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EMBRYOLOGY OF THE MANGROVE CRAB *UCIDES CORDATUS* (BRACHYURA: OCYPODIDAE)

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A B S T R A C T

Ovigerous females of *Ucides cordatus* were collected at different mangrove areas in Iguape, SP, Brazil, and reared in the laboratory in order to describe each embryonic stage. Accounts of the biometry, internal morphology, and coloration of the eggs were taken. The embryonic development took 19 ± 1 d (27°C, 12:12 h) with eight well-defined stages. A salinity test on embryonic development was conducted, and a better result was obtained in a rearing at 15‰. Eggs are slightly ellipsoid through development and undergo an increase of 13.9% in diameter to 91.7% in volume. Cluster analysis revealed three different groups for diameter (Stages I–II, III–VI, and VII–VIII) and volume (Stages I–III, IV–V, and VI–VIII), supporting the classification of embryos into initial, intermediate, and final stages, which are currently used in studies on the reproductive biology of decapod crustaceans. In this species, the identification of the different embryonic stages can be achieved only if biometric data are combined with information on the internal morphology of embryos and coloration of the eggs.

There is little information about the embryology of crustaceans in the literature (Bas and Spivak, 2000). Thus the classification provided by Boolootian *et al.* (1959), describing ten embryonic stages in brachyurans and anomurans, is often used. Their classification is based on the relative proportion of yolk compared to the animal pole and the differentiation of certain structures of the embryo. More recently, other authors have used a lower number of stages to distinguish embryos (Valdes *et al*., 1991; Sainte-Marie, 1993; Pinheiro and Terceiro, 2000).

The information available on the embryonic development of decapods is focused mainly on marketable species. Examples are the contributions on the shrimps *Palaemon serratus* (Pennant, 1777) and *Macrobrachium rosenbergii* (De Man, 1879), by Campillo (1979) and Clarke *et al.* (1990); on the clawed lobsters *Homarus gammarus* (Linnaeus, 1758) and *Homarus americanus* H. Milne Edwards, 1837, by Pandian (1970a) and Branford (1978), and by Pandian (1970b) and Attard and Hudon (1987), respectively; on the crab *Carcinus maenas* (Linnaeus, 1758) by Cheung (1966) and Hartnoll and Paul (1982); and the anomuran *Paralithodes platypus* Brandt, 1850, by Jensen and Armstrong (1989). No such information is available for the mangrove crab *Ucides cordatus* (Linnaeus, 1763), but Rodrigues (1982) and Geraldes and Calventi (1983) had reported changes in coloration and diameter of eggs through development.

According to Efford (1969), size increase and chromatic alterations are expected to occur through embryogenesis. In brachyurans, those characteristics may be related to developmental patterns (Kaestner, 1970; Sastry, 1983), but the available information is too scarce to draw general trends. Measuring the duration of embryonic development is also a valuable task, allowing one to predict the timing of larval release.

The present study describes the embryonic stages of *U. cordatus*, taking into account morphologic, biometric, and chromatic alterations over the development of embryos. The rationale of pooling different stages for analytical purposes and the use of biometric data for their differentiation and identification are discussed.

Materials and Methods

Females bearing recently extruded egg batches were captured from November/1998 to March/1999, along different mangrove areas in Iguape, SP, Brazil, and maintained in plastic 50-L tanks supplied with constant aeration, sandy sediments, and water from the capture sites. Each crab was marked on the carapace for identification.

Three experiments were undertaken using early embryos. In all cases, salinity (15 ± 1‰), temperature (27 ± 1°C) and photoperiod (12:12 h) were closely controlled. In experiment 1, egg samples were removed daily from females

to obtain biometry. In experiments 2 and 3, development was undertaken in 200-mL plastic vials and the water was changed daily and treated with 0.02% G-potassic penicillin. The effect of salinity in the embryonic development was evaluated in experiment 2; constant aeration was supplied, and the eggs were kept at 5‰, 15‰, 25‰, and 35‰, whereas in one case, no aeration was provided, and eggs were reared in brackish (15‰) water.

