

## Larval structure of *Passalus gravelyi* and sexual dimorphism in Passalid larvae

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Received 14-VIII-2014.      Corrected 16-III-2015.      Accepted 17-IV-2015.

**Abstract:** The adults and larvae of Passalidae are subsocial insects commonly found in tropical forests, living in decaying wood gallery systems constructed by adults. Currently, few reports on the larvae of Neotropical Passalidae have been published and information is scarce. In this study, the *Passalus (Pertinax) gravelyi* Moreira, 1922 larvae is described for the first time, based on ten larval specimens 1 (1<sup>o</sup> instar), 4 (2<sup>o</sup> instar), and 5 (3<sup>o</sup> instar) associated with three adults collected from a single colony at the Parque Nacional do Itatiaia (Itatiaia, Rio de Janeiro, Brazil). The description was carried out based on electronic and digital photographs of diagnostic structures, with some details on the systematic of the species. The larvae of *Passalus gravelyi* has the general setal ‘Pertinax’ pattern and differed from others by 16 to 18 setae on the anal ring, the other larvae data from Brazilian species show the anal ring with 10 to 12 setae. A discussion on the presence of sexual dimorphism in 62 species of two and three instars of Passalidae larvae is provided for the first time. Besides, a description of the *terminal ampulla* present as a cuticular structure found in the medial-ventral area of the 9th abdominal sternite in males is also given. The *terminal ampulla* was only observed in the Passalidae male larvae and was not visible in female larvae. The *terminal ampulla* are acknowledged now in males of 64 passalid species, that are taxonomically distributed in world tropical forests, at the Oriental and Australian subfamily Aulacocyclinae (Aulacocyclini & Ceracupini) and the cosmopolitan subfamily Passalinae (Solenocyclini, Macrolinini, Passalini, & Proculini). Rev. Biol. Trop. 63 (3): 695-704. Epub 2015 September 01.

**Key words:** immatures, morphology, sexual dimorphism, Neotropical, Passalinae, Passalini.

Larvae of the family Passalidae occur with relative abundance in tropical forest and they are associated with adults in fallen trunks. Only a few studies on the larvae of Neotropical Passalidae have been published (Costa & Fonseca, 1986; Costa, Vanin, & Casari-Chen, 1988; Schuster & Reyes-Castillo, 1981, 1990; Schuster, 1992), and up to date, the most important work on Brazilian species (Costa & Fonseca, 1986) has described the larvae of 21 species.

All known Passalidae are subsocial, with parental adults, immature adults and larvae, all living in a family group in a gallery system

constructed by the adults, almost exclusively within or beneath decaying wood (trunks, limbs, roots, and wood particles). This is associated with interesting behaviors including cooperation, parental care, defense, hierarchic systems and communication, including a complex acoustical repertoire (Reyes-Castillo, 1970; Schuster, 1983; Reyes-Castillo & Halffter, 1984).

The subgenus *Pertinax* in *Passalus* comprises 40 species, of which 23 have been recorded in Brazil (Hincks & Dibb, 1935; Fonseca & Reyes-Castillo, 2004). *Passalus*



(*Pertinax*) *gravelyi* Moreira, 1922 is an endemic species from the Atlantic Forest (Mata Atlântica) and known only from the states of Rio de Janeiro and Minas Gerais, and from elevations above 1 000 m.

Our current research includes a systematic study of the larvae of Neotropical Passalidae. While preparing the description of the 3<sup>rd</sup> instar larva of *Passalus* (*Pertinax*) *gravelyi* Moreira, 1922, we noted the occurrence of a sexual dimorphism in the 2<sup>nd</sup> and 3<sup>rd</sup> instar larvae of this species; the male larvae has a terminal ampulla on the margin of the 9<sup>th</sup> sternite, and investigated the occurrence of this character in the species from all of supra-generic taxa of Passalidae.

