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THE LITTLE BIVALVE *Planktomya* UNMASKED

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RESUMEN

El enigmático bivalvo *Planktomya henseni* ha sido considerado como un animal holoplantónico por casi un siglo. Allen and Scheltema (1972) demostraron que toda la evidencia indicaba hacia una concha bentónica con un estado larval inusualmente largo. Esta concha bentónica ha sido encontrada finalmente en la parte tropical del Atlántico occidental, y aparentemente pertenece a la familia Sportellidae. Al compararla con las especies fósiles de esta familia muestra un tendencia hacia una prodisoconcha grande y un largo estado larval planctónico, aparentemente largo.

ABSTRACT

The enigmatic bivalve *Planktomya henseni* has masqueraded as a holoplanktonic animal for nearly a century. Allen and Scheltema (1972) showed that all the evidence pointed to a benthic clam with an unusually long planktonic larval stage. This benthic clam has finally been found in the tropical western Atlantic, and appears to be a member of the Family Sportellidae. Comparison with fossil species in this family shows a trend toward a large prodissoconch and apparently a long planktonic larval stage.

A small number of gastropod molluscs, the pteropods and heteropods, have taken up a free swimming planktonic existence. It is not well known, however, that a bivalve mollusc has also been reported to be holoplanktonic. This lone bivalve, *Planktomya henseni*, was first described by Simroth (1896) in the results of the Plankton Expedition. Specimens had been collected at 21 stations of which 17 had been in the open sea far from any land. Simroth only saw the preserved specimens, and he apparently misinterpreted some of the structures that he observed. He evidently thought the specimens too large to be larvae, and so considered

them to be neotenous. Evidence given for this opinion was that *Planktomya henseni* had well developed adductor muscles, gills, and pigmented body. A contributing factor was the oceanic distribution of the species.

Planktomya was virtually ignored during the next 75 years. Few textbooks or manuals of the Mollusca mentioned the species, and no new information was published. Then Allen and Scheltema (1972) published the results of an extensive study of the species. They had more than 3000 specimens, and, furthermore, were able to study the animal alive. These authors saw that Simroth (1896) was mistaken about several features; there are no large "leaf-like" gills. Simroth also reported large palps, but Allen and Scheltema (1972) think that he had observed either the retracted velum or possibly the foot. The foot, on the other hand, was seen to be quite active and well developed.

Allen and Scheltema (1972), when they reviewed their findings, came to the following conclusions. *Planktomya henseni* is a planktonic bivalve widely distributed throughout the warm-temperate and tropical North and South Atlantic Ocean. Specimens have also been reported from the tropical Pacific. Although originally described as holoplanktonic, it has all the characteristics of a teleplanic bivalve larva. It has a large (sometimes more than one millimeter) non-calcified shell and prominent velum, and a pigmented body with large fat vacuoles. None of the specimens examined showed any evidence of reproductive activity, and no gonadial tissue was found. The most numerous smaller specimens were found near land while the few larger specimens were found far out in the open ocean. Evidence from abundance and geographical distribution suggested that it was the larva of a shallow water species. The morphological evidence suggested that the species belonged to the Superfamily Leptonacea.

I found my first post-larval specimen in 1970, and, over the past ten years, have found seven more. Since the material at hand, although sparse, is sufficient to connect the adult with the larval form, it was decided to publish the available information. It would be better, of course, if complete specimens of the full grown adult had been found, or if the anatomy of the animal could be described, but the adult appears to be rare. This is perhaps due to its habitat as it may be commensal with some deep burrowing large animal. At any rate, it is an unusual situation for a clam. Much is known about the larva, virtually nothing about the adult.

MATERIALS AND METHODS

I collect micromolluscs in shallow water by taking a bottom sample while free diving and from deeper water by a variety of methods. A number of friends have collected samples while scuba diving, while deeper water material is brought in by use of bottom grabs, dredges, and similar gear. These bottom samples are washed and dried in the laboratory, and then examined under a stereomicroscope. All of the material discussed in this paper was collected and treated in this manner. The micromolluscs are picked out of bottom samples and placed in micropaleo slides. Specimens are usually attached with gum tragacanth to reduce the danger of breakage.

