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Two new species of the genus *Symphylella* (Symphyla, Scolopendrellidae) from East China

Ya-Li Jin[1], Yun Bu[1]

1 *Natural History Research Center, Shanghai Natural History Museum, Shanghai Science & Technology Museum, Shanghai, 200041, China*

Corresponding author: Yun Bu (buy@sstm.org.cn)

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Abstract

Symphylella minuta **sp. nov.** and *Symphylella communa* **sp. nov.** from China are described and illustrated. *Symphylella minuta* **sp. nov.** is characterized by the delicate and minute body, a well-developed and thin central rod with a vestige of a transverse suture in the middle, eight setae on the first tergite, pointed processes on the tergites, and short cerci with sparse setae. *Symphylella communa* **sp. nov.** is characterized by the chaetotaxy of the first tergite with 4+4 setae, processes of the tergites somewhat longer or the same length with broad, most of lateromaginal setae long, anterolateral setae of tergites 2–4, 6, 7, 9, and 10 distinctly longer than other lateromarginal setae, approximately as long as the process of the same tergite, and cerci with numerous subequal and slightly curved setae. In addition, the chaetotaxic variation on the tergites, the distribution, the habitat, and the feeding habit of the genus *Symphylella* are discussed.

Keywords

Chaetotaxy, morphology, Myriapoda, taxonomy

Introduction

Symphyla is an ignored group of myriapods with about 200 species reported in the world and only six species are known from China (Bu and Jin 2018; Jin and Bu 2018, 2019; Jin et al. 2019). The genus *Symphylella* Silvestri, 1902 is a common group of symphylans in soil and litter, with 49 cosmopolitan species recorded (Szucsich and Scheller 2011; Bu and Jin 2018; Jin et al. 2019). However, the study of the diversity of this group in China is still insufficient, with only two species recorded so far, *S. macropora* Jin & Bu, 2019 and *S. zhongi* Jin & Bu, 2019, both from Tibet (Jin et al. 2019). From 2012 to 2020, the symphylans in East China were comprehensively investigated in several projects and plenty of specimens were obtained. After careful identification, two new species of the genus *Symphylella* were distinguished and are described in this paper.

Materials and methods

Specimens were collected using Berlese-Tullgren funnels and preserved in 80% ethanol. They were mounted under slides using Hoyer's solution and dried in an oven at 50 °C. Observations were performed under a phase contrast microscope (Leica DM 2500). Photographs were taken with a digital camera installed on the microscope (Leica DMC 4500). Line drawings were done using a drawing tube. All specimens are deposited in the collections of Shanghai Natural History Museum (**SNHM**), Shanghai, China.

Results

Taxonomy

Family Scolopendrellidae Bagnall, 1913

Genus *Symphylella* Silvestri, 1902

Type species. *Symphylella isabellae* (Grassi, 1886), described from Italy.

***Symphylella minuta* Jin & Bu, sp. nov.**
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Figures 1–3, Tables 1–3

Diagnosis. *Symphylella minuta* sp. nov. is characterized by the delicate and minute body, well-developed but thin central rod with a vestige of a transverse suture in the middle, eight setae on first tergite, pointed processes on tergites, and short cerci with sparse setae.

Material examined. ***Holotype***, female (slide no. JS-WX-SY2017020) (SNHM), China, Jiangsu Province, Wuxi City, Daji Mountain, extracted from soil samples of broad-leaf forest, alt. 5 m, 31°32'N, 120°12'E, 9-X-2017, coll. Y. Bu. ***Paratypes***, 1 female (slide no. JS-WX-SY2017031) (SNHM), same data as holotype; 2 females (slides no. JS-WX-SY2020001, JS-WX-SY2020002) (SNHM), ibidem, 14-VII-2020, coll.

Y. Bu; 3 females (slides no. SH-DJS-SY2015112, SH-DJS-SY2015114) (SNHM), China, Shanghai, Dajinshan Island, extracted from soil samples of broad-leaf forest, alt. 103 m, 30°41'N, 121°26'E, 22-IX-2015, coll. Y. Bu & Y. L. Jin; 3 females (slides no. ZJ-JLS-SY2019001, ZJ-JLS-SY2019002) (SNHM), China, Zhejiang, Lishui City, Suichang County, Jiulongshan National Nature Reserve, extracted from soil samples of broad-leaf forest, alt. 703 m, 28°13'N, 118°31'E, 27-V-2019, coll. Y. Bu & J. Y. Li. 1 female (slide no. ZJ-GTS-SY2012005) (SNHM), China, Zhejiang, Gutian Mountain, extracted from soil samples of broad-leaf forest, alt. 800 m, 29°15'N, 118°06'E, 11-IV-2012, coll. Y. Bu et al.; Non-type specimens: 7 juveniles with 8–10 pairs of legs, China, Shanghai, Dajinshan Island, extracted from soil samples of broad-leaf forest, alt. 103 m, 30°41'N, 121°26'E, 22-IX-2015, coll. Y. Bu & Y. L. Jin; 1 juvenile with 10 pairs of legs, China, Zhejiang, Lishui City, Suichang County, Jiulongshan National Nature Reserve, extracted from soil samples of broad-leaf forest, alt. 703 m, 28°13'N, 118°31'E, 27-V-2019, coll. Y. Bu & J. Y. Li; 3 juveniles with 9–10 pairs of legs, China, Zhejiang, Gutian Mountain, extracted from soil samples of broad-leaf forest, alt. 800 m, 29°15'N, 118°06'E, 11-IV-2012, coll. Y. Bu et al.; 1 juvenile with 10 pairs of legs, ibidem, 24-IV-2013; 1 juvenile with 10 pairs of legs, ibidem, 16-V-2012; 1 juvenile with 9 pairs of legs, ibidem, 19-VI-2012; 1 juvenile with 7 pairs of legs, ibidem, 15-VII-2012; 2 juveniles with 7 and 9 pairs of legs, ibidem, 14-X-2012; 2 juveniles with 9–10 pairs of legs, ibidem, 17-XI-2012, coll. Y. Bu et al.

Description. Adult body 1.5 mm long in average (1.2–2.2 mm, n = 8), holotype 1.4 mm (Fig. 1A).

Head length 150–170 μm, width 133–158 μm, with widest part somewhat behind the middle on a level with the points of articulation of mandibles. Central rod well developed but thin, with a vestige of a transverse suture in the middle. Anterior branches normally developed, without median branches. Dorsal side of head moderately covered with setae of different length, longest setae (18–25 μm) located most anterior on head, at least 3.0 times as long as central ones (4–6 μm). Cuticle of anterolateral part of head with rather coarse granules, around Tömösváry organ with moderate granules, other area with fine and faint granulation (Fig. 1F).

Tömösváry organ globular, diameter 11–14 μm, about half of greatest diameter of third antennomere (24–27 μm), opening small and round (5–8 μm), with distinct vertical inner striate (Fig. 1F).

Mouthparts. Mandible with two fused lamellae and 12 teeth in total (Fig. 3A). First maxilla has two lobes, inner lobe with four hooked teeth, palp bud-like and pointed (Fig. 3D). Anterior part of second maxilla with many small protuberances each carries one seta, distal setae thicker and spiniform; posterior part with sparse setae. Cuticle of maxilla and labium covered with dense pubescence (Fig. 1G).

Antennae with 14–19 antennomeres (holotype with 19 on left, 14 on right), length 320–380 μm (350 μm in holotype), about 0.2 of body length. First antennomere cylindrical, greatest diameter almost two times wider than long (23–27 μm, 14–16 μm), with three or four setae on inner side, longest inner seta 8–10 μm, outer side without seta. Second antennomere wider (22–29 μm) than long (16–19 μm),

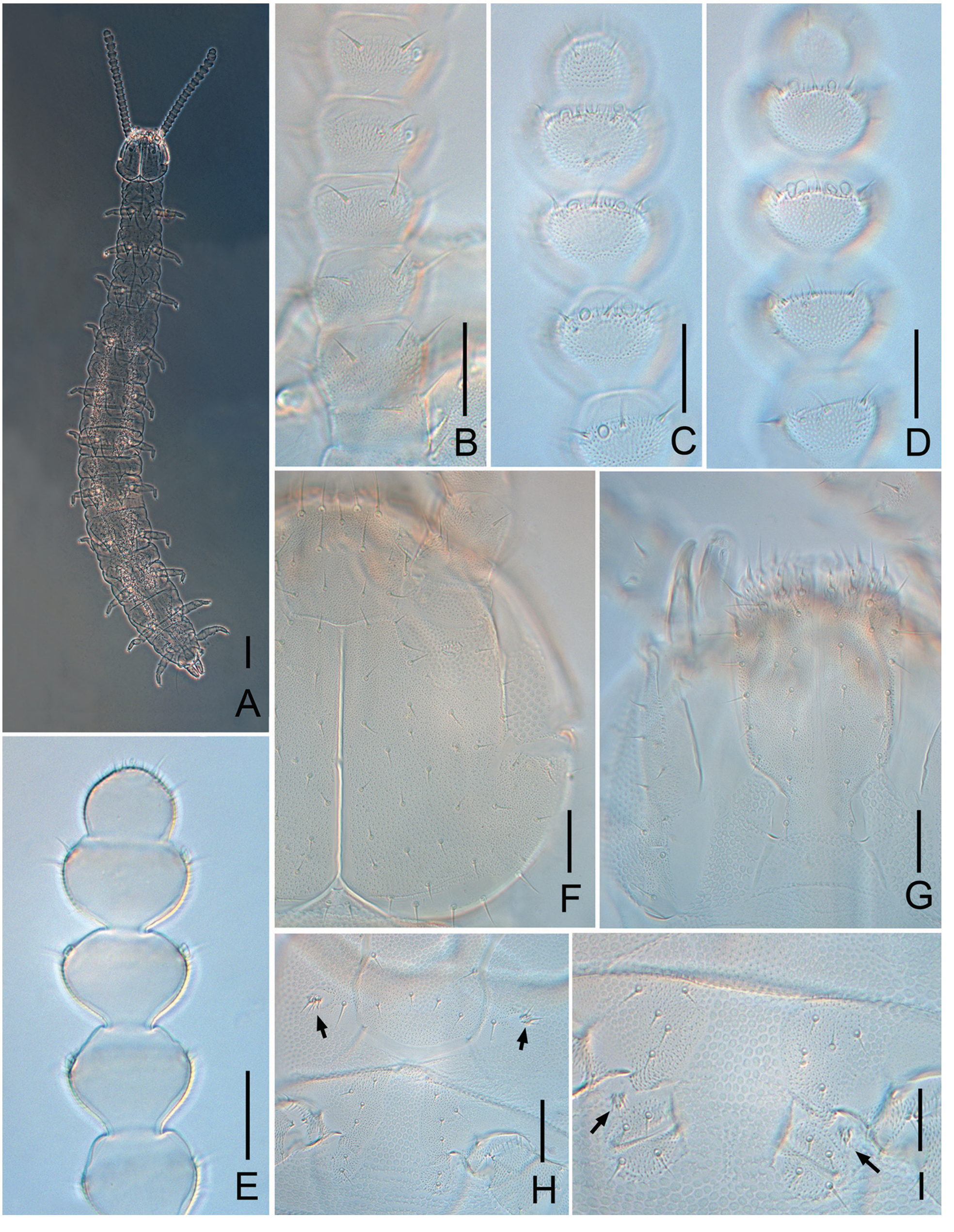

Figure 1. *Symphylella minuta* sp. nov. **A** habitus **B** left antenna, 1st–6th antennomeres, dorsal view **C** distal five antennomeres, dorsal view **D** distal five antennomeres, ventral view **E** distal five antennomeres, show lateral organs **F** head, right side, dorsal view **G** head, ventral view **H** first pair of legs (arrows indicate the reduced legs) and coxa of leg 2 **I** styli, and coxal sacs on base of 3rd leg (arrows indicate styli). Scale bars: 100 μm (**A**); 20 μm (**B–I**).

Table 1. Numbers of setae and sensory organs of antennae (holotype).

Antennomeres	No. of primary whorl setae	No. of secondary whorl setae	Rudimentary spined sensory organs	Cavity-shaped organs on dorsal side	Bladder-shaped organs
1st	4				
2nd	7				
3rd	7				
4th	8		1		
5th	8				
6th	8				
7th	8			1	
8th	9			1	
9th	9			1	
10th	9			1	
11th	9			1	
12th	9			1	
13th	8		1	1	
14th	11	1	1	1	
15th	10	4	1	1	2
16th	12	4		1	5
17th	11	5		1	12
18th		5		2	9

with six to eight setae evenly inserted around the antennal wall with interior setae (10–18 μm) slightly longer than exterior ones (6–7 μm). Chaetotaxy of third antennomere similar to preceding ones. Setae on proximal antennomeres longer than on distal ones. Proximal antennomeres with only primary whorl of setae, middle and subapical antennomeres with secondary whorl setae present. Three kinds of sensory organs observed on antenna: rudimentary spined sensory organs on dorsal side of middle antennomeres (Figs 1C, 3C); cavity-shaped organs on antennomeres 5–19 (Figs 1C, 3C); bladder-shaped organs on antennomeres 7–14 next to apical one increasing in number on subapical antennomeres to a maximum of 12 (Figs 1D, E, 3C). Apical antennomere subspherical, somewhat wider than long (width 22 μm, length 13–17 μm), with 10–13 setae on distal half; three or four spined sensory organs consisting of three or four curved spines around a central pillar in depressions on distal surface (Figs 1E, 3B). All antennomeres covered with short pubescence. Chaetotaxy and sensory organs of antennae of holotype are given in Table 1.

Trunk with 17 dorsal tergites. Tergites 2–13 and 15 each with one pair of sharp triangular processes. Length from base to tip of processes distinctly longer than its basal width except for the tergites 4, 7, 10 and 13, in which processes are almost as broad as long; basal distance between processes of tergites distinctly longer than their length from base to tip (Table 2). All processes with end-swellings. Anterolateral setae on all tergites longer than other lateromarginal setae, about 0.6–0.7 of the length of processes on same tergite. Inserted setae (setae between inner basal seta and apical setae) absent. All tergites pubescent (Fig. 2A–H).

