

ANATOMY AND SYSTEMATICS OF NORTHWESTERN ATLANTIC *DONAX*
(BIVALVIA, VENEROIDEA, DONACIDAE)

Luiz Ricardo L. Simone¹ & Joanne R. Dougherty²

ABSTRACT

A morphological examination of two nominal species of northwestern Atlantic donacids, *Donax fossor* and *D. variabilis*, was performed to resolve current taxonomic discrepancies. Specimens from New Jersey, South Carolina, and Florida were studied confirming the typical anatomical bauplan for the family as previously reported. Detailed investigation of all organ systems revealed a series of differences, mainly in the shell, mantle border papillae, siphonal tentacles and papillae, and digestive system, supporting separation of the two species. Other shared morphological features, such as the gill muscle, pallial muscles of the siphonal chamber, the glandular dorsal gastric caecum, and length of the style sac, have potential value for further functional and systematic studies.

Key words: *Donax fossor*, *Donax variabilis*, differentiation, distribution, western Atlantic.

INTRODUCTION

The systematics of the genus *Donax* along the Atlantic coast of the United States has been problematic for the last three decades. The nomenclature of *Donax variabilis* Say, 1822, which occupies the intertidal zone of sandy beaches from Virginia to Mississippi, has been particularly confusing. *Donax variabilis* became a primary junior homonym when *Latona variabilis* Schumacher, 1817, was proposed as a new name for *Donax cuneatus* Linnaeus, 1758 (Morrison, 1971). Because *Latona* is considered a subgenus of *Donax*, the name *D. variabilis* Say is thus preoccupied. Morrison's (1971) revision of the group identified the next available name for this species, *D. protracta* Conrad, 1849. Morrison considered *D. protracta*, from the southeastern coasts of the United States and eastern Gulf of Mexico, to be a subspecies of *D. roemeri* Philippi, 1849, from the northern and western Gulf of Mexico. Based on morphological differences between the two forms, Morrison designated the eastern forms as *D. roemeri protracta* Conrad, 1849, and the western forms as *D. roemeri roemeri* Philippi, 1849, because the publication date of *D. roemeri* was five months prior to that of *D. protracta*. Later, Boss (1970) proposed conservation of the name *D. variabilis* Say, 1822, to the International Commission on Zoological Nomenclature and

it was subsequently conserved (Melville, 1976).

In addition to his recognition of *D. roemeri roemeri* and *D. roemeri protracta*, Morrison (1971) recognized four other species of *Donax* inhabiting the eastern shores of the United States: *Donax fossor* Say, 1822, from Cape Hatteras, North Carolina, to New Jersey and occasionally the southern shores of Long Island; *D. parvula* Philippi, 1849, from North Carolina to southern Florida; *D. dorotheae* Morrison, 1971, along the shores of the northeastern Gulf of Mexico; and *D. texasianus* Philippi, 1847, along the shores of Louisiana, Texas and Mexico.

Subsequent analysis of RAPD DNA markers failed to support Morrison's distinction between the subspecies *D. roemeri roemeri* and *D. roemeri protracta* (Adamkewicz & Harasewych, 1996). The analysis also demonstrated that *D. parvula* was indistinguishable from *D. fossor*, and *D. dorotheae* was indistinguishable from *D. texasianus*, with the latter of each pair having taxonomic priority. That analysis simplified the biogeography of *Donax*; *D. variabilis* shares the Atlantic coast with *D. fossor* and the Gulf coast with *D. texasianus*.

Even in older literature, taxonomic problems are notable. Say (1822) described two similar species of *Donax*, *D. fossor* ("the digger"), a northern form inhabiting the coasts of New Jersey and Maryland, and *D. variabilis* ("highly

¹Museu de Zoologia da Universidade de São Paulo, Cx. Postal 42594, 04299-970 São Paulo, SP, Brazil; Irsimone@usp.br
²Department of Biology, Villanova University, Villanova, Pennsylvania 19085, USA; Joanne.dougherty@villanova.edu

variable"), a southern form from the coasts of Georgia and eastern shores of Florida. Based on the original species descriptions, differentiating the two species is quite difficult. Size, color, sculpture, and thickness of the shell valves are most often used to differentiate the two species (Say, 1822; Chanley, 1969). *Donax variabilis* reaches a length of 19 mm, exhibits an wide variety of colors, and displays radial shell sculpture that is more pronounced on the posterior slope (Say, 1822; Chanley, 1969; Morrison, 1971). *Donax fossor* reaches 13 mm length, exhibits only "yellowish" or "whitish" colors, has smooth radial sculpturing over the entire shell and exhibits thickened valves at the anterior end to produce "lips" (Say, 1822; Chanley, 1969; Morrison, 1971). The escutcheon area of *D. variabilis* juveniles of about 5 mm in length is more rounded toward the vertical, whereas in *D. fossor*, the same is regularly sloping parallel to the rounded posterior ridge (Morrison, 1971). *Donax fossor* is believed to inhabit the surf and subtidal zones in the winter, while *D. variabilis* inhabits the intertidal zone throughout the year (Morrison, 1971).

These two species are so similar that the populations of New Jersey have often been labeled *D. variabilis* (e.g., Johnson, 1927; A. E. Wood & H. E. Wood, 1927; McDermott, 1983; Alexander et al., 1993), which exacerbates taxonomic confusion in the northern limit of *Donax* on the Atlantic coast of North America. Some authors accept the validity of these two species (e.g., Johnson, 1934; Morris, 1947; Miner, 1950; Morrison, 1971; Abbott & Morris, 1995), while others suggest that the two are conspecific (Abbott, 1954, 1974; Chanley, 1969). For example, Chanley (1969) suggests that *D. fossor* is merely a summer range extension of *D. variabilis*, based on sporadic populations of *Donax* on Long Island, New York, that do not overwinter. Chanley (1969) hypothesized that these northern populations were actually *D. variabilis* recruited from larvae swept north of the sustainable species range due to fortuitous warm-water currents, and that conchological differences between the two species are merely ecophenotypic. However, Morrison's (1971) revision of Chanley's specimens concluded that *D. fossor* is not a summer range extension of *D. variabilis*, further supporting the distinction between the two species.

According to Morrison (1971), *Donax variabilis* is not found north of Virginia Beach, Virginia, and *D. fossor* is not found south of

Nag's Head, North Carolina. Thus, their ranges do not overlap until Virginia Beach, Virginia. The objective of this study was to compare the anatomy of specimens from Florida and South Carolina (supposedly *D. variabilis*) to that of specimens from Avalon, New Jersey (supposedly *D. fossor*), to provide evidence for confirming or refuting the biological validity of the two species along the east coast of the United States.

Anatomical investigations have been performed for about ten species of donacids (e.g., Ridewood, 1903; Pelseneer, 1911; Graham, 1934; Yonge, 1949; Duval, 1963; Nakazima, 1965; Wade, 1969; Narchi, 1972, 1978; Mouëza & Frenkiel, 1974, 1976, 1978; Odiete, 1981; Hodgson, 1982; Ansell, 1983; Salas-Casanova & Hergueta, 1990; Passos, 1998), however, none has been published on the species analyzed here. Those papers provide a secure scenario for discussion of the anatomical characters at the species and family level.

