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New species of *Endaeus* Schoenherr, 1826 (Curculionidae: Curculioninae: Ochyromerini) associated with Annonaceae and Clusiaceae

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Abstract. Representatives of the weevil tribe Ochyromerini (Coleoptera: Curculionidae: Curculioninae) have been increasingly reported as specialized pollinators of Annonaceae Juss., with some species in the genus *Endaeus* Schoenherr, 1826 engaging in brood-site pollination with their host. Recent investigations into the poorly documented life history of these pollinators have led to the discovery of new species in the genus *Endaeus* and provided details of their life histories. The following species are herein described: *E. canangae* Haran sp. nov. from Southeast Asia, associated with *Cananga odorata* (Lam.) Hook.f. & Thomson (Annonaceae); *E. lenticulatus* Haran sp. nov. from Central Africa, associated with *Uvariodendron molundense* (Diels) R.E.Fr. (Annonaceae); *E. xylopiae* Haran & Zelvelder sp. nov., *E. jaculifer* Haran & Zelvelder sp. nov. and *E. convexiculus* Haran & Zelvelder sp. nov. from Central Africa, associated with *Xylopia aethiopica* (Dunal) A.Rich. (Annonaceae) and *E. staminicola* Haran sp. nov. also from Central Africa, associated with *Allanblackia floribunda* Oliv. (Clusiaceae Lindl.). Pictures of habitus and terminalia of adults, molecular and morphological diagnostic tools along with life history data are provided for each species. These new associations are discussed in light of the general patterns of specialized brood-site pollination mutualism between plants and weevils.

Keywords. Africa, Asia, brood-site pollination, ciophily, integrative taxonomy.

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Introduction

Ochyromerini Voss, 1935 is a small palaeotropical tribe of weevils encompassing ca 200 species in 28 genera, with a centre of diversity in East-Asia (Kojima & Morimoto 1995a, 1995b, 1995c, 1996; Oberprieler 1993; Kojima 1997; Alonso-Zarazaga & Lyal 1999; Caldara *et al.* 2014). This tribe in its current concept (Kojima & Morimoto 1995a belongs to the true weevil subfamily (Curculioninae Latreille, 1802) and is distinct from Tychiini Gistel, 1848, of which it has often been considered as a subtribe (Clark *et al.* 1977; Oberprieler 1993; Haran *et al.* 2023b). Although the features used to identify this tribe have been unsatisfactory so far (Caldara *et al.* 2014), most species display a large profemoral tooth flanked with hairs on the outer margin, uncinate pro- and mesotibiae, appendiculate tarsal claws, elytro-tergal stridulation structures in both sexes, an endophallus with pairs of elongate sclerites and tegmen without parameres (Kojima & Morimoto 1995d). The genus *Endaeus* Schoenherr 1826 (type species *E. castus* Schoenherr, 1826) is the most species-rich genus in the tribe, it is widely distributed across the tropical regions of Africa and Asia and currently includes 104 valid species (Alonso-Zarazaga & Lyal 1999). *Endaeus* was diagnosed only at regional scale and lacks a comprehensive treatment (Oberprieler 1993; Kojima & Morimoto 1996). A revised definition of this genus is beyond the scope of this paper, but the following features should help to assign most species: funicle 6-segmented, integument of scutellar shield and elytra concolorous, surface of scutellar shield smooth and not raised laterally, profemora wider than meso- and metafemora (see Hsiao *et al.* 2025 for discussion on this feature and on the validity of *Endaenidius* Morimoto, 1962), profemora with a large triangular tooth bearing a row of erect setae on external margin, protibiae smooth and unarmed or either bicarinate or armed with a subapical internal spine (see Oberprieler 1993 and Kojima & Morimoto 1996 for more details).

The biological information available for Ochyromerini is scarce (Oberprieler 1993). The few records available indicate that larvae develop in fruits, leaves, petals or seeds of various angiosperm families, belonging in particular to magnoliid families (Annonaceae Juss., Ebenaceae Gürke, Myristicaceae R.Br.; see Hsiao *et al.* 2025 and the reviews of Oberprieler 1993; Caldara *et al.* 2014; Haran *et al.* 2023a). In recent years, however, a growing literature has indicated that several species belonging to the genera *Endaeus* and *Endaenidius* act as pollinators (Ratnayake *et al.* 2006; Lau *et al.* 2017; Saunders 2020), with some species involved in brood-site pollination mutualism (‘ciophily’, sensu Hsiao *et al.* 2023) with their hosts (Dao *et al.* 2023). In these systems, weevil larvae develop on the host plant’s tissues, while the adults move between plants, ensuring their pollination. To date, in Ochyromerini, such interactions have only been formally described between *Annona senegalensis* Pers. (Annonaceae) and *Endaeus castus* and *E. floralis* Marshall, 1907 with the larvae mining the fleshy petals of the plant while the adults are the only significant pollinators visiting the flowers (Deroin 1988b; Dao *et al.* 2023).

Brood-site pollination mutualism involving weevils is generally associated with a high degree of host specificity and phylogenetic niche conservatism at the genus level (Franz & Valente 2005; Toon *et al.* 2020; Haran *et al.* 2023a; Hsiao & Oberprieler 2025). Based on this finding, Haran *et al.* (2023a) suggested that the vast majority of undescribed species of *Endaeus* could be brood-site pollinators of the tropical flora. Recent fieldwork aiming at identifying such relationships has led to the discovery of new species and host-plant interactions which we report in this paper.

Material and methods

Sampling and taxonomic treatment

Detailed observations on flowers of forest trees and bushes in Gabon and Indonesia were conducted in 2023 to search for adults and larvae of Ochyromerini. Live specimens were collected in a vial with their host, imaged and then transferred to 96% ethanol. Adults were then dry mounted on a card using standard preparation techniques for weevils. Abdomens of adults were dissected and digested in KOH to obtain clean preparations of genital structures. Habitus and genitalia were photographed using a Keyence® VHX5000 imaging system. Measurements were taken with an optical micrometre. Body length refers to the distance from the apical margin of the head capsule (corresponding to the front margin of eyes in *Endaeus*) to the apex of the elytra in dorsal view. Rostrum length refers to the distance between the apical margin of the eyes and the apex of the mandibles in dorsal and lateral views (Fig. 1A–B). Eye width refers to the widest distance between the basal margin and apical margin of the eyes in lateral view (Fig. 1A–B). Ratios of width to length (W:L ratios) were measured at the widest point of the prothorax, the elytra, the club and the penis. The length of the elytra was measured between the anterior part of the scutellar shield and the apex of the elytra. The interstriae are counted from the elytral suture and include the sutural interstriae. The length of the penis was measured between the base of the penis body (apodemes excluded) and the apex. See Haran *et al.* (2022) for an illustration of all these measurements. The terminology used follows Lyal (2020). The identifications of weevil species were made based on the examination of type material housed at the MNHN, NHMUK, TUA (see below for details on abbreviations), and on original descriptions. The names of new species are attributed to the authors as indicated in the species treatment (ICZN 1999).

DNA barcodes

Whenever fresh material could be obtained, specimens of all putative species, except the ones collected on *Xylopia aethiopica* (Dunal) A.Rich. (see below), were sequenced for the standardized 658 bp barcode fragment of the mitochondrial cytochrome *c* oxidase subunit I (*COI*) gene (Hebert *et al.* 2003). DNA was extracted from a leg or entire specimens using a DNeasy Blood & Tissue kit (Qiagen, Hilden, Germany). PCR amplifications were carried out using a cocktail of *COI* primers for invertebrates (see primer details in Haran *et al.* 2022). PCR reactions were carried out on a Mastercycler® Nexus (Eppendorf, Hamburg, Germany) in a volume of 10 µL of PCR mix containing 5 µl of Multiplex Master Mix (Qiagen, Hilden, Germany), 2 µM of Forward and Reverse primers and 2 µl of DNA. 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 20 min at 72°C. The PCR products were sequenced by Eurofins Genomics (http://www.eurofinsgenomics.eu/). Specimens of new species collected on *Xylopia aethiopica* were sequenced for a 418 bp long fragment of *COI* using the primer pair BF3+BR2 (CCHGAYATRGCHTTYCCHCG/TCDGGRTGNCCRAARAAYCA) following the protocol described in Penel *et al.* (2025). Voucher specimens sequenced and type material are deposited in the Continental Arthropod Collection at Centre de Biologie pour la Gestion des Populations, Montpellier, France

(CBGP; https://doi.org/10.15454/D6XAKL). Barcode sequences were aligned using CodonCode Aligner ver. 3.7.1. (CodonCode Corporation, Centerville, MA, USA). Uncorrected *p*-distance values of pairwise genetic distances between species were computed with Mega ver. 11 (Tamura *et al.* 2021). Sequences are available in supplementary material of this article (Appendix 1).

Ecology

Detailed observations of the flowers hosting the *Endaeus* were made, to search for the traits typical of ciophilous (weevil-pollinated) plants (pollination chamber, flower structure, brood site for larval stage of weevils, etc.; Haran *et al.* 2023a). When larvae were located, part of the specimens were bred to obtain adults, while the rest was set in alcohol and later sequenced to match the immature stages with the species visiting flowers. When possible, we also made a preliminary assessment of the fragrance produced by the flowers that may play a functional role in the weevils' attraction. For two species of Annonaceae, *Xylopia aethiopica* and *Uvariodendron molundense* (Diels) R.E.Fr., volatile organic compounds (VOCs) released by one flower per species were extracted, using the SPME technique. Briefly, VOCs were sampled using solid phase micro extraction (StableFex SPME Fibre, 65 µm film thickness composed of polydimethylsiloxane-divinylbenzene (PDMS-DVB), SUPELCO, Bellefonte, USA). A static head-space was made by enclosing the subject in polyethylene terephthalate bags shut tightly with cotton string (Nalophane®, Kalle Nalo GmbH, Wursthüllen, Germany). An SPME fibre was then introduced into and was exposed to the vial headspace for 20 mins. Control samples were sampled in the same way without plant material. After extraction, fibre was introduced into the injector at 250°C in splitless mode of a gas chromatograph coupled to a mass spectrometer (GC-MS, QP2010-SE (Shimadzu, Kyoto, Japan)). The GC-MS was equipped with an Optima 5-MS fused silica capillary column (30 m × 0.25 mm × 0.25 µm film thickness, Macherey-Nagel, Düren, Germany) with helium as the carrier gas (1 ml/min). The oven temperature was programmed as follows: maintained at 40°C for 2 min., then increased to 200°C at 5°C min-1, and finally increased to 250°C at 10°C min-1 and maintained for 2 minutes. The transfer line and the ion source temperature were 250°C and 200°C, respectively, the ionization energy was 70 eV, and the acquiring spectra set from 38 to 350 m/z. Chromatograms were analysed with the resident software (GCMS Solution, Shimadzu, Kyoto, Japan). VOCs were identified using mass spectrum and retention index (RI) comparison to databases: NIST 2007, Wiley Registry 5th and Adams, 2007, Pubchem, https://pubchem.ncbi.nlm.nih.gov/, respectively. Mass RI were calculated from alkanes retention times injected in the same analysis conditions (Alkanes standard solution, 04070, Sigma-Aldrich, Darmstadt, Germany). After identification of all compounds and exclusion of those present in the control samples, we calculated the percentage of each compound in the mix relative to peak area based on the total ion current chromatogram (TICC).

Institutional abbreviations

The specimens on which this study was based are lodged in the following institutions and specimen collections.

CBGP = Continental Arthropod Collection, Centre de Biologie pour la Gestion des Populations, Montpellier, France
HNG = Herbier National du Gabon, Libreville, Gabon
MNHN = Muséum national d'Histoire naturelle, Paris, France
NHMUK = The National History Museum, London, UK
TUA = Tokyo University of Agriculture, Kanagawa, Japan

Results

Taxonomy

Class Insecta Linnaeus, 1758
Order Coleoptera Linnaeus, 1758
Family Curculionidae Latreille, 1802
Subfamily Curculioninae Latreille, 1802
Tribe Ochyromerini Voss, 1935
Genus *Endaeus* Schoenherr, 1826

Endaeus lenticulatus Haran sp. nov.
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Figs 1–2

Differential diagnosis

Endaeus lenticulatus Haran sp. nov. can be distinguished from the other known Afrotropical species of the genus by the following combination of characters: large size (4.0–4.5 mm), lenticular orange ochre elytra and black rostrum and funicle. It is morphologically closely related to *E. castus*, but the integument of the later species is uniformly pale brown. The two species show an uncorrected *p*-distance for the *COI* barcode fragment of 15.8%.

Etymology

This species is named in reference to its lentil-like (*Vicia lens* (L.) Coss. & Germ) general appearance, resulting in a preliminary name given by the authors at time of discovery. The specific epithet is the Latin translation of 'lens-shaped'.

