Carabidae (Coleoptera: Harpalinae: Harpalini: Harpalina) from an Upper Cretaceous Rock Deposit at Orapa Diamond Mine in Botswana[1]

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Abstract Four new species of carabid beetle—*Harpalus mckayi* sp. n., *Harpalus mnguni* sp. n., *Harpalus nkqwili* sp. n., and *Harpalus peteni* sp. n.—are described using relatively well-preserved compression fossils from an Upper Cretaceous lacustrine rock deposit at the Orapa Diamond Mine in Botswana. All the fossils are assigned in the extant subfamily Harpalinae based on key diagnostic characters, including the general habitus, mandibular scrobe without seta, elongated scutellum, and spiny mesotibia. They are assigned in genus *Harpalus* due to the following characters: glabrous habitus, hairless eyes, and narrow epilobes of mentum. Notably, all the fossils reported in this study can also be compared with members of the genera *Cratognathus*, *Dichaetochilus*, *Heterohyparpalus*, *Aulocoryssus*, *Acupalpus*, *Egadroma*, and many other genera. *Harpalus mckayi* sp. n. has unusual two supraorbital pits (instead of only one) located above each eye. *Harpalus mnguni* sp. n. and *H. nkqwili* sp. n. are rather similar; but *H. mnguni* sp. n. has elongated palps and slender antennomeres, whereas *H. nkqwili* sp. n. has a unique postorbital constriction. *Harpalus peteni* sp. n. differs by the shape of the eyes and anterior margins. The Harpalinae have been remarkably conservative in their evolution since the Cretaceous and possibly even longer. All of the fossils consolidate the widely documented diversity and widespread distribution of the Carabidae in the Cretaceous and in the Mesozoic at large.

Key Words fossils, carabids, ground beetles, *Harpalus*, Africa, Southern Hemisphere

The Carabidae was erected by Latreille in 1802 and has since become one of the most speciose families of the Coleoptera. It is known to be a cosmopolitan group that currently records 40,968 species nested within 36 subfamilies, 89 tribes, and 2,191 genera (Catalogue of Life, updated to October 2024; https://www.catalogueoflife.org/data/metadata). It is only outnumbered by the Curculionidae (with 74,095 species) and the Staphylinidae (with 66,928 species). The other most speciose families of the Coleoptera include the Cerambycidae (with 36,306 species) and the Scarabaeidae (with 36,303 species). These five major families alone make up 80% of the known Coleoptera fauna worldwide. The Carabidae are

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primarily ground-dwelling, highly mobile, predacious beetles that prefer moist microhabitats. They are morphologically homogeneous and can be found in almost every conceivable environment, including the tundra regions (Erwin 1979). As such, they are commonly used as model organisms in studies on biogeography and speciation. The Harpalinae constitutes 3,140 described species nested within four tribes and 177 genera, with the *Harpalus* being the largest contributor with 444 assigned species thus far (Catalogue of Life, updated to October 2024; https://www.catalogueoflife.org/data/metadata). The Harpalinae is predominantly phytophagous, and it is a cosmopolitan group that is found in most climates.

Authors have modeled the distribution and formulated the taxon pulse theory of the biogeography of the Carabidae through time (Erwin 1979, 1981, 1985). In addition, attempts have been made to reconstruct the phylogeny of the group. The Adephaga, a suborder within which the Carabidae belongs, is thought to have been derived from the Archostemata family Schizophoridae, the most dominant beetle group in the Triassic (Ponomarenko 1977). The Adephaga and Archostemata can be reliably separated from each other by the structure of the hind coxa. Nonetheless, the fossil record of Carabidae still remains poor and controversial. Their diagnostic characteristics include having an enlarged and immobile metacoxa, sclerotized abdominal sternites, and pygidial defense glands (Lawrence and Newton 1982). In Africa, the oldest described fossil Carabidae is *Umkoomasia depressa* Zeuner, 1961 from a Triassic deposit, Umkoomasi, located in the KwaZulu Natal Province in South Africa (Zeuner 1961). It is hypothesized to be an earliest representative of the Adephaga. Decades later, McKay (1991) described *Palaeoaxinidium orapensis* McKay, 1991 from a Cretaceous deposit named the Orapa Diamond Mine (ODM) in Botswana, within which the fossils reported herein were also found. Other fossil Carabidae known from the Mesozoic have been reported primarily from Russia, China, and Myanmar. Cretaceous deposits from Africa are rare. Many of them are recorded in the Northern Hemisphere; therefore, a study that describes more fossil Carabidae from a unique deposit in Africa is important in understanding the evolutionary attributes of the monophyletic group. Such a study contributes to improving our understanding of the diversity and biogeography of the Carabidae in the Cretaceous and Mesozoic.

