

Bostrycapulus heteropoma n. sp. and *Bostrycapulus tegulicius* (Gastropoda: Calyptraeidae) from Western Africa

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Abstract. Spiny slipper shells in the genus *Bostrycapulus* range worldwide in tropical and temperate oceans. Owing to the scarcity of samples that retain the defining characteristics of the genus, the species from tropical Africa and the Indo-Pacific are poorly known. Here we present data showing that samples of *Bostrycapulus* from the Cape Verde Islands and Senegal are distinct from each other and distinct from other known *Bostrycapulus* species. These two species can be distinguished from each other by the unique caplike protoconch found on the shells from Senegal and the coiled globose protoconchs typical of direct-developing species on the shells from the Cape Verde Islands. Genetically, samples from Senegal and the Cape Verde Islands are distinct. DNA sequences from Senegal are very similar to those of *Bostrycapulus odites*, which occurs in the South Atlantic (South Africa, Argentina, and Brazil) while those from Cape Verde are closest to *Bostrycapulus aculeatus* from Florida. The name *Bostrycapulus tegulicius* is available, and the single existing protoconch on the types in the Muséum National d'Histoire Naturelle, Paris, appears to match those from the Cape Verde Islands. Subtle variation in protoconch size and shape throughout the Cape Verde Islands suggests that there may be more than a single species in the archipelago. Unfortunately, too little material is available to rule out intraspecific variation or to support the description of additional new species from the Cape Verde Islands. Here, we augment the original description of *B. tegulicius* and describe the unique new species *Bostrycapulus heteropoma* n. sp. from Senegal.

INTRODUCTION

Recent phylogenetic analyses of calyptraeid gastropods and a review of the genus (Collin, 2003a, b, 2005) have shown that there are at least eight species of *Bostrycapulus* that were previously synonymized under the name *Crepidula aculeata* or *Bostrycapulus aculeatus* (Gmelin, 1791; Hoagland, 1977, 1983). These species are difficult or impossible to distinguish with any confidence on the basis of adult shell characters or adult anatomy (Simone, 2002). However, they can generally be distinguished using protoconch characters, developmental observations, and DNA sequence data (Collin, 2005). Samples that were recently collected from the Cape Verde Islands and Senegal show that animals from these locations are different from each other and that the species from Senegal is distinct from previously described *Bostrycapulus* species. The species from the

Cape Verde Islands is consistent with the description and type of *B. tegulicius* (Rochebrune, 1883).

Observations of protoconch morphology, using both light microscopy and scanning electron microscopy (SEM), show distinct differences between the two species (Figures 1 and 2). Shells from Senegal have a cap-shaped protoconch that is attached at right angles to the teleoconch (Figure 1), a morphology that is unknown in any other calyptraeid, and which suggests an unusual mode of development. Animals from the Cape Verde Islands have the coiled, globose protoconchs typical of other direct developing *Bostrycapulus* (Collin, 2005). Examination of the one type of *Bostrycapulus tegulicius* that retains a protoconch shows it to be similar to the material we obtained from São Vicente in the Cape Verde Islands (Figure 1). Subtle variation in protoconch size and shape, but not overall form, throughout the Cape Verde Islands suggests that there may be more than a single species in the archipelago (Figure 1). Alternatively, such variation could be the result of variation in nurse-egg allocation or intraspecific variation in egg size. Unfortunately, the mode of development of these

