An Eocene fossil scarab beetle (Coleoptera: Scarabaeoidea) from Tanzania

AUTHORS:
Werner P. Strümpher[1]
Clarke H. Scholtz[2]
Thomas Schlüter[3]

AFFILIATIONS:
[1]Ditsong National Museum of Natural History, Pretoria, South Africa
[2]Department of Zoology and Entomology, University of Pretoria, Pretoria, South Africa
[3]Department of Geography, Environmental Science and Planning, University of Eswatini, Kwaluseni, Eswatini

CORRESPONDENCE TO:
Werner Strümpher

EMAIL:
strumpher@ditsong.org.za

DATES:
Received: 02 Sep. 2022
Revised: 26 Dec. 2022
Accepted: 03 Jan. 2023
Published: 29 Mar. 2023

HOW TO CITE:
Strümpher WP, Scholtz CH, Schlüter T. An Eocene fossil scarab beetle (Coleoptera: Scarabaeoidea) from Tanzania. S Afr J Sci. 2023;119(3/4), Art. #14681. https://doi.org/10.17159/sajs.2023/14681

ARTICLE INCLUDES:
☒ Peer review
☐ Supplementary material

DATA AVAILABILITY:
☐ Open data set
☐ All data included
☐ On request from author(s)
☐ Not available
☒ Not applicable

EDITOR:
Jemma Finch

KEYWORDS:
Africa, Lagerstätte, Mahenge deposit, maar lake, new genus, new species, taxonomy

FUNDING:
None

A fossil scarabaeoid (Coleoptera: Scarabaeoidea) *Mahengea mckayi* new genus, new species – the only well-preserved insect fossil and one of only a few insects found at the site – is described from an otherwise rich Eocene (~ 45.6 mya) maar Lagerstätte at Mahenge in central northern Tanzania. Numerous fossil fishes and plants have been recovered from this site and described. The dearth of insect fossils is surprising considering their richness in other deposits of similar origin and age. We suggest that the rich fish fauna present in the oxygen-rich parts of the water in the former volcanic crater lake may have scavenged most of the terrestrial insects that fell into the water. Although the fossil described here is undoubtedly that of a member of the Scarabaeoidea, the family placement remains unsure.

Significance:

We describe the first Eocene fossil scarab from Africa. It is one of only a few scarab fossils from the continent and one of the best-preserved insect (invertebrate) fossils from the deposit.

Introduction

Unusually rich and well-preserved fossil assemblages are generally known under the term 'Lagerstätte' because the information they provide is not only concerned with details of the extinct animals and plants that once lived there, thus an indication of differing levels of diversity in the past, but because it is characteristic of them that more complete records of communities are preserved. Lagerstätte additionally afford insights into palaeoecological and evolutionary relationships in the geological context.

Classic Eocene deposits in Germany, like the famous Eckfelder Maar, are considered to be Lagerstätte, but these types of fossiliferous deposits have been largely limited to the northern hemisphere. The Orapa kimberlite pipe in north-central Botswana is one of the few maar deposits in the southern hemisphere (located in eastern Botswana), and is famous for its exceptionally well-preserved compression fossils of insects and other organisms in fine-grained mudstone.[1,2] Numerous maar deposits are known from central northern Tanzania (Figure 1), and at least one of them, the Mahenge maar deposit, has yielded various fossils.[3-5]

Beetles in general, and Scarabaeoidea in particular, usually yield only a few useful characters when fossilised. Scarabaeoids are mostly compact and evenly and strongly sclerotised and when compressed and fossilised, usually only the body outline and a few legs are recognisable. In less compact beetles often only elytra become fossilised. As a consequence, well-preserved beetle fossils in sediments are relatively rare.