The terminal ampulla was first described by Herold (1815) in the larvae of Lepidoptera and defined more specifically by Snodgrass (1941) in Hymenoptera. In Coleoptera the terminal ampulla was described in Scarabaeidae by Hurpin (1953), and subsequently the presence of sexual dimorphism in Passalidae, Lucanidae, Scarabaeidae and Melolonthidae larvae has been reported in literature of

Scarabaeoidea (Menees, 1957; Onore, 1994; Martínez & Lumaret, 2003, 2005; Ramírez-Salinas, Pacheco-Flores, Castro-Ramírez, & Morón, 2010). The sexual dimorphism in Passalidae has never been studied in detail, especially in larvae and pupae. The goal of our study was to describe the larvae of *Passalus* (*Pertinax*) *gravelyi* Moreira, 1922, and to begin the systematic study of larvae with the knowledge about the sexual dimorphism in larvae of the Neotropical Passalidae.

## MATERIAL AND METHODS

The samples were collected in decayed wood in the Parque Nacional do Itatiaia (Itatiaia, Rio de Janeiro, Brazil); a total of 10 specimens of larvae were collected from the same tunnel system as three adults, and all were preserved in ethanol 96 % until their evaluation.

At least 300 specimens of 62 species (Table 1) were comparatively studied about the *terminal ampulla* in the following Institutions: Coleção José Alfredo Pinheiro Dutra, Departamento de Zoologia, Universidade Federal do

TABLE 1  
List of species of Passalidae with larval sexual dimorphism

Subfamily	Tribe	Species
Aulacocyclinae	Aulacocyclini	<i>Aulacocyclus edentulus</i> (MacLeay, 1827)
	Ceracupini	<i>Taeniocerus bicanthatus</i> (Percheron, 1841)
Passalinae	Solenocyclini	<i>Ceracupes arrowi</i> Heller, 1911
	Macrolinini	<i>Cylindrocaulus patalis</i> (Lewis, 1883)
Passalinae	Passalini	<i>Erionomus planiceps</i> (Eschscholtz, 1829)
		<i>Pentalobus barbatus</i> (Fabricius, 1801)
		<i>Aceratius grandis</i> (Burmeister, 1847)
		<i>Ameripassalus tamaulipensis</i> Jimenez-Ferbans & Reyes-Castillo, 2014
		<i>Passalus (Mitrorhinus) zikani</i> Luederwaldt, 1929
		<i>Passalus (Passalus) aduncus</i> Erichson, 1847
		<i>Passalus (Passalus) alticola</i> Kirsch, 1885**
		<i>Passalus (Passalus) denticollis</i> (Kaup, 1869)
		<i>Passalus (Passalus) interstitialis</i> Eschscholtz, 1829
		<i>Passalus (Passalus) interruptus</i> (Linnaeus, 1752)
		<i>Passalus (Passalus) punctiger</i> Lepeletier & Serville, 1825
		<i>Passalus (Passalus) variiphyllus</i> Kuwert, 1891
		<i>Passalus (Pertinax) affinis</i> Percheron 1835
		<i>Passalus (Pertinax) caelatus</i> Erichson, 1847
		<i>Passalus (Pertinax) cognatus</i> Truqui, 1847



CUADRO 1 (Continuación) / TABLE 1 (Continued)

