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Abstract. Adults of three known species of *Ochodaeus* Dejean (Coleoptera: Scarabaeoidea: Ochodaeidae) in Madagascar have a strongly granulate pronotum. Three new species are described herein that have a smooth or weakly granulate pronotum: *Ochodaeus modopunctatus*, *O. polypollicatus*, and *O. meandrus*. A key to the species of *Ochodaeus* from Madagascar is provided.

Key words. Taxonomy, scarab, Africa, Madagascar.

Introduction

The subfamily Ochodaeinae (Coleoptera: Scarabaeoidea: Ochodaeidae) includes 10 genera and around 120 species of small, oval, usually testaceous to reddish-brown beetles that are most common in sandy habitats and nearly cosmopolitan. The family is distributed in Africa (Paulian 1976; Scholtz and Evans 1987), Europe (Pittino 2006; Huchet 2016), Asia (Ochi et al. 2006; Nikolajev 2009; Ochi et al. 2013; Huchet 2014a, 2014b, 2017), and the Americas (Carlson 1975; Paulsen 2007, 2011, 2012, 2014; Paulsen and Ocampo 2012), but is absent from Australia and Oceania. The best method of collecting these beetles, especially the diurnal species, are with flight intercept traps that are near the ground and where the beetles can drop into collecting pans. Some nocturnally active species are attracted to lights. The life history of the family is almost completely unknown, with the larvae of the largest subfamily Ochodaeinae remaining undiscovered.

The Madagascar species were first studied by Klug (1832) and Fairmaire (1868). Benderitter (1920) named an additional species, and then the fauna remained unstudied for decades. The most complete treatments of the ochodaeid fauna of Madagascar were provided by Paulian (1959, 1976). The relatively nondescript genus *Ochodaeus* Dejean, found in Eurasia and mainland Africa, also contains Madagascan representatives. Three Madagascan species are currently considered valid, all with a strongly tuberculate pronotum: *O. isoanalensis* Paulian, 1959; *O. miliaris* Klug, 1832; and *O. pygmaeus* Paulian, 1976. In the material of the California Academy of Sciences project on Madagascar Biodiversity, three undescribed species were found in relatively large series that each possess a pronotum that is either completely lacking tubercles or are only weakly tuberculate. These species are clearly distinct from the known taxa and are described herein as the first step toward a larger treatment of the island's ochodaeid fauna.

Materials and Methods

Specimens and taxonomic material. Approximately 100 specimens from or deposited in the following institutions and collections were examined for this study: (CASC) California Academy of Sciences, San Francisco, CA, USA; (DKC) Denis Keith Collection, Chartres, France; (FSCA) Florida State Collection of Arthropods, Gainesville, FL, USA; (JBHC) Jean-Bernard Huchet Collection, Paris, France; (MNHN) Muséum national d'Histoire naturelle, Paris, France; (MJPC) M.J. Paulsen Collection, Lincoln, NE, USA; (NHM) Natural History Museum, London, UK; (UNSM) University of Nebraska State Museum, Lincoln, NE, USA; (USNM) United States National Museum of Natural History, Washington, D.C., USA.

The majority of material studied originated from the Madagascan biodiversity surveys of CASC, and the holotypes are deposited there. Much of the material was stored in alcohol and was subsequently

pinned and labeled by me. Paratypes have the depository indicated if known, or if not indicated are predominantly CASC with some specimens to be distributed to the collections listed above.

Label data are presented verbatim, with each label denoted by a letter (a, b, etc.), and with each line separated by a slash. Entirely handwritten labels are noted, and handwritten portions of otherwise printed labels are indicated in brackets. Almost all CASC specimens studied have a unique identifying number, and if multiple specimens in series exist the numbers are given in brackets. The sex of these specimens, if known, may be indicated with the appropriate identifying number.

Size measurements given are length (total length from mandibular apex to pygidium) and width (greatest width, here medially across elytra). Characters that pertain to ochodaeids generally, such as pectinate spurs, are not discussed. Important characters that vary interspecifically are the form of the clypeal apex and bead, shape of the mentum, armature of the legs, and the shape of the stridulatory peg. This last structure can only be seen by separating the elytra from the abdomen and is located at the upper margin of the penultimate abdominal sternite. The peg is a sclerotized lobe that produces sound by acting as a plectrum rubbing against a striated thickening on the inner face of the elytra. The variable form of the peg is taxonomically informative.

Structures on the internal sac of the male genitalia are often used taxonomically when differentiating species of Ochodaeinae. The genitalia must be immersed in 10% potassium hydroxide solution until the internal sac is cleared sufficiently well to see the structures, then neutralized with 10% acetic acid and rinsed with ethanol. In the Madagascar *Ochodaeus* species the internal sac is relatively uninformative and it is not necessary to evert the sac. The only structure found to differ is a sclerotized patch located between the parameres (see Fig. 7–9).

Taxonomic Treatment

Ochodaeus modopunctatus Paulsen, new species

Type material. Holotype male (CASC; Fig. 1), labeled: a) "MADAGASCAR: Province / d'Antsiranana, Parc National / Montagne d'Ambre / el 1050 m, 25–29 Jan 2001"; b) "12° 31′ 13″ S, 49° 10′ 45″ E / California Acad of Sciences / M.E. Irwin, E.I. Schlinger / & R. Harin'Hala collectors / malaise trap MA-01-01C-02"; c) "CASENT / 8006869"; d) red paper "*Ochodaeus* / *modopunctatus* n. sp. / M.J. Paulsen det.".

Paratype male (MJPC) labeled a–b as holotype; c) "CASENT / 8006868". One paratype labeled: a) "MADAGASCAR: Province / d'Antsiranana, Parc National / Montagne d'Ambre, / elev 960 m 26–29 Jan 2001"; b) "12° 30′ 52″ S, 49° 10′ 53″ E / California Acad. of Sciences / M.E. Irwin, E.I. Schlinger / & R. Harin'Hala collectors, / malaise trap MA-01-01A-02"; c) "CASENT / 8011532". Two paratypes labeled: a) "MADAGASCAR: Diego- / Suarez Prov., Parc National / Montagne d'Ambre, / elev 960 m / 26–29.i.2001" malaise"; b) "12° 30′ 52″ S, 49° 10′ 53″ E / M.E. Irwin, E.I. Schlinger / & R. Harin'Hala MA-01-01A-02 / Calif. Acad. Sci. Collection"; c) "CASENT / #" (# = 8000057 or 8000058 [♂]). Two paratypes labeled: a) "MADAGASCAR: Province / d'Antsiranana, Parc National / Montagne d'Ambre, / elev 960 m, 29 January 2001"; b) "12° 30′ 52″ S, 49° 10′ 53″ E / California Acad. of Sciences / M.E. Irwin collector, netted / by hand MA-01-01A-05"; c) "CASENT / #" (# = 8011551 [♀] or 8011561). Three paratypes labeled: a) "MADAGASCAR: Province / d'Antsiranana, Parc National / Montagne d'Ambre, / elev 960 m 4–19 Mar 2001"; b) "12° 30′ 52″ S, 49° 10′ 53″ E / California Acad. of Sciences / Coll: M. Irwin, R. Harin'Hala, / malaise trap MA-01-01A-08"; c) "CASENT / #" (# = 8016282, 8016293, or 8016298). Four paratypes labeled: a) "MADAGASCAR: Province / d'Antsiranana, Parc National / Montagne d'Ambre, / elev 960 m 5–21 April 2001"; b) "12° 30′ 52″ S, 49° 10′ 53″ E / California Acad. of Sciences / Coll: M. Irwin, R. Harin'Hala, / malaise trap MA-01-01A-10"; c) "CASENT / #" (# = 8013900, 8013903, 8013914, or 8013922 [♀]). One paratype labeled: a) "MADAGASCAR: Province / d'Antsiranana, Parc National / Montagne d'Ambre / elev 975 m 21–25 Jan 2001"; b) "12° 31′ S, 49° 11′ E / California Acad. of Sciences / M.E. Irwin, E.I. Schlinger / & R. Harin'Hala collectors / malaise trap MA-01-01B-01"; c) "CASENT / 8000118". One female paratype labeled: a) "MADAGASCAR: Province / Diego-Suarez, Parc National / Montagne d'Ambre 975 m"; b) "25 Jan to 11 Feb 2001 / 12° 31′ S, 49° 11′ E / California Acad. of Sciences / M.E. Irwin, E.I. Schlinger / & R. Harin'Hala collectors / malaise trap MA-01-01B-04"; c) "CASENT / 8032442". One

