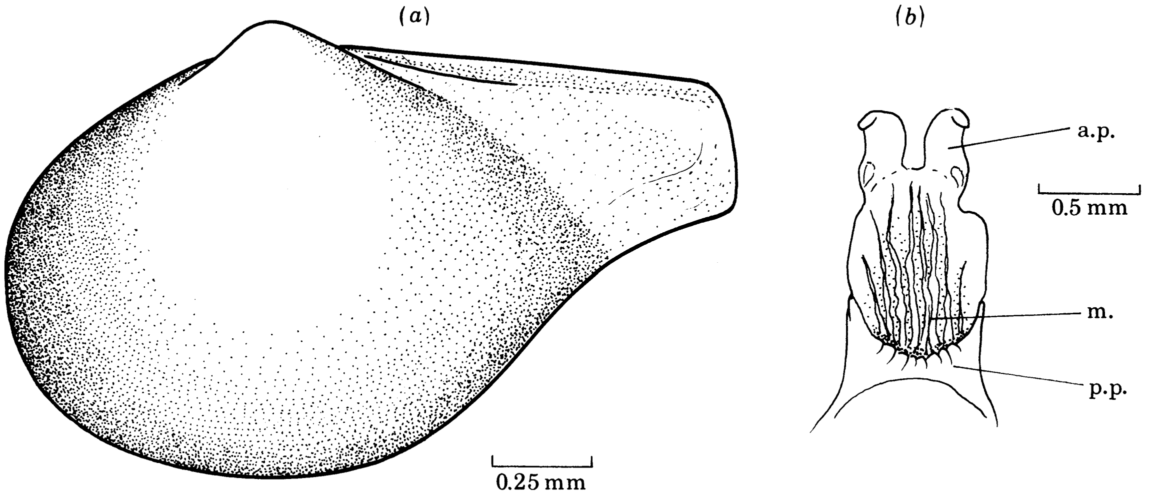


FIGURE 49. *Rhinoclama halimera*. (*a*) Lateral view of the shell from the left side. (*b*) Ventral view of mouth and palps.

Rhinoclama halimera (Dall, 1886) (figure 49)

1886 *Leiomya* (*Rhinoclama*) *halimera* Dall (pp. 300–301)

Material

ship	date	stn	latitude	longitude	depth/m	number
Atlantis II	06. 02. 67	147	10° 38.0′ N	17° 52.0′ W	2934	3
Discovery	17. 03. 68	6704	27° 44.9′ N	14° 25.0′ W	2129	1
	18. 03. 68	6709	27° 29.8′ N	15° 20.1′ W	2351	2

Distribution

North America Basin, Canaries Basin, Sierra Leone Basin. Depth range: 1360–2934 m.

Description

Shell fragile, transparent, elongate, inequivalve, ventral margin of left valve sinuate and overlapping right; anterodorsal margin slopes obliquely from umbo to join anterior and ventral margin in smooth curve, posterodorsal margin straight, left overlapping right, posteroventral margin concave; rostrum moderately long and broad, posteriorly truncate, faint oblique rostral ridge; umbones moderately large; ornamentation very faint concentric lines; hinge narrow, elongate posterior lateral tooth and small anterior lateral tooth in right valve.

Maximum shell measurements are: length, 1.9 mm; height, 1.2 mm.

This species was described but not figured by Dall (1886). The present specimens (figure 49), although much smaller, correspond to the type specimen in the United States National Museum and to the original description.

The anatomy is similar to that of *Cuspidaria obesa*. The palps are of type 1, the posterior palps being reduced to small swellings at the lateral limits of the lip. The septum is thin, with four pairs of pores. The testis is not greatly lobed, but three swellings are present. The foot is long and cylindrical.

Subgenus Luzonia

Although the anatomy of the subgenus has not been described previously in detail, the present collections reveal no difference between the species or from the general cuspidariid plan. Dall (1980) also noted this when he stated briefly that the anatomy of the type species of the subgenus, *L. chilensis*, was similar to that of both *Myonera* and *Cuspidaria* in having a thick septum, four pairs of pores, reduced palps, small foot, short siphons, and an ovary consisting of a mass of rounded lobules overlying the visceral mass.

Luzonia simplex new species (figure 50)

Holotype: *Atlantis II*, station 142, 10° 30.0′ N, 17° 51.0′ W, in 1624–1796 m (Museum of Comparative Zoology, Harvard).

Material

ship	date	stn	latitude	longitude	depth/m	number
Atlantis II	05. 02. 67	142	10° 30.0′ N	17° 51.0′ W	1624–1796	356
	05. 02. 67	144	10° 36.0′ N	17° 19.0′ W	2051–2357	1
	16. 05. 68	188	23° 00.0′ S	12° 58.0′ E	619–622	360
	16. 05. 68	189	23° 00.0′ S	12° 45.0′ E	1007–1014	1
	17. 05. 68	191	23° 05.0′ S	12° 31.5′ E	1546–1559	240
	17. 05. 68	192	23° 02.0′ S	12° 19.0′ E	2117–2154	19
Walda	12. 06. 71	DS10	18° 40.0′ S	10° 56.3′ E	1432	2

Distribution

Off the west coast of Africa from Sierra Leone to southwest Africa. Depth range: 619–2357 m.

Description

Shell small, polished, triangular, equivalve and more or less equilateral; rostrum short and tapering, no oblique rostral ridge; anterior and posterior dorsal margins slope obliquely from small domed umbo; anterior and ventral margins evenly rounded, posteroventral margin only slightly sinuate at the base of rostrum; although shell appears smooth, numerous fine concentric growth lines occur; right valve with hemispherical anterior cardinal tooth, left valve without teeth, but posterior dorsal hinge margin bears slight ridge and groove to accommodate margin of right valve; resilifer small, oblique and posteriorly directed; resilium oblique.

This species (figure 50) differs in shape from the type species *L. philippinensis* Hinds (B.M.N.H. no. 1961122), and from the other previously described species *L. chilensis* Dall (U.S.N.M. no. 224659).

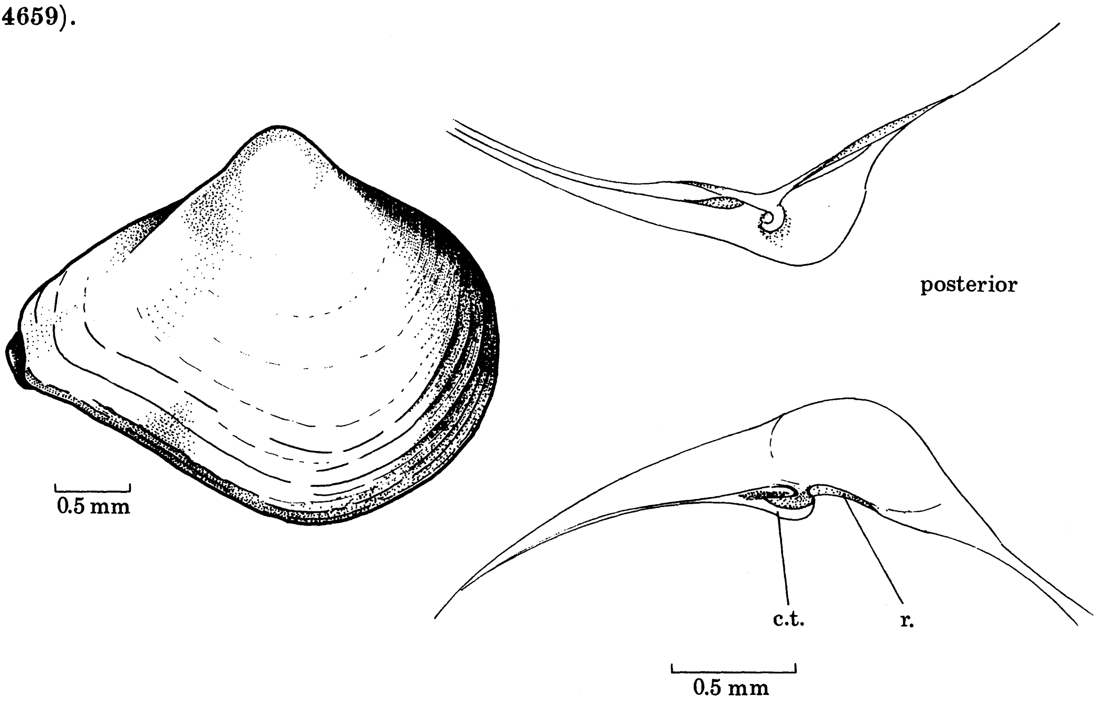


FIGURE 50. *Luzonia simplex*. Lateral view of the shell from the right side and dorsolateral view of the hinge of the right and left valves.

Maximum shell measurements are: length, 3.4 mm; height, 2.7 mm; width, 2.6 mm.

The anatomy is similar to that of *C. obesa*. Ostracods were present in the stomachs of some specimens.

Subgenus Tropidomya

Previously *Tropidomya* was considered a monospecific subgenus accommodating *Tropidomya abbreviata* (Forbes, 1843) and characterized by a single cardinal tooth in each valve. Although there is no description of the anatomy this study shows that *T. abbreviata* closely resembles that of *C. obesa*.

Tropidomya abbreviata (Forbes, 1843) (figures 51, 52)

1843 *Neaera abbreviata* Forbes (p. 75)
For numerous records from between 1843 and 1916 see Dautzenberg (1927, p. 340).
1935 *Cuspidaria (Tropidomya) abbreviata* Thiele (p. 947)
1966 *Cuspidaria (Tropidomya) abbreviata* Tebble (p. 205)
1969 *Tropidomya abbreviata* Nordsieck (p. 137)

Material

ship	date	stn	latitude	longitude	depth/m	number
Atlantis II	16. 05. 68	186	22° 57.0′ S	13° 00.5′ E	439–481	2 valves

Type specimen (B.M.N.H.); U.S.N.M. nos 171985 and 171989.

Distribution

West Europe, Aegean Sea, off west of Scotland to Canaries. Depth range: 125–481 m.

Description

A good description of this species is given by Tebble (1966). The hinge is simple and the teeth are little more than small swellings. The resilifer is long and, unlike in other cuspidariids, extends posteriorly within rather than below the hinge margin (figure 51). The internal ligament is oblique and a tongue-shaped lithodesma is present (figure 52).

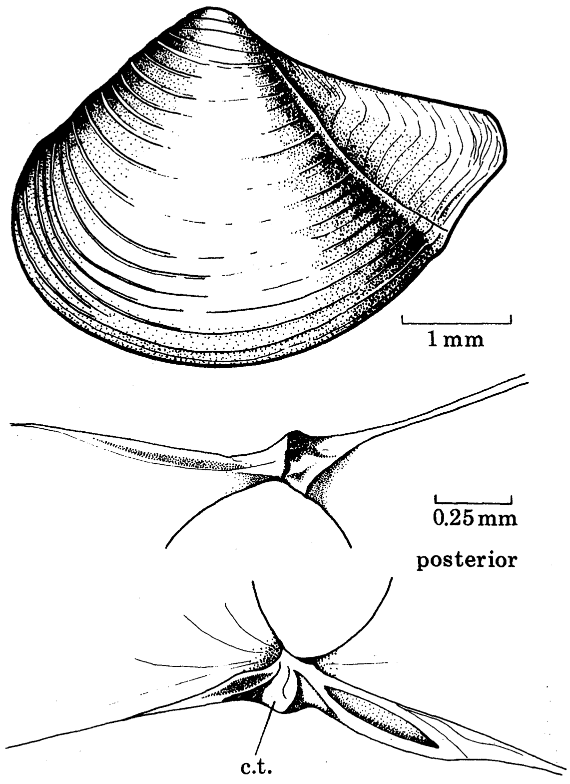


FIGURE 51. *Tropidomya abbreviata*. Lateral view of the shell from the left side and dorsolateral view of the hinge of both valves.

Tropidomya diagonalis new species (figures 53, 54)

Holotype: *Atlantis II*, station 203, 18° 48.0′ S, 12° 52.0′ E in 527–542 m (Museum of Comparative Zoology, Harvard).

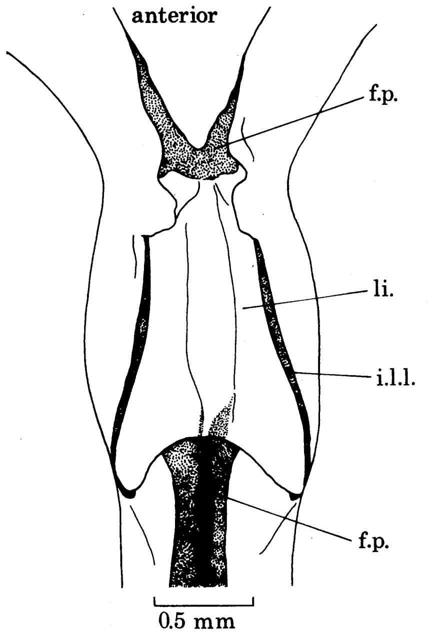
Material

ship	date	stn	latitude	longitude	depth/m	number
Atlantis II	23. 05. 68	203	18° 48.0′ S	12° 52.0′ E	527–542	1

Description

Shell large, triangular; high umbones; dorsal margins steep, anterior margin rounded, ventral margin deeply curved; rostrum short, tapering, slightly concave dorsally with four or five prominent, distal, dorsal corrugations with minor corrugations between, ventral limit defined with a faint striation and second faint striation dorsal to it; two moderately strong, curved radial ridges posterior to rostrum; anterior two-thirds of shell with 12 low, wide, concentric ridges which turn abruptly dorsally between first and second radial ridges giving characteristic vertically striated appearance (figure 53). Partially bifid cardinal tooth in right valve, resilifer, long, narrow, part external and part internal.

52



53

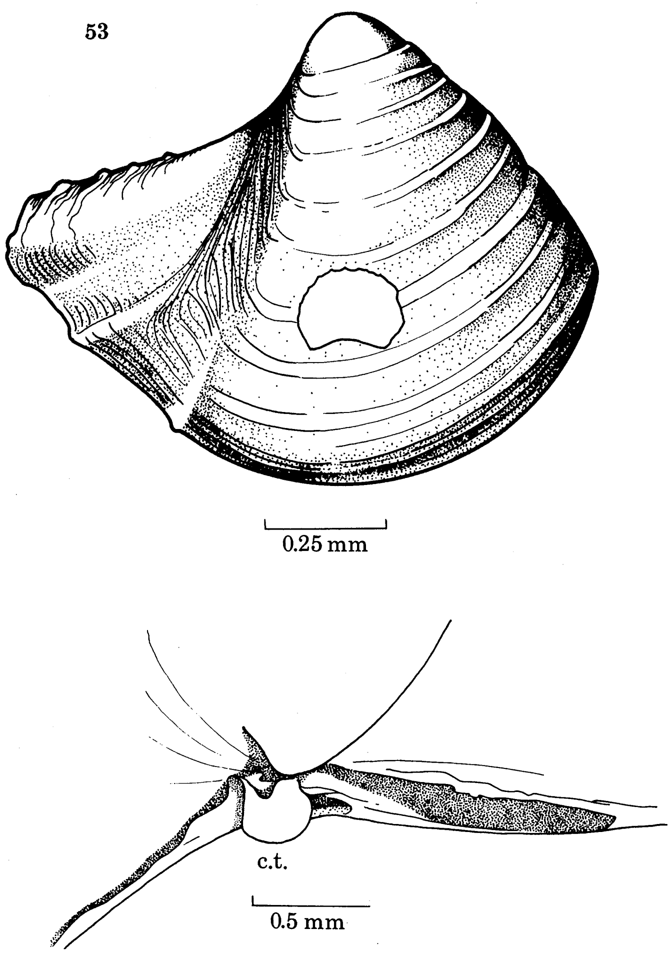


FIGURE 52. *Tropidomya abbreviata.* Ventral view of the hinge to show the lithodesma.

FIGURE 53. *Tropidomya diagonalis.* Lateral view of the shell from the right side and dorsolateral view of the hinge of the right valve.

The shell of *T. diagonalis* is similar to *T. abbreviata* except that the dorsal margins are steeper and the concentric lamellae are abruptly interrupted posteriorly.

Shell measurements are: length, 2.4 mm; height, 1.9 mm.

Unfortunately only the right valve of the specimen is intact. The bifid tooth is not referred to in the original definition of *Tropidomya* (Dall, 1886); however, because there are no lateral teeth such as are found associated with the bifid cardinal tooth of the subgenus *Leiomya* we prefer to assign this species to *Tropidomya* pending the acquisition of further material.

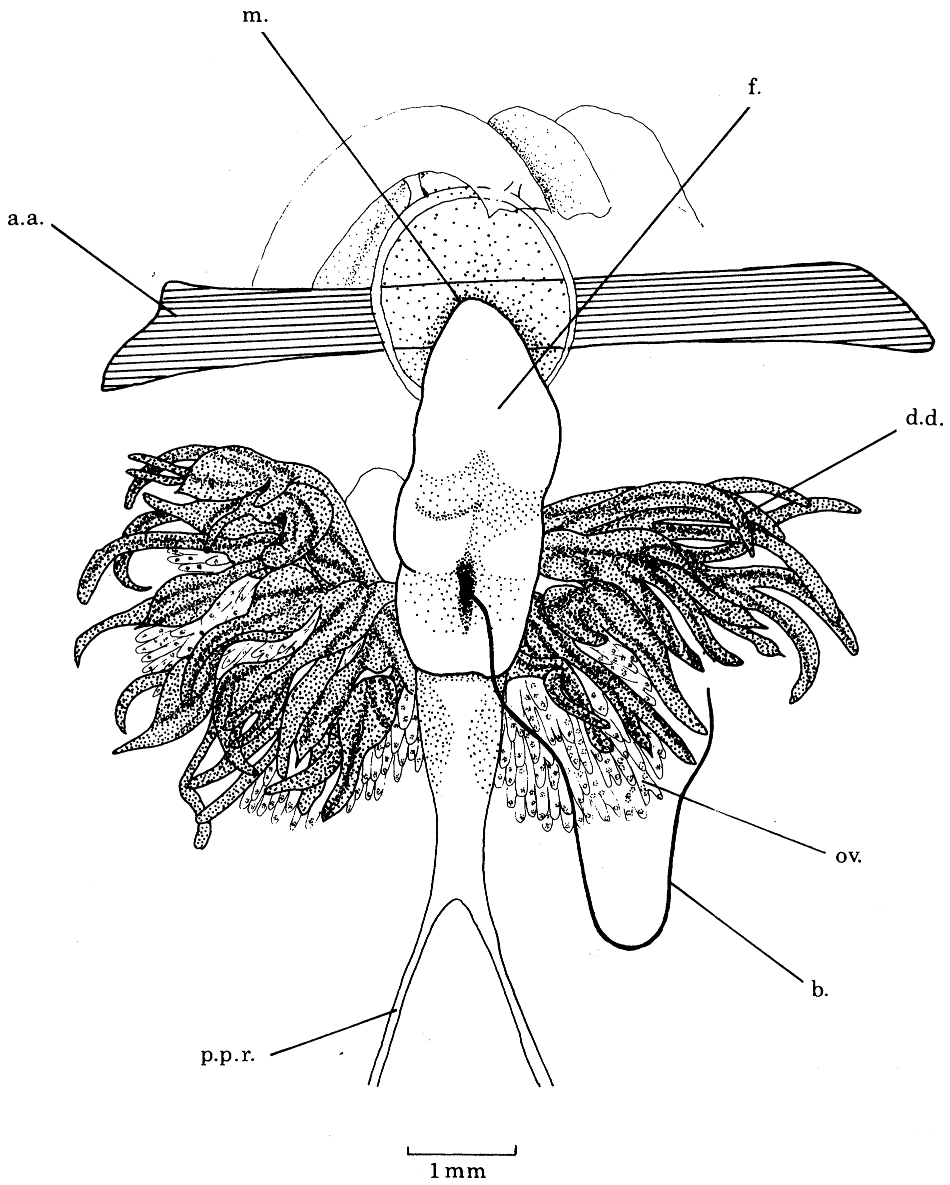


FIGURE 54. *Tropidomya diagonalis*. The viscera seen from the ventral side.

T. diagonalis differs from every other cuspidariid examined in having a multiple-lobed gonad and digestive gland (figure 54). The ovary consists of numerous narrow, finger-like, forked lobes bunched on each side of the stomach. Each lobe contains five or six eggs visible through an almost transparent epithelium. The digestive gland lies beneath the gonad, close to the floor of the stomach. It consists of approximately 24 long narrow tubes on either side of the foot, several of which are united at their base forming a swollen basal 'bulb'.

In other respects the anatomy is similar to that of other cuspidariids. The septum is very thick, but this may be a reflection of the size of the specimen. There are five pairs of pores and the lateral septal muscles are not divided. The palps are of type 1. The tentacles are club-ended and the bases of the exhalant tentacles are joined by a web whose margin is entire.

Genus Halonympha

In addition to differences in shell characters, *Halonympha* also differs in its anatomy from the genus *Cuspidaria*. Thus the septum has more than 5 pairs of pores, the number varying from 8 to 20 pairs, and it is also less muscular, lacking a posterior dorsal septal attachment to the shell. The posterior palps are large and cup-shaped. Other details of the anatomy are of the cuspidariid pattern.

Halonympha depressa (Jeffreys, 1881) (figures 55–59)

1881	*Neaera depressa*	Jeffreys (p. 940, pl. 71, fig. 3)
1885	*Neaera depressa*	Smith (p. 35)
1898	*Cuspidaria depressa*	Locard (p. 183)
1962	*Cuspidaria depressa*	Clarke (p. 71)

Material

ship	date	stn	latitude	longitude	depth/m	number
Sarsia	24. 07. 67	61	46° 20.1′ N	04° 36.0′ W	952	1
	24. 07. 67	63	46° 17.5′ N	04° 45.2′ W	1336	4
Discovery	18. 03. 68	6709	27° 29.8′ N	15° 20.1′ W	2351	2

Type specimen (B.M.N.H.).

Distribution

West Europe, Canaries, Bay of Biscay and Mediterranean. Depth range: 952–2351 m.

Description

Shell almost equivalve; anterior half large, rounded, with high-shouldered anterior dorsal margin, posterior half triangular, wedge-shaped; posterior dorsal margin slightly concave, slopes steeply from umbo, ventral margin smoothly curved, not sinuate; upturned, truncate rostrum; shell surface with numerous fine concentric striae that extend onto rostrum; without oblique rostral ridge; anterior cardinal tooth, rounded, knob-like, in right valve; long laminar ridge, or 'buttress' in both valves extending posteriorly from resilifer to dorsal edge of posterior adductor muscle scar, second ridge extends along ventral edge of posterior adductor muscle scar to join dorsal ridge posterior to scar; resilifer oblique, posteriorly directed; ligament opisthodetic.

The hinge was described by Dall (1886) as characteristic of the genus *Halonympha*. In *Halonympha claviculata*, the type species, the adductor muscle is said to be inserted on an expanded ridge, whereas here the adductor is bounded above and below by two ridges (figure 55).

The present specimens (figure 56) are identical to the type of *H. depressa* Jeffreys, 1881 housed in the British Museum. Jeffreys (1881) refers to the dorsal ridge as a lateral tooth and notes a ventral ridge but omits to mention an anterior cardinal tooth even though present in the type specimen. Smith (1885) does not include *H. depressa* in section K, although it is this section that Dall (1886) later synonymized with *Halonympha*. Dall (1886) also interpreted the dorsal ridge as a tooth.

Maximum shell measurements are: length, 6.4 mm; height, 3.95 mm.

The septum differs in two respects from that of *Cuspidaria*. First, there are more than five pairs of pores and, secondly, there are no posterior dorsal septal muscle attachments to the shell. Neither character has been reported previously. All species described here with more than five pairs of pores are without dorsal muscle attachments and have large palps.

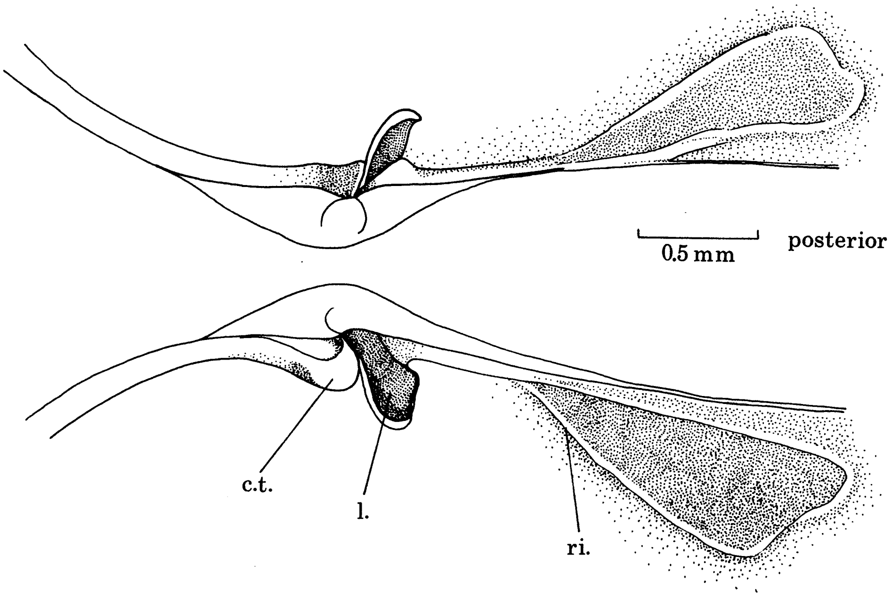


FIGURE 55. *Halonympha depressa*. Lateral view of the hinge of both valves with ligament attached.

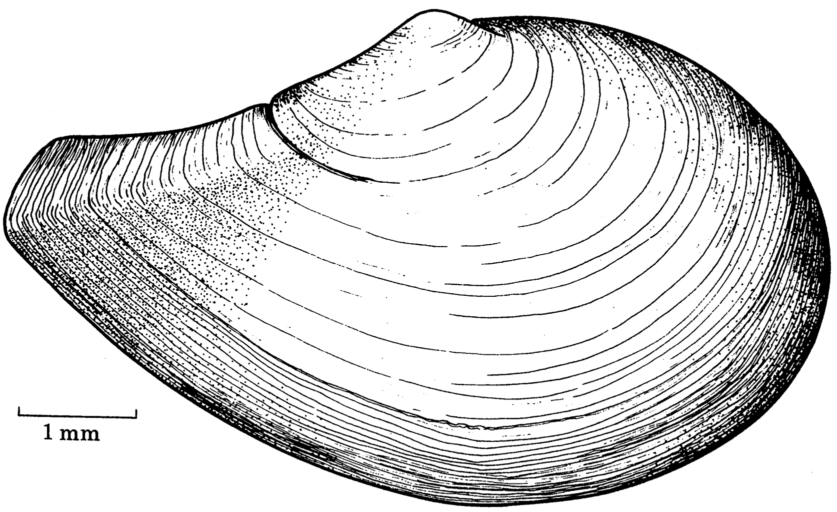


FIGURE 56. *Halonympha depressa*. Lateral view of the shell from the right side.

In *H. depressa* the septum is flimsy, with less muscle than is present in any species of *Cuspidaria*. Apart from differences in the attachment of the posterior dorsal septal muscles (see below), the septal muscles are arranged in a similar manner to other cuspidariids, but the septum is pierced by as many as 32 pores arranged in a single series on either side of the foot. Those anterior have wider apertures than those posterior (figure 57). The posterior pores tend to lie closer together than those anterior. The pores are simpler in their anatomy than those of *Cuspidaria* in that they lie more or less flush with the septal surface, and lack dorsally protruding lips; however, two bands of cilia are present, as too is a sphincter of plain muscle. Posteriorly the septal muscles terminate at the base of the siphons, dividing into two short narrow bands

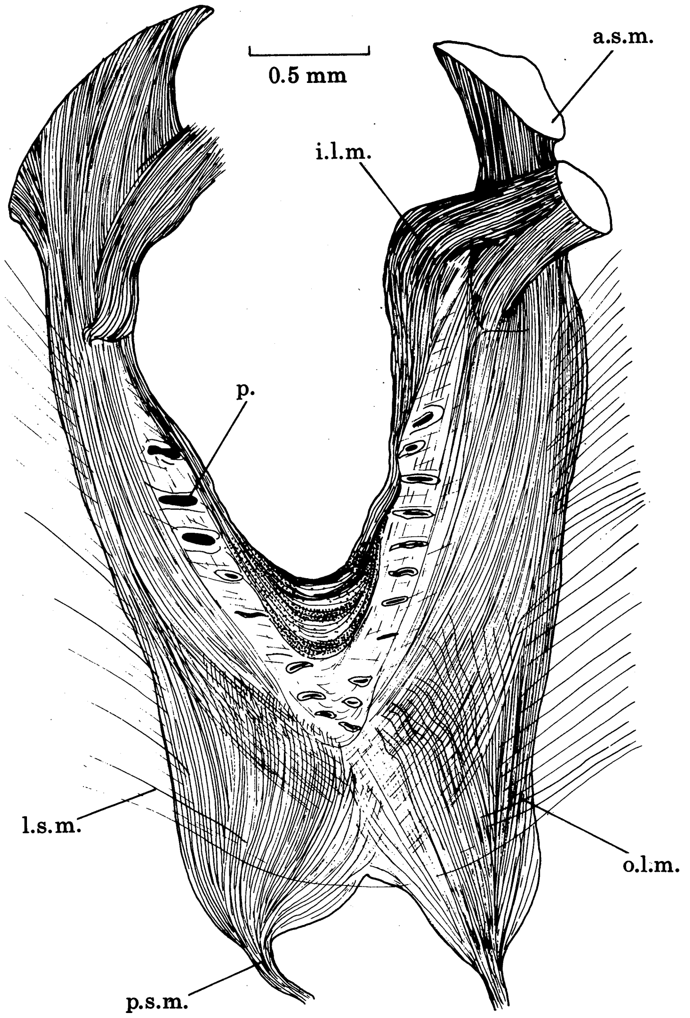


FIGURE 57. *Halonympha depressa*. Dorsal view of the septum.

that pass dorsolaterally (together with connective tissue and the septal nerve) to originate within the musculature of the siphonal retractor tube. This type of origin resembles that of the extra lateral septal muscles present in some species of *Cuspidaria*. Between the posterior muscles, the dorsal and ventral septal epithelia lie close together and form a relatively extensive intersiphonal membrane.

