Paleothius mckayi sp. n.: A New Species of Staphylininae (Arthropoda: Insecta: Coleoptera: Staphylinidae) from Orapa in Botswana[1]

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J. Entomol. Sci. 59(3): 275–288 (July 2024)
DOI: 10.18474/JES23-53

Abstract A new species of a staphylinid beetle, *Paleothius mckayi* sp. n. is described using a single fossil from the Orapa Diamond Mine in Botswana. *Paleothius* is placed in the extant subfamily Staphylininae based on its general symmetrical habitus, typical sub-limuloid and elongated medium-to-large body form, elongated head, remarkably long antennomere 1, antennal density increasing apically, antennal insertions closer to the eye than to each other, tapering abdomen with two pairs of paratergites, and intersegmental membranes with 'brick-wall' pattern. It is separated from its sister clade Paederinae by having exposed antennal insertions and a small post-coxal process. It can be distinguished from all other Staphylininae by its significantly curved temples and large subtriangular pro-, meta- and meso-coxae. The specimen is preserved with flexed, distally-sharpened, extended or protruding scissor-like mouthparts. It is possible that it was primarily using these extended or protruding scissor-like mouthparts to actively hunt prey in leaf litter and other microhabitats in and around the crater lake at Orapa. This fossil further confirms the widespread distribution of staphylinines during the Cretaceous. Moreover, similarly to other previously described fossil staphylinine staphylinid beetles, it portrays morphological stasis, or morphological conservatism. This is also known as arrested evolution. Therefore, it provides evidence for punctuated evolution dating back to the Cretaceous. Moreover, it highlights that morphological similarities between Staphylininae and Paederine date back to the Jurassic period.

Key Words fossil, rove/staphylinid beetle, crater lake, Cretaceous, Africa, southern Hemisphere

The Orapa Diamond Mine is a Cretaceous deposit from Botswana that is rich in compressions and impressions of fossil plants and insects. The existence of the deposit is of paramount importance when considering that the Cretaceous is widely accepted to be key in the history of insect evolution (Mayhew 2018, Nel 2015). The deposit is one of 60 kimberlitic pipes and dykes in the area, and is situated over a pair of adjoining diamondiferous kimberlitic pipes, recording 1,600 m in length and 1,000 m in width (McKay 1990, 1991; Rayner 1993; Rayner and McKay 1986; Rayner et al. 1991, 1997). About 93.1 Ma (Upper Cretaceous, Turonian), a pair of kimberlites from

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[1] Received 28 August 2023; accepted for publication 25 September 2023. The species is registered in ZooBank under: *Paleothius mckayi* sp. n.: urn:lsid:zoobank.org:pub:B6649C39-5DEE-4F99-B23D-3E47934FE563.

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the same kimberlitic source pipe erupted and formed a large volcanic crater at the surface (McKay 1990, 1991; Rayner 1993; Rayner and McKay 1986; Rayner et al. 1991, 1997). The kimberlite eruption was caused by deformed Archaean basement rocks overlain by volcanic and sedimentary rocks of the Permian-Jurassic Karoo Supergroup (McKay 1990, 1991; Rayner 1993; Rayner and McKay 1986; Rayner et al. 1991, 1997). Mining operations have removed the sediments, producing a large oval pit, thereby exposing lacustrine sediments preserving fossil plants and insects.

In the last decade, there has been an exponential increase in research involving Staphylinidae, which is widely accepted as the most speciose animal group on Earth, with 66,928 species nested within 35 subfamilies (Yamamoto 2021). The Jurassic was a period of diversification of Staphylinidae into subfamilies (Clarke and Chatzimanolis 2009, Grebennikov and Newton 2009, Schomann and Solodovnikov 2012, Solodovnikov et al. 2013, Thayer et al. 2012, Yue et al. 2011). This suggests that key diversification events within the tribes and subtribes occurred during the Cretaceous, although the rate of evolution was not constant. This diversity has resulted in the Staphylinidae being further subdivided into four informal subgroups of subfamilies, viz. omaliine (= 10 subfamilies), tachyporine (= 7 subfamilies), oxyteline (= 6 subfamilies), and staphylinine (= 11 subfamilies). Belonging in the staphylinine subgroup, the monophyletic Staphylininae has 9,071 described species and 411 genera, making it one of the most diverse subfamilies of the staphylinine informal subgroup (Tihelka et al. 2020). In terms of species diversity, richness and abundance, it is only outnumbered by two subfamilies, *viz.* Aleocharinae and Pselaphinae. Staphylininae has eight extant and one extinct monophyletic tribes: Arrowinini, Coomaniini, Diochini, Maorothiini, Othiini, Platyprosopini, Staphylinini, †Thayeralinini, and Xantholinini. Furthermore, Cai et al. (2019) provided nine proposed topologies between Staphylininae and Paederinae, which differed in morphological and molecular approaches.

