

Anatomical redescription of *Cyrenoida floridana* (Bivalvia, Cyrenoididae) from the Western Atlantic and its position in the Cyrenoidea

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Abstract

Members of the small bivalve family Cyrenoididae inhabit brackish waters of the eastern and western Atlantic Ocean. *Cyrenoida floridana* (Dall, 1896) from the western Atlantic is poorly known aside from shell descriptions. A detailed shell and anatomical study of *C. floridana* is here presented and compared with available data for Cyrenidae and Glauconomidae, two families of closest relationship according to recent phylogenetic studies. The species is characterized by valves externally covered by thin light brown periostracum; muscle scars and pallial line (without sinus) weakly impressed on the internal shell surface; a unique hinge pattern composed of cardinal and lateral teeth joining each other, right hinge with two laterals and two cardinals forming two inverted-V-shaped teeth and left hinge with two cardinals and one lateral forming a horizontal reversed F-shaped tooth; and microtubules inside the shell walls. Anatomically, the species presents unequal adductor muscles; demibranchs fused to each other along their posterior ends; a pair of totally fused, pigmented siphons; two pairs of siphonal retractor muscles; and a stomach with conjoined style sac and intestine, a single typhlosole, and three sorting areas. Evidence of shell parasitism is described.

Key Words

Anatomy, biodiversity, brackish water, Cyrenidae, freshwater, Glauconomidae, Heterodonta, Mollusca, taxonomy

Introduction

Cyrenoida Joannis, 1835, is the single genus of the small bivalve family Cyrenoididae and currently includes only six recognized extant species. Although previously assumed to extend into the Austral-Asian region (Pilsbry and Bequaert 1927), its known distribution includes temperate to tropical estuaries, marshes, and mangrove swamps of western Africa, both sides of the North American continent, and the western coast of Panama and adjacent islands (Joannis 1835; Morelet 1851; Dall 1896; Pilsbry and Zetek 1931; Morrison 1947; Huber 2010; MolluscaBase 2019). Because of its ecological position in the fringe area between freshwater and saltwater environments, the group has been left out from larger-scale

treatments of marine (e.g. Mikkelsen and Bieler 2007) and freshwater mollusks (e.g. Lydeard and Cummings 2019). *Cyrenoida* is poorly represented in museum collections, which, together with the fact that many of the original localities are difficult to access, has hindered detailed study of this taxon.

Several nominal species were introduced for West African members of this genus. These have been interpreted, based on shell morphology, as belonging to two fairly wide-ranging species (Huber 2010), the type species *Cyrenoida dupontia* Joannis, 1835, described from Senegal and extending to the Congo River (with synonyms *Cyrenella senegalensis* Deshayes, 1855, and *Cyrenoida rhodopyga*

Martens, 1891), and *C. rosea* (d'Ailly, 1896), described from Cameroon (including nominal subspecies *C. rosea brevidentata* Pilsbry & Bequaert, 1927 from Senegal). The fossil record of the group is poorly known, with a Pliocene species from southern Florida, *Cyrenoida caloosaensis* (Dall, 1896), recognized by Campbell (1993), and the modern species *Cyrenoida floridana* (Dall, 1896) interpreted as extending to the middle Pleistocene of Florida (Portell and Kittle 2010) and the Holocene of southern Texas (Neck and Herber 1981).

For the American Pacific coast (Coan and Valentich-Scott 2012), *Cyrenoida panamensis* Pilsbry & Zetek, 1931 was described from the western coast of mainland Panama (and is known from Costa Rica; Vargas-Zamora and Sibaja-Cordero 2011), and *C. insula* Morrison, 1946 from the Pearl Islands in the Gulf of Panama.

Another two species occur in the western Atlantic region, *Cyrenoida americana* Morelet, 1851, described from Cuba (and with published records from Puerto Rico and the Bahamas; Dall 1905), and *C. floridana* (Dall, 1896), the focus of the current treatment. Although rarely studied, the latter is a wide-ranging species along the western Atlantic and Gulf of Mexico coasts and has been cited as a prey item for both fish and bird species (Heard 1975, 1982; Kat 1978). It can be found living infaunally in muddy and sandy sediment colonized by halophytic plants, in estuaries and waters surrounding river mouths (Dall 1896, 1901; Kat 1982), the outer fringes of very low saline to freshwater marshes (Tunnell et al. 2010), as well as around freshwater ponds (this study).

The position of the family Cyrenoididae within the Heterodonta remained unresolved for a long time, with most authors including it in a broad concept of Lucinoidea (e.g. Prime 1860; Dall 1901; Lamy 1920; Chavan 1969; Vokes 1980; Boss 1982; Vaught 1989). Others placed it tentatively near the Corbiculidae (= Cyrenidae) (Thiele 1934) or as its own superfamily Cyrenoidoidea near groups such as Chamoidea and Galeommatoidea (Olsson 1961). A close relationship of Cyrenoididae with Lucinidae was questioned by Taylor and Glover (2006) and Williams et al. (2004) on anatomical grounds. The latter opinion was confirmed by Taylor et al. (2009) in the first molecular study that included a member of the family (*C. floridana*), which indicated a close relationship of Cyrenoididae with Cyrenidae (the latter as Corbiculidae) and Glauconomidae. They again elevated the rank to superfamily Cyrenoidoidea, which was adopted in some subsequent classifications (e.g. Bieler et al. 2010). Subsequent studies with additional molecular markers (Sharma et al. 2012; Combosch et al. 2017; Lemer et al. 2019) and combined morphological and molecular datasets (Bieler et al. 2014) confirmed the close relationship of Cyrenoididae, Cyrenidae, and Glauconomidae. The latter work combined them in the superfamily Cyrenoidea within the Neoheterodonte (the crown group of Imparidentia), its current position. The recent transcriptomic study by Lemer et al. (2019) included members of Cyrenidae [*Corbicula fluminea* (O. F. Müller, 1774) and *Polymesoda*

caroliniana (Bosc, 1801)], Glauconomidae (*Glauconome rugosa* Hanley, 1843), and Cyrenoididae (*C. floridana*). Interestingly, *Polymesoda* grouped with *Glauconome*, not *Corbicula* (which appeared as the basal taxon in this clade), indicating that Cyrenidae as currently understood (Bieler and Mikkelsen 2019) might not be monophyletic.

Whereas morpho-anatomical studies on this group have been limited, molecular data of *C. floridana* have been involved in several analyses, including recent transcriptomic studies exploring questions ranging from synonymous codon usage bias (Gerdol et al. 2015) to Imparidentia phylogeny (Lemer et al. 2019). To improve the morphological knowledge of Cyrenoididae and to contribute to the resolution in the Cyrenoidea clade, a detailed anatomical study of *C. floridana* is here presented. Its features are then compared to available data for members of Glauconomidae and several genera of Cyrenidae sensu lato.

Material and methods

A detailed list of examined material is presented following the anatomical description. The anatomical study is divided in two parts: shell analysis and soft part analysis. The shell analysis consisted of measurements and scanning electronic microscopy of the shell. The shell measurements were taken using a caliper or, in case of photos, using ImageJ software. The measurements used were shell length, height, and width; umbo length and height; dental shelf length and height; hinge teeth length and height; dorsal shell margin length; adductor muscle length, height, and area; and pallial line spacing from the ventral shell margin. The soft part analysis collected details of topology and morphology of systems and organs using photography and drawings under camera lucida. The soft part data were obtained from specimens preserved in ethanol. Dissection occurred with the specimens immersed in 70% ethanol. Final drawings were initially made in graphite and later remade on translucent paper with China ink, scanned, and edited using Photoshop CS3 software. The final drawings are average anatomical schemes based on information collected from several specimens. The number of specimens dissected varied according to the availability in collections and was expected to be sufficient to cover any feature affected by preservation methods, such muscular contractions, distensions limits, and presence or absence of delicate structures, or sexual stages of the specimens, and to detect maturation stages and gonadal filling. All soft parts here drawn are based on specimens in lot FMNH 328260.

The type materials of *C. floridana* and *C. guatemalensis* were examined from photographs, whereas additional samples were physically studied. Scanning electron microscopy (SEM) was provided by the Laboratório de Microscopia Eletrônica do Instituto de Biociências of the Universidade de São Paulo and by the Laboratório de Microscopia Eletrônica from Museu de Zoologia of the Universidade de São Paulo.

The following abbreviations are used in the anatomical descriptions and figures: **aa**: anterior adductor muscle; **an**: anus; **ar**: anterior pedal retractor muscle; **au**: auricle; **cc**: cerebral connective; **cg**: cerebral ganglia; **cn**: ctenidial nerve; **cp**: cerebropedal connective; **cv**: cerebrovisceral connective; **dd**: digestive diverticula; **dg**: digestive gland; **dh**: dorsal hood; **dm**: dorsal siphonal retractor muscles; **eo**: excurrent opening; **er**: esophageal rim; **es**: esophagus; **ex**: excurrent siphon; **fg**: food groove; **ft**: foot; **gf**: gill fusion; **gi**: gill; **go**: gonad; **gp**: genital pore; **gs**: gastric shield; **he**: heart; **id**: inner demibranch; **if**: mantle border inner fold; **in**: intestine; **io**: incurrent opening; **ip**: inner palp; **is**: incurrent siphon; **ki**: kidney; **lc**: left caecum; **lp**: left pouch; **lv**: large inverted-V-shaped tooth; **mf**: mantle border middle fold; **mo**: mouth; **mt**: major typhlosole; **na**: anterior adductor muscle nerve; **np**: nephropore; **nt**: minor typhlosole; **od**: outer demibranch; **of**: mantle border outer fold; **op**: outer palp; **pa**: posterior adductor muscle; **pg**: pedal ganglia; **pl**: pallial line; **pm**: pallial muscle; **pn**: pallial nerve; **pp**: papillae; **pr**: posterior pedal retractor muscle; **rc**: right caecum; **rn**: renal nerve; **sa1**: sorting area 1; **sa2**: sorting area 2; **sa3**: sorting area 3; **sm**: siphonal membrane; **sn**: dorsal siphonal muscle nerve; **sp**: siphons; **ss**: style sac; **st**: stomach; **sv**: small inverted-V-shaped tooth; **t1**: large lateral tooth of right valve; **t2**: large cardinal tooth of right valve; **t3**: small lateral tooth of right valve; **t4**: small cardinal tooth of right valve; **t5**: lateral tooth of right valve; **t6**: posterior cardinal tooth of left valve; **t7**: anterior cardinal tooth of left valve; **ve**: ventricle; **vg**: visceral ganglia; **vm**: ventral siphonal retractor muscles.

