

# Morphology of the female reproductive system and reproductive cycle of the mangrove land crab *Ucides cordatus* (L.) in the Baía de Antonina, Paraná, Brazil

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## Abstract

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*Ucides cordatus* is a species of considerable ecological and socioeconomic importance. The goal of this study is to contribute to the understanding of the reproduction biology of this species by describing the macroscopic anatomy, the histology of the female reproductive system and the reproductive cycle of *U. cordatus*. A total of 367 females were obtained from October of 2002 to March of 2005 during monthly collections in the Baía de Antonina, Paraná, Brazil. Specimens were submitted to necropsy and their reproductive systems (ovary and spermathecae) were analysed histologically. Permanent slides were stained with Harris' hematoxylin and eosin, Mallory's trichromic and the periodic acid-Schiff reaction. Ovarian analysis allowed for the determination of five developmental stages based on the prevalence of oocytes in different phases of vitellogenesis. During stage V, when ovaries recover from spawning, the presence of oocytes in advanced stages of vitellogenesis was detected, suggesting that there could be more than one spawning in a single reproductive period. Females in stage IV were most common in the spring (November through February), whereas females with their egg mass exposed were most frequent from November through March. The reproductive period of *U. cordatus* in mangroves of the study region occurred from October to March. The reproductive events observed in the present study suggest that spermatophores acquired during copulation, which takes place during the 'andada', are only used in the reproductive period of the following year.

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## Introduction

The mangrove land crab, locally known as 'caranguejo-uçá', is an ocypodid endemic to the New World Atlantic coast that represents an important source of food and income for traditional communities along the Brazilian coast (Gläser 2003). In addition, *Ucides cordatus* is considered a key biological component of mangrove areas in this region, particularly through its role in the cycling of organic matter (Wolff *et al.* 2000).

The study carried out by Mota-Alves (1975) in Ceará, Northeast of Brazil, analysed its reproductive cycle and was

the first to describe the histology and anatomy of the female reproductive system of *U. cordatus*. Since then, several studies have been carried out to further understand the reproductive biology of this species. Nakamura (1979) described the macro- and microscopic morphology of the ovaries and their relationship with the weight and total length of adult individuals, in Baía de Paranaguá, Southern Region. Góes *et al.* (2000) investigated behavioural aspects and the reproductive period of the mangrove land crab, in Vitória, Southeast Brazil, classifying the stages of ovarian maturation through the observation of the macroscopic aspect of the ovaries. Dalabona and

Silva (2005) investigated the reproductive period of *U. cordatus* in the Baía das Laranjeiras, Paraná, based on macroscopic observation and gonad histology, whereas Sampaio (2002) attempted to integrate the reproductive biology of the species with the laws regulating the protection of this species.

The study of the reproductive cycle of *U. cordatus* has been used as a tool to determine the no-fishing period (Sampaio 2002), as well as in the planning of harvesting policies that are less destructive through the management of natural stocks. However, species with broad geographical ranges can vary latitudinally in their reproductive period, leading to the need for studies in many different locations for efficient management initiatives (Dalabona and Silva 2005).

The reproductive period of *U. cordatus* is usually associated with the phenomenon known as ‘andada’ or ‘carnaval’, in which there is a considerable increase in walking activity of the species in the mangrove. This event is under lunar influence, taking place during the full and the new moons. The seasonal occurrence of the ‘andada’ is not precise, given that it can occur in different months, as observed by Góes *et al.* (2000) in Vitória, ES (Southeastern Brazil).

The impetus for this study was to provide an overview of the reproductive biology of this species by describing the macroscopic anatomy and the histology of the female reproductive system. In particular, a new classification of germinative cells and of the process of female gonadal maturation of *U. cordatus* is provided based on cell size and morphology, as well as an anatomical description of the spermathecae. Finally, a description of the reproductive cycle in mangroves of the Baía de Antonina, Paraná, is provided.

