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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. The family is confirmed as consisting of 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 Afrotropical (including Madagascan endemic) species; *Afomorgus* 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 in Appendix A.

Keywords

Afrotropical; Holarctic; keratin-feeding; *Omorgus*; *Phoberus*; *Polynoncus*; *Trox*

Introduction

Trogidae are a small family within the very large and diverse superfamily Scarabaeoidea (Browne & 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 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 & Caveney 1988; Hughes & 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,b, 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,b), 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 Palearctic 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, 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, see Baker (1968), Vaurie (1955) and Scholtz (1980, 1986a,b, 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*, which however was 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 synonymous with *Trox* (Lacordaire 1856; Harold 1872; Horn 1874; Loomis 1922); a subgenus of *Trox* (Gerstaecker 1873; Burmeister 1876; Péringuey 1900, 1908; Arrow 1912; Balthasar 1936; Robinson 1940; Scholtz 1980, 1982), or several species groups (Haaf 1953, 1954a; Vaurie 1955, 1962; 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-1980s classification of the Trogidae 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 (e.g., Vaurie 1955), (2) as a single genus (*Trox*) with several distinct subgenera (e.g., Burmeister 1876; Scholtz 1982), or (3) two genera (*Trox* and *Omorgus*) with unspecified internal relationships (e.g., 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 *Polynoncus* and *Omorgus* (with three subgenera, *Omorgus*, *Haroldomorgus* Scholtz and *Afromorgus* Scholtz).

Scholtz (1986a) found no phylogenetic justification for the retention of *Glareis* and *Cryptogenius* within Trogidae, because they shared no synapomorphies with *Trox*. Scholtz et al. (1987a, b) subsequently placed *Glareis* in a monotypic family, Glaresidae Kolbe, and transferred *Cryptogenius* to Hybosoridae Erichson. The family Glaresidae was until recently treated by some authors as a subfamily of Trogidae (Smith et al. 2006; Ratcliffe & Paulsen 2008), however several studies have clearly demonstrated its phylogenetic independence (Scholtz et al. 1994; Browne & Scholtz 1999; Bai et al. 2012a, b, Ahrens et al. 2014).

A series of studies that followed Scholtz (1986a) supported these findings: Scholtz & Peck (1990) and Grebennikov & Scholtz (2004) examined larval characters for the Trogidae and the basal groups in the Scarabaeoidea respectively; d'Hotmann & Scholtz (1990) assessed the phylogenetic significance of male genitalia; Nel & 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 & 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 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) 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

Our 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 & 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.

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). The subfamily Troginae is characterised by a round antennal scape, a metatibial spur longer than the first two tarsomeres, elytra and pronotum with complex body setae (plumose, spatulate or squamose), as well as several wing characters; the larvae are characterised by having biforous spiracles; an indistinct fronto-clypeal suture and the setae absent on the second mesothoracic dorsal lobe. The subfamily Omorginae is defined by an elongated antennal