The earliest fossil staphylinines are *Tunicopterus sigara* Tikhomirova and *Subcelytrinus antiquus* Tikhomirova, which were reported from the Jurassic Karatau Formation in Kazakhstan; and *Sinostaphylius xiejiajieensis* Hong, which was reported from the Jurassic Jiuda Formation in China. There are also 27 staphylinines that have been described in the Cretaceous (Table 1). There are also 57 staphylinines that have been described in the Cenozoic (Mnguni 2022). Some extant species of staphylinines are of forensic importance. Some species show strong seasonality and clear habitat preference, making them good potential indicators of the season of death of organisms (Mądra et al. 2014). The potential of using staphylinines for forensic investigations has been explored as a tool to validate conclusions drawn from using several species of Diptera (Mądra et al. 2014). To date, the Staphylininae have not been recorded from the Southern Hemisphere. A description of Staphylininae from the Southern Hemisphere, particularly Africa (especially from one of the major Cretaceous deposit in the region), has the potential to expand our knowledge about their biodiversity, biogeography, and early evolution.

Materials and Methods

A single specimen of an adult fossil preserving both dorsal and ventral structures is described. The specimen described in this study was excavated in Orapa Diamond Mine (ODM) (Fig. 1), a deposit located in the northeast of Botswana, approximately

Table 1. Species list of the Staphylininae (Arthropoda: Insecta: Coleoptera: Staphylinidae). Taken from Mnguni (2022).

Taxon	Deposit	Preservation
Jurassic		
Tunicopterus sigara Tikhomirova, 1968	Karatau, Kazakhstan	Rock
Subcelytrinus antiquus Tikhomirova, 1968	Karatau, Kazakhstan	Rock
Sinostaphylius xiejiajieensis Hong, 1992	Jiuda Formation, China	Rock
Cretaceous		
Paleothius mckayi Mnguni, Badenhorst and Bamford (this study)	Orapa, Botswana	Rock
Cretoquedius distinctus Solodovnikov and Yue, 2013	Yixian Fm., China	Rock
Cretoquedius dorsalis Solodovnikov and Yue, 2013	Yixian Fm., China	Rock
Cretoquedius infractus Solodovnikov and Yue, 2013	Yixian Fm., China	Rock
Cretoquedius oculatus Ryvkin, 1988	Magadanskaia, Russia	Rock
Cretoprosopus problematicus Solodovnikov and Yue, 2013	Yixian Fm., China	Rock
Durothorax creticus Solodovnikov and Yue, 2013	Yixian Fm., China	Rock
Laostaphylinus fuscus Zhang, 1988	Laiyang Fm., China	Rock
Laostaphylinus nigritellus Zhang, 1988	Laiyang Fm., China	Rock
Megolisthaerus minor Cai & Huang, 2013	Yixian Fm., China	Rock
Mesostaphylinus fraternus Zhang et al., 1992	Laiyang Fm., China	Rock
Mesostaphylinus laiyangensis Zhang, 1988	Laiyang Fm., China	Rock
Paleothius gracilis Solodovnikov and Yue, 2013	Yixian Fm., China	Rock
Paleowinus ambiguous Solodovnikov and Yue, 2013	Yixian Fm., China	Rock
Paleowinus chinensis Solodovnikov and Yue, 2013	Yixian Fm., China	Rock

Table 1. Continued.

