



Defining new dung beetle tribes to resolve discrepancies between phylogeny and tribal classification in the subfamily Scarabaeinae (Coleoptera: Scarabaeidae)

ADRIAN L. V. DAVIS, CHRISTIAN M. DESCHODT & CLARKE H. SCHOLTZ

Department of Zoology and Entomology, University of Pretoria, P/B X20, 0028 Hatfield, South Africa.

E-mail: adavis@zoology.up.ac.za; cdeschodt@zoology.up.ac.za; chsoltz@zoology.up.ac.za

Abstract

The monophyletic, dung beetle subfamily, Scarabaeinae, has a long history of subdivision into tribes and subtribes represented by groups of genera unified by designated characters. Various tribal names have been proposed although only 11 or 12 were considered valid in recent reviews. Three of these 12 tribes have now been invalidated due to extensive polyphyly indicated by both morphological and molecular phylogenies. Although partial revision of tribal classification was proposed in the most recent global molecular phylogeny of the subfamily, this was primarily limited to redefinition of membership or provision of support for pre-existing tribes. Complete revision was not attempted as the phylogeny examined interrelationships between only ~52% of the valid described genera. It was also hampered by inconsistencies in topology using different analytical methods, weakened by limited bootstrap support for many basal nodes, as well predicting several phylogenetic relationships that seemed anomalous with regards to biogeographical hypotheses. Nevertheless, using this phylogeny, we propose further revision of tribal classification in a clade of primarily African genera included within a group defined as “basal Scarabaeinae”. Using three different methods, the sister lineages of this clade were consistently recovered, mostly with strong bootstrap support for their molecular relatedness. Therefore, we provide a number of defining morphological characters to support their proposed designation as three new tribes: Byrrhidiini, Endroedyolini and Odontolomini. We also discuss approaches to a full tribal revision as well as the implications for historical biogeography of the Scarabaeinae.

Key words: dung beetle, historical biogeography, phylogeny, Scarabaeinae, tribal revision

Introduction

Division of the subfamily Scarabaeinae into tribes of genera with similar morphology commenced at the beginning of the 19th century with the designation of the Scarabaeini Latreille, 1802. Although various other tribal and subtribal names were proposed over the following two centuries, recent taxonomic publications recognized the validity of only 12 (Smith 2006) or 11 tribes (Bouchard *et al.* 2011), two of which were further subdivided into subtribes. Recent phylogenies developed from morphological (Philips *et al.* 2004; Tarasov & Génier 2015) and molecular data (Monaghan *et al.* 2007; Mlambo *et al.* 2015; Gunter 2016; Tarasov & Dimitrov 2016) suggest that only six regionally restricted and three globally widespread tribes are likely monophyletic. The remaining three globally widespread tribes are extensively polyphyletic. Thus, they require radical revision, particularly as they comprise ~59% of the valid genera in the subfamily.

The authors of the recent, most comprehensive, global molecular phylogeny (Tarasov & Dimitrov 2016) made a start to revising the tribal classification so that phylogeny and taxonomic classification are in agreement. However, only a partial revision was attempted as the study considered only ~52% of the valid genera. Also, the use of three different analytical methods yielded inconsistencies in topography. Consequently, there was poor bootstrap support at the basal nodes for some clades as well as several sister relationships that seemed biogeographically anomalous.

The partial revision (Tarasov & Dimitrov 2016) was primarily restricted to pre-existing tribes. Eight remained well-supported whereas one monophyletic and three polyphyletic tribes were redefined to fit in with the phylogeny. In the monophyletic tribe, the generic membership was expanded whereas in the polyphyletic tribes, the generic membership and their geographical extent were radically reduced. Using the same phylogeny, it is possible to define further new tribal divisions, based on consistent recovery of clades and strength of bootstrap support, tempered by

relative distance at nodes and degree of morphological difference. Thus, in the present study, we propose three new Afrotropical tribes from a clade within the “basal Scarabaeinae” of Tarasov & Dimitrov (2016).

Recent tribal revision

Using the 12 tribal divisions listed by Smith (2006) as a starting point, the partial revision proposed by Tarasov & Dimitrov (2016) left eight monophyletic tribes unchanged in status. Although only some of the generic membership was sequenced for most of the eight tribes, they were consistently recovered as sister lineages and were, thus, strongly supported as valid tribal divisions by bootstrapping (Table 1). They comprise three Afro-Eurasian centred tribes: Scarabaeini Latreille, 1802; Gymnopleurini Lacordaire, 1856; and Onitini Castelnau, 1840; plus the predominantly Neotropical-centred, Eurysternini Vulcano, Martínez & Pereira, 1961; Eucraniini Burmeister, 1873; and Phanaeini Hope, 1838 (also Nearctic). Although the globally widespread tribes, Onthophagini Burmeister, 1846, and Oniticellini Kolbe, 1905, were also retained, they were treated as a single strongly-supported clade. No bootstrap test was conducted to test the strength of the Onthophagini and Oniticellini as separate tribes. Although the Oniticellini are defined towards the terminal end of the phylogeny (Tarasov & Dimitrov 2016) at a more extreme distance from the basal node than the other tribes (Table 1), they are generically highly diversified.

TABLE 1. Support for pre-existing tribes of dung beetles in a molecular phylogeny for 137 genera using three different methods (ALL, G20, DT3): data presented or extrapolated from online supplementary files provided by Tarasov & Dimitrov (2016).

Valid monophyletic tribes defined prior to 2016* (N/N) = n out of total genera sequenced for phylogeny	Bootstrap support for clade ALL, G20, DT3	Scaled by factor, 1-0, from basal node of Scarabaeinae ALL, G20, DT3 (1:closer, 0:further from basal node)
Eucraniini (4/4)	98, 98, 96	0.730, 0.699, 0.699
Eurysternini (1/1)	89, 86, 96	0.869, 0.766, 0.605
Phanaeini (7/12)	83, 81, 71	0.730, 0.699, 0.699
Gymnopleurini (4/4)	97, 96, 95	0.775, 0.666, 0.633
Oniticellini (10/23)	-, -, -	0.330, 0.332, 0.306
Onitini (5/19)	98, 97, 97	0.586, 0.580, 0.574
Onthophagini (9/36) / Oniticellini	96, 97, 98	0.586, 0.580, 0.574
Scarabaeini (5/7)	77, 72, <50	0.669, 0.725, 0.793
Sisyphini (2/3) / <i>Epirinus</i>	DT3 = 95	0.782, 0.750, 0.575

*See Smith (2006); Bouchard *et al.* (2011).