Type material

Holotype

GABON • ♂; "GABON, Parc Nat. des / Monts de Cristal; 10.xi.2023; J. Haran coll. / JHAR07053-01; 0.464 10.277 [0°27′50.4″ N, 10°16′37.2″ E] / *Uvariodendron molundense* / Collection-Cirad / Holotype; *Endaeus lenticulatus* / Haran 2026"; JHAR07053-01; CBGP.

Paratypes

GABON • 1 ♂; Parc National des Monts de Cristal; 0°27′50.4″ N, 10°16'37.2″ E; 10 Nov. 2023; J. Haran leg.; emerging from petals of *Uvariodendron molundense* (Annonaceae); JHAR0753-02; HNG • 1 ♂; same data as for preceding; CBGP, JHAR0753-03 • 1 ♀; same data as for preceding; CBGP, JHAR0753-04 • 2 specs, preserved in ethanol, sex undetermined; same data as for preceding; CBGP, JHAR0753-05 and JHAR0753-06.

Description

Male

Body length. 4.0–4.5 mm.

Colour. Body integument entirely orange ochre, shiny, rostrum club and funicular segments 3–6 black; vestiture of elytra made of combination of suberect orange ochre setae, as long as ½ of interstriae width, forming 2–3 ill-defined longitudinal rows on each interstria and shorter recumbent setae forming dense cover of 6–8 setae per width of interstriae; setae not concealing integument.

Head. Rostrum as long as prothorax in lateral view, moderately downcurved, in dorsal view widening slightly from base to apex, with four deeply punctuated furrows extending from base to antennal insertion and smooth area at antennal insertion; integument black, shiny, covered with tiny recumbent setae up to apex; antennae inserted at apical ⅓ of length of rostrum; head capsule covered with tiny recumbent setae; eyes slightly protruding, moderately exceeding lateral curve of head capsule in dorsal view; interocular space narrow, ⅓ as wide as rostrum width at base, with small fovea; antennal funicle with segment 1 conical, about as long as wide, 2 twice as long as wide, 2–4 globular, isodiametric, 5–6 wider than long, 6 distinctly separated from club, ⅔ as wide as club width, bearing ring of erect setae reaching middle of length or apex of segment 1 of club; scape as long as funicle + segment 1 of club, widening at apical ⅓ of length.

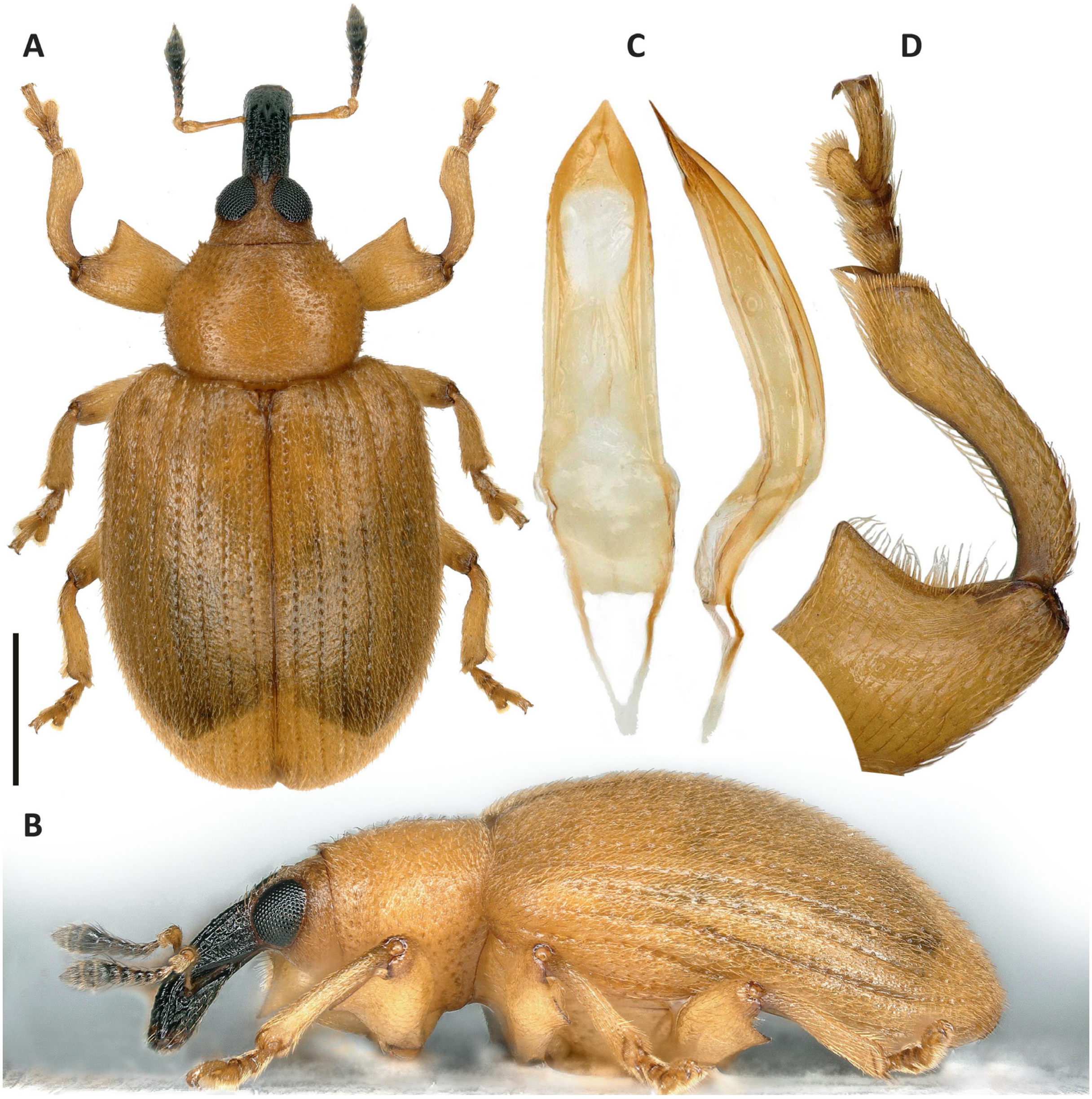

Fig. 1. Habitus and details of the morphology of *Endaeus lenticulatus* Haran sp. nov. from Gabon, holotype, ♂ (JHAR07053-01; CBGP). **A**–**B**. Habitus in dorsal and lateral views. **C**. Penis in dorsal and lateral views. **D**. Foreleg in dorsal view. Scale bar = 1 mm; C–D not to scale.

PROTHORAX. Wider than long (W:L ratio: 1.48), widest near middle of length, sides rounded, narrowed in apical ¼, apical margin ⅔ as wide as basal margin; integument shiny, with combination of larger punctures, subcircular, of diameter smaller than space between punctures, each bearing suberect seta, and minute background punctures of diameter as wide as space between them. Space between punctures micropunctate, as wide as or narrower than diameter of larger punctures; setae oriented toward median longitudinal line.

ELYTRA. Sides convex, widest near middle of length (W:L ratio: 0.85); humeri raised; each elytron separately rounded apically; striae ¼ as wide as interstriae, made of superficial and aligned circular punctures; interstriae flat; interstriae 10 with widening from base to level of metacoxae, middle of widening about 2 × as wide as interstriae 9 at same level; scutellar shield longer than wide, concolorous, bearing setae.

ABDOMEN. Underside covered with yellowish setae, longer on ventrite 5.

LEGS. Profemora clavate, with large triangular tooth bearing flange of erect setae on external margin extending from apex of tooth to close to apex of femora; protibiae strongly downcurved in basal ½, external margin straight in apical ½, internal margin bisinuate, carinate, with series of suberect setae forming tuft at apex, apex with strong mucro, larger than claw; meso-tibiae armed with mucro, on meta-tibiae mucro reduced to small spine; tarsal claws bifid.

TERMINALIA. Body of penis elongate (W:L ratio: 0.20), 4 × as long as apodemes, sides subparallel, widest at basal ⅓, narrowing from there to apex, narrowing strongly in apical ⅙, apex acuminate; in lateral view curvature strong, almost forming angle in basal ⅓, widest near middle of length, from there narrowing apicad regularly (Fig. 1C).

Female

Females can be distinguished from males by their rostrum which is longer than the prothorax in lateral view. Antennal insertion is located near the middle of the length of the rostrum in ♀♀ and at the apical ⅓ in ♂♂.

Life history

Larvae of *Endaeus lenticulatus* Haran sp. nov. mine the fleshy petals of *Uvariodendron molundense* (Annonaceae; Fig. 2A–E). Eggs are laid in shallow oviposition holes made by adults on the petals (Fig. 2C). First instar larvae start feeding on the sides of the holes and then dig galleries within the petals (Fig. 2D–E). From two to three larvae can coexist per petal. In the dissected flowers (n = 10), galleries were located at the edge of the petals (whitish areas), the central area being generally occupied by the larvae of an unidentified Lepidoptera (frass on Fig. 2B). After anthesis, larvae develop saprophagically in fallen petals. Last larval instars leave the petals and burrow a few centimetres deep in the soil into an earthen gallery where pupation takes place (Fig. 2F). Adults emerge after about two weeks. None of the flowers examined during the day contained adults, suggesting that this species has a crepuscular or night activity. This species does not seem to be attracted by UV light, since no specimens were collected using this collecting method in the vicinity of dense populations of the host plant. All adults used for the species description were obtained by rearing the larvae.

A preliminary assessment of scent of flowers at the anthesis stage of *U. molundense* shows a composition largely dominated by two Monoterpenes: Myrcene and 6,7-epoxy-Myrcene (Appendix 2).

Fig. 2. Illustration of the host plant and the life cycle of *Endaeus lenticulatus* Haran sp. nov. **A**. Flower of *Uvariodendron molundense* (Diels) R.E.Fr. in anthesis in the Monts de Cristal National Park, Gabon. Note the inner petals forming a 'cage', typical for cantharophilous Annonaceae Juss. **B**. Flower of *U. molundense* showing oviposition holes (arrow) as well the frass produced by lepidopteran larvae also mining the petals. **C**. Egg of *E. lenticulatus* in the oviposition hole. **D**. First instar larva starting to eat the edges of the oviposition hole. **E**. Last instar larva digging galleries in a declining petal. **F**. Teneral adult in the earthen cell. **G–H**. Newly emerged adults. Not to scale.

Distribution

This species is only known for the type locality in north-west Gabon (Estuaire Province). The distribution of its host plant, as currently accepted (Dagallier *et al.* 2023), is centred in Gabon and Cameroon, with some specimens occurring in the Republic of Congo and the Democratic Republic of Congo.

Endaeus staminicola Haran sp. nov.

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Figs 3–4

Differential diagnosis

Endaeus staminicola Haran sp. nov. can be distinguished from other Afrotropical *Endaeus* by its uniformly dark brown integument, its comparatively short rostrum, as long as prothorax in lateral view and its comparatively narrow prothorax (W:L ratio: 1.33) with the basal margin only a little wider (1.2 ×) than the apical margin. It is very close to *E. vicinus* Marshall, 1958 from Angola, but differs by the sides of elytra only moderately convex and the length of rostrum (shorter than prothorax in lateral view in *E. vicinus*). The body of penis is diagnostic between these species, in *E. vicinus* it is shorter (W:L ratio: 0.37) and the pointed apex is truncated. It is also related to *Endaeus carinifrons* Marshall, 1933 but the later species is distinctly longer (4.8 mm) and exhibits contrasting transverse pale brown shadings on elytra. The *COI p*-distance with the latter species ranges from 16.6 to 17.6%.

Etymology

This species is named in reference to its association with the phalanges of its host, structures resulting from transformed stamens. It is a combination of the Latin term for stamens (‘*stamina*’) and the suffix for inhabiting (‘*colo*’).

Type material

Holotype

GABON • ♂; “GABON, Parc Nat. des / Monts de Cristal / 10.xi.2023; L. Benoit coll. / JHAR07054-01; 0.412 10.259 [0°24′43.2″ N, 10°15′32.4″ E] / *Allanblackia floribunda*; Collection-Cirad / Holotype; *Endaeus staminicola*; Haran 2026”; CBGP, JHAR07054-01.

Paratypes

GABON • 1 ♂; Parc National des Monts de Cristal; 0°24′43.2″ N, 10°15′32.4″ E; 10 Nov. 2023; L. Benoit leg.; emerging from fallen flowers of *Allanblackia floribunda* Oliv. (Clusiaceae); HNG, JHAR0754-02 • 1 ♂; same data as for preceding; NHMUK, JHAR0754-03 • 6 ♂♂; same data as for preceding; CBGP, JHAR0754-04 to JHAR0754-09 • 1 ♀; same data as for preceding; CBGP, JHAR0754-10 • 3 ♂♂, preserved in ethanol; same data as for preceding; CBGP, JHAR0754-11 to JHAR0754-13 • 3 specs, preserved in ethanol, sex undetermined; same data as for preceding; TUA, JHAR0754-14 to JHAR0754-16 • 10 larvae, sex undetermined, preserved in ethanol; same data as for preceding; CBGP, JHAR0754-17 to JHAR0754-26.

