



Review

Dung beetle tribal classification (Coleoptera: Scarabaeidae: Scarabaeinae): progress, problems, and prospects

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The subfamily Scarabaeinae has been traditionally divided into tribes on the basis of morphological similarity between groups of genera or, even, dissimilarity shown by a single genus. Although various tribal units have been described over the past 220 years, they had been recently reduced to a maximum of only 12 through synonymies within some tribes. However, following the advent of morphological and molecular cladistic systematics, it is clear that there are many discrepancies between phylogeny and phenetic tribal classification. As a result the number of tribes has now been expanded to 20 by revalidating some tribes or describing new groupings although this revision is incomplete. Thus, this study provides a comprehensive review of the current status of dung beetle tribal classification with regards to validity in terms of monophyly versus polyphyly or paraphyly. We discuss the systematic position of tribes among Scarabaeinae and provide a summary of the generic and species structure for each tribe. Given the enduring polyphyly or paraphyly in several tribes, it is clear that further tribal units will need to be described or revalidated to resolve the discrepancies. Therefore, we discuss how to use multiple lines of evidence (molecular, morphological, biogeographical, and paleontological) to build the tree of life for dung beetles and consequently provide stability in the tribal classification of the lineage.

Key words: lineage, molecule, morphology, Scarabaeoidea, systematics

Scarabaeine dung beetles serve various functions within an ecosystem and provide ecosystem services that are beneficial to humans. To assist the conservation of these processes, an adequate knowledge of their classification and associated traits is required, particularly as dung beetles have a global distribution spanning all continents except Antarctica. The majority of dung beetles feed primarily on mammal dung although there are some species that feed primarily on carrion, rotting fruit, fungi, or decaying plant matter. As a result of manipulating these resources for feeding and breeding, dung beetles provide a series of ecosystem services including dung removal, nutrient recycling, soil fertilization, reduction of greenhouse gasses, secondary seed dispersal, pest control, and parasite suppression (Nichols et al. 2008, Scholtz et al. 2009, Raine and Slade 2019). Involvement in such processes highlights the importance of this group of beetles as both bio-indicators of environmental changes and as a model system for exploring ecosystem functioning (Nichols

and Gardner 2011). Furthermore, scarabaeine dung beetles have attracted attention as a promising model system in evolutionary developmental biology (evo-devo) and ecological development (eco-devo), especially horned dung beetles (Emlen et al. 2005, 2007, Emlen and Philips 2006, Moczek 2006, 2011).

The dung beetle subfamily, Scarabaeinae Latreille, 1802 (Coleoptera: Scarabaeidae) is the taxonomically richest in the superfamily Scarabaeoidea. It currently comprises 20 recognized tribes, 9 subtribes (Table 1) and various synonyms (see Davis et al. 2020) based on a synthesis derived from publications between 1985 and 2022 (Zunino 1985, Montreuil 1998, 2010, Smith 2006, Vaz-de-Mello 2008, Bouchard et al. 2011, Bousquet 2016, Philips, 2016, Tarasov and Dimitrov 2016, Tarasov 2017, Davis et al. 2019, Bouchard and Bousquet 2020, Daniel et al. 2020a, Rossini et al. 2022). It also comprises approximately 270 genera, 7,000 extant valid species (update from this study), and 23 fossil species (Tarasov et al. 2016, Tello et al. 2021, 2023).

Table 1. Breakdown of current recognized dung beetle tribes and subtribes with their respective type genera

Tribes	Subtribes	Type genus
Ateuchini Perty, 1830	Ateuchina Perty, 1830	<i>Ateuchus</i> Weber, 1801
	Scatimina Vaz-de-Mello, 2008	<i>Scatimus</i> Erichson, 1847
Byrrhidiini Davis, Deschodt & Scholtz, 2019		<i>Byrrhidium</i> Harold, 1869
Coprini Leach, 1815		<i>Copris</i> Leach, 1815
Deltochilini Lacordaire, 1855		<i>Deltochilum</i> Eschscholtz, 1822
Dichotomiini Pereira, 1954		<i>Dichotomius</i> Hope, 1838
Endroedyolini Davis, Deschodt & Scholtz, 2019		<i>Endroedyolus</i> Scholtz & Howden, 1987
Epactoidini Rossini, Grebennikov, Merrien, Miraldo, Viljanen & Tarasov, 2022		<i>Epactoides</i> Olsouffief, 1947
Epilissini van Lansberge, 1875		<i>Epilissus</i> Reiche, 1841
Epirinini van Lansberge, 1875		<i>Epirinus</i> Dejean, 1833
Eucraniini Burmeister, 1873		<i>Eucranium</i> Brullé, 1837
Eurysternini Vulcano, Martínez & Pereira, 1961		<i>Eurysternus</i> Dalman, 1824
Gymnopleurini Streubel, 1846		<i>Gymnopleurus</i> Illiger, 1803
Odontolomini Davis, Deschodt & Scholtz, 2019		<i>Odontoloma</i> Boheman, 1857
Oniticellini Kolbe 1905	Oniticellina Kolbe, 1905	<i>Oniticellus</i> Dejean, 1821
	Drepanocerina van Lansberge, 1875	<i>Drepanocerus</i> Kirby, 1828
	Helictopleurina Janssens, 1946	<i>Helictopleurus</i> d'Orbigny, 1915
	Attavicina Philips, 2016	<i>Attavicinus</i> Philips & Bell, 2008
	Liatongina Philips, 2016	<i>Liatongus</i> Reitter, 1892
Onitini Laporte, 1840		<i>Onitis</i> Fabricius, 1798
Onthophagini Streubel, 1846		<i>Onthophagus</i> Latreille, 1802
Parachoriini Tarasov, 2017		<i>Parachorius</i> Harold, 1873
Phanaeini Hope, 1838	Phanaeina Hope, 1838	<i>Phanaeus</i> MacLeay, 1819
	Gromphadina Zunino, 1985	<i>Gromphas</i> Brullé, 1837
Scarabaeini Latreille, 1802		<i>Scarabaeus</i> Linnaeus, 1758
Sisyphini Mulsant, 1842		<i>Sisyphus</i> Latreille, 1807