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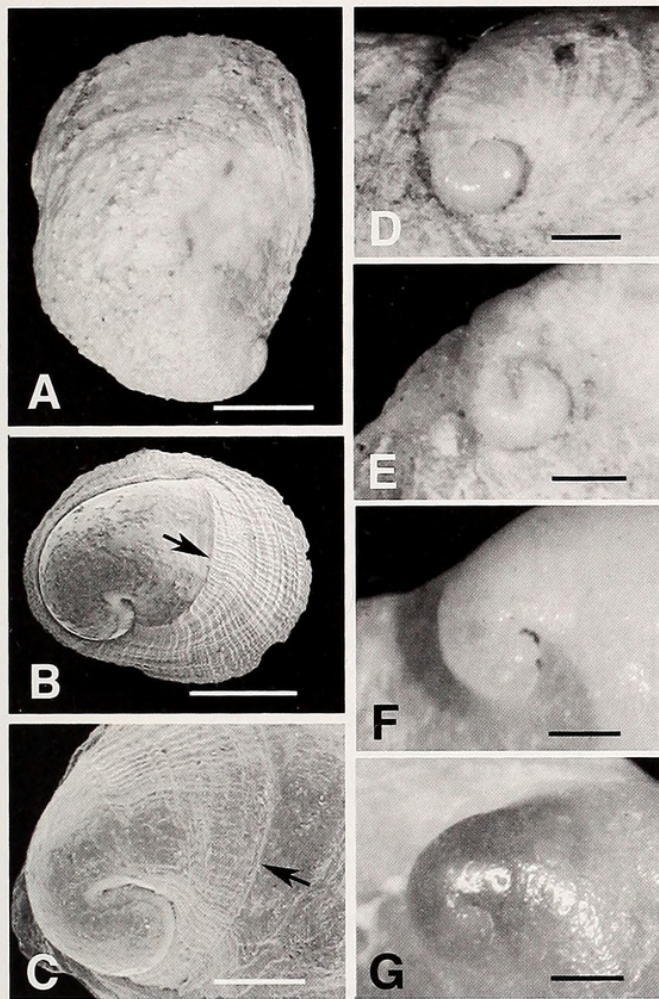


Figure 1. *Bostrycapulus tegulicius*. **A**. The lectotype of *B. tegulicius* that retains the protoconch. **B**. and **C**. SEMs of large globose protoconchs of *B. tegulicius* from Sal Island, Cape Verde. The arrow in **B** indicates the protoconch-teleoconch boundary and the arrow in **C** indicates the abrupt end of the radial sculpture. **D**. The tightly coiled protoconch of the lectotype of *B. tegulicius*. **E**. Protoconch of recently collected material from São Vicente. **F**. Globose protoconch from a pale shell from São Vicente. **G**. Globose protoconch from a dark shell from Sal. Scale bars: **A** = 5 mm; **B** = 500 μ m; **C** = 450 μ m; **D** = 700 μ m; **E** = 750 μ m; **F** = 450 μ m; **G** = 450 μ m.

species remains unknown, and too little material is available at this time to rule out intraspecific variation or to give strong support for the description of additional new species from the Cape Verde Islands.

Cytochrome oxidase subunit I (COI) and 16S DNA sequence data obtained and analyzed following Collin (2000, 2001, 2005) show that samples from Senegal are not genetically similar to those from the Cape Verde Islands. Despite being geographically proximate, they fall into completely different parts of the phylogeny of the genus. The single live-collected sample that was available to us from Sal Island in the Cape Verde Islands is genetically distinct from other *Bostrycapulus* species (Figures 3 and 4). There is a 6–7% Kimura 2-

