STUDIES ON THE DEEP SEA PROTOBRANCHIA (BIVALVIA);[1] THE FAMILY TINDARIIDAE AND THE GENUS *PSEUDOTINDARIA*

H. L. SANDERS[2] AND J. A. ALLEN[3]

ABSTRACT. In the present paper we have erected a new family of Protobranchia, the Tindariidae, to include those nuculanoid bivalves that lack a siphon but bear papillae on their posterior margin edge, have a single loop of the hind gut that penetrates the right side of the mantle, and possess a palp with few ridges. A new genus, *Pseudotindaria*, is created for those nuculanoid protobranch bivalves that have shell morphologies essentially similar to the Tindariidae but with soft parts that are markedly different. Siphons are present, the hind gut is a complex configuration of loops and coils on either side of the body and it does not penetrate the mantle, and palp ridges are numerous. The morphologies of the hard and soft part anatomies, the horizontal and vertical distributions, size-frequency histograms, and reproductive patterns of the tindariid and pseudotindariid species in our Atlantic samples are discussed. Two new species are described. On the basis of shell morphology, *Tindaria* and *Pseudotindaria* can be interpreted as recent descendants of the Paleozoic ctenodont Protobranchia.

INTRODUCTION

The objects and aims of our researches on the fauna of the deep sea, and on the Proto-branchia in particular, have been given in the prologue to these studies, (Sanders & Allen, 1973). This is the third paper in a series, all of which illustrate the initial problems that had to be resolved in our analysis and reappraisal of the deep-sea protobranch bivalves of the Atlantic.

As noted in the first paper (Sanders & Allen, 1973), the tindariid protobranchs represent an anomalous group within the Order Nuculanoidea, having features that divide them sharply from the remainder of the order. Verrill & Bush (1897), Theile (1935), Vokes (1967) and Knudsen (1970) all place the genus *Tindaria* (= *Tyndaria*) in the family Malletiidae, even though Verrill & Bush (1898) stated that "the genus *Tindaria* differs so widely from *Malletia* and other genera that it seemed necessary to establish a new subfamily (Tindarinae) for it."

Dall (1895) included the following subgenera: *Tindaria, Tindariopsis, Neilonella* and *Pseudoglomus* in the Malletiidae and Knudsen (1970) retained the genus *Neilonella* there as well. Theile (1935) divided the genus *Tindaria* into two sections each with a single subgenus, *Tindaria* and *Pseudoglomus*.

Because *Tindaria* differs so markedly in its morphology from both *Pseudoglomus* and *Neilonella* as well as other members of the family Malletiidae, we propose that a new family be erected, the Tindariidae.

The genera *Pseudoglomus*, *Neilonella* and *Malletia* will be the subjects of future papers.

The present study shows that some species, although having typical tindariid shells, have greatly different anatomies from the true tindariids. On the basis of these profound anatomical differences we find it impossible to include these species within the same family. We propose that those forms having papillae around the incurrent aperture, lacking well defined siphons, and having a hind gut configuration consisting of a single deep loop on the right side of the body, be included in the family Tindariidae. Excluded from the family are those forms with a well-developed siphon and complex hind gut configuration that extends on both sides of the body. These we include within a new genus *Pseudotindaria*, described here. The precise affinities of this genus will be deferred to a future paper. This interpretation in no way conflicts with earlier definitions of the genus *Tindaria*, all of which mention posterior papillae (e.g. Theile, 1935).

TINDARIIDAE New Family

The family is characterized as follows: valves rounded, ovate, robust, swollen, somewhat unequilateral, concentrically lined; umbo medially and somewhat anteriorly directed; hinge line strong, supporting a series of well-developed teeth that are continuous beneath the umbo; ligament external and opisthodetic; posterior sensory tentacle present or absent; true siphons lacking; incurrent region of mantle edge fringed with elongate papillae; palps small; sorting ridges of the palp broad, few in number; palp proboscides large, elongate; gill axis somewhat oblique to the antero-posterior axis of the body; gill filaments few; hind gut, with lumen of large diameter and a single typhlosole, making a single loop to the right side of the body and penetrating into the mantle to a greater or lesser extent; 'byssal' gland small.

Although they show several features that sharply differentiate them from other protobranchs, the tindariids clearly fall within our definition of the Order Nuculanoidea (Sanders & Allen, 1973). For example, all species of the family have a posterior incurrent current and an anterior mantle sense organ.

Tindaria Bellardi 1875
Type species *T. arata* Bellardi, by monotypy

Tindaria is the sole genus of the family, the generic characters of the genus are those that define the family. Many species are listed in the literature (see Smith, 1885; Clarke, 1962; Knudsen, 1970) but, for reasons that will become obvious, unless the soft parts have been described many of these species cannot be placed in the genus with confidence. Of the features that distinguish both the genus and family, the most distinctive are 1) the lack of siphons and the long fringing papillae of the incurrent region, 2) the small size of the palps relative to the size of the animal, 3) the very few ridges on the inner surface of the palps, 4) the oblique placement of the gill in relation to the anterior-posterior axis, 5) the relatively small number of gill filaments, 6) the small size of the 'byssal' gland, 7) the single loop of the hind gut on the right side of the body.

Tindaria callistiformis Verrill & Bush, 1897
Figures 1–11 & 27

Tindaria callistiformis, Verrill & Bush, 1897. Amer. J. Sci., p. 59, figs. 10, 20, 21 (Type locality: U.S. Fish Comm. Sta. 2566; Lat. 37°23'N, Long. 63° 8'W, type specimen: U.S. Nat. Mus.); Verrill & Bush, 1898. Proc. U.S. Nat. Mus., No. 1139, p. 881, pl. 78, fig. 1; 80, figs. 6, 7.
Previous records. Depth range = 3342 to 4795 m. North America Basin—2 stations. Refs. Verrill & Bush, 1897, 1898.
Present records. Depth range = 3305 to 5042 m.

Cruise		Station No.	Depth (m)	No. of specimens	Latitude	Longitude	Gear	Date
				North America Basin				
Chain 50		77	3806	622	38°0.7'N	69°16.0'W	ES	30.6.65
Chain 50		78	3828	181	38°0.8'N	69°18.7'W	ES	30.6.65
Chain 50		85	3832	882	37°59.2'N	69°26.2'W	ES	5.7.65
Atlantis II	40	175	4667	1	36°36.0'N–36°36.0'N	68°29.0'W–68°31.0'W	ES	29.11.67
Chain 50		84	4749	1	36°24.4'N	67°56.0'W	ES	4.7.65
Atlantis II	24	121	4800	2	35°50.0'N	65°11.0'W	ES	21.8.65
Atlantis II	24	122	4833	3	35°50.0'N–35°52.0'N	64°57.5'W–64°58.0'W	ES	21.8.65
Atlantis II	24	123	4853	1	37°29.0'N	64°14.0'W	ES	22.8.65
Atlantis II	24	124	4862	2	37°26.0'N–37°25.0'N	63°59.5'W–63°58.0'W	ES	22.8.65
Chain 50		81	5042	1	34°41.0'N	66°28.0'W	ES	2.7.65
				Angola Basin				
Atlantis II	42	197	4592–4597	2	10°29.0'S	9°04.0'E	ES	21.5.68
Atlantis II	42	196	4612–4630	1	10°29.0'S	9°04.0'E	ES	21.5.68
				Argentine Basin				
Atlantis II	60	259A	3305–3317	5	37°13.3'S	54°45.0'W	ES	26.3.71
Atlantis II	60	256	3906–3917	37	37°40.9'S	52°19.5'W	ES	24.3.71
				Guiana Basin				
Knorr 25		307	3835–3862	1	12°35.4'N 12°40.8'N	58°59.3'W 59°09.2'W	ES	3.3.72
Knorr 25		288	4417–4429	13	11°02.2'N 11°03.8'N	55°05.5'W 55°04.8'W	ES	25.2.72
Knorr 25		287	4934–4980	10	13°16.0'N 13°15.8'N	54°52.2'W 54°53.1'W	ES	24.2.72

Specific description. We can make but few additions to the excellent description of shell morphology given by Verrill & Bush (1898). The small medial teeth immediately below the umbo insert in a dorsal arc, away from the ventral edge of the hinge plate (Figs. 1 & 27a). The external ligament extends posteriorly in the mid-line of the escutcheon to about the posterior limit of the umbo at the insertion of the ninth tooth of the posterior plate series. The anterior ligament is short, not extending beyond the beak of the umbo.

The incurrent region has four or five papillae on each side and lacks mantle fusion between the posterior apertures. The gills are small, with 10 to 14 gill plates on each demibranch, and 7 to 10 palp ridges. The hind gut passes close to the anterior adductor muscle, but is not contiguous with it. The anterior adductor muscle is slightly larger than the obliquely orientated posterior adductor muscle (Fig. 2).

Morphology of the soft parts. No detailed account of the soft part anatomy has been given hitherto. Lack of mantle fusion and siphons (note, siphons may be formed in the Nuculanoidea without fusion of the mantle tissues, Yonge, 1959) is reminiscent of the condition in the Nuculoidea (Sanders and Allen, 1973). However, unlike the members of that order, the posterior mantle edge is highly specialized and divided into excurrent, incurrent and feeding regions in addition to the ventral pedal gape (Fig. 3).
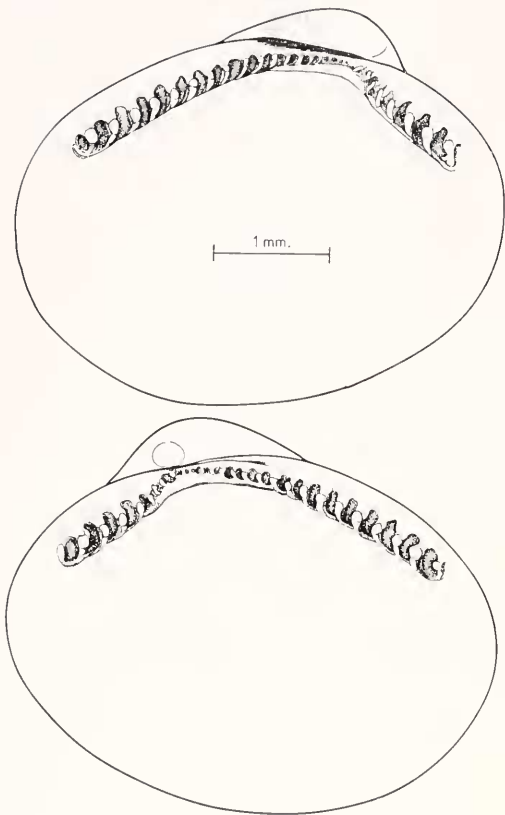
Figure 1. *Tindaria callistiformis* Verrill & Bush. Internal views of the left and right valves.

Figure 2. *Tindaria callistiformis* Verrill & Bush. Semidiagrammatic drawing of the body and mantle organs as seen from right and left sides.

The excurrent region occupies a very small portion of the posterior mantle margin. A narrow channel is defined by the ventral edge of the posterior adductor muscle and by a pair of low ridges, formed by the inner muscular mantle folds, to which the attenuate distal end of the gill axes are attached. The anus is positioned opposite this narrow channel. There is no development of the inner muscular fold of the mantle edge to form an incomplete siphon as Knudsen (1970) described for some other parts. The incurrent region is wider than the excurrent and defined by four to six pairs of short conical papillae, the number depending on the size of the specimen. On the right side immediately adjacent to the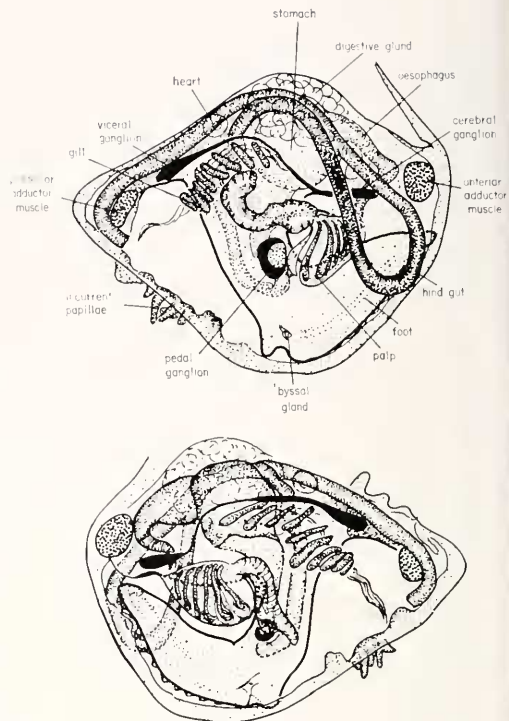 lower papilla there is a single sensory tentacle. The papillae are developed from the middle sensory lobe. In cross section, the papillae are radially divided into 12 to 15 haemocoelic cavities running the length of the papillae with longitudinal muscle fibres at the center.

Ventral to the incurrent region there is a feeding aperture which is formed by the extended overlapping and folded portions of the inner and middle mantle folds, and it is through this aperture that the palp proboscides are extended (Fig. 3). The inner muscular fold in the region of the posterior apertures is much broader than elsewhere. Gland cells are present in the outer mantle epithelium in the region immediately posterior to the feeding aperture. These extend anteriorly, although less densely, to the inside of the muscular fold in the region of the pedal aperture (Fig. 4).
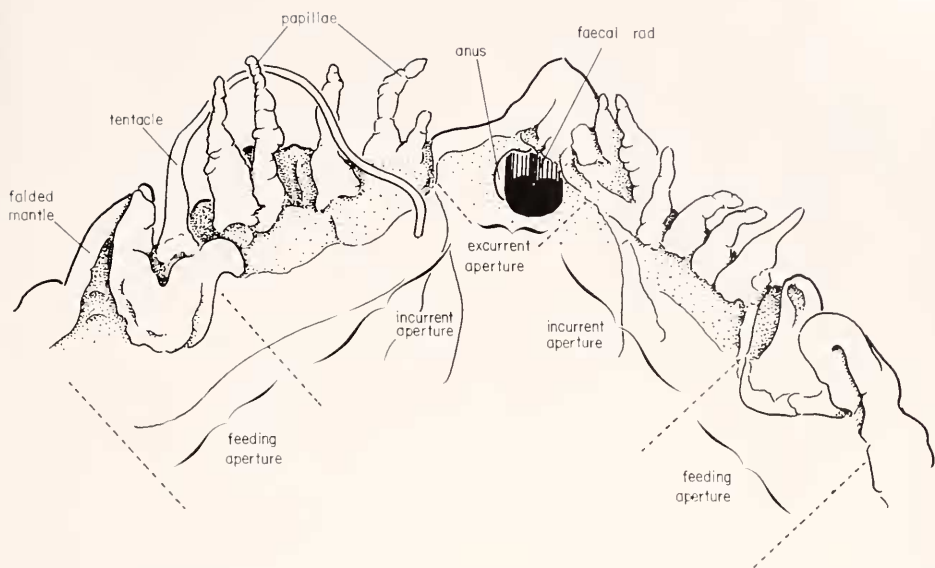
Figure 3. *Tindaria callistiformis* Verrill & Bush. Detail of the posterior mantle edge spread open and viewed from the ventral side; the limits of the various apertures indicated with dashed lines.

An anterior sense organ, derived from the middle sensory fold, is well-developed. The left sense organ is somewhat larger than the right, the latter positioned immediately below the ventral limit of the hind gut loop. For a comparatively robust shell, the adductor muscles are small and characteristically situated close to the pallial line and very near the shell margin. The 'quick' and 'catch' parts of the adductor muscles are clearly defined. The anterior muscle is circular in outline, while the posterior adductor is oval with the long axis oblique to the antero-posterior shell axis.

The gill axis lies parallel to the posterior dorsal margin of the shell and thus somewhat obliquely to the anterior-posterior axis of the body and shell. The number of gill plates is small, varying with the size of the animal. They are widely separate and alternate on either side of the axis (Fig. 2). The gill extends across the posterior third of the body to the ventral side of the excurrent region. Posteriorly, the gill plates do not extend much beyond the posterior limit of the body, thus the gill axes are extended posteriorly. The anterior limit of the gill axis is far removed from the insertion of the palp. The gill axis is highly muscular, with fibres extending its length and also reaching vertically to each gill plate (Fig. 5). The gill plates are finger-shaped and sub equal. There is no fusion between mantle and gill, and connections between the inner filaments of the two gills are apparently lacking.