The ODM in Botswana has a flat topography and it is one of the major Cretaceous deposits in Africa (Fig. 1). It is situated 960 m above sea level within the Kalahari Desert, ∼35 km south of the Makgadikgadi Pans, 824 km from Johannesburg in South Africa. It has a semiarid climate, a temperature range of 21–32°C, and an annual rainfall of 500 mm (McKay 1990, Mnguni 2022). The mopane tree (*Colophospermum mopane* (Bentham) Leonard) is the dominant vegetation in the area. The mine is situated over a pair of adjoining diamondiferous epiclastic kimberlitic pipes. It is one of 60 kimberlitic pipes in the area. There are also 397 other kimberlites in the country (Mnguni 2022). It has an oval outline at the surface, with a longer north–south axis of 1,600 m and a shorter east–west axis of 1,000 m (Rayner and McKay 1986). It is thought that the Orapa kimberlite consisted of fragments from the mantle that were transported in a calcite-rich fluid that included large amounts of gaseous CO_2 and water (Bamford 1990). It was first discovered in 1967 and started producing diamonds in 1971 (Mnguni 2022). A double eruption

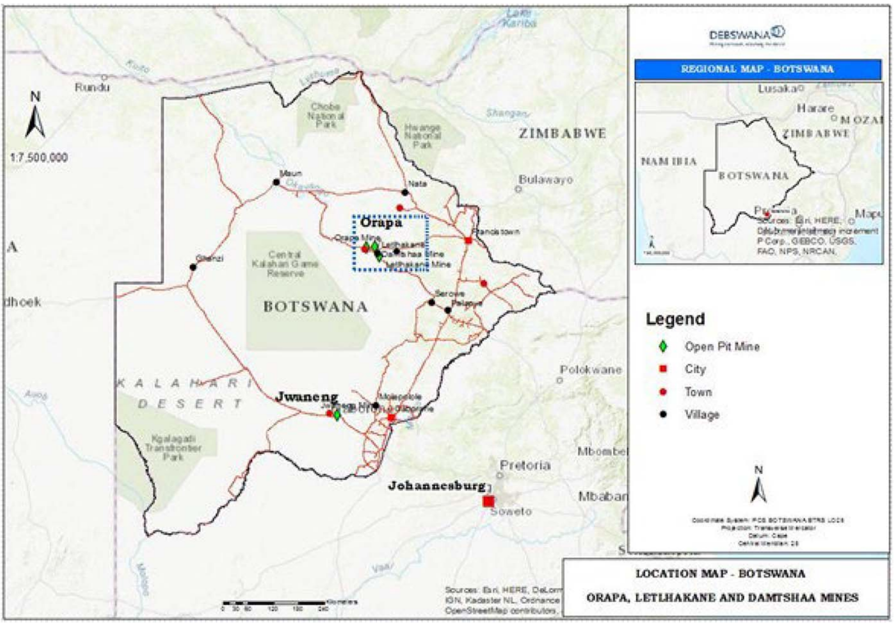

Fig. 1. Location of the Orapa Diamond Mine in Botswana (21°18.465′S; 25°22.177′E). Image taken from Mashabila (2019).

of diamondiferous kimberlites from north and south pipe formed a crater, with a maximum depth of 140 m, resulting in a deposition of fossiliferous sedimentary rocks. These rocks were subsequently uncovered by mining operations that exposed talus slopes, fluvial, debris flow, granular flow, and fine-grained sedimentary rocks that preserved fossil plants and insects that were collected from 18 sites between 1983 and 1988 (McKay 1990, Mnguni 2022).

