Male influence on the ovarian development of the crustacean parasite *Bopyrina abbreviata* (Isopoda, Bopyridae)

JESÚS ROMERO-RODRÍGUEZ[1], RAMIRO ROMÁN-CONTRERAS[2] AND JOSÉ LUIS BORTOLINI-ROSALES[3]

[1]Departamento de Biología Marina, Facultad de Veterinaria y Zootecnia, Universidad Autónoma de Yucatán (UADY), Km 15.5 carretera Mérida-Xmatkuil, Apartado Postal 4-116 Itzimná, Mérida Yucatán, Mexico, [2]Laboratorio de Carcinoparasitología, Unidad de Ecología y Biodiversidad Acuática, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México (UNAM), Apartado Postal 70-305, Mexico, DF 04510, Mexico, [3]Departamento de Biología Comparada, Facultad de Ciencias, Universidad Nacional Autónoma de México (UNAM), DF 04510, Mexico

The presence of a male in a population of terrestrial isopods can accelerate the onset of female reproduction, a feature that has been suggested also to occur in bopyrid isopods. This paper aims to estimate the influence of the male presence on the ovarian maturation of Bopyrina abbreviata. *Females of* B. abbreviata *of different sizes were collected at Términos lagoon, Campeche, Mexico. The organisms were morphometrically classified as immature or mature, the male presence or absence at female's marsupium was recorded, and the degree of ovarian development was determined histologically. The internal organization of* B. abbreviata *agrees with that described for bopyrids and isopods in general. The ovarian cells originate from a dorsal lamina germinal layer that extends horizontally. The ovarian development of lone and paired immature females was classified as incipient and medium, respectively. In mature females it was classified as advanced, in the paired females and in the one lone mature female studied. The lone mature female differed from paired mature females only in the presence of reabsorption process in some oocytes located closer to the ventral wall of the ovary. Morphology variations between lone and paired females suggests that the presence of a cryptoniscus larva or a male between the female's pleopods stimulates the onset of reproduction and accelerates the ovarian development of* B. abbreviata.

Keywords: reproductive onset, male influence, ovarian development, bopyrid, Laguna de Términos, Mexico

INTRODUCTION

Bopyrina abbreviata Richardson, 1904 is a bopyrid isopod that infests *Hippolyte zostericola* (Smith, 1873), an important caridean in the transferral of energy from primary producers to higher trophic levels in the lagoon systems of the south-west Gulf of Mexico (Sánchez *et al.*, 1996; Barba *et al.*, 2000, 2005). Information about the biology of *B. abbreviata* is limited to some reports about their population structure, reproduction and prevalence (Román-Contreras & Romero-Rodríguez, 2005; Romero-Rodríguez & Román-Contreras, 2013). Its distribution extends from the coast of North Carolina and Florida, USA (Markham, 1985) to the coast of the states of Espírito Santo, São Paulo and Santa Catarina, Brazil (Lemos de Castro & Brasil-Lima, 1980). But in Mexico it has been reported only in Laguna de Términos, south-western Gulf of Mexico (Román-Contreras & Romero-Rodríguez, 2005; Romero-Rodríguez & Román-Contreras, 2014).

Diversity among taxa of crustaceans is not limited to external morphological structures; there is also heterogeneity in their internal organization (McLaughlin, 1983). Wilson (1991) and Warburg (2011) noted that even though isopod crustaceans have wide morphological diversity and their

sexual adaptations have been addressed in several studies, the structure and function of their copulatory organs and reproductive systems are still poorly understood.

Multiple abiotic or biotic factors influence the reproductive patterns in isopod species, e.g. both temperature and photoperiod can regulate the onset of reproduction, mainly in terrestrial species. Population density can also affect fecundity since crowding shortens the reproductive period, slows down the rhythm of laying and reduces the number of eggs (Caubet *et al.*, 1998). Presence of males in a population of the terrestrial isopod *Armadillidium vulgare* (Latreille, 1804) stimulated female reproductive onset by reducing the duration of parturial intermoult by nearly 40%, from 54 days in lone females to 32 days in those paired with a male; this can also be appointed as a delay in the ovarian development of unpaired females (Jassem *et al.*, 1982; Lefebvre & Caubet, 1999).

The male influence on female reproductive onset in *A. vulgare* may be caused by physical stimulation of the female genital apparatus (Lefebvre & Caubet, 1999). However, if several females of the same species are grouped in a particular place this, too, may stimulate reproduction so its preparturial intermoult period is reduced. Further work is required to identify the cause of this stimulation (Caubet *et al.*, 1998), and to ascertain whether this trait is also present in other isopods, as has been suggested for the bopyrid isopod *Probopyrus ringueleti* Verdi & Schuldt, 1988 (Schuldt, 1993).