With the ecological importance of the dung beetle lineage, it should be no surprise that higher-level tribal classification has been a special focus of early dung beetle taxonomists since the time of Pierre André Latreille (1762–1833), who created the family Scarabaeidae. Although originally defined as ‘Scarabaeides’, this division was followed by subsequent separation into the subfamily Scarabaeinae Latreille, 1802, and subdivision into tribes, which commenced with the creation of the tribe, Scarabaeini Latreille 1802 based on its type genus, *Scarabaeus* Linnaeus, 1758 (Latreille 1802). A complex history of further subdivision (suffix ‘ides’, ‘aires’) or separation into groups (suffix ‘inae’, ‘idae’, ‘adae’) followed during the 19th century. However, these names were only formally (or not) designated as family-group names with an ‘ini’ suffix in the 20th century when rules on the structure of family-group names were introduced by the International Commission on Zoological Nomenclature [henceforth the Code] (Bock 1994). Thus, eleven of the 12 tribes recognized in the review of Smith (2006) had been already defined by the beginning of the 20th century (Table 1), with the exception of the Eurysternini Vulcano, Martínez & Pereira, 1961. Subsequent to 2006, a further 8 tribes and 4 subtribes have been added (Vaz-de-Mello 2008, Montreuil 2010, Philips 2016, Tarasov and Dimitrov 2016, Tarasov 2017, Davis et al. 2019, Daniel et al. 2020a, Rossini et al. 2022) by re-validating old names or defining new family-group names, partly,

though not entirely, driven by the development of phylogenies for the subfamily.

Phylogenies are responsible for an effort to provide a tribal classification that reflects evolutionary diversification within the subfamily Scarabaeinae. Following the advent of cladistic phylogenetic methods in the 1950s, the inferences of dung beetle phylogenies were first based on morphological characters but were succeeded from the early 2000s by the additional use of molecular data, a progression that was accompanied by the diversification of analytical methodology, such as parsimony, maximum likelihood and Bayesian (Baum and Smith, 2012). Details of the majority of earlier studies were thoroughly reviewed in Scholtz (2009) and Philips (2011). However, phylogenetic inferences based on molecular and morphological data are not always congruent, which led to a controversial discussion concerning which type of data is more reliable (Scotland et al. 2003, Jenner 2004, Wiens 2014). We concur that both molecular and morphological data are equally important in uncovering the evolutionary history and phylogeny of a given dung beetle lineage. However, the advantages of refined methods using molecular data include the large numbers of characters that are available, especially with the recent advent of targeted enrichment of ultraconserved elements (UCEs)-based phylogenomics (Faircloth et al. 2012), as well as sophisticated evolutionary models that may be implemented in molecular phylogenetic analyses (Hillis 1987).

Nevertheless, high technology notwithstanding, it is still challenging and extremely rare to obtain genetic material from fossils compared to morphological data that may be collected from both fossil and extant taxa. Fossils elucidate evolutionary history and generally maintain combinations of ancestral and derived characters (Hillis and Wiens 2000, Jenner 2004, Wiens 2004). Therefore, resolving the phylogenetic relationships of fossil taxa and their relationship to living taxa is the most compelling reason for the continued use of morphological data. Further evidence from fossils may illustrate patterns of evolution that are not apparent from purely molecular-based phylogenies.

Dung Beetle Tribal Classification

The first 3 attempts at collating and rationalizing tribal classification were empirical based on feeding or nesting behavior of dung beetles (Paulian 1933, Janssens 1949, Balthasar 1963). Balthasar's study divided the family Scarabaeidae into 2 subfamilies, Coprinae Leach, 1815 and Scarabaeinae Latreille, 1802, which were subdivided phenetically into 7 tribes of tunnelers, and 6 tribes of rollers. This system was followed by Halffter and Matthews (1966) and Halffter and Edmonds (1982), in their monographical studies of behavior and natural history of dung beetles as well as by Cambefort (1991). Subsequently, it was followed by most scarab workers until recent evidence of polyphyly in major groups and their breeding behavior indicated that the system was an artificial classification (Philips et al. 2004b).

The first morphologically-based phylogenetic analysis of the dung beetle subfamily of Scarabaeinae was conducted by Zunino (1983) followed by several regional and global studies based on both molecular and morphological data (for details see Scholtz 2009 and Philips 2011). This series of studies culminated in the 2 most comprehensive global phylogenies to date, 1 morphological (Tarasov and Génier 2015) and 1 molecular (Tarasov and Dimitrov 2016). Although these 2 studies did not provide a fully resolved phylogenetic tree for the subfamily, the molecular analysis provided a template for the current, complex, higher-level relationships between groups of dung beetle genera (Fig. 1). Based on this molecular phylogeny, a partial tribal revision of the subfamily was conducted and supported by diagnostic features with synapomorphies generated from the morphological phylogeny. Tarasov and Dimitrov's (2016) partial revision included a redefinition of concepts and diagnostic characters for the tribes Ateuchini Perty, 1830, Coprini Leach, 1815, Deltotomini Lacordaire, 1855, Dichotomiini Pereira, 1954 and Sisyphini Mulsant, 1842. Nevertheless, as a result of this revision, 100 genera are, in essence, currently unassigned to a tribe having been given the status of *incertae sedis* (Tarasov and Dimitrov 2016).

As a consequence of the latest global phylogenies (Tarasov and Génier 2015, Tarasov and Dimitrov 2016), partial tribal revisions are continuing with the revalidation or descriptions of new tribes (Tarasov 2017, Davis et al. 2019, Daniel et al. 2020a, Rossini et al. 2022; see summaries below) whilst driving a reevaluation of dung beetle biogeography. In essence, the molecular phylogeny (Fig. 1) supports earlier claims for an initial radiation of dung beetles from Africa (Sole and Scholtz 2010) that populated southern continents since basally derived elements are dominated by Afrotropical taxa and those in the center by clades of taxa dominated by Madagascar, Australasian, and Neotropical elements. The terminal clades are dominated by elements centered in the Afrotropical region, some of which have dispersed at a later date to both northern and southern continents along with a few taxa from more basally derived clades.

Although an over-simplification, these patterns are consistent with intercontinental faunal differences at either higher taxonomic level for older radiations or species level for more recent radiations (Davis et al. 2002, 2017, Davis 2009).

In this paper, we outline the current state of knowledge of tribal dung beetle classification and discuss the importance of taxon sampling for resolution in such a large phylogenetic tree. In addition, we discuss how morphology, and molecular data can be incorporated into our phylogenies to help to address questions in both dung beetle evolutionary biology and tribal classification.