## Materials and Methods

The crabs used in the present study were collected in mangroves of the Baía de Antonina (25°25'S; 48°42'W), Paraná, Southern Brazil. Adult females of *U. cordatus* were captured monthly from October of 2002 to March of 2005 and transported alive to the laboratory, where they were inspected to assess qualitatively their health state (individuals that were either moribund or dead from the transportation were not included in the study to avoid *post-mortem* artefacts). Each ovigerous female (carrying eggs by pleopods) had its cephalothoracic width (CW) measured with a caliper.

The reproductive system was dissected and described under a stereoscopic microscope and gonad and spermathecae colourations were recorded. Crabs were kept at  $-10^{\circ}\text{C}$  for approximately 15 min to reduce their metabolism, as indicated by their lethargy. Then, the dorsal region of the carapace was removed to allow for the dissection of the organs, which were fixated in AFA for 24 h, and processed according to standard histological methods. Ovary fragments from the proximal, medial and distal regions were processed, as well as spermathecae with the connection to the gonopores and the preserved ovaries. Tissues were sectioned into 5  $\mu\text{m}$  slides using a Leica RM2125RT microtome. Permanent slides were

stained with Harris' hematoxylin and eosin (HE), Mallory's trichromic and the periodic acid-Schiff reaction (PAS) according to Behmer *et al.* (1976). Photographs were taken using a QColor 5 digital camera.

The ovaries were classified histologically according to the prevalence of germinative cells during its development, including morphometric assessments. The percent of occurrence of specimens in each stage of ovarian development and the frequency of ovigerous females were recorded to determine their relative abundance over time.

## Results

### Macroscopic anatomy

A total of 367 females were analysed throughout the study, with an average CW of  $6.6 \pm 0.75$  (SD). Females of *U. cordatus* have a broad abdomen that covers completely the sternites. The internal side of the abdomen harbours the pleopods, which are structures in which the eggs remain attached during embryogenesis, until the eclosion of the larvae. Gonopores, which are operculated orifices located on the sternite of the sixth thoracic segment and that allow for the penetration of the spermatophores during copulations, are located medially. The female reproductive system of *U. cordatus* is bilateral and ‘H’ shaped. It is composed of a pair of ovaries, connected to one another by a bridge of ovarian tissue and a pair of spermathecae. The spermathecae are connected to the gonopores.

The ovaries are positioned dorsally on the cephalothorax. They are curved in their anterodorsal portion, extending until the posterior region of the cephalothorax. They communicate through a transversal expansion in their medial portion, which is located dorsally to the stomach. As vitellogenesis proceeds, the ovarian volume tends to increase and its colouration changes. The observed ovarian colourations during this study varied considerably, namely: transparent to white, beige, yellow, orange, brown and purple. In the latter, oocytes can be easily seen, even to the naked eye. However, there is little correspondence between macroscopic phenotypic traits such as gonadal colouration and the degree of ovarian maturation at the cellular level (Castilho 2006).

The spermathecae (seminal receptacles) are composed of a pair of spherical structures of a translucent, whitish or beige colouration, with occasional small gray or orange spots. Their function is to store the spermatophores until the female is ready for fertilisation. Spermathecae are located laterally to the midgut and posterior to the thoracic ganglion, between the pereiopod thoracic muscles. Each spermathecae is attached to a thin channel, which extends as a prolongation of the lumen of the ovary. This small channel is located parallel to the seminal vesicle wall until reaching the exit of the spermathecae.

### Histology

Ovaries are covered by conjunctive tissue. Internally, there are both germinative cells (oogonia and oocytes in different

degrees of maturation) and follicular cells (accessory cells and mesodermal stroma).

