# A Fossil Paederinae from a Lacustrine Deposit at Orapa Diamond Mine in Botswana[1]

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**Abstract** A staphylinid beetle morphotype, *Mesostaphylinus orapa* sp. n., is described based on a single well–preserved compression fossil from an Upper Cretaceous lacustrine deposit at Orapa Diamond Mine in Botswana. *Mesostaphylinus* Zhang is placed in the extant subfamily Paederinae based on general habitus and an unambiguous synapomorphy, the concealed antennal insertions. *Mesostaphylinus* is a genus of convenience for fossils belonging in Paederinae, but lacking diagnostic features (e.g., maxillary palpomeres) to assign and delineate them into appropriate tribes and subtribes. The fossil described here is morphologically similar to *M. laiyangensis* Zhang, *M. fraternus* Zhang, Wang and Xu, *M. elongatus* Solodovnikov and Yue, *M. yixianus* Solodovnikov and Yue, and *M. antiquus* Solodovnikov and Yue. Compared to other fossil staphylinid beetles that have been described thus far, the fossil also portrays morphological conservatism, morphological stasis, or arrested evolution dating back to the Cretaceous, thereby suggesting a punctuated equilibrium pattern of evolution.

**Key Words** Fossil, Staphylinid, Paederine, Kimberlite, Crater Lake, Africa, Southern Hemisphere

The Paederinae is one of the hyper–diverse Staphylinidae subfamilies with 7,982 species nested within 238 genera (Catalogue of Life, updated to 2023). It is known as one of the most challenging subfamilies for study (Żyła et al. 2021), and is one of few subfamilies in which social parasitism has evolved (Żyła et al. 2022). Initially it was divided into 4 tribes, namely: Pinophilini, Paederini, Cylindroxystini, and Lathrobiini (Schomann and Solodovnikov 2017). Recently, Żyła et al. (2021, 2022) conducted the most comprehensive phylogenetic analysis of the Paederinae, based on multiple genetic loci, incorporating the broadest sampling of the taxa. These studies reduced the Paederinae to 3 monophyletic tribes; the Pinophilini, Lathrobiini and Paederini. The sister relationships are unresolved. Żyła et al. (2021) resolved Pinophilini as sister group to Lathrobiini + Paederini; while in Żyła et al. (2022), Paederini was resolved as

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sister to Pinophilini + Lathrobiini. In the same study, Cylindroxystini was downgraded to a group within the Lathrobiini.

Most phylogenetic studies (e.g., Grebennikov and Newton 2009, McKenna et al. 2015, Schomann and Solodovnikov 2012, Solodovnikov et al. 2013) have grouped Paederinae and Staphylininae as sister taxa. Surprisingly, Lü et al. (2020) found only weak support for the relationship between Paederinae and Staphylininae. However, more recently, Paederinae + *Euaesthetus* were reported to be sister to Staphylininae, Xantholininae, Platyprosopinae, and Coomaniinae (Żyła et al. 2021). According to Hernando and Andujar (2021), the split between Paederinae and Staphylininae occurred during the Late Jurassic (156.6 Ma). Moreover, Lü et al. (2020), who analyzed 4 nuclear and 2 mitochondrial gene sequences, estimated that the two subfamilies originated between 160.41 and 147.58 Ma.

The Mesozoic fossil record of the Paederinae is restricted to the Cretaceous (Table 1). Two species, *Mesostaphylinus laiyangensis* Zhang and *M. fraternus* Zhang, Wang and Xu, were described from the Laiyang Formation of Shandong Province in China. Another two species, *Apticax solidus* Schomann and Solodovnikov and *A. volans* Schomann and Solodovnikov, from the Nova Olinda Member of the Crato/Santana Formation in Brazil were assigned to the Staphylininae + Paederinae lineage, but with the qualification that the small number of diagnostic features do not allow for their definite placement in any of the 35 subfamilies of the Staphylinidae. Three species, *Mesostaphylinus elongatus* Solodovnikov and Yue, *M. yixianus* Solodovnikov and Yue, and *M. antiquus* Solodovnikov and Yue, were described from the Yixian Formation of China, based on the phylogenetic analysis of both extinct and extant taxa. These were placed as "*incertae sedis*" within the Paederinae, due to lack of diagnostic features.

