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Larval development of the coquina clam, Donax variabilis Say, with a discussion of the structure of the larval hinge on the Tellinacea

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LARVAL DEVELOPMENT OF THE COQUINA CLAM, *DONAX VARIABILIS* SAY, WITH A DISCUSSION OF THE STRUCTURE OF THE LARVAL HINGE IN THE TELLINACEA[1]

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ABSTRACT

Adult specimens of *Donax variabilis* were spawned in the laboratory and the larvae reared to metamorphosis. Larval length increases from 70 μ to 340 μ during pelagic stages. Height is originally 10 μ to 15 μ less than length. Height increases less rapidly than length and may be 50 μ less than length at metamorphosis. Depth is originally 50 μ less than length. It also increases more slowly than length and may be 150 μ to 170 μ less than length at metamorphosis. Length of the hinge line is 50 μ to 60 μ. Round umbos form when larvae are 100 μ to 120 μ long. Umbos protrude above the shell as knobby projections at lengths above 170 μ. The anterior and posterior ends are equally rounded until, at about 250 μ, the posterior end becomes more pointed. Larvae metamorphose at lengths from 275 μ to 340 μ.

The hinges of the larvae of *D. variabilis* and *Tellina agilis* consist of numerous small irregular teeth. Descriptions of taxodont dentition in larvae of other Tellinacea are probably in error and refer to these small irregular teeth. The large special teeth, frequently described in larvae of this group, probably do not develop until after metamorphosis.

INTRODUCTION

Donax variabilis, the familiar surf-dwelling coquina, is a small (19 mm) inhabitant of ocean beaches in the United States from Virginia to Texas (Abbott, 1954). It occurs seasonally on the eastern shore of Virginia from the second half of June to November. Clams have mature gametes during this period but the spawning season in this area is not known. Adult coquinas have been the subject of many studies but their larval development has never been described.

MATERIAL AND METHODS

Coquinas were collected from the beaches of Cedar and Assateague islands. Several unsuccessful attempts to induce them to spawn were made by alternately raising and lowering the temperature of the water in the Pyrex spawning dishes in which they had been placed. The addition of stripped sperm also failed to induce spawning. On one occasion larvae were obtained when stripped eggs were placed in a 0.1 N ammonium hydroxide solution in sea water for 20 minutes before fertilization. Stripping

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was difficult because of the small size of the clams and was generally not practical because too few larvae developed normally. Clams spawned on several occasions, after unsuccessful day-long attempts to spawn them, when left in the spawning dishes overnight. Usually only a few eggs were released in these nocturnal spawnings, but on one occasion a few million eggs were obtained.

The techniques used in rearing the larvae were those described by Loosanoff & Davis (1963). Larvae were fed *Monochrysis* sp. and kept in polyethylene garbage pails and buckets. Water temperatures were maintained between 20° and 25°C.

Results

Gametes.—Dimensions of the unfertilized egg have not been determined. The spermatozoan head is 6 μ long and 2.5 μ wide at its base. It is sharply tapered anteriorly. The tail is about 40 μ long.

Larval Development.—Larvae increase in length (anteroposterior dimension) from 70 μ to about 340 μ during shelled stages. Height (dorsoventral dimension) is 10 μ to 15 μ less than length in early straight-hinge stages and 15 μ to 20 μ less later (Fig. 1). Length continues to increase more rapidly than height and is usually 20 μ to 25 μ greater than height at lengths from 130 μ to 190 μ, 25 μ to 35 μ greater than height from 190 μ to about 250 μ, and as much as 50 μ more than height above 325 μ. Depth (maximum dimension between the two halves) is about 50 μ less than length in early straight-hinge larvae. This dimension increases at about ⅔ the rate of the length and is about 150 μ to 170 μ less than length at metamorphosis (Fig. 1). Length of the hinge line remains constant at 50 μ to 60 μ.

