

Contribution to the study of the post-embryonic development and reproduction of the African millipede *Epibolus pulchripes* (Gerstäcker, 1873) (Diplopoda, Pachybolidae)

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ABSTRACT. A collection of 215 specimens of different stadia of the African millipede *Epibolus pulchripes* allowed studying its post-embryonic development, with special attention drawn to (i) the number of segments and ocelli at each stadium and (ii) the development of the copulatory organs of males and females. Laboratory rearing of adult *E. pulchripes* from Kenya revealed some aspects of reproduction, from the structure of the adult reproductive organs to mating behaviour and oviposition, as well as the first stadia of post-embryonic development. Based on histological observations and scanning electron microscopy, the position of the copulatory organs during mating and the function of the different parts of the reproductive organs are hypothesized.

KEY WORDS : *Epibolus pulchripes*, reproduction, development, morphology

INTRODUCTION

The post-embryonic development and life histories of Diplopoda have already been studied in Glomerida (JUBERTHIE-JUPEAU, 1967; IATROU & STAMOU, 1988), Spirobolida and Spirostreptida (DEMANGE & GASC, 1972; BERCOVITZ & WARBURG, 1988), Polydesmida (BHAKAT, 1987), Chordeumatida (BLOWER, 1987), Penicillata (KARMAOUNA, 1990), Colobognatha (DAVID & COURET, 1983) and a lot of Julida (see references in SAHLI 1974). A relevant synopsis dealing with these topics has also appeared (ENGHOFF et al., 1993). Apart from the ecological features, much of the attention in these studies has been drawn to ocular and segmental formulae, mostly culminating in a cone-shaped presentation of all the possible segmental formulae revealed for each stadium. In some papers, the development of the copulatory organs is considered (e.g. BERNS, 1968). However, knowledge of the ontogeny is a very important step in the understanding of the evolution and functions of the different parts of the reproductive system.

Only a few studies on the life history (reproduction and development) of pachybolid millipedes have hitherto been made (e.g.: VACHON, 1947; DEMANGE, 1972; AOUTI, 1980). None of them concerns the millipede *Epibolus pulchripes* Gerstäcker, 1873, even though this species is of significant ecological importance and potential use in biotope rehabilitation (HALLER & BAER, 1994).

In this paper, the most important features of the different stadia of the post-embryonic development are described including external morphology, segmental and ocular formulae and the development of the genitalia. The main objective is to describe the reproductive organs and

to formulate a hypothesis of the function of the different parts during copulation.

MATERIALS AND METHODS

Epibolus pulchripes is quite common along the coastal line of Kenya. A total of 215 specimens were collected by hand at Arabuko Sokoke, a mixed *Azelia* forest near Malindi. Adults were kept alive for rearing in the Royal Museum for Central Africa at Tervuren, Belgium (MRAC). The rest was stored in 70% ethanol. Millipedes were fed with fresh cucumbers and fish food (Tetramin) on a substrate of wet soil (Terrau Universel) in a terrarium at 18–20°C. One male with one female were accommodated in small mating arenas for observation of copulation and oviposition. Additional males were occasionally added to test male competition in *E. pulchripes*.

Developmental stadia were distinguished based on DEMANGE'S (1972) observations that each moult is followed by adding one row of ocelli. In spirobolidans, stadium I has one ocellus, stadium II has 3 ocelli in 2 rows, stadium III with 6 in 3 rows, and so forth. Thus, stadium number and the number of rows of ocelli are equal.

The study of the male genitalia was made using specimens previously anaesthetized with Nembutal and injected with Bouin's fixative to cause an extension of the penis and gonopods. Gonopodal and vulval nomenclature follows BERNS (1968) and ENGHOFF (1977), respectively.

For histological observations, the anterior body rings were removed from anaesthetized individuals (with Nembutal). They were fixed in Bouin's fixative, decalcified, embedded in paraplast, cut in 5-µm sections, and stained

with Masson's trichrome (GANTER & JOLLÈS, 1969–1970).

For scanning electron microscopy (SEM), samples were dried, mounted on aluminium stubs, coated with gold and observed with a JEOL JSM-5400LV microscope.

All the material studied here is deposited in the Royal Museum for Central Africa (MRAC)

RESULTS

External morphology of the adults

Epibolus pulchripes is a black millipede with red legs, commonly called the “Mombasa train”. It can reach 9–12 cm in length, while the head and anal valves are bright red in colour. Starting from ring 6, brown dots can be found on the sides, the so-called ozopores, the openings of the defensive glands. When mature, the *E. pulchripes* male can easily be distinguished from the female by its bright black body and white adhesive pads (Ad) on the tarsus (Ta) (Fig. 1). Females are generally larger and duller black in appearance, without adhesive structures on their legs.

