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Original paper

# Comparative aspects of the internal reproductive system of males in species of Melolonthinae, Dynastinae, and Rutelinae (Coleoptera: Scarabaeoidea) from Mexico

# Aspectos comparativos del sistema reproductivo interno de los machos en especies de Melolonthinae, Dynastinae y Rutelinae (Coleoptera: Scarabaeoidea) de México

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**ABSTRACT.** The anatomy of the internal male reproductive systems of 12 species of Melolonthinae (*Phyllophaga*, *Chlaenobia*, *Macrodactylus*, *Isonychus*), six species of Dynastinae (*Cyclocephala*), and three species of Rutelinae (*Paranomala*) (Coleoptera, Scarabaeoidea) of Mexico are described. A total of 350 male specimens representing 21 species were collected. From each species, the reproductive systems were obtained by micro-dissection, placed in a liquid fixative, stained, and drawn to scale. The internal genitalia of each species was described and compared among the species examined. The reproductive system of the Melolonthinae species is comprised of two testicles, each with six follicles, two deferent ducts, two accessory glands, two glandular ducts, an ejaculatory duct, and the aedeagus (not described for any of the species examined).

The number of testicular follicles per testicle is as reported in different species of other Scarabaeoidea subfamilies. The length of the accessory glands and the ejaculatory duct varies in the species studied. The ejaculatory bulb is present in all of the species of Dynastinae and Rutelinae examined but in only three species of Melolonthinae.

**Key words:** internal genitalia; comparative data; males; June bugs

**RESUMEN.** Se describió la anatomía del sistema reproductivo interno de los machos en 12 especies de Melolonthinae (*Phyllophaga*, *Chlaenobia*, *Macrodactylus*, *Isonychus*), seis de Dynastinae (*Cyclocephala*) y tres de Rutelinae (*Paranomala*) (Coleoptera, Scarabaeoidea) de México. Se recolectaron un total de 350 ejemplares machos representantes de 21 especies. De cada especie se obtuvieron los sistemas reproductivos por microdisección y fueron colocados en un líquido fijador, después teñidos y dibujados a escala. Se describió la genitalia interna de cada especie y se comparó entre las especies examinadas. El sistema reproductivo de las especies de Melolonthinae consta de dos testículos cada uno con seis folículos, dos conductos deferentes, dos glándulas accesorias, dos conductos glandulares, un conducto eyaculador y el edeago (no descrito en ninguna especie). El número de folículos testiculares por testículo es igual al conocido en diferentes especies de otras subfamilias de Scarabaeoidea. La longitud de las glándulas accesorias y del conducto eyaculador varían dependiendo de cada especie estudiada. Un bulbo eyaculador está presente sólo en tres especies de Melolonthinae y en todas las especies de Dynastinae y Rutelinae examinadas.

**Palabras clave:** genitalia interna; datos comparativos; machos; escarabajos de mayo

## INTRODUCTION

The species of Scarabaeidae exhibit great morphological and ecological diversity, which is reflected in the anatomy of their reproductive system. However, the anatomy of the male reproductive system in this family has received very little study, except for the aedeagus, which is often used for species identification (Sharp & Muir, 1912). Unfortunately, only some isolated descriptions of the male internal genitalia in representatives of different Scarabaeidae subfamilies are available.

In Melolonthinae, there are morphological descriptions of the male reproductive system for *Melolontha melolontha* (Linnaeus) (Dufour, 1825; Straus-Dürckheim, 1828; Bordas, 1900), *Anoxia villosa* (Fabricius) and *Hymenoplia strigosa* (Illiger) (Bordas, 1900), *Phyllophaga* sp. (Williams, 1945), *Amphimallon majale* (Razoumowsky) (Menees, 1963), *Costelytra zealandica* (White) (Fenemore, 1971; Stringer, 1990), *Phyllophaga anxia* (LeConte) (Berberet & Helms, 1972), *Phyllophaga sanctipauli* (Blanchard) (Diefenbach *et al*., 1998), *Prodontria lewisi* Broun (Ferreira & McKinlay, 2001), *Macrodactylus mexicanus* Burmeister (Benítez-Herrera *et al*., 2015) *Hoplia argentea* (Poda) (Bordas, 1900), *H*. *subcostata* Bates and *H*. *squamifera* Burmeister (Carrillo-Ruiz *et al*., 2008).

In Dynastinae the male reproductive system has been studied for *Oryctes nasicornis* (Linnaeus) (Straus-Dürckheim, 1828), *Oryctes rhinoceros* (Linnaeus) (Mathur *et al*., 1960; Jacob, 1989) and *Adoryphorus couloni* (Burmeister) (Hardy, 1981).

In Rutelinae it has been studied for *Anisoplia agricola* (Poda) (Bordas, 1900), *Anomala dubia* (Scopoli) and *Phyllopertha horticola* (Linnaeus) (Rittershaus, 1927), *Popillia japonica* Newman (Williams, 1945; Anderson, 1950), *Anomala ausonia* Erichson (Lupo, 1947), and *Chrysina costata* (Blanchard) (Morón, 2010).

Due to the limited knowledge of the internal genitalia of males in Scarabaeidae, here is described and illustrated for 21 Mexican June bug species. The systems of these species are compared with those reported in other published studies, differentiating between some subfamilies of Scarabaeidae and other families of Scarabaeoidea. The external genitalia were not studied because it is well known and used for taxonomic purposes (Sharp & Muir, 1912).

This study is a contribution to the line of research *Biología, Sistemática e Importancia de los Coleópteros Lamelicornios en América Latina*, established by the late Miguel Ángel Morón† several years ago.

