Taxonomy and phylogeny of western Atlantic Lucinidae: new genus for *Lucina costata* d'Orbigny, 1846, a new species of *Ferrocina* and neotype designation for *Venus orbiculata* (Montagu, 1808)

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ABSTRACT

A new genus, *Clathrolucina* Taylor and Glover, is proposed for the widely distributed western Atlantic species *Lucina costata* d'Orbigny, 1846, which has previously been placed in *Codakia*, *Ctena*, and *Parvilucina*. Molecular evidence indicates a closer relationship to *Radiolucina* and *Lucinisca*. A new species, *Ferrocina garciai* Taylor and Glover, is described from submerged pinnacles off the coasts of Louisiana and Alabama. It is similar to *Ferrocina* species described from the western Pacific and, in molecular analysis clusters, with *Parvilucina* and *Bathyaustriella*. Unusual features of this species include the large ctenidia and the lateral coiled pouches of the visceral mass. A neotype is designated for *Lucina orbiculata* Montagu, 1808 aka *Ctena orbiculata*, an abundant shallow water lucinid of the western Atlantic. The original type material is missing, the type locality is erroneous and considerable doubt exists about the identity of this species.

INTRODUCTION

More than 40 species of Lucinidae, well known for their chemosymbiosis with sulphide-oxidizing bacteria housed in the ctenidia (Taylor and Glover 2006; Heide et al., 2012), are recorded from the tropical–subtropical western Atlantic, including deeper water species. Many of the shallow water species are relatively well known and have been the subject of important studies of the symbiosis (e.g. Giere, 1985; Fisher and Hand, 1984; Distel and Felbeck, 1987; Frenkiel and Mouëza, 1995; Frenkiel et al., 1996; Gros, Frenkiel and Mouëza, 1998; Gros et al., 1998, 2012; Gros Liberge and Felbeck, 2003, Brissac et al., 2009). Nevertheless, there are unresolved taxonomic and nomenclatural problems even amongst abundant lucinids of the region including their phylogenetic relationships. Greater taxonomic refinement may also be needed since molecular analyses of other bivalves such as Arcidae and Mytilidae have revealed that species previously regarded as widespread in the western Atlantic are in fact complexes of genetically distinct taxa (Lee and Ó Foighil, 2005; Marko and Moran, 2009). From morphological evidence, species complexes are suspected within Lucinidae in the *Lucina pensylvanica* group (Gibson Smith and Gibson Smith, 1982) and *Ctena orbiculata* group (Taylor et al., 2011). Additionally, offshore exploration at hydrocarbon seeps has recovered several new Lucinidae for the region (Taylor and Glover, 2009).

In this paper we have three objectives. Firstly, we clarify, using molecular evidence, the phylogenetic position of "*Parvilucina*" *costata* (d'Orbigny, 1846), an abundant species that has been variously and confusingly classified in five different genera. A new genus is proposed for this species. Secondly, we describe an unexpected new species, dredged from depths of 58–86 m off Alabama and Louisiana. This lucinid is unlike any other from the western Atlantic and is most similar to species of *Ferrocina* from the western Pacific (Glover and Taylor, 2007; in press). Thirdly, we designate a neotype for *Venus orbiculata* Montagu, 1808 (i.e. *Ctena orbiculata*) perhaps the most abundant lucinid of the subtropical-tropical western Atlantic. This is necessary because the type material is missing, the original figure is equivocal, the type locality is in eastern Scotland and there is likely a complex of morphologically similar but genetically distinct species living in the western Atlantic.

MATERIALS AND METHODS

Molecular Methods: Two new sequences from the 28S rRNA nuclear gene and mitochondrial cytB genes were obtained from a single specimen of *Ferrocina garciai* (GenBank numbers: KF793275, KF793276). Extraction of DNA, PCR methods, and sequence editing were as in Taylor et al. (2011). The new sequences were analyzed along with a subset of previously published sequences primarily from Taylor et al. (2011), although distant outgroups and multiple exemplars of species were removed. The alignment of cytB was unambiguous but 28S required alignment with MAFFT (v 6.864; Katoh et al. 2002; online: http://mafft.cbrc.jp/alignment/server/). The G-INS-I option was used with '1PAM / κ=2' because the species were from two closely related subfamilies. Gap opening penalty was 1.5 with an offset value of 0.1 as long gaps were not expected based on previous analyses. A total of 1453 bp remained in the alignment after Gblocks was used to remove ambiguously aligned regions (97% of the original 1497 positions) (0.91b, Castresana, 2000; http://molevol.cmima.csic.es/castresana/Gblocks_server.html; using options for a less stringent selection).

A species tree was constructed using concatenated sequences from both genes and Bayesian inference as implemented in MrBayes (v. 3.2.1, Huelsenbeck and Ronquist, 2001). Nucleotide substitution models for both genes were GTR+I+G as determined by MrModelTest (v 2.1, J. Nylander, http://www.abc.se/~nylander). Bayesian analyses and tests for stationarity were performed following protocols in Williams (2012).

Abbreviations: NHMUK: The Natural History Museum, London; MNHN: Muséum National d'Histoire Naturelle, Paris; PRI: Paleontological Research Institution, Ithaca, New York; USNM: National Museum of Natural History, Washington; YPM: Peabody Museum, Yale University, New Haven; H: shell height; L: shell length; PI: Protoconch 1; PII: Protoconch 2; SEM: scanning electron microscopy; T: tumidity.

RESULTS

1. New Genus for *Lucina costata*

The lucinid species often called *Ctena* or *Parvilucina costata* (d'Orbigny, 1846) is widely distributed in the western Atlantic, ranging from Bermuda, North Carolina, through the Caribbean and Central America to Rio de Janeiro (Britton 1970; Schweimanns and Felbeck, 1985; Rios, 1994; Vokes and Vokes, 1984; Redfern, 2001; Hauser et al., 2007; Mikkelsen and Bieler, 2007). It is often abundant in shallow-water seagrass beds (Jackson, 1972; 1973). Despite being a common and widely distributed species, its systematic position is uncertain. It has been variously placed in the genera *Codakia*, *Ctena*, *Jagonia*, *Parvilucina*, and *Lucina* in taxonomic and biological literature. In the last major taxonomic revision of western Atlantic species, Bretsky (1976) listed some shell characters to differentiate *L. costata* from *Ctena* but placed it questionably in *Parvilucina*.

In common with all other investigated Lucinidae, *Lucina costata* possesses symbiotic sulphide-oxidizing bacteria housed in the ctenidia. Details of ctenidial structure and location of symbionts in the species were given by Giere (1985) and the bacteria characterized molecularly by Distel et al. (1994) (as *Codakia costata* GenBank L25712). Several other anatomical features of the species were described by Allen (1958).

Samples of *L. costata* from Guadeloupe and Bocas del Toro, Panama, were included in a molecular analysis of a wide range of lucinid species with broad taxonomic coverage (Taylor et al., 2011). The results (Figure 1) indicate that it does not group with *Codakia*, *Ctena*, *Lucina*, or *Parvilucina* but instead forms a clade with *Radiolucina* and *Lucinisca* species within the subfamily Lucininae. We are therefore introducing a new genus to accommodate *Lucina costata* and two fossil species.

SYSTEMATICS

Family Lucinidae Fleming, 1828
Subfamily Lucininae Fleming, 1828

Clathrolucina new genus Taylor and Glover

Type Species: *Lucina costata* d'Orbigny, 1846 here designated.

Diagnosis: Shell small, L to 15 mm, subcircular, inflated. Sculpture of numerous radial ribs of varying thickness, prominent ribs often bifurcated, crossed by fine commarginal lamellae. Lunule heart shaped, short. Hinge with two cardinal teeth and large anterior and posterior lateral teeth in each valve. Anterior adductor scar broad, medium long, ventrally detached from pallial line for about ½ length. Inner shell margin finely dentate.

Etymology: *clathrus*, Latin for basket and *Lucina*, in reference to the basket weave appearance of the external sculpture.

