

Afrinophilina orapa: a new genus and species of Paederinae (Coleoptera: Staphylinidae) from Cretaceous lacustrine deposits at Orapa Diamond Mine, Botswana.

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Abstract

A new genus and species of a staphylinid beetle, *Afrinophilina orapa* gen. et sp. n., is described using a single well-preserved compression fossil from an Upper Cretaceous fossil insect deposit, the Orapa Diamond Mine in Botswana. *Afrinophilina* is placed in the extant subfamily Paederinae based on concealed antennal insertions, and hypomeron with a well-developed post-coxal process. It is placed among the Pinophilini based on an elongated procoxae (as long as the profemora), broad, oval, fully exposed trochantin, and a conspicuous second abdominal segment. The new species is placed in the Pinophilina, rather than the Procirrina, based on the presence of well-preserved pair of paratergites on segments III-VIII. Characters which may distinguish this new species from other Pinophilina include the lack of an emarginate shape of the rear margins of the elytra, broad neck, and having two pairs of paratergites on each side of segments III-VI. This is the earliest occurrence of a member of the Pinophilina. It is the first member of the Pinophilina from the Southern Hemisphere, particularly the African continent. Similarly, compared to other fossil staphylinids, the fossil also portrays morphological stasis dating back to the Cretaceous, thereby suggesting a punctuated equilibrium pattern of evolution.

1 Introduction.

The Paederinae is one of the hyper-diverse subfamilies of the Staphylinidae with 225 (1 extinct) genera, and approximately 7 584 (35 extinct) species (Bogri et al. 2020). This subfamily remains largely unexplored, both phylogenetically and taxonomically (Schomann and Solodovnikov 2017), and is known as one of the most challenging subfamilies to study (Żyła et al. 2021). This is due to the shortage of phylogenies undertaken. In addition, its phylogeny-based tribal and sub-tribal classification schemes still need an extensive revision, while many genera await proper delimitation (Bogri et al. 2020). The challenge is exacerbated by its high species richness, diversity and abundance, and having few experts studying this group (Żyła et al. 2021). Recently, more researchers are studying the subfamilies of the Staphylinidae.

The Paederinae was divided into four tribes, namely: Pinophilini, Paederini, Cylindroxystini and Lathrobiini (Schomann and Solodovnikov 2017). Recently, Żyła et al. (2021) conducted the most comprehensive phylogenetic analysis of the Paederinae, based on multiple genetic loci, incorporating the broadest sampling of the taxa. The study reduced the Paederinae into three monophyletic tribes, namely the Pinophilini and Paederini which are sister groups of one another, and which together are the sister group of the Lathrobiini. In the study, the Cylindroxystini were subsequently demoted to a group within the Lathrobiini (Żyła et al. 2021). Furthermore, according to Żyła et al. (2021), the sister clades of the Paederinae are either the Euasthetinae or Staphylininae. However, most phylogenetic studies (e.g., Grebennikov and Newton 2009; Solodovnikov et al. 2013; and McKenna et al. 2015) found that the Paederinae and Staphylininae are sister groups. Surprisingly, the relationship between Paederinae and Staphylininae only found weak support in a recent study by Lü et al. (2020).

The split between Paederinae and Staphylininae is estimated to have occurred during the Late Jurassic (156.6 Ma), using mitogenomic sequencing (Hernando and Andujar 2021). More recently, this notion has been supported by Lü et al. (2020), who analysed four nuclear and two mitochondrial gene sequences, and estimated that the two subfamilies originated between 147.58 and 160.41 million years ago, respectively.

The Mesozoic fossil record of the Paederinae is restricted to the Cretaceous (Table 1). So far, none have been recorded between the Triassic and Jurassic ages. Schomann and Solodovnikov (2012) assigned the genus *Apticax* and *A. solidus* from the Nova Olinda Member of the Crato/Santana Formation in north-eastern Brazil to the Staphylininae + Paederinae lineage, but disclosed that the small number of diagnostic features do not allow for a definite placement in any of the 33 subfamilies of the Staphylinidae.

Solodovnikov et al. (2013) described *Mesostaphylinus elongatus*, *M. yixianus*, and *M. antiquus* from the Early Cretaceous deposit, Yixian Formation of China, based on phylogenetic analysis of both extinct and extant taxa. These were placed “*incertae sedis*” within the Paederinae, due to lack of diagnostic features. Żyła et al. (2019) described two inclusions from the Cretaceous Burmese amber of Myanmar, *Diminudon schomannae* and *D. kachinensis* (Lathrobiini), by a combination of morphological and molecular datasets. Shaw et al. (2020) described the earliest record of the Pinophilini, *Cretoprocirrus trichotos* from Burmese amber of Myanmar. Bogri et al. (2018) described *Dysanabatium kechrimparens*, *D. aenaum*, *D. damgaardi*, and *D. johannes* from the Baltic amber of Russia, to address a connection between co-occurrence of thermophilic and temperate insect taxa and Eocene climate change. In addition, Bogri et al. (2020) described *Micrilus electrus* and *Scymbalium phaethoni* from the Baltic amber of Russia, based on diagnostic morphological character matrices of both genera.

In total, the fossil record of the Paederinae encompasses 40 species from 12 genera: *Achenium* Curtis 1826, *Apticax* Schomann and Solodovnikov 2012, *Cretoprocirrus* Shaw et al. 2020, *Diminudon* Żyła et al. 2019, *Dysanabatium* Bernhauer 1915, *Lathrobium* Gravenhorst 1802, *Lithocharis* Dejean 1833, *Miolithocharis* Wickham 1913, *Medon* Stephens 1833, *Mesostaphylinus* Zhang 1988, *Orsunius* Assing 2011 and *Paederus* Lin et al. 2018; ranging from Cretaceous to Miocene. This summary is given by Żyła et al. (2019), with an addition of *Cretoprocirrus* (Shaw et al. 2020). Notably, all the Cenozoic fossils have been assigned to the tribe Lathrobiini (Żyła et al. 2019).

