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Research article

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**Revision of the palm-pollinating weevil genus
Elaeidobius Kuschel, 1952 (Curculionidae, Curculioninae,
Derelomini) with descriptions of two new species**

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Abstract. The genus *Elaeidobius* Kuschel, 1952 (Curculionidae, Curculioninae, Derelomini) is an Afrotropical genus associated with the male inflorescences of the oil palm *Elaeis guineensis* Jacq. The activity of species in this genus is critical for pollen transportation and for the fruit set of this economically important palm. In this study, the genus *Elaeidobius* was revised using an integrative taxonomic approach, combining traditional taxonomic treatment of species and an analysis of sequences of mitochondrial genes (*COI* and *COII*). A total of eight species is now recognized: five now formally included within it [*E. bilineatus* Hustache, 1924) comb. nov., *E. kamerunicus* (Faust, 1898) comb. nov., *E. plagiatus* (Fåhræus, 1844) comb. nov., *E. singularis* (Faust, 1898) comb. nov., *E. subvittatus* Faust, 1898)], one transferred here from the genus *Prosoestus* to the genus *Elaeidobius*, *E. spatulifer* (Marshall, 1950) comb. nov., and two newly described species (*E. pilimargo* Haran & Kuschel sp. nov., *E. piliventris* Haran & Kuschel sp. nov.). The following new synonymies are proposed: *Prosoestus armatus* Voss, 1956 = *E. bilineatus* (Hustache, 1924) comb. nov. and *Derelomus uelensis* Hustache = *E. singularis* (Faust, 1898). An illustrated key to the species is provided with photographs of the adult habitus and male genitalia.

Keywords. Pollination, *Elaeis guineensis*, new species, Afrotropical Region, integrative taxonomy.

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Introduction

The Derelomini Lacordaire, 1865 (Curculionidae, Curculioninae) constitute a tribe of weevils mainly associated with the inflorescences of angiosperms, containing around 265 species assembled in 40 genera (Lacordaire 1865; Alonso-Zarazaga & Lyal 1999; Franz 2006; Caldara *et al.* 2014). Species diversity, host plants and generic splits have been quite well documented in the New World (Kuschel 1952, see Franz & Valente 2005 for a review). By contrast, the species of the Old World remain very poorly known (see postscript at the end of this section). In the Afrotropical region itself, 6 genera are recognized: *Adisius* Fairmaire, 1903, *Elaeidobius* Kuschel, 1952, *Liothenus* Fairmaire, 1901, *Lomederus* Marshall, 1932, *Derelomus* Schoenherr, 1825 and *Psilocaulus* Fairmaire, 1901 (Alonso-Zarazaga & Lyal 1999).

Among these genera, the genus *Elaeidobius* has received attention due to its association with the inflorescences of the African oil palm (*Elaeis guineensis* Jacq., Arecaceae) a species native to tropical Africa, where it is traditionally used by local populations for its oil (Sheil *et al.* 2009). The activity of species belonging to *Elaeidobius* is critical for pollen transportation and for the fruit set of this plant (Mariau *et al.* 1991; Li *et al.* 2019). In return, the palm provides these weevils with support for larval development, constituting an exemplary case of mutualism. In a context of widespread cultivation of this oil palm across its native range and elsewhere, there is a need to review the identity of species of *Elaeidobius* to gain a better understanding of their exact role in pollinating their host.

The genus *Elaeidobius* was first created by Kuschel (1952) for *Derelomus elaeisae* Bondar, 1942 in a key of New World genera of Derelomini. Apart from this key, no diagnosis was provided for this monobasic new genus (Alonso-Zarazaga & Lyal 1999), but among other genera the species of *Elaeidobius* were distinguished by the presence of transversal eyes, of a prosternal process forming a protruding lamina and of a lateral carina on the pronotum. Later, Kuschel (1955) recognized the synonymy between *Elaeidobius elaeisae* (Bondar, 1942) and *Derelomus subvittatus* Faust, 1898, an African species associated with *Elaeis guineensis* that was accidentally introduced into South America with this palm. As a consequence of this synonymy, other African species closely related to *E. subvittatus* (Faust, 1898) fell into this genus, although no transfer has been formally made (*E. bilineatus* Hustache, 1924, *E. kamerunicus* Faust, 1898, *E. plagiatus* Fähræus, 1844 and *E. singularis* Faust, 1898).

As a result of this, the genus *Elaeidobius* is lacking a formal taxonomic treatment. In this study, the genus is revised. An integrative taxonomic approach, combining traditional taxonomic treatment of species and sequencing of mitochondrial gene fragments, is used to clarify species identity. An illustrated key to the species is provided with photographs of the adult habitus and male genitalia. An update of known distribution and host plant records is also provided.

Postscript: Unfinished work on Derelomini by Guillermo (Willy) Kuschel

[Samuel Brown & Rich Leschen]

Guillermo Kuschel undertook extensive revision work on all Old World Derelomini, including a description of new genera more than 10 years ago. Unfortunately, he passed away before he could complete the work on this tribe (Oberprieler *et al.* 2018). Completing this work is an important and difficult task, as the tribe is large and still very poorly known in the Old World. GK's unpublished manuscripts are held at NZAC and contain a wealth of insights into weevil taxonomy, biology and evolution. This study only reports on his contribution to the genus *Elaeidobius*. More precisely, GK wrote the core of this paper, checked type specimens and wrote a preliminary key, diagnosis and description of new species. We have reported his work as faithfully as possible. The other authors have added localities and biological data, produced figures and the molecular part of the study. They also formatted diagnoses and descriptions and wrote the introduction, material and methods and discussion sections.

Material and methods

Preparation and photographs

The abdomens of adult specimens were extracted and digested in KOH to obtain clean preparations of genital structures, as these are commonly used to distinguish between closely related species in Curculioninae (Caldara 1990; Haran & Perrin 2017; Haran 2018). The descriptions and illustrations of genital structures is limited to the male penis. The spermatheca and sternum VIII of female genitalia did not show stable diagnostic characters to support species identification between closely related species. The habitus and male genitalia were photographed at CBGP using a Keyence® VHX5000 imaging system. All measurements were taken with an optical micrometer. The body length of specimens refers to the distance from the apical margin of the head (excluding the rostrum) to the apex of the elytra in dorsal view. The rostrum length refers to the distance between the apical margin of the eyes and the apex of the mandibles. The ratio of width to length (w/l) was measured at the widest point of the prothorax, the elytra and the penis. The length of the elytra was measured between the anterior part of the scutellum and the apex of the elytra. The length of the penis was measured between the base of the penis body (telsones excluded) and the apex. The terminology of external and internal morphology used follows Lyal (2017). Stable external morphological characters to distinguish between species are mainly found in males in the genus *Elaeidobius*. The main characters are: the presence/absence of a fringe of semi-erect hairs on each side of the median depression of the first two abdominal ventrites, the presence of erect hairs on the margin of the elytra, along the suture and at the base of interstria 4, the base of this interstria being raised to a swelling (Fig. 5). Some species can be distinguished by the strongly developed sternal process of males (Figs 2A–B, 5B), but as this character is lacking in some smaller specimens, it is critical to examine long series of specimens for reliable identification. Females are very difficult to distinguish between in the *E. plagiatus* species group, so the key provided for this group is focussed on male specimens. The identity of species was established by comparison with types borrowed from IRSNB, MRAC, NHMB, NHMUK and MTD (*Derelomus bilineatus* Hustache, 1924; *D. callosus* Hustache, 1924; *D. ciliatus* Hustache, 1924; *D. congoanus* Hustache, 1924; *D. elaeisae* Bondar, 1942; *D. kamerunicus* Faust, 1898; *D. maynei* Hustache, 1924; *D. singularis* Faust, 1898; *D. subvittatus* Faust, 1898; *D. uelensis* Hustache, 1932; *Prosoestus armatus* Voss, 1956 and *P. spatulifer* Marshall, 1950). The holotype of *D. plagiatus* Fåhræus, 1844 was examined via a high definition image of the specimen and of the labels sent by NHRS. The designation of lectotypes from series of syntypes was made following article 74 of the ICZN (ICZN 1999).

Molecular analysis

An analysis of interspecific genetic distance was carried out in order to validate the new species recognized morphologically and to provide a molecular diagnostic tool for each species of the genus. DNA was extracted from whole specimens, or from a single leg, using a DNeasy Blood & Tissue kit (Qiagen, Hilden, Germany). PCR amplification was carried out using a mix of primers for amplification of the standard Barcode region (mitochondrial cytochrome c oxidase subunit I, *COI*) of invertebrates (Table 1). PCR reactions were carried out on a Mastercycler® Nexus (Eppendorf, Hamburg, Germany) in a final volume of 10 µL containing 5 µL of Multiplex PCR Master Mix (Qiagen, Hilden, Germany), 2 µM of each primer and 2 µL of DNA template. The PCR conditions were as follows: initial DNA denaturation at 94°C for 15 minutes, followed by 35 cycles of 30 s at 94°C, 1 min at 52°C, and 1 min at 72°C with a final extension of 15 min at 72°C. Due to difficulties with the amplification of the Barcode region in some species, a fragment of mitochondrial Cytochrome oxidase II (*COII*) was also amplified for each species. For this second gene, PCR conditions followed Hernández-Véra *et al.* (2013). All PCR products were paired-end sequenced by Eurofins Genomics (<http://www.eurofinsgenomics.eu/>). Voucher specimens were mounted, dried and deposited at CBGP, Montpellier, France in the CIRAD collection (<https://doi.org/10.15454/D6XAKL>). DNA sequences were aligned and manually checked using CodonCode Aligner ver. 3.7.1. (CodonCode Corporation, Centerville, MA, USA) to verify the

Table 1. PCR primers. M13 tails from Ivanova *et al.* (2007) are highlighted.

Gene	Primer	Reference
COI	CAGGAAACAGCTATGACTAAACYTCDGGATGBCCAAARAATCA	Folmer <i>et al.</i> (1994), modified in Germain <i>et al.</i> (2013)
	HCO2198 CAGGAAACAGCTATGACTAAACYTCAGGATGACCAAAAAYCA	
	CAGGAAACAGCTATGACTAAACTTCWGGRTGWCCAAARAATCA	
	LCO1490 TGTA AACGACGGCCAGTTTTC AACTAAYCATAARGATATYGG	
	TGTA AACGACGGCCAGTTTTC AACWAATCATAAAGATATTGG	

absence of pseudogenes using standard detection methods (Haran *et al.* 2015). Uncorrected *p*-distance values of pairwise genetic distances between species were computed with Mega 7 (Kumar *et al.* 2016). Interspecific phylogenetic relationships were preliminarily reconstructed on *COII* sequences using PhyML (Guindon & Gascuel 2003) with 1000 bootstrap replicates. A specimen of the species *Derelomus piriformis* Hoffmann (Macinalio, Corsica, France) was used as the outgroup of the tree.

Depositories

- CBGP = Centre de Biologie pour la Gestion des Populations, Montpellier, France
- IRSNB = Institut royal des Sciences naturelles, Brussels, Belgium
- MNHN = Muséum national d'histoire naturelle, Paris, France
- MRAC = Musée Royal de l'Afrique centrale, Tervuren, Belgium
- MTD = Senckenberg Museum für Tierkunde, Dresden, Germany
- NHMB = Naturhistorisches Museum, Basel, Switzerland
- NHMUK = The Natural History Museum, London, UK
- NHRS = Swedish Museum of Natural History, Stockholm, Sweden
- NZAC = New Zealand Arthropod Collection, Landcare Research, Auckland, New Zealand
- SDEI = Senckenberg Deutsches Entomologisches Institut, Munich, Germany
- TMP = Ditsong National Museum of Natural History, South Africa
- USNM = United States National Museum, Washington D.C., USA
- ZMB = Zoologisches Museum, Humboldt Universität, Berlin, Germany

Results

Class Insecta Linnaeus, 1758
 Order Coleoptera Linnaeus, 1758
 Family Curculionidae Latreille, 1802
 Subfamily Curculioninae Latreille, 1802
 Tribe Derelomini Latreille, 1865
 Subtribe Derelomina Latreille, 1865

Genus *Elaeidobius* Kuschel, 1952

Elaeidobius Kuschel, 1952: 272; 1955: 310.

Type species

Derelomus elaeisae Bondar, 1942 [= *Derelomus subvittatus* Faust, 1898].