MATERIAL AND METHODS

Specimens were collected and fixed directly in 70% ethanol. Gross dissections were performed with the specimen immersed in fixative under a stereomicroscope. Histological 5- μ m serial sections of partial regions were stained with Mallory's trisain. All drawings were made with the aid of a camera lucida.

Abbreviations used in figures: am, anterior adductor muscle; an, anus; au, auricle; cm, cruciform muscle; cv, ctenidial (efferent) vessel; dd, ducts to digestive diverticula; dg, digestive diverticula; dh, dorsal hood; di, inner demibranch; do, outer demibranch; dv, dorsal portion of outer demibranch covering visceral mass; es, esophagus; fe, foot elevator muscle; ff, fecal furrow; fm, posterior foot retractor muscle; fp, foot protractor muscle; fr, anterior foot retractor muscle; ft, foot; gf, ventral gastric fold; gm, gill retractor muscle; go, gonad; gs, gastric shield; id, insertion of outer demibranch in mantle; in, intestine; ip, inner hemipalp; is, septum in siphonal base separating infra- and suprabranchial chambers; ki, kidney; mb, mantle border; mm, mantle muscles of siphonal chamber; mp, mantle papillae; op, outer hemipalp; pa, posterior adductor muscle; pc, pericardium; pd, dorsal caecum; pp, palp; sc, siphonal chamber; se, excurrent siphon; ri, ridge in esophageal insertion in stomach; rt, rectum; sh, shell; si, in-

current siphon; sm, siphonal retractor muscle; ss, style sac; st, stomach; ty, typhlosole; um, fusion between left and right mantle lobes; ve, ventricle; vg, visceral ganglia; vm, visceral mass.

Abbreviations of institutions: FMNH, Field Museum of Natural History, Chicago; MZSP, Museu de Zoologia da Universidade de São Paulo, Brazil; USNM, National Museum of Natural History [United States National Museum], Washington, DC.

SYSTEMATICS

Donax fossor Say, 1822
(Figs. 1–5, 11, 12, 14, 16–26)

Synonymy (for additional references, see Morrison, 1971: 456):

Donax fossor: Abbott, 1974: 509 (as form of *D. variabilis*); Emerson & Jacobson, 1976: 415–416, pl. 43, fig. 15; Abbott & Morris, 1995: 91; Adamkewicz & Harasewych, 1996: 97–103.

Donax variabilis: McDermott, 1983: 529–538; Alexander et al., 1993: 289–303.

Diagnosis

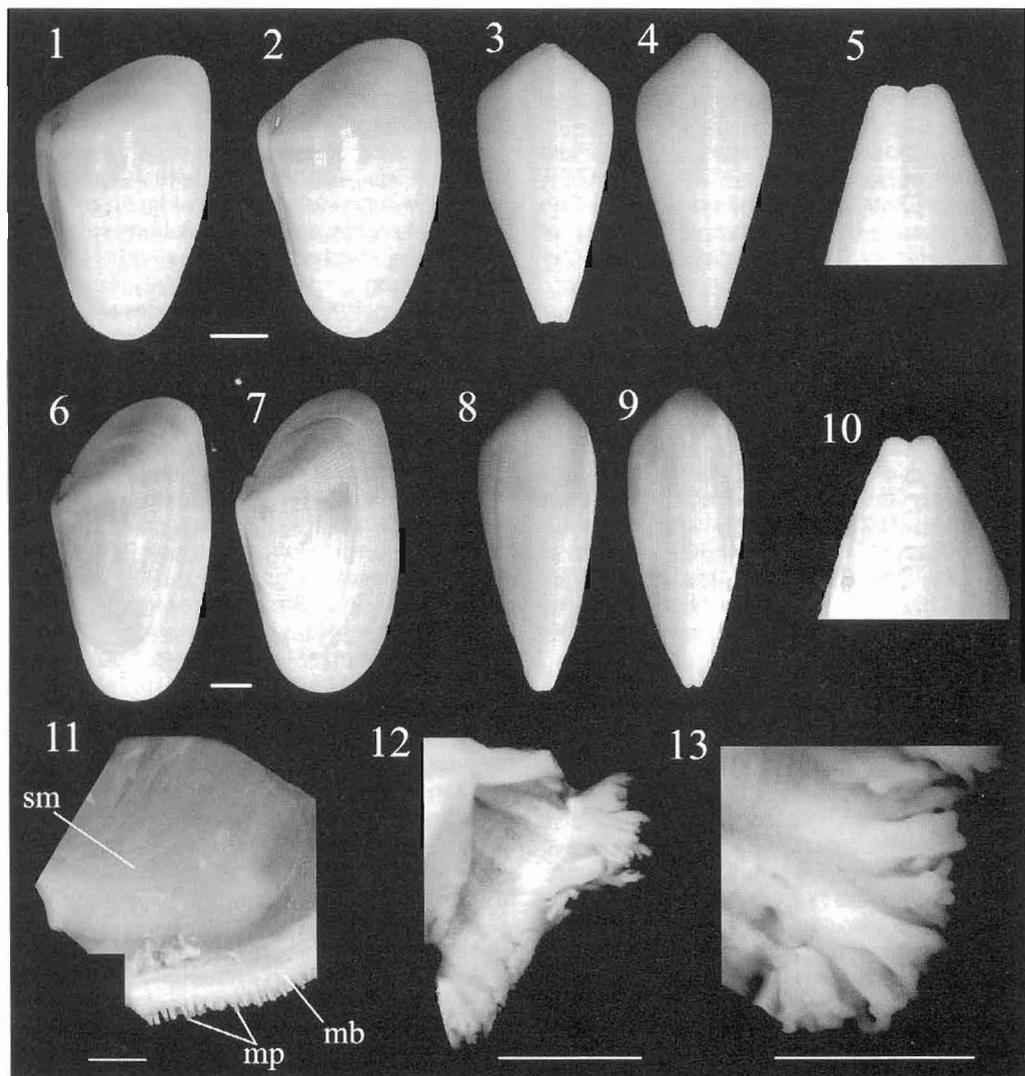
Shell triangular; anterior (pedal) edge very thick; posterior region flattened, with a flattened posterior margin. Mantle edge and siphons with large number of papillae. Gastric style sac almost straight, with distal region positioned in ventral region of visceral sac. Intestine bearing few undulations.

Description

Shell (Figs. 1–5, 14): Up to 13 mm length. Color varying from pure white to yellowish. Outline somewhat triangular; general shape cuneiform; anterior region with very thick edge, producing a strong slope. Umbo located in posterior third of hinge, weakly protruded, rounded. Outer surface smooth, bearing only concentric undulations. Hinge with three teeth in left valve, including small tooth just anterior to umbo, another two cardinal teeth at posterior level of ligament (Fig. 14, arrows) of similar size, transverse, separated by short depression. Right valve with single small, transverse tooth articulating between two cardinal teeth of left valve; also bearing sockets for teeth of left valve.