paratype labeled: a) "MADAGASCAR: Province / d'Antsiranana, Parc National / Montagne d'Ambre 975 m 4–19 Mar 2001"; b) "12° 31′ S, 49° 11′ E / California Acad. of Sciences / M.E. Irwin, E.I. Schlinger / & R. Harin'Hala collectors / malaise trap MA-01-01B-06"; c) "CASENT / 8013823". One paratype labeled: a) "MADAGASCAR: Province / d'Antsiranana, Sakalava / Beach, dwarf littoral forest / elev 10 m, 6–20 Mar 2001"; b) "12° 15′ 46″ S, 49° 23′ 51″ E / California Acad. of Sciences / Coll: M. Irwin, R. Harin'Hala / malaise trap - across sandy / trail MA-01-04B-04"; c) "CASENT / 8011513". Two paratypes labeled: a) "MADAGASCAR: Province / d'Antsiranana, Sakalava / Beach, dwarf littoral forest / elev 10 m, 20 Mar–7 April 2001"; b) "12° 15′ 46″ S, 49° 23′ 51″ E / California Acad. of Sciences / Coll: M. Irwin, R. Harin'Hala / malaise trap - across sandy / trail MA-01-04B-05"; c) "CASENT / #" (# = 8011542 [♂] or 8011544). One female paratype labeled: a) "MADAGASCAR: Province / d'Antsiranana, Sakalava / Beach, dwarf littoral forest / elev 10 m, 27 April–2001"; b) "12° 15′ 46″ S, 49° 23′ 51″ E / California Acad. of Sciences / Coll: M. Irwin, R. Harin'Hala / malaise trap - across sandy / trail MA-01-04B-08"; c) "CASENT / 8013984". One paratype labeled: a) "MADAGASCAR: Province / Diego-Suarez, Sakalava / Beach, dwarf littoral forest / elev 10 m, 20 Mar–7 April 2001"; b) "12° 15′ 46″ S, 49° 23′ 51″ E / California Acad. of Sciences / Coll: M. Irwin, R. Harin'Hala / malaise trap - across sandy / trail MA-01-04B-09"; c) "CASENT / 8014033". One paratype labeled: a) "MADAGASCAR: Province / Diego-Suarez, Sakalava / Beach, dwarf littoral forest / elev 10 m, 16–31 May 2001"; b) "12° 15′ 46″ S, 49° 23′ 51″ E / California Acad. of Sciences / Coll: M. Irwin, R. Harin'Hala / malaise trap - across sandy / trail MA-01-04B-10"; c) "CASENT / 8014100". One female paratype labeled: a) "MADAGASCAR: Province / d'Antsiranana, Sakalava / Beach, dwarf littoral forest / elev 10 m, 7–25 May 2001"; b) "12° 15′ 46″ S, 49° 23′ 51″ E / California Acad. of Sciences / Coll: M. Irwin, R. Harin'Hala / malaise trap - across sandy / trail MA-01-04B-12"; c) "CASENT / 8016232". Two paratypes labeled: a) "MADAGASCAR: Province / d'Antsiranana, Sakalava / Beach, dwarf littoral forest / elev 10 m, 25 June–6 July 2001"; b) "12° 15′ 46″ S, 49° 23′ 51″ E / California Acad. of Sciences / Coll: M. Irwin, R. Harin'Hala / malaise trap - across sandy / trail MA-01-04B-13"; c) "CASENT / #" (# = 8013588 [♀] or 8013595). One male paratype labeled: a) "MADAGASCAR: Province / Diego-Suarez, Sakalava / Beach, dwarf littoral forest / elev 10 m, 28 July–6 August 2001"; b) "12° 15′ 46″ S, 49° 23′ 51″ E / California Acad. of Sciences / Coll: M. Irwin, R. Harin'Hala / malaise trap - across sandy / trail MA-01-04B-16"; c) "CASENT / 8032553″. One paratype labeled: a) "MADAGASCAR: Province / d'Antsiranana, Sakalava / Beach, dwarf littoral forest / elev 10 m, 13–20 August 2001"; b) "12° 15′ 46″ S, 49° 23′ 51″ E / California Acad. of Sciences / Coll: M. Irwin, R. Harin'Hala / malaise trap - across sandy / trail MA-01-04B-17"; c) "CASENT / 8025601". One paratype labeled: a) "MADAGASCAR: Province / d'Antsiranana, Parc National / Montagne d'Ambre 1125 m / 29 Jan to 11 Feb 2001"; b) "12° 31′ 13″ S, 49° 10′ 45″ E / California Acad. of Sciences / Coll: M. Irwin, R. Harin'Hala / malaise trap MA-01-01D-03"; c) "CASENT / 8016175". One paratype labeled: a) "MADAGASCAR: Province / Diego-Suarez, Parc National / Montagne d'Ambre 1125 m / 11 Feb to 4 March 2001"; b) "12° 31′ 13″ S, 49° 10′ 45″ E / California Acad. of Sciences / Coll: M. Irwin, R. Harin'Hala / malaise trap MA-01-01D-04"; c) "CASENT / 8014060". Three paratypes labeled: a) "MADAGASCAR: Province / Diego-Suarez, Parc National / Montagne d'Ambre 1125 m / 19 March to 5 April 2001"; b) "12° 31′ 13″ S, 49° 10′ 45″ E / California Acad. of Sciences / Coll: M. Irwin, R. Harin'Hala / malaise trap MA-01-01D-06"; c) "CASENT / #" (# = 8014203, 8014204 [♀], or 8014205 [♀]). One paratype labeled: a) "MADAGASCAR: Province / d'Antsiranana, Parc National / Montagne d'Ambre 1125 m / 5–21 April 2001"; b) "12° 31′ 13″ S, 49° 10′ 45″ E / California Acad. of Sciences / Coll: M. Irwin, R. Harin'Hala / malaise trap MA-01-01D-07"; c) "CASENT / 8006346". One female paratype labeled: a) "MADAGASCAR: Province / d'Antsiranana, Parc National / Montagne d'Ambre 1125 m / 21–26 April 2001"; b) "12° 31′ 13″ S, 49° 10′ 45″ E / California Acad. of Sciences / Coll: M. Irwin, R. Harin'Hala / malaise trap MA-01-01D-08"; c) "CASENT / 8016143". One paratype labeled: a) "MADAGASCAR: Province / d'Antsiranana, Parc National / Montagne d'Ambre 1125 m / 12–14 May 2001"; b) "12° 31′ 13″ S, 49° 10′ 45″ E / California Acad. of Sciences / Coll: M. Irwin, R. Harin'Hala / malaise trap MA-01-01D-10"; c) "CASENT / 8016164". Two female paratypes labeled: a) "MADAGASCAR: Province / d'Antsiranana, Parc National / Montagne d'Ambre 1125 m / 14–30 May 2001"; b) "12° 31′ 13″ S, 49° 10′ 45″ E / California Acad. of Sciences / Coll: M. Irwin, R. Harin'Hala / malaise trap MA-01-01D-11"; c) "CASENT / #" (# = 8016113 or 8016118). Three paratypes labeled: a) "MADAGASCAR: Province / Diego-Suarez, Montaigne / Francais, elev 150 m / 15 Feb–6 March 2001"; b) "12° 19.5′ S, 49° 20′ E / California Acad. of Sciences / coll: M. Irwin, R. Harin'Hala / malaise, forested limestone / ridge MA-01-06-06"; c) "CASENT / #" (# =

8032601, 8032602, or 8032603). One female paratype labeled: a) "MADAGASCAR: Province / Diego-Suarez, dry forest / 7 km N of Joffreville, 360 m"; b) "6–20 March 2001 / 12° 20′ S, 49° 15′ E / R. Harin'Hala collector / malaise trap MA-01-07-08"; c) "CASENT / 8014117". One paratype labeled: a) "MADAGASCAR: Province / Diego-Suarez, dry forest / 7 km N of Joffreville, 360 m"; b) "7–27 April 2001 / 12° 20′ S, 49° 15′ E / R. Harin'Hala collector / malaise trap MA-01-07-10"; c) "CASENT / 8025772". One paratype labeled: a) "MADAGASCAR: Province / d'Antsiranana, dry forest / 7 km N of Joffreville, 360 m"; b) "27 April–13 May 2001 / 12° 20′ S, 49° 15′ E / R. Harin'Hala collector / malaise trap MA-01-07-11"; c) "CASENT / 8011458".