The Current Status of Dung Beetle Tribal Classification

In this section, we give summaries of characteristics and relationships for each of the 20 currently recognized tribes (Table 1). A discussion is made of their validity in terms of monophyly versus non-monophyly with an indication of any revision needed to balance phylogeny with phenetically-based classification.

Tribe Ateuchini Perty, 1830

There has been a complex and utterly confused recent history of nomenclature and tribal or subtribal affiliations claimed for genera included in the tribes Ateuchini and Dichotomiini (see Martínez 1951, Pereira 1954, Montreuil 1998, Smith 2006, Vaz-de-Mello 2007, Bouchard et al. 2011, Tarasov and Dimitrov 2016, Davis et al. 2020). Until redefinition by Montreuil (1998) and Tarasov and Dimitrov (2016), these 2 names were used interchangeably for the same group of genera (Martínez 1951, Pereira 1954) and sometimes cited as subtribes of the Coprini (e.g., Halffter and Matthews 1966). Montreuil (1998) conducted a morphology-based phylogenetic analysis using 26 genera, then ascribed to the tribes Coprini or Dichotomiini, which supported division into 2 tribal groups, but with re-arrangement of membership. Because the 'Coprini-like' type genus of the Dichotomiini (*Dichotomius* Hope, 1838) was then placed in the Coprini, it was necessary to redefine the other clade, represented by *Ateuchus* and its relatives. Consequently it was defined as the tribe, Ateuchini, to accommodate the majority of scarabaeine genera with apically expanded mesotibiae and metatibiae (Montreuil 1998, Vaz-de-Mello 2008). Subsequently, Vaz-de-Mello (2008) divided this tribe into 2 subtribes, the Ateuchina and Scatimina (Table 1), describing a number of new genera for the Scatimina.

Although it was already known from previous phylogenies that the Ateuchini were polyphyletic (Philips et al. 2004b, Monaghan et al. 2007, Tarasov and Génier 2015), Tarasov and Dimitrov (2016) sequenced 21 of the genera studied by Montreuil (1998) and showed that they occurred in 13 different lineages scattered across the phylogeny. They redefined the Ateuchini to accommodate only 21 genera and 181 valid species distributed in the Neotropical and Nearctic regions (Vaz-de-Mello 2008, Génier 2015, Génier and Cupello 2018, Kohlmann and Vaz-de-Mello 2018, Lopera-Toro et al. 2020, Cupello 2022, Cupello et al. 2023) awarding all other former members of Afrotropical, Oriental, and Australasian genera the status of *incertae sedis*. Nevertheless, as recently redefined, the Ateuchini remain polyphyletic. *Ateuchus* is placed as sister to *Dichotomius* and *Canthidium* Erichson, 1847 whereas the Scatimina are split between 2 separate lineages with the type genus, *Scatimus* on one lineage and the other comprising the genera *Trichillum* Harold, 1868, *Trichilidium* Vaz-de-Mello, 2008 and *Leotrichillum* Vaz-de-Mello, 2008. These arrangements contrast with the morphological phylogeny published in the previous year (Tarasov and Génier 2015) in which *Ateuchus* and

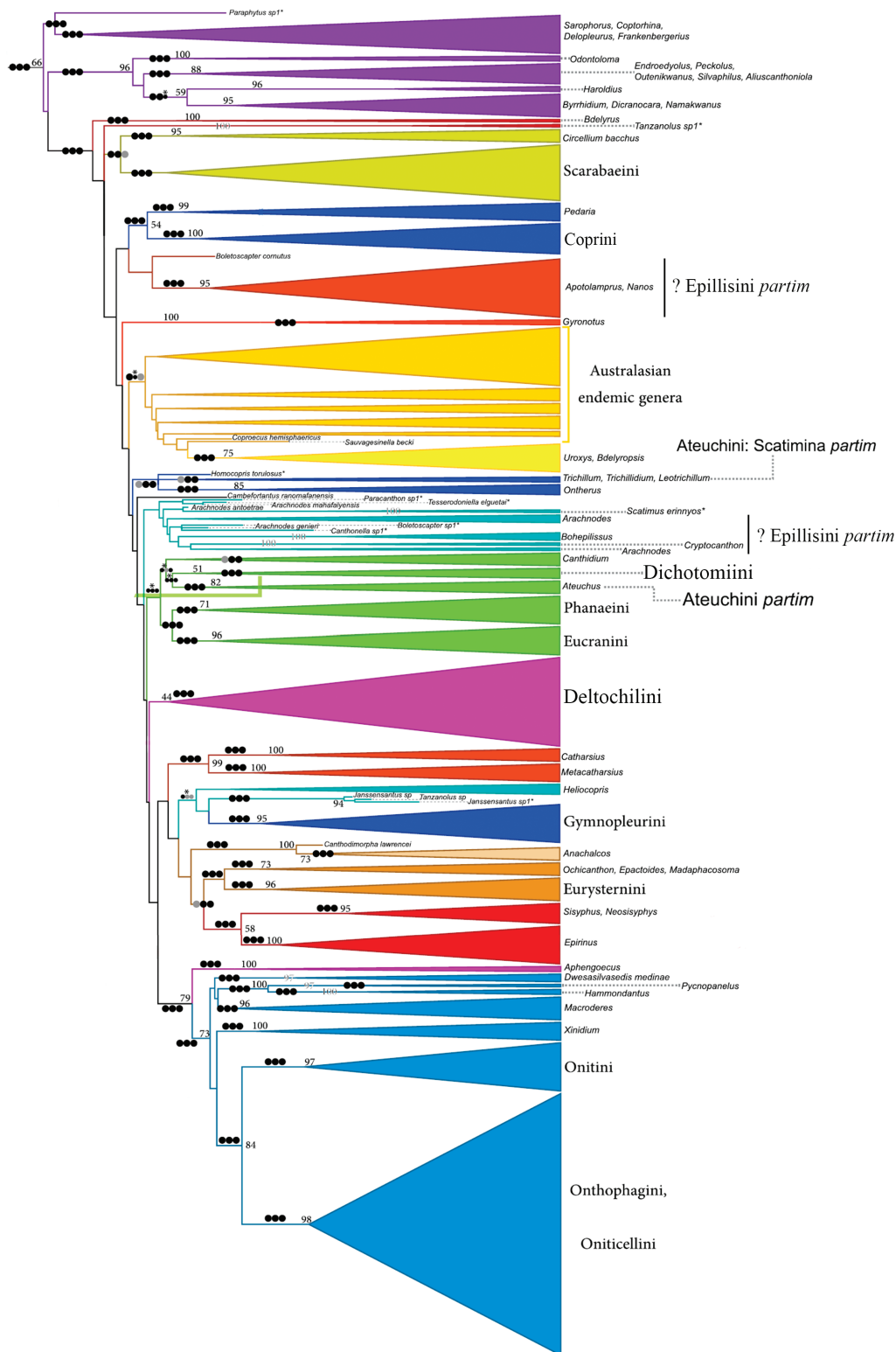


Fig. 1. Phylogram extracted and redrawn from Tarasov and Dimitrov (2016)—representing the most updated phylogeny of Scarabaeinae based on molecular data.