The sedimentary rocks are dated to be 98.5 and 81.7 Ma, with a midpoint of 90.1 Ma (Haggerty et al. 1983) and 93.1 Ma (Davis 1977). The mine has sedimentary rocks of the Permian–Jurassic Karoo Supergroup. Today, the mine is considered to be the largest conventional open-pit diamond mine producer by carats worldwide. In this study, we describe four new species of the Carabidae from this deposit. They are all compression fossils preserved in brown-red and olive-green fine-grained lacustrine sedimentary rocks.

Materials and Methods

The early infilling of the crater was caused primarily by gravity-driven catastrophic processes that consisted of kimberlitic material and chunks of surrounding country rock that the kimberlite possibly collected on its journey to the surface (McKay 1990). Mining operations have revealed a large oval pit that is 80 m in depth. The deposit was dated using radioactive U in zircon crystals involving two dating techniques (i.e., low contamination hydrothermal U-Pb and fission track) and by using fossil plants and fossil pollen. The lacustrine sedimentary rocks have interbedded fine-grained sedimentary rocks, with coarser grained sedimentary rocks. It is thought that the deposit had a rapid rate of sedimentation of approximately half a million years (Dobbs 1978). The specimens were collected from the spoil heap that is the dumping ground for both fine-grained sedimentary rocks and coarser grained sedimentary rocks that have been collected from the Orapa pit.

The specimens described in this study are relatively well-preserved compression fossils. The holotypes are all housed in the herbarium at the Evolutionary Studies Institute (ESI), University of the Witwatersrand, Braamfontein, Johannesburg, South Africa. Observation and photography were done using an Axio Zoom V16 microscope (Zeiss, with Axiocam 512 color camera, identification no. 195-42829) housed in the Biosystematics Microscopy Imaging System, Agricultural Research Council Plant Health and Protection (ARC-PHP), Roodeplaat, Pretoria, South Africa. Multiple photographs were stacked and measured using the Axio Zoom V16 microscope. All the photographs were prepared using Photoshop 5.6.5.58 (Adobe Creative Cloud, University of the Witwatersrand). The photographs are with and without glare for each specimen.

The specimens were examined under cross polars to clarify the outlines. Polarizing filters were attached to swan-necked lights (the objective lens of the microscope), and they were rotated to polarize the light and remove reflection. For each species, a single specimen of an adult fossil with carbonaceous material preserving both dorsal and ventral structures was used for the description. One of the specimens is preserved as part and counterpart (reverse photograph). Only the counterpart was found and used for the description. Owing to the fragile nature and the oxidation of Fe on the surfaces of the rocks, the fossils were studied without alcohol. Unfortunately, several diagnostic features are not well preserved on the fossils. Their study is still warranted. The scale in all the photographs provided in this work is 2.0 mm. The diagnosis and descriptions of the four new species were extracted from McKay (1990), where they were not assigned in any genera due to lack of reliable characters due to the limitations of the machinery at the time.

Results

Systematic Palaeontology

Class: Insecta Linnaeus, 1758
Order: Coleoptera Linnaeus, 1758
Suborder: Adephaga Schellenberg, 1806
Superfamily: Caraboidea Latreille, 1802
Family: Carabidae Latreille, 1802
Subfamily: Harpalinae Bonelli, 1810
Tribe: Harpalini Bonelli, 1810
Subtribe: Harpalina Bonelli, 1810
Genus: Harpalus Latreille, 1802

Incertae sedis

Type species. *Harpalus* (*Harpalus*) *affinis* (Schrank, 1781).

Composition. *Harpalus mckayi* sp. n., *Harpalus mnguni* sp. n., *Harpalus nkqwili* sp. n., and *Harpalus peteni* sp. n.

Diagnosis. General habitus, mandibular scrobe without seta, elongated scutellum, and spiny mesotibia. The fossils are assigned in *Harpalus* due to the following characters: glabrous habitus, hairless eyes, and narrow epilobes of mentum. Notably, all of the fossils reported in this study are comparable to members of the *Cratognathus*, *Dichaetochilus*, *Heterohyparpalus*, *Aulocoryssus*, *Acupalpus*, *Egadroma*, and other genera. Moreover, *H. mnguni* sp. n. and *H. nkqwili* sp. n. are rather morphologically similar.

Harpalus mckayi Mnguni, new species (Figs. 2, 3)

Measurements. Length = 9.98 mm and width = 3.49 mm.