In contrast to the abundance of reports on bopyrid taxonomy and the damage caused by bopyrids to their hosts,

Corresponding author:
J. Romero-Rodríguez
Email: bopiride@gmail.com

knowledge about their reproductive organs is scant, probably because the small body size of most of these parasites inhibits study of their internal anatomy (Hiraiwa, 1934).

Among the first authors who studied the internal anatomy of bopyrid isopods, Rathke (1837) and Cornalia & Panceri (1858) described the internal organization of both sexes in *Bopyrus squillarum* (Latreille, 1802) and *Gyge branchialis* Cornalia & Panceri, 1861, respectively; however, description of the gonads was limited to their position and aspect. Kossmann (1881) noted that the appearance of the female gonads of *Bopyrina ocellata* (Czerniavsky, 1868) (referred to as *B. virbii*) is modified during growth.

A detailed description of the reproductive organs of female and male *Parapenaeon japonica* (Thielemann, 1910) (as *Epipenaeon japonica*) defined the shape and development of the gonads and provided diagrams of the germ cells (Hiraiwa, 1933, 1934). A microanatomical study of the ovaries of *P. ringueleti* revealed a gradient of dorsoventral laminar maturation of the germ cells. The development of the region of vitellogenesis II in the ovary appeared to be related to the presence of the male over the female's abdomen, since vitellogenesis II was not seen in oocytes of lone mature females (Schuldt, 1993).

Oliveira & Masunari (1998) did not record lone immature females of *Aporobopyrus curtatus* (Richardson, 1904), i.e. all these females were paired with a cryptoniscus larva or a bopyridium, and they proposed that the presence of an immature female accelerates the development of the larvae into males. Similarly, Romero-Rodríguez & Román-Contreras (2014) reported ovigerous females of *Bopyrinella thorii* (Richardson, 1904) of smaller size than unpaired immature females and suggest that the establishment of pairs of parasites encourages the sexual maturation of both individuals. The present study aims to determine the influence of the male on the gonadal maturation in the female of *Bopyrina abbreviata*.

MATERIALS AND METHODS

Individuals of the caridean *Hippolyte zostericola* parasitized by *Bopyrina abbreviata* were collected during February and April 2010 with a Colman–Seagrove sledge net in meadows of *Thalassia testudinum* Banks ex König, 1805 on the inner margin of Isla del Carmen, Términos lagoon, Campeche, Mexico (19°10′–18°05′N 92°12′–91°10′W). For a more detailed description of the study area see Yáñez-Arancibia *et al.* (1988) and Raz-Guzmán & Sánchez (1996).

The biological material was fixed with Davidson's solution, a suitable fixative for histological techniques in crustaceans (Bell & Lightner, 1988), by a period of 72–100 h to ensure that the fixative could pervade the internal organs of the parasites (Bortolini & Álvarez, 2008). Afterwards, the material was washed with running water for 6 h and transferred into 70% ethanol until histological processing.

Because collection and subsequent handling of the biological material might damage the gill chamber of the host, thereby risking loss of the parasites settled therein, we considered only *B. abbreviata* females that were completely covered by the intact branchiostegite of the host. The total length (TL) of each *B. abbreviata* was recorded: in symmetric females, TL was measured from the anteromedial margin of the head to the posterior margin of the pleon; in asymmetric females, TL was measured from the posterior margin of the pleotelson to

the edge of the first thoracic somite of the longer side (Cash & Bauer, 1993; Romero-Rodríguez & Román-Contreras, 2008).

Developmental stages were defined according to the criteria proposed by Beck (1980), McDermott (1998) and Masunari *et al.* (2000) for other bopyrids: (a) Immature females – symmetric or asymmetric body, oostegites absent or moderately developed, coxal plates absent or poorly developed in pereomeres 1–3 of the longer side of the body; (b) Mature females – clearly asymmetric body, oostegites fully developed, coxal plates developed in pereomeres 1–3 of the longer side of the body; and (c) Ovigerous females – similar to mature females but with eggs or epicaridium larvae in the marsupium. Presence or absence of male or cryptoniscus larvae in the marsupium was recorded so that the immature and mature females could be grouped as lone or paired.