Fossil beetles can only be reliably identified as belonging to Scarabaeoidea (other than Lucanidae and Passalidae) by at least one of four character suites: antennae with lamellate club; pronotum and fore legs adapted for burrowing (procoxae enlarged, pronotum enlarged to include enlarged coxal musculature, protibiae dilated apically, usually with teeth on their outer margin), albeit that similar adaptations also occur in some other burrowing beetles; reduced wing venation and intrinsic spring mechanism for folding wings; prosternal intercoxal process widened apically behind procoxae.[6]

The fossil record of Scarabaeoidea and a comprehensive molecular study of the origin of major beetle groups hypothesised a Triassic origin for the group[6,7], postulated the establishment of most extant families during the Jurassic and suggested extensive radiation of groups within families during the Cretaceous, especially of phytophagous taxa in co-radiation with the expanding angiosperm flora. Yet, despite the presence of well-placed Scarabaeoidea fossils from as far back as the Middle Jurassic[8], a total of only about 230 species have been described[6,9]; this from one of the largest beetle groups with about 30 000 extant species and probably many thousand more extinct. Furthermore, besides a detailed study of a late Cretaceous (~ 91 mya) Melolonthinae (Scarabaeidae) species[10], only a few Scarabaeidae of Palaeocene[9], seven of Eocene[9,11], another few of Oligocene age[9], and two from the Pliocene[12] are known. Most of the fossil species of all scarabaeoid groups are from the Miocene and younger.[6,9] The Miocene was also the period when grasslands and herbivorous mammals radiated in Africa, which is when and where dung beetles (Scarabaeinae) co-radiated.[13] Three Miocene (13–12 mya) fossil species purportedly belonging to extant dung beetle genera have been described from Kenya.[14]

In spite of several well-studied and extensive Eocene fossil sites (in the northern hemisphere), only a few have produced scarabaeoid fossils, and then in very low numbers: three Aphodiinae (one each from Menat, France; Baltic amber; Bognor Regis, UK) and three Melolonthinae (two species from Geiseltal, Germany and one from the Green River Formation in USA). The one described in this paper is the only Eocene scarabaeoid known from Africa.

Scarabaeoid fossils are rare in African fossil records and have only been recorded from the very rich Cretaceous deposit at Orapa in Botswana (one species: *Ceafornotensis archratiras* Wooley, 2016)[10], a Miocene deposit in Kenya (three species)[14], and a Pliocene site in northern Tanzania (two species)[12]. The specimen described in this paper lies chronologically about midway between the Orapa and Kenyan fossils, the Eocene. Earlier deposits such as the Triassic Molteno Formation yielded many insect fossils, including beetle fossils, but no scarabaeoids.[15,16]

The Orapa fossil belongs to an extinct genus and species (*Ceafornotensis archratiras*) of the scarabaeid subfamily Melolonthinae[10], and the three Kenyan fossils are members of three extant genera of dung beetles (Scarabaeinae); *Anachalcos* Hope, 1837 (the name subsequently synonymised with *Chalconotus* Dejean, 1833), *Copris* Geoffroy, 1762 and *Metacatharsius* Montreuil, 1998[14]. The two Pliocene fossils from Tanzania (Laetoli) are assigned to two different scarabaeid subfamilies – Dynastinae (of the extinct genus *Calcitoryctes* Krell, 2011) and Melolonthinae (one unnamed species of extant melolonthine tribe Schizonychini).[12]

Material and methods

Geographical position

The Mahenge deposit (4°47’50.2”S, 34°15’54.5”E) is located close to the village of Mwaru, about 65 km west of the town Singida and east of the Wembere Steppe (Figure 1).[5]

Geology and palaeoenvironmental reconstruction

Geologists prospecting for diamonds in the area of Singida in the early 1930s recorded the occurrence of superbly preserved fossils contained in lake beds overlying the diamondiferous kimberlite pipes.[2] The fossils were found in sediments largely consisting of shales and mudstones, originally deposited in the former crater lake. One of many in the area, the Mahenge maar deposit has yielded various fossils.[3-5] The Mahenge deposit has been interpreted as a small, previously roughly circular lake, about 400 m in diameter, which was formed in a kimberlite intrusion.[17,18]