Tergites. Tergite 1 reduced, with eight short setae in a row. Tergite 2 complete, with two triangular posterior processes, four lateromarginal setae, one central seta, anterolateral setae 0.6–0.7 of length of process, longer than other lateromarginal ones,

Table 2. Chaetotaxy of tergites (holotype in brackets).

No. of tergites	lateromarginal	Central setae	Other setae
1st		8*	
2nd	4 (4)	1 (1)	4 (4)
3rd	4–5 (5)	1–2 (1)	9–10 (9)
4th	4 (4)	1–3 (2)	4–9 (4)
5th	4 (4)	2 (2)	4–5 (4)
6th	4–5 (5)	2–3 (2)	10–12 (10)
7th	4 (4)	2–3 (2)	4–5 (4)
8th	4 (4)	2 (2)	4–6 (4)
9th	5 (5)	2 (2)	10–12 (12)
10th	4 (4)	2–3 (2)	4–5 (4)
11th	4 (4)	2 (2)	4 (4)
12th	5 (5)	2 (2)	8–15 (14)
13th	4 (4)	2–3 (3)	4 (4)
14th			5–14 (5)
15th	4–5 (5)	1–2 (2)	6–10 (10)
16th			4–13 (4)
17th			6–17 (6)

* With 8 setae in a row.

Table 3. Measurements of tergites and processes (mean ± se, in μm, n = 6) (holotype in brackets).

No. of tergites	Length	Width	Length of processes	Basal width of processes	Basal distance between processes
1st	24 ± 3 (20)	96 ± 8 (108)			
2nd	37 ± 2 (40)	100 ± 6 (108)	21 ± 2 (23)	18 ± 2 (21)	31 ± 3 (28)
3rd	64 ± 5 (70)	106 ± 1 (108)	22 ± 1 (24)	16 ± 4 (20)	30 ± 3 (30)
4th	39 ± 5 (43)	114 ± 5 (120)	20 ± 2 (22)	22 ± 3 (25)	39 ± 1 (37)
5th	40 ± 2 (43)	103 ± 4 (108)	25 ± 3 (25)	20 ± 1 (21)	42 ± 1 (43)
6th	77 ± 6 (85)	135 ± 11 (135)	27 ± 2 (30)	21 ± 3 (26)	42 ± 4 (40)
7th	43 ± 4 (45)	136 ± 11 (150)	24 ± 2 (26)	24 ± 2 (27)	49 ± 4 (50)
8th	45 ± 4 (50)	118 ± 11 (135)	25 ± 4 (31)	21 ± 2 (24)	49 ± 4 (50)
9th	79 ± 8 (85)	154 ± 10 (155)	28 ± 2 (31)	20 ± 3 (24)	48 ± 6 (55)
10th	44 ± 6 (45)	148 ± 19 (160)	24 ± 2 (26)	90 ± 3 (27)	52 ± 3 (55)
11th	36 ± 5 (38)	120 ± 4 (125)	24 ± 4 (29)	20 ± 2 (22)	53 ± 1 (53)
12th	76 ± 8 (85)	141 ± 6 (150)	24 ± 1 (24)	21 ± 5 (19)	51 ± 5 (58)
13th	45 ± 4 (50)	136 ± 13 (155)	23 ± 3 (27)	22 ± 3 (27)	54 ± 4 (59)
14th	47 ± 5 (50)	125 ± 24 (160)			
15th	65 ± 7 (75)	135 ± 11 (150)	22 ± 2 (25)	20 ± 3 (22)	44 ± 8 (53)
16th	53 ± 7 (63)	113 ± 8 (125)			
17th	74 ± 3 (75)	81 ± 7 (75)			

processes 1.1 or 1.2 times as long as broad, basal distance between processes 1.2–1.7 times as long as their length (Fig. 2A). Tergite 3 complete, broader and longer than preceding one with ratios of 0.6–0.8, 1.2–2, and 1.2–1.5 respectively, four or five lateromarginal setae (Fig. 2B). Tergite 4 broader than tergite 3, with ratios 0.7–0.9, 0.9–1, and 1.7–2.2 respectively, four lateromarginal setae (Fig. 2C). Chaetotaxy of tergites 5–7, 8–10, and 11–13 similar as tergites 2–4 (Fig. 2D, E). Pattern of alternating tergite lengths of two short tergites followed by a long tergite only disrupted at the caudal end (Table 2). Tergites 14 and 16 without processes, with 5–14 and 4–13 setae respectively (Fig. 2F, H). Tergite 17 with 6–17 setae. Chaetotaxy and measurements of tergites are given in Tables 2, 3.

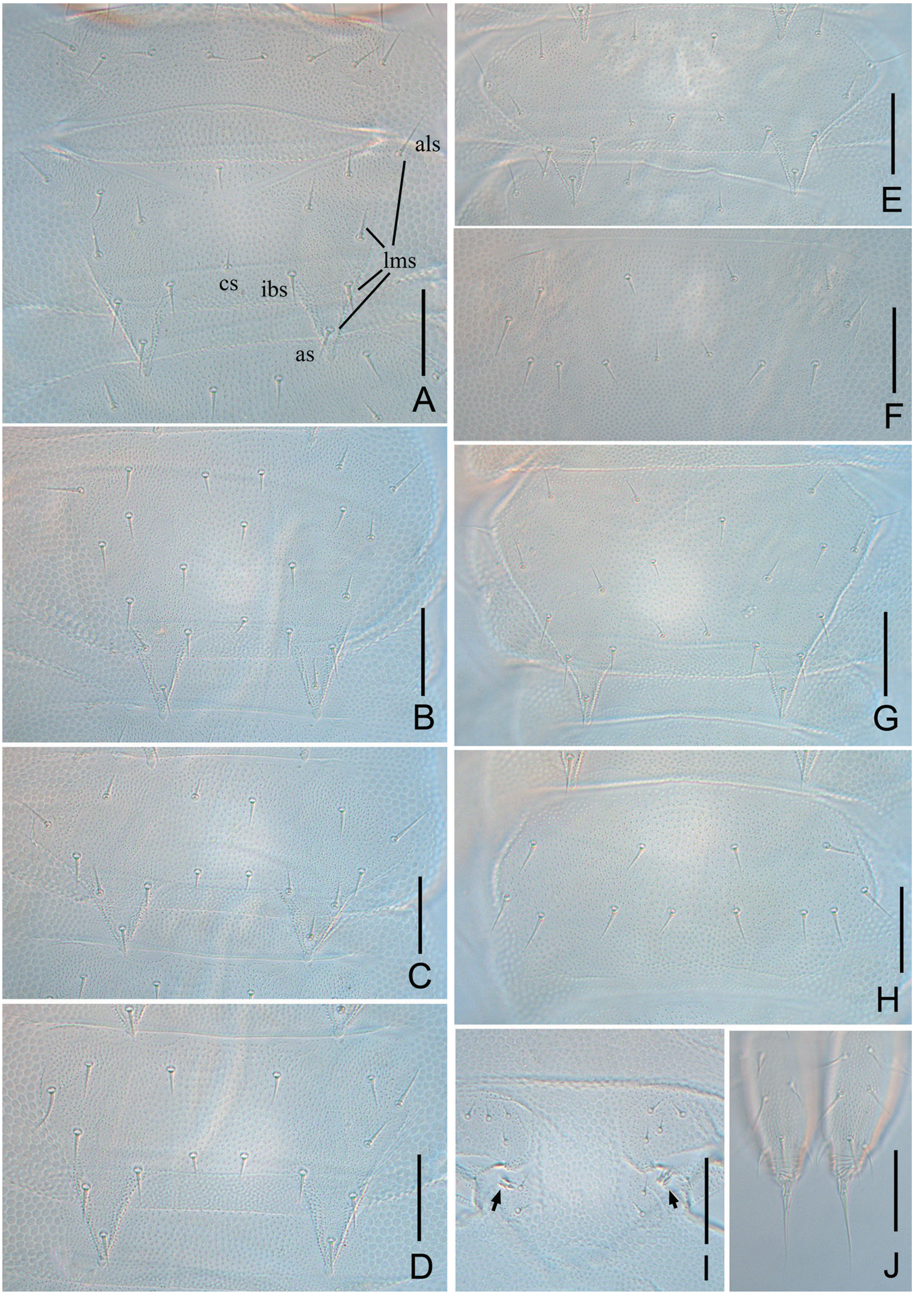

Figure 2. *Symphylella minuta* sp. nov. **A** 1st and 2nd tergites (als-anterolateral seta, as-apical seta, cs-central seta, ibs-inner basal seta, lms-lateromarginal seta) **B** 3rd tergite **C** 4th tergite **D** 5th tergite **E** 13th tergite **F** 14th tergite **G** 15th tergite **H** 16th tergite **I** styli and base of 4th leg (arrows indicate styli) **J** cerci, dorsal view. Scale bars: 20 µm.

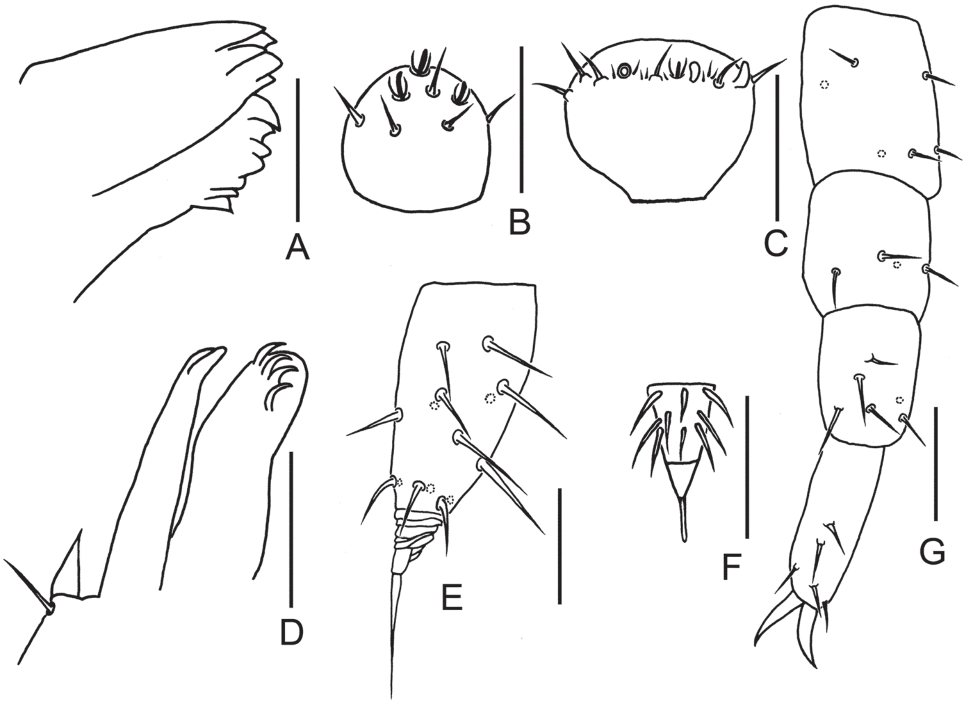

Figure 3. *Symphylella minuta* sp. nov. **A** mandible **B** right apical antennomere, dorsal view **C** right 14th antennomere, dorsal view **D** first maxilla **E** right cercus, dorsal view **F** stylus on base of 4th leg, right side **G** 12th leg. Scale bars: 20 μm (**A–E, G**); 5 μm (**F**).

Legs. First pair of legs reduced to two small hairy cupules, each with two long setae (Fig. 1H). Basal areas of legs 2–12 each with four to six setae (Figs 1H, I, 2I). Leg 12 about 0.1 of the body (Fig. 3G). Trochanter 1.1–1.7 times longer than wide (30–46 μm, 24–35 μm), with six subequal setae totally. Femur almost as long as wide (19–25 μm, 20–23 μm), with four setae, three dorsal ones (9–12 μm) distinctly longer than ventral one (5–6 μm); femur pubescent dorsally, laterally with cuticular thickenings in pattern of scales. Tibia nearly 1.2–2.3 times longer than wide (20–26 μm, 11–18 μm), with four or five dorsal setae and one or two ventral setae, longest one 10–12 μm. Tarsus subcylindrical, 2.3–3.0 times as long as wide (16–30 μm, 10–12 μm) with four dorsal setae: two straight and protruding, two slightly curved and depressed; longest setae (20–22 μm) about same length of greatest width of podomere; one to three ventral setae close to claw and distinctly shorter than dorsal ones. Claws curved, anterior one somewhat longer than posterior one, the latter more curved than the former. All legs covered with dense pubescences except areas with cuticular thickenings.

Coxal sacs present at bases of legs 3–9, fully developed, each with three to five setae on surface (Fig. 1I). Relevant area of leg 2, 11 and 12 replaced by two, two or three, and one to three setae respectively (Figs 1H, 2I).

Styli present at base of legs 3–12, subconical (length 2–4 μm, width 2–3 μm), basal part with straight hairs; with a distal blunt apex (2–3 μm) (Figs 1I, 2I, 3F).

Sense calicles with smooth margin to pit, about same length as outer diameter. Sensory seta inserted in cup center, extremely long (90–100 μm).

Cerci short and stout (Figs 1A, 2J, 3E), about one-third of head and one-half of length of leg 12, 2.5 times as long as its greatest width (48–55 μm, 20–22 μm), inserted with sparse subequal setae, six to eight dorsal, five or six ventral, one or two outer, most setae straight, a whorl of six distal setae slightly curved, longest outer seta (14–16 μm) slightly longer than greatest width of cerci, terminal area (8–17 μm) short, 0.3–0.6 time as long as greatest width of cerci, circled by six to eight layers of curved ridges, terminal seta (20–23 μm) long, distinctly longer than terminal area.

Etymology. The species name "*minuta*" refers to the delicate and minute body of the species.

Distribution. China (Jiangsu, Shanghai, Zhejiang).