Table 1: Species list of the Paederinae (Coleoptera: Staphylinidae). Updated from Żyła et al. (2019).

Taxon	Deposit	Pres
Cretaceous	Cretaceous	Cret.
<i>Afrinophilina orapa</i> Mnguni, McKay and Badenhorst, 2023 (this study)	Orapa, Botswana	Rock
<i>Apticax solidus</i> Schomann and Solodovnikov, 2012	Crato/Santana Fm., Brazil	Rock
<i>Apticax volans</i> Schomann and Solodovnikov, 2012	Crato/Santana Fm., Brazil	Rock
<i>Cretoprocirrus trichotos</i> Shaw et al., 2020	Burmese Amber, Myanmar	Ambe
<i>Diminudon kachinensis</i> Żyła et al., 2019	Burmese Amber, Myanmar	Ambe
<i>Diminudon schomannae</i> Żyła et al., 2019	Burmese Amber, Myanmar	Ambe
<i>Mesostaphylinus antiquus</i> Solodovnikov and Yue, 2013	Yixian Fm., China	Rock
<i>Mesostaphylinus elongatus</i> Solodovnikov and Yue, 2013	Yixian Fm., China	Rock
<i>Mesostaphylinus laiyangensis</i> Zhang, 1988	Laiyang Fm., China	Rock
<i>Mesostaphylinus yixianus</i> Solodovnikov and Yue, 2013	Yixian Fm., China	Rock
<i>Paederus fuscipes</i> Lin et al. 2018	Zhengzhou Fm., China	Rock
Palaeocene and Eocene	Palaeocene and Eocene	Palae
<i>Dysanabatium aenaum</i> Bogri et al., 2018	Baltic Amber, Russia	Ambe
<i>Dysanabatium damgaardi</i> Bogri et al., 2018	Baltic Amber, Russia	Ambe
<i>Dysanabatium johannes</i> Bogri et al., 2018	Baltic Amber, Russia	Ambe
<i>Dysanabatium kechrimparens</i> Bogri et al., 2018	Baltic Amber, Russia	Ambe
<i>Lathrobium ambricum</i> Paśnik and Kubisz, 2002	Baltic Amber, Russia	Ambe
<i>Lathrobium antediluvianum</i> Wickham, 1913	Florissant Fm., United States of America	Rock

Taxon	Deposit	Pres
<i>Lathrobium balticum</i> Pašnik and Kubisz, 2002	Baltic Amber, Russia	Ambe
<i>Lathrobium jantarticum</i> Pašnik and Kubisz, 2002	Baltic Amber, Russia	Ambe
<i>Lathrobium succini</i> Pašnik and Kubisz, 2002	Baltic Amber, Russia	Ambe
<i>Lathrobium whitei</i> Abdullah and Abdullah, 1968	Baltic Amber, Russia	Ambe
<i>Lithocharis scotti</i> Casey, 1886	Florissant Fm., United States of America	Rock
<i>Miolithocharis lithographica</i> Wickham, 1913	Florissant Fm., United States of America	Rock
<i>Orsunius electronefelus</i> Kypke and Solodovnikov, 2020	Baltic Amber, Russia	Ambe
<i>Paederus adumbratus</i> Frank, 1988	Florissant Fm., United States of America	Rock
Oligocene	Oligocene	Oligo
<i>Achenium ingens</i> Goss, 1878	Aix en Provence, France	Rock
<i>Lathrobium gensium</i> Zhang, 1989	Shanwang Fm., China	Rock
<i>Lathrobium homorum</i> Zhang, 1989	Shanwang Fm., China	Rock
<i>Lathrobium phthartum</i> Zhang, 1989	Shanwang Fm., China	Rock
<i>Lathrobium provinciale</i> Goss, 1878	Aix en Provence, France	Rock
<i>Lathrobium sobrinum</i> Zhang, 1989	Shanwang Fm., China	Rock
<i>Lathrobium xiejiaheense</i> Zhang, 1989	Shanwang Fm., China	Rock
<i>Lithocharis varicolor</i> Heer, 1856	Aix en Provence, France	Rock
<i>Lithoplanes deleta</i> Heer, 1856	Aix en Provence, France	Rock
<i>Lithoplanes elongata</i> Heer, 1856	Aix en Provence, France	Rock
<i>Lithoplanes elongata</i> Heer, 1856	Armissan, Aude, France	Rock
<i>Medon stenus</i> Zhang, 1989	Shanwang Fm., China	Rock
<i>Sunius demersus</i> von Heyden and von Heyden, 1866	Rott Bonn, Germany	Rock
Miocene	Miocene	Mioc
<i>Lathrobium oeningense</i> Heer, 1862	Öningen Fm., Germany	Rock
<i>Palaminus</i> spp. Seevers 1971	Mexican Amber, Mexico	Ambe
Pleistocene and Holocene	Pleistocene and Holocene	Pleis
<i>Pinostygus galapagoensis</i> Campbell and Peck, 1989	Galapagos Islands, Ecuador	Rock

2 Materials and Methods.

The specimen described in this study was excavated at Orapa Diamond Mine (ODM) (Fig. 1), located in the north-east of Botswana, approximately 240 km due west of Francistown (McKay 1991). A double eruption of diamondiferous kimberlites from North and South pipe 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 81.7 and 98.5 Ma, with a midpoint of 90.1 Ma (Haggerty et al. 1983), and 93.1 Ma (Davis 1977), respectively. Thus, the deposits are considered as Upper Cretaceous (Turonian, but possibly Cenomanian or Coniacian). Orapa is the only major insect deposit from the Cretaceous in Africa (Grimaldi and Engel 2005). The palaeofauna of the Orapa deposit has been reviewed (McKay and Rayner 1986; Rayner and McKay 1986; Rayner 1987; Rayner and Waters 1989, 1990; Waters 1989, 1990; McKay 1990, 1991; Brothers 1992; Rayner 1993; Rayner et al. 1991, 1994, 1997; Kuschel et al. 1994; Brothers and Rasnitsyn 2003, 2008; Dlussky et al. 2004; Rasnitsyn and Brothers 2007, 2009; Kopylov et al. 2010; Woolley 2016; Mnguni 2022; and Mnguni et al. 2022).