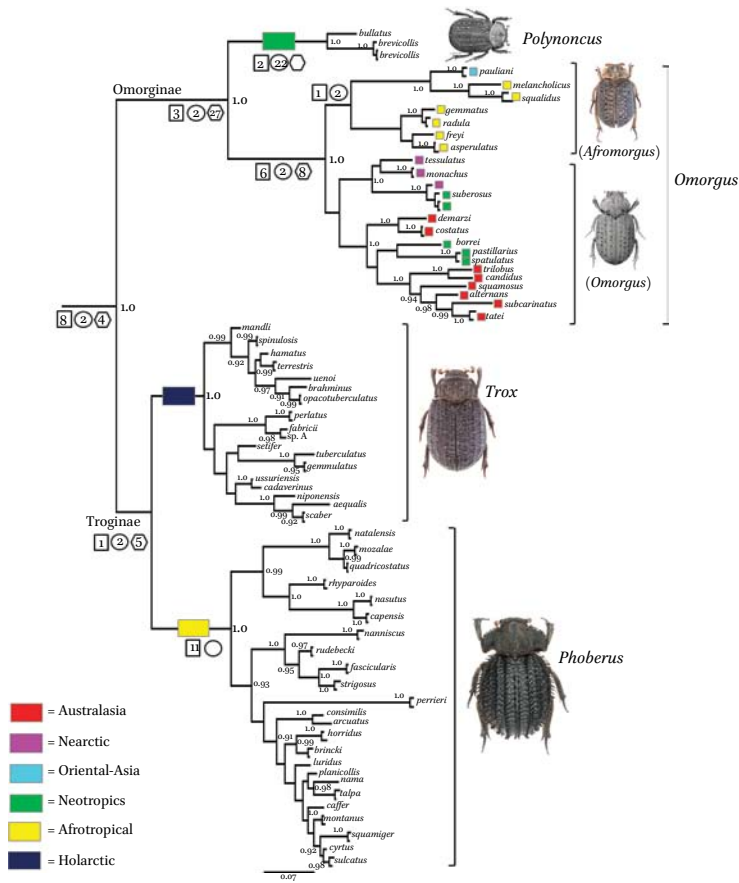


Fig. 1. Molecular phylogeny of the Trogidae (redrawn from Strümpher et al. 2014b). Numbers next to each node are the posterior probability support. Only nodes with posterior probabilities $\geq 90\%$ are shown. Images depict the type species of the genus or subgenus. Synapomorphic character sets (see Strümpher et al. 2014b) which unite each node are plotted on the phylogram. Branches colour-coded for geographic distributions. This figure is published in colour in the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/journals/1876312x>.

scape, a metatibial spur as long as the first two tarsomeres, 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 (Fig. 1). Two monophyletic lineages within each subfamily were clearly diagnosable by synapomorphies (Fig. 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. We maintain the status of both subfamilies as currently defined by Nikolajev (2005).

