

# Current advances in Scarabaeoidea research

*Edited by*

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# Does your preservative preserve? A comparison of the efficacy of some pitfall trap solutions in preserving the internal reproductive organs of dung beetles

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## Abstract

Eight pitfall trap preservatives, brine, saturated borax solution, propylene glycol (33%, 50%, 75%), white vinegar, 100% ethylene glycol, FAACC (Formaldehyde 4%, Acetic acid 5%, Calcium chloride 1.3%), 4% phosphate buffered formaldehyde and 96% ethanol, were compared for their ability to preserve the internal reproductive organs of the dung beetle *Liatongus militaris* (Laporte) (Scarabaeidae: Scarabaeinae) for up to 28 days in the field. Relative evaporation rates of the preservatives in riparian vine thicket and low open woodland environments were also compared. 96% ethanol, FAACC and 4% phosphate buffered formaldehyde were the only solutions found to preserve all of the internal reproductive organs. Evaporation rates were lower in the vine thicket and some preservatives such as ethanol completely evaporated within seven days. 4% phosphate buffered formaldehyde is recommended as a preservative for pitfall traps left in the field for periods longer than one week. Possible ways to prevent trap interference by mammals and risks to the environment due to overspill are also discussed.

## Keywords

Pitfall traps, preservative, killing agent, dung beetles, reproductive organs, ovary, oocytes, formaldehyde, ethylene glycol, propylene glycol, mammal exclusion, evaporation

## Introduction

Pitfall traps have long been recognised as an effective and inexpensive technique for sampling arthropods, including Coleoptera (Greenlade and Greenlade 1971; Gist and Crossley 1973; Luff 1975; Newton and Peck 1975; Topping and Sunderland 1992; Weeks and McIntyre 1997). The efficiency of pitfall traps may be influenced by aspects of construction, such as shape, size and materials (Luff 1975; Brennan et al. 1999); spacing and transect design (Luff 1975; Ward et al. 2001; Perner and Schueler 2004; Larsen and Forsyth 2005); and the use of various baits, killing agents, and preservatives (Luff 1968; Greenlade and Greenlade 1971; Weeks and McIntyre 1997; Pekar 2002). Although various killing agents and preservatives are commonly used in pitfall traps, there is a lack of studies testing the efficacy of preservative type in preventing the decomposition of collected samples. This gap in the literature is particularly evident in regards to the deterioration of insects' internal organs (Sasakawa 2007). The examination of internal organs and, in particular, reproductive organs can provide useful ecological information such as the reproductive seasonality and physiological age of insects (Tyndale-Biscoe 1978, 1984; Stork and Paarmann 1992; Tyndale-Biscoe and Walker 1992). The time during which preservatives remain effective is also a largely unknown component of this trapping technique. A probable reason that this duration had not been investigated is that most researchers either service their pitfall traps within a few days of setting or baiting or do not require internal organs of specimens to be preserved.

However, short-term trap servicing is not always feasible and this is especially true for broad scale studies that require trapping to be conducted at many locations or in situations where trapping sites are difficult to access. This results in traps containing captured insects being left *in situ* in preservative for prolonged periods (e.g. up to one month), and presents a serious problem for the study of the internal organs of insects, especially with preservatives prone to evaporation. This makes the choice of a suitable preservative critical. For these reasons, the ideal preservative must: 1) adequately preserve the target organism and its internal organs, and 2) not completely evaporate between consecutive servicing intervals. The aim of this study was to identify a preservative suitable for use in long-term field studies that maintains the internal organs of insects and arthropods for periods of up to one month.

## Methods

**Specimens and location.** This experiment was performed on *Liatongus militaris* (Laporte), an African species of dung beetle introduced to Australia. Individuals were hand collected on 30<sup>th</sup> October 2006 from dung within a cow paddock behind the James Cook University campus grounds in Townsville, tropical north Queensland, Australia (19°19' S, 146°45'E). This species was chosen because specimens were very abundant and easily obtained.

**Preservatives.** A total of eight preservatives were tested for their efficacy in preserving the internal organs of *L. militaris*. These preservatives were chosen based on their previous use or recommendation as pitfall trap solutions (see Hall 1991; Weeks and McIntyre 1997; Pekar 2002; Perner and Schueler 2004; Norden et al. 2005; Schmidt et al. 2006; Jud and Schmidt-Entling 2008). Water is also commonly used as a killing agent in pitfall traps but due to its obvious lack of preservative properties it was not tested. The eight preservatives were:

1. Saturated salt solution – NaCl dissolved in hot water until the saturation point was reached (hereafter referred to as brine).
2. Saturated borax solution – Harper’s Powdered Borax dissolved in hot water until the saturation point was reached.
3. White vinegar
4. Propylene glycol (33%, 50%, 75%)
5. Ethylene glycol (100%)
6. Ethanol (96%)
7. FAACC (Formaldehyde 4%, Acetic acid 5%, Calcium chloride 1.3%)
8. 4% phosphate buffered formaldehyde (hereafter referred to as 4% PBF)

Forty dung beetles were immediately killed in the field by submersion in each of the eight preservatives, and in the case of propylene glycol in each of the three different concentrations. The dead beetles and 400 ml of preservative were placed into round plastic take away containers (11 cm diameter, 800 ml capacity). These containers were placed in the ground approximately 5 m apart in a riparian vine thicket forest type within the James Cook University campus grounds. Due to the high evaporation rate of 96% ethanol specimens were kept in this preservative within sealed vials in the laboratory. Gardening mesh (3 mm × 3mm gap size) was tied around the opening of the container to prevent other dung beetles, especially *L. militaris*, from entering the preservative at a later date. A plastic roof was placed above the trap to prevent rainfall from diluting the preservative. This ensured that the dung beetles and the preservatives would experience similar environmental conditions to that of a pitfall trap in the field.

**Dissections.** After one week submerged in the preservatives, ten dung beetles from each preservative were removed and dissected. Since it is common practise to store pitfall catches in ethanol once they have been cleared from the field (regardless of the type of preservative actually used in the pitfall trap) some individuals from propylene glycol, FAACC and 4% PBF were also transferred to 96% ethanol one day before they were dissected in order to test if later transference to ethanol alters the final preservation of specimens. All dung beetles were dissected under water in a wax-lined Petri dish with the visual aid of a stereo microscope. During dissection, preservation of internal organs was noted. The internal organs / structures that were used to test the preservation strength of the preservatives were selected based on their previous use in

physiological age grading studies (Tyndale-Biscoe 1978, 1984). These included the: germarium, ovariole wall, small oocytes, large oocytes, calyx, male follicles / testes, vas deferens, accessory glands, fat bodies and the gut. Internal organ condition was assessed qualitatively. As a result all comparisons were based on observations rather than measurements.

**Preservation categories.** An overall preservation category was assigned to each preservative. The preservation categories depended on how well a preservative preserved the internal organs of individuals when compared to freshly killed individuals. Preservation of the female ovary was regarded as more important, since most of the characteristics used to identify the various physiological stages of dung beetles are derived from the female ovary. Nonetheless, preservation of other organs including the male reproductive system, fat bodies and gut was also taken into consideration. The four preservation categories were poor, moderate, good and very good and are defined as follows:

Poor – Female reproductive organs not preserved or highly degraded. Size and shape of oocytes cannot be determined. Ovariole base and calyx degraded thus not allowing presence of yellow body (corpus luteum) to be detected. Male reproductive organs may still be detectable but size, shape and colour distorted. Gut lining not preserved leading to the release of gut contents into the abdominal cavity. Head, thorax and abdomen easily detach.

Moderate – Female reproductive organs partially preserved. Oocytes may be preserved but their size, shape and colour cannot be determined. Ovariole base and calyx degraded thus not allowing presence of yellow body to be detected. Male reproductive organs partially preserved but size, shape and colour distorted. Male and female reproductive organs cannot be manipulated without causing irreversible damage. Gut lining not preserved leading to the release of gut contents into the abdominal cavity. Head, thorax and abdomen easily detach.

Good – Female reproductive organs sufficiently preserved. Oocytes retain size, shape and colour. Ovariole base and calyx adequately preserved thus allowing presence of yellow body to be detected. Male reproductive organs preserved retaining their size, shape and colour. Male and female reproductive organs cannot be manipulated without causing irreversible damage. Gut lining preserved retaining gut contents. Head, thorax and abdomen do not easily detach.

Very good – Female reproductive organs ideally preserved. Oocytes retain size, shape and colour. Ovariole base and calyx adequately preserved thus allowing presence of yellow body to be detected. Male reproductive organs preserved retaining their size, shape and colour. Male and female reproductive organs can be freely manipulated without causing irreversible damage. Gut lining preserved retaining gut contents. Head, thorax and abdomen do not easily detach.

If the category was poor or moderate after the first seven days then no more individuals were dissected from that specific preservative since further submergence would have not increased the preservation quality of the specimens. If the category was good

or very good then the remaining specimens were left in the preservative and ten more individuals were dissected after seven more days. This continued up until 28 days.

**Evaporation rates.** Four pitfall traps containing 400 ml of each of the above preservatives/propylene glycol concentrations and water (control) were placed in the ground approximately 5 m apart in both low open woodland and riparian vine thicket forest types within the James Cook University campus grounds during a spring period (7<sup>th</sup> September until 10<sup>th</sup> October 2007). The two forest types provided different levels of shading at the ground surface (hence different environmental conditions) allowing evaporation rates of the preservatives to be compared in response to contrasting habitat conditions. Since the low open woodland forest had an open canopy pitfall traps placed here experienced mostly sunny and dry conditions. The closed canopy riparian forest was maintained by the university gardeners by daily misting of the area. Pitfall traps placed here experienced mostly shady and humid conditions. A plastic roof placed above the containers prevented any rainwater or artificial spray from entering the traps. The volume of each preservative was re-measured every seven days. This was repeated until either the preservatives had completely evaporated or until 28 days had passed. A critical preservative volume of 100 ml was used, since below this volume specimens would not be fully submerged limiting their preservation. Note that the critical volume chosen was based on the dimensions of the pitfall trap containers used in this experiment and will thus change if different containers are used.

## **Results**

Observations made during dissections are stated below under appropriate subheadings for each preservative. The relevant internal structures from freshly killed and dissected individuals are described first, followed by individual summaries of preservation success associated with each of the preservatives examined. The preservation category and the total number of days that the specimens were submerged are mentioned in brackets next to each preservative.

### **Freshly killed specimens**

After removing the abdominal tergites the gut was exposed. A network of white trachea was readily visible along with elongated fat bodies which were either opaque white or yellow in colour. The entire gut could be carefully uncoiled and removed in one mass.

In females this exposed a single telotrophic ovary on the left side of the abdomen, as expected in the Scarabaeinae (Tyndale-Biscoe and Watson 1977). The ovary was made up of a number of oocytes, opaque white to yellowish orange in colour, in sequential stages of development. The oocytes were contained within a thin transparent ovariole wall. The largest most developed basal oocyte joined to the calyx and then

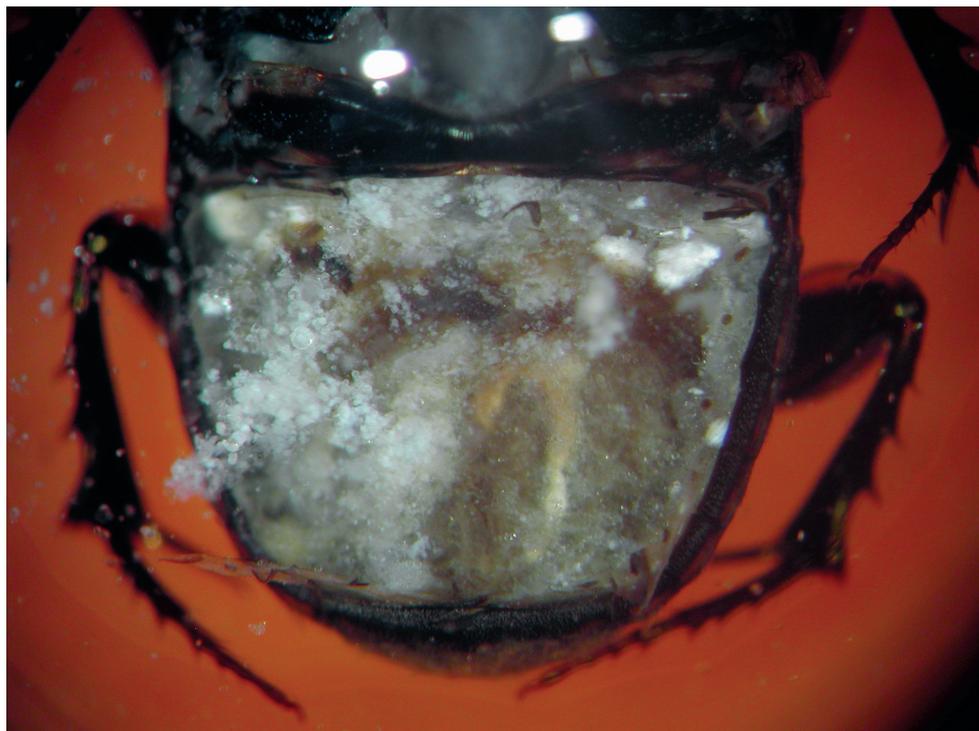
to the oviduct. The yellow body or corpus luteum forms on the base of the terminal oocyte and the calyx once egg laying commences (Tyndale-Biscoe 1978). A yellow body was not observed, possibly due to the individuals being nulliparous i.e. not laid eggs yet. Nonetheless, the ovariole base and calyx were clearly visible, thus allowing the detection of a yellow body to be made if it was present. The tip of the ovary consisted of the germarium which was slightly coiled and opaque white in colour.

In males the aedeagus along with the follicles were found lying on the inner bottom centre of the abdomen. The testicular follicles were round and opaque white in colour. The vas deferens was thick and opaque white in colour but was brighter than the follicles. The accessory glands were thin, elongate tubular in shape and opaque white in colour.

**Brine (Poor – after seven days of submergence)** (Figure 1). All the internal organs were dissolved and unpreserved. The gut was liquefied and the fat bodies were reduced to small white globules which sometimes formed large white coagulations. These white coagulations were not oocyte remnants as they were found in both male and female specimens. In females the ovary could not be detected. The male testes were partially preserved. They changed to a brown colour and became partially transparent revealing the seminiferous tubules, which had an opal like appearance. The follicles became supple and easily flaked apart. The vas deferens and accessory glands retained their original shape and size but changed to a dark brown and translucent colour respectively. The muscles and membranes connecting the thorax to the abdomen were also deteriorated since the two easily separated when the beetles were pinned for dissection. Due to the inadequate preservation of specimens in brine after the first seven days, no more individuals were dissected after this period, as further submergence would have not increased preservation success.

**Saturated Borax solution (Poor – after seven days of submergence).** Identical to brine.

**Propylene glycol 33%, 50%, 75% (Moderate – after seven days of submergence).** Since no difference in preservation between the three concentrations of propylene glycol could be found, they are summarised here under the same category. The gut was soft and spongy and was easily cut apart. Fat bodies were reduced to white grains or escaped as oil droplets once the abdominal tergites were removed. The ovariole wall, germarium and small oocytes were not preserved and only the larger oocytes were partially preserved. These oocytes were distorted in shape and flaked apart easily when handled. The ovariole base of the terminal oocyte and calyx could not be determined in order to check for an accumulation of yellow body. The male follicles were brown and partially transparent, revealing the seminiferous tubules, which had an opal like colour. The vas deferens and accessory glands retained their shape and colour but were easily distorted when handled. The thorax easily detached from the abdomen when individuals were pinned. Due to the inadequate preservation of specimens in the



**Figure 1.** *L. militaris* (female) after seven days of submersion in brine showing the unpreserved internal organs.

three different concentrations of propylene glycol after the first seven days, no more individuals were dissected after this period, as further submersion would have not increased preservation success.

There was no notable difference in preservation between specimens kept in propylene glycol or transferred to 96% ethanol the day before they were dissected.

**Ethylene glycol (Moderate – after seven days of submersion).** The gut was partially deteriorated and the abdomen was filled with a brown liquid. The fat bodies were reduced in size and turned a light brown colour. The ovariole wall and germarium were not preserved and only the larger oocytes were partially preserved. In some individuals, but not all, these retained their shape. In both instances they were easily damaged and flaked apart once handled. The terminal oocyte was not connected to the calyx and oviduct so a yellow body category could not be determined. The male follicles were partially preserved. Only a few remained and these were a brown transparent colour and they were very supple. The vas deferens and accessory glands were only partially preserved. The thorax easily detached from the abdomen when individuals were pinned. Due to the inadequate preservation of specimens in ethylene glycol after the first seven days, no more individuals were dissected after this period, as further submersion would have not increased preservation success.

**White vinegar (Moderate – after seven days of submergence).** The gut was not preserved. The abdomen was filled with small white particles of deteriorated matter, possibly fat bodies. The ovariole wall and germarium were not preserved. The larger oocytes were partially preserved but did not retain their original shape and colour. They were easily damaged once handled and were not connected to the calyx and oviduct so a yellow body could not be determined. The male follicles, vas deferens and accessory glands retained their shape and colour but were easily distorted once handled. Due to the inadequate preservation of specimens in white vinegar after the first seven days, no more individuals were dissected after this period, as further submergence would have not increased preservation success.

**FAACC (Good – after seven and up to 28 days of submergence).** The gut, fat bodies and ovary were preserved retaining their original shape and colour. All the organs were fixed onto each other making it difficult to remove the gut and fat bodies that surrounded the ovary without breaking the oocytes. The ovariole wall was not preserved and the oocytes were only held in position because they were fixed to each other. The male follicles, vas deferens and accessory glands were preserved retaining their original shape and colour but they too were easily broken or snapped apart. No major difference to the above was observed after 28 days of submergence in FAACC.

There was no notable difference in preservation between specimens kept in FAACC or transferred to 96% ethanol the day before they were dissected.

**4% PBF (Very good - after seven and up to 28 days of submergence)** (Figure 2). The gut, fat bodies and reproductive organs were properly preserved and retained their original shape and colour. These structures could still be moved apart and had not fused together. The entire ovary was preserved with the germarium and all of the developing oocytes still intact within the thin ovariole wall. The terminal oocyte was still attached to the calyx and oviduct and so the area could be inspected for the presence of a yellow body. The ovary was also very rigid and could be moved around without the fear of breaking apart. Male follicles were no exception and they too were highly preserved along with the vas deferens and accessory glands. No major difference to the above was observed after 28 days of submergence.

There was no notable difference in preservation between specimens kept in 4% PBF or transferred to 96% ethanol the day before they were dissected.

**96% Ethanol (Very Good – after seven and up to 28 days of submergence).** Identical to 4% PBF

### **Evaporation rates**

Since the preservative volumes were measured every seven days and not daily the evaporation rates are based on a linear rate of evaporation with time, therefore the predicted days to critical volume should be regarded as approximations. All of the

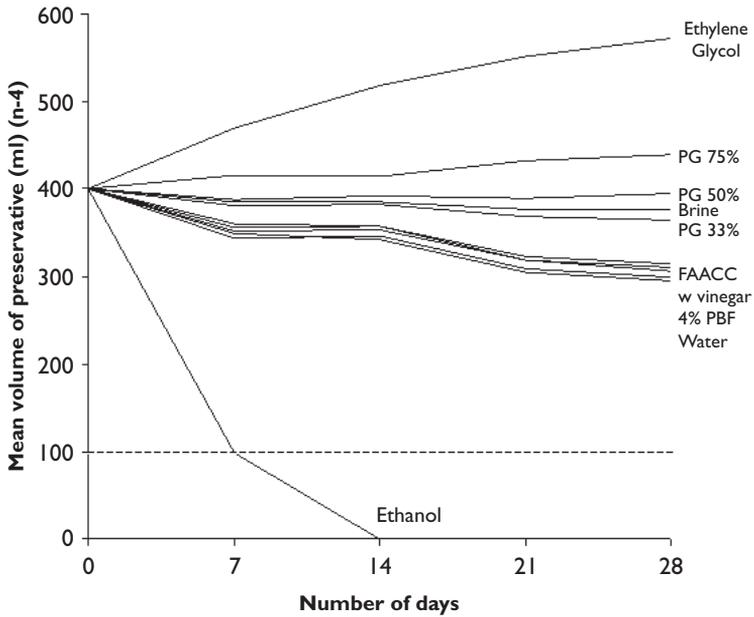


**Figure 2.** *L. militaris* (female) after 28 days of submersion in 4% PBF showing the well preserved ovary and oocytes.

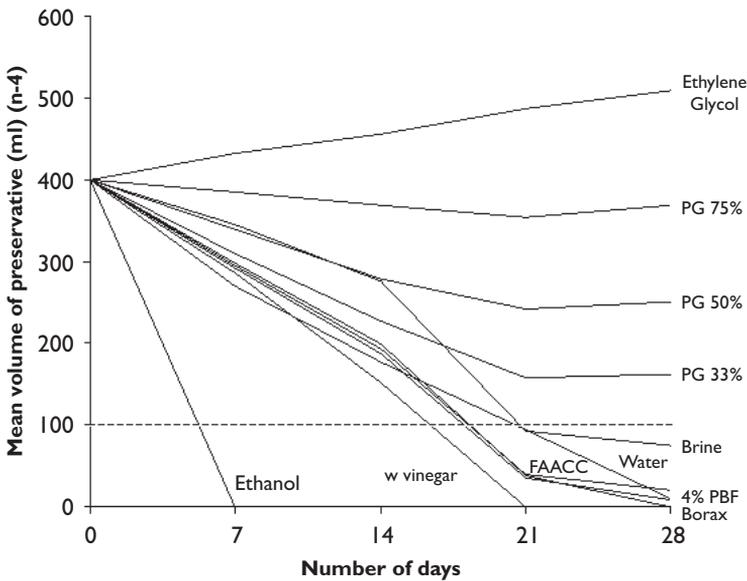
preservatives evaporated at a slower rate within the shady and humid riparian vine thicket (Figure 3) in comparison to the sunny and dry, low open woodland (Figure 4). All of the preservatives in the vine thicket, except ethanol, remained above the critical volume after 28 days (Figure 3). However, in the open woodland FAACC, 4% PBF and the saturated Borax solution reached the critical volume in 18 days and brine in 21 days (Figure 4). Ethanol evaporated most readily out of all the preservatives, reaching critical volume within seven days in the vine thicket (Figure 3) and within the first five days in the open woodland (Figure 4). The hygroscopic property of ethylene glycol resulted in an increase in volume throughout the duration of the experiment at both sites (Figures 3 & 4). Propylene glycol was also observed to display hygroscopic activity especially at higher concentrations (Figure 3) or when the majority of water had evaporated from the lower concentrations (Figure 4).

## Discussion

Only 4% PBF, 96% ethanol and FAACC adequately preserved all the dung beetle internal reproductive organs after 28 days of submersion (Table 1). Since 96% ethanol



**Figure 3.** Evaporation rates of the eight preservatives in the riparian vine thicket environment. Water is also shown for comparison. The dotted line represents the critical volume. PG = propylene glycol, w vinegar = white vinegar.



**Figure 4.** Evaporation rates of the eight preservatives in the low open woodland environment. Water is also shown for comparison. The dotted line represents the critical volume. PG = propylene glycol, w vinegar = white vinegar.

evaporates within a week in the field, and FAACC fused most of the internal organs together, 4% PBF is recommended as a suitable pitfall trap preservative for arthropod samples likely to remain in situ in the field for periods greater than one week and up to one month. Specimens remaining in 4% PBF for 54 days in the field have been dissected and found with well preserved reproductive organs (pers. obs). Since identical preservation occurred between beetles kept in 4% PBF or transferred to 96% ethanol, specimens can be removed from 4% PBF and stored in 96% ethanol until their subsequent dissection.

FAACC and formaldehyde are commonly used as gonad and cell fixatives, so it is unsurprising that they would preserve the internal organs of arthropods; similar results were also obtained with 96% ethanol. The low internal preservation strength of propylene glycol should be highlighted as it is a commonly used and often recom-

**Table 1.** Relative preservation of the dung beetle internal organs/structures by different preservatives in comparison to freshly killed specimens. All preservatives were tested in pitfall traps placed in the field, except for 96% ethanol which was tested in sealed vials in the lab.

	Preservative							
	Brine	Saturated borax solution	Propylene glycol 33%, 50%, 75%	Ethylene glycol	White vinegar	FAACC	4% PBF	99 % Ethanol
No. days beetles sub-merged in preservative	7	7	7	7	7	28	28	28
<b>Internal organ/structure</b>								
Germarium	Not preserved	Not preserved	Not preserved	Not preserved	Not preserved	Good	Very good	Very good
Ovariole wall	Not preserved	Not preserved	Not preserved	Not preserved	Not preserved	Not preserved	Very good	Very good
Small oocytes	Not preserved	Not preserved	Not preserved	Not preserved	Not preserved	Good	Very good	Very good
Large oocytes	Not preserved	Not preserved	Poor	Moderate	Moderate	Good	Very good	Very good
Calyx	Not preserved	Not preserved	Not preserved	Not preserved	Not preserved	Good	Very good	Very good
Male follicles / testes	Moderate	Moderate	Moderate	Poor	Moderate	Good	Very good	Very good
Vas deferens	Moderate	Moderate	Moderate	Poor	Moderate	Good	Very good	Very good
Accessory glands	Poor	Poor	Moderate	Poor	Moderate	Good	Very good	Very good
Fat bodies	Poor	Poor	Poor	Moderate	Poor	Good	Very good	Very good
Gut	Not preserved	Not preserved	Moderate	Poor	Not preserved	Good	Very good	Very good
<b>Overall preservation category</b>	<b>Poor</b>	<b>Poor</b>	<b>Moderate</b>	<b>Moderate</b>	<b>Moderate</b>	<b>Good</b>	<b>Very good</b>	<b>Very good</b>

mended preservative for pitfall traps (Weeks and McIntyre 1997; Schmidt et al. 2006; Thomas 2008). The reduced preservation effect of brine and ethylene glycol was also reported for a study involving carabid beetles (Sasakawa 2007). Interestingly, Sasakawa (2007) was able to determine egg maturation, but not egg volume. The present study shows that this is not the case for dung beetles. These differences in egg preservation may be attributed to the differing egg maturing strategies/rates of the Carabidae and Scarabaeinae. Scarabaeinae dung beetles possess a single telotrophic ovary with one ovariole (Tyndale-Biscoe 1978). Eggs are matured sequentially and there can only be one mature egg possessing a chorion within the ovariole at any one time (Richards and Davies 1977). Thus, the remaining undeveloped (but developing) oocytes do not possess a chorion. On the other hand, Carabidae mature many eggs, which possess a chorion, that are stored in the oviducts (van Dijk and den Boer 1992). The chorion protects the egg against dehydration and physical damage (Hinton 1981). Thus, its presence may be responsible for the partial preservation of Carabid eggs in brine and ethylene glycol reported by Sasakawa (2007). This may also explain why the larger oocytes (more mature and likely to possess a chorion) of dung beetles submerged in ethylene glycol in this experiment were preserved in some individuals but not in others. Therefore, the lack of preservation of Scarabaeinae eggs by many pitfall trap solutions may be attributed to, but is not limited to, the late deposition of the protective chorion around the oocytes.

It should also be noted that most preservatives may act as either an attractant or repellent to certain species or groups of arthropods (Luff 1968; Greenslade and Greenslade 1971; Luff 1975; Weeks and McIntyre 1997; Pekar 2002; Schmidt et al. 2006). There does not seem to be any repulsive effect on dung beetles when using dung baited pitfall traps containing 4% PBF (pers. obs); it may be possible that the attractiveness of dung may mask or overpower any possible repulsive effects of formaldehyde and substantial numbers of dung beetles have been caught using this method (Aristophanous, unpublished data). However, since attractive or repulsive properties of formaldehyde on dung beetles were not tested for, in this or other studies, they remain unknown. Nonetheless, there are reported repellent effects of formaldehyde on Opiliones (Pekar 2002) and attractive effects on lycosid and theridiid spiders (Pekar 2002), carabid, staphylinid (Luff 1968; Pekar 2002), curculionid, and hydrophilid beetles (Luff 1968). In formaldehyde stored specimens, isolation of DNA is often difficult due to degradation and is thus not recommended for genetic studies (Gurdebeke and Maelfait 2002). Specialised techniques are required for the effective extraction of DNA and RNA sequences from formalin-fixed, paraffin embedded tissue (see Coombs et al. 1999).

The evaporation experiment revealed that the environment in which a pitfall trap is placed can affect the evaporation rate of the preservative (Figures 3, 4). Pitfall traps placed in an open woodland environment evaporated at a faster rate than the ones placed in the riparian vine thicket. 96% ethanol evaporated the fastest and should not be used for periods longer than a few days. Similar results were found by Schmidt et al. (2006) even when ethanol was mixed with glycerine or water i.e. lower con-

centrations of ethanol. Care should be taken if ethylene glycol is to be used, since its hygroscopic properties may lead to overspilling if it is left in the field for too long, alternatively lower concentrations may be used. Propylene glycol also showed hygroscopic properties at higher concentrations, thus a 50% concentration is recommended. FAACC and 4% PBF may be used for periods longer than four weeks in humid shady environments but in sunny drier environments their use will be limited to just below three weeks.

If long term trapping is to be undertaken with no desire to examine the internal organs then propylene glycol is recommended. Brine and borax solutions should not be used since within these preservatives crystallisation occurred on the exoskeleton of the dung beetle specimens. This will make identification of specimens difficult since many external features are hidden and any attempts in removing the crystals leads to the breaking of certain structures, especially the antennae and legs. Ethylene glycol should be avoided since it is toxic to wildlife (Hall 1991) and has similar preservative strength to propylene glycol (see Results and Table 1). Thus, propylene glycol is probably the easiest and safest to use since it is not toxic, is odourless and can remain in the field for prolonged periods. However, pitfall traps containing propylene glycol have been observed to be repeatedly disturbed by wild pigs and rats when placed in Australian rainforests (K. Staunton, pers. comm.) whereas pitfall traps containing 4% PBF in the same area were not disturbed (pers. obs.). Similarly, birds and mammals have been reported to consume ethylene glycol voluntarily even when water was available (Hall 1991). White vinegar is also a good candidate since it is cheap and easily obtainable. Norden et al. (2005) have successfully used rice vinegar to preserve mosquito ovaries, but only for short periods of time.

The results of this study emphasises the *a priori* need to determine the type and concentration of preservative that should be used. Clearly, this choice is dependent on the target species or group of species, their scientific use and storage (e.g. for dissection or genetics) and the habitat in which the pitfall traps will be placed.

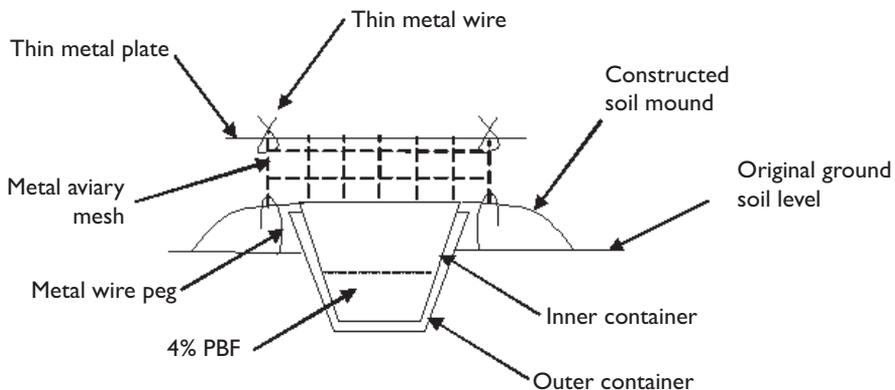
## **Safety issues**

Formaldehyde is classified as carcinogenic to humans (Group 1) by the International Agency for Research on Cancer (IARC 2006). However, a recent comprehensive review of cancer has concluded that there was no excess risk for a number of cancers in industry workers and professionals exposed to formaldehyde (Bosetti et al. 2008). Nonetheless, all concentrations of formaldehyde should be treated with care, and it is highly recommended that appropriate precautions be taken when handling formaldehyde or any other hazardous chemicals e.g. use of latex gloves. Regardless of some views against the use of formaldehyde the author agrees with Pekar (2002) in that the majority of preservatives are toxic, but their use is sometimes unavoidable.

## Protective caging and mound for pitfall traps

When placing pitfall traps containing formaldehyde in the field, two important factors should be taken into consideration: 1) mammals should be prevented from interfering with or gaining access to formaldehyde, and 2) formaldehyde should not leak or overspill the container into the surrounding soil.

To prevent mammal interference it is recommended that protective caging be placed around the trap (Newton and Peck 1975). This will also protect the pitfall containers from being chewed and destroyed by rats (a common problem in Australian rainforests). The easiest and most effective way to do this is to place a ring of aviary mesh wire (the mesh gaps should be big enough so as to allow the target organism to fit through) around the pitfall container. The ring of mesh wire is then pegged into the soil using pegs constructed from metal wire (similar to tent pegs). To protect the trap from precipitation a thin metal (zincal or aluminium) roof should be placed on-top of the mesh ring and attached in position by tying it with thin metal wire (Figure 5). To prevent water from entering the pitfall trap by surface runoff the containers should be placed 1/2 or 1/3 into the soil and a mound should be constructed around the containers (Figure 5). This will ensure that surface runoff will flow around the trap and not into it. Care must be taken to ensure that the lip of the container is flush with the soil. Two containers should be used so that the outer one will always remain in the soil and only the inner container removed when the trap is serviced. This makes clearing the trap easier and efficient as the soil is not disturbed every time the trap is visited.



**Figure 5.** Pitfall trap with protective caging and cover placed on-top of a manually constructed soil mound so as to prevent interference from mammals and dilution and/or overspilling from precipitation and surface runoff.

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# Chromosomal separation of difficult species of *Copris* Geoffroy, 1762 and *Onthophagus* Latreille, 1802 (Coleoptera, Scarabaeidae), with discussion of *O. massai* Baraud as a British Pleistocene fossil

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## Abstract

Karyotype analysis shows that *Copris hispanus cavolinii* Petagna should be regarded as a separate species from *C. hispanus* Linnaeus, and that *Onthophagus massai* Baraud is a valid species, not a synonym of *Onthophagus fracticornis* Preysslner. Chromosomal variation between populations of *O. fracticornis* is discussed, and Spanish material is shown to be the most distinct of the populations studied, but it is not considered that it should be placed as a separate species. Pleistocene fossil *O. massai* and Bronze Age *O. fracticornis* from England are discussed and illustrated. The distinctive elytral puncturation of *O. massai* is shown by the Pleistocene material, while Bronze Age *O. fracticornis* resembles modern material of that species.

## Keywords

*Copris hispanus*, *Copris hispanus cavolinii*, *Onthophagus fracticornis*, *Onthophagus massai*, chromosomes, karyotypes, Last (Eemian) Interglacial

## Introduction

A number of recent studies on Scarabaeoidea have demonstrated the usefulness of chromosomal analysis in establishing the limits of species which may be difficult to

distinguish from one another morphologically. For example Wilson (2001) showed that the common and widespread European dung beetle *Aphodius fimetarius* (Linnaeus, 1758) (Aphodiidae) in fact comprised two distinct species, *A. fimetarius* itself and *Aphodius pedellus* (DeGeer, 1774) with completely different karyotypes and with absolutely no evidence of hybridisation between them. Further work (Wilson and Angus, 2004) confirmed the initial separation and extended the database. More recently, Angus (2008) was able to show that *Onthophagus similis* (Scriba, 1790) and *Onthophagus opacicollis* Reitter, 1893 (Scarabaeidae) are completely separate species with no evidence of hybridisation between them, contrary to the suggestion of Martín-Piera and Boto (1999), who used allozyme analysis.

The work on *O. similis* and *O. opacicollis* also included *Onthophagus fracticornis* (Preyssler, 1790), whose chromosomes were clearly very distinct from those of the other two species, and this suggests that a detailed comparison of the chromosomes of *O. fracticornis* and *Onthophagus massai* Baraud, 1975, a Sicilian endemic morphologically very similar to *O. fracticornis* would be useful, especially as *O. massai* has been recorded as a fossil from the Last Interglacial (about 120,000 years ago) in England (Coope, 2001).

Work by Angus et al. (2007) showed that the chromosomes of *Copris hispanus hispanus* (Linnaeus, 1764) do not match the published account of those of *Copris hispanus cavolinii* (Petagna, 1792) (Salamanna, 1972), raising the possibility that these are in fact separate species, a view supported by small differences in the form of their male genitalia (e.g. Baraud, 1992). Salamanna's work was done using squash preparations from testis, and his figures do not enable karyotypes to be assembled, so that fresh work is necessary.

### *Chromosome features used and rationale behind their use*

The chromosome features used here, in addition to the total number of chromosomes present, are the size and shape of the chromosomes, expressed as Relative Chromosome Length (RCL: the length of each chromosome as a percentage of the total haploid autosome length in the nucleus) and Centromere Index (CI: the length of the short arm of a chromosome as a percentage of the total length of the chromosome), and the relative amounts and distribution of constitutive heterochromatin (repetitive DNA detected by C-banding). These features allow a high level of distinction between different karyotypes, but care is needed when considering the implication of these differences. Differences in chromosome number may result from the presence of variable numbers of B-chromosomes, e.g. *Pterostichus nigrita* (Paykull, 1790) and *Pterostichus rhaeticus* Heer, 1837 (Angus et al., 2000), or may reflect polyploidy often associated with parthenogenesis, as well as indicating differences between species. Fusion-fission polymorphisms involving different chromosomes are also known in Coleoptera, an example being *Ilybius montanus* Stephens, 1828 (Aradottir & Angus, 2004). The key to understanding these infraspecific differences is the occurrence of heterozygotes. Differ-

ences in CI may result from addition or deletion of heterochromatin, or pericentric inversions, and may occur as polymorphisms within species, e.g. autosome 5 of *Aphodius pedellus* (Wilson, 2001), and differences in RCL may reflect differences in the amount of constitutive heterochromatin present, as in the long and short X chromosome of *Helophorus grandis* Illiger, 1798 (Helophoridae) (Angus, 1989). A key feature of these infraspecific chromosomal variations is that they are likely to occur as heterozygotes, though only if the two arrangements occur sympatrically. Intraspecific variation in chromosome sizes, revealed by differences in the sequence of RCLs along a karyotype, unless reflecting differences in heterochromatic blocks, are likely to result from translocation of material between chromosomes. Such translocational differences may result in mispairings of chromosomes at first division of meiosis, and hence reduced fertility (or even sterility), and are thus prima facie evidence that different species are involved. Some caution is needed here: translocational differences will only be detectable if they result in noticeable alterations in a chromosome's size. There may be reciprocal translocations which would not be detected but which would nevertheless result in reduced fertility or sterility of hybrids. In this sense the results of chromosomal studies are unidirectional – demonstrable differences may indicate that different species are involved, but a lack of such differences does not prove conspecificity.

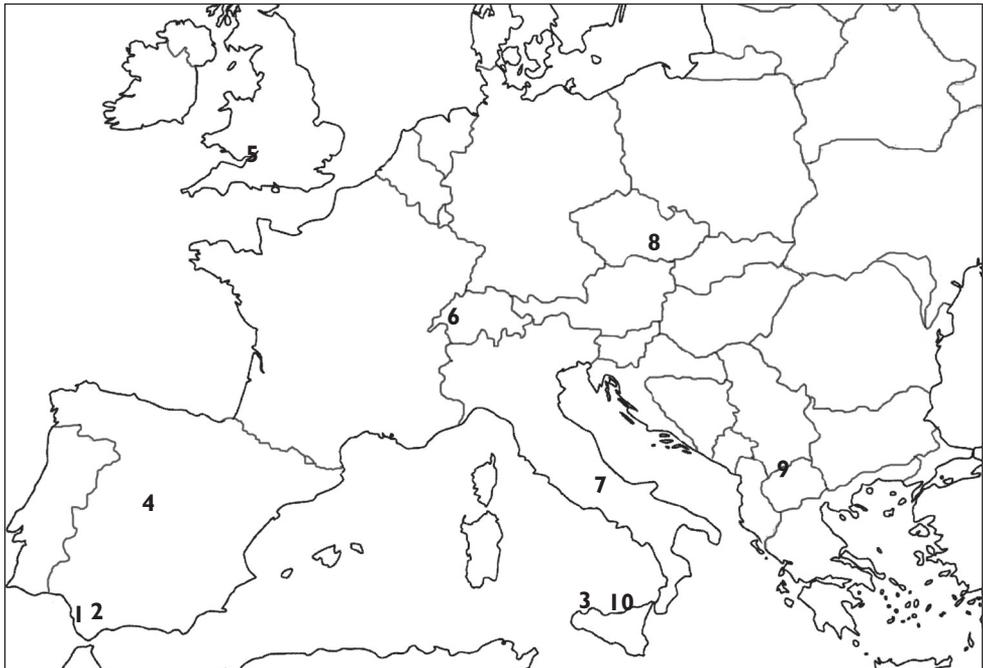
## Material and methods

Table 1 lists the material used in these analyses, with the localities of capture and the number of specimens analysed. This refers to the number of beetles from which distinctive chromosome spreads were used in the RCL and CI analyses. Additional material checked for distinctive chromosomes is given in parentheses. The localities are numbered, and their geographical locations are shown on the map in Fig. 1. Note that when two localities are fairly close together they have been given the same number.

Chromosome preparations are from mid-gut and testis of adult beetles, as described by Angus (1982) and Shaarawi and Angus (1991). Slides were stained in 1–2 % Giemsa, dried and photographed under oil immersion. Immersion oil was removed using xylene followed by absolute ethanol, and the 2-day old slides were C-banded using saturated barium hydroxide at room temperature (ca 22 °C). Treatment in barium hydroxide was for 3 minutes and was followed by washing in 3 changes of Sørensen at pH 6.8, and incubation in salt-sodium citrate (2 X SSC: 0.3 M sodium chloride and 0.03 M trisodium citrate) for 1 hour at 55 °C. The slides were then washed in a further 3 changes of Sørensen at room temperature, and stained in Giemsa as before. This enables the same nucleus to be studied both plain and C-banded, and has been done throughout this study. Photographs were printed at a magnification of 3000 X, and the chromosomes were cut out and arranged as karyotypes. At this stage they were scanned into a computer and further arrangement and measurement done using Adobe Photoshop. The use of the total

**Table 1.** Material used, localities, map numbers, numbers of specimens used for chromosome measurements, with additional checked material given in parentheses.

Species	Locality with No. on Map	Number of specimens analysed
<i>Copris hispanus hispanus</i> (L.)	Spain, Provincia de Cádiz, Facinas (No. 1)	3♂
	Spain, Provincia de Cádiz, San Roque (No. 2)	2♂
	Spain, Provincia de Cádiz, La Línea (No. 2)	(1♂)
	Spain, Provincia de Málaga, Parque de los Alcornocales, La Saucedá (No. 2)	2♂
<i>Copris hispanus cavolinii</i> (Pettagna)	Sicily, Provincia di Trapani, Segesta (No. 3)	2♂, (1♀)
	Sicily, Provincia di Trapani, Scopello (No. 3)	1♀
<i>Onthophagus fracticornis</i> (Preysslér)	Spain, Provincia de Madrid, Lozoya (No. 4)	4♂, 2♀
	England, Somerset, Compton Bishop (No. 5)	2♂, (1♀)
	Switzerland, Valais, Chandolin (No. 6)	1♂
	Italy, Abruzzo, Provincia di L'Aquila, Campo Imperatore (No. 7)	3♂
	Czech Republic, southern Moravia, Podyji National Park (No. 8)	2♀
	Macedonia, Šar Planina, (No. 9)	3♂, 1♀
	Macedonia, Mavrovo National Park (No. 9)	1♂
<i>Onthophagus massai</i> Baraud	Sicily, Provincia di Palermo, Parco delle Madonie, Piano Zucchi (No. 10)	2♂, 2♀
	Sicily, Provincia di Messina, Parco dei Nebrodi, Muto (No. 10)	3♂, 1♀

**Figure 1.** Map showing the collection sites of the material used in this paper. See Table 1 for explanation of the numbers, and note that neighbouring sites may share the same number.

haploid autosome length in RCL calculations follows the procedure used with human chromosomes (Paris Conference, 1971) and means that, although the X and Y chromosomes can have calculated RCL values, it is the RCL values of the autosomes that should add up to 100. The CI calculations, again following the Paris Conference, are the basis of morphological classification of the chromosomes. Based on Sumner (2003), these are: metacentric, CI 50–46; submetacentric, CI 46–26; subacrocentric, CI 25–15; and acrocentric (including telocentric), CI less than 15. The beetles from which the preparations were obtained were card-mounted and are in R. B. Angus' collection.

The fossil material was photographed using a Zeiss photomicroscope with oblique surface illumination from a standard bench light. The elytra were very crumpled and only small portions were in focus at any one time. However, the resolution was good and the resulting photographs are sufficient to show the diagnostic features.

## Results

### *Copris hispanus hispanus* and *C. h. cavolinii*

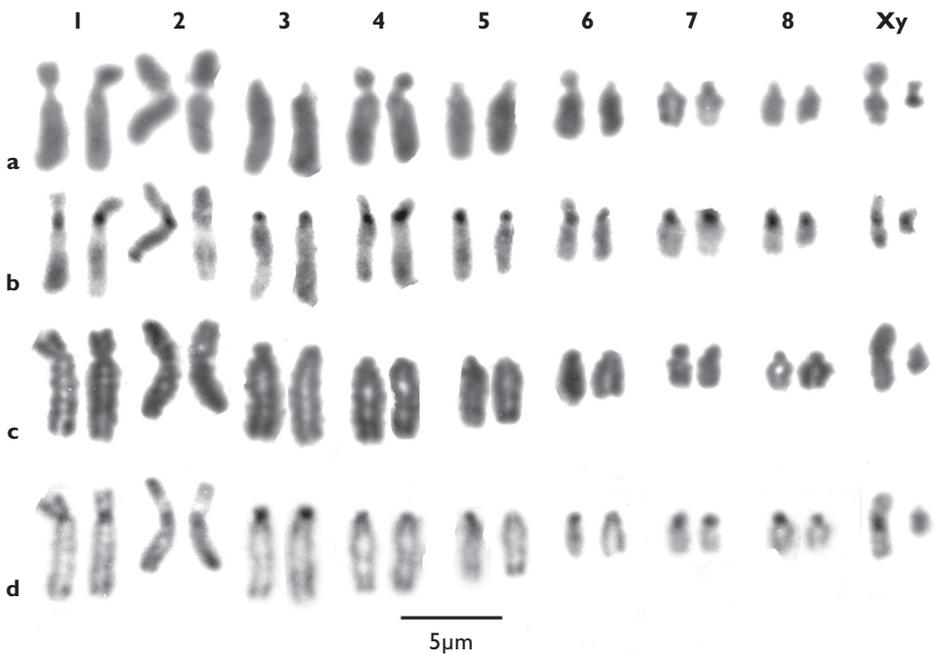
$$2n = 16 + Xy (\text{♂}), 16 + XX (\text{♀}).$$

Plain (Giemsa stained) and C-banded karyotypes are shown in Fig. 2, while RCL and CI data are shown in Table 2, where values showing differences between the two forms significant at the 95% level are indicated by yellow highlight. For practical reasons (difficulty of accurate measurement) CI values below 15 are listed as acrocentric, without further analysis. Points to note are the RCL differences in autosomes 3, 6 and 7, and the Y chromosome, and the CI differences in autosomes 4 and 7. Autosome 6 of *C. h. hispanus* appears to show a pericentric inversion in the specimen illustrated, but not in the other analysed material. In both forms the heterochromatic blocks are very small and confined to the centromere region, so differences in the RCLs of the chromosomes are almost certainly due to translocation.

### *Onthophagus fracticornis* and *O. massai*

$$2n + 18 + Xy (\text{♂}), 18 + XX (\text{♀}).$$

Plain and C-banded karyotypes are shown in Fig. 3, while RCL and CI data are shown in Tables 3 and 4. In the tables instances where the values for chromosomes from different populations of *O. fracticornis* differ at the 95% significance level are indicated by yellow highlight, while cases in which the chromosomes of *O. massai* differ from those of *O. fracticornis* are indicated by green highlight. Within *O. fracticornis* the most



**Figure 2.** Mitotic chromosomes of *Copris hispanus hispanus* (a, b) and *C. h. cavolinii* (c, d) arranged as karyotypes. a, c, plain, b, d, the same nuclei C-banded.

notable size differences are shown by autosomes 5 and 9 of Spanish material (Fig. 3a, b), and the y chromosome of the Italian material (Fig. 3k, l). The large Italian y chromosome is very striking in all preparations, resulting in no clear size difference between it and autosome 9. C-bands are heavy on all the autosomes and in some preparations small intercalated C-bands may be present, possibly sites of nucleolus organisers. The C-band of the y chromosome is clearly weaker than that of autosome 9. CI differences are shown by the y chromosome, with a fairly median (metacentric) centromere in Macedonian (Fig. 3 e–h) and Italian material (Fig. 3k, l) – and the single Swiss specimen (not shown here), and the subterminal (subacrocentric) centromere of Spanish and English material (Fig. 3a–d). In one Macedonian specimen (Fig. 3g, h) autosome 5 is heterozygous for a pericentric inversion, and this specimen also has one B-chromosome.

The chromosomes of *O. massai* (Fig. 3 m, n) show an extensive suite of RCL differences from those of *O. fracticornis* (Fig. 3a–l). Thus the RCL values for autosomes 1, 5, 8 and 9 are different at the 95% level. The y chromosome is as large as that of Italian *O. fracticornis*, but differs from it in having a subterminal centromere. There is also an extensive suite of CI differences, involving autosomes 1, 5 and 7–9, as well as the X chromosome. The subterminal centromere of the X chromosome is very distinctive.

**Table 2.** *Copris hispanus* and *C. h. cavolinii*, chromosome parameters. Mean, 95% confidence intervals by t-test, number of chromosomes analysed. Significant differences are indicated by gray background.

Chromosome	RCL		CI	
	<i>Copris hispanus hispanus</i>	<i>C. hispanus cavolinii</i>	<i>Copris hispanus hispanus</i>	<i>C. hispanus cavolinii</i>
1	18.54 18.14–18.93 N = 38	18.97 18.61–19.33 N = 44	submetacentric 29.01 27.47–30.56 N = 28	submetacentric 28.48 26.89–30.08 N = 36
2	16.81 16.44–17.17 N = 38	17.07 16.75–17.39 N = 44	submetacentric 40.60 38.43–42.77 N = 28	submetacentric 41.43 40.26–42.60 N = 36
3	15.20 14.75–15.65 N = 38	16.41 16.09–16.72 N = 42	acrocentric N = 28	acrocentric N = 36
4	14.79 14.43–15.14 N = 38	13.96 13.70–14.22 N = 44	subacrocentric 24.40 22.91–25.89 N = 28	acrocentric N = 36
5	12.09 11.71–12.48 N = 38	11.96 11.66–12.29 N = 44	acrocentric N = 28	acrocentric N = 36
6	9.50 9.15–9.87 N = 38	8.33 7.97–9.02 N = 44	acrocentric N = 28	acrocentric N = 36
7	6.69 6.42–6.95 N = 38	7.41 7.07–8.59 N = 44	acrocentric N = 28	subacrocentric 17.73 16.46–18.99 N = 36
8	6.29 6.05–6.52 N = 38	6.59 6.38–6.79 N = 44	subacrocentric 17.55 16.58–18.52 N = 28	subacrocentric 17.65 16.66–18.63 N = 36
X	10.07 9.69–10.46 N = 19	10.75 10.30–11.21 N = 26	submetacentric 44.24 40.16–48.32 N = 14	metacentric 48.04 46.23–49.85 N = 22
y	4.56 4.17–4.94 N = 19	5.59 5.26–5.92 N = 18	metacentric 46.74 44.05–49.44 N = 14	submetacentric 40.06 35.11–45.02 N = 14

## Discussion

### *Copris hispanus hispanus* and *C. h. cavolinii*

The RCL differences between the karyotypes of these two beetles, taken in combination with their very small heterochromatic regions, similar in size in the two taxa, suggest very strongly that the karyotypes differ as a result of translocation of material



**Figure 3.** Mitotic chromosomes of *Onthophagus fracticornis* (a–l) and *O. massai* (m, n), arranged as karyotypes. **a, c, e, g, i, k, m**, plain; **b, d, f, h, j, l, n**, the same nuclei C-banded. **a, b**, Spain; **c, d**, England; **e, f**, Macedonia, Šar Planina; **g, h**, Macedonia, Mavrovo National Park, with one B-chromosome and autosome 5 heterozygous for a pericentric inversion; **i, j**, Czech Republic; **k, l**, Italy; **m, n**, Sicily, Piano Zucchi.

**Table 3.** *Onthophagus fracticornis* and *O. massai*, Relative Chromosome Length. Mean, 95% confidence intervals by t-test, number of chromosomes analysed. Significant differences between populations of *O. fracticornis* are indicated by light gray background, and those between *O. fracticornis* and *O. massai* by dark gray background.

Chromosome	Spain	England	Macedonia	Czech Rep.	Italy	<i>O. massai</i>
1	16.06 15.54– 16.58 N = 16	15.96 15.41– 16.50 N = 16	16.05 15.59– 16.51 N = 26	15.72 15.28– 16.17 N = 18	14.98 14.40– 15.55 N = 16	14.93 14.60– 15.26 N = 28
2	14.13 13.86– 14.39 N = 16	13.95 13.58– 14.32 N = 16	14.26 13.84– 14.68 N = 26	13.54 13.07– 14.02 N = 18	14.14 13.68– 14.59 N = 16	13.70 13.46– 13.94 N = 28
3	12.88 12.48– 13.28 N = 16	13.16 12.79– 13.53 N = 16	13.20 12.86– 13.55 N = 26	12.64 12.17– 13.11 N = 18	13.24 12.89– 13.59 N = 16	12.66 12.35– 12.96 N = 28
4	11.49 11.07– 11.90 N = 16	11.95 11.53– 12.36 N = 16	12.48 12.17– 12.80 N = 26	11.88 11.42– 12.34 N = 18	11.75 11.35– 12.15 N = 16	11.54 11.24– 11.83 N = 28
5	10.98 10.64– 11.33 N = 16	12.76 12.38– 13.13 N = 16	12.12 11.73– 12.50 N = 26	12.29 11.79– 12.80 N = 18	11.66 11.50– 11.81 N = 16	10.86 10.62– 11.11 N = 28
6	10.47 10.10– 10.85 N = 16	9.89 9.56– 10.22 N = 16	10.44 10.18– 10.70 N = 26	10.15 9.54– 10.76 N = 18	10.18 9.72– 10.64 N = 16	9.99 9.74– 10.24 N = 28
7	8.77 8.45–9.09 N = 16	8.61 8.35–8.88 N = 16	8.73 8.40–9.06 N = 26	9.04 8.59–9.49 N = 18	9.44 9.12–9.76 N = 16	9.48 9.20–9.76 N = 28
8	7.81 7.61–8.02 N = 16	7.41 7.08–7.73 N = 16	7.78 7.41–8.16 N = 26	8.03 7.62–8.44 N = 18	7.73 7.43–8.03 N = 16	8.66 8.45–8.87 N = 28
9	7.39 7.09–7.68 N = 16	6.24 5.93–6.56 N = 16	6.68 6.40–6.95 N = 26	6.59 6.30–6.88 N = 18	6.86 6.54–7.18 N = 16	8.14 7.90–8.38 N = 28
X	13.89 13.16– 14.62 N = 8	15.03 13.33– 16.72 N = 8	14.42 12.57– 16.28 N = 13	14.86 14.23– 15.50 N = 18	14.10 13.06– 15.14 N = 8	14.48 13.09– 15.87 N = 21
y	4.86 4.40–5.31 N = 8	4.46 4.44–5.08 N = 8	5.12 4.61–5.62 N = 13		6.25 5.92–6.58 N = 8	6.40 4.67–8.13 N = 7

**Table 4.** *Onthophagus fracticornis* and *O. massai*, Centromere Index. Mean, 95% confidence intervals by t-test, number of chromosomes analysed. Significant differences between populations of *O. fracticornis* are indicated by light gray background, and those between *O. fracticornis* and *O. massai* by dark gray background.

