Biogeographical and co-evolutionary origins of scarabaeine dung beetles: Mesozoic vicariance vs Cenozoic dispersal and dinosaur vs mammal dung

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Abstract

The subfamily Scarabaeinae (Coleoptera: Scarabaeidae) may have originated in Gondwanaland, through Mesozoic vicariance or dispersal in association with dinosaur dung, or, through Cenozoic dispersal in association with mammal dung. We review evidence from age-calibrated phylogenies, fossil records, biogeographical patterns, and ecological associations. Fossil calibrated phylogenies for Scarabaeoidea predict Cretaceous origin for Scarabaeinae although age estimates would rely on other scarabaeoid groups given doubtful validity of Mesozoic "scarabaeine" fossils. Molecular clock calibrated phylogenies for Scarabaeinae predict early Cenozoic origin coeval with modern mammal diversification. Trace fossil evidence suggests exploitation of dinosaur dung by fossorial insects although scarabaeine fossils are only validated for the Cenozoic. Although we discuss fossil evidence for dinosaur dung as a faunal resource, origin of modern scarabaeines from an earlier Mesozoic vicariant or dispersal fauna remains unsupported. Although clock-constrained, phylogram topography is consistent with early Cenozoic palaeoclimatic and palaeoecological events, Eocene marine barriers would demand dispersal to explain distributional origins of Scarabaeinae. Inconsistencies between classification and phylogeny complicate biogeographical analysis but earlier southern radiation of basally-derived tribes has probably been followed by later diversification and global dispersal of both basally and terminally-derived taxa, primarily via restored land links.

INTRODUCTION

Questions on evolutionary origins of dung beetles in the subfamily Scarabaeinae (Coleoptera: Scarabaeidae) have focused on evidence from food specialization (Scholtz & Chown, 1995), fossil records (Chin & Gill, 1996; Krell, 2000), spatial distribution patterns (Davis, Scholtz & Philips, 2002; Davis, 2009), and temporal frameworks derived from classification (Cambefort, 1991a) or morphological (Philips, Pretorius & Scholtz, 2004; Tarasov & Génier, 2015) and molecular phylogenies (Monaghan *et al*., 2007; Sole & Scholtz, 2010; Ahrens, Schwarzer & Vogler, 2014; Gunter *et al*., 2016**)**. Two evolutionary biogeographical hypotheses have resulted. Different studies support spatio-temporal origins in Mesozoic vicariance, Mesozoic dispersal or Cenozoic dispersal with trophic origins on dinosaur or mammal dung. The present review examines the merits of hypotheses with regard to trophic, spatial, temporal and fossil evidence.

Food specialization has led to dominance of dung-feeding and has clearly played an important role in driving evolution of the subfamily. Early opinion considered scarabaeine beetles to be established (Halffter, 1972) and associated with dinosaurs (Jeannel, 1942) by the mid to late Mesozoic. However, there is only limited fossil evidence for exploitation of dinosaur dung by a fossorial Cretaceous fauna (Chin & Gill, 1996). Whilst some have considered such associations not unlikely for scarabaeines (Davis *et al*., 2002, Gunter *et al*., 2016**)** others have viewed them as questionable (Arillo & Ortuño, 2008; Davis, 2009**)**. As association with mammal dung dominates in the extant scarabaeine fauna, Cambefort (1991b) considers that dung beetle specialization was driven by co-evolution with early Cenozoic diversification of modern mammals **(**Halliday & Goswami, 2016**)**. However, accurate determination of scarabaeine temporal origins is required to ascertain the most likely historical drivers of subfamily food associations.

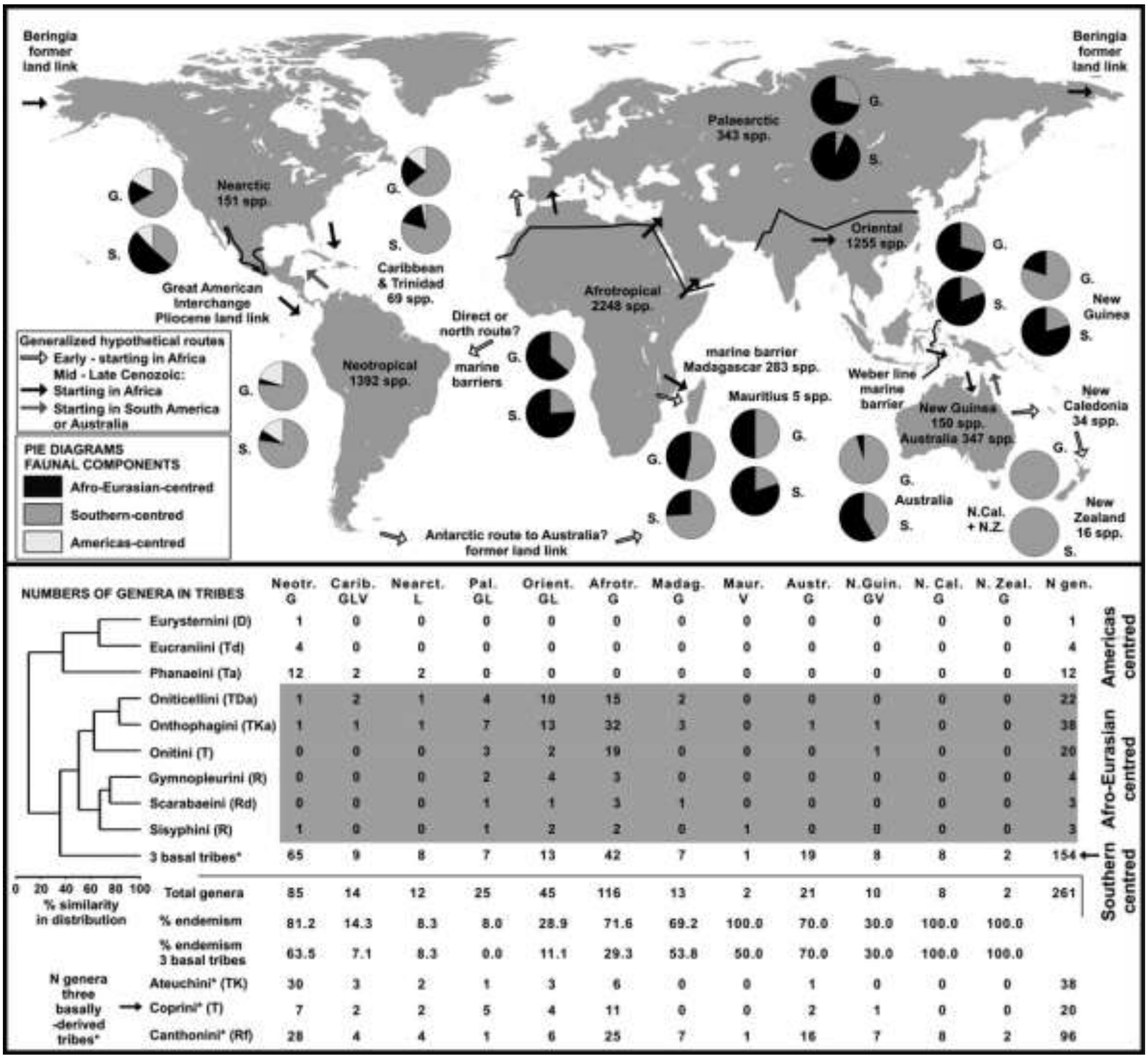
Several methods have been used to determine temporal origins of Scarabaeinae. Based on plesiomorphic versus apomorphic characterization, Cambefort (1991a) used the classification system to divide the subfamily into old, intermediate and modern tribes. A subsequent global morphological phylogeny (Philips *et al*., 2004) supported the old, basal derivation of some tribes (Canthonini and Dichotomiini) and added one other (Coprini). It also suggested polyphyly in basally-derived tribes and monophyly in the remaining, nine, terminally-derived tribes. A subsequent global molecular phylogeny (Monaghan *et al*., 2007) emphasized extensive polyphyly in three basally-derived tribes but suggested paraphyly in the most-diversified of the derived tribes (Onthophagini). Subsequent fitting of absolute age scales to molecular phylogenies supports Cenozoic origin for those calibrated using sequence divergence rates (Davis, 2009; Sole & Scholtz, 2010; Mlambo, Sole & Scholtz, 2015) but suggests Mesozoic origin for those calibrated using fossils (Ahrens *et al*., 2014; Gunter *et al*., 2016).

Global distribution data have been used to define geographical patterns and predict both temporal origins and generalized intercontinental tracks. Using multivariate analyses of generic distribution patterns in each tribe, Davis *et al*. (2002) defined three principal patterns predominantly centred on southern Gondwanaland fragments (Canthonini, Dichotomiini, Coprini), the Americas (Eucraniini, Eurysternini, Phanaeini) or Afro-Eurasia (Scarabaeini, Gymnopleurini, Sisyphini, Onitini Onthophagini, Oniticellini). These patterns were hypothesized to represent an early origin in Gondwanaland vicariance followed by Cenozoic dispersal via northern continents. One hypothesized Cenozoic track has subsequently been supported by a phylogeny of species in the tribe, Onthophagini (Emlen *et al*., 2005). This extends northwards from Africa into Eurasia, continues to Australia and both North and South America. Reciprocal invasions from South to North America and vice versa (Davis, 2009) were hypothesized as dating from the Pliocene during the Great American Interchange. The northwards track had been previously supported by phylogenetic relationships within the predominantly Neotropical genera, *Ateuchus* Weber and *Canthon* Hoffmannsegg (Kohlmann & Halffter, 1988; 1991).

The extensive polyphyly in basally-derived tribes (Monaghan *et al*., 2007) suggests that early diversification and biogeographical history is poorly understood compared to that supported for the later Cenozoic (Emlen *et al*., 2005; Kohlmann & Halffter 1988; 1991). Furthermore, this polyphyly weakens an earlier, global, multivariate biogeographical analysis (Davis *et al*., 2002) that was based on the now suspect "classic" tribal classification system. However, in essence, the same three groups were generated by a subsequent analysis in which the generic membership of basally-derived tribes was collapsed into a single unit (Davis, 2009). Even so, there is current conflict in all lines of investigation. Therefore, this review re-examines some principal areas of contention, particularly those relating to evolutionary age, origin of coprophagy and processes responsible for current biogeographical patterns.