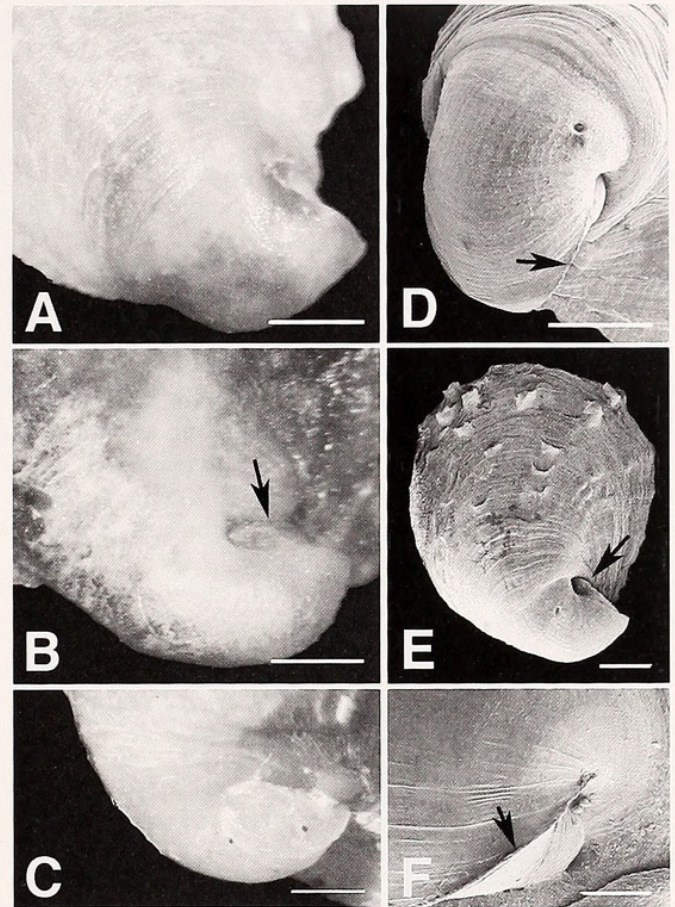


Figure 2. Protoconchs of *B. heteropoma* from Senegal showing the distinctive protoconch morphology and the basis for the specific name *heteropoma*. **B** and **E** arrows point to protoconch. **D** and **F** arrows point to the ridge at the protoconch-teleoconch boundary. Scale bars: **A** = 500 μ m; **B** = 500 μ m; **C** = 500 μ m; **D** = 500 μ m; **E** = 500 μ m; **F** = 200 μ m.

parameter divergence in COI sequences between this sample from the Cape Verde Islands and its sister species, *B. aculeatus* (Figure 3). A COI divergence of 6–7% is similar to, or greater than, divergences between other distinct, well-recognized calyptraeid species (e.g., Collin, 2000, 2001, 2003b). The 16S sequences recover the same sister-species relationship but show lower levels of divergence (Figure 4), as is typical of this gene region. *Bostrycapulus aculeatus* has direct development with large, yolky eggs and a protoconch similar to those observed on shells from the Cape Verde Islands.

Analysis of the COI and 16S sequences from animals collected in Senegal placed this species as sister to *Bostrycapulus odites* Collin 2005 from the South Atlantic, with only a 1.5–2.5% Kimura 2-parameter divergence in COI. This is a small COI divergence for sister species, but some other morphologically distinct calyptraeid species with similar or smaller interspecific distances have been reported (Collin, 2003b; Collin et al., 2007). *Bostrycapulus odites* has direct development

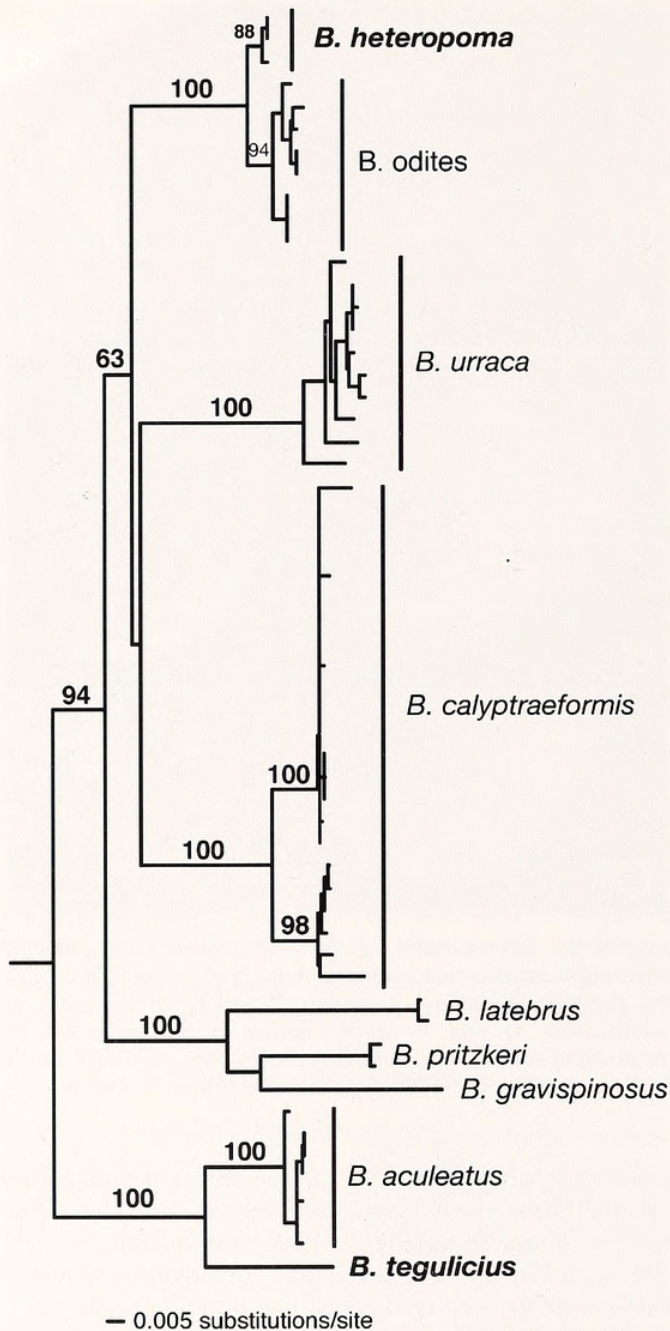


Figure 3. Neighbor-joining tree of *Bostrycapulus* based on 611 base pairs of mt COI DNA sequence data. All data are from Collin (2005) except for three individuals of *B. heteropoma*. Numbers above the branches show bootstrap support for the major nodes. More details can be found in Collin (2005).

