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Cretafrica orapensis: a new genus and species of Mycetoporinae (Coleoptera: Staphylinidae) from lacustrine deposits at Orapa Diamond Mine, Botswana

Sandiso Mnguni[a,b,*], Ian James McKay[a] and Shaw Badenhorst[a]

[a]Evolutionary Studies Institute (ESI), School of Geosciences, University of the Witwatersrand, Johannesburg, Private Bag 3, Wits 2050, South Africa.
[b]GENUS: DSI-NRF Centre of Excellence in Palaeosciences (DSI-NRF CoE-Pal), University of the Witwatersrand, Johannesburg, Private Bag 3, Wits 2050, South Africa.
*Corresponding author: Sandiso.Mnguni@wits.ac.za, msandiso@gmail.com
ZooBank registration: https://zoobank.org/Editor/SandisoMnguni
ORCiD iDs: Mnguni: 0000-0002-3077-2162; Badenhorst: 0000-0002-6651-9660

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Abstract

A new genus and species of staphylinid beetle, *Cretafrica orapensis* **gen. nov. et sp. nov.** is described using a single well-preserved impression fossil from an Upper Cretaceous fossil insect deposit, the Orapa Diamond Mine in Botswana. *Cretafrica* is placed in the extant subfamily Mycetoporinae based on its general habitus, typical sublimuloid medium-to-large body form, elongated head, visible ridge on ventral side of head under eyes, antennomeres increasing in length and width apically, scutellum with basal carina that is distinctly divided medially, elevated area along suture of the elytra, and presumably large metacoxae, and tapering abdomen. It differs from other Mycetoporinae by its triangular head and elytra with broadly rounded apico-lateral margins. A possible preservation distortion illustrates brush-like or fork-like mouthparts. The fossil insect may have been found in forest litter or fresh and rotting mushrooms at Orapa. It confirms the widespread distribution of mycetoporines with phytophagous or mycophagous lifestyles during the mid-Cretaceous. Moreover, like other described fossil staphylinids, the fossil portrays morphological stasis dating back to the Cretaceous. It further confirms the proposed punctuated equilibrium pattern of evolution.

Keywords:

Fossil insect, Staphylinid, Craterlake, Africa, Southern Hemisphere, Forest microhabitat.

ZooBank: https://zoobank.org/B1CC15AA-3075-4769-9ED5-676B90356AC4

Introduction

The Mycetoporinae has approximately 444 species within 16 genera (Yamamoto 2021). The fossil record of this group is minimal during both the Mesozoic and Cenozoic. Ryvkin (1990) described *Cuneocharis elongata* Ryvkin, 1990 from the Lower Cretaceous Daya Formation of Russia (Ryvkin 1990). In addition, Yue at al. (2009) described *Glabrimycetoporus amoenus* Yue, Zhao & Ren, 2009 from the Lower Cretaceous Yixian Formation of China (Yue et al. 2009). Some taxa once assigned to Tachyporinae have been revised and moved to Mycetoporinae. For example, Ryvkin (1990) also described *Ryvkinius gracilis* (Ryvkin, 1990) from the Lower Cretaceous Daya Formation of Russia and *Undiatina pilosa* Ryvkin, 1990 from another Lower Cretaceous Semyon Formation of Russia (Ryvkin 1990). These were initially assigned to Tachyporinae. However, after re-examination and revision, Yamamoto (2021) has since assigned them to Mycetoporinae.

To date, there are no fossil mycetoporines that have been recorded from any Mesozoic amber. However, there are several Cenozoic specimens that belong to the genera *Lordithon* and *Mycetoporus* that have been described from the Eocene Florissant Formation of the United States of America. Generally, extant Mycetoporinae are commonly found in forest litter, near water settings, or mammal nests and middens; while some are associated with fresh and rotting mushrooms (Yamamoto 2021). Until recently, the Tachyporinae consisted of five tribes, namely: Deropini Smetana, 1983; Megarthropsini Cameron, 1919; Mycetoporini Thomson, 1859; Tachyporini MacLeay, 1825; and Vatesini Seevers, 1958 (Yamamoto 2021). Herman (2001) recognised two more tribes, *viz.* the Symmixini Bernhauer, 1915 and the Cordobanini Bernhauer, 1910. The Symmixini Bernhauer, 1915 are now synonymised under Tachyporini, while the Cordobanini Bernhauer, 1910 have now been transferred to the subfamily Aleocharinae (Yamamoto 2021).