Subfamily	Tribe	Species
Proculini		<i>Passalus (Pertinax) convexus</i> Dalman, 1817
		<i>Passalus (Pertinax) gravelyi</i> Moreira, 1922
		<i>Passalus (Pertinax) inops</i> Truqui, 1847
		<i>Passalus (Pertinax) punctatostriatus</i> Percheron, 1835
		<i>Passalus (Passalus) unicornis</i> Le Peletier et Serville, 1825**
		<i>Paxillus jamaicensis</i> Hincks, 1950
		<i>Paxillus leachi</i> MacLeay, 1819
		<i>Ptichopus angulatus</i> (Percheron, 1835)
		<i>Spasalus crenatus</i> (MacLeay, 1819)
		<i>Chondrocephalus debilis</i> (Bates, 1886)
		<i>Chondrocephalus purulensis</i> (Bates, 1886)
		<i>Heliscus tropicus</i> (Percheron, 1835)
		<i>Odontotaenius cerastes</i> Castillo, Rivera-C. & Reyes-Castillo, 1988
		<i>Odontotaenius disjunctus</i> (Illiger, 1800)*
		<i>Odontotaenius striatopunctatus</i> (Percheron, 1835)
		<i>Odontotaenius zodiacus</i> (Truqui, 1857)
		<i>Oileus bifidus</i> (Zang, 1905)
		<i>Oileus rimator</i> (Truqui, 1857)
		<i>Oileus heros</i> (Truqui, 1857)
		<i>Oileus sargi</i> (Kaup, 1871)
		<i>Ogyges cackchiqueli</i> Schuster & Reyes-Castillo, 1990
		<i>Ogyges championi</i> (Bates, 1886)
		<i>Petrejoides haagi</i> (Kaup, 1868)
		<i>Petrejoides jalapensis</i> (Bates, 1886)
		<i>Petrejoides orizabae</i> Kuwert, 1897
		<i>Petrejoides silvaticus</i> Castillo & Reyes-Castillo, 1984
		<i>Proculejus brevis</i> (Truqui, 1857)
		<i>Proculus goryi</i> (Melly, 1833)
		<i>Proculus mniszechi</i> Kaup, 1868
		<i>Pseudacanthus mexicanus</i> (Truqui, 1857)
		<i>Pseudacanthus subopacus</i> (Bates, 1886)
		<i>Spurius bicornis</i> (Truqui, 1857)
		<i>Spurius depressifrons</i> (Bates, 1886)
		<i>Spurius dichotomus</i> Zang, 1905
		<i>Undulifer incisus</i> (Truqui, 1857)
		<i>Verres hageni</i> Kaup, 1871
		<i>Verres intermedius</i> Kaup 1871
		<i>Veturius (Ouayana) cirratus</i> Bates, 1886
		<i>Veturius (Veturius) marilucae</i> Boucher, 2006
		<i>Veturius (Veturius) sinuaticollis</i> Kuwert, 1891
		<i>Veturius (Veturius) sinuosus</i> (Drapiez, 1817)
		<i>Vindex agnoscendus</i> (Percheron, 1841)
		<i>Vindex sculptilis</i> Bates, 1886
		<i>Xylopassalooides schusteri</i> Reyes-Castillo, Fonseca & Castillo, 1987
		<i>Yumtaax recticornis</i> (Burmeister, 1847)

\* species cited by Menees (1957).

\*\* Species cited by Martínez &amp; Lumaret (2003, 2005).



Rio de Janeiro, Rio de Janeiro (DZ RJ) and Colección Entomológica del Instituto de Ecología Xalapa (IEXA).

The morphological characters and the illustrations were made with the aid of a Leica MZ 7.5 stereomicroscope with a drawing tube and integrated digital camera Leica 3.0 CMOS. The larvae terminology followed the primary setal patterns proposed by Schuster & Reyes-Castillo (1981), the general terms of structures as Costa et al. (1988), and the general taxonomic classification followed Boucher (2006).

The electronic photographs were made after the dehydration of some larval structures in a graded ethanol series (70-100 %), air dried, and mounted on aluminum stubs and palladium gold covered. Subsequently, the samples were photographed in a JEOL model JSM 5600 LV Scanning electron Microscope.

In order to study the *terminal ampulla*, the larvae were fixed following the techniques described by Martínez (1999, 2002) using Black of chlorazol and Feulgen-woven green. We investigated the occurrence of the sexual dimorphism in passalid larvae, with the dimorphism present in the structure of the terminal ampulla. We observed the terminal ampulla in male larvae of the 62 passalid species across the two subfamilies and six tribes.

## RESULTS

### *Passalus (Pertinax) gravelyi* Moreira, 1922, larva

*Passalus (Pertinax) gravelyi* Moreira, 1922:276-278; Luederwaldt, 1931:116; Fonseca & Reyes-Castillo 2004:15 (cat.) (Fig. 1, Fig. 2, Fig. 3, Fig. 4, Fig. 5, Fig. 6, Fig. 7, Fig. 8, Fig. 9).