A number of taxa have been described from amber deposits (Betz et al. 2018). Bogri et al. (2018) described *Dysanabatium kechrimparense* Bogri, Solodovnikov and Żyła, *D. aenaum* Bogri, Solodovnikov and Żyła, *D. damgaardi* Bogri, Solodovnikov and Żyła, and *D. johannesi* Bogri, Solodovnikov and Żyła from the Baltic amber, to address a connection between co–occurrence of thermophilic and temperate insect taxa, and Eocene climate change. Żyła et al. (2019) described 2 inclusions, *Diminudon schomannae* Żyła, Yamamoto and Jenkins Shaw and *D. kachinensis* Żyła, Yamamoto and Jenkins Shaw, from the Burmese amber (Myanmar), based on a combination of morphological and molecular datasets. The earliest record of the Pinophilini, also from the Burmese amber, was described by Jenkins Shaw et al. (2020a) as *Cretoprocirrus trichotos* Jenkins Shaw, Wang, Bai and Żyła. In addition, Bogri et al. (2020) described *Micrillus electrus* Bogri, Solodovnikov, Kypke and Żyła, and *Scymbalium phaethoni* Bogri, Solodovnikov, Kypke and Żyła, possibly from the Baltic amber, based on diagnostic morphological character matrices of both genera.

In total, the fossil record of Paederinae includes 40 species from 12 genera: *Achenium* Curtis; *Apticax* Schomann and Solodovnikov; *Cretoprocirrus* Jenkins Shaw et al.; *Diminudon* Żyła et al.; *Dysanabatium* Bernhauer; *Lathrobium* Gravenhorst; *Lithocharis* Dejean; *Miolithocharis* Wickham; *Medon* Stephens; *Mesostaphylinus* Zhang; *Orsunius* Assing; and *Paederus* Lin et al. These genera range from the Cretaceous to the Miocene, particularly in the Tertiary period. The taxa are summarized by Żyła et al. (2019), with an addition of *Cretoprocirrus* (Jenkins

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**Table 1. Species list of the Mesozoic Paederinae (Coleoptera: Staphylinidae).**

| Taxon | Stratigraphy | Deposit | Preservation |
|---|---|---|---|
| **Paederinae** | | | |
| Paederinae *incertae sedis* (morphotype described here) | Upper Cretaceous | Orapa, Botswana | Rock |
| *Apticax solidus* Schomann and Solodovnikov, 2012 | Lower Cretaceous | Crato Fm., Brazil | Rock |
| *Apticax volans* Schomann and Solodovnikov, 2012 | Lower Cretaceous | Crato Fm., Brazil | Rock |
| *Cretoprocirrus trichotos* Jenkins Shaw et al., 2020 | Lower Cretaceous | Burmese Amber, Myanmar | Amber |
| *Diminudon kachinensis* Żyła et al., 2019 | Lower Cretaceous | Burmese Amber, Myanmar | Amber |
| *Diminudon schomannae* Żyła et al., 2019 | Lower Cretaceous | Burmese Amber, Myanmar | Amber |
| *Mesostaphylinus antiquus* Solodovnikov and Yue, 2013 | Lower Cretaceous | Yixian Fm., China | Rock |
| *Mesostaphylinus elongatus* Solodovnikov and Yue, 2013 | Lower Cretaceous | Yixian Fm., China | Rock |
| *Mesostaphylinus fraternus* Zhang, Wang and Xu 1992 | Lower Cretaceous | Yixian Fm., China | Rock |
| *Mesostaphylinus laiyangensis* Zhang, 1988 | Lower Cretaceous | Laiyang Fm., China | Rock |
| *Mesostaphylinus yixianus* Solodovnikov and Yue, 2013 | Lower Cretaceous | Yixian Fm., China | Rock |

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

Shaw et al. 2020a). Many species are described from Cenozoic deposits such as the Florissant Formation of the United States of America, and the Baltic amber, and it has been suggested that the majority of these have been incorrectly assigned to the genus *Lathrobium* Gravenhorst (Chatzimanolis 2018). Among these are *Lathrobium provinciale* Goss that has been described formally from the Aix–en–Provence Formation of France (11.6–7.2 Ma), and several *Lathrobium* spp. from the Shanwang Formation of China (Chatzimanolis 2018).

