Overview and revision of the extant genera and subgenera of Trogidae (Coleoptera: Scarabaeoidea)

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Abstract

Extant genera and subgenera of the Trogidae (Coleoptera: Scarabaeoidea) are reviewed. Contemporary classifications of this family have been based exclusively on morphological characters. The first molecular phylogeny for the family recently provided strong support for the relationships between morphologically defined genera and subgenera. On the basis of morphological, molecular and biogeographical evidence, certain taxonomic changes to the genus-level classification of the family are now proposed. Trogidae is confirmed as being divided into two subfamilies, Omorginae Nikolajev and Troginae MacLeay, the former with two genera, *Omorgus* Erichson and *Polynoncus* Burmeister; and the latter with two genera, *Trox* Fabricius and *Phoberus* MacLeay **stat. rev.** *Phoberus* is restored to generic rank to include all of the Afrotropical (including Madagascan endemic) species; *Afromorgus* is confirmed at subgeneric rank within the genus *Omorgus*; and the monotypic Madagascan genus *Madagatrox* **syn. n.** is synonymised with *Phoberus.* The current synonymies of *Pseudotrox* Robinson (with *Trox*), *Chesas* Burmeister, *Lagopelus* Burmeister and *Megalotrox* Preudhomme de Borre (all with *Omorgus*) are all accepted to avoid creating speculative synonyms before definitive phylogenetic evidence is available. New combinations resulting from restoring *Phoberus* to a monophyletic genus are listed as an Appendix.

Introduction

Trogidae represents a small family within the very large and diverse superfamily Scarabaeoidea (Browne and Scholtz 1999). Trogids are relatively secretive and elusive beetles, which can be attributed to their remarkable feeding specialisation. Adults and larvae

of all known species are considered truly keratinophagous (keratin-digesting) beetles. Of the insects, only some clothes moth (Tineidae) larvae, bird lice (Mallophaga), and adult and larval hide and museum beetles (Dermestidae) are adapted to digesting keratin. Trogids are the only members of the Scarabaeoidea with this adaptation which is undoubtedly of major evolutionary significance (Scholtz 1980, 1986a; Scholtz and Caveney 1988; Hughes and Vogler 2006).

The family comprises some 330 species that primarily inhabit the temperate and arid savanna regions of the world (Scholtz 1982, 1986a; Smith 2003; Pittino 2006; Zidek 2013). Africa and Eurasia have the richest faunas with about 100 species each, followed by Australia (55 species) and South and North America (around 50 species each) (Scholtz 1982, 1986a, 1986b, 1990; Zidek 2013). The fauna of each of the zoogeographical regions has been revised, mostly over the past 60-odd years; some of the most important revisions include those by Blackburn (1904) and Haaf (1954a; 1954b), who treated the Australian and Afrotropical-Oriental faunas, respectively; Vaurie (1955; 1962) the Nearctic and Neotropical faunas; Balthasar (1936), Pittino (1983, 1985) and Scholtz et al. (2007) the Palaearctic fauna; and Scholtz (1980, 1986b, 1990) the Afrotropical (Sub-Saharan Africa), Australasian and Neotropical faunas, respectively. Scholtz (1982) and Zidek (2013) catalogued the species of the world.

Taxonomic history

The taxonomic history of the Trogidae extends back 257 years to when the first 'trogid' species, *Scarabaeus sabulosus* Linnaeus, was described. Numerous systematists subsequently contributed and by the end of the nineteenth century all of the major taxonomic groups had been established. As the extant genera and subgenera are taxonomically well-defined by their morphological characters, only a brief overview of their taxonomic history is presented here. For a more detailed account refer to Baker (1968), Vaurie (1955) and Scholtz (1980, 1986a, 1986b, 1990).

Fabricius (1775) described the genus *Trox*, (from the Greek *trog*, which means to gnaw). MacLeay (1819) proposed the family name Trogidae, and described the genus *Phoberus*. The latter, was however, not generally recognised as a genus; it was either considered to be a monotypic subgenus (Burmeister 1876; Preudhomme de Borre 1886), a synonym of *Trox*

(Harold 1872; Scholtz 1979a), a species group (Haaf 1953) or a subgenus of *Trox* (Péringuey 1900; Arrow 1912; Scholtz 1980, 1982).

In 1847 Erichson erected the genus *Omorgus* for two American species originally placed in *Trox*, separating the North American species into two genera, *Trox* and *Omorgus*. Other authors, however, considered *Omorgus* either as synonymous with *Trox* (Lacordaire 1856; Harold 1872; Horn 1874; Loomis 1922); as a subgenus of *Trox* (Burmeister 1876; Péringuey 1900, 1908; Gerstaecker 1873; Arrow 1912; Balthasar 1936; Robinson 1940; Scholtz 1980, 1982) or several species groups (Vaurie 1955, 1962; Haaf 1953, 1954a; Scholtz 1979b). Baker (1968) restored *Omorgus* to a valid genus based on differences in larval and adult morphology between *Trox* and *Omorgus*.

Arrow (1912) placed three well-defined genera in the family: *Trox*, *Glaresis* Erichson and *Cryptogenius* Westwood. Petrovitz (1968) described the genus *Afroglaresis* in the Trogidae, to be later synonymised with *Glaresis* (Scholtz et al. 1987). Robinson (1948) proposed the genus *Pseudotrox* for one North American species, *T. laticollis* LeConte, but it was subsequently synonymised with *Trox* (Vaurie 1955).

Several other subgenera have been proposed for various species or species groups. Burmeister (1876) reviewed trogids of Argentina and split them into different groups, *Omorgus*, *Chesas*, *Lagopelus* and *Polynoncus*, which he treated as subgenera of the genus *Trox*. Preudhomme de Borre (1886) established the subgenus, *Megalotrox* (of *Trox* Fabricius) for some of the very large flightless Australian species. *Chesas*, *Lagopelus* and *Megalotrox* were later synonymised with *Omorgus* (Vaurie 1962). *Polynoncus* has remained a well-defined group. Other authors followed Burmeister and treated *Polynoncus* as a subgenus of *Trox* (Preudhomme de Borre 1886; Arrow 1912; Scholtz 1982).

Until the mid-nineteen eighties Trogidae classification was based mainly on overall physical similarity of species and limited character sets and none of the earlier revisions addressed evolutionary patterns or relationships in the family. The problem was whether to classify Trogidae (1) as a large, variable genus (*Trox*) with numerous species groups (for example Vaurie 1955), (2) as a single genus (*Trox*) with several distinct subgenera (for example Burmeister 1876; Scholtz 1982); or (3) two genera (*Trox* and *Omorgus*) with unspecified internal relationships (for example Erichson 1847; LeConte 1854).

Morphological phylogeny

The first comprehensive phylogenetic approach to classification for this group was made by Scholtz (1986a), who was the first to infer relationships among and within genera based on synapomorphic character states. The resulting phylogenetic classification, which has remained relatively stable for the last three decades, divided the family into two distinct lineages, a morphologically plesiomorphic *Trox* lineage (with two subgenera, *Trox* and *Phoberus*) and a relatively apomorphic lineage consisting of *Polynoncu*s and *Omorgus* (with three subgenera, *Omorgus*, *Haroldomorgus* Scholtz and *Afromorgus* Scholtz).

Scholtz (1986a) found there was no phylogenetic justification for the retention of *Glaresis* and *Cryptogenius* within Trogidae because they shared no synapomorphies with *Trox*. Scholtz et al. (1987a, b) subsequently placed *Glaresis* in a monotypic family, Glaresidae Kolbe and transferred *Cryptogenius* to Hybosoridae Erichson. Glaresidae until recently was still treated, by some authors, as a subfamily of Trogidae (Smith et al. 2006; Ratcliffe and Paulsen 2008), however recent studies have clearly demonstrated their phylogenetic independence (Bai et al. 2012a, b; Ahrens et al. 2014).

A series of studies that followed Scholtz (1986a) supported these findings: Scholtz and Peck (1990) and Grebennikov and Scholtz (2004) examined larval characters for the Trogidae and the basal groups in the Scarabaeoidea respectively; d'Hotmann and Scholtz (1990) assessed the phylogenetic significance of male genitalia; Nel and Scholtz (1990) compared the morphology of mouthparts of adult Scarabaeoidea; Browne et al. (1993) examined wing articulation and wing base characters; and Scholtz (1991, 1993) investigated the phylogenetic importance of larval morphology of congeneric trogids from different geographical regions. All of these studies demonstrated that: (1) Trogidae is a monophyletic group within the superfamily Scarabaeoidea; and (2) monophyletic genera can be defined on the basis of synapomorphic character states of the morphology of both adults and larvae.

Current classification

Despite these comprehensive treatments of the family, some subsequent authors have proposed changes to the classification established by Scholtz (1986a) and Scholtz and Peck (1990): Nikolajev (2005) revised the morphological characters of the family and split the Trogidae into two subfamilies, Troginae MacLeay, containing only the genus *Trox*, and Omorginae Nikolajev, comprising the genera *Omorgus* and *Polynoncus*. Pittino (2006)

elevated the subgenus *Afromorgus* to genus status on the basis of apomorphic character states on the male genitalia and biogeography. Zidek (2013) in his checklist of the Trogidae considered the generic status of *Afromorgus* (as proposed by Pittino) as nomenclaturally incorrect and reconsidered *Afromorgus* as a subgenus of *Omorgus* (*sensu* Scholtz 1986a). Recently Pittino (2010) described a new genus, *Madagatrox*, to accommodate a single flightless species from Madagascar.