The palps are remarkable for their small size and the small number of ridges (seven to nine), the exact number being dependent on the size of the animal (Fig. 6). The palp ridges are broad, high and deeply grooved on the mid-anterior face. The most posterior ridge is well anterior to the posterior thickened edge of the palp.

The foot is typically nuculanoid with a well-defined neck at its junction with the body. Within the neck are large pedal ganglia and associated statocysts. Small papillae fringe the entire edge of the divided sole. The heel is small and triangular and internally there is a small 'byssal' gland with paired apertures opening at the junction be-
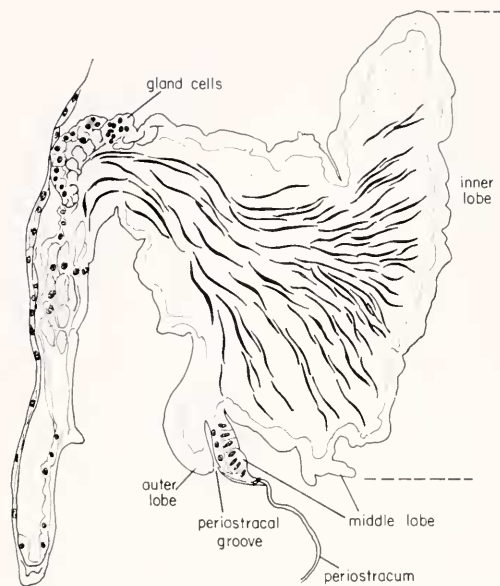
Figure 4. *Tindaria callistiformis* Verrill & Bush. Transverse section through the mantle edge.

tween heel and foot. Numerous subepithelial mucous glands open on to the sole of the foot on either side and in the mid line (Fig. 7).

The gut also is basically nuculanoid with a single loop of the hind gut on the right side of the body. The mouth is posterior to and some distance from the anterior adductor muscle. This may be due in part to its displacement by the loop of the hind gut, which passes close to the adductor muscle. It may also have functional significance in relation to the posterior ingress of food material into the mantle cavity. The oesophagus is long, first taking an anterior course to the posterior dorsal edge of the anterior adductor muscle where it is displaced slightly to the left of the sagittal plane. At this point it turns dorsally and posteriorly to open on the left anterior side of a huge stomach. The oesophagus is inflated close to its junction with the stomach and the stomach occupies much of the body space (Figs. 2 & 8). Although the stomach is large, there are only six very low crested
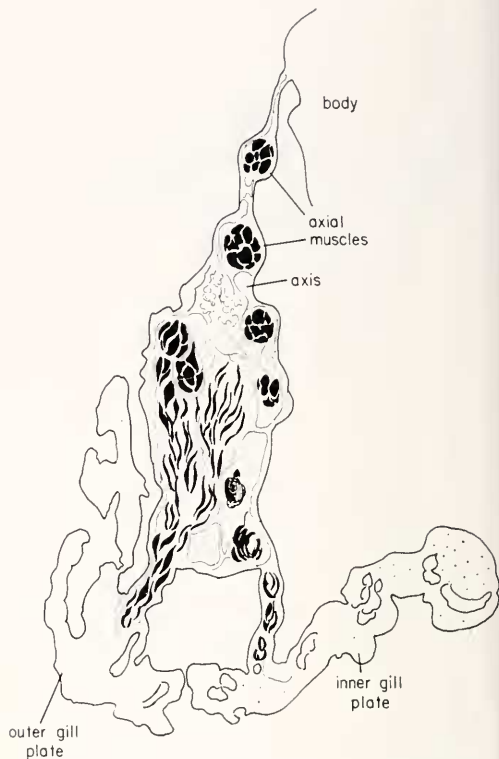

Figure 5. *Tindaria callistiformis* Verrill & Bush. Transverse section through the left gill showing axial muscles and outline of gill plates.

sorting ridges on its right side. Much of the remainder of the stomach is lined with a gastric shield which has a well-defined tooth on the anterior dorsal side close to the apertures of the three ducts of the digestive diverticula. The combined mid gut and style sac penetrate the neck of the foot, pass to the posterior and left side of the pedal
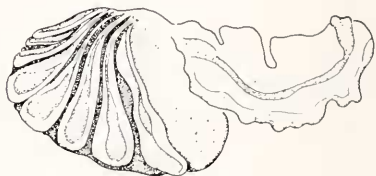

Figure 6. *Tindaria callistiformis* Verrill & Bush. Lateral view of inner surface of a proximal palp to show detail of ridging.

Figure 7. *Tindaria callistiformis* Verrill & Bush. Transverse section of the foot to show position of the muscles and pedal glands.

Figure 8. *Tindaria callistiformis* Verrill & Bush. Transverse section through the body to show detail of stomach, hind gut and digestive gland.

ganglion and join with the hind gut just ventral to the latter. The hind gut turns and follows a dorsal course parallel with the style sac, with a shallow, ill-defined U-bend posterior to the stomach. The hind gut then forms a single loop to the right and the loop together with some body tissue penetrates the right mantle to a position close to the pallial line. A typhlosole is present throughout the length of the hind gut.

The ganglia and their connectives are large, as the visceral and cerebral ganglia are elongated. A pair of statocysts dorsal and postero-lateral to the pedal ganglia are filled with small crystals (which are not calcium carbonate) lacking ducts to the outside. Transverse muscle fibres in the foot are found dorsal and ventral to the ganglia and the statocysts.

The kidney is small and multilobed. Sexes are separate.

Size, Reproduction and Age. All three stations from which large numbers of *T. callistiformis* were collected showed similar population histograms. Each was strongly skewed to the left (Fig. 9). Yet, we might not adequately be sampling the smallest juvenile stages which could pass through the 0.42 mm openings in our screens. The eggs on hatching are at least 0.15 mm long and the size of the metamorphosed post-
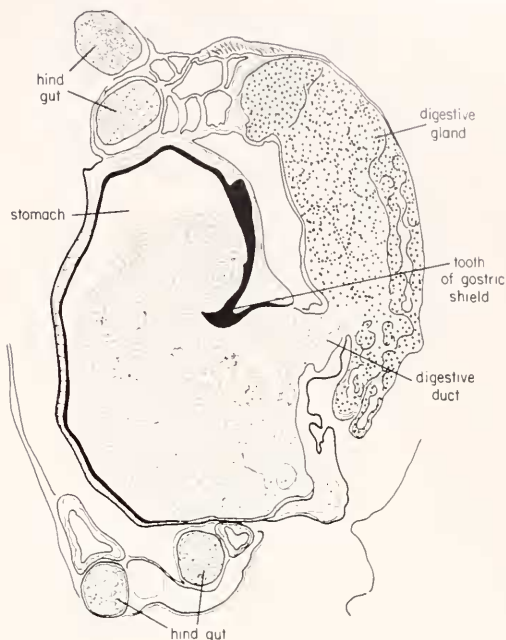
larvae settling onto the bottom (assuming a lecithotrophic mode of reproduction) must be somewhat larger. We feel our histograms do not significantly distort the length-frequency composition of *T. callistiformis* at the sampling sites. Analysis of 60 specimens from Station 77, representative of the size range, indicates that gonadal development does not occur until this species reaches a size of between 4.0 and 4.5 mm total length. This was confirmed by examination of the specimens from Stas. 78 and 85 which show that all specimens larger than 4.5 mm had some gonadal development and the larger the specimen the more mature was the gonad. Only in an exceptionally small percentage (2.6 to 3.0 per cent depending on the sample) of the total population was any sign of gametogenesis evident. Great disparity exists in the sex ratio with only one female to every five males. The most mature female (6.5 mm

total length) was dissected and the eggs counted; these numbered 230 having a maximum length of 145 μ. From our past observations on a wide range of abyssal protobranchs, we would estimate this specimen to be 3/4 mature. The eggs were maturing simultaneously. There is no evidence of brooding.

Growth rate measurements using [228]Ra chronology (Turekian et al., 1975) show that *Tindaria callistiformis* having a length of 4 mm are about 50 to 60 years old, while the largest specimen, having a length of 8.4 mm, has an age of 100 years or longer.

The moderate degree of variation in shell shape appears to have no intimate relation to the size of the specimen. Thus, the height/total length ratio varies from 0.62 to 0.83 over much of the size range (Figs. 10

and 11). However, if the five largest specimens are ignored, there is a tendency for the height/total length ratio to decrease with increasing size. Similarly, there appears to be no increase in length posterior to the umbo with increasing length. Although anterior in position, there is considerable variation in the position of the umbo, the extreme limits being between 55 per cent and 76 per cent of the total length. The maximum total length recorded is 8.4 mm.

Tindaria hessleri, new species
Figures 12–16 & 27

Holotype: MCZ 279902, from *Atlantis II*, Cruise 31, Station 141, in 2031 m.
Depth range = 1739 to between 2051 and 2357 m.

Cruise No.		Station No.	Depth (m)	No. of Specimens	Latitude	Longitude	Gear	Date
				W. Europe Basin				
Sarsia		S–44	1739	19	43°40.8'N	3°35.2'W	ES	16.7.67
				Cape Verde Basin				
Atlantis II	31	138	1944–1976	2	10°36.0'N	17°52.0'W	ES	4.2.67
Atlantis II	31	141	2131	3	10°30.0'N	17°51.5'W	ES	5.2.67
Atlantis II	31	139	2099–2187	1	10°33.0'N	17°53.0'W	ES	4.2.67
Atlantis II	31	145	2105–2192	1	10°36.0'N	17°49.0'W	ES	6.2.67
Atlantis II	31	144	2051–2357	7	10°36.0'N	17°49.0'W	ES	5.2.67

Specific description. Shell stout, robust, with strong, uniform, concentric ridges, somewhat oval in outline and extended posteriorly; umbos anterior in position, moderately swollen beaks prominent and strongly curved medio-anteriorly; escutcheon present and forms moderate concavity (Fig. 27B); elongate, narrow, external ligament extends posteriorly along the escutcheon to about the insertion of the eleventh tooth on the posterior hinge plate and anteriorly to about the insertion of the sixth or seventh tooth of the anterior hinge plate; dorsal shell margin strongly convex; antero-dorsal margin short, sloping rapidly to form a continuous curve with the anterior margin; postero-dorsal margin long, sloping more gradually to form a smooth

curve with posterior margin; posterior end narrow, evenly rounded; anterior end broad, rounded, but with dorso-anterior shorter than ventro-anterior margin; ventral margin long and only slightly convex. Hinge plate broad and strong with a continuous row of teeth; posterior hinge plate long with about 21 to 22 teeth, 14 through 21 or 22 large and robust, more medial teeth progressively smaller and very reduced in size at confluence of the anterior and posterior hinge plates; anterior hinge plate short and thick bearing about 10 teeth, distal five large and strong, more proximal teeth as on posterior hinge plate become gradually smaller with minute proximal teeth inserting dorsally (Fig. 12).

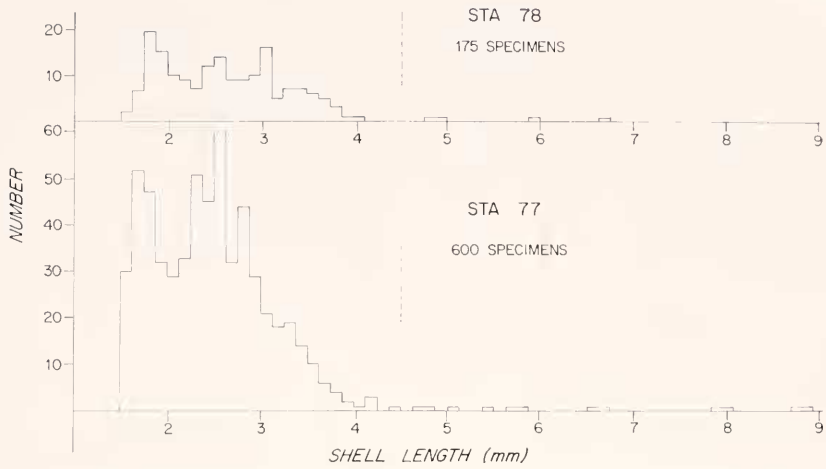*Tindaria hessleri* differs from *T. callisti-*

Figure 9. *Tindaria callistiformis* Verrill & Bush. Size frequency histograms of samples from two stations. The dashed lines indicate the sizes at which gametogenesis is evident.
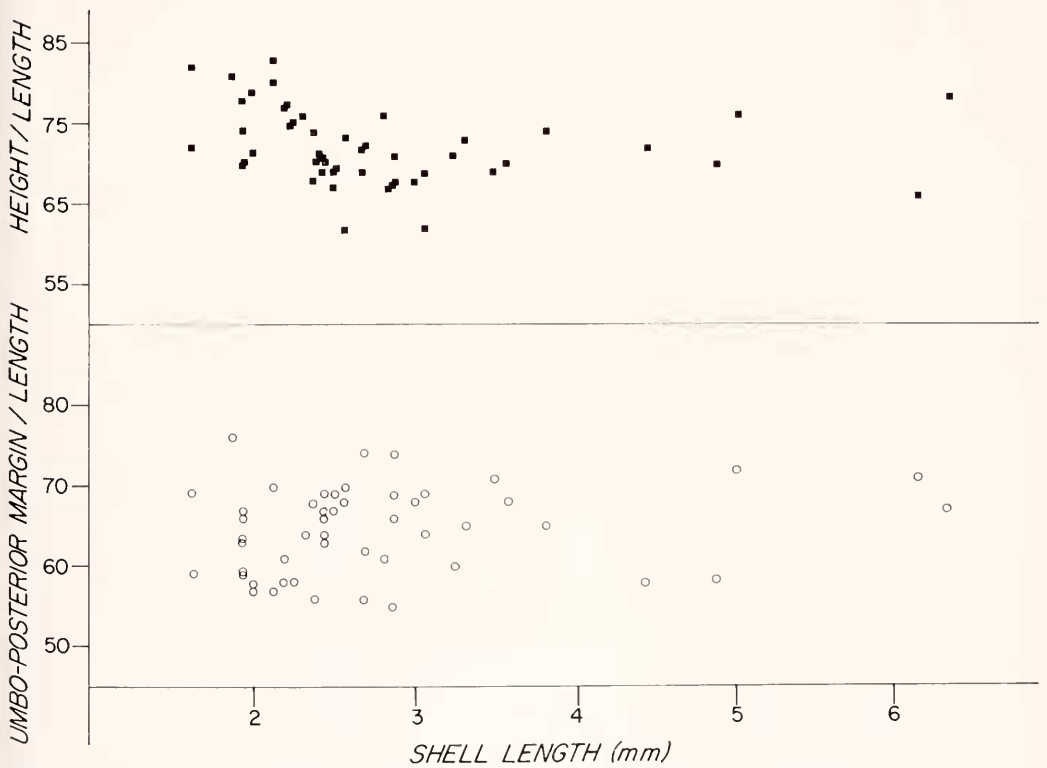

Figure 10. *Tindaria callistiformis* Verrill & Bush. Graph showing height/total length (■) and umbo to posterior margin/total length (○) plotted against total length.
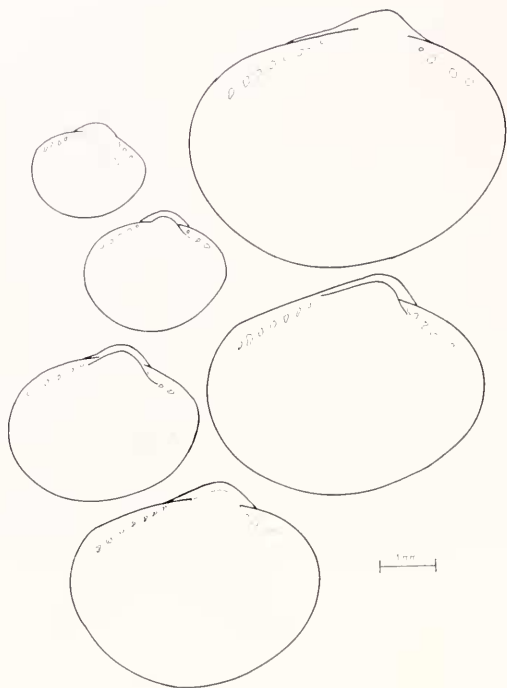
Figure 11. *Tindaria callistiformis* Verrill & Bush. Growth series in lateral view.