Taxon	Deposit	Preservation
Paleowinus fossilis Solodovnikov and Yue, 2013	Yixian Fm., China	Rock
Paleowinus mirabilis Solodovnikov and Yue, 2013	Yixian Fm., China	Rock
Paleowinus rex Solodovnikov and Yue, 2013	Yixian Fm., China	Rock
Philonthus kneri Alroy et al., 2017	Lulworth Fm., Middle Purbeck	Rock
Quedius cretaceous Cai & Huang, 2013	Yixian Fm., China	Rock
Sinostaphylina nanligezhuangensis Hong and Wang, 1990	Laiyang Fm., China	Rock
Thayeralinus fieldi Solodovnikov and Yue, 2013	Yixian Fm., China	Rock
Thayeralinus fraternus Zhang et al., 1992	Laiyang Fm., China	Rock
Thayeralinus giganteus Solodovnikov and Yue, 2013	Yixian Fm., China	Rock
Thayeralinus glandulifer Solodovnikov and Yue, 2013	Yixian Fm., China	Rock
Thayeralinus longelytratus Solodovnikov and Yue, 2013	Yixian Fm., China	Rock
Vetatrecus adelfiae Kypke et al., 2019	Burmese Amber, Myanmar	Amber
Vetatrecus secretum Kypke et al., 2019	Burmese Amber, Myanmar	Amber

824 km away from Johannesburg, 240 km due west of Francistown (McKay 1991). The sediments are aged between 98.5 and 81.7 Ma, with a midpoint of 90.1 Ma (Haggerty et al. 1983), and 93.1 Ma (Davis 1977), based on the decay of ^{238}U in zircons in the kimberlite. Thus, the deposits are considered as Upper Cretaceous (Turonian, but possibly Cenomanian or Coniacian). The fossil is a well-preserved compression fossil, and both dorsal and ventral structures are visible on top of each other. It was photographed in McCarthy and Rubidge (2005: 254). It has been previously reported in Rayner and McKay (1986: 60) and Rayner and Waters (1991: 281) without description. The specimen was photographed in the Herbarium of the Evolutionary Studies Institute (ESI), at the University of the Witwatersrand, Johannesburg, South Africa. Observations and photography were done using an Olympus SZX7 binocular microscope

Fig. 1. A top view of the Orapa Diamond Mine showing the open pit left after the removal of the crater lake facies and kimberlite (21°18.465'S; 25° 22.177'E). Photo by I.J. McKay, June 2018.

(with Olympus U-TV0.36XC camera). The specimen was examined under cross polars to clarify the outlines, and non-polarized light was used at various angles to show relief. Polarizing filters were attached to the swan necked lights (the objective lens of the microscope), and were rotated to polarize the light and remove reflection. All the images were prepared using Adobe Photoshop version 5.6.5.58 (Adobe Creative Cloud, University of the Witwatersrand, Johannesburg, South Africa). All the measurements are given in mm.

Results

Systematic Palaeontology.
Order: Coleoptera Linnaeus, 1758
Series: Staphyliniformia Latreille, 1802
Superfamily: Staphylinoidea Latreille, 1802
Family: Staphylinidae Latreille, 1802
Subfamily: Staphylininae Latreille, 1802
Genus: *Paleothius* Solodovnikov and Yue, 2013

Incertae sedis

Type species: Paleothius gracilis sp. n. Solodovnikov and Yue, 2013.

Etymology: The generic epithet was described by Solodovnikov and Yue (Solodovnikov et al. 2013).

Composition: Only type species *Paleothius mckayi* sp. n.

Diagnosis: The specimen is separated from the Paederinae by its exposed antennal insertions and small post-coxal process. It is placed in the genus *Paleothius* of the subfamily Staphylininae based on characters listed in Solodovnikov et al. (2013), including: general symmetrical habitus, typical sub-limuloid and elongated medium-to-large body form, elongated head, ridges on ventral side of head under eyes, remarkably long antennomere 1, antennal density increasing apically, antennal insertions closer to the eye than to each other, tapering abdomen with two pairs of paratergites, and intersegmental membranes with ‘brick-wall’ pattern. It differs from *Paleothius gracilis* and other known

Fig. 2. The whole body of *Paleothius mckayi* species nov. holotype, Orapa Diamond Mine, polarised light, scale bar = 1 mm. Taken from McCarthy and Rubidge (2005, figure 9.9, page 254).

Staphylininae by its significantly curved temples and relatively large subtriangular pro-, meta- and meso-coxae.

Paleothius mckayi sp. n. (Figs. 2, 3, 4).

Etymology: The epithet of the new species is named in honor of Dr. Ian James McKay (1963–2022), who was a palaeoentomologist and Geosciences Outreach Education Specialist at the University of the Witwatersrand, Johannesburg, South Africa. He spent many years describing fossil insects from the Orapa Diamond Mine (McKay and Rayner 1986; McKay 1990, 1991; Mnguni 2022; Mnguni et al. 2022, 2023; Rayner and McKay 1986; Rayner et al. 1991, 1997). He also trained various undergraduate and postgraduate students, including Dr. Sandiso Mnguni (lead author), as the first black palaeoentomologist in South Africa.