EVOLUTIONARY HYPOTHESES

Hypothesis (1): Origin in Mesozoic vicariance or dispersal between fragments of Gondwanaland followed by diversification and global dispersal across restored late Cenozoic land links or narrow marine barriers between continents. Dietary specialization driven, variously, by increasing spatial frequency, suitability and size of vertebrate droppings, either those of dinosaurs, mammals or both. Hypothesis supported by the centring of basally-derived tribes on southern fragments of Gondwanaland (Davis *et al*., 2002; Fig. 1) with renewed support from recent molecular phylogenies calibrated using fossils (Ahrens *et al*., 2014; Gunter *et al*., 2016).



NUMBERS OF GENERA IN TRIBES	Neotr. G	Carib. GLV	Nearct. L	Pal. GL	Orient. GL	Afrotr. G	Madag. G	Maur. V	Austr. G	N.Guin. GV	N. Cal. G	N. Zeal. G	N gen.
Eurysternini (D)	1	0	0	0	0	0	0	0	0	0	0	0	1
Eucraniini (Td)	4	0	0	0	0	0	0	0	0	0	0	0	4
Phanaeini (Ta)	12	2	2	0	0	0	0	0	0	0	0	0	12
Oniticellini (TDa)	1	2	1	4	10	15	2	0	0	0	0	0	22
Onthophagini (TKa)	1	1	1	7	13	32	3	0	1	1	0	0	38
Onitini (T)	0	0	0	3	2	19	0	0	0	1	0	0	20
Gymnopleurini (R)	0	0	0	2	4	3	0	0	0	0	0	0	4
Scarabaeini (Rd)	0	0	0	1	1	3	1	0	0	0	0	0	3
Sisyphini (R)	1	0	0	1	2	2	0	1	0	0	0	0	3
3 basal tribes*	65	9	8	7	13	42	7	1	19	8	8	2	154
Total genera	85	14	12	25	45	116	13	2	21	10	8	2	261
% endemism	81.2	14.3	8.3	8.0	28.9	71.6	69.2	100.0	70.0	30.0	100.0	100.0	
% endemism 3 basal tribes	63.5	7.1	8.3	0.0	11.1	29.3	53.8	50.0	70.0	30.0	100.0	100.0	
Ateuchini* (TK)	30	3	2	1	3	6	0	0	1	0	0	0	38
Coprini* (T)	7	2	2	5	4	11	0	0	2	1	0	0	20
Canthonini* (Rf)	28	4	4	1	6	25	7	1	16	7	8	2	96

Figure 1. Dendrogram defining three, main, global distribution patterns for genera in 12 dung beetle tribes dominated by different behavioural habits (T = tunneler, R = roller, D = dweller or endocoprid, K = kleptocoprid, d = dragger, f = forest litter, a = ant or termite association) and map of their proportional contribution to generic (G.) and species diversity (S.) in different biogeographical regions (two or three-way pie diagrams). Generic and species numbers are primarily from a synthesis of data in Schoolmeesters (2015). Proportional generic endemism is also cited for each region, including the proportion contributed by three basally-derived tribes. Combined generic endemism for Australia and New Guinea is 91.7%. Biogeographical regions are labeled according to whether they constitute fragments of Gondwanaland (G) or Laurasia (L), are entirely of volcanic origin (V), or are primarily a composite of these origins (GL, GLV). Arrows show some hypothetical directions of range expansion ultimately from Africa (early or late Cenozoic routes, open and black arrows, respectively) or northwards from the Neotropical region or Australia (late Cenozoic, grey arrows). Dendrogram showing dissimilarities in distribution pattern derived from cluster analysis of square root transformed data for generic numbers in each region using the non-parametric Bray-Curtis similarity coefficient and group average linking contained in Primer 5 (Clarke & Gorley, 2001).

Hypothesis (2): Origin in early Cenozoic dispersal across wide oceanic barriers (Figs 2, 3) followed by diversification and late Cenozoic dispersal via restored land links or narrow marine barriers. Co-evolution with early Cenozoic diversification and increase in body size of mammals and their dung types. Hypothesis supported by current dominance of scarabaeine beetle associations with mammalian dung (Cambefort, 1991b) and age scales based on measured extremes in base-pair sequence divergence rates for insects (Juan, Oromi & Hewitt, 1995; Farrell, 2001). These rates were used to calibrate a molecular phylogeny of *Helictopleurus* d'Orbigny (Wirta, Orsini & Hanski, 2008). Ages for a basal node between clades of *Helictopleurus* species provided ages for a node between the same species in the molecular phylogeny of Monaghan *et al*. (2007). These ages were used to convert the clock-constrained, proportional age calibration of Monaghan *et al*. (2007: 0-1 scale) to age scales in Myr (Davis, 2009; Fig. 2).

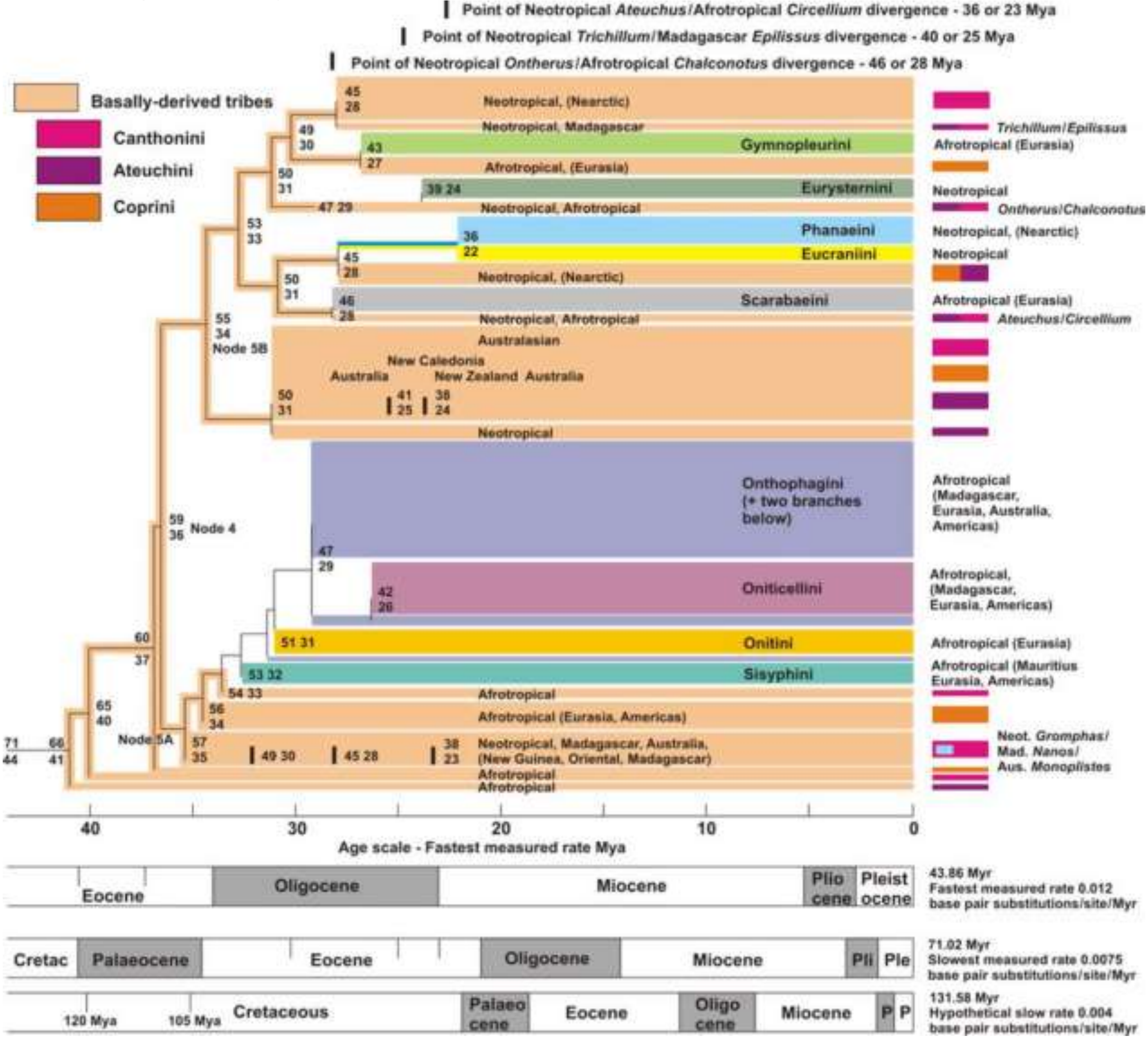


Figure 2. Seven-partition, Bayesian molecular phylogeny of the Scarabaeinae with clock-constrained maximum likelihood branch lengths redrawn from Monaghan *et al*. (2007). Tree simplified and colour-coded to show monophyly or polyphyly in three basally or nine terminally-derived tribes. Basal branching sand-coloured, with polyphyly in three basally-derived tribes indicated by colour-coding in right column (Canthonini: magenta; Ateuchini: violet; Coprini: orange). Absolute age scales are fitted using measured base-pair substitution rates, which support Cenozoic dispersal (Hypothesis 2), or, a hypothetical much slower rate that is required for consistency with Mesozoic vicariance (Hypothesis 1). Geographical occurrences for each colour coded clade are cited according to whether they are considered pre-Miocene or late Cenozoic in origin (latter in brackets).