Figure 12. *Tindaria hessleri* Sanders & Allen. Internal views of the left and right valves.

formis in the following ways: *T. hessleri* is less smoothly convex and more triangular in outline; the ventral margin of the valve is deepest directly beneath the umbo rather than more posteriorly; the dorsal margin is more strongly convex; the anterior margin is not as broadly rounded; and the hinge plates are less massive.

Incurrent region, three papillae on each side; adductor muscles oval and equal in size; gill small with 7 to 14 plates on each side of the axis; palp with 8 to 10 ridges; hind gut extends into the mantle of the right side to a position short of the pallial line, part of hind gut lies adjacent to the posterior face of the anterior adductor muscle; visceral ganglion placed anterior to the posterior adductor muscle.

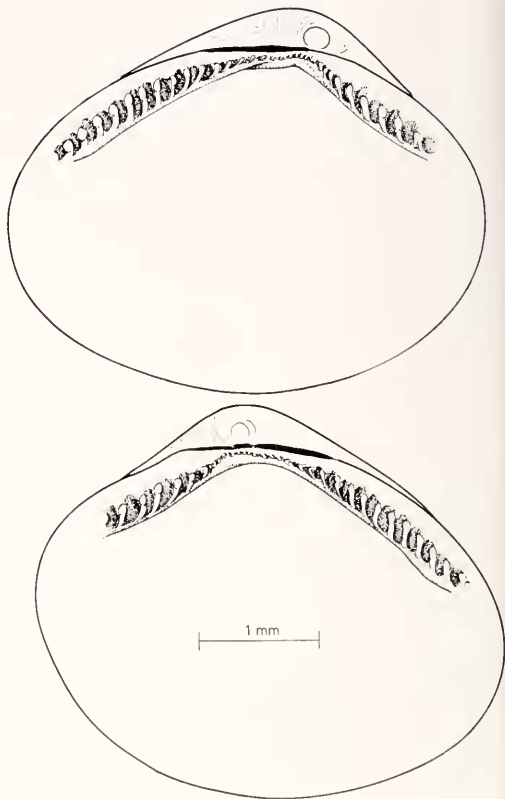*Morphology of the soft parts.* The morphology of *T. hessleri* is very similar to that of *T. callistiformis* (Fig. 13). How-ever, unlike the latter species, there is a permanent excurrent aperture formed by the fusion of the muscular lobe and the inner part of the sensory fold of the mantle, between the incurrent and excurrent regions (Fig. 13). There are only three pairs of papillae on each side of the incurrent region and sectioned material suggests that mantle fusion dorsal to this region involves the homologue of a pair of papillae that have fused together. There is no single sensory tentacle but mantle extensions at the dorsal side of the feeding aperture may possibly serve the same function. The latter aperture is well-developed with the muscular and sensory folds of the mantle showing considerable hypertrophy. These are folded in preserved specimens but in life they must be capable of considerable extension.
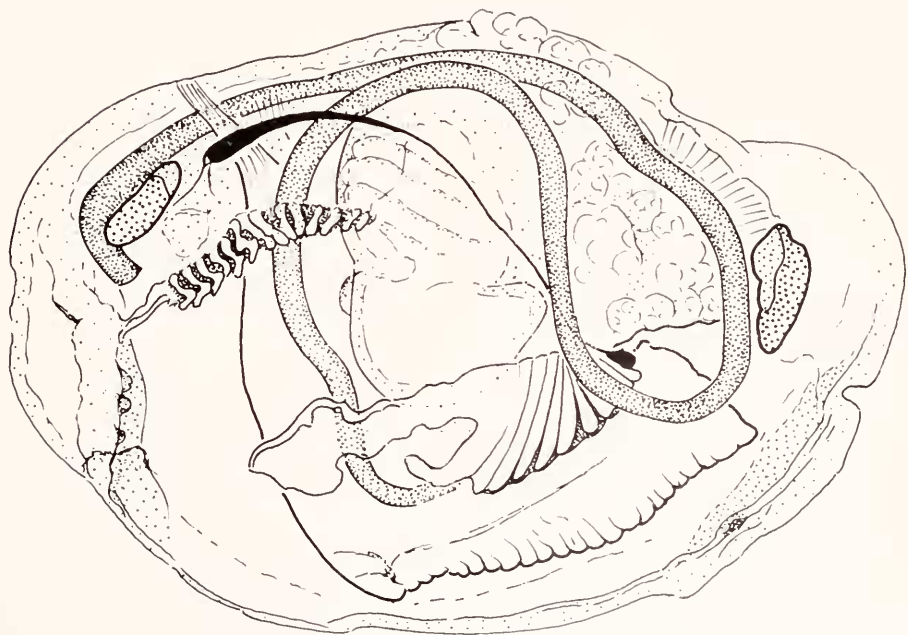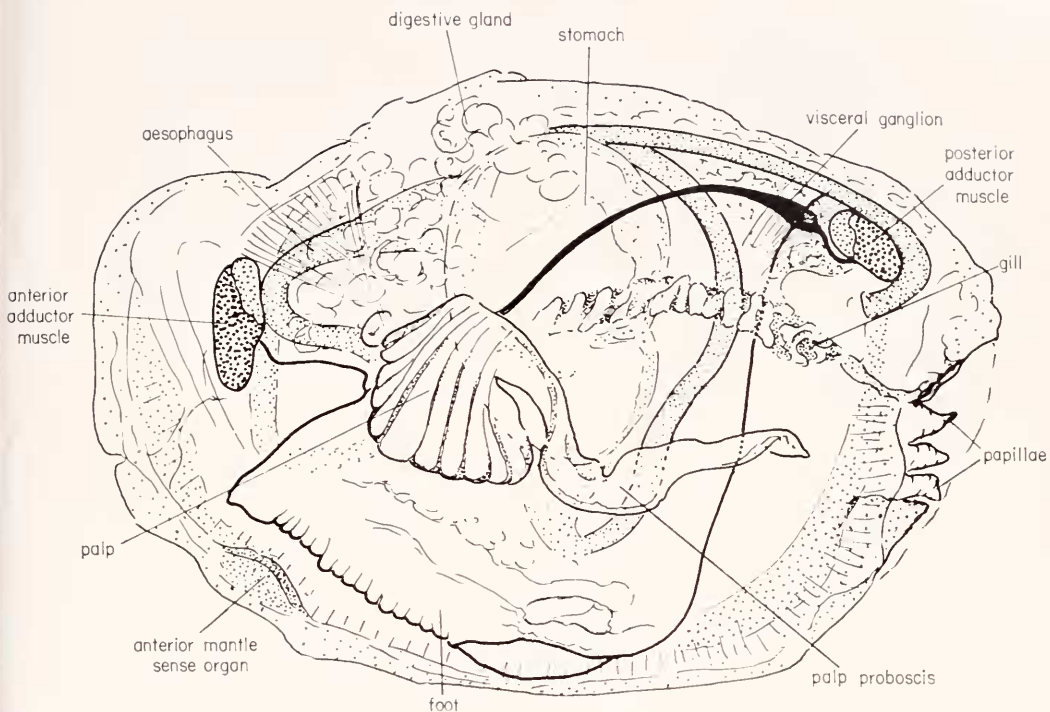
Figure 13. *Tindaria hessleri* Sanders & Allen. Semidiagrammatic drawings of the body and mantle organs as seen from the left and right sides.
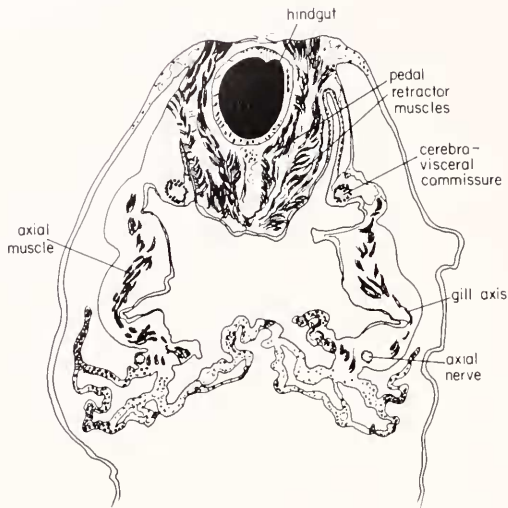
Figure 14. *Tindaria hessleri* Sanders & Allen. Transverse section through the posterior part of the body and gills to show axial and pedal retractor muscles.
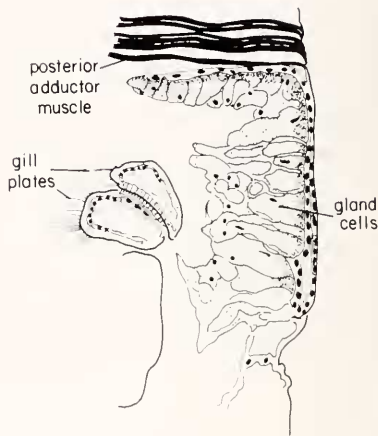

Figure 15. *Tindaria hessleri* Sanders & Allen. Transverse section through the right margin of the hypobranchial cavity showing the distribution of basiphilic gland cells.

There is no mantle fusion either dorsal or ventral to the feeding aperture, but aposition or overlapping of the mantle edges at these points makes an efficient functional separation. Adjacent to this region is a well-defined area of acidophilic mucus secreting cells at the surface of the inner mantle epithelium. The adductor muscles are oval in cross section with the longitudinal axis vertical in the anterior muscle and oblique in the posterior muscle. To the inside of the inner muscular lobe and at 90 degrees to it are a series of fine pallial retractor muscles extending inwards for a short distance; these are present along the entire perimeter of the mantle (Fig. 13).

In specimens of a similar size there are more gill filaments than in *T. callistiformis* and, as in the latter species, they are arranged alternately along the axis. Behind the body, the tips of the filaments of the inner demibranch are extended and fuse with the filaments of the inner demibranch of the opposite gill and with adjacent filaments of the same demibranch, thus forming a membranous junction. The filaments

of the outer demibranches are also extended and make a strong ciliary junction with the mantle (Fig. 14). The gill axis is very muscular and it must be concluded that in life the gills form a pumping system in many ways analogous to that of the Septibranchia. The hypobranchial cavity is thus entirely separate from the rest of the mantle, the lateral mantle walls of the cavity being lined with basiphilic gland cells (Fig. 15). No fecal material passes into the mantle cavity. When the gill is contracted the volume of the hypobranchial cavity is very small.

The palps are very similar to those of *T. callistiformis* except that, depending on the size of the animal, the number of ridges is somewhat greater, and these lie relatively closer together than in the latter species. The palps (and mouth) lie far posterior to the anterior adductor muscle. The course of the gut is essentially the same as in the previous species but the lumen is relatively smaller and does not extend as far into the mantle, never reaching the inner muscular lobe of the mantle—even in the smallest specimens. The foot is similar to that of *T. callistiformis*, however, the 'byssal' gland is somewhat larger. Nervous

system and kidney are as in the previous species; sexes are separate.

Size and Reproduction. The small number of specimens and the opaqueness of the shell makes an analysis of reproductive potential similar to that given for *T. callistiformis* impossible. However, sections show that a specimen of 2.5 mm total length contains approximately 350 ova with a maximum length of 110 μ. The ova are maturing simultaneously.

Relatively few shells (eight) were available for studies on dimensional variation (Fig. 16). It appears to be of the same order as *Tindaria callistiformis* and *Pseudotindaria galatheae* with the height/length ratio varying from 0.69–0.81 and with the total length/umbo to posterior margin length varying from 58 per cent to 67 per cent, the umbo being anterior in position.

It gives us great pleasure to name this species after Dr. R. R. Hessler, of the Scripps Institution of Oceanography—colleague, collaborator and friend—who has contributed so significantly to our knowledge of the abyssal fauna.

Tindaria cytherea (Dall, 1881)
Figures 17–22

Nucula cytherea Dall, 1881, Bull. M.C.Z., 9, No. 2: 123 (*Blake* Station without number Yucatan Strait, 640 fms. (= 1171 m)). Holotype. U. S. Nat. Mus. 63137.

Malletia veneriformis Smith, 1885, Chall. Rep. 13: 246, pl. 20, figs. 9, 9a. (*Challenger* Station 33, off Bermuda, 435 fms (= 796 m).)

Malletia cytherea (Dall), 1886, Bull. M.C.Z., 12, No. 6: 254, pl. 8, figs. 1, 1a. [in part, figure only.]

Malletia amabilis Dall, 1889, Bull. M.C.Z., 18: 438, pl. 40, fig. 8. [New name for *Malletia cytherea* Dall 1886 in part, description only, not figure.]

Tindaria cytherea (Dall) Verrill & Bush, 1898, Proc. U.S.N.M. No. 1139.

Previous records. Depth range = 711 to 1325 m. North America Basin—1 station. Ref. Smith, 1885. Gulf of Mexico Basin—1 station. Ref. Dall, 1886. Caribbean Basin—4 stations. Refs. Dall, 1881, 1886; Smith, 1885.

Present record. Depth 1000 m.

Cruise	Station No.	Depth (m)	No. of Specimens	Latitude	Longitude	Gear	Date
			North America Basin				
Panulirus	Bermuda #1	1000	1	32°16.5'N	66°42.5'W	AD	13.4.60

We have collected a single large specimen of a tindariid species off Bermuda in 1000 meters that is similar to or identical with a number of forms described from the same general region and depth. These are *T. cytherea*, (Dall) *T. amabilis* (Dall) and *T. veneriformis* (Smith) (Fig. 17). Dall (1886) synonymized *T. cytherea* and *T. veneriformis* and later Verrill and Bush (1898) synonymized *T. cytherea* and *T. amabilis*, although Dall (1889) believed that they were separate. Dall (1881, 1886, 1889) described two specimens, one in 1881 as *Nucula cytherea*, and the second in 1886 as *Malletia cytherea*. In 1889 he stated that the second specimen described in 1886 was sufficiently different from the specimen described in 1881 to warrant the erection of a second species which he named *M. ama-* *bilis*. The position is confused by the fact that the specimen described as *N. cytherea* (Dall, 1881) is figured in his second paper (Dall, 1886) while the specimen described in 1886 is figured in his third paper (Dall, 1889). We agree with Verrill and Bush (1898) that these all refer to the same species as indicated in the synonymy.

