The morphology of deep-sea Thyasiridae (Mollusca: Bivalvia) from the Atlantic Ocean

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SUMMARY

Twenty-five species and three subspecies of the family Thyasiridae (Bivalvia: Lucinacea) are described from the deep Atlantic. They belong to two genera and five subgenera. Eleven of the species and all of the subspecies are described for the first time.

The number of demibranchs in the gill and shape of the lobes of the lateral body pouches are characteristic features which are additionally used to clarify taxonomic divisions that have been previously based on shell features alone.

One species, *Axinus grandis* Verrill & Bush (1898), is thought to be the sole living representative of the predominantly Tertiary fossil genus *Axinus* Sowerby (1821). This genus has been regarded by most previous authors as a synonym of *Thyasira* Leach (1818). *Axinus grandis*, as here defined, is morphologically distinct from all other thyasirids and possesses primitive characters. It shows affinities to the lucinacean family Ungulinidae, suggesting that the Thyasiridae may have an origin close to the ungulinid stem.

The morphology of the species described here is extremely conservative, all sharing a number of key features. The most important of these is the form of the lateral body pouches. Shell shape and morphology relate in part to different life habits. Some species which have vertically elongate shape are probably immobile deep-burrowers, while others, principally the smallest species, which are horizontally elongate are adapted for a more active existence. All are infaunal.

The deep-water species are thought to be pre-adapted to life at depth through their ability to inhabit impoverished deoxygenated habitats. Few morphological differences could be detected between the populations of species that occur in both shallow and deep waters. The small size of all but a few species may be one of their greatest adaptive features. The greatest reduction in size and greatest simplification of morphology are seen in species of the subgenera *Thyasira* and *Parathyasira*. The subgenera *Axinulus* and *Mendicula* show the greatest radiation in deep water. The latter subgenera are thought to have arisen from the larger subgenera by neoteny.

The thyasirids, unlike the deep-sea protobranch and septibranch bivalves, are predominantly inhabitants of slope depths. Very few are truly abyssal. Many have very wide depth distributions extending from shelf to abyssal depths. This, together with the production of planktotrophic larvae, has ensured that most thyasirid species, unlike other deep-sea bivalves, are very widely distributed. Thus species extend into Arctic waters, including the Norwegian Basin and into the Pacific and are truly cosmopolitan.

INTRODUCTION

The species described in this study were obtained largely from samples taken in the Atlantic by research vessels of the Woods Hole Oceanographic Institute. Other material has also been obtained from French campaigns in the Bay of Biscay and in the southeast Atlantic Basin. Additional collections came from British research ships. Most of the material was collected by means of the epibenthic sledge and the anchor dredge.

The Lucinacea are one of three major groups which dominate the infaunal bivalves of the deep-sea, the others being the Protobranchia and the Septibranchia. Only one lucinacean family penetrates to any degree to abyssal depths: this family is the Thyasiridae. Although most numerous in species numbers at slope depths thyasirids occur to the greatest hadal depths. Thus a *Thyasira* species was the most numerous bivalve recovered by the Soviet research vessel *Vitjaz* from the Kermadec trench at 9995–10002 m. Two further species have been recorded from even greater depths, 10687–10415 m in the Tonga trench (Knudsen 1970). It is also worth noting that a lucinid species has also been recorded from the Kurile Kamchatka trench at 7210–7230 m (Filatova 1959).

The conditions under which shallow water thyasirids occur has been reviewed by Kauffman (1967). They are characteristic of infaunal communities in cool or cold waters in sandy mud, soft mud or clay substrates, which are sometimes sulphide rich. Species are also present in the Galapagos and Guaymas rift communities, and these have sulphur reducing bacteria present in their gills (J. A. Allen, unpublished data).

In the past, deep water thyasirids have received little attention, especially with respect to their internal morphology. The earliest literature on the family resulted from the upsurge of interest in deep-sea dredging which occurred in the latter half of the nineteenth century and takes the form of records and descriptions of species from the Atlantic and Mediterranean. This work was carried out mainly by Jeffreys (1868, 1870*a*, *b*, 1876*a*, *b*, 1880, 1881), Forbes (1844), M. Sars (1870), G. O. Sars (1878), Monterosato (1877, 1878, 1880, 1882), Locard (1898), and Dauztenberg & Fischer (1897, 1912, 1927). Similar work in the United States on western Atlantic and eastern Pacific species, was carried out by Verrill (1872, 1880, 1882, 1884, 1885) and Verrill & Bush (1898), and Dall (1881, 1889, 1901, 1927). The American Thyasiridae were revised by Dall (1901) in his 'Synopsis of the Lucinacea', while Lamy (1920) based a further revision on specimens in the Paris museum. The greater part of the work on Pacific species from Australian and Japanese waters has been carried out by Iredale (1924, 1930) and Okutani (1964, 1966, 1968). Thyasirids have been recorded from Iceland (Madsen 1949) and from East Greenland (Ockelmann 1958). Some species described by Verrill & Bush (1898) have been synonymized by Ockelmann (1961).

A detailed study has been made of Cretaceous species of *Thyasira* from the western interior of North America by Kauffman (1967).

In 1870 Michael Sars described the morphology of *T.*(*T.*) *sarsi* (Philippi) and *T.* (*Axinulus*) *eumyaria* (Sars). This established that *T.* (*A.*) *eumyaria* has only a single demibranch to each gill. Thereafter, the morphology of the Thyasiridae received almost no attention until Allen (1958) made a detailed study on 13 species of the Lucinacea. This work included a description of the British shallow water species *T.* (*T.*) *flexuosa* (Montagu) and established the basic morphology of the Thyasiridae upon which subsequent work has been based. It showed the uniqueness of the thyasirid foot, the tip of which is used to construct an anterior inhalent tube in the substrate. This is fundamental to the interpretation of the functional morphology of the deep-sea thyasirids described here. Also in 1958 Nakazima made a brief study of a large species *T.* (*Conchocele*) *disjuncta* (Gabb) and later Soot-Ryen (1966) figured the internal structure of a relatively large deep water species *T.* (*Parathyasira*) *tortuosa* (Jeffreys) in his revision of bivalves of the *Michael Sars* deep-sea expedition. Bernard (1972) described four large thyasirids from western Canadian waters. Thus, morphological work has been mainly confined to the larger species. Blacknell & Ansell (1974) showed *T.* (*T.*) *gouldi* (Philippi) to have direct development, but otherwise development in most species has been thought to be lecithotrophic with a short pelagic larval stage (Ockelmann 1958).

Since the studies by Allen (1958) there has been debate as to the primitive or specialized nature of the morphological adaptations of the Lucinacea particularly with regard to the anterior inhalent feeding current and, the specialized posterior exhalent siphon which can be inverted into the supra-branchial cavity. These features were interpreted as secondary adaptations by Allen (1958). In contrast, McAlester (1964, 1965, 1966) believed the anterior inhalent current to be evidence of the primitive nature of the Lucinacea. He noted that the lucinids occur earliest in the fossil record (mid-Ordovician), followed by the thyasirids (mid-Triassic) and the ungulinids (Upper Cretaceous), i.e. an order of evolution reverse to that suggested by Allen. These arguments are summarized by Bretsky (1976) in an extensive evolutionary and taxonomic study of the Family Lucinidae. Evidence from the present work suggests that the Thyasiridae may have an origin close to the Ungulinidae.

Not all the thyasirid genera or subgenera known to occur in the Atlantic Ocean have been obtained during the course of this study. Thus *Axinopsida* Keen and Chavan and *Conchocele* Gabb are not included here. Conversely some species described here have been assigned to genera or subgenera previously used for Pacific species; these are *Mendicula* Iredale and *Parathyasira* Iredale.

METHODS

The gross anatomy and internal structure of each species has been described from whole mount specimens and from serial transverse sections.

The shells were removed using a saturated solution of ethylenediaminetetra-acetic acid (EDTA) in water. The remaining periostracum was normally removed using fine needles. Specimens to be sectioned were dehydrated in a series of alcohols, cleared in xylene or cedar wood oil, transferred to paraffin wax at 55–60 °C, infiltrated, embedded and sectioned at 10–12 mm. They were then stained in Masson's trichrome stain or haematoxylin with eosin (Pantin 1964). Whole specimens were stained in Ehrlich's acid haematoxylin (Pantin 1964), differentiated in acid alcohol, 'blued' in alkaline water, cleared in xylene and mounted on cavity slides.

For shell detail, the tissues were removed by 4% sodium hypochlorite, the valves separated and examined by light and scanning microscopy.

Type specimens have been deposited in the British Museum (Natural History) (BMNH) and the Museum National d'Histoire Naturelle, Paris (MNHN).

DESCRIPTIONS OF SPECIES OBTAINED FROM THE ATLANTIC

AXINUS Sowerby, 1821

Type species: *Axinus angulatus* Sowerby, 1821.
Type locality: Islington; London clay (Eocene).

In the original definition of the Genus (Sowerby 1821) it was stated that it was a 'free equal valved, transverse, bivalve; anterior side very short; posterior side produced, truncated, with a lunette near the beaks; hinge with a long oblique ligament placed in a furrow.... I suspect it has no teeth'.

The type species (figure 5) was further described as 'a depressed shell whose greatest length is nearly perpendicular to the hinge cartilage; the base (front) rounded, terminated at each end by an angle from which two obtuse keels run up to the beaks; the anterior keel is sharpest near to and almost parallel with the hinge: the posterior keel is very obtuse, from it to near the lunette the surface is almost flat, but just upon its border the shell rounds with an obtuse angle upon its edge; the lunette is impressed, ovate, pointed and curved'.

From this it is clear that Sowerby (1821) confused the anterior and posterior ends of the shell.

The genus is now redefined, to include both fossil and living species: shell thin, moderate to large in size, usually greater than 10 mm in length; subhexangular, inequilateral; small, pointed, strongly prosogyrous beaks; two main ridges radiate from beaks, first posterior, more or less parallel to posterior margin, second less distinct central to mid anterior in position and extending to ventral margin; sculpture fine concentric grooves forming characteristic wave-like undulating ridges; lunule well defined; hinge plate edentulous, thickened; ligament partly external,

inserted into the margin of the hinge plate; extant species are characterized by unlobed lateral body pouches concealed beneath gill; adductor muscles oval and not particularly elongated; mantle edge modified bearing sensory papillae and tentacles.

Axinus grandis (Verrill & Smith, 1885)

Type species: *Cryptodon grandis*, Verrill & Smith, 1885.
Type locality: 38° 29′N, 73° 00′W; 1765 m.
Type specimen: Holotype MCZ, Harvard.

Synonymy

Cryptodon grandis Verrill (1885, p. 436, fig. 22, pl. 44).
Cryptodon grandis Dall (1889, p. 50, fig. 22, pl. 46).
Schizothaerus grandis Locard (1896, p. 180).
Schizothaerus grandis Locard (1898, p. 222).
Cryptodon grandis Verrill & Bush (1898, p. 785).
Schizothaerus grandis Locard (1899, p. 136).
Thyasira grandis Dall (1901, p. 785).
Schizothaerus grandis Lamy (1915, p. 19).
Schizothaerus grandis Lamy (1917, p. 380).
Thyasira grandis Lamy (1920, p. 302–304).
Thyasira grandis Clarke (1962, p. 64).
Thyasira piriformis Nordsieck (1969, p. 81).

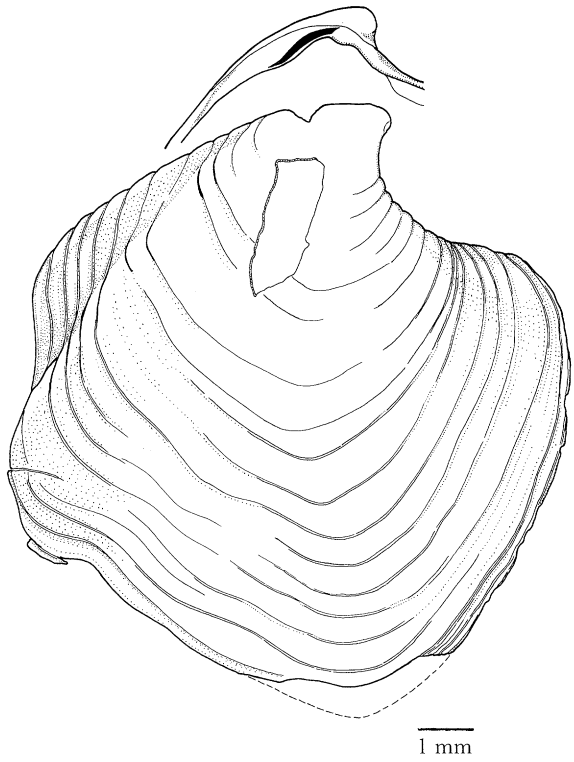

Figure 1. *Axinus grandis*: hinge plate of left valve and lateral view of right valve; specimen from *Challenger*, station 10.

Historical

Dall (1901) synonymized *Cryptodon pyriformis* Dall with this species. Although *C. grandis* is recorded from 1715–2893 m, *C. pyriformis* is from shallower depths, 155–1337 m. We have not examined specimens of *C. pyriformis*. Dall (1901) notes that the genus *Schizothaerus* as applied to this species arose from the confusion of *Cryptodon* Conrad (= *Schizothaerus* Conrad = *Tresus* Gray), Family Mactridae, with *Cryptodon* Turton. Lamy (1915, 1917, 1920) who re-examined the Locard specimen, found it edentulous and thus clearly not a mactrid.

Material

ship/cruise	no.	date	sta.	position	depth/m	number	gear
West European Basin							
Challenger		04.07.73	10	56° 37.0′N 11° 04.0′W	2540	1	es
North America Basin							
Atlantis II	12	21.08.73	64	38° 46.0′N 70° 06.0′W	2886	1	es

Distribution

North Atlantic, isolated records; North-West Atlantic, between 38° 29′N, 73° 09.0′W, and 35° 09.5′N, 74° 57.4′W; 1715–2893 m; Azores (1266 and 1385 m); Bay of Biscay (1710 m); Cape Verde Basin; Rockall Trough.

Records of *T. pyriformis* are geographically separate from these above, from off Cape Fear to Florida, 155–1337 m; Yucatan Stait, 1170 m.

Shell description (figure 1)

Shell large, fragile, white, chalky in texture, equivalve, markedly inequilateral, strongly inflated, sculpture, fine closely spaced concentric grooves forming irregular raised wave-like ridges, sometimes sharply defined, small amounts of ferruginous material may adhere around beaks; beaks small, raised, prosogyrous; deep lunule emphasized by marginal ridge; antero-dorsal margin upturned, ventral margin mid-ventral region where median radial ridge meets ventral margin, posterior margin indented by shallow, distinct curved posterior sulcus; hinge plate without teeth; internal shell white, glossy with faint radial striae, muscle scars indistinct.

The specimen from *Challenger* sta. 10 measures 11.1 mm long × 11.6 mm high.

Internal morphology (figures 1, 2, and 3)

Because only one damaged specimen was available, sections were not made.

The anterior and posterior adductor muscles are relatively large and moderately elongate. The posterior muscle is approximately two-thirds as large as the anterior. The anterior muscle is split into three separate blocks. The antero-ventral surface of the anterior adductor bears a centrally positioned conical projection which may be sensory in function (figure 4).

The mantle edge of *Axinus* is distinguished from that of all other thyasirid genera by the sensory papillae developed from the middle mantle fold adjacent to the anterior adductor (in the position of the anterior inhalent current) and mid-ventally between the area of

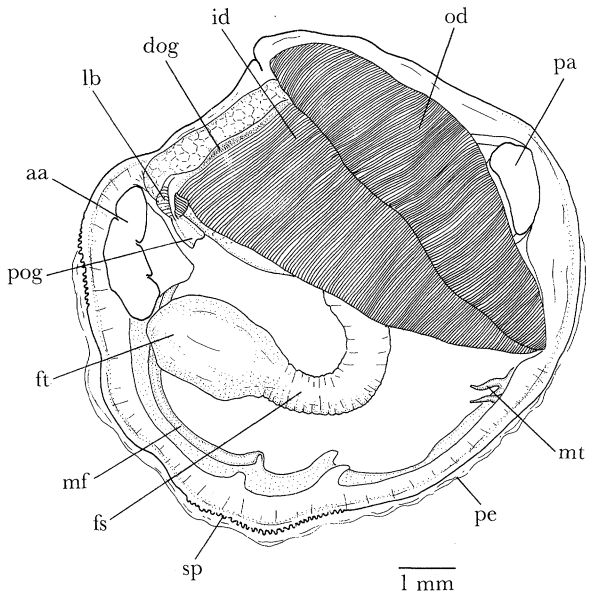

Figure 2. *Axinus grandis*: internal morphology as seen from the left side; specimen from *Challenger*, station 10. (List of abbreviations: see p. 561.)

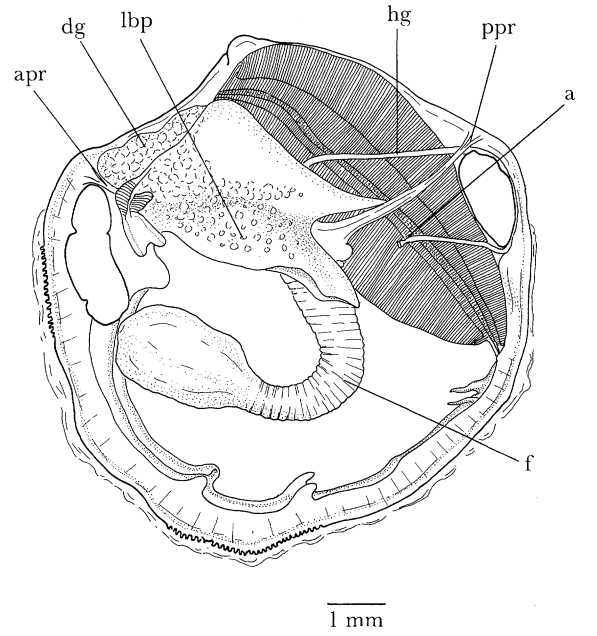

Figure 3. *Axinus grandis*: internal morphology from the left side after removal of the left gill; specimen from *Challenger*, station 10. (List of abbreviations: see p. 561.)

posterior mantle adhesion and the mantle flaps (see below). There is a pair of inwardly directed tentacles at the ventral margin of the inhalent aperture. These are formed from the inner mantle fold. Extending from the anterior adductor to a mid-ventral position on each side is a glandular mantle flap which also is a development of the inner mantle fold. These flaps cover the main rejection tract on the dorsal surface of the inner mantle fold and which carries pseudofaeces posteriorly. At the dorsal margin of the posterior inhalent aperture is a second pair of curved, inwardly directed, tentacles formed from the inner fold. These may be concerned with the manipulation of pseudofaeces. *Axinus grandis* has *two* posterior mantle apertures.

The posterior exhalent aperture is formed by tissue fusion of the inner and middle mantle folds. Ventral to it a posterior 'inhalent' aperture is formed by tissue adhesion of the middle folds. This adhesion is extremely strong but can be parted without damaging the mantle tissues.

The eulamellibranch homorhabdic gill consists of a pair of demibranchs, the outer demibranch being approximately two-thirds the size of the inner. Numerous tissue connections occur between adjacent filaments. The ascending and descending lamellae of each demibranch are similarly connected. The filaments are remarkably thick from frontal to abfrontal surfaces giving the gills a solid fleshy appearance. The gill axis joins the mantle edge at the point of ventral fusion of the exhalent aperature.

The foot is long and vermiform and lacks a heel and a sagittal groove. The stem is broader than that of large species of *Thyasira*. The tip of the foot is differentiated from the stem, and is bulbous. The tip is not divided into two distinctly grooved parts as seen in some species of *Thyasira*.

The external shape of the lateral pouches of the body is distinct from that in other thyasirids of a similar size. The pouches are small and elongate along an antero-dorsal postero-ventral axis. Posteriorly they form a flattened point. They do not project ventral to the gill. Species of *Thyasira* of a similar size invariably have extensively branched or arborescent lateral pouches.

The digestive diverticula are positioned antero-dorsally within the body cavity and also extend into the pouches. The hindgut is narrow and without convoluted loops. It passes over the posterior adductor and opens unusually far anterior in the supra-branchial cavity. The gonad also penetrates the lateral pouches.

Two individuals of a species of undescribed parasitic polychaete were taken from the posterior part of the gill. Parasitic polychaetes have not been recorded from any other thyasirid species.

To summarize: *Axinus grandis* has a unique morphology which necessitates at least generic separation from other thyasirids.

Comparison with the fossil species of the genus, e.g.

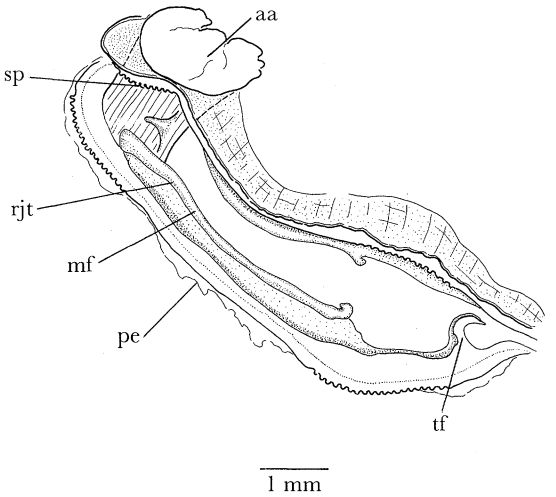

Figure 4. *Axinus grandis*: antero-ventral mantle edge, showing mantle flaps and senory papillae; specimen from *Challenger*, station 10. (List of abbreviations: see p. 561.)

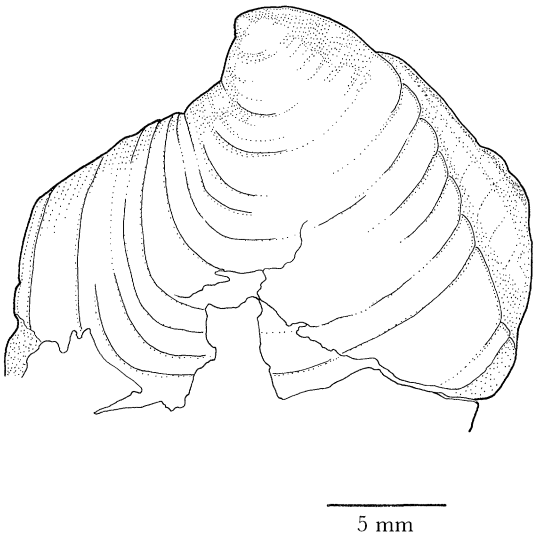

Figure 5. *Axinus angulatus*: type specimen from the London clay; Wrigley collection, BM(NH).

the type species *Axinus angulatus* from the early Eocene (BM (NH) Reg. No. LL3118) (figure 5), shows that the two species are closely related and congeneric. They have in common the following characteristics: an unusual shell sculpture of concentric lines which form wave-like undulations of the shell; a prominent broad radial ridge in a central or mid-anterior position in addition to the posterior shell ridges; small, strongly prosogyrous beaks; a well defined lunule. *A. angulatus* differs from *A. grandis* in having a more oblique shape and a less upturned antero-dorsal shell margin. *A. grandis* is the only known living member of the genus.

THYASIRA Leach, 1817

Type species: *Tellina flexuosa*, Montagu, 1803.
Type locality: 'Cornwall and Devon'. England.

Original description of type species:

'*Tellina* with a thin, pellucid, fragile, convex, suborbicular, white shell: from behind the umbo to the lower angle of the margin, a sulcus runs parallel with the cartilage slope, and forms a sinus or flexure at the edge. It is finely but irregularly striated concentrically and is not very glossy; umbo placed central, much produced and turns to one side at the apex; hinge with an obsolete tooth; along the margin from behind the umbo, a groove in which is fixed the connecting cartilage: inside smooth, glossy white.... This shell seldom exceeds three-eights of an inch in diameter and never arrives at half an inch, and in length is rather more than in breadth'.

Description

Shell, usually white, suborbicular or oblique or elongate ovate, frequently sulcate, hinge without true teeth, but may have small protrusions, ligament opisthodetic and indented, lateral brood pouches present, gills may be reduced to single demibranch, anterior adductor muscle elongate.

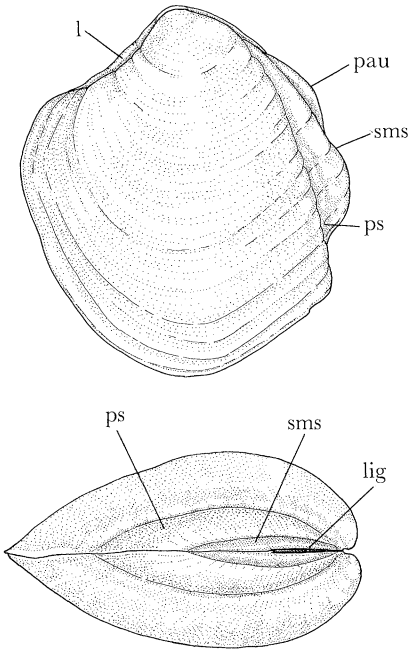

Figure 6. *Thyasira* (*Thyasira*) *trisinuata*: lateral view of the shell from the left side and postero-dorsal view; *Atlantis II*, station C. (List of abbreviations: see p. 561.)

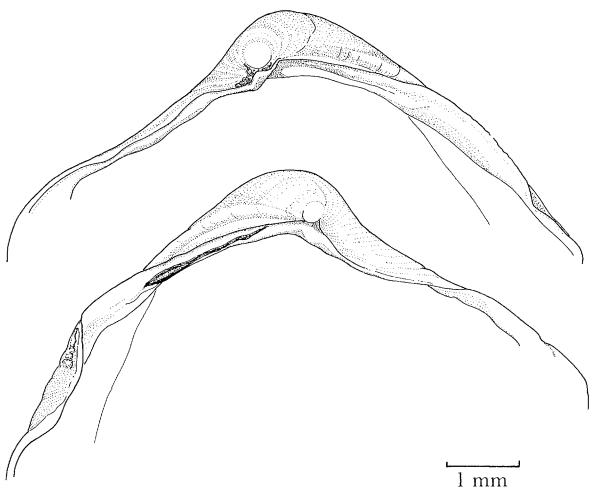

Figure 7. *Thyasira* (*Thyasira*) *trisinuata*: hinge plates of left and right valves; USNM No. 45715.

Subgenus: ***THYASIRA*** s.s.

Description

Shell white, fragile, suborbicular or oblique, height normally exceeds length, hinge plate narrow, no true hinge teeth but small knob may be present ventral to beak of right valve, no lateral teeth, postero-dorsal labial sulci variously developed, better developed in large species; adductor muscles unequal in size, lateral body pouches lobed, outer demibranch present but may be reduced in size.

Thyasira* (*Thyasira*) *trisinuata (d'Orbigny, 1846)

Type species: *Lucina trisinuata*, d'Orbigny, 1846.
Type locality: Martinique and Guadeloupe.
Type specimen: not known.

Synonymy

Lucina trisinuata d'Orbigny (in Sagra (1846) p. 300–301, atlas fig. 46–49, pl. 27)
Cryptodon obesus Verrill (1872, p. 287, fig. 2, pl. 7).
Crypton obesus Verrill (1880, p. 399)
Cryptodon obesus Verrill (1882, p. 569–70)
Cryptodon obesus Verrill (1884, p. 279)
Cryptodon obesus Dall (1889, p. 50, fig. 12, pl. 58)
Thyasira trisinuata Dall (1901, p. 786)
Thyasira trisinuata Johnson (1915, p. 63)
Thyasira trisinuata Lamy (1920, p. 301–302)
Thyasira trisinuata Oldroyd (1924, p. 121)
Thyasira trisinuata Johnson (1934, p. 39)
Thyasira trisinuata trisinuata La Rocque (1953, p. 57)
Thyasira trisinuata polygona La Rocque (1954, p. 57)
Thyasira trisinuata Ockelmann (1954, p. 197)
Thyasira trisinuata Clarke (1962, p. 65)
Thyasira trisinuata Keen (1971, p. 131)
Thyasira trisinuata Bernard (1972, p. 366)

Historical

Dall (1901) synonymized *Cryptodon obesus* Verrill and *Axinus flexuosus* var. *polygona* Jeffreys with *T. trisinuata* (d'Orbigny) a West Indian species. Jeffreys (1881) however, regarded *Cryptodon obesus* as synonymus with *T. flexuosa*. Verrill (1872) believed that while *C. obesus* was probably closely related to *T. flexuosa* there were enough differences to merit a specific separation. No type specimens of *T. trisinuata* have been found, nevertheless Dall's synonymy has been accepted. The identity of *Axinus flexuosus* var. *polygona* Jeffreys remains in doubt. Again, type specimens were not found by Warén (1980) or by ourselves.

Material

ship/cruise	no.	date	sta.	position	depth/m	number	gear
North America Basin							
Atlantis	264	25.05.61	C 1	40° 20.5′N 70° 47.0′W	97	44	ad
	283	28.08.62	Sl.3	39° 58.4′N 70° 40.3′W	300	1	ad
	298	04.09.63	55	40° 27.2′N 70° 47.5′W	75	12	
Atlantis II	40	27.11.67	171	40° 34.0′N 70° 51.0′W	68–71	1	ad
			—	40° 31.5′N 70° 51.5′W			
		27.11.67	172	40° 12.3′N 70° 44.7′W	119	20	es
			—	40° 10.8′N 70° 43.6′W			
		28.11.67	173	40° 10.8′N 70° 43.6′W	123	1	ad
			—	40° 10.6′N 70° 44.0′W			

Distribution

Off the Atlantic coast of America from Labrador (Verrill 1872) to Martinique (d'Orbigny 1846) from 22–351 m with isolated records (probably dead shells) down to 2359 m. It is also recorded from Sitka harbour, Alaska, 18 m (Dall 1901) to San Diego, California (Oldroyd 1924) and from the Korean coast (Dall 1901). Bernard (1972) could not confirm the records of Dall from the west coast, and considers that the species occurring in western Canada is *T. flexuosa*. One of us (J.A.A.) confirms the presence of *T. flexuosa* from Puget Sound. The present material is all taken from off Martha's Vineyard, the type locality of *C. obesus*.

Shell description (figures 6 and 7)

Shell thin, white, inflated, equivalve, inequilateral, sculpture fine concentric grooves with clear growth stages, periostracum thin, transparent, small quantities of ferruginous deposit may adhere to anterior and posterior margins; small strongly prosogyrous beaks on or just posterior to midline, antero-dorsal margin shelf-like sloping from beaks in concave curve, upturned anteriorly to form an angulation, margin prolonged mid-ventrally, postero-dorsal margin slopes rapidly from beaks in concave curve, indented by deep primary and submarginal sulci giving rise to two prominent notches in posterior shell margin; submarginal sulcus forms projecting auricle in the area of the escutcheon; lunule broad but defined by slight ridge of antero-dorsal slope; hinge of right valve with pseudo-cardinal projection ventral to beak, left valve with elongate swelling just anterior to beak, an indentation ventral to beak accommodates projection on right valve; ligament opisthodetic, internal, lying in curved inset groove which extends approximately one third of the distance to posterior margin, anteriorly more external; interior covered with fine radiating grooves, sulci visible as two prominent ridges.

Shells measure up to 18 mm in height (Verrill 1882). The largest specimen from the present material measures 9 mm in height × 7.6 mm in length and × 6.1 mm in width. Except in juveniles, shell height typically exceeds length.

Both shell and tissue morphology are similar to those of *T. flexuosa* as decribed by Allen (1958). *T. trisinuata* is distinguished from *T. flexuosa* by a more upturned antero-dorsal margin, deeper posterior sulci and a larger posterior auricle.

Internal morphology

The mantle is thin, composed of outer and inner epithelia of regular vacuolated cells. The mantle edge (figure 10) has three folds but lacks a pallial fold over the main rejection tract (Allen 1958). The mantle margin is broad on each side of the anterior inhalent region. The inner fold is muscular; a group of longitudinal muscle fibres run below and parallel to the shelf-like rejection tract on the inner margin of the fold. Transverse pallial muscles extend from the inner fold (pallial line) into the outer and middle folds. The middle fold forms a small frill, but no sensory tentacles are developed. The periostracal groove lies between the middle and outer mantle folds. The epithelium and subepithelium of the inner fold are specialized, in particular gland cells are associated with the rejection

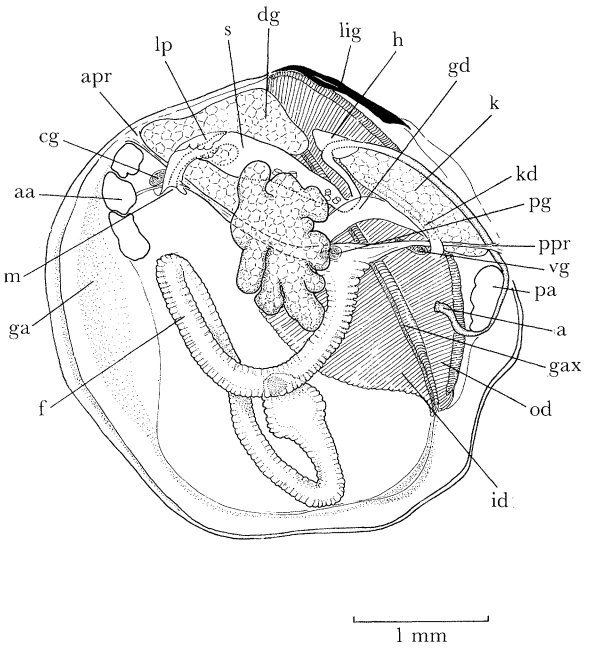

Figure 8. *Thyasira* (*Thyasira*) *trisinuata*: internal morphology as seen from the left side with the gill removed; *Atlantis II*, station 55. (List of abbreviations: see p. 561.)

tract. These are closely packed, irregular in shape, and filled with granular secretory material. Ventral to the anterior adductor where the anterior inhalent tube opens into the mantle cavity this glandular tissue is particularly well developed. A large blood space is central within the mantle margin. Mantle fusion is restricted to a narrow inter-connection below the posterior adductor so forming a posterior exhalent aperture. The aperture is encircled by well developed pallial muscles. There is no mantle adhesion of the postero-ventral or antero-ventral mantle edges to form other apertures.

The adductor muscles (figure 8) are very unequal in size, the anterior adductor is elongate and curved parallel to the anterior mantle margin. The posterior adductor is slightly more than half its length, broader and oval in shape. The 'catch' and 'quick' components are clearly visible.

The gills have two demibranchs, the outer approximately half the size of the inner. The gills cover the greater part of the lateral body pouches. Both the ascending and descending lamellae of the inner demibranch are well developed, but the descending lamella of the outer demibranch is reduced. Each demibranch is composed of about 60 homorhabdic filaments, in a specimen 4.0 mm in length. The gill axis lies at an angle across the mantle cavity. Anteriorly the axis fuses with the mantle and the visceral wall. Posterior to this (and in sequence) it is joined to the pericardial wall, the kidney wall and the mantle edge at the point of mantle fusion. Posterior to the foot the dorsal margins of the ascending lamellae of the inner demibranchs are joined by stiff ciliary junctions. The abfrontal surfaces of the filaments of ascending and descending lamellae are joined by a tissue junction (interlamella fusion) over most of their length. Horizontal cross connections (interfilamentar septa) occur at intervals between adjacent filaments. Muscles fibres which originate from the gill axis extend the length of each filament. Sections show the filaments are thickened abfrontally (figure 12). This part is made up of large cells some of which are mucus filled while others are vacuolate. The abfrontal surface has terminal mucus secreting cells (Allen 1958). At the centre of the gill filament is a haemocoele, supported laterally by skeletal rods. The frontal cilia are short and brush-like, flanked by longer curved laterofrontals. The lateral cilia are long and located close to the frontal surface.

The labial palps (figure 8) are very small triangular extensions of the posterior margins of the proximal oral groove. They bear 6–7 ridges on the inner surface, in a specimen 4.0 mm long. They lie close to the antero-ventral corner of the gill. The inner surface of the palp is covered by a ciliated columnar epithelium that overlies loosely packed connective tissue.

The foot (figures 8 and 9) is extremely long, slender and vermiform. When retracted it lies coiled within the mantle cavity. The tip of the foot is bulbous and divided from the stem by a constriction. There is no heel or sagittal groove at the base of the foot. Of two pairs of narrow pedal retractor muscles, the anterior pair pass as a single sheet of muscle from the base of the foot, ventral to the lateral body pouches, and con-

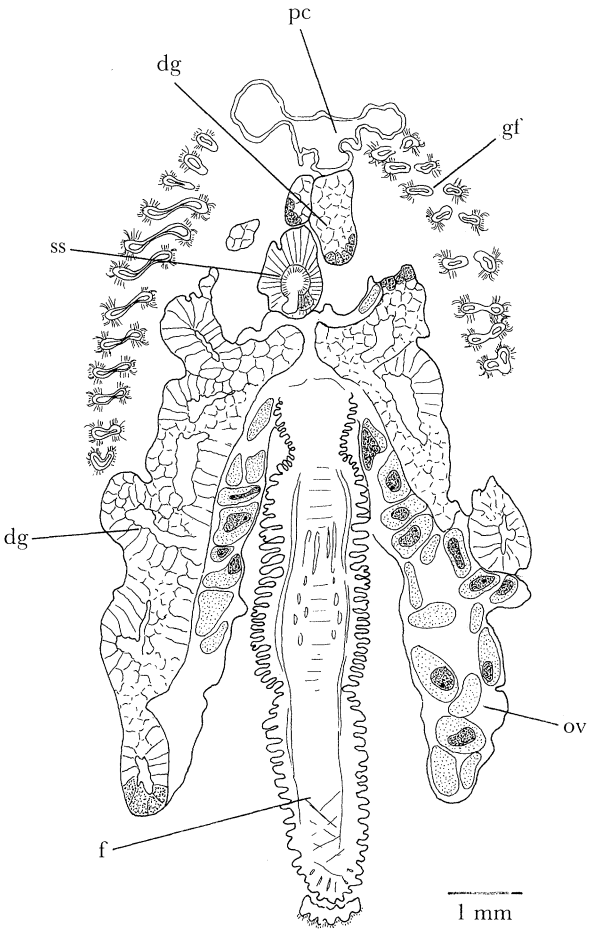

Figure 9. *Thyasira* (*Thyasira*) *trisinuata*: median transverse section through the body. (List of abbreviations: see p. 561.)

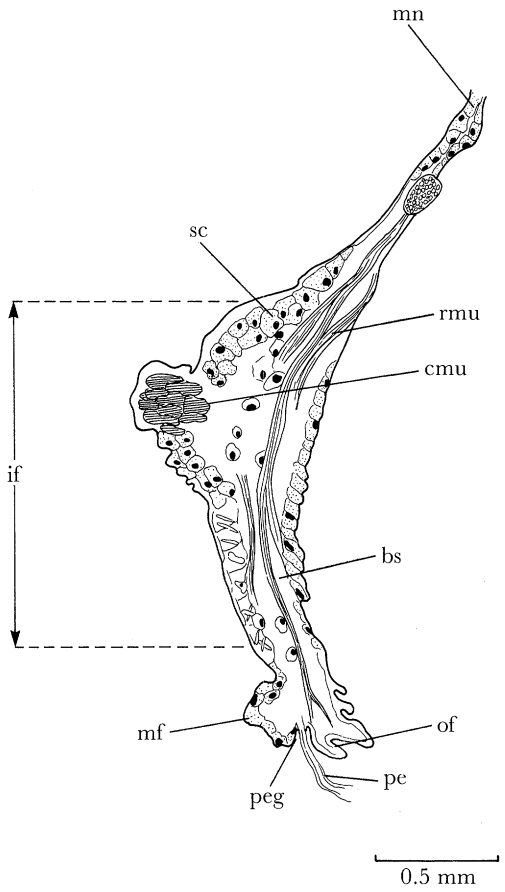

Figure 10. *Thyasira* (*Thyasira*) *trisinuata*: transverse section through the mid-ventral mantle edge. (List of abbreviations: see p. 561.)

tribute to the musculature of the pouch wall. The paired components then separate and pass to either side of the oesophagus and attach to the mantle or shell immediately dorsal to the anterior adductor muscle. The combined posterior pedal retractors pass from the base of the foot to separate dorsally at the anterior limit of the visceral ganglia and attach dorsal to the posterior adductor muscle. Both stem and tip of the foot are ciliated, the tip heavily so. Contraction of the foot causes the epithelium to be thrown into deep annular corrugations. A narrow outer layer of circular muscle lies directly beneath the ciliated epithelium and beneath the circular muscle are two layers of longitudinal muscle. The outer longitudinal layer is thin with narrow fibres, while the fibres of the inner layer are much broader and link with the pedal retractor muscles. A large blood space is at the centre of the foot and is crossed by fine transverse muscle fibres. The cavity is filled with loosely packed blood cells with a granular cytoplasm. The tip of the foot contains a discrete mass of gland cells which stain deeply with haematoxylin. A large pedal ganglion is located at the base of the foot.

A short oesophagus enters the stomach mid-dorsally on the anterior face (figure 8), anterior and dorsal to the digestive apertures. The stomach is short and broad, and is separated from the tapering combined style sac and midgut by a constriction of the stomach wall. The style sac extends to a position immediately dorsal to the pedal ganglion. The hind gut then forms an anterior loop dorsal to the style sac before passing through the heart and then dorsal to the kidney and the posterior adductor muscle to open into the suprabranchial cavity anterior to the posterior adductor. Food remains present in the hindgut and stomach include intact diatoms, broken diatom frustules and unidentifiable fine particles. The hindgut is not grossly distended as it is in other species (p. 515 and figure 39).

Transverse sections show the lumen of the oesophagus to be narrow and lined with a ciliated epithelium thrown into a number of longitudinal folds. The stomach has a small dorsal hood. The ciliated sorting area in the dorsal hood is continuous with the ciliated epithelium of the oesophagus. As described for *T. flexuosa* (Allen 1958), digestive ducts are not differentiated from tubules. There are two enormous apertures in the anterior, ventro-lateral stomach wall which open directly to the digestive tubules. Each aperture serves two series of tubules. The dorsal series on each side passes to each side of the dorsal hood. The larger ventral series lie somewhat posterior to the dorsal pair and lead directly to the lateral body pouches.

The dorsal and lateral walls of the stomach are protected by a gastric shield which anteriorly is narrow and pointed. The stomach wall beneath the gastric shield is thickened, comprising of a tall columnar cells containing granules of refractory material. Ventrally the stomach wall is thin and has a ventral groove which leads to the midgut. The wall of the style sac (figure 11) is composed of extremely thick regular columnar cells, with basal nuclei and bearing stiff brush-like cilia. The thin-walled midgut forms a deep ventral groove along the length of the style sac. A typhlosole consisting of deeply staining cells protects and partially separates the midgut from the style sac (figure 11). These cells

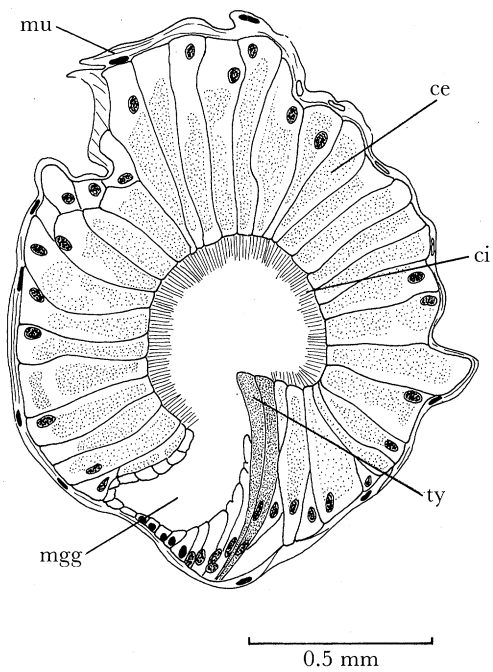

Figure 11. *Thyasira* (*Thyasira*) *trisinuata*: transverse section through the style sac showing the midgut groove. (List of abbreviations: see p. 561.)

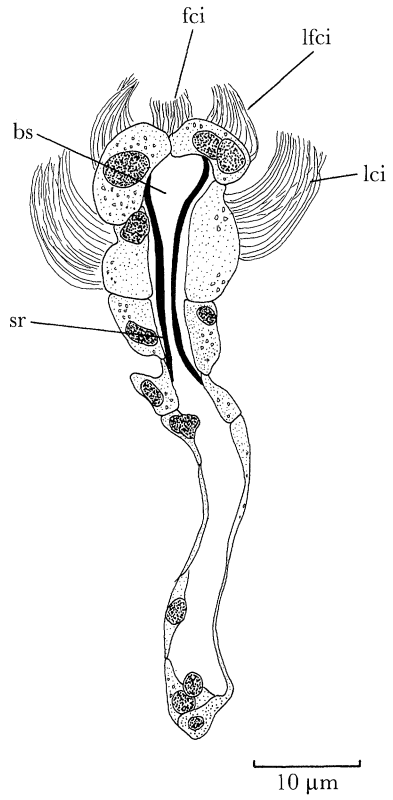

Figure 12. *Thyasira* (*Thyasira*) *trisinuata*: transverse section through a gill filament. (List of abbreviations: see p. 561.)

differ from those of the remainder of the style sac epithelium in staining with Light Green and may be associated with the production of the crystalline style.

The lateral pouches in *T.* (*T.*) *trisinuata* are extensively lobed, each lobe is a small finger-like process. The lumena of the digestive diverticula extend from the neck of the pouches into the processes, so that in transverse section each lobe consists of a central lumen surrounded by tubule cells. The dorsal digestive diverticula consist of a pair of unbranched tubules, which are contiguous along the midline. The digestive diverticula are lined with large vacuolated cells measuring about 50 μm in height. Smaller, deeply staining cells are found at the blind ends of tubules. These are probably homologous with juvenile cells of Yonge (1926) and interstitial cells of Allen (1958). The walls of the pouches have a well defined muscle layer which is probably used to eject eggs or sperm, as well as to move food material in and out of the lumen of the digestive gland.

The gonad occupies the inner side of the lateral pouches. Paired gonadial ducts, one from each pouch, pass postero-dorsally to open into the supra-branchial cavity close to the ventral wall of the kidney. Sexes are separate and in mature individuals the gonadial ducts as well as the gonad are filled with eggs or sperm. The eggs are oval or polygonal in shape, measuring 105–111 μm in length. Eggs and digestive cells were measured in section and it must be assumed that shrinkage will have occurred during fixation and dehydration.

The paired kidneys are extremely large unlobed sacs. They occupy a postero-dorsal position between the posterior pedal retractors and the heart (figure 8). The sacs are laterally compressed and dorso-ventrally elongate. An anterior arm extends forward from each side of the kidney lateral to the pericardium. Posteriorly the inner epithelia of the kidneys lie close together, separated by a lightly muscularised central wall in which is a single posterior aperture allowing communication between the two lumena. The walls of the kidneys are made up of large vacuolated cells, some of which contain plate-like concretions of varying sizes and unknown composition. A pair of slender kidney ducts (figure 8) originate immediately posterior to the two anterior arms and run along the ventral wall of the kidney to open posteriorly as paired funnels into the suprabranchial cavity.

The heart and pericardial cavity (figure 8) lie between the kidney and the posterior end of the dorsal digestive diverticula. The very small relatively thick-walled ventricle, is perforated by the hindgut. On each side there is a thin walled auricle. An extensive thin walled pericardial cavity surrounds the heart. Reno-pericardial ducts were not identified and if present must be very small in size.

Three pairs of ganglia (figure 8), the cerebro-pleural, pedal and visceral, with their associated connectives comprise the major part of the nervous system. All are well developed and of large size. The pedal ganglion is particularly large. The cerebro-pleural ganglia lie anterior and to each side of the oesophagus. They are joined by a stout, broad, supra-oesophageal commissure. Transverse sections show that in each cerebropleural ganglion the two components are identifiable. The pedal ganglia are fused to form a single body. Each ganglion gives rise to a broad pedal nerve. The visceral ganglia lie ventral to the postero-ventral wall of the kidney the two being joined posteriorly. Anterior to the junction the posterior pedal retractors pass between the ganglia.

Thyasira* (*Thyasira*) *excavata plicata (Verrill, 1885)

Type species: *Cryptodon plicatus*, Verrill, 1885.
Type locality: Off Martha's vineyard, Massachusetts 2052 m.
Type specimen: Holotype USNM. No. 44825.

Synonymy
Cryptodon plicatus Verrill (1885, p. 437).
Cryptodon plicatus Verrill & Bush (1898, p. 786; fig. 6, pl. 89).
Thyasira plicata Dall (1901, p. 786).
Thyasira excavata Lamy (1920, p. 302).
Thyasira plicata Lamy (1920, p. 298).
Thyasira plicata Johnson (1934, p. 39).
Thyasira plicata Clarke (1962, p. 64).
Thyasira excavata Knudsen (1970, p. 179).

A new species of *Thyasira* was described as *Cryptodon plicatus* by Verrill (1885), however, it was later realised that this name was preoccupied by *C. plicatus* Adams from Japan (Lamy 1920).

C. plicatus is very similar to the type specimen of *T.* (*T.*) *excavata* (USNM No. 107449) a Pacific species

Material

Material obtained from *Walda* Sta. CY13 (MNHN, Paris) is identical to the type specimen of *T.* (*T.*) *excavata plicata* (USNM No. 44825).

ship/cruise	no.	date	sta.	position	depth/m	number	gear
West European Basin							
Sarsia	—	13.07.67	33/2	43° 41.8′N 03° 36.0′W	1573	1 sh.	nd
Angola Basin							
Walda	—	.06.71	DS07	19° 57.0′S 11° 02.0′E	1277	1	ds
	—	.06.71	CY13	12° 03.7′S 12° 22.3′E	2044	4	cv

(figure 13). The type specimen of *T.* (*T.*) *excavata* is a larger size and has a thicker shell. Here we recognize two subspecies: *T.* (*T.*) *excavata excavata* in the Pacific and *T.* (*T.*) *excavata plicata* in the Atlantic. The small differences in shell morphology may reflect differences developed during the long separation of the Atlantic and Pacific Oceans, however, Bernard's (1972) description of the internal morphology of *T.* (*T.*) *excavata* s.s. shows it to be identical to that of specimens from *Walda* Sta. CY13.

Because *T.* (*T.*) *tricarinata* Dall, was unfigured, and occurs at almost the same locality and depth as *T.* (*T.*) *excavata*, led Lamy (1920) and Knudsen (1970) to question the validity of the former species. Knudsen found that the types to be similar and suggested that they may be synonymous. The principal difference which we have observed is the more upturned antero-dorsal margin in *T.* (*T.*) *excavata*. *T.* (*T.*) *tricarinata* is figured in figure 18. Here we retain the distinction between the species.

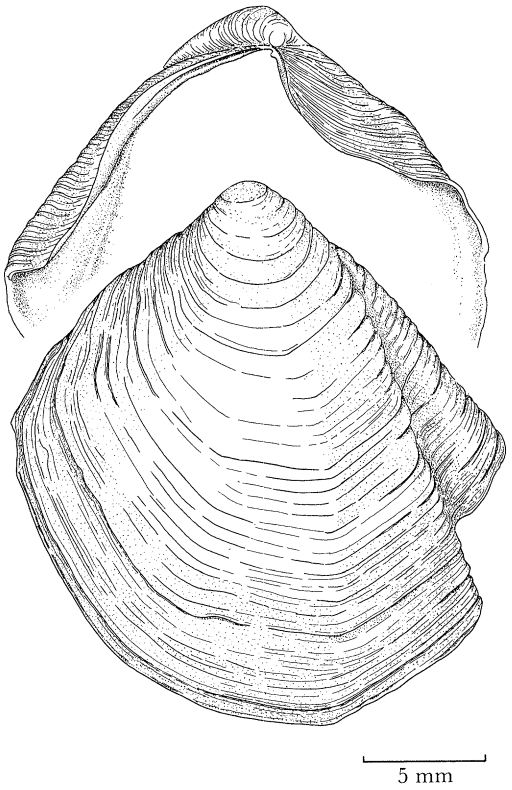

Figure 13. *Thyasira* (*Thyasira*) *excavata excavata*: lateral view of right valve and hinge plate of left valve; Holotype, USNM No. 107449, Gulf of California.