Diagnosis

Eyes flat, following contour of head. Head not or hardly depressed above forehead. Elytra with interstria 9 or 10 costate in part, with costa at apex flat, not extending to apical margin; area on declivity between interstriae 3 and 9 not impressed. Fore and middle tibiae mucronate, hind tibiae with or without mucro. Claws free, simple. Tergites well-pigmented, divided or not along midline; spiracle surrounding not darkened.

Among the Afrotropical Derelomini, the genus *Elaeidobius* is close to the genera *Derelomus* and *Prosoestus* Faust, 1899, which both contain species associated with inflorescences of Arecaceae Bercht. & J.Presl. The species belonging to the genus *Elaeidobius* can be distinguished by the key provided at the end of the results section.

Distribution

This genus is native to West and central Africa (Table 2). It has been introduced into Madagascar, Asia (Burma, India, Indonesia, Malaysia, Thailand and Solomon Islands) and to the Americas (Brazil, Colombia, Ecuador, Guatemala, North America and Peru) (O'Brien & Woodruff 1986; Mariau & Genty 1988).

Life history

Larvae of the genus *Elaeidobius* develop in male flowers of the African oil palm, *Elaeis guineensis* (Arecales, Arecaceae), adults settle on the inflorescences and feed on pollen (Fig. 7, see Li *et al.* 2019 for a review). Adults fly during the day, attracted by the odour emitted by the inflorescences (Beaudoin-Ollivier *et al.* 2017). They transfer the pollen to female flowers, lured by their odours, which are similar to the male ones (Opute 1975; Lajis *et al.* 1985; Hussein *et al.* 1989).

Species-group: subvittatus

Diagnosis

Characterised by a smaller size (1.4–3.0 mm) and a more compact body. Prosternum in male armed with a protruding process, variable in shape and size, occasionally absent in smaller specimens. Pronotum lacking depressions and fold on anterior half and fovea on middle of disc on either side of midline. Lateral carina of prothorax forming a constriction near collar (Fig. 5A), followed by a distinct indentation. Three species in this group.

Elaeidobius bilineatus (Hustache, 1924) comb. nov.

Figs 1A, 2A, 4A, 5D–F

Derelomus bilineatus Hustache, 1924: 75.

Prosoestus armatus Voss, 1956: 629. **syn. nov.**

Material examined

Lectotype (here designated)

DEMOCRATIC REPUBLIC OF CONGO • “HOLOTYPUS [red label]” “Musée du Congo. Haut-Uelé: Moto. -1922. L. Burgeon” “Lectotype ♀ [here designated]. *Derelomus bilineatus*. Hustache 1924. Kuschel 2009 [red label]” “*Derelomus bilineatus*. Type Hust” “*Elaeidobius bilineatus*. (Hust. 1924) Kuschel 2009”; MRAC.

Table 2. List and verified geographical distribution of species of the genus *Elaeidobius* Kuschel, 1952. Abbreviation: DRC = Democratic Republic of Congo.

Genus <i>Elaeidobius</i>	Native distribution (verified specimens)
species-group: <i>E. subvittatus</i>	
<i>E. bilineatus</i> (Hustache, 1924)	Angola, Benin, Cameroon, Congo, DRC, Ghana, Guinea, Nigeria, Senegal, Sierra Leone, Tanzania, Togo
<i>E. spatulifer</i> (Marshall, 1950)	Cameroon, DRC, Ivory Coast
<i>E. subvittatus</i> (Faust, 1898)	Angola, Cameroon, DRC, Gabon, Ghana, Guinea, Ivory Coast, Nigeria, Senegal, Sierra Leone, Togo
species-group: <i>E. plagiatus</i>	
<i>E. kamerunicus</i> (Faust, 1898)	Angola, Benin, Cameroon, DRC, Gabon, Ghana, Guinea, Ivory Coast, Madagascar, Nigeria, Togo
<i>E. pilimargo</i> Haran & Kuschel sp. nov.	Benin, Cameroon, Ghana, Nigeria
<i>E. piliventris</i> Haran & Kuschel sp. nov.	Angola, Cameroon, DRC, Ghana
<i>E. plagiatus</i> (Fahraeus, 1844)	Angola, Benin, Cameroon, DRC, Ghana, Nigeria, Togo
<i>E. singularis</i> (Faust, 1898)	Benin, Cameroon, DRC, Gabon, Ghana, Ivory Coast, Nigeria, Togo

Paralectotype (here designated)

DEMOCRATIC REPUBLIC OF CONGO • 1 ♀; “Musée du Congo. Haut-Uelé: Moto. -1922. L. Burgeon” [labelled as follows] “Paralectotype *Derelomus. bilineatus*. Hustache 1924. Kuschel 2009”; MRAC.

Other material

DEMOCRATIC REPUBLIC OF CONGO – **Haut-Uelé Province** • 2 ♀♀; Moto; 1922; L. Burgeon leg.; MRAC • 1 ♀; same collection data as for preceding; 1920; MRAC • 1 ♀; same collection data as for preceding; Jan. 1927; MRAC • 1 ♀; Watsa; 1922; L. Burgeon leg.; MRAC.

ANGOLA • 6 ♂♂, 15 ♀♀; C.E.Salazar; 9.16° S, 14.55° E; 14 May 1973; P. Carvalho leg.; oil palm inflorescence; TMP.

IVORY COAST • 1 ♂; Boudoukal; 2014; JHAR00286_0104; CBGP.

SENEGAL • 1 ♂, holotype of *Prosoestus armatus* Voss, 1951; La Digue near Rufisque; 8 Apr. 1951; Bechyné leg.; NHMB.

Other specimens identified and labelled by G. Kuschel at IFPE, MNHN, MRAC, NHMUK, NZAC, USNM and ZMB.

Diagnosis (♂♀)

BODY LENGTH. 2.2–3.0 mm.

COLOUR. Reddish or yellowish brown with dark markings on pronotum and elytra, also sterna darkened.

HEAD. Forehead in both sexes not impressed. Rostrum relatively long, in male $1.5 \times$ as long as prothorax, lacking a postmental tubercle, in female $1.8\text{--}1.9 \times$ as long, slender, slightly downcurved.

PROTHORAX. Disc with a pair of dark stripes, slightly convergent; lateral carina continued to apex with a distinct indentation or interrupted, in lateral view strongly curving upwards before apical collar.

ELYTRA. Presence of irregular dark stripes, generally with a short one in middle of interstria 2, and an elongate one along interstria 6 from basal quarter to top of declivity, often expanding on interstriae 5 and 7, a further stripe on interstria 9; punctures of striae as wide as width of interstriae or slightly smaller; interstriae with a row of very short recumbent hairs. Prosternal process in male variously developed, from a large spatulate structure to a reduced or even absent one.

ABDOMEN. Tergites 1 to 6 medially membranous, tergite 4 on sides subtruncate, anteriorly angulate, tergite 7 truncate at apex; row of approximately 15 plectral pegs flanked by narrow, clear sides, area between plectral rows parallel-sided, dark, smooth.

GENITALIA. Penis as long as last two ventrites and half of ventrite 3, body $2.17 \times$ as long as apodemes, about $2 \times$ as long as wide (ratio w/l: 0.56), symmetrical, gradually widening apicad, abruptly apiculate (Fig. 4A); internal sac with straight, stiff, robust sclerite half length of body.

Life history

Adults are found on inflorescences of *Elaeis guineensis* (Arecaceae), the African oil palm. (JH pers. obs.).

Distribution

Angola (C.E. Salazar (?)); **Benin** (Cotonou, Dassa, Niaouli); **Cameroon** (Likomba, Moliwe); **Congo** (Brazzaville); **Democratic Republic of Congo** (Haut-Uelé: Moto, Moku Moto, Watsa, Yambula); **Ghana** (Kumasi, Aburi); **Guinea** (Nimba); **Ivory Coast** (Boudoukal); **Nigeria** (Ibadan, Ife, Lagos); **Senegal** (Dakar, La Digue); **Sierra Leone** (Njala); **Tanzania** (Morogoro); **Togo** (Kloto).

Remarks

Elaeidobius bilineatus has, in lateral view, the marginal carina of the prothorax strongly upcurved, a character that safely distinguishes this species from all others of the genus. As *Elaeidobius* is said to be a West African genus, its presence in Tanzania is unexpected and it has to be confirmed whether it is a native or an introduced element. *Elaeidobius bilineatus* was described by Hustache as *Derelomus bilineatus* based on two female specimens from Haut Uelé (Democratic Republic of Congo) (Hustache 1924). These two specimens were located in the MRAC collection, bearing a red “holotype” label. As the original description of this species did not designate a holotype, one of them was designated as the lectotype for this species and was labelled accordingly. The second syntype was labelled as paralectotype. The other specimens from the same collecting event (2 ♀♀) are not part of the type series. We examined the holotype of the species *Prosoestus armatus* Voss, 1956, described from a single male specimen from Senegal (La Digue nr Rufisque). A detailed observation of the external and internal morphology of this specimen showed no difference from the lectotype of *Elaeidobius bilineatus*. As a result of this, *Prosoestus armatus* Voss, 1956 should be considered as a junior synonym of *E. bilineatus*.

Elaeidobius spatulifer (Marshall, 1950) comb. nov.
Figs 1B, 2B, 4B

Prosoestus spatulifer Marshall, 1950: 264.

Material examined

Holotype

DEMOCRATIC REPUBLIC OF CONGO • “Musée du Congo. Thysville. -XI-1935. 2445. J Ghesquière” “HOLOTYPUS. *spatulifer* ♂. Marsh [red label]” “*Prosoestus spatulifer*. Mshl. TYPE ♂” “Holotype ♂. *Prosoestus spatulifer*. Marshall 1950. Kuschel 2009 [red label]” “*Elaeidobius spatulifer*. (Marshall 1950). Kuschel 2009”; MRAC.

Paratypes

DEMOCRATIC REPUBLIC OF CONGO • same collection data as for holotype; “PARATYPUS. ♀ [red label]” “*Prosoestus spatulifer*. Mshl. Cotype ♀” “Paratype. *Prosoestus spatulifer*. Marshall 1950. Kuschel 2009” “*Elaeidobius spatulifer*. (Marshall 1950). Kuschel 2009”; MRAC • 1 ♀; same collection data as for holotype; NHMUK.

Other material

Other specimens identified and labelled by G. Kuschel at NHMUK and NZAC.

Diagnosis (♂♀)

BODY LENGTH. 2.5–2.9 mm.

COLOUR. Derm dorsally reddish brown, ventrally dark brown, elytra vaguely darker on interstria 2 and laterally on interstriae 6 and 7; antennae and legs reddish or yellowish.

HEAD. Forehead not impressed in either sex. Rostrum in male about as long as prothorax, in female $1.2 \times$ as long, moderately robust and downcurved, with a slight postmental elevation in male.

PROTHORAX. Uniformly coloured, lacking stripes and foveae; lateral carina in dorsal view uninterrupted at apex, with conspicuous cuticular expansion in male, carina in lateral view moderately upcurved in male, gently in female towards apical collar.

ELYTRA. A low costa on interstria 9 gradually fading towards end; pubescence inconspicuous, very sparse, with a row of more conspicuous hairs on interstriae. Prosternal process of male variable in size, the apex rounded without a lateral lobe.

ABDOMEN. Tergites 1–6 divided on midline; pruinose patches on tergites 5–7; tergite 7 in male impinging slightly into 6, subtruncate at apex; plectral rows on basal two thirds, each with 12 pegs.

GENITALIA. Penis as long as last four ventrites; body deeply pigmented, $2.9 \times$ as long as apodemes (ratio w/l: 0.19), widest near basal third, then tapering to less than one third of its width, widening moderately to an asymmetrical apex (Fig. 4B); internal sac without sclerite.

Life history

Unknown, *Elaeis guineensis* (Arecaceae), oil palm, on inflorescences.

Distribution

Cameroon (Yaoundé); **Democratic Republic of Congo** (Thysville); **Ivory Coast** (Toumodi).

Remarks

The species is distinguished by a uniform dark colour, and in the male by a prominent spade-like prosternal process and lack of a postmental tubercle. No DNA-grade material of this species could be obtained in the course of this study.

Elaeidobius subvittatus (Faust, 1898) Figs 1C, 2C, 4C, 5A–B, E, G, M, 7

Derelomus subvittatus Faust, 1898: 224.

Derelomus maynei Hustache, 1924: 75 [syn. by Marshall 1930: 575].