from small eggs, where the embryos consume other eggs and embryos, and it has a coiled protoconch that is clearly different from those from Senegal. The unique protoconch on shells from Senegal (Figure 2), which is unlike the protoconch of any other *Bostrycapulus* species (Collin, 2005) and is, in fact, of a type unknown for any other calyptraeid, leaves no doubt that this is a distinct species.

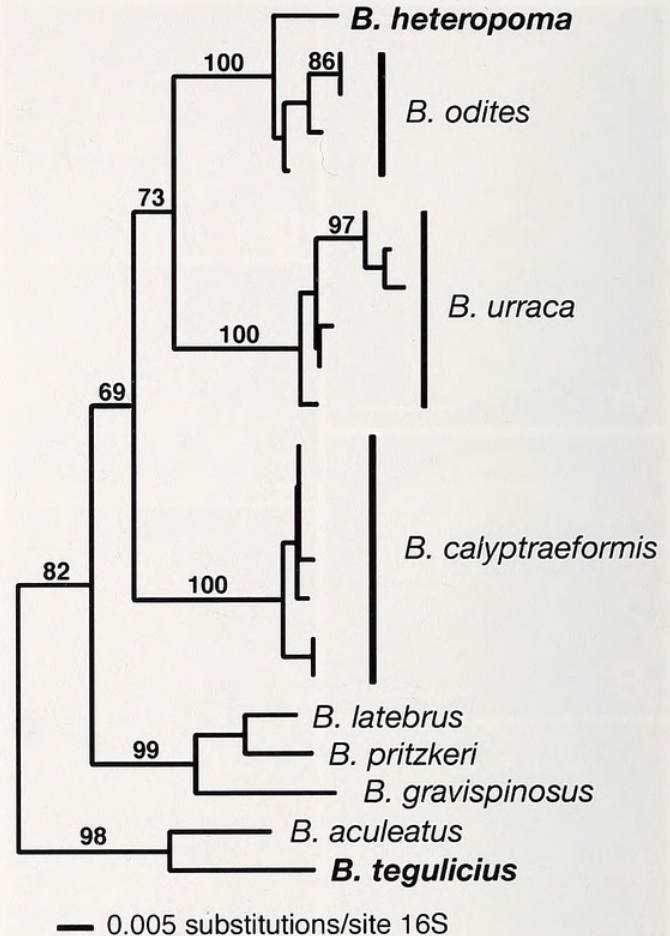


Figure 4. Neighbor-joining tree of *Bostrycapulus* based on 481 base pairs of mt 16S DNA sequence data. All data are from Collin (2005) except for three individuals of *B. heteropoma*. Numbers above the branches show bootstrap support for the major nodes. More details can be found in Collin (2005).

SYSTEMATICS

Genus *Bostrycapulus* Olsson & Harbison, 1953

Type Species *Bostrycapulus aculeatus* (Gmelin) by original designation

Bostrycapulus tegulicius (Rochebrune, 1883)

(Figure 1)

Synonymy:

Crypta tegulicia Rochebrune 1883:4.

Crepidula aculeata (Gmelin, 1791), Lamy 1911:318 (in part); Hoagland 1977:364 (in part); Hoagland, 1983:7 (in part).

Crepidula cf. *tegulicia* Collin, 2003a: 541–593. Collin, 2003b:618–640.

Bostrycapulus cf. *tegulicius* Collin, 2005.

Types: Two syntypes are in the Muséum National d'Histoire Naturelle, Paris (MNHN) (Hoagland, 1983).

Both figured in Hoagland (1983, fig. 9). The shell figured as 9a in Hoagland (1983) retains a protoconch (Figure 1). We hereby designate this shell as the lectotype of *Bostrycapulus tegulicius*. The shell length is 17.6 mm.