The Sisyphini Mulsant, 1846, were expanded to Sisyphini *sensu novo* by transferring the sister genus, *Epirinus* Dejean, 1830, from the Deltochilini Lacordaire, 1856 (Table 2). This decision has since been questioned (Daniel *et al.*, submitted) on the basis of inconsistent bootstrap support, estimated Oligocene age of separation, morphological dissimilarity and differing biogeographical origins. It was proposed that they should be separated into two tribes: Sisyphini *stat. rev.* and the revalidated, *Epirinini* van Lansberge, 1874 *stat. rev.*

Although names of the three, remaining, globally-distributed, polyphyletic tribes were retained, they were also redefined as *sensu novo* (Table 2) with reduced membership following the combined removal of 100 genera to the status of *incertae sedis*, of which 69 had been sequenced and included in the phylogeny of Tarasov & Dimitrov (2016). The Deltochilini *sensu novo* were reduced to ten Neotropical or Neotropical/Nearctic genera although this new tribe was poorly supported, possibly due to polyphyly within included genera. Although possibly not universally accepted, a morphological phylogeny (Montreuil 1998) had previously split membership of the other two polyphyletic tribes into coprine-like genera assigned to the Coprini Leach, 1815, with the remaining non-coprine-like genera assigned to the Ateuchini Perty, 1830. Tarasov & Dimitrov (2016) redefine Coprini *sensu novo* based on only two sister genera, including the globally widespread genus, *Copris* Geoffroy, 1762. The Ateuchini were redefined to comprise 20 genera restricted to Neotropical, or, Neotropical and Nearctic regions. Further reassessment would be required as they consistently comprise three separate lineages *Ateuchus* Weber, 1801, *Scatimus* Erichson, 1847,

and further members of the subtribe, Scatimina Vaz-de-Mello, 2008 (*Trichillum* Harold, 1868; *Leotrichillum* Vaz-de-Mello, 2008; *Trichilidium* Vaz-de-Mello, 2008). This suggests that as redefined by Tarasov & Dimitrov (2016), the Ateuchini and, even the subtribe, Scatimina, remain polyphyletic. Finally, they redefined the tribe, Dichotomiini *sensu novo* based on the single genus *Dichotomius* Hope, 1838. It is noteworthy that *Dichotomius* was formerly classified in the Ateuchini under the tribal name Dichotomiini, which has no valid status as it lacks a formal description (Smith 2006). In the morphological phylogeny of Montreuil (1998), the coprine-like *Dichotomius* was placed in a clade with the Coprini. However, the consistent sisterhood of *Dichotomius* and *Ateuchus*, in the molecular phylogeny of Tarasov & Dimitrov (2016) perhaps supports their redefinition as the tribe, Ateuchini *sensu novo*.

TABLE 2. Support for revised tribes of dung beetles proposed by Tarasov & Dimitrov (2016) in a molecular phylogeny for 137 genera using three different methods (ALL, G20, DT3): data presented or extrapolated from online supplementary files.

Old tribes redefined by Tarasov & Dimitrov (2016)* (N/N = n out of total genera sequenced for phylogeny)	Bootstrap support for clade ALL, G20, DT3	Scaled by factor, 1-0, from basal node of Scarabaeinae ALL, G20, DT3 (1:closer, 0:further from basal node)
Coprini <i>sensu novo</i> (2/2)	100, 100, 100	0.671, 0.662, 0.744
Deltotrichilini <i>sensu novo</i> (10/10)	<50, <50, <50	0.725, 0.709, 0.746
Dichotomiini <i>sensu novo</i> (1/1)	83, 78, 51	0.734, 0.698, 0.699
Sisyphini <i>sensu novo</i> (3/4)	81, 77, 58	0.861, 0.797, 0.643

*See text for redefinition of tribe, Ateuchini.

Subsequent to the phylogeny of Tarasov & Dimitrov (2016), several further unpublished and published proposals have been made for changes to tribal or subtribal divisions. Using molecular and morphological results, Tarasov (2017) removed the Oriental genera, *Cassolus* Sharp, 1875, and *Parachorius* Harold, 1873, from the list of species given the status of *incertae sedis* (Tarasov & Dimitrov 2016), and assigned them to the new tribe, Parachoriini Tarasov, 2017. Using an analysis of morphological characters Philips (2016) provided support for retaining three older subtribal divisions in the Oniticellini (*Drepanocerina* van Lansberge, 1875; *Helictopleurina* Janssens, 1946; *Oniticellina* Kolbe, 1905) but proposed two others (*Liatongina* Philips, 2016; *Attavicina* Philips, 2016) to maintain subtribal monophyly. Finally, in an unpublished Ph.D. thesis, Medina Uribe (2015) proposed that two groups of endemic southern African genera should be assigned to new tribes, Byrrhidiini and Circelliini, and these are discussed in the present study.

Proposed further tribal revision

In the molecular phylogeny of Tarasov & Dimitrov (2016), two clades of scarabaeine genera were described as “basal Scarabaeinae” as they diverged close to the basal node. One of these clades comprised three lineages of primarily Southern African centred genera and species and was shown to have very strong support (Table 3) despite the inclusion of the Afro-Eurasian genus, *Haroldius* Boucomont, 1914, on a fourth lineage for which internal support was very weak. Additional files provided by Tarasov & Dimitrov (2016) show that the sequenced *Haroldius* specimens were from Taiwan. This constitutes the eastern distributional extreme for a genus that is known by 33 Oriental and only four Afrotropical species (Schoolmeesters 2018) showing forest litter or myrmechophilous habits (Krikken 2006). Although the phylogeny of Tarasov & Dimitrov (2016) consistently places *Haroldius* in the “basal Scarabaeinae”, Paulian (1985) previously assigned the genus to the tribe Onthophagini on morphological grounds. In view of poor bootstrap support and biogeographical bias, it is considered that *Haroldius* would best remain as *incertae sedis* for the present. Therefore, redefined tribal status is only provided for the other three sister lineages with extremely strong support for their common ancestry.