A number of undescribed fossil staphylinid beetles are known to be stored in collections. These include taxa from the Burmese amber, and others from the Green River Formation of the United States of America, and the Kishenehn Formation of the United States of America (Chatzimanolis 2018). Notably, all the Cenozoic fossils have been assigned to the tribe Lathrobiini (Żyła et al. 2019). Here, we describe the first record of Paederinae from Africa. The specimen was initially assigned to Pinophilina, and was named *Afrinophilina orapa* (Mnguni 2022, Mnguni et al. 2022), and has since been later renamed *Mesostaphylinus orapa* in earlier versions of this work.

## Materials and Methods

The specimen was excavated from Orapa Diamond Mine (ODM) (Fig. 1), located in the north–east of Botswana, approximately 240 km due west of Francistown, and 824 km away from Johannesburg (McKay 1991). A double eruption of diamondiferous kimberlites from North and South pipe resulted in a deposition of fossiliferous sediments. 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

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98.5 and 81.7 Ma, with a midpoint of 90.1 Ma (Haggerty et al. 1983) and 93.1 Ma (Davis 1977), respectively. Thus, the deposit is considered to be Upper Cretaceous (Turonian, but possibly Cenomanian or Coniacian). The Orapa Diamond Mine is one of the major insect deposit from the Cretaceous in Africa (Grimaldi and Engel 2005). The palaeofauna of the deposit has been reviewed elsewhere (Brothers 1992; Brothers and Rasnitsyn 2003, 2008; Dlussky et al. 2004; Kopylov et al. 2010; Kuschel et al. 1994; McKay 1990, 1991; McKay and Rayner 1986; Mnguni 2022; Mnguni et al. 2022, 2023; Rasnitsyn and Brothers 2007, 2009; Rayner 1987, 1993; Rayner and McKay 1986; Rayner and Waters 1989, 1990; Rayner et al. 1991, 1994, 1997; Waters 1989a,b, 1990; Woolley 2016).

The specimen described here is a well–preserved compression fossil. The morphotype is housed in the Herbarium of the Evolutionary Studies Institute (ESI), at the University of the Witwatersrand, Johannesburg, South Africa. Observation and photography were effected 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 specimen is preserved as part (120 × 90 × 38 mm) and counterpart (73 × 62 × 30 mm) in large pieces of brown lacustrine mudstones. Owing to the fragile nature and the oxidation of iron on the surfaces of the rocks, the fossil was studied without alcohol. Several key diagnostic features, especially on the head region, such as maxillary palpomeres, are not well preserved. The scale in all the photographs provided in this work is 1 mm.

## Results

### Systematic Palaeontology.

Order: Coleoptera Linnaeus, 1758
Series: Staphyliniformia Latreille, 1802
Superfamily Staphylinoidea Latreille, 1802
Family: Staphylinidae Latreille, 1802
Subfamily: Paederinae Fleming, 1821
Genus: *Mesostaphylinus* Zhang, 1988

***Incertae sedis***

*Type species: Mesostaphylinus laiyangensis* Zhang, 1988.

*Etymology:* The generic epithet was described in Zhang (1988).

*Composition*: Only type species *Mesostaphylinus orapa* sp. n.

*Diagnosis:* The new morphotype is placed in Paederinae based on general habitus and unambiguous synapomorphy of the subfamily, the antennal insertions concealed under “shelf” (and therefore not visible from above). It is assigned to *Mesostaphylinus* based on general habitus, sharing key diagnostic morphological characters with *M. laiyangensis* Zhang, *M. fraternus* Zhang, Wang and Xu,

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*M. elongatus* Solodovnikov and Yue, *M. yixianus* Solodovnikov and Yue, and *M. antiquus* Solodovnikov and Yue. It differs from them by having an expanded tarsomere 1.

### ***Mesostaphylinus orapa*** sp. n. (Figs. 2–4).

*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."

*Material studied:* Morphotype, 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, Haggerty et al. 1983).

*Diagnosis:* As for the genus ***Mesostaphylinus*** described by Zhang (1988).

*Diagnosis: Body* long, slender, measuring 8.81 mm in length (from tip of mandibles to tip of abdomen, posterior to head + neck region) 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. 2–4).