Material studied: Paratype, adult, BP/2/26888, Evolutionary Studies Institute (ESI), Johannesburg, South Africa.

Fig. 3. The whole body of *Paleothius mckayi* species nov. holotype, Orapa Diamond Mine, polarised light, scale bar = 1 mm. Taken from Rayner and Waters (1991, figure 1, page 281).

Type locality and horizon: Botswana, Orapa, Orapa Diamond Mine, lacustrine deposit, Upper Cretaceous (Davis 1977, Haggerty et al. 1983).

Diagnosis: As for the genus *Paleothius* described by Solodovnikov and Yue (Solodovnikov et al. 2013).

Description: Narrow, slender and cylindrical body shape, measuring 7.70 mm in length (from tip of mandibles to tip of abdomen) and 0.80 mm in width (from exterior edge of left elytron to edge of right elytron). Last abdominal segment seemingly covered with setae.

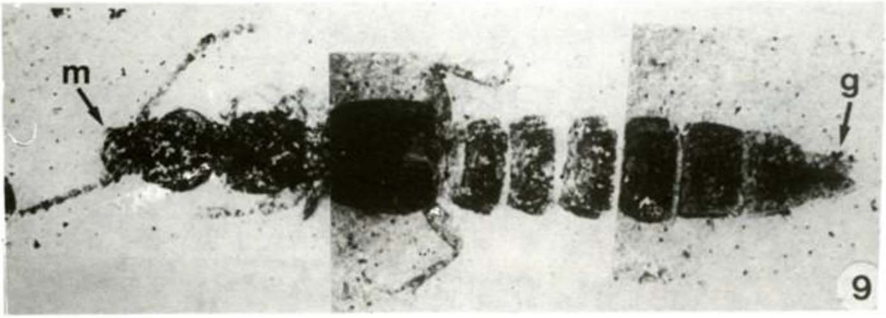

Fig. 4. The whole body of *Paleothius mckayi* species nov. holotype, Orapa Diamond Mine, polarised light, scale bar = 1 mm. Abbreviations: m = mandibles and g = genitalia. Taken from Rayner and McKay (1986, figure 9, page 60).

Head capsule rounded, with distinctly curved temples, broader than pronotum, longer than wide (1.30 long and 0.70 wide), width of head broader than width of thick neck constriction. Eyes small, circular to slightly oval, located behind antennal insertions, left eye more visible than right. Infraorbital ridges below eyes and basolateral ridges distinct and complete. Gular sutures indistinct. Antennae filiform, right antennae with 11 segments, left antennae with 9 segments. Antennal proximal bases exposed under “shelf”; antennal insertions exposed (not concealed), seemingly located at anterior margin of head capsule; distance between antennal insertions slightly longer than distance to eyes (i.e., significantly closer to the eyes than to each other); antennomeres funnel-shaped (subquadrate), without a club, antennomere 1 (proximal bases) remarkably long, antennomeres 2–6 seemingly subquadrate, antennomere 7-8 longer than wide, antennomere 9–11 more or less of equal length and width. Mandible large, extended, with broad base, apically curved, narrow, pointy and sharp-edged. Maxillary palpi extremely long, fusiform, right side more visible than left. Labial palpi indistinct. Neck constriction (0.20 mm long, and 0.30 wide) clearly visible, broad, wider than long, about 0.6 times as wide as head.

Pronotum rectangular with curved sides, with equal length and width (0.60 mm long, and 0.60 mm wide); slightly narrower than head; anterolateral angles well developed; lateral and posterior margins well-rounded; anterior margin strongly curved, forming slight collar around the neck; posterior margin gently curved; with indistinct post-coxal process of hypomeron. Elytra rectangular, slightly wider than long (1.80 mm long, from posterior margin of pronotum to anterior margin of elytron, 1.0 mm wide each side); 1.4 times longer than pronotum; surface smooth, apparently without striae; anterolateral corners well rounded; seemingly without epipleural ridge; elytral posterior margins evenly curved. Legs very long, with relatively large subtriangular coxae, small post-coxal process; femur thick; tibia long and thick, gradually widening apically; protibia curved, thicker than metatibia, with tibial combs; tarsi long, with sharp apical spur; tarsomeres poorly preserved, presumably 5-segmented.