Distribution

T. (*T.*) *excavata plicata* is previously recorded only from off Martha's Vinyard, Massachusetts, 1962–2052 m. The present material is from the Angola Basin and the Bay of Biscay. The latter is represented only by a dead shell. The species is thus sparsely but widely distributed in the Atlantic. Depth range: 1277–2100 m.

Shell description

Shell large, opaque, white, subtriangular, extremely inflated, equivalve, sculpture, fine concentric ridges incised close to ventral margin, surface chalky, partly flaked away; inequilateral, small beaks in midline turned slightly anteriorly; antero-dorsal and postero-dorsal margins descend rapidly from beaks, antero-dorsal margin somewhat shelf-like forming a broad lunule, joins antero-ventral margin in an obtuse angulation; two prominent posterior ridges define deep primary and sub-marginal sulci, primary sulcus straight, sharply incised, forming deep notch in postero-ventral shell margin, submarginal sulcus outlines deep sunken escutcheon; posterior auricle not developed; two faint median ridges extend across shell from umbones to ventral margin causing ventral angulation; hinge plate very narrow, small pseudocardinal projection ventral to beak of right valve fits into depression in left, (the projection is at shell margin, consequently interlocking is visible externally); interior white, smooth, with fine radiating striae, obverse sulci form prominent internal folds, anterior adductor muscle scar elongate, dorsal to anterior marginal angle, posterior adductor muscle scar and pallial line indistinct.

The largest specimen examined is 14.1 mm long × 15.6 mm high × 9.6 mm broad.

T. (*T.*) *excavata plicata* is characterized by a straight, deep, primary sulcus. The ventral margin is characteristically angulate.

Internal morphology

The anterior adductor muscle (figures 14 and 15) is extremely long, and curves parallel to the anterior shell margin. An epithelial membrane connects the adductor muscle to the ventral margin of the oral groove. The posterior adductor is minute and oval, about one quarter the size of the anterior adductor. It is positioned dorsal to the posterior exhalent aperture.

Although larger and more complex, the basic form and histology of the mantle edge is similar to that of *T.*

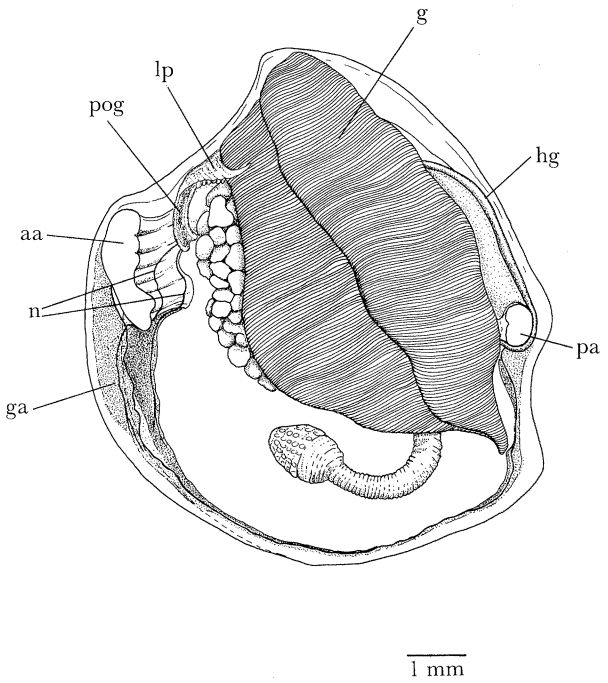

Figure 14. *Thyasira* (*Thyasira*) *excavata plicata*: internal morphology as seen from the left side; specimen from *Walda*, station CY 13. (List of abbreviations: see p. 561.)

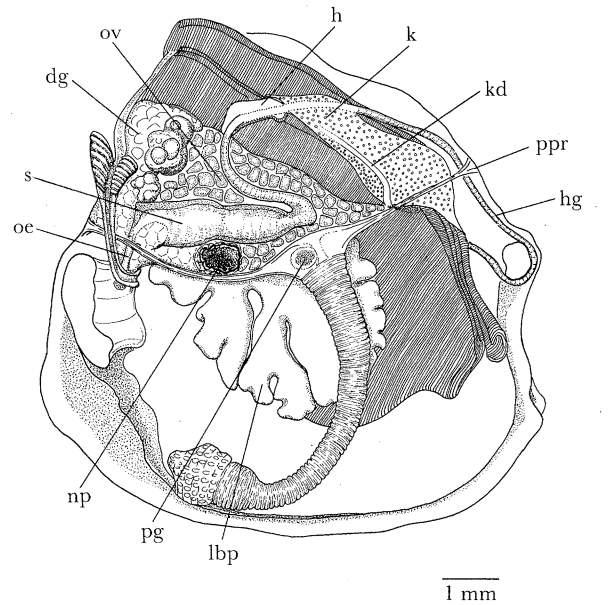

Figure 15. *Thyasira* (*Thyasira*) *excavata plicata*: internal morphology as seen from the left side with left gill and body pouch removed; specimen from *Walda*, station CY 13. (List of abbreviations: see p. 561.)

(*T.*) *trisinuata*. The concentric musculature of the inner fold is particularly well developed below the projecting inner shelf (figure 16). A rejection tract on the shelf forms an indented groove. Underlying the rejection tract are large numbers of sub-epithelial gland cells each with a granular cytoplasm. As in *T.* (*T.*) *trisinuata* there is also a broad glandular region on each side of the anterior inhalent aperture. The cells stain blue with Masson's trichrome stain. The inner mantle fold is fused at a point position posteriorly to form a narrow exhalent aperture. This position coincides with the

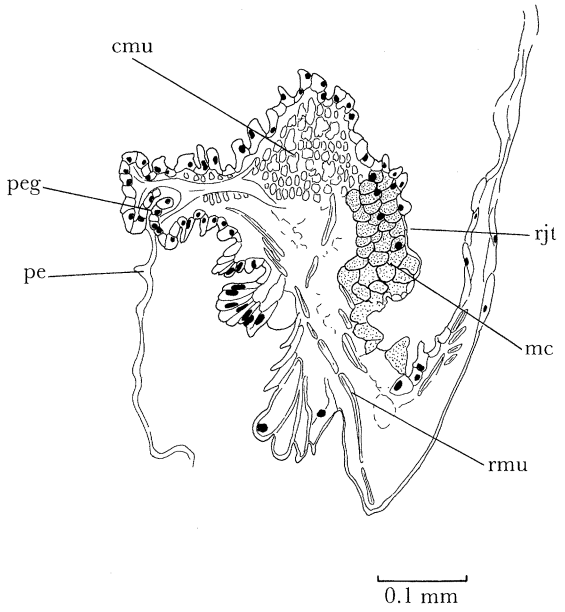

Figure 16. *Thyasira* (*Thyasira*) *excavata plicata*: transverse section through the mid-ventral mantle edge; specimen from *Walda*, station CY 13. (List of abbreviations: see p. 561.)

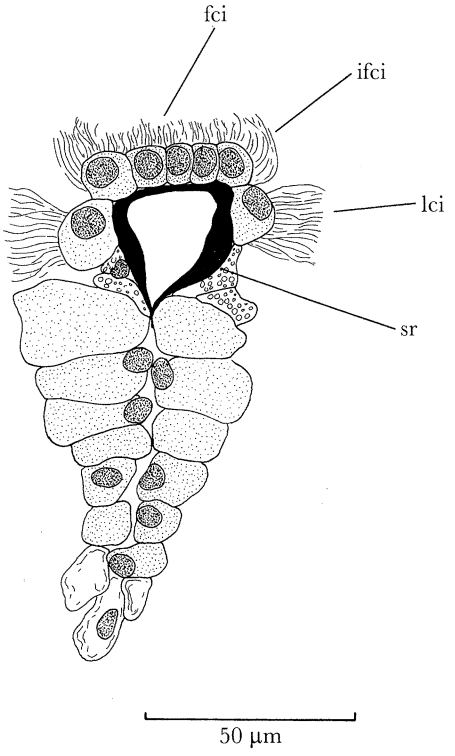

Figure 17. *Thyasira* (*Thyasira*) *excavata plicata*: transverse section through a gill filament; specimen from *Walda*, station CY 13. (List of abbreviations: see p. 561.)

indentation formed by the sulcus. No other mantle fusion or adhesion was observed.

The demibranchs of the gill (figure 14) are well developed, but the outer is only half the size of the inner. The lamellae of the inner demibranchs are equal while the descending lamella of the outer demibranch is shorter than the ascending lamella. Each is composed of more than 100 homorhabdic filaments which have well-developed abfrontal tissue extensions (figure 17).

The labial palps are two small flaps at the outer

limits of a long proximal oral groove. The upper overlaps the lower and is drawn out postero-dorsally to form a narrow 'wing'. The inner surfaces bear 9–10 ridges. The foot is long and vermiform, without a heel. Narrow anterior and posterior retractor muscles extend from the base and attach to the mantle or shell dorsal to the adductor muscles but are not strongly developed. The bulbous tip of the foot is differentiated into two parts. The distal part has a thickened irregular surface, while the proximal part bears transverse corrugations like the rest of the stem.

The course of the gut is similar to that of *T.* (*T.*) *trisinuata* and no description is given here. The antero-dorsal wall of the stomach bears a dorsal hood which is more prominent than in any other species examined. The stomach and style sac are broad and tubular in shape, with a small constriction separating them. The stomach occupies a horizontal position in relation to the rest of the body.

The lateral pouches are very large arborescent structures. Each pouch is connected to the body by a narrow neck. They project beneath the ventral margin of the gill and extend far dorsally (figure 15). This is the only species of those studied in which the dorsal digestive diverticula are also branched. They extend just anterior and dorsal to the stomach. Digestive ducts are not present.

The gonad is located to the inner side of the pouches. Paired gonadial ducts pass through the posterior half of the neck of the pouches and to each side of the style sac before opening ventral to the posterior margin of the kidney. In this species the gonad also occupies a considerable area dorsal to the style sac and stomach. The number of eggs in each ovary of a specimen 15.3 mm in height exceeds 1000. Eggs are 193 μm in length (measured from sectioned material).

The kidneys are large and occupy the area between the pericardium and the posterior pedal retractors. Despite their size, they are not lobed. A pair of ducts, like those in *T.* (*T.*) *trisinuata* extend from the anterior end of the kidneys along the ventral wall to open into the supra-branchial cavity.

The heart although small is relatively well developed. It is located anterior to the kidneys and surrounds the hindgut.

The nervous system resembles that of *T.* (*T.*) *trisinuata*. Of note is a particularly broad pair of nerves from the cerebral ganglia to the anterior adductor muscle and the 'glandular' area of the mantle edge.

Thyasira* (*Thyasira*) *obsoleta (Verrill & Bush, 1898)

Type species: *Cryptodon obsoletus*, Verrill & Bush, 1898.
Type locality: Off Martha's Vineyard, Massachusetts: 183–713 m.
Type specimen: Holotype USNM No. 159886.

Synonymy

Axinus croulinensis Jeffreys (1863, p. 250–251).
Axinus croulinensis Jeffreys (1868, p. 301).
Axinus croulinensis Jeffreys (1869, fig. 2, pl. 33).
Axinus croulinensis (error) Jeffreys (1870*a*, p. 441).
? *Axinus croulinensis* Monterosato (1872, p. 24).
? *Axinus croulinensis* Monterosato (1877, p. 30).
? *Axinus croulinensis* Monterosato (1878, p. 69).
Axinus croulinensis Sars (1878, p. 62, fig. 8*a–b*, pl. 19).
Axinus croulinensis Jeffreys (1880, p. 316).
Axinus croulinensis Jeffreys (1881, p. 703).
Axinus flexuosis var. *rotunda* Jeffreys (1881, p. 701–702).
? *Axinus croulinensis* Monterosato (1882, p. 98).
? *Cryptodon croulinensis* Smith (1885, p. 193).
Axinus croulinensis Kobelt (1888, p. 375).
Cryptodon croulinensis Norman (1893, p. 344).
Axinus croulinensis (in part) Marshall (1897, p. 353–354).
Axinus croulinensis var. *transversa* Locard (1898, p. 291–292).
Axinus flexuosus var. *rotundata* Locard (1898, p. 288).
Axinus croulinensis (in part) Posselt (1898, p. 78–79).
Axinus flexuosus var. *rotunda* Posselt (1898, p. 80).
Cryptodon obsoletus Verrill & Bush (1898, p. 789–790, figs. 1–2, pl. 89).
? *Cryptodon croulinensis* Verrill & Bush (1898, p. 786–787, figs. 3–4, pl. 90).
Cryptodon obsoletus Dall (1901, p. 787).
Thyasira croulinensis Dall (1901, p. 787).
Thyasira rotunda Dall (1901, p. 787).
? *Axinus croulinensis* Friele & Greig (1901, p. 32).
? *Thyasira croulinensis* Dautzenberg & Fischer (1912, p. 487).
? *Cryptodon croulinensis* Cooke (1914, p. 115).
Axinus croulinensis var. *truncatus* Marshall (1914, p. 186–187).
Thyasira (*Axinulus*) *obsoleta* Johnson (1915, p. 64).
Thyasira croulinensis Johnson (1915, p. 64).
Thyasira croulinensis (in part) Lamy (1920, p. 306–307).
Thyasira rotunda Lamy (1920, p. 295–296).
? *Thyasira croulinensis* Dautzenberg (1927, p. 312).
? *Thyasira croulinensis* Thiele & Jaeckel (1931, p. 218).
Thyasira croulinensis Johnson (1934, p. 39).
Thyasira rotunda Johnson (1934).
Thyasira croulinensis La Rocque (1953, p. 56).
Thyasira rotunda La Rocque (1953, p. 57).
Thyasira croulinensis Ockelmann (1958, p. 110, 197).
Thyasira croulinensis (in part) Clarke (1962, p. 64).
Thyasira rotunda Clarke (1962, p. 64).
Thyasira obsoleta Ockelmann (in Bowden & Heppell (1968), pp. 262–263).
? *Thyasira croulinensis* Petersen (1968, p. 21, 52).
Axinus croulinensis, var. *truncatus* Nordsieck (1969, p. 60, not fig. 48.10, pl. 13).
Axinus croulinensis, var. *transversus* Nordsieck (1969).
Thyasira flexuosa var. *rotunda* Nordsieck (1969, p. 79).

Note: the references prefixed with a question mark may refer to either *Clausina croulinensis* Jeffreys, or the present species. Those marked (in part), probably include both species. See also *Thyasira* (*Axinulus*) *croulinensis* p. 525.

Historical

In much of the literature this species has been regarded as a variety or form of *Clausina croulinensis* (Jeffreys 1847) (figures 72 and 73). The confusion arose from a misconception by Jeffreys (1869) that *Clausina croulinensis* is a juvenile of the present species.

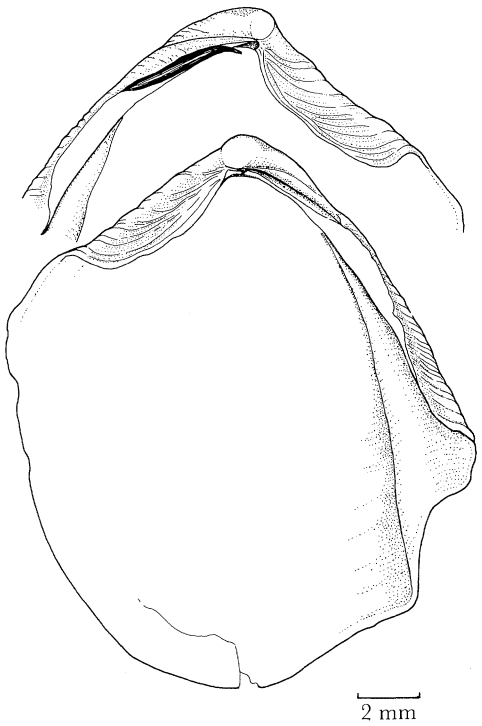

Figure 18. *Thyasira* (*Thyasira*) *tricarinata*: interior of left hinge plate and right valve of paratype; USNM No. 749073.

Ockelmann (in Bowden & Heppell 1968) notes that:

> '*Clausina croulinensis* Jeffreys (1863:250; 1869: pl. 33, fig. 2) a species of *Thyasira* s.s. is.... a different species from *Clausina croulinensis* Jeffreys (1847), which is placed in the subgenus *Axinulus*. The oldest available name for the former species is stated to be *Thyasira obsoleta* (Verrill & Bush 1898).'

We have examined the type specimen of *T.* (*T.*) *obsoleta* and confirm that it is the same species as that described as *Clausina croulinensis* by Jeffreys in 1863.

T. rotunda (Jeffreys), originally taken by the *Lightning* and *Porcupine* Expeditions, 1868–1870, and described as *Axinus flexuosus* var. *rotunda* (Jeffreys 1881) was subsequently elevated to specific status by Dall (1901). We have specimens in our samples that correspond to the description of this species (figure 23). We believe them to be large laterally compressed specimens of *T.* (*T.*) *obsoleta* and have therefore included this species in our synonymy. The type specimens of *T.* (*T.*) *rotunda*, obtained at a depth of 419–823 m between the Hebrides and the Faroes, could not be found by Warén (1980) nor by us.

Material

ship/cruise	no.	date	sta.	position	depth/m	number	gear
North America Basin							
Atlantis	264	21.05.61	HH 3	38° 47.0′N 70° 08.0′W	2900	3	ad
Atlantis	277	23.05.62	D 1	39° 54.5′N 70° 35.0′W	509	2	ad
Atlantis II	12	25.08.64		73 39° 46.5′N 70° 43.3′W	1330–1470	3	es
Chain	50	06.07.65	87	39° 48.7′N 70° 40.8′W	1102	70	es
Chain	88	21.02.69	207	39° 51.3′N 70° 54.3′W	805–811	216	es
			—	39° 51.0′N 70° 56.4′W			
	88	22.02.69	209	39° 47.6′N 70° 49.9′W	1501–1693	4	es
			—	39° 46.0′N 70° 51.5′W			
West European Basin							
Chain	106	17.08.72	313	51° 32.2′N 12° 35.9′W	1491–1500	15	es
Polygas		21.10.72	DS16	47° 36.1′N 08° 40.5′W	2325	1	ds
		01.11.72	DS26	44° 08.2′N 04° 15.0′W	2076	6	ds
		22.10.72	DS17	47° 32.0′N 08° 45.5′W	2103	2	ds
		22.10.72	DS18	47° 32.2′N 08° 44.9′W	2138	2	ds
		01.11.72	DS25	44° 08.2′N 04° 15.7′W	2096	2	ds
Biogas II		19.04.73	DS31	47° 32.5′N 09° 04.2′W	2813	1	ds
		10.04.73	DS32	47° 32.2′N 08° 05.3′W	2138	2	ds
		20.04.73	DS33	47° 39.7′N 08° 05.5′W	2338	1	ds
Biogas III		24.08.73	DS35	47° 34.4′N 08° 40.7′W	2226	1	ds
		24.08.73	DS37	47° 31.8′N 08° 34.6′W	2110	3	ds
		25.08.73	DS38	47° 32.5′N 08° 35.8′W	2138	1	
		01.09.73	DS49	44° 05.9′N 04° 15.6′W	1845	1	ds
		01.09.73	DS50	44° 08.9′N 04° 15.9′W	2124	1	ds
Thalassa		22.10.73	Z400	47° 33.4′N 07° 19.0′W	1175	38	gbs
		25.10.73	Z429	48° 28.0′N 09° 50.0′W	1300	3	pbs
		26.10.73	Z436	48° 39.8′N 09° 56.4′W	1210	1	pbs
		26.10.73	Z439	48° 42.0′N 10° 23.4′W	500	2	pbs
		27.10.73	Z445	48° 52.2′N 11° 07.0′W	1200	1	pbs
Thalassa		27.10.73	Z449	48° 41.3′N 10° 33.8′W	730	1	pbs
Biogas IV		18.02.74	DS52	44° 06.3′N 04° 22.4′W	2006	36	ds
		26.02.74	DS63	47° 32.8′N 08° 35.0′W	2126	1	ds
Biogas V		15.06.74	DS65	47° 36.1′N 08° 40.5′W	2360	6	ds

Material

ship/cruise	no.	date	sta.	position	depth/m	number	gear
Biogas VI		20.10.74	DS71	47° 34.3′N 08° 33.8′W	2194	1	ds
		31.10.74	DS86	44° 04.8′N 04° 18.7′W	1950	9	ds
		01.11.74	DS87	44° 05.2′N 04° 19.4′W	1913	2	ds
		01.11.74	DS88	44° 05.2′N 04° 15.7′W	1894	3	ds
Sierra Leone Basin							
Atlantis II	31	05.02.67	142	10° 30.0′N 17° 51.5′W	1624–1796	1	ds
		05.02.67	144	10° 36.0′N 17° 40.0′W	2051–2357	2	es
Angola Basin							
Atlantis II	42	23.05.68	201	09° 25.0′S 11° 35.0′E	1964–2031	11	es
			—	09° 05.0′S 12° 17.0′E			
		23.05.68	202	08° 56.0′S 12° 15.0′E	1427–1693	10	es
			—	08° 40.0′S 12° 47.0′E			
Walda		.06.71	DS16	10° 31.0′S 11° 57.8′E	1787	1	ds

In addition, we have examined the Sykes collection in the British Museum of Natural History, and the Jeffreys and Verrill and Bush material in the U.S. National Museum.

Past records of this species are numerous but in many cases it is impossible to distinguish them from than those of *T.* (*Axinulus*) *croulinensis*. The following are definitely referable to *T.* (*T.*) *obsoleta*: North America Basin (Verrill & Bush 1898); Norway (Sars 1878; Marshall 1914); West European Basin (Jeffreys 1880, 1881; Locard 1898; Marshall 1914). Our material extends the range to the Sierra Leone Basin and Angola Basin and provides additional material from the North America and West European Basins. Depth range: 24–2900 m.

Shell description (figures 19, 20, 22 and 23)

Shell small, white or semi-transparent, oblique or pyriform, equivalve, inequilateral, height normally exceeds length, but specimens occur in which length equals height or may exceed it; often inflated, sculpture, fine concentric lines more distinct at ventral margin; small prosogyrous beaks positioned posterior to midline; antero-dorsal and postero-dorsal margins slope rapidly from beaks, antero-ventral margin very broadly curved, postero-ventral margin flattened or faintly concave where a shallow posterior sulcus indents the shell margin, postero-dorsal margin indented by well defined submarginal sulcus forming characteristic projecting auricle which varies in degree of development; escutcheon shallow; lunule ill defined; hinge plate variable usually without any distinct swellings, although always a little thickened ventral to beaks, small distinct tubercle ventral to beak of right valve in a few specimens, latter fits elongated tubercle of left valve, internally postero-dorsal section of hinge plate reflected outwards; ligament opisthodetic, in curved groove at surface of hinge plate, invisible externally, extends one quarter the distance to posterior margin; interior white, glossy, with faint concentric lines and radial striae, muscle scars indistinct.

Three specimens from *Biogas* sta. DS86 measure (length × height × breadth) 3.9 × 3.9 × 2.1 mm; 3.1 × 3.2 × 2.0 mm; 2.1 × 1.8 × 0.9 mm; while a 'typical' specimen from *Chain* sta. 207 measures 2.2 × 2.4 × 1.6 mm. Prodissoconch 117–128 μm in length.

The identification of *T.* (*T.*) *obsoleta* is particularly difficult due to the variation in its shell characters. It

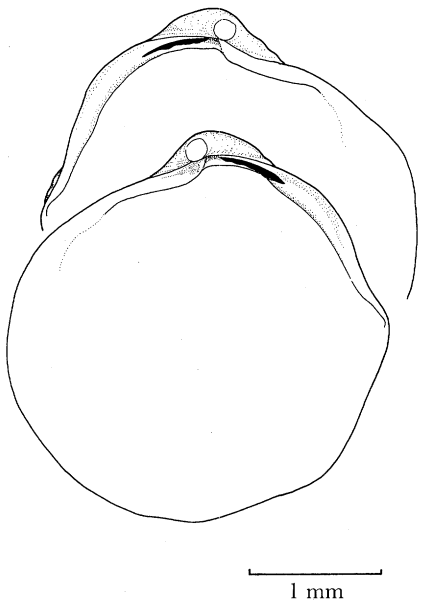

Figure 19. *Thyasira* (*Thyasira*) *obsoleta*: hinge plate of left valve and interior of right valve; specimen from *Biogas VI*, station DS 86.

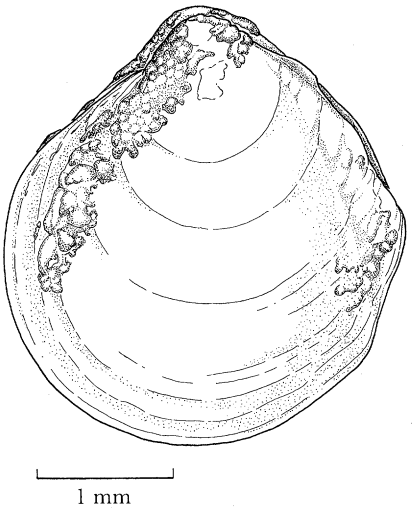

Figure 20. *Thyasira* (*Thyasira*) *obsoleta*: lateral view of the shell from the left side; specimen from *Chain* 106, station 313.

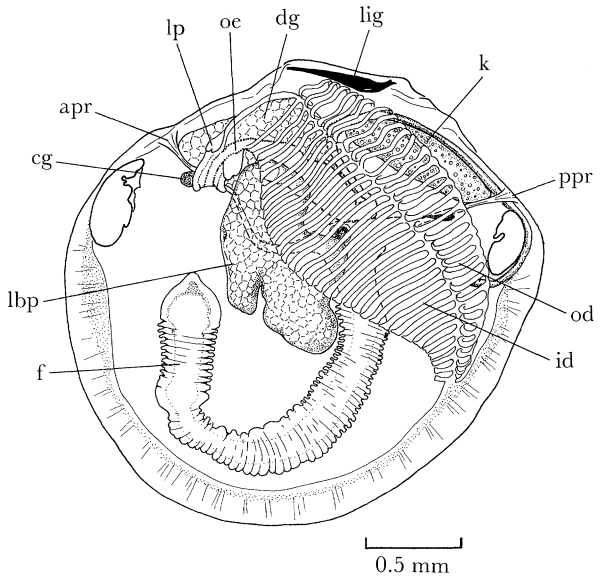

Figure 21. *Thyasira* (*Thyasira*) *obsoleta*: internal morphology as seen from the left side of a wholemount; specimen from *Biogas*, station DS 887. (List of abbreviations: see p. 561.)

differs from the closely related *T.* (*P.*) *equalis* (figures 34 & 35) principally by its more oblique shape and the presence of a projecting posterior auricle. Shells from a range of geographical localities show variation in the size of the posterior auricle, the obliqueness of the shell and the depth of the primary sulcus. Thus, specimens from Drobak, Norway (110–183 m) are more oblique than those from the West European and North America Basins.

Internal morphology (figure 21)

The anterior and posterior adductor muscles are oval and dorso-ventrally elongated. The anterior adductor is narrow dorsally and a small constriction separates this part from the broader ventral region. The posterior adductor is about two thirds the size of the anterior muscle.

A single point of mantle fusion forms the posterior exhalent aperture. No adhesion was observed between opposing mantle edges at any other point along the mantle margin. Transverse sections of the mantle edge do not show any important differences from that of species already described. Concentric and pallial musculature is well developed. The gland cells of the inner mantle lobe typically form an expanded area on each side of the anterior inhalent region.

The gills comprise both inner and outer demibranchs. This feature immediately distinguishes *T.* (*T.*) *obsoleta* from *T.* (*A.*) *croulinensis* which has only a single demibranch in each gill. In lateral view the inner demibranch is approximately twice as large as the outer demibranch; its ventral edge covers the dorsal margin of the lateral pouches. The ascending lamella of the inner demibranch is about three quarters the size of the descending lamella. In contrast the outer demibranch has a very short descending lamella which, in small specimens is almost non-existent. Thus the outer demibranch may appear to be completely reflected above the gill axis. In the largest specimens each demibranch is composed of about 36 homorhabdic filaments but usually there are fewer. Tissue connections between adjacent filaments occur at broad intervals. A maximum of three such connections occur in the inner demibranch, and from none to two in the outer. The gill axis is characteristically curved at its posterior end paralleling the curvature of the shell margin. In transverse section the filaments are elongated by abfrontal tissue, but less so than in the previous two species described. The blood space which lies close to the frontal surface does not extend into the abfrontal tissue. Except dorsally, the filaments are joined by interlamellar tissue as described for *T.* (*T.*) *trisinuata* (p. 488).

The foot is long, narrow and without a heel. It is served by slender anterior and posterior retractor muscles. The tip is bulbous and is more heavily ciliated than the stem. It is separated from the stem by a constriction. A group of deeply staining cells are present at the extreme tip.

Since they follow the same basic plan as all other *Thyasira* species, the stomach and course of the gut require little description. The stomach wall is thin except adjacent to the gastric shield where deep columnar epithelial cells contain spherules of proteinaceous material. The gastric shield covers the dorsal and lateral walls; there is a gastric tooth on the left side. The thin ventral wall has a rejection groove leading to the midgut. The style sac is lined dorsally and laterally by heavily ciliated columnar epithelial cells.

Two enormous ventro-lateral apertures are present at the anterior end of the stomach. Each opens into two digestive tubules. The most dorsal of the latter leads to the dorsal side of the stomach while the larger ventral tubule leads to the lateral pouch. The arrangement of the digestive diverticula is the same as in *T.* (*T.*) *trisinuata* (figure 8) except that here the situation is more simple owing to the smaller size of the species. Thus, the pattern of lobes of the lateral pouches is similar to that of juvenile specimens of *T.* (*T.*) *trisinuata*. The pouches are characteristically divided into two parts, an antero-dorsal lobe and a postero-ventral lobe. The antero-dorsal lobe overlaps the postero-dorsal and from which it is almost completely separated. Small specimens have less well developed lobes. Large specimens may be more complicated. The digestive diverticula are lined with large vacuolated tubule cells except at the blind ends where smaller more deeply staining cells are present.

The gonad is similar to that of other species. Eggs measure up to 71 μm in length in preserved specimens. The kidney, pericardium and nervous system are also similar to those of the larger species. No reno-pericardial ducts were seen.

Thyasira* (*Thyasira*) *succisa succisa (Jeffreys, 1876)

Type species: *Axinus incrassatus* var. *succisa*, Jeffreys, 1876.

Type locality: Adventure bank, Mediterranean: 168 m.

Type specimen: Lectotype. USNM No. 61973.

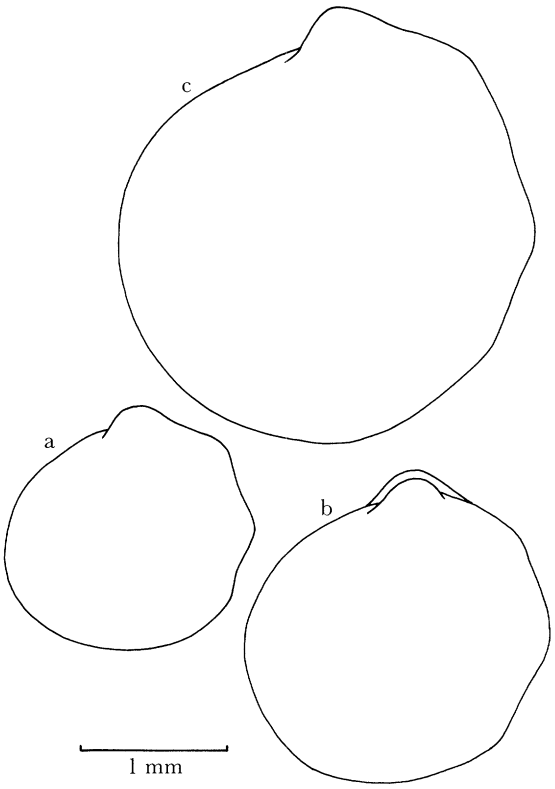

Figure 22. *Thyasira* (*Thyasira*) *obsoleta*: outline drawings to show variation in shell shape of specimens from different sampling stations. (*a*) *Thalassa*, station Z400, (*b*) *Chain* 88, station 207, and (*c*) *Biogas VI*, station DS 86.

Synonymy

Axinus incrassatus (*nomen nudum*) Jeffreys (1876*a*, p. 191, 199).
Axinus incrassatus var. *succisa* Jeffreys (1876*b*, p. 492–493).
Axinus incrassatus var. *succisa* Jeffreys (1881, p. 703; fig. 7, pl. 61).
? *Cryptodon incrassatus* var. Smith (1885, p. 193).
Axinus incrassatus Kobelt (1888, p. 376).
Axinus incrassatus Posselt (1898, p. 77–78).
Thyasira (*Axinulus*) *succisa* Dall (1901, p. 788).
Thyasira (*Axinulus*) *succisa* Johnson (1915, p. 65).

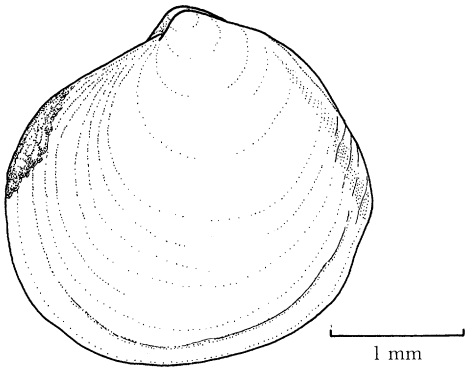

Figure 23. *Thyasira* (*Thyasira*) *obsoleta*: a rounded and laterally compressed variant similar to the description by Jeffreys of *Axinus flexuosus var. rotunda*: specimen from *Polygas*, station DS 26.

Axinus succisus Lamy (1920, p. 315).
Thyasira (*Axinulus*) *succisa* Dall (1927, p. 15).
Thyasira (*Axinulus*) *succisa* Johnson (1934, p. 39).
Thyasira succisa La Rocque (1953, p. 58).
Thyasira (*Axinulus*) *succisa* Clarke (1962, p. 65).
Leptaxinus incrassatus var. *succisus* Nordsieck (1969, p. 81; fig. 48.12, pl. 13).
Axinus incrassatus succisa Warén (1980, p. 46).

Historical

T. (*T.*) *succisa* was originally described as *Axinus incrassatus* var. *succisa*. The two varieties were separated by Dall (1901) as *Leptaxinus incrassatus* (figures 55 and 57) and *Thyasira* (*Axinulus*) *succisa* (figures 24 and 25). Although Dall placed *T.* (*T.*) *succisa* in the subgenus *Axinulus*, it is here considered to be a species of the subgenus *Thyasira* s.s. and is closely related to *T.* (*T.*) *obsoleta*.

T. (*T.*) *succisa* is well figured by Jeffreys (1881) although he does not make it clear that it is this species, rather than *T.* (*L.*) *incrassatus*. Nevertheless, the difference between the two is clear from Jeffreys (1876*b*) description. Specimens from Adventure bank, Mediterranean, were selected by Ockelmann as Lectotype (Warén 1980).

Material

ship/cruise	no.	date	sta.	position	depth/m	number	gear
West European Basin							
Biogas II		19.04.73	DS31	47° 32.5′N 09° 04.2′W	2813	1	ds
		20.04.73	DS33	47° 39.7′N 08° 05.5′W	2338	1	ds
		20.04.73	DS34	47° 42.4′N 08° 03.4′W	1031	2	ds
Thalassa		21.10.73	Z392	47° 34.9′N 07° 01.3′W	390	2	gbs
		22.10.73	Z393	47° 33.0′N 07° 04.7′W	750	1	gbs
		22.10.73	Z397	47° 33.8′N 07° 12.6′W	511	8	gbs
		22.10.73	Z399	47° 34.8′N 07° 18.1′W	825	1	gbs
		24.10.73	Z413	48° 03.1′N 08° 29.4′W	805	2	pbs
		24.10.73	Z414	48° 05.0′N 08° 29.8′W	650	13	pbs
		24.10.73	Z415	48° 07.2′N 08° 26.2′W	380	1	pbs
		24.10.73	Z416	48° 13.5′N 09° 07.5′W	480	36	pbs
		24.10.73	Z417	48° 12.0′N 09° 09.5′W	865	9	pbs
		24.10.73	Z420	48° 19.8′N 09° 37.8′W	507	4	pbs
		25.10.73	Z426	48° 28.2′N 09° 39.1′W	860	1	pbs
		25.10.73	Z427	48° 27.0′N 09° 48.4′W	330	1	pbs
		25.10.73	Z428	48° 27.2′N 10° 49.7′W	850	5	pbs

Material

ship/cruise	no.	date	sta.	position	depth/m	number	gear
		25.10.73	Z431	48° 38.2′N 09° 47.3′W	800	3	pbs
		26.10.73	Z438	48° 33.7′N 10° 25.0′W	1400	2	pbs
		26.10.73	Z440	48° 41.4′N 10° 21.5′W	860	5	pbs
		25.10.73	Z442	48° 54.8′N 11° 02.0′W	975	4	pbs
		27.10.73	Z443	48° 56.0′N 11° 02.0′W	660	2	pbs
		29.10.73	Z457	48° 38.2′N 09° 52.6′W	800	7	gbs
		29.10.73	Z459	48° 37.3′N 09° 53.0′W	1180	6	gbs
		29.10.73	Z456	48° 39.3′N 09° 50.2′W	400	5	gbs
Biogas IV		24.02.74	DS59	47° 31.7′N 09° 06.2′W	2790	1	ds
		25.02.74	DS61	47° 34.7′N 08° 38.8′W	2250	2	ds
Biogas VI		31.10.74	DS86	44° 04.8′N 04° 18.7′W	1950	1	ds
		01.11.74	DS87	44° 05.2′N 04° 19.4′W	1913	1	ds

Distribution

This species has been recorded from the West European Basin, from the Faroes, southwest Ireland, to the Bay of Biscay, Spain, Portugal and the Mediterranean (Jeffreys 1881). In the northwest Atlantic it has been recorded off New England (Johnson 1915), off Florida (Dall 1901), and possibly off Culebra Island, West Indies, (Smith 1885). Depth range: 73–2813 m.

Shell description (figures 24, 25 and 28)

Shell small, white or semi-transparent, equivalve, inequilateral, shell length exceeds height, characteristic oblique shape, anteriorly broadly curved and elongate, fragile fine concentric lines, patches of ferruginous deposit adhere to shell margins, inside rather glossy, with faint radial and concentric striae, muscle scars indistinct; small prosogyrous beaks posterior to midline; ventral margin curved, posterior margin strongly angulated at junction of postero-dorsal and postero-ventral margins; primary sulcus almost obsolete, defined only by a slight flattening of the postero-dorsal margin, shallow submarginal sulcus indents the postero-dorsal shell margin to form prominent auricle; lunule ill-defined; hinge plate of right valve bears a small protruberance immediately anterior to beak, this fits a declivity in left hinge plate; ligament opisthodetic,

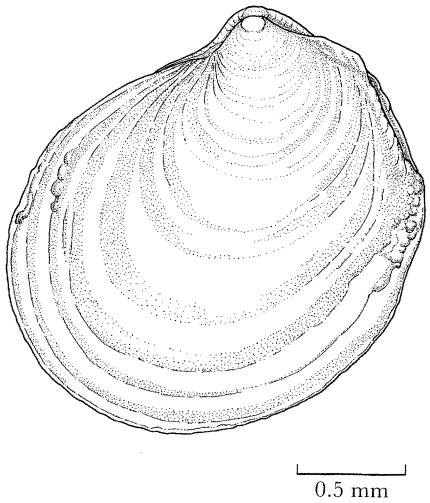

Figure 24. *Thyasira* (*Thyasira*) *succisa succisa*: lateral view of shell from the left side; specimen from *Thalassa*, station Z416.

Figure 25. *Thyasira* (*Thyasira*) *succisa succisa*: lateral view of the hinge plate and right valve; specimen from the *Porcupine* expedition; BM(NH) No. 61971.

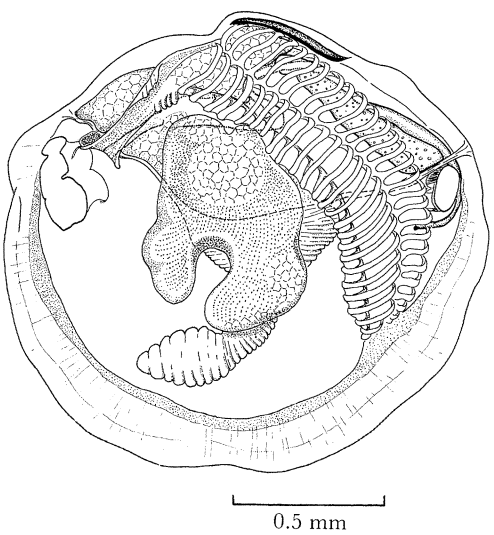

Figure 26. *Thyasira* (*Thyasira*) *succisa succisa*: internal morphology as viewed from the left side of a wholemount; specimen from *Thalassa*, station Z428. (For identification of parts see figures 2 and 3.)

in a curved groove on face of hinge plate, extends one quarter distance to posterior margin.

Shells measure up to 2 mm in length; the largest specimen (from Thalassa sta. Z414) measures (length × height × breadth) 2.0 × 1.9 × 1.05 mm.

T. (*T.*) *succisa* is distinguished by its characteristic oblique shell shape and pronounced posterior angulation.

Internal morphology (figure 26)

In most respects the mantle edge is similar to that of other species of *Thyasira*. The inner fold is well developed and forms an inner ledge, along which runs the main rejection tract. Underlying this ledge is a sizeable block of concentric muscle fibres which encircle the mantle edge. Radial pallial musculature is also well developed and extends into the three folds. A small, bifurcate, sensory frill comprises the middle fold and this is separated from the outer fold by the periostracal groove. The mantle edge is fused posteriorly at a single point to define the posterior exhalent aperture. The anterior adductor muscle is elongate and in cross section approximately three times the size of the small oval posterior adductor.

Each gill comprises two demibranchs. The ventral margin of the gill does not cover the dorsal part of the lateral pouches. In lateral view the two demibranchs are approximately equal in size, in some specimens the inner demibranch may be slightly the larger. The descending lamella of the outer demibranch is extremely short and the ascending lamella is almost entirely reflected above the level of the gill axis. The ascending lamella of the inner demibranch is about one third the length of the descending lamella. The angle of the gill axis reflects the posterior angulation of the shell. Interlamellar fusion occurs ventrally necessarily being restricted by the small extent of the descending lamella of the outer demibranch. In transverse section (figure 27) the filaments are broad and short. Little abfrontal tissue is present. Cilia-bearing frontal and lateral cells have a swollen appearance. Centrally there is a large blood space supported by well developed skeletal rods. Filamentar musculature is well developed. The frontal cilia occupy a narrow strip; large groups of latero-frontal cilia occur to each side. The lateral cilia are also well developed.

A pair of small triangular palps is situated at the outer limits of the extremely long proximal oral groove. The palps have four indistinct grooves on their inner surface.

The foot is short and broad with a pointed, but bulbous, tip and well developed heel. The heel is ventrally flattened and grooved sagittally. In appearance the foot is more spade-like than that of *T.* (*T.*) *trisinuata* and *T.* (*T.*) *obsoleta*. Internally, transverse muscle fibres cross the stem of the foot and are also present internally between the outer parts of the heel and the walls of the groove.

The course of the gut is shown in figure 26. The stomach is of moderate size with a well developed gastric shield covering its dorsal and lateral walls. Dorsal and ventral pairs of digestive tubules join the stomach at a single aperture in the anterior stomach wall. As in previously described species the style sac and the midgut are combined. The hindgut immediately anterior to the posterior adductor muscle may be dilated with food remains.

The digestive diverticula occupy the outer part of the body pouches and are present dorsal and lateral to the stomach. Although the body pouches characteristically have two main lobes separated by a deep indentation, some specimens from shallower depths were found to have rather more subsidiary lobing than that illustrated (figure 26).

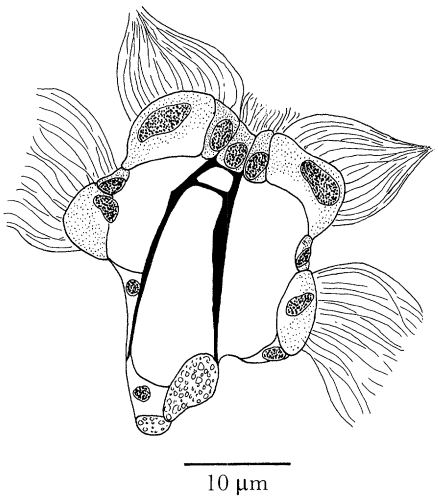

Figure 27. *Thyasira* (*Thyasira*) *succisa succisa*: transverse section through a gill filament; specimen from *Thalassa*, station Z416. (For identification of parts see figure 12.)

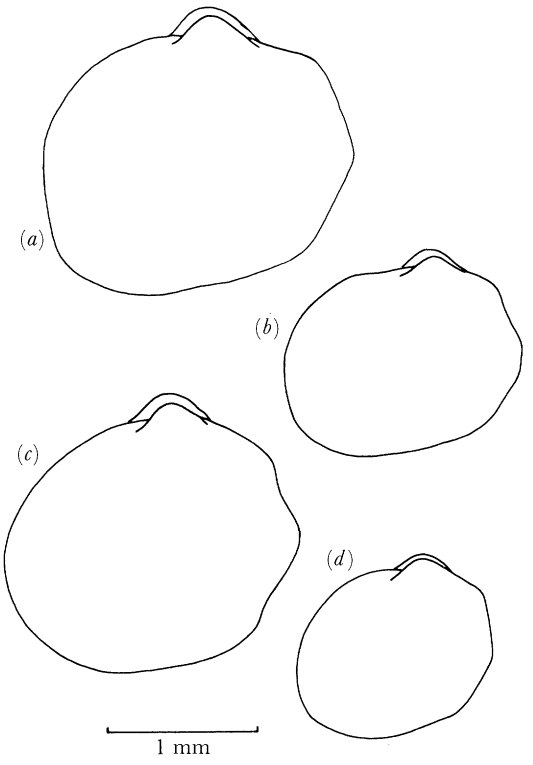

Figure 28. *Thyasira* (*Thyasira*) *succisa atlantica* (*a*, *b*) and *T.* (*T.*) *succisa succisa* (*c*, *d*): comparison by shell shape: specimens from a number of sampling stations: (*a*, *b*) *Atlantis*, station 202; (*c*) *Biogas*, station DS 34; (*d*) *Thalassa*, station Z443.

The gonad occupies the inner part of the body pouches. A total of 87 eggs were counted in one individual measuring 1.5 mm long. The eggs of sectioned individuals measure up to 95 μm in length.

The pericardium is thin walled and located anterior and dorsal to the anterior end of the paired kidneys. As in other species, the kidney cells are large, vacuolated and contain large angular concretions.

Although the nervous system is similar to those described before, the pedal ganglia in this species are fused to form an unpaired body as viewed externally.

Thyasira* (*Thyasira*) *succisa atlantica (new subspecies)

Type locality: Cape Basin: 23° 05′S, 12° 31.5′E; 1546–1559 m.
Type specimen: Holotype BM(NH) No. 1990041.

Distribution

Widely distributed in the Atlantic Ocean, in the North American, Angola, Argentine and Guiana Basins. Depth range: 508–2500 m.

Shell description (figures 28, 29 and 30)

Shell small, fragile, white or semi-transparent with small quantity of ferruginous deposit adhering, equivalve, inequilateral, obliquely oval with posterior angulation, more broadly rounded than *T.* (*T.*) *succisa succisa*; rounded beaks just posterior to midline; posterior sulcus forms faint radial undulation at posterior shell margin, submarginal sulcus small, forming posterior auricle; hinge plate of right valve bears a small swelling below beak, a similar swelling in left valve fits ventral to that of right; narrow opisthodetic ligament reaches one quarter of the distance to posterior margin; muscle scars and pallial line indistinct.

Material

ship/cruise	no.	date	sta.	position	depth/m	number	gear
North America Basin							
Atlantis II	24	18.08.66	118	32° 19.4′N 64° 34.9′W	1150	1	es
Sierra Leone Basin							
Atlantis II	31	05.02.67	142	10° 30.0′N 17° 51.5′W	1624–1796	15	es
Angola Basin							
Atlantis II	42	23.05.68	202	08° 56.0′S 12° 15.0′E	1427–1643	92	es
			—	08° 46.0′S 12° 47.0′E			
Cape Basin							
Atlantis II	42	17.05.68	191	23° 05.0′S 12° 31.5′E	1546–1559	24	es
		17.05.68	194	22° 54.0′S 11° 55.0′E	2864	19	es
Argentine Basin							
Atlantis II	60	11.03.71	239	36° 49.0′S 53° 15.4′W	1661–1679	6	es
		27.03.71	262	36° 05.2′S 52° 17.9′W	2440–2480	20	es
		28.03.71	264	36° 12.7′S 52° 42.7′W	2041–2048	5	es
Guiana Basin							
Knorr	25	28.02.72	295	08° 04.2′N 54° 21.3′W	1000–1022	72	es
		28.02.72	297	07° 45.3′N 54° 24.0′W	508–523	5	es
		29.02.72	299	07° 55.1′N 55° 42.0′W	1942–2076	2	es
		29.02.72	301	08° 12.4′N 55° 50.2′W	2487–2500	13	es

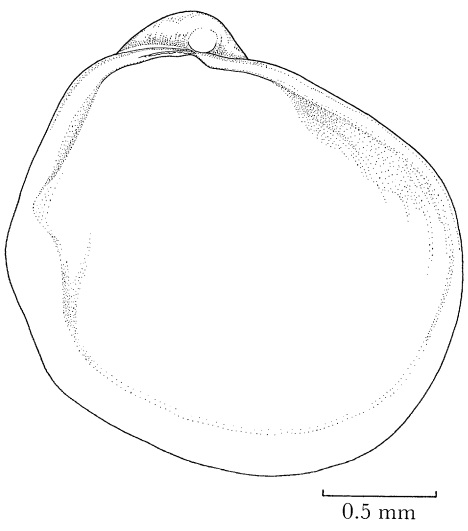

Figure 29. *Thyasira* (*Thyasira*) *succisa atlantica*: interior view of the left valve; specimens from *Atlantis II*, station 191.

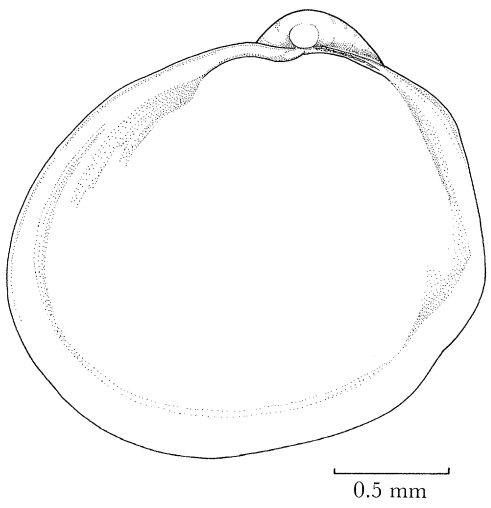

Figure 30. *Thyasira* (*Thyasira*) *succisa altantica*: interior view of the right valve; specimen from *Atlantis II*, station 191.

Five specimens (Atlantis II Sta. 194) measure (length × height × breadth) 2.10 × 2.00 × 1.20 mm; 1.80 × 1.80 × 1.00 mm; 1.70 × 1.70 × 0.90 mm; 1.40 × 1.40 × 0.70 mm; and 1.30 × 1.25 × 0.70 mm.

This subspecies differs from *T.* (*T.*) *succisa succisa* in having a more broadly rounded outline and more inflated shell. The small swellings on the hinge plate are also better developed. Although in shape the shell appears intermediate between that of *T.* (*T.*) *succisa* and *T.* (*T.*) *obsoleta*, the rounded shell is also very similar in shape to that of a number of *Axinulus* species, e.g. *T.* (*A.*) *brevis*, however, the internal morphology shows that it is more closely related to species of the subgenus *Thyasira*.