Females of every group and stage of development were processed in sequential dehydration, leaving the specimens for 30 min in each step. Tissue samples were cleared in xylene for 30 min before embedding in paraplast with a melting point of 56–58°C. Sections 7 μm thick were obtained with a rotary microtome Leica RM212RT and stained with standard haematoxylin and eosin, an overall staining technique that allows a broad overview of tissue (Torres & Bortolini, 2002; Bortolini & Álvarez, 2008; Álvarez *et al.*, 2010). Finally, samples were mounted in synthetic resin for later observation by optical microscopy.

Ovarian maturation in *B. abbreviata* was recorded according to the scale of sexual maturity proposed by Schuldt (1993) for *Probopyrus ringueleti*, which recognizes four stages of maturity: (a) Incipient – ovary poorly developed, in cross section occupies less than 30% of the surrounding loose connective tissue, germ cells at the end of vitellogenesis I, therefore plaques of eosinophilic yolk are not present (Figure 1A, D); (b) Medium – ovary more developed, oocytes in vitellogenesis II occupy most of the available frame (Figure 1E); (c) Advanced – ventrolaterally the mass of oocytes in vitellogenesis II almost reaches the body wall, oocyte size varies from one organism to another; and (d) Ovulation or post-spawn – the follicular cavity or *cisterna follicularis* appears empty or with some residual oocytes in advanced or total vitellogenesis (Figures 2D & 3D).

RESULTS

Of the 604 *Bopyrina abbreviata* females collected, 255 met the criterion of protection by the intact branchiostegite of the host. Of the 124 classified as immature, 48 were unpaired, 54 were paired with a cryptoniscus larva and 22 were paired with a male. Only one female classified as mature was lone, whilst 29 were paired with a male but without embryos in the marsupium and 101 mature females paired with a male were ovigerous. No mature female was paired with a cryptoniscus larva. Each of these groups was represented in the 21 females of different sizes that were selected for the histological treatment (Table 1).

Ovarian characterization of *Bopyrina abbreviata*

The ovary of *B. abbreviata* lies in the pereon and is a paired structure that runs lengthwise over the digestive tract. In
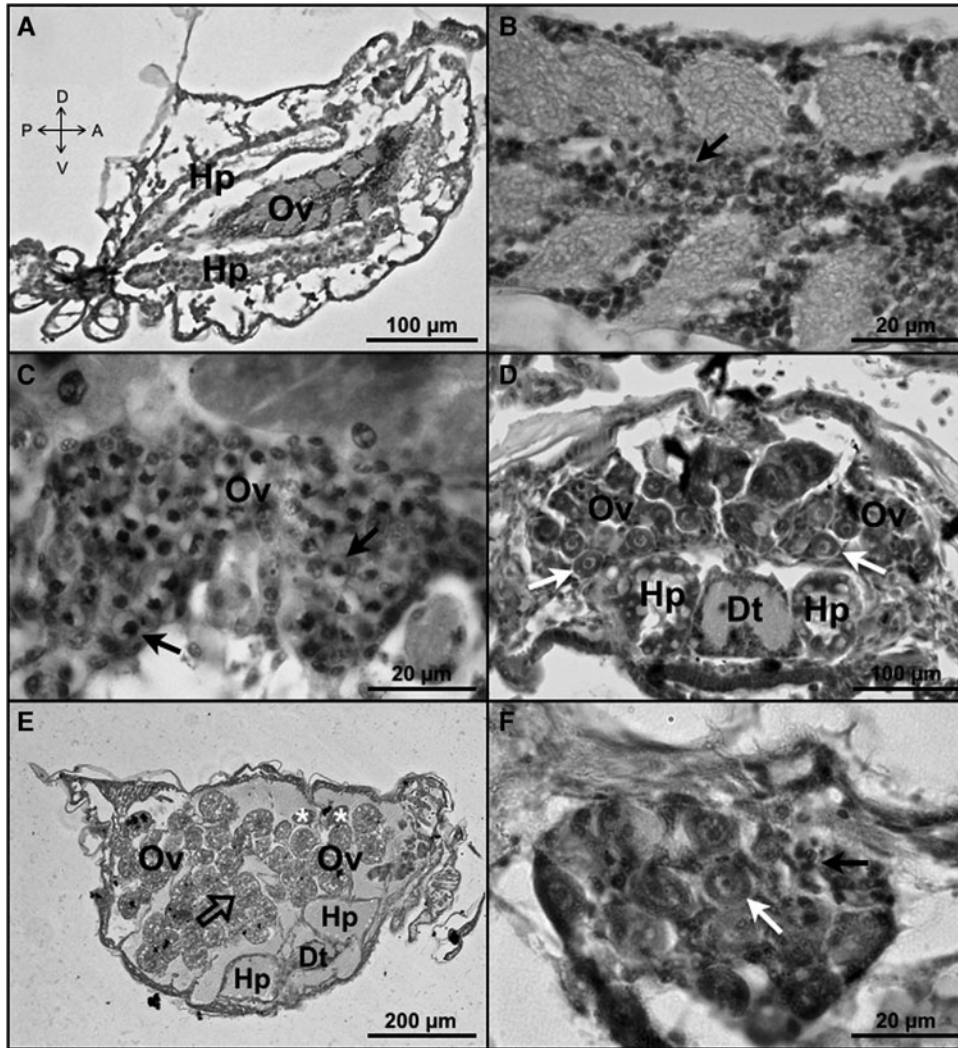
Fig. 1. Location, aspect and ovary development of *Bopyrina abbreviata* Richardson, 1904. (A) paired and compacted gonads of lone immature female, longitudinal section; (B) ovary detail of lone immature female; (C) development of lateral protuberance at distal sides in ovary of lone immature female, longitudinal section; (D) ovary on incipient stage of development of immature female paired with a cryptoniscus larva, transverse section; (E) ovary in advance stage of development of a mature female settle on host left side, transverse section. (F) dorsal lamina germinal layer detail of mature female, transverse section. (Ov, ovary; Hp, hepatopancreas; Dt, digestive tract; black arrow, oogonia II; white arrow, oocytes in vitellogenesis I; clear arrow, oocytes in vitellogenesis II; *, dorsal lamina germinal layer; D, dorsal; V, ventral; P, posterior; A, anterior).

