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Wingless *Paocryptorrhinus* (Coleoptera: Curculionidae) rediscovered in Tanzania: synonymy, four new species and a mtDNA phylogeography

VASILY V. GREBENNIKOV

Canadian Food Inspection Agency, K.W. Neatby Bldg., 960 Carling Ave., Ottawa, ON K1A 0Y9, Canada.
E-mail: vasily.grebennikov@inspection.gc.ca

Abstract. The weevil genus *Paocryptorrhinus* Voss, 1965 is revised. The nominal taxon *Anchonidium hustachei* Hoffmann, 1965 is transferred to *Paocryptorrhinus* as *P. hustachei* (Hoffmann, 1965) comb. n. The nominal taxa *Anchonidium hustachei* Hoffmann, 1965 and *Paocryptorrhinus obsitus* Voss, 1965 are considered conspecific and the name *A. hustachei* Hoffmann, 1965 is a senior subjective synonym of *P. obsitus* Voss, 1965 syn. n. The genus, previously known for a single species from the wet forests on geologically young volcanic mountains in northeastern Tanzania, is reported from two other forest types: the old crystalline East Arc Mountains and the lowland forest. Four new species, all from Tanzania, are described: *P. atropos* sp. n. (North and South Pare), *P. clotho* sp. n. (West Usambara), *P. hanangensis* sp. n. (Mt. Hanang) and *P. lachesis* sp. n. (Kimboza forest). A single specimen of an unnamed species is reported from East Usambara. The mtDNA barcoding sequences are analysed phylogeographically. Even though the genus was not recovered as a monophyletic clade in two of the molecular phylogenetic analyses, it is nevertheless hypothesized as being monophyletic based on numerous similarities in adult morphology, biology and based on the geographical proximity of all records. The uncertain phylogenetic position of *Paocryptorrhinus* is briefly discussed and the genus is transferred from Brachycerinae: Erirhinini to Molytinae *incertae sedis*.

Key words. COI, DNA barcoding, Eastern Arc Mountains, East Africa

Introduction

Taxonomic literature contains numerous poorly known taxa that are mentioned only when described and that are then seemingly forgotten. A significant, if not the predominant number of genus- and, particularly, species-group Coleoptera taxa from "exotic" localities (i.e. far from the historical taxonomic centres of expertise located in Europe and elsewhere) can be classified as such. Once introduced, the names are repeatedly mentioned in catalogues, while their true identity, taxonomic diversity and distribution, monophyly and phylogenetic position, immature stages and habitat remain elusive. Such state of affairs might continue indefinitely, unless the taxon suddenly turns out to be of economic significance and gains importance and attention. This was the case with *Agrilus planipennis* Fairmaire, a jewel beetle from the Asian Pacific Region. This was a taxonomically neglected and poorly known species until it suddenly spread over most of eastern North America and became an invasive ash killer of cosmic proportions (Jendek & Grebennikov 2011). Such examples form the negligible minority within poorly known taxa, while the overwhelming majority continues to drag along their ghostly existence decade after decade. One such example among the weevils is the subject of the present paper.

The generic name *Paocryptorrhinus* was introduced a half century ago by Eduard Voss (1965) for his new species *P. obsitus* from the geologically young volcanic mountains in northeastern Tanzania. The holotype was sampled from "humus" (=leaf litter) in the forest on the eastern slopes of Mount Kilimanjaro at 2700 m, while 12 paratypes came either from the vicinities of Marangu village on the south-eastern slope of the same mountain, or from nearby Mount Meru, Mount Oldeani and the Ngorongoro highlands (Fig. 11). These localities correspond closely to the geologically young (<2 Ma) volcanic highlands of the so-called Ngorongoro-Kilimanjaro Volcanic Belt (NKVB, Nonnotte et al. 2008). The type series was collected by the Belgian entomologists Pierre Basilewsky and Narcisse Leleup of the Royal Museum for Central Africa in Tervuren during their epic 1957 journey to sample the East African biota. All weevils from their samples were given to Voss for study, who delivered the results in two parts published in 1962 and 1965, respectively. The latter contained the description of the new genus, accompanied by an adult habitus drawing in dorsal view and the head and prothorax in lateral view (Voss 1965: Fig. 7). Until present, this was the only time the genus has been mentioned in original literature (i.e. excluding catalogs).

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This project was triggered by the necessity to identify *Paocryptorrhinus* specimen #3081 included as an outgroup representative in the phylogenetic analysis of new wingless species of *Notaris* Germar from southwest China (Grebennikov & Kolov, unpublished). Comparison of the specimen's morphology with that of the other seemingly congeneric and newly sampled specimens suggested existence of other species, aside from the type species. This was further supplemented by the differences in their mtDNA barcodes. Another unexpected discovery was that the type species had already been named and assigned to a different genus (Hoffmann 1965) about one month before the genus *Paocryptorrhinus* was formally established by Voss. These discoveries necessitated the completion of the present paper, which had the following main goals: (1) to document the course of the work highlighted above; (2) to revise the genus taxonomically; and (3) to propose a phylogeographic scenario for the low-dispersing *Paocryptorrhinus* species biologically linked to highly isolated Afrotropical wet forests of contrasting origin and age.

Material and Methods

This study is based on examination of 18 adults of *Paocryptorrhinus* sampled from Tanzania and assigned to six species (*P. hustashei*, four formally named as new, and one consciously left unnamed as *Paocryptorrhinus* sp. #3081). Sixteen specimens were successfully sequenced for the Cytochrome Oxidase subunit 1 (5-prime end, i.e. the Barcoding fragment). Parts of the historical type series pertaining to two synonymous names of the type species were examined. Fifteen other specimens representing various species of mainly Molytinae and Brachycerinae were added to the DNA-based phylogenetic analysis as an extended outgroup. All 31 specimens used for DNA extraction have at least one unique identifier label pinned underneath with the code CNCCOLVG0000XXXX (shortened to #XXXX when specimens are cited in the text below). Some specimens with more than one unique identifier (for example a specimen with labels #5231, #7270, #7271) required repeated sequencing attempts. GenBank accession numbers for 16 *Paoctyptorrhynus* sequences are given in the species descriptions; those of the 15 outgroup representatives are: HM417724, HQ986868, HQ987003, HQ987029, KJ445698, KJ445708, KJ672224, KJ672228, KJ672239, KJ672247, KJ672251, KJ672255, KJ672276, KJ841714 and KJ841726. A list of all species, specimen images, georeferences, primers, sequences, original chromatograms and other relevant data for all 31 sequenced specimens can be found online in the publicly accessible dataset "*Paocryptorrhinus*" on the Barcode of Life Database portal (doi: dx.doi.org/10.5883/DS-PAOCRYPT).

All methods used in the present work are the same as those explained in detail for a similarly structured work on the genus *Niphadomimus* (Grebennikov 2015). This includes specimen collecting and dissection, diagnostic species descriptions, process of DNA extraction, as well as the logic, software and implementation of phylogenetic analyses using Maximum Likelihood (ML) and Bayesian analysis as implemented in MEGA6 (Tamura et al. 2013) and BEAST v1.8.0 (Drummond et al. 2012), respectively. The matrix used for both analyses had a length of 658 base pairs (bp) and contained 31 sequences. The resulting topologies were visualized in FigTree v1.4 (Rambaut 2014). The ML tree was rooted with both representatives of Anthribidae (Choraginae genus *Styphlochoragus* Frieser and Anthribinae genus *Disphaerona* Jordan). The BEAST analysis was performed without rooting and without enforcing monophyly of any group. In the absence of relevant fossil data, time calibration was made by assuming strict linear molecular clock and the rate of 0.018% of nucleotide substitution per million years (Papadopoulou et al. 2010). Tracer 1.6 (Rambaut et al., 2014) was used to graphically determine stationarity and to check convergence of runs.

Labels of holotypes (HT) and paratypes (PT) of the newly described species are cited in quotation marks. Letters [p] and [h] in square brackets denote printed and handwritten text on historical labels, respectively, while back slash \ separates text on individual labels. Weevil taxonomy follows Alonso-Zarazaga & Lyal (1999), with subsequent modifications by Oberprieler (2014) and Lyal (2014). Distribution maps are generated using the on-line SimpleMappr tool (Shorthouse 2010). The chronostratigraphic timing is that of Cohen et al. (2013). Terminology for male genitalia follows Wanat (2007). The length of the body was measured in dorsal aspect from the elytral apex to the anterior edge of the pronotum (standard length).

The following abbreviations were used to indicate the Museum depositories (followed by the name of the curator):

BSUM Department of Biological Sciences, the University of Memphis, Memphis, USA (D. McKenna);
CNC Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Canada (P. Bouchard);
MRAC Musée Royal de l'Afrique Centrale, Tervuren, Belgium (M. De Meyer);
NMW Naturhistorisches Museum, Wien, Austria (H. Schillhammer).

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Taxonomy

Paocryptorrhinus Voss, 1965

Type species. *Paocryptorrhinus obsitus* Voss, 1965: 361 fixed by original designation.

