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Revision of the endemic Madagascan stag beetle
genus *Ganelius* Benesh, and description of a new, related genus
(Coleoptera: Lucanidae: Lucaninae: Figulini)

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Revision of the endemic Madagascan stag beetle genus *Ganelius* Benesh, and description of a new, related genus (Coleoptera: Lucanidae: Lucaninae: Figulini)

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Abstract. This paper revises the genus *Ganelius* Benesh, which is endemic to Madagascar, in the stag beetle tribe Figulini Burmeister (Coleoptera: Lucanidae: Lucaninae). Species in the genus are striking in their highly sexually dimorphic mandibles, a character that rarely occurs in the tribe. The genus was previously comprised of four species, but three of these names were problematic or questionably applied. A **lectotype** is designated for *G. madagascariensis* Laporte, a **neotype** is designated for *Ganelius oberndorferi* Nonfried, and *Nigidius passaliformis* Benesh is **newly synonymized** with *G. oberndorferi*. Two **new species**, *G. gnamptus* Paulsen and *G. zombi* Paulsen, are described from western Madagascar. The identity of the overlooked *Ganelius nageli* (Kriesche) is fixed through a **neotype** designation, and the species is moved to the **new genus** *Agnelius*, which is distinguished from *Ganelius* by a lack of sexual dimorphism, serrate protibiae, and a more flattened body.

Key Words. Figuline, taxonomy, Africa, Madagascar, new genus, *Agnelius*

Introduction

This paper revises the Madagascan genus *Ganelius* Benesh of the tribe Figulini Burmeister. Figulines are distributed almost exclusively in the Old World and are notable among the Lucaninae in their limited presentation of sexual dimorphism. They have eyes that are completely divided by an ocular canthus and frequently display a flattened or elongate form and may be modified for termitophily. Three genera in the Mascarene Islands are flightless. Although sexual dimorphism is rare among figulines, it reaches one of its zeniths in *Ganelius* mandibles, which are strikingly different between males and females.

The distinctly sexually dimorphic mandibles and pronotum that appears almost smooth with only fine punctures (lacking a strongly indicated midline) distinguish the genus *Ganelius* from *Nigidius* MacLeay. *Ganelius* is a small genus of stag beetles from Madagascar, and includes four available names that are poorly understood (Bartolozzi and Werner 2004). Two of these names, *N. madagascariensis* Laporte and *N. oberndorferi* (Nonfried) are frequently applied to specimens in collections when these infrequently collected stag beetles are present, but it is clear that the names were not being used appropriately or precisely. The two other names are dubious or rarely used. Bartolozzi and Werner (2004) illustrated the type of *G. passaliformis* Benesh, which was described from a single, abraded female with dubious locality information. The species treated as *G. nageli* (Kriesche) in Bartolozzi and Werner (2004) does not conform to the generic description of *Ganelius* and is moved to a new genus below.

Due to the Madagascan biodiversity project of Dr. Brian Fisher and other researchers from the California Academy of Sciences, recent material has been made available for study in this genus. This material, together with historical specimens from Paris, has made it possible to distinguish between previously named species and also to discover new species, two of which are described here.

Materials and Methods

Specimens and taxonomic material. The following institutions and private collections provided specimens examined for this study. A total of 184 *Ganelius s.l.* specimens formed the basis of this research. For *Ganelius*, the dorsal ramus of the mandibles could give false total length measurements if confused with the true mandibular apex, so lengths given are measured from the apex of the clypeus

to the elytral apex. The greatest width is measured across the pronotum. Acronyms for collections providing material or data for this study include:

CASC	California Academy of Sciences, San Francisco, CA, USA (J. Schweikert)
FMNH	Field Museum of Natural History, Chicago, IL, USA (C. Maier)
IRSNB	Royal Belgian Institute of Natural Sciences, Brussels (A. Drumont)
LBC	Luca Bartolozzi Collection, Florence, Italy
MHNG	Muséum d'Histoire Naturelle, Geneva, Switzerland (G. Cuccodoro)
MJPC	M.J. Paulsen Collection, Lincoln, NE, USA
MNHN	Muséum National d'Histoire Naturelle, Paris, France (A. Mantilleri, S. Boucher)
NLMH	Niedersächsisches Landesmuseum, Hannover, Germany (A. Eichler)
NHM	The Natural History Museum, London, UK (M. Barclay, B. Garner, M. Kerley)
ZMHB	Museum für Naturkunde de Humboldt Universität, Berlin, Germany (Johannes Frisch, Joachim Willers)

Madagascar place names are sometimes repeated and political subdivisions have frequently changed. Historic localities required additional research to locate. The provinces used here are those found on the labels of the most recent specimens and in the current versions of common geo-referencing programs.

Taxonomic Treatments

Figulini Burmeister, 1847

Nigidiini Jakobson, 1911, synonym
 Penichrolucanini Arrow 1950, synonym
 Brasilucanini Nikolajev 1999, synonym

***Ganelius* Benesh, 1955**

Eudora Laporte, 1840: 174 (not *Eudora* Péron and Leseur, 1810; *Eudora* Rafinesque, 1815; *Eudora* De Haan, 1833)

Nagelius Benesh, 1955a: 62 (not *Nagelius* Lewis, 1909)

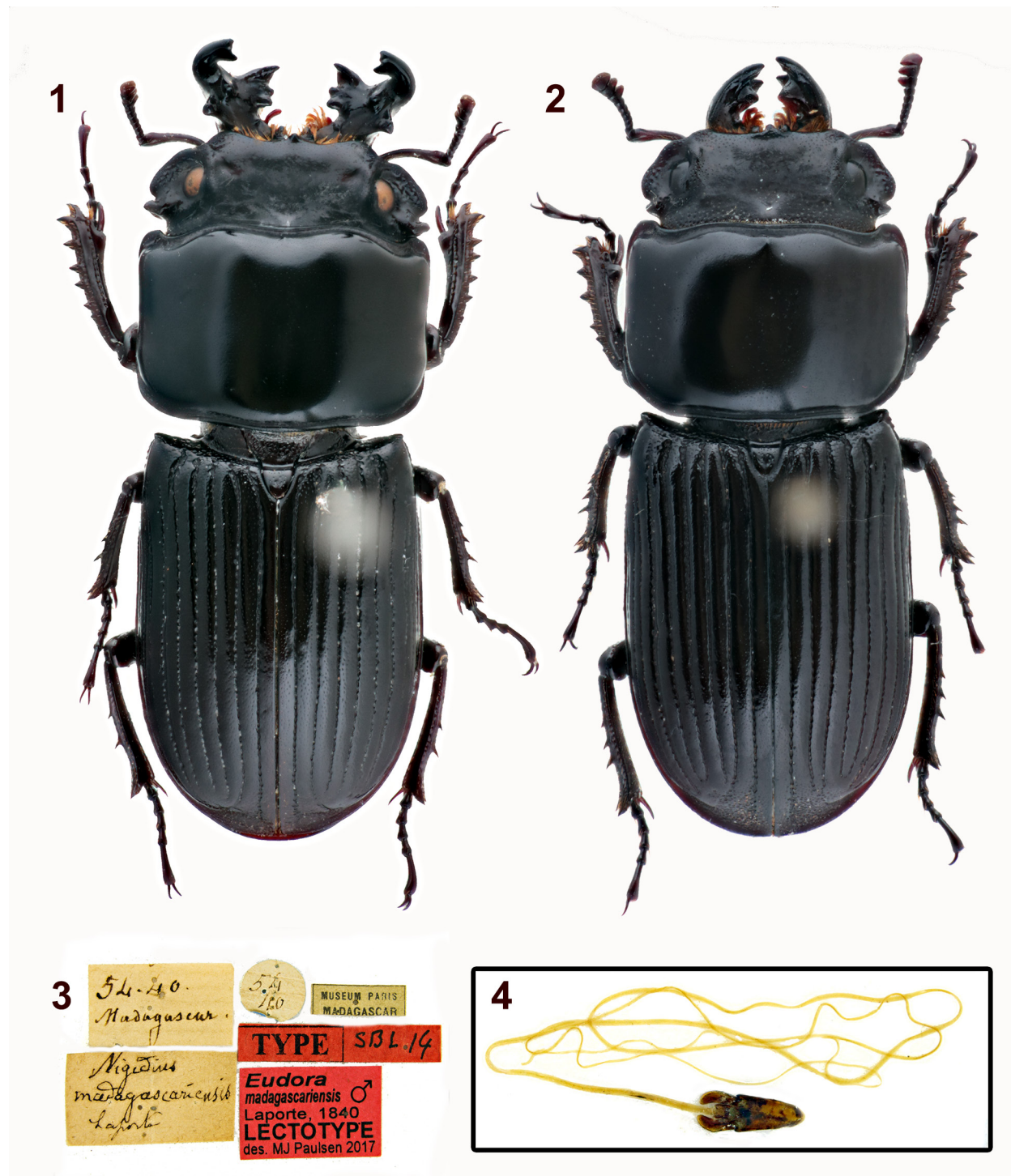
Ganelius Benesh, 1955b: 70 (new name for *Nagelius* Benesh)