In common with all other species (except *Cuspidaria circinata*) with more than five pairs of pores in the septum, *H. depressa* possesses large, type III palps (figure 58). The mouth is wide, opens ventrally, with the palps at the anterior and posterior margins. The anterior palps are thin and broad, while the posterior pair are larger and cup-shaped, with the 'bowl' facing towards the mouth. The anterior palps are connected to the mantle along their anterior edge. Both contain a sparse layer of subepithelial longitudinal muscle and a few scattered transverse fibres. The rim of the mouth has a thick band of muscle within it, the fibres being orientated along its length. Both palps have a ciliated tract along their outer edge.

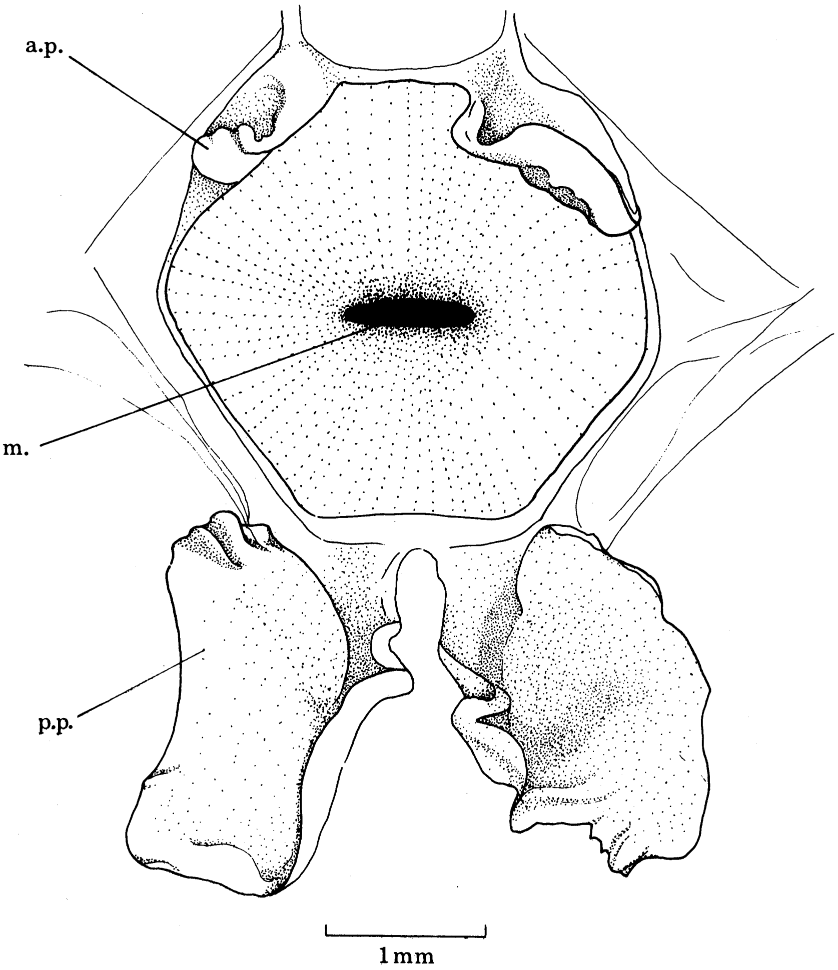


Figure 58. *Halonympha depressa.* Ventral view of the mouth and palps.

The nervous system differs in two important respects from that of *Cuspidaria* (figure 97). (i) The outer septal nerve, which in *Cuspidaria* runs from the visceral to cerebropleural ganglion, here stops well short of the cerebropleural ganglion, and thus confirms its visceral origin. (ii) The inner septal nerve, which in *Cuspidaria* runs within the septum, from the cerebropleural to pedal ganglion, does not extend as far as the pedal ganglion.

In other respects the anatomy of *Halonympha* is similar in form to that of *C. obesa* or *C. parva* (figure 59). The only minor exception is that the lacunal cells are more distinct and more widely distributed than in *C. obesa*, being found around the base of the exhalant siphon and at the edges of the intersiphonal septum.

Halonympha atlanta new species (figure 60)

Holotype: *Atlantis II*, station 64, 38° 46.0′ N, 70° 6.0′ W, in 2886 m (Museum of Comparative Zoology, Harvard).

Material

ship	date	stn	latitude	longitude	depth/m	number
Atlantis II	21. 08. 64	64	38° 46.0′ N	70° 06.0′ W	2886	4
	24. 08. 64	72	38° 16.0′ N	71° 47.0′ W	2864	1
	22. 05. 68	200	09° 43.5′ S	10° 57.0′ E	2644–2754	1
Walda		DS23	00° 15.3′ S	05° 47.8′ E	3138	5
		DS22	00° 35.6′ S	06° 49.4′ E	3025	3

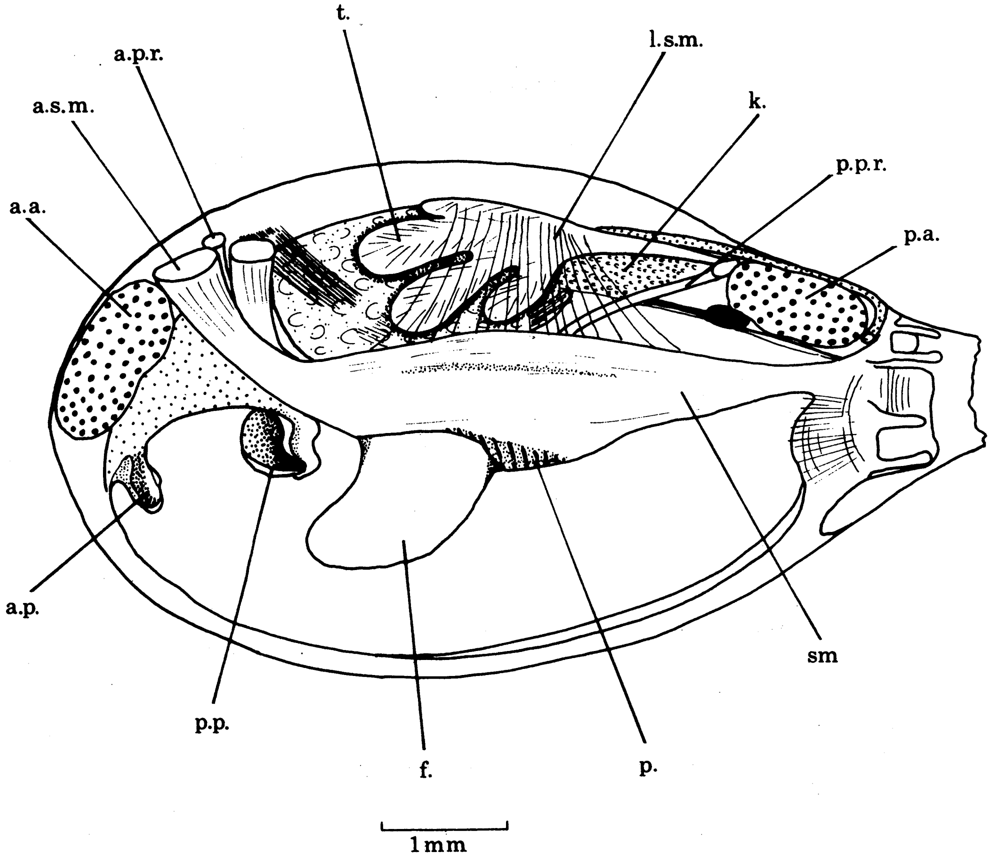


FIGURE 59: *Halonympha depressa*. Lateral view of the male anatomy.

Distribution

North America Basin, Guinea Basin, Angola Basin, Depth range: 2644–3128 m.

Description

Shell thin, oval-rostrate, very slightly sinuate ventral margin; posterodorsal margin steeply sloping and concave, anterior dorsal margin raised, rounded, continuously curved with anterior and anteroventral margins, posteroventral margin slightly concave, umbones prominent and large; rostrum posteriorly truncate, with moderately long wedge-shaped, very faint oblique rostral ridge; shell surface with numerous fine, concentric striae; hinge feeble, consists of small cardinal swelling in right valve, dorsal ridge defining posterior adductor muscle scar not very distinct (figure 60).

Maximum shell measurements are: length, 3.7 mm; height, 2.4 mm.

Anatomy as for *Halonympha depressa*.

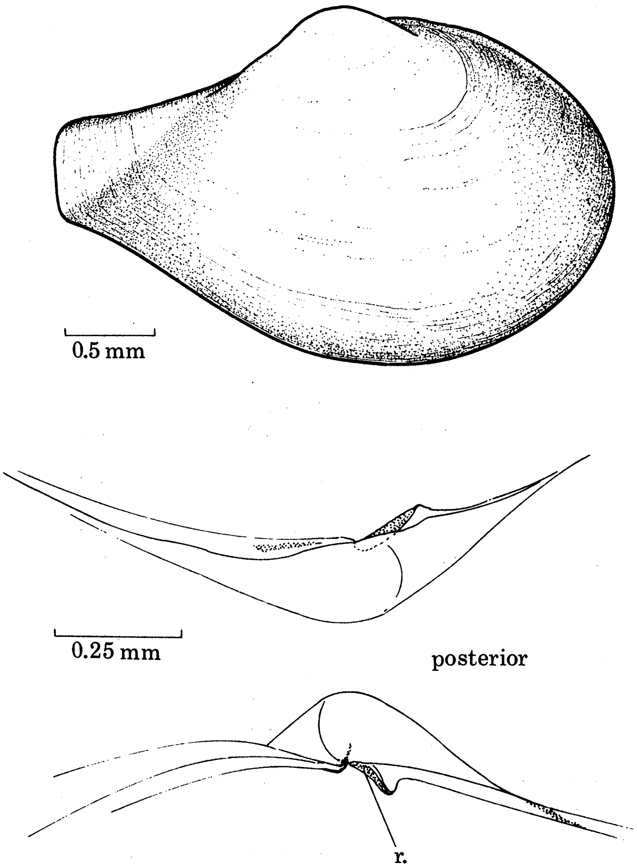


FIGURE 60. *Halonympha atlanta*. Lateral view of the shell from the right side and lateral view of the hinge of both valves.

Genus Protocuspidaria new genus

Type species: *Protocuspidaria* (*Protocuspidaria*) *verityi* n.sp.

Protocuspidaria is presented as a new genus† divisible into the three subgenera (*Protocuspidaria*, *Edentaria* and *Bidentaria*) on the basis of hinge characters. All species have a similar external appearance, in that they are small, rounded, laterally flattened with a very short rostrum.

Subgenus Protocuspidaria new subgenus

Type species: *P.* (*P.*) *verityi* n.sp.

Shell small, rounded, laterally compressed, equivalve, inequilateral; umbo small, hemispherical; anterior dorsal margin short, posterior dorsal margins straight or nearly so with right

---

† *Myonera ruginosa* (Jeffreys, 1881) may prove to be a species of *Protocuspidaria*.

overlapping left, anterior dorsal margin usually slightly flattened, ventral margins evenly curved; slight sinuation in ventral margin at base of rostrum; rostrum short, wide, variably truncate; shell surface with innumerable, close-set, thread-like concentric striae, more fibrous and irregular in appearance towards rostrum; hinge line simple, left valve without tooth, right valve with single, anterior lateral tooth, forming shallow crescent-shaped shelf, resilium oblique; resilifer small and central.

Protocuspidaria verityi new species (figures 61, 62)

Holotype: *Atlantis II*, station 167, 7° 58.0′ S, 34° 17.0′ W to 7° 50.0′ S, 34° 17.0′ W, in 943–1007 m (Museum of Comparative Zoology, Harvard).

Material

ship	date	stn	latitude	longitude	depth/m	number
Atlantis II	20. 02. 67	167	07° 58.0′ S 07° 50.0′ S	34° 17.0′ W 34° 17.0′ W	943–1007	3
	29. 11. 67	175	36° 36.0′ N 36° 36.0′ N	68° 29.0′ W 68° 31.0′ W	4667–4693	1
	23. 05. 68	201	09° 25.0′ S	11° 35.0′ E	1964–2031	1
	28. 03. 71	267	36° 17.1′ N	52° 56.1′ W	1472	1
Discovery	17. 03. 68	6704	27° 44.9′ N	14° 25.0′ W	2129	1
Atlantis II	27. 03. 71	262	36° 05.2′ S	52° 17.9′ W	2440–2480	2
La Perle (Biogas I)	08. 08. 72	DS11	47° 35.5′ N	08° 33.7′ W	2205	1
J. Charcot (Polygas)	31. 10. 72	CV16	44° 06.5′ N	04° 16.9′ W	2226	1
(Biogas III)	24. 08. 73	DS35	47° 34.4′ N	08° 40.7′ W	2226	1
	24. 08. 73	DS36	47° 32.7′ N	08° 36.5′ W	2147	4
(Biogas IV)	18. 02. 74	DS51	44° 11.3′ N	04° 15.4′ W	2430	2
	18. 02. 74	DS52	44° 06.3′ N	04° 22.4′ W	2006	1 s
	21. 02. 74	DS54	46° 31.1′ N	10° 29.2′ W	4659	1
	23. 02. 74	DS58	47° 34.1′ N	09° 08.2′ W	2775	3
	24. 02. 74	DS59	47° 31.7′ N	09° 06.2′ W	2790	2
	26. 02. 74	DS62	47° 31.8′ N	08° 40.0′ W	2175	1
	24. 02. 74	CV38	47° 30.9′ N	08° 59.5′ W	2695	1
	[illegible]6. 02. 74	CPO1	47° 34.6′ N	08° 38.8′ W	2245	1
(Biogas VI)	[illegible]4. 10. 74	DS77	47° 31.8′ N	09° 34.6′ W	4240	1
	25. 10. 74	DS78	46° 31.2′ N	10° 23.8′ W	4706	1
	31. 10. 74	DS86	44° 04.8′ N	04° 18.7′ W	1950	1
	20. 10. 74	CPO8	44° 33.2′ N	08° 38.5′ W	2177	1 s
	20. 10. 74	CPO9	47° 33.0′ N	08° 44.1′ W	2171	1

Distribution

West European Basin, Canary Basin, Guinea Basin, Argentine Basin, Surinam Basin, North America Basin. Depth range: 943–4706 m.

Description

As for subgenus (figures 61 and 62).

There are some variations in shell characters. These can be divided into two types. The first is related to shell damage and subsequent growth. This damage is most frequently associated with the rostrum which, although always short, can vary considerably in length and in the angle and form of the posterior margin. The second is related to the development of the anterior lateral tooth in the right valve; this varies somewhat in both length and breadth and has the secondary effect of emphasizing or not a slight angulation of the anteroventral margin. Shells with a more strongly developed tooth are more angular.

Maximum shell measurements are: length, 6.0 mm; height, 4.5 mm.

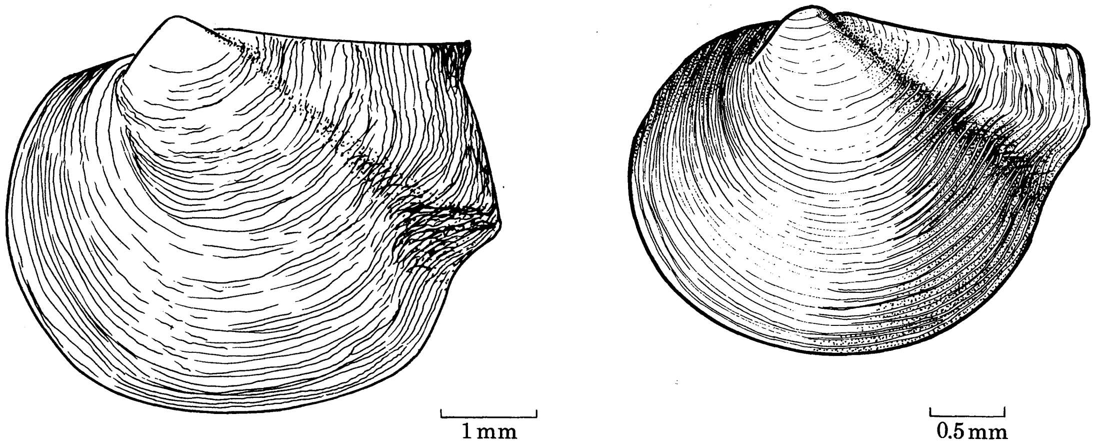


FIGURE 61. *Protocuspidaria verityi*. Lateral views of shells from the left side to show variation in form.

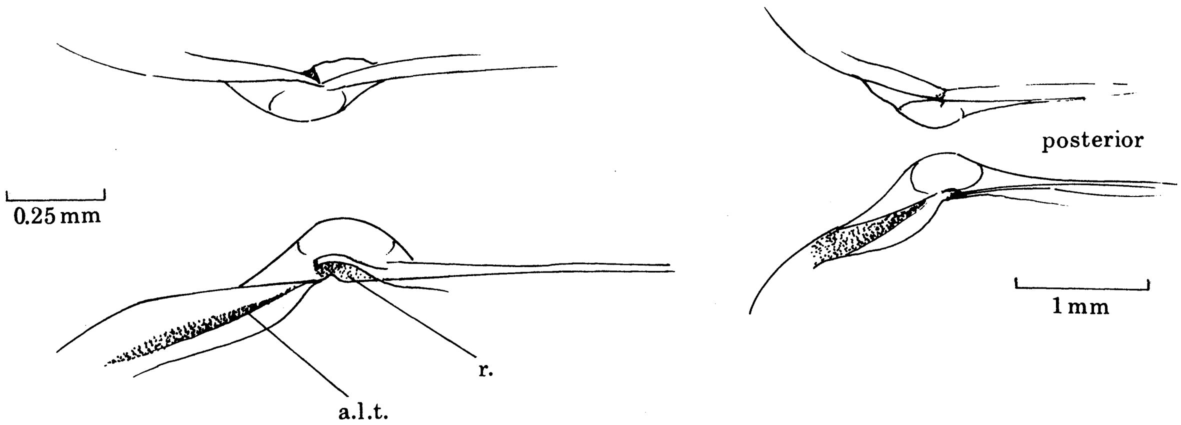


FIGURE 62. *Protocuspidaria verityi*. Lateral views of the hinge of both valves of specimens to show variation in the anterior lateral tooth.

Subgenus Edentaria new subgenus

Type species: *Protocuspidaria* (*Edentaria*) *simplis* n.sp.

Shell rounded, laterally compressed, equivalve, slightly inequilateral; umbones relatively prominent, somewhat angular as opposed to hemispherical; anterior dorsal margin short and evenly rounded, posterior dorsal margin very slightly concave with the right margin slightly overlapping left, anterior and ventral margins evenly and deeply curved; rostrum short, little or no sinuation of ventral margin at base of rostrum, no well defined oblique rostral ridge but usually a prominent oblique line of crossed striae present in this position, sculpture numerous fine close-set concentric striae; no hinge teeth, resilium oblique.

Edentaria simplis new species (figure 63)

Holotype: *Jean Charcot*, station KR33, 47° 30.4′ N, 9° 6.9′ W in 2963 m (Museum of Comparative Zoology, Harvard).

Material

ship	date	stn	latitude	longitude	depth/m	number
Chain	04. 07. 65	84	36° 24.4′ N	67° 56.0′ W	4749	2
Atlantis II	23. 08. 66	125	37° 24.0′ N	65° 54.0′ W	4825	2
	05. 02. 67	142	10° 30.0′ N	17° 51.5′ W	1624–1796	2
Discovery	18. 03. 68	6709	27° 29.8′ N	15° 20.1′ W	2351	1
La Perle (Biogas I)	08. 08. 72	DS11	47° 35.5′ N	08° 33.7′ W	2205	2
J. Charcot (Polygas)	21. 10. 72	DS15	47° 35.2′ N	08° 40.1′ W	2246	4
	22. 10. 72	DS18	47° 32.2′ N	08° 44.9′ W	2138	3
J. Charcot (Biogas IV)	22. 02. 74	DS55	47° 34.9′ N	09° 40.9′ W	4125	6
	24. 02. 74	DS60	47° 26.8′ N	09° 07.2′ W	3742	1
	24. 02. 74	KR33	47° 30.4′ N	09° 06.9′ W	2963	1 s

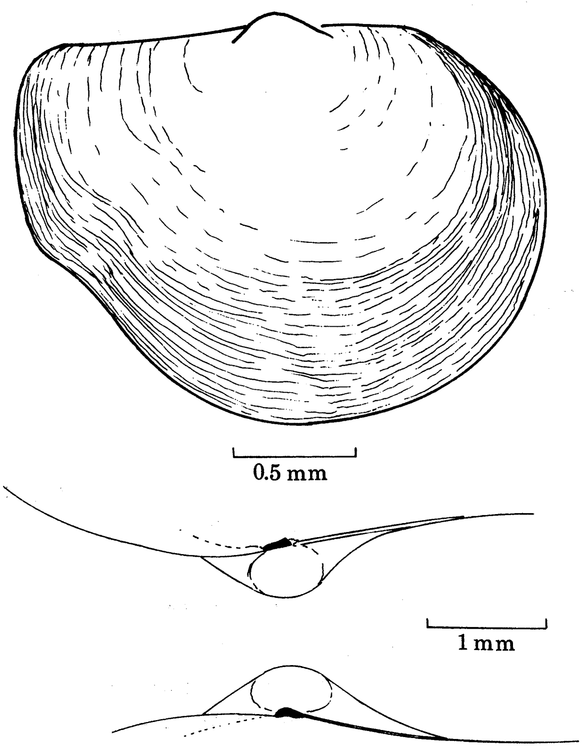


FIGURE 63. *Protocuspidaria simplis*. Lateral view of the shell from the right side and lateral views of the hinge of both valves.

Distribution

West European Basin, North Atlantic, North America Basin, Canaries Basin and Cape Verde Basin. Depth range: 1624–4825 m.

Description

As given under the subgenus (figure 63).

The specimens show some variation in height. The posterior margin of the rostrum may be angled rather than vertical, but as in other species this is probably due to predator damage.

Maximum shell measurements are: length, 4.4 mm; height, 3.4 mm.

Subgenus Bidentaria new subgenus

Type species: *Protocuspidaria* (*Bidentaria*) *atlantica* n.sp.

Shell, laterally compressed, equivalve, inequilateral, hemispherical umbones; anterior dorsal margin short, posterior dorsal margin straight; anterior and ventral margins evenly curved; rostrum short, truncate; surface sculpture numerous concentric striae that continue onto rostrum; no rostral ridge, but faint, fibrous irregularities in striae in this position at base of rostrum; hinge simple, single anterior lateral tooth in both valves; resilium oblique.

This subgenus is similar to the subgenus *Protocuspidaria* except that the rostrum is longer and narrower, and that there is an anterior lateral tooth in left valve (figure 64).

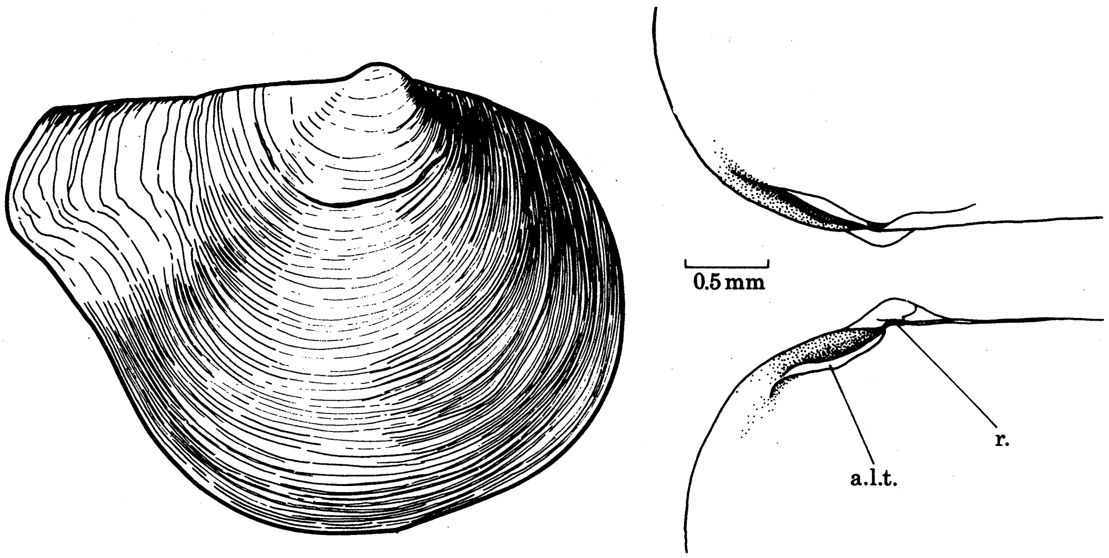


FIGURE 64. *Protocuspidaria atlantica*. Lateral view of the shell from the right side and lateral views of the hinge of both valves.

Bidentaria atlantica new species (figures 64–67)

Holotype: *Discovery*, station 6696, 28° 6.0′ N, 13° 28.0′ W, in 1780 m (Museum of Comparative Zoology, Harvard).

Material

ship	date	stn	latitude	longitude	depth/m	number
Discovery	15. 03. 68	6696	28° 06.0′ N	18° 28.0′ W	1780	1
Atlantis II	18. 07. 66	118	32° 19.4′ N 32° 19.0′ N	64° 34.9′ W 64° 34.8′ W	1150	1 s
	24. 08. 66	126	39° 37.0′ N	66° 47.0′ W	3806	2
J. Charcot (Biogas VI)	25. 10. 74	DS78	46° 31.2′ N	10° 23.8′ W	4706	1
	26. 10. 74	CP17	46° 30.8′ N	10° 19.5′ W	4706	1

Distribution

West European Basin, Canaries Basin, North America Basin. Depth range: 1150–4706 m.

Description

Shell small, laterally compressed, equivalve, inequilateral; small, hemispherical umbones; anterior dorsal margin short and evenly rounded, posterior dorsal margin straight; anterior and ventral margins evenly and deeply curved, rostrum fairly short, wide, truncate, with little or no ventral sinuation; surface sculpture numerous moderately coarse, close-set, concentric striae that continue onto rostrum, no oblique rostral ridge, but faint, fibrous irregularities in striae along line of base of rostrum; hinge simple, single anterior lateral tooth in both valves, resilifer oblique.

Maximum shell measurements are: length, 7.4 mm; height, 5.2 mm.

Apart from differences in the hinge dentition the morphology of the three species is broadly similar and there is sufficient variation between individuals to make identification other than by reference to dentition extremely difficult. Figures 61–64 of lateral views of the shells of the three species are of forms most frequently observed, but as will be seen individual variation is marked. We have debated whether the hinge characters themselves may also be individual variations within a single species. At present we believe that the three typical forms are sufficiently distinct for us to regard them as species.

Anatomy of Protocuspidaria

Despite some marked anatomical differences from the genus *Cuspidaria*, species of *Protocuspidaria* are obviously cuspidariid in form (figure 65).

The siphons, though short, bear the seven tentacles typical of the Cuspidariidae. The internal partition in the inhalant siphon is as in *Cuspidaria*, and not similar to the valve present in the Verticordiidae (Allen & Turner 1974) and the Poromyidae. The palps are of type III, in keeping with there being more than five pairs of pores in the membranous septum. The foot, sinuses, kidney, digestive and reproductive systems are similar to those described for *C. obesa*. The septum, however, differs markedly from species described so far.

The septum is unique, with a morphology intermediate between that of the verticordiid, in which the gill may be reduced to the descending lamella of the inner demibranch alone and where it is attached to body and mantle by membrane junctions, and that of *Halonympha*, in which the septum has numerous cuspidariid-like pores set in a slightly muscular horizontal sheet of tissue.