We have but a single specimen, measuring 9.2 mm total length, height 7.6 mm. Its description is as follows:

Description of Shell. Shell stout, robust, straw-colored, with strong, uniform, concentric ridges; oblong oval in outline with anterior end slightly truncate, inequilateral; umbo anterior in position, prominent, with beaks strongly curved antero-medially; escutcheon present; external ligament elongate, moderately large, extending posteriorly
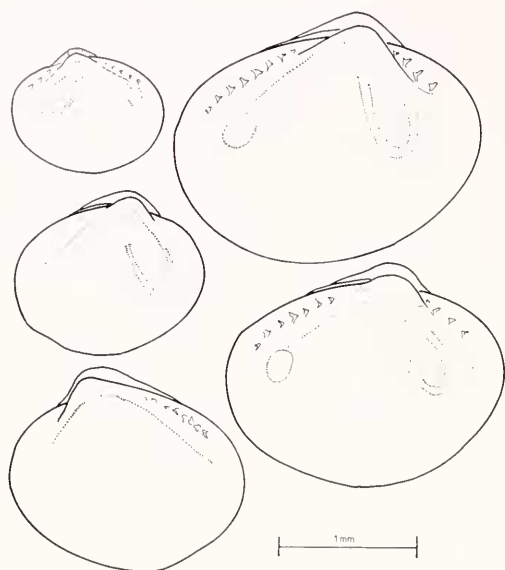
Figure 16. *Tindaria hessleri* Sanders & Allen. Growth series in lateral view.

to about the insertion of the fourteenth tooth of the posterior hinge plate series and anteriorly to about the sixth tooth of the anterior series; inner layer forms a small crescent-shaped section immediately below the beaks; dorsal shell margin strongly convex with both antero- and postero-dorsal shell margins steeply sloping away from the umbos; long postero-dorsal margin forms a smooth curve with the rather broadly rounded posterior end; antero-dorsal margin forms a smooth curve with the slightly truncated anterior end; ventral margin smooth, long, and only shallowly convex; hinge plate strong, moderately broad with teeth continuous beneath the umbo; long posterior hinge plate bearing about 24 teeth which are directed primarily medially, proximal teeth smallest, distal teeth increasingly larger to tooth 16 to 18, the latter being large, long, and robust, thereafter teeth diminish in length but remain robust; anterior hinge plate with about 14 medially directed teeth, teeth 6 to 13 strong and long, more proximal teeth progressively smaller.
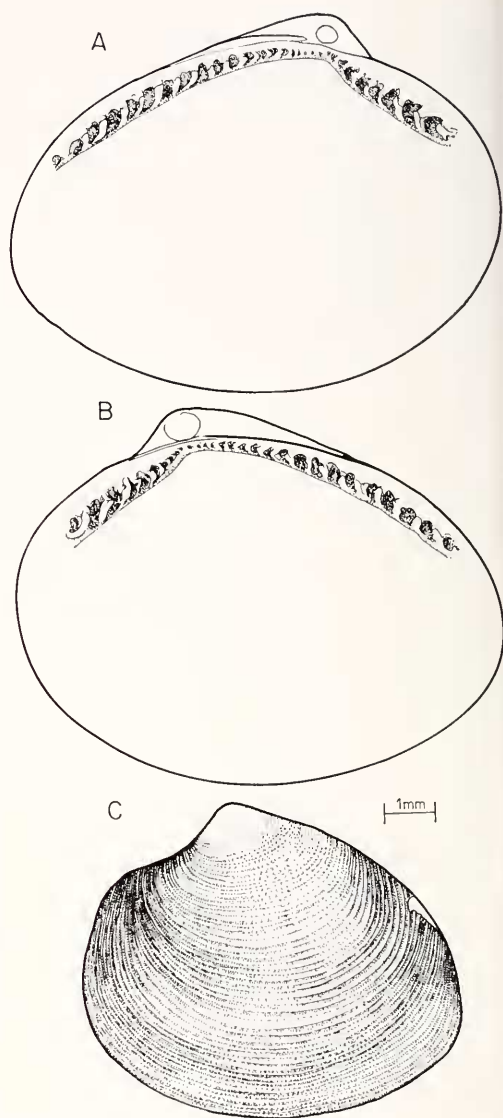

Figure 17. *Tindaria cytherea* (Dall). A & B, internal views of the valve (Type specimen USNM No. 63137, Blake Collection, Yucatan Strait 640 fm); C, external lateral view of specimen collected by authors.

Remarks. This specimen differs from the descriptions given by Dall (1881, 1886) and Smith (1885) primarily by the somewhat more obvious external ligament and the straight ventro-medial edge of the anterior margin. In this respect it resembles the
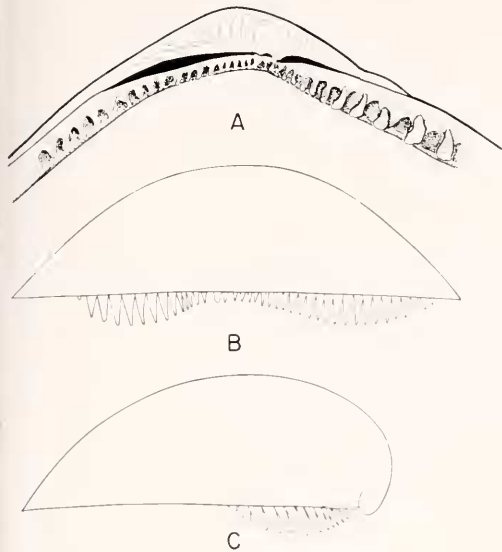
Figure 18. *Tindaria cytherea* (Dall). Detail of the hinge and teeth of the specimen collected by the authors. A, left valve, umbonal region; semidiagrammatic presentation of right valve in dorsal (B) and posterior view (C).

type specimen of *M. amabilis* (Dall) rather than the type specimen of *M. cytherea* (Dall) (Fig. 17) in which the ventro-medial edge is curved. Shell proportion, shape and thickness alter with growth in many deep-sea protobranch species. These changes are most evident in the very largest specimens. Our single individual is larger than any of the other specimens that we refer to this species and we attribute the differences in our specimen to its larger size.

Description of the soft parts. Incurrent region with 7 papillae on either side, no single tentacle; adductor muscles very small, oval and dorsal in position, anterior adductor muscle somewhat larger than the posterior; gills moderately large, 24 gill plates on each side of the axis; hind gut penetrates slightly into the mantle, ventral limit of hind gut loop scarcely ventral to the ventral edge of the anterior adductor muscle; vis-
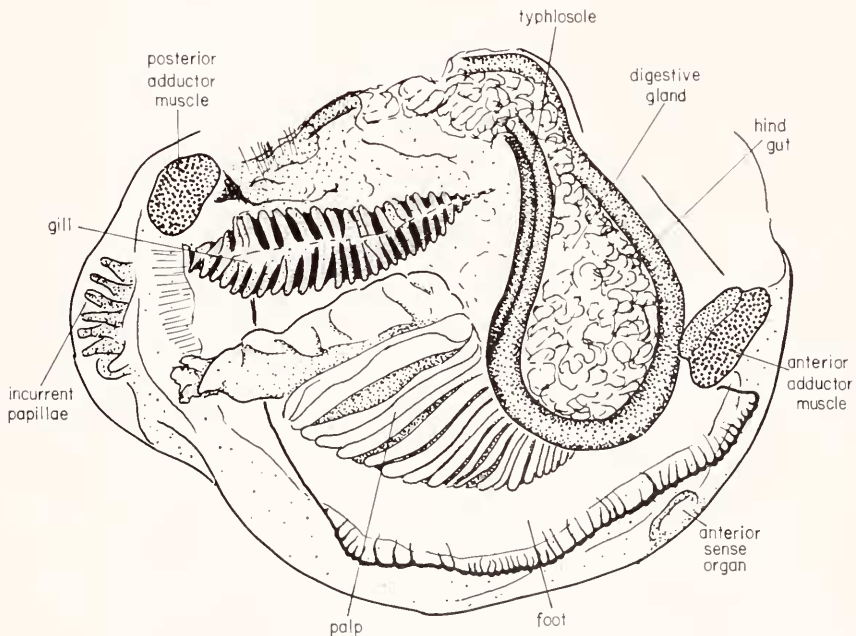

Figure 19. *Tindaria cytherea* (Dall). Semidiagrammatic drawing of the body and mantle organs as seen from the right side.
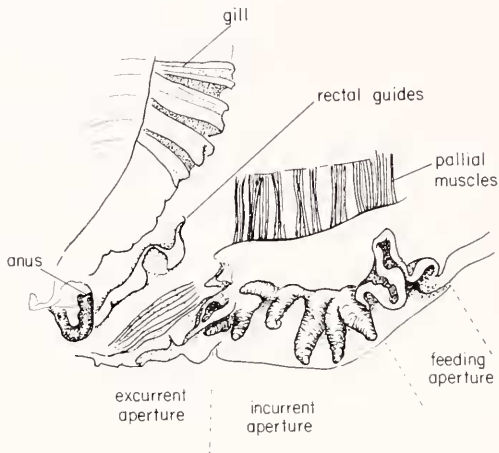
Figure 20. *Tindaria cytherea* (Dall). Detail of the posterior part of the left mantle margin.

Figure 21. *Tindaria cytherea* (Dall). Latero-ventral view of gill.

ceral ganglion close to the posterior adductor muscle.

Remarks. Fortuitously, the soft parts of our single specimen had become detached from the shell on preservation. There are no great differences in the morphology of the soft parts from those of other species, many being the consequence of the large size of the specimen (Fig. 19). Hence, the development and the extension of the inner mantle fold to form a feeding aperture below the incurrent region is particularly well marked (Fig. 20). Similarly, the anterior sense organ is well-developed. The gills are large (Fig. 21) but not fused to form an obvious pumping organ, although in life,

with the aid of peripheral interlocking cilia, they could possibly function as such. The gill axes which connect with the ventral side of the excurrent region probably act as guides during the expulsion of faeces from the anus. The palps, probably because of the large size of this specimen, have a greater number of ridges (18) than in other species of *Tindaria*, but they are small in comparison with other protobranch genera of the same size. The palp proboscides are extremely large and elongate. The mouth, unlike the other species here described, is close to the anterior adductor muscle. The course of the gut is similar to that of *T. callistiformis* and *T. hessleri*. The stomach is extremely large, with an extensive gastric shield on the left dorsal side, and bears a tooth close to the three apertures of the digestive diverticula. There are 10 sorting ridges on the right side (Fig. 22). The ganglia are extremely large.

Tindaria miniscula, new species
Figures 23–28

Holotype: M.C.Z. 279901, from *Atlantis II* cruise 42, Station 197, in 4565 to 4595 m.
Depth range: 4559–4566 to 4612–4630 m.

Cruise	Station No.	Depth (m)	No. of Specimens	Latitude	Longitude	Gear	Date
			Angola Basin				
Atlantis II	198	4559–4566	7	10°24.0'S–10°29.0'S	9°04.0'E–9°09.0'E	ES	21.5.68
Atlantis II	197	4565–4595	27	10°29.0'S	9°09.0'E	ES	21.5.68
Atlantis II	196	4612–4630	2	10°29.0'S–10°29.0'S	9°03.0'E–9°04.0'E	ES	21.5.68

Specific Description. Shell minute, strong, elongate, oval in outline, with uniform concentric ridges; umbo large and swollen; beaks prominent and strongly curved medially; escutcheon forms a conspicuous concavity in dorsal margin (Fig.
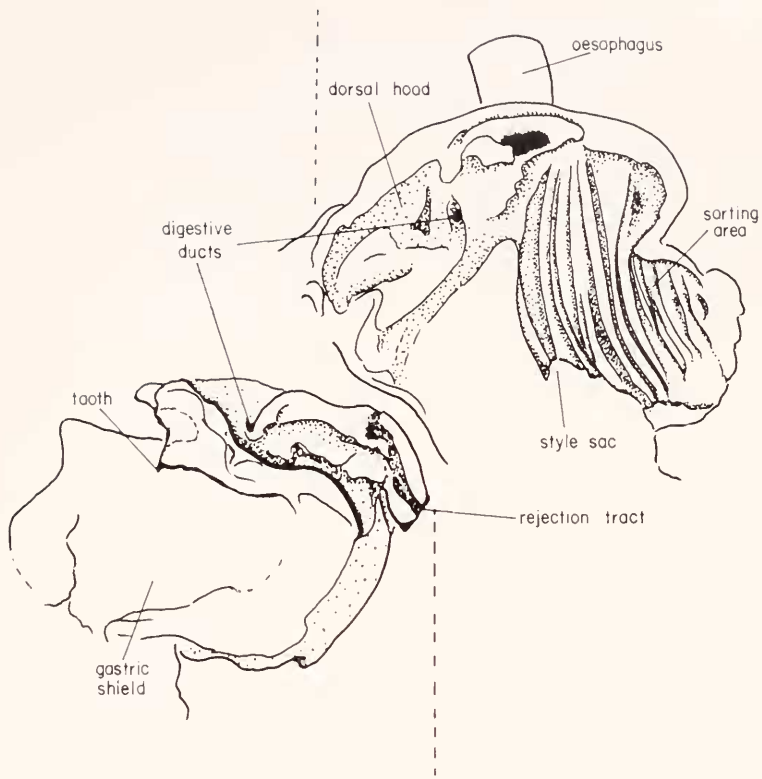
Figure 22. *Tindaria cytherea* (Dall). Internal detail of the left and right sides of the stomach.

27c); external ligament elongate, narrow, extending posteriorly to near the insertion of the second tooth of posterior hinge plate series and extending anteriorly to the insertion of the first tooth of anterior series; dorsal shell margin weakly convex; antero-dorsal margin short, rather straight and, distally, sloping ventrally to form a smooth curve with the anterior margin; postero-dorsal margin longer, slightly convex to form continuous curve with the posterior margin; anterior and posterior margins evenly rounded; ventral margin elongate and moderately convex.

Hinge plate thin, rather weak with a relatively broad edentulous space separating the anterior and posterior rows of teeth; posterior hinge series with six chevron-shaped teeth; anterior hinge series shorter, with three similar teeth (Fig. 23).

Tindaria miniscula differs from *T. callistiformis*, *T. hessleri* and *T. cytherea* in its small size, oval shape, few teeth on thin hinge plate, the extensive endentulous space on hinge plate beneath umbo and the more medial position of the umbo.

Morphology of the soft parts. Incurrent region with three papillae to the left side and two to the right; adductor muscles small, unequal in size; gill very small with six to seven plates to each demibranch; palp with five to six ridges; hind gut penetrates mantle of right side almost to the pallial line; part of hind gut lies adjacent to the posterior face of the anterior adductor
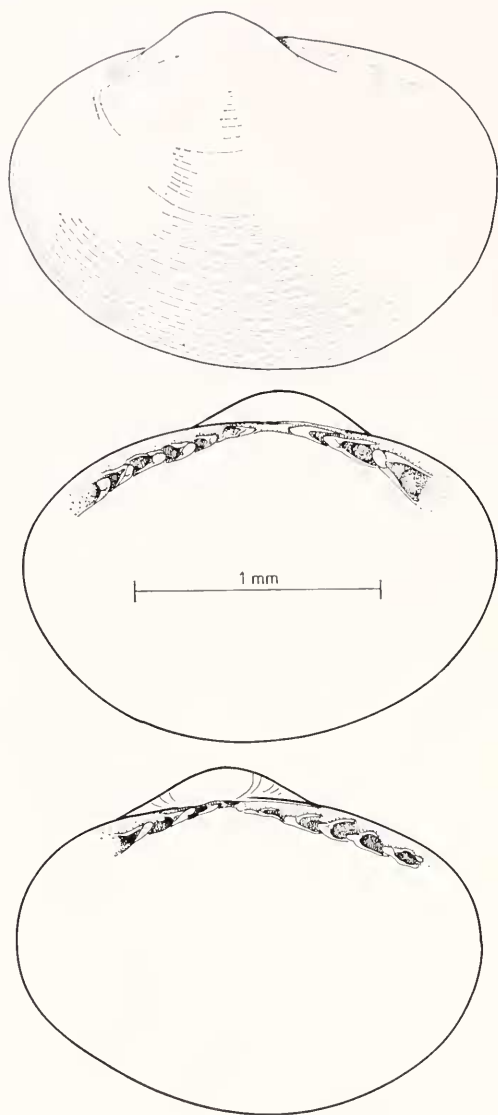
Figure 23.   *Tindaria miniscula* Sanders and Allen. External view of the left valve and internal view of the left and right valves.

muscle; visceral ganglion contiguous with the posterior adductor muscle.