Description. *Ganelius* are moderately sized (12–22 mm) figuline species that display distinctly sexually dimorphic mandibles in which males have a short mandible with a long, vertically produced dorsal ramus or branch, while females lack the dorsal ramus and have a simple, more-or-less tricuspid mandible. The pronotum appears smooth, bearing only fine punctures and always lacking a strongly indicated midline. In both sexes the pronotum has an anterior tubercle that varies from distinct to almost obsolete (especially in larger males that have the anterior margin produced on either side), and is generally elevated. The male genitalia of *Ganelius* species have an exceptionally long, thin, and gradually narrowing flagellum that varies from 20–65 mm in length. The genus only occurs in Madagascar. Species within the genus vary most importantly in the form of the mandibles, shape of the ocular canthus and anterior margin of the head, and extent of punctation of the elytra. The male genitalia between species is fairly uniform but with apparent interspecific variation in the length of the flagellum.

***Ganelius madagascariensis* (Laporte)**

Eudora madagascariensis Laporte 1840: 175 (original combination).

Type material. Lectotype male of *Eudora madagascariensis* (Fig. 1), MNHN, **here designated**, labeled (Fig. 3): a) handwritten, “54–40 / Madagascar”; b) on underside of blue circular label, “54 | 40”; c) handwritten, “*Nigidius* / *madagascariensis* / Laporte”; d) “Museum Paris / Madagascar”; e) on red paper “TYPE SBL 14”; f) on red paper “*Eudora* / *madagascariensis* ♂ / Laporte, 1840 / LECTOTYPE /



Figures 1–4. *Ganelius madagascariensis* (Laporte, 1840). 1) Male lectotype, dorsal habitus. 2) Female, dorsal habitus. 3) Lectotype labels. 4) Male genitalia, flagellum ~ 60 mm.

des. M.J. Paulsen 2017”; g) “*Ganelius / madagascariensis* / (Laporte, 1840) / det. M.J. Paulsen 2017”. Paralectotype female, MNHN, labeled: a) on underside of blue circular label, “54 | 40”; b) handwritten, “*Nigidius / madagascariensis* / Laporte / Madagascar”; c) on yellow paper “*Eudora / madagascariensis* ♀ / Laporte, 1840 / PARALECTOTYPE / des. M.J. Paulsen 2017”; d) “*Ganelius / madagascariensis* / (Laporte, 1840) / det. M.J. Paulsen 2017”.

Non-type material (Fig. 33). **MADAGASCAR:** ANTSIRANANA: Antsiranana [Diego Suarez] (11♂, 18♀; CASC, IRSNB, MNHN); Forêt d’Antsahabe (2♂, 1♀; CASC, MJPC). Mt. D’Ambre (8♂, 8♀; FMNH, LBC, MNHN, NHM, ZMHB); Reserve l’Ankarana (2♂, 1♀; CASC, MNHN). FIANARANTSOA: Ambositra (1♀, MNHN); Ivohibe (1♀, MNHN); Mananjary (1♂, 2♀, IRNSB, NHM); Midongy (1♂, MNHN). TOAMASINA: Alahakato Forest/Tamatave (1♂, 1♀; MNHN); Ambodisaina (1♂, MNHN); Fampanambo (1♂, 1♀; MNHN); Fenerive (2♀, MNHN); Rogez (1♂, MHNG); Antanambe/S. of Baie Antongil (6♂, 8♀; CASC, FMNH, LBC, MNHN, ZMHB); Lake Alaotra/Antsianaka (1♂, 1♀; MNHN); Maroantsetra /Ambodivoangy (1♂, 3♀; NHM, MNHN); Ste. Marie de Madagascar (1♀, MNHN). TOLIARA: Cape Andrahomana (1♂, MNHN); 20 km N of Fort Dauphin [Taolagnaro] (1♀, MNHN).

Diagnosis. The male mandibles have an acute basal tooth on the dorsal ramus that is near the median denticle (Fig. 1, 26), and this tooth remains subacute in smaller specimens. In males of *G. oberndorferi*, the homologous tooth is poorly developed and obtuse (Fig. 5, 27). Females (Fig. 2) are difficult to distinguish from those of *G. oberndorferi*, but the ocular canthus of female *G. madagascariensis* (Fig. 28) is straight to weakly concave, while that of *G. oberndorferi* is distinctly concave, and the suprantennal tubercle is less elevated in *G. madagascariensis*. The male genitalia possess a flagellum that is much longer than the insect itself (Fig. 4).

Remarks. Laporte (1840) described this species from an unknown number of specimens. Two specimens from MNHN, a male and female of nearly identical size, bear labels corresponding to the accession log entry for “Séries 1854-40”, which translates to 60 insect specimens from Madagascar bought from Mr. Deyrolle for 339 francs. The lectotype male chosen bears a type label added by S. Boucher (MNHN, pers. comm.) who selected it as certainly having been studied by Laporte while in the Deyrolle collection before accession. The other specimen is a female that bears similar labels and therefore must be treated as a paralectotype. The lectotype lacks specific locality data, however it is indistinguishable from males from the locality of Ambodivoangy and others around Antongil Bay. Although somewhat variable in mandibular form, additional specimens from farther south along the entire eastern side of the island cannot be separated from *G. madagascariensis*.

Two female specimens of *G. madagascariensis* are imaged and listed as ‘types’ on the website of IRSNB. I have examined the two specimens, which appear to be more recent Oberthür specimens and determined that they are not part of the type series. They are not labeled as types.