Description

Male

Body length. 2.8–3.1 mm.

Colour. Body integument dark brown to reddish brown; vestiture of elytra made of recumbent yellowish setae, truncated at apex, as long as ⅔ of interstriae width, generally aligned in one row on even interstriae and two rows on odd interstriae, and of narrower, shorter and recumbent setae, not aligned on interstriae, forming dense and homogeneous background cover; vestiture not concealing integument.

HEAD. Rostrum as long as prothorax in lateral view (1.10 ×), moderately downcurved; underside straight in apical ¾; in dorsal view with 5 longitudinal carinae only visible in basal ½, covered with recumbent setae in basal ½, apical ½ almost glabrous, with few scattered setae; antennae inserted at apical ⅓ of

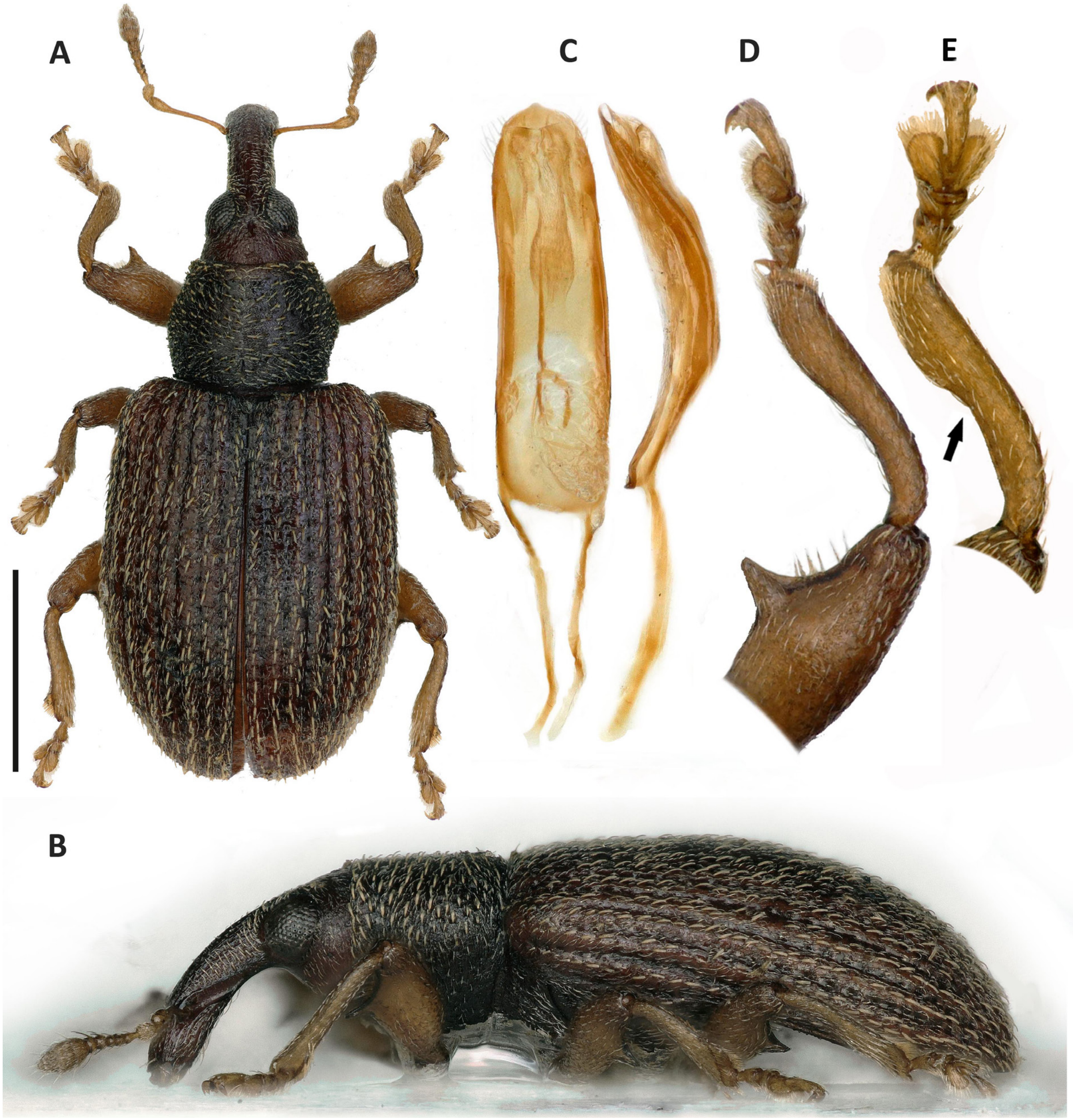

Fig. 3. Habitus and details of the morphology of *Endaeus staminicola* Haran sp. nov. from Gabon, holotype, ♂ (JHAR07054-01; CBGP). **A**–**B**. Habitus in dorsal and lateral views. **C**. Penis in dorsal and lateral views. **D**–**E**. Protibia in dorsal view, with illustration of variation encountered in this species. Arrow pointing to the curved shape of the internal margin of protibiae in some specimens. Scale bar = 1 mm; C–E not to scale.

length of rostrum; head capsule with minute punctures, covered with recumbent setae oriented toward interocular fovea; eyes slightly convex, moderately exceeding lateral curve of head capsule in dorsal view; antennal funicle with segment 1 slightly longer than wide, slightly longer than 2, 3 isodiametric, 4–6 wider than long, 6 distinctly separated from club, ½ as wide as club width, bearing ring of erect setae reaching middle of length or apex of segment 1 of club; scape as long as funicle + segment 1 of club, widening at apical ⅓ of length.

PROTHORAX. Wider than long (W:L ratio: 1.33), widest near middle of length, sides rounded, apical margin 0.8 × as wide as basal margin; integument dull, space between punctures 2–3 × as large as diameter of punctures, finely reticulate; setae as long as space between punctures, oriented toward middle of median line.

ELYTRA. Sides slightly convex, widest near middle of length (W:L ratio: 0.83–0.78); humeri raised; elytra jointly rounded at apex; interstriae striae 2–3 × as wide as striae, slightly convex, 5–6 moderately but distinctly raised at apex; interstriae 10 with a widening from base to level of metacoxae, middle of widening as wide as interstriae 9 at same level; scutellar shield rounded, isodiametric, almost concealed by setae.

ABDOMEN. Underside covered with recumbent and contiguous whitish setae.

LEGS. Profemora thickened in middle of length, bearing acute tooth and 6–8 erect setae located at distance from apex of tooth and apex of femora equal to length of seta; protibiae downcurved in basal ½, external margin straight in apical ½, internal margin bisinuate, carinate, apex with mucro similar in size to claws; meso-tibiae armed with mucro, on meta-tibiae mucro reduced to small spine; tarsal claws appendiculate, only with smooth internal thickening on metatarsi.

TERMINALIA. Body of penis elongate (W:L ratio: 0.26), about 2 × as long as apodemes, widest near base, narrowing from base to apical ⅓ of length, sides subparallel or slightly convex in apical ⅓, apex acuminate, bearing erect setae laterally; in lateral view curvature moderate, regular; internal sclerite 0.5 × as long as body of penis, forming asymmetrical bifid fork (Fig. 3C).

Female

Females can be distinguished from males by their rostrum which is longer than the prothorax in lateral view, with the underside distinctly downcurved.

Life history

The larvae of *Endaeus staminicola* Haran sp. nov. mine the phalanges, the flower receptacle and the pedicel of male flowers of *Allanblackia floribunda* Oliv. (Clusiaceae; Fig. 4A–C, 4E). Eggs are laid in shallow oviposition holes made by females on these structures and larval development takes place in feeding galleries (Fig. 4C). Several larvae can coexist in one phalange and in the receptacle, and a single male flower can host up to 10–15 individuals of this species. The larval development is mostly saprophagous, as it continues on the leaf litter in the declining abscised flowers (Fig. 4B–D). Pupation takes place in the host's tissues, in the galleries formed by the larva (Fig. 4E). Adults emerge about two weeks after pupation. Large populations of adults were found during the day on post-anthesis flowers fallen to the ground, up to six individuals were collected on a single flower, but most flowers contained only one individual when sampled (from 10 am to 3 pm). It should be noted that at time of collecting, the flowering season of *A. floribunda* was ending, which may have caused specimens to concentrate on the last available flowers. This species was not collected by the UV light traps set up in the vicinity of the population recorded. At the sampling site, *Endaeus staminicola* was found on fallen flowers with

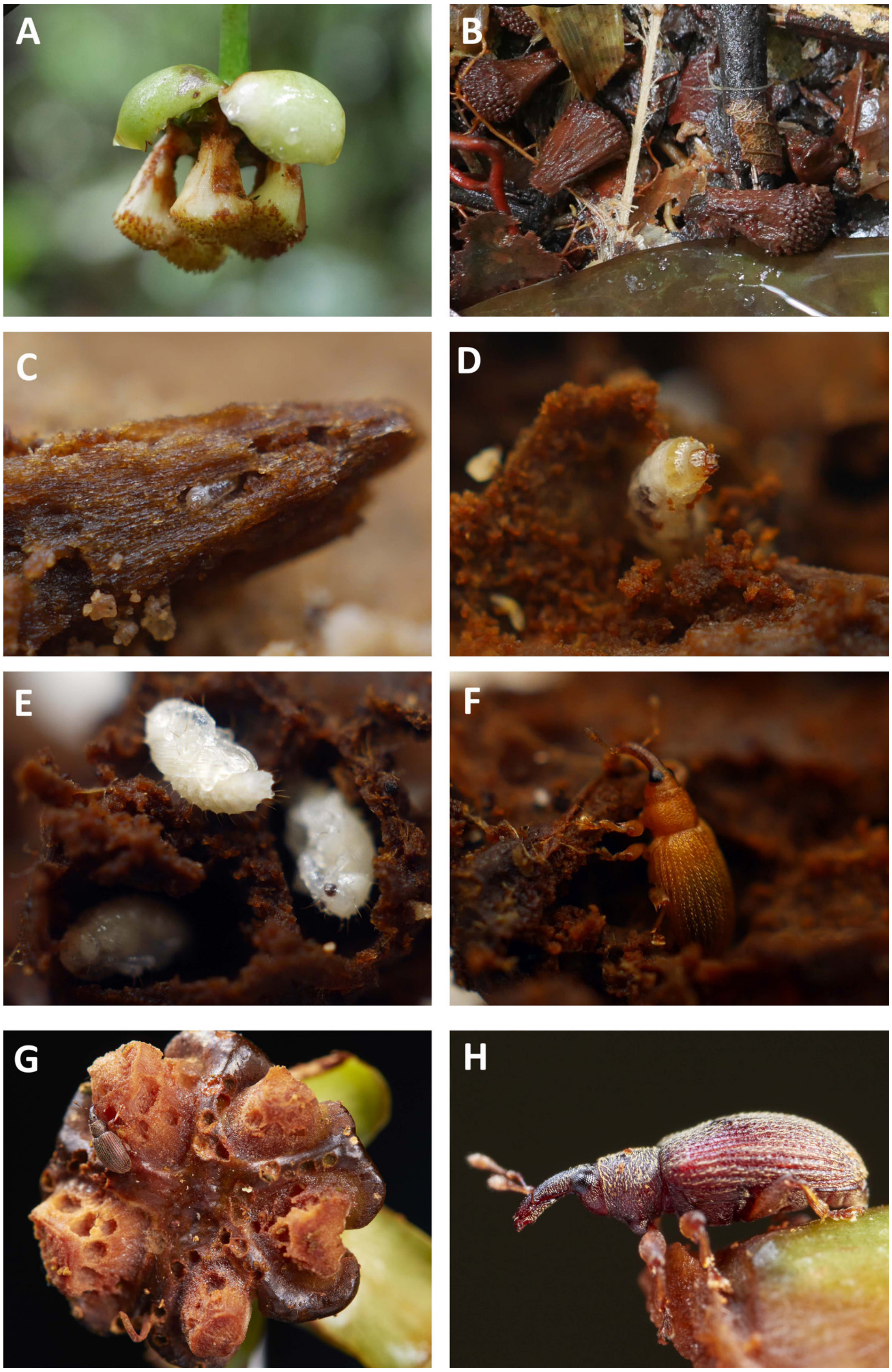

Fig. 4. Illustration of the host plant and the life cycle of *Endaeus staminicola* Haran sp. nov. in the Monts de Cristal National Park, Gabon. **A**. Post anthesis male flower of *Allanblackia floribunda* Oliv. (Clusiaceae Lindl.) on which adult specimens were collected. See feeding damages on phalanges. **B**. Fallen and declining phalanges of *A. floribunda* in which larval development takes place. **C**. First instar larva mining a declining phalange. **D**. Last instar larva in gallery of flower receptacle. **E**. Transversal cut of a phalange showing pupae in galleries. **F**. Emergence of adults from the leaf litter. **G**. Adult and feeding damage on declining flower receptacle, note the mimicry of adults on substrate. **H**. Adult on substrate. Not to scale.

