

ANOTHER LAST WORD ON *CREPIDULA CONVEXA* WITH A
DESCRIPTION OF *C. USTULATULINA* N. SP. (GASTROPODA:
CALYPTRAEIDAE) FROM THE GULF OF MEXICO AND
SOUTHERN FLORIDA

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ABSTRACT

The taxonomy of *Crepidula* has a history of instability due to the low number of informative shell characters and their phenotypic plasticity. Molecular and developmental data show that *Crepidula convexa* sensu Hoagland 1977 is composed of two distinct species. Animals of the northern species are relatively larger, and have darker shells and direct development, while animals from the Gulf of Mexico and southeastern Florida have smaller, pale spotted shells and produce pediveligers. *C. convexa* Say, 1822 is re-described and a single neotype is designated for *C. convexa* and *C. glauca* Say, 1822 to represent the northern species and to formalize the synonymy of these two names. The southern species, which is distributed throughout the Gulf of Mexico, is described as a new species, *C. ustulatulina*.

Marine slipper-shell 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). Although the *Crepidula* fauna of the east coast of North America is well known and contains only a few species (Hoagland, 1977), the taxonomy of even these species is still being refined (e.g., Collin, 2000a). Animals with small speckled shells from eastern North America are generally referred to as *Crepidula convexa* Say, 1822. Although originally used to refer to a species from the east coast of the United States the name *C. convexa* has also been applied to animals from Mexico (Carnes, 1975; Bolivar de Carranza and Hidalgo-Escalante, 1990), the West Indies (Abbott, 1974), and Columbia (Bandel, 1976). However, detailed research on the development and genetics of *C. convexa* (Hoagland, 1984, 1986) suggested that, as previously recognized, *C. convexa* is made up of two distinct species.

Genetic data from both allozymes (Hoagland, 1984) and mtDNA sequences (Collin, 2001) demonstrate that there are two distinct clades of '*C. convexa*' in North America. A northern species extends from New England to Georgia and a southern species ranges from southeast Florida through the Gulf Coast of the United States and the Yucatán Peninsula (Collin, 2001). These clades show a divergence of 5% in 640 base pairs of mitochondrial cytochrome oxidase c subunit I DNA (Collin, 2001) and they do not share alleles at 12 of 24 enzyme loci examined (Hoagland, 1984). These data show that gene flow does not occur between these clades.

Developmental and morphological observations using the methods of Collin (2000a) corroborate the results of the genetic analyses. Embryos of the northern species hatch as crawling juveniles and embryos of the southern species hatch as pediveligers which settle and metamorphose within minutes to hours of hatching (Hoagland, 1984; Collin, 2001). Morphologically the two species differ in shell size and color, salivary gland position, and the number of osphradial filaments (Table 1). This evidence clearly reflects the presence of two distinct species, the taxonomy of which is formalized below.

TAXONOMIC DESCRIPTIONS

Genus *Crepidula* Lamarck, 1822*Crepidula convexa* Say, 1822

(Fig. 1, Table 1)

C. glauca Say, 1822; *C. convexa* Say (Verrill and Smith, 1874); *C. convexa* Say (Franz and Hendler, 1970); *C. convexa* Say (Hoagland, 1977) in part; *C. convexa* Say (Hoagland, 1984; 1986); *C. convexa* northern species, (Collin, 2001)

Fate of Original Type Material.—Say's types were originally deposited in the ANSP (All institutions are referred to by the acronyms given in Leviton et al. (1985)). They were removed in 1825, many were subsequently destroyed in a fire and those that survived were returned to the ANSP after his death. The types of *C. convexa* and *C. glauca* were considered lost by Hoagland (1977) and cannot be located in the ANSP collection (Franz and Hendler, 1970; Hoagland, 1977; G. Rosenberg, pers. comm.; pers. observ.).

Neotype.—ANSP A19269;—ethanol preserved female (Fig. 1); length 13.3 mm; width 10.9 mm; height 3.3 mm.

Locality of Neotype.—West side of the barrier island, Wildwood Crest, Cape May, New Jersey (38°57'N, 74°50'W), intertidal on rocks.

Other Material Examined.—Wildwood Crest, New Jersey ANSP A19270; FMNH 282261, 282262, 282299; Galilee, Rhode Island FMNH 282300; St. Catherine's Island, Georgia FMNH 282259, FMNH 282260; All ethanol preserved material.