In an attempt to introduce some objectivity into revision of tribal divisions, distance values at basal nodes were determined for each pre-existing and revised tribe using additional data provided by Tarasov & Dimitrov (2016) (Tables 1–3). Mean nodal distance \pm S.D. (0.681 ± 0.120) from the basal node for the subfamily, Scarabaeinae (=1 on a 1–0 scale), yielded a range in deviation from 0.801 to 0.561, which encompassed most of the 49 measured distances for basal nodes of tribes named in the tables. Only six values lay outside of this range, three each at either

the basal or terminal ends of the phylogeny. The terminal values represented nodal distances for the pre-existing tribe, Oniticellini, whereas the three basal values were scattered between three different tribes. Thus, is it useful to use nodal distance to assist in defining insect tribes or should topology take precedence as in other recent studies (e.g., Rousse *et al.* 2016; Ban *et al.* 2018)? Although emphasizing topology would favour one tribe in the present case, it would be defined entirely outside of the average range of nodal distance values (Table 3: 0.924-0.982; see “3 defined tribes + *Haroldius*”), like the Oniticellini. Therefore, because we were, also, unable to identify a suite of unifying characters to link the three sister lineages, we defined them as three separate tribes (Table 3) with nodal distance values that fall almost entirely within the limits of the average range (0.561 to 0.801). However, should a suite of linking characters be noted in the future, there might be a case for reducing these three tribes to subtribes within the tribe Odontolomini new tribe.

We have not considered the proposed assignment of the endemic South African genus, *Circellium* Latreille, 1825, to the new tribe Circelliini, as proposed by the unpublished study of Medina Uribe (2015), since weakly supported sister relationships are shown to the Afro-Eurasian tribe, Scarabaeini, and a Neotropical genus, *Bdelyrus* Harold, 1869, in the phylogeny of Tarasov & Dimitrov (2016). Nevertheless, *Circellium* is a morphologically distinct, monotypic outlier in the South African dung beetle fauna.

TABLE 3. Support for three new proposed tribes of dung beetles based on a molecular phylogeny for 137 genera using three different methods (ALL, G20, DT3): data presented or extrapolated from online supplementary files provided by Tarasov & Dimitrov (2016).

New tribes and subtribes defined within “basal Scarabaeinae”** (N/N) = n out of total genera sequenced for phylogeny	Bootstrap support for clade ALL, G20, DT3	Scaled by factor, 1-0, from basal node of Scarabaeinae ALL, G20, DT3 (1:closer, 0:further from basal node)
3 new tribes + <i>Haroldius</i> (10/15)	98, 98, 96	0.982, 0.925, 0.924
Byrrhidiini + <i>Haroldius</i> (4/8)	<50, <50, 59	0.783, 0.734, 0.673
Byrrhidiini (3/7)	DT3 = 95	-----*, -----*, 0.589
Endroedyolini (5/6)	92, 96, 96	0.833, 0.785, 0.660
Odontolomini (1/1)	DT3 = 100	0.783, 0.734, 0.771

*See Byrrhidiini + *Haroldius*, **See Tarasov & Dimitrov (2016)

Descriptions of the new tribes

Below, we identify characters that may be used to separate the membership of the new tribes from all other genera or combinations of genera. As there are few, unique, diagnostic morphological characters (autapomorphies or synapomorphies), their separation at tribal level relies strongly on their published molecular relationships and biogeography together with putative, unique combinations of characters.

Tribe Byrrhidiini Davis, Deschodt & Scholtz, new tribe

Type genus. *Byrrhidium* Harold, 1869, here designated (Figs. 1, 4).

Head. Punctate; anterior clypeal margin often with forklike small to large teeth protruding anteriorly; single very small median tooth on lower margin of clypeus; never with a horn on the frons or vertex; antenna nine segmented; mouthparts varying between genera but labrum always strongly sclerotized apically, inside margins of glossae with sclerotized denticles.

Pronotum. Pronotum convex, with sub-parallel sides; punctation indistinct.

Elytra. Convex; fused without humeral umbones; elytra with seven to eight feebly visible striae followed by an acute sub-lateral pseudoepipleural carina and inflexed pseudopipleuron; interstriae intervals flat; metathoracic wings absent; scutellum not visible from above.

Sterna. Smooth to punctate; sutures well defined.



FIGURE 1. *Byrrhidium ovale* Harold, 1869, type species of the type genus of the tribe Byrrhidiini Davis, Deschodt & Scholtz, new tribe.

Protibia. With a terminal spur; two or three denticles on anterior outside margin; posterior outside margin serrated or smooth; tarsi short.

Meso- and metatibia. Unmodified, long and thin; each meso- and metatarsus of uniform width, often setate.

Pygidium. Somewhat convex; punctate.

Aedeagus. Phallobase unmodified; parameres symmetrical and extremely variable.

Body size. Small to medium with size varying between 4.9 mm × 3.8 mm for the smallest and 11.8 mm × 7.5 mm for the largest known species.

Diagnosis and known distribution. The Byrrhidiini new tribe, can be distinguished from all other dung beetle tribes by the combination of the following characters: flightless with body medium sized, sparsely setate and strongly convex; antennae nine segmented; labrum sclerotized apically, inside margins of glossae with sclerotized denticles; punctures on pronotum visible but indistinct; an acute sub-lateral pseudoepipleural carina and inflexed pseudepipleuron; striae and punctures on the elytra indistinctly visible; no humeral umbone visible; scutellum not visible from above; unmodified meso- and metatibiae of the same width; distributed in the arid to hyper-arid region along the southwest seaboard of Namibia and South Africa between about 21 and 31 degrees south with most known species occurring in Namibia (Fig. 4).

Generic list:

Ausmontins Deschodt & Davis, 2018 (1 sp.)

Byrrhidium Harold, 1869 (2 spp.: both sequenced)

Dicranocara Frolov & Scholtz, 2003 (4 spp.: 3 sequenced)

Drogo Deschodt, Davis & Scholtz, 2016 (1 sp.)

Namakwanus Scholtz & Howden, 1987 (4 spp.)

Namaphilus Deschodt & Davis, 2017 (5 spp.: 1 sequenced as *Namakwanus davisii*)

Versicorpus Deschodt, Davis & Scholtz, 2011 (2 spp.)

Tribe Odontolomini Davis, Deschodt & Scholtz, new tribe

Type genus. *Odontoloma* Boheman, 1857, here designated (Figs. 2, 5).

Head. Clypeus with a small median tooth flanked by two others; frons and vertex without horns; antenna nine segmented.

Pronotum. More or less flat dorsally; strongly curving downward both anteriorly and laterally; antero-lateral margins often explanate.