Endaeus carinifrons, a species developing in seeds of *Allanblackia* sp. and *Pentadesma* sp. (Marshall 1933, Clusiaceae).

Distribution

This species is only known for the type locality in north-west Gabon (Estuaire Province). The host *A. floribunda* is distributed from Benin to the Democratic Republic of Congo (WFO 2024).

Remarks

The population used to describe this species shows an unusual degree of morphological variation for the intraspecific level in *Endaeus*. Several specimens exhibit more downcurved protibiae (Fig. 3D–E), more or less downcurved rostrum and great variation of the ratio of elytra (W:L ratio: 0.78–0.83). Uncorrected *COI p*-distance ranged up to 2.2% in this species (four specimens sequenced). However, this divergence is not associated with stable morphological features and all male specimens dissected have the same penis morphology. These divergences possibly reflect a process of recent reconnection of formerly isolated populations, as has been reported in other weevil lineages in Central Africa (Haran *et al.* 2021).

Endaeus canangae Haran sp. nov.

urn:lsid:zoobank.org:act:3E7EAE7B-312C-4E3E-9D9D-F99619B1D9D7

Figs 5–6

Differential diagnosis

Endaeus canangae Haran sp. nov. is similar in general appearance to some species of the related genus *Endaenidius*, such as *En. sarawakensis* Kojima & Morimoto, 1995, *En. kemae* Kojima & Morimoto, 1995, *En. crassipes* Kojima & Morimoto, 1995 and *En. spinipes* Kojima & Morimoto, 1995, all described from East Malaysia (Sarawak and Sabah) by having the profemora not thicker than the posterior femora, and the erect setae pointed outwards along sides and apical margin of prothorax (for details see Kojima & Morimoto 1995a). However, profemora each bear a comb of 5–6 erect setae beyond the triangular tooth in *E. canangae* (the setae are very short or absent in aforementioned species of *Endaenidius*). Among the known *Endaeus*, this species is also similar to *E. hikosanus* Kojima & Morimoto, 1995 from Japan, in the absence of a series of suberect setae along the internal margin of the protibiae. *Endaeus canangae* can be distinguished from it by the subequal thickness of the femora across all pairs of legs (profemora slightly thicker than the posterior femora in *E. hikosanus*). *Endaeus canangae* is also closely related to *E. inexpectatus* Hsiao & Kojima, 2025, recently described from northern Vietnam. It differs by having a paler body integument, a narrower prothorax (W:L ratio 1.44, versus 1.60 in *E. inexpectatus*), the eyes are more convex and the ventrite 5 in females lacks a rounded patch. The body of penis is widest at base and regularly converging apicad in dorsal view, while it is widest in apical ¼ in *E. inexpectatus* (Hsiao *et al.* 2025). Among the species of *Endaeus* for which a barcode sequence is available, this species is closest to *E. castus* (*COI p*-distance of 14.6%), which is a brood-site pollinator of *Annona senegalensis* in Africa.

Etymology

This species is named in reference to its association with flowers of ylang-ylang (*Cananga odorata* (Lam.) Hook. f. & Thomson, 1855; Annonaceae).

Type material

Holotype

INDONESIA • ♂; "INDONESIA, SUMATRA / Martebing; 4.vii.2023; J. Haran coll. / JHAR05725-01; 3.329 99.035 [3°19′44.3″ N, 99°02′05.6″ E] / *Cananga odorata* / Collection-Cirad / Holotype; *Endaeus canangae* / Haran 2026"; CBGP, JHAR05725-01.

Paratypes

INDONESIA • 4 ♂♂; Sumatra Island; Martebing; 3°19′44.3″ N, 99°02′05.6″ E; 4 Jul. 2022; J. Haran leg.; on flowers of *Cananga odorata* (Annonaceae); TUA, JHAR05725-02 to JHAR05725-05 • 1 ♀; same data as for preceding; CBGP, JHAR05725-06 • 2 ♂♂; same data as for preceding; CBGP, JHAR05725-07 to JHAR05725-08 • 2 ♀♀; same data as for preceding; CBGP, JHAR05725-09 to JHAR05725-10 • 10 adult specs, sex undetermined, preserved in ethanol; same data as for preceding; CBGP, JHAR05725-11 to JHAR05725-20 • 10 larvae, sex undetermined, preserved in ethanol; same data as for preceding; CBGP, JHAR05725-21 to JHAR05725-30 • 1 ♀; Sumatra Island; Martebing; 3°20′08.8″ N, 99°02′34.9″; 4 Jul. 2022; J. Haran leg.; sweeping flowers of *Turnera* sp. (Passifloraceae Juss. ex Roussel); CBGP, JHAR05727-01.

Description

Male

Body length. 2–2.7 mm.

Colour. Body integument entirely pale yellow; vestiture of head, prothorax and elytra made of whitish setae, not concealing integument; vestiture of elytra made of combination of short, recumbent setae, ½–¾ as wide as width of interstria, forming 3–4 ill-defined longitudinal rows on each interstria and suberect setae, 2 × as long as former ones, forming one row per interstria.

Head. Rostrum slightly shorter than prothorax (0.9 ×) in lateral view, 2.2 × as long as width of eye, moderately downcurved; antennae inserted at apical ⅓ of rostrum; head capsule covered with recumbent, centripetal setae in dorsal view; eyes convex, exceeding lateral curve of head capsule in dorsal view but not in lateral view, space between eyes about ½ as wide as base of rostrum; antennal funicle with segments 1 and 2 equal in length, 1 globular, slightly longer than wide, 2 twice as long as wide, 3 isodiametric, 4–6 wider than long, 6 fused to club, ⅔ as wide as club width, bearing ring of erect setae reaching the apex of segment 1 of club; scape as long as segments 1–5 of funicle, widening at apical ⅓ of length.

Prothorax. Wider than long (W:L ratio 1.44), widest near middle of length, sides rounded, narrowing apically and basally, with basal margin only slightly wider than apical margin; integument shiny, micropunctuate, with uniformly distributed, medium-sized, circular punctures; space between punctures as wide as diameter of punctures or larger; sides and apical margin of prothorax with erect setae pointing outwards; recumbent setae on dorsum pointing towards scutellar shield.

Elytra. Sides subparallel on basal ½, widest near middle of length (W:L ratio: 0.80); humeri raised; interstriae 3–4 × as wide as striae; interstriae 10 with widening from base to level of metacoxae, middle of widening about 1.5 × as wide as interstriae 9 at same level; scutellar shield rounded and shiny.

Abdomen. Underside covered with recumbent, whitish setae, forming slightly denser coating than on elytra.

Legs. Profemora subequal in thickness to meso- and metafemora, thickened in middle of length, bearing acute tooth and comb of 5–6 erect setae located at distance from apex of tooth equal to length of tarsomere 1+2, at distance from apex of profemora equal to length of seta; protibiae downcurved in basal ½, external margin straight in apical ¾, internal margin bisinuate, apex with mucro slightly larger than claws; meta-tibiae faintly emarginate internally in apical ⅓ and with suberect incurved setae; meso-tibiae armed with mucro, on meta-tibiae mucro reduced to small spine; tarsal claws appendiculate, only with smooth internal thickening on metatarsi.

Terminalia. Body of penis elongate (W:L ratio: 0.26), about 1.8 × as long as apodemes, sides subparallel, narrowing in apical ⅕, apex acuminate; curvature in lateral view moderate and regular, narrowing in apical ¼; internal sclerite 0.5 × as long as body of penis, forming a reversed 'y' at base (Fig. 5C).

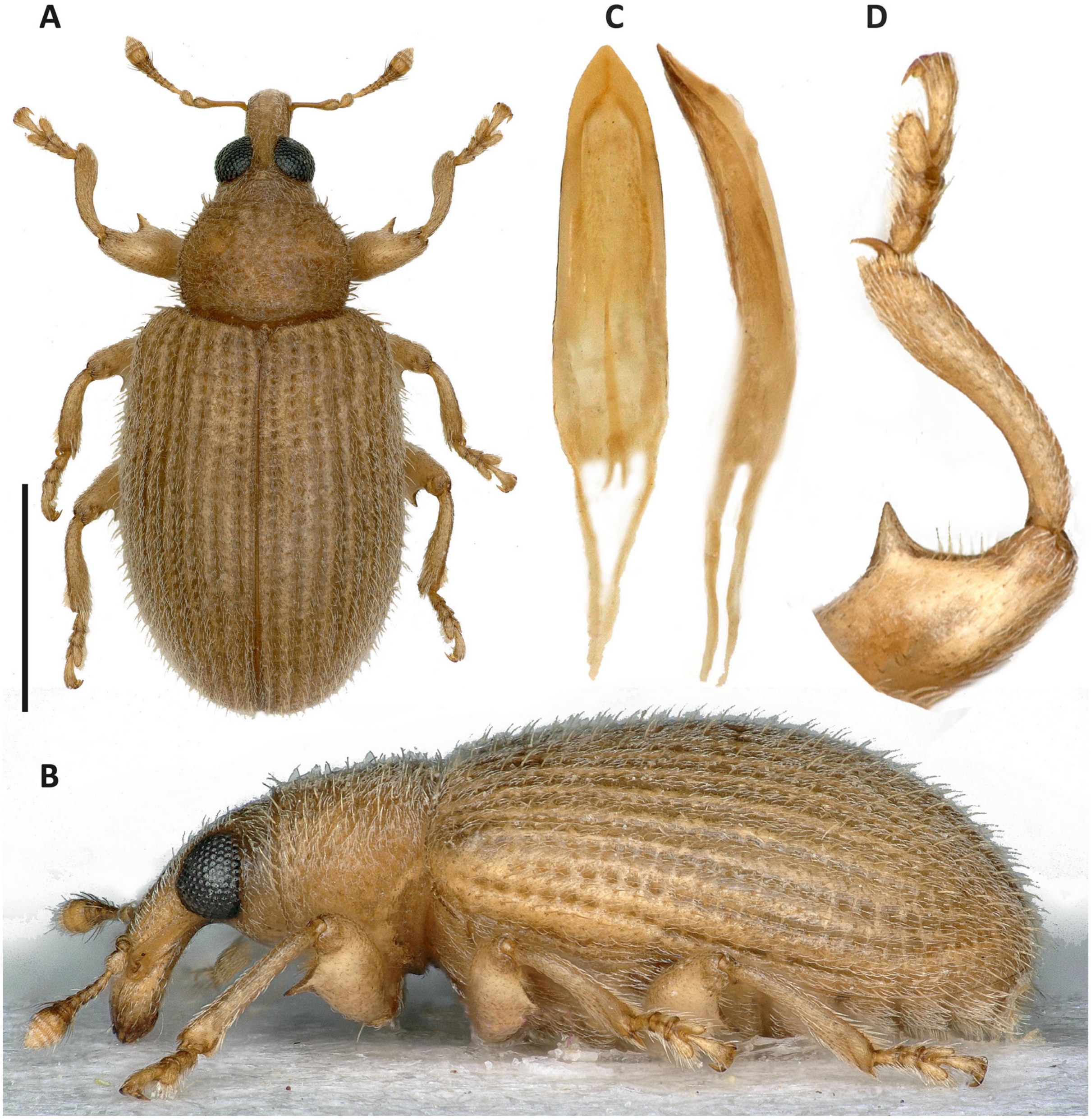

Fig. 5. Habitus and details of the morphology of *Endaeus canangae* Haran sp. nov., paratype, ♂ (JHAR05727-04; CBGP). **A–B.** Habitus in dorsal and lateral views. **C**. Penis in dorsal and lateral views. **D**. Foreleg in dorsal view. Scale bar: 1 mm, B–D not to scale.