For each experiment, eggs were removed and examined under a stereomicroscope (Boolootian *et al*., 1959). The morphology of each embryo was recorded in a computer image analysis system, and schematic drawings were produced using the terminology proposed by Nagao *et al*. (1999). The pattern of coloration at each stage was also noted and compared during ontogeny of embryos.

Fifteen eggs of each stage were mounted in excavated slides with habitat water, and analyses were made on embryos positioned in lateral view. Images were then digitized and morphometric procedures were carried out using the KS-100 3.0 (Carl Zeiss, GMBH) software. Meristic variables included the large (LA: from the funiculus to the opposite margin) and small (SA: between lateral margins opposite to the funiculus) axes, the area covered by embryonic tissues (EA), the yolk area (YA), the ocular area (OA), and the area covered by ocular pigments (POA).

The average LA/SA ratio and respective 1% confidence intervals were calculated for each stage as to categorize the egg shape in either spherical (LA/SA = 1) or ellipsoid (LA/SA $\neq$ 1). For spherical eggs, the volume was calculated as $V = 1/6(\pi d^3)$ (where d = average between the larger and smaller diameter), and for ellipsoid eggs the formula $V = 4/3(\pi r^2 R)$ (where, r = SA/2 and R = LA/2) was used.

The biometric variables were compared among the different embryonic stages using a balanced ANOVA design, and the Tukey test was used for post-hoc comparisons ($\alpha = 0.05$). A Cluster Analysis with Single Linkage was performed to examine the relationship between the morphometric similarity groups in both the diameter and volume data (according to Romesburg, 1984; Krebs, 1989). These results were then used to evaluate the statistical confidence of biometric data as a single criterion to discriminate among embryonic stages.

Chromatic patterns and the variability of the embryo (EA) and yolk (YA) areas were compared among stages and used to characterize the embryos.

Results

Only 44% of the 63 ovigerous females collected during this study were successfully monitored until hatching. The remaining females either lost their eggs soon after extrusion or the development of embryos ceased in a more advanced stage.

After egg laying, eight embryonic stages were recognized. Each stage averaged 2.7 $\pm$ 0.9 d, so that the duration of the total incubation was 19 d at 27°C. Free-swimming larvae were only obtained when reared at 15‰. The results obtained for each salinity follow below.

Salinity 5‰.—After 24 h, the eggs swelled more noticeably than in other salinities and yolk droplets were dissolved, as detected by the accumulation of a reddish translucent fluid. Egg development ceased completely after the third day and funiculus spiraling was not observed. A significant proportion of the eggs (which showed no further development) were infested by microscopic algae, hipotrichid ciliated protozoans, and fungi hyphae.

Salinity 15‰.—Half of the eggs did not survive beyond the 17th day, whereas the others developed into living zoea. Algae and peritrichan ciliated protozoans were very common over the surface of developing eggs.

Salinity 25‰.—Egg development ceased in Stage 2, with no further development after day 5. Microscopic algae, ciliated protozoans, and fungi hyphae were abundant.

Salinity 35‰.—Egg development ceased in Stage 2, with no further development after day 3. The abundance of encrusting algae over the egg surface, fungi hyphae, and protozoans was much higher than in any other treatment.

The eight embryonic stages (Fig. 1) were characterized in terms of time from egg-laying, appearance of morphologic structures, coloration, and relative proportion of yolk. Growth of some embryonic structures and yolk reduction are reported in Table 1. The average length of the large (LA) and small (SA) axes was similar in Stages IV–V and VI–VII (Table 1). From Stage I to Stage VIII, the increase of egg size was 22% to 25.6%. Confidence intervals around the average LA/SA ratio showed that eggs were slightly ellipsoid through embryogenesis ($P < 0.01$). The eggs of *U. cordatus* increased in diameter 13.9%, with a volumetric increase of 91.7%.

Cluster analysis (Fig. 2) revealed three groups according to diameter (Stages I–II; III–VI; and VII–VIII), with egg volume resulting in a very similar cluster (Stages I–III; IV–V; and VI–VIII). The arbitrary cut line was established in euclidian distance of 100 μm diameter and 50 ($\times 10^6$) μm^3 volume.