**Description:** Larva of third instar ( $n = 5$ ). Length = 8.09-15.99 mm; head width = 1.89-2.66 mm; prothorax width = 2.98-3.83 mm. **Head**, with short and sparse pubescence (Fig. 2 and Fig. 3); two or three post-antennal setae (2-3 HPA), elongate, reaching antennal tip when extended and folded forward. Epicranial

suture present with distinct frontal stem in V shaped. Coronal suture almost half of head capsule length. Clypeus distinctly transverse and pubescent. Labrum transverse, with anterior margin rounded and with moderately elongate and sparse setae. Epipharynx (Fig. 4) with *corypha* rounded and with setose, *clithrum* small and pigmented, *acanthoparia* with elongate setae, *acroparia* smooth, *chaetoparia* with long and sparse setae, *pedium* marked by the presence of many setae in the central area, *laeotorma* and *dextiotorma* strongly pigmented. Mouthparts protracted (Fig. 5, Fig. 6 and Fig. 7): mandibles (Fig. 5) symmetrical, movable, triangular, tridentate at apex, external margin distinctly angulate, with many sparse setae (except in apical part), mesal surface curved and smooth, inner cutting edge with a blunt tooth, mola developed, baso-lateral area, near the mola, with a declivity and with one tuft

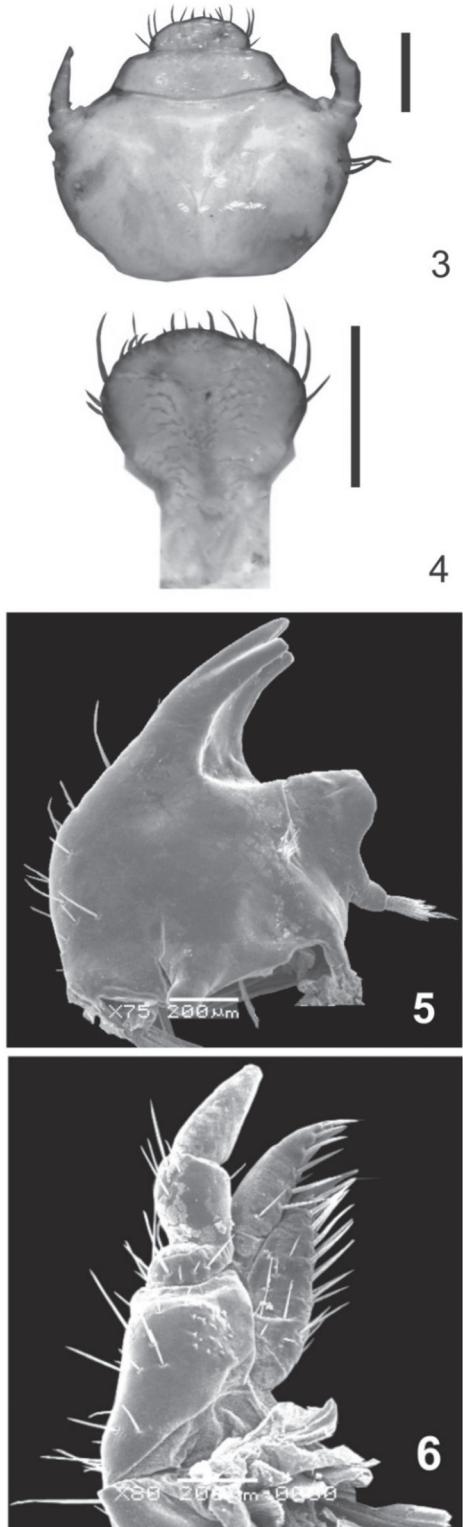


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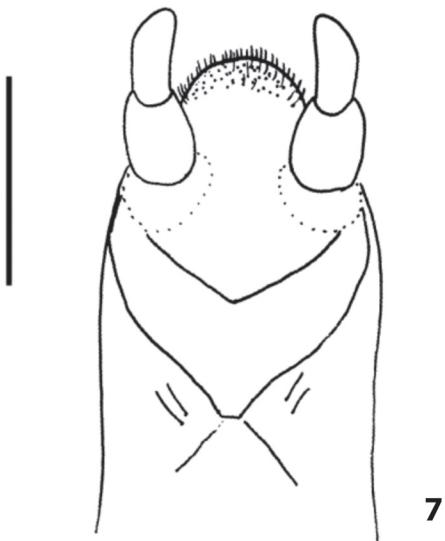
Figs. 1-2. *Passalus (Pertinax) gravelyi*. (1) Larva of first instar, lateral view. (2) Larva of third instar, lateral view. Scale bars = 1.0 mm.