The maximum parsimony phylogenetic analysis of the Tachyporinae by Yamamoto (2021) is the most recent and comprehensive phylogenetic analysis of the group. In the analysis, Yamamoto (2021) divided the subfamily into two monophyletic units, *viz*. the Mycetoporinae and the Tachyporinae. In that study, Tachyporinae are subdivided into four tribes, *viz.* the Tachyporini, Vatesini, Tachinusini and the Deropini; while the Mycetoporinae were found to be distantly related to the Tachyporinae, and are the sister taxon of the Olisthaerinae.

To date, there are only four Mesozoic mycetoporines that have been reported (Table 1). Here we describe *Cretafrica orapensis* from Orapa Diamond Mine in Botswana, the only major Cretaceous deposit rich in compressions and impressions fossil flora and fauna in Africa. The lacustrine deposit bears a rare example of a kimberlite pipe that still has its crater lake facies preserved, termed epiclastic kimberlite. Other examples of epiclastic kimberlites are known from neighbouring countries in Africa such as Tanzania, Zambia, Angola, Democratic Republic of the Congo, Mali and South Africa (McKay 1990). The Cretaceous is key in the history of insect evolution, as many of the families and subfamilies of the Coleoptera were already present. We assign the fossil to an extant subfamily Mycetoporinae, and subsequently draw inferences of its probable microhabitats during the Cretaceous at Orapa, Botswana.

Table 1. Species list of the Mesozoic Mycetoporinae (Coleoptera: Staphylinidae). From Yamamoto (2016).

Taxon	Stratigraphy	Deposit	Preservation
Mycetoporinae			
Cretafrica orapensis (new species described here)	Upper Cretaceous	Orapa, Botswana	Rock
Cuneocharis elongata Ryvkin, 1990	Lower Cretaceous	Obeschayushchiy (Daya Fm.), Russia	Rock
Glabrimycetoporus amoenus Yue et al., 2009	Lower Cretaceous	Yixian Fm., China	Rock
Ryvkinius gracilis (Ryvkin, 1990)	Lower Cretaceous	Obeschayushchiy (Daya Fm.), Russia	Rock
Undiatina pilosa Ryvkin, 1990	Lower Cretaceous	Semyon Fm., Russia	Rock

Materials and Methods

The specimen described in this study was excavated at Orapa Diamond Mine (Figure 1), located in the northeast of Botswana. It is approximately 824 km away from South Africa, and 240 km due west of Francistown (McKay & Rayner 1986; McKay 1991). It is the largest conventional open-pit diamond mine producer by carats in the world (Brook 2019), with a length of 1 600 m and a width of 1 000 m (Rayner & McKay 1986; McKay 1991). A double eruption of diamondiferous kimberlites resulted in a deposition of fossiliferous sediments in a crater lake. These were subsequently uncovered by mining operations, and collected from 18 sites between 1983 and 1988 (McKay 1990). Based on the decay of ^{238}U in zircons in the kimberlite, the sediments are aged between 98.5 and 81.7 Ma, with a midpoint of 90.1 Ma (Haggerty et al.

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 IJ McKay, June 2018.

1983), and 93.1 Ma (Davis 1977), respectively. Thus, the deposits are considered as Upper Cretaceous (Turonian, but possibly Cenomanian or Coniacian). The palaeofauna of the deposit has been reviewed elsewhere (e.g., McKay & Rayner 1986; Rayner & McKay 1986; Rayner 1987; Rayner & Waters 1989, 1990, 1991; Waters 1989a, b; Bamford 1990; McKay 1990, 1991; Waters 1990; Brothers 1992; Rayner 1993; Rayner et al. 1991, 1994, 1997; Kuschel et al. 1994; Brothers & Rasnitsyn 2003, 2008; Dlussky et al. 2004; Rasnitsyn & Brothers 2007, 2009; Kopylov et al. 2010; Woolley 2016; Mnguni 2022; Mnguni et al. 2022, 2023).