Derelomus elaeisae Bondar, 1942: 461 [syn. by Kuschel 1955: 310].

Elaeidobius subvittatus – Kuschel, 1955: 310.

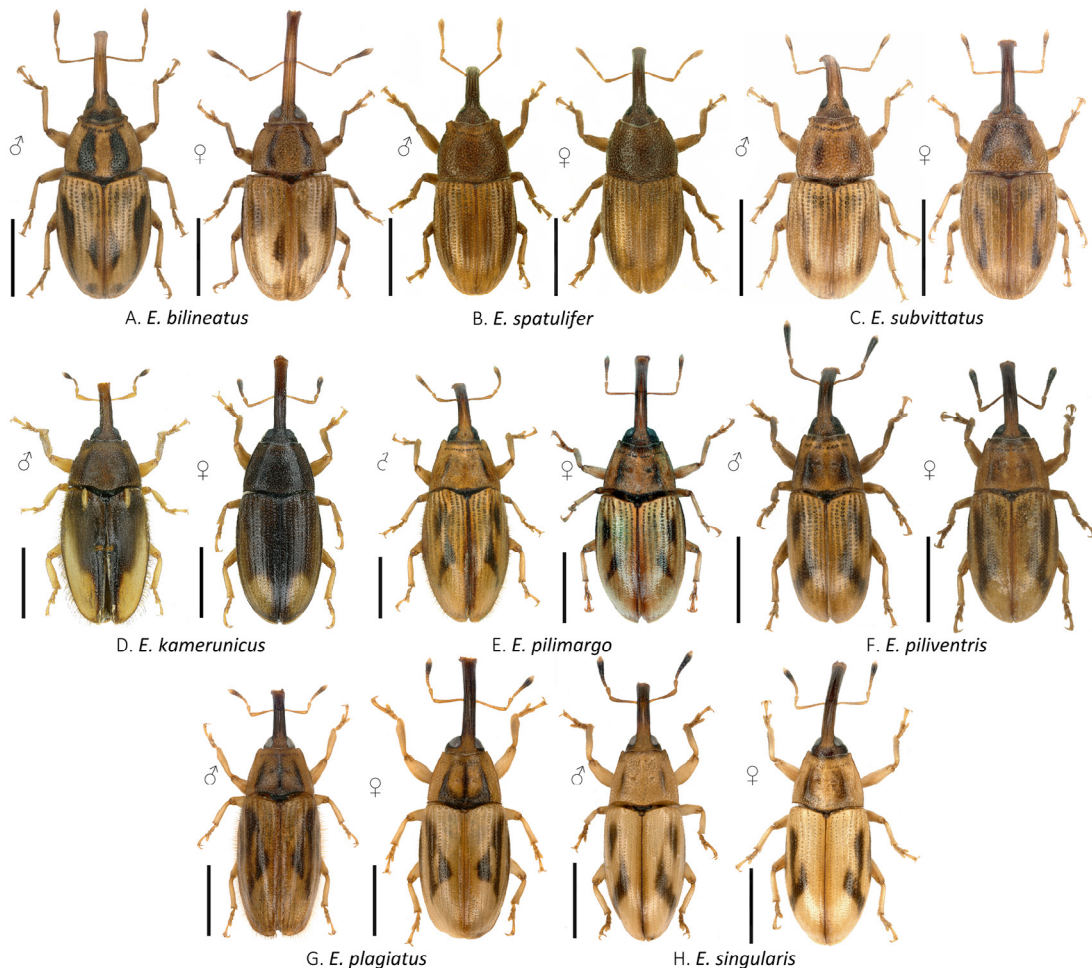


Fig. 1. Habitus of males and females of species of *Elaeidobius* Kuschel, 1952. **A.** *E. bilineatus* (Hustache, 1924) comb. nov., Dakar, Senegal. **B.** *E. spatulifer* (Marshall, 1950) comb. nov., holotype, Thysville, Democratic Republic of Congo (MRAC). **C.** *E. subvittatus* (Faust, 1898), Dakar, Senegal. **D.** *E. kamerunicus* (Faust, 1898) comb. nov. (JHAR00209). **E.** *E. pilimargo* Haran & Kuschel sp. nov. (JHAR00409). **F.** *E. piliventris* Haran & Kuschel sp. nov. (JHAR02182). **G.** *E. plagiatus* (Fåhræus, 1844) comb. nov. (JHAR00272). **H.** *E. singularis* (Faust, 1898) comb. nov. (JHAR00283). Scale bars = 1 mm.

Material examined

Holotype

DEMOCRATIC REPUBLIC OF CONGO • “Landana. Congo. Oberthur” “*subvittatus* Fst.” “Coll. J. Faust. Aukauf 1900” “type” “Staatl. Museum für. Tierkunde Dresden” “Holotype ♀. *Derelomus subvittatus* Faust, 1898. Kuschel 2013” “*Elaeidobius subvittatus* (Faust, 1898). Kuschel 2013”; MTD.

Other material

ANGOLA • 10 ♂♂, 13 ♀♀; CE Salazar; 9.16° S, 14.55° E; 14 May 1973; Carvalho leg.; oil palm inflorescence; TMP.

CAMEROON • 1 ♂; Bertoua, Bindzia; 15 Mar. 2019; J. Haran leg.; JHAR02229_0101; CBGP.

DEMOCRATIC REPUBLIC OF CONGO • 1 ♂, lectotype of *Derelomus maynei* Hustache, 1924 [here designated], labelled as “*Elaeidobius. subvittatus* (Faust 1898). Kuschel 2009”; Yambata; 10 Dec. 1912; R Mayné leg.; MRAC • 2 ♀♀, paralectotypes of *Derelomus. maynei* Hustache, 1924; same collection data as for preceding; MRAC • 1 ♂; Haut-Uelé, Moto; 1922; L. Burgeon leg.; MRAC • 1 ♀; Mbwasa; 30 Nov. 1912; MRAC • 4 specs, sex not determined; same collection data as for preceding; IRSNB.

TOGO • 1 ♂; Toné; 2015; JHAR00275_0101; CBGP.

Diagnosis (♂♀)

BODY LENGTH. 1.4–2.2 mm.

COLOUR. Variable in colour, partly or entirely yellowish or dark brown, on more western populations usually with a pair of abbreviated dark stripes on prothorax, and a stripe on interstriae 4–5, with a slightly darkened suture; on eastern specimens prevailing darker colour, especially with prothorax usually becoming more extensively or entirely dark, and markings on elytra vaguer or obliterated.

HEAD. Forehead slightly impressed. Rostrum in male as long as prothorax, in female 1.2 to 1.3 × as long as prothorax, with small postmental tubercle in male visible in lateral view.

PROTHORAX. Disc lacking impressions; carina interrupted or not at collar, with small cuticular expansion, in lateral view gently curved upwards towards apex.

ELYTRA. Interstriae with a distinctive row of elongate hairs on middle, hairs as long as width of interstriae; striae with a row of very short recumbent hairs; prosternum in male large and trilobed, or rudimentary and reduced to a cuticular elevation, sometimes absent.

ABDOMEN. Ventrites 1–2 medially flattened, 5 gently rounded at apex. Tergites 1–6 medially divided; tergite 7 in males truncate; plectral pegs 4 on pale line.

GENITALIA. Penis as long as last three ventrites plus $\frac{1}{3}$ of ventrite 2; body 3 × as long as apodemes, about 4 × as long as wide (ratio w/l: 0.24), slightly asymmetrical, tilted to the right (Fig. 4C); internal sac without an obvious sclerite.

Life history

Elaeis guineensis (Arecaceae) the oil palm, on inflorescences (Mariau & Genty 1988).

Distribution

Angola (Landana); **Benin** (Cotonou, Dassa, Niaouli, Pobè); **Cameroon** (Bota, Edu Ngat, Likomba, Moliwe, Tiko); **Democratic Republic of Congo** (Haut-Lopori, Yambula); **Gabon** (Kome estate, Bokové); **Ghana** (Kwae); **Ivory Coast** (Banoua, Boudoukal); **Nigeria** (Obaretin); **Senegal** (Malika – Dakar); **Sierra Leone** (Njala); **Togo** (Toné). Introduced populations: **Brazil** (Bahía); **Colombia** (Campo Alegre); **French Guiana** (Kourou).

Remarks

Elaeidobius subvittatus is readily distinguished from all other species by its smaller size, and in males by a small tubercle on the underside at the rostrum apex. The populations of South America were introduced accidentally. This taxon was described on a single female from Landana. In the collection of J. Faust housed at MTD, we found this specimen bearing a red “type” label with the identification “*subvittatus* Fst.”, “Landana, Congo”. This specimen is the holotype of *Derelomus subvittatus* Faust, 1898 and was labelled accordingly.

Derelomus maynei Hustache, 1924, was described from three specimens (1 ♂, 2 ♀♀) from Yambata, 10 Dec. 1912 (Democratic Republic of Congo). This species was then put in synonymy with *D. subvittatus* (= *Elaeidobius subvittatus* Faust) by Marshall (1930). The three syntypes of *D. maynei* were located in MRAC. The male is designated here as the lectotype of this species and the two females are labelled as paralectotypes.

Species-group plagiatus

Diagnosis

Characterised by larger size and slender body. Prosternum in male never armed with a protruding process. Pronotum with depressions and fold on anterior half and fovea on middle of disc on either side of midline. Lateral carina of prothorax regular, not forming a constriction or indentation near collar (Fig. 5C). Five species in this group.

Elaeidobius kamerunicus (Faust, 1898) comb. nov.

Figs 1D, 2D, 4D, 5I

Derelomus kamerunicus Faust, 1898: 225.

Derelomus callosus Hustache, 1924: 76 [syn. by Marshall 1930: 575].

Derelomus congoanus Hustache, 1924: 77 [syn. by Marshall 1930: 575].

Material examined

Holotype

CAMEROON • ♀; “Kamerun. Kraatz” “*kamerunicus* Fst.” “type” “Coll. J. Faust. Aukauf 1900” “Staatl. Museum für. Tierkunde Dresden” “Holotype ♀. *Derelomus kamerunicus* Faust, 1898. Kuschel 2013” “*Elaeidobius kamerunicus* (Faust, 1898). Kuschel 2013”; MTD.

Other material

CAMEROON • 2 ♂♂, 2 ♀♀; Edu Ngat; 2008; JHAR00209_0101; CBGP.

DEMOCRATIC REPUBLIC OF CONGO • 1 ♂, lectotype of *Derelomus callosus* Hustache, 1924 [here designated], labelled as “*Elaeidobius kamerunicus* (Faust 1898). Kuschel 2009”; Yambata; 10 Dec. 1912; R. Mayné leg.; MRAC • 2 ♂♂, paralectotypes of *Derelomus callosus* Hustache, 1924, labelled as “*Elaeidobius kamerunicus* (Faust 1898). Kuschel 2009”; Kindu; Nov. 1913; L. Burgeon leg.; MRAC