Generally, the formation of a kimberlite pipe begins after its eruption, when the overlying basement rock material is scattered around and a crater produced, which is subsequently surrounded by a tuffaceous cone of largely fine-grained ashes. In Mahenge, this steep-sided cone created a rather small shoreline for the original lake, made of the sediments from the surrounding pyroclastic kimberlitic rocks.[19] Thus, the centre of the Mahenge palaeolake is now characterised by well-stratified, micro-laminated shales and mudstones in which the majority of the fossils are found (Figure 2).[3,18,19]

The age of the fossiliferous beds at Mahenge has been determined using radiometric methods. Originally, based on a comparison of elements in the fossil ichthyofauna, a Miocene age was suggested[20], but this changed later to Oligocene[21]. Kimberlites from elsewhere in the Singida region (Figure 1) have been dated using U-Pb and fission track radiometric methods, giving an age between 51 and 54 Ma for some kimberlites (Paleocene to Lower Eocene). A single zircon crystal, collected in 1996 from the stream bed at Mahenge and linked by its origin to the Mahenge diatreme, was dated at 45.83±0.17 Ma, based on 206Pb/238U radiometric measurements (Middle Eocene = Lutetian).[3] Consequently, it is assumed to be only slightly older than the palaeolake at Mahenge, because it is well known from comparable maar lakes in Europe and Africa that lacustrine sediments accumulate soon after formation of the original lake.[22] The age of the Mahenge Lagerstätte can therefore be assumed to be about 45.6 Ma old. Estimates of the sedimentation rate at Mahenge indicate that the fossiliferous deposits in the crater represent an interval ranging from 8000 to 22 700 years.[3]

From palaeobotanical evidence, it has been suggested that the palaeoflora of Mahenge structurally resembled ‘miombo’ savanna woodlands still widespread in much of southern and East Africa, including Tanzania, and that the region was subjected to an overall dry climate with pronounced seasonality.[5,23]

All the fossils are embedded as compressions in fine-laminated, pale beige, clayey-calcareous lake sediments. The rocky material seems to be extremely hard. The surfaces of the fossils are characterised at least partly by a darker film of possibly organic (coaly) or iron-containing material, varying in colour from reddish, brownish to blackish. Fine details to a size of less than 1 mm can often clearly be seen under a microscope, but processes of increasing weathering are also indicated by subsequent exuding of hardened small bubbles of iron or manganese along the body surfaces. In total, 1900 fossils have been recovered; fish make up the largest part (51%), followed by plant remains (36%) while only nine insect fossils have been identified, most of which are poorly preserved.[5]