Institutional abbreviations: **ANSP**, Academy of Natural Sciences of Drexel University, Philadelphia, Pennsylvania, USA; **UF**, Florida Museum of Natural History, Gainesville, Florida, USA; **FMNH**, Field Museum of Natural History; **USNM**, National Museum of Natural History [United States National Museum], Smithsonian Institution, Washington, DC, USA.

Systematics

Family Cyrenoididae H. Adams & A. Adams, 1857 (1853). Synonym: Cyrenellidae J.E. Gray, 1853.

Genus *Cyrenoida* Joannis, 1835 (type species by monotypy: *Cyrenoida dupontia* Joannis, 1835). Synonyms include: *Cyrenella* Deshayes, 1836 (established in synonymy of *Cyrenoida*; available because it was used as valid before 1960, e.g. by Gray 1853); *Cyrenoidea* Dall, 1896 (unjustified emendation; the earlier use by Hanley (1846) is considered an incorrect subsequent spelling); *Cyrenodonta* has been credited by some authors to H. Adams & A. Adams, 1857, but it was introduced in synonymy of *Cyrenoida* and no pre-1960 use as a valid name has been located); *Cyrenoides* auct. is an incorrect subsequent spelling for *Cyrenoida* (G.B. Sowerby II, 1839).

Cyrenoida floridana (Dall, 1896)

Figs 1–41

Cyrenoidea floridana Dall 1896: 52; Simpson 1887–1889: 66 [nomen nudum]; Dall 1889: 50, 208 [nomen nudum]; Rhoads 1899: 48; Heard 1975: 22; 1982a: 23, fig. 24; 1982b: 131.

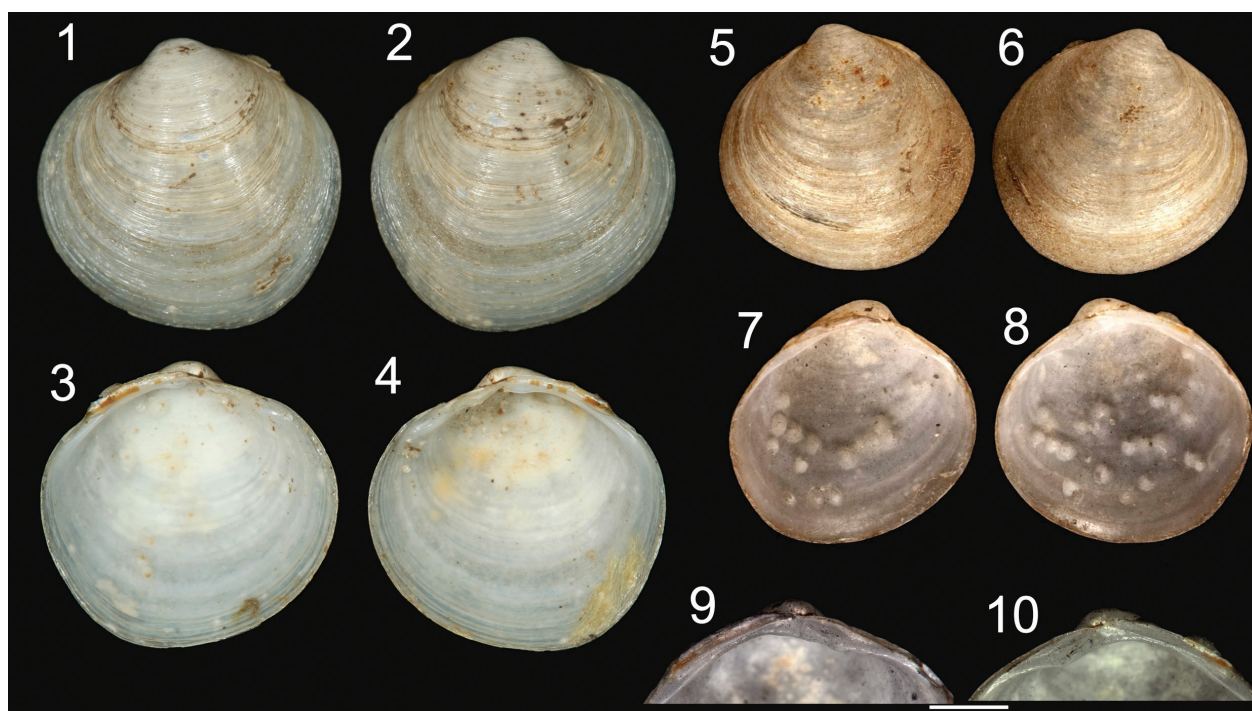
Cyrenoida floridana—Dall 1901: 817, pl. 42, fig. 7; Lamy 1920: 388; Pilsbry and Zetek 1931: 69; Smith 1951: 45 (pl. 16, fig. 11, pl. 18, fig. 8); Pulley 1952: 114–115, pl. 9, fig. 15; Morrison 1954: 9–10; Van Regteren Altena 1968: 157, 176; 1971: 5, 41, fig. 14; Waas 1972: 123; Abbott 1974: 466 (fig. 5383); Leathem et al. 1976: 93, figs 1–3; Kat 1978: 1–168, figs 1–91, tables 1–7; A1–A6; Neck and Herber 1981: 35–39; Kat 1982: 47, figs 1–3 (oocytes); Heard 1982a: 25, fig. 28j; Vokes and Vokes 1983: 39, 62, pl. 39, fig. 7; Neck 1985: 5; Bishop and Hackney 1987: 141, fig. 6; Turgeon et al. 1988: 36; 1998: 39; Camp et al. 1998: 11; Abbott and Morris 1995: 53, pl. 24, fig. 12; Redfern 2001: 219, pl. 92, fig. 898; Reece et al. 2004: 1116; Mikkelsen and Bieler 2000: 373; 2004a: 513; 2004b: 596; Lee 2009: 28, fig.; Turgeon et al. 2009: 728; Taylor et al. 2009: 10 (figs 4–8); Tunnell et al. 2010: 345; Redfern 2013: 400, fig. 1067; Bieler et al. 2014: 45 (fig. 3N); Arzul and Carnegie 2015: 33; González et al. 2015: 4, figs 1, 2; Combosch et al. 2017: table 1, figs 1, 2; Lemer et al. 2019: figs 1, 2.

Cyrenella floridana—Walker 1918: 88, fig. 232.

Cyrenoidea guatemalensis Pilsbry 1920: 221 (pl. 11, fig. 9); Clench and Turner 1962: 60.

Cyrenoida guatemalensis—Pilsbry and Zetek 1931: 69; Morrison 1946: 45.

Description. Shell (Figs 11–23): **External features:** Outline rounded, subcircular with ventral margin slightly posteriorly carinated (Figs 11, 12); equivalve, equilateral, ~6% longer than high, reaching maximum length of ~15 mm. Laterally inflated, width ~59% of total shell length (Figs 13–15). Externally white, adorned only with growth lines, showing ~3 thicker commarginal growth increments. Periostracum thin, slightly wrinkled, light brown. Walls thin, fragile. Umbones prosogyrous, low, ~5% of total shell height, large, length ~25% of total shell length, located at midpoint of shell length. Ligament parivincular, opisthodetic, long, ~39% of total shell length (Figs 15–17). Nymph long, ~20 times longer than wide, rectangular. Lunule and escutcheon absent. **Internal features:** Internal surface opaque white (Figs 16, 17). Adductor muscle scars and pallial line weak, very faintly impressed (outlined in Fig. 16). Anterior adductor muscle scar reniform, occupying ~1.5% of total internal surface; ventral portion ~2 times wider than dorsal portion; positioned at median third of valve height. Posterior adductor muscle scar oval, slightly pointed dorsally, occupying ~1.6% of total internal surface; located slightly more ventral than anterior muscle scar. Pallial line weak, formed by row of small pallial muscle scars, connected to middle portion of ventral surface of anterior adductor muscle to middle portion of ventral surface of posterior adductor muscle, inset from ventral shell margin by ~19.5% of total shell height, without pallial sinus. Microtubules of elongated conical shape, beginning with circular opening in interior shell wall, tapering toward but not reaching external surface (Figs 20–22). Internal surface of shell usually with aragonitic nodules of various sizes and quantities (Figs 16, 17, 23).