Elytra. Seventh stria or eighth interstria interval partly carinate anteriorly; inflexed pseudepipleuron, epipleuron narrow; metathoracic wings well developed to greatly reduced.

Sterna. Prosternum fairly well developed; metasternum mostly with clear punctures; sutures clearly visible.

Protibia. Front tibia truncate and obtuse, widening apically with three teeth on outside margin.

Meso- and metatibia. Widening apically, with setae.

Pygidium. Basal transverse groove or depression present, groove terminating in a fovea on each side near margin.

Aedeagus. Parameres symmetrical and short.

Body size. All species are small, less than 5 mm in length with some size variation observed within species.

Diagnosis and known distribution. Body oval and moderately convex; black; densely punctate with scattered semi-erect setae; clypeus five-dentate; all tibiae widening anteriorly, anterior tibiae with three denticles, truncated and obtuse. Widespread in the Afrotropical region but with a strong bias in species diversity centred on southern Africa.

Generic list:

Odontoloma Boheman, 1857 (20 spp.: 2 sequenced)



FIGURE 2. *Odontoloma pauxillum* (Boheman, 1857), type species of the type genus of the tribe Odontolomini Davis, Deschodt & Scholtz, new tribe.

Tribe Endroedyolini Davis, Deschodt & Scholtz, new tribe

Type genus. *Endroedyolus* Scholtz & Howden, 1987, here designated (Figs. 3, 6).

Head. Clypeus bidentate with a notch to the side of each denticle. Antennae nine segmented.

Pronotum. Very convex with lateral margins explanate, sometimes carinate laterally.



FIGURE 3. *Endroedyolus paradoxus* Scholtz & Howden, 1987, type species of the type genus of the tribe Endroedyolini Davis, Deschodt & Scholtz, new tribe.

Elytra. Strongly convex; setae in straight and slightly converging lines; metathoracic wings always absent.

Sterna. Smooth to punctate with punctures of varying density and size; prosternum fairly well developed; metasternum smooth to punctate, sometimes with deep fovea extending from anterior to sometimes half way between mesocoxae.

Protibia. With three small denticles on outside margin.

Meso- and metatibia. Unmodified with setae.

Pygidium. With small setiferous punctures; with or without depression or fovea.

Aedeagus. Parameres symmetrical.

Body size. Very small to small: 1.5mm to 4.8 mm.

Diagnosis and known distribution. The combination of extreme small size, very convex body, unique clypeal shape and explanate lateral pronotal margins, distinguishes members of this tribe from any other. They are restricted to forest patches of south east South Africa where they are associated with forest litter.

Generic list:

Aliuscanthoniola Deschodt & Scholtz, 2008 (1 sp. sequenced)

Endroedyolus Scholtz & Howden, 1987 (1 sp. sequenced)

Nebulasilvius Deschodt & Scholtz, 2008 (2 spp.)

Outenikwanus Scholtz & Howden, 1987 (1 sp. sequenced)

Parvuhowdenius Deschodt & Scholtz, 2008 (1 sp.)

Peckolus Scholtz & Howden, 1987 (3 spp.: 1 sequenced)

Silvaphilus Roets & Oberlander, 2010 (1 sp. sequenced)

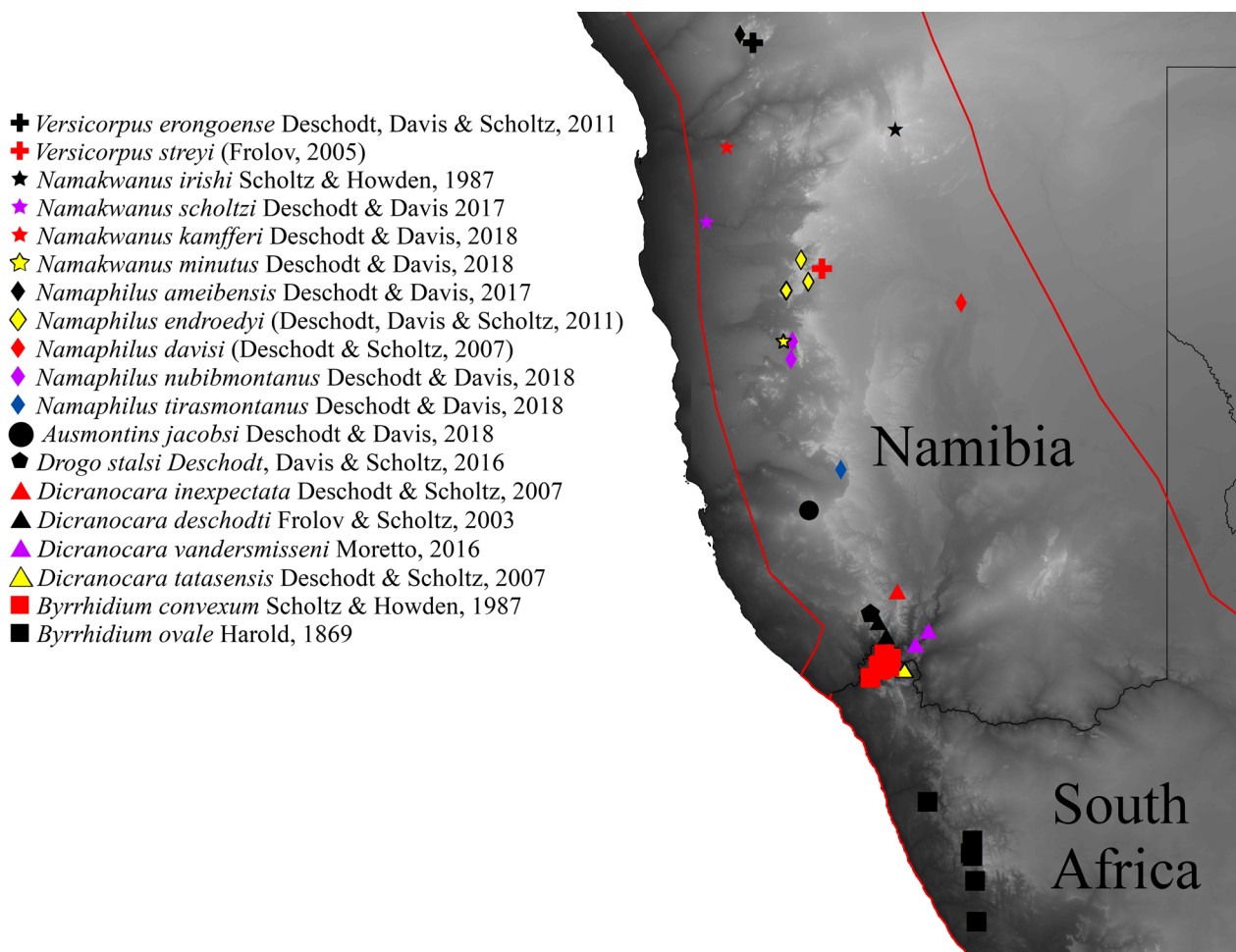


FIGURE 4. Map showing the distribution of known species in the tribe, Byrrhidiini Davis, Deschodt & Scholtz, new tribe. Map adapted from Deschodt & Davis (2018).