The septum in *Protocuspidaria* consists of a membranous horizontal partition across the mantle cavity with very little muscle within it. Longitudinal sections show that what appears to be transverse ridging on the membrane surface to be 16 pairs of very short gill filaments, held horizontally within the septum and arranged in a single series on either side of the foot, and converging behind it. Each filament is relatively broad, and is joined to its neighbour at inner and outer limits by a membrane formed by interfilamentar connections and axis tissue. Each filament with its usual complement of blood space and supporting skeletal rod bears only lateral cilia. The latter are not divided into two separate bands as is found in a typical cuspidariid pore (figure 66). Muscles associated with the membranous septum are a few short unstriated lateral fibres that pass into the dorsal part of the mantle, and which appear to be homologous to the cuspidariid lateral septal muscles (figure 67). There are no well defined posterior septal muscles (also true of *Halonympha*) and no well defined anterior septal muscles. The dorsal and ventral epithelia fuse posteriorly with the intersiphonal septum, laterally with the mantle and foot, and anteriorly close to the mouth. Unlike in other cuspidariids, in which the posterior pedal retractor muscles form a single band until just before their attachments onto the shell, here both anterior and posterior pedal retractors form two bands of muscle along the base of the foot below the viscera. Thus, there are two well developed bands of muscle adjacent to the attachment of the septum with the foot. In transverse section these pedal muscle blocks are arranged

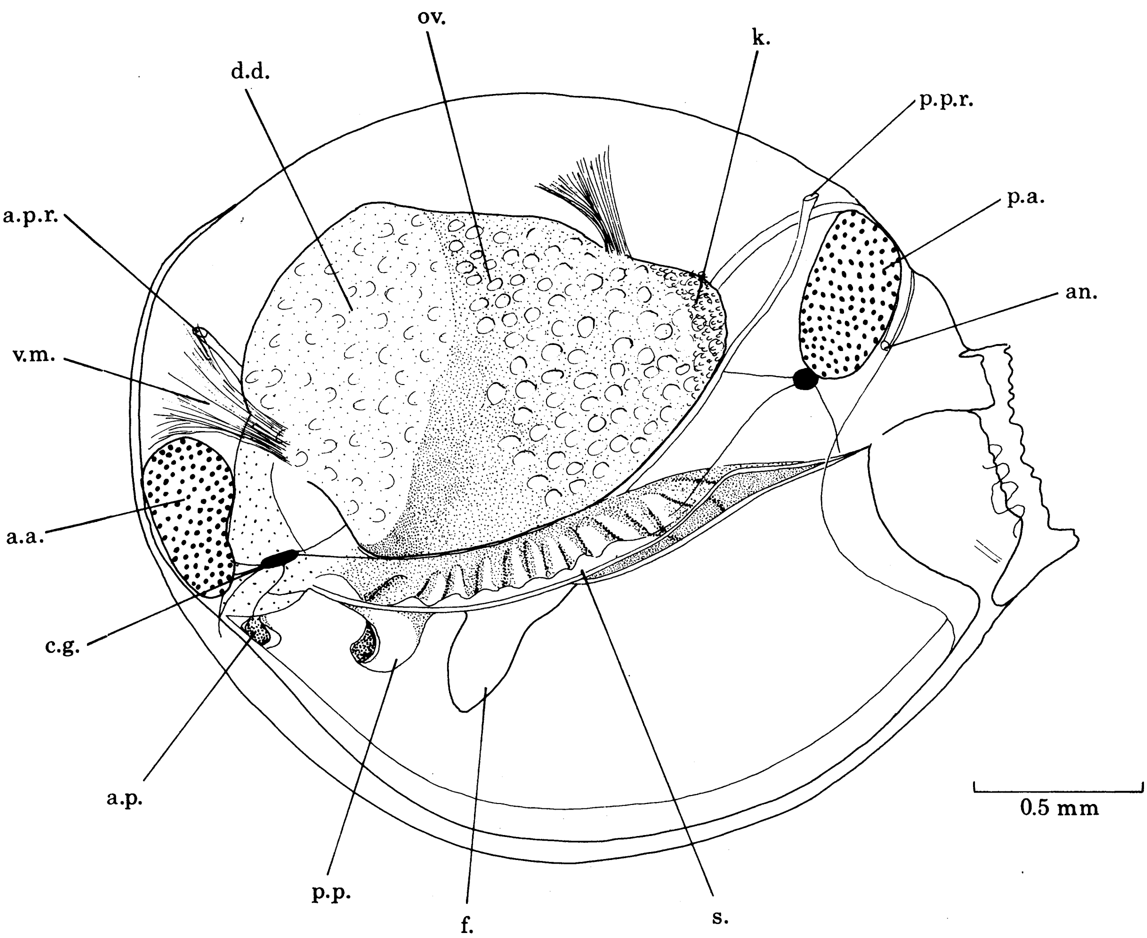


FIGURE 65. *Protocuspidaria atlantica*. Anatomy as seen from the left side.

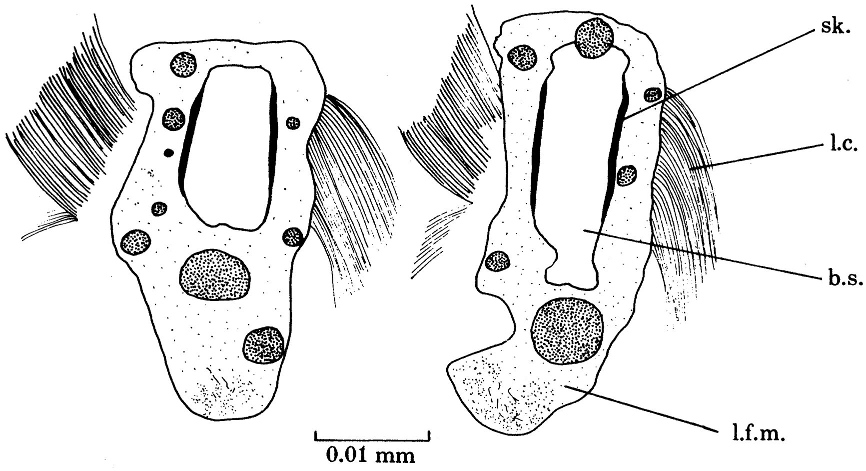


FIGURE 66. *Protocuspidaria atlantica.* Transverse section through the gill filaments.

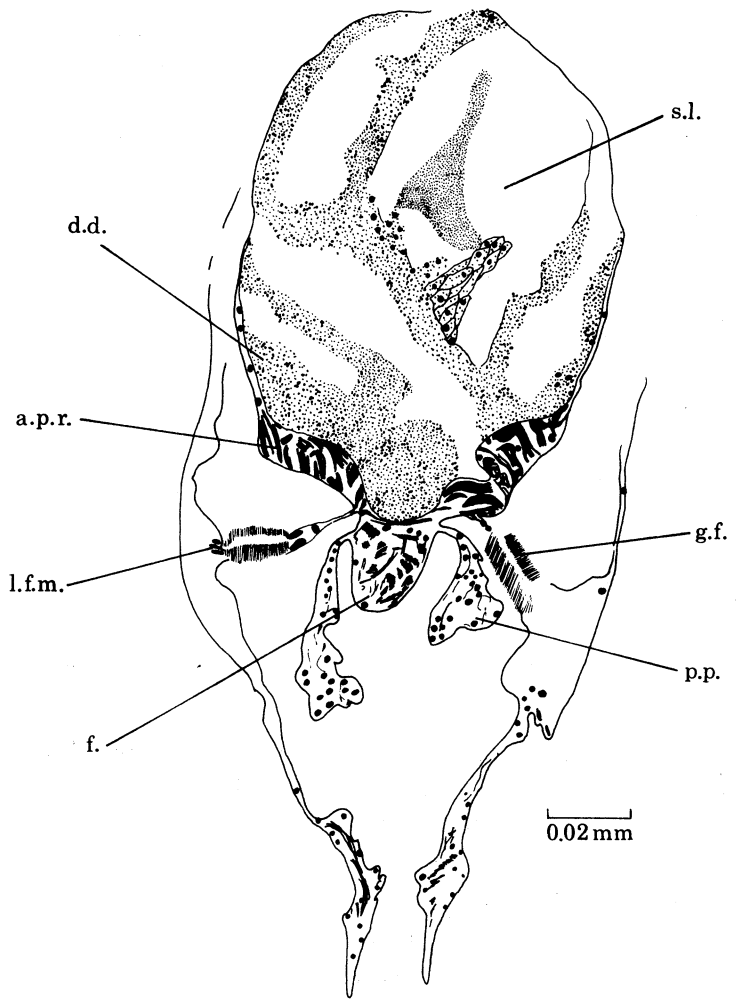


FIGURE 67. *Protocuspidaria atlantica.* Transverse section of anterior part of body through the region of the gill and posterior palp.

in a pattern remarkably similar to that of the inner longitudinal septal muscle of a typical cuspidariid.

The septum of *Protocuspidaria* is thus similar to the condition seen in some verticordiids, such as *Lyonsiella perplexa* or *Verticordia quadrata* (Allen & Turner 1974). *Protocuspidaria* is obviously cuspidariid in form by virtue of its siphonal structure, large cup-shaped posterior palps, and that it is dioecious. The fact that gill filaments can be recognized in the septum is extremely important for, taken together with the fact that the septum is innervated by a nerve derived from the *visceral* ganglia, it strongly suggests that the septibranch septum is, for the most part, ctenidial in origin.

The arrangement of nerves is similar to that of *Halonympha*. Inner and outer septal nerves do not reach the pedal and cerebral ganglia, respectively. Lacunal cells are particularly conspicuous, being scattered within the lateral walls of the exhalant chamber, and overlie the visceral ganglion. They are also concentrated in dense groups in the roof of the exhalant chamber and the intersiphonal septum.

Genus Poromya

Some morphological features of *Poromya* are well known, particularly those that distinguish the genus from *Cuspidaria*, but, despite the studies by Pelseneer (1881, 1891, 1911), Dall (1890), Ridewood (1903) and Yonge (1928), a detailed comparison of the septum with those of *Cetoconcha*, *Verticordia* and *Cuspidaria* has not been given before.

Dall (1881, 1886, 1890) and Pelseneer (1888*a*, *b*, 1891, 1911) gave the first accounts of poromyid anatomy and compared it with what was then known of *Cetoconcha* and *Cuspidaria*. Ridewood (1903) described the structure of the septum and branchial sieves and later Yonge (1928), the only person to do so, examined living *P. granulata* and observed branchial sieves and feeding. Since then Odhner (1960) has briefly described the anatomy of *P. romanchensis*, noting that the number of gill filaments in the branchial sieves of the different species varies, even in different individuals within a species. Knudsen (1970), who described three species of *Poromya*, also noted variability in the number of filaments and siphonal tentacles. Bernard (1974) describes the shell characteristics of eleven species and the anatomy of one, while Yonge & Morton (1980) describe the poromyid ligament.

Poromya tornata (Jeffreys, 1876) (figures 68–77)

1876	*Pecchiola tornata*	Jeffreys (p. 494)
1884	*Poromya sublevis*	Verrill (p. 221)
1885	*Verticordia tornata*	Smith (p. 170)
1888	*Verticordia tornata*	Pelseneer (p. 10)
1889	*Poromya sublevis*	Dall (p. 68)
1889	*Poromya tornata*	Dall (p. 68)
1889	*Poromya sublevis*	Dall (p. 448)
1889	*Verticordia (Pecchiola) tornata*	Dautzenberg (p. 68)
1890	*Poromya microdonta*	Dall (p. 290)
1895	*Poromya (Cetoconcha) tornata*	Smith (p. 11)
1897	*Poromya (Cetoconcha) isocardioides*	Dautzenberg (p. 230)
1898	*Poromya sublevis* var. *microdonta*	Verrill & Bush (p. 183)
1898	*Verticordia tornata*	Locard (p. 200)
1927	*Poromya (Cetoconcha) isocardioides*	Dautzenberg (p. 351)
1940	*Cetoconcha tornata*	Winckworth (p. 28)
1949	*Poromya (Poromya) sublevis microdonta*	Haas (p. 7)
1960	*Poromya romanchensis*	Odhner (p. 375)
1961	*Poromya sublevis*	Clarke (p. 379)
1962	*Poromya sublevis*	Clarke (p. 70)

1962	*Poromya* (*Cetomya*) *tornata*	Clarke (p. 70)
1962	*Cetoconcha isocardioides*	Clarke (p. 70)
1967	*Poromya tornata*	Knudsen (p. 332)
1970	*Poromya tornata*	Knudsen (p. 124)

Knudsen (1970) synonymized *P. microdonta*, *P. isocardioides*, *P. sublevis* and *P. romanchensis* with *P. tornata.*

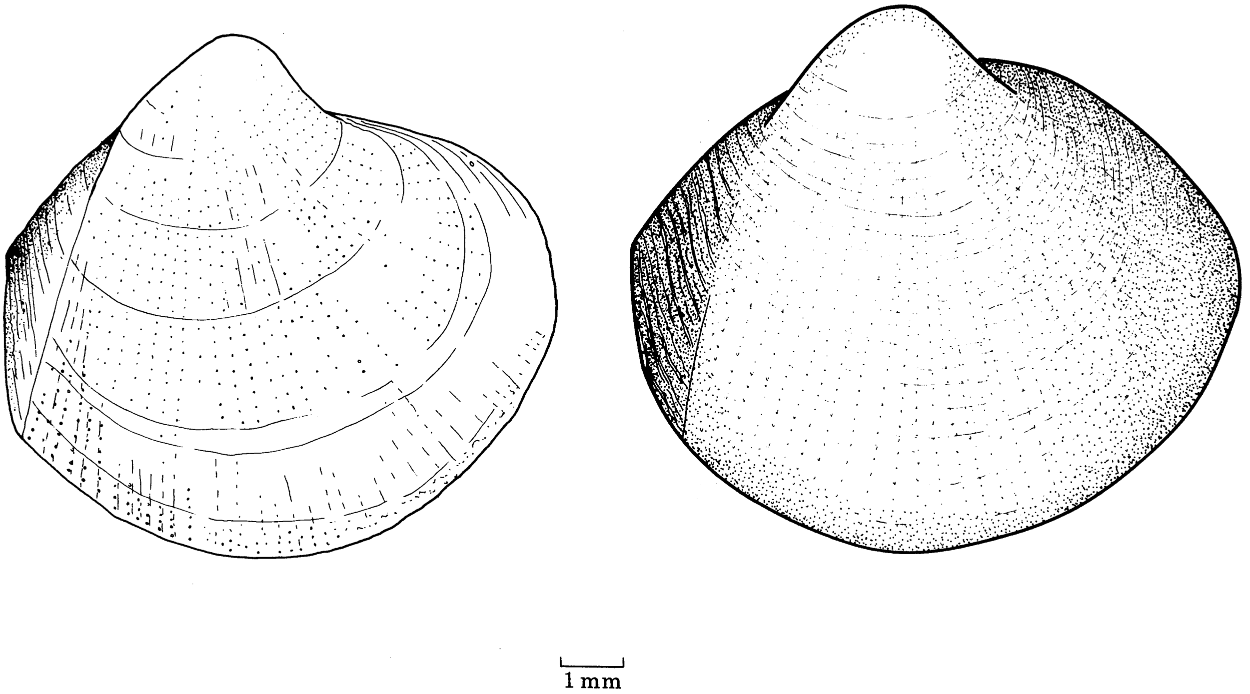


FIGURE 68. *Poromya tornata*. Lateral view of shells from the right side to show variation in outline.

Material

ship	date	stn	latitude	longitude	depth/m	number
Galathea	09. 04. 51	280	01° 56.0′ N	77° 00.5′ E	4350	1
Akad.Kurchatov	—	1233	14° 39.0′ N	73° 39.0′ W	3500	2
	—	1240	19° 26.0′ N	80° 28.0′ W	3060	1
Walda	20. 06. 71	DS31	03° 17.5′ N	02° 01.7′ E	4279	1
	01. 08. 71	CY20	02° 39.5′ S	05° 43.2′ E	4088	4
Atlantis II	13. 02. 67	155	00° 03.0′ S	27° 45.0′ W	3730–3783	2
	14. 02. 67	156	00° 46.0′ S	29° 28.0′ W	3459	1 + 3 valves
J. Charcot (Polygas)	24. 10. 72	DS21	47° 31.5′ N	09° 40.7′ W	4190	1
Cryos (Biogas V)	16. 06. 74	CV41	47° 27.0′ N	09° 01.0′ W	3800	2
J. Charcot (Biogas VI)	23. 10. 74	DS76	47° 34.8′ N	09° 33.3′ W	4228	2
	23. 10. 74	CP13	47° 34.4′ N	09° 38.0′ W	4134	1
	25. 10. 74	CP16	46° 27.3′ N	10° 25.8′ W	4825	2
	26. 10. 74	CP17	46° 30.8′ N	10° 19.5′ W	4706	7
	26. 10. 74	CP16	46° 30.5′ N	10° 26.0′ W	4721	2

Distribution

North and central Atlantic, west and central Indian Ocean. Depth range: 2085–5300 m.

Description

Shell rhomboidal, inequilateral, slightly inequivalve, with high swollen umbos; dorsal margins slope steeply, ventral margin curved and slightly produced centrally, posterior margin not rostrate but roundly truncate with short, deep slightly gaping, siphonal opening; anterior cardinal tooth in right valve fitting in socket in left; ligament external, opisthodetic, resilifer oblique and posteriorly directed; shell surface with very faint concentric growth lines and numerous granular radial striae, striae most distinct posteriorly and ventrally; single, oblique, rostral keel in right valve only extends from umbo to posteroventral margin.

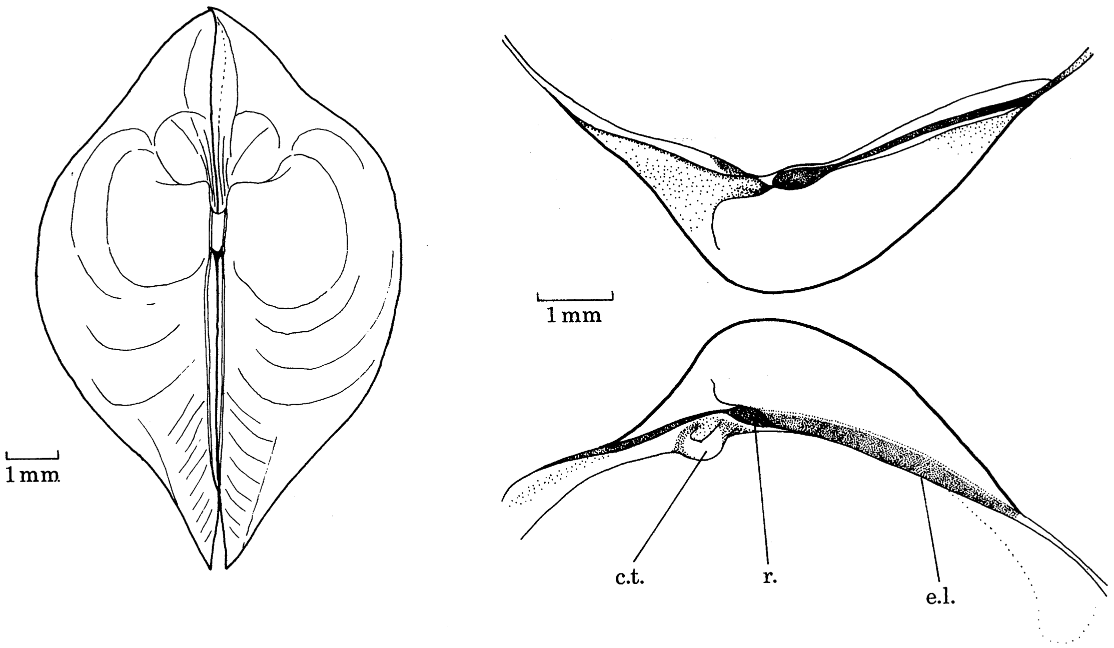


FIGURE 69. *Poromya tornata*. Dorsal view of shell and dorsolateral view of the hinge of both valves.

The pedal gape is greater in *P. tornata* than in any cuspidariid species examined (figure 70). The well developed marginal folds are fused at the extreme anterior end and beneath the inhalant siphonal valve. The fusion involves the inner lobe and the inner face of the middle lobe. In general there appears to be more muscle present, although the animals are large. There is no concentration of gland cells beneath the main mantle rejection tract that extends the length of the ventral mantle edge, suggesting a difference in the quality and/or quantity of pseudofaecal material.

The structure of the foot is similar to that in the Cuspidariidae. It is long, cylindrical and externally ciliated. There are two anterior pedal retractor muscles and a single posterior muscle that bifurcates close to its dorsal insertions. The musculature of the foot consists of an inner circular layer, with a layer of longitudinal muscles to the outside, plus several bands of transverse muscle. A byssal groove and a byssogenous cavity are present but, relative to the size of the foot, both are much smaller and nearer to the tip of the foot than in the Cuspidariidae. There are few gland cells adjacent to the byssogenous cavity and no byssus threads were seen.

The epithelial seal between the foot and septum in the genera *Cuspidaria* and *Halonympha*, while tenuous, is complete. In contrast, the pedal muscle of *P. tornata* extends laterally into the septum from an anterior position between the posterior palps to a point level with the posterior wall of the style sac, thus forming a strong, muscular connection with the septum. Furthermore, although it is held close to the posterior pedal retractor, for a short distance posterior to the anterior branchial sieve the septum is free of the foot.

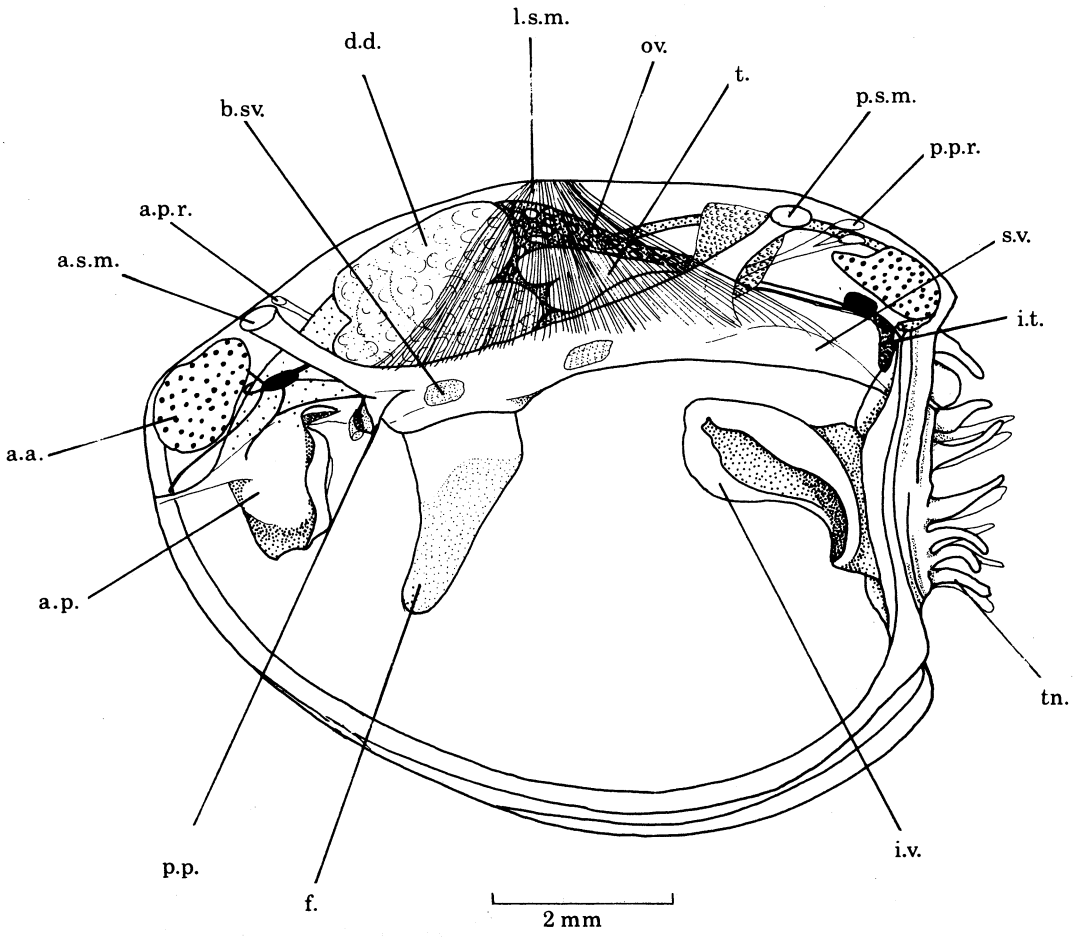


FIGURE 70. *Poromya tornata*. Anatomy as seen from the left side.

The septum is comparable to that of *Cuspidaria* in that it is a strong, muscular, horizontal partition that divides the mantle cavity into infra- and supraseptal cavities with the foot passing through it. It is pierced by two paired groups of apertures.

All the muscles previously described are present (figure 71), though they are not as well developed as in some cuspidariids. The muscles are not striated. The inner longitudinal muscle lacks an independent dorsal attachment to the shell and originates within the membrane around the mouth. A strong anterior septal muscle extends from an anterodorsal attachment to the shell, to curve behind the foot and the posterior branchial sieve. Left and right posterior septal muscles consist of discrete narrow bands of muscle from a dorsal shell attachment and curve ventrally in a semicircle behind the foot, where they meet medially. There is no separate outer longitudinal muscle but lateral septal muscles are obvious; these penetrate the mantle and come together and attach to the shell laterodorsally, forming a lateral triangular area. These lateral bands of muscle are much stouter than those in *Cuspidaria* (figures 3, 71).

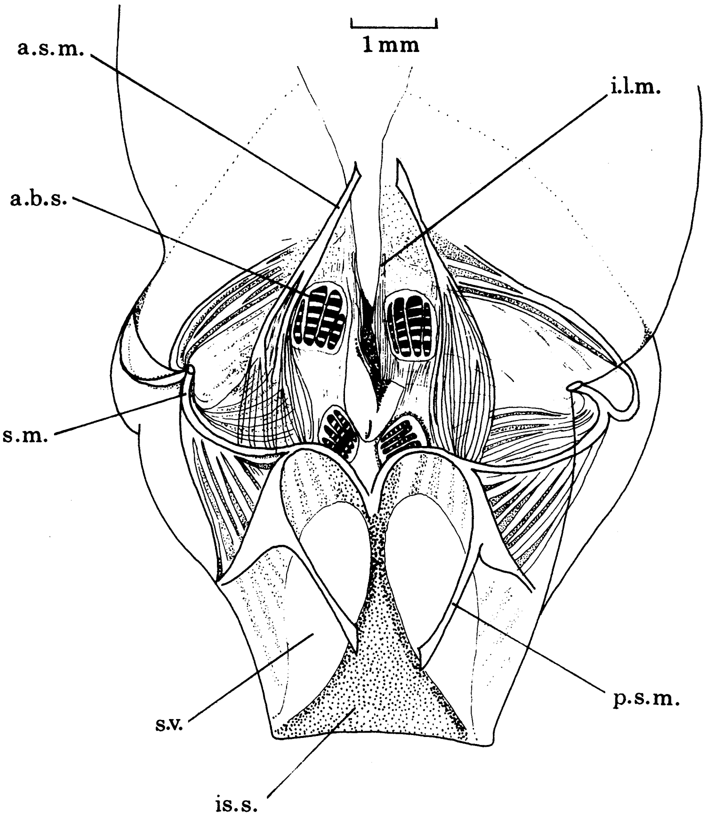


FIGURE 71. *Poromya tornata*. Dorsal view of the septum.

Behind the posterior septal muscles, instead of thin epithelia connecting with the intersiphonal septum, there are two thick longitudinal pear-shaped pads (figure 72). These were first reported by Pelseneer (1891); Odhner (1960) termed them the 'septal valvulae' and described them in some detail. Odhner (1960) thought that they strengthened the posterior part of the septum. They are present in all species of *Poromya* so far examined. Sections show a central lumen, posteriorly continuous with the siphonal sinuses and anteriorly continuous with the septal sinuses. The walls are thick, with numerous muscle fibres and round, darkly staining cells. Dorsal and ventral epithelia come together in the midline. The significance of the organ is discussed later.

The septum of *P. tornata* contains gill filaments that are arranged in two paired groups and which have been variously termed 'branchial sieves', 'sieve plates' or 'oscula' in the literature. The filaments are very short and set horizontally in the surrounding septum, the anterior and posterior being joined to the septum along a lateral face, i.e. they appear as half filaments. The posterior group lies behind the foot, immediately anterior to the posterior septal muscle, and therefore is situated in the posterior part of the anterior septal muscle. The posterior group

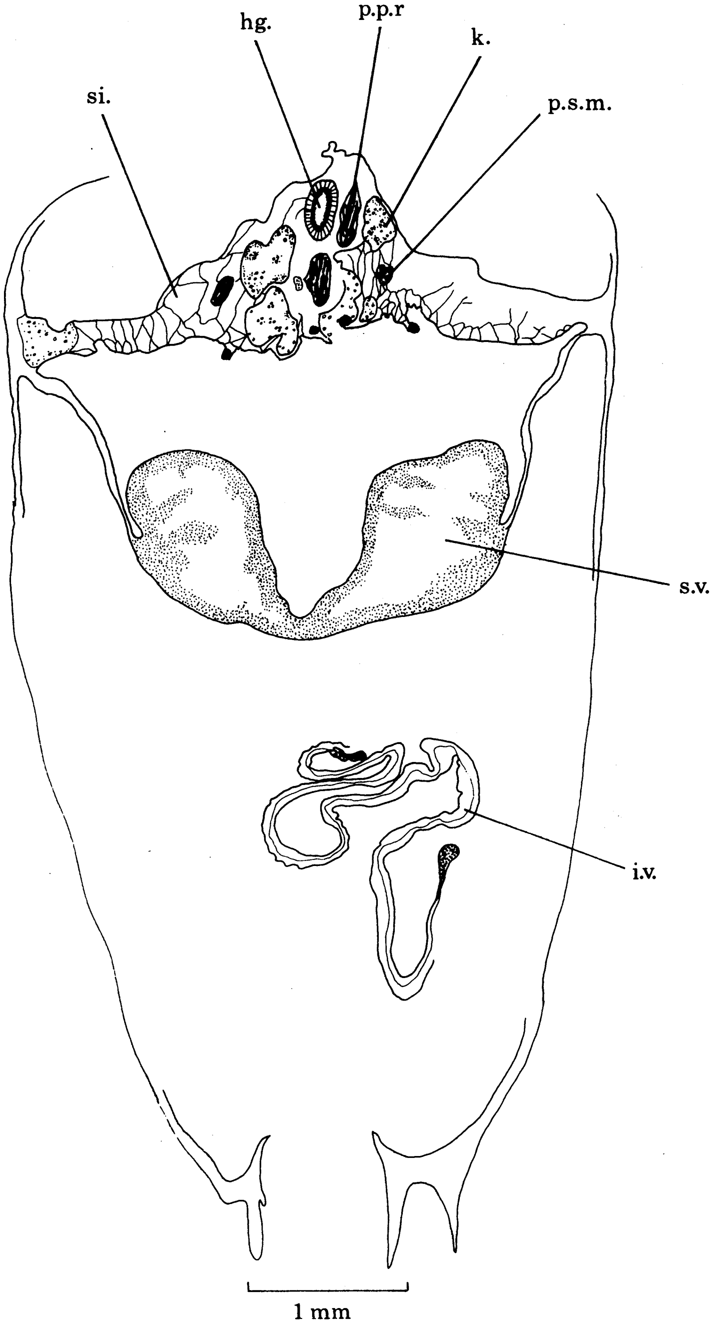


FIGURE 72. *Poromya tornata*. Transverse section through the posterior part of the body to show the kidney and septal valvulae.

consists of five filaments and two half end filaments, thus forming six slits. The anterior group lies close to the inner longitudinal septal muscle and foot, posterior to the palps, and consists of four filaments and two half end filaments, forming five slits. In addition, each group has three rows of interfilamentar tissue connections joining the dorsal surfaces of the filaments. Together filaments and connections form a lattice-like structure resembling a sieve. In transverse section, the filaments are seen to be typical triangular gill filaments similar to those of the Verticordiidae (Allen & Turner 1974) (figure 73), with a central blood space, two skeletal rods against the lateral walls and a dorsal band of longitudinal muscle. Lateral cilia line the slit between the filaments, with a more extensive band of short frontal cilia on the ventral (frontal) surface of each filament. Yonge (1928) notes that *P. granulata* has no frontal cilia on the gill filaments. Although this is true, *P. granulata* has branchial sieves that differ markedly in form from those of *P. tornata*.

