

Crepidula badisparsa sp. nov. (Gastropoda: Calyptraeidae) from Bocas Del Toro Province, Panama

RACHEL COLLIN

Smithsonian Tropical Research Institute, Apartado Postal 0843-03092, Balboa, Ancon, Republic of Panama.
collinr@naos.si.edu

ABSTRACT.—The taxonomy of calyptraeid gastropods is made difficult by their morphologically simple, plastic shells and the numerous instances of morphological convergence within the family. The small speckled species of *Crepidula* from the West Atlantic have all previously been referred to as *C. convexa* Say, 1822. Recent developmental and genetic work has shown that there are two species along the coast of North America, *C. convexa* and *C. ustulatulina*, and that there are at least two other species in the southern Caribbean. Here I describe, *Crepidula badisparsa* sp. nov., the small speckled species from the Caribbean coast of Panama and augment the original description of *C. navicula* from Venezuela and the Lesser Antillies. These species are easily distinguished from the more northern *C. convexa* and *C. ustulatulina* by the absence of the right muscle scar, and from each other by genetic, conchological, and anatomical characters.

KEYWORDS.—Calyptraeidae, *Crepidula riisei*, *Crepidula convexa*, *Crepidula navicula*

INTRODUCTION

Slipper snails in the genus *Crepidula* are well known for the taxonomic difficulties posed by their plastic shells and conservative anatomy (Hoagland 1977, 1984, 1986; Collin 2000a, 2002, 2003b, 2005). Although the *Crepidula* fauna of the east coast of North America is well known after considerable scientific study, the southern extent of the species ranges are still not well-documented. Likewise, the identities and geographic ranges of calyptraeid species from the Caribbean and the tropical Americas are poorly known. Animals from these regions with shells similar to species found in North America are generally referred to by the northern names and, therefore, single species are often cited as ranging along an entire coast of the Americas. For example, Hoagland (1977) lists *C. plana* Say, 1822 as ranging from Canada to Argentina. Subsequent examination of developmental and genetic data showed that *C. plana* ranges only as far south as Georgia, USA

and that a morphologically similar species, *C. depressa* Say, 1822 occurs along the coast of the Gulf of Mexico (Collin 2000, 2001). Other species that were previously thought to be wide-ranging (e.g., *Bostrycapulus aculeatus*) are also comprised of several more narrowly distributed cryptic species (Collin, 2005).

Animals with small, speckled shells from eastern North America are generally referred to as *Crepidula convexa* Say, 1822. This name has also been applied to animals from Mexico (Carnes 1975; Bolivar de Caranza and Hidalgo-Escalante 1990), the West Indies (Abbott 1974), Columbia (Bandel 1976) and Venezuela (Simone 2002). Detailed research on the development and genetics of *C. convexa* s. l. (Hoagland 1984, 1986; Collin 2000) in North America showed that it was comprised of two species, *C. convexa* Say, 1822 and *C. ustulatulina* Collin, 2002. *Crepidula convexa* extends from New England to Georgia and *C. ustulatulina* ranges from southeastern Florida through the Gulf Coast of the United States and the Yucatan Peninsula (Collin 2001). The southern range endpoint of this species has not yet been determined.

Animals with similar habits and external

ms. received August 23, 2004; accepted March 31, 2005

shell morphology to *C. ustulatulina* also occur along the Caribbean coast of Panama and in Venezuela (Fig. 1 and 2). Samples of both were included in previous comparative studies of calyptraeid development (Hoagland 1986; Collin 2003a; Miloslavich et al. 2003), morphology (Collin 2003b) and DNA sequence data (Collin 2003c). Morphologically, these animals are easily distinguished from *C. convexa* and *C. ustulatulina*, because shells of the latter have a large muscle scar on the animal's right side which is absent in the Caribbean species. Although the development of animals from both Venezuela and Panama is similar and both hatch as pediveligers (Miloslavich et al. 2003; Collin 2003a), mitochondrial cytochrome oxidase c subunit I and 16S ribosomal DNA sequence data show they are two distinct species (Collin 2003c). Phylogenetic analysis of DNA sequence data for 95 calyptraeid species shows that the spe-

cies from Panama is most closely related to *C. cf. incurva* from Peru, while the small spotty *Crepidula* from Venezuela is genetically very similar to a larger brown species referred to as *C. aphysioides* form Venezuela (Fig. 3; Collin 2003c). These two speckled species can also be distinguished from each other by subtle morphological differences.