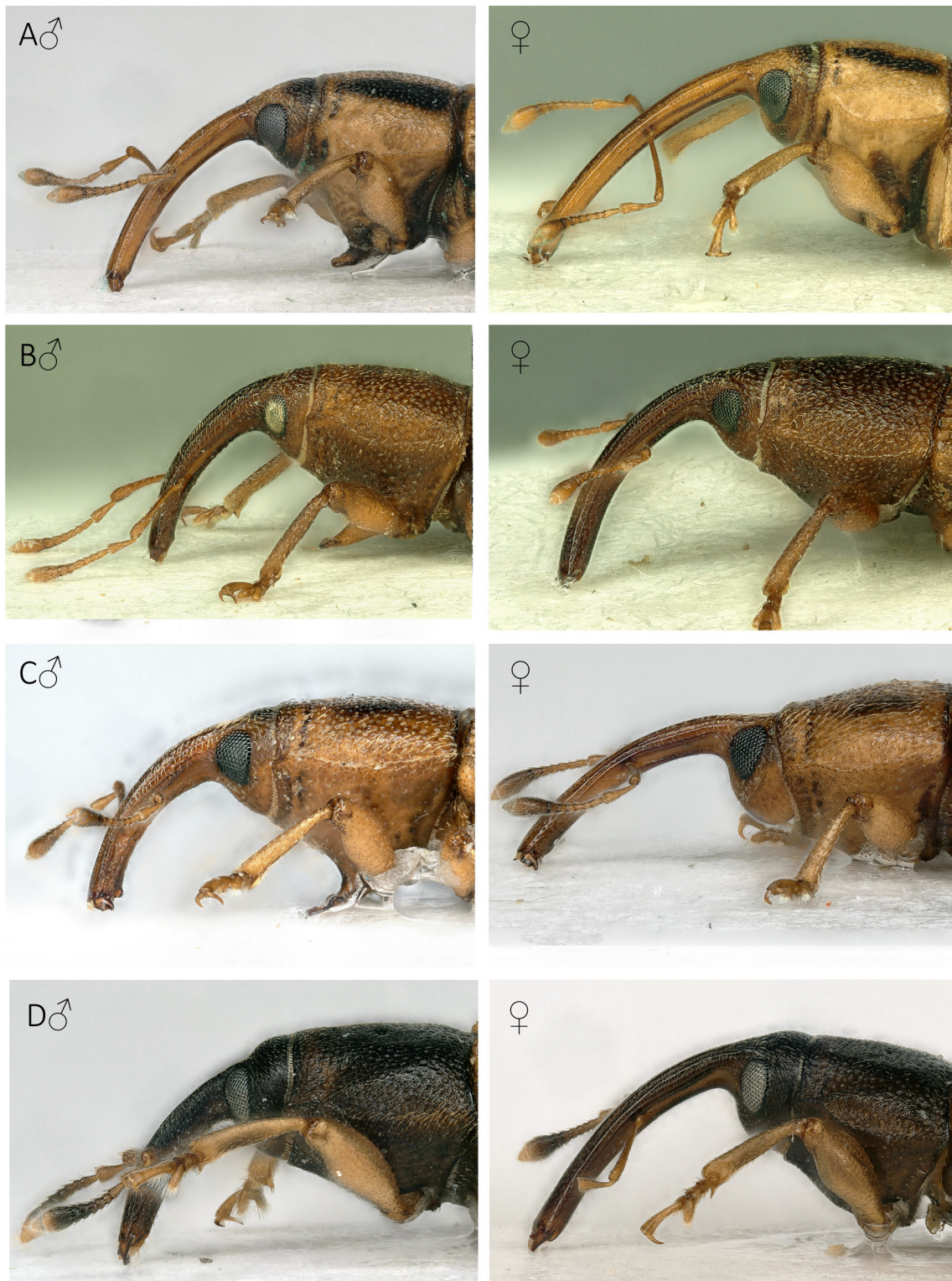


Fig. 2. Head and prothorax in lateral view of species of *Elaeidobius* Kuschel, 1952 (Part 1). **A.** *E. bilineatus* (Hustache, 1924) comb. nov., Dakar, Senegal. **B.** *E. spatulifer* (Marshall, 1950) comb. nov., holotype, Thysville, Democratic Republic of Congo (MRAC). **C.** *E. subvittatus* (Faust, 1898), Dakar, Senegal. **D.** *E. kamerunicus* (Faust, 1898) comb. nov. (JHAR00209). Not to scale.

• 1 ♀, lectotype of *Derelomus congoanus* Hustache, 1924 [here designated], labelled as “*Elaeidobius kamerunicus* (Faust 1898). Kuschel 2009”; Haut-Uelé, Moto; 1920; L. Burgeon leg.; MRAC • 8 ♀♀, paralectotypes of *Derelomus congoanus* Hustache, 1924 [here designated], labelled as “*Elaeidobius kamerunicus* (Faust 1898). Kuschel 2009”; Yambata; 10 Dec. 1912; R. Mayné leg.; MRAC • 1 ♀; Mobwasa; 30 Nov. 1912; R. Mayné leg.; MRAC • 1 ♂, 1 ♀; Haut-Uelé, Moto; 1922; L. Burgeon leg.; MRAC • 1 ♀; Kindu; Nov. 1913; L. Burgeon leg.; MRAC. Other specimens identified and labelled by G. Kuschel in MRAC, MNHN, NHMUK, NZAC, MTD, USNM and ZMB.

ANGOLA • 12 ♂♂, 18 ♀♀; CE Salazar; 9.16° S, 14.55° E; 14 May 1973; Carvalho leg.; oil palm inflorescence; TMP.

Diagnosis (♂♀)

BODY LENGTH. 2.5–3.5 mm.

COLOUR. Dull dark brown, elytra with large yellow or reddish brown spot on either side at apex and on all or part of base, in male with long erect setae on margins, erect setae and a setiferous tuft on suture.

HEAD. Forehead in male with prominent carinae against eyes and depressed between them, in female with low or obsolescent carina and not depressed; rostrum in male 1.1 × as short as prothorax, in female 1.5 × as long as prothorax, cylindrical, 5-carinate in basal half, underside in male with short erect hairs and no postmental tubercle.

PROTHORAX. Disc in lateral view nearly flat, usually with minute fovea on either side of middle; carina fine, in male obsolete or obsolescent on basal half, ending in prominent, somewhat auriculate carina without constriction at base of collar.

ELYTRA. In male alutaceous, dull, moderately curved from shoulders to apex; base of interstria 4 usually raised to a yellow tumour or swelling bare of erect hairs; apical $\frac{2}{3}$ of sutural interstria raised, bearing long erect setae; interstria 9 in male swollen, somewhat inflated, bearing long curved erect setae, in female costate, with costa flat, not continued to apex.

ABDOMEN. Tergites heavily pigmented; tergite 7 strongly advancing forward against 6 in middle, with well-pigmented stridulatory rods, each rod containing about 15 granules.

GENITALIA. Penis as long as last three ventrites; body about 3 × longer than wide (ratio w/l: 0.36), symmetrical, sides sub-parallel, relatively broadly rounded at apex (Fig. 4D); with small median sclerites in the body.

Life history

On and in flowers of *Elaeis guineensis* (Arecaceae), the oil palm. Males and females show a peak of flight activity around the inflorescences between 3 and 6 hours after sunrise (Auffray *et al.* 2017).

Distribution

Benin (Cotonou, Dassa, Niaouli, Pobè); **Cameroon** (Edu Ngat, Kienke, Moliwe, N’Kongsamba); **Democratic Republic of Congo** (Beni: Ituri Forest, Haut-Uelé: Moto, Kindu, Mobwasa, Yambata, Yambula); **Gabon** (Kome Estate); **Ghana** (Kwae); **Ivory Coast** (Bonoua, Lamé); **Madagascar** (Melville); **Nigeria** (Ibaden, Obaretin, Cowan); **Togo** (Kloto). Introduced to other countries to aid pollination of oil palms in plantations: Americas: **Brazil** (Moju); **Colombia** (Campo Alegre, Finca la Roca, Girardot, La Cabana, Palmar del Casanare); **Ecuador** (Shushufindi); **Guatemala** (Tecum Uman); **Peru** (Palmas de Shanusi). Asia: **Burma** (Thanintharyi); **Indonesia** (Aek Loba, Bangun Bandar, Kota

Gelanggi, Lae Butar, Mata Pao, Negeri Lama, Seumanyam, Sungei Liput, Tanah Gambus, Bangka, Belitung, Kalimantan Center, East Kalimantan, Lampung, North Sumatra, Papua, Riau, West Kalimantan, South Kalimantan, South Sumatra); **Malaysia** (Tun Razak); **Thailand** (Banhariz, Sji Nigena Toem, Koandi, Konho, Krabi Noi).

Remarks

Elaeidobius kamerunicus is distinctive in its dark body colour and yellow spots on elytra. This species is being imported by increasing numbers of countries to facilitate pollination of oil palms in plantations (Syed 1982). In its native range, *E. kamerunicus* exhibits two genetically differentiated populations that are roughly distributed on each side of the cameroon volcanic line (Haran *et al.* 2020). This taxon was described based on a single female from Cameroon without more detailed indications. In the collection of J. Faust housed at MTD, we found this specimen with the identification “*kamerunicus*” and bearing a red “type” label. This specimen is the holotype of *Derelomus kamerunicus* Faust, 1898 and was labelled accordingly. *Derelomus callosus* Hustache, 1924 was described based on a series of individuals from two localities of the Democratic Republic of Congo (Yambata, 10 Dec. 1912 and Kindu, Nov. 1913). This species was later put in synonymy with *D. kamerunicus* (= *Elaeidobius kamerunicus*) by Marshall (1930), but no particular specimen from these series was designated as holotype. In the collections of the MRAC, three male specimens from these localities and bearing the red labels “Holotypus” and “Paratypus” were located. The specimen from Yambata and bearing the label “Holotypus” is here designated as the lectotype for *D. callosus*. The two specimens from Kindu and bearing the label “Paratypus” are labelled as paralectotypes. *Derelomus congoanus* was described based on a series of individuals from two localities of the Democratic Republic of Congo (Yambata, 10 Dec. 1912 and Haut-Uelé, Moto, 1920). This species was also put in synonymy with *D. kamerunicus* (= *Elaeidobius kamerunicus*) by Marshall (1930). The specimens used to describe *Derelomus congoanus* are in fact females of *Elaeidobius kamerunicus* that Hustache took to be a distinct species. As for the previous species, no particular specimen from the type series was designated as holotype. In the collection of the MRAC, one female from Haut-Uelé (1920) and bearing a red label “Holotypus” was located. It is here designated as the lectotype of *Derelomus congoanus* and labelled accordingly. In the same collection, 8 females from Yambata (10 Dec. 1912) and bearing a red “Paratypus” label were labelled as paralectotypes of this species.

Elaeidobius pilimargo Haran & Kuschel sp. nov.

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Figs 1E, 3A, 4E

Etymology

The species name *pilimargo* is derived from ‘pilus’ for ‘hair’, and ‘margo’ for ‘margin’.

Material examined

Holotype

GHANA • “GOLD COAST [Ghana]. Accra. 11.X.1920. Mrs W. H. Patterson” “On Oil Palm flowers” “*Elaeidobius* sp. indet. B. R.T. Thompson det. 2004” “Holotype [red label]. *Elaeidobius. pilimargo*. Haran & Kuschel. Haran & Kuschel 2019”; NHMUK.

Paratypes

GHANA • 2 ♂♂; same collection data as for holotype; “Paratype. *Elaeidobius. pilimargo*. Haran & Kuschel. Haran & Kuschel 2019”; NHMUK.