Remarks. *Symphylella minuta* sp. nov. is similar to *S. oligosetosa* Scheller, 1971 from India and Sri Lanka in the shape of the central rod on head and the shape and chaetotaxy of the tergites. They can be distinguished by the chaetotaxy of the first tergite (eight setae in *S. minuta* sp. nov. vs six in *S. oligosetosa*), shape of the processes (pointed and with swollen ends in *S. minuta* sp. nov. vs strongly pointed and without swollen ends in *S. oligosetosa*), shape and chaetotaxy of cerci (short and stout, about 2.5 times as long as wide in *S. minuta* sp. nov. vs slender, 3.5–3.6 times as long as wide in *S. oligosetosa*). It is also similar to *S. abbreviata* Scheller, 1971 from Sri Lanka in the chaetotaxy of the tergites and shape of the processes, but can be easily separated by the chaetotaxy of the first tergite (with eight setae in *S. minuta* sp. nov. vs six setae in *S. abbreviata*), shape of the third tergite (without indentation in *S. minuta* sp. nov. vs with a distinct middle lateromarginal indentation in *S. abbreviata*), shape of cerci (tapering in *S. minuta* sp. nov. vs with outer side strongly bulging in *S. abbreviata*).

Symphylella communa **Jin & Bu, sp. nov.**

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Figures 4–6, Tables 4–6

Diagnosis. *Symphylella communa* sp. nov. is characterized by the chaetotaxy of the first tergite composed by 4+4 setae, processes of tergites somewhat longer or the same length with broad, most of lateralmaginal setae long, anterolateral setae of tergites 2–4, 6, 7, 9, and 10 distinctly longer than other lateromarginal setae, approximately as long as processes of the same tergite, cerci with numerous subequal and slightly curved setae.

Material examined. ***Holotype***, male (slide no. SH-DJS-SY2015048) (SNHM), China, Shanghai, Dajinshan Island, extracted from soil samples of broad-leaf forest, alt. 103 m, 30°41'N, 121°26'E, 30-VI-2015, coll. Y. Bu & Y. L. Jin. ***Paratypes***, 1 male (slide no. SH-DJS-SY2015023) (SNHM), 10 females (slides no. SH-DJS-SY2015001, SH-DJS-SY2015018–SH-DJS-SY2015022, SH-DJS-SY2015024, SH-

DJS-SY2015025, SH-DJS-SY2015048, SH-DJS-SY2015055) (SNHM), same data as holotype; 2 males (slides no. SH-DJS-SY2015099, SH-DJS-SY2015108) (SNHM), 1 female (slide no. SH-DJS-SY2015107) (SNHM), ibidem, 22-IX-2015; 4 males (slides no. SH-DJS-SY2015083, SH-DJS-SY2015124, SH-DJS-SY2015125) (SNHM), 5 females (slides no. SH-DJS-SY2015058, SH-DJS-SY2015059, SH-DJS-SY2015079, SH-DJS-SY2015122, SH-DJS-SY2015123) (SNHM), ibidem, extracted from soil samples of bamboo forest, 22-IX-2015, coll. Y. Bu & Y. L. Jin; 5 females (slides no. SH-DJS-SY2015117, SH-DJS-SY2015118, SH-DJS-SY2015120, SH-DJS-SY2015121) (SNHM), ibidem, extracted from soil samples of broad-leaf forest, 22-IX-2015, coll. Y. Bu & Y. L. Jin; 1 female (slide no. ZJ-GTS-SY2012018) (SNHM), 1 male (slide no. ZJ-GTS-SY2012009) (SNHM), Zhejiang, Gutian Mountain, extracted from soil samples of broad-leaf forest, alt. 800 m, 29°15'N, 118°06'E, 11-IV-2012, coll. Y. Bu et al.; 1 male (slide no. ZJ-GTS-SY2012021) (SNHM), ibidem, 16-V-2012; 1 female (slide no. ZJ-GTS-SY2012041) (SNHM), ibidem, 19-VI-2012; 1 female (slide no. ZJ-GTS-SY2012045) (SNHM), ibidem, 14-X-2012; 1 female (slide no. ZJ-GTS-SY2012054) (SNHM), ibidem, 17-XI-2012, coll. Y. Bu et al.; 4 females (slides no. JS-WX-SY2017012, JS-WX-SY2017017, JS-WX-SY2017018, JS-WX-SY2017033) (SNHM), 1 male (slide no. JS-WX-SY2017035) (SNHM), China, Jiangsu, Wuxi, Daji Mountain, extracted from soil samples of broad-leaf forest, alt. 5 m, 31°32'N, 120°12'E, 9-X-2017, coll. Y. Bu. Non-type specimens: 37 juveniles with 7–10 pairs of legs, same data as holotype; 6 juveniles with 7–10 pairs of legs, ibidem, 22-IX-2015; 32 juveniles with 7–10 pairs of legs, 22-IX-2015; 8 juveniles with 7–10 pairs of legs, 23-IX-2015, ibidem, extracted from soil samples of bamboo forest, 22-IX-2015, coll. Y. Bu & Y. L. Jin; 1 juvenile with 9 pairs of legs (slide no. ZJ-GTS-SY2012011), Zhejiang, Gutian Mountain, 11-IV-2012; 1 juvenile with 9 pairs of legs, ibidem, 19-VI-2012; 4 juveniles with 8 pairs of legs, ibidem, 15-VII-2012; 1 juvenile with 9 pairs of legs, ibidem, 19-IX-2012; 3 juveniles with 8 or 10 pairs of legs, ibidem, 14-X-2012; 3 juveniles with 8–10 pairs of legs, ibidem, 17-XI-2012; 6 juveniles with 8–9 pairs of legs, ibidem, 12-XII-2012; 1 juvenile with 8 pairs of legs, ibidem, 23-I-2013; 2 juveniles with 8 or 10 pairs of legs, ibidem, 27-III-2013; 1 juvenile with 10 pairs of legs, ibidem, 24-IV-2013, coll. Y. Bu et al.; 12 juveniles with 7–10 pairs of legs, Jiangsu, Wuxi, Daji Mountain, 9-X-2017, coll. Y. Bu.

Description. Adult body 2.2 mm long in average (1.7–3.1 mm, n = 40), holotype 2.1 mm (Fig. 4A).

Head length 200–290 μm, width 200–350 μm, with widest part somewhat behind the middle on a level with the points of articulation of mandibles (Fig. 4F). Central rod distinct, divided into two parts by a node-like interruption in the middle. Anterior branches normal, median branches vestigial. Head dorsally covered with setae of different length, longest setae (25–38 μm) located most anteriorly, at least 3.0 times as long as central shortest ones (8–11 μm). Cuticle on anterolateral part of head with fine coarse granules.

Tömösváry organ globular (Fig. 4F), diameter 13–25 μm, 0.4–0.6 of greatest diameter of third antennomere (34–45 μm), opening round with length about half of greatest diameter of the organ, inner margins of openings covered with uniform vertical striae.

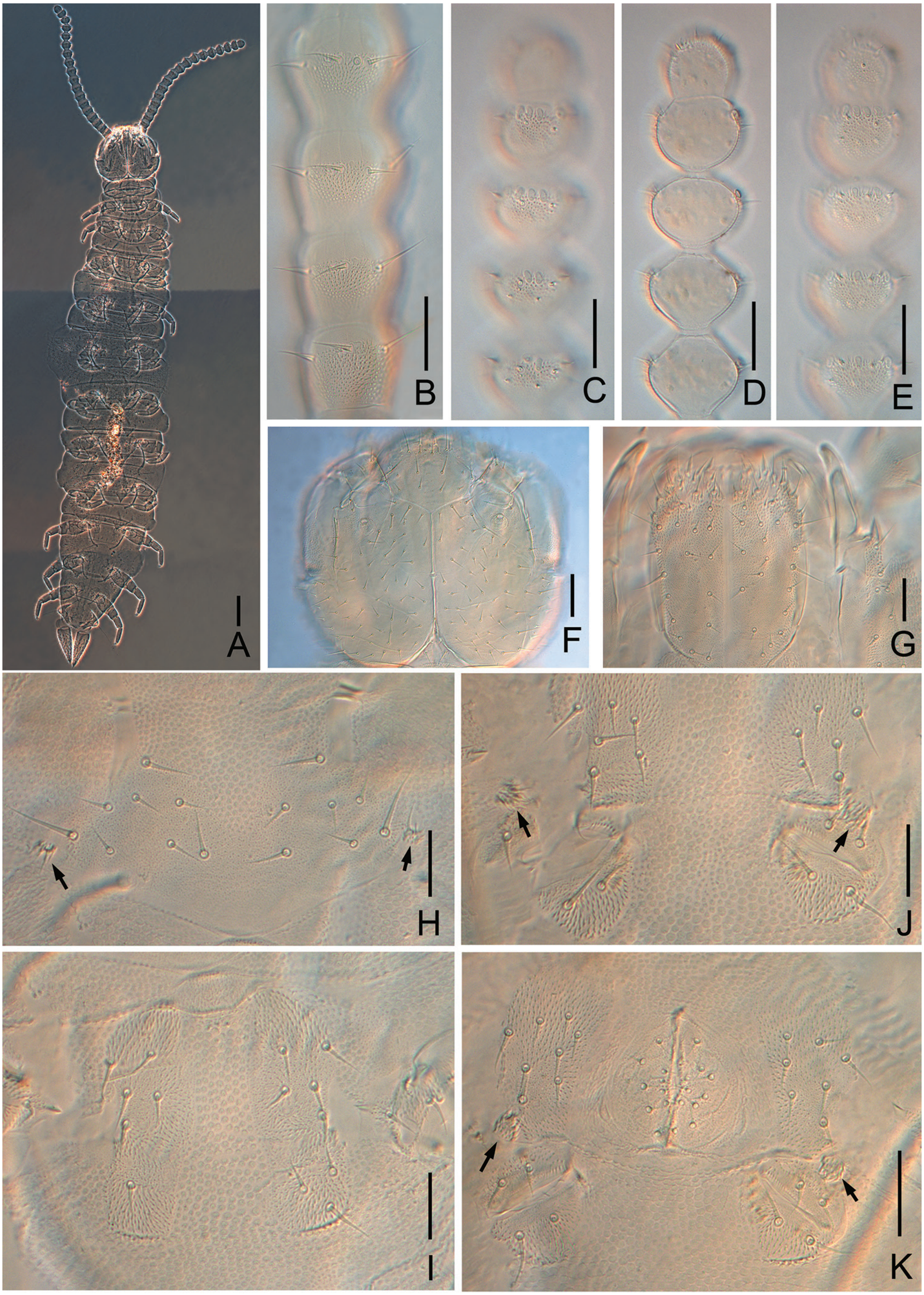

Figure 4. *Symphylella communa* sp. nov. **A** habitus **B** left 2nd–5th antennomeres, dorsal view **C** distal five antennomeres, dorsal view **D** distal five antennomeres, show lateral organs **E** distal five antennomeres, ventral view **F** head, dorsal view **G** head, ventral view **H** first pair of legs (arrows indicate the reduced legs) **I** coxa of leg 2 **J** coxa of leg 3 (arrows indicate styli) **K** coxa of leg 4 and male genital plate (arrows indicate styli). Scale bars: 100 µm (**A**); 20 µm (**B–K**).

Mouthparts. Mandible with two fused lamellae and 11 teeth in total (Fig. 6A). First maxilla has two lobes, inner lobe with four hooked teeth, outer lobe with teethed apex, palp straight, conical, pointed (Fig. 6B). Anterior part of second maxilla with numerous small protuberances which carry one seta each, distal setae thicker and spiniform; posterior part with sparse setae (Fig. 4G). Cuticle of maxilla and labium covered with dense pubescence (Fig. 4G).

Antennae with 15–20 antennomeres, length 500–720 μm (550 μm in holotype), about one-quarter of body length. First antennomere shorter than second one, greatest diameter 1.2–1.7 times as wide as long (34–43 μm, 20–35 μm), with five to seven setae in one whorl, longest seta (20–21 μm) inserted at inner side and distinctly longer than outer ones (11–12 μm). Second antennomere wider (29–44 μm) than long (23–35 μm), with 6–10 setae evenly inserted around the antennal wall with interior setae (20–22 μm) slightly longer than exterior ones (13–15 μm). Chaetotaxy of third antennomere similar to preceding ones. Setae on proximal antennomeres longer and on distal antennomeres shorter. Proximal antennomeres with only primary whorl of setae (Fig. 4B). Secondary whorl appearing ventrally on antennomeres 6–12 (Fig. 4E). Three kinds of sensory organs on antenna: rudimentary spined sensory organs on dorsal side of most antennomeres except first antennomere (Figs 4D, 6D); cavity-shaped organs on antennomeres 3–6 next to apical one, occasionally on apical antennomere (Figs 4D, 6D); bladder-shaped organs on antennomeres 6–11 next to apical one increasing in number on subdistal antennomeres to a maximum of 16 (Figs 4C, E, 6D). Apical antennomere subspherical, somewhat longer than wide (length 26–38 μm, width 25–28 μm), with 12–18 setae on distal half; two to five spined sensory organs consisting of three or four curved spines around a central pillar in depressions in distal surface (Figs 4D, E, 6C). All antennomeres covered with short pubescence. Chaetotaxy and sensory organs of antennae are given in Table 4.

Trunk with 17 dorsal tergites. Tergites 2–13, and 15 each with one pair of triangular processes. Length from base to tip of processes somewhat shorter than or the same as its basal width; basal distance between processes of tergites 4–13, and 15 longer than their length from base to tip (Table 5). All processes with round swollen ends (Figs 5B–E, G). Anterolateral setae of tergites 2, 3, 4, 6, 7, 9 and 10 distinctly longer than other lateromarginal setae, approach length of process of same tergite (Fig. 5B–D), that of tergites 5, 8, 11, 13 and 15 subequal or slightly shorter than longest ones of other lateromarginal (Fig. 5E, G). Processes with one to three inserted setae. All tergites pubescent (Fig. 5B–G).

Tergite. Tergite 1 reduced, with eight or nine unequal length setae in two groups (4+4 or 4+5) (Fig. 5A). Tergite 2 complete, with two broad posterior processes, five to seven lateromarginal setae, one to three inserted setae, two or three central setae, with anterolateral setae 0.8–1.2 times as long as length of process, processes 0.8–1.0 time as long as broad, basal distance between processes 0.3–0.9 time as long as their length (Fig. 5B). Tergite 3 complete, broader and longer than preceding one with ratios of 0.7–1.3, 0.7–1, and 0.5–1.1 respectively, 7–10 lateromarginal setae (Fig. 5C). Tergite 4 broader than tergite 3, with ratios 1–1.7, 0.8–0.6, and 1–2.6 respectively, six to eight

Table 4. Numbers of setae and sensory organs of antennae (holotype).