There are two possibly available names for these Caribbean species. The syntypes of *Crepidula navicula* (Mörch 1877) collected by Riise from St. Thomas (ZMUC GAS-237), and other possible syntypes of this species collected by Hornbeck from Vieques (ZMUC collection) (Fig. 4) are similar to the shells from both Panama and Venezuela. The other possible name is *C. riisei* Dunker 1852 from Puerto Rico. This species is described as pale with brown speckles, the apex is terminal, and the edge of the shelf is sinuous medially and deeply emarginate on the left. The synonym of *C. riisei*

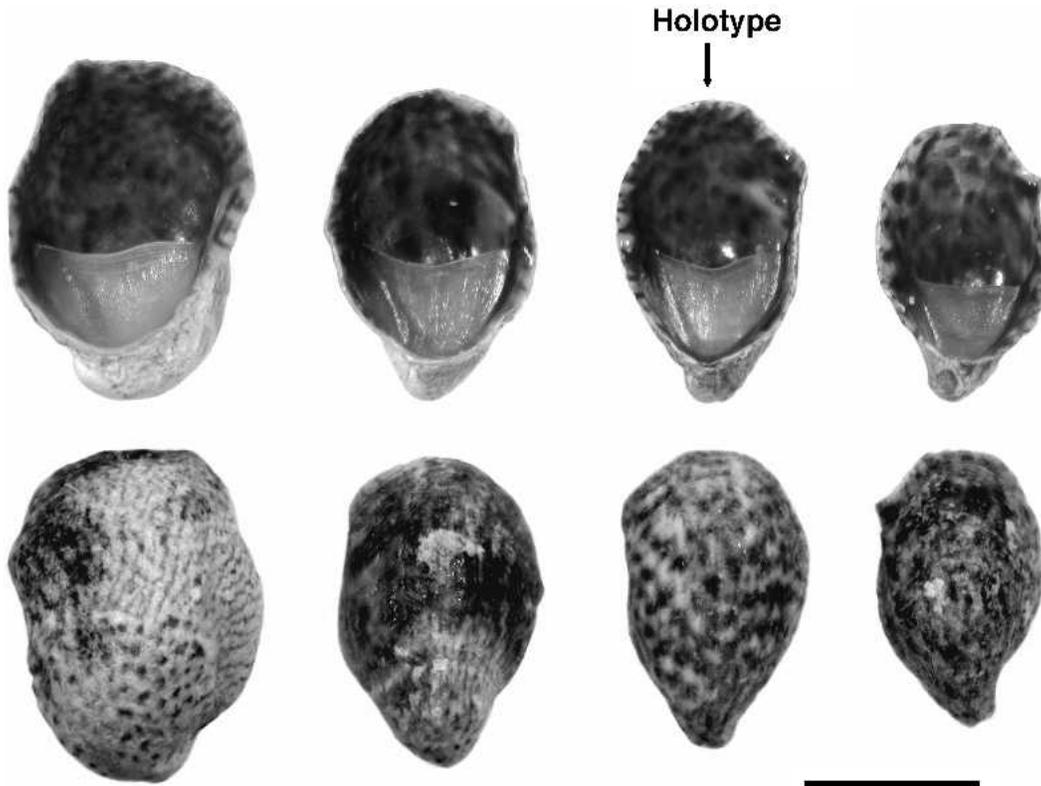


FIG. 1. Photographs of the shells of *C. badisparsa*. The type of *C. badisparsa* is indicated with an arrow. Scale bar = 5.0 mm.