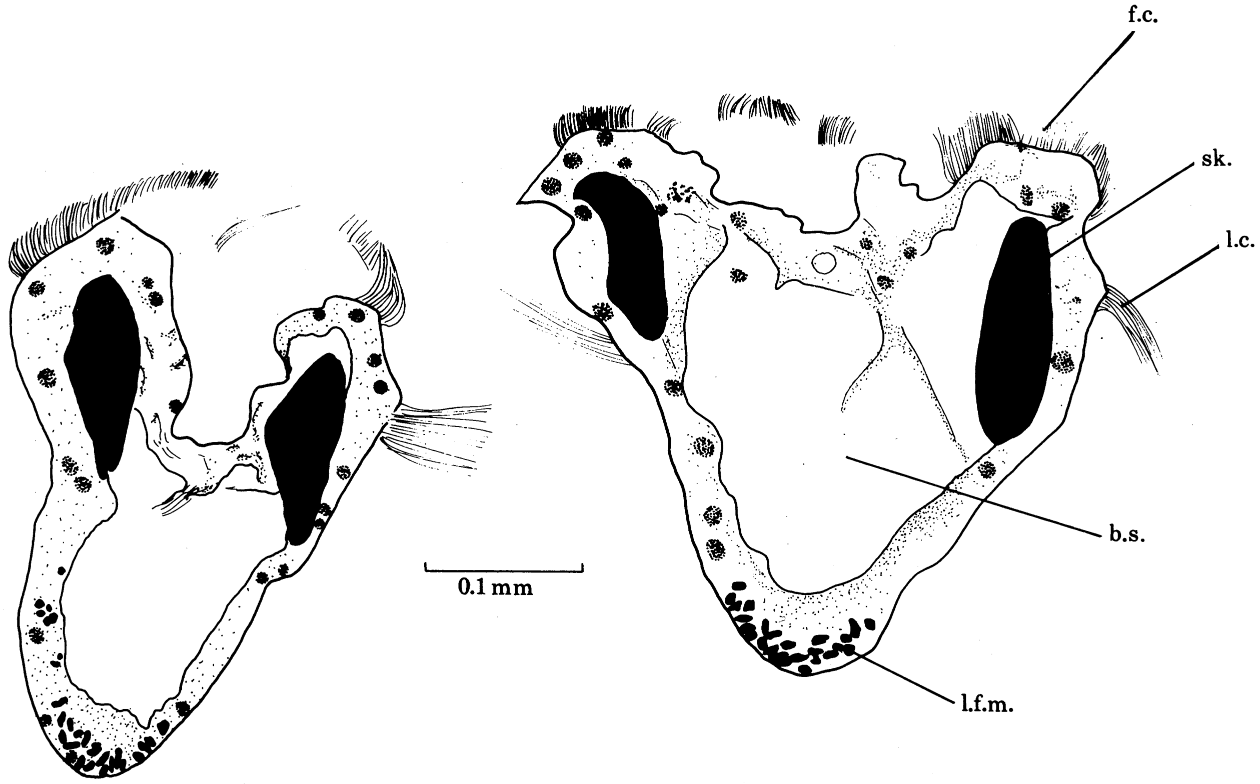


FIGURE 73. *Poromya tornata*. Longitudinal section of two filaments.

In contrast to those of *Cuspidaria*, the palps of *P. tornata* are large and well developed, but unlike in *Protocuspidaria* and *Halonympha*, it is the anterior and not the posterior pair that are large cup-shaped structures curving over the mouth. The posterior pair of palps form smaller, pendulous cups (figure 74). Both pairs of palps contain much longitudinal muscle, are heavily ciliated on their inner surface, but are not ridged. As in the Cuspidariidae, the mouth is a ventral-facing funnel, whereas in the Verticordiidae the mouth is posteriorly directed (Allen & Turner 1974). We have been unable to examine any living *Poromya* and so are unable to confirm Yonge's (1928) observation, in life, that the palps push food into the mouth.

The gut takes the same course as that in the Cuspidariidae and Verticordiidae. The oesophagus is heavily folded and ciliated, and is surrounded by a thick coat of muscle, consisting of an inner circular layer and an outer longitudinal layer, and which further extends over the whole stomach. In contrast to the scanty, incomplete muscle layer seen in *C. obesa*, the muscle layer here is 0.02 mm thick in a stomach measuring 0.9 mm × 1.04 mm. The ventral half of the

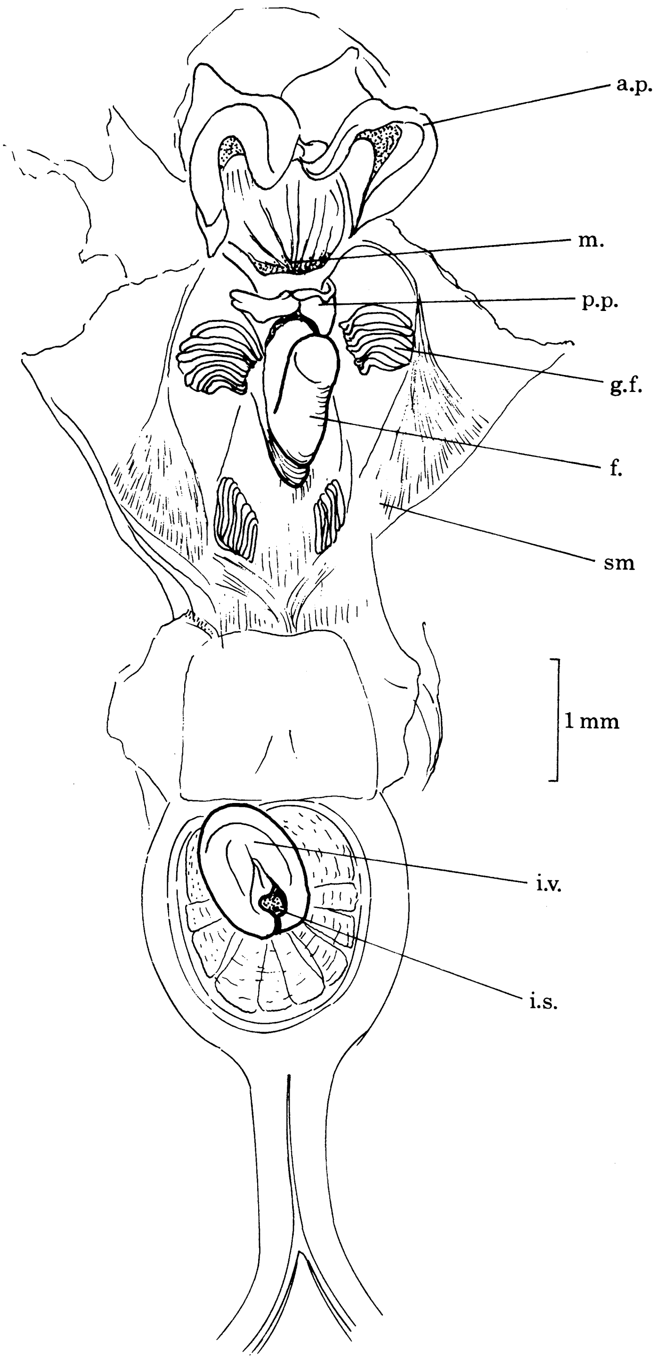


Figure 74. *Poromya tornata*. Ventral view of inhalant aperture body, palps and septum.

stomach, from the oesophagus to the digestive ducts, is lined with densely ciliated columnar cells, while the dorsal epithelium consists of non-ciliated columnar cell containing spherules of pale-staining material. This epithelium is covered with a thick gastric shield. Except that they appear to be relatively longer, the digestive ducts and style sac are as in the Cuspidariidae. No style was seen, but a typical brush border is present and it is probable that the style was dissolved before preservation.

The digestive gland is more extensive than in the Cuspidariidae and surrounds the stomach ventrally and laterally (figure 75), where it forms two short dorsal horns that fill the space beneath the umbones. The constituent tubules are smaller and more numerous than in *C. obesa*. There are also small groups of muscle fibres scattered in the epithelium between the tubules which were not seen in any cuspidariid.

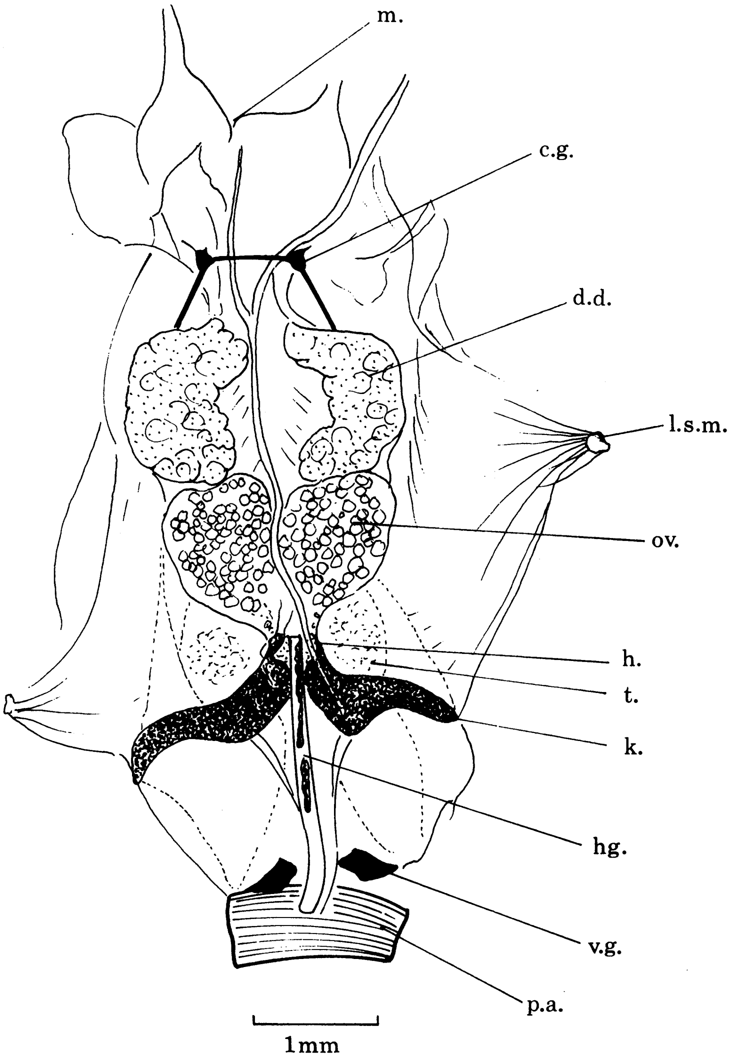


FIGURE 75. *Poromya tornata*. Dorsal view of body.

Siphons

Although *Poromya* and *Cetoconcha* have similar siphons, these differ substantially from those of the Cuspidariidae. In *Poromya tornata* the siphons are short and wide with the inhalant siphon much larger than the exhalant. There is no common siphonal sheath within which the siphons can retract. In preserved specimens the siphons appear to be slightly domed, barely projecting from the posterior shell margin, but in life they are widespread, extended and flat on the surface of the mud (Yonge 1928). The apertures of the two siphons are surrounded by a ring of tentacles whose number appears to be species specific (figure 76). As Knudsen (1970) has shown, the form of the tentacles in *P. tornata* is totally different from that of the Cuspidariidae. There are 13 short, tapering tentacles which are neither club-ended nor 'frilled'. Six pairs occur around the ventral inhalant siphon, and there is a single dorsal tentacle above the exhalant siphon. In addition, there are four pairs of small, characteristic knobs or papillae between certain of the tentacles. From the ventral side of the inhalant siphon, there are two papillae close to each other on the fused mantle edge beneath the first pair of tentacles; a second pair is present between the third and fourth pair of tentacles, a third pair between the fourth and fifth pair of tentacles and a fourth pair of papillae above the sixth pair of tentacles, at either side and below the ventral edge of the exhalant siphon (figure 76).

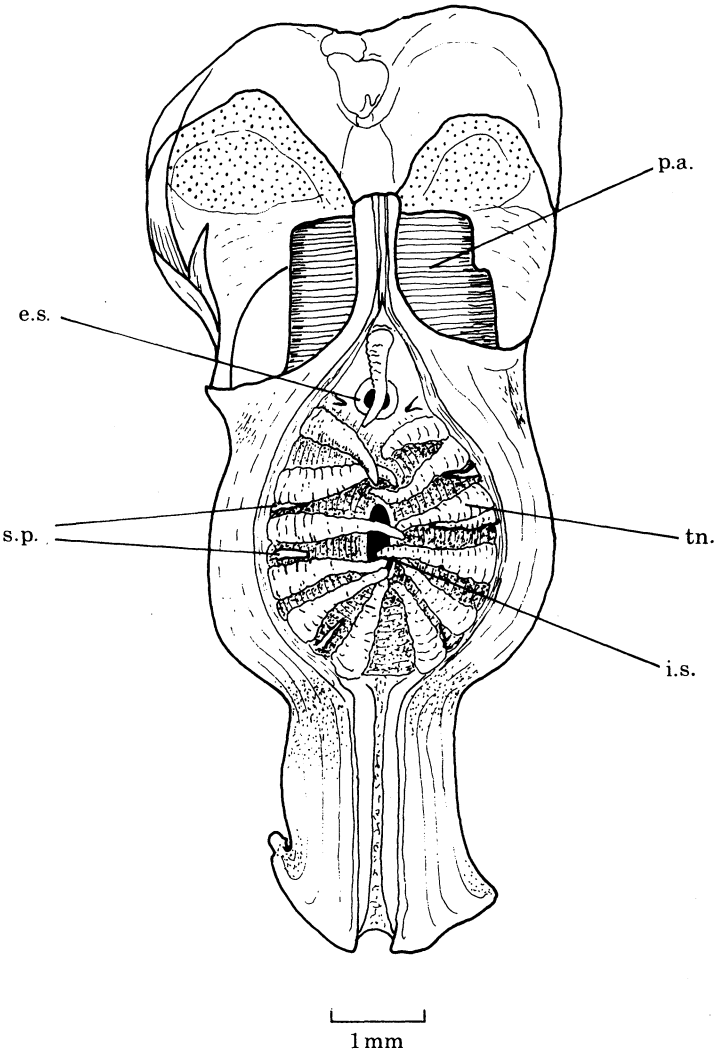


FIGURE 76: *Poromya tornata*. Posterior view of siphonal region.

A pair of longitudinal sinuses, continuous with the septal sinuses, run the length of each tentacle. The tentacular sinuses are surrounded by a layer of longitudinal muscle and, within, numerous radial muscle fibres. The papillae appear to be without sinuses, although they contain several radial and longitudinal muscle fibres.

In addition to the external tentacles, there is also a pair of internal tentacles attached to the dorsal epithelium of the supraseptal cavity posterior to the posterior adductor muscle. These hang below the visceral ganglion close to the internal aperture of the exhalant siphon (figure 70). These structures have never been described before but are present in *Poromya* and *Cetoconcha*. They appear to consist of connective tissue, and a few scattered transverse muscle fibres, with a restricted sinus space continuous with the mantle sinus. Their function is as yet unknown, but they may help to cleanse the suprabranchial cavity of faecal material.

The siphons are separated by an intersiphonal septum that is continuous with the septal valvulae. The epithelia of the intersiphonal septum are separated by connective tissue and some scattered muscle fibres. The siphons differ slightly from those in the Cuspidariidae in that, while each siphon has two layers of circular muscle (as in the Cuspidariidae), they have only one layer of longitudinal muscle. The inhalant siphon has inner and outer layers of circular muscle, with an *outer* longitudinal muscle layer, while the exhalant siphon has inner and outer circular muscle layers, with an *inner* layer of longitudinal muscle. The siphonal retractor muscles are much shorter than those in the Cuspidariidae.

The inhalant valve is a large, muscular, hood-shaped structure, projecting inwards from the internal margin of the inhalant aperture (figure 70). It is roughly tubular, but shorter and narrower ventrally than dorsally. It is attached to the intersiphonal septum, and sections show that it has inner and outer layers of circular muscle with an outer layer of longitudinal muscle and thus is comparable to the inhalant siphon. The free inner margins contain a thick layer of circular muscle, contraction of which may close the inhalant aperture. The valve of the Poromyidae is similar to that of the Verticordiidae.

Nervous system

The nervous system is similar to that described for *Cuspidaria* and *Halonympha*. There are three pairs of ganglia, a pair of visceral and a pair of pallial connectives running between the visceral to cerebropleural ganglia, a siphonal ring nerve from the pallial connectives, and a pair of pedal connectives passing back from the cerebropleural to pedal ganglion. The septal innervation differs in two respects from that of the Cuspidariidae. The inner septal nerve, which in *Cuspidaria* runs from the cerebropleural to pedal ganglion, and which in *Halonympha* never connects with the pedal ganglion, is absent in *Poromya*. The outer septal nerve from the visceral ganglion passes along the inner edge of the posterior septal muscle and forward within the septum. In contrast to *Cuspidaria*, but like *Halonympha*, the latter nerve does not extend as far as the cerebropleural ganglion (figure 97).

Reproductive system

There is no dispute that *Poromya* (and *Cetoconcha*) are hermaphrodite. The gonads are in the same relative position as they are in the Cuspidariidae, with the ovary overlying the testes. The ovary in *P. tornata* consists of a pair of slightly lobulated, elongate sacs, one either side of the midline, that cover the roof and the posterior wall of the stomach (figure 75). The testes lie ventral to the ovary and consist of a pair of lobulated sacs (figure 77). Behind the stomach the gonads taper into four ducts, the female pair dorsal to the male pair. At a point close to the anterior end of the kidney the male and female ducts of each side come together to form a hermaphrodite duct that continues for a short distance before opening into the exhalant cavity above the septal valvulae.

The heart is dorsal to the hindgut. The mantle sinuses dorsal to the viscera, barely discernible in *Cuspidaria*, are well developed. In contrast the siphonal sinuses are less well developed. The mantle sinuses extend within the tissues lining the dorsal side of the posterior part of the exhalant cavity and into the siphons.

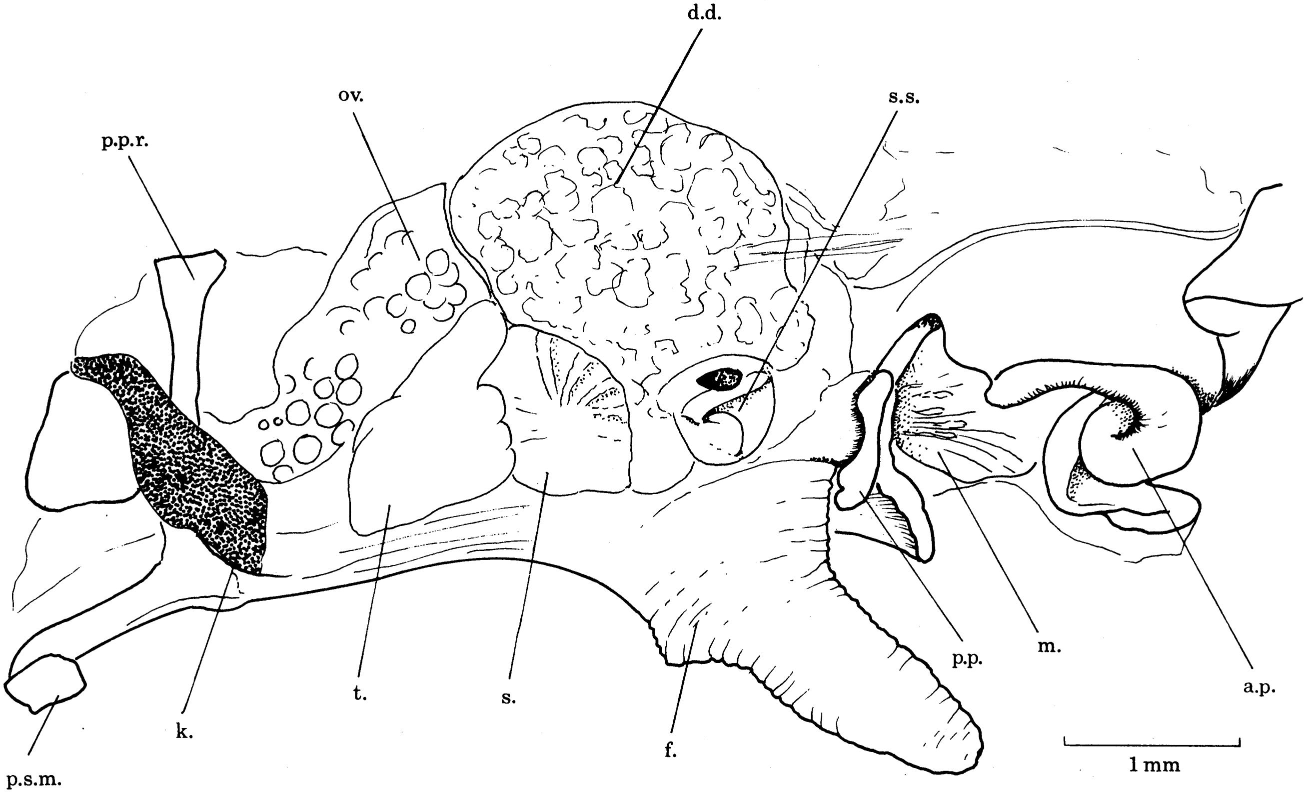


FIGURE 77. *Poromya tornata*. Lateral view of viscera from the right side.

The kidneys occupy approximately the same position as those in the Cuspidariidae, being situated posterodorsally between the ovary and the posterior adductor muscle (figure 70), above the posterior pedal retractor muscles and below the gut. They are more deep and obvious than in any cuspidariid examined and comprise two triangular sacs, one either side of the midline. Anteriorly these fuse below the gut but remain separate posteriorly, where they extend laterally into the space between the posterior septal muscles and the horizontal septal valvulae.

Whereas in *Cuspidaria* the material in the lumen consists of small cells and granules, in *Poromya* the granules are large, spherical and refractile, and similar to those seen in the Verticordiidae (Allen & Turner 1974).

In *P. tornata* the lacunal cells are more numerous than in the Cuspidariidae but not as numerous as in the Verticordiidae. They consist of two groups of about ten cells on either side of the anterior end of the intersiphonal septum, dorsal and lateral to the siphonal sinuses. A further few cells are scattered in the posterior walls of the suprabranchial cavity.

This, the type species of the genus, was described from a Pliocene Coralline Crag fossil. Pelseneer (1891) also used this species to give the first good description of the anatomy of *Poromya*. Since then there has been little further work on the species, although the morphological variability of its shell form (figure 78) is of some renown in the literature.

Poromya granulata (Nyst & Westendorp, 1839) (figures 78–94, 96)

1839	*Corbula granulata*	Nyst & Westendorp (p. 6, pl. 3, fig. 3)
1843	*Poromya anatinoides*	Forbes (p. 191)
1844	*Poromya anatinoides*	Forbes (p. 103)
1853	*Poromya granulata*	Forbes & Hanley (p. 204)
1868	*Poromya granulata*	Jeffreys (p. 308)
1881	*Poromya granulata*	Dall (p. 108)
1881	*Poromya granulata*	Jeffreys (p. 936)
1882	*Poromya granulata*	Verrill (p. 546)
1888	*Poromya granulata*	Pelseneer (pp. 1–42)
1891	*Poromya granulata*	Pelseneer (pp. 147–312)
1897	*Poromya granulata*	Dautzenberg & Fischer (p. 229)
1911	*Poromya granulata*	Pelseneer (p. 78)
1912	*Poromya granulata*	Dautzenberg & Fischer (p. 528)
1916	*Poromya granulata*	Hidalgo (p. 567)
1928	*Poromya granulata*	Yonge (p. 221)
1960	*Poromya granulata*	Odhner (p. 377)

Material

ship	date	stn	latitude	longitude	depth/m	number
Ingolf	11. 05. 1895	32	66° 35.0′ N	56° 38.0′ W	599	1
	18. 05. 1895	35	65° 16.0′ N	56° 00.5′ W	682	1
T.B.S.†	10. 06. 71	T 71031	Stornfjord, Norway		50–100	3
	13. 04. 72	T 72051	Trondheimsfjord, Norway		60–80	1
K.S.†	1971				60–120	15
C.U.M.†		E 80				25

† T.B.S., Trondheim Biological Station; K.S., Kostuomandet Sacken; C.U.M., Copenhagen University Museum.

Distribution

Widely distributed, northwest Europe, North Atlantic, tropical America, northwest America. Depth range: 30–682 m.

Description

Shell equivalve, slightly inequilateral; anterior dorsal, anterior and ventral margins join in unbroken curve, posterior dorsal margin short, slightly convex, posterior margin oblique and truncate; umbos high, width narrow, anteriorly inclined; relatively flat posterior triangular area rather than ridge present from umbo to posterior ventral margin; numerous, faint, concentric growth lines, innumerable closely spaced, radial lines of tiny granules, most obvious ventrally and on triangular portion of shell posterior to the umbo; single anterior cardinal tooth, anterior to resilifer in right valve with corresponding notch in left valve; resilifer oblique, triangular, divided by diagonal ridge between anterior dorsal and posterior ventral corners; ligament external, opisthodetic, thick band of posterior outer layer extends posteriorly between hinge margins (figure 79).

The outstanding difference that distinguishes *P. granulata* from *P. tornata* and other species such as *P. perla* and *P. tenuiconcha* is that in *P. granulata* the gill filaments are much shorter than in the other species, and are ventrally swollen to produce a lipped pore. There are no interfilamentar connections; consequently the apertures do not appear as a lattice but as a close-set series of slit-like pores, similar to those of *Cuspidaria* except that there is little muscle between individual pores within a group (figures 80, 81). Apart from this there is little difference between the anatomy of *P. granulata* and that of *P. tornata*. The septal valvulae in *P. granulata* are not lozenge-shaped as in *P. tornata* but dish-shaped with swollen edges; moreover, they contain fewer muscle fibres and contain innumerable large, densely staining cells similar in form to lacunal cells (figure 83). These cells are aggregated in large numbers around the few muscle fibres that extend across the lumina of the valvulae. There are also a few similar scattered cells in the tissue around the inhalant and exhalant siphons.

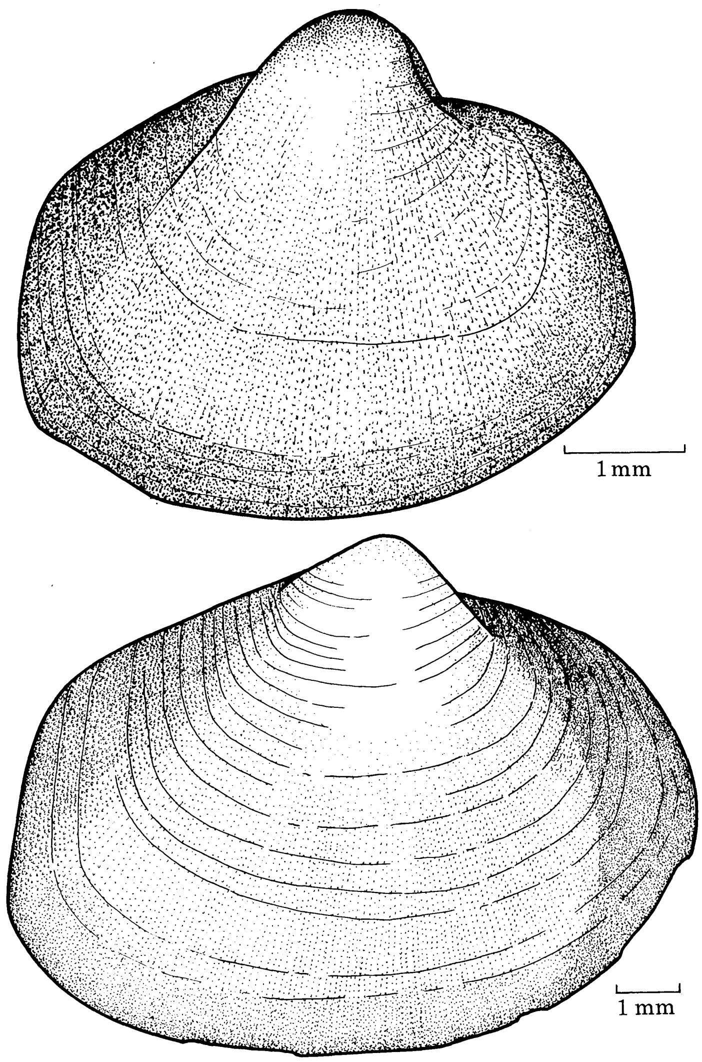


FIGURE 78. *Poromya granulata*. Lateral view of two shells from the right side to show variation in outline.