young females the ovaries extend between the first and fifth pereomere, are tubular and compact carrying oogonia and oocytes, mainly in prophasic stage (Figure 1A, B).

Ovarian structure changed throughout female development; laterally, several lateral protrusions evolved discontinuously over the distal margin of each gonad, giving each an undulate appearance (Figure 1C). The ovaries progressively wrap dorsoventrally round the digestive organs (Figure 1D), which in some sections are completely surrounded by the gonads. This was observed mainly in some females larger than 2.0 mm TL (Figure 1E).

Relative ovarian size reflects the asymmetry of the whole body, which in turn is related to which of the branchial chambers of *Hippolyte zostericola* the female occupies, i.e. if a female *B. abbreviata* is attached to the right branchial chamber of its host, the parasite and its ovary are smaller on the right, and vice versa (Figure 1E). In a mature female the ovary length extends from the middle part of its head to the first pleomere.

The ovarian cells originate from a dorsal lamina germinal layer that extends dorsally (Figure 1F, 3D, E) and leads to the following dorsoventral maturation sequence of the germ cells: Oogonia I and follicular cells. The oogonia I, 2.5–3.6 μm, exhibit a clear nucleus, round or ovoid and about 0.9–1.1 μm in diameter and granular chromatin (Figure 3E). The follicular cells, 2.3–2.6 μm, have an ovoid nucleus with a diameter of 0.6–0.8 μm (Figure 3B, C). Next, there is a layer of oogonia II (4.1–6.2 μm) with a round nucleus 1.8–3.0 μm in diameter, and a small number of mesodermal cells (Figure 3A, F). Further on, towards the ventral region, oocytes in vitellogenesis I (10.8–13.2 μm) have a nucleus of 2.7–3.7 μm diameter, and basophilic and granular cytoplasm (Figure 3A, F). At the end of the maturation sequence are found oocytes in vitellogenesis II, and this forms the most massive ventral layer in a mature ovary. These oocytes, 40.7–68.6 μm, have a nucleus diameter from 8.7 to 11.7 μm, cytoplasmic vacuolations of 8–10 μm and eosinophilic droplets of about 1 μm (Figure 3B, C). The
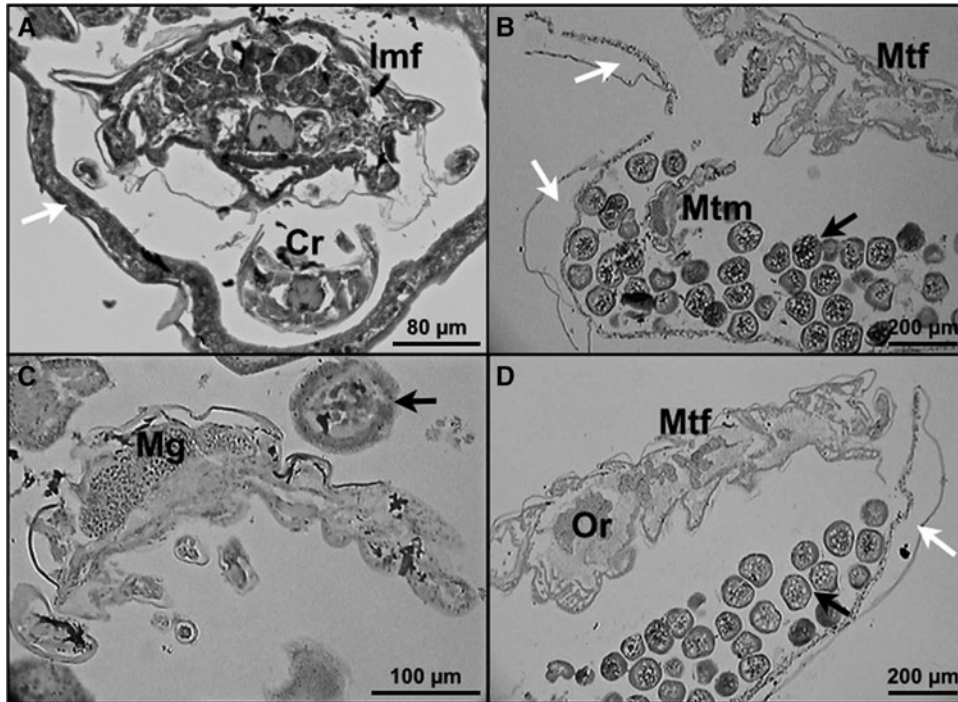
Fig. 2. Female *Bopyrina abbreviata* Richardson, 1904 paired with a cryptoniscus larva or a male. (A) immature female with a cryptoniscus larva, transverse section; (B) ovigerous female with a mature male, longitudinal section; (C) mature male detail, longitudinal section; (D) ovigerous female with ovary in post-spawn stage, longitudinal section. (Cr, cryptoniscus larva; Imf, immature female; Mtf, mature female; Mtm, mature male; Mg, male gonad; Or, oocytes in reabsorption; black arrow, embryos in egg stage; white arrow, host branchiostegite).