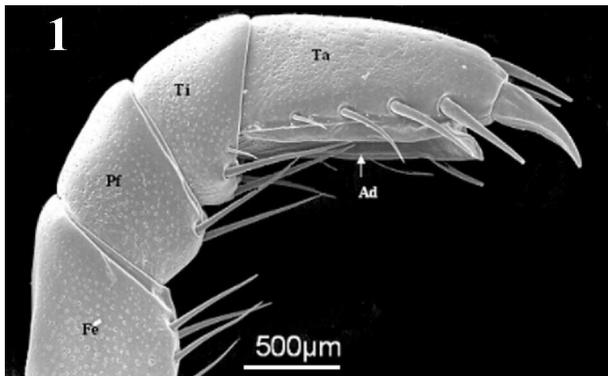


Fig. 1. – Posterior view of a male leg with a detail presentation of an adhesive pad: Ad: Adhesive pad; Fe: Femur; Pf: Postfemur; Ta: Tarsus; Ti: Tibia.

Structure of adult genitalia

Male genitalia: The male has two essential structures for copulation: the so-called penis (P) and the gonopods.

The penis: The penis is the differentiated end of a ladder-shaped testis. As the penis in *E. pulchripes* takes no part in direct sperm transfer, this structure cannot properly be termed as penis. To emphasize its double structure due to fusion of two leg anlagen, the penis in Diplopoda is often referred to in plural, as penes. Like the gonopores in any Diplopoda, it lies on ring 2 and is only everted during copulation. When extended, the penis reaches up to body ring 6 (10–15 mm) and shows a typical bifurcated apical end. The two apical tips bend back to the front, thus shaping like an anchor (Fig. 2).

Histological observations reveal that both spermal ducts (Sd) form a single channel when entering the first part of the penis. Towards the end, this channel splits again into two apical tips. A longitudinal section of a

retracted penis shows the anterior membrane as being more rugose than the posterior one. A cross-section reveals retractor muscles (Rm) at the base of the penis (Fig. 5).

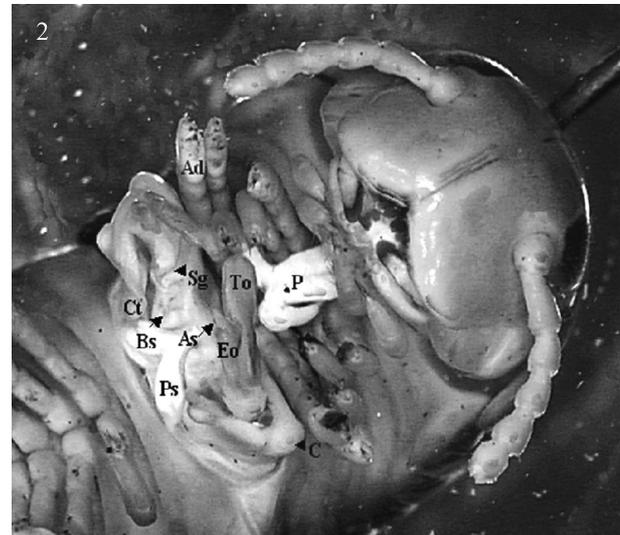


Fig. 2. – Photo of the anterior segments of a male with artificially extended reproductive organs, ventral view:

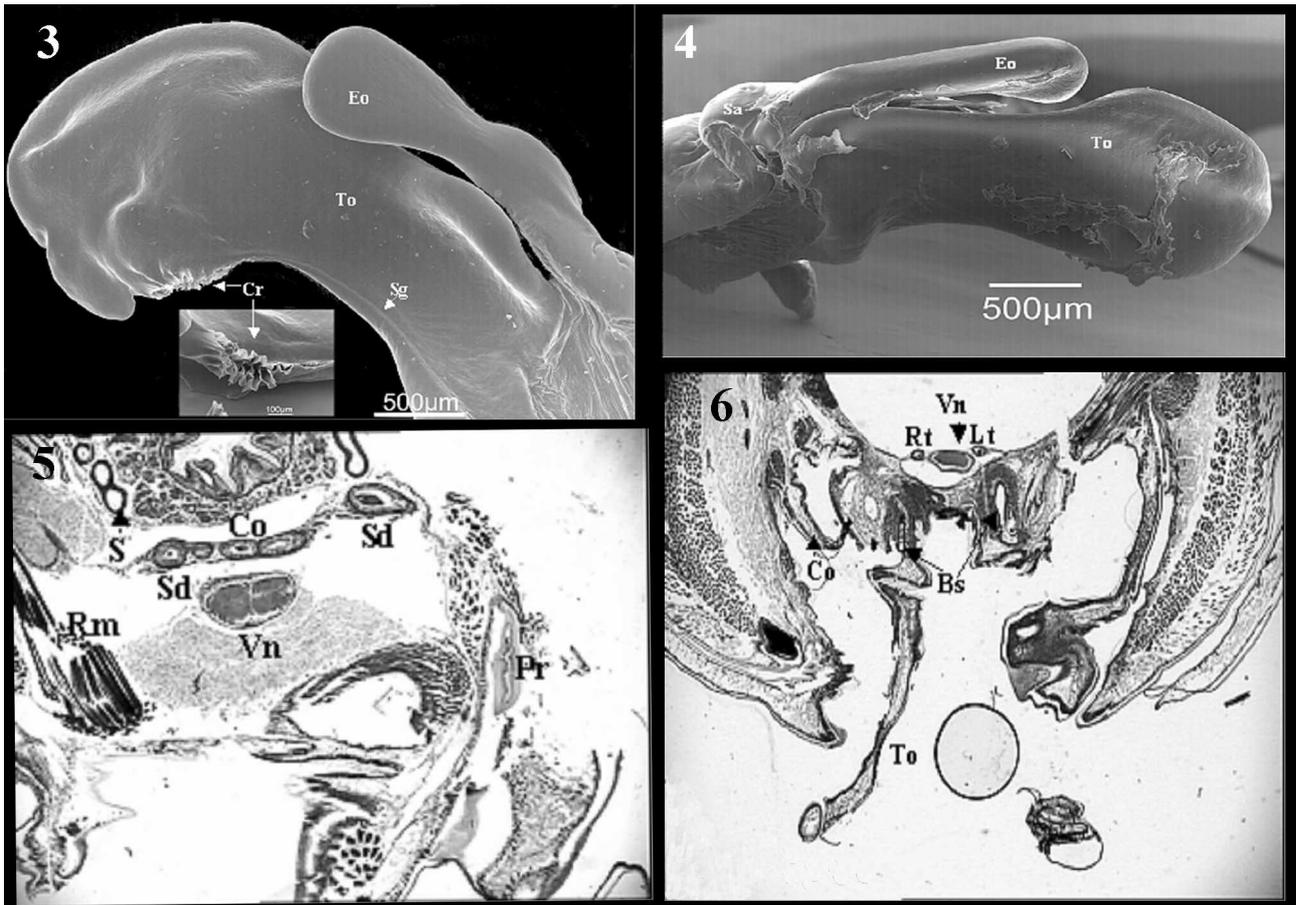
Ad: Adhesive pad; As: Anterior sternum; Bs: Bursae seminalis; C: Coxa; Ct: Coxal telepodite; Eo: Endite of opisthomere; P: Penis; Ps: Posterior sternum; To: Telopodite of opisthomere.

The gonopods: The gonopods are modified legs used for the transfer of sperm; they consist of two main parts: the anterior gonopod (Ag), or coxoid, and the posterior gonopod (Pg), or opisthomere. Functionally, the gonopods are not a penis either, instead they serve as spermato-positors. The Ag includes a coxa (C), a coxal bar, a coxal endite and a telopodite (Fig. 2). The Ag protects the Pg, which consist of a pair of telopodites (To) and its spatuliform endites (Eo) (Fig. 3). This endite is attached to the base of the telopodite in a spring-like way and bends back when moved aside. The Pg telopodite shows two small excavations at its base and a groove (Sg) that runs from these excavations to a membranous crown (Cr) at the tip (Figs 2 & 4). In cross-section, the groove appears to be a tube formed by the integument of the anterior side overlapping that of the posterior side.

Histological observations show that the two excavations at the base of the telopodites are in fact two small receptacles (Bs) that are connected to the groove (Fig. 6). They also reveal retractor muscles at the base of each gonopod (Fig. 6).

Female genitalia: The female genitalia consist of two vulvae, each located in a vulval sac (Vs) on the posterior side of the coxae of the second pair of legs.

Each vulva consists of four sclerites: a caudal valve (Vca), a rostral valve (Vr), a ventral ridge (R) in-between and a median operculum (O) (Fig. 7). The ridge can be seen from outside as a structure that is folded between the two valves; in the middle of the vulva it disappears between these valves. On the opposite side of the operculum, an apical cluster of setae (S) can be found on the valves.



Figs. 3-6. – SEM and histological images of male reproductive system :

3 : Posterior gonopod or opisthomere with details of membranous crown at the end of seminal groove; 4 : Details of a spring-like attachment of the endite to the telepodite of opisthomere; 5 : Section through the second segment with a retracted penis; 6 : Section through the seventh segment with retracted gonopods.

As : Anterior sternum; Bs : Bursae seminalis; C : Coxa; Co : Connection; Cr : (membranous) Crown; Ct : Coxal telepodite; Eo : Endite of opisthomere; Lt : Left testis; P : Penis; Pr : Penis : right part; Ps : Posterior sternum; Rm : Retractor muscle; Rt : Right testis; S : Salivary gland; Sa : Spring-like attachment; Sd : Spermal duct; Sg : Seminal groove; To : Telepodite of opisthomere; Vn : Ventral nerve chord.

