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SHELL MORPHOLOGY AND MORPHOMETRY OF LARVAL AND POST-LARVAL *DONAX FOSSOR* SAY (BIVALVIA: DONACIDAE)

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ABSTRACT Scanning electron micrograph sequences are presented of the disarticulated shell valves of laboratory-reared larval and post-larval stages of *Donax fossor* obtained from adult specimens collected in the oceanic surf zone of beaches along the east coast of Assateague Island, VA. These sequences accurately depict the gross morphologies/morphometries and hinge (provinculum) structures of consistently-oriented, disarticulated shell valves of the larvae and/or postlarvae of this species. It is emphasized, however, that a scanning electron microscope is not necessary to observe even fine hinge structures associated with the early ontogenetic stages of the individual specimens depicted in these sequences. Such structures are readily visible using a wide range of optical compound microscopes equipped with high-intensity reflected light sources. The depicted morphologic and morphometric characters provide researchers with invaluable aids for discriminating (using routine optical microscopic techniques) the early life history stages of *D. fossor* from those of other sympatric species of bivalves isolated from plankton and benthic samples.

KEY WORDS: *Donax fossor*, morphology, morphometry, bivalve, larvae, postlarvae, identification

INTRODUCTION

Say (1822) provided the first description of *Donax fossor* Say, an oceanic surf zone species that he indicated inhabited the coasts of New Jersey and Maryland. Over subsequent years, the range of the species has been extended from Long Island to mid-east Florida (Adamkewicz & Harasewych 1996). The presence of a similar species (*Donax variabilis* Say) with a range along the Atlantic Coast that partially overlaps with that of *D. fossor* has led to considerable taxonomic confusion (Adamkewicz & Harasewych 1996). As articulated by Simone and Dougherty (2004, p. 460), *D. fossor* and *D. variabilis* "are so similar that the populations of New Jersey have often been labeled *D. variabilis* (e.g., Johnson 1927, Wood & 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 have accepted the validity of these two species (e.g., Johnson 1934, Morris 1947, Miner 1950, Morrison 1971, Abbott & Morris 1995), whereas others have suggested that the two are conspecific (Abbott 1954, 1974, Chanley 1969a). For example, Chanley (1969a) suggested 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 (1969a) 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." (Simone & Dougherty 2004).

Based on their studies with RAPD DNA markers, Adamkewicz and Harasewych (1996) concluded that the distribution of *Donax variabilis* along the Atlantic Coast is from south of Chesapeake Bay to mid-east Florida, which is consistent with the statement of Morrison (1971, p. 548) that "All of the *Donax* from the Wachapreague region of Virginia studied by Chanley (1969a), belong to the species *fossor* Say." Morrison (1971, p. 548) further states that Chanley "experimentally raised young from *fossor* parents that 'set' as *fossor*" and that they "cannot be identified as any other species" [presumably this statement refers to the larvae reared and depicted by Chanley (1969b) and Chanley and Andrews (1971) that they identified as "*D. variabilis*"]. The adult *Donax fossor* that were spawned to obtain the larval and post-larval shells depicted in the present study were collected from north of Virginia Beach, VA (and north of the Wachapreague region of Virginia) on the oceanic beaches of Assateague Island, VA.

The present study provides aids to discriminate larval and post-larval stages of *Donax fossor* from those of other species of bivalves along the Atlantic Coast of the United States. Over the years, numerous authors have articulated the difficulties associated with the identification of bivalve larvae and early postlarvae in planktonic and benthic samples from marine, estuarine, and freshwater environments (Stafford 1912, Odhner 1914, Lebour 1938, Werner 1939, Jørgensen 1946, Sullivan 1948, Rees 1950, Miyazaki 1962, Loosanoff & Davis 1963, Newell & Newell 1963, Loosanoff et al. 1966, Le Pennec & Lucas 1970, Chanley & Andrews 1971, de Schweinitz & Lutz 1976, Lutz & Jablonski 1978a, 1978b, 1981, Lutz & Hidu 1979, Jablonski & Lutz 1980, Le Pennec 1980, Lutz et al. 1982a, 1982b, 2018, Lutz 1988, 2012, Fuller & Lutz 1989, Kennedy et al. 1989, 1991, Goodsell et al. 1992, Hu et al. 1992, 1993, Baldwin et al. 1994, Hare et al. 2000, Garland & Zimmer 2002, Tiwari & Gallager 2003a, 2003b, Hendriks et al. 2005, Larsen et al. 2005, 2007, Wang et al. 2006, North et al. 2008, Henzler et al. 2010, Thompson et al. 2012a, 2012b, Goodwin et al. 2014, 2016a, 2016b, 2018). Hendriks et al. (2005, p. 151) stated that "Despite the importance of the planktonic larval stage in intertidal bivalves, our understanding of this stage is still insufficient. A major obstacle in the quantification of planktonic larval distributions is the identification of sampled larvae."