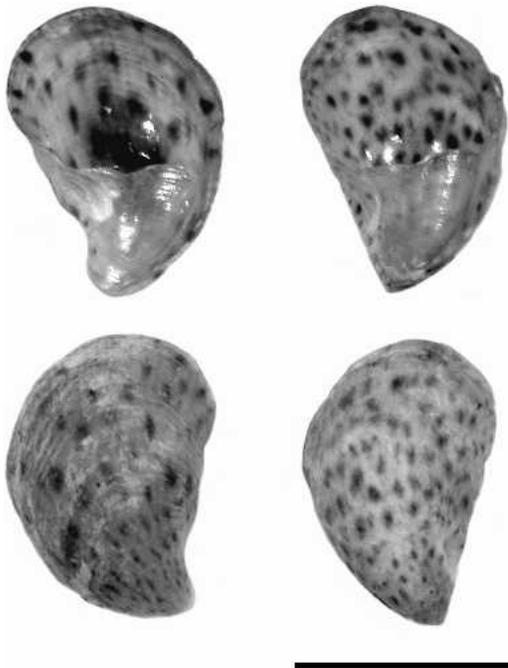


FIG. 2. Photographs of the shells of *C. navicula* from Morrocoy National Park, Venezuela. Scale bar = 5.0 mm.

with *C. plana* in Yong and Coomans (1988) is dubious, but *C. riisei* has also been synonymized with *Crepidula fornicata* (Tryon 1886; Hoagland 1977). It is not clear to which side of the shell the “left” refers as several works of this age illustrate the animal inverted with respect to the shell. Although there is a subtle notch on the right side of the shelf of shells from Venezuela, neither of the species discussed here has a deep notch on either side of the shell. The shell length of “7 lin” cited by Dunker (1852) is somewhat large for this species (15.3 mm based on a Prussian inch of 26.15 mm employed by Dunker) but is small for *Crepidula fornicata*. I have been unable to locate the types of this species, which Hoagland (1977) lists as lost. There are no records of these types in Berlin (M. Glaubrecht pers. com. 2004), and they cannot be located in Copenhagen (A. Joergensen pers. com. 2004), Stockholm (A. Warén pers. com. 2005) or London (pers. obs. 2001 and K. Way pers. com. 2005). Since there is no figure in the original description, it will be difficult to resolve the identity of this spe-

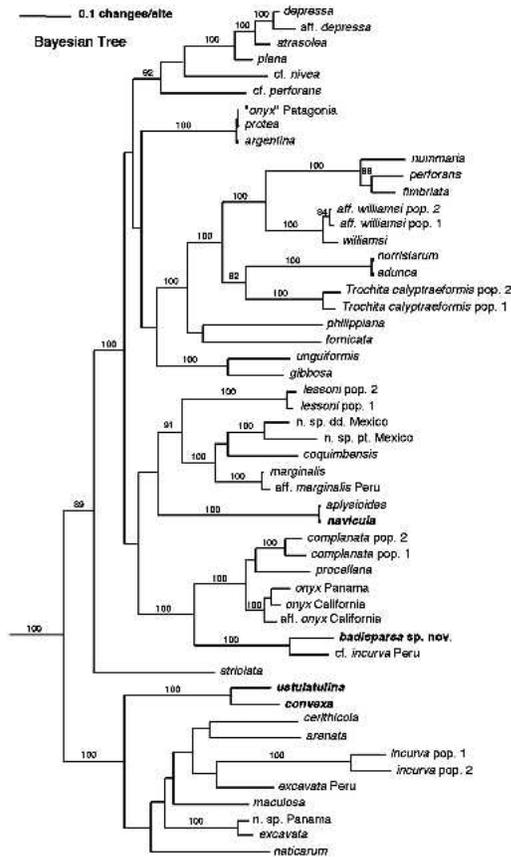


FIG. 3. Bayesian estimate of the phylogeny of *Crepidula* s.s. showing the relationships of *C. convexa*, *C. ustulatulina*, *C. badisparsa* and *C. navicula*. Topology from Collin (2003c).

cies. The types of *C. navicula* come from localities close to the origin of the Venezuelan animals and therefore it is appropriate to apply that name to the Venezuelan species and to describe the Panamanian species as new. I formalize this taxonomic scheme below.