Abdomen long, narrow, cylindrical, almost parallel-sided until segment IX; approximately 3 x length of elytra, 3 x as long as wide (4.40 mm long, and 0.70 mm wide);

narrows posteriorly; with six visible abdominal segments, seemingly with abdominal intersegmental membranes; widest at segment VII; tapers from abdominal segment VIII to apex; segment IV-VII with two pairs of paratergites, segment VIII with single pair of paratergites; segment IX significantly long, with setae, with pair of setiferous latero-apical processes separated by pair of pointed structures interpreted as tergal plates (Naomi 2018).

Palaeoenvironment: At Orapa, the specimen was probably an active general predator of small invertebrates in and around the crater lake, and would have been found in leaf litter and other kinds of debris, or floating mats of vegetation. It is equally probable that it would have been found in dead decaying organic matter, or was an inhabitant of bird and mammal nests. The specimen possibly had inter-specific competition with another staphylinid that has been previously described from Orapa, *Afristenus orapensis* Mnguni, McKay and Badenhorst (2023), as well as others that are still in the process of being published, including a Paederinae.

Remarks: The staphylinine tribes such as Diochini, Xantholinini, Maorothiini and Othiini are excluded for a possible taxonomic and systematic assignment because the antennal insertions of the specimen are extremely closer to the eye than to each other. However, tribes such as Arrowinini, Thayeralinini, Staphylinini and Platyprosopini typically have cylindrical parallel-sided body shapes and, therefore, remain possibilities. Interestingly, the tribe Platyprosopini is found to be a sister group to the Paederinae in Brunke et al. (2016) and in Schomann and Solodovnikov (2017), while Cai et al. (2019) report that some researchers have considered raising it to a subfamily rank. This has led to several researchers proposing that the tribe Platyprosopini may be an important link between subfamilies Staphylininae and Paederinae (Cai et al. 2019). More work is still needed to accept or reject this conjecture. Nonetheless, the tribe Arrowinini is considered to be the most primitive and phylogenetically isolated lineages of the Staphylininae (Cai et al. 2019).

Discussion

This is the first fossil staphylinine from the Southern Hemisphere, particularly from Africa. Previously, staphylinines have been described from localities in Myanmar, Purbeck, China, and Russia (Fig. 5). The addition of a locality in Botswana offers diversity, geography, and evolution insights. The Staphylininae and Paederinae are estimated to be 156.6 Ma, which marks the Late-Jurassic period (McKenna et al. 2015a, b). An estimate by Solodovnikov et al. (2013) is much older, projecting 180–145 Ma. The subsequent split of Staphylininae into main lineages is estimated to be between 152.9–143.9 Ma, during the Late-Jurassic and Early-Cretaceous (Hernando and Andujar 2021). Finding a staphylinine from one of the major Cretaceous deposits in Africa, the Orapa Diamond Mine in Botswana is consistent with the fossil record. It complements the description of a paederine from the same deposit, which is currently in the process of being published. The Staphylininae is sister to Paederinae, and has an impressive variation of shapes, biologies, distributions, and several other taxonomic features. The fossil described in this study ascertains that the Staphylininae (and possibly its sister clade Paederinae) was more diverse in the Early Cretaceous than previously thought.

The specimen shares several characteristics with *Quedius cretaceous* Cai and Huang, 2013, including having small eyes, broad neck and large robust mandibles.