Remarks: Molecular analysis (Figure 1) shows that *Clathrolucina costata* falls within the subfamily Lucininae and forms a subclade with *Radiolucina* and *Lucinisca* (Taylor et al., 2011) rather than its previous placements within *Ctena* and *Codakia* based on morphology. There are superficial shell characters in common with *Ctena* Mörch, 1861 (type species: *Codakia (Jagonia) mexicana* Dall, 1901) including the bifurcating radial ribs and posterior dorsal areas that lack radial sculpture. The anterior adductor scar of *Ctena* is longer and more widely detached from the pallial line (Figure 25). *Jagonia* Récluz, 1869 (type species: *Venus eburnea* Gmelin, 1791) has been used for *C. costata* by earlier authors such as Dall (1901) and Chavan (1937) but it is now considered a junior synonym of *Ctena* (Bretsky, 1976). In more recent publications, *Clathrolucina costata* has been classified

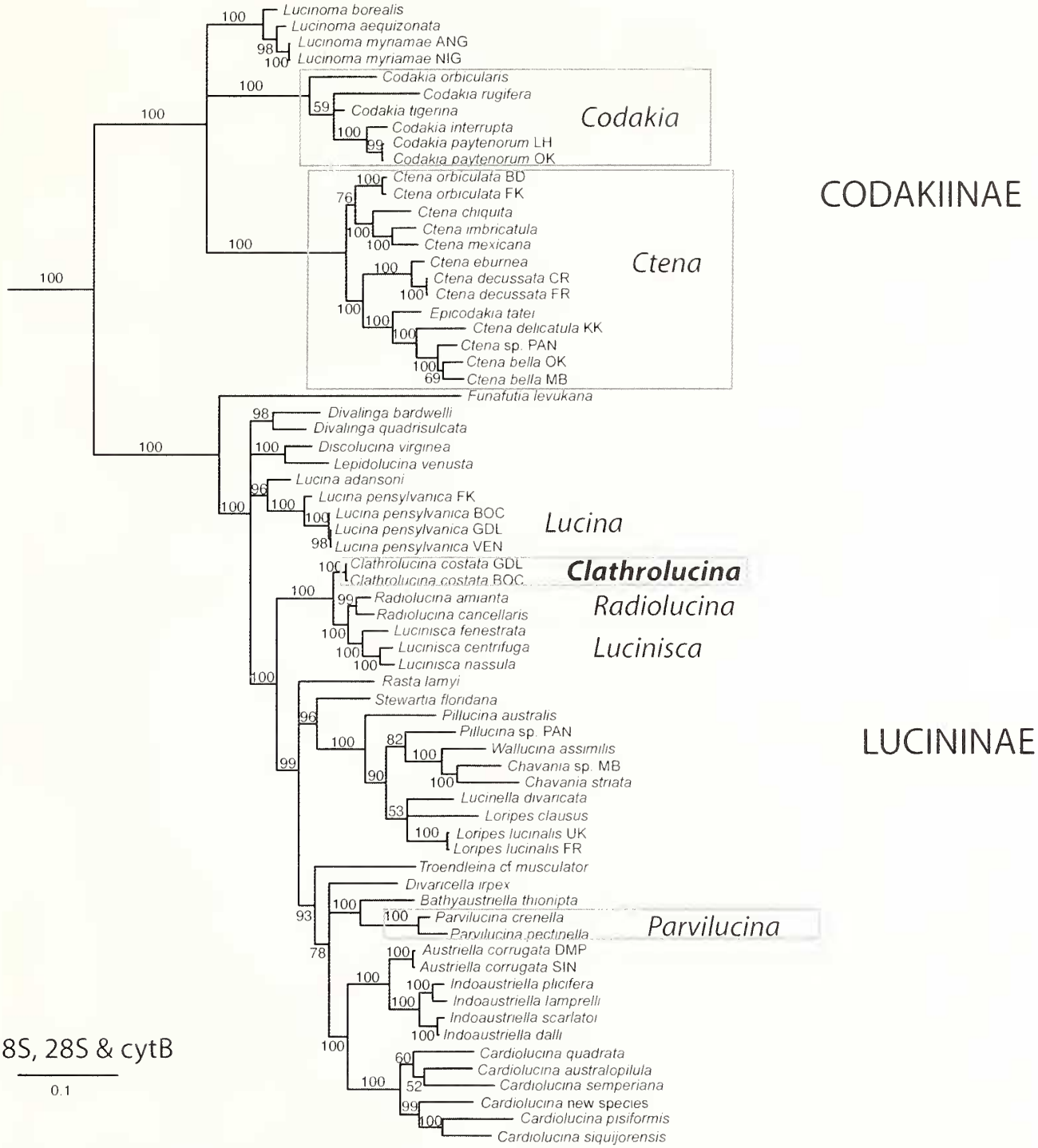


Figure 1. Molecular phylogeny of Lucinidae produced by Bayesian analysis of concatenated sequences of 18S rRNA, 28S rRNA, and cytochrome *b* genes (adapted from inset in figure 4 from Taylor et al., 2011). The position of *Clathrolucina costata* is highlighted, as are the genera where it has previously been assigned. Subfamily names are indicated on the right. Further details given by Taylor et al. (2011).

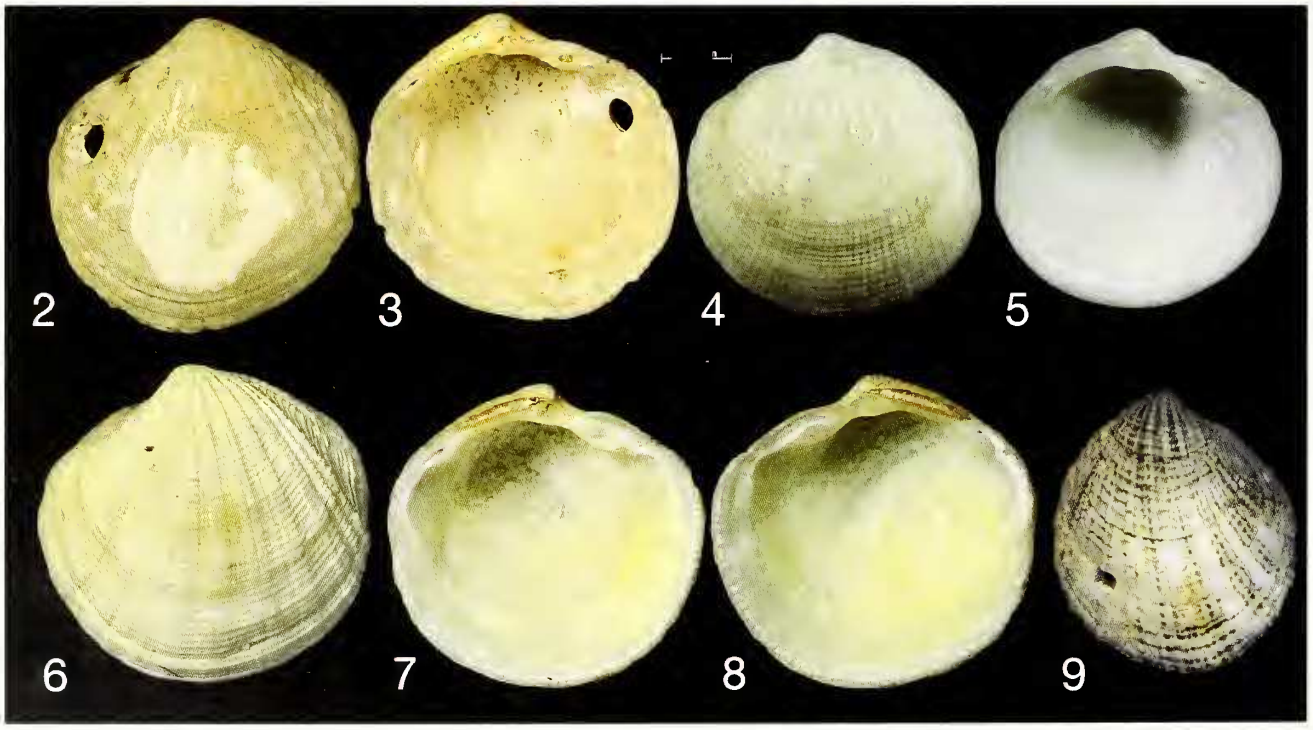
as a species of *Parvilucina* Dall, 1901 (type species: *Lucina tenuisculpta* Carpenter, 1864, from the northeastern Pacific). However, in the molecular analysis, although *C. costata* and two western Atlantic *Parvilucina* species occur in the same major lucinid clade (subfamily Lucininae; Taylor et al., 2011), they are not closely related. *Parvilucina* species have fine radial ribs that do not bifurcate, an extremely short anterior adductor

scar detached for only about ¼ of length (Figure 26), and the shell margin is finely denticulate. *Clathrolucina* groups with *Lucinisca* Dall, 1901 (type species: *Lucina nassula* Conrad, 1846) and *Radiolucina* Britton, 1972 (type species: *Phacoides (Bellucina) amiantus* Dall, 1901) from the western Atlantic. *Lucinisca* has fine, non-birfurcating radial ribs, crossed by low, thin commarginal lamellae forming raised scales where they cross the radial ribs. Radial ribs project beyond the ventral shell margin as denticles. The lunule in the type species is short and deeply inset and the anterior adductor scar is ventrally detached for about ½ of its length (Figure 24). The three living species of *Radiolucina* were recently reviewed by Garfinkle (2012); *Radiolucina amianta* has about 9–11 prominent radial ribs with deep interspaces, a short heart-shaped lunule with the anterior adductor scar detached for about ½ of length (Figure 23). The inner shell margin is coarsely denticulate. Dall (1901) originally placed *R. amianta* in a subgenus *Bellucina* (= *Cardiolucina* Sacco, 1901) but Britton's (1972) recognition of *Radiolucina* is corroborated by molecular results in which *Radiolucina amianta* and *R. cancellaris* are distantly separated from *Cardiolucina* species (Taylor et al., 2011).