Chromosome	Spain	England	Macedonia	Czech Rep.	Italy	<i>O. massai</i>
1	submetacentric 40.82 39.08–42.55 N = 16	submetacentric 41.03 39.55–42.51 N = 16	submetacentric 38.12 34.87–41.37 N = 26	submetacentric 39.11 37.13–41.08 N = 18	submetacentric 39.59 37.8–41.39 N = 16	submetacentric 44.27 43.08–45.47 N = 27
2	submetacentric 45.17 43.42–46.92 N = 16	submetacentric 45.36 43.56–47.15 N = 16	metacentric 46.50 44.90–48.11 N = 26	submetacentric 43.23 38.25–48.21 N = 18	submetacentric 44.42 42.5–46.34 N = 16	submetacentric 45.97 42.64–49.29 N = 28
3	submetacentric 44.76 42.71–46.83 N = 16	metacentric 46.09 44.42–47.77 N = 16	submetacentric 44.70 42.72–46.68 N = 26	metacentric 47.57 45.86–49.28 N = 18	metacentric 46.71 45.67–47.75 N = 16	metacentric 46.76 45.67–47.85 N = 28
4	metacentric 46.60 45.52–47.68 N = 16	submetacentric 45.99 44.37–47.61 N = 16	metacentric 48.76 47.53–49.99 N = 26	submetacentric 44.53 42.23–46.82 N = 18	submetacentric 44.08 41.34–46.81 N = 16	metacentric 47.40 45.53–49.27 N = 28
5	submetacentric 28.96 27.41–30.51 N = 16	submetacentric 31.41 29.93–32.88 N = 16	submetacentric 31.81 29.40–34.22 N = 26	submetacentric 32.07 29.89–34.24 N = 18	submetacentric 34.29 32.39–36.18 N = 16	metacentric 48.56 47.06–50.06 N = 28
6	metacentric 46.28 44.62–47.93 N = 16	submetacentric 43.93 40.80–47.05 N = 16	submetacentric 44.66 43.19–46.13 N = 26	submetacentric 45.37 43.15–47.58 N = 18	metacentric 46.31 44.16–48.46 N = 16	metacentric 48.16 46.70 – 49.63 N = 28
7	submetacentric 41.09 37.75–44.44 N = 16	submetacentric 41.21 39.63–43.61 N = 16	submetacentric 41.52 39.88–43.15 N = 26	submetacentric 43.64 42.19–45.10 N = 18	submetacentric 43.06 40.59–45.53 N = 16	metacentric 47.13 45.24–49.01 N = 28
8	submetacentric 40.08 38.03–42.13 N = 16	submetacentric 41.57 39.53–43.61 N = 16	submetacentric 40.50 38.94–42.06 N = 26	submetacentric 42.52 39.93–45.10 N = 18	submetacentric 42.23 40.46–43.99 N = 16	metacentric 46.94 45.30–48.57 N = 28
9	submetacentric 43.08 41.34–44.83 N = 16	submetacentric 44.55 43.25–45.85 N = 16	submetacentric 45.92 44.08–47.76 N = 26	metacentric 47.14 44.77–49.51 N = 18	submetacentric 42.45 40.21–44.70 N = 16	metacentric 49.88 48.31–51.44 N = 28
X	submetacentric 42.75 41.05–44.45 N = 8	submetacentric 44.24 40.80–47.68 N = 8	submetacentric 44.68 42.60–46.76 N = 12	submetacentric 43.46 41.78–45.14 N = 18	submetacentric 44.58 41.94–47.21 N = 8	submetacentric 35.40 33.51–37.28 N = 21
y	subacrocentric 25.92 21.68–30.17 N = 8	submetacentric 33.08 27.85–38.31 N = 8	submetacentric 43.09 39.82–46.36 N = 12		submetacentric 44.66 41.86–47.46 N = 8	subacrocentric 24.20 20.04–28.36 N = 7

between non-homologous chromosomes, and thus provide good evidence that they should be considered as separate species, *Copris hispanus* and *C. cavolinii*.

*Copris cavolinii* was described, as a species, by Petagna (1792) on the basis of material from the Naples area, but most subsequent works, including the Catalogue of Palaearctic Coleoptera (Löbl et al., 2006a) place it as a subspecies of *C. hispanus*.

The morphological and geographical characteristics of *C. hispanus* and *C. cavolinii* (which she regarded as a subspecies of *C. hispanus*) were discussed in depth by Rommel (1965). She figured details of the cephalic horns and pronotal carinae, but not the genitalia. She gave the distribution of *C. hispanus* as extending from southern France, Corsica and Sardinia, via the Iberian Peninsula to North Africa, where its range is shown as extending as far as Egypt. No local variation was noted. *C. cavolinii* was noted from Italy, the Balkans, Turkey, Israel, and extending eastwards through northern Iran to the former Middle Asian republics of the USSR. She distinguished three forms. The western form occurs in Italy and the former Yugoslavia, and Albania, the eastern form in Greece (including Crete), Turkey, Cyprus and Israel, and the northeastern form occurs in middle Asia. Dellacasa (1968) reviewed the morphological characteristics of *C. hispanus* and *C. cavolinii* and, although he left them as subspecies, pointed out that *C. cavolinii* was in fact very distinct.

As far as *C. cavolinii* is concerned, it is important to note that our data refer only to Italian (Sicilian) material, and therefore to Rommel's western form. In the case of *C. hispanus*, the situation at first appears more straightforward as no geographical variation was noted. However Ebied et al. (2000) record and figure a completely different karyotype, with 20 mainly metacentric chromosomes, from Egyptian *C. hispanus*. This is so different from those reported here that it cannot refer to *C. hispanus*, and means that, unless their material is misidentified, the species passing as *C. hispanus* in Egypt is something entirely different.

It would be useful to study material from a wider area. The *C. hispanus* localities lie at the apices of an equilateral triangle with 40 km sides, but at least Spanish material must be considered typical of *C. hispanus*. The two Sicilian localities are only about 16 km apart, but nevertheless the results from all the material are consistent so that there is no reason to doubt their validity. The main unanswered question is whether study of material from a wider area, especially of the different forms of *C. cavolinii*, would reveal the presence of other species. This question is given added weight by the differences between some of the populations of *O. fracticornis*, to be discussed next.

### *Onthophagus fracticornis* and *O. massai*

In the case of *O. fracticornis*, in contrast to those of the two *Copris* species, material from populations over a wide area of Europe has been studied. While, in terms of RCL at least, this has revealed a considerable level of stability, the Spanish material, in particular, shows some significant differences: autosome 5 (recognisable in all populations because of its low CI) is significantly smaller than in other populations,

while autosome 9 is significantly larger. One effect of this is that in some preparations autosome 5 actually appears shorter than autosome 6. The centromeric C-bands of Spanish material appear similar in size to those of other populations, so it is difficult not to believe that some interchromosomal translocation of material has taken place. It would therefore seem logical to suggest that there is a *prima facie* case for regarding the Spanish material as representing a separate species. However, we have detected no morphological difference between Spanish and other material, so that for the moment it seems prudent to leave it as *O. fracticornis*, but note the problem. At this stage it is interesting to note that Angus (2008) found that autosome 5 of Spanish *O. opacicollis* was significantly larger than that of Sardinian and Cyprus material. It may appear a curious coincidence that this same chromosome is involved in both cases, but there is a simple explanation: autosome 5 in all the species concerned has a distinctly lower CI than those of autosomes 4 and 6, so autosome 5 is clearly recognisable. This raises the question as to whether this autosome is homologous in all the species, and whether the observed differences in its length are the only ones involved. As mentioned in the introduction, only translocational differences resulting in obvious changes to the length of a chromosome can be detected – and one requirement for this is that the chromosome concerned is itself clearly identifiable. Altering the RCLs of metacentric autosomes occupying adjacent positions in a karyotype might simply reverse the order in which they were placed, without this being apparent.

Apart from the Spanish situation, the Italian material has a significantly larger y chromosome than those of other populations (only females were available from the Czech material, so we have no data on its y chromosome), meaning that, without C-banding, which shows the small heterochromatic block on the y, it could be difficult to distinguish from autosome 9. It is difficult to assess the significance of this larger y chromosome. The sex chromosomes of most Polyphaga pair via a cytoplasmic vesicle (the parachute or  $Xy_p$  association, cf. Smith and Virkki, 1978), and the small y chromosomes of these *Onthophagus* species suggest that they are likely to follow this pattern. This would mean that no impaired meiosis need be involved in hybrids, and we have no idea what, if any, extra genes the Italian y chromosome may be carrying.

When the CI data are considered, the only variation is found in the y chromosome, more or less metacentric in Macedonian and Italian material, as well as the single Swiss example, but subacrocentric in English and Spanish material. This is of no taxonomic significance as it would not affect the  $Xy_p$  pairing at meiosis. It is worth noting that the sequence of CI values along the karyotype of Spanish material does not differ from those of the other populations, suggesting that the amount of chromosomal difference between Spanish and other material is small.

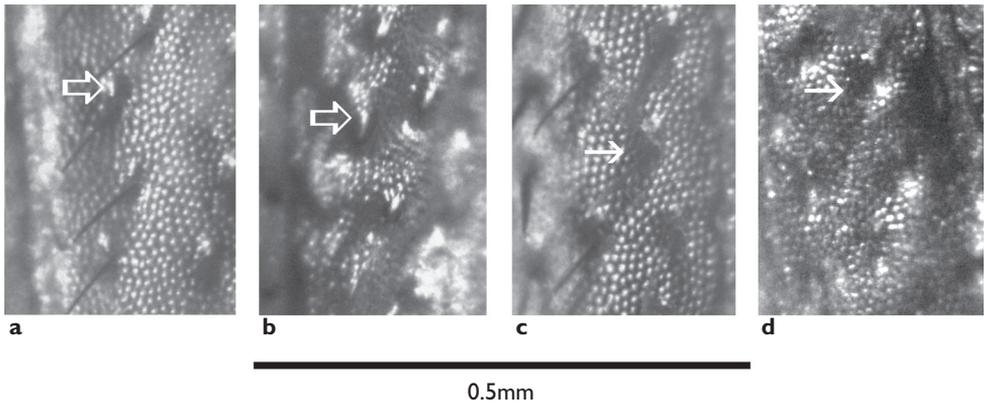
Comparison of the karyotypes of *O. fracticornis* and *O. massai* reveals a very different situation, with four of the nine pairs of autosomes of *O. massai* having significantly different RCLs from their apparent counterparts in *O. fracticornis*. When the CIs are compared, five pairs of autosomes appear different, as does the X chromosome. This degree of difference is clearly far more than that shown by populations of *O. fracticornis* and vindicates the placing *O. massai* as a separate species.

*Onthophagus massai* was described, as a distinct species, by Baraud (1975) on the basis of material from the Piano Battaglia in the mountains of the Parco delle Madonie in northern Sicily. We were unable to find it on the Piano Battaglia in early November 2008, but it was present on the Piano Zucchi slightly lower down the same mountains. The species status of *O. massai* was denied by Palestrini (1981), who placed it as a synonym of *O. fracticornis*. Baraud (1992) reasserted its species status and reviewed the morphological distinctions, especially as regards the sculpture of the elytral striae, between it and *O. fracticornis*. Subsequent authors (e.g. Carpaneto and Piatella (1995), Sparacio (1995), Pesarini (2004) and Lapiana and Sparacio (2006)) have followed Baraud's assessment, and this view is maintained in the Palaearctic Catalogue of Löbl et al. (2006b). Thus our chromosomal data are in agreement with the current taxonomic consensus.

### *Onthophagus massai* as a Pleistocene fossil in England

As mentioned in the introduction, *O. massai* has been recorded as a fossil from the Last (Eemian or Ipswichian) Interglacial in England. Coope (2001) reviewed its occurrences and showed that it occurs, sometimes abundantly, in deposits of that interglacial, but not in the immediately preceding one.

Validation of *O. massai* as a species separate from *O. fracticornis*, rather than as a local variant of it, means that there is no theoretical difficulty with its fossil distribution, since many species of beetle have altered their geographical ranges on a dramatic scale in response to the glacial/interglacial oscillations (Coope, 2001). Nevertheless the occurrence in Britain of what is now an endemic confined to a small region of northern Sicily is so unexpected that it requires special verification. It is therefore appropriate to consider the characters on which the identification was and is based. Russell Coope first encountered this species in material from Trafalgar Square (see Franks et al., 1958), where at least 49 individual specimens were represented. The material clearly belonged to the *O. fracticornis* group on details of the head and pronotum, and the strength of the basal portion of the cephalic horn of the males was too great for either *O. opacicollis* or *O. similis*. The specimens appeared consistently small and dark when compared with *O. fracticornis*, but did match a small series of *O. massai*. The fossil pronota had the punctures large, especially towards the basolateral edge, matching the *O. massai*, but not the *O. fracticornis* available for study, and the basal portion of the cephalic horns of the males seemed more like the *O. massai* than the *O. fracticornis*. Coope also felt that the puncturation of the elytral interstices was somehow coarser in the fossils and in *O. massai* than in *O. fracticornis*, but at the time he did not know that this elytral puncturation character was the one Baraud now uses (e.g. Baraud, 1992) to key out *O. massai*. Much of the Trafalgar Square fossil material is now in a parlous state having been dry-mounted on cards for many years, but in some cases the elytral puncturation is adequately preserved. It should at this stage be noted that in Pleistocene fossil material the lipid components of the cuticle are lost and the structure tends to collapse on drying. However, as well as the Trafalgar Square fossil material, we have been able to study



**Figure 4.** Elytral sculpture of *Onthophagus fracticornis* (a, b) and *O. massai* (c, d), to show the prominent presetal granules of the interstices in *O. fracticornis* (white-bordered black arrow) and the prominent perisetal punctures in *O. massai* (white arrow). a, modern, Šar Planina, Macedonia; b, Bronze Age, Wilsford, Wiltshire, England, age about 4000 years; c, modern, Parco dei Nebrodi, Sicily; d, Last Interglacial, Trafalgar Square, London, age about 120,000 years.

fossil *O. fracticornis* from Bronze Age deposits (aged about 4000 years) from Wilsford in Wiltshire, England (see Osborne, 1969). This material, though much younger than that from Trafalgar Square, shows a similar fragility due to loss of the lipid components.

Details of modern and fossil elytra of *O. fracticornis* and *O. massai* are shown in Fig. 4. The presetal granules of *O. fracticornis* (indicated by white-bordered black arrows) are very clear, and partial collapse of the fossil material serves merely to enhance them. In the case of the *O. massai* these granules are less conspicuous, but the perisetal punctures (indicated by white arrows) are clear and distinct in both the modern and fossil material. The fact that this character, unknown to Russell Coope when he originally studied the material, leads to the same identification, gives ample support for the recognition of *O. massai* as a Pleistocene fossil, and graphically illustrates how modern restricted distributions may not reflect the former ranges of the species concerned.

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The research reported here forms part of an MSc project by Sarah Falahee, supervised by Robert Angus. We thank the School of Biological Sciences, Royal Holloway, for the opportunity to carry it out. We also thank Eleanor Slade for collecting *O. fracticornis* in the Czech Republic, and Russell Coope for the loan of his fossil material and for all his help in working with it.

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# Studies on palearctic *Onthophagus* associated with burrows of small mammals. IV. A new Iranian species belonging to the *furciceps* group (Coleoptera, Scarabaeidae, Onthophagini)

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## Abstract

*Onthophagus* (*Palaeonthophagus*) *psychopompus* **sp. n.** is described based on 75 specimens from Iran. The new species belongs to the *furciceps* species group, and has pholeophile habits, as the other species of the group. It appears to have a wide distribution in Iran, from 600 to 1950 m above sea level. A revised dichotomous key to the group is given.

## Keywords

Scarabs, pholeophily, dens, rodents, Middle East

## Introduction

At least since Falcoz (1914), it has been known that several species of *Onthophagus* Latreille, 1802, and other scarabaeoids, have a more or less exclusive association with rodents (pholeophily). Whereas burrow specialists are fairly well-known in the New

World, they are still poorly investigated in the Palearctic. Rodents associated pholeobiont scarabs do not use dung deposited on open ground but exclusively droppings inside rodent burrows. Such dung beetle species are rarely collected outside burrows, and if so, usually under stones and most likely during their passage from one burrow to another.

During a research project undertaken by the authors on the scarabaeoid fauna of Iran associated with burrows of rodents, one of us (M. Moradi) has had the chance to collect some *Onthophagus* specimens belonging to an undescribed species.

In this paper, which is a continuation of the works by Ziani and Gudenzi (2006; 2007; 2009) on palearctic pholeophile *Onthophagus*, the new species is described.

## Material and methods

75 specimens from the following collections were studied:

- ABCB** A. Ballerio private collection, Brescia (Italy)  
**ANCR** A. Napolov private collection, Riga (Latvia)  
**EBCT** E. Barbero private collection, Torino (Italy)  
**GCCR** G. Carpaneto private collection, Rome (Italy)  
**LNCB** L. Nádai private collection, Budapest (Hungary)  
**MHNG** Muséum d'Histoire Naturelle, Genève (Switzerland)  
**TBCP** T. Branco private collection, Porto (Portugal)  
**SZCM** S. Ziani private collection, Meldola, Forlì (Italy)

Methods and terminology follow Ziani and Gudenzi (2006).

## Description

### *Onthophagus (Palaeonthophagus) psychopompus* sp. n.

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Figs 1–7, 9–10

**Type locality.** Iran, Tehran prov.: Hashtgerd, 35°57'N, 50°40'E.

**Type series.** Holotype ♂: IRAN, Tehran prov., Hashtgerd, 1250 m, IV.2009, M. Moradi leg. Allotype: same data as holotype. Other paratypes: 73 specimens as follows: IRAN, West Azarbaijan prov., Kelisa Kandi, 1684 m, IV.2009, M. Moradi leg. 5 males and 1 female; IRAN, East Azarbaijan prov., Haris, 1900 m, IV.2009, M. Moradi leg. 3 males and 1 female; IRAN, Zanjan prov., Garmab, 1590 m, M. Moradi leg. 2 males and 1 female; IRAN, Kordestan prov., Saqez, 1500 m, IV.2009, M. Moradi leg. 1 male and 3 females; IRAN, Qazvin prov., Sirdan, 1308 m, IV.2009, M. Moradi leg. 8 males and 3 females; IRAN, Hamedan prov., Razan, 1840 m, IV.2009, M. Moradi leg. 5 males and

4 females; IRAN, Kermanshah prov., Islam Abad, 1335 m, IV.2009, M. Moradi leg. 4 males; IRAN, Qum prov., Dastjerd, 1680 m, IV.2009, M. Moradi leg. 2 males and 3 females; IRAN, Tehran prov., Hashtgerd, 1250 m, IV.2009, M. Moradi leg. 1 male and 4 females; IRAN, Ilam prov., Saleh Abad, 620 m, IV.2009, M. Moradi leg. 4 males; IRAN, Chaharmahal Bakhtiari prov., Chelgard, 1950 m, IV.2009, M. Moradi leg. 4 males and 3 females; IRAN, Razavi Khorasan prov., Torbat-e-Jam, 1390 m, M. Moradi leg. 1 male; IRAN, Southern Khorasan prov., Birjand, 1480 m, V.2009, M. Moradi leg. 1 male; IRAN, Yazd prov., Abarkooh, 1510 m, VI.2009, M. Moradi leg. 3 males and 1 female; IRAN, Yazd prov., Taft, 1560 m, VI.2009, M. Moradi leg. 1 female; IRAN, Kerman prov., Rafsanjan, 1510 m, VI.2009, M. Moradi leg. 1 female; IRAN, Kerman prov., Ravar, 1175 m, VI.2009, M. Moradi leg. 1 male and 1 female; IRAN, Sistan and Baluchestan prov., Iranshahr, 1570 m, VI.2009, M. Moradi leg. 1 female.

**Type depositaries.** Holotype and allotype in MHNG. Other paratypes in SZCM and in ABCB, ANCR, EBCT, GCCR, LNCB, TBCP.

**Type labelling.** Holotype bears three labels, as follow. 1<sup>st</sup>, white, printed in black: "IRAN-Tehran / Hashtgerd 1250m / 35° 57' N, 50° 40' E / IV.2009 M. Moradi leg."; 2<sup>nd</sup>, white, printed in black: "in burrows of *Microtus* sp. / probably *M. socialis* Pall."; 3<sup>rd</sup>, red, printed in black: "Holotype / *Onthophagus* (*Palaeonthophagus*) / *psychopompus* nobis / S. Ziani & M. Moradi, 2009".

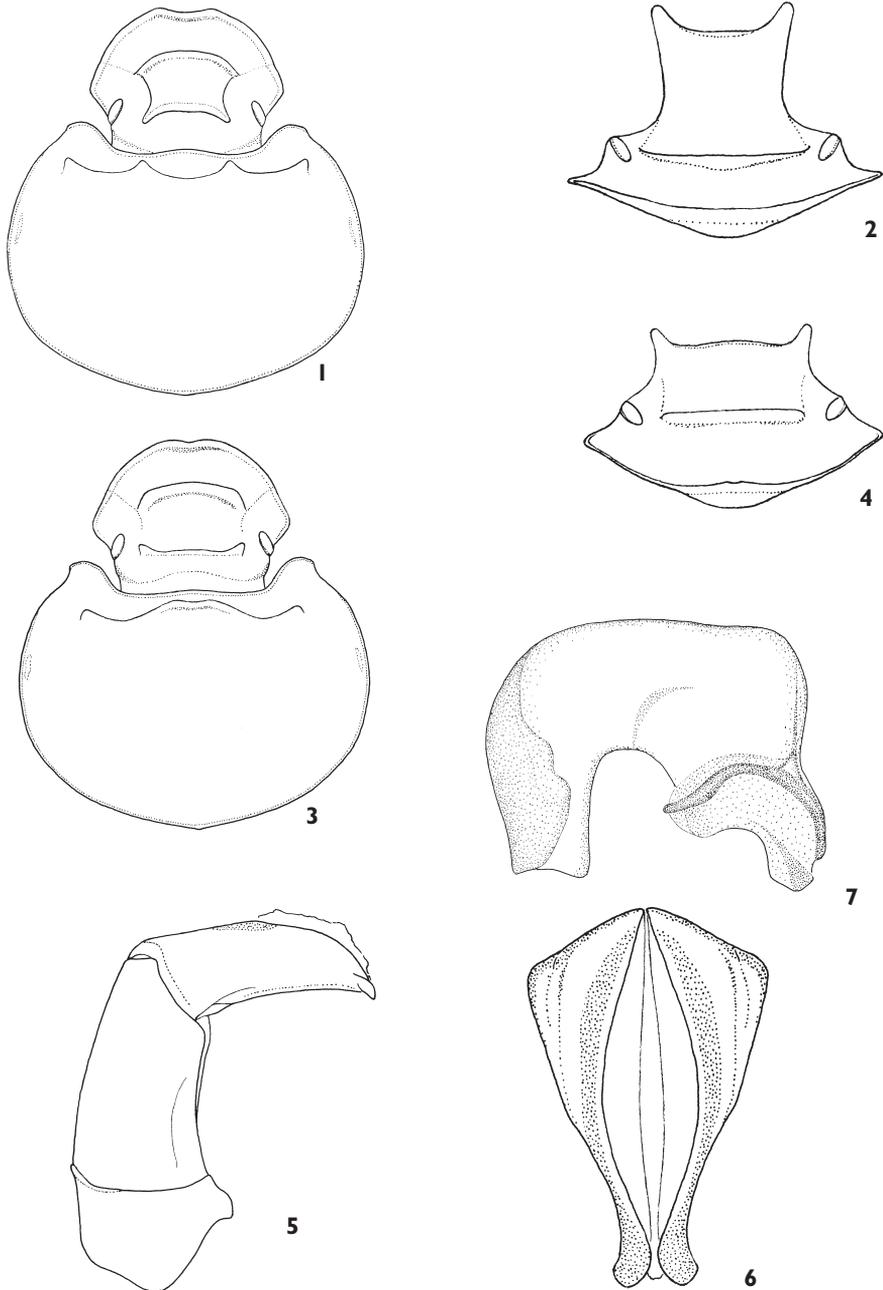
**Etymology.** Latinized from the classical Greek ψυχοπομπός ("*psyche*", soul and "*pompós*", guide). In the mythology, psychopomps were figures who usually escorted the souls of the dead men to the netherworld. It is here referred to the subterranean habits of the new species. The noun is in apposition.

**Description.** Holotype. Length 8.8 mm, width 5.2. Pronotum shorter than elytra (length ratio = 0.90).

Black, dorsal side moderately shiny with a distinct isodiametric microreticulation, pubescence yellowish white, antennal scape, pedicel and funicle red, antennal club dark red.

Head (Fig. 2) short, clearly wider than long (width/length ratio = 1.73), clypeus round, weakly reflexed anteriorly, only very slightly emarginate at middle, anterior angles very broadly round, sides evenly arcuate with no sinuations, genae distinctly protruding from eyes; clypeo-frontal carina distinct, strongly bent backwards, its edge in contact with a very barely traced clypeo-genal suture; occipital carina extended in a high, slender, terminally expanding and bifurcate horn, very weakly dentate at middle apically, twice as long as width of its base; clypeal and frontal surface with rather coarse setigerous punctures, more spaced on frons than on clypeus, with long erected bristles clearly thicker basally, gradually thinner apically.

Pronotum (Fig. 1) convex, strongly declivous towards anterior edge, with four anterior, equidistant, slender and apically almost sharp tubercles, the middle two slightly more prominent and projected upwards, the two anterolateral slightly projected outwards; base margined; anterolateral angles round, subtruncate, dorsal surface with setigerous punctures, separated by half to one diameter anteriorly, gradually more spaced towards base, where punctures are separated by two to four diameters; each puncture



**Figures 1–7.** *Onthophagus (Paleonthophagus) psychopompus* sp. n. Male, holotype, and female, allotype (Iran, Hashtgerd, Tehran prov.). **1** Male: head and pronotum, dorsal view **2** Male: head, frontal view **3** Female: head and pronotum, dorsal view **4** Female: head, frontal view **5** Parameres, lateral view **6** Parameres, dorsal view **7** Lamella copulatrix, ventral side. Drawings by I. Gudenzi.

bears a small granule at its anterior margin; bristles yellowish white, moderately long, scale-shaped, usually bifid or trifid at about two thirds of their length.

Elytral striae thin, shallow, slightly shining, their punctures only barely crenating interstriae; the latter flat, granulose, granules minute, as big as striae punctures or a little smaller, each granule bearing at its base a long yellowish white bristle which is sometimes bifid or trifid, or lanceolate.

Pygidium with setigerous, large punctures, widely spaced, with long thin yellowish white hairs.

Fore tibial spur bent inwards and downwards. Fore, middle and hind femora ventrally with small, rather sparse setigerous punctures.

Male genital armature as in Figs 5–6. Lamella copulatrix as in Fig. 7.

Allotype. Length 8.9 mm, width 5.2 mm. Pronotum shorter than elytra (length ratio = 0.85).

Head (Fig. 4) short, clearly wider than long (width/length ratio = 1.75), clypeus sub-truncate, clypeo-frontal carina distinct, slightly more elevate than in male, slightly bent backwards, frontal carina with a narrow lamina ending in a pair of erect horns, margin between horns straight or slightly sinuate in frontal view.

Pronotum (Fig. 3) with distinct, male-like, anterolateral tubercle on either side, and with an anteromedian transverse sunk gibbosity, only very slightly sinuate at middle.

**Variability.** Length 5.8 – 9.9 mm, width 3.4 – 5.7 mm. Occipital carina is female-like in minor males. In some males, usually but not necessary minor specimens, pronotal anteromedian gibbosities are closer to each other than in most of the examined specimens. Some minor males, less than 6.0 mm long, have pronotal anteromedian tubercles joined together in a small projection, but always divided in two by a shallow depression. In one minor male (the smallest of the type series) anterolateral tubercles are only vestigial and the occipital carina is reduced to a straight transverse and very low ridge. On the other hand pronotal morphology is quite homogenous in both major or minor females. Only the occipital carina is clearly lower and straighter in minor than in major females.

**Distribution.** The new species appears to be widespread all over Iran (Fig. 8) from 620 to 1950 m above sea level.

**Remarks.** *Onthophagus psychopompus* sp. n. belongs to the subgenus *Palaeonthophagus* Zunino, 1979, and can be placed in the *furciceps* group, characterized by medium size (6.0 to 10.0 mm), black colour, the occipital carina of the head with a high slender lamina, which is expanding and bifurcate apically in major males, broader basally and more or less elevate and horned in females, pronotum with anterior angles subtruncate, with a distinct anterolateral tubercle on either side and a more or less bilobate anteromedian gibbosity, elytra with yellowish white to reddish yellow stout bristles, sometimes bifid or trifid along their length or lanceolate, and a lamella copulatrix of quadrangular shape, excluding the basal emargination (Ziani and Gudenzi, 2006). *O. psychopompus* sp. n. can be assigned to the lineage of *O. ponticus*, characterized by both pronotal and elytral bristles stout, lanceolate, always distinctly thicker basally than distally, sometimes bifid or trifid

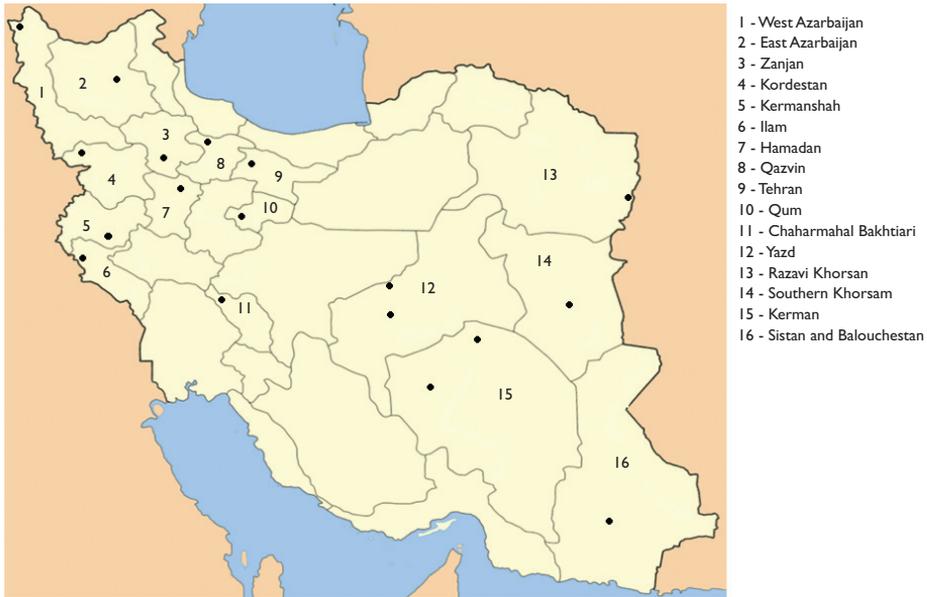


Figure 8. *Onthophagus (Paleonthophagus) psychopompus* sp. n. Distribution map.

along their length, and by the dorsal surface dull, with distinct microreticulation. The new species can be easily distinguished from the other species of the group, particularly *O. ponticus*, apparently its closest relative, by the characters given in the key to *furciceps* species group proposed by Ziani and Gudenzi, 2006, modified as follows:

**Key to the *O. furciceps* species group**

- 1. Bristles on elytral disc simple; dorsal surface shining, disc of pronotum barely or not at all microreticulate..... **4**
- Bristles on elytral disc bifid or trifid, or lancelolate; dorsal surface dull, with distinct microreticulation..... **2**
- 2. Lamellae of antennal club thin and elongate, much longer than in most *Onthophagus* species, somewhat resembling those of some Melolonthini..... ***O. parmatus* Reitter, 1892**
- Lamellae of antennal club normally shaped..... **3**
- 3. Relatively small species (length 4.8–8.2 mm). Pronotum equally densely punctate on disc and basally. Male: pronotum with four tubercles, the two anteromedian very closely placed and smaller than the two anterolateral; female: pronotum with an anteromedian narrow regularly convex gibbosity.... ***O. ponticus* Harold, 1883**

- Relatively large species (length 5.8–9.9 mm). Pronotum densely punctate on disc, punctures gradually more spaced toward base. Male: pronotum with four equidistant tubercles, the two anteromedian more prominent than the two anterolateral; female: pronotum with an anteromedian transverse sunk gibbosity..... *O. psychopompus* sp. n.
- 4. Pronotal sides obviously sinuate behind anterior angles; pronotum approximately as long as elytra..... *O. furciceps* Marseul, 1869
- Pronotal sides not sinuate behind anterior angles; pronotum longer than elytra..... *O. bytinskii* Balthasar, 1960

In Balthasar (1963), the last taxonomic monograph covering Iranian territory, *O. psychopompus* sp. n. can be inserted in the key at thesis 24 (21), p. 199, to form a couplet with *O. ponticus* from which is easily distinguished by the characters mentioned above. Moreover, the shape of the lamella copulatrix, with the right branch, in ventral view, bifurcate, is very characteristic for the new species.



**Figures 9–10.** *Onthophagus* (*Paleonthophagus*) *psychopompus* sp. n. Male, paratype (Iran, Sirdan, Qazvin prov.) and female, paratype (Iran, Saqqez, Kordestan prov.). **9** Dorsum of male **10** Dorsum of female. Photos by A. Ballerio, scanned by G. Fiumi.

## Discussion

All the specimens of the type series were collected in burrows of rodents belonging to three genera: *Meriones* Illiger, 1811, *Microtus* Schrank, 1798 and *Allactaga* Cuvier, 1837. The rodents in the first two genera tend to inhabit both arid and grassy areas, while the genus *Allactaga* includes hopping rodents of desert and semi-arid regions. *O. psychopompus*, which appears to be a strictly pholeobiont species, is distributed almost all over the Iranian territory and is associated to rodents of at least the three mentioned genera. The new species shows a strict but generalized preference for small rodents' burrows, without host specificity or restrictions to particular soil types. Its occurrence is not associated to a narrow altitudinal range, because it was collected from a wide belt ranging from 620 to 1950 m above sea level. Probably the constant temperature inside the burrows and the regular presence of food allows this scarab to avoid less favourable conditions outside.

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# ***Formicdubius* Philips & Scholtz from South Africa, a junior synonym of *Haroldius* Boucomont, and a survey of the trichomes in the African species (Coleoptera, Scarabaeidae, Onthophagini)**

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## **Abstract**

*Formicdubius* Philips & Scholtz, 2000, a genus of South African scarab dung beetle, is synonymised with *Haroldius* Boucomont, 1914. All four African species of *Haroldius*, formerly in the genus *Afroharoldius* Janssens, possess trichomes. Trichome location and degree of development in the African species are discussed. The first record of *Haroldius modestus* Janssens from Malawi is given.

## **Keywords**

Afrotropics, dung beetles, myrmecophiles, taxonomy

## **Introduction**

Philips and Scholtz (2000) described a new genus and species of a tiny, myrmecophilous Scarabaeinae, *Formicdubius convexus* (Figs 1–6), based on 16 specimens found in a nest of *Pheidole megacephala* (F.) ants collected in a suburb of Pretoria, South Africa. The circular and convex body shape and a length less than 2 mm resemble those in the Oriental *Haroldius* Boucomont, 1914, but the possession of trichomes was considered unique within Scarabaeinae.

The genus *Afroharoldius* Janssens, 1949a, also of similar appearance, was classified in the tribe Alloscelini or subtribe Alloscelina (Janssens 1949b; Ferreira 1972). *Afroharoldius* contained three species from central Africa but was synonymised with *Haroldius* by Paulian (1985), because the only single differential diagnostic character, the number of antennomeres, was based on an incorrect observation. Janssens (1949a, b; 1953) erroneously claimed that *Afroharoldius* has nine antennomeres, but both *Afroharoldius* and *Haroldius* have eight antennomeres. Other characters differentiating these taxa remain unknown.

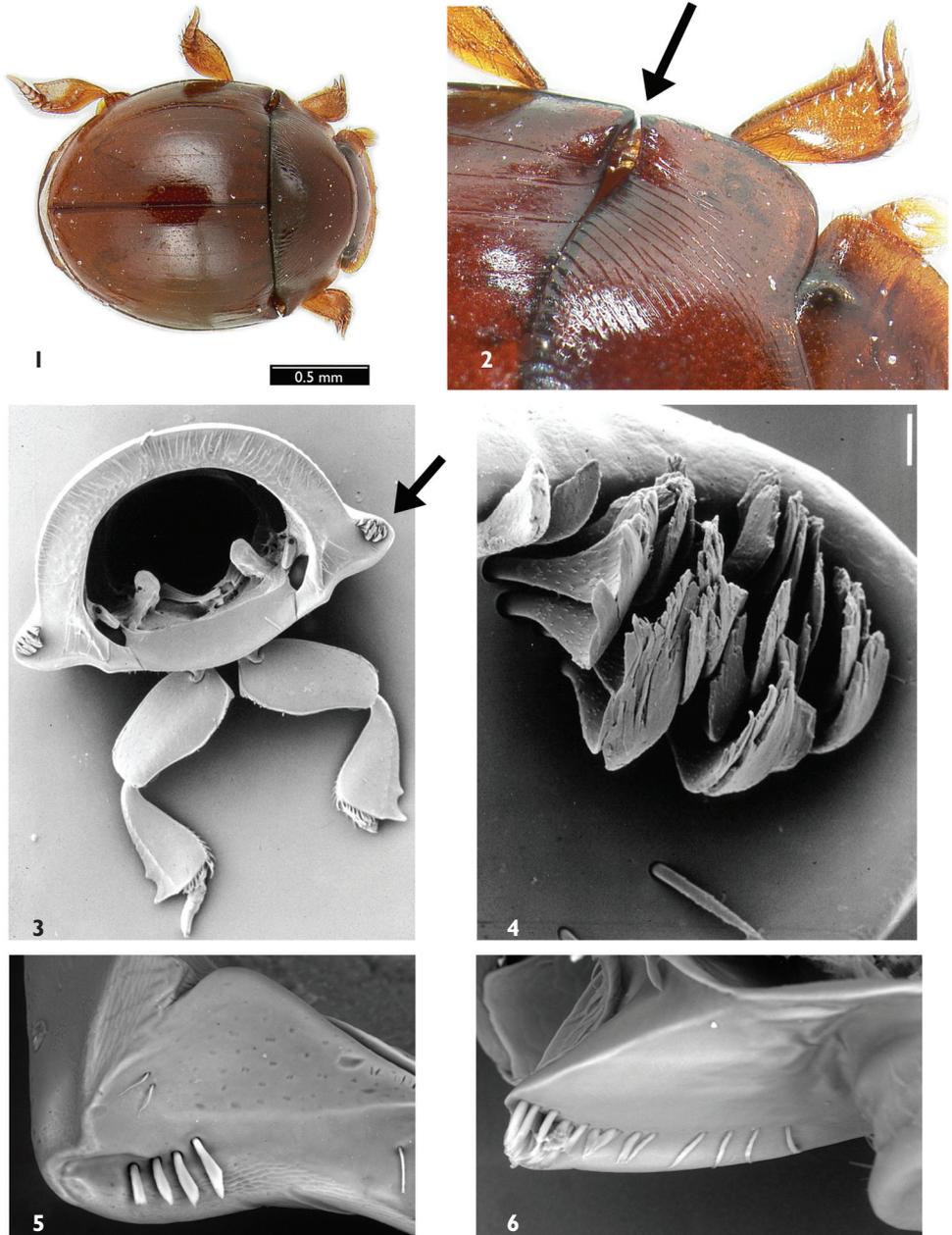
The three former *Afroharoldius* species were overlooked for comparison when *Formicdubius* was described. Furthermore, due to the earlier placement of this genus in the now unused “Alloscelina,” it was not included or studied in the revision of the southern African “Canthonina” (Scholtz and Howden 1987). Recently, the resemblance of *Formicdubius* with *Haroldius* and *Afroharoldius* became obvious and has already entered the scientific record in form of an “unpublished synonymy of *Formicdubius* Philips and Scholtz 2000” with *Haroldius* Boucomont (Davis et al. 2008: 216), which relates to the present paper, and Krikken and Huijbregts’ (2006: 168; 2009: 259) statement that *Formicdubius* should be placed in or near *Haroldius*. With this paper, we formalize the synonymy between *Formicdubius* with *Haroldius*.

Tribal placement for *Haroldius* is unsettled. Although currently placed in the tribe Canthonini (Hanski and Cambefort 1991; Krikken and Huijbregts 2006), a preliminary phylogenetic analysis (Philips 2005) placed this taxon in the Onthophagini. This is also where *Formicdubius* was provisionally placed in Philips and Scholtz (2000).

### **African *Haroldius* species**

All African species of *Haroldius* appear to have trichomes on the mesepimeron, the pronotal base, and the elytral base. Trichomes appear as distinct and relatively tight clusters of setae while others are looser or even single rows of thick setae such as those on the elytral base. Without microsections we are unable to decide whether those might be proper trichomes associated with glands or mechanoreceptors. However, as further evidence of a glandular association, longitudinal grooves at the pronotal base are also present that may facilitate the spreading of allomone secretions onto the pronotal surface, increasing the attractiveness of these beetles to their host ants.

*Formicdubius convexus* (Figs 1–6) (and the very similar or conspecific *Haroldius leleupi* Janssens, 1953; Figs 11–13) can easily be distinguished from the remaining *Haroldius* species by the presence of a distinct notch between the pronotum and the elytral base accommodating the pronotal trichomes (Figs 2, 12). In *Haroldius ennearthrus* Janssens, 1949 (Figs 14–19), the basal margins of pronotum and elytra are straight with the pronotal margin slightly emarginate close to the edge (Figs 15, 18); a notch is missing, but a slight lateral depression towards the bases of the pronotum and elytra is visible. *H. modestus* Janssens, 1953 shares the general shape of the pronotal and elytral bases with *H. ennearthrus* but the pronotal margin is slightly more strongly emarginate laterally (Figs 8–9).



**Figures 1–6.** *Haroldius convexus*: **1** Dorsal habitus **2** Trichomes within cleft between prothorax and mesothorax and showing pronotal sulci **3** SEM (scanning electron microscope) view of pronotal trichome **4** SEM view of pronotal trichome showing possibly ant-gnawed tips of the setae **5** SEM view of possible trichomes on the elytral base **6** SEM view of trichome on the mesepisternum and additional setal row proximally.

The trichomes on these species are located on the mesepisternum anterolaterally, the elytra anterolaterally (on the vertical surface facing the pronotum), and on the pronotal base posterolaterally. One should be aware that these setae may be damaged from the effects of gnawing by their host ants and the actual number of setae may vary in number more than we report due to our limited sample sizes. Regardless, the degree of development of these structures in each species is as follows:

Specimens of *H. ennearthrus* possess a large rounded cluster of setae on the mesepisternum (Fig. 19) and no additional setae proximally. They also appear to have two short and relatively thick setae on the elytral base. Three to five thick setae are present on the pronotum (Figs 16–18) as well as a row of similar aligned setae proximal to these, all of which may be trichomes (Fig. 16).

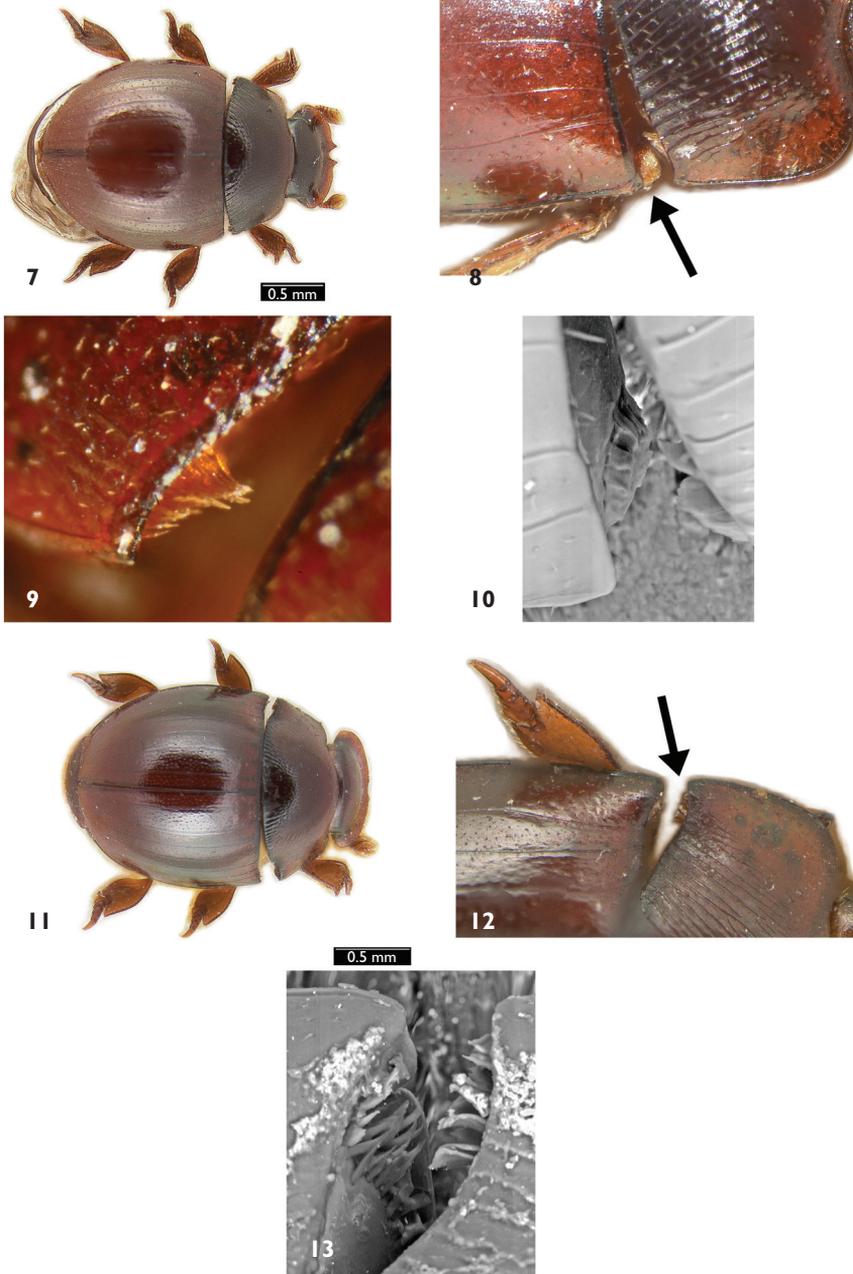
*Haroldius modestus* (Figs 7–10) also has a large, rounded cluster of setae on the mesepisternum (Fig. 10) and lacks any thick setae proximally. There are two to three thick setae on the elytral base. On the pronotum a brush-like trichome is well developed, consisting of six to sometimes ten or more, long, thick setae (Figs 8–9).

The third described *Haroldius* species from Africa, *H. leleupi* (Figs 11–13), is strikingly similar to *Formicdubius convexus* (Figs 1–6). They both have a small cluster of stout setae on the mesepisternum (Figs 6, 13) and proximal to this are a few more thick and elongate setae arranged in a transverse row (Fig. 6). These same setae become more slender and slightly more widely separated the further from the mesepisternal trichome. Additionally, there are four to five short, thick setae at the base of the elytra near the lateral margin (Fig. 5). Both species also have a well developed trichome on the pronotal base consisting of 20 or more lobe shaped setae (Figs 3–4, 12–13).

We are unsure whether *H. leleupi* and *F. convexus* are distinct taxa. *H. leleupi* is generally larger; the five specimens studied measure 1.80–2.20 mm in length (average 2.06 mm), whereas the 14 sampled types of *F. convexus* measure 1.63–1.90 mm (average 1.78 mm). *Haroldius leleupi* also has slightly stronger (more clearly defined) punctures on the disk of the pronotum and the elytral intervals and slightly deeper elytral striae, particularly near the suture. Additional material will be required from localities between the Congo and South Africa to decide to what extent these minor differences indicate taxonomic differentiation.

## Synonymy

*Haroldius leleupi* and *Formicdubius convexus* are difficult to distinguish at the species level, but there is no doubt that *Formicdubius* is identical with *Haroldius* at the generic level. *Formicdubius* fully matches Boucomont's (1914) original description of *Haroldius*. It also agrees with the extended diagnosis of *Haroldius* recently published by Krikken and Huijbregts (2006) with the exception that all African species currently subsumed under *Haroldius* possess trichomes.



**Figures 7–13.** *Haroldius* species. Figures 7–10. *H. modestus* 7 Dorsal habitus 8 Trichomes within cleft between prothorax and mesothorax and showing pronotal sulci 9 Pronotal trichome 10 SEM view of trichomes on the pronotum and mesepisternum. Figures 11–13. *Haroldius leleupi*: 11 Dorsal habitus 12 Trichomes within cleft between prothorax and mesothorax and showing pronotal sulci 13 SEM view of trichomes on the pronotum and mesepisternum.

We propose the following synonymy:

*Haroldius* Boucomont, 1914 (type species by subsequent designation by Arrow, 1931: *Haroldius rugatulus* Boucomont, 1914)

= *Formicdubius* Philips & Scholtz, 2000 (type species by original designation: *Formicdubius convexus* Philips & Scholtz, 2000), syn. n.

Consequently, the following new combination is established:

*Haroldius convexus* (Philips & Scholtz, 2000) Krell & Philips, 2010, comb. n.

We refrain from determining the taxonomic status of the African species of the *Haroldius/Afroharoldius* group. All African *Haroldius* species have more or less distinct trichomes which could be a synapomorphy justifying a genus or subgenus *Afroharoldius*. However, we neither know if trichomes (vestigial or distinctive) are common in Asian *Haroldius* species, or whether the trichome-bearing species are the sister group of the trichome-less *Haroldius*, or whether their exclusion from *Haroldius* would leave *Haroldius* or *Afroharoldius* paraphyletic. In *Haroldius brendelli* Krikken & Huijbregts, antehumeral elytral trichomes are described (Krikken and Huijbregts 2009). Based on the illustrations in Krikken and Huijbregts (2006), it appears as though pronotal grooves are present on at least some Asian species and, moreover, trichomes seem to be present in *H. tangkoko* Krikken & Huijbregts and *H. cambeforti* Krikken & Huijbregts (see their figs 5 and 6). A revision and phylogenetic analysis of the whole group, including species of *Phaedotrogus* Paulian and probably *Ponerotrogus* Silvestri and *Cyclo-trogus* Wasmann (both currently considered to be junior synonyms of *Haroldius*), will probably be necessary to establish a sound genus-level classification. Currently we see no reason to change the status of *Afroharoldius* as junior synonym of *Haroldius*.

## Material studied

40 Afrotropical *Haroldius* specimens from the following collections were studied:

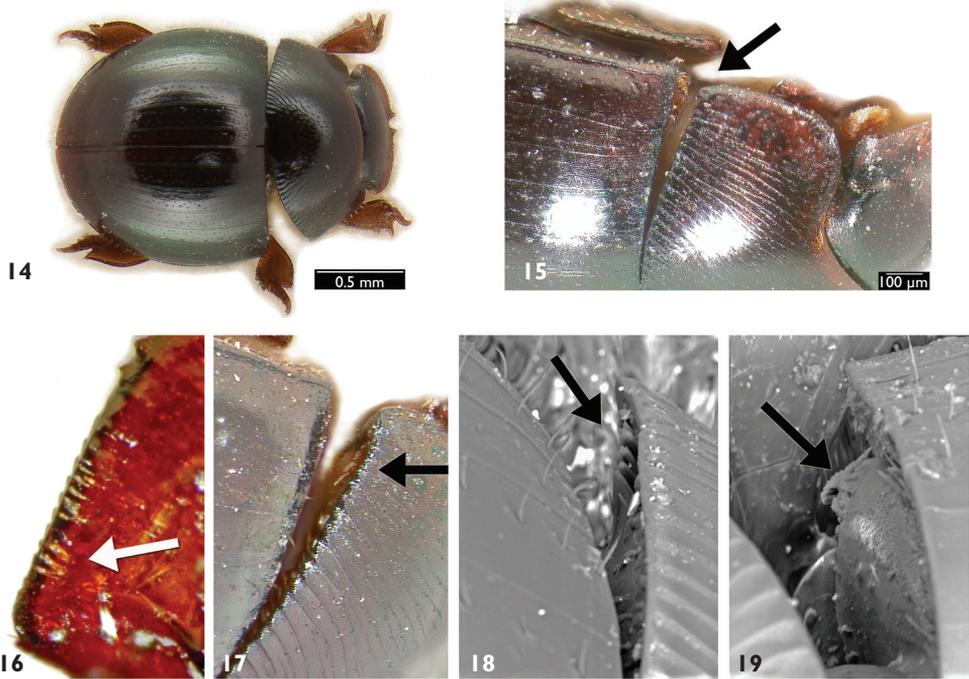
**BMNH** The Natural History Museum, London, UK.

**MRAC** Musée Royal de l’Afrique Centrale, Tervuren, Belgium.

**TKPC** T. Keith Philips Collection, Western Kentucky University, Bowling Green, USA.

*Haroldius ennearthrus* (7 spm.): Holotype: DR Congo, Katanga, Elisabethville [Lubumbashi], “dans petites termitières”, leg. N. Leleup 3.i.1949 [MRAC]. Additional material: 6 spm. Kasai [now Lulua Province], Luluabourg [Kananga], “Récolté sous des pierres (avec fourmis)”, leg. N. Leleup 3.ii.1953 (det. Janssens) [MRAC].

*Haroldius modestus* (22 spm.): Holotype: DR Congo, Katanga, Kundelungu, 1750m, “savane herb.”, “Myrmécophile”, leg. N. Leleup 23.iii.1950 [MRAC]. Paratypes: 1 spm., Massif des Kundelungu, leg. N. Leleup 7.ii.1950, “Rives d’une mare”, “Récolté dans pet. fourmilière”; 5 spm., dto., 1750 m, ii.1950, “savane herbeuse”, “Récolté dans petite fourmilière”; 1 spm., dto., 18.ii.1950; 8 spm., same data as holotype; 1 spm., 4.iii.1950, “Rives d’une mare”, “Myrmécophile”; 1 spm., dto.,



**Figures 14–19.** *Haroldius ennearthrus*. **14** Dorsal habitus **15** Trichomes within left between prothorax and mesothorax and showing pronotal sulci **16** Pronotal trichome and adjacent setae **17** Close-up view of trichome on the pronotum **18** SEM view of trichome on the pronotum **19** SEM view of trichome on the mesepisternum.

10.iii.1950; 1 spm., dto., 20.iii.1950, “Récolté dans pet. fourmilière”; 1 spm., dto. 24.iv.1950, “Myrmécophile”, “savane – parc”; 1 spm., dto., “savane boisée”, “Récolté sous écorce d’arbre” [MRAC]. Additional material: 1 spm., Malaŵi, Chisasira (Chinteche), leg. R. Jocqué 3.i.1978 [MRAC], **new record for Malaŵi**.

*Haroldius leleupi* (5 spm.): Holotype: DR Congo, Katanga [now in Lualaba Province], Kanzenze, “Récolté dans fourmilière”, leg. N. Leleup 5.ii.1949 [MRAC]. Paratypes: 4 spm., dto., 12.ii.1949 [MRAC].

*Haroldius convexus* (6 spm.): Paratypes: South Africa, Pretoria, The Willows, 25°45'S, 28°21'E, under stone with *Pheidole megacephala* (F.) [det. H.G. Robertson], leg. R. Oberprieler 1.i.1996 [2 spm. BMNH, 1 spm. MRAC, 3 spm. TKPC].

## Acknowledgements

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# A new genus and species of myrmecophilous aphodiine beetle (Coleoptera, Scarabaeidae) inhabiting the myrmecophytic epiphyte *Platyserium* sp. (Polypodiaceae) in the Bornean rainforest canopy

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## Abstract

*Pterobius itiokai* Maruyama, **gen. n.** and **sp. n.**, (Coleoptera: Scarabaeidae: Aphodiinae) is described from Lambir Hills National Park, Borneo based on specimens collected from a *Crematogaster difformis* ant nest in the myrmecophytic epiphytic fern genus *Platyserium*. *Pterobius* belongs to the tribe Eupariini and is closely related to the Indo-Australian genus *Cnematoplatys*.

## Keywords

Myrmecophily, *Crematogaster difformis*, Aphodiinae, Eupariini, *Cnematoplatys*

## Introduction

The Bornean lowland rainforest is dominated by dipterocarp trees, in whose canopies the ant, *Crematogaster difformis* (F. Smith), is a common and predominant species in arboreal ant community (Inui et al. 2009; Tanaka et al. 2009). This ant nests under the bark of trees and in myrmecophytic epiphytic ferns *Platyserium* sp. and *Lecanopteris* sp. Roth (1995) described a myrmecophilous cockroach, *Pseudoanaplectinia yumotoi*,

which was found in the nests of *C. difformis* in the domatia of the epiphytic ferns in Lambir Hills National Park, Borneo. Recently, Dr. T. Itioka of Kyoto University collected a series of a remarkable aphodiine scarab species from a colony of *C. difformis* in the domatia of *Platyserium* sp. in the same locality, together with *P. yumotoi*. Both adults and larvae of this aphodiine were found in the nest. The unusual adult morphology was indicative of its integration in the ant society. The beetle was not able to be assigned to any known genus and species. While many myrmecophilous aphodiines are known in the Neotropics (Stebnicka 2009), none have been reported previously from Southeast Asia. This paper describes the first myrmecophilous aphodiine from Southeast Asia as a new genus and species.