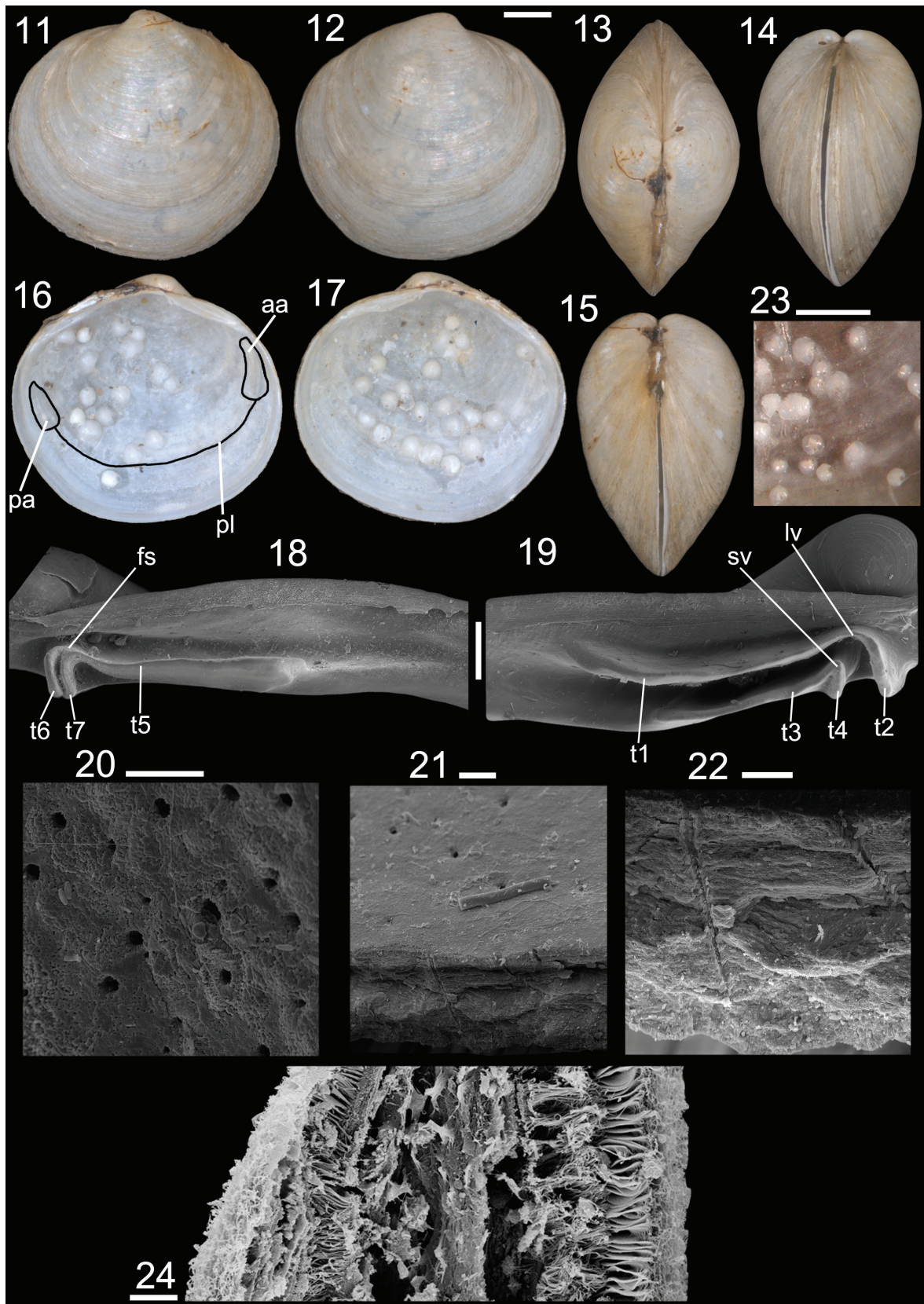


Figures 1–10. Syntypes of *Cyrenoida floridana* and lectotype of *C. guatemalensis*. **1–4.** *Cyrenoida floridana* (USNM 46846, length 12 mm, height 13 mm). **1.** Left valve, external view; **2.** Right valve, external view; **3.** Left valve, internal view; **4.** Right valve, internal view; **5–10.** *Cyrenoida guatemalensis* (ANSP 107532; length 8.6 mm, height 8.9 mm). **5.** Left valve, external view; **6.** Right valve, external view; **7.** Left valve, internal view; **8.** Right valve, internal view; **9.** Detail of left hinge; **10.** Detail of right hinge. Scale bar: 2 mm.

Hinge (Figs 16–19): Hinge restricted to central and anterior portion of dorsal margin, composed of lateral and cardinal teeth. **Right hinge** (Figs 17, 19): Dental shelf short and wide, triangular, running along entire length of anterior portion of dorsal margin, height equivalent to ~10 times dorsal margin width; composed of two laterals and two cardinals. Each cardinal tooth joining posteriorly with a lateral tooth, forming two inverted-V-shaped teeth, one large (Fig. 19: **lv**), one small (Fig. 19: **sv**). Large V-shaped tooth located near dorsal shell margin, formed by long and laminar lateral tooth (Fig. 19: **t1**) and short cardinal one (Fig. 19: **t2**). Lateral tooth length equivalent to ~56% of total dental shelf length, cardinal tooth length equivalent to ~22% of lateral tooth length; small V-shaped tooth located ventral to large V-shaped tooth (**lv**). Small lateral tooth (Fig. 19: **t3**) length ~30% shorter than large lateral tooth, whereas small cardinal tooth (Fig. 19: **t4**) ~40% shorter than dorsally located cardinal tooth (Fig. 19: **t2**). **Left hinge** (Figs 16, 18): Dental shelf narrow, fusiform, running along 30% of anterior portion of dorsal margin, height equivalent to ~3 times dorsal margin width; composed of three cardinal teeth, two cardinal and one lateral, forming horizontal reversed F-shaped tooth (Fig. 18: **fs**). Both cardinal teeth originating parallel and close to each other, (Fig. 18: **t6**, **t7**). Lateral tooth laminar (Fig. 18: **t5**), joining anterior cardinal tooth (Fig. 18: **t7**), length equivalent to 50% of total length of dorsal shelf. Both cardinal teeth equivalent to 20% of lateral tooth length. When articulated, left

valve tooth complex (**t5**–**t7**) fits within groove between right valve **t3**–**t4** and **t1**–**t2**.

Muscular system (Figs 25–27, 31, 34, 33): Anterior adductor muscle (**aa**) reniform in cross section, ~3 times taller than wide; ventral portion ~2 times wider than dorsal portion; occupying ~3% of total shell internal volume; located at middle third of shell height; clearly divided into quick and slow components (Figs 25, 26, 35), quick component occupying ~39% of anterior portion of muscle, dark grey in color, slow component occupying ~61% of posterior portion of muscle, light cream in color. Posterior adductor muscle (**pa**) elliptical in cross section, ~1.5 times wider than tall, ~20% shorter and ~2 times wider than anterior adductor muscle, occupying ~3% of total shell internal volume; located slightly ventral to anterior adductor muscle; clearly divided into quick and slow components (Figs 25–27, 34, 35), quick component occupying ~52% of posterior portion of muscle, dark grey in color, slow component occupying ~48% of anterior portion of muscle, light cream in color. Paired anterior pedal retractor muscles (**ar**) oval in section, thin, attached on shell at posterodorsal side of anterior adductor muscle insertion, area ~3% of that of adductor, length ~20% of shell length, left and right branches fused at mid-length. Paired posterior pedal retractor muscles (**pr**) oval in cross section, slightly laterally compressed, thin, ~40% longer than anterior pedal retractors; inserting on shell dorsally posterior adductor muscle, in area ~3% of that adductor, left and right branches fusing at dorsal ~20% of total muscle length. Pedal protractor



Figures 11–24. *Cyrenoida floridana*, shell and gills details. 11–22, 23. UF 246126; 24. FMNH 328260. 11. Left valve, external view; 12. Right valve, external view; 13. Dorsal view of shell; 14. Anterior view of shell; 15. Posterior view of shell; 16. Left valve, internal view, muscle scars and pallial line outlined; 17. Right valve, internal view; 18. Left hinge, SEM; 19. Right hinge, SEM; 20. Internal surface of shell, SEM, showing microtubule orifices; 21. Detail of microtubule patch; 22. Fractured shell showing microtubules partially through shell thickness; 23. Detail of nodules at shell internal surface; 24. Gill fragment, transverse section, SEM. Scale bars: 1 mm (11–17, 23); 200 μ m (18, 19); 20 μ m (20–22), 0.5 mm (23); 10 μ m (24).

muscles absent. Two pairs of siphonal retractor muscles (Figs 27, 31, 33); dorsal siphonal retractors (**dm**) ~3 times longer than wide; insertion at mantle bifid for half of total muscle length, 2 times as long as excurrent opening, originating laterally at half of siphonal base height; ventral siphonal retractors (**vm**) thin and translucent, ~3 times longer than wide, length ~50% of total length of dorsal siphonal muscle, originating at ventral end of incurrent siphon base.

Foot (Figs 25, 26, 33): Foot short, wedged-shaped, length equivalent to ~35% of total shell length, contracted height equivalent to ~27% of total shell height, laterally compressed, with small heel of length equivalent to ~23% of total foot length. Distal end acuminate. Byssal groove and byssus absent in adults.

