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RESEARCH PAPER

Out of the Palaearctic: the *Helophorus* water beetles of the Afrotropical Region (Coleoptera: Helophoridae)

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Abstract. *Helophorus* Fabricius, 1775 (Coleoptera: Hydrophiloidea: Helophoridae) is an old and largely Holarctic genus of beetles, with most extant diversity concentrated in the Palaearctic. As with a number of primarily northern temperate lineages, the genus has colonised the Afrotropical Region, with species described from the Ethiopian Highlands and southern Africa. Here, the Afrotropical *Helophorus* fauna is revised, based on a study of all primary types and additional material, including extensive recent collections from South Africa. The known Afrotropical fauna is shown to be comprised of six species, only three of which were previously described: *H. aethiopicus* Régimbart, 1907, from southern highland areas of Ethiopia, *H. aethiops* J. Balfour-Browne, 1954 known from summer and year-round rainfall areas of South Africa and Namibia and *H. cooperi* Orchymont, 1948, stat. nov., described as a subspecies of *H. aethiopicus* and still only known from the type locality in Ethiopia. To these, three new species are added: *H. brumopluvialis* sp. nov., widespread in winter rainfall areas of the Western and Northern Cape Provinces of South Africa, *H. nyandaruaensis* sp. nov. from mountains of the East African Rift in Kenya and *H. simiensis* sp. nov. from the Simien Mountains of northern Ethiopia. All species are (re)described in detail and illustrated with high-resolution photos. Known distributions are mapped and a key to species provided. It is suggested that the two South African species may have speciated allochronically, due to seasonal shifts in life cycle associated with the development of the winter rainfall regime in the Cape during the Plio-Pleistocene. *Helophorus* are hypothesised to have colonised the Afrotropics on at least two occasions from separate Palaearctic ancestors.

Key words. Coleoptera, Helophoridae, new records, new species, taxonomy, Afrotropical Region

Zoobank: http://zoobank.org/urn:lsid:zoobank.org:pub:D982BDAC-CB44-41BE-A35C-92D630F96BF7

Introduction

Helophorus Fabricius, 1775, the only recognised genus within the Helophoridae, is a widespread and relatively old lineage of (mostly) true water beetles (sensu Jäch 1998), dating to at least the late Jurassic (ca. 150 Ma), with crown-group *Helophorus* apparently originating in the Early Cretaceous (ca. 136 Ma) (Fikáček et al. 2012). Some individual lineages/species within the genus also seem to be old, fossils of apparent *Helophorus sibiricus* (Motschulsky, 1860), for example, being known from the early Miocene of Russia (Fikáček et al. 2011). Today, *Helophorus* is a primarily Holarctic genus, with just over 200 species described. Some species are fully terrestrial, others associated with the margins of running water, but most are characteristic of shallow, temporary standing waters, including "vernal pools" flooded by spring rains or snowmelt, where they can be the most abundant macroinvertebrates and clearly of significant ecological importance. *Helophorus* diversity is especially high in mountainous regions, particularly Anatolia, the Caucasus and the Western Cordilleras of North America (e.g. Smetana 1985; Angus 1988a, 1992). Whilst the adults of most species are aquatic herbivores/detritivores, most known larvae are terrestrial and predatory (Angus 1973).

The rich *Helophorus* fauna of the Holarctic has been extensively studied during the last 50 years, much of this work being summarised by Angus (1992) and Smetana (1985). The systematics of the genus are notoriously difficult, particularly due to the relatively high degree of variability observed within many species (e.g. Angus 1992), including in features of the male genitalia and, on the other hand, the presence of morphologically cryptic taxa. Angus (1982) pioneered the use of karyotype analysis in *Helophorus* as a consequence, and this approach has aided the interpretation of many species complexes, particularly in Europe (e.g. Angus 1983, 1986, 1988b, 1996). Surprisingly, DNA-based studies of *Helophorus* remain rare, however and have not been employed to aid taxonomic interpretations to date.

In Africa, most *Helophorus* are restricted to areas of the continent north of the Sahara, and comprise species or lineages which are also present further north within the Palaearctic (e.g. Angus 1987). As with a number of other primarily Holarctic water beetles, however, *Helophorus* have colonised the Afrotropical Region, being known from east and southern Africa. To date, only two species have been described: *Helophorus aethiopicus* Régimbart, 1907 from Ethiopia and *H. aethiops* J. Balfour-Browne, 1954 from South Africa; the former having a named subspecies *H. aethiopicus cooperi* Orchymont, 1948, also described from Ethiopia. The present work began almost ten years ago, when I found large numbers of a *Helophorus* in KwaZulu-Natal, South Africa, geographically distant from all published records of the genus. In the field, these beetles looked very different from Western Cape material that I had long considered to be *H. aethiops*. Both morphological and genetic analysis showed that this was indeed a different species from specimens collected in winter-rainfall areas, prompting me to review all Afrotropical material of the genus I could access. As stated above, *Helophorus* are difficult and this work is unlikely to be the last word on the biodiversity of the genus in the region, particularly given the limited volume of material available from outside South Africa. Any significant improvements will require further fieldwork in African mountains and DNA-based assessments of populations; hopefully both will be possible in the future.

Materials and methods

Specimens were studied using Leica MZ8 and M205C stereomicroscopes, with LED gooseneck lights diffused using a tracing paper collar and tubes derived from opaque white plastic film canisters. Habitus photographs were taken with a Canon EOS 5D Mark IV camera fitted to a Leica M205C stereomicroscope, with a 1× objective lens. Specimens were illuminated with gooseneck lights, diffused with a film canister tube. Genitalia were mounted on glass slides in Kisser's glycerol gelatine (see Riedel 2005) and imaged using an Olympus CX31 microscope and a Canon EOS 500D camera. All image stacks were produced by hand and combined using Zerene Stacker software (www.zerenesystems.com).

For scanning electron microscopy (SEM), card mounted beetles were removed from pins and cards attached to metal stubs using double-sided carbon conducting tape and a blob of silver paint at the margin of the card to aid conduction. Specimens were gold sputter coated using an Emitech K550 Coating Unit and examined and photographed in a JEOL JSM5600LV Scanning Electron Microscope.

Terminology for pronotal grooves and intervals follows Angus (1992). Exact label data are cited for specimens. Slashes "//" indicate a new line in the label text. [Hw.] indicates handwriting.

The following abbreviations are used in the text:

BMNH	Natural History Museum, London, United Kingdom;
CBP	Collection D. T. Bilton, Plymouth, United Kingdom;
CTP	Collection C. R. Turner, Plymouth, United Kingdom;
ISAM	Iziko South African Museum, Cape Town, South Africa;
MNHN	Muséum national d'Histoire naturelle, Paris, France;
NMNW	National Museum of Namibia, Windhoek, Namibia;
NMPC	National Museum of the Czech Republic, Prague, Czech Republic;
NMW	Naturhistorisches Museum in Wien, Wien, Austria;
RBINS	Royal Belgian Institute of Natural Sciences, Brussels, Belgium;
BL	body length (front of labrum to elytral apices);
EL	elytral length (outer angle of shoulder to apex);
EW	elytral width at widest point.

Taxonomy

Helophorus (*Ropalohelophorus*) *aethiopicus* Régimbart, 1907

(Figs 1A, 2A–B, 3A, 5)

Helophorus aethiopicus Régimbart, 1907: 127.

Type locality. Ethiopia, Oromiya Region, Karsa (Kersa), approximately 7°45′S 37°00′E, > 1,740 m. Exact details imprecise. Karsa (or Kersa) is a woreda (district) in the Oromiya Region of southern Ethiopia, whose altitude ranges from 1,740–2,660 m.

Type material. Lectotype: ♂, labelled: "♂" "LECTO- // TYPE" [circular label with purple margin] "MUSEUM PARIS // ÉTHIOPIE MÉRID // KARSSA // Maurice de Rothschild // 1905" "Helophorus // aethiopicus Rég. typus" [Hw.] "LECTOTYPE 1974 // H. aethiopicus Rég. // R. B. Angus det." [LECTOTYPE, 74 and name and describer Hw.] "1974 // H. mervensis Sem. // R. B. Angus det." [74 and name and describer Hw.] (MNHN). Paralectotypes: 1 ♂, "PARA- // LECTO- // TYPE" [circular label with blue margin] "MUSEUM PARIS // ÉTHIOPIE MÉRID // KARSSA // Maurice de Rothschild // 1905" "Helophorus // aethiopicus Rég. // n. sp. // Type - 1906" [Hw.] "PARALECTOTYPE Sept1974 // H. aethiopicus Rég. // R. B. Angus det." [LECTOTYPE, Sept, 74 and name and describer Hw.] "1974 // H. mervensis Sem. // R. B. Angus det." [74 and name and describer Hw.] (MNHN); 1 ♀, "♀" "PARA- // LECTO- // TYPE" [circular label with blue margin] "MUSEUM PARIS // ÉTHIOPIE MÉRID // KARSSA // Maurice de Rothschild // 1905" "TYPE" [red label] "PARALECTOTYPE Sept1974 // H. aethiopicus Rég. // R. B. Angus det." [LECTOTYPE, Sept, 74 and name and describer Hw.] (MNHN); 1 ♀, "PARA- // LECTO- // TYPE" [circular label with blue margin] "TYPE" [red printing] "MUSEUM PARIS // ÉTHIOPIE MÉRID // KARSSA // Maurice de Rothschild // 1905" "Helophorus // aethiopicus // Rég. n. sp. // Type // 1906" [Hw.] "PARALECTOTYPE Sept1974 // H. aethiopicus Rég. // R. B. Angus det." [LECTOTYPE, Sept, 74 and name and describer Hw.] "1974 // H. mervensis Sem. // R. B. Angus det." [74 and name and describer Hw.] (MNHN).