TAXONOMIC DESCRIPTION

GENUS: *Crepidula* Lamarck, 1822
Crepidula navicula (Mörch 1877)
 (Fig. 2 and 4; Table 1)

Synonymy:

Crypta navicula Mörch, 1877: 105.
Crepidula cerithicola Guppy, 1894 from Trinidad and Tobago (non *C. cerithicola* Adams, 1852).

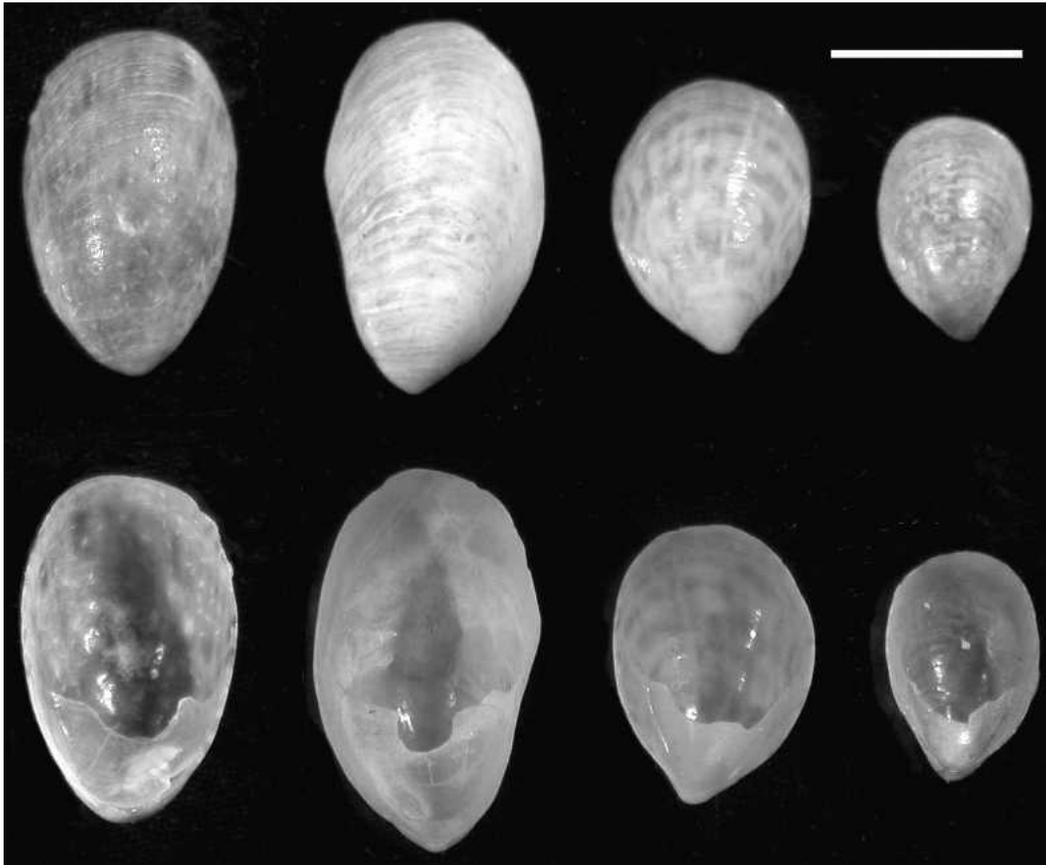


FIG. 4. Photographs of the syntype of *Crepidula navicula* (Mörch, 1877) collected by Riise from St. Thomas (ZMUC GAS-237) (left), and other 3 possible syntypes of this species collected by Hornbeck from Vieques (ZMUC collection). Scale bar = 5.0 mm.

TABLE 1. Summary of species differences.