All paratypes ($n = 43$) with label: on yellow paper, "*Ochodaeus* / *modopunctatus* / Paulsen / PARATYPE".

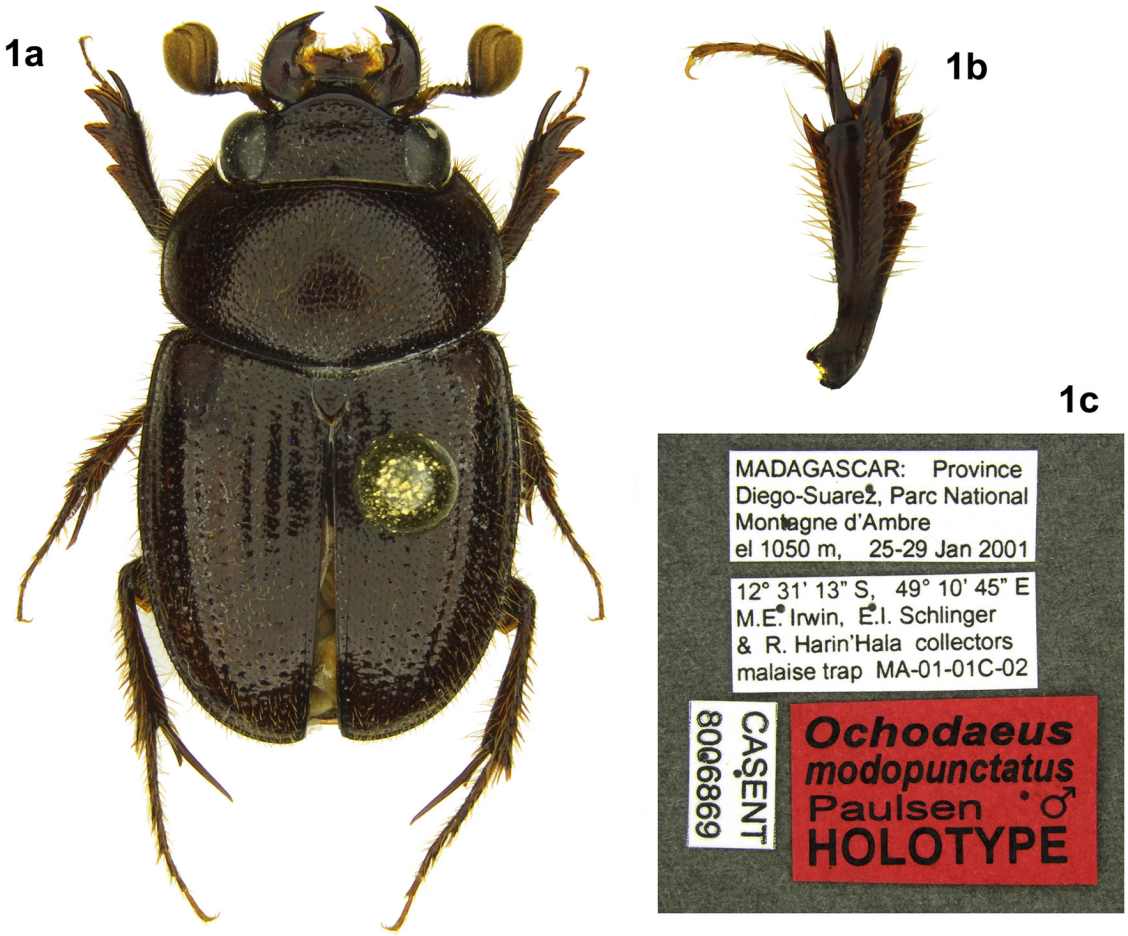


Figure 1. *Ochodaeus modopunctatus* Paulsen, new species, male holotype. **a)** Dorsal habitus. **b)** Right front leg, dorsal view. **c)** Labels.

Description. Holotype male (Fig. 1a). Coleoptera: Scarabaeoidea: Ochodaeidae. **Length:** 9.9 mm. **Width:** 4.1 mm. **Color:** Everywhere uniformly dark reddish brown; surface nitid. **Head:** Surface lacking tubercles, irregularly punctate; punctures moderately large, setose, separated by ~ 4 puncture diameters. Eyes large, globose; lacking ventral projection of canthus. Antennal club subequal to eye in size. Mandibles broadly scooped, basal angle prominent, apices falcate; left mandible with large rectangular internal tooth; right mandible with complimenting tooth reduced, second tooth large, obtuse. Frons weakly convex. Clypeus flat with disc short (at most 1/5 as long as wide), anterior margin strongly beaded; bead thick, rounded, almost as long as disc. Mentum (Fig. 4) slightly wider than long, tumid (not flat); most strongly tumid near base, decreasing anteriorly; surface with 2 lateral and 1 median depression near base, median depression contiguous with oval fovea on disc; fovea continuing anteriorly. **Pronotum:**

Form convex. Surface densely punctate, appearing smooth between punctures, lacking distinct tubercles (at 40× minute tubercle anterior to seta); punctation mixed, with large setose punctures and smaller naked punctures interspersed. **Elytra:** Form convex, relatively elongate, elytra together longer than wide. Surface with striae moderately impressed, punctate, surface smooth between punctures (except sutural stria with connecting groove); strial punctures separated by > 5 diameters, lacking setae. Intervals irregularly punctate; punctures small, setose, with minute tubercle anteriorly. **Legs:** Protibia tridentate externally, with short, acute pollex directed anteriorly (Fig. 1b). Profemur and mesofemur with apical tooth reduced to rounded lobe. Metafemur with apical fin-like projection with weak tooth in distal fourth. **Venter/Abdomen:** Metasternum and abdomen sparsely punctate; punctures large with long, erect, golden setae. Pygidium punctate, setose. Stridulatory peg with narrow neck and rounded apex (Fig. 10). **Male genitalia:** Sclerotized patch on internal sac between parameres broadly oblong with bifurcate end (Fig. 7).

Paratype variation. The paratypes show little variation from the holotype, and negligible sexual dimorphism. The clypeus may appear more trapezoidal (truncate medially), and although this is a common sexual dimorphism in ochodaeids this does not appear to be sexually diagnostic in *O. modopunctatus*. The subapical tooth on the metafemur is present in the holotype and the three largest males but is obsolete in all smaller males and females.

Remarks. Due to the lack of any useful sexual dimorphism in the specimens that had open pygidia with visible genitalia, the majority of the remaining specimens were not subjected to potential damage during genitalic dissection. The sex is indicated only for paratypes with everted genitalia.

Etymology. The name is constructed from the Latin adverb 'modo' meaning 'only' and the adjective for 'punctate'. This refers to the apparent lack of tubercles on the pronotum of this species, which is unique among the Madagascan species. The other species treated below have at least weak indications of tubercles between punctures, and the known taxa all have a distinctly tuberculate pronotum.