When larvae reach a length of 100 μ to 120 μ, the hinge line becomes slightly rounded as the umbo is formed (Fig. 2). At first the umbo is broadly rounded, but at 170 μ it forms a knobby projection above the shell margin (Fig. 2). The dorsal areas (shoulders) slope gradually between the umbo and the ends with the posterior slope shorter and steeper. The height from the ventral margin to the beginning of the shoulders exceeds the height from the umbo to the shoulders. The anterior end is longer than the posterior, although this difference is slight until larvae exceed 200 μ. The ends are almost equally rounded until larvae are approximately 250 μ long, at which time the posterior (short) end becomes more pointed than the anterior. This feature is helpful in identification, since the anterior end is more pointed than the posterior in most bivalve larvae with dissimilar ends.

The internal structure of larvae is indistinct in early straight-hinge stages (Fig. 3). Within hours the digestive diverticulae, stomach, and velar retractor muscles become evident. The gut is originally straight, but becomes

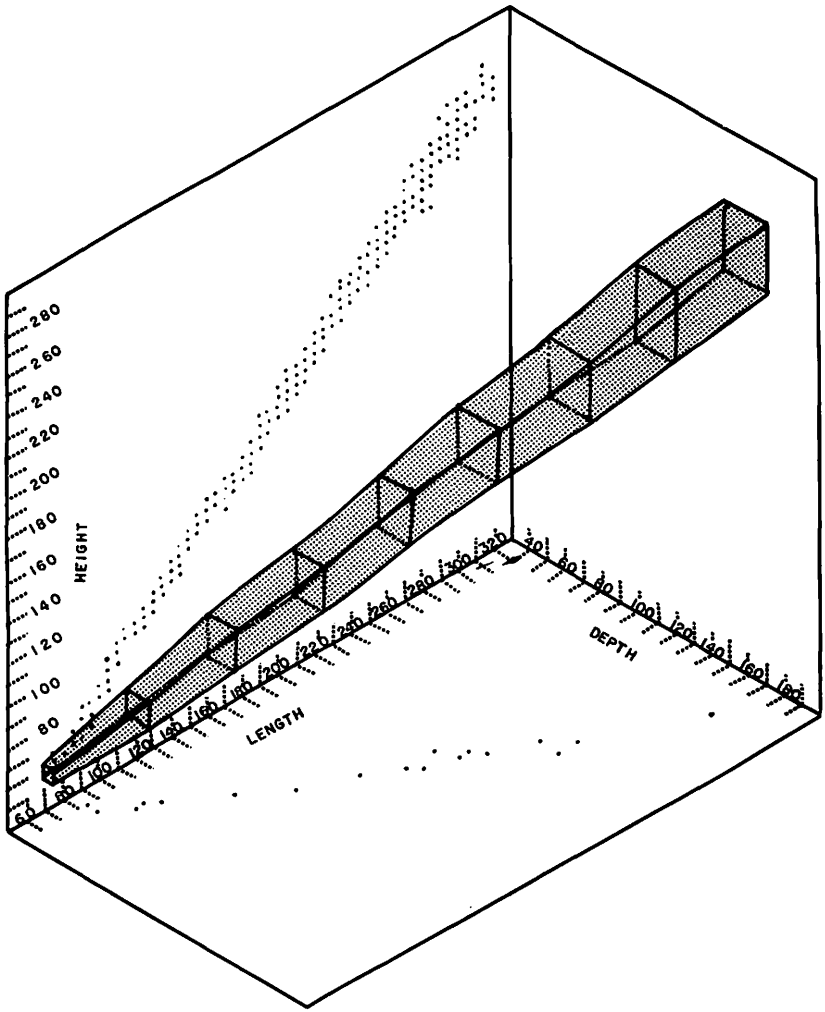

FIGURE 1. Length × height × depth relationship of larval specimens of *Donax variabilis*. The length *vs.* height is plotted along the "back wall," while length *vs.* depth is plotted on the "floor." The suspended three-dimensional figure encloses all possible length-height-depth combinations of larval individuals of *D. variabilis*.