The fossil is a well-preserved impression fossil, and both dorsal and ventral structures are superimposed, and thus visible on top of each other. On the right, the specimen is accompanied by a small coleopteran (0.9 mm in length) with an attenuated elytra, possibly a myxophagan, belonging to the family Hydroscaphidae. The holotype is housed in the Herbarium of the Evolutionary Studies Institute (ESI), at the University of the Witwatersrand, Johannesburg, South Africa. Observation and photography were done using a combination of an Olympus SZX7 binocular microscope (with Olympus U-TV0.36XC camera) and an Olympus DSX 110 digital microscope. Multiple images were stacked and measured using an Olympus Stream 2.4. All the images were prepared using Adobe Photoshop version 5.6.5.58 (Adobe Creative Cloud, University of the Witwatersrand, Johannesburg, South Africa). The specimen was also examined under cross polars to clarify the outlines, and non-polarised light was used at various angles to show relief. Polarising filters were attached to the swan necked lights (the objective lens of the microscope), and were rotated to polarise the light and remove reflection. A single specimen of an adult fossil preserving both dorsal and ventral structures is described. It is preserved in pink lacustrine mudstone block (135 x 65 x 30 mm in size) from Orapa Diamond Mine in Botswana. All the images are scaled.

Results

Systematic Palaeontology

Order: Coleoptera Linnaeus, 1758
Series: Staphyliniformia Lameere 1900
Superfamily Staphylinoidea Latreille, 1802
Family: Staphylinidae Latreille, 1802
Subfamily: Mycetoporinae Thomson, 1859
Genus: ***Cretafrica* gen. nov.**

Type species: Cretafrica orapensis **sp. nov.**, by monotype and present designation.
Etymology: The generic epithet is a combination of Cret-, from 'Cretaceous', and Africa.
ZooBank: https://zoobank.org/D046A6E7-C813-4783-B080-E5A203B3A3D4
Composition: Only the type species *Cretafrica orapensis* **sp. nov.**

Diagnosis: Sublimuloid medium-to-large body form, moderately elongated head, visible ridge on ventral side of head under eyes, lacking mid-cranial suture, antennal

density increasing apically, lacking a distinct neck, has scutellum with basal carina that is distinctly divided medially, with presumably large hind coxae, pronotal hypomeron with transverse ridge, and abdomen with six visible tapering segments. It differs from other Mycetoporinae by its triangular head and broadly rounded apico-lateral margins.

***Cretafrica orapensis* sp. nov.** (Figures 2, 3, 4, 5 A, 5 B, 5 C & 5 D).
ZooBank: https://zoobank.org/D67D7406-CBD6-436C-A28A-B75927AE54E2

Etymology: The epithet of the new species is a combination of Orap- from 'Orapa', the deposit where the specimen was discovered, which in itself is derived from Sesarwa

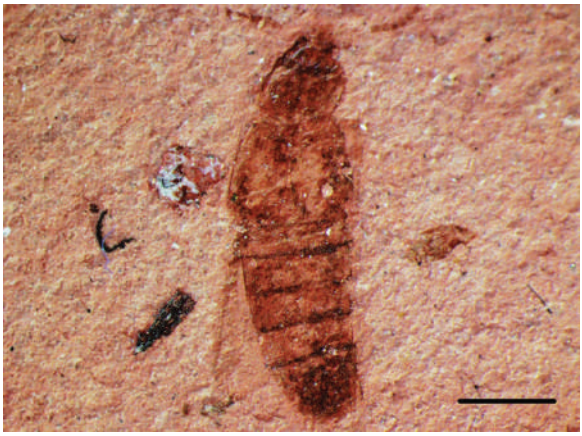

Fig. 2. The whole body of *Cretafrica orapensis* **gen. nov. sp. nov.** holotype, BP./2/27480, Orapa Diamond Mine, polarised light, scale bar = 1 mm.