Distribution. This species is thus far known only from the extreme northern tip of the island in the vicinity of the type locality, Montagne d'Ambre (Fig. 19).

Ochodaeus polypollicatus Paulsen, new species

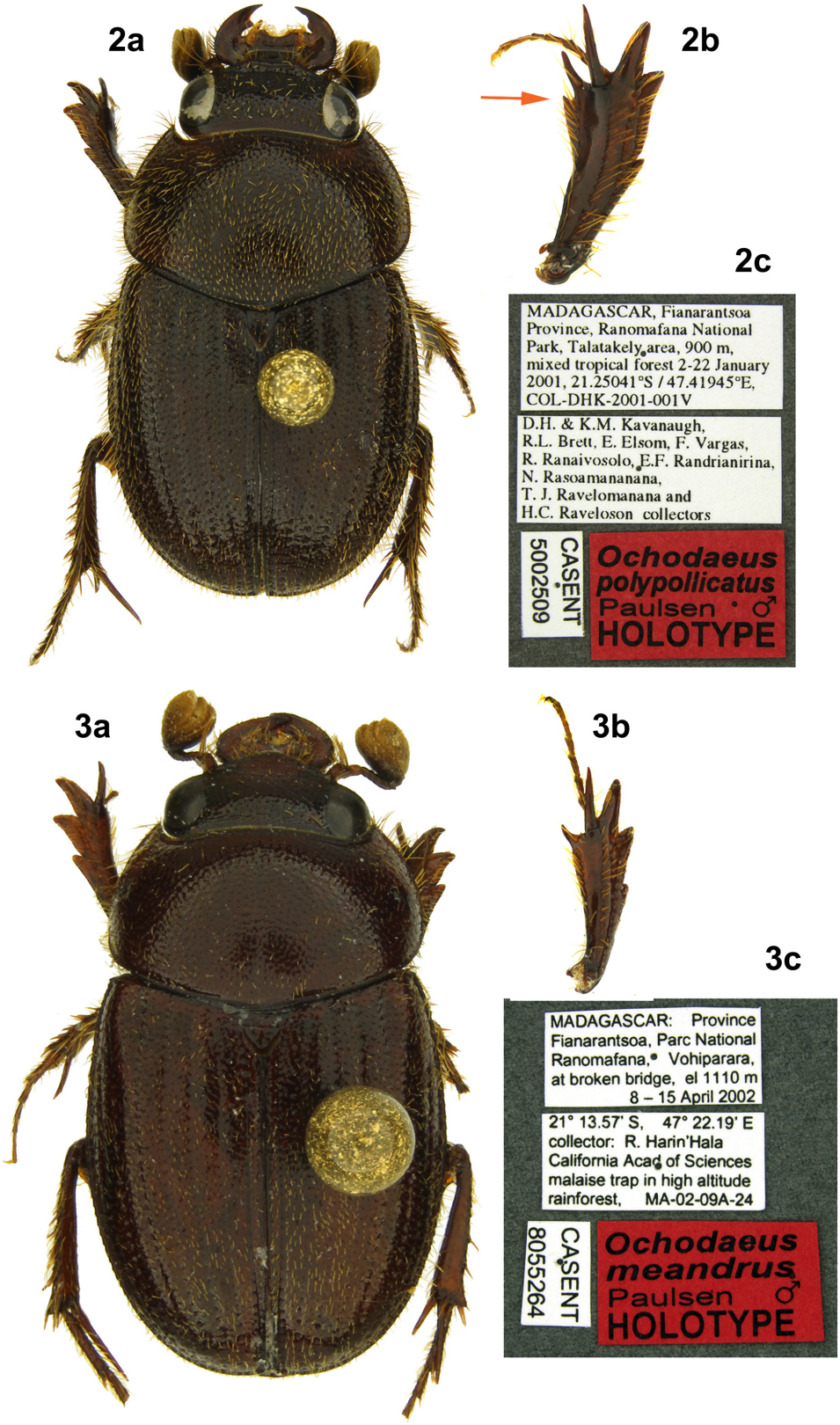
Type material. Holotype male (CASC; Fig. 2), labeled: a) "MADAGASCAR, Fianarantsoa / Province, Ranomafana National / Park, Talatakely area, 900 m, / mixed tropical forest 2–22 January / 2001, 21.25041° S | 47.41945° E, / COL-DHK-2001-001V"; b) "D.H. & K.M. Kavanaugh, / R.L. Brett, E. Elsom, F. Vargas, / R. Ranaivosolo, E.F. Randrianirina, / N. Rasoamananana / T.J. Ravelomanana and / H.C. Raveloson collectors"; c) "CASENT / 5002509".

Two male, two female paratypes labeled: a, b as holotype; c) "CASENT / #" (# = 5002518, 5002522, 5002535, 5002584). One male paratype labeled: a) "MADAGASCAR, Province / Fianarantsoa, Ranomafana / National Park, Talatakely / area, 900 m, mixed tropical / forest 4–16 January 2001" b) "21.25041° S 47.41945° E / D.H. & K.M. Kavanaugh, / R.L. Brett, E. Elsom, and / F. Vargas colls. pitfall traps / COL-DHK-2001-001TN"; c) "CASENT / 8003738". One male, two female paratypes labeled: a) "MADAGASCAR: Province / Fianarantsoa, Parc National / Ranomafana, Belle Vue at / Talatakely, elev 1020 m / 12–19 February 2002"; b) "21° 15.99′ S, 47° 25.21′ E / coll: M. Irwin, R. Harin'Hala / California Acad of Sciences / malaise, secondary tropical / forest MA-02-09C-16"; c) "CASENT / #" (# = 8055451, 8055453, 8055454). One female paratype labeled: a) "MADAGASCAR: Province / Fianarantsoa, Parc National / Ranomafana, Belle Vue at / Talatakely, elev 1020 m / 26 February–4 March 2002"; b) "21° 15.99′ S, 47° 25.21′ E / coll: M. Irwin, R. Harin'Hala / California Acad of Sciences / malaise, secondary tropical / forest MA-02-09C-18"; c) "CASENT / 8055994". One female paratype labeled: a) "MADAGASCAR: Province / Fianarantsoa, Parc National / Ranomafana, Belle Vue at / Talatakely, elev 1020 m / 10–21 March 2003"; b) "21° 15.99′ S, 47° 25.21′ E / coll: M. Irwin, R. Harin'Hala / California Acad of Sciences / malaise, secondary tropical / forest MA-02-09C-56". Two female paratypes labeled: a) "MADAGASCAR: Province / Fianarantsoa, Parc National / Ranomafana, Vohiparara, / at broken bridge, el 1110 m / 2–10 January 2002 / 21° 13.57′ S, 47° 22.19′ E"; b) "coll: M. Irwin, R. Harin'Hala / California Acad