Diagnosis. Adult beetles of the genus *Paocryptorrhinus* are rather distinctive in their appearance and can be recognised relatively easily. The presence of postcoxal flanges on the prosternum (Figs 7I, J; Figs 9A–G) forming lateral walls along the canal for accommodating the rostrum in repose immediately separates *Paocryptorrhinus* from the majority of weevils not only in East Africa but also worldwide (except Molytinae: Aedemonini, a few Sophrorhinini and a few other stray genera). From the latter, *Paocryptorrhinus* can be recognized by having any two of the following three characters: (A.) eyes much reduced in size and seemingly consisting of a single, relatively large ommatidum (Fig. 9I) subequal in diameter to that of any funicular antennomere; (B.) the dorsal outline of the frons-to-rostrum junction in lateral view not forming an even curve, but marked by a depression (Fig. 3C), and (C.) elytra flattened, nearly parallel-sided most of their length (Figs 1A, C), and not shorter than 1.55 times their maximum width. Adults of two other weevil genera (*Ocladius* Schoenherr and *Isorhamphus* Faust) with a rostral canal were sifted together with *Paocryptorrhinus*. Those, however, have eyes with several ommatidia and vaulted elytra which are either rounded (*Ocladius*) or posteriorly tapered (*Isorhamphus*) in dorsal view.

Description. Integument uniformly dark-brown, often covered by waxy, white-brown coating obscuring colour and surface texture; standard length 2.31–3.96 mm; body notably elongate. Head capsule almost completely retracted into prothorax and not visible from above when rostrum in repose or directed ventrally. Eyes located lateroventrally, small, flat, seemingly consisting of single ommatidium not exceeding in diameter maximum diameter of scapus (Fig. 9I). Rostral attachment to head capsule abruptly constricted laterally (in dorsal view) to half rostral width (Fig. 9A) and gently depressed dorsally in lateral view (Fig. 9I). Rostrum in lateral view almost straight; in dorsal view almost parallel-sided and slightly and evenly constricted at middle. Antennal attachments in apical 30–40% of rostral length; funicle with seven antennomeres; compact club consisting of three antennomeres. Pronotum weakly to markedly constricted laterally in anterior quarter; widest at middle; prosternum with deep rostral canal delimited laterally by lamellae anterior and posterior to procoxae (Figs 9A–G). Pro- and mesofemora without ventral tooth; hind femur with or without. Tibiae mucronate (Fig. 9J). Elytra parallel-sided; elytron with 10 striae each marked by single line of setiferous punctures; striae 7 and 8 short, not reaching base (Fig. 9J) or apex of elytra. Hind wings absent. Metaventrite forming ventrally extended posterior wall of rostral canal (Fig. 9H); metepisternum and metaventrite fused without trace of metepisternal suture (Figs 7I–J, 9J); sclerolepidia absent (Fig. 9J). Male tergite 7 (Fig. 2I) without deep notch at posterior margin; sternite 8 (Fig. 2K) entire, not separated into hemisternites. Aedeagus weakly sclerotized, dorsally membranous; endophallus with weak sclerotization (Figs 2E–G).

Biology and distribution. All known *Paocryptorrhinus* specimens were collected by sifting wet leaf litter on the floor of wet primary Afrotropical forests. Host plants and larvae of this genus are unknown, together with all other more specific biological characteristics of these cryptic and rarely encountered beetles. The known distribution of *Paocryptorrhinus* is relatively small and limited to 12 localities in northeastern Tanzania (Fig. 11) at altitudes between 288 and 2700 meters.

Key to species of *Paocryptorrhinus*

1. Elytral stria 1 or 2 subequal in width to any of striae 4, 5 or 6 (Figs 1A, C; 6A, C); prosternum with postcoxal flanges smaller, postcoxal section of rostral canal half as deep as anterior section (Fig. 9A, B); pronotum with fine and numerous punctures (Figs 1A,C, 2A,C ……..... 2
– Elytral stria 1 or 2 markedly narrower than any of striae 4, 5 or 6 (Fig. 3A); prosternum with postcoxal flanges greater, post- and antecoxal sections of rostral canal subequal in depth (Fig. 9C–G); pronotum with large and relatively few punctures (Figs 3A, C, 4A,C, 7A, C) …… 3

2. Smaller, body length 2.31–3.05 mm (Figs 1A–D; 2) …… ***P. hustachei* comb. n.**
– Greater, body length 3.75–3.92 mm (Fig. 6) …….. ***P. hanangensis* sp. n.**

3 Ridges on interstriae 2, 4 and 6 markedly higher and longer than those on interstriae 1, 3, 5 (Figs 3, 4A–D); lateral outline of elytra in dorsal view formed by raised ridge on interstria 6 (Figs 3A, 4A) …….. 4
– Ridges on interstriae 1 to 6 subequal in height and length (Fig. 5); lateral outline of elytra in dorsal view formed by raised ridge on interstria 5 (Figs 5A, 7A, 8A) ……... 5

4 Elytral intervals 3 and 5 without raised ridges …….. ***P. atropos* sp. n.** (North Pare)
– Elytral intervals 3 and 5 with raised ridges in posterior half …… ***P. atropos* sp. n.** (South Pare)

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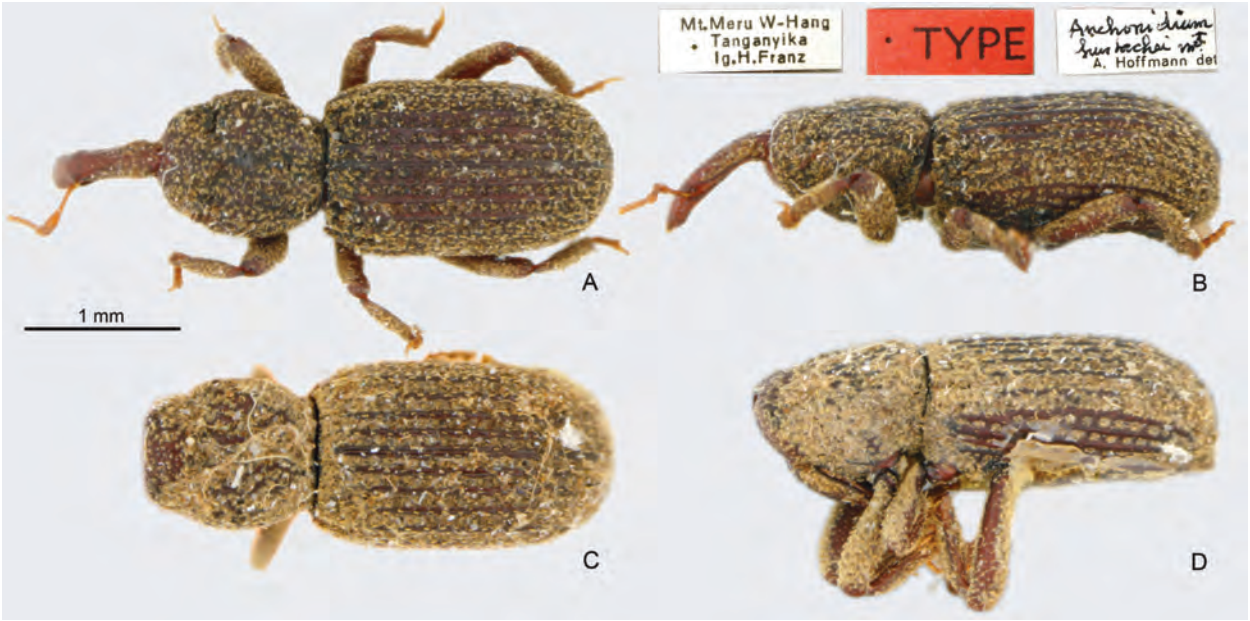

Fig. 1. *Paocryptorrhinus hustachei* comb. n., A–B: holotype of *hustachei*, unsexed, with three original labels; C–D: paratype of *obsitus*, unsexed.

5 Hind femur with large ventral tooth (Fig. 5C) …… ***P. clotho* sp. n.**
– Hind femur without ventral tooth …….. 6

6 Combined maximal width of elytral striae 4 and 5 subequal to that of striae 1 to 3 (Fig. 8A, C) …… ***Paocryptorrhinus* sp.** #3081
– Combined maximal width of elytral striae 4 and 5 not more than 80% of that of striae 1 to 3 (Fig. 7A, C) ……. ***P. lachesis* sp. n.**

***Paocryptorrhinus hustachei* (Hoffmann, 1965) comb. n.**
Figs 1, 2, 9A, I, J

Anchonidium hustachei Hoffmann, 1965: 397–398.

Type locality. Tanganyika, Mount Meru [Tanzania].

Type specimens. HT (Figs 1A–B) stated as male, not dissected (NMW): "Mt. Meru W-Hang Tanganyika lg. H. Franz [p] \ TYPE [p] [red label] \ Anchonidium hustachei m. [male sign] [h] A. Hoffmann det [p]". 2 PT (NMW): not studied (see Remarks on the status of a specimen labelled as PT). Described from three specimens.

Paocryptorrhinus obsitus Voss, 1965: 361–362, Abb. 7, syn. n.

Type locality. Mt. Kilimanjaro, Versant Est, 2700 m, for. mont., humus [Tanzania].

Type specimens. HT (MRAC): not studied. 1 PT (MRAC) (Figs 1C–D): "PARATYPUS [p] [red label] \ étrépage sous Hagenia [p] [blue label] \ I.R.S.A.C. - MUS. CONGO Kilimanjaro, Marangu 2400 m. 20–II–1956 J. et N. Leleup [p] \ R. DET. 7680 [p] A. [h]"; 1 PT (MRAC): "PARATYPUS [p] [red label] \ forêt mont., humus [p] [blue label] \ COLL. MUS. CONGO Tanganyika Terr. Mt. Meru, Olkokola, versant N.O. 2600 m. 8–VII–1957 [p] \ R. DET. 7680 [p] A. [h]"; 1 PT (MRAC): "PARATYPUS [p] [red label] \ étrépage sous forêt claire [p] [blue label] \ COLL. MUS. CONGO Tanganyika Terr. Mt. Meru, Olkokola, versant N.O. 2500 m. 8–VII–1957 [p] \ R. DET. 7680 [p] A. [h]"; all three paratypes have additional label: "Mission Zoolog. I.R.S.A.C. en Afrique orientale (P. Basilewsky et N. Leleup) [p]". Described from 13 specimens.