Diagnosis.—*C. convexa* can be distinguished from other species of *Crepidula* by the following suite of characters. Shell small and convex; usually brown or purplish brown often with darker spots or streaks. Shelf white sometimes with brown streaks. Periostracum dark. Body gray with yellowish or cream spots on tentacles, in life. Shelf margin extends further forward on animal's left, sometimes straight, often slightly arched. Muscle scar anterior to shelf on animal's right. Apex often slightly rostrate, excavated ventral to the shelf. Salivary glands extend from buccal mass to nerve ring. Female genital papilla pointed with slight thickening at distal end, longitudinal groove shallow. Direct development.

Distribution and Habitat.—East coast of North America from New England to Georgia; Introduced in British Columbia (Collin, 2001) and San Francisco Bay (Vokes, 1935). Low intertidal and shallow subtidal on rocks, shells and sea grass.

Description.—The shell is generally convex and oval with shape strongly dependent on habitat. Animals from sea grass blades are much smaller and more highly arched than those from rocks. Externally and internally brown, ranging from light tan to chocolate, usually with darker spots or streaks. Often purplish or grayish externally, especially near the apex, sometimes pale. Often with brown periostracum. The shelf is flat or slightly convex and the left side extends farther forward than does the right side. The margin is straight or slightly arched. Oval muscle scar just anterior to the shelf on the animal's right side. The slightly rostrate apex is usually directly posterior, slightly above the aperture and usually excavated ventral to the shelf. The smooth protoconch is often eroded. No sculpture other than growth lines. Length up to 20 mm.