Type material studied. Specimen number BP/2/18669b, herbarium, ESI, University of the Witwatersrand, Braamfontein, Johannesburg, South Africa.

Diagnosis. As for genus. *Harpalus. mckayi* sp. n. has unusual two supraorbital pits (instead of only one) located above each eye.

Fig. 2. ***Harpalus mckayi* sp. nov., holotype, part, BP./2/18669b, Orapa Diamond Mine. Photograph of habitus, polarized light with glare. Scale bar = 2.0 mm.**

Fig. 3. *Harpalus mckayi* sp. nov., holotype, part, BP./2/18669b, Orapa Diamond Mine. Photograph of habitus, polarized light without glare. Scale bar = 2.0 mm.

Type locality and horizon. ODM in Botswana, lacustrine deposit, Upper Cretaceous (Cenomanian–Campanian, possibly Turonian) (21°18.465′S; 25°22.177′E).

Etymology. The species epithet is named in honor of the late I.J.M., who diligently worked on these fossil carabid beetles from ODM and supervised S.M. (July 2018–June 2022) as a doctoral student.

Description. A well-preserved coalified compression embedded in micaceous olive-green fine sandstone. It is represented as both part and counterpart. However, the part consists only of the mesothorax, metathorax, and abdomen. Also, the counterpart is missing the anterior portion of the head and the right portion of the prothorax.

Head short, broad, triangular in outline (ratio of width of head between antennae to width of neck = 0.67) with no postorbital constriction; antennae represented by pair of incomplete scapes; with two poorly preserved but distinguishable segments of left maxillary palp, right maxillary palp not preserved; mandibles incomplete, mandibular scrobe without seta; compound eyes small, hairless, convex, and protrude slightly; pair of supraorbital pits on either side of head; posterior portion of head raised in prominent half dome.

Prothorax transverse (ratio of maximum width of prothorax to its length = 1.45), narrower between posterior angles than elytra between humeral angles; width at widest point is far narrower than elytra at widest point (ratio of maximum width of prothorax to maximum width of elytra = 0.60); anterior margin, posterior angles, and posterior margin not preserved; anterior angles prominent and acute; lateral margins curve gradually outward from anterior angles, until about one third down length of prothorax where they straighten, become subparallel and curve gently until posterior of prothorax; lateral border visible only on left; posterior side of prothorax narrow and parallel to lateral margin as epipleura; longitudinal ridge runs down length of prothorax; epipleura parallel to lateral margin; coxa not visible; right leg represented by poorly preserved femur and tibia; left leg represented by remnants of femur.

Mesothorax with scutellum at base of elytra; elytra with gently rounded humeral angles, with parallel sides curving gradually toward apex in last third of length before apex turn sharply inward so that apex of elytra is almost flat (this effect may be compounded by incomplete tips of elytra); with nine pairs of nonpunctate stria, stria 1 intersected basally by scutellary stria, stria 1 and 2 parallel, stria 3 to 4 and stria 5 to 6 connected to form two U shapes, U formed by stria 3 to 4 longer than U formed by stria 5 to 6, stria 7 and 8 parallel, and stria 9 very close to and converges with edge of elytron near its apex, stria 8 with expansions along its length, three expansions visible at distal end on right elytron of counterpart and two expansions visible at proximal end on left elytron of counterpart (these could have been sites of seta); mesepimera not forming part of border of coxal cavities (visible on left side of part) that are therefore conjunct; right leg not preserved; left leg consists of portions of femur, tibia with distinct longitudinal ridge and seta on anterior margin; with five-segmented tarsus; tarsal segments triangular, unexpanded, with seta at basal corners; tarsal segments 1 and 2 are 1.5 times as long as tarsal segments 3 and 4 (that are in turn a third of the length of tarsal segment 5), tarsal segment 5 has pair of claws with third appendage, which may be long seta.

Metathorax with pair of metepimera and pair of legs; right leg with trochanter, femur, elongated tibia with pair of apical spurs (only one is visible on part), and poorly preserved tarsus; left leg with coxa, trochanter, femur, tibia, and poorly preserved tarsus; tarsal segments with hairs and spines (number of segments undetermined), and terminal segment has pair of diverging claws; trochanters are elongated, three times as long as wide (ratio of length of trochanter to length of femur = 0.56); tibia have prominent longitudinal groove.