Diagnosis. This species is recognized by the uniformly shaped six striae and interstria on the elytral disk in combination with its relatively small body length (not greater than 3.05 mm).

Description. Holotype, unsexed specimen (Figs 1A–B). Not sequenced for DNA barcode. Length: 2.94 mm. Smaller prosternal postcoxal flanges forming rostral canal twice shallower than that anterior of procoxae; raised elytral interstriae 1 to 6 reaching elytral base, subequal in height; lateral elytral outline in dorsal view formed by ridge on interstria 6; elytral striae 4 and 5 not markedly wider than others; hind femur without ventral tooth.

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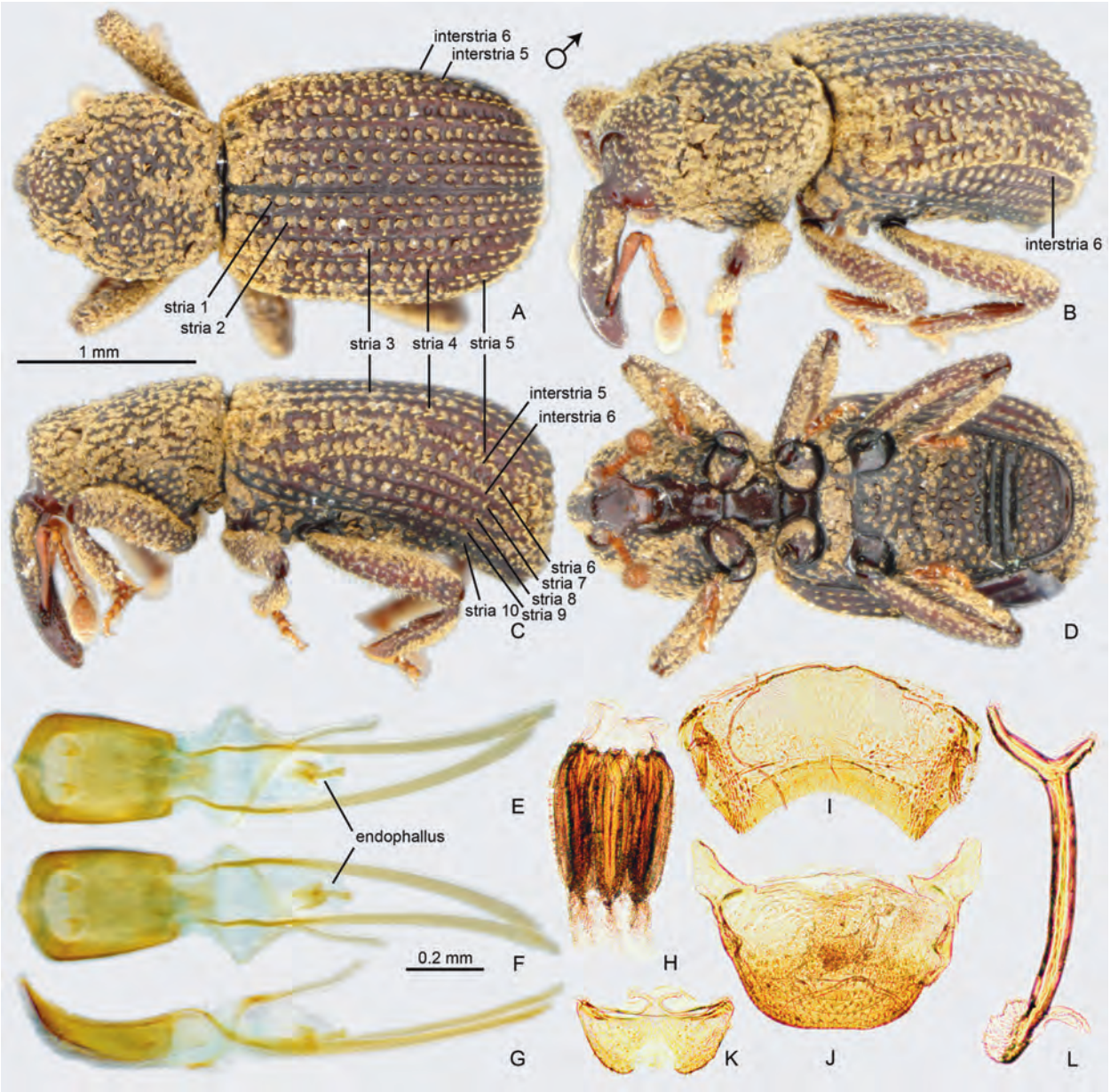

Fig. 2. *Paocryptorrhinus hustachei* comb. n., #4893 from Mt. Kilimanjaro, male. A–D: habitus; E–G: aedeagus & tegmen, dorsal (E), ventral (F) and lateral (G); H: proventriculus; I: tergite 7; J: tergite 8; K: sternite 8; L: sternite 9.

Intraspecific variation. GenBank accessions: KJ841713, KJ841717, KJ841719, KJ841722–KJ841724, KJ841728. Length: 2.31–3.05 mm.

Additional material examined. 12 exx in total. 5 exx (NMW): 1 ex, "Mt. Monduli Tanganyika lg. H. Franz [p] \ PARATYPE [p] [rad label] / Anchonidium hustachei m. [male sign] [h] A. Hoffmann det [p]"; 4 exx, "Gebirgswald oc. Marangu lg. H. Franz [p] \ Kilimanjaro Tanganyika [p]". 7 exx (CNC): 1 ex, #4801 "TANZANIA, Mt. Kilimanjaro, Marangu route, S3.18424° E37.51344°, 2668 m, 25.xi.2012, sift01, V. Grebennikov"; 2 exx, #4844, #4845 "TANZANIA, Mt. Kilimanjaro, Marangu route, S3.21470° E37.51822°, 2198 m, 28.xi.2012, sift05, V. Grebennikov"; 1 ex, #4864, "TANZANIA, Mt. Kilimanjaro, Marangu route, S3.20141° E37.51903°, 2370m, 6.xii.2012, sift09, V. Grebennikov"; 2 exx, #4869, #4870 "TANZANIA, Mt. Kilimanjaro, Machame route, S3.14954° E37.24532°, 2124 m, 7.xii.2012, sift11, V. Grebennikov"; 1 ex, #4893 "TANZANIA, Mt. Kilimanjaro, Umbwe route, S3.16197° E37.28464°, 1993 m, 8.xii.2012, sift13, V. Grebennikov".

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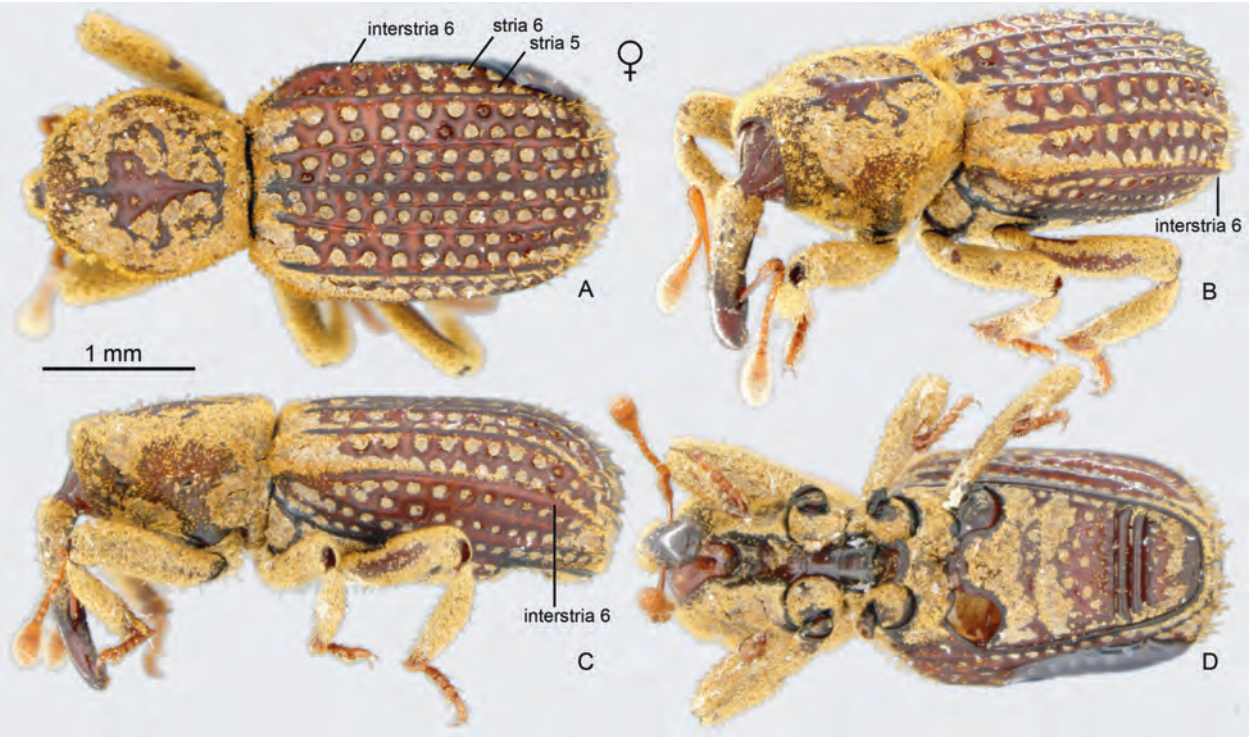

Fig. 3. *Paocryptorrhinus atropos* sp. n., #7271 from North Pare, female. A–D: habitus.