Mantle (Figs 25–29): Mantle lobes symmetrical, thin, translucent white. Pallial muscles long, triangular, inserting from inner mantle fold region to ~16% of total mantle lobe height, arranged sparsely at ventral margin of mantle lobe; separated from each other by ~4 times pallial muscle basal width (Fig. 25: **pm**). Mantle border with three folds (Fig. 29); outer fold (**of**) thin, width ~5% of shell thickness, 5 times higher than wide; middle fold (**mf**) similar to outer fold, ~30% shorter; inner fold (**if**) short, ~3 times taller than wide. Middle fold with 30 small and short papillae, bordering entire pedal gape portion (Fig. 26: **pp**); each papilla taller than wide, with rounded tip, separated from adjacent papillae by width equivalent to 4 times papillar width. Periostracum between outer and middle folds. Mantle lobes totally free except for siphonal area. Anterior mantle fusion occurring at ~42% of anterior adductor muscle height; posterior mantle fusion occurring at ~70% of posterior adductor muscle height (Fig. 26). Siphonal area corresponding to ~30% of total mantle lobe length (Fig. 26). Incurrent and excurrent siphons originating from inner mantle fold; siphonal area equivalent to ~35% of total animal height and ~7% of length (Figs 26, 27); siphons externally fused, covered by small brown spots, internally separated by thick, smooth muscular wall (Figs 27, 28, 31); siphonal internal openings free, opening directly into pallial cavity; incurrent and excurrent siphons similar in size; ~5 times longer than wide; incurrent siphonal external tip bordered by one row of short papillae, papillae length equivalent to ~10% of total siphon length (Fig. 28: **pp**); excurrent siphonal tip with siphonal membrane (Fig. 28: **sm**).

Pallial cavity (Figs 25, 26, 30, 32, 33): Occupying ~50% of total internal shell volume (Fig. 25). Labial palps small, ~2% of total internal shell volume, triangular (Figs 26, 32), external surface smooth; outer (**op**) and inner hemipalps (**ip**) of similar size, ~60% narrower and 55% shorter than anterior adductor muscle insertion; outer hemipalp connected to mantle lobe by dorsal edge, at ~30% of palp length; inner hemipalp connected to visceral mass by dorsal edge, at ~20% of palp length; internal surface of each palp with ~10 tall, rounded transverse folds covering ~90% of inner palp surface, leaving thin smooth area at palp edges, corresponding to ~10% of total inner palp area. Folds decreasing in length toward

mouth, forming shallow channels directed to anterior and posterior portions of mouth (Fig. 32). Gill wide, ~60% times wider than outer hemipalp, equivalent to ~30% of total valve area (Fig. 25). Ctenidia eulamellibranch with two demibranchs (Fig. 30). Outer demibranch, fusiform, twice as long as wide; folded upon ~30% of its own area; covering pericardial and renal areas; connected to mantle lobe by tissue for ~15% of posterodorsal border length (Fig. 25); inner demibranch triangular, ~1.5 times longer than wide; folded upon 50% of its own area; covered by outer demibranch in area equivalent to ~20% of its own area; food groove along ventral surface of inner demibranch (Figs 30, 33: **fg**); demibranchs connected to each other at posterior end by tissue (**gf**), fusion length equivalent to 25% of total gill length (Figs 25, 33); each demibranch thin, fragile, without signs of chemosymbiotic bacteria (Figs 24, 30). Suprabranchial chamber ~1/3 of infrabranchial chamber volume (Fig. 26).

Visceral mass (Fig. 26): Triangular, occupying half of total internal shell volume, laterally flattened, 2 times as wide as muscular base; ~40% of anterodorsal portion filled by brown digestive gland (**dg**); remaining area filled by cream-colored gonad (**go**). Stomach and style sac located vertically in central portion of visceral sac.

Circulatory and excretory systems (Figs 26, 34): Pericardium located in posterodorsal region of visceral sac, between posterior region of umbonal cavity and dorsal surface of kidney (Fig. 34), ~2 times as long as wide; occupying ~25% of total visceral mass volume. Paired auricles (**au**) anteroposteriorly elongated, connecting to main axis of gills along ~1/3 of gill length; walls thin, translucent. Ventricle (**ve**) elongated, thick, located at central pericardial region, surrounding ~45% of intestine crossing pericardial area, connected to auricles at median portion of lateral walls. Kidney light brown, triangular, located posteroventral to visceral mass, between ventral wall of pericardium and dorsal surface of posterior pedal retractor muscles, occupying ~25% of total visceral mass volume. Nephropores (Fig. 26: **np**) small, located at anterior third of kidney length, near genital pore (Fig. 26: **gp**).

Digestive system (Figs 35–37): Palps and digestive gland as described above. Mouth small, located centrally between pairs of inner and outer labial palps. Esophagus (**es**) long, narrow, length ~30% and height ~10% of visceral sac length and height (Fig. 35), cylindrical, running separate from anterior adductor muscle between and parallel to anterior portion of paired anterior pedal retractor muscles; internal surface covered by longitudinal folds, forming esophageal rim at stomach entrance (Fig. 37, **er**) in anteroventral region. Stomach (**st**) wide, occupying ~30% of visceral sac volume, conical, funnel-like, located anterior to umbo (Fig. 35); length ~60% of total visceral sac length, ~30% of its height; posterior portion ~60% taller than anterior portion. Paired apertures to digestive caeca located ventrolaterally, turned toward ventral portion of visceral sac, located side by side at anterior portion of stomach. Dorsal hood (**dh**) long, thin, length ~40% of total stomach length, anteriorly bluntly pointed.

Left pouch (**lp**) located below anterior portion of dorsal hood, shallow, wide, occupying ~20% of external area of left stomach wall, with ducts to digestive gland connecting at its central region (Fig. 36: **dd**). Stomach internal surface mostly smooth, with three well-developed sorting areas (Fig. 37); first sorting area starting at left side of esophageal rim, running along dorsal wall of anterior stomach chamber, penetrating dorsal hood, narrow, comprised of small transverse folds (**sa 1**). Second sorting area originating ventral to first sorting area, at left side of esophageal rim, running along left wall of anterior stomach chamber, entering left pouch and dorsal hood, both on their ventral surfaces, broad, formed by thickening of stomach wall (**sa 2**). Third sorting area starting inside dorsal wall of dorsal hood, running along dorsal and right walls of posterior stomach chamber, until diffusing on ventral portion of right wall (**sa 3**). Gastric shield (**gs**) located at central dorsal wall, occupying ~40% of total gastric area, with two anterior projections, one dorsal at left border, penetrating dorsal hood, and one left ventral, penetrating left pouch. Two narrow, tall gastric ridges running along ventral stomach chamber, forming major and minor typhlosoles at style sac entrance (Fig. 37). Longer ridge originating posterior to left caecum, penetrating caecum and exiting its anterior end, running toward anterior portion of stomach, performing curve, penetrating anterior end of right caecum, exiting that caecum at its posterior end, penetrating style sac at its right side, forming major typhlosole (**mt**). Shorter fold originating at style sac entrance, at region of major typhlosole penetration into style sac, forming rim bordering style sac entrance and ultimately minor typhlosole (**nt**). Style sac (**ss**) connecting stomach ventrally (Fig. 35), tapering ventrally, ~3.3 times longer than wide, occupying ~12% of visceral sac total volume; style sac height equivalent to 50% of visceral sac length, and ~10% of its width. Intestine (**in**) thin, long, originating between typhlosoles, merging with style sac initially, narrowing after ventral end of style sac, passing ventrally below central stomach, penetrating pedal musculature at ~5% of foot height, contacting dorsal surface of posterior pedal retractor muscles, curving toward right, following posterodorsal portion of visceral sac, parallel to style sac; intestine total length ~7 times longer than style sac. Anus simple, sessile, on ventral surface of posterior adductor muscle (Fig. 31, 35: **an**).

Reproductive system (Fig. 26): Gonads with branched aspect, opaque, cream-colored. Paired gonoducts connected to gonadal acini branches along posterodorsal portion of visceral sac. Genital pores simple (**gp**), located at posterior portion of visceral mass, at ~20% of visceral mass height, near nephropore (**np**).

Central nervous system (Figs 38–41): Paired cerebral ganglia (Figs 38, 41: **cg**) surrounding dorsal surface of anterior esophagus, dorsal to external surface of outer labial palp, triangular, longer than wide (Fig. 38), length 50% of esophageal length. Each cerebral ganglion ~50% width of transverse section of esophagus. Cerebral commissure ~50% longer than ganglia length; anterior ad-