Antennomeres	No. of primary whorl setae	No. of secondary whorl setae	Rudimentary spined sensory organs	Cavity-shaped organs on dorsal side	Bladder-shaped organs
1st	6				
2nd	8		1		
3rd	9		1		
4th	10		1	1	
5th	11			1	
6th	11			1	
7th	11	2		1	
8th	11	2	1	1	1
9th	12	5		2	2
10th	13	6	1	2	3
11th	14	6	1	1	2
12th	14	5	1		6
13th	15	5	1	1	6
14th	14	5		2	7
15th	13			1	8
16th	12		1	1	7
17th	12		1	1	4

Table 5. Chaetotaxy of tergites (holotype in brackets).

No. of tergites	lateromarginal	Inserted seta	Central setae	Other setae
1st		4+4/5 (4+4)*		
2nd	5–7 (6)	1–2 (1)	2–5 (2)	6–14 (8)
3rd	7–10 (8)	1–3 (2)	2–5 (2)	14–27 (19)
4th	6–8 (6)	1–2 (1)	3–6 (4)	7–18 (11)
5th	5–8 (6)	1–3 (2)	2–5 (2)	8–18 (12)
6th	8–11 (8)	1–3 (1)	3–6 (5)	21–36 (26)
7th	5–7 (6)	0–2 (1)	4–8 (5)	7–20 (15)
8th	5–8 (6)	1–3 (2)	3–6 (4)	8–20 (11)
9th	7–11 (8)	1–3 (2)	3–6 (4)	21–36 (29)
10th	5–7 (6)	0–2 (1)	3–7 (4)	6–19 (11)
11th	5–8 (6)	0–3 (1)	3–8 (4)	6–18 (11)
12th	6–10 (6)	1–2 (1)	2–6 (4)	9–33 (14)
13th	4–7 (5)	0–2 (1)	2–6 (5)	2–15 (7)
14th				12–23 (18)
15th	5–8 (5)	0–2 (1)	1–4 (3)	5–29 (14)
16th				10–16 (14)
17th				18–27 (19)

* With 4+4 or 4+5 setae in a row.

lateromarginal setae (Fig. 5D). Chaetotaxy of tergites 5–7, 8–10, and 11–13 similar as tergites 2–4 (Fig. 5E). Pattern of alternating tergite lengths of two short-tergites followed by a long-tergite only disrupted at the caudal end (Table 5). Tergites 14 and 16 without processes and with 12–26 and 9–16 setae respectively (Fig. 5F). Tergite 17 with 18–27 setae. Chaetotaxy and measurements of tergites are given in Tables 5 and 6.

Legs. First pair of legs reduced to two small, hairy cupules, each with at least one long setae (4–10 μm) (Fig. 4H). Leg 12 about same length of head (Fig. 6F), trochanter 1.2–1.8 times as long as wide (50–90 μm, 36–60 μm), with five to eight subequal setae; femur almost as long as wide (31–53 μm, 30–46 μm), with five or six setae and the

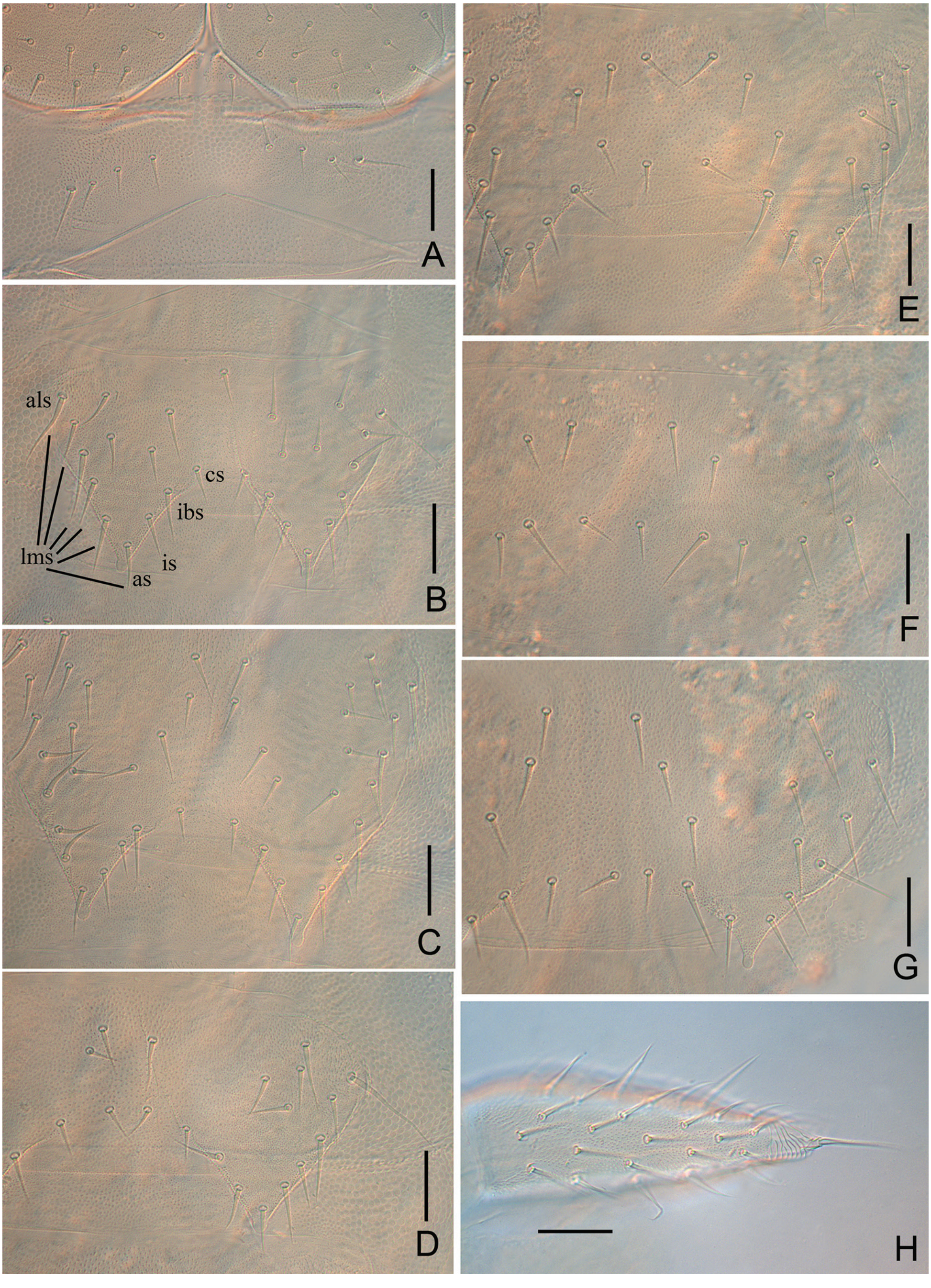

Figure 5. *Symphylella communa* sp. nov. **A** posterior of head and 1st tergite **B** 2nd tergite (als-anterolateral seta, as-apical seta, cs-central seta, is-inserted seta, ibs-inner basal seta, lms-lateromarginal seta) **C** 3rd tergite **D** 4th tergite, right side **E** 5th tergite **F** 14th tergite **G** 15th tergite **H** right cercus, dorsal view. Scale bars: 20 μm.

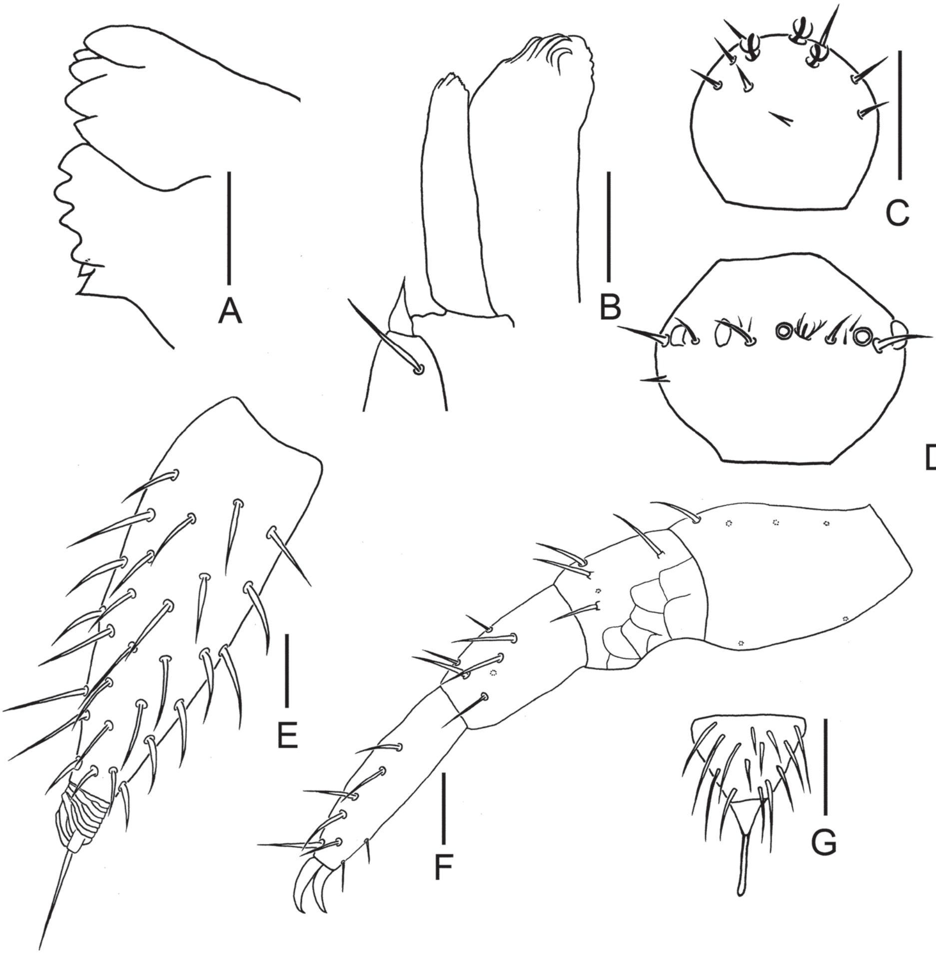

Figure 6. *Symphylella communa* sp. nov. **A** mandible **B** first maxilla **C** left apical antennomere, dorsal view **D** left 13th antennomere, dorsal view **E** left cercus, dorsal view **F** 12th leg **G** stylus on base of 3rd leg, right side. Scale bars: 20 µm (**A–F**); 5 µm (**G**).

dorsally protruding longest setae (20–27 µm) about 0.4–0.7 time of greatest diameter of podomere, laterally with cuticular thickenings in pattern of large scales; tibia nearly 1.3–1.9 times longer than wide (40–65 µm, 23–41 µm), with four to six dorsal setae: three straight and protruding, others slightly curved and depressed, longest seta 0.7–0.9 of greatest diameter of tibia; ventral setae distinctly shorter than dorsal ones; tarsus subcylindrical, about 3.1–4.2 times as long as wide (50–89 µm, 15–22 µm) with six dorsal setae: four straight and protruding, two curved and depressed; longest setae (16–25 µm) about same length or a little longer than greatest width of podomere; one or two ventral setae close to claw distinctly shorter than dorsal ones. Claws curved, anterior one somewhat longer and broader than posterior one, the latter more curved than the former. All legs covered with dense pubescences except areas with cuticular thickenings.

Table 6. Measurements of tergites and processes (mean ± se, in μm, *n* = 22) (holotype in brackets).

No. of tergites	Length	Width	Length of processes	Basal width of processes	Basal distance between processes
1st	33 ± 7 (25)	175 ± 25 (150)			
2nd	53 ± 4 (58)	135 ± 4 (130)	38 ± 6 (38)	45 ± 7 (43)	23 ± 5 (25)
3rd	89 ± 5 (95)	178 ± 10 (168)	41 ± 5 (38)	48 ± 7 (40)	33 ± 5 (40)
4th	61 ± 10 (50)	192 ± 12 (178)	36 ± 6 (25)	56 ± 11 (43)	54 ± 9 (65)
5th	69 ± 6 (75)	185 ± 13 (180)	43 ± 5 (45)	51 ± 8 (53)	55 ± 11 (48)
6th	117 ± 10 (125)	234 ± 12 (225)	49 ± 6 (45)	54 ± 11 (45)	59 ± 11 (53)
7th	67 ± 8 (75)	236 ± 13 (232.5)	40 ± 5 (45)	59 ± 10 (63)	79 ± 16 (68)
8th	72 ± 4 (75)	194 ± 9 (200)	46 ± 6 (45)	54 ± 10 (50)	70 ± 12 (65)
9th	121 ± 4 (120)	258 ± 18 (240)	52 ± 8 (50)	61 ± 13 (50)	63 ± 10 (58)
10th	70 ± 9 (75)	239 ± 10 (230)	38 ± 6 (33)	60 ± 15 (55)	81 ± 12 (75)
11th	83 ± 8 (75)	219 ± 9 (213)	43 ± 6 (40)	54 ± 11 (43)	73 ± 10 (75)
12th	111 ± 10 (100)	258 ± 11 (250)	42 ± 7 (40)	57 ± 14 (50)	68 ± 9 (70)
13th	71 ± 4 (70)	233 ± 4 (230)	30 ± 4 (30)	58 ± 9 (50)	72 ± 12 (70)
14th	75 ± 13 (70)	198 ± 4 (195)			
15th	82 ± 6 (75)	218 ± 14 (208)	31 ± 5 (25)	54 ± 12 (38)	58 ± 9 (58)
16th	75 ± 5 (70)	171 ± 7 (163)			
17th	111 ± 3 (113)	157 ± 16 (145)			

Coxal sacs present at bases of legs 3–9, fully developed, each with four or five setae on surface (Fig. 4J, K). Relevant area of leg 2, 11, and 12 replaced by 1–3, 1–2, and 1–2 setae respectively (Fig. 4I).