Distribution. This species is known from five isolated wet forests on volcanic mountains of the geologically young NKVB (Fig. 11) in northeastern Tanzania. Elevation: 1993–2700 m.

Remarks. The type specimens of both nominal historical names pertaining to *P. hustachei* are similar to each other (Fig. 1), while their type localities are about 60–70 km apart (Fig. 11). Each name was proposed by two authors, respectively, unaware of each other and published a month apart. These considerations suggest that both species names are subjective synonymous. Hoffmann's (1965) paper came out in the issue of the journal published on May 26, 1965 (endleaf), while the volume containing Voss (1965) paper was printed in June 1965 (verso of title page). Consequently, the name introduced by Hoffman is a senior subjective synonym of Voss' name.

Hoffmann (1965: 398) stated that he had studied three *hustachei* specimens: two males from Mount Meru (one of them designated by him as the "type" (=holotype, ICZN Article 73.1.1, Figs 1A–B) and a female from Machame, Mount Kilimanjaro. The series of this species received on loan from NMW contained six conspecific specimens all collected by Herbert Franz, two of them with red labels "TYPE" and "PARATYPE", respectively. The former specimen from Mount Meru is considered herein as the holotype (Figs 1A–B). The latter is labeled as originating from Mount Monduli (Fig. 11), which is a separate, thinly forested and much smaller volcanic cone about 30 km West of Mount Meru, which itself is situated 60–70 km West of Mount Kilimanjaro (Fig. 11). The specimen with the paratype label does not agree geographically with any of the two paratypes mentioned in the original description and, therefore, its paratype status is refuted.

***Paocryptorrhinus atropos* sp. n.**
Figs 3, 4, 9C, D, H

Diagnosis. This species is recognized by the unique arrangement of elytral interstriae, of which 1, 3 and 5 are absent in at least the basal half of the elytra, while interstriae 2, 4 and 6 are markedly enlarged along their entire length.

Description. Holotype, male, (Fig. 5). GenBank accession: KJ841721. Length: 4.29 mm. Greater prosternal postcoxal flanges forming rostral canal subequal in depth to that anterior of procoxae; elytral interstriae 1, 3 and 5 without raised ridged entirely (Figs 3A–C, North Pare population) or in anterior half only (Figs 4A–C, South Pare population); raised ridges on interstriae 2, 4 and 6 markedly enlarged; lateral elytral outline in dorsal view formed by ridge on interstria 6; elytral striae 4 and 5 not markedly wider than others; hind femora without ventral tooth.

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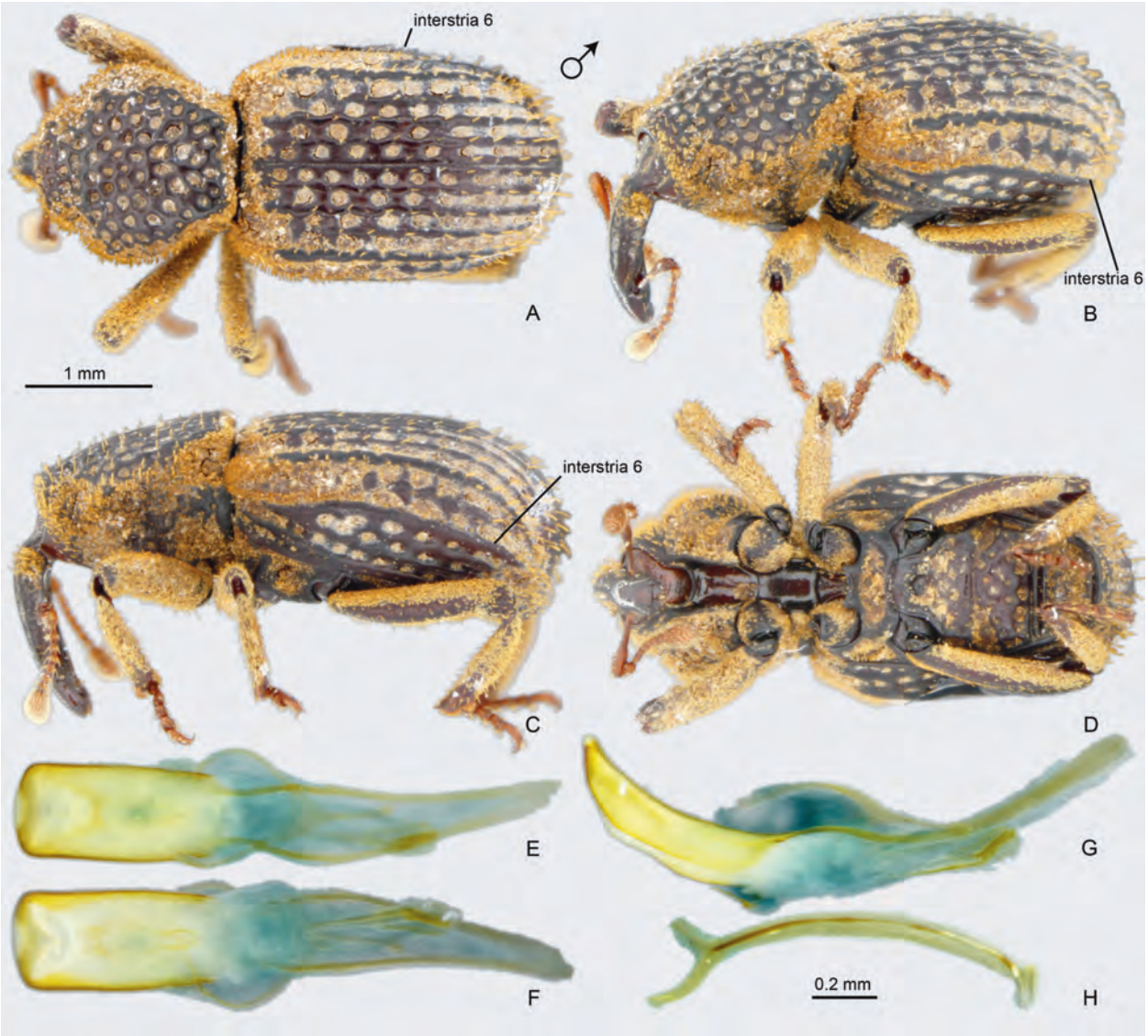

Fig. 4. *Paocryptorrhinus atropos* sp. n., holotype, #5438 from South Pare, male. A–D: habitus; E–G: aedeagus and tegmen, dorsal (E), ventral (F) and lateral (G); H: sternite 9.

Intraspecific variation. GenBank accession: KJ841718. Length: 3.73–4.34 mm.

Material examined. HT (Fig. 4) male (CNC): #5488 (= #5439), "TANZANIA, South Pare Mts., Chome For., S4.27145° E37.92347°, 2072m, 4.i.2013, sift40, V.Grebennikov". PT (CNC, BSUM): 1 ex, #5436 (=#5467), same data as the holotype; 3 exx, #5231 (= #7270, = #7271), #5232 (= #7272, = #7273) and one not numbered, "TANZANIA, North Pare Mts., Kindoroko For., S3.74313° E37.65022°, 1987m, 23.xii.2012, sift25, V.Grebennikov".

Distribution. This species is known from both South and North Pares in northeastern Tanzania. Elevation: 1987–2072 m.

Etymology. The species epithet is the Latinized Greek mythical name of Atropos, one of three Morai (= Fates), who cut the thread of life; noun in apposition.

Remarks. Three attempts to amplify DNA from each of two North Pare specimens failed (hence three unique identifiers on each specimen) and, therefore, they are not represented on the phylogenetic tree (Fig. 10).