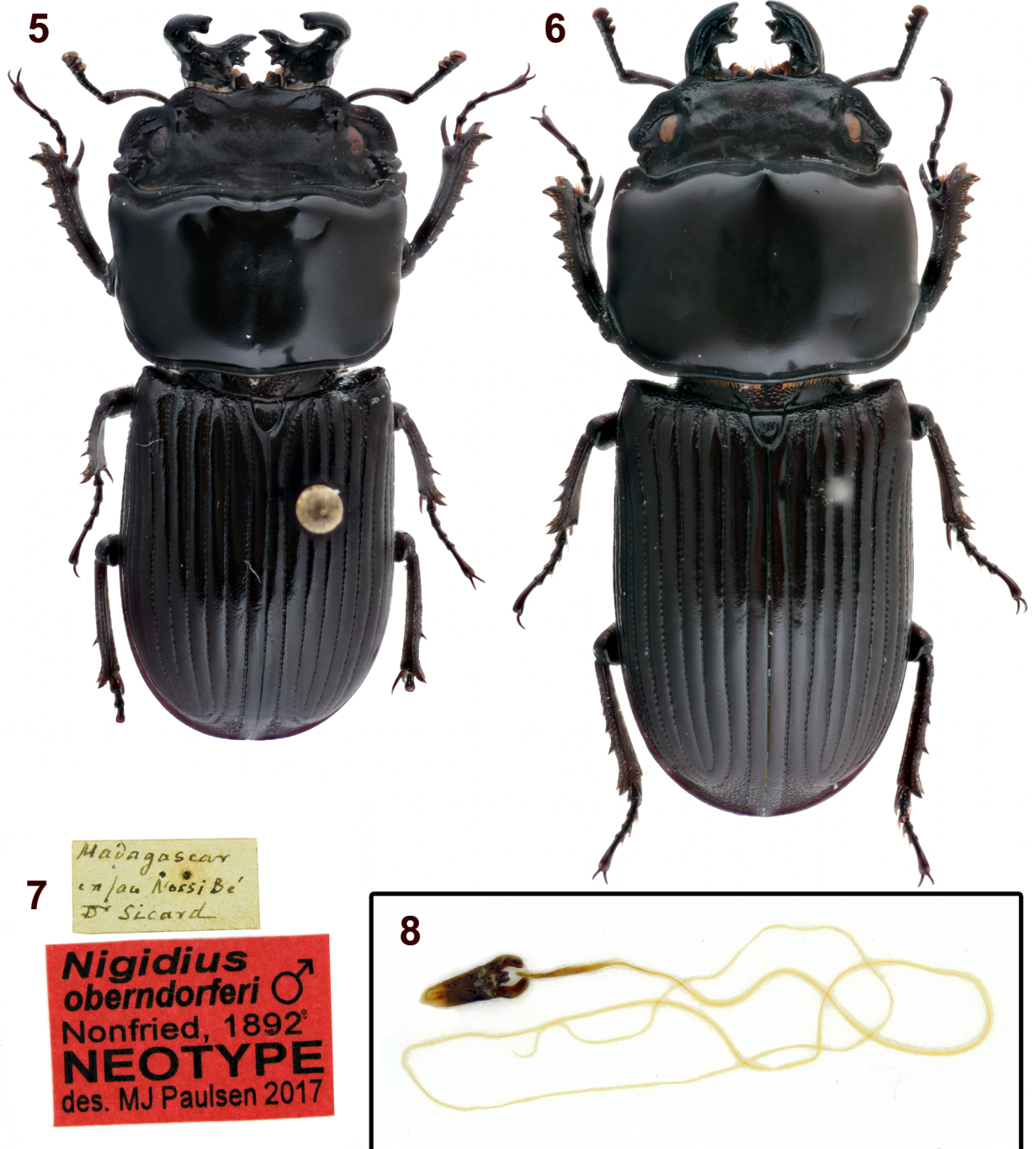
Ganelius oberndorferi (Nonfried)

Nigidius oberndorferi Nonfried 1892: 118 (original combination)

Nigidius passaliformis Benesh, 1943: 44 (original combination), **new synonymy**

Type material. Neotype male of *Nigidius oberndorferi* Nonfried (Fig. 5), MNHN, **here designated**, labeled (Fig. 7): a) “Madagascar / en | au Nossi Bé / Dr. Sicard”; b) on red paper “*Nigidius / oberndorferi* ♂ / Nonfried, 1892 / NEOTYPE / des. M.J. Paulsen 2017”; b) “*Ganelius / oberndorferi* / (Nonfried, 1892) / det. M.J. Paulsen 2017”.

Holotype female of *Nigidius passaliformis* Benesh, Museum of Comparative Zoology, labeled: a) handwritten, “West Africa / coll. Harvard”; b) handwritten, “*Eudora / passaliformis* / (Benesh)”; c) on red paper, “HoloTYPE / B. Benesh”; d) on red paper, “M.C.Z. / Type / 25913”; e) handwritten, “*Nigidius / passaliformis* / Benesh”; f) on orange paper, “Allotype” (sic); g) “H. Bomans det. 196 [72] / [= ♀ *Ganelius / madagascariensis* / Cast.]”; h) handwritten, “Origin certainly / inaccurate – / This insect seen only in Madagascar / !”. Images studied (Perkins 2010).



Figures 5–8. *Ganelius oberndorferi* (Nonfried, 1892). 5) Male neotype, dorsal habitus. 6) Female, dorsal habitus. 7) Neotype labels. 8) Male genitalia, flagellum, 41 mm.

Non-type material (Fig. 34). **MADAGASCAR:** ANTSIRANANA: Ambanja (2♂, 1♀; MNHN); Ambilobe (1♂, MNHN); “Ambodinadiro” (Fort Ambodimadiro, Passandava Bay) (1♂, 1♀; MHNG); Ankarana (1♂; MNHN); Nosy Be (1♂, 3♀; MNHN). **MAHAJANGA:** Forêt d’Anobohazo (1♂ MJPC). **TOAMASINA:** Maroantsetra (1♂, 2♀; IRSNB).

Diagnosis. In males of *G. oberndorferi* the dorso-basal tooth on the vertical ramus is weakly produced and obtuse and much lower than the interior median denticle of the ramus; in *G. madagascariensis* the external dorso-basal tooth is strongly produced and near to the interior median denticle of the ramus (see Fig. 26–27). In females of *G. oberndorferi* the canthus is sloping and concave (Fig. 29), not straight or almost rounded as with female *G. madagascariensis*. In addition, the tubercle above the antennal insertion is usually much more elevated in females of *G. oberndorferi* (Fig. 6). The flagellum of the male genitalia (Fig. 8) is somewhat shorter than in *G. madagascariensis*.

Remarks. The number of specimens examined by Nonfried (1892) is not stated, but may have consisted of only a single specimen. The following information was contributed by S. Boucher, MNHN, concerning the whereabouts of Nonfried’s type (pers. comm.). No probable type specimens of *G. oberndorferi* Nonfried have been located in MNHN, where Nonfried specimens received a special label printed by Oberthür and thus are readily identifiable. This part of Nonfried’s collection arrived in Paris from Oberthür in 1952, but another large part of Nonfried’s scarabaeoids were deposited at ZMHB, Berlin. All *Ganelius* material from Berlin was examined and does not appear to have originated with Nonfried. Therefore a neotype specimen is chosen from the original locality to stabilize the nomenclature and tie the name to the appropriate species. The identity of *G. oberndorferi* was confused with *A. nageli* by Benesh (1955b), in part. His second figure of *G. oberndorferi* (Benesh’s fig. 15) is a specimen of *A. nageli* from ‘Sandramora’ forest, near Vohilava in eastern Madagascar. Because Benesh (1955b) mixed two different species under the name, and Didier (1928) erroneously considered the species to belong to the genus *Figulus* MacLeay, a neotype is clearly necessary to resolve the identity of *G. oberndorferi*.