Subgenus

Genus

Subfamily

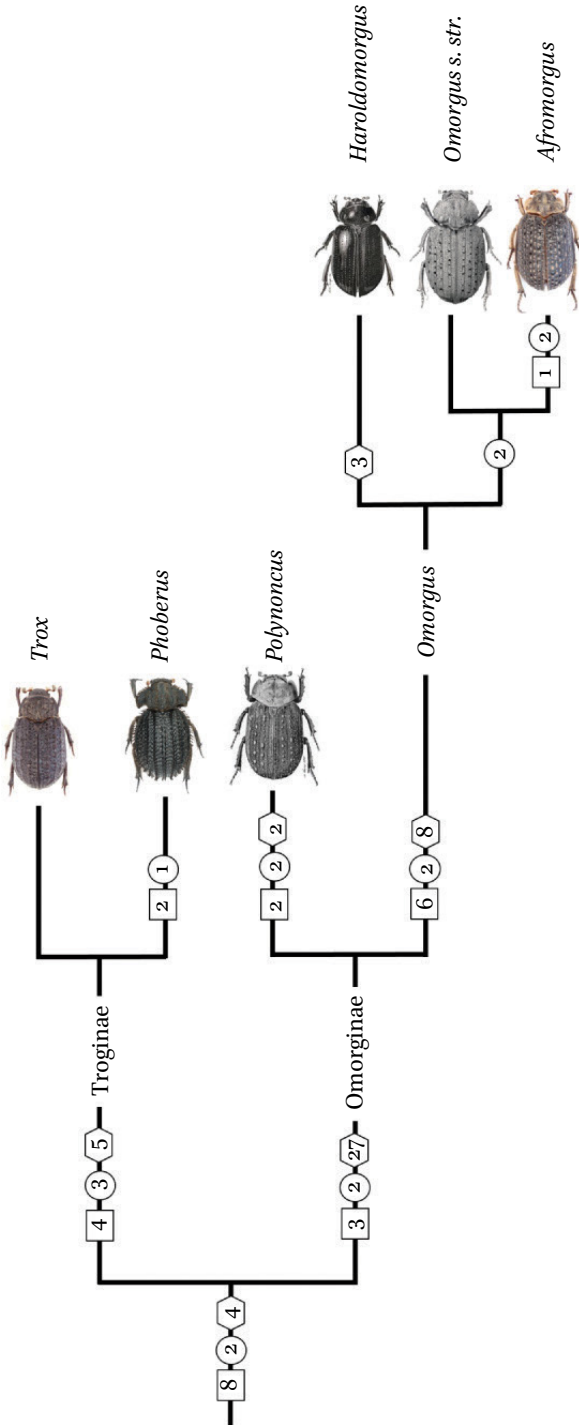


Fig. 2. Proposed classification of the Trogidae based on the phylogenetically important morphological characters and the molecular phylogeny presented by Strümpher et al. (2014b). The larval (boxes), adult (circles) and hind-wing (hexagons) synapomorphic characters which unite each node are plotted on the phylogram. Numbers represent the number of characters that unite each clade. For details on larval characters see Scholtz & Peck (1990), Scholtz (1993) and Grebennikov & Scholtz (2004); for adult (excluding hind wing) characters, see Scholtz (1986a) and Browne & Scholtz (1999); for hind-wing characters, see Browne et al. (1993) and Browne & Scholtz (1995). Images depict the type species of the genus or subgenus. This figure is published in colour in the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/journals/1876312x>.

Trox

The genus *Trox* was described by Fabricius (1775) for the Palaearctic species *T. sabulosus* (Linnaeus). The defining adult and larval characters of this genus (in the strictest sense), which essentially distinguished Holarctic (and a small number of Afrotropical) trogid species from those of other zoogeographic regions, were: (for adults) oval scutellum; round antennal scape; apical attachment of pedicel to scape; reticulated eyes; base of pronotum not restricted; quadrangular serrated hind legs; metatibial spur longer than first tarsomere; adults usually small (4–12 mm) (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 he therefore divided it into 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 known at the time to the subgenus *Phoberus*. The remaining nine species (*Trox nasutus* Harold, *T. capensis* Scholtz, *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 the 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*.

We 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*) from the nomenclatural hierarchy, since Troginae and *Trox* would otherwise be defined by the same synapomorphies. Robinson's monotypic Nearctic genus *Pseudotrox* was synonymised with *Trox* (Vaurie 1955), a decision that is not at odds with our proposals. Similarly, based on these results we also reinstate the genus *Phoberus* **stat. rev.** to accommodate all the Afrotropical species (Scholtz 1980, 1982, 1986b, 1993; van der Merwe & Scholtz 2005; Strümpher & Scholtz 2009, 2011). This also has the advantage of removing an uninformative level (subgenus *Phoberus*) from 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 of *Phoberus* (Strümpher & 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 foveae) 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 protarsomere is deeply recessed in the apex of the foretibia, 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, we 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), its morphological description suggests very strongly that phylogenetic analysis would place it in or very near the *natalensis* group within the *Phoberus* clade (Strümpher & 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, we 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 & 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 & Peck 1990; Browne et al. 1993), we 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* in the Afrotropical and Oriental Regions. The molecular phylogeny of Strümpher et al. (2014), which did not include *Haroldomorgus*, shows that *Omorgus* comprises 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 of the subgenera and their clear morphological diagnosability (Scholtz 1986a, 1993; Scholtz & Peck 1990; Browne et al. 1993), we 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 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 *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 alate 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 that 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 for drawing any concrete conclusions (Strümpher et al. 2014b), and we prefer to wait for unequivocal evidence rather than to risk creating unnecessary synonyms. Therefore, *Omorgus* s. str. is retained as the nominal subgenus of *Omorgus* and the current synonymies of *Chesas*, *Lagopelus* and *Megalotrox* (all with *Omorgus* s. str.) are all accepted.

Omorgus (*Haroldomorgus*)

Specimens of this rare monotypic subgenus were not included in the molecular phylogeny of the Trogidae, and without molecular data its placement 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 we 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 unstable taxonomic history. It was originally described as a subgenus of *Omorgus* (Scholtz 1986a), elevated to genus (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). We intuitively follow the classification system for the genus *Omorgus* and its subgenera as proposed by Scholtz (1986a; see also Zidek 2013). *Afromorgus* is therefore 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 & 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 mandates the same status for *Polynoncus* in phylogenetic systematics.