The specimen described here is a well-preserved compression fossil. 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 taken 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 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. A single specimen of an adult fossil with carbonaceous material preserving both dorsal and ventral structures is described. The antennae, eyes, legs, elytra, and mouthparts are preserved as part (120 x 90 x 38 mm) and counterpart (73 x 62 x 30 mm) in large pieces of brown lacustrine mudstones. The scale in all the photographs is 1 mm.

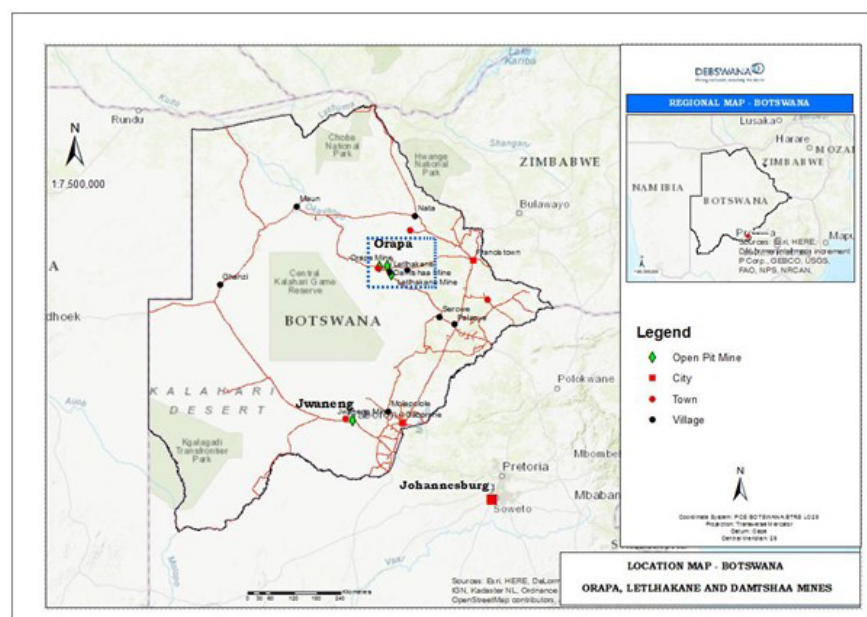


Figure 1. The location of Orapa Diamond Mine in Botswana. Taken from Mashabila (2019, page 9).

3 Systematic Palaeontology.

Order: Coleoptera Linnaeus, 1758

Series: Staphyliniformia Latreille, 1802

Superfamily Staphylinoidea Latreille, 1802

Family: Staphylinidae Latreille, 1802

Subfamily: Paederinae Fleming, 1821

Tribe: Pinophilini Nordmann, 1837

Subtribe: Pinophilina Nordmann, 1837

Genus: *Afrinophilina* gen. nov.

Type species: *Afrinophilina orapa* species nov., by monotype and present designation.

Etymology: The generic epithet is a combination of Afri-, from 'Africa', and nophilina, from subtribe suffix 'Pinophilina'.

Composition : Only type species *Afrinophilina orapa* species nov.

Diagnosis: The new species is placed in Paederinae using the following diagnostic characters of the subfamily: antennal insertions concealed under "shelf" (and therefore not visible from above), and hypomeron of prothorax with well-developed post-coxal process. It is placed in Pinophilini based on an elongated procoxae

(as long as the profemora), broad, oval, fully exposed trochantin, and a conspicuous second abdominal segment. It is placed in Pinophilina, rather than Procirrina, based on the presence of well-preserved pair of paratergites on segments III-VIII. Characters which distinguishes this new species from other Pinophilina include the lack of an emarginate shape of the rear margins of the elytra (Herman 2010), broad neck and having two pairs of paratergites on each side of segments III-VI.

Afrinophilina orapa species nov. (Figs 2, 3, 4 and 7).

Etymology: The epithet of the new species is a name of the deposit where the specimen was discovered, which in itself is derived from Sesarwa (a San or Bushmen language), and is named after a nearby cattle post, meaning ‘the resting place of lions’ (De Beers Group website <https://www.debeersgroup.com/about-us/our-operations/our-mines/botswana>).

Material studied: Holotype, adult (specimen number BP./2/27586a (part) and BP./2/27596 (counterpart), Herbarium, Evolutionary Studies Institute (ESI), University of the Witwatersrand, Johannesburg, South Africa).

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

Diagnosis: As for the genus *Afrinophilinagen. nov.* .

Description: Body slender measuring 8.81 mm in length (from tip of mandibles to tip of abdomen) and 1.82 mm in width (from exterior edge of one elytron to edge of another elytron, at widest point). Covered with setae of variable length throughout (Figs. 2, 3, 4 and 7).

Head (Fig. 5), 1.44 mm long (from tip of mandible to anterior margin of pronotum) and 1.01 mm wide at widest point just anterior to neck, making it approximately 1.4 x longer than wide, with distinct curved temples; width of head 1.4 x broader than width of neck constriction, with broad neck. Eyes (Fig. 5) not well preserved, circular to slightly oval, located closer to base of antennae, covering 1/3 of temple. Antennae filiform (Figs. 2 and 3), approximately length of head and prothorax, bases hidden under “shelf” at base of head; proximal antennomeres incomplete, but antennomere 1 appears less or equal length as antennomeres 2 and 3, antennomeres 9 and 10 funnel shaped, antennomere 11 poorly preserved, but with funnel shape, suggesting that it had spiniform pencil of setae, in general antennae with setae visible in many places. Mandibles curved, sickle-shaped, left mandible curved over right, possibly with traces of teeth posteriorly. Pair of long setae posterior to base of mandibles. Labial palps, represented only by indistinct segment or portion of segment adjacent to left mandible. Labrum poorly preserved. Several indistinct structures in region which could be interpreted as spines or lobes. Margin between labrum and frontoclypeus apparently straight, curved at corners. Gular sutures fully separate, apparently reaching posterior margin of head.