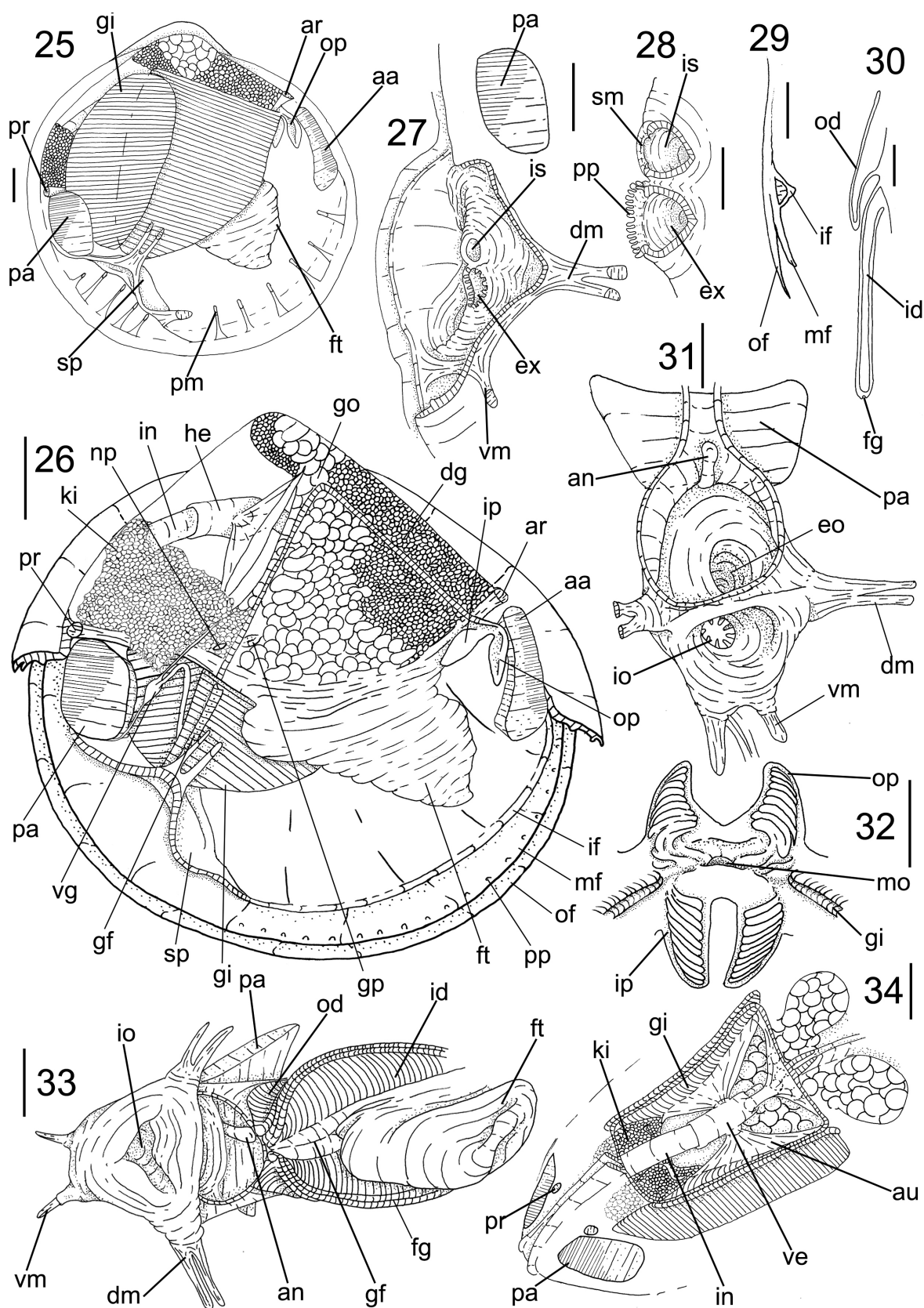
ductor muscle nerve (**na**) originating at anterior end of cerebral ganglion, contacting posterior surface of anterior adductor muscle, bifurcating into two main branches; internal branch penetrating posterodorsal third of muscle, diffusing into muscle; outer branch bordering posterior surface of anterior muscle until contacting pallial region and diffusing into muscle. Two additional pairs of nerves originating dorsally on cerebral ganglia, anterior to cerebrovisceral connective (**cv**) crossing visceral mass, contacting gonopore dorsally, bordering anterior portion of kidney and connecting dorsally with visceral ganglia, connecting cerebropedal connective (**cp**) running immersed in pedal muscles, connecting to anterior region of paired pedal ganglia (Figs 40, 41: **pg**). Paired visceral ganglia (Figs 39, 41: **vg**) fusiform, of similar length and height, length ~60% of cerebral ganglia length, partially fused medially, with subcentral groove; located ventral to paired posterior pedal retractor muscle, parallel with posterior adductor muscle, at dorsal tip connecting to cerebrovisceral connective (**cv**, as described above) and renal nerve (**rn**), penetrating kidney area; laterally originating ctenidial nerves (**cn**) running through central axis of posterior portion of gills; dorsally originating posterior adductor muscle nerve, penetrating mid-region of anterior surface of posterior adductor muscle; at ventral tip originating pallial nerve (**pn**), contacting anterior surface of ventral portion of posterior adductor muscle, running toward incurrent and excurrent siphonal muscles, reaching excurrent opening, originating single, short nerve (**sn**) that runs parallel to ~25% of dorsal siphonal muscle length, continuing parallel to mantle border, diffusing into mantle lobe edge. Paired pedal ganglia totally fused (Figs 40, 41: **pg**), oval, longer than wide, ~20% wider than visceral ganglia; located internal to posterior pedal retractor muscles, dorsal to foot insertion, at anterior tip connecting with cerebropedal connectives from cerebral ganglia; at posterior tip connecting two pairs of nerves, with dorsal pair running toward posterior region, inside posterior pedal retractor muscles; posteroventral pair curving ventrally, running into foot.

Habitat. Infaunal, in muddy sand; usually positioned vertically in about 2 cm depth (Kat 1978), in mangrove areas and brackish waters.

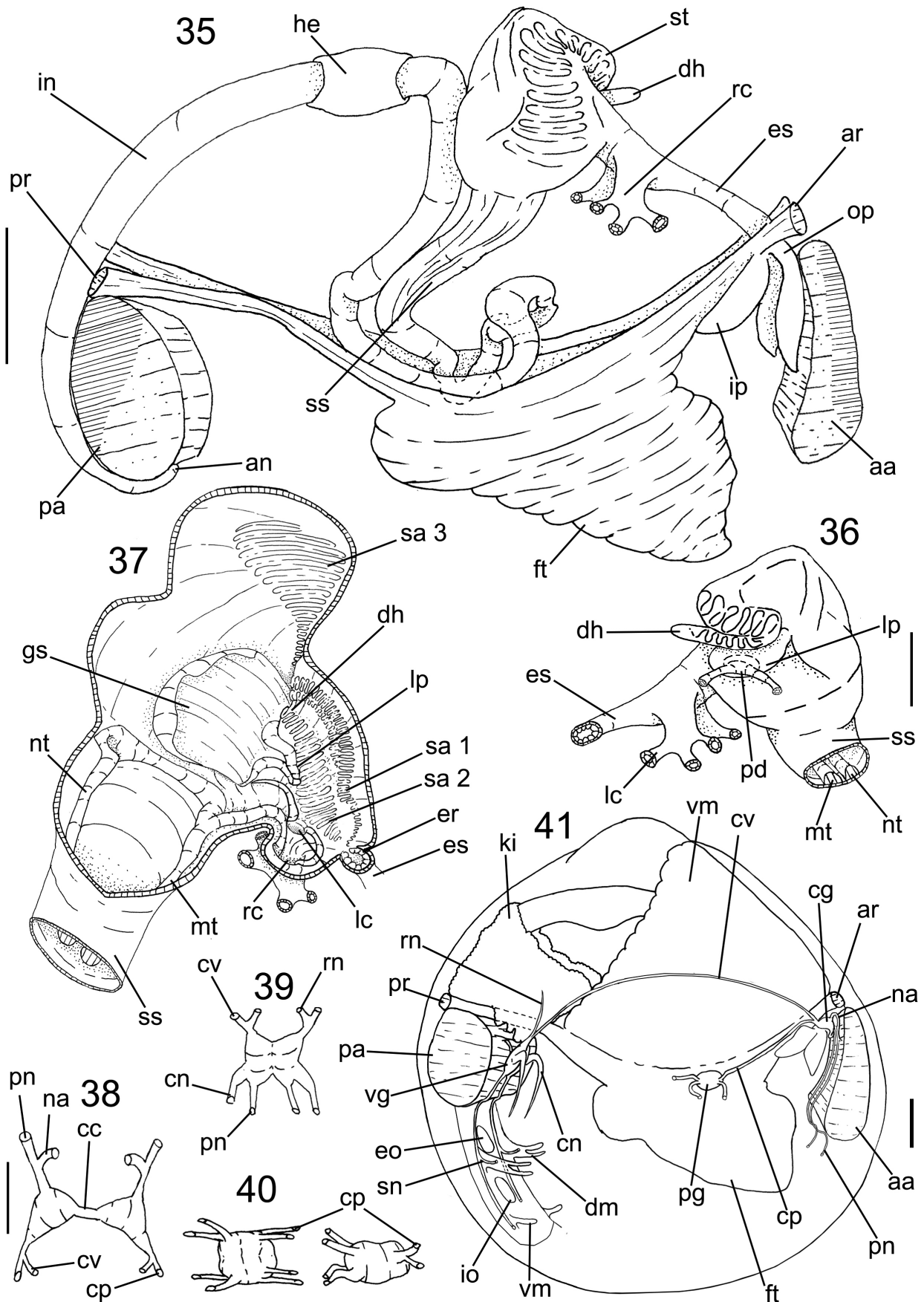
Measurements. (length by height by width, in mm): FMNH 328260 (specimen #1 of 4): 14.2×13.4 by 8.5; UF 122840 #1: $12.5 \times 11.4 \times 8$; UF 264025 #1: $10.8 \times 10.3 \times 5.6$; #2: $14.18 \times 13.55 \times 8.55$.

Distribution. USA: eastern coast from Delaware to the Florida Keys, and Gulf of Mexico coast from western Florida to Texas; **Bahamas;** **Mexico:** Yucatan, Quintana Roo; **Guatemala;** **Bonaire** (Lee 2009); **Suriname.**

Type material. Syntypes: *Cyrenoidea floridana*: UNITED STATES OF AMERICA • **Florida**, Fort Myers, Everglades; 2 specimens; USNM 87735. Marco Island; 3 specimens;



Figures 25–34. Anatomy of *Cyrenoida floridana* (FMNH 328260). **25.** Right view valve removed, some structures seen by transparency of mantle lobe; **26.** Same, with mantle and gill removed; **27.** Incurrent and excurrent siphons, posterolateral view, right mantle lobe partially removed, some adjacent structures shown; **28.** Siphonal tips; right view, both partially sectioned longitudinally; **29.** Mantle border, section in its ventromedial portion; **30.** Gill, transverse section in its central portion; **31.** Incurrent and excurrent siphons, interior view, with details of their base and siphonal muscles; **32.** Labial palps, ventral view, outer hemipalps deflected dorsally; **33.** Posteroventral visceral region, ventral view, showing fusion of inner demibranchs in siphonal base; **34.** Pericardial region, posterodorsal view, dorsal mantle wall partially removed. Scale bars: 2 mm (25–28, 31, 33–34); 1 mm (29, 30, 32).