Nonfried (1891) clearly described the mandibles and ocular canthus of this species. The mandibles are described as long, bent nearly vertically and reinforced at the bottom of the base with a large tooth, while the tip is made of two bifurcated small teeth. This description confuses the actual apex with the dorsal ramus, but it nevertheless clearly refers to a male *Ganelius*. In the original description, Nonfried (1892) noted that it differed by its slimmer construction and differences in pronotal shape and mandibular form. The first two characters are variable based on body size. However, based on the male mandibles of material examined from the type locality as described in the diagnosis, this species is distinct from *G. madagascariensis*. Based on the relatively few specimens available for study, the species may be restricted to extreme northern Madagascar near the type locality (Fig. 34). A series of specimens from the Lemoult collection in IRSNB are labeled as being from Maroantsetra. If correct these specimens are geographically separated from all others and possibly sympatric with *G. madagascariensis*, which seems unlikely. However, I do not have any information about whether these might be mislabeled with the locality actually referring to the port from which they were shipped, or if this is a common distributional pattern.

Benesh (1943) described *G. passaliformis* from ‘West Africa’, which Bartolozzi and Werner (2004) proposed might be referring to Madagascar since the genus is not known from mainland Africa. Benesh discusses the specimen as male, however it is a female, which he confirmed with a subsequent dissection (Benesh 1955a). The holotype is entirely consistent with females of *G. oberndorferi*. Specimens of that species on hand are indistinguishable from images of Benesh’s type, especially in the concave, sloping anterior margin of the head, elevated suprantennal tubercles, and vaulted appearance of the pronotum anteriorly in lateral view. Thus a name based on a single, abraded female specimen rather unsurprisingly is reduced here to synonymy.

***Ganelius gnamptus* Paulsen, new species**

Type material. Holotype male (Fig. 9), CASC, labeled (Fig. 11): a) “MADAGASCAR: Mahajanga / Prov: Parc National Tsingy / de Bemaraha, 2.5 km 62° ENE / Bekopaka, Ankidrodra River / elev 100 m 11–15 Nov. 2001”; b) “19° 7' 56" S 44° 48' 53" E / coll: Fisher, Griswold et al. / California Acad. of Sciences /



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MADAGASCAR: Mahajanga Prov: Parc National Tsingy de Bemaraha, 2.5 km 62° ENE Bekopaka, Ankidrodroa River elev 100m 11-15 Nov. 2001	CASENT 8030423	***** Collection of the CALIFORNIA ACADEMY OF SCIENCES, San Francisco, Calif. *****
19° 7' 56" S 44° 48' 53" E coll: Fisher, Griswold et al. California Acad. of Sciences general collecting - tropical dry forest on Tsingy, BLF4342		



Figures 9–12. *Ganelius gnampus* Paulsen, n.sp. 9) Male holotype, dorsal habitus. 10) Female paratype, dorsal habitus. 11) Holotype labels. 12) Male genitalia, flagellum, 21 mm.

general collecting – tropical dry / forest on Tsingy, BLF4342”; c) “CASENT / 8030423”; d) “Collection of the / California Academy of Sciences, San / Francisco, Calif.”; e) on red paper, “*Ganelius / gnampthus* ♂ / HOLOTYPE / des. M.J. Paulsen 2017”.

Two paratype females (CASC, MJPC) labeled: a) “MADAGASCAR: Toliara Prov. / Forêt de Kirindy, 15.5 km 64° / ENE Marofandilia, elev 100 m / 28 Nov. – 3 Dec. 2001 / 20° 2' 42" S 44° 39' 44" E”; b) “coll: Fisher, Griswold et al. / California Acad. of Sciences / at light – in tropical dry forest / coll. code: BLF4603”; c) on yellow paper, “*Ganelius / gnampthus* ♀ / PARATYPE / des. M.J. Paulsen 2017”.

Description, holotype male. Length: 12.0 mm. Width: 4.9 mm. **Color:** Piceous black. **Head:** Surface matte on disc, becoming shiny near margins, evenly punctate; punctures small, sparse (separated by 5 or more diameters). Clypeus short, emarginate on each side, apex acuminate with small denticle. Clypeolabral suture obsolete. Labrum bifurcate, visible dorsally, almost on same plane as clypeus. Suprantennal tubercle small but distinct. Ocular canthus wide, broadly convex (almost semicircular); canthus subcontiguous with anterior and posterior margins of head; postocular process almost obsolete. Antennal club small, short (shorter than scape), antennomeres tomentose only distally. Mandibles (to true apex) shorter than head, apex acute, internal tooth subrectangular. Dorsal surface produced into long, vertical ramus (false apex); ramus with apex acute, triangular subapical tooth, serrate margin internally, and basal lobe reduced to carina. Mentum broad, surface coarsely, semicircularly but shallowly punctate. **Pronotum:** Form broad, wider than elytra. Anterior angles subacute. Surface appearing smooth, actually finely shagreened and with finer punctures than head. Anteromedial tubercle almost obsolete. **Elytra:** Form slightly wider posteriorly. Surface with serially punctate striae, striae impressed basally becoming weakly impressed towards apex, striae 7–9 almost obsolete, striae with punctures not crenulating intervals. Intervals convex basally, becoming flat elsewhere, punctate with fine, shallow punctures in 3–5 irregular rows. **Legs:** Protibia with 5 acute teeth decreasing in size proximally. Mesotibiae and metatibiae with 1 large external tooth below middle with 1–3 smaller accessory teeth proximally. **Abdomen:** Male genitalia (Fig. 12) with permanently everted internal sac (flagellum) whip-like, 21 mm.

Paratype variation. Females ($n = 2$). Length: 14.9–15.2 mm. Width: 6.1–6.4 mm. The females (Fig. 10) differ from the holotype male in the following characters: Clypeal apex with median tooth larger. Labrum lower than clypeus, not distinctly visible in dorsal view. Suprantennal tubercles more strongly elevated. Antennal club smaller. Mandibles lacking dorsal ramus, subapical dorsal tooth large, obtuse. Anteromedial pronotal tubercle distinct.