Histological observations show that the single ovary splits into two oviducts (Od). Each oviduct enters a vulva dorsally through the bottom of the vulval sac and between the two valves.

The bottom of the ridge is extremely digitised and shows two peculiar glands (Bg) just beneath the setae on the valves (Figs 8 & 9). They are formed of club-shaped ciliated cells which bear an apical cilium. Between both the glands, a long cilium is located. The glands are flanked by two bands of muscles (M). One band connects the outer epidermis of the valves with the epidermis of the ridge, while the other band is attached to the two outer epidermis layers of the two valves.

Reproduction and egg-laying

Reproduction : Several copulations were observed in captivity. Once a male finds an adult female, he mounts her back using the adhesive structures on his legs. If he succeeds to climb entirely onto her back, he taps his legs

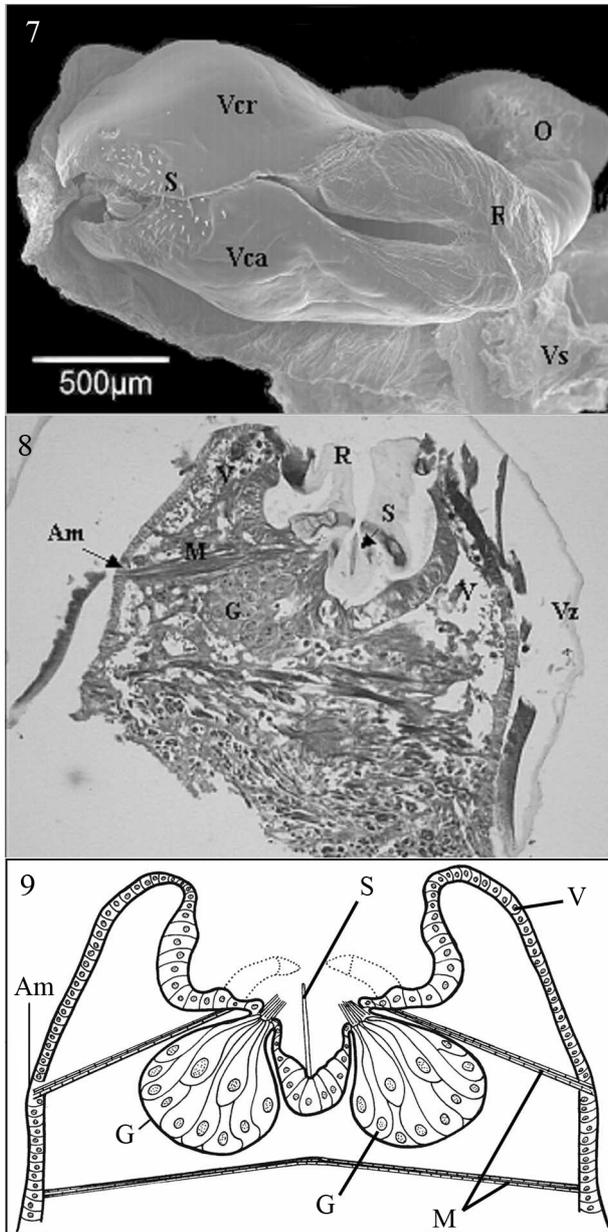
against her flanks in an undulating fashion to stimulate her. This process can last hours, resulting in the female carrying the male around over considerable distances. When the female is ready for copulation, she raises her head and the male entwines his body around hers until their copulatory organs come in contact. He then inserts his posterior gonopods placed inside the seventh ring into the vulvae of the female which are positioned inside the second ring. Then sperm transfer takes place.

When further males were placed inside the mating arena, they did try to compete and interfere with this male by climbing on top of the mating pair.

Egg-laying : The female can lay eggs several times following one copulation. In captivity, the first egg-laying event was observed two weeks after copulation, followed by a second egg-laying event one week later.

For egg-laying, the female makes a small depression in the soil. She then rolls up and starts depositing the eggs one by one. As the eggs come out of the vulvae, she picks

them up by her front legs to coat them with a mixture of soil and saliva, making them look exactly like faeces. Each time she produces 10 to 15 eggs, depositing them while defecating.



Figs. 7-9. – Female reproductive system :
7 : SEM image of vulva and second pair of legs ; 8 : Section through bursal glands (place of section indicated by arrows in Fig. 7) ; 9 : Scheme of the section given in Fig. 8.
Am : Attachment of muscle ; G : Bursal gland ; M : Muscle ; O : Operculum ; R : Ridge ; S : Setae ; V : Valve ; Vca : Caudal valve ; Vr : Rostral valve ; Vs : Vulval sac.

Development

Eleven stadia have been recognized during the development, the most important features of the different stadia being summarized in Table 1.