Consequently, there are currently four nomenclaturally valid extant genera in the family: *Trox* (with subgenera *Trox* and *Phoberus*), *Omorgus* (with subgenera *Omorgus*, *Afromorgus* and *Haroldomorgus*), *Polynoncus*, and *Madagatrox.* However, these changes to the classification were not based on formal phylogenetic analyses.

Molecular phylogeny

My recent molecular phylogeny (Strümpher et al. 2014b; Fig 1), based on partial DNA sequences of three ribosomal gene regions (two nuclear and one mitochondrial), is the first for the family and provides robust support for the relationships of genera and subgenera, cross-validating the morphological phylogeny (Scholtz 1986a; Scholtz and Peck 1990) in most aspects. On the basis of this study and the morphological evidence, certain taxonomic changes to the genus-level classification of the family are proposed here. The arguments supporting the classification of the extant crown group genera and subgenera are assessed.

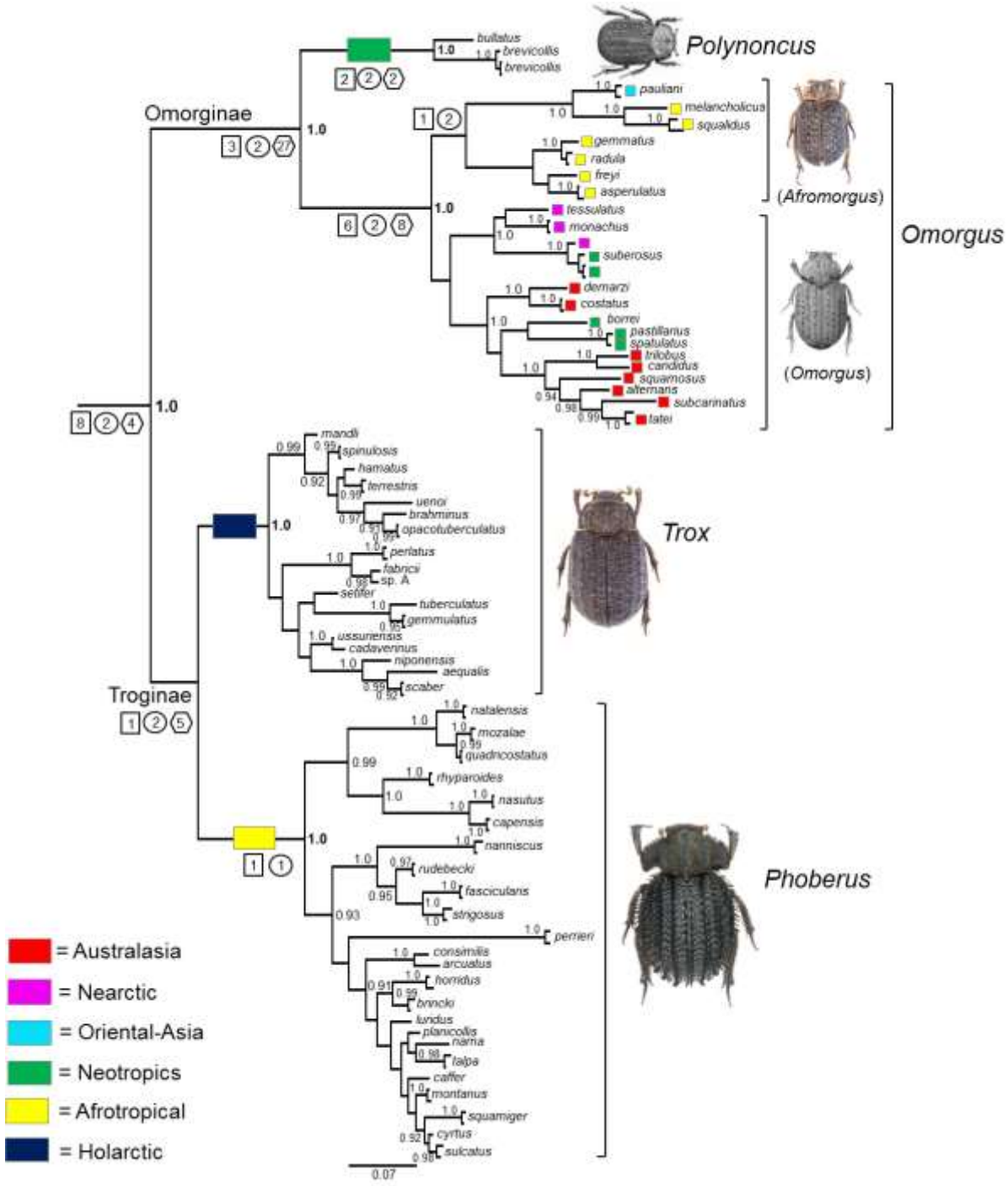

Figure 1. Molecular phylogeny of the Trogidae (redrawn from Strümpher et al. 2014b). Numbers next to each node are the posterior probability support. Only nodes with posterior probabilities ≥ 90% are shown. Images depict the type species of the genus or subgenus. Synapomorphic characters sets (see Strümpher et al. 2014b) which unite each node are plotted on the phylogram. Branches colour coded for geographic distributions.

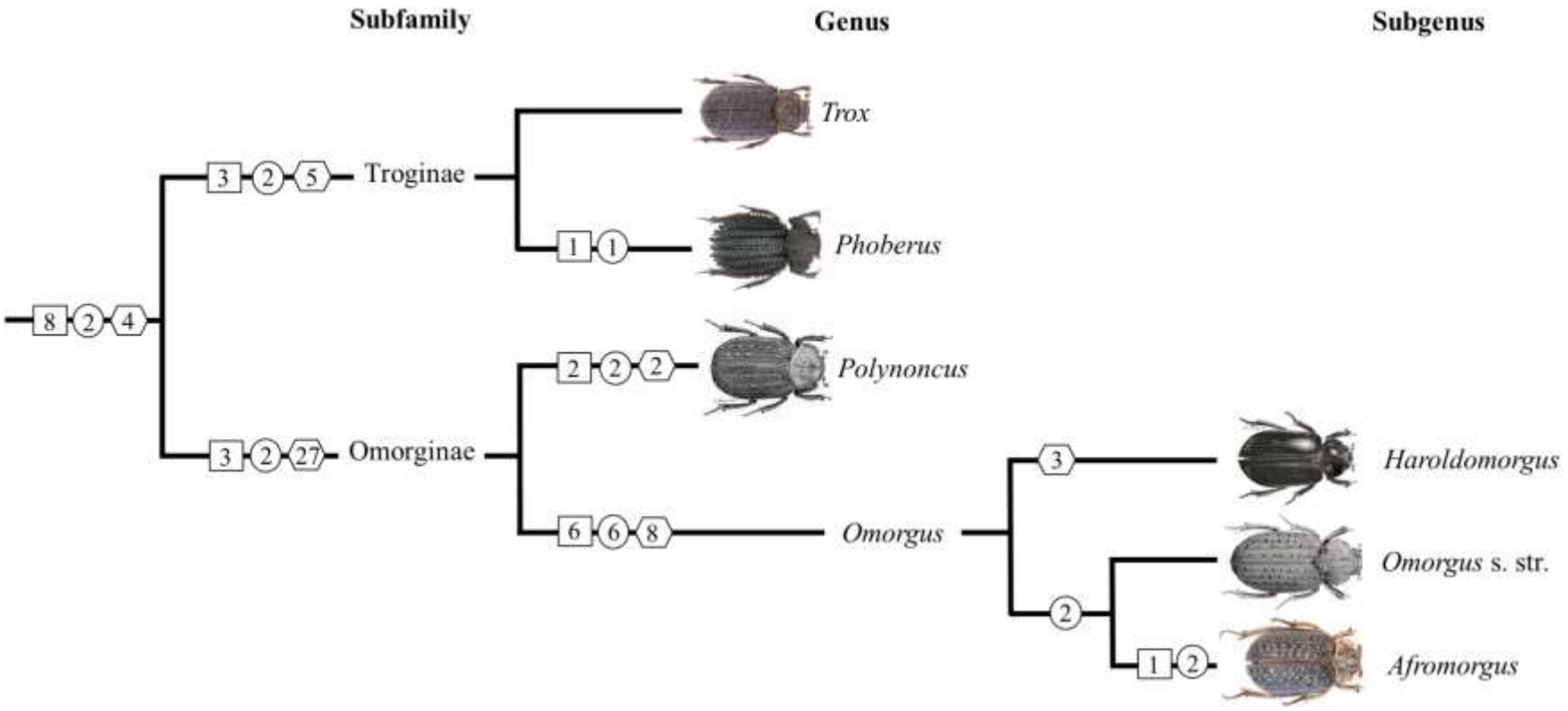

Figure 2. Proposed classification of the Trogidae, based on the phylogenetically important morphological characters and the molecular phylogeny presented by Strümpher et al. (2014b). The larval (boxes), adult (circles) and hind wing (hexagons) synapomorphic characters which unite each node are plotted on the phylogram. Numbers represent the number of characters that unite each clade. For details on larval characters, see Scholtz and Peck (1990), Scholtz (1993) and Grebennikov and Scholtz (2004); for adult (excluding hind wing) characters, see Scholtz (1986a) and Browne and Scholtz (1999); for hind wing characters, see Browne et al. (1993) and Browne and Scholtz (1995). Images depict the type species of the genus or subgenus.