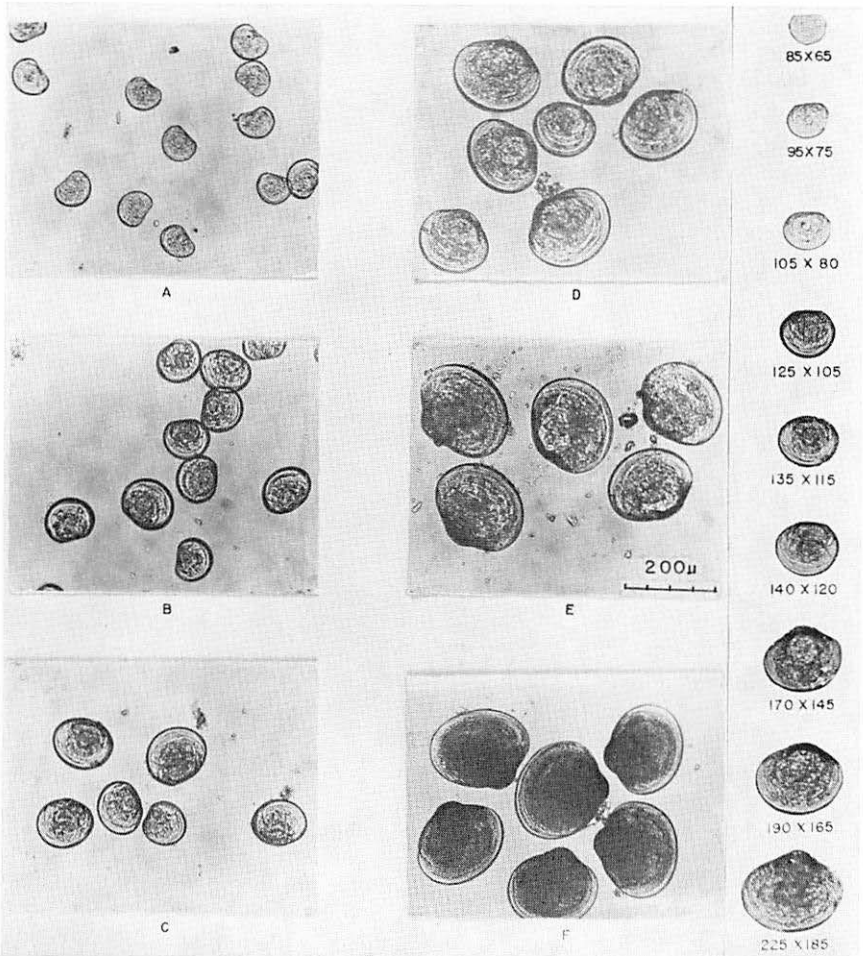

FIGURE 2. Photomicrographs of larval specimens of *Donax variabilis*: A, 2 days old; B, 8 days old; C, 12 days old; D, 19 days old; E, 19 days old; F, 22 days old. (Dimensions are in microns.)