Fossils

The fossil taxa are not dealt with in this paper. Details concerning them 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 family Trogidae is accepted as consisting of two subfamilies, Omorginae and Troginae, following Nikolajev (2005). The subgenus

Phoberus is restored to genus, and the subgenus *Trox* becomes a separate genus because of the promotion of *Phoberus*. The Afrotropical species of *Trox* are transferred to *Phoberus*; and the Madagascan genus *Madagatrox* is synonymised with *Phoberus*, with its only species being 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. We 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).

Diagnosis

Length: 4–30 mm.

Colour: Flavescent, reddish brown, grey or black.

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

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

Scutellum: Hastate or oval.

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

Hind wing: Present or absent, if present then 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 medial vein, mesial of 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 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 trilobed, but vary from simple to complex and asymmetrical; basal piece either longer or shorter than 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 either small and without armature, or large and armed or unarmed, or large and armed with sclerites; temones present or absent, if present then long or short; genital segment either well-developed genital capsule or well-developed U-shaped spiculum gastrale.

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

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

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 ventrite against a file on the inside margin of the elytra (Vaurie 1955; Lawrence & Britton 1991). Adults of some species are attracted to lights. 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 & Hamm 1985, Van Emden 1948), some reports and field observations from Australia indicate that a group of large flightless species appears to feeds on various insects (or insect remains), mostly ants and termites, rather than on carrion (Houston et al. 2009). Surprisingly, none of these large, flightless species appear to have ever been found at carrion, and attempts to make them feed 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 Holarctic Region

Trox

- Aedeagus with complex median lobe; restricted to Afrotropical Region *Phoberus* **stat. rev.**
- 3. Scutellum oval, clypeus deflexed, pedicel attached apically to scape *Polynoncus*
- Scutellum hastate, clypeus reflexed or straight, pedicel attached subapically 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: 4–17 mm.

Head: Antennal scape round, pedicel attached apically, 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 constricted at base.

Hind wing: With two apically detached veins between cubitus and first complete anal vein in alate 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 tarsomeres combined; metatarsal setae isolated or sparse.

Male genitalia: Aedeagus elongate and characteristically arched; basal piece longer than parameres, evenly sclerotized; parameres simple; median lobe hollow and simple (in *Trox*) to complex (in *Phoberus*); internal sac small, without armature, not extending beyond median lobe; temones long and thin, but may form a spoon-shaped expansion proximally; genital segment either well-developed genital capsule (Holarctic taxa) or spiculum gastrale (Afrotropical taxa).

Larvae: Easily distinguishable from Omorginae by their biforous spiracles; indistinct fronto-clypeal suture; second antennomere with sensory cone; prothorax with two small lateral lobes; setae on prothoracic margin absent; setae present on second dorsal lobe of abdomen (in dorsal view).

Distribution: Holarctic and Afrotropical Regions. Absent from Australasian and Neotropical Regions, except for *Trox scaber* (Linnaeus), which was undoubtedly introduced by man (Scholtz 1986b, 1990).

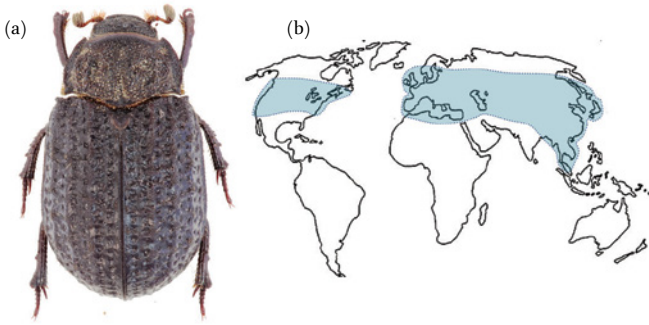


Fig. 3. (a) The type species of the genus *Trox* Fabricius, *Trox sabulosus* Linnaeus (b) Distribution of the genus *Trox*. This figure is published in colour in the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/journals/1876312x>.