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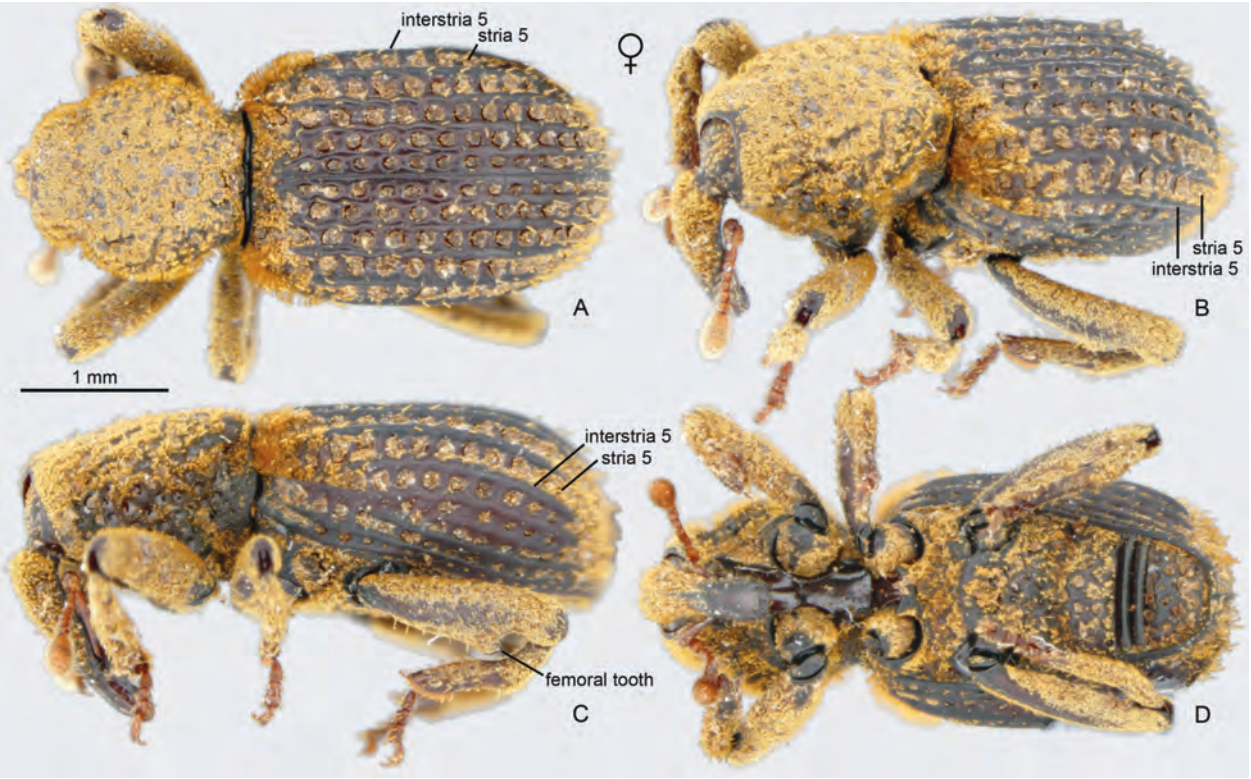

Fig. 5. *Paocryptorrhinus clotho* sp. n., holotype, #5476 from West Usambara, female. A–D: habitus.

***Paocryptorrhinus clotho* sp. n.**
Figs 5, 9E

Diagnosis. This species is unique by having a markedly developed ventral tooth on each hind femur (Fig. 5C).

Description. Holotype, female (Figs 5, 9E). GenBank accession: KJ841727. Length: 4.13 mm. Greater prosternal postcoxal flanges forming rostral canal subequal in depth to that anterior of procoxae; raised elytral interstriae 1 to 6 reaching elytral base, subequal in height; lateral elytral outline in dorsal view formed by ridge on interstria 5; elytral striae 4 and 5 not markedly wider than others; hind femur with ventral tooth (Fig. 5C).

Intraspecific variation. GenBank accessions: KJ841712, KJ841716. Length: 3.68–4.13 mm.

Material examined. HT (Figs 5, 9E) female (CNC): #5476, "TANZANIA, W. Usambara Mts., Mazumbai For., S4.81054° E38.49858°, 1618m, 11.i.2013, sift43, V.Grebennikov". PT (CNC): 1 ex, #5477, same data as the holotype; 1 female, #5478, "TANZANIA, W. Usambara Mts., Mazumbai For., S4.82634° E38.49690°, 1860m, 12.i.2013, sift46, V.Grebennikov".

Distribution. This species is known only from the Mazumbai forest in West Usambara, northeastern Tanzania. Elevation: 1618–1680 m.

Etymology. The species epithet is the Latinized Greek mythical name of Clotho, one of three Morai (= Fates), who spun the thread of life; noun in apposition.

***Paocryptorrhinus hanangensis* sp. n.**
Figs 6, 9B

Diagnosis. This species is recognized by the uniformly shaped six elytral discal striae and interstria, in combination with its relatively greater body length (not smaller than 3.75 mm).

Description. Holotype, female (Figs 6, 9B). GenBank accession: KJ841725. Length: 3.75 mm. Smaller prosternal postcoxal flanges forming rostral canal twice shallower than that anterior of procoxae; raised elytral interstriae 1 to 6 reaching elytral base, subequal in height; lateral elytral outline in dorsal view formed by ridge on interstria 6; elytral striae 4 and 5 not markedly wider than others; hind femur without ventral tooth.

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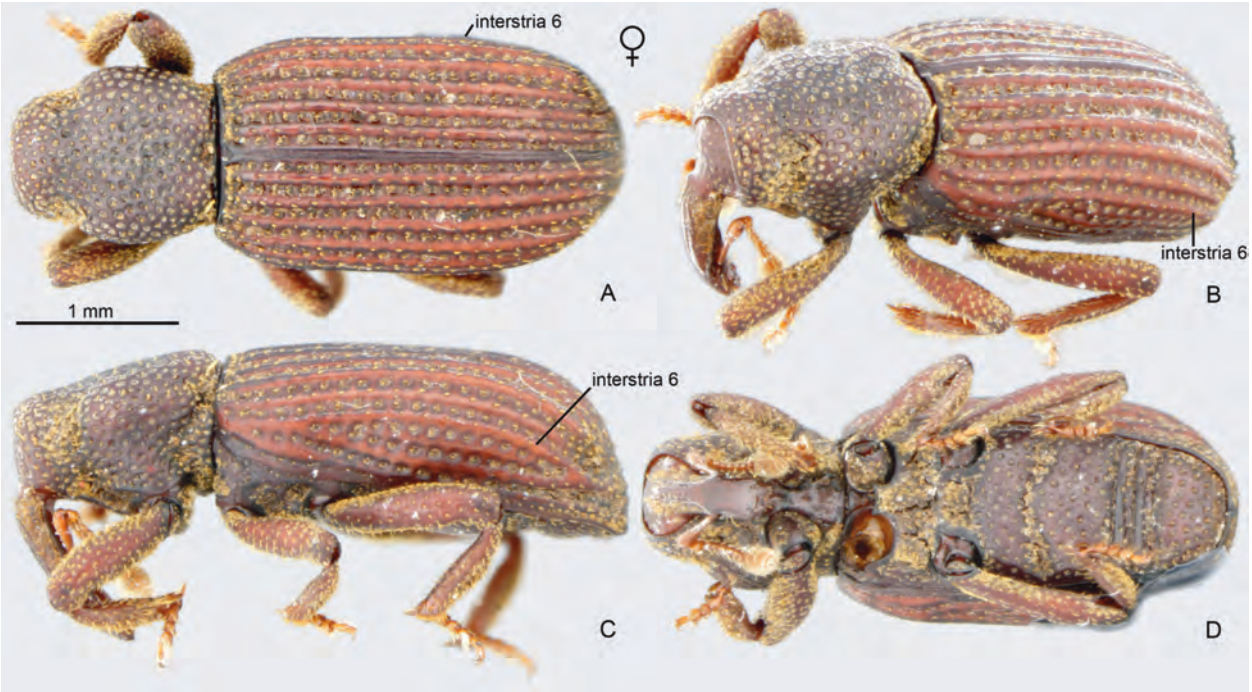

Fig. 6. *Paocryptorrhinus hanangensis* sp. n., holotype, #5086 from Mt. Hanang, female. A–D: habitus.

Intraspecific variation. GenBank accessions: KJ841720. Length: 3.75–3.92 mm.

Material examined. HT (Figs 6, 9B) female (CNC): #5086, "TANZANIA, Mt. Hanang, NE slope, S4.41621° E35.40281°, 2652m, 13.xii.2012, sift15, V.Grebennikov". PT (CNC): 1 female, #5147 (=#5148) "TANZANIA, Mt. Hanang, NE slope, S4.43077° E35.41593°, 2283m, 15.xii.2012, sift20, V.Grebennikov".

Distribution. This species is known only from Mount Hanang, northeastern Tanzania. Elevation: 2283–2652 m.

Etymology. The species epithet is an adjective derived from the name of its type locality, Mount Hanang in northeastern Tanzania.

***Paocryptorrhinus lachesis* sp. n.**
Figs 7, 9F.

Diagnosis. This species is most easily recognized by the deep and abrupt lateral constriction of the pronotum in the anterior quarter (Fig. 7A).

Description. Holotype, male (Fig. 7, 9F). GenBank accession: KJ841715. Length: 3.96 mm. Greater prosternal postcoxal flanges forming rostral canal subequal in depth to that anterior of procoxae; raised elytral interstriae 1 to 6 reaching elytral base, subequal in height; lateral elytral outline in dorsal view formed by ridge on interstria 5; elytral striae 4 and 5 not markedly wider than others; hind femur without ventral tooth.

Material examined. HT (Fig. 7) male (CNC): #3603, "TANZANIA, Kimboza forest, 7°01'20"S 37°48'13"E, 8.i.2012, 288m, sift.24, V.Grebennikov".

Distribution. This species is known only from the holotype found in the Kimboza forest. Elevation: 288 m.

Etymology. The species epithet is the Latinized Greek mythical name of Lachesis, one of three Morai (=Fates), who measured the thread of life; noun in apposition.

Remarks. External morphological peculiarity of the single known male specimen (Figs 7, 9F), along with its distinct DNA sequence (though relatively short and consisting of only 407 nt) and a large geographical gap separating it from the rest of the genus (Fig. 11) triggered its recognition as a formally named species (unlike *Paocryptorrhinus* sp. #3081; see below).