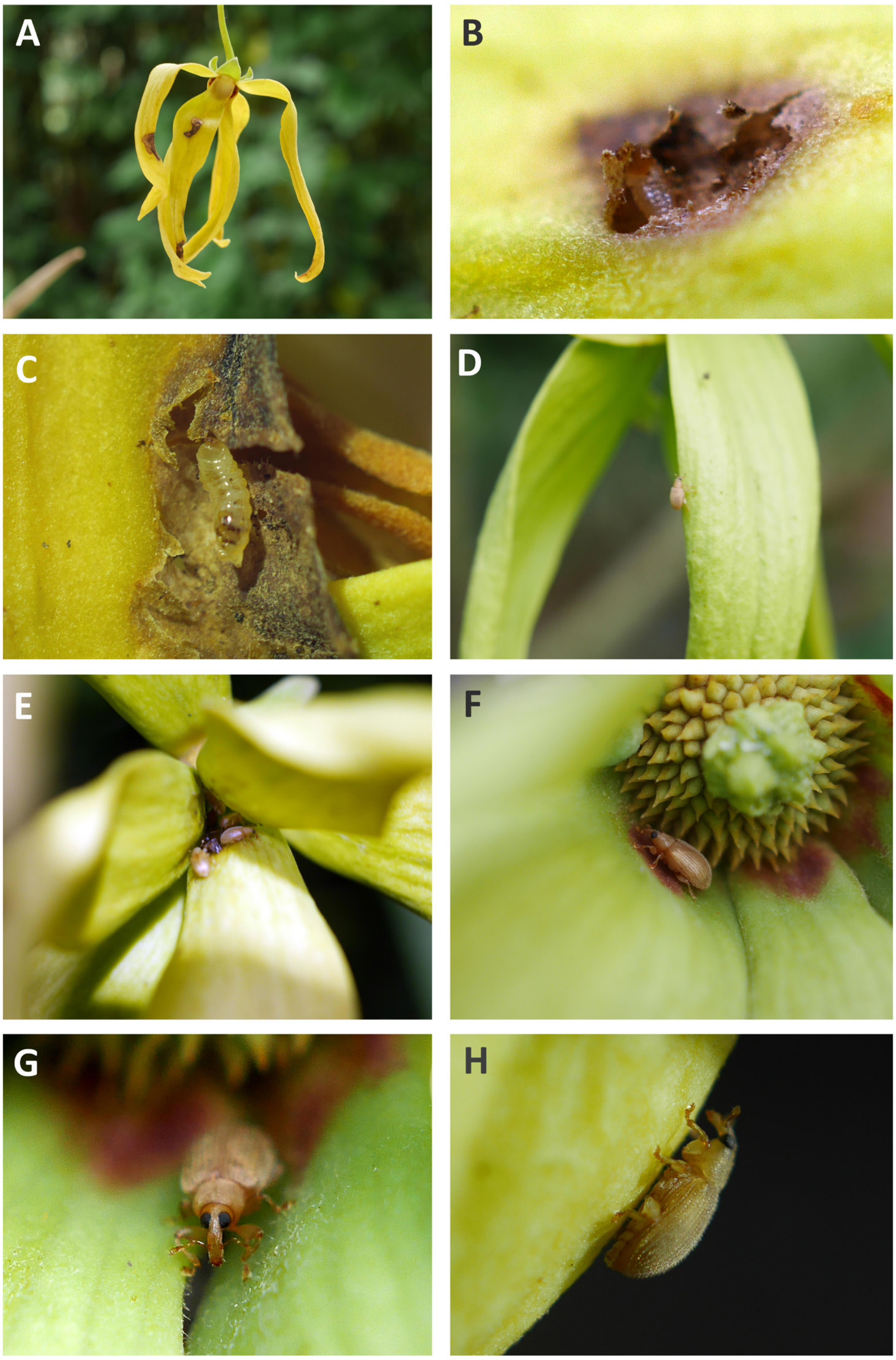

Fig. 6. Illustration of the host plant and the life cycle of *Endaeus canangae* Haran sp. nov. on Sumatra Island, Indonesia. **A**. Flower of *Cananga odorata* (Lam.) Hook.f. & Thomson (Annonaceae Juss.) in anthesis. Note the mines on petals. **B**. First instar larva in its mine, protected under the epidermis. **C**. Last instar larva in a senescent petal. **D**. Adult landing on petals in late afternoon during anthesis. **E**. Adults hiding in the "cage" formed by the petals around stigma and stamens. The conformation of the base of the inner petal forces the specimens into contact with receptive stigma when specimens are entering the cage. Note the presence of sap beetle (Nitidulidae Latreille, 1802) standing at the entrance of the cage as well. **F–H**. Adults standing hidden on the red spots in the cage in the evening (F–G), actively moving, mating and ovipositing on the petals in the night (H). Not to scale.

Feamle

Males and females can be distinguished by their rostrum which is longer (as long as the prothorax in lateral view in ♀♀; 0.8 × as long as the prothorax in ♂♂) and more downcurved in females than in males.

Life history

Endaeus canangae Haran sp. nov. is associated with the flowers of ylang-ylang (*Cananga odorata*; Annonaceae). Adults were observed flying toward flowers in anthesis in late afternoon. This activity coincides with the emission of a distinct scent (JH pers. obs.). Once on a petal (Fig. 6D), the adults move up to hide in the flower chamber, between the base of petals and apex of stamens (Fig. 6E). Multiple individuals may stay in this chamber together with an unidentified species of sap beetle (Nitidulidae). In the chamber, specimens generally stand on the red spots at the base of petals (Fig. 6F). Later in the night (around 9 pm), some adults were observed mating on the petals, out of the chamber. Oviposition takes place in a shallow hole made by females and the larvae develop by digging a gallery in the petals, forming a brown mine (Fig. 6A–C). Pupae were not observed in the mines, suggesting that pupation and eclosion takes place in the ground. Among the dozens of flowers in anthesis observed over several days, only one was exhibiting mines at time of observation. Despite intensive examination of receptive flowers of other flowering species of Annonaceae at the vicinity, *E. canangae* was only observed on *Cananga odorata*, suggesting a specialized relationship. The single observation of a specimen on flowers of *Turnera* Plum. ex L. (Passifloraceae) is likely accidental. *Cananga odorata* is widely cultivated for ylang-ylang production but is unable to reproduce out of its native range in absence of its pollinators, except in Ivory Coast where an association with local nitidulid beetles enables the development of fruits (Deroin 1988a).

Distribution

This species is currently only known for the type locality on Sumatra Island, but its host is widely distributed in Southeast Asia and planted across the tropics (WFO 2024).

Remarks

Endaeus canangae Haran sp. nov. exhibits profemora that are similar in thickness to the meso- and metafemora – a trait considered diagnostic for the genus *Endaenidius*. However, recent observations of both *Endaenidius* and *Endaeus* have revealed intermediate forms, casting doubt on the validity of *Endaenidius* as a distinct genus. To avoid potential future nomenclatural acts and pending a clearer definition of *Endaenidius*, this species is provisionally placed within the genus *Endaeus*. See Hsiao *et al.* (2025) for a comparable case.

Endaeus xylopiae Haran & Zelvelder sp. nov.

urn:lsid:zoobank.org:act:AFABF503-2DC4-4361-B80B-11E9ECB43133

Figs 7–8

Differential diagnosis

Endaeus xylopiae Haran & Zelvelder sp. nov. is morphologically very close to *E. baikieae* Marshall, 1933, *E. jaculifer* Haran & Zelvelder sp. nov. and *E. convexiculus* Haran & Zelvelder sp. nov. It differs by having a shorter and very moderately downcurved rostrum. Males of the three species differ greatly in the shape of their penis, that of *E. xylopiae* being the only one bearing strong hook-like setae at apex and hook-like processes laterally in dorsal view. Among the species of *Endaeus* for which a barcode sequence is available, this species is closest to *E. jaculifer*, also found on *Xylopia aethiopica* (*COI p*-distance of 16.0%).

Etymology

This species is named in reference to its association with flowers of *Xylopia aethiopica* (Annonaceae).

Type material

Holotype

GABON • ♂; "GABON, Parc de la Lékédi / 26.x.2023 / J. Haran & R. Allio coll. / JHAR06086-04; -1.778 13.000 [1°46′40.8″ S, 13°00′00.0″ E], 25m, 20h45 / *Xylopia aethiopi*.[ca] / Collection-Cirad / Holotype / *Endaeus xylopiae* Haran & Zelvelder 2026"; CBGP, JHAR06086-04.

Paratypes

GABON • 1 ♂; Parc de la Lékédi; 1°46′40.8″ S, 13°00′00.0″ E; 26 Oct. 2023; J. Haran and R. Allio leg.; on flower of *Xylopia aethiopica* (Annonaceae); CBGP, JHAR06086-01 • 1 ♀; same data as for preceding; CBGP, JHAR06086-03 • 1 ♂; same data as for preceding; HNG, JHAR06086-05 • 1 ♀; Parc de la Lékédi; 1°46′40.8″ S, 13°00′00.0″ E; 26 Oct. 2023; J. Haran leg.; beating understory vegetation, 4:00 pm; CBGP, JHAR06081-01.

Description

Male

Body length. 2.2–2.45 mm.

Colour. Body integument uniformly pale brown; vestiture of head, prothorax and elytra made of pale yellow to light orange setae, not concealing the integument; vestiture of prothorax and elytra made of combination of short, subrecumbent setae, ½ to ¾ as wide as width of interstriae, forming 3–4 ill-defined longitudinal rows on each interstria and long suberect setae, forming a row on each interstria, on average 3 × as long as subrecumbent setae, about as long as width of interstriae.

Head. Head capsule with short, pale, subrecumbent setae and longer, pale suberect setae forming two ill-defined rows on forehead; rostrum slightly shorter than prothorax (0.9 ×) in lateral view, 2.2 × as long as width of eye, moderately downcurved; antennae inserted near apical ⅓ of length of rostrum; eyes convex, strongly exceeding lateral curve of head capsule in dorsal view and dorsal curve of head capsule in lateral view; space between eyes about half as wide as base of rostrum; antennal scape slightly longer than segments 1–5 of funicle, widening at apical ⅓ of length; funicle with segment 1 globular; 2 twice as long as wide, 3–6 isodiametric; club slightly longer than wide (W:L ratio 0.55–0.6).

Prothorax. Wider than long (W:L ratio 1.3), widest near middle of length, sides rounded, apical margin about 0.75 × wider than basal margin; dorsum flat in lateral view; integument shiny, micropunctuate, with uniformly distributed, medium-sized, roughly circular punctures; space between punctures as wide as diameter of punctures or larger; sides and apical margin of prothorax with erect setae pointing upwards and forwards, respectively; subrecumbent setae pointing towards median line of prothorax on dorsum.

Elytra. Sides slightly convex in dorsal view, widest near middle of length (W:L ratio: ~0.70); humeri raised; interstriae 3–4 × as wide as striae; interstriae 10 widening from base to the level of metacoxae, about 1.5 × as wide as interstriae 9 at widest point; in lateral view, dorsum of elytra almost flat on basal ¾ of length, then declivity; scutellar shield shiny, rounded.

Abdomen. Underside covered with recumbent whitish setae longer than subrecumbent setae of elytra.

Legs. Femora subequal in thickness, thickened in middle of length, each armed with flat triangular tooth, profemoral tooth followed by row of 6 erect setae located between base of the triangular tooth and distance from apex of femora equal to length of tarsomere 1; protibiae curved in basal ½, external margin straight in apical ⅔, internal margin bisinuate, carinate, apex with sharp, slightly curved mucro located medially on corbel, similar in size to claw, curvature pointing inwards to almost perpendicular; apex of meso-tibiae with robust, slightly downcurved mucro located on inner part of corbel, erected almost perpendicularly; tarsal claws widely divergent, appendiculate with dull triangular inner tooth.

Terminalia. Body of penis elongate (W:L ratio: 0.33), about 1.7 × as long as apodemes, sides bisinuate in dorsal view, strongly narrowed in apical ⅔ to 0.66 × its maximum width and narrowing towards apex from apical ¾; lateral processes of body gradually translucent, oriented backwards, each bearing 6-7 dull, flattened hooks directed towards apex; apex rounded, bearing 5–7 strong anteapical hook-like setae laterally; tip forming button-like shape; inner part of apical ⅔ coated with sclerified papillae pointing forward; in lateral view, widest near middle of length, curvature irregular, stronger near middle of length; internal sclerite not distinct in specimens examined (Fig. 7C).