Pronotum (Fig. 2, 3 and 4) rectangular with curved sides, longer than wide (0.59 mm wide, 0.68 mm long); length 0.9 x less than that of head, width 1.1 x broader than head, anterior margin forms slight collar around the neck, posterior margin gently curved. Superior marginal line apparently deflexed, reaching from anterior margin of prothorax and tapering off just before posterior corner of prothorax. Distinct post-coxal process of hypomeron visible. Longitudinal carina of furcasternum present, sharp, apparently extending anterior towards longitudinal carina of basisternum, crossed by transverse basisternum carina anteriorly.

Elytra (Figs. 2, 3 and 4) jointly 1.6 x wider and 1.1 x longer than pronotum. Elytra oval, collectively wider than long (each 1.61 mm long, from posterior margin of pronotum to anterior margin of elytron, 1.76 mm wide); with epipleural margin, but no obvious epipleural ridge; separated at base by small scutellum, with faint striae. Elytral posterior margins curved evenly, non-emarginate, apparently with long setae.

Prothoracic legs (Figs. 2, 3 and 4) with broad coxa, long as femur, trochanter large and oval, tibia narrow at base, becoming broader distally, lacking any distinct medial expansion, with row of setae in posterior mid-section, possibly representing longitudinally arranged protibial combs (Fig. 6), distal surface with grooves which also represent ctenidium, only tarsomere 1 preserved, moderately expanded, triangular, with curved

distal surface fringed with short setae. Mesocoxae indistinct, remainder of leg represented by poorly preserved fragments of femur and tibia, femur covered with long setae, remnants of tarsal segments visible. Thorns on mesotibia not visible. Metathoracic coxae apparently large and extended, trochanter difficult to discern, femurs projecting beyond side of body, tibia $1\frac{1}{2}$ x long as femur, with tibial thorn at apex, tarsomere 1 about $1\frac{1}{2}$ x longer than tarsomere 2, approximately same for tarsomere 5, although with poorly-preserved distal segments.

Abdomen (Fig. 2, 3 and 4) approximately 3 x elytral length and 1.2 x elytral width, $3\frac{1}{2}$ x as long as wide (4.96 mm long, 1.56 mm wide), apparently with waist (but this may be due to poor preservation of first visible segment), tapering strongly from segment VI. Segments II-VIII visible, segment II distinct, without paratergites, with intercoxal carina in the middle that extends into segment III, segments III-VIII each with pair of paratergites, segments III-VI each with two pairs of paratergites, segment IX with pair of setiferous latero-apical processes, separated by pair of pointed structures interpreted as tergal plates (Naomi 1989).

Palaeoenvironment: There has been no recent review of the Pinophilina. Apparently, most of them prefer wet tropical forest environments (Campbell and Peck 1989), a view shared with the Procirrina (Herman 2010). Extant paederines are commonly found in damp places, under logs, litter or foliage, while some have been recorded inhabiting caves and ant nests.

Remarks: The maxillary palps crucial for differentiating the tribes within the Paederinae are not preserved. Its first protarsal segment (protibial combs) is dilated with a setiferous margin as for the Pinophilini. However, there are other taxa, for example, *Scymbalium* and *Micrillis* (classified as *Lathrobiini incertae sedis*), with similar features (Bogri et al. 2020). The tribe Lathrobiini was ruled out based on an invisible, typical small and unmodified apical (fourth) maxillary palpomere. Interestingly, this species shares the characters of having an elongated procoxae and well-developed abdominal segment II with *Mesostaphylinus* (Solodovnikov et al. 2013), but is more similar to the Pinophilina in other features. The elongated procoxae are not typical for *Mesostaphylinus*. The abdominal segment II is not usually preserved in fossils, as it is mostly hidden behind the elytra, making it difficult to compare this character.