Figures 35–41. Anatomy of *Cyrenoida floridana* (FMNH 328260). **35.** Digestive tubes as *in situ*; right lateral view; **36.** Stomach, left lateral view; **37.** Stomach, right lateral view, right wall opened and deflected to show inner gastric surface; **38.** Cerebral ganglia, ventral view; **39.** Visceral ganglia, ventral view; **40.** Pedal ganglia; right figure in lateral right view, left figure in dorsal view; **41.** Nervous system topology, right lateral view. Scale bars: 2 mm (35–41, 40); 0.5 mm (38–40).

USNM 60974. 3 specimens, USNM 60975; Boca Ciega Bay; 3 specimens; USNM 60973. St Johns River mouth; 10 specimens; USNM 46846 (Figs 1–4). **Georgia**, Brunswick Island; 30 specimens; USNM 129197. *Cyrenoida guatemalensis*: **Lectotype**: GUATEMALA • Livingstone; ANSP 107532 (Figs 5–10). Note: Pilsbry's (1920) description of *C. guatemalensis* can be read as having been based on a single specimen and Van Regteren Altena (1971: 41) interpreted the specimen of ANSP 107532 as a holotype. However, Pilsbry is known for imprecisely indicating the type material at hand (P. Callomon, G. Rosenberg pers. comm.) and the existence of more than one original type specimen cannot be excluded. We accept Van Regteren Altena's (1971) action as a fixation of lectotype by inference of holotype under ICZN (1999) Article 74.6.

Examined material. UNITED STATES OF AMERICA • 10 valves; **Delaware**, Kent County, Bombay Hook; 01 Aug. 1954; Morrison and Rosso leg.; USNM 777892. • 10 valves; **New Jersey**, Delaware Bay, Cumberland County, Fortescue; 15 Jul. 1957; J.P.E. Morrison leg.; USNM 777894. • 6 valves; Delaware Bay, Cumberland County, Dividing Creek; J.P.E. Morrison leg.; 15 Jul. 1957; USNM 777895. • 20 valves; **Maryland**, Dorchester County; J.P.E. Morrison leg.; 11 Jul. 1954; USNM 777893. • 10 valves; Dorchester County, near Elliot, gullet of black duck; F.M. Uhler leg.; USNM 592260. • 8 valves; Queen Anne's County; 11 Jul. 1954; J.P.E. Morrison leg.; USNM 777890. • 12 valves; Arundel County, Deale, marshy, head of small inlet; 11 Jul. 1953; J.P.E. Morrison leg.; USNM 777887. • 6 valves; Arundel County; 15 Jul. 1953; J.P.E. Morrison leg.; USNM 777889. • 4 valves; Arundel County, Deale; 13 Jun. 1954; J.P.E. Morrison leg.; USNM 777888. • 6 valves; **North Carolina**, Beaufort, under algal mats; R.W. Heard leg.; USNM 678947. • 1 specimen; **South Carolina**, Horry/Georgetown counties, Murrell's Inlet, in black muddy sand under log near high tide line, S. edge of inlet along road; 03 Dec. 1955; J.P.E. Morrison leg.; USNM 1437782. • 6 valves; **Georgia**, McIntosh County, Fort King George Historic Site, Darien, exposed under drift logs and boards; 15 Dec. 1954; Cmdr. Miller leg.; USNM 707264. • 4 valves; Glynn County, Saint Simons Island; Oct. 1938; H.A. Rehder leg.; USNM 535386. • 1 valve; **Mississippi**, Jackson County, Halstead Bayou; Gulf Coastal Marine Laboratory leg.; UF 246126. • 15 valves; **Florida**, Wakulla County, St. Marks; 17 Jun. 1958; United States Fish and Wildlife Service leg.; USNM 612256. • 5 valves; Saint Johns County, Saint Augustine; F.E. Spinner leg.; ANSP 54330. • 6 valves; Saint Johns County, Halifax River; USNM 253659. • 12 valves; Volusia County, Daytona [Beach]; C.W. Johnson leg.; USNM 336943. • 2 valves; Marion County, creek SE of Ocala; 15 May. 1928; T. Van Hyning leg.; ANSP 152656. • 8 valves; Citrus County, Homosassa; E. Roper leg.; USNM 131462. • 4 specimens; Hernando County; G. Prime leg.; ANSP 68457. • 25 specimens; Hernando County, Aripeka; G. Prime leg.; ANSP 73905. • 20 valves; Pasco/Hernando counties,

Aripeka; L. Pine leg.; USNM 149932. • 10 valves; Hernando County, Little Blind Creek; 04 Dec. 1927; T. Van Hyning leg.; ANSP 149568. • 1 valve; Pasco/Hillsborough counties, Hillsborough River; E.J. Post leg.; USNM 591792. • 6 valves; Charlotte County, Punta Gorda; 1928; J.L. Madden leg.; USNM 592290. • 1 specimen; Glades County, Caloosahatchee River; C.W. Johnson leg.; ANSP 62888. • 5 valves; W Florida; C.W. Johnson leg.; ANSP 59610. • 30 valves; Collier County, Carnestown; 12 Apr. 1928; T. Van Hyning leg.; ANSP 152655. • 4 valves; Dade County, Miami; Olsen leg.; USNM 153404. • 10 valves; Dade County, Miami; 07 Apr. 01; Benedict leg.; USNM 330959. • 10 specimens; Dade County, Miami; S. N. Rhoads leg.; ANSP 77046. • 8 valves; Dade County, Miami; S. N. Rhoads leg.; ANSP 189416. • 16 valves; Lee County, Fort Myers; Hend. leg.; USNM 455820. • 16 valves; Lee County, Fort Myers; Henderson leg.; USNM 425820. • 2 valves; Lee County, Fort Myers, Everglades; 1896; C.W. Johnson leg.; USNM 87735; syntype. • 20 valves; Monroe County, Big Pine Key; C. Margaret leg.; UF 122840. • 14 valves; Florida Keys, Monroe County, Big Pine Key; 27–28 Dec. 1956; C. Phillips, F. Philips leg.; FMNH 63059. • 31 valves; Florida Keys, Monroe County, pond on Big Pine Key; 1968; M. Teskey leg.; FMNH 293174. • 4 specimens + 15 valves; Florida Keys, Monroe County, Blue Hole quarry on Big Pine Key, Florida Keys; 024°42'21"N, 081°22'49"W; shoreline sediment at base of vegetation, salinity measured at 3 ppt; sta. FK-727; 03 May. 2004; R. Bieler, P.M. Mikkelsen leg.; FMNH 328260. • 67 valves; Florida Keys, Monroe County, Blue Hole quarry on Big Pine Key; 024°42'24"N, 081°22'48"W; sta. FK-794; 18 Nov. 2007; R. Bieler, P. Sierwald, E.A. Glover, J.D. Taylor leg.; same locality as in study by Taylor *et al.*, 2009; FMNH 333534. • 5 valves; Florida Keys, Monroe County, off mangrove island SE of Cudjoe Key; 024°38'12"N, 081°18'12"W; 1 m; sta. FK-745; 15 May. 2005; R. Bieler, P. Mikkelsen leg.; FMNH 333533. • 11 valves; Florida Keys, Monroe County, quarry on Big Pine Key, in sediment on shoreline rock; 024°41'56"N, 081°23'03"W; sta. FK-728; 03 May. 2005; R. Bieler, P. Mikkelsen leg.; FMNH 333535. • 3 valves; Florida Keys, Monroe County, mosquito ditch on Big Pine Key; 024°42'30"N, 081°23'02"W; sta. FK-939; 25 Apr. 2010; R. Bieler, P. Mikkelsen leg.; FMNH 333532. • 3 valves; Florida Keys, Monroe County, Spanish Harbor Key; sta. JG-708-0; 08 Jun. 2000; J. Gerber leg.; FMNH 308431. • 1 valve; Florida Keys, Monroe County, Ohio Key, land-locked pond adjacent to Ohio–Missouri Key bridge; 024°40'20"N, 081°14'36"W; sta. FK-723; 29 Apr. 2004; R. Bieler, P. Mikkelsen leg.; FMNH 314324. • 4 valves; Monroe County, Boca Chica Key; H. Hemphill leg.; ANSP 7983. **BAHAMAS** • 14 valves; **Grand Bahama Island**; 26°31'00"N, 78°46'30"W; J.N. Worsfold leg.; ANSP 374956. • 1 valve; Dover Sound, 26°35'05"N, 78°13'20"W, May. 1983; J. N. Worsfold leg.; ANSP 374350. • 2 valves; 26°31'00"N, 78°46'30"W; J.N. Worsfold leg.; ANSP 374957. • 6 valves; **Abaco**; C.W. Johnson leg.; USNM 425821. • 2 valves; S side of Abaco;

O. Bryant leg.; USNM 180503. MEXICO • 10 valves (1 figured specimen); **Quintana Roo**, Boca de Paila; Tulane University leg.; UF 264025. • 20 valves; Tulane University; Emily & Harold Vokes leg.; UF 264026. GUATEMALA • 2 valves; **Livingstone**; 1913; A. A. Hinkley leg.; syntype; ANSP 107532.

Discussion

Cyrenoida floridana and other *Cyrenoidea* anatomy

Recently, the family Cyrenoididae was classified together with Cyrenidae and Glauconomidae based on analyses of nuclear 18S and 28S rRNA genes (Taylor et al. 2009). This statement was corroborated using an integrative approach, with anatomical, molecular, and ontogenetic views (Bieler et al. 2014). In both cases, only one species each from Cyrenidae and Glauconomidae was used, and a robust discussion comparing morphological characters among the families was still lacking. Here a detailed discussion is provided, including morphological traits of the three families using available data from general traits of the family to details of species anatomy.