Major features shared by all members of the subgenus *Thyasira* are an inequilateral shell in which the beaks are positioned posterior to the midline and a shell in which height normally exceeds length. In small species (*T.* (*T.*) *obsoleta* and *T.* (*T.*) *succisa*) the shell is oblique. In all the hinge plate is narrow, but there is a tendency to develop a very small pseudo-cardinal tooth below the beak in the right valve. No lateral teeth are present. Although the posterior radial sulci are conspicuous in the larger species (*T.* (*T.*) *trisinuata* (figure 6) and *T.* (*T.*) *excavata* (figure 13)), they are reduced in smaller species to the extent that in *T.* (*T.*) *succisa atlantica* (figures 29 and 30) they approach the condition in the subgenus *Axinulus* (p. 521). Radial sulci cannot therefore be regarded as being characters particular to the subgenus *Thyasira*, however, sulci are best developed in large species of the subgenus *Thyasira* and in the subgenus *Conchocele* which includes the largest of all thyasirid species.

Morphological features which characterize the subgenus *Thyasira* include the large size difference of the anterior and posterior adductor muscles. This difference is more marked than in most species of the related subgenus *Parathyasira* (compare figures 14 and 36). The heteromyarian condition may be related in part the inequilateral shape of the shell and in part to the position of the anterior inhalent tube and the need to process effectively incoming particles. In large species the differentiation of the tip of the foot into two parts indicates a particularly specialized form of tube building activity. Nothing similar is seen in species of *Parathyasira* or in *Axinus grandis*. The subgenus *Thyasira* like *Parathyasira*, possesses extensively lobed lateral body pouches. The pattern of the lobes may be very complex. For example, in *T.* (*T.*) *excavata atlantica* the pouches resemble bunches of grapes. The kidneys are extensive in all of the species examined, but this is typical of deep-sea bivalves in general. There is a lack of internal convolution of the kidney epithelium. All species have a similar internal morphology although there is a trend of reduction and simplification the largest (14 mm) to the smallest species (2 mm) in the subgenus. Although smaller species have gills composed of a relatively small number of filaments, outer demibranchs are never lost. Similarly, the lobes of the lateral body pouches are simpler and fewer in the smaller species e.g. *T.*(*T.*) *obsoleta* and *T.* (*T.*) *succisa*.

T. (*T.*) *trisinuata*, is closely related to *T.* (*T.*) *flexuosus*, the type species of the subgenus. Both species are characteristic of shallow waters and belong to a closely related group or 'complex', similar to those described for fossil thyasirids by Kauffman (1967). This Recent complex is represented off northwest Europe by *T.* (*T.*) *flexuosa* and off the northeast United States by *T.* (*T.*) *trisinuata*. *T.* (*T.*) *trisinuata* can be considered as a typical shallow-water thyasirid species to which true deep-sea species can be compared.

Three types of distribution can be identified within the subgenus: (i) shallow shelf species (*T.* (*T.*) *trisinuata* like *T.* (*T.*) *flexuosa*) present in relatively shallow boreal waters but with restricted depth and geographical ranges; (ii) widely distributed species from relatively shallow water to almost 3000 m in depth (*T.* (*T.*) *obsoleta* and *T.* (*T.*) *succisa*), both species being widely distributed in the Atlantic and extremely variable in shape; (iii) lower slope and abyssal species (*T.* (*T.*) *excavata*) restricted to depths below 1000 m. Only small numbers of this latter species were obtained. It is possible that because it is relatively large, and probably deep burrowing it may have been missed by the epibenthic sledge.

Subgenus: **PARATHYASIRA** Iredale, 1930

Type species: *Parathyasira resupina* Iredale, 1930.
Type locality: Off Port Kembla, New South Wales, 119–137 m.

Original description

The genus *Parathyasira* was not defined separately from the original description of *P. resupina*:

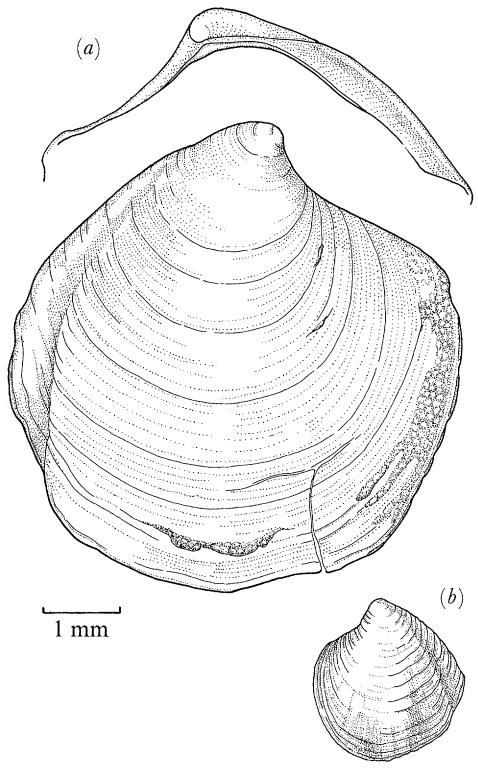

Figure 31. (*a*) *Thyasira* (*Parathyasira*) *granulosa*: hinge plate and lateral view of the right valve; specimen from the *Porcupine* expedition BM(NH) No. 61979. (*b*) *Parathyasira resupina*: after Iredale (1930).

'Shell small, thin, inequilateral, equivalve, umbones touching subcircular, anterior side nearly straight enclosing a deep, long ligamental pit, ligament semi-external; posterior side concave with an ill-defined elongate lunule; ventral margin rounded; a double very shallow fold present. Sculpture of very fine radial lines, with a delicate brownish silky periostracum present. Dead shell transluscent, muscle scars indistinct. Hinge toothless. Length 5.5 mm; height 5.5 mm; depth of conjoined valve 3.5 mm'.

Parathyasira resupina is very similar to *Thyasira granulosa* (Monterosato). The latter species was not obtained in our samples, but is figured in figure 31 for comparison with other species.

Redefinition of the subgenus *Parathyasira*

The subgenus *Parathyasira* as used here includes species which have an almost equilateral shell with the beaks close to the midline, with the anterior and posterior dorsal shell margins descending at almost equal angles from the beaks. Posteriorly there is a shallow double angulation. The hinge plate is thicker in the area immediately below the beaks than it is in *Thyasira* s.s. and does *not* bear a prominent projecting tubercle, but a very faint posterior lateral tooth and a faint central tubercle may be present. When specimens of equal size are compared the posterior radial sulcus is less deep in *Parathyasira* than in *Thyasira* sg and the ventral shell margin is more smoothly rounded.

The internal morphology is characterized by two demibranchs to each gill (**note:** *T.* (*P.*) *simplex* is exceptional in having only a single demibranch in the gill) and by extensive division of the lateral body pouches. Mantle fusion occurs at a single point posteriorly to form posterior exhalent aperture however, in some species at least, adhesion of the opposing inner mantle lobes occurs postero-ventrally and antero-ventrally.

Two small species *T.* (*Parathyasira*) *tortuosa* and *T.* (*Parathyasira*) *subovata* are with some doubt referred to this subgenus. These show deviation from the general shell shape and hinge plate characters of larger species, but are included here because their internal morphology is so similar to that of *T.* (*Parathyasira*) *atlantica*.

Thyasira* (*Parathyasira*) *subcircularis (new species)

Type locality: West European Basin, 47° 33.4′N, 07° 19.0′W; 1175 m.

Type specimen: Holotype: MNHN Paris.

Distribution

The species is widely distributed in the eastern Atlantic, West European Basin, Sierra Leone Basin and Angola Basin. Depth range: 800–2357 m.

Shell description (figure 32)

Shell fragile, white or semi-transparent, sub-circular moderately inflated, equivalve, length and height approximately equal, sculptured, fine concentric lines, at margins, fine radiating rows of tiny projections, possibly periostracal in origin, are visible under microscope, no ferruginous material adheres to shell, some specimens indented anteriorly by small irregularities, interior glossy, shows in obverse the small dents in anterior part of shell; moderately prominent prosogyrous beaks, slightly anterior of midline; antero-dorsal margin short, concave, postero-dorsal margin short, almost straight, posterior margin not indented; primary sulcus very faint, only visible in certain light; very distinct sunken escutcheon; no projecting auricle; hinge plate broad, thickened beneath beaks, almost smooth; no tooth-like swellings visible, little difference in form between right and left hinge plates; ligament opisthodetic in shallow curved groove close to margin of hinge plate, reaches to more than one third the distance to posterior margin, ligament externally visible along its whole length.

The largest specimen (Polygas Sta. DS25) measures 7.2 mm long × 7.2 mm high × 4.5 mm broad; most other specimens are considerably smaller.

T. (*P.*) *subcircularis* (figure 32) most closely resembles *T.* (*P.*) *granulosa* (Jeffreys) (figure 31) with which it shares a microsculpture of radiating rows of fine projections. *T.* (*P.*) *subcircularis* is distinguished by its sub-circular outline and less concave antero-dorsal margin.

Although this species bears an external resemblance

Material

ship/cruise	no.	date	sta.	position	depth/m	number	gear
West European Basin							
Polygas		01.11.72	DS25	44° 08.2′N 04° 15.7′W	2096	1	ds
Biogas II		20.04.73	DS34	47° 42.4′N 08° 03.4′W	1031	1	ds
Thalassa		22.10.73	Z400	47° 33.4′N 07° 19.0′W	1175	5	gbs
		27.10.73	Z445	48° 52.2′N 11° 07.0′W	1200	1	gbs
		29.10.73	Z457	48° 38.2′N 09° 52.6′W	800	1	gbs
Biogas IV		18.02.74	DS52	44° 06.3′N 04° 22.4′W	2006	1	ds
Biogas V		21.06.74	DS70	44° 08.8′N 04° 17.4′W	2150	1	ds
Biogas VI		31.10.74	DS86	44° 04.8′N 04° 18.7′W	1950	1	ds
Sierra Leone Basin							
Atlantis II	31	05.02.67	142	10° 30.0′N 17° 51.5′W	1624–1796	2	es
		05.02.67	144	10° 36.0′N 17° 49.0′W	2051–2357	1	es
Angola Basin							
Walda		06.71	DS10	18° 40.0′S 10° 56.3′E	1432	2	ds

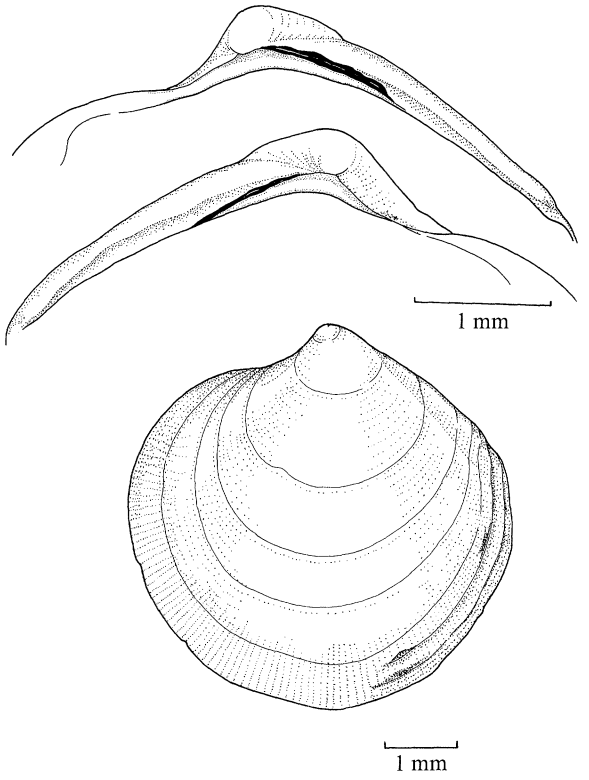

Figure 32. *Thyasira* (*Parathyasira*) *subcircularis*: hinge plate of right and left valves and lateral view of the left valve; specimen from *Walda*, station DS 10.

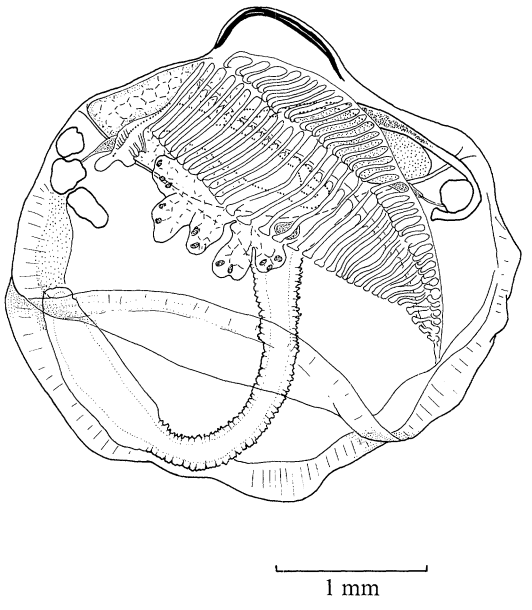

Figure 33. *Thyasira* (*Parathyasira*) *subcircularis*: internal morphology as seen from the left side of a wholemount: specimen from *Walda*, station DS 10. (For identification of parts see figures 2 and 3.)

to species of *Axinopsida* the hinge plate lacks any trace of the well developed cardinal tooth which characterizes that genus. The shell sculpture is also similar to a valve taken from Eastport, Maine which Verrill & Bush (1898) doubtfully refer to *Thyasira* (*Axinulus*) *simplex*. Our specimens are distinct from the type specimen of the latter species (USNM No. 159888).

Internal morphology (figure 33)

The anterior adductor muscle is narrow, dorso-ventrally elongated, curved and divided into three clear muscle blocks. The posterior adductor muscle is oval in shape, and approximately one third the size of the anterior adductor.

Mantle fusion is limited to a single posterior point to form a posterior exhalent aperture. The mantle folds are similar to those of the subgenus *Thyasira*. In *T.* (*P.*) *subcircularis* the inner fold is particularly broad and well supplied with gland cells in the anterior inhalent region. Nevertheless, this latter is somewhat less pronounced than that in larger species of *Thyasira*. Gland cells are also numerous at the posterior limit of the rejection tract of the inner mantle fold. Radial pallial muscles are particularly well developed being visible to the eye in both whole mounts and transverse sections. They are most strongly developed in the anterior inhalent region and close to the posterior exhalent aperture.

Both inner and outer demibranchs are present. The ventral margin of the inner demibranch covers the dorsal lobes of the lateral body pouches. The outer demibranch is less than half the size of the inner demibranch. The descending lamella of the outer demibranch is short and the ascending lamella is mainly reflected dorsal to the gill axis. The ascending and descending lamellae of the inner demibranch are similar in length. Each demibranch has 35 filaments in a specimen 3.5 mm in length. In this specimen there are six interfilamentar cross connections which connect the adjacent filaments of the inner demibranch and three which connect the filaments of the outer demibranch. These junctions are strong and distort the gill filaments somewhat. As in other species there are interlamellar junctions attaching the ventral sections of opposing filaments. The gill filaments lack abfrontal tissue extensions which characterize the subgenus *Thyasira*. Ciliation is well developed; the lateral and latero-frontal cilia are particularly long reflecting the wide separation of the filaments. Although labial palps are typically small, the palp ridges on the inner face are unusually distinct and number four to five in a specimen 3.5 mm in length.

The foot is long and narrow, lacking a heel and sagittal groove. Although the tip is elongate it is relatively undifferentiated from the stem. The extreme tip contains a discrete group of cells which stain deeply with haematoxylin.

The course of the gut and arrangement of the digestive diverticula are as in species of the subgenus *Thyasira*. The lateral body pouches have a distinctive shape. They are deeply divided with blunt-ended finger-like lobes at their perimeter (figure 33). The specimen 3.5 mm in length has ten such lobes. The most dorsal are concealed beneath the gill. Each lobe contains a separate branch of the digestive tubules. One specimen in whole mount contained very large oval granular bodies in the tubule cells. The identity of these is uncertain but they may be parasitic ciliates. It

is noteworthy that these bodies also occurred within the digestive diverticula of two other thyasirid species from the same sampling station (p. 512 & p. 528).

No specimens containing eggs or sperm were seen, however, the largest specimens which may have been mature, were not dissected owing to the paucity of material.

The kidney is similar in morphology to that of *Thyasira* sg. It occupies the area between the posterior adductor muscle and the pericardium. Small concretions occur within the epithelial cells. The arrangement of the heart is also similar to other *Thyasira* species.

The ganglia and the nervous system as a whole are well developed. A particularly well developed pair of nerves originating from the cerebral ganglia serves the anterior adductor muscle.

Thyasira* (*Parathyasira*) *equalis (Verrill & Bush, 1898)

Type species: *Cryptodon equalis*, Verrill & Bush, 1898.
Type locality: North America Basin.
Type specimen: Holotype USNM No. 74302.

Synonymy

Cryptodon equalis Verrill & Bush (1898, p. 788; fig. 5–6).
? *Cryptodon croulinensis* var. *altus* Verrill & Bush (1898, p. 787–788; fig. 1–2, pl. 88).
Thyasira equalis Dall (1901, p. 787).
Axinus flexuosus Friele & Greig (1901) in part (see Ockelmann 1958) (p. 31).
Thyasira equalis Johnson (1915, p. 64).
Axinopsis orbiculata Greig (1931, p. 4).
Thyasira equalis Johnson (1934, p. 39).
Thyasira equalis La Rocque (1953, p. 56).
Thyasira sp. A. Ockelmann (1958, p. 109, 197).
Thyasira equalis McIntyre (1961, p. 604, 605).
Thyasira equalis Clarke (1962, p. 64).
Thyasira equalis Soot-Ryen (1966, p. 27; fig. 11, pl. 1).
Thyasira equalis Bowden & Heppell (1968, p. 244, 263).
Thyasira equalis Nordsieck (1969, p. 79, footnote).
Thyasira equalis Knudsen (1970, p. 170).

Historical

In the literature this species has been confused with a number of other species. The species recorded by Ockelmann (1958) from east Greenland as *T. equalis* was later thought by him (McIntyre 1961) to be an undescribed species. *Thyasira* species A, described by Ockelmann and recorded from west Greenland and northern and southern Norway (Ockelmann 1958), is now regarded as *T.* (*P.*) *equalis* (McIntyre 1961). In his revision of the molluscs of the *Michael Sars* expedition, Soot-Ryen (1966) found *Axinopsis orbiculata* (Greig) to be synonymous with *T.* (*P*). *equalis* and the photograph (Ockelmann 1958) confirms this. We include *Cryptodon croulinensis* var. *altus* (Verrill & Bush) in the synonymy on the grounds that the reported difference of a longer and straighter shell margin (Verrill & Bush 1898) comes within the normal variation in shell shape of this species.

Material

ship/cruise	no.	date	sta.	position	depth/m	number	gear
North America Basin							
Atlantis	264	21.05.61	HH3	38° 37.0′N 70° 08.0′W	2900	2	ad
		25.05.61	C1	40° 20.5′N 70° 47.0′W	97	2	ad
Atlantis	277	23.05.62	D1	39° 54.5′N 70° 35.0′W	509	34	ad
Atlantis	283	28.08.62	Sl2	40° 01.8′N 70° 42.0′W	200	4	ad
		30.08.62	Sl4	39° 46.5′N 70° 39.9′W	400	9	ad
Atlantis II	12	25.08.64	73	39° 46.5′N 70° 43.3′W	1330–1470	5	es
Chain	50	29.06.65	76	39° 38.3′N 67° 57.8′W	2862	1	es
Chain	58	04.05.66	103	39° 43.6′N 70° 37.4′W	2022	1	es
		05.05.66	105	39° 56.6′N 71° 03.6′W	530	117	es
Chain	88	21.02.69	207	39° 51.3′N 70° 57.5′W	805–811	311	es
			—	39° 51.0′N 70° 56.4′W			
		22.02.69	209	39° 47.6′N 70° 49.9′W	1501–1693	12	es
			—	39° 46.0′N 70° 51.5′W			
West European Basin							
Knorr	25	28.02.68	295	08° 04.2′N 54° 21.3′W	1000–1022	3	es
Chain	106	17.08.72	313	51° 32.2′N 12° 35.9′W	1491–1500	2	es
Polygas		25.10.72	DS22	47° 34.1′N 09° 38.4′W	4144	1	ds
		26.10.72	DS23	46° 32.8′N 10° 21.0′W	4734	2	ds
		01.11.72	DS26	44° 08.2′N 04° 15.0′W	2076	2	ds
Biogas II		18.04.73	DS30	47° 38.3′N 09° 33.9′W	4106	3	ds
		19.04.73	DS32	47° 32.2′N 08° 05.3′W	2138	1	ds
Biogas III		25.08.73	DS38	47° 32.5′N 08° 35.8′W	2138	5	ds
		27.08.73	DS42	47° 32.1′N 09° 35.6′W	4104	1	ds
		27.08.73	DS44	47° 33.2′N 09° 42.0′W	3992	1	ds
		27.08.73	DS45	47° 33.9′N 09° 38.4′W	4260	1	ds
Biogas IV		18.02.74	DS51	44° 11.3′N 04° 15.4′W	2430	3	ds
		18.02.74	DS52	44° 06.3′N 04° 22.4′W	2006	2	ds
		22.02.74	DS55	47° 34.9′N 09° 40.9′W	4125	1	ds

Material

ship/cruise	no.	date	sta.	position	depth/m	number	gear
Biogas V		21.06.74	DS70	44° 08.8′N 04° 17.4′W	2150	2	ds
Biogas VI		23.10.74	DS76	47° 34.8′N 09° 33.3′W	4228	1	ds
		25.10.74	DS78	46° 31.2′N 10° 23.8′W	4706	2	ds
		30.10.74	DS85	44° 23.2′N 04° 50.8′W	4462	1	ds
		31.10.74	DS86	44° 04.8′N 04° 18.7′W	1950	4	ds
		01.11.64	DS87	44° 05.2′N 04° 19.4′W	1913	1	ds
		01.11.74	DS88	44° 05.2′N 04° 15.7′W	1894	3	ds
Sarsia		09.76	7627	43° 47.1′N 03° 46.0′W	1925–1990	2	ag
Shackelton		28.04.77	X/3	48° 28.1′N 10° 20.6′W	1500–1900	6	ad
		20.04.77	7/3	47° 47.5′N 08° 11.5′W	1620–1700	2	ag
Sierra Leone Basin							
Atlantis II	31	05.02.67	142	10° 30.0′N 17° 51.5′W	1624–1796	16	es
		06.02.67	145	10° 36.0′N 17° 49.0′W	2185	2	es
		06.02.67	147	10° 38.0′N 17° 52.0′W	2934	10	es
Angola Basin							
Atlantis II	42	23.05.68	203	08° 48.0′S 12° 52.0′E	527–542	3	es
Walda		06.71	DS10	18° 40.0′S 10° 56.3′E	1432	14	ds
		06.71	DS19	03° 48.0′S 09° 17.7′E	2243	1	ds
Cape Basin							
Atlantis II	42	16.05.68	187	22° 58.0′S 13° 01.0′E	626–631	3	ad
		16.05.68	188	23° 00.0′S 12° 58.0′E	619–622	14	es
Argentine Basin							
Atlantis II	60	11.03.71	236	36° 27.0′S 53° 31.0′W	497–518	1	es
		14.03.71	245	36° 55.7′S 53° 01.4′W	2707	1	es

Distribution

T. (*P.*) *equalis* is distributed off the coast of northeast America from Nova Scotia to Chesapeake Bay (Verrill & Bush 1898; Dall 1901) from west Greenland and the Norwegian coast (Ockelmann 1958), and Sweden (USNM) and in the North Sea, Fladen ground (McIntyre 1961).

The present material is from the North America Basin, West European Basin, Sierra Leone Basin, Angola Basin, Cape Basin and Argentine Basin. Depth range: 37–4734 m.

Shell description (figures 34, 35 and 37)

Shell small, thin, chalky white or semi-transparent, equivalve and moderately inflated, interior white, slightly glossy, covered by fine radial striae and concentric grooves, sculpture, fine concentric lines with growth stages at intervals, small patches of ferruginous deposit sometimes adhere to beaks and margins, pyriform, height exceeding length, (in early growth stages height and length equal); raised prosogyrous beaks, central or just anterior to midline; anterior and posterior margins slope steeply from beaks, anterior margin straight or sometimes slightly concave, joins evenly curved ventral margin dorsal to mid horizontal line, antero-dorsal margin frequently distorted where inhalent tube joins shell, postero-dorsal margin convex, indented by shallow primary and sub-marginal sulci, primary sulcus makes a characteristic vertical and slightly concave flattening of posterior shell margin, dorsal to this margin angulated, sub-marginal sulcus outlines sunken escutcheon, without projecting auricle; lunule indistinct, hinge plate edentulous, somewhat thickened and swollen below beak; ligament occupies broad, curved groove on face of hinge plate, slightly inset posteriorly, reaches about one third of distance to posterior margin, dorsal surface visible externally.

Specimens from sta. 207 measure (length × height × breadth) 4.15 × 4.35 × 2.7 mm; 2.33 × 2.40 × 1.50 mm;

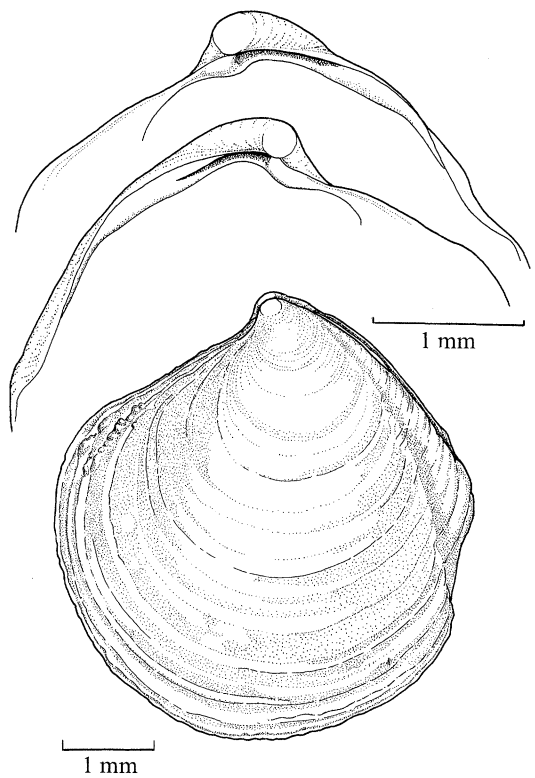

Figure 34. *Thyasira* (*Parathyasira*) *equalis*: hinge plate of right and left valves; specimen from *Atlantis II*, station D1 and lateral view of the shell from the left side; specimen from *Chain*, station 207.

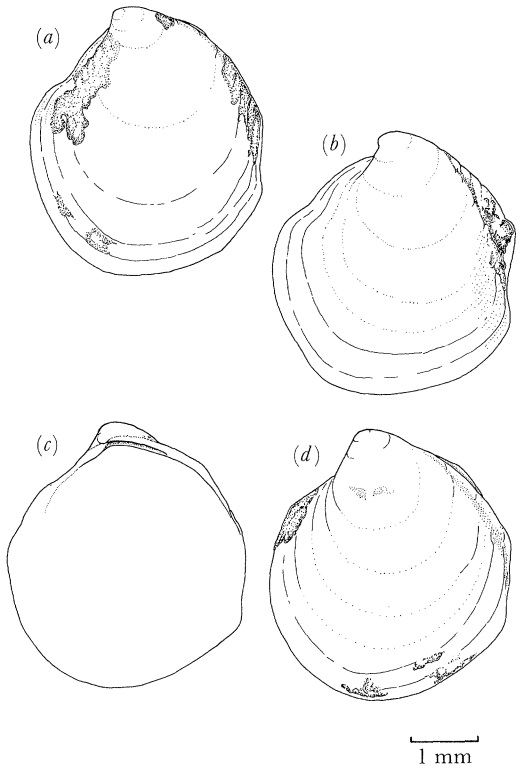

Figure 35. *Thyasira* (*Parathyasira*) *equalis*: shells from a number of stations to show variation in shape: (*a*) Bay of Biscay; (*b*) *Chain*, station 105 and (*c*, *d*) from *Atlantis II*, station 73.

2.70 × 2.90 × 1.70 mm; 2.25 × 2.35 × 1.40 mm; 1.40 × 1.40 x 0.85 mm.

The characteristic features which distinguish *T.* (*P.*) *equalis* are the centrally positioned beaks with the anterior and posterior limits of shell at the same horizontal level and the vertical flattening of the posterior shell margin. The shell is not oblique as it is in *T.* (*T.*) *obsoleta* and the sunken escutcheon lacks a projecting auricle. The hinge plate is broad and is lacking distinct tubercles.

There is a great range of variation in shape in this species (figure 35). So called typical specimens only occur in samples from off northeast America in 466–811 m (figure 34). Specimens from deeper water are usually thinner shelled and more angular in shape. Some specimens from the Bay of Biscay have smaller, but strongly curved beaks. The variations are not such as to constitute good species of their own and are regarded as phenotypic variations.

Internal morphology (figure 36)

The anterior adductor muscle is about twice the size of the posterior, both are narrow and dorso-ventrally elongate. The posterior muscle lies slightly below the horizontal level of the anterior.

The mantle edge is fused posteriorly at a single point. Fusion involves the inner muscular part of the inner mantle fold. There is extensive adhesion of the opposing inner folds anteriorly a short distance ventral to the anterior adductor thus forming an anterior inhalent aperture, and postero-ventrally, forming an aperture ventral to the exhalent aperture. These adhesions relate to the water flow into the mantle cavity and the rejection of pseudofaeces from the posterior end of the main rejection tract. The glandular area beneath the anterior adductor is somewhat less well developed in *T.* (*P.*) *equalis* than in *T.* (*T.*) *trisinuata*.

Inner and outer demibranchs are present the outer demibranch being about half the size of the inner. The ascending lamella of the inner demibranch is approximately three quarters the length of the descending lamella and the descending lamella of the outer demibranch is about half the length of the ascending lamella. The ventral margin of the gill covers from a half to two thirds of the lateral body pouches. Each demibranch has 40 filaments in a specimen 3 mm in length. Except dorsally the ascending and descending lamellae of each demibranch are united by interlamellar junctions. Fine interfilamentar cross-connections also occur at intervals. Transverse sections show that abfrontal tissue is not extensive as in *T.* (*T.*) *trisinuata*. A marginal food groove is present at the ventral margin of both demibranchs.

The labial palps are triangular in shape, small in size and situated at the distal end of short proximal oral grooves. The inner palp surface bears up to five very distinct ridges and grooves. The palps are generally heavily ciliated. Although the foot is vermiform, it is shorter than that of *T.* (*T.*) *trisinuata*. The tip is distinguished from the stem by its heavier ciliation and reduced longitudinal musculature, but it is not divided into two parts as in other large species of *Thyasira*.

The course of the gut and arrangement of the digestive ducts is similar to previous descriptions. There is a small, triangular dorsal hood antero-dorsally. The stomach wall is not thickened except beneath the gastric shield and the latter is small and narrow covering the dorsal and the left lateral wall of the stomach. There is a small gastric tooth. The ventral wall of the stomach is thin with a broad ventral rejection tract that leads to the midgut. The walls of

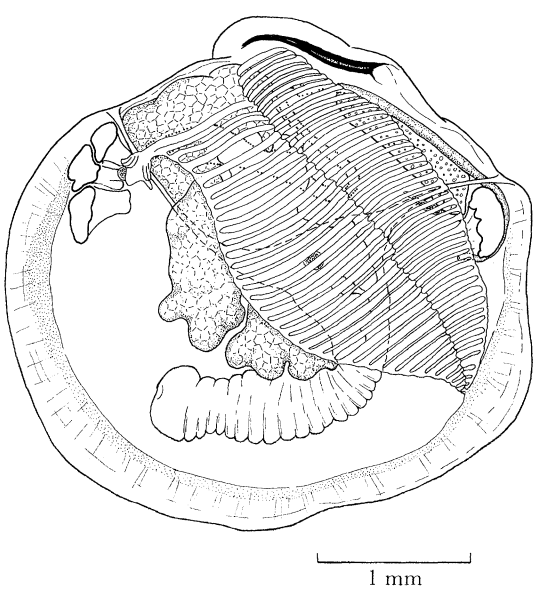

Figure 36. *Thyasira* (*Parathyasira*) *equalis*: internal morphology as seen from the left side; specimen from *Chain*, station 207. (For identification of parts see figures 2 and 3.)

the style sac are formed by regular columnar epithelial cells bearing short brush-like cilia. The midgut is combined with the style sac. The hindgut has a small ventral typhlosole where it traverses the ventricle. Dorsal to the kidney, the hindgut is dilated with stored but unrecognizable remains.

The lateral pouches are slightly compressed. The lobes of the pouches are formed by deep divisions at their perimeter. Some of the dorsal-most lobes cover the area of body wall adjacent to the stomach and style sac.

Sexes are separate, the gonad is located in the inner part of the pouches. The gonadial ducts pass to each side of the style sac to open ventral to the kidney.

The arrangement of both the kidney and pericardium is similar to that of *T.* (*T.*) *trisinuata*, except that instead of being laterally compressed and dorsoventrally elongated, the paired halves are oval in section. The vacuolated kidney cells contain rounded concretions which in section are concentrally layered and measure up to 14 μm in diameter.

The nervous system is similar to that of other species described here.

Thyasira* (*Parathyasira*) *subequatoria (new species)

Type locality: Argentine Basin: 38° 16.9′S, 51° 56.1′W; 4382–4402 m.
Type specimen: Holotype BM(NH) No. 1990038.

Material

ship/cruise	no.	date	sta.	position	depth/m	number	gear
Angola Basin							
Atlantis II	42	19.05.68	195	14° 40.0′S 09° 54.0′E	3797	8	es
			–	10° 29.0′S 09° 03.0′E			
Argentine Basin							
Atlantis II	60	13.03.71	242	38° 16.9′S 51° 56.1′W	4382–4402	11	es
		24.03.71	256	37° 40.9′S 52° 19.3′W	3906–3917	14	es

Distribution

Known only from the abyssal depths in the Angola and the Argentine Basins. Depth range: 3797–4405 m.

Shell description (figure 38)

Shell thin, fragile, white or semi-transparent, moderately inflated, equivalve, pyriform, height exceeds length, sculpture fine, ill-defined growth lines, interior glossy white, muscle scars indistinct; small beaks positioned central or slightly posterior to midline, turned inward and anterior; antero-dorsal and postero-dorsal margins slope steeply from beaks, ventral margin evenly rounded, posterior margin somewhat angulate at point where postero-dorsal margin joins ventral margin, posterior margin indented by primary and sub-marginal sulci; primary sulcus shallow; sub-marginal sulcus outlines escutcheon, no posterior auricle present; beaks and margins frequently encrusted by ferruginous depost; hinge plate of right valve swollen ventral to and immediately anterior to beak, ventral to beak small projection fits declivity in left hinge plate; ligment short, broad, in curved groove, more sunken posteriorly, extends one third of the distance to the posterior margin.

Specimens measured as follows: (length × height × breadth) 3.3 × 3.5 × 2.3 mm; 2.9 × 3.1 × 2.0 mm; 1.3 × 1.5 × 0.9 mm; (sta. 242).

The shell is similar to *T.* (*P.*) *equalis* but more rounded and the ligament is shorter and broader than that in the latter species. The principal distinguishing

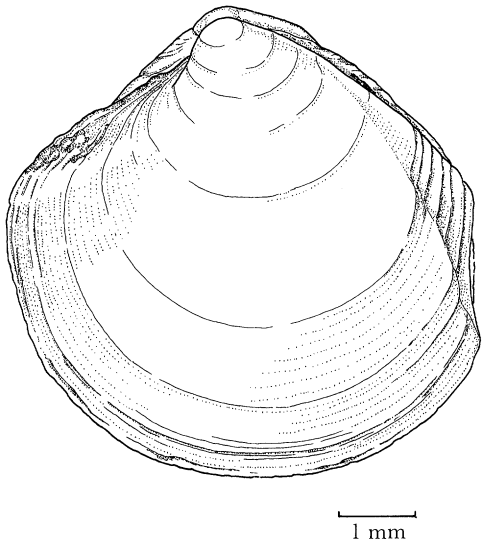

Figure 37. *Thyasira* (*Parathyasira*) *equalis*: shell viewed from the left side; USNM No. 69002 from Sweden.

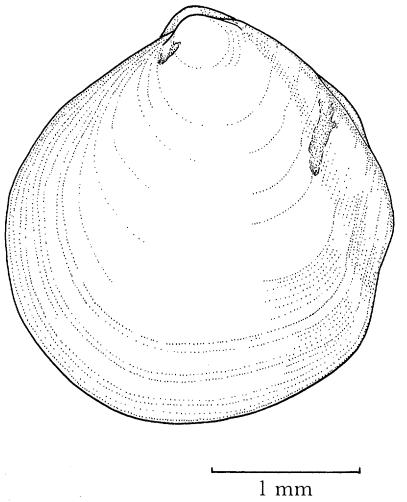

Figure 38. *Thyasira* (*Parathyasira*) *subequatoria*: shell viewed from the left side; specimen from *Atlantis II*, station 242.

character is the presence of a *single* demibranch in each gill of *T.* (*P.*) *subequatoria*.

This is not a juvenile condition for single demibranchs are found in mature specimens, but is probably related to the depth at which this species occurs. Reduction in the size of gills is common in abyssal bivalve species. The shape of the shell and the lobed lateral body pouches (figure 39) distinguish it from species of the subgenus *Axinulus* (p. 521).

Internal morphology (*figure* 39)

Apart from the single demibranch the internal morphology is similar to that of *T.* (*P.*) *equalis*. The anterior adductor muscle is elongate, lying parallel to the mantle edge, and about twice the length of the oval posterior muscle. There is a single point of mantle fusion to form the posterior inhalent aperture and adhesion of the inner folds is as in *T.* (*P.*) *equalis*. The inner mantle fold is particularly well developed and projects into the mantle cavity. The middle fold forms a short, double sensory frill. The outer fold has a large blood space.

A number of small peripheral lobes of the lateral body pouches are present and are similar to, but less deeply divided than those of *T.* (*P.*) *equalis*.

T. (*P.*) *subequatoria* one of the few truly abyssal thyasirid bivalves is the only recorded species of the subgenus *Parathyasira* with the gill consisting of the inner demibranch alone. In the largest specimens there are 30 filaments. The ascending lamella is about half the length of the descending lamella. Ventrally the filaments are joined by interlamellar junctions. Abfrontal tissue is not well developed but skeletal rods and axial musculature are well developed. Large specimens were mature and sexes separate.

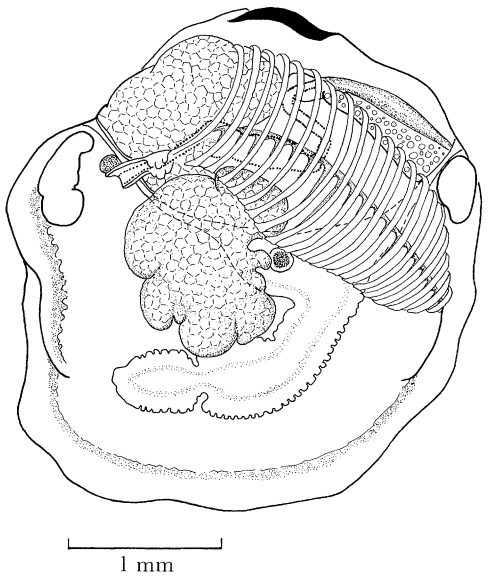

Figure 39. *Thyasira* (*Parathyasira*) *subequatoria*: internal morphology as viewed from the left side; specimen from *Atlantis II*, station 242. (For identification of parts see figures 2 and 3.)

Thyasira* (*Parathyasira*) *biscayensis (new species)

Type locality: Bay of Biscay: 46° 29.5′N, 10° 29.5′W; 4720 m.

Type specimen: Holotype: MNHN, Paris.

Material

ship/cruise	date	sta.	position	depth/m	number	gear
West European Basin						
Biogas VI	27.10.74	DS80	46° 29.5′N 10° 29.5′W	4720	2	ds

Distribution

This species was only taken from the type locality in the Bay of Biscay at a depth of 4720 m.

Shell description (figure 40)

Shell relatively large, white or semi-transparent, moderately inflated, obliquely curved, ventral margin prolonged anteriorly, sculpture irregular indented concentric growth lines, interior white, with faint radial striae, muscle scars clearly visible; small, strongly prosogyrous beaks in midline or just anterior to midline; anterior dorsal margin descends steeply and almost straight from beaks then forms smooth curved shallow anterior arc, postero-dorsal margin forms smooth curve meeting posterior margin in obtuse angle; primary sulcus very shallow, forms small indentation at shell margin, sub-marginal sulcus outlines sunken escutcheon; hinge plate of right valve particularly broad, slightly thickened ventral to beaks but lacking distinct tubercles or pseudo-cardinal swelling; ligament in long groove at margin hinge plate, extends about half the distance to posterior shell margin.

The larger specimen measures (length × height × breadth) 8.2 × 9.1 × 5.8 mm, the smaller specimen is 7.3 × 8.1 × 4.2 mm.

The oblique and prolonged antero-ventral shell margin and very reduced shell sulci are characteristic of the species. While the shell of this species is rather similar to large species of *Axinulus*, the internal morphology differs significantly.

Internal morphology (figures 41 and 42)

Because of the small number of specimens only the gross morphology was studied.

The anterior adductor is long and narrow, twice the length of the posterior muscle and is curved parallel to the mantle edge. The posterior adductor muscle is also elongate but oval in shape. There is a single permanent point of mantle fusion to form a posterior exhalent aperture and opposing inner mantle folds adhere to each other along the ventral margin. The glandular area adjacent to the anterior adductor muscle is not particularly extensive in this species.

The gill is large with some 150 filaments in each demibranch. The outer demibranch is approximately

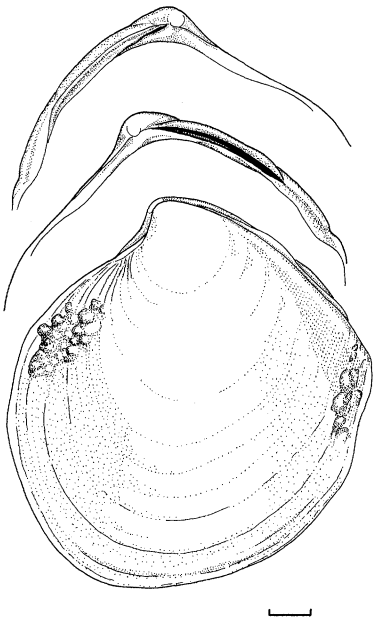

Figure 40. *Thyasira* (*Parathyasira*) *biscayensis*: hinge plate of right and left valves and lateral view of the shell from the left side; specimen from *Biogas VI*, station DS 80.

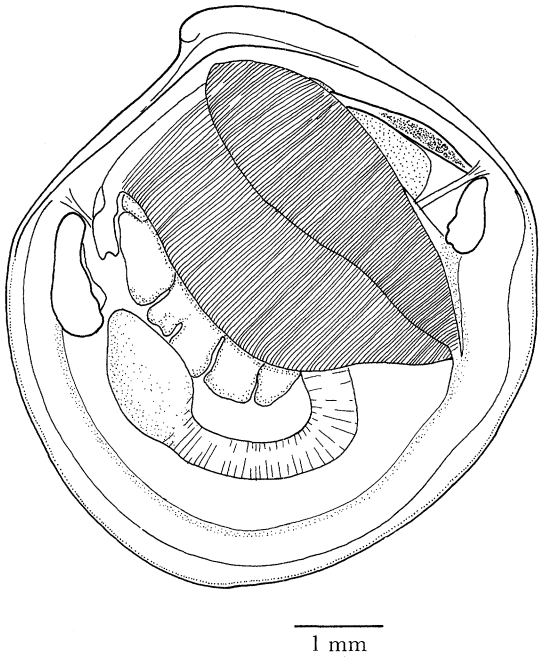

Figure 41. *Thyasira* (*Parathyasira*) *biscayensis*: internal morphology as viewed from the left side; specimen from *Biogas VI*, station DS 80. (For identification of parts see figures 2 and 3.)

one third as large as the inner demibranch. Interfilamentar junctions occur at broadly spaced intervals but offset to form a zig-zag pattern on the gill. The labial palps are small, and bear 6–8 distinct ridges and grooves on their inner surfaces. The foot is relatively short and the rounded base lacks a heel. The tip is differentiated from the stem only in being spear shaped. It is not divided into two distinct parts. The anterior and posterior pedal retractor muscles are well developed.

The stomach and gut (figure 42) are similar to those

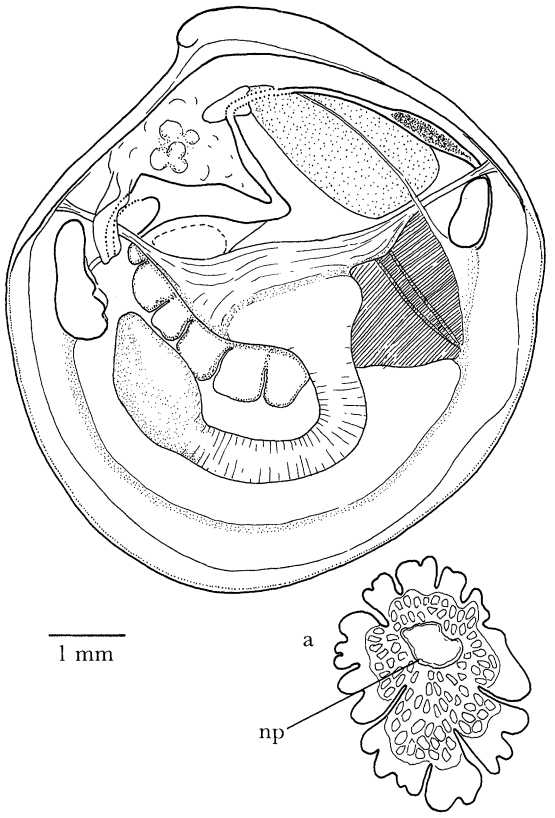

Figure 42. *Thyasira* (*Parathyasira*) *biscayensis*: internal morphology viewed from the left side with the gill and the lateral body pouch, removed; specimen from *Biogas VI*, station DS 80. (*a*) Inner face of lateral body pouch of same specimen. (For identification of parts see figures 2 and 3.)

of other species of the subgenus *Parathyasira*. The lateral body pouches are arborescent, bearing numerous small projecting lobes. The inner side of each pouch contains the gonad and developing ova were present in the whole mount specimen examined (figure 42*a*).

Thyasira* (*Parathyasira*) *atlantica (new species)

Type locality: North America Basin, 37° 26.0′N, 63° 59.5′W; 4862 m.
Type specimen: Holotype BM(NH) No. 1990039.

Distribution

Known only from the North America Basin at abyssal depths.

Shell description (figure 43)

Shell small, elongate, oval, thin, chalky in texture, small patches of ferruginous deposit adhere posteriorly, equivalve, sculpture concentric lines indented towards ventral margin, interior white, indistinct muscle scars, viewed from inside antero-dorsal margin is reflected outwards; small prosogyrous beaks on or just posterior to midline; antero-dorsal and postero-dorsal margins long, almost straight, descend at a small angle from beaks, anterior and ventral margins in continuous curve, posterior margins almost vertical; primary sulcus shallow, forms posterior undulation; postero-dorsally a small submarginal sulcus outlines escutcheon; lunule indistinct; hinge plates endentulous, slightly

Material

ship/cruise	no.	date	sta.	position	depth/m	number	gear
North America Basin							
Atlantis II	24	22.10.66	124	37° 26.0′N 63° 59.5′W	4862	2	es

swollen ventral to beaks; ligament inset, curved, reaches one third of distance to posterior margin.

Specimens from *Atlantis II* sta. 124 measure (height × length × breadth) 2.15 × 2.70 × 1.20 mm and 1.87 × 2.30 × 1.10 mm. Prodissoconch prominent, 155 μm in diameter.

The shape of the shell and the internal morphology suggest a close relationship to *T.* (*P.*) *tortuosa* (figure 45). *T.* (*P.*) *atlantica* differs from the latter species in having a convex rather than upturned antero-dorsal margin, a more prominent primary sulcus and a chalky texture to the shell. In further contrast the shell of *T.* (*P.*) *tortuosa* is inequivalve, smoother, more lustrous and the ligament is extremely short and wedge-shaped.

Internal morphology (figure 44)

The internal morphology was studied from a single whole mount. Only two specimens were obtained.

The glandular area on each side of the anterior inhalent region occupies a smaller area than that in *T.* (*P.*) *tortuosa* while the anterior adductor muscle is more strongly angular at the dorsal margin. The gills are reduced in size as compared with the condition in *T.* (*P.*) *tortuosa* (figure 46). Thus, the outer demibranch is reflected above the gill axis and lacks a descending lamella. There are about 30 filaments in each demibranch. The inner surface of the labial palps bears three or four ridges that are more distinct than those of *T.* (*P.*) *tortuosa*.

Although the foot appears to be short (figure 44), this is largely the result of contraction following fixation. The heel is less well developed and the tip of the foot relatively undifferentiated as compared to *T.* (*P.*) *tortuosa*. The perimeter of the lateral body pouch is divided into short bilobed branches similar to those of small specimens of *T.* (*P.*) *tortuosa*. The specimen examined was a mature male.

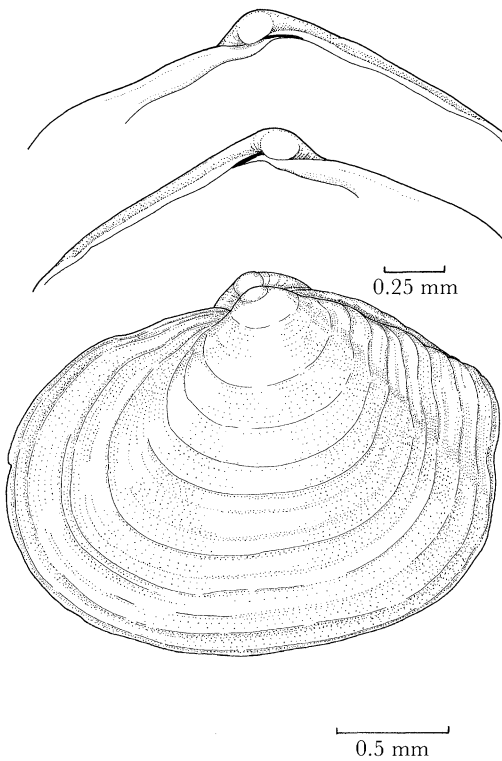

Figure 43. *Thyasira* (*Parathyasira*) *atlantica*: hinge plate of right and left valves and lateral view of the shell from the left side; specimen from *Atlantis II*, station 124.

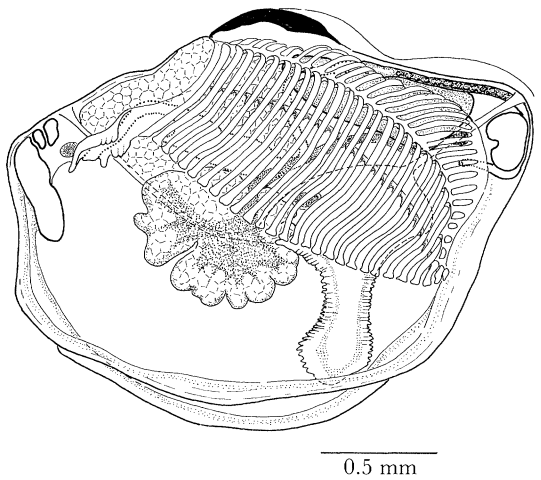

Figure 44. *Thyasira* (*Parathyasira*) *atlantica*: internal morphology as viewed from the left side of a wholemount; specimen from *Atlantis II*, station 124. (For identification of parts see figures 2 and 3.)

Thasira* (*Parathyasira*) *tortuosa (Jeffreys, 1881)

Type: *Axinus tortuosus* Jeffreys, 1881.
Type locality: Not designated by Jeffreys.
Type material: Paralectotypes include one shell from Cape Espichel, off Portugal (BM(NH) 85.11.5.1181) and USNM No. 683898 (Warén 1980). A lectotype, selected by K. W. Ockelmann, USNM No. 61904.