Natural history: Many of the species are often found on carnivore faeces and owl pellets, in birds' nests or in burrows.

Composition: About 150 species in two extant genera, the type genus *Trox* Fabricius and *Phoberus* MacLeay **stat. rev.**

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: 4–12 mm.

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, pedicel attached apically, first segment of club (in lateral view) flat and same width throughout.

Pronotum: Usually not constricted, with base appressed closely to elytra; pronotal margins densely setose.

Scutellum: Oval, not constricted at base.

Legs: Metatibia with one or more teeth or spines externally; metatarsus with isolated setae, longest metatibial spur exceeds length of first two tarsomeres combined; metatarsomere ventrally only sparsely setose, claw with one seta.

Male genitalia: Aedeagus slender, with simple median lobe, usually with apex divided, pars basalis fused dorsally; genital segment in form of primitive genital capsule.

Larvae: Phobae on proximal region of hypopharynx united basally. For diagnosis of Holarctic taxa see Baker (1968: 21), Scholtz & Lumaret (1991) and Shabalin (2013).

Distribution: Widespread throughout 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 & Kawai 2006; Scholtz et al. 2007). The largest of these, the “*terrestris*” group (Pittino & Kawai 2006), consists of mostly eastern Palaearctic species, but contains also some Nearctic species. The second largest group, “*hispidus*”, is mainly Mediterranean. The “*sabulosus*” group consists of eastern Palaearctic species. Another typical Holarctic group is the “*scaber*” group, widespread across the Palaearctic and with related species in the Nearctic. *Trox scaber* (Linnaeus) is now virtually cosmopolitan. The remaining two groups, “*unistriatus*” and “*tuberculatus*”, are restricted to the Nearctic (Vaurie 1955).

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 1986a: 361, Zidek 2013: 6.

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

Diagnosis

Length: 4–17 mm.

Colour: Grey or reddish brown to black.

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

Pronotum: Margins attenuated anteriorly, smooth or irregular; sides narrow to broadly flattened; margins densely setose, or with fringes of stiff setae, or with scattered setae (as in *P. brincki*), setae spatulate and squamose or pubescent; surface tomentose to smooth; length at least half or more of elytral length in flightless species, or small relative to abdomen in winged species; discal area varies from smoothly rounded with ridges and vestigial tubercles to ridges and tubercles distinctly raised and depressions well-defined.

Scutellum: Oval, relatively large in winged forms and small in flightless forms.

Elytra: Elongated, with sharp humeral angle and distinct humeral calli in winged taxa, or rounded, with rounded humeral angle and no humeral calli in flightless taxa; 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 at or behind midlength.

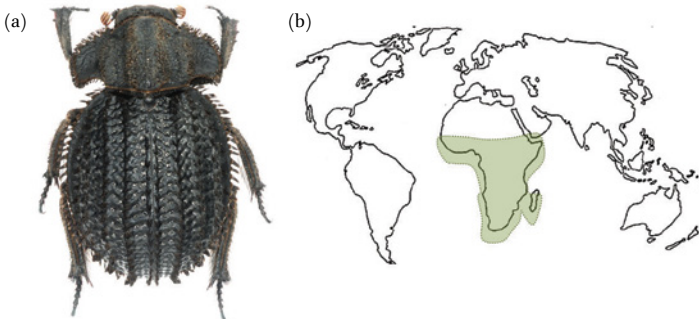


Fig. 4. (a) The type species of the genus *Phoberus* MacLeay, *Phoberus horridus* (Fabricius) **comb. nov.** (b) Distribution of the genus *Phoberus*. This figure is published in colour in the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/journals/1876312x>.

Legs: Metatarsomeres ventrally with isolated setae or sparsely setose; longest metatibial spur either longer than first two tarsomeres combined, or scarcely longer, or no longer than first tarsomere; 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 form of spiculum gastrale.

Larvae: 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). Most species are distributed along the temperate eastern montane faunal exchange route (Endrödy-Younga 1978), with a few penetrating into the arid regions of southern Africa (Scholtz 1979a, 1980).