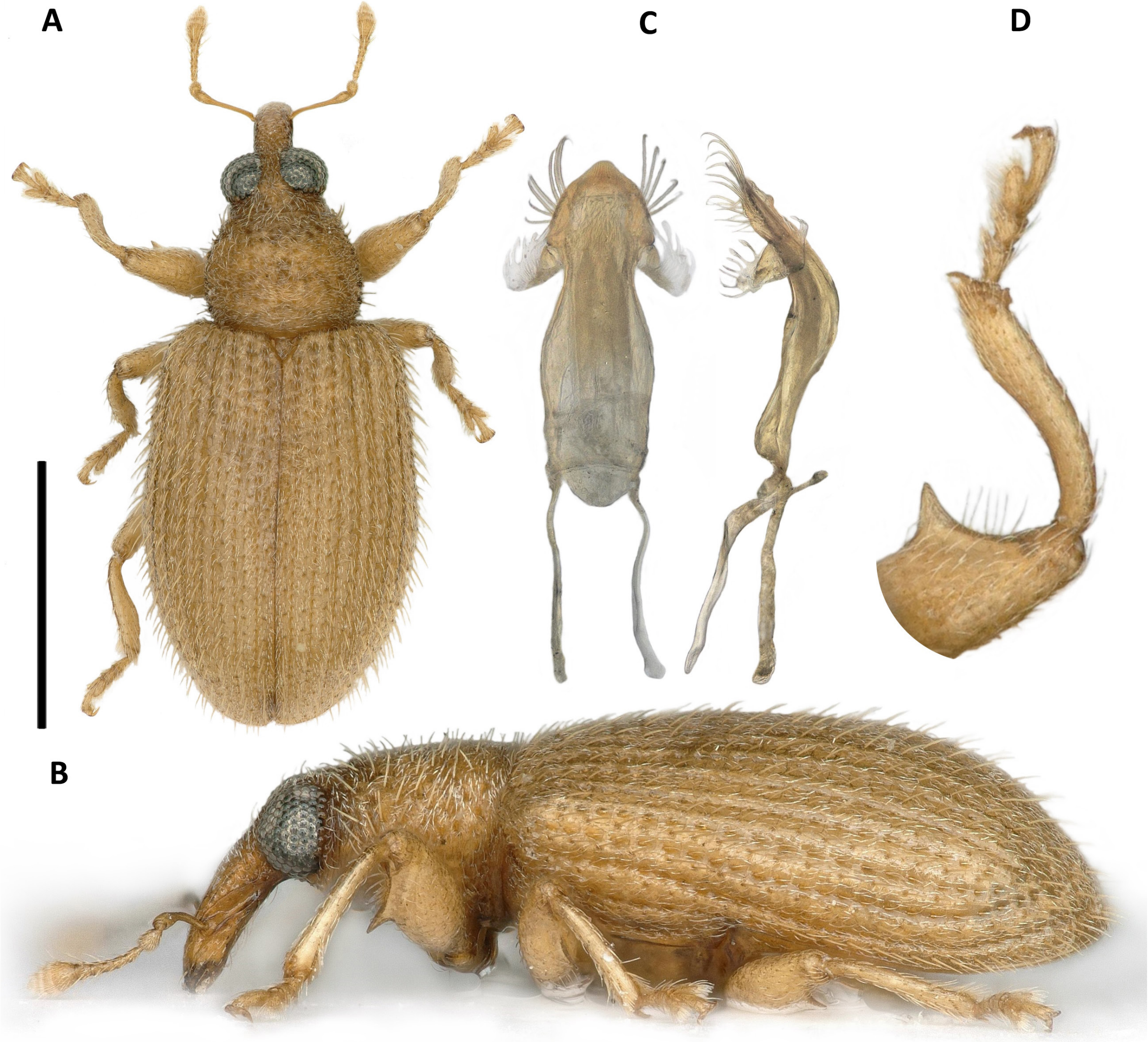

Fig. 7. Habitus and details of the morphology of *Endaeus xylopiae* Haran & Zelvelder sp. nov., holotype, ♂ (JHAR006086-04; CBGP). **A**–**B.** Habitus of male in dorsal and lateral views. **C**. Penis in dorsal and lateral views. **D**. Foreleg in dorsal view. Scale bar: 1 mm; B–D not to scale.

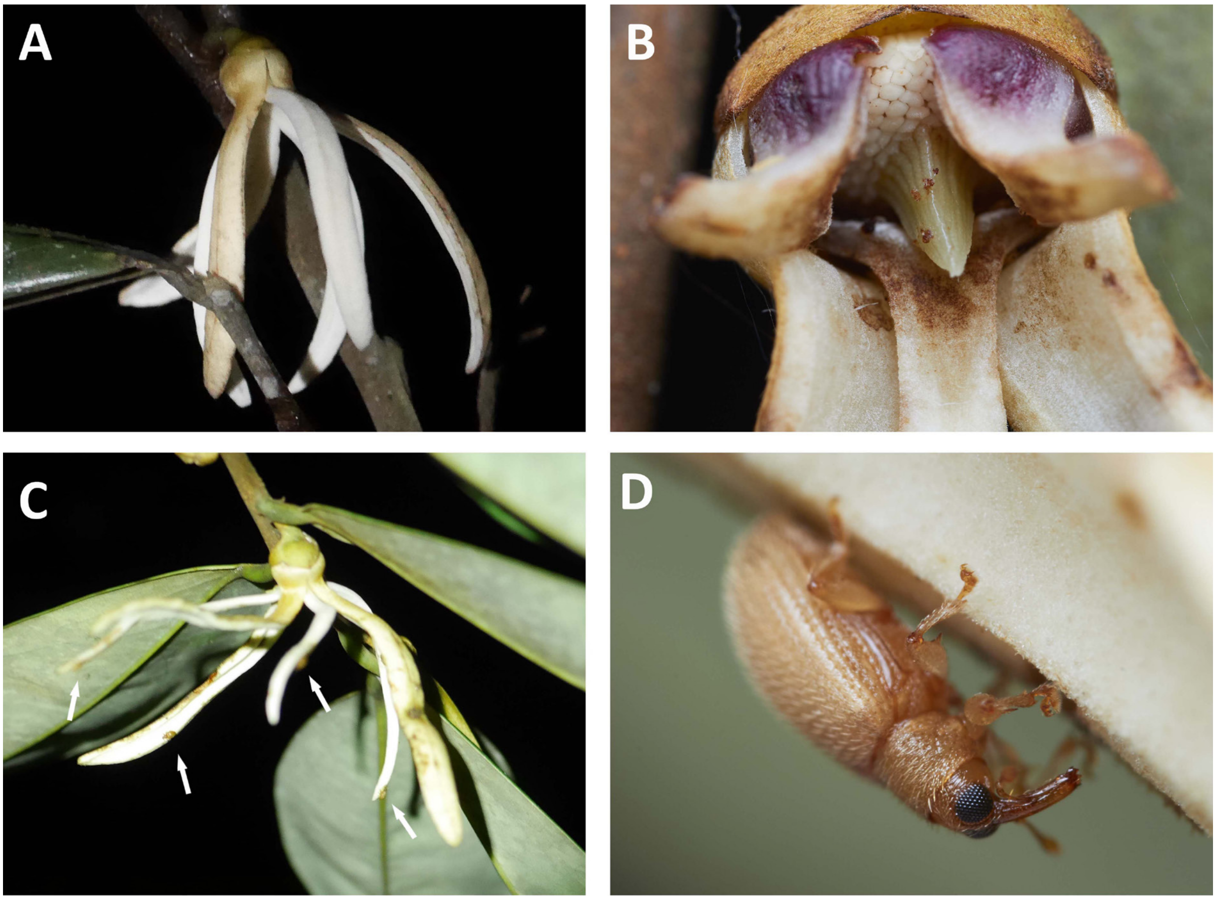

Fig. 8. Illustration of the host plant and the habitus *in natura* of *Endaeus xylopiae* Haran & Zelvelder sp. nov. in Gabon. **A**. Flower of *Xylopia aethiopica* (Dunal) A.Rich. (Annonaceae Juss.) in anthesis. **B**. Floral chamber where *E. xylopiae* adults were observed. **C**. Adults reaching the flower at time of emission of the scent (white arrows). **D**. Female on petal. Not to scale.

Sexual dimorphism

Females can be distinguished from males by their rostrum which is narrower and longer in lateral view (2.5 × as long as width of eye). Antennal insertion is located near middle of length of rostrum in ♀♀ (near apical ⅓ in ♂♂). Meso-tibial mucro more broadly downcurved in ♀♀.

Life history

This species was collected on a flower of *Xylopia aethiopica* in anthesis (Fig. 8A–C). The flower was located at 25 m high in the tree and started producing a strong scent at dusk. Adults were observed reaching this flower and standing on petals around 8 pm (Fig. 8C). Most specimens then moved into the floral chamber. The flower sampled contained four individuals of this species. These biological data echos with the observations made for *Xylopia championii* Hook.f. & Thomson in Sri Lanka, where an *Endaeus* was identified pollinating this species via a synchronization of floral phenology and beetle activity (Ratnayake *et al.* 2007). Despite detailed searches, the immatures of this species could not be found in the petals of the flower sampled, nor in the flowers that had fallen at the base of the tree. Flowers hosting larvae of *Endaeus* can be rare, see life history section under *E. canangae* Haran sp. nov. Given the trend in ciophily and in *Endaeus*-Annonaceae interactions (host specificity, flower structure, etc.), it is very likely that larvae of this species develop in the petals of *X. aethiopica*. *Endaeus xylopiae* Haran & Zelvelder sp. nov. was found in sympatry, in the same flower, with *E. jaculifer* Haran & Zelvelder sp. nov. and *E. convexiculus* Haran & Zelvelder sp. nov. One specimen of *E. xylopiae* was also collected by beating understorey vegetation at 4 pm. This species is seemingly not attracted by UV light, since it was not observed at a UV light trap set in an *X. aethiopica* tree in the vicinity of the flowers in anthesis on which specimens were observed.

A first assessment of floral scent emitted by flowers in anthesis of *Xylopia aethiopica* revealed a scent composed of several groups of chemicals, mainly terpenoids, and largely dominated by one unique terpene derivative, showing a chemical skeleton similar to Farnesyl although it could not be precisely identified (Unknown terpene derivatives 2, see Appendix 2).

Distribution

This species is currently only known for the type locality in La Lékédi park, in south-east Gabon (Haut-Ogooué Province). Its host is widely distributed in tropical Africa, from Senegal to Ethiopia and from Mozambique to Chad (WFO 2024).

Endaeus jaculifer Haran & Zelvelder sp. nov.

urn:lsid:zoobank.org:act:DA84520E-74E4-4215-B4CD-87CF3D78F000

Fig. 9

Differential diagnosis

Endaeus jaculifer Haran & Zelvelder sp. nov. is morphologically very close to *E. baikieae*, *E. xylopiae* Haran & Zelvelder sp. nov. and *E. convexiculus* Haran & Zelvelder sp. nov. Males differ by having a long spear-shaped tooth on its metafemora, more elongate antennal club and mucros exceeding the inner part of protibiae. Males of the four species differ greatly in the shape of their penis, that of *E. jaculifer* having very short apodemes, a robust body of penis and comparatively small brushes of 7–8 setae at apex (more than 10 in *E. baikieae*). Among the species of *Endaeus* for which a barcode sequence is available, this species is closest to *E. convexiculus*, also found on *Xylopia aethiopica* (*COI* *p*-distance of 11.0%).

Etymology

This species is named in reference to the 'spear-shaped' ('*jaculi*-', combining form of Latin '*jaculum*' = 'dart' and '-fer') tooth on its metafemora.

Type material

Holotype

GABON • ♂; "GABON, Parc de la Lékédi / 26.x.2023 / J. Haran & R. Allio coll. / JHAR06086-08 / -1.778 13.000 [1°46′40.8″ S, 13°00′00.0″ E], 25m, 20h45 / *Xylopia aethiopi*. [ca]; Collection-Cirad / Holotype / *Endaeus jaculifer* Haran & Zelvelder 2026"; CBGP, JHAR06086-08.

Description

Male

Body length. 2.45 mm.

Colour. Body integument uniformly pale brown, head sometimes slightly darker, legs slightly lighter; vestiture of head, prothorax and elytra made of pale yellow to light orange setae, not concealing integument; vestiture of prothorax and elytra made of combination of short, subrecumbent setae, slightly shorter than elytral interstriae, forming 3–4 ill-defined longitudinal rows on each interstria and long suberect setae, forming row on each interstria, 1.5–2 × as long as subrecumbent setae, as long as or longer than width of interstriae.

HEAD. Head capsule with short, pale, subrecumbent setae and longer, pale suberect setae forming two ill-defined rows on forehead; rostrum slightly shorter than prothorax (0.85 ×) in lateral view, 2.5 × as long as width of eye, moderately downcurved; antennae inserted at apical ⅓ of rostrum; eyes convex, strongly exceeding lateral curve of head capsule in dorsal view and slightly exceeding dorsal curve of head capsule in lateral view; space between eyes about half as wide as base of rostrum; antennal scape longer than segments 1–5 of funicle, widening at apical ⅓ of length; funicle with segment 1 globular; 2 twice as long as wide, 3–6 isodiametric; club longer than wide (W:L ratio 0.4–0.5).