Discussion

The embryonic development of crustaceans may be divided into stages, which can be identified by examining the development of morphological structures, marked by biometric alterations (Pinheiro and Hattori, 2002). The eight stages for *U. cordatus* do not coincide with the ten stages established by Boolootian *et al*. (1959).

Temperature is known to be negatively

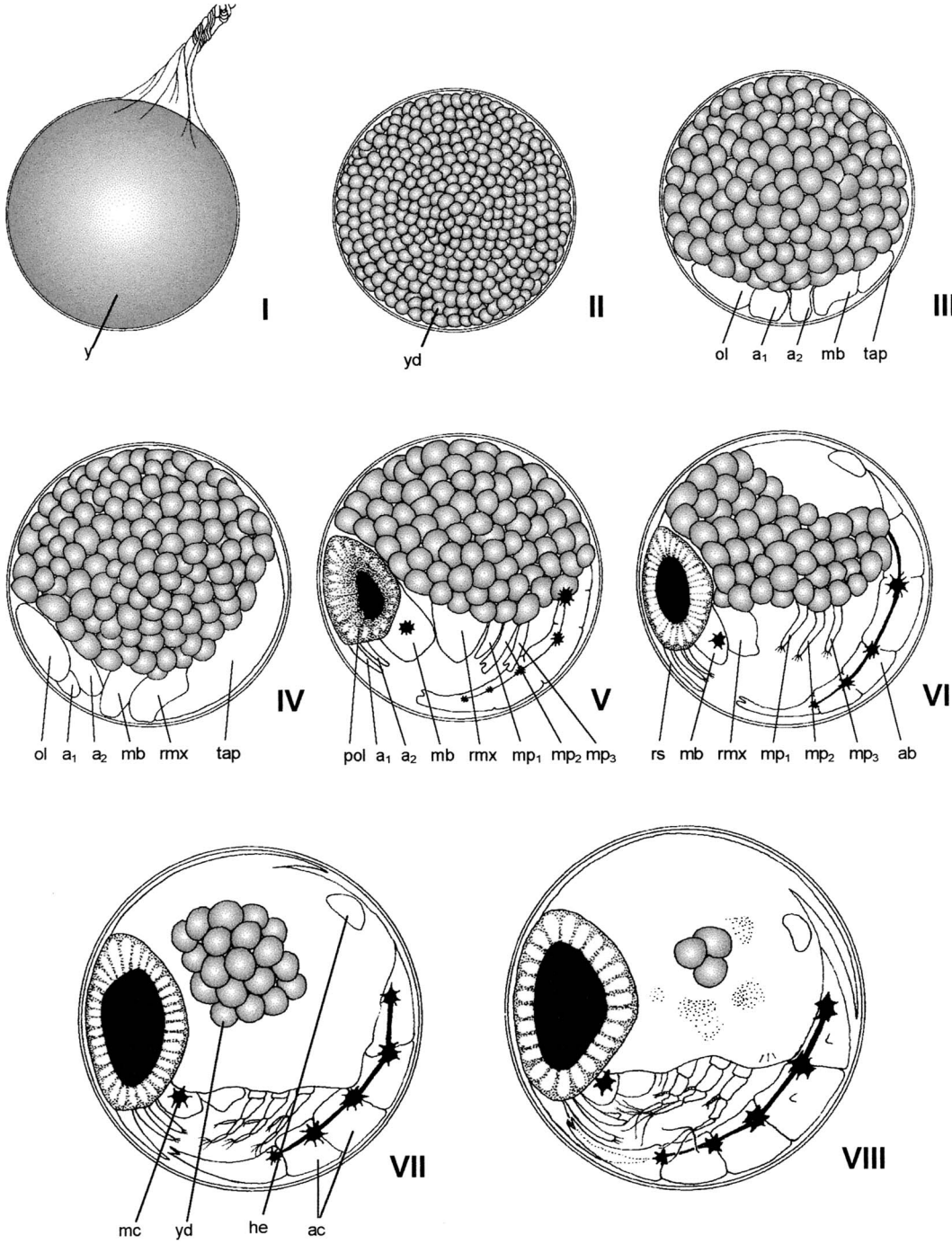

Fig. 1. *Ucides cordatus* (Linnaeus, 1763). Schematic drawings of the eight embryonic stages, showing the main morphologic structures (a_1 = antennule; a_2 = antenna; ab = abdomen; ac = abdominal chromatophores; h = heart; mb = mandible; mc = mandibular chromatophore; mp_1 to mp_3 = maxillipeds 1 to 3; ol = optic lobe; pol = pigmented optic lobe; rmx = rudiment of maxilla and maxillule; rs = rostral spine; tap = thoracic-abdominal process; y = yolk; yd = yolk droplets).

Table 1. *Ucides cordatus* (Linnaeus, 1763). Average and standard deviation for both the length of larger and smaller diameter, mean diameter, volume, and for the areas of the embryo, yolk pole, ocular lobe, and ocular pigmentation, in all embryonic stages. The growth percentage (G) from the first stage, or from the first appearance of a given structure, is also shown. Average values sharing the same letter in a given column are not statistically different ($P > 0.05$). Sample size for each stage is 15.

Stages	Length of larger diameter (μm)	Length of smaller diameter (μm)	Mean diameter (μm)	Volume ($\mu m^3 \times 10^6$)	Embryo area ($\mu m^2 \times 10^3$)	Yolk area ($\mu m^2 \times 10^3$)	Area of ocular lobe ($\mu m^2 \times 10^3$)	Area of ocular pigmentation ($\mu m^2 \times 10^3$)	Description