Mantle: Mantle border of somewhat uniform width along its length; mostly not fused, except in siphonal area and short portion ventral to them (Figs. 18, 20, um). Mantle border with two folds, each with series of small papillae of uniform size; each papilla long, slender (Figs. 11, 18, 20), with longitudinal, narrow furrow along outer side; tip concave, edges slightly projecting. Siphons separated from each other, similarly sized (Figs. 18, 20), each protected by cavity formed by mantle, depth about one-quarter of animal's length. Siphonal walls thickly muscular, basal region thinner, with muscle fibers arranged radially like a fan (Figs. 11, 20), originating from pallial sinus of shell. Incurrent siphon with 6–7 larger folds projecting inwardly, each bearing several papillae on outer surface (Figs. 12, 16, 17, 20), smaller and simpler tentacles among large papillae (Figs. 16, 17). Excurrent siphon with simpler tentacles than incurrent siphon (Fig. 20); tentacles narrow, with 2–3 papillae on distal end; fecal groove narrow, shallow, running longitudinally along internal ventral surface of excurrent siphon (Fig. 20, ff), terminating in a furrow on siphonal edge between two tentacles. Cruciform muscle located on ventral edge between middle and posterior thirds of mantle edge, at base of incurrent siphon (Figs. 18, 20), inside mantle fusion (Fig. 21); anterior branches longer and narrower, inserted on shell tangentially; posterior branches broader, shorter, inserted on shell almost perpendicularly (Fig. 21). Several radial muscle fibers connecting posterior edge of posterior adductor muscle with mantle border, becoming successively larger ventrally, abruptly terminating in middle region of siphonal area; ventral fibers thicker, branched distally (Fig. 23).

Mantle Organs: Pallial cavity very ample (with only narrow dorsal portion not covered by cavity) (Fig. 18). Gills small, occupying about one-third of pallial cavity (Fig. 18). Outer demibranch shorter than inner demibranch anteriorly, gradually becoming about same width posteriorly. Both demibranch ventral edges simple, lacking food grooves (Figs. 18, 19). Gill insertion on visceral mass between demibranchs, that of inner demibranch (on visceral mass) more ventral; outer demibranch with portion dorsal to gill insertion, covering visceral mass (Fig. 19), with shallow longitudinal furrow separating



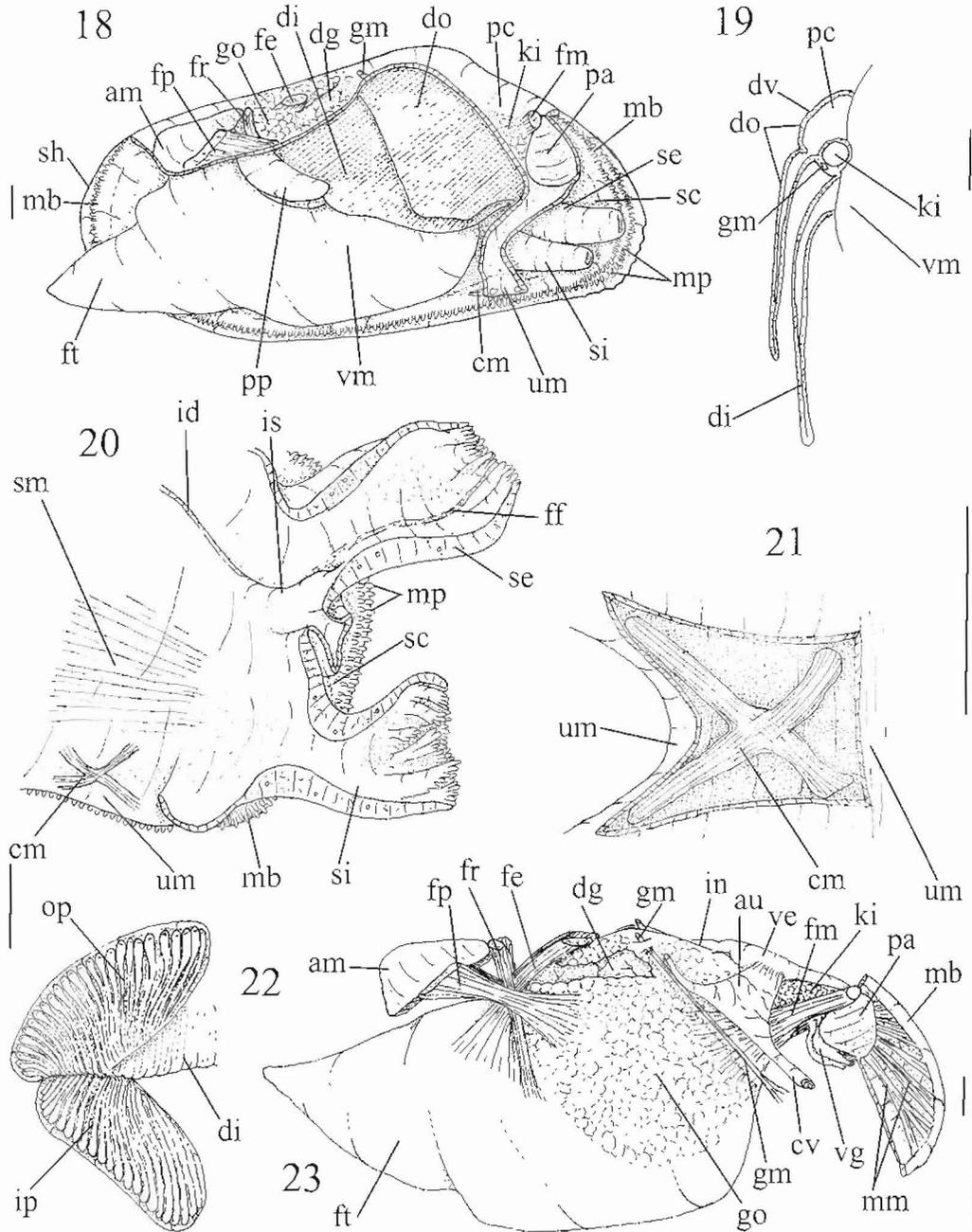
FIGS. 1–13. *Donax* shells and mantle. FIGS. 1–5: *Donax fossor* shells, two specimens MZSP 36508 (New Jersey); FIGS. 1, 2: Right lateral view; FIGS. 3, 4: Ventral view; FIG. 5: Detail of anterior region of Fig. 4; FIGS. 6–10: *Donax variabilis* shells, two specimens MZSP 36509 (South Carolina); FIGS. 6, 7: Right lateral view; FIGS. 8, 9: Ventral view; FIG. 10: Detail of anterior (foot) region of Fig. 9; FIG. 11: *D. fossor*, left mantle lobe, inner view, detail of siphonal basal region; FIG. 12: *D. fossor*, incurrent siphon, detail of apical region opened longitudinally, showing tentacles and papillae on inner edge; FIG. 13: Same for *D. variabilis*, showing more weakly developed tentacles and papillae. Scales = 2 mm.

this portion from remaining demibranch, connecting to visceral mass far dorsal of gill insertion. Gill dorsal and ventral connections to visceral mass ciliary only. Gills connected to one another posterior to visceral mass in median line; no other anatomical gill connec-

tion, either with mantle (only by cilia) or with posterior adductor muscle. A communication between infra- and suprabranchial chambers remaining in contracted gill condition (Fig. 20). Mantle transverse septum in ventral base of excurrent siphon, separating infra-



FIGS. 14–17. *Donax* hinges and siphons. FIG. 14: *Donax fossor* hinge, left valve at left, arrows indicating teeth. Scale = 1 mm; FIG. 15: Same for *D. variabilis*; FIG. 16: *D. fossor*, extended incurrent siphon, dorsal-slightly apical view. Scale = 0.5 mm; FIG. 17: Same, apical view, showing fully extended tentacles and papillae. Scale = 0.5 mm.