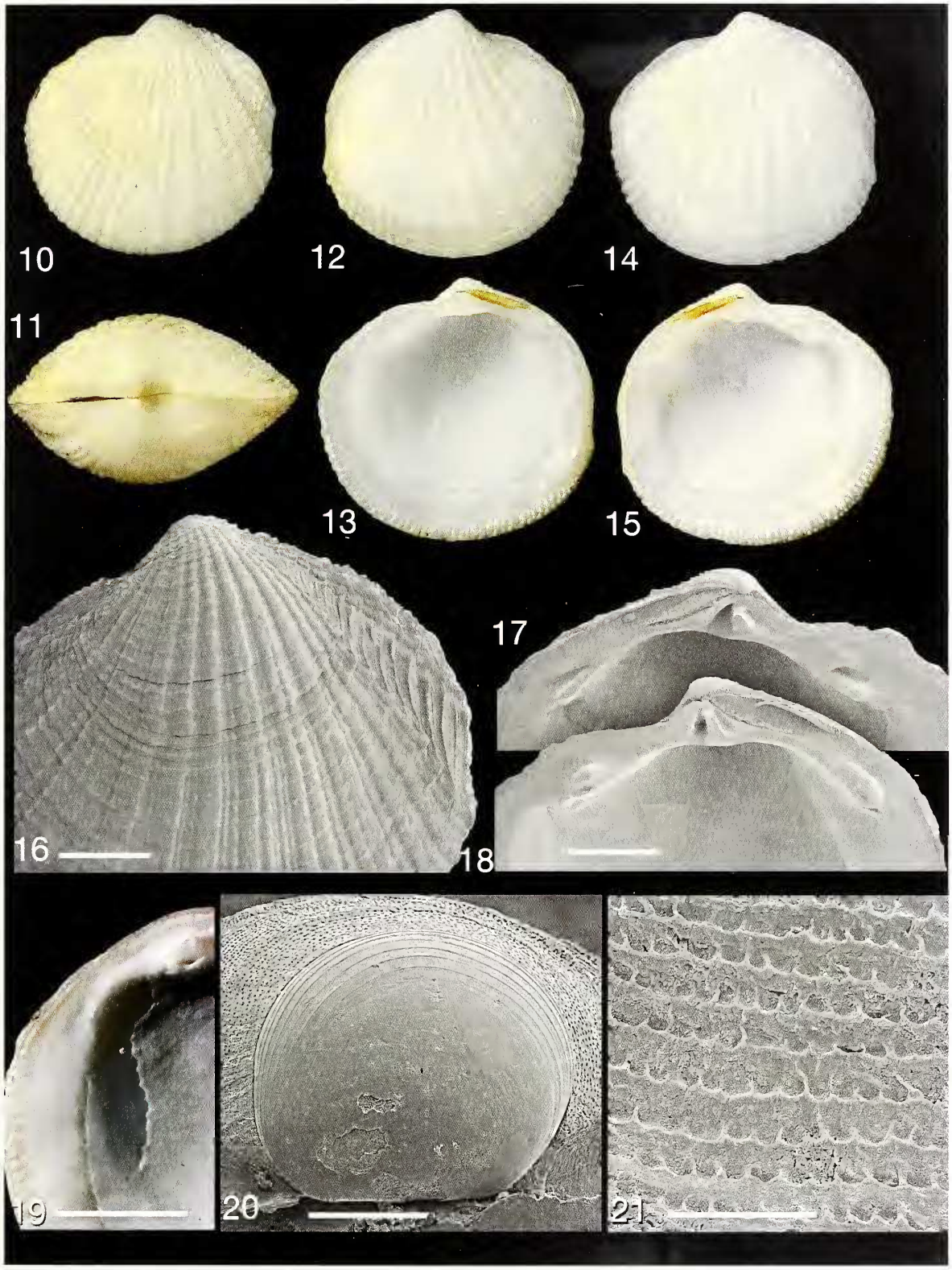
Included Species: *Codakia (Jagonia) vendryesi* Dall, 1903 from the Pliocene, Bowden Formation, Jamaica (3 syntypes USNM 135720; see Woodring 1925: 109 pl. 14, figs. 1–4.) and *Codakia (Jagonia) umbonicostata* Weisbord (1964: 234, pl. 31, figs 7–8) from the Pliocene of Venezuela (holotype PRI 1519a).

***Clathrolucina costata* (d'Orbigny, 1846)**
(Figures 2–22)

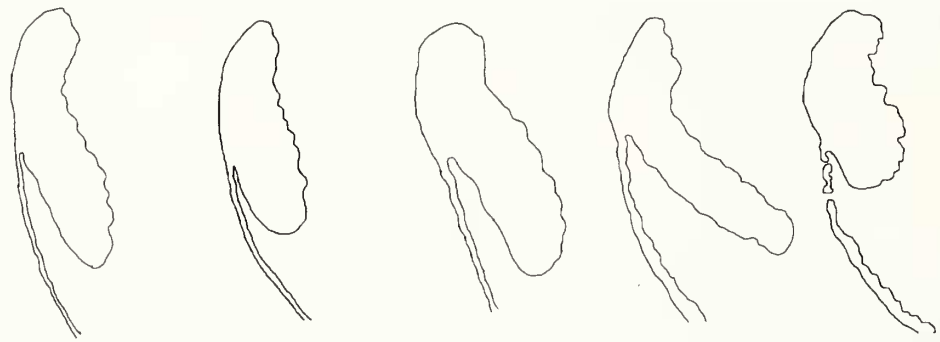
Lucina costata d'Orbigny, 1846: 586, 1853: 296, pl. 27, figs 40–42.
Lucina antillarum Reeve, 1850: pl. 10, fig. 37.
Lucina textilis Philippi, 1850: 104, pl. 2, fig. 7.
Lucina nux Verrill and Bush, 1900: 518, pl. 58, figs 12, 13.
Codakia (Jagonia) costata.—Dall, 1901: 800; Lamy, 1920: 262–263).
Jagonia (Jagonia) costata.—Chavan, 1937: 260.
Codakia (Codakia) costata.—Abbott, 1954: 390; Vokes and Vokes, 1984: 38, pl. 38, fig. 5.
Codakia costata.—Allen, 1958: 426, fig. 64; Warmke and Abbott, 1961:178; Abbott, 1974: 460, fig. 5298; Rios, 1994: 253, pl. 87, fig. 1236.
Parvilucina (Parvilucina) costata.—Britton, 1972: fig. 5.
Lucina (Parvilucina?) costata.—Bretsky, 1976: 263, pl. 28, figs 1–5.
Parvilucina costata.—Redfern, 2001: pl. 91, figs. 887 A, B; Jensen and Pearce, 2009: 330; Turgeon et al., 2009: 727.
"Parvilucina" costata.—Mikkelsen and Bieler, 2007: 234.
Ctena orbiculata.—Tunnell et al., 2010: 341 and figure, non Montagu, 1808.



Figures 2–9. Type material of *Clathrolucina costata*. **2–3.** Exterior and interior of the holotype of *Lucina costata*, Rio de Janeiro, Brazil, NHMUK 1854.12.4.765, L= 12.8 mm. **4–5.** Paratype of *L. costata*, exterior and interior of left valve, St. Thomas, NHMUK 1854.10.4.564. L = 8.9 mm. **6–8.** Syntype of *Lucina antillarum* NHMUK1963192-3, exterior of left valve and interior of left and right valves L = 12.0 mm. **9.** Holotype *Lucina nux* Bermuda, YPM 8760, exterior of right valve. L = 7 mm.