Very little information regarding *Cyrenoida floridana* has been available. What morphological data have been published are fragmented and lack details (e.g. Taylor et al. 2009; Bieler et al. 2014). Kat (1978) provided a histological and ecological study on the species, but only part of those results were formally published (Kat 1982).

Habitat: All three families that comprise *Cyrenoidea* are infaunal in soft sediments, inhabiting fresh to brackish waters worldwide. Most species present geographic distributions in Asia (e.g., Glauconomidae), but Cyrenidae includes species naturally distributed worldwide, except for Arctic and Antarctic regions, as well as introduced invasive species (Bieler and Mikkelsen 2019). Cyrenoididae is known only from African and American continents in brackish waters. Kat (1978) commented that *C. floridana* presents hermaphroditism, brooding behavior, juvenile dispersion by buoyance, thermal resistance, and site selection as adaptations to survive in intertidal areas of severe conditions subject to rapid environmental change.

Additional details about *C. floridana* habitat in Canary Creek, Delaware were provided by Kat (1978). There, the species lives buried horizontally in the first two centimeters of sediment. High sulfide concentration in the sediment appears to inhibit colonization, although the species can tolerate a wide range of salinity, suspended particles, temperature, pH, and moisture content. Highest population densities were found in moist sediment protected by a primary layer of halophytic vegetation and a secondary cover of filamentous algae.

Shell: As is common in fresh and brackish water bivalves (Cummings and Graf 2015), *C. floridana* presents a persistent periostracum covering the entire shell surface. In contrast to African *Cyrenoida* species, Cyrenidae,

and Glauconomidae that are covered in thick, brown to greenish periostracum (Huber 2015), *C. floridana* bears a thin periostracum. Periostracum in fresh and brackish water bivalves is a common feature, because such environments present much more corrosive properties (Cummings and Graf 2015) and this organic layer protects against shell corrosion. Kat (1978) noted that *C. floridana* periostracum is thicker near the shell border and almost invisible and iridescent near the umbo. Kat (1978) also described parallel folds in the thicker portions of periostracum in adult specimens of *C. floridana*. In living specimens, these folds create ridges that act to channel water when the bivalve is partially exposed, helping the animal to stay hydrated and thermally stable.

Shape among *Cyrenoidea* varies from rounded (Cyrenoididae), trigonal (Cyrenidae), to anteroposteriorly elongated with a straightening of the posterior shell margin (Glauconomidae) (Joannis 1835; Owen 1959; Boss 1982; Huber 2015). Some representatives present a gap between the valves at the posterior end of the shell, as in *Polymesoda* (Morton 1976) and *Glauconome* (Owen 1959).

Shell size among *Cyrenoida* species can be variable. The African *Cyrenoida* can reach 30 mm (e.g. *C. dupontia*) whereas the American *C. floridana* reaches only 14 mm. Despite the size difference, ecological and morphological characteristics allow African and American species assignment to the same genus, i.e., the habitat in brackish waters and the unique hinge pattern. Compared with other *Cyrenoidea*, *C. floridana* can be considered the smallest representative of the superfamily; Cyrenidae attain lengths of 39 to more than 150 mm and Glauconomidae between 20 and 79.5 mm (Huber 2015). Cyrenidae is the only family within this group that presents concentric ribs; the remaining species are adorned only with growth lines (Boss 1982; Huber 2015). Commarginal growth increments are here described for *C. floridana*. These thickened lines could be associated with seasonal growth anomalies or seasonal metabolic changes (Lewis and Cerrato 1997).

Hinge: Hinge pattern in *Cyrenoidea* is somewhat variable. Glauconomidae and Cyrenidae share the presence of at least three cardinal teeth positioned perpendicular to the shell umbo, and one of these teeth can be bifid (Boss 1982; Huber 2015). Members of Cyrenidae share with *C. floridana* the presence of lateral teeth, but those in Cyrenidae can be either smooth or serrate. Cyrenoididae, including African *Cyrenoida* and *C. floridana*, presents a combination of lateral and cardinal teeth forming a unique pattern.

Microtubules: The *C. floridana* shell presents microtubules that partially penetrate the shell. This feature is shared with some Cyrenidae, e.g., *Corbicula* species (Araújo et al. 1994), but is absent in others, e.g., *Polymesoda* (see Tan Tiu and Prezant 1989). According to Waller (1980), microtubules are more common in epifaunal than in infaunal bivalves and, based on studies in Arcidae, could be associated with photoreception, anchorage sites for the mantle, improvement of the surface for res-

piratory change, protection against boring organisms, or sites of ionic regulation. Rosso (1954) commented that microtubules could be involved in embryonic nourishment. Robertson and Coney (1979) stated that they could be used for monitoring water conditions, although this is unlikely given that they do not fully penetrate the shell. Tiu Tan and Prezant (1989) hypothesized that microtubules could act to lighten juvenile shells, aiding in planktonic dispersal, and to assist in anchoring the mantle to shell during locomotion or biomineralization. At any rate, microtubules occur in several bivalve families as a post-larval feature (Malchus 2010) and resemble the aesthetes found in some gastropods and polyplacophorans (Simone 2011), which mostly have receptor functions. Kat (1978) observed that the vast majority of tubules in *C. floridana* do not fully penetrate the shell and are filled with non-secretory, finger-like projections from the external layer of the mantle. The mantle includes blood sinuses that, when filled, could extend the projections inside the tubules, improving tissue attachment to the shell. Therefore Kat (1978) discarded any notion of secretory or sensory function and believed that the microtubules serve to anchor the mantle to the inner shell surface.

Pallial line: Another feature variable among Cyrenoidea is the pallial line. In *Cyrenoida floridana* it is weak, discontinuous, and without a sinus, whereas Glauconomidae presents a narrow, deep sinus, and in Cyrenidae, it varies between entire to including a shallow or deep sinus (Huber 2015). The difference between the presence of a sinus and pallial line intensity is due to size and form of the siphonal muscles, and the quantity of pallial muscles, respectively. Siphonal muscles in *C. floridana* are paired, short, and thin and insert on the pallial muscle insertion line; Glauconomidae and Cyrenidae have strong, long muscular bands that dislocate the pallial muscle insertion toward the interior of the valve (Owen 1959; Kurniushin and Glaubrecht 2002). Pallial muscles in *C. floridana* are spaced along the mantle border, creating a discontinuous pallial line, whereas Glauconomidae and Cyrenidae present powerful pallial muscles strongly marked on the internal surface of the shell (Owen 1959; Glaubrecht et al. 2003).

Main muscular system: All known species of Cyrenoidea present anterior and posterior adductor muscles, a pair of anterior pedal retractor muscles, and a pair of posterior retractor muscles (Owen 1859; Huber 2015); a pair of pedal protractor muscles are present in some Cyrenidae (Simone et al. 2015). The overall symmetry of the adductor muscles in Cyrenoidea and Glauconomidae is slightly anisomyarian, with the anterior adductor muscle reniform and the posterior adductor muscle oval, but some Cyrenidae are isomyarian (Morton 1976; Simone et al. 2015; Huber 2015).

Foot: Foot shape among Cyrenoidea varies between Cyrenidae, which bear a well-developed, strong, wide, axe-shaped foot, whereas Cyrenoididae and Glauconomidae have a wedged-shaped foot (Owen 1959; Mansur and Meier-Brook 2000; Huber 2015). Dall (1898) de-

scribed the *Cyrenoida floridana* foot as filiform, and this condition was used to classify the species in Lucinidae. The image of a living specimen included by Bieler et al. (2014, fig. 3 N) can be referenced to verify shape and color of foot in living condition. Kat (1978) commented that the foot of *C. floridana* can be extended by more than one shell length in the sediment, lacks a byssal gland, and in large individuals required up to 10 minutes to complete a burrowing cycle.

Mantle: The number of mantle folds and presence of papillae are very diverse among Cyrenoidea. In Cyrenidae, mantle papillae are relatively common (Boss 1982; Huber 2015), although they are not shared among all genera and species (Simone et al. 2015). Although three mantle folds are found in Cyrenidae (Morton 1976), the genera *Corbicula* and *Cyanocyclus* present four mantle folds, with the middle one doubled and forming papillae at the anteroventral portion of mantle border (Mansur and Meier-Brook 2000). *Cyrenoida floridana* and Glauconomidae present a three mantle folds arrangement, but in *C. floridana* the middle fold bears papillae, whereas this does not occur in Glauconomidae (Owen 1959). The degree of mantle fusion of both mantle lobes varies greatly. In Cyrenidae (Huber 2015; Simone et al. 2015) and *C. floridana*, fusion occurs only at the siphonal area, whereas Glauconomidae presents a wider fusion along the inner fold and internal surface of middle fold (Owen 1959), forming an anterior pedal gape.

Siphon: In Cyrenidae, the siphons can originate from the inner fold, as in *Polymesoda* (see Morton 1976) and *Cyanocyclus* (see Mansur and Meier-Brook 2000; as *Neocorbicula*) or from fusion of the inner fold and the internal surface of middle fold, as in *Corbicula* (see Mansur and Meier-Brook 2000). This second pattern is also found in Glauconomidae (Owen 1959), classified as type B by Yonge (1957). In *C. floridana*, the siphon originates as in *Polymesoda*, classified as a type A (Yonge 1957), but it presents a row of papillae described as type B by Yonge (1982).