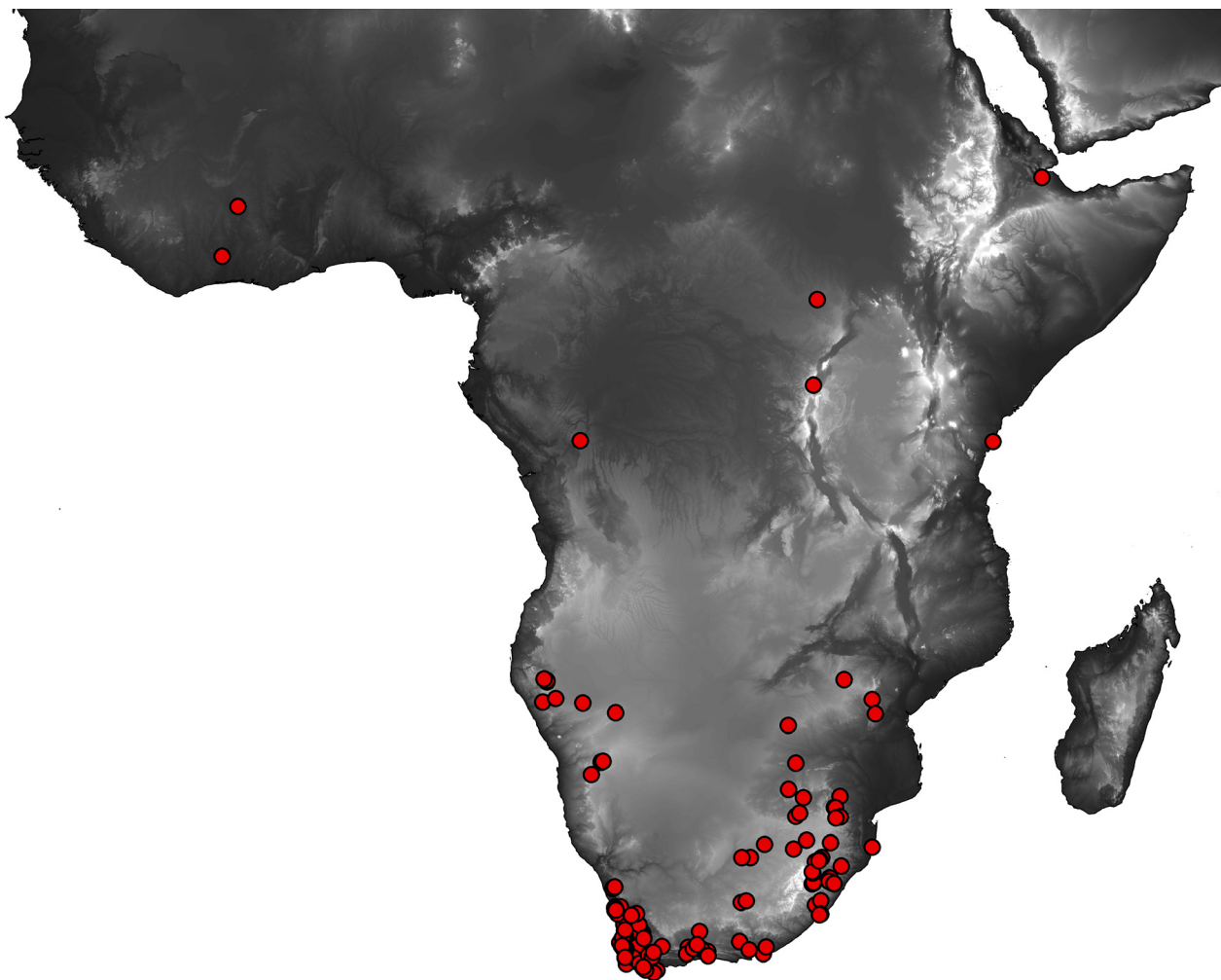


FIGURE 5. Map showing the distribution of known species in the tribe, Odontolomini Davis, Deschodt & Scholtz, new tribe.

Topology, taxonomic classification and historical biogeography

Topology of the most recent global molecular phylogeny has been arranged in ladderized sequence (Tarasov & Dimitrov 2016). Groups of clades that emanate from either basal or terminal nodes are dominated, primarily, by endemic Afrotropical or Afro-Eurasian centred genera. Groups of clades emanating from intermediate nodes are dominated by endemic genera of Madagascar, Australasia or the Americas. Nevertheless, there are a few biogeographical anomalies such as the Neotropical genera, *Bdelyrus* and *Eurysternus* Dalman, 1824, embedded, respectively, in groups of basal or terminally-derived clades. It is unclear if this split between clades dominated by Afro-Eurasian genera is real or an artefact of topology as nodal distances are very short and poorly-supported along the spine of the topology. Across the entire phylogeny of Tarasov & Dimitrov (2016), clades are variously represented by regionally-restricted genera with limited species diversification or geographically widely-radiated genera with extensive species diversification.

Previous analyses of global distribution patterns have hypothesized two major radiations of scarabaeine taxa (Davis *et al.* 2002, 2017; Davis 2009). Chronology and tracks followed by the earlier radiation are uncertain but they are represented, primarily, by taxa that are endemic to southern biogeographical regions at generic level, either Afrotropical, Neotropical, Madagascar or Australasia. The second radiation is dated to the late Cenozoic and is represented by genera that are centred in both northern and southern biogeographical regions or by closely-related endemic southern genera. An ultimately African origin has been postulated for the global scarabaeine fauna due to the dominance of African genera in basally-derived lineages showing closest relationships to outgroups (Monaghan *et al.* 2007, Sole *et al.* 2010). A major contribution by taxa of African origin is also postulated for the second global

radiation to Eurasia, and, thereafter, to the Americas and Australia, supported by molecular phylogenies for the tribe, Onthophagini (Emlen *et al.* 2005, Breeschoten *et al.* 2016, Zunino & Halffter 2019). Regional late Cenozoic radiations have also occurred within the Americas during the Great American Interchange (Kohlmann & Halffter 1988, 1991) and from Africa to Madagascar (Miraldo *et al.* 2011).