Abdomen with three sternal sutures, probably representing six sternites as in many carabids.

Harpalus mnguni **McKay, new species**
(Figs. 4, 5)

Measurements. Length = 7.7 mm and width = 2.64 mm.

Type material studied. Specimen number BP/2/26255, herbarium, ESI, University of the Witwatersrand, Braamfontein, Johannesburg, South Africa.

Diagnosis. As for genus. *Harpalus mnguni* sp. n. has elongated maxillary and labial palps and slender antennomeres.

Type locality and horizon. ODM in Botswana, lacustrine deposit, Upper Cretaceous (Cenomanian–Campanian, possibly Turonian) (21°18.465′S; 25°22.177′E).

Etymology. The species epithet is named in honor of S.M., who was supervised by the late I.J.M. as a doctoral student (July 2018–June 2022), becoming the first and only palaeoentomologist in South Africa.

Fig. 4. ***Harpalus mnguni*** **sp. nov., holotype, part, BP./2/26255, Orapa Diamond Mine. Photograph of habitus, polarized light with glare. Scale bar = 2.0 mm.**

Description. A well-preserved coalified compression embedded in micaceous red mudstone. It is a positive image preserved with portions of the head, thorax, and abdomen and their associated appendages.

Head without postorbital constriction, slightly narrower between antennae than at neck (ratio of width of head between antennae to width of neck = 0.72); compound eyes hairless; antennae slender, filiform, with portions of all 11 segments visible, scape twice as long as segment 2, which is just over half length of segment 3; segment 3 same length as segments 4–10; and segment 11 is 1.4 times length of scape; maxillary palps represented by three elongated segments (visible on left side) that protrude beyond mandibles, mandibular scrobe without seta; only distal portions of labial palps are preserved; labial and gular sutures visible.

Prothorax transverse (ratio of maximum width of prothorax to its length = 1.48); anterior angles gently curved, oblique; anterior margin (dorsal or ventral) straight; posterior margin (dorsal or ventral) slightly concave and gently curved; posterior angles obtuse; lateral margins curved evenly from anterior-to-posterior angles; width between posterior angles less than width of elytra between humeral angles; width at widest point less than that of elytra at widest point (ratio of maximum width of prothorax to maximum width of elytra at widest point = 0.92); median longitudinal depression runs from posterior to coxal cavities to anterior angles; epipleura parallel to lateral margin (except at anterior angles where they become broader); coxal cavities poorly preserved; each leg represented by portions of femur and tibia.

Fig. 5. ***Harpalus mnguni*** **sp. nov., holotype, part, BP./2/26255, Orapa Diamond Mine. Photograph of habitus, polarized light without glare. Scale bar = 2.0 mm.**

Mesothorax with scutellum rounded and situated at base of elytra; elytra with pair of oblique humeral angles, with subparallel sides, curved gently and evenly until last quarter of their length, where they curve more sharply toward apex; with indistinct stria, left elytron with three, right elytron with five; elytral epipleura visible; coxal cavities poorly preserved, probably conjunct because mesepimera (visible on right side) do not form part of boundary; mesepisternal sutures present; legs represented by pair of femora, left leg also has tibia with longitudinal groove.

Metathorax with pair of metepisterna, antecoxal suture and legs represented by pair of contiguous coxa that do not reach as far as elytral epipleura, pair of oblong trochanters that are twice as long as wide, and pair of femora (ratio of length of trochanter to length of femur = 0.48); left leg also has tibia with longitudinal groove and tarsus with three square-shaped tarsal segments.

Abdomen with at least four sternal sutures, probably representing six sternites as in many carabids.

Harpalus nkqwili McKay and Mnguni, new species (Figs. 6, 7)

Measurements. Length = 7.04 mm and width = 2.4 mm.

Type material studied. Specimen number BP/2/26260, herbarium, ESI, University of the Witwatersrand, Braamfontein, Johannesburg, South Africa.

Diagnosis. As for genus. *Harpalus nkqwili* sp. n. has a unique postorbital constriction.