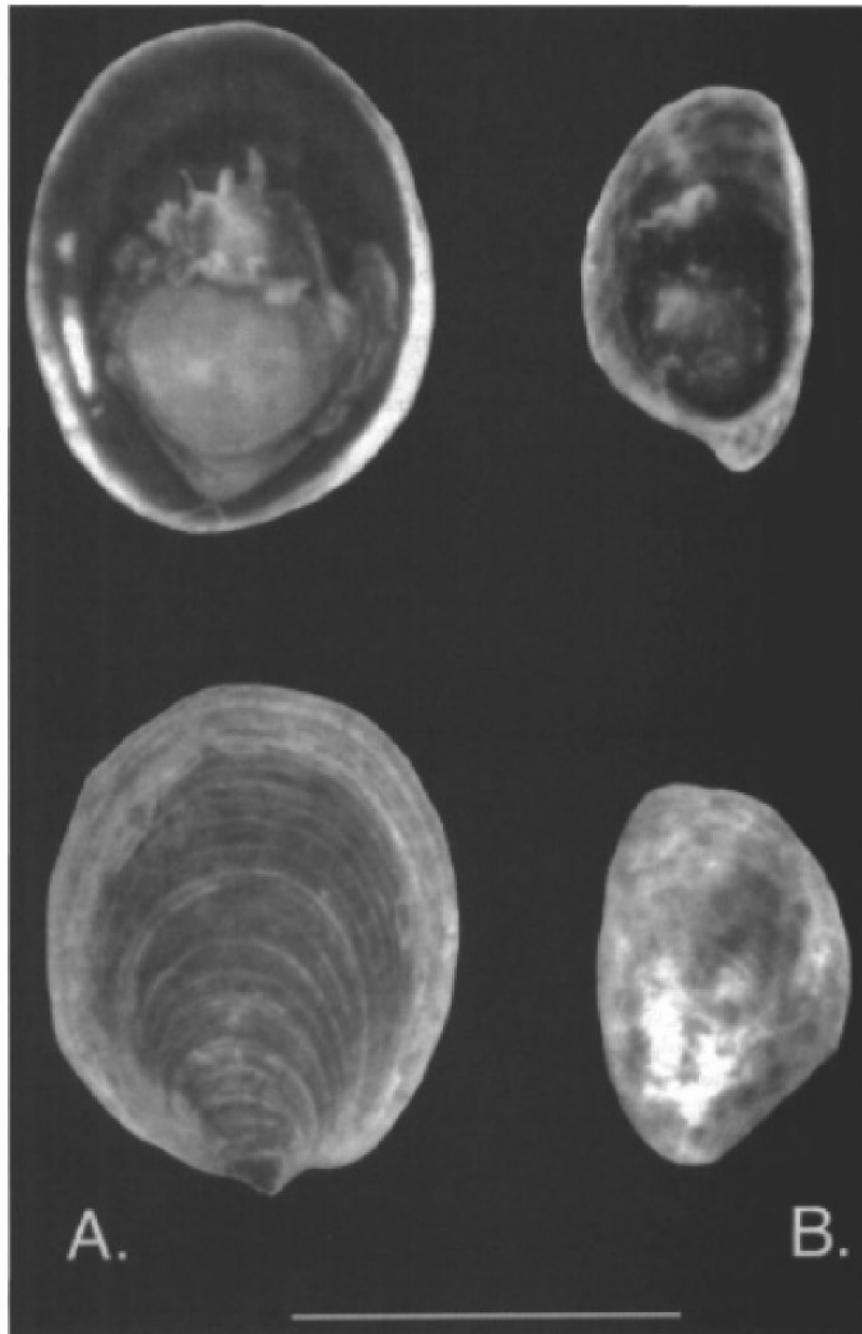


Figure 1. The neotype of *Crepidula convexa* Say and *Crepidula glauca* Say, ANSP A19269 left (A) and the holotype of *Crepidula ustulatulina* sp. nov. ANSP A19271 right (B). Scale bar = 10 mm.

Morphology.—Foot, mantle, neck lappets dark gray; tips of tentacles and lips opaque cream or yellow, in life. Osphradium darker than body. There are sometimes large yellow pigment splotches along the neck lappets and the edge of the mantle but these are not visible in preserved material. General morphology typical of all *Crepidula* and similar to that described in detail for *C. fornicata* (Werner and Grell, 1950) with the following exceptions. The gill extends half-way to three-quarters of the way to the end of the viscera. The anterior end of the style sac bulges dorsally into the mantle cavity. The viscera are covered with strikingly yellow or greenish yellow superficial tissue. The gill is black. Large shell muscle extends from the foot to the shell roof on the animal's right side. The osphradium is an evenly spaced, tightly packed, cluster of 10–20 monopectinate leaflets. The mesopodial flaps and propodium are especially well developed in females. The long and narrow food pouch lies at the mantle margin directly above head. Thin, tubular salivary glands extend from buccal mass to the nerve ring. The female genital papilla extends well into mantle cavity with a shallow but distinct groove, a slight distal thickening, and a pointed distal end. In females there are usually four sperm receptacles embedded in opaque yellow tissue. In males the slightly flattened penis tapers gradually to the distal end.

Radula.—Similar to radula of other *Crepidula* species (Collin, 2000a). Rachidian has 3–5 denticles on each side of the central cusp. The marginal tooth has 3–5 denticles on the inner side and 6–12 on the outer side. The inner lateral has 7–11 denticles on the inner side and 3–6 on the outer side. The outer lateral has 2–5 denticles on the inner side. There are no denticles on the outer side of the outer lateral.

Development.—The large eggs (280–300 μm , Hendler and Franz, 1971; Hoagland, 1986) produce typical directly developing embryos with a smooth shell, 950–1000 μm at hatching (Hendler and Franz, 1971; Hoagland, 1986; pers. observ.). The embryonic velum is a ciliated ridge at the base of the tentacle, slightly larger than in *C. adunca* (Collin, 2000b) with no pigmentation. Operculum absent. Embryonic kidney single cell. About 13–16 eggs/capsule, but the number of eggs per capsule increases with female size.

Discussion.—*C. convexa* Say 1822 and *C. glauca* Say 1822 have a long and intertwined history. After being recognized as distinct by Reeve (1859), they were synonymized by Verrill and Smith (1874; the first revisers) under the name *C. convexa*. However considerable debate ensued (Dall, 1889; Ford, 1889, 1890; Stone, 1892; Stearns, 1899). Part of the confusion is due to the vagueness of the original descriptions (Say, 1822). Both descriptions could fit individuals of either northern or southern species, with one important exception. In both the northern and southern clades the edge of the shelf is somewhat diagonal, extending further forward on the left side than on the right side. The shelf edge is straight or slightly curved. Say's description states that the edge of the shelf of *C. convexa* is "simply arquated" (arched or curved) and that the edge of the shelf in *C. glauca* is "widely contracted in the middle". This is somewhat unclear but as described for *C. glauca* it does not fit the shells of either the northern or southern species but is similar to the shelf of *C. fornicata*. However in Say's description of *C. fornicata*, which corresponds to *C. fornicata* in every other way, the shelf is described as reclivate (sloped). It appears, therefore, that the descriptions of the shelves of *C. glauca* and *C. fornicata* were exchanged in Say's paper. When this lapse is taken into account Say's description of *C. glauca* and *C. convexa* could both describe either the northern or southern species. As he does not appear to have collected material from along the Gulf coast (Say, 1822), it is

most likely that the majority of the shells in Say's collection were from the northern species and that his *C. glauca* and *C. convexa* represent situs forms of a single species.