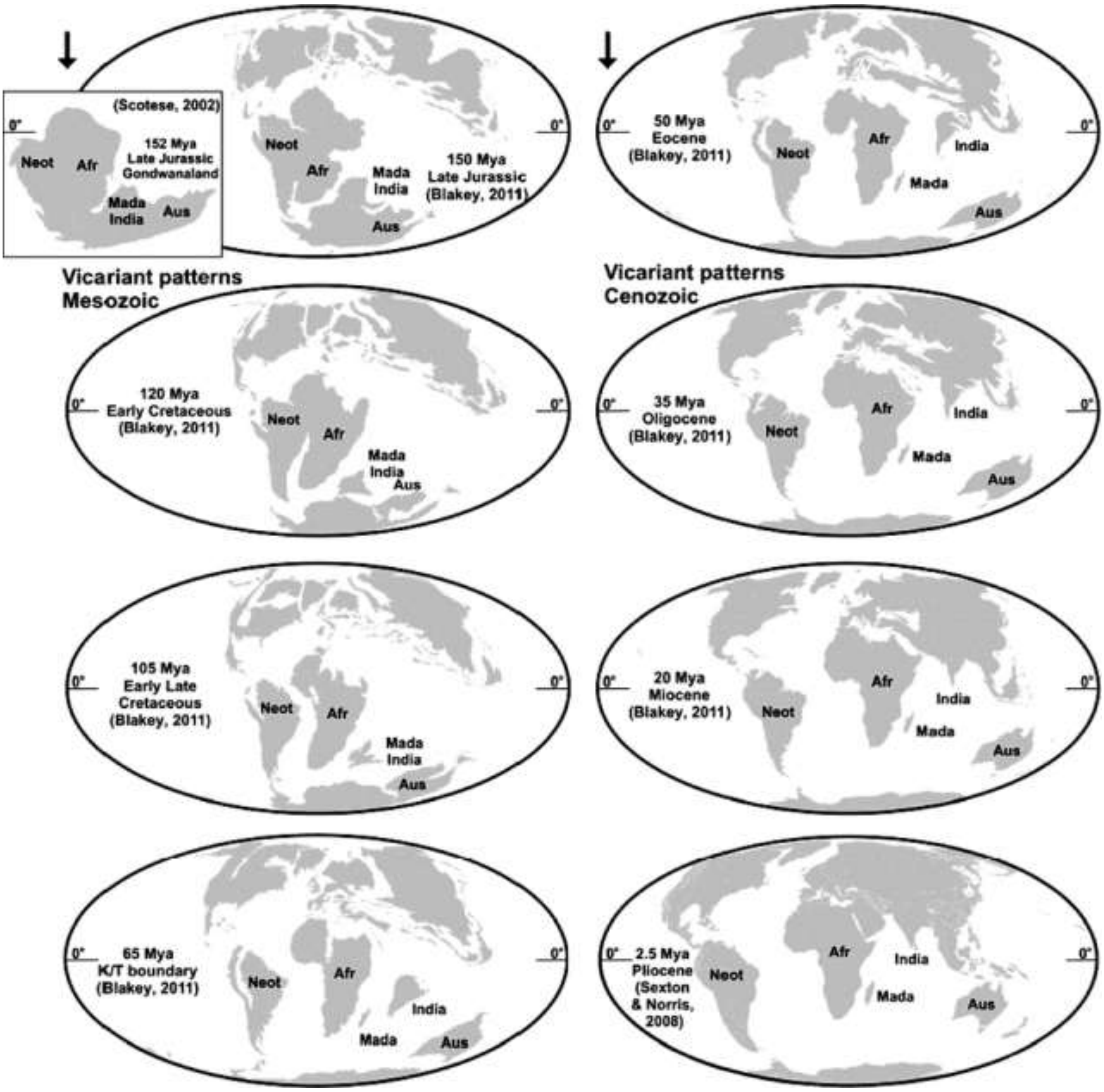


Figure 3. Mollweide global projections redrawn from Blakey (2011) or Sexton & Norris (2008), showing hypothesized changes in the position, exposure, and isolation or connection of principal land masses at eight points in time since the late Jurassic. A comparison is also made between redrawn late Jurassic predictions for Gondwanaland at 150 Myr (Blakey, 2011) and 152 Myr (Scotese, 2002).

All aging methods show weaknesses. Molecular clock methods are claimed to often underestimate age owing to omissions of genetic character through extinctions or missing extant taxa (Wilke, Schultheiß & Albrecht, 2009). Also, rates of base-pair substitution are applied as an average across phylogenies although they differ between gene regions and at different nodes. Fossils may be used to adjust rates at different nodes. However, accuracy is dependent on validity of morphological identification and estimated geological age. The Mesozoic fossil, *Prionocephale*, used in superfamily phylogenies (Ahrens *et al*., 2014; Gunter *et al*., 2016) has not been validated as a scarabaeine (Tarasov *et al*., 2016) and it may be significant that it was recorded together with fossil insects, characteristic of an aquatic environment (Lin, 1994). However, estimated Mesozoic ages for Scarabaeinae may also be constrained by fossils of other families or subfamilies. Thus, the present range of age estimates may err towards the Cenozoic using sequence divergence rates to calibrate subfamily Scarabaeinae phylogenies or towards the Mesozoic using fossils to calibrate superfamily Scarabaeoidea phylogenies but the degree of bias is unknown.

FOSSIL EVIDENCE

Convincing evidence for exploitation of dung in the Mesozoic is limited to putative dinosaur coprolites and adjacent soil tunneled by an unidentified fauna at a single, 1x1 km^2, fossil locality in the Nearctic region (Chin & Gill, 1996). The tunnels comprise a range of diameters (1-3 cm). Some are backfilled with organic material that is of smaller average particle size than the fossil woody matrix of the coprolites. These findings suggest a diverse and specialist dinosaur dung fauna with similar behaviour to modern Scarabaeinae. However, their occurrence in the Nearctic Cretaceous (74-80 Myr) clashes with evidence for late Cenozoic derivation of the extant Nearctic scarabaeine fauna from Afro-Eurasia and the Neotropical regions (Kohlmann & Halffter, 1988; 1991; Davis *et al*., 2002; Emlen *et al*., 2005). An alternative possibility is the allied subfamily Geotrupinae that includes extant dung feeding taxa (Holter, 2004), is found primarily in the Holarctic region, and has a Northern Hemisphere fossil history extending back to the Upper Jurassic / early Cretaceous (Nikolajev & Ren, 2010).

Trace evidence for scarabaeine dung beetle activity based on fossil brood balls is primarily from the Neotropical Cenozoic with dates extending back from the Pleistocene possibly to the Upper Cretaceous (Krell, 2000). Although fossil broods have been found in other geographical regions, records are few in number: four from the Miocene to Pleistocene of Africa and Southern Asia and, remarkably, three from the Eocene to Oligocene of North America and Antarctica (Krell, 2000).

Table 1. Summary of the fragmentary fossil record for scarabaeine dung beetles from Tarasov *et al.* (2016) showing bias to Cenozoic species from the Northern Hemisphere (*doubtful scarabaeine fossils in brackets*) (Neotr. = Neotropical, Nearc. = Nearctic, Afrotr. = Afrotropical, Palae. = Palaearctic)

	Number of fossil species					
EPOCH	Neotr.	Nearc.	Afrotr.	Palae.	Total	Genera
L. Cretaceous	-	-	-	(*1*)	(*1*)	*(*Cretonitis*)
U. Cretaceous	-	-	-	(*1*)	(*1*)	*(*Prionocephale*)
Palaeocene	-	-	-	(*1*)	(*1*)	(*Onthophagus*)
Eocene	-	-	-	1 (*1*)	1 (*1*)	**Lobateuchus*, (*Gymnopleurus*)
Oligocene	-	-	-	1 (*3*)	1 (*3*)	*(*Ateuchites*), *Onthophagus* (*Onthophagus*), (*Onitis*)
Miocene	2^	-	3	9 (*5*)	14 (*5*)	*Canthochilum*, *Chalconotus*, *Gymnopleurus* (*Gymnopleurus*), *Metacatharsius*, *Copris* (*Copris*), *Onthophagus* (*Onthophagus*), (*Oniticellus*), *Heliocopris*, *(*Scelocopris*)
Pliocene	-	-	-	-	-	
Pleistocene	1	3 (*2*)	-	1	5 (*2*)	*Phanaeus* (*Phanaeus*), *Copris*, *Onthophagus*, (*Ateuchus*), *Eodrepanus*
Total	3	3 (*2*)	3	12 (*12*)	21 (*14*)	

*Genera not known from extant faunas. ^Caribbean.

Despite the hypothesized African origin of the Scarabaeinae (Monaghan *et al*., 2007; Sole & Scholtz, 2010), the fossil beetle record is primarily from the Northern Hemisphere on fragments of Laurasia (Tarasov *et* *al*., 2016; Table 1). Furthermore, validated fossil taxa are mostly from mid or late Cenozoic sediments that postdate re-establishment of land links between northern and southern continents (Miocene in Afro-Eurasia, Pliocene in Americas; Fig. 3). Most validated taxa belong to extant genera from either terminal (Gymnopleurini, Phanaeini, Onthophagini, Oniticellini) or basally-derived tribes (Coprini, Canthonini). The few fossils of Mesozoic to early Cenozoic age remain non-validated as Scarabaeinae (Russia: early Cretaceous, *Cretonitis*; China: late Cretaceous, *Prionocephale*; France: Oligocene, *Ateuchites*) or are affiliated with the basally-derived tribe, Ateuchini (France: Lower Eocene, *Lobateuchus*) (Montreuil, Génier & Nel, 2011; Tarasov *et al*., 2016). All are globally extinct as none is represented in modern faunas.

A putative late Mesozoic to earliest Cenozoic fossil history remains unsupported due to the absence of validated scarabaeines, which reflects the poor fossil insect record for this period (Smith & Marcot, 2015). Therefore, any effect of the catastrophic extinction event at the end of the Cretaceous (Gunter *et al*., 2016) remains speculative although the earliest validated fossil could equally be a basal or derived element in the hierarchy of scarabaeine evolution. There is a disparity between the geological age for *Lobateuchus* (Eocene: 53 Myr) (Montreuil *et al*., 2011) and the molecular ages estimated for *Ateuchus* (Fig. 2: 36 or 23 Myr), a hypothesized close relative (Tarasov *et al*., 2016). However, this relationship would presumably be based on few external morphological characters.

During the Cenozoic, a principal driver of change may have been the steepening of latitudinal thermal stratification from pole to equator as reflected by development of south polar glaciation (Barker, Diekmann & Escutia, 2007). In particular, the hot, wet, early Eocene was followed by Oligocene cooling (Zachos *et al*., 2001) that may have driven extinction of basally-derived *Lobateuchus* in Western Europe as supported by recorded extinctions at the Eocene / Oligocene Climatic Transition (Hansen, Kelley & Haasl, 2004) and the loss of tropical forest from higher latitudes (Fine & Ree, 2006)**.** The Miocene fossil record is dominated by extant genera but was followed by further cooling (Zachos *et al*., 2001), cyclic oscillations in the extent of Plio / Pleistocene polar glaciation (Lisiecki & Raymo, 2007), and local extinction or southwards retreat by extant warm temperate and tropical genera now represented only as fossils in the north, e.g. Japan (Miocene: *Heliocopris* Hope; Fugiyama, 1968), England (Pleistocene: *Eodrepanus* Barbero, Palestrini & Roggero, 2009).