Fig. 6. ***Harpalus nkqwili*** **sp. nov., holotype, part, BP./2/26260, Orapa Diamond Mine. Photograph of habitus, polarized light with glare. Scale bar = 2.0 mm.**

Type locality and horizon. ODM in Botswana, lacustrine deposit, Upper Cretaceous (Cenomanian–Campanian, possibly Turonian) (21°18.465′S; 25°22.177′E).

Etymology. The species epithet is named in honor of the late Cambridge Nkqwili, who groomed S.M. to become an academic professional.

Description. A well-preserved coalified compression embedded with a fragment of an insect wing in micaceous red mudstone. It is a positive image, with the whole body and portions of its associated appendages preserved.

Head with slight postorbital constriction, broader at neck than between antennae (ratio of width of head between antennae to width at neck = 0.72), left antenna represented by portions of all 11 segments, right antenna represented by portions of 7 segments; part of projecting scape almost same size as segment 2, segments 3–10 of equal size and same size as scape, segment 11 about 1.25 times longer than scape; mandibles large and curved, mandibular scrobe without seta; left maxillary palp with three distinct segments, terminal segment 3 times as long as wide, penultimate segment 0.66 times as wide as long; right maxillary palp indistinct and represented by one segment; compound eyes small, hairless, convex, and protruding; portions of gular sutures visible.

Prothorax transverse (ratio of maximum width of prothorax to its length = 1.32), anterior angles prominent and acute, anterior margin (dorsal or ventral) concave, shaped like wide V; posterior angles oblique, posterior margin not distinct; lateral margins of prothorax curved evenly from anterior-to-posterior angle; median and longitudinal depression runs across length of prothorax; coxal cavities closed

Fig. 7. ***Harpalus nkqwili*** **sp. nov., holotype, part, BP./2/26260, Orapa Diamond Mine. Photograph of habitus, polarized light without glare. Scale bar = 2.0 mm.**

behind by postcoxal bar; legs represented by pair of femora and pair of tibia; right tibia with comb, longitudinal groove and four spines or seta on anterior outer surface; right leg has tarsus with four square segments of similar proportions and left leg remnant of poorly preserved tarsus.

Mesothorax elytra with poorly preserved sides; sides subparallel, gently rounded for 0.66 of length, curving more sharply toward apex; stria indistinct; right elytron with two visible stria, left elytron with five visible stria; coxae indistinct, probably conjunct; right leg with trochanter, femur, and tibia with longitudinal groove and four-segmented tarsus; left leg with poorly preserved femur and tibia.

Metathorax represented by pair of legs, pair of metepisterna and antecoxal suture; each leg has coxa, elongated oblong trochanter (about twice as long as wide), slender tibia with tibial spur (visible on left side), and tarsus with five segments; coxa contiguous, not reaching elytral epipleura; first four tarsal segments similar in size and shape, terminal segment 3 times as long as terminal segment 4.

Abdomen with four sternal sutures, probably representing six sternal plates as in many carabids.

Harpalus peteni McKay and Mnguni, new species (Figs. 8, 9)

Measurements. Length 4.85 mm and width 1.6 mm.

Type material studied. Specimen number BP/2/24006, herbarium, ESI, University of the Witwatersrand, Braamfontein, Johannesburg, South Africa.

Fig. 8. *Harpalus peteni* sp. nov., holotype, part, BP./2/24006, Orapa Diamond Mine. Photograph of habitus, polarized light with glare. Scale bar = 2.0 mm.

Diagnosis. As for genus. *Harpalus peteni* sp. n. differs by the shape of the eyes and anterior margins.

Type locality and horizon. ODM in Botswana, lacustrine deposit, Upper Cretaceous (Cenomanian–Campanian, possibly Turonian) (21°18.465′S; 25°22.177′E).

Etymology. The species epithet is named in honor of the late Thamsanqa Peteni, the biological father of S.M.

Description. The specimen is an impression that has been stained brown, perhaps by the remains of organic material, and is embedded in micaceous buff-colored mudstone along with fragments of organic matter. The whole body with its associated appendages is preserved. It is a negative image of a small beetle with a pedunculate body.