Synonymy

Axinus tortuosus (nomen nudum) Jeffreys (1880, p. 316; preliminary list).
Axinus tortuosus Jeffreys (1881, p. 702; fig. 6, pl. 61).
Cryptodon tortuosus Verrill (1884, p. 226).
Axinus tortuosus Locard (1886, p. 256).
Axinus tortuosus Kobelt (1888, p. 376).
Cryptodon tortuosus Dall (1889, p. 50).
Axinus tortuosus Locard (1898, p. 290–291).
Axinus tortuosus Locard (1899, p. 149).
Thyasira (*Axinulus*) *tortuosa* Lamy (1920, p. 311–312).
Thyasira tortuosa Johnson (1934, p. 39).
Thyasira tortuosa Clarke (1962, p. 65).

Axinulus tortuosus Soot-Ryen (1966, p. 27–28, fig. 15, figs 12–13, pl. 1).
Axinulus tortuosus Nordsieck (1969, p. 80, fig. 48.12, pl. 13).
Thyasira tortuosa Knudsen (1970, p. 171, 176).

Historical

Although *T.* (*P.*) *tortuosa* was first mentioned in a preliminary list of molluscs from the 'Travailleur' Expedition by Jeffreys (1880) the species was not described by him until 1881. Since then *T.* (*P.*) *tortuosa* has been widely recorded and well illustrated in the literature. It is not easily mistaken for any other species although Locard (1898) describes *T. tortuosa* var. *alta* from three stations off Northern Spain which is said to be less transversely curved than the type.

A number of authors (Lamy 1920; Soot-Ryen 1966; Nordsieck 1969) have placed *T.* (*P.*) *tortuosa* within the subgenus *Axinulus*. This is probably due to its unusually elongate shell and shallow primary sulcus. We include it in the subgenus *Parathyasira* because the internal morphology although showing certain specialized features, is not dissimilar to that of *T.* (*P.*) *equalis*.

619–2359 m. Knudsen (1970) reports that *T.* (*P.*) *tortuosa* occurs at temperatures of 2.4–10 °C.

Shell description (figure 45)

Shell thin, smooth, white, rather compressed and inequivalve, longitudinally oval, anteriorly elongate, very slightly twisted to right, sculpture consists of fine concentric grooves at irregular intervals, covered by a thin, glossy, almost lustrous, periostracum, occasional patches of ferruginous material adhere to shell margin, interior smooth with faint radial striae, muscle scars indistinct; small prosogyrous beaks posterior to mid-line, not raised; antero-dorsal margin somewhat concave, occasionally almost straight, upturned where it joins antero-ventral margin, postero-dorsal margin descends at a small angle, posterior margin broadly concave and angulate at dorsal and ventral limits; primary sulcus very faint, sub-marginal sulcus small, outlines sunken escutcheon; lunule indistinct, hinge plates narrow, swollen anterior to beaks, tubercles not present; ligament wedge-shaped and characteristic in shape within deep marginal groove reaching less than one quarter of distance to posterior margin, barely visible externally.

Material

ship/cruise	no.	date	sta.	position	depth/m	number	gear
North America Basin							
Atlantis II	12	25.08.64	73	39° 46.5′N 70° 43.3′W	1330–1470	4	es
Chain	50	06.07.65	87	39° 48.7′N 70° 40.8′W	1102	33	es
Chain	58	04.05.66	103	39° 43.6′N 70° 37.4′W	2022	4	es
Chain	88	21.02.69	207	39° 51.3′N 70° 54.3′W	805–811	20	es
			—	39° 51.0′N 70° 56.4′W			
		22.02.69	209	39° 47.6′N 70° 49.9′W	1501–1693	12	es
			—	39° 46.0′N 70° 51.5′W			
West European Basin							
Thalassa		25.10.73	Z426	48° 28.2′N 09° 39.1′W	860	6	pbs
		20.10.73	Z457	48° 38.2′N 09° 52.6′W	800	1	gbs
Sarsia		.09.76	7610	43° 44.7′N 03° 48.6′W	1100–1100	2	ag
		.09.76	7627	43° 47.1′N 03° 46.0′W	1925–19	5	ag
Cape Verde Basin							
Atlantis II	31	05.02.67	142	10° 30.0′N 17° 51.5′W	1624–1796	2	es
		06.02.67	145	10° 30.0′N 17° 49.0′W	2185	3	es
Angola Basin							
Walda		06.71	DS10	18° 40.0′S 10° 56.3′E	1432	68	ds
Cape Basin							
Atlantis II	42	16.05.68	187	22° 58.0′S 13° 01.0′E	626–631	7	ad
		16.05.68	188	23° 00.0′S 12° 58.0′E	619–622	4	es
		16.05.68	189	23° 00.0′S 12° 45.0′E	1007–1014	20	es
		17.05.68	190	23° 05.0′S 12° 45.0′E	974	2	es
		17.05.68	191	23° 05.0′S 12° 31.5′E	1546–1559	40	es
		17.05.68	192	23° 02.0′S 12° 19.0′E	2117–2159	1	es

Distribution

T. (*P.*) *tortuosa* has been previously recorded from the North America Basin from Nova Scotia to North Carolina (Soot-Ryen 1966; Verrill 1884) and the West European Basin from west Portugal and the Bay of Biscay (Jeffreys 1881; Locard 1898, and the material listed here). Other material here examined is from the Cape Verde, Angola and Cape Basins. Depth range:

The largest specimen from *Atlantis II* sta. 187 measures (length × height × breadth) 3.2 × 2.8 × 1.4 mm. Prodissoconch prominent, 133 μm in diameter. Small concentric wrinkles are present on prodissoconch in SEM photographs.

The shell is characteristically elongate and, as noted by Jeffreys (1881), when viewed from above the anterior end is turned slightly to the right. The oblique

Figure 45. *Thyasira* (*Parathyasira*) *tortuosa*: hinge plate of left and right valves, specimen from *Atlantis II*, station 187; specimen from Travailleur expedition, USNM No. 61983.

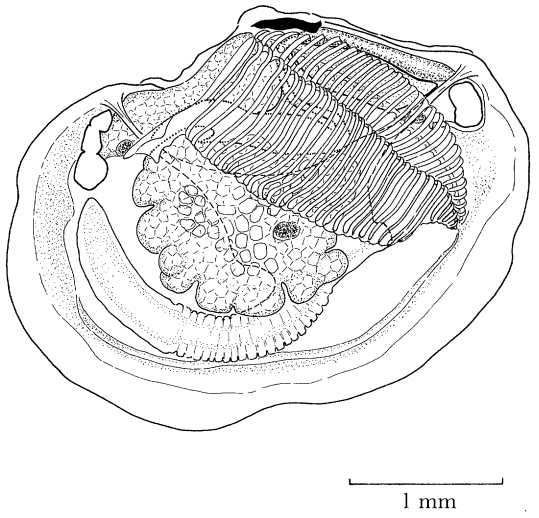

Figure 46. *Thyasira* (*Parathyasira*) *tortuosa*: internal morphology as seen from the left side of a wholemount; specimen from *Walda*, station DS 10. (For identification of parts see figures 2 and 3.)

wedge-shaped ligament is also distinctive. The presence of both inner and outer demibranchs, distinguishes it from species of the subgenera *Mendicula* and *Axinulus*.

Internal morphology (figure 46)

The anterior adductor muscle is narrow, elongate and curved parallel to the mantle edge. It is approximately twice as large as the small oval posterior adductor muscle. There is a single point of tissue fusion at the posterior mantle edge forming a posterior exhalent aperture. Fusion involves the inner mantle fold. The inner lobe is also modified postero-ventrally to form a pair of muscular flattened pads. These are thought to adhere together in the living animal thus forming an aperture ventral to the exhalent aperture.

The mantle edge consists of three typical mantle folds. The inner is the largest forming a broad platform with a rejection tract at its margin. Pallial muscles are well developed as are concentric muscles associated with the rejection tract. The outer and middle folds are small.

There are two demibranchs to each gill. The outer demibranch is short and about half the size of the inner. The lamellae of the inner demibranch are similar in length but the descending lamella of the outer demibranch is approximately half the length of the ascending lamella. As in all thyasirid species examined, the tips of the filaments of the ascending lamellae of the left and right inner demibranchs posterior to the foot are joined together by an interlocking short brush-like cilia. Horizontal interfilamentar junctions occur at intervals and interlamellar junctions are also present. Abfrontal tissue is not developed. The cells bearing the lateral cilia are very large and are remote from the frontal surface. A large blood space is present in the centre of the filament.

The labial palps are minute, triangular extensions of the elongate proximal oral groove. They bear a few indistinct ridges on their inner surface.

The contracted foot has a small heel which is deeply grooved in the sagittal plane, The epithelium within the groove lacks cilia whereas the region on each side of the groove is ciliated. There is no byssus gland. Anterior and posteror pedal retractor muscles are unusually broad. The posterior retractor muscles are approximately twice as broad as the anterior pair. The stem of the foot is separated from the heel by a small constriction. The stem itself is long, narrow and vermiform; when contracted it lies in an even curve in the mantle cavity. The tip is differentiated externally only in being smoother and more heavily ciliated than the stem.

The course of the gut is similar to that of other thyasirids. The oesophagus enters the stomach close to the dorsal hood. The stomach is small and for the most part thick-walled, with a well developed dorsal gastric shield (figure 47). The ventral wall is thin, with a rejection tract originating close to the digestive apertures which leads to the midgut. The latter is combined with the style sac. The hindgut is frequently grossly distended with ingested remains which consist of fine particulate matter and small spicules. The configuration of the digestive diverticula is similar to that of to other species of *Parathyasira*.

The lateral body pouches have a charactristic shape. They are laterally compressed and the outer surface is formed of many small rounded lobes. These are not deeply divided. The dorsal section of the digestive diverticula occupies an area dorsal to the oesophagus and stomach and consists of a single pair of unbranched tubules. The diverticula are lined with tubule cells. Small deeply staining cells occur at the blind ends of tubules. Some tubule cells contain dark pigmented oval inclusions with a granular texture. Similar

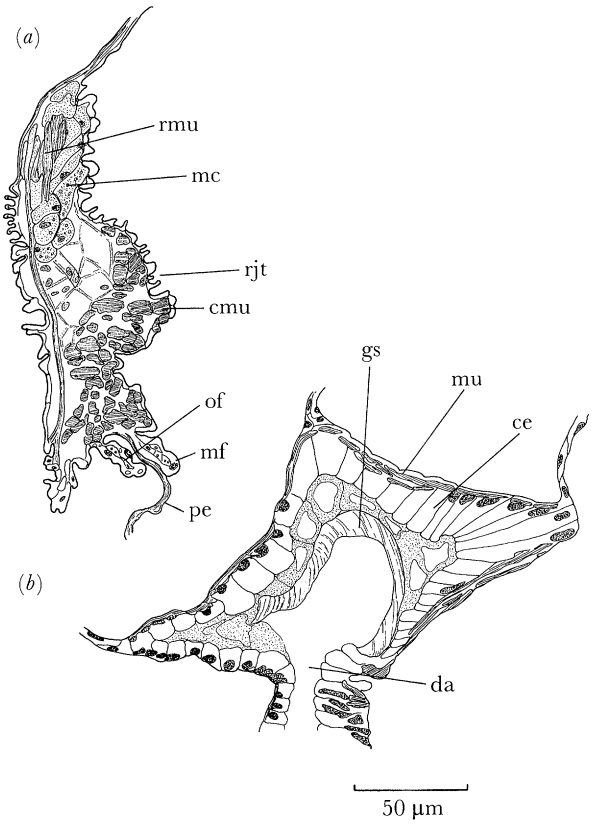

Figure 47. *Thyasira* (*Parathyasira*) *tortuosa*: (*a*) transverse section through the mid-ventral mantle edge; and (*b*) transverse section through the anterior part of the stomach showing the entrance to the the digestive diverticula of the left side; specimen from *Walda*, station DS 10. (List of abbreviations: see p. 561.)

inclusions were seen in *T.* (*P.*) *subcircularis* and *T.* (*M.*) *transversa* from the same Station.

The gonads are to the inner side of the lateral pouches. When mature they extend around the margins of each lobe. Sexes are separate. The kidneys are large, oval and sac-like. Except anteriorly they are contiguous with a central longitudinal dividing wall. Anteriorly they are extended by anterior arms, one on each side of the pericardium. Ducts similar to those described for *T.* (*T.*) *trisinuata* and *T.* (*T.*) *excavata verrilli* extend along the length of the kidney. They are closely applied to the central dividing wall with postero-ventral funnel-like extensions. Some kidney cells contain small concretions, similar to those seen in other species. The nervous system is similar to that of other species.

Thyasira* (*Parathyasira*) *subovata subovata (Jeffreys, 1881)

Type: *Axinus subovatus* Jeffreys, 1881.
Type locality: Not designated by Jeffreys.
Type specimen: Syntype from the *Porcupine* expedition, USNM No. 61895 gives no station number, but another syntype BM(NH) No. 85.11.5.395 destroyed on some earlier occasion, was from 56° 24.0′N, 11°40′W; 2524 m.

Synonymy
Axinus subovatus (nomen nudum) Jeffreys (1880, p. 316).
Axinus subovatus Jeffreys (1881, p. 704, fig. 8, pl. 61).
? *Cryptodon subovatus* Verrill (1882, p. 570).
Cryptodon subovatus Verrill (1884, p. 279).
Axinus subovatus Locard (1886, p. 257).
Axinus subovatus Kobelt (1888, p. 376).
Axinus subovatus Locard (1898, p. 295).
Axinus subovatus Locard (1899, p. 150).
Thyasira (*Axinulus*) *subovata* Lamy (1920, p. 312).
Thyasira (*Axinulus*) *subovata* Johnson (1934, p. 40).
Axinulus subovata Madsen (1949, p. 9, 53, fig. 6).
Axinulus subovatus Ockelmann (1958, p. 197).
Thyasira subovata Clarke (1962, p. 65).
Axinulus subovata Nordsieck (1969, p. 80. fig. 48.13, pl. 13).
Thyasira subovata Knudsen (1970, p. 170).

Historical

This species is described and figured by Jeffreys (1881) from the 1869 cruise of the *Porcupine*, although confuses the anterior with the posterior shell margin. The species was named earlier (Jeffreys 1880) in a preliminary list of molluscs from the *Travailleur* expedition to the Bay of Biscay.

Distribution

Recorded from Iceland, 216 m (Madsen 1949); queried from New England 914 m (Verrill 1882); North Atlantic between the Hebrides and Faroes, 988 m (Jeffreys 1881); west of Ireland, 1492 and 2524 m (Jeffreys 1881); north of Spain, 2651 m and west of Sahara, 2376 m (Locard 1898).

The present material is from the Cape Verde Basin, 1624–2185 m; the Angola Basin, 1432 m; the Cape Basin, 1007–2154 m; and the Argentine Basin, 2440–3917 m. Additional records have been obtained from the Bay of Biscay and the west of Ireland. A single specimen from the North Atlantic Basin suggests that Verrill's earlier record from New England may well be correct. Thus, *T.* (*P.*) *subovata* s.s. is widely distributed in both the South Atlantic and the North Atlantic as far north as Iceland where it is found at relatively shallow depths. Depth range: 216–3917 m.

Shell description (figures 48 and 53)

Shell small, smooth, triangulate, thin, white or semi-transparent, covered by fine concentric lines, sometimes small patches of ferruginous deposit occur, moderately inflated, equivalve, inequilateral with flattened wedge-shaped posterior angulation; beaks prosogyrous, small rounded, positioned just posterior to midline; antero-dorsal margin raised, before descending in smooth curve and becoming more flattened ventrally, postero-dorsal margin long gentle curve to posterior margin; primary sulcus very faint corresponding to posterior angulation of shell, sub-marginal sulcus sharply defined, outlines a lanceolate escutcheon extending along entire postero-dorsal margin; lunule extended but poorly defined; hinge plates thickened with small swelling ventral and anterior to

Material

ship/cruise	no.	date	sta.	position	depth/m	number	gear
North America Basin							
Chain	50	06.07.65	87	39° 48.7′N 70° 40.8′W	1102	1	es
West European Basin (Rockall Trough)							
Challenger	6/73	02.07.73	6	55° 03.0′N 12° 29.0′W	2900	91	es
		04.07.73	10	56° 37.0′N 11° 04.0′W	2540	336	es
Challenger	14B	17.11.75	55	40° 40.0′N 12° 16.0′W	2878	20	es
West European Basin (Bay of Biscay)							
Biogas II		19.04.73	DS31	47° 32.5′N 09° 04.2′W	2813	1	ds
Biogas III		26.08.73	DS41	47° 28.3′N 09° 07.2′W	3548	1	ds
Biogas IV		24.02.74	DS59	47° 31.7′N 09° 06.2′W	2790	2	ds
		26.02.74	DS64	47° 29.2′N 08° 30.7′W	2156	1	ds
		21.10.74	DS74	47° 33.0′N 09° 07.8′W	2777	1	ds
Cape Verde Basin							
Atlantis II	31	05.02.67	142	10° 30.0′N 17° 51.5′W	1624–1796	34	es
		06.02.67	145	10° 36.0′N 17° 49.0′W	2185	13	es
Angola Basin							
Walda		06.71	DS10	18° 40.0′S 10° 56.3′E	1432	28	ds
Cape Basin							
Atlantis II	42	16.05.68	189	23° 00.0′S 12° 45.0′E	1007–1014	40	es
		17.05.68	191	23° 05.0′S 12° 31.5′E	1546–1559	29	es
		17.05.68	192	23° 02.0′S 12° 19.0′E	2117–2154	5	es
Argentine Basin							
Atlantis II	60	24.03.71	256	37° 40.9′S 52° 19.3′W	3906–3917	18	es
		27.03.71	262	36° 05.2′S 52° 17.9′W	2440–2480	1	es

beak; ligament in groove at margin of hinge plate, reaches one third of the distance to posterior margin, just visible externally.

Four specimens from *Challenger* sta. 10 measure (length × height × breadth) 1.98 × 1.65 × 1.23 mm; 1.80 × 1.55 × 1.10 mm; 1.75 × 1.55 × 0.93 mm; 0.90 × 0.78 × 0.50 mm. Prodissoconch 128 μm in diameter.

The shell is characteristically elongate. No other species has this somewhat triangular shape with a wedge-shaped posterior angulation and sharply defined sunken escutcheon. Subspecific differences exist and a new subspecies is described in the next section and illustrated in figure 53.

Internal morphology (figures 49 and 50)

The anterior adductor muscle is small, the posterior muscle minute, oval and attached close to the postero-

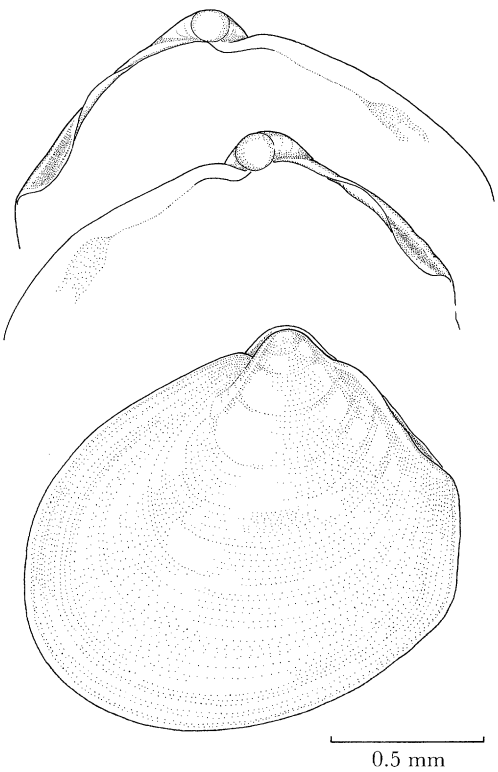

Figure 48. *Thyasira* (*Parathyasira*) *subovata subovata*: hinge plate of left and right valves and lateral view of the shell from the left side; specimens from *Challenger*, station 55.

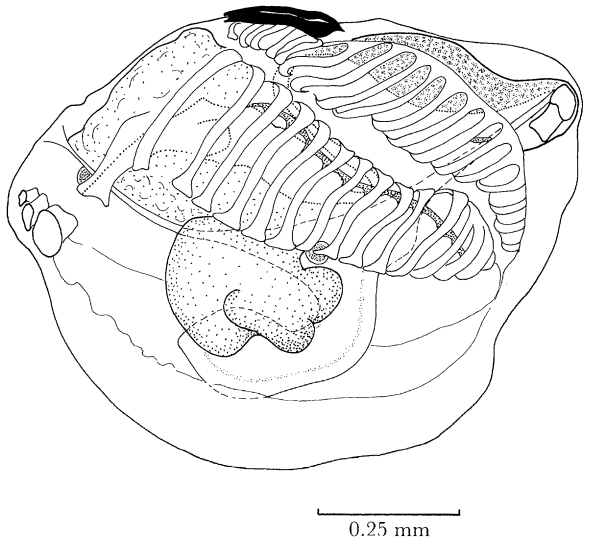

Figure 49. *Thyasira* (*Parathyasira*) *subovata subovata*: internal morphology as seen from the left side of a wholemount, specimen from *Challenger*, station 6. (For identification of parts see figures 2 and 3.)

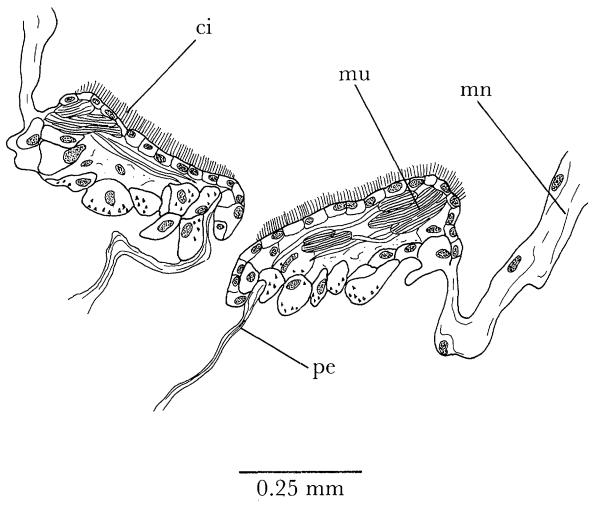

Figure 50. *Thyasira* (*Parathyasira*) *subovata subovata*: transverse section through the postero-ventral mantle edge to show 'ciliated' pads of the inner mantle fold; specimen from *Challenger*, station 10.

dorsal margin. The anterior adductor is elongate and more than twice as large as the posterior.

The mantle edge is fused at a single point posteriorly, there is also ciliary attachment of the opposing inner folds for a short distance ventral to the posterior inhalent aperture (figure 50). Adhesion as distinct from interlocking of cilia of the opposing inner folds also occurs along the ventral mantle edge. A rejection tract is present on a narrow shelf formed by the muscular inner mantle fold. Pallial musculature is well-developed. The epithelial cells of the middle fold contains refractory inclusions and include eosinophilic cells. A deep periostracal groove separates the middle from the outer fold. The outer fold contains a blood space. Below the anterior adductor muscle the inner fold is expanded to form a glandular region. This area is also highly muscularized with both pallial and longitudinal muscles. The middle fold is particularly well developed anteriorly.

The gill has both inner and outer demibranchs the former covering the dorsal-most part of the lateral body pouches. In lateral view the inner and outer demibranchs are approximately equal in size. The outer demibranch is almost completely reflected above the gill axis and thus the outer gill face is essentially reduced to a single combined lamella. Each demibranch has up to 22 filaments. There are two horizontal interfilamentar junctions in the inner demibranch, but none in the outer demibranch. The inner demibranchs have interlamellar junctions along most the length of the opposing filaments. The gill filaments are short in cross section, with little abfrontal tissue.

The labial palps are minute triangular extensions of the proximal oral groove and bear about three indistinct ridges. The oral groove itself is extremely long.

The foot is relatively short and compact, with a small sagittally grooved heel. The tip is more densely ciliated than the stem, but not differentiated in any other respect. Transverse sections show that the pedal retractors form the inner layer of longitudinal muscles in the foot. The fibres of the inner layer are broader than those of the outer longitudinal layer. Central transverse fibres and a narrow outer layer of circular muscle are also present.

The digestive system is similar to that of other thyasirids. The gastric shield is well developed with a small tooth on the left side. The hindgut is frequently grossly swollen with food remains which are arranged in polygonally shaped masses. Although *T.* (*P.*) *subovata* is small the lateral body pouches have two or three ventral lobes and a number of smaller undulations along the dorsal edge. The number is dependent on the size of the animal.

The gonad is located in a broad layer to the inner side of the pouches. Sexes are separate. A total of 136 eggs were found in the ovaries of one large specimen (distributed 73 in the left pouch and 63 in the right). Mature eggs measured 66 × 48 μm.

The kidney is large and sac-like. The epithelial cells contain large plate-like concretions of the type noted in other species. From transverse sections the cerebral and pleural parts of the combined ganglia can be identified. The pedal ganglion is large and almost completely fused to form a single body. The visceral ganglia are joined by a posterior connective.

Thyasira* (*Parathyasira*) *subovata minuta (new subspecies)

Type locality: Angola Basin; 08° 48.0′S, 12° 52.0′E; 527–542 m.
Type specimen: Holotype BM(NH) No. 1990040.

Taxonomy

Although clearly closely related to each other the morphologies of *T.* (*P.*) *subovata* s.s. and *T.* (*P.*) *subovata minuta* are sufficiently different to make a taxonomic separation. Differences lie in the shell shape and the hinge plate. *T.* (*P.*) *subovata minuta* is without the posterior wedge-shaped angulation that is characteristic of *T.* (*P.*) *subovata subovata*. Other shell differences are described below. There is little or no difference in their internal morphologies. *T.* (*P.*) *subovata minuta* occurs in the Cape Basin, although a lesser depths than *T.* (*P.*) *subovata* s.s.

Distribution

Only recorded from off Angola and Namibia in 439–631 m.

Shell description (figures 51 and 53)

Shell thin, white or semi-transparent, inflated, equivalve, inequilateral, broadly ovate with posterior end drawn out as mid-posterior angulation, smooth, covered by fine concentric striae, small amounts of ferruginous deposit adhere to umbones and posterior margin, interior with minute radial striae, muscle scars indistinct; small beaks turned inwards and slightly anterior, central or just posterior to midline; antero-dorsal margin slightly convex (sometimes straight) descending at gentle angle, postero-dorsal margin descends in even curve to mid-posterior angle; primary sulcus faint, corresponding to slight postero-ventral

Material

ship/cruise	no.	date	sta.	position	depth/m	number	gear
Cape Basin							
Atlantis II	42	16.05.68	185	22° 56.0′S 13° 02.0′E	458–463	3	ad
		16.05.68	186	22° 57.0′S 13° 05.0′E	439–481	4	es
		16.05.68	187	22° 58.0′S 13° 01.0′E	626–631	32	ad
		16.05.68	188	23° 00.0′S 12° 58.0′E	619–622	23	es
		16.05.68	203	08° 48.0′S 12° 52.0′E	527–542	86	es

flattening of shell margin, submarginal sulcus sharp defines escutcheon; lunule extensive, ill defined; hinge plate of right valve somewhat swollen ventral and anterior to beak; left hinge plate narrow and not thickened; ligament in shallow groove reaching one third of distance to posterior margin.

Four specimens from *Atlantis II*, sta. 203 measure (length × height × breadth): 1.65 × 1.55 × 1.12 mm, 1.50 × 1.40 × 1.00 mm, 1.39 × 1.24 × 0.77 mm, 1.12 × 0.94 × 0.65 mm. A particularly large specimen from *Atlantis II*, sta. 186 measures 1.54 × 2.21 × 1.81 mm.

Features which distinguish this subspecies (figures 53*c–d*) include an ovate rather than a triangular inflated shell. Although the posterior angulation is distinct, it is not wedge-shaped. The antero-dorsal margin is shorter and the beaks are more central in position than in *T.* (*P.*) *subovata subovata*. The hinge plate of the left valve is more swollen ventral and anterior to the beaks. As in *T.* (*P.*) *subovata subovata* (figure 48) the escutcheon is extensive and sharply defined. This latter feature distinguishes both subspecies from *T.* (*T.*) *succisa* (figure 24).

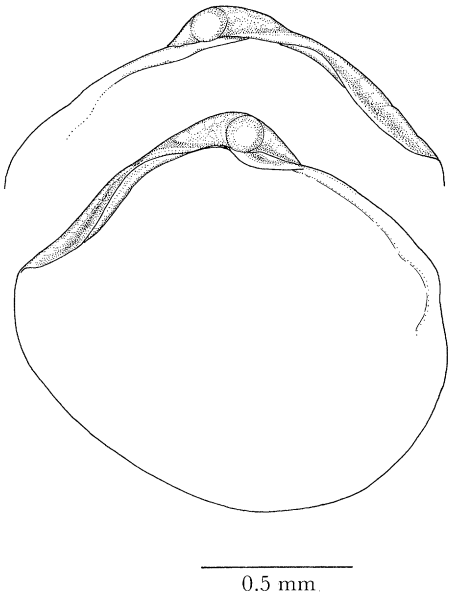

Figure 51. *Thyasira* (*Parathyasira*) *subovata minuta*: hinge plate of the left valve and internal view of the right valve; specimen from *Atlantis II*, station 203.

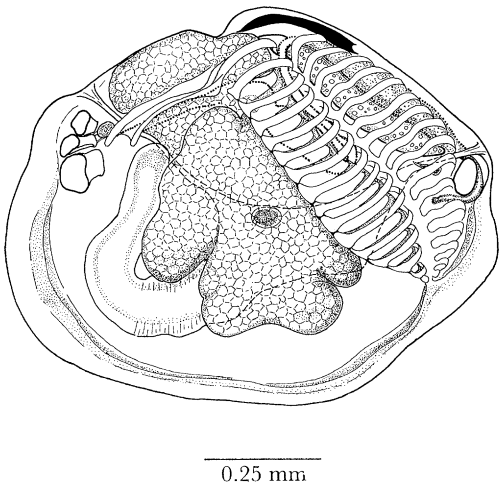

Figure 52. *Thyasira* (*Parathyasira*) *subovata minuta*: internal morphology as seen from the left side of a wholemount; specimen from *Atlantis II*, station 203. (For identification of parts see figures 2 and 3.)

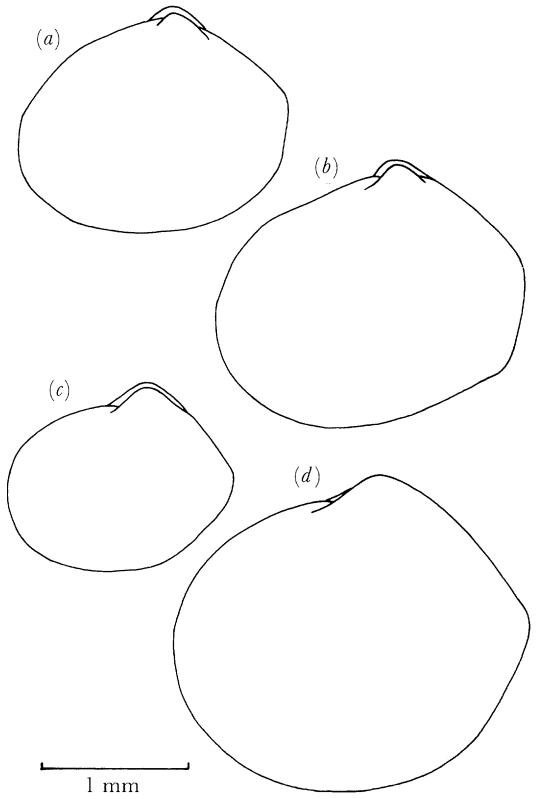

Figure 53. *Thyasira* (*Parathyasira*) *subovata subovata* and *T.* (*P.*) *subovata minuta*: lateral views of shells from various stations to show variations in outline: (*a*) *T.* (*P.*) *subovata subovata*, *Challenger*, station 10; (*b*) *T.* (*P.*) *subovata subovata*, *Atlantis II*, station 256; (*c*) *T.* (*P.*) *subovata minuta*, *Atlantis II*, station 203 and (*d*) *T.* (*P.*) *subovata minuta*, *Atlantis II*, station 186.

Internal morphology (figure 52)

The internal morphology is similar in all respects to that of *T.* (*P.*) *subovata subovata*; no differences were seen in sectioned material.

Of the species of *Parathyasira* described here that which most closely relates to the type species is *T.* (*P.*) *subcircularis*. It resembles *T.* (*P.*) *resupina* (figure 31*b*) in having what for thyasirids is an unusual feature namely shell ornamentation consisting of radial rows of minute spines. No other species included in the subgenus possess this feature.

Although the subgenus *Parathyasira*, unlike (*Thyasira*), appears to consist of a relatively diverse assemblage of shell morphologies, nevertheless, all have a number of morphological features in common. Typically the shell is equilateral with the beaks positioned approximately on the mid-line. Anterior and posterior margins descend at an almost equal angle and for an equal distance from the beaks. Although radial shell sulci are present they are neither sharp nor deep as they are in larger species of the subgenus *Thyasira* (e.g. figure 6). The submarginal sulcus outlines a deeply incised escutcheon but usually a projecting auricle at the shell margin is lacking. The sunken escutcheon is particularly distinctive in *T.* (*P.*) *subovata* (figure 48) and distinguishes it from apparently similar small species of the subgenus *Mendicula* (p. 534). The hinge plate is generally much broader ventral to the beaks than it is in *Thyasira* sg. It is also smooth and generally devoid of tooth-like tubercles of any prominence.

The ligaments of *T.* (*P.*) *desiderata* and *T.* (*P.*) *equalis* are long, narrow and positioned at the margin of the hinge plate. In contrast the ligament of *T.* (*P.*) *tortuosa* is deeply inset and is short and wedge shaped. *T.* (*P.*) *tortuosa* also differs in that the shell is elongate, inequivalve and flexed slightly to the right. This possibly reflects a horizontal position in life as it does in genera such as *Tellina*.

Despite these differences members of the subgenus *Parathyasira* also possess a number of common characteristic internal morphological features. For instance, the gill is extensive. Outer demibranchs are larger than are found in species of *Thyasira* of similar size. *T.* (*P.*) *subequatoria* is exceptional in that the outer demibranch is lost. This presents an additional problem in defining the subgenus, particularly so as all other species with single demibranchs have been placed in the subgenera *Leptaxinus*, *Axinulus*, or *Mendicula*. The lobes of the lateral body pouches in *T.* (*P.*) *subequatoria* are also less marked than those of other *Parathyasira* species, yet, *T.* (*P.*) *subequatoria* has such obvious affinities both in shell and internal morphology with *T.* (*P.*) *equalis* that it is difficult to do other than include it in this subgenus. *T.* (*P.*) *subequatoria* is found at a great depths and it is likely that the reduction of the gill may simply relate to this (Allen 1983). *T.* (*P.*) *subovata*, which has been previously regarded by a number of authors as a species of *Axinulus*, has a well developed gill with both demibranchs present and lateral body pouches that are lobed. These characters indicate a closer relationship with the subgenera *Thyasira* and *Parathyasira*.

Other anatomical characters peculiar to the subgenus include the form of the lobes of the lateral body pouches, the relatively undifferentiated tip to the foot and extensive adhesion of the mantle edges, more than is seen in the other subgenera of *Thyasira*. Adhesion was not observed in *Thyasira* sg. and elsewhere has only been observed in *Axinulus grandis*. In other respects *Parathyasira* differs very greatly from *A. grandis*.

Three of the species of *Parathyasira* described here are confined to depths below 3000 m, other species occur at slope depths down to 3000 m. *T.* (*P.*) *equalis* and *T.* (*P.*) *subovata* have been previously recorded from shallower shelf depths in arctic waters, a not uncommon occurrence in deep sea bivalves that range into Arctic waters. In general it appears that *Parathyasira* is present in deeper waters than is *Thyasira* sg.

Subgenus: ***LEPTAXINUS*** Verrill & Bush, 1898

Type species: *Leptaxinus minutus* Verrill & Bush, 1898.
Type locality: 40° 03.00′N, 70° 31.00′W; 183 m.

Original description (figure 54)

Originally described as a new genus, *Leptaxinus* was said to differ from *Thyasira* in having distinct lateral teeth and a more internal ligament (Verrill & Bush 1898). The genus was not defined separately from the type species. The species description is as follows: 'shell small, short-ovate, inequilateral, with the anterior end the longer, and rounded, and the posterior end tapered and angulated, with a slight plication. Hinge plate well developed, with a delicate lateral tooth on both sides of the beak in the right valve, and one posterior lateral

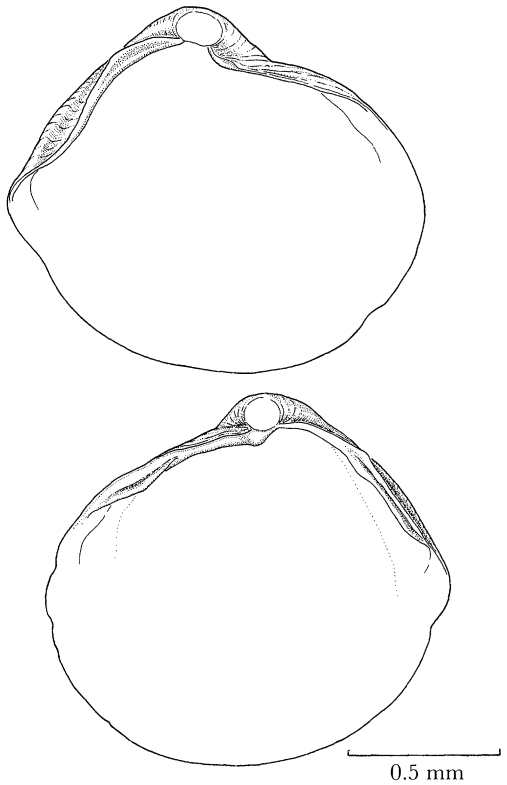

Figure 54. *Thyasira* (*Leptaxinus*) *minuta*: internal view of the left and right valves; holotype, USNM No. 45686, from 183 m off Martha's Vineyard.

tooth in the left valve; in both valves with the proximal end of the hinge plate enlarged and thickened near the beak, that of the left valve most developed and rising into a blunt tooth-like prominence. Ligament commencing under the beak and running back on the ventral side of the posterior hinge plate, so that for the greater part of its length it is internal'.

Leptaxinus as described above differs so little from *Thyasira* s.s. that we would *not* wish to separate them other than at subgeneric level (see below).

Thyasira* (*Leptaxinus*) *incrassata (Jeffreys, 1876)

Type species: *Axinus incrassatus* Jeffreys, 1876.
Type locality: North Atlantic, Valorous expedition, sta. 9, 1750 fms.
Type material: Lectotype, USNM No. 61969.

Synonymy

Axinus incrassatus Jeffreys (1876*b*, p. 492).
Axinus incrassatus Jeffreys (1881, p. 703; not fig. 7, pl. 61 which is *T.* (*T.*) *succisa*).
Axinus incrassatus Kobelt (1888, p. 376).
Axinus dubius Dautzenberg & Fischer (1897, p. 215–216; figs. 18–21, pl. 6).
Axinus incrassatus Posselt (1898, p. 77–78).
Leptaxinus incrassatus Dall (1901, p. 789).
Axinus incrassatus Lamy (1920, p. 315–316).
Thyasira dubia Dautzenberg (1927, p. 312; figs. 35–38, pl. 8).
Leptaxinus incrassatus Johnson (1934, p. 40).
Leptaxinus incrassatus Ockelmann (1958, p. 197),
Thyasira dubia Belloc (1962, p. 4).
Thyasira dubia Clarke (1962, p. 64).
Thyasira incrassata Clarke (1962, p. 64).
Thyasira dubia Harry (1969, p. 179).
Thyasira dubia Nordsieck (1969, p. 79–80; fig. 48.09, pl. 13).
Leptaxinus incrassatus Nordsieck (1969, p. 81 not fig. 48.21, pl. 13 which is *T.* (*T.*) *succisa*).
Axinus incrassatus Warén (1980, p. 44).

Historical

Jeffreys (1876*b*) original description of the species included a variety called *succisa* which was later recognized by Dall (1901) as a separate species. It is clear from Jeffreys (1876*b*, 1881) and an examination of museum specimens, that the specimen illustrated (Jeffreys 1881) as *Axinus incrassatus* is the variety *succisa* (figures 24–25) and that *T.* (*L.*) *incrassata* (figure 55) was not figured. As a result, subsequent authors have confused the two species. Dall (1901) placed *T.* (*L.*) *incrassata* in the genus *Leptaxinus*, basing his conclusion on similarities of the hinge plate. Following a comparison of museum specimens (cf. figures 55 and 56), *T.* (*L.*) *incrassata* is synonymized with *T.* (*L.*) *dubia* (Dautzenberg & Fischer 1897).

Distribution

T. (*L.*) *incrassata* has been recorded from Baffin Bay and the North Atlantic 2652–3264 m (Jeffreys 1876*a*, *b*, 1881); northwest Ireland, 2158 m (Jeffreys 1881); Azores 1850–1550 m (Dautzenberg & Fischer 1897) and the Bay of Biscay 2110–3548 m (material listed here). This species is therefore distributed both in the northeast and the north west Atlantic and as far south as the Azores. Depth range: 1550–3448 m.

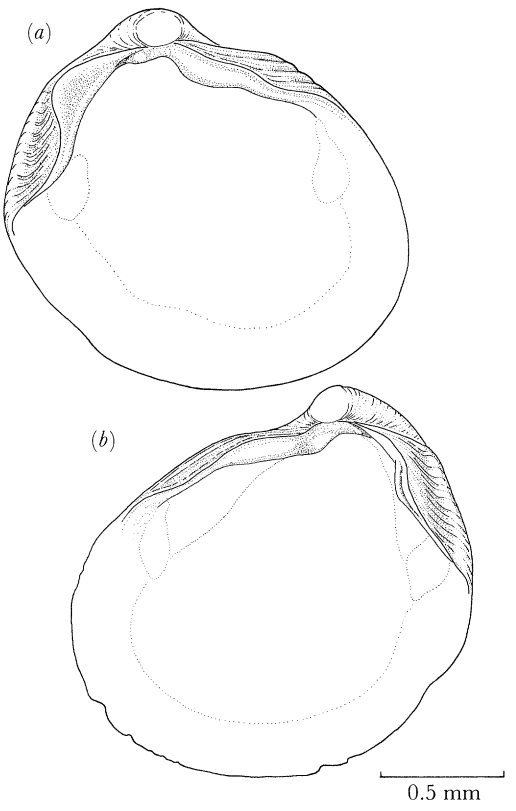

Figure 55. *Thyasira* (*Leptaxinus*) *incrassata*: (*a*) internal view of the left valve; specimen from *Biogas*, station DS 65; and (*b*) internal view of the right valve; specimen from *Valorous* expedition, 2652 m, USNM No. 62095.

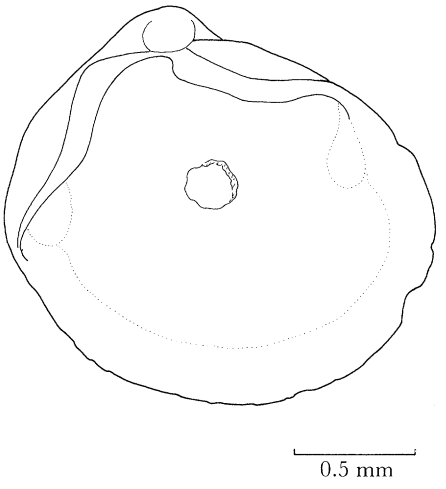

Figure 56. *Thyasira dubia*: interior view of the left valve of a specimen from the Azores; Musée Oceanographique de Monaco.

Shell description (figure 55)

Shell small, strong, sub-ovate, becoming oblique in older specimens, unusually thickened, inflated, semi-transparent, and straw-coloured, height normally exceeds length, although in large specimens the length and height are approximately equal, sculpture nu-

Material

ship/cruise	date	sta.	position	depth/m	number	gear
West European Basin						
Polygas	21.10.72	DS16	47° 36.1′N 08° 40.5′W	2325	2	ds
Biogas II	19.04.73	DS31	47° 32.5′N 09° 04.2′W	2813	3	ds
Biogas II	19.04.73	DS32	47° 32.2′N 08° 05.3′W	2138	5	ds
Biogas III	24.08.73	DS35	47° 34.4′N 08° 40.7′W	2226	5	ds
	24.08.73	DS36	47° 32.7′N 08° 36.5′W	2147	4	ds
	24.08.73	DS37	47° 31.8′N 08° 34.6′W	2110	3	ds
	26.08.73	DS41	47° 28.3′N 09° 07.2′W	3548	3	ds
Biogas IV	23.02.74	DS58	47° 34.1′N 09° 08.2′W	2775	11	ds
	24.02.74	DS59	47° 31.7′N 09° 06.2′W	2790	1	ds
	24.02.74	CV38	47° 30.9′N 08° 59.5′W	2695	2	cv
	25.02.74	DS61	47° 34.7′N 08° 38.8′W	2250	6	ds
	26.02.74	DS62	47° 32.8′N 08° 40.0′W	2175	4	ds
	26.02.74	DS63	47° 32.8′N 08° 35.0′W	2126	8	ds
	26.02.74	DS64	47° 39.2′N 08° 30.7′W	2256	2	ds
Biogas V	15.06.74	DS65	47° 36.1′N 08° 40.5′W	2360	73	ds
Biogas VI	20.10.74	CP09	47° 33.0′N 08° 44.1′W	2171	2	cp
	20.10.74	DS71	47° 34.3′N 08° 33.8′W	2194	2	ds
	20.10.74	DS72	47° 38.6′N 08° 36.1′W	2250	1	ds
	21.10.74	DS74	47° 33.0′N 09° 07.8′W	2777	3	ds

merous fine concentric lines, more prominent close to ventral margin, some larger specimens direction of growth of margin turns inwards producing ventral broadening of the shell; antero-dorsal margin almost horizontal anterior to beak, postero-dorsal margin descends at a steeper angle, angulated posteriorly, anteriorly smoothly curved; primary sulcus outlines deep postero-dorsal escutcheon; lunule an indented groove each side of antero-dorsal margin; hinge plate extremely thickened, right valve with rounded longitudinal swelling ventral and anterior to beak, elongate lateral projection postero-dorsally, socket receives lateral projection from left valve, hinge plate of left valve swollen to each side of central indentation ventral to beak, postero-dorsal lateral projection fits socket of right valve, but less well-defined than a true lateral tooth, formed from outer shell margin rather than inner hinge plate; interior glossy, muscle scars strongly impressed, radial scars produce lines marking path of muscle attachment during growth; ligament

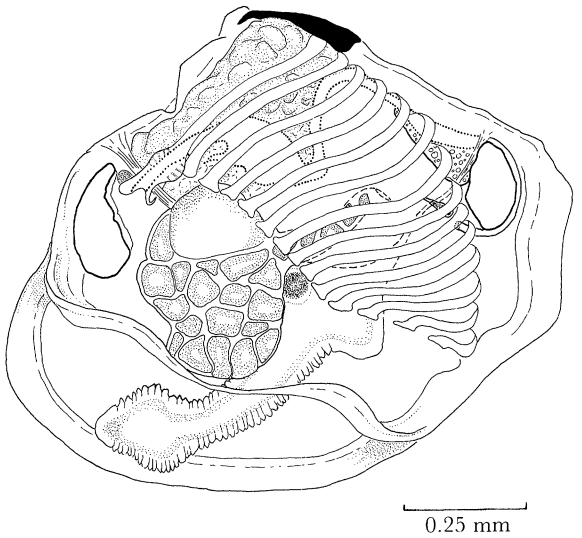

Figure 57. *Thyasira* (*Leptaxinus*) *incrassata*: internal morphology as seen from the left side of a wholemount, specimen from *Biogas*, station DS 58. (For identification of parts see figures 2 and 3.)

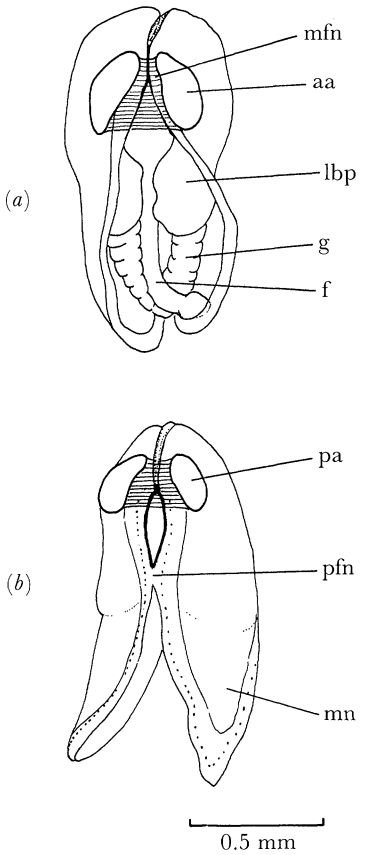

Figure 58. *Thyasira* (*Leptaxinus*) *incrassata*: (*a*) anterior view of the body with the shell removed; and (*b*) posterior view of the body to show extent of mantle fusion ventral to the posterior exhalent aperature; specimen from *Biogas*, station DS 58. (List of abbreviations: see p. 561.)

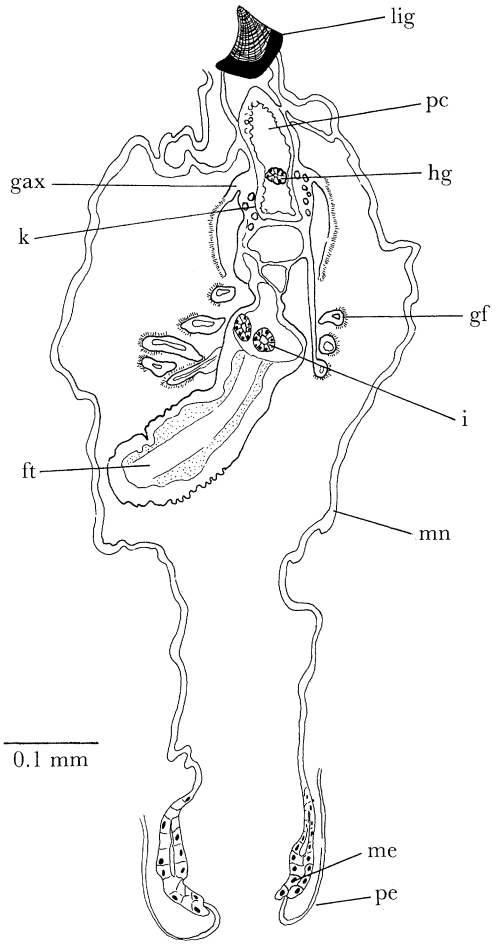

Figure 59. *Thyasira* (*Leptaxinus*) *incrassata*: median transverse section through the body; specimen from *Biogas*, station DS 58. (List of abbreviations: see p. 561.)

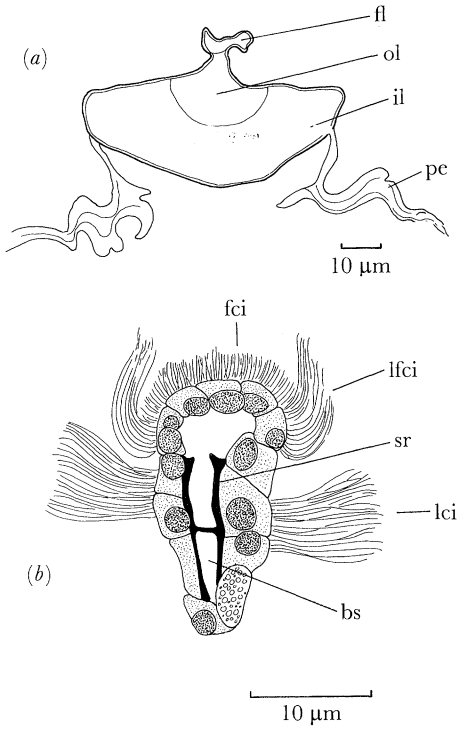

Figure 60. *Thyasira* (*Leptaxinus*) *incrassata*: (*a*) transverse section through the ligament; and (*b*) transverse section through a gill filament; specimen from *Biogas*, station DS 65. (List of abbreviations: see p. 561.)

inset, in short broad groove, reaching about one quarter of distance to posterior margin.