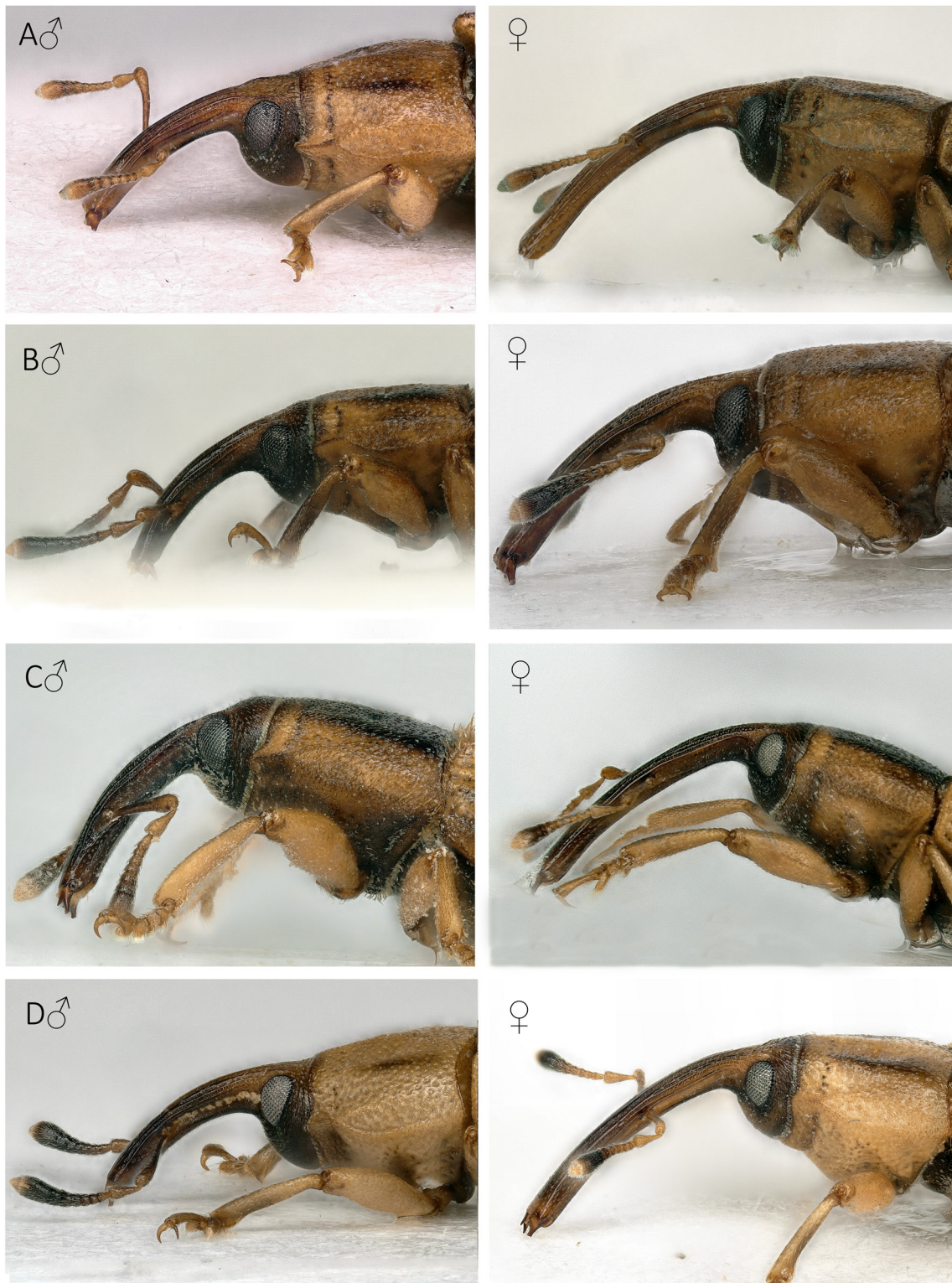


Fig. 3. Head and prothorax in lateral view of species of *Elaeidobius* Kuschel, 1952 (Part 2). **A.** *E. pilimargo* Haran & Kuschel sp. nov. (JHAR00409). **B.** *E. piliventris* Haran & Kuschel sp. nov. (JHAR02182). **C.** *E. plagiatus* (Fåhraeus, 1844) comb. nov. (JHAR00272). **D.** *E. singularis* (Faust, 1898) comb. nov. (JHAR00283). Not to scale.

NIGERIA • 3 ♂♂; “Nigeria. Ife, W State. 15.xii.1974. J.T. Medler coll.” “*Elaeidobius* sp. indet. B. R.T. Thompson det. 2004” “Paratype. *Elaeidobius. pilimargo*. Haran & Kuschel. Haran & Kuschel 2019”; NHMUK.

SENEGAL • 1 spec.; Dakar, Malika; 4 Oct. 2017; J. Haran leg.; *Elaeis guineensis*; JHAR00409_0201; CBGP.

Description (♂♀)

BODY LENGTH. 2.5–3.0 mm.

COLOUR. Yellow or reddish brown metasternum, antennal club in part darker; often prothorax and elytra with dark stripes or oblique bands; in male, elytra with long erect setae on margins and on suture but not on base of interstria 4.

HEAD. Strongly punctate, punctuation partly confluent towards frontal fovea; forehead in male with prominent carinae against eyes and depressed between them, in female with low or obsolescent carina and not depressed; rostrum in male as long as prothorax, in female 1.2–1.4 × longer, cylindrical, 5-carinate in basal $\frac{2}{3}$, median carina widening near antennal insertion, apical $\frac{1}{3}$ smooth and punctate, underside in male lacking erect hairs and postmental tubercle; antennae yellowish or reddish brown, insertion on rostrum median in male, antemedian in female; scape slightly curved, gradually thickening toward apex, first segment of funicle elongate, in male as long as segments 2–4, in females longer than segments 2–4, segment 2 longer than wide, 3 isodiametric, 4–7 transverse, gradually widening to width of club.

PROTHORAX. Sub-trapezoidal (w/l ratio: 1.46), converging in a straight or nearly straight line, deeply bisinuous at base, concavely curved at apex; apical collar at base with a transverse row of black dots; disc in lateral view nearly flat, with four impressions anteriorly, and a pair of large, deep foveae on either side of middle; integument with double punctuation, glabrous in appearance, with a very short pubescence mainly on sides at basal half; carina in lateral view obsolete or obsolescent towards base, weakly sinuous near apex, sharply carinate on collar.

ELYTRA. Widest near middle (w/l ratio: 0.70), in male not tectiform, base of interstriae 3–5 raised to a tumour or swelling, apical $\frac{2}{3}$ of suture darker, slightly raised with a row of erect setae, interstria 10 in male swollen, somewhat inflated bearing long upwardly curved erect setae, interstria 9 in female costate in basal $\frac{2}{3}$; striae as wide as width of interstriae or slightly narrower, gradually fading apicad; stria 9 absent basally, starting from near height of fore coxae; dark stripe on elytra generally present on interstria 6 in basal half and between middle of interstriae 3 or 4 to 8 before declivity.

LEGS. Integument pale yellow, mostly glabrous, with whitish suberect hairs in apical $\frac{2}{3}$ of tibiae and on tarsus; tibiae bisinuate on ventral side, with a small mucro apically; tarsi with first segment elongate, 0.7 as long as segments 2+3; segment 3 deeply bilobate; segment 4 elongate, slightly shorter than 1+2+3; claws free, not apendiculate.

ABDOMEN. Tergite 7 with about 14 plectral granules; ventrites with short suberect, scattered whitish hairs; in male ventrites 1 and 2 impressed in middle, without specific pilosity on margin on impression.

GENITALIA. Penis as long as last three ventrites; body 1.7 × longer than apodemes, symmetrical, more than 2 × longer than wide (w/l ratio: 0.40), parallel-sided, blunt at apex (Fig. 4E), with a pair of small median sclerites.

Life history

All the specimens collected recently were found on inflorescences of the oil palm, *Elaeis guineensis* (Arecaceae) (JH pers. obs.).

Distribution

Benin (Cotonou); **Cameroon** (Bota); **Ghana** (Aburi); **Nigeria** (Ife); **Senegal** (Malika-Dakar).

Remarks

Elaeidobius pilimargo sp. nov. is characterised by its elytral margins bearing long erect setae and presence of a swelling on base of interstria 4 without erect setae in males (Fig. 5J–K). The likely females examined are not part of the type series because their identity cannot be guaranteed based on morphology. *Elaeidobius pilimargo* sp. nov. is morphologically close to *E. singularis*. Both species show a genetic distance of 2.01% on *COII* (JHAR00409_0201, Senegal / JHAR00283_0101, Ghana). The sequencing of the *COI* gene for specimens of *E. singularis* failed repetitively, probably due to polymorphism in the primer sequences. Within the *E. plagiatus* species group, the *COI* sequence of *E. pilimargo* sp. nov. showed a genetic distance of 2.88% with *E. piliventris* sp. nov. (JHAR02182_0101).

Elaeidobius piliventris Haran & Kuschel sp. nov.

[urn:lsid:zoobank.org:act:0B74EAD6-28CE-4DC7-B12E-E8362448470C](https://zoobank.org/act:0B74EAD6-28CE-4DC7-B12E-E8362448470C)

Figs 1F, 3B, 4F, 5J–K

Etymology

The name *piliventris* is a Latin adjectivised noun derived from ‘pilus’ for ‘hair’, and ‘venter’ for ‘belly’.

Material examined

Holotype

GHANA • “GHANA. Kumasi. 21.x.1977. R.A. Syed” “ex ♂ inflorescence. oil palm” “*Elaeidobius* sp. indet. A R.T. Thompson det. 2004” “Holotype [red label] *Elaeidobius. piliventris*. Haran & Kuschel. Haran & Kuschel 2019”; NHMUK.

Paratypes

GHANA • 1 ♂, 1 ♀; “GHANA (Central Reg.). Egyirkom (site 8). CABI study sample” “*Elaeidobius* sp. indet. A R.T. Thompson det. 2004” “Paratype. *Elaeidobius. piliventris*. Haran & Kuschel. Haran & Kuschel 2019”; NHMUK.

Other material

ANGOLA • 1 ♂; CE Salazar; 9.16° S, 14.55° E; 14 May 1973; Carvalho leg.; oil palm inflorescence; TMP.

DEMOCRATIC REPUBLIC OF CONGO • 9 specs; Yambula; 23 Jan. 2018; *E. guineensis*; JHAR02182; CBGP.

CAMEROON • 1 ♂; Kienké; 2009; JHAR293_0102; CBGP.

Description (♂♀)

BODY LENGTH. 2.3–3.0 mm.

COLOUR (♂). Yellowish or reddish brown, pronotum usually with vague, dark stripe, elytra with a short dark stripe on interstria 6 in basal third, and an oblique stripe from near middle of interstriae 3 or 4

to 8; integument with very short, scattered recumbent white hairs, usually forming 1–2 series on each interstria of elytron; in male elytra lacking long erect setae on margins, suture and at base of interstria 4.

HEAD. Strongly punctate, punctuation partly confluent towards frontal fovea; forehead flat between eyes; rostrum in male as long as or $1.1 \times$ as long as prothorax, in female $1.2\text{--}1.4 \times$ longer, cylindrical, 5-carinate in basal $\frac{2}{3}$, median carina widening near antennal insertion, apical $\frac{1}{3}$ smooth and punctate, underside in male lacking erect hairs and postmental tubercle; antennal scape and segments 13 of funicle reddish brown, segments 4–7 and club usually dark brown; insertion of antennae on rostrum in apical $\frac{2}{3}$ in male, antemedian in female; scape slightly curved, gradually thickening towards apex, first segment of funicle elongate, in male slightly shorter than segments 2–4, in females longer than segments 2–4, segment 2 longer than wide, 3–7 transverse, gradually widening to width of club.

PROTHORAX. Sub-trapezoidal (ratio w/l: 1.33), in male sides converging in straight or nearly straight line, in female moderately rounded, deeply bisinuous at base, concavely curved at apex; apical collar at base with a transverse row of black dots; disc in lateral view nearly flat, with a pair of large, deep foveae on either side of middle; integument with double punctuation, glabrous in appearance, with a very short pubescence mainly on sides on basal half; carina in lateral view weak towards base, sharply carinate on collar.

ELYTRA. Widest near middle (ratio w/l: 0.70), in male not tectiform, base of interstria 4 slightly swollen, not raised to a tumour, apical $\frac{2}{3}$ of suture darker, lacking row of erect setae; interstria 10 in male flat, not inflated and lacking long erect setae, interstria 9 in female costate in basal half; striae as wide as width of interstriae or narrower, gradually fading apicad; stria 9 absent basally, starting from near height of fore coxae; dark stripe on elytra generally present on interstria 6 in basal half and between middle of interstriae 3 or 4 to 8 before declivity.

LEGS. Integument pale yellow, occasionally darkened in fore and middle tibiae, mostly glabrous, with whitish suberect hairs in apical $\frac{2}{3}$ of tibiae and on tarsus; tibiae bisinuate on ventral side, with a small mucro apically; tarsi with first segment $0.5 \times$ as long as segments 2+3; segment 3 deeply bilobate; segment 4 elongate, as long as 1+2+3; claws free, not apiculate.

ABDOMEN. Tergites 3–6 undivided on midline; tergite 7 strongly impinging into 6, with a row of granules on basal $\frac{2}{3}$ and about 15 granules on basal half visible at $50 \times$ magnification; ventrites with short suberect, scattered whitish hairs; in male ventrites 1–2 deeply impressed, depression flanked by longer, semi-erect hairs.

GENITALIA. Penis a little longer than combined length of last three ventrites, body about $2 \times$ as long as wide (ratio w/l: 0.48), symmetrical, with relatively long, tapering apex (Fig. 4F); internal sac with a pair of small median sclerites.

Life history

All the specimens collected recently were found on the inflorescences of the oil palm, *Elaeis guineensis* (Arecaceae) (JH pers. obs.).

Distribution

Angola (Amboim); **Cameroon** (Bota); **Democratic Republic of Congo** (Haut-Lopori); **Ghana** (Egyirkom, Kumasi).