Head wider at neck than at antennae (ratio of width of head between antennae to width of neck = 0.51), with no postorbital constriction; antennae slender and filiform, scape 1.6 times as long as segment 2, segment 2 half-length of segment 3, segment 3 slightly longer than segments 4–9, shorter than incomplete terminal segment; mandibles curved, left mandible longer than right, mandibular scrobe without seta; portions of both maxillary and labial palps visible; compound eyes indistinct, hairless; remnants of gular sutures distinguishable.

Prothorax transverse (ratio of maximum width of prothorax to its length = 1.36); anterior angles acute; anterior margin (dorsal or ventral) concave and rounded gently; posterior margin (probably ventral) convex and curved evenly; lateral margins curved slightly from anterior-to-posterior angles; prothorax narrower at posterior angles than elytra between humeral angles (ratio of width of prothorax between

Fig. 9. ***Harpalus peteni*** **sp. nov., holotype, part, BP./2/24006, Orapa Diamond Mine. Photograph of habitus, polarized light without glare. Scale bar = 2.0 mm.**

posterior angles to width of elytra between humeral angles = 0.8); maximum width equal to width of elytra between humeral angles, narrower than maximum width of elytra (ratio of maximum width of prothorax to maximum width of elytra = 0.85); median longitudinal ridge runs down length of prothorax; epipleura narrow and parallel to lateral border, except at anterior angles where they widen slightly; coxal cavities indistinct; legs represented by pair of femora and tibia.

Mesothorax scutellum oval; elytra unfused, with pair of obtuse humeral angles, sides curving gently and evenly toward apex, with poorly preserved nonpunctate stria; left elytron with two parallel stria, right elytron with four parallel stria; legs represented by pair of conjunct but poorly preserved coxal cavities, femora and tibia; right leg with indistinct tarsus.

Metathorax legs represented by pair of coxa, pair of oblong trochanters (twice as long as wide), pair of femora (ratio of length of trochanter to length of femur = 0.53), pair of slender tibia with median longitudinal ridges, and pair of indistinct tarsi; five segments of left tarsus, two or three of right tarsus visible; terminal segment of left tarsus has pair of tarsal claws.

Abdomen with four sternal sutures, probably representing six sternal plates as in many carabids.

Remarks. *Harpalus mckayi* sp. n. is similar to members of the *Harpalus*, *Cratognathus*, *Dichaetochilus*, *Egadroma*, and many other genera. The two supraorbital pits above each eye are not typical of the Harpalinae: they usually only have one supraorbital pit above each eye. However, in other Carabidae, which have two supraorbital setae above each eye (e.g., the Pterostichinae), the setae are usually situated further back and closer to the eye than the pits, as observed in the specimen. *Harpalus mnguni* sp. n. resembles members of the *Harpalus*, *Heterohyparpalus*, *Aulocoryssus*, *Acupalpus*, and *Egadroma*. *Harpalus nkqwili* sp. n. is very similar in shape to *Harpalus mnguni* sp. n. The key differences between the two specimens include the postorbital constriction of *H. nkqwili* sp. n., the difference in the shape of the eyes and the elongated palps of *H. mnguni* sp. n., the difference in the shape of the anterior margins of the specimens, and the slenderer antennal segments of *H. mnguni* sp. n.

Discussion

The deposit offers examples of early plant–insect and insect–insect reciprocal interactions. At ODM in Botswana, the Carabidae may have been found feeding on the flowers and preying on other insects before being buried by the fine-grained and coarser sedimentary rocks. Attempts were made to compare them with extant Carabidae in the Coleoptera Collection housed in the Biosystematics Building at the ARC-PHP in Roodeplaat. This comparative approach was imperative because some of the diagnostic features, such as seta, genitalia, the position of tibial spurs, and ventral sclerites, are, in most cases, either not preserved or are rather difficult to interpret on the fossils, as is the case with the four new species reported in this study. There are also other Coleoptera belonging to Curculionidae (Kuschel et al. 1994), Scarabaeidae (Woolley 2016), and Staphylinidae (Mnguni et al. 2022, 2023, 2024a,b,c) that have been described by several authors from the same deposit. Most of the fossil plants and insects are intact and well preserved in brown-red lacustrine sedimentary rocks. These tend to have a pitted pattern at the surface that resembles raindrop impressions. Moreover, there is no sign of animal activity in a form of burrowing or tracks (bioturbation) in the sedimentary rocks.