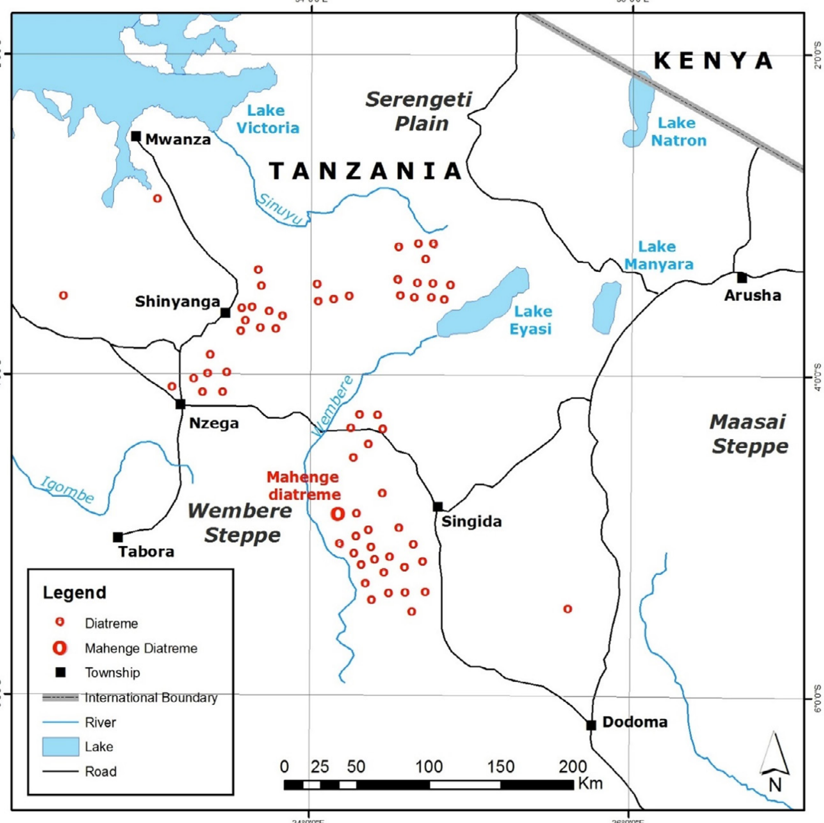

Figure 1: Overview of the Mahenge area in northern Tanzania. Potentially similar kimberlite deposits are indicated as red circles (modified after Kaiser et al.[4]).

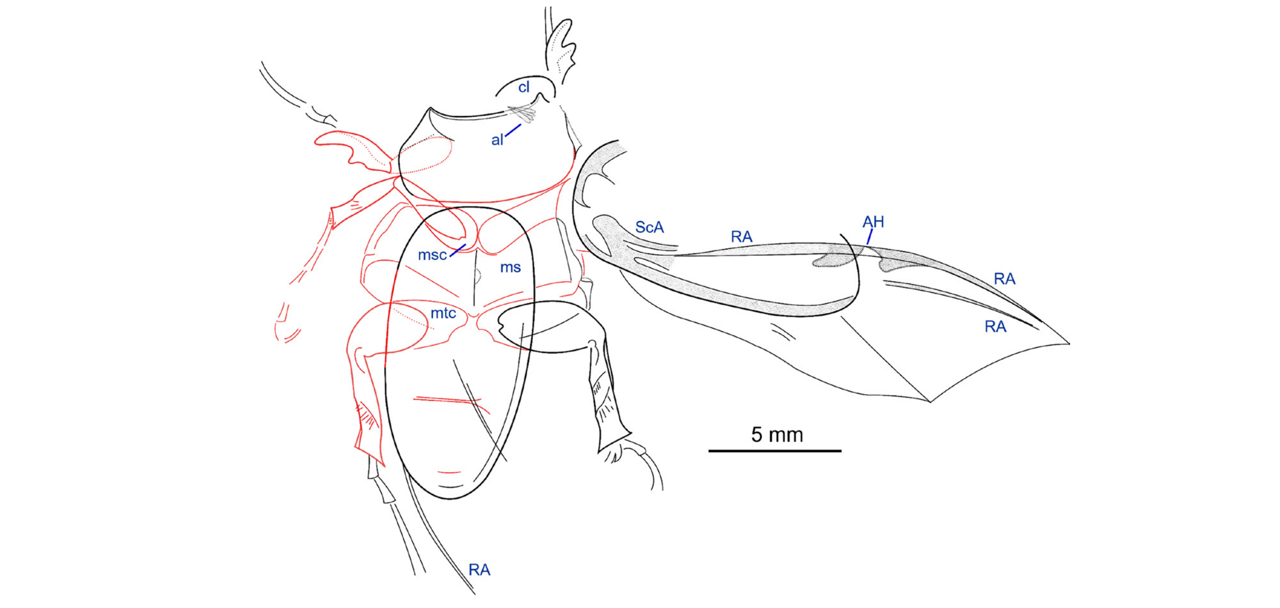

Figure 2: Composite line drawings of *Mahengea mckayi* Strümpher, Scholtz & Schlüter, new genus, new species. Black lines, plate. Red lines, counter plate. Abbreviations: AH, apical hinge; al, antenna lamellae; cl, clypeus; ms, metasternum; msc, mesocoxa; mtc, metacoxa; hindwing venation: RA, radius anterior veins; ScA, subcosta anterior vein.