yolk is made up of plates of 10–13 µm. Some oocytes in vitellogenesis I and II had processes of cellular reabsorption, similar to the oocytes in vitellogenesis II showed in Figure 3D.

Effect of male presence on ovarian development of *Bopyrina abbreviata*

Ovarian development of *B. abbreviata* was classified as incipient in all lone immature females analysed. Most of these females had a tubular ovary (Figure 1A, B), but even when it was more developed it never filled more than 30% of the internal anatomy of the female (Figure 1D). The germ cells in the gonads of these immature females were mainly oogonia, but in some cases it was possible to observe some oocytes in vitellogenesis I.

Despite the difference in size of the lone immature females, their external morphology was similar. In only one of these females (67 mm TL) the pleomeres were well defined on both sides of the pleon, while in the remaining females the pleomeres were moderately fused onto one of the pleon edges. The greatest difference among these lone immature females was in the two largest (0.91 and 0.92 mm TL), whose bodies were moderately asymmetrical due to the poor development of the coxal plates in the first three pereomeres and whose dorsal facie was slightly pigmented.

In the three immature females paired with a cryptoniscus larva the degree of ovarian development was classified as medium, since among the germinal cells set on the gonads oocytes in vitellogenesis II were observed with a cell size of 45 µm and the yolk was in drops of medium size. Furthermore, the ovarian dorsoventral development exceeded 50% of the internal space available but in no cases reached the

abdominal body wall of the female. The largest immature female paired with a cryptoniscus larva had a bulging white abdomen, an appearance attributable to a further ovarian development. The coxal plates in two of these immature females were poorly developed in the first three pereomeres, and in the other one only the first pereomere had a coxal plate. The degree of fusion of the pleomeres on one of the two pleon edges ranged from medium to completely fused.

The degree of development of the ovaries in immature females paired with a male was variable. In the smallest of these females (Table 1) paired with an immature male of 0.5 mm TL, the ovary was classified as incipient since it had characteristics similar to those described for the lone immature females. In the two larger females of this group, one of 1.12 mm TL paired with a mature male of 0.65 mm TL, and another of 1.15 mm TL accompanied by an immature male of 0.45 mm TL, the ovaries contained oocytes in vitellogenesis II and due to their dorsoventral development the gonads were very close to the female abdominal wall but without reaching it, so ovarian development was classified as medium. Immature females paired with a male had a bulging white abdomen, and a body with a slightly more pronounced asymmetry that the previous group of females owing to the further development of the coxal plates in pereomeres 2–3. Except for the smallest of these females, all had the pleomeres fused on the shorter side margin of the pleon.