Several other small speckled species of *Crepidula* have also been suggested as synonyms of *C. convexa*. The absence of any muscle scars on the syntypes of *Crepidula navicula* (Mörch, 1877) collected by Riise from St. Thomas (ZMUC GAS-237), and other possible syntypes collected by Hornbeck from Vieques on Isla Margarita (ZMUC collection) show that this species is distinct from *C. convexa*. Hoagland's *Crepidula* cf. *convexa* from Panama (Hoagland, 1986) also lacks muscle scars. *Crepidula cerithicola* Guppy 1894 from Trinidad and Tobago is a junior homonym of *C. cerithicola* C. B. Adams (1852) and is probably the same as *C. navicula*. The Japanese fossil species *Crepidula convexa* Yokoyama 1925 is a junior homonym of *C. convexa* Say.

Crepidula glauca Say, 1822
(Fig. 1)

Junior synonym of *C. convexa* Say, 1822

Fate of Original Type Material.—See above

Neotype.—ANSP A19269

Discussion.—*C. convexa* and *C. glauca* as described by Say (1822) are situs forms of the same species and have traditionally been considered simple synonyms. I designate the same individual as the neotype of both *C. convexa* and *C. glauca* in order to formalize this relationship and to ensure subsequent nomenclatural stability.

Crepidula ustulatulina new species
(Fig. 1, Table 1)

C. convexa Say Hoagland, 1977 in part; *C. cf. convexa* from Florida (Hoagland, 1984, 1986); *C. convexa* Southern species (Collin, 2001)

Holotype.—ANSP A19271; ethanol preserved female (Fig. 1); length 9.9 mm; width 5.7 mm; height 4.5 mm.

Type Locality.—Beach next to Mote Marine Laboratory, Lido Key, Florida (27°20'N, 82°35'W). On small rocks, shells and turtle grass in about 40 cm water.

Live Material Examined.—Lido Key, Florida, ANSP A19272; FMNH 282190, 282191, 282253, 282254, 282268; Key Largo, Florida FMNH 282249, 282250; Fort Pierce, Florida FMNH 282251, 282252; Galveston, Texas FMNH 282307; Port Aransas, Texas FMNH 282257, 282258; Cancún, Mexico FMNH 282315; Dzilam de Bravo, Mexico FMNH 282316.

Diagnosis.—*C. ustulatulina* can be distinguished from other species of *Crepidula* by the following suite of characters. Shell small convex; usually cream with distinct chestnut brown spots or streaks, sometimes brown overall with darker spots. Inside markings same as exterior. Body gray, sometimes with yellowish splotches. Shelf margin extends further forward on the animal's left, or sometimes straight across the shell, margin often slightly arched. Large oval muscle scar anterior to shelf on animal's right. Apex directed posterior, slightly rostrate, excavated ventral to shelf. Salivary glands small, tubular nestled

Table 1. Summary of species differences

Character	<i>Crepidula convexa</i>	<i>Crepidula ustulatulina</i> n. sp.
Maximum length	20 mm	13.2 mm
Shell color	Usually brown or purplish brown often with darker spots or streaks	Usually white with chestnut spots, sometimes tan or brown
Stage at hatching	Crawling juvenile	Pediveliger
Egg size	280–300 μm	300–340 μm
Hatching size	950–1000 μm	744 μm
Osphradium	10–20 filaments	5–11 filaments
Salivary glands	extending along neck	around buccal mass

around buccal mass. Female genital papilla with shallow epithelial groove and blunt end. Embryos hatch as pediveligers.

Distribution and Habitat.—Throughout the Gulf of Mexico and along the east coast of Florida north at least to Fort Pierce. Low intertidal and shallow subtidal. Often on oyster shells at the base of mangroves, columbellids in sea grass, cerithiids, and trash.