Fig. 3. The whole body of *Cretafrica orapensis* **gen. nov. sp. nov.** holotype, BP./2/27480, Orapa Diamond Mine, non-polarised light, scale bar = 1 mm.

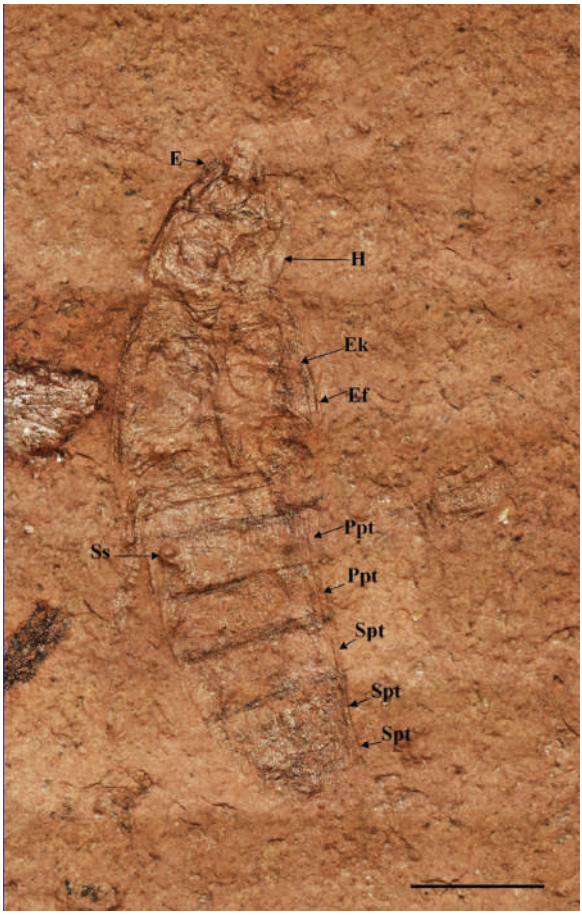

Fig. 4. The whole body of *Cretafrica orapensis* **gen. nov. sp. nov.** holotype, BP./2/27480, Orapa Diamond Mine, non-polarised light, scale bar = 1 mm. Abbreviations: e = eye, h = hypomeron, ek = epipleural keel, ef = epipleural fold, ppt = paired paratergite, spt = single paratergite, ss = spiral structure.

(a San or Bushmen language), and is named after a nearby cattle post, meaning 'the resting place of lions' (https://www.debeersgroup.com/about-us/our-operations/our-mines/botswana); and -ensis, a Latin suffix meaning 'from'.

Material studied: Holotype, adult [specimen number BP./2/27480, Herbarium, Evolutionary Studies Institute (ESI), University of the Witwatersrand, Johannesburg, South Africa].

Type locality and horizon: Botswana, Orapa Diamond Mine, lacustrine deposit, Upper Cretaceous (21°18.465'S; 25°22.177'E) (Davis 1977; Haggerty et al. 1983).

Diagnosis: As for the genus ***Cretafrica*** **gen. nov.**.

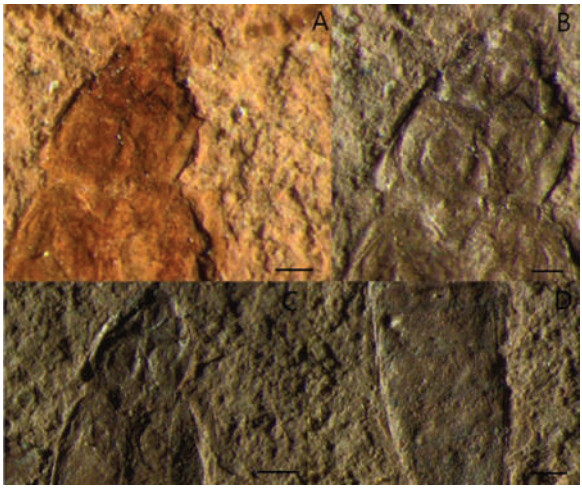

Fig. 5. *Cretafrica orapensis* **gen. nov. sp. nov.** under different light angles, holotype, BP/2/27480, Orapa Diamond Mine, (a) head + thorax (low polarised light), (b) head + thorax (non-polarised light), (c) head + thorax + elytra (non-polarised light) and (d) abdomen (non-polarised light), scale bar = 1 mm.