Comments: *Phoberus* is restored to genus. Afrotropical (including Madagascan) species are transferred to *Phoberus* (see Appendix A). *Phoberus* has the highest incidence of flightless species (about 35%), making the group morphologically diverse. The genus can be roughly divided into 10 informal species groups based on external morphology and male genital anatomy (Scholtz 1980; Strümpher & Scholtz 2011).

SUBFAMILY: **Omorginae** Nikolajev

Original spelling and citation: Omorgini Nikolajev, 2005: 322.

Type genus: *Omorgus* Erichson, 1847: 107.

Diagnosis

Length: 6–30 mm.

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 cubitus and first complete anal vein (for comprehensive overview of hind wing morphology in Trogidae, see Browne et al. 1993).

Abdomen: With eight functional spiracles.

Legs: Metatibial spur as long as first tarsal segment; metatarsal setae dense.

Male genitalia: Aedeagus robust; basal piece shorter than parameres; pars basalis dorsally fused or open; parameres simple, symmetrical, may or may not be fused basally; median lobe either simple or specialised; internal sac large, armed or unarmed; temones present or absent; genital segment well-developed, U-shaped spiculum gastrale.

Larvae: Distinguished from those of Troginae by their cribriform spiracles; distinct fronto-clypeal suture; second antennal joint with sensory disc or small cone and sensory area; prothorax with single large lateral lobe; setae present on prothoracic margins and on second dorsal lobe of abdomen (in 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: Throughout arid regions of southern continents, extending into southern Nearctic and Oriental Regions.

Composition: Two genera, type genus *Omorgus* Erichson and *Polynoncus* Burmeister.

GENUS: ***Omorgus*** Erichson

Omorgus Erichson, 1847: 111; LeConte 1854: 211, Baker 1968: 1, Scholtz 1986a: 361, 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: 5–30 mm.

Colour: Flavescent to black.

Head: Frons bituberculate or smooth; clypeus with rim reflexed; antennal scape elongate, pedicel attached apically; well-developed prosthema 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 of hind wing morphology in Trogidae, see Browne et al. 1993).

Legs: Metatarsomeres ventrally with dense setae; longest metatibial spur either no longer or scarcely longer than first tarsomere.

Male genitalia: Aedeagus varies considerably between continental groups; basal piece membranous in New World/Australasian taxa or dorsally sclerotized in Afro-Oriental taxa; parameres usually simple and symmetrical; median lobe simple in New World/Australasian groups or complex in Afro-Oriental groups; internal sac large, usually armed with sclerites, spines or setae, armature varies among taxa; sclerites present in

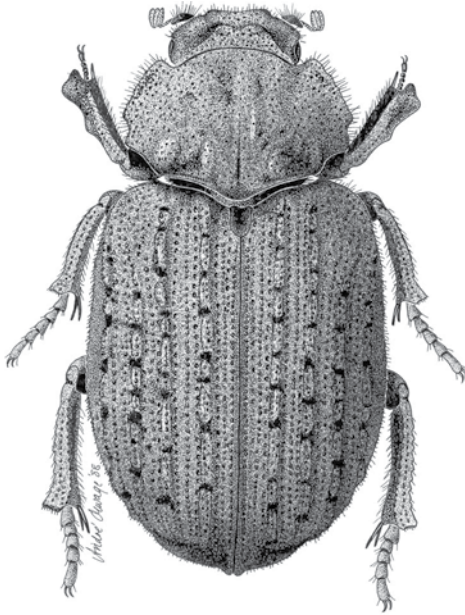


Fig. 5. The type species of the subgenus *Omorgus* (*Omorgus*) Erichson, *O. (Omorgus) suberosus* Fabricius. Image redrawn from Scholtz (1990).

Afro-Oriental taxa, absent in New World/Australasian taxa; temones present in Afro-Oriental taxa, 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, 1990: 1404, 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: 5–30 mm.