***Pterobius* Maruyama, gen. n.**

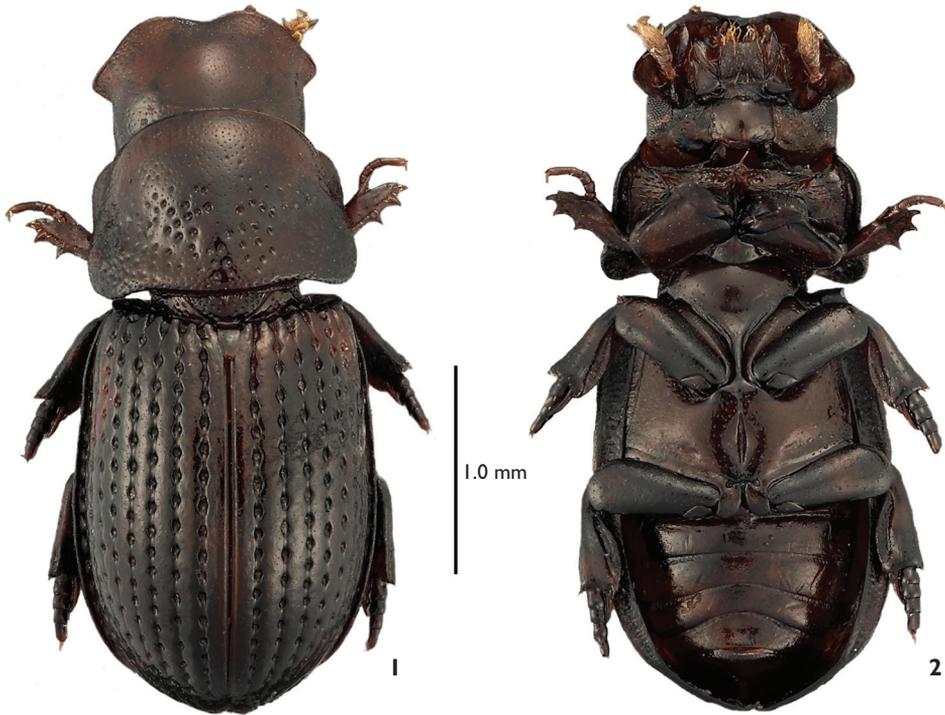
urn:lsid:zoobank.org:act:A3912CE4-BFFE-4177-9FA1-A80C1C29EEFD

**Type species.** *Pterobius itiokai* Maruyama, sp. n.

**Etymology.** Combination of the Greek *ptēris* and *-bios*, meaning inhabitant of ferns. Gender masculine.

**Description.** *Body* (Figs 1–2) elongate, glabrous above; coloration reddish brown. *Head* large, slightly narrower than anterior edge of pronotum, strongly convex medially; clypeal margin with acutely triangular, deflexed process at middle; genae right-angled, protruding; mouthparts adapted for soft saprophagy. *Antennae* 9-segmented, with 3 lamellae. *Pronotum* evenly convex with narrowly explanate anterior half; posterior angles broadly rounded, protruding; pronotal base without marginal line; surface roughly covered with variably-sized punctures. *Elytra* long, strongly convex dorsally and declivous laterally, widely margined from base to apical 1/9; humerus with epipleural denticle; striae impressed, coarsely punctate; intervals smooth. Metathoracic wings functional. *Venter* with prosternal process very large, elevated; mesosternum unevenly convex, glabrous, shining; mesocoxae slightly separated by meso-metasternal carina; metasternum convex, lateral metasternal triangle shallow; abdominal sternites long, finely fluted along sutures, medially narrowed, sutures arch anteriorly at middle. *Pygidium* with deep medial groove from base to middle; disc impunctate, not eroded. *Legs* (Figs 5–7) short; profemur with perimarginal groove; meso- and metafemora not lobed at knee; protibia with 3 lateral teeth and stout terminal spur; meso- and metatibiae (Figs 2, 6–7) flattened dorsoventrally, deplanated inwards, widened toward apex; apical spurs large, s-curved outwards; tarsi short, stout; tarsomeres cylindrical; claws hair-like; metatarsus 4-segmented. *Epipharynx* (Fig. 3) characteristic for Eupariini. Male genitalia are weakly differentiated among species of Eupariini and are generally similar in shape to species of *Saprosites*.

**Remarks.** This genus is similar to *Cnematoplatys* Schmidt in general appearance, but it is easily distinguishable from it by the posterior angles of the pronotum that are broadly rounded and protruding, the widely margined elytra, the meso- and metatibiae widened toward the apex, the stout tarsi, and the 4-segmented metatarsus.



**Figures 1–2.** Habitus of *Pterobius itiokai*, new genus and species (paratype). **1** dorsal view **2** ventral view.

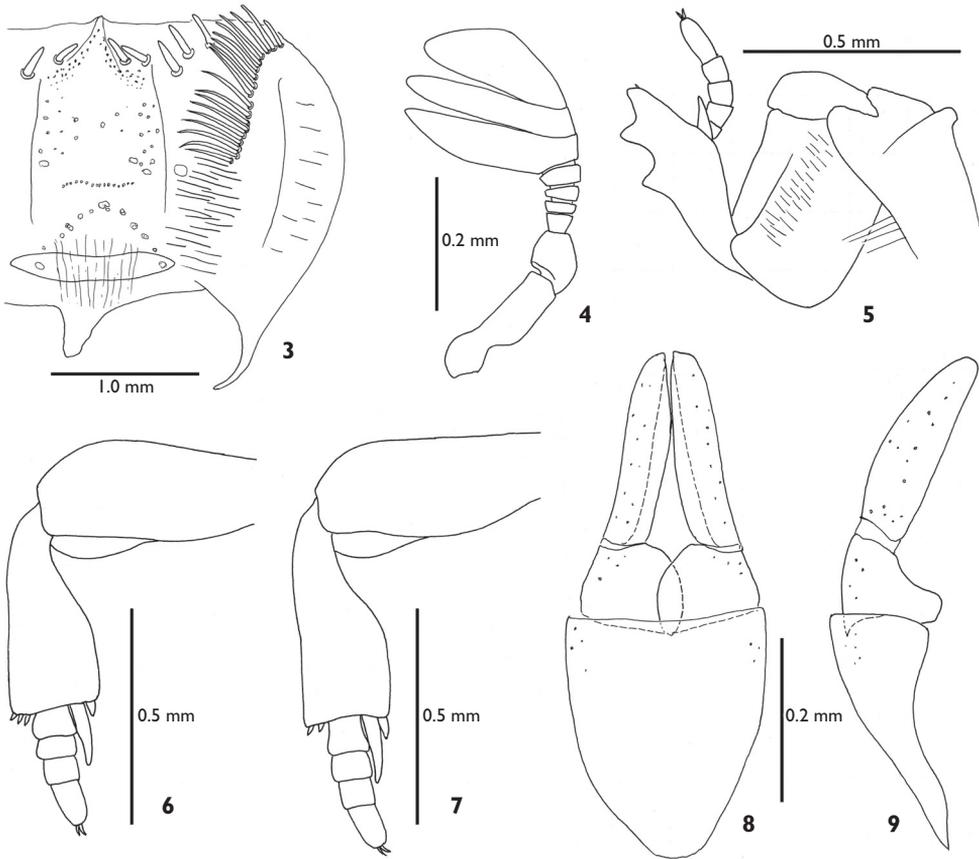
***Pterobius itiokai* Maruyama, sp. n.**

urn:lsid:zoobank.org:act:BB668AEE-029A-4FDC-8127-E0DA27AC3C29

**Etymology.** Dedicated to the collector of the type series, Dr. Takao Itioka.

**Type series.** *Holotype*, male, “MALAYSIA: Sarawak, Taman Negara Bukit Lambir [Lambir Hills National Park], 16.IX.2005, leg. ITIOKA-K.” Mouthparts, left legs and genitalia dissected and mounted on a small glass slide pinned under the specimen. Deposited at the Forest Department of Sarawak, Malaysia. Six paratypes with same data as holotype (deposited in the Kyushu University Museum).

**Description.** Length 3.05–3.30 mm. *Body* (Figs 1–2) elongate oval, reddish brown, glabrous shining. *Head* strongly gibbose medially; clypeal margin narrowly reflexed, broadly rounded on each side of shallow, median emargination; sides distinctly emarginate in front of right-angled, protruding genae; clypeal surface densely and finely punctate, with microreticulations. *Pronotum* rectangular, convex, side margin narrowly deplanate; posterior angles broadly rounded; surface punctures variably-sized, coarse and deep mesally, separated by 1–3 times their diameters. *Scutellum* narrowly subtriangular. *Elytra* slightly wider than base of pronotum and about 2.3 times as long



**Figures 3–9.** *Pterobius itiokai*, new genus and species (holotype). **3** epipharynx **4** left antenna, ventral view **5** foreleg, dorsal view **6** middle leg, dorsal view **7** hindleg, dorsal view **8** aedeagus, dorsal view **9** aedeagus, lateral view.

as pronotum, epipleural margin slightly reflexed, forming obtuse tooth at shoulder; striae finely impressed, strial punctures coarse, deep; intervals slightly convex, smooth, impunctate. Ventral sclerites shining; mesosternum gibbose and smooth in anterior half, posterior half concave, finely and sparsely punctate, at middle with triangular, smooth convexity prolonged to metasternum; metasternum convex, midline fine; surface finely and sparsely punctate; abdominal sternites with fine fluting along sutures and smooth, impunctate surface including that of pygidium. *Legs* (Figs 5–7) short; all femora sparsely and finely punctate; profemur subquadrate; meso- and metafemora with posterior lines; metatarsus stout,  $2/3$  times as long as tibia.

*Male.* Penultimate abdominal sternite and disc of pygidium shorter than female; aedeagus as in Figs 8–9.

**Remarks.** This species is similar to species of the genus *Cnematoplatys* in general appearance but are easily distinguished from them by the margined elytra, the thick meso- and metatarsi. and the 4-segmented metatarsi.

## Discussion

*Pterobius* is similar to the Indo-Australian genus *Cnematoplatys* of the tribe Eupariini in general appearance and in sharing the following character states: head large and strongly gibbose, genae acutely prominent; tibiae broad, flattened; tarsomeres of meso- and metatarsi stout; and abdominal sutures anterior. In her revision, Stebnicka (2006) stated that *Cnematoplatys* belongs to a group of related euparine genera including the Gondwanan *Saprosites* Redtenbacher, the Neotropical *Iguazua* Stebnicka, and *Passaliolla* Balthasar. These genera share a number of similar characters with *Pterobius*, which should belong to this group of genera. Nevertheless, *Pterobius* displays several unique character states that distinguish it as a distinct genus, especially the thick meso-metatarsi and the 4-segmented metatarsi. *Pterobius itiokai* is a myrmecophilous species living inside of the host ant nest, whereas the species of *Cnematoplatys*, *Iguazua*, and *Passaliolla* are found under the bark of rotten logs and on dead trunks of large trees. Thickened and shortened (including reduction of segment) tarsi are commonly found in a variety of myrmecophilous and termitophilous beetles such as of Paussinae (Carabidae), Staphylinidae, and Scarabaeidae. This is considered to be a morphological adaptation to integrate into ant society. In the case of *Pterobius*, the host ant *Crematogaster difformis* is an active and aggressive ant species, and the thick tarsi of the beetle may be protection against the hosts' bite.

## Acknowledgments

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# A new genus and species and a revised phylogeny of Stereomerini (Coleoptera, Scarabaeidae, Aphodiinae), with notes on assumedly termitophilic aphodiines

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## Abstract

A new genus and species of Stereomerini, *Cheleion malayanum* **gen. n.** and **sp. n.**, are described based on a single specimen from the Malacca peninsula in Malaysia. It is the first stereomerine found on the mainland of the Asian continent. A key to genera of Stereomerini and a phylogenetic estimate of the stereomerines using 24 species representing 7 tribes of Aphodiinae based on 53 morphological characters. The phylogenetic analysis places the new species within the tribe Stereomerini as a sister to the monophyletic group including *Adebrattia*, *Austaloxenella*, *Bruneixenus*, *Pseudostereomera* and *Stereomera*. A survey is given of the various taxa of Aphodiinae that are termite and/or ant inquilines, or have been presumed to be so based on morphology, and their phylogeny is discussed.

## Keywords

termite association, Aphodiinae tribes, synechthran morphology

## Introduction

The aphodiine tribe Stereomerini was erected by Howden and Storey in 1992 for four genera of minute, rare and supposedly termite-associated aphodiines *Stereomera* Arrow, *Termitaxis* Krikken, *Australoxenella* Howden and Storey, and *Bruneixenus* Howden and Storey (Howden and Storey 1992). In 1995 Bordat and Howden excluded *Termitaxis* from the tribe and described 3 new genera and species: *Adebrattia depressa* Bordat and Howden, *Danielssonia minuta* Bordat and Howden and *Pseudostereomera mirabilis* Bordat and Howden (Bordat and Howden 1995). Since then one new genus (*Daintreeola* Howden and Storey) and 11 new species of the genera *Daintreeola*, *Bruneixenus* and *Australoxenella* have been described (Storey and Howden 1996; Howden and Storey 2000). The number of genera of Stereomerini is presently 7 and the number of species 18, all from insular south east Asia and Australia.

Synapomorphies for the Stereomerini include a grooved head as well as a particular pattern of carinae and grooves on the pronotum with three pronotal carinae concentrated in median third and one transverse groove, plus convex body shape, wide epipleura and reduced eyes. Characters that may be either apomorphic or plesiomorphic are a more or less lanceolate posterior prosternal process, clypeus without dentation and flattened tibiae (Forshage 2002).

In the collections of the Swedish Museum of Natural History (NHRS) we found a remarkable specimen clearly belonging to Stereomerini but representing a new undescribed taxon, the first one from a locality on the Eurasian continent (the Malaysian Peninsula). As it has not been possible to accommodate the new taxon in one of the existing genera we felt impelled to describe a new genus as well. In order to test this, we performed a phylogenetic analysis of all the genera of Stereomerini. As the relationships between various aberrant tribes within the Aphodiinae, and between those tribes and the poorly delineated Eupariini, we included a wealth of other genera in the analysis.

## Methods

Images of the new species were obtained with a digital Olympus DP70 camera mounted on an Olympus SZX12 stereo microscope using the imaging software AnalySIS 5.0 to montage section images with different focus. Micrographs were taken with a Zeiss Supra35VP scanning electron microscope on low vacuum. The low vacuum scanning electron microscopy does not require the specimen to be prepared in the traditional manner including critical point drying and gold-coating and is thus particularly suitable for type material. Character coding of the new taxon and other taxa at hand were done from a combination of stacked digital images and direct observation in stereo microscope. Taxa not at hand were coded from scorings and images found in literature. These include *Australoxenella humptydooensis* Howden and Storey, *Bruneixenus squamosus* Howden and Storey, *Cartwrightia intertribalis* Islas, *Ascharhyparus peregrinus* (Hinton), *Termitodiellus es-*

*akii* Nomura and *Stereomera pusilla* Arrow and *Termitaxis holmgreni* Krikken coded from Howden and Storey (1992), *Daintreeola grovei* Howden and Storey coded from Howden and Storey (2000) and *Termitoderus ultimus* Krikken coded from Krikken (2008a).

Our images of the following taxa are deposited on Morphbank (<http://www.morphbank.net>); the new taxon (*Cheleion malayanum* n.sp.) (image numbers 480710–480723) and of the types of the rare *Danielssonina minuta* (image numbers 497197–497199), *Pseudostereomera mirabilis* (image numbers 497204–497207) and *Adebrattia depressa* (image numbers 497200–497203) (all Bordat and Howden 1995)

### Character selection

Several of the characters have been used in previous phylogenetic analyses (Howden and Storey 1992; Bordat and Howden 1995, Forshage 2002). In an attempt to further define the tribe Stereomerini based on morphological characters, we have added several characters (see Table 2) on the head (characters 4, 5, 10, 11), pronotum (characters 15, 18, 20, 22, 23, 24), legs (characters 34, 35), wings (characters 37, 38, 39, 44, 45), abdomen (characters 46, 53). We did not want to dissect the single type specimen of the new taxon so we have not been able to compare mouthparts and genitalia which are potential valuable sources of additional characters.

### Taxon selection

For the phylogenetic analysis we included representatives from all genera of the tribe Stereomerini, as this was our primary group of interest. In addition we wanted to include representatives of the tribes believed to be closely related to the Stereomerini based on morphology as well as some taxa of unclear taxonomic status and phylogenetic position. In addition to the 8 Stereomerini species, we thus coded 5 species of Rhyparini (*Aschna-rhyparus peregrinus*, *Termitodiellus esakii*, *Rhyparus suturalis* Schmidt, *Cartwrightia intertribalis* and *Sybacodes simplicicollis* Fairmaire), 1 species of Termitoderini (*Termitoderus ultimus* Krikken), 1 species of Termitotrogini (*Termitotrox consobrinus* Reichensperger), 2 species of Corythoderini (*Corythoderus loripes* Klug and *Neochaetopisthes heimi* Wasmann) as well as *Termitaxis holmgreni* (incertae sedis). As these aberrant taxa are of uncertain relationships with Eupariini – possibly differently to different parts of Eupariini – we wanted to include a fair representation of the diversity of that tribe. Thus we included a representative of an aberrant genus, morphologically similar to some of the truly or assumedly termitophilous tribes (*Notocaulus sculpturatus* Boheman), plus the largest genera of the tribe (*Ataenius scabrelloides* Petrovitz and *Saprosites laeviceps* Harold), as well as the type genus of the tribe (*Euparia castanea* LePeletier and Serville). As outgroup taxa we chose Aphodiini, since they are the major group of Aphodiinae that we expect to be safely outside the group of interest here; we included one more or less typical and one aberrant representative of Aphodiini (*Aphodius elegans* Allibert and *Sybx impressicollis* Boheman).

## A note on the type specimen of *Termitotrox*

The type specimen of the type species of the type genus of Termitotrogini, *Termitotrox consobrinus* Reichensperger 1915, was long considered lost (Paulian 1985), but was recently rediscovered by author MF in a cabinet at the Lund museum, where it was left forgotten many years ago by B-O Landin who was acting as a courier between the Gothenburg museum where it was originally deposited and professor Balthasar in Prague who had borrowed it. The specimen is now again available at the Natural History Museum in Gothenburg.

## Phylogenetic estimate

Fifty three morphological characters (Table 2) were coded for 24 species from 7 tribes of Aphodiinae (Table 3). Fourteen of the species were coded from specimens, whereas 10 were coded from literature. Character 10 is ordered, while all other multistate characters are unordered. Uniform weights were applied. The phylogenetic analyses were performed in Paup\* Portable version 4.0b10 for Unix (Swofford 2002). Character evolution was explored using MacClade 4.08 (Maddison and Maddison 2005). Heuristic searches produced three equally parsimonious trees with 195 steps. Ensemble consistency index is 0.345 and retention index is 0.589.

## Results

An identification key for the genera of Stereomerini is given in Table 1.

**Table 1. Identification key to the genera of Stereomerini**

1.	Elytra modified laterally or posteriorly .....	2
–	Elytra flattened or evenly convex.....	5
2.	Margin of clypeus with pronounced inflexion, triangular at apex; pronotum with conspicuous depressions laterally; deep lateral longitudinal furrow on each elytron .....	<i>Danielsonia</i> Bordat & Howden
–	Margin of clypeus weakly inflexed; pronotum not laterally depressed; elytra conspicuously declivous posteriorly, deep elytral furrow missing .....	3
3.	Elytra with strong transversal ridges .....	<i>Stereomera</i> Arrow
–	Elytra without strong transversal ridges.....	4
4.	Elytral costae strongly twisted .....	<i>Pseudostereomera</i> Bordat & Howden
–	Elytral costae subparallell, posterior elytral corners protruding.....	<i>Bruneixenus</i> Howden & Storey
5.	Each elytron with pronounced and widely separated longitudinal costae; transverse striation missing or inconspicuous; elytral epipleura wide .....	6
–	Each elytron lacking or with inconspicuous longitudinal costae; strong transverse striation on each elytron; elytral epipleura narrow .....	7

6. Posterior prosternal process lanceolate; body covered by appressed circular scales giving surface a granular appearance ..... *Australoxenella* Howden & Storey  
 – Posterior prosternal process hastate; body covered with large punctures/tubercles giving surface a rough appearance..... *Cheleion* gen. n.
7. Body flattened; longitudinal elytral striae very weak, transverse striations profound; apical segment of maxillary palp securiform.....  
 ..... *Adebrattia* Bordat & Howden  
 – Body convex; longitudinal elytral striae pronounced with transverse striations only on the lateral elytron; apical segment of maxillary palp cylindrical .....  
 ..... *Daintreeola* Howden & Storey

**Table 2.** List of characters used in data matrix for phylogenetic analysis

<b>General</b>	
1	Entire dorsum with longitudinal costae: absent (0) or present (1)
2	Body shape cylindrical (0), flattened (1) or strongly convex (2) (unordered)
<b>Head</b>	
3	Head forward-pointing (0) or strongly retractable (1)
4	Antenna shorter than (0) or longer than (1) length of head
5	Maxillary palpi oval (0) or securiform (1)
6	Eyes with distinct dorsal portion (0), reduced (lacking dorsal portion) (1), or absent (2) (unordered)
7	Head posteriorly margined (1) or not (0)
8	Head wide (1) or not wide (0)
9	Anterior edge of clypeus inflexed (0), straight or slightly rounded (1) or pointed (2) (unordered)
10	Reflexed apical portion of clypeus absent (0), perpendicular (1), fully inflexed (2) (ordered 0-1-2)
11	Head grooves absent (0), present, parallel (1) or present, radial (2) (unordered)
<b>Pronotum</b>	
12	Prosternal process inconspicuous (0) flattened (1) or raised (2) (unordered)
13	Prosternal process inconspicuous (0) lanceolate (1) or hastate (2) (unordered)
14	Scutellum minute (0) or absent (1)
15	Pronotal anterior lateral angles evenly convex (0) or conspicuously depressed (1)
16	Pronotal sides concave (0), parallel (1) or convex (2)
17	Pronotal transverse furrow absent (0), basal (1), medial (2) or frontal (3) (unordered)
18	Pronotal transverse furrow absent (0), shallow (1), or deep (2) (unordered)
19	Pronotal posterior lateral angles protruding (1) or not protruding (0)
20	Pronotal basal medial lobe protruding (1) or basal border evenly convex (0)
21	Pronotum with (1) or without (0) broad lateral depressions
22	Bulbous posterior submedian lobes on pronotum absent (0) or present (1)
23	Pronotum anteriorly tapering (1) or of equal width (0)
24	Anterior median pronotal knob absent (0), present (1)
<b>Legs</b>	
25	Denticulation of fore tibiae normal (three distinct teeth) (0) or reduced (1)
26	Mid and hind tibial apical spurs pronounced (0) or reduced (1)
27	Mid and hind tibial apical spurs adjacent (0) or separated (1)

28	Transverse tibial ridges on mid and hindleg absent (0) or present (1)
29	Longitudinal tibial ridges on mid and hindleg absent (0) or present (1)
30	Legs of normal length (0) or very short (1)
31	Row of sulci on hind femora absent (0) or present (1)
32	Tarsomere count 555 (0) or 544(1)
33	Tibiae straight (0) or distinctly curved (1)
34	Midlegs not longer than other legs (0) or distinctly longer than others (1)
35	Midcoxae adjacent (0), widely separated (1)
<b>Wings</b>	
36	Elytral base margined (1) or not (0)
37	General orientation of longitudinal structures in posterior part of elytra roundly converging (0) or diverging (1)
38	Deep longitudinal elytral fold absent (0), present, straight (1) or present, twisted in posterior half (2) (ordered) (unordered)
39	Elytra with flat or weakly convex interstices between longitudinal rows of sulci (0), conspicuously elevated, cariniform interstices between rows of sulci (1), or costae apparently not corresponding to the rows of sulci (2) (unordered)
40	Elytra posteriorly evenly convex (0), flattened (1), bulbous (2), or abruptly declivous (3)
41	Elytral transverse ridges absent (0) or present (1) (unordered)
42	Epipleura inconspicuous (0) broadly inflexed (1)
43	Alae present (0) or absent (1)
44	Flaplike elytral apex absent (0) or present (1)
45	Hindleg emargination at elytra absent (0) or present (1)
<b>Abdomen</b>	
46	Pygidium covered by elytra (0) or free (1)
47	Transverse pygidial furrow absent (0) or present (1)
48	Ventrites mobile (0) or fused (1)
49	Punctures on ventrites scattered (0), arranged in rows (1) or arranged in dense rows (“fluting”) (2) (unordered)
50	Trichomes absent (0) or present (1)
51	Pygidium reflexed (1) or perpendicular (0)
52	Physogastry absent (0) or present (1)
53	Emargination of pygidial border absent (0) or present (1)

***Cheleion* gen. n.**

urn:lsid:zoobank.org:act:CC1002E4-849C-437A-BAEF-678474600B59

**Type species.** *Cheleion malayanum* sp. n., here designated.

**Etymology.** Genus name after the ancient Greek name for shell; gender is neuter.

**Diagnostic characters.** The body shape of the imago is strongly convex and the elytra are not conspicuously modified posteriorly. Large tubercles on the entire body surface give a rough appearance. Longitudinal grooves on the pronotum converge into a median transversal groove giving it an hourglass pattern. The posterior prosternal process is hastate.

**Table 3.** Data matrix based on characters in Table 1

		Characters					
Species		1–10	11–20	21–30	31–40	41–50	50–53
1	<i>Aphodius elegans</i>	0210?11010	0000010000	0000000100	0000000000	000000?000	00?
2	<i>Euparia castanea</i>	0210010100	0000110011	0000001010	0010110000	0000001120	00?
3	<i>Ataenius scabrelloides</i>	0110011100	0000010000	0000000010	0000110000	000000?110	001
4	<i>Saprosites laeviceps</i>	0010000100	0000010000	0000000100	0010100000	0000011120	100
5	<i>Adebrattia depressa</i>	1111111112	1210011201	0011111011	1100001001	1100011111	101
6	<i>Australoxenella humptydooensis</i>	111?11011?	1210012201	000111?001	?100011011	0100111110	100
7	<i>Bruneixenus squamosus</i>	110?11011?	2210012211	0001110001	?10001?011	0101111110	101
8	<i>Cartwrightia intertribalis</i>	110?1011??	?000112100	000?10??10	?000?1???2	0000?????1	00?
9	<i>Corythoderus loripes</i>	1011110120	0000100011	0000110001	0011010020	0000110101	000
10	<i>Danielssonina minuta</i>	1211111111	12?1022100	1001111011	0200010020	1100111110	001
11	<i>Daintreeola grovei</i>	121?01110?	1211022200	000111?000	?100010010	100001?100	00?
12	<i>Neochaetopisthes heimi</i>	1011100120	0000000011	0000100000	0000010012	0000010001	000
13	<i>Notocaulus sculpturatus</i>	1210100110	2000110010	1000100010	0010110010	0000011110	00?
14	<i>Cheleion malayanum</i>	1211111111	2220012200	1101110001	1100001010	0100111110	001
15	<i>Pseudostereomera mirabilis</i>	1111111110	2220012211	0010111011	010001?223	0100111111	101
16	<i>Rhyparus suturalis</i>	1110110111	12211?2100	0000110010	0000010012	0001010011	101
17	<i>Stereomera pusilla</i>	111??1001?	2211012211	00111100?1	?100010013	11001?????	10?
18	<i>Sybacodes simplicicollis</i>	1210110111	0221020000	0000111010	0000000010	0000010011	101
19	<i>Sybx impressicollis</i>	0100011000	0000110000	0000000100	0000000000	000000?001	00?
20	<i>Termitoderus ultimus</i>	1211?0011?	0??0121111	1001100000	?000011010	00000100?0	?10
21	<i>Termitodiellus esakii</i>	111??111??	1?21022100	100001???1	?000011012	00010????1	01?
22	<i>Aschnarhyparus peregrinus</i>	111??111??	??211?2210	1000010?1	0000011012	100100?0?1	01?
23	<i>Termitaxis holmgreni</i>	1010?21111	0211020010	0000110001	?000011020	1110???0?1	11?
24	<i>Termitotrox consobrinus</i>	101??2?11?	0?01102200	1101110000	0001111110	101011?0?0	00?

Immature stages unknown.

**Description.** *Dorsal surface.* Head very wide, subrectangular dorsally, clypeus apically pointed and reflexed under head, frons slightly bulbous with 5 divergent furrows; posterior transverse furrow running across the head from the posterolateral side of the one eye across to the posterolateral side of the other eye. Antennae long, length equivalent to width of head; amber-color, with long setae. Maxillary palpi length equivalent to length of head, amber-color, with securiform apical segment. Labial palpi with long setae on apices. Eyes have no distinct dorsal part and mouthparts are retracted.

Pronotum large and transverse, sides evenly curved, anterior edge bisinuate, posterior edge with a broad median protrusion. Disc of pronotum medially with 5 furrows, converging towards the middle in an hourglass pattern, midfurrow shallower than lateral furrows. Anteromedial disc with distinctly raised tubercle, posteromedial disc and posterolateral sides with slightly lower tubercles. Lateral of the furrows are large elliptical depressions, delineated by furrows.

Hindbody narrower than pronotum, elytra only slightly longer than pronotum plus head.

Elytra posteriorly tapering, apically rounded, evenly, not abruptly (declivous) posteriorly. Each elytron with 6 longitudinal ridges before the lateral edge, elytral interstices alternating in height, elevated but discontinuous, consisting of series of longitudinal setae-bearing tubercles. Even interstices lower, rugose. Epipleura broadly inflexed, posterior two thirds of lateral edge slightly recurved to allow free movement of hindlegs.

Pygidium exposed, strongly punctured proximally, less strongly apically. Small emargination on proximal pygidial border.

*Ventral surface.* Prosternal process strongly elevated and apex expanded, transversely split anterior to procoxae, hastate posterior to procoxae. Mesosternum narrow with alutaceous and punctured surface. Metasternum triangular widest in front and tapering posteriorly, groove along midline, surface nitid and punctured. Abdomen with 5 segments visible ventrally.

Ventrites apparently fused.

Legs short with broad femora and tibiae, tarsi 4-segmented and short. Fore tibiae moderately wide, with finely serrated outer edge and one strong apical lateral tooth, tarsus inserted well before apex. Mid and hind tibiae broad with finely serrated outer edge and concave apex; each with at least two inconspicuous tibial spurs.

### ***Cheleion malayanum* sp. n.**

urn:lsid:zoobank.org:act:D8732C0E-4747-4276-8F27-2354509159F3

**Material.** Holotype: Malaysia, Pahang, Bukit Frazer, 1200 m, 7-9/4 – 1992, Malaise-trap in jungle, Heikki Hippa leg. Swedish Museum of Natural History (NHRS).

**Etymology.** The first specimen of the species was collected in Malaysia.

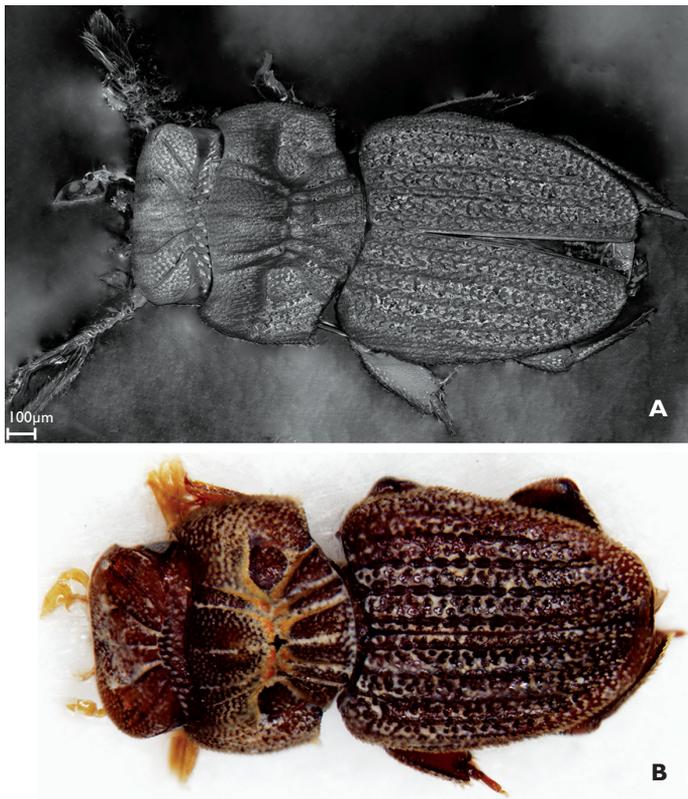
**Diagnostic characters.** Structures such as the hastate posterior prosternal process, pattern on the pronotum with a strong anteromedial knob as well as bulbous areas

medially and laterally on each side at the posterior end of the pronotum, the very long antennae and the strongly tuberculate and rugose surface of the body will easily separate this species from other known Stereomerini.

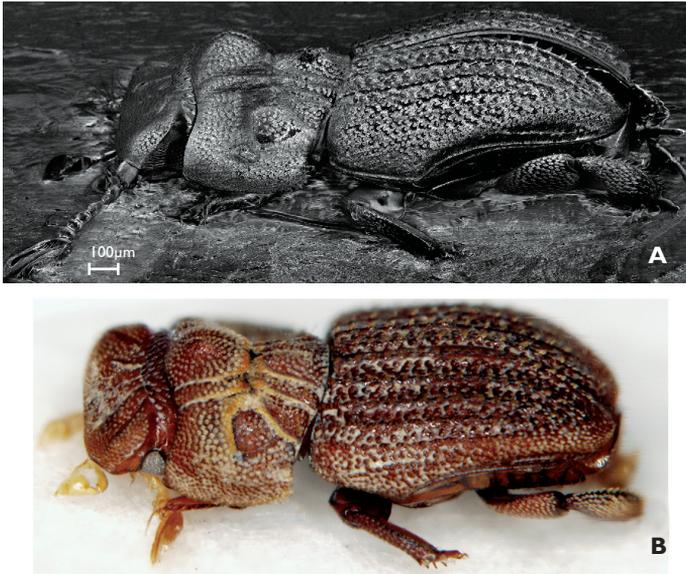
**Description.** Length 1.8 mm, width at broadest point 0.9 mm. Chestnut brown, whole body rather densely covered with strong puncture; strongly convex. Morphology as in generic description and as in Figures 1–6.

### Phylogenetic estimate

The three resulting most parsimonious trees (Figure 7A–C) differ only in the internal relationships within the Stereomerini genera *Australoxenella*, *Bruneixenus*, *Pseudostereomera*, *Stereomera* and *Adebrattia* (as shown in the consensus tree, Figure 7D). The rest of the Stereomerini species, namely the new taxon, *Danielssonia* and *Daintreeola* appear in the same positions in all three trees (Figure 7A–C). None of the three configurations corresponds very well with Bordat and Howden's (1995) cladogram (we do not compare with Storey and Howden as they only included three representatives of



**Figure 1.** Dorsal view of *Cheleion malayanum* sp. n. **A** scanning electron micrograph **B** stereo microscope image.



**Figure 2.** Lateral view of *Cheleion malayanum* sp. n. **A** scanning electron micrograph **B** stereo microscope image.

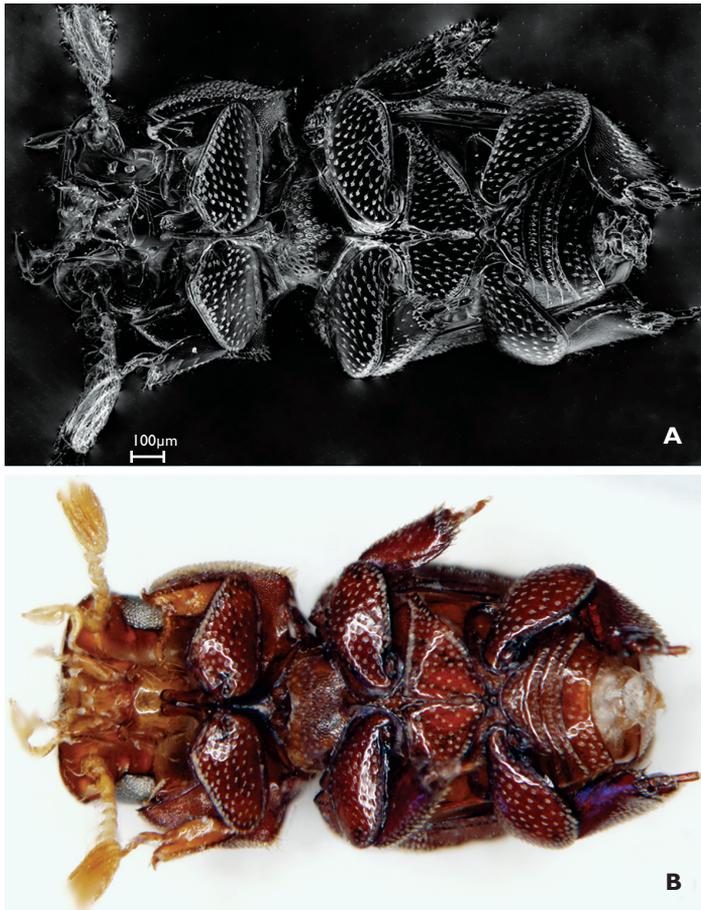
Stereomerini in their 1992 analysis) in which the sister species *Adebrattia-Bruneixenus* forms a sister group to *Danielsonia-Australoxenella*-(*Stereomera-Pseudostereomera*). One reason for this may be that neither the new taxon nor *Daintreeola* were included in the Bordat and Howden (1995) analysis. Our results rather points to a close relationship between *Adebrattia* and *Pseudostereomera* and between *Australoxenella* and *Bruneixenus*. *Stereomera* was placed as a sister group to the *Adebrattia-Pseudostereomera* in 2 of the 3 trees and as sister group to *Australoxenella-Bruneixenus* in the third tree.

Concerning the relationships outside Stereomerini, our results point to a close relationship between Stereomerini and the genus *Termitaxis*, that was formerly included in Stereomerini but is now considered *incertae sedis* (Bordat and Howden 1995), and the Termitotrogini (*Termitotrox*). Corythoderini appears monophyletic, as does a core of Rhyparini (if excluding *Sybacodes*, the position of which has been ambiguous, and *Cartwrightia*, previously classified in Eupariini and recently transferred to Rhyparini). All representatives of the aberrant tribes form a monophyletic group together, while the more typical Eupariini genera form a grade basal to this group.

## Discussion

### History of classification of inquiline Aphodiinae

There are several taxa in Aphodiinae which have inquiline or inquiline-like morphologies (listed in Table 4). They are usually small, have integumental bulbs and ridges, particularly longitudinal dorsal ridges; sometimes contracted body shapes; short, broad



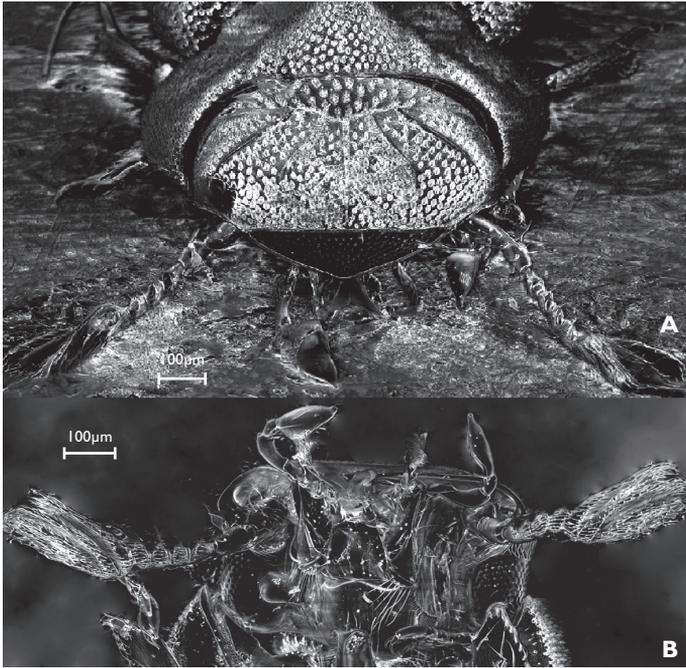
**Figure 3.** Ventral view of *Cheleion malayanum* sp. n. **A** scanning electron micrograph **B** stereo microscope image.

extremities, sometimes less so; and occasionally hair tufts or inflated abdomen. Their classification has included some moments of confusion.

In the first tribal division of Aphodiinae (Schmidt 1910), all the termitophilic or termitophile-like species were classified as Rhyparini and Corythoderini (only later were *Termitotrox* considered to be part of or closely related to Aphodiinae).

Termitoderini was added explicitly as a probable sister group to Corythoderini (Tangelder and Krikken 1982), and Stereomerini in a similar way as the sister group to Rhyparini (Howden and Storey 1992). The boundaries between all these tribes have been somewhat confused due to the uncertain status of some genera, and to the citing of all recent or problematic taxa as Termitoderini in Dellacasa's catalogue (Dellacasa 1987–88).

Termitoderini was erected as monotypic, but Dellacasa listed six genera there (including several from Rhyparini), which may have been a mere mistake, or a conscious reclassification with no arguments presented in the series of corrigenda to the cata-



**Figure 4.** Head of *Cheleion malayanum* sp. n. **A** frontal view, scanning electron micrograph **B** ventral view, scanning electron micrograph.

logue. The genera that actually belonged to Ceratocanthidae were deleted (“dropped”) but no further information given on the others (Dellacasa 1991).

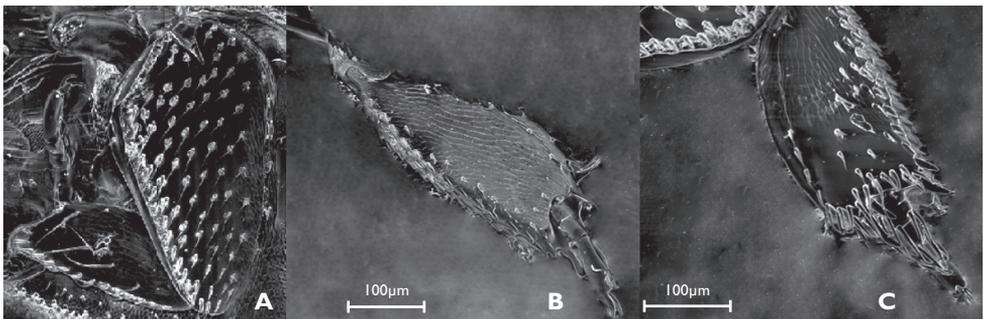
If disregarding Dellacasa’s classification, it becomes rather straightforward: *Termitaxis* was described in Rhyparini (Krikken 1970) but removed to become *incertae sedis* (Howden and Bordat 1995), *Cartwrightia* was classified as Eupariini, but transferred to Rhyparini (Galante et al. 2003; Stebnicka 2009), *Sybacodes* were always considered Rhyparini but it has been questioned (Howden and Bordat 1995), *Notocaulus* were classified as Rhyparini, but transferred to Eupariini (Krikken and Huijbregts 1987; Howden and Storey 1992).

A number of more or less aberrant genera have been added to the Rhyparini in recent years (Howden 1995, 2003; Howden and Storey 2000; Makhan 2006; Pittino 2006), with Skelley (2007) making an effort to straighten up the classification and listing several papers describing new species or otherwise forwarding knowledge which are not listed here. Krikken (2008a, b) recently reconsidered and described new species in Termitoderini and Termitotrogini.

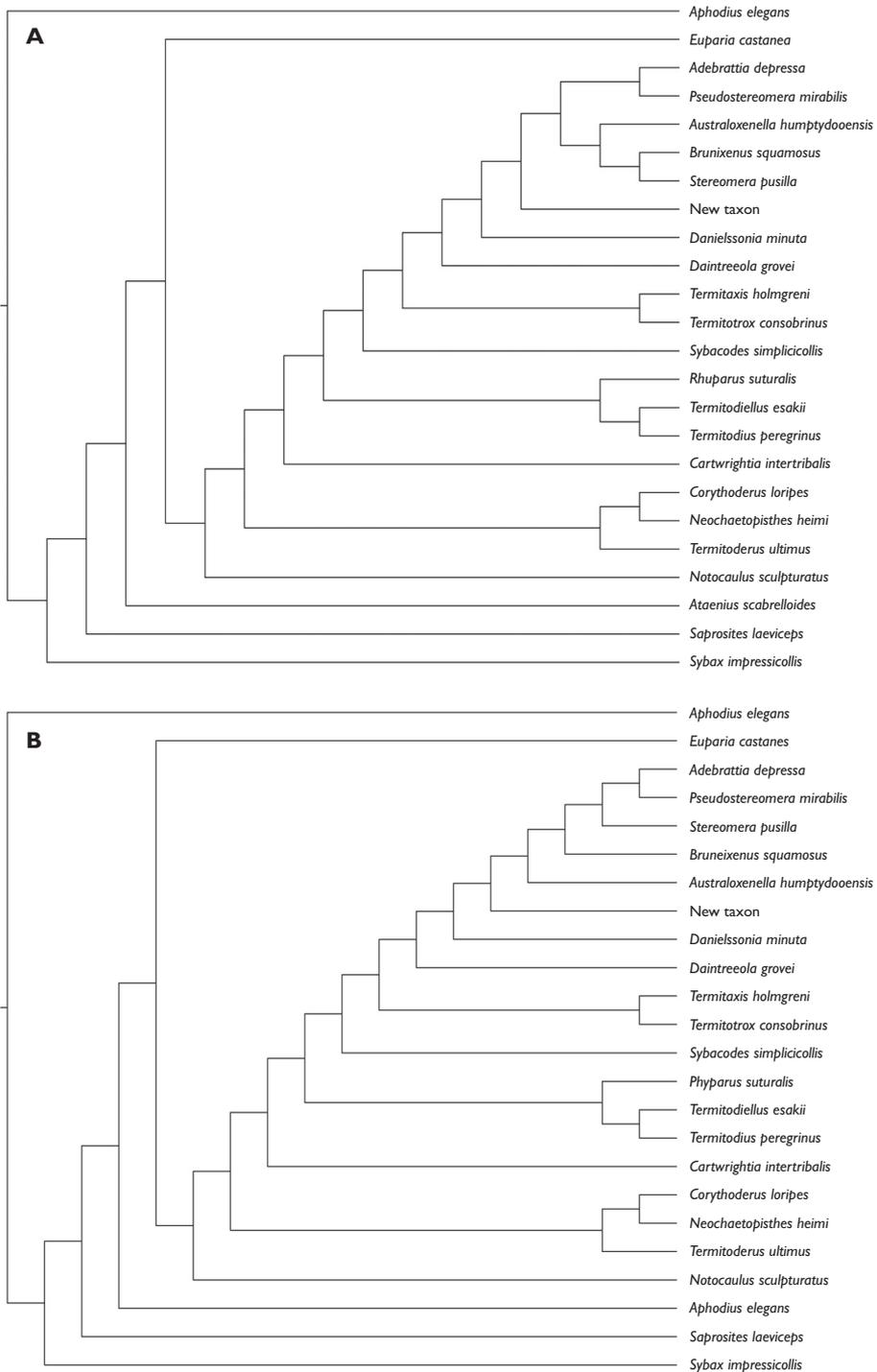
In addition to these, a number of ant inquilines have always been present in the Eupariini, including the type genus *Euparia*, and two species which are termite inquilines. At one point, Stebnicka erected the tribe Lomanoxiini for the most aberrant Neotropical ant inquilines (Stebnicka 1999), but that was synonymized into Eupariini (Skelley and Howden 2003). All these Neotropical forms were recently reviewed and pictured in Stebnicka (2009).



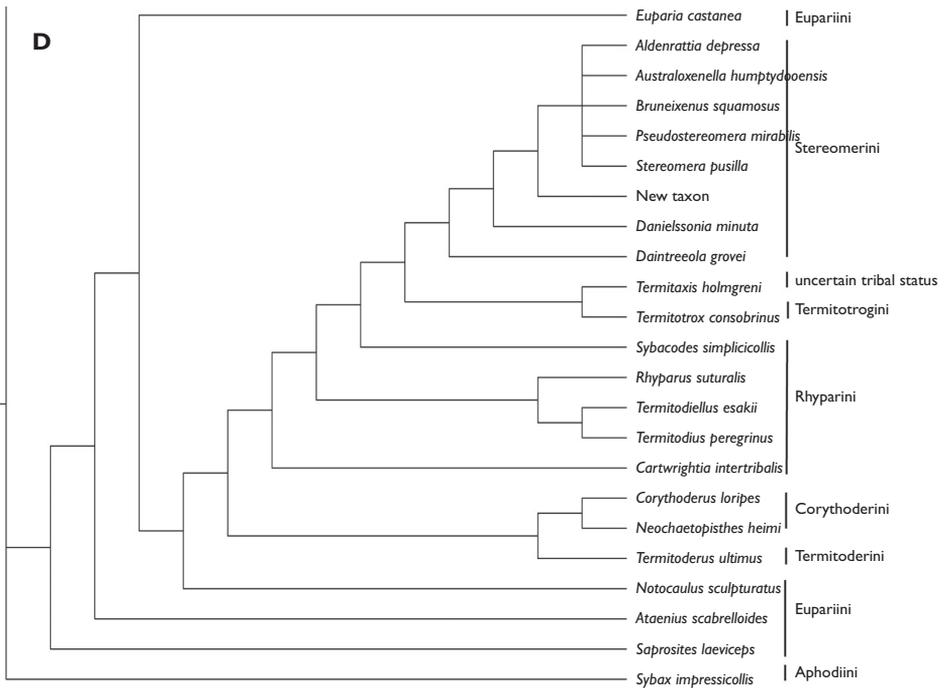
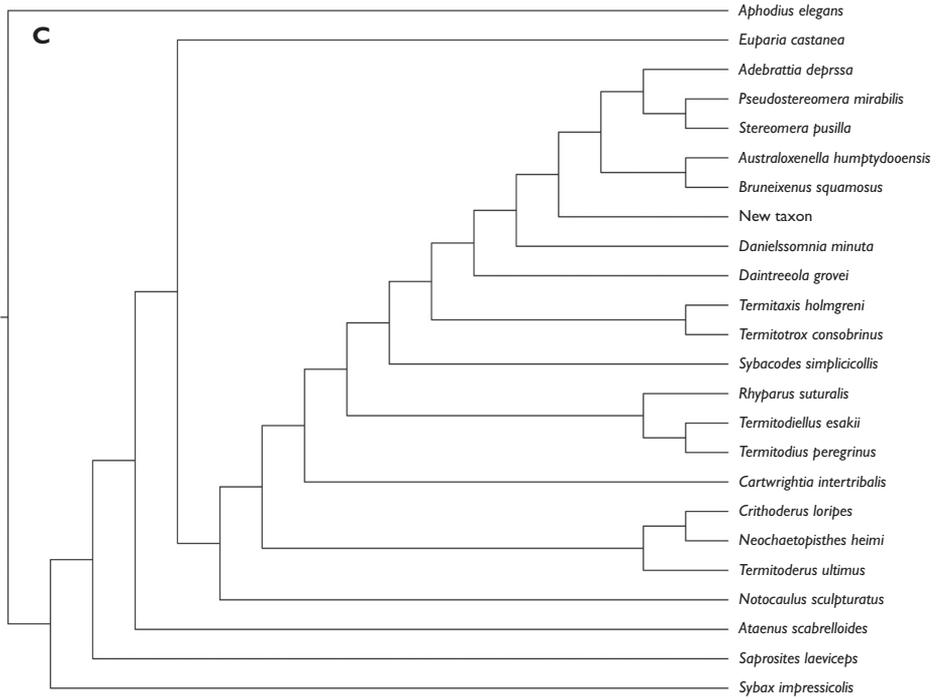
**Figure 5.** Posterior prosternal process of *Cheleion malayanum* sp. n. **A** scanning electron micrograph **B** stereo microscope image.



**Figure 6.** Legs of *Cheleion malayanum* sp. n. **A** scanning electron micrograph of foreleg **B** scanning electron micrograph of midleg showing un conspicuous tibial spurs **C** scanning electron micrograph of hindleg.



**Figure 7.** Resulting trees from phylogenetic analysis of morphological data of representatives of **A–C** The 3 most parsimonious trees **D** the strict consensus tree.



Stereomerini, Rhyparini, Corythoderini, Termitoderini, Termitotrogini, Aphodiini and Eupariini.

Table 4. Inquilines and suspected inquilines of Aphodiinae

Taxa	Habitat	Distribution	Species	Trichomes	Morphology type	Classification
Stereomerini	unknown; forest litter	South East Asian + Australian	19	trichomes	strongly synechthran	Stereomerini
Termitotrogini	termite inquilines	Afrotropical + Indian	10	not trichomes	strongly synechthran	Termitotrogini
<i>Rhyparus</i>	unknown; forest litter	Pantropical	56	trichomes	intermediate type	Rhyparini
<i>Termitodius</i> & <i>Termitodiellus</i> (+ <i>Aschnarhyparus</i> )	termite inquilines	Pantropical except Africa	10	trichomes	intermediate type	Rhyparini
Recent odd genera in Rhyparini ( <i>Hadorhyparus</i> Howden, <i>Leptorhyparus</i> Howden, <i>Lioglyptoxenus</i> Pittino, <i>Microtermitodius</i> Pittino, <i>Montitheolus</i> Howden and Storey, <i>Nanotermitodius</i> Howden)	termite inquilines	Pantropical except Africa	6	trichomes	often intermediate	Rhyparini
Corythoderini	termite inquilines	Afrotropical + Indian	35	trichomes	symphilic type	Corythoderini
<i>Termitoderus</i>	termite inquilines	Afrotropical	4	not trichomes	symphilic type	Termitoderini
<i>Termitaxis</i>	termite inquilines	Neotropical	1	trichomes	symphilic type	incertae sedis
<i>Cartwrightia</i>	ant inquilines	Neotropical	3	trichomes	intermediate type	Rhyparini (recently Eupartiini)

<b>Taxa</b>	<b>Habitat</b>	<b>Distribution</b>	<b>Species</b>	<b>Trichomes</b>	<b>Morphology type</b>	<b>Classification</b>
<i>Sybacodes</i>	unknown	Oriental	3	?trichomes	weakly synechthran	Rhyparini?
<i>Notocaulus</i>	mostly dung	Afrotropical	13	not trichomes	weakly synechthran	Eupariini (recently Rhyparini)
<i>Sybas</i>	unknown	Afrotropical	3	?trichomes	weakly synechthran	Aphodiini
<i>Euparotrix</i> Stebnicka and Howden	unknown	Australian	1	trichomes	more or less conventional aphodiine	Eupariini
<i>Napoa</i> Ross and <i>Batesiana</i> Chalumeau	termite inquilines	Neotropical	2	not trichomes	more or less conventional aphodiines	Eupariini
<i>Euparia</i> and relatives ( <i>Jarupea</i> Martinez, <i>Arupaia</i> Stebnicka, <i>Selviria</i> Stebnicka, <i>Flehtmanniella</i> Stebnicka, <i>Myrmecaphodius</i> Martinez, <i>Martineziana</i> Chalumeau & Ozdikmen, <i>Lomanoxoides</i> Stebnicka, <i>Paraplesiataenius</i> Chalumeau, <i>Bruchaphodius</i> Martinez)	mostly ant inquilines	Neotropical	>30	not trichomes	conventional aphodiines	Eupariini
<i>Lomanoxia</i> Martinez and relatives ( <i>Euparixia</i> Brown & <i>Euparixoides</i> Hinton)	ant inquilines	Neotropical	22	not trichomes	more or less conventional aphodiines	Eupariini (briefly Lomanoxiini)

The classification, and above all the relationships between the inquiline tribes, remains unsure because of the more or less far-reaching morphological specializations, including both obvious strongly derived specializations in habitus and integument, as well as reductions in characters traditionally used for distinguishing aphodiine tribes. Many of these specializations often overlap between the inquiline tribes, thus obscuring relationships between each other and between them and the large aphodiine tribe Eupariini, which is speciose in the tropics and characterized mainly by plesiomorphies visavis most other tribes of Aphodiinae.

Often, the appearance of tibial ridges and position of tibial apical spurs are used as diagnostic characters between Eupariini and Aphodiini. These characters are often useless in inquiline-type aphodiines with highly modified, short tibiae and reduced spurs. The abdominal characters traditionally used (fusing of sternites, pygidial furrow, etc.) often unite several but not all inquiline-type taxa with most Eupariini. Perhaps the dissection-requiring mouthparts and aedeagus, which both have provided characters considered important for aphodiine classification (Dellacasa et al. 2001 and elsewhere), but were not studied here, may provide useful information in this respect.

### Status of knowledge of biology of alleged inquilines

Strangely enough, it is only some of these inquiline-looking taxa that are actually found in association with social insects. Actually associated with termites are Termitotrogini, Corythoderini, Termitoderini, several small genera in Rhyparini (*Termitodius*, *Termitodiellus*, et al.), plus *incertae sedis Termitaxis*. One genus of similar morphology (*Cartwrightia*) and many more genera with more normal appearances are actually associated with ants. In several of the inquiline-type taxa, inquiline lifestyles have never been demonstrated; Stereomerini, a major part of Rhyparini (including *Rhyparus*), plus *Notocaulus* and *Sybacodes* (and *Sybox*). Instead, these are often found in forest litter, *Notocaulus* and *Sybacodes* also in dung. Of course, sifting forest litter and various trapping methods (light traps, Malaise traps, flight intercept traps) are far more common collecting methods than actually breaking into termite mounds. Thus, these taxa might be inquilines not yet encountered in their true habitat, or they may not live with social insects.

Typologies of social insect inquilines are from Wasmann (1894, 1903, 1918), who also studied many of these aphodiines, like Kolbe (1909). Balthasar (1963) summarized the knowledge. Later, Wilson (1971) and Kistner (1979, 1982) provided general discussion of inquiline types.

The basic division is between symphilic inquilines (those actually cared for by the hosts), and inquilines which are synoeketes (ignored by the hosts) or synechthrans (treated with hostility by the hosts). Morphologically, a symphilic lifestyle is often indicated by particular phenomena as possession of specialized tufts of glandular setae (trichomes) or enlarged abdomen (physogastry). Often, symphilic organisms display some kind of general morphological mimicking of their hosts. Synechthrans on the other hand are usually characterized with a “defensive” morphology, often very compact

body (sometimes referred to as “limuloid” body shape, after horseshoe crabs (*Limulus*)), with reinforcing ridges and the capacity to withdraw protruding appendages into folds or grooves.