Family **Trogidae**

Molecular phylogenetic characters (Strümpher et al. 2014b; Fig 1) clearly support the subfamily division of Trogidae MacLeay proposed by Nikolajev (2005). Both subfamilies (Omorginae Nikolajev and Troginae MacLeay) are monophyletic and diagnosable by adult and larval synapomorphies (Fig 2; Appendix B). Troginae is characterised by their round antennal scape, a metatibial spur longer than first two tarsal segments, elytra and pronotum with complex body setae (plumose, spatulate or squamose) as well as several wing characters; the larvae are characterised by a having biforous spiracles; an indistinct fronto-clypeal suture and the setae absent on the second mesothoracic dorsal lobe. Omorginae on the other hand are defined by an elongated antennal scape, a metatibial spur as long as first two tarsal segments, dense metatarsal setae and a large number of synapomorphic wing characters; the larvae have cribriform spiracles; a distinct fronto-clypeal suture and setae present on the second mesothoracic dorsal lobe.

The phylogenetic relationships within the two subfamilies were well resolved (Figs 1). Two monophyletic lineages within each subfamily were clearly diagnosable by synapomorphies (Figs 2, Appendix B), and are regarded here as distinct genera: the Holarctic *Trox* Fabricius and African *Phoberus* MacLeay within Troginae; and *Omorgus* Erichson and *Polynoncus* Burmeister within Omorginae. I maintain the status of both subfamilies as currently defined by Nikolajev (2005).

Trox

The genus *Trox* was described by Fabricius (1775) for the Palaearctic species *T. sabulosus* (Linnaeus). The defining adult and larval characteristics of this genus (in the strictest sense), which essentially distinguished Holarctic (and a small number of Afrotropical) trogid species from that of other zoogeographic regions, were: [for adults] the oval scutellum, round antennal scape; apical attachment of the pedicel to the scape; reticulated eyes; base of pronotum not restricted; quadrangular serrated hind legs; metatibial spur longer than the first tarsal segment; adults usually small (4-12mm) (Balthasar 1936; Haaf 1953; Vaurie, 1955); [for larvae] biforous spiracles; indistinct fronto-clypeal suture; and second antennal segment with sensory cone (Baker 1968).

From this nomenclatural basis, a phylogenetic analysis of a larger suite of morphological characters led Scholtz (1986a) to conclude that the genus was paraphyletic and divided the genus in two subgenera, *Trox* s. str. and *Phoberus*. *Phoberus* was originally described as a

genus by MacLeay (1819) for the flightless Afrotropical species *P. horridus* (Fabricius). However, assigning species to *Phoberus* remained problematic with some Afrotropical species not fitting clearly into either *Trox* or *Phoberus* (Péringuey 1900; Haaf 1953; Scholtz 1979b, 1980). The lack of defining morphological characters can to some extent be attributed to the high incidence of flightlessness among the Afrotropical taxa making the group morphologically diverse. Scholtz (1986a) transferred all, but nine, of the Afrotropical *Trox* species described at the time to the subgenus *Phoberus*. The remaining nine Afrotropical species (*Trox nasutus* Harold, *T. capensis* Scholtz and *T. natalensis* Haaf, *T. rhyparoides* Harold, *T. pusillus* Péringuey, *T. fascicularis* Wiedemann, *T. strigosus* Haaf, *T. nanniscus* Péringuey, *T. rudebecki* Haaf) were placed together with all the Holarctic species in the subgenus *Trox*.

However, molecular phylogenetic analysis (Strümpher et al. 2014b) clearly demonstrated the existence of two geographically distinct monophyletic lineages within this genus (Fig 1); the Holarctic *Trox* and Afrotropical *Phoberus*. All nine Afrotropical species previously placed in the subgenus *Trox* s. str. group naturally within the Afrotropical *Phoberus*. Even the Madagascan species, *T. perrieri* Fairmaire, currently placed in the subgenus *Trox*, is phylogenetically nested within the Afrotropical *Phoberus* lineage (Strümpher et al. 2014; Fig 1). Fairmaire (1899) and Haaf (1953) considered *T. perrieri* related to other members on the mainland, which is supported by molecular evidence (Strümpher et al. 2014b; Fig 1). The close relationship of *T. perrieri* to the Afrotropical *Phoberus* points to an African origin for the Madagascan trogid fauna (Strümpher et al. 2014b). The clade into which *P. horridus* falls is confined to Africa and Madagascar and can be defined by synapomorphies of adult and larval morphology that are not part of the original definition of *Phoberus* (Fig 2, Appendix B). The Holarctic clade containing the type species of *Trox* can also be characterised in this way. *Phoberus* and *Trox* can therefore be made reciprocally monophyletic. Therefore, all Afrotropical species of *Trox* can be reassigned to *Phoberus*.

I consider the molecular and morphological monophyly, geographic distributions and defining morphological synapomorphies sufficient to rank them equivalent to genera. Dispensing with the subgeneric divisions would simplify the classification of the family by removing an uninformative level (subgenus *Trox*) in the nomenclatural hierarchy, since Troginae and *Trox* would otherwise be defined by the same synapomorphies. Robinson's (1948) monotypic Nearctic genus *Pseudotrox* was synonymised with *Trox* (Vaurie 1955), a

decision that is not at odds with my proposals. Similarly, based on these results I also reinstate the genus *Phoberus* **stat. rev.** to accommodate all the Afrotropical species (Scholtz 1980; 1982; 1986b; 1993; van der Merwe and Scholtz 2005; Strümpher and Scholtz 2009, 2011). This also has the advantage of removing an uninformative level (subgenus *Phoberus*) in the nomenclatural hierarchy. The list of species, including new combinations, belonging to *Phoberus* is presented in Appendix A.

Madagatrox

Pittino (2010) described the new genus *Madagatrox* from a single, incomplete female specimen. This flightless representative of the genus is morphologically very similar to other flightless species on the mainland, especially those species belonging to the *natalensis*-group in *Phoberus* (Strümpher and Scholtz 2009, 2011), and is based on problematic diagnostic characteristics.

Pittino (2010) listed several pronotal and elytral characters (autapomorphies) that distinguish this taxon from other trogids (Pittino 2010) but these characters should be treated with caution. Some of these characters (autapomorphies), apart from not having any phylogenetic value in recognizing *Madagatrox*, are characteristic of flightless southern African and other trogid species with extreme morphological changes as a result of "old aptery" (see Scholtz 1980, 2000). Moreover, in small flightless trogids, external characters vary greatly with size of the individual. In very small specimens, for example, many features tend to become irregular or obscured (for example intercostal punctures and fovae) and/or pronounced (like tubercles and ridges), thus making it generally difficult to identify taxonomically relevant characters (personal observations WPS). These observations mean that such characters are of dubious value in diagnosing *Madagatrox*. Similarly, in some of the flightless species on the mainland, and especially in very small individuals, the fifth segment on the protarsus is deeply recessed in the apex of the fore tibia, giving the appearance of a four-segmented protarsus or a pseudotetramerous condition (personal observations WPS). The single specimen of *Madagatrox* differs from all other trogids in having a four-segmented, rather than a five-segmented protarsus on its only intact protibia (Pittino 2010), but the latter condition is likely pseudotetramery, because of the small size of the representative specimen and its flightless condition. Until such time as additional (male and female) specimens become available for study, I consider the condition pseudotetramerous (see also Zidek 2013) and therefore a dubious defining autapomorphy. This leaves *Madagatrox* effectively undiagnosed.

Although the genus was not included in the molecular analysis (Strümpher et al. 2014b), but consideration of its morphological description suggests very strongly that phylogenetic analysis would place it in or very near the *natalensis*-group within the *Phoberus* clade (Strümpher and Scholtz 2009, 2011). This would render the *Phoberus* clade (and *Trox* as currently defined) paraphyletic and several phylogenetically and biologically insignificant taxa would have to be described to preserve *Madagatrox* under the principle that (crown) taxa should be monophyletic.

Consequently, I propose that the genus *Madagatrox* be synonymised with *Phoberus* **stat. rev.** This also has the advantage of removing a redundant monotypic taxon from the classification.

Omorgus

Omorgus is a monophyletic group supported by a large number of adult and larval morphological synapomorphies (Scholtz 1986a; Scholtz and Peck 1990; Browne et al. 1993) and molecular evidence (Strümpher et al. 2014b, Fig 2). Because of the strong support for the monophyly for this genus and its clear morphological diagnosability (Scholtz 1986a, 1993; Scholtz and Peck 1990; Browne et al. 1993), I maintain its status as delineated by Scholtz (1986a).