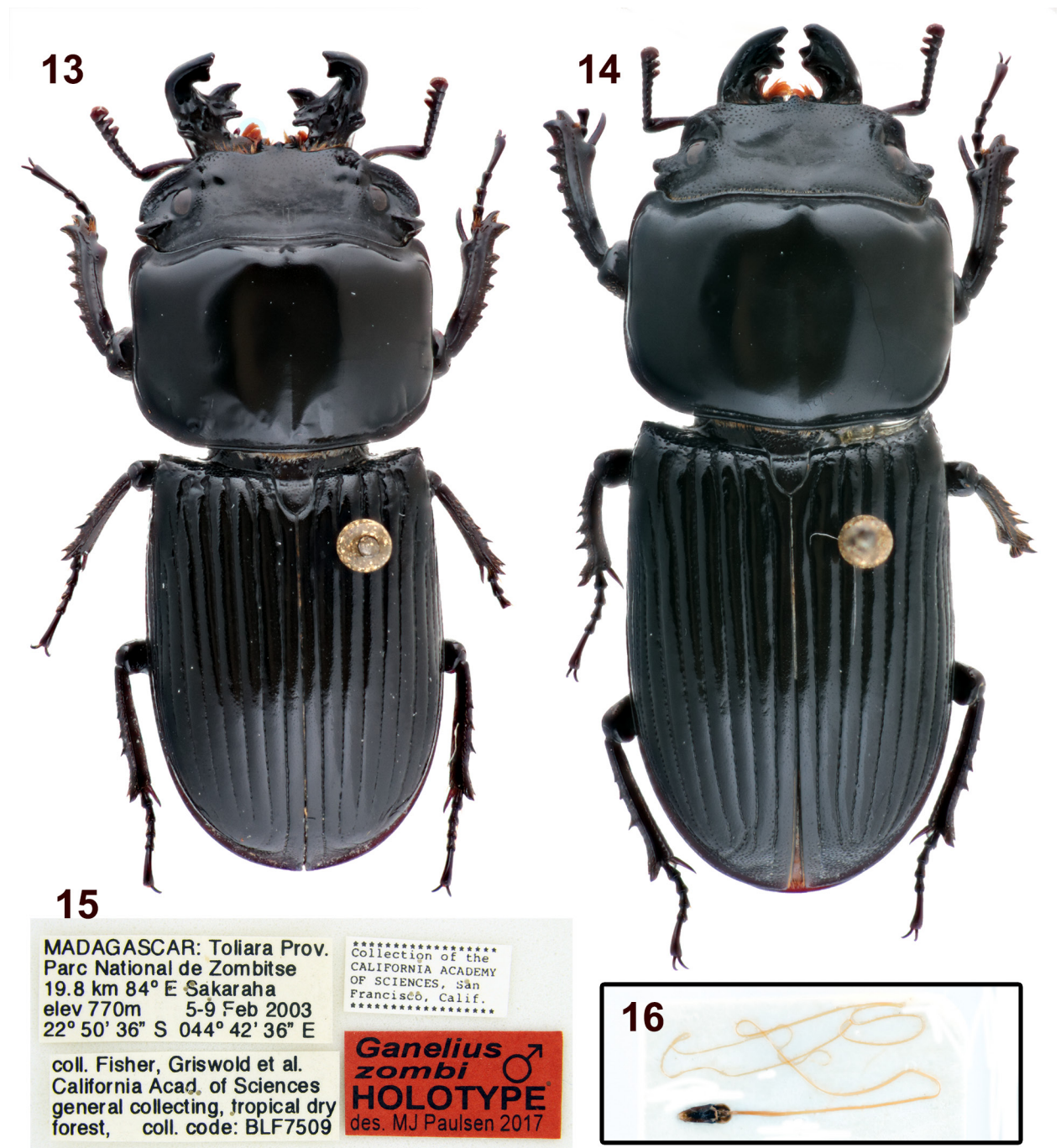
Remarks. The broadly convex canthus (Fig. 9, 10, 30) of this species makes it immediately distinguishable. The male holotype is the smallest *Ganelius* specimen studied, and larger males would likely have a more distinct pronotal tubercle on a more convex pronotum, with more developed mandibles. The female mandibles in this species are unique in being sharply bent internally in the basal third (Fig. 30), with females of other species have simply rounded mandibles. The females display the same rounded head and relatively flat pronotum with a weak tubercle that is seen in the male holotype.

Etymology. The specific epithet is a Latinized adjective derived from the Greek *gnampotos* meaning curved, in reference to the head shape of this species that is broadly curved anteriorly.

Distribution (Fig. 35). **MADAGASCAR:** MAHAJANGA: P.N. Tsingy de Bemaraha. **TOLIARA:** Forêt de Kirindy near Mandofandilia.

Ganelius zombi Paulsen, new species

Type material. Holotype male (Fig. 13), CASC, labeled (Fig. 15): a) “MADAGASCAR: Toliara Prov / Parc National de Zombitse / 19.8 km 84° E Sakaraha / elev 770 m 5–9 Feb 2003 / 22° 50' 36" S 044° 42' 36" E”; b) “coll. Fisher, Griswold et al. / California Acad. of Sciences / general collecting, tropical dry / forest, coll. code: BLF7509”; c) “Collection of the / California Academy of Sciences, San / Francisco, Calif.”; d) on red paper, “*Ganelius / zombi* ♂ / HOLOTYPE / des. M.J. Paulsen 2017”.



Figures 13–16. *Ganelius zombi* Paulsen, n.sp. 13) Male holotype, dorsal habitus. 14) Female paratype, dorsal habitus. 15) Holotype labels. 16) Male genitalia, flagellum, ~50 mm.

Three female paratypes, 2 CASC, 1 MJPC, labeled: a–c) as holotype. One male, one female paratypes, CASC, labeled: a) “MADAGASCAR: Mahajanga / Prov: Parc National Tsingy / de Bemaraha, 3.4 km 93° E / Bekopaka, Tombeau Vazimba / Elev 50 m 6–10 Nov. 2001 / 19° 8' 31" S 44° 49' 41" E"; b) “coll: Fisher, Griswold et al. / California Acad. of Sciences / general collecting, tropical dry / forest, coll. code: BLF4231”; c) as holotype. One female paratype (CASC), labeled: a) MADAGASCAR: Mahajanga / Prov: Parc National Tsingy / de Bemaraha, 2.5 km 62° ENE / Bekopaka, Ankidrodroa River / elev 100 m 11–15 Nov. 2001”; b) “19° 7' 56" S 44° 48' 53" E / coll: Fisher, Griswold et al. / California Acad. of Sciences / general collecting – tropical dry / forest on Tsingy, BLF4342”; c) as holotype. One male, one female paratypes (CASC, MJPC) labeled: a) “MADAGASCAR: Mahajanga / Prov. Forêt de Tsimembo, / 8.7 km 336° NNW Soatana / elev 20 m 21–25 Nov. 2001 / 19° 1' 17" S 44° 26' 26" E”; b) “coll: Fisher, Griswold et al. / California Acad. of Sciences / general collecting in tropical / dry forest code: BLF4509”; c) as holotype. One male paratype (CASC) labeled: a) “MADAGASCAR: Mahajanga / Prov: Parc National Tsingy / de Bemaraha, 10.6 km ESE / 123° Antsalova, elev 150 m / 16–20 November, 2001 / 19° 42' 34" S 44° 43' 5" E”; b) “coll: Fisher, Griswold et al. / California Acad. of Sciences / at light in tropical dry forest / on Tsingy, BLF4431”; c) as holotype. One paratype male (CASC) labeled: a) handwritten, “*Nigidius / madagas- / cariensis*”; b) “Collection of the / California Academy of Sciences, San / Francisco, Calif.”. One paratype female (MNHN) labeled: a) “Forêt de l' / Ankarafantsika”; b) “Museum Paris”. All paratypes labeled on yellow paper, “*Ganelius / zombi* (♂ or ♀) / PARATYPE / des. M.J. Paulsen 2017”.