DRIVERS OF DUNG SPECIALIZATION

Support of a specialist dung fauna evolved from possibly saprophagous ancestors would depend on a sufficiently high spatial and temporal frequency of fresh droppings of suitable size, composition and consistency. During the Cenozoic, diversification of endothermic eutherian mammals (Halliday & Goswami, 2016) and their droppings would have fulfilled these criteria. However, the possibility of earlier, Mesozoic drivers of specialization have also been considered, particularly the dung of Cretaceous mammals and/or dinosaurs. Evidence is lacking for specialization driven by the dung of Cretaceous mammals, which were primarily small-bodied insectivores or herbivores (Lillegraven, 1972). The putative Mesozoic dinosaur coprolites that are found coevally with dinosaur fossils would be better candidates due to their more suitable size range from 2-15 cm long to 2-10 cm wide (Thulborn, 1991). However, there is little fossil evidence for the use or suitability of their droppings to a Cretaceous dung fauna other than surface markings (Thulborn, 1991) and tunneled coprolites from a single North American locality (Chin & Gill, 1996). Nevertheless, recent arguments for (Davis *et al*., 2002; Gunter *et al*., 2016) or against a dinosaur dung fauna (Arillo & Ortuño, 2008; Davis, 2009) have concentrated on two criteria. One is the rate and amount of dung production using evidence for physiological condition extrapolated from fossil bone microstructure and statistical modeling. The second is suitability of dung composition and consistency extrapolated from fossil evidence for available diet, dentition, digestion, and coprolite microstructure, or, characteristics of defaecation in extant relatives.

Dung production in dinosaurs would have depended on food intake driven by energy requirements. Energy and food requirements would be low if body temperature fluctuated with the environment resulting in both low basal metabolic rate (BMR) and low maximum growth rates as in extant ectotherms (Grady *et al*., 2014). However, to fuel metabolic heat production and a high body temperature, energy requirements would be much increased as reflected by a high BMR and fast growth rate in extant, endothermic birds and eutherian mammals (Grady *et al*., 2014). Dinosaurs have been assumed to be physiologically close to mammals as their bone histology is dominated by fibro-lamellar structure perforated by haversian canals, indicating highly vascular condition. Such structure is linked with fast growth rates. These have been estimated using visible lines of arrested growth (=LAGs) (Benton, 2009) that are assumed seasonal in origin. However, as dinosaurs were diversified into five main lineages (Benton, 2009), they may have shown a range of physiological conditions commensurate to a wide range of body sizes and ecological habits (Clarke, 2013) under different thermal environments.

Recently, the interrelationship between maximum growth rate, body size and BMR has been used to estimate BMR in 21 dinosaur taxa representing four major clades (Grady *et al*., 2014). This study shows that the BMRs of some dinosaur taxa overlapped with those in extant ectotherms or endotherms but most were intermediate and similar to a few extant mesothermic taxa that are able to generate metabolic heat without active regulation of body temperature. These results would be consistent with the absence in dinosaurs of respiratory turbinates housed in widenings of the nasal passages that are directly linked to active thermoregulation in endothermic birds and mammals (Ruben *et al*., 1996). They would also be consistent with the high body temperatures (36-38 ^{o}C) predicted from oxygen isotope ratios in fossil sauropod teeth (Eagle *et al*., 2011). Thus, as a gross generalization based on BMR plus food and energy requirements, dinosaur dung production would probably have been greater than many extant reptilian ectotherms but lower than extant eutherian endotherms of similar body size.

Nevertheless, amount of dinosaur defaecation could have exceeded that in endotherms as dinosaur mass is strongly skewed to large body size (Gorman & Hone, 2012). For instance, assuming a 50% lower BMR, a 30 tonne sauropod would have had an estimated dry mass food intake that was circa 1.5 times greater than a seven tonne endothermic elephant (Hummel *et al.*, 2008). However, the Cretaceous was dominated by herbivorous ornithischian dinosaurs with a body size not exceeding ~5 tonnes and by theropod carnivores not exceeding 7 tonnes (Gorman & Hone, 2012). Scaled to the results of Hummel *et al*. (2008), this suggests a much lower food intake than in elephants of similar body size, given that the nutritional quality of some dominant Mesozoic and Cenozoic plants were comparable. Furthermore, high digestive retention times in sauropods (Hummel *et al*., 2008), and other dinosaurs, might have resulted in slower release of droppings than in elephants. Thus, despite a suitable average coprolite size of 8x4 cm (Thulborn, 1991), low spatial and temporal frequency of droppings might have limited diversification of specialized dung faunas. Notably, in extant scarabaeine assemblages, low spatial frequency of droppings results in low species numbers and abundance (Lobo *et al*., 2006).

Suitable composition and consistency of droppings would also be important. This depends on diet and the processes of feeding, digestion and defaecation. Arillo & Ortuño (2008) postulate a Mesozoic origin for scarabaeine dung beetles driven by the dung of Cretaceous mammals despite their mostly small body-size. They argue that composition of dinosaur dung would have been relatively unsuitable owing to combined voiding of both faecal and high nitrate urinary products through a single cloacal opening. Cloacae are a plesiomorphic reptilian character found in extant crocodiles and birds (Oliveira *et al*., 2004), which represent, respectively, the Archosaur ancestors of dinosaurs (Benton, 2009) plus the only surviving derived dinosaur lineage (Brusatte *et al*., 2014). Although cloacae are not confirmed in Cretaceous dinosaurs, external parts of a few dinosaur coprolites have been identified as urolites owing to structural differences to the interior (Thulborn 1991). By contrast, separate dinosaur coprolites and fossil urolite "splash deformations" of the soil surface have been recorded from South America (Souto & Fernandes, 2015). Similar variation occurs in extant reptiles and birds. The combined urinary and faecal products of iguanas and boa constrictors have been shown to be poor attractants of dung beetles compared to dung of eutherian mammals (Young, 1981). Furthermore, low taxonomic diversity is shown by the derived dung beetle faunas of Mauritius and, also, New Zealand (Fig. 1) where the largest-bodied native vertebrates comprised ratite birds. However, unlike most birds in which urinary and faecal products are voided as a single dropping (McWhorter, Caviedes-Vidal & Karasov, 2009), release of urinary products of the ostrich (ratite bird) precedes that of faecal products (C. M. Deschodt, pers. comm.). Furthermore, the dung of tortoises shows no inclusion of urinary products (C. M. Deschodt pers. obs.). Both ostrich and tortoise dung have been observed to attract dung beetles although there are no quantitative data on relative attractiveness.

There is currently only limited information on the original consistency of dung that was fossilized as coprolites although this would be expected to vary greatly according to dinosaur diet that included carnivores, high or low-fibre herbivores and omnivores (Barrett & Rayfield, 2006). Consistency would also be expected to vary according to dentition and digestive processes. Tearing and swallowing of chunks from prey by carnivores and cutting or crushing action of fibrous vegetation or foliage by dentition of different herbivores may have been augmented by further maceration of food during digestion by gastroliths although the mechanism may have differed between different dinosaur groups (Wings & Sander, 2007). Coprolite collections show a bias to preservation of carnivore droppings that are often identified by bone and undigested muscle inclusions (Thulborn 1991). Coprolites of herbivores are recorded as containing plant matter although size of particles has, apparently, only been recorded explicitly on few occasions. Putative finer consistency reflected by the inclusion of grass phytoliths in dinosaur coprolites has been recorded only at the very end of the Cretaceous (65-67 Myr) (Prasad *et al*., 2005).

On the basis of some of their age predictions, Gunter *et al.* (2016) considered the possibility that scarabaeine specialization was driven by increasing suitability of herbivorous dinosaur dung consistency during the late Cretaceous. However, there is little supporting evidence that this was linked to change in dinosaur dentition and diet during the diversification of the angiosperms. This taxon comprised only 20% of the flora by the mid-Cretaceous based on pollen samples (Feild & Arens, 2004) and did not constitute a substantial proportion of Mesozoic floral biomass until the late Cretaceous (Barrett & Willis, 2001) when at least some coprolites from India still included mostly gymnosperm plant tissues (Ghosha *et al*., 2003). In fact, the only evidence for Mesozoic exploitation of dinosaur dung is Chin & Gill's (1996) North American observations of tunneled late Cretaceous, ornithischian coprolites containing woody fragments. It may be noteworthy that an extant specialist scarabaeine genus in Afro-Asian tropical forests (*Paraphytus* Harold) uses wood fragments and xylophagous insect frass in rotten tree trunks to make brood ovoids (Cambefort & Walter, 1985). As other beetles of the subfamily use their modified membranous mouthparts (Bai *et al*., 2015) to triturate and ingest juices and colloidal particles held amongst the dung fibre (Holter, Scholtz & Wardaugh, 2002), it is presumed that *Paraphytus* is able to feed in a similar manner using wood particles, frass or fungi in the logs. These observations suggest that a Southern Hemisphere Mesozoic dung fauna was possible, irrespective of dinosaur diet, but there is currently no fossil evidence of their existence let alone taxonomic affiliations and possible drivers of specialization.

INCONSISTENCIES: CLASSIFICATION VS PHYLOGENY

The monophyletic subfamily Scarabaeinae (Philips *et al*., 2004) currently remains divided into 12 tribes based on morphological characters although nomenclature for three basally-derived tribes is now controversial. The present analyses and illustrations (Figs 1, 2) are little influenced by use of the morphological classification of

Montreuil (1998 - Ateuchini, Coprini) as opposed to the “classic” tribal classification (Dichotomiini, Coprini) used by Monaghan *et al.* (2007). The only differences are the transfer of coprine-like “dichotomiine” genera to the Coprini, including *Macroderes* Westwood and the type genus of the Dichotomiini, *Dichotomius* Hope, which necessitates a change in tribal name for the remaining genera (Ateuchini). However, even with these modifications, it is no longer tenable to use the "classic" classification in its entirety due to the extensive polyphyly in the three basally-derived tribes, which is illustrated by lack of topological grouping in colour-coding for each tribe, Ateuchini, Coprini, Canthonini (=Deltochilini by precedence versus long-term, common usage of Canthonini) (Fig. 2). This disarray in classification complicates biogeographical analyses leading to past (Davis, 2009) and present treatment of the three basally-derived tribes as a single unit (Fig. 1). Such an approach is supported by the extensively dichotomous but uninterrupted monophyletic relationships between taxa of the basally-derived tribal unit (Fig. 2).

Errors or confusion in classification may result from extensive morphological convergence due to constraints of behavioural habit. Four major types have been described, tunnelers, ball rollers, kleptocoprids (use dung buried by other scarabaeine taxa), and endocoprids (dwellers within droppings). Ordinations of morphometric data from four different biogeographical regions show clear overlap coupled with different trajectories of morphological separation according to habit (Inward *et al*., 2011). Phylogenies suggest that there has been much morphological plasticity and interchange between the two major habits of tunneling (dominates in six tribes) or ball rolling (dominates in five tribes) (Philips *et al*., 2004; Fig. 1). Thus, reliance on purely morphological characters for classification has led to differences in opinion. For instance, convergence in body shape associated with behavioural habit has, presumably, been responsible for the recent suggested transfer of the endocoprid genus, *Eurysternus* (tribe Eurysternini), to the tunneler and endocoprid tribe, Oniticellini (Génier, 2009). Although these taxa show close morphological similarity they show only distant phylogenetic relationships (Monaghan *et al*., 2007; Tarasov & Génier, 2014; Fig. 2). In like manner, flightless desert genera in the tribe, Eucraniini (Neotropical) and flightless desert species in the genus, *Pachysoma* (Afrotropical) show strong morphological and behavioural similarity but distant phylogenetic relationships (Monaghan *et al*., 2007).