Siphon length is variable in Cyrenoidea from long or short, fused or separated (Huber 2015). Glauconomidae presents long siphons totally fused, whereas Cyrenidae can show separated short to long siphons (Owen 1959; Morton 1976; Mansur and Meier-Brook 2000; Huber 2015). The siphons of *C. floridana* were shown in living condition by Bieler et al. (2014, fig. 3N); showing siphons with different lengths, with the excurrent siphon two times longer than incurrent, although the incurrent one has a wider opening than the excurrent; this can be explained by the different degree of contraction of the two siphons. Kat (1978) illustrated *C. floridana* siphons with the excurrent one being longer, but half of its length is due to the extroverted siphonal membrane. At any rate, the cyrenoidid siphons are not as long as those of the Glauconomidae, which reach ~50% of the animal length, but they are not as short as those of the cyrenid *Polymesoda erosa* (Solander, 1786) (Morton 1976). All three families share the pattern of the incurrent opening wider than the excurrent (Owen 1959; Morton 1976; Boss 1982;

Mansur and Meier-Brook 2000; Simone et al. 2015). The different sizes of incurrent and excurrent siphons in *C. floridana* is a reversed pattern from that of the Glauconomidae, in which the excurrent siphon is slightly shorter than the incurrent (Owen 1959); Cyrenidae presents siphons of similar lengths (Morton 1976; Mansur and Meier-Brook 2000; Simone et al. 2015).

The presence of papillar rows at the siphonal apertures is a common feature in all three families. They have, at least, one row of papillae at the external rim of the incurrent siphon (Morton 1956; Owen 1959; Glaubrecht et al. 2003). Glauconomidae, *C. floridana*, and some Cyrenidae present a siphonal membrane in the external excurrent siphonal opening, but some Cyrenidae genera, e.g. *Corbicula*, also can present papillar rows at this opening (Araújo et al. 1993; Glaubrecht et al. 2003). Glauconomidae and some Cyrenidae, such as *Corbicula* and *Polymesoda erosa* present papillae beyond the siphonal tip. In Glauconomidae, the external surfaces of both siphons present small papillae, especially on the ventral and dorsal surfaces (Owen 1959). In *Corbicula* and *P. erosa*, the papillae occur at the siphonal base in parallel rows, which can surround the siphonal base, as in *P. erosa* (see Morton 1976), or can be distributed along the entire mantle border up to the siphonal tip, as in *Corbicula* (Glaubrecht et al. 2003). According to Kat (1978), the siphonal papillae in *C. floridana* serve a regulatory function for the incurrent siphon. When incurrent water presents a high concentration of suspended material or the siphon tips are below the sediment surface, the papillae are positioned over the siphonal entrance, whereas in conditions of low suspended material, the siphons are held at maximum dilatation with the papillae away from the entrance.

The siphonal base or tips in all three families show pigment as rings or spots in pale to dark brown, orange, or black (Owen 1959; Morton 1976; Araújo et al. 1993; Glaubrecht et al. 2003).

Siphonal musculature is composed of siphonal retractor muscles that can be present as only one muscle band or divided into two bands, one dorsal and one ventral. In Glauconomidae and most Cyrenidae, the siphonal retractor muscle appears as one wide muscular band; it is fan-shaped in Glauconomidae (Owen 1959; Korniushev and Glaubrecht 2002), but in *C. floridana* and *Polymesoda floridana* (Conrad, 1846) each present two muscular bands (Simone et al. 2015) with the dorsal band bifid in *C. floridana*.

Gills: Gills in Cyrenoidea are eulamellibranch and both demibranchs are present (Huber 2015). Both demibranchs are wide in *C. floridana*, and the anterior portion of the inner demibranch inserts between the labial palps. In Cyrenoidea, gill size is usually small, without insertion of the inner demibranch between the palps (Owen 1959; Morton 1976; Simone et al. 2015).

Stomach: The stomach of *C. floridana* presents the style sac and the midgut conjoined, the major typhlosoles penetrating both left and right caeca, presence of a normal gastric shield that penetrates at dorsal hood and left pouch, ducts from digestive diverticula opening into

the stomach via left pouch and both caeca, presence of sorting area at roof of anterior side of the dorsal hood and sometimes extending over the right wall of stomach, sorting area in the left pouch, and a sorting area at anterior roof of stomach from esophagus to dorsal hood. Gastric shield teeth and a cuticular lining of the stomach, coded in the morphological/molecular analysis by Bieler et al. (2014) and reaffirmed as having been observed by I. Temkin who conducted that part of the study (2019 pers. comm.), were not detected in the histological study by Kat (1978) nor in the present study. Kat (1978) also described two short caeca, one adjacent to the gastric shield and another near the intestinal groove, but those structures were not observed during this study. The main differences between *C. floridana* and other Cyrenoidea is that in Corbiculidae and Glauconomidae, digestive ducts open independently on the lateral wall of the stomach and Cyrenidae presents a sorting area on the anterior roof and posterior wall of the stomach.

Intestinal coiling among Cyrenoidea shows a simple, loose pattern, with few loops. Midgut course can be summarized as starting as style sac, running ventrally in the visceral sac, followed by a portion running anteriorly, forming a dorsal loop directing the intestine posteriorly, then following parallel to the style sac until leaving visceral sac, passing through the pericardium, crossing the dorsal surface of the kidney, and ending on the surface of posterior adductor muscle (Owen 1959; Morton 1976; Simone et al. 2015). This pattern is a little more complex in *Corbicula*, which presents several spiral coils at the anterior portion of the midgut (Araújo et al. 1993).

The anus of *C. floridana* is located on the ventral surface of the posterior adductor muscle (Fig. 35: **an**). This is a unique position. The anus in the Cyrenidae can be found at different points on the posterior surface of the posterior adductor muscle (Owen 1959; Morton 1976; Araújo et al. 1993; Simone et al. 2015).

In living specimens of *C. floridana*, Kat (1978) observed that the portion of the intestine posterodorsal to the anterior adductor muscle is folded when the intestine was empty, but straightened when the intestine was filled.

Excretory system: The kidney did not present any unusual gross features during this study. In histological sections, Kat (1978) described U-shaped tubules differentiated into anterior and posterior portions based on cell type. Also Kat (1978) described soft, rounded concretions of unknown composition in the kidney lumen and, because some were too large to be expelled, hypothesized that the kidney acts as a storage area for such concretions as a strategy to survive in intertidal environments.

Reproductive cycle: Little is known about the reproductive cycle of *C. floridana*. Kat (1978, 1982) described the reproductive physiology of *C. floridana*, identifying the species as a simultaneous hermaphrodite, describing four gonadal stages and observing developing juveniles in the demibranchs, indicative of brooding behavior, as in many Cyrenidae (Huber 2015). Kat (1978) also noticed that a few specimens in the studied population were purely males.

Based on the reproductive cycle of *C. floridana*, Kat (1978) discussed differing fertilization strategies, based on the number of embryos developing inside the gonad. Kat (1978) noticed that southern populations of *C. floridana* present a characteristic gonadal development and spawn twice a year, whereas northern populations present discreet alterations on gonadal development and successfully spawn only once. Due these differences Kat hypothesized that both populations are in process of differentiation.

Nervous system: Kat (1978) performed a histological study on *C. floridana* specimens and provided additional details about the nervous system, especially regarding microscopic nerve branching and the presence of statocysts on the pedal ganglia.

Parasitism: Calcareous nodules on the inside of *C. floridana* shells are sometimes visible in published photographs of this species, e.g. those by Abbott (1974) and Abbott and Morris (1995). They have been variously reported, e.g. by Van Regteren Altena (1971: 41) who referred to their presence on the type material of *Cyrenoida guatemalensis* (see Figs 7, 8) and stated that “the present Suriname specimens also possess blisters interiorly and I think that their presence is caused by some outward influence in all.” Nodules were noted frequently during this study, although the small numbers of specimens examined do not present a reliable percent occurrence in the species or any living population. They were neither mentioned nor figured in the morphological study by Kat (1978), which involved an unquantified “large number” of shells collected over nine months from the coast of Delaware. Each nodule seen during the present study presents as a small orifice on an igloo-shaped structure that could indicate parasitism by Trematoda (Huntley and De Baets 2015). Kat (1978) detected trematodes in sporocyst stages throughout the bivalve’s soft tissues in a small percentage of histological sections and notice that the infection negatively affected gonadal development and excretion. Also, histozoic and coelozoic parasitism by the haplosporidian protist *Minchinia* sp. has been reported in samples of *C. floridana* (Reece et al. 2004; Arzul and Carnegie 2015).

Conclusions

1. *Cyrenoida floridana* is morphologically characterized by valves externally covered by thin light brown periostracum; muscle scars and pallial line only faintly visible on the internal shell surface, and a unique hinge pattern.
2. The species presents microtubules on the interior shell wall.
3. Anatomically the species presents slightly unequal adductor muscles; few pallial muscles that are well separated from each other; an inner demibranch inserted between the labial palps; demibranchs fused to each other along their posterior ends; totally fused and pigmented siphons that originate from the inner mantle fold; two pairs of siphonal retractor muscles;

loose intestinal coiling; and the anus located on the ventral surface of the posterior adductor muscle.

4. *Cyrenoida floridana* shares a similar habitat, its gill morphology, most of the stomach complexity, and siphonal pigmentation with members of Cyrenidae and Glauconomidae. It differs from the latter two families in its hinge composition, small size, weak and discontinuous pallial line, few and separated pallial muscles at the mantle border, the presence of papillae along the entire ventral border of the mantle except the siphonal area, an excurrent siphon longer than the incurrent one, a bifid dorsal siphonal retractor muscle tip, demibranchs inserting between the labial palps, the absence of independently digestive ducts opening into the lateral side of stomach, and the anus located at the ventral surface of the posterior adductor muscle.
5. Calcareous nodules presenting single circular openings are common on the internal shell surface and could be associated with trematode parasitism.

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