Among the aphodiines, Corythoderini, Termitoderini and *Termitaxis* clearly correspond to the “symphilic” type (and are indeed found with termites). The clearest examples corresponding to the “synechthran” type are presented by Termitotrogini and Stereomerini (the one found with termites, the other not recognized). The Rhyparini are probably best considered synechthran in general morphology, but less so than Termitotrogini and Stereomerini, and also have symphilic-type trichomes. The typical Rhyparini are not found with termites, and could be described as weakly synechthran in morphology. Within Rhyparini, only the more or less aberrant taxa are actually found among termites, often being intermediate between the weaker synechthran-type and symphilic-type morphologies.

### **The rationale for classification of inquiline tribes**

It is unsatisfactory that this cluster of characters is regarded as an indication of a particular lifestyle in so many taxa where that lifestyle has not been observed. Some of them are commonly collected under circumstances giving no support whatsoever for that assumption. In aphodiine classification, various selections from this cluster are utilized to diagnose several aberrant tribes, while still being assumed to be intimately connected with a particular lifestyle and therefore largely homoplastic, and so not necessarily indicating a relationship between these different tribes while still keeping them together one by one. This is a problematic line of reasoning. A Darwinist framework still rests on interpreting similarities as the result of shared ancestry *unless* in conflict with other similarities. In this data set, the number of characters is small and the taxon sampling, particularly in various groups of possibly related Eupariini, is limited. For this reason, our results are uncertain and do not form the basis for any confidence in suggesting a revised tribal classification. Indeed the consistency is relatively low, but not extremely low, and there is a small number of most parsimonious trees, indicating that there is a fairly strong signal in the data. The Stereomerini, the core Rhyparini (excluding *Sybacodes* and *Cartwrightia*), and the Corythoderini, are all retained as monophyletic groups without conflict. All the representatives of aberrant taxa form a monophyletic group together.

Again, this is not a strong test, but the possibility that their similarities are to a significant extent due to shared ancestry rather than just shared lifestyle must be considered, especially since this particular lifestyle has in fact not been observed in so many of them. The aberrant or termitophilous tribes have been suggested to possibly be related to each other in a few works (Nikolajev 1993; Forshage 2002). Nikolajev suggests they could be related to each other and to Aulonocnemini. The phylogenetic status of Aulonocnemini is not well investigated, and it too might prove to be near or in Eupariini.

The few representatives of Eupariini included, on the other hand, admittedly covering very little of the diversity of the group but nevertheless representing its three most principal genera, did not form a clade together, but instead a grade basal to a single clade of all the “termitophilic” tribes. Eupariini is historically delineated in contrast with Aphodiini, and most of its diagnostic characters are defined in that contrast. As the phylogeny of Aphodiinae remains uncertain, the polarity of most of these characters is not known. Regardless of whether the character states found in Eupariini are plesiomorphic or apomorphic visavis Aphodiini, they are either shared with or clearly plesiomorphic visavis Psammodiini and most minor tribes. In fact it seems impossible to circumscribe Eupariini as a monophyletic group. Eupariini may perhaps be a paraphyletic grade of basal groups of Aphodiini, or it may be a huge possibly monophyletic complex, but in both cases very possibly with Psammodiini and several smaller tribes intermixed.

A more robust phylogenetic analysis including a wealth of eupariine taxa, several of the minor tribes, and many more characters than used here, will highlight the difficulties of keeping Eupariini in its present form, and suggest a revised tribal classification. Whether this will result in the synonymy of several tribes into a solid Eupariini *sensu lato*, or identify monophyletic lineages that will allow for even further splitting into more tribes, will be up to the judgment of that revisor.

## Acknowledgements

We express our gratitude to Bert Viklund for presenting the specimen of the new species to us. We thank Gary Wife at Department at the Biological Structure Analysis Group at the Evolutionary Biology Centre at Uppsala University for assistance with the scanning electron microscope. The *Termitotrox* type was found in material presented to MF by Roy Danielsson at the Museum of Zoology in Lund, Sweden, who also kindly provided the types of *Adebrattia depressa*, *Pseudostereomera mirabilis* and *Danielssonia minuta*. Torsten Nordander, The Natural History Museum in Gothenburg, was helpful in the return of the *Termitotrox* type. The constructive comments of two anonymous reviewers improved the manuscript considerably.

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# The Ceratocanthinae of Ulu Gombak: high species richness at a single site, with descriptions of three new species and an annotated checklist of the Ceratocanthinae of Western Malaysia and Singapore (Coleoptera, Scarabaeoidea, Hybosoridae)

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## Abstract

The remarkable species richness of Ceratocanthinae (Coleoptera: Scarabaeoidea: Hybosoridae) found at Ulu Gombak (Selangor, West Malaysia), a secondary rainforest research station, is discussed. Eighteen species have been collected, mainly in nests of termites (Isoptera) and bess beetles (Coleoptera: Passalidae). Among them at least seven are new species, three of them here described: *Madrasotes hashimi* **sp. n.**, *Madrasotes mirificum* **sp. n.**, and *Pterorthochaetes tsurui* **sp. n.** Four other species (*Madrasotes agostii* Paulian, *Madrasotes clypeale* Paulian, *Madrasotes depressum* Paulian, and *Madrasotes simplex* Paulian) are recorded for the first time for West Malaysia and three for new states within West Malaysia (*Pterorthochaetes insularis* Gestro, *Madrasotes malayanum* Paulian and *Madrasotes sculpturatum* Paulian). A checklist of the 34 Ceratocanthinae recorded so far from West Malaysia and Singapore is provided with taxonomic, distributional and morphological remarks on some species.

## Keywords

Coleoptera, Hybosoridae, Ceratocanthinae, *Besuchetostes*, *Madrasostes*, *Pterorthochaetes Ebbrittoniella*, *Cyphopisthes*, *Eusphaeropeltis*, taxonomy, biology, termitophily, Passalidae, Isoptera, rainforest, Selangor, Malaysia

## Introduction

The feeding habits of the Ceratocanthinae (Coleoptera: Scarabaeoidea: Hybosoridae) are still unknown. Because many species are found in termite nests or in leaf litter, they have been supposed to feed on fungi (Scholtz and Grebennikov 2005) or to feed on termitaria (Iwata et al. 1992), although up to now no evidence has been obtained to support these hypotheses. The increasing information on the diversity of their mouthparts morphology and, to a lesser extent, of their life histories (e.g. Ballerio 2008, Ballerio 2009, Ballerio and Wagner 2005) however makes reasonable to expect a diversity in feeding habits too. Because of this lack of knowledge any ecological approach to the Ceratocanthinae diversity is very difficult and merely speculative. The aim of this paper is to shed some more light on Ceratocanthinae natural history by briefly discussing a massive finding of several Ceratocanthinae species at a single site in West Malaysia. We describe also three new species found at that site and take the occasion to provide an annotated checklist of the species so far recorded for West Malaysia and Singapore.

## Methods and acronyms

We refer to Ballerio (2000a, 2000b, 2008, 2009) for methods and terminological conventions. In giving label data author's comments are in square brackets, while depository collection acronyms are in parenthesis.

Micrographs were obtained with a Zeiss EVO 40 XVP Scanning Electron Microscope at the Museo Tridentino di Scienze Naturali (Trento, Italy), after gold coating.

Habitus photographs were taken with Microptic System and mounted with the automontage software CombineZM, or obtained with a Canon PowerShot S80 connected to a Leica MZ 12.5 stereomicroscope and then mounted with the automontage software Syncrosopy.

Habitus photographs of living individuals were taken in the field using Nikon D70 and Tamron 1:2.8 macro lens, with Konica Minolta Twin Flash 2400.

In the descriptions for ocellate punctures we refer to the definitions given by Howden and Gill (2003).

### Abbreviations:

<b>EL</b>	maximum elytral length
<b>EW</b>	maximum total elytral width
<b>FIT</b>	flying interecept trap

<b>HL</b>	maximum head length
<b>HW</b>	maximum head width
<b>L</b>	length
<b>PL</b>	maximum pronotal length at middle
<b>PW</b>	maximum pronotal width at middle
<b>W</b>	width
<b>ABCB</b>	Alberto Ballerio collection, Brescia, Italy.
<b>KUM</b>	The Kyushu University Museum, Fukuoka, Japan.
<b>MHNG</b>	Muséum d'histoire naturelle collection, Genève, Switzerland.

### **The Ceratocanthinae of Ulu Gombak**

From 2003 onwards, the second author conducted field work at the University of Malaya Ulu Gombak Studies Centre (West Malaysia, Selangor, 3°19'N 101°45'E, 250 m a.s.l.), for research on various groups of termitophilous and myrmecophilous insects. The area is mostly covered with advanced secondary forest of the lowland dipterocarp type. The topography is rough, mostly steep hillsides and narrow valley bottoms (Wiedemann 1969).

The total number of Ceratocanthinae collected at Ulu Gombak from 2003 to 2009, scores respectively 600 specimens and 18 species, although the majority of them (500 specimens representing 16 species) were collected in an one-month stay in 2007 (from April 5 to May 7).

The number of species recorded is particularly remarkable. Eighteen species represent about half the number of the species known from West Malaysia and appears to be a high number for a single secondary forest site. Interestingly no flightless species of Ceratocanthinae have been collected and this could be due to the circumstance that Ulu Gombak is a secondary forest, which after its re-growth has never been connected to any primary forest. The second author samplings from the area did not yield any flightless beetle species.

Currently the knowledge of the alpha diversity of Ceratocanthinae for a single site is limited to two contributions: Ballerio and Wagner (2005) listed five species occurring in the Budongo forest (Uganda) and Erwin et al. (2005) and Erwin and Geraci (2009) listed eleven morphospecies (no identifications were made) from the Yasuni National Park in Ecuador. Both lists resulted from mainly canopy fogging surveys, hence with an underestimated representation of the leaf litter fauna (often made of flightless species). The number of species collected in Ulu Gombak reveals therefore the highest species richness recorded for a single site.

## Ulu Gombak species list and collecting data

The number of specimens collected is in parenthesis.

- 1) *Madrasostes variolosum* Harold  
21. V – 3. VI 2003, M. Maruyama, by FIT (6); 7. IV – 6. V. 2007, M. Maruyama et al., from termite nest(s) (195); 6 – 13. III. 2009, M. Maruyama et al., from termite nest(s) (101).
- 2) *M. simplex* Paulian  
7. IV – 6. V, M. Maruyama et al. (27); 6 – 13. III. 2009, M. Maruyama et al. (7). All from termite nest(s).
- 3) *M. hashimi* sp. n.  
19. IV. 2007, M. Maruyama et al. (1); 24. IV. 2007, M. Maruyama (1); 29. IV. 2007, M. Maruyama (1); 5. V. 2007, M. Maruyama (1). All from termite nest(s).
- 4) *M. depressum* Paulian  
15. IV. 2007, M. Maruyama et al. (2); 26. IV. 2007, M. Maruyama (2); 3. V. 2007, M. Maruyama (1); 5. V. 2007, M. Maruyama (1). All from termite nest(s).
- 5) *M. boucomonti* Paulian  
2 – 18. III 2004, M. Maruyama, by FIT (1); 11. V 2005, K. Yamada, by sifting (1); 29. IV. 2007, M. Maruyama, at light (1); 6 – 13. III. 2009, M. Maruyama et al., from termite nest(s) (6).
- 6) *M. sculpturatum* Paulian  
7. IV – 6. V. 2007, M. Maruyama et al. (114); 6 – 13. III. 2009, M. Maruyama et al. (24). All from termite nest(s).
- 7) *M. agostii*  
7. IV – 6. V. 2007, M. Maruyama et al. (14); 6 – 13. III. 2009, M. Maruyama et al. (2). All from termite nest(s).
- 8) *M. clypeale* Paulian  
7. IV – 6. V. 2007, M. Maruyama et al. (71); 6 – 13. III. 2009, M. Maruyama et al. (42). All from termite nest(s).
- 9) *M. malayanum* Paulian  
15. IV. 2007, M. Maruyama et al. (1); 16. IV. 2007, M. Maruyama et al. (1); 20. IV. 2007, M. Maruyama (1); 28. IV. 2007, M. Maruyama (1); 29. IV. 2007, M. Maruyama (1); 30. IV. 2007, M. Maruyama (1); 3. V. 2007, M. Maruyama et al. (1); 7. III. 2009, Maruyama et al. (1). All from termite nest(s).
- 10) *M. mirificum* sp. n.  
15. IV. 2007, M. Maruyama et al. (2); 16. IV. 2007, M. Maruyama et al. (1); 17. IV. 2007, M. Maruyama (1); 19. IV. 2007, M. Maruyama (3); 20. IV. 2007, M. Maruyama (3); 26. IV. 2007, M. Maruyama (5); 28. IV. 2007, M. Maruyama (3); 30. IV. 2007, M. Maruyama (1); 1. V. 2007, M. Maruyama (3); 3. V. 2007, M. Maruyama (7); 7. III. 2009, M. Maruyama et al. (2); 10. III. 2009, M. Maruyama et al. (1). All from termite nest(s).

- 11) *Pterorthochaetes insularis* Gestro  
7. V. 2005, M. Maruyama, from termite nest(s) (1); 18. VI. 2006, Y. Katayama, from bess beetle nest(s) gallery (9); 24. IV. 2007, M. Maruyama, from termite nest(s) a (1); 28. IV. 2007, M. Maruyama, from termite nest(s) (1); 30. IV. 2007, M. Maruyama, from termite nest(s) (1); 3. V. 2007, M. Maruyama, from termite nest(s) (3).
- 12) *P. tsurui* sp. n.  
15.IV.2007, M. Maruyama (1) ; 26. IV. 2007, M. Maruyama et al. (2); 28. IV. 2007, M. Maruyama (1); 29. IV. 2007, M. Maruyama (1); 30. IV. 2007, M. Maruyama (2); 3.V.2007, M. Maruyama (1) ; 4. V. 2007, M. Maruyama (1). All from termite nest(s).
- 13) *Pterorthochaetes* sp.  
20. IV. 2007, M. Maruyama (1); 24. IV. 2007, M. Maruyama (2); 26. IV. 2007, M. Maruyama (1); 28. IV. 2007, M. Maruyama (1); 29.IV.2007, M. Maruyama (1) ; 5. V. 2007, M. Maruyama (1); 7. III. 2009, S. Befu (3). All from termite nest(s).
- 14) *Eusphaeropeltis* sp. a (large, green)  
27 XI 2005, M. Maruyama, by FIT (1).
- 15) *Eusphaeropeltis* sp. b (small, rainbow)  
10 IV 2007, M. Maruyama, from termite nest(s) (1).
- 16) *Eusphaeropeltis* sp. c (small, red)  
15 IV 2007, T. Tsuru, by net sweeping (1).
- 17) *Cyphopisthes* sp.  
7. IV – 6. V. 2007, M. Maruyama et al. from termite nest(s) (121); 9. IV. 2007, T. Tsuru, by net sweeping (3).
- 18) *Ebbrittoniella ignita* (Westwood)  
9. III. 2009, Y. Matsumura, by net sweeping (1).

### Biological notes on the Ceratocanthinae of Ulu Gombak

All the *Madrasotes* species found in Ulu Gombak were associated with termites (Isoptera). Almost all the specimens and all species but *M. boucomonti* were collected from the nests of *Coptotermes* sp. The termites nested in dead standing trees, whose surface was covered by a muddy wall made by the termites. Both larvae and adults of *Madrasotes* beetles were found inside the wall (which is about 1–1.5 cm thick, allowing the digging of tunnels inside). *Madrasotes boucomonti* were only (with the sole exception of one specimen that was attracted at light) collected in the foraging galleries of *Macrotermes* sp. (not in the nest), which were wet and soft clayey, or by sifting the soil where the host termites were foraging. The *Madrasotes* species observed remained concealed under the surface of the nest material in the daytime, while they were walking and mating on the surface of the nest at night. Some specimens of *M. variolosum* (the most abundant species) were obtained also by flight interception traps.

*Pterorthochaetes* species were collected from the surface of nests of *Coptotermes* termites at night, but the condition of the nest was different from the ones where *Madrasotes* species were found: it was not wet and not muddy, and with more wood debris

(the first author in 1999 collected several *Pterorthochaetes* species inside dead logs occupied by termites in various localities of Perak, Pahang and Kelantan). *Pterorthochaetes* were also abundant in the galleries of Passalidae (e.g. *Leptaulax* sp.): both larvae and adults were found in the wood debris of the galleries. Association with Passalidae has already been reported for some New World species of Ceratocanthinae by Ohaus (1909) and Woodruff (1973). A single specimen of *Pterorthochaetes* was found in the arboreal nest of *Hospitalitermes* sp.

*Eusphaeropeltis* and *Ebbrittoniella* were usually collected by net sweeping of bushes in the daytime, or by flight interception traps (the genus *Eusphaeropeltis* elsewhere has also been collected by canopy fogging, Ballerio and Wagner 2005), but *Eusphaeropeltis* sp. b was collected inside a mound of *Dicuspidermes* sp. termites.

*Cyphopisthes* sp. were collected in similar condition as *Madrasostes* species, but preferred more clayey nest material. Once the termite nest was excavated, specimens of *Cyphopisthes* sp. flew attracted to the nest material at night (interestingly this behaviour was not observed in *Madrasostes*), a similar behaviour is reported by Howden and Gill (2000) for the Neotropical genus *Astaenomoechus* Martínez and Pereira, 1959, *Cyphopisthes* sp. were also collected by net sweeping of bush in the daytime.

### **Annotated checklist of the Ceratocanthinae of West Malaysia and Singapore with description of three new species from Ulu Gombak**

An alphabetic list of the Ceratocanthinae currently recorded for West Malaysia and Singapore is provided below, based on published records plus the new species hereinafter described and the new records from Ulu Gombak. For each species the known distribution is recorded (“Known distribution”), limited to the country (or to the state if within West Malaysia) and the original bibliographical source is added in brackets. West Malaysia is simply indicated for old records from “Malacca”, since this name in ancient literature had a broader meaning than in present days (being now the name of a small coastal state south of Negeri Sembilan). “New material examined” refers only to unpublished data extending the known distribution to West Malaysia or to new state records within West Malaysia (the Ulu Gombak material, being already listed above, is not reported). Some taxonomic and morphological remarks on various species are added. The record of *Madrasostes feae* (Gestro, 1899) (sub *Pterorthochaetes feae*) for “Malacca” found in Paulian (1978) is erroneous as demonstrated by Ballerio (1999).

With the three new species hereinafter described, the number of species known to occur in West Malaysia increases to 34 (about the 10% of all known Ceratocanthinae species worldwide and the 60% of the species recorded from South East Asia). This figure is however far from being complete: the first author has examined at least 10 further undescribed species occurring in West Malaysia and it is reasonable to think that other species, especially flightless members of the *Perignamptus* genus group, could occur in the primary rainforests still present in the area, so that the final figure could be well over 50 species, making the Malay Peninsula a hot spot of Ceratocanthine diversity.

***Besuchetostes howdeni* Paulian, 1979**

Known distribution: West Malaysia (Pahang) (Paulian 1979).

Remarks. This is a flightless species known up to now by the type series only. Examination of the type series revealed that this species does not belong to *Besuchetostes* Paulian, 1972 (see below, under *B. jaccoudi*, for more details).

***Besuchetostes jaccoudi* Paulian, 1977**

Known distribution: West Malaysia (Pahang) (Paulian 1977).

Remarks. This is another flightless species known up to now by the holotype (in the collection of the Museum National d'Histoire naturelle, Paris) and a few further specimens from the type locality (MHNG, ABCB). Examination of all available material revealed that this species does not belong to *Besuchetostes*. Paulian placed this species in the genus *Besuchetostes* mainly because of the lack of genal canthus/dorsal ocular area, a character to which he gave much importance. However, according to a preliminary analysis carried out by the first author, the presence/absence of a genal canthus seems often the result of the fusion of the genal canthus with the occipital area of the head surface, a character that could be related to an adaptation to live in dark environments (leaf litter, dead logs), so it is highly homoplastic in the group and not particularly reliable for defining genera. Based on the aforesaid analysis the genus *Besuchetostes* is now characterized by a combination of characters involving mouthparts morphology, pronotum posteriorly swollen and protruding backwards, male genitalia and, above all, the shape of antennal scape and pedicellus. In *Besuchetostes* the antennal scape is regularly gradually swollen proximad and the pedicellus is very large (about as wide as the apical portion of scape), whereas in *B. jaccoudi* the scape is securiform, with pedicellus smaller than the apical portion of the scape. The overall morphology of *B. jaccoudi* would suggest its placement in the *Perignamptus* genus group, as defined by Ballerio (2009), although currently it is not possible to assign it to any given genus, due to the messy systematics of the genera belonging to the group.

***Cyphopisthes crux* (Sharp, 1875)**

Known distribution: Indonesia (Kalimantan), West Malaysia (Perak, Selangor) (Paulian 1942)

***Cyphopisthes minutus* Paulian, 1978**

Known distribution: Malaysia (Perak) (Paulian 1978).

***Cyphopisthes wallacei* (Pascoe, 1860)**

Known distribution: Indonesia, West Malaysia (Perak) (Paulian 1978).

Remarks. The West Malaysian record is doubtful, as stated by Paulian himself (1978). The occurrence of *C. wallacei* outside Borneo has to be confirmed. The synonymy between *Cyphopisthes wallacei* and *Cyphopisthes humeralis* Gestro, 1899 (described from Borneo) established by Paulian (1978) doesn't seem acceptable. The majority of

published records for *C. wallacei* outside Borneo seems to be wrong. The genus *Cyphopisthes* Gestro, 1899 is in need of a revision.

***Ebbrittoniella gestroi* (Paulian, 1942)**

Known distribution: Indonesia (Sumatra, Kalimantan), East Malaysia (Sabah, Sarawak), West Malaysia (Pahang, Perak) (Ballerio 2000b).

***Ebbrittoniella ignita* (Westwood, 1883) (Fig. 4D)**

Known distribution: Indonesia (Sumatra, Kalimantan), East Malaysia (Sabah), West Malaysia (Selangor, Pahang, Johor) (Ballerio 2000b).

***Eusphaeropeltis aureola* Gestro, 1899**

Known distribution: West Malaysia (Perak) (Gestro 1899)

***Eusphaeropeltis aurora* (Lansberge, 1887)**

Known distribution: West Malaysia (Perak) (Gestro 1899)

***Eusphaeropeltis iris* Gestro, 1899**

Known distribution: West Malaysia (Perak) (Paulian 1978)

***Eusphaeropeltis kedahensis* Paulian, 1942**

Known distribution: West Malaysia (Kedah) (Paulian 1978)

***Eusphaeropeltis punctatissimus* (Lansberge, 1887)**

Known distribution: Brunei, West Malaysia (Paulian 1978)

***Madrasostes agostii* Paulian, 1993 (Fig. 2C, Fig. 6B)**

Known distribution: Indonesia (Sumatra) (Paulian 1993).

Remarks. First record for West Malaysia.

***Madrasostes boucomonti* Paulian, 1978 (Fig. 2B)**

Known distribution: West Malaysia (Selangor) (Paulian 1978), Indonesia (Sumatra) (Paulian 1992).

***Madrasostes clypeale* Paulian, 1993 (Fig. 2D, Fig. 6C, D)**

Known distribution: Indonesia (Sumatra) (Paulian 1993).

New material examined: West Malaysia, Perak, 25 km NE of Ipoh, Banjaran Titi Wangsa Mounts, Gunung Korbu, 1400–1800 mt., 11–31.I.1999, leg. P. Cechovsky (ABCB); West Malaysia, Perak, Penang Island, above botanical garden, 250 mt., 12.XI.1999, #4a, leg. Cuccodoro & Loebl, sifting forest leaf litter (MHNG, ABCB). Remarks. First record for West Malaysia (Perak and Selangor). The amazing sexual dimorphism of this species has already been described (Ballerio 2006). An examination of the microsculpturing of pronotum through scanning electron microscopy re-

vealed that the pronotal punctures bottom surface is areolate (Fig. 5A, B). The larger punctures of females have the areolate surface limited to a portion of the bottom and slightly raised (Fig. 5C, D, E). Each puncture is often preceded by a short fine seta. It was not possible to detect any pore inside the punctures, so that the dirt which usually fills the punctures comes probably from outside. The species closest to *M. clypeale* is *Madrasostes thai* Paulian, 1987, known only by the male holotype from Thailand (Chanthaburi province, well north of the isthmus of Kra, which is the boundary between the Sundaland and Indochinese subregions, see Corlett 2009). Both *M. clypeale* and *M. thai* represent a distinctive group within *Madrasostes* and their current generic placement in the genus *Madrasostes* must be regarded as provisional in the framework of a revision of the *Perignamptus* generic group.

***Madrasostes depressum* Paulian, 1992** (Fig. 2A)

Known distribution: Indonesia (Sumatra) (Paulian, 1992).

Remarks. First record for West Malaysia (Selangor). This species has two distinctive paired thick sclerites in the internal sac of aedeagus. The shape of these sclerites in the Ulu Gombak material is slightly different from the shape of the sclerites of the holotype, however, due also to the circumstance that the Sumatran population is known by the type only, we were unable to find further differences that could allow a taxonomic separation of the Sumatran populations from Peninsular Malaysian specimens.

***Madrasostes malayanum* Paulian, 1979** (Fig. 2E)

Known distribution: West Malaysia (Pahang).

Remarks. First record for Selangor. This species was known only by its type series, which consists only on females. The overall morphology suggests a close similarity to *Madrasostes parcepunctatum* Paulian, 1989 from Borneo (Sabah).

***Madrasostes mirificum* sp. n.**

urn:lsid:zoobank.org:act:903EBB4B-72C9-4463-9784-10F08C856EBC

(Fig. 2F, G, H, I, J)

**Type locality.** West Malaysia: Ulu Gombak (Selangor), 3°19' N 101°45' E.

**Material examined.** *Holotype*, male: West Malaysia, Selangor, Ulu Gombak, 250 mt., 17.IV.2007, Leg. M. Maruyama / *Madrasostes mirificum* sp. n. det. Ballerio & Maruyama 2009 Holotypus (KUM) [distended specimen, glued on a card, dissected, genitalia mounted in DMHF resin on a separate card, same pin]. *Paratypes* [three males dissected]: same locality as holotype but: 15 IV 2007, M. Maruyama et al. (1 male and 1 female); 16 IV 2007, M. Maruyama et al. (1 male); 19 IV 2007, M. Maruyama (3 males); 20 IV 2007, M. Maruyama (2 males and 1 female); 26 IV 2007, M. Maruyama (3 males and 2 females); 28 IV 2007, M. Maruyama (1 male and 2 females); 30 IV 2007, M. Maruyama (1 male); 1 V 2007, M. Maruyama (3 females); 3 V 2007, M. Maruyama (5 males and 2 females), 7.III.2009, M. Maruyama (2 males) ; 10.III.2009,

M. Maruyama (1 male).(20 KUM, 2 MHNG, 6 ABCB) ; 5 males and 9 females [two males and one female dissected]: West Malaysia, Perak, 25 km NE of Ipoh, Banjaran Titi Wangsa Mounts, Gunung Korbu, 1400–1800 mt., 11–31.I.1999, leg. P. Cechovsky (ABCB).

**Description.** HL = 0.58 mm; HW = 1.16 mm; PL = 1.53 mm; PW = 1.93 mm; EL = 2.32 mm; EW = 1.88 mm.

Small Ceratocanthinae, body shiny, setose; “rolling up” coaptations perfect; volant.

Dorsum black, setation yellow/whitish, sternum reddish, antennae reddish.

*Head:* wide (W/L ratio = 2), subpentagonal, sexually dimorphic, fore portion triangular, apex forming an obtuse angle (about 120°), both sides of the angle rectilinear, irregularly serrated, not reflexed upward, tip of triangle blunt; genae aligned with fore margin, acutely protruding outwards, genal canthus present, reaching the occipital area of head, dorsal ocular area small, dorsal interocular area about 18 times the maximum width of the dorsal ocular area, ventral ocular area small; head dorsal surface with dense impressed fine comma-shaped punctures, fore margin with a few very fine shallow transverse striae. Near each comma-shaped puncture a very short erect simple seta.

*Pronotum:* subrectangular, wider than long (W/L ratio = 1.25), wider than elytra; fore margin feebly bisinuate; fore angles gently subtruncate at apex; fore edge continuously finely margined, edges of sides without any visible margin (dorsal view), base continuously strongly margined; base at middle not protruding backwards; pronotal surface regularly convex without paradiscal depressions. Shiny, smooth, with dense impressed horseshoe-shaped punctures, with opening centrifugally oriented, their distance from each other being inferior than their diameter, two smooth areas with sparser puncturation near base at each side of disc. Each puncture bearing in the middle a short erect simple seta, about as long as the puncture diameter.

*Scutellum:* about as wide as long, sides proximally subparallel and distinctly notched by elytral articular process, then convergent to form a triangle with elongate acute apex and sides slightly curved inward. Surface slightly depressed in the middle, covered by dense impressed horseshoe-shaped punctures, with opening directed backwards. Apical portion of mesepisterna visible from above.

*Elytra:* longer than wide (W/L ratio = 0.81), apical fourth regularly rounded (dorsal view), apex slightly re-entering inward (lateral view); elytra regularly convex, although slightly flattened at disc; elytral suture not or very finely raised; inferior sutural stria present, ending just before humeral area; marginal area with sparse irregular puncturation, articular area with striation, not visible in lateral view; humeral callus small; elytral articular process large, smooth and shiny. Elytra smooth, shiny, with four longitudinal, weakly raised, blunt carinae, the first carina corresponding to the sutural stria, starting at medial third, the second one more raised apically, starting near elytral base, the third and fourth ones starting at apical third. Elytral puncturation made of irregular longitudinal rows of medium sized impressed elongate horseshoe-shaped punctures (each one bearing in the middle a simple erect seta), with opening backwards, their distance from each other being inferior to their diameter, mixed with simple impressed

punctures. Between sutural carina and the second carina in the distal third of elytra punctures often merging into three longitudinal impressed lines.

Clypeopleuron short and transversely slightly grooved at each side. Apex of head forming a thick protrudent process, more developed in males. Labrum wide and short, semicircular, bearing six long semierect setae and distally fringed by long fine setae directed forward. Distal epipharynx (Fig. 5G) semicircular, longitudinally divided by a strong anterior median process; pariae distinctly raised with respect to the haptolachus; median brush and corypha absent; apical fringe made of long fine setae, absent in the middle. Mentum (Fig. 5F) ventrally flat, widely emarginated in the middle, emargination regularly wide-U-shaped; labial palpi (including palpiger) two jointed, first joint short and transverse, joint two longer and plumper than preceding one, joint four flattened, apically bearing some short sensilla, all joints, apart from the last one, fringed with long setae. Maxillae (Fig. 5J) with an elongate single membranous lacinia, covered with fine long setae, monolobed galea proximally sclerotized and distally clothed with very coarse long fine setae with distinctive comb-like tip (galeal brush) (Fig. 5I), maxillary palpi (including palpiger) four jointed, palpiger very small, joint two wide and relatively short, joint three relatively short, joint four long and subconical, about as long as preceding two together, apically bearing some short sensilla. Mandibles (Fig. 5H) short, regularly curved, apicalis with very short and blunt apical tooth, not protruding over mesal brush, lateral sclerite of apicalis bearing a distinct large pore, conjunctive present, mesal brush wide and well developed, basalis with molar lobe relatively strong. Antennae 10-segmented, scape long (about half the total length of antenna), distally securiform, pedicellus plump and rounded, flagellum short and thin, distinctly wider than long short articles, antennal club with three articles, articles uniformly setose.

Ventral areas of prothorax slightly alutaceous, setigerously punctured, with setae fine and long. Procoxae transversely oriented, apices nearly touching each other; fore trochanters relatively wide, with fore tips bearing a tuft of long setae; profemora slender, fore margin slightly curved inwards, surface almost smooth with few recumbent setae; protibiae straight, sexually dimorphic, apical spur relatively long, sharp, distally curved downward, protarsi with first article longer than the following three articles together, articles two to four relatively plump, article five slightly longer than four, bearing two short curved claws, each tarsomere, except tarsomere five, ventrally bearing a tuft of fine setae. Mesosternum narrow, short and plump. Mesocoxae large, almost adjacent to each other, transversely oriented. Trochanters narrow, with hind tip acute. Mesofemora slender, surface smooth, with hind edge emarginated at distal third. Mesotibiae slender, thick, inner angle of apex with one straight apical spur, mesotarsi inserted near the inner angle of apical edge, slightly longer than apical edge of tibia, with first four articles plump and subequal, fifth slightly longer than the preceding one, bearing two small curved claws; each tarsomere, except the last one, ventrally bearing a tuft of coarse setae; trochanters of metafemora narrow, with hind tip acute, metafemora plumper than mesofemora, surface hairy, hind edge distally with a small emargination, metatibiae triangular, elongate, flat, inner side not sinuated, ending with two straight and sharp fine spurs paired at the inner angle of the tibia, metatarsi almost as long as the apical edge of tibia,

first article almost as long as the following two together, articles two to four short and plump, fifth longer than the fourth, with ends with two claws small and feebly curved; each tarsomere, with the exception of the last one, ventrally bearing a tuft of coarse setae. Outer face of meso- and metatibiae with longitudinal striae along inner margin.

*Wings:* normally developed.

*Sexual dimorphism:* males with strongly modified head and pro- and mesotibiae. Male head with distal portion, before fore margin, lowered compared to median and proximal portions of head, tip truncated swollen (nose-like) and directed upwards, overall head shape more subrectangular than subpentagonal. Male protibiae thicker than female protibiae, twisted, median and distal third disaligned compared to basal third, median and distal third arched in lateral view, outer margin ending with two strong teeth, other three outer teeth present medially and basally, protibia ending with an apical spur plumper than in females and with distal third more dramatically bent downwards, ventral side fringed by rows of thick setae. Male mesotibiae ending with a straight apical spur and with the inner apical angle with an acute expansion (false spur) replacing the hooked apical spur usually present in other genera of Ceratocanthinae. Females with head normally shaped (Fig. 2H) protibiae normally developed, with two apical teeth and a row of four denticles, apical spur of protibiae slender and more gently bent downwards, mesotibiae ending with a straight apical spur, lacking any false transverse spur.

*Male genitalia:* genital segment fairly sclerotized, Y-shaped (Fig. 8A), with manubrium about as long as basal triangle. Aedeagus with basal piece distally curled (Fig. 8B), about six times longer than parameres; parameres slightly asymmetrical, dorsally flattened (Fig. 8C).

**Variability.** The type series shows a strong variability in the development of the smooth areas near the base of pronotum as well as in the microsculpturing of elytra, especially in the shape and density of punctures between carinae and in the development of the longitudinal striae.

**Identification.** Easily identifiable among all other *Madrasostes* because of the very thick pro- and mesotibiae and the sexually dimorphic characters (male shape of protibia and nose-like process on head), which are unique among all other known Ceratocanthidae.

**Etymology.** *Mirificum*, Latin adjective meaning wonderful, due to the striking morphological features that characterize this species.

**Distribution and habitat.** This species occurs in Perak and Selangor in both lowland and submontane rainforest. The paratypes from Gunung Korbu were collected in a termite nest (Petr Checovsky, pers. comm.). For more details on the Ulu Gombak series see the introductory paragraphs.

**Remarks.** *Madrasostes mirificum* sp. n. displays a series of unique characters (most of which likely to be autoapomorphic), which place this species in a very isolated position within the genus *Madrasostes* and which would represent good points for the erection of a distinct genus in the framework of a complete revision of the *Perignamptus* genus group: a) male's apex of head modified, b) male protibiae shaped as in Fig. 2I, J, d) mesotibiae thick, e) male mesotibiae ending with only one apical spur.

***Madrasostes rafflesi* Paulian, 1979**

Known distribution: Malaysia (Pahang) (Paulian 1979).

Remarks. An enigmatic species. The holotype only is known, most probably a female. This species shows an unusual morphology and its placement in *Madrasostes* must be regarded as doubtful.

***Madrasostes hashimi* sp. n.**

urn:lsid:zoobank.org:act:EADB4ADB-ED02-4F5F-A1EC-C0AEB4F53371

(Fig. 1C, D)

**Type locality:** West Malaysia: Ulu Gombak (Selangor), 3°19' N 101°45' E.

**Material examined.** *Holotype*, male: West Malaysia, Selangor, Ulu Gombak, 250 mt., 24.IV.2007, Leg. M. Maruyama / *Madrasostes hashimi* sp. n. det. Ballerio & Maruyama 2009 Holotypus (KUM) [distended specimen glued on a card, dissected, genitalia mounted in DMHF resin on a separate card, same pin]. *Paratypes* [all dissected]: 19. IV. 2007, M. Maruyama et al. (1 male); 29. IV. 2007, M. Maruyama (1 female); 5. V. 2007, M. Maruyama (1 male). All from termite nest(s). (2 KUM, 1 ABCB)

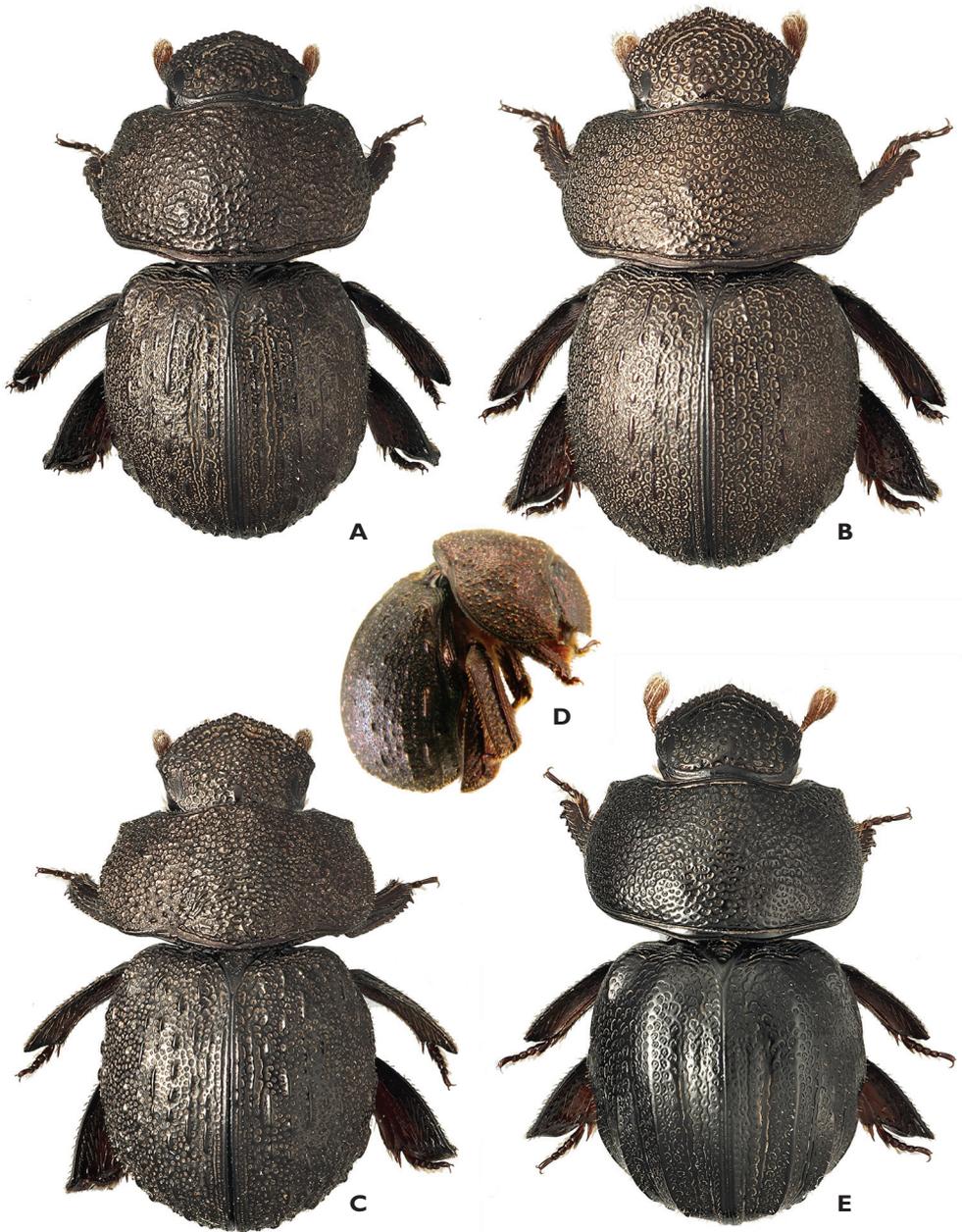
**Description.** HL = 1.21 mm; HW = 2 mm; PL = 1.28 mm; PW = 3.42 mm; EL = 3.57 mm; EW = 3.5 mm.

Medium sized Ceratocanthinae, surface shiny, finely setose (45x); "rolling up" adaptations perfect; wings present and fairly developed.

Dorsum dark brown with bronze sheen, sternum reddish, antennae reddish.

*Head:* wide (W/L ratio = 1.64) pentagonal, fore portion triangular, apex forming an obtuse angle (about 120°), both sides of the angle slightly convex, irregularly finely serrated, not reflexed upward, tip of triangle blunt; genae almost aligned with fore margin, slightly protruding outwards, while forming a rounded acute angle, genal canthus normally developed, reaching the occipital area of head, dorsal ocular area small, dorsal interocular area about 18 times the maximum width of the dorsal ocular area, ventral ocular area relatively large; head dorsal surface slightly convex, with dense puncturation, punctures deeply impressed, their distance being inferior than their diameter, intervals between punctures irregularly raised, giving a granulose appearance to head sculpturing, punctures ocellate, bearing a short fine seta, fore margin with two deep, fine, transverse striae.

*Pronotum:* subtrapezoidal, wider than long (W/L ratio = 2.66), almost as wide as elytra; fore margin feebly bisinuate; fore angles slightly, but distinctly protrudent forward, broadly subtruncate at apex, outer apex of truncation acute and distinctly protruding, a distinct sinuature at the outer side of the apex; fore edge continuously finely margined, edges of sides without any visible margin (dorsal view), base strongly margined; base at middle very slightly protruding backwards, basal edge neither swollen nor raised; pronotal surface regularly convex with one shallow depression at each side of disc (paradiscal depressions). Surface shiny, smooth, with dense strong irregular puncturation; punctures deep, ocellate, their distance being less than their diameter,



**Figure 1.** Ceratocanthinae of Ulu Gombak. **A** *Madrasostes variolosum* habitus dorsal **B** *Madrasostes simplex* habitus dorsal **C** *Madrasostes hashimi* sp. n. habitus dorsal **D** idem habitus lateral **E** *Madrasostes sculpturatum* habitus dorsal.

intervals between punctures irregularly raised, giving a granulose appearance to pronotal sculpturing, punctures bearing often a fine short seta.

*Scutellum*: wider than long, sides proximally subparallel and distinctly notched by elytral articular process, then convergent to form a triangle with elongate acute apex and sides slightly curved inward. Surface slightly depressed in the middle. Apical portion of mesepisterna visible from above. Scutellum uniformly densely punctured; punctures about as large and shaped as on head.

*Elytra*: slightly longer than wide (W/L ratio = 0.98), apical fourth regularly rounded (dorsal view), apex slightly re-entering inward (lateral view); elytra regularly convex, although slightly flattened at disc; elytral suture very finely raised; inferior sutural stria present, ending just before humeral area, delimiting a small marginal elytral area; marginal area poorly developed, smooth, articular area with striation, visible in lateral view; humeral callus small; elytral articular process small, smooth and shiny. Elytra strongly densely punctured, basal and median third covered by a mix of horseshoe-shaped impressed punctures, their distance from each other being shorter than their diameter, each one bearing a very short fine seta and simple impressed punctures, distal third covered by dense ocellate punctures, discal surface with sparse longitudinal short carinae, distal third and sides with sparse, short tubercles. Wings present.

Clypeopleuron very short and transversely slightly grooved at each side. Labrum wide and short, semicircular, distally fringed by long fine setae directed forward. Distal epipharynx semicircular, longitudinally divided by a strong anterior median process; pariae distinctly raised with respect to the haptolachus; median brush and corypha absent; apical fringe made of long fine setae, absent in the middle. Mentum ventrally flat, widely emarginated in the middle, emargination regularly wide-U-shaped; labial palpi (including palpiger) four jointed, first joint very short and transverse, joint two short, joint three longer and plumper than joint two, joint four subconical, apically bearing some short sensilla, all joints, except four, fringed with long setae. Maxillae with an elongate single membranous lacinia, covered with fine long setae, monolobed galea proximally sclerotized and distally clothed with very coarse, long, fine setae, with distinctive comb-like tip (galeal brush), maxillary palpi (including palpiger) four jointed, palpiger very small, joint two wide and relatively short, joint three relatively short, joint four long and subconical, about as long as two and three together, apically bearing some short sensilla. Mandibles short, regularly curved, apicalis with pointed apical tooth short and blunt, not protruding over mesal brush, lateral sclerite of apicalis bearing a distinct large pore, conjunctive present, mesal brush wide and well developed, basalis with molar lobe relatively strong. Antennae 10-segmented, scape long (about half the total length of antenna), securiform, pedicellus plump and rounded, flagellum short, with articles distinctly wider than long, antennal club with three uniformly setose articles.

*Sexual dimorphism*: males with protibiae ending with an apical spur plumper than in females and with distal third more dramatically bent downwards, mesotibiae ending with a straight apical spur and an inner apical spur bent inwards at a right angle, almost fused with the apex of mesotibia. Females with apical spur of protibiae slender and more gently bent downwards, mesotibiae ending with two straight apical spurs.



**Figure 2.** Ceratocanthinae of Ulu Gombak. **A** *Madrasostes depressum* habitus dorsal **B** *Madrasostes boucomonti* habitus dorsal **C** *Madrasostes agostii* sp. n. habitus dorsal **D** *Madrasostes clypeale* male habitus dorsal **E** *Madrasostes malyanum* habitus dorsal **F** *Madrasostes mirificum* sp. n. habitus dorsal **G** habitus lateral of male **H** fore body of female **I** male protibia dorsal view **J** male protibia lateral view.

*Male genitalia*: genital segment fairly sclerotized, V-shaped (Fig. 8D). Aedeagus with basal piece twisted, about three times longer than parameres; internal sac relatively small, containing a large very thick asymmetrical spiraliform sclerite (Fig. 8F); parameres asymmetrical (Fig. 8E), laterally flattened.

**Variability.** The type series shows variability mainly in the development of longitudinal carinae of elytra.

**Identification.** *Madrasostes hashimi* sp. n. can be mistaken only with *M. thoracicum* Paulian, 1989 known from Borneo (Sabah). The new species however differs from the former because of a) the puncturation of elytra which in *M. thoracicum* is slightly larger and denser, b) the shape of elytral carinae that in *M. hashimi* sp. n. are usually longer than in *M. thoracicum*, c) the sculpturing of pronotum which is much stronger in *M. thoracicum*, with puncturation deeper and more transverse, and finally d) the shape of the sclerite of the internal sac of aedeagus, which in the new species is larger and distinctly spiraliform (Fig. 8F), whereas in *M. thoracicum* is short and shaped in a different way (Fig. 8G)

**Etymology.** Dedicated to Dr. Rosli Hashim, who always helps Munetoshi Maruyama's research in Malaysia.

**Distribution and habitat.** This new species is known only from the type locality. For details on collecting circumstances see the introductory paragraphs.

***Madrasostes sculpturatum* Paulian, 1989** (Fig. 1E)

Known distribution: Indonesia (Sumatra) (Paulian, 1989), West Malaysia (Perak) (Paulian, 1989, Grebennikov et al. 2005), East Malaysia (Paulian, 1989).

Remarks. First record for Selangor.

***Madrasostes simplex* Paulian, 1989**

Known distribution: East Malaysia (Sabah) (Paulian 1979) (Fig. 1B)

Remarks. First record for West Malaysia (Selangor). *Madrasostes simplex* is extremely similar to *M. variolosum* and to *M. reticulatum* (Lansberge, 1887). *Madrasostes variolosum* is a very common species and has a wide distribution, ranging from Thailand to Borneo (based on first author's unpublished data) and showing a clinal morphological variation in the sculpturing of elytra, while *Madrasostes reticulatum* is restricted to Sulawesi and the Philippines (although the Philippine population shows intermediate characters between *M. variolosum* and *M. reticulatum*). *Madrasostes simplex* can be easily distinguished from *M. variolosum* because of the sculpturing of elytra and pronotum and the shape of parameres.

***Madrasostes variolosum* (Harold, 1874)** (Fig. 1A, Fig. 6A)

Known distribution: Indonesia, West Malaysia (Paulian 1978).

Remarks. See under *Madrasostes simplex*.

***Paulianostes acromialis* (Pascoe, 1860)**

Known distribution: Singapore, West Malaysia (Pahang, Perak) (Ballerio 2000a)

***Paulianostes georyssoides* (Gestro, 1899)**

Known distribution: Indonesia, West Malaysia (Pahang) (Ballerio 2000a).

***Pterorthochaetes brevisetosus* Gestro, 1899**

Known distribution: Singapore (Gestro 1899).

Remarks. The record from Sumatra published by Paulian (1992) seems incorrect.

***Pterorthochaetes gestroi gestroi* (Harold, 1874)**

Known distribution: Indonesia, Malaysia (Paulian 1978).

***Pterorthochaetes gestroi longisetosus* Gestro, 1899**

Known distribution : Singapore (Gestro 1899).

Remarks. *Pterorthochaetes gestroi gestroi* and *P. gestroi longisetosus* shows differences strong enough to warrant their separation at specific level.

***Pterorthochaetes haroldi* (Sharp, 1875)**

Known distribution: Indonesia, East Malaysia, West Malaysia (Pahang), Singapore (Paulian 1978).

Remarks. The first author began a revision of the genus *Pterorthochaetes* in the late 90's, the revision is still in progress. Based on the preliminary results of this revision the majority of records of *P. haroldi* (and *P. incertus*, which will probably become a junior synonym of *P. haroldi*) reported by Paulian (1978) (e.g. Java, Thailand, Vietnam, Sri Lanka, etc.) are wrong.

***Pterorthochaetes incertus* Gestro, 1899**

Known distribution: Indonesia, West Malaysia (Paulian 1978).

Remarks. See under *P. haroldi*.

***Pterorthochaetes insularis* Gestro, 1899 (Fig. 3A)**

Known distribution: Indonesia, Philippines (Paulian 1978), Nepal (Ballerio 1999), West Malaysia (Kelantan) (Grebennikov et al. 2005).

New material examined: West Malaysia, Perak, 25 km NE of Ipoh, Banjaran Titi Wangsa Mountains, Gunung Korbu, 1400–1800 mt., 11–31.I.1999, leg. P. Cechovsky (ABCB).

Remarks. First record for Perak and Selangor. Based on unpublished data of the senior author, *P. insularis* is a quite common species with a wide distribution, spanning from Nepal to Borneo, with a strong geographical morphological variation, whose taxonomic meaning still needs to be evaluated.

***Pterorthochaetes latus* (Sharp, 1875)**

Known distribution: Singapore (Paulian 1978).

***Pterorthochaetes montanus* Ballerio, 1999**

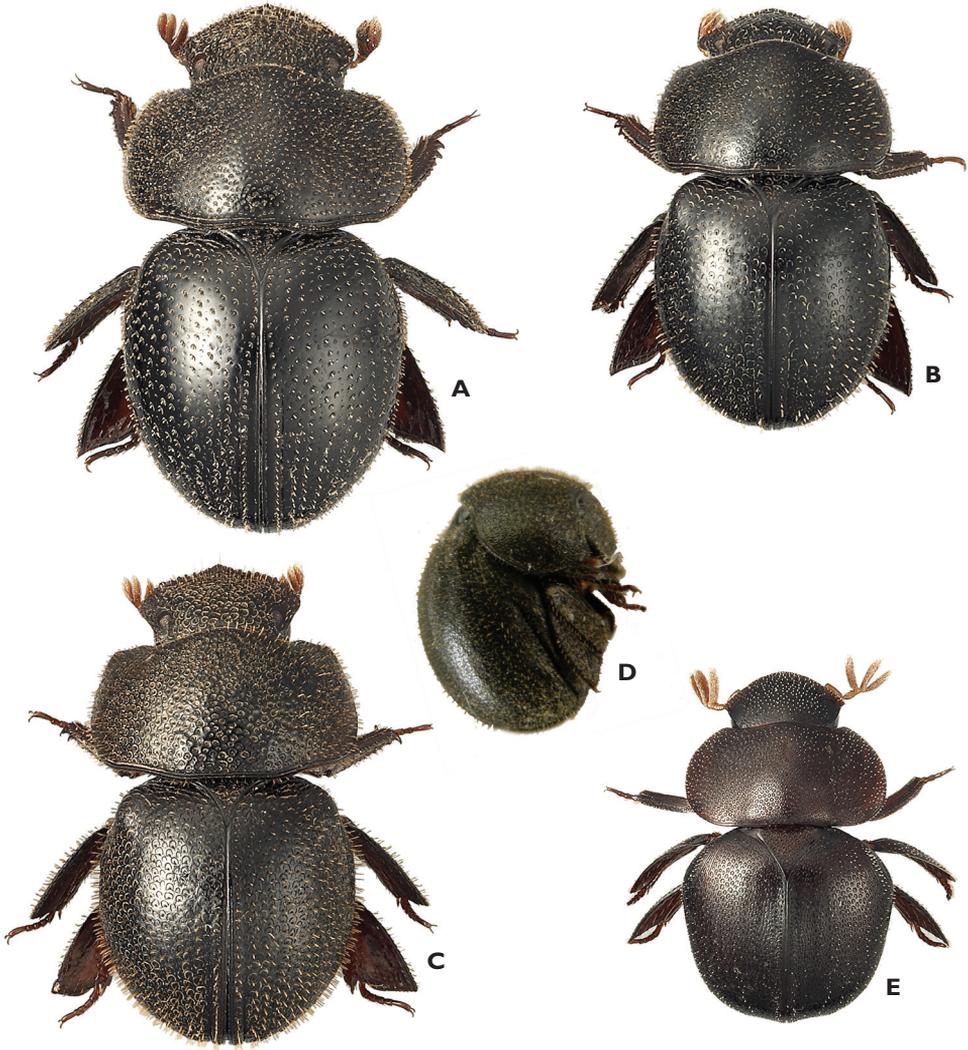
Known distribution: West Malaysia (Pahang, Perak). (Ballerio 1999).

***Pterorthochaetes tsurui* sp. n.**

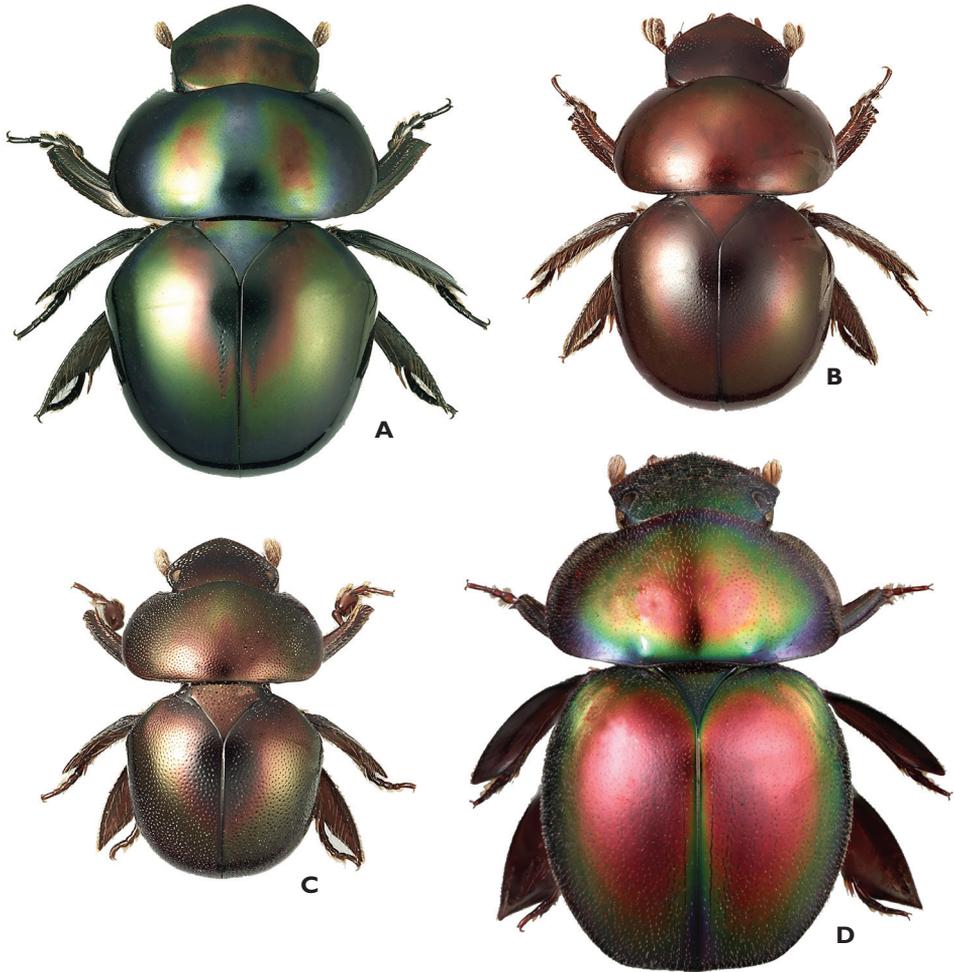
urn:lsid:zoobank.org:act:E8ACB7E2-9473-4521-B654-F8A923F10AF0  
(Fig. 3C, D)

**Type locality:** West Malaysia: Ulu Gombak (Selangor), 3°19'N 101°45' E.

**Material examined.** *Holotype*, male: West Malaysia, Selangor, Ulu Gombak, 250 mt., 29.IV.2007, Leg. M. Maruyama / *Pterorthochaetes tsurui* sp. n. det. Ballerio & Maruyama 2009 Holotypus (KUM). [distended specimen glued on a card, dissected,



**Figure 3.** Ceratocanthinae of Ulu Gombak. **A** *Pterorthochaetes insularis* habitus dorsal **B** *Pterorthochaetes* sp. habitus dorsal **C** *Pterorthochaetes tsurui* sp. n. habitus dorsal **D** idem habitus lateral **E** *Cyphopisthes* sp. habitus dorsal.