Styli present at base of legs 3–12, subconical (length 6–10 μm, width 3–6 μm), basal part with dense straight hairs; distal quarter hairless and blunt (3–5 μm) (Figs 4J, K, 6G).

Sense calicles with smooth margin to pit. Sensory seta inserted in cup center, extremely long (120–180 μm).

Cerci about 0.4–0.8 of head length and leg 12, 2.4–3.3 times as long as its greatest width (115–178 μm, 37–63 μm), moderately covered with subequal length setae (Figs 5H, 6E). Two types of setae inserted on cercus: slightly curved and depressed ones and three or four long and erect outer ones. Longest outer seta (23–32 μm) 0.5–0.7 of greatest width of cerci, terminal area (20–29 μm) short, circled by 7–10 layers of curved ridges. Terminal setae (25–30 μm) 1.0–1.4 times as long as terminal area.

Etymology. The species name "*communa*" is derived from "common" which refer to the common morphology and wide distribution of the species.

Distribution. China (Jiangsu, Shanghai, Zhejiang).

Remarks. *Symphylella communa* sp. nov. is most similar to *S. asiatica* Scheller, 1971 from India and Sri Lanka and *S. macropora* Jin & Bu, 2019 from Tibet in the shape of the central rod, tergites, processes, anterolateral setae, and leg 12. It differs from *S. asiatica* and *S. macropora* in the size of the opening of the Tömösváry organ (moderate in *S. communa* sp. nov. vs very small in *S. asiatica*, extremely large in *S. macropora*) and chaetotaxy of the first tergite (4+4 in *S. communa* sp. nov. and *S. macropora* vs 3+3 setae in *S. asiatica*). It is also affiliated to *S. neotropica* (Hansen, 1903) from Brazil in the shape of tergites and processes, but can be easily distinguished by the central rod (both the anterior and posterior parts are in the same width in *S. communa* sp. nov. vs the anterior part is distinctly narrow than the posterior part in *S. neotropica*).

Discussion

The genus *Symphylella* is well defined by the presence of 17 tergites with 13 of them having triangular processes present on posterior margins, the first pair of legs replaced by two protuberances with a few setae inserted on, and short styli present on the base of legs 3–9. The shapes of the central rod, Tömösváry organ, tergites and their processes, and cerci, as well as the chaetotaxy of the tergites and cerci, are good characters for the species identification. The measurements of anterolateral setae on tergites are also taxonomically informative for the species definition. The number of lateromarginal setae, inserted setae, central setae, and other setae on tergites often show considerable variations among adult individuals. Asymmetrical setae are usually observed on tergites. In *Symphylella communa* sp. nov., most specimens with 4+4 setae on the first tergite while several specimens exhibits 4+5 and one specimens with 5+5 setae, and the same variation is also observed in *S. macropora*. The shape of the cerci is a relative stable character of the species, but the ratio of the length and width of the cercus may be affected by the mounting process of specimens. Therefore, caution is advised when identify the species of *Symphylella*, which should be based on multiple differential stable characters of fully mature specimens.

The members of the genus *Symphylella* are distributed in almost all faunal regions of the world: 17 species (34.7%) in Nearctic Region, 12 (24.5%) in Ethiopian Region, 11 (22.5%) in Oriental Region, 7 (14.3%) in Palaearctic Region, 6 (12.2%) in Australian Region, and two (4.1%) in Neotropical Region. Most of the species occur in Nearctic, Ethiopian, and Oriental regions. It seems they are more adaptable to the temperate climate. In China, *Symphylella* are often found with high density in the tropical and subtropical area. More species are expected to be discovered in East and South China in the future.

According to the previous studies, the species of the genus *Symphylella* are adapted to diverse habitats and a variety of biotopes: from litter and moss, soil and leaf litter in bamboo and broad-leaf forest, pineapple field, to the plantation of bananas and coco, lawn, botanical garden, tea plantation, orchards, and unoccupied sites. They can live on moist slopes of hills, along streams, in silty soil of agricultural lands, and in caves. They are also present under stone or bricks, in decaying vegetable matter, under bark, in heaps of rotten coconut shells, and under coco trunks on grassy ground (Scheller 1961, 1971). Studies have shown that *Symphylella* species occupy a broad range of habitats, from the littoral intertidal areas to high mountain forests. Some species, *S. asiatica* Scheller, 1971, *S. brincki* Scheller, 1971, *S. foucquei* Scheller, 1971, and *S. tentabundna* Scheller, 1971 for instance, live in mountain areas more than 2000 m above the sea level (Scheller 1971).

Symphylella species are supposed to be phytophagous or saprophagous (Rohrbach and Johnson 2003). During our observation of the mounted specimens of *S. communa* sp. nov., we noticed that the intestinal tract of some individuals have many appendages, mandibles, antennae, and cuticle fragments of some other micro-arthropods such as pauropods and collembolans, so this species may be also omnivorous.

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RESEARCH ARTICLE

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Review of *Mesocallis* Matsumura from China (Hemiptera, Aphididae), with one new species

Jing Chen[1], Li-Yun Jiang[1], Ge-Xia Qiao[1,2]

1 *Key Laboratory of Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Sciences, No. 1-5 Beichen West Road, Chaoyang District, Beijing 100101, China* **2** *College of Life Science, University of Chinese Academy of Sciences, No. 19, Yuquan Road, Shijingshan District, Beijing 100049, China*

Corresponding author: Ge-Xia Qiao (qiaogx@ioz.ac.cn)

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Abstract

The aphid genus *Mesocallis* Matsumura in China is reviewed. A total of seven species are recognised using morphological characteristics, including six known species, *Mesocallis* (*Mesocallis*) *alnicola* Ghosh, *M.* (*Paratinocallis*) *corylicola* (Higuchi), *M.* (*M.*) *pteleae* Matsumura, *M.* (*M.*) *sawashibae* (Matsumura), *M.* (*P.*) *yunnanensis* (Zhang) and *M.* (*M.*) *taoi* Quednau, and one new species, *M.* (*M.*) *platycaryae* Qiao, **sp. nov.** The new species, collected on *Platycarya strobilacea* (Juglandaceae) in Anhui Province, China, is described and illustrated. A key to *Mesocallis* species from China is presented.

Keywords

Aphids, Calaphidinae, embryo, new host plant

Introduction

The aphid genus *Mesocallis* was erected by Matsumura (1919), with *Myzocallis sawashibae* Matsumura, 1917 as the type species. The genus has distinct morphological characteristics; a narrow body, antennae much shorter than the body, antennal segments IV–VI scarcely imbricated, segment III of the alatae with one row of oblong, secondary rhinaria along all or most of its length, and empodial setae distinctly longer than the claws (Higuchi 1972; Quednau 2003; Qiao et al. 2005). Currently, this genus includes 10 species placed in two subgenera: *Mesocallis* (*Mesocallis*) *alnicola* Ghosh, *M.* (*Paratinocallis*) *corylicola* (Higuchi), *M.* (*M.*) *carpinicola* Lee, *M.* (*M.*) *fagicola* Matsumura, *M.* (*M.*) *obtusirostris* Ghosh, *M.* (*P.*) *occulta* Lee, *M.* (*M.*) *pteleae* Matsumura, *M.* (*M.*) *sawashibae* (Matsumura), *M.* (*P.*) *yunnanensis* (Zhang), and *M. taoi* Quednau (Blackman and Eastop 2020; Favret 2020). These species all are associated with plants of the family Betulaceae and are mainly distributed in East Asia. Six species are hitherto recorded from China: *M. alnicola*, *M. corylicola*, *M. pteleae*, *M. sawashibae*, *M. taoi*, and *M. yunnanensis*. Recently, some apterous specimens on *Platycarya strobilacea* (Juglandaceae) were collected in Anhui Province (Dabieshan Mountain), which were identified as a new species in this genus. Herein, the genus *Mesocallis* from China is reviewed, a key to Chinese species is provided, and the new species is described and illustrated.

Materials and methods

The brief procedure of making aphid slide-mounted specimens follows that of Jiang et al. (2016). The descriptions and drawings provided here were produced from slide-mounted specimens using a Leica DM4000B and drawing tube. The photomicrographs were prepared with a Leica DM2500 using DIC illumination and processed with Automontage and Photoshop software.

Aphid terminology in this paper generally follows that of Quednau (2003) and Qiao et al. (2005). The unit of measurements is millimetres (mm). All specimens, including the holotype and paratypes, are deposited in the National Zoological Museum of China, Institute of Zoology, Chinese Academy of Sciences, Beijing, China (**NZMC**).

Taxonomy

***Mesocallis* Matsumura, 1919**

Mesocallis Matsumura 1919: 103. Type species: *Myzocallis sawashibae* Matsumura, 1917; by original designation.

Subgenus *Mesocallis* Matsumura 1919: 103

Synonym: *Neocallis* Matsumura 1919: 104.

Synonym: *Nippochaitophorus* Takahashi 1961: 247.

Subgenus *Paratinocallis* Higuchi 1972: 30. Type species: *Paratinocallis corylicola* Higuchi,1972; by original designation. Given subgenus status by Quednau (2003: 20).

Mesocallis Matsumura: Higuchi 1972: 22; Raychaudhuri et al. 1980: 291; Ghosh and Quednau 1990: 114; Quednau 2003: 19; Qiao et al. 2005: 194; Lee et al. 2018: 3.

Generic diagnosis. In alatae, eyes with ocular tubercles. Antennae 6-segmented, processus terminalis 0.80–1.20× as long as the base of the segment. Ultimate rostral segment with 2–16 accessory setae. First tarsal segments with five to seven ventral setae and two dorsal setae. Empodial setae flabellate. Siphunculi truncated, without flange, without any setae surrounding at base. Cauda knobbed. Anal plate bilobed. Gonapophyses fused, with eight gonosetae. In apterae, nymphs and embryo, dorsal body setae with spinulose shafts, and round knobs at apex. Abdominal tergites I–IV with one pair of marginal setae in subgenus *Mesocallis*, or two or three pairs of marginal setae in subgenus *Paratinocallis*. Compound eye of apterous morph often smaller and with fewer facets than in the alate morph, and inner setae of antennal segment III inconspicuous. Apterae with 5- or 6-segmented antennae, dorsal setae of tibiae similar to other tibial setae in subgenus *Mesocallis*, or strongly differentiated from other tibial setae in subgenus *Paratinocallis*; first tarsal segments with five ventral setae, without dorsal setae. In embryo, dorsal body setae capitate at apex; spinal setae of metanotum and tergites I, III, and V short or minute, pleural setae absent. Viviparae alate and apterous in some species.

Distribution. China, Japan, Korea, and India.

Host plants. *Alnus*, *Carpinus*, *Corylus*, and *Ostrya* (Betulaceae), and *Platycarya* (Juglandaceae).

Comments. Of the known *Myzocallis* species, most infest plants of Betulaceae. Two species (*obtusirostris* and *taoi*) are primarily associated with *Alnus*; and three species (*corylicola*, *occulta*, and *yunnanensis*) are associated with *Corylus*. *Myzocallis carpinicola* is recorded only on *Carpinus*. Additionally, *M. alnicola* infests both *Alnus* and *Corylus*, and *M. sawashibae* occurs on both *Carpinus* and *Corylus* (Lee et al. 2018). Only *M. pteleae* infests plants in several different genera of Betulaceae (*Alnus*, *Betula*, *Corylus*, *Carpinus*, and *Ostrya*) (Holman 2009). So, *Mesocallis* species have distinct host specialization. However, the new species, *M. platycaryae* Qiao was found on *Platycarya* (Juglandaceae). All species occur only in East Asia and are endemic to this region.

***Mesocallis* (*Mesocallis*) *alnicola* Ghosh, 1974**

Mesocallis alnicola Ghosh 1974: 425.
Mesocallis alnicola Ghosh: Raychaudhuri et al. 1980: 292; Ghosh and Quednau 1990: 116; Quednau 2003: 20; Qiao et al. 2005: 195.

Specimens examined. Two alate viviparous femlaes, **China:** Gansu (Yuzhong County: Xinglong Mountain, alt. 2300 m), 1 Aug. 1986, no. 8579, on *Corylus heterophylla*, coll. G.X. Zhang, J.H. Li, and T.S. Zhong (NZMC).

Distribution. China (Gansu), India.

Host plants. *Corylus heterophylla* in China (first record from this host), *Alnus nepalensis* in India.

Biology. Yellow in life. Infesting the underside of leaves of host plants.

***Mesocallis* (*Paratinocallis*) *corylicola* (Higuchi, 1972)**

Paratinocallis corylicola Higuchi 1972: 30; Qiao et al. 2005: 210.
Mesocallis (*Paratinocallis*) *corylicola* (Higuchi): Quednau 2003: 21; Lee et al. 2018: 8.

Specimens examined. Four alate viviparous females and 2 nymphs, **China:** Heilongjiang (Harbin City), 27 Jul. 1976, no. 6423, on *Corylus heterophylla*, coll. G.X. Zhang and T.S. Zhong (NZMC); 3 alate viviparous females, Liaoning (Shenyang City), 25 May 1984, no. Y4994, on *Corylus heterophylla*, coll. L.J. Liu and Y.Q. Wang (NZMC); 2 alate viviparous females, Liaoning (Dandong City), 22 Jun. 1984, no. Y4914, on *Corylus heterophylla*, coll. G.X. Zhang and L.J. Liu (NZMC); 7 alate viviparous females, Shandong (Taian City), 12 Jun. 1975, no. 5990, on *Corylus heterophylla*, coll. T.S. Zhong (NZMC); 2 alate viviparous females, Gansu (Yuzhong County: Xinglong Mountain, alt. 2170 m), 30 Jul. 1986, no. 8556, on *Corylus heterophylla*, coll. G.X. Zhang, J.H. Li, and T.S. Zhong (NZMC).

Distribution. China (Liaoning, Heilongjiang, Shandong, Gansu), Japan, Korea.

Host plants. *Corylus sieboldiana* and *C. heterophylla*; however, in the Russian Far East it was collected from *Quercus dentata* (Holman 2009).

Biology. Beige or pale green in life; scattered on the underside of leaves of host plants.