of short and dense setae near the condilum, and brustia developed with a dense, compact tuft of elongate setae. Maxillae (Fig. 6) mobiles and elongate, with galea elongate, almost as long as apical segment of maxillary palp, falcate at apex, with elongate setae at inner edge; lacinia entire, reaching the apical third of galea, with single apex, inner margin with fringe of elongate setae; palpifer present with six basal setae; maxillary palp with two segments, the apical segment slightly longer than basal segment and narrowing near the apex, basal segment with four setae. Labium with prementum, mentum and submentum; ligula (Fig. 7) rounded at apex and dense and short setae; prementum with a single fringe of setae near base; mentum short, smooth, and posterior margin converging back in V-shaped; submentum with one pair of elongate setae at the sides the suture between mentum and submentum; submentum fused at the gula; gula laterally with many setae, medially glabrous. **Thorax.** Segments glabrous, with prothoracic spiracles larger than and directed opposite to mesothoracic, metathoracic and abdominal spiracles. Pronotum entirely pubescent and with two lateral sclerotized areas, each with 3-5 long lateral setae (3-5 PSL); median area between sclerotized pronotal areas distinct glabrous. Mesonotum no dorsal mesonotal setae (MSD) and one pair of lateral mesonotal setae (0MSD; 2 MSL). Metanotum with one pair dorsal metanotal setae and two lateral metanotal setae (1 MTD; 2 MTL). Pro and mesothoracic legs well developed (with coxa, trochanter, femur, tibia and tarsungulus) and pubescent. Metathoracic legs reduced (Fig. 8) with only one segment bearing six small, lateral teeth basal to the apex. **Abdomen.** Ten segments visible when viewed dorsally or laterally. Abdominal segments each with one pair of medial tergal setae and one pair of lateral tergal setae (1 TM; 1 TL). Anal opening (Fig. 9) V-shaped; anal ring with 16-20 setae (18-20

Figs. 3-6. *Passalus (Pertinax) gravelyi*. (3) Head, dorsal view. (4) Epipharynx, ventral view. (5) Mandible, dorsal view. (6) Maxillae, dorsal view. Scale bars, Figs. 3-4 = 1.0 mm.





**Fig. 7.** *Passalus (Pertinax) gravelyi*, labium, ventral view. Scale bars = 1.0 mm.

AR); IX abdominal ventrite with one pair of setae in medial area (AV9).

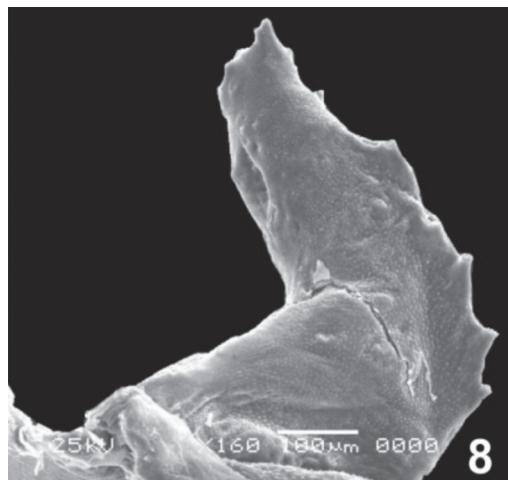
**Setal Pattern 2° and 3° instars:** 2-3 HPA; 3-4 PSL; 0 MSD; 2 MSL; 1 MTD; 2 MTL; 1 TM; 1 TL; 1 AV9; 16-18 AR.

**Setal Pattern 1° instar** (Fig. 1): 3 HPA; 4 PSL; 1 MSD; 2 MSL; 1 MTD; 2 MTL; 1 TM; 1 TL; 1 AV9; 18 AR. Measurements of first instar - Length = 7.49 mm; head width = 1.49 mm; prothorax width = 2.66 mm.

**Material examined:** BRAZIL. Rio de Janeiro: Itatiaia (Parque Nacional do Itatiaia, Estrada para Agulhas Negras, 44°36'25.3" W - 22°26'3.3" S, 2,091 m), 20.VII.2012, 1 larva (1° instar), 4 larvae (2° instar), 5 larvae (3° instar), 3 adults, Mermudes et al. leg. (DZRJ).