## MATERIALS AND METHODS

The adults of most of the species studied were collected in May and June over several years, from different places where it was known that they could be found. Beetles were collected manually, at random, mainly near Xalapa City, Veracruz, Mexico. A total of 350 males of the different species were collected. The species were determined by Miguel Angel Morón†.
The species studied were the following:

**Melolonthinae.** *Phyllophaga testaceipennis* (Blanchard) (El Sumidero, Xalapa, Veracruz), *Phyllophaga* (*Phytalus*) *obsoleta* (Blanchard) (El Sumidero, Xalapa, Veracruz), *Phyllophaga* (*s. str.*) *opaca* (Moser) (Valle del Carrizo, Ahome, Sinaloa), *Phyllophaga* (*Phytalus*) *pruinosa* (Blanchard) (Coatepec, Veracruz), *Phyllophaga* (*s. str.*) *ravida* (Blanchard) (El Haya, Xalapa, Veracruz), *Phyllophaga* (*s. str.*) *rugipennis* (Schauffus) (Briones, Coatepec, Veracruz), *Phyllophaga* (*s. str.*) *setifera* (Burmeister) (La Higuera, Xalapa, Veracruz), *Phyllophaga* (*s. str.*) *subrugosa* (Moser) (Briones, Coatepec, Veracruz), *Phyllophaga* (*s. str.*) *tenuipilis* (Bates) (Las Ánimas, Xalapa, Veracruz), *Chlaenobia latipes* Bates (Las Ánimas, Xalapa, Veracruz), *Macrodactylus nigripes* Bates (Las Vigas, Veracruz) and *Isonychus neglectus* Moser (Briones, Coatepec, Veracruz).

**Dynastinae.** *Cyclocephala jalapensis* Casey (Rancho Guadalupe, Xalapa, Veracruz), *Cyclocephala picta* Burmeister (Briones, Coatepec, Veracruz), *Cyclocephala sexpunctata* Castelnau (Briones, Coatepec, Veracruz), *Cyclocephala mafaffa* Burmeister (Briones, Coatepec, Veracruz), *Cyclocephala lunulata* Burmeister (Briones, Coatepec, Veracruz), and *Cyclocephala weidneri* Endrödi (Briones, Coatepec, Veracruz).

**Rutelinae.** *Paranomala marginicollis* (Bates) (Briones, Coatepec, Veracruz). *Paranomala semicincta* (Bates) (Briones, Coatepec, Veracruz), and *Paranomala cupricollis* (Chevrolat) (Briones, Coatepec, Veracruz).

The suprageneric classification used follows the proposal of Smith (2006). All examined specimens were deposited in the collection of Miguel Ángel Morón, Xalapa, Veracruz, Mexico (MXAL).

For each species two to ten live males were selected and dissected in Ringer's saline solution to obtain their reproductive system. The complete system from each male was placed and extended in AFATD fixer (96% ethanol-formaldehyde-trichloroacetic acid-dimethylsulfoxide), and later completely stained using the Feulgen light green and chlorazol black staining techniques (Martoja & Martoja, 1967; Gabe, 1968; Carayon, 1969; Martínez, 2002). The internal genitalia of several specimens of each species were initially observed and drawn to scale using a stereomicroscope with a camera lucida (Zeiss® SV11). For each species Chinese ink was used for the line drawings (unpublished techniques, learned by the first author directly from J. Carayon and Dominique Pluot-Sigwalt). The figures were edited into plates using Corel Photo-Paint® software. The descriptions use the terminology of Snodgrass (1935) and Matzuda (1976) for the general morphology of the internal genitalia.