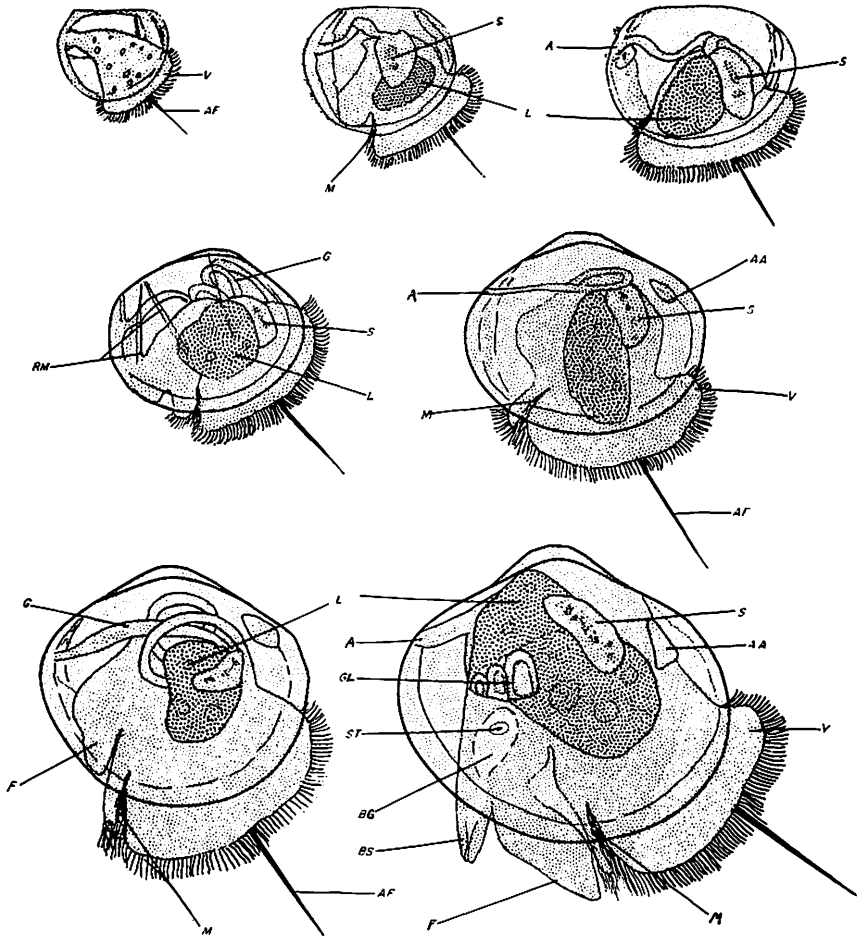

FIGURE 3. Diagrams of conspicuous features of the internal anatomy of the larvae of *D. variabilis*. a = anus; aa = anterior adductor muscles; af = apical flagellum; b = byssus gland; bs = byssal spur; f = foot; g = gut; gl = gill; l = liver; m = mouth; ma = mantle; pa = posterior adductor muscle; r = retractor muscles; s = stomach; st = statocyst; v = velum.