Dichotomius are distantly related and the genera of the Scatimina constitute a monophyletic group as also indicated by the phylogeny of Vaz-de-Mello (2007). Thus, further revision of the Ateuchini is required due to lack of published diagnostic traits and enduring discrepancies between phylogenies and classification (Fig. 1).

Tribe Byrrhidiini Davis, Deschodt & Scholtz, 2019

The flightless tribe, Byrrhidiini, was erected to accommodate 7 basally derived genera that were defined from within a clade of genera defined as ‘basal Scarabaeinae’ in the molecular study of Tarasov and Dimitrov (2016) but were previously included within

the Deltochilini. This monophyletic lineage is distributed in the arid to hyper-arid region along the southwest seaboard of Namibia and South Africa, where it seems to be associated, especially, with concentrations of dung found in communal middens of the rock hyrax or around heuweltjies comprising fossil termite mounds that attract small rodent communities (Deschodt et al. 2007, 2011, 2018). It comprises 13 valid species from 7 genera (Davis et al. 2019) that are sister to the new tribes Endroedyolini and Odontolomini (Fig. 1).

Tribe Coprini Leach, 1815

The tribe Coprini is shown to be polyphyletic in both global morphological and molecular phylogenies (Philips et al. 2004b, Monaghan et al. 2007, Tarasov and Génier 2015, Gunter et al. 2016, Tarasov and Dimitrov 2016). Tarasov and Dimitrov (2016) reduced the Coprini to only 5 genera comprising 300 species of which 1 genus (*Copris*) was widely distributed from the Afrotropical, Oriental and Palearctic to the Nearctic and Neotropical regions (Davis et al. 2008, 2020). To maintain monophyly within the Coprini, this decision leaves some former Afrotropical, Oriental, Australasian and Neotropical genera without certain tribal placement. Although past tribal names had been proposed for some elements from these regional faunas, these were cited as synonyms of the Coprini by Smith (2006) (Australian Coptodactylini Paulian, 1933) and Davis et al. (2020) (Neotropical Dichotomiini Hope, 1838). Although the recently phylogenetically-defined Coprini has not been fully resolved using morphological data (Tarasov and Génier 2015), this monophyletic lineage has been supported by other molecular studies (Monaghan et al. 2007, Gunter et al. 2016). Tarasov and Dimitrov (2016) provided tentative diagnostic characters for the redefined Coprini, which is crucial for taxonomic purposes. But, they failed to define the synapomorphies for the lineage due to a lack of morphological resolution. As 3 of the traditionally assigned genera were not included in the study and are, currently, *incertae sedis*, perhaps their inclusion in a full analysis of former Coprini may resolve the problem with synapomorphies of the redefined tribe. Such an approach would also aid the description of putative new tribes, such as the Catharsiini suggested for the genera *Catharsius* Hope, 1837, and *Metacatharsius* Paulian, 1939, by the unpublished study of Takano (2018) based on a clade in the phylogeny of Tarasov and Dimitrov (2016) that is distant from *Copris* (Fig. 1).

Tribe Deltochilini Lacordaire, 1855

Although Canthonini van Lansberge, 1875 (type genus *Canthon* Hoffmannsegg, 1817), was recommended as the name for this tribe on the basis of long-term usage (Smith 2006), it has recently been superseded by Deltochilini on the basis of precedence. This tribe formerly comprised the bulk of the scarabaeine genera (~60% = ~140 genera) based on just a few shared morphological features (see Scholtz 2009). However, both molecular and morphological systematics analyses have shown it to be highly polyphyletic and composed of numerous lineages (Philips et al. 2004b, Monaghan et al. 2007, Tarasov and Génier 2015, Tarasov and Dimitrov 2016). Tarasov and Dimitrov (2016) reduced the tribe, Deltochilini, to just 20 genera comprising 457 valid species that are endemic to the Neotropical and Nearctic regions where they are, essentially, sister to other prominent tribes and lineages of these 2 regions (Halffter and Martínez 1977, Vaz-de-Mello et al. 2011, González-Alvarado and Vaz-de-Mello 2014, 2021a, 2021b, Valois et al. 2015, Cupello and Vaz-de-Mello 2018, Nunes et al. 2018, 2020, Vaz-de-Mello and Cupello 2018, González-Alvarado et al. 2019, Sawaris et al. 2019, Silva and Valois 2019, Edmonds 2022, Halffter et al.

2022, Nunes and Vaz-de-Mello 2022, Cupello et al. 2023). To maintain monophyly within the Deltochilini this decision leaves many former Afrotropical, Madagascar, Oriental, Australian, and further Neotropical deltochiline genera without a certain tribal placement. Although past tribal names had been proposed for some elements from these regional faunas, these were cited as synonyms by Smith (2006) (Australian Mintophilini Lacordaire, 1855, Oriental Panelini Arrow, 1931, Afrotropical Epirinini van Lansberge, 1875, Madagascar Epilissini van Lansberge, 1875) with the latter 2 having been revalidated.

Tribe Dichotomiini Pereira, 1954

A phylogeny derived from analysis of morphological characters for 26 genera, then ascribed to the tribes Coprini or Dichotomiini, transferred the type genus of the Dichotomiini (*Dichotomius* Hope, 1838) to the Coprini (Montreuil 1998) making it a junior objective synonym. This was not recognized by the review of Smith (2006) who cited Dichotomiini as a synonym of Ateuchini and deemed the name unavailable, claiming that it did not meet the requirements of Article 13.2.1 of the Code (ICZN 1999), as it lacked formal description. However, having been published by Pereira (1954), Dichotomiini has been cited as valid on several subsequent occasions (Halffter and Matthews 1966, Halffter and Edmonds 1982, Zunino 1983, Montreuil 1998), which renders this tribal name available as corrected by Bouchard et al. (2011) and Tarasov and Dimitrov (2016). The last cited authors reerected the tribe Dichotomiini with a new concept for just 4 Nearctic and Neotropical genera comprising 215 valid species (Smith and Génier 2001, Rossini and Vaz-de-Mello 2015, 2017, Nunes and Vaz-de-Mello 2016, 2019, Montoya-Molina and Vaz-de-Mello 2021, Solís and Kohlmann 2022, Cupello et al. 2023). These dichotomiine genera are distantly related to members of the Coprini but sister to *Ateuchus* (Tarasov and Dimitrov 2016), which is the type genus of the Ateuchini as currently defined (Table 1).