A large specimen from *Biogas* sta. DS65 measures (length × height × breadth) 1.90 × 1.95 × 1.25 mm. A smaller specimen from the same station is 1.30 × 1.20 × 0.75 mm. Prodissoconch 147 μm in length.

The extreme thickening of the hinge line, the position of the swellings on the hinge plate, the thick periostracum and strong muscle scars distinguish this species from *T.* (*L.*) *minuta* (figure 54).

Internal morphology (figures 57–62)

The anterior and posterior adductor muscles are oval, relatively large, and although anterior muscle is a little longer, and narrow dorsally, they have a similar cross sectional area.

Posterior mantle fusion is limited to a single point ventral to the posterior exhalent aperture and involves the inner mantle folds alone. No mantle adhesion occurs ventrally and sensory tentacles are not developed at any part of the mantle edge. Pallial musculature is particularly well developed adjacent to the posterior exhalent aperture. The inner muscular fold is also well developed with muscles extending into the middle and outer folds. It forms a small shelf along which the main rejection tract of the mantle runs. The middle and outer folds are small and separated by a broad and deep periostracal groove. The cells adjacent to the groove are filled with granules and are particularly noticeable and presumably relate to the unusually thick periostracum.

The gills comprise a single inner demibranch on each side and thus the gill axis is at the dorsal margin of the descending lamella. The ascending filaments are about half the length of the descending. Each demibranch contains 13–14 filaments. Interlamellar junctions occur along the ventral part of the gill and a small number of horizontal inter-filamentar connections also occur. There is little extension of the abfrontal surface of the filaments but a number of terminal cells with a granular cytoplasm occur. Frontal cilia are short and brush-like and adjacent to them are eulatero-frontal cilia. The lateral cilia are longer and slightly removed from the frontal surface (figure 60).

The labial palps are little more than small flaps at the outer limits of the proximal oral grooves. Each has four or five shallow ridges on the inner surface.

The foot of *T.* (*L.*) *incrassata* is characteristically short with a well developed, sagittally grooved heel and a swollen tip (figures 59 and 62). It has a spade-like appearance when retracted. The epithelium of stem, tip and each side of the heel is ciliated but there is no ciliation at the base of the foot dorsal to the heel. The anterior pedal retractor muscles which are less well developed than the posterior pair extend from the anterior base of the foot, passing to each side of the oesophagus to attach to the mantle or shell dorsal to the anterior adductor muscle. The posterior retractors pass between the anterior limits of the visceral ganglia before separating to attach above the posterior adductor. The course of the gut and form of the stomach is the same in this subgenus as in others already described (figure 61).

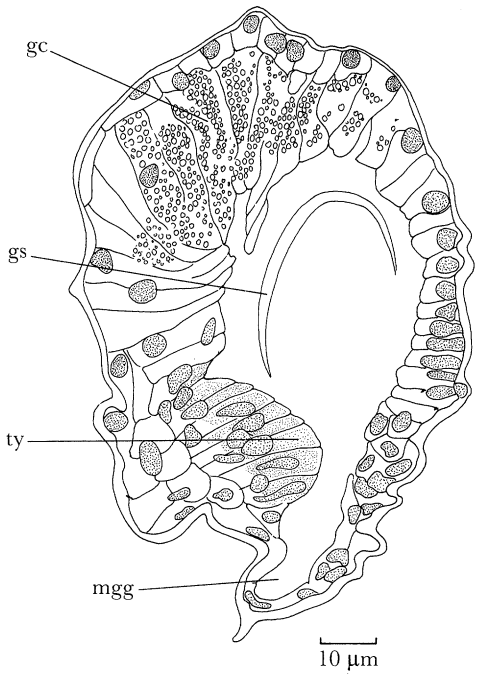

Figure 61. *Thyasira* (*Leptaxinus*) *incrassata*: tangential section through the posterior dorsal part of stomach and anterior to ventral limit of midgut. (List of abbreviations: see p. 561.)

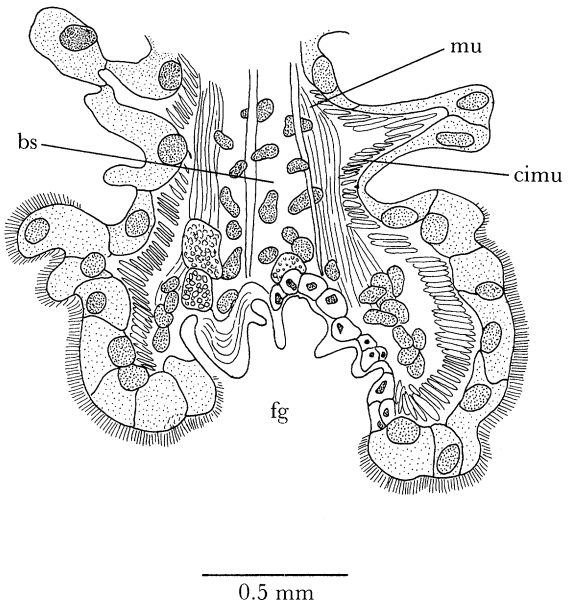

Figure 62. *Thyasira* (*Leptaxinus*) *incrassata*: transverse section through the heel of the foot showing the sagittal groove. (List of abbreviations: see p. 561.)

T. (*L.*) *incrassata* is distinguished from species of the subgenera *Thyasira* and *Parathyasira* in that the body pouches are small, rounded and never divided into lobes. Although small, the pouches are swollen and this may relate to the shell's globosity. The four tubules comprising the digestive diverticula are extensive, the tubule within each pouch is only slightly larger than each of the pair dorsal to the oesophagus and stomach.

The sexes are separate. The gonads are restricted to the postero-ventral part of the body pouches. The number of eggs is small, in the order of 14 (seven in each ovary) and measure 70 × 40 μm in preserved specimens.

The kidney occupies the dorsal area of the body between the posterior and adductor and the heart. Anteriorly the two halves are separated by the pericardium (figure 59), posteriorly they come together but remain divided by a central wall. The ducts are short and open mid-ventrally into the supra-branchial cavity. The kidney wall is membranous comprising a single layer of vacuolated epithelial cells some of which contain large plate-like inclusions, similar to those seen in other species.

The heart and pericardial cavity lie anterior to and between the anterior parts of the kidney. The hindgut passes through the pericardium (figure 59). The nervous system is similar to those described before.

Species of the subgenus *Leptaxinus* have a particularly well-developed hinge plate which bears a number of pseudo-cardinal and pseudo-lateral teeth. The form of the 'teeth' is important in distinguishing between species of *Leptaxinus* and *Mendicula*. *Mendicula* also has 'teeth' but these are in different positions (p. 534).

The right valve of *T.* (*L.*) *minutus* (Verrill & Bush) and of *T.* (*L.*) *incrassata* has a characteristic rounded raised tubercle ventral to the beak, a lateral antero-dorsal tooth-like projection and a postero-dorsal lateral tooth socket on the hinge plate. The postero-dorsal margin is reflected outwards alongside a well-defined escutcheon. The escutcheon is edged by a submarginal sulcus. *T.* (*L.*) *incrassatus* while similar to the type species (figure 54) has an unusually thickened shell and periostracum. As described by Verrill (1898), the ligament of *Leptaxinus* is deeply inset and lies along the ventral surface of the hinge plate. This is also characteristic of species of *Mendicula*.

T. (*L.*) *incrassata* is also characterized by a reduced gill (the outer demibranch being lost), small rounded, unlobed lateral body pouches, adductor muscles which differ little in size and a short, heeled foot.

T. (*L.*) *minutus* has only been recorded from a single locality of the northeast United States in relatively shallow water (183 m). *T.* (*L.*) *incrassata* has a wider distribution in the Northern Atlantic where it occurs between approximately 1500–3500 m.

Subgenus: ***AXINULUS*** Verrill & Bush, 1898

Type species: *Cryptodon* (*Axinulus*) *brevis*, Verrill & Bush, 1898.

Type locality: Off northeast United States between 40° 16.50′N, 67° 05.15′W, and 38° 22.00′N, 70° 17.30′W; 1799–3338 m.

Original description of the subgenus

Axinulus was described as a genus or subgenus by Verrill & Bush (1898) although these authors only used it in a subgeneric sense. They defined it as: '..... those species which agree with *Cryptodon* (*i.e. Thyasira*) in the character of the hinge and ligament, but lack the plications of the shell, and have, therefore a smaller posterior adductor muscle.'

The subgenus *Axinulus* here has been further restricted to include only those species with a small upright, ovate shell in which the height normally exceeds the length in adult specimens. We can find no relationship in the size of the posterior adductor muscle however the posterior angulation of the shell is less well defined than in the subgenera *Leptaxinus* and *Mendicula*. There is a single demibranch to each gill and large simple lateral body pouches are also characteristic. The foot is long and vermiform.

Thyasira* (*Axinulus*) *brevis (Verrill & Bush, 1898)

Type species: *Cryptodon* (*Axinulus*) *brevis* Verrill & Bush, 1898.

Type locality: Off the northeast United States between 40° 16.50′N, 67° 05.15′W, and 38° 22.00′N, 70° 17.30′W; 1799–3338 m.

Type specimen: Holotype USNM No. 159873.

Synonymy

Cryptodon (*Axinulus*) *brevis* Verrill & Bush (1898, p. 790; fig. 7–8, pl. 89).
Thyasira (*Axinulus*) *brevis* Dall (1901, p. 787).
Axinulus brevis Lamy (1920, p. 314).
Thyasira brevis Johnson (1934, p. 39).
Thyasira (*Axinulus*) *brevis* Clarke (1962, p. 65).
Thyasira brevis Knudsen (1970, p. 170, 176).

Although Dall (1901) considered *Crytodon obsoletus* Verrill & Bush, to be synonymous with the present species, they are now known to differ (Ockelmann, in Bowden & Heppell (1968)).

Material

ship/cruise	no.	date	sta.	position	depth/m	number	gear
North America Basin							
	264	21.05.61	HH3	38° 47.0′N 70° 08.0′W	2900	1	ad
	264	22.05.61	II2	38° 05.0′N 69° 36.0′W	3752	1	ad
	273	27.09.61	GH1	39° 25.5′N 70° 35.0′W	2500	3	ad
	273	03.10.61	GH3	39° 27.5′N 70° 33.5′W	2478	2	ad
	273	03.10.61	GH4	39° 29.0′N 70° 34.0′W	2469	3	ad
Atlantis II	12	21.08.64	64	38° 46.0′N 70° 06.0′W	2886	22	es
	12	23.08.64	70	36° 23.0′N 67° 58.0′W	4680	22	es
Chain	50	29.06.65	76	39° 38.3′N 67° 57.8′W	2862	5	es
	50	30.06.65	78	38° 00.8′N 69° 18.7′W	3828	3	es
	50	05.07.65	85	37° 59.2′N 69° 26.2′W	3834	4	es
	58	04.05.66	103	39° 43.6′N 70° 37.4′W	2022	1	es
West European Basin (Rockall Trough)							
Chain	106	21.08.72	323	50° 08.3′N 13° 53.7′W	3338–3356	12	es
			—	50° 08.3′N 13° 50.9′W			
Challenger		02.07.73	6	55° 03.0′N 12° 29.0′W	2900	37	es
		04.07.73	10	56° 37.0′N 11° 04.0′W	2540	12	es
West European Basin (Bay of Biscay)							
Polygas		21.10.72	DS15	47° 35.2′N 08° 40.1′W	2246	1	ds
		22.10.72	DS18	47° 32.2′N 08° 44.9′W	2138	1	ds
Polygas		26.10.72	DS23	46° 32.8′N 10° 21.0′W	4734	12	ds
		01.11.72	DS26	44° 08.2′N 04° 15.0′W	2076	26	ds
		02.11.72	DS28	44° 23.8′N 04° 47.5′W	4413	18	ds
Biogas II		18.04.73	DS30	47° 38.3′N 09° 33.9′W	4106	1	ds
Biogas III		24.08.73	DS35	47° 34.4′N 08° 40.7′W	2226	3	ds
		24.08.73	DS36	47° 32.7′N 08° 36.5′W	2147	8	ds
		24.08.73	DS37	47° 31.8′N 08° 34.6′W	2110	1	ds
		25.08.73	DS38	47° 32.5′N 08° 35.8′W	2138	5	ds
		29.08.73	DS46	46° 28.6′N 10° 23.0′W	4521	5	ds
		31.08.73	DS48	44° 29.0′N 04° 54.0′W	4203	2	ds
Biogas IV		18.02.74	DS51	44° 11.3′N 04° 15.4′W	2430	19	ds
		18.02.74	DS52	44° 06.3′N 04° 22.4′W	2006	78	ds
		19.02.74	DS53	44° 30.4′N 04° 56.3′W	4425	20	ds
		21.02.74	DS54	46° 31.1′N 10° 29.2′W	4659	2	ds
		22.02.74	DS55	47° 34.9′N 09° 40.9′W	4125	3	ds
		23.02.74	DS58	47° 34.1′N 09° 08.2′W	2775	4	ds
		25.02.74	DS61	47° 34.7′N 08° 38.8′W	2250	4	ds
		26.02.74	DS62	47° 32.8′N 08° 40.0′W	2175	4	ds
		26.02.74	DS63	47° 32.8′N 08° 35.0′W	2126	9	ds
Biogas V		26.02.74	DS64	47° 29.2′N 08° 30.7′W	2156	5	ds
		18.06.74	KR50	46° 33.5′N 10° 23.3′W	4750	2	kr
		21.06.74	DS69	44° 21.9′N 04° 52.4′W	4510	9	ds
Biogas VI		21.10.74	DS74	47° 33.0′N 09° 07.8′W	2777	1	ds
		29.10.74	DS82	44° 25.4′N 04° 52.8′W	4462	1	ds

Material

ship/cruise	no.	date	sta.	position	depth/m	number	gear
		30.10.74	DS85	44° 23.2′N 04° 50.8′W	4462	28	ds
		31.10.74	DS86	44° 04.8′N 04° 18.7′W	1950	146	ds
		01.11.74	DS87	44° 05.2′N 04° 19.4′W	1913	53	ds
Sierra Leone Basin							
Walda			DS22	00° 35.6′S 06° 49.4′E	3025	1	ds
			DS25	02° 19.8′N 07° 49.1′E	2470	1	ds
			DS27	03° 30.7′N 05° 31.8′E	1376	1	ds
			DS28	04° 21.2′N 04° 35.2′E	1261	3	ds
Angola Basin							
Atlantis II		21.05.68	198	10° 24.0′S 09° 09.0′E	4559–4566	8	es
			—	09° 47.0′S 10° 29.0′E			
		22.05.68	200	09° 43.5′S 10° 57.0′E	2644–2754	1	es
			—	09° 29.0′S 11° 34.0′E			
Walda		06.71	DS13	14° 21.5′S 09° 46.2′E	3985	1	ds
		06.71	DS15	12° 27.2′S 11° 01.5′E	3367	1	ds
		06.71	DS16	10° 31.0′S 11° 57.8′E	1787	2	ds
Cape Basin							
Atlantis II	42	17.05.68	194	22° 54.0′S 11° 55.0′E	2864	99	es
Walda		06.71	DS05	21° 45.0′S 11° 07.8′E	2992	3	ds
		06.71	DS06	22° 50.2′S 11° 57.9′E	2745	2	ds
Argentine Basin							
Atlantis II		14.03.71	245	36° 55.7′S 53° 01.4′W	2707	74	es
		27.03.71	262	36° 05.2′S 52° 17.9′W	2440–2480	267	es

Distribution

Previous records of this species are those of Verrill & Bush (1898) from the North America Basin. The present material is from the West European, Sierra Leone, Angola, Cape and Argentine Basins. Depth range: 1261–4750 m.

T. (*A.*) *brevis* is one of the commonest species in our samples and most records are from depths below 2000 m.

Note: depth ranges quoted by Dall (1901) and Clarke (1962) include the records of *T.* (*T.*) *obsoleta* (see p. 493).

Shell description (figures 63 and 68)

Shell small, variable in shape and thickness, higher than long, with an upright oval outline, white or semi-transparent, inflated, smooth and glossy when dry, sculpture of very fine concentric growth lines, small patches of ferruginous deposit adhere to anterior and posterior margins; beaks approximately central; antero-dorsal margin descends in steep convex curve to anteriorly prolonged ventral margin, postero-dorsal margin descends in steep curve, large specimens may have mid-posterior angulation in region of sulcus; primary sulcus faint, no more than radial undulation between umbo and postero-ventral margin, making small marginal indentation, submarginal sulcus faint; no sunken escutcheon; lunule ill defined; hinge plate with small swelling ventral to beak of right valve, slightly thickened; ligament long, evenly curved, anteriorly lying external to hinge plate, but becoming inset posteriorly.

A range of specimens from *Biogas* sta. DS86 measure (length × height × breadth) 2.70 × 3.19 × 2.25 mm; 2.40 × 2.70 × 1.72 mm; 2.06 × 2.25 × 1.50 mm; and 1.27 × 1.35 × 0.75 mm. Prodissoconch measures 135–175 μm.

T. (*A.*) *brevis* is distinguished by its smooth oval upright shape in which the anterior and posterior

Figure 63. *Thyasira* (*Axinulus*) *brevis*: hinge plate of the left and right valves and lateral view of the left valve; specimen from *Biogas*, station DS 86.

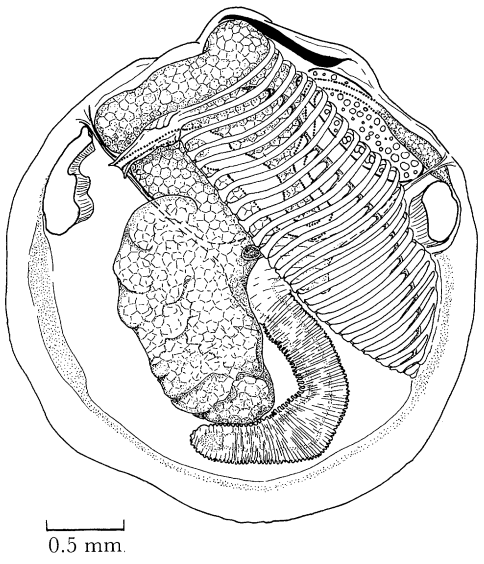

Figure 64. *Thyasira* (*Axinulus*) *brevis*: internal morphology as seen from the left side of a wholemount, specimen from *Biogas*, station DS 87. (For identification of parts see figures 2 and 3.)

margins descend from the beaks more steeply than those of *T.* (*A.*) *croulinensis*. Large specimens have a much stronger, whiter shell than that in the latter species.

Internal morphology (figures 64–67)

The anterior adductor is almost twice the length of the posterior adductor. Dorsally it is narrow and curved inwards while ventrally it is broad and rounded. The posterior muscle is oval but not greatly elongate. The mantle folds (figure 66) are considerably more pronounced than those of *T.* (*L.*) *incrassata*. There is a single posterior point of fusion to form the posterior exhalent aperture. This fusion involves the inner mantle fold, the bridge containing well developed muscle fibres. Postero-ventrally a second aperture ventral to the exhalent aperture is formed by opposing pads of heavily ciliated tissue (figure 65). The inner mantle fold, forms a projecting shelf along which lies the main rejection tract of the mantle. Radial and concentric muscles are well-developed in the inner fold. The middle and outer folds are divided by a deep periostracal groove; cells secreting periostracum are relatively few in number. The middle fold has a double sensory frill but, no sensory papillae are present. An extensive area of deeply staining gland cells is present ventral to the anterior adductor at the point where the inhalent tube joins the shell margin.

Each gill is composed of an inner demibranch with up to 29 gill filaments. The ventral margins of the gills do not cover the lateral body pouches. Each demibranch consists of both ascending and descending lamellae, the ascending lamella being slightly the shorter. The opposing filaments are joined by interlamellar junctions along most of their length. A small number of fine horizontal, muscular, interfilamentar junctions occur. A food groove is present at the ventral margin of the demibranchs. In transverse section the filaments are elongate, but have less abfrontal tissue

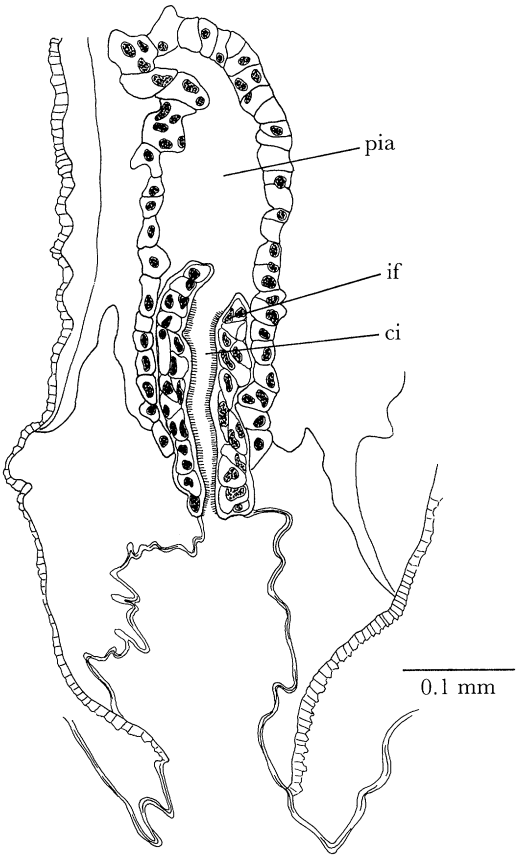

Figure 65. *Thyasira* (*Axinulus*) *brevis*: transverse section through the postero-ventral mantle edge showing paired ciliated 'pads' forming a second posterior aperture; specimen from *Biogas*, station DS 86. (List of abbreviations: see p. 561.)

present than in larger species of *Thyasira* sg. (figure 67). Filamentar muscles, skeletal rods and ciliation are well developed.

Extremely small triangular labial palps, *ca.* 100 μm in length are extensions of the proximal oral grooves.

The foot is long and vermiform and, depending upon its state of contraction, may either form several coils within the mantle cavity or form a shorter straight stem with a markedly bulbous tip. There is little tissue differentiation of heel or tip. The stem and tip are ciliated with ciliation being most dense on the tip. Internally an inner layer of longitudinal muscles is present. The fibres forming this layer are broader than those of the outer longitudinal layer. Muscles are better developed at the base of the foot than at the tip. The anterior and posterior retractors are narrow.

The combined stomach and style sac is elongate. A short oesophagus opens into the stomach antero-dorsally. A constriction divides the stomach from the style sac. A pair of anterior apertures each open to two digestive diverticula. A dorsal tubule on each side passes lateral to the oesophagus and dorsal to the stomach. A ventral tubule opens to each lateral body pouch. The tubules are not branched or convoluted and, relatively, are exceptionally large, up to 100 μm in length, and contain unidentifiable particulate material. The stomach wall is thickened beneath the gastric shield, the elongate epithelial cells contain refractile inclusions. The gastric shield forms a thin

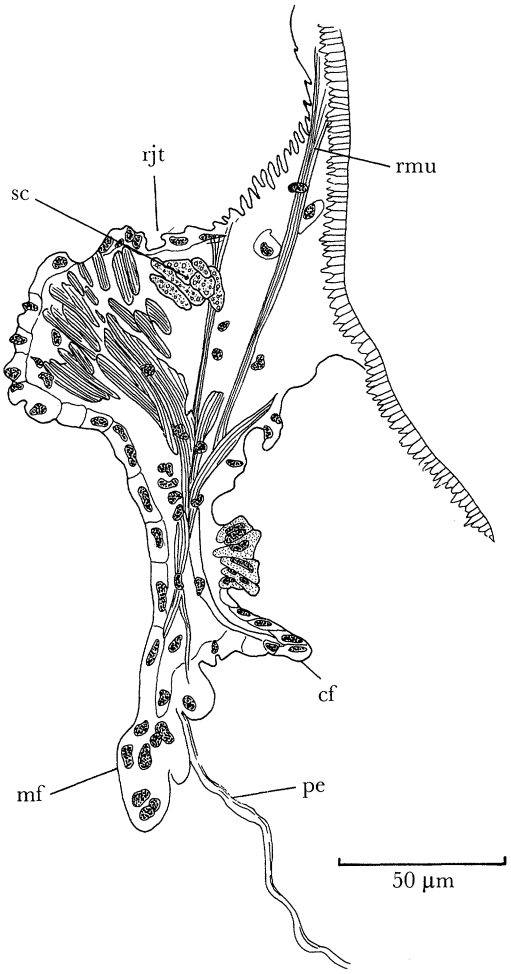

Figure 66. *Thyasira* (*Axinulus*) *brevis*: transverse section through the mid-ventral mantle edge; specimen from *Biogas*, station DS 86. (List of abbreviations: see p. 561.)

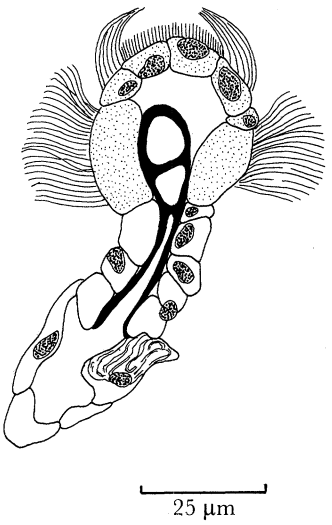

Figure 67. *Thyasira* (*Axinulus*) *brevis*: transverse section through a gill filament, specimen from *Biogas*, station DS 86. (For identification of parts see figure 12.)

curved band across the dorsal wall of the stomach. The lateral pouches are elongate, oval in outline, the longitudinal plane of the pouch lying parallel to the margin of the gill. There are no marked lobes or

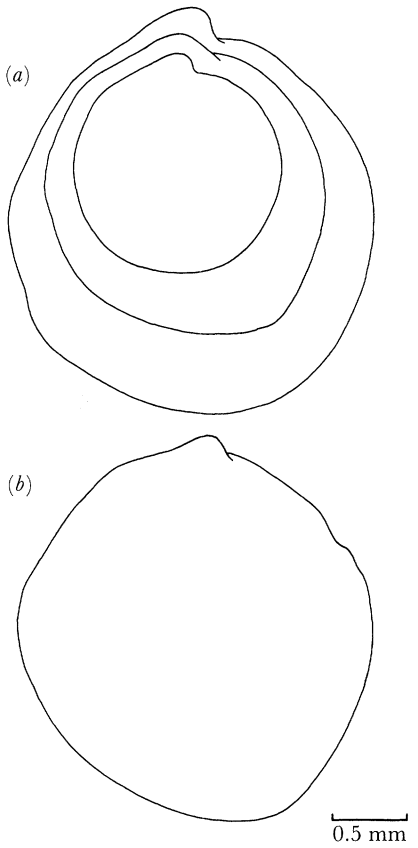

Figure 68. *Thyasira* (*Axinulus*) *brevis*: (*a*) shell outlines showing the change in shape with growth; specimen from *Biogas*, station DS 86; and (*b*) variation in shell from the same station.

divisions, a feature which distinguishes *Axinulus* from the subspecies *Thyasira* and *Parathyasira*.

The sexes are separate. When mature the gonads fill the inner and ventral parts of the lateral pouches and the eggs or sperm fill the gonadial ducts. Up to 70 eggs were counted and these measure 100 μm in length in preserved specimens.

Paired sac-like kidneys lie between the heart and the posterior adductor muscle. Their arrangement is similar to that described before, although in transverse section the lumen is either round or triangular rather than dorso-ventrally elongate. A number of large plate-like concretions are present in the epithelial cells. A thin walled pericardial cavity contains a large central ventricle with an auricle on each side. The ventricle is penetrated by the hindgut. Reno-pericardial ducts were not identified.

The arrangement of the nervous system is similar to that described before. The pedal ganglia are fused to form a single mass.

Thyasira* (*Axinulus*) *croulinensis (Jeffreys, 1847)

Type locality: Originally dredged close to the Crowlin Islands, Skye, west Scotland.

Type specimen: A neotype selected by K. W. Ockelmann is from Loch Fyne (USNM No. 62048).

Synonymy

Clausina croulinensis Jeffreys (1847, p. 19).
Clausina croulinensis Forbes & Hanley (1853, p. 60).
Clausina croulinensis Jeffreys (1858, p. 122, figs. 2*a–c*, pl. 5).
? *Axinus croulinensis* Jeffreys (1868, p. 301).
? *Axinus croulinensis* Jeffreys (1870*a*, p. 441).
? *Axinus croulinensis* Sars (1870, p. 87).
? *Axinus croulinensis* Monterosato (1875, p. 14).
? *Axinus croulinensis* Monterosato (1877, p. 30).
? *Axinus croulinensis* Monterosato (1878, p. 69).
? *Axinus croulinensis* Jeffreys (1880, p. 316).
? *Axinus croulinensis* Jeffreys (1881, p. 703).
? *Axinus croulinensis* Monterosato (1882, p. 98).
? *Cryptodon croulinensis* Smith (1885, p. 193).
? *Axinus croulinensis* Jeffreys (1887, p. 21).
? *Axinus croulinensis* Kobelt (1888, p. 375).
? *Cryptodon croulinensis* Norman (1893, p. 344).
Axinus croulinensis Marshall (1897, p. 353–354).
? *Axinus croulinensis* Posselt (1898, p. 78–79).
? *Axinus croulinensis* Locard (1898, p. 291–292).
? *Axinus croulinensis* Friele & Greig (1901, p. 32).
? *Thyasira croulinensis* Dautzenberg & Fischer (1912, p. 487).
? *Cryptodon croulinensis* Cooke (1914, p. 115).
? *Thyasira croulinensis* Johnson (1915, p. 64).
? *Thyasira croulinensis* Lamy (1920, p. 306–307).
? *Thyasira croulinensis* Dautzenberg (1927, p. 312).
? *Thyasira croulinensis* Thiele and Jaeckel (1931, p. 218).
? *Thyasira croulinensis* Winckworth (1932, p. 218).
? *Thyasira croulinensis* Johnson (1934, p. 39).
? *Thyasira croulinensis*, La Rocque (1953 p. 56).
? *Thyasira croulinensis* Ockelmann (1958, p. 197, 110).
? *Thyasira croulinensis* Allen (1962, p. 59).
? *Thyasira croulinensis* Clarke (1962, p. 64).
? *Thyasira croulinensis* Tebble (1966, p. 79–80; fig. 34*a–b*).
? *Thyasira croulinensis* Bowden & Heppell (1968, p. 244, 263).
? *Thyasira croulinensis* Hopner Petersen (1968, p. 21, 52).
? *Thyasira croulinensis* McMillan (1968, p. 83).
Axinulus croulinensis Nordsieck (1969, p. 60; fig. 48.10, pl. 13).
Thyasira croulinensis Turk (1973, p. 62).

Note: because earlier workers did not recognize two species, references prefixed with a question mark may refer to either *T.* (*T.*) *obsoleta* (p. 493) or *T.* (*A.*) *croulinensis* or to a mixture of the two.

The following references and illustrations do not refer to this species:
Axinus croulinensis Jeffreys (1864, p. 250, fig. 2, pl. 33).
Axinus croulinensis Sars (1878, p. 62; figs. 8*a–b*, pl. 19).
Cryptodon croulinensis Verrill & Bush (1898, p. 786–788, figs. 3–4, pl. 87).
Thyasira croulinensis Dall (1901, p. 787).

Historical

The confusion between this species and *T.* (*T.*) *obsoleta* is discussed in the section dealing with the latter species (p. 493) (figures 72–73).

Material

ship/cruise	no.	date	sta.	position	depth/m	number	gear
North America Basin							
Atlantis	264	24.05.61	E1	39° 50.5′N 39° 35.0′W	1000	1	ad
	264	24.05.61	G1	39° 42.0′N 70° 39.0′W	2000	9	ad
Chain	22	23.05.62	D1	39° 54.5′N 70° 35.0′W	467–509	242	ad
Atlantis	283	28.08.62	Sl2	40° 01.8′N 70° 42.0′W	200	146	ad
		28.08.62	Sl3	39° 58.4′N 70° 40.3′W	300	713	ad
		28.08.62	Sl4	39° 56.5′N 70° 39.9′W	400	154	ad
Atlantis II	12	21.08.64	64	38° 46.0′N 70° 06.0′W	2886	9	es
		24.08.64	72	38° 16.0′N 71° 47.0′W	2864	3	es
		25.08.64	73	39° 46.5′N 70° 43.3′W	1220–1470	40	es
Chain	50	29.06.65	76	39° 38.3′N 67° 57.8′W	2862	2	es
		06.07.65	87	39° 48.7′N 70° 40.8′W	1102	10	es
	58	05.05.66	105	39° 56.6′N 71° 03.6′W	530	37	es
Atlantis II	30	18.12.66	131	39° 38.5′N 70° 36.5′W	2178	1	es
Chain	88	22.02.69	209	39° 47.6′N 70° 49.9′W	1501–1693	17	es
			—	39° 47.6′N 70° 49.9′W			
West European Basin							
Thalassa		22.10.73	Z399	47° 34.8′N 07° 18.1′W	825	3	gbs
		24.10.73	Z417	48° 12.0′N 09° 09.5′W	865	6	pbs
		25.10.73	Z424	48° 27.9′N 09° 44.3′W	475	25	pbs
		25.10.73	Z426	48° 28.2′N 09° 39.1′W	860	18	pbs
		25.10.73	Z428	48° 27.2′N 10° 49.7′W	850	27	pbs
		25.10.73	Z431	48° 38.2′N 09° 47.3′W	800	1	pbs
		26.10.73	Z434	48° 40.7′N 09° 54.1′W	720	94	pbs
		26.10.73	Z438	48° 33.7′N 10° 25.0′W	1400	3	pbs
		26.10.73	Z439	48° 42.0′N 10° 23.4′W	500	286	pbs
		26.10.73	Z440	48° 41.4′N 10° 21.5′W	860	111	pbs
		26.10.73	Z442	48° 54.8′N 11° 02.0′W	975	2	pbs
		27.10.73	Z443	48° 56.0′N 11° 02.0′W	660	178	pbs
		27.10.73	Z444	48° 58.2′N 10° 58.5′W	380	27	pbs

Material

ship/cruise	no.	date	sta.	position	depth/m	number	gear
		27.10.73	Z445	48° 52.2′N 11° 07.0′W	1200	4	pbs
		27.10.73	Z449	48° 41.3′N 10° 33.8′W	730	5	pbs
		29.10.73	Z457	48° 38.2′N 09° 52.6′W	800	22	gbs
		29.10.73	Z458	48° 41.6′N 09° 52.9′W	350	1	gbs
Sarsia		09.76	7627	43° 47.1′N 03° 46.0′W	1925–1990	5	ag
Cape Verde Basin							
Atlantis II	31	05.02.67	142	10° 30.0′N 17° 51.5′W	1624–1796	10	es
		06.02.67	145	10° 36.0′N 17° 49.0′W	2185	30	es
		06.02.67	147	10° 38.0′N 17° 52.0′W	2934	6	es
		07.02.67	149	10° 30.0′N 18° 18.0′W	3861	2	es
Angola Basin							
Atlantis II	42	22.05.68	200	09° 43.5′S 10° 57.0′E	2644–2754	28	es
		23.05.68	201	09° 25.0′S 11° 35.0′E	1964–2031	24	es
			—	09° 05.5′S 12° 17.0′E			
		23.05.68	202	08° 56.0′S 12° 15.0′E	1427–1643	1	es
			—	08° 46.0′S 12° 47.0′E			
		23.05.68	203	08° 48.0′S 12° 52.0′E	527–542	1	es
Cape Basin							
Atlantis II	42	16.05.68	185	22° 56.0′S 13° 02.0′E	458–463	45	ad
		16.05.68	187	22° 58.0′S 13° 01.0′E	626–631	2	ad
		16.05.68	188	23° 00.0′S 12° 58.0′E	619–622	385	es
		16.05.68	189	23° 00.0′S 12° 45.0′E	1007–1014	2	es
		17.05.68	191	23° 05.0′S 12° 31.5′E	1546–1559	48	es
		17.05.68	192	23° 19.0′S 12° 19.0′E	2117–2154	22	es
Argentine Basin							
Atlantis II	60	11.03.71	236	36° 27.0′S 53° 31.0′W	497–518	1319	es
			—	36° 28.1′S 53° 32.3′W			
		11.03.71	237	36° 32.6′S 53° 23.0′W	993–1011	3	es
		11.03.71	239	36° 49.0′S 53° 15.4′W	1661–1679	13	es
Guiana Basin							
Knorr	25	28.02.72	295	08° 04.2′N 54° 21.3′W	1000–1002	27	es
		28.02.72	297	07° 45.3′N 54° 24.0′W	508–523	17	es
		29.02.72	300	08° 14.2′N 55° 53.5′W	2524–2542	3	ad

Distribution

It has proved almost impossible to establish exactly which of the earlier records are referable to this species and which to *T.* (*T.*) *obsoleta*.

T. (*A.*) *croulinensis* is known to occur from Norway to the Shetland Isles, in the West European Basin, from west coast of Scotland to the Bay of Biscay in the Mediterranean. The species also occurs in the North America, Cape Verde, Angola, Cape, Argentine and Guiana Basins. Depth range: 40–3861 m. This is one of the more common species represented in our samples.

Shell description (figures 69, 72, 73, 74 and 75)

Shell small, thin and fragile, white or semi-transparent, inflated, sculpture of fine concentric lines, ferruginous material adheres to anterior and posterior ends of shell, very variable in shape, height normally exceeds length, but may be almost equal, thus shell may be upright oval or almost circular in outline; beaks rounded, positioned approximately at the mid vertical line; antero-dorsal margin characteristically projects almost horizontally for short distance before descending in even curve to antero-ventral margin; postero-dorsal margin descends from beaks at modest angle, primary and submarginal sulci very faint, marked only by minute undulation of margin; escutcheon and lunule indistinct; hinge plates edentulous, but slightly swollen ventral to beak, reflected outwards anterior to beak; ligament long, curved, in groove on hinge plate reaching about one third of distance to posterior margin.

Specimens from *Thalassa* sta. Z439 measure as

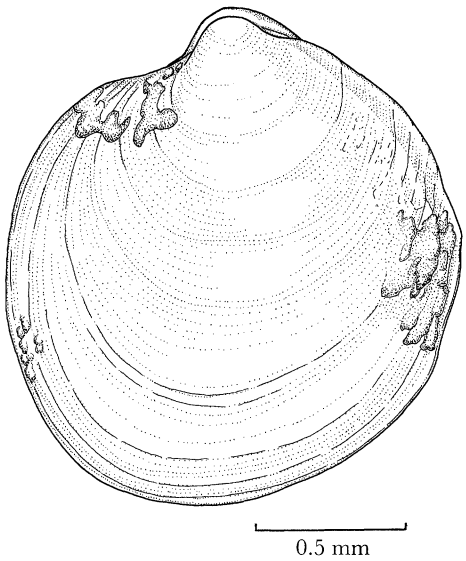

Figure 69. *Thyasira* (*Axinulus*) *croulinensis*: lateral view of the shell from the left side; USNM No. 61894, specimen from Shetland.

follows (length × height × breadth): 1.8 × 2.0 × 1.3 mm; 1.3 × 1.5 × 0.85 mm; 1.1 × 1.1 × 0.65 mm. The prodissoconch of specimens from *Thalassa* sta. Z439 range from 121–135 μm.

The projecting antero-dorsal margin and reflected hinge plate distinguish typical specimens of *T.* (*A.*) *croulinensis* from *T.* (*A.*) *brevis*. Usually the shell of *T.* (*A.*) *croulinensis* is more fragile and more transparent than that of *T.* (*A.*) *brevis*, however small specimens of the latter may also be thin shelled. This makes juveniles extremely difficult to distinguish. It was found that large specimens from the Angola and Cape Basins, like large *T.* (*A.*) *brevis*, are more angular and have a more solid shell which looks different from the typical form. Figures 74–75 show the extent of variation in shell shape.

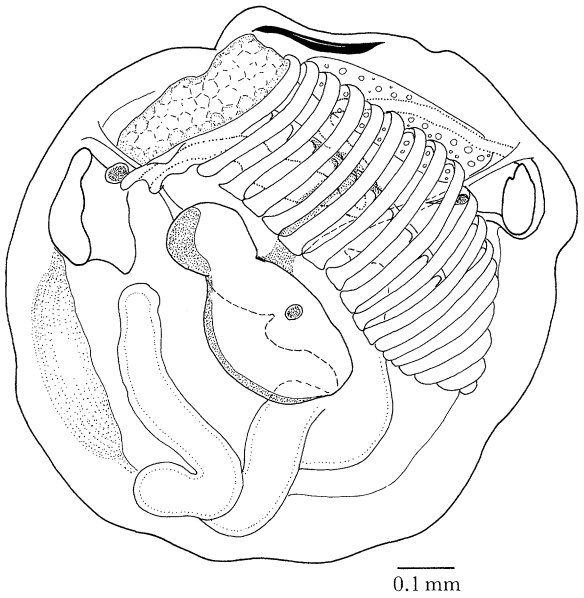

Figure 70. *Thyasira* (*Axinulus*) *croulinensis*: internal morphology as seen from the left side of a wholemount; specimen from *Atlantis II*, station 203. (For identification of parts see figures 2 and 3.)

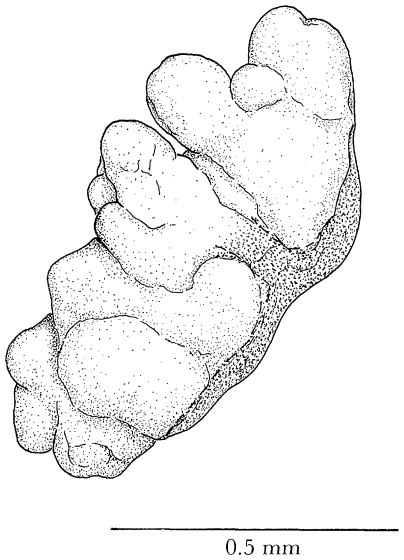

Figure 71. *Thyasira* (*Axinulus*) *croulinensis*: lateral view of a body pouch of a large specimen from *Atlantis II*, station 182.

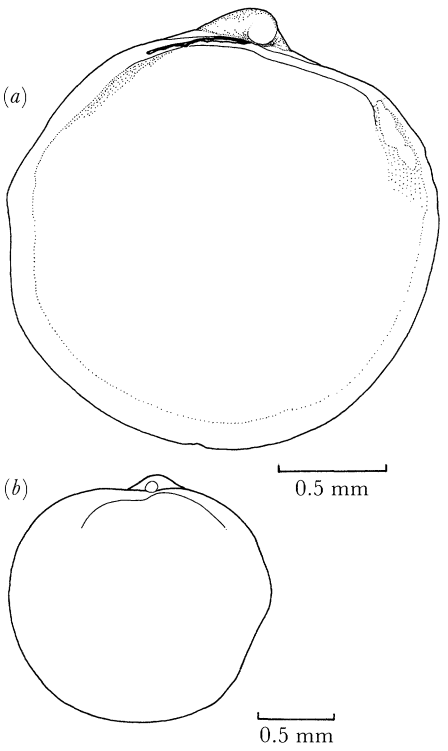

Figure 72. *Thyasira* (*Axinulus*) *croulinensis*: (*a*) Neotype from Loch Fyne, Scotland, selected by K. W. Ockelmann, USNM No. 62048; and (*b*) specimen from Drobak, Norway, BM(NH), Sykes collection.

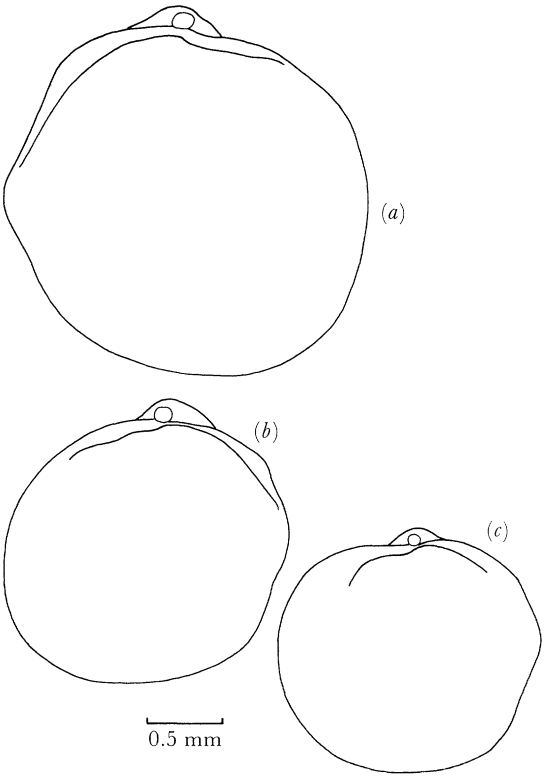

Figure 73. Outline drawings to show differences in shell shape between *Thyasira* (*Thyasira*) *obsoleta* and *Thyasira* (*Axinulus*) *croulinensis*: (*a*) *Thyasira* (*Thyasira*) *obsoleta*, large specimen from 110–183 m, Drobak, Norway; (*b*) *Thyasira* (*Thyasira*) *obsoleta*, small specimen from same locality as (*a*); and (*c*) *Thyasira* (*Axinulus*) *croulinensis* from same locality as (*a*).

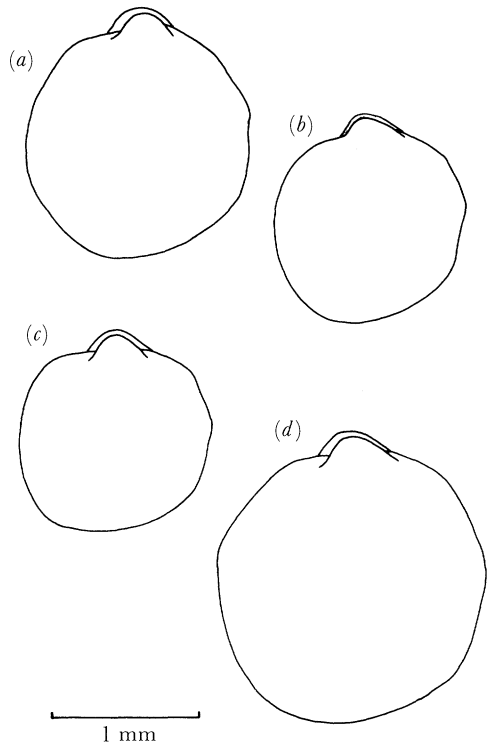

Figure 74. *Thyasira* (*Axinulus*) *croulinensis*: variation in shell shape of different sized specimens from a number of sampling stations: (*a*) and (*b*), *Thalassa*, station Z439; (*c*) *Atlantis II*, station sl. 3; and (*d*) *Atlantis II*, station 186.

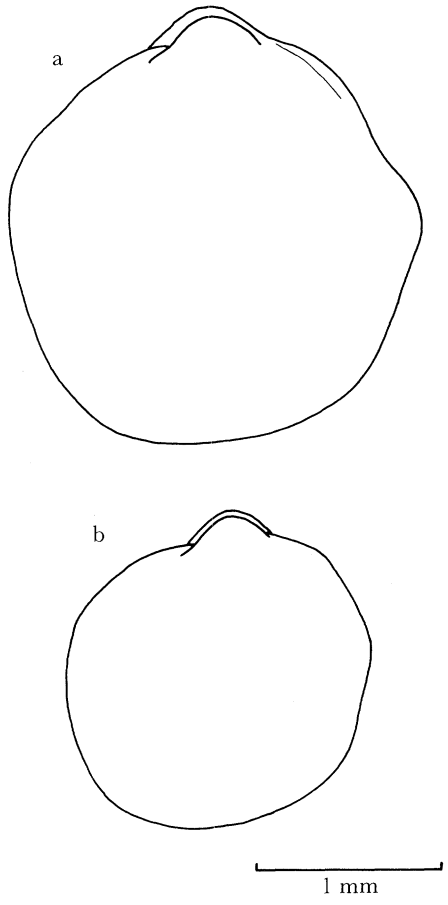

Figure 75. *Thyasira* (*Axinulus*) *croulinensis*: outline drawings of shells to show the change in shape with growth: a large specimen from (*a*) *Atlantis II*, station 203; and (*b*) a small specimen from the same station.

Internal Morphology (figure 70)

The internal morphology of this species is so similar to that of *T.* (*A.*) *brevis* that it is not described in detail. The main difference between the two lies in the shape of the lateral body pouches which in large specimens of *T.* (*A.*) *croulinensis* have small projecting lobes along the dorsal margin (figure 71). Specimens bearing these lobes generally occur in relatively shallow water (greater than 500 m). The postero-ventral mantle edge does not have interlocking ciliated pads like those seen in *T.* (*A.*) *brevis*.

Thyasira* (*Axinulus*) *eumyaria (M. Sars 1870)

Type species: *Axinus eumyarius* M. Sars, 1870.
Type locality: ? Oslo fjord.
Type specimen: Not known.

Synonymy

Axinus eumyarius Sars (1870, p. 87–89; figs. 7–10, pl. 12).
Axinus eymyarius Jeffreys (1870*a*, p. 441).
Axinus eymyarius Monterosato (1875, p. 14).
Axinus eumyarius Jeffreys (1876, p. 492).
Axinus eumyarius Monterosato (1877, p. 31).
Axinus eumyarius Monterosato (1878, p. 69).
Axinus eumyarius Sars, G. O. (1878, p. 62).
Axinus eumyarius Monterosato (1880, p. 58).
Axinus eumyarius Jeffreys (1881, p. 703).
Axinus eumyarius Locard (1886, p. 257).
Axinus eumyarius Kobelt (1888, p. 374).
Cryptodon eumyarius Norman (1893, p. 344).
Axinus eumyarius Dautzenberg & Fischer (1897, p. 215).
Axinus eumyarius Marshall (1897, p. 355).
Axinus eumyarius Locard (1898, p. 293).
Axinus eumyarius Posselt (1898, p. 77).
Thyasira (*Axinulus*) *eumyaria* Dall (1901, p. 788).
Thyasira (*Leptaxinus*) *eumyaria* Dautzenberg & Fischer (1912, p. 000).
Thyasira (*Axinulus*) *eumyaria* Lamy (1920, p. 310–311).
Thyasira (*Axinulus*) *eumyaria* Dautzenberg (1927, p. 315).
Thyasira (*Axinulus*) *eumyaria* Johnson (1934, p. 39).
Thyasira eumyaria Madsen (1949, p. 53).
Thyasira eumyaria La Rocque (1953, p. 58).
Axinulus eumyarius Ockelmann (1958, p. 197).
Thyasira eumyaria Clarke (1962, p. 64).
Leptaxinus eumyarius Nordsieck (1969, p. 81, fig. 48.20, pl. 13).
Leptaxinus eumyarius Carozza (1981).

Historical

Some authorities (Dauztenberg & Fischer, 1912; Nordsieck 1969; Carroza; 1981) refer *T. eumyaria* to the subgenus *Leptaxinus*, however the hinge lacks tubercles and lateral teeth which characterize *Leptaxinus*. The shape of the shell also differs from the latter subgenus.

T. (*A.*) *eumyaria* was well figured by M. Sars (1870) and the figures show the main features of the internal morphology, the single demibranch, the vermiform foot and the unlobed lateral body pouches.

Material

ship/cruise	no.	date	sta.	position	depth/m	number	gear
West European Basin							
Chain	106	17.08.72	313	51° 32.2′N 12° 35.9′W	1491–1500	8	es
Thalassa		22.10.73	Z400	47° 33.4′N 07° 19.0′W	1,175	64	gbs
		25.10.73	Z426	48° 28.2′N 09° 39.1′W	860	3	pbs
		25.10.73	Z428	48° 27.2′N 10° 49.7′W	850	18	pbs
		26.10.73	Z438	48° 33.7′N 10° 25.0′W	1,400	1	pbs
		26.10.73	Z442	48° 54.8′N 11° 02.0′W	975	3	pbs
		27.10.73	Z443	48° 56.0′N 11° 02.0′W	660	2	pbs
		27.10.73	Z445	48° 52.2′N 11° 07.0′W	1200	3	pbs
		29.10.73	Z457	48° 38.2′N 09° 52.6′W	800	2	gbs
		29.10.73	Z459	48° 37.3′N 09° 53.0′W	1180	5	gbs
Sarsia		09.76	7627	43° 47.1′N 03° 46.0′W	1925–1990	1	ag
Cape Verde Basin							
Atlantis II	31	05.02.67	142	10° 30.0′N 17° 51.5′W	1624–1796	41	es
Sierra Leone Basin							
Walda		07.71	DS28	04° 21.2′N 04° 35.2′E	1261	1	ds
Angola Basin							
Walda		06.71	DS16	10° 31.0′S 11° 57.8′E	1787	1	ds
Cape Basin							
Atlantis II	42	17.05.68	191	23° 05.0′S 12° 31.5′E	1546–1559	1	es

Distribution

Past records of *T.* (*A.*) *eumyaria* are numerous; Baffin Bay (Johnson 1934); Davis Strait (*Valorous* expedition); Iceland (Madsen 1949); Norwegian coast (M. Sars 1870; G. O. Sars 1878); West European Basin (Jeffreys 1881; Locard 1898); Azores (Dautzenberg & Fischer 1897) and Mediterranean (Jeffreys 1881). The material obtained in this study came from the West European, Cape Verde, Sierra Leone, Angola and Cape Basins. Depth range: 42–2663 m.