I	444.7 ± 16.4 a	419.3 ± 16.2 a	432.0 ± 14.4 a	41.1 ± 4.2 a	–	144.0 ± 8.3 g	–	–	Precleavage Stage—Immediately after extrusion, egg still undivided, fully filled with yolk, color of dark bordeaux and opaque, and funiculus not spiraled.
II	458.7 ± 12.5 b	436.7 ± 15.9 b	439.0 ± 7.6 ab	45.9 ± 4.4 b	–	150.0 ± 9.3 fg	–	–	From Cleavage to Blastula—Two days after egg-laying, egg totally divided with yolk droplets of similar size. Egg colored dark bright bordeaux, and embryo not yet defined in lateral view. Egg funiculus now spiraled.
III	473.3 ± 9.0 c	454.0 ± 9.9 c	447.7 ± 13.3 bc	51.1 ± 2.7 c	14.0 ± 6.3 a	153.3 ± 8.2 f	–	–	Naupliar Stage—Five days after egg-laying, fragmentation of yolk more evident, and yolk droplets larger. Egg color dark bright bordeaux. In lateral view, embryo appeared as whitish, translucent pole, comprising 1/6 to 1/5 of egg volume. Three naupliar appendages (antennule, antenna, and mandible) identifiable between ocular lobe and thoracic-abdominal process.
IV	495.3 ± 11.3 d	478.0 ± 7.7 d	455.0 ± 9.3 cd	59.3 ± 2.5 d	73.3 ± 9.8 b	106.7 ± 9.8 e	12.0 ± 4.1 a	–	Metanaupliar Stage—Eight days after extrusion, embryo occupied 1/4 to 1/3 of dark ochre egg. Embryonic ocular region well delimited but still not pigmented. Six embryonic characteristics (ocular lobe, antennule, mandible, maxilla-maxillule rudiment, and thoracic-abdominal process) distinguishable. Embryo's heart distinguished as tenuous beating structure. Thoracic-abdominal process still not metamerized, five times larger than in previous stage.

Table 1. Continued.