Original description: “Testa subovata, crassiuscula, irregulari, oblique curvata, extus albida, concentric striata, et squamis minutis teguliformibus, subdistantibus ornata; intus nitide castaneo violacea; lamella opalina, ad medio et ad latus subemarginata. Long 0.019, Lat 0.014.”

Type locality and distribution: The original description cites “Dakar, Joalles, Pointe de Cap Vert” Senegal as the locality. However, all of the *Bostrycapulus* shells collected by one of us (ER) in Senegal retain protoconchs that demonstrate them to be distinct from *B. tegulicius*. Material collected from the Cape Verde Island on São Vicente Island matches the protoconch morphology of the type of *B. tegulicius* (Figure 1). Therefore, we believe that the locality cited by Rochebrune (1883) is in error. This is likely, since type localities from the nineteenth century are often approximate, and Rochebrune examined material collected by a variety of people and is unlikely to have examined the protoconchs in detail.

Habitat: Most of the material examined was collected by dredging at 30–40 m, and living material was most often found on dead bivalve shells on soft bottoms. One animal was collected from the shell of a living *Comus* sp. from 2 m depth.

Material examined: Cream morphotypes with gracile protoconchs (*B. tegulicius* s. s.):

- 2 juveniles, 3 females, São Vicente, Cape Verde (MNHN).
- 2 specimens, Porto Mindelo, São Vicente, Cape Verde, 15 m (MHNS : Museo de Historia Natural of the University of Santiago de Compostela).
- 1 shell, Mاتیota, São Vicente, Cape Verde (MHNS).

Material examined: Brown morphotypes with globose protoconchs:

- 5 juveniles, Santa Maria, Sal, 30 m (MHNS).
- 1 shell, Algodoeiro, Sal, Cape Verde (MHNS).
- 3 shells, Palmeira, Sal, Cape Verde, 30 m (MHNS).
- 1 shell, Pau Seco, Maio, Cape Verde, 30 m (MHNS).
- 50 shells, 17 juveniles, Sal, Cape Verde (MNHN, coll. Marche-Marchad).
- 1 shell, Boavista, Cape Verde (coll. Michele) (the shell represented in Ardovini & Cossignani, 2004:100).
- 1 juvenile, Sal, Cape Verde, FMNH282359

Diagnosis: *Bostrycapulus tegulicius* can be distinguished from all other known species of *Bostrycapulus* by a combination of protoconch morphology, DNA sequence data, and biogeography. The protoconch has

a single 850–1000 μ m whorl, available sequence data for the DNA barcoding gene COI, GenBank #AY061776, is distinct from other species, and this species is known to occur only in Cape Verde.

Description: Examination of dead material from several localities throughout the Cape Verde Islands shows that there is subtle variation both in shell color and in protoconch size (cream and brown morphotypes above) and that this variation may represent intraspecific or interspecific variation (see below). The following description is based on samples (cream morphotypes) that match the protoconch of the type of *B. tegulicius* and that are generally typical of samples from São Vicente.

Bostrycapulus tegulicius sensu stricto (cream morphotype) has adult morphology typical of all *Bostrycapulus* species. The spiny shells, up to 25 mm in length, are convex and retain distinct coiling. There is a lunate muscle scar anterior to the septum on the animal's right side, and the edge of the septum is sinuous (see Collin, 2005, for detailed description). The shells of *B. tegulicius* are generally pale with sparse brown markings and can be distinguished from the shells of other species of *Bostrycapulus* by protoconch morphology. The protoconch is large and globose, and it constitutes about one whorl, with a length from the posterior of the shell to the protoconch–teleoconch boundary of about 850–1000 μ m (Figure 1E). The protoconch–teleoconch boundary is not clearly demarcated. The samples available to us are all uniformly smooth, and there is no indication of the fine, granular sculpture that is present on the shells of several other *Bostrycapulus* species. Many of the shells we examined were slightly eroded. Because the granular sculpture on the shells of other species erodes easily (Collin, 2005), it is possible that newly hatched individuals of this species have granular sculpture. No embryos have been observed in live-collected material, and therefore the details of embryonic development and egg-size measurements are not available. Neither DNA sequence data nor appropriate tissue for molecular work for samples that unambiguously match the type are available at this time.