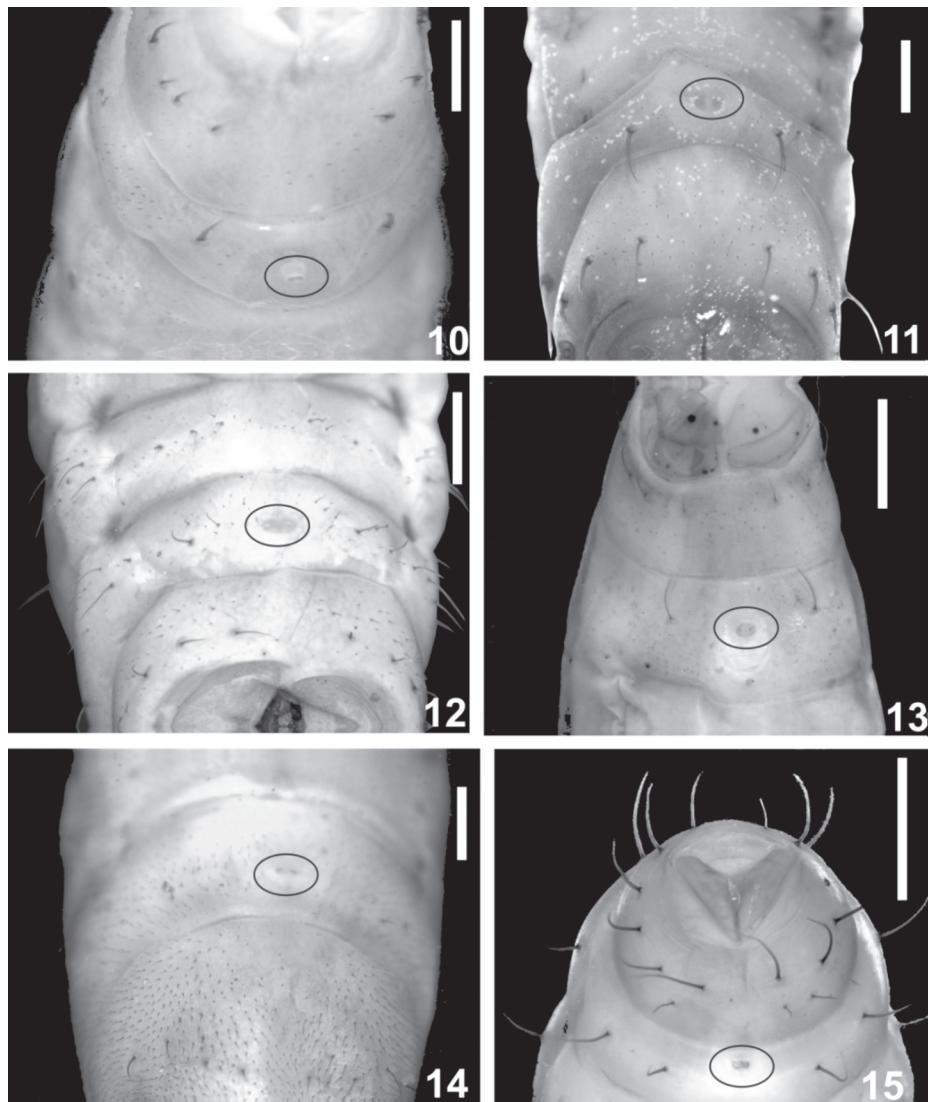
#### AN OVERVIEW ON SEXUAL DIMORPHISM IN PASSALID LARVAE

In this study sexual dimorphism in passalid larvae is characterized in detail for the first time, with the dimorphism present in the



**Figs. 8-9.** *Passalus (Pertinax) gravelyi*. 8. Metathoracic leg. 9. Anal ring, ventral view. Scale bar, Fig. 9 = 1.0 mm.

structure of the *terminal ampulla* (sometimes referred to as “genital ampula”). The *terminal ampulla* has been reported and described in various holometabolous insects (Herold, 1815; Snodgrass, 1941; Hurpin, 1953; Menees, 1957; Matsuda, 1976; Onore, 1994; Martínez & Lumaret, 2005) as the cuticular structure in medial-ventral area of the 9<sup>th</sup> abdominal sternite in males (Fig. 10, Fig. 11, Fig. 12, Fig. 13, Fig. 14 and Fig. 15). Ramírez-Salinas et al. (2010) reported that the terminal ampulla (referred to as “genital ámpula”) was present in the last (tenth) abdominal sternite of the pupae of the dynastine scarab, *Ligyrus nasutus* (Burmeister) but that it was less prominent than the terminal ampulla in male pupae.