Other material examined. 1 ♂, "ETHIOPIA: Oromia // Bale Mountains NP // 5 km NW Dinsho // small lake" "07°07′15.62″N/39°43′10.52″E // 3057 m a.s.l. // 22.II.2014 // leg. M.A. Jäch (12)" (NMW); 2 ♀♀, "ETHIOPIA: Oromia // Bale Mountains NP // 5 km NW Dinsho // stream" "07°07′24.47″N/39°44′26.31″E // 3044 m a.s.l. // 20.II.2014 // leg. M.A. Jäch (12)" (NMW); 1 ♂, "♂" "Ethiopie : Goba // R. de Meulenaere // 1934-1935" "R. Mus. Hist. Nat. // Belge. I.G 10.738" "A. d'Orchymont det. // Helophorus s. str. // aethiopicus Rég." [name and describer Hw.] (RBINS); 9 exx., "Ethiopie : Goba // R. de Meulenaere // 1934-1935" "R. Mus. Hist. Nat. // Belge. I.G 10.738" (RBINS); 2 ♂♂ 1 ♀ "Ethiopie

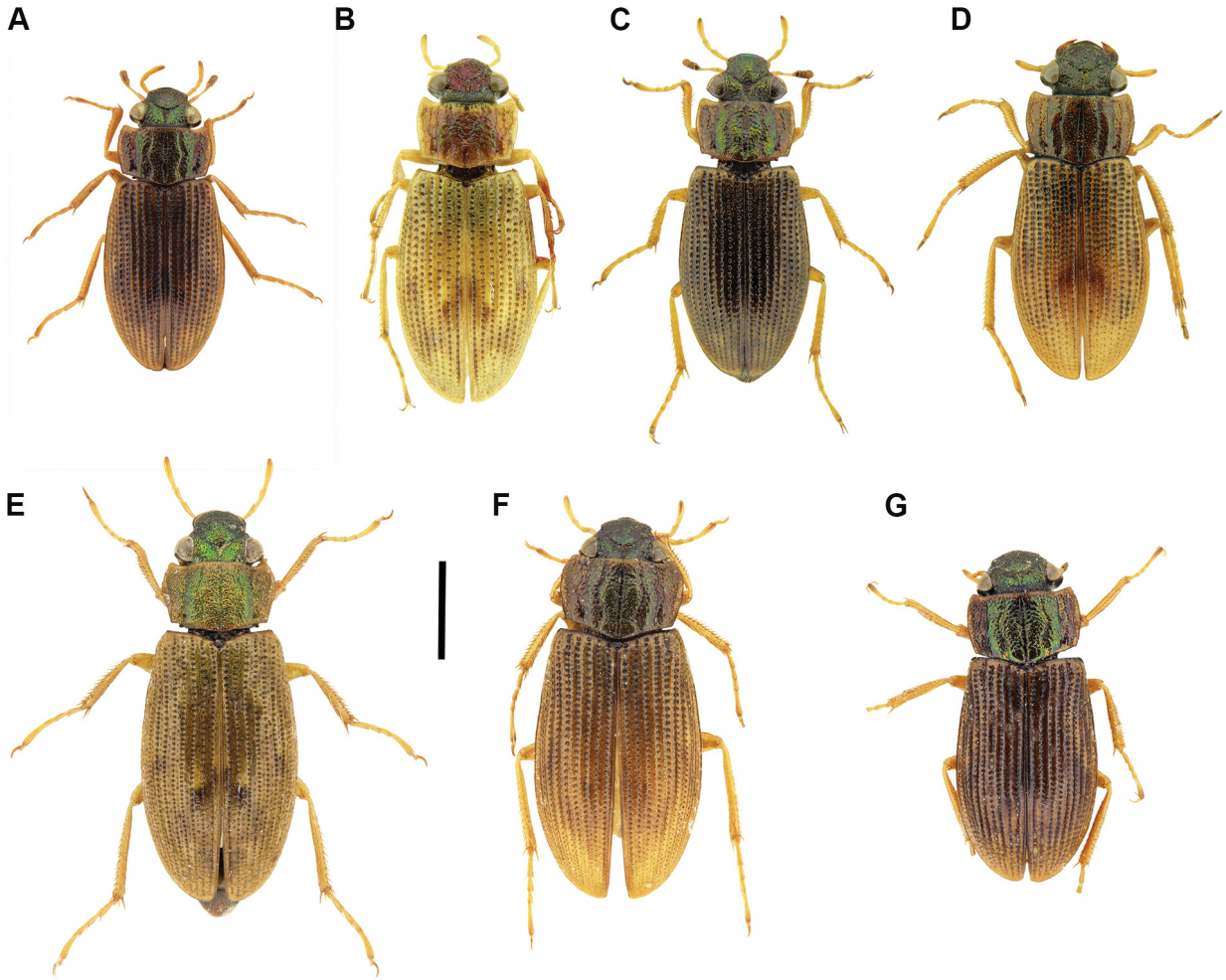

Fig. 1. Afrotropical *Helophorus*, habitus. A – *H. aethiopicus* Régimbart, 1907, lectotype; B – *H. aethiops* J. Balfour-Browne, 1954, holotype; C – *H. aethiops* J. Balfour-Browne, 1954, Kokstad, South Africa; D – *H. cooperi* Orchymont, 1947, holotype; E – *H. brumopluvialis* sp. nov., holotype; F – *H. nyandaruaensis* sp. nov., holotype; G – *H. simiensis* sp. nov., holotype. Scale bar = 1 mm.

: Goba // R. de Meulenaere // 1934-1935" "Ethiopie : Goba // R. de Meulenaere // 1934-1935" "R. Mus. Hist. Nat. // Belge. I.G 10.738" "Coll. I.R.Sc.N.B." (RBINS) [blue label].

Redescription. ***Male*** (Fig. 1A). *Head* dark brown to black, with strong green to purplish aeneous reflection; strongly shining. Granules mostly absent, reduced to a central seta-bearing pore over central areas of frons and clypeus; more evident inside compound eyes, laterally on clypeus and immediately in front of Y-groove. Y-groove relatively deep; floor of stem with dense, coarse, rugose punctures, punctures in lateral branches smaller, shining as rest of head; stem evenly diverging anteriorly; lateral branches narrow, particularly over apical 0.5, straight proximally then weakly arcuate laterally in front of eyes. Clypeus strongly elevated in centre; anterior margin almost straight. Labrum with shining, impunctate, basal portion with anterior margin acuminate at centre; anterior portion with coarse, rugose punctures, each puncture bearing a short, stout, whitish semi-erect seta; anterior margin arcuate with shallow anteromedian emargination. Antennae 9-segmented, yellowish brown, with cupule and club segments darker. Maxillary palpi yellow, apex of terminal segment infuscated; moderately elongate, terminal segment longest, curved and clearly asymmetrical.

Pronotum (Fig. 3A), reddish brown, with strong green to purple aeneous reflections, particularly on internal intervals; anterior border narrowly and lateral borders more widely paler, yellowish brown; shining over entire dorsal surface. Broadest between middle and anterior margins; weakly arched in frontal and dorsal views and somewhat flattened over internal intervals, particularly anteriorly. Anterior margin slightly concave over central 0.5, then sinuate to broadly rounded front angles; posterior margin broadly bisinuate around centre. Sides straight over posterior 0.4, then weakly arcuate around broadest point to anterior angles. Lateral margins setose and weakly crenulated to serrate. Internal and middle intervals slightly arched, strongly shining; most granules reduced to pore and seta; granules more evident on anterior portion of both intervals, particularly middle. External interval, surface strongly shining with evident granules anteriorly. Grooves smooth and shining, median and submedian with almost coalescent, shallow punctures, giving a somewhat rugose appearance; submarginal and marginal with irregular small bumps. Median groove narrowed anteriorly, less so posteriorly, open at both ends more widely so posteriorly. Submedian and submarginal grooves broadly open anteriorly and po-

Fig. 2. Afrotropical *Helophorus*, aedeagi. A – *H. aethiopicus* Régimbart, 1907, lectotype; B – *H. aethiopicus*, paralectotype; C – *H. aethiops* J. Balfour-Browne, 1954, holotype; D–F – *H. aethiops* J. Balfour-Browne, 1954, Kokstad, South Africa; G – *H. cooperi* Orchymont, 1947, holotype; H – *H. brumopluvialis* sp. nov., holotype; I–J – *H. brumopluvialis* sp. nov., Hopefield, South Africa; K – *H. nyandaruaensis* sp. nov., holotype; L – *H. simiensis* sp. nov., holotype. Scale bar = 100 μm.

steriorly. Submedian grooves relatively broad, distinctly sinuate. Submarginal grooves weakly arcuate, broader than submedian. Marginal grooves curved parallel to the side of pronotum, width uniform. All grooves relatively deep, with intervals curving down towards their margins, which are well-defined but somewhat sloping rather than vertical.

Elytra (Fig. 1A) brown, with diffuse paler markings, particularly posteriorly. Shape elongate oval, sides rounded to bluntly rounded apex. In lateral profile flat over anterior 0.5, then gradually descending to apex. Puncture rows moderately striate, particularly on disc and laterally; intervals arched.

Legs yellowish-brown, apex of last tarsal segment and claws infuscated. Swimming hairs distinct and clearly visible.

Venter black, with pronotal hypomeron, antennal pocket and pseudepipleura and epipleura brown to yellow. Mentum shining, centre without microreticulation, with sparse, medium punctures; lateral marginal areas with weak isodiametric microreticulation centrally; margins with fine yellow setae, denser towards posterolateral angles. Submentum shining, without microreticulation; anterior 0.5 with sparse, shallow, coarse punctures and fine, hair-like vestiture. Gula and genae rugose, with dense hydrofuge

vestiture. Gular sutures well marked as pits anteriorly. Vestiture only absent around margin of compound eyes and their posterolateral corners. Prosternum dull, rugose, with dense hydrofuge vestiture and sparse, long, erect setae approximately 2× length of vestiture. Pronotal hypomeron dull, with dense hydrofuge vestiture. Pronotal epipleura shining, glabrous, with sparse shallow punctures. Anterior antennal pocket well developed, with long, dense setae internally and long, curved setae at posterolateral margins. Elytral epipleura dull, glabrous, narrowing posteriorly at level of metaventrite and continuing until posterior margin of ventrite. Elytral flanks very narrowly visible from below. Ventral surface of mesothorax, metathorax and abdomen dull, with dense hydrofuge vestiture and longer, erect setae; longer setae concentrated on centre of metaventrite and abdominal ventrites 2–5; setae on ventrites arising from longitudinal tubercles, which sometimes appear as shining patches. Hind margin of abdominal ventrite 5 weakly crenulate.

Aedeagus (Figs 2A–B), elongate, 0.45 mm in length. Parameres longer than basal piece; outer margins of parameres straight almost to apex; interior margins of parameres rather straight, apices pointed. Median lobe narrow, with weakly pointed apex; sides diverging slightly posteriorly to base of struts, weakly concave; struts distinctly shorter than tube.

Female. Externally as male.

Measurements. Lectotype: BL = 2.90 mm; EL = 2.00; EW = 1.25 mm. Males: BL = 2.75–2.80 mm; EL = 1.15–2.00 mm; EW = 1.20–1.25 mm. Females: BL = 2.60–3.50 mm; EL = 1.80–2.50 mm; EW = 1.20–1.50 mm.

Variation. Some variation in colour of elytra, some of the paralectotypes and additional specimens being somewhat paler than the lectotype illustrated. Punctation of pronotal grooves also varies somewhat, being more pronounced in some specimens, including paralectotypes, than in the lectotype.

Differential diagnosis. This species can be distinguished by its 9-segemented antennae, relatively small size, weak pronotal granulation and the structure of the aedeagus.

Distribution and ecology. Only known from Ethiopia (Fig. 5), from three collections from two separate areas of the southern highlands; the Oromiya Region in the southwest (type locality) and the Bale Mountains across the Ethiopian Rift Valley to the East. Potentially widespread in these southern high mountain districts, all localities being over 2,500 m.

Comment. Robert Angus had considered that this species could be a synonym of *H. mervensis* Semenow, 1900 known from Armenia, through Arabia to Iran, Central Asia and Kashmir, something reflected by labels on part of the material examined (see above). Despite this, the two were never formally synonymised (Angus 1971, 1986). My assessment is that, whilst these taxa are similar, they are not conspecific. The aedeagi of these species are very close indeed, but the beetles themselves differ. Based on my examination of specimens from Iran, Kashmir and Central Asia (Golodnya Steppe, Uzbekistan and Shymkent, Kazakhstan) *H. mervensis* is comparatively more elongate and paler that *H. aethiopicus* (ground colour of pronotum pale brown with aeneous reflections; elytra pale brown to yellow). In addition, the pronotal granulation of *H. mervensis* is typically more reduced than in all the *H. aethiopicus* I have seen, internal intervals in particular lacking any evident granules in most specimens. The pronotal grooves also appear shallower in *H. mervensis*, and the elytral striae less deep apically, with flatter intervals than in *H. aethiopicus*, although, as stated by Angus (1986) this character varies. Given the similarities, particularly in aedeagi, it may be that *H. mervensis* and *H. aethiopicus* share a relatively recent common ancestor, one sublineage of which colonised Ethiopia. Clearly this hypothesis should be tested with DNA sequence data when practicable. Angus (1986) lists four species described by David Sharp as synonyms of *H. mervensis* and notes the variability of the species as currently defined. Whether it represents a single, widespread, Palaearctic species, or a complex, seems impossible to resolve without genetic data.