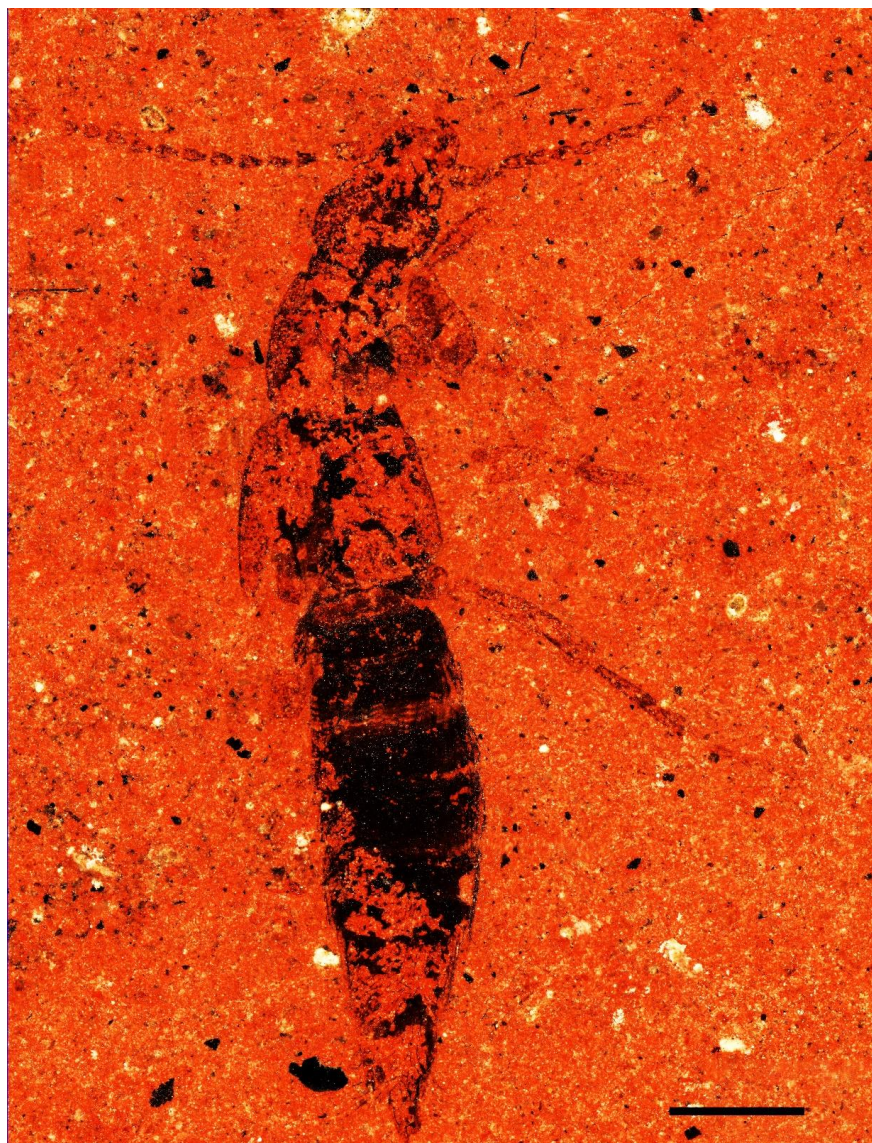


Figure 2. The whole body of *Afrinophilina orapa* gen. nov., species nov. holotype, part, BP./2/27586a, Orapa Diamond Mine, polarized light, scale bar = 1 mm.

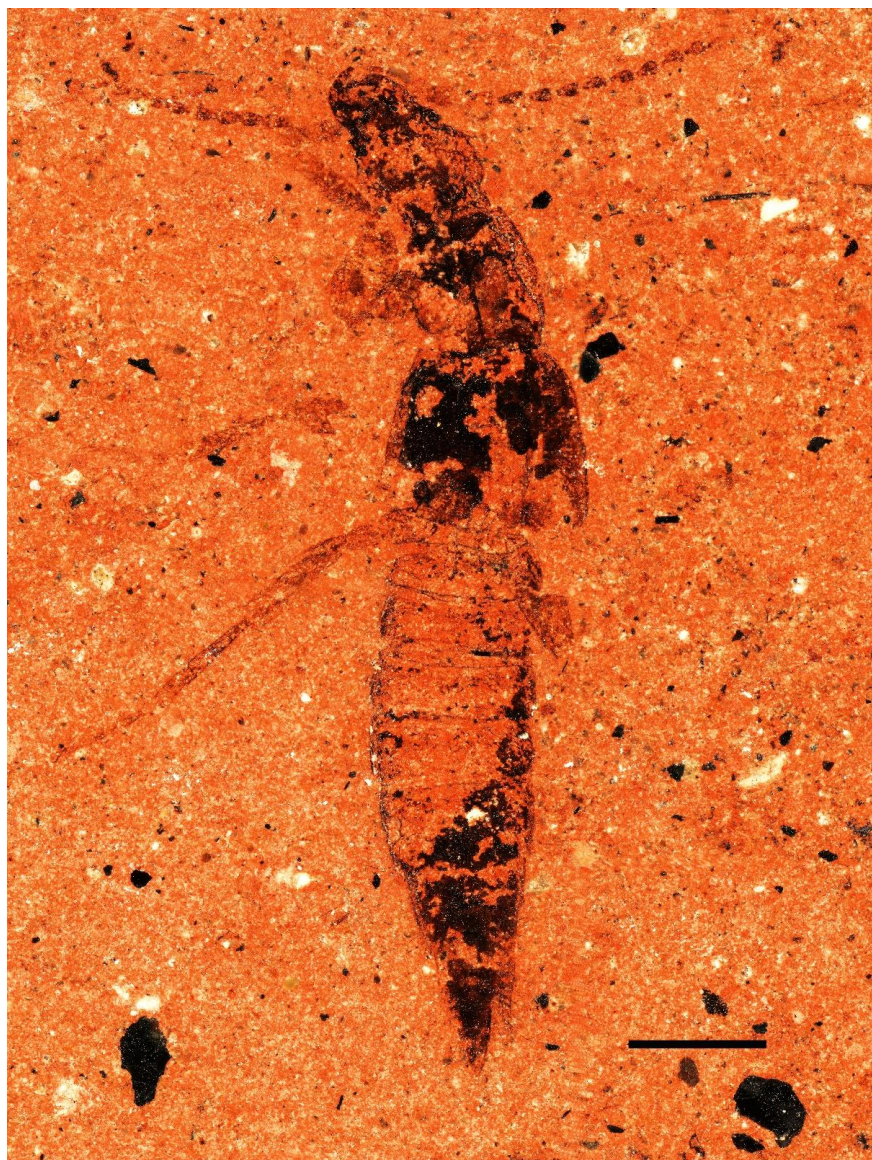


Figure 3. The whole body of *Afrinophilina orapa* gen. nov., species nov. holotype, counterpart BP./2/27596, Orapa Diamond Mine, polarized light, scale bar = 1 mm.



Figure 4. The whole body of *Afrinophilina orapa* gen. nov., species nov. holotype, counterpart, BP./2/27596, Orapa Diamond Mine, non-polarized light, scale bar = 1 mm.