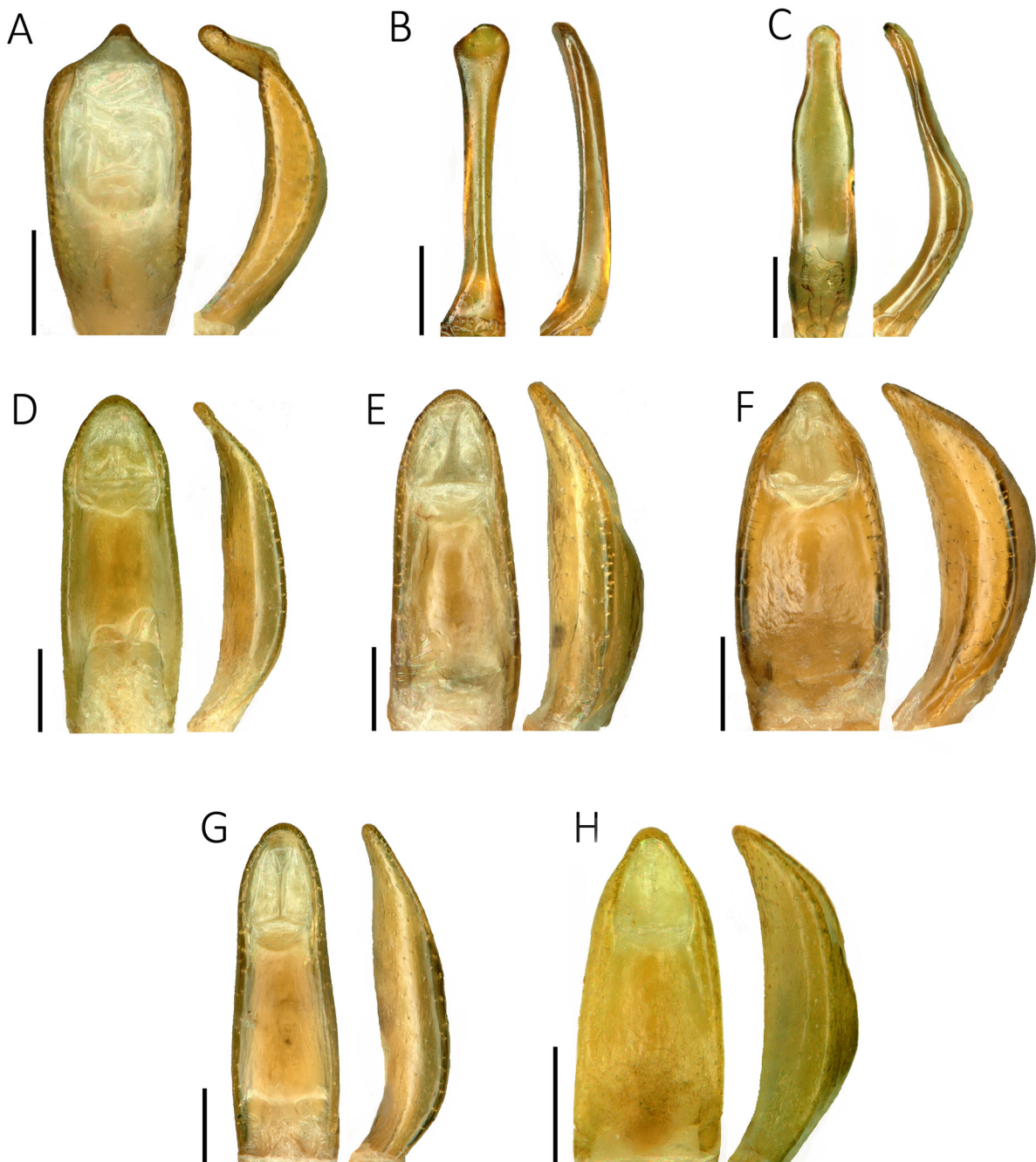


Fig. 4. Penis of males of species of the genus *Elaeidobius* Kuschel, 1952 in dorsal (left) and lateral (right) view. **A.** *E. bilineatus* (Hustache, 1924) comb. nov., Dakar, Senegal. **B.** *E. spatulifer* (Marshall, 1950) comb. nov., holotype, Thysville, Democratic Republic of Congo (MRAC). **C.** *E. subvittatus* (Faust, 1898), Dakar, Senegal. **D.** *E. kamerunicus* (Faust, 1898) comb. nov. (JHAR00209). **E.** *E. pilimargo* Haran & Kuschel sp. nov. (JHAR00409). **F.** *E. piliventris* Haran & Kuschel sp. nov. (JHAR02182). **G.** *E. plagiatus* (Fähræus, 1844) comb. nov. (JHAR00272). **H.** *E. singularis* (Faust, 1898) comb. nov. (JHAR00283). Scale bars = 100 μ m.

Remarks

Elaeidobius piliventris sp. nov. is distinguished in the male by sides of the ventral impression flanked by longer semi-erect hairs (Fig. 5J–K). Females of *E. piliventris* sp. nov., *E. pilimargo* sp. nov. and *E. singularis* cannot be assigned to their specific males based on morphology of the current material of this study. *Elaeidobius piliventris* sp. nov. is closest to *E. pilimargo* sp. nov. (2.88% and 2.7–3.0% on *COI* and *COII* respectively) and *E. singularis* (2.6–2.9% on *COII*).

Elaeidobius plagiatus (Fåhraeus, 1844) comb. nov.
Figs 1G, 3C, 4G, 5C–L, 7

Derelomus plagiatus Fåhraeus, 1844: 94.

Derelomus ciliatus Hustache, 1924: 74 [syn. by Marshall 1930: 575].

Material examined

Lectotype

BETWEEN GHANA AND CONGO RIVER • ♀; “Guinea. Westermann” “♀” “Typus” “*Derelomus plagiatus* (Fahr. 1844) Kuschel 2007” “Holotype ♀ *Derelomus plagiatus* Fåhraeus 1844 Kuschel 2007” “NHRS-JLKB000065509” “Lectotype ♀ *Derelomus plagiatus* Fåhraeus 1844 Haran 2020”; NHRS.

Other material

ANGOLA • 3 ♂♂, 1 ♀; CE Salazar; 9.16° S, 14.55° E; 14 May 1973; Carvalho leg.; oil palm inflorescence; TMP.

DEMOCRATIC REPUBLIC OF CONGO • 1 ♂, lectotype of *Derelomus ciliatus* Hustache, 1924 [here designated], labelled as “*Elaeidobius plagiatus* (Fåhraeus 1844) Kuschel 2009”; Haut-Uelé, Moto; 1922; L. Burgeon leg. MRAC • 1 ♂, paralectotype of *Derelomus ciliatus* Hustache, 1924 [labelled as] “*Elaeidobius plagiatus* (Fåhraeus 1844) Kuschel 2009”; same collection data as for preceding; MRAC • 1 ♂, paralectotype of *Derelomus ciliatus* Hustache, 1924, [labelled as] “*Elaeidobius plagiatus* (Fåhraeus 1844) Kuschel 2009”; Kindu; Nov. 1913; L. Burgeon leg.; MRAC.

GHANA • 3 ♀♀; Western region, Pretsea; 4.55° N, 1.52° W; 30 m a.s.l.; 26 Aug. 1967; Endrödy-Younga leg.; beating oil palms; TMP • 2 ♂♂; Godbe; 2015; on inflorescences of *E. guineensis*; JHAR00283_0102/0103; CBGP.

NIGERIA • 1 ♂; Obaretin; 2006; JHAR00272_0103; CBGP.

CAMEROON • 1 ♂; Edu Ngat; 2008; JHAR00291_0101; CBGP • 1 ♂; Kienké; 2009; JHAR00293_0101; CBGP.

Diagnosis (♂♀)

BODY LENGTH. 2.1–3.4 mm.

COLOUR. Yellowish or pale reddish brown; reddish or dark brown on head, rostrum, underside, a large trapezoidal central area on pronotum, a stripe on interstria 6 in basal half and an oblique band between interstriae 3 or 4 to 8 before declivity; male with long erect setae on elytral margins and erect setae on suture and swelling at the base of interstria 4.

HEAD. Forehead in male sharply carinate on sides near eyes, flat or impressed, in female not or obsolete carinate on sides, not impressed; rostrum in male as long as prothorax, or a fraction longer,

robust, moderately downcurved, without erect hairs or tubercle on underside, in female $1.5 \times$ as long as prothorax.

PROTHORAX. Trapezoidal, with nearly straight sides; disc nearly flat in lateral view, medially with two shallow impressions and two vague impressions between middle and apex; median impressions with small fovea on either side of middle; marginal carina in male obsolescent at least on basal half, carinate at apex near collar, distinctly projecting forward.

ELYTRA. In both sexes shiny, with slightly rounded sides, widest near middle, in male tectiform, distinctly sloping to the sides; striae gradually fading towards apex; base of interstria 4 in male not or slightly tumescent, with erect setae on the swelling similar to those on suture; interstria 9 in male swollen and bearing long erect setae throughout, in female costate on basal half, here rendering stria 8.

ABDOMEN. Tergites well-pigmented, entire; tergite 7 advancing strongly forward, with 9–11 plectral granules.

GENITALIA. Penis nearly as long as combined length of last 3 ventrites, Body symmetrical, $3.3 \times$ as long as apodemes, about $3 \times$ as long as than wide (ratio w/l: 0.32), with rather large frena (Fig. 4G).

Life history

In inflorescences of the oil palm, *Elaeis guineensis* (Arecaceae) (Mariau & Genty 1988).

Distribution

Benin (Cotonou, Lobé); **Cameroon** (Bota, Kienke, Mbalmayo, Moliwe, Tiko); **Democratic Republic of Congo** (Beni: Ituri Forest, Haut-Lopori, Haut-Uelé: Moto, Kindu, Yambula); **Ghana** (Aburi, Accra, Kumasi); **Nigeria** (Ibadan, Ife); **Togo** (Kolo)

Remarks

Elaeidobius plagiatus is distinguished in the male by long erect setae on margin of elytra, on suture and at base of interstria 4, in female by a large dark trapezoidal central area on the pronotum and a rather wide apical half of the foretibiae. The usually long marginal erect setae of males can be very short as well, as is the case with the paralectotype of *D. ciliatus* from Kindu (Congo) that Hustache took to be a female. Such males are also observed in low proportions in Angola.

Elaeidobius plagiatus was described by Fåhraeus as *Derelomus plagiatus* from “Guinea”, an area that comprised the current zone between Ghana and the Congo River. In the collection of Fåhraeus housed at NHRS, a female specimen with the locality “Guinea Westermann” and bearing a red “Typus” label was located. As no particular holotype specimen was designated in the original description, this specimen was designated as the lectotype for *Derelomus plagiatus* Fåhraeus, 1844 and labelled accordingly. *Derelomus ciliatus* Hustache, 1924 was described based on a series of individuals from two localities in the Democratic Republic of Congo (Haut-Uelé, Moto, 1922 and Kindu, 1913). This species was later put in synonymy with *D. plagiatus* Fåhraeus (= *Elaeidobius plagiatus* Fåhraeus) by Marshall (1930) but no particular specimen from these series was designated as holotype. In the collections of the MRAC, three male specimens from these localities and bearing the red labels “Holotypus” and “Paratypus” were located. The specimen from Haut-Uelé and bearing the label “Holotypus” is here designated as the lectotype for *D. ciliatus* Hustache. The second specimen from Haut-Uelé and the one from Kindu, both bearing the label “Paratypus” are labelled as paralectotypes for this species.