**Figs. 10-15.** Nine ventrite abdominal larvae, ventral view, showing the terminal Ampulla with the circles. (10) *Passalus (Pertinax) convexus* Dalman, 1817. (11) *Passalus (Passalus) interruptus* (Linnaeus, 1752). (12) *Ptichopus angulatus* (Percheron, 1835). (13) *Paxillus leachi* MacLeay, 1819. (14) *Odontotaenius zodiacus* (Truqui, 1857). (15) *Cylindrocaulus patalis* (Lewis, 1883). Scale bars = 1.0 mm.

In other Scarabaeoidea, the *terminal ampulla* is evident in all larval instars and it is observed at apex of the aedeagus at the last abdominal ventrite in male pupae (Martínez & Lumaret, 2005). We were unable to detect the *terminal ampulla* in the first instar passalid larvae, but in the second and third instar larvae and in pupae, the sex of the immatures can be determined. We observed the *terminal ampulla*

only in male larvae of the 62 passalid species across the two subfamilies and six tribes (*sensu* Boucher, 2006) of Passalidae (Table 1), using the techniques of Martínez (1999) for dissecting and staining the *terminal ampulla* in the Scarabaeinae.

The *terminal ampulla* of late-instar passalid male larvae is visible ventrally as a distinct patch of cuticular tissue of the 9th sternite,

between and internal to the pair of ventral abdominal setae (AV) of this segment (Fig. 10, Fig. 11, Fig. 12, Fig. 13, Fig. 14 and Fig. 15). This structure, *terminal ampulla*, it is a very thin layer, with no apparent differences among species.

## DISCUSSION

Our current examination included a systematic study of the larvae of Neotropical Passalidae, with the description of the larva of *Passalus (Pertinax) gravelyi* Moreira, 1922. Based on the three larval instars studied and the absence of some primary setae in the later instars (2° and 3°), the following general setal pattern is proposed for *Passalus (Pertinax) gravelyi*: 2-3 HPA; 3-5 PSL, 0-1 MSD; 2 MSL; 1 MTD; 2 MTL; 1 TM; 1 TL 1 AV9; 16-18 AR. The larvae of *Passalus gravelyi* has the general setal ‘*Pertinax*’ pattern (Schuster & Reyes-Castillo, 1981) and differ from others of *Pertinax* subgenus larvae by the high number of setae in the anal ring (16-18 AR). *Passalus (Pertinax) affinis* Percheron, 1835, *P. (Pertinax) anguliferus* Percheron, 1835, *P. (Pertinax) mancus* Burmeister, 1847, *P. (Pertinax) latifrons* Percheron, 1841, and also *P. (Pertinax) dubitans* Kuwert, 1891 present the typical anal ring with 10 setae (10AR). While, *P. (Pertinax) convexus* Dalman, 1817 reveal variation between 10-12 AR.

The descriptions of Passalidae larvae were based on ornamentalizations or setae for chaetotaxy analysis (see Costa & Fonseca, 1986; Costa et al., 1988; Schuster & Reyes-Castillo, 1981, 1990; Schuster, 1992). Nevertheless, in all previous descriptions of Passalidae larvae, the authors did not report the presence of a *terminal ampulla* (sensu Snodgrass, 1941; Matsuda, 1976). The *terminal ampulla* structure was originally described on Lepidoptera larva by Herold (1815), it was described in Hymenoptera by Snodgrass (1941), and in Coleoptera: Scarabaeidae larvae by Hurpin (1953) and it was reported at three instars larvae of *Canthon c. cyanellus* LeConte by Martínez and Lumaret (2003, 2005); it was cited from

immature stages of six species of *Sphaenognathus* (Lucanidae) by Onore (1994).

The reports to larval species of the families assemblage in Scarabaeoidea published by Menees (1957), cited the Passalidae *Popilius disjunctus* (Illiger) transferred to *Odontotae-nius* by Reyes-Castillo (1970), and by Martínez and Lumaret (2003, 2005), that mentioned 26 species from Scarabaeidae, Aphodiidae, Trogidae, Orphnidae, Dynastidae, and two species of Passalidae: *Passalus unicornis* Saint-Fargeau (a species from Lesser Antilles endemic to Guadeloupe) and *P. alticola* Kirsch (a species described from Ecuador), which have not been described.