FIGS. 18-23. *Donax fossor* anatomy. FIG. 18: Whole specimen, left view, left mantle lobe partially removed (except for portion in siphonal base); FIG. 19: Left gill, transverse section at mid-region, with some adjacent structures. FIG. 20: Siphonal region, left view, both siphons opened longitudinally along their left side; FIG. 21: Detail of posteroventral union of mantle lobes, at base of incurved siphon, inner view, with inner layer of tissue removed; FIG. 22: Left labial palp, outer hemipalp deflected, with adjacent region of inner demibranch; FIG. 23: Foot and visceral mass, left view, emphasizing main muscle system, pericardial structures, topology of visceral glands, gill muscle and mantle muscles shown in situ. Scale bars = 1 mm.

and suprabranchial chambers, somewhat short (Fig. 20, is). Palps long, curved, slightly triangular, located in anteroventral corner of inner demibranch, relatively small (Fig. 18); outer surface smooth; inner surface (Fig. 22) with several uniform transverse folds, somewhat parallel to palp posterodorsal edge; dorsal portion of folds very narrow, ventral portion broader, a short transverse whitish furrow located in distal end of each fold of outer demibranch (Fig. 22, op); folds ending short distance from palp inner edge, producing a narrow smooth margin. Palps and palp folds gradually becoming shorter toward anterior, a smooth inner area in palp portion surrounding mouth.

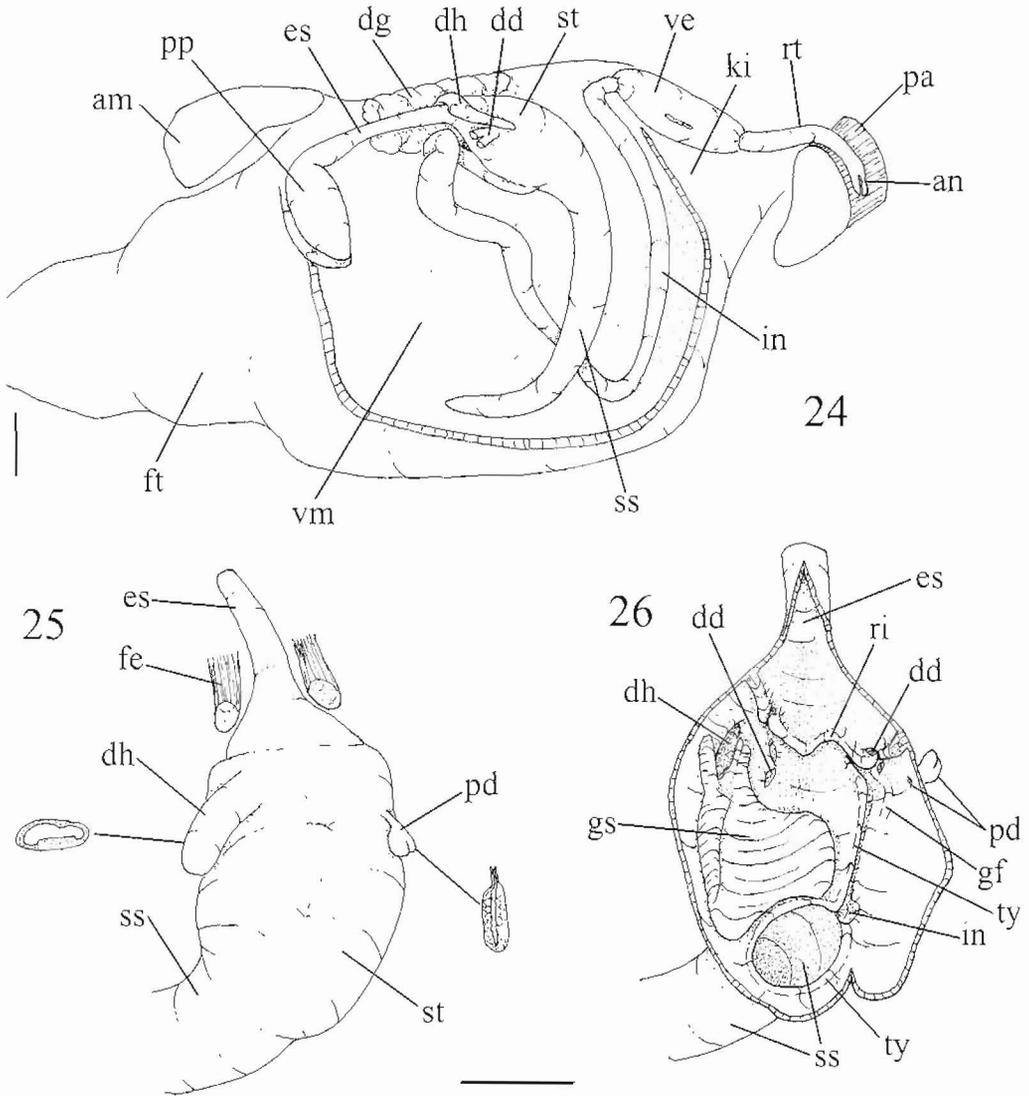
Foot and Main Muscle System: Foot large, about half of body size; triangular, tip broadly pointed, laterally flattened, bent in retracted condition (Figs. 18, 23). Adductor muscles similarly sized (Figs. 18, 23); each with ventral region somewhat circular, dorsal somewhat pointed. Anterior adductor muscle close to anterodorsal shell edge. Posterior adductor muscle at middle level of posterior shell edge. Paired anterior protractor muscles broad, thin, flat, originating in posteroventral edge of anterior adductor muscle, passing posteroventrally to insert fan-like on lateral wall of visceral mass (Figs. 18, 23, fp). Paired anterior pedal retractor muscles (Figs. 18, 23, fr) long, flat, narrow, slender, originating on shell just posterior to anterior adductor muscle, internally crossing anterior protractor muscles, passing superficially posteroventrally, inserting fan-like in middle region of transitional area of foot-visceral mass. Paired pedal levator muscles (Figs. 18, 23, 25, fe) narrow, long, cylindrical, originating in umbonal cavity at some distance posterior to anterior adductor muscle, running ventrally and anteriorly close to median line and close to one another, covered laterally by anterior retractor muscles, inserting in transitional area of foot-visceral mass. Paired posterior pedal retractor muscles (Figs. 18, 23, fm) originating on shell just dorsal to posterior adductor muscle, passing anteroventrally, narrow in posterior half, gradually becoming broad in anterior half, inserting on outer surface of posterior region of visceral mass. Paired gill retractor muscles very narrow, thin (Figs. 18, 19, 23, gm), originating on very small area of umbonal cavity at some distance posterior to levator muscles, penetrating pallial cavity between

demibranchs, passing along gill to posterior end, becoming thinner and more diffuse (Fig. 23).

Visceral Mass: Internal organs visible by transparency only in narrow dorsal umbonal region (Fig. 18). Digestive diverticula pale green in preserved specimens, somewhat small, surrounding gastric area in dorsal region of visceral cavity. Gonad very large (Fig. 23), cream-colored, occupying most of visceral cavity, surrounding all visceral structures except renopericardial organs and some portions of digestive diverticula.