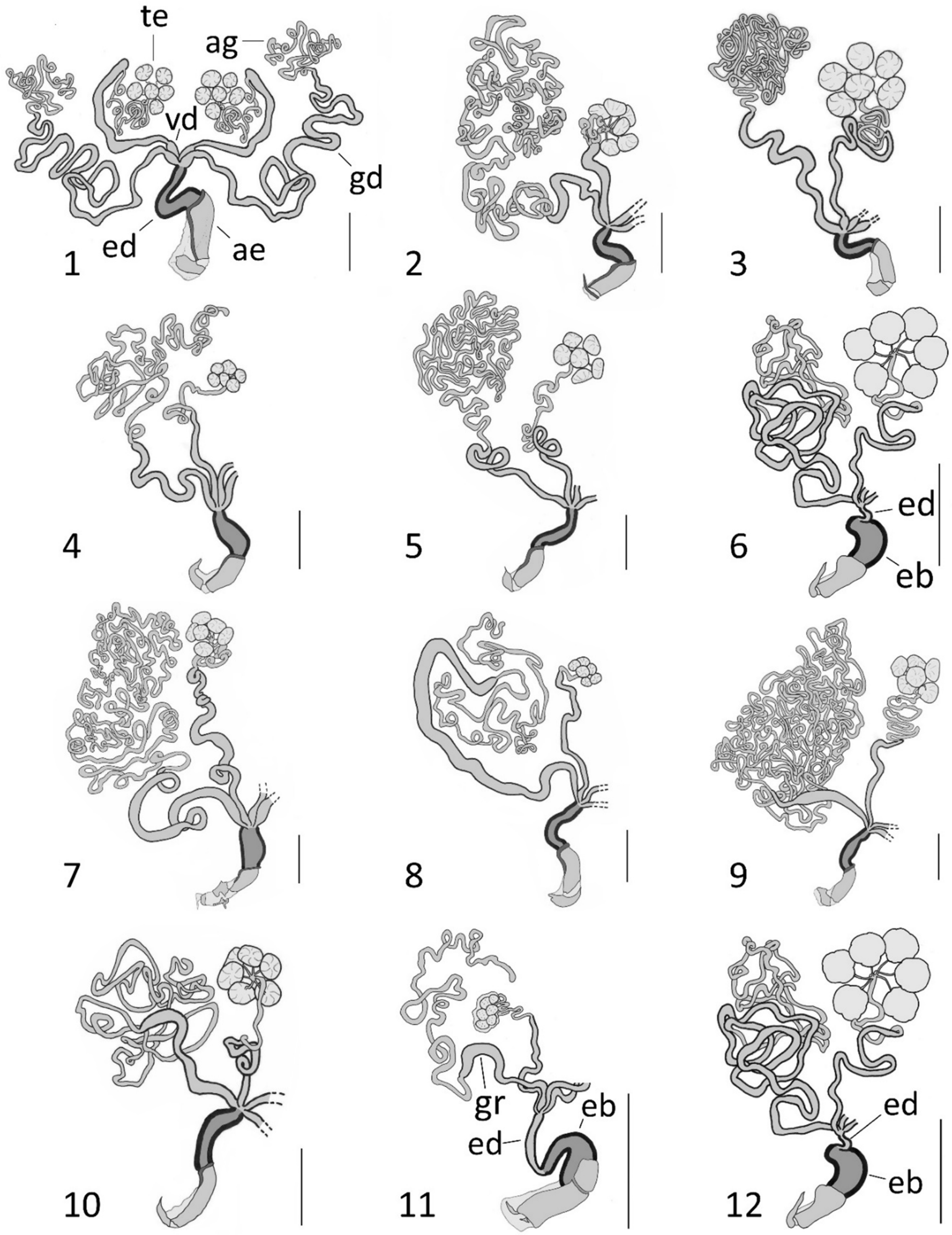
## RESULTS

In general terms, the males of these three subfamilies have similar reproductive systems, though there are some differences between them.

**Melolonthinae** (Fig. 1–12). The male reproductive system of *P. testaceipennis* (Fig. 1) is typical of all of the Melolonthinae species examined. It consists of two testes, each with six lobed and dorsoventrally flattened testicular follicles, without an outer membrane to group them together. Each testicular follicle has a long and very visible vas efferens, which emerges from the ventral region. The six vas efferens flow into the vas deferens of each testis.

Each vas deferens has an anterior region that is smaller in diameter than the posterior region, and both ducts flow into the anterior region of the ejaculatory duct. The ejaculatory duct is a very elongated organ, with a thick muscular wall that opens to the inner sac, inside the aedeagus (Fig. 1).

There are two accessory glands, each with the anterior glandular region and a posterior glandular duct greater in diameter than the previous one. The glandular region is filamentous, small in diameter, which rolls over on itself and measures approximately 42 mm long. The glandular duct, larger in diameter than the glandular region, measures approximately 34 mm. Both glandular ducts open into the anterior part of the ejaculatory duct, next to the vas deferens (Fig. 1).




**Figures 1–12.** Male reproductive system of 12 species of Melolonthinae. **1.** *Phyllophaga testaceipennis* **2.** *Ph. obsoleta* **3.** *Phy opaca* **4.** *Ph. pruinosa* **5.** *Ph. ravida* **6.** *Ph. rugipennis* **7.** *Ph. setifera* **8.** *Ph. subrugosa* **9.** *Ph. tenuipilis* **10.** *Chlaenobia latipes* **11.** *Macrodactylus nigripes* **12.** *Isonychus neglectus*. Only in *P. testaceipennis* is the complete reproductive system shown, in the other figures only half is shown. (ae= aedeagus, ag= accessory glands, eb= ejaculatory bulb, ed= ejaculatory duct, gd= glandular duct, gr=glandular reservoir, te= testis, vd= vas deferens). Scale= 4 mm.

The males of all the *Phyllophaga* species examined have two testes with six testicular follicles and their respective vasa deferens, and two accessory glands open to the ejaculatory duct, which continue with the inner sac inside the aedeagus. Only in *P. rugipennis* (Fig. 6), *M. nigripes* (Fig. 11) and *I. neglectus* (Fig. 12) is the ejaculatory duct shorter, and it opens to an ejaculatory bulb with thick muscular walls.

Testes. In all species of Melolonthinae there are six follicles per testis (Fig. 1–12). In *Phyllophaga*, the six testicular follicles are free, lobed, and dorsoventrally flattened. In *I. neglectus* they are free, flattened, and lobed as in the species of *Phyllophaga*, while in *M. nigripes* (Fig. 11) the testicular follicles are spherical and grouped within an outer membrane. The vas efferens are long and thin, and the vas deferens is long, with thicker walls, as in all species. Likewise, the anterior part of the vas deferens is smaller in diameter than the posterior part.

Accessory glands. The two accessory glands in all species have an anterior region that is glandular, filamentous, long, and small in diameter, but their length varies among species (Table 1). The longest glands, more than 300 mm long, were found in *Ph. tenuipilis* (Fig. 9). Glands of 100 to 164 mm in length were found in *Ph. obsoleta* (Fig. 2), *Ph. ravida* (Fig. 5), *Ph. rugipennis* (Fig. 6), and *Ph. setifera* (Fig. 7), and glands 41 to 86 mm long were found in *Ph. testaceipennis* (Fig. 1), *Ph. opaca* (Fig. 3), *Ph. pruinosa* (Fig. 4), *Ph. subrugosa* (Fig. 8) and *Ch. latipes* (Fig. 10). The glandular duct varies in size between nine and 34 mm, depending on the species (Table 1). The smallest accessory glands were found in *M. nigripes* (Fig. 11). Only in this species was a widening observed in the anterior part of the glandular duct, as a glandular reservoir, but it does not occur in any other of the species studied in Melolonthinae.

Ejaculatory duct. This duct is very elongated and occurs in all species of *Phyllophaga*, though in some species it is slightly thicker towards the back (Table 1), as in *Ph. testaceipennis* (Fig. 1), *Ph. pruinosa* (Fig. 4) and *Ph. rugipennis* (Fig. 6).