Helophorus (*Ropalohelophorus*) *aethiops* J. Balfour-Browne, 1954

(Figs 1B–C, 2C–F, 3B, 4A, C, E, G, 5)

Helophorus aethiops J. Balfour-Browne, 1954: 105.

Type locality. South Africa, Eastern Cape Province, Albany District, Gowie's Kloof, Makhanda (formerly Grahamstown), 33°18′58.71″S 26°31′29.68″E, 570 m.

Type material. Holotype: ♂, labelled: "♂" "Type" [circular label with red margin] "SOUTH AFRICA // Albany Dist. // Gowies Kloof // 6.viii.39." "J. Omer Cooper // coll." "Helophorus (s.str.) // aethiops Type!/ J. Balfour-Browne det." [genus and species name and Type! Hw.] (BMNH). Paratypes: 2 ♀♀, same data as holotype; 2 ♂♂, "SOUTH AFRICA // Albany Dist. // Grahamstown. // v. 1939." "J. Omer Cooper // coll." "Brit. Mus. // 1939–625."; 2 ♂♂, "SOUTH AFRICA // Grahamstown. // Teafontein Farm // 29.vii.1939." "J. Omer Cooper // coll." "Brit. Mus. // 1939–625."; 1 ♂, "SOUTH AFRICA // Albany Dist. // Piggot Bridge // Rd. 10.ii.39." "J. Omer Cooper // coll." "Brit. Mus. // 1939–625."; 1 ♂, "SOUTH AFRICA // Albany Dist. // Piggot Bridge // Rd. 20.iii.39." "J. Omer Cooper // coll." "Brit. Mus. // 1939–625." "Helophorus (s.str.) // aethiops Paratype!/ J. Balfour-Browne det." [genus and species name and Paratype! Hw.]; 2 ♂♂, "SOUTH-WEST AFRICA. // Windhoek, Avis Dam. // 7.vii.37. // J. Omer-Cooper." "J. Omer Cooper // coll." "Brit. Mus. // 1939–625." All BMNH and with circular Paratype labels with yellow border.

Other material examined. 24 ♂♂ 21 ♀♀, "29/xii/2013 South Africa KZN // Temp. pond in grassland beside // R56 road ca. 25 km ENE of // Kokstad D T Bilton leg." (AMG, CBP, ISAM, MNHN, NMPC, NMW); 1 ♂, "29/xii/2013 South Africa KZN // Temp. pond in grassland beside // R56 road ca. 25 km ENE of // Kokstad D T Bilton leg." "DNA voucher // IBE-DV277" (CBP); 1 ♀, "29/xii/2013 South Africa KZN // Temp. pond in grassland beside // R56 road ca. 25 km ENE of // Kokstad D T Bilton leg." "DNA voucher // IBE-DV278" (CBP); 7 ♂♂ 14 ♀♀, "Stn, No. // 111" "S. AFRICA: // Matatiele // 4800ft., 28.iii.1954" "Shallow, muddy // roadside ditch // very weedy, // grasses and Juncus" "J. Balfour-Browne // Brit. Mus. 1954–797" (BMNH); 2 ♀♀, "Stn. No. // 134" "S. AFRICA: // Farm Dam, 4250ft., // nr. Mooi River, // 2.iv.1954" "Mud with Juncus // and Nitella" "J. Balfour-Browne // Brit. Mus. 1954–797" (BMNH); 1 ♂, "Stn. No. // 84" "S. AFRICA: // E. Cape Province // van Staaden's Pass, // 21.iii.1954" "In gravel at edge // of fast stream" "J. Balfour-Browne // Brit. Mus. 1954–797" "Helophorus (s. str.) aethiops J. B-B // J. Balfour-Browne det. // v. 1975" (BMNH); 1 ♀, "Stn. No. // 160" "S. SAFRICA: // O.F.S., nr. // Harrismith, // 5500ft., 7.iv.1954" "Farm dam, // very grassy." "J. Balfour-Browne // Brit. Mus. 1954–797" (BMNH); 2 ♂♂, 8 exx., "S. AFRICA: // Riversdale Dist. // nr. Albertinia // 16.ii/1947 // J. Omer-Cooper" "Brit. Mus. // 1978-162" (BMNH); 1

♂ 1 ♀, "S. AFRICA: // ca. 12 mi. from Queenstown // on road to Lady Frere, // ca. 3800ft., 26.iii.1954" "in small // grassy dam" "J. Balfour--Browne // Brit. Mus. 1954–797" (BMNH); 1 ♂ 4 ♀♀, "TRANSVAAL // Middleburg Dist. // Middleburg // 29.xi.1948" "SOUTH AFRICA // J. Omer-Cooper" "J. Omer-Cooper // B.M. 1981–272" (BMNH); 2 ♂♂, 5 exx., "Dry stream // with pools" "TRANSVAAL // Waterburg Dist. // Potgietersrust. // ? Matini R. // 25.xi.1948" "SOUTH AFRICA // J. Omer-Cooper" "J. Omer-Cooper // B.M. 1981–272" (BMNH); 2 ♀♀, "TRANSVAAL // Pietersburg Dist. // Bandolier Kop // 23.xi.1948" "SOUTH AFRICA // J. Omer-Cooper" "J. Omer-Cooper // B.M. 1981–272" (BMNH); 3 ♀♀, "TRANSVAAL // Pietersburg Dist. // Dam, 18 mls South // of Pietersburg // 25.xi.1948" "SOUTH AFRICA // J. Omer-Cooper" "J. Omer-Cooper // B.M. 1981–272" (BMNH); 2 ♂♂, 18 exx., "ORANGE FREE STATE // Kroonstad Dist. // Vredefort // Nr. Honing Spruit // 29.viii.1947" "SOUTH AFRICA // J. Omer-Cooper" "J. Omer-Cooper // B.M. 1981–272" (BMNH); 1 ♂, 7 exx., "CAPE PROV. // Cathcart Dist. // Cathcart // 20.ii.1950" "SOUTH AFRICA // J. Omer-Cooper" "J. Omer-Cooper // B.M. 1981–272" (BMNH); 1 exx., "CAPE PROV. // Colesburg Dist. // Colesburg. Dam // outside town. // 22.ii.1947" "SOUTH AFRICA // J. Omer-Cooper" "J. Omer-Cooper // B.M. 1981–272" (BMNH); 1 exx., "CAPE PROV. // Aliwal North Dist. // Dam in mountains // 13.iii.1948" "SOUTH AFRICA // J. Omer-Cooper" "J. Omer-Cooper // B.M. 1981–272" (BMNH); 1 exx., "TRANSVAAL. // Lydenburg Dist. // Belfast. // 30/xi/1948" "SOUTH AFRICA // J. Omer-Cooper" "J. Omer-Cooper // B.M. 1981–272" (BMNH); 2 exx., "CAPE PROV. // Cathcart Dist. // Cathcart // 20.ii.1950" "SOUTH AFRICA // E. M. Rodgers" "J. Omer-Cooper // B.M. 1981–272" (BMNH); 2 exx., "CAPE PROV. // Queenstown Dist. // Dam nr. Sterkstroom // 25 mls. Queenstown - // Aliwal. 13.ii.1948." "SOUTH AFRICA // J. Omer-Cooper" "J. Omer-Cooper // B.M. 1981–272" (BMNH); 1 exx., "S. W. AFRICA // Okarupa, ca. 17 ml. // E. of Okahandja, // 4900ft. 22.v.1954." "Pools in overflow // stream from dam, // much weed and algae." "J. Balfour-Browne // Brit. Mus. 1954–797" (BMNH); 1 exx., "CAPE PROV. // Uniondale Dist. // Lange Kloof Mts. // 22.xi.1947" [all except CAPE PROV. Hw] "SOUTH AFRICA // J. Omer-Cooper" "J. Omer-Cooper // B.M. 1981–272" (BMNH); 1 ♂, "Stn. No. // 78" [78 Hw.] "S. AFRICA // Witte Elbosch, // Groote River, // 19.iii.1954" "Rapid stream, // weeds and moss, // dead edges" "SOUTH AFRICA // J. Omer-Cooper" "J. Omer-Cooper // B.M. 1981–272" (BMNH); 1 ♂, "Namibia: WINDHOEK // DIST. Krumneck 20 // Farm dam on Oanob R. // SE 2216 Dd // 25.iii.1987 // B.A. Curtis // SMI 3210" "Namibian National // Insect Collection, // National Museum, // OP.O. Box 1203, // Windhoek, Namibia." (NMNW); 1 ♂, "SOUTH AFRICA: // Aliwal North, // 18-25.viii.1954." "'in tank' // H. Andreae" "Helophorus // aethiops J. B-B. // J. Balfour-Browne det. // 1975 [name and date Hw] "SAM-COL/ AO 01926" (ISAM); 2 ♂♂, 3 exx., "SOUTH AFRICA: // Aliwal North, // 18-25.viii.1954." "'in tank' // H. Andreae" "Helophorus // aethiops // Balf.- Browne" [Hw.] "SAM-COL/ AO 01926" (ISAM); 1 ♂ 3 ♀♀, "SUDAFRIKA, Natal // 40km S Bethlehem // 30.12.1993 // leg. Wewalka (10)" "1997 // H. aethiops J B-B // R. B. Angus det." [name and year Hw.] (NMW); 1 ♂, "9/iii/2018 South Africa EC // Winterberge – seepage // below Fenella Falls // D T Bilton leg." "DNA specimen // E.E. IBE-AN1090" (NMW); 1 ♂, "12/iii/2018 South Africa EC // Compassberg, small stream // above farmhouse // D T Bilton leg." "DNA specimen // E.E. IBE-AN1092" (NMW); 1 ♂, "11/iii/2018 South Africa EC // Toorberg – temporary pool // 1 km NW of Longfontein // D T Bilton leg." "DNA specimen // E.E. IBE-AN1095" (NMW); 1 ♂, "SOUTH AFRICA, W. Cape, 4 Sept 2003 // leg. C.R. Turner, 33º39'19"S 21º01'05"E, alt: 310m, // R62 c.32km east of Ladismith, Large Bridge // with waning river slight flow with silty/fine sand, // rock based pools with sparse vegetation, // some sedges and little reeds." (CBP); 1 ♂ 2 ♀♀, "SOUTH AFRICA, W. Cape, 4 Sept 2003 // leg. C.R. Turner, 33º39'19"S 21º01'05"E, alt: 310m, // R62 c.32km east of Ladismith, Large Bridge // with waning river slight flow with silty/fine sand, // rock based pools with sparse vegetation, // some sedges and little reeds." (CTP).