A number of techniques have been refined in recent years and show promise for use in routine identifications of larval and post-larval bivalves (e.g., single-step nested multiplex PCR; *in*

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situ hybridization protocols through color-coding with taxon-specific, dye-labeled DNA probes; coupled fluorescence *in situ* hybridization and cell sorting; image analysis techniques using species-specific shell birefringence patterns under polarized light; Larsen et al. 2005, 2007, Henzler et al. 2010, Thompson et al. 2012a, 2012b, Goodwin et al. 2014, 2016a, 2016b). However, Lutz et al. (2018, p. 248) emphasized that "no adequate comprehensive reference source exists that accurately depicts the morphology and morphometry of the shells of larval and post-larval stages of target bivalve species in a consistent format." To this end, scanning electron micrograph sequences of the disarticulated shell valves of laboratory-reared larval and post-larval stages of 56 species of bivalve molluscs were compiled from a wide spectrum of freshwater, estuarine, and marine habitats. In the resulting monograph (Lutz et al. 2018), the morphology and morphometries of consistently-oriented, disarticulated shell valves and associated hinge (provinculum) structures provide powerful tools for discriminating the early life history stages of these various bivalve species. Most of the species depicted in the monograph are from environments along the east coast of North America. Noticeably absent in the monograph is *Donax fossor* which, as mentioned earlier, is a common species along the east coast of the United States from Long Island, NY to mid-east Florida (Adamkewicz & Harasewych 1996). In the present article, scanning electron micrograph sequences of disarticulated shell valves of *D. fossor* are depicted in a similar format to that presented for the 56 bivalve species included in the monograph (Lutz et al. 2018) in an effort to provide aids for the discrimination of larvae and postlarvae of *D. fossor* from those of other sympatric species of bivalves isolated from planktonic and benthic samples.

MATERIALS AND METHODS

Sexually mature adults of *Donax fossor* were collected in the oceanic surf zone of beaches along the east coast of Assateague Island, VA in August 1982. Spawning of the adults was induced using a variety of protocols described by various workers (see Loosanoff & Davis 1963, Lutz et al. 1982b, Fuller & Lutz 1989). The larvae and postlarvae were reared in cultures using standard hatchery techniques [e.g., techniques described by Loosanoff & Davis (1963) and Chanley & Andrews (1971)].

Larval and post-larval specimens were sampled at frequent intervals (frequency dependent on the growth of organisms since the previous sampling period) from the various cultures and placed in distilled water for 30 min (Calloway & Turner 1978). Immediately following this treatment, specimens were preserved in 95% ethanol. After various lengths of time (up to 2 mo), specimens were removed from the ethanol, rinsed in distilled water, and immersed in a 5% solution of sodium hypochlorite (Rees 1950) for approximately 10 min to facilitate separation of shell valves. After rinsing in distilled water, disarticulated valves were mounted on copper or silver tape, coated (under vacuum) with approximately 400 Å of gold–palladium or a combination of gold and carbon, and examined under an ETEC Autoscan scanning electron microscope (SEM).

Procedures used for accurate documentation of shapes and dimensions of the larval and post-larval shells using scanning electron microscopy were those of Fuller et al. (1989) and are outlined in the following text.

Before imaging individual larval or post-larval specimens under the SEM, great care was taken to adjust the microscope so that x and y dimensions were equal on a calibration sphere that was approximately the same size as the specimen being photographed. In turn, these adjustments were made at a magnification close to that at which the specimen was to be photographed. The calibration spheres used were sandblasting beads that were selected for roundness by comparing measurements of the diameter on photomicrographs taken at 0°, 45°, and 90° rotations [see Fuller et al. (1989) for further details].