*Head* tilted, 1.44 mm long (from tip of mandible to anterior margin of pronotum) and 1.01 mm wide at widest point (tilted measure, anterior to neck); 1.4× longer than wide, with distinct curved temples; width of head 1.4× broader than width of neck constriction, neck broad. Eyes poorly preserved, somewhat circular to slightly oval, located closer to base of antennae, covering 1/3 of temple. Antennae filiform (Figs. 2–3); antennal bases concealed, hidden under "shelf"; proximal antennomeres incomplete, appear to be more or less equal in length and width to antennomeres 2–3 combined, antennomeres 4–8 of equal length and width, antennomeres 9 and 10 funnel shaped, antennomere 11 poorly preserved, but apparently funnel–shaped; in general antennae bearing setae. Mandibles complete, curved, sickle–shaped, very sharp apically. Labrum poorly preserved. Margin between labrum and frontoclypeus straight, curved at corners. Gular sutures separate, reaching posterior margin of head. Several indistinct structures.

*Pronotum* tilted (Figs. 2–4), semi–rectangular with curved sides, longer than wide (0.59 mm wide, 0.68 mm long at widest point); 0.9× shorter and 1.1× wider than head; anterior margin with slight strip around the neck, posterior margin gently curved. Superior marginal line apparently deflexed; with distinct post–coxal process of hypomeron. Longitudinal carina of furcasternum present, extending towards longitudinal basisternum carina, anteriorly crossed by transverse basisternum carina.

*Elytra* slightly tilted (Figs. 2–4), jointly 1.6× wider and 1.1× longer than pronotum. Semi–rectangular, wider than long (each 1.76 mm wide, 1.61 mm long at widest point); with epipleural margin, but no obvious epipleural ridge; separated at base by small scutellum, with faint striae. Elytral posterior margins curved evenly, non–emarginate, with long setae.

*Prothoracic legs* (Figs. 2–4) with coxa broad; length as for femur; trochanter large and ovoid; tibia narrow at base, becoming broader distally, lacking distinct medial expansion; distal surface with grooves which represent ctenidium, with row of setae in posterior mid–section (protibial combs). Femur covered with long setae; remnants of tarsal segments visible. First pro–tarsal segment dilated, with

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**Fig. 2. The whole body of *Mesostaphylinus orapa* sp. n. holotype, part, BP./ 2/27586a, Orapa Diamond Mine, polarized light, scale bar = 1 mm.**

setiferous margins. Metathoracic coxae apparently large and extended; tibia 1.5× long as femur, with tibial thorn at apex; tarsomere 1 about 1.5× longer than tarsomere 2, approximately same for tarsomere 5, although with poorly preserved distal segments.

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**Fig. 3. The whole body of *Mesostaphylinus orapa* sp. n. holotype, counterpart BP./2/27596, Orapa Diamond Mine, polarized light, scale bar = 1 mm.**

*Abdomen* (Figs. 2–4) curved on one side; approximately 3× elytral length and 1.2× elytral width, 3.5× as long as wide (4.96 mm long, 1.56 mm wide), apparently with waist (may be preservation artefact), tapering strongly from segment VI. Segments III–VIII visible; segment III distinct, without paratergites, with intercoxal

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**Fig. 4. The whole body of *Mesostaphylinus orapa* sp. n. holotype, counterpart, BP./2/27596, Orapa Diamond Mine, non-polarized light, scale bar = 1 mm.**

carina in middle, extending into segment IV; segments IV–VIII each with pair of paratergites, but segments IV–VII each with two pairs of paratergites, segment VIII with pair of setiferous latero–apical processes, separated by pair of pointed structures interpreted as tergal plates (Naomi 2018).

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*Palaeoenvironment:* Extant paederines are commonly found in damp places, under logs, litter or foliage, while some have been recorded inhabiting caves, as well as ant and termite nests.

*Remarks:* The fossilized staphylinid beetle has the first pro–tarsal segment dilated and its margin setiferous as for Paederinae, but diagnostic features crucial for differentiating the tribes within the subfamily, such as the form of the maxillary palps, are not preserved. Similar features are seen in other fossil taxa such as *Scymbalium* Erichson and *Micrillis* Raffray that were classified as Lathrobiini *incertae sedis* by Bogri et al. (2020), and with members of the tribes Lathrobiini and Paederini. The African fossil paederine also shares with *Mesostaphylinus* Solodovnikov and Yue characteristics of having elongated procoxae and a well–developed abdominal segment III (Solodovnikov et al. 2013). Elongated procoxae are rather typical for all tribes belonging to Paederinae. In Paederinae, the abdominal segment II is reduced and not fully developed, and is mostly hidden behind the elytra, making it difficult to compare.