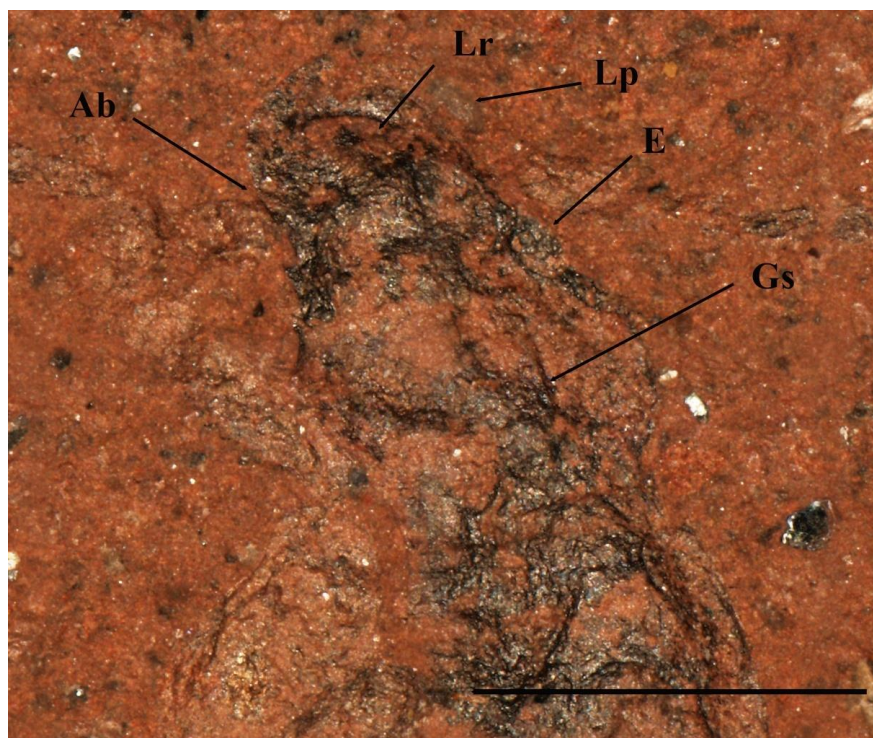


Figure 5. Details of head of *Afrinophilina orapa* gen. nov., species nov. holotype, counterpart, BP./2/27596, scale bar = 0.5 mm. Abbreviations: ab = antennal base, e = eye, gs = gular suture, lp = portion of labial palp, lr = possible left labrum.

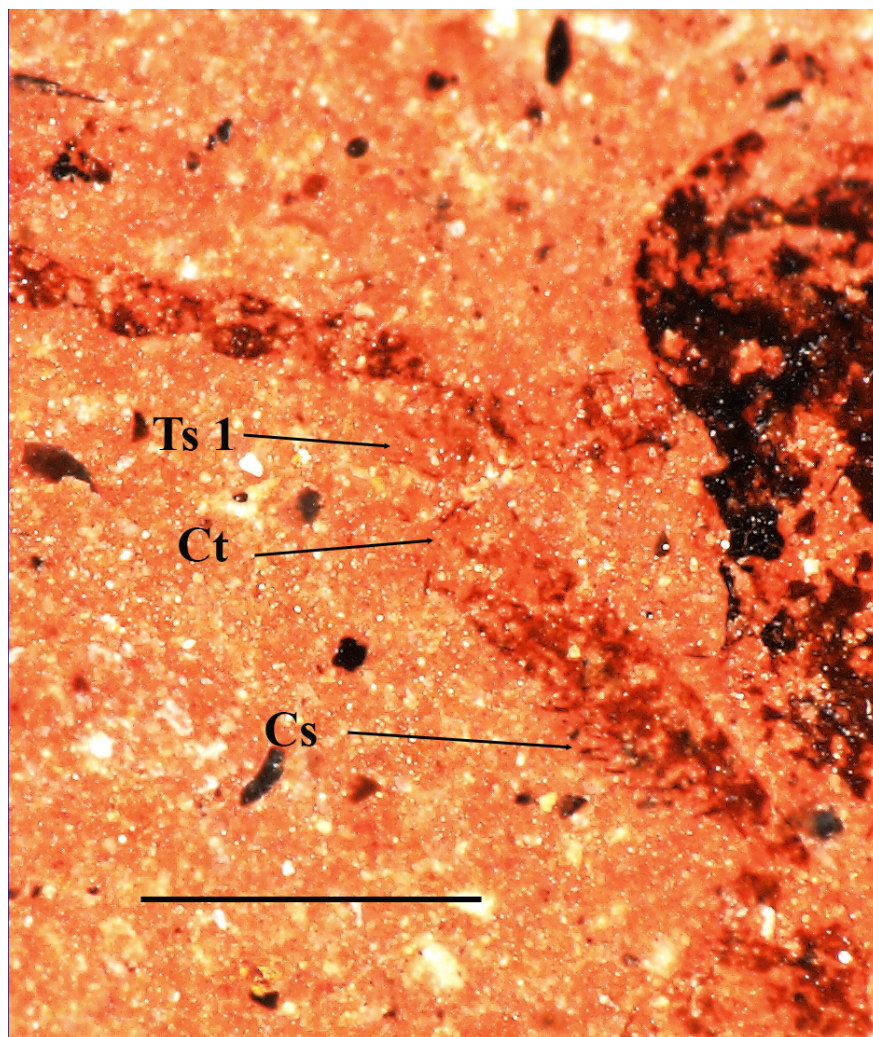


Figure 6. Details of protibia, *Afrinophilina orapa* gen. nov., species nov. holotype, counterpart, BP./2/27596, scale bar = 0.5 mm. Abbreviations: ts = tarsal segments, cs = ctenidial setae, ct = ctenidial (protibial) combs.