Figures 10–21. *Clathrolucina costata* from Bocas del Toro, Panama, NHMUK 20130562. **10.** Exterior of left valve, L = 8.1 mm. **11.** Dorsal view of shell in Figure 10. **12–13.** Exterior and interior of right valve, L = 8.3 mm. **14–15.** Exterior and interior of left valve, L = 8.3 mm. **16.** Detail of sculpture. Scale bar = 1.0 mm. **17–18.** Detail of hinge teeth of left and right valves. Scale bar = 1.0 mm. **19.** Detail of anterior adductor muscle scar. Scale bar = 2 mm. **20.** Protoconch, note micropunctae of post-settlement shell. Scale bar = 50 μm. **21.** Microsculpture. Scale bar = 10 μm.



Figures 22–26. Outline drawings of anterior adductor muscle scars. Traced from digital images.

Types: *Lucina costata*, holotype, NHMUK1854.12.4.765, one left valve, L = 12.8 mm, H = 12.7 mm, T = 4.5 (Figures 2–3); paratypes NHMUK 1854.10.4.564, St Thomas, US Virgin Islands, 8 valves (4R, 4L); Gray Cat No. 497 (Figures 4–5); *Lucina antillarum*, 3 whole syntypes, NHMUK 1963192-3 (Figures 6–8), L = 12.0 mm, 15.1 mm, 12.4 mm, St. Johns, Antigua; *Lucina nux* holotype, YPM 8760, single right valve, L = 7 mm, H = 8 mm, T = 3 mm (Figure 9).

Type Locality: d'Orbigny (1846: 586) cited Baie de Rio Janeiro near St Christophe and gave other localities – Antilles and Cuba.

Description: Shell small (L to 15.2, H to 14.3 mm), subcircular (H/L=0.95, n=10) moderately inflated, posterior margin slightly truncated, umbones prominent. Sculpture of numerous (ca. 35) rounded radial ribs, varying in width, that occur in bundles of two to three ribs, sometimes bifurcated ventral to umbo (Figure 16). Ribs crossed by low, regularly spaced commarginal lamellae. Posterior dorsal area without radial ribs but with more prominent commarginal lamellae, posterior dorsal margin with two low radial ribs with raised scales. Anterior dorsal area marked by lower and broader radial ribs. Lunule short, heart shaped, smooth, slightly asymmetrical with right side larger. Ligament, external, short, set in shallow groove. Microsculpture of rows of shallow pits (Figure 21) or micropunctate in juvenile shell (Figure 20). Protoconch (Figure 20): PI = 121 μm, PI + PII = 146 μm, PII with 5–8 growth increments. Hinge (Figures 17–18): LV with 2 cardinal teeth, the anterior larger, prominent anterior and posterior lateral teeth; RV with 2 cardinal teeth, the posterior much larger and slightly bifid, anterior and posterior laterals prominent. Anterior adductor muscle scar broad (Figures 19, 22), medium-long, with rounded ventral tip, ventrally detached from pallial line for about ½ of length and diverging at an angle of 5–10°. Posterior adductor scar reniform. Pallial blood vessel track visible. Pallial line entire. Inner shell margin finely denticulate. Colour yellowish-white externally, white internally.

Distribution: Western Atlantic and throughout Caribbean from North Carolina to Santa Catarina, Brazil (Britton, 1970; Rios, 1994).

Remarks: The holotype is a worn shell in poor condition but has the features of the species. Other d'Orbigny specimens in NHMUK from St. Thomas and regarded as paratypes are worn but in better condition. No locality was given for *Lucina textilis* Philippi, 1850 and the type has not been located. Syntypes of *Lucina antillarum* Reeve, 1850 are in good condition and one is figured (Figures 6–8). *Lucina nux* Verrill and Bush, 1900 described from Bermuda (Figure 9) is regarded as a higher than long shape variant of *C. costata*.

2. A New Species from the Northern Gulf of Mexico

This unusual species, a surprising addition to the shallow water bivalve fauna of the Gulf of Mexico sent to us by Emilio Garcia, was dredged from submarine pinnacles on the Alabama and Louisiana shelf.

SYSTEMATICS

Subfamily Lucininae Fleming, 1828

***Ferrocina* Glover and Taylor, 2007**

Type species: *Ferrocina multiradiata* Glover and Taylor, 2007.

Diagnosis: Shell to 20 mm, thin, subovate, posteriorly truncate, sculpture of numerous fine to indistinct radial ribs crossed by fine commarginal threads. Hinge plate thin, small single cardinal tooth in RV, two in LV, lateral teeth small or absent. Anterior adductor scar short, detached for 1/3 of length. Interior shell margin coarsely to finely dentate. Color bright to pale orange or rusty

red-brown, external color paler, often blotchy, stronger in umbonal area.

Included species: *Ferrocina multiradiata*, (Vanuatu, Fiji, New Caledonia): *Ferrocina* new species Glover and Taylor (in press), Philippines; and *F. brunei* from off Brunei (Taylor and Glover, 2013).

Remarks: This distinctive, rare, and highly colored genus with fine radial ribs was originally described from Fiji, New Caledonia, and Vanuatu with other species known from the Philippines and Brunei.

***Ferrocina garciai* Taylor and Glover new species**
(Figures 27–44)

Type Material: Holotype (Figures 27–34), USNM 1227857, L = 19.7 mm, H = 19.0 mm, T = 5.2 mm, from type locality; Paratype 1 (Figures 35–37), USNM 1227858, L = 13.9 mm, H = 11.7 mm, T = 3.5, off Alabama, 29°15.681′ N, 88° 20.237′ W, 78–86 m, dredged by R/V Pelican, 27 August 2012; Paratype 2 (Figures 38–39), Emilio García collection 30783, L = 11.7 mm, from type locality.

Type Locality: USA, northern Gulf of Mexico, off Louisiana, 27°56.835′ N, 92°01.464′ W, 58 m, rubble, dredged by R/V Pelican, 26 August 2012.

Description: Small, L = 14.0 mm, H = 11.7 mm, subcircular, slightly longer than high, less mature paratypes more elongate with posterior margin truncate; thin-shelled, moderately inflated, T/L = 0.26. Shallow posterior sinus and posterior dorsal area. Sculpture of numerous fine, low, radial ribs that become obscure on ventral parts of shell, commarginal sculpture of growth lines and halts. Posterior dorsal area without radials. Protoconch (Figure 32): PI =113 μm, PI+PII =160 μm, PII with many growth increments. Lunule long, slightly asymmetric, larger in RV. Ligament long, set in shallow groove. Hinge narrow: RV with single cardinal tooth and irregular anterior folds; tiny posterior lateral teeth present on smaller paratype; LV with two cardinal teeth and anterior folds but posterior laterals present on paratype. Anterior adductor scar medium long, ventrally detached from pallial line for ½ of length at angle of ca. 10° (Figure 40). Pallial line entire, dorsally lobate. Posterior adductor scar ovoid. Impression of pallial blood vessel prominent, broad, terminating ventral to anterior adductor scar (Figures 40–41). Shell margin finely dentate and linearly grooved. Exterior color pale pink-orange to off white, umbonal area darker. Interior colour uniformly bright apricot-orange, extreme shell margin creamy white.