Mesocallis (*Mesocallis*) *platycaryae* Qiao, sp. nov.

http://zoobank.org/F0D1DBB8-684E-4983-8CA1-47EF630AFC21

Figures 1–24, Table 1

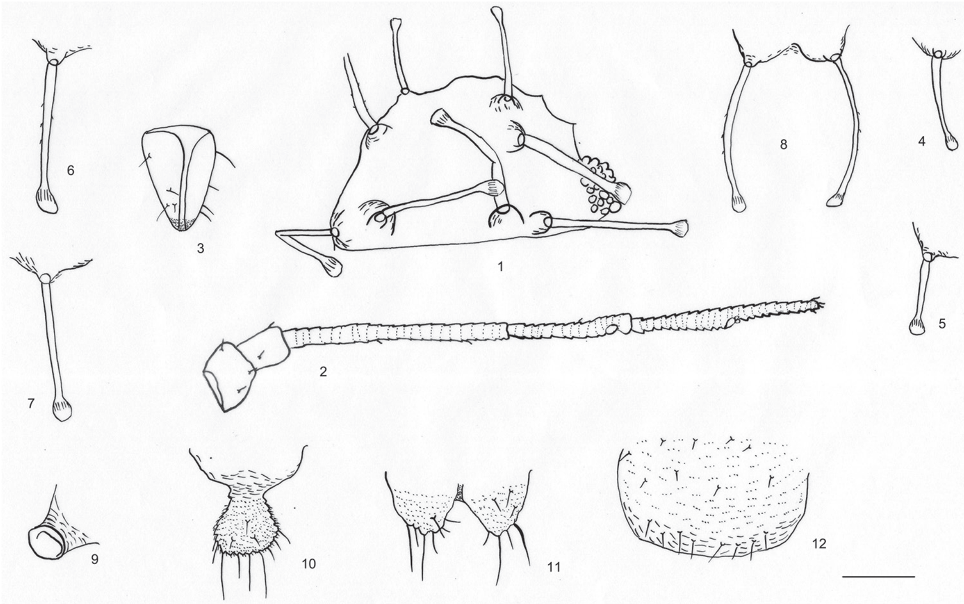
Etymology. The specific name *platycaryae* is based on the host plant (*Platycarya*) of the species.

Description. Apterous viviparous female: body oval (Fig. 13), translucent white in life. For morphometric data, see Table 1.

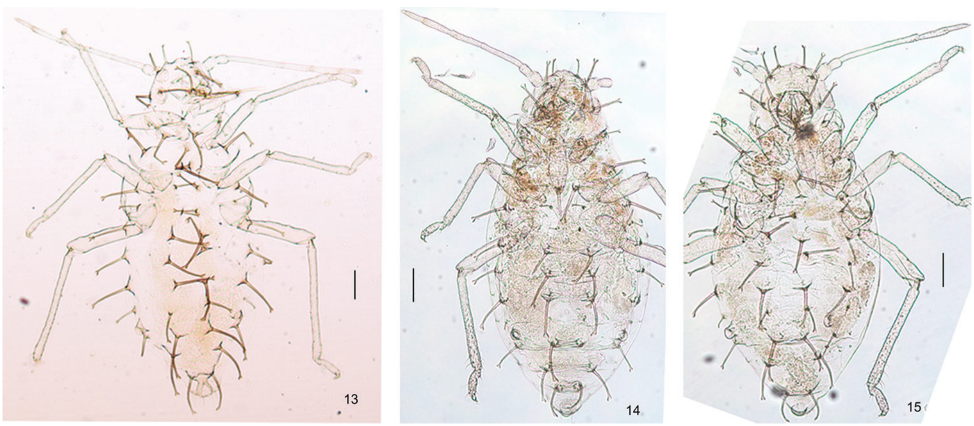
Mounted specimens. Body dorsum pale; antennae, legs, cauda, anal plate, and genital plate pale, apex of rostrum brown (Fig. 13). Dorsal body setae thick long and dark brown, with elevated bases, sparsely spinulose shafts on part of length and large round knobs at apices (Figs 4–8, 13, 20–22, 24).

Head. Frons convex (Figs 1, 17). Dorsal setae on head similar to dorsal body setae. Head with one pair of frontal setae (Figs 4, 16, 17), one pair of setae between antennae and two pairs of posterior marginal setae between eyes (Figs 1, 16, 17). Frontal setae 5.67–6.00× as long as basal diameter of antennal segment III. Eyes with relatively few facets (Figs 1, 16). Antennae 5-segmented, 0.29–0.33× as long as body (Figs 2, 18), segments III–V with spinulose transverse imbrication; processus terminalis 0.81–0.88× as long as the base of the segment. Antennal setae very few short and pointed; segments I–V each with 2, 2, 2 or 3, 2, 1 setae, respectively; processus terminalis with four apical setae. Length of setae on segment III 0.33–0.40× as long as basal diameter of the segment. Primary rhinaria not ciliated (Figs 2, 18). Rostrum (Figs 3, 17) reaching back to between fore and mid-coxae; ultimate rostral segment thick wedge-shaped, 1.39–1.56× as long as its basal width, 0.74–0.78× as long as second hind tarsal segment, with two accessory setae

Thorax (Fig. 13). Pronotum with 1 pair of short, pale brown, anterior spinal setae and 2 pairs of thick, long, dark brown marginal setae; meso- and metanotum each with one pair of spinal and one pair of marginal thick, long, dark brown setae. Mesosternal



Figures 1–12. *Mesocallis platycaryae* sp. nov. Apterous viviparous female **1** dorsal view of head **2** antennal segments I–V **3** ultimate rostral segment **4** frontal seta **5** marginal seta on abdominal tergite I **6** spinal seta on abdominal tergite III **7** marginal seta on abdominal tergite III **8** spinal seta on abdominal tergite VIII **9** siphunculus **10** cauda **11** anal plate **12** subgenital plate. Scale bars: 0.05 mm.



Figures 13–15. *Mesocallis platycaryae* sp. nov. Dorsal view of body **13** apterous viviparous female **14** 4th nymph **15** 3rd nymph. Scale bars: 0.1 mm.

furca separated (Fig. 5). Femur and trochanter partially fused; hind femur and trochanter 4.66–5.00× as long as greatest width of segment; 1.42–1.48× as long as antennal segment III. Distal half of tibiae and tarsi with spinulose transverse striae (Fig. 19); hind tibia 0.35–0.36× as long as body. Setae on legs fine, pointed; tibial distal setae similar to other tibial setae; length of setae on hind tibiae 1.38–1.50× as long as middle

Table 1. Morphometric data for apterous viviparous females and nymphs of *Mesocallis* (*Mesocallis*) *platycaryae* sp. nov.

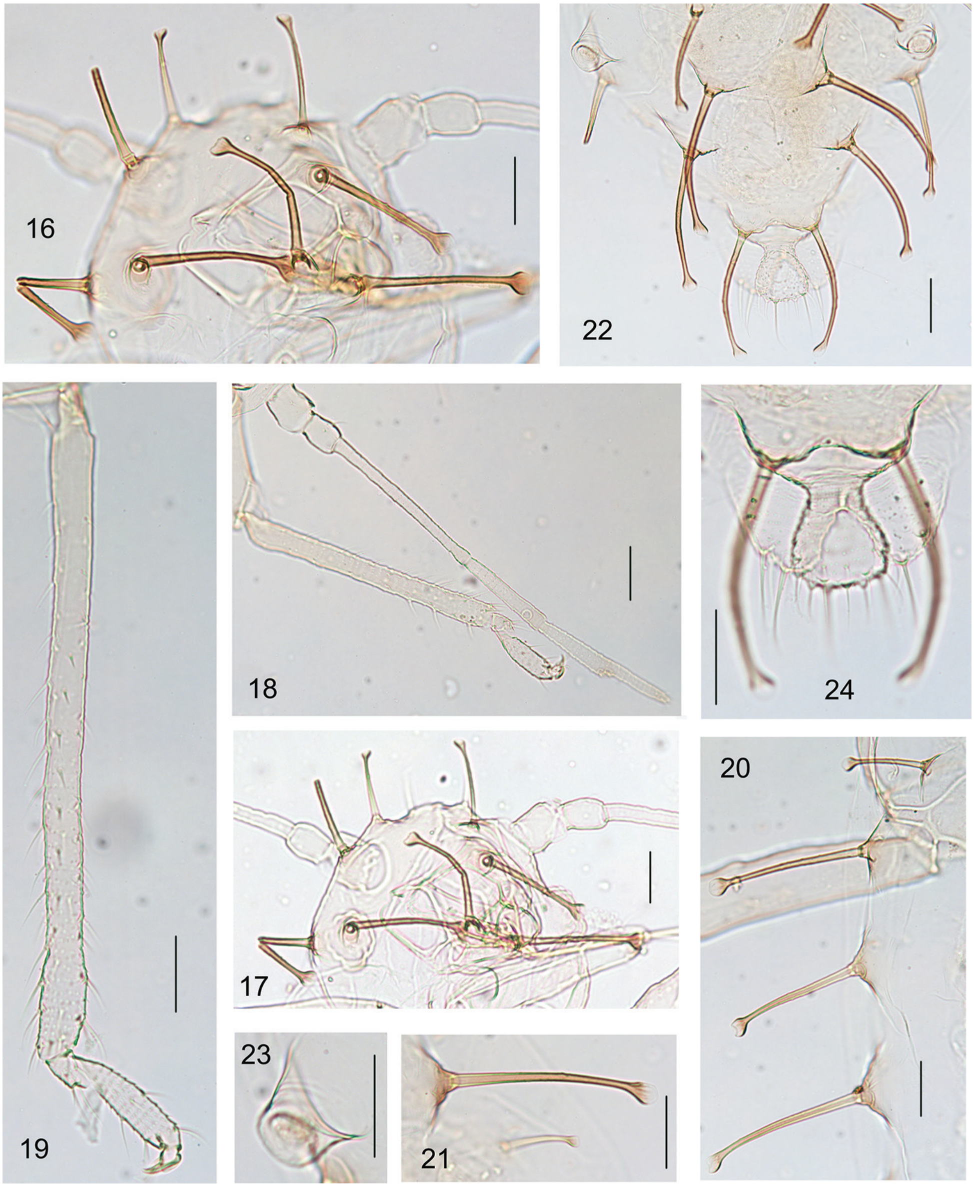
Characters	Apterous viviparous female (holotype)	Apterous viviparous female (paratype)	3rd nymph (*n* = 1)	4th nymph (*n* = 1)
Body length	1.120	1.010	1.020	1.030
Body width	0.470	0.450	0.490	0.490
Antenna	0.532	0.470	0.465	0.483
Antennal segment I	0.047	0.040	0.045	0.042
Antennal segment II	0.037	0.035	0.037	0.042
Antennal segment III	0.183	0.166	0.151	0.144
Antennal segment IV	0.106	0.092	0.087	0.097
Base of antennal segment V	0.084	0.077	0.082	0.089
Processus terminalis	0.074	0.062	0.064	0.069
Ultimate rostral segment	0.062	0.062	0.062	0.062
Hind femur	0.260	0.230	0.225	0.218
Hind tibia	0.396	0.361	0.342	0.302
Second hind tarsal segment	0.084	0.079	0.079	0.077
Siphunculus	0.037	0.037	0.027	0.030
Basal width of siphunculus	0.054	0.050	0.050	0.054
Distal width of siphunculus	0.032	0.035	0.032	0.030
Cauda	0.099	0.099	–	–
Basal width of cauda	0.089	0.094	–	–
Basal diameter of antennal segment III	0.015	0.012	0.012	0.015
Widest width of hind femur	0.052	0.050	0.050	0.050
Width of hind tibia at mid length	0.020	0.020	0.027	0.025
Longest dorsal cephalic seta	0.084	0.074	0.074	0.057
Longest marginal seta on abdominal tergite I	0.079	0.114	0.059	0.040
Longest seta on abdominal tergite VIII	0.151	0.129	0.092	0.094
Longest seta on antennal segment III	0.005	0.005	0.005	0.005
Longest seta on hind tibia	0.027	0.030	0.040	0.030

diameter of segment. First tarsal segments each with five ventral setae, and without dorsal setae. Second hind tarsal segment 1.13–1.28× as long as processus terminalis, 0.79–0.86× as long as antennal segment IV. Empodial setae flabellate.

Abdomen. Abdominal tergites I–VII each with a single pair of spinal and a pair of marginal setae (Figs 5–7, 13, 20–22), marginal setae on tergites I and V distinctly shorter than ones on tergites II–IV (Figs 20, 21), setae on tergite VII very much shorter and pointed, not elevated at base; sometimes spinal setae on tergites III and V slightly shorter than other spinal setae; tergite VIII with one pair of thick long and dark brown dorsal setae (Figs 8, 24). Marginal setae on tergite I are 5.33–9.20× as long as basal diameter of antennal segment III; dorsal setae on tergite VIII 10.17–10.40× as long as basal diameter of antennal segment III. Siphunculi truncated (Figs 9, 22, 23), 0.68–0.75× as long as their basal widths, 0.38× as long as cauda. Cauda knob-shaped, with spinulose short striae (Figs 10, 24); 0.27–0.28× as long as its basal width, with 6–8 long and short pointed setae. Anal plate bilobed, with short spinulose striae (Figs 11, 24). Subgenital plate transversely oval (Fig. 12), with sparse spinulosity in transverse lines; with nine anterior setae, six to eight posterior setae. Gonapophyses fused, with eight short gonosetae.

Third instar nymph. Body oval (Fig. 14), pale brown. Cauda circular at apex, otherwise similar to apterous viviparous female.

Fourth instar nymph. Body oval (Fig. 15), pale brown. Cauda circular at apex, otherwise similar to apterous viviparous female.



Figures 16–24. *Mesocallis platycaryae* sp. nov. Apterous viviparous female **16** dorsal view of body, dorsal setae shown **17** dorsal view of head, antennal segments I–II, and ultimate rostral segment **18** antenna, fore tibia and tarsal segment **19** hind tibia and tarsal segments **20** marginal setae on antennal segments I–IV **21** marginal setae and marginal setae on abdominal tergites IV–V **22** siphunculi, spinal and marginal setae on abdominal tergites VI–VIII, cauda and anal plate **23** siphunculus **24** dorsal setae on abdominal tergite VIII, cauda, and anal plate. Scale bars: 0.05 mm.