Description, holotype male. Length: 16.4 mm. Width: 6.6 mm. **Color:** Piceous black. **Head:** Surface velvety shagreened, impunctate basally, anterior half of frons shagreened with fine, shallow punctures, becoming shiny near margins with larger punctures laterally. Clypeus short, emarginate on each side, apex acuminate with median denticle. Clypeolabral suture obsolete. Labrum bifurcate, visible dorsally, just below clypeus. Suprantennal tubercle weakly elevated but distinct, elongate. Ocular canthus broad, rounded, laterally produced, convex; canthus not contiguous with anterior and posterior margins of head; postocular process a large, compressed, transverse plate. Antennal club moderate, short (shorter than scape), antennomeres tomentose only distally. Mandibles (to true apex) shorter than head, apex triangular, internal tooth bifurcate. Dorsal surface produced into long, vertical ramus (false apex); ramus with apex truncate, conjoined to triangular subapical tooth, margin not serrate internally, basal lobe forming an obtuse tooth remote from smaller internal tooth. Mentum broad, distinctly emarginate, surface coarsely, contiguously punctate. **Pronotum:** Form broad, wider than elytra. Anterior angles transversely truncate. Surface smooth with minute punctures. Anteromedial tubercle small, anterior margin produced on either side. **Elytra:** Form subparallel, widest at middle. Surface with serially punctate striae, striae impressed basally (rugose at base) becoming weakly impressed towards apex, striae 7–9 almost obsolete except medially, striae very with regular sides without punctures crenulating intervals; strial punctures elongate. Intervals strongly convex basally, becoming flat towards apex, punctate with fine, shallow punctures in 3–5 irregular rows. **Legs:** Protibia with 7 acute teeth decreasing in size proximally. Mesotibiae and metatibiae with 1 large external tooth below middle with 1–3 smaller accessory teeth proximally. **Abdomen:** Male genitalia (Fig. 16) with permanently everted internal sac (flagellum) whip-like, 45 mm.

Paratype variation. Males ($n = 4$). Length: 13.0–16.1 mm. Width: 5.2–6.9 mm. Postocular process varying from compressed as in holotype to bulbous; reduced in smaller males. Females ($n = 7$). Length: 13.2–18.9 mm. Width: 5.2–6.9 mm. The females (Fig. 14) differ from the holotype male in the following characters: Clypeal apex with median tooth larger. Labrum lower than clypeus, not distinctly visible in dorsal view. Suprantennal tubercles more strongly elevated. Antennal club smaller. Mandibles lacking dorsal ramus, subapical dorsal tooth moderately large, obtuse. Anteromedial pronotal tubercle strongly produced in large females.

Remarks. The strongly concave ocular canthus of females of this species is immediately recognizable (Fig. 14). Males are somewhat less distinctive, but the elytral striae of the disc are narrower and have straight margins that are not crenulated by the punctures as in *G. madagascariensis* and *G. oberndorferi*.

Etymology. The specific epithet is a shortened form of the type locality Zombitse with which I originally labeled the specimens during the revision, and which gradually stuck. It is used as a noun in apposition based on an arbitrary (non-Latin) combination of letters.

Distribution (Fig. 36). **MADAGASCAR:** MAHAJANGA: Forêt d'Ankarafantsika; Forêt de Tsimembo near Soatana; P.N. Tsingy de Bemaraha. TOLIARA: P.N. Zombitse.

Agnelius Paulsen, new genus

Type species. *Nigidius nageli* Kriesche, here designated.

Description. *Agnelius* are moderately sized (12.0–17.2 mm) figuline species that lack sexually dimorphic mandibles. The mandibles of both sexes in this species are identical and are relatively simple but have a bifurcate dorsomedial tooth that is not found in other genera (Fig. 32). In both sexes the smooth, minutely punctate pronotum has a weak anterior tubercle, but the anterior margin is simply concave and not produced on either side of the tubercle as in *Ganelius*. The pronotum disc is almost flat, never elevated anteriorly, and the longitudinal midline is weakly indicated by a slight depression. The male genitalia have a gradually narrowing flagellum that is less than 20 mm in length.

Remarks. The species described as *Nigidius nageli* Kriesche differs morphologically from *Ganelius* species in significant ways, and as indicated by Fujita (2010) its placement within *Ganelius* is problematic. Among the Figulini, it shares the long flagellum of the male genitalia with *Ganelius* species, as well as a trilobed conjoined clypeus and labrum. However, unlike *Ganelius*, it lacks sexual dimorphism in the shape of the mandibles (males lacking the vertical ramus), the pronotum has a simply concave anterior margin with a weak anteromedial tubercle (vs. bisinuate margin and usually stronger tubercle), and its body is distinctly flattened and more elongate (Fig. 21–25). The protibial dentition is different than in *Ganelius*, with large, contiguous teeth rather than isolated smaller teeth. For these reasons a new genus is erected for the species.

Etymology. The name, gender masculine, is formed by corruption of *Ganelius* through rearranging letters to echo the name of the nearby and somewhat similar Mascarene figuline genus *Agnus* Burmeister.

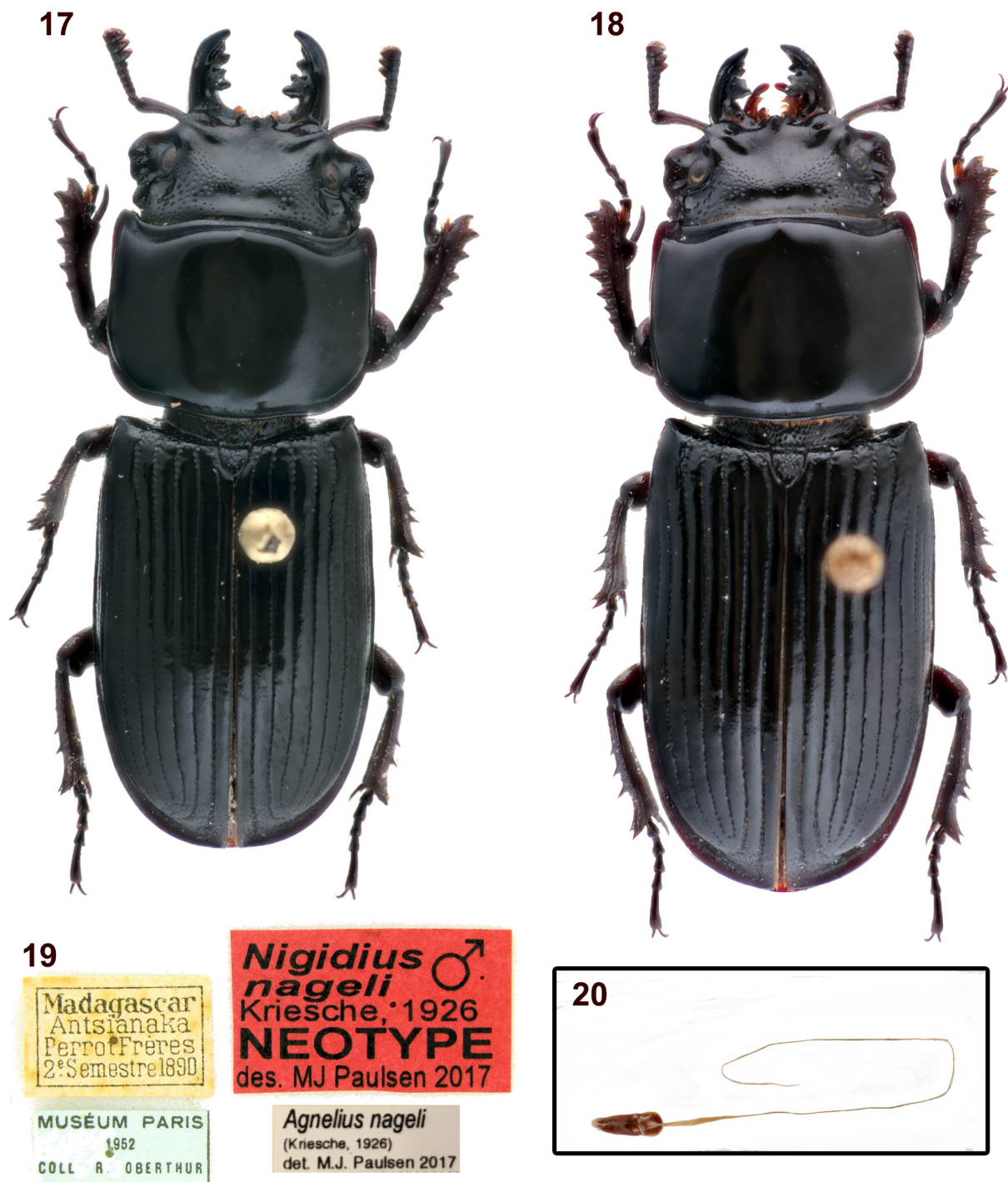
Agnelius nageli (Kriesche), new combination