Scholtz (1986a) divided *Omorgus* into three phylogenetically (and geographically) distinct subgenera; *Haroldomorgus*, *Omorgus* s. str. and *Afromorgus*. The monotypic subgenus *Haroldomorgus* occurs in South America, *Omorgus* in the southern Nearctic, Neotropical and Australasian Regions, and *Afromorgus* occurs in the Afrotropical and Oriental Regions. The molecular phylogeny of Strümpher et al. (2014), which did not include *Haroldomorgus*, shows that *Omorgus* comprise two well-supported sister lineages, one (the *Omorgus*-lineage) containing the New World and Australasian species, and the other (the *Afromorgus*-lineage) comprising the Afrotropical and Oriental species, which to a large extent supports the morphological subdivisions of Scholtz (1986a). Because of the strong support for the monophyly for the subgenera and their clear morphological diagnosability (Scholtz 1986a, 1993; Scholtz and Peck 1990; Browne et al. 1993), I maintain them as delineated by Scholtz (1986a). Even though one can equally argue that the subgenera can be treated as genera based on the morphological diagnosability and unique geographical distributions of these taxa (as for *Phoberus* and *Trox*); maintaining the subgeneric classification provides a better indication of the phylogenetic relationships within *Omorgus*.

Omorgus (***Omorgus***)

All of the Australasian and New World *Omorgus* species group phylogenetically in this taxon (Scholtz 1986a; Strümpher et al. 2014b). In the past, the New World and Australasian *Omorgus* has been the subject of many attempts at species groupings. Apart from *Omorgus*, other subgenera (of *Trox* Fabricius) proposed for species included, *Megalotrox* Preudhomme de Borre (1886), *Lagopelus* Burmeister (1876) and *Chesas* Burmeister (1876). Preudhomme de Borre (1886) established the genus *Megalotrox* for one of the very large, flightless Australian species, *T. gigas* Harold, and six species are currently placed in the taxon (Arrow 1912; Haaf 1954b). Similarly, Burmeister (1876) considered *O. pastillarius* Blanchard unique among the Argentine species, on account of it being flightless, and placed it in the monotypic subgenus *Chesas*, to which no other species have been added. *Lagopelus* was established for a single, winged species, *Trox ciliatus* Blanchard, and the genus remains monotypic. *Chesas*, *Lagopelus* and *Megalotrox* were later synonymised with *Omorgus* (Vaurie 1962; Baker 1968; Scholtz 1986b).

Results from the molecular phylogeny of the Trogidae indicated the subgenus *Omorgus* may well comprise several lineages equivalent to subgenera (Strümpher et al. 2014b). Strümpher et al. (2014) discussed the resurrection of *Megalotrox* and *Chesas*. The former is assignable to some Australian *Omorgus* species and the latter to some Neotropical representatives. However, evidence for their monophyly is inadequate to draw any concrete conclusions (Strümpher et al. 2014b) and I prefer to not risk creating unnecessary synonyms and to wait for unequivocal evidence of their membership. Therefore, *Omorgus* s. str. is retained as the nominal subgenus of *Omorgus* and the current synonymies *Chesas*, *Lagopelus* and *Megalotrox* (all with *Omorgus* s. str.) are all accepted.

Omorgus (***Haroldomorgus***)

Exemplars of this rare monotypic subgenus were not included in the molecular phylogeny of the Trogidae and without molecular data the placement of this subgenus remains uncertain. The morphology suggests that *Haroldomorgus* is the sister clade to *Omorgus* s. str. (Scholtz 1986a; Browne et al. 1993; see also Vaurie 1962). For the time being I consider *Haroldomorgus* a close relative of *Omorgus*. Therefore, *Haroldomorgus* retains its status as a subgenus within the genus *Omorgus*.

Omorgus (***Afromorgus***)

Afromorgus has had an inconstant taxonomic history. It was originally described as a subgenus of *Omorgus* (Scholtz 1986a), elevated to genus rank (Pittino 2006) and recently treated again as a subgenus of *Omorgus* (Zidek 2013). Molecular evidence clearly indicates that *Afromorgus* is a well-defined clade containing all the Afrotropical and Asian species within the genus *Omorgus* (Strümpher et al. 2014b; Fig 1) and can be defined by synapomorphies of adult and larval morphology (Fig 2, Appendix B).

I intuitively follow the classification system for the genus *Omorgus* and its subgenera, as proposed by Scholtz (1986a; see also Zidek 2013). *Afromorgus* is, consequently retained as a subgenus of the genus *Omorgus*.

Polynoncus

Polynoncus remains a well-defined group and is the sister-group to the genus *Omorgus* (see also Scholtz 1986a; Scholtz and Peck 1990; Browne et al. 1993). Molecular and morphological data support the monophyly of the group. Its generic status is maintained since recognising *Omorgus* as a genus obliges according *Polynoncus* the same status in phylogenetic systematics.

Fossils: The fossilised taxa are not dealt with in this paper. Details regarding the fossilised taxa are provided by Krell (2007) and Nikolajev (2007; 2009).

In conclusion, the phylogenetic classification proposed here basically follows the system proposed by Scholtz (1986a), except that the Trogidae are accepted as consisting of two subfamilies, Omorginae and Troginae following Nikolajev (2005). The subgenus *Phoberus* is restored to genus and the subgenus *Trox* falls away because of the promotion of *Phoberus*. The Afrotropical species of *Trox* are transferred to *Phoberus*; and the Madagascan genus *Madagatrox* is synonymised with *Phoberus* and its only species is transferred to *Phoberus*. The classification of the genus *Omorgus* and its subgenera, as proposed by Scholtz (1986a), is maintained with *Afromorgus* confirmed as a subgenus. The current synonymies of *Pseudotrox* Robinson (= *Trox*), *Chesas* Burmeister (= *Omorgus*), *Lagopelus* Burmeister (= *Omorgus*) and *Megalotrox* Preudhomme de Borre (= *Omorgus*) are all accepted to avoid creating speculative synonyms before definitive phylogenetic evidence is available. I are confident that the proposed changes produce a balanced and stable classification for this

unique beetle family (Fig 2). New combinations resulting from restoring *Phoberus* to a monophyletic genus are listed in Appendix A.

Taxonomy

FAMILY: Trogidae MacLeay

Trogidae MacLeay, 1819: 36

Type genus: *Trox* Fabricius, 1775: 31

Lists of references to the family are provided in Scholtz (1982), see additional sources cited within Zidek (2013)

Diagnosis

Length: 4–30mm.

Colour: Flavescent, reddish brown, grey or black.

Head: Eyes not divided by genae; mandibles vertical, robust; frons smooth, bi- or quadrituberculate or ridged; 10-segmented antennae with basal segment robust, three-segmented club, free, setose; antennal scape may be virtually round with apical pedical attachment, elongate with apical pedicel attachment, or elongate with subapical pedicel attachment; clypeus usually triangular or broadly rounded, it may be horizontal (straight) or slightly bent down; with the apex distinctly deflexed at right angles to the clypeal disc, or slightly reflexed.

Pronotum: Convex; usually wider than long, pronotal margins attenuated anteriorly; the sides may be broad and flat, obsolete or intermediate between them; the total pronotal width may be narrower than the elytra, as wide or wider; pronotal lateral margin may be straight, attenuated anteriorly or posteriorly, smooth, notched posteriorly, dentate or with one or two distinct incisions; pronotal disc may be prominently sculpted with distinct median ridges and sub-median ridges and tubercles, smooth or setose.

Scutellum: Hastate or oval.

Elytra: Convex or flat; elongated with sharp humeral angle and distinct humeral calli in winged individuals or rounded with rounded humeral angle and no humeral calli in flightless individuals; elytra striate, convex, declivous behind, usually tuberculate or setose or both, seldom smooth; epipleurae distinct.

Hind wing: Wings present or absent, where present, with M-Cu loop and one or two apical detached veins, RP3+4 vein lost; wing articulation characterised by 2Ax subalare tendon attachment point short, narrow and apically rounded; 2BP with transverse crimps on the

medial vein, mesal of the bridge and distal of 2BP, BMP-CuA brace either reduced or modified (for comprehensive overview on hind wing morphology in Trogidae see Browne et al. 1993).

Abdomen: Completely covered by hind wings; with five distinct fused ventral sternites; pygidium concealed by elytra; with seven or eight functional spiracles.

Legs: Profemora enlarged; coxae virtually contiguous; claws simple; tarsi 5-5-5.

Male genitalia: Typically trilobite type but varies from simple to complex and asymmetrical; the basal piece may be longer or shorter than the parameres, membranous or fused dorsally; parameres usually simple and symmetrical; median lobe may be hollow, simple or asymmetrical and varies from complex to highly complex; internal sac small without armature, large and armed or unarmed or large and armed with sclerites; temones present or absent, when present it can be long or short; genital segment is a well-developed genital capsule or a well-developed u-shaped spiculum gastrale.

Larvae: Typically scarabaeiform, white or cream in colour, heavily sclerotized cranium and prominent sclerotized shields on either side of the prothorax; 3-segmented antenna; with well-developed lateral ocelli; distinct or faint fronto-clypeal suture; galea and lacinia distinctly separated; galea 2-segemented; 4-segmented maxillary palpi; presence of maxillary and mandibular stridulatory apparatus; epipharyngeal tormae symmetrical or asymmetrical, fused or divided; left mandible with 2-3 mandibular teeth; spiracles biforous or cribriform, the latter have a closing apparatus; legs four-segmented and well developed, with prominent claw; larvae lack a stridulatory apparatus.