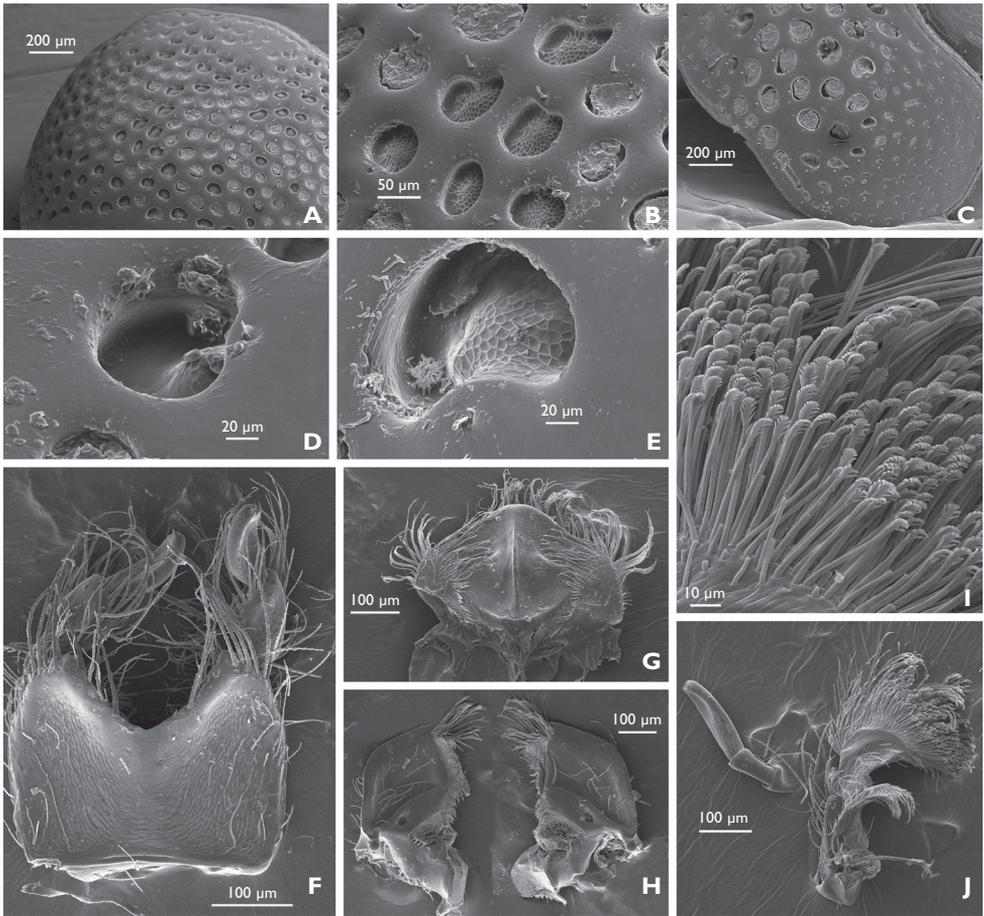
**Figure 4.** Ceratocanthinae of Ulu Gombak. **A** *Eusphaeropeltis* sp. a habitus dorsal **B** *Eusphaeropeltis* sp. b habitus dorsal **C** *Eusphaeropeltis* sp. c habitus dorsal **D** *Ebbrittoniella ignita* habitus dorsal.

genitalia mounted in DMHF resin on a separate card, same pin]. *Paratypes* [one male and four females dissected]: 15.IV.2007, M. Maruyama (1 male); 26.IV.2007, M. Maruyama (1 female and 1 male); 28. IV. 2007, M. Maruyama (1 female); 29. IV. 2007, M. Maruyama (1 female); 30. IV. 2007, M. Maruyama (1 male and female); 3. V. 2007, M. Maruyama (1 female); 4. V. 2007, M. Maruyama (1 female). All from termite nest(s). (2 ABCB, 7 KUM)

**Description.** HL = 0.69 mm; HW = 1.44 mm; PL = 1.38 mm; PW = 2.33 mm; EL = 2.36 mm; EW = 2.27 mm.

Medium sized *Pterorthochaetes*, surface shiny, setose; “rolling up” coaptations perfect; volant.

Dorsum brown, setation yellowish, sternum reddish, antennae reddish.



**Figure 5.** SEM photographs of: **A** *Madrasotes clypeale*: male pronotum **B** detail of male pronotum puncture **C** female pronotum **D** detail of female pronotum punctures **E** and **F** *Madrasotes mirificum* sp. n. mouthparts: labium **G** epipharynx **H** mandibles **I** detail of galear brush **J** maxilla.

*Head*: subrectangular, wider than long, fore margin irregularly sinuated, serrated, tip acute, interocular distance about 9 times the maximum width of dorsal ocular area, dorsal ocular area large, sculpure distally made of very coarse and deep wrinkles and proximally of impressed small dense horseshoe-shaped punctures, each one having a pore in the middle bearing an erect simple seta.

*Pronotum*: wider than long (W/L ratio= 1.68), fore angles normally shaped, elytral lateral margins fringed with a row of long simple setae, spaced out by an interval about half of their length, the whole pronotal surface covered by medium sized round, shallow, ocellate punctures, each one having a pore in the middle bearing a long simple erect seta; puncturation relatively dense, the distance between punctures being inferior to their diameter, denser on disc and at sides, only at sides the ocellate punctures are replaced by horseshoe-shaped punctures with openings outwards. Pronotal pubescence relatively long, approximately as long as marginal setae.

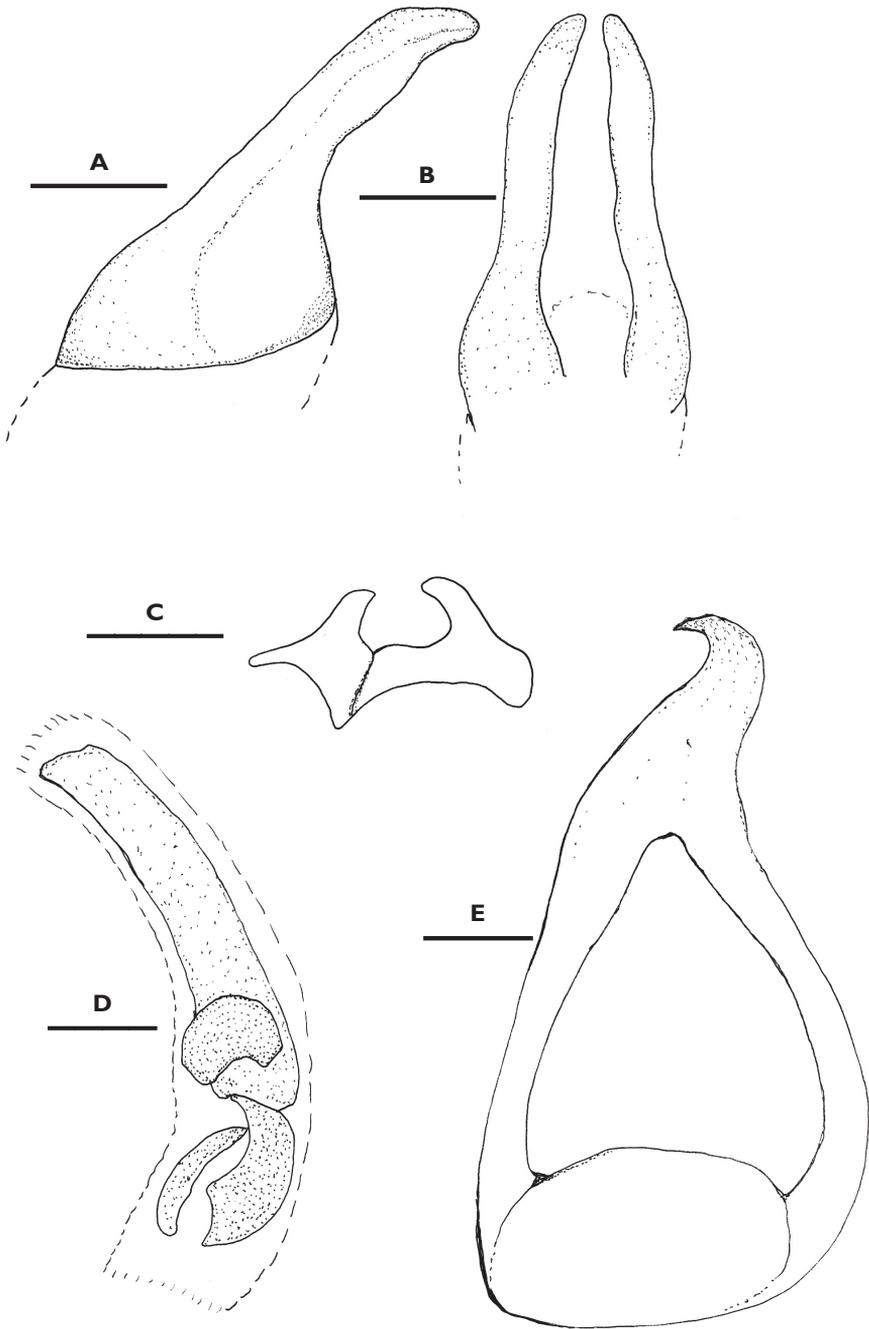


**Figure 6.** Photos of alive specimens taken in habitat at Ulu Gombak (photos © M. Maruyama, 2008). **A** *Madrasostes variolosum* **B** *Madrasostes agostii* **C** *Madrasostes chypeale* male **D** idem female **E** *Eusphaeropeltis* sp. b **F** *Eusphaeropeltis* sp. c.

*Scutellum*: punctures horseshoe-shaped, thick and coarse.

*Elytra*: shape oval, longer than wide (W/L ratio= 0.96); elytral surface covered by medium sized shallow horseshoe-shaped punctures with opening directed backwards, spaced out by an interval inferior to their diameter. Each horseshoe-shaped puncture containing a pore bearing a long erect simple seta.

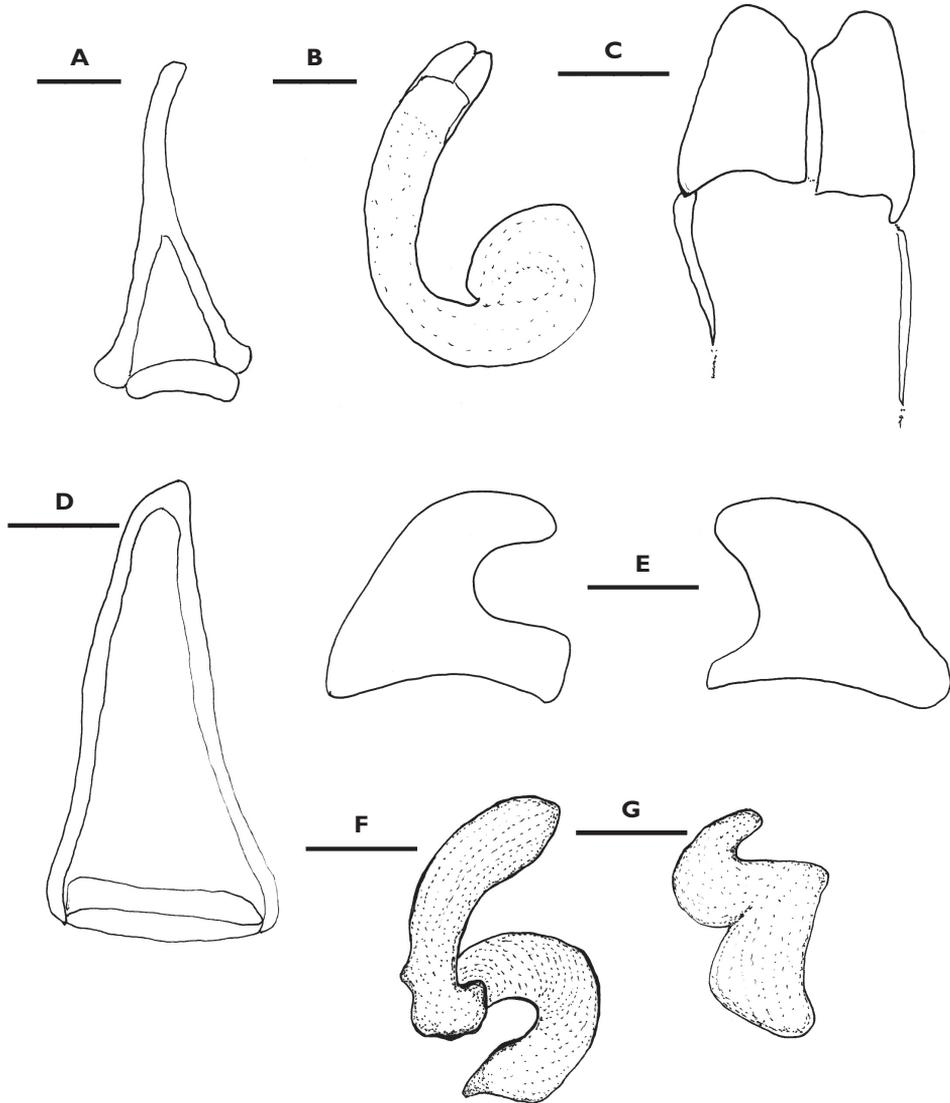
*Male genitalia*: parameres about as long as basal piece, slightly asymmetrical (Fig. 7A, B), apex distinctly bent, internal sac armed with longitudinal subrectangular sclerotization about as long as the basal piece with three short distal sclerites (Fig. 7D), genital segment with manubrium long but strongly bent/twisted, so that in dorsal view it appears very short (Fig. 7E).



**Figure 7.** *Pterorthochaetes tsurui* sp. n.: **A** parameres in lateral view (scale bar: 0,1 mm) **B** parameres in dorsal view (scale bar: 0,1 mm) **C** female bursal sclerites (scale bar: 0,1 mm) **D**, sclerites of the internal sac of aedeagus (scale bar: 0,1 mm) **E** male genital segment (scale bar: 0,1 mm).

*Female genitalia*: bursal sclerites weakly sclerotized and shaped as in Fig. 7C.

**Identification.** This species is characterized by the following combination of characters: a) pronotal puncturation made of ocellate, shallow, medium sized punctures, b) lateral margins of pronotum fringed by long, simple setae, setae relatively spaced out, c) elytral puncturation made of medium sized horseshoe-shaped punctures with opening backwards and bearing a long erect seta, d) shape of parameres (about as long as



**Figure 8.** *Madrasostes mirificum* sp. n.: **A** male genital segment (scale bar: 0,2 mm) **B** aedeagus (scale bar: 0,1 mm) **C** parameres in dorsal view (scale bar: 0,05 mm) **D** *Madrasostes hasimi* sp. n.: male genital segment (scale bar: 0,1 mm) **E** parameres (scale bar: 0,1 mm) **F** sclerite of internal sac of aedeagus (scale bar: 0,1 mm) **G** *Madrasostes depressum*: sclerite of internal sac of aedeagus (scale bar: 0,1 mm).

basal piece and with bent apex, e) shape of genital segment of males, with manubrium strongly twisted, f) shape of female bursal sclerites and, g) head subrectangular, with fore margin somewhat sinuated in a way very unusual for *Pterorthochaetes*. Perhaps the species closest to it could be *Pterorthochaetes brevisetosus*, which, however, has pronotal and elytral puncturation much less dense and shorter setae.

**Variability.** The type series shows a strong uniformity as for size, shape, setation and microsculpturing.

**Etymology.** Dedicated to Mr. Tomoyuki Tsuru, who found the huge termite nest from which the junior author collected more than 400 *Ceratocanthinae*, among which *P. tsurui* sp. n.

**Distribution and habitat.** This new species is known only from the type locality. For details on collecting circumstances see the introductory paragraphs.

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We thank Giulio Cuccodoro (MHNG), Olivier Montreuil (MNHN), and Roberto Poggi (MCSN) for permission to study material kept in the collections under their care. Nicola Angeli and Valeria Lencioni (Museo Tridentino di Scienze naturali, Trento, Italy) are thanked for SEM photographs. Alberto Ballerio thanks Petr Chceovsky (Brno, Czech Republic) for providing Malaysian *Ceratocanthinae*. Munetoshi Maruyama thanks Shinichi Befu, Rosli Hashim, Takashi Komatsu, Yoko Matsumura, Tomoyuki Tsuru, and Yoshihiro Senda for their assistance in the field, and Alfred F. Newton and Margaret K. Thayer for allowing to use Microptic System at the Field Museum of Natural History.

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# A review of the *Blaesiina* (Coleoptera, Scarabaeidae, Cetoniinae, Gymnetini)

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## Abstract

The two genera comprising the subtribe *Blaesiina* (Scarabaeidae: Cetoniinae: Gymnetini) are reviewed. Each genus contains two species, with *Blaesia* Burmeister occurring in southern South America and *Halfferinetis* Morón & Nogueira occurring in northern Mexico. Descriptions, keys, distributions, biology, and illustrations are provided. The biogeography of the *Blaesiina* is discussed with a hypothesis to explain the current disjunct distributions. I provide a new state record for *Halfferinetis gonzaloi* Morón & Nogueira in San Luis Potosí, Mexico.

## Keywords

Scarabaeidae, Cetoniinae, Gymnetini, *Blaesiina*

*Who knows not the name, knows not the subject.*

– Linnaeus, 1773

*Critica Botanica*

## Introduction

The purpose of this paper is to provide a comprehensive review of the gymnetine subtribe *Blaesiina* by re-describing the two genera and four species, providing illustrations and a key for identification, mapping their distributions, and recording observations on life history when known. This review is a continuation of my series of studies on the New World Gymnetini genera (Deloya and Ratcliffe 1988; Morón

and Ratcliffe 1984; Ratcliffe 1978, 2004, 2005; Ratcliffe and Mico 2001). Two species in the genus *Blaesia* occur in southern South America, and one of them (*B. subrugosa* Moser) is uncommon in collections, possibly a result of unusual life history traits that conceals them from general collecting methods. Two other species in the genus *Halffierinetis* are found in northern Mexico, and each is known by several specimens only, again possibly a result of secretive life history traits or limited occurrence in space and time.

## Methods

In order to ascertain species limits (both morphological and geographic), I examined (or recorded from the literature) 238 specimens of *Blaesia* and *Halffierinetis* species from the research collections listed below. The collections and their acronyms (as given in Arnett et al. 1993) are as follows. The curators and/or collection managers who provided the material are also indicated.

- AMIC** Antonio Martínez Collection, then at Salta, Argentina (currently at the Canadian Museum of Nature, Ottawa, Canada).
- AMNH** American Museum of Natural History, New York, NY, USA (Lee Herman).
- BCRC** Brett C. Ratcliffe Collection, Lincoln, NE, USA.
- BMNH** The Natural History Museum, London, England (Malcolm Kerley, Michael Bacchus).
- CASC** California Academy of Sciences, San Francisco, CA, USA (Norman Penny, David Kavanaugh).
- CMNC** Canadian Museum of Nature, Ottawa, Canada (François Génier).
- FMNH** Field Museum of Natural History, Chicago, IL, USA (Al Newton).
- GMNC** Guillermo Nogueira Collection, Zapopan, Jalisco, Mexico.
- IEXA** Instituto de Ecología, Xalapa, Mexico (Miguel Morón).
- ISNB** Institut Royal de Sciences Naturelles de Belgique, Brussels, Belgium (Alain Drumont).
- MACN** Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina (Axel Bachmann).
- MCZC** Museum of Comparative Zoology, Cambridge, MA, USA (Phil Perkins).
- MGFT** Georg Frey Collection, then at the Zoologische Staatssammlung, Munich, Germany (Gerhard Scherer, Max Kühbandner), now at the Naturhistorisches Museum, Basel, Switzerland (Daniel Burkhardt).
- MLPA** Museo de La Plata, La Plata, Argentina (Analia Lanteri).
- MNHN** Museum National d'Histoire Naturelle, Paris, France (Jean Menier, Roger-Paul Dechambre).
- MXAL** Miguel Morón Collection, Xalapa, Veracruz, Mexico.
- MZSP** Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (Cleide Costa).

- QBUM** Museu Nacional, Rio de Janeiro, Brazil (Miguel Monné).  
**RMNH** Nationaal Natuurhistorische Museum Leiden, the Netherlands (Jan van Tol).  
**USNM** U. S. National Museum, currently at University of Nebraska State Museum, Lincoln, NE, USA.  
**WBWC** William B. Warner Collection, Chandler, AZ, USA.  
**ZMHU** Museum für Naturkunde der Humboldt Universität, Berlin, Germany (Manfred Uhlig, Joachim Schulze, Hella Wendt).

The generic and species descriptions were based on the following characteristics: length (from apex of clypeus to apex of elytra), color and markings, interocular width (number of transverse eye diameters across the frons), form and sculpturing of the frons, clypeus, antennae, pronotum, mesepimeron, elytra, pygidium, legs, venter (mesometasternal process, abdominal sternites), form of the apex of the metatibia, and parameres.

Geographical localities are arranged alphabetically by province, state, or department within each country and then alphabetically by locality within each province. Temporal data is provided, but these data should be used with caution because many specimens in old collections lack these data.

I use the phylogenetic species concept as outlined by Wheeler and Platnick (2000). This concept defines species as the smallest aggregation of (sexual) populations diagnosable by a unique combination of character states.

## **Taxonomic history**

The cetoniine tribe Gymnetini is currently comprised of 26 genera in the New World (Krikken 1984; Krajcik 1998; Morón and Nogueira 2007) distributed from the eastern and central United States south to Argentina (Blackwelder 1944). Keys to the tribes of Cetoniinae and subtribes of Gymnetini can be found in Krikken (1984). Krikken (1984) recognized the subtribe Blaesiina to accommodate the genus *Blaesia* based upon the presence of approximate mesocoxae, the absence of a distinct mesometasternal process, the greatly enlarged metafemora, and the modified apex of the metatibia in the males of *Blaesia* species. *Blaesia atra* Burmeister and *Blaesia subrugosa* Moser occur in Bolivia, Paraguay, Uruguay, Argentina, and southern Brazil.

Morón and Nogueira (2007) established the genus *Halffterinetis* for their new species, *H. gonzaloi* Morón and Nogueira and *H. violetae* Morón and Nogueira, from arid regions of northern Mexico. The morphological similarities between *Blaesia* and *Halffterinetis* are obvious, thus leading Morón and Nogueira to place *Halffterinetis* in the Blaesiina.

Specimens of Blaesiina are not commonly found in collections, thus suggesting either their relative rarity in nature or our lack of knowledge regarding their habitat. Krikken (1984) suggested that *Blaesia* species are termitophilous, while Monné (1969) described the larvae of *B. atra* from the nest of *Acromyrmex* species (Formicidae) in

Uruguay. Morón and Nogueira (2007) suggested myrmecophily for both genera. If this is so, sampling ant and termite nests might yield additional specimens and reveal more of their life history, which is, at present, completely unknown. In spite of the broad array of collections consulted, I have seen only about two dozen examples of *B. subrugosa*, and specimens of *Halffterinetis* are known from only 11 specimens.

### Key to the genera of adult *Blaesiina*

1. Clypeal apex broadly rounded, surface slightly longitudinally tumid at middle. Metafemora enlarged in both sexes (Fig. 1). Male with apex of metatibia elongated into stout, acute spine and with 1 articulated spur (Fig. 1). Southern South America .....*Blaesia*
- 1'. Clypeal apex broadly truncate and weakly to distinctly emarginate at middle, surface concave. Metafemora not enlarged. Male with apex of metatibia with 2 angulate lobes and with 2 articulated spurs. Northern Mexico .....*Halffterinetis*

### *Blaesia* Burmeister, 1842

*Blaesia* Burmeister 1842: 615. Type species: *Blaesia atra* Burmeister, 1842, by monotypy.

**Description.** Scarabaeidae, Cetoniinae, Gymnetini. *Form:* Rhomboidal, robust, sides slightly tapering toward apex of elytra, dorsum nearly flat. Color on dorsum black to dark reddish brown, venter shiny black. Surface of head, pronotum, elytra, and pygidium with or without distinct setae. *Head:* Shape subrectangular, longer than wide. Clypeus with apex broadly rounded, surface slightly longitudinally tumid at middle. Antenna 10-segmented, club subequal in length to segments 1–7. Eyes small. *Pronotum:* Shape subtrapezoidal, widest near base, gradually convergent to anterior angles, basomedian lobe strongly produced, lobe covering all but tip of scutellum. *Elytra:* Widest at base, post-humeral emargination distinct. *Pygidium:* Surface punctate and/or with transverse strigulae. *Legs:* Protibia tridentate in both sexes, teeth subequally spaced. Metatrochanter with long, acute spur, spur with apex projecting almost perpendicular to posterior margin of metafemur in both sexes (Fig. 2). Metafemur greatly enlarged, broad. Metatibia in male with apex extended into long, thick, acute spine and with 1 long, articulated spur; metatibia at apex in female with short, subtriangular extension and with 2 long, articulated apical spurs. *Venter:* Mesometasternal process short, flat, apex rounded, nearly obsolete.

**Diagnosis.** Species of *Blaesia* can be easily recognized by the presence of the enlarged metafemora in both sexes. In addition, males have the apex of the metatibia elongated into stout, acute spine and with only one articulated spur, both of which are unique characters in the Gymnetini.

**Distribution.** Species of *Blaesia* are known from Bolivia, Paraguay, Uruguay, Argentina, and southern Brazil.

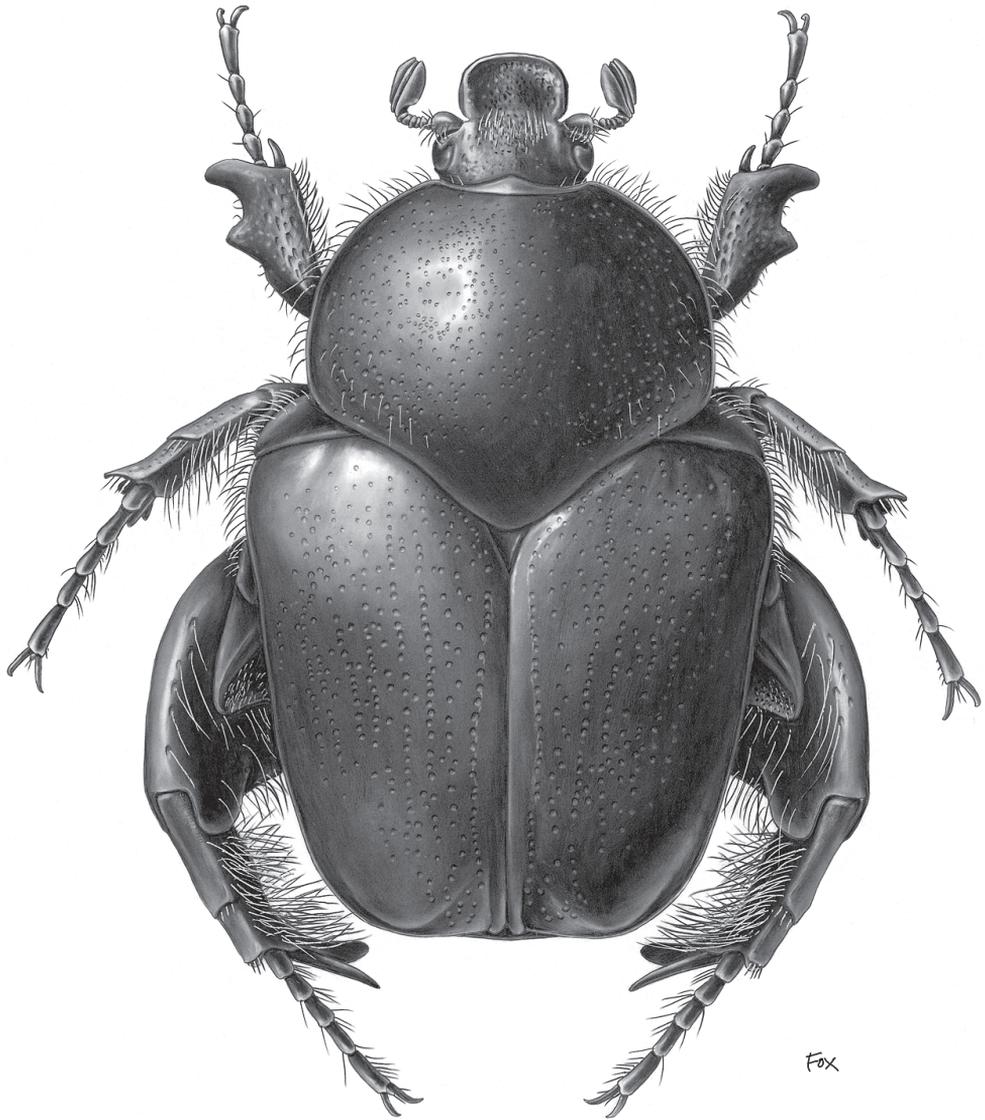
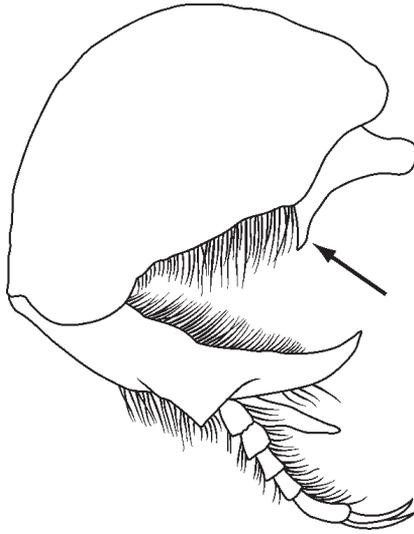


Figure 1. *Blaesia atra*, habitus drawing of male.

**Key to the species of adult *Blaesia***

- 1. Pronotum with small punctures, punctures becoming large on lateral margins. Elytra with several large punctures in incomplete rows. Setae on venter rust colored to tawny ..... ***atra* Burmeister**
- 1'. Pronotum completely punctate, with large, deep, dense punctures. Elytra densely punctate to rugopunctate, punctures moderate to large. Setae on venter black ..... ***subrugosa* Moser**



**Figure 2.** *Blaesia atra*, right posterior leg, ventral view.

***Blaesia atra* Burmeister, 1842**

Figs 1–3, 5

*Blaesia atra* Burmeister 1842: 615. Type not found; not present in Burmeister collection at Martin-Luther-Universität Halle-Wittenberg, Halle, Germany (Karla Schneider, personal communication, September 2009) or at the Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina (personal observation, 2003).

**Description.** Length 13.9–20.5 mm; width 8.5–12.4 mm. Color usually completely black, shining occasionally pronotum and elytra dark reddish brown and only weakly shining. *Head:* Surface densely punctate; punctures moderate to large, deep, nearly confluent to rugose on clypeus and between eyes. Frons and clypeus with distinct, median, longitudinal ridge. Frons with sparse, rust colored to tawny setae. Clypeus with apex evenly, broadly rounded, thickened, slightly reflexed, subapex slightly wider than base, surface slightly longitudinally tumid at middle. Interocular width equals 5.5–6.0 transverse eye diameters. Antenna black, with 10 segments, club slightly shorter than antennomeres 1–7. *Pronotum:* Most of surface moderately densely punctate; punctures small in males, slightly larger in females, round to slightly transverse, becoming large, setigerous and dense on sides; setae long, rust colored to tawny; base at center not modified. Apex at center with margin thickened. Sides margined. Mesepimeron with dense, large, setigerous punctures anteriorly, setae long, rust colored to tawny. *Elytra:* Surface finely shagreened, usually with; 3–4 distinguishable punctate, incomplete striae; punctures round to  $\cap$ -shaped, moderate to large, some setigerous in unworn specimens; setae sparse, long, rust colored to tawny. Intervals with sparse, irregularly spaced punctures similar to those of striae. Bead present on lateral margin. Apical umbone

pronounced. Apices rounded into right-angles. *Pygidium*: Surface varies from moderately densely punctate with small to slightly transverse punctures to densely, transversely strigulate. Base usually with sparse, long, rust colored to tawny setae. In lateral view surface weakly convex in male, nearly flat in female. *Venter*: Setae rust colored to tawny. Mesometasternal process short, flat, apex rounded, nearly obsolete. Abdominal sternites with transverse, irregular row of large punctures; punctures mostly large with rust colored to tawny setae. *Legs*: Femora and tibiae with dense fringe of mostly short, rust colored (most common) to tawny (less common) setae on both median and lateral surfaces. Protibia tridentate, apical tooth longer, narrower, slightly curving. Metafemur greatly enlarged, broad (Fig. 2). Metatibia in male with apex extended into long, thick, acute spine and with 1 long, articulated spur with acute apex; metatibia at apex in female with short, subtriangular extension and with 2 long, articulated apical spurs with apices rounded. Metatrochanter with long, acute spur, spur with apex projecting almost perpendicular to posterior margin of metafemur in both sexes (Fig. 2). *Parameres*: Fig. 3.

**Distribution** (Fig. 5). 200 specimens examined from AMIC, BCRC, BMNH, CASC, CMNC, FMNH, ISNB, MACN, MGFT, MLPA, MNHN, MZCZ, MZSP, QBUM, RMNH, USNM, WBWC, ZMHU.

**ARGENTINA** (30). BUENOS AIRES (14): Buenos Aires, La Plata; CORRIENTES (2): Santo Tomé; MISIONES (1): Loreto; SAITA (1): No data; SANTA FÉ (4): Rosario; NO DATA (9).

**BRAZIL** (28). PARANÁ (1): No data; RIO GRANDE DO SUL (21): Porto Alegre; SÃO PAULO (5): Campinas, Itatiba, Pres. Epitácio; NO DATA (1).

**PARAGUAY** (7). GUAÍRA (2) Sapucay, Villarrica; NO DATA (5).

**URUGUAY** (107). CANELONES (3): La Tuna; DISTRITO FEDERAL (80): Montivideo; TACUAREMBÓ (2): Pozo Honso; TRIENTA Y TRES (17): Santa Clara de Olimar; NO DATA (5).

**NO DATA** (28).

**Temporal Distribution.** January (7), February (3), June (1), September (2), October (3), November (4), December (6 adults, 11 larvae). Too few specimens have label data with the month of collection to indicate a reliable temporal distribution.

**Biology.** Monné (1969) described the larvae of *B. atra* from the nest of *Acromyrmex* species (Formicidae) in Uruguay, thus demonstrating myrmecophily for this species. Krikken (1984) suggested, without any supporting commentary, the possibility that this species is termitophilous.

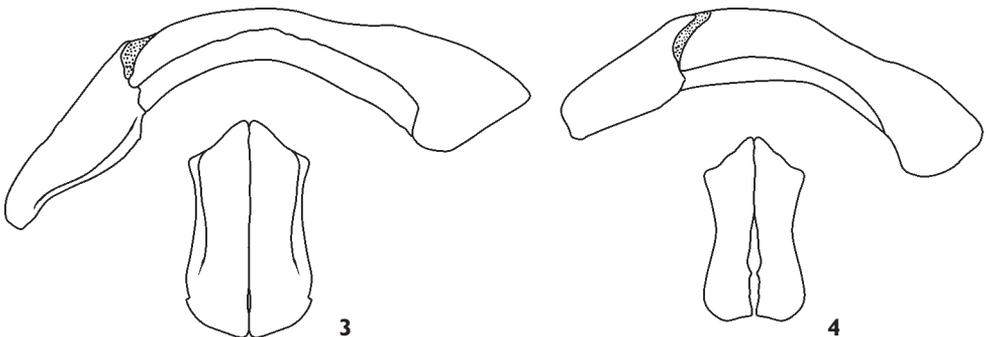
### ***Blaesia subrugosa* Moser, 1905**

Figs 4–5

*Blaesia subrugosa* Moser, 1905: 211. Lectotype female (Fig. 9) at ZMHU, labeled: S. Cruz de la Sierra, Bolivia / *Blaesia subrugosa* Moser, Type / *Blaesia subrugosa* Moser, Type, G. Ruter det. 1966 / Type / with my red lectoallotype label. Paralect-

otype female at ZMHU with same locality label as lectotype and with my yellow paralectotype label (Ratcliffe 2004).

**Description.** Length 12.0–19.5 mm; width 7.5–11.8 mm. Color completely black, shining. *Head:* Surface densely punctate; punctures moderate to large, deep, nearly confluent to rugose on clypeus and between eyes. Frons and clypeus with weak, median, longitudinal ridge. Frons with sparse, dark brown setae. Clypeus with apex evenly, broadly rounded, thickened, slightly reflexed, subapex slightly wider than base, surface slightly longitudinally tumid at middle. Interocular width equals 5.0 transverse eye diameters. Antenna black, with 10 segments, club slightly shorter than antennomeres 1–7. *Pronotum:* Surface densely punctate; punctures large, deep, round to slightly transverse, becoming confluent or rugose on sides; base at center narrowly depressed, impunctate or with numerous small, shallow punctures. Apex at center with small, broad, flattened, opaque tumosity. Sides margined. Mesepimeron with a few large, setigerous punctures anteriorly, setae long, black. *Elytra:* Surface densely punctate to rugopunctate, punctures moderate (on sides) to large (on disc), round to  $\cap$ -shaped. Bead present on lateral margin. Apical umbone pronounced. Apices nearly right-angled. *Pygidium:* Surface with short, transverse strigae (on disc) (often reduced) to transversely strigose (on base and sides). Base usually with sparse, short, black setae. In lateral view surface weakly convex. *Venter:* Setae black. Mesometasternal process short, flat, apex rounded, nearly obsolete. Abdominal sternites with transverse, irregular row of large punctures; punctures mostly large with short, black setae. *Legs:* Femora and tibiae with fringe of mostly short, black setae on both median and lateral surfaces. Protibia tridentate, apical tooth longer, narrower, curving slightly. Metafemur greatly enlarged, broad. Metatibia in male with apex extended into long, thick, acute spine and with 1 long, articulated spur with acute apex; metatibia in female with short, subtriangular extension and with 2 long, articulated apical spurs with apices rounded. Metatrochanter with long, acute spur, spur with apex projecting almost perpendicular to posterior margin of metafemur in both sexes. *Parameres:* Fig. 4.



**Figures 3–4.** Parameres, caudal and lateral views, of **3** *B. atra* and **4** *B. subrugosa*.

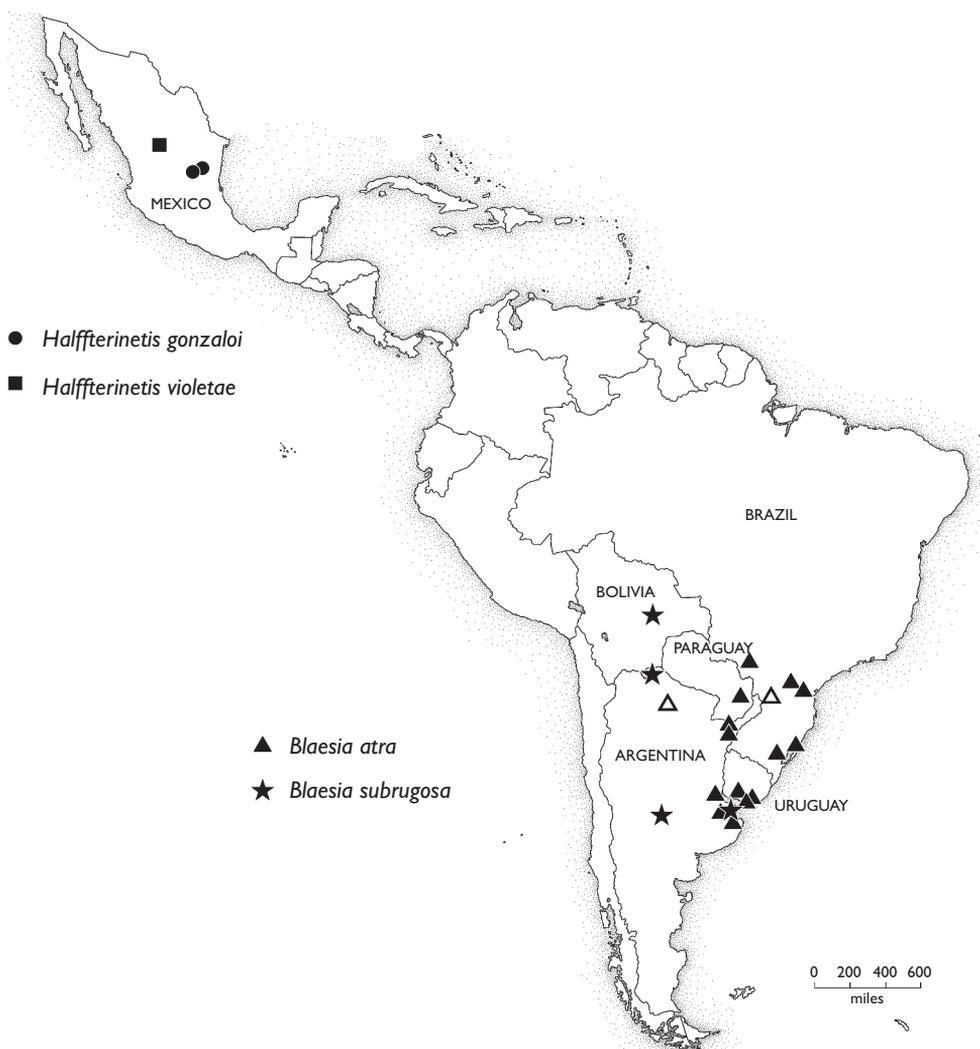
**Distribution** (Fig. 5). 27 specimens examined from AMIC, BMNH, CASC, CMNC, FMNH, ISNB, MACN, MLPA, MNHN.

**ARGENTINA** (23). BUENOS AIRES (8): Buenos Aires; SALTA (4): Tobatirenda, No data; TUCUMAN (1): Buruyacú; NO DATA (10): Gran Chaco region.

**BOLIVIA** (4). SANTA CRUZ (2): Santa Cruz de la Sierra; NO DATA (2).

**Temporal Distribution.** March (5), December (1). Too few specimens have label data with the month of collection to indicate a reliable temporal distribution.

**Biology.** Nothing is known of the biology of this species. Krikken (1984) suggested the possibility that this species is termitophilous, while Morón & Nogueira (2007) suggested myrmecophily.



**Figure 5.** Distribution map of *Blaesia* and *Halffterinetis* species. Open symbol is state record only.

### ***Halffterinetis* Morón & Nogueira, 2007**

*Halffterinetis* Morón & Nogueira 2007: 52. Type species: *Halffterinetis gonzaloi* Morón & Nogueira, by original designation.

**Description.** Scarabaeidae, Cetoniinae, Gymnetini. *Form:* Rhomboidal, robust, sides slightly tapering toward apex of elytra, dorsum nearly flat. Color shiny black, males of *H. gonzaloi* with chalky white marks on lateral margin of pronotum (Fig. 6) and sides of 4<sup>th</sup> sternite; males of *H. violetae* and females lacking cretaceous marks (Fig. 7). Surface of frons densely punctate to rugopunctate, usually with short setae. *Head:* Shape subrectangular, longer than wide. Clypeus with apex broadly truncate, distinctly emarginate at middle, surface distinctly concave (Fig. 8). Antenna 10-segmented, club in males longer than antennomeres 1–7 (Fig. 8), club in females subequal in length to antennomeres 2–7. Eyes small. *Pronotum:* Shape subtrapezoidal, widest near base, gradually convergent to anterior angles, basomedian lobe with margin arcuate, weakly to moderately produced, most of scutellum visible. *Elytra:* Widest at base, posthumeral emargination distinct. *Pygidium:* Surface varies from moderately densely punctate to having strong, concentric, vermiform strigulae (Fig. 9). *Legs:* Protibia tridentate in both sexes, teeth subequally spaced. Metatrochanter triangular, elongated, flush with posterior margin of metafemur in both sexes, not projecting as a spur. Metafemur slightly enlarged. Metatibia at apex with 2 broad lobes and with 2 long, articulated, apical spurs. *Venter:* Mesometasternal process short, nearly obsolete, flat, apex rounded.

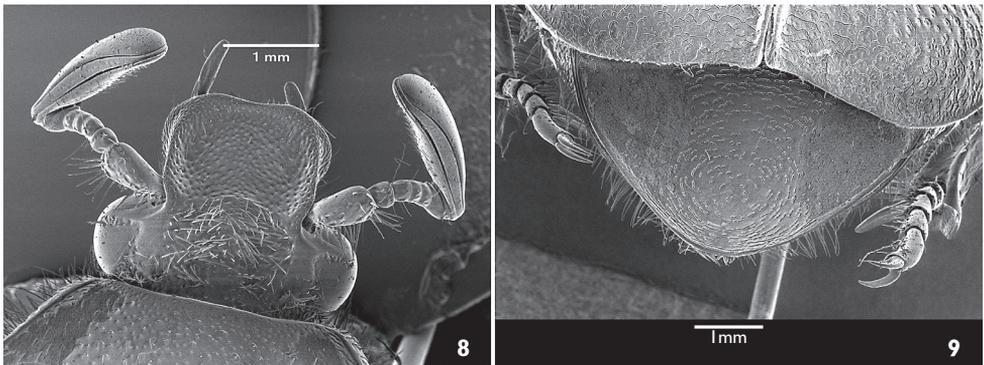
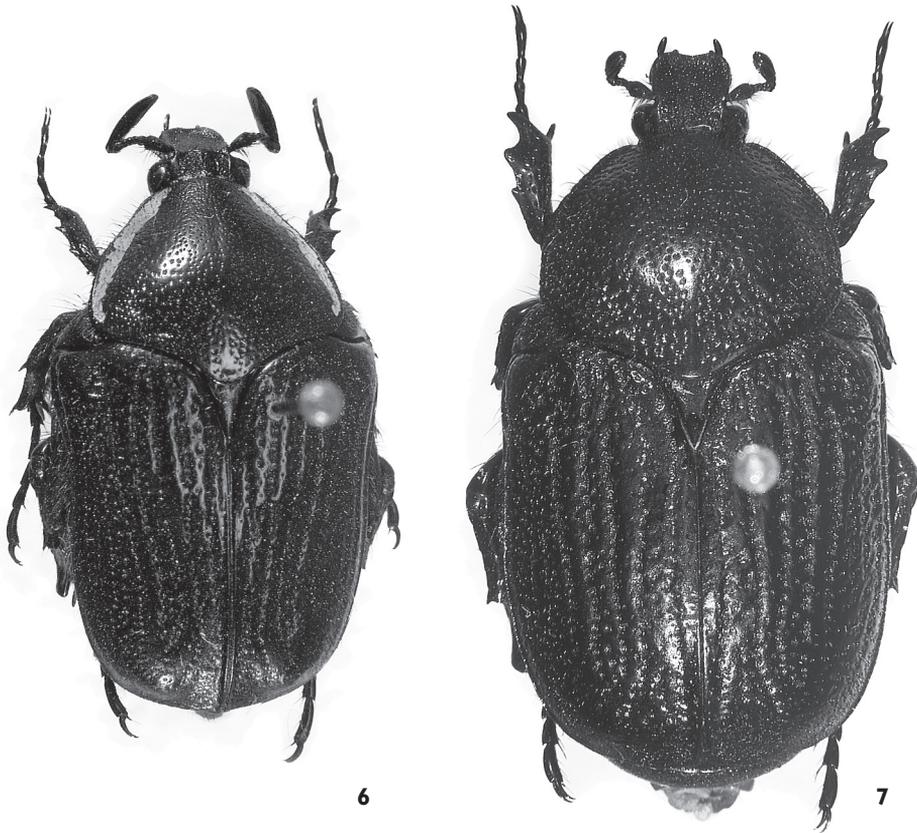
**Diagnosis.** The genus *Halffterinetis* is unique among the American Gymnetini, because the basomedian lobe of the pronotum is only arcuate to moderately produced (not covering most of the scutellum) instead of strongly produced posteriorly (covering all but the extreme tip of the scutellum) as in the other genera of the tribe. Morón and Nogueira (2007) proposed *Halffterinetis* as a member of the Blaesiina pending further studies, and I am in agreement with their placement. I have a single female (AMNH) collected in August from Guadalupe in the state of Coahuila (a NEW STATE RECORD for the genus) that I am unable to assign to the species level; characteristics of the specimen do not coincide with the description of *H. gonzaloi*, and the female of *H. violetae* remains unknown.

**Distribution.** *Halffterinetis* species are known from northern Mexico only.

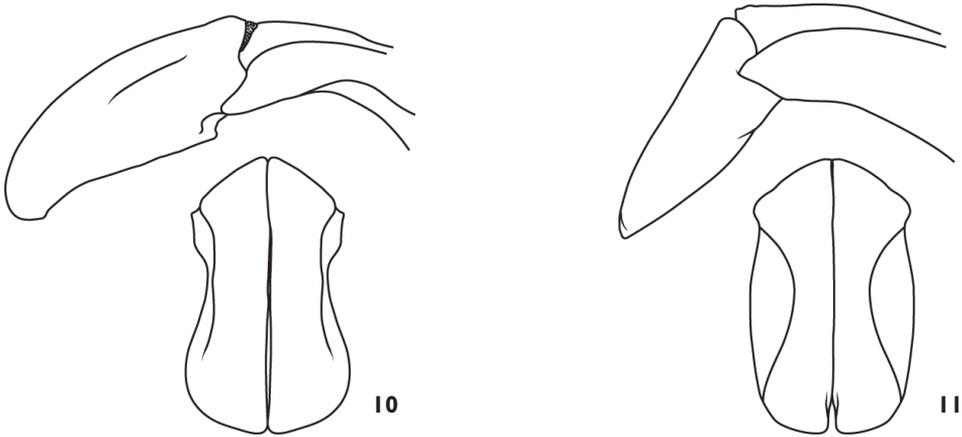
### **Key to the species of adult Male *Halffterinetis***

(females of *H. violetae* are unknown)

1. Frontoclypeal region with transverse carina. Clypeal apex weakly emarginate. Cretaceous marking present on lateral margins of pronotum and pygidium. Parameres as in Fig. 10..... ***gonzaloi* Morón & Nogueira**
- 1'. Frontoclypeal region without transverse carina. Clypeal apex strongly emarginate. Cretaceous markings absent. Parameres as in Fig. 11 .....  
..... ***violetae* Morón & Nogueira**



**Figures 6–9.** *Halffterinetis gonzaloi*: **6** male, dorsal view **7** female, dorsal view **8** head of male, dorsal view **9** pygidium of male. Images courtesy of M. Morón, Instituto de Ecología, Xalapa, Mexico (Figs 6–7 taken by R. Woodruff and Figs 8–9 taken by P. Skelley, both Florida State Collection of Arthropods, Gainesville, FL).



**Figures 10–11.** Parameres, caudal and lateral views, of **10** *H. gonzaloi* and **11** *H. violetae*.

***Halffterinetis gonzaloi* Morón & Nogueira, 2007**

Figs 5–10

*Halffterinetis gonzaloi* Morón & Nogueira 2007: 52.

Holotype male and allotype female at MXAL. Holotype labeled MEXICO: Tamaulipas, Palmillas, 1130 m, 23-VII-2005, G. Nogueira; allotype with same data but 19-VII-2005 and 1030 m. Five paratypes with same data deposited at IEXA (2), CMNC (1), and GNGC (2).

**Description.** Length 14.9–18.5 mm; width 8.4–10.1 mm. Color black, shining; male with lateral margins of pronotum (Fig. 6), sides of 4<sup>th</sup> sternite, and usually a spot on pygidium cretaceous; female lacking cretaceous marks. *Head:* Surface densely punctate to rugopunctate; punctures small to large, deep. Frontoclypeal region with weak, transverse ridge in male, ridge absent in female. Frons with dense, moderately long, black setae in male (Fig. 8), setae absent in female. Clypeus with apex broadly truncate, weakly emarginate at middle in male, more so in female, thickened, slightly reflexed, subapex slightly wider than base, surface concave in male, slightly less so in female. Interocular width equals 5.0 transverse eye diameters. Antenna black, with 10 segments, club in male slightly longer than antennomeres 1–7 (Fig. 8), club in female subequal in length to antennomeres 2–7. *Pronotum:* Surface densely punctate; punctures moderate to large, deep, round to slightly transverse, punctures becoming larger to rugopunctate on sides (more pronounced in female), and with short, black setae. Sides margined. Mesepimeron completely punctate to rugose, with sparse, black setae. *Elytra:* Surface superficially and irregularly striate, rugopunctate, punctures moderate to large, round to mostly  $\cap$ -shaped. Bead present on lateral margin. Apical umbone pronounced. Apices nearly right-angled in male, rounded in female. *Pygidium:* Surface in male with oval punctures or with short, transverse strigae (on disc) (often reduced) to transversely strigose (on base and sides) (Fig. 9); surface in

female densely, concentrically strigulate. Base usually with sparse, short, black setae. In lateral view surface in male weakly convex, female with surface usually strongly convex. *Venter*: Setae black. Mesometasternal process short, nearly obsolete, flat, apex rounded. Abdominal sternites with transverse, irregular field of large punctures; punctures sparser in central third, mostly large, shallow, with short, black setae. *Legs*: Meso- and metaemora and meso- and metatibiae with sparse fringe of mostly long, black setae on median surface. Protibia tridentate, apical tooth longer, slightly narrower. Metafemur normal, not enlarged. Metatibia at apex with 2 broad lobes and with 2 long, articulated apical spurs with apices rounded. Metatrochanter triangular, elongate, flush with posterior margin of metafemur, acuminate apex not projecting perpendicularly. *Parameres*: Fig. 10.

**Distribution** (Fig. 5). 8 specimens recorded (7 from Morón & Nogueira 2007). The San Luis Potosí specimen is a NEW STATE RECORD.

**MEXICO** (8): SAN LUIS POTOSÍ (1): km 200 carretera SLP a Ciudad del Maíz TAMAULIPAS (7): Palmillas.

**Temporal Distribution.** July (8).

**Biology.** Morón & Nogueira (2007) reported that the seven specimens were crepuscular, that some were collected in flight, while others were found on dead trunks of mesquite trees (*Prosopis juliflora* [Swartz]) (Mimosaceae), all near the nests of *Atta* ants at elevations ranging from 1030–1130 meters. A search of the *Atta* nest found no larvae or pupae, but these authors surmised there might be some association with the ants. The habitat was semiarid with an annual precipitation of 500–600 mm and an average annual temperature of 20–22°C. Dominant plants consisted of *Prosopis* species (Mimosaceae), *Acacia* species (Leguminosae), *Hechtia* species (Bromeliaceae), *Yucca* species (Lilaceae), *Opuntia* species (Cactaceae), *Agave* species (Amarilidaceae), and *Helietta* species (Rutaceae). Adults were not attracted to banana traps.

### ***Halffterinetis violetae* Morón & Nogueira, 2007**

Figs 5, 11

*Halffterinetis violetae* Morón & Nogueira 2007: 56.

Holotype male at CMNC and one paratype male at MXAL. Types labeled MEXICO: Durango, 40 mi SW Torreón, Hwy 40, 18-VI-1961, D. H. Janzen.

**Description.** Male (female unknown). Length 14.6–15.3 mm; width 7.9–8.4 mm. Color black, shining, lacking cretaceous marks. *Head*: Surface densely punctate to rugopunctate; punctures small to large, deep. Frontoclypeal region lacking transverse ridge. Frons with short, moderately dense, black setae. Clypeus with apex broadly truncate, strongly emarginate at middle, slightly reflexed, subapex distinctly wider than base, surface weakly concave. Interocular width equals 3.9 transverse eye diameters. Antenna black, with 10 segments, club almost twice as long as antennomeres 2–7. *Pronotum*: Surface densely punctate; punctures moder-

ate to large, deep, round to slightly transverse, punctures becoming larger to rugopunctate on sides, and with short, tawny setae. Sides margined, bead reduced in anterior fifth. Mesepimeron completely punctate, with sparse, black setae. *Elytra*: Surface superficially and irregularly striate, rugopunctate, punctures moderate to large, round to mostly  $\cap$ -shaped, setigerous; setae short, sparse, black. Bead present on lateral margin. Apical umbone pronounced. Apices nearly right-angled. *Pygidium*: Surface with oval punctures or with short, transverse strigae (often reduced) to transversely strigose. Base usually with sparse, short, black setae. In lateral view surface weakly convex. *Venter*: Setae black. Mesometasternal process short, nearly obsolete, flat, apex rounded. Abdominal sternites with transverse, irregular field of large punctures; punctures sparser in central third, mostly large, shallow, with short, black setae. *Legs*: Femora and tibiae with sparse fringe of mostly short, black setae on median surface. Protibia tridentate, apical tooth longer, slightly narrower. Metafemur normal, not enlarged. Metatibia at apex with 2 broad lobes and with 2 long, articulated apical spurs with apices rounded. Metatrochanter triangular, elongate, flush with posterior margin of metafemur, acuminate apex not projecting perpendicularly. *Parameres*: Fig. 11.