The two papillae to the left of the incurrent region alternate with the three to the right so that the dorsalmost papilla is on the right, i.e., the two most ventral are on the left. The third left ventral papilla may possibly be homologous to the single nuculanid tentacle but in form and histology it cannot be separated from the others. A pair of well marked faecal guides or ridges mark the ventral limit of the excurrent aperture. Below the incurrent region the extended inner mantle folds overlap to form a feeding aperture. Separation of the aperture is not permanent. Inward of the feeding aperture and the incurrent aperture is a band of very large epithelial gland cells. Adductor muscles are small and the posterior is larger. The gills are very small, approximately seven pairs of alternating gill plates set tangentally across and behind the posterior part of the body. The gill axes are attached to the mantle edge at the level of the faecal guides. There are a few muscle fibers in the axes and two well-developed muscles in the plate. The palp is relatively large, extending approximately half the total length of the animal; the palp proboscides are stout (Fig. 24). The mouth is set posterior to the anterior adductor muscle, the oesophagus extends forwards, turning short of the anterior adductor muscle, posterodorsally to the stomach. The lumen of the oesophagus is exceptionally large, as is the stomach. The latter occupies the bulk of the body space. The stomach is almost entirely lined with the gastric shield, and is surrounded by a fine network of muscle fibers. Diatom frustules are the main organic content of the stomach. It is possible that the digestive gland is composed of two regions, the umbo non-pigmented and the remainder a pale brown color, but sections indicate no obvious histological differences. The hind gut forms a single loop to the right-hand side of the body, penetrating the lumen of the mantle and skirting the anterior adductor muscle, but not reaching the inner mantle lobe. At its maximum point of penetration it lies some distance dorsal to the anterior mantle sense organ. The hind gut also extends deep into the foot ventral to the pedal ganglia. A typhlosole is present along the entire length of
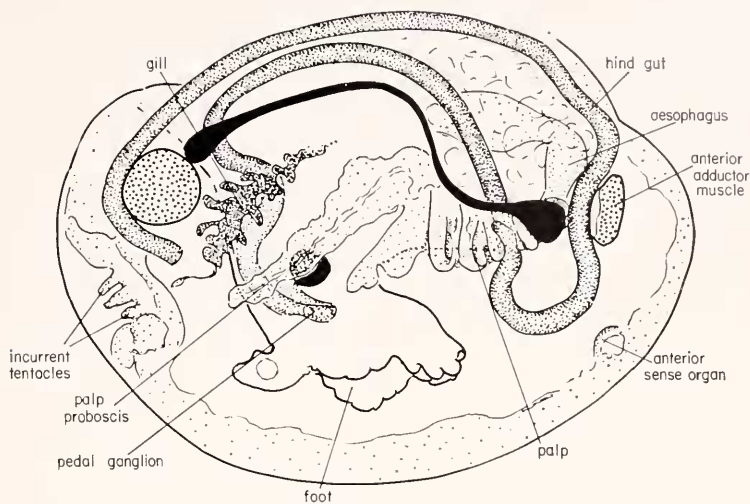
Figure 24. *Tindaria miniscula* Sanders & Allen. Semidiagrammatic drawing of the body and mantle organs as seen from the right side.

the gut. The foot is relatively small, and placed far back on the visceral mass. It bears a relatively large, triangular, posteriorly directed heel and a small 'byssal' gland. The sole of the foot is small, divided and peripherally papillate with glands to the inside of the papillae. The ganglia are large, particularly the pedal, the visceral and cerebral ganglia are attenuate pear-shape. There is a pair of small but typical protobranch statocysts dorsal to the pedal ganglia. The kidney is very small; sexes are separate, whole mounts showing initial stages in ovarian development with approximately 12 ova lateral to the stomach.

Although the total number of specimens in our samples is small, and the size range is so much smaller than in other species (0.8 to 2.5 mm), the population histogram remains clearly skewed to the left as it is in *Tindaria callistiformis* (Fig. 25). Similarly, the height/length ratio shows a wide range of values varying from 0.66 to 0.78 over the length range (Fig. 26). However, we may not have sampled the smaller juvenile stages which might have passed through the
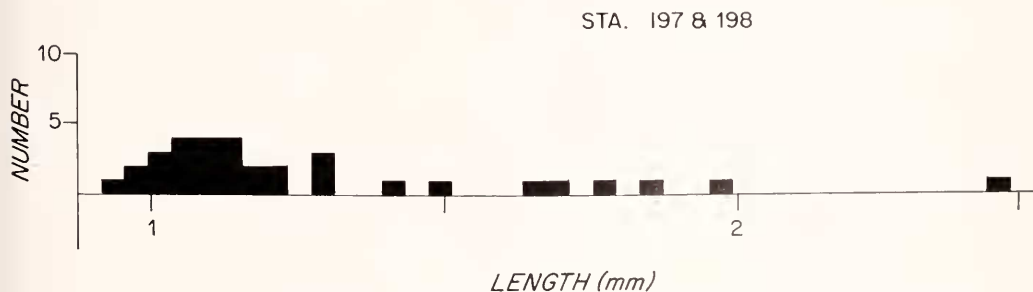

Figure 25. *Tindaria miniscula* Sanders & Allen. Size frequency histogram of specimens collected at Stations 197 and 198.
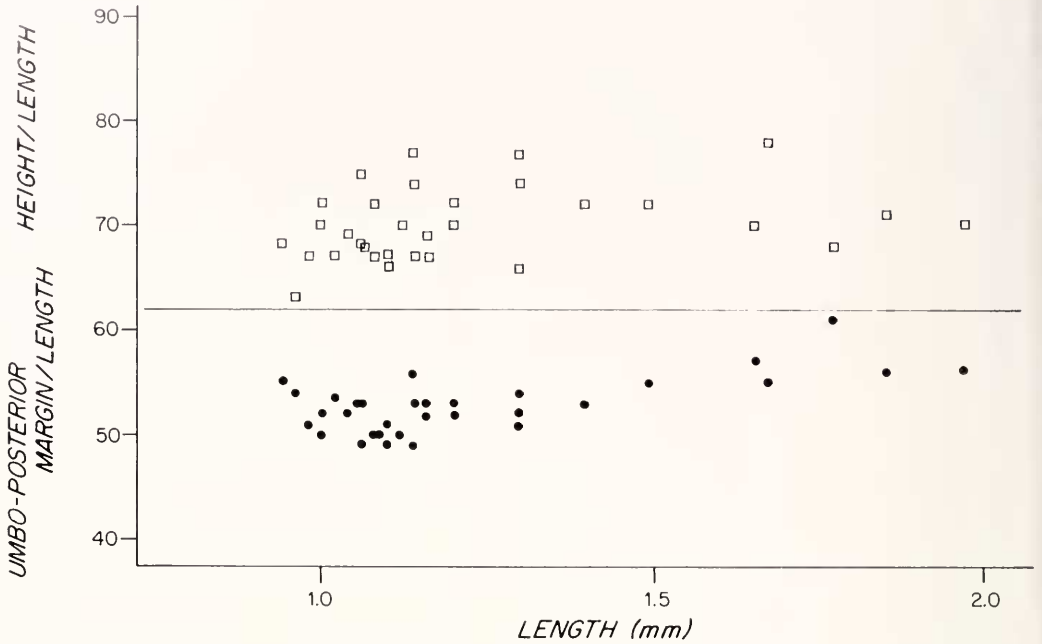
Figure 26. *Tindaria miniscula* Sanders & Allen. Graph showing height/total length (□) and umbo to posterior margin/total length (●) plotted against total length.

0.42 mm apertures of our screen. The umbo, unlike other species of *Tindaria*, is almost central in position in the smallest specimens and becomes progressively more anterior as the size of the shell increases (52 per cent to 57 per cent), i.e., there is an increase in length of the posterior part of the body with increasing age (Fig. 28).
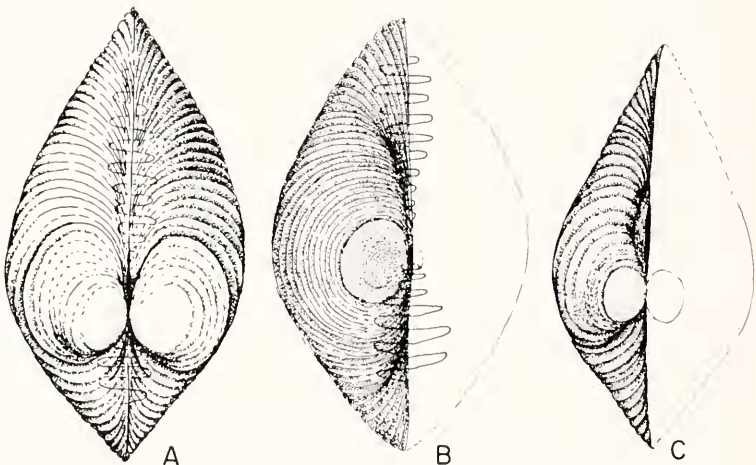

Figure 27.   Dorsal views of A, *Tindaria callistiformis*; B, *Tindaria hessleri*; C, *Tindaria miniscula*.

Family INCERTAE SEDIS[1]
Pseudotindaria new genus

Type species: *P. erebus* (Clarke, 1959)

Shell stout, oval in outline, inequilateral and with strong, uniform, concentric ridges; external ligament extends anterior and posterior to the umbo; hinge plate strong and continuous below umbo, with at most a minute endentulous area between the anterior and posterior hinge teeth series; siphons present and fused ventrally; siphonal embayment shallow; gills horizontal to the anteroposterior axis, or nearly so; palps moderately large with many narrow ridges on the inner faces; mouth opens close to the anterior adductor muscle; hind gut coils on both sides of the body and does not penetrate the mantle.

[1] Considering the present systematic state of the protobranchiate bivalves and the need to erect a number of additional families to include the diversity of morphologies, we feel that it is premature at this time to assign the genus *Pseudotindaria* to a presently defined family.

	Tindaria		*Pseudotindaria*
1)	Rounded, robust shell concentrically lined	1)	Same
2)	Hinge line strong, supporting a series of well-developed teeth, continuous below the umbo	2)	Same
3)	Ligament external	3)	Same
4)	Tentacle present or absent	4)	Tentacle present
5)	No siphons, fringing papillae around inhalent region	5)	Siphonate, without papillae
6)	Palp with few ridges	6)	Palp with many ridges
7)	Relatively few gill plates	7)	Relatively many gill plates
8)	Hind gut with typhlosole, single loop to the right of body penetrating the mantle	8)	Hind gut without typhlosole, loops and/or coils to right and left of body crossing before and behind the stomach, does not penetrate mantle
9)	'Byssal' gland small and ovoid	9)	'Byssal' gland very large and cylindrical
10)	Ganglia very large, pedal ganglia in a median position within foot	10)	Ganglia small, pedal ganglia in upper half of foot

Pseudotindaria erebus (Clarke, 1959)
Figures 29–40

Tindaria erebus Clarke, 1959. Proc. Malacol. Soc. London, 33: 236. Text. fig. 1(1). (Type locality: m/v *Theta*, Station 9, Lat. 31°42'N, Long. 68°08'W; type specimen, Mus. Comp. Zool., No. 218182.)

Neilonella galathea Knudsen, 1970. Galathea Rep., XI, p. 58. Text fig. 38, B–D; Plate 5, fig. 2, Plate 6, fig. 6. (Type locality: Galathea Station 66, Lat. 4°00'S, Long. 8°25'E; type specimen, Zool. Mus. Univ. Copenhagen.)

Previous records: Single station west of Bermuda at 31°42'N, 68°08'W in 5203 m (Clarke, 1959). Single station off W. Africa 4°00'S, 8°25'E at 4018 m depth (Knudsen, 1970).

Present record: Depth range = 2644–2754 to 5007 m.

Cruise No.		Station No.	Depth (m)	No. of Specimens	Latitude	Longitude	Gear	Date
				North America Basin				
Chain 50		85	3834	1	37°59.2'N	69°26.2'W	ES	5.7.65
Atlantis 11	24	123	4853	1	37°59.2'N	64°14.0'W	ES	22.8.66
Atlantis 11	17	93	5007	2	34°39.0'N	66°56.0'W	ES	14.12.65
				Canaries Basin				
Discovery		6714	3301	1	27°13'N	15°41'W	ES	20.3.68

Cruise No.		Station No.	Depth (m)	No. of Specimens	Latitude	Longitude	Gear	Date
				Cape Verde Basin				
Atlantis 11	31	148	3814–3828	2	10°37.0′N	18°14.0′W	ES	7.2.67
Atlantis 11	31	149	3861	12	10°30.0′N	18°18.0′W	ES	7.2.67
				Brazil Basin				
Atlantis 11	31	156	3459	3	00°46.0′S– 00°46.5′S	29°28.0′W– 29°24.0′W	ES	14.2.67
Atlantis 11	31	155	3730–3783	2	00°03.0′S	27°48.0′W	ES	13.2.67
				Guiana Basin				
Knorr 25		307	3835–3862	22	12°35.4′N– 12°40.8′N	58°59.3′W– 59°09.2′W	ES	3.3.72
Knorr 25		288	4417–4429	9	11°02.2′N– 11°03.8′N	55°05.5′W– 55°04.8′W	ES	25.2.72
Knorr 25		287	4934–4980	87	13°16.0′N– 13°15.8′N	54°52.2′W– 54°53.1′W	ES	24.2.72
				Angola Basin				
Atlantis 11	42	200	2466–2754	36	9°41.0′S– 9°43.5′S	10°55.0′E– 10°57.0′E	ES	22.5.68
Atlantis 11	42	195	3797	145	14°40.0′S	9°54.0′E	ES	19.5.68

Description of Shell. The specimens in our collection depart from Knudsen's (1970) description only by having a very narrow and not a 'rather wide' edentulous space separating the anterior and posterior hinge teeth series. They differ from the specimen described by Clarke (1959) by having one more tooth in both the anterior and posterior hinge series.

With the additional material from our collections we can add further observations to the precise descriptions given by Clarke (1959) and Knudsen (1970) (Figs. 29, 30 & 31). Shell stout, with strong, uniform concentric ridges, oval in outline and slightly extended posteriorly; umbones low, anterior in position; beaks not prominant, curved medially and slightly anteriorly; escutcheon forms a shallow concavity; external ligament elongate, narrow, extending posteriorly in escutcheon to about insertion of sixth or seventh tooth on the posterior hinge plate and anterior to the third tooth of the anterior hinge plate; hinge plate strong and moderately thick with a minute edentulous gap immediately below the umbonal beak; posterior hinge plate with about 14 teeth, medial teeth small, and on the dor-

sal side of the hinge plate, distally the teeth enlarge the bases nearly spanning the width of the hinge plate; anterior hinge plate with about 11 teeth, medial three or four teeth minute, rod-shaped and restricted to the upper half of the hinge plate; distally the teeth enlarge becoming chevron-shaped and rather stout; postero-dorsal shell margin slightly convex forming a smooth curve with the posterior margin; antero-dorsal margin short but longer than in *T. callistiformis* or *T. hessleri*, margin straight medially or even slightly concave, anteriorly convex forming a continuous curve with anterior end; ventral margin long and relatively convex.

Morphology of the soft parts. Siphons are developed posteriorly from the inner muscular fold (Figs 32 & 33). They are fused dorsally but not ventrally so that the lumen of the excurrent siphon is not separated by tissue from the incurrent, nor is the latter separated by tissue fusion from the mantle gape below. Central and ventral ridges are present and when these are apposed they effectively separate the lumen of the excurrent and incurrent siphons as well as the feeding aperture below. A single tentacle is inserted below the incur-
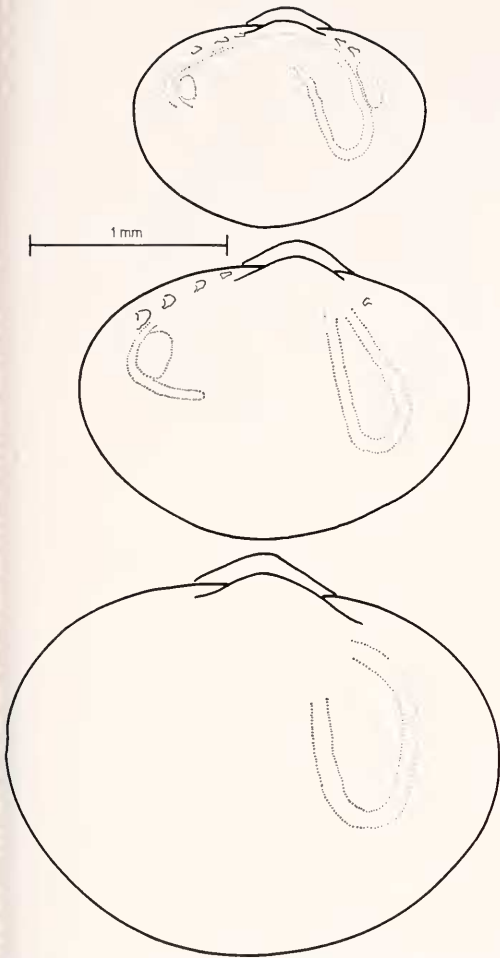
Figure 28. *Tindaria miniscula* Sanders & Allen. Growth series in lateral view.
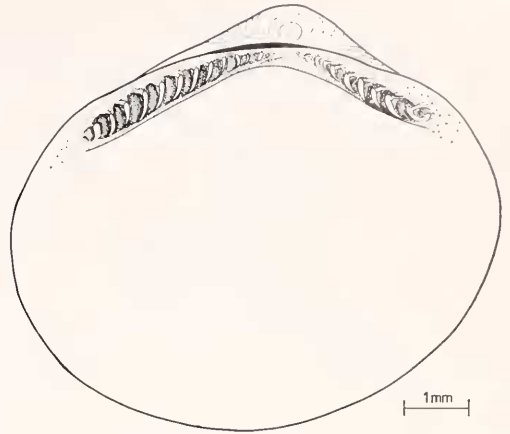