Stadium I : After hatching, the pupoid moults into the first true larval stadium. This was not observed during our study.

Stadium II : Seven juveniles of stadium II were recovered from the nursery. They were slightly transparent and measured 0.5 cm in length. They can easily be recognized by their unique segmental formula consisting in a collum, 6 podous and 14 apodous rings, as well as a telson (6+14+T).

Since the fifth ring is the first diplosegment like in all Spirobolida, seven pairs of legs can be found. The number of ocelli is 3, they are arranged in two rows : 1+2 ocelli. At this stadium the first defensive gland is visible as a black dot through the transparent cuticle.

Stadium III : Slightly longer than stadium II, juveniles of stadium III are 0.7–0.8 cm long. They show 20 podous and 6 apodous rings (20+6+T), as well as three rows of ocelli, bringing the total up to six ocelli (1+2+3); 15 defensive glands are visible through the white cuticle on each side of the body.

Stadium IV : At stadium IV, juveniles measure about 1 cm in length and have a black body with white legs. Each specimen shows 26 podous and 6 apodous rings (26+6+T), as well as four rows of ocelli (1+2+3+4). At this stadium, male and female can be distinguished; in males, the legs of the seventh ring have disappeared, being replaced by two pairs of gonopod primordia (Table 1, IV a, c).

Stadium V : At stadium V, the millipedes are 1.5–2.0 cm long and show the typical adult colour pattern of a black body with red legs. The defensive glands are visible as small brown circles on the cuticle around the pores. All 21 males and 27 females observed have a segmental formula of 32+6+T, as well as five rows of ocelli (1+2+3+4+5) (Table 1, Va).

Although the development of the vulvae in females has not started yet, the anterior gonopod (Ag) and posterior gonopod (Pg) primordia in males are clearly distinguishable. The Pg primordia have migrated between the two primordia of the Ag, both pairs, especially the Pg, being elevated above a sclerotized sternum (Table 1, Vc).

Stadium VI : At stadium VI, the juveniles measure 2.5 ± 0.2 cm in length. Only one segmental formula has been found : 38+6+T. All 52 millipedes observed had six rows of ocelli bringing the number up to a total of 1+2+3+4+5+6 = 21 ocelli (Table 1, VIa).

The gonopods start forming distinctive structures. Each Ag is divided into two pieces : a future coxa (C) and telopodite (Ct). Each Pg has now clearly sunk into the sternum to start showing the first curve which will be best recognized in an adult Pg telopodite (Table 1, VIc).

This is also the first stadium where the primordia of the vulvae can be seen behind the coxae of the second pair of legs. Three small protuberances represent the future valves and the ridge (R) of the vulva. They are placed in a triangular way, the valves forming the two longest sides, the ridge making out the top of the triangle (Table 1, VIb).

Stadium VII : At stadium VII, the millipedes are 3.9 ± 0.4 cm in length. This is the first stadium where two different segmental formulae have been observed : 43+5+T and 44+5+T. The total number of ocelli is no longer con-

stant, as the rows that are added vary in the number of ocelli. However, the number of rows, here seven, can still be used to determine the stadium (Table 1, VIIa).

The gonopods now have a triangular anterior sternum, while the Pg coxa and telopodite are placed around the Pg (Table 1, VIIc). The vulvae are a little larger, the only difference from the preceding stadium lying in that the ridge starts bending (Table 1, VIIb).

Stadium VIII : At this stadium the millipedes are 5.0 ± 0.5 cm long. Two different segmental formulae have likewise been found : $49+3+T$ and $48+3+T$. The ocular field has also gained one row of ocelli, resulting in 8 rows (Table 1, VIIIa). The gonopods are more compact, the Pg fitting into the cavity formed by the Ag. Only the Pg telopodite has grown significantly (Table 1, VIIIc).

The valves of the vulvae are now almost fully separated from the coxae; the ridge shows its first curve, being folded between the two valves. A primordial operculum (O) can be distinguished on the opposite side of the vulva. The posterior valve is significantly larger, but narrower than the anterior one (Table 1, VIIIb).

Stadium IX : At stadium IX, the millipedes measure 7.1 ± 0.9 cm in length and show 9 rows of ocelli; only one segmental formula has been revealed ($52+0+T$; Table 1, IXa).

The gonopods are very similar to those of an adult, but they are not functional yet, because each Pg is not completely developed, being very small and still showing its typical curved shape absent (Table 1, IXc).

Being larger, the vulvae differ from the preceding stadium only by the occurrence of a dozen setae (S) on each valve just above the ridge. The operculum is shell-shaped (Table 1, IXb).

Stadium X : At stadium X, specimens are 8.3 ± 0.7 cm in length and also count 52 podous rings and a telson. Only the addition of an extra row of ocelli (10 rows) indicates that the millipedes are at stadium X (Table 1, Xa).