Character	<i>C. badisparsa</i> sp. nov.	<i>C. navicula</i> (Mörch 1877)
Maximum length	13 mm	10 mm
Shell color	White with brown spots or streaks, with more than 50% brown	White with brown spots or streaks, predominantly pale
Shelf margin	Slightly bowed or slightly sinuous	Slightly sinuous, notch on the right
Apex	Excavated	Not excavated
Stage at hatching	Pediveliger	Pediveliger
Egg size	286 μm	350 μm (Miloslavich et al. 2003)
Hatching size	515 μm	550-1170 μm (Miloslavich et al. 2003)
Osphradium	6-11 filaments	3-6 filaments
Salivary glands	Near the buccal mass	Extend along neck
Right shell muscle	Small and in lateral position	Absent

Crepidula convexa Say: Hoagland, 1977: 369 (partly).

Crepidula navicula (Mörch): Collin, 2003a,b,c. Miloslavich et al., 2003.

Original description: "T. convexa, angusta, maculis oblongis fuscis. Long. 10 mm, lat 5 mm."

Types: Hoagland (1977) lists the types of

C. navicula as lost. However a syntype collected by Riise from St. Thomas, (Copenhagen, ZMUC GAS-237; length = 9.3 mm), and other possible syntypes collected by Hornbeck from Vieques (ZMUC collection; lengths = 1.0, 7.4, 6.0 mm) were located in Copenhagen Museum of Zoology (Figure 4). The status of the Vieques material as types is questionable as only Isla Margarita was mentioned in the original description. The location of the syntypes collected by Krebs in St. Martin is unknown. None of the types were figured by Mörch.

Type locality: Mörch lists the habitat as "Terra firma" (Hornbeck) St. Martin (Krebs), St. Thomas (Riise), and I. Margarita (Hornbeck).

Distribution and habitat: The extent of the distribution of *C. navicula* is not well documented. However this species is known from the coast of Venezuela (type description and the material examined here) and the Lesser Antillies (the syntypes). It commonly occurs on other snails in shallow water. In Morrocoy National Park, Falcón, Venezuela they occur commonly on *Modulus modulus* in *Thalassia* beds (Miloslavich et al. 2003).

Description: The anatomical description presented here is drawn from lot FMNH293349 and ANSP 412185 from Morrocoy, Venezuela.

Shell. Fig. 2 and 4. The shell is small somewhat convex and curved laterally. Shell shape is strongly dependent on the shape of the substrate. Animals living on small snails often have a compressed left side or are compressed on both sides. The shell is usually white with dark brown spots and streaks, with white predominating. The periostracum is not visible. The shell apex is at the level of the aperture and is not noticeably excavated. The protoconch is usually eroded from the edge of the aperture. There is no sculpture other than growth lines. There are no muscle scars. The shelf is flat and white, and extends slightly less than half the length of the shell. The anterior margin of the shelf is often slightly sinuous, with a medial inflection. There is a small notch where the shelf connects to the shell on the left side. This notch is just intact on the syntype from St. Tho-

mas but the shelves are broken, obscuring this feature on the other possible syntypes. Maximum length is 10 mm.

Morphology: External body color is dark gray and black along the dorsal side of the head and neck. Because the available material was all preserved, the presence of yellow or cream pigment could not be assessed. The general anatomy is similar to *Crepidula fornicata* described in detail by Werner and Grell (1950), and to general *Crepidula* s.s. anatomy as described by Simone (2002) and Collin (2003b). The black gill extends about two thirds to three quarters of the way to the end of the viscera. There is no shell muscle but the small dorsal attachment muscle is present in the mantle anterior to the heart. The monopectinate osphradium consists of 3-6 closely spaced simple leaflets. These occur in a tight cluster that does not overlap with the food pouch and covers less than half of the mantle opening. The tubular salivary glands extend along the neck halfway to the nerve ring. The visceral mass does not bulge into mantle cavity on the left side. Female genital papilla (fgp) extends well into the mantle cavity with a wide, shallow groove and blunt, rounded distal tip. The capsule gland and albumen gland together form a round bulge in the mantle cavity at the base of the fgp. The penis is slightly flattened, and tapers gradually to the long, thin distal papilla which is not as distinct from the rest of the penis as in many species.