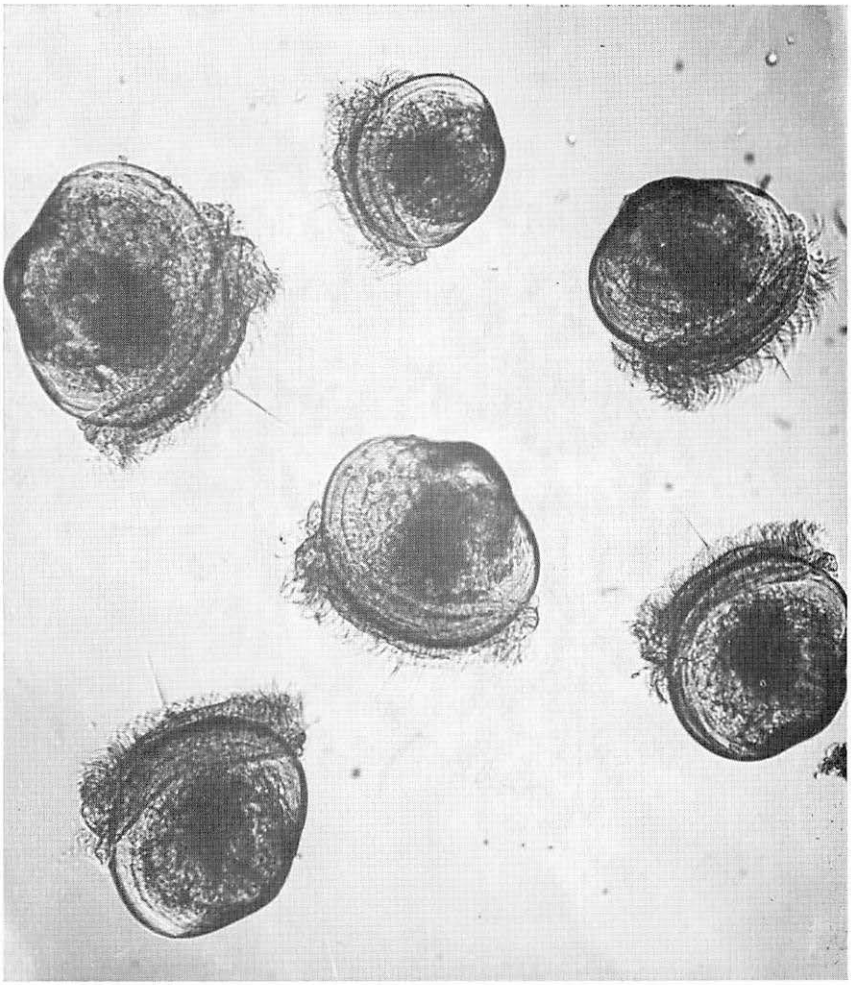

FIGURE 4. Larval specimens of *D. variabilis* with vela extended. Multiple apical flagella are visible in the two middle larvae.

coiled. The velum increases in size during larval development and, as with most pelagic lamellibranch larvae, constitutes a large portion of the tissues. The apical flagellum is inconspicuous in early straight-hinge larvae but soon becomes prominent and is conspicuous until the velum is lost. In later stages two large flagella are sometimes evident (Fig. 4). As metamorphosis begins, a foot develops posterior to the velum. At the base of the foot a centrally located, clear byssal gland lies just beneath the statocyst.