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

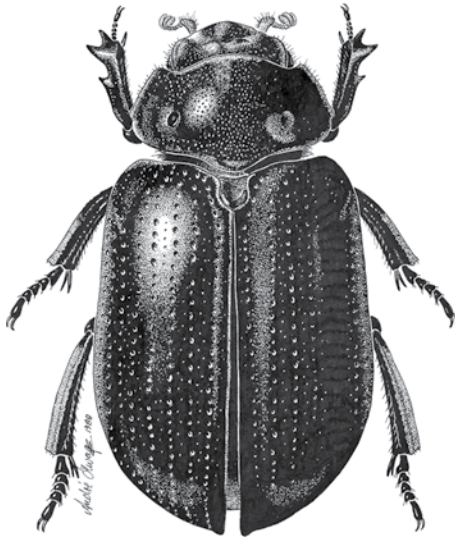


Fig. 6. The type species of the subgenus *Omorgus* (*Haroldomorgus*) Scholtz, *O. (Haroldomorgus) batesi* Harold. Image redrawn from Scholtz (1990).

Larvae: New World and Australasian taxa characterised by concave sensory disc on second antennomere (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.

SUBGENUS: *Omorgus* (*Haroldomorgus*) Scholtz

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

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

Diagnosis

Length: 9–10 mm.

Colour: Flavescent.

Head: Frons bituberculate, clypeus horizontal; antennal scape elongate, pedicel attached subapically.

Pronotum: Glabrous.

Scutellum: Oval.

Elytra: Smooth, glabrous.

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

Legs: Metatarsi ventrally with dense setae; longest metatibial spur either no longer or scarcely longer than first tarsomere.

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

Larvae: Unknown.



Fig. 7. The type species of the subgenus *Omorgus* (*Afromorgus*) Scholtz, *O. (Afromorgus) squalidus* Olivier. This figure is published in colour in the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/journals/1876312x>.

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

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

SUBGENUS: *Omorgus (Afromorgus)* Scholtz

Omorgus (Afromorgus) Scholtz, 1986a: 362; Zidek 2013: 6.

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

Afromorgus: Pittino 2006: 26.

Diagnosis

Length: 8–21 mm.

Colour: Grey, brown to black.

Head: Clypeus with rim reflexed; antennal scape elongate, pedicel attached subapically.

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

Larvae: Larvae from Oriental Asia unknown; in African species characterised by convex sensory cone on distal end of second antennomere. For diagnosis of African taxa see Scholtz (1993: 2).

Distribution: Afrotropical and Oriental Regions (Fig. 8).

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

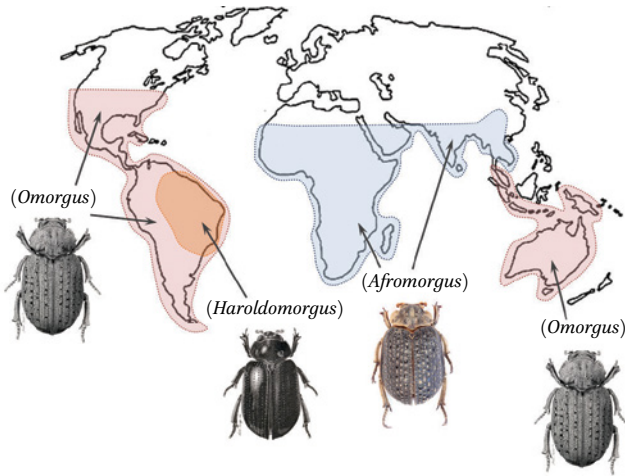


Fig. 8. Distribution of the subgenera of *Omorgus* Erichson: *O.* (*Omorgus*), *O.* (*Afromorgus*) and *O.* (*Haroldomorgus*). This figure is published in colour in the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/journals/1876312x>.

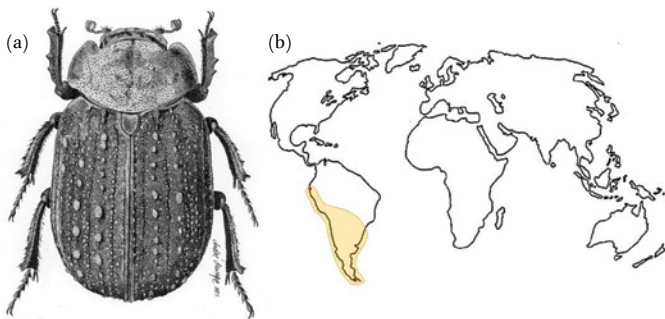


Fig. 9. (a) The type species of the genus *Polynoncus* Burmeister, *Polynoncus pedestris* (Harold). (b) Distribution of the genus *Polynoncus*. Image of type species redrawn from Scholtz (1990). This figure is published in colour in the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/journals/1876312x>.