The Adephaga appeared in the late Permian or early Triassic. Many researchers consider that the first true Carabidae were members of the Protorabinae that appeared in the Jurassic (a time of global aridity), which were diagnosed by the metepisterna reaching the mesocoxal cavities and metacoxal plates (McKay 1990). Cretaceous Carabidae include *Carabites vitimensis* Ponomarenko, *Carabites nigriventris* Ponomarenko, and *Carabites creta* Ponomarenko. The Cretaceous, Tertiary, and Quaternary Carabidae are modern and similar to extant taxa in nature, and those of Eocene and Oligocene ages are known from the Baltic, Dominican, and Mexican ambers. These are well known because they tend to be well preserved. Even those found in tarpits and peatbogs seldom have an excellent preservation (McKay 1990). Early Adephaga had their metepisterna forming part of the wall of mesocoxal cavities as in the Dytiscidae. They also had an enlarged metacoxae that extend to the elytral epipleura as is commonly observed in the Hydradephaga and the Trachypachidae. These are considered to be pleisiomorphic, and they are deemed to be more widespread than previously thought.

In the Cretaceous, the deposit would have been slightly to the south and east of Cape Town (McKay 1990). Moreover, the general elevation of the land surface was between 50 and 100 m higher than it is today. The Cretaceous global temperatures were apparently very similar to those that we are experiencing today. An example of evidence supporting this notion involves an analysis of O isotopes of planktonic from Cretaceous tropical waters that have recorded surface temperatures in the range of 27–32°C, which is similar or warmer than those of the present day. In the Cretaceous, temperatures at the tropics were higher or similar than those of today, whereas temperatures in the midlatitudes and polar regions were above those of today (McKay 1990). In the Cretaceous, there were cooler sea-surface temperatures (Frakes 1979, Frakes et al. 1992), suggesting that there would have been less evaporation. An inference can be made that there was less moisture in the air moving over the continent and therefore low precipitation.

The ODM in Botswana probably experienced similar or even warmer temperatures than those of today. The Orapa crater was possibly a damp minienvironment in an arid region. The sea level is hypothesized to have been 100 m higher than the sea level today (McKay 1990). The paleoenvironmental reconstructions using fossil plants and insects suggest that the climate was strongly seasonal, with warm, high-humidity, wet summers and dry, cold winters. The evaporite layers in the lacustrine sedimentary rocks may indicate periods of drought, whereas varves suggest a seasonal climate. According to McKay (1990), the palaeolake was poisoned by volcanic residues or excess salinity. Phytophagous, saprophagous, and mycophagous insects previously reported from the deposit suggest continuous vegetation cover. Some of the vegetation in the crater was deciduous (Bamford 1990). Many insects are completely preserved (articulated), possibly suggesting a slow deposition of weak water currents. It also suggests that there would have been few predators and scavengers.

The similarity of the carabids to modern forms indicates that they have been remarkably conservative in their evolution since the Cretaceous and possibly even longer. They support a punctuated pattern of evolution, with morphological stasis linked to continued presence of preferred habitats. At the ODM in Botswana, it is hypothesized that plants and insects flew, walked, or were washed into the palaeolake by current and were subsequently buried by mudflows, turbidity currents, or gradual lacustrine deposition. They eventually became fossilized over time. Furthermore, aquatic insects have been reported previously (Rayner and McKay 1986), but no aquatic or terrestrial vertebrates have been reported so far. The preliminary taphonomy of the deposit has been studied by Mnguni (2022).

In conclusion, in the Cretaceous, the ODM in Botswana would have been situated in the high-pressure belt and therefore possibly experienced dry climatic conditions. Furthermore, Orapa would have had a relatively low rainfall; however, it is probable that the rainfall at Orapa would have been much higher than it is today. Evidence from the predominance of mass flows and granular flows suggests that the Orapa crater had an arid environment with occasional torrential rainstorms. Seasonality may have been expressed as either seasonal fluctuations in temperature or seasonal fluctuations in rainfall, or both. The carabids reported herein are indicative of ferns, thick bush, and forest. They must have lived in and around the outside of the crater. All the carabids are modern in form and may be placed in the more derived and recent taxa. Studies of global climate in the Cretaceous suggest that southern Africa was warmer, wetter, and more humid than it is today.

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