Examined material

The fossil specimen can be examined and interpreted from both plate and counter plate. On both pale-coloured plate sides it is shown as a dorso-ventral compression. The specimen was examined dry and wet (submerged in water) using a LEICA MZ12.5 dissecting microscope; measurements were made using digital electronic callipers and are here given in millimetres. The plates were photographed with a Canon EOS 5D camera equipped with a 100 mm macro lens. The specimen was illustrated from the photographs with the aid of vector graphics software.[24] The adult specimen is nearly complete, but parts of the head and legs are poorly preserved (Figures 2–4). The body has a cylindrical form. The fore legs are well-visible, distally broadened, and thus apparently suitable for digging. One partial outstretched metathoracic wing is visible (Figures 2, 3).

Taxonomy

Order: **Coleoptera** Linnaeus, 1758[25]

Superfamily: **Scarabaeoidea** Latreille, 1802[26]

Family: ***incertae sedis*** **[uncertain]**

Mahengea Strümpher, Scholtz & Schlüter, **new genus**

(Figures 2–4)

Type species: *Mahengea mckayi*, here designated.

Generic diagnosis

This genus can be diagnosed as follows: *Body* moderately large (~18 mm long), somewhat robust, cylindrical form, broadly oval. *Head*. Clypeal margin rounded. Antenna with lamellate club. *Pronotum*. About twice as wide as long, widest at middle. Shape subquadrate, anterior margin of pronotum concave, basal margin relatively straight, only slightly rounded; lateral margin strongly curved, with basal half rounded, anterior half straight. Anterior angles acute, posterior angles broadly rounded. *Elytra*. Shape parabolic, about twice as long as wide medially, indistinct striae. *Metathoracic wings*. Fully developed, apical hinge discernible. *Legs.* Protibiae widening apically, tridentate, mesotibiae and metatibiae slender, each with medial transverse carinae. Mesocoxa near contiguous at midline. Metafemora large, broadly ovate.

Etymology

The generic name *Mahengea* is based on the name of the palaeolake, Mahenge, in Tanzania from which the fossil originates.

Mahengea mckayi Strümpher, Scholtz & Schlüter, **new species**

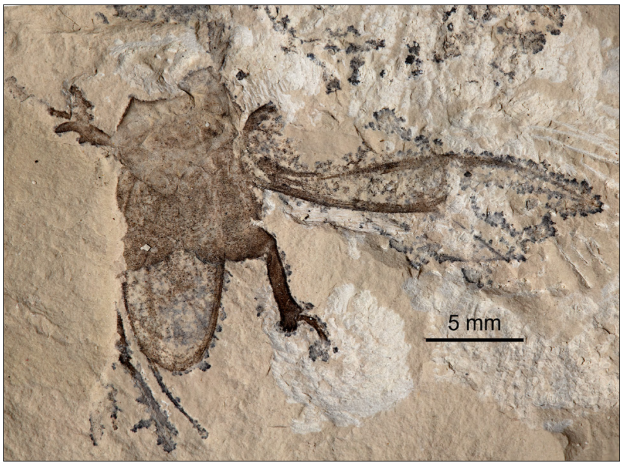

Figure 3: Habitus of *Mahengea mckayi* Strümpher, Scholtz & Schlüter, new genus, new species, holotype specimen (plate).

Holotype

Sex unknown, plate and counter plate. The specimen is deposited in the collection of the Ditsong National Museum of Natural History (TMSA; Coll. No. 811) (Figures 3 and 4).