The occurrence of the sexual dimorphism in passalid larvae was characterized in detail for the first time based in the structure of this *terminal ampulla*. This structure was localized on the margin of the 9th sternite in male larvae, in species of the supra-generic taxa of Passalidae: all subfamilies and tribes, except the Leptaulacini, sensu Boucher (2006). In this study, we were unable to detect the *terminal ampulla* in first instar passalid larvae, but in second and third instar male larvae, and pupae (only clearly evaginated aedeagus in males), the sex of immatures was determined for species of subfamilies Aulacocyclinae and Passalinae. Data from this study included the largest world range of information to Passalidae, comprising 62 passalid species, 29 genera in six tribes –Aulacocyclini, two species from Brunei & Australia, and Ceracupini, two species from Japan & Taiwan; Solenocyclini, two species from Ivory Coast; Macrolinini, one species from Brunei; Passalini, 19 species from Mexico, Guatemala, Colombia, Ecuador, Jamaica, Guadeloupe Lesser Antilles & Brazil; and Proculini, 36 species from United States of America, Mexico, Guatemala, Colombia & Brazil–. Obviously is easier to determine the sexual dimorphism in larvae than in adults, for which the recent studies pointed specific areas of the adult pubescent body (e. g., species of *Paxillus*, see Mattos & Mermudes, 2013). Finally, the testicle, deferent ducts and other structures observed in Scarabaeidae by



Martínez and Lumaret (2005), were not seen in Passalidae species, possibly because sexual maturation occurs later, which can be further investigated.

## ACKNOWLEDGMENTS

We would like to thank Imelda Martínez from Instituto de Ecología (INECOL, México) for help with literature and techniques of dissection and pigmentation, and also to Tiburcio Laez Aponte for help with the Scanning electron Microscope photographs. We are grateful to people who made material available, and Alan Gillogly (Orma J. Smith Museum of Natural History) for the revision of the English and anonymous reviewers for comments. This study was supported by FAPERJ (process, 100.927/2011, 100.030/2014) and partially by the project 169604 from the Consejo Nacional de Ciencia y Tecnología (CONACYT, México).

## RESUMEN

**Estructura larval de *Passalus gravelyi* y dimorfismo sexual en larvas de Passalidae.** Passalidae son insectos subsociales, los adultos y larvas son comunes en bosques tropicales, viven dentro de troncos podridos en un sistema de galerías construido por los adultos. A la fecha, pocos estudios han sido publicados sobre larvas de Passalidae neotropicales. En el presente trabajo, se describe por primera vez la larva de *Passalus (Pertinax) gravelyi* Moreira, 1922, con base en 10 especímenes: uno de primer estadio, cuatro de segundo estadio y cinco de tercer estadio, asociados con tres adultos de un grupo familiar recolectado en el Parque Nacional de Itatiaia (Río de Janeiro, Brasil). La descripción esta fundamentada en microfotografías electrónicas y digitales de los caracteres diagnósticos que muestran detalles sobre la sistemática de la especie. La larva de *Passalus gravelyi* muestra el patrón setal general de 'Pertinax' y difiere de otras larvas del subgénero *Pertinax* por tener el anillo anal con 16 a 18 setas, las seis especies de larvas descritas del Brasil tienen en el anillo anal con 10 a 12 setas. Por primera vez se discute la presencia de dimorfismo sexual en larvas de 62 especies de Passalidae, describiendo el *ampulla terminal* presente en el macho y localizada en el área cuticular media ventral del noveno esternito abdominal. El *ampulla terminal* es visible ventralmente solo en la larva macho y no es visible en la larva hembra; esta estructura cuticular es común en el macho sobre el noveno esternito abdominal del segundo y tercer estadio larval y no está presente en la larva de primer

estadio. El *ampulla terminal* es conocida en 62 especies agrupadas taxonómicamente en la subfamilia oriental y australiana Aulacocylinae (Aulacocylini & Ceracupini) y en la subfamilia cosmotropical Passalinae (Solenocyclini, Macrolinini, Passalini, & Proculini).

**Palabras clave:** inmaduro, morfología, dimorfismo sexual, Neotropical, Passalinae, Passalini.

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