The method used for consistent orientation of the disarticulated shell valves, in which each larval or post-larval valve is positioned with points of the hinge and shell margin aligned in a plane normal to the axis of the electron optical system, is described by Fuller et al. (1989, p. 59) as follows. "Specifically, a disarticulated valve with the interior shell surface visible on the microscope screen is rotated until the anterior and posterior margins are at equal working distances. A digital voltmeter (monitoring the reference voltage of the lens control) is used to measure carefully the differences in working distance when opposite margins of the shell are successively focused at 30,000X. A difference of 1 mV on the meter is equal to a change in working distance of about 0.34 μm. Subsequently, the specimen is tilted perpendicularly to the first axis until the dorsal and ventral margins of the valve also are at the same working distances. A photomicrograph of the shell in this position documents its characteristic shape."

The dimensions of the larval and post-larval shells were determined by positioning a flat 400-mesh copper transmission electron microscope grid (on the same specimen mount, near the shell valve) normal to the electron optical axis and photographing this grid at the identical magnification at which the shell valve was photographed. Measurements of the shell dimensions are based on the 63.5 μm grid spacings of the 400-mesh grid, rather than on magnification or scale bar displays on the SEM screen [for further details, see Fuller et al. (1989)]. The numbers depicted above each of the scanning electron micrographs in Figures 1–4 indicate the maximum linear distance measured along any axis of the shell. This maximum distance represents "shell length" as defined by numerous authors (e.g., Fuller & Lutz 1989, Kennedy et al. 1989, 1991, Goodsell et al. 1992, Gustafson & Lutz 1992).

DISCUSSION

Figures 1–4 depict scanning electron micrograph sequences of the gross shell morphologies, morphometries, and details of the hinge regions of disarticulated shell valves of larval and post-larval specimens of *Donax fossor* at various stages of development. We have attempted to present these sequences in a manner (i.e., consistent orientation) that will facilitate comparison of the shell morphologies and morphometries of larvae and postlarvae of this species with those of other species of bivalves depicted in Lutz et al. (2018). The term "provinculum" is herein used in the sense of Bernard (1898) and Rees (1950). Provinculum length represents the linear distance between the lateral extremes of the hinge apparatus in larval and early post-larval shells (see Bayne 1976, p. 87, for a diagrammatic illustration of this dimension). The morphological features of various ontogenetic stages of the disarticulated larval and post-larval shell valves of *D. fossor* are distinct from those of any of