Circulatory and Excretory Systems: Pericardial cavity relatively small, located just anterior to posterior adductor muscle (Figs. 18, 23). Paired auricles triangular, with thin, transparent walls, central region connecting directly to gill, anterior and posterior verticles connecting to relatively short efferent gill vessels (Fig. 23). Auricles connecting to ventricle laterally. Ventricle surrounding intestine. Kidney whitish, mostly solid, located ventral to pericardium, compressed by posterior pedal retractor muscles, gonad and posterior adductor muscle.

Digestive System: Mouth somewhat small, in central region between palps. Esophagus relatively long, dorsoventrally flattened, away from anterior adductor muscle (Fig. 24). Stomach (Figs. 24–26) ovoid, located in umbonal region of visceral mass totally surrounded by digestive gland. Gastric dorsal hood narrow, about half of stomach length, originating close to median line, situated on left side covering dorsal surface of stomach (Figs. 24, 25, dh); inner surface smooth, except for broad, low longitudinal fold on ventral surface (Figs. 25–26). Dorsal gastric caecum (Figs. 25, 26, pd) small, generally bifid; walls whitish, glandular, with inner space narrow; connecting to stomach by very narrow duct to anterior third of stomach left-dorsal side (Fig. 25). Inner surface of posterior esophagus smooth; esophageal junction with stomach marked by tall, transverse typhlosole almost entirely surrounding this insertion, except at two narrow portions in lateroventral region where pair of furrows begin, running toward ducts of digestive diverticula (Fig. 26). Digestive diverticular apertures located lateroventrally in anterior gastric region. Dorsal hood aperture just dorsal of left apertures of digestive diver-



FIGS. 24–26. *Donax fossor* anatomy. FIG. 24: Visceral mass showing digestive system in situ, left view, with some adjacent structures; left wall of visceral sac, gonad and part of digestive diverticula removed; FIG. 25: Stomach, dorsal view, with some adjacent structures; with transverse sections of dorsal hood and dorsal caecum; FIG. 26: Same. Left wall sectioned longitudinally and deflected, exposing inner surface. Scale bars = 1 mm.

ticula; transverse, low fold (closer to dorsal hood aperture) separating the two digestive diverticula apertures, bearing short projection of gastric shield (Fig. 26). Aperture of gastric dorsal caecum immediately dorsal to right aperture of digestive diverticula; deep, narrow furrow running posteriorly from right

aperture of digestive diverticula, along ventral-right inner gastric surface, to intestinal origin. Gastric shield occupying about one-third of inner gastric surface, located in ventral and left inner regions (Fig. 26). Intestine and style sac origins adjacent (that of intestine right-anterior); narrow low fold almost

entirely surrounding style sac origin, except for short portion adjacent to intestinal origin (Fig. 26). Style sac entirely separated from intestine, very long (longer than dorsoventral height of visceral cavity), passing ventrally, gradually narrowing, with tip somewhat pointed, curved forward (Fig. 24). Intestine mostly narrow, from origin in posteroventral region of stomach, to right of style sac, passing anteriorly, contouring ventral gastric region to left-anterior side, abruptly twisting towards right, passing sinuously posteroventrally, crossing right side of style sac ventral third; in posteroventral region of visceral cavity curving dorsally, to region just posterior to stomach; curving abruptly toward anterior, crossing pericardium and posterodorsal surface of posterior adductor muscle (Fig. 24). Anus in middle region of posterior adductor muscle, bearing short longitudinal, narrow notch on median line (Fig. 24, an).

Genital System: Gonad apparently dioecious.

Central Nervous System: Not seen in detail, except for pair of large visceral ganglia (Fig. 23) close to one another on posteroventral surface of posterior adductor muscle.

Measurements (length x dorsoventral height x lateral width, in mm): MZSP 36508: no. 7, 16.5 x 9.1 x 5.8; no. 8, 10.4 x 6.0 x 3.6.

Material Examined: U.S.A.: New Jersey; 66th St., Avalon, MZSP 36508, 13 specimens (Joanne Dougherty, coll., 01/ix/2001).

Donax variabilis Say, 1822
(Figs. 6–10, 13, 15, 27)

Synonymy (for additional references, see Morrison, 1971: 550–551):

Donax variabilis: Boss, 1970: 205–206; Tiffany, 1971: 82–85; Melville, 1976: 19–21; Abbott, 1974: 509, fig. 5753; Emerson & Jacobson, 1976: 414, pl. 43, fig. 14; Mikkelsen, 1981: 230–239; Leber 1982: 297–301; Mikkelsen, 1985: 308–311; Vega & Tunnell, 1987: 97–135; Ruppert & Fox, 1988: 158, pl. B28; Estes & Adamkewicz, 1991: 321–332; Bonsdorff & Nelson, 1992: 358–365; Nelson et al., 1993: 317–322; Adamkewicz & Harasewych, 1994: 97–103; Meinkoth, 1995: 556, pl. 321; Ellers, 1995a: 120–127; 1995b: 128–137, 1995c: 138–147; Abbott & Morris, 1995: 91, pl. 4, fig. 37; Adamkewicz & Harasewych, 1996: 97–103;

Wilson, 1999: 61–83; Manning & Lindquist, 2003: 415–422.

Diagnosis

Shell elongated-elliptic; anterior (pedal) edge thin; posterior region compressed, anterior slope weak. Mantle edge and siphons with few weakly branched papillae. Gastric style sac curved, with distal region positioned in anterodorsal region of visceral sac. Intestine bearing several loops.

Description

Shell (Figs. 6–10, 15): Up to 20 mm. Color very variable, from pure white to yellowish, grayish, brownish and reddish (see Morrison, 1971, for further comments). Outline somewhat elongated and elliptical; general shape weakly cuneiform, somewhat compressed; anterior (pedal) region with edge about half as thin as that of preceding species. Umbos located between middle and posterior third of hinge, weakly protruded, rounded. Remaining characters similar to those of *Donax fossor*, differing in: (1) larger size; (2) surface with more developed radial sculpture; (3) anterior pedal region thinner, narrowing gradually, with a more rounded anterior margin (Figs. 8–10); (4) posterior siphonal slope longer (Figs. 6, 7), less abrupt than in *D. fossor*. This last difference is reflected in the position of umbo, which is in posterior quarter of dorsal edge in *D. fossor*, between middle and posterior third of dorsal edge in *D. variabilis*; (5) cardinal teeth shorter (Fig. 15), total hinge somewhat narrower.

Mantle: Features similar to those of *D. fossor*, with the following differences: Mantle border entirely bearing single series of papillae on inner fold; outer fold double, smooth or with very small, low papillae between papillae of inner fold, with two series of papillae in region of siphonal chamber similar to those in *D. fossor*. Mantle border papillae similar to those of *D. fossor*, but smaller. Distal end of incurrent siphon with 5–6 folds proportionally smaller than those of *D. fossor*, bearing fewer papillae on outer surface (Fig. 13); that of excurrent siphon with 4–5 folds lacking papillae or bearing few, very small papillae; fecal furrow also present (Fig. 27, se).

Mantle Organs: Similar to those of *D. fossor*, including characters of gill and palps (Fig. 27).