Tribe Endroedyolini Davis et al. (2019)

The flightless tribe, Endroedyolini, was erected to accommodate 8 basally derived genera and 12 species (Davis et al. 2019) that were defined from within a clade of genera defined as 'basal Scarabaeinae' in the molecular study of Tarasov and Dimitrov (2016) but were formerly included in the polyphyletic tribe, Deltochilini. This monophyletic lineage is primarily distributed in coastal and escarpment forest patches along the extreme southwest, southern, and eastern seaboard of South Africa where they are found in the leaf litter (Deschodt and Scholtz 2008, Davis et al. 2019, 2020, Deschodt et al. 2020, Daniel et al. 2022). This endemic South African tribe is sister to the Byrrhidiini and Odontolomini.

Tribe Epactoidini Rossini et al. (2022)

The genera, *Ochicanthon* Vaz-de-Mello, 2003, *Epactoides* Olsouffief, 1947, and *Madaphacosoma* Paulian, 1975 (now *Grebennikovius* Mlambo, Scholtz & Deschodt, 2019), are included in the tribe Epilissini as defined by Montreuil (2010). However, in the molecular phylogeny of Tarasov and Dimitrov (2016), they are placed together in a clade that is distant from many genera of Epilissini but close to lineages of other former Afrotropical Deltochilini, plus the Sisyphini and Neotropical Eurysternini. Further combined morphological and molecular analysis of the group confirmed their monophyletic relationship and led to their inclusion in the new tribe, Epactoidini (Rossini et al. 2022) comprising 3 genera and 92 valid species. The tribe occupies disjunct forest distributions hypothesized to represent

past radiation from Tanzania to Madagascar, Réunion (extinct species) and the Oriental region (Rossini et al. 2021, 2022).

Tribe Epilissini van Lansberge, 1875

Although this tribe has not been recognized in 2 recent global phylogenies (Tarasov and Génier 2015, Tarasov and Dimitrov 2016), it has been cited in other systematic works (Montreuil 2010, 2011, 2021, Montreuil and Théry 2011, 2016, Montreuil and Viljanen 2011, 2022, Montreuil et al. 2014, Gunter et al. 2016). It was revalidated on morphological grounds for a group of former deltochiline genera characterized by apically truncated protibiae with a straight margin and a well-marked cavity on each side of the prosternum (Montreuil 2010). It includes 25 genera from 5 biogeographical regions: Madagascar, New Caledonia, Afrotropical, Neotropical, Oriental. However, these genera are scattered between different lineages on the phylogenetic trees of Tarasov and Génier (2015), Gunter et al. (2016), plus Tarasov and Dimitrov (2016). Based on the latter phylogeny, 3 lineages assigned to the tribe Epilissini have been, subsequently, classified in other tribes (see Davis et al. 2019, Rossini et al. 2022). On phylogenetic grounds, the Epilissini comprises a non-natural group and requires revision, so the number of its constituent taxa will not be provided until further phylogenetic assessment.

Tribe Epirinini van Lansberge, 1875

Formerly assigned to the Deltochilini (Philips et al. 2004b, Medina and Scholtz 2005, Mlambo et al. 2015), the genus *Epirinus* Dejean, 1833, has been consistently shown as sister to the Sisyphini (Monaghan et al. 2007, Tarasov and Génier 2015, Gunter et al. 2016, Tarasov and Dimitrov 2016). Thus, Tarasov and Dimitrov (2016) transferred the genus to the tribe, Sisyphini *sensu novo*. Subsequently, Daniel et al. (2020a) pointed out morphological, evolutionary, and biogeographical differences between the 2 sister-lineages, and re-separated them into 2 tribes. The Epirinini is monobasic comprising 31 valid species endemic to southern Africa (Deschodt et al. 2019, Daniel et al. 2021). Although species are distributed from north-east to southwest regions of South Africa, the highest diversity is recorded in the south-east. Single species are also recorded in eSwatini (*Epirinus davis* Scholtz & Howden, 1987) and jointly in South Africa and Namibia (*Epirinus flagellatus* Fabricius, 1775) (Deschodt et al. 2019, Daniel et al. 2020a, 2021, Davis et al. 2020).

Tribe Eucraniini Burmeister, 1873

The endemic, Neotropical tribe, Eucraniini, has been consistently recovered as a monophyletic lineage (Philips et al. 2002) and sister group to the Neotropical and Nearctic tribe Phanaeini (Philips et al. 2004) plus a lineage comprising Ateuchini + Dichotomiini and *Canthidium* (Ocampo and Hawks 2006, Gunter et al. 2016, Tarasov and Dimitrov 2016). It comprises 14 valid species in 4 genera with distributions in desert-thorn habitats of the Chaco and Monte biogeographical provinces of Argentina (Ocampo 2004, 2005, 2007, 2010a, 2010b).

Tribe Eurysternini Vulcano, Martínez & Pereira, 1961

Described to accommodate a single genus, the Eurysternini is a somewhat enigmatic tribe on the basis of its various hypothesized sister relationships and specialized endocoprid breeding behavior within droppings (Halfpter and Matthews 1966, Halfpter and Edmonds 1982). The morphological phylogeny of Philips et al. (2004b) recovered the Eurysternini as monophyletic and sister to a lineage

composed of Onitini, Onthophagini and Oniticellini. Subsequent molecular phylogenies did not support this finding placing the tribe as sister to the Neotropical genus, *Canthidium* (Ocampo and Hawks 2006, Monaghan et al. 2007). Nevertheless, Génier (2009) downgraded the Eurysternini to a subtribe of the Oniticellini while revising the genus *Eurysternus*. However, recent morphological (Tarasov and Génier 2015) and molecular studies (Gunter et al. 2016, Tarasov and Dimitrov 2016) unequivocally support monophyly and tribal status of the Eurysternini. But, in the latter 2 molecular studies, it has been recovered as sister to the tribes Epactoidini + Sisyphini + Epirinini. The Eurysternini is monobasic comprising 53 valid species, all endemic to the Neotropical Region (Génier 2009).