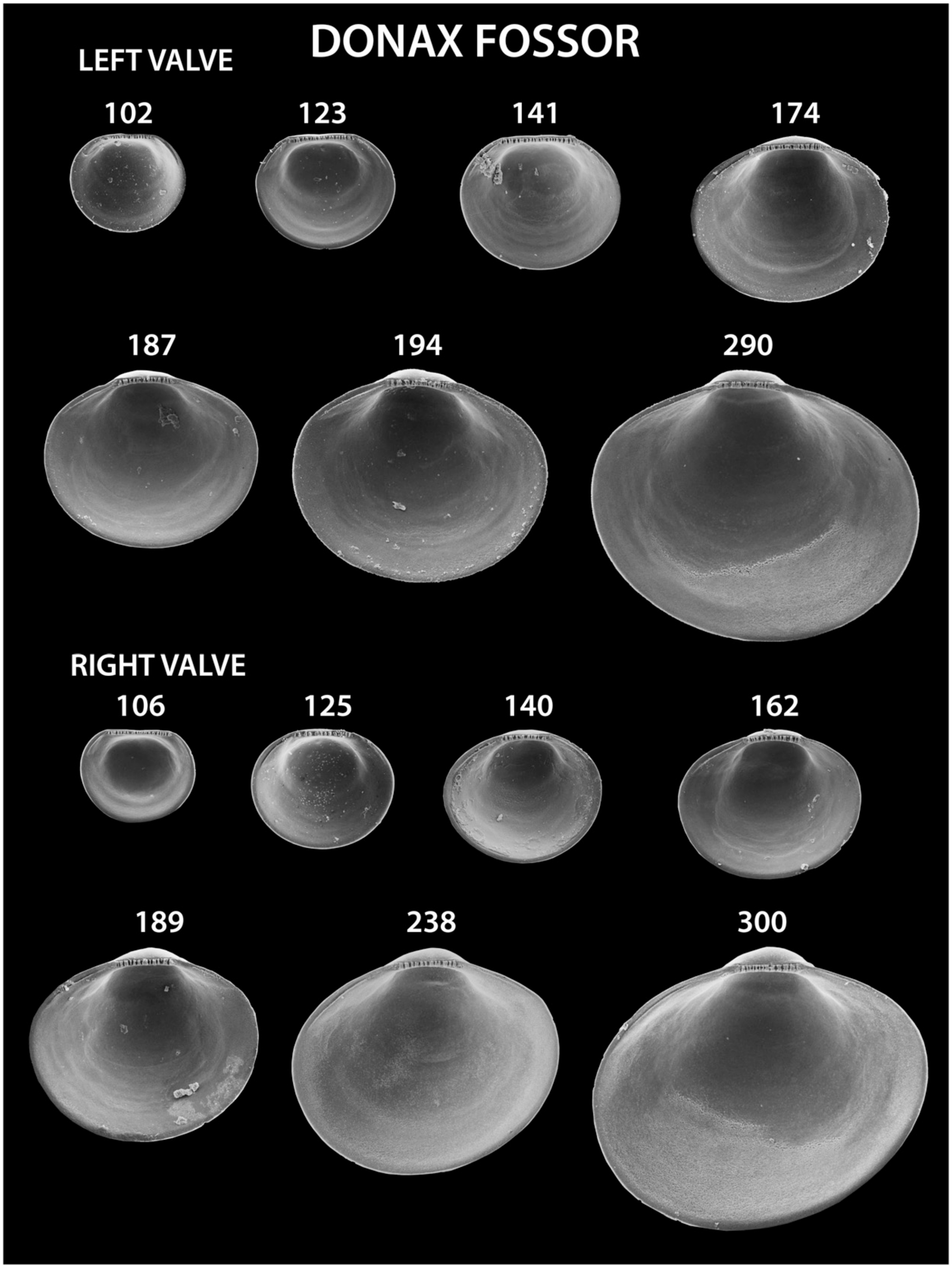

Figure 1. Scanning electron micrographs of disarticulated shell valves of *Donax fossor* larvae. Numbers indicate the maximum linear shell dimension in micrometers.