Individuals of the brown morphotype of *Bostrycapulus tegulicius* have brown shells with cream markings that are typical of samples from Sal Island and Boavista Island. They have larger, more globose protoconchs (Figure 1B) than the pale morphs from São Vicente. The protoconch is large, globose, and constitutes about half a whorl with a length from the posterior of the protoconch to the protoconch–teleoconch boundary of about 800–900 μ m (Figure 1). The protoconch–teleoconch boundary is clearly marked by the abrupt initiation of spiral cords (Figure 1). The spiral cords give way to an underlying

smooth sculpture with occasional plicate spines after an additional 800–900 μm . There is no indication of fine granular sculpture.

The protoconch morphology and the DNA sequences described in Collin (2005) and attributed to *B. cf. tegulicius* correspond to the brown morphotype of *B. tegulicius*. In general, protoconchs from darker shells are slightly larger and less coiled than those from pale shells (Figure 1). However, shells with similar globose protoconch morphologies have also been observed on pale shells from São Vicente (e.g., Figure 1F), demonstrating that the general association between shell color, protoconch morphology, and locality is not rigid.

Development: unknown. The protoconch morphology is consistent with direct development from large yolky eggs.

Sequences in GenBank: COI AY061776, 16S AY061775 for FMNH282359 Sal Island, Cape Verde.

Remarks: The taxonomic status of the two *Bostrycapulus* morphotypes present in Cape Verde is not clear. It is clear that the pale morphotype with the more coiled protoconch matches the type of *B. tegulicius*. However, whether differences in protoconch morphology and/or shell color indicate the presence of one or several additional species is unclear. In general, the protoconchs from darker shells are larger and less coiled than those from pale shells. However, all combinations of color and protoconch morphology do occur. Some of these differences may simply be the result of geographic variation within a species, as shell color and sculpture varies among populations of other *Bostrycapulus* species (Collin, 2005). Alternatively, it is possible that these differences indicate the presence of two very closely related species. The Cape Verde Islands are the site of very recent explosive radiations of other marine gastropods with direct development (e.g., *Conus* [Duda & Rolán, 2005; Cunha et al., 2005]) and therefore interspecific divergences may also be very recent. Because protoconch morphology usually varies little within a species, we anticipate that distinct specific status of animals with each protoconch morphology will be supported as more material becomes available for study. However, we prefer the conservative approach of waiting until more than one line of evidence is available to support the introduction of additional species names.

Bostrycapulus heteropoma Collin & Rolán,
sp. nov.

(Figures 2, 5)

Synonymy:

Crepidula aculeata (Gmelin, 1791) Adam & Leloup, 1935:358 (in part). Hoagland 1977:364 (in part).

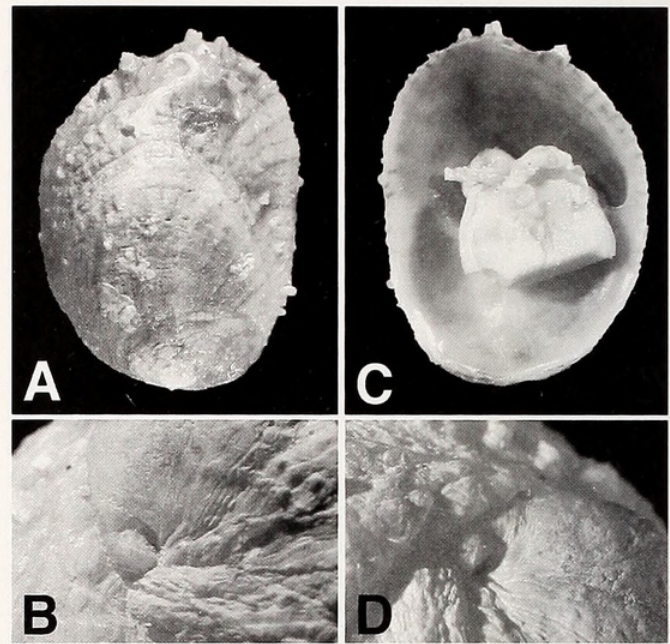


Figure 5. The holotype of *Bostrycapulus heteropoma* MNHN 21222. A. Dorsal view of the shell. B. and D. Different views of the protoconch. C. Ventral view of the holotype showing the tissue that was removed for sequencing.

Holotype: Gorée, Dakar, Senegal. Individual #282. GenBank #DQ314567; DQ314570. Muséum National d'Histoire Naturelle, Paris. MNHN 21222. Figure 5. Shell length = 25.5mm.

Paratypes: Gorée, Dakar, Senegal. Individual #284. GenBank #DQ314569. ANSP A21823. Shell length = 20.6 mm.