Description: Sublimuloid body shape, medium to relatively large, measuring 4.92 mm in length (from tip of mandibles to tip of abdomen, although tergite VIII is missing) and 1.58 mm in width (from exterior edge of one elytron to edge of other elytron) (Figures 2, 3, 4, 5 A, 5 B, 5 C & 5 D).

Head triangular, elongated (Figures 5 A, 5 B & 5 C), 0.82 mm long (from tip of mandible to anterior margin of pronotum) and posteriorly 0.76 mm wide at base, longer than wide, widest posteriorly at base, narrower than pronotum (Figures 5 A, 5 B & 5 C), without distinct neck constriction, seemingly with visible ridge on ventral side of head under eyes. Eyes (Figures 5 A, 5 B & 5 C) small, oval, located posteriorly on head, covering 1/3 of temple. Antennal insertions poorly preserved. Antennomeres increasing in length and width apically, probably with 11 segments, each antenna represented by 7 distal antennomeres. Antennomere 11 oval, almost twice as long as wide; antennomere 10 slightly longer than wide; antennomeres 6, 7, 8, 9 rectangular, slightly wider than long; antennomere 5 roughly twice as long. Anterior position of antennae, and lack of clear evidence for insertions between eyes suggest they were located anterior to eyes. Mandibles, maxillary and maxillary palps visible, but poorly preserved, details indistinct. Mouthparts anteriorly seemingly with brush-like or fork-like protrusions (although this could be a preservation distortion). Pair of parallel dark pigmented structures running down either side of head, terminating in dark oval structure, connected posteriorly. These are interpreted as dorsal tentorial arms, while the ovals are interpreted as dorsal tentorial pits (Blackwelder 1936). Similar structures are figured in Yamamoto (2021, Figure 9 A, page 18).

Pronotum (Figures 5 A, 5 B & 5 C) difficult to interpret as margins are partially covered with sediment. Appears transverse, rectangular with curved sides (1.08 mm

wide, 0.69 mm long); greatest width about halfway down length; anterior margin concave. Left side distinctly curved, probably representing original condition. Right side straight from right angles to posterior margins, forming rectangular corner. However, this may be due to poor preservation. Hypomeron visible on left side, lacking postcoxal bar, with transverse ridge at apical 1/3 to 1/4 (Yamamoto 2021); scutellum with basal carina distinctly divided medially; procoxal cavities large and open posteriorly. Elytra slightly less than 1/3 of the body length, exposing 6 abdominal segments, oval-shaped (each 1.37 mm long, 0.76 mm wide); with epipleural keel and fold; with visible elevated area along suture; no prominent punctations or striae, some evidence of setae, posterior edges poorly preserved, appears convex posterad. Coxae large, oval, diverging, contiguous or almost contiguous, reaching edge of body. Prothoracic leg preserved on right side, metathoracic leg preserved on left side, with thin femora, tibia and tarsi.

Abdomen (Figure 5 D) gradually tapering posteriorly, 1.44 mm at widest point and 2.55 mm long; with segments III-IX preserved, segments VIII-IX seemingly partially fused; segment IX incomplete (seemingly damaged or dissected); segments IV-VII seemingly with two pairs of paratergites; segment VIII-IX seemingly with one pair of paratergites; segment III probably with two pairs of paratergites, but obscured, incomplete; segment IX with hook-like structures. Abdomen covered with fine setae.

Palaeoenvironment: The specimen provides evidence for dead-decaying organic matter such as dung, carrion, fresh and rotting mushrooms, or compost (Yamamoto 2016, 2021; Yamamoto & Takahashi 2016). It also provides evidence for leaf litter and moist debris near streams, similarly to extant Mycetoporinae and morphologically-similar Tachyporinae.