Distribution: Cosmopolitan. Species primarily inhabit the temperate and arid/savanna regions of the world.

Natural history: Adult trogids exhibit thanatosis when alarmed or disturbed, retracting their legs and head and remaining motionless, which probably helps them to escape potential predators (Ratcliffe 1991). Adults are able to stridulate by rubbing a coarse plate (plectrum) on the outer surface of the first ventral segment of the abdomen against a file on the inside margin of their elytra (Vaurie 1955; Lawrence and Britton 1991). Adults of some species are attracted to light. Adults and larvae feed primarily on keratin. Trogids are among the last insects to visit the dried remains of dead animals where adults and larvae may be found feeding on various sources of keratinous matter (e.g. hair, skin, hooves, nails and feathers). Keratin is an important structural component (a fibrous protein) of hair, fur, hooves and feathers. Even though there are records of opportunistic feeding on insects (Young and Hamm 1985; Van Emden 1948) some reports and field observations from Australia indicate

that a group of large flightless species appear to feeds on various insects (or insect remains), mostly ants and termites, rather than carrion (Houston et al. 2009). Surprisingly, none of these large, flightless species appear to have ever been found at carrion, and attempts at feeding them on carcasses were unsuccessful (Houston et al. 2009).

Key to the extant subfamilies, genera and subgenera of adult Trogidae

1. Antennal scape round ..... Troginae … **2**
- Antennal scape elongate ..... Omorginae … **3**
2. Aedeagus with simple, apically divided median lobe, restricted to the Holarctic Region ..... *Trox*
- Aedeagus with complex median lobe, restricted to the Afrotropical Region .... *Phoberus* **stat. rev.**
3. Scutellum oval, clypeus deflexed, pedicel attached apically to scape..... *Polynoncus*
- Scutellum hastate, clypeus reflexed or straight, pedicel attached sub-apically to scape..... *Omorgus* … **4**
4. Clypeus straight ..... *Omorgus* (*Haroldomorgus*)
- Clypeus reflexed **5**
5. Aedeagus with pars basalis fused dorsally..... *Omorgus* (*Afromorgus*)
- Aedeagus with pars basalis membranous dorsally ..... *Omorgus* (*Omorgus*)

SUBFAMILY: **Troginae** MacLeay

Troginae MacLeay 1819: 59; Nikolajev 2005: 322

Type genus: *Trox* Fabricius, 1775: 31

See also Scholtz (1982) for a list of references for the subfamily

Diagnosis

Adults

Length: 4–17mm

Head: Antennal scape round, pedicel apically attached, clypeus straight, triangular or broadly rounded; prostheca on mandibles well-developed.

Pronotum and elytra: setae complex or specialized, usually plumose, spatulate or squamose.

Scutellum: Round or oval, not restricted at base.

Hind wing: With two apically detached veins between the cubitus and first complete anal vein in winged species (for comprehensive overview on hind wing morphology of Trogidae see Browne et al. 1993).
Abdomen: with seven functional spiracles.
Legs: metatibial spur longer than first two tarsal segments, metatarsal setae isolated or sparsely distributed.
Male genitalia: Aedeagus elongate and characteristically arched; basal piece longer than the parameres, evenly sclerotized; parameres simple; median lobe hollow, and simple (in *Trox*) to complex (in *Phoberus*); internal sac small, without armature, and does not extend beyond the median lobe; temones long and thin and but may form a spoon-shaped expansion proximally; genital segment may be a well-developed genital capsule (Holarctic taxa) or a spiculum gastrale (Afrotropical taxa).
Larvae: The larvae of the subfamily can easily be distinguished from members of the other subfamily by their biforous spiracles; an indistinct fronto-clypeal suture; second antennal segment with sensory cone; prothorax with two small lateral lobes; setae on prothoracic margin absent; setae present on the second dorsal lobe on the abdomen (in the dorsal view).
Distribution: The Holarctic Region and the Afrotropical Region. Troginae are absent from Australasian and Neotropical Regions, except for one ubiquitous species, *Trox scaber* (Linnaeus), which was undoubtedly introduced by man (Scholtz 1986b; 1990).
Natural history: Many of the species are often found on carnivore faeces and owl pellets, in birds' nests or in burrows.
Composition: Contains two extant genera, the type genus *Trox* Fabricius and *Phoberus* MacLeay **stat. rev.**, and about 150 species.

GENUS: ***Trox*** Fabricius
Trox Fabricius 1775: 31.
Type species: *Scarabaeus sabulosus* Linnaeus, 1758 (by subsequent designation, Latreille 1810) (Fig 3a).
List of synonyms and references to the genus (and as subgenus) is provided in Scholtz (1982), see also Zidek (2013).

Diagnosis
Length: 4–12mm.
Colour: Flavescent to black, habitus relatively setose.

Head: Frons bituberculate or quadrituberculate, or flat, with setose ridges or smooth; clypeus horizontal, broadly rounded or triangular; antennal scape rounded, attached apically, first segment of club (in lateral view) flat and same width throughout.
Pronotum: Usually not constricted, with base applied closely to elytra; pronotal margins densely setose.
Scutellum: Oval, not restricted at base.
Legs: Hind tibia with one or more teeth or spines externally; metatarsal segment with isolated setae, longest spur on metatibia longer than first two tarsal segments; hind tarsal segment ventrally with only scattered setae, claw with one seta.
Male genitalia: Aedeagus slender, with simple median lobe, usually with apex divided, pars basalis fused dorsally; genital segment in the form of a primitive genital capsule.
Larvae: Members of the genus has the phobae on proximal region of hypopharynx united basally. For diagnosis of Holarctic taxa see Baker (1968: 21), Scholtz and Lumaret (1991) and Shabalin (2013).
Distribution: Widespread throughout the Nearctic and Palaearctic Regions, with a small number of species occurring in the Oriental Region (Fig 3b).
Comments: Although formal testing is required, the Palaearctic and Nearctic species can be roughly divided into six groups based on external morphology and male genitalia (Vaurie 1955; Pittino 1985; Pittino and Kawai 2006; Scholtz et al. 2007). The largest of these groups, the "*terrestris*"-group (Pittino and Kawai 2006), consists of mostly eastern Palaearctic species, but also comprises species from the Nearctic. The second largest group "*hispidus*" is mainly distributed in the Mediterranean. The "*sabulosus*" group consists of eastern Palaearctic species. Another typical Holarctic group is the "*scaber*"-group; it is the most widespread across the Palaearctic and has related species in the Nearctic. The (now) virtually cosmopolitan species, *Trox scaber* (Linnaeus) is included in the latter. The remaining two groups, "*unistriatus*" and "*tuberculatus*" are restricted to the Nearctic (Vaurie 1955).

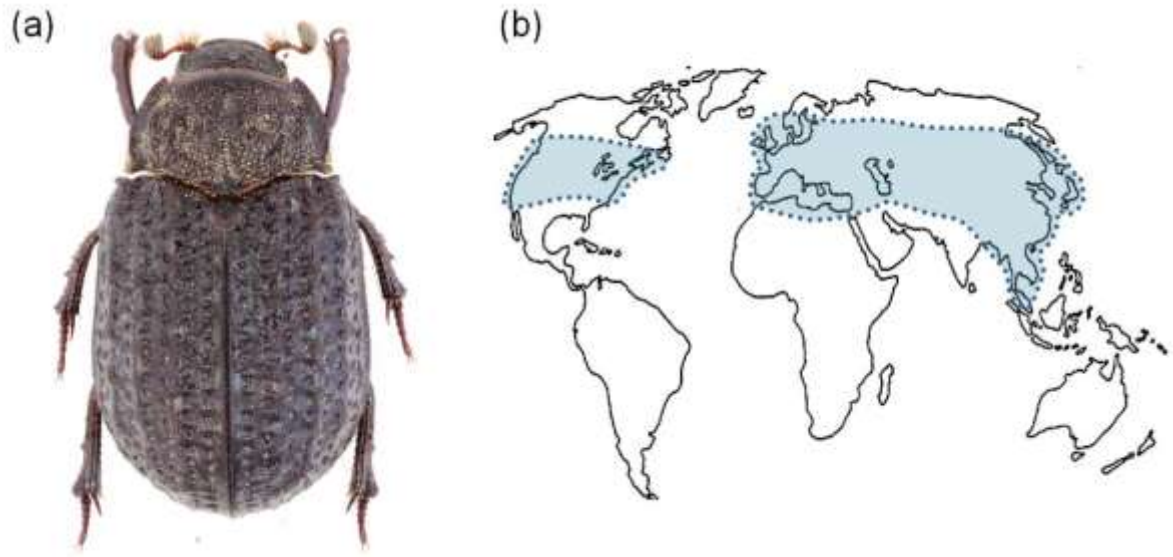

Figure 3. (a) The type species of the genus *Trox* Fabricius, *Trox sabulosus* Linnaeus (b) Distribution of the genus *Trox.*

GENUS: *Phoberus* MacLeay **stat. rev.**

Phoberus MacLeay, 1819: 137-138.

Type species: *Trox horridus* Fabricius, 1775, by monotypy (Fig 4a).