Development: Development of this species was described by Miloslavich et al. (2003). All of the uncleaved 350 μ m eggs develop initially but a slight decrease in the number of eggs per capsule during development was noted (Miloslavich et al. 2003). This was attributed to intrabrood cannibalism, but different broods were examined at different stages and female size was not taken into account. Therefore it may also be an artifact of differences in maternal size. The small differences are most likely due to the occasional consumption of disintegrating embryos rather than development specialized for the consumption of nurse eggs as observed in *Crepidula coquimbensis* or *Crepidula dilatata*. Pediveligers hatch at about

800 μm (Miloslavich et al. 2003) but are reported to be retained below the female until they crawl away, so it is unclear if they were ever observed to swim.

Available DNA sequences: DNA sequences are available from GenBank from a single individual from Morrocoy, Venezuela for mitochondrial cytochrome oxidase I and 16S rDNA, and nuclear 28S rDNA #AF546040, AF545980, AF545903, respectively.

Notes: I have chosen to attribute these animals to *C. navicula* on the basis of similarities between their shells and the types, and on geographic proximity. The shells of the types are slightly larger and more robust than the material from Morrocoy. They are certainly more similar to this material than to the flatter, more gracile samples from Isla Margarita attributed to *C. aplysioides* (Miloslavich et al. 2003; Collin 2003a,b,c). *Crepidula riisei* appears to be similar but the animals described here do not have a deep notch on either side of the shelf. Examination of the anatomy, development, and DNA of material from throughout the Caribbean and especially Puerto Rico is necessary before we can determine how many species are present and can therefore assess the validity of this older name.

Crepidula badisparsa sp. nov.
(Fig. 1 and 3, Table 1)

Synonymy:

Crepidula convexa Say: Hoagland, 1977: 369 (partly).

C. cf. convexa: Hoagland, 1986.

"*C. convexa* Bocas": Collin, 2003a,b

C. cf. navicula: Collin, 2003c

Holotype: ANSP 412182. Figure 1. Female. Length = 9.0 mm; width = 5.5 mm; height 3.7 mm; 3 figured paratypes from type locality ANSP 412183.

Other material from the type locality: FMNH 282355, ANSP 412184.

Type locality: *C. badisparsa* were collected from *Cerithium* living on the *Thalassia* meadow behind the Smithsonian's Bocas del Toro Research Station (9°21'4.3"N, 82°15'25.6"W) at 1-2 meters depth.

Diagnosis: *Crepidula badisparsa* is distinguished from other similar species of *Crepidula* by the following suite of characters. Small, speckled shell with a slightly arched shelf margin and no muscle scar, a small right shell muscle located ventro-laterally in the visceral mass, and development with a pediveliger.

Distribution and habitat: I have collected *C. badisparsa* from Bocas del Toro, Panama and Hoagland (1986) collect animals that may be the same species (see below) from Coco Solo, Limon Bay, Panama (ANSP A12043 and ANSP A12044). In both cases the animals were collected living attached to other snails and were found in shallow (1-2 m) water.

Description:

Shell. Fig. 1. The shell is small and convex or arched dorsal-ventrally, but not curved laterally. Shell shape is strongly dependent on the shape of the substrate. Animals living on small snails often have a compressed left side or are compressed on both sides. The shell is usually white with dark brown spots and streaks, with the brown predominating over the white. The periostracum is not visible. The shell apex is well-excavated ventral to the shelf, directed posteriorly, and curves ventrally to the level of the aperture. The protoconch is smooth and often eroded. There is no sculpture other than growth lines. There are no muscle scars. The white shelf is flat and extends slightly less than half the length of the shell. The anterior margin of the shelf is often slightly bowed with the half on the animal's left side running laterally and the right side extending slightly further forward. In others the shelf margin runs laterally across the entire shell, but it is still bowed near the midline. There is no notch where the shelf connects to the shell on the left side.