Tribe Gymnopleurini Streubel, 1846

Monophyly of the ball-rolling tribe, Gymnopleurini, has been supported in all earlier global phylogenies of the subfamily (Philips et al. 2004b, Monaghan et al. 2007) up to the most recent where it emerged as sister to *Eurysternus* + *Onthophagus* + *Heliocopris* and *Epirinus* + *Neosisyphus* Müller, 1942 in the morphological phylogeny of Tarasov and Génier (2015) but sister to *Janssensantus* Paulian, 1976 + *Tanzanolus* Scholtz & Howden, 1987 and *Heliocopris* Hope, 1837, in molecular phylogenies (Gunter et al. 2016, Tarasov and Dimitrov 2016). The tribe is Afro-Eurasian comprising 121 valid species classified in 4 genera, 1 Afro-Eurasian, 2 Afro-Oriental, and 1 Oriental (Kabakov 2006, Davis et al. 2008, 2020, Pokorný and Zidek 2009, Pokorný and Zidek 2018, Davis and Deschodt 2018).

Tribe Odontolomini Davis, Deschodt & Scholtz, 2019

The monobasic Odontolomini was erected to accommodate a single genus, *Odontoloma*, which was defined from within a clade of genera defined as ‘basal Scarabaeine’ in the molecular study of Tarasov and Dimitrov (2016) having been formerly included with the Deltochilini. The monophyly of the tribe has not been tested since previous phylogenies used only 1 to 2 representative species of the genus. It was recovered as sister to the Endroedyolini and Byrrhidiini in the molecular phylogeny of Tarasov and Dimitrov (2016). Although found to be sister to the former ateachine genera *Frankenbergerius* Balthasar, 1938, + *Sarophorus* Erichson, 1847 + *Coptorhina* + *Delopleurus* Erichson, 1848, by Mlambo et al. (2015) these genera comprise a second clade in the ‘basal Scarabaeine’ of Tarasov and Dimitrov, 2016. The Odontolomini is endemic to the Afrotropical region and, currently, comprises 20 extremely small-bodied species (~ 2.5 mm in length) although ongoing revision suggests dozens of new species await description (GM. Daniel unpublished). *Odontoloma* shows a wide, disjunct occurrence with the majority of described species restricted to southern Africa. The remaining species are distributed in West, Central, and East Africa. Their ranges are primarily situated in cooler southern climates, upland regions, or forests (Howden and Scholtz 1987, Davis et al. 2020), however, their behavior remains unknown.

Tribe Oniticellini Kolbe 1905

The tunneling or endocoprid Oniticellini emerged as monophyletic or paraphyletic depending on the weighting applied to morphological data (Philips 2016) whereas the sister Onthophagini was always monophyletic. Conversely, monophyly for the Oniticellini was supported in several phylogenies using both molecular and morphological data (Monaghan et al. 2007, Tarasov and Solodovnikov 2011, Tarasov and Génier 2015, Mlambo et al. 2015, Breeschoten et al. 2016, Tarasov and Dimitrov 2016, Guo et al. 2022) although

these studies consistently recovered the Oniticellini nested within the Onthophagini, which rendered the latter tribe paraphyletic. Although the 2 tribes have been traditionally distinguished by 2 morphological characteristics, some members of both tribes share these features; viz. the number of antennomeres and visibility of the scutellum. Because of insufficient morphological differences between these tribes, there is enough evidence to downgrade Oniticellini from tribal to subtribal status within the Onthophagini. Although we recognize that a revision is needed to balance the phylogenetic evidence with tribal classification (see Kabakov 2006, Wirta et al. 2008, Tarasov and Solodovnikov 2011), there is a problem in that Oniticellini are currently, themselves, divided into 5 subtribes (Afro-Oriental and Caribbean Drepanocerina van Lansberge, 1875; Afro-Eurasian and Caribbean Oniticellina Kolbe, 1905, Madagascar Helictopleurina Janssens, 1946; Afro-Oriental and western Nearctic Liatongina Philips, 2016; northern Neotropical Attavicina Philips, 2016). The latter 2 subtribes were created to maintain monophyly within the oniticelline lineages. As currently constituted, the Oniticellini comprise 24 genera and 257 valid species (Roggero et al. 2015, Philips 2016).

Tribe Onitini Laporte, 1840

Monophyly of the tunneling Onitini, has been supported by most morphological and molecular phylogenies together with a clear sister relationship to the Oniticellini and Onthophagini (Villalba et al. 2002, Philips et al. 2004b, Monaghan et al. 2007, Mlambo et al. 2015, Breeschoten et al. 2016, Gunter et al. 2016, Tarasov and Dimitrov 2016, Guo et al. 2022). The morphological study of Tarasov and Génier (2015) is an exception where the Onitini emerged as a sister to *Dwesasilvasedis* Deschodt & Scholtz, 2008, with both nested within a clade composed of *Catharsius* Hope, 1837 + *Metacatharsius* Paulian, 1939 + *Macroderes* Westwood, 1842 + *Xinidium* Harold, 1869. The Onitini comprises 18 genera and 238 species (Davis et al. 2008, 2020). *Cheironitis* van Lansberge, 1875 and *Onitis* Fabricius, 1798, show the highest species diversity with a distribution extending across the Afrotropical, Palearctic and Oriental Regions. The other 16 genera each comprise 1 to 5 species and are endemic to the Afrotropical Region, bar for the genus, *Bubas* Dejean, 1833, which is endemic to the Palearctic (Janssens 1937, Davis et al. 2008, 2020, Scholtz et al. 2009).

Tribe Onthophagini Streubel, 1846

In several molecular studies, the primarily tunneling Onthophagini is shown to be paraphyletic with respect to the nested tribe, Oniticellini (Ocampo and Hawks 2006, Monaghan et al. 2007, Mlambo et al. 2015, Breeschoten et al. 2016, Tarasov and Dimitrov 2016, Guo et al. 2022). Nevertheless, in the latest morphological phylogeny devoted to just the Oniticellini and Onthophagini, Philips (2016) recovered the latter tribe as a monophyletic lineage, probably due to the high level of homoplasies for morphological characters used in the study. Revisionary work is required to develop a natural classification for Onthophagini, based on a phylogenetic reassessment using both morphological and molecular data for representatives of all genera traditionally classified in the Onthophagini. At the present time, the Onthophagini comprises approximately 42 genera and over 3000 species (d'Orbigny 1913, Davis et al. 2008, 2020, Scholtz et al. 2009, Philips 2016, Josso and Génier 2019, Dierkens 2022, Daniel et al. 2023, Josso 2023, Schoolmeesters 2023) with various new genera added recently by raising the status of species groups in the most speciose genus, *Onthophagus* Latreille, 1802 (Dierkens et al. 2017, Roggero et al. 2017, Ochi et al. 2017). Some of the genera are widespread in 2 or

all 3 regions comprising AfroEurasia whereas *Onthophagus* shows a global distribution in warmer parts of the world. However, many of the genera are Afrotropical or Oriental endemics.