Specimens from any one station are usually placed all together on a faunal slide. These can then be examined quickly and easily under magnification, and unusual specimens can be removed and placed in single species slides. The material was observed using a Wild Heerbrug M5 stereomicroscope, or with a Nikon SMZ-2.

MATERIAL EXAMINED

The first specimen that I collected was during "Gerda" cruise G7018 to Cay Sal Bank, Bahamas. This specimen was a single left valve only 1.54 mm in length, and it still had the golden brown uncalcified prodissoconch in place. It was collected just inside the lagoon entrance, Cay Sal, on the west side of the island in 4.5 m depth. It was examined and the large prodissoconch noted, but its true significance was not realized at the time.

The second specimen was collected during "Gerda" cruise G7124 to the north central Bahama Islands. The locality was a tiny beach at the east end of Black Rock, on the southern edge of Little Bahama Bank southwest of Mores Island. A very abundant fauna of micromolluscs was noticed at the high tide line and some of this material was scraped up and bagged. The *Planktomya* specimen was a large left valve 3.35 mm in length. The original prodissoconch was lost, but this area was covered by calcified layer that had been laid down while the original prodissoconch had been in place. This specimen was only recently discovered as the Black Rock material had been picked and sorted by a student assistant. He had put the specimen on a faunal slide with a large number of specimens of *Ervila concentrica* which are almost the same size, shape, and color.

Additional material was collected in Colombia while on a visit to the Instituto de Investigaciones Marinas de Punta de Betín (INVEMAR),

ex-ICAL, Santa Marta. Two specimens, both left valves, were found in a bottom sample taken just offshore from the fishing village of Taganga, about 2 km north of Santa Marta. The sample came from a depth of 5 m on open sandy bottom. One specimen, although fairly fresh, was a broken adult; the other was a large, 3.8 mm specimen in excellent condition.

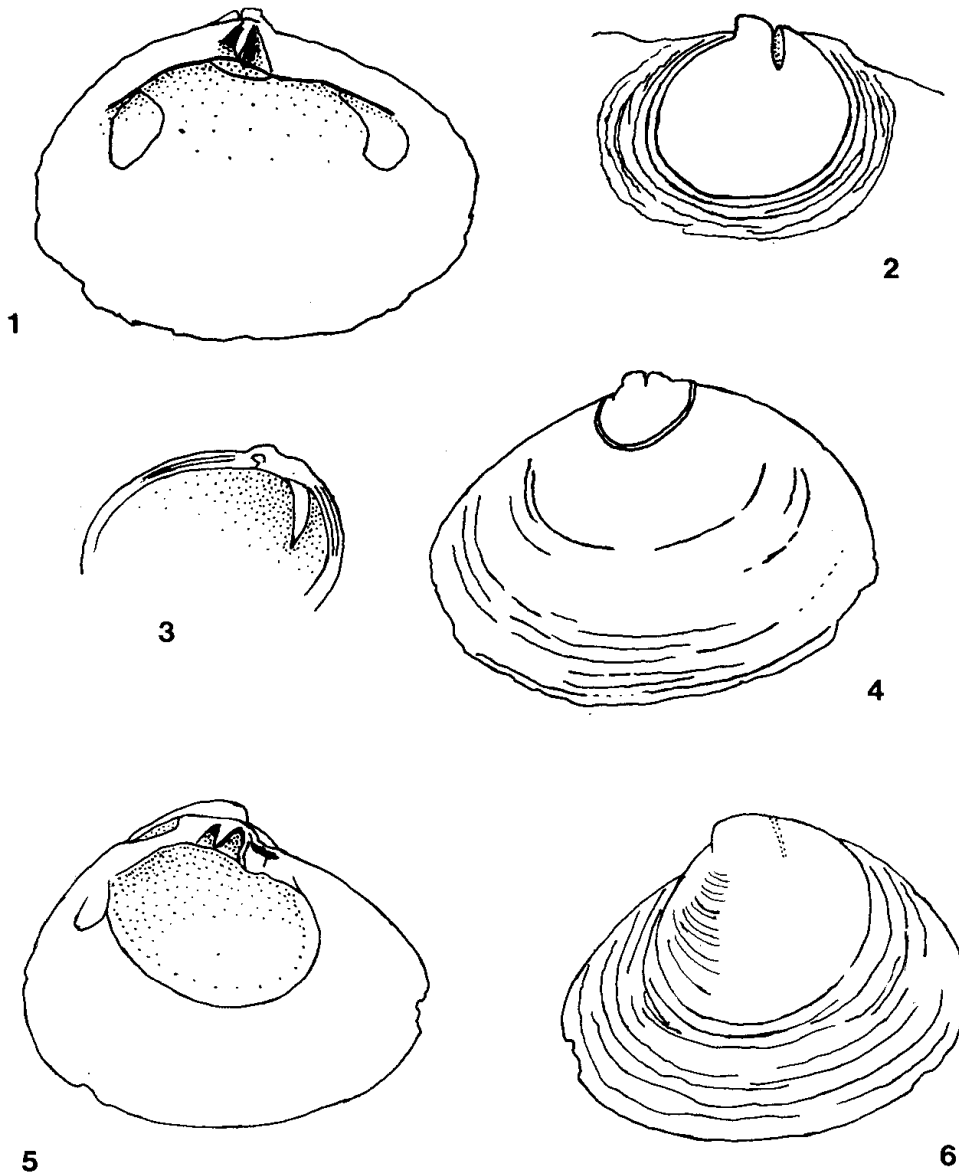
Other material was collected in Ensenada de Concha, a small but deep bay about 10 km N E of Santa Marta. Two bottom samples were collected from a small coral reef on one side near the head of the bay in 6 to 7 m. This locality is unusual as the calcareous sand from around the corals is made up almost entirely of coral fragments. In these samples were found three young adults 1.64, 1.70, and 1.72 mm long. The largest specimen was complete, enabling me to examine the right valve hinge. These three specimens still had the original golden brown prodissoconch in place, but in somewhat deteriorated condition. There were also a number of larval shells in the samples, four complete and three single valves. These showed no indication of any adult shell growth, and ranged in size from 0.9 to 1.0 mm long.