Ejaculatory bulb. Only *Ph. rugipennis* (Fig. 6), *M. nigripes* (Fig. 11), and *I. neglectus* (Fig. 12) have an ejaculatory bulb (Table 1). This organ was not seen in all the species of *Phyllophaga* examined, though in *Ph. pruinosa* (Fig. 4) and *Ph. setifera* (Fig. 7) the muscular walls of the ejaculatory duct are thickened and are wider than long, which would represent an incipient ejaculatory bulb.

**Table 1.** General characteristics of the male reproductive system of 12 species of Melolonthinae, 6 species of Dynastinae, and 3 species of Rutelinae (n = number, * = presence, - = absence).

| **Subfamily species** | **Follicles per testis (n)** | **Accessory gland length (mm)** | **Glandula duct length (mm)** | **Ejaculatory duct** | **Ejaculatory bulb** |
|---|---|---|---|---|---|
| **MELOLONTHINAE** | | | | | |
| *Phyllophaga testaceipennis* | 6 | 41.9 | 34.1 | * | - |
| *Phyllophaga obsoleta* | 6 | 116 | 9 | * | - |
| *Phyllophaga opaca* | 6 | 86.6 | 13.9 | * | - |
| *Phyllophaga pruinosa* | 6 | 77 | 12 | * | - |

| Subfamily species | Follicles per testis (n) | Accessory gland length (mm) | Glandula duct length (mm) | Ejaculatory duct | Ejaculatory bulb |
|---|---|---|---|---|---|
| *Phyllophaga ravida* | 6 | 117.6 | 14.9 | * | - |
| *Phyllophaga rugipennis* | 6 | 103.1 | 31.5 | * | * |
| *Phyllophaga setifera* | 6 | 164 | 30.2 | * | - |
| *Phyllophaga subrugosa* | 6 | 73 | 25.3 | * | - |
| *Phyllophaga tenuipilis* | 6 | 312 | 10 | * | - |
| *Chlaenobia latipes* | 6 | 63 | 7.5 | * | - |
| *Macrodactylus nigripes* | 6 | 21.2 | 4.5 | * | * |
| *Isonychus neglectus* | 6 | 37.3 | 31.3 | * | * |
| **DYNASTINAE** | | | | | |
| *Cyclocephala jalapensis* | 6 | 44.1 | 9.8 | * | * |
| *Cyclocephala picta* | 6 | 270. 1 | 20.5 | * | * |
| *Cyclocephala sexpunctata* | 6 | 178. 2 | 14 | * | * |
| *Cyclocephala mafaffa* | 6 | 348.6 | 33.2 | * | * |
| *Cyclocephala lunulata* | 6 | 219 | 24.3 | * | * |
| *Cyclocephala weidneri* | 6 | 298.7 | 8.6 | * | * |
| **RUTELINAE** | | | | | |
| *Paranomala marginicollis* | 6 | 35.7 | 15.5 | * | * |
| *Paranomala semicincta* | 6 | 17. 9 | 29.9 | * | * |
| *Paranomala cupricollis* | 6 | 144.1 | 57.5 | * | * |

**Dynastinae** (Fig. 13–18). The male reproductive system in *C. jalapensis* (Fig. 13) exemplifies the system seen in all the species examined of this subfamily. It consists of two testicles, each with six dorsoventrally flattened free testicular follicles (Table 1), two vas deferens, two accessory glands with their respective glandular duct, and an ejaculatory bulb that opens into the aedeagus.

Testes. The six species studied have two testicles, each with six flattened and lobed testicular follicles, and the vas efferens are long. The vas deferens are small in diameter in their anterior region and much larger diameter, with thick walls in the posterior region (Fig. 13–18).

Accessory glands. The longest—almost 349 mm long—were found in *C. mafaffa* (Fig. 16), and the smallest (44 mm) in *C. jalapensis* (Fig. 13) (Table 1). In all species, these glands are small in diameter. The glandular duct is long, with thick walls.

Ejaculatory duct. This duct is present in all six species (Table 1), although it is very small in *C. jalapensis* (Fig. 13), *C. sexpunctata* (Fig. 15), and *C. weidneri* (Fig. 18). In the other three species, it is elongated (Fig. 14, 16, 17).

Ejaculatory bulb. In the six species studied, there is a well-developed ejaculatory bulb (Table 1), with thick muscular walls (Fig. 13–18).