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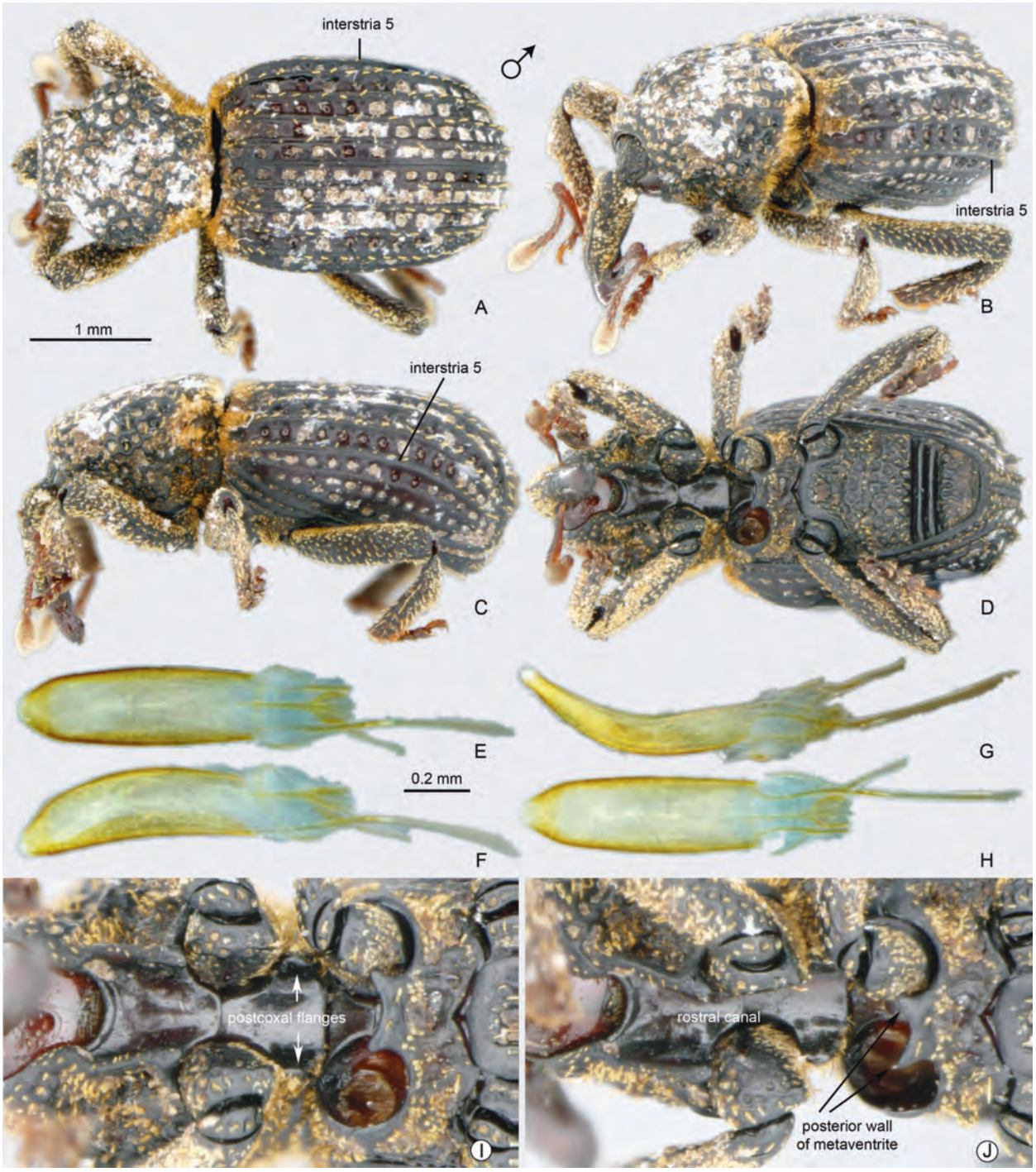

Fig. 7. *Paocryptorrhinus lachesis* sp. n., holotype, #3603 from Kimboza forest, male. A–D: habitus; E–H: aedeagus and tegmen, dorsal (E), ventro-lateral (F), lateral (G) and ventral (H); I–J: prosternum, meso- and metaventrum showing rostral canal, ventral (I) and latero-ventral (J).

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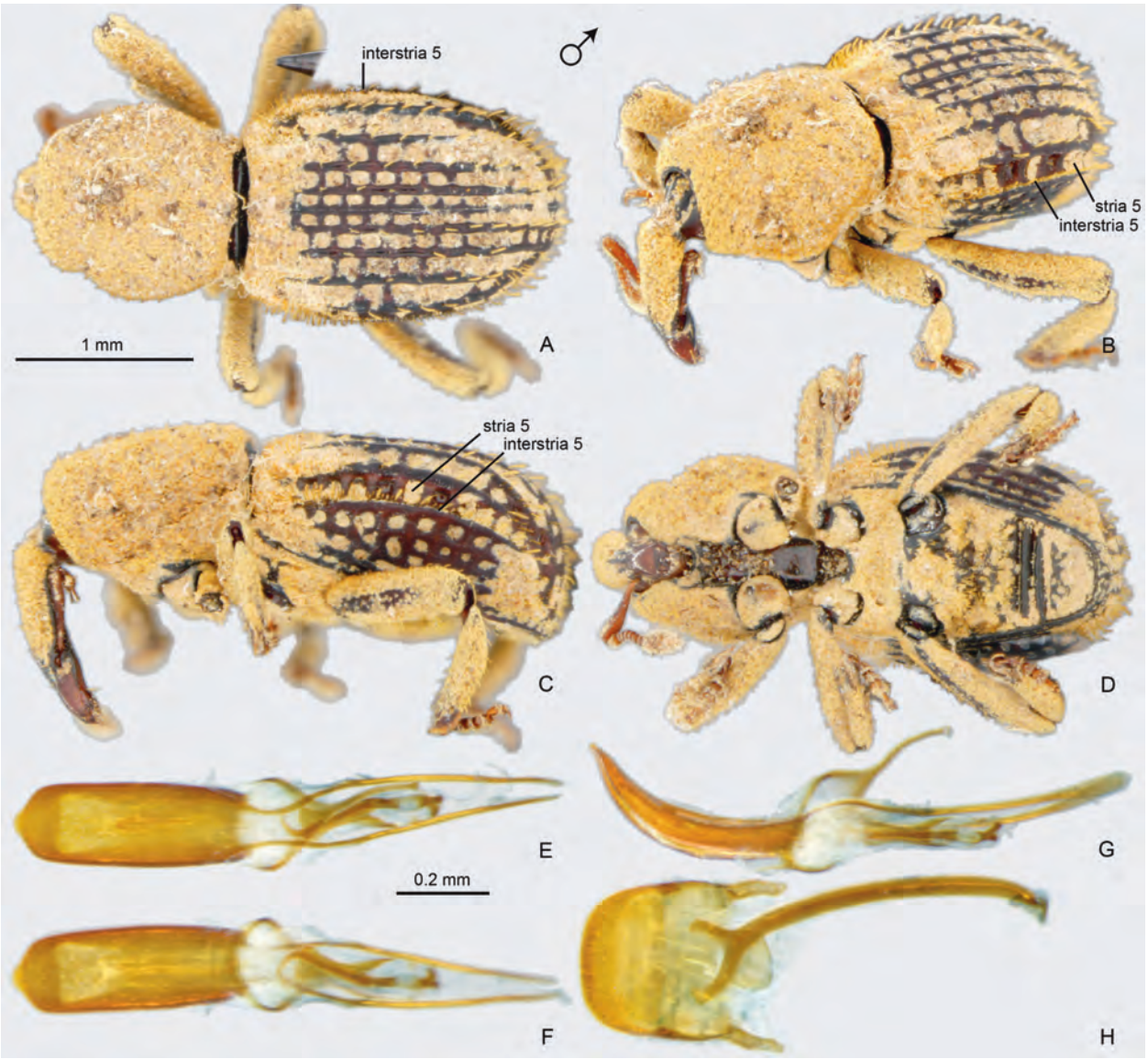

Fig. 8. *Paocryptorrhinus* sp. #3801, #3801 from East Usambara, male. A–D: habitus; E–G: aedeagus and tegmen, dorsal (E), ventral (F), lateral (G); H: tergite 8 and sternite 9, ventral.

***Paocryptorrhinus* sp. #3081**
Figs 8, 9G

Diagnosis. This species is unique by having markedly widened elytral striae 4 and 5 (Fig. 8C).

Description. Male (Fig. 8, 9G). GenBank accession: KJ672257. Length: 3.10 mm. Greater prosternal postcoxal flanges forming rostral canal subequal in depth to that anterior of procoxae; raised elytral interstriae 1 to 6 reaching elytral base, subequal in height; lateral elytral outline in dorsal view formed by ridge on interstria 5; elytral striae 4 and 5 markedly wider than others; hind femur without ventral tooth.

Material examined. Male (CNC): #3081, "TANZANIA, E Usambara Mts., Amani NR, 5°05'56"S 38°37'18"E, 16.xii.2011, 970m, sift.07, V.Grebennikov".

Distribution. This species is known from a single specimen found in East Usambara, northeastern Tanzania. Elevation: 970 m.

Remarks. Unlike *P. lachesis* sp. n. also known from a male singleton, this potentially new species is consciously left unnamed, mainly due to uncertainties suggested by its geographical proximity to the majority of other species of *Paocryptorrhinus*.