The gonopods are now almost completely developed. The Ag are completely developed in shape, but still are a little smaller, while the apical part of the Pg is different from the adult stadium : the membranous crown is not yet formed and only wrinkles of the integument around the end of the seminal groove can be seen (Fig. 10) (Table 1, Xc).

The valves of the vulvae are now shaped like those of a functional vulva and 20–30 setae occur on the valves on the opposite side of the operculum. The ridge is very small and still located on the side opposite to the operculum of the vulva (Table 1, Xb).

Stadium XI : Both males and females are now sexually mature and have eleven rows of ocelli. During the last moult towards sexual maturity in males, only the telopodite of the Pg undergoes a last change, i.e. formation of the membranous crown around the apical pore (Figs 1 & 4). The vulvae undergo one last big change as well; this is a migration of the ridge lying between the two valves to the other side of the vulva, thus creating an opening between the two valves and the folded ridge (Fig. 7).

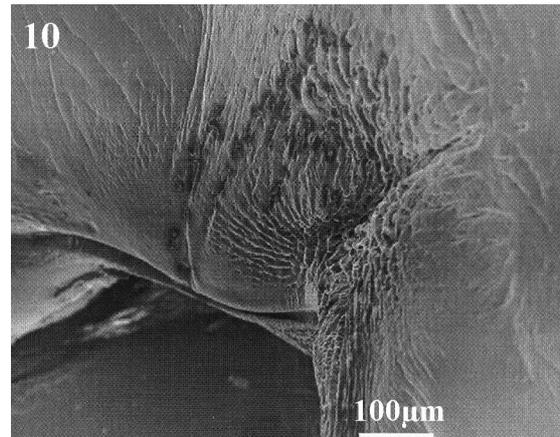


Fig. 10. – Details of membranous crown of opisthomere at stage X.

DISCUSSION

Development patterns

Like in the spirobolid *Narceus annularis* (Rafinescue, 1820), maturity of *E. pulchripes* is attained at stadium XI. The eggs of *E. pulchripes* are laid individually in earthen capsules carefully manufactured by the female. Stadium I remains inside the capsule and is likely to have only one ocellus, as all other spirobolidans (pachybolids) studied (VACHON, 1947; DEMANGE, 1972; AOUTI, 1980). Based on the literature (NGUYEN DUY-JACQUEMIN, 1992; ENGHOFF et al., 1993), the first stadium probably has three podous and four apodous rings with a telson. This hexapodous larva moults into the first free larval stadium, which is also the first stadium with one diposegment. Up to stadium IX, the post-embryonic development seems to be anamorphic, meaning that each moult results in an addition of podous and apodous rings. The presence of immature specimens without apodous rings at stadia IX and X suggests that anamorphosis is followed by epimorphosis. Thus, as in most species of Spirobolida, the post-embryonic development of *E. pulchripes* appears to be hemianamorphic.

Like in *Pelmatojulus ligulatus* (Voges, 1880) (see ENGHOFF et al., 1993), the development of *E. pulchripes* is remarkable for its very modest variability in segmental formulae. Up to stadium VI ($38+6+T$), all show a single segmental formula for each stadium. Looking at stadium VII, however ($44+5+T$ and $43+5+T$), other possible options might exist at stadium VI as well : $37+6+T$ or $38+5+T$. Such a variation has already been well documented (e.g. SAHLI, 1969; ENGHOFF et al., 1993) that, from a certain stadium on, two possible segmental formulae are evident that can give rise to two new possible formulae, and so on. Thus, a cone-shaped scheme can be constructed with most of the possible segmental formulae observed at the last stadia before adulthood. No conform presentation could be obtained in our study, because we have apparently failed to discover all segmental formulae. Although in almost all pachybolid millipedes the variation in ring number is known to be somewhat more modest than in the other millipedes (ENGHOFF, 1977), *E. pul-*

chripes studied here shows an extremely low variation in segmental formulae in the course of development. This might be due to the fact that all material was collected in the same place and represented the same population. SAHLI (1969) showed that variation within a single population is usually smaller than that between two separated

populations, while ENGHOFF (1977), in his revision of the genus *Epibolus* Cook, 1897, found a higher degree of variation in the adult number of rings of *E. pulchripes* between populations stemming from different geographical regions (51+0+T up to 54+0+T).

| Stage | a) Ocellular field (ocelli indicated by [®]) | b) Development of the vulvae | c) Development of the gonopods |
|---------------------------|---|---------------------------------|-----------------------------------|
| IV Segm.:26+6 | | | |
| V Segm.:32+6 | | | |
| VI Segm.:38+6 | | | |
| VII Segm.:44+5 | | | |
| VIII Segm.:49+3 | | | |
| IX Segm.:52+0 | | | |
| X Segm.:52+0 | | | |