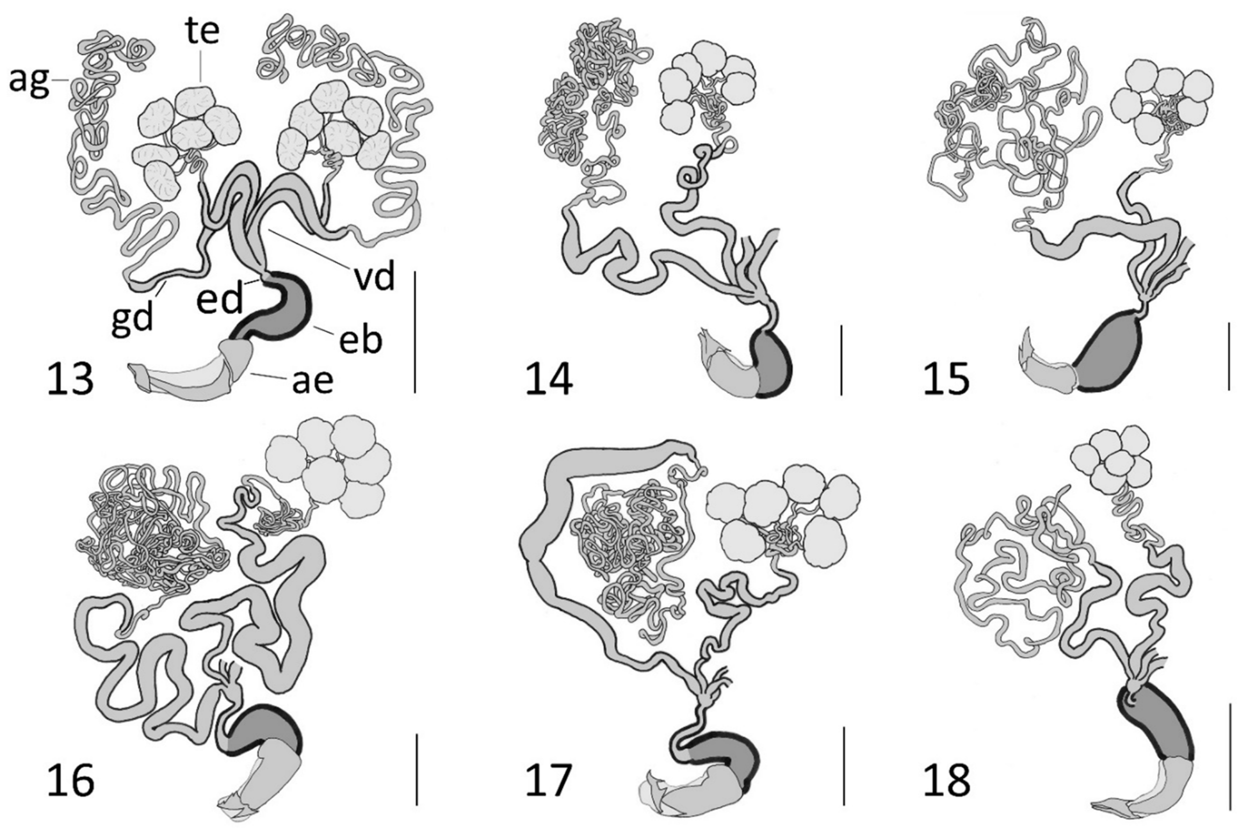
**Rutelinae** (Fig. 19–21). The male reproductive system of *Paranomala marginicollis* (Fig. 19) is typical of all the Rutelinae species examined. It consists of two testicles, each with six testicular follicles (Table 1), with their respective vas efferens, and a vas deferens. There are two very long accessory glands, with their respective glandular duct, the ejaculatory duct, and the ejaculatory bulb. The organs of the reproductive system of these three species have the same distribution plane.

Testes. The three species studied have two testicles, each with six-lobed and dorsoventrally flattened testicular follicles. The vas deferens are large in diameter.

Accessory glands. The accessory glands are 144 mm long in *P. cupricollis* (Fig. 20), but only 17.9 mm in *P. semicincta* (Fig. 21) (Table 1).

Ejaculatory duct. The ejaculatory duct is short and is present in all species.

Ejaculatory bulb. In the three species studied, there is a well-developed ejaculatory bulb.




**Figures 13–18.** Male reproductive system of six species of Dynastinae species. **13.** *Cyclocephala jalapensis* **14.** *C. picta* Burmeister **15.** *C. sexpunctata* **16.** *C. mafaffa* **17.** *C. lunulata* **18.** *C. weidneri*. Only in *C. jalapensis* is the complete reproductive system shown, in the other figures only half is shown. (ae= aedeagus, ag= accessory glands, eb= ejaculatory bulb, ed= ejaculatory duct, gd= glandular duct, gr=glandular reservoir, te= testis, vd= vas deferens). Scale= 4 mm.

**Comparative aspects between the males of Melolonthinae, Dynastinae and Rutelinae.** The species examined in this study were similar in terms of the general morphology of their internal genitalia, however, some differences were found.

Testes. In all the species studied there are two testicles with six lobes and flattened testicular follicles and without an outer membrane to contain them (Table 2), except in *M. nigripes* (Melolonthinae) in which they are spherical and have a membrane that contains them (Fig. 11). The vas deferens is similar in all species and has no seminal vesicle.

**Table 2.** Species of Scarabaeoidea with two testes and six testicular follicles.

| Species | References |
|---|---|
| **MELOLONTHINAE** | |
| *Anoxia villosa* (Fabricius) | Bordas, 1900 |
| *Amphimallon majale* (Razoumowsky) | Menees, 1963 |
| *Costelytra zealandica* (White) | Fenemore, 1971, Stringer, 1990 |
| *Chlaenobia latipes* Bates | Martínez *et al*., present paper |
| *Hymenoplia strigosa* (Illiger) | Bordas, 1900 |
| *Isonychus neglectus* (Moser) | Martínez *et al.*, present paper |
| *Macrodactylus nigripes* Bates | Martínez *et al*., present paper |
| *Melolontha melolontha* (Linnaeus) | Dufour, 1825; Straus-Dürckheim, 1828; Bordas, 1900 |
| *Phyllophaga anxia* LeConte | Berberet & Helms, 1972 |
| *Phyllophaga obsoleta* (Blanchard) | Martínez *et al.,* present paper |
| *Phyllophaga opaca* (Moser) | Martínez *et al.,* present paper |
| *Phyllophaga pruinosa* (Blanchard) | Martínez *et al*., present paper |
| *Phyllophaga ravida* (Blanchard) | Martínez *et al*., present paper |
| *Phyllophaga rugipennis* (Schauffus) | Martínez *et al*., present paper |
| *Phyllophaga setifera* (Burmeister) | Martínez *et al.,* present paper |
| *Phyllophaga subrugosa* (Moser) | Martínez *et al.,* present paper |
| *Phyllophaga tenuipilis* (Bates) | Martínez *et al.,* present paper |
| *Phyllophaga testaceipennis* (Blanchard) | Martínez *et al*., present paper |
| **DYNASTINAE** | |
| *Cyclocephala jalapensis* Casey | Martínez *et al.,* present paper |
| *Cyclocephala lunulata* Burmeister | Martínez *et al*., present paper |
| *Cyclocephala mafaffa* Burmeister | Martínez *et al*., present paper |
| *Cyclocephala picta* Burmeister | Martínez *et al*., present paper |
| *Cyclocephala sexpunctata* Castelnau | Martínez *et al*., present paper |
| *Cyclocephala weidneri* Endrödi | Martínez *et al.,* present paper |
| *Oryctes nasicornis* (Linnaeus) | Straus-Dürckheim, 1828 |
| *Oryctes rhinoceros* (Linnaeus) | Mathur *et al*., 1960; Jacob 1989 |
| **RUTELINAE** | |
| *Anisoplia agricola* (Poda) | Bordas, 1900 |
| *Anomala ausonia* Erichson | Lupo, 1947 |