HISTORY AND PHYLOGENY

The global history of the Scarabaeinae may span anything from *ca* 143 to 44 Myr. Recent molecular phylogenies of the Scarabaeoidea generate a wide range of age predictions for Scarabaeinae during the Cretaceous. These vary from 86-100 Myr for subfamily origins and 72-86 Myr for dung specialization based on 16 scarabaeine species (Ahrens *et al*., 2014). Or, 83-143 Myr for subfamily origins and 66-111 Myr for dung specialization based on 177 scarabaeine species (Gunter *et al*., 2016) that are primarily a subset of the Genbank data of Monaghan *et al*. (2007: 213 species) with a few new measurements from the Australian fauna. Both sets of analyses are calibrated using various fossil scarabaeoids of Mesozoic age, although the late Cretaceous fossil, *Prionocephale deplanate* Lin (83.6-93.9 Myr) is doubtfully assignable to the Scarabaeine (Tarasov *et al*., 2016). Using measured base-pair substitution rates, calibration of the Monaghan tree (2007) for 37.9% (99) of the valid genera suggests subfamily ages of 71 or 44 Myr (Late Cretaceous or Eocene) (Davis, 2009). Sequence divergence rate calibration of several recent phylogenies of regional faunas generate similar ages of 56.3 Myr (Palaeocene) for the ultimate origin of African taxa assigned to the three basally-derived tribes (Sole & Scholtz, 2010), 45.3 Myr (Eocene) for the ultimate origin of the African scarabaeine fauna (Mlambo *et al*., 2015), and, 79 or 49 Myr (late Cretaceous or Eocene) for the first invasion of Madagascar by scarabaeines (Miraldo *et al*., 2011).

The disparity between ages predicted by use of fossils and those predicted using sequence divergence rates have differing implications for historical biogeography of the Scarabaeinae. Some older age predictions are more or less coeval with Mesozoic fragmentation of Gondwanaland from 150-105 Myr onwards whereas younger ages suggest origins in Late Cretaceous or Cenozoic dispersal owing to large marine separations between continents (Fig. 3). The phylogeny of Ahrens *et al*. (2014) postulates a Cretaceous origin for the subfamily (up to 114 Myr) followed by diversification on mammal dung in the Cenozoic. However, Gunter *et al*. (2016) hypothesize a Mesozoic scarabaeine fauna (origin up to 143 Myr) that became specialized to dinosaur dung as early as 111 Myr but suffered extinctions along with the dinosaurs at the end of the Cretaceous, thus supporting possible origins in both vicariance and/or dispersal. These age predictions predate those generated using measured sequence divergence rates that suggest a history primarily restricted to dispersal during the Cenozoic. Although an origin in vicariance at 132 Myr (Fig. 2) would require a hypothetical sequence divergence rate that is twice as slow as those measured to date, a scenario based on partial extinction of an earlier dung fauna (Gunter *et al*., 2016) might be compatible with measured rates for the extant fauna.

Topology and calibration (Fig. 2) of the clock-constrained tree of Monaghan *et al*. (2007) are used to generate insights into historical biogeography of the subfamily at global scale. The base of the tree is characterized by endemic African representatives of all three basally-derived tribes. A major dichotomy occurs at Node 4 and the two resulting major clades differ in biogeographical bias that is accentuated by identification of earlier pre-Miocene geographical affiliations (Fig. 2) and later radiations (in brackets). A strong bias to presence in Africa dominates clades derived from Node 5A. Although the first clade comprises basally-derived taxa found in all fragments of Gondwanaland, taxa in the two following clades are most diversified in Africa whereas all further terminal clades comprise Afro-Eurasian centred tribes. There is greater biogeographical diversity in clades derived from Node 5B. Subsequent, coeval branching (31 Myr) separates three clades of basally-derived taxa dominated by diversification in Australasian or both Neotropical and Afrotropical regions. The Australasian clade shows the earliest separation with final divergences between Neotropical and Afrotropical taxa occurring later. It seems paradoxical that the two latter branches include a biogeographical mix of basally-derived taxa, terminally-derived Americas-centred tribes and terminally-derived, ball-rolling tribes with a modern centre of distribution restricted to Afro-Eurasia (Scarabaeini, Gymnopleurini). These tribes have a clearly different history to other, primarily tunneling, Afro-Eurasian-centred taxa. However, six terminally-derived tribes now centred in Afro-Eurasia (26-32 Myr or 42-53 Myr) and three in the Americas (22-24 Myr or 36-39 Myr) originate at similar times, together with some major derived clades of basally-derived taxa. Similarity in time of origin suggests diversification in response to more or less coeval events towards the end of the Oligocene or earlier in the Eocene. These ranges are younger but overlap with those predicted for terminal tribes using fossils for calibration (Americas: 33-89 Myr; Afro-Eurasia: 34-86 Myr; Gunter *et al.* 2016).

SPATIAL PATTERNS AND HYPOTHETICAL TRACKS

Global biogeographical analysis is based on generic distribution data (Schoolmeesters, 2015) for the basally-derived taxonomic unit and the nine remaining tribes across six continental regions and six island complexes. The results divide the extant global fauna into three major groups (Fig. 1). These comprise (1) basally-derived taxa with plesiomorphic characterization (Cambefort, 1991a) centred across southern continents, and, more terminally-derived tribes with apomorphic characterization (Cambefort, 1991a) centred on (2) Afro-Eurasia or (3) the Americas (Figs 1, 2). On two of the islands, the dung beetle faunas comprise only basally-derived taxa (New Zealand, New Caledonia). In the remaining 10 regions and island complexes, they are a composite of basally and more terminally-derived taxa from two or, all three biogeographical groups. Group proportions differ between regions and, mostly, between generic and species levels (Fig. 1). The differences presumably reflect contrasts in regional evolutionary histories and regional faunal exchanges (Davis *et al*., 2002; Davis, 2009).

Phylogenies and geographical data support the Afrotropical region as the ultimate origin of both basally-derived (Monaghan *et al*., 2007; Sole & Scholtz, 2010) and terminally-derived Afro-Eurasian groups (Emlen *et al*., 2005) whereas the Americas group originates in the Neotropics (Kohlmann & Halffter, 1988; 1991). Vicariant origins seem more plausible in terms of population of Gondwanaland by land prior to fragmentation. However, most age predictions for Scarabaeinae are consistent with dispersal, which is less plausible because of the already wide sea barriers in the late Cretaceous and early Cenozoic.

Hypothesized tracks (Fig. 1) reflect direct tribal or generic level similarities between faunas and may or may not be the most likely routes of dispersal. They are divided into putative early routes (open arrows, older than 23 Myr, ultimately from Africa) when there were sea barriers and later routes when land links had been largely re-established (solid arrows, younger than 23 Myr, ultimately from Africa (black), South America or Australia (grey)). Evidence and relative plausibility for routes of dispersal are discussed in following paragraphs regarding earlier routes to the Neotropics, Australasia, India and Madagascar and later routes followed by terminally-derived taxa.

A direct early Cenozoic dispersal route to South America from Africa seems unlikely given their separation across the already wide Atlantic Ocean (Fig. 3). However, there is no fossil evidence for a circuitous northern route across more narrow marine barriers (Fig. 3) between warm, Eocene, land masses of Europe, North and South America, other than the Eocene fossil ateuchine from France (Montreuil *et al*., 2011; Tarasov *et al*., 2016) and fossil Eocene brood balls from North and South America (Krell, 2000). Similar problems for explanation of origins arise from the phylogenetic relationships between African and South American primates (Pozzi *et al*., 2014), their first known appearance as Neotropical fossils in the Oligocene (Fleagle, 2013), and routes of dispersal that remain hypothetical without clear support, either across major Eocene oceanic barriers (Atlantic, Antarctic, or Pacific) or via the more narrow waterways separating Europe and North America, (Jameson Kiesling *et al*., 2015), with the latter at odds with palaeocurrents flowing northwards between North and South America (Berggren & Hollister, 1974).

A possible early Cenozoic route for dung beetle dispersal to Australia via Antarctica is supported by records of a fossil Eocene brood ball in Antarctica (Krell, 2000) and of *Tesserodoniella* Vaz de Mello & Halffter (2006) in the temperate Araucarian region of southern Chile, a genus that shows morphological affiliations with African, Australian and tropical Neotropical taxa (Tarasov & Génier, 2015). A recent climate re-construction based on fossil leaves from the Antarctic Peninsula predicts a middle Eocene climate similar to that of Japan (Jacques *et al*., 2014) where there is an extant dung beetle fauna. Studies of the onset of the Antarctic Circum Polar Current suggest a break in land links between Tasmania and Antarctica by the late Eocene at 35.5 Myr (Barker *et al*., 2007) close to one estimated age of origin of the main Australian clade at 34 Myr (Fig. 2). Origins of the New Caledonia and New Zealand faunas are embedded within this clade.

There is, currently, no support for late Cretaceous or Eocene vicariance on the Indian subcontinent (Fig. 3) as an origin of basally-derived Oriental taxa. In fact, recent origin is indicated by the low generic diversity of Oriental Canthonini and Ateuchini compared to Africa. Furthermore, some forest and savanna genera are still shared between the two regions (*Paraphytus* Harold, *Haroldius* Boucomont, *Panelus* Lewis, *Delopleurus* Erichson). A dry-adapted *Delopleurus* species was recently discovered on Socotra (Král, 2014), possibly representing a relictual northern track. In addition, calibration of the clock-constrained tree (Monaghan *et al*., 2007) suggests recent derivation of the Oriental genus, *Ochicanthon* Vaz de Mello, at only 19.2 or 11.9 Myr.

Three occasional invasions from Africa are hypothesized to account for the older fauna of Madagascar (Miraldo *et al*., 2011) comprising basally-derived Canthonini. These have occurred over a long time period (79-30 Myr or 49-19 Myr) but postdate Gondwanaland fragmentation (Fig. 3). An invasion route across a narrow sea barrier may account for the highly endemic and quite different dung beetle fauna compared to the nearby

East African mainland. Equally, similar processes must account for the limited fauna on the isolated oceanic island of Mauritius given its recent origin in volcanism at 8.9 Myr (Moore *et al*., 2011).