Stages	Length of larger diameter (μm)	Length of smaller diameter (μm)	Mean diameter (μm)	Volume ($\mu m^3 \times 10^6$)	Embryo area ($\mu m^2 \times 10^3$)	Yolk area ($\mu m^2 \times 10^3$)	Area of ocular lobe ($\mu m^2 \times 10^3$)	Area of ocular pigmentation ($\mu m^2 \times 10^3$)	Description
V	506.0 ± 15.5 d	486.0 ± 15.0 d	463.7 ± 7.7 de	62.7 ± 5.5 d	96.7 ± 10.5 c	87.3 ± 8.8 d	13.5 ± 3.8 a	1.5 ± 0.4 a	Pigmented Stage—Ten days after egg-laying, yolk now convoluted in dorsal view, occupying half of egg volume. Egg coloration dark ochre. Ocular lobes now more evident, with black pigmentation in central area. Eyes oval in lateral view, semicircular in dorsal or ventral views. Abdominal chromatophores already visible, connected. Metamerization of thoracic-abdominal process, with terminal tip overreaching rostral spine, apparent.
VI	520.7 ± 10.3 e	504.7 ± 13.0 e	474.7 ± 7.7 e	69.5 ± 4.8 e	139.3 ± 8.8 d	60.7 ± 7.0 c	11.9 ± 1.0 b	3.0 ± 0.3 b	Double Chromatophoric Bridge Stage—In lateral view 14 days after egg-laying, two bilobed yolk occupied 1/3 of egg volume and V-shaped in dorsal view. Egg color dark ochre. In ventral view, chromatophore pair in each abdominal somite, joined together by double chromatophoric bridge. Heart now larger and beating evident. Terminal setae of maxillipeds visible, and metamerization of thoracic-abdominal process still incomplete.
VII	526.7 ± 11.1 e	511.3 ± 14.6 e	486.7 ± 7.5 f	72.2 ± 5.2 e	162.0 ± 8.6 e	44.7 ± 64 b	14.6 ± 1.4 c	4.2 ± 0.3 c	Pre-Hatching Stage—Sixteen days after egg-laying. In lateral view, embryo occupied 3/4 of egg volume, and yolk two small connected patches. Coloration of eggs light ochre. Ocular area ovoid and intensively pigmented, covering from 1/8 to 1/6 of whole egg in lateral view. Beating heart much more noticeable and cardiac chromatophore visible. Six abdominal somites and telson already differentiated.

Table 1. Continued.

Stages	Length of larger diameter (μm)	Length of smaller diameter (μm)	Mean diameter (μm)	Volume ($\mu m^3 \times 10^6$)	Embryo area ($\mu m^2 \times 10^3$)	Yolk area ($\mu m^2 \times 10^3$)	Area of ocular lobe ($\mu m^2 \times 10^3$)	Area of ocular pigmentation ($\mu m^2 \times 10^3$)	Description
VIII	542.7 ± 9.6 f	526.7 ± 10.5 f	492.0 ± 9.0 f	78.8 ± 3.5 f	200.7 ± 8.0 f	16.7 ± 6.2 a	15.4 ± 2.9 c	5.0 ± 1.0 c	Hatching Stage—Nineteen days after extrusion, larva totally formed, fills egg space (13/15). Color of eggs light ochre. In lateral position, two small yolk droplets (1/8 of egg volume) at dorsal region of carapace. These yolk droplets a similar size and shape as the embryo eyes. Carapace, maxillipeds, and abdominal somites evident.
G (%)	+ 22.0	+ 25.6	+ 13.9	+ 91.7	+ 1333.6	+ 762.3	+ 28.3	+ 233.3	

correlated to the duration of embryonic (Efford, 1969; Wear, 1974; Fukui, 1988; Furota, 1988) and larval (Sastry, 1983; Lindley, 1990a, b; Pinheiro *et al.*, 1994) development of decapod crustaceans. The duration of the embryonic development can vary between species in different temperatures, i.e., 1 yr (5.7 ± 1.6°C) in *Erimacrus isenbeckii*, according Nagao *et al.* (1999), compared to 19 d (27 ± 1°C) in *U. cordatus*. Waterman and Chace (1960) mentioned an evolutive tendency towards an increase of the duration of the embryonic development in crustaceans with a reduction of larval stages as observed in *U. cordatus* (see Rodrigues, 1982).