Redescription. ***Male*** (Fig. 1B). *Head* black, with strong purple aeneous reflection; strongly shining. Granules effaced, most reduced to a central seta-bearing pore; more evident laterally on clypeus and immediately in front of Y-groove, where some coalesce into irregular, transverse ridges. Y-groove shallow; floor with dense, coarse, rugose punctures, shining as rest of head; stem evenly diverging anteriorly; lateral branches narrow, straight proximally then weakly arcuate laterally in front of eyes. Clypeus slightly elevated in centre; anterior margin weakly arcuate. Labrum with shining, impunctate, basal portion with anterior margin bisinuous around centre; anterior portion with coarse, rugose punctures, each puncture bearing a short, stout, whitish semi-erect seta; anterior margin arcuate with broad, shallow anteromedian emargination. Antennae 8-segmented, yellowish brown, with cupule and club segments darker. Maxillary palpi yellow, apex of terminal segment infuscated; moderately elongate, terminal segment longest, curved and clearly asymmetrical.

Pronotum (Figs 3B & 4C, E) predominantly reddish brown, with strong purple aeneous reflections, particularly on internal intervals; anterior and lateral borders paler, yellowish brown; shining over entire dorsal surface. Broadest between middle and anterior margins; weakly arched in frontal and dorsal views and somewhat flattened over internal intervals, particularly anteriorly. Anterior margin almost straight over central 0.5, then sinuate to broadly rounded front angles; posterior margin broadly bisinuate around centre. Sides straight over posterior 0.4, then weakly arcuate around broadest point to anterior angles. Lateral margins setose and very weakly crenulated to serrate. Internal and middle intervals flat, very weakly to weakly granulate, strongly shining; most granules reduced to pore and seta; granules more evident on external interval, surface strongly shining and somewhat rugose. Grooves smooth and shining, with sparse, shallow punctures and small raised areas but no clear trace of granules. Median groove narrowed anteriorly and posteriorly, open at both ends more widely so posteriorly. Submedian and submarginal grooves broadly open anteriorly and posteriorly. Submedian grooves relatively broad, sinuate. Submarginal grooves straight internally, weakly sinuate externally, broader than submedian. Marginal grooves curved parallel to the side of pronotum, width uniform. All grooves relatively shallow, but with sides abrupt and vertical, particularly evident in submedian, submarginal and marginal grooves.

Elytra (Fig. 1B) brownish-yellow, with diffuse, irregular infuscation; sometimes coalescing into more or less discrete patches around suture and on disc. Shape elongate oval, bluntly rounded at apex. In lateral profile flat over anterior 0.5, then gradually descending to apex. Puncture rows weakly to moderately striate, particularly laterally; intervals weakly arched, more evident laterally.

Legs yellowish-brown, apex of last tarsal segment and claws infuscated. Swimming hairs distinct and clearly visible.

Venter black, with pronotal hypomeron, antennal pocket and pseudepipleura and epipleura orange-brown to straw yellow. Mentum shining, centre without microreticulation, with sparse, medium punctures; lateral marginal areas with weak isodiametric microreticulation centrally; margins with fine yellow setae, denser towards posterolateral angles. Submentum shining, without microreticulation;

anterior half with sparse, shallow, coarse punctures and fine, hair-like vestiture. Gula and genae rugose, with dense hydrofuge vestiture. Gular sutures well marked as pits anteriorly. Vestiture only absent around margin of compound eyes and their posterolateral corners. Prosternum dull, rugose, with dense hydrofuge vestiture and sparse, long, erect setae approximately 2× length of vestiture. Pronotal hypomeron dull, with dense hydrofuge vestiture. Pronotal epipleura shining, glabrous, with sparse shallow punctures. Anterior antennal pocket well developed, with long, dense setae internally and long, curved setae at posterolateral margins. Elytral epipleura dull, glabrous, narrowing posteriorly at level of metaventrite and continuing until posterior margin of ventrite. Elytral flanks very narrowly visible from below. Ventral surface of mesothorax, metathorax and abdomen dull, with dense hydrofuge vestiture and longer, erect setae; longer setae concentrated on centre of metaventrite and abdominal ventrites 2–5; setae on ventrites arising from longitudinal tubercles, which sometimes appear as shining patches. Hind margin of abdominal ventrite 5 weakly crenulate.

Aedeagus (Fig. 2C), elongate, 0.5 mm in length. Basal piece equal in length to parameres; outer margins of parameres weakly and evenly arcuate to apex; interior margins of parameres very weakly concave apically. Median lobe with apex weakly pointed; sides diverging posteriorly to base of struts, weakly concave; struts slightly longer than to tube.

Female. Externally as male, but most somewhat larger.

Measurements. Males: Holotype: BL = 3.50 mm; EL = 2.40; EW = 1.40 mm. Males: BL = 2.60–3.60 mm; EL = 1.90–2.45 mm; EW = 1.10–1.45 mm. Females: BL = 3.45–4.20 mm; EL = 2.30–2.70 mm; EW = 1.35–1.70 mm.

Variation. As with most *Helophorus* from which long series are available, there is some variation in many characters, both within and between populations. In particular, the aeneous reflections on the head and pronotum vary from purplish to greenish, with the background colour of the pronotum varying from pinkish brown to pitchy and the elytral colouration varying from relatively pale to relatively dark (see Figs 1B–C). The degree of elytral infuscation also varies, from almost absent to dominant over the disc. (Figs 1B–C). In some specimens the granulation of the pronotal intervals is more evident than others, but granules, if evident, are always weak and flat. The degree of sculpture visible in the pronotal grooves also varies somewhat, this being correlated with the degree of interval granulation evident, but grooves are always as described above in terms of their relative widths, and their abrupt, vertical margins. In the aedeagus, there is variation in the size (0.50–0.55 mm) and in the shape of paramere apices between specimens, this variation being seen within populations when longer series are available (Figs 2C–F). In some specimens the paramere apices appear pointed, as in the holotype; in others they are internally produced. The basal piece varies from being equal to or slightly longer than the parameres and on the median lobe the struts vary from being equal to or slightly longer than the tube.

Differential diagnosis. This species can be distinguished by its 8-segmented antennae, a pronotum with relatively weak granulation but relatively broad, sharply-defined grooves, relatively large serial punctures on the elytra, with narrow intervals and features of the aedeagus, including the shape of the paramere apices and relatively small size.

Distribution and ecology. Apparently widely distributed in summer and year-round rainfall regions of South Africa, extending along the Great Escarpment into Namibia (Fig. 5). Gaps between known South African and Namibian records likely reflect lack of collecting rather than genuine absences. In the southwest extends as far west as the Riversdale district in the Western Cape Province. Not to date known to overlap geographically with *H. brumopluvialis* sp. nov. Most collections are from the austral summer, but some are from other months in areas of year-round rainfall. Characteristic of shallow, seasonally flooded waters, typically with aquatic grasses, algae and macrophytes. Cytochrome oxidase-I DNA sequence divergence between this species and *H. brumopluvialis* sp. nov. is 5.5–6.0% (I. Ribera, pers. comm.), suggesting that these two species diverged during the Plio-Pleistocene.

Helophorus (*Ropalohelophorus*) *cooperi* Orchymont, 1947, stat. nov.

(Figs 1D, 2G, 3C, 5)

Helophorus aethiopicus cooperi Orchymont, 1947: 722

Type locality. Ethiopia, Oromiya Region, Wourambouchi, close to Djem-Djem Forest, ca. 60 km W of Addis-Abbaba, approximately 9°03′N 38°09′E, ca. 2,750 m. Exact details imprecise. Wouramboulchi is a frequent locality on historical specimens from the region and was close to Djem-Djem Forest.

Type material. Holotype: ♂, labelled: "♂" "Abyssinia // Wouramboulchi // 9,000ft. // 2-7.x.1926. // J. Omer-Cooper." "TYPE" [pink label] "A. d'Orchymont det. // Helophorus (s.str.) aethio // picus cooperi m." [name Hw.] (BMNH). Paratypes: 1 ♀, "♀" otherwise same data as Holotype (BMNH); 1 ♀, "♀" "Abyssinia // Wouramboulchi // 9,000ft. // 2-7.x.1926. // J. Omer-Cooper." "A. d'Orchymont det. // Helophorus (s.str.) aethio // picus cooperi m." [name Hw.] "Para- // type" [pink label) (RBINS).

Redescription. ***Male*** (Fig. 1D). *Head* dark brown to black, with green aeneous reflection; shining. Granules evident over entire frons and clypeus, but partly or fully coalescent with adjacent granules in places. Y-groove relatively shallow; floor shining, with dense, shallow, coarse, rugose punctures; stem weakly diverging anteriorly; lateral branches narrow, particularly over apical 0.5, straight. Clypeus strongly elevated in centre; anterior margin weakly arcuate. Labrum with shining, impunctate, basal portion with anterior margin produced and rounded at centre; anterior portion with coarse, rugose punctures, each puncture bearing a short, stout, whitish semi-erect seta; anterior margin arcuate with shallow anteromedian emargination. Antennae 9-segmented, yellowish brown, with cupule and club segments darker. Maxillary palpi yellow, apex of terminal segment infuscated; moderately elongate, terminal segment longest, curved and clearly asymmetrical.

Pronotum (Fig. 3C) pale reddish brown, with pale green aeneous reflections weak and restricted to sublateral groove; anterior and lateral borders paler, but contrast with remainder of pronotum indistinct; shining over entire