The material enumerated above, six left valves and a complete specimen, were taken in very shallow water around or near corals and coral reefs. The eighth specimen is from a depth of 29 m, but this was from a steep reef in front of Carrie Bow Cay, Belize. This was from a bottom sample collected by John F. Meeder in June, 1980. One broken left valve was found in this sample, but the prodissoconch was undamaged making identification easy. The valve is only in fair condition, and is 2.1 mm long. The bottom sample material was apparently washed down from much shallower water.

DESCRIPTION OF PLANKTOMYA HENSENI

Mature prodissoconch of *P. henseni* (Figs. 1-6) is transparent and golden brown in color. The shell is oval, uncalcified, light, marked only by concentric lines. Umbos prominent, face forward; ligament difficult to observe in complete specimen. Single tooth lying in front of ligament; margins of shell locking together in tongue and groove principle. Umbo prodissoconch I, rather deeply cupped, thickened before strengthened by buttress behind. Posterior buttress is prominent feature and easily seen in larval shell. Posterior buttress is distinctive feature which simplifies identification of planktonic larvae and mature adult.

Mature teleoconch oval, equivalve, and with beaks slightly posterior off center. Sculpture made up of very narrow low concentric irregular ribs, difficult to count. No lunule, and no escutcheon. Inner margins of shell



Figures 1-6. *Planktomya henseni*. 1. Interior of adult left valve from Black Rock, Bahamas, total length 3.35 mm. 2. Exterior view of prodissoconch of Black Rock specimen. 3. Interior of larval prodissoconch, right valve one mm long, with ventral margin tilted up to show the posterior buttress, Ensenada de Concha, Colombia. 4. Exterior view of Black Rock specimen. 5. Interior view of Cay Sal specimen, left valve 1.54 mm long. 6. Exterior view of Cay Sal specimen.

are smooth. Two adductor muscle scars, posterior oval, anterior more elongate. Irregular pallial line connects muscle scars.