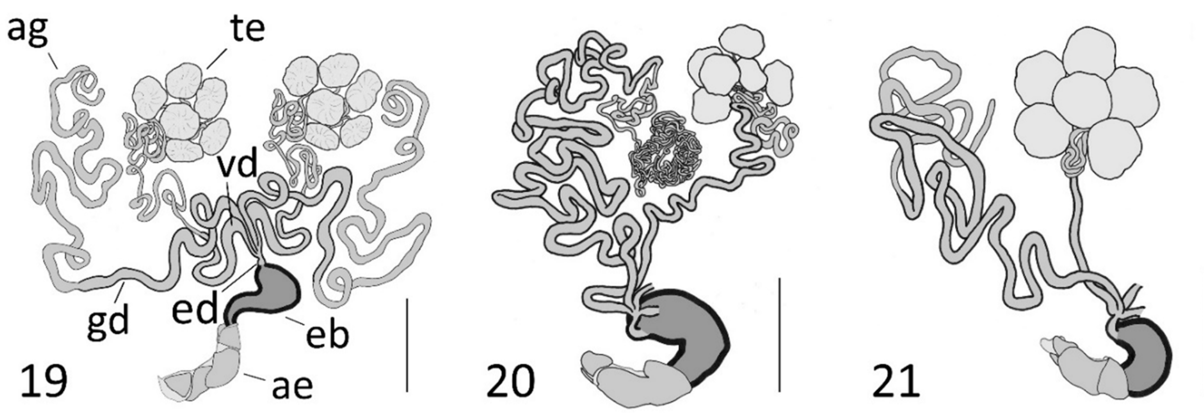
| **Species** | **References** |
|---|---|
| *Paranomala cupricollis* (Chevrolat) | Martínez *et al.*, present paper |
| *Paranomala marginicollis* (Bates) | Martínez *et al.*, present paper |
| *Paranomala semicincta* (Bates) | Martínez *et al.*, present paper |
| *Phyllopertha horticola* (Linnaeus) | Rittershaus, 1927 |
| *Popillia japonica* Newman | Williams, 1945; Anderson, 1950 |
| **HOPLIINI** | |
| *Hoplia argentea* (Poda) | Bordas, 1990 |
| *Hoplia squamifera* Burmeister | Carrillo-Ruiz *et al.*, 2008 |
| *Hoplia subcostata* Bates | Carrillo-Ruiz *et al.*, 2008 |
| **TROGIDAE** | |
| *Omorgus omacanthus* (Harold) | Sharp & Muir, 1912 |
| *Trox scaber* (Linnaeus) | Sharp & Muir, 1912 |
| **GEOTRUPINAE** | |
| *Anoplotrupes stercorosus* (Scriba) | Pluot & Martínez, 1998; Martínez & Cruz, 1999 |
| *Bolbocerosoma farctum* (Fabricius) | Williams, 1945 |
| *Bolbelasmus gallicus* (Mulsant) | Bordas, 1900 |
| *Ceratotrupes bolivari* Halfft. & Mtz. | Pluot & Martínez, 1998; Martínez & Cruz, 1999 |
| *Geotrupes mutator* (Marsham) | Bordas, 1900 |
| *Geotrupes stercorarius* (Linnaeus) | Bordas, 1900 |
| *Halffterius rufoclavatus* (Jekel) | López-G., 1987; Martínez & Cruz, 1999; Trotta *et al.*, 2007 |
| *Megatrupes cavicollis* Bates | Pluot & Martínez, 1998; Martínez & Cruz, 1999 |
| *Onthotrupes herbeus* (Jekel) | Pluot & Martínez, 1998; Martínez & Cruz, 1999 |
| *Onthotrupes nebularum* (Howden) | Pluot & Martínez, 1998; Martínez & Cruz, 1999 |
| *Onthotrupes sobrinus* (Jekel) | Pluot & Martínez, 1998; Martínez & Cruz, 1999 |
| *Trypocopris vernalis* (Linnaeus) | Pluot & Martínez, 1998; Martínez & Cruz, 1999 |
| *Typhaeus typhoeus* (Linnaeus) | Bordas, 1900 |
| **SCARABAEINAE** | |
| *Ateuchetus semipunctatus* (Fabricius) | Dajoz, 1972 |
| *Ateuchus illaesus* Harold | Martínez & Cruz, 1999 |
| *Canthidium moestum* Harold | Martínez & Cruz, 1999 |
| *Canthidium puncticolle* Harold | Pluot & Martínez, 1998 |
| *Canthon cyanellus* LeConte | Mtz. & Benítez, 1988; Pluot & Mtz., 1998; Mtz. & Cruz, 1999 |
| *Canthon femoralis* Chevrolat | Martínez & Cruz, 1999 |
| *Canthon humectus* (Say) | Pluot & Martínez, 1998; Martínez & Cruz, 1999 |
| *Canthon indigaceus* LeConte | Martínez, 1991; Pluot & Martínez, 1998 |
| *Canthon pilularius* (Linnaeus) | Cooper, 1938 |
| *Canthon subhyalinus* Harold | Martínez & Cruz, 1999 |
| *Canthon viridis* Palisot de Beauvois | Martínez & Cruz, 1999 |
| *Copris armatus* Harold | Pluot & Martínez, 1998; Martínez & Cruz, 1999 |
| *Copris incertus* Say | Cruz & Huerta, 1998; Pluot & Mtz., 1998; Mtz. & Cruz, 1999 |