Nigidius nageli Kriesche 1926: 385 (original combination)

Type material. Neotype male, MNHN, **here designated**, labeled: a) “Madagascar / Antsianaka / Perrot Frères / 2° Semestre 1890”; b) on light blue paper, “Museum Paris / 1952 / Coll. R. Oberthur”; c) on red paper, “*Nigidius nageli* / ♂ Kriesche / NEOTYPE / des. MJ Paulsen”; d) “*Agnelius / nageli* / (Kriesche, 1926) / det. M.J. Paulsen 2017”.

Non-type material (Fig. 37). **MADAGASCAR:** FIANARANTSOA: Ambatofitorahana (1; LBC); Ambositra (1 ♂; MNHN); Talakately (1 ♂; CASC); Vondrozo (2 ♂; MNHN). TOAMASINA: Antsianaka/Lake Alaotra (11 ♂, 6 ♀, MNHN); Beparasy (1; LBC); Fanovana (1♂, 1♀; MNHN); Fenerive (2 ♂, 1 ♀; CASC, MNHN); Maroantsetra, (1 ♀; MNHN); Perinet (1♂, 1 ♀; MNHN); Rogez (5 ♂, 4 ♀; MHNG, MJPC); Tamatave/Toamasina (3; MNHN).

Diagnosis. This species is immediately separable from other Madagascan stag beetles by the characters discussed above. It is the only species with mandibles with a bifurcate median tooth (Fig. 32). The flattened, elongate form is also distinctive.



Figures 17–20. *Agnelius nageli* (Kriesche, 1926). 17) Male neotype, dorsal habitus. 18) Female, dorsal habitus. 19) Neotype labels. 20) Male genitalia, flagellum, <20 mm.

Remarks. Bartolozzi and Werner (2004) indicated that the type of *G. nageli* (Kriesche), which was originally deposited in Hannover, Germany, is presumably lost. The stag beetle primary types from Hannover were taken to Hamburg for study by Paul Nagel (A. Eichler, NLMH, pers. comm.) where they were destroyed during WWII (Klapperich 1948).

Although Kriesche's holotype is lost, when comparing the available material with his original description, his species *N. nageli* can be distinguished. I had originally considered the species in question to be an undescribed species of *Ganelius* from the eastern Madagascan forests that oddly lacked visible sexual dimorphism. The species was illustrated by Benesh (1955) as *Nigidius oberndorferi*, in part (Benesh's fig. 15), and in Fujita (2010) as "*Ganelius?* spp." (species 1279). Characteristics described by Kriesche that cannot be ignored are the fitting description of the canthus, mentum with a button-like elevation, shiny and finely punctate frons, and especially the more elongate form. Most examined specimens are identical to Kriesche's values of 19 mm in length (including mandibles) and 6 mm in width. Kriesche indicated that the specimen was female, which would be expected for a species that lacks sexual dimorphism in a time when genitalic dissections were rarely performed.

A neotype is designated to tie the name to this species and eliminate confusion about its previously unknown identity. Kriesche's original locality was simply 'Madagaskar' and a female indicated, however without genitalic dissection the lack of sexual dimorphism makes the sex equivocal; a neotype male is chosen from the MNHN material from Antsianaka.

Acknowledgments

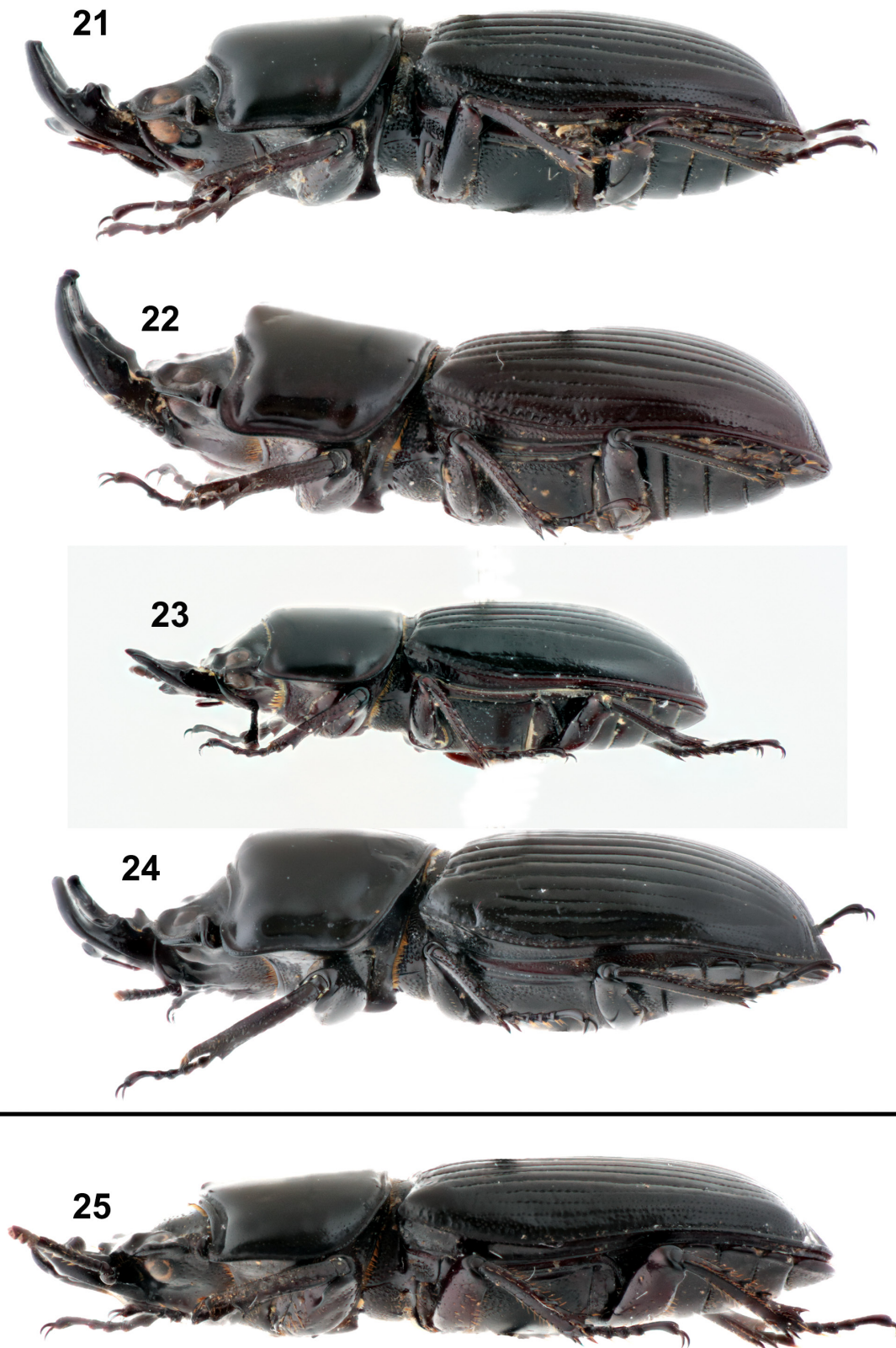
I thank the individuals and institutions listed above for loaning the specimens necessary to complete this research, especially the researchers of CASC for spearheading and making possible the study of Madagascan biodiversity. Dr. Stéphane Boucher (MNHN) provided critical information about the probable lectotype specimens in the Paris collection. I also thank David C. Hawks (Riverside, CA) and Dr. Andrew Smith (Canadian Museum of Nature) for reviewing the manuscript.