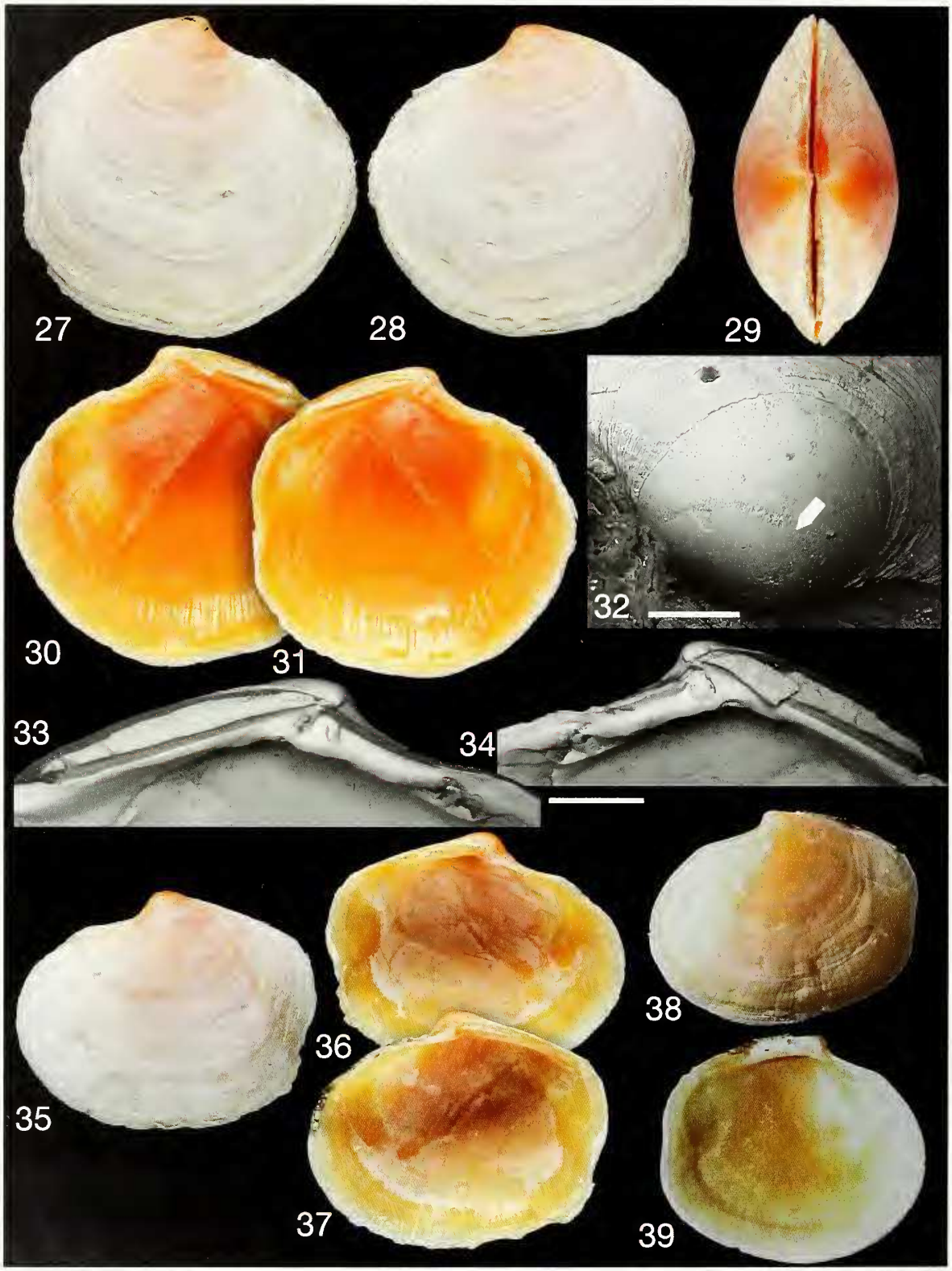
Anatomy: Very large, thick ctenidal demibranchs occupying most of mantle cavity (Figure 42). Mantle gills absent. Foot large, fat, with short heel. Body wall immediately anterior to the foot extended on each side into posteriorly directed "ramshorn-like" coiled projection (Figures 43–44). Labial palps as short ridges. Rectum passing dorsally and posterior to posterior adductor muscle. Posterior exhalant aperture with an inverted tube, inhalant aperture edged with papillae on middle mantle fold. Posterior mantle fusion short.

Phylogenetic Position: The results of a molecular analysis using sequences from two genes, 28S rRNA and cytochrome B (Figure 45), show the position of *Ferrocina garciai* (tissue from holotype) in relation to a diverse range of lucinid species from the subfamilies Codakiinae and Lucininae. Other more distantly related lucinid subfamilies of Pegophyseminae, Leucosphaerinae, and Myrteinae (see Taylor et al., 2011) were excluded from this analysis. The results show that *Ferrocina garciai* belongs in the Lucininae and that it is sister to two species of *Parvilucina* from the western Atlantic (PP=100%). This subclade is sister to *Bretskya* sp. and *Bathyaustriella thionipta* (PP=100%). The four genera are in turn a sister clade to *Troendleina* and *Epicodakia falklandica* although support is lower (PP=82%).

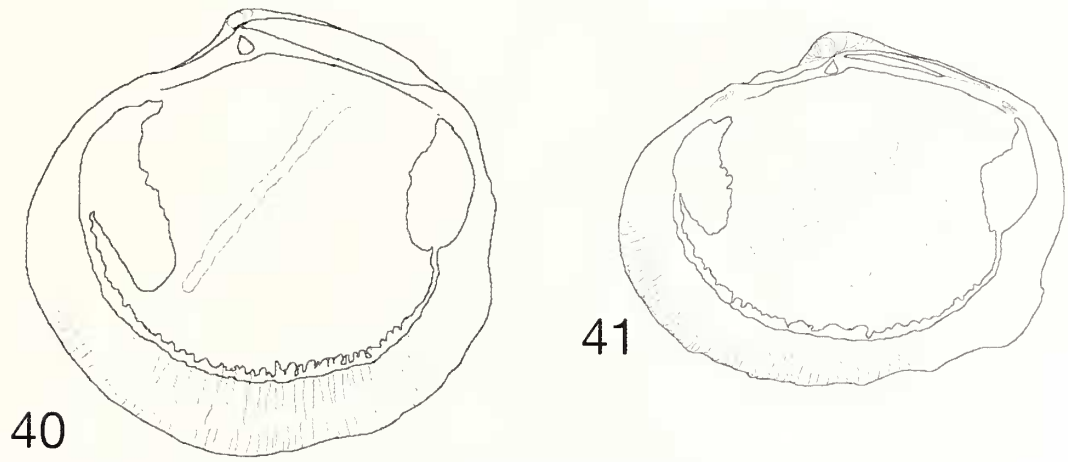
Bretskya (type species: *B. scapula* Glover and Taylor, 2007) is an Indo-Pacific genus of irregularly shaped lucinids that are strongly associated with sunken wood (Glover and Taylor, 2007; in press). *Bathyaustriella thionipta* is recorded from a 500 m deep hydrothermal vent on the Kermadec Ridge off New Zealand (Glover et al., 2004). *Troendleina* (type species: *T. marquesana* Cosel and Bouchet, 2008) includes several deeper water species (150–800 m) from the Pacific Ocean (Cosel and Bouchet, 2008, Glover and Taylor, in press). *"Epicodakia" falklandica* Dell, 1964 from the southern Atlantic occurs at depths of 100–400 m but the molecular results show that it should not be classified in the Codakiinae as *Epicodakia* but in the Lucininae with uncertain generic placement. The two *Parvilucina* species analyzed are known from shallow water habitats (1–100 m) in the western Atlantic.

Distribution and Habitat: The three individuals of *Ferrocina garciai* were dredged from submerged calcareous pinnacles and banks at depths of 58–86 m off Louisiana and Alabama. These pinnacles occur along the northern Gulf of Mexico shelf from Alabama to Texas and form islands of hard substrate surrounded by mud (Parker and Curray, 1956). The unusual molluscan faunas of the pinnacles, including many endemic species and new records for the Gulf, have been documented by Garcia (2000; 2008) and Garcia and Lee (2002; 2013).