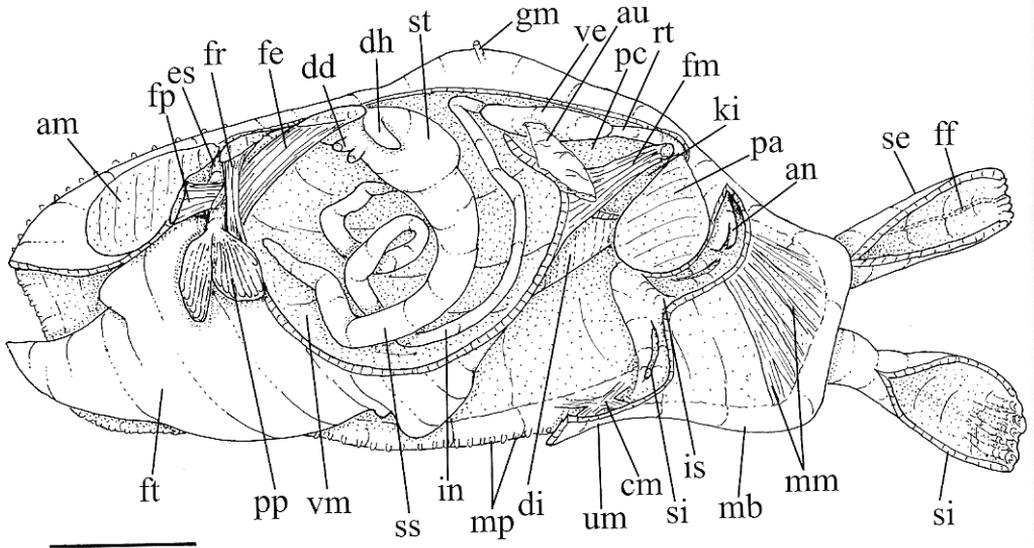


FIG. 27. *Donax variabilis* anatomy, whole specimen, left view, left mantle lobe partially removed (except at siphonal base), left gill, left wall of visceral sac, gonad and digestive diverticula removed, palps deflected. Scale = 2 mm.

Foot and Main Muscle System, Visceral Mass, and Circulatory and Excretory Systems: Similar to those of *D. fossor* (Fig. 27).

Digestive System: General organization similar to that of *D. fossor*, with following differences. Dorsal gastric caecum proportionally larger, with glandular portion more greatly developed. Gastric style sac proportionally longer (Fig. 27, ss), passing surrounding ventral border of visceral sac, decreasing gradually, in mid-ventral region of visceral mass ascending anteriorly, slightly sinuously, with distal end in mid-dorsal region of visceral sac at short distance from mouth. Intestine more convolute (Fig. 27, in), bearing a strong loop in region ventral to stomach.

Measurements (length x dorsoventral height x lateral width, in mm): MZSP 36509: no. 1, 12.4 x 7.5 x 5.5; no. 3, 17.7 x 7.8 x 5.5.

Material Examined: U.S.A.: South Carolina; Pawleys Islands, south end, MZSP 36509, 15 specimens (David Bushek, coll., 11/viii/2002). Florida; Franklin County, south corner of St. George Island, MZSP 36507, 12 specimens (Harry G. Lee & R. L. Whipple, coll., 29/vii/2002); Florida Keys; Monroe County, Matecumbe Key, FMNH 202068, 17 shells, 202070, 12 shells, 202071, 3 shells (A. Koto, coll.).

DISCUSSION

Donax fossor and *D. variabilis* are very similar in their morphology. The most significant difference in the shell is the pedal region, which is thicker and with a narrow slope in *D. variabilis* (Fig. 5), whereas in *D. fossor* is of a shape more typical of donacids, and with a thinner shell border (Fig. 10). The outline is also different; *D. fossor* has a more developed posterior slope and this region is shorter and more blunt (Figs. 1–2, 6–7). *Donax fossor* has many more papillae both at the mantle border and the siphons, with two series of somewhat long papillae (Fig. 11), while most specimens of *D. variabilis* have a single row, although some bear very small and short papillae on the outer mantle border fold. The incurrent siphon of *D. fossor* (Figs. 14, 15) has larger apical folds with proportionally more papillae on the outer surface than in *D. variabilis* (Figs. 12, 13). The tip of the excurrent siphon generally lacks papillae in *D. variabilis* (Fig. 27), or has very small papillae, while that of *D. fossor* has well-developed papillae (Fig. 20). The gastric style sac is longer in *D. variabilis*, being curved and slightly sinuous, with its distal end close to the mouth (Fig. 27); in *D. fossor*, the style sac is almost straight, with the distal end in the ventral region of the visceral mass (Fig. 24).

It is important to emphasize that the style sac proportions were consistent among specimens of different sizes of both species. The intestine of *D. variabilis* is more highly looped than that of *D. fossor*, mainly in its proximal region ventral to the stomach (Fig. 27).

Both *Donax* species show anatomy consistent with previous reports for the family, such as the siphons being separated from each other beginning at their base, the presence of a cruciform muscle, and the separation of the gastric style sac from the adjacent intestine. The circulatory system is very similar to that of *Donax trunculus* (Linnaeus, 1758) (Mouëza & Frenkiel, 1978). The cruciform muscle (Fig. 21) is cited as a character of the superfamily Tellinoidea (Yonge, 1949); it matches that previously reported in both species studied (Mouëza & Frenkiel, 1974: figs. 2-5).

The siphonal constitution is also similar to those described for other species of the family, with a clear siphonal septum separating supra- and infrabranchial chambers (Mouëza & Frenkiel, 1978; Hodgson, 1982). This septum (Fig. 20, id) aids in directing water flow to the gills, because the gills are not anatomically connected to the siphons. This study is the first report of a fecal furrow (Figs. 20, 27, ff) in any donacid species. The shape, number and constitution of the siphonal tentacles and papillae (Figs. 11, 12) are obviously associated with the high energetic environment that donacids normally inhabit; their differences have been very useful in comparative analysis among sympatric species (e.g., Ansell, 1981; 1983: fig. 6). Species of the genera *Iphigenia* (Narchi, 1972) and *Egeria* (Purchon, 1963) have weakly developed siphonal papillae and inhabit low energy environments. The well-developed radial pallial muscles connecting the posterior edge of the posterior adductor muscle with the mantle edge (Figs. 22, 27, mm) is a unique feature of the two species studied herein, and has not been described for any other species. The more dorsal of these muscles is short and thin, gradually becoming thicker, longer and more distinct ventrally, where it abruptly terminates.

A portion of the outer demibranch covering the visceral sac (Fig. 19, dv) is as previously reported in other donacids; this portion has been called supra-axial extension of the ctenidium (Ansell, 1983). The two species studied here differ from other known donacids in lacking a food groove on the ventral edge

of the inner demibranch; this groove has been found in other species (Purchon, 1963; Yoloze, 1977; Ansell, 1981; Passos, 1998). Another interesting feature is the well-developed gill muscle (Fig. 22, gm), which occurs in both studied species, originating inside the umbonal cavity (Figs. 18, 27) and penetrating the mantle along the gill just between the demibranchs. The posterior region of the gill muscle is more diffuse and thin. Only one similar structure has been reported in the literature on donacids, the so-called "demibranch muscle" in *Donax gouldii* Dall, 1921, studied by Pohlo (1967). However, some confusion with the levator muscle of the foot exists in that description (Pohlo, 1967: 330). The gill muscle could be an exclusive feature of the three species (*D. fossor*, *D. variabilis*, *D. gouldii*).