Figure 29. *Pseudotindaria erebus* (Clarke). Internal view of left valve of type specimen No. 218182 Museum of Comparative Zoology, Harvard.
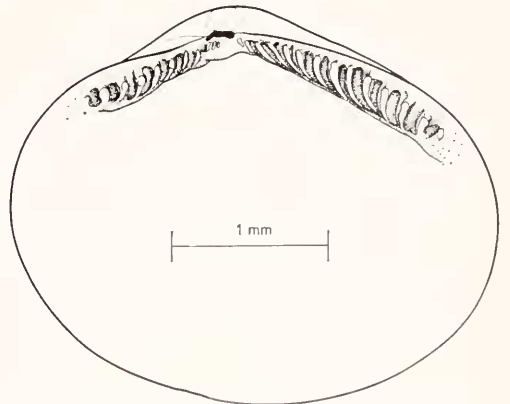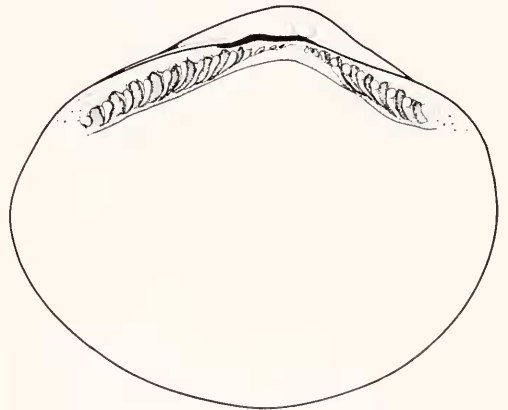

Figure 30. *Pseudotindaria erebus* (Clarke). Internal view of left and right valves of specimen from Station 195.

rent aperture on the right side and, histologically, it is similar to that of *Tindaria*. A food aperture is also developed from the hypertrophied inner muscular fold giving rise to a third, but smaller, channel. The anterior sense organ is well-developed. Adductor muscles are oval, although not greatly elongate, and situated at a relatively greater distance in from the shell margin than is the case in *Tindaria*. Although there is no marked development of the siphonal embayment, the siphons can be retracted within the valves; the retractor muscles are
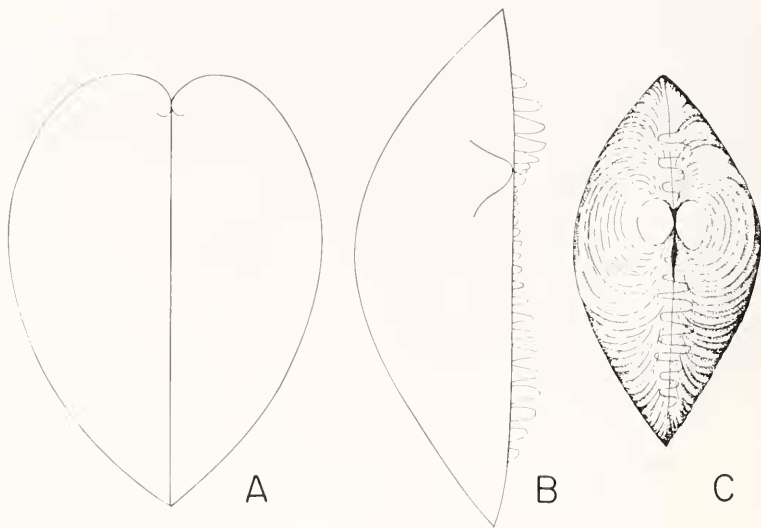
Figure 31. *Pseudotindaria erebus* (Clarke). A, anterior view of shell in outline; B, dorsal view of valve in outline; C, dorsal view of entire shell.

not particularly well-developed. There is no great concentration of gland cells internal to the feeding aperture; although there are small mucous cells lining the main mantle rejectory tract leading to this area.

The gills are more or less horizontal with 14 to 16 plates on each side of the axis, the plates on either side alternating. The gill plates are approximately equal in size, those of the inner demibranch slightly larger than those of the outer, particularly posterior to the body; each has a fan of three muscles in the transverse plane which penetrate the axis as a retractor muscle, and on either side of the retractor muscle are longitudinal muscles running the length of the axis (Fig. 34). There is no tissue fusion to the mantle and/or the body opposite to form a diaphragm because the separation of the hypobranchial cavity from the remainder of the mantle cavity is accomplished by ciliary junctions. Note that the

cerebro-visceral connectives lie close to the junction of the gill axis with the body.

The palps are relatively larger than those of *Tindaria* with many more ridges (17 to 30). The mouth is close to the anterior adductor muscle and the palps extend more than half way across the body. The palp proboscides are relatively large. The foot is moderately large with a well-defined neck; the fringing papillae and heel are very small. A large 'byssal' gland is present, the hyaline central portion of which is elongate, cylindrical and different in shape from any of those described to date (Sanders and Allen, 1973; Allen and Sanders, 1973) (Fig. 35). As in other genera, there is a central sagittal strip of tissue dividing the gland in half, the gland opening just posterior to the sole of the foot.

The oesophagus extends dorsally, and posteriorly, opening into a relatively simple stomach which has a few low-crested sort-

→

Figure 32. *Pseudotindaria erebus* (Clarke). Semidiagrammatic drawings of the body and mantle organs as seen from the right and left sides.
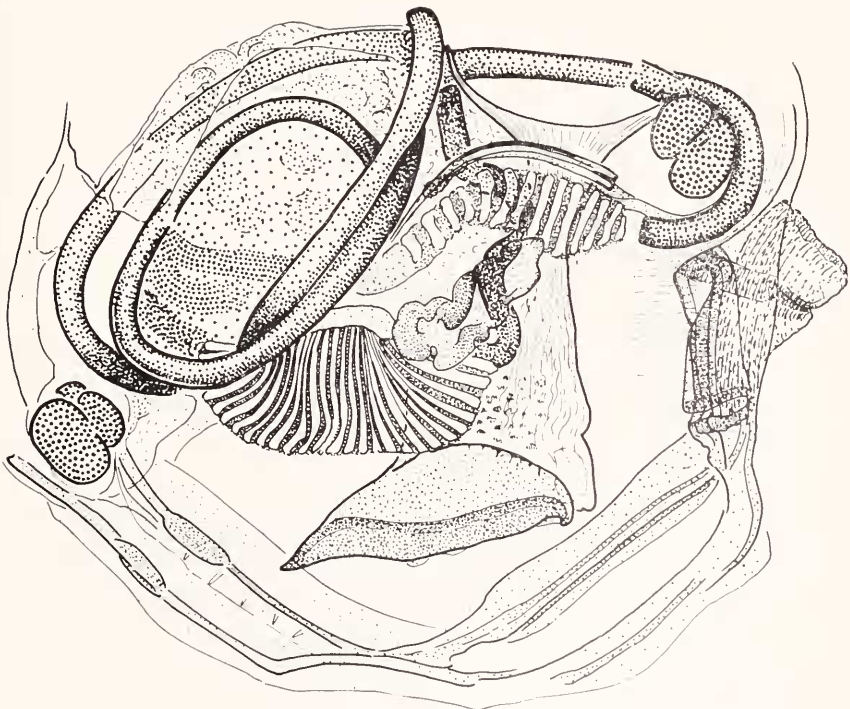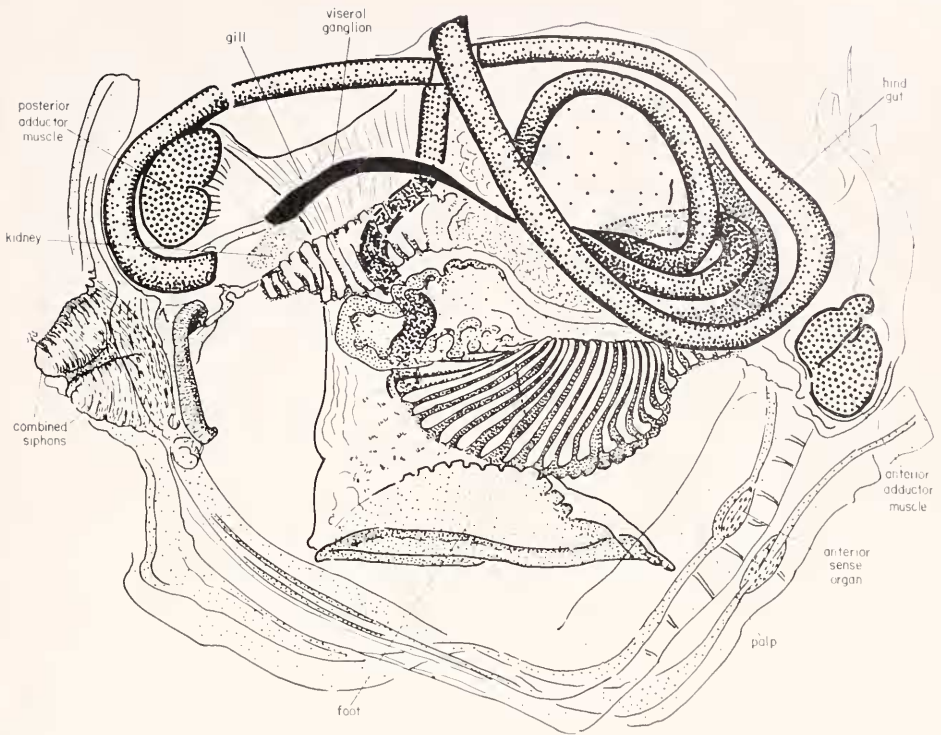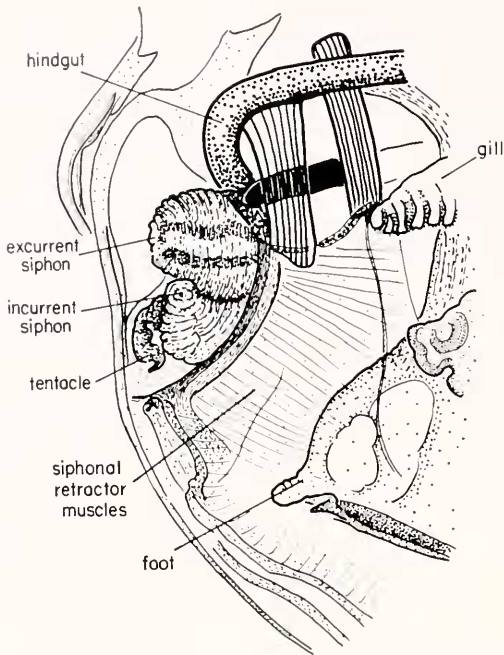
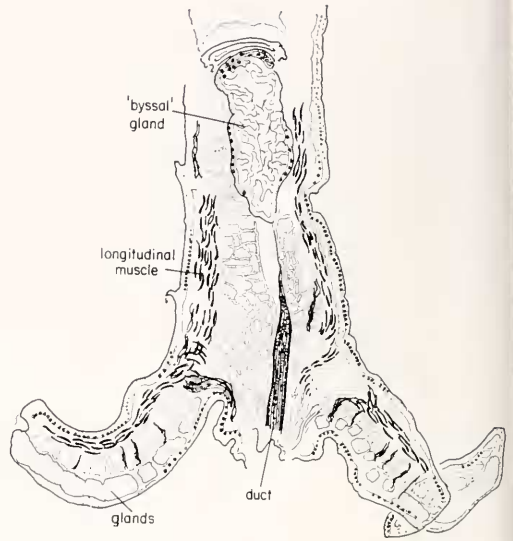Figure 33. *Pseudotindaria erebus* (Clarke). Detail of siphonal region.

Figure 35. *Pseudotindaria erebus* (Clarke). Transverse section through the foot to show the position of muscles and gland.
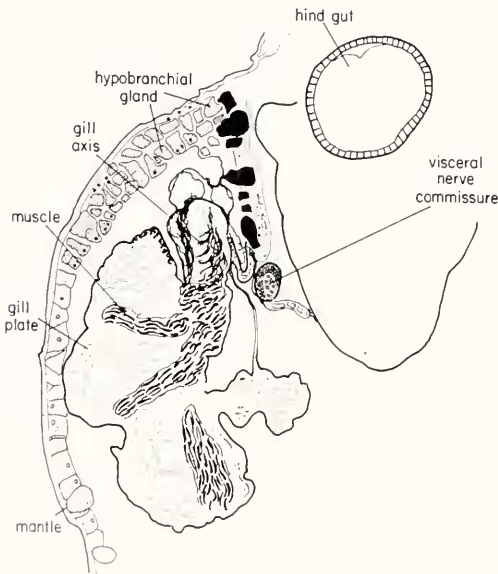
ing ridges on the right side (Fig. 36). The long axis of the stomach and style sac is oblique to the body axis and directed postero-ventrally. The hind gut does not penetrate far into the foot before turning dorsally to the left ventral side of the body. Thereafter it passes to the right side of the body in front of the stomach (posterior to the oesophagus) forming a small loop before returning to the left where it outlines the periphery of the stomach and the digestive gland (Fig. 37). After forming this single

Figure 34. *Pseudotindaria erebus* (Clarke). Transverse section through gill and mantle to show musculature and glands.
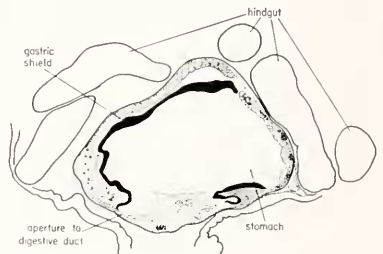

Figure 36. *Pseudotindaria erebus* (Clarke). Transverse section through body to show stomach and outline of hind gut sections.

Figure 37. *Pseudotindaria erebus* (Clarke). Dorsal diagrammatic view of stomach and hind gut.
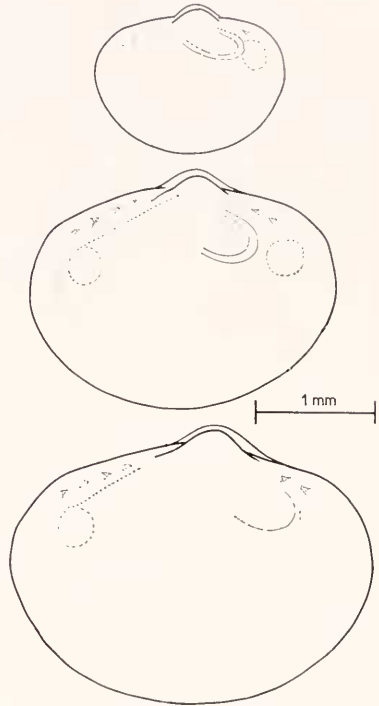
Figure 39. *Pseudotindaria erebus* (Clarke). Growth series in lateral view.

coil it returns to the right side of the body passing dorsal to the style sac and the anterior part of the hind gut. Here it forms a second loop to the outside of the first before continuing to the anus via the mid-dorsal line. The second loop on the right side and the single coil on the left are approximately the same diameter and pass close to the posterior face of the anterior adductor muscle. No typhlosole is present nor does the hind gut penetrate the mantle.

The ganglia are not particularly large, the

Figure 38. *Pseudotindaria erebus* (Clarke). Size frequency histograms of samples from two stations. The dashed lines indicate the size at which gametogenesis is evident.