Alterations of the color of eggs through embryogenesis are common in crustaceans (Pinheiro and Hattori, 2002). Generally orange early eggs develop into dark brown pre-hatching eggs (Costa and Negreiros-Fransozo, 1996; Pinheiro and Hattori, 2002) reddish eggs to light ochre in other species, such as *Pachycheles monilifer* (Dana, 1852) (Hattori and Pinheiro, 2002) and *U. cordatus*. However, some species do not have color changes, i.e., red eggs in *Macrobrachium potiuna* (Müller, 1880) and light brown in *M. iheringi* (Ortmann, 1897) studied by Bueno (1981). Carotenoid pigments are very abundant in yolk, promoting absorption of harmful UV radiation with embryo protection (Green, 1957), a function not very important for the gallery-dwelling *U. cordatus*.

During the adult phase, *U. cordatus* is physiologically capable of tolerating salinities common to the mangrove environment from 2‰ to 30‰ (Rodrigues, 1982). However, eggs and larvae are very sensitive to sudden salinity alterations. Rodrigues and Hebling (1989) reported higher larval survival for *U. cordatus* at 24‰, whereas Geraldes and Calventi (1983) mentioned lethal effects for juveniles at salinities higher than 20‰. Best results were obtained in our experiments at a salinity of 15‰, where all embryonic stages were obtained. However, half of the eggs were lost, possibly due to a great abundance of algae and protozoans.

Rodrigues (1982) reported that eggs of *U. cordatus* are spherical, but in the present study, we found the eggs to be slightly ellipsoid and similar to the egg shape in *A. cribrarius* (see Pinheiro and Hattori, 2002). Nagao *et al.* (1999) also described the eggs of *E. isenbeckii* as spherical. Although egg shape often varies throughout development, it does not in *U. cordatus*. The variation of the egg biometry