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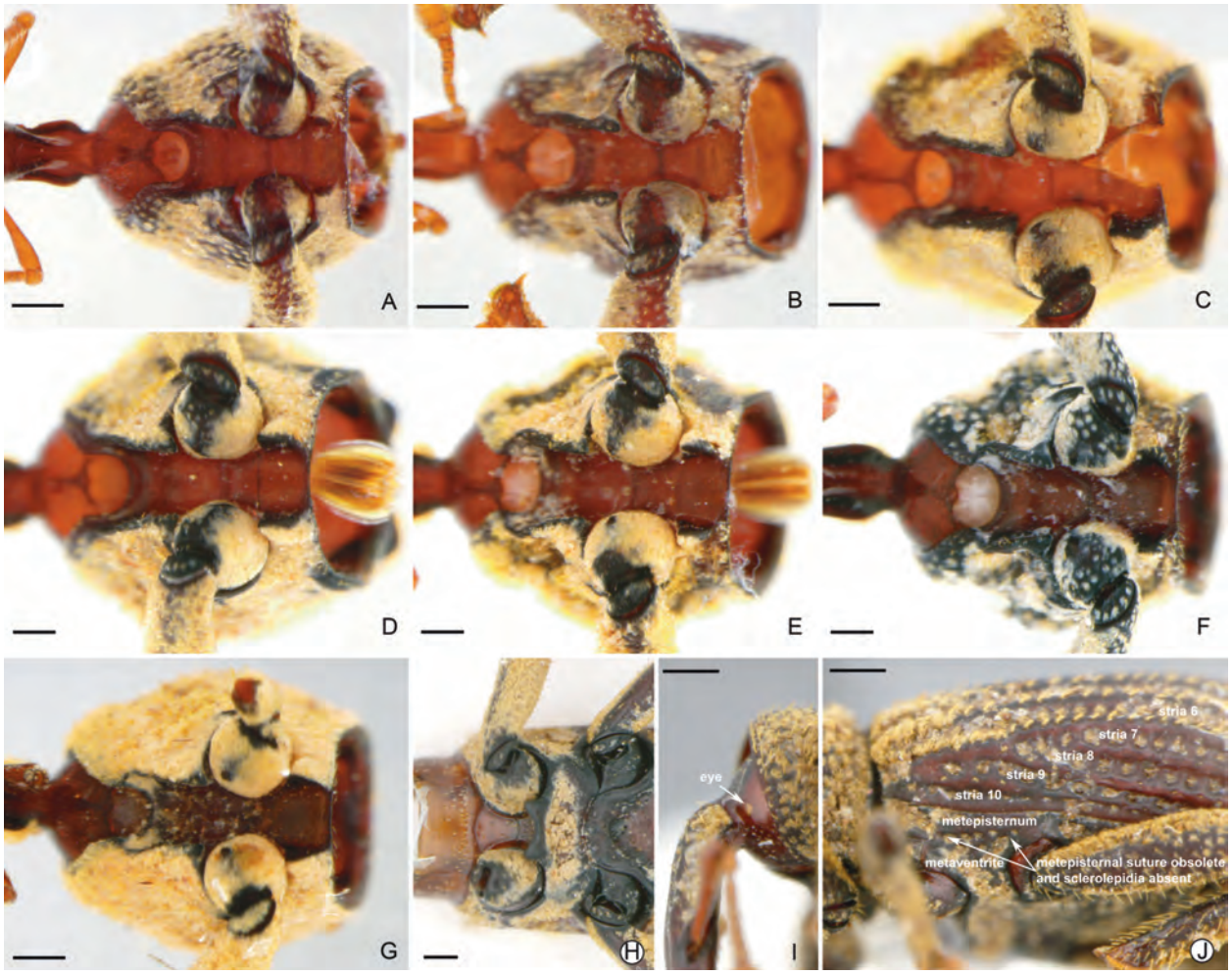

Fig. 9. *Paocryptorrhinus* spp., ventral view. (A–G): prothorax in ventral view showing prosternal canal and variously developed postcoxal flanges forming its lateral walls; (H): meso- and metaventrum with two basal abdominal ventrites in ventral view showing rostral canal and its posterior vertical wall formed by metaventrum; (I): head in left lateral view showing small eye; (J): left elytron and left metathorax showing lack of metepisternal suture and sclerolepidia. (A): *P. hustachei* comb. n., #4893 from Mt. Kilimanjaro, male; (B): *P. hanangensis* sp. n., #5086 from Mt. Hanang, female; (C): *P. atropos* sp. n., #7271 from North Pare, female; (D, H): *P. atropos* sp. n., holotype, #5438 from South Pare, male; (E): *P. clotho* sp. n., #5476 from West Usambara, female; (F) *P. lachesis* sp. n., holotype, #3603 from Kimboza Forest, male; (G): *Paocryptorrhinus* sp. #3081, #3081 from East Usambara, male; (I, J): *P. hustachei*, #4801 from Mt. Kilimanjaro, unsexed. Scale: 0.2 mm.

Results of DNA analyses

The model search in MEGA6 detected the generalized time-reversible model with gamma distributed rate heterogeneity and inferred proportion of invariable sites (GTR+G+I) as the best fit. The best ML tree (not shown and with *Paocryptorrhinus* branching pattern identical to that in Fig. 10) had the highest log likelihood of –7223.19. The representatives of *Paocryptorrhinus* were not monophyletic being separated in two clades, *P. hustachei* comb. n. plus *P. hanangensis* sp. n. versus all other species, respectively (as in Fig. 10). The BEAST analysis (Fig. 10) recovered a topology identical to that of the ML analysis, although the exact placement of both ingroup clades among the members of the extended outgroup was different. The time tree hypothesis from BEAST revealed for the *Paocryptorrhinus* evolution an interval from 14.16 MY to present (Fig. 10).

Discussion

While the present report greatly increases the amount of information available on *Paocryptorrhinus* weevils, all attempts to interpret the results are still much hindered by the acute shortage of data and concomitant phylogenetic resolution. The results, therefore, should be taken with caution.

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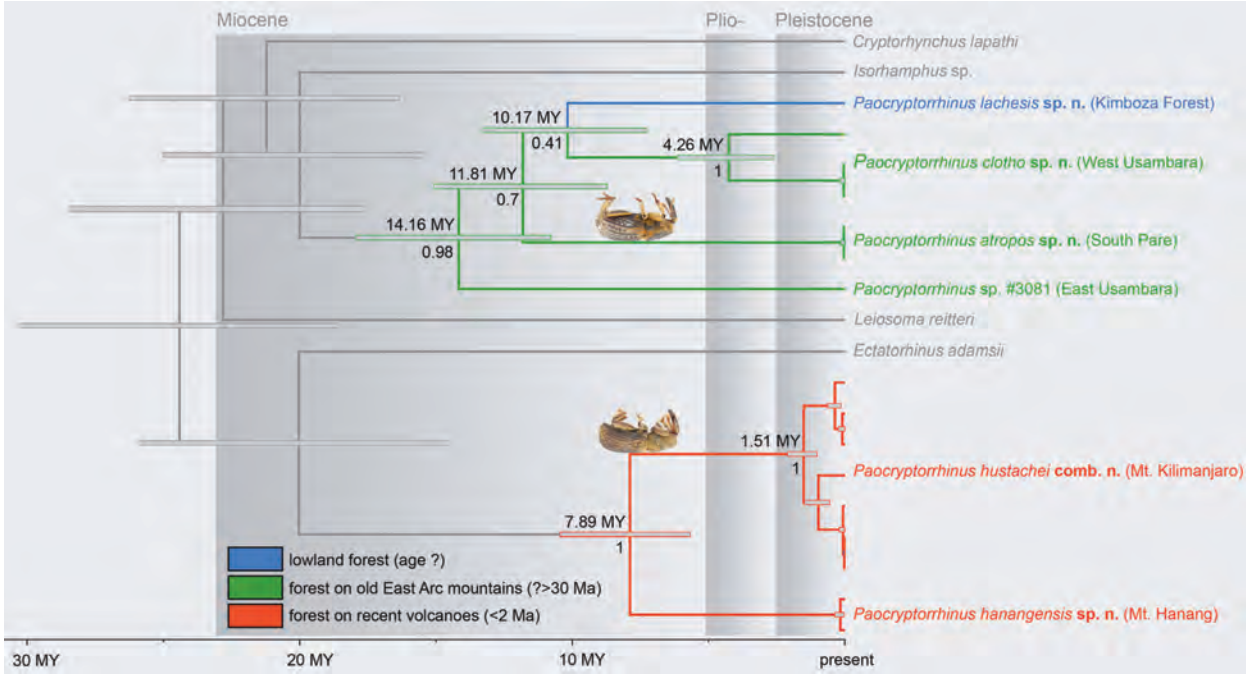

Fig. 10. Relevant part of an ultrametric time tree of *Paocryptorrhinus* obtained by using BEAST software calibrated at a rate 0.018 substitutions/site/MY. Note that the genus was not recovered as monophyletic. Values above nodes and on scale below are million years before present (MY); values below nodes are bootstrap support for identical clades recovered in ML analysis. Node bars represent 95% confidence interval of the age estimate.