Pelseneer (1911), Ridewood (1903) and Odhner (1960) have shown that the number of interfilamentar connections in *Poromya* can vary, from six in *P. eximia* to none in *P. granulata* and *P. oregonensis*. In addition, as both Pelseneer (1891) and Odhner (1960) noted, there is great variability in the number of pores per branchial group in *P. granulata*. This study shows that not

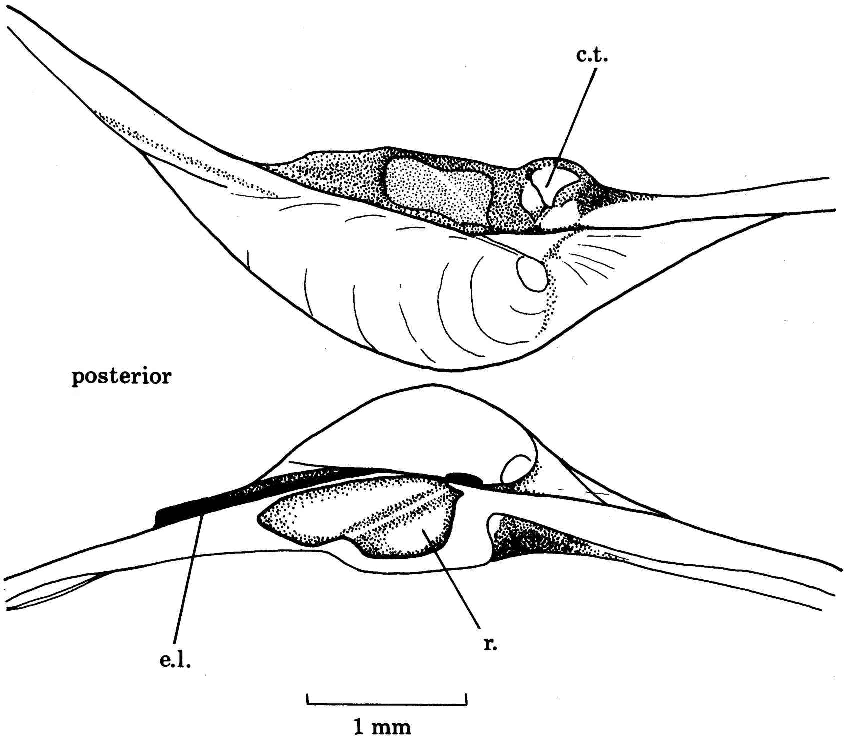


FIGURE 79. *Poromya granulata*. Dorsolateral views of the hinge of both valves.

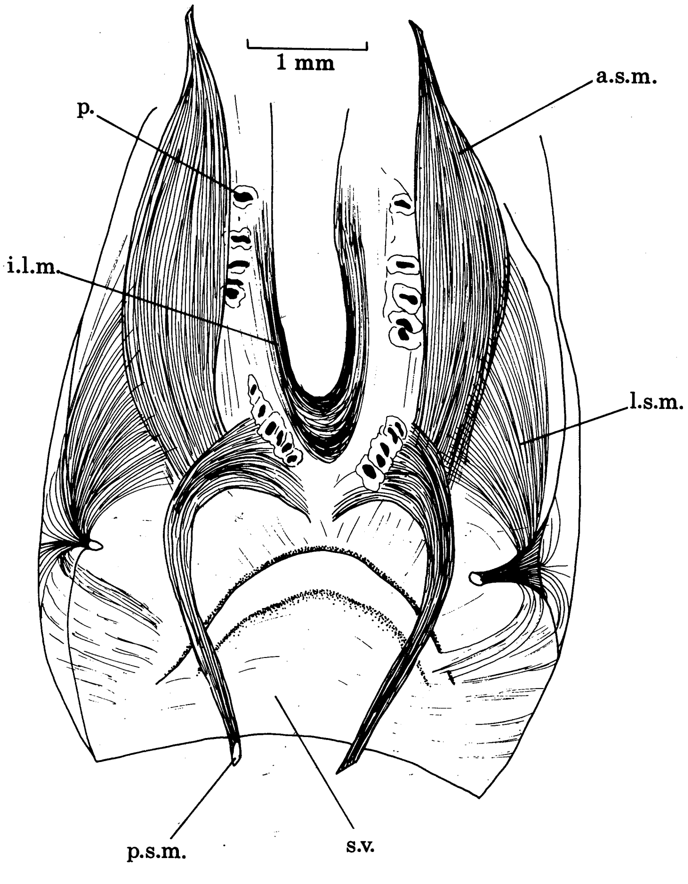


FIGURE 80. *Poromya granulata*. Dorsal view of the septum.

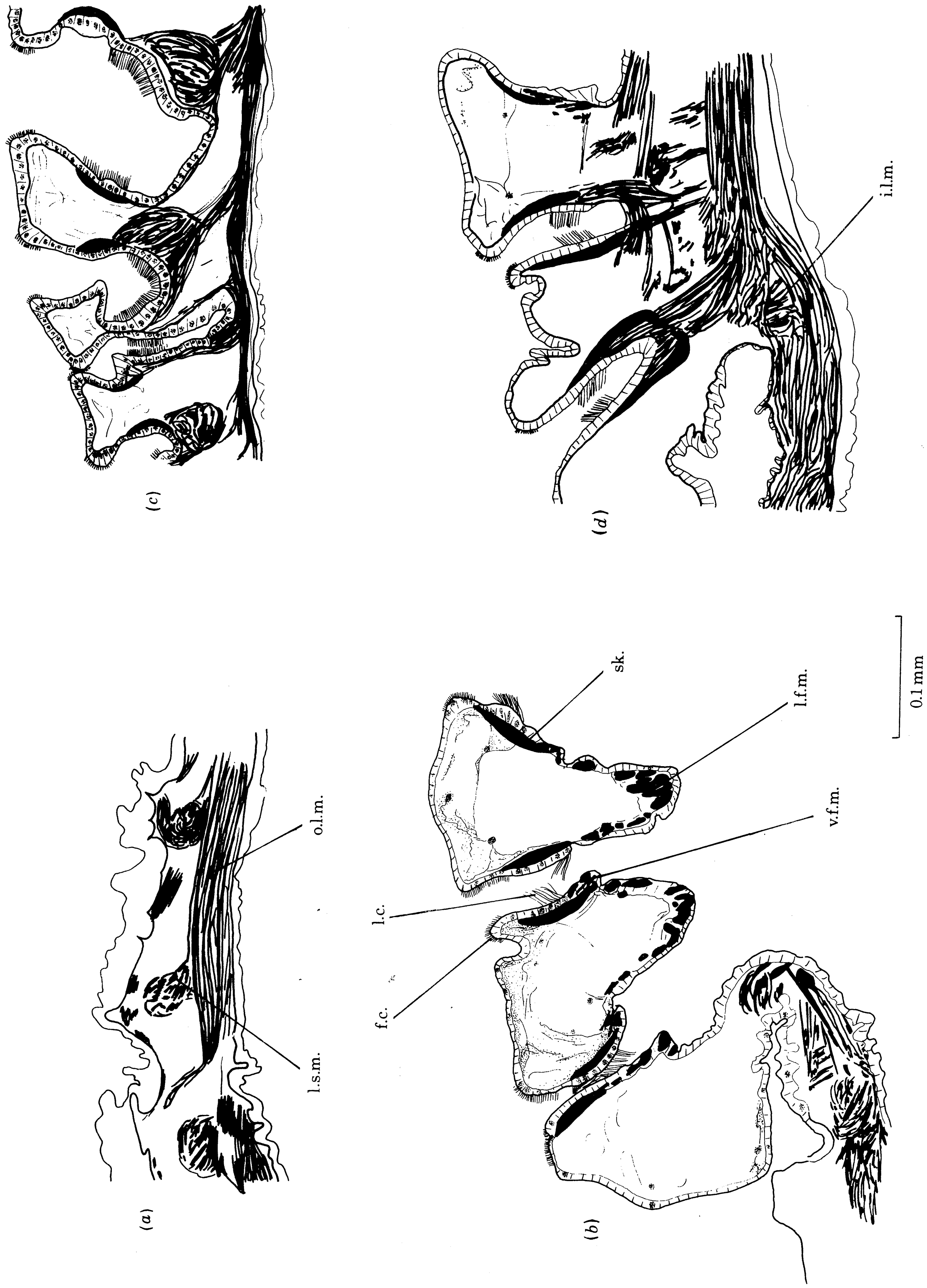


FIGURE 81. *Poromya granulata.* Four consecutive transverse sections through the septum and filaments.

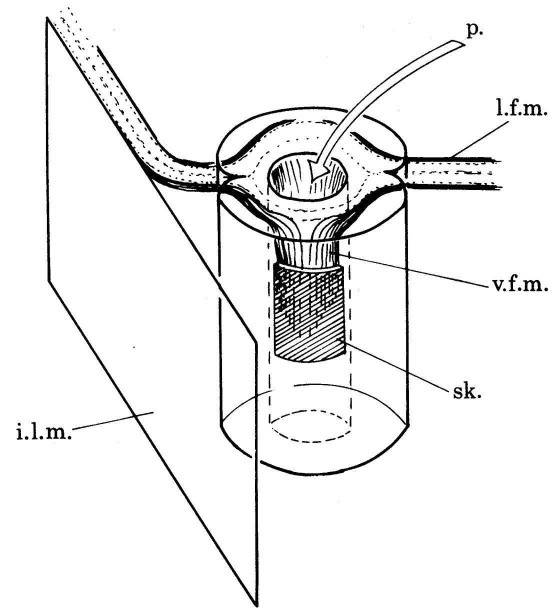


FIGURE 82. Diagram to show the arrangement of the muscles of the pore-closing mechanism.

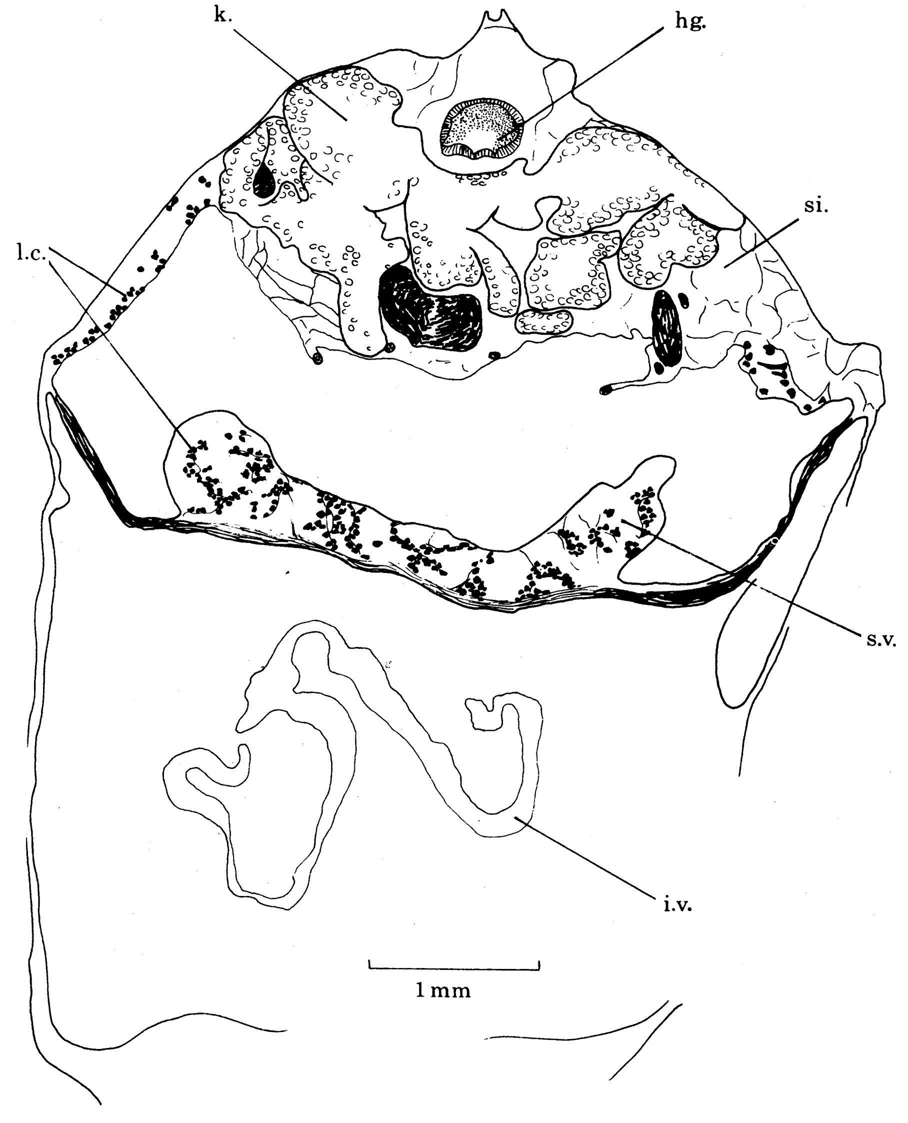


FIGURE 83. *Poromya granulata*. Transverse section of the posterior part of the body to show septal valvulae and lacunal cells.

only does the number in each individual vary but also the number may occasionally vary from one side to the other, within the same individual (table 3).

Ridewood (1903) showed in *P. oregonensis* that the margins of the pores are modified gill filaments. The filament, like those of *Protocuspidaria* and *Poromya tornata*, is triangular in section with the frontal surface facing ventrally. There is a central blood space, traversed by several connective tissue strands, and a pair of skeletal rods lying beneath the epithelium, one on each side of the filament (figure 81). In addition, there is a dorsal longitudinal band of muscle that is homologous to the longitudinal filamentar muscle present in eulamellibranch bivalves. Because the short filaments lie in the horizontal plane, the muscles lie laterally across the septum. Beyond lateral margins of the pores the filamentar muscles lie adjacent to each other forming externally the lateral septal muscles, while internally they merge with the inner longitudinal muscle. The filamentar muscles form a pore-closing mechanism similar to that in *Cuspidaria*, and here their origin is clear. Associated with the longitudinal filamentar muscles are several fibres running vertically within the pore walls. These lie between the skeletal rod and the epithelium and run from the ventral edge of the rod to the dorsal surface of the septum and are concentrated close to the lateral margins of the pore. Beyond the pore these too lie close to their neighbours and merge with either the inner longitudinal muscles or the lateral septal muscles. Contraction of the longitudinal filamentar muscles closes the pore by bringing the margins together in the transverse plane of the septum. The vertical muscles extend this contraction through the depth of the pore and allow alteration of the shape of the pore (figure 82). Although vertical muscles were not observed in *Cuspidaria*, when the pores close and the septum contracts the ventral lips of the pores are protruded; this is probably due to the action of vertical muscles.

TABLE 3

sample	number of filaments per group on each side of septum			
	posterior group		anterior group	
	left	right	left	right
Kostuomandet	4	4	5	5
	4	4	5	5
	6	6	4	4
	6	5	5	5
	6	4	5	5
	5	5	4	4
E. 80	4	4	5	5
	5	5	5	5
	6	6	5	5
†Odhner specimen	6		5	
†Pelseneer specimen	6		5	

† Only one number for both sides given.

As in *P. tornata*, the pore bears two rings of cilia, one of long cilia within the pore itself and another of shorter cilia near the ventral opening (figure 81), but, whereas in *P. tornata* the latter extend over the whole ventral surface of the filament, in *P. granulata* the cilia are confined to the lateral corners of the pore. It is possible that they are homologous to laterofrontal cilia or are simply frontal cilia that are reduced in their extent. Yonge (1928) states there are no frontal cilia in *P. granulata* but Ridewood (1903), who recorded them in *P. malespinae* though not in *P. oregonensis*, also debated their possible homology to laterofrontal cilia.

The siphons of *P. granulata* are very short and are surrounded by a ring of short tapering tentacles. The inhalant siphon has an inwardly projecting valve and a pair of internal tentacles close to the visceral ganglion. There are 15 and not 13 external tentacles, 7 pairs of which surround the inhalant siphon, and a single dorsal tentacle above the exhalant siphon. There are no intertentacular papillae.

Genus Cetoconcha

The anatomy of the septum of *Cetoconcha* has been described several times (Pelseneer 1888*a*, *b*, 1891; Dall 1890; Ridewood 1903; Odhner 1960; Knudsen 1970), and only those species whose anatomy has been studied can be considered as *Cetoconcha*. In fact only 6 of 14 recorded species of *Cetoconcha*, together with 2 new species described here, can be designated with certainty as species of *Cetoconcha*. These are *C. bulla* Dall, *C. ceylonensis* Knudsen, *C. galatheae* Knudsen, *C. margarita* Dall, *C. pelseneeri* Pelseneer and *C. sarsi* Smith.

Cetoconcha braziliensis new species (figures 84–87)

Holotype: *Atlantis II*, station 155, 0° 0.3′ S, 27° 48.0′ W, in 3730 m (Museum of Comparative Zoology, Harvard).

Material

ship	date	stn	latitude	longitude	depth/m	number
Atlantis II	13.02.67	155	00° 00.3′ S	27° 48.0′ W	3730	1
J. Charcot (Biogas IV)	25.02.74	DS61	47° 34.7′ N	08° 35.0′ W	2250	1

Distribution

Off northeast coast of Brazil, Bay of Biscay. Depth range: 2250–3730 m.

Description

Shell oval, slightly inequilateral, posterior dorsal margin of right valve overlapping left; posterior dorsal margin short and slightly convex, posterior margin deep and truncate, ventral margin wide and shallowly curved, anterior margin slightly extended, anterodorsal margin steeply sloping; umbones very prominent, and twisted anteriorly; shell surface with faint, concentric growth lines, about 13 posterior radial lines of granules, more distinct ventrally; no rostral ridge, but discontinuity in growth lines delimits triangular, posterior dorsal region; internal shell with numerous fine radiating striations, anterior muscle scar much larger than posterior; hinge narrow, except beneath umbones where it supports long, narrow, opisthodetic and mainly external ligament; no teeth in either valve (figure 84).

Maximum shell measurements are: length, 19 mm; height, 16 mm.

As in *Poromya* the pedal gape extends from the anterior adductor muscle to the base of the inhalant siphon. Fusion beyond these points involves the inner fold, and inner face of the middle fold, but the periostracal grooves never lie as close together as they do in the Cuspidariidae. The mantle margins are very muscular, with a central band of longitudinal muscle running within the inner fold. A ciliated rejectory tract is present and, as in *Poromya*, there are few gland cells.

The structure of the foot is similar to *Poromya*. Two long narrow anterior pedal retractor muscles pass under the stomach and round the oesophagus. Posteriorly a wide band of muscles around the lower half of the viscera converges to form part of a single narrow posterior pedal retractor muscle. This bifurcates close to the shell to attach between the posterior septal muscles (figure 85). There is a shallow byssal groove leading, via a short ciliated duct, to a very small ciliated byssogenous cavity. There appears to be only one type of gland cell present, homologous to the large cells in *Cuspidaria*, that are restricted to the end of the groove and around the byssal duct, the latter being few in number.

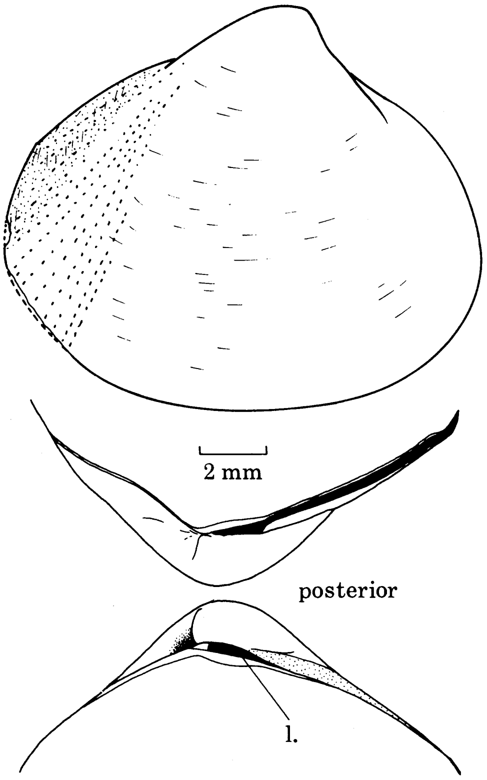


FIGURE 84. *Cetoconcha braziliensis*. Lateral view of the shell from the right side and lateral view of the hinge of both valves.

The septum of *Cetoconcha* is as muscular as that of *Cuspidaria*, although, as in *Poromya*, the muscle is unstriated. Although the septal apertures are pores, the prominent development of the lateral septal muscles relates more closely to *Poromya* than to *Cuspidaria* (figure 86). The lateral septal muscles extend across the dorsal surface of the septum and dorsally within the mantle to a point of attachment on the shell posterior to the posterior septal muscles. Anterior and posterior septal muscles are better developed than in *Poromya*. The anterior is divided into a main inner muscle and a small outer longitudinal muscle and forms a double anterior attachment. The septal valvulae are small and crescent-shaped.

Ridewood (1903) showed that the branchial apertures were spaces between modified gill

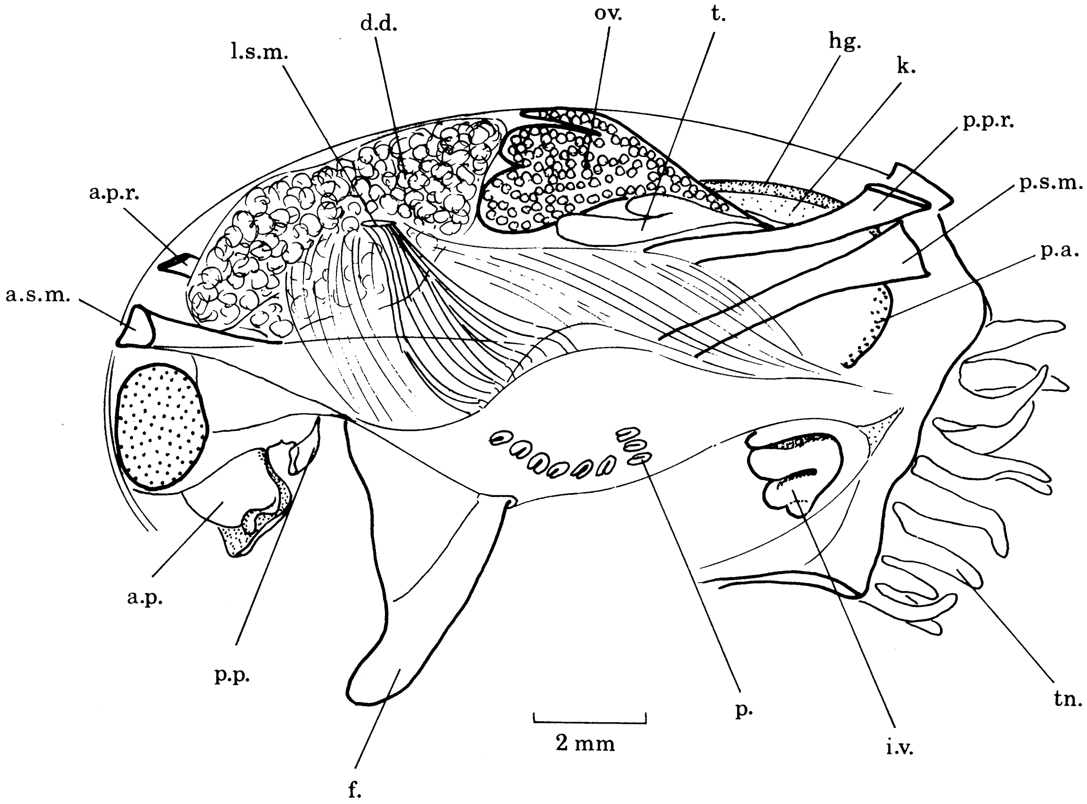


Figure 85. *Cetoconcha braziliensis*. Anatomy as seen from the left side.

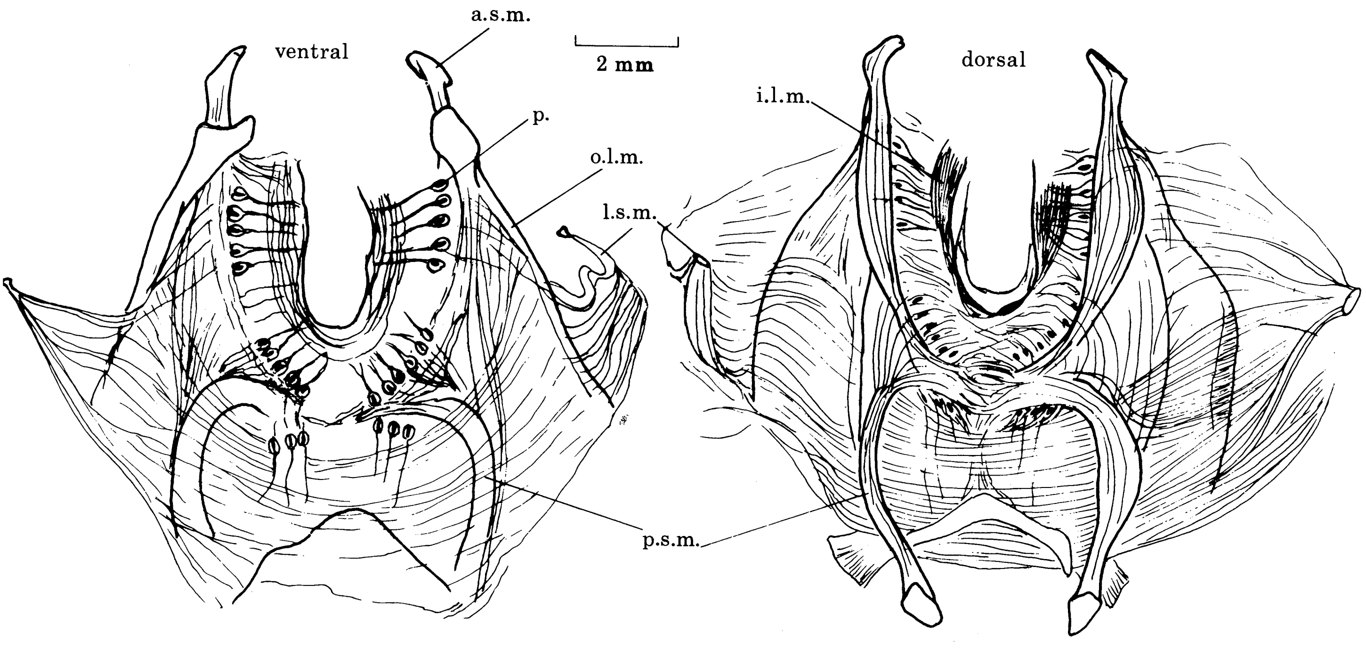


Figure 86. *Cetoconcha braziliensis*. Dorsal and ventral views of the septum.

filaments, though he failed to locate any cilia. The two anterior groups lie in a similar position to those in *Poromya*. The third and smallest group lies behind the posterior septal muscles and anterior to the septal valvulae. There are five pairs of pores in the anterior group, six in the middle and three in the posterior group. Although *C. angolensis*, described here, has a similar number of pores, numbers appear to vary in other species, for example *C. sarsi* is described as having five, five and three pairs of pores respectively. The filaments of *Cetoconcha* are shorter and flatter than those of *Poromya*. The blood space is more restricted, there are no skeletal rods or interfilamentar connections and there is much more muscle present. This muscle extends over the dorsal edge of the filament and laterally, and is a development of the longitudinal filamentar muscle already described in *Poromya* (figure 81). In poromyids, such as *P. granulata*, with no interfilamentar connections the longitudinal filamentar muscle is contiguous with its neighbour only at the inner and outer ends of the pore. In *P. tornata*, what little muscle there is comes together with adjacent muscles at each interfilamentar connection, suggesting that the 'pored' condition is derived from the 'sieved' condition by a simple process of reduction. Thus the septum of *Cetoconcha* is intermediate between the condition in *P. granulata* and *Cuspidaria*.

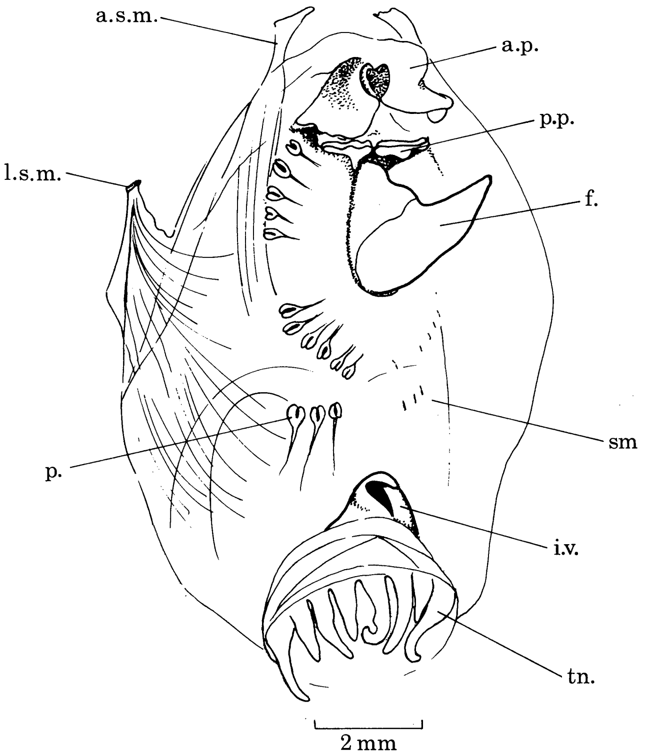


FIGURE 87. *Cetoconcha braziliensis*. Lateroventral view of the body.

It must be emphasized that *Cetoconcha* differs from *P. granulata* in that there is a third group of pores situated behind the posterior septal muscles.

The palps of *Cetoconcha* are similar to those of *Poromya* (figure 89).

Cetoconcha, like *Poromya*, has a very muscular stomach wall with longitudinal and circular muscles similar to those surrounding the oesophagus. It differs only in that in addition to the

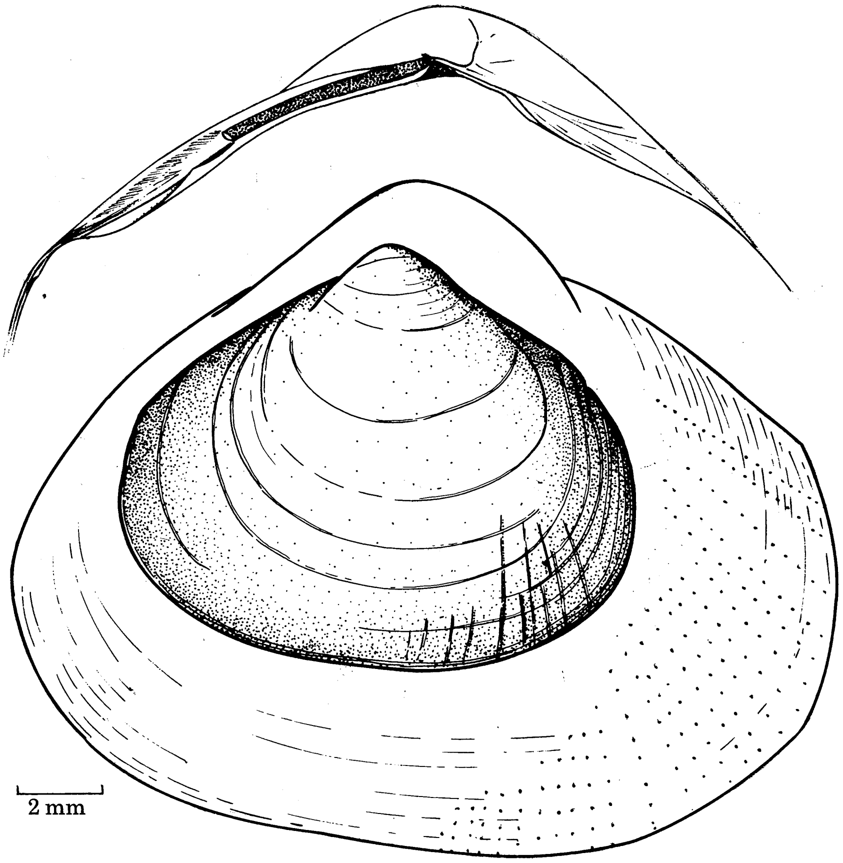


FIGURE 88. *Cetoconcha angolensis*. Lateral view of the shell from the right side and lateral view of the hinge of the left valve. Inset is a smaller shell seen from the left side.