**Distribution** (Fig. 5). Two specimens recorded from Morón and Nogueira (2007).

**MEXICO** (2): DURANGO (2): Torreón (40 mi SW on Hwy 40).

**Temporal Distribution.** June (2).

**Biology.** Morón & Nogueira (2007) indicated the habitat where this species was collected is semiarid with an average annual temperature of 12–18°C and located at 1287–1300 meters above sea level. Dominant plants consisted of *Parthenium* species (Asteraceae), *Fouquieria* species (Fouquieriaceae), *Larrea* species (Zygophiliaceae), *Hechtia* species (Bromeliaceae), *Opuntia* species (Cactaceae), *Agave* species (Amarillidaceae), and *Euphorbia* species (Euphorbiaceae).

## Biogeography

The distribution of blaesiine species (Fig. 5) nearly mirrors that of *Hologymnetis* species, another genus within the Gymnetini. The biogeography of *Hologymnetis* species was reviewed by Ratcliffe and Deloya (1992) and is reviewed here to understand the similar distribution of the Blaesiina. Lacking fossil evidence for the Gymnetini, it is necessary to rely upon data from plate tectonics, present and paleodistribution of other plants and animals, and ecological factors to formulate a hypothesis to best explain the current distribution of these insects.

As with most other genera of New World Gymnetini, the ancestral Blaesiina were present in South America prior to the establishment of the Panamanian land bridge in the Miocene. Given the current distribution and ecological requirements of Blaesiina species, it is assumed that they evolved in drier habitats. Drier habitats have been present in South America since middle Tertiary time (Webb 1978). The Quaternary (*i.e.*, the last two million years) is characterized by great environmental instability (Bigarella and

Andrade-Lima 1982; Whitmore & Prance 1987). These climatic changes caused, in relatively short geologic time, successive expansions and contractions of either forest or open, drier vegetation. Forest and nonforest biomes broke up into isolated blocks or expanded and coalesced depending on varying humid or arid climatic conditions (Haffer 1969, 1982; Vuilleumier 1971; Müller 1973; Prance 1973, 1982; Brown et al. 1974; Brown 1977; Tricart 1974; Simpson and Haffer 1978). With the reduction of forest vegetation during drier periods, there was a corresponding increase in nonforest formations that penetrated into the Amazon region from both north and south. Such formations consisted of large blocks or corridors connecting the open vegetation associations of the Central Brazilian Plateau with those of Venezuela and the Guianas (Eden 1974; Sarmiento 1975; Bigarella and Andrade-Lima 1982; Marshall 1985).

Present day *Blaesia* species inhabit the mesic to semiarid, relatively open vegetation habitats of Bolivia, Paraguay, Uruguay, Argentina, and southern Brazil. The broad, continuous band of present-day Amazonian rainforest is a barrier preventing further dispersal northward. Ancestral *Blaesiina* would have been afforded suitable avenues for traversing previously inhospitable lowland forested regions in Amazonia by the extensions of savanna-like habitat (Fig. 12). With the establishment or re-establishment of rain forest in the Amazon basin, populations of ancestral *Blaesiina* became divided and isolated both to the north and south of the Amazon region. The northern lineage (today's *Halffterinetis* species) ultimately dispersed to nuclear northern Mexico, and the southern lineage (today's *Blaesia* species) became isolated in the woodland savannas south of the Amazon basin. As habitats changed through time, ancestral *Blaesiina* disappeared entirely from between northern Mexico and southern South America.

Pre-Miocene dispersal of the biota between North and South America was probably rare, and a small amount of biotic interchange agrees with the geologic evidence suggesting a relatively wide separation of the Americas in Cretaceous through Oligocene times (Raven and Axelrod 1974; Smith and Briden 1977; Gose et al. 1980). Consideration of climate is important both before and after establishment of a land connection (Stehli and Webb 1985b). For example, the existence of clear evidence of mountain glaciation along the continental divide in Guatemala suggests that simply extending present-day conditions back in time will not suffice to allow a real understanding of the physical nature of the link between the two Americas or of its effect on biotic interchange. After Mesoamerica coalesced during the Pliocene 3.0 MYBP (Marshall 1988) to 5.7 MYBP (Lloyd 1963; Kaneps 1979), an extensive faunal exchange began (Webb 1978; Stehli & Webb 1985a). Formation of the Panamanian isthmus dispersal route permitted separate invasions of plants and animals at widely separated periods when climates and topographic features were different than today.

After the formation of the isthmus of Panama, members of the Gymnetini began their northward dispersal from South America into Central America, Mexico, and the United States. Webb (1978, 1985) provided an excellent analysis of the interamerican biotic exchange, pertinent parts of which are described here. The interval from 2.5–1.5 MYBP shows an extensive movement of savanna-adapted mammal faunas from south temperate to north temperate latitudes and vice versa. All of the animals that



**Figure 12.** Maps showing approximate distribution of savannas (gray areas) in South America at **a** about 4.0 MYBP, **b** during glacial maxima, and **c** today. Arrow in **b** shows most likely dispersal route of taxa living in savanna habitats (after Marshall 1985).

are known to have dispersed between the Americas in the late Tertiary were tolerant of, or specifically adapted to, savanna woodland habitats. The savanna elements were not incidental parts of the interchange but represent the vast majority of the taxa involved. Notable among them were horses, llamas, armadillos, and ground sloths. The extent of savanna adaptations among the land mammals of the interchange indicates the presence of a uniformly nonforested corridor or a moving mosaic of such habitats between South America and North America. The more arid conditions that must be postulated for the isthmian region during its early history probably supported seasonal forests grading into thorn scrub savannas. Similar habitats exist today in northern Venezuela and eastern Colombia and on the Pacific slopes of Central America from western Panama northward. Less mesic conditions in the isthmian corridor were a result of a combination of factors having to do with climatic fluctuations associated with northern hemisphere glaciations, lowering of sea levels (with a concomitant increase in land area), regional uplift with large-scale volcanic extrusion, and creation of rain shadow regions.

The glacial maxima at and following the emergence of the Panamanian land bridge, combined with the presence of a north-south corridor over the bridge, occurred only twice in the late Tertiary (Shackelton and Opdyke 1977; Cronin 1981). These times (2.5 and 1.8 MYBP) represent “optimal ecological windows” that permitted dispersal of taxa living in savanna habitats between the Americas (Marshall 1985). The earliest known South American mammals to disperse to North America across the Panamanian land bridge occur in rocks dated at 2.8–2.6 MYBP. This reciprocal event favoring savanna-adapted forms could not have occurred earlier due to absence of a suitable corridor, habitat, and climate. Subsequent opportunities did not exist until the next glacial maxima at about 2.0–1.9 MYBP (Marshall 1985). “Thus, two synchro-

nous and reciprocal dispersal events of late Tertiary age are recognized. The first event (2.8–2.6 Ma) included dispersal of *Erethizon* Cuvier, *Neochoerus* Hay, *Glyptotherium* Osborn, *Glossotherium* *Glossotherium* Owen, *Othrotheriops* Hoffstetter, *Kraglievichia* Casatellanos, and *Dasyops* L. (and the ground bird *Titanis* Brodkorb) to North America, and *Conepatus* Gray, *Hippidion* Roth, and *Platygonus* LeConte to South America. The second event (2.0–1.9 Ma) included dispersal of *Hydrochoerus* Brisson, *Eremotherium* Spillmann, and *Holmesina* Simpson to North America, and *Arctodus* Leidy, *Galictis* Bell, *Felis* L., *Smilodon* Lund, *Tapirus* Brünnich, *Hemiauchenia* Gervais and Ameghino, *Onohippidium* Moreno, and *Cuvieronius* Osborn (and possibly *Stipanicia* Reig, *Dusicyon* Smith, and *Protocyon* Giebel) to South America. Only one dispersal event of early Pleistocene age is evident, and this occurred at about 1.4 Ma. It corresponds to the earliest of the Pleistocene glacial maxima recognized by Cronin (1981) and follows the one at 2.0–1.9 Ma. During this event, *Canis* L., *Lutra* Brisson, *Chrysocyon* Hamilton-Smith, *Cerdocyon* Hamilton-Smith, *Leo* (= *Panthera* Oken), and *Stegomastodon* Pohlig dispersed to South America, and *Didelphis* L. and *Palaeolama* Gervais dispersed to North America” (Marshall 1985). The last glacial maximum permitting dispersal of savanna biotas over the land bridge occurred 12,000–1,000 years B.P. (Bradbury 1982; Markgraf and Bradbury 1982). A savanna corridor formed along the eastern side of the Andes connecting the now disjunct habitats in South America (Fig. 12).

The major obstacles to such dispersal events were distance and potential competitive exclusion. Given that cetoniines are capable of such powerful flight, distance may not have been such a deterrent to long distance dispersal. The Japanese beetle (*Popillia japonica* Newman) (Scarabaeidae: Rutelinae), for example, has spread from the east coast of North America (where it was introduced) to the central states (1,900 km away) in only 70 years; that averages 27 km/year. *Aphodius fimetarius* (L.) (Scarabaeidae: Aphodiinae), introduced into North America from Europe probably in colonial times, is now found over much of the continent. *Digitonthophagus gazella* (Fabr.) has dispersed from 43 to 808 (!) km/year in Mexico and the U.S. (Barbero and López-Guerrero 1992). The tussock moth, monarch butterfly, European corn borer, and honeybee all represent contemporary examples of long distance dispersal by insects in short periods of time. The Africanized honeybee, *Apis mellifera scutellata* Lepeletier, has dispersed 300–500 km per year from southern Brazil to northern Mexico in only 30 years (Camazine & Morse 1988). The rapid and historically near-instantaneous colonization of the Australian continent by the European hare, *Lepus europaeus* Pallas, highlights the phenomenal dispersal ability of a small mammal (Marshall 1985). The opossum, *Didelphis marsupialis* L., had an average dispersal rate of 50 km/year during the 26 years following its introduction into California (Tyndale-Biscoe 1973). At such a rate this species could extend its range 25,000 km in only 500 years (Savage and Russell 1983). Martin (1973) noted that a conservative dispersal rate of 16 km/year would have permitted prehistoric humans to spread from Canada to Tierra del Fuego in less than 1,000 years. The dispersal of insects between the mid-continental regions of North and South America may have occurred in only a few thousand years with the availability of suitable habitat. The vertebrate fossil evidence clearly indicates

that dispersal of savanna-adapted animals occurred twice in the late Tertiary. South American ancestral *Blaesiina*, adapted to dry habitats, was part of that dispersal. Webb (1978) observed that it may be difficult for some biologists to accept so short a time scale for such evolutionary change, but the paleontological record of the interamerican interchange demonstrates that two or three million years is sufficient time to produce fundamental evolutionary reorganization of a major biota.

The late Pleistocene shift to more humid conditions in lower Central America produced a major set of savanna disjunctions spanning the isthmian gap (Webb 1978). The disjunct distribution across the American tropics shared by many present-day organisms provides additional evidence of a previous woodland savanna corridor. Within the temperate to subtropical *Areodina* (Scarabaeidae: Rutelinae), six genera are found ranging from the United States to Guatemala, and three genera are found in South America (Jameson 1990). None of these genera occur in the remainder of Central America, which, for the most part, has been historically covered by tropical rainforest. This Central American gap might seem like a paradox until, noticing its occurrence in other groups, we recognize a pattern. Many birds adapted to savanna or thorn scrub show a wide interamerican disjunction. These include the Green Jay, Military Macaw, Melodious Blackbird, Homed Lark, Vermillion Flycatcher, small woodpeckers, and the Grasshopper Sparrow (Griscom 1950; Mengel 1970). Cricetid rodents such as *Reithrodontomys* Giglioli skip from semiarid habitats in Nicaragua to similar habitats in the Andes, and *Crotalus* L. vipers (preferring scrub habitats) now have a large gap across the rainforest of the isthmus (Webb 1985). The distributional gap across the isthmian region is well known for many plants as well as many bees that specialize on these plants (Raven 1963; Solbrig 1972; Rzedowski 1973; Simpson and Neff 1985). Webb (1985) observed that one of the most convincing indications of former continuity is a string of relict populations of *Larrea* Cav. in Peru and Bolivia partly connecting its main south temperate and north temperate ranges. This idea is strengthened by the fact that one of the principal foods of the extinct ground sloth (*Nothrotheriops* Hoffstetter species), as indicated by its dung, was *Larrea*, and that both genera clearly came to North America from temperate South America (Martin et al. 1961; Hunziker et al. 1973). By the late Pleistocene, as now, woodland savanna taxa were excluded from the isthmian region due to the dissolution of savanna habitats and replacement by tropical rainforest. Late Pleistocene pollen samples from Lake Gatun in Panama reveal a forest flora much like that of present lowland Panama (Webb 1978). About 1,700 km of tropical wet forest extending from Costa Rica and Panama through northern Colombia now separates the nearest areas of savanna and thorn forest (Sarmiento 1976). Consequently, ancestral *Blaesiina* were also excluded from this region because they could not survive in tropical wet forests. Northern Central America retained a woodland savanna fauna as evidenced by the present biota and Pleistocene samples from Guatemala, Honduras and El Salvador (Stirton and Gealey 1949; Carr 1950; Duellman 1966; Savage 1966; Woodburne 1969; Howell 1969). Species of *Halffterinetis* are today found in mesic to xeric habitats in north central Mexico.

Based on his analysis of the entomofauna, Halffter (1976) formulated several different dispersal patterns to explain the present distribution of taxa in the Mexican Transition Zone. The distribution of *Halffterinetis* species coincides well with Halffter's "Typical Neotropical Dispersal Pattern". In this pattern, South American elements penetrated into the Mexican Transition Zone after the formation of the Panamanian land bridge and after most of the elevation of the Mexican Plateau. As ancestral Blaesiina spread northward, they used as their principal expansion route from Central America the mountains of Oaxaca and the Sierra Madres, which funneled the dispersal of Blaesiina to the west and north, respectively, where *Halffterinetis* species occur today.

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# Phylogenetic analysis of the myrmecophilous *Cremastocheilus* Knoch (Coleoptera, Scarabaeidae, Cetoniinae), based on external adult morphology

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## Abstract

The genus *Cremastocheilus* (Coleoptera: Scarabaeidae: Cetoniinae) is a myrmecophilous group of approximately 45 species distributed throughout North America. Authors previously recognized anywhere between two and five subgenera. We present the first cladistic analysis of *Cremastocheilus* based on 51 external adult morphological characters. The monophyly of the subgenera *Macropodina*, *Trinodia* and *Cremastocheilus* is supported. *Cremastocheilus* (*Anatrinodia*) *wheeleri* is most closely related to other *C.* (*Cremastocheilus*). The three species groups comprising *C.* (*Myrmecotonus*) are paraphyletic with respect to *C.* (*Cremastocheilus*). The pronotum, which bears most of the glands that enable beetles to interact with ants, provides important characters, while characters associated with setae and tomenta are homoplastic. Based on examination of the strict consensus of 24 equally parsimonious trees *C.* (*Myrmecotonus*) and *C.* (*Anatrinodia*) are synonymized with *C.* (*Cremastocheilus*).

## Keywords

Scarabaeidae, *Cremastocheilus*, phylogeny, myrmecophily

## Introduction

*Cremastocheilus* Knoch is a unique scarab genus that can be recognized by a suite of characters related to its myrmecophilous habit. It can be distinguished from other

genera by distinct anterior and posterior pronotal projections or “angles” that bear exocrine glands and associated trichomes (clumps of setae typically associated with glands). The pronotal angles are highly variable within the genus, particularly in *C. tibialis* which lacks posterior pronotal trichomes entirely. Similarly, posterior pronotal trichomes are found in the New World related genus *Centrochilus* Krikken (see Krikken 1976) as well as Old World genera *Aspilus* Shaum and *Lecanoderus* Kolbe, although none of these genera have modified anterior pronotal angles or associated trichomes (Krikken 1982). In comparison to related genera *Cremastocheilus* is one of the more speciose and probably best studied groups within the tribe Cremastocheilini (Krikken 1984), which includes 51 genera worldwide (Krikken 1984) and ten in the New World, including *Cremastocheilus*. There are approximately 45 recognized species, including several subspecies found throughout North America. As adults, all species are presumed predaceous on ant larvae and, in some cases, pupae, based on collection records and behavioral studies on certain species (see Cazier and Mortenson 1965). Related beetles are also known to be predaceous on other insects, e.g. *Pseudospilophorus plagosus* Boheman preys on soft scale insects in southern Africa (Buttiker 1955), and *Spilophorus maculatus* (Gory and Percheron) from southern India has been documented feeding on membracids (Ghorpade 1975). It is presumed that related species in the tribe Cremastocheilini are also predaceous based on the expanded mentum (Krikken 1984). In addition, no genus, except *Centrochilus* and Old World genera *Aspilus* and *Lecanoderus* bear trichomes like those of *Cremastocheilus*; however, the presence of associated glands makes *Cremastocheilus* a distinctive genus within the tribe as well as the scarab subfamily Cetoniinae.

Horn (1879) was the first to suggest that trichomes in *Cremastocheilus* species are associated with glands that secrete substances somehow pleasing to ants. In contrast, Wheeler (1908) proposed that pronotal glands emit substances that are irritants that “distract” ants from attacking more vulnerable organs. Others have proposed that trichomes allow the beetles to gain access to ant nests by rapid diffusion of aromatic substances that would allow beetles to be carried into ant nests as food (Cazier and Mortenson 1965). In support of Wheeler, Alpert (1994) recently found that ants “lick” the pronotal glands and are subsequently ignored within the brood chambers, while feeding uninterruptedly on ant larvae. Given the above scenarios it is possible that different *Cremastocheilus* species use various means to gain access to ant mounds or be expelled from them. Alpert (1994) has shown that exocrine glands and their associated trichomes vary greatly among species. In addition, he found that clusters of glandular cells are often located underneath or close to external patches of hair called tomenta, particularly in the abdomens of several species. The frontal tomenta which largely distinguish the subgenus *C. (Trinodia)* also indicate closeness with glands inside the head of these beetles, but there is no evidence that pores or other secretive structures are associated with these patches of hair. Alpert’s (1994) definitions of various species groups suggested that ant host, habitat, and position of glands and trichomes are good indicators of relatedness or similarity among different species.

In Horn's (1879) revision of *Cremastocheilus* the mentum was used to distinguish between 17 species known at the time. Mann (1914) created a new subgenus named *Myrmecotonus* that would divide *Cremastocheilus* into two groups based on geographic range and emarginated mentum (Table 1). Typical *Cremastocheilus* species bear a mentum that is notched at the base and are distributed throughout the eastern United States. All other known species are distributed throughout the western United States and northern Mexico, and lack a notched mentum. Mann also suggested that an unusual species described by LeConte as *C. wheeleri* would belong to *C. (Myrmecotonus)* given the angulate, non-emarginate mentum. Noting the variability of mentum, pronotal, and leg structure within the group, Casey (1915) later described 15 new species and two new subspecies. He proposed two new genera including *Macropodina*, which was named for distinctive enlarged fore tarsi, and *Trinodia*, which included specimens with a distinctive tri-lobed pronotum. Casey also rejected Mann's (1914) subgenus *Myrmecotonus*, noting that most species bear a non-emarginate mentum, which would put all atypical *Cremastocheilus* species and other genera in the subgenus. The subgenus *Myrmecotonus* has been problematic, due to what most authors would admit is a lack of synapomorphies or good subgeneric definition. In contrast with Mann's (1914) suggestion it was treated as a synonym of *C. (Cremastocheilus)* by Krikken (1982), and was later recognized by other authors as an ill-defined subgenus (Howden 1971). Alpert (1994) reinstated *C. (Myrmecotonus)* due to geographic range.

Casey (1915) also suggested the recognition of one new monotypic subgenus *Anatrinodia* for *C. wheeleri*, based on a transverse, lobiform mentum, but still related to other typical *Trinodia* by possessing a somewhat similar tri-lobed pronotum. Later, Cazier (1938) synonymized the genus *Macropodina* with the genus *Cremastocheilus* based on what he believed to be few supportive characters for generic status. Cazier also synonymized.

**Table 1.** History of major subgeneric changes in the genus *Cremastocheilus*. Indented names indicate subgenera that are included in the given genus.

Horn 1879	Mann 1914	Casey 1915	Cazier 1938	Potts 1945
<i>Cremastocheilus</i>	<i>Cremastocheilus</i> <i>Cremastocheilus</i> <i>Myrmecotonus</i> *	<i>Cremastocheilus</i> <i>Macropodina</i> <i>Trinodia</i> <i>Anatrinodia</i>	<i>Cremastocheilus</i> <i>Crematocheilus</i> <i>Macropodina</i> <i>Trinodia</i> <i>Anatrinodia</i>	<i>Cremastocheilus</i> <i>Cremastocheilus</i> <i>Macropodina</i> <i>Trinodia</i> <i>Anatrinodia</i>
Howden 1971	Krikken 1982	Alpert 1994	Mynhardt and Wenzel 2010	
<i>Cremastocheilus</i> <i>Cremastocheilus</i> * <i>Macropodina</i>	<i>Cremastocheilus</i> <i>Cremastocheilus</i> <i>Macropodina</i> <i>Trinodia</i> <i>Anatrinodia</i>	<i>Cremastocheilus</i> <i>Cremastocheilus</i> <i>Macropodina</i> <i>Trinodia</i> <i>Anatrinodia</i> <i>Myrmecotonus</i>	<i>Cremastocheilus</i> <i>Cremastocheilus</i> * <i>Macropodina</i> <i>Trinodia</i>	

\* Indicates inclusion of *C. wheeleri*

*Trinodia* and the subgenus *Anatrinodia* with *Cremastocheilus* and suggested that *C. wheeleri* is an intermediate form between *C. (Trinodia)* and *C. (Cremastocheilus)*. Similar to Cazier, Potts (1945) only recognized *Macropodina* and *Cremastocheilus* as well defined subgenera, and united *Anatrinodia* and *Trinodia* informally into what he called a single “*Trinodia* group” in *Cremastocheilus*, following Cazier’s (1938) suggestion. Howden (1971) also did not recognize *C. (Anatrinodia)* but provided no information on the placement of *C. wheeleri*. It is assumed that Howden’s key would place *C. wheeleri* in *C. (Cremastocheilus)*. Krikken (1982) later reinstated *Anatrinodia* as a unique subgenus due to its unique pronotum and mentum. Recently, Alpert (1994) recognized all subgenera, including *C. (Myrmecotonus)* and *C. (Anatrinodia)* based on differences in geographic range previously recognized by Mann (1914).

The aim of this study is to test the monophyly of currently recognized *Cremastocheilus* subgenera and species groups suggested formally by Alpert (1994), and to determine evolutionary relationships among subgenera. We also aim to elucidate the importance of characters for future phylogenetic analysis, with particular focus on characters related to a myrmecophilous habit.

## Methods

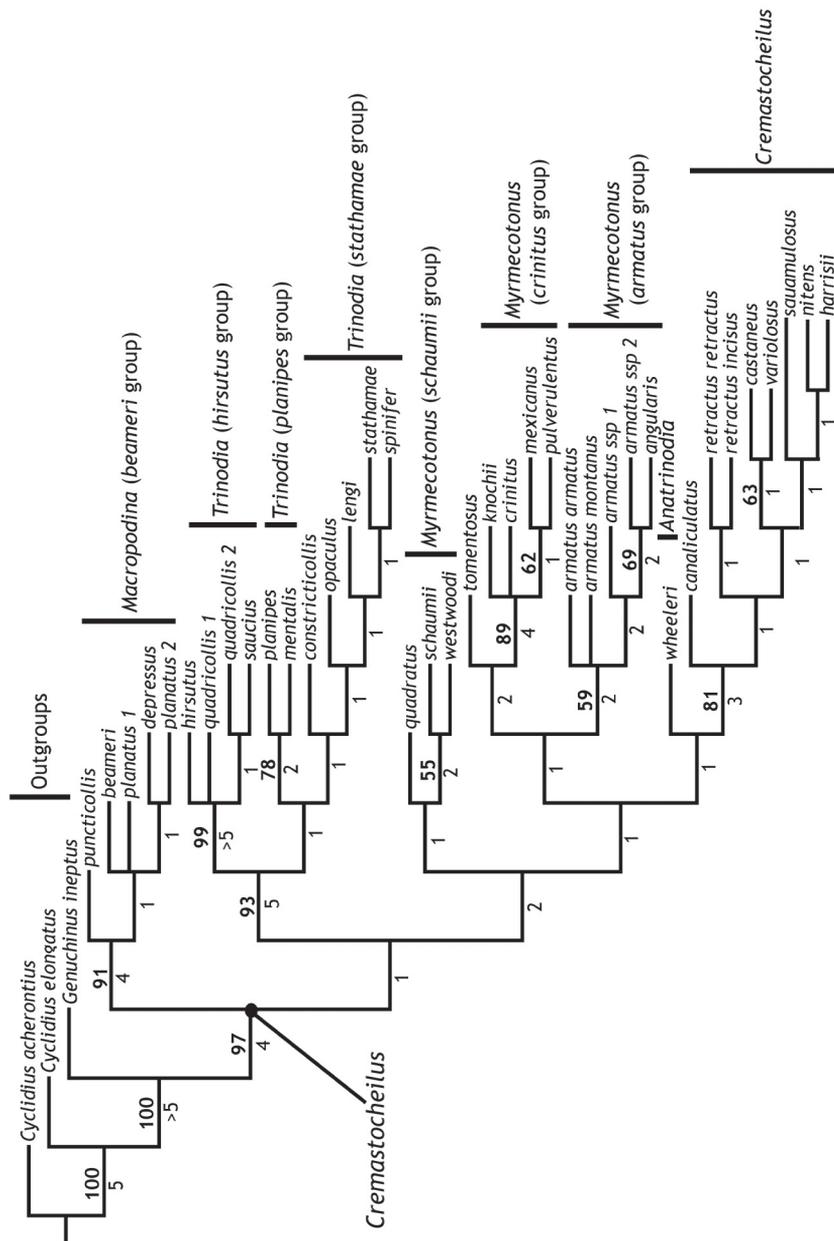
A total of 450 *Cremastocheilus* specimens were borrowed from The Ohio State University Insect Collection, University of California-Riverside Entomology Research Museum, University of Nebraska State Museum, Los Angeles County Museum of Natural History, Albert J. Cook Arthropod Research Collection at Michigan State University, and the Museo de Zoologia, Universidade de Sao Paulo. Three species, including *C. robinsoni* Cazier, *C. academicus* Krikken, *C. setosifrons* and *C. chapini* Cazier were not included in the analysis due to unavailability of specimens. The inclusion of *C. (Macropodina) depressus* in the analysis follows Warner (unpublished thesis) who recognized it as a unique species, although previous authors have synonymized it with *C. (Macropodina) planatus*. Three related Nearctic *Cremastocheilini* were used as outgroups, namely *Genuchinus ineptus*, *Cyclidius acherontius* and *Cycl. elongatus*. *Genuchinus* is assumed to be a close relative based on overall morphological similarity (Alpert 1994) and other *cremastocheilines* are rare in collections. Alpert’s key was used to identify numerous misidentified specimens, particularly species that appear to be part of larger species complexes (see Alpert 1994). A total of 52 adult external morphological characters were used in this analysis (see Appendix A). Inapplicable characters were coded as “-”, while missing, unknown or highly variable characters were coded as “?” (see Appendix B for character coding used). The choice of characters was based in part on previous suggestions by Krikken (1982), who was the first to propose a set of characters only for *C. (Trinodia)*. Characters related to genitalia and wing venation were not used because they have previously been established as invariant within the genus (Cazier 1938). Uninformative characters were removed from the analysis. Species that vary in relevant characters were coded as morphotypes of a spe-

cies to recognize this variability. Male and female characters were not coded separately as sexes are not known to differ in external morphology except for the presence of a tibial tooth in the males (Alpert 1994).

Initially, all characters were run equally weighted and non-additive. The final matrix included seven characters coded as additive (see Appendix A). The Parsimony Ratchet (Nixon 1999a) was implemented in NONA (Goloboff 1999), and run within Winclada (Nixon 1999b) with 50 iterations, beginning with one starting tree and weighting approximately 21% of characters (11/52). The trees obtained by the Ratchet were used as starting trees in a "max\*" (TBR branch swapping) search that produced 24 equally parsimonious trees of 149 steps. Suboptimal trees were searched, but none were found, leaving 24 equally parsimonious trees of 149 steps. A more thorough search using mult\*100 and a successive max\* search algorithm was performed, but the same 24 equally parsimonious trees were found. A strict consensus of the optimal trees was performed, with 4 collapsed nodes, yielding a tree of 153 steps (CI = 0.46 and RI = 0.80, Fig. 1). Bremer support was determined using Nona, and was set to a support level of 5. Clade support was estimated using jackknifing where each search consisted of 1000 replications, 5 reiterations of random additions of taxa, and holding a maximum of 10000 trees per replication. TBR (max\*) was initiated with one starting tree per replication.

## Results

The strict consensus of 24 equally parsimonious trees (CI = 0.46, RI = 0.80) reveals several monophyletic, resolved clades. The genus *Cremastocheilus* is a well-defined, monophyletic group (Jackknife support = 97) comprised of several clades. The subgenera *C. (Macropodina)*, *C. (Trinodia)*, and *C. (Cremastocheilus)* are monophyletic. The *hirsutus* species group within *C. (Trinodia)* is well supported (Bremer support = 5; Jackknife support = 99). In contrast, *C. (Myrmecotonus)* is not a monophyletic group. The *armatus* and *crinitus* species groups within *C. (Myrmecotonus)* form a single monophyletic group, while the *schaumii* species group appears to be the sister group of the *Cremastocheilus sensu str.* + *Myrmecotonus* clade (including only *armatus* and *crinitus* groups). The recently described *C. (Myrmecotonus) tomentosus* Warner is closely related to the *crinitus* group, although it has been proposed as a sister to *C. (Myrmecotonus) robinsoni* (Warner 1985) in the *C. robinsoni* species group, which was not included in the analysis. Diagnosis of all equally parsimonious trees indicates that *C. wheeleri* [in (*C. Anatrindia*)] is the sister of *C. (Cremastocheilus)*. Overall, the trees found in this analysis agree with those of Krikken (1982), whereby *C. (Myrmecotonus)* and *C. (Cremastocheilus)* are closely related; however *C. (Anatrindia)* is more closely connected with the *C. (Myrmecotonus)* + *C. (Cremastocheilus)* clade than with *C. (Trinodia)*, which disagrees with original hypotheses (Casey 1915, Potts 1945) about a close relationship between *C. (Trinodia)* and *C. (Anatrindia)*.



**Figure 1.** Strict consensus of 24 equally parsimonious trees (153 steps, CI = 0.46, RI = 0.80) of *Cremastocheilus*. Dark bars indicate monophyletic groups that correspond with Alpert's (1994) subgenera and respective species groups. Jackknife values are shown above branches, with support <50 not shown. Bremer support values are shown in bold below branches. Black dot indicates the genus *Cremastocheilus*.

## Discussion

Based on all equally parsimonious trees found, the monophyly of the genus *Cremastocheilus* is well supported. Diagnostic characters include the presence of modified anterior and posterior pronotal angles and associated trichomes. Relationships within the genus support some previous hypotheses, but renders the validity of certain subgenera invalid. While subgenera *C. (Macropodina)*, *C. (Trinodia)*, and *C. (Cremastocheilus)* are monophyletic, *C. (Myrmecotonus)* is not. Similarly, the monotypic subgenus *C. (Anatrinodia)* is more closely related to *C. (Cremastocheilus)* than to *Trinodia*, with which it was previously united by similarity in pronotal shape.

Monophyly of *C. (Macropodina)* is supported by enlarged protarsi, frontolateral carinae bearing glands (Alpert 1994), carinate pygidium, and generally rectangular body shape. Within *C. (Macropodina)* there is poor support for species relationships below the subgeneric level, and Alpert also only suggested one species group, the *C. (Macropodina) beameri* group, which includes all species within this subgenus. There is little information regarding the hosts for this subgenus, although the species *C. (Macropodina) beameri* has been collected in and near rodent burrows. Cazier and Mortenson (1965) suggested that *C. beameri* uses rodent burrows, particularly those of *Neotoma* as sites for mating and overwintering for adults, as well as development of immature beetles. Ant colonies are often found within or near rodent mounds, and it is possible that these colonies are a source of brood for adults, although beetles have not been found in surrounding ant mounds in the field (Alpert 1994). The species *C. (Macropodina) planatus*, which is likely a widely distributed species complex, as well as its previously recognized synonym *C. (Macropodina) depressus* have been collected with *Camponotus* and there is no evidence that it is associated with rodent mounds. Similarly, *C. puncticollis* has been collected in *Myrmecocystus mexicanus* mounds, although this particular host record has been cited as accidental (see Alpert 1994 for host accounts for all species). While these beetles have never been observed to interact with ants, it has been suggested that the long forelegs can be used to wipe ants from the beetles' bodies while attempting to enter ant nests (Alpert 1994). Similarly, true functions of the frontolateral and protarsal glands are unknown, although they probably function together since the glands are identical in structure (Alpert 1994).

The monophyletic subgenus *C. (Trinodia)* is united by several unique synapomorphies that make it one of the most distinctive subgenera in the genus. All species bear a very prominent trilobed pronotum, a character that gave this subgenus its name. The presence of an upcurved proepisternum, which appears dorsally as a separate nodular lobe, is unique in this subgenus. Although a few unrelated species appear to have a slight frontoclypeal ridge, it is highly developed in *C. (Trinodia)*. It is suspected that many of these characters are related to myrmecophily. Alpert's (1994) three species groups are all monophyletic. The *C. (Trinodia) hirsutus* group is a unique and well supported species group, with all species bearing an emarginate posterior pronotal angle. All species within this species group are found with ants in the genus *Pogonomyrmex*. It is likely that the robust and excised posterior angles in this species group is involved

in their interaction with these aggressive ant hosts. Two species in the species group *C. (Trinodia) planipes* are united by very broadly flattened hind tibiae and femora. Both *C. (Trinodia) planipes* and *C. (Trinodia) mentalis* are found with the ant genus *Aphaenogaster*. The *C. (Trinodia) stathamae* group is supported by unique elytral punctures that appear elongate and fused. This is the only monophyletic group that is united by a character related to punctation, as it appears highly homoplastic throughout the genus. Species in this group are collected with various species of the honeypot ants, *Myrmecocystus*, as well as *Pheidole*.

Species in *C. (Cremastocheilus)* comprise a monophyletic group and are united by several unique synapomorphies, including strongly delimited posterior angles and nodulose anterior angles. All species in *C. (Cremastocheilus)* bear a notched mentum of various sizes, except for *C. nitens* and *C. chapini*, although the monophyly of the subgenus is still preserved given the pronotal characters. In contrast, all species groups within *C. (Cremastocheilus)* suggested by Alpert (1994) are paraphyletic. His division of species groups relied mainly on characters related to shape of angles on the pronotum, shape of mentum, and elytral punctures; however, many characters related to elytral punctation show high incidences of homoplasy. The *C. (Cremastocheilus) canaliculatus* group is often defined by the presence of a secondary trichomes situated by the anterior pronotal angles; however, this character does not seem to be useful in defining the group.

The subgenus *C. (Myrmecotonus)* is not monophyletic, without removal of the *C. (Myrmecotonus) schaumii* group. This species group lacks highly developed pronotal angles as well as a notch in the proepisternum that is present in all other *C. (Myrmecotonus)*. The analysis indicates that the *C. (Myrmecotonus) schaumii* group is the sister group to the *C. (Cremastocheilus) + C. (Myrmecotonus)* clade (with removal of the *schaumii* species group). Given that the host records indicate that a western United States distribution for all *C. (Myrmecotonus)* species, it is possible that specific ant hosts play an important role in the relationships indicated. The close relationship of *C. (Cremastocheilus)* and *C. (Myrmecotonus)* with removal of the *C. schaumii* group could be explained by similar ant hosts. With exception of a few other ant host genera, including *Aphaenogaster* and other accidental records (see Alpert 1994), all species in *C. (Cremastocheilus)* and the *C. (Myrmecotonus) crinitus*, *C. (Myrmecotonus) armatus*, and *C. (Myrmecotonus) robinsoni* species groups, are found with *Formica* ant hosts. Species in the *C. (Myrmecotonus) schaumii* group have only been collected with *Messor* species and was accidentally recorded with *Pogonomyrmex subnitidus* (Alpert 1994).

The relationship of the species *C. (Anatrinodia) wheeleri* with other species and subgenera has never been well understood due to its odd mentum and pronotal structures. Its initial union with *Trinodia* was based on elements of the pronotum. Unlike the tri-lobed pronotum, with the lateral lobes holding large muscles in *Trinodia*, the pronotum in *C. wheeleri* contains enlarged glandular clusters (Alpert 1994). The distinctly trilobed pronotum, up-curved proepisternum, and carinate clypeus support the monophyly of *C. (Trinodia)*, characteristics that are not found in *C. wheeleri*. The strict consensus indicates that *C. wheeleri* is be a basal species of *C. (Cremastocheilus)*, but

some have suggested that it is a highly derived relative of the subgenus (Warner, pers. comm.). The deeply cup-shaped mentum and notched proepisternum places it close to other *C.* (*Cremastocheilus*), but overall body shape does not match character definitions of any other subgenus. We are hereby synonymizing *C.* (*Myrmecotonus*) and *C.* (*Anatrinodia*) with *C.* (*Cremastocheilus*). Note that taxonomic perspective regarding species and subgenera should be cited as Mynhardt 2009 (in Mynhardt and Wenzel 2010).

The role of glands and associated trichomes and tomenta in beetle/ant interactions are not well understood and thus not described herein (but see Alpert 1994 for extensive histological study). Low consistency index (CI) values indicate a high occurrence of homoplasy, which could be due to myrmecophilous habits. Some behavioral work has shown that even species that are closely related do not interact with ant hosts in the same way. For example, *C.* (*Trinodia*) *hirsutus* enters nests on its own, without aid from ants, while closely related *C.* (*Trinodia*) *saucius* is pulled into mounds by ants (Alpert 1994). This could suggest that characters related to certain myrmecophilous behaviors are homoplastic. It might also suggest a divergence in behaviors that could lead to speciation. Ants are known to “lick” or bite pronotal angles of *Cremastocheilus*, which is likely to be rather host-specific with respect to the mandibles of the ants and may drive the evolution of the pronotal projections. Wheeler (1908) suggested that the shape of the posterior pronotal angles is likely shaped by ant mandibles. As such, the only pronotal characters that indicate relatively low CI values are the shape of the posterior angles (Wheeler 1908) and the appearance of a notch in the anterior pronotal angle in unrelated species of *C.* (*Trinodia*) and *C.* (*Cremastocheilus*). Ant hosts of these two groups differ, suggesting separate selective pressures by different ant hosts. Characters related to the patches of setae (tomenta) distributed across the body are also supported by low CI's. The frontoclypeal tomentum, elytral disk tomentum, and ventral abdominal tomentum appear in various unrelated *Cremastocheilus* species. Similarly, there is a strip of tomentum along the base of the mesepimeron, which is found in five species, only two of which are closely related. These tomenta are probably linked to interactions with ants, and may have associated exocrine glands. For example, the frontal tomentum is has been shown to be associated with the frontal glands found in histological sections in *C. wheeleri* and the *hirsutus* group of *C.* (*Trinodia*) (Alpert 1994). The placement of glands, which were coded by using external trichomes or tomenta, appears to be a relatively good character in distinguishing subgenera or even species groups, particularly in the case of trichomes. For example, tarsal glands are found only in *C.* (*Macropodina*) and frontal glands are found in closely related *C. wheeleri* and species in *C.* (*Cremastocheilus*). Externally, tomenta above the antennal insertions are associated with the frontal glands in *C.* (*Cremastocheilus*). Most species in the genus bear tomenta on the metepimeron and many species have tomentose areas along or on the lateral portion of the abdominal sterna. Alpert (1994) found evidence of glands in *C.* (*Trinodia*), *C.* (*Myrmecotonus*) *armatus* and *C.* (*Myrmecotonus*) *pulverulentus*. Other tomentose areas are not at all associated with internal glands, especially those tomenta on the elytra of many species, which appears to be highly homoplastic. Tomentum at the base of the mesepimeron in several species is also homoplastic. Similar tomenta are

found throughout the Cetoniinae. Alpert (1994) suggested that the elytral punctures were reliable in defining species groups and even identifying species in many cases. Elytral characters used in this analysis did not prove to be useful in uniting species groups, and three of the four elytral characters used had very low CI values. However, because most of Alpert's species groups appear to be well-defined, monophyletic clades, it is evident that many other useful characters still unite those groups.

While tomenta and other myrmecophilous structures may be under strong selective pressures by ants, it is also likely that distinct monophyletic groups revealed in this analysis are associated with specific ant host genera, a pattern that has been shown in sceptobiine staphylinids associated with ants (Danoff-Burg 1994). Alpert's (1994) *hirsutus* group in *C. (Trinodia)* is almost exclusively collected with *Pogonomyrmex* ant hosts; the *C. (Trinodia) planipes* group is associated only with *Aphaenogaster* spp; and *C. (Cremastocheilus)* species as well as *C. wheeleri* and the majority of species in *C. (Myrmecotonus)* are most often collected in *Formica* mounds. A few exceptions to this pattern includes *C. (Anatrinodia) wheeleri*, which is most often collected in *F. obscuripes* mounds. The unrelated *C. (Myrmecotonus)* is also most often found with this particular species; however, there is an indication that closely related *Cremastocheilus* species are more likely to be found with ant hosts of the same genus.

## Conclusion

True interactions between beetles and their respective ant hosts should elucidate evolutionary patterns regarding strategies used by different *Cremastocheilus* species. Based on the characters used in this study, it is evident that many characters related to myrmecophily are informative at the subgeneric level, but others are not. Trichomes, which are assumed to play an integral part in beetle/ant host interactions, show low instances of homoplasy, while some tomenta and the elytral punctures indicate multiple origins and are less phylogenetically informative. This work presents a framework for future studies, but also presents some important taxonomic changes regarding subgenera. We suggest that any future work should include characters related to myrmecophilous habits, and addition of molecular data would be very useful.

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## Appendix A.

List of the characters and character states used in the analysis. doi:10.3897/zookeys.34.262.app.1.ds.

Note: Consistency index (CI) and retention index (RI) resulting from analysis are indicated in parentheses. Characters are numbered beginning with “0”. File format: PDF.

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## Appendix B.

Morphological character matrix of analyzed species of *Cremastocheilus*, with states used for each character. doi:10.3897/zookeys.34.262.app.2.ds.

Note: States are numbered beginning at “0”. File format: PDF.

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# Synopsis of the aroid scarabs in the genus *Peltonotus* Burmeister (Scarabaeidae, Dynastinae, Cyclocephalini) from Sumatra and description of a new species

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## Abstract

We provide a synopsis of the Sumatran species in the scarab beetle genus *Peltonotus* Burmeister (Scarabaeidae: Dynastinae: Cyclocephalini), describe a new species of *Peltonotus* from Sumatra, and describe the male of *P. cybele* Jameson & Wada from Sumatra (previously known only by the female holotype). To enable identification, we include a key to the five Sumatran species of *Peltonotus*, comparative images and diagnoses for all species, and temporal and geographical distributions.

## Keywords

Araceae, Indonesia, beetle

## Introduction

The southeast Asian scarab beetle genus *Peltonotus* Burmeister (Scarabaeidae: Dynastinae: Cyclocephalini) is associated with aroid flowers (Araceae) (Jameson and Wada 2004, 2009; Grimm 2009). The natural history, distribution, identification,

and history of classification of species in the genus were reviewed by Jameson and Wada (2009). With the addition of the species that we describe herein, the genus *Peltonotus* includes 25 species, including the following species that are distributed in Sumatra: *P. animus* Jameson & Wada 2009, *P. cybele* Jameson & Wada 2009, *P. gracilipodus* Jameson & Wada 2004, *P. sisyrus* Jameson & Wada 2004, and *P. talangensis* Jameson & Jakl, sp. n. All species that reside in Sumatra are endemic to the island. Ongoing biodiversity surveys will likely reveal additional species that await discovery. Based on the high species diversity within central Sumatra (four species in 100 miles<sup>2</sup>), it is possible that the species diversity of Sumatra approximates that in Sabah, Borneo (six species in 100 miles<sup>2</sup>). We provide a synopsis of the five Sumatran species in the genus *Peltonotus*, including a key to species, comparative images, species diagnoses, the description of a new species, information on natural history, and distribution maps.

With the inclusion of the new species and the male of *P. cybele*, only one species of *Peltonotus* from Sumatra lacks known females (*P. animus*). The males of all species from Sumatra are known. This is contrasted with our lack of knowledge for many species of *Peltonotus* in which identification is complicated by the absence of associated male and female specimens. Overall, five species of *Peltonotus* lack known males: *P. kyojinus* Jameson & Wada 2004, *P. mushiyaus* Jameson & Wada 2009, *P. nethis* Jameson & Wada 2004, *P. pruinus* Arrow 1910, and *P. tigerus* Jameson & Wada 2009. Four species lack known females: *P. animus* Jameson & Wada 2009, *P. deltoementum* Jameson & Wada 2004, *P. favonius* Jameson & Wada 2009, and *P. karubei* Muramoto 2000.

Little natural history information is available for the Sumatran species of *Peltonotus*, and most species are known from very few specimens and localities. Collection localities reveal that species are concentrated on the western side of the island (coinciding with montane habitat) and at elevations from 1000–1500 m. Specimens have been collected from February to April, June to July, and October to November.

## Methods

Characters and specimens were examined using a dissecting microscope (6.3–50.0 times magnification) and fiber-optic illumination. Morphological characters used for species identification (including puncture size and density, type of setae, form of male protibia, form of female epipleuron) are defined in Jameson and Wada (2004). Digital images of specimens and structures were captured using the Auto-Montage imaging system by Syncroscopy. Images were edited in Adobe Photoshop CS2 (background removed, contrast manipulated). We follow the phylogenetic species concept (Wheeler and Platnick 2000) which states that “A species is the smallest aggregation of (sexual) populations or (asexual) lineages diagnosable by a unique combination of character states.” Formation of specific epithets follows conventions in the International Code of Zoological Nomenclature (1999) and Blackwelder (1967). The generic name *Peltonotus* is considered masculine in gender

(Jameson and Wada 2004). Specimens examined during this research are deposited in the following institutional and private collections: Brett C. Ratcliffe Collection, Lincoln, NE, USA (BCRC); The Natural History Museum, London, England (BMNH; Malcolm Kerley); Field Museum of Natural History, Chicago, IL, USA (FMNH; Al Newton, Margaret Thayer); Masayuki Fujioka Collection, Tokyo, Japan (FUJI); Museum National d'Histoire Naturelle, Paris, France (MNHN; Olivier Montreuil); Mary Liz Jameson Collection, Wichita, KS, USA (MLJC); National Museum (Natural History), Prague, Czech Republic (NMPC); National Science Museum (N.H.), Tokyo, Japan (NSMT; Shuhei Nomura); Nationaal Natuurhistorische Museum ("Naturalis"), Leiden, Netherlands (RMNH); Stanislav Jakl Collection, Prague, Czech Republic (SJC); United States National Collection, Washington, D.C., USA (USNM; currently housed at UNSM); University of Nebraska State Collection, Lincoln, NE, USA (UNSM); Kaoru Wada Collection, Tokyo, Japan (WADA); Museum fur Naturkunde der Humboldt Universitat zu Berlin, Berlin, Germany (ZMHB; Manfred Uhlig).

### Key to the Sumatran species of *Peltonotus*

*Males*: Protibial claws with one claw enlarged and expanded; elytral epipleuron not developed in ventral view.

*Females*: Protibial claws similar in size and shape; elytral epipleuron developed or simple in ventral view.

1. Apical half of mentum acute, triangular (Figs 9–10) ..... **2**
- 1'. Apical half of mentum rounded (*e.g.*, Fig. 8)..... **3**
2. Surface of frons and clypeus multisetigerous; male genitalia as in Fig. 21a–b; female epipleuron incised and with elongate-oval emargination at sternite 4 in ventral view (Fig. 16) ..... ***P. sisyrus* Jameson & Wada**
- 2'. Surface of frons and clypeus unisetigerous; male genitalia as in Fig 22a–b; female epipleuron simple, not incised and emarginated in ventral view (Fig. 17)..... ***P. talangensis* Jameson & Jakl, sp. n.**
3. Protibia tridentate (Fig. 12); male genitalia as in Fig. 19a–b; female epipleuron incised and with rounded emargination in ventral view (Fig. 14)..... ***P. cybele* Jameson & Wada**
- 3'. Protibia bidentate (Fig. 11); male genitalia not as in Fig. 19a–b; female epipleuron not as in Fig. 14..... **4**
4. Apex of metatibia in male with longer spur produced to apex of metatarsomere 2; male genitalia as in Fig. 18a–b; female unknown ..... ***P. animus* Jameson & Wada**
- 4'. Apex of metatibia in male with longer spur produced to middle of metatarsomere 2; male genitalia as in Fig. 20a–b; female epipleuron incised and with moderately developed emargination in ventral view (Fig. 15)..... ***P. gracilipodus* Jameson & Wada**

***Peltonotus animus* Jameson & Wada, 2009**

Figs 1, 5, 11, 18a–b, 23

**Diagnosis.** *Peltonotus animus* (Fig. 1) is distinguished from other Sumatran species of *Peltonotus* based on the following characters: apex of metatibia in male with longer spur produced to apex of metatarsomere 2 (shared with *P. sisyrus*; spur shorter in *P. cybele*, *P. talangensis*, and *P. gracilipodus*); mala with setae curled at the apices (Fig. 5) (shared with *P. gracilipodus*; not curled in *P. cybele*, *P. talangensis*, and *P. sisyrus*); protibia bidentate (Fig. 11) (shared with *P. gracilipodus* and *P. sisyrus*; tridentate in *P. cybele* and *P. talangensis*); and form of the male genitalia (Fig. 18a–b). Outside of Sumatra, *P. animus* shares many character states with *P. silvanus* Jameson & Wada 2004 from Sarawak and Kalimantan on the island of Borneo (see Jameson and Wada 2009).

**Locality records** (n=1) (Fig. 23). SUMATRA. West Sumatra Province (1): Bukittinggi.

**Temporal data.** July (1).

**Remarks.** *Peltonotus animus* is known only from the male holotype specimen (housed in WADA).

***Peltonotus cybele* Jameson & Wada, 2009**

Figs 2–3, 6, 12, 14, 19a–b, 23

*Peltonotus cybele* was previously known only by the female holotype specimen (Fig. 3). Discovery of the first male specimens (e.g., Fig. 2) and a second female facilitates identification of the species.

**Description of male (n=2).** The male differs from the female holotype in the following respects. Length 16.4–16.5 mm. Widest width 8.0 mm. *Color* (Fig. 2): Head, pronotum, scutellum, propygidium, pygidium, and venter castaneous; elytra dark reddish-brown with iridescent bloom. *Head*: Maxilla (Fig. 6) as in holotype, mala lacking lamellate setal brush; stipes with setae sparse, long, not flattened, not curled at apex; palpomere 2 with weak internomedial bump. *Elytron*: Surface with 5 poorly developed, punctate, longitudinal striae between suture and humerus, lateral-most striae poorly defined. *Propygidium*: Surface shagreened and moderately densely punctate (base to mid-disc) to moderately densely punctate (mid-disc to apex); punctures simple, unisetigerous or lacking setae; setae minute, tawny. *Pygidium*: Surface moderately densely punctate; punctures ocellate, moderately large and large, some unisetigerous; setae minute. *Venter*: Prosternal keel elongate; apex projecting anteriorly at about 90° with respect to ventral plane; apex extends to about mid-height of protrochanter, quadrate. *Legs*: Protibia (Fig. 12) of male tridentate; lateral margin with short, dense setae. Protarsomere 5 of male subequal in length to tarsomeres 1–4; protarsomere 3–4 with apices expanded, dorsal and ventral apices clothed with dense, short setae. Anterior claws of male with inner claw curved, about 4 times thicker than outer claw; outer claw simply arcuate, about half length of inner claw; empodium bulbous at base. Meso- and metatibial claws with 2 setae. Metatibia with apical spurs weakly curved;



1 *Peltonotus animus*, male



2 *Peltonotus cybele*, male



3 *Peltonotus cybele*, female



4 *Peltonotus talangensis*, holotype male

**Figures 1–4.** *Peltonotus* species dorsal habitus. 1 *P. animus* (holotype, male) 2 *P. cybele*, male 3 *P. cybele* (holotype, female) 4 *P. talangensis* (holotype, male).

ventral spur produced to middle of metatarsomere 1, dorsal spur produced to apex of metatarsomere 2. *Parameres*: Figs 19a–b.

**Diagnosis.** Within Sumatra, *P. cybele* is distinguished from other species of *Peltonotus* based on the dark reddish-brown elytral coloration in the male (elytra castaneous and suffused with reddish brown in the female). Additional characters that enable identification include: protibia of the male tridentate (Fig. 12) (shared with *P. talangensis*; bidentate in *P. animus*, *P. gracilipodus*, and *P. sisyrus*); mentum with rounded apex (shared with *P. animus* and *P. gracilipodus*; apex triangular in *P. talangensis* and *P. sisyrus*); unisetigerous punctures on the head (shared with *P. talangensis*; punctures clearly multisetigerous in *P. animus*, *P. sisyrus*, and *P. gracilipodus*); form of the male genitalia (Fig. 19a–b); and female epipleuron incised and with rounded emargination in ventral view (Fig. 14). Outside of Sumatra, *P. cybele* shares several similarities with *P. similis* Arrow 1931 and *P. adelphosimilis* Jameson & Wada 2004 from Sabah on the island of Borneo (Jameson and Wada 2009).

**Locality records** (Fig. 23) (n=4). SUMATRA. *West Sumatera Province* (4): Padang, Mt. Sanngul (20–30 km N. Payakumbuh, 1000–1300m).

**Temporal data.** June (1), April (2), October (1).

**Remarks.** *Peltonotus cybele* was previously known only from the holotype female (housed in WADA). We record the first known male specimens and an additional female specimen (housed in MLJC and SJC). The second known female greatly resembles the female holotype in size, coloration, and other respects.

### *Peltonotus gracilipodus* Jameson & Wada, 2004

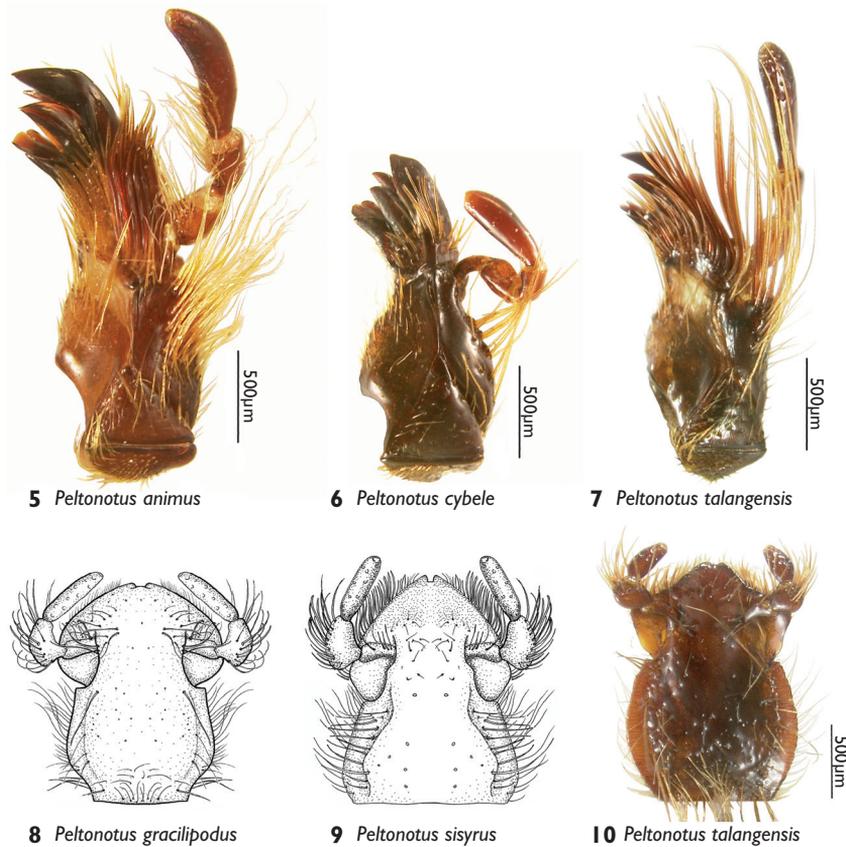
Figs 8, 15, 20a–b, 23

**Diagnosis.** Within Sumatra, *P. gracilipodus* is separated from other species of *Peltonotus* based on the surface of the frons and clypeus that has multisetigerous punctures (shared with *P. animus* and *P. sisyrus*; unisetigerous in *P. cybele* and *P. talangensis*); form of the mentum that is rounded in the apical half (Fig. 8) (shared with *P. animus* and *P. cybele*; triangular in *P. sisyrus* and *P. talangensis*); form of the male genitalia (Fig. 20a–b); and form of the female epipleuron in ventral view (Fig. 15). Outside of Sumatra, *P. gracilipodus* closely resembles *P. podocrassus* Jameson & Wada 2004 from peninsular Malaysia. In fact, males of both species have very similar genitalic forms and females have very similar eplipleural forms. Other characters differ between the species (*e.g.*, length of the metatibial spur, slender versus robust form of the fifth protarsomere in the male). Similarity in the genitalic form may provide evidence of recent isolation of ancestral populations in Sumatra and peninsular Malaysia.