As basally-derived taxa, show primarily southern-centred distributions, it is hypothesized that earlier radiations have been followed by later dispersal via the Northern Hemisphere, particularly Afro-Eurasian taxa (Fig. 1: black arrows; Fig. 2). Evidence persists in the modern fauna as proportional composition of southern-centred genera is greater towards the ends of hypothetical tracks from Africa (Fig. 1: open arrows), particularly in Australasia and the Neotropical region. Closer to Africa, proportional compositions of terminally-derived, Afro-Eurasian-centred taxa are much greater than southern-centred taxa at both generic and species levels (Fig. 1). It is suggested that late Cenozoic tracks followed by the Onthophagini (Emlen *et al*., 2005), were also partly followed by other Afro-Eurasian-centred taxa and some Coprini, firstly across land links from Africa to Eurasia (Onthophagini, Oniticellini, Onitini, Sisyphini, Scarabaeini, Gymnopleurini). Some then dispersed from the Orient across a permanent sea barrier (Sunda Strait) to New Guinea and onwards to Australia via an occasional land link (Onthophagini: *Onthophagus*). Others dispersed from the Palaearctic to North America via the occasional Pliocene/Pleistocene land link at Beringia (Coprini, Oniticellini, Sisyphini, Onthophagini) (Davis, 2009). In both Australia and the Nearctic, they now constitute larger proportions of the species level fauna than basally-derived, southern-centred taxa (Fig. 1). Although Afro-Eurasian taxa have also reached the Neotropical Region during the Great American Interchange they currently constitute only a small proportion of the dung beetle fauna at species level. Reciprocal northwards movement from South America and Australia (Fig. 1: grey arrows) modify the Nearctic (Kohlmann & Halffter, 1988; 1991) and New Guinea faunas. Low generic diversity and low proportions of Afro-Eurasian-centred species isolated on Madagascar mostly result from species diversification by one now endemic genus (*Helictopleurus*) after invasion at the Oligocene / Miocene boundary (37-23 Myr).

Patterns of generic sharing or endemism differ between regions. Generic endemism would support older radiations, sharing would support more recent radiations (Fig. 1). Most genera of northerly-lying, Laurasian continents (North America, Eurasia) are also represented in southern continents (South America and/or Africa; Supplementary Table 1) so that differences are primarily at species level. By contrast many of the genera found in southerly-lying, Gondwanaland fragments are restricted to a single region (Supplementary Table 1) so that generic endemism is much greater than in the north (Fig. 1). Thus, separation between the southern faunas (Africa, Madagascar, Australia, South America) is also mainly at tribal or generic level, apart from species of four genera dispersed from Afro-Eurasia (*Scarabaeus* Linnaeus, *Copris* Geofrroy, *Onthophagus* Latreille, *Mimonthophagus* Balthasar). Except in Africa, most of the endemism is contributed by basally-derived tribes (Fig. 1). It is not clear if the modern scarabaeine complement of northern continents represents a novel fauna derived from the Southern Hemisphere or replacement of extinct lineages.

Although reclassification of basally-derived tribes is required to resolve the inconsistencies between morphological taxonomy and phylogenetic relationships, it is difficult to predict exactly how it will affect future historical biogeographical analyses. However, the likely result would be more regionalism, such as in the endemic Neotropical subtribe Scatimina created within the Ateuchini (Vaz de Mello, 2008). Major dichotomy in basally-derived taxa (Fig. 2) suggest that further regional higher taxa might be described although these divisions would still be primarily centred on southern continents.

EVOLUTIONARY ECOLOGICAL TRENDS

Scarabaeine beetles may be derived from mycetophagous ancestors (Scholtz & Chown, 1995**)** that co-evolved with vertebrate droppings culminating in dominance of feeding and breeding on mammalian dung (Cambefort, 1991b). Historical trends in scarabaeine taxon diversification have varied asymmetrically between biogeographical regions (Fig. 1) related to both differences in vegetation ecotype and mammal diversification.

Currently, the fossil record and ecological associations of the extant dung beetle fauna are a limited guide to past trends in habitat or food associations as the fossil record is fragmentary and quantitative assessments are available for only a small proportion of the >6000 known valid species.

The earliest validated fossil ateuchine dung beetle genus (*Lobateuchus*) is preserved in amber (Montreuil *et al*., 2011) suggesting forest associations. Its Lower Eocene age places the fossil site (Seine Valley) within the tropical forest band that occupied a more northerly position (Fine & Ree 2006) during the warmer than present early Eocene climatic optimum (Zachos *et al*., 2001). Hypothetical origins of basally-derived taxa in early Cenozoic forests would be best supported by the extant fauna of the Neotropical region where forest has declined little during Pleistocene glaciations and assemblages contain high proportions of Ateuchini and Canthonini (44.8% out of 1369 individuals in mainland Brazilian forest (Klein, 1989); 90.9% out of 514 in undisturbed Mexican forest (Arellano *et al*., 2008)). In Africa, Canthonini primarily show a relict distribution in the arid southwest and moist southeast of the continent (Davis, 2009; 23 out of 25 genera) after extreme decline in Pleistocene rain forest cover (Fine & Ree, 2006). Afrotropical rain forest faunas are now dominated by terminally-derived tribes, particularly Onthophagini and Sisyphini **(**95.4% out of 1051 individuals in unlogged Ghana forest, Canthonini 2.3% (Davis & Philips, 2005); 93.8% or 97.4% out of 795 or 496 in virgin Uganda Forest, Canthonini 0.6% (Nummelin & Hanski, 1989)).

As regards later trends, clock-constrained age calibration (Fig. 2) suggests an Eocene or Oligocene origin for terminally-derived tribes with further coeval diversification of elements still classified in basally-derived tribes. However, according to Sole & Scholtz (2010), the main diversification of extant Afrotropical genera occurred in the Miocene as supported by their first validated appearance in the fossil record (Table 1). Ahrens *et al*. (2014) suggest this history is related to expansion of savanna during late Cenozoic climatic cooling and the diversification of herbivorous Artiodactyla. However, terminally-derived scarabaeine tribes show a mixture of trends. Some Afro-Eurasian-centred tribes are, apparently, biased to occurrence in open habitats with few forest elements, including, Scarabaeini, Gymnopleurini and Onitini. Others are well-represented in both open and forest habitats including, Sisyphini, Onthophagini and Oniticellini. Evolutionary history of the onthophagine genus, *Diastellopalpus* van Lansberge, supports initial diversification in wet forest followed by a trend to drier forest and savanna woodland during the late Cenozoic cooling phase (Davis & Scholtz, 2010). Similarly, in the Americas, whereas Eucraniini are biased to arid open vegetation in response to the uplift of the Andes and development of a rain shadow in southeast South America (Davis, 2009), many Phanaeini and Eurysternini are, apparently, found in forest, except those phanaeine and other taxa that radiated northwards into the Nearctic region.

Although more quantitative support is required, asymmetric regional patterns of evolution in floral ecotype, mammal and dung type diversity have been major driving forces in regional dung beetle evolution during the Cenozoic. For instance, current mammal and dung type diversity is lower in Madagascar and Australia resulting in fewer species (Fig. 1) and lower functional diversity compared to the Neotropical and Afrotropical regions (Inward *et al*., 2011). Thus, in comparison with extant relatives, a study of the fossil mammal record might provide insights into effects of past to present regional variation in proportional forest cover (Fine & Ree, 2006), expansion of woodland and grassland plus different proportions of omnivores, monogastric and ruminant herbivores and their different dung types.

CONCLUSIONS

1. Morphological convergence and parallelism in geographically isolated taxa may have masked many true relationships. Therefore, tribal classification requires revision so that it is consistent with phylogeny. Such revision will facilitate more accuracy in historical biogeographical analysis and comparative ecological studies.

2. Accuracy of age predictions may err towards earlier or later epochs. Scarabaeoidea phylogenies calibrated using fossils predict Mesozoic ages for Scarabaeinae compatible with origin in Gondwanaland vicariance or dispersal on dinosaur dung. Scarabaeinae phylogenies calibrated using sequence divergence rates predict ages compatible with origin in Cenozoic dispersal on mammal dung.
3. Different phylogenetic studies have generated many different topologies. In order to resolve differences, molecular phylogenies need to be expanded to include all genera as well as representatives of major species groups in larger genera. Particularly, those classified in basally-derived tribes whose history is least well known.
4. Some key subjects for research would be molecular phylogenetic relationships between basally-derived taxa (Ateuchini, Canthonini) found in East Africa, Madagascar and the Oriental region. Also, those between the most basally-derived taxa from Africa, Australia, tropical and Araucarian regions of South America. In addition, Cenozoic radiations all Afro-Eurasian-centred genera require investigation to determine if they parallel those of the Onthophagini, particularly given the polyphyletic relationships of some ball-rolling and tunneling tribes.
5. Further research into habitat and food data for the >6000 species of the entire subfamily may provide further and more accurate insights into evolutionary ecological trends, particularly if matched to improved phylogenies.

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Supplementary Material

Supplementary Table 1. Occurrence of 261 genera of Scarabaeinae in three biogeographical centres and 12 geographical regions according to data from Schoolmeesters (2015).