The ovaries of all mature females paired with a male were at an advanced stage of ovarian development. The germ cell stratification in the gonads of these females showed a great number of oocytes in vitellogenesis II very close to each other, giving them a rectangular or trapezoidal appearance (Figure 1D). These oocytes in vitellogenesis II ranged from 49 to 65 µm.
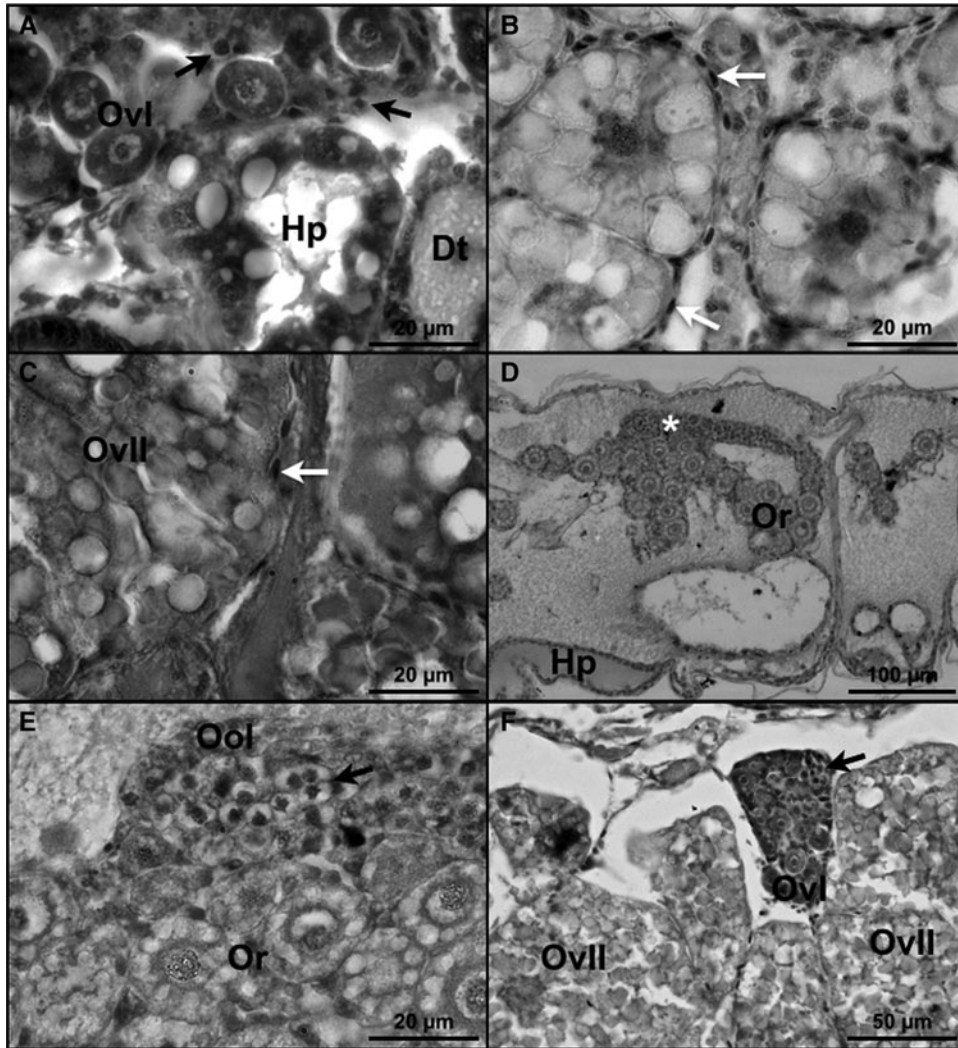
Fig. 3. Maturation of germ cells in female *Bopyrina abbreviata* Richardson, 1904. (A) ovarian detail of immature female, transverse section; (B) oocytes in vitellogenesis II of mature female, longitudinal section; (C) oocytes in vitellogenesis II of lone mature female, transverse section; (D) ovary in post-spawn stage, longitudinal section; (E) detail of ovary in post-spawn stage with cells in reabsorption and new oocytes generation, longitudinal section; (F) detail of ovary in advance development stage, transverse section. (OoI, oogonia I; Ov, ovary; Hp, hepatopancreas; Dt, digestive tract; Ov I, oocytes in vitellogenesis I; Ov II oocytes in vitellogenesis II; Or, oocytes in reabsorption; black arrow, oogonia II; white arrow, follicular cells; *, dorsal lamina germinal layer).