Trox (*Phoberus*): Burmeister, 1876: 264; Preudhomme de Borre, 1886:59; Péringuey, 1900: 453 (*pars*); Arrow, 1912: 53 (*pars*); Scholtz, 1980:17; Scholtz, 1982: 15; Scholtz, 1986a: 361; Scholtz, 1993: 6 [larvae]; Zidek, 2013: 6.

Madagatrox Pittino, 2010: 75. **syn. n.**

Diagnosis

Length: 4–17mm.

Colour: Grey or reddish brown to black.

Head: Clypeus triangular; apex pointed with apical portion bent down at right angles to disk or straight; frons bituberculate, rounded or ridged, setose ridges or smooth; surface of frons and clypeus punctuate; antennal scape rounded or slightly elongate, and pedicel attached to apex of scape (except for *P. brincki* Haaf, where it is attached sub-apically) with setae; eyes large and rounded (diameter of eye approximately half the distance between the eyes) in flight capable species, eye small (diameter approximately one-third the distance between the eyes) in flightless species.

Pronotum: Pronotal margins attenuated anteriorly, smooth or irregular; pronotal sides narrow to broadly flattened; margins densely setose or with fringes of stiff setae or with irregular

setae (as for *P. brincki*), setae spatulate and squamose or pubescent; pronotal surface tomentose to smooth; pronotal length at least half or more the elytral length in flightless species or small relative to abdomen in winged species; pronotal discal area varies from smoothly rounded with ridges and tubercle vestigial to ridges and tubercles distinctly raised and depressions well-defined.

Scutellum: Oval, distinct in winged forms and small in flightless forms.

Elytra: Elongated with sharp humeral angle and distinct humeral calli in winged individuals or rounded with rounded humeral angle and no humeral calli in flightless individuals; sides flattened; lateral margins usually with fringes of setae; even numbered costae prominent with tubercles, or with fused tubercles to form distinct costal ridges; ridges and tubercles usually with tufts of setae; profile convex attaining maximum height in the middle or behind the middle.

Legs: Metatarsal segments ventrally with isolated setae or sparsely setose; longest metatibial spur longer than first two tarsal segments or scarcely longer or not than first tarsal segment; five segmented protarsus, but four-segmented in *Madagatrox* **syn. n.** (the latter is probably a pseudotetramerous condition).

Male genitalia: Aedeagus slender, symmetrical; simple to complex median lobe usually consisting of various blades, plates and hooks; pars basalis fused dorsally, usually as long or longer than parameres; genital segment in a form of a spiculum gastrale.

Larvae: Members of the genus has the phobae on proximal region of hypopharynx not united basally. For diagnosis of Afrotropical taxa see Scholtz (1993: 6).

Distribution: Restricted to Africa, mainly southern Africa and Madagascar (Fig 4b). The majority of the species are distributed along the temperate eastern montane faunal exchange route (Endrödy-Younga 1978), with a few species penetrating into the arid regions of southern Africa (Scholtz 1979a, 1980).

Comments: *Phoberus* MacLeay is restored to genus. Afrotropical (including Madagascan) species are transferred to *Phoberus* (see Appendix A). *Phoberus* is the genus with the highest incidence of flightless species (about 35 % of the genus), making the group morphologically diverse. The genus can be roughly divided into ten informal species-groups based on external morphology, male genital anatomy (Scholtz 1980; Strümpher and Scholtz 2011).

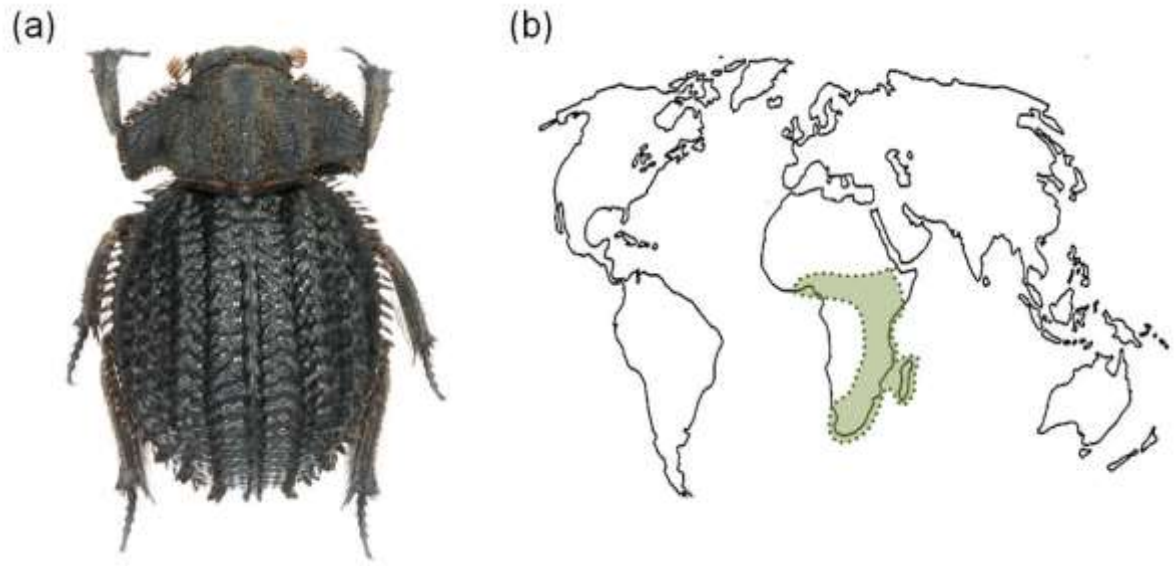

Figure 4. (a) The type species of the genus *Phoberus* MacLeay, *Phoberus horridus* (Fabricius) **comb. nov.** (b) Distribution of the genus *Phoberus*

SUBFAMILY: **Omorginae** Nikolajev
Original spelling and citation: Omorgini Nikolajev 2005: 322
Type genus: *Omorgus* Erichson, 1847: 107

Diagnosis
Length: 6–30mm.
Head: Antennal scape elongate; pedicel attached apically or subapically; clypeus straight, reflexed or deflexed.
Scutellum: Hastate or oval.
Pronotum and elytra: setae simple, straight, elongated and pointed.
Hind wing: With one or two apically detached veins between the cubitus and first complete anal vein (for comprehensive overview on hind wing morphology in Trogidae see Browne et al. 1993).
Abdomen: with eight functional spiracles.
Legs: metatibial spur as long as the first tarsal segments; metatarsal setae dense.
Male genitalia: Aedeagus robust; basal piece shorter than the parameres; pars basalis can be dorsally fused or open; parameres simple, symmetrical, may or may not be fused basally; median lobe may be simple or specialised; internal sac large, armed or unarmed; temones present or absent; genital segment a well-developed u-shaped spiculum gastrale.

Larvae: The larvae of the subfamily can easily be distinguished from members of the other subfamily by their cribriform spiracles; a distinct fronto-clypeal suture; second antennal joint with sensory disc, or small cone and sensory area; prothorax with large single lateral large lobe; setae present on prothoracic margins; setae present on the second dorsal lobe on the abdomen (in the dorsal view); glossa with eight or more setae; two rows of parallel hypopharyngeal phobae present; anterior angle of frons with more than three setae.
Distribution: Occur throughout the arid regions of the southern continents, extending into the southern Nearctic and Oriental Regions.
Composition: Contains two genera, the type genus *Omorgus* Erichson and *Polynoncus* Burmeister.

GENUS: ***Omorgus*** Erichson
Omorgus Erichson, 1847: 111; LeConte, 1854: 211; Baker, 1968: 1; Scholtz, 1986a: 361; Scholtz, 1993:2 [larvae]; Zidek, 2013: 6
A list of references to the genus [as *Trox* (*Omorgus*)] is provided in Scholtz (1982, 1986a, 1986b, 1990).
Type species: *Trox suberosus* Fabricius (by subsequent designation, Lacordaire, 1856).

Diagnosis
Length: 5–30mm.
Colour: Flavescent to black.
Head: Frons bituberculate or smooth; clypeus with rim reflexed; antennal scape elongate, pedicel attached apically; well-developed prostheca on mandibles.
Pronotum: Usually constricted at base; pronotal margins with isolated, pointed, simple setae.
Scutellum: Hastate, constricted at base.
Hind wing: With one apically detached vein (for comprehensive overview on hind wing morphology in Trogidae see Browne et al. 1993).
Legs: Metatarsal segments ventrally with dense setae; longest spur on hind tibia not or scarcely longer than the first tarsal segment.
Male genitalia: Aedeagus varies considerably between continental groups; basal piece membranous (New World/Australasian taxa) or sclerotized (Afro-Oriental taxa) dorsally; parameres usually simple and symmetrical; median lobe simple (New World/Australasian groups) or complex (Afro-Oriental groups); internal sac large, usually armed with sclerites, spines or setae but the armature varies between taxa; sclerites may be present (Afro-Oriental

taxa) or absent (New World/Australasian taxa); temones present (in Afro-Oriental taxa) and absent in (New World/ Australasian taxa).

Larvae: *Omorgus* larvae from different geographical regions can be distinguished from each other by phylogenetically important characters (see Scholtz 1991, 1993)

Distribution: Southern Nearctic, Neotropical, Afrotropical, Oriental and Australasian Regions (Fig 8).