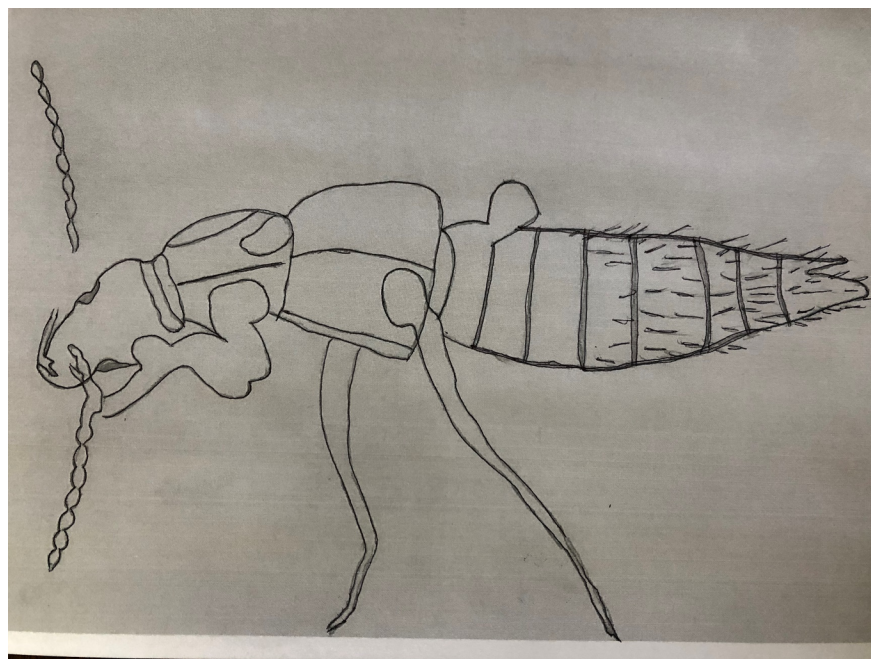


Figure 7. The whole body of *Afrinophilina orapa* gen. nov., species nov. holotype, counterpart, BP./2/27586a, Orapa Diamond Mine, drawing, scale bar = 1 mm.

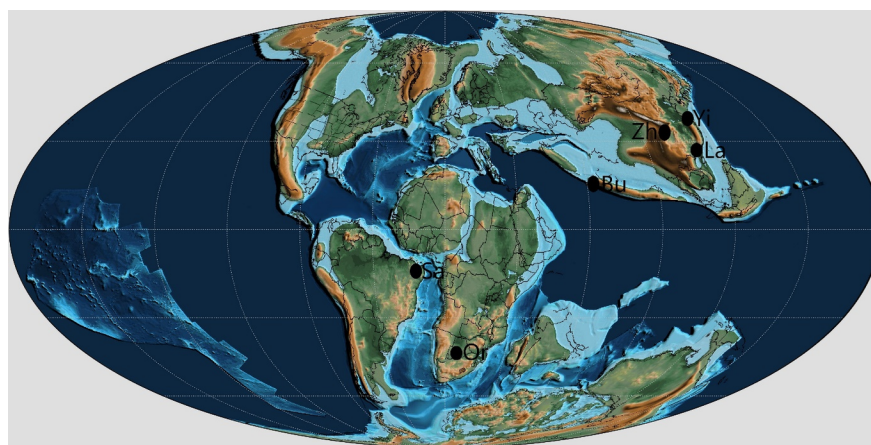


Figure 8. Global palaeogeographic reconstruction of the mid-Cretaceous (100 Ma) showing the localities where the fossil Paederinae have been recovered. The map in Mollweide projection was sourced from Scotese (2021). The position of the localities was adapted from Rasnitsyn and Quicke (2002). Abbreviations: Bu = Burmese amber, Myanmar; Sa = Santa/Crato Formation, Brazil; Or = Orapa, Botswana; La = Laiyang Formation, China; Yi = Yixian Formation, China; Zh = Zhezou Formation, China.

4 Discussion.

The Paederinae is one of the most challenging subfamilies to study (Żyła et al. 2021). However, Bogri et al. 2020 and Żyła et al. 2019, 2021 have made considerable progress in creating a comprehensive, well-supported phylogenetic framework for this hyper-diverse group. The species (*Afrinophilina orapa* species. nov., Figs. 2, 3, 4 and 7) described in this study has antennae that are concealed under the “shelf”, and a hypomeron with

a post-coxal process, which are both diagnostic features for this group (Herman 2010, Bogri et al. 2020, and Żyła et al. 2019, 2021). Unfortunately, the characters which are generally used to separate Paederinae tribes, in particular the maxillary palps, are poorly preserved on the fossil. Therefore, this hinders an accurate and reliable interpretation of the mouthparts.

The specimen has its first pro-tarsal segment (also known as protibial combs) dilated with a setiferous margin as for the Pinophilini (Herman 2010). However, it is seemingly not as dilated in comparison to the examined extant pinophilines housed at the Ditsong National Museum of Natural History (DNMNH) (Pretoria, South Africa). It would be useful to have the rest of the tarsus preserved, because there are other genera assigned to other tribes, for example, *Scymbalium* Erichson, 1839 and *Micrillis* Raffray, 1873, that have similar features (Bogri et al. 2020). Other characters which may be important in assisting to place this specimen among the Pinophilini are the elongate procoxae, which are as long as the profemora (Campbell and Peck 1989; Herman 2010; and Shaw et al. 2020); broad, oval, fully exposed trochantin, and presence of a conspicuous second abdominal segment (Campbell and Peck 1989).

The new species is placed in the Pinophilina, rather than the Procirrina, based on the presence of well-preserved pair of paratergites on segments III-VIII (Campbell and Peck 1989; Herman 2010; and Shaw et al. 2020). Characters which may distinguish this new species from all the other Pinophilina is the lack of an emarginate shape of the rear margins of the elytra, broad neck and having two pairs of paratergites on each side of segments III-VI (Herman 2010). It is also interesting to note, however, that two recent matrices of morphological characters (i.e., Bogri et al. 2020; and Żyła et al. 2021), do not include characters like extended procoxae, and fully exposed protrachant. It is possible that these characters are not useful for distinguishing amongst other tribes of the Paederinae. However, it is equally probable that the characters could be widely variable among the Paederinae genera. The reason behind this is unclear at the moment, and needs further investigation.