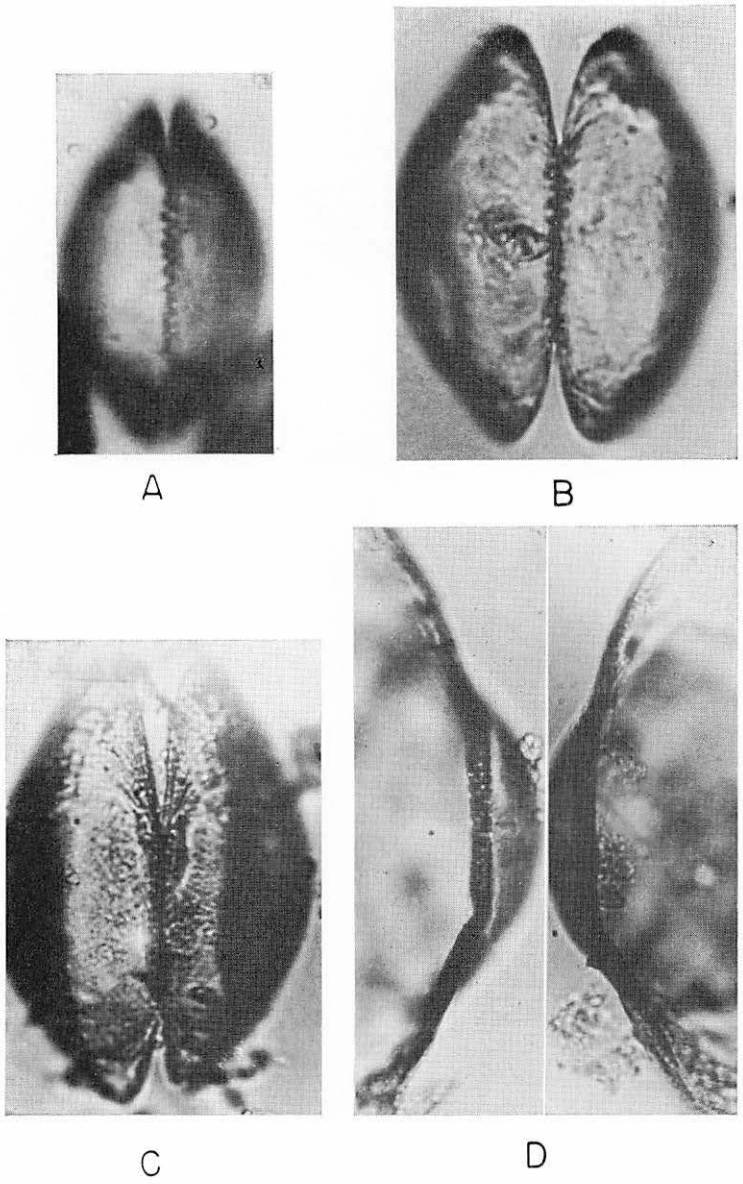

FIGURE 5. Hinge structure of larvae of *Donax variabilis* (anterior end is at top): A, dorsal view of larval shell about 85 μ long; B, internal view of larval shell 97 μ long; C, internal view of larval shell 140 μ long; D, internal view of larval shell 275 μ long.

The byssus is applied by a long "byssal spur" at the heel of the foot. Gill bars develop while the velum is still functional and there may be as many as three gill loops before the velum is lost (Fig. 3). Larvae are not distinctively colored nor is a pigmented eyespot obvious in any stage of development.

The entire hinge line of the larval *D. variabilis* consists of unevenly spaced minute teeth that are unequal in size (Fig. 5). These teeth are evident in small straight-hinge larvae and persist throughout larval development, though they are difficut to see in large larvae.

Discussion

Larval Characteristics of the Donacidae.—Larval development has been described in only two species of Donacidae. Rees (1950) tentatively identified larvae of *Donax vittatus* in plankton samples. He described these larvae as yellow-brown, but rose-red at the "narrow" end. His photomicrograph shows a larva with more steeply sloping, longer shoulders and a less conspicuous umbo than is found in *D. variabilis*. Advanced larvae of *D. venustus* have a round umbo and equally rounded ends, though the anterior end is longer (Zakhvatkina, 1959). The larvae of *D. variabilis* differ from larvae of these species by their prominent knobby umbo and lack of distinctive coloration.

Hinge Structure of Larval Tellinacea.—Larval Tellinacea (the superfamily including the Donacidae) vary considerably in form and appearance, with some species having non-pelagic development (Werner, 1939; Jørgensen, 1946; Loven, 1848; Miyazaki, 1938; Odhner, 1914; Thorson, 1936). However, in many of the species a distinctly tellinid shape and a reddish umbo are common to late-stage larvae.

At least three different hinge structures have been described for larval Tellinacea. Zakhvatkina (1959) described a dentition similar to that of *D. variabilis* in larvae of *Gastrana fragilis*. Borisiak (1909, fig. 6) also reported a similar structure of the hinge in an unidentified larva. The hinges of larval *Tellina donacina* (Zakhvatkina, 1959), *T. crassa,* and *T. fabula* (Newell & Newell, 1963) have been described as having minute teeth "resembling the taxodont condition." These descriptions were apparently based on the observations of Rees (1950). Rees also illustrated two large teeth in each valve. In most references to the hinge structure of larval Tellinacea these large teeth are described without reference to the minute teeth. Sullivan (1948) published photomicrographs of the large teeth in juvenile *Tellina tenera* (*Tellina agilis*), yet larvae of this species have a hinge structure similar to that described for *Donax variabilis* (Fig. 6). Because of this and because the large teeth commonly reported for the Tellinacea were not observed in larval specimens of *D. variabilis,* it seems likely that