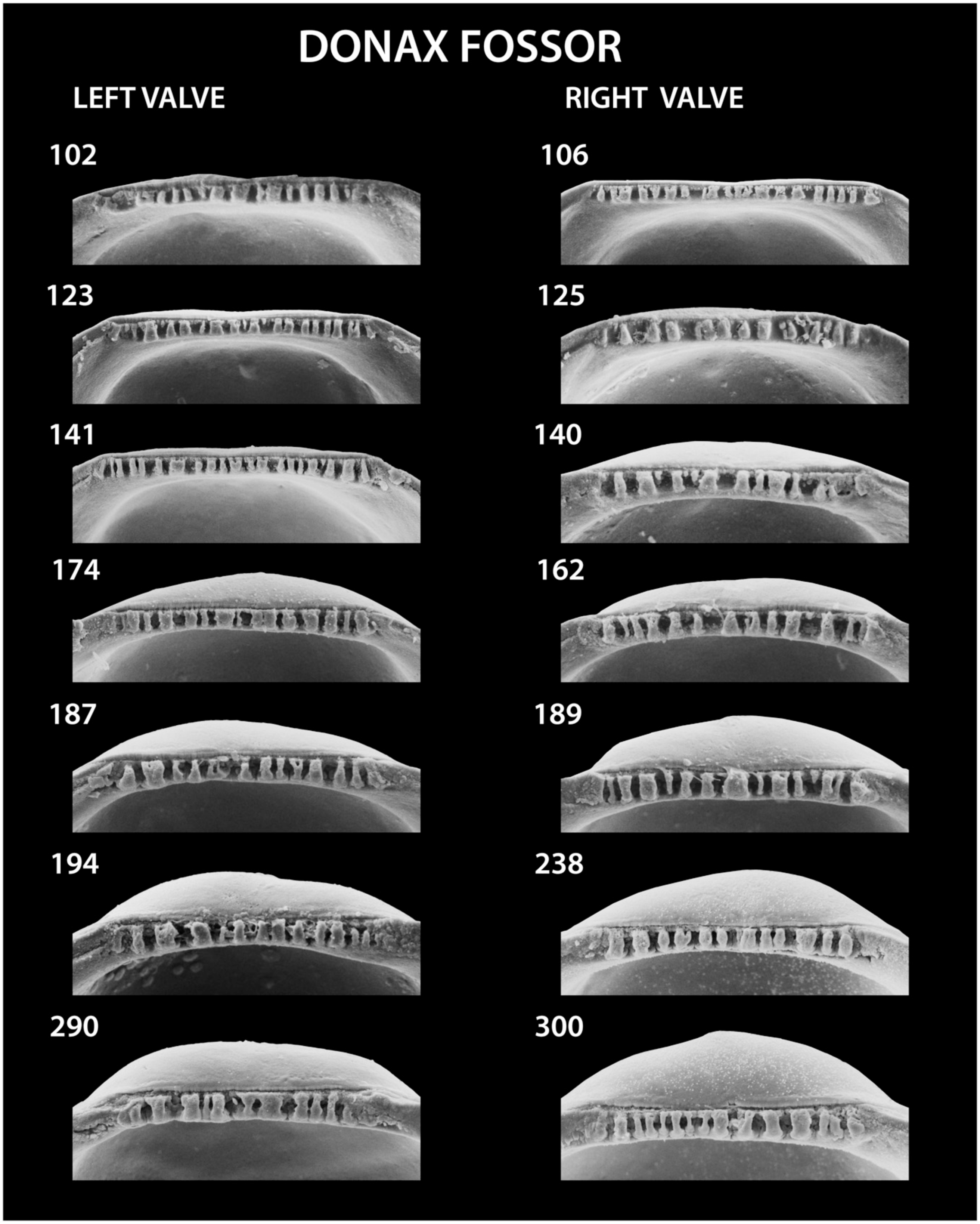

Figure 2. Scanning electron micrographs of the hinge of disarticulated shell valves of *Donax fossor* larvae seen in Figure 1. Numbers indicate the maximum linear shell dimension in micrometers.