Remarks: The tapering abdomen of the specimen, moderately sublimuloid shape, lack of distinct neck constriction, and head retractile into prothorax suggest that it belongs to the tachyporine subgroup of subfamilies (Lawrence & Newton 1982, 1995). The specimen is assigned to Mycetoporinae and distinguished from Tachyporinae based on having an elongated head and lacking mid-cranial suture. Among these, it can be separated from two closely related subfamilies, *viz.* Habrocerinae and Trichophyinae, because it lacks their characteristic verticillate antennae. It lacks the slender shape and characteristic pronotal postcoxal process of Olisthaerinae (Cai et al. 2015), which would be probably visible on this specimen if it was present. Separating the specimen from Phloeocharinae is rather difficult, since the diagnostic features such as procoxae lacking mesal groove, antennal insertions concealed from above, and cuticular combs on the abdominal terga (Chatzimanolis et al. 2013) are not preserved.

Finally, separating the specimen from Aleocharinae is an even more challenging task, because the taxonomy of the hyper-diverse group is indefinite and under revision (Orlov et al. 2021 a), and the few features that distinguish this group are associated with genitalia that are not visible on the fossil (Orlov et al. 2021 b). In addition, the specimen has thin setae on the abdomen which are commonly found on some Tachyporinae (Yamamoto 2021, page 117). However, it is distinct from other Tachyporinae because of its triangular head, which is almost the same length as the transverse thorax. The

thoracic margins are not well preserved and were probably more curved than apparent on the fossil.

Discussion

The fossil described here has a general habitus of Mycetoporinae, including a sublimuloid medium-to-large body form, moderately elongated head (almost the same length as the prothorax), visible ridge on ventral side of head under eyes, lacking mid-cranial suture, antennomeres increasing in length and width apically, lacking distinct neck constriction, scutellum with basal carina that is distinctly divided medially, with apparently large hind coxae, having pronotal hypomeron with transverse ridge, and with six visible tapering abdominal segments. The shape of the posterior margin of the elytra is somewhat difficult to interpret. Evidence shows that the Mycetoporinae originated in the Early Cretaceous age (Yamamoto 2021), suggesting that they could have had a Pangean distribution. Therefore, it is reasonable and expected to find such a specimen at the Orapa Diamond Mine in Botswana, the only major Cretaceous deposit from Africa that is rich is palaeobiota.

The tapering abdomen and moderately sublimuloid shape of the fossil suggest that it belongs to the tachyporine subgroup of subfamilies (Lawrence & Newton 1982, 1995). Within the tachyporine group of subfamilies, *Cretafrica orapensis* **sp. nov.** can be separated from two closely related subfamilies, Habrocerinae and Trichophyinae, and Olisthaerinae. Separating the specimen from the Phloeocharinae and Aleocharinae is challenging due to poor preservation of the respective diagnostic features of the subfamilies. The Aleocharinae are presently under revision (Orlov et al. 2021 a, b). Its synapomorphies: laterotergal struts of male tergum IX present; lateral lobe of aedeagus (paramere) broad, enclosing median lobe; and apical lobe of female gonocoxites reduced or absent (Orlov et al. 2021 a, b) are not visible on the fossil. More importantly, to date, due to their high species richness, diversity and abundance, Aleocharinae remains one of the most taxonomically challenging groups of Coleoptera (Betz et al. 2018; Klimaszewski et al. 2018).

During the Cretaceous, Mycetoporinae were present in widely distributed localities (Figure 6), suggesting a much earlier, common point of origin. They were distributed in several countries, including Russia, China and Botswana. Given the general placement of this fossil in Mycetoporinae, which are associated with forest microhabitats, as well as fresh and rotting mushrooms, it unequivocally supports all previous research findings concerning the Orapa Diamond Mine in Botswana, which suggests a moist, well-vegetated habitat in and around the volcanic crater (e.g., McKay & Rayner 1986; Rayner & McKay 1986; Rayner 1987; Rayner & Waters 1989, 1990, 1991; Waters 1989a, b; Bamford 1990; McKay 1990, 1991; Waters 1990; Brothers 1992; Rayner 1993; Rayner et al. 1991, 1994, 1997; Kuschel et al. 1994; Brothers & Rasnitsyn 2003, 2008; Dlussky et al. 2004; Rasnitsyn & Brothers 2007, 2009; Kopylov et al. 2010; Woolley 2016; Mnguni 2022; Mnguni et al. 2022, 2023). The fossil portrays morphological stasis, which, as previously suggested by other researchers, may have