PROTHORAX. Wider than long (W:L ratio 1.3), widest near middle of length, sides rounded, apical margin about 0.75 × as wide as basal margin; dorsum flat in lateral view; integument shiny, micropunctuate, with uniformly distributed, medium-sized, roughly circular punctures; space between punctures as wide as

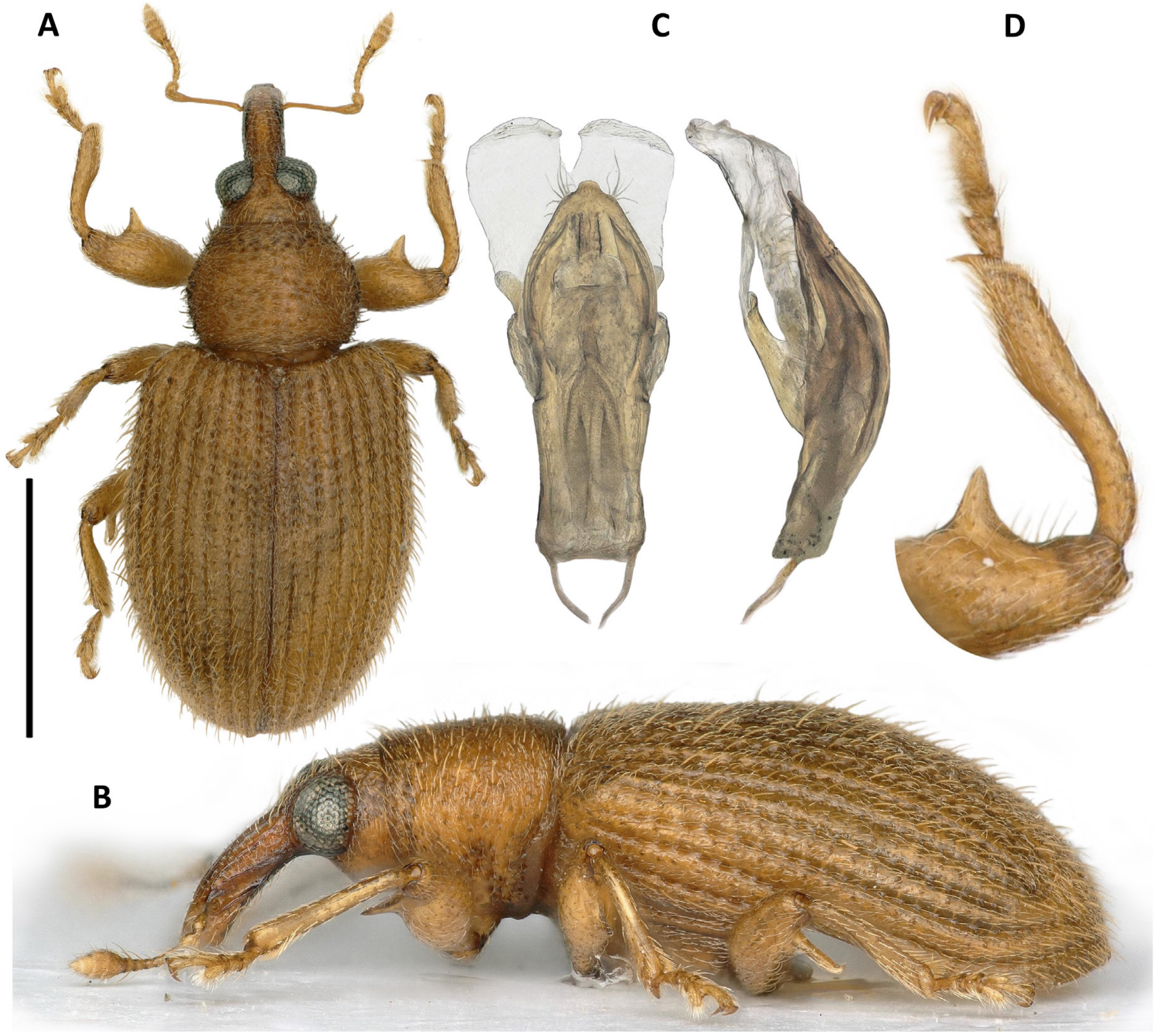

Fig. 9. Habitus and details of the morphology of *Endaeus jaculifer* Haran & Zelvelder sp. nov., holotype, ♂ (JHAR006086-08; CBGP). **A**–**B.** Habitus in dorsal and lateral views. **C**. Penis in dorsal and lateral views. **D**. Foreleg in dorsal view. Scale bar = 1 mm; B–D not to scale.

diameter of punctures or larger; sides and apical margin of prothorax with erect setae pointing upwards and forwards respectively; subrecumbent setae pointing towards inner line of prothorax on dorsum.

ELYTRA. Sides slightly convex in dorsal view, widest near middle of length (W:L ratio: ~0.75); humeri raised; interstriae 3–4 × as wide as striae; interstriae 10 weakly widening from base to level of metacoxae, about 1.5 × as wide as interstriae 9 at widest point; in lateral view, dorsum of elytra almost flat on basal ½ of length, then declivity; scutellar shield shiny, rounded.

ABDOMEN. Underside covered with recumbent whitish setae about as long as subrecumbent setae of elytra.

LEGS. Pro- and meso-femora subequal in thickness, thickened in middle of length, armed with flat triangular tooth, profemoral tooth followed by row of 5 erect setae located between base of triangular tooth and distance from apex of femora equal to length of tarsomere 1, curve formed between apex of tooth to apex of femora uneven, sunken at base of tooth; meta-femora slightly thinner, bearing spear-shaped tooth, about ½ as long as length of meta-tibiae, often bearing long subrecumbent setae at apex; protibiae curved in basal ½, external margin straight in apical ¾, internal margin bisinuate, carinate, apex with long, robust, almost straight mucro located basally on corbel, exceeding inner margin of protibiae; apex of meso-tibiae with robust, slightly downcurved mucro located on inner part of corbel; tarsal claws widely divergent, appendiculate with dull triangular inner tooth.

TERMINALIA. Body of penis elongate (W:L ratio: 0.35), about 5.6 × as long as apodemes, sides subparallel, narrowing in apical ⅕; apex trapezoidal, bearing few hairs of variable size and orientation on both sides; tip forming button-like shape; lateral extensions of body oriented ventrally, extended into two flat, translucent rectangular areas extending beyond apex at distance equal to size of apodemes (but can be missing or folded beneath penis); curvature in lateral view moderate and regular on dorsal side, almost flat on ventral side, widest in its basal ½; internal sclerite not visible (Fig. 9C).

Female

Females of this species are currently unknown.

Remarks

In the same sampling event, three additional specimens related to this species were collected. They exhibit a slightly divergent external morphology (ratio of elytra, insertion of antennae on rostrum, etc.) and *p*-distance ranking up to 7.4% for the 418 bp long fragment of *COI*. The penis of males, however, shows no significant divergence with the holotype. Thus, *E. jaculifer* Haran & Zelvelder sp. nov. is likely a species complex and more material is needed to clarify the species boundaries in the additional lineages identified. The corresponding specimens (JHAR06086-06/09) were labelled "*Endaeus* nr. *jaculife*r" pending further exploration of this complex.

Life history

This species was collected in the same conditions as *E. xylopiae* Haran & Zelvelder sp. nov., see details under that species.

Distribution

This species is currently only known for the type locality in La Lékédi park, in south-east Gabon (Haut-Ogooué Province). Its host is widely distributed in tropical Africa, from Senegal to Ethiopia and from Mozambique to Chad (WFO 2024).

Endaeus convexiculus Haran & Zelvelder sp. nov.

urn:lsid:zoobank.org:act:083F03C8-A62A-4851-B815-1D85D343B3D0

Fig. 10

Differential diagnosis

Endaeus convexiculus Haran & Zelvelder sp. nov. is morphologically very close to *E. baikieae*, *E. xylopiae* Haran & Zelvelder sp. nov. and *E. jaculifer* Haran & Zelvelder sp. nov. It differs by having a longer and less downcurved rostrum. Males of the four differ greatly in the shape of their penis, that of *E. convexiculus* having ear-shaped lateral processes and an angled 'three-sided' profile. Among the species of *Endaeus* for which a barcode sequence is available, this species is closest to *E. jaculifer*, also found on *Xylopia aethiopica* (*COI p*-distance of 11.0%).

Etymology

This species is named in reference to its convex body shape in lateral view.

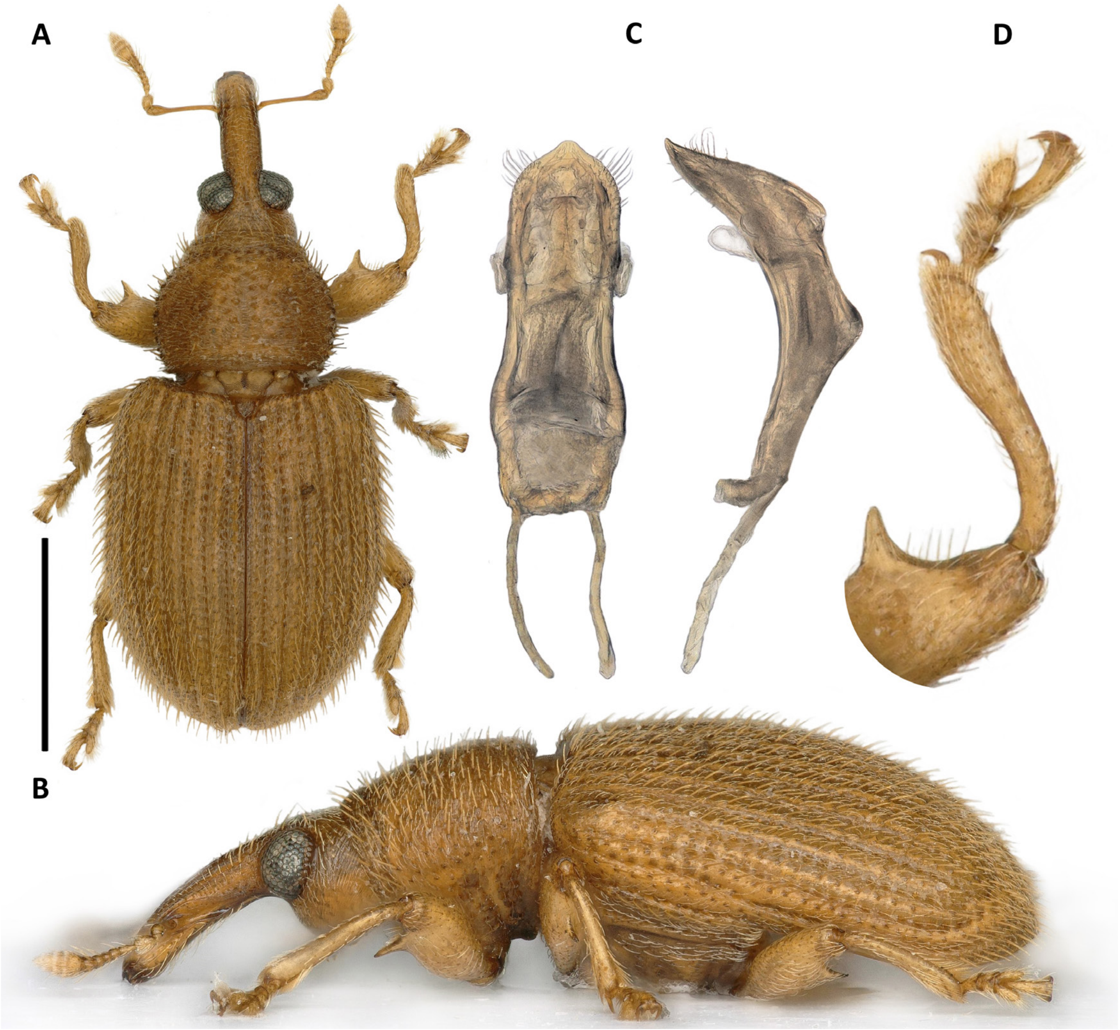

Fig. 10. Habitus and details of the morphology of *Endaeus convexiculus* Haran & Zelvelder sp. nov., holotype, ♂ (JHAR006086-07; CBGP). **A**–**B**. Habitus in dorsal and lateral views. **C**. Penis in dorsal and lateral views. **D**. Foreleg in dorsal view. Scale bar: 1 mm; B–D not to scale.

Type material

Holotype

GABON • ♂; “GABON, Parc de la Lékédi / 26.x.2023 / J. Haran & R. Allio coll. / JHAR06086-07 / -1.778 13.000 [1°46′40.8″ S, 13°00′00.0″ E], 25m, 20h45 / *Xylopia aethiopi*. [ca] / Collection-Cirad / Holotype / *Endaeus convexiculus* Haran & Zelvelder 2026”; CBGP, JHAR06086-07.

Description

Male

Body length. 2.6 mm.

Colour. Body integument uniformly pale brown, legs slightly lighter; vestiture of head, prothorax and elytra made of pale yellow to light orange setae, not concealing the integument; vestiture of prothorax and elytra made of a combination of short, subrecumbent setae, almost as long as interstriae, forming 3–4 ill-defined longitudinal rows on each interstria and long suberect setae, forming row on each interstria, 1.5–2.5 × as long as subrecumbent setae, as long as or longer than width of interstriae.