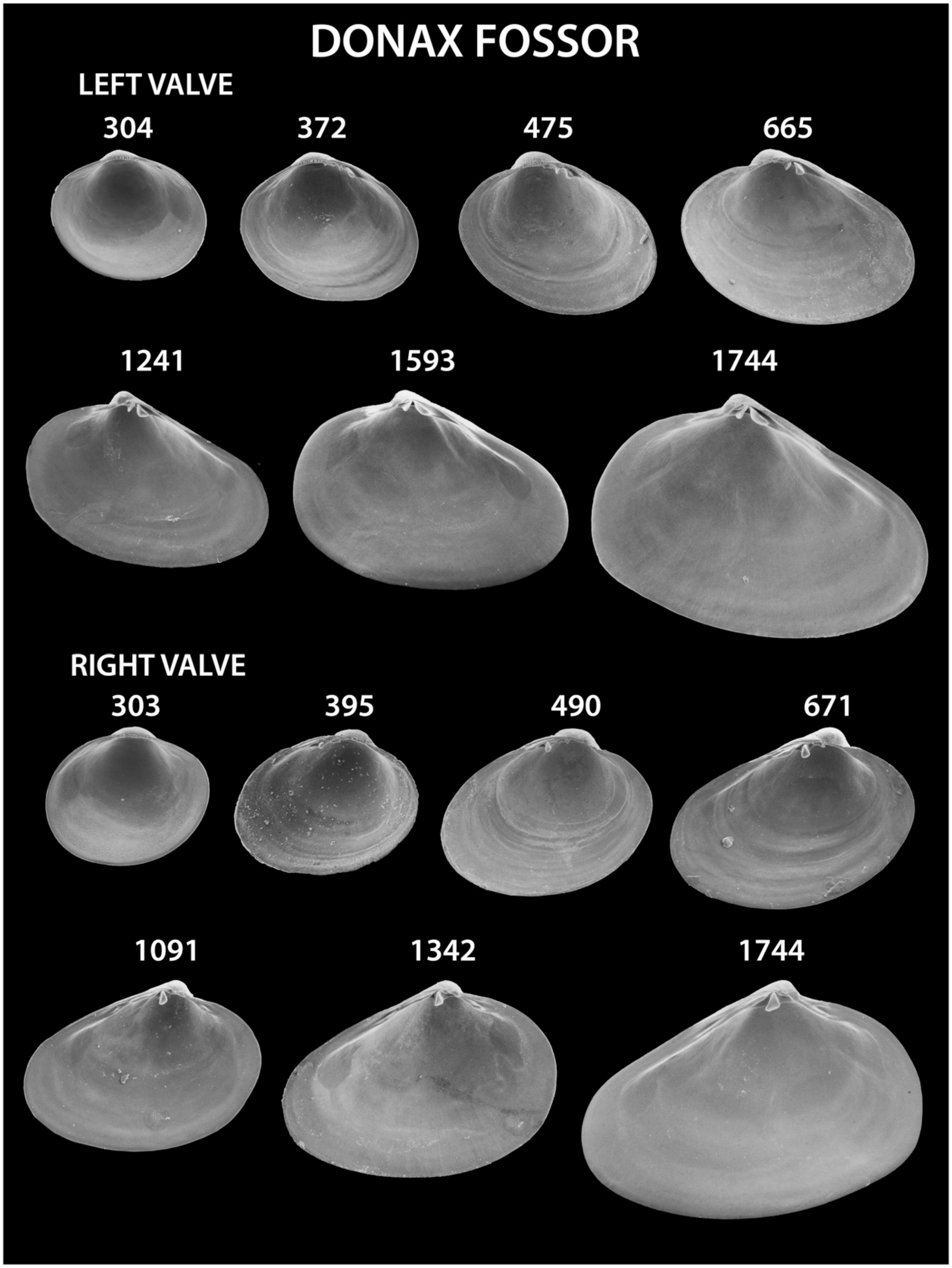

Figure 3. Scanning electron micrographs of disarticulated shell valves of *Donax fossor* postlarvae. Numbers indicate the maximum linear shell dimension in micrometers.