## Discussion

The African fossil paederine has antennae that are concealed under the "shelf," which is one of the two unambiguous synapomorphies for Paederinae (Bogri et al. 2020; Herman 2010; Żyła et al. 2019, 2021, 2022). While the tribes and subtribes of the subfamily are quite clearly defined, assignation of the specimen beyond Paederinae is hindered by poor preservation of diagnostic features, such as the form of maxillary palpomeres. The African fossil paederine has its first pro–tarsal segment dilated with setiferous margin as for the Pinophilini and Lathrobiini (Herman 2010). However, it is not as dilated as seen in extant pinophilines housed at the Ditsong National Museum of Natural History (DNMNH) (Pretoria, South Africa).

Despite studies by Schomann and Solodovnikov (2017), Żyła et al. (2019, 2021, 2022), Bogri et al. (2020), and Jenkins Shaw et al. (2020a) published on Paederinae; and those such as Solodovnikov et al. (2013), Jenkins Shaw et al. (2020b, c) published on Staphylininae, more research is still needed to refine the classification and phylogeny of Paederinae, before new specimens can be reliably assigned to existing tribes, subtribes and genera of the subfamily. For example, the genus *Apticax* Schomann and Solodovnikov was formally described from the Santana/Crato Formation, and 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 of the 35 subfamilies of the Staphylinidae.

Cretaceous Paederinae have been found in widely disjunct deposits (Fig. 5), in Brazil, China, Myanmar, and Botswana, suggesting a much earlier point of origin. So far, no paederines have been described from Triassic and Jurassic deposits. Finding a paederine at Orapa Diamond Mine in Botswana is highly significant as the third staphylinid beetle described from this deposit. Others include a stenine, *Afristenus orapensis* Mnguni, McKay and Badenhorst, and a staphylinine, *Paleothius mckayi* Mnguni, Badenhorst and Bamford, a study on a staphylinid beetle mentioned by

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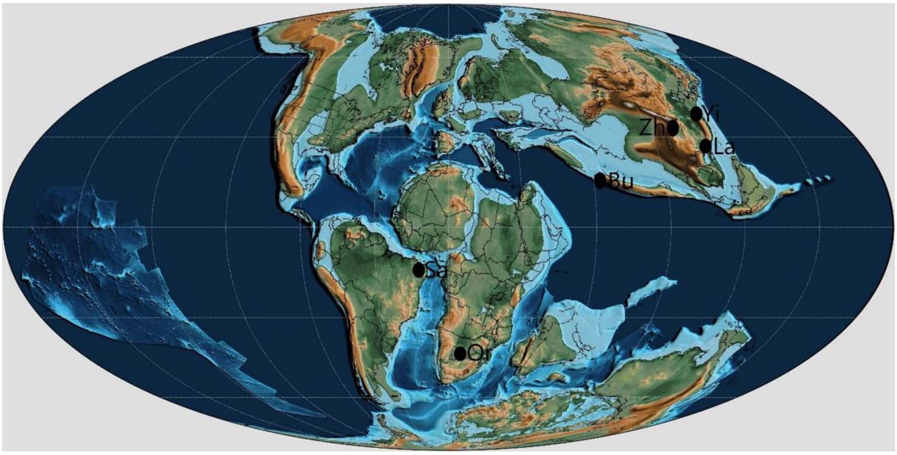

**Fig. 5. Global palaeogeographic reconstruction of the mid-Cretaceous (100 Ma) showing the localities where the fossil Paederinae have been recovered. The map in Mollweide projection was sourced from Scotese (2021, Appendix 2, Mollweide_Maps.zip). The position of the localities was adapted from Rasnitsyn 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.**

Rayner and McKay (1986), Rayner and Waters (1991), and McCarthy and Rubidge (2005). So far, these are the only documented fossil staphylinid beetles from Africa. We anticipate recovery of more staphylinid beetles from the Orapa Diamond Mine in Botswana.

In conclusion, the Mesozoic fossil record of Paederinae is restricted to the Cretaceous. The paederine morphotype described here represents the second record of the subfamily from the Southern Hemisphere, and extends the Cretaceous record for the subfamily, now known from Brazil, China, Myanmar and Botswana. Notwithstanding land connections, the widespread and disjunct Cretaceous records suggest that the subfamily Paederinae arose at an earlier time.

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

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

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

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