Head. Head capsule with short, pale, subrecumbent setae and longer, pale suberect setae forming two ill-defined rows on forehead; rostrum slightly shorter than prothorax (0.83 ×) in lateral view, 3.4 × as long as width of eye, almost straight; antennae inserted near apical ⅓ of length of rostrum; eyes convex, strongly exceeding lateral curve of head capsule in dorsal view but not exceeding dorsal curve of head capsule in lateral view; space between eyes about ⅔ as wide as base of rostrum; antenna scape longer than segments 1–5 of funicle, widening at apical ⅓ of length; funicle with segment 1 globular; 2 twice as long as wide, 3–6 slightly wider than long; club slightly longer than wide (W:L ratio 0.55).

Prothorax. Wider than long (W:L ratio 1.3), widest near middle of length, sides rounded, apical margin about 0.7 × as wide as basal margin; dorsum slightly convex in lateral view; integument shiny, micropunctuate, with uniformly distributed, medium-sized, roughly circular punctures; space between punctures as wide as diameter of punctures or larger; sides and apical margin of prothorax with erect setae pointing upwards and forwards, respectively; subrecumbent setae pointing towards inner line of prothorax on dorsum.

Elytra. Sides slightly convex in dorsal view, widest near middle of length (W:L ratio: 0.83); humeri raised; interstriae 3–4 × as wide as striae; interstriae 10 widening from base to level of metacoxae, about 1.5 × as wide as interstriae 9 at widest point; in lateral view, dorsum of elytra gradually curves downward towards apex; interstriae 2 and 9 meet forming acute angle at apex; scutellar shield shiny, rounded.

Abdomen. Underside covered with recumbent whitish setae longer than subrecumbent setae of elytra.

Legs. Femora subequal in thickness, thickened in middle of length, armed with flat triangular tooth, profemoral tooth followed by comb of 6 erect setae located between base of triangular tooth and distance from apex of femora equal to length of tarsomere 1; protibiae curved in basal ½, external margin straight in apical ¾, internal margin bisinuate, carinate, apex with long, robust, strongly curved mucro located medially on apex; apex of meso-tibiae with robust, slightly downcurved mucro located on inner part of corbel, erected almost perpendicularly; tarsal claws widely divergent, appendiculate with dull triangular inner tooth.

Terminalia. Body of penis elongate (W:L ratio: 0.36), about 2.1 × as long as apodemes, sides subparallel, widest in basal ⅓, narrowing in apical ⅕, apex rounded, bearing anteapical comb of hairs of variable size on both sides; tip forming button-like shape; lateral extensions of body oriented ventrally, forming two small, translucent, ear-shaped extensions slightly longer than anteapical setae; curvature in lateral view moderate and regular on ventral side, three-sided on dorsal side, forming two right angles at apical ½ and apical ¼ of its length; internal sclerite not visible (Fig. 10C).

Female

Females of this species are currently unknown

Life history

This species was collected in the same conditions as *E. xylopiae* Haran & Zelvelder sp. nov., see details under that species.

Distribution

This species is currently only known for the type locality in La Lékédi park, in south-east Gabon (Haut-Ogooué Province). Its host is widely distributed in tropical Africa, from Senegal to Ethiopia and from Mozambique to Chad (WFO 2024).

Discussion

The formal description of a brood-site pollination mutualism requires specific protocols (see Lau *et al.* 2017; Rocamundi *et al.* 2023) that are difficult to apply in a field situation when multiple interactions are uncovered. However, converging traits in plant and weevils engaged in such relationships and the overall phylogenetic conservatism observed at genus level in weevils helps indicate where this type of interaction is likely to happen (Haran *et al.* 2023a). This paper resulted in the description of six new species in the genus *Endaeus* and provided details on their life histories that agree in several respects with the traits known in brood-site pollination mutualism involving the genus *Endaeus* and weevils in general.

All these species are associated with typical cantharophilous flowers: large, pale, fragrant flowers forming a chamber around the reproductive structures (individual flower type). The cases of *Endaeus canangae* sp. nov. on *Cananga odorata* and *E. lenticulatus* Haran sp. nov. on *Uvariodendron molundense* are remarkably convergent with the pollination syndrome described in *Annona senegalensis* (Dao *et al.* 2023). These weevils oviposit and develop in the fleshy petals of their hosts, while the activity of the adults on the receptive flowers occurs in close contact with stigma and anthers (Fig. 6E), thereby promoting pollination if these specimens are carrying pollen. In this respect, it is interesting to note the presence of red areas on the inner part of the floral chamber in all these species of Annonaceae, including *Xylopia aethiopica* (Figs. 2B, 6F–G, 9B). These structures were interpreted as 'pollination reception areas' in *Cananga odorata* (Deroin 1988b), because the nitidulid beetles visiting the floral chambers of this species were observed standing preferentially on these spots, thus receiving pollen loads at the staminate phase of the flower cycle (release of anthers). The observation of this behaviour in *Endaeus canangae* (Fig. 6F), and in the three species found on *Xylopia aethiopica* argues for a role of these species as pollinators of their hosts as well. Additional similarities between *Cananga odorata, Xylopia aethiopica* and other Annonaceae pollinated by weevils include the apparently timed visit of flowers and the association of a weevil and a Nitidulidae (in *Cananga* only) as floral visitors (Lau *et al.* 2017). In *Uvariodendron* (Engl. & Diels) R.E.Fr., the presence of an *Endaeus* as floral visitor is consistent with previous reports made in Cameroon on *U. calophyllum* R.E.Fr. and *U. connivens* (Benth.) R.E.Fr. (Gottsberger *et al.* 2011). In these species, the weevils (specimens from this study were not examined) are active during the anthesis stages, associated with peaks of thermogenesis in the protogynous flowers, in line with general patterns of ciophily. The genus *Xylopia* L. was already reported as being pollinated by species of the genus *Endaeus* in Asia (*X. championii*; Ratnayake *et al.* 2007) and the present report of a homologous system in Africa suggests that these trees are more broadly engaged in such pollination systems. The presence of multiple closely related weevil species in sympatry pollinating a unique host is a common trend in ciophily (Haran *et al.* 2023a) and probably applies to the case of *Endaeus convexiculus* Haran & Zelvelder sp. nov., *E. jaculifer* Haran & Zelvelder sp. nov. and *E. xylopiae* Haran & Zelvelder sp. nov. on *Xylopia aethiopica*. The complex 3-dimensional structures on the body of the penis in these species are very rare in weevils and have possibly emerged as strategies to enhance mating success in such multispecies communities in sympatry. Finally, the preliminary analysis of flower scent in *Xylopia* and *Uvariodendron* showed a composition largely dominated by one or two compounds, some of which are rare in floral scents (Knusden *et al.* 2006). This pattern is typical for ciophily (Haran *et al.* 2023a), in which plants have been shown to produce large amounts of a few rare compounds to attract their specific pollinators, also known as a "private channel" strategy (Chen *et al.* 2009; Svensson *et al.* 2010).

The association of *Endaeus staminicola* Haran sp. nov. with the flowers of *Allanblackia floribunda* is also suggestive of a brood-site pollination mutualism system. In addition to the floral structure typical of such interaction (and also including red areas on phalanges where the pollen is produced) species of *Allanblackia* Oliv. ex Benth. are dioecious trees with a strong resemblance between male and female flowers, previously interpreted as a sign of a pollination by deceit system (for *A. stuhlmannii* Engl.; Mathayo *et al.* 2009). Our observations suggest that the phalanges and the receptacle in *A. floribunda* male flowers represent transformed structures providing a brood-site to host the larvae of the *Endaeus*. In this context, the phalanges would be another example of transformed stamens emerging in ciophilous plants promoting weevil attraction and nutrition in a context of pollination mutualism (i.e., staminodes; Armstrong & Irvine 1990; Franz 2007; Teichert *et al.* 2018). This case is the second example of association of a species of *Endaeus* with a representative of the Clusiaceae (*Endaeus carinifrons* in seeds of *Pentadesma butyracea* Sabine and *Allanblackia* sp.; Marshall 1933) and the first report of a possible brood-site pollination mutualism between weevils and this family. The pattern of niche partitioning between a species developing on male flowers (*E. staminicola* Haran sp. nov.) and a second in female reproductive structures (*E. carinifrons*) of a dioecious and cantharophilous plant agrees with the pattern of pollination systems as reported in the palm *Elaeis guineensis* Jacq. (*Elaeidobius* Kuschel, 1952 and *Prosoestus* Faust, 1899; Haran *et al.* 2021) and further argue for the existence of an *Endaeus*-based pollination mutualism in *Allanblackia*. Given the growing economic importance of *Allanblackia* for producing edible oil in tropical Africa (Crockett 2015), these relationships deserve specific attention. More generally, multiple species in the genera *Allanblackia* and *Garcinia* L. exhibit staminal phalanges (Sosef *et al.* 2013), indicating that additional *Endaeus*-Clusiaceae interactions may exist.

This study documents a series of new pollination interactions between the species-rich genus *Endaeus* and various palaeotropical tree species, some of which are of economic importance. While these cases warrant targeted investigations to confirm the effective transfer of pollen to receptive stigmas by the weevils, the observations lend further support to our previous assertion that *Endaeus* functions as a widespread pollinator of the tropical flora (Haran *et al.* 2023a). The genus still comprises a large number – likely hundreds – of species awaiting formal description and life history documentation (Hustache 1924; Marshall 1926; Oberprieler 1993; Momose *et al.* 1998).

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Appendix 1 (continued next page). *COI* sequences of the new species of *Endaeus* Schoenherr, 1826 described and of other representatives of the genus available (*E. castus* Schoenherr, 1826, *E. floralis* Marshall, 1907 and *E. carinifrons* Marshall, 1933).

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Appendix 1 (continued).

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Appendix 2 (continued on next page). List of identified volatile compounds emitted by flowers of *Xylopia aethiopica* Dunal (A.Rich) and *Uvariodendron molundense* (Diels) R.E.Fr. (Annonaceae). Compounds are sorted by chemical family. Numbers indicate the percentage of each compound in the floral scent, based on the peak areas in Mass Spectrometry analyses. Compounds that could not be identified are listed as "unknown compounds". When their chemical structure provides enough information, they are assigned to a chemical family and listed as unknown within that family.

Family	COV	*X. aethiopica*	*U. molundense*
Shikimic acid derivatives			
	Methyl benzoate	1.50	0.00
	Ethyl benzoate	5.43	0.00
	Methyl salicylate	7.57	0.00
Fatty acid derivatives			
	Hexyl acetate	0.17	0.00
	(Z)-Hexenyl butanoate	0.27	0.00
Monoterpenes and derivatives			
	Sabinen	0.61	0.35
	beta-Pinene	1.60	2.80
	Myrcene	1.80	59.15
	delta-3-Carene	0.00	4.31
	alpha-Terpinene	0.14	0.00
	p-Cymene	0.25	1.90
	beta-Phellandrene	0.00	0.15
	(Z)-beta-Ocimene	1.26	0.46
	(E)-beta-Ocimene	0.60	0.76
	gamma-Terpinene	0.23	0.00
	(Z)-Linalool oxide (furanoid form)	1.63	0.00
	(E)-Linalool oxide (furanoid form)	2.70	0.00
	6,7-epoxy-Myrcene	0.00	20.86
	Linalool	9.46	0.80
	2,2,6-trimethyl-3-keto-6-vinyltetrahydropyran	0.94	0.00
	(Z)-Linalool oxide (pyranoid form)	7.97	0.00
	(E)-Linalool oxide (pyranoid form)	0.94	0.00
	Terpinen-4-ol	0.43	0.00
	alpha-Terpineol	0.00	0.26
	Nerol	0.18	1.76
Sesquiterpenes			
	delta-Elemene	0.90	0.00
	alpha-Cubebene	0.17	0.00
	alpha-Copaene	0.27	0.83
	unknown sesquiterpene 1	0.47	0.00
	(E)-Caryophyllene	0.55	0.54
	beta-Copaene	0.14	0.76
	gamma-Elemene	0.51	0.00
	Aristolene	0.52	0.51
	alpha-Humulene	0.13	0.00
	gamma-Muurolene	0.36	0.00
	delta-Cadinene	0.19	0.00

Appendix 2 (continued).

Family	COV	*X. aethiopica*	*U. molundense*
Terpene derivatives			
	beta-Ionon epoxide	0.47	0.00
	unknown terpene deriv. 1	4.27	0.00
	unknown terpene deriv. 2	43.53	0.69
Other compounds		0.00	0.00
	unknown compound 1	0.21	2.65
	unknown compound 2	0.00	0.46
	unknown compound 3	0.76	0.00
	unknown compound 4	0.43	0.00