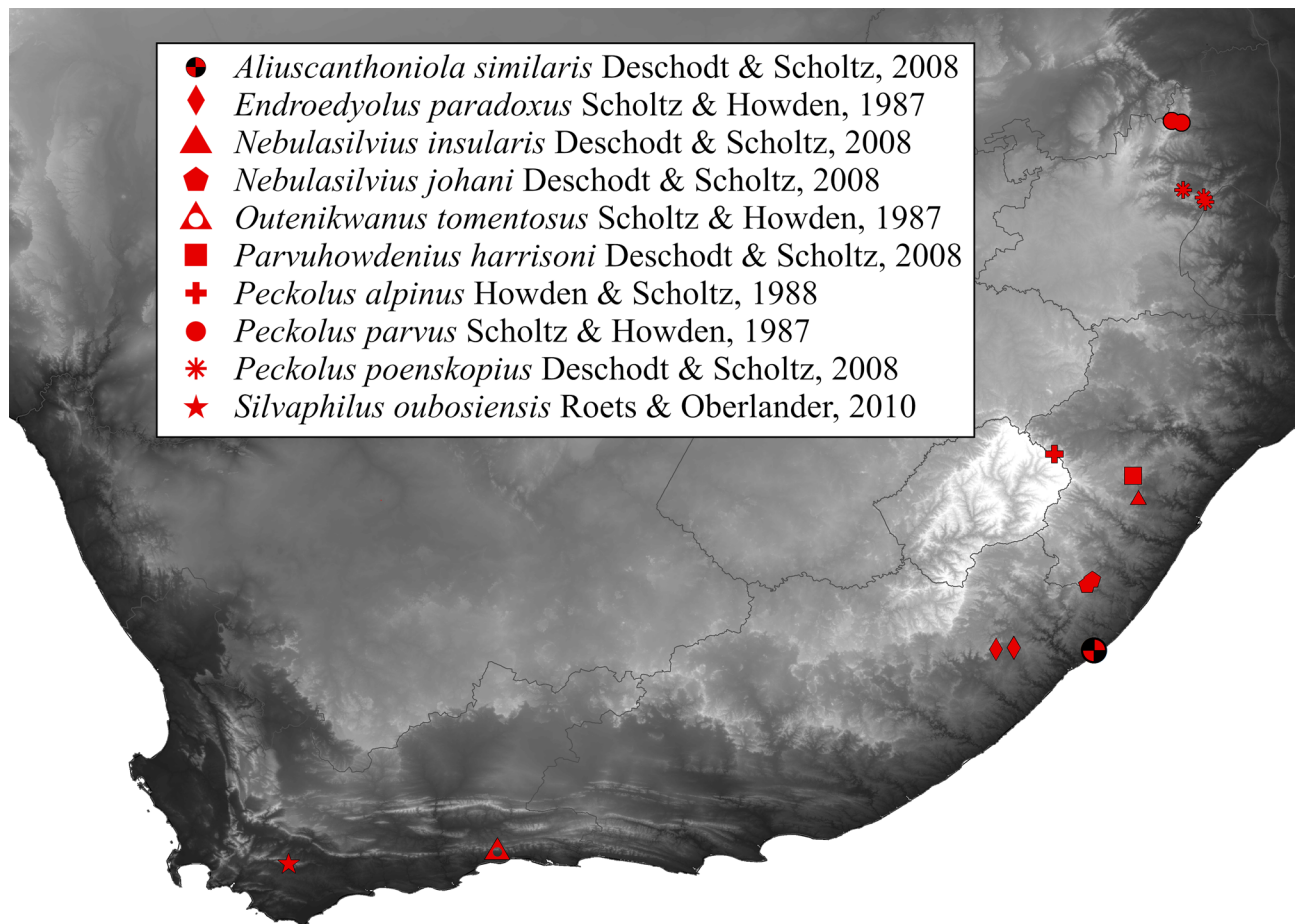


FIGURE 6. Map showing the distribution of the known species in the tribe, Endroedyolini Davis, Deschodt & Scholtz, new tribe.

Earlier historical biogeographical analyses (Cambefort 1999; Davis *et al.* 2002) relied on the division of the subfamily into 12 tribes. Those tribes dominated by intercontinental separation at generic level were considered relatively older and those dominated by species level separation were considered relatively younger (Davis *et al.* 2002). Following the demonstration of polyphyly in the Ateuchini, Deltochilini and Coprini, this approach was continued by collapsing their membership into a single unit (Davis 2009; Davis *et al.* 2017) on the basis that basal phyletic linkages between their membership remained uninterrupted by any of the other nine tribes. The phylogeny and partial tribal revision of Tarasov & Dimitrov (2016) suggest that this approach is insupportable and that future tribal revision is likely to modify the current definition of three main biogeographical patterns: Afro-Eurasian-centred, Neotropical-centred, or, widespread across southern continents.

Davis *et al.* (2017) point out that revision and subdivision of polyphyletic tribes will likely be along geographical lines, resulting in greater regional endemism at tribal level. It will remove the widespread pattern between southern continents suggested by their former classification as the tribes Ateuchini, Deltochilini or Coprini. Given the monophyly of the subfamily, distant affinities would remain between these new, endemic tribes of Afrotropical, Madagascar, Australasian and Neotropical regions. However, a reassessment of historical biogeography of the subfamily will be necessary based on integration of a new complete tribal revision with phylogenetic structure and geographical patterns. Nevertheless, it might, again, be predicted that tribes dominated by regionally endemic genera would result from older radiations whereas those comprising many regionally-shared genera would result from more recent radiations, as in the nine pre-existing tribes that remain well-supported by phylogeny.