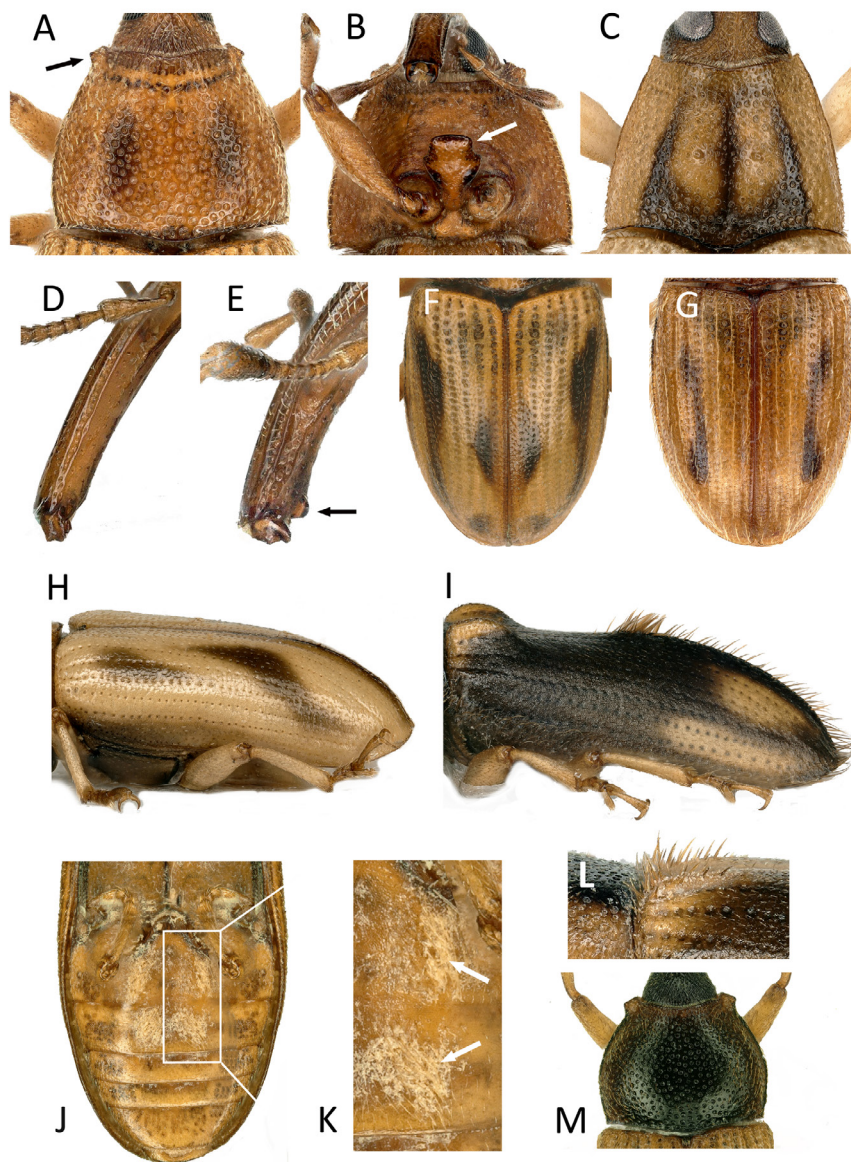


Fig. 5. Details of morphology of *Elaeidobius* spp. **A.** Pronotum of *E. subvittatus* (Faust, 1898) in dorsal view showing the flat pronotum and the lateral cuticular expansion near head. **B.** Pronotum of *E. subvittatus* (Faust, 1898) in ventral view, showing the trilobate cuticular expansion between the coxae. **C.** Pronotum of *E. plagiatus* (Fåhræus, 1844) comb. nov. in dorsal view showing the fovea on either side of midline. **D.** Apex of rostrum of *E. bilineatus* (Hustache, 1924) comb. nov. in lateral view. **E.** Apex of rostrum of *E. subvittatus* (Faust, 1898) in lateral view showing the protruding tubercle on underside. **F.** Elytra of *E. bilineatus* (Hustache, 1924) comb. nov. in dorsal view. **G.** Elytra of *E. subvittatus* (Faust, 1898) in dorsal view. **H.** Elytra of *E. singularis* (Faust, 1898) comb. nov. in lateral view. **I.** Elytra of *E. kamerunicus* (Faust, 1898) comb. nov. in lateral view. **J–K.** Abdominal sternites of male of *E. piliventris* Haran & Kuschel sp. nov. showing the median impression of the first two segments, flanked by a fringe of semi-erect hairs. **L.** Scutellum of *E. plagiatus* (Fåhræus, 1844) comb. nov. in lateral view showing erect setae on tumescent base of interstria 4. **M.** Pronotum of dark specimens of *E. subvittatus* (Faust, 1898) in dorsal view. Not to scale.

Elaeidobius singularis (Faust, 1898) comb. nov.
Figs. 1H, 3D, 4H, 5H

Derelomus singularis Faust, 1898: 224.

Derelomus uelensis Hustache, 1932: 68. **syn. nov.**

Material examined

Lectotype (here designated)

DEMOCRATIC REPUBLIC OF CONGO • ♂; “Landana. Congo. Oberthur” “*D singularis* Fst.” “Coll. J. Faust. Ankauf 1900” “type” “Staatl. Museum für. Tierkunde Dresden” “Lectotype ♂ [here designated]. *Derelomus singularis* Faust, 1898. Kuschel 2013” “*Elaeidobius singularis* (Faust, 1898). Kuschel 2013”; MTD.

Paralectotype (here designated)

DEMOCRATIC REPUBLIC OF CONGO • 1 ♀; same collection data as for lectotype; “Paralectotype ♀. *Derelomus singularis* Faust, 1898. Kuschel 2013” “*Elaeidobius singularis* (Faust, 1898). Kuschel 2013”; MTD.

Other material

DEMOCRATIC REPUBLIC OF CONGO • ♂, lectotype of *Derelomus uelensis* Hustache, 1932 [here designated], labelled as “*Elaeidobius singularis* (Faust 1898) Kuschel 2009”; Haut-Uelé, Moto; 1922; L. Burgeon; MRAC • 3 ♂♂, 2 ♀♀; Kindu; Nov. 1913; L. Burgeon leg.; MRAC • 1 ♀; Haut-Loporiv; 1927; J. Ghesquiere leg.; MRAC • 1 ♀; Haut-Uelé, Watsa; 1922; L. Burgeon leg.; MRAC.

ANGOLA • 2 ♂♂; CE Salazar; 9.16° S, 14.55° E; 14 May 1973; Carvalho leg.; oil palm inflorescence; TMP.

GHANA • 1 ♂; Godbe; 2015; on inflorescences of *E. guineensis*; JHAR00283_0101; CBGP.

Diagnosis (♂♀)

BODY LENGTH. 2.2–3.0 mm.

COLOUR. Yellowish or reddish brown, shiny rostrum in part, meso and metasternum dark; prothorax with vague, dark stripe on sides of discal foveae, elytra usually dark near basal 1/3 of interstria 6 and an oblique band from middle of interstria 3 or 4 to 2/3 of interstria 8.

HEAD. Forehead in male impressed. Rostrum in male a fraction shorter than prothorax, without erect hairs or tubercle on underside, in female 1.5 × longer than prothorax.

PROTHORAX. Disc with a pair of large, deep foveae; apical collar at base usually with a transverse row of black dots; lateral carina fine, continued to apex.

ELYTRA. Without long erect setae on margin and suture, in male often with a conspicuous swelling at base of interstria, in small males reduced or absent; prosternum without protruding process.

ABDOMEN. Ventrite 1–2 flattened on middle, not impressed, with fine, appressed pubescence and no semi-erect hairs. Tergites 3–6 undivided on midline, tergite 7 strongly advancing forward against tergite 6; granules of stridulatory organ evenly distributed on entire line, up to 18 in number per row.

GENITALIA. Penis a little longer than the last three ventrites; body $2.3 \times$ as long as apodemes, about $2 \times$ as long as wide (ratio w/l: 0.48), symmetrical, tapering with slight curve to apex (Fig. 4H); internal sac with a pair of small frena.

Life history

In inflorescences of the oil palm, *Elaeis guineensis* (Arecaceae) (Mariau & Genty 1988).

Distribution

Benin (Cotonou, Dassa, Niaouli, Pobè); **Cameroon** (Edu Ngat, Ekondo Titi, Kienke, Mbalmayo, Moliwe); **Democratic Republic of Congo** (Haut-Lopori, Haut Uelé: Moto, Watsa, Kindu, Landana, Luluabourg); **Gabon** (Kome Estate); **Ghana** (Gobbe); **Ivory Coast** (Bonoua, Boudoukal); **Nigeria** (Obaretin); **Togo** (Kloto).

Remarks

Elaeidobius singularis is readily distinguished in the male by having a tumescent 4th interstria at the base (though reduced or even absent at times in some small individuals), and no semi-erect hairs on the abdomen, and by the elytra without long erect setae on the margin and on the suture. This taxon was described on a male and a female from Landana in the current Democratic Republic of Congo. In the collection of J. Faust housed at MTD, we found a male and a female pinned on the same pin with the identification “*D singularis* Faust.” “Landana, Congo” and bearing a red “type” label. The description of this species does not refer to a holotype, therefore the male syntype was designated as the lectotype of *Derelomus singularis* Faust, 1898 and was labelled accordingly. The female syntype was labelled as the paralectotype of this species.

Hustache described *D. uelensis* based on five specimens collected by L. Burgeon in Moto (Democratic Republic of Congo). In the collections of the MRAC, only one specimen from Moto could be located and bore a red paratypus label. This specimen is here designated as the lectotype for *D. uelensis* and labelled accordingly. The other four specimens of this series are from Kindu and not from Moto as reported by Hustache (1932). These specimens also bear paratypus labels and were labelled as paralectotypes of this species. Observations made on the external and internal morphology of specimens of this series showed no difference from the holotype of *Elaeidobius singularis*. Consequently, the name *Derelomus uelensis* should be considered as a junior synonym of *Elaeidobius singularis*.

Key to the genera of Derelomini found on inflorescences of Afrotropical Arecaceae

1. Eyes convex, the external margin exceeding the contour of head in dorsal view. On inflorescences of Arecaceae and various Dicotyledonous plants *Derelomus* Schoenherr, 1825
– Eyes flat, following contour of head. On inflorescences of *Elaeis guineensis* Jacq. 2
2. Body integument (head, prothorax and elytra) entirely dark brown *Prosoestus* Faust, 1899
– Body integument at least partly yellow *Elaeidobius* Kuschel, 1952

Key to species of *Elaeidobius*

1. Prothorax on middle of disc without a fovea on either side of midline (Fig. 5A); without a shallow depression on distal half on either side of a midline fold. Lateral carina of prothorax forming a constriction near collar (Fig. 5A), followed by a distinct indentation. In male, prosternum between coxae generally with prominent process (Figs 2A, 5B) (*subvittatus*-group) 2
– Prothorax on middle of disc with a fovea on either side of midline (Fig. 5C); with a shallow depression on distal half on either side of a midline fold (Fig. 5C). Lateral carina of prothorax

- regular, not forming a constriction or indentation near collar (Fig. 5C). In male, prosternum between coxae without cuticular process (*plagiatus*-group) 4
2. Rostrum distinctly longer than prothorax (Fig. 2A). In males, rostrum in lateral view on underside at apex smooth, without a tubercle or elevation (Fig. 5D). Elytra with dark markings on middle of interstriae 2–3, on each side of suture forming a central circular marking (Fig. 5F) *E. bilineatus* (Hustache, 1924) comb. nov.
- Rostrum as long as prothorax in males, 1.2 × longer in females (Fig. 2B–C). In males, rostrum in lateral view on underside at apex with a protruding tubercle or cuticular elevation (Fig. 5E). Elytra yellowish brown or homogeneously reddish brown lacking a central circular marking on disc (Fig. 5F–G) 3
3. Body length under 2.3 mm. Pronotum and elytra yellowish brown with dark markings on prothorax and elytra (Fig. 5G). In males, process between procoxae trilobate at apex (when present) *E. subvittatus* (Faust, 1898)
- Body length over 2.4 mm. Prothorax and elytra uniformly chestnut-brown, without contrasting darker markings (Fig. 1B). In males, process between procoxae rounded at apex (when present) *E. spatulifer* (Marshall, 1950) comb. nov.
4. Elytra of male without long erect setae on margins and on suture (Fig. 5H) 5
- Elytra of male with long erect setae on margins and on suture (Fig. 5I) 6
5. First two ventrites of male with deep median impression flanked by a fringe of semi-erect hairs (Fig. 5J–K). Elytra of male at base of interstria 4 flat, not raised to a swelling *E. piliventris* Haran & Kuschel sp. nov.
- First two ventrites of male with shallow median depression and recumbent hairs only. Elytra of male at base of interstria 4 usually raised to a distinct swelling ... *E. singularis* (Faust, 1898) comb. nov.
6. Elytra of male with long erect setae on tumescent base of interstria 4 (Fig. 5L). Apical half of protibiae of females widening apicad, as wide as apex of rostrum *E. plagiatus* (Fåhraeus, 1844) comb. nov.
- Elytra of male lacking erect setae on tumescent base of interstria 4 (Fig. 5I). Apical half of protibiae of females distinctly narrower than rostrum width 7
7. Elytra yellowish-brown with dark markings. In male, row of erect setae along elytral suture not forming a condensed spot near middle of length. Ventrites 1 and 2 of male with median impression flanked with semi-erect hairs (Fig. 5J–K) *E. pilimargo* Haran & Kuschel sp. nov.
- Elytra dark brown, with one or two yellowish spots on either side of apical third, yellow often also on and around base of interstria 4 (Fig. 5I). In male, row of erect setae along elytral suture forming a condensed spot near middle (Fig. 5I). Ventrites 1 and 2 in male lacking erect hairs on sides of median impression *E. kamerunicus* (Faust, 1898) comb. nov.