of Sciences / malaise trap in high altitude / rainforest, MA-02-09A-10". Two female paratypes labeled: a) "MADAGASCAR: Province / Fianarantsoa, Parc National / Ranomafana, Vohiparara, / at broken bridge, el 1110 m / 19–26 February 2002 / 21° 13.57′ S, 47° 22.19′ E"; b) "coll: M. Irwin, R. Harin'Hala / California Acad of Sciences / malaise trap in high altitude / rainforest, MA-02-09A-17". One female paratype labeled: a) "MADAGASCAR: Province / Fianarantsoa, Parc National / Ranomafana, radio tower / at forest edge, elev 1130 m / 28 Nov–6 Dec 2001"; b) "21° 15.05′ S, 47° 24.43′ E / coll: M. Irwin, R. Harin'Hala / California Acad of Sciences / malaise, mixed tropical / forest MA-02-09B-05"; c) "CASENT / 8055993". One male, two female paratypes labeled: a) "MADAGASCAR: Province / Fianarantsoa, Parc National / Ranomafana, radio tower / at forest edge, elev 1130 m / 14–21 January 2002"; b) "21° 15.05′ S, 47° 24.43′ E / coll: M. Irwin, R. Harin'Hala / California Acad of Sciences / malaise, mixed tropical / forest MA-02-09B-12"; c) "CASENT / #" (# = 8055768, 8055770, 8055771). One male paratype labeled: a) "MADAGASCAR: Province / Fianarantsoa, Parc National / Ranomafana, radio tower / at forest edge, elev 1130 m / 24 May–4 June 2002"; b) "21° 15.05′ S, 47° 24.43′ E / coll: M. Irwin, R. Harin'Hala / California Acad of Sciences / malaise, mixed tropical / forest MA-02-09B-30"; c) "CASENT / 8055873". One male paratype labeled: a) "MADAGASCAR: Province / Fianarantsoa, Parc National / Ranomafana, radio tower / at forest edge, elev 1130 m / 22 July–8 August 2004"; b) "21° 15.05′ S, 47° 24.43′ E / coll: M. Irwin, R. Harin'Hala / California Acad of Sciences / malaise, mixed tropical / forest MA-02-09B-97". One female paratype labeled: a) "MADAGASCAR: Province / Fianarantsoa, Ranomafana / JIRAMA water works / 28 Jan–4 Feb 2002 / 21° 14.91′ S, 47° 27.13′ E"; b) "coll: M. Irwin, R. Harin'Hala / California Acad of Sciences / malaise trap near river / elev 690 m, MA-02-09D-14". One male paratype labeled: a) "MADAGASCAR: Toamasina / Corridor Forestier Analamay-Mantadia, Ambatoharanana / el 995 m 12–19 Dec 2012 /18° 48′ 08″ S 048° 24′ 21″ E"; b) "California Acad of Sciences / coll. B.L. Fisher et al. / malaise trap rainforest / collection code: BLF30260". One male paratype labeled: a) "MADAGASCAR: Toamasina / Réserve Nationale Intégrale / Betampona, Betampona / 35.1 km NW Toamasina / 27 July–3 Aug 2008 / 17°54′58″ S 049°12′07″ E"; b) "California Acad of Sciences / coll. B.L. Fisher rainforest / malaise trap elev 550 m / coll. code: BLF19593_32". One female paratype labeled: a) "MADAGASCAR: Toamasina / Réserve Nationale Intégrale / Betampona, Betampona / 35.1 km NW Toamasina / 20–27 January 2008 / 17°55′11″ S 049°12′01″ E"; b) "California Acad of Sciences / coll. B.L. Fisher rainforest / malaise trap elev 525 m / coll. code: BLF19594_05". One female paratype labeled: a) "MADAGASCAR: Toliara / Parc National Andohahela, / Col de Tanatana, 33.3 km / NW Tolagnaro, elev 275 m / 22–24 November 2006 / 24° 45′ 31″ S 046° 51′ 13″ E"; b) "California Acad of Sciences / coll. B.L. Fisher et al. / malaise trap rainforest / collection code: BLF15102". One female paratype labeled: a) "MADAGASCAR: Toamasina / Prov., Mobot site, Analalava / 7 km SW of Foulpointe / 17° 41′ 36″ S, 49° 27′ 37″ E / 28 Dec 2007–3 Jan 2008"; b) "California Acad of Sciences / coll: M. Irwin, R. Harin'Hala / malaise trap on sand in low / altitude dense humid forest, / elev 60 ft MG-37B-16". One female paratype labeled: a) "MADAGASCAR: Toamasina / Prov., Mobot site, Analalava / 7 km SW of Foulpointe / 17° 41′ 36″ S, 49° 27′ 37″ E / 15–22 February 2008"; b) "California Acad of Sciences / coll: M. Irwin, R. Harin'Hala / malaise trap on sand in low / altitude dense humid forest, / elev 60 ft MG-37B-23". One female paratype labeled: a) "MADAGASCAR: Toamasina / Prov., Mobot site, Analalava / 7 km SW of Foulpointe / 17° 41′ 36″ S, 49° 27′ 37″ E / 25 July–1 Aug 2008"; b) "California Acad of Sciences / coll: M. Irwin, R. Harin'Hala / malaise trap on sand in low / altitude dense humid forest, / elev 60 ft MG-37B-46". Two male, four female paratypes labeled: a) "MADAGASCAR: Province / d'Antsiranana, Montaigne / Francais, elev 150 m / 30 Jan–15 Feb 2001 / 12° 19.5′ S, 49° 20′ E"; b) California Acad. of Sciences / coll: M. Irwin, R. Harin'Hala / malaise, forested limestone / ridge MA-01-06-05"; c) "CASENT / #" (# = 8032521, 8032522, 8032523, 8032528, 8032529, 8032537). One male, two female paratypes labeled: a) "MADAGASCAR: Province / d'Antsiranana, Montaigne / Francais, elev 150 m / 6–20 March 2001 / 12° 19.5′ S, 49° 20′ E"; b) California Acad. of Sciences / coll: M. Irwin, R. Harin'Hala / malaise, forested limestone / ridge MA-01-06-07"; c) "CASENT / #" (# = 8014195, 8014196, 8014197).

All paratypes (n = 12 male, 25 female) with label: on yellow paper, "*Ochodaeus* / *polypollicatus* / Paulsen / PARATYPE".

Description. Holotype male (Fig. 2a). Coleoptera: Scarabaeoidea: Ochodaeidae. **Length:** 8.4 mm. **Width:** 4.1 mm. **Color:** Everywhere uniformly dark reddish brown; surface nitid. **Head:** Surface lacking tubercles, irregularly punctate; punctures mixed, moderately large and setose or smaller and lacking



Figures 2–3. Madagascar *Ochodaeus* species. **2)** *Ochodaeus polypollicatus* Paulsen, new species, male holotype. **a)** Dorsal habitus. **b)** Right front leg, dorsal view, arrow indicating second pollex. **c)** Labels. **3)** *Ochodaeus meandrus* Paulsen new species, male holotype. **a)** Dorsal habitus. **b)** Right front leg, dorsal view. **c)** Labels.

setae, separated by ~ 4 puncture diameters. Eyes large, globose; lacking ventral projection of canthus. Antennal club large, subequal in size to eye. Mandibles broadly scooped, basal angle rounded, apices falcate; left mandible with large triangular internal tooth; right mandible with complimenting tooth obtuse, second tooth larger, bicusped. Frons weakly convex; surface impunctate behind frontoclypeal suture. Clypeus flat with disc short (at most 1/10 as long medially as wide), anterior margin strongly beaded; bead thick (at least 2× as thick as clypeal disc), anterior margin of bead subtrapezoidal, posterior margin of bead bisinuate. Mentum (Fig. 5) with strongly excavated rounded furrow on nearly entire length, lateral margins of furrow roughly thickened. **Pronotum:** Form convex. Surface densely punctate, appearing smooth between punctures laterally, disc with slight indication of tiled granules; punctation mixed, predominantly large setose punctures with few smaller naked punctures interspersed. **Elytra:** Form convex, relatively elongate, elytra together longer than wide. Surface with striae moderately impressed, punctate, surface smooth between punctures (except sutural stria with connecting groove); strial punctures large, separated by 1 diameter, lacking setae. Intervals irregularly punctate; punctures small, setose, with tubercle anteriorly. **Legs:** Protibia tridentate externally, internal side with strong, acute pollex ½ length of apical spur, with second triangularly acute pollex proximally (Fig. 2b). Profemur lacking apical tooth. Mesofemur and metafemur with strong subapical tooth connected by fin-like extension to apex. **Venter/Abdomen:** Metasternum and abdominal segments 1 to 5 sparsely punctate; punctures large with long, erect, golden setae; abdominal segment 6 with dense, small punctures resulting in setal patch. Pygidium roughly punctate. Stridulatory peg long, arcuate (Fig. 11). **Male genitalia:** Internal sac with elongate-oval patch of sclerites between parameres (Fig. 8).

Paratype variation. In males the second pollex becomes less distinct as body size decreases, with only the smallest of the 13 males lacking any sort of angulation. Females lack the second pollex, and also lack the setal patch on the last abdominal segment, instead displaying only sparse setation.