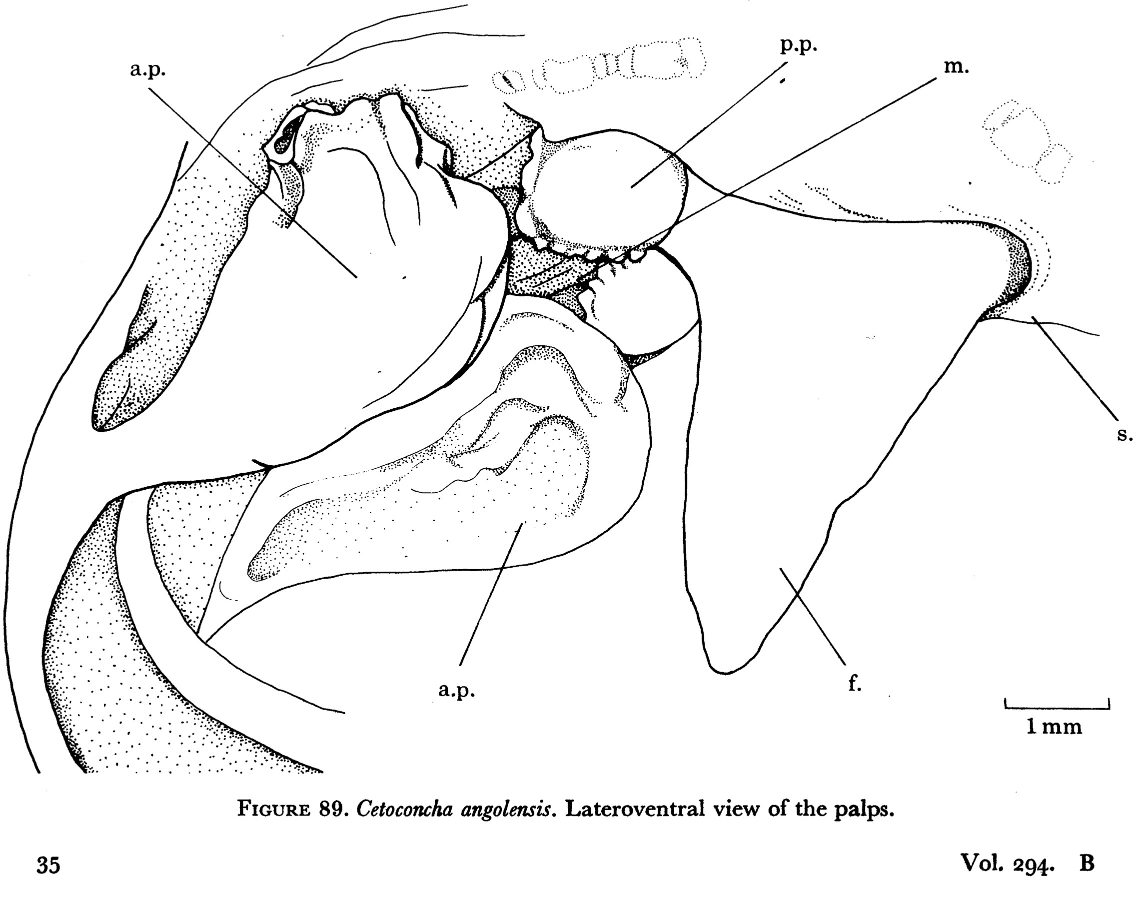


FIGURE 89. *Cetoconcha angolensis*. Lateroventral view of the palps.

pair of narrow ciliated tracts running from the entrance of digestive ducts to the style-sac/midgut opening, there is a ciliated circumoesophageal ring and a tract that connects with the digestive ducts.

The siphons of *Cetoconcha* are similar to those of *Poromya*. While *Poromya* species such as *P. tornata* and *P. romanchensis* have 13 tentacles and three or four pairs of tiny intertentacular papillae, others, such as *P. granulata*, have 15 tentacles and no papillae. Both species of *Cetoconcha* described here have 15 tentacles and no papillae (figure 90).

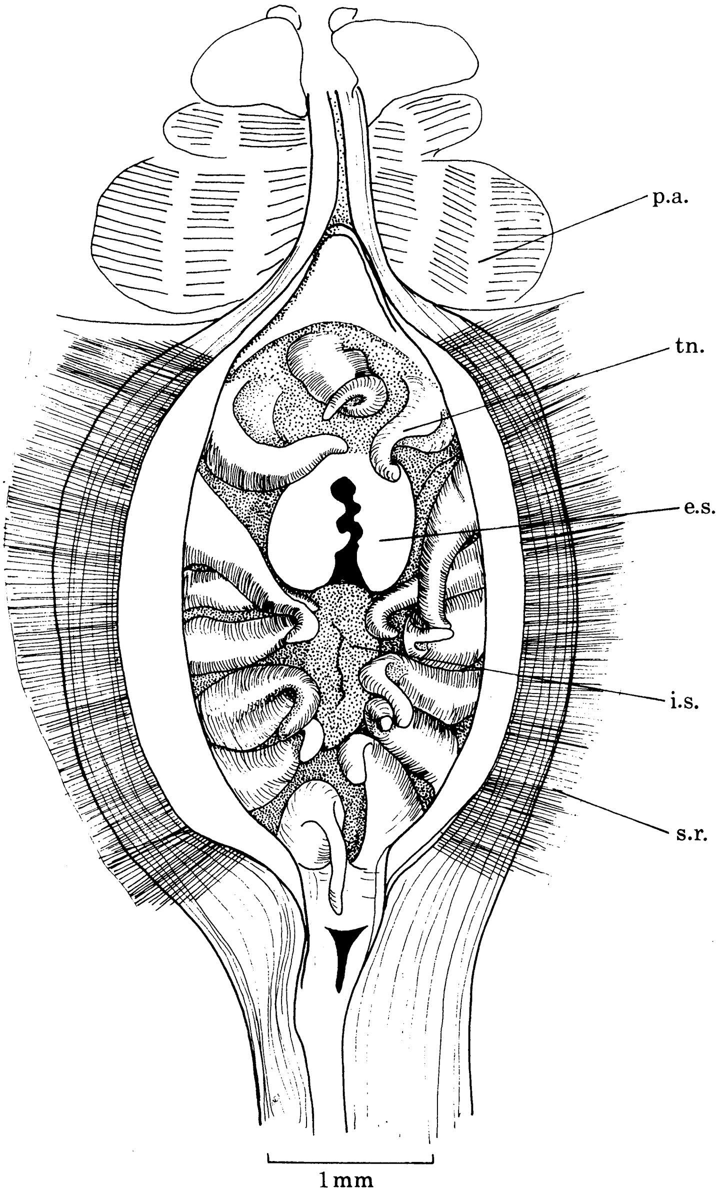


FIGURE 90. *Cetoconcha angolensis*. Posterior view of the siphons.

Sinuses are conspicuous in the posterior region of the roof of the supraseptal cavity of *Cetoconcha* They are compartmented by numerous membranes and extend within the mantle into

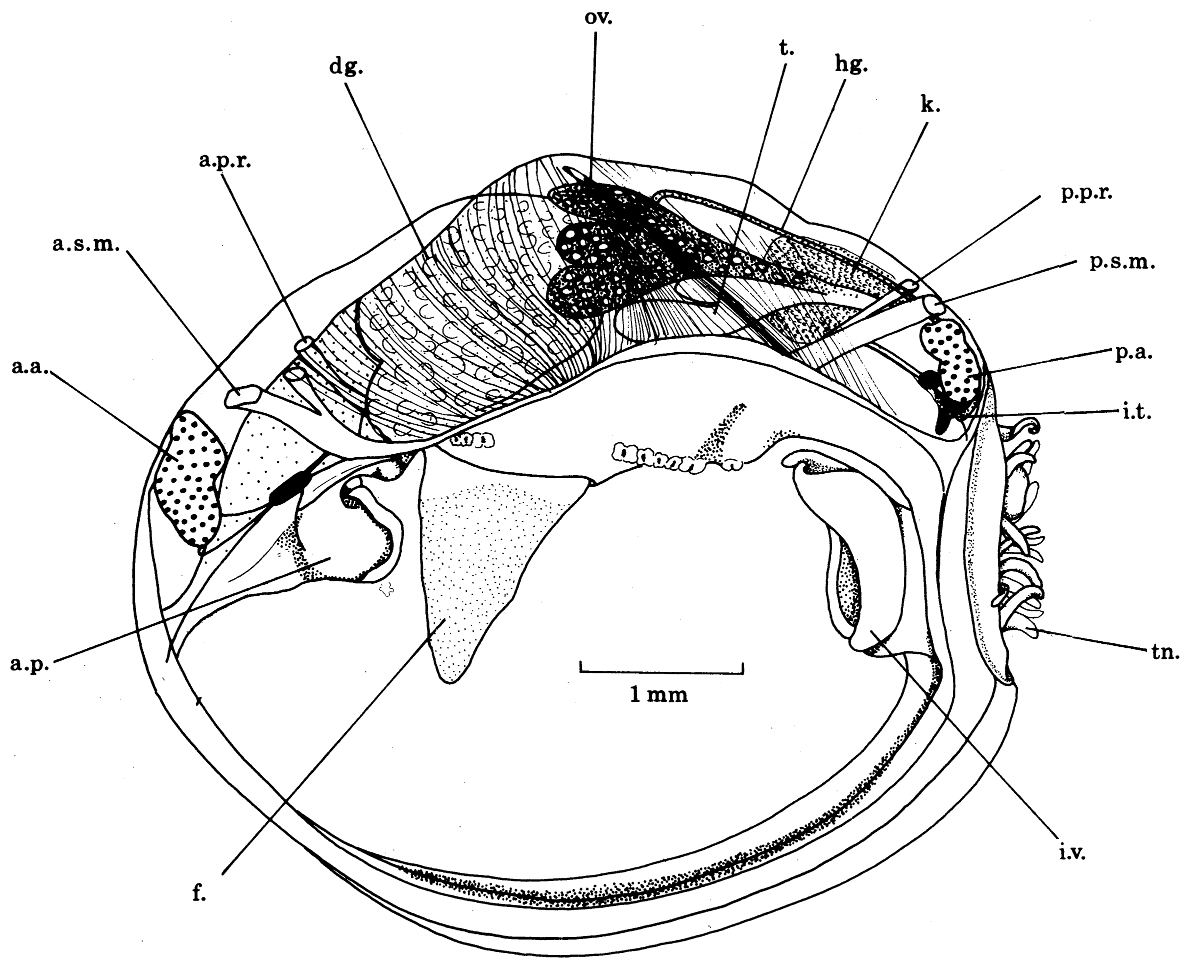


FIGURE 91. *Cetoconcha angolensis*. Anatomy as seen from the left side.

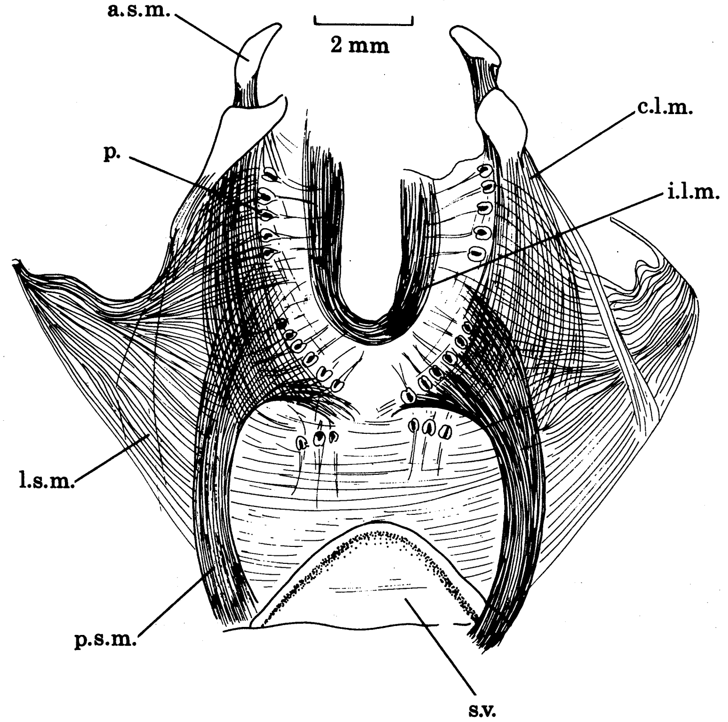


FIGURE 92. *Cetoconcha angolensis*. Dorsal view of the septum.

the septum and intersiphonal septum. Lacunal cells are not as obvious as they are in *P. tornata* and are restricted to a few scattered cells in the walls of the exhalant cavity. The septal valvulae are also much reduced in comparison with the condition seen in *Poromya*. They contain numerous scattered peripheral muscle fibres and are not packed with lacunal cells.

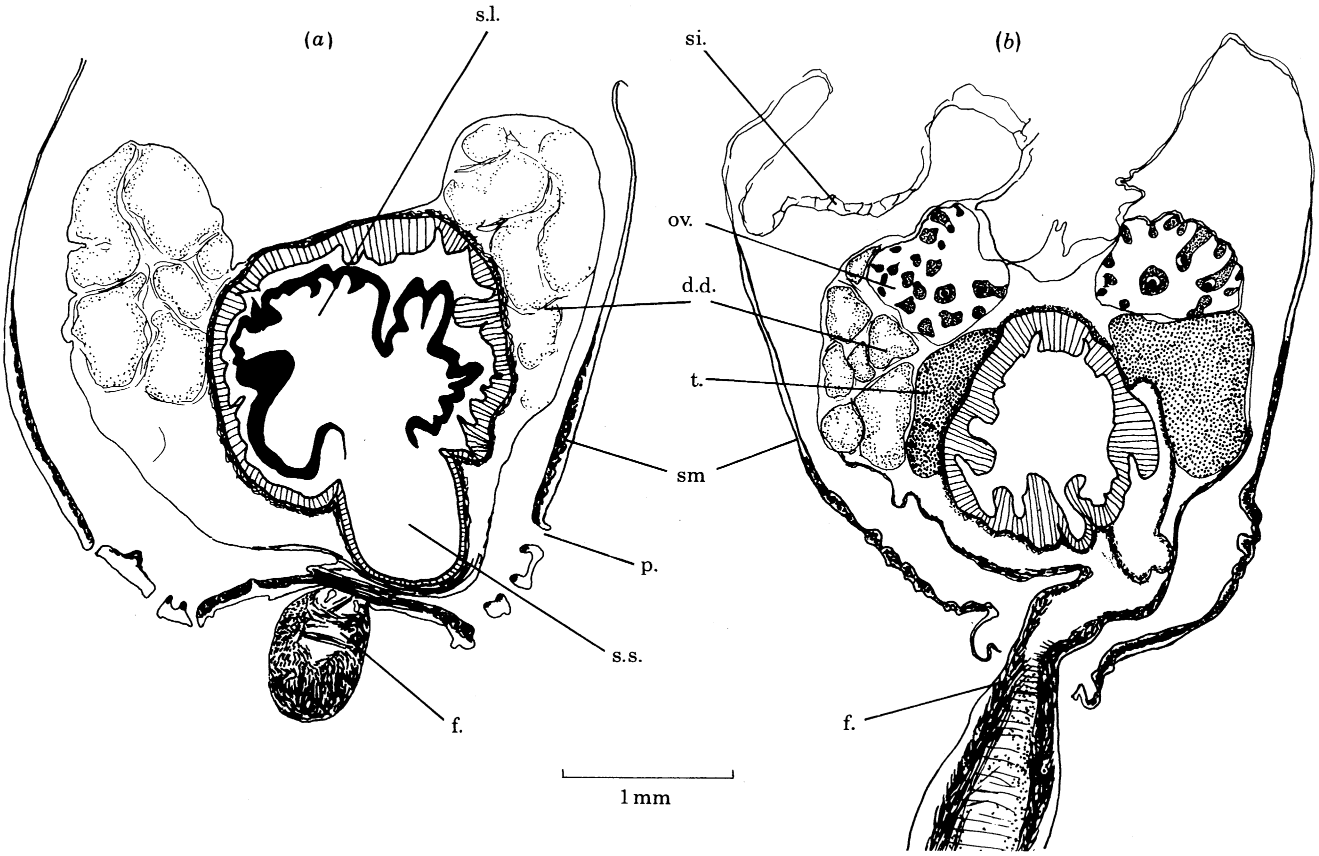


FIGURE 93. *Cetoconcha angolensis*. Transverse sections through the stomach and the gonads.

Cetoconcha angolensis new species (figures 88–93)

Holotype: *Walda*, station CY 02, 18° 52.1′ S, 7° 23.1′ E, in 5124 m (Museum of Comparative Zoology, Harvard).

Material

ship	date	stn	latitude	longitude	depth/m	number
Walda		CY 02	18° 52.1′ S	07° 23.1′ E	5124	1 + 1s

Distribution

South Atlantic off the coast of Angola. Depth: 5124 m.

Description

Shell relatively elongate; right valve overlaps left at posterodorsal margin; anterior and posterior dorsal margins slope more or less evenly from umbo; little difference between anterior and posterior margins but latter less deep, with posterodorsal angle, ventral margin little curved, almost straight in midventral section; shell surface with few well marked concentric growth lines, several radial lines of granules of varying length at posterior ventral margin, mostly incomplete, not extending more than half height of shell; hinge slightly thickened centrally to accommodate narrow opisthodetic resilifer, ligament predominantly external. No teeth (figure 88).

Maximum shell measurements are: length, 26 mm; height, 21 mm.

Anatomy as for *C. braziliensis* (figures 89–93).

OBSERVATIONS ON THE SEPTUM OF LIVING SPECIMENS OF *CUSPIDARIA CUSPIDATA*

Yonge (1928) was the first to describe the function of the septum in living cuspidariids from observations on *C. cuspidata* and *C. rostrata*. More recently Reid & Reid (1974) have examined feeding and burrowing behaviour in *C. obesa*, and the following observations confirm and extend many of these findings.

Specimens were collected by a 2 mm mesh Agassiz trawl at a depth of approximately 80 m off Northumberland (55° 10.0′ N, 1° 5.0′ W) from fine mud. They were kept in separate dishes containing about 2 cm of mud and placed in a larger tray through which cooled sea water (10 °C) was flowing. As described by Reid & Reid (1974) the animals burrow into mud anterior end first and come to lie vertically with the posterior end uppermost. Only the inhalant siphon and the seven tentacles are visible and these extend 1–2 mm above the sediment surface.

Except around the thin mobile distal end, the inhalant siphon of *C. cuspidaria* has numerous scarlet pigment cells scattered over its surface. These cells are also present between the bases of the tentacles and between the bases of the papillae on the siphonal sheath. There are none on the remainder of the sheath nor on the exhalant siphon itself.

To observe siphonal movements the dishes were placed in a small cooling bath beneath a binocular microscope. To observe septal movements, and correlate these with siphonal movements, it was necessary to remove the animal from the sediment and cut a window in the shell. After an attempt to seal a glass window over the hole, it was found best to remove some of the shell without removing the underlying mantle and place the animal in a small tube made of thin, flexible, clear plastic. This served to seal over the window. It also provided a surface against which the mantle could press and prevented the accumulation of debris on the exposed surface.

Animals were first observed after 1 week in laboratory conditions, when their activities seemed erratic and no feeding was seen. After a period of 6 weeks several patterns of activity were established.

Reid & Reid (1974) describe three combinations of siphon and septum movements, namely:

(i) the extension of the exhalant siphon, extrusion of faecal strings accompanied by the contraction of the septum;

(ii) the extension of the inhalant siphon, production of an inhalant current accompanied by the contraction of the septum;

(iii) the ejection of pseudofaeces via the extended inhalant siphon while the septum is depressed ventrally.

Our observations on *C. cuspidata* show that the first two are combined: they occur simultaneously and were never seen to occur separately.

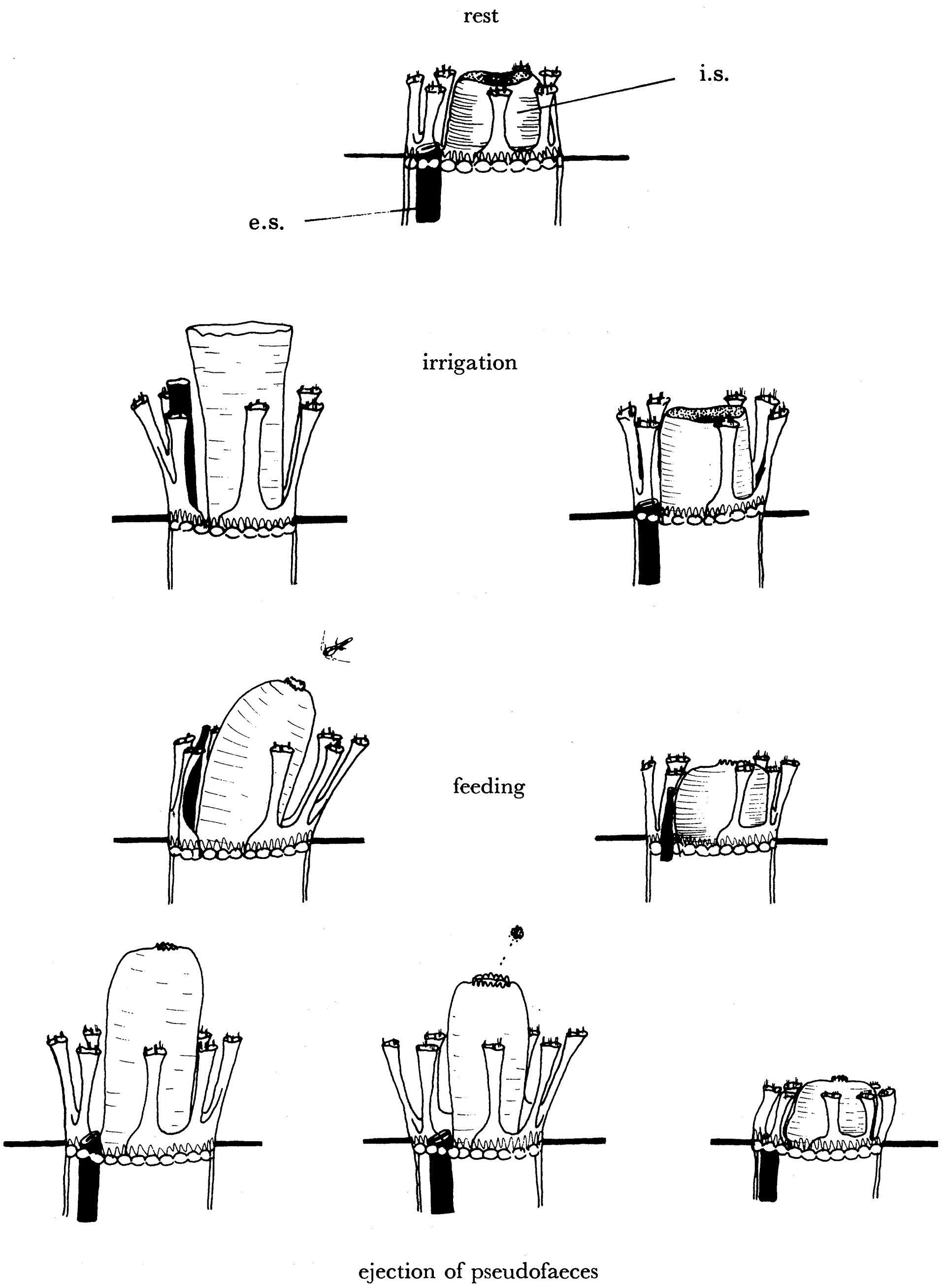


FIGURE 94. *Cuspidaria cuspidata*. Diagram to show siphonal movements observed in live specimens (for further explanation see text).

In *C. cuspidata* there are three distinct activities involving feeding, irrigation, and ejection of pseudofaeces respectively. The first two involve similar but distinct movements.

The siphons are extremely sensitive to mechanical disturbance and rapidly retract within the shell. When they emerge, they do so slowly at first, the thin frilled edges of the common siphonal sheath held closely together across the siphons and tentacles, forming a dorsoventrally orientated slit. This then opens and the ring of 15–20 papillae to the inside of the sheath are arranged level with the sediment, while the inhalant siphon, together with the spreading dorsal (exhalant) and ventral (inhalant) tentacles, is extended to approximately 1–2 mm above the sediment. This we refer to as the *rest* position, which the animal assumes most of the time and which Reid & Reid (1974) have described in *C. obesa* (figure 94). The inhalant siphon is relaxed, slightly protruded, with the rim folded in and over, but not quite occluding, the lumen. At the same time the exhalant siphon is held invaginated within the supraseptal cavity and the sphincter at its base closes, forming a transverse slit. The seven tentacles are held motionless in a ring around the siphons, their expanded, sucker-like tips being level with the unfolded end of the inhalant siphon (figure 94). At rest, the septum is held in a ventral position with the pores open and there is little space between it and the mantle margin. This is not the maximum ventral extension, but even in the rest position the infra septal cavity is somewhat restricted (figure 95).

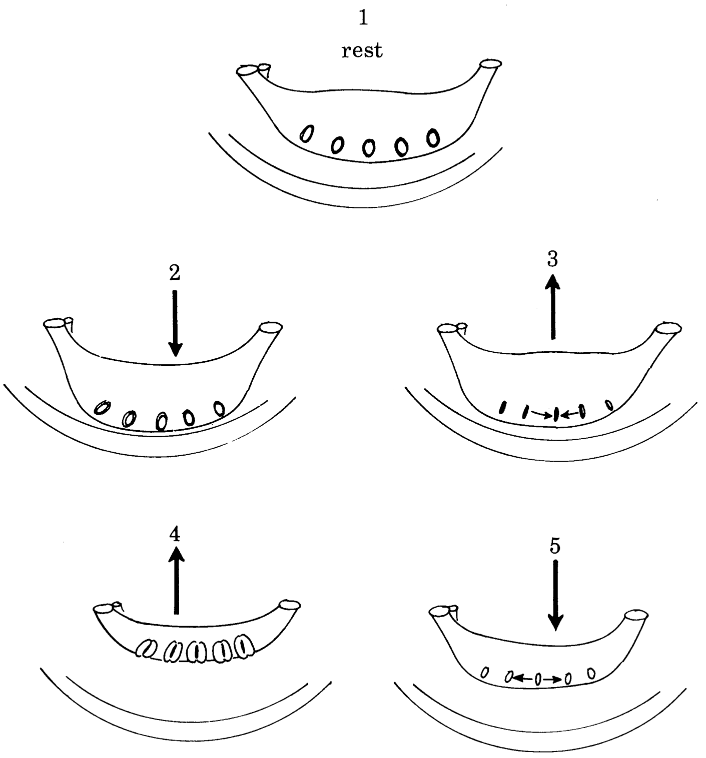


FIGURE 95. *Cuspidaria cuspidata*. Diagram to show septal movements observed in live specimens. Large arrows indicate direction of movement of septum, small arrows closure (3) and opening (5) of pores (for further explanation see text).

Irrigation movement

This is a rhythmic activity involving the combined action of the septum and siphons which causes a flow of water through the mantle cavity. It occurs on average once per minute but can occur as often as once every $\frac{1}{2}$ min. If the animal is disturbed and retracts its siphons then it takes of the order of 5 min to re-establish the rhythm. The irrigation movement takes about 2–3 s to accomplish.

In detail, the septum relaxes very slightly with the pores open, and the volume of the supraseptal cavity increases momentarily, then the pores shut and the septum contracts dorsally. This produces a reduced pressure in the infraseptal cavity, and an increased pressure in the supraseptal cavity, and coincides with the extrusion of both siphons and the production of inhalant and exhalant currents. The extrusion of the siphons occurs when fluid from the mantle sinuses passes into the siphonal and rostral sinuses (Reid & Reid 1974). The inhalant siphon extends to its maximum length (approximately 5 mm) with the distal end splayed out, trumpet fashion. When water has entered the infraseptal cavity, the siphon returns slowly to its rest position. The exhalant siphon is extended momentarily, water passes out and the siphon is then retracted. The two currents flow simultaneously when both siphons are at their fullest extent. Thus, from its inverted position in the supraseptal cavity and with the base of the siphon closed by a sphincter, the exhalant siphon first contracts, turns inside out, and is then shot out to its full extent, almost to the level of the inhalant siphon. On contraction it inverts to its original position (figure 94); however, the sphincter takes approximately 30 s to close again. As the inhalant siphon returns to its rest position the septum, with its pores open, relaxes slowly, water passing from infra- to supraseptal cavity. The inhalant siphon remains slightly open, with the septal pores wide open with their cilia beating. A very weak through current was seen at times. Yonge (1928) says that there is no continuous current, and certainly after irrigation the exhalant siphon appears to be firmly shut, but there is some passage of water in through the inhalant siphon and through the pores for a time after irrigation. The pore cilia play at least a minor part in the movement of water between the mantle cavities.