Phylogenetic analysis

The preliminary phylogenetic reconstruction of the genus *Elaeidobius* was performed based on *COII* sequences due to unsuccessful amplification of *COI* in several species and populations (probably due to a primer mismatch). Sequences of *COII* showed no traces of ambiguous sites that could be assigned to pseudogenes or heteroplasmy. The species *E. bilineatus* and *E. subvittatus* showed a condon insertion (GAC) in position 716 of the *COII* sequences amplified. This insertion was removed to compute uncorrected p-distances, but was kept for phylogenetic analysis. The best model for the *COII* fragment was GTR+G+I (AIC: 5104.8) and was used to run the maximum likelihood analysis. The tree obtained

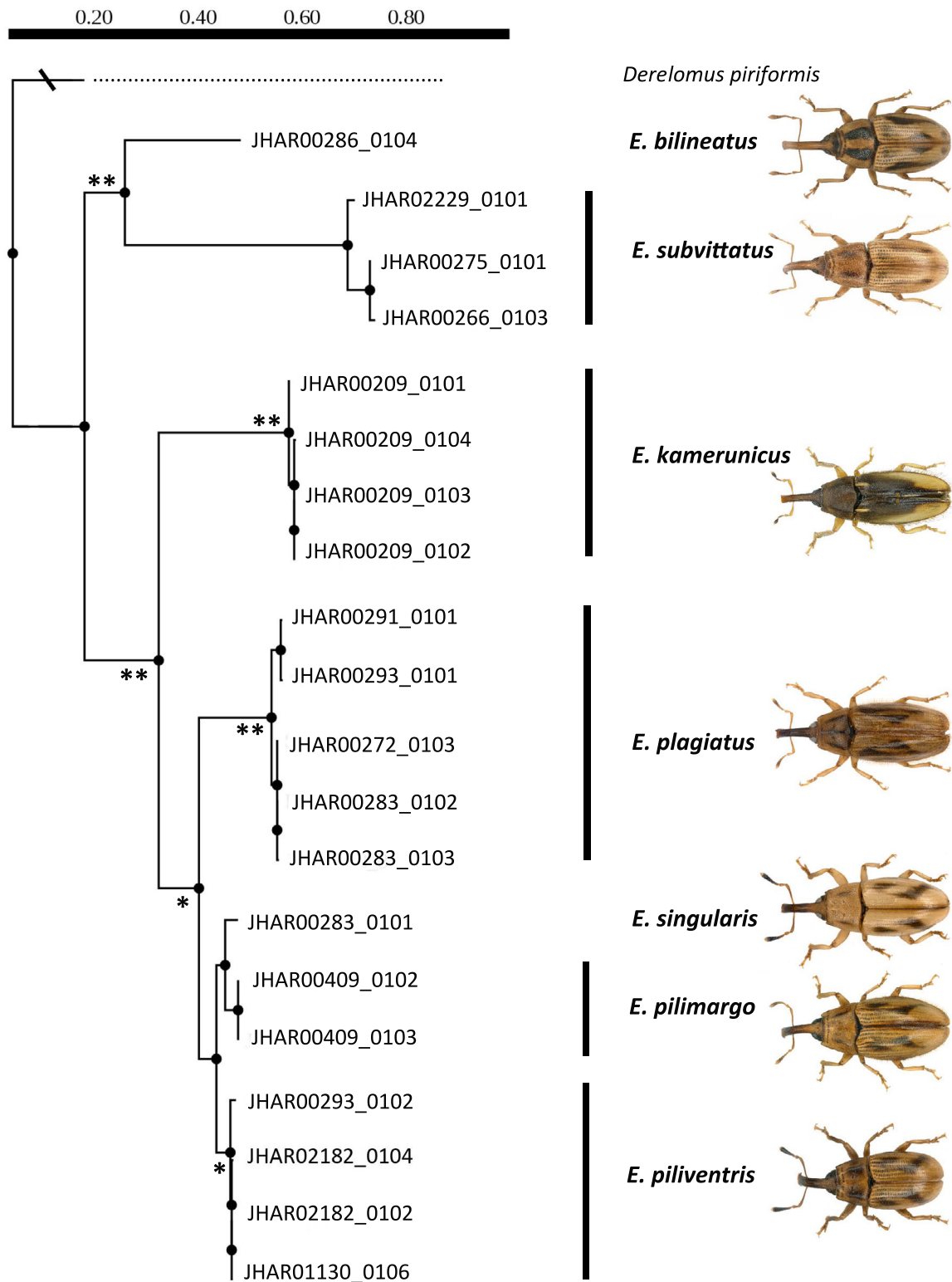


Fig. 6. Preliminary phylogenetic tree of the genus *Elaeidobius* Kuschel, 1952 inferred from *COII* fragment sequences (730 bp). Bootstrap support values were obtained for 1000 replicates. * = bootstrap values above 70; ** = bootstrap values above 90.

confirmed the interspecific splits recognized morphologically with all species forming a distinct cluster (Fig. 6). All intraspecific genetic distances were below 1.3% apart from *E. subvittatus*, which showed 2.5% between the central and West African populations. The tree topology was also consistent with the species groups recognized based on morphology, with the *E. subvittatus* species group forming a cluster separated from all the species of the *E. plagiatus* group. The genebank accessions for the *COI* and *COII* sequences used are reported in Table 3.

Discussion

This study recognized eight valid species in the genus *Elaeidobius*, two of them described as new here. The new species *E. pilimargo* sp. nov. and *E. piliventris* sp. nov. were probably confused under *E. singularis* in previous studies (Desmier de Chenon 1982; Beaudoin-Ollivier *et al.* 2010; Yalamoussa *et al.* 2011; Li *et al.* 2019). As a result, all previous work dealing with this species should be considered with care. The genus *Elaeidobius* exemplifies the critical importance of detailed integrative taxonomic studies to clarify species identity, especially for groups of economic importance occurring in tropical areas where the entomofauna is generally poorly known.

Apart from *E. kamerunicus*, the species of *Elaeidobius* show a remarkable homogeneous general appearance, with a dark elytral pattern on a yellowish cuticular background. This homogeneity probably originates from strong selective constraints to mimic the colour and shape of the inflorescences of *Elaeis guineensis* (Fig. 7). Despite this homogeneity, species can be readily distinguished from each other by the long erect setae on the elytra, the cuticular sculptures and the penis of males. Females of *E. singularis*, *E. pilimargo* sp. nov. and *E. piliventris* sp. nov., however, show no external morphological features enabling species to be distinguished from each other. As all the species of this group are sympatric and found together on the same inflorescence, only males can be reliably identified based on morphology. The standard Barcode (*COI*) and *COII* showed interspecific genetic distances that corroborate morphological recognition of species. Within the *plagiatus* species group, low genetic distances of about 2% were observed between the closely related species *E. singularis* and *E. pilimargo* sp. nov. Morphological and molecular close relations between these species suggests that somewhat recent speciation processes have occurred in this group. A formal phylogenetic analysis of the genus and related genera was beyond the scope of the present work and will be developed in a future study.

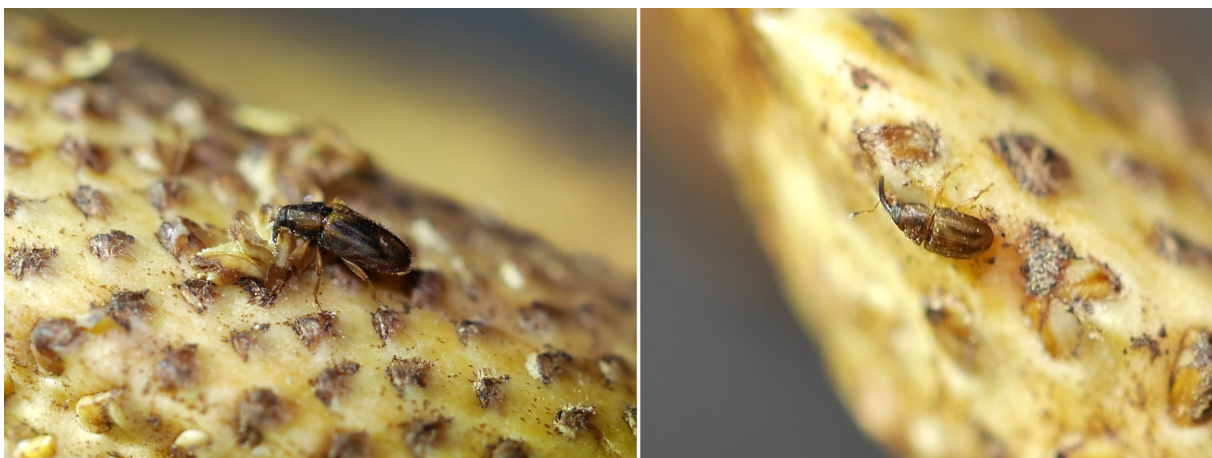


Fig. 7. Adults of *Elaeidobius plagiatus* (Fåhraeus, 1844) comb. nov. (left) and *E. subvittatus* (Faust, 1898) (right) feeding on male inflorescence of *Elaeis guineensis* Jacq.

Table 3. GenBank accession number for the genes COI and COII of *Elaeidobius* spp.

Species	CBGP code	COII	COI
<i>E. bilineatus</i>	JHAR00286_0104	MN635541	–
<i>E. subvittatus</i>	JHAR02229_0101	MN635538	MN627256
<i>E. subvittatus</i>	JHAR00275_0101	MN635539	–
<i>E. subvittatus</i>	JHAR00266_0103	MN635540	–
<i>E. kamerunicus</i>	JHAR00209_0101	MN635527	–
<i>E. kamerunicus</i>	JHAR00209_0102	MN635528	–
<i>E. kamerunicus</i>	JHAR00209_0103	MN635529	–
<i>E. kamerunicus</i>	JHAR00209_0104	MN635530	–
<i>E. piliventris</i>	JHAR01130_0106	MN635526	MN627255
<i>E. piliventris</i>	JHAR02182_0102	MN635522	MN627254
<i>E. piliventris</i>	JHAR02182_0104	MN635523	–
<i>E. piliventris</i>	JHAR00293_0102	MN635537	–
<i>E. pilimargo</i>	JHAR00409_0103	MN635525	MN627252
<i>E. singularis</i>	JHAR00283_0101	MN635532	–
<i>E. plagiatus</i>	JHAR00272_0103	MN635531	–
<i>E. plagiatus</i>	JHAR00283_0102	MN635533	–
<i>E. plagiatus</i>	JHAR00283_0103	MN635534	–
<i>E. plagiatus</i>	JHAR00291_0101	MN635535	MN627259
<i>E. plagiatus</i>	JHAR00293_0101	MN635536	MN627260
<i>Derelomus piriformis</i>	JHAR02980_0101	MN635542	–

Of all the species, only males of *E. kamerunicus*, *E. pilimargo* sp. nov. and *E. plagiatus* display long hairs on the elytra that are a typical adaptation to pollen transport. The exact role of the other species in pollen transportation is unclear. Interestingly, most efforts have been focused on *E. kamerunicus* for the pollination of *Elaeis guineensis* from Africa, while this species is sometimes far less abundant on inflorescences than *E. pilimargo* sp. nov. and *E. plagiatus* in that region (JH pers. obs.). The exact role of each species in pollinating this palm remains unclear (Li *et al.* 2019) and should be explored, especially in the light of the new species described here.

More generally, the inflorescences of *Elaeis guineensis* show a remarkable assemblage of eight sympatric weevil species in a single genus. In addition to this diversity, two species of the genus *Prosoestus*, *P. minor* Marshall, 1935 and *P. sculptilis* Faust, 1899, have also been reported to develop on the same host (Mariau *et al.* 1991). The maintaining of this high diversity of species on a single host is unexpected. A recent detailed study of the assemblage of species pollinating the Neotropical palm *Syagrus coronata* Becc. showed a contrasting case where only one specialist species of Derelomini was associated with inflorescences (Medeiros *et al.* 2019). The diversity of *Elaeis*-associated Derelomini raises the question of the driver of speciation processes in this group, and of the stability of this assemblage over evolutionary times.

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