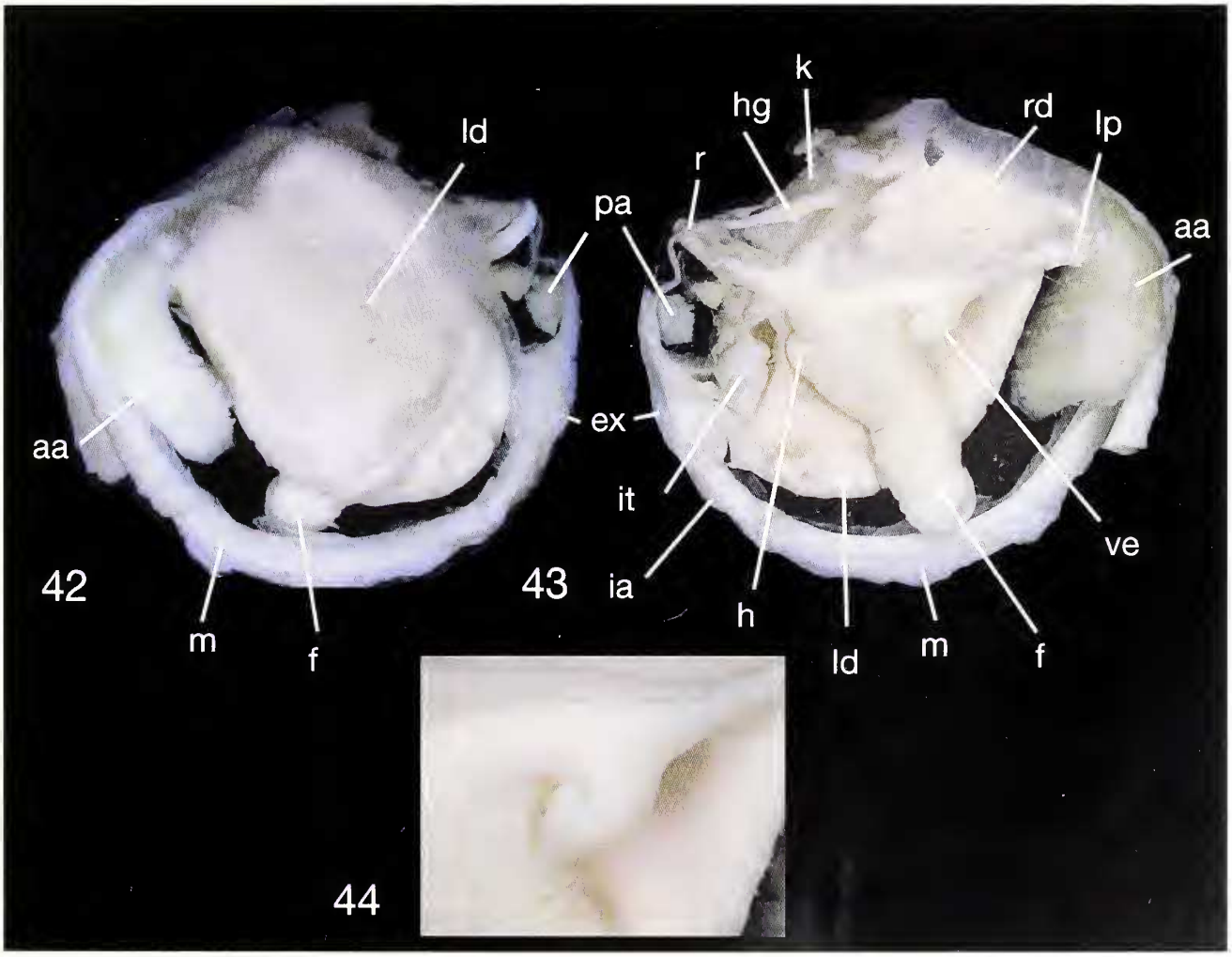
Remarks: Although presently known from only three specimens, *Ferrocina garciai* is a highly distinctive species and cannot be confused with any other lucinid from the western Atlantic. It differs from the type species *Ferrocina multiradiata* (Vanuatu, Fiji, New Caledonia) (Figures 46–47), depth range 80–400 m, in having finer, less prominent radial ribs and differs in shape and ribbing from a new *Ferrocina* species from the Philippines (Glover and Taylor, in press). The



Figures 27–39. *Ferrocina garciai*. **27–28.** Exterior of right and left valves of holotype, L = 19.7 mm. **29.** Dorsal view of holotype. **30–31.** Interior of right and left valves of holotype. **32.** Protoconch of holotype, boundary between P1 and P11 indicated with arrow. Scale bar = 50 µm. **33–34.** Details of hinge of left and right valves of holotype (SEM). Scale bar = 2 mm. **35.** Exterior of left valve of paratype 1. L = 13.9 mm. **36–37.** Interior of left and right valves of paratype 1. **38–39**. Exterior and interior of left valve of paratype 2, L = 11.7 mm.



Figures 40–41. Outline drawings of shell interiors of *Ferrocina*. **40.** Holotype. **41.** Paratype 1.



Figures 42–44. *Ferrocina garciai*, body of holotype. **42.** Left side with mantle removed showing large, thick, left ctenidial demibranch. **43.** Right side with mantle and part of right demibranch removed showing foot and coiled lateral visceral extension. **44.** Detail of ramshorn visceral extension. Abbreviations: **aa,** anterior adductor muscle; **ex,** exhalant aperture; **f,** foot; **h,** heel of foot; **hg,** hindgut; **ia,** inhalant aperture; **it**, invertible tube of posterior exhalant aperture; **k,** kidney; **ld,** left demibranch; **lp,** labial palps; **m,** mantle margin; **pa,** posterior adductor muscle; **r,** rectum; **rd,** right demibranch; **ve,** visceral 'ramshorn' extension.

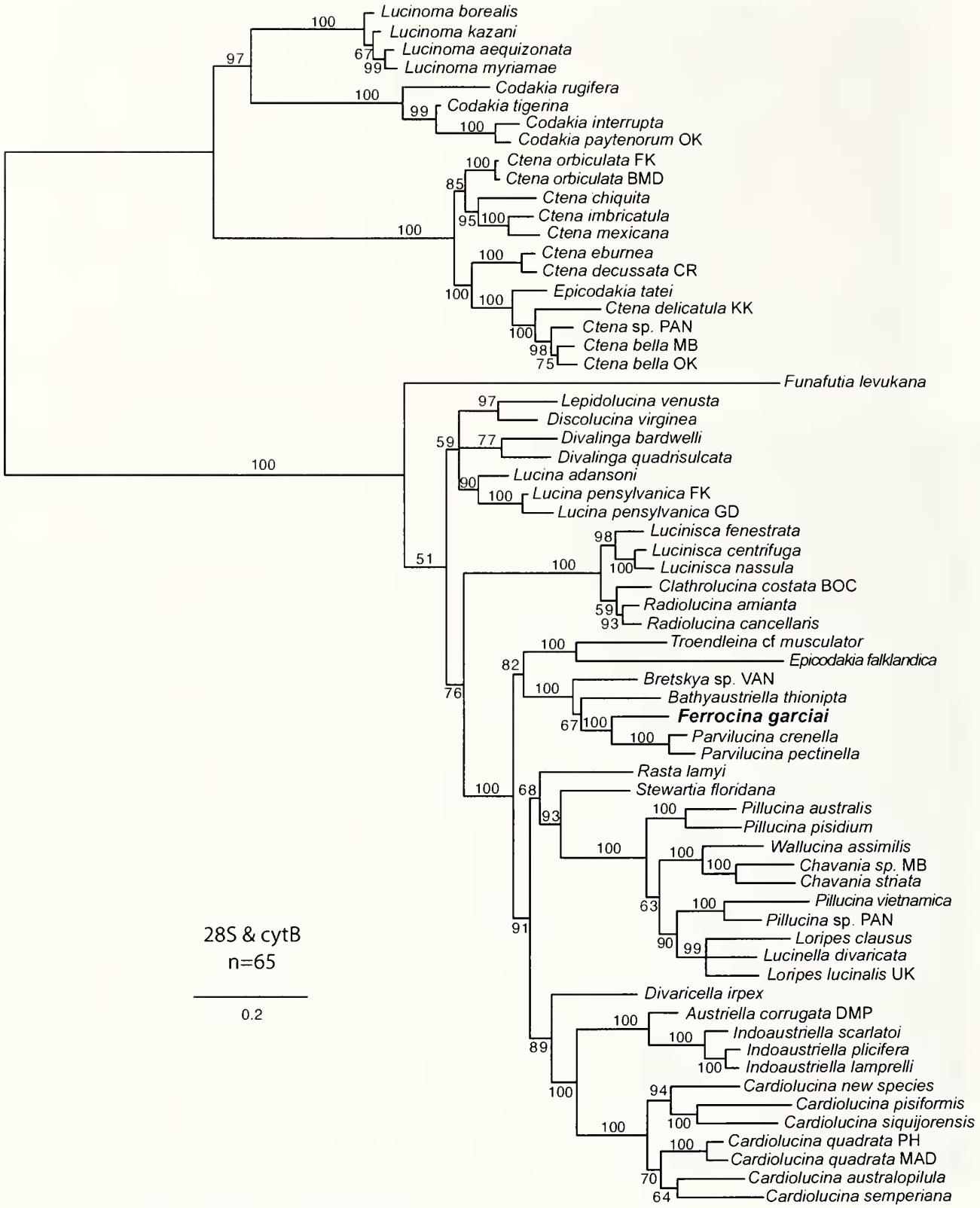
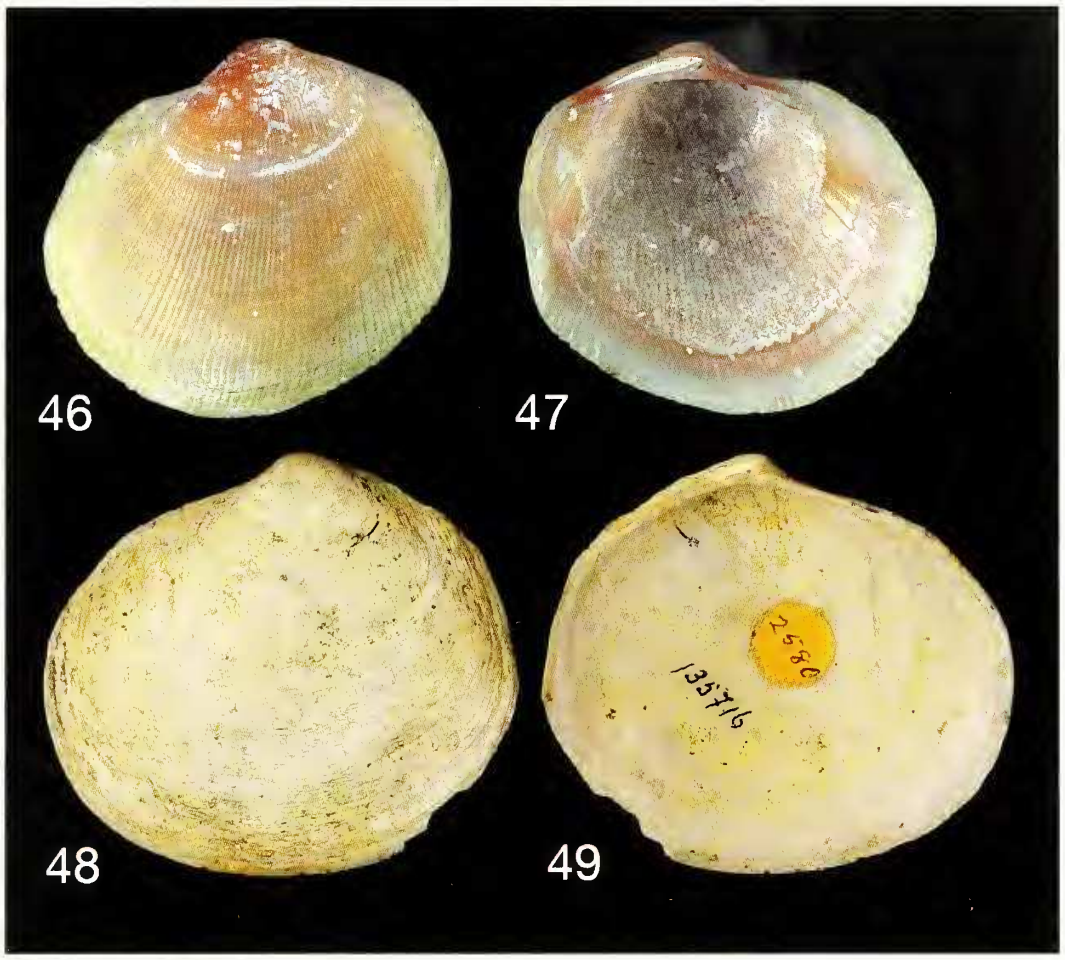