| **Species** | **References** |
|---|---|
| *Copris laeviceps* Harold | Pluot & Martínez, 1998; Martínez & Cruz, 1999 |
| *Copris lugubris* Boheman | Pluot & Martínez, 1998; Martínez & Cruz, 1999 |
| *Copris sierrensis* Matthews | Pluot & Martínez, 1998; Martínez & Cruz, 1999 |
| *Coprophanaeus corythus* (Harold) | Pluot & Martínez, 1998; Martínez & Cruz, 1999 |
| *Coprophanaeus lancifer* (Linnaeus) | Edmonds, 1974 |
| *Coprophanaeus pluto* (Harold) | Pluot & Martínez, 1998; Martínez & Cruz, 1999 |
| *Deltochilum gibbosum* (Fabricius) | Martínez & Cruz, 1999 |
| *Deltochilum lobipes* Bates | Pluot & Martínez, 1998; Martínez & Cruz, 1999 |
| *Deltochilum pseudoparile* Paulian | Pluot & Martínez, 1998; Martínez & Cruz, 1999 |
| *Dichotomius carolinus* (Linnaeus) | Williams, 1945, Pluot & Martínez, 1998 |
| *Dichotomius centralis* (Harold) | Pluot & Martínez, 1998; Martínez & Cruz, 1999 |
| *Dichotomius satanas* (Harold) | Pluot & Martínez, 1998; Martínez & Cruz, 1999 |
| *Euoniticellus intermedius* (Reiche) | Pluot & Martínez, 1998; Martínez & Cruz, 1999 |
| *Eurysternus caribaeus* (Herbst) | Pluot & Martínez, 1998; Martínez & Cruz, 1999 |
| *Eurysternus mexicanus* Harold | Pluot & Martínez, 1998; Martínez & Cruz, 1999 |
| *Gromphas inermis* Harold | Martínez & Cruz, 1999 |
| *Liatongus rhinocerulus* (Bates) | Pluot & Martínez, 1998; Martínez & Cruz, 1999 |
| *Ontherus mexicanus* Harold | Pluot & Martínez, 1998; Martínez & Cruz, 1999 |
| *Onthophagus aureofuscus* Bates | Martínez & Cruz, 1999 |
| *Onthophagus batesi* Howden & Cart. | Pluot & Martínez, 1998; Martínez & Cruz, 1999 |
| *Onthophagus chevrolati* Harold | Pluot & Martínez, 1998; Martínez & Cruz, 1999 |
| *Onthophagus cyanellus* Bates | Pluot & Martínez, 1998; Martínez & Cruz, 1999 |
| *Onthophagus hippopotamus* Harold | Pluot & Martínez, 1998; Martínez & Cruz, 1999 |
| *Onthophagus incensus* Say | Pluot & Martínez, 1998; Martínez & Cruz, 1999 |
| *Onthophagus rhinolophus* Harold | Pluot & Martínez, 1998; Martínez & Cruz, 1999 |
| *Onthophagus rostratus* Harold | Pluot & Martínez, 1998 |
| *Onthophagus vacca* Linnaeus | Pluot & Martínez, 1998 |
| *Phanaeus amethystinus* Harold | Martínez & Cruz, 1999 |
| *Phanaeus demon* Castelnau | Martínez & Cruz, 1999 |
| *Phanaeus endymion* Harold | Pluot & Martínez, 1998; Martínez & Cruz, 1999 |
| *Phanaeus scutifer* Bates | Pluot & Martínez, 1998 |
| *Phanaeus tridens* Castelnau | Pluot & Martínez, 1998; Martínez & Cruz, 1999 |
| *Sulcophanaeus menelas* (Castelnau) | Martínez & Cruz, 1999 |

Accessory glands (Table 1). These glands differ in length depending on the species of each subfamily. In Melolonthinae, they range from 21.2 mm as in *M. nigripes* (Fig. 11) to 117.6 mm as in *Ph. ravida* (Fig. 5), except in *Ph. tenuipilis* (Fig. 9) in which they measured 312 mm. In Dynastinae, these glands were very long in five of the six species examined: 178.2 mm in *C. sexpunctata* (Fig. 15), 219 mm in *C. lunulata* (Fig. 17), 270 mm in *C. picta* (Fig. 14), 298.7 mm in *C. weidneri* (Fig. 18) and 348.6 in *C. mafaffa* (Fig. 16); whereas in *C. jalapensis* (Fig. 13) they only measured 44.1 mm. In the three species of Rutelinae, the length of these glands also varied among species, in *P. semicincta* (Fig. 21) they measured 17.9 mm, in *P. marginicollis* (Fig. 19) 35.7 mm and in *P.*

*cupricollis* (Fig. 20) 144.1 mm. Only in *M. nigripes* (Fig. 11) is there a glandular reservoir on each side, which was not observed in any other species.

Ejaculatory duct (Table1). This duct is present in all species but varies in length. This duct is long in Melolonthinae species (Fig. 1–5, 7–10), except in *Ph. rugipennis* (Fig. 6), *M. nigripes* (Fig. 11) and *I. neglectus* (Fig. 12), in which the back of the ejaculatory duct thickens forming an ejaculatory bulb. Ejaculatory bulb (Table 1). This organ occurs in three species of Melolonthinae: *Ph. rugipennis* (Fig. 6), *M. nigripes* (Fig. 11) and *I. neglectus* (Fig. 12), and in all Dynastinae (Fig. 13–18) and Rutelinae (Fig. 19–21) species.