Phylogeny, taxonomic classification, morphology and habit

Morphological variation in the subfamily may have been constrained by the two main behavioural habits of tunnelling or ball-rolling (Davis *et al.* 2017). This has led to repeated independent evolution of one or the other (Philips *et al.* 2004) along trajectories of morphological change indicated by Inward *et al.* (2011). However, the mostly small-bodied taxa in the new tribes show relatively specialized habits. The flightless Byrrhidiini new tribe have diversified between rocky often mountainous terrain across a region of south western Africa that has become increasingly arid since the mid-Miocene (Diekmann *et al.* 2003; Hoetzel *et al.* 2015). They appear localized around concentrations of dung, especially, communal middens of the Rock Hyrax. The flightless Endroedyolini new tribe have diversified between naturally-isolated, southern and eastern forest patches of South Africa where they occur in leaf litter. The mostly fully-winged Odontolomini new tribe are characterized by very small body size and, although more widespread than the other two tribes, they are primarily diversified across cooler climates of Southern Africa with extremely limited representation in tropical Africa. Their behavioural habits are, essentially, unknown, but, at least four species are flightless (Howden & Scholtz 1987).

Concluding remarks

Because of the degree of diversification within the subfamily, it is useful to retain the systematic division into tribes. However, it is essential to revise current classification so that it becomes consistent with phylogeny, even though some new tribes will comprise single genera. Owing to poor bootstrap support for many basal nodes in the phylogeny of Tarasov & Dimitrov (2016), completion of tribal revision might be assisted by a new phylogeny that also includes the ~68 remaining genera of the former polyphyletic tribes (Ateuchini, Deltochilini, Coprini) that remain unsequenced. It is less clear if it would be useful to also include the ~60 currently unsequenced genera of the nine, well-supported, pre-existing tribes. However, further phylogenies of individual genera would be useful as some are probably polyphyletic, particularly those comprising many species. In conclusion, we suggest that approaches to a full tribal revision should use a combination of topology, strength of support, nodal distance, morphological similarity/dissimilarity and biogeographical pattern, assisted by an even more comprehensive, new phylogeny. For the present, we propose revision to tribal divisions of just a single clade in the phylogeny of Tarasov & Dimitrov (2016) comprising sister Afrotropical taxa that are primarily diversified within Southern Africa and were formerly assigned to the tribe, Deltochilini.

References

- Ban, X., Jiang, N., Cheng, R., Xue, D. & Han, H. (2018) Tribal classification and phylogeny of Geometrinae (Lepidoptera: Geometridae) inferred from seven gene regions. *Zoological Journal of the Linnean Society*, 184, 653–672.
<https://doi.org/10.1093/zoolinnean/zly013>
- Bouchard, P., Bousquet, Y., Davies, A.E., Alonso-Zarazaga, M.A., Lawrence, J.F., Lyal, C.H.C., Newton, A.F., Reid, C.A.M., Schmitt, M., Slipinski, S.A. & Smith, A.B.T. (2011) Family-group names in Coleoptera. *ZooKeys*, 88, 1–972.
<https://doi.org/10.3897/zookeys.88.807>
- Breeschoten, T., Doorenweerd, C., Tarasov, S. & Vogler, A.P. (2016) Phylogenetics and biogeography of the dung beetle genus *Onthophagus* inferred from mitochondrial genomes, *Molecular Phylogenetics and Evolution*, 105, 86–95.
<http://dx.doi.org/10.1016/j.ympev.2016.08.016>
- Cambefort, Y. (1991) Biogeography and evolution. In: Hanski, I. & Cambefort, Y. (Eds.), *Dung beetle ecology*. Princeton University Press, Princeton, pp. 51–68.
- Daniel, G.M., Sole, C.L., Davis, A.L.V., Strümpher, W.P. & Scholtz C.H. (2019) The dung beetle tribe, Sisyphini Mulsant *sensu novo* (Scarabaeidae: Scarabaeinae): An evolutionary and systematic assessment inferred from molecular phylogeny and geographical distribution of southern African species. *Systematic Entomology*. [submitted]
- Davis, A.L.V. (2009) Section D: Historical biogeography of the Scarabaeinae and its physical and biotic drivers. In: Scholtz, C.H., Davis, A.L.V. & Kryger, U. (Eds.), *Evolutionary biology and conservation of dung beetles*. Pensoft Publishers, Sofia and Moscow, pp. 330–385.
- Davis, A.L.V., Scholtz, C.H. & Philips, T.K. (2002) Historical biogeography of scarabaeine dung beetles. *Journal of Biogeography*, 29, 1217–1256.
<https://doi.org/10.1046/j.1365-2699.2002.00776.x>