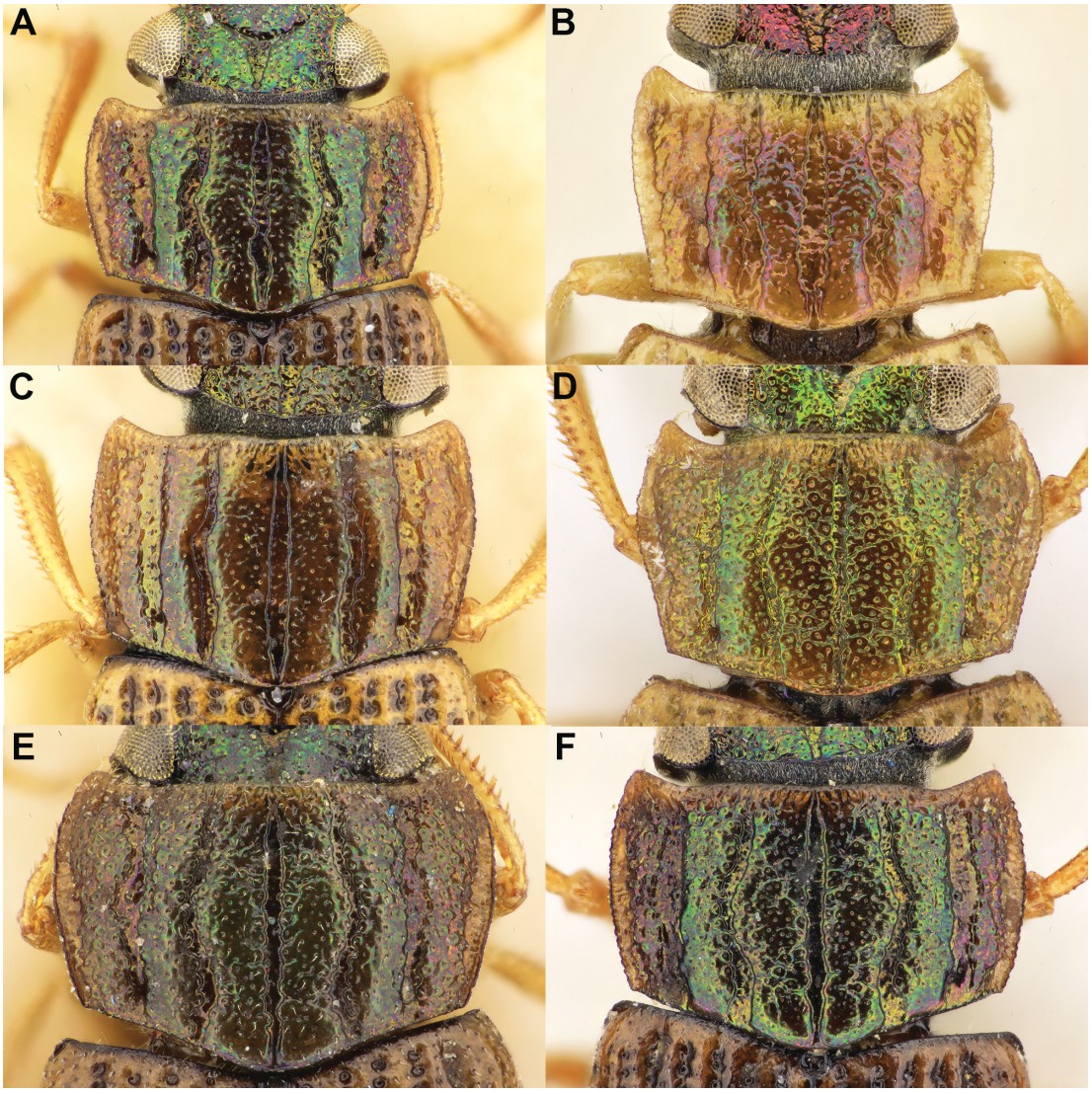

Fig. 3. Afrotropical *Helophorus*, pronota. A – *H. aethiopicus* Régimbart, 1907, lectotype; B – *H. aethiops* J. Balfour-Browne, 1954, holotype; C – *H. cooperi* Orchymont, 1947, holotype; D – *H. brumopluvialis* sp. nov., holotype; E – *H. nyandaruaensis* sp. nov., holotype; F – *H. simiensis* sp. nov., holotype.

dorsal surface. Broadest between middle and anterior margins; weakly arched in frontal and dorsal views and somewhat flattened over internal intervals, particularly anteriorly. Anterior margin slightly concave over central 0.5, then sinuate to broadly rounded front angles; posterior margin broadly bisinuate around centre. Sides straight over posterior 0.4, then weakly arcuate around broadest point to anterior angles. Lateral margins setose and crenulated to serrate. Internal and middle intervals slightly arched, strongly shining; granules reduced to pore and seta. External interval strongly shining with weak granules evident, particularly anteriorly. Grooves smooth and shining, with sparse punctures and wrinkles, particularly in sublateral and lateral. Median groove narrowed anteriorly, more so posteriorly, open at both ends more widely so anteriorly. Submedian and submarginal grooves broadly open anteriorly and posteriorly. Submedian grooves relatively narrow, weakly sinuate. Submarginal grooves almost straight, much broader than submedian. Marginal grooves curved parallel to the side of pronotum, width uniform. All grooves relatively deep, with intervals curving down towards their margins, which are well-defined but somewhat sloping rather than vertical.

Elytra (Fig. 1D) brown, with diffuse paler markings, particularly posteriorly. Shape elongate oval, sides rounded to bluntly rounded apex. In lateral profile flat over anterior 0.5, then gradually descending to apex. Puncture rows weakly striate, more so laterally; intervals slightly arched anteriorly and flatter posteriorly.

Legs yellowish-brown, apex of last tarsal segment and claws infuscated. Swimming hairs distinct and clearly visible.

Venter black, with pronotal hypomeron, antennal pocket and pseudepipleura and epipleura brown to yellow. Mentum shining, centre without microreticulation, with sparse, medium punctures; lateral marginal areas with weak isodiametric microreticulation centrally; margins with fine yellow setae, denser towards posterolateral angles. Submentum shining, without microreticulation; anterior half with sparse, shallow, coarse punctures and fine, hair-like

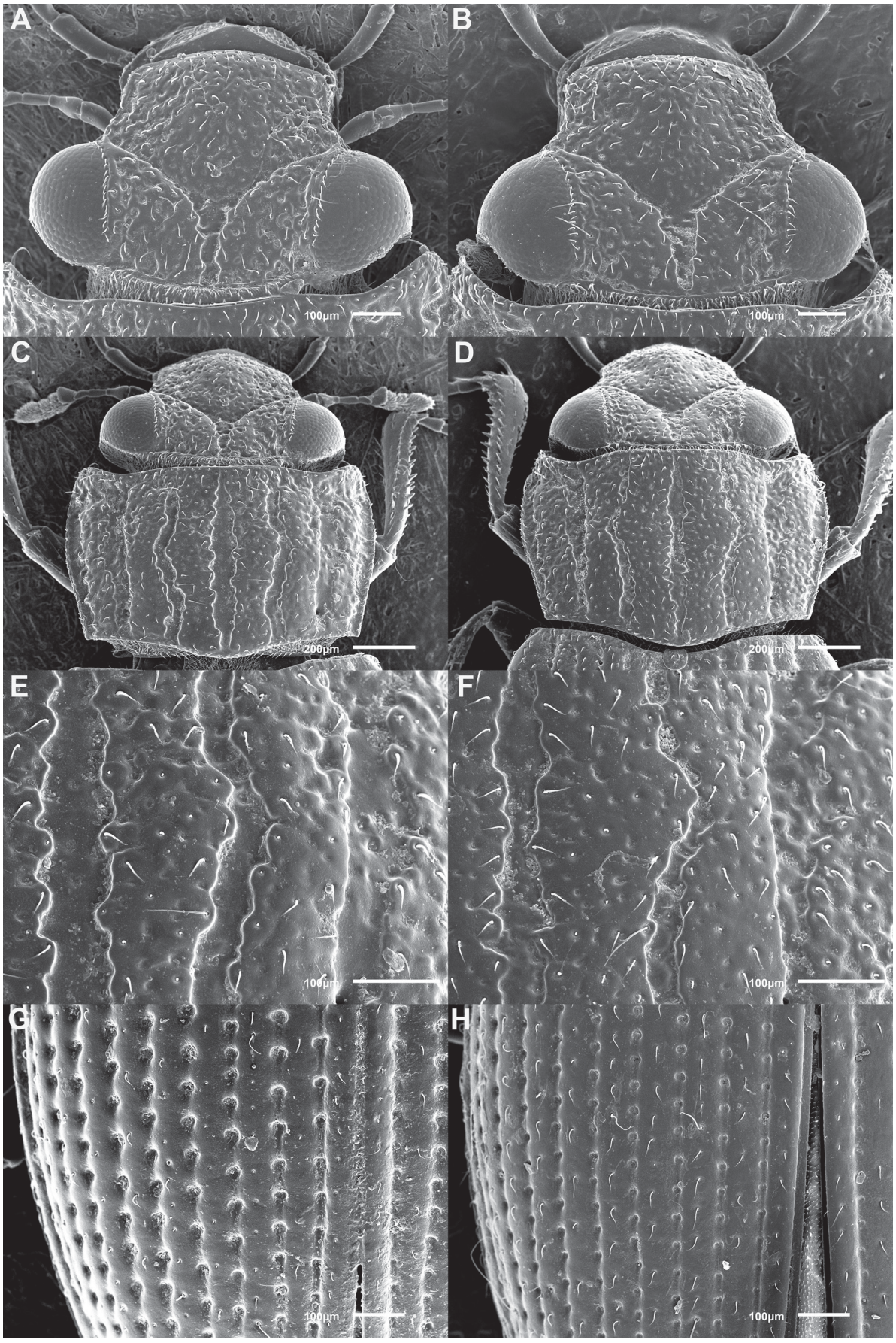

Fig. 4. South African *Helophorus*, SEMs. A, C, E & G – *H. aethiops* J. Balfour-Browne, 1954, Kokstad, South Africa; B, D, F & H – *H. brumopluvialis* sp. nov., Hopefield, South Africa. A–B – head detail; C–D – pronota; E–F – pronotal detail, median groove to far left; G–H – left elytral striation close to apex.

vestiture. Gula and genae rugose, with dense hydrofuge vestiture. Gular sutures well marked as pits anteriorly. Vestiture only absent around margin of compound eyes and their posterolateral corners. Prosternum dull, rugose, with dense hydrofuge vestiture and sparse, long, erect setae approximately 2× length of vestiture. Pronotal hypomeron dull, with dense hydrofuge vestiture. Pronotal epipleura shining, glabrous, with sparse shallow punctures. Anterior antennal pocket well developed, with long, dense setae internally and long, curved setae at posterolateral margins. Elytral epipleura dull, glabrous, narrowing posteriorly at level of metaventrite and continuing until posterior margin of ventrite. Elytral flanks very narrowly visible from below. Ventral surface of mesothorax, metathorax and abdomen dull, with dense hydrofuge vestiture and longer, erect setae; longer setae concentrated on centre of metaventrite and abdominal ventrites 2–5; setae on ventrites arising from longitudinal tubercles, which sometimes appear as shining patches. Hind margin of abdominal ventrite 5 weakly crenulate.

Aedeagus (Fig. 2G) elongate, 0.65 mm in length. Parameres slightly shorter than basal piece; outer margins of parameres sinuate approximately 0.5 from apex; interior margins of parameres initially sloping, then rather straight, apices acuminated. Median lobe narrow, with weakly pointed apex; sides diverging posteriorly to base of struts, weakly concave; struts as long as tube.

Female. Externally as males.

Measurements. Males: Holotype: BL = 3.45 mm; EL = 2.30; EW = 1.40 mm. Females: BL = 3.50–4.00 mm; EL = 2.50–2.65 mm; EW = 1.45–1.65 mm.

Variation. Limited, other than in size – note that only three specimens of this taxon are available, however.

Differential diagnosis. *Helophorus cooperi* has a very distinctive pronotal sculpture, with smooth internal and middle intervals, 9-segmented antennae and a characteristic aedeagus.

Distribution and ecology. Known only from the type locality, Wourambouchi, close to Djem-Djem Forest in the Oromiya Region, ca. 60 km W of Addis-Ababa at approximately 2,750 m (Fig. 5). *Helophorus aethiopicus* is recorded both north and south of this locality and the precise distribution of, and possible ecological differences between, the two species remain unknown.

Helophorus (*Ropalohelophorus*) *brumopluvialis* sp. nov.

(Figs 1E, 2H–J, 3D, 4B, D, F, H, 5)

Helophorus aethiops (partim, misidentification): Balfour-Browne (1954: 105).

Type locality. South Africa, Northern Cape Province, Bokkeveld Plateau, Avontuur Reserve, pools in drying temporary stream, 31°17′38.92″S 19°01′12.03″E, 795 m.