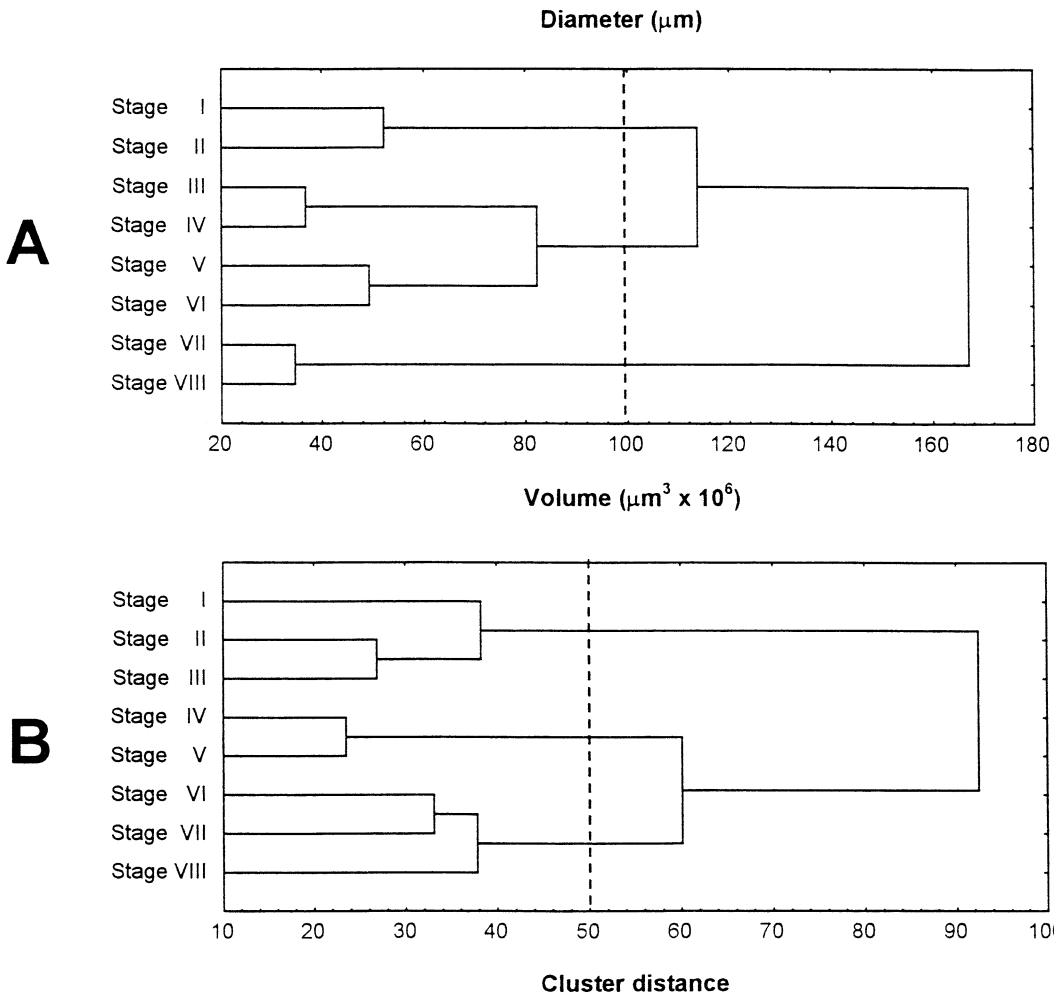

Fig. 2. *Ucides cordatus* (Linnaeus, 1763). Cladogram obtained in the cluster analysis (Euclidian Distance–Weighted Pair-Group Average) for embryo size in terms of diameter (A) and volume (B).

may be related to female size, age (Stella *et al.*, 1996; Giménez and Anger, 2001), or even genetics (Mashiko, 1992). In *U. cordatus*, Rodrigues (1982) estimated an egg increase of 22.9%, similarly to what was found in this study, i.e., 25.6% and 22% considering the smaller and larger axes, respectively.

The eggs of *U. cordatus* are small (390 μm to 540 μm) and similar to those of portunids (Pinheiro and Hattori, 2002). Their cleavage corresponds to the mesolecital pattern, as in *E. isenbeckii* and *A. cribrarius* (Nagao *et al.*, 1999; Pinheiro and Hattori, 2002). Smaller eggs imply extended larval development, with a larger number of larval stages, whereas larger eggs are commonly associated with abbreviated development (Lindley, 1990a, b; Pinheiro *et al.*, 1994).

Environmental factors may also play a role in the determination of the duration of embryonic development (Fukui, 1988; Furota, 1988), whereas physiological factors are the main variables determining the biometric variability of eggs (Crisp and Costlow, 1963; Efford, 1969; Nishino, 1980). According to Valdes *et al.* (1991), the embryonic development of *Necora puber* (Linnaeus, 1767) can be divided into five stages. The first two stages are similar to those described for *A. cribrarius* by Pinheiro and Hattori (2002), but the remainder correspond to the fifth, seventh, and eighth stages of the latter. Nagao *et al.* (1999) defined nine stages in *E.*

isenbeckii, while Yoshida (1940) *apud* Nagao *et al.* (1999), have only distinguished three stages for the same species without clearly describing their diagnostic characteristics. The sixth embryonic stage described for *U. cordatus* is similar to the fifth one defined by Nagao *et al.* (1999).

Statistical analyses revealed that the eight stages of *U. cordatus* may be separated into three groups with satisfactory biometric resolution, both in terms of diameter and volume. According to Pinheiro and Hattori (2002), these groups corroborate a more didactical classification of the embryonic development (initial, intermediate, and final) facilitating the statistical procedures in crustacean reproductive biology, followed by Costa and Negreiros-Fransozo (1996), Mantelatto and Fransozo (1997), Santos and Negreiros-Fransozo (1998), and Pinheiro and Fransozo (2002).

Therefore, the embryonic stages of *U. cordatus* can be adequately identified by verifying the morphology of embryos and chromatic patterns of eggs. Although contributing to their identification, biometric data alone are not sufficient to achieve a precise discrimination.

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