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

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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 bauplas 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 proctacta, 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. texanus 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 proctacta (Adamkewicz & Harasewych, 1996). The analysis also demonstrated that D. parvula was indistinguishable from D. fossor, and D. dorotheae was indistinguishable from D. texanus, 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. texanus.

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

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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 a 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). 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, 1933; 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; Mouéza & Frenkeli, 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-μm serial sections of partial regions were stained with Mallory's tristain. All drawings were made with the aid of a camera lucida.

Abbreviations used in figures: am, anterior adductor muscle; an, anus; au, auricle; 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; sh, 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);


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;ecal 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, incumbent 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 connection, 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 incumbent 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 incumbent 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 incurrent 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 posteroventral 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). 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 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 ventricles 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-
Icosa; 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 posteroventral 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.

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 on the right 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 incipient 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 & Frenkiiel, 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 & Frenkiiel, 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 infrabranial chambers (Mouëza & Frenkiiel, 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 rectal 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; Yoloye, 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 postero-dorsal caecum (Yonge, 1949; Purchon, 1963; Mouëza & Frenkiiel, 1976; Salas-Casanova & Herguet, 1990). These last authors demonstrated that in *D. venustus* (Pol, 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 & Frenkiiel (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.

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LITERATURE CITED


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