Type material. Holotype: ♂, labelled: "6/x/2015 South Africa NC // Avontuur Reserve – pools in drying // temporary stream 795m 31 17 38.92S // 19 01 12.03 E D T Bilton leg." (AMG) with red holotype label. Paratypes: 2 ♂♂ 1 ♀, same data as Holotype (CBP); 10 ♂♂ 7 ♀♀, "27/ix/2010 South Africa WC // Hopefield pools beside // Berg River on dirt road N of // Bergrivier D.T. Bilton leg." (AMG, CBP, ISAM, MNHN, NMPC, NMW); 1 ♂, "27/ix/2010 South Africa WC // Hopefield pools beside // Berg River on dirt road N of // Bergrivier D.T. Bilton leg." "DNA voucher // IBE-DV275" (CBP); 1 ♀, "27/ix/2010 South Africa WC // Hopefield pools beside // Berg River on dirt road N of // Bergrivier D.T. Bilton leg." "DNA voucher // IBE-DV276" (CBP); 2 ♂♂ 1 ♀, "Sept. 2002 South Africa WC // Temporary pond along R315 road // ca. 10 km E of Darling // D.T. Bilton leg." (CBP); 2 ♂♂ 1 ♀, "18/ix/2010 South Africa NC // Temporary pools on R27 road ca. 2 km E. of // Vanrhynspas – pools on sandy soils // D. T. Bilton leg." (CBP); 2 ♂♂, "17/ix/2014 South Africa NC // Kamiesberg- seepage pools // beside road 2 km SE of // Leliefontein D.T. Bilton leg." (BMNH); 1 ♀, "19/ix/2009 South Africa WC // Temp. pool beside R324 road 12 km S of // Barrydale below Tradouw Pass // D.T. Bilton leg." (BMNH); 2 ♂♂ 1 ♀, 4 exx., "Stn. No. // 326" [326 Hw.] "S. AFRICA // Kalabaskraal // ca. 350ft. 27.vii.1954 // J. Balfour-Browne" "roadside pond, // much Juncus and Nitella" "J. Balfour-Browne // Brit. Mus. 1954–797" (BMNH); 1 ♀, "Para- // type" [circular label with yellow border] "SOUTH AFRICA: // Milnerton, // Diep River, // 28.ix.1949 // A.D. Harrison." [date Hw.] "Brit. Mus. // 1951–35" "Helophorus (s.str.) // aethiops Paratype! // J. Balfour-Browne det. [name and Paratype! Hw.] (BMNH); 1 ♀, "Para- // type" [circular label with yellow border] "SOUTH AFRICA: // Milnerton, // Diep River, // 21.vi.1948 // A.D. Harrison." [date Hw.] "Brit. Mus. // 1951–35" "Helophorus (s.str.) // aethiops Paratype! // J. Balfour-Browne det." [name and Paratype! Hw.] (BMNH); 1 ♀, "Stn. No. // 319" [319 Hw.] "S. AFRICA // 6ml. S. of Garies // 2,500ft. 18.vii.1954 // J. Balfour-Browne" "Small muddy // ephemeral pool" "J. Balfour-Browne // Brit. Mus. 1954–797" (BMNH); 1 exx., "S. AFRICA // near Paarl // 420ft. 10.viii.1954 // J. Balfour-Browne" "Shallow weedy // rivulet" (BMNH); 1 exx., "Stn. No. // 322" [322 Hw.] "S. AFRICA // Van Rhynsdorp // 400 ft. 19.vii.1954" "shallow grassy // farm dam" "J. Balfour-Browne // Brit. Mus. 1954–797" (BMNH); 1 exx., "Stn. No. // 320" [320 Hw.] "S. AFRICA // Bitterfontein // 1,126ft. 18.vii.1954" "ephemeral road- // side pool" "J. Balfour-Browne // Brit. Mus. 1954–797" (BMNH); 1 ♀, "Para- // type" [circular label with yellow border] "SOUTH AFRICA: // Milnerton, // Diep River, // 28.ix.1948 // A.D. Harrison." [date Hw.] "Helophorus (s.str.) // aethiops Paratype! // J. Balfour-Browne det." [name and Paratype! Hw.] "Type // SAM/Ent. // 3610 [3610 Hw.] (ISAM); 3 ♂♂ 5 ♀♀, "SOUTH AFRICA, W. Cape, 2 Sept 2003, // leg. C.R. Turner, 33º06'11"S 18º25'22"E, alt: 41m, // Pools in field margins, fine silty with crops protruding, // opposite large grain silos on // R45 east of Hopefield" (CBP); 156 exx., "SOUTH AFRICA, W. Cape, 2 Sept 2003, // leg. C.R. Turner, 33º06'11"S 18º25'22"E, alt: 41m, // Pools in field margins, fine silty with crops protruding, // opposite large grain silos on // R45 east of Hopefield" (CTP), all with red paratype labels.

Description. ***Male*** (Fig. 1E). *Head* black, with golden-green aeneous reflection; strongly shining. Granules weak, central seta-bearing pore always evident, but most granules coalesce with adjacent ones into irregular raised areas; discrete granules more evident laterally on frons and clypeus and immediately in front of Y-groove. Y-groove shallow; floor with dense, coarse, rugose punctures, shining as rest of head; stem evenly diverging anteriorly; lateral branches narrow, straight proximally then weakly arcuate laterally in front of eyes. Clypeus slightly elevated in centre; anterior margin weakly arcuate. Labrum with shining, impunctate, basal portion with anterior margin bisinuous around centre; anterior portion with coarse, rugose punctures, each puncture bearing a short, stout, whitish semi-erect seta; anterior margin arcuate with broad, shallow anteromedian emargination. Antennae 8-segmented, yellowish brown, with cupule and club segments darker. Maxillary palpi yellow, apex of terminal segment infuscated; moderately elongate, terminal segment longest, curved and clearly asymmetrical.

Pronotum (Figs 3D & 4D, F) predominantly reddish brown, with golden-green aeneous reflections, particularly on internal and middle intervals; anterior and lateral borders paler, yellowish brown; shining over entire dorsal surface. Broadest between middle and anterior margins; very weakly

arched in frontal and dorsal views and flattened over internal and middle intervals. Anterior margin almost straight over central 0.5, then sinuate to broadly rounded front angles; posterior margin broadly bisinuate around centre. Sides straight over posterior 0.4, then weakly arcuate around broadest point to anterior angles. Lateral margins setose and distinctly minutely crenulated to serrate. Internal and middle intervals flat, distinctly granulate, strongly shining; granules flattened and partly coalescent, but evident, all with pore and seta; granules similar on external interval, but more discrete, surface strongly shining and somewhat rugose. Grooves with dense, somewhat rugose, shallow punctures and small raised areas but no clear, discrete, granules. Median groove narrow and parallel-sided, open anteriorly and posteriorly. Submedian and submarginal grooves open anteriorly and posteriorly. Submedian grooves relatively narrow, weakly sinuate. Submarginal grooves straight, broadest anteriorly and broader than submedian. Marginal grooves curved parallel to the side of pronotum, width uniform. All grooves shallow, particularly median and submedian, with sides rounded; transition between grooves and intervals involving relatively small step.

Elytra (Fig. 1E) brownish-yellow, with limited diffuse infuscation, coalescing into two discrete patches either side of suture on disc; paler spots visible anterior to dark patches. Shape elongate oval, bluntly rounded at apex. In lateral profile flat over anterior 0.5, then gradually descending to apex. Puncture rows weakly striate, particularly laterally; intervals relatively broad and flat.

Legs yellowish-brown, apex of last tarsal segment and claws slightly infuscated. Legs relatively long; swimming hairs distinct and clearly visible on tarsi.

Venter black, with pronotal hypomeron, antennal pocket and epipleura orange-brown to straw yellow. Mentum shining, centre without microreticulation, with sparse, medium punctures; lateral marginal areas with weak isodiametric microreticulation centrally; margins with fine yellow setae, denser towards posterolateral angles. Submentum shining, without microreticulation; anterior 0.5 with sparse, shallow, coarse punctures and fine, hair-like vestiture. Gula and genae rugose, with dense hydrofuge vestiture. Gular sutures well marked as pits anteriorly. Vestiture only absent around margin of compound eyes and their posterolateral corners. Prosternum dull, rugose, with dense hydrofuge vestiture and sparse, long, erect setae approximately 2× length of vestiture. Pronotal hypomeron dull, with dense hydrofuge vestiture. Pronotal epipleura shining, glabrous, with sparse shallow punctures. Anterior antennal pocket well developed, with long, dense setae internally and long, curved setae at posterolateral margins. Elytral epipleura dull, glabrous, narrowing posteriorly at level of metaventrite and continuing until posterior margin of ventrite. Elytral flanks not visible from below. Ventral surface of mesothorax, metathorax and abdomen dull, with dense hydrofuge vestiture and longer, erect setae; longer setae concentrated on centre of metaventrite and abdominal ventrites 2–5; setae on ventrites arising from longitudinal tubercles, which sometimes appear as shining patches. Hind margin of abdominal ventrite 5 weakly crenulate.

Aedeagus (Fig. 2H) elongate, 0.66 mm in length. Basal piece distinctly longer than parameres; outer margins of parameres sinuous approximately 0.5 from apex and then narrowed more abruptly close to apex; interior margins of parameres abruptly widened subapically, then almost straight. Median lobe with apex rounded; sides diverging posteriorly to base of struts, weakly concave; struts slightly longer than tube.

Female. Externally as males, but typically slightly larger in overall body size.

Measurements. Males: Holotype: BL = 4.00 mm; EL = 2.75; EW = 1.60 mm. Paratype: BL = 3.25–4.20 mm; EL = 2.10–2.85; EW = 1.20–1.65 mm. Females: BL = 4.20–4.65 mm; EL = 2.70–3.25 mm; EW = 1.65–1.90 mm.

Variation. This species exhibits some variation, both within and between populations. In particular, the aeneous reflections on the head and pronotum vary from greenish to purplish to absent, with the background colour of the pronotum varying from pinkish brown to yellowish. In some specimens the granulation of the pronotal intervals is less evident than others, but granules, whilst they are weak and flat, are always evident somewhere on each interval. In some specimens the median groove is widened in the middle. The degree of sculpture visible in the pronotal grooves also varies somewhat, this being correlated with the degree of interval granulation evident, but grooves are always as described above in terms of their relative widths, and their rather weakly-defined margins. The degree of elytral infuscation also varies, from almost absent to being present over much of the disc. In the aedeagus, there is variation size (0.58–0.66 mm – all except smallest male examined (BL = 3.25 mm), from Kalabaskraal, Western Cape Province > 0.60 mm) and in the relative lengths of the basal piece and parameres, these sometimes being subequal and the precise shape of the paramere sides and apices between specimens, this variation being seen within populations when slightly longer series are available (Figs 2H–J).

Differential diagnosis. *Helophorus brumopluvialis* sp. nov. is distinguished by its 8-segmented antennae, rather flat, granulate pronotum with a very narrow submedian groove as well as its relatively large aedeagus, usually with relatively broad tips to the parameres. Some paratypes were originally included in the type series of *H. aethiops*.

Etymology. From the Latin *bruma*, winter and *pluvial*, rain, reflecting the distribution and ecology of the species; adjective.

Distribution and ecology. Apparently restricted to areas of the Western and Northern Cape Provinces of South Africa, in regions experiencing predominantly winter rainfall (Fig. 5). Not so far known to overlap geographically with *H. aethiops*. Like the latter species, characteristic of shallow, seasonally flooded waters, typically with aquatic grasses, algae and macrophytes, in this case sites that flood following winter rains. Cytochrome oxidase-I DNA sequence divergence between this species and *H. aethiops* is 5.5–6.0% (I. Ribera, pers. comm.), suggesting that these two species diverged during the Plio-Pleistocene.

Helophorus (*Ropalohelophorus*) *nyandaruaensis* sp. nov.

(Figs 1F, 2K, 3E, 5)

Helophorus aethiopicus (misidentification): Balfour-Browne (1954: 105).

Type locality. Kenya, Abadare (Nyandarua) Mountains, south-west face, 2,600–2,700m, ca. 0°44′S 36°43′E. Likely in "Prairies découvertes" (open meadows) above a forest hut Alluaud and Jeannel travelled to from Naivasha (see Jeannel 1950).