Hinge broad, especially under beaks, one strong cardinal tooth in each valve. That of left valve in advance of beak; tooth in right valve directly under beak. Left valve has socket directly posterior of tooth, a smaller tooth separates socket from resilium. Small nymph also present, external ligament not observed.

After settlement, the young clam forms a white shell which is more elongate than the larval form. At first, the large golden brown prodissoconch is the dominant feature, but probably deteriorates and flakes away by the time the shell is 2 mm in length.

The mature teleoconch ranges from just over 3 mm to about 4 mm. This is based on two unbroken valves which show all the signs of maturity (Moore, 1977), and which measure 3.35 and 3.8 mm respectively. The prodissoconch is now an internal mold of the larval shell, laid down while the proteinaceous larval shell was still in place. Thus the posterior blade-like buttress becomes a narrow slit while the anterior internal thickening is reproduced as a cut away area at the front of the beak. The thick internal edge of the larval shell is reproduced as a deep groove all around the margin of the prodissoconch in the adult shell.

The adult of *P. henseni* is an elusive animal. After more than 20 years of collecting in the tropical western Atlantic, I have a total of seven single valves and one young complete adult. It may not be as rare as it seems, but the small size of the adult plus a possible deep dwelling habitat would conceal it from all but the most persistent investigators. However, the strange prodissoconch makes it possible to identify even broken specimens with ease.

OBSERVATIONS

The distribution of *Planktomya henseni* as plotted by Allen and Scheltema (1972) shows an oceanic distribution in the Atlantic from several degrees south of the equator to more than 45° north. No specimens came from the coast of Europe although some material was taken off northern Morocco. More material was collected around the Canary Islands, but not close to Africa until south of Cape Blanc. *Planktomya* was present in the Gulf of Guinea and in the equatorial current across to Brasil. Other material was collected in the Caribbean, the Gulf of México, and off the east coast of the United States. It has also been collected throughout much of the central north Atlantic.

This map suggests an amphi-Atlantic distribution. The known distribution of the adults indicates warm shallow water and carbonate banks; a very different environment from that found off the west coast of Africa. It is possible that there is suitable habitats around small islands in the Gulf of Guinea, such as Annobon or Sao Tome, but the mainland coast does not appear at all suitable. It is quite possible that some larval *Planktomya* make a complete circuit of the North Atlantic before finding a compatible environment for adult existence. By far the vast majority of individuals, however, must finally die far out at sea. Robertson (1964) has discussed this larval wastage in a paper on *Philippia krebsii*, a gastropod with long lived larvae. The larvae of *P. krebsii*, however, apparently do not have the staying power of larval *Planktomya*. Thiede (1974) considered the distribution of bivalve larvae in the eastern north Atlantic, and decided that the great majority were produced on the continental shelves or sub-surface elevations in that region.

Adult *Planktomya* have a fairly extensive geographic range, even with small amount of material at hand. The straight line distance between Santa Marta, Colombia and Black Rock, Bahamas, is over 1600 km. Since this is based on just eight specimens, the actual distribution is probably considerably more extensive. Material should be looked for throughout the Antilles, the Gulf of México, and Bermuda, as well as more of the coast of South America.

Allen and Scheltema (1972), on the advice of Kurt Ockelman, postulated that *Planktomya* was a member of the Leptonacea. With this I concur, although they were wrong in stating that it was probably a common species. It appears to me that this species should fit into the family Sportellidae. This is based on the oval shape, the broad hinge plate scarcely hollowed out for the ligament, sub-central prodissoconch, and strong tooth in each valve. There doesn't seem to be any closely related species, so *Planktomya* will stand as a monotypic genus in the Sportellidae.