SUBGENUS: *Omorgus* (*Omorgus*) Erichson

Omorgus (*Omorgus*) Erichson: Scholtz, 1986a: 362; Scholtz, 1990: 1404; Scholtz, 1993: 2 [larvae]; Zidek, 2013: 1

Type species: *Trox suberosus* Fabricius (by subsequent designation, Lacordaire, 1856) (Fig 5).

Trox (*Chesas*) Burmeister, 1876: 264; Preudhomme de Borre, 1886: 59; Arrow, 1912: 53

Type species: *Trox pastillarius* Blanchard, 1846, original designation. Syn. by Vaurie (1962: 109, 115).

Trox (*Lagopelus*) Burmeister, 1876: 265; Preudhomme de Borre, 1886: 59; Arrow, 1912: 53

Type species: *Trox ciliatus* Blanchard, 1846, original designation. Syn. by Vaurie (1962: 109, 115).

Trox (*Megalotrox*) Preudhomme de Borre, 1886: 59; Arrow, 1912: 53

Type species: *Trox gigas* Harold, subsequent designation by Scholtz (1982).

Diagnosis

Length: 5–30mm.

Male genitalia: Aedeagus robust; median lobe simple; pars basalis small, membranous dorsally.

Larvae: New World and Australasian taxa are characterised by the concave sensory disc on the second antennal segment (see also Scholtz 1993). For diagnosis of New World and Australasian taxa see Baker (1968: 39) and Scholtz (1991, 1993).

Distribution: Southern Nearctic, Neotropical and Australasian Regions (Fig 8).

Comments: All New World and Australasian species belong to this subgenus.

Figure 5. The type species of the subgenus *Omorgus* (*Omorgus*) Erichson, *O*. (*Omorgus*) *suberosus* Fabricius. Image reproduced from Scholtz (1990).

SUBGENUS: *Omorgus* (*Haroldomorgus*) Scholtz

Omorgus (*Haroldomorgus*) Scholtz, 1986a: 362; Scholtz, 1990: 1418; Zidek, 2013: 6

Type species: *Trox batesi* Harold 1872: 126, by original designation and monotypy (Fig 6).

Diagnosis

Length: 9–10 mm.

Colour: Flavescent.

Head: Frons bituberculate, clypeus horizontal; antennal scape elongate, pedicel attached sub-apically.

Pronotum: Glabrous.

Scutellum: Oval.

Elytra: Smooth, glabrous.

Hind wing: Reduced (for comprehensive overview on hind wing morphology in Trogidae see Browne et al. 1993).

Legs: Metatarsi ventrally with dense setae; longest spur on metatibia not or scarcely longer than first tarsal segment.

Male genitalia: Aedeagus robust, simple, median lobe pointed; pars basalis membranous dorsally.

Larvae: Unknown

Distribution**:** Central to eastern South America (Fig 8).

Comments: *Haroldomorgus* is monotypic. Members of this rare species display incipient winglessness (Browne et al. 1993).

Figure 6. The type species of the subgenus *Omorgus* (*Haroldomorgus*) Scholtz, *O*. (*Haroldomorgus*) *batesi* Harold. Image reproduced from Scholtz (1990).

SUBGENUS: *Omorgus* (*Afromorgus*) Scholtz

Omorgus (*Afromorgus*) Scholtz, 1986a: 362; Scholtz, 1993: 2 [larvae]; Zidek, 2013: 6

Type species: *Trox squalidus* Olivier, 1789: 12 (by subsequent designation, Scholtz, 1986a: 362) (Fig 7).

Afromorgus: Pittino, 2006: 26

Diagnosis

Length: 8–21mm.

Colour: Grey, brown to black.

Head: Clypeus with rim reflexed; antennal scape elongate and pedicel attached sub-apically.

Male genitalia: Aedeagus robust; median lobe complex, with ridges, knobs, foveae; pars basalis large, fused dorsally.

Larvae: Larvae from Oriental-Asia unknown, but African members of the subgenus are characterised by a convex sensory cone on distal end of segment two. For diagnosis of African taxa see Scholtz (1993: 2).

Distribution: Afro-Oriental Regions (Fig 8).

Comments: All the African, Arabian and Oriental species belong to this subgenus.

Figure 7. The type species of the subgenus *Omorgus* (*Afromorgus*) Scholtz, *O*. (*Afromorgus*) *squalidus* Olivier

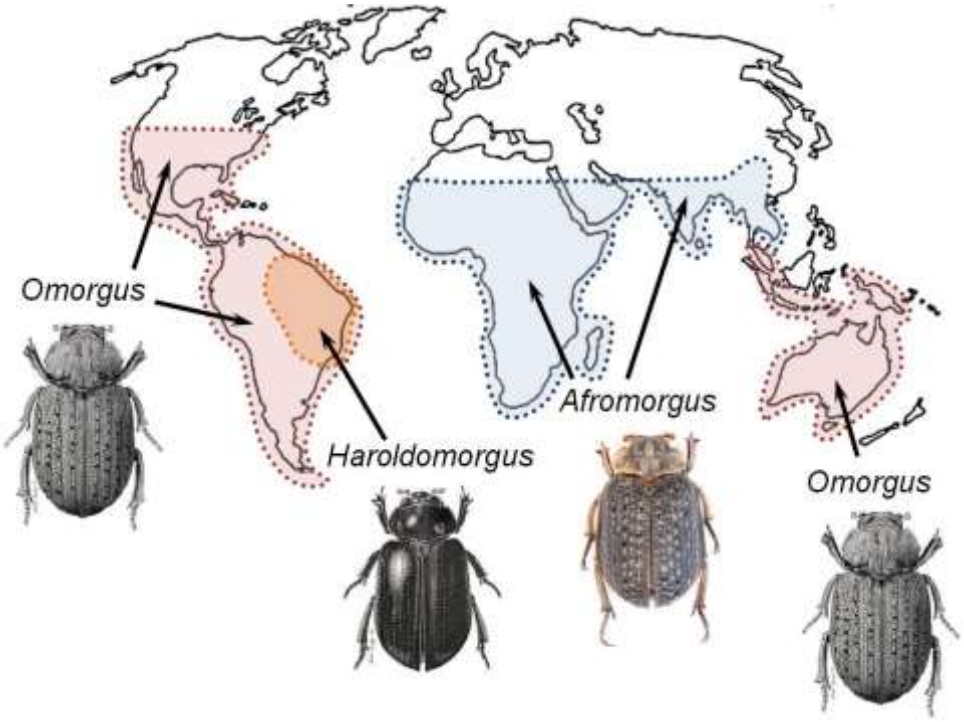

Figure 8. Distribution of the subgenera of *Omorgus* Erichson: *O*. (*Omorgus*), *O*. (*Afromorgus*) and *O*. (*Haroldomorgus*)

GENUS: ***Polynoncus*** Burmeister

Trox (*Polynoncus*) Burmeister, 1876:264 (*pro. parte*); Preudhomme de Borre, 1886:59 (*pro. parte*); Arrow, 1912:53; Scholtz, 1982: 15.

Type species: *Trox pedestris* Harold, 1872:128 (by subsequent designation, Scholtz, 1986a: 362) (Fig 9a).

Polynoncus: Scholtz, 1986a: 362; Scholtz, 1990: 1419; Zidek, 2013: 6.

Diagnosis

Length: 10–20 mm.

Colour: Varies from grey to black.

Head: Frons bituberculate; clypeus with apical portion bent down abruptly, at right angles to disc of clypeus; antennal scape elongate, pedicel attached apically; prostheca on mandibles reduced.

Pronotum: Margins with isolated, pointed, simple setae.

Scutellum: Oval.

Hind wing: With two apically detached veins (for comprehensive overview on hind wing morphology in Trogidae see Browne et al. 1993).

Legs: Metatarsi ventrally with dense setae; longest spur on metatibia, not or scarcely longer than first tarsal segment.

Male genitalia: Aedeagus robust, complex; with the basal piece shorter than the parameres; pars basalis membranous dorsally; parameres are simple and symmetrical and not fused basally; median lobe specialised and varies from complex to highly complex, narrow, ligulate, sometimes asymmetrical; temones short; genital segment a u-shaped spiculum gastrale; internal sac large, armed or unarmed.

Larvae: For diagnosis of the genus see Scholtz and Peck (1990).

Distribution**:** Neotropical Region. Members of the genus are endemic to South America (Fig 9b).

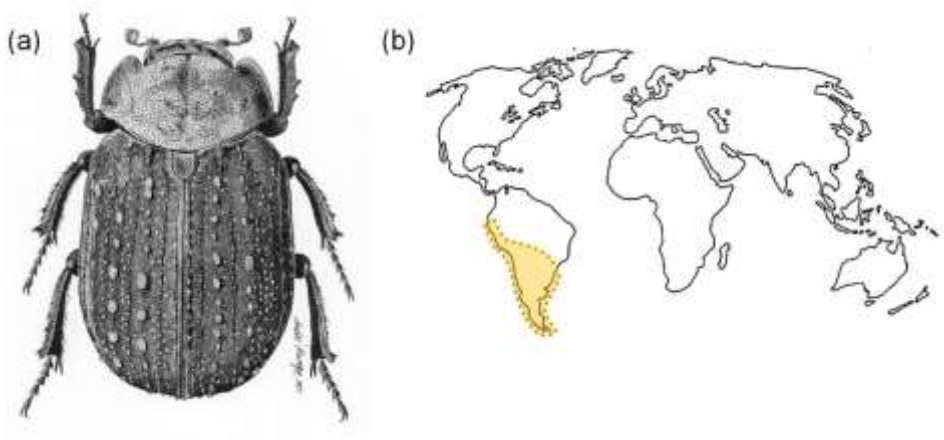

Figure 9. (a) The type species of the genus *Polynoncus* Burmeister, *Polynoncus pedestris* (Harold) (b) Distribution of the genus *Polynoncus.* Image of type species reproduced from Scholtz (1990).