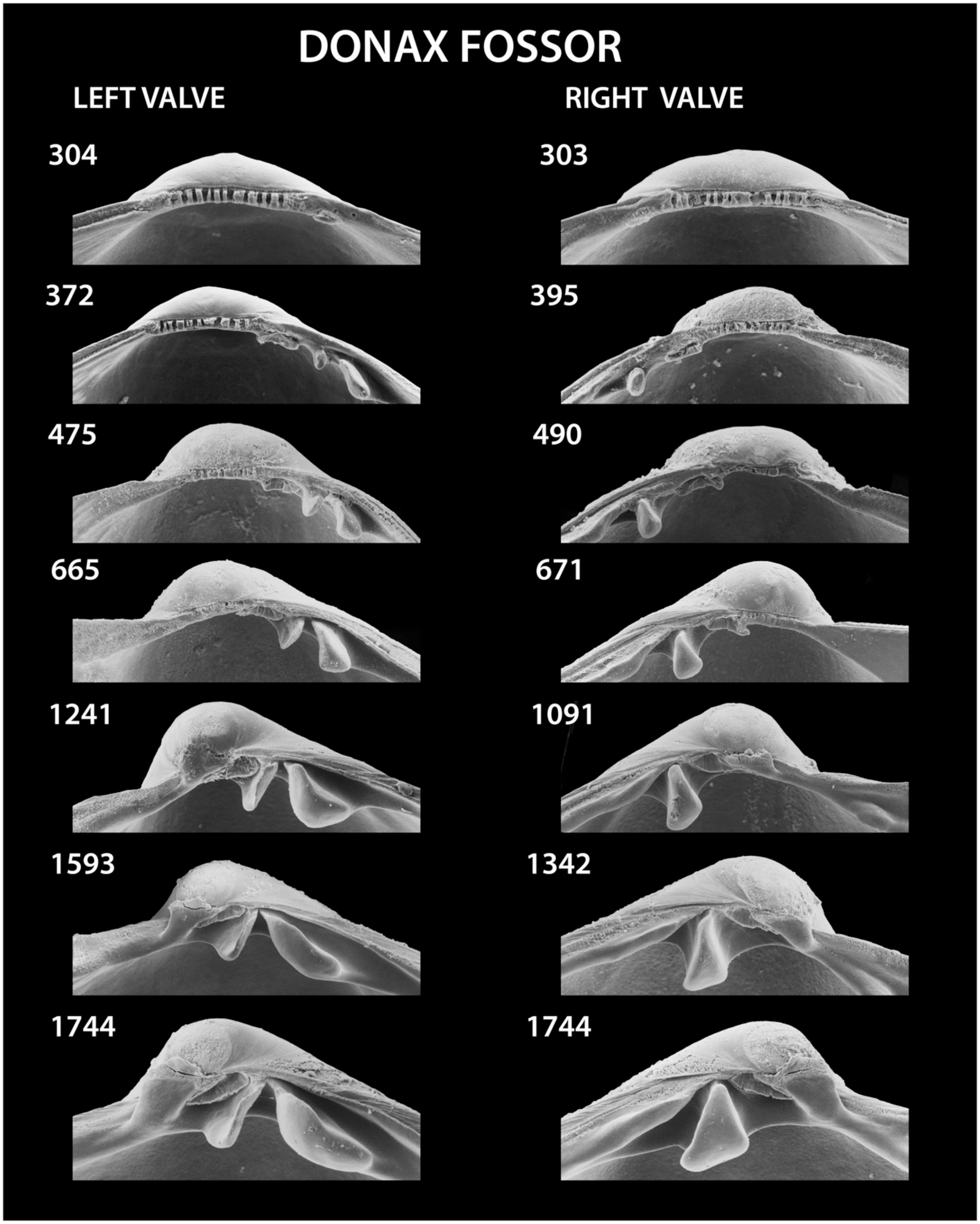

Figure 4. Scanning electron micrographs of the hinge of disarticulated shell valves of *Donax fossor* postlarvae seen in Figure 3. Numbers indicate the maximum linear shell dimension in micrometers.

the 56 species of bivalves depicted in the monograph published by Lutz et al. (2018).

No "primary" (after Trueman 1950; "primitive" of Le Pennec 1980) ligament pits ("fossette ligamentaire" of Bernard 1896a) were observed in *Donax fossor* specimens with shell lengths less than 300 μm. Since the classic studies of Bernard in the late 19th century (Bernard 1895, 1896a, 1896b, 1897, 1898), numerous workers have commented on the presence of ligaments or ligament pits in "larval" specimens (Rees 1950, Ansell 1962, Loosanoff et al. 1966, Chanley & Andrews 1971, Bayne 1976); for further discussion concerning the significance of the presence or absence of ligament pits in the shells of early ontogenetic stages of bivalves, see Lutz et al. (1982b). Lutz and Hidu (1979) suggested that "primary" (after Trueman 1950) ligament pits do not form until metamorphosis has been initiated (see also Lutz 1979). It has been further suggested that changes associated with metamorphosis proceed in an orderly fashion (Bayne 1965, 1971, Turner 1976a) and that "any interruption … in the normal sequence of events affects the ability of the larvae to progress to the next step whether that be the loss of a larval organ or the acquisition of a postlarval one" (Turner 1976b). Ligament pits were first observed in shells of a number of specimens of *D. fossor* with shell lengths ranging between 300 and 340 μm. If, as suggested by Lutz and Hidu (1979, pp. 117–118), development of the primary ligament pit is "one of the first morphological changes that occurs during metamorphosis," it is reasonable to conclude that larvae within this size range are at least capable of metamorphosis (Lutz 1979). This conclusion is compatible with the observations of the lengths of prodissoconch II shells (indicative of the size at metamorphosis) on post-larval specimens of *D. fossor* (see Fig. 5). It is interesting that ligament pits were not observed in any specimens with shell lengths less than 300 μm. This observation strongly suggests the larvae of this species are not capable of metamorphosing at shell lengths below this size.