Type locality: Gorée, Senegal. 14°24'N 19°30'W.

Other Material Examined:

One shell, Gouye Teni M'Both, Dakar, Senegal, 25 m (J. Pelorce collection, Paris).

One shell, Cap Vert, Dakar, Senegal (MHNS).

Three juveniles, Goute Teni M'Both, Dakar, Senegal, 28 m (J. Pelorce collection, Paris).

One shell, Petit Corniche, Dakar, Senegal, 40 m (J. Pelorce collection, Paris).

Three specimens, Cap Vert, Dakar, Senegal, 40 m (J. Pelorce collection, Paris).

Eight juveniles, Gorée, Dakar, Senegal, 8–15 m (MHNS).

One juvenile, N'Gor, Dakar, Senegal, 7 m (MHNS).

One female, Gorée, Dakar, Senegal. Individual #283. GenBank #DQ314568. ANSP A21822; shell length = 25.5 mm; shell very eroded by epibionts.

Distribution and Habitat: This species has been collected from Dakar, Senegal. The material examined here was collected attached to large rocks from subtidal sandy habitats.

Diagnosis: *Bostrycapulus heteropoma* can be distinguished from all other known species of *Bostrycapulus* by its unique protoconch morphology, its distribution in Senegal, and the sequence of the COI gene. The cap-shaped protoconch is slightly curved and attaches to the teleoconch at a right angle along a prominent ridge.

Description: The adult shell morphology and anatomy are typical of *Bostrycapulus* species (see Collin, 2005, and Simone, 2002, for detailed descriptions). Externally, the shell is relatively flattened and somewhat coiled. The internal septum extends about half the length of the shell, and the anterior margin is indented medially and notched on the animal's left. There is a distinct but small medial ridge or crease from the medial indentation to the posterior shell margin near the apex. There is a small lunar muscle scar on the animal's right side anterior to the septum. The apex is appressed, usually slightly above the posterior shell margin on the right and is not excavated. The external shell sculpture varies from widely spaced, large, scalelike plicate spines to tightly packed, pointed, granular bumps along fine spiral ribs. Shell color varies from overall cream with scattered brown markings to solid chocolate brown, sometimes with pale streaks and occasionally solid tan. Markings are sometimes speckled and often streaky.

The protoconch is a large, elongate cap with pointed, asymmetrical apex and shows a slight curve but little sign of coiling (Figures 2 and 5). The 700 µm protoconch is attached at right angles to the teleoconch, and the boundary is marked by a distinct ridge (Figures 2 and 5). This morphology is so distinct that, without direct observations of development, it is not possible to verify that this ridge does indeed represent the protoconch–teleoconch boundary. We decide to call the ridge the protoconch–teleoconch boundary simply because there are no other clear demarcations on the shell that could be interpreted in this way, and because most calyptraeid shells include a clear protoconch–teleoconch boundary. It is possible that the ridge represents the boundary between protoconch I, laid down by the embryo prior to ingestion of nurse eggs or intracapsular albumin, and that the smooth area after the ridge is a later stage of a protoconch (protoconch II). However, if this is the case, there is no clear protoconch–teleoconch boundary. The protoconch is smooth, with some indication of growth lines prior to the ridge. The shell has more distinct growth ridges and some indistinct radial sculpture subsequent to the ridge. Some specimens retain very fine granular sculpture on the early teleoconch (Figure 2).

The pigmentation of the living animals is similar to that of other *Bostrycapulus* species. The body is generally creamish in large animals and translucent in very small animals. In large animals, the foot is a darker yellowish and the head is often orange. The

tentacles and snout have creamish or yellowish pigment splotches, and the mantle is decorated with numerous small, irregular white or cream spots. The osphradium is bipectinate with a brown border. Unlike other *Bostrycapulus* species, the animals we examined did not have black pigment along the edge of the foot or on the head or neck. We did not detect any diagnostic differences in the internal anatomy of ethanol-preserved samples. However, there were generally more distinct lobes on the capsule gland and the albumin gland than are usually observed in other *Bostrycapulus* species.

Development: Unknown.

Sequences in GenBank: COI: 3 sequences, GenBank # DQ314567–69; 16S: 1 sequence, GenBank # DQ314570.

Etymology: The neuter Greek noun heteropoma means “strange cover” and refers to this species’ unusual protoconch morphology.

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