Shell description (figure 76)

Shell small, fragile, inflated, sculpture of fine concentric lines, ferruginous material frequently adheres to anterior and posterior parts of shell, internal raised muscle scars project from shell surface and bear prominent concentric growth marks, outline ventrally ovate/dorsally triangulate, semi-transparent except for two white radiating scars; beaks fractionally posterior to midline, curved slightly anteriorly and inwards; antero-dorsal and postero-dorsal margins descend rapidly from beaks to join somewhat flattened antero-ventral and posterior margins; submarginal sulcus faint, primary sulcus indistinguishable; radiating muscle scars cross shell anteriorly and posteriorly from beak towards anterior and posterior margins; scars appear white because the shell layer is extensively thickened at ventral margin of adductors during migration of the muscles during growth; hinge plate featureless, not thickened and without tubercles; ligament opisthodetic, lying in curved ligamental groove extending one quarter of the distance to posterior margin, becoming sunken posteriorly.

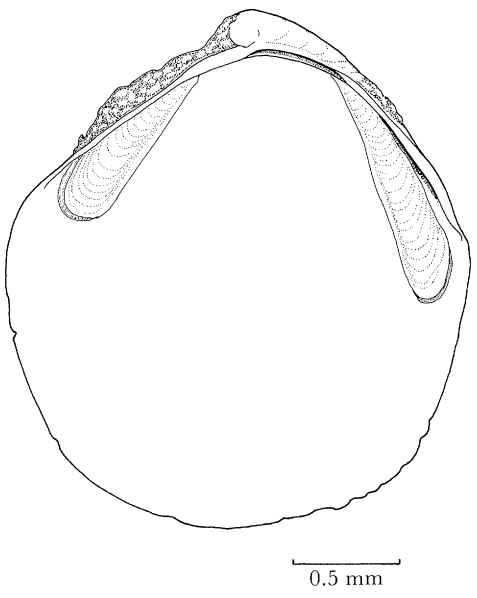

Figure 76. *Thyasira* (*Axinulus*) *eumyaria*: interior view of the right valve, specimen from USNM No. 620216.

A large and a smaller specimen from *Chain* sta. 313 measure (length × height × breadth) 1.30 × 2.70 × 1.60 mm and 1.92 × 2.08 × 1.28 mm.

The white muscle scars make *T.* (*A.*) *eumyaria* an easy species to identify. The only other species which posesses similar scars is *T.* (*M.*) *ultima* (figure 110), but the shell shape and hinge plate of the latter distinguish it clearly from the present species.

Morphologically *T.* (*A.*) *eumyaria* is similar to *T.* (*A.*) *croulinensis* and *T.* (*A.*) *brevis*, which it resembles in body orientation and in the structure of gill, pouch and foot. The only noticeable difference is the smaller size of the anterior adductor muscle in the present species.

Internal morphology (figure 77)

The anterior adductor muscle is small and oval. Despite this the anterior muscle is almost twice as large as the posterior. The scars are formed as the muscles migrate down the shell as growth continues and thus the adductor muscles are positioned at the ventral end of each radiating scar. The thickened shell probably serves as a mechanism for strengthening what is

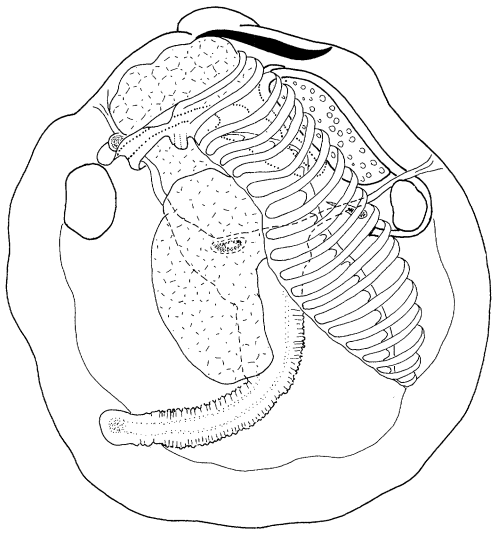

Figure 77. *Thyasiria* (*Axinulus*) *eumyaria*: internal morphology as seen from the left side of a wholemount; specimen from *Thalassa*, station Z400. (For identification of parts see figures 2 and 3.)

elsewhere fragile shell at the point where most stress is applied.

There is a single posterior point of mantle fusion. As in *T.* (*A.*) *brevis*, the opposing postero-ventral mantle edges are thickened and ciliated. These probably interlock in the living animal to form a second posterior aperture. The inner fold of the mantle edge below the anterior adductor muscle is glandular. Posteriorly the mantle edge resembles that of *T.* (*A.*) *ferruginea* (p. 537) in having an extended flap-like middle fold.

Each gill is formed of a single inner demibranch. Each demibranch is made up of 16–20 filaments in larger specimens. The ascending lamella is approximately two thirds the size of the descending lamella. Ventrally the opposing filaments are joined by interlamellar junctions. In transverse section the structure of the filaments is the same as described for *T.* (*A.*) *brevis*. The labial palps are triangular with two to three grooves on their inner surfaces.

The foot is narrow and vermiform, it appears slightly shorter than that of other *Axinulus* species. It has no heel and no sagittal groove at the base. The tip is pointed, but not much differentiated from the stem.

The gut and digestive diverticula although examined in detail showed no important differences to those of *T.* (*A.*) *brevis*. The lateral pouches are not lobed or subdivided. The digestive tubules are unbranched, with a small central lumen surrounded by large tubule cells which contain fine unidentifiable particulate material. The walls of the pouches have a thin layer of muscle below the epithelium.

Sexes are separate. The gonad occupies a narrow area along the ventral and inner part of the pouch. A pair of gonadial ducts open separately ventral to the kidney. Eggs seen in the suprabranchial cavity measure 70 μm × 30 μm.

The arrangement of the kidney, pericardium and nervous system resembles that of *T.* (*A.*) *brevis*.

Thyasira* (*Axinulus*) *alleni Carozza 1981

Type locality: Off Cape Comino, north eastern Sardinia 350–1600 m.
Type specimen: Holotype in personal collection of F. Carrozza.
Paratypes: Museum of Natural History, Milan.

Synonymy

? *Leptaxinus intermedius* Monterosato (1878).
Thyasira alleni Carrozza (1981, p. 223–228, figs. 1*a*, *b*, 2, 3*a* and *b*).

Twelve specimens of *T.* (*A.*) *alleni* from Palermo are present in the BM(NH) Sykes collection (unregistered) and are labelled *Axinus eumyarius*.

Taxonomy

Monterosato (1878) reported on a species which he named *Axinus intermedius*. Jeffreys (1881) considered this species to be a variety of *T.* (*A.*) *eumyaria* possibly a juvenile in which the muscle scars are less pronounced. Monterosato (1882) refuted Jeffreys suggestion, saying that both adults and juveniles were consistent in form, and different from *T.* (*A.*) *eumyaria*. Unfortunately Monterosato did not provide a figure and inadequately described his species for identification purposes. *Axinus intermedius* is therefore regarded as a *nomen nudum* (Carozza 1981).

Material

ship/cruise	no.	date	sta.	position	depth/m	number	gear
Angola Basin							
Atlantis II	42	23.05.68	203	08° 48.0′S 12° 52.0′E	527–542	335	es
Walda		06.71	DS10	18° 40.0′S 10° 56.3′E	1432	6	ds
Cape Basin							
Atlantis II	42	16.05.68	186	22° 57.0′S 13° 05.0′E	439–481	10	es
		16.05.68	187	22° 58.0′S 13° 01.0′E	626–631	38	ad
		16.05.68	188	23° 00.0′S 12° 58.0′E	619–622	856	es
		16.05.68	189	23° 00.0′S 12° 45.0′E	1007–1014	250	es
		17.05.68	190	23° 05.0′S 12° 45.0′E	974–979	35	ad
		17.05.68	191	23° 05.0′S 12° 31.5′E	1546–1559	65	es

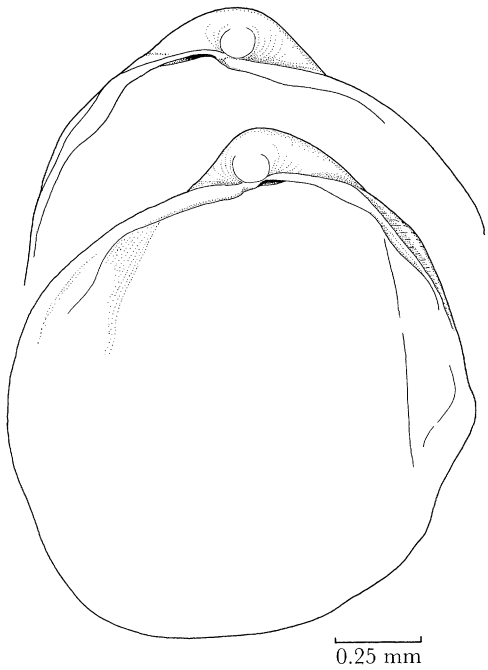

Figure 78. *Thyasira* (*Axinulus*) *alleni*: hinge plate of left and right valves; specimen from *Altantis II*, station 188.

Distribution

Mediterranean BM(NH) Sykes collection and Carrozza (1981); Angola and Cape Basins. Depth range: 439–1559 m.

Shell description (figures 78 and 81)

Shell small, white or semi-transparent, very inflated, height slightly exceeds length, sculpture fine concentric lines with growth stages at intervals, ferruginous encrustations occur anteriorly and posteriorly; rounded beaks positioned just posterior to midline; anterior margin broadly curved, somewhat prolonged antero-ventrally, ventral margin somewhat flattened, postero-ventral margin indented, apart from slight projecting auricle, postero-dorsal margin rather straight, angulated at posterior ventral margin; primary sulcus shallow, forms faint ridge from beak to postero-ventral margin, postero-dorsal margin and submarginal sulcus form small auricle; lunule broad and distinct; hinge plate somewhat thickened anterior to beaks to form elongate swelling, one specimen with rounded swelling ventral to beak in left valve, not present in others, right valve with the suggestion of a small tubercle ventral to beak, faint lateral projection at postero-dorsal margins; ligament lies in shallow, curved groove, reaching less than one third the distance to posterior margin, visible externally.

The shell is distinguished from *T.* (*A.*) *croulinensis* (figure 69) by being much more inflated, and have a more distinct posterior shell angle. Fully grown specimens are very globose and specimens appear to become more inflated after reaching a definitive length. The development of very shallow interlocking postero-dorsal lateral margins of the hinge plate differs from that of other species of *Axinulus*. Otherwise the morphology suggest a very close affinity to *T.* (*A.*) *croulinensis*.

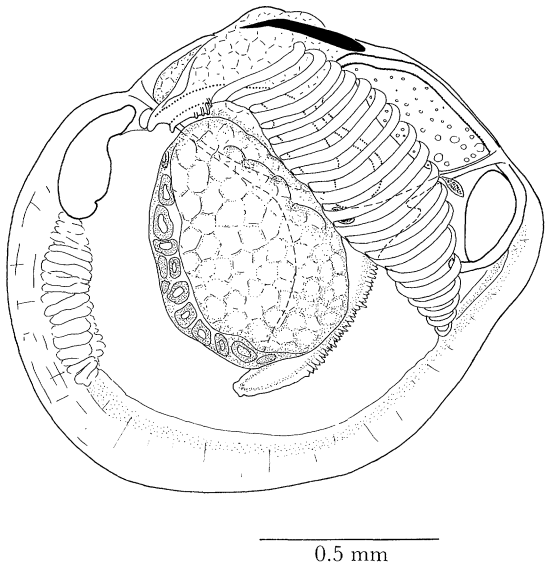

Figure 79. *Thyasira* (*Axinulus*) *alleni*: internal morphology as seen from the left side of a wholemount; specimen from *Atlantis II*, station 187. (For identification of parts see figures 2 and 3.)

Internal morphology (figure 79)

The anterior and posterior adductor muscles are well developed and are a little larger and broader than those of specimens of *T.* (*A.*) *croulinensis* of a similar size. The posterior adductor muscle is approximately two thirds the size of the anterior and oval in cross section. Both adductor muscles are clearly divided into 'quick' and 'catch' muscle blocks.

Posteriorly the inner mantle folds are fused at a single point to form a posterior exhalent aperture. Adhesion of the mantle to form a posterior inhalent aperture was not seen. The inner fold is well developed and forms a projecting shelf underlain by gland cells. Anteriorly, adjacent to point of attachment of the inhalent tube, the inner lobe is expanded and contains many more secretory cells. These latter are in irregular shape with a granular cytoplasm which either stains blue with Masson's trichrome or are eosinophilic. Thus, either two types of cell may be present or there is a change of pH in the product (figure 80). The cells are arranged in groups radial to the mantle edge. The area is well supplied with pallial circular muscles and less well developed radial muscles.

Each gill is reduced to a single demibranch with approximately 17–22 filaments. The ascending lamella is approximately four fifths the size of the descending lamella. Except dorsally the filaments of the opposing lamellae are attached by abfrontal interlamellar junctions. Gill axes and filaments are well supplied with muscles. In transverse section the filaments are similar in appearance to those of *T.* (*A.*) *brevis* (figure 67). Each filament has a broad frontal surface, raised lateral cells bear the latero-frontal cilia. A large and swollen cell posterior to the latero-frontals, bears the lateral cilia.

The inner surface of the labial palps has four distinct raised ridges. The foot is a little shorter than that of the other species of *Axinulus*. The tip is pointed but not well differentiated from the stem. A small heel is present

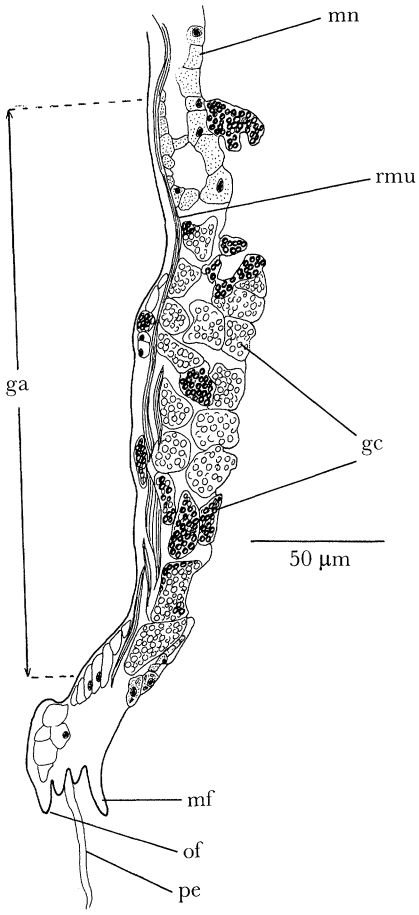

Figure 80. *Thyasira* (*Axinulus*) *alleni*: transverse section through the anterior glandular area of the mantle edge; specimen from *Atlantis II*, station 188. (List of abbreviations: see p. 561.)

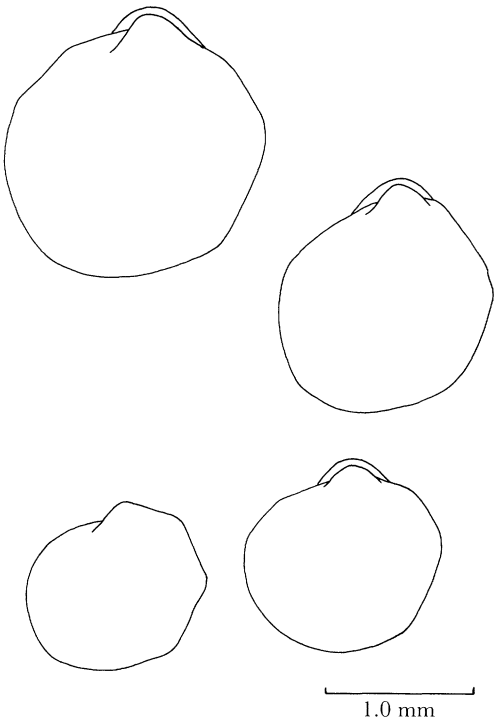

Figure 81. *Thyasira* (*Axinulus*) *alleni*: outline drawings of shells of various sizes; specimens from *Atlantis II*, station 188.

which is grooved sagittally. The heel is much less well defined than those of *T.* (*L.*) *incrassatus* and *T.* (*M.*) *ferruginea*.

The gut and digestive diverticula are similar to those of related species. The posterior section of the hindgut has unusually thick walls which contain a number of large swollen cells with a fine particulate cytoplasm. The function of these cells is not known. The lateral pouches are very swollen and occupy a large proportion of the mantle cavity, it is the space required by the pouches which gives the shell its characteristic globose shape. There are no deep divisions of the pouches, but as in *T.* (*A.*) *croulinensis*, the dorsal margin is thrown into a number of small lobes. The tubules within are thus also slightly lobed.

Sexes are separate. A relatively large number of (160–200) eggs are produced. The eggs measure 94 μm in length in preserved specimens.

The heart, kidney and nervous system are similar to those in *T.* (*A.*) *brevis*.

The subgenus *Axinulus* comprises a discrete group of species. All four species described here have an upright ovoid shell in which the height usually exceeds the length although occasionally the two parameters may be about equal. The radial sulci are much less obvious than in the larger species of other subgenera (*e.g.* *Thyasira* and *Parathyasira*). The sulci such as they are give rise to a faint radial undulation at the posterior margin of the shell. The shell margin tends to be prolonged mid-ventrally. The maximum size of species of *Axinulus* is just over 3 mm and they are similar in size to small species of the subgenus *Thyasira*.

The hinge plate of *Axinulus* species is generally featureless, but may be slightly thickened and very small swellings may be present ventral to the beak in both valves. *T.* (*A.*) *alleni* additionally has an ill-defined interlocking hinge margins to some extent resembling those of the *Mendicula* species (p. 534). The ligament is long and narrow at the outer margin of the hinge plate.

The internal morphology of the species examined are similar. All possess a gill with only the inner demibranch present. The foot is vermiform, sometimes with a small heel close to its base. Lateral body pouches are usually unlobed but, if lobes are present they are small and largely confined to the dorsal margin. The anterior adductor muscle is approximately twice as large as the posterior.

Large specimens of *T.* (*A.*) *brevis* and *T.* (*A.*) *croulinensis* occur at some localities. As they age they take on a different shape to that of the juveniles. The shells become more angular posteriorly and similar in appearance to *T.* (*Parathyasira*) *equalis*. This, together with the simple hinge and the single demibranch suggests that species of *Axinulus* may have been derived from the *Parathyasira* and stem from a morphology similar to that of *T.* (*P.*) *equalis*.

Two of the species described, *T.* (*A.*) *brevis* and *T.* (*A.*) *croulinensis* are very widely distributed in the North and South Atlantic. *T.* (*A.*) *brevis* is confined to depths below 1000 metres and the closely related *T.* (*A.*)

croulinensis occurs from shallow depths just offshore, to almost 4000 metres deep. Shells of *T.* (*A.*) *croulinensis* are highly variable in form and we believe that the species may be in process of further speciation. In contrast *T.* (*A.*) *eumyaria* is only found in the northeast and southeast Atlantic where it occurs at slope depths, while *T.* (*A.*) *alleni*, has been found so far only in the Mediterranean and southeast Atlantic also at slope depths. It could well be that the two latter are sibling species. *T.* (*A.*) *eumyaria* has a similar geographical but shallower depth distribution to that of *T.* (*A.*) *alleni*.

Subgenus: ***MENDICULA*** Iredale 1924

Type species: *Lucina induta* Hedley, 1907.
Type locality: 35 miles east of Sidney, 1463 m.

Original description

The definition of the subgenus *Mendicula* is based on the original description of *Lucina induta* (Hedley 1907) (figure 82). Because the latter name was preoccupied Iredale (1924) proposed *Mendicula memorata* as a replacement name. The original description reads: 'Shell minute, very thin, brittle, glossy, white, concealed beneath a thick hard brown mass which cakes, cracks and splits off when dry. In shape sub-cordate, rounded anteriorly, sub-angled posteriorly, beaks prominent, incurved. Lunule absent. Sculpture, irregular concentric undulations and striations. No muscle scars visible. Hinge, the valve margin is produced under the umbo to simulate a cardinal tooth, the ligament occupies a narrow groove. Length 3 mm; height 2.65 mm.'

The subgenus *Mendicula* is used here to include small species in which the shell is longer than high and in which there is a strong posterior marginal angle. The hinge plate usually bears cardinal tubercles and sometimes lateral teeth. Internally the anatomy is characterized by a gill with a single demibranch. Lateral body pouches sometimes bear small lobes and exceptionally may be divided. A heel to the foot is usually present.

Thyasira* (*Mendicula*) *ferruginea (Locard, 1886)

Type species: *Kellia ferruginosa* Forbes, 1844.
Type locality: Crete, 218 m.
Type specimen: Not known

Synonymy

Lucina ferruginosa (nomen nudum) Forbes (1844, p. 143, 168).
Kellia ferruginosa Forbes (1844, p. 192).
Clausina ferruginosa Jeffreys (1847, p. 18).
Lucina ferruginosa Forbes & Hanley (1849, p. 60; fig. 1, pl. 34).
? *Cryptodon ferruginosum* Wood (1853, p. 135; fig. 19*a–b*, pl. 12).
Clausina ferruginosa Jeffreys (1858, p. 122).
Clausina ferruginosa Sowerby (1859, fig. 20, pl. 5).
Axinus ferruginosus Jeffreys (1863, vol. 2, p. 251–252; vol. 4, p. 180).

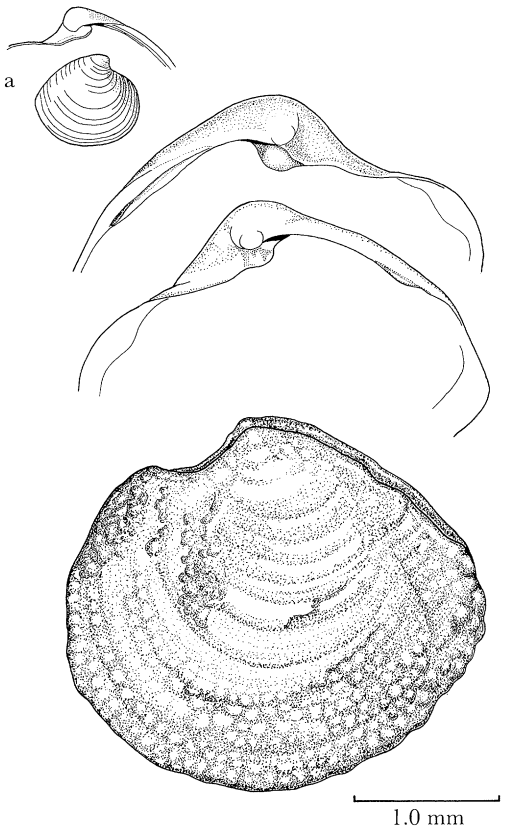

Figure 82. *Thyasira* (*Mendicula*) *ferruginea*: hinge plate of left and right valves; specimen from Loch Fyne, Scotland (150 m). Lateral view of the shell from the left side, a specimen from Norway (110 m); (*a*) *Mendicula memorata*, after Hedley (1907).

Axinus ferruginosus Jeffreys (1868, p. 307).
Axinus ferruginosus Jeffreys (1870*a*, p. 441).
Axinus ferruginosus Jeffreys (1870*b*, p. 71).
Axinus ferruginosus Sars (1870, p. 86–87).
Axinus ferruginosus Monterosato (1877, p. 31).
Axinus ferruginosus Sars, G. O. (1878, p. 63; fig. 10*a–b*, pl. 19).
Axinus ferruginosus Jeffreys (1880, p. 316).
Axinus ferruginosus Monterosato (1880, p. 59).
Crytodon ferruginosus Verrill (1880, p. 400).
?*Crytodon ferruginosus* Verrill (1880, p. 392).
Axinus ferruginosus Jeffreys (1881, p. 703–704).
Axinus ferruginosus Monterosato (1882, p. 98).
Cryptodon ferruginosus Verrill (1882, p. 570–571).
Axinus ferrugineus Locard (1886, p. 256).
Axinus ferruginosus Kobelt (1888, p. 374).
Axinus ferruginosus Locard (1892, p. 316).
Crytodon ferruginosus Norman (1893, p. 344, 365).
Crytodon ferruginosus Chaster & Heathcote (1894, p. 310).
Axinus ferruginosus Marshall (1897, p. 354).
Axinus ferrugineus (amended name) Locard (1898, p. 293–294).
Axinus ferruginosus Posselt (1898, p. 80–81).
Crytodon (*Axinulus*) *ferruginosus* Verrill & Bush (1898, p. 793, figs. 7–8, pl. 87).
Thyasira (*Axinulus*) *ferruginosa* Dall (1901, p. 791, 787, 788).
Axinus ferruginosus Friele & Greig (1901, p. 32–33).
Thyasira (*Axinulus*) *ferruginosa* Johnson (1915, p. 65).

Thyasira (Axinulus) ferruginosa Lamy (1920, p. 307–309).
Thyasira (Axinulus) ferruginosa Oldroyd (1924, p. 122).
Thyasira (Axinulus) ferruginosa Dautzenberg (1927, p. 313–314).
Thyasira ferruginea Winckworth (1932, p. 242, 251).
Thyasira (Axinulus) ferruginosa Johnson (1934, p. 39).
Axinulus ferruginosus Madsen (1949, p. 53).
Thyasira (Axinulus) ferruginosa La Rocque (1953, p. 58).
Axinulus ferruginosus Ockelmann (1958, p. 197).
?*Thyasira ferruginosa* Clarke (1961, p. 379).
Thyasira ferruginea Allen (1962, p. 59).
Thyasira (Axinulus) ferruginosa Clarke (1962, p. 65).
Thyasira ferruginea Tebble (1966, p. 80; fig. 35*a–b*).
Thyasira (Axinulus) ferruginea Bowden & Heppell (1968, p. 245, 263).
Thyasira ferruginea Petersen (1968, p. 52).
Thyasira ferruginea McMillan (1968, p. 83).
Lucina ferruginosa Harry (1969, p. 179).
Axinulus ferruginosus Nordsieck (1969, p. 80; fig. 48.11, pl. 13).
Thyasira ferruginea Knudsen (1970, p. 170).
Thyasira ferruginea Turk (1973, p. 62).

Historical

This species was first described as *Kellia ferruginosa*, a name preoccupied by *Kellia ferruginosa* Morris. Winckworth (1932) changed the name to *Thyasira ferruginea* but had overlooked earlier emendation by Locard (1886) to *Axinus ferrugineus*. Although Locard's emendation was subsequently disregarded by most authors, Bowden & Heppell (1968) consider it to be a valid replacement name.

Jeffreys (1863) considered *Cryptodon rotundatum* S. Wood and *Kellia abyssicola* Forbes to be synonymous with *T. (M.) ferruginea*. Later Jeffreys (1881) added *Kellia transversa* Forbes and *Axinus oblongus* Monterosato to the synonymy. Lamy (1920) noted that *Axinus oblongus* is preoccupied by *Cryptodon oblongus* A. Adams.

Material

ship/cruise	no.	date	sta.	position	depth/m	number	gear
North America Basin							
Atlantis	264	24.05.61	F1	39° 47.0′N 70° 45.0′W	1500	3	ad
		24.05.61	G1	39° 42.0′N 70° 39.0′W	2000	6	ad
	273	27.09.61	GH1	39° 25.5′N 70° 35.0′W	2500	4	ad
		03.10.61	GH2	39° 26.0′N 70° 34.0′W	2488	2	ad
		03.10.61	GH3	39° 27.5′N 70° 33.5′W	2478	2	ad
		03.10.61	GH4	39° 29.0′N 70° 34.0′W	2469	4	ad
	277	23.05.62	D1	39° 54.5′N 70° 35.0′W	467–509	256	ad
Atlantis II	12	21.08.64	64	38° 46.0′N 70° 06.0′W	2886	1	es
		24.08.64	72	38° 16.0′N 71° 47.0′W	2864	9	es
		25.08.64	72	39° 46.5′N 70° 43.3′W	1330–1470	136	es
Chain	50	29.06.65	76	39° 38.3′N 67° 57.8′W	2862	2	es
Atlantis II	24	23.08.66	125	37° 24.0′N 65° 50.0′W	4825	8	es
			—	37° 26.0′N 65° 50.0′W			
		24.08.66	126	39° 27.0′N 66° 47.0′W	3806	6	es
			—	39° 37.5′N 66° 44.0′W			
	30	18.12.66	131	39° 38.5′N 70° 36.5′W	2178	49	es
			—	39° 39.0′N 70° 37.1′W			
	40	29.11.67	175	36° 36.0′N 68° 29.0′W	4667–4693	16	es
			—	36° 36.0′N 68° 31.0′W			
Chain	88	21.02.69	207	39° 51.3′N 70° 54.3′W	805–811	474	es
			—	39° 51.0′N 70° 56.4′W			
		22.02.69	209	39° 47.6′N 70° 51.5′W	1501–1693	58	es
West European Basin							
Chain	106	17.08.72	313	51° 32.2′N 12° 35.9′W	1491–1500	3	es
Biogas II		18.04.73	DS30	47° 38.3′N 09° 33.9′W	4106	1	ds
Biogas III		31.08.73	DS48	44° 29.0′N 04° 54.0′W	4203	2	ds
Thalassa		23.10.73	Z410	47° 50.7′N 08° 09.3′W	1180	6	pbs
		24.10.73	Z413	48° 03.1′N 08° 29.4′W	805	3	pbs
		24.10.73	Z417	48° 12.0′N 09° 09.5′W	865	1	pbs
		24.10.73	Z422	48° 21.0′N 09° 39.5′W	1175	3	pbs
		25.10.73	Z424	48° 27.9′N 09° 44.3′W	475	3	pbs
		25.10.73	Z426	48° 28.2′N 09° 39.1′W	860	6	pbs
		25.10.73	Z427	48° 27.0′N 09° 48.4′W	330	1	pbs
		25.10.73	Z428	48° 27.2′N 10° 49.7′W	850	2	pbs
		25.10.73	Z429	48° 28.0′N 09° 50.0′W	1300	2	pbs
		26.10.73	Z434	48° 40.7′N 09° 54.1′W	720	16	pbs
		26.10.73	Z436	48° 39.8′N 09° 56.4′W	1210	3	pbs
		26.10.73	Z438	48° 33.7′N 10° 25.0′W	1400	3	pbs
		26.10.73	Z439	48° 42.0′N 10° 23.4′W	500	37	pbs
		26.10.73	Z440	48° 41.4′N 10° 21.5′W	860	33	pbs
		26.10.73	Z441	48° 35.4′N 10° 33.2′W	1180	2	pbs

Material

ship/cruise	no.	date	sta.	position	depth/m	number	gear
		26.10.73	Z442	48° 54.8′N 11° 02.0′W	975	1	pbs
		27.10.73	Z443	48° 56.0′N 11° 02.0′W	660	42	pbs
Thalassa		27.10.73	Z444	48° 58.2′N 10° 58.5′W	380	30	pbs
		27.10.73	Z445	48° 52.2′N 11° 07.0′W	1200	5	pbs
		27.10.73	Z449	48° 41.3′N 10° 33.8′W	730	4	pbs
		28.10.73	Z451	48° 39.3′N 10° 36.4′W	1400	2	pbs
		29.10.73	Z457	48° 38.2′N 09° 52.6′W	800	16	gbs
		29.10.73	Z459	48° 37.3′N 09° 53.0′W	1180	3	gbs
Biogas IV		18.02.74	DS51	44° 11.3′N 04° 15.4′W	2430	1	ds
		18.02.74	DS52	44° 06.3′N 04° 22.4′W	2006	2	ds
		19.02.74	DS53	44° 30.4′N 04° 56.3′W	4425	3	ds
		22.02.74	DS55	47° 34.9′N 09° 40.9′W	4125	8	ds
		23.02.74	DS56	47° 32.7′N 09° 28.2′W	4050	1	ds
		23.02.74	DS58	47° 34.1′N 09° 08.2′W	2775	2	ds
		24.02.74	DS60	47° 26.8′N 09° 07.2′W	3742	1	ds
		26.02.74	DS62	47° 32.8′N 08° 40.0′W	2175	1	ds
		26.02.74	DS64	47° 29.2′N 08° 30.7′W	2156	1	ds
Biogas V		16.06.74	DS66	47° 28.2′N 09° 00.0′W	3480	11	ds
		17.06.74	DS67	47° 31.0′N 09° 35.0′W	4150	4	ds
		20.06.74	DS69	44° 21.9′N 04° 52.4′W	4510	5	ds
		21.06.74	DS70	44° 08.8′N 04° 17.4′W	2150	7	ds
Biogas VI		23.10.74	CP14	47° 32.0′N 09° 35.9′W	4237	1	cp
		24.10.74	DS76	47° 34.8′N 09° 33.3′W	4228	8	ds
		24.10.74	DS77	47° 31.8′N 09° 34.6′W	4240	15	ds
		29.10.74	DS82	44° 25.4′N 04° 52.8′W	4462	2	ds
		29.10.74	DS84	44° 30.0′N 04° 53.9′W	4466	3	ds
		30.10.74	DS85	44° 23.2′N 04° 50.8′W	4462	13	ds
		31.10.74	DS86	44° 04.8′N 04° 18.7′W	1950	7	ds
		30.10.74	CP21	44° 21.2′N 04° 49.3′W	4453	2	cp
		30.10.74	CP22	44° 22.9′N 04° 54.8′W	4475	1	cp
Sarsia		09.76	7601	43° 51.8′N 03° 43.3′W	3080–3100	3	nd
		09.76	7610	43° 44.7′N 03° 48.6′W	1100–1185	1	ag
		09.76	7622	43° 44.5′N 03° 43.3′W	1600	7	ad
		09.76	7627	43° 47.1′N 03° 46.0′W	1975–1990	13	ag
Cape Verde Basin							
Atlantis II	31	04.02.67	138	10° 36.0′N 17° 52.0′W	1944–1976	3	es
		05.02.67	141	10° 30.0′N 17° 51.5′W	2131	20	es
		05.02.67	143	10° 30.0′N 17° 51.5′W	1624–1796	65	es
		05.02.67	144	10° 36.0′N 17° 49.0′W	2051–2357	10	es
		06.02.67	145	10° 36.0′N 17° 49.0′W	2185	2	es
		06.02.67	147	10° 38.0′N 17° 52.0′W	2934	14	es
Angola Basin							
Atlantis II	42	22.05.68	200	09° 43.5′S 10° 57.0′E	2644–2754	3	es
		23.05.68	201	09° 25.0′S 11° 35.0′E	1964–2031	3	es
			—	09° 05.0′S 12° 17.0′E			
		23.05.68	202	08° 56.0′S 12° 15.0′E	1427–1643	8	es
Cape Basin			—	08° 46.0′S 12° 47.0′E			
Atlantis II	42	17.05.68	191	23° 05.0′S 12° 31.5′E	1546–1559	144	es
		17.05.68	192	23° 02.0′S 12° 19.0′E	2117–2154	219	es
		17.05.68	193	22° 56.0′S 12° 18.0′E	2094–2191	16	ad
		17.05.68	194	22° 54.0′S 11° 55.0′E	2864	452	es
Walda		06.71	DS05	21° 45.0′S 11° 07.8′W	2992	138	ds
Argentine Basin							
Atlantis II	60	11.03.71	236	36° 27.0′S 53° 31.0′W	497–518	1	es
		11.03.71	239	36° 49.0′S 53° 15.4′W	1661–1679	19	es
		13.03.71	242	38° 16.9′S 51° 56.1′W	4382–4402	28	es
		24.03.71	256	37° 40.9′S 52° 19.3′W	3906–3917	42	es
		26.03.71	259	37° 13.3′S 52° 45.0′W	3305–3317	13	es
		27.03.71	262	36° 05.2′S 52° 17.9′W	2440–2480	7	es
		28.03.71	264	36° 12.7′S 52° 42.7′W	2041–2048	10	es
Guiana Basin							
Knorr	25	28.02.72	295	08° 04.2′N 54° 21.3′W	1000–1022	30	es
		28.02.72	297	07° 45.3′N 54° 24.0′W	508–523	49	es
		29.02.72	299	07° 55.1′N 55° 42.0′W	1942–2076	4	es
		29.02.72	301	08° 12.4′N 55° 50.2′W	2487–2500	1	es

Distribution

T. (A.) ferruginea has an extremely wide geographical distribution and depth range. It is found in both the Atlantic and the Pacific Oceans. In the Pacific it is recorded from the Aleutian Islands and the Bering Sea. In the Atlantic it occurs in the North America Basin, west Greenland, Finmark, Novaya Zemblia, Atlantic coast of Europe, West European Basin, Bay of Biscay, Mediterranean, Adriatic, northwest Africa and the Azores. Clarke (1961) also gave doubtful records from the Cape Basin, Angola Basin, and the Scotia Sea. The present material confirm the records from the two former localities and provides additional records from the Cape Verde, Argentine and Guiana Basins.
Depth range: 50–4,825 m.

Shell description (figures 82 and 87)

Shell small, thin, fragile, variable in outline, typically ovate with distinct posterior angulation, height and length are approximately equal or length is slightly greater, white or semi-transparent, moderately inflated, surface covered with fine irregular concentric grooves, obscured by rough ferruginous coating which may also exhibit concentric ridging, juvenile specimens not always encrusted, thin periostracum beneath ferruginous layer; beak small, positioned on or just behind midline; antero-dorsal margin markedly convex, with anterior limit hook-like, postero-dorsal margin long, smoothly concave, anterior margin deep, continuous curve with ventral margin; primary sulcus faintly defined as flattening of postero-ventral margin, sub-marginal sulcus forms, small, faint radial indentation of postero-dorsal shell margins; hinge plate extremely variable, generally more thickened in shallow water specimens from off Norway and west Scotland, right valve with thickened projecting marginal flange ventral to beak, left valve with projecting tubercle ventral to beak fits ventral to flange of right, postero-dorsal margin forms indistinct lateral ridge, socket for lateral ridge on right valve, in specimens from deep water hinge plate reduced and may lack distinct tubercles, (examination of many specimens from different localities shows continuous variation depending on thickness of shell).

Largest specimen *Atlantis II*, sta. 256 measures (length × height × breadth) 4.4 × 4.3 × 2.4 mm, including the ferruginous coating. A number of specimens from *Atlantis II*, sta. 131 measure 3.5 × 3.5 × 2.3 mm; 2.7 × 2.5 × 1.6 mm; 1.9 × 1.6 × 1.1 mm; and 1.4 × 1.1 × 0.8 mm.

Shells do vary in shape (figure 87). Unfortunately the ferruginous deposit on the shell adheres so closely that we found it nigh impossible to remove it without breaking the shell. It proved difficult to check whether differences are related to particular geographical locations or depths and thus whether varieties are recognizable. Thus, we follow previous authors in referring this to one cosmopolitan species.

Internal morphology (figures 83–86)

The adductor muscles are relatively large, broadly oval, and approximately equal in size. The anterior muscle is prolonged dorsally. Both are clearly divided into 'quick' and 'catch' portions. Mantle fusion is limited to a posterior point where fusion of the inner mantle fold forms the posterior exhalent aperture. As in other species of *Thyasira* the mantle edge is anteriorly expanded as a glandular area ventral to the anterior adductor (figure 84). Radial and circular muscles in the mantle edge are well developed, particularly in the glandular region and around the posterior exhalent aperture.

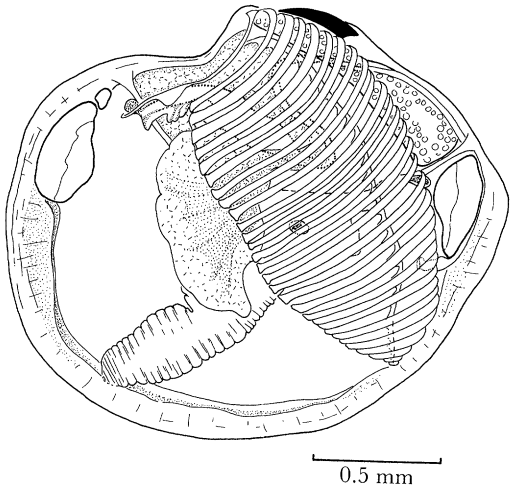

Figure 83. *Thyasira (Mendicula) ferruginea*: internal morphology as seen from the left side of a wholemount, specimen from *Chain*, station 207. (For identification of parts see figures 2 and 3.)

Figure 84. *Thyasira (Mendicula) ferruginea*: transverse section through the antero-ventral mantle edge; specimen from *Thalassa*, station Z440. (For identification of parts see figure 80.)

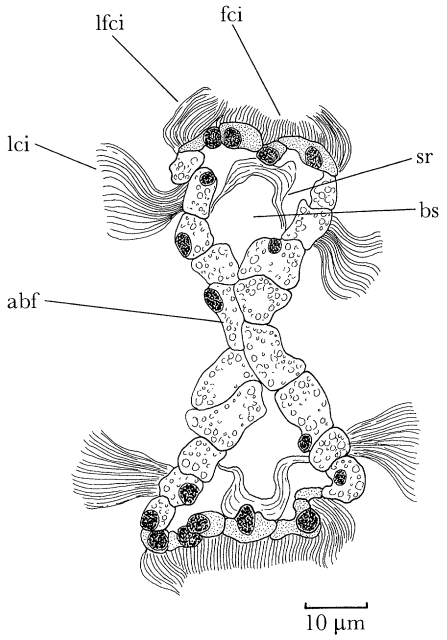

Figure 85. *Thyasira* (*Mendicula*) *ferruginea*: transverse section through a pair of gill filaments to show interlamellar fusion of the abfrontal surfaces. (List of abbreviations: see p. 561.)

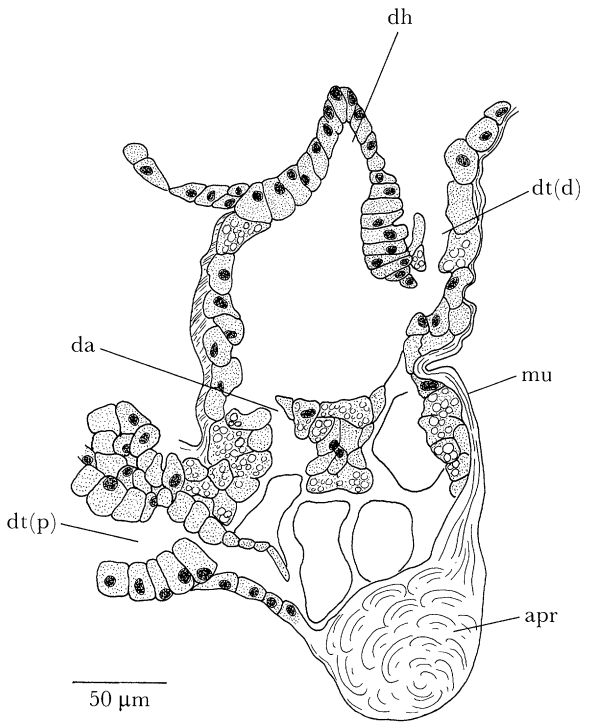

Figure 86. *Thyasira* (*Mendicula*) *ferruginea*: transverse section through anterior part of the stomach to show the digestive apertures and tubules. (List of abbreviations: see p. 561.)

Each gill is formed of a single demibranch with 13–33 filaments, depending upon the size of the specimen. The ascending lamella is two thirds as large as the descending lamella. The lamellae are connected ventrally by the fusion of the abfrontal filamentar surfaces but are free dorsally. There is a food groove at the ventral margin of the gill. In transverse section (figure 85) the gill filaments are triangular with a broad frontal surface, there is little abfrontal tissue. In this respect they differ from most species of the subgenera and *Thyasira* and *Parathyasira* and, to a lesser extent from *Axinulus*. The ciliation and musculature of the gills are well developed.

The foot is vermiform but with a broad muscular base and a well-developed heel that is sagittally grooved at its posterior end. Cilia are present on either side of the groove but not within it.

The course of the gut is similar to other species. The digestive apertures open into the stomach ventral to the oesophageal opening. A pair of digestive tubules pass one to each side of the oesophagus to the dorsal part of the body. A second and ventral pair pass to the lateral pouches (figure 86). The gastric shield is well developed and underlain by a thick columnar epithelium. The style sac is long and tapering and lined by regular cuboid cells bearing a stiff brush border. Typhlosoles formed by a row of guard cells cover the midgut groove. The hindgut is thin-walled but not swollen, at its posterior limit a short ventral groove is present. This groove was not seen in other species.

The lateral pouches are elongate, slightly lobed structures. There are no marked indentations but some convolution of the digestive tubules within gives an uneven external appearance. The structure of the digestive tubules differs from that of the species *Axinulus* in that the tubules are discrete and circular in section with a large lumen surrounded by moderately small tubule cells.

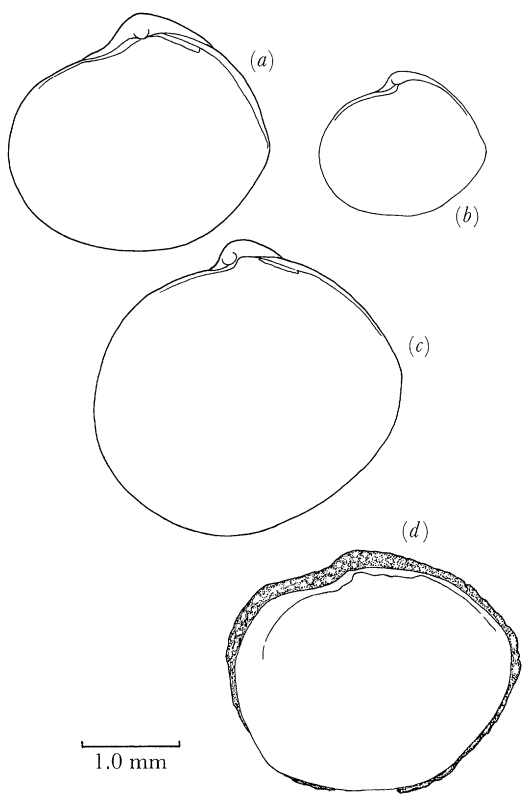

Figure 87. *Thyasira* (*Mendicula*) *ferruginea*: outline drawings of shells from a number of stations to show variation in shape; (*a*) and (*b*) *Chain*, station 207; (*c*) *Atlantis II*, station 256; and (*d*) Norway, USNM No. 225205.

The gonads are located to the inside of the body pouches and open by way of a pair of gonadial ducts to the supra-branchial cavity. The paired kidney is large. It occupies the space ventral to the posterior end of the ligament and the posterior adductor muscle. The two halves are separate at their anterior end where they lie either side of the pericardium. The latter is penetrated by the hindgut. The kidney is roughly triangular in cross section and lined with vacuolated cells some of which contain large spherical concretions. A pair of short kidney ducts open into the supr-branchial cavity anterior to the posterior adductor muscle. The arrangement of the nervous system is no different from those described before.

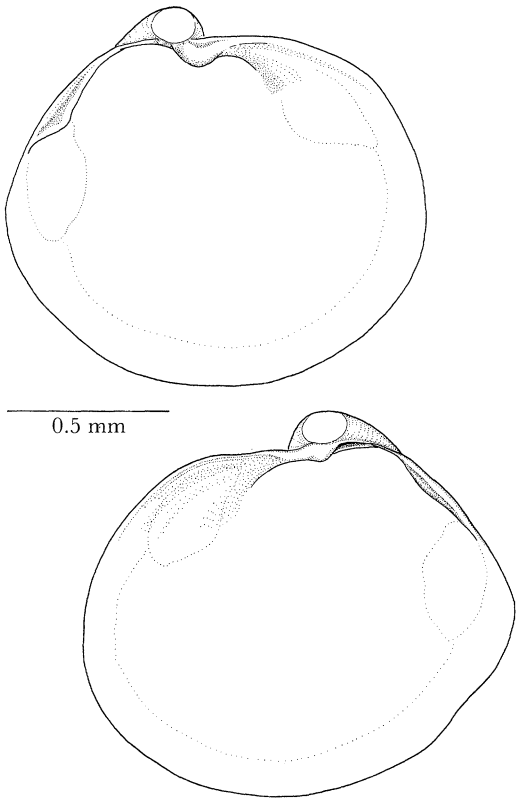

Figure 88. *Thyasira* (*Mendicula*) *ovata*: interior view of the left and right valves; specimen from *Atlantis II*, station sl. 3.

Thyasira* (*Mendicula*) *ovata (Verrill & Bush, 1898)

Type species: *Cryptodon* (*Axinulus*) *ovatus* Verrill & Bush, 1898.
Type locality: Off northeast United States from 40° 03.00′N, 70° 31.00′W; 183 m.
Type specimen: Holotype. USNM No. 159887.

Synonymy
Cryptodon (*Axinulus*) *ovatus* Verrill & Bush (1898, p. 793–4, fig. 7, pl. 91, fig. 1, pl. 92).
Thyasira (*Axinulus*) *ferruginosa* Dall (1901, p. 787).
Axinulus ovatus Lamy (1920, p. 314).

Material

ship/cruise	no.	date	sta.	position	depth/m	number	gear
North America Basin							
Atlantis	273	28.08.62	Sl2	40° 01.8′N 70° 42.0′W	200	331	ad
		28.08.62	Sl3	39° 58.4′N 70° 40.3′W	300	1320	ad
		28.08.62	Sl4	39° 56.5′N 70° 39.9′W	400	71	ad
Atlantis II	40	27.11.67	172	40° 12.3′N 70° 44.7′W	119	4	es
			—	40° 10.8′N 70° 43.6′W			

Distribution

This species has only been recorded from off the coast of northeast United States (Verrill & Bush 1898). As stated by Dall (1901) three larger specimens recorded by Verrill & Bush from 35° 20.30′N, 75° 19.00′W are probably specimens of *T.* (*M.*) *ferruginea*. Depth range: 119–400 m.

Shell description (figure 88)

Shell small, ovate, thin, transparent and fragile, completely covered by smooth ferruginous crust, chestnut brown in colour, interior transparent, with fine concentric lines; beaks small, rounded, positioned posterior to midline; posterior margin a little produced and angulate where it joins ventral margin, in some specimens with beaks in midline the angulation is stronger (Verrill & Bush 1898), antero-dorsal margin almost horizontal for a short distance anterior to beaks, then descends to broadly rounded antero-ventral margin; primary sulcus ill-defined but produces small amount of flattening of shell margin ventral to posterior angulation; hinge plate of right valve bears projecting, swollen tubercle ventral to beak, small elongated lateral tooth at postero-dorsal margin, hinge plate of left valve bears projecting, swollen tubercle, posterior to this is an indentation to receive tubercle of right valve; postero-dorsal margin of left valve with large, projecting, pointed lateral 'tooth' and shallow lateral socket; ligament relatively large, in sunken groove on ventral surface of hinge plate, it reaches one quarter of distance to posterior margin.

Externally this species resembles *T.* (*M.*) *ferruginea* in being completely covered with iron deposit. However, the encrustation in this species is smoother and is a different and distinct chestnut brown colour. In *T.* (*M.*) *ferruginea* the deposit is rougher and is dark brown in colour. The two species reach a different size, thus *T.* (*M.*) *ferruginea* reaches 3.5 mm in length but *T.* (*M.*) *ovata* only 1.5 mm. The hinge plate of *T.* (*M.*) *ovata* is much stronger than that of *T.* (*M.*) *ferruginea*.