Type material. Holotype: ♂, labelled: "♂" "Afrique or. anglaise // Monts ABERDERE // VERSANT SUD-OUEST // ALLUAUD & JEANNEL" "LISIÈRE INFÉR. DES FORÊTS // et Prairies découvertes // 2600–2700m // Févr. 1912 Stn. 57" "A. d'Orchymont det. // Helophorus s. str.) // aethiopicus Rég." [aethiopicus & Rég. Hw.] "Coll.I.R.Sc.N.R." [blue label] and red Holotype label (RBINS). Paratypes: 1 ♀, "♀" otherwise same data as Holotype (RBINS); 2 exx., same data as Holotype, but Helophorus also Hw. (RBINS); 1 ♂, "♂" "Afrique or. anglaise // Monts ABERDERE // VERSANT SUD-OUEST // ALLUAUD & JEANNEL" "LISIÈRE INFÉR. DES FORÊTS // et Prairies découvertes // 2600–2700m // Févr. 1912 Stn. 57" "A. d'Orchymont det. // Helophorus s. str.) // aethiopicus Rég." [aethiopicus & Rég. Hw.] "Coll. et det. // A. d'Orchymont: // Helophorus // aethiopicus Rég. // R.M.H.N.B. 15.962" [name and describer Hw.] (RBINS); 1 ♂, "♂" "Afrique or. anglaise // Monts ABERDERE // VERSANT SUD-OUEST // ALLUAUD & JEANNEL" "LISIÈRE INFÉR. DES FORÊTS // et Prairies découvertes // 2600–2700m // Févr. 1912 Stn. 57" "A. d'Orchymont det. // Helophorus s. str.) // aethiopicus Rég." [aethiopicus & Rég. Hw.] "compare // à aethiopicus" [Hw.] "Coll.I.R.Sc.N.R." [blue label] (RBINS);1 ♂, "water // tank" [Hw.] "VAN SOMEREN // NGONG SCARP // MAY, 1943" "IMP. INST. ENT. // COLL. NO. 10643" (BMNH); 1 ♀, "water // tank" [Hw.] "VAN SOMEREN // NGONG SCARP // MAY, 1943" "IMP. INST. ENT. // COLL. NO. 10643" "Helophorus (s. str.) // aethiopicus Rég. // J. Balfour-Browne det." [species name Hw.] (BMNH); 2 exx., "AFRIQUE ORle ANGLAISE // NAIROBI // (WA-KIKUYU ET MASAI) // CH. ALLUAUD. 2e SEM. 1903" "Helophorus // pallidipennis Muls." [Hw] on same card (MNHN) all with red paratype labels.

Description. ***Male*** (Fig. 1F). *Head* dark brown, with green aeneous reflections; very strongly shining. Granules weak, central seta-bearing pore always evident, often at least partly confluent over central area of frons and clypeus; discrete granules more evident laterally on frons, close to compound eyes and clypeus laterally, in front of Y-groove. Y-groove relatively deep; floor with scattered pits, shining as rest of head; stem evenly diverging anteriorly; lateral branches narrow, relatively straight. Frons either side of Y-groove stem and clypeus slightly elevated in centre; anterior clypeal margin weakly arcuate, almost straight. Labrum with shining basal portion with sparse micropunctures, anterior margin bisinuous around centre; anterior portion with medium punctures, each puncture bearing a short, stout, whitish semi-erect seta; anterior margin arcuate with shallow anteromedian emargination. Antennae 8-segmented, yellowish brown, with cupule and club segments darker. Maxillary palpi yellow, apex of terminal segment infuscated; moderately elongate, terminal segment longest, curved and clearly asymmetrical.

Pronotum (Fig. 3E) dark brown, with green aeneous reflections; anterior and lateral borders paler brown, anterior pale border narrower than lateral; shining over entire dorsal surface. Broadest between middle and anterior margins; arched in frontal and dorsal views and slightly flattened over internal and middle intervals. Anterior margin weakly bisinuous over central 0.5, then sinuate to broadly rounded front angles; posterior margin broadly bisinuate around centre. Sides straight over posterior 0.3, then weakly arcuate around broadest point to anterior angles. Lateral margins setose and distinctly crenulated to serrate. Internal intervals slightly tumid, granules weak but visible, particularly anteriorly; many reduced to pore and seta centrally and posteriorly; strongly shining. Middle intervals similar to internal, but flatter and granules more evident towards middle. External interval more evidently granulate throughout, particularly on internal side. Grooves shining, with shallow punctures and small raised areas but no clear, discrete, granules. Median groove narrow and rather parallel-sided, open narrowly anteriorly and somewhat wider posteriorly. Submedian and submarginal grooves open anteriorly and posteriorly. Submedian grooves relatively narrow as median, moderately sinuate. Submarginal grooves weakly arcuate, broadest anteriorly and broader than submedian. Marginal grooves curved parallel to the side of pronotum, width uniform. All grooves moderately deep, particularly median and submedian, with margins sloping but distinct; intervals curving down into grooves.

Elytra (Fig. 1F) brownish, with limited diffuse paler markings. Shape elongate oval, bluntly rounded at apex. In lateral profile flat over anterior 0.6, then gradually descending to apex. Puncture rows strongly striate, particularly on disc and anterolaterally; intervals slightly raised, rounded.

Legs pale brown, apex of last tarsal segment and claws infuscated. Swimming hairs distinct and clearly visible on tarsi.

Venter black, with pronotal hypomeron, antennal pocket and epipleura brown to yellow. Mentum shining, centre without microreticulation, with sparse, medium punctures; lateral marginal areas with weak isodiametric microreticulation centrally; margins with fine yellow setae, denser towards posterolateral angles. Submentum shining, without microreticulation; anterior 0.5 with sparse, shallow, coarse punctures and fine, hair-like vestiture. Gula and genae rugose, with dense hydrofuge vestiture. Gular sutures well marked as pits anteriorly. Vestiture only absent around margin of compound eyes and their posterolateral corners. Prosternum dull, rugose, with dense hydrofuge vestiture and sparse, long, erect setae approximately 2× length of vestiture. Pronotal hypomeron dull, with dense hydrofuge vestiture. Pronotal epipleura shining, glabrous, with sparse shallow punctures. Anterior antennal pocket well developed, with long, dense setae internally and long, curved setae at posterolateral margins. Elytral epipleura dull, glabrous, narrowing posteriorly at level of metaventrite and continuing until posterior margin of ventrite. Elytral flanks visible from below, but narrower than epipleura. Ventral surface of mesothorax, metathorax and abdomen dull, with dense hydrofuge vestiture and longer, erect setae; longer setae concentrated on centre of metaventrite and abdominal ventrites 2–5. Hind margin of abdominal ventrite 5 with irregular microserrations in centre only.

Aedeagus (Fig. 2K) elongate, 0.85 mm in length. Basal piece longer than parameres; outer margins of parameres weakly diverging basally, then weakly converging and strongly converging approximately 0.2 from apex;

narrowing to distinctly acuminate tips; interior margins of parameres widening after apex, first 0.5 with different angle to second and with a concave margin. Median lobe with apex bluntly pointed; sides diverging posteriorly to base of struts, distinctly concave; struts approximately 1.25× length of tube.

Female. Externally as males, but slightly larger in overall body size.

Measurements. Holotype: BL = 3.90 mm; EL = 2.65; EW = 1.55 mm. Paratype males: BL = 3.25–3.45 mm; EL = 2.35–2.45 mm; EW = 1.35–1.50 mm. Paratype females: BL = 3.70–4.55 mm; EL = 2.60–3.20 mm; EW = 1.55–1.65 mm.

Variation. Variation evident in size and the degree of paler pigment on elytra. Some paratypes have slightly weaker, or slightly stronger granulation on head and pronotum than in the holotype and a more purplish aeneous sheen. Some variation in size of aedeagus (0.78–0.85 mm), but always very large.

Differential diagnosis. *Helophorus nyandaruaensis* sp. nov. can be separated from all known African species by its very large aedeagus, with acuminate tips to the parameres. In addition, the species has 8-segmented antennae and is relatively robust, with raised, granulate pronotal intervals.

Etymology. Named after the Nyandarua, the Kikuyu name for the Abadares Range, where the holotype was collected; adjective.

Distribution and ecology. To date, known from only three collections, all in mountains of the East African Rift, close to Nairobi, Kenya (Fig. 5). The holotype and most paratypes were taken by Alluaud and Jeannel in 1912, in the southwestern portion of the Abadare (Nyandarua) Range, in open meadows at 2,600–2,700 m. An additional male and female (BMNH) were collected in 1943 by Victor Van Someren on the Ngong Scarp, most likely in the present-day Ngong Hills Forest Reserve, which reaches almost 2,500 m in altitude, southwest of Nairobi. Finally, I have seen two examples in MNHN, collected by Alluaud close to Nairobi in 1903.

Helophorus (*Ropalohelophorus*) *simiensis* sp. nov.

(Figs 1G, 2L, 3F, 5)

Type locality. Ethiopia, Gondar province, Simien Mountains, Inatye (Enatye) plateau, approximately 13°15′N 39°09′E, 4,000 m.

Type material. Holotype: ♂, labelled: "ÄTHIOPIEN: Prov. Gondar // Simien: Inatye 4000m // 17.4.1976 // leg. Löffler" "1997 // H. aethiopicus Rég. // R. B. Angus det." [97, name and describer Hw.], with red holotype label (NMW). Paratypes: 1 ♂ 4 ♀♀, same data as holotype, with red paratype labels (NMW).

Description. ***Male*** (Fig. 1G). *Head* dark brown to black, with strong green to gold aeneous reflection; strongly shining. Granules strong, sometimes coalescent, particularly on lateral margins of Y-groove stem; individual granules most strongly developed inside compound eyes and laterally on clypeus. Y-groove deep; floor of stem with dense, coarse, rugose punctures, extending into base of lateral branches, shining as rest of head; stem strongly diverging anteriorly; lateral branches very narrow, particularly over apical 0.5, broadly arcuate laterally in front of eyes. Clypeus strongly elevated in centre; anterior margin almost straight. Labrum with shining, impunctate, basal portion with anterior margin acuminate at centre; anterior portion with coarse, rugose punctures, each puncture bearing a short, stout, whitish semi-erect seta; anterior margin arcuate with small anteromedian emargination. Antennae 9-segmented, yellowish brown, with cupule and club segments darker. Maxillary palpi yellow, apex of terminal segment infuscated; moderately elongate, terminal segment longest, curved and clearly asymmetrical.

Pronotum (Fig. 3F) reddish brown, with strong green to golden aeneous reflections, particularly on internal and middle intervals; anterior border narrowly and lateral borders more widely paler, yellowish brown; shining over entire dorsal surface. Broadest between middle and anterior margins; weakly arched in frontal and dorsal views and somewhat flattened over internal intervals, particularly anteriorly. Anterior margin slightly concave over central 0.3, then sinuate to broadly rounded front angles; posterior margin broadly bisinuate around centre. Sides straight over posterior 0.4, then weakly arcuate around broadest point to anterior angles. Lateral margins setose and weakly crenulated to serrate. Internal intervals distinctly arched, middle intervals relatively flat, strongly shining; granules distinct, but often partly coalescent with adjacent ones. External interval, with distinct granules, surface strongly shining. Grooves smooth and shining, with coarse, shallow punctures, giving a somewhat rugose appearance in places. Median groove narrowed anteriorly and posteriorly, open at both ends more widely so posteriorly. Submedian and submarginal grooves broadly open anteriorly and posteriorly. Submedian grooves relatively narrow and arcuate. Submarginal grooves weakly arcuate, broader than submedian. Marginal grooves curved parallel to the side of pronotum, width uniform. All grooves relatively shallow, with intervals curving down towards their margins, which are well-defined but somewhat sloping rather than vertical.