Figure 40. *Pseudotindaria erebus* (Clarke). Graph showing height/total length (□) and umbo to posterior margin/total length (●) plotted against total length.
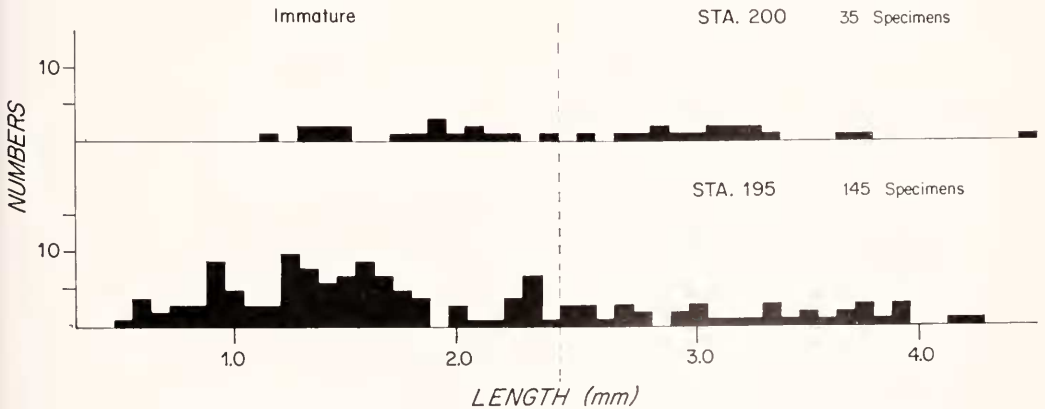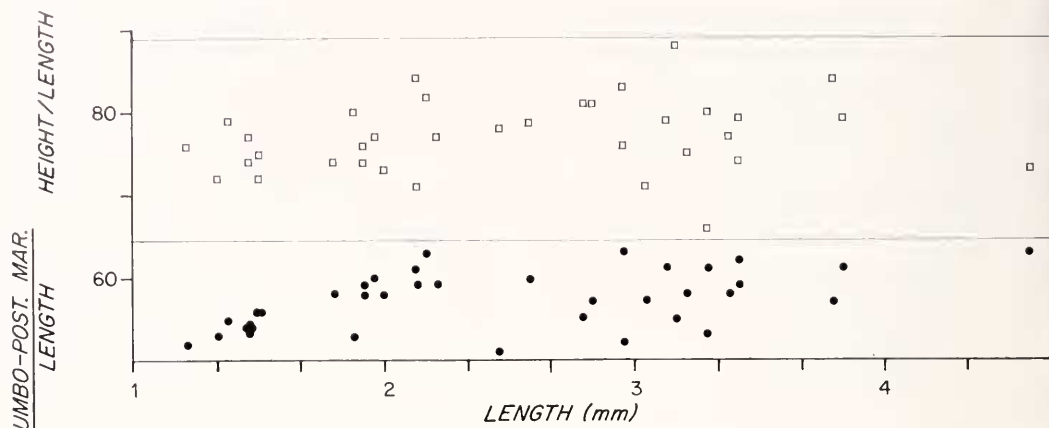
visceral and cerebral are elongate, the pedal ganglia are positioned high in the foot, the visceral ganglia about the posterior adductor muscle (Fig. 32). Note that the foot can

Figure 41. *Pseudotindaria championi* (Clarke). Internal views of left valve of type specimen No. 224957 Museum of Comparative Zoology, Harvard with enlarged detail of the umbonal region.

be extended backwards far into the posterior part of the mantle cavity and, as in other protobranch species, may well assist in pushing rejected faecal material out of the mantle cavity.

Size and Reproduction. The population histograms of stations 195 and 200 (Fig. 38) show that the skew to the left is not nearly so marked as it is in *T. callistiformis.* Specimens less than 2.5 mm in total length are all immature and those 3 mm or more show signs of gonad development. Sexes are separate, the sex ratio is even. Maturity increases with increasing size. A fully mature female measuring 6.0 mm total length contained approximately 800 ova having a maximum length of 142 μ. The gonads initially develop at the ventral perimeter of the body to the inside of the outer hind gut loop. Eggs mature simultaneously. On an average, 42 per cent of a given population is maturing, samples ranging from 33 per cent to 49 per cent.

As in *T. callistiformis,* there is a relatively high degree of variation in shell dimensions, particularly in respect to the height/total length ratio, which varies from 0.71 to 0.87. There is no relation between this variation and the increasing size of the shell. The lat-
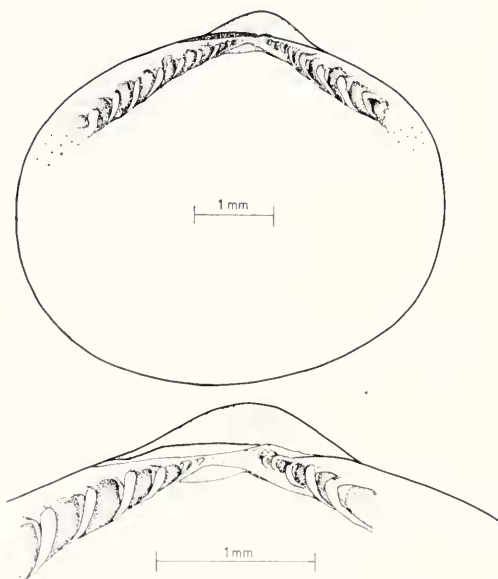
ter also applies to the total length umbo-posterior margin length ratio. The umbo, although anterior, is not so far forward as it is in *T. callistiformis* (51–63 per cent of the total length). There is a slight trend for the posterior umbonal length to increase with increasing size although the variation remains wide throughout the size range (Figs. 39 and 40). Maximum total length recorded is 6.0 mm.

Pseudotindaria championi (Clarke, 1961)
Figures 41–43

Tindaria championi, Clarke, 1961. Bull. M.C.Z. 125, 372. Plate 2, figs. 1 and 4. (Type locality: r/v *Vema*, Biology Station 12, Lat. 38°58.5′S, Long. 41°45′W, type specimen M.C.Z. 224957).
Previous records: Depth range = 3116 to 5133 m. Argentine Basin—1 station. Ref. Clarke, 1961. Cape Basin—1 station. Ref. Clarke, 1961.
Present records:

Cruise	Station No.	Depth (m)	No. of Specimens	Latitude	Longitude	Gear	Date
			Argentine Basin				
Atlantis II 60	269A	3305–3317	5	37°13.3′S	52°45.0′W	ES	26.3.71
Atlantis II 60	242	4382–4405	3	38°16.9′S	51°56.1′W	ES	13.3.71

Description of Shell. Since we are able to add a number of further observations to Clarke's (1961) very adequate description of the hard parts of *Pseudotindaria championi*, a fairly extensive redescription follows.

Shell stout, with strong concentric ridges, subovate in outline, and slightly extended posteriorly; umbos low, anterior in position, beaks moderately prominent and curved medially; escutcheon forms a shallow concavity; external ligament elongate, narrow, extends from about the insertion of fourth tooth on the posterior hinge plate to about second tooth of the anterior hinge plate; hinge plate strong and somewhat angular with moderately extensive edentulous gap below umbo; posterior hinge plate with about eight chevron-shaped teeth medial three teeth becoming progressively smaller and restricted to upper margin, distally teeth enlarge in size with bases almost spanning the width of the hinge plate, distalmost teeth rather massive; anterior hinge plate with about seven teeth, medial tooth small, rudimentary and confined to middle of hinge plate, more distal teeth chevron-shaped and progressively larger inserted progressively further from the dorsal shell margin; entire shell margin smoothly rounded in outline; postero-dorsal shell margin much more convex than short, al-most straight antero-dorsal margin; posterior margin broad; ventral margin long and moderately convex. Total length of 3.56 mm. *Pseudotindaria championi* is readily distinguished from *P. erebus* by its more rounded outline, a more medial positioning of the umbo and its fewer teeth.

Morphology of the soft parts. The morphology of the animal is very similar to that of *P. erebus*; combined incurrent and excurrent siphons are present, the respective channels being separated by approximation of the tissues along the length of the midline of the siphon. Similarly the incurrent siphon is separated from the pedal gape by apposition of the right and left ventral edges. There is a shallow embayment formed by the extension of the mantle edge between the insertion of the pallial muscles and the outer part of the sensory lobe. Inserted on the right-hand side at the ventral limit of the embayment is a small single sensory tentacle (Figs. 42, 43). The food aperture is not very clearly defined in *P. championi*, and barely separates from the extensive pedal gape—its ventral limit is marked by the posterior edge of a well-marked ridge of glandular tissue to the inside of the inner muscular lobe of the mantle edge in the posterior half of the pedal gape (Fig. 42). A pair of well-developed anterior mantle sense organs are present below
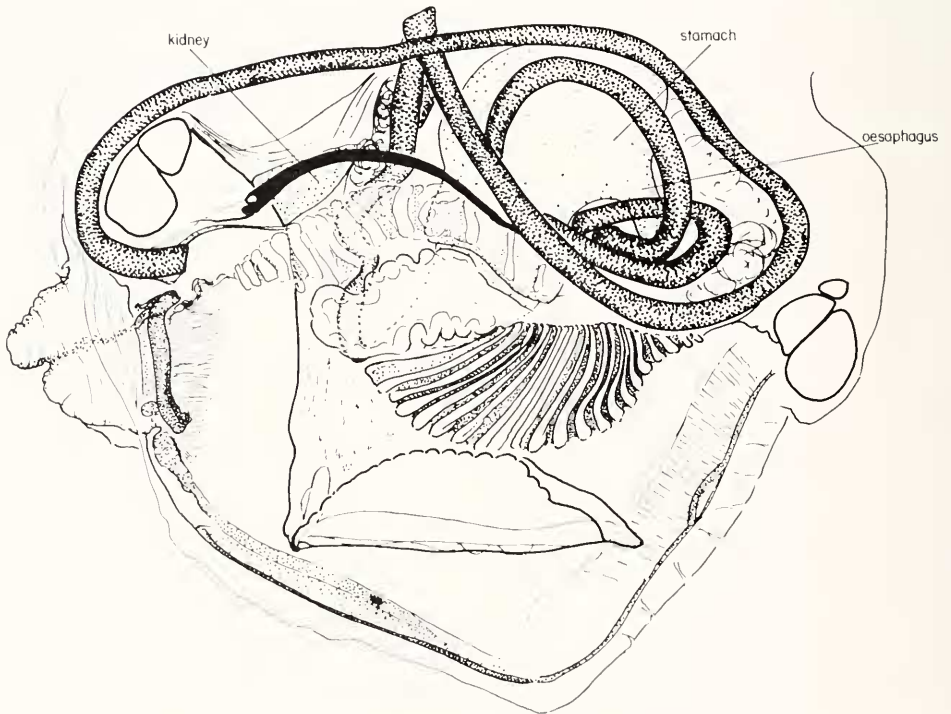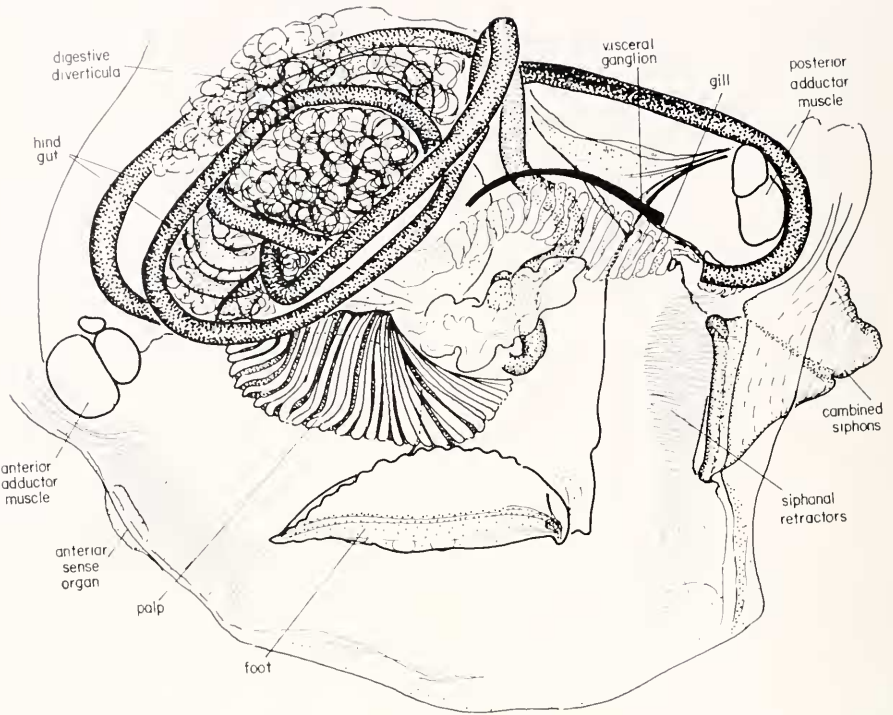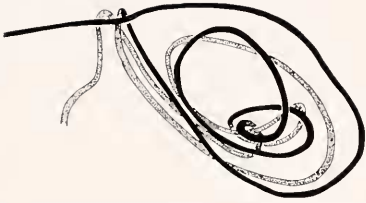
Figure 43. *Pseudotindaria championi* (Clarke). Lateral view of the course of the hind gut as seen from the right side. Stippled sections are positioned on the left side of body, blacked sections on the right.
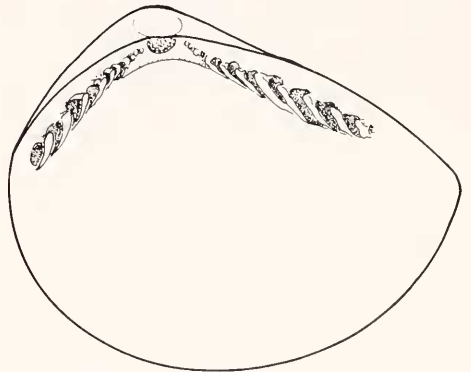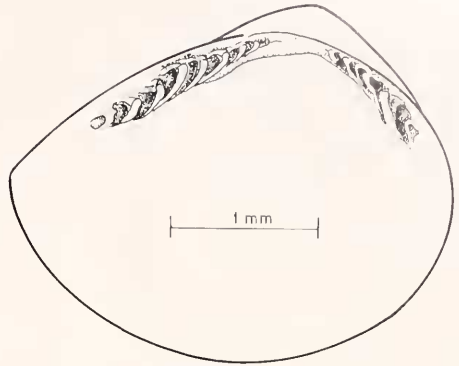
the anterior adductor muscle. The adductor muscles are oval, equal in size, with the 'quick' and 'catch' portions clearly seen.

The gills are horizontal, each with 10 or 11 pairs of plates. The gill axis extends beyond the posterior plates to fuse with the siphonal tissue at the junction of incurrent and excurrent channels, and as in *T. erebus* there is no fusion between gill and mantle, body or opposite gill. It seems likely that as in other protobranchs, the posterior limits of the gill axes act as guide rails to facilitate the removal of bulky faecal rods. The palps are moderately large and extend from the mouth partly across the foot; the dorsal limit of the ridged area is attached to the body in front of the junction of the anterior edge of the muscular part of the foot to the viscera. The many ridges (approximately 25) spread fanwise, posteriorly. The retracted palp proboscides do not extend beyond the posterior margin of the foot. The foot is dorso-ventrally elongate, the sole is not exceptionally large, the tip is pointed, with the fringing papillae moderately small, rounded and low crowned. The heel is produced as a small, short process with a moderately large 'byssal' gland, similar to that described for *P. erebus*. The gut is also similar to that of *P. erebus* (Fig. 42), with the hindgut arranged in the same configuration. However, the relative diameter

Figure 44. '*Tindaria*' *acinula* Dall. Internal views of the left and right valves.

of the hind gut is greater in *P. championi*, in which the gut occupies much more of the body space (Figs. 32, 42).