Vitellogenesis is observed during oogenesis. The latter can be divided into several phases and is characterised by the production and maturation of female gametes. The maturation phases in females of *U. cordatus* were determined based on the morphological changes observed in the germinative cells. Cells were classified as:

- 1 Oogonia (incipient germinative cells): cells with an average diameter of  $9.68 \pm 1.0 \mu\text{m}$  ( $n = 117$  cells) and a clear nucleus, with chromatin granules located near the nuclear membrane. A narrow layer of basophile cytoplasm surrounds the nucleus. Oogonia are located in germinative centres (GCs) (proliferation regions) and often are observed in the process of cell division. GCs are surrounded by follicular cells, which form a simple squamous epithelium and are located near the lumen of the gonad (Fig. 1A).
- 2 Oocytes I (basophile oocytes with reduced cytoplasm): cells with an average diameter of  $16.78 \pm 2.73 \mu\text{m}$  ( $n = 116$  cells). Oocytes I are located in the germinative centres, near the oogonia. Their cytoplasm is narrow and basophile, with a clear nucleus and nucleoli near the nuclear cell membrane. One nucleolus that is larger than the rest is often observed (Fig. 1A).
- 3 Oocytes II (previtellogenic oocytes): cells with a basophile cytoplasm, although eosinophilic globules and vacuolisation can also be present. Their nucleus is clear in its centre, with several small nucleoli and a large nucleolus averaging  $3.94 \pm 0.90 \mu\text{m}$  that is usually near the nuclear membrane. Oocytes II average  $39.14 \pm 7.24 \mu\text{m}$  ( $n = 123$  cells) in diameter and can be seen within germinative centres or dispersed throughout the ovary (Fig. 1A,B).
- 4 Oocytes III (oocytes in vitellogenesis with a slightly eosinophilic cytoplasm): cells with an average diameter of  $68.53 \pm 12.48 \mu\text{m}$  ( $n = 124$  cells) and a clear nucleus, with dispersed granular chromatin and a lateralised nucleolus. Lipid droplets are observed in the cytoplasm, as well as slightly eosinophilic droplets that stain positive to the PAS reaction (Fig. 1B).
- 5 Oocytes IV (oocytes in vitellogenesis with an eosinophilic cytoplasm and a condensed nucleus): In this phase, the nuclei experience a severe reduction in diameter, are highly basophilic and display chromatin granules. The nucleus is located closer to the cell membrane. The average cell diameter in this stage is  $122.22 \pm 19.79 \mu\text{m}$  ( $n = 130$  cells). The cytoplasm harbours many lipid and eosinophilic droplets that also stain positive for the PAS reaction (Fig. 1C).
- 6 Oocytes V (mature oocytes): By the time vitellogenesis is complete, oocytes V have an average diameter of  $196.44 \pm 26.85 \mu\text{m}$  ( $n = 136$  cells), with polyhedral shapes and rounded corners. The nuclei and the cyto-

plasm are similar to the previous stages, although large droplets are no longer found near the nucleus. Given the considerable increase in cell volume, follicular cells that surround oocytes become distended and assume a squamous appearance (Fig. 1D).