Yonge (1928), who describes the irrigation movement in *C. obesa* and *C. rostrata*, records that when the animal is at rest the septum lies 'drawn up dorsally to its maximum extent'. Here the rest position of the septum is well ventral to its dorsal contracted position, there being only a small space between it and the inside of the mantle edge. Yonge (1928) removed both valves during his observations: this possibly affected the tonus of the muscles and the state of the contraction of the septum. Yonge (1928) did not describe a specific feeding movement and assumed that the irrigation movement also served to bring small animals or carrion into the mantle cavity as food but, as Reid & Reid (1974) have shown and we confirm here, there is a capture and feeding movement distinct from rhythmic irrigation (figures 94, 95).

Feeding movement

The feeding movement is much more rapid. It is triggered by the presence of prey within about 2 mm of the outspread tentacles. In our investigation of this movement *Artemia* larvae were used as food. Not only are the inhalant siphon and septum involved, but also the exhalant siphon. When no prey is present or prey is distant from them the seven tentacles are held motionless in a ring around the two siphons. There are groups of short bristles around the edge of each sucker-like tip of the tentacle, which are seen clearly in fresh material but are difficult to demonstrate histologically. In each group there are six to ten bristles of different lengths, the largest being in the centre of the group. If the prey swims within approximately 2 mm of these tentacles a capturing response is elicited, in which, starting from the *rest* position, both tentacles and inhalant siphon slightly extend and bend towards the prey. The tentacles do not hold the prey during capture. The inhalant siphon is then very rapidly extended with the distal aperture still closed by the contracted rim. Simultaneously the septum contracts, the exhalant siphon is shot out, the inhalant aperture opens momentarily and the prey is sucked in. The inhalant siphon contracts again to just below the resting level. Three or four seconds elapse before the aperture rim relaxes to the slightly open resting position, during which time the septum relaxes and the exhalant siphon contracts. The exhalant siphon is not extended as far as it is during irrigation and its diameter distally is smaller. A short, sharp, exhalant current counterbalances the inhalant suction. In approximately 50 % of the captures seen, the exhalant siphon inverted immediately within the mantle cavity. In other cases, it remained everted, relaxed and flaccid with the aperture closed distally and remained so until the next irrigation or capture. There appears to be no pattern as to whether it inverts or not, and the reason for the difference is not known. Reid & Reid (1974) report that their experimental animals fed four times in 20 min every hour for 6 h. We found no such set pattern, though this may have been due to the artificiality of the experimental environment. If the animals had had no food for several days, they would attempt to catch any *Artemia* larvae that came within their range, in one case 18 larvae in 1 h, frequently with only 30 s between successive captures (figure 96).

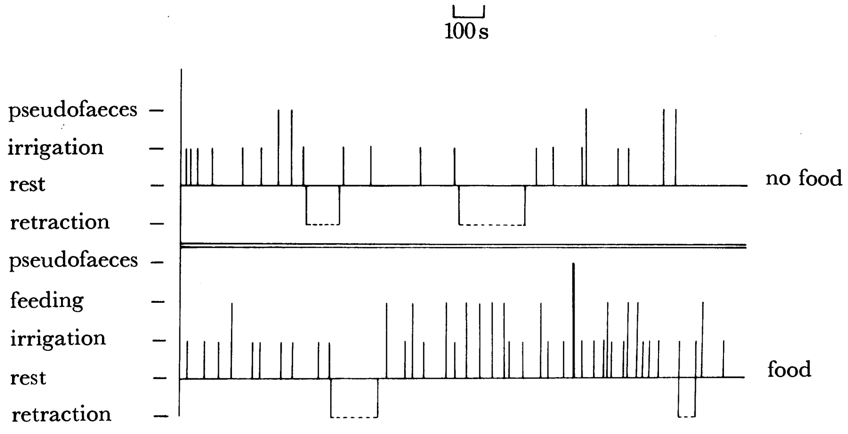


FIGURE 96. *Cuspidaria cuspidata.* Diagram of the frequency of the various activities observed in live specimens.

The tentacles are extremely sensitive to mechanical disturbance and Reid & Reid (1974) suggest that this is how cuspidariids sense their prey. They found that they could elicit the feeding response by the production of low-frequency vibrations. We have also observed this, when the stimulus is very gentle, such as when a fine hair, mounted on a needle, is vibrated at a frequency similar to the swimming movements of *Artemia*. Stronger movements cause the siphons to retract into the shell. No response was elicited from *Artemia* extract that was allowed to fall passively from a pipette clamped in position near the siphons, nor from the mere presence of several larvae in the dish. Only if a larva swam close enough was the feeding response elicited.

Ejection of pseudofaeces

Ejection of pseudofaeces is the only activity that does not involve the exhalant siphon. It was the least common movement observed (figure 96). It occurs during burrowing and sometimes after the animal has been retracted or covered by sediment for some time.

With the aperture almost closed the inhalant siphon extends even farther than it is during feeding and the tentacles also extend a little. The septum is then depressed slightly until it touches the mantle edge, the pores close and the valves clap together producing a short excurrent, during which time the inhalant siphon momentarily opens widely. The aperture closes and the siphon relaxes as the septum contracts slightly and the pores open until the rest position is assumed again.

Small unwanted particles sucked in during irrigation are rejected by the palps. Particles carried to the tip of the posterior palp fall off onto the narrow ciliated rejectory tract passing back along the length of the mantle edge to the inhalant siphon where they are ejected as described above. The palps were also seen to wipe over the anterior pair of pores, removing any debris, while the mobile foot periodically swept over both septum and mantle surfaces, collecting material on its ciliated surface and passing it either to the palps or the mantle edge.

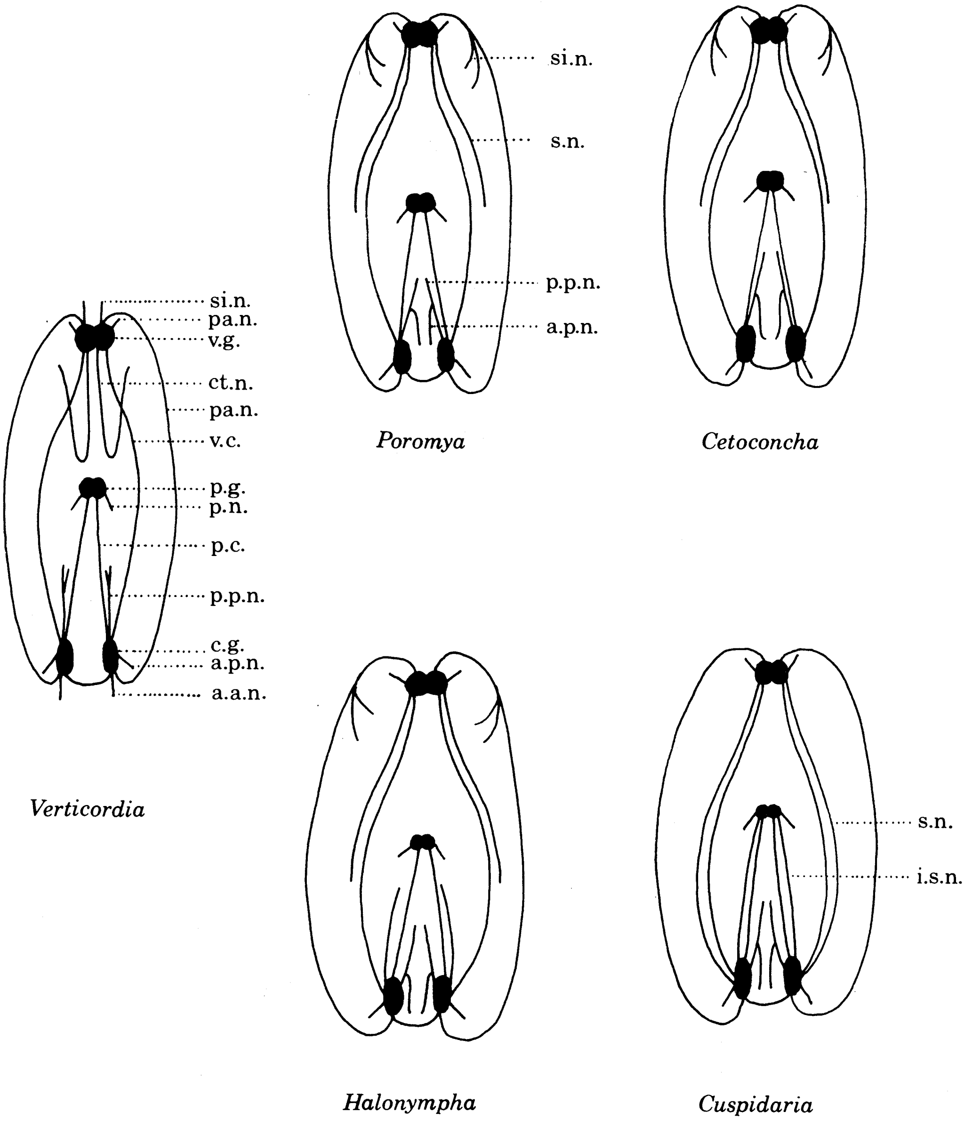
The evolution of the septum

The origin of the septibranch septum frequently has been the subject of discussion (Dall 1890; Pelseneer 1888*a*, *b*; Grobben 1892; Plate 1897; Yonge 1928; Bernard 1974), but owing to paucity of material little evidence has ever been presented to substantiate the theories offered. Fortunately, from the material available for the present study two hitherto unknown intermediate types of septum have been recognized, one in the previously known genus *Halonympha* and the other in a new genus *Protocuspidaria*. These two genera possess recognizable gill filaments.

Dall (1890) maintained that the septum was derived from a forward extension of the siphonal retractor muscles and the intersiphonal septum. He considered the series of branchial pores in the septibranchs to be a secondary development, and that the septum served three functions, namely to delimit the anal cavity, to drastically reduce the gill area and to act as a marsupium for brooding developing eggs. Pelseneer (1888*a*, *b*, 1891, 1911), Grobben (1892) and Ridewood (1903) all believed that the septum could be derived from the gills by a process of reduction in the number of branchial apertures and an increase in the musculature. All believed that the septum was innervated by nerves originating in the visceral ganglion just as do the branchial nerves serving a normal gill. Plate (1897), however, maintained that the septal innervation was cerebropleural not visceral and like Dall (1890) considered the septum to be mainly pallial. Yonge (1928) did not enter the argument but considered that since the septum performs the same water-propelling function as the gills it is more likely that Pelseneer's view is correct, and that the septum is branchial in origin.

In the most recent reference to the subject, Bernard (1974) dismisses the idea that the septum or its pores are in any way homologous with the gills. Like Plate (1897) he claims that the septum in the Cuspidariidae and Poromyidae is innervated from the cerebropleural ganglion. Bernard (1974) uses his assumption on the innervation of the septum as evidence to justify separating the Poromyidae and Cuspidariidae from the Verticordiidae. From the present studies it is clear that the septum in all three families is innervated from the visceral ganglion (figure 97).

Bernard (1974) postulates an evolutionary series in which the gill area is reduced in relation to an increasing secondary outgrowth of a sheet of pallial tissue, which he terms the 'supractenidial flap'. This is equivalent to the 'free lamina' of Ridewood (1903) or the 'septal valvulae' of Odhner (1960). Bernard (1974) maintains that the flap grows over the dorsal surface of the gill until the separation into supra- and infraseptal mantle cavities is complete, thus rendering the gill obsolete. He deduces that the septum in the Poromyidae and the Cuspidariidae probably arose from the growth of this flap in an ancient, gill-less taxon, and that the branchial apertures developed secondarily. Despite the present discovery of cuspidariids possessing gill filaments and confirmation of the ctenidial origin of the 'flap' or septal valvulae the theory ignores the great morphological similarities between the Poromyidae and Verticordiidae.



Verticordia

Poromya

Cetoconcha

Halonympha

Cuspidaria

FIGURE 97. Comparison of the nervous systems of various septibranch genera.

Within the Verticordiidae there are species with reduced eulamellibranch gills in which both demibranchs are present and others where the gills are reduced to a state similar to that seen in the *Protocuspidaria* (Allen & Turner 1974). The supra-ctenidial flap in *Verticordia triangularis* is formed at the margins of the filaments of the outer demibranchs, posterior to the point where the gill axes converge behind the foot (figure 98). The marginal abfrontal epithelium of the filament is enlarged, glandular, and fused with that of the adjacent filaments and laterally with a shallow shelf-like outgrowth of the mantle tissue. The longitudinal filamentar muscles of filaments are

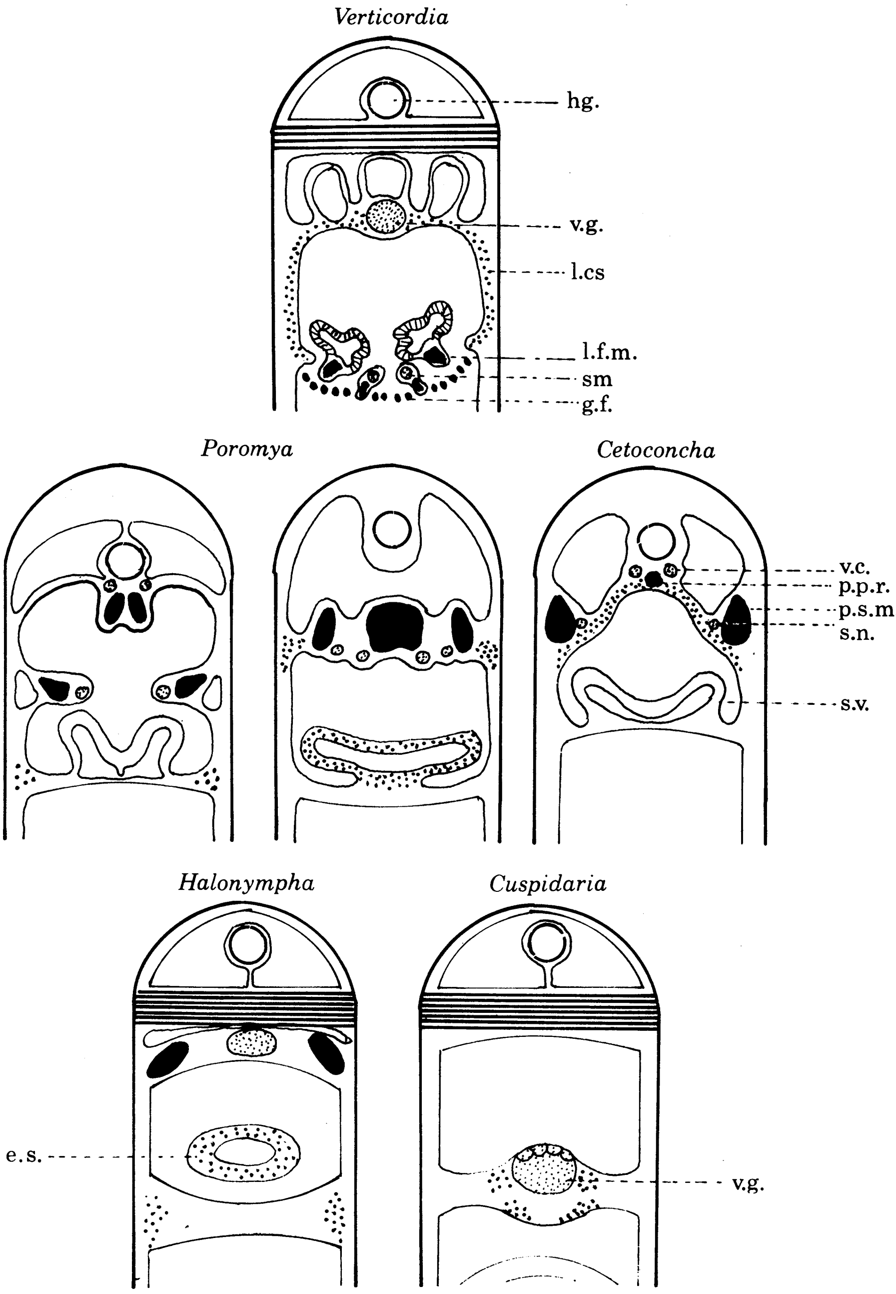


FIGURE 98. Diagrammatic transverse sections to show relationship between the fused posterior part of the outer demibranch in *Verticordia* and the septal valvulae, posterior septal muscle insertion and the distribution of lacunal cells in other septibranchs.

enlarged and coalesce to form a muscle that passes posteriorly and laterally into the adjacent mantle and there turns dorsally. The ctenidial nerve passes down the inner face of the muscle into the septum and along the axial muscle.

In *Poromya* and *Cetoconcha* there is a dorsally directed, posterior septal muscle with the septal nerve running down the inner face. In addition a swollen sheet of glandular and muscular tissue is present on the dorsal side of the septum, i.e. the septal valvulae. It must be concluded that the septal valvulae of *Poromya* and *Cetoconcha* and the supra-ctenidial flap of *Verticordia* are homologous.

The largest septal valvulae are found in *Poromya*, which has weak posterior septal muscles. The septal valvulae are not so large in *Cetoconcha*, where the muscles are more developed. Odhner (1960) believed that the septal valvulae serve to strengthen the posterior end of the septum, the posterior septal muscle not being sufficiently strong to support a fully developed pumping mechanism as it does in the Cuspidariidae. In the Cuspidariidae, at most, only a few scattered cells and vertical muscle struts between two epithelial layers are possibly homologous with the septal valulae, but here the posterior septal muscles are very large. However, in *Halonympha* there are two small masses of connective tissue containing gland cells and a few muscle fibres at the posterior end of the multipored septum. The muscle fibres extend from the septum into the mantle lining the supraseptal cavity to merge with the siphonal retractor muscles. These may be homologous to the posterior septal muscle of *Cuspidaria*, *Poromya* and *Cetoconcha*.

In the Poromyidae and the Cuspidariidae, contrary to the view of Plate (1897) and Bernard (1974) the septal nerve originates in the visceral ganglion, passes down the inside of the posterior septal muscles and along the outer edge of the septum. In *Poromya*, *Cetoconcha* and the less-specialized cuspidariids *Protocuspidaria* and *Halonympha*, this nerve does not reach the cerebropleural ganglion although it does so in the genus *Cuspidaria*. The septal nerve is homologous with the branchial nerve of other bivalves, thus suggesting that part, at least, of the septum is derived from gill axis.

If one assumes that the septum, at least in part, is derived from the gill, then the muscles of the gill consisting of longitudinal axial muscle from mouth to intersiphonal septum and small filamentar muscles at right angles to the axis should be homologized with at least some of the septal muscles (figure 99).

Within the family Verticordiidae, there are species such as *V. triangularis* in which the gills are reduced and consist largely of the shortened descending lamellae of the inner demibranch with, posteriorly, a few filaments of the descending lamellae of the outer demibranch (Allen & Turner 1974). The filaments lie in the horizontal plane. The axis, with an enlarged longitudinal muscle, is for the most part detached from the body. The gill margins fuse with the mantle laterally, the foot and palps anteriorly and the opposing demibranch and siphonal septum posteriorly, all by means of a thin epithelial membrane.

In *Poromya* and *Cetoconcha* the anterior septal muscle, external to the septal pores, corresponds in position to the axial muscle in the Verticordiidae. In comparison it is further enlarged and has acquired a dorsal attachment to the shell. In the Cuspidariidae the anterior septal muscle is variously developed. In *Protocuspidaria*, it is ill defined and lacks an anterior dorsal attachment to the shell, but it follows the same course as the axial muscle in running along the outer edge of the filaments to behind the foot. In *Halonympha* the muscle has an anterior dorsal attachment and is more distinct, and in *Cuspidaria* it is comparable to *Poromya* in size and structure.

A well developed posterior septal muscle with a dorsal attachment to the shell is present in *Poromya*, *Cetoconcha* and *Cuspidaria*, but not in *Verticordia*, *Protocuspidaria* and *Halonympha*. In *Verticordia* the fused filamentar muscles of the much reduced outer demibranch extend into the mantle. There is a similar, very narrow strand of tissue in *Halonympha* which extends dorsally from the back of the septum and which consists mainly of connective tissue and a few muscle fibres. If the position of the axial nerve is taken into account it is probable that the posterior

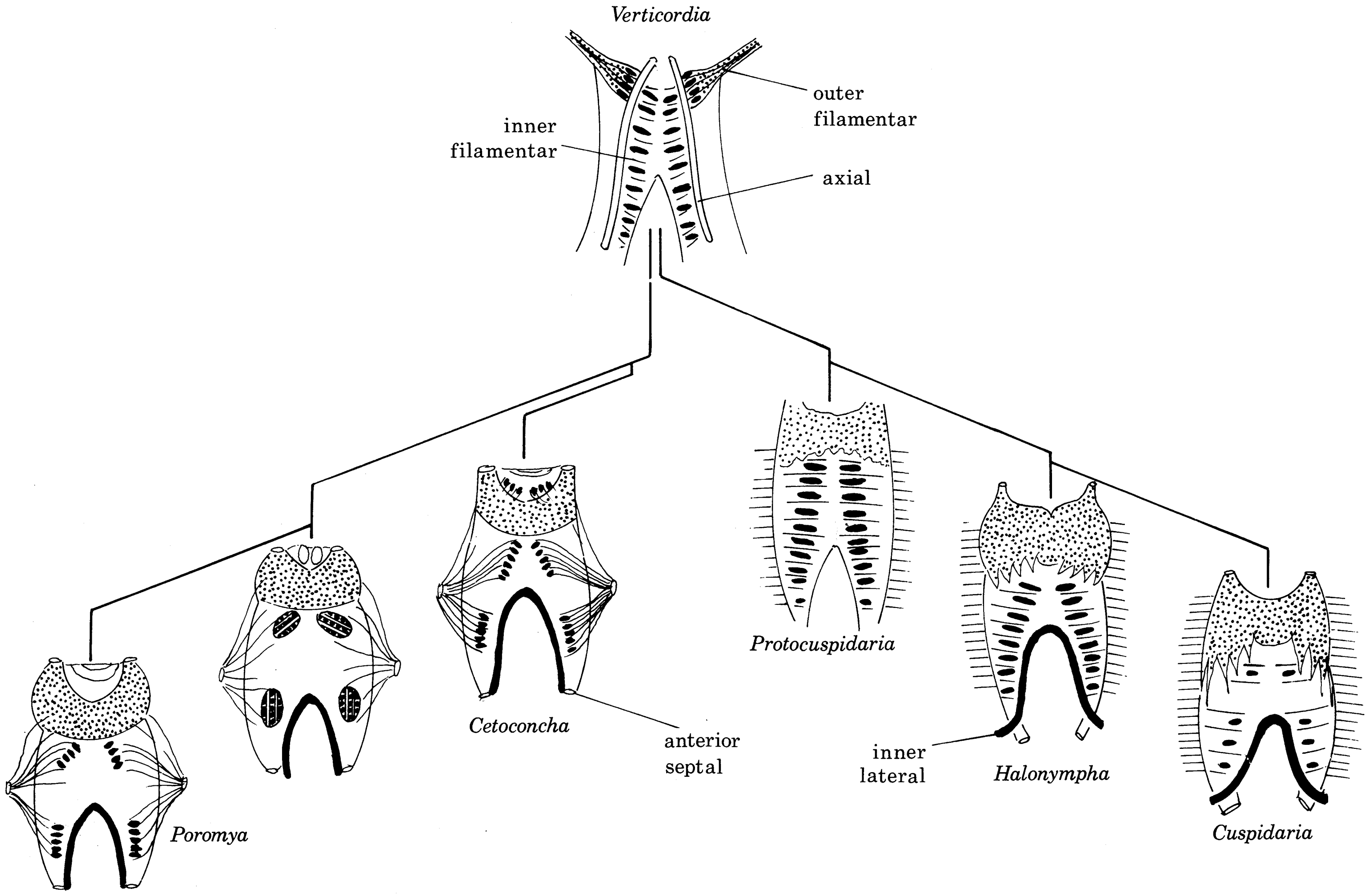


FIGURE 99. Diagram to show the origin and development of the septal muscles in the genera of the Septibranchia.

septal muscle, characteristic of the Poromyidae and *Cuspidaria*, may be derived from rudiments of the filamentar muscles of the last few gill filaments of outer demibranch (n.b. *Cetoconcha*).

Lateral septal muscles are very prominent in the Poromyidae, where they act as the main supporting muscles of the septum and are attached in groups to the shell. In the Cuspidariidae, where the anterior and posterior septal muscles are much stronger, the lateral septal muscles are less important. Even in those few species of the genus *Cuspidaria* where the lateral septal muscles are attached in groups, they are always weak. In *Poromya* and *Cetoconcha* the lateral muscles, which run transversely across the dorsal surface of the septum into the mantle, can be homologized as extensions of the longitudinal filamentar muscles. It is recognized that there are far more lateral septal muscles in *Cuspidaria* than there are remaining modified gill filaments, and it must be assumed that additional lateral septal muscles are derived from the filamentar muscles of lost gill filaments. It remains uncertain as to whether in *Cuspidaria* they are derived solely from filaments of the inner demibranch.

As described earlier, the pore-closing mechanism in *Poromya*, *Cetoconcha* and *Cuspidaria* also can be derived from the longitudinal filamentar muscles.

The outer longitudinal septal muscle, which is obvious only in *Cuspidaria*, is an additional muscle lateral to the anterior septal muscle. It may be simply a branch of the latter muscle that, instead of curving behind the foot, continues posteriorly to make a posterior attachment to the shell, or it may be derived from pallial muscle.

When fully developed (*Halonympha*, *Cuspidaria*) the inner longitudinal muscle has an anterior dorsal attachment separate from that of anterior septal muscle. The muscle passes posterior to the foot and is connected to it by complete tissue fusion. In *Poromya* and *Cetoconcha*, there is no separate attachment of the inner longitudinal septal muscle and the septum is free from the posterior part of the foot. It should be noted that pedal muscles pass into the septum anteriorly. The inner longitudinal muscle is innervated by a nerve of different origin from other nerves supplying the septum. The inner septal nerve originates in the cerebropleural ganglion, and in *Halonympha*, *Poromya* and *Cetoconcha* passes posteriorly along the inner edge of the septum into musculature of the foot. In *Cuspidaria*, where the muscle is better developed, the inner septal nerve extends further and connects with pedal ganglion. The inner longitudinal muscle is probably derived from the anterior pedal retractor muscle by an anterolateral invasion of the septum, at a point corresponding to the anterior attachment of a gill to the body–foot wall.

Plate (1897), in his work on *C. obesa*, described a single tract of muscle fibres running out from the anterior part of the foot and thought that, perhaps, part of the foot musculature was involved in the septum formation. It is probable that he was describing the inner longitudinal septal muscle, although he presented no other supporting evidence.

Although Dall (1889*a*, *b*) and Bernard (1974) claim that the branchial apertures in the Poromyidae and Cuspidariidae are secondarily developed, comparison with the Verticordiidae, together with the evidence of the derivation of the septal muscles, leaves little doubt that the branchial apertures in both families are derived from modified gill filaments. The verticordiid gill is a modified eulamellibranch form and is set horizontally across the mantle cavity so that the frontal surfaces of the filaments face ventrally. The filaments have a large central blood space bounded by a pair of characteristic skeletal rods, and a distinct longitudinal filamentar muscle running the length of the filament beneath the dorsal (abfrontal) surface. Lateral cilia are present on either side and short frontal cilia are present over the entire ventral surface. In *Poromya* the filaments are arranged in two separate paired groups. Some species have longer filaments than others, with interfilamentar connections giving the appearance of sieves. Others have five or six short filaments in each group, with lipped, pore-like apertures, within the margins of which the longitudinal muscles form a closing mechanism. In both a modified gill filament is recognizable, containing muscle, blood space, skeletal rods, lateral cilia within the aperture, and frontal cilia restricted to the ventral edge.

Cetoconcha differs from *Poromya* in that the branchial apertures are arranged in three paired groups. The anterior two are homologous to those in *Poromya*. The third and smallest group, consisting of two or three filaments, is posterior to the small posterior septal muscles and aligned in a more longitudinal plane than are the anterior groups. If one assumes that the posterior septal muscle is derived from the filamentar muscles of the outer demibranch, then it follows that this group of branchial apertures is also derived from the same demibranch. In *Cetoconcha* the filaments are more shallow than those of *Poromya* and lack skeletal rods; however, muscle is well developed around the dorsal and lateral surfaces, forming an efficient closing mechanism. Lateral cilia are present as in *Poromya*, but the lateral/frontal cilia are more restricted.

The septibranchs, with the possible exception of *Propeammussium* (Knudsen 1970), are the only group of lamellibranchs with a specialized carnivorous habit, all others being either suspension or deposit feeders using gills to filter particles entering the mantle cavity. The evolution of the carnivorous habit from a filtration system involves the development of a prey-capturing mechanism. Two such mechanisms have been adopted by the septibranchs; one, an external trapping mechanism, involves adhesive tentacles that passively collect small, bottom-dwelling animals (Verticordiidae); the second involves the use of a muscular pumping mechanism to suck in detected passing prey (Cuspidariidae).

How *Poromya* and *Cetoconcha* feed is a matter of debate. They possess a muscular septum and pores that can close, but the posterior septal muscles are rather weak and are associated with septal valvulae. Furthermore, the supra- and infraseptal cavities are not sealed by tissue posterior to the foot. It is possible that the pumping mechanism of *Poromya* and *Cetoconcha* is not as efficient as that in *Cuspidaria*. However, the tentacles, though similar to those of verticordiids, do not appear to be adhesive.

Similarly, neither *Halonympha* nor *Protocuspidaria* have posterior septal muscles but possess numerous septal apertures. The septum therefore may also be incapable of pumping as efficiently as in *Cuspidaria*. These genera have siphons of the *Cuspidaria* type and thus are probably adapted to detecting and capturing prey in the same manner and thus it might be assumed that the septal apertures can close completely. Without examining living specimens it is not possible to define, with certainty, how they feed, but it seems probable that *Poromya* and *Cetoconcha*, and possibly *Halonympha* and *Protocuspidaria*, rely on both pumping and ciliary action for respiration and possibly capture of small prey. All have the typical, crushing, septibranch stomach.