Description.—The shell is generally convex and oval with shape strongly dependent on habitat. Externally and internally usually white with chestnut-brown spots or streaks. Sometimes tan or brown with darker markings. Periostracum pale and thin if visible. Those attached to other small gastropods are usually smaller and more convex than those living on sea grass and are often compressed on left side. Shelf white, flat or slightly convex, left side usually extends somewhat farther forward than does the right side. Shelf margin straight or slightly bowed. Oval muscle scar just anterior to the shelf on the animals right side. The small apex is usually directly posterior, slightly rostrate, excavated ventral to the shelf. Protoconch smooth, often eroded. No sculpture other than growth lines. Length to 13.2 mm.

Morphology.—External body color is light to dark gray with opaque white or cream on the tips of the tentacles and the lips. Usually large yellow pigment splotches on the mantle, neck and sometimes foot, visible only in life. Osphradium is often darker than surrounding tissue. General morphology is typical of all *Crepidula* and is similar to that described in detail for *C. fornicata* (Werner and Grell, 1950). The black gills extend half-way to three-quarters of the way to the end of the visceral mass. Large shell muscle extends from the foot to the shell roof on the animal's right side. Osphradium with 5–11 tightly-packed, evenly-spaced monopectinate leaflets. Mesopodial flaps and propodium especially well developed in females. Long and narrow food pouch at mantle margin directly above head. Tubular salivary glands nestled around buccal mass. Style sac does not bulge dorsally into the mantle cavity anteriorly. Female genital papilla extends well into mantle cavity with a shallow groove and blunt end. Penis tapers evenly towards distal end.

Radula.—Similar to radula of other *Crepidula* species (Collin, 2000a). Rachidian has 3–5 denticles on each side of the central cusp. In very small animals there may be as few as two denticles. The marginal tooth has 3–4 denticles on the inner side and 5–10 on the outer side. The inner lateral has 5–11 denticles on the inner side and 2–5 on the outer side. The outer lateral has 1–4 denticles on the inner side. Usually there are no denticles on the outer side of the outer lateral but the occasional tooth has a single denticle on the outer side. Radulae from larger animals have slightly more teeth but there is more variation among teeth within an individual than there usually is between individuals.

Development.—The large eggs (300–340 μm $n = 8$; 1 female pers. observ.; ~300 μm according to Hoagland 1984) produce typical direct developing embryos with a smooth shell, and an average length of 744 μm ($n = 31$; five females; 630–880 μm ; 630–700 μm in Hoagland 1984; 840 μm in Hoagland 1986) at hatching. The large embryonic velum is not absorbed prior to hatching and the embryo hatches as a swimming pediveliger. The velum has 5–7 large yellow pigment spots just medial to the food groove. Operculum absent. Embryonic kidney single. The pediveliger settles a few minutes to several hours after hatching. The velum contracts and is subsequently absorbed. Yellow pigment from the velum forms dense patches along the neck on each side of the esophagus. Two broods from Mote Marine Lab, Florida, developed a large embryonic velum which was absorbed prior to hatching, in the laboratory. This also occurred in two broods from Key Largo while the other broods hatched as swimming larvae. Between 3 and 16 eggs per capsule; the number of eggs per capsule increases with female size.

Etymology.—The species name *ustulatulina* is a double diminutive of the Latin *ustulata* (a burnt brown color) meaning small and slightly burnt, referring to the smaller size and fewer brown spots or streaks on the shell of this species as compared to *C. convexa*.

Discussion.—Not *C. convexa* Yokoyama 1925, *C. cf. convexa* from Panama of Hoagland (1986), *C. cerithicola* Guppy 1894, or *C. navicula* (Mörch 1877), as discussed above.

ACKNOWLEDGMENTS

I thank R. Bieler, B. Chernoff, A. Kohn, R. Robertson, P. Willink and an anonymous reviewer for comments on the manuscript, G. Rosenberg for discussion, the curators and collection managers of USNM, BMNH, CAS, ANSP, MCZ, ZMUC and LACM for loans of type material in their care and the BMNH, FMNH, and ANSP for accepting voucher material for this study. I am especially grateful to T. Rawlings for help in the field and logistical support and S. Padowitz for helping me collect the neotype of *C. convexa*. Financial support for this research was provided by NSF (DIG DEB #9972555) and the National Geographic Society (#6335-89).

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DATE SUBMITTED: September 19, 2000.

DATE ACCEPTED: July 9, 2001.

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