- Davis, A.L.V., Scholtz, C.H. & Sole, C.L. (2017) Biogeographical and co-evolutionary origins of scarabaeine dung beetles: Mesozoic vicariance versus Cenozoic dispersal and dinosaur versus mammal dung. *Biological Journal of the Linnean Society*, 120, 258–273.
<https://doi.org/10.1111/bij.12893>
- Deschodt, C.M. & Davis, A.L.V. (2018) New deltochiline (Coleoptera: Scarabaeidae: Scarabaeinae) taxa associated with hyrax dung in arid south western Namibia. *Zootaxa*, 4450 (1), 66–76.
<https://doi.org/10.11646/zootaxa.4450.1.4>
- Diekmann, B., Falker, M. & Kuhn, G. (2003) Environmental history of the south-eastern South Atlantic since the Middle Miocene: evidence from the sedimentological records of ODP Sites 1088 and 1092. *Sedimentology*, 50, 511–529.
<https://doi.org/10.1046/j.1365-3091.2003.00562.x>
- Emlen, D.J., Marangelo, J., Ball, B. & Cunningham, C.W. (2005) Diversity in the weapons of sexual selection: horn evolution in the beetle genus *Onthophagus* (Coleoptera: Scarabaeidae). *Evolution*, 59, 1060–1084.
<https://doi.org/10.1111/j.0014-3820.2005.tb01044.x>
- Gunter, N.L., Weir, T.A., Slipinksi, A., Bocak, L. & Cameron, S.L. (2016) If dung beetles (Scarabaeidae: Scarabaeinae) arose in association with dinosaurs, did they also suffer a mass co-extinction at the K-Pg boundary? *PLoS ONE*, 11, e0153570.
<https://doi.org/10.1371/journal.pone.0153570>
- Hoetzel, S., Dupont, L.M. & Wefer, G. (2015) Miocene–Pliocene vegetation change in south-western Africa (ODP Site 1081, offshore Namibia). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 423, 102–108.
<https://doi.org/10.1016/j.palaeo.2015.02.002>
- Howden, H.F. & Scholtz, C.H. (1987) A revision of the African genus *Odontoloma* Boheman (Coleoptera: Scarabaeidae: Scarabaeinae). *Journal of the Entomological Society of Southern Africa*, 50, 155–192.
- Inward, D.J.G., Davies, R.G., Pergande, C., Denham, A.J. & Vogler, A.P. (2011) Local and regional ecological morphology of dung beetle assemblages across four biogeographic regions. *Journal of Biogeography*, 38, 1668–1682.
<https://doi.org/10.1111/j.1365-2699.2011.02509.x>
- Kohlmann, B. & Halffter, G. (1988) Cladistic and biogeographical analysis of *Ateuchus* (Coleoptera: Scarabaeidae) of Mexico and the United States. *Folia Entomologica Mexicana*, 74, 109–130.
- Kohlmann, B. & Halffter, G. (1991) Reconstruction of a specific example of insect invasion waves: the cladistic analysis of *Canthon* (Coleoptera: Scarabaeidae) and related genera in North America. *Quaestiones Entomologicae*, 26, 1–20.
- Krikken, J. & Huijbregts, J. (2006) Miniature scarabs of the genus *Haroldius* on Sulawesi, with notes on their relatives (Coleoptera: Scarabaeidae). *Tijdschrift voor Entomologie*, 149, 167–187.
<https://doi.org/10.1163/22119434-900000197>
- Medina Uribe, C.A. (2015) *Canthonini (Scarabaeidae: Scarabaeinae) of Gondwana: comparison of male genitalia, evolutionary trends and phylogeny*. Ph.D. thesis, University of Pretoria, Pretoria, 125 pp. [unpublished]
- Miraldo, A., Wirta, H. & Hanski, I. (2011) Origin and Diversification of Dung Beetles in Madagascar. *Insects*, 2, 112–127.
<https://doi.org/10.3390/insects2020112>
- Mlambo, S., Sole, C.L. & Scholtz, C.H. (2015) A molecular phylogeny of the African Scarabaeinae (Coleoptera: Scarabaeidae). *Arthropod Systematics and Phylogeny*, 73, 303–321.
- Monaghan, M.T., Inward, D.J.G., Hunt, T. & Vogler, A.P. (2007) A molecular phylogenetic analysis of the Scarabaeinae (dung beetles). *Molecular Phylogenetics and Evolution*, 45, 674–692.
<https://doi.org/10.1016/j.ympev.2007.06.009>
- Montreuil, O. (1998) Analyse Phylogénétique et Paraphylie des Coprini et Dichotomiini. Scénario Biogéographique. *Annales de la Société Entomologique de France*, New Series, 34, 135–148.
- Paulian, R. (1985) Notes sur les Coléoptères Scarabaeidae du Muséum de Genève. II. *Revue Suisse de Zoologie*, 92, 189–203.
<https://doi.org/10.5962/bhl.part.81609>
- Philips, T.K. (2016) Phylogeny of the Oniticellini and Onthophagini dung beetles from morphological evidence. *ZooKeys*, 579, 9–57.
<https://doi.org/10.3897/zookeys.579.6183>
- Philips, T.K., Pretorius, E. & Scholtz, C.H. (2004) A phylogenetic analysis of dung beetles (Scarabaeinae: Scarabaeidae): unrolling an evolutionary history. *Invertebrate Systematics*, 18, 53–88.
<https://doi.org/10.1071/IS03030>
- Rousse, P., Quicke, D.L.J., Matthee, C.A., Lefevre, P. & van Noort, S. (2016) A molecular and morphological reassessment of the phylogeny of the subfamily Ophioninae (Hymenoptera: Ichneumonidae). *Zoological Journal of the Linnean Society*, 178, 128–148.
<https://doi.org/10.1111/zoj.12405>
- Schoolmeesters, P. (2018) Scarabs: World Scarabaeidae Database. In: Roskov, Y., Abucay, L., Orrell, T., Nicolson, D., Bailly, N., Kirk, P.M., Bourgoin, T., DeWalt, R.E., Decock, W., De Wever, A., Van Nieukerken, E., Zarucchi, J. & Penev, L. (Eds.), *Species 2000 & ITIS Catalogue of Life*. Naturalis, Leiden, the Netherlands. ISSN 2405-8858. Available from: www.catalogueoflife.org/col/ (accessed 15th April 2018)
- Smith, A.G. (2006) A review of the family-group names for the superfamily Scarabaeoidea with corrections to nomenclature and a current classification. *Coleopterists Society Monograph*, 5, 144–204.
[https://doi.org/10.1649/0010-065X\(2006\)60\[144:AROTFN\]2.0.CO;2](https://doi.org/10.1649/0010-065X(2006)60[144:AROTFN]2.0.CO;2)

- Sole, C.L. & Scholtz, C.H. (2010) Did dung beetles arise in Africa? A phylogenetic hypothesis based on five gene regions. *Molecular Phylogenetics and Evolution*, 56, 631–641.
<https://doi.org/10.1016/j.ympev.2010.04.023>
- Tarasov, S. (2017) A cybertaxonomic revision of the new dung beetle tribe Parachoriini (Coleoptera: Scarabaeidae: Scarabaeinae) and its phylogenetic assessment using molecular and morphological data. *Zootaxa*, 4329 (2), 101–149.
<https://doi.org/10.11646/zootaxa.4329.2.1>
- Tarasov, S. & Dimitrov, D. (2016) Multigene phylogenetic analysis redefines dung beetles relationships and classification. *BMC Evolutionary Biology*, 16, 1–19.
<https://doi.org/10.1186/s12862-016-0822-x>
- Tarasov, S. & Génier, F. (2015) Innovative Bayesian and Parsimony Phylogeny of Dung Beetles (Coleoptera, Scarabaeidae, Scarabaeinae) Enhanced by Ontology-Based Partitioning of Morphological Characters. *PLoS ONE*, 10, e0116671.
<https://doi.org/10.1371/journal.pone.0116671>
- Zunino, M. & Halfpfer, G. (2019) About the origin of American *Onthophagus* (Coleoptera: Scarabaeidae). A critical appraisal of a recent paper by Breeschoten et al. (2016) on phylogenetics and biogeography. *Molecular Phylogenetics and Evolution*, 133, 141.
[https://doi: https://doi.org/10.1016/j.ympev.2019.01.001](https://doi.org/10.1016/j.ympev.2019.01.001)