The larval and post-larval specimens depicted in Goodwin et al. (2018, Figure 9, p. 456) were obtained from the same cultures from which the larval and post-larval specimens depicted in the present study were obtained (J. Goodwin, personal communication). Goodwin et al. (2018) refer to these specimens as "*Donax variabilis*." As mentioned in the Introduction, Adamkewicz and Harasewych (1996) concluded, based on their studies with RAPD DNA markers, that the distribution of *D. variabilis* along the Atlantic Coast is from south of Chesapeake Bay to mid-east Florida. This is consistent with the statement of Morrison (1971, p. 548) that "All of the *Donax* from the Wachapreague region of Virginia studied by Chanley (1969a) belong to the species *fossor* Say." Also, as articulated in the Introduction, Morrison (1971, p. 548) further states that Chanley "experimentally raised young from *fossor* parents that 'set' as *fossor*" and that they "cannot be identified as any other species" [presumably this statement refers to the larvae reared and depicted by Chanley (1969b) and Chanley and Andrews (1971) that they identified as "*D. variabilis*"]. In light of this, the larval and post-larval specimens depicted by Goodwin et al. (2018, Figure 9, p. 456) should have been labeled as *Donax fossor*, not *D. variabilis*. It is further concluded that the larval specimens of "*D. variabilis*" described and depicted by Chanley (1969b) and Chanley and Andrews (1971) were those of *D. fossor*, not *D. variabilis*.

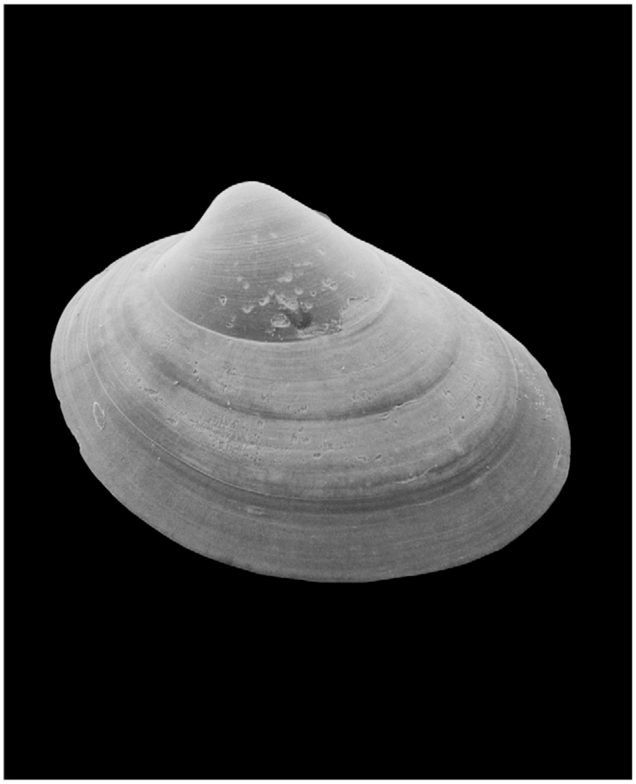

Figure 5. Right shell valve of a *Donax fossor* postlarva with a shell length (maximum linear shell dimension) of 759 μm. The prodissoconch II shell (indicative of the size at metamorphosis) measuring 339 μm is seen in the umbonal region of this specimen.

The scanning electron micrograph sequences presented in Figures 1–4 accurately depict the gross morphologies/morphometries and hinge structures of the disarticulated shell valves of the larvae and/or postlarvae of *Donax fossor* [see Fuller et al. (1989) for details concerning procedures for accurate documentation of the shapes and dimensions of the depicted shell valves]. It is important to emphasize, however, that a scanning electron microscope is not necessary to observe even fine hinge structures associated with the ontogenetic stages of the *D. fossor* specimens comprising these sequences. Such structures are readily visible using a wide range of optical compound microscopes equipped with high-intensity reflected light sources, although the disarticulated shell valves must be viewed in several planes of focus to discern the often subtle details seen clearly in Figures 1–4 (Lutz et al. 2018). In conclusion, the scanning electron micrograph sequences of disarticulated shell valves of larval and post-larval specimens depicted in the present study provide researchers with invaluable aids for discriminating the early life history stages of *D. fossor* from those of other sympatric species of bivalves isolated from plankton and benthic samples.

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