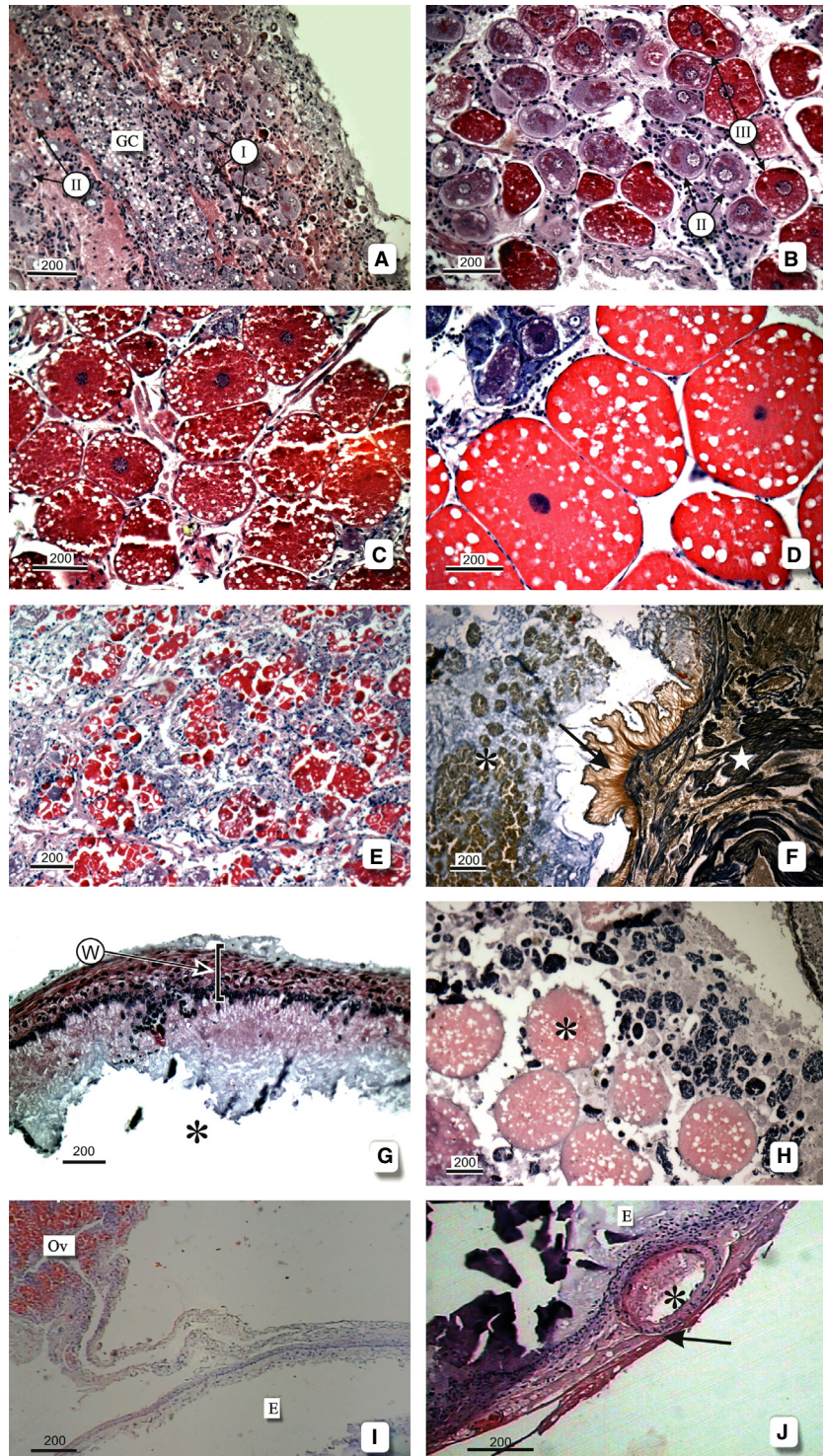
During the process of oogenesis, there is an increase in cell diameter, resulting in oocytes V being nearly 20 times larger than oogonia. The prevalence and distribution of germinative cells in different developmental phases varied throughout ovarian development, thus allowing for the determination of maturation stages. In this study, a classification of ovarian development into the following five stages is proposed:

- 1 E1 (Stage 1 – immature ovary): germinative centres (oogoniae and oocytes I) are present, together with oocytes II, which account for most of the volume in the ovary.
- 2 E2 (Stage 2 – ovary in initial maturation): oogonia and oocytes I, II and III are present, although the latter are the most prevalent.
- 3 E3 (Stage 3 – ovary in final maturation): oogonia and oocytes I, II, III and IV are present, with a predominance of the latter.
- 4 E4 (Stage 4 – mature ovary): Only oogonia and oocytes I, II and V are observed in this stage. Oocytes V are the most prevalent, taking up most of the gonadal volume, with a small number of oocytes I.
- 5 E5 (Stage 5 – regenerating ovary): Oocytes V are in the process of reabsorption and gonadal restructuring, with an increase in the number of germinative centres and oocytes II. Empty spaces throughout the gonad are also observed in this stage (Fig. 1E).