Historical

Dall (1901) considered *T.* (*M.*) *ovata* identical to *T.* (*M.*) *ferruginea*. Subsequent authors have followed Dall. Except for one feature, material obtained near the type locality agrees with figures by Verrill & Bush

(1898). The latter specimens have a strong projecting lateral 'tooth' at the postero-dorsal margin of the left valve (figure 88). This tooth is less well defined in our specimens. Although the species is closely related to *T.* (*M.*) *ferruginea* the differences in the hinge plate are great and it is here regarded as a separate species.

Internal morphology (figures 89–90)

The anterior and posterior adductor muscles are particularly large in relation to the size of the body. The anterior adductor is an elongate oval, with a short, narrow, dorsal prolongation. The posterior muscle is oval and similar in cross sectional area to the anterior muscle. Both are clearly divided into 'quick' and 'catch' parts.

The mantle edge is similar to that of *T.* (*M.*) *ferruginea*. Ventral to the shelf-like dorsal surface of the inner fold there is a flap which overlies the middle fold. Postero-ventrally these flaps are ciliated and it is assumed that they interlock to form a second posterior exhalent aperture. A single postero-ventral point of tissue fusion closes the posterior exhalent aperture. Adhesion of the inner mantle folds occurs ventral to the anterior inhalent region.

Each gill is composed of an inner demibranch with 16–18 filaments in a fully grown specimen. The ascending lamella is approximately half as large as the descending lamella. Interlamellar junctions are present ventrally but there are no horizontal interfilamentar connections. The structure of the filaments is similar to those of *T.* (*M.*) *ferruginea*. Ciliation is well developed, lateral cilia are located midway between frontal and abfrontal surfaces, the latero-frontal cilia are strongly curved to each side of the frontal surface and the frontal cilia are about half the length of the latter.

The gut and stomach are similar to those in *T.* (*M.*) *ferruginea*. A large trematode parasite was present in the stomach of the sectioned individual and (figure 90) entirely filled the lumen. Lateral pouches are elongate, oval, with characteristic small lobes along the dorsal margin. The lobes are just visible below the ventral edge of the gill. Approximately 50% of each lateral pouch is occupied by the gonad. Forty-four eggs were present in one large individual (27 in the right ovary, 17 in the left). The gonadial ducts originate from the inner side of each gonad, they are oval in section and wide enough to accommodate two eggs side by side.

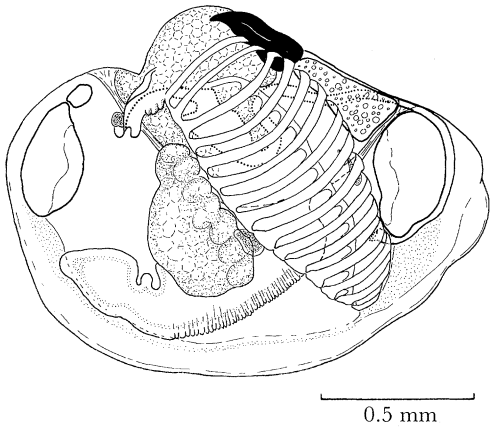

Figure 89. *Thyasira* (*Mendicula*) *ovata*: internal morphology as seen from the left side of a wholemount, specimen from *Atlantis II*, station sl. 3. (For identification of parts see figures 2 and 3.)

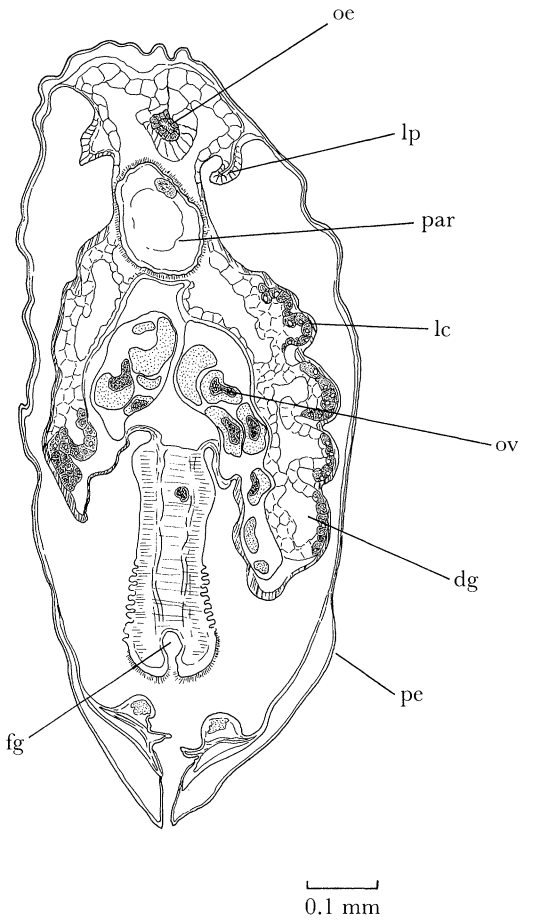

Figure 90. *Thyasira* (*Mendicula*) *ovata*: median transverse section through the body showing a trematode parasite in the stomach; specimen from *Atlantis II*, station sl. 3. (List of abbreviations: see p. 561.)

The kidneys are paired elongate sacs which communicate in the central section, but are separate at their anterior and posterior ends. In sectioned specimens the epithelial cells did not contain refractory concretions.

Thyasira* (*Mendicula*) *pygmaea (Verrill & Bush, 1898)

Type species: *Cryptodon* (*Axinulus*) *pygmaeus* Verrill & Bush, 1898.
Type locality: East of Newfoundland. 47° 50.00′N, 57° 35.30′W; 377 m.
Type specimen: Lectotype USNM No. 78368.

Synonymy
Cryptodon (*Axinulus*) *pygmaeus* Verrill & Bush (1898, p. 792–93; pl. 86, figs. 3–4).
? *Thyasira* (*Axinulus*) *pygmaea* Dall (1901, p. 788).
Axinulus pgymaeus Lamy (1920, p. 312).
Thyasira (?) *pygmaea* Johnson (1934, p. 40).
Axinulus pygmaeus Madsen (1949, p. 54–55, figs. 7*a–d*).
Thyasira (?) *pygmaea* La Rocque (1953, p. 58).
Axinulus pygmaeus Ockelmann (1958, p. 197).

Since Dall (1901) stated that this species may be a

juvenile of *T.* (*M.*) *ferruginea*, *T.* (*M.*) *pygmaea* has been largely ignored in the literature. More recently it has been recorded and figured by Madsen (1949) from Iceland. Although the shape of the shell and the internal morphology strongly suggests a close relationship with *T.* (*M.*) *ferruginea*, the more elongate shape and less robust and more simple hinge plate distinguishes it from the latter species.

Material

ship/cruise	no.	date	sta.	position	depth/m	number	gear
North America Basin							
Atlantis	273	23.05.61	D1	39° 54.5′N 70° 35.0′W	467–509	374	ad
		24.05.61	E3	39° 50.5′N 70° 35.0′W	824	49	ad
	283	28.08.62	S14	39° 56.5′N 70° 39.9′W	400	51	ad
Atlantis II	12	25.08.64	73	39° 46.5′N 70° 43.3′W	1330–1470	5	es
Chain	50	06.07.65	87	39° 48.7′N 70° 40.8′W	1102	10	et
	58	05.05.66	105	39° 56.6′N 71° 03.6′W	530	459	es
	88	21.02.69	207	39° 51.3′N 70° 54.3′W	805–811	851	es
			—	39° 51.0′N 70° 56.4′W			

Distribution

Off the northeast American coast from Martha's Vineyard, Massachusetts, to a position east of Newfoundland (Verrill & Bush 1898), also from south Iceland (Madsen 1949). The present material is from the North America Basin. Depth range: 377–1,470 m.

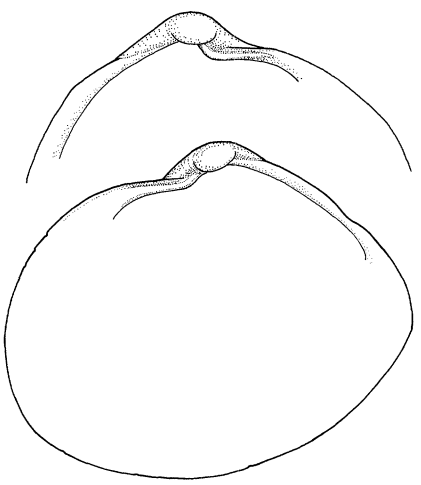

Figure 91. *Thyasira* (*Mendicula*) *pygmaea*: hinge plate of left valve and interior of right valve; specimens from *Chain*, station 207.

Shell description (figures 91 and 96)

Shell small, thin, white to semi-transparent, slightly inflated with very fine concentric growth lines, small patches of ferruginous deposit adhere to anterior and posterior shell margins, longitudinally ovate with a posterior angulation; beaks rounded, immediately posterior to midline; antero-dorsal margin horizontal for short distance before descending steeply to gently curved ventral margin, postero-dorsal margin slopes evenly to posterior angulation, in region escutcheon forms small posterior auricle, primary sulcus defined by faint postero-ventral flattening of shell margin; lunule distinct; hinge plate narrow, ventral to beaks, narrow projecting ridge anterior to beak of right valve fits into similar ridge on left valve; ligament in short groove inset in ventral margin of hinge plate; indistinct muscle scars.

Specimens from *Atlantis II*, sta. 207 measure (length × height × breadth): 2.0 × 1.65 × 1.1 mm; 1.4 × 1.2 × 0.7 mm and 1.25 × 1.00 × 0.6 mm.

Internal morphology (figure 92)

The internal morphology is similar to that of *T.* (*M.*) *carrozae* (described below).

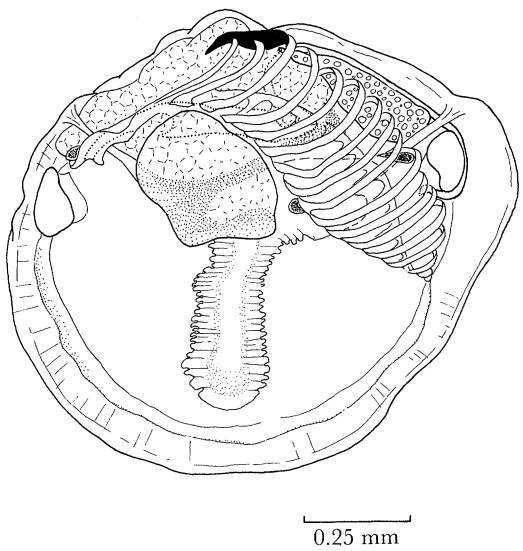

Figure 92. *Thyasira* (*Mendicula*) *pygmaea*: internal morphology as seen from the left side of a wholemount; specimen from *Chain*, station 207. (For identification of parts see figures 2 and 3.)

Thyasira* (*Mendicula*) *carrozae (new species)

Type locality: Cape Basin, 23° 00.0′S, 12° 58.0′E; 619–622 m.

Type specimen: BM(NH) 1990035.

Taxonomy

T. (*M.*) *carrozae* is similar to *Axinus oblongus* Monterosato, taken off Palermo at a depth of 210 m (Monterosato 1875). The name *A. oblongus* is preoccupied by *Cryptodon oblongus* A. Adams. Monterosato

(1875, 1880, 1882) questioned if *A. oblongus* could possibly be synonymous with *Kellia transversa* Forbes, which latter species Jeffreys (1881) believed was synonymous with *Thyasira ferruginea*. Monterosato (1882) totally disagreed with the latter view.

This species is distinguished from *T.* (*M.*) *pygmaea* (figure 96) by the beak being approximately equidistant from the anterior and posterior margins, by hinge teeth rather than rounded tubercles and by the short ligament. The species is somewhat variable in shape (figure 95). Specimens from *Atlantis II* sta. 203 are particularly distinctive in that the beaks are immediately posterior to the midline, the long antero-dorsal margin forms a blunt posterior angle and the pseudo-cardinal 'teeth' are particularly well developed. Nevertheless, the specimens from sta. 203 are

Material

ship/cruise	no.	date	sta.	position	depth/m	number	gear
North America Basin							
Chain	88	22.02.69	209	39° 47.6′N 70° 49.9′W	1501–1693	29	es
			—	39° 46.0′N 70° 51.5′W			
Cape Verde Basin							
Atlantis II	31	05.02.67	142	10° 30.0′N 17° 51.5′W	1624–1796	43	es
Angola Basin							
Atlantis II	42	23.05.68	201	09° 25.0′S 11° 35.0′E	1964–2031	1	es
		23.05.68	203	08° 48.0′S 12° 52.0′E	527–542	235	es
Walda		06.71	DS10	18° 40.0′S 10° 56.3′E	1432	44	ds
Cape Basin							
Atlantis II	42	16.05.68	182	22° 53.0′S 13° 23.0′E	307	9	ad
		16.05.68	185	22° 56.0′S 13° 02.0′E	458–463	50	ad
		16.05.68	187	22° 58.0′S 13° 01.0′E	626–631	110	ad
		16.05.68	188	23° 00.0′S 12° 58.0′E	619–622	3899	es
		16.05.68	189	23° 00.0′S 12° 45.0′E	1007–1810	1810	es
		17.05.68	190	23° 05.0′S 12° 45.0′E	974–979	68	ad
		17.05.68	191	23° 05.0′S 12° 31.5′E	1546–1559	174	es
Argentine Basin							
Atlantis II	60	11.03.71	239	36° 49.0′S 53° 15.4′W	1661–1679	196	es
		14.03.71	245	36° 55.7′S 53° 01.4′W	2707	4	es
		28.03.71	264	36° 12.7′S 52° 42.7′W	2041–2048	20	es

Distribution

Widely distributed in the North America, Cape Verde, Angola, Cape and Argentine Basins. Possibly in the Mediterranean should this prove to be identical to *Axinus oblongus* Monterosato. Depth range: 307–2707 m.

Shell description (figures 93 and 95)

Shell small, white, triangulate when fully grown, smaller specimens less triangular and more longitudinally oval, length greater than shell height, moderately inflated, sculpture, fine concentric lines with growth stages at intervals, thin ferruginous deposit frequently adheres to posterior shell margin and beaks, interior with fine concentric lines, muscle scars indistinct; rounded beaks positioned at or immediately posterior to midline; posterior margin flattened and wedge-shaped, antero-dorsal and postero-dorsal margins straight descending at low angle from beaks, ventral margin broad even curve; primary sulcus only indicated by flattening of posterior shell margin; escutcheon present; lunule indistinct; hinge plate of right valve with small projecting 'tooth' ventral to beak, left valve with similar 'tooth' anterior to beak, lateral 'teeth' absent, hinge plate not thickened; ligament extremely short, broad, in short sunken groove reaching only one sixth of distance to posterior margin; postero-dorsal margin frequently covered by growth of hydroids.

Specimens from *Atlantis II*, sta. 188 measure (length × height × breadth): 1.72 × 1.50 × 1.12 mm; 1.57 × 1.19 x 0.97 mm; 1.05 × 0.90 × 0.52 mm.

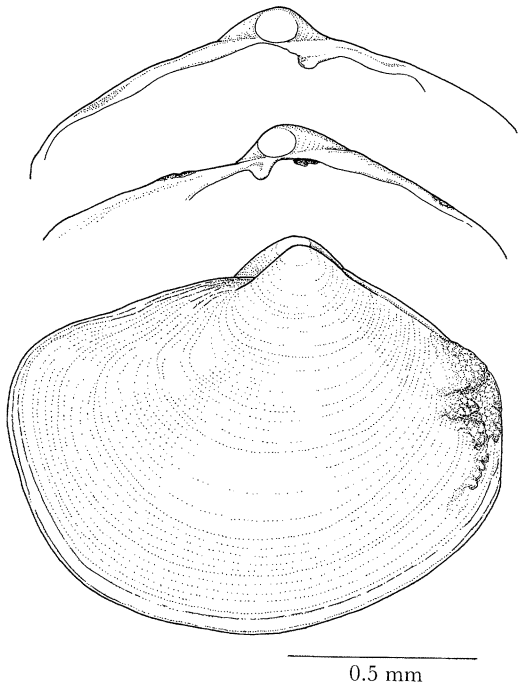

Figure 93. *Thyasira* (*Mendicula*) *carrozae*: hinge plate of the left and right valves and a lateral view of the left valve; specimen from *Atlantis II*, station 203.

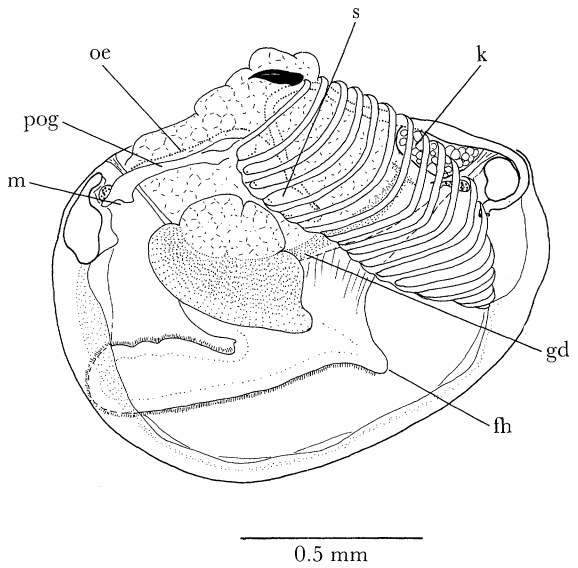

Figure 94. *Thyasira* (*Mendicula*) *carrozae*: internal morphology in lateral view of a wholemount; specimen from *Atlantis II*, station 188. (List of abbreviations: see p. 561.)

regarded as exhibiting no more than population differences.

Internal morphology (figure 94)

Both adductor muscles are relatively small, the anterior is oval in cross section with a narrow dorsal prolongation. The posterior adductor muscle is also oval but about half as large as the anterior adductor. There is a single posterior point of mantle fusion and it is to this point that the gill axes join. There is no evidence of mantle adhesion at the anterior or posterior end of the pedal gape. The inner lobe is expanded below the anterior adductor muscle to form a glandular region and a similar expansion occurs at the posterior exhalent aperture. The rejection tract on the inner fold is relatively ill defined. The middle fold is well developed, and forms a single sensory frill.

Each gill comprises an inner demibranch, the ascending lamella being approximately two thirds the size of the descending lamella. Each demibranch comprises 14–18 filaments in large specimens. Except dorsally, interlamellar junctions are present. A small number of interfilamentar cross connections are also present. A row of large cells to each side of the frontal surface bear the lateral cilia. There is little abfrontal tissue. The central blood space is bordered by skeletal rods and muscle fibres.

The labial palps are minute, triangular structures at the ends of the very long proximal oral groove. Although they are heavily ciliated, there are no distinct grooves on the inner surface of the palps. The foot is short and somewhat spade-like and it has a well-defined heel that is pointed posteriorly. The heel of the foot is grooved in the sagittal plane. The base of the foot is more broad and more muscular than that of *T.* (*M.*) *pygmaea*. The posterior pedal retractor muscles are considerably larger than the anterior pair. The ciliated epithelium of the foot is not thrown into extensive folds in the contracted state, suggesting that the foot is less extensible than that of other species. Externally the tip of the foot is not differentiated from the stem. Longitudinal muscles from the base of the foot extend to each side of the heel.

The course of the gut is simple and similar to that of other species. The oesophagus is long; and opens on the anterior dorsal face of the broad stomach. The digestive apertures open antero-ventrally. The junction between stomach and style sac is marked by a constriction of the stomach wall. The hindgut loops anteriorly before turning posteriorly, it penetrates the ventricle, and then passes dorsally over the posterior adductor muscle. The oesophagus is not internally grooved but is lined with a heavily ciliated epithelium. The digestive apertures open to dorsal and lateral parts of the digestive diverticula the apertures to the lateral tubules being the wider. The entire inner dorsal surface of the stomach is covered by a gastric shield. The lateral pouches are ovate and are characteristically inflated but with a blunt, but narrow postero-ventral extremity. There are no lobes or divisions to the pouch wall.

The sexes are separate. Eggs measure up to 65 μm in length.

The kidneys are small in size and oval in section and the epithelium is without concretions in these specimens examined.

Thyasira* (*Mendicula*) *inflata (new species)

Type locality : Angola Basin, 10° 29.0′S, 09° 04.0′E; 4595–4597 m.

Type specimen: BM(NH) No. 1990034.

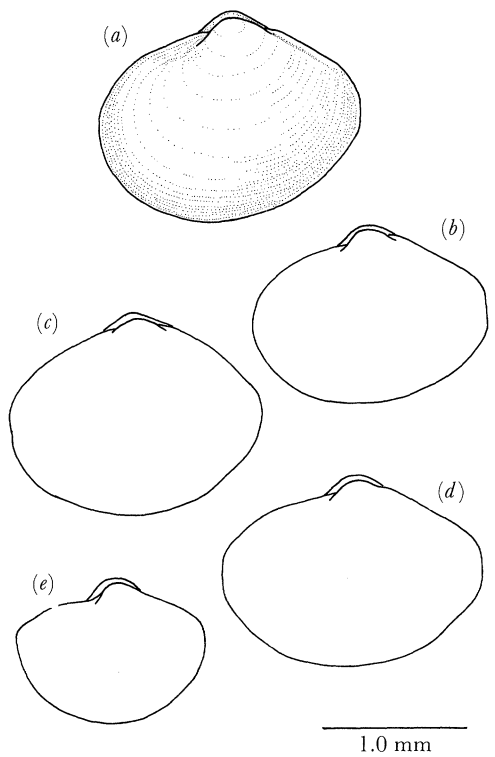

Figure 95. *Thyasira* (*Mendicula*) *carrozae*: outline drawings of shells from a number of stations to show variation in shape; (*a*) *Atlantis II*, station 189; (*b*) and (*c*) *Atlantis II*, station 188; (*d*) *Atlantis II*, station 189; and (*e*) *Atlantis II*, station 203.

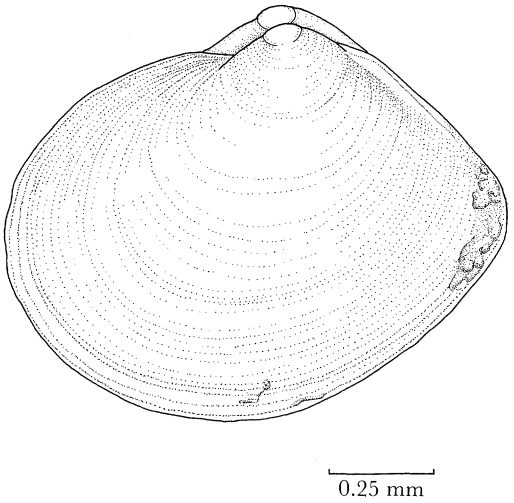

Figure 96 *Thyasira* (*Mendicula*) *pygmaea*: lateral view of the shell from the left side; USNM No. 6833897.

This species differs from *T.* (*M.*) *transversa* in being more obliquely oval, with beaks closer to the midline and with a less flattened posterior shell angulation. It differs from *T.* (*M.*) *carrozae* in size, shape and form of the hinge plate. Specimens from a number of different sampling stations are outlined in Figure 99.

Internal morphology (figure 98)

The anterior and posterior adductor muscles are almost equal in size and approximately oval in shape. The anterior muscle is the more dorsally elongate. The structure of the mantle edge is similar to that described for other species of *Mendicula*. The inner mantle fold is fused at a single point to form the posterior exhalent aperture. The gland cells of the inner fold are particularly numerous in the area ventral to the anterior adductor muscle.

Each gill is made up of a single demibranch. The ascending lamella is approximately half the length of the descending lamella. Each demibranch comprises about 12 filaments. The labial palps are extremely small, the inner surfaces are heavily ciliated and thrown into a small number of indistinct folds. The foot is relatively short with a heavily ciliated rounded tip

Material

ship/cruise	no.	date	sta.	position	depth/m	number	gear
West European Basin							
Biogas IV		21.02.74	DS54	46° 31.1′N 10° 29.2′W	4659	1	ds
Biogas VI		30.10.74	CP22	44° 22.9′N 04° 54.8′W	4475	1	cp
Angola Basin							
Atlantis II	42	21.05.68	197	10° 29.0′S 09° 04.0′E	4595–4597	43	es
		21.05.68	198	10° 24.0′S 09° 09.0′E	4559–4566	16	es
			—	09° 47.0′S 10° 29.0′E			
Argentine Basin							
Atlantis II	60	13.03.71	242	38° 16.9′S 51° 56.1′W	4382–4402	4	es
		24.03.71	256	37° 40.9′S 52° 19.3′W	3906–3917	8	es

Shell description (figure 97)

Shell minute, thin, white, globose, obliquely oval with distinct posterior angulation, sculpture, very fine concentric lines, growth stages indistinct, thin layer of ferruginous material occurs around beaks and shell margins, interior glossly, covered with fine radiating and concentric lines; beaks posterior to midline, prominent, inward and anteriorly turned; anterior dorsal margin almost horizontal for short distance then descends gradually to broadly curved, obliquely prolonged antero-ventral margin, postero-dorsal margin convex and evenly curved; primary sulcus not present, postero-dorsal margin indented by small indistinct sub-marginal sulcus; lunule small, oval; hinge plate of left valve with protruberance immediately anterior to beak, socket ventral to beak houses similar protruberance of right valve, left valve with postero-dorsal lateral groove which houses lateral projection of margin of right valve; ligament recessed in ventral face of hinge plate, reaches one quarter to one third of distance to posterior margin.

Specimens from *Atlantis II*, sta. 198 measure as follows (length × height × breadth): 1.15 × 1.00 × 0.85 mm; 1.08 × 0.90 × 0.70 mm and 1.05 × 0.90 × 0.63 mm.

Distribution

West European Basin (Bay of Biscay), off Angola, and in the Argentine Basin. Depth range: 3865–4659 m.

Figure 97. *Thyasira* (*Mendicula*) *inflata*: hinge plate of the left valve and interior view of the right valve; specimen from *Atlantis II*, station 197.

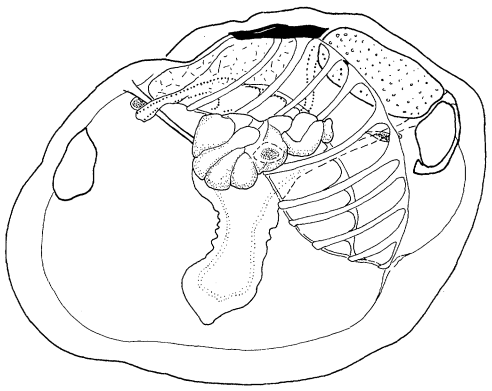

Figure 98. *Thyasira* (*Mendicula*) *inflata*: internal morphology as seen in lateral view from the left side of a whole mount; specimen from *Atlantis II*, station 197. (For identification of parts see figures 2 and 3.)

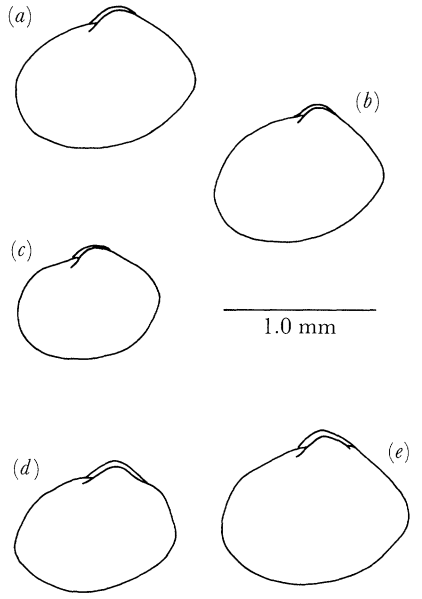

Figure 99. *Thyasira* (*Mendicula*) *inflata*: outline drawings of shells from a number of stations showing variation in shape: (*a*) *Atlantis II*, station 197; (*b*) *Atlantis II*, station 198; (*c*) *Atlantis II*, station 256; (*d*) *Biogas VI*, station CP 22; and (*e*) *Biogas IV*, station DS 54.

and a distinct heel which is sagittally grooved. It is similar to that of *T.* (*M.*) *pygmaea*.

The gut and digestive apertures follow the same plan of other species of *Mendicula*. The stomach, although small has a well developed gastric shield, but the most noticeable feature of the digestive system was the inordinately swollen hindgut anterior to the posterior adductor. The distension is such that in some specimens the hindgut obscures the kidney when viewed laterally. No specialized cells were seen in this section of wall of the hindgut. The lateral pouches are extremely small, ovate but bluntly pointed posteriorly. They are not lobed or divided and the tubules within are unbranched. The digestive diverticula are not extensive. The dorsal sections are located above the oesophagus and stomach. The lateral sections occupy the antero-dorsal portion of the lateral pouches. The digestive cells are arranged around a very narrow central lumen.

Much of the lateral pouch is occupied by gonad. Sexes are separate. In whole mounts of mature specimens the pouches appear to be almost entirely filled with eggs or sperm. The eggs measure 62 μm in length.

The structure of the heart and kidney is similar to species previously described.

Thyasira* (*Mendicula*) *transversa (new species)

Type locality: Argentine Basin, 36° 12.7′S, 52° 42.7′W; 2041–2048 m.

Type material: Holotype BM(NH) No. 1990033.

Material

ship/cruise	no.	date	sta.	position	depth/m	number	gear
North America Basin							
Chain	50	04.07.65	84	36° 24.4′N 67° 56.0′W	4749	3	es
		05.07.65	85	37° 59.2′N 69° 26.2′W	3834	12	es
Atlantis II	24	21.08.66	121	35° 50.0′N 65° 11.0′W	4800	72	es
		21.08.66	122	35° 50.0′N 64° 57.5′W	4833	195	es
			—	35° 52.0′N 64° 58.0′W			
		22.08.66	124	37° 26.0′N 63° 59.5′W	4862	4	es
			—	37° 25.0′N 63° 58.0′W			
		23.08.66	125	37° 24.0′N 65° 54.0′W	4825	67	es
			—	37° 26.0′N 65° 50.0′W			
		24.08.66	126	39° 37.0′N 66° 47.0′W	3806	54	es
			—	39° 37.5′N 66° 44.0′W			
West European Basin							
Chain	106	21.08.72	323	50° 08.3′N 13° 53.7′W	3338–3356	1	es
			—	50° 08.3′N 13° 50.9′W			
North America Basin							
		23.08.72	328	50° 04.7′N 15° 44.8′W	4426–4435	42	es
		24.08.72	330	50° 43.5′N 17° 51.7′W	4632	20	es
			—	50° 43.4′N 17° 52.9′W			

Material

ship/cruise	no.	date	sta.	position	depth/m	number	gear
Cape Verde Basin							
Atlantis II	31	06.02.67	145	10° 36.0′N 17° 49.0′W	2185	46	es
		06.02.67	147	10° 38.0′N 17° 52.0′W	2934	2	es
Angola Basin							
Atlantis II	42	21.05.68	197	10° 29.0′S 09° 04.0′E	4595–4597	21	es
			—	10° 29.0′S 09° 04.0′E			
		21.05.68	198	10° 24.0′S 09° 09.0′E	4559–4566	6	es
			—	09° 47.0′S 10° 29.0′E			
		22.05.68	200	09° 43.5′S 10° 57.0′E	2644–2754	13	es
			—	09° 29.0′S 11° 34.0′E			
		23.05.68	203	08° 48.0′S 12° 52.0′E	527–542	1	es
Walda		06.71	DS10	18° 40.0′S 10° 56.3′E	1432	2	ds
Cape Basin							
Atlantis II	42	17.05.68	190	23° 05.0′S 12° 45.0′E	974–979	7	ad
		17.05.68	191	23° 05.0′S 12° 31.5′E	1546–1559	68	es
		17.05.68	192	23° 02.0′S 12° 19.0′E	2117–2154	27	es
		17.05.68	193	22° 56.0′S 12° 18.0′E	2094–2191	30	ad
Argentine Basin							
Atlantis II	60	11.03.71	237	36° 32.6′S 53° 23.0′W	993–1011	3	es
		11.03.71	239	36° 49.0′S 53° 15.4′W	1661–1679	169	es
		13.03.71	242	38° 16.9′S 51° 56.1′W	4382–4402	2	es
		17.03.71	247	43° 39.0′S 48° 58.1′W	5208–5223	6	es
		24.03.71	256	37° 40.9′S 52° 19.3′W	3906–3917	4	es
		27.03.71	262	36° 05.2′S 52° 17.9′W	2440–2480	52	es
		28.03.71	264	36° 12.7′S 52° 42.7′W	2041–2048	169	es
Brazil Basin							
Atlantis II	31	14.02.67	156	00° 46.0′S 29° 28.0′W	3459	2	es
			—	00° 46.5′S 29° 24.0′W			
Guiana Basin							
Knorr	25	28.02.72	297	07° 45.3′N 54° 24.0′W	508–523	3	es

Shell description (figure 100)

Shell small, transparent or semi-transparent, outline characteristically elongate, moderately inflated, length greater than height, sculpture very fine, shell appears smooth, black deposit adheres to shell margin; beaks posterior to midline; long evenly curved antero-ventral margin, posterior dorsal margin slightly convex, wedge-shaped posterior angulation; submarginal sulcus well defined, visible inside shell, primary sulcus ill-defined; hinge plate not greatly thickened, small, distinct, projecting 'tooth' present ventral and anterior to beak of right valve, left hinge 'tooth' similar but more elongate, no lateral 'teeth'; ligamental groove lies to ventral side of hinge plate, reaches one quarter of the distance to posterior margin.

Specimens from *Atlantis II*, sta. 264 measured as follows (length × height × breadth): 1.60 × 1.45 × 0.90 mm; 1.65 × 1.40 × 0.90 mm; 1.35 × 1.15 × 0.65 mm; 1.20 × 1.99 × 0.55 mm, and 0.85 × 0.68 × 0.40 mm.

This species is distinguished by (i) the elongate outline with beaks clearly posterior to the midline, (ii) the broad, flattened posterior wedge-shaped angulation and (iii) the distinct sub-marginal sulcus. The hinge plate and internal morphology are similar to *T.* (*M.*) *carrozae* while the shell shape is more similar to that of small specimens of *T.* (*P.*) *subovata*. The present species is distinguished from the latter by differences in the internal morphology and in the hinge plate. Variation in the shell shape of *T.* (*M.*) *transversa* is shown in figure 105.

Distribution

Distributed widely from the North America, West European, Cape Verde, Angola, Cape, Brazil and

Figure 100. *Thyasira* (*Mendicula*) *inflata*: hinge plate of the left and right valves and a lateral view of the shell from the left side; specimen from *Atlantis II*, station 191.

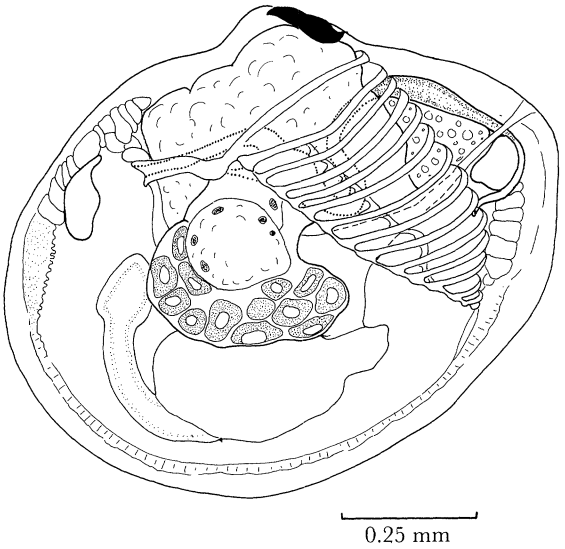

Figure 101. *Thyasira* (*Mendicula*) *transversa*: internal morphology from left side; specimen from *Walda*, station DS 10. (For identification of parts see figures 2 and 3.)

Guiana Basins. Depth range: 508–5223 m but the majority of specimens are from depths below 1500 m.

Internal morphology (figure 101)

The anterior and posterior adductor muscles are small and oval in cross section. The anterior muscle is somewhat more elongate with a narrow dorsal extension.

The inner fold of the mantle is fused at a single point, to form the posterior exhalent aperture. In preserved specimens the opposing mantle edges adhere along the entire ventral margin and probably do so in life. The adhesion must *a priori* be temporary and the mantle edges are easily separated in preserved specimens. An unusual feature of the mantle is the presence of very large gland cells adjacent to the anterior and posterior adductor muscles (figure 103). Of these the anterior are the most extensive and they are clearly visible in whole mounts. The cells have a fine amorphous cytoplasm which stains with eosin. The mantle edge (figure 102) is narrow. The inner fold forms a small dorsal shelf indented by a deep longitudinal rejection tract. Ventrally the inner mantle fold contains eosinophilic gland cells with a granular cytoplasm. These cells are smaller than those adjacent to the adductor muscles and are possibly involved in the adhesion of the inner folds. The middle mantle fold forms a small bilobed frill. A periostracal groove separates the middle fold from a narrow outer fold. Radial musculature extends from the pallial line into the middle and outer folds.

The gill consists of a single demibranch, the ascending lamella being approximately one third as large as the descending lamella. The ventral edges of the gills do not cover the lateral body pouches. In the largest specimens each demibranch contains 13–16 filaments. In transverse section (figure 104) the filaments have little abfrontal tissue but there are strong supporting skeletal rods. Ciliation is similar to that of other species of *Mendicula*.

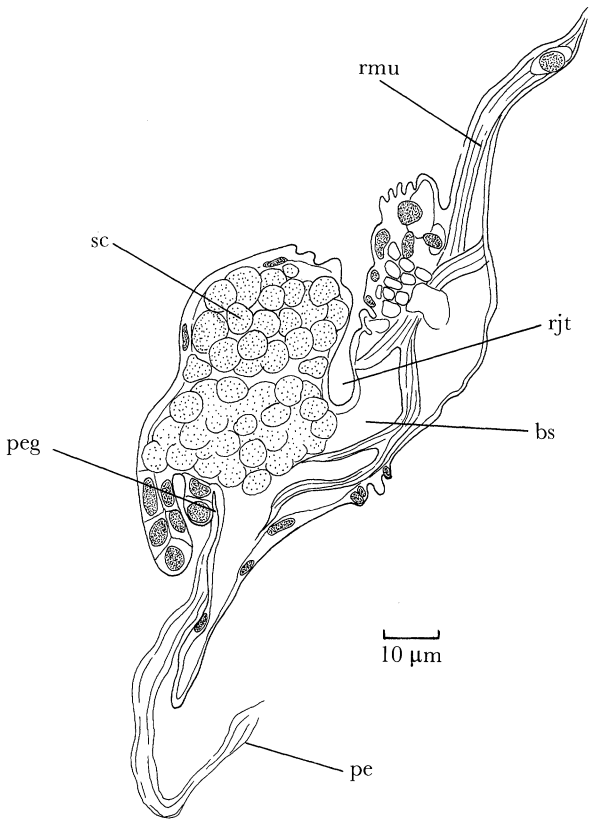

Figure 102. *Thyasira* (*Mendicula*) *transversa*: transverse section through the antero-ventral mantle edge. (List of abbreviations: see p. 561.)

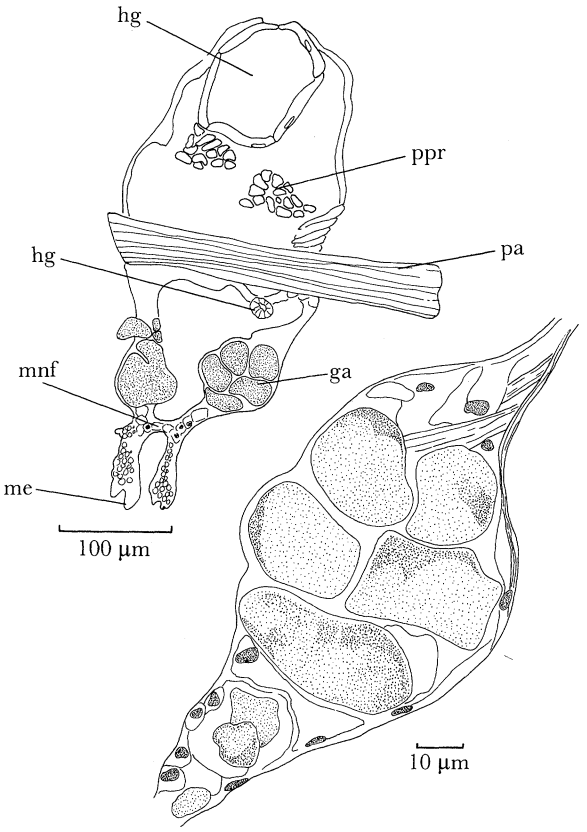

Figure 103. *Thyasira* (*Mendicula*) *transversa*: (*a*) transverse section through the posterior exhalent aperture; and (*b*) detail of the glandular part. (List of abbreviations: see p. 561.)

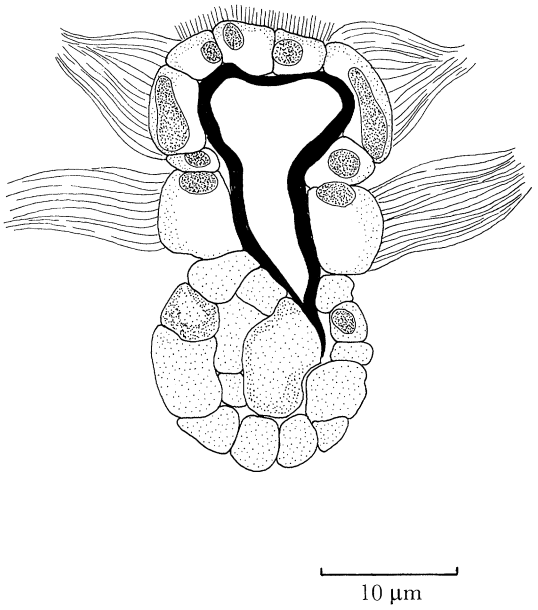

Figure 104. *Thyasira* (*Mendicula*) *transversa*: transverse section through a gill filament. (For identification of parts see figure 12.)

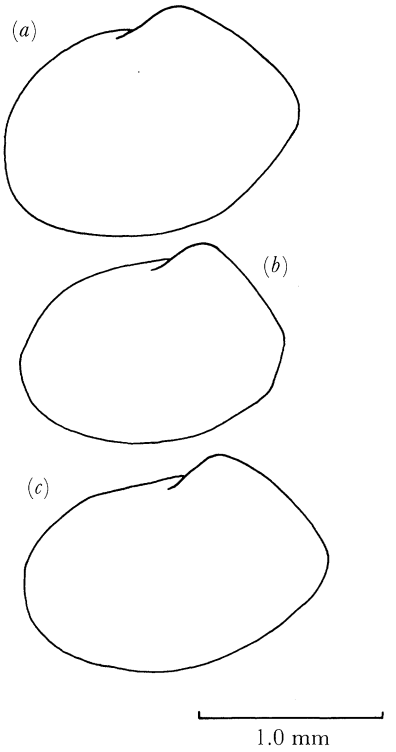

Figure 105. *Thyasira* (*Mendicula*) *transversa*: outline drawings of shells from a number of stations to show variation in shape of specimens: (*a*) *Atlantis II*, station 239; (*b*) *Atlantis II*, station 126 and (*c*) *Atlantis II*, station 262.

The labial palps are little more than raised borders at the end of the proximal oral groove. Each palp bears three or four indistinct grooves on its inner surface. The foot is narrow and elongate, with a broad muscular base and a sagittally grooved heel. When the foot is contracted, the base is grossly swollen in the region of the heel. The tip and stem of the foot and heel are ciliated, but there are no cilia within the groove. The anterior and posterior retractor muscles are broad, the posterior pair being particularly well developed.

The course of the gut is similar to that of other species of *Mendicula*. The stomach and style sac have thick walls composed of columnar epithelial cells which, in the dorsal part of the stomach below the gastric shield, contain refractile inclusions. The gastric shield is well developed. The style sac is relatively short and thickly lined with short brush-like cilia. The hindgut is extremely broad and thick walled. The walls have exceptionally large cells which are best seen where the gut is not distended. Extreme distension of the hind gut occurs dorsal to the kidney the lumen being filled with fine particulate material. The lateral pouches are small, oval and without lobes. The dorsal part contains the lateral digestive tubules whilst the ventral part contains the gonad. As in most small species of the subgenera *Axinulus* and *Mendicula* the digestive diverticula are composed of two pairs of unlobed tubules, on each side of the body and which open from the stomach. Two dorsal tubules lie on either side of the dorsal part of the body cavity, while each of two ventral tubules penetrates a lateral pouch. A small number of ovate deeply pigmented inclusions were present in the digestive cells of some whole mounts. The nature of these is not known for certain but, they may be ciliates. These were observed in other species taken from the same station (*Walda* DS10).

The majority of specimens examined were mature females. Fifty seven eggs were recorded in one specimen, the eggs measuring 72 μm in length.

The structure of the heart and kidney is similar to that of other species. Similarly the nervous system although well developed with all ganglia large in size, is also described in other species.

Thyasira* (*Mendicula*) *verrilli (new species)

Type locality: North America Basin, 32° 15.8′N, 64° 31.6′W; 2095 m.

Type material: Holotype BM (NH) No. 1990032.

Material

ship/cruise	no.	date	sta.	position	depth/m	number	gear
North America Basin							
Atlantis II	24	29.08.66	119	32° 15.8′N 64° 31.6′W	2095	40	es
			—	32° 16.1′N 64° 32.6′W			
Guiana Basin							
Knorr	25	29.02.72	299	07° 55.1′N 55° 42.0′W	1942–2076	15	es
		29.02.72	301	08° 12.4′N 55° 50.2′W	2487–2500	33	es

Shell description (figure 106)

Shell minute, characteristically elongate, fragile, transparent, moderately inflated, surface smooth, rather glossy, covered with fine growth lines but without distinct growth stages, some specimens with soft ferruginous deposit at ventral margin, others lack encrustation, internally thickened in region of anterior and posterior adductor muscles to form two radial lines from umbo to shell margin; beak posterior to midline, large and rounded; antero-dorsal margin straight, postero-dorsal margin steeply angled, flexed, forms oblique, wedge-shaped posterior angulation, posterior margin almost straight, meets broadly curved ventral margin in obtuse angle; primary sulcus faint, forms shallow radial indentation which joins margin at posterior shell angle, sub-marginal sulcus small, well defined; escutcheon present; hinge plates slightly thickened, narrow ventral to beak, antero-dorsal and postero-dorsal margins of hinge plates of right valve thickened, with narrow groove between shell margin and hinge plate, antero-dorsal and postero-dorsal shell margins of left valve fit the grooves, but projections indistinct and do not form lateral 'teeth'; ligament extremely short, broad, in sunken groove reaching one fifth of distance to posterior margin.

Specimens from *Knorr*, sta. 301 and *Atlantis II*, sta. 119 measure: 1.06 × 0.88 × 0.70 mm (*Knorr* 301): 1.00 × 0.85 × 0.68 mm; 0.85 × 0.73 × 0.55 mm; 0.78 × 0.68 × 0.46 mm; 0.68 × 0.58 × 0.35 mm, (*Atlantis II*, sta. 119). Only one specimen exceeds 1.00 mm in length.

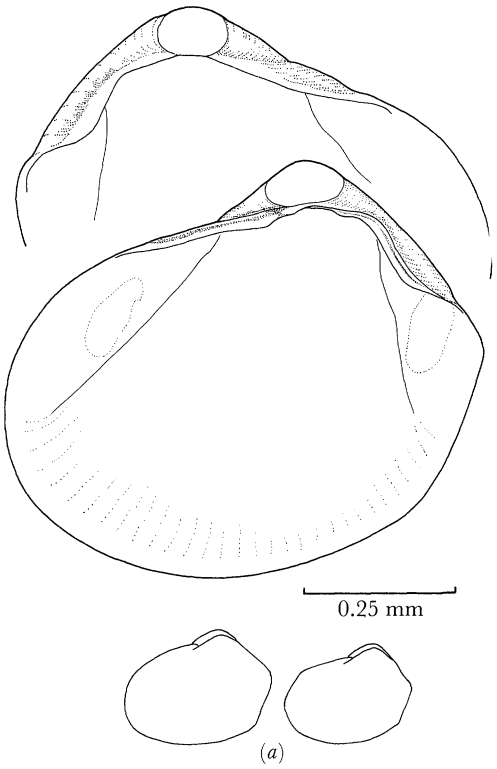

Figure 106. *Thyasira* (*Mendicula*) *verrilli*: hinge plate of left valve and interior view of the right valve; (*a*) outline drawings of whole shells; specimens from *Atlantis II*, station 119.

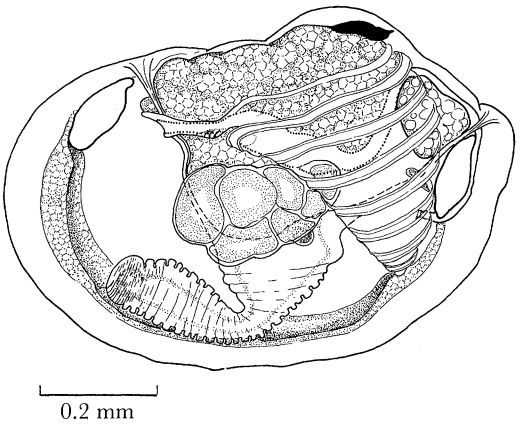

Figure 107. *Thyasira* (*Mendicula*) *verrilli*: internal morphology as seen from the left side of a wholemount; specimen from *Knorr*, station 301. (For identification of parts see figures 2 and 3.)

Distribution

Only obtained from the west Atlantic, from the North America and Guiana Basins. Depth range: 1942–2500 m.

This species can be distinguished from all other species of *Mendicula* by the form of the hinge plate and the thickened radial lines on the inside of the shell. This is the smallest species of *Thyasira* to be described to date and one of the smallest of known bivalves.

Internal morphology (figure 107)

The adductor muscles are relatively large and unusual in being almost equal in size and shape. Both are oval and dorso-ventrally elongate, positioned at approximately the same horizontal level. There is a single point of mantle fusion to form the posterior exhalent aperture. There is no visible sign of adhesion elsewhere along the mantle edge. As in other species, the inner lobe is expanded ventral to the anterior adductor muscle.

The gills consist of an inner demibranch only which is further reduced in that the ascending lamella is either completely lost, or so short that it cannot be differentiated in wholemounts. Between seven and nine broad, frontally grooved filaments are present in the largest specimens. Lateral cilia are well developed. The structure of the filaments is essentially the same as in other species of *Mendicula*. In cross section the filaments are short with little abfrontal tissue. A row of cells project to each side of the frontal surface thus forming a broad frontal gutter.

The labial palps are minute, positioned at the end of the long proximal oral grooves. No distinct grooves are visible on the inner surfaces of the palp. The foot is short and with a heel. Although the heel is well defined and sagittally grooved, it is not swollen as in *T.* (*M.*) *transversa*.

The course and form of the gut is conventional except that the hindgut is short and not distended dorsal to the kidney. The lateral pouches are extremely small, oval, and not lobed. They project from beneath the ventral edge of the gill. The pouches of females with eggs are more swollen than those of the male. Although

the digestive diverticula do extend into the dorsal part of the lateral pouches the diverticula are mainly composed of the antero-dorsal branch above the stomach.

Sexes are separate and each ovary contains 8–10 eggs.

The arrangement of the kidney and heart is similar to that of other species. The kidney is small and oval in lateral view, being broadest the heart is minute. The nervous system is also similar in all import and respects to that of other species.

Thyasira* (*Mendicula*) *bushae (new species)

Type locality: Angola Basin, 08° 48.0′S, 12° 52.0′E; 527–542 m.

Type material: Holotype BM(NH) No. 1990037.