Embryo. Dorsal body setae thick, long, and with terminal large round knobs. Head with three pairs of anterior dorsal setae, and two pairs of posterior marginal setae; pronotum with two pairs of spinal setae and one pair of marginal setae, some anterior spinal setae minute; meso- and metanotum each with one pair of spinal and one pair of marginal setae; abdominal tergites I–VII each with one pair of spinal and one pair of marginal setae; among spinal setae of metanotum and tergites I, III, and V are minute, marginal setae on tergites I–III and V–VII; spinal setae on tergites III, V, and VII are displaced.

Specimens examined. ***Holotype*:** apterous viviparous female, **China** (Anhui Province: Yuexi County, Yaoluoping Reserve, Xiaoqiling, alt. 1100 m), 19 Jul. 2007, no. 20714-1-1-1, on *Platycarya strobilacea*, coll. J.J. Yu (NZMC). ***Paratypes*:** 1 apterous viviparous female, 1 third instar nymph, and 1 fourth instar nymph (NZMC), the collection data is the same as in the holotype.

Taxonomic notes. Based on the following morphological characteristics in apterae and nymphs of dorsal body setae with round knobbed apex, 5-segmented antennae, much shorter than the body, hind tibial distal setae similar to other setae on the segment, distal part of tibiae and tarsi spinulose, and abdominal tergites I–VII each with one pair of marginal setae, the new species should clearly be placed in *Mesocallis*. The species is characterised by the dark-brown dorsal body setae, which are placed on unsclerotized tuberculate bases, and by its colonisation of *Platycarya strobilacea* (Juglandaceae). *Mesocallis platycaryae* resembles *M. taoi* in the number of antennal segments, the ratio of antennae to body length, the length and the number of accessory setae of ultimate rostral segment etc., but apterae differ from those of *M. taoi* as follows: dorsal body setae dark brown, not arising from sclerites (*M. taoi* has the dorsal body setae pale but on pigmented sclerites); shafts of dorsal body setae largely smooth, only sparsely spinulose on part of length (vs long dorsal body setae with spinulose shafts); antennae and tarsi pale (vs distal part of antennal segments III–V and tarsi brown). The new species differs from *M. carpinicola* and *M. pteleae* in: ultimate rostral segment 0.06 mm long, and with two accessory setae (*M. carpinicola* and *M. pteleae*: 0.10–0.14 mm long, with four or more accessory setae), head vertex and antennal segments I–III pale (vs blackish), cauda with 6–8 setae (vs 7–15 setae). In addition, the new species may be distinguished from *M. obtusirostris* by: antennae 0.46–0.48× as long as body (*M. obtusirostris*: antennae 0.61–0.75× as long as body), ultimate rostral segment 0.74–0.78× as long as second hind tarsal segment (vs 0.50–0.55×). The difference between the new species and other species of subgenus *Mesocallis* may be found in the key below.

Distribution. China (Anhui).

Host plant. *Platycarya strobilacea* (Juglandaceae).

Biology. The species lives scattered on the underside of leaves of host plant.

Mesocallis (*Mesocallis*) *pteleae* Matsumura, 1919

Mesocallis pteleae Matsumura 1919: 103. Higuchi 1972: 23; Quednau 2003: 20; Qiao et al. 2005: 196; Lee et al. 2018: 4.

Agrioaphis hashibamii Shinji 1935: 287; Tseng and Tao 1938: 209; Tao 1963: 57.
Myzocallis colyricola Shinji 1941: 1148.

Specimens examined. Two alate viviparous females, **China:** Hebei (Wulin Mountain), 15 Jul. 1983, no. Y4357, on *Corylus mandshurica*, coll. S.B. Tian (NZMC); 1 alate viviparous female, Hebei (Wulin Mountain), 13 Sep. 1983, no. Y4354, on *Corylus heterophylla*, coll. S.B. Tian (NZMC); 1 alate viviparous female, Gansu (Yuzhong County: Xinglong Mountain, alt. 2170m), 30 Jul. 1986, no. 8556, on *Corylus heterophylla*, coll. G.X. Zhang, J.H. Li, and T.S. Zhong (NZMC); 3 alate viviparous females, Gansu (Tianshui City: Maijishan Mountain, alt. 1700 m), 24 Jul. 1985, no. 8556, on *Corylus heterophylla*, coll. G.X. Zhang and T.S. Zhong (NZMC).

Distribution. China (Hebei, Sichuan, Gansu), Japan, Korea.

Host plants. *Corylus heterophylla*, *C. sieboldiana* var. *mandshurica*, *Alnus cremastogyne* in China; but, in Japan, *Alnus matsumurae*, *Corylus heterophylla* var. *thunbergii* (Shinji 1935); *C. sieboldiana*, *C. sieboldiana* var. *mandshurica* (Higuchi 1972), also recorded from *Ostrya japonica* and *Carpinus* sp. (Quednau 2003), and *Betula* spp. (Holman 2009).

Biology. Pale green in life; scattered on the underside of leaves of host plants.

Mesocallis (*Mesocallis*) *sawashibae* (Matsumura, 1917)

Myzocallis sawashibae Matsumura 1917: 374; Matsumura 1919: 103.
Mesocallis sawashibae (Matsumura): Higuchi 1972: 24; Quednau 2003: 20; Qiao et al. 2005: 198; Lee et al. 2018: 8.
Neocallis carpinicola Matsumura 1919: 105.
Nippochaitophorus moriokaensis Takahashi 1961: 247.

Specimens examined. Nine alate viviparous females, **China:** Hebei (Changli County), 30 May 1984, no. 5518, on *Corylus heterophylla*, coll. S.B. Tian (NZMC); 1 alate viviparous female, Hebei (Wulin Mountain), 15 Sep. 1983, no. Y4357, on *Corylus mandshurica*, coll. S.B.Tian (NZMC).

Distribution. China (Hebei), Japan, Korea.

Host plants. *Corylus heterophylla* and *C. mandshurica* in China; in Japan, *Corpinus cordata* (Higuchi 1972), *Corpinus erosa*, *C. coreana* (Quednau 2003).

Biology. White in life; scattered on the underside of leaves of host plants.

Mesocallis (*Mesocallis*) *taoi* Quednau, 2003

Mesocallis taoi Quednau 2003: 20, 53.

Distribution. China (Sichuan).

Host plants. *Alnus cremastogyne.*

Mesocallis (*Paratinocallis*) *yunnanensis* (Zhang, 1985)

Paratinocallis yunnanensis Zhang 1985: 220; Qiao et al. 2005: 211.
Mesocallis (*Paratinocallis*) *yunnanensis* (Zhang): Quednau 2003: 21.

Specimens examined. Three alate viviparous females, China: Yunnan (Lijiang City: Yulongxueshan Mountain), 30 May 1984, no. 7192, on *Corylus heterophylla*, coll. T.S. Zhong (NZMC).

Distribution. China (Yunnan).

Host plants. *Corylus heterophylla*.

Biology. Beige in life; infesting the underside of leaves of host plants.

Key to the species of *Mesocallis* in China

1 Abdominal tergites I–IV each with one pair of marginal setae..................... **2**

– Abdominal tergites I–IV each with two or three pairs of marginal setae **6**

2 Dorsal body setae dark brown; shafts of setae mainly smooth, only sparsely spinulose for part of length; on *Platycarya strobilacea* (Juglandaceae)............ .... ***M. platycaryae* sp. nov.**

– Dorsal body setae unpigmented; with spinulose shafts; on plants of Betulaceae **3**

3 In the alatae anterior part of head black; antennal segment III black; ultimate rostral segment 0.7–1.4× as long as hind second tarsal segment **4**

– In the alatae anterior part of head pale; antennal segment III black in whole, or dorsal half, or only apex; ultimate rostral segment 0.6–0.9× as long as hind second tarsal segment.. **5**

4 In alatae: processus terminalis 0.6–0.8× as long as the base of the segment; ultimate rostral segment 0.7–0.9× as long as hind second tarsal segment; first tarsal segments with five ventral setae; in apterae and nymph: marginal setae of abdominal tergites V and VII minute or very short...................... ***M. taoi****

– In alatae: processus terminalis 0.9–1.2× as long as the base of the segment; ultimate rostral segment 1.2–1.4× as long as hind second tarsal segment; first tarsal segments with six ventral setae; in alatoid nymph: marginal setae of abdominal tergites V and VII slightly shortened than those on other tergites..... ***M. pteleae***

5 Some abdominal tergites with duplicated spinal setae and/or with an intercalary seta developed amidst spinal setae; processus terminalis 0.6–0.7 × as long as the base of the segment; in alatae antennal segment III black except for its very base, antennal segment IV sometimes with secondary rhinaria....... ***M. alnicola***

– Abdominal tergites each with one pair of spinal setae; processus terminalis 1.0–1.2× as long as the base of the segment; in alatae antennal segment III pale with apex, antennal segment IV without secondary rhinaria........... ***M. sawashibae***

* The information on *M. taoi* is based on the original description by Quednau (2003).

6 In alatae: processus terminalis 0.9–1.0× as long as the base of the segment; antennal segment IV with secondary rhinaria; ultimate rostral segment 0.9–1.0× as long as hind second tarsal segment................................***M. corylicola***

– In alatae: processus terminalis 0.6–0.7× as long as the base of the segment; antennal segment IV without secondary rhinaria; ultimate rostral segment 1.5–1.7× hind second tarsal segment .... ***M. yunnanensis***

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RESEARCH ARTICLE

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Ancyronyx lianlabangorum sp. nov., a new spider riffle beetle from Sarawak, and new distribution records for *A. pulcherrimus* Kodada, Jäch & Čiampor based on DNA barcodes (Coleoptera, Elmidae)

Ján Kodada[1], Manfred A. Jäch[2], Hendrik Freitag[3,4,5], Zuzana Čiamporová-Zaťovičová[6], Katarína Goffová[1], Dávid Selnekovič[1], Fedor Čiampor Jr[6]

1 *Department of Zoology, Faculty of Natural Sciences, Comenius University in Bratislava, Mlynská dolina B-1, SK-842 15, Bratislava, Slovakia* **2** *Naturhistorisches Museum Wien, Burgring 7, A–1010, Wien, Austria* **3** *Ateneo de Manila University, Biology Department, School of Science and Engineering, Loyola Heights, Quezon City, 1108, Philippines* **4** *Universiti Brunei Darussalam, Environmental and Life Sciences, Faculty of Science, Jalan Tungku Link, Gadong, BE1410, Brunei* **5** *Museum für Naturkunde, Leibniz Institute for Evolution and Biodiversity Science, Invalidenstraße 43, Berlin, 10115, Germany* **6** *Zoology Lab, Plant Science and Biodiversity Centre, Slovak Academy of Sciences, Dúbravská cesta 9, SK-84523, Bratislava, Slovakia*

Corresponding author: Ján Kodada (jan.kodada@uniba.sk)

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Abstract

Ancyronyx lianlabangorum **sp. nov.** (Coleoptera, Elmidae), a new spider riffle beetle from the Kelabit Highlands (Sarawak, northern Borneo), is described. Illustrations of the habitus and diagnostic characters of the new species and the similar, polymorphic *A. pulcherrimus* Kodada et al. are presented. Differences to closely related species, based on COI nucleotide sequences and morphological characters, are discussed. *Ancyronyx pulcherrimus* is here recorded from Sarawak for the first time, based on DNA barcoding.

Keywords

Ancyronyx, Coleoptera, Elmidae, taxonomy, variability

Introduction

Borneo, the third-largest island of the world, possesses a very diverse fauna with numerous endemic species including riffle beetles (e.g., Kodada et al. 2014, 2020; Freitag et al. 2018). Tragically, the primary forests of Borneo continually decrease together with their specific aquatic habitats, which are disappearing or deteriorating at an alarming rate (Faridah-Hanum et al. 2018). In the scope of our recent research on the diversity of Dryopidae and Elmidae (Insecta, Coleoptera) in Sarawak, we examined numerous streams in the Kelabit Highlands, Gunung Mulu National Park (NP), and in the Kuching Division. During several months of fieldwork in 2018 and 2019, we noticed that especially the sensitive cloud forest ecosystems are now drastically influenced by climate change. This phenomenon was extremely notable in the Kelabit Highlands and Gunung Mulu NP, with very unpredictable weather conditions, local floods and increased temperatures.

So far, seven species of *Ancyronyx* Erichson have been recorded from Borneo: *A. acaroides* Grouvelle (Brunei, Sabah, Sarawak); *A. clisteri* Kodada et al. (Brunei, Sabah, Sarawak); *A. malickyi* Jäch (Sabah, Sarawak); *A. procerus* Jäch (Brunei, Sabah, Sarawak); *A. pulcherrimus* Kodada et al. (Brunei); *A. reticulatus* Kodada et al. (Sabah); and *A. sarawacensis* Jäch (Brunei, Sabah, Sarawak). Interestingly, all these species belong to the *Ancyronyx variegatus* (Germar) species group, representing larger species inhabiting submerged wood (Freitag and Jäch 2007). Contrarily, in the neighboring islands of the Philippines and Sulawesi, the majority of the species belongs to the *A. patrolus* Freitag & Jäch species group, preferring rocky substrates (Freitag and Balke 2011; Freitag 2013; Freitag and Kodada 2017a, b).

The macropterous *Ancyronyx acaroides*, *A. malickyi*, and *A. procerus* are good flyers and considered to be widespread in Southeast Asia (Jäch et al. 2016); however, the taxonomic and distributional data have been confirmed at a molecular level for only *A. procerus* (Kodada et al. 2020). The remaining four species seem to have restricted ranges and are obviously endemic to Borneo. Fully developed long wings were found in several specimens of *A. sarawacensis* and *A. clisteri.* The remaining individuals studied are most probably macropterous too, considering the elytral shape.

During our fieldwork in the Kelabit Highlands we found a new, large and flightless species resembling *A. pulcherrimus* and *A. reticulatus*. Besides, we discovered populations of *A. pulcherrimus* in the Gunung Mulu NP and in the Kuching Division, which differ to some extent in coloration and morphological characters from the type specimens from Brunei.