The stomach of *Donax variabilis* and *D. fossor* (Figs. 25, 26) is also typical of donacids, having a transverse typhlosole in the esophageal insertion and a dorsal hood at left. However, the dorsal caecum found on the right side of stomach can be absent in some species (Nakazima, 1965) and has been called a stomach appendix (Pohlo, 1967; Wade, 1969; Narchi, 1972, 1978; Passos, 1998) or posterodorsal caecum (Yonge, 1949; Purchon, 1963; Mouëza & Frenkiel, 1976; Salas-Casanova & Hergueta, 1990). These last authors demonstrated that in *D. venustus* (Poli, 1795) sand grains and similar coarse particles pass by the dorsal caecum; in the present species the caecum appears to be a gland, because it is almost entirely filled by glandular tissue and has a narrow duct separating it from the stomach (Figs. 25, 26, pd). Dorsal caeca have been reported in members of other tellinoidean families (Yonge, 1949: figs. 28-29), but they differ from those of donacids in being larger and amply opened to the stomach. The species studied here also lack tall gastric typhlosoles as those reported in the above-mentioned papers. The highly curved style sac is a unique feature of *D. variabilis* (Fig. 27); however, Mouëza & Frenkiel (1976) showed a long style sac for *D. trunculus*, figuring it as a semi-circle.

The configuration of the intestinal coils is also useful for species distinction (e.g., Ansell, 1983: fig. 7) reinforcing the distinction between the two species studied here. The donacid intestine is normally weakly coiled, however, *Egeria radiata* (Lamarck, 1804) is an exception (Purchon, 1963: fig. 10).

CONCLUSIONS

- (1) Specimens from New Jersey (attributable to *Donax fossor*) and South Carolina and Florida (attributable to *D. variabilis*) are confirmed as separate species, distinguishable by morphological features of shell and soft parts, in agreement with the molecular findings of Adamkewicz & Harasewych (1996).
- (2) Morphological study of *Donax fossor* and *D. variabilis* confirmed the typical bauplan of the family as revealed by previous authors. Detailed investigation of all organ systems showed useful distinguishable differences that are consistent in each sample and sufficient for specific separation.
- (3) At the present time, the radial pallial muscles of the siphonal chamber are unique to *Donax fossor* and *D. variabilis*, not having been described for any other donacid species. The gill muscle is an exclusive feature of these two species and *D. Gouldii*.

ACKNOWLEDGMENTS

This study is one result of the International Marine Bivalve Workshop, held in the Florida Keys, 19–30 July 2002, funded by U.S. National Science Foundation award DEB-9978119 (to co-organizers R. Bieler and P. M. Mikkelsen), as part of the Partnerships in Enhancing Expertise in Taxonomy [PEET] Program. Additional support was provided by the Bertha LeBus Charitable Trust, the Comer Science & Education Foundation, the Field Museum of Natural History, and the American Museum of Natural History. This study was also part of the junior author master's thesis, supported by the Lerner-Gray Fund of the American Museum of Natural History, Conchologists of America, and Sigma Xi, and is in part supported by Brazilian Fundação de Amparo a Pesquisa do Estado de São Paulo, process nos. 00/11074-5 and 00/11357-7, to the senior author. We are grateful to Flavio Dias Passos (Instituto de Biociências, Universidade de São Paulo) for bibliographical support and suggestions related to anatomy. We are also grateful to David Bushek and Harry Lee for providing specimens.

LITERATURE CITED

- ABBOTT, R. T., 1954, *American seashells*. Van Nostrand, Princeton, New Jersey. 541 pp., 32 pls.
- ABBOTT, R. T. & P. A. MORRIS, 1995, *Shells of the Atlantic & Gulf coasts & the West Indies*. Peterson Field Guide, Houghton Mifflin Company, Boston, Massachusetts. 350 pp., 74 pls.
- ADAMKEWICZ, L. & M. G. HARASEWYCH, 1994, Use of randomly amplified polymorphic DNA (RAPD) markers to assess relationships among beach clams of the genus *Donax*. *The Nautilus*, Supplement 2: 51–60.
- ADAMKEWICZ, L. & M. G. HARASEWYCH, 1996, Systematics and biogeography of the genus *Donax* (Bivalvia: Donacidae) in eastern North America. *American Malacological Bulletin*, 13: 97–103.
- ALEXANDER, R. R., R. J. STANTON, JR. & J. R. DODD, 1993, Influence of sediment grain size on the burrowing abilities of bivalves: correlation with distribution and stratigraphic persistence of selected neogene clams. *Palaos*, 8: 289–303.
- ANSELL, A. D., 1981, Functional morphology and feeding of *Donax serra* Röding and *Donax sordidus* Hanley (Bivalvia: Donacidae). *Journal of Molluscan Studies*, 47: 59–72.
- ANSELL, A. D., 1983, Species of *Donax* from Hong Kong; morphology, distribution, behaviour, and metabolism. Vol. 1: 19–47, in: B. MORTON & D. DUDGEON, eds., *Proceedings of the Second International Workshop on the Malacofauna of Hong Kong and Southern China*. Hong Kong University Press, Hong Kong.
- BONSDORFF, E. & W. G. NELSON, 1992, The ecology of coquina clams *Donax variabilis* Say, 1822, and *Donax parvula* Philippi, 1849, on the east coast of Florida. *The Veliger*, 35: 358–365.
- BOSS, K. J., 1970, *Donax variabilis* Say, 1822 (Mollusca: Bivalvia): proposed validation under the plenary powers. *Bulletin of Zoological Nomenclature*, 27: 205–206.
- CHANLEY, P., 1969, *Donax fossor*: a summer range extension of *Donax variabilis*. *The Nautilus*, 83: 1–14.
- DUVAL, D. M., 1963, The comparative anatomy of some lamellibranch siphons. *Proceedings of the Malacological Society of London*, 35: 289–295.
- ELLERS, O., 1995a, Behavioral control of swash-riding in the clam *Donax variabilis*. *Biological Bulletin*, 189: 120–127.
- ELLERS, O., 1995b, Discrimination among wave-generated sounds by a swash-riding clam. *Biological Bulletin*, 189: 128–137.
- ELLERS, O., 1995c, Form and motion of *Donax variabilis* in flow. *Biological Bulletin*, 189: 138–147.
- EMERSON, W. & M. K. JACOBSON, 1976, *The American Museum of Natural History guide to shells*. Alfred A. Knopf, New York. 482 pp.
- ESTES, J. H. & S. L. ADAMKEWICZ, 1991, A comparison over time of two Virginia populations of the coquina clam, *Donax variabilis*. *Virginia Journal of Science*, 42: 321–332.