Remarks. The double pollex on male protibiae is diagnostic and not seen in other species. The widely separated localities represented by such males suggested either that multiple species possessed this character or they comprised a single species with a large distribution and elevational range. The genitalia of all male specimens were dissected and found to possess a diagnostic elongate-oval sclerotized patch on the internal sac just between the parameres, confirming that they constituted a single species. For females and the smallest males, the first pollex is longer than in other species and the mentum deeply and entirely furrowed (Fig. 5).

Etymology. The name is an adjective from Latin meaning 'multiple thumbs'. Males of the species have two 'thumbs' on the internal margin of the protibia, which is unique among Madagascan *Ochodaeus* species.

Distribution. This species is widely distributed along the eastern, forested edge of Madagascar (Fig. 19).

Ochodaeus meandrus Paulsen, new species

Type material. Holotype male (CASC; Fig. 3), labeled: a) "MADAGASCAR: Province / Fianarantsoa, Parc National / Ranomafana, Vohiparara, / at broken bridge, el 1110 m / 8–15 April 2002 / 21° 13.57′ S, 47° 22.19′ E" b) "coll: M. Irwin, R. Harin'Hala / California Acad of Sciences / malaise trap in high altitude / rainforest, MA-02-09A-24"; c) "CASENT / 8055264".

One male, two female paratypes labeled: a, b as holotype; c) "CASENT / #" (# = 8055260, 8055262, 8055300). One female paratype labeled: a) "MADAGASCAR: Province / Fianarantsoa, Parc National / Ranomafana, Vohiparara, / at broken bridge, el 1110 m / 6–15 December 2001 / 21° 13.57′ S, 47° 22.19′ E" b) "coll: M. Irwin, R. Harin'Hala / California Acad of Sciences / malaise trap in high altitude / rainforest, MA-02-09A-06"; c) "CASENT / 8055632". One female paratype labeled: a) "MADAGASCAR: Province / Fianarantsoa, Parc National / Ranomafana, Vohiparara, / at broken bridge, el 1110 m / 19–26 March 2001 / 21° 13.57′ S, 47° 22.19′ E" b) "coll: M. Irwin, R. Harin'Hala / California Acad of Sciences / malaise trap in high altitude / rainforest, MA-02-09A-21"; c) "CASENT / 8055999". Two male paratypes labeled: a) "Two male paratypes labeled: a) "MADAGASCAR: Province / Fianarantsoa, Parc National / Ranomafana, Vohiparara, / at broken bridge, el 1110 m / 19–26 March 2001 / 21° 13.57′ S, 47° 22.19′ E" b) "coll: M. Irwin,

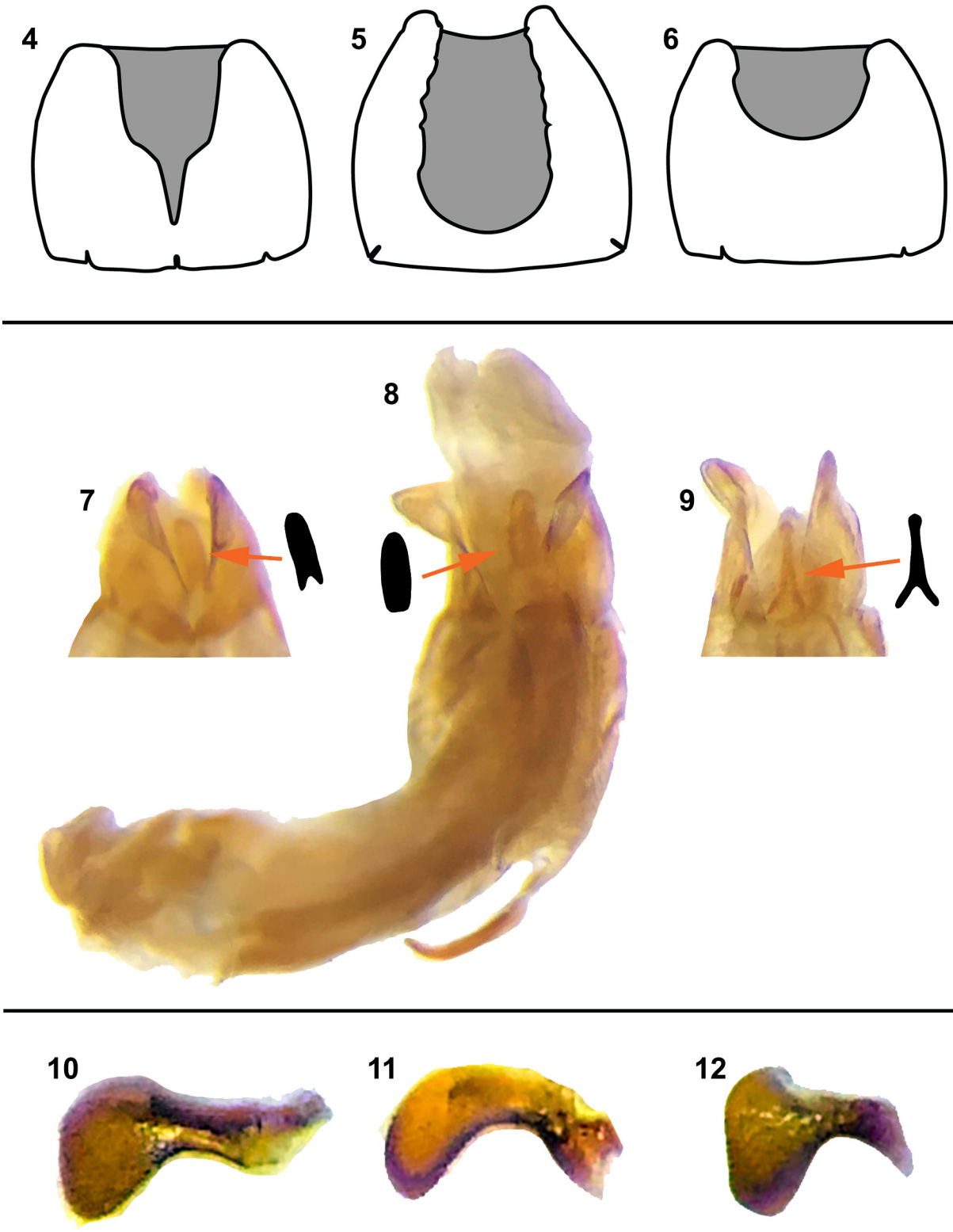
R. Harin'Hala / California Acad of Sciences / malaise trap in high altitude / rainforest, MA-02-09A-22"; c) "CASENT / 8055999". Two male, two female paratypes labeled: a) "MADAGASCAR: Province / Fianarantsoa, Parc National /Ranomafana, radio tower / at forest edge, elev 1130 m / 19–26 February 2002 / 21° 15.05′ S, 47° 24.43′ E"; b) "coll: M. Irwin, R. Harin'Hala / California Acad of Sciences / malaise, mixed tropical / forest MA-02-09B-17"; c) "CASENT / #" (# = 8055520, 8055521, 8055522, 8055544). One male paratype labeled: a) "MADAGASCAR: Province / Fianarantsoa, Parc National / Ranomafana, radio tower / at forest edge, elev 1130 m / 20 Sept–5 Oct 2006 / 21° 15.05′ S, 47° 24.43′ E"; b) "coll: M. Irwin, R. Harin'Hala / California Acad of Sciences / malaise, mixed tropical / forest MA-02-09B-160". One female paratype labeled: a) "MADAGASCAR: Province / Fianarantsoa, Parc National / Ranomafana, radio tower / at forest edge, elev 1130 m / 1–11 November 2006 / 21° 15.05′ S, 47° 24.43′ E"; b) "coll: M. Irwin, R. Harin'Hala / California Acad of Sciences / malaise, mixed tropical / forest MA-02-09B-163". One male paratype labeled: a) "MADAGASCAR: Province / Fianarantsoa, Ranomafana / JIRAMA water works / 21–24 December 2001 / 21° 14.91′ S, 47° 27.13′ E"; b) "coll: M. Irwin, R. Harin'Hala / California Acad of Sciences / malaise trap near river / elev 690 m, MA-02-09D-08"; c) "CASENT / 8056011". One female paratype labeled: a) "MADAGASCAR: Province / Fianarantsoa, SE of Fandriana, / Ranomena, 5 March, 2000 / 20° 23′ 37″ S, 47° 39′ 09″ E"; b) "M.E. Irwin & E. I. Schlinger / California Acad. of Sciences / el. 1345 m coll. code: SI-010"; c) "CASENT / 8003859". One paratype (NHM; on glueboard, unsexed) labeled: a) "MADAGASCAR, 2007 / Ranomafana Nat. Park / near Ranomafana vill. / M. Trýzna leg., 26.-31.i (sic)"; b) "BMNH (E) / 2016-44 / M. Trýzna".