Tribe Parachoriini Tarasov, 2017

The tribal placement of the genus, *Parachorius* Harold, 1873, has been problematic with previous researchers placing it in the Pinotini (=Dichotomiini) (Balthasar 1963) followed by transfer to the Coprini (Vaz-de-Mello 2008). Using both molecular and morphological data, Tarasov (2017) investigated its tribal position and found a well-supported monophyletic lineage composed of *Parachorius* + *Cassolus* Sharp, 1875, after removal of several species misidentified as *Cassolus*. The misidentifications may be the reason *Cassolus* was classified as a canthonine (Halffter and Matthews 1966) and then as an onthophagine (Hanski and Cambefort 1991), a placement that was studied but questioned by Philips (2016). The corrected results of Tarasov (2017) supported the synonymy of the former deltochiline/onthophagine *Cassolus* with *Parachorius*. As the lineage emerged as sister to the tribes Epactoidini and Eurysternini on the phylogeny of Tarasov (2017), it was described as a new monobasic tribe, Parachoriini. *Parachorius* comprises 19 species of unknown habits and is widely distributed across much of the Oriental region, except Borneo and the Philippines, with some representatives in the south-east Palearctic (Tarasov 2017).

Tribe Phanaeini Hope, 1838

Although the morphological phylogeny of Philips et al. (2004a) showed the Neotropical *Dichotomius* Hope, 1838 + Oriental/Palearctic *Synopsis* Bates, 1868 + Afrotropical/Oriental *Heliocopris* Hope, 1837, as the sister group of the tunneling tribe of Phanaeini, all other morphological and molecular phylogenies support the Neotropical Eucraniini as the sister tribe (Philips et al. 2004b, Ocampo and Hawks 2006, Monaghan et al. 2007, Vaz-de-Mello 2007, Tarasov and Génier 2015, Gunter et al. 2016, Tarasov and Dimitrov 2016, Gillett and Toussaint 2020). But, whilst the earliest morphological phylogeny supported monophyly (Philips et al. 2004b), a more recent molecular analysis indicated that the tribe was paraphyletic with the genus *Gromphas* Brullé, 1837, closely related to the Neotropical/ Nearctic genera, *Ateuchus* + *Dichotomius*, and, remarkably, to the Madagascar *Apotalamprus* d'Olsouffief, 1947 + *Nanos* Westwood, 1842. This suggests the need for a systematic reassessment and redefinition of the tribe although it is already separated taxonomically into 2 subtribes comprising the Phanaeina Hope, 1838, and the Gromphadina Zunino, 1985, which include just *Gromphas* and *Oruscatus* Bates, 1870, with the latter not sequenced by Gillett and Toussaint (2020). However, they show some paraphyly within the Phanaeina where 1 species of *Coprophanaeus* (*Metallophanaeus*) Olsouffief, 1924 was nested in the lineage of *Dendropaemon* Perty, 1830, and *Megatharsis* Waterhouse, 1891 and several species of *Oxysternon* Laporte, 1840 were nested in the lineage of *Phanaeus* MacLeay, 1819 (Gillett and Toussaint 2020). Nevertheless, there is strong morphological evidence for monophyly in *Coprophanaeus* (Philips et al. 2004b). As it presently stands, the Phanaeini is endemic to the Neotropical and Nearctic regions where it comprises 216 valid species in 11 genera (Génier and Patrick 2016, Gillett and Toussaint 2020, Moctezuma and Halffter 2021, Cupello et al. 2022, 2023, Halffter et al. 2022).

Tribe Scarabaeini Latreille, 1802

The Scarabaeini has been retrieved as monophyletic in all morphological and molecular phylogenies (Mostert and Scholtz 1986,

Villalba et al. 2002, Forgie et al. 2005, 2006, Monaghan et al. 2007, Mlambo et al. 2015, Gunter et al. 2016) and was shown to be sister to the former deltochiline, *Circellium* Latreille, 1829, by both the morphological study of Philips et al. (2004b) and the molecular study of Tarasov and Dimitrov (2016). However, there has been a much recent conflict regarding the status of included taxa. Forgie et al. (2005) reduced the membership to only 2 genera, *Pachylomera* Griffiths & Pidgeon, 1831, and *Scarabaeus* Linnaeus 1758. Three genera were made subgenera of *Scarabaeus* and another 6 were synonymized with that genus. Subsequently, some of these taxa plus various others have been revalidated at generic level or newly described, so that this Afro-Eurasian tribe currently comprises 11 genera and 172 species (Forgie et al. 2006, Davis et al. 2008, 2020, Zidek and Pokorný 2008, 2011, Ziani and Gudenzi 2012, Moretto 2016, Moretto and Deschamps 2023).