In mature females with a male, the ovaries occupied almost the entire internal space available, so other organs were compressed anteriorly. The largest mature females paired with a male (Table 1) had a whitish bulging abdomen; a large number of oocytes were visible dorsally through the exoskeleton, which may be an indication that egg laying was imminent. Morphologically, mature females paired with a male were all very similar, with coxal plates well developed in the first three pereomeres, the pleomeres fused on the shorter lateral margin of the pleon and the dorsal body surface unpigmented.

The lone mature female was very similar morphologically and histologically to those accompanied by a male described previously. The ovaries of this female were in advanced development, the oocytes in vitellogenesis II being rectangular and 45–65 μm; however, some of them were observed with process of reabsorption, especially in those nearer to the ventral wall of the female (Figure 3C), which may indicate that they would not be released into the marsupium. The ovarian size of this lone mature female caused its abdomen

to bulge appreciably. The first three pereomeres had well developed coxal plates, while the pleomeres on the shorter side margin of the pleon were completely fused and the dorsal part of the female was unpigmented.

DISCUSSION

Ovarian characterization of *Bopyrina abbreviata*

The internal organization of *Bopyrina abbreviata* agrees with the description by Wägele (1992) for isopods in general, and it also supports the organ arrangement described by Kossmann (1881) for *Bopyrina ocellata* (as *B. virbii*) and by Hiraiwa (1933, 1934) for *Parapenaeon japonica* (as *Epipenaeon japonica*).

The paired ovaries lie in the pereon and run lengthwise over the digestive organs, with oviducts that end in a small

Table 1. Sizes of female *Bopyrina abbreviata* Richardson, 1904 selected for histological analysis.

Stage of development	N	Total length (mm)		
		Minimum	Maximum	Mean ± SD
Lone immature	5	0.65	0.92	0.76 ± 0.12
Immature with larva	3	0.92	1.17	1.02 ± 0.11
Immature with male	5	0.87	1.15	1.02 ± 0.10
Mature with male	5	1.17	2.17	1.60 ± 0.37
Lone mature	1	1.45	1.45	1.45 ± 0.00
Ovigerous female	2	1.27	1.57	1.42 ± 0.15

N, number; SD, standard deviation.

cleft-like ventral gonopore near the ventral margin of the insertion of the fifth pereiopod; the gonads are connected to the wall of the digestive organs and to the inner wall of the body by suspensory ligaments (Kossmann, 1881; Hiraiwa, 1933; Wägele, 1992).

The shape and position of the ovaries of immature females of *B. abbreviata* coincide with the descriptions of the gonads of young females of *B. ocellata* (see Kossmann, 1881), *P. japonica* (see Hiraiwa, 1934) and *Probopyrus rigueleti* (see Schuldt, 1993). In these species, including *B. abbreviata*, the increase in female size is accompanied by a rapid extension of the ovaries. Kossmann (1881) noted that with lateral development of the ovary in *B. ocellata* it twists and adopts a zigzag form with follicular protuberances, a feature also observed in immature females of *B. abbreviata*.

Likewise, Hiraiwa (1934) described in the ovaries of young female *P. japonica* the presence of a laminar structure with various projections or branches that extends from the first anterior thoracic segment to the posterior region of the abdomen and is occupied by oogonia and oocytes. Wägele (1992) noted that in the ovaries of isopods, in general, the different cells (epithelial cells, follicular cells, oogonia and oocytes) originate from a lateral germinal zone that forms a band along the ovary. For *P. japonica*, Hiraiwa (1934) described germ cells generated in the ovary wall and running inwards in a parallel arrangement. The present observations in *B. abbreviata* differ, since these germ cells originate from a dorsal laminar layer that extends horizontally, from which the maturation gradient occurs towards the ventral region; this agrees with observations of *P. ringueleti* (Schuldt, 1993).

Oogonia have been observed in the ovaries of *P. ringueleti* from very early sizes (Schuldt, 1993), and they persist through the four stages of maturity established for this species. Hiraiwa (1934) noted that even when some oocytes have accumulated yolk and develop to occupy most of the space available within the ovary, it is possible to find oocytes at early stages of development within the same gonad. Both patterns are consistent with that observed in *B. abbreviata* because even when the gonads of some females, mainly mature females, were filled with oocytes in vitellogenesis II, there were some 'nodes' in the laminar layer where oogonia and/or oocytes were in early vitellogenesis. The process of reabsorption observed in various kinds of germ cells throughout the oogenic cycle of *B. abbreviata* coincides with that reported in *P. ringueletii*, and has been proposed as a regulatory factor of fecundity, i.e. the number of oocytes is adjusted to the real spawning possibilities of the species (Schuldt, 1993).