GENUS	BIOGEOGRAPHICAL CENTRE	TRIBE	PRESENCE IN BIOGEOGRAPHICAL REGION											
			Afr	Or	Pal	Neo	Car	Nea	Aus	NG	NC	NZ	Mad	Mau
Allogymnopleurus Janssens	Afro-Eurasian-centred	Gymnopleurini	1	1	1									
Garreta Janssens	Afro-Eurasian-centred	Gymnopleurini	1	1										
Gymnopleurus Illiger	Afro-Eurasian-centred	Gymnopleurini	1	1	1									
Paragymnopleurus Shipp	Afro-Eurasian-centred	Gymnopleurini		1										
Afrodrepanus Krikken	Afro-Eurasian-centred	Oniticellini	1											
Anoplodrepanus Simonis	Afro-Eurasian-centred	Oniticellini					1							
Attavicinus Phillips	Afro-Eurasian-centred	Oniticellini				1								
Cyptochirus Lesne	Afro-Eurasian-centred	Oniticellini	1											
Drepanocerus Kirby	Afro-Eurasian-centred	Oniticellini	1	1	1									
Drepanoplatynus Boucomont	Afro-Eurasian-centred	Oniticellini	1											
Eodrepanus Barbero	Afro-Eurasian-centred	Oniticellini	1	1										
Euoniticellus Janssens	Afro-Eurasian-centred	Oniticellini	1	1	1		1							
Helictopleurus d'Orbigny	Afro-Eurasian-centred	Oniticellini											1	
Heterosyphus Paulian	Afro-Eurasian-centred	Oniticellini											1	
Ixodina Kraatz	Afro-Eurasian-centred	Oniticellini	1	1										
Latodrepanus Krikken	Afro-Eurasian-centred	Oniticellini	1											
Liatongus Reitter	Afro-Eurasian-centred	Oniticellini	1	1	1			1						
Nitiocellus Branco	Afro-Eurasian-centred	Oniticellini	1											
Oniticellus Lep. Aud. Serville	Afro-Eurasian-centred	Oniticellini	1	1										
Paroniticellus Balthasar	Afro-Eurasian-centred	Oniticellini			1									
Scaptocnemis Peringuey	Afro-Eurasian-centred	Oniticellini	1											
Sinodrepanus Simonis	Afro-Eurasian-centred	Oniticellini		1										
Tibiodrepanus Krikken	Afro-Eurasian-centred	Oniticellini	1	1										
Tiniocellus Peringuey	Afro-Eurasian-centred	Oniticellini	1	1										
Tragiscus Klug	Afro-Eurasian-centred	Oniticellini	1											
Yvescambefortius Ochi & Kon	Afro-Eurasian-centred	Oniticellini		1										
Acanthonitis Janssens	Afro-Eurasian-centred	Onitini	1											
Allonitis Janssens	Afro-Eurasian-centred	Onitini	1											
Anonychonitis Janssens	Afro-Eurasian-centred	Onitini	1											
Aptychonitis Janssens	Afro-Eurasian-centred	Onitini	1											
Bubas Mulsant	Afro-Eurasian-centred	Onitini			1									
Cheironitis van Lansberge	Afro-Eurasian-centred	Onitini	1	1	1									
Gilletellus Janssens	Afro-Eurasian-centred	Onitini	1											
Heteronitis Gillet	Afro-Eurasian-centred	Onitini	1											
Janssensantus Paulian	Afro-Eurasian-centred	Onitini	1											
Janssensellus Cambefort	Afro-Eurasian-centred	Onitini	1											
Kolbeellus Jacobson	Afro-Eurasian-centred	Onitini	1											
Lophodonitis Janssens	Afro-Eurasian-centred	Onitini	1											
Megalonitis Janssens	Afro-Eurasian-centred	Onitini	1											
Neonitis Peringuey	Afro-Eurasian-centred	Onitini	1											
Onitis Fabricius	Afro-Eurasian-centred	Onitini	1	1	1					1				
Paronitis Balthasar	Afro-Eurasian-centred	Onitini	1											
Platyonitis Janssens	Afro-Eurasian-centred	Onitini	1											
Pleuronitis van Lansberge	Afro-Eurasian-centred	Onitini	1											
Pseudochironitis Ferreira	Afro-Eurasian-centred	Onitini	1											

Tropidonitis Janssens	Afro-Eurasian-centred	Onitini	1											
Alloscelus Boucomont	Afro-Eurasian-centred	Onthophagini	1											
Amietina Cambefort	Afro-Eurasian-centred	Onthophagini	1											
Anoctus Sharp	Afro-Eurasian-centred	Onthophagini		1										
Caccobiomorphus Balthasar	Afro-Eurasian-centred	Onthophagini	1											
GENUS	**BIOGEOGRAPHICAL**	**TRIBE**	**PRESENCE IN BIOGEOGRAPHICAL REGION**											
	CENTRE		**Afr**	**Or**	**Pal**	**Neo**	**Car**	**Nea**	**Aus**	**NG**	**NC**	**NZ**	**Mad**	**Mau**
Caccobius Thomson	Afro-Eurasian-centred	Onthophagini	1	1	1									
Cambefortius Branco	Afro-Eurasian-centred	Onthophagini	1											
Cassolus Sharp	Afro-Eurasian-centred	Onthophagini		1										
Cleptocaccobius Cambefort	Afro-Eurasian-centred	Onthophagini	1	1	1									
Clypeodrepanus Krikken	Afro-Eurasian-centred	Onthophagini	1											
Cyobius Sharp	Afro-Eurasian-centred	Onthophagini		1										
Diastellopalpus van Lansberge	Afro-Eurasian-centred	Onthophagini	1											
Digitonthophagus Balthasar	Afro-Eurasian-centred	Onthophagini	1	1										
Disphysema Harold	Afro-Eurasian-centred	Onthophagini		1										
Dorbignyolus Branco	Afro-Eurasian-centred	Onthophagini	1											
Euonthophagus Balthasar	Afro-Eurasian-centred	Onthophagini	1		1									
Eusaproecius Branco	Afro-Eurasian-centred	Onthophagini	1											
Haroldius Boucomont	Afro-Eurasian-centred	Onthophagini	1	1									1	
Heteroclitopus Peringuey	Afro-Eurasian-centred	Onthophagini	1											
Hyalonthophagus Palestrini	Afro-Eurasian-centred	Onthophagini	1											
Krikkenius Branco	Afro-Eurasian-centred	Onthophagini	1											
Larhodius Balthasar	Afro-Eurasian-centred	Onthophagini		1										
Milichus Peringuey	Afro-Eurasian-centred	Onthophagini	1											
Mimonthophagus Balthasar	Afro-Eurasian-centred	Onthophagini	1										1	
Neosaproecius Branco	Afro-Eurasian-centred	Onthophagini	1											
Onthophagus Latreille	Afro-Eurasian-centred	Onthophagini	1	1	1	1	1	1	1	1			1	
Phalops Erichson	Afro-Eurasian-centred	Onthophagini	1	1	1									
Pinacopodius Branco	Afro-Eurasian-centred	Onthophagini	1											
Pinacotarsus Harold	Afro-Eurasian-centred	Onthophagini	1											
Proagoderus van Lansberge	Afro-Eurasian-centred	Onthophagini	1	1	1									
Pseudosaproecius Balthasar	Afro-Eurasian-centred	Onthophagini	1											
Stiptocnemis Branco	Afro-Eurasian-centred	Onthophagini	1											
Stiptopodius Harold	Afro-Eurasian-centred	Onthophagini	1											
Stiptotarsus Branco	Afro-Eurasian-centred	Onthophagini	1											
Strandius Balthasar	Afro-Eurasian-centred	Onthophagini		1	1									
Sukelus Branco	Afro-Eurasian-centred	Onthophagini	1											
Tomogonus d'Orbigny	Afro-Eurasian-centred	Onthophagini	1											
Unidentis Walter	Afro-Eurasian-centred	Onthophagini	1											
Walterantus Cambefort	Afro-Eurasian-centred	Onthophagini	1											
Pachylomera (Hope)	Afro-Eurasian-centred	Scarabaeini	1											
Pachysoma MacLeay	Afro-Eurasian-centred	Scarabaeini	1											
Scarabaeus Linnaeus	Afro-Eurasian-centred	Scarabaeini	1	1	1								1	
Neosisyphus Muller	Afro-Eurasian-centred	Sisyphini	1	1										
Nesosisyphus Vinson	Afro-Eurasian-centred	Sisyphini												1
Sisyphus Latreille	Afro-Eurasian-centred	Sisyphini	1	1	1	1								
Anomiopsoides Blackwelder	Americas-centred	Eucraniini				1								
Ennearabdus van Lansberge	Americas-centred	Eucraniini				1								
Eucranium Brulle	Americas-centred	Eucraniini				1								
Glyphoderus Westwood	Americas-centred	Eucraniini				1								
Eurysternus Dalman	Americas-centred	Eurysternini				1								
Bolbites Harold	Americas-centred	Phanaeini				1								
Coprophanaeus Olsoufieff	Americas-centred	Phanaeini				1		1						

Dendropaemon Perty	Americas-centred	Phanaeini				1								
Diabroctis Gistel	Americas-centred	Phanaeini				1								
Gromphas Brulle	Americas-centred	Phanaeini				1								
Homalotarsus Janssens	Americas-centred	Phanaeini				1								
Megatharsis Waterhouse	Americas-centred	Phanaeini				1								
Oruscatus Bates	Americas-centred	Phanaeini				1								
GENUS	**BIOGEOGRAPHICAL**	**TRIBE**	**PRESENCE IN BIOGEOGRAPHICAL REGION**											
	CENTRE		**Afr**	**Or**	**Pal**	**Neo**	**Car**	**Nea**	**Aus**	**NG**	**NC**	**NZ**	**Mad**	**Mau**
Oxysternon Laporte de Castelnau	Americas-centred	Phanaeini				1								
Phanaeus MacLeay	Americas-centred	Phanaeini				1	1	1						
Sulcophanaeus Olsoufieff	Americas-centred	Phanaeini				1	1							
Tetramereia Klages	Americas-centred	Phanaeini				1								
Anomiopus Westwood	Southern-centred	Ateuchini				1	1							
Aphengium Harold	Southern-centred	Ateuchini				1								
Ateuchus Weber	Southern-centred	Ateuchini				1	1	1						
Bdelyropsis Pereira, Vulcano, Martinez	Southern-centred	Ateuchini				1								
Bdelyrus Harold	Southern-centred	Ateuchini				1								
Besourenga Vaz de Mello	Southern-centred	Ateuchini				1								
Bradypodium Vaz de Mello	Southern-centred	Ateuchini				1								
Canthidium Erichson	Southern-centred	Ateuchini				1		1						
Coptorhina Hope	Southern-centred	Ateuchini	1											
Degallieridium Vaz de Mello	Southern-centred	Ateuchini				1								
Delopleurus Erichson	Southern-centred	Ateuchini	1	1	1									
Deltorrhinum Harold	Southern-centred	Ateuchini				1								
Demarziella Balthasar	Southern-centred	Ateuchini							1					
Eutrichillum Vaz de Mello	Southern-centred	Ateuchini				1								
Feeridium Vaz de Mello	Southern-centred	Ateuchini				1								
Frankenbergerius Balthasar	Southern-centred	Ateuchini	1											
Genieridium Vaz de Mello	Southern-centred	Ateuchini				1								
Hypocanthidium Balthasar	Southern-centred	Ateuchini				1								
Leotrichillum Vaz de Mello	Southern-centred	Ateuchini				1								
Lobidion Vaz de Mello	Southern-centred	Ateuchini				1								
Martinezidium Vaz de Mello	Southern-centred	Ateuchini				1								
Nunoidium Vaz de Mello	Southern-centred	Ateuchini				1								
Onoreidium Vaz de Mello	Southern-centred	Ateuchini				1								
Onychothecus Boucomont	Southern-centred	Ateuchini		1										
Paraphytus Harold	Southern-centred	Ateuchini	1	1										
Pedaria Laporte de Castelnau	Southern-centred	Ateuchini	1											
Pedaridium Harold	Southern-centred	Ateuchini				1								
Pereiraidium Vaz de Mello	Southern-centred	Ateuchini				1								
Pseuduroxys Balthasar	Southern-centred	Ateuchini				1								
Pteronyx van Lansberge	Southern-centred	Ateuchini				1								
Sarophorus Erichson	Southern-centred	Ateuchini	1											
Scatimus Erichson	Southern-centred	Ateuchini				1								
Scatonomus Erichson	Southern-centred	Ateuchini				1								
Scatrichus Genier & Kohlmann	Southern-centred	Ateuchini				1								
Silvinha Vaz de Mello	Southern-centred	Ateuchini				1								
Trichillidium Vaz de Mello	Southern-centred	Ateuchini				1								
Trichillum Harold	Southern-centred	Ateuchini				1								
Uroxys Westwood	Southern-centred	Ateuchini				1	1							
Agamopus Bates	Southern-centred	Canthonini				1								
Aliuscanthoniola Deschodt & Scholtz	Southern-centred	Canthonini	1											
Amphistomus Lansberge	Southern-centred	Canthonini							1	1				
Anisocanthon Martinez & Perreira	Southern-centred	Canthonini				1								