**Locality records** (Fig. 23) (n=13). SUMATRA. *West Sumatera Province* (10): Harau Valley (Payakumbuh near Bukittinggi), Padang, Pang Kavan, Siboga. *No data* (3).

**Temporal data.** March (2), April (2), June (2), July (1), October (3), November (1).

**Remarks.** Male and female specimens of *P. gracilipodus* are housed in BCRC, WADA, MLJC, MNHN.



**Figures 5–10.** Maxilla (dorsal view) showing mala with or without lamellate setal brush and form. **5** *P. animus* (holotype) **6** *P. cybele* (holotype) **7** *P. talangensis* (holotype). Mentum (ventral view) showing form **8** *P. gracilipodus* **9** *P. sisyrus* **10** *P. talangensis* (holotype).

### *Peltonotus sisyrus* Jameson & Wada, 2004

Figs 9, 16, 21a–b, 23

**Diagnosis.** *Peltonotus sisyrus* is separated from other Sumatran *Peltonotus* species based on the form of the mentum that is triangular in the apical half (Fig. 9; shared with *P. talangensis*); surface of frons and clypeus that is multisetigerous (shared with *P. gracilipodus* and *P. animus*; unisetigerous in *P. talangensis* and *P. cybele*); and the form of the female epipleuron (Fig. 16). Outside of Sumatra, only one additional species, *P. deltoementum* (from Kalimantan on the island of Borneo) shares the triangular apex of the mentum.

**Locality records** (Fig. 23) (n=2). SUMATRA. Aceh Province (2): Banda Aceh, Brastagi.

**Temporal data.** June (1), November (1).

**Remarks.** This species is known from one male and one female specimen housed in FUJI.

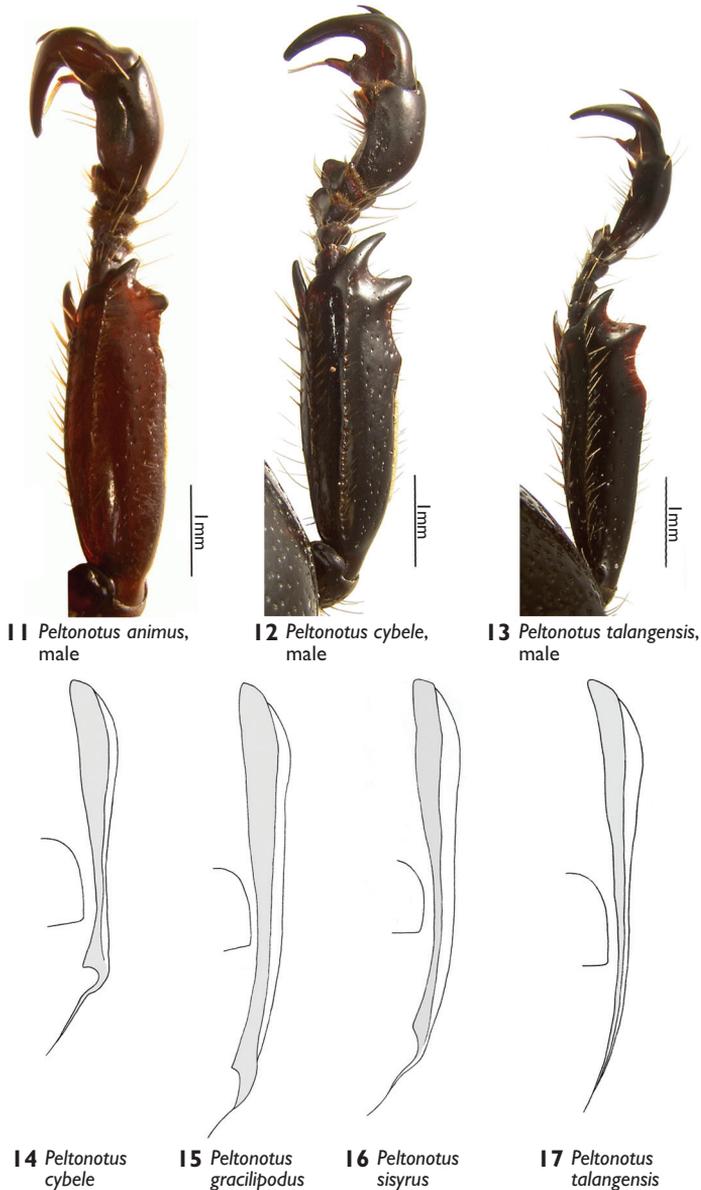
***Peltonotus talangensis* Jameson & Jakl, sp. n.**

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Figs 4, 7, 10, 13, 17, 22a–b, 23

**Type Material.** Holotype male housed at NMPC with the following label data and with male genitalia, mentum, and maxillae mounted beneath specimen: a) “West Sumatra, Mt. Talang, 1500m, II-2006, Col. Stan Jakl” (type set), b) our holotype label. Allotype female labeled as male but with our allotype label (deposited at NMPC). 116 paratypes (95 males, 21 females) with label data as holotype and our paratype labels. Fifty eight paratypes deposited in SJC, ten in MLJC, and four in each of the following institutions: BCRC, BMNH, FMNH, FUJI, MNHN, NMPC, NSMT, RMNH, UNSM, USNM, WADA, ZMHB.

**Description of holotype** (male). Length 14.1 mm. Widest width 6.8 mm. *Color* (Fig. 4): Head, pronotum, scutellum, pygidium, elytron, and venter castaneous. Elytra lacking iridescent bloom. *Head*: Surface of frons at base sparsely punctate, disc and apex moderately densely (base) to densely (apex) punctate; punctures simple, moderate in size, some unisetigerous; setae short and moderately long, mixed. Surface of clypeus moderately densely punctate (base) to densely punctate (margins); punctures simple, moderate in size (base) to small (apex), some unisetigerous; setae moderately long. Clypeus laterally weakly arcuate, corners square, apex truncate, beaded; bead not weakly arcuate posteriorly. Labrum broadly emarginate at middle. Mandible with external edge rounded, inner apex with 1 poorly developed tooth. Mentum with apical half triangular (Fig. 10), notched at middle; palpomere 2 dorsoventrally flattened, about 1.5 times width of palpomere 1, setose; setae dense, moderately long, rufous, weakly thickened, not curled at apices. Maxilla (Fig. 7): Mala with lamellate setal brush; stipes with setae dense, long, not flattened at apex, not curled at apices; palpomere 2 with poorly developed internomedial bump. Antennal club slightly longer than segments 2–7 combined. *Pronotum*: Basal bead lacking anterior to scutellum; anterior bead incomplete. Surface moderately densely punctate, more so laterally; punctures simple, lacking setae. Lateral margin lacking long setae. *Elytron*: Sutural length about 4.0 times length of scutellum. Surface shagreened with 5 moderately developed, impressed, punctate, longitudinal striae between suture and humerus; punctures ocellate, moderate in size, moderately dense, lacking setae. Intervals similarly sculptured. *Propygidium*: Surface densely punctate, some contiguous (disc) to confluent punctate (laterally); punctures simple, moderate in size, unisetigerous; setae short, tawny and rufous. *Pygidium*: Surface densely punctate, more so laterally; punctures ocellate, unisetigerous; setae short, rufous. *Venter*: Prosternal keel elongate; apex projecting anteriorly at about 90° with respect to ventral plane, extends to about a quarter of the height of protrochanter, truncate. *Legs*: Protibia (Fig. 13) of male tridentate; lateral margin lacking short, dense setae. Protarsomere 5 subequal in length to tarsomeres 1–4 combined, moderately thickened; protarsomeres 3–4 with apices weakly expanded, dorsal and ventral apices of tarsomeres 1–4 clothed with dense, short setae. Anterior claws with inner claw broadly curved, about 2 times thicker than outer claw; outer

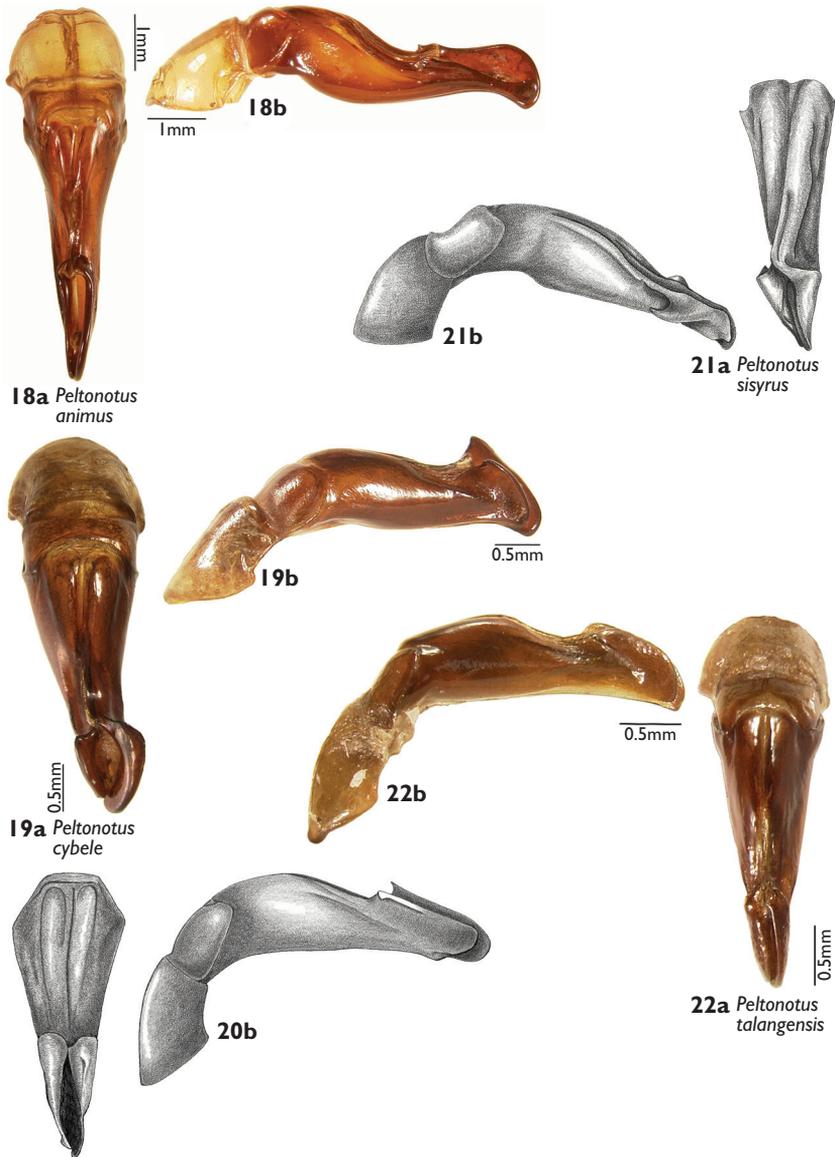


**Figures 11–17.** Right foreleg of male, dorsal view, showing form. 11 *P. animus* (holotype, male) 12 *P. cybele* (male) 13 *P. talangensis* (paratype, male). Female elytral epipleuron (gray, ventral view) with position of metacoxa 14 *P. cybele* (holotype) 15 *P. gracilipodus* 16 *P. sisyrus* 17 *P. talangensis* (allotype, female). Epipleura all the same scale.

claw elongate-arcuate, about half length of inner claw; empodium bulbous at base. Meso- and metatibial claws of male with 2 setae, claw angled toward venter, about half length of metatarsomere 5. Metatibia of male with apical spurs nearly straight; ventral

spur produced to middle of metatarsomere 1, dorsal spur produced to apex of metatarsomere 1. *Parameres*: Fig. 22a–b.

**Allotype** (female). Differs from the holotype male in the following respects: Length 15.2 mm. Widest width 7.2 mm. *Elytron*: Epipleuron (Fig. 17) in ventral view simple, terminating adjacent to sternite 3; in dorsal view, expansion not developed.



**Figure 18.** Male genitalia in dorsal and left lateral view. **18a–b** Phallobase and parameres of *P. animus* (holotype) **19a–b** Phallobase and parameres of *P. cybele* **20a–b** Parameres **a** and phallobase plus parameres **b** of *P. gracilipodus* **21a–b** Parameres **a** and phallobase plus parameres **b** of *P. sisyrus*. **22a–b** Phallobase and parameres of *P. talangensis* (holotype).

*Propygidium*: Surface moderately densely punctate, some punctures confluent laterally; punctures simple, small, moderate in size (mixed). *Legs*: Anterior claws half length of protarsomere 5, angled toward venter.

**Paratypes** (females=21, males=95). Differ from the holotype and allotype in the following respects: *Color*: Elytron castaneous with weak reddish undercolor.

**Diagnosis.** *Peltonotus talangensis* is distinguished from other Sumatran *Peltonotus* species based on the form of the mentum that is triangular in the apical half (Fig. 10; shared with *P. sisyrus*); surface of frons and clypeus unisetigerous (shared with *P. cybele*; multisetigerous in *P. sisyrus*, *P. gracilipodus* and *P. animus*); the short prosternal keel that extends to about a quarter of the height of the protochanter (in all other species of *Peltonotus*, the prosternal keel extends one third to three quarters the height of the protochanter); and the simple female epipleuron (Fig. 17). Outside of Sumatra, *P. talangensis* shares the triangular apex of the mentum with *P. deltomentum* from Kalimantan on the island of Borneo.

**Locality records** (Fig. 23) (n=118). SUMATRA. *West Sumatera Province* (118): Mt. Talang (1500m).

**Temporal data.** February (118).



**Figure 23.** Distribution of *Peltonotus* species in Sumatra.

**Remarks.** *Peltonotus talangensis* was collected at 1450 m elevation on the southern slopes of Mt. Talang in the Diatas Lake region (February 15–16, 2006). This locality is home to a number of endemic species (including a new species of Cetoniinae) and is climatically much cooler (even at 1000 m elevation) than other volcanoes in the region. Specimens were collected at lights for two nights only, after which adult flight activity completely ceased, although collecting in the region was on-going.

## Acknowledgments

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# Synopsis and key to the genera of Dynastinae (Coleoptera, Scarabaeoidea, Scarabaeidae) of Colombia

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## Abstract

An illustrated key to identify the adults at the generic level of Dynastinae known from Colombia is provided. A synopsis for each genus is given with updated information on the diversity and distribution of species in Colombia and worldwide.

## Keywords

Illustrated key, Scarabaeidae, Dynastinae, Colombia, Biodiversity.

## Introduction

The subfamily Dynastinae is a cosmopolitan group of beetles widely distributed in most biogeographical regions of the world (except in the polar regions), and the majority of species are distributed in the tropics, especially in the Neotropics. There are approximately 220 genera and 1500 species within the Dynastinae world wide (Ratcliffe 2003). Endrödi (1985) estimated about 2000 species world wide. Some authors (e.g.,

Baraud 1985; Dechambre 1986) referred to this taxon at the family level. In groups belonging to Scarabaeoidea, the phylogenetic relationships and taxonomic hierarchy are poorly studied. A comparative analysis including all known tribes and genera would provide a much needed evolutionary and taxonomic foundation in the Scarabaeoidea. To date, however, many genera lack complete taxonomic revisions and most larvae remain undescribed (Morón et al. 1997).

Adult Dynastinae are characterized by exposed mandibles in dorsal view; small and thin labrum with the border usually not surpassing the clypeal margin; antennae with nine or ten segments with the base of the scape hidden by the clypeus; scutellum visible; mesepimeron hidden; pygidium exposed; procoxae transverse; middle and hind tarsal claws simple; and apex of the fifth meso- and metatarsomeres lacking a longitudinal slit. The body shape is generally robust, and the color is generally dark brown, black or reddish, occasionally testaceous yellow, with maculae or dark symmetrical lines or spots. Body length ranges from 4 to 160 mm (including the head and pronotal projections in males).

The dynastine beetles are important in nutrient recycling. The larvae are able to fragment large amounts of wood during their feeding, greatly expediting decomposition time (Morón 1985). In the process, they produce detritus and excretions that facilitate the action of other decompositional agents in the microfauna and microflora. This ecological role makes them essential for nutrient recycling in tropical forest ecosystems (Morón 1985).

Adults of most species are nocturnal or crepuscular and are attracted to lights at night. Dynastines feed on foliage, sap secretions, fruits, flowers, and pollen of plants. Larvae are saprophagous or phytophagous, feeding on roots, stems, decaying logs, or organic matter. Some species are economically important, causing damage to crops such as corn and sugarcane (Morón 2004). Males in several species (mainly in the tribes Dynastini, Agaoccephalini, and Oryctini) possess prominent horns on the head and/or the thorax, which, because of their great size, give rise to vernacular names such as “rhinoceros beetle”, “elephant beetle”, “Hercules beetle” or “unicorn beetle” (Ratcliffe 2003).

In the last ten years in Colombia, the Dynastinae subfamily has been the subject of increasing interest. One of the most remarkable pioneering studies was Restrepo's (1998) undergraduate thesis that provided the first contribution to the study of the phytophagous scarab beetles in Colombia. In this work, the author compiled and analyzed information about the phytophagous scarabs and presented an identification key to 76 genera and a descriptive synopsis of important agricultural species. For the subfamily Dynastinae, Restrepo reported 40 genera and 195 species in Colombia, and seven species were of agricultural importance. From this study, and as a posthumous tribute, two important reference papers for the study of the Dynastinae were published that increased the number of species in Colombia to 200: *Especies de Chisas (Coleoptera: Melolonthidae) de importancia agrícola en Colombia* (Restrepo and López-Avila 2000) and *Catálogo de Coleoptera Melolonthidae (Scarabaeidae: Pleurosticti) de Colombia* (Restrepo et al. 2003).

Recent works have continued the study of the Dynastinae in Colombia. Pardo-Locarno et al. (2006), Neita et al. (2007), Vallejo and Morón (2008), Neita and Orozco (2009), and Neita and Ratcliffe (2009) provided descriptions of immature stages of species found in the country. Additional contributions that improve the knowledge of the dynastine fauna in Colombia include publications by Young and LeTirant (2005), Pardo-Locarno et al. (2006) and Ratcliffe (2008).

This faunistic survey recorded 42 genera and 213 species of Dynastinae in Colombia. At the genus level, Colombia surpasses other countries with great diversity such as Mexico and Costa Rica. Colombia possesses approximately 20% of the generic richness in the world (Table 1). Ten genera are represented by a single species each, whereas genera such *Haplophileurus* Kolbe, *Horridocalia* Endrödi, *Pucaya* Ohaus, and *Thronistes* Burmeister have all of the species comprising each genus. In recent years the monotypic South American genus *Acrobolbia* Ohaus was removed from the subfamily Rutelinae and transferred to the tribe Cyclocephalini (Jameson et al. 2002). According to the known geographical distribution (Ecuador, Peru and Venezuela), *Acrobolbia* should be found in Colombia. However, *Acrobolbia* has not yet been recorded in Colombia. Accordingly, *Acrobolbia* is not included in the identification key below.

In this contribution we present an illustrated identification key to the adults of the genera of Dynastinae found in Colombia. In addition, a diagnosis, world and national distributions, and the current species number in the world and in Colombia are included for each genus.

## Materials and methods

For the construction of the identification key, we used minimally variable characters that were consistently expressed when using routine observation techniques (following Ratcliffe 2003).

**Table 1.** Dynastinae generic diversity in the World, Colombia, and other regions of the Neotropics.

Tribe	World <sup>1</sup>	Mexico <sup>2</sup>	Brazil <sup>3</sup>	Costa Rica Panama <sup>4</sup>	Honduras Nicaragua El Salvador <sup>5</sup>	Colombia <sup>6</sup>	National Percentage
Agaoccephalini	11	1	4	2	1	6	54.54 %
Cyclocephalini	14	6	12	7	7	8	57.14 %
Dynastini	13	3	3	3	3	3	23.08 %
Oryctini	28	7	7	9	8	7	25.00 %
Pentodontini	108	8	11	6	5	8	7.40 %
Phileurini	36	5	15	9	7	10	27.78 %
<b>TOTAL</b>	210	30	52	36	31	42	20 %

<sup>1</sup> Endrödi (1985); Morón and Ratcliffe (1996); Jameson et al. (2002); Jameson and Wada (2004); Ratcliffe and Cave (2006); <sup>2</sup> Morón et al. (1997); <sup>3</sup> Endrödi (1985); <sup>4</sup> Ratcliffe (2003); <sup>5</sup> Ratcliffe and Cave (2006); <sup>6</sup> Current study.

This work is based on data obtained from specimens deposited in the entomological collection of the Instituto de Ciencias Naturales, Universidad Nacional, Bogotá [ICN-MHN], on the original descriptions by Endrődi (1966, 1969, 1970, 1976a-b, 1977, 1985), Ratcliffe (1981b, 2003), Morón et al. (1997), Ratcliffe and Cave (2006), Ide (1998) and on the identification keys by Endrődi (1985), Restrepo (1998), Delgado et al. (2000), Ratcliffe (2003), Ratcliffe and Cave (2006) and Gasca et al. (2008). For this work, was followed the classification adopted by Browne and Scholtz (1995), Lawrence and Newton (1995, 1999) and Jameson and Ratcliffe (2002) at the family level and Endrődi (1985) at the subfamily level.

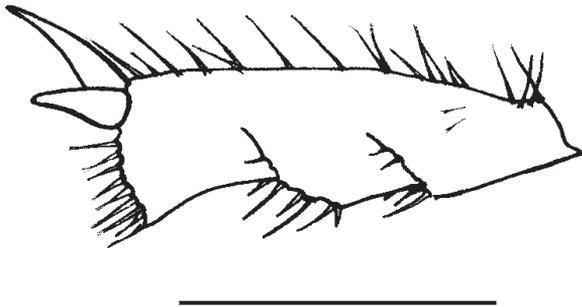
### Key to the tribes of adult *Dynastinae* of Colombia

1. Mentum widened or expanded, covering bases of labial palpi. Body more or less dorsoventrally flattened..... **Phileurini**
- Mentum narrow, not covering bases of labial palpi. Body not dorsoventrally flattened..... **2**
2. Head and pronotum convex, without horns, tubercles or fovea in both sexes, or with inconspicuous tubercles posterior to frontoclypeal suture. Males in many species with front claws enlarged. Tarsomeres of all legs usually long and cylindrical ..... **Cyclocephalini**
- Head and/or pronotum with horns, tubercles or fovea. Males with front claws of variable size, enlarged or not. Protarsomeres and mesotarsomeres usually short and triangular ..... **3**
3. Protarsus in males longer than protibiae. Metatarsal segments usually cylindrical, basal segment with strong apical spur ..... **Dynastini**
- Protarsus in males shorter than or subequal the same size to protibiae. Metatarsal segments triangularly expanded, basal segment variable in form..... **4**
4. Elytra tomentose or irregularly punctate. Punctures slightly impressed. Body slightly dorsoventrally flattened..... **Agaocephalini**
- Elytra smooth or with punctures usually in distinct rows (except for some *Heterogomphus* species). Punctures strongly or moderate impressed. Body not dorsoventrally flattened..... **5**
5. Apex of metatibia truncate or smooth (Fig 1). Sexual dimorphism usually not well-pronounced..... **Pentodontini**
- Apex of metatibia usually strongly crenulate or with distinct teeth (Fig 2) (except for *Coelosis* species). Sexual dimorphism usually pronounced.... **Oryctini**

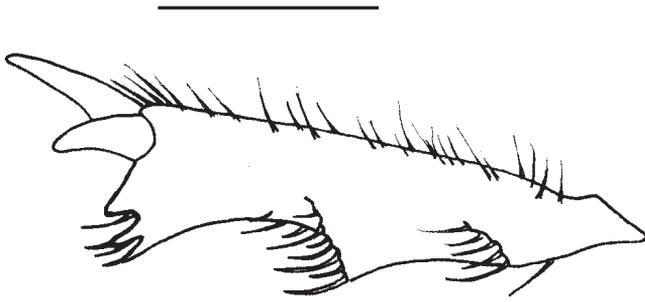
### Key to the genera of adult *Agaocephalini* of Colombia

1. Body surface tomentose, grayish brown color..... **2**
- Body surface glabrous, irregularly punctate ..... **3**

2. External edge of mandibles with 3 teeth (Fig 3). Prosternal process short or moderately long. Pronotum with strong horn, short to large, flat, narrow, usually directed upwards (Fig 4)..... ***Lycomedes Bréme***  
 – External edge of mandibles with 2 teeth (Fig 5). Prosternal process absent. Pronotum with large horn, directed forward, thin and curved (Fig 6) .....  
 ..... ***Spodistes Burmeister***
3. Protibia quadridentate, basal tooth short in minor males. Head of males with two large, divergent, forward directed horns; horns curved upward, apices rounded (Fig 7). Females lacking horns..... ***Aegopsis Burmeister***  
 – Protibia tridentate. Head with thick horn, curved upward, apex bifurcated ..... **4**
4. Males with frontal horn short and thick, slightly curved. Pronotum with forward directed knob with acute apex, surface smooth. Females lacking horn on head and knob on pronotum. Head and pronotum black, elytra reddish brown ..... ***Mitracephala Thomson***  
 – Males with frontal horn large, curved upwards, apex bifurcate. Pronotum convex or with high knob. Body black, brown, or with dark spots ..... **5**
5. Apex of frontal horn in males bifurcate. Pronotum with wide, high knob; apex rounded, surface densely punctate. Females lacking frontal horn. Elytra with punctures strongly impressed. Prosternal process high, apex dilated. Body black or brown..... ***Horridocalia Endrödi***  
 – Apex of frontal horn in males emarginated or bifurcated. Head of females with 2 transversal tubercles. Pronotum convex, smooth. Elytra strongly reticulated and finely punctate. Prosternal process absent. Body yellowish brown with dark spots ..... ***Brachysiderus Prell***



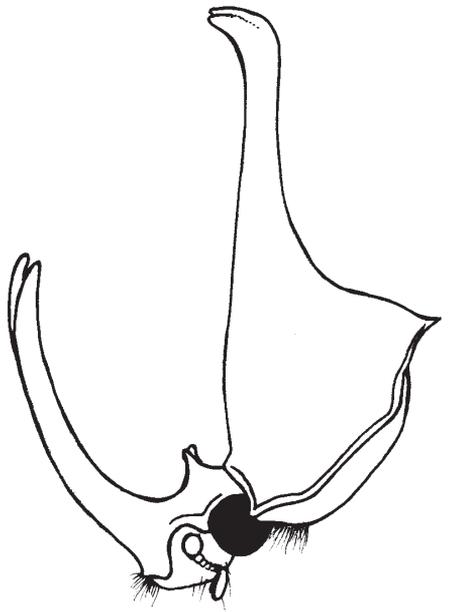
**Figure 1.** Metatibia of *Tomarus* sp. (scale bar: 5 mm).



**Figure 2.** Metatibia of *Heterogomphus schoenherri* Burmeister (scale bar: 5 mm).



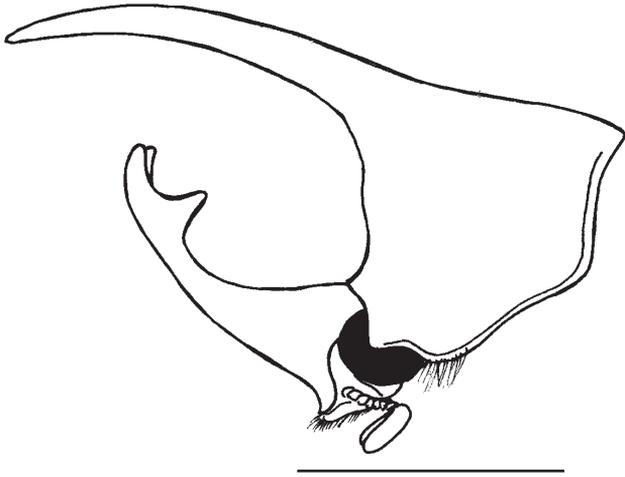
**Figure 3.** Right mandible of *Lycomedes* sp. (scale bar: 1 mm).



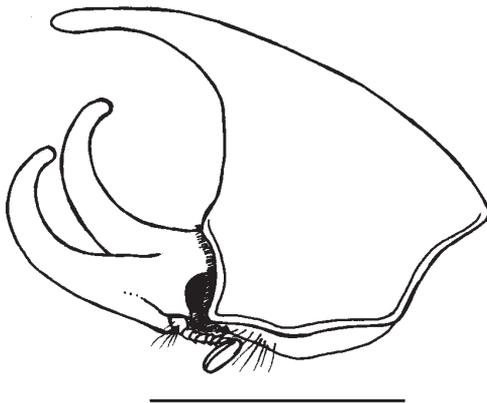
**Figure 4.** Male head and pronotum (lateral view) of *Lycomedes* sp. (scale bar: 1 cm).



**Figure 5.** Right mandible of *Spodistes* sp. (scale bar: 1 mm).



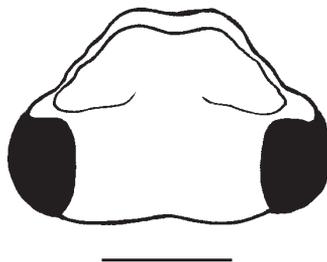
**Figure 6.** Male head and pronotum (lateral view) of *Spodistes* sp. (scale bar: 1 cm).



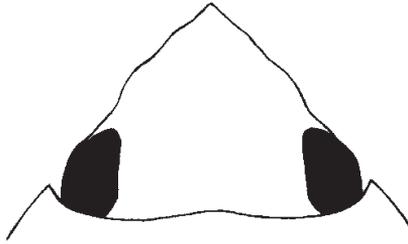
**Figure 7.** Male head and pronotum (lateral view) of *Aegopsis curvicornis* Burmeister (scale bar: 1 cm).

## Key to the genera of adult Cyclocephalini of Colombia

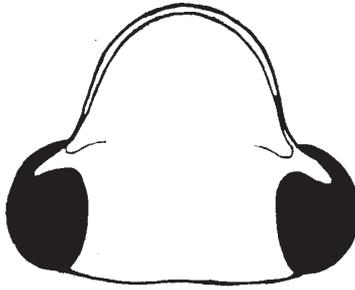
1. Protarsomeres in males enlarged; external claws larger than internal. Females with protarsomeres and claws simple. Clypeal length subequal to or longer than length of frons; apex parabolic, quadrate, weakly emarginated, or rounded. Metatibia semicircular in cross section ..... **2**
- Protarsomeres in males and females simple, not enlarged; tarsal claws simple. Clypeal length shorter than length of frons; apex trapezoidal (Fig. 8). Metatibia flattened dorsoventrally, not semicircular in cross section ..... **Stenocrates Burmeister**
2. Propygidium with numerous long setae ..... **Chalepides Casey**
- Propygidium without long setae..... **3**
3. Clypeus with apex acute or narrowly parabolic..... **4**
- Clypeus with apex rounded, truncate, trapezoidal, or emarginate..... **5**
4. Clypeus with apex acuminate (Fig. 9). Mentum with apex emarginate, surface not furrowed in apical third. Base of pronotum with marginal bead..... **Mimeoma Casey**
- Clypeus with apex narrowly parabolic (Fig. 10). Mentum with apex deeply emarginated, surface with furrow in apical third. Base of pronotum without marginal bead ..... **Ancognatha Erichson**
5. Clypeus trapezoidal or subtrapezoidal. Anterior margin of pronotum weakly produced anteriorly at middle (Fig. 11)..... **Dyscinetus Harold**
- Clypeus quadrate, rectangular or parabolic. Anterior margin of pronotum not produced anteriorly at middle..... **6**
6. Clypeus with sides usually divergent from base, apex broadly rounded (Fig. 12). Maxilla without teeth (except for *Aspidolea fuliginea*) ..... **Aspidolea Bates**
- Clypeus with sides parallel or convergent from base, apex rounded, truncate or emarginate. Maxilla with visible teeth ..... **7**
7. Clypeus with sides convergent, apex rounded, parabolic or emarginated (Fig. 13). Males with protarsus enlarged..... **Cyclocephala Dejean**
- Clypeus subquadrate, sides weakly converging, apex truncate or emarginate. Males with protarsus simple not enlarged..... **Erioscelis Burmeister**



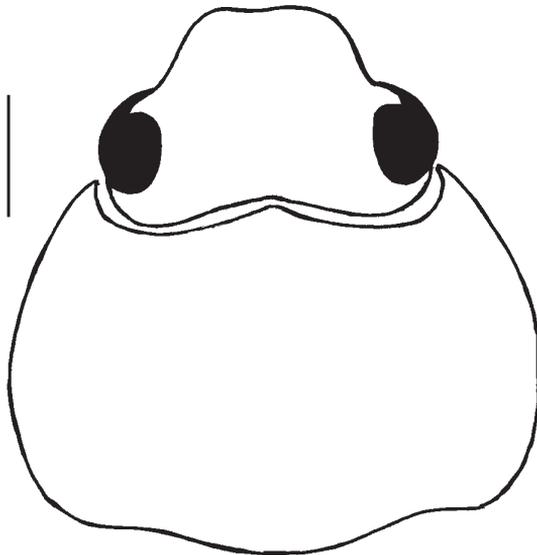
**Figure 8.** Head of *Stenocrates* sp. (scale bar: 2 mm).



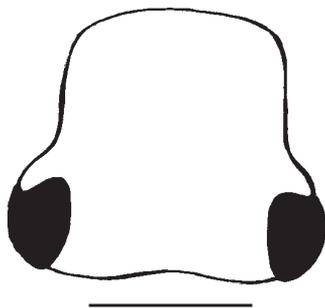
**Figure 9.** Head of *Mimeoma* sp. (scale bar: 2 mm). (Figure taken from Ratcliffe 2003).



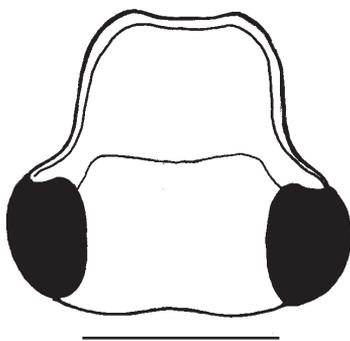
**Figure 10.** Head of *Ancognatha scarabaeoides* Erichson.



**Figure 11.** Head and pronotum of *Dyscinetus dubius* (Olivier) (scale bar: 2 mm).



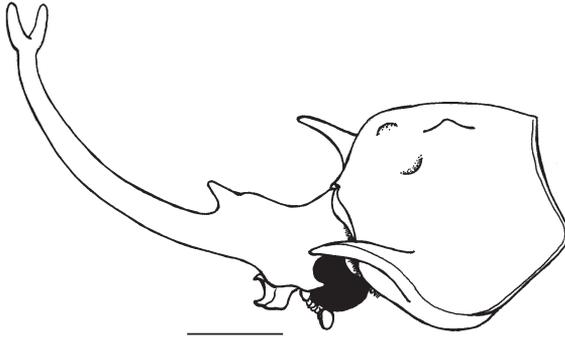
**Figure 12.** Head of *Aspidolea* sp. (scale bar: 2 mm).



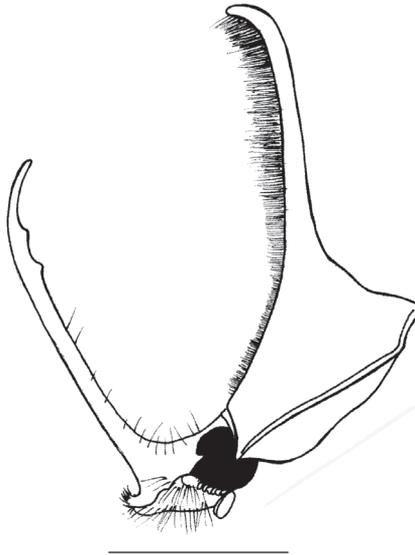
**Figure 13.** Head of *Cyclocephala* sp. (scale bar: 2 mm).

### Key to the genera of adult Dynastini of Colombia

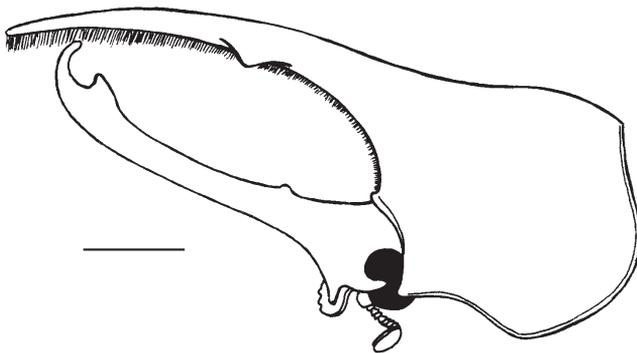
1. Clypeus emarginate or with 2 spiniform teeth widely separated. Males with head horn large and slightly flattened, apex bifurcate. Pronotum in males with 2 acute horns, 1 at each anterior angle (Fig. 14). Females on head with simple or double tubercle; pronotum simply convex ..... ***Megasoma* Kirby**
  - Clypeus truncate or with 2 adjacent teeth. Males with head horn large, with teeth on dorsal surface, apex acuminate or rounded. Pronotum in males with a central horn. Females with frontal tubercle, pronotum simply convex ..... **2**
2. Mandibles with apex entire or weakly notched. Pronotum in males with horn directed upwards, apex acuminate or with erect and wide tubercle (Fig. 15). Pronotum in females usually strongly punctate ..... ***Golofa* Hope**
  - Mandibles with 2 apical teeth. Pronotum in males with forward directed horn, apex acute (Fig. 16). Pronotum in females usually strongly rugose.....  
..... ***Dynastes* MacLeay**



**Figure 14.** Male head and pronotum (lateral view) of *Megasoma mars* (Reiche) (scale bar: 1 cm).



**Figure 15.** Male head and pronotum (lateral view) of *Golofa* sp. (scale bar: 1 cm).



**Figure 16.** Male head and pronotum (lateral view) of *Dynastes hercules* (Linnaeus) (scale bar: 1 cm).

## Key to the genera of adult Oryctini of Colombia

1. Protibia tridentate ..... **2**
- Protibia quadridentate ..... **3**
2. Elytra smooth, black, shiny. Clypeus emarginate or truncate (bidentate in *M. philoctetes*). Mandibles bidentate (Fig. 17) ..... **Megaceras Hope**
- Elytra with 5 distinct rows of punctures on relatively smooth surface. Clypeus with apex sharply bidentate. Mandibles tridentate (Fig. 18) .... **Coelosis Hope**
3. Elytra with deeply furrowed rows of punctures. Mandibles broad, with 2 lobes, strongly projecting from beneath clypeus. Clypeus with conical tubercle on dorsal surface. Pronotal fovea of males broadly triangular, extending almost to posterior margin of pronotum ..... **Gibboryctes Endrödi**
- Elytra smooth, rugose, or with punctures, never with deeply furrowed rows of punctures. Mandibles variably toothed, never with 2 large lobes. Head with 1–2 conical tubercles in frontoclypeal region, never with 1 on top of clypeus. Males with pronotal fovea variable in form ..... **4**
4. Body form elongate, subparallel. Protibia with teeth projecting almost at right angles. Apex of metatibia with 2 strong teeth. Males with anterior half of pronotum nearly smooth and with single, median horn or tubercle (Fig. 19). Females without fovea on pronotum ..... **Podischnus Burmeister**
- Body form broader, sides rounded (not subparallel). Protibia with teeth projecting obliquely. Apex of metatibia crenulate or with 1, 3, or 4 teeth. Males with anterior half of pronotum densely punctate or rugose or, if nearly smooth, then with lateral horns or tubercles. Females with or without fovea on pronotum ..... **5**
5. Both males and females with head horn. Prosternal process short, not produced beyond middle of protrochanters. Pronotum with anterior margin distinctly emarginate at center (Fig. 20)..... **Enema Hope**
- Males with or without head horn; females never with head horn, instead tuberculate at most. Prosternal process long, produced beyond middle of protrochanters. Anterior margin of pronotum lacking emargination at center. **6**
6. Frons in males and females unarmed or with 2 tubercles, never with horn on the head. Mandibles tridentate. Pronotum in males with subapical horn and usually with lateral horn or elevated, triangular ridge on each side (Fig 21). Females with fovea in anterior third of pronotum ..... **Strategus Kirby**
- Males usually with distinct head horn; females with single tubercle. Mandibles without teeth, or with 1–2 rounded teeth. Pronotum in males with horn or prominence arising from posterior half and with or without lateral horns; females usually lacking pronotal fovea..... **Heterogomphus Burmeister**

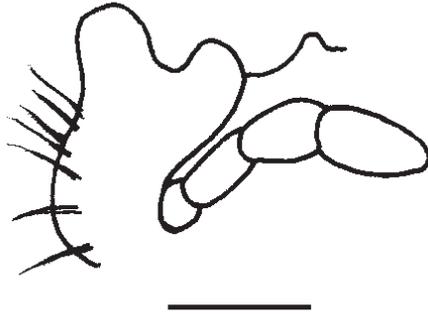


Figure 17. Right mandible of *Megaceras* sp. (scale bar: 1 mm).



Figure 18. Right mandible of *Coelosis biloba* (Linnaeus) (scale bar: 1 mm).

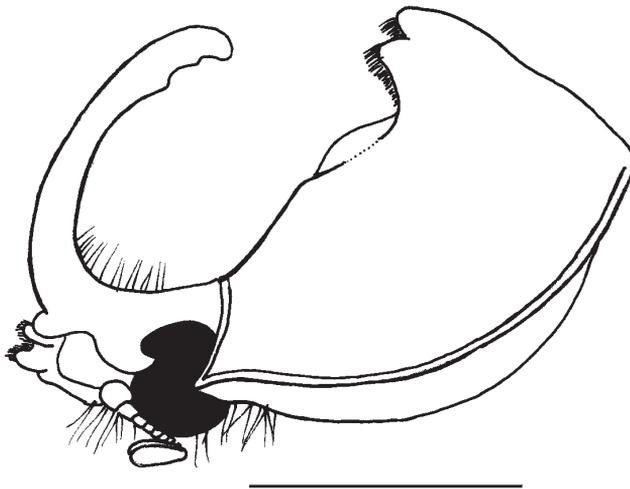
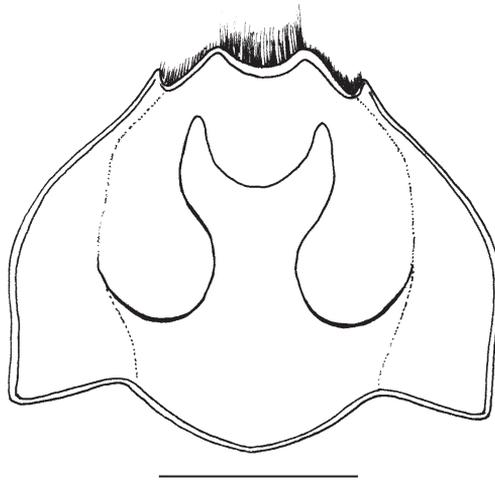
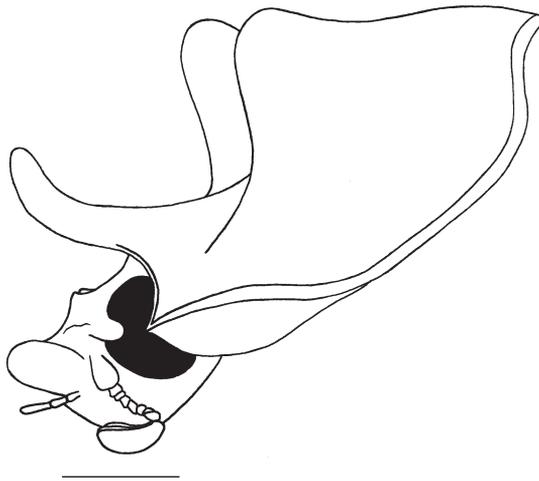


Figure 19. Male head and pronotum (lateral view) of *Podischmus agenor* (Olivier) (scale bar: 1 cm).



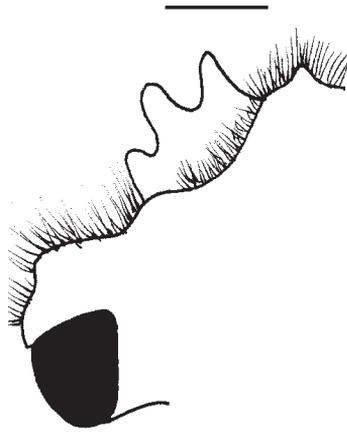
**Figure 20.** Pronotum of *Enema pan* (Fabricius) (scale bar: 1 cm).



**Figure 21.** Male head and pronotum (lateral view) of *Strategus aloeus* (Linnaeus) (scale bar: 5 mm).

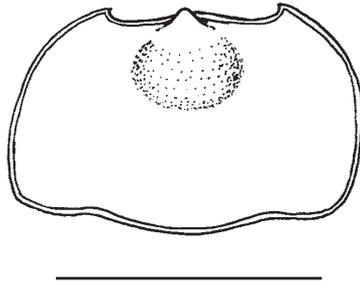
**Key to the genera of adult Pentodontini of Colombia**

- 1. Body black or dark brown, almost black ..... 2
- Body brownish-yellow, brown, red or reddish brown ..... 6
- 2. Mandibles with 3 teeth (Fig. 22). Propygidium with stridulatory area..... 3
- Mandibles with 2 teeth or without teeth. Propygidium without stridulatory area ..... 4

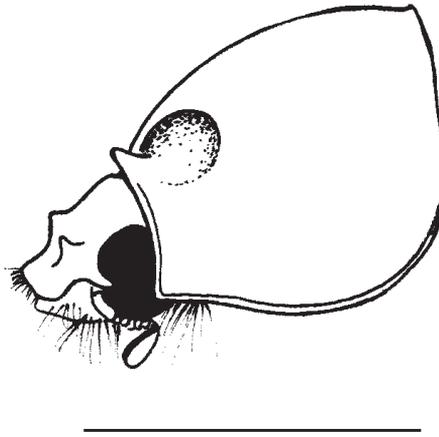


**Figure 22.** Right mandible of *Bothynus complanus* (Burmeister) (scale bar: 1 mm).

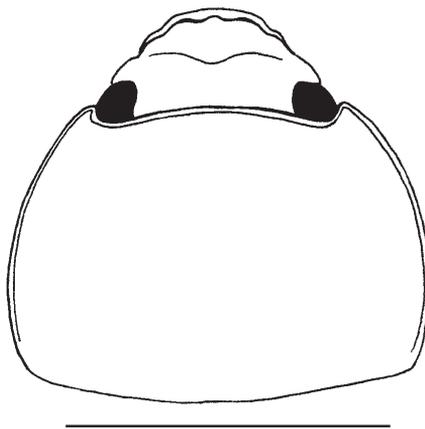
3. Protibia quadridentate. Pronotum with apical tubercle, subapical fovea deep (Fig. 23). Elytra smooth or moderately punctate. Propygidium elongated, pygidium short ..... ***Bothynus* Hope**
- Protibia tridentate. Pronotum convex, without tublercle. Elytra with rows of impressed punctures. Propygidium short, pygidium normal.....  
.....***Hylobothynus* Ohaus**
4. Clypeus truncate or relatively contracted at apex, bidentate. Pronotum with or without apical tubercle and subapical fovea..... **5**
- Clypeus acuminate, strongly reflexed. Pronotum with large apical tubercle, fovea wide and deep. Both sides of pronotum with obtuse carina.....  
.....***Oxyligyris* Arrow**
5. Mandibles with 2–3 teeth, third tooth obtuse. Pronotum with apical tubercle and deep subapical fovea (Fig. 24)..... ***Tomarus* Erichson**
- Mandibles without teeth, external edge sinuate, rounded. Pronotum convex, without tubercle and fovea (Fig. 25).....***Euetheola* Bates**
6. Mandibles small, narrow, external edge curved. Clypeus truncate. Pronotum convex, with deep transverse fovea or with 2 small tubercles behind anterior margin. Protibia tridentate..... **7**
- Mandibles broad, with 2 apical teeth. Clypeus contracted, emarginate. Pronotum in males with high and wide knob, apex bifurcate. Fovea broad. Females with convex pronotum. Head of males with small horn, apex rounded; females with tubercle. Protibia quadridentate..... ***Thronistes* Burmeister**
7. Frontal suture impressed (Fig. 26). Frons without tubercles or horns. Pronotum convex, with 2 small tubercles behind anterior margin .....  
.....***Parapucaya* Prell**
- Frontal suture absent. Frons with tubercle or semiconical horn close to each eye. Pronotum binodose, with transversal fovea (Fig. 27) ..... ***Pucaya* Ohaus**



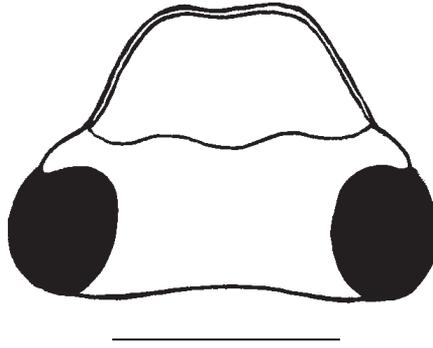
**Figure 23.** Pronotum of *Bothynus complanus* (Burmeister) (scale bar: 1 cm).



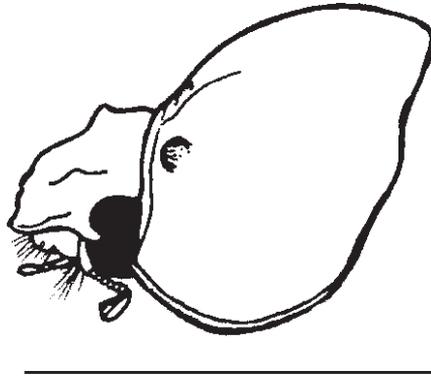
**Figure 24.** Head and pronotum (lateral view) of *Tomarus* sp. (scale bar: 1 cm).



**Figure 25.** Head and pronotum of *Euetheola bidentata* (Burmeister) (scale bar: 5 mm).



**Figure 26.** Head of *Parapucaya* sp. (scale bar: 1 mm).

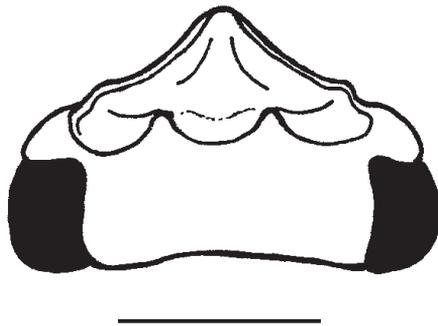


**Figure 27.** Head and pronotum (lateral view) of *Pucaya pulchra* Arrow (scale bar: 1 cm).

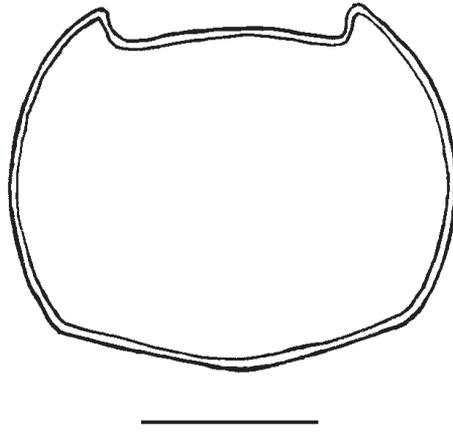
### Key to the genera of adult Phileurini of Colombia

1. Outer side of mandibles tridentate..... 2
- Outer side of mandibles simply curved ..... 3
2. Body dorsoventrally flattened. Frons with 2 tubercles. Protibia with 3 small teeth. Apical margin of metatibia with 3 teeth. Pygidium strongly punctate...  
..... *Metaphileurus* Kolbe
- Body not dorsoventrally flattened. Frons with tubercle or posteriorly curved horn. Protibia with 4 teeth, basal tooth reduced. Apical margin of metatibia with 5 teeth. Pygidium convex, finely wrinkled..... *Oryctophileurus* Kolbe
3. Apex of metatibia truncate, without teeth ..... 4
- Apex of metatibia acute or with 2–3 teeth..... 5

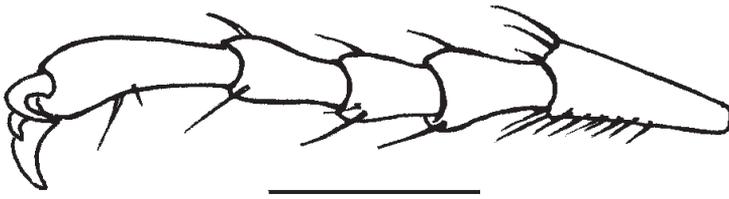
4. Frons with small tubercle. Prosternal process moderately elevated, anterior region convex, densely setose. Protibia quadridentate..... ***Haplophileurus* Kolbe**  
 – Frons with 2 tubercles or horns placed near lateral margins (Fig. 28). Prosternal process variable, punctate. Protibia tridentate..... ***Archophileurus* Kolbe**
5. Apex of metatibia tridentate..... **6**  
 – Apex of metatibia with acute tooth or with 1–2 large teeth ..... **7**
6. Mentum trapezoidal short. Pronotum with longitudinal, broad furrow, with or without small tubercle in middle of apical margin. Protibia with 3 teeth ...  
 ..... ***Amblyoproctus* Kolbe**  
 – Mentum trapezoidal elongated. Pronotum with anterior margin rugose, convex, or with pronotal cavity and 4 subequal tubercles ..... ***Homophileurus* Kolbe**
7. Pronotum convex, without longitudinal furrow (Fig. 29). Elytra opaque, with rows of punctures slightly impressed or absent. First tarsomere of metatibia without apical, spiniform process (Fig. 30)..... ***Palaeophileurus* Kolbe**  
 – Pronotum with longitudinal furrow, with or without tubercles or fovea. Elytra shiny, with impressed rows of punctures. First tarsomere of metatibia with apical, spiniform process (Fig. 31)..... **8**
8. Tubercles or horns of frons placed near center of head (Fig. 32). Pronotum without fovea, longitudinal furrow usually incomplete (not reaching anterior margin) ..... ***Hemiphileurus* Kolbe**  
 – Tubercles or horns of frons placed near lateral margin of head. Pronotum with anterior, wide fovea, longitudinal furrow usually complete, anterior margin with tubercle at center (Fig 33) ..... **9**
9. Prosternal process triangular, with angulate projection or large conical knob of posterior surface..... ***Paraphileurus* Endrődi**  
 – Prosternal process variable, never with angulate projection.....  
 ..... ***Phileurus* Latreille**



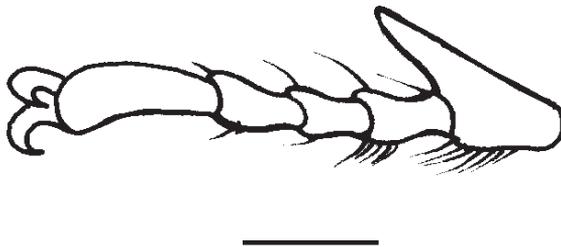
**Figure 28.** Head of *Archophileurus* sp. (scale bar: 2 mm).



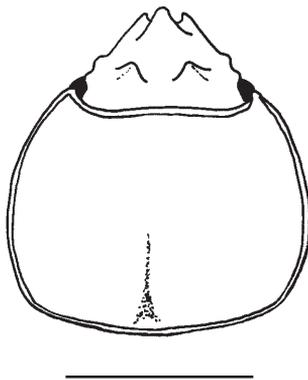
**Figure 29.** Pronotum of *Palaeophileurus sclateri* (Bates) (scale bar: 5 mm).



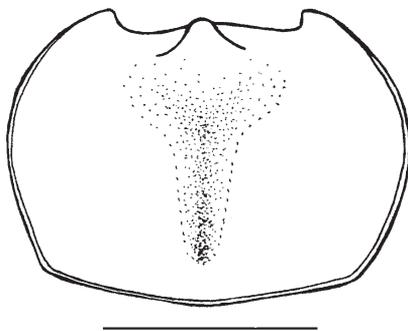
**Figure 30.** Metatarsus of *Palaeophileurus sclateri* (Bates) (scale bar: 2 mm).