Tribe Sisyphini Mulsant, 1842

The Sisyphini have been retrieved as monophyletic in several morphological and molecular studies (Philips et al. 2004b, Monaghan et al. 2007). Although the history of different cited sister groups is complex (Daniel et al. 2020a, 2020b), the tribe was recently placed as sister to the Afrotropical, former deltochiline genus, *Epirinus* (Tarasov and Dimitrov 2016). This juxtaposition led Tarasov and Dimitrov (2016) to combine the 2 lineages as the tribe, Sisyphini *sensu novo*. Subsequently, this arrangement was overturned on evolutionary, morphological and biogeographical grounds (Daniel et al. 2020a) resulting in separation of the 2 lineages as the Sisyphini, in its former strictest sense, and the revalidated tribe, Epirinini. Recent phylogenetic studies using molecular (Daniel et al. 2020a, 2020c) and morphological data (Daniel 2019) supported the monophyly of the tribe and its sister relationship with the Epirinini. However, the studies of Daniel et al. (2020a) and Daniel et al. (2020c) on southern African sisyphines showed that the genus *Sisyphus* Latreille, 1802 was paraphyletic relative to *Neosisyphus* Müller 1942. A partial taxonomic revision of the tribe was effected by reinstating the subgeneric status of *Neosisyphus* and downgrading the status of the genus *Parasisyphus* Barbero, Palestini & Zunino, 1991 to a subgeneric rank. Currently, the tribe is now composed of 104 valid species classified in 3 genera, the Oriental *Indosisyphus*, Barbero, Palestini & Zunino, 1991, the Mauritius *Nesosisyphus* Vinson, 1946 and the Afro-Eurasian and north Neotropical *Sisyphus* comprising 3 subgenera, the nominotypical *Sisyphus*, *Neosisyphus* and *Parasisyphus* (Daniel, 2019, Daniel et al. 2020c). Nevertheless, an unpublished phylogenetic study on Mauritius sisyphines suggests that *Nesosisyphus* comprises a lineage nested within the genus *Sisyphus* (F. Losacco et al. unpublished), suggesting that a global revision of generic classification of sisyphines is urgently needed.

Conclusions

Progress, Problems and Prospects

Progress would be represented by support for phenetic classification from global phylogenies with efforts to resolve any discrepancies. The most recent global phylogeny (Tarasov and Dimitrov 2016) provided variable statistical support for 8 tribes and generated redefined generic membership for the other 4 listed in the review of Smith (2006). Further tribes have subsequently been defined based on phylogeny (Tarasov 2017, Davis et al. 2019, Daniel et al. 2020a, Rossini et al. 2022).

Problems would be represented by difficulties in developing a consistent method for defining tribes from phylogenies. For instance,

along a standardized 1-0 distance from the basal node for the subfamily (Fig. 1), basal nodes for current tribes are defined at an inconsistent range that varies between 0.8-0.3 (Davis et al. 2019). At the mean distance, the topology defines a complex arrangement of sister-lineages that would represent many putative new tribes, up to 50 or more, several comprising a single genus. The high potential number of tribes raises questions on whether the tribal system is a useful tool. Answering this question requires further study.

Thus, prospects would be represented by 2 principal efforts. It is (i) necessary to improve phylogenies through inclusion of further rare and common genera to both increase biogeographical coverage and better resolve within group relationships and membership. It is also necessary (ii) to improve phylogenetic inference using new methodologies that provide more comprehensive results by including powerful computing facilities to process high amounts of data.

A Road Map to Build a High-resolution Phylogeny of Dung Beetles and Natural Tribal Classification

It is clear that a well resolved, densely sampled tree will be needed to answer many key questions in the evolutionary biology of dung beetles at various time scales, from deep to shallow phylogenetic divergences. A dense sampling of genera and species is necessary as studies of diversification patterns are sensitive to taxon sampling biases. Furthermore, studies of trait evolution benefit from the increased power of large numbers of gains and losses. Although it is easier to generate a well represented morphology-based global phylogeny of dung beetles, for a more comprehensive understanding of relationships, it is necessary to develop a more integrated approach using both molecular and morphological data. The main problem lies in how we get fresh material suitable for DNA extraction that covers all global representatives of all genera in the subfamily Scarabaeinae.

Given the challenges of obtaining fresh samples for rare dung beetle taxa suitable for DNA extraction. Therefore, it is, perhaps, time to shift to phylogenomic methods that are less-demanding in terms of quality, such as target-enrichment procedures that focus on Ultraconserved Elements (UCEs), which are highly conserved regions within the genome that are shared among evolutionary distant taxa (Faircloth et al. 2012, Faircloth 2017). In particular, 2 new UCEs probe sets have been recently designed for the subfamily Scarabaeinae (Scarabaeidae) and superfamily Hydrophiloidea (Gustafson et al. 2023). Compared to similar methods, such as Anchored Hybrid Enrichment, BaitFisher (Mayer et al. 2016), and Hyb-Seq (Weitemier et al. 2014), UCEs have proven useful in resolving phylogenies at both shallow and deep phylogenetic scales in several groups of Coleoptera, including Adephaga (Baca et al. 2017, 2021, Gustafson et al. 2020), Elmidae (Kobayashi et al. 2021), Carabidae (Sota et al. 2022), Curculionidae (Van Dam et al. 2017) and Scirtidae (Bradford et al. 2022) although they have not yet been applied in dung beetles. This phylogenomic technique is focused on selecting and capturing genomic regions from DNA prior to sequencing, thus targeting many more loci (>1000—Zhang et al. 2019) than previous global molecular phylogenies for the subfamily Scarabaeinae. These studies were based on the Sanger, sequencing-based, multilocus, molecular phylogenetic method that used only a few gene regions, i.e., 3 gene regions (Monaghan et al. 2007, Gunter et al. 2016), 4 gene regions (Ahrens et al. 2014) and 8 gene regions (Tarasov and Dimitrov 2016).

Besides generating a high volume of data compared to traditional, restriction enzyme-based, Sanger sequencing methods, the UCEs approach offers a high rate of success with degraded or low quantity DNA samples (Zhang et al. 2019). With that in mind, we

can generate global molecular data for Scarabaeinae using specimens in museum collections that are mostly old and dried but represent both rare and common taxa from all biogeographical regions. In contrast to the UCEs approach, the restriction enzyme-based technique requires high-quality DNA or RNA from fresh or carefully preserved specimens (Blaimer et al. 2016, Lim and Braun 2016, Ruane and Austin 2017, Zhang et al. 2019). This new phylogenomic approach should be integrated with morphology-based phylogeny as the main objective is to provide a tree of life and natural tribal classification of dung beetles. Only a morphological-based phylogenetic assessment will provide the required tools for diagnosing and identifying dung beetle taxa. Furthermore, a recent revision of dung beetle fossils (Tarasov et al. 2016) should also be used as paleontological evidence for phylogenetic and biogeographical inferences in dung beetle lineages.

Author Contributions

Gimo Daniel (Conceptualization [Lead], Data curation [Lead], Formal analysis [Equal], Investigation [Lead], Methodology [Lead], Project administration [Lead], Validation [Equal], Writing—original draft [Lead], Writing—review & editing [Lead]), and Adrian Davis (Conceptualization [Lead], Data curation [Equal], Formal analysis [Lead], Investigation [Equal], Methodology [Equal], Resources [Equal], Validation [Equal], Writing—original draft [Supporting], Writing—review & editing [Lead])

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