The earliest Paederinae are described from the Yixian Formation of China, and were initially assigned as ‘*incertae sedis*’ to the genus *Mesostaphylinus* (Chatzimanolis 2018). These have since been described as *M. antiquus*, *M. elongatus*, and *M. yixianus* Solodovnikov et al., 2013 (Solodovnikov et al. 2013). There are also several described Mesozoic Paederinae such as *Apticax solidus* and *Apticax volans* Schomann and Solodovnikov, 2012 known from the Santana/Crato Formation of Brazil (122.46-112.6 Ma) (Chatzimanolis 2018). Many species of Paederinae are described from Cenozoic deposits such as the Florissant Formation of the United States of America, and the Baltic amber of Russia and many other countries, and it is thought that the majority of these have been incorrectly assigned to the genus *Lathrobium* Gravenhorst, 1802 (Chatzimanolis 2018).

Furthermore, there are other notable Cenozoic taxa belonging to the above-mentioned genus, such as *Lathrobium provinciale* Goss, 1878 that has been formally described from the Aix-en-Provence of France (11.6-7.2 Ma), and several *Lathrobium* spp. from Shanwang of China (Chatzimanolis 2018). According to Betz et al. (2018), there are taxa that continue to await description from Burmese amber of Myanmar, Green River Formation of the United States of America, and Kishenehn Formation of the United States of America.

Despite studies by Schomann and Solodovnikov (2017); Żyła et al. (2019, 2021); Bogri et al. (2020); and Shaw et al. (2020), more research is still required regarding the classification and phylogeny of Paederinae, before new descriptions can be reliably assigned to existing tribes, subtribes and genera of the subfamily. For example, the genus *Apticax* proposed by Schomann and Solodovnikov, 2012 was formally described from the Santana/Crato Formation, and it was assigned to the Paederinae + Staphylininae lineage; whereas more phylogenetic analysis by Solodovnikov et al. (2013) argued that the genus is missing some of its key features, and could therefore, not be assigned with confidence to any subfamily of the Staphylinidae. A reclassification is required, especially after the latest hypothesis by Cai et al. (2021) that downgraded the Silphidae to a subfamily level within the Staphylinidae.

During the Cretaceous, the Paederinae were found in widely distributed localities (Fig. 8), suggesting a much earlier, common point of origin. They were distributed in several countries, including Brazil, China,

Myanmar and Botswana. Finding a paederine fossil at Orapa Diamond Mine in Botswana is not surprising, given that Schomann and Solodovnikov (2012) suggested that the genus *Apticax*, from the Lower Cretaceous Santana/Crato Formation of Brazil, is possibly, if not conclusively, a paederine. In addition, Solodovnikov et al. (2013) described the genus *Mesostaphylinus* from the Lower Cretaceous, Yixian Formation of China as “Paederinae, *incertae sedis*”. These were later described as *M. elongatus*, *M. yixianus*, and *M. antiquus*.

In addition, there is also *M. laiyangensis* Zhang, 1988 from Laiyang Formation of China. Solodovnikov et al. (2013) pronounced that the discovery of the Paederinae and Staphylininae lineage from the Lower Cretaceous Yixian Formation sets the split between these groups back to the Jurassic. Interestingly, *Mesostaphylinus* Solodovnikov et al., 2013 shares three characters with *Afrinophilina*, in a form of an extended procoxae, well-developed segment II of the abdomen, and seemingly dilated protibial combs.

Afrinophilina resembles the Pinophilina based on the shape of the antennae and arrangement of the setae on the protarsi. Perhaps it would be worth reanalysing *Mesostaphylinus* for affinities with Pinophilina. Shaw et al. (2020) have recently described the first fossil Procirrina, *Cretoprocirrus trichotos*, from the Burmese amber of Myanmar, and it is therefore to be expected that the sister group of this taxon would have appeared around this time. *Afrinophilina orapa* is therefore the first fossil paederine belonging to the subtribe Pinophilina from the Cretaceous. It is the first fossil Paederinae from Africa, the second from the Southern Hemisphere. Similarly to other fossil staphylinids that have been described in the past, the new species demonstrates morphological conservatism dating back to the Cretaceous.

5 Conclusions.

To date, the fossil record of Paederinae is restricted to the Cretaceous. However, their presence at localities as far apart as Brazil, Botswana, China and Myanmar during the Cretaceous suggests that they must have arisen at a far earlier time. The new species has diagnostic characters of the Paederinae: antennal insertions concealed under “shelf” (and therefore not visible from above), and hypomeron of prothorax with a well-developed post-coxal process. It also has characters of the Pinophilini: elongated procoxae (as long as the profemora), broad, oval, fully exposed trochantin and a conspicuous second abdominal segment. Moreover, it has characters of the Pinophilina: well-preserved pair of paratergites on segments III-VIII. It differs from other Paederinae because it lacks an emarginate shape of the rear margins of the elytra (Herman 2010), and has two pairs of paratergites on each side of segments III-VI.

Rock fossils and amber fossils offer different palaeoenvironment reconstructions. As such, understanding how rock fossils are fossilized can lead to more accurate interpretations (Mnguni 2022; and Mnguni et al. 2022). Finally, at Orapa, *Afrinophilina orapa* gen. nov., species nov. would have possibly been found in damp places, under logs, litter or foliage, suggesting a habitat preference fidelity, correlated with arrested evolution (i.e., morphological stasis) for this group over a long evolutionary time. It was probably an active predator which hunted near the crater-lake at Orapa, together with *Afristenus orapensis*, which has also been recently described by Mnguni et al. (2022). Using extant species, it is worth investigating the possible insect-insect relationships between predators belonging in Paederinae and Steninae.

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7 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.

8 Competing interests.

We declare that there are no competing or financial interests.

9 Author contributions.

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

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11 Data availability.

Datasets related to this article will be shared with the audience upon request. The new species will be registered on ZooBank.

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