Anatomy: External body color is dark gray and black along the dorsal side of the head and neck, with splotches of cream and yellow along the neck lappets, tentacles and lips. The general anatomy is similar to *Crepidula fornicata* described in detail by Werner and Grell (1950), and to general *Crepidula* s.s. anatomy as described by Si-

mone (2002) and Collin (2003b). The black gill extends about three quarters of the way to the end of the visceral mass. A shell muscle extends dorsally from the anterior right portion of the foot to attach the animal to the shell. This muscle attaches to the anterior margin of the shelf from the underside of the viscera and wraps around to the right side of the viscera (ventral and lateral to the capsule and albumin glands) attaching to the shell at the intersection of the shell and the shelf. In other *Crepidula* species with a right shell muscles the muscle extends from the dorsal side of the viscera and attaches to the shell roof. The osphradium consists of 5-11 tightly packed monopectinate leaflets. The most medial leaflets are covered by the left side of the food pouch. The osphradium covers most of the mantle cavity opening. The tubular salivary glands are clustered around the buccal mass and the neck is full of connective tissue making it difficult to find them. The visceral bulges extensively into mantle cavity on the left side. Female genital papilla (fgp) extends well into the mantle cavity with a wide shallow groove and somewhat angled or pointed tip. The capsule gland and albumin gland together form a round bulge into the mantle cavity at the base of the fgp. The penis is evenly tapered and the seminal groove extends to the distal tip.

Development: In Bocas del Toro, Panama, *C. badisparsa* lay eggs in thin transparent capsules typical of most calyptraeids. Uncleaved eggs are 286 μm ($n = 11$; s.d. = 5.8 μm). Embryos develop into encapsulated pediveligers which have a clear mid-sized head vesicle, and a single embryonic kidney on each side. Embryos hatch as pediveligers with a shell length of 515 μm ($n = 10$; s.d. = 30 μm). The hatchlings have an operculum, unpigmented velum, a clear intestine, and a smooth, transparent shell. Although this is a small hatching size with respect to the egg size and the larvae clearly had yolk reserves at hatching, they settled within several hours of hatching. Because these larvae were release by undisturbed females that were maintained in the laboratory, it is unlikely that they hatched prematurely.

Available DNA sequences: DNA sequences

are available from GenBank from a single individual of *C. badisparsa* from Bocas del Toro, Panama for mitochondrial cytochrome oxidase I and 16S rDNA, and nuclear 28S rDNA AF546036, AF545975, AF545898, respectively.

Etymology: The species name *badisparsa* is a Latin adjective, referring to the brown spots on the shell of this species.

Notes: Hoagland (1986) describes the development of what appears to be the same species (her *C. cf. convexa*) from Limon Bay, Panama, but she obtained slightly different results. She reports a larger egg size (300 μm ; 260-400 μm) and a larger hatching size (800 μm) than *C. badisparsa* from Bocas del Toro. The presence of a single nurse egg per capsule (Hoagland 1986, Table 3) is not in accordance with her observation of "extensive brood cannibalism" (Hoagland 1986, pg. 182) and so the exact nature of the nurse eggs and the details of embryonic development remain unclear. Hoagland's formalin-preserved vouchers, however, do demonstrate the diagnostic morphology of the left shell muscle and the pointed fgp that distinguish *C. badisparsa* from *C. navicula*. Unfortunately, no living material from Limon Bay is currently available to repeat Hoagland's observations of development.

Acknowledgments.—I thank the Smithsonian's Marine Science Network and the Smithsonian's Women's Committee for their support of invertebrate taxonomic work in Bocas del Toro. I am grateful to R. Cooke for translating the species description of *C. riisei*, T. Schiøtte for finding the types of *C. navicula*, A. Valdés and A. Warén for commenting on the manuscript, and the curators and collection managers of USNM, BMNH, CAS, ANSP, MCZ, ZMUC and LACM for loans of type material and for accepting vouchers. I also thank the Autoridad Marítima de Panamá for issuing me collecting and export permits.

LITERATURE CITED

- Abbott, R. T. 1974. *American seashells*. 2d ed.: New York, Van Nostrand Reinhold Company.