Anonthobium Paulian	Southern-centred	Canthonini									1			
Aphengoecus Peringuey	Southern-centred	Canthonini	1											
Apotolamprus Olsoufieff	Southern-centred	Canthonini											1	
Aptenocanthon Matthews	Southern-centred	Canthonini							1					
Apterepilissus Montreuil	Southern-centred	Canthonini											1	
Arachnodes Westwood	Southern-centred	Canthonini											1	
Aulacopris White	Southern-centred	Canthonini							1					
GENUS	**BIOGEOGRAPHICAL**	**TRIBE**	**PRESENCE IN BIOGEOGRAPHICAL REGION**											
	CENTRE		**Afr**	**Or**	**Pal**	**Neo**	**Car**	**Nea**	**Aus**	**NG**	**NC**	**NZ**	**Mad**	**Mau**
Baloghonthobium Paulian	Southern-centred	Canthonini									1			
Bohepilissus Paulian	Southern-centred	Canthonini	1											
Boletoscapter Matthews	Southern-centred	Canthonini							1					
Byrrhidium Harold	Southern-centred	Canthonini	1											
Caeconthobium Paulian	Southern-centred	Canthonini									1			
Cambefortantus Paulian	Southern-centred	Canthonini											1	
Canthochilum Chapin	Southern-centred	Canthonini					1							
Canthodimorpha Davis, Scholtz, Harrison	Southern-centred	Canthonini	1											
Canthon Hoffmansegg	Southern-centred	Canthonini				1	1	1						
Canthonella Chapin	Southern-centred	Canthonini				1	1							
Canthonidia Paulian	Southern-centred	Canthonini				1								
Canthonosoma MacLeay	Southern-centred	Canthonini							1					
Canthotrypes Paulian	Southern-centred	Canthonini				1								
Cephalodesmius Westwood	Southern-centred	Canthonini							1					
Chalconotus Dejean	Southern-centred	Canthonini	1											
Circellium Latreille	Southern-centred	Canthonini	1											
Coproecus Reiche	Southern-centred	Canthonini							1					
Cryptocanthon Balthasar	Southern-centred	Canthonini				1								
Deltepilissus Pereira	Southern-centred	Canthonini				1								
Deltochilum Eschscholtz	Southern-centred	Canthonini				1		1						
Dicranocara Frolov & Scholtz	Southern-centred	Canthonini	1											
Diorygopyx Matthews	Southern-centred	Canthonini							1					
Dwesasilvasedis Deschodt & Scholtz	Southern-centred	Canthonini	1											
Endroedyolus Scholtz & Howden	Southern-centred	Canthonini	1											
Epactoides olsoufieff	Southern-centred	Canthonini											1	
Epilissus Reiche	Southern-centred	Canthonini											1	
Epirinus Reiche	Southern-centred	Canthonini	1											
Eudinopus Burmeister	Southern-centred	Canthonini				1								
Falsignambia Paulian	Southern-centred	Canthonini									1			
Gyronotus van Lansberge	Southern-centred	Canthonini	1											
Hammondantus Cambefort	Southern-centred	Canthonini	1											
Hansreia Halffter & Martinez	Southern-centred	Canthonini				1								
Holocanthon Martinez & Pereira	Southern-centred	Canthonini				1								
Ignambia Heller	Southern-centred	Canthonini									1			
Labroma Sharp	Southern-centred	Canthonini							1					
Lepanus Balthasar	Southern-centred	Canthonini							1	1				
Macropanelus Ochi & Kon & Araya	Southern-centred	Canthonini		1										
Madaphacosoma Paulian	Southern-centred	Canthonini	1											
Malagoniella Martinez	Southern-centred	Canthonini				1								
Megathopa Eschscholtz	Southern-centred	Canthonini				1								
Megathoposoma Balthasar	Southern-centred	Canthonini				1								
Melanocanthon Halffter	Southern-centred	Canthonini						1						
Mentophilus Laporte de Castelnau	Southern-centred	Canthonini							1					
Monoplistes van Lansberge	Southern-centred	Canthonini							1					
Namakwanus Scholtz & Howden	Southern-centred	Canthonini	1											

Nanos Westwood	Southern-centred	Canthonini											1	
Nebulasilvius Deschodt and Scholtz	Southern-centred	Canthonini	1											
Nesovinsonia Martinez & Pereira	Southern-centred	Canthonini												1
Ochicanthon Vaz de Mello	Southern-centred	Canthonini		1										
Odontoloma Boheman	Southern-centred	Canthonini	1											
Oficanthon Paulian	Southern-centred	Canthonini								1				
Onthobium Reiche	Southern-centred	Canthonini									1			
Outenikwanus Scholtz & Howden	Southern-centred	Canthonini	1											
GENUS	**BIOGEOGRAPHICAL**	**TRIBE**	**PRESENCE IN BIOGEOGRAPHICAL REGION**											
	CENTRE		**Afr**	**Or**	**Pal**	**Neo**	**Car**	**Nea**	**Aus**	**NG**	**NC**	**NZ**	**Mad**	**Mau**
Panelus Lewis	Southern-centred	Canthonini	1	1	1									
Paracanthon Balthasar	Southern-centred	Canthonini				1								
Parachorius Harold	Southern-centred	Canthonini		1										
Paracryptocanthon Howden & Cook	Southern-centred	Canthonini				1								
Paraphacosomoides Balthasar	Southern-centred	Canthonini								1				
Paronthobium Paulian	Southern-centred	Canthonini									1			
Parvuhowdenius Deschodt and Scholtz	Southern-centred	Canthonini	1											
Peckolus Scholtz & howden	Southern-centred	Canthonini	1											
Penalus Paulian	Southern-centred	Canthonini								1				
Phaedotrogus Balthasar	Southern-centred	Canthonini		1										
Pseudignambia Paulian & Pluot-Sigwalt	Southern-centred	Canthonini							1					
Pseudocanthon Bates	Southern-centred	Canthonini				1	1	1						
Pseudonthobium Paulian	Southern-centred	Canthonini									1			
Pycnopanelus Arrow	Southern-centred	Canthonini	1	1										
Saphobiamorpha Brookes	Southern-centred	Canthonini										1		
Saphobius Sharp	Southern-centred	Canthonini										1		
Sauvagesinella Paulian	Southern-centred	Canthonini							1					
Scybalocanthon Martinez	Southern-centred	Canthonini				1								
Scybalophagus Martinez	Southern-centred	Canthonini				1								
Silvaphilus Roets	Southern-centred	Canthonini	1											
Sinapisoma Boucomont	Southern-centred	Canthonini				1								
Streblopus van Lansberge	Southern-centred	Canthonini				1								
Sylvicanthon Halffter & Martinez	Southern-centred	Canthonini				1								
Tanzanolus Scholtz & Howden	Southern-centred	Canthonini	1											
Temnoplectron Westwood	Southern-centred	Canthonini							1	1				
Tesserodon Hope	Southern-centred	Canthonini							1	1				
Tesserodoniella Vaz de Mello & Halffter	Southern-centred	Canthonini				1								
Tetraechma Blanchard	Southern-centred	Canthonini				1								
Versicorpus Deschodt	Southern-centred	Canthonini	1											
Vulcanocanthon Pereira & Martinez	Southern-centred	Canthonini				1								
Xenocanthon Martinex	Southern-centred	Canthonini				1								
Zonocopris Arrow	Southern-centred	Canthonini				1								
Catharsiocopris Balthasar	Southern-centred	Coprini	1											
Catharsius Hope	Southern-centred	Coprini	1	1	1									
Chalcocopris Burmeister	Southern-centred	Coprini				1								
Copridaspidus Boucomont	Southern-centred	Coprini	1											
Copris Muller	Southern-centred	Coprini	1	1	1	1		1						
Coptodactyla Burmeister	Southern-centred	Coprini							1	1				
Dichotomius Hope	Southern-centred	Coprini				1	1	1						
Heliocopris Hope	Southern-centred	Coprini	1	1	1									
Holocephalus Hope	Southern-centred	Coprini				1								
Homocopris Burmeister	Southern-centred	Coprini				1								
Isocopris Pereira & Martinez	Southern-centred	Coprini				1								
Litocopris Waterhouse	Southern-centred	Coprini	1											

Macroderes Westwood	Southern-centred	Coprini	1											
Metacatharsius Paulian	Southern-centred	Coprini	1		1									
Ontherus Erichson	Southern-centred	Coprini				1	1							
Pseudocopris Ferreira	Southern-centred	Coprini	1											
Pseudopedaria Felsche	Southern-centred	Coprini	1											
Synapsis Bates	Southern-centred	Coprini		1	1									
Thyregis Blackburn	Southern-centred	Coprini							1					
Xinidium Harold	Southern-centred	Coprini	1											
TOTAL GENERA			116	45	25	85	14	12	20	10	8	2	13	2

KEY TO GEOGRAPHICAL REGIONS
Afr = Afrotropical
Or = Oriental
Pal = Palaearctic
Neo = Neotropical
Car = Caribbean
Nea = Nearctic
Aus = Australia
NG = New Guinea
NC = New Caledonia
NZ = New Zealand
Mad = Madagascar
Mau = Mauritius