DISTRIBUTION PATTERNS

Of the six species considered in this paper, four members of the genus *Tindaria* and two representatives of the genus *Pseudotindaria*, two are cosmopolitan while the remaining four appear to be confined to restricted regions of the Atlantic. The two widely distributed species *Tindaria callistiformis* and *Pseudotindaria erebus* are abyssal species and have been collected from the North America, Guina and Angola

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Figure 42. *Pseudotindaria championi* (Clarke). Semidiagrammatic drawings of the body and mantle organs as seen from the left and right sides.
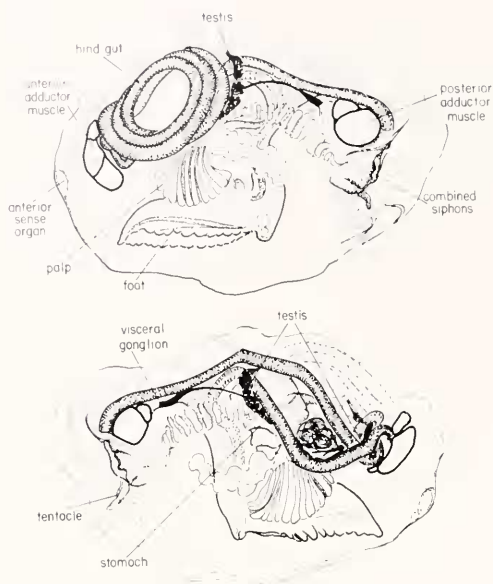
Figure 45. 'Tindaria' acinula Dall. Semidiagrammatic drawings of the body and mantle organs as seen from left and right sides.

is present, *T. callistiformis* makes up but a minor fraction of the protobranch fauna, 0.08 to 1.97 per cent at ten stations 4600 m or deeper. At the shallowest station, in 3305 to 3317 m of water, it constitutes 4.48 per cent. In the remaining six samples, taken in 3806, 3828, 3834, 3906 to 3917, 4417 to 4429, and 3825 to 3862 m, this species formed 20.84, 18.99, 13.80, 27.61, 3.82 and 0.74 per cent respectively of the protobranch specimens. The first three samples were taken from the North American Basin, the fourth was from the Argentine Basin, and the remaining two, from the Guiana Basin.

Despite its broad horizontal distribution, *Pseudotindaria erebus* must be a very rare animal at least in part of its range. Of more than 22,500 protobranchs collected from the Gay Head-Bermuda transect in the North America Basin, only four specimens of *P. erebus* have been taken. Alternatively, in the Angola Basin it may be numerically important, 19.05 per cent at station 200 and 20.03 per cent at station 195. The values found in the Canaries, Cape Verde, Guiana, Brazil and Argentine Basins fall between these extremes.

Of the remaining species, *Tindaria hessleri* appears to be a lower slope–upper abyssal rise inhabitant of the northeast Atlantic. We have taken it at a single station in the West Europe Basin and from five of the six stations in its depth range in the Cape Verde Basin. Thus it appears to be a constant faunal constituent within the appropriate depth range and in the latter basin comprises, numerically, nearly one to ten per cent of the protobranch bivalves.

Tindaria cytherea has a narrow depth range, restricted to intermediate slope depths in the northwest Atlantic. It has so far been reported from a few localities in the North America, Gulf of Mexico and Caribbean Basins. We have collected but a single specimen in 1000 m depth off Bermuda. It is probably not present at equivalent depths at the New England end of the Gay Head-Bermuda traverse, which have been extensively sampled.

Basins. In addition, *P. erebus* has been taken in the Canaries, Cape Verde and Brazil Basins and *T. callistiformis* in the Argentine Basin. *Pseudotindaria erebus*, which occurs in shallower depths, has been found in about 2650 m in the Angola Basin, but *T. callistiformis* has never been collected shallower than about 3300 m. The only region so far examined where *P. erebus* has not been obtained is the West Europe Basin. However, the samples analysed to date from that region have been limited to depths less than 2380 m. Similarly, on the basis of depth distribution of *T. callistiformis*, there are only four stations of appropriate depths where it has not been found (two stations in the Angola Basin and two stations in the Brazil Basin). Probably these forms are present throughout the Atlantic wherever there are adequate depths. Our data suggest that *Tindaria callistiformis* may be numerically significant only in a small subset of its vertical and perhaps its horizontal range. In most samples where it

Pseudotindaria championi is an abyssal species of the high southern latitudes known from three localities in the Argentine Basin and a single sample in the Cape Basin.

The remaining species, *Tindaria minis-cula*, is probably limited to the deeper abyssal depths of the southeast Atlantic. We have found it at three stations in the Angola Basin where it formed 0.99, 2.04 and 3.29 per cent of the protobranch fauna.

PALEONTOLOGICAL RELATIONSHIPS

Pojeta (1971) has pointed out that all known 'nuculoids' from the early Paleozoic (Ordovician) lacked a resilifer but had instead a hinge plate continuous beneath the umbo. In addition, these forms possessed a continuous row of teeth rather than teeth that were separated into an anterior and posterior hinge series. Among the living protobranchs, the genera *Tindaria, Pseudotindaria* and *Neilonella* have a similar combination of morphological characters.

Most Ordovician nuculoids have been placed in the extinct family Ctenodontidae. However, the careful studies of Pojeta (1971) clearly show that the Ordovician nuculoids were a "highly varied and successful group," a fact masked by the pronounced conservatism of the systematics.

Earlier, Verrill & Bush (1897) noted that the ctenodont *Palaeoneilo* "agree in nearly all essential characteristics with the living genus Tindaria." Within the complex of Ordovician ctenodont shell morphologies cited by Pojeta (1971) can be found apparent homologues of *Tindaria* and *Pseudotindaria*; e.g., *Palaeoneilo fecunda* (Hall), and *Neilonella*; e.g., *Decaptrix* aff. *D. hartsvillensis* (Stafford) and *Decaptrix baffinense* (Ulrich).

In the present paper we have documented the profound differences in the soft part anatomy of *Tindaria* and *Pseudotindaria*, two genera which have almost identical shells. *Neilonella* is more elongate and rostrate but the soft part anatomy resembles that of *Pseudotindaria*, e.g., they have si-phons, many gill plates and palp ridges and lack posterior papillae. Thus, these few modern genera also represent a varied complex of morphologies. Yet, on the basis of shell morphology, there is no reason why these living genera should not be the modern descendants of the Paleozoic ctenodonts, the oldest lineage of protobranchs with typical chevron-shaped teeth, representing a group or groups of bivalves with remarkably conservative shell features.

In comparison, we have pointed out elsewhere that the modern nontaxodont protobranchs such as the families Nucinellidae (Allen & Sanders, 1969), Lametilidae and Siliculidae (Allen & Sanders, 1973) are analogs of the Palaeozoic actinodonts and may, indeed, be direct derivatives.

DISCUSSION

The present paper, in addition to defining a morphology that stands apart from all other protobranchs, emphasizes more clearly than in any other group of the Protobranchia the danger of relying on shell character to define a taxon. Thus, *Tindaria* and *Pseudotindaria* on shell characters alone would have been (indeed were) placed in the same genus, but the soft parts show that they are greatly different. This has the unhappy consequence that anatomical studies must be made to confirm the placement of many of the species referred to the genus *Tindaria*.

Pseudotindaria is difficult to place in relation to other known protobranch genera at this stage in our researches. Some species of *Neilonella* described by Knudsen (1970) certainly resemble *Pseudotindaria* and it is our intention to analyze the "*Neilonella* complex" in a subsequent paper of this series. Similarly, so-called *Tindaria acinula* (a species that occurs in our samples) is an example of a species wrongly described in the literature as a tindariid which, like *Pseudotindaria*, has siphons, not tentacles, and a large palp with many ridges. The hind gut does not penetrate the mantle and

the large posterior adductor is not close to the shell margin (Figs. 44, 45). However, unlike *Pseudotindaria*, the hind gut crosses to the left side of the body *in front* of the mouth and there forms four coils, and the valves are posteriorly rostrate rather than oval. Again, this species will be considered in a later paper.

The species of *Tindaria* are characterized by the lack of posterior mantle fusion and, in this sense, as well as in having a gill placed obliquely across the mantle cavity, they are at first sight akin to the Nuculoidea. We hypothesize that the tindariids may have similar habits to some species of *Nucula* (see below). Nevertheless, the posterior mantle edge is highly specialized and, in addition to the pedal gape, it forms functional posterior incurrent, excurrent and feeding apertures. The apertures are formed by the apposition or overlapping of the inner and, sometimes, middle lobes of the mantle. The excurrent region is particularly circumscribed, the space between the adductor muscle and the first papillae being only wide enough to allow the passage of the faecal rod. Knudsen (1970) reports a simple flap-like extension of the mantle on the dorsal side of the aperture in two Pacific species. In *T. bengalensis* and *T. compressa*, at the ventral limit of the excurrent region and extending across the mantle edge on each side is a shallow ridge which might possibly be considered to be the first stage in the development of a siphon, to which the attenuate part of the gill axis attaches. The anus opens opposite this channel. In many specimens the dorsal-most papilla on each side of the incurrent region point inwards, parallel to this channel. The number of papillae on either side of the aperture varies between species. An unpaired papilla or tentacle, which in some cases is longer than the other papillae, may be present on the right or left side at the ventral limit of the inhalent region. This may or may not be equivalent to the unpaired siphonal tentacle of other nuculanids. Histologically there is no difference between

the two. The papillae consist of a central pair of longitudinal muscle bands with a haemocoele between the muscles and the outer epithelium. There are no major nerves supplying the papillae and innervation is probably in the form of a number of fine fibers. There are also no concentrations of gland cells, thus the papillae are in no way comparable to the feeding tentacles of the deep sea carnivorous Verticordiidae (Allen & Turner, 1974). We can only assume that the papillae have a generalized sensory function and possibly act as a coarse filter for the incurrent flow generated by the pumping action of the gills.

We have been able to keep *T. callistiformis* alive for approximately one month. The soft parts are virtually colorless in life. Although the metabolism of these animals was clearly affected by their long journey to the surface, to reduced pressure and through the varying changes of temperature of the water column, their condition was sufficiently good to confirm that the papillate region defines the incurrent area and that the palp proboscides are extended from the feeding aperture. The inner mantle folds are extended beyond the shell margin in this region. Although gross movements of the gills occurred, no definite pumping rhythm was observed. Ciliary movement was particularly languid and we hesitate to say more than that the ciliary patterns within the mantle cavity are similar to those described by Yonge (1939) for more shallow-living nuculanids.

The stomach takes up much of the body space and it may be that the extension of the hind-gut into the mantle is in part related to the lack of space between the body wall and the stomach. Undoubtedly the refractile nature of the food (diatom frustules, etc.) to enzyme action is correlated with the considerable extension of the gut in deep-sea deposit feeding bivalves (Allen & Sanders, 1966; Allen, 1971, 1973). One of the many strategies used by the deep-sea protobranch for housing the hind gut is exemplified in the tindariids by their utiliza-

tion of mantle space. Exploitation of mantle space occurs in other bivalves, as for the gonads of mytilids—but deep-sea protobranchs are unique in the accomodation of the hind-gut in this manner. There is much evidence that material entering the stomach in deep-sea protobranchs is less rigorously sorted than that in shallow-water species. Thus the ciliated sorting ridges are reduced in number and size. The large tooth of the gastric shield deserves mention because it presumably does not act in the same manner as in the Lamellibranchia. The material coming forward from the style sac in the protobranchs is a soft particulate mixture and not a hard crystalline style. Hence it is difficult to imagine that the tooth either serves as a stop to the forward movement of the style or as a cutting surface which 'turns' the head of the style with subsequent release of style material. We believe that it may act here as a barrier to the encroachment of space immediately posterior to the oesophageal aperture by the style and/or acts as a 'breakwater' in front of the ducts to the digestive diverticula preventing material from being forced into the ducts. It may also act as a baffle to enhance the mixing of the stomach contents in a fashion analogous to the blade in a cement mixer. There is evidence that selection of particles does occur because a high proportion of the stomach contents consists of diatom frustules.

We believe that it is possible to deduce something about the habits of the genus *Tindaria*. The strong robust concentrically ornamented shell and rounded shape, together with an attached growth of hydroids on many of the specimens, indicate a surface dwelling rather than the infaunal habit for the genus. The presence of tentacles around the inhalent region and a pumping gill can also be correlated to a stationary habit close to the surface. The foot is by no means as highly developed as in the smooth, glossy, thin-shelled genera without epifauna such as *Silicula* and *Spinula*, which have all the hallmarks of fast-burrowing infaunal

bivalves (Allen & Sanders, 1973). Nevertheless, the foot is moderately developed and, in addition to any cleansing function, it may well be involved in occasional rapid movement, necessitated by predators or for reorientation.

Tindaria species do not show an inverse relationship between the size of the palp and the size of the gill with increasing depth, first shown in *Abra* (Allen & Sanders, 1966) and later for some genera of Protobranchia (Allen, 1973). We think that a possible explanation is that gill size is critical in relation to efficient pumping action. Elsewhere (Allen & Sanders, 1966) we have also shown that hind gut length is much greater in deep water species as compared with related shallow water forms. In this, *Tindaria* is more consistent with the general pattern. Thus, estimations of hind gut volume per unit animal volume shows that gut volume is half as large again in *T. callistiformis* (3305 to 5042 m) as compared with *T. hessleri* (1739 to 2339 m). However, *T. miniscula* (3797 to 4566 m) is an exception for it has a similar gut volume/animal volume ratio, as in the two shallower-dwelling tindarid species (see below). This anomaly may be explained by the small size of *T. miniscula* as compared with the other species. Perhaps of more significance is the fact that the gut volume of *Pseudotindaria* (2644 to 5007 m) is similar to that of *Tindaria*, i.e., that irrespective of the great difference in hind gut configuration the volume is not significantly different in the two genera.

	Gut volume/unit	shell volume
T. cytherea	1000 m	1.005
T. hessleri	1739–2339 m	0.903
T. miniscula	3797–4546 m	0.954
T. callistiformis	3305–5042 m	1.413
P. championi	3305–4405 m	?
P. erebus	2644–5007 m	0.915

The reproductive strategies of the genera *Tindaria* and *Pseudotindaria* are greatly different. *Pseudotindaria* follows the typical

deep-sea pattern of approximately 50 per cent of the population maturing at any one time. The largest animals are the most mature and the sex ratio is 1:1 (Sanders & Allen, 1973; Allen and Sanders, 1973; Scheltema, 1972). (It must be noted that both dioecious and hermaphroditic species occur in the deep sea.) Our collections of *Tindaria callistiformis* differ in the extremely low percentage of the population that was maturing and also in the male-female ratio of 5:1. However, it appears that the largest animals are the most mature. We have argued elsewhere (Sanders & Allen, 1973) that, in the sparsely populated abyss, it is an advantage to have large numbers of sperm produced (and have a free planktonic larva, even though of a short duration). We may be observing, in this case, an exceptional condition even for *Tindaria* and if so we have fortuitously encountered a remarkably successful and isolated larval settlement. However, there are reasons to doubt this; not only is the pattern maintained at three widely spaced stations but also the analysis of the *T. miniscula* specimens indicates that this species is showing a similar population structure, i.e., that these are features common to the genus. It is our intention to re-investigate these stations at a different time of year following an interval of some years to see whether the structure has been maintained. More striking and less easily explained is the small number of eggs present in the ovary, which conflicts with the dominance of this species in the samples and the large number of small specimens in the sample.

SUMMARY

A new family of the Protobranchia, the Tindariidae, is erected and included in the Order Nuculanoidea. As of present, the family is monogeneric; previously associated genera, namely *Pseudoglomus*, *Neilonella* and *Malletia* are not included because of their markedly different morphologies.

Two new species are described—*Tindaria hessleri* and *T. miniscula*.

The species of *Tindaria* described here show a number of common anatomical features that are of particular note.

1)   The posterior mantle edge bears papillae on either side of the non-siphonate incurrent aperture, the number varying according to the species and to the size of the animal.

2)   The single loop of the hind gut and associated visceral tissue penetrates the right mantle to a greater or lesser extent. In *T. callistiformis* the loop approaches close to the mantle margin immediately above the anterior mantle sense organ while in *T. cytherea* it barely penetrates the mantle.

3)   Palp ridges are few in number.

4)   Gametogenesis was observed in less than 5 per cent of the specimens of *T. callistiformis* (the most common species in our collection), males outnumbering females by 5:1. In only the largest specimens could gonads be recognized.

A new genus, *Pseudotindaria* (not included in the family Tindariidae), is described. This includes species with shell morphologies very similar to those of *Tindaria* but with soft parts that are markedly different. The taxonomic affinities of *Pseudotindaria* will be discussed in a later paper.

Pseudotindaria is siphonate. The hind gut is arranged in a complex series of loops and coils on either side of the body and does not penetrate the mantle. Palp ridges are numerous. In the case of *P. erebus*, the most common species in our samples, more than 40 per cent of the specimens have recognizable gonads and the sex ratio is even.

Shell morphologies indicate that *Tindaria* and *Pseudotindaria* could well be considered as recent descendants of the Paleozoic ctenodont Protobranchia.

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