Description

Broadly oval, elongate, cylindrical form; body length: about 18 mm, body width: 11 mm. *Head*. Clypeus partly visible, anterior margin rounded. Antennal club lamellate with at least three lamellae discernible, lamellae elongate and narrow (Figure 2). *Pronotum*. length 3.8 mm, width about 7.5 mm. Shape and form as in genus. Scutellum not preserved. *Elytra and metathoracic wing*. Elytron: length 12.5 mm, width 6.2 mm. Shape parabolic, about twice as long as wide medially, widest at middle, tapering slightly posteriorly, rounded apically, without discernible striae or tubercles on surface. Metathoracic wings: Fully developed. *Legs*. Protibiae with three teeth on the outer margin. Mesocoxae close, round; mesofemora and mesotibia slender, latter not strongly dilated at the apex, not wider than mesofemur; mesotarsi distinctly longer than mesotibia. Metacoxae transverse, narrowly separated; metafemora broad, ovate, widest medially; metatibiae slightly dilated apically. Transverse carinae present on the mesotibia and metatibiae, with presence of spine-like setae.

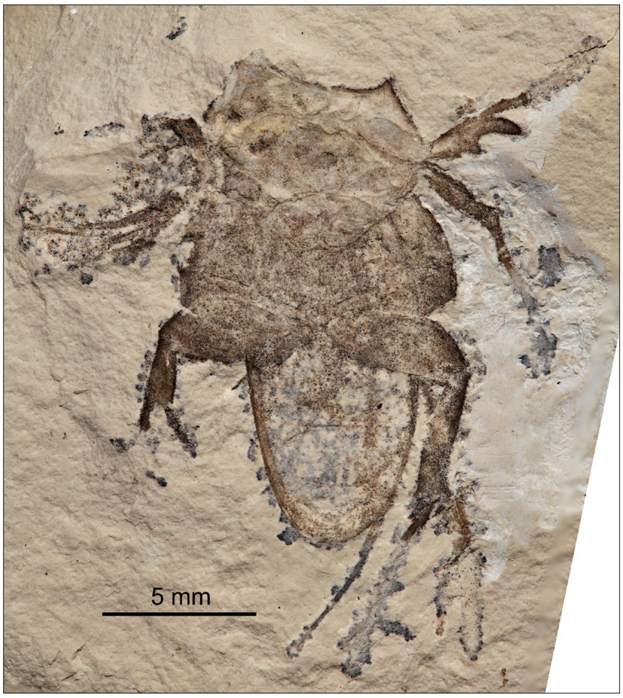

Figure 4: Habitus of *Mahengea mckayi* Strümpher, Scholtz & Schlüter, new genus, new species, holotype specimen (counter plate).

Diagnosis

Same as the genus.

Etymology

This species is named in honour of Ian Mckay (1963–2022) who died suddenly and unexpectedly recently – he was an insect fossil curator, palaeoentomologist and geoscience outreach educationist extraordinaire at the University of the Witwatersrand, Johannesburg, South Africa.

Age and significance of the Mahenge fossil

Based on the geological and palaeontological evidence now known from the Mahenge site, it can be concluded that the maar and related deposits in this area represent one of the very few sampled temporal and geographical windows of freshwater and terrestrial ecosystems in sub-Saharan Africa. Although an Eocene age is not of particular significance because of the undisputed older origin of scarabaeoids, its significance lies in the fact that few scarab fossils of older than Oligocene age have been described, and only one (Cretaceous) from Africa. It is also the only Eocene fossil scarab from Africa and one of only a few worldwide. Furthermore, its description brings to seven the total number of scarabaeoid fossils from the continent.

Possible family placement

All currently recognised families of the Scarabaeoidea (and their subfamilies) are undoubtedly older than the Eocene and the distinguishing characters outlined above could equally apply to most of these taxa. The environment was postulated to be 'savanna', so conditions conducive to habitation by almost all of the known higher taxa would have been possible and none can be excluded on ecological grounds. Consequently, we are left with little option other than to conclude that, although the fossil undoubtedly is that of a scarabaeoid species, the family should be considered *incertae sedis*.