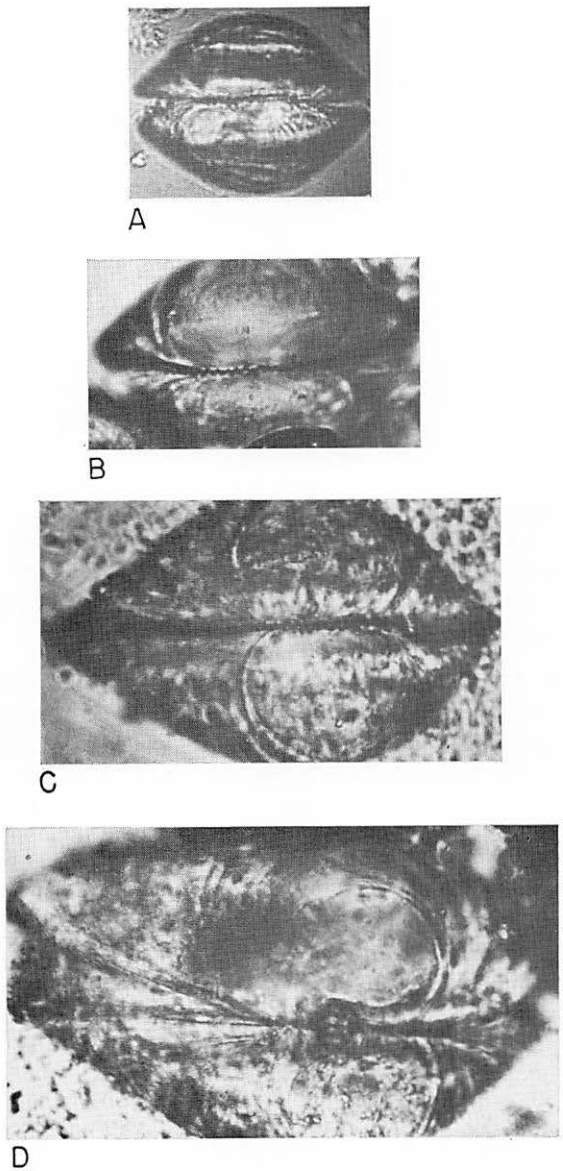

FIGURE 6. Hinge structure of larval specimens of *Tellina agilis* (anterior end is to the right): A, internal view of larval shell 110 μ long; B, dorsal view of larval shell about 130 μ long; C, dorsal view of larval shell 195 μ long; D, larval shell 250 μ long, showing ligament.

these two teeth are probably typical of the structure of the juvenile hinge and do not appear until late larval life or until after metamorphosis. The "minute" teeth frequently described are the larval hinge teeth of the present description and are not taxodont.

ACKNOWLEDGMENT

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SUMARIO

DESARROLLO LARVAL DEL MOLUSCO, *Donax variabilis* SAY, CON DISCUSION SOBRE LA ESTRUCTURA DE LA CHARNELA LARVAL EN TELLINACEA

Ejemplares adultos de *Donax variabilis* fueron desovados en el laboratorio y las larvas se desarrollaron hasta la metamorfosis. Durante los estados pelágicos, la longitud de las larvas aumentó de 70 μ a 340 μ. La altura es originalmente de 10 μ a 15 μ menos que la longitud. La altura aumenta menos rápidamente que la longitud y en la metamorfosis puede tener 50 μ menos que ésta. El espesor es originalmente 50 μ menos que la longitud. También aumenta más lentamente que ella y puede ser de 150 μ a 170 μ menos que la longitud, en la metamorfosis. La longitud de la línea de la charnela es de 50 μ a 60 μ. Los umbos redondos se forman cuando las larvas tienen de 100 μ a 120 μ de longitud. Los umbos sobresalen sobre la concha como proyecciones en forma de nudos o perillas a longitudes de más de 170 μ. Los extremos anterior y posterior son igualmente redondeados hasta que alrededor de las 250 μ, el extremo posterior se vuelve más puntiagudo. Las larvas sufren su metamorfosis con longitudes de 275 μ a 340 μ.

Las charnelas de las larvas de *D. variabilis* y *Tellina agilis* consisten de numerosos dientes irregulares pequeños. Las descripciones de la dentición taxodonta en las larvas de otras Tellinacea son probablemente erróneas y se refieren a estos pequeños dientes irregulares. El diente especial grande, que frecuentemente es descrito en las larvas de este grupo, probablemente no se desarrolla hasta después de la metamorfosis.

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