Table 1. – Most important features of different stadia of the post-embryonic development. Ag : Anterior gonopod; As : Anterior sternum; C : Coxa; Ct : Coxal telepodite; O : operculum; Pg : Posterior gonopod; R : Ridge; S : Setae; Vca : Caudal valve; Vr : Rostral valve

The gonopods of spirobolidan millipedes have long been assumed to represent modified appendages of the seventh body ring (e.g. KEETON, 1960). BERNIS (1968) was the first to study the development of the copulatory organs in the spirobolid *Narceus annularis*. He showed that the gonopods actually originate from the elliptical primordia that arise when the legs of the seventh ring fall off during the stadium IV to V transition. In *E. pulchripes*, the legs on the seventh body ring also fall off, but this occurs during the moult of stadium III to IV. This looks like an evolutionary imperfection, when considering entropy, since the development of the legs on the seventh body ring during the earlier stadia seems to be unnecessary. Based on the present observations, it seems impossible to determine the evolutionary advantages of this process.

BRÖLEMANN (1922) was the first to study the structure of the vulva in millipedes. According to him, the vulva consists of four sclerites: a ridge, an operculum, a caudal valve and an apical valve. Although ENGHOFF (1977) mentions that, in *Epibolus*, the apical valve is divided into two different sclerites, we agree with Brölemann, as in our study of the ontogeny of the vulva only four sclerites could be distinguished. On the other hand, in adult females one of the two valves is partly divided, creating the illusion that it consists of two parts instead of one. In their histological study of the vulvae of several diplopods, BRÖLEMANN & LICHTENSTEIN (1919) described the structure of two glands called 'glandes de la bourse' in the vulvae of *Archispirostreptus tumuliporus sudanicus* (Brölemann, 1905) (Spirostreptidae, Spirostreptida). The histological observations we made of the vulva of *E. pulchripes* also reveal the presence of two glands at the lateral end of the vulva. The location and structure of these glands are very similar to the "glandes de la bourse" as described by BRÖLEMANN & LICHTENSTEIN (1919). According to these authors, the position of the excretion pore indicates that the secretion is to be spread at the lateral end at the bottom of the ridge, which acts as a receptaculum seminis (Rs). The glands can be emptied by contraction of the muscles after some stimulation by the setae. The secretion could then cover the sperm at the bottom to preserve it until the eggs are laid.

Mating

Earlier observations show that the first rains after a dry season initiate a mass activity during which the millipedes seek a mate. The adhesive structures on the tarsus of the legs of males are used to obtain a better contact during copulation. These structures have been suggested to have evolved as a result of male competition, if males can be seen trying to take over the female from copulating pairs (TORNHILL & ALCOOK, 1983; EBERHARD, 1985). TADLER (1996) could not support this hypothesis by his study of the reproduction in Julida, since he never observed a male trying to steal a female from another male during copulation. In *E. pulchripes*, however, this behaviour has been observed during this study, adding more support to the male competition hypothesis.

Before mating, the male must evert his penis and gonopods in order to inseminate the female. The julid species *Unciger foetidus* (C. L. Koch, 1838) and *Cylindroiulus*

boleti (C. L. Koch, 1847) (see VERHOEFF, 1928; TADLER, 1996) possess a "gonopodal sac" which forms a conspicuous eversible hydraulic structure with intersegmental membranes for a protrusion of the gonopods. Such an elaborate hydraulic system exists neither in *Nemasoma varicorne* C. L. Koch, 1847 (Nematomatidae, Julida), nor *Brachyiulus lusitanus* (Verhoeff, 1898) (Julidae, Julida) (see TADLER, 1996), nor *E. pulchripes* (present paper). Several observations suggest that, in *E. pulchripes*, the reproductive structures of the male are only everted due to an increased inner body pressure: (i) both penis and gonopods can be extended artificially when an anaesthetized animal is injected with a fluid at its rear end; (ii) during copulation and an artificial extension of the gonopods, a white inflated membrane can be seen at their base; and (iii) on the histological slides, only retractor muscles are found for both penis and gonopods.

When the penis is everted, and even when artificially extended, it bends back toward the gonopods. This can be accounted for by the structure of the penis which has the anterior wall longer than the posterior one, constraining to fold it automatically when extended.

As soon as the penis is everted, the millipede bends its head down and the two apical ends of the penis, which are shaped like an anchor, reach exactly the posterobasal parts of the Pg telopodites, where two excavations are observed. These two pouch-shaped structures are in connection with the grooves that run up to the apical membranous crowns of these telopodites. This strongly suggests that these structures are in fact two so-called bursae seminales. Before or during copulation, the bursae seminales are charged with sperm through the two tips of the penis. As observed by ENGHOFF (unpublished), a male can charge his gonopods several times during one copulation. The sperm will then be conducted from the bursae seminales via the seminal grooves towards the membranous crown, through which it will be delivered inside the vulvae of the female.