Elytra (Fig. 1G) brown, with diffuse paler markings, particularly posteriorly. Shape elongate oval, sides rounded to bluntly rounded apex. In lateral profile flat over anterior 0.5, then gradually descending to apex. Puncture rows moderately striate, particularly laterally; intervals relatively broad and weakly arched, particularly so laterally.

Legs yellowish-brown, apex of last tarsal segment and claws infuscated. Swimming hairs distinct and clearly visible.

Venter black, with pronotal hypomeron, antennal pocket and pseudepipleura and epipleura brown. Mentum shining, centre without microreticulation, with sparse, medium punctures; lateral marginal areas with weak isodiametric microreticulation centrally; margins with fine yellow setae, denser towards posterolateral angles. Submentum shining, without microreticulation; anterior 0.5 with sparse, shallow, coarse punctures and fine, hair-like vestiture. Gula and genae rugose, with dense hydrofuge vestiture. Gular sutures well marked as pits anteriorly. Vestiture only absent around margin of compound eyes and their posterolateral corners. Prosternum dull, rugose, with dense hydrofuge

vestiture and sparse, long, erect setae approximately 2× length of vestiture. Pronotal hypomeron dull, with dense hydrofuge vestiture. Pronotal epipleura shining, glabrous, with sparse shallow punctures. Anterior antennal pocket well developed, with long, dense setae internally and long, curved setae at posterolateral margins. Elytral epipleura dull, glabrous, narrowing posteriorly at level of metaventrite and continuing until posterior margin of ventrite. Elytral flanks not visible from below. Ventral surface of mesothorax, metathorax and abdomen dull, with dense hydrofuge vestiture and longer, erect setae; longer setae concentrated on centre of metaventrite and abdominal ventrites 2–5; setae on ventrites arising from longitudinal tubercles, which sometimes appear as shining patches. Hind margin of abdominal ventrite 5 weakly crenulate.

Aedeagus (Fig. 2L) elongate, 0.55 mm in length. Parameres longer than basal piece; outer margins of parameres straight basally, then broadly arcuate to apex; interior margins of parameres sloping strongly at apex, then rather straight, apices bluntly rounded. Median lobe narrow, with weakly pointed apex; sides diverging slightly posteriorly to base of struts, weakly concave; struts distinctly shorter than tube.

Female. Externally as males, but on average slightly larger.

Measurements. Holotype: BL = 3.40 mm; EL = 2.45 mm; EW = 1.45 mm. Paratype male: BL = 3.15 mm; EL = 2.20; EW = 1.40 mm. Paratype females: BL = 3.55–3.85 mm; EL = 2.60–2.75 mm; EW = 1.55–1.70 mm.

Variation. Some variation in the degree of development of pronotal granulation, some specimens having this somewhat stronger than in the holotype. In some specimens the aeneous reflections on the head and pronotum are purplish as well as green/golden.

Differential diagnosis. This new species has 9-segmented antennae and is closest to *H. aethiopicus*, from which it can be distinguished on the basis of its larger body size and relatively granulate pronotum, with a more weakly angled submedian groove. In addition the aedeagus is larger and the parameres more expanded at their apices. These differences are relatively slight, but are consistent across all specimens of the two species that I have examined, including a relatively large number of *H. aethiopicus* from three separate localities. Given experience of *Helophorus* in the Palaearctic, the differences strongly suggest that two species are involved here.

Etymology. Named in reference to the type locality in the Simien Mountains; adjective.

Distribution and ecology. Known only from the type locality at 4,000 m in the Simien Mountains, in northern Ethiopia (Fig. 5).

Key to the Afrotropical species of *Helophorus*

1 Antennae 9-segmented. 2
– Antennae 8-segmented. 4
2 Pronotal internal and middle intervals smooth, granulation reduced to pores and setae over most of surface (Figs 1D & 3C); median lobe of aedeagus with struts as long as tube (Fig. 3G); habitus relatively robust (Fig. 1D), body length 3.45–4.0 mm. .... ***H. cooperi*** Orchymont, 1947
– Pronotal internal and middle intervals with evident granulation over most of surface (Figs 1A & G, 3A & F); median lobe of aedeagus with struts distinctly shorter than tube. 3
3 Granulation on pronotal internal and middle intervals weaker (Figs 1A, 3A); prontoal submedian groove more strongly angled medially (Fig. 3A); parameres relatively straight, with evenly pointed tips (Figs 2A–B); body size smaller, 2.60–3.50 mm; aedeagus smaller, 0.45 mm. ... ***H. aethiopicus*** Régimbart, 1907
– Granulation on pronotal internal and middle intervals stronger (Figs 1G, 3F); pronotal submedian groove more weakly angled medially (Fig. 3F); paramere tips more broadly rounded (Fig. 3L); body size larger, 3.15–3.85 mm; aedeagus larger, 0.55 mm. .... ***H. simiensis*** **sp. nov.**
4 Aedeagus very large, 0.78–0.85 mm, parameres with acuminate tips (Fig. 2K); pronotal intervals raised and granulate (Figs 1F, 3E); body robust (Fig. 1F) and relatively large, 3.25–4.55 mm; species from East African Rift. ..... ***H. nyandaruaensis*** **sp. nov.**
– Aedeagus smaller, maximum length 0.66 mm, paramere tips various, but not strongly acuminate (Figs 2C–F, H–J); pronotal intervals flatter (Figs 1B–C, E, 3B, E, 4C–F). 5
5 Pronotal submedian groove broader, granulation on middle and internal intervals weaker (Figs 1B–C, 3B, 4C, E); walls of pronotal grooves straighter and sharper (Figs 4C, E); punctures of elytral striae larger and intervals narrower and more arched apically (Fig. 4G); aedeagus smaller, 0.50–0.55 mm, parameres with relatively narrow apices (Figs 2C–F). .... ***H. aethiops*** J. Balfour-Browne, 1954
– Pronotal submedian groove narrower, granulation on middle and internal intervals stronger (Figs 1E, 3D, 4D, F); walls of pronotal grooves more rounded and indistinct (Figs 4D, F); punctures of elytral striae smaller and intervals broader and flatter apically (Fig. 4H); aedeagus larger, 0.58–0.66 mm, parameres usually with relatively broad apices (Figs 2H–J). .... ***H. brumopluvialis*** **sp. nov.**

Discussion

The *Helophorus* fauna of the Afrotropical Region, whilst still relatively modest, is now shown to be much more diverse than previously appreciated. Given the limited amount of material available from East African mountains, particularly those between Kenya and South Africa, it seems highly probable that additional species remain undetected. Whilst the absence of a molecular phylogeny makes detailed discussion of the geographical and evolutionary origins of Afrotropical *Helophorus* somewhat speculative, known species likely stem from two independent colonisation events, one comprising species with 8-, the other 9-segmented antennae; antennal segmentation apparently

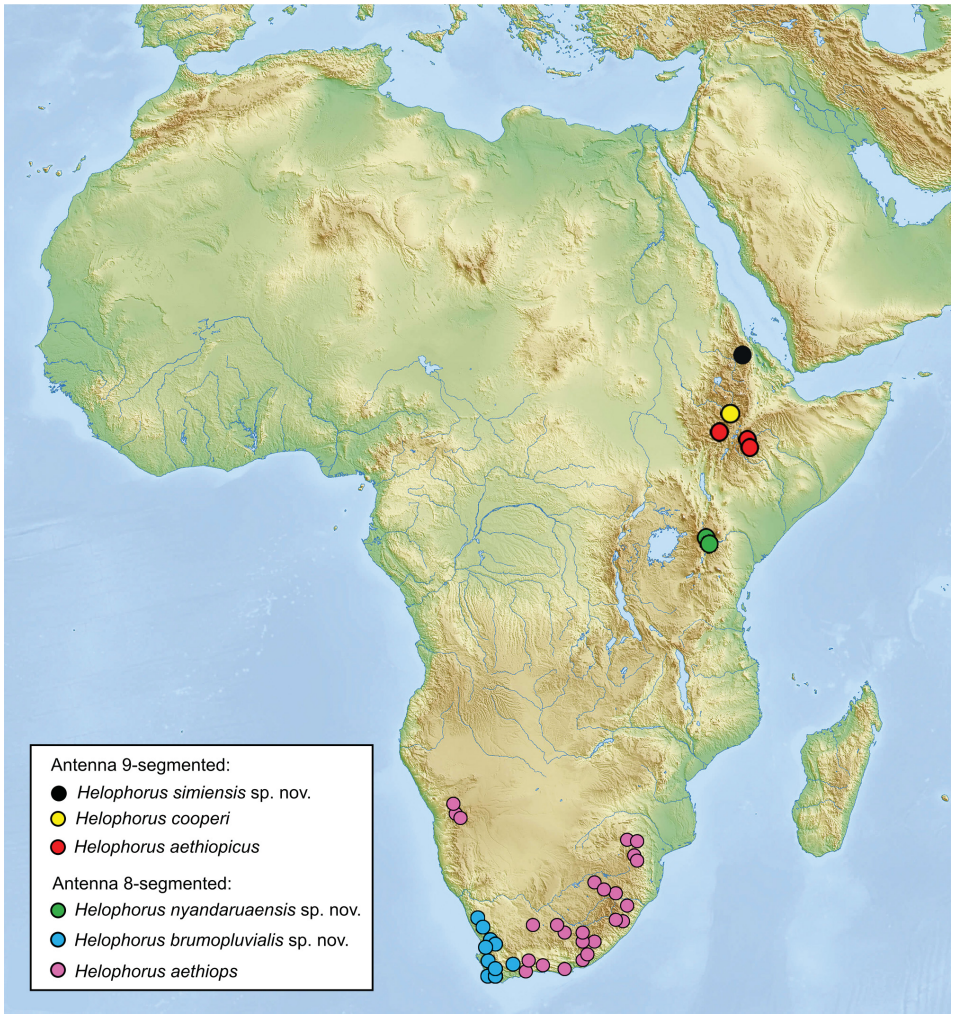

Fig. 5. Afrotropical *Helophorus,* known distributions. Map by https://mapswire.com.

being constant in known Afrotropical species. Taxa with 9-segmented antennae all share a similar habitus, being relatively small, short beetles, restricted to Ethiopia. Those with 8 antennal segments are generally more robust and distributed in Kenya and South Africa. Clearly this hypothesis should be tested in the future using DNA. The distribution of the two southern African species *H. aethiops* and *H. brumopluvialis* sp. nov., is apparently driven by rainfall seasonality, the former being widespread in summer and year-round rainfall zones, the latter restricted to areas with strong winter rainfall. COI sequence data for this species pair suggests that they diverged during the Plio-Pleistocene, this likely being driven by changes in the intensity, extent and location of the winter rainfall climate during this time period (deMenocal 2004, Chase & Meadows 2007). Speciation through seasonal allochrony is particularly well studied in sympatric, phytophagous insects, but can occur under any geographical scenario, including allo-parapatry as envisaged here (Taylor & Friesen 2017).

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