It cannot be without significance that, as the septum becomes a stronger and more complete partition, the palps are reduced and the shell becomes more rostrate. The Verticordiidae, Poromyidae and *Protocuspidaria* are at most barely rostrate; they have short siphons and therefore are confined to the uppermost layers of the sediment. In contrast, with a better developed pumping mechanism and a larger rostrum with only the siphon tip and tentacles exposed, *Cuspidaria* can penetrate further into the sediment.

The discovery of the intermediate types of septum represented by the cuspidariid genera *Halonympha* and *Protocuspidaria* indicates the likelihood that the group evolved from a common gilled ancestor but that the component families diverged at an early stage. The Verticordiidae and Poromyidae diverged as short-siphoned, hermaphrodite animals with a reduced gill area; only the Poromyidae increased the musculature of the septum. The Cuspidariidae on the other hand, while showing clear similarities between the primitive genus *Protocuspidaria* and *Verticordia*, become long-siphoned dioecious animals in which the pores remain as a single series and in which the septum becomes increasingly muscular, giving rise to *Halonympha* and *Cuspidaria*.

Thus we conclude, in contrast to Dall (1889) and Bernard (1974), but in general agreement with Pelseneer (1888*a*, *b*, 1891, 1911), that the origin of the septibranch septum is mainly ctenidial. In the course of evolution the gill was first reduced to the descending lamella of the inner demibranch together with a few posterior filaments of the descending lamella of the outer demibranch, the total number of filaments being greatly reduced. The axial muscle increased and formed the anterior septal muscle, developing an anterior shell attachment. The longitudinal filamentar muscles of the inner demibranch gave rise to the lateral septal muscles and the sphincter closing the pore, while the remnants of outer demibranch were transformed into the posterior septal muscles, which also form a dorsal insertion on the shell.

There is no evidence to support Dall (1889) and Bernard (1974) in their theory that the branchial apertures in the Septibranchia are secondarily developed. A series can be traced from a typical eulamellibranch filament in which the filamentar apertures become very much shorter, fewer in number, lose their skeletal rods and whose musculature increases while the lateral and reduced frontal cilia remain in a modified form. There is evidence that the pedal musculature is also involved in the septum, forming the inner longitudinal septal muscle. There is also possibly some pallial involvement giving rise to the outer longitudinal muscle.

Familial relationships

From evidence of this study the taxonomy of the group proposed here is as set out in table 1 and figure 99.

Here all three families (Verticordiidae, Poromyidae and Cuspidariidae) are combined in the Anomalodesmata as the suborder Septibranchia by virtue of the similarities in their septal and digestive systems. Although Yonge & Morton (1980) from evidence of their studies on the ligament came to a different conclusion we separate the Verticordiidae and Poromyidae in the superfamily Poromyoidea from the Cuspidariidae in the superfamily Cuspidaroidea.

It is clear that although the Verticordiidae (Allen & Turner 1974), Poromyidae and Cuspidariidae have many characters in common, such as the variously developed septum, the muscular and scleroprotein-lined stomach, the form of the gut, nervous, sinus and excretory systems, there are characters, the ligament apart, that separate the Verticordiidae and Poromyidae from the Cuspidariidae and which suggest that divergence from a common ancestor may have occurred early in their evolutionary history. Jurassic cuspidariids (the earliest recorded fossils) were already similar in shell shape and form to the recent species and, therefore, then distinct from poromyids. The similarities in the septal and stomach structure between the families could be a result of parallel evolution, possibly related to a comparable carnivorous habit.

The similarities between the Verticordiidae (Allen & Turner 1974) and the Poromyidae are very great and do not warrant their separation to the extent of placing the former within the Eulamellibranchia, and the latter within the Septibranchia, as did Pelseneer (1891, 1911). Nor is it possible, as Bernard (1974) would have it, to retain the Verticordiidae in the subclass Anomalodesmacea and place the Cuspidariidae and Poromyidae together, close to the

Protobranchia. The Verticordiidae and Poromyidae resemble each other very much more than either do the Cuspidariidae. Both have short siphons surrounded by a ring of short tapering tentacles, a conspicuous inwardly projecting inhalant valve and large anterior palps, and are hermaphrodite. In contrast the Cuspidariidae have longer, separate siphons encased in a common siphonal sheath, seven distinct club-ended or frilled tentacles, and an inhalant valve that is merely a thin vertical partition across the inner end of the inhalant siphon that is pierced by a slit. Most cuspidariid species are dioecious. While they normally have reduced palps, those with more than five pairs of pores in the septum have larger palps, but it is the posterior, not the anterior that are the larger.

The form of the ligament is an exception in that in this respect the Cuspidariidae are much more similar to the Verticordiidae than are the Poromyidae (Yonge & Morton 1980).

Although it would appear that the Verticordiidae and Poromyidae are not in direct evolutionary line with the Cuspidariidae, it seems that the differences between the three families are not so great that they cannot be combined in a single taxon, the Septibranchia. The primitive cuspidariid genera, *Protocuspidaria* and *Halonympha*, whose anatomy is here described for the first time, differ from the Verticordiidae and Poromyidae in having cuspidariid-type siphons, but have a comparable septum. A scale of increasing complexity of septal musculature with a corresponding reduction in the number of apertures can be seen in the series Verticordiidae, Poromyidae and Cuspidariidae. The verticordiids and *Protocuspidaria* have no anterior and posterior septal attachments on to the shell, *Halonympha* has anterior septal attachments and the poromyids and *Cuspidaria* have both anterior and posterior attachments.

We wish to thank and acknowledge our indebtedness to the following for their assistance and for providing specimens for this study: Sir Maurice Yonge, who so kindly added his comments and corrections to the manuscript and gave much of his experience and advice; Dr H. L. Sanders, Woods Hole Oceanographic Institution; Dr J. Gage, Scottish Marine Biological Association; M. M. Segonzac, Centre Océanologique de Bretagne; Dr J. Taylor and Mrs S. Whybrow, British Museum; Dr J. Rosewater and Dr W. J. Byas, Smithsonian Institution; Dr A. Warén, University of Gothenburg; Dr K. Ockelmann and Dr J. Knudsen, University of Copenhagen and Mr P. B. Wikander, University of Bergen. We wish to thank the Natural Environment Research Council for a Grant (no. GR3/1895A) to support this study.

We would also like to acknowledge the great assistance that came via the referees of the Royal Society.

REFERENCES

Adams, A. 1864 On the species of *Neaera* found in the seas of Japan. *Ann. Mag. nat. Hist.* (3) **13**, 206–209.

Adams, H. & Adams, A. 1854–1858 *The genera of recent* Mollusca *arranged according to their organization*, vol. 2. London: van Voorst.

Allen, J. A. 1960 The ligament of *Cochlodesma praetenue* (Pultney). *J. mar. biol. Ass. U.K.* **39**, 445–447.

Allen, J. A. 1968 The functional morphology of *Crassinella mactracea* (Linsley) (Bivalvia: Astartacea). *Proc. malac. Soc. Lond.* **38**, 27–40.

Allen, J. A. 1978 Evolution of the deep sea protobranch bivalves. *Phil. Trans. R. Soc. Lond.* B **284**, 387–401.

Allen, J. A. 1979 The adaptations and radiation of deep-sea bivalves. *Sarsia* **64**, 19–27.

Allen, J. A. & Sanders, H. L. 1973 Studies on deep sea Protobranchia. The families Siliculidae and Lametilidae. *Bull. Mus. comp. Zool. Harv.* **145**, 263–310.

Allen, J. A. & Sanders, H. L. 1981 Studies on the deep sea Protobranchia. The subfamily Spinulinae (family Nuculanidae). *Bull. Mus. comp. Zool. Harv.* (In the press.)

Allen, J. A. & Turner, J. F. 1974 On the functional morphology of the family Verticordiidae (Bivalvia) with descriptions of new species from the abyssal Atlantic. *Phil. Trans. R. Soc. Lond.* B **268**, 401–536.

Bernard, F. R. 1969 Preliminary diagnoses of new septibranch species from the E. Pacific (Bivalvia, Anomalodesmata). *J. Fish. Res. Bd Can.* **26**, 2230–2234.

Bernard, F. R. 1974 Septibranchs of the Eastern Pacific (Bivalvia, Anomalodesmata). *Allan Hancock Monogr. mar. Biol.* **8**, 1–279.

Brown, T. 1844 *Illustrations of the conchology of Great Britain and Ireland* (2nd edn). Edinburgh: Fullerton.

Bush, K. J. 1885 Mollusca of Cape Hatteras. *Trans. Conn. Acad. Arts Sci.* **4**, 472–473.

Carpenter, P. P. 1864 Supplementary report on the present state of our knowledge with regard to the Mollusca of the west coast of N. America. *Rep. Br. Ass. Advmt Sci.*, pp. 517–686.

Clarke, A. H. 1962 Annotated list and bibliography of the abyssal marine molluscs of the world. *Bull. natn. Mus. Can.* **181**, 1–114.

Dall, W. H. 1878 Preliminary note on mollusks of the 'Blake' Expedition. *Bull. Mus. comp. Zool. Harv.* **5**, 55–64.

Dall, W. H. 1881 Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico, and in the Caribbean Sea, 1877–79, by the U.S. coast survey steamer 'Blake' XV. Preliminary report on the Mollusca. *Bull. Mus. comp. Zool. Harv.* **2**, 33–144.

Dall, W. H. 1886 Report on the Mollusca. Part I. Brachiopoda and Pelecypoda. Reports on the results of dredging by the U.S. coast survey steamer 'Blake'. *Bull. Mus. comp. Zool. Harv.* **12**, 171–318.

Dall, W. H. 1889*a* Report on the Mollusca. Addenda and corrigenda to part I 1886. Reports on the results of dredging by the U.S. coast steamer 'Blake'. *Bull. Mus. comp. Zool. Harv.* **18**, 1–492.

Dall, W. H. 1889*b* A preliminary catalogue of the shell bearing marine molluscs and brachiopods of the S.E. coast of the United States. *Bull. U.S. natn. Mus.* **37**, 1–221.

Dall, W. H. 1890 Preliminary report on the collection of molluscs and Brachiopoda obtained in 1887–1888. Scientific results of explorations by the U.S. Fish. Commission steamer 'Albatross'. No. 7. *Proc. U.S. natn. Mus.* **12**, 219–362.

Dall, W. H. 1903 Contribution to the Tertiary fauna of Florida with special reference to the silex beds of Tampa and the Pliocene beds of the Caloosahatchie River, including in many cases, a complete revision of the generic groups treated and of their American Tertiary species. Part VI. *Trans. Wagner. free Inst. Sci. Philad.* **3**, 1219–1654.

Dall, W. H. 1908 The Mollusca & Brachiopoda. Report on the dredging operations off the west coast of Central America by the U.S. Fish. Commission steamer 'Albatross'. *Bull. Mus. comp. Zool. Harv.* **43**, 428–434.

Dall, W. H. 1916 Diagnoses of new species of marine bivalve molluscs from the north west coast of America in the collection of the United States National Museum. *Proc. U.S. natn. Mus.* **52**, 393–417.

Dall, W. H., Bartsch, P. & Rehder, H. A. 1938 A manual of the recent and fossil marine pelecypod molluscs of the Hawaiian Islands. *Bull. Bernice P. Bishop Mus.* **153**, 1–233.

Dautzenberg, Ph. 1889 Contribution à la faune malacologique des iles Açores. *Résult. Camp. scient. Prince Albert I*, **1**, 1–112.

Dautzenberg, Ph. 1891 Campagnes scientifiques du yacht l'Hirondelle en 1886. Contributions á la faune malacologique du Golfe de Gascogne. *Mém. Soc. zool. Fr.* **4**, 604–619.

Dautzenberg, Ph. 1927 Mollusques provenant des campagnes scientifiques du Prince Albert Ier e Monaco dans l'Ocean Atlantique et dans le Golfe de Gascogne. *Résult. Camp. scient. Prince Albert I*, **72**, 1–400.

Dautzenberg, Ph. & Fischer, H. 1897 Dragages effectués par l'Hirondelle et par la Princesse Alice. 1888–1896. *Mém. Soc. zool. Fr.* **10**, 139–234.

Dautzenberg, Ph. & Fischer, H. 1912 Mollusques provenant des campagnes de l'Hirondelle et de la Princess-Alice dans les mers du nord. *Résult. Camp. scient. Prince Albert I*, **37**, 1–629.

Fischer, P. H. 1880–1887 *Manuel de conchyliologie et de paléontologie conchyliologique*, vol. 24. Paris: Savy.

Forbes, E. 1843 On the species of *Neaera* (Gray) inhabiting the Eegean (*sic*) Sea. *Proc. zool. Soc. Lond.* **11**, 75.

Forbes, E. 1844 Report on the Mollusca and Radiata of the Aegean Sea, and on their distribution, considered as a bearing on geology. *Rep. Br. Ass. Advmt Sci.* (1843), pp. 130–193.

Forbes, E. & Hanley, S. 1849–1853 *History of British Mollusca and their shells*, vol. **1**. London: van Voorst.

Friele, H. & Grieg, J. A. 1901 Mollusca. III. *Norw. N Atl. Exped.* 1876–1878 **6**, 1–131.

Gould, A. A. 1861 Descriptions of new genera and species of shells. *Proc. Boston Soc. nat. Hist.* **8**, 280–285.

Gray, J. E. 1834 Cited in E. Griffith & E. Pidgeon 1834 The Mollusca and Radiata. An appendix in *Animal kingdom* (by D. Cuvier), vol. 12, p. 601.

Gröbben, C. 1892 Beiträge zur Kentniss des Baues, von *Cuspidaria* (*Neaera*) *cuspidata*. Olivi. *Arb zool. Inst. Univ. Wien* **10**, 101–146.

Haas, F. 1949 On some deep sea mollusks from Bermuda. *Butll. Inst. catal. Hist. nat.* **37**, 69–72.

Hedley, C. 1907 The results of deep sea investigations in the Tasman Sea. 3. Mollusca from eighty fathoms off Narrabeen, Sydney, N.S.W. *Rec. Aust. Mus.* **6**, 283–304.

Hedley, C. & Petterd, F. W. 1906 Mollusca from three hundred fathoms off Sydney. Sydney N.S.W. *Rec. Aust. Mus.* **6**, 211–225.

Hinds, R. B. 1843 Descriptions of new species of *Neaera*, from the collections of Sir Edward Belcher, C. B., made during a voyage round the world, and from that of Hugh Cuming, esq., obtained during his visit to the Philippines; with notices of synonymy. *Proc. zool. Soc. Lond.* **11**, 75–79.

Iredale, T. 1930 More notes on the marine Mollusca of New South Wales. *Rec. Aust. Mus.* **17**, 384–407.

Jeffreys, G. 1862–1869 *British conchology*. London: John van Voorst.

Jeffreys, G. 1876 New and peculiar Mollusca of the *Kellia*, *Lucina*, *Cyprina* and *Corbula* families produced in the 'Valorous' Expedition. *Ann. Mag. nat. Hist.* (4) **18**, 490–499.

Jeffreys, G. 1881 On the Mollusca procured during the 'Lightening' and 'Porcupine' expeditions 1868–70, part V. *Proc. zool. Soc. Lond.* (1882), pp. 656–687.

Johnson, C. W. 1934 List of the marine Mollusca of the Atlantic. *Proc. Boston Soc. nat. Hist.* **40**(1), 1–203.

Keen, A. M. 1963 *Marine molluscan genera of western North America. An illustrated key.* Stanford: University Press.

Knudsen, J. 1970 The systematics and biology of abyssal and hadal Bivalvia. *Galathea Rep.* **11**, 7–241.

Locard, A. 1898 Mollusques testacés. II. *Expéditions scientifiques du Travailleur et du Talisman*, vol. 2, pp. 1–515. Paris: Masson.

Locard, A. 1899 *Les coquilles marines des côtes de France.* Paris: Baillière.

Lövén, S. 1846 Nordens Hafs-Mollusker. Index Molluscorum litora Scandinaviae occidentalia habitantium. *K. svenska VetenskAkad. Handl.* **3**, 134–160, 182–204.

Melville, J. C. & Standen, R. 1907 The marine Mollusca of the Scottish National Antarctic Expedition. 1. *Trans. R. Soc. Edinb.* **46**, 119–157.

Moore, R. C. (ed.) 1969 Mollusca 6, Bivalvia. *Treatise on invertebrate palaeontology*, pt N, vol. 1. Kansas: Geol. Soc. Am. and University of Kansas.

Mörch, O. A. L. 1875 Prodromus faunae Groenlandiae. In *Manual of the natural history, geology and physics of Greenland and the neighbouring regions, Great Britain and Ireland.* London: Admiralty.

Morgan, R. E. & Allen, J. A. 1976 On the functional morphology and adaptations of *Entodesma saxicola* (Bivalvia: Anomalodesmacea). *Malacologia* **15**, 233–240.

Morgan, R. E. & Heppell, D. 1981 *Rhinoclama* Dall & Smith, 1886 (Pelecypoda: Cuspidariidae). Proposed validation of the customary usage by description of the reputed type-species. *Bull. zool. Nom.* (In the press.)

Nardo, G. D. 1840 Sopra un nuovo genere di conchioglie de mare Adriatico Atti della Prima Riunione degli Scienziata Italiani tenuta in Pisa nell ottobre del 1839. *Rev. zool., Paris*, p. 30.

Newell, D. N. 1965 Classification of the Bivalvia. *Am. Mus. Novit.* **2206**, 1–25.

Nicol, D. 1966 Descriptions, ecology and geographic distribution of some antarctic pelecypods. *Bull. Am. Paleont.* **51**, 5–84.

Nordsieck, F. 1969 *Die europaischen Meeresmuscheln (Bivalvia) von Eismeer bis Kapverden, Mittelmeer und Schwarzes Meer.* Stuttgart: Gustav Fischer.

Nyst, H. & Westendorp, G. D. 1839 Nouvelles recherches sur les coquilles fossiles de la provence d'Anvers. *Bull. Acad. r. Belg. Cl. Sci.* **6**, 393–414.

Ockelmann, W. K. 1958 Marine Lamellibranchiata. *Meddr Grønland* **122**, 1–256.

Odhner, N. H. 1960 Mollusca. *Rep. Swed. deep Sea Exped.* **2**, 367–400.

Okutani, T. 1962 Report on the archibenthal and abyssal Lamellibranchiata Mollusca mainly collected from Sagami Bay and adjacent waters by the R.V. Soyo-Maru during the years 1955–60. *Bull. Tokai. reg. Fish. Res. Lab.* **32**, 1–40.

Okutani, T. 1968 Bathal and abyssal Mollusca trawled from Sagami Bay and south of Boso Peninsula by the Soyo-Maru, 1965–67. *Bull. Tokai. reg. Fish. Res. Lab.* **56**, 6–49.

Okutani, T. & Sakurai, K. 1964 Genus *Cardiomya* (Mollusca Lamellibranchiata) from Japanese waters. *Bull. natn. Sci. Mus., Tokyo* **7**, 17–32.

Oliver, G. & Allen, J. A. 1980 The functional and adaptive morphology of the deep sea species of the superfamily Arcacea (Mollusca Bivalvia) from the Atlantic. *Phil. Trans. R. Soc. Lond.* B **291**, 45–76.

Oliver, G. & Allen, J. A. 1980 The functional and adaptive morphology of the deep sea species of the family Limopsidae (Bivalvia Arcoida) from the Atlantic. *Phil. Trans. R. Soc. Lond.* B **291**, 77–125.

Olivi, G. 1792 *Zoologica Adriatica, ossia catalogo ragionata degli animati del Golfe e delle Lagune di Venezia.* Bassano.

Pelseneer, P. 1888*a* Report on the scientific results of the Voyage of H.M.S. Challenger in the years 1873–76. *Rep. scient. Res. Challenger* **27**, 1–42.

Pelseneer, P. 1888*b* Les pelecypodes (ou lamellibranches) sans branchies. *C. r. hebd. Séanc. Acad. Sci. Paris* **106**, 1029–1031.

Pelseneer, P. 1891 Contribution à l'étude des Lamellibranches. *Archs Biol. Paris* **11**, 147–312.

Pelseneer, P. 1911 Les Lamellibranches de l'expédition du Siboga, partie anatomique. *Siboga Exped.* A **53**, 1–125.

Philippi, R. A. 1836 *Enumeratio Molluscorum Siciliae cum viventium, tum in Tellure Tertiaria fossilium qual in itinere suo observavit.* Berolini: Sumptibus Cimonis Schroppi et Sociorum.

Plate, L. 1897 Giebt es septibranchiate Muscheln? *Sber. Ges. naturf. Freunde Berl.*, pp. 24–28.

Powell, A. E. B. 1937 New species of marine Mollusca from New Zealand. *'Discovery' Rep.* **15**, 153–222.

Prashad, B. 1932 The Lamellibranchia of the Siboga Expedition. Systematic. Part II. *Siboga Exped.* C **53**, 1–353.

Purchon, R. D. 1963 Phylogenetic classification of the Bivalvia, with special reference to the Septibranchia. *Proc. malac. Soc. Lond.* **35**, 71–80.

Reid, G. B. & Reid, A. M. 1974 The carnivorous habit of members of the septibranch genus *Cuspidaria* (Mollusca: Bivalvia). *Sarsia* **56**, 47–56.

Ridewood, W. G. 1903 On the structure of the gills of the Lamellibranchia. *Phil. Trans. R. Soc. Lond.* B **195**, 147–284.

Risso, A. 1826 *Histoire naturelle des principales productions de l'Europe méridionale et principalement de celles des environs de Nice et des Alpes Maritimes*, vol. 4. Paris and Strasbourg: Lavrault.

Sanders, H. L. & Allen, J. A. 1973 Studies on deep sea Protobranchia (Bivalvia), prologue and the Pristiglomidae. *Bull. Mus. comp. Zool.* **145**, 237–262.

Sanders, H. L. & Allen, J. A. 1977 Studies on the deep-sea Protobranchia (Bivalvia), the family Tindariidae and the genus *Pseudotindaria*. *Bull. Mus. comp. Zool. Harv.* **48**, 23–59.

Sanders, H. L., Hessler, R. R. & Hampson, G. R. 1965 An introduction to the study of deep-sea benthic faunal assemblages along the Gay Head – Bermuda transect. *Deep Sea Res.* **12**, 845–867.

Sars, G. O. 1878 *Bidrag til Knudskaben om Norges arktiske Fauna 1. Mollusca regionis arcticae Norvegiae.* Christiania: A. W. Brogger.

Smith, E. A. 1885 Report on the Lamellibranchiata collected by H.M.S. Challenger during the years 1873–76. *Rep. scient. Res. Challenger* **13**, 1–341.

Smith, E. A. 1896 Natural history notes from H.M. Indian Marine Survey Steamer 'Investigator', ser. II, no. 22 Descriptions of new deep-sea Mollusca. *Ann. Mag. nat. Hist.* (6) **18**, 367–375.

Sowerby, G. B. 1859 *Illustrated index of British shells.* London: Simpkin & Marshall.

Stoliczka, F. 1870–1871 The Pelecypoda, with a review of all known genera of this class, fossil and recent. *Mem. geol. Surv. India Palaeont. indica* **3**, 1–538.

Tate, R. 1892 Descriptions of some new species of marine Mollusca from Australia. *Trans. Proc. R. Soc. S. Aust.* **15**, 125–132.

Tebble, N. 1966 *British bivalve seashells. A handbook for identification.* Edinburgh: H.M.S.O.

Thiele, J. 1935 *Handbuch der systematischen Weichtierkunde 2. Classis Bivalvia.* Jena: Gustav Fischer.

Thiele, J. & Jaeckel, S. 1931 Muscheln der Deutschen Tiefsee Expedition. *Wiss. Ergebn. dt. Tiefsee-Exped. 'Valdivia'* **21**, 159–268.

Verrill, A. E. 1882 Catalogue of marine Mollusca added to the fauna of the New England region during the past ten years. *Trans. Conn. Acad. Arts Sci.* **5**, 447–587.

Verrill, A. E. 1884 Second catalogue of mollusca recently added to the fauna of the New England coast and the adjacent parts of the Atlantic. *Trans. Conn. Acad. Arts Sci.* **6**, 223.

Verrill, A. E. 1885 Third catalogue of Mollusca recently added to the fauna of the New England coast and the adjacent parts of the Atlantic, consisting mostly of deep-sea species, with notes on others previously recorded. *Trans. Conn. Acad. Arts Sci.* **6**, 397–452.

Verrill, A. E. & Bush, K. 1898 Revision of the deep water Mollusca of the Atlantic coast of North America with descriptions of new genera and species. Part I: Bivalvia. *Proc. U.S. natn. Mus.* **20**, 777–901.

Vokes, H. E. 1967 Genera of the Bivalvia, a systematic and bibliographic catalogue. *Bull. Am. Paleont.* **51**, 111–394.

Winckworth, R. 1940 A systematic list of the 'Investigator' Mollusca. *Proc. malac. Soc. Lond.* **24**, 19–29.

Yonge, C. M. 1928 Structure and function of the organs of feeding and digestion in the septibranchs, *Cuspidaria* and *Poromya*. *Phil. Trans. R. Soc. Lond.* B **216**, 221–261.

Yonge, C. M. 1952 Studies on Pacific Coast mollusks. V. Structure and adaptation in *Entodesma saxicola* (Baird) and *Mytilimeria nuttallii* Conrad. *Univ. Calif. Publs Zool.* **55**, 439–450.

Yonge, C. M. 1957 Mantle fusion in the Lamellibranchia. *Pubbl. Staz. zool. Napoli* **23**, 151–171.

Yonge, C. M. 1976 Primary and secondary ligaments with the lithodesma in the Lyonsiidae (Bivalvia: Pandoracea). *J. mollusc. Stud.* **42**, 395–408.

Yonge, C. M. & Morton, B. 1980 Ligament and lithodesma in the Pandoracea and the Poromyacea with a discussion on evolutionary history in the Anomalodesmata (Mollusca: Bivalvia). *J. Zool.* **191**, 263–292.

ABBREVIATIONS USED IN FIGURES

a.a.	anterior adductor muscle
a.a.n.	anterior adductor nerve
a.b.s.	anterior branchial sieve
a.l.t.	anterior lateral tooth
an.	anus
a.p.	anterior palp
a.p.n.	anterior palp nerve
a.p.r.	anterior pedal retractor muscle
a.s.m.	anterior septal muscle
b.	byssus
b.a.	byssal aperture
b.c.	byssogenous cavity
b.g.	byssal groove
b.g.I	byssal gland cell (type 1)
b.g.II	byssal gland cell (type 2)
b.s.	blood space
b.sv.	branchial sieve
c.c.	cerebral commissure
c.g.	cerebropleural ganglion
c.l.m.	lateral muscle
c.m.	circular muscle
c.t.	cardinal tooth
ct.n.	ctenidial nerve
d.d.	digestive diverticula
d.d.a.	aperture to digestive diverticula
d.s.e.	dorsal septal epithelium
e.l.	external ligament
e.l.i.	extra lateral insertion
e.s.	exhalant siphon
e.s.a.	exhalant aperture
f.	foot
f.c.	frontal cilia

f.p.	fused periostracum
g.c.	gland cell
g.d.	gonadial duct
g.f.	gill filament
h.	heart
hg.	hindgut
i.l.l.	inner layer of ligament
i.l.m.	inner lateral muscle
i.s.	inhalant siphon
i.s.a.	inhalant aperture
i.s.n.	inner septal nerve
is.s.	intersiphonal septum
i.t.	internal tentacle
i.v.	inhalant valve
i.w.	intertentacular web
k.	kidney
l.	ligament
l.c.	lateral cilia
l.cs	lacunal cells
l.f.m.	longitudinal filamentar muscle
li.	lithodesma
l.m.	longitudinal muscle
l.s.m.	lateral septal muscle
m.	mouth
mg.	midgut
m.r.t.	rejection tract
m.s.	membranous septum
mu.	muscle
oe.	oesophagus
o.l.l.	outer layer of ligament
o.l.m.	outer longitudinal muscle
ov.	ovary
p.	pore
p.a.	posterior adductor muscle
p.a.n.	pallial nerve
p.c.	pedal connective
p.c.m.	pore-closing muscles
p.ga.	pedal ganglion
p.l.t.	posterior lateral tooth
p.n.	pedal nerve
p.p.	posterior palp
p.p.n.	posterior palp nerve
p.p.r.	posterior pedal retractor
p.r.m.	pedal retractive muscle
p.s.m.	posterior septal muscle
r.	resilifer
ri.	ridge
s.	stomach
sc.l.	scleroprotein layer
s.e.	stomach epithelium
si.	sinuses
si.n.	siphonal nerve
sk.	skeletal rod
s.l.	lumen of stomach
s.n.	septal nerve
sm	septum
s.p.	siphonal papilla
s.r.	siphonal retractor muscle
s.s.	style sac
st.	style
s.v.	septal valvulae
t.	testes
tn.	siphonal tentacle
v.	viscera
v.c.	visceral connective
v.f.m.	vertical filamentar muscle
v.g.	visceral ganglion
v.m.	visceral muscle
v.p.c.	ventral pore cilia
v.p.n.	ventral pedal nerve
v.s.e.	ventral septal epithelium

APPENDIX

Cuspidaria (*Rhinoclama*) *adamsi* Morgan & Heppell new species
Rhinoclama philippinensis (A. Adams)
Rhinoclama adamsi Thiele

Holotype: British Museum specimen no. 1878.1.28.416.

Shell small, equivalve, inequilateral, moderately extended to form posterior rostrum; anterior dorsal margin slopes gradually from small umbones; posterior dorsal margin sloping, slightly concave, ventral margin wide, evenly curved, with slight sinuation at base of rostrum; shell surface with 20 concentric striations, absent from umbones, wider apart ventrally, striations turn dorsally on rostrum and become irregular; oblique rostral ridge runs from umbo to ventral posterior edge of rostrum, second rostral ridge follows line of posterior dorsal margin; hinge line narrow, right valve with inflected triangular anterior and posterior lateral teeth, left valve without teeth; small central oblique resilifer.

Shell measurements are: length, 3.18 mm; height, 1.85 mm.