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Appendix A

List of Afrotropical (including Madagascar) species belonging to the genus *Phoberus* MacLeay stat. rev. (in alphabetical order)

All new combinations resulting from restoring *Phoberus* to a monophyletic genus are indicted below. *Species previously in the genus *Trox* (Fabricius). **Species previously in the genus *Madagatrox* Pittino. Synonyms not listed: for details on synonyms see Scholtz (1982) and Zidek (2013).

Genus: *Phoberus* MacLeay, 1819: 137. **stat. rev.**
Type species: *Trox horridus* (Fabricius 1775: 818), by monotypy.
Trox (*Phoberus*): Burmeister 1876: 264; Preudhomme de Borre 1886: 59; Péringuey 1900: 453 (*pars*); Arrow 1912: 53 (*pars*); Scholtz 1980: 17; Scholtz 1982: 15; Scholtz 1986a: 361; Zidek 2013: 6.
Madagatrox Pittino 2010: 75. **syn. n.**

aculeatus (Harold 1872: 37) **comb. nov.**
arcuatus (Haaf 1953: 323) **comb. nov.**
braacki (Scholtz 1980: 87) **comb. nov.**
brincki (Haaf 1958a: 475) **comb. nov.**
caffer caffer (Harold 1872: 41) **comb. nov.**
caffer lilianae, (Scholtz 1980: 96) **comb. nov.**
* *capensis* (Scholtz 1979: 174) **comb. nov.**
consimilis (Haaf 1953: 324) **comb. nov.**
cyrtus (Haaf 1953: 333) **comb. nov.**
elmariae (van der Merwe and Scholtz 2005: 184) **comb. nov.**
* *fascicularis fascicularis* (Wiedemann 1821: 129) **comb. nov.**
* *fascicularis rowei* (Scholtz 1980: 78) **comb. nov.**
gunki (Scholtz 1980: 86) **comb. nov.**
horridus (Fabricius, 1775: 818) **comb. nov.**
levis (Haaf 1953: 325) **comb. nov.**
luridus (Fabricius 1781: 496) **comb. nov.**
miliarius (Gmelin 1790: 1587) **comb. nov.** (*Incertae sedis* - see Scholtz, 1980: 99)

montanus (Kolbe 1891: 22) **comb. nov.**

mozalae (Strümpher & Scholtz 2009: 73) **comb. nov.**

nama (Kolbe 1908: 125) **comb. nov.**

* *nanniscus* (Péringuey 1900: 458) **comb. nov.**

* *nasutus* (Harold 1872: 34) **comb. nov.**

* *natalensis* (Haaf 1954: 97) **comb. nov.**

necopinus (Scholtz 1986b: 29) **comb. nov.**

ngomensis (van der Merwe & Scholtz 2005: 182) **comb. nov.**

nigrociliatus nigrociliatus (Kolbe 1904: 292) **comb. nov.**

nigrociliatus nyansanus (Haaf 1953: 330) **comb. nov.**

nigrociliatus nyassicus (Haaf 1953: 330) **comb. nov.**

penicillatus (Fahraeus 1857: 383) **comb. nov.**

* *perrieri* (Fairmaire 1899: 519) **comb. nov.**

planicollis (Haaf 1953: 337) **comb. nov.**

puncticollis (Haaf 1953: 330) **comb. nov.**

pusillus (Péringuey 1908: 634) **comb. nov.**

quadricostatus (Strümpher & Scholtz 2009: 76) **comb. nov.**

** *ranotsaraensis* (Pittino 2010: 77) **comb. nov.**

* *rhyparoides* (Harold 1872: 32) **comb. nov.**

* *rudebecki* (Haaf 1958a: 474) **comb. nov.**

squamiger (Roth 1851: 133) **comb. nov.**

sternbergi (van der Merwe & Scholtz 2005: 183) **comb. nov.**

* *strigosus* (Haaf 1953: 319) **comb. nov.**

sulcatus (Thunberg 1787: 38) **comb. nov.**

talpa (Fahraeus 1857: 380) **comb. nov.**

youngai (Strümpher & Scholtz 2011: 340) **comb. nov.**

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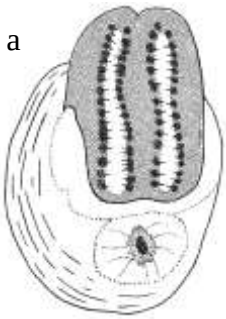
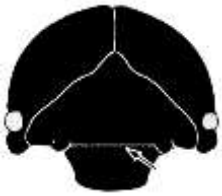
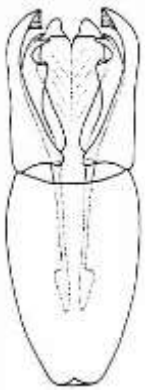
Appendix B

Phylogenetically important larval and adult characters of subfamilies, genera and subgenera.

Subfamily: Troginae ° Antennal scape round ° Metatibial spur longer than first two tarsal segments ° With complex body setae (plumose, spatulate or squamose) ° With five autapomorphic wing characters (Browne et al. 1993) † Spiracle Biforous (a) † Fronto-clypeal suture indistinct (b) † Setae absent on the second mesothoracic dorsal lobe **Genus: *Trox*** ° Median lobe simple ° Genital segment in the form of a primitive genital capsule † Phobae on proximal region of hypopharynx united basally **Genus: *Phoberus* stat. rev.** ° Median lobe exhibiting complex structure with hooks, blades and spines (c) ° Genital segment in the form of a spiculum gastrale † Phobae on proximal region of hypopharynx not united basally	a  b  c 
Subfamily: Omorginae ° Antennal scape elongate ° Metatibial spur as long as first two tarsal segments ° Metatarsal setae dense ° With 27 synapomorphic wing characters (Browne et al. 1993) † Spiracle Cribriform (d) † Fronto-clypeal suture distinct † Setae present on the second mesothoracic dorsal lobe **Genus: *Omorgus*** ° Pedicel attachment – sub-apical (e)	d  e 

° Wing venation – one apical detached vein

° With 8 autapomorphic wing characters (Browne et al. 1993)

† 2nd antennal joint with sensory disc (f)

† Left mandible with three mandibular teeth (g)

† Haptolachus with sensory cone

† Epicranial stem long

† Epipharynx shape, complexity – rounded , bilobed

† Setae on prothoracic disk – present

Subgenus: *Afromorgus*

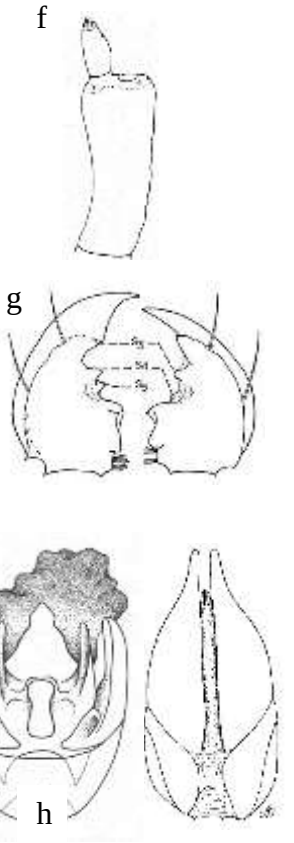
° Median lobe complex usually characterised by dorsal knobs, fovea and or ridges, frequently with erect lamina on either side of median lobe (features absent in *Omorgus* s.s.)

° Pars basalis forms an unbroken sclerified segment (h) (in *Omorgus* s.s. divided median membranous lamina)

† Antenna with convex sensory cone on distal end of segment two

Subgenus: *Haroldomorgus*

° With three autapomorphic wing characters (= reductions) which may be indicative of incipient flightlessness (Browne et al. 1993)



(Afromorgus) (Omorgus)

Genus: *Polynoncus*

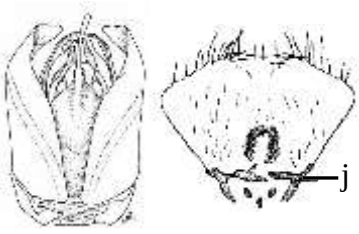
° Median lobe complex, specialised, even asymmetrically (i)

° Clypeus deflexed

° With two autapomorphic wing characters (Browne et al. 1993)

† 2nd antennal joint – sensory cone and area

† Epipharyngeal tormae – asymmetrical, divided (j)



i

○ = Adult characters, † = Larval characters

Images reproduced from: (Baker 1968; Scholtz 1980, 1990, 1993; Scholtz and Peck 1990; Browne and Scholtz 1999; Grebennikov and Scholtz 2004; Ratcliffe and Paulsen 2008)

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