Figure 45. Molecular phylogeny of Lucinidae produced by Bayesian analysis of concatenated sequences of 28S rRNA, and cytochrome *b* genes including new sequences for *Ferrocina garciai*. Only lucinids from subfamilies Codakiinae and Lucininae included in the analysis. Locality and GenBank details of other lucinid taxa given in Taylor et al. (2011). GenBank numbers for *Ferrocina garciai*: 28S rRNA KF793276, cytochrome b KF793275.



Figures 46–49. Other species discussed under the "Remarks" for *Ferrolucina garciai*. **46–47.** *Ferrocina multiradiata* Glover and Taylor, 2007, holotype Vanuatu, 90–200 m, MNHN, exterior and interior of left valve, L = 11.2 mm. **48–49.** Syntype of *Codakia (Jagonia) pertenera* Dall, 1903, exterior and interior of left valve, L = 35 mm, USNM 135716, Pliocene, Bowden Formation, Jamaica.

juvenile paratype shells of *F. garciai* have stronger radial ribs and a shape more similar to *F. multiradiata*.

The curled body extension of *F. garciai* is similar to that described from *Bathyastriella thionipta*, a species from a hydrothermal vent on the Kermadec Ridge, New Zealand (Glover et al., 2004). *Bathyanstriella thionipta* also has very large enveloping etenidial demibranchs and a papillate inhalant aperture. We have no anatomical data for the type species *Ferrocina multiradiata* but the recently described, small, *Ferrocina brunei* from off Brunei, Borneo (Taylor and Glover, 2013) also has the curled body extension but the demibranchs are relatively small. *Troendleina* cf. *musculator* from the Philippines has the visceral mass extended into a ventral lobe and *Parvilucina crenella* has prominent lateral pouches to the visceral mass (unpublished observations) that may be homologous with the curled body extensions of *Ferrocina*. Visceral extensions may be an apomorphy of this subclade of Lucininae.

Ferrocina garciai has many shell features similar to the *Ferrocina* species known from the tropical Pacific, but it is a surprising addition to the western Atlantic fauna because the western Pacific species are also rare and known from only a few specimens. However, there is a probable fossil antecedent in the Caribbean (Figures 48–49). This is *Codakia (Jagonia) pertenera* (Dall, 1903: 1347 pl. 51, fig. 4., four syntypes, USNM 135716) from the Late Pliocene, Bowden Formation of Jamaica, later reclassified as *Myrtaea (Myrteopsis) pertenera* by Woodring (1925: 113, pl. 14, figs 13–16). Subsequently, Bretsky (1976: 284) discussed the species, apparently not recorded from mainland North America and supported an assignment to *Ctena*. It is larger than *F. garciai* (L = 35 mm) and the life color is unknown but it is similar in shape, dentition, and anterior adductor scar, with weak radial ribs on the dorsal part of the shell, and (according to Woodring) the inner shell margin is sometimes slightly fluted.

Etymology: Named for Emilio García who collected this distinctive species.

3. Neotype for *Venus orbiculata* Montagu, 1808 (= *Ctena orbiculata*)

Ctena orbiculata (Montagu, 1808) is one of the most abundant shallow water bivalves of the western Atlantic (Britton, 1970; Bretsky, 1976; Jackson, 1972, 1973) with a reported geographical range from Bermuda to Brazil. *Venus orbiculata* was described by Montagu (1808: 42) from a locality on the east coast of Scotland: "Found on the shore near Dunbar by Mr Laskey." No *Ctena* species are known to live around Scotland or the British Isles and the record is regarded as adventitious despite findings of two shells of the Mediterranean *Ctena decussata* (da Costa) from the Scilly Islands and Cornwall – see McMillan, 1971. How the species came to be recorded from Dunbar is a mystery. Dunbar is on the eastern coast of Scotland, to the east of Edinburgh and in the late 18th and 19th centuries was a busy fishing port and for a while, a whaling port. Western Atlantic mollusc species occasionally wash up on British shores but they usually occur on the west coast (Oliver et al., 2009). The specimen could have been dumped from ship ballast or there was an accidental confusion of localities. Cleevely (1995: 391) noted that collectors such as Laskey from whom Montagu obtained shells are known to have been less than scrupulous over the provenance of their specimens.

Original Description from Montagu (1808 p. 42): *"Shell white, orbicular, depressed, and cancellated: the umbo remarkably small, beneath which is a minute cordiform depression. Inside white; margin plain, teeth, two primary approximate, and one remote standing transverse; the margin where the lateral tooth is placed projects into an angle. Diameter five eighths of an inch* (approx. 16 mm). *The shell has probably been confounded with* Venus tigerina, *but it differs somewhat in contour, is not so flat, more orbicular, and more coarsely decussated, and the lateral tooth is more remote than in* tigerina. *Found on the shore near Dunbar, by Mr Laskey."*

Since Dall (1901) the name has been accepted for the western Atlantic species and the type locality of Dunbar, Scotland, was regarded as erroneous. No type material exists among Montagu specimens either at the Royal Albert Memorial Museum, Exeter, or The Natural History Museum, London. Furthermore, Montagu's figure (see Figure 50) is equivocal and cannot with confidence be assigned to any *Ctena* species. Nevertheless, Lamy (1920) listed *Venus orbiculata* Montagu as a synonym of the western African species now known as *Ctena eburnea* (Gmelin, 1791). Other names introduced for western Atlantic *Ctena* species (*Lucina occidentalis* Reeve, 1850; *Lucina imbricatula* C. B. Adams, 1845 and variety names for *C. orbiculata* var. *filiata* and var. *recurvata* introduced by Dall (1901)), have usually been placed in synonymy with *C. orbiculata* (Britton, 1971; Bretsky, 1976). The name *Ctena orbiculata* has become firmly entrenched in publications concerning western Atlantic mollusks (e.g. Warmke and Abbott, 1961; Abbott, 1954, 1974; Bretsky, 1976; Vokes and Vokes, 1984; Redfern, 2001; Mikkelsen and Bieler, 2007) and variously classified under other generic and subgeneric combinations of *Codakia* (*Jagonia*), *Codakia* (*Ctena*), or *Codakia* (*Codakia*).