Material

ship/cruise	no.	date	sta.	position	depth/m	number	gear
Angola Basin							
Atlantis II	42	23.05.68	203	08° 48.0′S 12° 52.0′E	527–542	737	es

Shell description (figure 108)

Shell small, ovate or triangular, white, inflated, slightly inquivalve, the postero-dorsal margin of left valve projects over that of right, sculpture fine, concentric lines, becoming very smooth towards beak, many specimens encrusted with ferruginous deposit at posterior and ventral shell margin, fine internal concentric lines; beaks raised, approximately central, turned inwards and anteriorly; postero-dorsal margin with characteristic curved flange, antero-dorsal and postero-dorsal margins descend at an equal angle from the beaks, ventral margin evenly curved, somewhat flattened anteriorly; postero-dorsal margin indented by broad escutcheon, outlined by sub-marginal sulcus and ridge, primary sulcus not defined, but shell slightly flattened forming sharp, wedge-like posterior angulation; lunule faint; hinge plate lacks distinct tubercles, right valve thickened ventral to beak and along antero-dorsal margin to form ridge beneath lunule, ligament narrow, lying in groove on ventral side of hinge plate reaching approximately one quarter of distance to posterior margin.

Specimens measure (length × height × breadth); 1.50 × 1.35 × 1.01 mm; 1.27 × 1.12 × 0.75 mm and 0.75 × 0.64 × 0.34 mm.

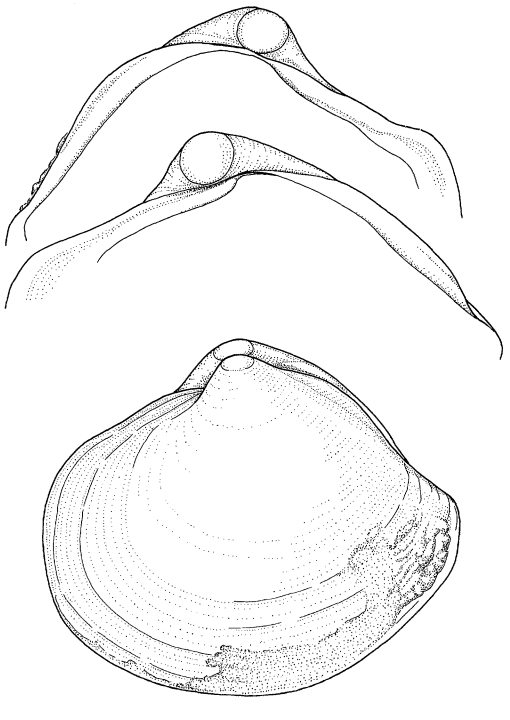

Figure 108. *Thyasira* (*Mendicula*) *bushae*: hinge plate of left and right valves and lateral view of the shell from the left side, specimen from *Atlantis II*, station 203.

Distribution

Only obtained from the type locality where a large number of specimens were found.

This species differs from other species of *Mendicula* in its more triangular outline, raised beaks and flanged postero-dorsal margin. The hinge plate also differs from that of other species.

Internal morphology (figure 109)

The adductor muscles are particularly large. The posterior muscle is ovate and positioned dorsal to the posterior shell angle, the anterior adductor muscle is predominantly ovate, but has a short dorsal prolongation. The mantle edge is fused posteriorly to form the posterior exhalent aperture. Adhesion of the

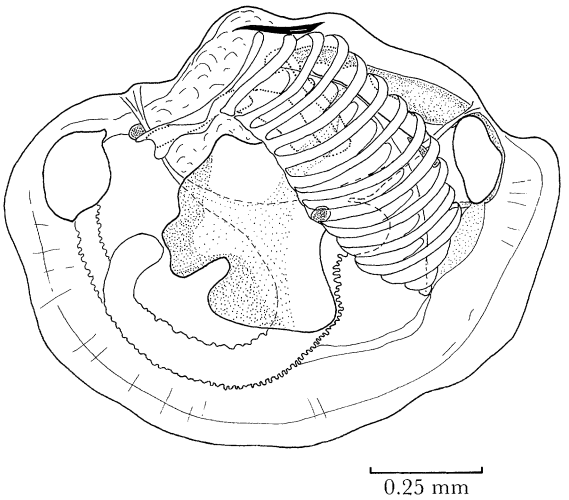

Figure 109. *Thyasira* (*Mendicula*) *bushae*: internal morphology as seen from the left side of a wholemount; specimen from *Atlantis II*, station 203. (For identification of parts see figures 2 and 3.)

opposing inner mantle folds occurs antero-ventrally, ventral to the anterior glandular region. The inner fold typically forms an inner shelf along which the main tract of the mantle runs. The middle and outer folds are of similar size, the middle fold forming a short sensory frill.

The gill is composed of an inner demibranch. The ascending lamella is relatively well developed, being approximately three quarters the size of the descending lamella. Each demibranch has 15 filaments in the largest specimens. The gill filaments are typical of species of *Mendicula* having little abfrontal tissue. Lateral cilia are thick, long and arranged in distinct groups. There are well developed latero-frontal cilia while frontal cilia are extremely short and brush-like. Filamentar muscles are well developed and the central blood space is large.

The foot is small, vermiform, with a sagittally grooved heel. The base of the foot is less broad and muscular than that of *T.* (*M.*) *carrozae*. The tip of the foot is variable in shape, this probably relates to the varying state of contraction of the specimens.

The course of the gut and shape of the stomach are similar to other species. Dorsal to the kidney, the hindgut is swollen and filled with fine particulate material.

The lateral pouches are unique within the subgenus *Mendicula* in that they are divided into a number of lobes which are most pronounced in large specimens. The pouches are also characterized by a fairly deep ventral division to form two large lobes. Two smaller lobes extend from the dorsal surface beneath the ventral margin of the gill. The form of digestive tubules reflects that of the lobes, the tubules extending into the lobes. As in other species there is a section of the diverticula located dorsal to the stomach.

Sexes are separate and the gonads occupy the ventral and inner side of the pouches.

Heart, kidney and nervous system are usual in their arrangement.

Thyasira* (*Mendicula*) *ultima (new species)

Type locality: Cape Verde Basin, 10° 30.0′N, 17° 51.5′W; 1624–1796 m.

Type material: Holotype BM(NH) No. 1990036.

Shell description (figure 110)

Shell small, thin, white, moderately inflated, characteristically pyriform, height exceeds length except in small specimens, surface smooth, white and glossy, without growth stages, two curved radiating lines extend from beaks to antero-ventral and postero-ventral margins respectively, formed by internal thickening associated with anterior and posterior adductor muscles, large specimens thickly encrusted with black or dark brown ferruginous deposit at ventral margin, internally white, well defined anterior and posterior adductor muscle scars, anterior pedal retractor scar also visible; beaks raised, posterior to midline; antero-dorsal margin straight, descending at steep angle from beaks, postero-dorsal margin descends in long steep curve, joins ventral margin at posterior angulation, antero-ventral margin smoothly curved; primary sulcus defined by faint flattening of postero-ventral shell margins, sub-marginal sulcus extends from beaks to posterior shell angle; hinge plate of right valve with elongate, flattened, swollen projection

Material

ship/cruise	no.	date	sta.	position	depth/m	number	gear
West European Basin							
Thalassa		23.10.73	Z410	47° 50.7′N 08° 09.3′W	1180	27	pbs
		25.10.73	Z429	48° 28.0′N 09° 50.0′W	1300	15	pbs
		25.10.73	Z430	48° 37.0′N 09° 52.2′W	1080	1	pbs
		26.10.73	Z438	48° 33.7′N 10° 25.0′W	1400	67	pbs
		26.10.73	Z442	48° 54.8′N 11° 02.0′W	975	1	pbs
		27.10.73	Z445	48° 52.2′N 11° 07.0′W	1200	26	pbs
		28.10.73	Z450	48° 40.0′N 10° 36.1′W	1170	1	pbs
		29.10.73	Z459	48° 37.3′N 09° 53.0′W	1180	3	gbs
Biogas VI		31.10.74	DS86	44° 04.8′N 04° 18.7′W	1950	1	ds
		01.11.74	DS87	44° 05.2′N 04° 19.4′W	1913	1	ds
Sarsia		09.76	7626	43° 47.1′N 03° 46.0′W	1925–1990	4	ag
Cape Verde Basin							
Atlantis II	31	05.02.67	142	10° 30.0′N 17° 51.5′W	1624–1796	38	es
		05.02.67	144	10° 36.0′N 17° 49.0′W	2051–2357	1	es
		06.02.67	145	10° 36.0′N 17° 49.0′W	2185	38	es
Sierra Leone Basin							
Walda		07.71	DS28	04° 04.2′N 04° 35.2′E	1261	1	ds
		07.71	DS27	03° 30.7′N 05° 31.8′E	1376	2	ds
Angola Basin							
Atlantis II	42	23.05.68	201	09° 25.0′S 11° 35.0′E	1964–2031	3	es
			—	09° 05.0′S 11° 35.0′E			
		23.05.68	202	08° 56.0′S 12° 15.0′E	1427–1643	31	es
			—	08° 46.0′S 12° 47.0′E			

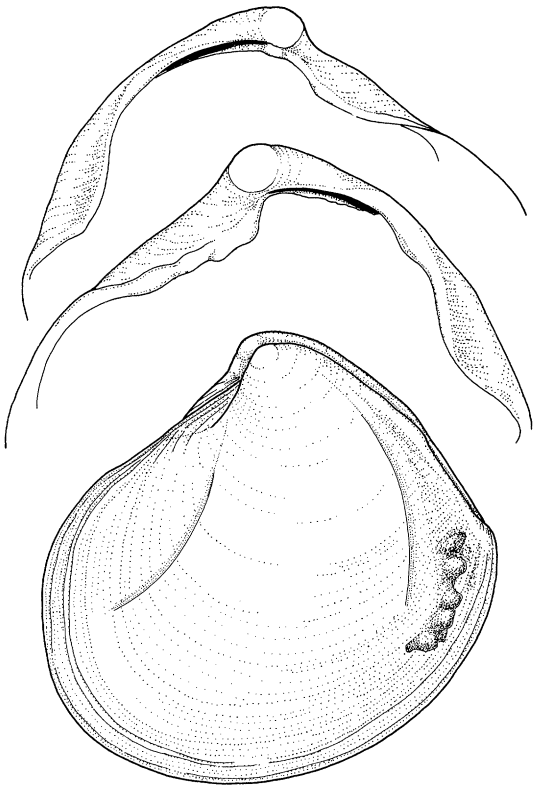

Figure 110. *Thyasira* (*Mendicula*) *ultima*: hinge plate of the left and right valves and a lateral view of the whole shell; specimen from *Thalassa*, station Z438.

anterior to beak, ill-defined lateral projection at postero-dorsal margin, left valve with very small swelling ventral to beak, anterior to beak small flattened projection which fits ventral to that of right valve, faint socket for lateral projection of right valve formed at postero-dorsal margin of left; ligament lies in curved groove, more sunken posteriorly.

Specimens from *Atlantis II*, sta. 145 measure (length × height × breadth): 1.80 × 1.90 × 1.10 mm: 1.40 × 1.50 × 0.85 mm; 9.80 × 0.85 × 0.40 mm.

Distribution

Obtained from the eastern Atlantic; in the West European, Cape Verde, Sierra Leone and Angola Basins. Depth range: 975–2,357 m.

The shell shape of *T.* (*M.*) *ultima* is characteristic and this in combination with the radial lines make it particularly easy to identify. The thickened shell layer which forms the radial scars is not whiter than the rest of the shell, as it is in *T.* (*A.*) *eumyaria*. The ferruginous or manganeous deposit which adheres to the shell differs from that of *T.* (*M.*) *ferruginea* in being black or very dark brown in colour. Small specimens lack the encrustation. Shell variations are shown in figure 114.

Internal morphology (figure 111)

The anterior and posterior adductor muscles are similar in size, the posterior muscle is broadly ovate while the anterior muscle is narrowed dorsally and curves parallel to the mantle edge. The mantle edge

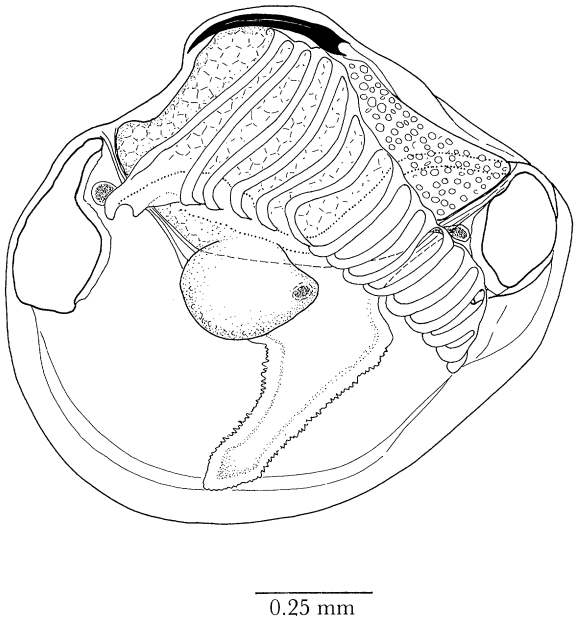

Figure 111. *Thyasira* (*Mendicula*) *ultima*: internal morphology as seen from the left side of a whole mount; specimen from *Thalassa*, station Z438. (For identification of parts see figures 2 and 3.)

(figure 112) is fused posteriorly to form the posterior exhalent aperture. The fusion involves the inner musculature part of the inner mantle lobe at a single point. The gill axis joins the mantle edge at this point. The mantle edge is similar to that of other species of *Mendicula* and the inner fold typically forms a shelf along which runs the main rejection tract of the mantle. As in other species, the inner fold is expanded on each side of the anterior inhalent region to form a glandular area, which is well supplied with radial and concentric muscles.

The gills consist of a single inner demibranch, the ascending lamella of which is almost as extensive as the descending lamella. Up to 19 gill filaments are present in each demibranch. Interlamellar junctions join opposing abfrontal surfaces and a small number of interfilamentar connections also occur.

The filaments in transverse section (figure 113) show the frontal surface as having a lobed appearance, a result of the swollen cells bearing the frontal cilia. The lateral and latero-frontal cilia are positioned well posterior to the frontal surface. There is a moderate depth of abfrontal tissue and thus the filaments are relatively deeper in section than those of most other species of *Mendicula*.

The labial palps are extremely small. The foot is spade-like and similar to that of *T.* (*M.*) *ferruginea*. A small heel is present but this lacks a well defined sagittal groove. Both the anterior and posterior pairs of pedal retractor muscles are broad. The arrangement of the gut, stomach and digestive apertures is also similar to those of other species. Both the gastric shield and the style sac are well developed. The lateral body pouches are notably small and, except posteriorly where they are somewhat pointed, they are characteristically rounded. They are not covered by the ventral margin of the gill and are without lobes. The digestive diverticula

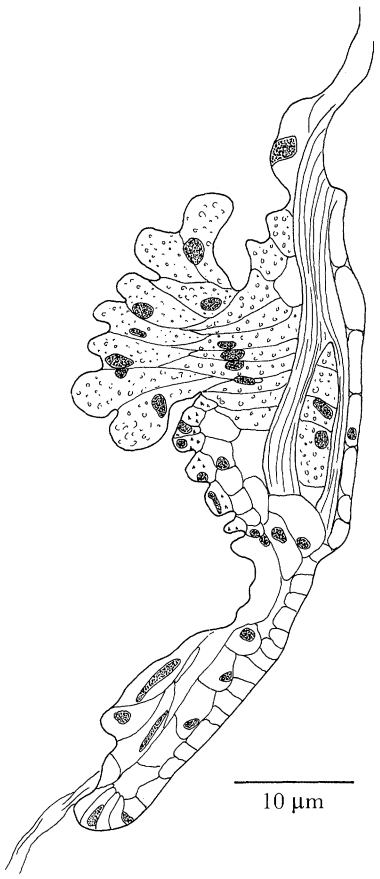

Figure 112. *Thyasira* (*Mendicula*) *ultima*: transverse section through the mid-ventral mantle edge; specimen from *Thalassa*, station Z438. (For identification of parts see figure 10.)

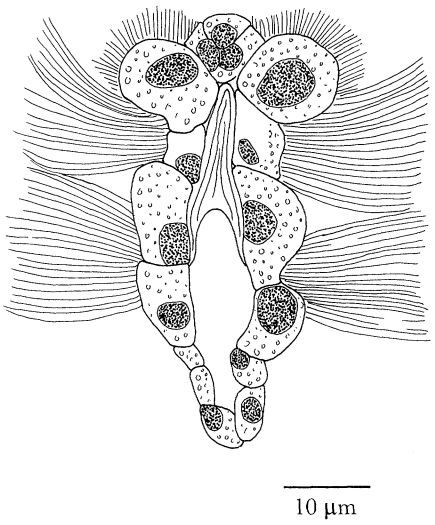

Figure 113. *Thyasira* (*Mendicula*) *ultima*: transverse section through a gill filament; specimen from *Thalassa*, station Z438. (For identification of parts see figure 12.)

are located antero-dorsally in the body and in the anterior part of the lateral pouches. Each pouch contains one convoluted digestive tubule, likewise the dorsal diverticula comprises one tubule. The posterior portion of the lateral pouches is occupied by the gonad. The kidney lies between the pericardium and the posterior adductor muscle. It is very obvious in wholemounts owing to the presence of large numbers of

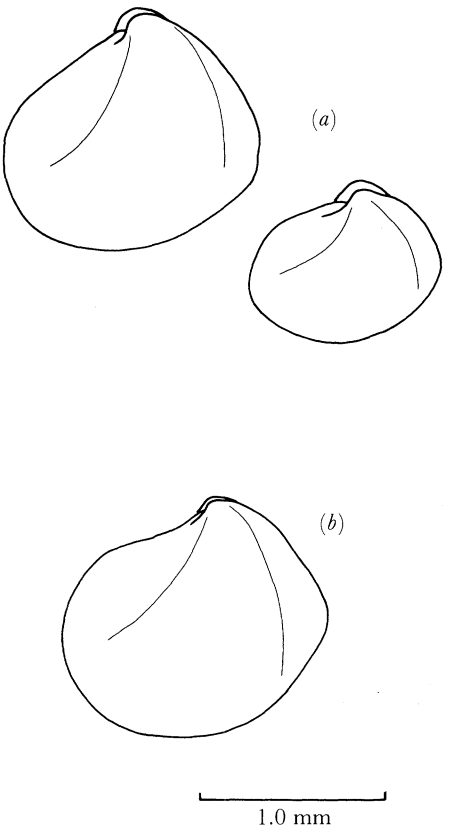

Figure 114. *Thyasira* (*Mendicula*) *ultima*: outline drawings of shells to show variation in shape; (*a*) *Thalassa*, station Z438, a large and a small specimen, and (*b*) *Atlantis II*, station 142.

golden refractory concretions within the epithelial cells. These concretions are similar to those observed in other species but are particularly large many being equal in size to the diameter of the hindgut.

The shells of species of *Mendicula* differ from those of *Axinulus* in that, excepting for the occasional species where length and height are approximately equal, length exceeds height. All species of *Mendicula* are small and usually less than 2 mm in length, although exceptionally *T.* (*M.*) *ferruginea* may reach 3.5 mm. Nevertheless, *T.*(*Mendicula*) *ferruginea* is similar to the type species, *T.* (*M.*) *memorata* Iredale, and may be regarded as typical of the subgenus. Invariably the species have strongly angled posterior shell margins but with radial sulci reduced to form a faint flattening of the posterior part of the shell. The development of the hinge plate is generally more marked than in any of the other subgenera except *Leptaxinus*. The position of tubercles differs in the two subgenera, thus whereas a well formed postero-dorsal lateral tooth maybe present in the left valve of *Mendicula*, it is antero-dorsal in the right valve in *Leptaxinus*.

Overall the degree of development of the hinge plate in species of *Mendicula* is variable, but is best developed in the thickest shells. The morphology of the hinge plate is therefore thought to be of limited diagnostic value, except when used in combination with other features.

There is a trend of decreasing shell height and increasing shell length from the condition seen in *T.*

(*M.*) *bushae*. This culminates in a number of minute, closely related, species of which *T.* (*M.*) *pygmaea* is an example. These latter are distinguished mainly by subtle differences in shell shape and internal morphology.

All species of *Mendicula* have a gill composed of the inner demibranch alone and which has a reduced number of gill filaments. There may be as few as seven filaments in the demibranch of the smallest species. Unlike the gills of *Parathyasira* and *Thyasira* the gill filaments are not extended by abfrontal tissue. A relatively short, heeled foot is characteristic. Lateral pouches are normally small and unlobed, although there are exceptions e.g. *T.* (*M.*) *bushae* is unusual in having relatively large, divided, lateral pouches.

The morphology of two species, *T.* (*M.*) *ultima* and *T.* (*M.*) *bushae*, differs sufficiently from that of other members of the subgenus, as well as from each other, perhaps to suggest a different derivation. If this is the case then the subgenus *Mendicula* will prove to be an assemblage of small thyasirids whose similarities derive from their small size.

Most species of *Mendicula* have a wide distribution from shallow slope depths to 2000–5000 m deep. Exceptions are *T.* (*M.*) *ferruginea* and *T.* (*M.*) *ovata* which occur in relatively shallow waters, and *T.* (*M.*) *verrilli* and *T.* (*M.*) *inflata* which are found only below 1900 m and 3800 m respectively. One species, *T.* (*M.*) *bushae* has a restricted distribution to upper slope of the Angola Basin.

DISCUSSION

Taxonomy

The deep water species of the Atlantic have been assigned to the genera *Axinus* and *Thyasira* and those of the latter genus to the subgenera *Thyasira*, *Parathyasira*, *Leptaxinus*, *Axinulus* and *Mendicula*. *Axinus*, Sowerby, *Parathyasira* Iredale, and *Mendicula*, Iredale, are applied for the first time to Recent Atlantic species. *Axinus* was previously only known as a fossil whereas *Parathyasira* and *Mendicula* were previously restricted to Pacific species. The other subgenera *Thyasira*, *Axinulus* and *Leptaxinus* are well established in the literature (Verrill & Bush 1898; Dall 1901). Two genera, previously recorded from the Atlantic, *Axinopsida* Keen and Chavan, and *Conchocele* Gabb, were not present in the samples.

Problems of classifying and identifying thyasirids have arisen because the generic divisions have had to be based on subtle and variable shell characters. Most authors have not attempted, or have been unable, to support the taxonomy from examination of the internal anatomy. This study shows that relationships between species of similar shell form, especially the smaller ones such as *T.* (*P.*) *subovata*, *T.* (*T.*) *succisa*, *T.* (*T.*) *obsoleta* and *T.* (*A.*) *croulinensis* often can be clarified by reference to the internal anatomy.

Axinus is the critical genus in the consideration of the evolution of the group. Although it has genuine thyasirid features: an edentulous shell with posterior radial sulci, two demibranchs in each gill and lateral body pouches, its differences from other thyasirids are great. Thus, the anterior adductor muscle is not markedly long and narrow, but is similar in size and shape to the posterior muscle, there is great specialization of the mantle edge with a *second* permanent posterior aperture to the mantle cavity. The lateral body pouches are small and lack the division of the lobes which is found in other *large* thyasirids. Thus, some of the features of *Axinus*, are similar to those of ungulinids (Allen 1958) and the origin of the Thyasiridae may well lie close to the ungulinid stem.

Of the subgenera, *Parathyasira* is the closest in shell character and internal morphology to *Axinus grandis*. Externally the main similarity is the presence of radial ridges from the umbones to the mid-ventral and anterior margins and which are additional to the posterior sulci (figure 115). Although similar but very faint ridges are also present in species of other subgenera they are not as particularly marked as in *Axinus* and in, say, *T.* (*P.*) *granulosa*. Of the subgenera the degree of mantle fusion and the extent of the outer demibranch is also greatest in *Parathyasira*, similarly the tip of the foot is not divided into two distinct regions in *Axinus* or *Parathyasira* as it is in *Thyasira*. Yet, despite its similarities to *Axinus*, *Parathyasira* remains more closely related to *Thyasira* than to the latter genus. Features emphasizing this closer relationship include an elongate anterior adductor muscle, well developed and strongly divided lateral body pouches and a long vermiform foot. In addition *Parathyasira* has no tentacles or specialized structures at the mantle margin such as are present in *Axinus grandis*.

Thyasira is the most specialized subgenus of those studied here. The shell has departed from the more equilateral form of *Axinus*. The anterior adductor muscle in *Thyasira* is particularly narrow and elongate, the outer demibranch of the fleshy gill is reduced and the tip of the foot is clearly distinct and may be divided into two regions in larger species. The mantle is relatively simple with the minimum of fusion and with few points of adhesion. With regard to the shell, the hinge plate of *Thyasira* is extremely narrow ventral to the beaks, and the posterior radial sulci tend to be strongly incised particularly in the larger species.

Reduction and simplification of the internal morphology

Previously the Lucinacea were classified partly on the basis of the form and the number of demibranchs in the gill (Allen 1958). Thus the Lucinidae possess a single (inner) demibranch the filaments of which are abfrontally thickened, the Ungulinidae have both demibranchs present but without abfrontal thickening and the Thyasiridae were regarded as possessing two demibranchs with the outer demibranch somewhat reduced but with abfrontal thickening to some degree (Allen 1958; Bernard 1972).

It is now clear that the outer demibranch is not present in many species of *Thyasira*. When a demibranch is 'lost' it is always the outer one (Allen 1958). The genera and the subgenera can be partially defined on the basis of the number of demibranchs present. Thus, the subgenera *Leptaxinus*, *Axinulus* and *Mendicula*

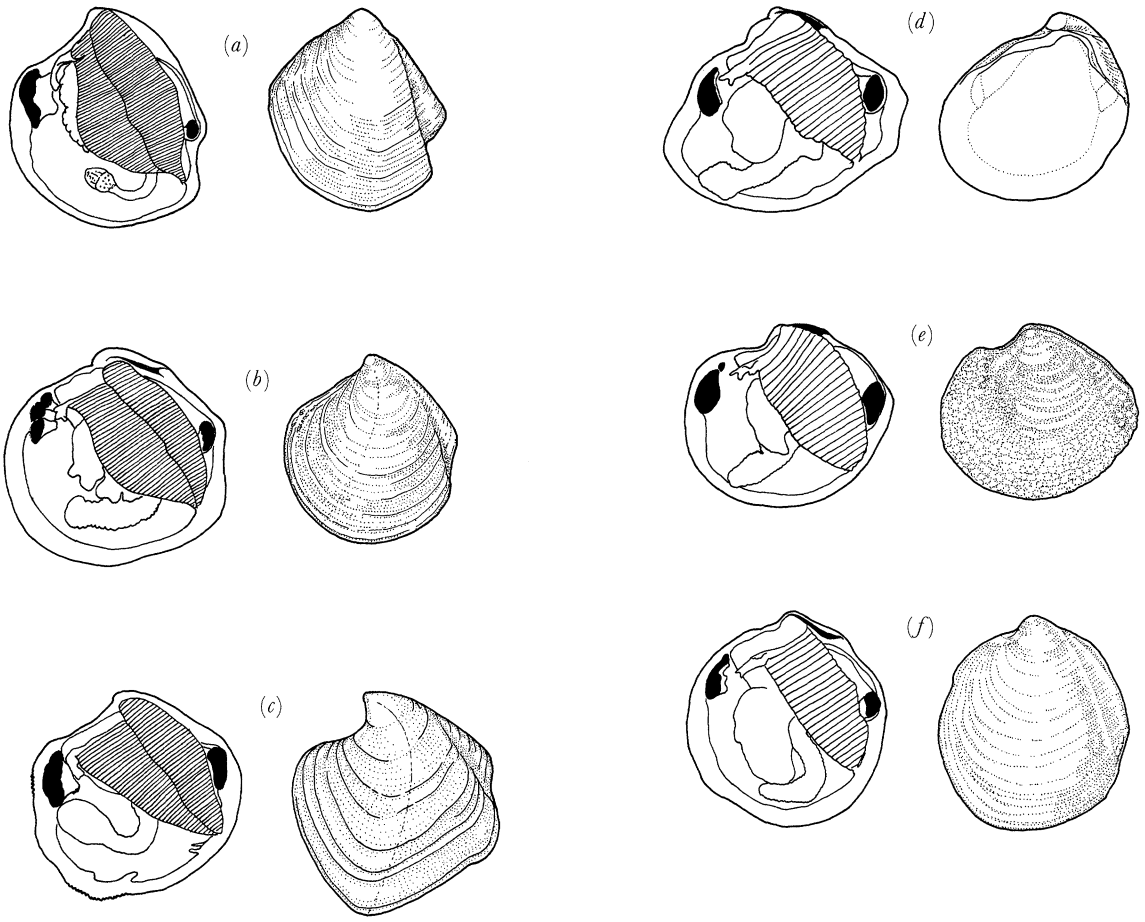

Figure 115. Major distinguishing features of the shell and internal anatomy in: (*a*) *Thyasira* (*Thyasira*); (*b*) *Thyasira* (*Parathyasira*); (*c*) *Axinus*; (*d*) *Thyasira* (*Leptaxinus*); (*e*) *Thyasira* (*Mendicula*); and (*f*) *Thyasira* (*Axinulus*). Note the decrease in relative size of the posterior adductor muscle and steeper angle of the gill in the mantle cavity from *Axinus* through to *T.* (*Parathyasira*) to *T.* (*Thyasira*), and greater differentiation in size of the adductor muscles in *T.* (*Axinulus*) as compared with *T.* (*Leptaxinus*) and *T.* (*Mendicula*).

have only the inner demibranch present (figure 115). The genus *Axinus* has both present and the subgenera *Thyasira* and *Parathyasira* generally have both present. It is also clear that possession or not of the outer demibranch is related to the size of the species. Species without an outer demibranch are invariably less than 4 mm in length. While none of the larger species have lost the outer demibranchs, a number of very small species have retained them. The reasons for this, if any, are not apparent, although species retaining the outer demibranch are most closely related to one of the larger species. It should be noted that one of these small species, *T.* (*P.*) *subovata*, also possesses deeply lobed body pouches which are also characteristic of the larger subgenera.

The absence of a demibranch is physiologically possible in small species since they can no doubt satisfy respiratory demand via the general body epithelium. Thus small species particularly those of the subgenus *Mendicula* possess characters common to juvenile bivalves in general (a single demibranch, heeled foot, small oval shell, and simple gut morphology), i.e. small thyasirids may well be neotenous.

It would be thought that this might apply also to species of the subgenera *Parathyasira* and *Thyasira*. Yet, *T.* (*P.*) *subovata*. *T.* (*T.*) *obsoleta* and *T.* (*T.*) *succisa* are equally small and the reason why these species should have, despite their small size, two demibranchs to each gill is not clear. The loss of the outer demibranch may have occurred on more than one occasion during the course of evolution of a subgenus. It may be that species of subgenera *Axinulus* and *Mendicula*, as here defined, have mixed origins, thus some species of *Mendicula* may be derived from small species with two demibranchs, while others may be derived from *Axinulus* stock.

Shell morphology

The shells of species studied fall into two main groups; those in which shell height is greater than the length and those in which the reverse is true. Examples of the former include most of the species of the genus *Axinus*, and the subgenus *Thyasira*, *Parathyasira* and *Axinulus*. The latter group includes most species of *Leptaxinus* and *Mendicula* together with *T.* (*P.*) *tortuosa*, *T.* (*P.*) *subovata* and *T.* (*P.*) *atlantica*. These two shapes are thought to reflect a difference in life style, position and attitude in the sediment and also movement or not through the sediment.

Some of the differences in hinge detail and in internal morphology are associated with the differences

in shell shape. For example, the hinge 'teeth' or tubercles are less well developed in species where shell height is greater than length and developed in *some* species where shell length is the greater.

Although radial shell sulci are characteristic of large thyasirids, they are not unique to the family Thyasiridae. They are also well developed in some species of the Lucinidae (Abbott 1954). One major sulcus occurs in thyasirids, this has been defined as the primary sulcus by Kauffman (1967). The submarginal sulcus which additionally is found in most species appears to outline the perimeter of the escutcheon. Its ridged appearance is emphasized by the primary sulcus adjacent to it and thus the shells have a characteristic double ridge. A posterior auricle is present in species in which the shell margin of the posterior part of the escutcheon projects instead of being sunken. The purpose of the primary sulcus is unknown although Bernard (1972) suggested that the sulcus may help to direct the posterior exhalent current and Allen (1958) related it to the line of attachment of the gill axis. The point at which the primary sulcus meets the shell margin is invariably ventral to the posterior exhalent aperture and corresponds to the point of posterior mantle fusion and where gill axis meets mantle edge. The sulcus is very pronounced in large species of *Thyasira* and may relate to the upright attitude of the shell which in itself relates to the ventral position of the posterior mantle fusion as distinct from the mid-posterior position as seen in *Axinus*. This results in the gill of *Thyasira* sg. being set at a steep angle within the mantle cavity. The most prominent sulcus recorded was that of *T.* (*T.*) *excavata*, the largest species studied and probably the most deeply buried within the sediment.

Thyasirid shells are usually frail, invariably white in colour, although some species may be covered by a yellowish periostracum. The latter is mostly thin and transparent, an exception being *T.* (*L.*) *incrassata* where the periostracum is particularly thick.

Other than sulci, shell ornamentation is unusual in the Thyasiridae and only found in *Parathyasira*. In the latter subgenus, ornamentation, when it occurs, consists of radiating rows of minute projections which are unusally worn away at the centre of the valves. In addition, many species acquire a partial or, in a few species, a complete coating of ferruginous material. Primarily this deposit occurs where the inhalent and exhalent currents enter and leave the shell. It is also found frequently around the beaks and to a lesser extent at the ventral shell margin. Although it may simply be deposited as a result of physical precipitation of iron and manganese salts on the matt shell surface, the deposit may reinforce the strength of a thin shell and serve to cement more securely the anterior inhalent tube to the shell margin, Thus, it is advantageous in a functional sense as well as a cryptic sense in shallow water species. Only in *T.* (*M.*) *ferruginea* and *T.* (*M.*) *ovata* is the shell completely coated with deposit and it is extremely difficult to remove the deposit without damage to the underlying shell. It may well be that in these two species the coating is essential to the species. There is no evidence that like the similarly coated *Montacuta ferruginosa* (Bivalvia: Erycinacea) that they live in association with another animal or its burrow.

The hinge plate varies in its development. Without true cardinal teeth, pseudo-cardinal and lateral tooth-like protruberances may occur. Their presence is sufficiently consistent to be a useful diagnostic at subgeneric as well as species level. A few species are inequivalve and ridges may be developed at the shell margin which overlap those in the opposing valve (Harry 1969).

Internal morphology

The anterior and posterior adductor muscles of *Axinus* are of different size but similar in shape. The posterior adductor is about two thirds as large as the anterior. In contrast species of *Thyasira* sg. and *Parathyasira* have anterior adductor muscles that are greatly elongate or parallel to the mantle edge. The size differential of the muscles vary, thus in *T.* (*T.*) *excavata*, the posterior adductor is only one quarter the size of the anterior whereas in the subgenera *Leptaxinus* and *Mendicula* the muscles are of a similar size. Conversely, in species of *Axinulus* with a more upright form the adductors are similar to those of species of *Parathyasira*. Elongation of the anterior adductor muscle is not only related to the height of the shell but also the anterior inhalent tube and the processing of particles within the mantle cavity (Allen 1958).

The structure of the mantle edge is similar in all species studied (Allen 1958). A single point of mantle tissue fusion of the inner fold forms the posterior exhalent aperture. There appears to be variation in the degree of mantle adhesion along the pedal gape. In *Axinus grandis* adhesion, as distinct from fusion, forms a second aperture below the exhalent aperture. A second posterior aperture has also been reported by Bernard (1972) in *Thyasira cygnus* Dall. A number of species of *Parathyasira* posteriorly have interlocking ciliated pads developed from the middle mantle folds. These do not form such a well defined second aperture as that formed in *Axinus* by adhesion.

In the great majority of species described, the inner fold forms a well defined glandular shelf along which runs the main rejection tract of the mantle. Particles entrapped in mucus secreted by epithelial gland cells are passed to a postero-ventral point where they are collected as pseudo-faeces before being expelled. In *Axinus grandis* alone is there a glandular mantle flap which roofs over the rejection tract. *Axinus* also possesses sensory papillae along two sections of the ventral mantle edge. In this *Axinus* resembles the condition in species of the family Ungulinidae. Tentacles at the posterior end of the tract in *Axinus* are probably involved in the expulsion of the pseudo-faeces.

An expanded area of mantle richly provided with secretory cells is present ventral to the anterior adductor. The area appears to be a development of the inner mantle fold and is particularly large and well developed in large species of the subgenus *Thyasira* (Allen 1958). It may be associated with the production of mucus for the construction of the anterior inhalent

tube or the secretion is used to entrap particles entering the mantle cavity via the anterior inhalent current.

The variation in the gill structure has already been discussed (p. 554). The filaments, particularly in larger species, may be abfrontally thickened. A further feature of the thyasirid gill is that filaments in opposing lamellae are joined by extensive interlamellar connections. In most other lamellibranchs interlamellar junctions occur only at intervals along the gill. The gill filaments are additionally joined by inter-filamentar junctions at broadly spaced intervals. Skeletal support rods and muscles are well developed. Abfrontal extension of the filaments is greatest in the largest species such as *Axinus grandis* and *T.* (*T.*) *excavata*. These species almost certainly are deeply buried in the substrata, almost certainly in anoxic sediments, and are probably adapted to sulphur metabolism. In contrast, abfrontal extension is non-existent in species of *Mendicula*, which are almost certainly shallow burrowers and possibly mobile.

Labial palps are universally small in the Thyasiridae but never lost. They occur at the outer limit of the proximal oral grooves, close to the ventral margin of the gill. At their greatest development palps consist of small triangular flaps with up to 12 ridges on their inner surface (Allen 1958), but most deep-sea species bear only three or four ridges. A distal oral groove is present linking the gill axis to the palps. Usually the ventral margin of the gill has a groove conveying particles to the palps.

Allen (1958) described how the specialized vermiform foot of *T.* (*T.*) *flexuosa* is used to construct an anterior inhalent tube. *T.* (*T.*) *excavata* and *T.* (*T.*) *trisinuata* have a similar foot in which the tip is also divided into two parts. Species of the subgenera *Parathyasira*, *Axinulus*, *Leptaxinus* and *Mendicula* have a less well defined tip at most it being simply bulbous and more heavily ciliated than the stem. The foot of these subgenera appears to be shorter than that of the large species of *Thyasira* sg. The length and shape of the foot is related to the manner of burrowing, tube building and the depth to which the animal is buried. Species with a heeled foot are likely to be shallow burrowers and to crawl through the sediment. No byssus gland was found although a sagittal groove is present in a number of small species.

The digestive tract is in the sagittal plane and the hindgut is not extended and looped as it is in many deep-sea bivalves. All species have a short stomach, that is broad anteriorly and has a small dorsal hood. Large openings ventral to the oesophagus lead to the digestive diverticula. In all species the two apertures each open directly to two tubules. The midgut and style sac are combined. Identifiable material was observed only in the stomach of *T.* (*T.*) *trisinuata* where large intact diatom frustules were present. In other species the remains in both the stomach and the hindgut consist of very fine particles. In a large number of species these latter particles build up in the posterior region of the hindgut until it is grossly swollen to many times its empty diameter. The reason for this accumulation is unknown, but the same phenomenon has been described by Allen & Turner (1974) in deep-sea verticordiids. It seems probable that some further absorption or digestion must take place in this region, this being the specialism of thyasirid digestion to meet the problems of energy supply in the deep sea. Faecal pellets were not observed. The labial palps are so small in thyasirids as to indicate that they do not select material arriving via the gills. In any case they must obtain most of their food via the anterior inhalent tube and this will move directly across the inner face of the anterior adductor to the mouth (Allen 1958). The most noteworthy feature of the thyasirid digestive tract is the small number of digestive tubules, the lack of primary and secondary ducts and the basic similarity of all the species studied.

The most striking feature of the internal morphology which distinguishes thyasirids from other lucinaceans are the lateral pouches of the body wall which contain a large part of the digestive diverticula and the greater part of the gonad. Although the Ungulindae and Lucinidae have a tendancy to develop lateral swellings of the body (Allen 1958), these are never so pronounced as in thyasirids and never lobed or arborescent. Unlike the thyasirids they are also always without a distinct neck at the junction with body. *Axinulus grandis* may be primitive in possessing small, but distinct, pouches which are undivided and not lobed. Some species of the subgenera *Leptaxinus*, *Axinulus* and *Mendicula* also have unlobed pouches, but, in all probability, this relates to simplication that small size brings. Sub-divided pouches are found for the most part in the subgenera *Thyasira* and *Parathyasira*. The shape of the pouch and the pattern of lobing is characteristic for each species and is an important feature in identification. Lateral pouches have the effect of increasing the surface area of the body and may allow for increased epithelial exchange and thus may be correlated to the small size of the gills.

The digestive diverticula are little branched. Only in species with lobed pouches do tubules have simple diverticulations to match the form of the lobes. Each tubule is lined by an epithelium of large digestive cells. Interstitial cells are mostly limited to the blind end of the tubules. Extreme simplicity is reached in *T.* (*A.*) *brevis* and many small *Mendicula* species where the digestive diverticula consist of four simple short tubes.

The gonads are located in the inner and ventral parts of the lateral pouches. When mature they may extend into the area ventral to the style sac. Sexes are separate. The gonads open into the suprabranchial cavity via paired ducts separate from the kidney ducts. Egg numbers vary from about 20 in the smallest species to more than 2000 in *T.* (*T.*) *excavata*. Eggs are relatively small in size (80–100 μm) and thus there must be a larval phase. No evidence of direct development was seen.

The kidney follows a common plan. As in most deep sea bivalves it is relatively large. It is composed of paired sacs lacking any internal divisions. In two large species *T.* (*T.*) *trisinuata* and *T.* (*T.*) *excavata* paired excretory ducts lead from the anterior end of the kidney to open into the posterior suprabranchial chamber. Very large spherical concretions of varying sizes within the epithelial cells are common to all but

one or two species. Some of the largest concretions are found in species of *Mendicula*. A thin walled pericardial cavity is located anterior to the kidney. This contains a small central ventricle and lateral auricles. The latter are tenuous and lack well developed musculature. The heart is particularly ill-defined in smaller species. The hind gut passes through the heart.

The position and size of the ganglia of the nervous system differ little between the species. Cerebropleural, pedal and visceral ganglia are always prominent.

Adaptation of deep-sea thyasirids

The prevalence of the family Thyasiridae in deep water suggests that they may have features not possessed by other lucinacean families that allow them to exploit this environment. Comparison of deep-sea and coastal specimens of the same species that have an extremely wide depth range, e.g. *T.* (*M.*) *ferruginea*, shows no major differences. This suggests that thyasirids may be pre-adapted for life in deep water. Apart from small size, morphological features which have enabled thyasirids to inhabit the deep waters might include the possession of lateral body pouches, the long vermiform foot, the simple structure of stomach and digestive diverticula and large kidney of simple construction. Lack of predation, selectivity of food, physiological adaptation and low metabolic activity must also play a large part in their exploitation of the deep-sea environment.

Based on recent studies (Cavanaugh 1985) rift bivalves (which include large thyasirids) have gills that are unusual in containing chemoautotrophic bacteria that provide an additional energy source. Some of the species described here may have these in the abfrontal filamentar tissue but many others, particularly the smaller species, have no bacteria within the gills and the abfrontal region is not extended.

Undoubtedly one of the major features of deep-sea thasirids is their small size and size in itself may be a preadaptive character to successful colonization of the deep sea. The smallest species *T.* (*M.*) *verrilli* matures at less than 1 mm in length. Such small species are thus able to reproduce within a relatively short time in an environment where organic material is scarce and refractile and thus enforcing low growth rates. Very large numbers of small thyasirids were obtained from certain stations. Successful fertilization in relatively dense populations of a small species producing few eggs is more likely to be achieved than in larger species producing a modest number of eggs but in low population density.

It should be noted that there are few truly abyssal thyasirid species, the vast majority of the species being taken from slope depths. Down slope migration is indicated

Life habits

The two main shell shapes probably reflect a difference in orientation and in habit. Upright shells in which the height exceeds the length tend to have a reduced hinge plate lacking lateral teeth. At most only small cardinal tubercles are present. These species are usually laterally inflated and have a long foot which is lacking a heel. Horizontal movement through the sediment must be difficult, if not impossible. These species are therefore thought to be deeply buried and largely static, constructing a long anterior inhalent tube as in the case of *T.* (*T.*) *flexuosa* (Allen 1958).

Species with elongate shells in which the length exceeds the height have a foot that is shorter and usually with a differentiated heel. The shell has relatively well developed pseudo-cardinal and pseudo-lateral teeth essential in a shell that opens and closes frequently. It is thought that these species are buried just beneath the surface of the sediment. In the case of some species, this is confirmed by attached hydroids on the postero-dorsal shell margin. The anterior and posterior adductor muscles of this group of species are usually less dissimilar in size and shape. A different lifestyle is indicated by this shell morphology. Although not confirmed, the inhalent tube must be shorter and may be less well developed. A more active mode of life, perhaps similar to that of small erycinancean bivalves (which they resemble) is suggested for this group.

Distribution

Analysis of the distributions of the 28 species and subspecies described here (figure 11) shows that there are only four (*T.* (*M.*) *inflata*, *T.* (*P.*) *biscayensis*, *T.* (*P.*) *atlantica*, *T.* (*P.*) *subequatoria*) that are confined solely to the abyss. The great majority (20) are present at slope depths. Some of this majority have extremely wide depth distributions from shallow water less than 100 m to lower slope depths (nine) with a few of these (four) extending further on to the abyssal plane to between 2500–3500 m. Finally, there are species (four) which occur at lower slope depths into mid abyssal depths.

In terms of geographical distribution the majority (17) are widely distributed throughout the Atlantic. It is notable that a significant number of these occur in Arctic and Mediterranean waters and a few *T.* (*M.*) *ferruginea* and *T.* (*T.*) *trisinuata* also occur in the Pacific. Of the other eleven species, four are widely distributed in the eastern Atlantic, three are widely distributed in western Atlantic, and the remaining four have been only recorded in a single basin, two from the east and two from the west. Thus, a restricted distribution is unusual in this group. This is probably related in part to the wide depth distribution and in part to the clear indication from egg size that most species produce a planktotrophic larva. Thus, there are few topographical and inherent restrictions on the spread of the species.

These depth distributions are remarkably different in a number of aspects from those of the other major deep-sea groups, in particular the protobranchs and septibranchs. First, is the very great depth range of species for example, *T.* (*P.*) *equalis*, 37–4000 m; *T.* (*P.*) *subovata subovata*, 216–3916 m; *T.* (*A.*) *croulinensis*, 40–3861 m; *T.* (*M.*) *ferruginea*, 50–4825 m. Second, is that the thyasirids predominantly occur at slope depths. Third, is that a significant number are present at shelf depths as well as in the deep-sea. Fourth, is that

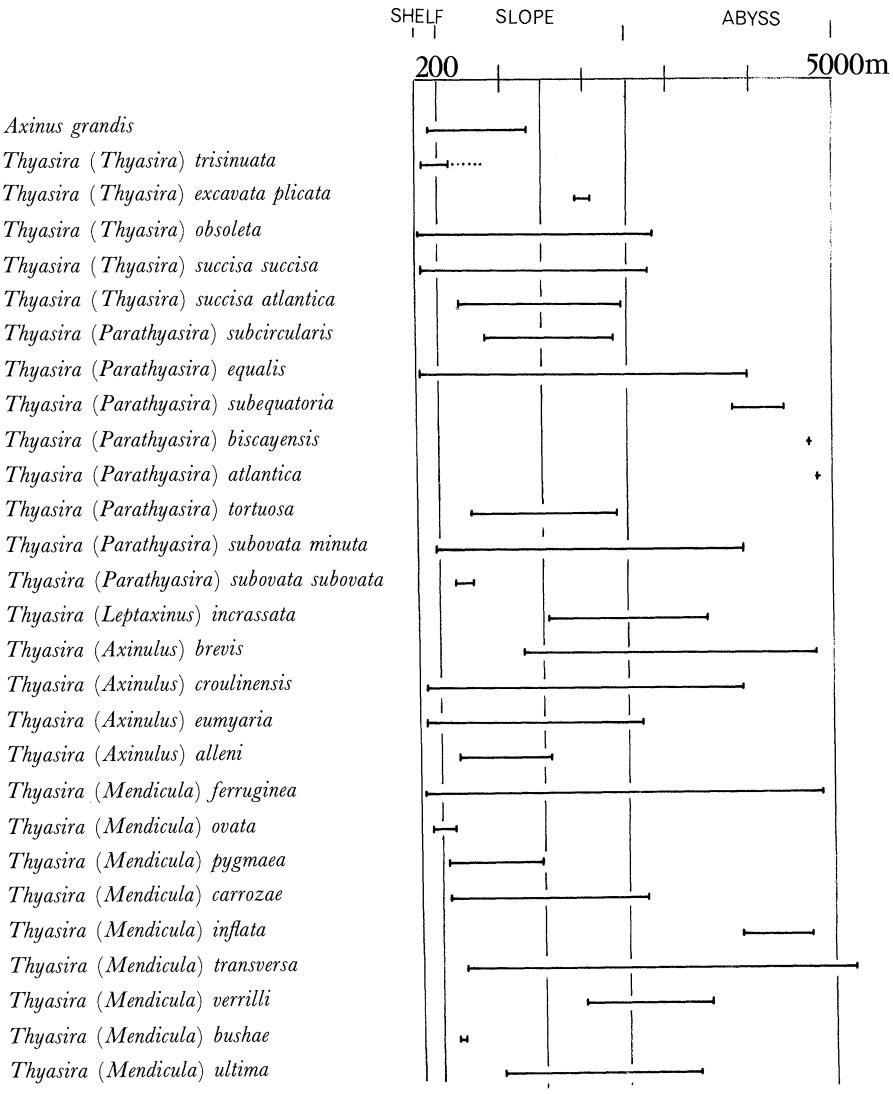

Figure 116. The depth distribution of species of *Thyasira* in the Atlantic.

because of their wide depth range species are not excluded from the Norwegian Basin. Fifth, is that many have particularly wide geographical distributions and unlike most other groups of Atlantic deep-sea bivalves, several are cosmopolitan species extending into the Pacific and Arctic Oceans.

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KEY TO ABBREVIATIONS USED IN FIGURES

a	anus
aa	anterior adductor muscle
abf	abfrontal fusion
apr	anterior pedal retractor muscle
bs	blood space
ce	columnar epithelium
cg	cerebral ganglion
ci	cilia
cimu	circular musculature
cmu	concentric musculature
da	digestive aperture
dg	digestive gland (diverticula)
dh	dorsal hood
dog	distal oral groove
dt (d/p)	digestive tubule (dorsal branch/branch to pouch)
f	foot
fci	frontal cilia
fg	groove in heel of foot
fh	heel of foot
fl	fusion layer
fs	stem of foot
ft	tip of foot
g	gill
ga	glandular area
gax	gill axis
gc	gland cells
gd	gonadial duct
gf	gill filament
gs	gastric shield
h	heart
hg	hindgut
i	intestine
ic	interstitial cell
id	inner demibranch
if	inner mantle fold
il	inner layer
k	kidney
kd	kidney duct
lbp	lateral body pouch
lci	lateral cilia
lfci	latero-frontal cilia
lig	ligament
lp	labial palps
m	mouth
mc	mucous cells
me	mantle edge
mf	middle mantle fold
mfn	mantle fusion
mgg	midgut groove
mn	mantle
mt	mantle tentacle
mu	muscle
n	nerve
np	neck of body pouch (cut)
od	outer demibranch
oe	oesophagus
of	outer mantle fold
ol	outer layer
ov	ovary
pa	posterior adductor muscle
par	parasite
pau	posterior shell auricle
pc	pericardium
pe	periostracum

pg	pedal ganglion
peg	periostracal groove
pfn	posterior mantle fusion
pia	posterior inhalent aperture
pog	proximal oral groove
ppr	posterior pedal retractor muscle
ps	primary shell sulcus
rjt	rejection tract
rmu	radial musculature
s	stomach
sc	secretory cells
sms	submarginal shell sulcus
sp	sensory papillae
sr	skeletal rod
ss	style sac
tf	tentacle
ty	typhlosole
vg	visceral ganglion

KEY TO ABBREVIATIONS USED IN TABLES

ad	anchor dredge
ag	agassiz trawl
cp	chalût à perche
cv	chalût blake
ds	sanders dredge
es	epibenthic sledge
gbs	grande drague boillot
kr	carottier reineck
nd	naturalist's dredge
pbs	petite drague boillot.