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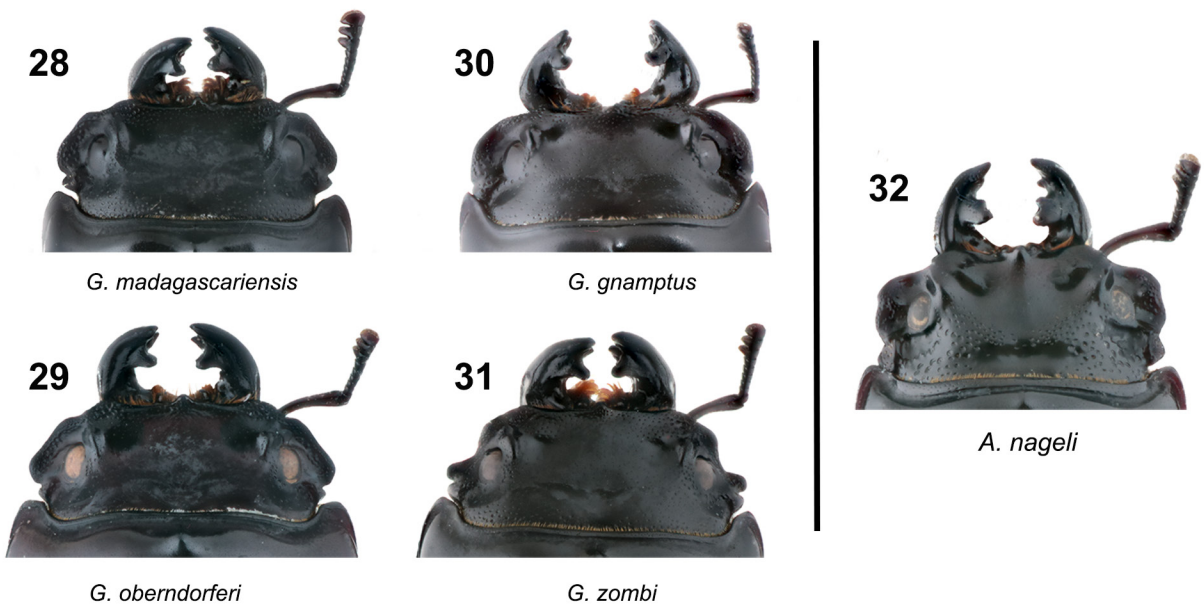
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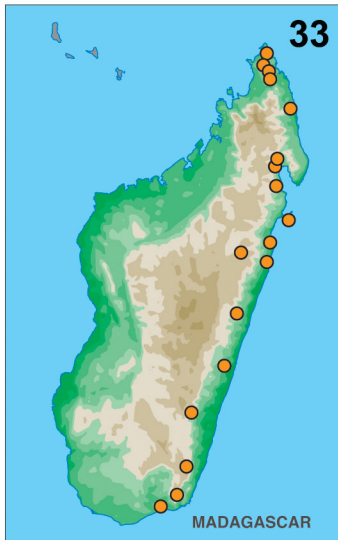
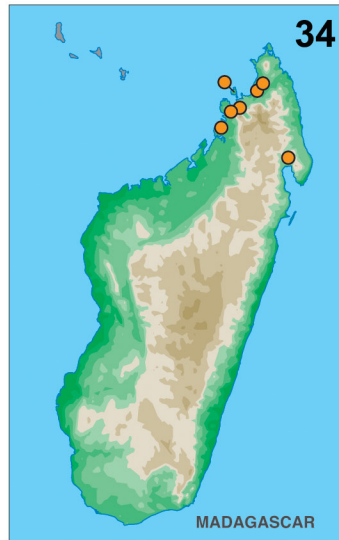
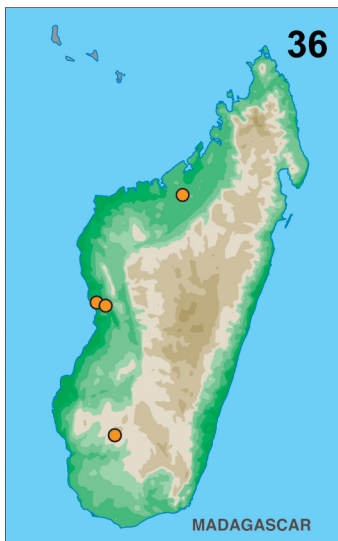
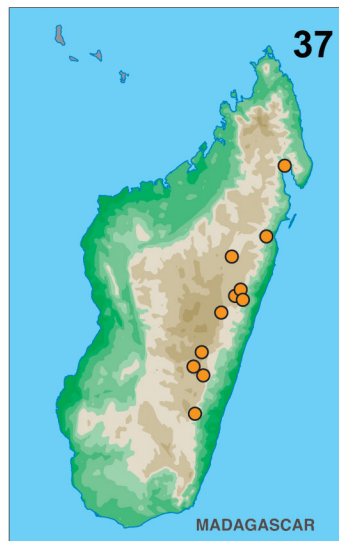
Figures 21-25. Lateral view, males. 21) *Ganelius madagascariensis*. 22) *G. oberndorferi*. 23) *G. gnamptus*. 24) *G. zombi*. 25) *Agnelius nageli*.



Figures 26–27. Comparison of male mandibles. Arrows indicate relative position of dorsal basal teeth and median denticles. **26)** *Ganelius madagascariensis*. **27)** *G. oberndorferi*.



Figures 28–32. Comparison of ocular canthi, females. **28)** *Ganelius madagascariensis*. **29)** *G. oberndorferi*. **30)** *G. gnamptus*. **31)** *G. zombi*. **32)** *Agnelius nageli*.

*G. madagascariensis**G. oberndorferi**G. gnamptus**G. zombi**A. nageli*

Figures 33–37. Species distributions. **33)** *Ganelius madagascariensis*. **34)** *G. oberndorferi*. **35)** *G. gnamptus*. **36)** *G. zombi*. **37)** *Agnelius nageli*.