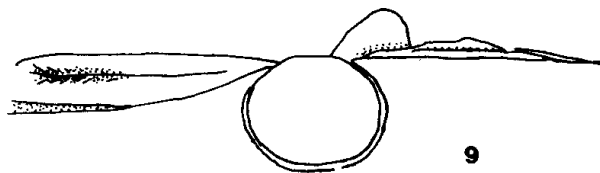
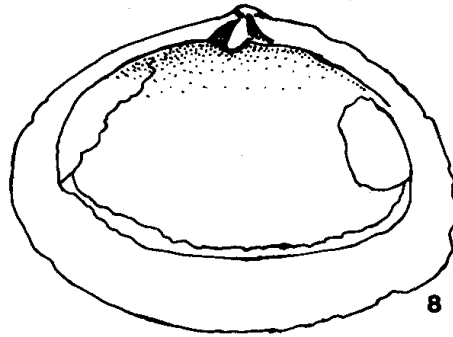
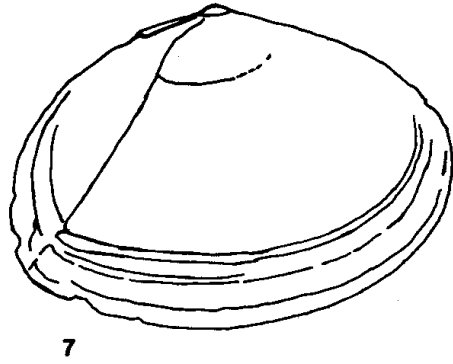
I have been unable to find the adult described in either the Recent or fossil literature. However, there is one tantalizing description and figure in Weisbord (1964). This is described as *Gouldia diffidentia* Weisbord 1964, and is based on one left valve 1.7 mm in length. The shape is very close to my 3 small specimens from Santa Marta. The umbonal region is described as somewhat swollen, surface sculptured by small, faint, subregular concentric riblets, lunule not defined and the escutcheon wanting. This could be used for a description of *Planktomya henseni*. I have not seen Weisbord's specimen, but it should be compared with adult *Planktomya*. The Mare Formation, in which *Gouldia diffidentia* was

found, is Lower Pliocene according to Weisbord, so this species might be a precursor of *Planktomya henseni* if not conspecific.

The prodissoconch of bivalves has usually received scant attention from systematists. However, those of some leptonids have been reasonably well illustrated by some workers. The Miocene species, *Sportella unicarinata* Dall, is shown as having a prodissoconch about half a millimeter across. It is difficult to know how far one can trust an old drawing, but I was able to obtain material which showed that at least some old illustrations are carefully drawn. I was working through the vast Dominican Republic fossil collection amassed by Peter Jung of the Basel Natural History Museum, where I found two specimens of leptonids with large prodissoconchs. One, a right valve from locality number 15860, is a specimen of *Sportella unicarinata* Dall, 1900, and is 8.8 mm long (Figs. 7-9). The prodissoconch is 650 μm across, and is surrounded by a rather strong groove, a feature that suggests that the prodissoconch was originally uncalcified. The other specimen is not so spectacular as the prodissoconch is only 400 μm across, still rather large for a clam just 5.0 mm long. This specimen, from Dominican Republic locality 15000, appears to be close to *Sportella petropolitana* Dall 1900, if not actually that species. The groove around the prodissoconch is weak indicating that it may not have been entirely uncalcified when a member of the plankton. Although the prodissoconch of this species is not spectacular, it is large compared to those of most species of the Bivalvia.

It can be seen from above that there appears to be a trend in the Sportellidae toward large poorly calcified larval shells. This has doubtless led to wide distribution of those species so endowed. *Planktomya* appears to be the culmination of this trend as no other species in the family has such a large prodissoconch.

Finally, I should mention that, while there are no living species of Bivalvia that are holoplanktonic, there were some in the past. At least that is the theory proposed by Jefferies and Minton (1965) for two Jurassic species of 'Posidonia'. The two species are thin shelled Pectinacea, and are considered to be nekton on facies grounds. There are very few benthic animals where fossils of *Bositra buchi* (Romer, 1836) and 'Posidonia radiata' Goldfuss, 1836, are found, and extremely few fossils of these two species where there are many benthic animal fossils. Since the Pectinacea are swimming animals, and these two species show no sign of attachment to drifting wood or to seaweed, they are considered to be holoplanktonic.



Figures 7-9. *Sportella uncarinata*. 7. Right valve from Dominican Republic, Basel Natural History Museum, Peter Jung station 15860, total length 8.8 mm, exterior view. 8. Interior view of right valve of *S. uncarinata*. 9. Enlarged view of prodissoconch, 650 in total length.

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