It is important to note that, although uncommon, some ovigerous females showed regenerating ovaries with large quantities of oocytes III and IV. These females show few atretic oocytes V and many germinative cells in the process of vitellogenesis. Also, some specimens showed the presence of spongy connective tissue (SCT) surrounding the ovaries in different stages of maturation.

The walls of the spermathecae are thin and fragile, being composed of a stratified squamous epithelium (Fig. 1G). Spermatophores containing either viable or unviable spermatozooids are commonly observed in the lumen of the spermathecae, being immersed in a secretion that stains positive to the PAS reaction. The characterisation of spermatozoid viability was carried out based on the results of HE staining and PAS reaction, given that unviable spermatozooids cease being acidophile and become slightly basophile, as well as being negative to the PAS reaction. It is noteworthy that all females had viable spermatozooids in their spermathecae throughout the study period. Oocytes V, on the other hand, were not so common in within spermathecae (Fig. 1H).

The ovary is attached to the spermatheca by a thin, whitish canaliculus (oviduct). One to three small pores were observed microscopically along the walls of the spermatheca, possibly

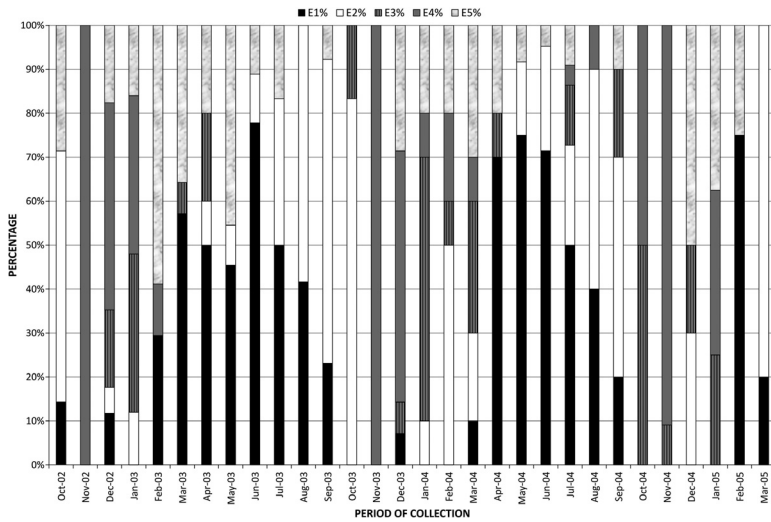


**Fig. 1**—Ovary of *Ucides cordatus* in a longitudinal section, HE staining. —**A**. Immature ovary containing oocytes II and a large germinative centre (GC) with a oocyte I in an inset. —**B**. Ovary in initial maturation, with the presence of oocytes II and III. —**C**. Ovary in final maturation, with a predominance of oocytes 4 (IV). —**D**. Mature ovary, with oocytes V. —**E**. Regenerating ovary, showing the reabsorption of oocytes V. Spermatheca of *U. cordatus* in a longitudinal section. —**F**. Wall of the spermatheca with a layer of dense connective tissue (star) and spermatozoa in its lumen (\*). Stratified squamous epithelium (arrow) near the vagina. Staining with Mallory's trichomic. —**G**. Wall of the spermatheca (W) and lumen (\*). Staining with HE. —**H**. Oocyte-like cells in phase V in the lumen of the spermatheca (\*). Staining with HE. —**I**. Oviduct connecting the ovary (Ov) and the spermatheca (E). Staining with HE. —**J**. Opening (\*) of the wall (arrow) of the spermatheca (E). Staining with HE.

related to the transit of oocytes from the oviduct to the spermatheca. However, the exit point of the oocytes is located at the base of the spermatheca, in its connection with the vagina. The vaginal canal is supported by two exoskeleton plates and displays a thick wall of conjunctive tissue, which is connected

to the gonopore. The gonopores are openings located in the abdomen, in the segment corresponding to the third pair of pereiopods, and allow the transit of spermatophores and eggs.