Acknowledgements

We are grateful to Ruth Muller (Pretoria, South Africa) for photographing the fossil specimen for this publication. We thank the anonymous reviewers for their valuable comments that have improved this article.

Competing interests

We have no competing interests to declare.

Authors' contributions

T.S. was responsible for the conception of this study, provided the fossil scarab described herein and reviewed drafts of the paper. C.H.S. and W.P.S. wrote and prepared the various drafts leading up to the submission of this article. W.P.S examined and described the new scarab fossil, and prepared figures. All authors read and approved the final manuscript.

References

1. McKay IJ, Rayner RJ. Cretaceous fossil insects from Orapa, Botswana. J Entomol Soc South Afr. 1986;49:7–17.
2. Rayner RJ, Waters SB, McKay IJ, Dobbs PN, Shaw AL. The mid-Cretaceous palaeoenvironment of central southern Africa (Orapa, Botswana). Palaeogeogr Palaeoclimatol Palaeoecol. 1991;88(1–2):147–156. https://doi.org/10.1016/0031-0182(91)90020-R
3. Harrison T, Msuya CP, Murray A, Jacobs BF, Baez AM, Ludwig KR, et al. Paleontological investigations at the Eocene locality of Mahenge in north-central Tanzania, East Africa. In: Gunnell G, editor. Eocene biodiversity: Unusual occurrences and rarely sampled habitats. New York: Kluwer/Plenum; 2001. p. 39–74. https://doi.org/10.1007/978-1-4615-1271-4_2
4. Kaiser TM, Alberti G, Bullwinkel V, Michalik P, Msuya C, Schulz E. Mahenge – Ein Fenster zum Mitteleozän Afrikas [Mahenge - A window to the Middle Eocene of Africa]. Nat.wiss Rundsch. 2003;56:540–546. German.
5. Kaiser TM, Ansorge J, Arratia G, Bullwinkel V, Gunnell GF, Herendeen PS, et al. The maar lake of Mahenge (Tanzania) – unique evidence of Eocene terrestrial environments in sub-Saharan Africa. Z Dtsch Ges Geowiss. 2006;157(3):411–431. https://doi.org/10.1127/1860-1804/2006/0157-0411
6. Krell F-T. The fossil record of Mesozoic and Tertiary Scarabaeoidea (Coleoptera: Polyphaga). Invertebr Taxon. 2000;14:871–905. https://doi.org/10.1071/IT00031
7. Zhang SQ, Che LH, Li Y, Liang D, Pang H, Ślipiński A, et al. Evolutionary history of Coleoptera revealed by extensive sampling of genes and species. Nat Commun. 2018;9, Art. #205. https://doi.org/10.1038/s41467-017-02644-4
8. Bai M, Ahrens D, Yang X-K, Ren D. New fossil evidence of the early diversification of scarabs: *Alloioscarabaeus cheni* (Coleoptera: Scarabaeoidea) from the Middle Jurassic of Inner Mongolia, China. Insect Sci. 2012;19(2):159–171. https://doi.org/10.1111/j.1744-7917.2011.01460.x
9. Krell F-T. Catalogue of fossil Scarabaeoidea (Coleoptera: Polyphaga) of the Mesozoic and Tertiary – Version 2007. Denver Mus Nat Sci Rep. 2007–8:1–79.
10. Woolley C. The first scarabaeid beetle (Coleoptera, Scarabaeidae, Melolonthinae) described from the Mesozoic (Late-Cretaceous) of Africa. Afr Invertebr. 2016;57:53–66. https://doi.org/10.3897/AfrInvertebr.57.8416
11. Ratcliffe B, Smith D, Erwin D. *Oryctoantiquus borealis*, new genus and species from the Eocene of Oregon, U.S.A., the world's oldest fossil dynastine and largest fossil scarabaeid (Coleoptera: Scarabaeidae: Dynastinae). Coleopt Bull. 2005;59:127–135. https://doi.org/10.1649/0010-065X(2005)059[0127:OBNGAS]2.0.CO;2
12. Krell F-T, Schawaller W. Beetles (Insecta: Coleoptera). In: Harrison T, editor. Paleontology and geology of Laetoli: Human evolution in context. Fossil hominins and the associated fauna. Vol. 2. Dordrecht: Springer; 2011. p. 535–548. https://doi.org/10.1007/978-90-481-9962-4_19
13. Mlambo S, Sole CL, Scholtz CH. A molecular phylogeny of the African Scarabaeinae (Coleoptera: Scarabaeidae). Arthropod Syst Phylogeny. 2015;73(2):303–321.
14. Paulian R. Three fossil dung beetles (Coleoptera: Scarabaeidae) from the Kenya Miocene. J East Afr Nat Hist Soc Natl Mus. 1976;31(158):1–4.
15. Anderson JM, Kohring R, Schlüter T. Was insect biodiversity in the Triassic akin to today? – A case study from the Molteno Formation (South Africa). Entomol Gener. 1998;23(1/2):15–26. https://doi.org/10.1127/entom.gen/23/1998/15