An additional problem arising from ongoing molecular analyses, including our own results (Barnes and Weigt, 1998; Taylor et al., 2011), is that *Ctena orbiculata* is likely a complex of morphologically similar species as have been documented for other western Atlantic bivalves. Certainly, our own results separate *Ctena orbiculata* from the Florida Keys and specimens from Bocas, Panama that on shell characters resemble the type of *Lucina imbricatula* C. B. Adams, 1845, a species that is usually synonymized with *C. orbiculata* (e.g. Bretsky, 1976).

Ctena orbiculata in its varying name combinations is the subject of continuing investigations into the biology of the bacterial symbiosis, host-symbiont relationships (e.g. Giere, 1985; Schweimanns and Felbeck, 1985; Gros et al., 1998; Gros and Felbeck, 2003; Brissac et al., 2009, Gros et al., 2012) and reproductive biology (Bigatti et al., 2004). Because of the biological interest in *Ctena orbiculata*, its abundance in the western Atlantic and the possible existence of sibling species, it has become important to stabilise this well-established name by the designation of a neotype from an appropriate western Atlantic type locality and for which genetic data is available. The International Code of Zoological Nomenclature (ICZN, 1999) specifies (Article 75.3.6) that the neotype should come from a place as near as practicable to the original type locality. In this case, the geographical range of the species lies several thousand kilometres west of the original (likely erroneous) type locality and we have chosen the locality in the Florida Keys because we have published molecular data from a co-occurring, morphologically similar specimen to the neotype.

SYSTEMATICS

Subfamily Codakiinae Iredale, 1937

Genus *Ctena* Mörch, 1861

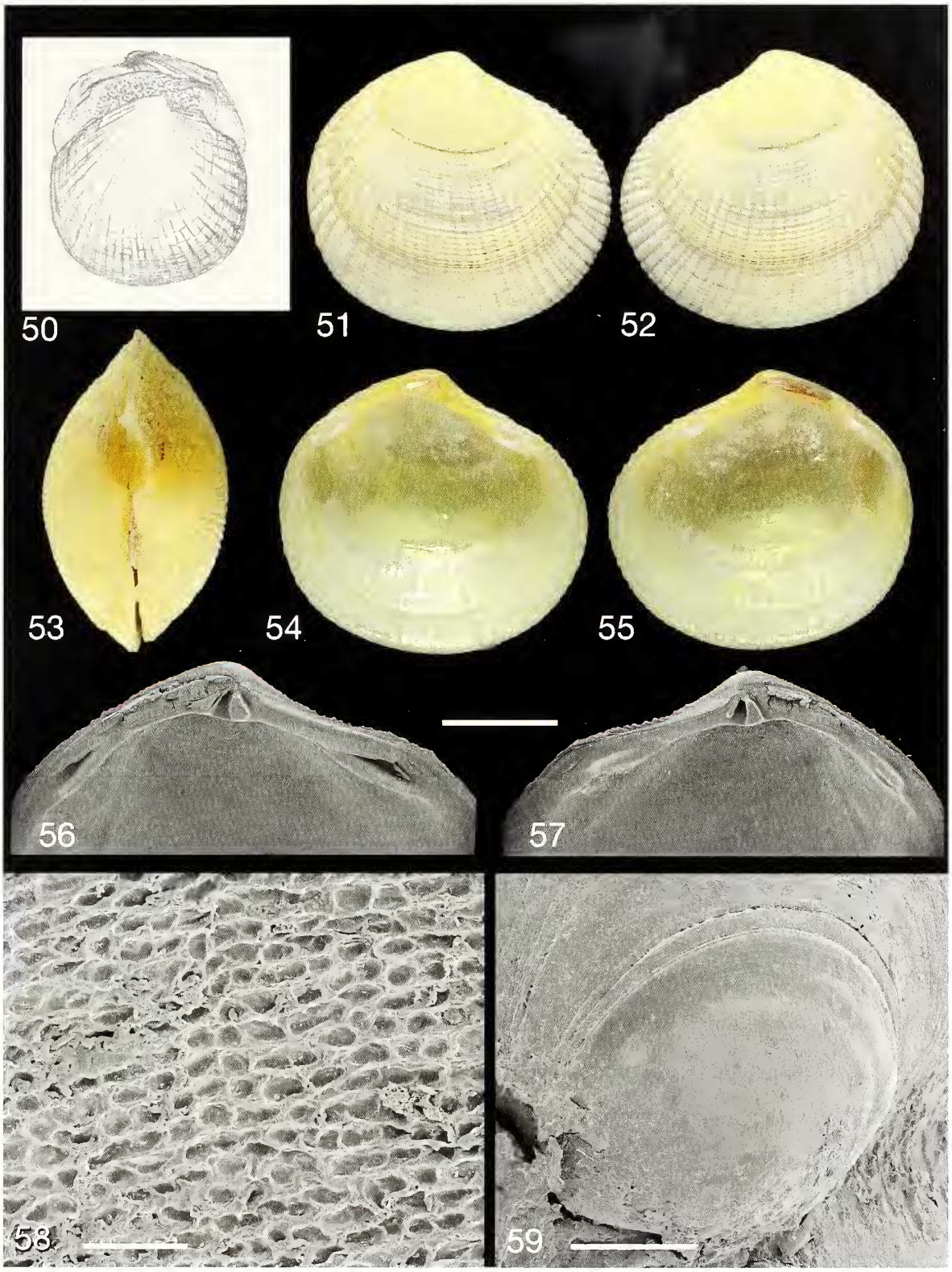
Type Species: *Codakia (Jagonia) mexicana* Dall, 1901, subsequent designation Dall, Bartsch and Rehder, 1938.

Ctena orbiculata (Montagu, 1808)

(Figures 50–59)

Venus orbiculata Montagu, 1808: 42, pl. 29, fig. 7.

Neotype: Whole shell, live-collected, FMNH 339457, collected by G. Bigatti, M. Perhada, J. Taylor and E. Glover during the International Marine Bivalve Workshop 2002, stn. IMBW-FK-622A, 22nd July 2002 (Mikkelsen and Bieler, 2004).



Figures 50–59. *Ctena orbiculata*. **50.** *Venus orbiculata*, copy of original figure from Montagu (1808). **51–55.** Neotype, *Venus orbiculata*, Long Key, FMNH 339457, L=13.6 mm. **51–52.** Exterior of right and left valves. **53.** Dorsal view of conjoined valves. **54–55.** Interior of left and right valves. **56–59.** *Ctena orbiculata*, SEM details of coated specimen from same sample and location as neotype, NHMUK 20130563. **56–57.** Hinge teeth of left and right valves. Scale bar = 2 mm. **58.** Microsculpture. Scale bar = 10 μm. **59.** Protoconch. Scale bar = 50 μm.

Type Locality: USA, Florida Keys, Long Key, bayside, 24°49.5′ N, 80°48.9′ W. 0.5–1.0 m, thin sand over rock platform with *Halodule wrightii*, *Thalassia testudinum*, and *Syringodium filiforme* (Mikkelsen and Bieler, 2004).

Description of Neotype: Shell small, L = 13.6 mm, H = 12.5 mm, T (single valve) = 4.2, longer than high, H/L = 0.92, moderately inflated, T/L = 0.31, exterior and interior pale, yellowish white. Sculpture of many radial ribs (55 at periphery), crossed by fine commarginal lamellae producing scales on summits of ribs. Ribs both divide and intercalate. Prominent major growth halts present. Lunule lanceolate. Ligament short, set in shallow groove. Hinge robust; RV with two cardinal teeth, anteriormost very small, anterior and posterior lateral teeth present, LV with two cardinal teeth, posterior tooth thin, anterior and posterior lateral teeth present. Anterior adductor scar short, broad, detached from pallial line for ½ length at an angle of 15°. Posterior adductor scar reniform. Shell interior within pallial line with radial grooves. Pallial line entire. Inner shell margin denticulate.

Remarks: Details of surface microsculpture and protoconch were examined by SEM on another coated specimen collected with the neotype (NHMUK 20130563). The microsculpture consists of a meshwork of irregular, shallow punctations, ca. 3–6 µm in size (Figure 58) similar to structures seen in other Codakiinae (Glover and Taylor, in press). The protoconch (Figure 59) PI+PII= 165 µm, PI=142 µm is irregularly lumpy, PII a narrow rim with fine growth increments.

A specimen (NHMUK 20100254) included in molecular analyses (Taylor et al., 2011) was collected at the same locality and time as the neotype and is very similar in shell characters. GenBank numbers for sequences of three genes: 18S rRNA (AJ 581853), 28S rRNA (AJ581887), cytochrome B (FR686627).

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