The inner wall of the spermatheca has villousities near the vagina (Fig. 1F), which are formed by cylindric epithelium



**Fig. 2**—Monthly distribution of the relative occurrence of females of *Ucides cordatus* in each stage of gonadal development. See text for a description of each developmental stage.

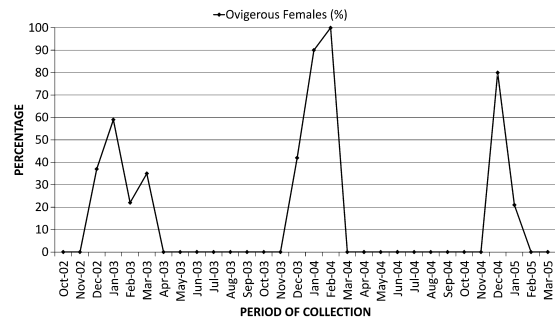
covered by a fine cuticle in its apical portion. Loose conjunctive tissue is located immediately underneath this epithelium, followed by a thick layer of dense conjunctive tissue which, together with the villositities, extends until the vagina. In some specimens, the wall of one or both spermathecae showed strong pigmentation, at times becoming black.

*Reproductive cycle*

The study of the ovarian histology showed a seasonal tendency in the occurrence of different ovarian developmental stages (Fig. 2), as well as in the frequency of ovigerous females, generally from November to March (Fig. 3 and Table 1). Stage E1 females were most common from early March to September, coinciding with the fall and winter in 2003, 2004 and part of 2005. The E2 developmental stage was nearly absent in 2003 until the period between July and October, yet showed a strong peak of occurrence in February of 2004 and was again absent in February of 2005, indicating a strong interannual variability in occurrence patterns. The occurrence of E3 females peaked around January of 2003, 2004 and 2005, yet a second peak was observed in October of 2004 that was not present in the previous year. Stage E4 females dominated the samples in November of all 3 years and gradually decreased in frequency afterwards, whereas stage E5 females were present almost all year round.

**Discussion**

The overall anatomy of the ‘H’ shaped ovary of *U. cordatus* is common to other ocypodids, including *Uca rapax* (Castiglioni et al. 2007). However, the new classification of germinative cells and of the process of female gonadal maturation of *U. cordatus* based on cell size and morphology provided in this study used anatomical and histological aspects of the female



**Fig. 3**—Monthly distribution of the percentage of ovigerous ( $n = 67$ , average =  $2.23 \pm 4.37$ /months) females of *Ucides cordatus* collected randomly in the Baía de Antonina, PR, Brazil.

reproductive system of this species that had not been investigated in previous studies.

Nakamura (1979) classified oocytes into four stages, such that intracytoplasmatic basophilic granules would be present on oocytes IV. This study identified five stages, with the last being composed of eosinophilic granules without any intracytoplasmatic basophilic content. It is important to underscore that germinative centres (proliferation zones) were located throughout the entire lumen of the ovary, as opposed to Nakamura (1979), who only observed this cell structures in the transversal commissure of the ovary. The results of this study are similar to those described by Castiglioni et al. (2007) in the case of *U. rapax*, in which germinative centres are grouped at the centre of the ovary.

Oocytes II have been frequently observed in stage 5 ovaries in this study, contrary to the lack of such cell type in the study by Dalabona and Silva (2005). In addition, oocytes II were present in all developmental stages. During stage 5, a large proportion of the studied individuals only showed phase I and II viable germinative cells, possibly as a source of reserve

**Table 1** Number of the ovigerous females of *Ucides cordatus* collected in the Baía de Antonina, from October 2002 to March 2005

Date	Collected	Ovigerous female
October-02	8	0
November-02	5	0
December-02	11	4
January-03	33	19
February-03	17	4
March-03	14	5
April-03	11	0
May-03	11	0
June-03	10	0
July-03	11	0
August-03	12	0
September-03	15	0
October-03	9	0
November-03	13	0
December-03	14	6
January-04	10	9
February-04	10	10
March-04	11	0
April-04	10	0
May-04	12	0
June-04	32	0
July-04	10	0
August-04	10	0
September-04	10	0
October-04	12	0
November-04	11	0
December-04	10	8
January-05	9	2
February-05	8	0
March-05	10	0
Total	369	67

whereas oocytes V were atresic and being reabsorbed. Therefore, one can assert that *U. cordatus* displays a complete spawning strategy given that, after mature oocytes are released, the remaining oocytes are reabsorbed.