**Figures 19-21.** Male reproductive system of three species of Rutelinae. **19.** *Paranomala marginicollis* **20.** *Paranomala cupricollis* **21.** *Paranomala semicincta*. Only in *P. marginicollis* is the complete reproductive system shown, in the other figures only half is shown. (ae= aedeagus, ag= accessory glands, eb= ejaculatory bulb, ed= ejaculatory duct, gd= glandular duct, gr=glandular reservoir, te= testis, vd= vas deferens). Scale= 4 mm.

## DISCUSSION

Testes and vasa deferens. In all species studied there are six testicular follicles as occurs in the species of other Scarabaeoidea subfamilies (Table 2). However, in species of Passalidae there are two testicular follicles (Krause, 1946; Cruz & Castillo, 2008; Salazar *et al*., 2016), whereas species of Aphodiinae have six to seven testicular follicles, while some species of Eupariini have two testicular follicles (Martínez *et al*., 2001) and Lucanidae have twelve (Reyes-Castillo *et al*., 2004).

The vas deferens are similar in all the species of the three subfamilies studied and in none of them was a seminal vesicle observed. Nevertheless, the presence of a seminal vesicle has been observed in other Melolonthinae species: *Prodontria lewisii* Broun, 1904 and *Costelytra zealandica* (White, 1846) (Ferreira & McKinlay, 2001; Stringer, 1990). But, in two species of *Hoplia* (Carrillo-Ruiz *et al*., 2008) in reality the seminal vesicle is only a dilation of the final part of the vas deferens. In one species of Dynastinae, *Oryctes rhinoceros* (Linnaeus, 1758) (Jacob, 1989; Mathur *et al*., 1960), the seminal vesicle appears as an elongated dilation in the middle of the vas deferens. And in one species of Rutelinae, *Plusiotis costata* (Blanchard, 1851), it appears as two independent hemispherical dilations between the anterior and posterior vas deferens (Morón, 2010).

Accessory gland. These glands are very long in Melolonthinae, Dynastinae, and Rutelinae. In fact, these glands are much longer than those of the other scarab species that have been studied (Berberet & Helms, 1972; Jacob, 1989; Diefenbach *et al*., 1998; Stringer, 1990; Carrillo-Ruiz *et al*., 2008; Morón 2010). The glandular reservoir, which is located between the gland and the glandular duct, was only observed in *M*. *nigripes* (Fig. 11). This organ was also observed in *M*. *mexicanus* and *O*. *rhinoceros* (Mathur *et al*., 1960; Benítez-Herrera *et al*., 2015). Some authors call the final part of the glandular duct the "glandular reservoir", perhaps because that region is very wide, but it is not a glandular reservoir.

Ejaculatory duct. This duct is straight and long in the Melolonthinae species studied (Fig. 1-5, 7-10) except in *Ph*. *rugipennis*, *M*. *nigripes* and *I*. *neglectus*, in which the back of the ejaculatory duct thickens to form an ejaculatory bulb (Fig. 6, 11, 12). A long duct is also reported for other Melolonthinae such as *C*. *zealandica* and *M*. *mexicanus* (Stringer, 1990; Benítez-Herrera *et al*., 2015). It has also been described as a short duct in *P*. *anxia* and *P*. *sanctipauli* (Berberet & Helms, 1972; Diefenbach *et al*., 1998). In Dynastinae and Rutelinae, the ejaculatory duct is short before entering the ejaculatory bulb in all the species examined, as observed in *O*. *rhinoceros* and *Ch*. *costata* (Mathur *et al*., 1960; Jacob, 1989; Morón, 2010).

Ejaculatory bulb. This organ occurs in three species of Melolonthinae, *Ph*. *rugipennis*, *M*. *nigripes*, and *I*. *neglectus*, and in all species of Dynastinae and Rutelinae (Table 1). It has also been observed in *Ph*. *anxia* (Berberet & Helms, 1972), though these authors refer to it as the "erection fluid pump". It is also present in *Ph*. *sanctipauli* (Diefenbach *et al*., 1998) and *C*. *zealandica* (Stringer 1990), for which the latter author calls it the "muscular sheath of ductus ejaculatorius", and in *M*. *mexicanus* (Benítez-Herrera *et al*., 2015). In the genus *Hoplia*, the ejaculatory bulb is found in *H*. *squamifera* and *H*. *subcostata* (Carrillo-Ruiz *et al*., 2008), and these authors referred to it as the "ejaculatory duct". In Dynastinae there is an ejaculatory bulb in *O*. *rhinoceros* (Mathur *et al*., 1960; Jacob, 1989), which the latter author refers to as the "spermatophore sac". In Rutelinae it occurs in *C*. *costata* (Morón, 2010).

In species of Aphodiinae and Scarabaeinae, it is known that the ejaculatory bulb, a complex muscular structure that contains the ejaculatory duct of ectodermal origin, is well developed. In *Aphodius pseudolividus* (Aphodiinae), the ejaculatory bulb is formed by a thick (50 μm) muscular wall, inside of which is the ejaculatory duct and a part of the internal sac. In *Canthon indigaceus* (Scarabaeinae) this structure is more complicated, with a 100 μm thick muscular wall and, in addition to the ejaculatory duct, there is a third gland that is ectodermal in origin (an ectadenia). Its structure indicates that it has a pumping function; the muscular contractions probably ensure the emission of the secretions of the accessory glands and the seminal fluid with the spermatozoa, which participate in the formation of the spermatophore (Pluot-Sigwalt & Martínez, 1998). Perhaps the complexity of the ejaculatory bulb is related to the shape of the spermatophore. The spermatophore of several Scarabaeinae species is more elaborate than that of Aphodiinae species (Cruz & Martínez, 1992; Martínez, 2003) and in other Scarabaeoidea species its shape is very simple, including *Melolontha melolontha* (Landa, 1960), *Costelytra zealandica* (Striger, 1988) and *Phyllopertha horticola* (Rittershaus, 1927). In the species studied, the spermatophore is still unknown.

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