**Figure 31.** Metatarsus of *Phileurus didymus* (Linnaeus) (scale bar: 2 mm).



**Figure 32.** Head and pronotum of *Hemiphileurus* sp. (scale bar: 5 mm).



**Figure 33.** Pronotum of *Phileurus didymus* (Linnaeus) (scale bar: 1 cm).

### Clave para los adultos de las tribus de Dynastinae de Colombia

1. Mentón ensanchado o expandido, cubriendo la base de los palpos labiales. Cuerpo mas o menos dorsoventralmente aplanado..... **Phileurini**
- Mentón estrecho o angosto, sin cubrir la base de los palpos labiales. Cuerpo no dorsoventralmente aplanado ..... **2**
2. Cabeza y pronoto convexos, sin cuernos, tubérculos o foveas, en ambos sexos, o con tubérculos inconspicuos detrás de la sutura fronto-clipeal. Machos con las uñas anteriores más desarrolladas en muchas especies. Tarsos de todas las piernas generalmente largos y cilíndricos..... **Cyclocephalini**
- Cabeza y/o pronoto con cuernos, tubérculos o foveas en ambos sexos. Machos con uñas anteriores de tamaño variable, desarrollados o no. Protarsos y mesotarsos generalmente cortos y triangulares..... **3**

3. Tarsos anteriores de los machos más largos que las tibias respectivas. Segmentos tarsales posteriores generalmente cilíndricos, segmento basal con fuerte espina apical..... **Dynastini**
- Tarsos anteriores de los machos más cortos o de igual tamaño que las tibias respectivas. Segmentos tarsales expandidos en forma de triángulo, segmento basal de forma variable..... **4**
4. Élitros tomentosos o irregularmente punteados. Puntuaciones ligeramente marcadas. Cuerpo ligeramente deprimido ..... **Agaocephalini**
- Élitros lisos o con puntuaciones dispuestas en hileras distinguibles (excepto en algunas especies de *Heterogomphus*). Puntuaciones fuerte o moderadamente marcadas. Cuerpo no deprimido, robusto..... **5**
5. Ápice de las metatibias generalmente truncado, liso o ligeramente prolongado (Fig 1). Dimorfismo sexual poco acentuado..... **Pentodontini**
- Ápice de las metatibias generalmente crenulado o con dientes agudos notorios (excepto para las especies de *Coelosis*) (Fig 2). Dimorfismo sexual evidente ..... **Oryctini**

### Clave para los géneros de **Agaocephalini** adultos de Colombia

1. Superficie de los élitros tomentosa, de color pardo grisáceo ..... **2**
- Superficie de los élitros glabra, irregularmente punteada..... **3**
2. Lado exterior de las mandíbulas con 3 dientes (Fig. 3). Proceso prosternal corto o moderadamente largo. Pronoto con cuerno fuerte, corto a largo, plano, estrecho, generalmente dirigido hacia arriba, recto (Fig. 4) ..... **Lycomedes Brême**
- Lado exterior de las mandíbulas con 2 dientes (Fig. 5). Proceso prosternal ausente. Pronoto con cuerno largo, dirigido hacia delante, delgado y curvo (Fig 6)..... **Spodistes Burmeister**
3. Tibia anterior con 4 dientes, diente basal muy corto en los machos braquíceros. Cabeza con dos cuernos largos, divergentes, proyectados hacia delante; curvados hacia arriba, ápices redondeados (Fig. 7) ..... **Aegopsis Burmeister**
- Tibia anterior con 3 dientes bien definidos. Cabeza con cuerno o grueso, curvado hacia arriba, ápice bifurcado ..... **4**
4. Machos con cuerno cefálico corto y grueso, ligeramente curvo. Pronoto con prominencia dirigida hacia delante de ápice agudo, superficie lisa. Machos sin cuernos y tubérculos en cabeza y pronoto. Cabeza y pronoto de color negro, élitros marrón rojizo..... **Mitracephala Thomson**
- Machos con cuerno cefálico largo, curvado hacia arriba, ápice bifurcado. Pronoto convexo o con prominencia alta. Cuerpo de color negro, marrón o con manchas oscuras..... **5**

5. Machos con cuerno cefálico bifurcado en el ápice. Pronoto con prominencia ancha y alta de ápice redondeado, superficie densamente punteada. Machos sin cuerno frontal. Elitros con hileras de puntuaciones fuertemente marcadas. Proceso prosternal alto, ápice dilatado. Cuerpo de color negro o marrón.....  
..... ***Horridocalia* Endrődi**
- Machos con cuerno cefálico emarginado o bifurcado. Hembras con dos tubérculos transversales en la cabeza. Pronoto convexo y liso. Élitros fuertemente reticulados y finamente punteados. Proceso prosternal ausente. Cuerpo de color pardo amarillo con manchas oscuras..... ***Brachysiderus* Prell**

### Clave para los géneros de Cyclocephalini adultos de Colombia

1. Tarsos anteriores de los machos engrosados; uña externa más grande que la interna. Hembras con tarsos anteriores y uñas simples. Longitud del clípeo subigual o mayor que la longitud de la frente; apice parabólico, cuadrado, ligeramente emarginado, o redondeado. Tibia posterior semicircular en sección transversal ..... **2**
- Tarsos anteriores de los machos y hembras sin engrosamiento. Uñas tarsales simples. Longitud del clípeo mas corta que la longitud de la frente; apice trapezoidal (Fig 8). Tibia posterior aplanada dorsoventralmente, no semicircular en sección transversal..... ***Stenocrates* Burmeister**
2. Propigidio con numerosas sedas largas, visibles..... ***Chalepides* Casey**
- Propigidio sin sedas largas y abundantes..... **3**
3. Clípeo con ápice puntiagudo o estrechamente parabólico ..... **4**
- Clípeo con ápice redondeado, truncado, trapezoidal o emarginado ..... **5**
4. Clípeo con ápice acumindo (Fig. 9). Mentón con ápice emarginado, superficie sin surco en el tercio apical. Base del pronoto con línea marginal.....  
..... ***Mimeoma* Casey**
- Clípeo con ápice estrechamente parabólico (Fig 10). Mentón con ápice profundamente emarginado, superficie con surco en el tercio apical. Base del pronoto sin línea marginal ..... ***Ancognatha* Erichson**
5. Clípeo trapezoidal o casi trapezoidal. Margen anterior del pronoto con una proyección central (Fig. 11) ..... ***Dyscinetus* Harold**
- Clípeo cuadrado, cuadrangular o parabólico. Margen anterior del pronoto simple ..... **6**
6. Clípeo con los lados generalmente divergentes desde la base, ápice ampliamente redondeado (Fig. 12). Maxila sin dientes (excepto en *Aspilodea fuliginea*)..... ***Aspilodea* Bates**
- Clípeo con lados convergentes desde la base, ápice redondeado, truncado o emarginado. Maxila con dientes evidentes..... **7**

7. Clípeo con los lados convergentes, ápice redondeado, parabólico o emarginado (Fig. 13). Machos con los tarsos anteriores engrosados ..... *Cyclocephala* Dejean
- Clípeo subcuadrado, lados ligeramente convergentes, ápice truncado o emarginado. Machos con los tarsos anteriores simples no engrosados..... *Erioscelis* Burmeister

### Clave para los géneros de *Dynastini* adultos de Colombia

1. Clípeo emarginado o con 2 dientes espiniformes ampliamente separados. Machos con cuerno cefálico largo y ligeramente aplanado dorso ventralmente, bifurcado en el ápice. Pronoto de los machos con 2 cuernos agudos, 1 en cada ángulo exterior (Fig. 14). Hembras con tubérculo frontal doble o simple, pronoto convexo ..... *Megasoma* Kirby
- Clípeo truncado o con 2 dientes apicales próximos. Machos con cuerno cefálico largo, con dientes en la superficie dorsal, ápice acuminado o redondeado. Pronoto de los machos con cuerno central. Hembras con tubérculo frontal, pronoto convexo..... 2
2. Mandíbulas con ápice entero, o con una muesca. Pronoto de los machos con cuerno dirigido hacia arriba de ápice acuminado, o con tubérculo erecto y ancho (Fig. 15). Pronoto de las hembras generalmente punteado ..... *Golofa* Hope
- Mandíbulas con 2 dientes apicales. Pronoto de los machos con cuerno dirigido hacia delante, ápice agudo (Fig. 16). Pronoto de las hembras generalmente rugoso..... *Dynastes* MacLeay

### Clave para los géneros de *Oryctini* adultos de Colombia

1. Tibia anterior tridentada ..... 2
- Tibia anterior cuadridentada ..... 3
2. Élitros lisos, brillantes, de color negro. Clípeo emarginado o truncado (Bidentado en *M. philoctetes*). Mandíbulas bidentadas (Fig. 17) ..... *Megaceras* Hope
- Élitros con 5 filas de puntuaciones sobre una superficie opaca, de color pardo-rojo. Clípeo estrecho con ápice bidentado. Mandíbulas tridentadas (Fig. 18) ..... *Coelosia* Hope
3. Élitros con filas de puntuaciones en surcos profundos. Mandíbulas con 2 lóbulos arredondados, similarmente grandes, proyectados desde la parte inferior del clipeo. Cabeza con tubérculo cónico cerca de la margen anterior del clipeo. Machos con prominencia pronotal formando una cavidad triangular y alcanzando la margen posterior del pronoto ..... *Gibboryctes* Endrődi

- Élitros lisos, rugosos o cubiertos densamente de puntuaciones, nunca en filas. Mandíbulas variablemente dentadas, nunca con 2 lóbulos grandes arredondados. Cabeza con 1–2 tubérculos cónicos, nunca cerca del clipeo. Machos con prominencia pronotal de forma variable ..... **4**
- 4. Cuerpo alargado y subparalelo. Tibia anterior con dientes proyectados casi en ángulos rectos. Ápice de la tibia posterior con dos dientes fuertes. Machos con la mitad anterior del pronoto casi liso, con un cuerno (o tubérculo) medio (Fig. 19). Hembras sin cavidad pronotal en el pronoto..... **Podischnus Burmeister**
- Cuerpo ancho, lados arredondados. Tibia anterior con dientes proyectados oblicuamente. Ápice da tibia posterior crenulado o con 1,3 o 4 dientes. Machos con la mitad anterior del pronoto densamente cubierto de puntuaciones o rugoso. Hembras con o sin cavidad pronotal en el pronoto ..... **5**
- 5. Machos y hembras con cuerno em la cabeza. Proceso prosternal corto, no producido después de la mitad de los protrocanteres. Pronoto con margen anterior emarginada hacia el centro (Fig. 20) ..... **Enema Hope**
- Machos con o sin cuerno en la cabeza. Hembras nunca con cuerno. Proceso prosternal largo, producido después de la mitad de los protrocanteres. Pronoto con margen anterior no emarginada hacia el centro ..... **6**
- 6. Frente de los machos e hembras con dos tubérculos cónicos, nunca con cuerno. Mandíbulas con tres dientes. Pronoto en los machos con cuerno subapical e generalmente con cuernos laterales o una crista triangular elevada a cada lado (Fig. 21); hembras con cavidad pronotal en el tercio anterior del pronoto.....**Strategus Hope**
- Frente de los machos con cuerno. Frente de las hembras con dos pequeños tubérculos. Mandíbulas simples o con dos dientes arredondados. Pronoto en los machos con cuerno o protuberancia originándose desde la mitad posterior y con o sin cuernos laterales; hembras generalmente sin cavidad pronotal ....  
..... **Heterogomphus Burmeister**

### Clave para los géneros de Pentodontini adultos de Colombia

- 1. Especies de color negro o marrón muy oscuro casi negro..... **2**
- Especies de color amarillo ocre, pardo claro, rojo o marrón rojizo ..... **6**
- 2. Mandíbulas con 3 dientes (Fig. 22). Propigidio con área estridulatoria..... **3**
- Mandíbulas con 2 dientes o sin dientes. Propigidio sin área estridulatoria.....**4**
- 3. Tibia anterior con 4 dientes. Pronto con tubérculo apical, fóvea subapical profunda (Fig. 23). Élitros lisos o moderadamente punteados. Propigidio muy desarrollado, placa pigidial corta ..... **Bothynus Hope**

- Tibia anterior con 3 dientes. Pronoto conexo, sin tubérculo. Élitros con filas de puntuaciones profundas. Propigidio corto, placa pigidial larga ..... *Hylobothynus* Ohaus
- 4. Clípeo truncado o relativamente contraído en el ápice, bidentado. Pronoto con o sin tubérculo apical y fóvea subapical..... 5
- Clípeo acuminado, fuertemente dirigido hacia arriba. Pronoto con tubérculo apical grande, fóvea amplia y muy profunda. Ambos lados del pronoto con una carina obtusa..... *Oxyligyrus* Arrow
- 5. Mandíbulas con 2–3 dientes, tercer diente obtuso. Pronoto con tubérculo apical y fóvea profunda subapical (Fig. 24)..... *Tomarus* Ericsson
- Mandíbulas sin dientes, borde externo sinuado, redondeado. Pronoto convexo, sin tuberculo o fóvea (Fig. 25)..... *Euetheola* Bates
- 6. Mandíbulas pequeñas, estrechas, borde externo curvo. Clípeo truncado. Pronoto convexo, con fóvea profunda transversa o con dos pequeños tubérculos detrás de la margen anterior. Tibia anterior con 3 dientes..... 7
- Mandíbulas anchas, con dos dientes apicales. Clípeo contraído, emarginado. Pronoto de los machos con prominencia alta y ancha, ápice bifurcado. Fóvea ancha. Hembras con pronoto convexo. Cabeza de los machos con cuerno de ápice redondeado. Hembras con tubérculo. Tibia anterior con 4 dientes ..... *Thronistes* Burmeister
- 7. Sutura frontal sobresaliente (Fig. 26). Frente sin tubérculos o cuernos. Pronoto convexo, con dos pequeños tubérculos detrás de la margen anterior..... *Parapucaya* Prell
- Sutura frontal ausente. Frente con un tubérculo o cuerno semicónico junto a cada ojo. Pronoto bilobulado, con fóvea transversal profunda (Fig. 27) ..... *Pucaya* Ohaus

### Clave para los géneros de *Phileurini* adultos de Colombia

- 1. Borde externo de las mandíbulas con 3 dientes ..... 2
- Borde externo de las mandíbulas recurvado, simple..... 3
- 2. Cuerpo aplanado dorsoventralmente. Frente con dos tubérculos. Tibia anterior con tres dientes pequeños. Margen apical de la tibia posterior con 3 dientes. Pigidio fuertemente punteado ..... *Metaphileurus* Kolbe
- Cuerpo no aplanado dorsoventralmente. Frente con tubérculo o cuerno curvado para atrás. Tibia anterior con 4 dientes, diente basal reducido. Margen apical de la tibia posterior con 5 dientes. Pigidio convexo y finamente rugoso ..... *Oryctophileurus* Kolbe
- 3. Margen apical de la tibia posterior truncado, sin dientes ..... 4
- Margen apical de la tibia posterior agudo o con 3 dientes..... 5

4. Frente con pequeño tubérculo. Proceso prosternal moderadamente elevado, región anterior convexa, densamente setoso. Tibia anterior con 4 dientes..... *Haplophileurus* Kolbe
- Frente con 2 tubérculos o cuernos localizados cerca de las margenes laterales (Fig. 28). Proceso prosternal variable, punteado. Tibia anterior con 3 dientes ..... *Archophileurus* Kolbe
5. Ápice de la tibia posterior con 3 dientes ..... 6
- Ápice de la tibia posterior con 1 diente ángulo con 1–2 dientes grandes..... 7
6. Mento trapezoidal corto. Pronoto con surco longitudinal ancho, con o sin un pequeño tubérculo en la mitad de la margen apical. Tibia anterior con 3 dientes ..... *Amblyoproctus* Kolbe
- Mento trapezoidal alargado. Pronoto con pargen anterior rugosa, convexo o con cavidad pronotal y cuatro tubérculos subiguales.... *Homophileurus* Kolbe
7. Pronoto convexo, sin surco longitudinal (Fig. 29). Élitros opacos, con filas de puntuaciones ligeramente marcadas o ausentes. Primer tarsómero de la tibia posterior sin proceso espiniforme (Fig. 30)..... *Palaeophileurus* Kolbe
- Pronoto con surco longitudinal, con o sin tubérculos o foveas. Élitros billantes, con filas de puntuaciones bien definidas. Primer tarsómero de la tibia posterior con proceso espiniforme (Fig. 31) ..... 8
8. Tubérculos o cuernos de la frente cerca del centro de la cabeza (Fig. 32). Pronoto sin fovea, surco longitudinal incompleto (sin alcanzar la margen anterior) ..... *Hemiphileurus* Kolbe
- Tubérculos o cuernos de la frente cerca del margen lateral de la cabeza. Pronoto con fovea anterior amplia, surco longitudinal completo, margen anterior con tubérculo en la parte media (Fig. 33)..... 9
9. Proceso prosternal triangular, con una proyección cónica en la superficie posterior..... *Paraphileurus* Endrődi
- Proceso prosternal de forma variable, sin proyecciones ..... *Phileurus* Latreille

## Synopsis of Dynastinae genera of Colombia

### Tribe Agaoccephalini

#### *Aegopsis* Burmeister, 1847

*Aegopsis* Burmeister 1847: 281.

**Distribution:** Costa Rica and Panama to northwestern South America. Colombia: Caquetá, Cundinamarca, Meta, Putumayo, Tolima, Valle.

**Diversity:** 4 species. Colombia: 2 species; *A. curvicornis* Burmeister, *A. westwoodi* Thomson (Endrődi 1985; Ratcliffe 2003; Restrepo et al. 2003).

***Brachysiderus* Waterhouse, 1881**

*Brachysiderus* Waterhouse 1881: 409.

**Distribution:** Ecuador, Colombia, Peru, Bolivia, Brazil. Colombia: Huila.

**Diversity:** Worldwide: 6 species. Colombia: 1 subspecies; *B. quadrimaculatus tridentiger* (Prell) (Endrődi 1985; Joly 1992; Grossi and Grossi 2005; Abadie et al. 2008).

***Horridocalia* Endrődi, 1974**

*Horridocalia* Endrődi 1974: 49.

**Distribution:** Colombia: Valle

**Diversity:** Monotypic genus: *H. delislei* Endrődi (Endrődi 1985; Restrepo et al. 2003).

***Lycomedes* Brėme, 1844**

*Lycomedes* Brėme 1844: 298.

**Distribution:** Colombia, Ecuador. Colombia: Antioquia, Boyacá, Caldas, Cauca, Cundinamarca, Huila, Tolima, Valle.

**Diversity:** 7 species. Colombia: 4 species; *L. burmeisteri* Waterhouse, *L. hirtipes* Arrow, *L. ramosus* Arrow, *L. reichei* Brėme (Endrődi 1985; Restrepo et al. 2003).

***Mitracephala* Thomson, 1859**

*Mitracephala* Thomson 1859: 34.

**Distribution:** Peru, Colombia, Ecuador, Bolivia. Colombia: Huila.

**Diversity:** 2 species. Colombia: 1 species, *M. humboldti* Thomson (Endrődi 1985; Dechambre 1992; Joly 1992; Mizinuma 1999).

***Spodistes* Burmeister, 1847**

*Spodistes* Burmeister 1847: 286.

**Distribution:** southern Mexico to Colombia and Ecuador. Colombia: Antioquia, Meta, Valle.

**Diversity:** 8 species. Colombia: 4 species; *S. angulicollis* Dechambre, *S. grandis* Sternberg, *S. hopei* Arrow, *S. mniszewski* (Thomson) (Endrődi 1985; Dechambre 1992, 1999; Restrepo et al. 2003).

### Tribe Cyclocephalini

#### *Ancognatha* Erichson, 1847

*Ancognatha* Erichson 1847: 97.

**Distribution:** Southern United States to Ecuador, Peru and Bolivia. Colombia: Antioquia, Atlántico, Boyacá, Caldas, Cauca, Chocó, Cundinamarca, Huila, Meta, Nariño, Quindío, Risaralda, Santander, Tolima, Valle,

**Diversity:** 18 species. Colombia: 7 species; *A. lutea* Erichson, *A. matilei* Dechambre, *A. scarabaeoides* Erichson, *A. ustulata* Burmeister, *A. veliae* Pardo-Locarno, Gonzalez and Montoya-Lerma, *A. vulgaris* Arrow (Endrődi 1985; Ratcliffe 1992; Dechambre 2000a; Restrepo et al. 2003; Pardo-Locarno et al. 2006).

#### *Aspidolea* Bates, 1888

*Aspidolea* Bates 1888: 296.

**Distribution:** Mexico to Argentina. Colombia: Amazonas, Antioquia, Bolivar, Boyacá, Caldas, Cauca, Cundinamarca, Meta, Risaralda, Santander, Tolima, Valle.

**Diversity:** 25 species. Colombia: 13 species (Endrődi 1985; Ratcliffe 1992; Restrepo et al. 2003).

#### *Chalepides* Casey, 1915

*Chalepides* Casey 1915: 176.

**Distribution:** Venezuela to Chile, including West Indies. Colombia: Antioquia, Bolívar.

**Diversity:** 8 species. Colombia: 1 species, *C. comes* Prell (Endrődi 1985; Restrepo et al. 2003).

#### *Cyclocephala* Dejean, 1821

*Cyclocephala* Dejean 1821: 51.

**Distribution:** Southeastern Canada to Argentina. Colombia: Amazonas, Antioquia, Boyacá, Caldas, Cauca, Cesar, Chocó, Córdoba, Cundinamarca, Magdalena, Meta, Santander, Tolima, Valle.

**Diversity:** 325 species. Colombia: 70 species (Endrődi 1985; Ratcliffe 2003; Restrepo et al. 2003; Young and Le Tirant 2005; Ratcliffe 2008).

***Dyscinetus* Harold, 1869**

*Dyscinetus* Harold 1869: 123.

**Distribution:** Worldwide: Central United States to Argentina. Colombia: Antioquia, Boyacá, Casanare, Córdoba, Caquetá, Huila, Meta, Nariño, Tolima, Valle.

**Diversity:** 15 species. Colombia: 6 species; *D. dubius* (Olivier), *D. dytiscoides* Arrow, *D. frater* Bates, *D. laevipunctatus* Bates, *D. olivaceus* Höhne, *D. ornaticaudus* Ratcliffe (Endrödi 1985; Ratcliffe 1986; Joly and Escalona 2002; Restrepo et al. 2003)

***Erioscelis* Burmeister, 1847**

*Erioscelis* Burmeister 1847: 72.

**Distribution:** Honduras to Argentina. Colombia: Cundinamarca, Meta.

**Diversity:** 5 species. Colombia: 2 species: *E. columbica* Endrödi, *E. proba* Sharp (Endrödi 1985; Ratcliffe 2003; Restrepo et al. 2003).

***Mimeoma* Casey, 1915**

*Mimeoma* Casey 1915: 111.

**Distribution:** Mexico to Brazil, Bolivia and Dominican Republic. Colombia: Meta.

**Diversity:** 5 species. Colombia: 3 species; *M. acuta* Arrow, *M. signatoides* Höhne, *M. maculata* Burmeister (Endrödi 1985; Ratcliffe 2003; Restrepo et al. 2003).

***Stenocrates* Burmeister, 1847**

*Stenocrates* Burmeister 1847: 83.

**Distribution:** Mexico to Argentina. Colombia: Antioquia, Meta, Santander, Tolima, Cundinamarca, Valle.

**Diversity:** 41 species. Colombia: 7 species; *S. cognatus* Endrödi, *S. difficilis* Endrödi, *S. holomelanus* (Germar), *S. laborator* (Fabricius), *S. laevicollis* Kirsch, *S. omissus* Endrödi, *S. rufipennis* (Fabricius) (Endrödi 1985; Delgado 1991; Dupuis and Dechambre 1995; Restrepo et al. 2003).

## Tribe Dynastini

### ***Dynastes* MacLeay, 1819**

*Dynastes* MacLeay 1819: 22.

**Distribution:** Southern United States to South America and West Indies. Colombia: Amazonas, Antioquia, Chocó, Cundinamarca, Putumayo, Santander, Valle.

**Diversity:** 7 species. Colombia: 2 species, *D. hercules* (Linnaeus), *D. neptunus* Quenzel (Endrődi 1985; Hardy 2003; Restrepo et al. 2003).

### ***Golofa* Hope, 1837**

*Golofa* Hope 1837: 42.

**Distribution:** Mexico to Argentina and Chile. Colombia: Antioquia, Boyacá, Cauca, Cundinamarca, Quindio, Tolima, Valle.

**Diversity:** 26 species. Colombia: 7 species; *G. aegeon* (Drury), *G. antiqua* Arrow, *G. claviger* (Linnaeus), *G. eacus* Burmeister, *G. paradoxa* Dechambre, *G. pelagon* Burmeister, *G. porteri* Hope (Endrődi 1985; Lauchame 1985; Morón 1995; Restrepo et al. 2003).

### ***Megasoma* Kirby, 1825**

*Megasoma* Kirby 1825: 566.

**Distribution:** Southwestern United States to northern Argentina. Colombia: Amazonas, Antioquia, Chocó, Córdoba, Magdalena, Nariño, Norte de Santander, Valle.

**Diversity:** 14 species. Colombia: 3 species; *M. actaeon* (Linnaeus), *M. elephas* (Fabricius), *M. mars* (Reiche) (Endrődi 1985; Morón 2005; Restrepo et al. 2003).

## Tribe Oryctini

### ***Coelosis* Hope, 1837**

*Coelosis* Hope 1837: 88.

**Distribution:** Mexico to Argentina. Colombia: Antioquia, Risaralda, Santander, Tolima, Valle.

**Diversity:** 7 species. Colombia: 2 species; *C. bicornis* (Leske), *C. biloba* (Linnaeus) (Endrődi 1985; Restrepo et al. 2003).

***Enema* Hope, 1837**

*Enema* Hope 1837: 83.

**Distribution:** Mexico to Bolivia and Argentina. Colombia: Amazonas, Antioquia, Boyacá, Cundinamarca, Huila, Magdalena, Nariño, Risaralda, Valle.

**Diversity:** 2 species. Colombia: 2 species: *E. endymion* Chevrolat, *E. pan* (Fabricius) (Endrődi 1985; Restrepo et al. 2003).

***Gibboryctes* Endrődi, 1974**

*Gibboryctes* Endrődi 1974:13.

**Distribution:** Panama to Brazil, Paraguay and Argentina. Colombia: Putumayo.

**Diversity:** 4 species. Colombia: 1 species: *G. waldenfelsi* (Endrődi) (Dechambre 2006; Restrepo et al. 2003; Abadie et al. 2008).

***Heterogomphus* Burmeister, 1847**

*Heterogomphus* Burmeister 1847: 224.

**Distribution:** Mexico to Argentina. Colombia: Antioquia, Cauca, Chocó, Cundinamarca, Huila, Magdalena, Risaralda, Tolima, Valle.

**Diversity:** 48 species. Colombia: 12 species (Dechambre 1986 1998a; Ratcliffe 2006; Restrepo et al. 2003).

***Megaceras* Hope, 1837**

*Megaceras* Hope 1837: 82.

**Distribution:** Honduras and Nicaragua to Brazil. Colombia: Boyacá, Cundinamarca, Tolima, Valle.

**Diversity:** 19 species. Colombia: 7 species: *M. crassum* Prell, *M. inflatum* Prell, *M. laevipenne* Prell, *M. morpheus* Burmeister, *M. pauliani* Dechambre, *M. philoctetes* (Olivier), *M. septentrionis* Bates (Endrődi 1985; Dechambre 1981, 1998b-c; Ratcliffe 2007; Restrepo et al. 2003)

***Podischnus* Burmeister, 1847**

*Podischnus* Burmeister 1847: 237.

**Distribution:** Mexico to Peru and Brazil. Colombia: Antioquia, César, Cundinamarca, Meta, Santander, Tolima, Valle.

**Diversity:** 3 species. Colombia: 2 species, *P. agenor* (Olivier), *P. sexdentatus* (Taschenberg) (Endrődi 1985; Restrepo et al. 2003).

### ***Strategus* Kirby, 1828**

*Strategus* Kirby 1828: 349.

**Distribution:** United States, West Indies, to central Argentina. Colombia: Amazonas, Antioquia, Boyacá, Caquetá, Chocó, Cundinamarca, Huila, Magdalena, Meta, Santander, Tolima, Valle, Vichada.

**Diversity:** 37 species (1 fossil). Colombia: 4 species: *S. aloeus* (Linnaeus), *S. fascinus* Burmeister, *S. hipposiderus* Ratcliffe, *S. jugurtha* Burmeister (Ratcliffe 1976; Endrődi 1985; Restrepo et al. 2003; Morón and Nogueira 2008)

### **Tribe Pentodontini**

#### ***Bothynus* Hope, 1837**

*Bothynus* Hope 1837: 95.

**Distribution:** Mexico and Honduras to Peru and Brazil. Colombia: Antioquia, Cundinamarca, Norte de Santander, Tolima.

**Diversity:** 25 species. Colombia: 4 species: *B. complanus* (Burmeister), *B. herbivorus* (Arrow), *B. medon* (Germar), *B. quadridens* (Taschenberg) (Martínez 1983; Endrődi 1985; Restrepo et al. 2003).

#### ***Euetheola* Bates, 1888**

*Euetheola* Bates 1888: 314.

**Distribution:** United States to Argentina. Colombia: Antioquia, Bolívar, Boyacá, Caldas, Caquetá, Córdoba, Cundinamarca, Huila, Magdalena, Meta, Risaralda, Tolima, Sucre, Valle.

**Diversity:** 4 species. Colombia: 2 species: *E. bidentata* (Burmeister), *E. humilis* (Burmeister) (Endrődi 1985; Restrepo et al. 2003).

#### ***Hylobothynus* Ohaus, 1910**

*Hylobothynus* Ohaus 1910: 677.

**Distribution:** Colombia, Ecuador. Colombia: Amazonas, Putumayo.

**Diversity:** 4 species. Colombia: 2 species: *H. columbianus* Endrődi, *H. obesus* Ohaus (Dechambre 1979; Ratcliffe 1981a; Endrődi 1985; Restrepo et al. 2003).

***Oxylygyrus* Arrow, 1908**

*Oxylygyrus* Arrow 1908: 341.

**Distribution:** French Guiana to Bolivia and Argentina. Colombia, Ecuador. Colombia: Amazonas, Putumayo.

**Diversity:** 9 species. Colombia: 1 species: *O. zoilus* (Olivier) (Endrődi 1985; Restrepo et al. 2003).

***Parapucaya* Prell, 1934**

*Parapucaya* Prell 1934: 162.

**Distribution:** Honduras to northwestern South America. Colombia: Antioquia, Cauca, Cundinamarca, Meta, Risaralda, Valle.

**Diversity:** 2 species. Colombia: 2 species: *P. amazonica* Prell, *P. nodicolis* (Kirsch) (Endrődi 1985; Restrepo et al. 2003).

***Pucaya* Ohaus, 1910**

*Pucaya* Ohaus 1910: 675.

**Distribution:** Panama to Colombia and Ecuador. Colombia: Antioquia, Bolivar, Caquetá, Huila, Valle.

**Diversity:** 3 species. Colombia: 3 species (Endrődi 1985; Restrepo et al. 2003).

***Thronistes* Burmeister, 1847**

*Thronistes* Burmeister 1847: 177.

**Distribution:** Colombia, Brasil, Argentina, Uruguay. Colombia: Cundinamarca, Santander.

**Diversity:** Monotypic genus: *T. rouxi* Burmeister (Endrődi 1985; Restrepo et al. 2003; Abadie et al. 2008).

***Tomarus* Erichson, 1847**

*Tomarus* Erichson 1847: 95.

**Distribution:** United States to Argentina and Chile. Colombia: Amazonas, Antioquia, Atlántico, Caldas, Casanare, Cauca, Meta, Putumayo, Valle.

**Diversity:** 27 species. Colombia: 6 species: *T. bituberculatus* (Palisot de Beauvois), *T. ebenus* (Degeer), *T. fossor* Latreille, *T. gyas* Erichson, *T. maimon* (Erichson), *T. mater-*

*nus* Prell (Endrődi 1985; Dechambre and Lumaret 1985; Restrepo et al. 2003; Escalona and Joly 2006; Abadie et al. 2008).

### Tribe Phileurini

#### ***Amblyoproctus* Kolbe, 1910**

*Amblyoproctus* Kolbe 1910: 335.

**Distribution:** Nicaragua, Costa Rica, Panama to Colombia and Brazil. Colombia: Amazonas.

**Diversity:** 7 species. Colombia: 3 species: *A. piliger* (Perty), *A. torulosus* Kolbe, *A. chalumeaui* Endrődi (Endrődi 1985; Ratcliffe 1988, 2003; Restrepo et al. 2003).

#### ***Archophileurus* Kolbe, 1910**

*Archophileurus* Kolbe 1910: 334.

**Distribution:** Southern United States to Colombia, Ecuador, Bolivia, Brazil and Argentina. Colombia: No data.

**Diversity:** 26 species. Colombia: 2 species: *A. elatus* (Prell), *A. ovis* (Burmeister) (Endrődi 1985; Morón 1990; Restrepo et al. 2003).

#### ***Haplophileurus* Kolbe, 1910**

*Haplophileurus* Kolbe 1910: 335.

**Distribution:** Ecuador, Colombia. Colombia: Tolima, Valle.

**Diversity:** Monotypic genus: *H. unidonis* Burmeister (Endrődi 1985; Ide 1998; Restrepo et al. 2003).

#### ***Hemiphileurus* Kolbe, 1910**

*Hemiphileurus* Kolbe 1910: 340.

**Distribution:** United States to Brazil, including West Indies. Colombia: Antioquia, Boyacá, Chocó, Cundinamarca, Meta, Norte de Santander, Tolima, Valle.

**Diversity:** 42 species. Colombia: 10 species (Endrődi 1985; Ratcliffe 1988, 2001; Dechambre 2000b; Restrepo et al. 2003).

***Homophileurus* Kolbe, 1910***Homophileurus* Kolbe 1910: 336.**Distribution:** Mexico to Brazil, Paraguay and Cuba. Colombia: Putumayo, Santander, Valle.**Diversity:** 9 species. Colombia: 2 species: *H. quadrituberculatus* (Palisot de Beauvois), *H. waldenfelsi* Endrödi (Endrödi 1978, 1985; Restrepo et al. 2003).***Metaphileurus* Kolbe, 1910***Metaphileurus* Kolbe 1910: 334.**Distribution:** Colombia and Brazil. Colombia: No data.**Diversity:** 3 species. Colombia: 1 species: *M. explanatus* (Burmeister) (Endrödi 1985; Ide 1998; Restrepo et al. 2003).***Palaeophileurus* Kolbe, 1910***Palaeophileurus* Kolbe 1910: 335.**Distribution:** Panama, Colombia, Ecuador, Guyana, French Guiana, Brazil. Colombia: Amazonas, Meta.**Diversity:** 8 species. Colombia: 1 species: *P. sclateri* (Bates) (Endrödi 1985; Ratcliffe 2002; Restrepo et al. 2003).***Paraphileurus* Endrödi, 1978***Paraphileurus* Endrödi 1978: 98.**Distribution:** Panama, Venezuela, Colombia, French Guiana. Colombia: Cauca.**Diversity:** 3 species. Colombia: 1 species: *P. impressus* Endrödi (Endrödi 1978, 1985; Restrepo et al. 2003; Ratcliffe 2003).***Phileurus* Latreille, 1807***Phileurus* Latreille 1807: 103.**Distribution:** United States to Argentina. Colombia: Amazonas, Antioquia, Boyacá, Casanare, Cauca, Cundinamarca, Tolima, Valle.**Diversity:** 19 species. Colombia: 5 species: *P. didymus* (Linnaeus), *P. hospes* Burmeister, *P. kaszabi* Endrödi, *P. rufus* Dechambre, *P. valgus* (Olivier) (Endrödi 1978, 1985; Restrepo et al. 2003).

***Oryctophileurus* Kolbe, 1910**

*Oryctophileurus* Kolbe 1910: 334.

**Distribution:** Colombia, Peru, Bolivia. Colombia: Boyacá, Cauca.

**Diversity:** 3 species. Colombia: 1 species: *O. nasicornis* (Burmeister) (Endrődi 1985; Ide 1998; Restrepo et al. 2003).

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# The rare rhinoceros beetle, *Ceratophileurus lemoulti* Ohaus, 1911, in French Guiana and Suriname (Coleoptera, Scarabaeidae, Dynastinae, Phileurini)

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## Abstract

The rare dynastine, *Ceratophileurus lemoulti* Ohaus, 1911, previously known only from French Guiana, is here reported for the first time from Suriname. All biological, distributional and temporal data available for the species in both territories are presented and discussed.

## Keywords

*Ceratophileurus lemoulti*, Dynastinae, Phileurini, scarab beetle, Suriname, French Guiana, new country record, distribution

## Introduction

The tribe Phileurini belongs to the scarab beetle subfamily Dynastinae (commonly called rhinoceros beetles) and contains approximately 225 described species in 36 genera. It is worldwide in distribution. Tropical regions have the most diverse fauna of these beetles, especially in the New World, which has the highest species richness; more than half of all known species occur there (Ratcliffe and Cave 2006). The beetles be-

longing to this tribe are easily recognised by the enlarged mentum that covers the base of the labial palpi. In the New World, all species are black, flattened beetles, usually having the elytral striae clearly visible. They are nocturnally active and are attracted to artificial light, where they are often collected, although they are also found in decaying trunks and logs, where presumably the majority of species undertake their larval development. Some species have been associated with the nests of termites or ants (Ratcliffe and Cave 2006). Most adult Phileurini do not exhibit distinctive sexual dimorphism or obvious secondary sexual characters as is common in many other Dynastinae, although some do possess horns and other protuberances on the head and/or pronotum. One such species is *Ceratophileurus lemoulti* Ohaus.

The genus *Ceratophileurus* contains only the species, *C. lemoulti*, described from the French overseas Département of Guyane (French Guiana) and which has, until now, been recorded only rarely from that territory. French Guiana has a rich diversity of Dynastinae, with no fewer than 138 species, including 35 species of Phileurini, recorded from there (Ponchel, unpublished data). The diversity of Dynastinae in neighbouring Suriname is much less known, with few species recorded in the literature and only about 30 species presently represented in the National Zoological Collections of Suriname (Gillett, personal observation), including four species of Phileurini. French Guiana, Suriname and Guyana (the Guianas) have mostly escaped large-scale human induced alteration of their natural habitats, and consequently still contain vast areas of pristine Amazonian rainforest.

*Ceratophileurus lemoulti* is a distinctive species of Phileurini that can be easily identified with the keys of Endrödi (1977, 1985). The most striking character is the long, recurved and acuminate horn arising from the frons, which is present in *both* sexes. The pronotum of major specimens also bears on each side a short, laterally compressed projection, which is truncate apically (Figs 1–2). It is difficult to separate the sexes based on external morphology alone; the only reliable method is to dissect the abdomen to look for the sclerotised parameres found in the male. Thouvenot (2007) indicated that the only external difference between the single male specimen he studied and female specimens was the reduced size of the male. However our data indicate that this is not a reliable character, because female specimens we examined fell within the size range of the few males available for study. This paper aims to summarise and consolidate all known biological and distributional data available for *C. lemoulti*.

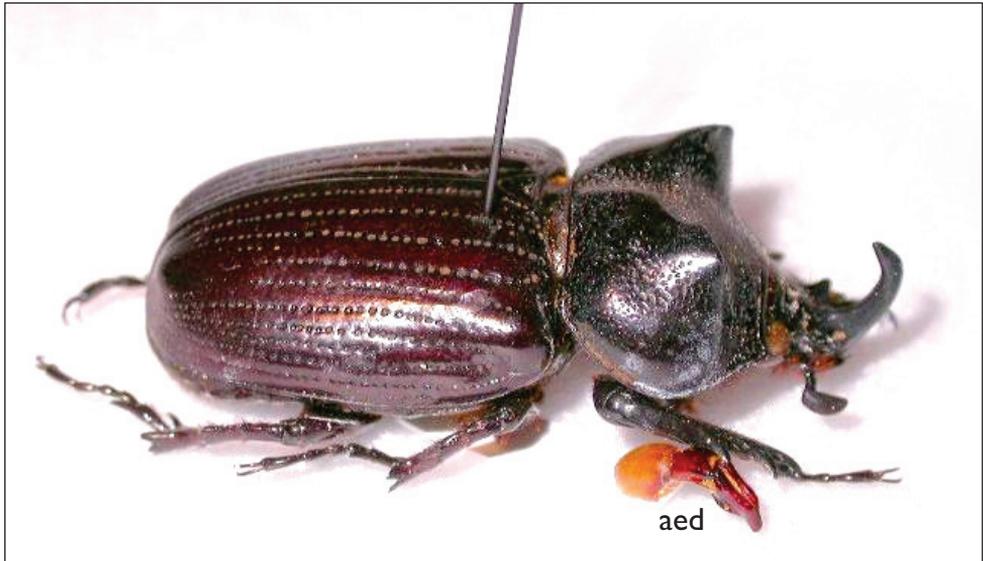
## Materials and methods

Specimens of *C. lemoulti* were studied from several institutional and private collections. The label data are reproduced below. Collection repositories are indicated by the following acronyms:

**ADC** Alain Drumont Collection, Bruxelles, Belgium

**GSC** Guy Silvestre Collection, Bédoin, France

**IRSNB** Institut royal des Sciences naturelles de Belgique, Bruxelles, Belgium



**Figure 1.** Male specimen of *Ceratophileurus lemoulti* Ohaus collected in French Guiana (YPC). Photograph by Yannig Ponchel. Aedeagus (**aed**) attached to card mount underneath specimen, in oblique view.

**RPDC** Roger-Paul Dechambre Collection, Paris, France

**YPC** Yannig Ponchel Collection, Kourou, Guyane, France

**Specimens Examined.** 15: 4♂♂ and 11♀♀ (ADC, IRSNB, RDCE, GSC, YPC)

**French Guiana** (France, Département outre mer de la Guyane). St-Laurent-du-Maroni, V.1980, 1 male (RPDC); Crique Nancibo, VI.1987, 1 female (RPDC); No data, 1 female (RPDC); Cacao, no date, 1 female (RPDC); Piste Coralie, IV.1989, 1 female (RPDC); Route de Régina, PK 35, 05.XI.1989, 1 female (GSC); Piste FRG, 09.V.1997, 1 male (YPC); Piste de Coralie, PK 2, V.1999, 1 female (YPC); Piste de Patagaïe, PK 27, VIII.2000, 1 female (YPC); Piste de Bélizon, PK 12–16.II.2001, 1 male (YPC;specimen shown in Fig. 1); Route de Petit Saut, PK 9, II.2000, 1 female (YPC); Cacao, VII.2000, 1 female (YPC); Cacao, V.2001, 1 female (YPC); RN 1, PK 20.IX.2000, 1 female (IRSNB).

**Suriname.** Sipaliwini, Central Suriname Nature Reserve, Raleighvallen, 14-16-II-2000, 1 male (Fig. 2), **new country record.**

Collecting localities for specimens examined are in Fig. 3.

**Literature Records.** Ohaus (1911) - French Guiana: St-Laurent-du-Maroni (Type locality); Blackwelder (1944) - French Guiana; Endrödi (1977) - French Guiana: St-Laurent-du-Maroni; Endrödi (1985) - French Guiana; Lachaume (1992) - French Guiana; Thouvenot (2007) - French Guiana: Petit Saut, PK 18 + PK 3, 15.VII.1993; Route Nationale 2, PK 79, 12.V.1997.

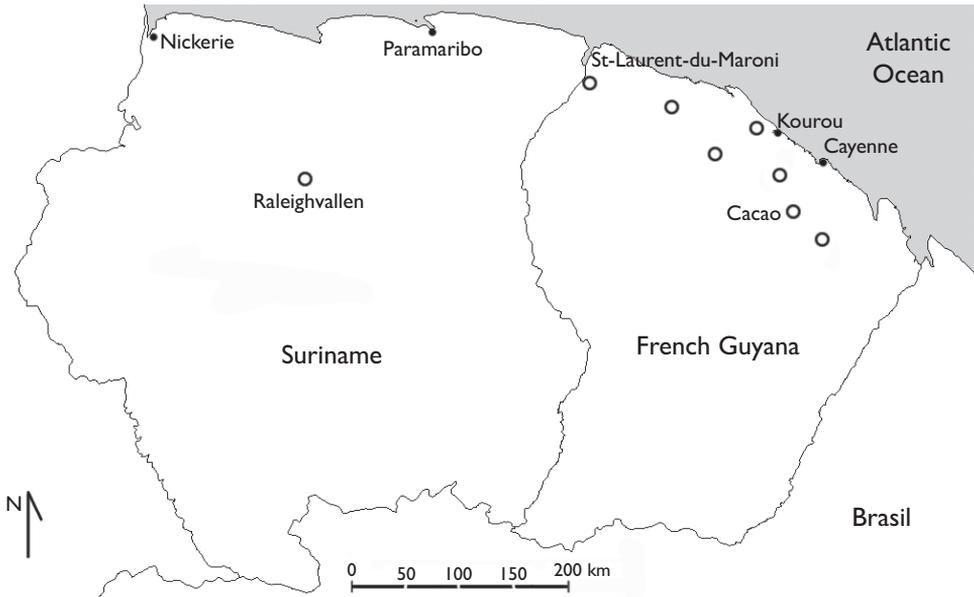
**Temporal data.** February (2), April (1), May (5), June (1), July (2), August (1), September (2), November (1)



**Figure 2.** Male specimen of *Ceratophileurus lemoulti* Ohaus collected at Raleighvallen, Suriname. Photograph by Alain and Marcel Galant.

## Discussion

*C. lemoulti* is a rare species. The holotype was collected by E. Le Moulton at St-Laurent-du-Maroni, French Guiana. Since its description, few other records have been published. It appears that the males are particularly scarce in collections; Thouvenot (2007) was able to collect only three females in more than 20 years of collecting in French Guiana. Of the 15 specimens we were able to study, only four were males. Whether males are truly less abundant or are less easily attracted to lights remains to be determined.



**Figure 3.** Distribution map for *Ceratophileurus lemoulti* Ohaus. Collection localities in black circles.

The possession of well developed horns in box sexes is exceptional within the Scarabaeoidea; usually only the male is armed. This condition is also seen in species of *Megaphanaeus* (Scarabaeinae: Phanaeini), which also exhibit little sexual dimorphism, but in which both sexes possess well developed cephalic and pronotal horns.

Although the species has been collected during different months, the temporal data indicates a peak activity in May, which represents approximately the onset of the main rainy season in the Guianas (lasting until August). Many adult Dynastinae are known to be most abundant during the beginning of rainy seasons across the Neotropics (e.g., Ratcliffe 2003; Gillett and Ponchel, personal observations). Equally interesting is the lack of captures during the months of December and January, which approximately coincides with the start of the short rainy season in the Guianas. This is a period of known activity for many Coleoptera and it may be significant that it has not been collected during those months.

As far as is known, all the specimens examined for this paper were collected at artificial light (especially mercury vapour light traps) in areas of primary or secondary lowland Amazonian rainforest. The species has usually been collected between the hours of 19:00 and 22:00, as is common for many Dynastinae (Ponchel, personal observation). In French Guiana its distribution is scattered, but most localities occur along the north of the territory (Fig. 3). However, because access to the remote forested interior of the Département is usually difficult, there is a good possibility that this species is also present there.

No other biological information is available, and the immature stages remain completely unknown. It appears that this species is an endemic and enigmatic element of the fauna of the Guianan shield.

The single male specimen collected at Raleighvallen in the Central Suriname Nature Reserve is the only specimen recorded to date from Suriname. Raleighvallen is an area of pristine lowland Amazonian rainforest, renowned for its rich biodiversity that remains virtually unknown entomologically. This record represents a modest range extension for the species, increasing its distribution by some 250 km to the west of the westernmost locality in French Guiana.

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# Stag beetles of the genus *Dorcus* MacLeay in North America (Coleoptera, Lucanidae)

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## Abstract

General confusion has surrounded the status of Nearctic *Dorcus* species since the 19<sup>th</sup> Century. In this paper the two Nearctic species are clarified and compared, and morphological characters discussed that will readily distinguish them. Examination of the type specimens of *D. mexicanus* reveals that they are actually mislabeled specimens and that the species is a new synonym of the Palearctic *D. parallelipedus* (L.).

## Keywords

Systematics, Lucanidae, Nearctic, *Dorcus brevis*, *Dorcus parallelus*, *Dorcus mexicanus*, synonym

## Introduction

The status of the North American species of *Dorcus* MacLeay has been the subject of debate since the late 1800s. On more than one occasion I have been asked how many species are present in our fauna, and so the purpose of this paper is to discuss the morphology of the North American species and provide the relevant characters for identification. Factors that have complicated the taxonomy are the relatively small numbers of known specimens of *D. brevis*, the markedly different morphology of large and small specimens due to allometric growth, and the general trend in *Dorcus* species for larger individuals to be less punctate.

Say described both *Lucanus parallelus* (1823) and *L. brevis* (1825). The former was subsequently transferred to *Dorcus* by Burmeister (1847), and the name *L. oblongus* de Charpentier, 1825 (based on a pair mislabeled as coming from the Pyrenees) was treated as a synonym. The description of new species based on mislabeled specimens is a frequent occurrence in Lucanidae, especially in *Dorcus*; *D. caucasicus* Ganglbauer, 1886 (mislabeled as coming from the Caucasus Mountains) was reduced to a synonym of *D. brevis* by Reitter (1892). Angell (1916) described the form *D. carnochani*, a synonym of *D. parallelus*.

A history of the ensuing debate over the distinctness of *D. brevis* and *D. parallelus* was provided in Benesh (1937). These species were frequently declared to be identical or merely forms of the same species (Parry 1870; Fuchs 1882; Horn 1892; Wickham 1899). Skinner (1911) planted the first seeds of doubt concerning the synonymy but stopped short of arguing for the ‘specific value’ of *D. brevis*.

Benesh (1937) distinguished the two species by the form of their posterior angles of the pronotum and overall body shape. His concepts of both species appear to be more or less correct based on specimens illustrated. However, his illustration of the male genitalia of *neither* species matches the actual morphology, which could indicate that the genitalia studied were broken during dissection or improperly relaxed. If male specimens with short flagella were identified by Benesh as *D. parallelus*, the locality information given in that paper and in Benesh (1942) may be suspect. Also, his characterization of the female mandibles as unidentate in *D. brevis* and bidentate in *D. parallelus* does not appear to be correct because no obvious difference in the dentition of female mandibles occurs in these species. However, based on the specimens examined it appears that *D. brevis* is widely distributed in the eastern United States.

Benesh (1944) described a third North American species, *Dorcus mexicanus*, from a male and female specimen in the Field Museum (FMNH) collection, the male with the locality as Jalapa, Mexico. Reyes-Castillo and Boucher (2003) noted that the distribution of the species in Mexico was unknown. Other than the type series, no other specimens of this species have been reported. Only one element of the Nearctic lucanid fauna, *Lucanus mazama* (LeConte), is known to extend into northern Mexico (Paulsen 2005). In a biogeographical sense, it seems unlikely that a species in the Holarctic genus *Dorcus* would be endemic to Neotropical Mexico. For this reason, I examined and compared the type specimens of *D. mexicanus* with the known species in the genus.

## Results

### *Dorcus brevis* and *D. parallelus*

The overall broader form of the body of *D. brevis* (Fig. 1) is often adequate to distinguish it from the relatively narrower *D. parallelus* (Fig. 2). However, the most useful and obvious external character for separating the North American species is the shape of the posterior pronotal angle. In *D. brevis*, the posterior angles are in close proximity to the elytral bases

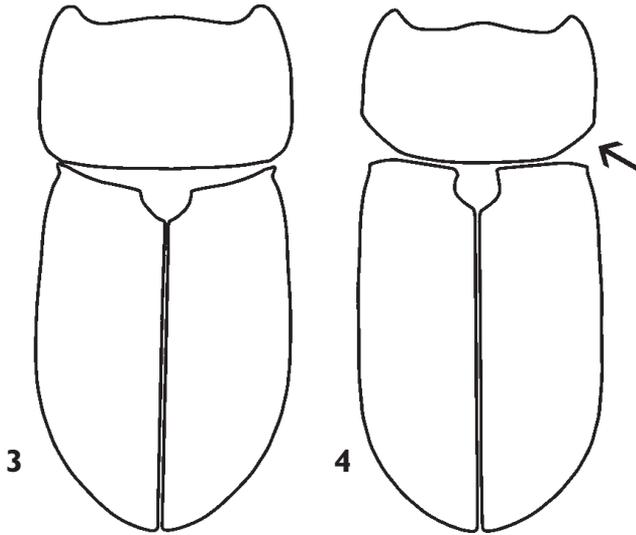


**Figures 1–2.** Dorsal habitus of major males. **1** *Dorcus brevis* (length 30mm) **2** *Dorcus parallelus* (length 26mm). Scale bar = 5mm.

(Fig. 3). In *D. parallelus*, the angles are distinctly removed from the base of the elytra (Fig. 4). The humeral angles of *D. brevis* are generally more strongly dentate and the humeri produced forward of the scutellum, while in *D. parallelus* the humerus is less strongly dentate and more or less in line with the scutellum. In addition, males of *D. parallelus* have a dense field of setae on the internal face of the metatibia (Fig. 5), but this patch is not present on males of *D. brevis* (Fig. 6). The clypeus is distinctly broader in males of *D. parallelus*.

In both species, the mandibles of major males have a single large dorsal tooth, but the dentition of the mandibles of minor males is clearly distinct. Even the smallest minor males of *D. parallelus* have mandibles that are of the same basic shape as major males, but they are simply reduced in size (Fig. 7). In contrast, minor males of *D. brevis* have two distinct internal teeth below the dorsal tooth and are abruptly curved internally (Fig. 8).

The form of the male genitalia is radically different in the two species. The flagellum of *D. parallelus* is longer than the entire length of the body and is weakly flared at the apex (Fig. 9). The flagellum of *D. brevis* is less than half as long, with a large lobe-like sac at the apex (Fig. 10). The genitalia of the European species, *D. parallelipipedus*, differs from either species in being more strongly expanded medially and in possessing a trilobed apex (Fig. 11).



**Figures 3–4.** Outline of body shape in females. **3** *Dorcus brevis* **4** *Dorcus parallelus*, arrow pointing to posterior pronotal angle distinctly removed from the base of the elytra.

### *Dorcus mexicanus*

Examination of the type specimens of *D. mexicanus* revealed that they are *Dorcus parallelipipedus* (L.), a Palearctic species. The identical male genitalia (Fig. 11), protruding clypeus of males, irregularly punctate elytra, and bituberculate frons of the female provide overwhelming evidence to support this conclusion. Thus, the name *D. mexicanus* Benesh is here reduced to a synonym of *D. parallelipipedus* (new synonymy).

Coincidentally, I encountered a second pair of *D. parallelipipedus* recently accessioned at the FMNH that bore handwritten labels indicating “Mexico, Nuevo Leon, Monterey (sic), Aug 1976”. The presence of a second, more recent pair of *D. parallelipipedus* from Mexico at first suggested that the species might be introduced there. However, on further examination I found that other handwritten locality labels of the same style from the accessioned collection were erroneous (with incorrect countries). While it is not impossible that the species is adventive in Mexico, it is more likely given the nomenclatural history of *Dorcus* that the common *D. parallelipipedus* has been mislabeled in these two instances.

### *Dorcus brevis* (Say, 1825)

*Lucanus brevis* Say 1825: 202, original combination. Type material: Not listed among the existing Say type material by Mawdsley (1993).

*Dorcus caucasicus* Ganglbauer 1886: 81, synonym (Reitter 1892). Type material (NMW- Vienna), not examined.



**Figures 5–6.** Left metatibia of males, ventral view. **5** *Dorcus parallelus*, arrow pointing to dense field of setae **6** *Dorcus brevis*.

**Distribution.** Specimens examined from Florida, Georgia, Illinois, Missouri, New Jersey, South Carolina, Tennessee, and Virginia. In addition to these states, Benesh (1937) listed Alabama, Indiana, Mississippi, North Carolina, and Oklahoma, while Benesh (1944) added Kansas, Maryland, and Michigan.

***Dorcus parallelus* (Say, 1823)**

*Lucanus parallelus* Say 1823: 248, original combination. Type material: Not listed among the existing Say type material by Mawdsley (1993).

*Lucanus oblongus* Charpentier 1825: 214, synonym (Burmeister 1847). Type not examined.

*Dorcus costatus* LeConte 1866: 35, synonym. Type material: Holotype female (MCZ) labeled a) red disk; b) handwritten “var. *costatus* / LeC.”; c) reddish-orange label “Type / [3688]”.

*Dorcus parallelus nanus* Casey 1909: 278, synonym. Type material: Syntype male (USNM) labeled a) “CASEY / bequest / 1925”; b) reddish-orange label “TYPE USNM / [36202]”. Syntype female (UNSM) labeled a) as male; b) reddish-orange label “[*nanus* – 2] / PARATYPE USNM / [36202]”.



**Figures 7–8.** Head of minor males, dorsal view. Inset showing dentition of right mandible. **7** *Dorcus parallelus* **8** *Dorcus brevis*.

*Dorcus carnochani* Angell 1916: 70, synonym. Type material: Two syntype males and one syntype female, possibly located in storage at the Brooklyn Museum, not examined.

**Distribution.** Specimens examined from Alabama, Illinois, Indiana, Iowa, Maryland, Michigan, Nebraska, New York, Ohio, South Carolina, Tennessee, and Virginia.

***Dorcus parallelipedus* (Linnaeus, 1758)**

*Scarabaeus parallelipedus* Linnaeus 1758: 354, original combination. Palearctic synonymy given in Bartolozzi and Sprecher-Uebersax (2006).

*Dorcus mexicanus* Benesh 1944: 45, syn. n. Type material: Holotype male (FMNH) labeled a) “JALAPA / MEX”; b) male symbol; c) “FIELD MUSEUM / (F. Psota



**Figures 9–11.** Male genitalia (parameres and flagellum). **9** *Dorcus parallelus* **10** *Dorcus brevis* **11** *Dorcus parallepipedus*. Scale bar = 5 mm.

Coll.)”; d) reddish-orange paper “Holotype / male symbol CNHM / [*Dorcus / mexicanus* / Benesh]”; e) handwritten “*Dorcus / mexicanus* / MS Benesh”, on reverse “Det. Dec. 15, 1943 / B. Benesh”. Female allotype labeled a) female symbol; b) as c of holotype; c) on reddish-orange paper “Allotype / CNHM female symbol / [*Dorcus / mexicanus* / Benesh]”.

This species is distributed in Europe, Asia, and Northern Africa (Bartolozzi & Sprecher-Uebersax 2006).

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