However, some ovigerous females present large numbers of oocytes III and IV. Although this finding was not observed in all analysed females, it suggests that part of the population occasionally carries out a second spawning on the same reproductive season, given that the spermathecae remain constantly filled with viable spermatozooids, which allows for new fertilisations.

Góes *et al.* (2000) classified the maturation stages of *U. cordatus* based on macroscopic appearance, variation in the gonadossomatic index of the females and reproductive behaviour, thus proposing the ‘partially spawned’ category, which would include features of both mature and regenerating stages. Sampaio (2002), on the other hand, also observed partially spawned ovaries, but interpreted them as evidence for multiple spawning in this species. The SCT was observed attached to the ovaries in some specimens. This tissue had not been reported in ovaries of *U. cordatus*, but has been reported

by Johnson (1980) in *Callinectes* sp. and in *Libinia emarginata* (Leach, 1815). According to that author, SCT would correspond to a large site for the storage of glycogen. Therefore, the presence of this tissue near the ovaries suggests the accumulation of glycogen to be later allocated to oocytes during vitellogenesis.

Sant’Anna *et al.* (2007) studied the spermathecae of *U. cordatus* using histological and histochemical methods and found oocytes V in the spermathecae, as well as an orange pigment in the distal region of the spermatheca that was very similar to oocytes, suggesting that internal fertilisation in this species takes place immediately prior to spawning.

The pigmented cells observed in the walls of the spermathecae in the present study were also observed by Beninger *et al.* (1988) in the snow crab (*Chionoecetes opilio*). All analysed spermathecae were filled with a viscous substance that stains intensely with PAS, as described by Beninger *et al.* (1988) and Sant’Anna *et al.* (2007).

Based on the observed anatomical traits of *U. cordatus*, one can infer that the oocytes enter the spermatheca through the pores located dorsally on the wall, and leave it at the base across the vagina, contrary to the case described by Diesel (1989) for *Inachus phalangium*, in which the spermatheca has two chambers. In this case, the spermatozoa remain in the dorsal chamber and fertilisation takes place in the ventral chamber.

The temporal distribution of females with mature gonads in the Baía de Antonina ranged from October to March, a pattern consistent with studies in other bays in the State of Paraná (Nakamura 1979; Dalabona and Silva 2005). However, differences can be observed in comparisons with studies in other Brazilian states, with an apparent trend to delay maturation toward lower latitudes (Table 2).

Given that: (i) males have constant spermatogenesis throughout the year (Castilho 2006; Castilho *et al.* 2008); (ii) spermatophores containing viable spermatozooids are observed all year long in the spermathecae, which is a common characteristic of crustaceans according to Brusca and Brusca (2007); (iii) fertilisation takes place immediately prior to spawning; (iv) females with mature ovaries begin appearing in October, with a peak in November; (v) a reduction in the proportion of females with mature ovaries and the onset of appearance of ovigerous females takes place in November, these results lead one to infer that the spermatozooids used in fertilisation were obtained in copulations that occurred one or more months prior to October. This observation is based on reports of the ‘andada’, which is the moment when copulation would take place, from December to May (Oliveira 1946; Costa 1979; Freire 1998; Botelho *et al.* 1999; Vasconcelos *et al.* 1999; Góes *et al.* 2000). Therefore, we suggest that the ‘andada’ is a moment of replenishing spermatozoa into the spermathecae for their later use during the reproductive period.

Therefore, if the ‘andada’ is associated with mating, it would account for the replenishment of spermatozooids in the



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