The asymmetry in extension of the ovaries caused by the increase in size of females of *B. abbreviata* is similar to that reported by Schuldt (1993) in *P. ringueleti*, although it is not mentioned in the anatomical description of other species such as *B. ocellata* and *P. japonica* (Kossmann, 1881; Hiraiwa, 1933, 1934). In agreement with the description of *P. japonica* by Hiraiwa (1934), when the ovary in *B. abbreviata* does not occupy the entire body of the female, in immature females mainly, the available space is occupied by a mass of connective tissue formed by small irregular cells that surround the internal organs, which are enveloped and compressed by the mass of developing oocytes.

Effect of male presence on ovarian development of *Bopyrina abbreviata*

Overall, two reproductive patterns are known in isopods: discrete or seasonal and continuous or non-seasonal (Warburg, 2013). They can be influenced by the environment through abiotic factors such as temperature, photoperiod or humidity and/or by biotic factors such as population density, crowding, sex ratio or the presence/absence of the male (Caubet *et al.*, 1998). Jassem *et al.* (1982, 1991) noted that temperature and photoperiod determine the beginning of the breeding season of *Armadillidium vulgare*, and also reported that the reproductive onset of females of this species is accelerated by the presence of males; this 'male effect' is characterized by the reduction in duration of the preparturial intermoult and of the secondary vitellogenesis period. This effect is produced by a physical (tactile) and/or chemical stimulus, requiring direct physical contact between male and female, in which the male copulatory organs come into contact with the female genital apparatus. Whether or not insemination occurs, this stimulates the neurosecretory cells on the protocerebrum that control synthesis of the hormone that inhibits vitellogenesis; the hormone concentration is lowered and this decline allows rapid synthesis of vitellogenin thus reducing the period of vitellogenesis (Picaud *et al.*, 1989; Caubet *et al.*, 1998; Lefebvre & Caubet, 1999).

In bopyrids this 'male effect' has been reported only in *P. ringueleti* (Schuldt, 1993), a species that has shown an absence or scant presence of oocytes in vitellogenesis II in mature females unpaired with a male. The pattern observed in *B. abbreviata* contrasts with that reported by Schuldt (1993), since the only difference recorded in ovarian development between the lone mature female and those paired with a male was that the lone female showed evidence of cellular reabsorption in some oocytes with secondary vitellogenesis. Nevertheless, because the ovary of immature females of similar sizes was more developed when they were paired with a male, it could be suggested that the presence of a cryptoniscus larva or a male between the pleopods should trigger the gonadal maturation process of the *B. abbreviata* female. Therefore, if the pairing occurs when the female is small, it may still be relatively small when reproduction begins. This would explain the presence of ovigerous females of *B. abbreviata* of lower TL than that of unpaired females (Romero-Rodríguez & Román-Contreras, 2013), as has been reported for *Bopyrinella thorii* (Romero-Rodríguez & Román-Contreras, 2014). These authors suggested that despite the absence of a male the female is capable of producing oocytes, since they recorded lone mature females of *B. thorii*

with ovaries filled with oocytes, which were visible through the exoskeleton. The present results support this, because oocytes of lone mature and immature females of *B. abbreviata* reached the stage of vitellogenesis II, although oocytes of the immature females were much less numerous than those recorded in mature females.

Because the shape of the gonads is related to the size of the female and as through its development it shows external morphological variations, we may assume that if the presence of a male promotes accelerated development of the ovaries it will also influence the morphology of the female. This could explain the differences between lone and paired immature females in body symmetry, the development of coxal plaques in pleomeres 1–3, and the degree of fusion of pleomeres at any edge of the pleon, since such features were more developed in females paired with a male. However, it is necessary to perform more detailed studies in order to confirm the possible relationship between the degree of ovarian development and the morphological characteristics of females of *Bopyrina abbreviata*. Although this study suggests that the male influences the ovarian development some females were able to produce oocytes without a male presence, so it is important to describe if the influence of the male on the ovarian development is just mechanical or by a humoral factor which also could determine the release of the oocytes into the marsupium.

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Correspondence should be addressed to:
J. Romero-Rodríguez
Departamento de Biología Marina, Facultad de Veterinaria y Zootecnia, Universidad Autónoma de Yucatán (UADY), Km 15.5 carretera Mérida-Xmatkuil, Apartado Postal 4-116 Itzimná, Mérida Yucatán, Mexico
email: bopiride@gmail.com