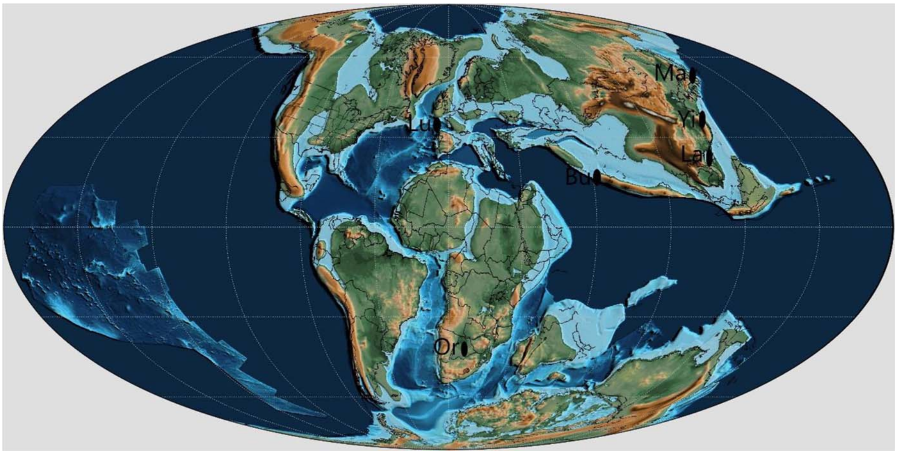

Fig. 5. Global palaeogeographic reconstruction of the mid-Cretaceous (100 Ma) showing the localities where the fossil Staphylininae have been recovered. The map in Mollweide projection was sourced from Scotese (2016, 2021; Appendix 2, Mollweide_Maps.zip). The position of the localities was adapted from Rasnitsyn and Quicke (2002). Abbreviations: Bu = Burmese amber, Myanmar; La = Laiyang Formation, China; Or = Orapa Diamond Mine, Botswana; Yi = Yixian Formation, China; Ma = Magadanskaia, Russia and Lu = Lulworth Formation, Middle Purbeck.

It also shares similar characteristics with *Cretoquedius* Ryvkin, 1988, in terms of its general habitus, and having a sub-parallel abdomen. However, the specimen differs in having a larger body size, smaller eyes (not typically occupying most of lateral side of head), and slightly shorter elytra. The specimen also shares characteristics with *Megolisthaerus* Yue and Solodovnikov, 2010, such as having a large, elongated and cylindrical body, antennae inserted at the anterior margin of the head, elytron without epipleural keel, and having two pairs of paratergites on abdominal segments. The specimen shares several characteristics with *Platydracus* Thomson, 1858, such as general habitus, relatively small eyes and robust mandibles with sharply pointed apex.

The specimen differs from *Cretoprosopus problematicus* Solodovnikov and Yue, 2013 by having a neck constriction, longer antennae, and a well-developed abdominal segment II. *Paleothius* Solodovnikov and Yue, 2013 is significantly smaller than any of the species of *Thayeralinus* Solodovnikov and Yue, 2013, or *Paleowinus* Solodovnikov and Yue, 2013, and additionally differs from species of both of those genera by having a more gracile body, especially the distinctly elongated pronotum. *Paleothius* Solodovnikov and Yue, 2013 differs from *Cretoquedius* Ryvkin, 1988 by its less developed neck constriction, and having only one (contrary to two) transverse carina at the base of the scutellum. Unlike *Durothorax* Solodovnikov and Yue, 2013, *Paleothius* Solodovnikov and Yue, 2013 has basally-confluent (as opposed to separate) gular sutures, and has no large sclerite at the base of the prothorax behind the anterior coxae.

In addition, *Paleothius mckayi* sp. n. Mnguni, Badenhorst and Bamford has a remarkably long antennomere 1 that is confined to the extant subfamilies Paederinae and Staphylininae, which have always been considered to be distinct monophyletic groups (Brunke et al. 2016; Cai et al. 2019; Grebennikov and Newton 2009; McKenna et al. 2015a, b; Tihelka et al. 2020; Toussaint et al. 2016). The close affinity between Staphylininae and Paederinae is supported by several larval and adult apomorphies such as mandibles without preapical teeth, abdominal terga and sterna longitudinally divided medially by membranous area, metacoxae projecting medially with posterior margin of metaventrite strongly sinuate, as well as having a flat, blade-like, and protruding adult protrochantin (Cai et al. 2019). However, several researchers propose that Staphylininae may be paraphyletic (Solodovnikov et al. 2013), and this notion is being strongly supported by molecular and fossil-integrated morphology-based phylogenies (e.g., Brunke et al. 2016, Kypke et al. 2018), thereby strongly contradicting the conventional larval and adult morphological studies (e.g., McKenna et al. 2015a, b). This uncertainty pertaining the paraphyly of the Staphylininae is still on-going.

It is rather difficult to place the specimen in any of the tribes of Staphylininae due to the inability to view some key diagnostic characters under non-polarised light. Superficially, it resembles some representatives of Platyprosopini and Staphylinini in its general habitus (i.e., large, elongated and parallel-sided body, curved and elongated head, and similar structure of abdominal segments IX); but it differs significantly in having significantly curved temples and relatively large subtriangular pro-, meta- and meso-coxae. Curved temples are known to be limited to some extant staphylinine genera such as *Leistotrophus* Perty, 1830, *Naddia* Fauvel, 1867, *Ontholestes* Ganglbauer, 1895, and in some species of *Platydracus* Thomson, 1858. However, *Paleothius mckayi* sp. n. Mnguni, Badenhorst and Bamford challenges this notion. It unequivocally shows that this characteristic is much more common than previously thought. It confirms that this characteristics dates back to the Cretaceous.