All paratypes (n = 6 male, 9 female, 1 unsexed) with label: on yellow paper, "*Ochodaeus* / *meandrus* / Paulsen / PARATYPE".

Description. Holotype male (Fig. 3a). Coleoptera: Scarabaeoidea: Ochodaeidae. **Length:** 7.4 mm. **Width:** 3.9 mm. **Color:** Everywhere uniformly dark reddish brown; surface nitid. **Head:** Surface lacking tubercles, irregularly punctate; punctures mixed, moderately large and setose, separated by 1–2 diameters. Eyes large, globose; lacking ventral projection of canthus. Antennal club large, subequal to eye in size. Mandibles broadly scooped, shortened (shorter than head), apices falcate; left mandible with large triangular, subacute internal tooth; right mandible with complimenting tooth obsolete, second tooth larger, subacute. Frons weakly convex; surface punctate behind frontoclypeal suture. Clypeus flat with disc relatively long (1/4 as long medially as wide), subtrapezoidal; anterior margin beaded, bead roughly circular but wavy (Fig. 18). Mentum flat emarginated by round fovea in apical half (Fig. 6). **Pronotum:** Form convex. Surface densely punctate, appearing smooth between punctures laterally, disc with slight indication of tiled granules; punctation mixed, predominantly large setose punctures with few smaller glabrous punctures interspersed. **Elytra:** Form convex, relatively elongate, elytra together longer than wide. Surface with striae moderately impressed, punctate, surface smooth between punctures (except sutural stria with connecting groove); strial punctures large, separated by 2 diameters, lacking setae. Intervals irregularly punctate; punctures small, setose, with tubercle anteriorly. **Legs:** Protibia tridentate externally, internal side with short, ventrally directed pollex < 1/3 length of apical spur (Fig. 3b). Profemur with strong apical tooth. Mesofemur and metafemur with isolated subapical tooth not strongly connected to apex. **Venter/Abdomen:** Metasternum and abdominal segments sparsely punctate; punctures large with long, erect, golden setae. Pygidium roughly punctate. Stridulatory peg short, capitate (Fig. 12). **Male genitalia:** Internal sac with narrow arrowhead-shaped patch of sclerites between parameres (Fig. 9).

Paratype variation. Sexual dimorphism is not readily apparent in this species. The acute, apical tooth on the profemur is not present in females or smaller males, and the subapical tooth on the mesofemur is also obsolete on most female specimens. The subapical tooth on the metafemur may be reduced but is present on all specimens.

Remarks. This species may be confused with smaller males and females of *O. polypollicatus*. The much shorter, ventrally-directed pollex, less furrowed mentum, and isolated subapical tooth on the metafemur are all consistent differences and diagnostic. Males of this species lack the setal patch on the last abdominal segment, and second pollex of most male *O. polypollicatus*. The best character for specimens of both sexes of *O. meandrus* is the wavy appearance of the clypeal bead when viewed from directly above. Positioning the specimen in the correct plane so that the light reflects on the crest of the



Figures 4–12. Additional characters of Madagascar *Ochodaeus* species. **4–6)** Mentum, shading indicates foveae. **7–9)** Male genitalia, inset with arrow illustrating shape of sclerotized patch on internal sac between parameres. **10–12)** Right stridulatory peg, dorsal view. **4, 7, 10)** *O. modopunctatus* Paulsen, new species. **5, 8, 11)** *O. polypollicatus* Paulsen, new species. **6, 9, 12)** *O. meandrus* Paulsen, new species.

bead is necessary to best see the wavy form. The clypeal bead of *O. modopunctatus* may also appear wavy, but that species has no indication of granules on the pronotum and a mentum with a furrow that becomes acute posteriorly.

Etymology. The name is formed from "meandrus", a noun in apposition derived classically from the Meandros River of antiquity and used then figuratively for 'a wavy border' in embroidery and continuing into modern usage as 'meandering'. It is a reference to the wavy margin on the clypeus that is the most recognizable character of the species.

Distribution. The species is known only from the vicinity of Ranomafana National Park (Fig. 20).

Generic Catalog of the Madagascar Fauna

Ochodaeus isoanalensis Paulian, 1959: 129
Ochodaeus meandrus Paulsen, new species
Ochodaeus miliaris Klug, 1832: 164
    Ochodaeus cannellinus Fairmaire, 1868: 785
    Ochodaeus infuscatus Fairmaire, 1868: 785
Ochodaeus modopunctatus Paulsen, new species
Ochodaeus polypollicatus Paulsen, new species
Ochodaeus pygmaeus Paulian, 1976: 151

Key to species of *Ochodaeus* in Madagascar

1. Pronotum everywhere strongly, densely granulate with elevated tubercles (Fig. 13) **2**
— Pronotum either entirely smooth and punctate or with weak granulation confined to disc (Fig. 14) **4**

2(1). Elytral tubercles on intervals sparse; body length less than 4 mm . . . . ***O. pygmaeus* Paulian**
— Elytral tubercles dense; body length greater than 4 mm **3**

3(2). Median thickening of clypeal bead variable, lateral thickening always evident (Fig. 15); body usually > 9.0 mm . . . . . ***O. isoanalensis* Paulian**
— Median thickening of clypeal bead simply convex, bead thin laterally (Fig. 16); body length usually 4.5–8.0 mm . . . . . ***O. miliaris* Klug**

4(1). Pronotal surface simply punctate . . . . . ***O. modopunctatus* Paulsen, new species**
— Pronotal surface weakly granulate on disc **5**

5(4). Clypeal bead evenly curved (Fig. 17). Mentum deeply, entirely furrowed (Fig. 5). Males usually with 2 pollices on protibia . . . . . ***O. polypollicatus* Paulsen, new species**
— Clypeal bead wavy (Fig. 18). Mentum with furrow not reaching past middle (Fig. 6). Males with a single pollex on protibia . . . . . ***O. meandrus* Paulsen, new species**

Acknowledgments

I thank the researchers of CASC for undertaking the Madagascan biodiversity projects that resulted in the collection of such important material. I also thank Andrew B.T. Smith (Canadian Museum of Nature), Brett Ratcliffe (UNSM), and Jean-Bernard Huchet (MNHN) for reviewing the manuscript. Special thanks to J. Schweikert (CASC), J.-B. Huchet, and Andrey Frolov (Universidade Federal de Mato Grosso, Brazil) for help in locating additional specimens.