16. Anderson HM, Anderson JM. Molteno sphenophytes: Late Triassic biodiversity in southern Africa. Palaeontol Afr. 2018;53(SI):1–391.

17. Mannard GW. The geology of the Mckayi Kimberlite Pipes, Tanganyika [PhD thesis]. Montreal: McGill University; 1962.

18. Murray AM. Eocene cichlid fishes from Tanzania, East Africa. J Vertebr Paleontol. 2000;20(4):651–664. https://doi.org/10.1671/0272-4634(2000)020[0651:ECFFTE]2.0.CO;2

19. Schlüter T. Eocene insects from a Maar Lagerstätte at Mahenge, northern Tanzania. Entomol Gener. 2018;37(3/4):375–392. https://doi.org/10.1127/entomologia/2017/0653

20. Greenwood PH. Fossil denticipitid fishes from East Africa. Bull Br Mus Nat Hist Geol. 1960;5:1–11.

21. Greenwood PH, Patterson C. A fossil osteoglossoid fish from Tanzania (E. Africa). Zool J Linnean Soc. 1967;47(311):211–223. https://doi.org/10.1111/j.1096-3642.1967.tb01404.x

22. Rayner RJ, McKay IJ. The treasure chest of the Orapa diamond mine. Botsw Notes Rec. 1986;18:55–61.

23. Jacobs BF, Herendeen PS. Eocene dry climate and woodland vegetation in tropical Africa reconstructed from fossil leaves from northern Tanzania. Palaeogeogr Palaeoclimatol Palaeoecol. 2004;213:115–123. https://doi.org/10.1016/j.palaeo.2004.07.007

24. InkScape version 1.1.1. Boston, MA: Free Software Foundation, Inc. Available from: https://inkscape.org/

25. Linnaeus C, Salvius L. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis [System of nature through the three kingdoms of nature, according to classes, orders, genera, species, with characters, differences, synonyms, places]. 10th ed. Vol. 1. Stockholm: Laurentii Salvii; 1758. Latin. https://doi.org/10.5962/bhl.title.542

26. Latreille PA. Histoire naturelle, générale et particuliére des Crustacés et des Insectes. Ouvrage faisant suite aux oeuvres de Leclerc de Buffon, et partie du cours complet d'Histoire naturelle rédigé par C. S. Sonnini, membre de plusieurs sociétés savantes. Familles naturelles des genres [Natural, general and particular history of crustaceans and insects. Book following the works of Leclerc de Buffon, and part of the complete Natural History course written by C. S. Sonnini, member of several learned societies. Natural families of genera]. Vol. 3. Paris: F. Dufart; 1802. French. https://doi.org/10.5962/bhl.title.15764