- GRAHAM, A., 1934, The structure and relationships of lamellibranches possessing a cruciform muscle. *Proceedings of the Royal Society of Edinburgh*, 54(2): 158-187.
- HODGSON, A. N., 1982, Studies on wound healing and regeneration of the siphons of the bivalve *Donax serra* (Röding). *Transactions of the Royal Society of South Africa*, 44(4): 489-498.
- JOHNSON, C. W., 1927, *Donax fossor*, not *D. variabilis*. *The Nautilus*, 41: 140.
- JOHNSON, C. W., 1934, List of marine Mollusca of the Atlantic coast from Labrador to Texas. *Proceedings of the Boston Society of Natural History*, 40: 1-204.
- LEBER, K. M., 1982, Bivalves (Tellinacea: Donacidae) on a North Carolina beach: contrasting population size, structure, and tidal migrations. *Marine Ecology - Progress Series*, 7: 297-301.
- MANNING, L. & N. LINDQUIST, 2003, Helpful habitant or pernicious passenger: interactions between an infaunal bivalve, an epifaunal hydroid and three potential predators. *Oecologia*, 134: 415-422.
- MCDERMOTT, J. J., 1983, Food web in the surf zone of an exposed sandy beach along the mid-Atlantic coast of the United States. Pp. 529-539, in: A. MCLACHLAN & T. ERASMUS, eds., *Sandy beaches as ecosystems*. Dr. W. Junk Publishers, The Hague.
- MEINKOTH, N., 1995, *National Audubon Society field guide to North American seashore creatures*. Alfred A. Knopf, New York. 799 pp.
- MELVILLE, R. V., 1976, Opinion 1057, *Donax variabilis* Schumacher 1817 (Mollusca: Bivalvia) suppressed under the plenary powers; type-species designated for *Latona* Schumacher 1817. *Bulletin of Zoological Nomenclature*, 33: 19-21.
- MIKKELSEN, P. S., 1981, A comparison of two Florida populations of the coquina clam, *Donax variabilis* Say 1822. I. Intertidal density, distribution, and migration. *The Veliger*, 23: 230-239.
- MIKKELSEN, P. S., 1985, A comparison of two Florida populations of the coquina clam *Donax variabilis* Say, 1822 (Bivalvia: Donacidae). II. Growth rates. *The Veliger*, 27: 308-311.
- MINER, R. W., 1950, *Field book of seashore life*. G. P. Putnam's Sons, New York. 888 pp.
- MORRIS, P. A., 1947, *A field guide to shells of our Atlantic coast*. Peabody Museum of Natural History, Boston. 236 pp., 45 pls.
- MORRISON, J. P. E., 1971, Western Atlantic *Donax*. *Proceedings of the Biological Society of Washington*, 83: 545-568.
- MOUÉZA, M. & L. FRENKIEL, 1974, Contribution à l'étude des structures paléales des Tellinacea. Morphologie et structure du manteau de *Donax trunculus* L. *Proceedings of the Malacological Society of London*, 41(1): 1-19.
- MOUÉZA, M. & L. FRENKIEL, 1976, Contribution à l'étude de la biologie de *Donax trunculus* (Mollusque Lamellibranche). Morphologie fonctionnelle - anatomie microscopique - histologie de l'appareil digestif. *Journal of Molluscan Studies*, 42(1): 1-16.
- MOUÉZA, M. & L. FRENKIEL, 1978, Le système circulatoire et le jeu des siphons chez *Donax trunculus*, mollusque lamellibranche. *Malacologia*, 17(1): 117-124.
- NAKAZIMA, M., 1965, On the differentiation of the crenated-folds in the midgut-gland of Eulamellibranchia. VII. Crenated-fold in *Donax semigranosus*. *Venus*, 23(4): 218-222.
- NARCHI, W., 1972, On the biology of *Iphigenia brasiliensis* Lamarck, 1818 (Bivalvia, Donacidae). *Proceedings of the Malacological Society of London*, 40(2): 79-91.
- NARCHI, W., 1978, Functional anatomy of *Donax hanleyanus* Philippi, 1847 (Donacidae - Bivalvia). *Boletim de Zoologia da Universidade de São Paulo*, 3: 121-142.
- NELSON, W. G., E. BONSDORFF & L. ADAMKEWICZ, 1993, Ecological, morphological, and genetic differences between the sympatric bivalves *Donax variabilis* Say, 1822 and *Donax parvula* Philippi, 1849. *The Veliger*, 36: 317-322.
- ODIETE, W. O., 1981, The cruciform muscle complex in *Egeria radiata* L. (Bivalvia, Tellinacea, Donacidae). *Basteria*, 45: 57-63.
- PASSOS, F. D., 1998, *Anatomia funcional de Donax gemmula Morrison, 1971 (Bivalvia: Donacidae)*. M. S. Thesis, Instituto de Biociências da Universidade de São Paulo. São Paulo, Brazil. 70 pp.
- PELSENEER, P., 1911, *Les lamellibranches de l'expédition du Soboga*. Siboga Expeditie, Partie Anatomique, 53a: 1-125.
- POHLO, R. H., 1967, Aspects of the biology of *Donax gouldi* and a note on evolution in Tellinacea (Bivalvia). *The Veliger*, 9(3): 330-337.
- PURCHON, R. D., 1963, A note on the biology of *Egeria radiata* Lam. (Bivalvia, Donacidae). *Proceedings of the Malacological Society of London*, 35: 251-271.
- RIDEWOOD, W. G., 1903, On the structure of the gills of the Lamellibranchia. *Philosophical Transactions of the Royal Society of London, Biological Sciences*, 195B: 147-284.
- RUPPERT, E. & R. FOX, 1988, *Seashore animals of the Southeast*. University of South Carolina Press. Columbia. 429 pp.
- SALAS-CASANOVA, C. & E. HERGUETA, 1990, The functional morphology of the alimentary canal of *Donax venustus* Poli and *D. semistriatus* Poli. Pp. 213-222, in: B. MORTON, ed., *The Bivalvia. Proceedings of a Memorial Symposium in Honour of Sir Charles Maurice Yonge (1899-1986)*, Edinburgh, 1986. Hong Kong University Press. Hong Kong. 355 pp.
- SAY, T., 1822, An account of some of the marine shells of the United States. *Journal of the Academy of Natural Sciences*, 2: 302-325.
- TIFFANY, W. J., 1971, The tidal migration of *Donax variabilis* Say. *The Veliger*, 14: 82-85.
- VEGA, R. R. & J. W. TUNNELL, 1987, Seasonal abundance, zonation, and migratory behavior

- of *Donax* (Donacidae: Bivalvia) on Mustang and North Padre Island, Texas. *Malacology Data Net (Ecosearch Series)*, 1: 97–135.
- WADE, B. A., 1969, Studies on the biology of the West Indian beach clam, *Donax denticulatus* Linné. 3. Functional morphology. *Bulletin of Marine Science*, 19(2): 306–322.
- WILSON, J. G., 1999, Population dynamics and energy budget for a population of *Donax variabilis* (Say) on an exposed South Carolina beach. *Journal of Experimental Marine Biology and Ecology*, 239: 61–83.
- WOOD, A. E. & H. E. WOOD, 1927, A quantitative study of the marine mollusks of Cape May County, New Jersey. *The Nautilus*, 41: 8–18.
- YOLOYE, V., 1977, The biology of *Iphigenia truncata* (Monterosato) (Bivalvia, Tellinacea). *Malacologia*, 16(1): 295–301.
- YONGE, C. M., 1949, On the structure and adaptations of the Tellinacea, deposit-feeding Eulamellibranchia. *Philosophical Transactions of the Royal Society*, 234B: 29–76.