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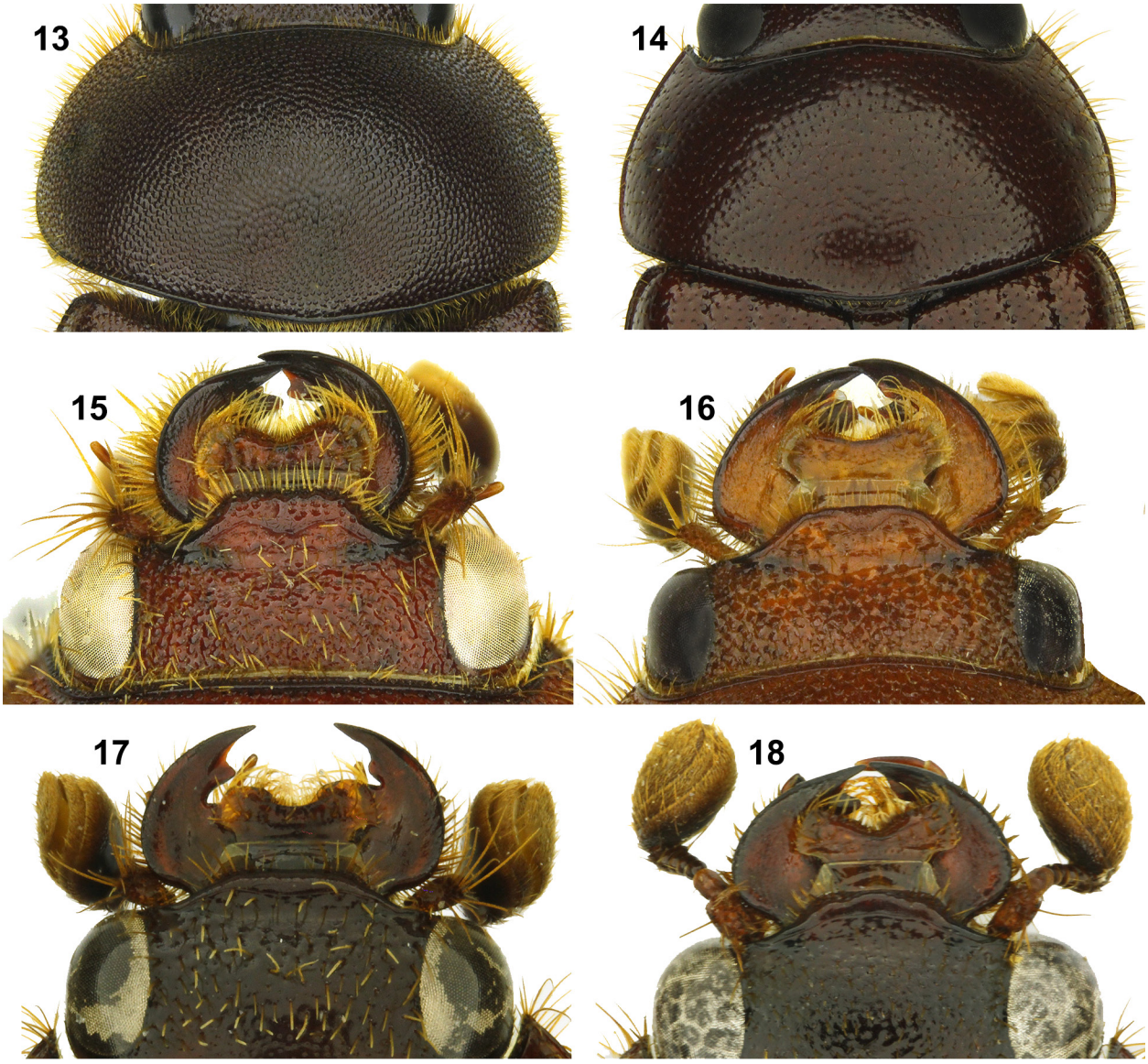

Figures 13–18. Key characters of Madagascar *Ochodaeus* species. **13)** Granulate pronotum of *O. isoanalensis* Paulian. **14)** Punctate pronotum of *O. modopunctatus* Paulsen, new species. **15)** Head of *O. isoanalensis* Paulian showing broadly thickened clypeal margin. **16)** Head of *O. miliaris* (Klug), showing narrowly thickened clypeal margin. **17)** Head of *O. polypollicatus* Paulsen, new species, showing smoothly curved clypeal margin. **18)** Head of *O. meandrus* Paulsen, new species, showing wavy clypeal margin.

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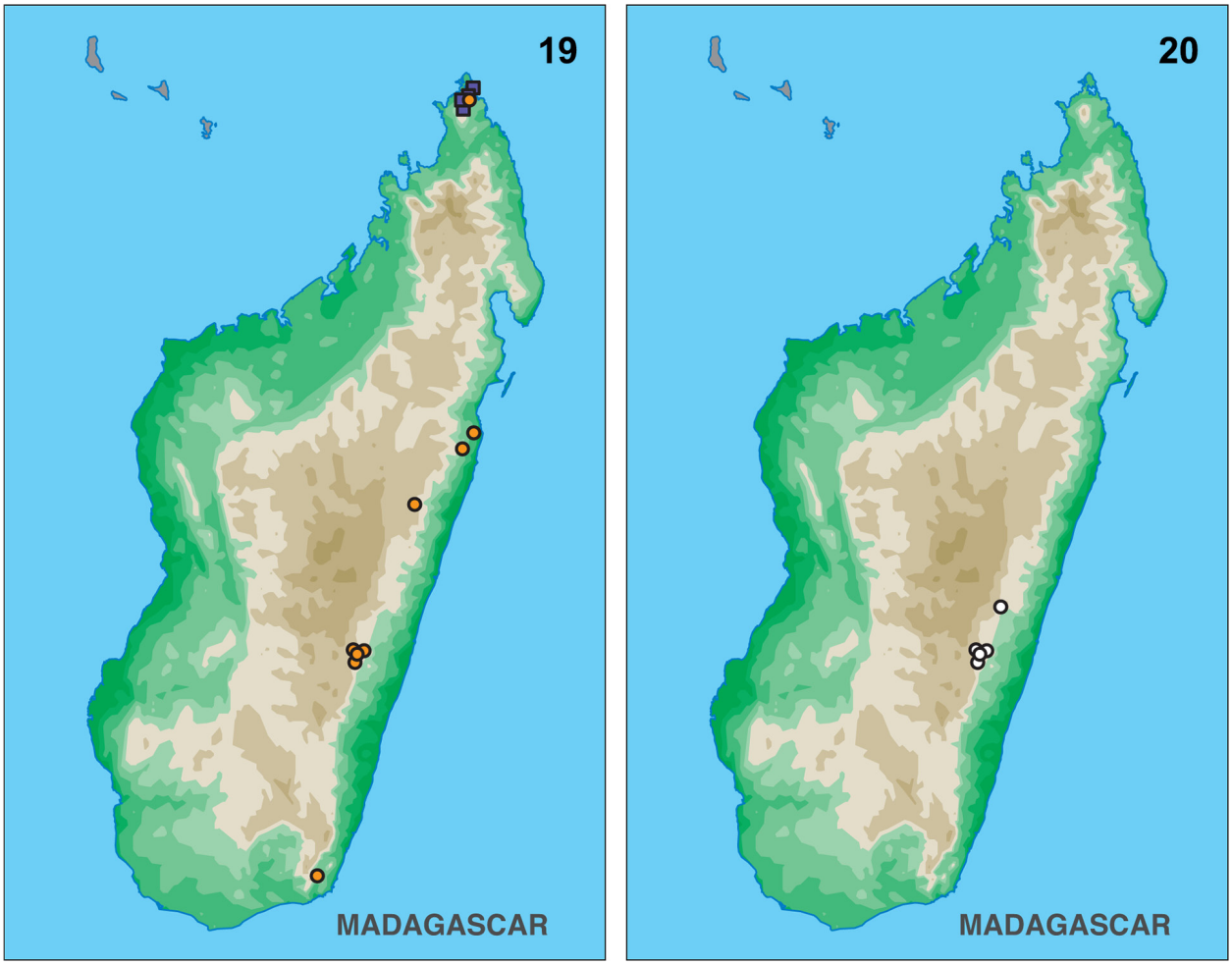

Figures 19–20. Distributions of new species of Madagascar *Ochodaeus*. **19)** Blue squares = *O. modopunctatus* Paulsen, new species; orange circles = *O. polypollicatus* Paulsen, new species. **20)** White circles = *O. meandrus* Paulsen, new species.

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