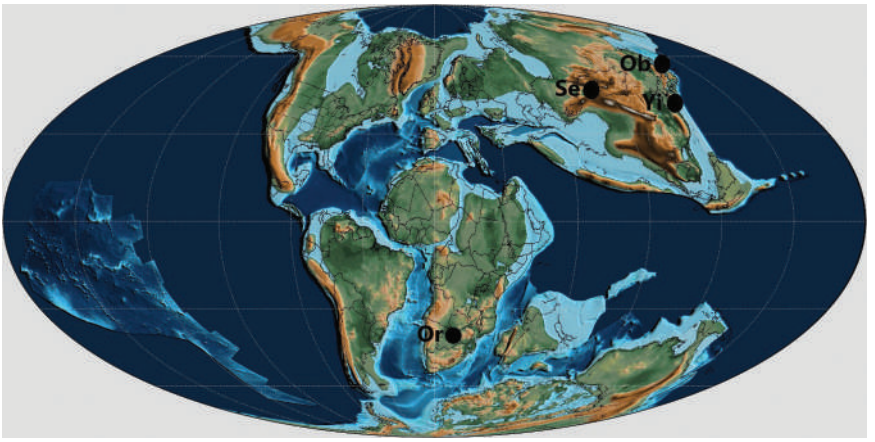

Fig. 6. Global palaeogeographic reconstruction of the mid-Cretaceous (100 Ma) showing the localities where fossil Mycetoporinae have been recovered. The map in Mollweide projection was sourced from Scotese (2016; 2021, Appendix 2, Mollweide_Maps.zip). The position of the localities were referenced from Rasnitsyn and Quicke (2002). Abbreviations: (1) Ob = Obeschayushchiy locality (Daya Formation), Russia; (2) Se = Semyon Formation, Russia; (3) Yi = Yixian Formation, China; and (4) Or = Orapa, Botswana. Adapted from Scotese (2021).

been caused by continuous presence of mesic habitats over geological time (Clarke & Chatzimanolis 2009; Grebennikov & Newton 2009). Similarly to other staphylinid beetles, it also further supports and confirms the proposed punctuated equilibrium pattern of evolution.

Conclusions

The presence of fossil mycetoporines with their synapomorphies at localities as far apart as Botswana, China, and Russia during the Cretaceous confirms their early appearance dating back to Early Cretaceous, and possibly Jurassic ages. The interpretation of some of the diagnostic features on the fossil was very challenging. It further confirms that researchers need to understand how rock fossils are fossilised, as that will assist with better interpretation, since rock fossils offer different palaeoenvironments compared to amber fossils. Finally, *Cretafrica orapensis* **gen. nov. et sp. nov.** would have been found in forest environment; possibly near leaf litter, moist debris, dead-decaying organic matter such as dung, carrion, or fresh and rotting mushrooms, and compost near the crater-lake at the Orapa Diamond Mine in Botswana. This fossil is important as the first mycetoporine from the Southern Hemisphere and Africa. Moreover, it is currently the 5th in the world.

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Dedication

SM would like to dedicate this publication to his late supervisor, Dr I.J. McKay. This work would not have been possible without his valuable contribution.

Competing interests

We declare that there are no competing or financial interests.

Author contributions

SM & IJM - Conceptualization; SM & IJM - Data curation; SM & IJM - Formal analysis; SM & IJM- Funding acquisition; SM & IJM - Investigation; SM & IJM - Methodology; IJM & SB - Project administration; SM & IJM - Resources; IJM - Software; IJM & SB - Supervision; IJM & SB - Validation; SM & IJM - Visualization; SM - Roles/Writing - original draft; SM, IJM & SB - Writing - review and editing.

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Data availability

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

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