Although copulation has been observed in captivity, the position of the copulatory organs during insemination has not been monitored clearly enough. So the following hypothesis of the position of the copulatory organs during copulation (Fig. 11) is mainly based on detailed observations of both male and female genitalia.

The telopodite of the posterior gonopod is inserted into the vulvae through the ridge, while the endite bends over the overlapping valves. This way the endite contacts the setae at the apical end of the two valves and thus might stimulate contraction of the muscles that flank the bursal glands. The contraction of the gland is to initiate the secretion and release of a product that might fix and protect the sperm that is being deposited. When the posterior gonopod is drawn back, the endite would bend back into its original position. In this hypothesis, the endites are essential for the stimulation of females. So egg fertilization depends also on stimulation quality.

Since copulations have been observed neither during the period between the first copulation and the first oviposition nor between two ovipositions, it is apparent that the female is capable of carrying about fertile sperm for several weeks. When the eggs leave the vulvae, they might be fertilized by sperm stored in the ridge.

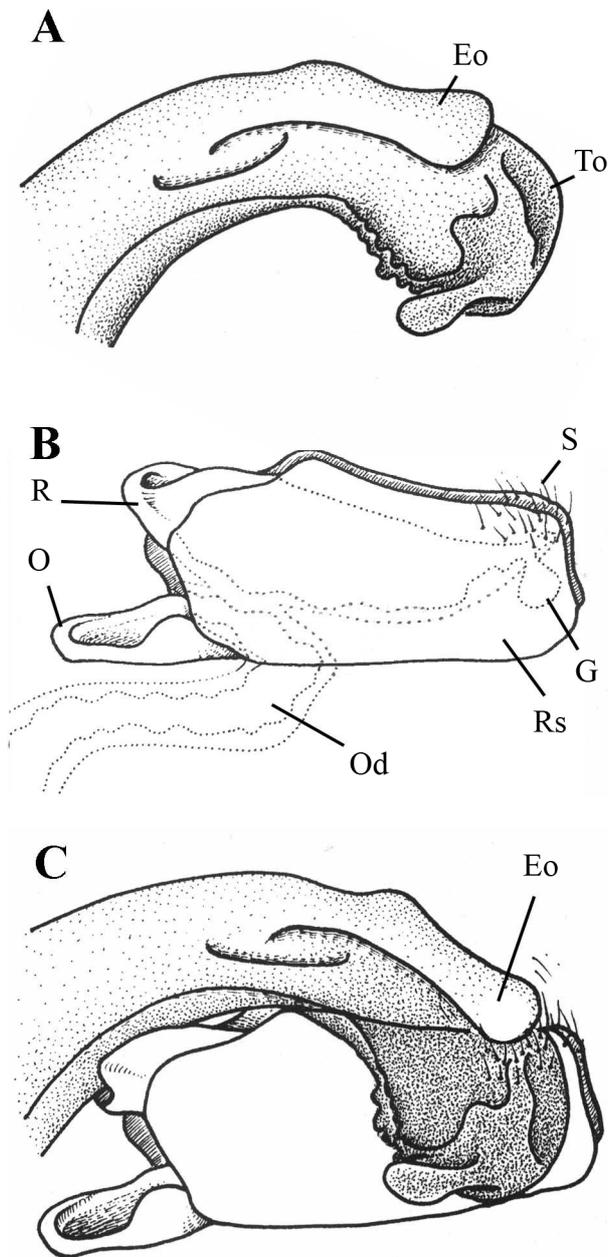


Fig. 11. – Position of reproductive organs during copulation : A : Posterior gonopod; B : Female reproductive system; C : Position of genitalia during copulation. Eo : Endite of opisthomere; G : Bursal gland; M : Muscle; O : Operculum; Od : Oviduct; R : Ridge; Rs : Receptaculum seminis; S : Setae; To : Telepodite of opisthomere.

Several mechanisms in the process of oviposition can be interpreted as adaptations in order to ensure the best survival of the offspring : by coating the eggs with a mixture of soil particles and saliva the female not only protects the eggs against desiccation, mould and other hazards, but she also camouflages them, since they can hardly be distinguished from the faeces. Upon a single copulation, a female lays 10–15 eggs every two weeks. This way she spreads her offspring in time and space, an evident adaptation against predation.

ACKNOWLEDGEMENTS

We would like to thank Dr Koen Maes for his hospitality at the National Museum of Kenya in Nairobi. For staining the histological preparations, we would like to thank Prof. G. Toubeau and Ms. A. Maes of the 'Service Histologique de l'Université de Mons'. We also would like to thank N. VanNoppen and Tim De Vocht for their drawings.

Special thanks go to Dr Sergei Golovatch for his critical review of an advanced draft.

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Received : March 26, 2004

Accepted : October 14, 2005