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, 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 angle to disc; 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 of hind wing morphology in Trogidae see Browne et al. 1993).

Legs: Metatarsi ventrally with dense setae; longest metatibial spur either no longer or scarcely longer than first tarsomere.

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

Larvae: For diagnosis see Scholtz & Peck (1990).

Distribution: Neotropical Region, endemic to South America (Fig. 9b).

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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, 1982: 15, 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 & 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.** (*Incerta 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.**
 * *rhyparoides* (Harold, 1872: 32) **comb. nov.**
 ** *ranotsaraensis* (Pittino, 2010: 77) **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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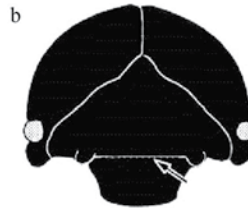
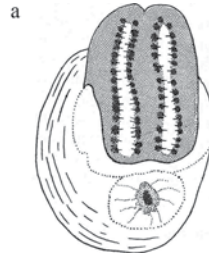
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Appendix B

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)
- † Fronto-clypeal suture indistinct (a)
- † Spiracle biforous (b)
- † Setae absent on second mesothoracic dorsal lobe

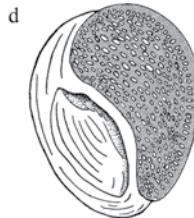


Genus: **Trox**

- Median lobe simple
- Genital segment in 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 form of a spiculum gastrale
- † Phobae on proximal region of hypopharynx not united basally



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**

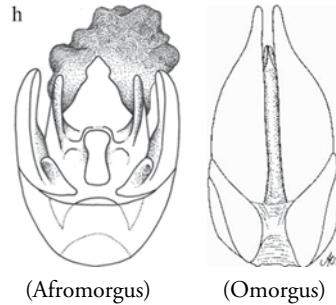
- Pedicel attachment – subapical (e)
- Wing venation – one apical detached vein
- With 8 autapomorphic wing characters (Browne et al. 1993)
- † 2nd antennal joint with sensory disc (f)
- † Left mandible with three mandibular teeth (g)
- † Haptolachus with sensory cone
- † Epicranial stem long
- † Epipharynx shape, complexity – rounded, bilobed
- † Setae on prothoracic disk – present



(Continued)

Appendix B: (*Cont.*)Subgenus: *Afromorgus*

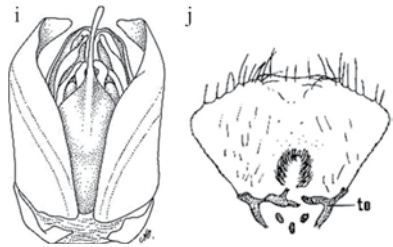
- ° Median lobe complex, usually characterised by dorsal knobs, foveae and/or ridges, frequently with erect lamina on either side of median lobe (features absent in *Omorgus* s.str.)
- ° Pars basalis forms unbroken sclerified segment (h) (in *Omorgus* s.str. divided median membranous lamina)
- † Antenna 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)

Genus: *Polynoncus*

- ° Median lobe complex, specialised, even asymmetrical (i)
- ° Clypeus deflexed
- ° With two autapomorphic wing characters (Browne et al. 1993)
- † 2nd antennal joint – sensory cone and area
- † Epipharyngeal tormae – asymmetrical, divided (j)



° Adult characters, † larval characters. Images redrawn from Baker (1968), Scholtz (1980, 1990, 1993), Scholtz & Peck (1990), Browne & Scholtz (1999), Grebennikov & Scholtz (2004) and Ratcliffe & Paulsen (2008).

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