Monophyly of *Paocryptorrhinus*

Even though monophyly of *Paocryptorrhinus* was rejected in both DNA analyses (Fig. 10), the genus is likely monophyletic. This assumption is based on three independent sources of evidence. The seemingly strongest support comes from rather uniform adult morphological characters: the similar unique arrangement of sclerites forming the rostral canal (Figs 7A–B, 9A–H) potentially represents a complex synapomorphy. The small adult eyes formed by a seemingly single and relatively flat ommatidium might be another synapomorphy. The deep retraction of the head capsule into pronotum (Fig. 1), lateral constriction of the pronotum in apical fourth, and the peculiar sclerotization of the endophallus (Fig. 2E) might be other synapomorphies. Thus, a broadly designed morphology-based phylogenetic analysis, presently outside of the scope of this study, has the potential of recovering the genus as a monophyletic clade. Such a hypothesis could be coherent with two other lines of evidence: (a) the similar biological preferences (=inhabitants of wet leaf litter in primary forests), and (b) the restricted distribution of the genus, with all species limited to northeastern Tanzania (Fig. 11).

Phylogenetic position of *Paocryptorrhinus*

The sister group of *Paocryptorrhinus* and its phylogenetic position among other weevils are presently entirely unknown. The genus was described as a member of "Notarini" and was retained there ever since (although under a different tribe name of Brachycerinae: Erirhinini; see Alonso-Zarazaga & Lyal 1999). This assignment is rather an historical artefact than an evidence-based hypothesis. When described by Voss, *Paocryptorrhinus* was only compared with the genus *Pachytychius* Jekel, which then was kept in Brachycerinae: Erirhinini. The latter genus, however, was transferred from Erirhinini to Curculioninae, and retained either in Storeini (Alonso-Zarazaga & Lyal 1999) or *incertae sedis* (Caldara et al. 2014). Consequently, the original assignment of *Paocryptorrhinus* to Erirhinini via its similarity with *Pachytychius* was the only reason why the former remained in Brachycerinae: Erirhinini (although with some reservations; see Oberprieler 2014).

The current assignment of *Paocryptorrhinus* to Erirhinini is not corroborated in the present analysis (Fig. 10), since *Paocryptorrhinus* did not form a clade with *Notaris*, the latter being the type genus of Erirhinini. This is not surprising, since adults of *Paocryptorrhinus* neither display the pedotectal-type of male genitalia characteristic

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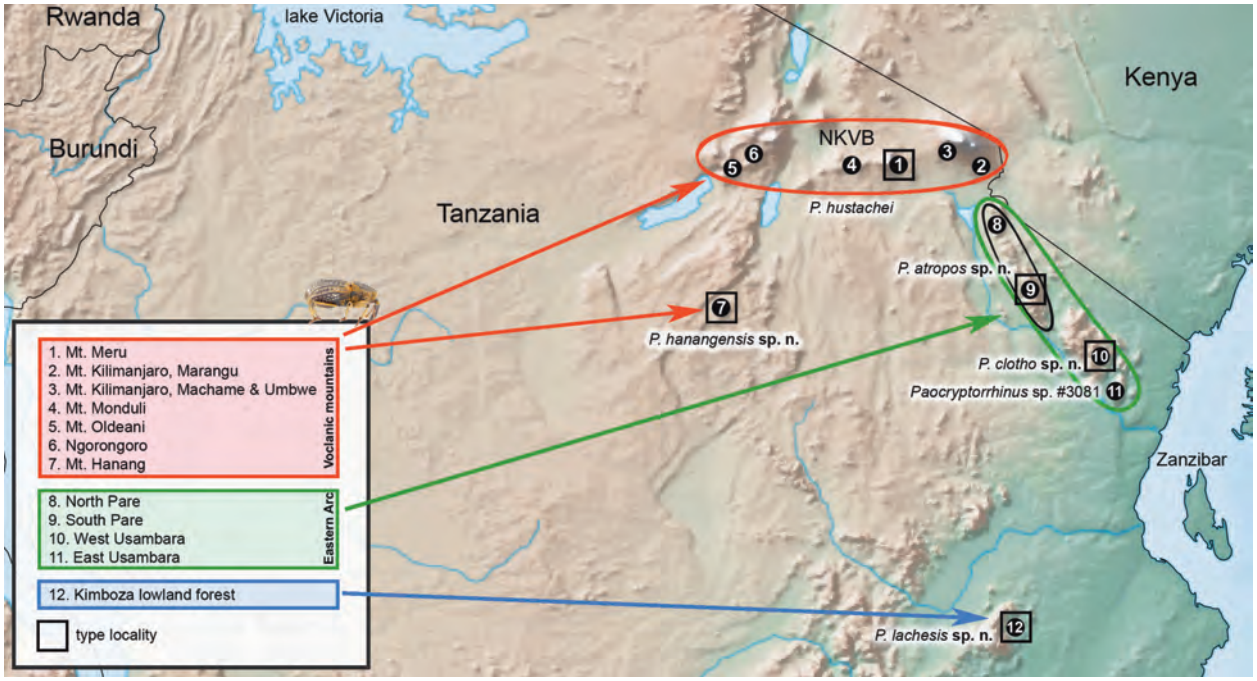

Fig. 11. Known distribution of *Paocryptorrhinus* weevils. NKVB: Ngorongoro-Kilimanjaro Volcanic Belt.

to *Notaris* and most Brachycerinae, nor do they have a lateral setiferous groove on either side of the rostral apex characteristic for most of Erirhinini (Oberprieler 2014, Figs 3.7.1.2D–G). The presence of prosternal postcoxal flanges forming lateral walls of the rostral canal seemingly suggests affinities to Molytinae: Aedemonini, a group of 35 genera from most of the warm and temperate regions of the World (except Europe, New Zealand and both Americas; Lyal 2014). Unlike adults of Aedemonini, those of *Paocryptorrhinus* have a rostral canal with a markedly developed transverse posterior metaventral wall (Figs 7I, J) and the posterior margin of the male tergite 7 is only weakly emarginated (Fig. 2I). Alternative states of these two characters were suggested as synapomorphies for Aedemonini (Lyal 2014) and, therefore, this tribe cannot accommodate *Paocryptorrhinus*. Any attempt to place the genus in the relatively weakly understood phylogenetic framework of weevils is at present doomed by the lack of adequate data and pre-existing hypotheses. With all this in mind, the most rational temporal action is the herein proposed transfer of the genus from Brachycerinae: Erirhininae to Molytinae *incertae sedis*.

Phylogeography of *Paocryptorrhinus*

Adults of *Paocryptorrhinus* are most likely low-dispersing and humidity-dependant, specialized litter inhabitants, as suggested by sampling circumstances, flightlessness, and eye reduction. As presently known, all species of *Paocryptorrhinus* are strictly allopatric (Fig. 11) and all are found within a coherent geographical area in northeastern Tanzania (Fig. 11). These observations appear to favour the simplified model of vicariant speciation for low-dispersing habitat-dependent organisms (but see below on *P. hustachei* comb. n. and *P. hanangensis* sp. n.). Remarkably, the genus *Paocryptorrhinus* has not been detected by us in other seemingly suitable and similarly extensively sampled parts of the Eastern Arc Mountains in Tanzania, such as Nguru, Kaguru, Rubeho, Udzungwa and Uluguru. The lack of *Paocryptorrhinus* records from Uluguru is particularly puzzling, since the forest edge is only 10 km west of the minute (about 3 km square) Kimboza forest, the type locality of *P. lachesis* sp. n.

Among all species, *P. hustachei* comb. n. has the largest known distribution on forested slopes of five volcanic mountains forming a nearly straight latitudinal chain some 220 km long: Mt. Kilimanjaro, Mt. Meru, Mt. Mulundi, Mt. Oldeani and the adjoining Ngorongoro highlands (NKVB, Fig. 11). Only Mt. Kilimanjaro specimens from two localities (Fig. 11) were available for DNA analysis (Fig. 10), while morphological similarity was the main criterion to group all specimens into a single species, including those not barcoded. A similar approach was used with morphologically homogenous *P. atropos* sp. n. known from North and South Pare mountains, but only the latter locality was represented on the DNA-based topology. The ancient lowland or Eastern Arc Mountains in Tanzania were long believed to harbour numerous ancient moisture-dependent low-dispersal animals (Tolley et al. 2011 and references therein), such as *Paocryptorrhinus* weevils. The presence of two species in the geologically young forests on volcanic cones (Fig. 11) is, therefore, a remark-

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able result strongly implying their relatively recent colonization. The same species grouping (i.e. those from old versus young forests), is upheld with the ML and Bayesian phylogenetic trees (Fig. 10), and morphologically (see the first couplet of the key). Only a few other similarly habitat-dependent and locally abundant radiations such as horned chameleons (Ceccarelli et al. 2014), brevicipitid frogs (Loader et al. 2014) or bush crickets (Hemp et al. 2014 and references therein) were studied in sufficient detail and to evaluate distributional patterns, which were found to be similar to that reported for *Paocryptorrhinus*.

Equally remarkable is the fact that the split between both species inhabiting young forests on volcanic highlands is dated at 7.89 MY (Fig. 10). This is about four times older than the origin of these mountains and, subsequently, predates the origin of the wet forest habitat suitable for these beetles. The last observation strongly suggests that (A.) separation between *P. hustachei* comb. n. and *P. hanangensis* sp. n. is not attributable to their currently observed allopatry (Fig. 11) and that (B.) the most recent common ancestor of each of these two species had means to colonize both localities across presently unsuitable dry savannah landscapes. A similar phenomenon was hypothesized for a radiation of flightless *Galapaganus* Lanteri endemic to, and markedly older than, the Galápagos Islands (Sequeira et al. 2000).

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