Cai et al. (2019) advocates that without a robust phylogeny of the Staphylininae, time-trees of the group cannot be reconstructed confidently; while further sampling of more taxa of the group (especially key taxa from the Southern Hemisphere, or Africa) should undoubtedly provide further insights into the diversity, geography, phylogeny and early evolution of the subfamily. This remark necessitates an acceleration of descriptions of the group. Here, we provide the first attempt to address this important knowledge gap. Any new fossil descriptions of any staphylinid group are of great interest to taxonomists and systematists, especially one recovered from the Southern Hemisphere, or Africa. This is largely because the staphylinid fossil record from the region is very scarce, but has inadvertently become a subject of research interest very recently (e.g., Mnguni 2022; Mnguni et al. 2022, 2023). As a start, a fossil stenine staphylinid beetle, *Afristenus orapensis* Mnguni, McKay and Badenhorst, 2023 has recently been described from the same deposit.

A proper description and delineation of fossils is important for understanding an early evolution of the subfamilies of the Staphylinidae. The Staphylininae is one of the most speciose subfamilies of the Staphylinidae. To date, inter-tribal and inter-subtribal relationships within the Staphylininae are still not completely resolved. This is because more descriptions of the group are still needed. The descriptions have been scarce from Africa. Morphological and molecular character analyses of the Staphylininae continue to be unresolved completely, as studies yield ambivalent results, as readily established in many other morphologically-diverse taxa. Nonetheless, the general consensus is that the Staphylininae and all its tribes are monophyletic. The fossil described here, *Paleothius mckayi* sp. n. Mnguni, Badenhorst and Bamford, is the first from Africa. This fossil further confirms the diversity and widespread distribution of staphylinines during the Cretaceous. Moreover, similarly to other described fossil staphylinid beetles, the fossil also portrays morphological stasis or conservatism (i.e., arrested evolution), demonstrating punctuated evolution dating back to the Cretaceous. It distinctly and unequivocally highlights that the morphological similarities between the Staphylininae and Paederine date back to the Jurassic.

Acknowledgments

We thank the editors and reviewers for their unequivocal contributions. We also thank The Office of the President of Botswana, Botswana National Museum (BNM) and De Beers Botswana Mining Company for the invitation to collect the material. We acknowledge Mr. J. Claase from Wirsam Scientific and Precision Equipment (Pty) Ltd. for monitoring and repairing our Olympus microscope.

The support of the GENUS [DSI-NRF Centre of Excellence in Palaeosciences (DSI-NRF CoE-Pal), UID 86073] towards this research is hereby acknowledged. Previously, S.M. was also funded by the National Research Foundation of South Africa Innovation Doctoral Scholarship (Grant UID: 113518 and 131055), the Palaeontological Scientific Trust (PAST), Johannesburg, and the GENUS [DSI-NRF Centre of Excellence in Palaeosciences (DSI-NRF CoE-Pal) Top-Up (References: COE2018-16PHD, COE2019-D11, COEPH2020-11 and COE2021-SM)]. Opinions expressed and conclusions arrived at in this publication are those of the authors and are not necessarily to be attributed to the sources of funding and support.

The authors declare that there are no potential conflict of interests; in a form of competing, financial, funding sources, owning of shares, and other payments.

S.M. would like to dedicate this publication to his late supervisor, Dr. Ian James McKay (1963–2022) and his former colleague, Ms. Lumka Anita Mdodana (1988–2023).

Contributions to this work by the authors are as follows: S.M. - Conceptualization; S.M. - Data curation; S.M. - Formal analysis; S.M., M.K.B., and S.B. - Funding acquisition; S.M. - Investigation; S.M. - Methodology; S.M. and S.B. - Project administration; S.M. - Resources; S.M. - Software; S.B. and M.K.B. - Supervision; S.B. and M.K.B. - Validation; S.M. - Visualization; S.M. - Roles/Writing - original draft; S.M., S.B., and M.K.B. - Writing - review and editing.

Data sets related to this article will be shared with the audience upon request.

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