- Adams, C. B. 1852. Catalogue of shells collected at Panama. *Ann. Lyceum Nat. Hist.* New York, 5:5-334.
- Bandel, K. 1976. Observations on spawn, embryonic development, and ecology of some Caribbean lower Mesogastropoda (Mollusca). *Veliger* 18:249-271.
- Bolivar de Carranza, A. M., and E. Hidalgo-Escalante. 1990. Lista de moluscos gastrópodos y pelecípodos del Golfo de México y el Caribe. *An. Esc. Nac. Cienc. Biol. Méx.* 33:53-72.
- Carnes, S. F. 1975. Mollusks from southern Nichupté Lagoon, Quintana Roo, Mexico. *Sterkiana* 59:21-50.
- Collin, R. 2000. Phylogeny of the *Crepidula plana* (Gastropoda: Calyptraeidae) cryptic species complex in North America. *Can. J. Zool.* 78:1500-1514.
- Collin, R. 2001. The effects of mode of development on the phylogeography and population structure of North Atlantic *Crepidula* (Gastropoda: Calyptraeidae). *Mol. Ecol.* 10:2249-2262.
- Collin, R. 2002. Another last word on *Crepidula convexa* and a description of *C. ustulatulina* sp. nov. (Gastropoda: Calyptraeidae) from the Gulf of Mexico. *Bull. Mar. Sci.* 70(1):177-184.
- Collin, R. 2003a. World-wide patterns of development in calyptraeid gastropods. *Mar. Ecol. Prog. Ser.* 247: 103-122.
- Collin, R. 2003b. The utility of morphological characters in gastropod phylogenetics: An example from the Calyptraeidae. *Biol. J. Linn. Soc.* 78:541-593.
- Collin, R. 2003c. Phylogenetic relationships among calyptraeid gastropods and their implications for the biogeography of speciation. *Syst. Biol.* 52(5):618-640.
- Collin, R. 2005. Development, phylogeny, and taxonomy of *Bostrycapulus* (Caenogastropoda: Calyptraeidae), an ancient cryptic radiation. *Zool. J. Linn. Soc.* 144:75-101.
- Dunker, G. 1852. Diagnoses Molluscorum novorum. *Zeitschr. Malakozool.* 9:189-191.
- Guppy, R. J. L. 1894. Observations upon the physical conditions and fauna of the Gulf of Paria. *Proc. Victoria Inst. Trinidad* 1894(2):115-125.
- Hoagland, K. E. 1977. Systematic review of fossil and recent *Crepidula* and discussion of evolution of the Calyptraeidae. *Malacologia* 16(2):353-420.
- Hoagland, K. E. 1984. Use of molecular genetics to distinguish species of the gastropod genus *Crepidula* (Prosobranchia: Calyptraeidae). *Malacologia* 25(2):607-628.
- Hoagland, K. E. 1986. Patterns of encapsulation and brooding in the Calyptraeidae (Prosobranchia: Mesogastropoda). *Am. Malacol. Bull.* 4(2):173-183.
- Jong, K. M. de, and H. E. Coomans. 1988. Marine gastropods from Curaçao, Aruba and Bonaire. *Stud. Fauna Curaçao Other Caribb. Islands* 69 (214):1-261.
- Mörch, O. A. L. 1877. Synopsis molluscorum marinarum Indiarum occidentalium imprimis insularum danicarum. *Malakozool. Blätt.* 24:93-123.
- Miloslavich, P., E. Klein, and P. E. Penchaszadeh. 2003. Reproduction of *Crepidula navicula* Morch, 1877 and *Crepidula aphysioides* Reeve, 1859 (Caenogastropoda) from Morrocoy and La Restinga Lagoon, Venezuela. *Nautilus* 117:121-134.
- Say, T. 1822. An account of the marine shells of the United States. *J. Acad. Nat. Sci. Philadelphia* 2:221-227.
- Simone, L. R. L. 2002. Comparative morphological study and phylogeny of representatives of the superfamilies Calyptraeoidea (including Hipponicoidea) (Mollusca, Caenogastropoda). *Biota Neotropica* 2(2). http://www.biotaneotropica.org.br/v2n2/pt/fullpaper?bn01602022002_1+en t
- Werner, B., and K. G. Grell. 1950. Die amerikanische Pantoffelschnecke, *Crepidula fornicata* L. Jena: Fischer.