Here, we present the description of the new species, *A. lianlabangorum* sp. nov. and provide an analysis of the COI variation along with the examination of the morphological variability in the *A. pulcherrimus* clade with an attempt to discuss possible taxonomic solutions.

Material and methods

Most of the specimens examined were collected from numerous watercourses in Sarawak during three field trips in 2018 and 2019. Adults were collected individually from submerged wood and preserved in 96% ethanol, specifically for the use of DNA barcoding, and samples were as soon as possible stored at –22 °C.

The material used for the study is deposited in the following collections: **BM** (Brunei Museum, Brunei); **CFDS** (Forest Department Sarawak, Kuching, Malaysia); **CKB** (collection of Ján Kodada, Bratislava, Slovakia); **NMW** (Naturhistorisches Museum Wien, Austria); **UB** (Department of Biology, Universiti Brunei, Darussalam, Brunei); **UBDM** (Universiti Brunei Darussalam Museum, Brunei).

In addition to the fresh material, older dry-pinned specimens were soaked in warm water with several drops of concentrated acetic acid and cleaned. Abdomina with genitalia or genitalia only were placed in lactic acid for one or two days and temporarily mounted onto microscopic slides. Specimens were examined and measured using a Leica M205C stereomicroscope with fusion optics and diffuse lighting at magnifications up to 160×. For measurements, an eyepiece graticule (5 mm: 100) or the Leica MC190-HD camera attached to the microscope and LAS software were used. The specimens were photographed under a Zeiss Axio Zoom.V16 stereomicroscope using diffuse LED lighting and a Canon 5D Mark IV camera attached. Dissected genitalia and pregenital segments were studied and illustrated while mounted on a temporary microscope cavity slide covered with a cover glass at magnifications up to 640× with a Leica DM 1000 microscope using a Leica drawing device.

For examination of the wing polymorphism, one elytron was entirely removed, which, unfortunately, resulted often in breaking the elytron due to the firm interlocking devices. Because of the limited number of specimens available, we therefore dissected only a few specimens with different elytral shapes.

Principal component analyses (PCA) were performed separately for male and female specimens using software PAST 3.12 (Hammer et al. 2001) and a variance-covariance matrix with log-transformed variables. PCA plots were subsequently edited in Adobe Illustrator CC.

Metric characters of 13 males and nine females of *A. lianlabangorum* sp. nov. as well as 12 males and 16 females of *A. pulcherrimus* were used for the PCA analyses; all intact specimens identified by mtDNA characters are in the dataset of measurements. Morphometric parameters are provided in tables as range and mean ± standard deviation. The following characters were measured: **BL** (body length without head, length of pronotum and elytra measured along midline); **EL** (elytral length, measured along suture from level of the most anterior point to the most posterior tip in dorsal view); **EW** (maximum combined elytral width); **HW** (head width including eyes); **ID** (interocular distance); **MW** (maximum pronotal width); **PL** (pronotal length along midline).

DNA was extracted from 39 adults representing five species of *Ancyronyx* and three species of *Graphelmis*. Of these, 31 were sequenced successfully, and their datasets were submitted to GenBank (see accession numbers in Table 1). DNA was extracted from the whole specimen or one entire hind leg including the metacoxa with some muscles using E.Z.N.A. Tissue DNA kit (OMEGA bio-tek) or Qiagen Blood and Tissue kit according to the manufacturer's protocols for DNA Extraction from Tissue. A fragment of the 5' end of the mitochondrial gene for cytochrome

Table 1. Samples used in the molecular analyses: origin of samples, GenBank accession numbers.

Specimens, voucher IDs	Origin	GenBank no.
Ancyronyx lianlabangorum JK147	Malaysia, Sarawak	MT367499
Ancyronyx lianlabangorum JK146	Malaysia, Sarawak	MT367500
Ancyronyx lianlabangorum JK144	Malaysia, Sarawak	MT367501
Ancyronyx lianlabangorum JK145	Malaysia, Sarawak	MT367502
Ancyronyx pulcherrimus FZ1632A	Malaysia, Sarawak	–
Ancyronyx pulcherrimus FR324	Brunei	MT568725
Ancyronyx pulcherrimus JK100	Malaysia, Sarawak	MT367503
Ancyronyx pulcherrimus JK101	Malaysia, Sarawak	MT367504
Ancyronyx pulcherrimus JK102	Malaysia, Sarawak	MT367505
Ancyronyx pulcherrimus JK214	Malaysia, Sarawak	MT367506
Ancyronyx pulcherrimus JK215	Malaysia, Sarawak	MT367507
Ancyronyx pulcherrimus JK213	Malaysia, Sarawak	MT367508
Ancyronyx pulcherrimus JK208	Malaysia, Sarawak	MT367509
Ancyronyx pulcherrimus JK195	Malaysia, Sarawak	MT367510
Ancyronyx pulcherrimus JK106	Malaysia, Sarawak	MT367511
Ancyronyx pulcherrimus JK193	Malaysia, Sarawak	MT367512
Ancyronyx pulcherrimus FR344	Malaysia, Sarawak	MT568724
Ancyronyx pulcherrimus JK12	Malaysia, Sarawak	MT367513
Ancyronyx pulcherrimus JK199	Malaysia, Sarawak	MT367514
Ancyronyx pulcherrimus JK105	Malaysia, Sarawak	MT367515
Ancyronyx pulcherrimus JK197	Malaysia, Sarawak	MT367516
Ancyronyx procerus JK143	Malaysia, Sarawak	MT367517
Ancyronyx procerus JK142	Malaysia, Sarawak	MT367518
Ancyronyx procerus JK37	Malaysia, Sarawak	MT367519
Ancyronyx sarawacensis JK38	Malaysia, Sarawak	MT367520
Ancyronyx sarawacensis JK39	Malaysia, Sarawak	MT367521
Ancyronyx clisteri H44	Brunei	LR735553
Ancyronyx clisteri FZ1640	Malaysia, Sarawak	MK505421
Graphelmis monticola FZ530	Malaysia, Kelantan	MK505416
Graphelmis anulata FZ510	Malaysia, Pahang	MK505424
Graphelmis obesa FZ544	Malaysia, Sabah	MK505408

c oxidase subunit I (COI) was amplified with primers LCO1490 and HCO2198 (Folmer et al. 1994). PCR was amplified according to the protocol on https://zsm-entomology.de/wiki/The_Beetle_D_N_A_Lab. Amplification products were mainly purified with Exo-CIP Rapid PCR Cleanup Kit (New England Biolabs), and both strands sequenced by the commercial service of Macrogen Europe Inc. (Amsterdam, Netherlands). Raw sequences were assembled and edited in Geneious v. 6.1.8 (https://www.geneious.com). The genetic distances and maximum likelihood (ML) tree were measured by the K2P model with bootstrap support (1,000 replicates) and performed in MEGA v. 7 software (Kumar et al. 2016). The best-fitted substitution model (GTR+I+G) was selected by jModelTest 2 (Darriba et al. 2012). The maximum likelihood tree based on amino acid sequences was measured by the JTT matrix-based model with bootstrap support (1,000 replicates) and performed in MEGA v. 7 software. Voucher IDs for sequenced specimens are provided between square brackets.

The general morphological terminology follows Kodada et al. (2016) and Lawrence and Ślipiński (2013).

Results

DNA analysis

The COI sequences used in the analysis are 648 bp long, with no ambiguous sites or indels. The ML analysis revealed several well-separated and highly supported, monophyletic clades representing at least five *Ancyronyx* species (Fig. 1). The interspecific divergences

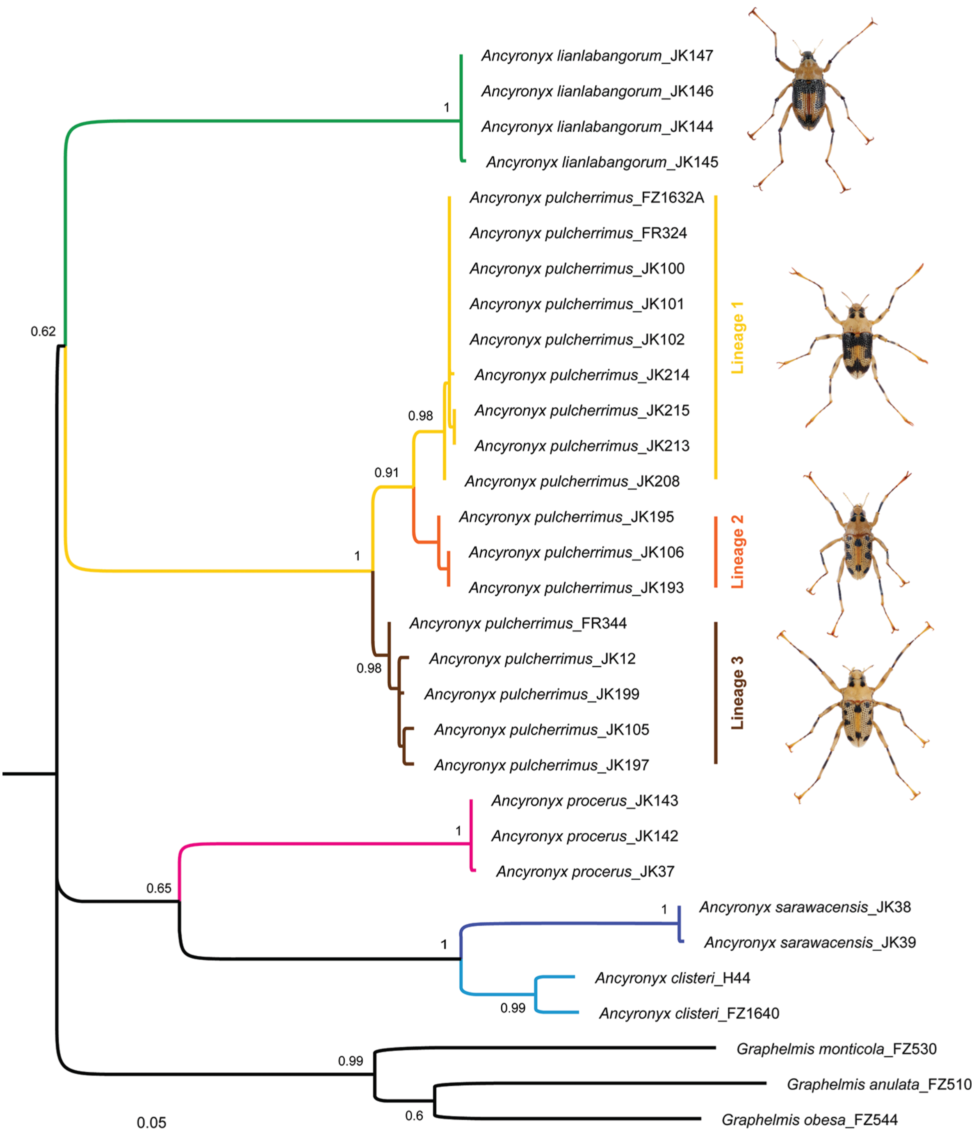

Figure 1. Maximum Likelihood tree inferred from aligned COI mtDNA nucleotides sequences.

were high and varied from 9.4% to 20.0% (Table 2, Suppl. material 1: Table S1). The intraspecific distance ranged from 0.0% to 0.2% in *Ancyronyx lianlabangorum* sp. nov.; it was 2.5% in *A. clisteri*, 0.2% in *A. sarawacensis*, and ranged from 0.0 to 0.2% in *A. procerus.* Mean genetic distances within species are shown in Table 2. More complex divergences for the two latter species were calculated on larger sample sizes from different populations studied by Kodada et al. (2020). Surprisingly, 17 new sequences obtained from two widely separated, allopatric populations of the well-supported *A. pulcherrimus* clade, showed higher pairwise genetic distances ranging from 0.0% to 3.7%. Specimens grouped in three lineages with high statistical support (Fig. 1), two of them appeared to be distinguishable by the elytral color pattern. The first lineage involves sequences of specimens from Gunung Mulu NP sampled from a stream ca 15 km from the type locality and of one specimen from Brunei. This dataset shows only a minimal nucleotide substitution pattern (Suppl. material 2: Table S2) and morphological characters correspond to those of the type specimens of *A. pulcherrimus.* Beyond any doubt, they are conspecific. The second and the third lineages are morphologically similar to each other. Still, they differ from the first lineage in the elytral color pattern, and their genetic distances differs from the first lineage in 1.7% to 3.2% respectively. Although the second and third lineages are sympatric, they differ in the pattern of nucleotide substitutions and their genetic divergence ranges from 2.5% to 3.7% (Suppl. material 1: Table S1). Contrarily, the examination of the external and genital morphology as well as the measurements of the specimens sequenced failed to provide characters useful to distinguish these sympatric lineages (Fig. 2, Table 4). Despite the relatively high divergences within the entire *A. pulcherrimus* clade based on the consensus nucleotide sequences, all specimens were grouped in a single well-supported and unstructured lineage in the tree inferred from amino acid sequences (Suppl. material 3: Figure S1, Suppl. material 4: Table S3). The very uniform genital morphology also confirms this status. Thus, we consider all specimens of this clade being conspecific.

PCA analysis

We performed PCA analyses based on seven characters to quantify and display morphometric variations among *Ancyronyx pulcherrimus* and *A. lianlabangorum* sp. nov. (Fig. 2, Table 4). The first principal component (PC 1) explained 98.87% of the variance in males and 98.45% in females (Table 3). According to the loadings (Table 3),

Table 2. Pairwise genetic distances (*p*-distance) between five *Ancyronyx* species and the genus *Graphelmis* (outgroup) and mean interspecific genetic distance of five *Ancyronyx* species.

		1	2	3	4	5	within species (mean)
1	*A. lianlabangorum* sp. nov.						0.1 %
2	*A. pulcherrimus*	16.9 %					1.8 %
3	*A. procerus*	16.7 %	17.2 %				0.1 %
4	*A. sarawacensis*	19.6 %	19.0 %	17.8 %			0.2 %
5	*A. clisteri*	20.0 %	18.9 %	15.4 %	9.4 %		2.5 %
6	*Graphelmis* (outgroup)	20.0 %	20.0 %	19.1 %	20.7 %	20.7 %	

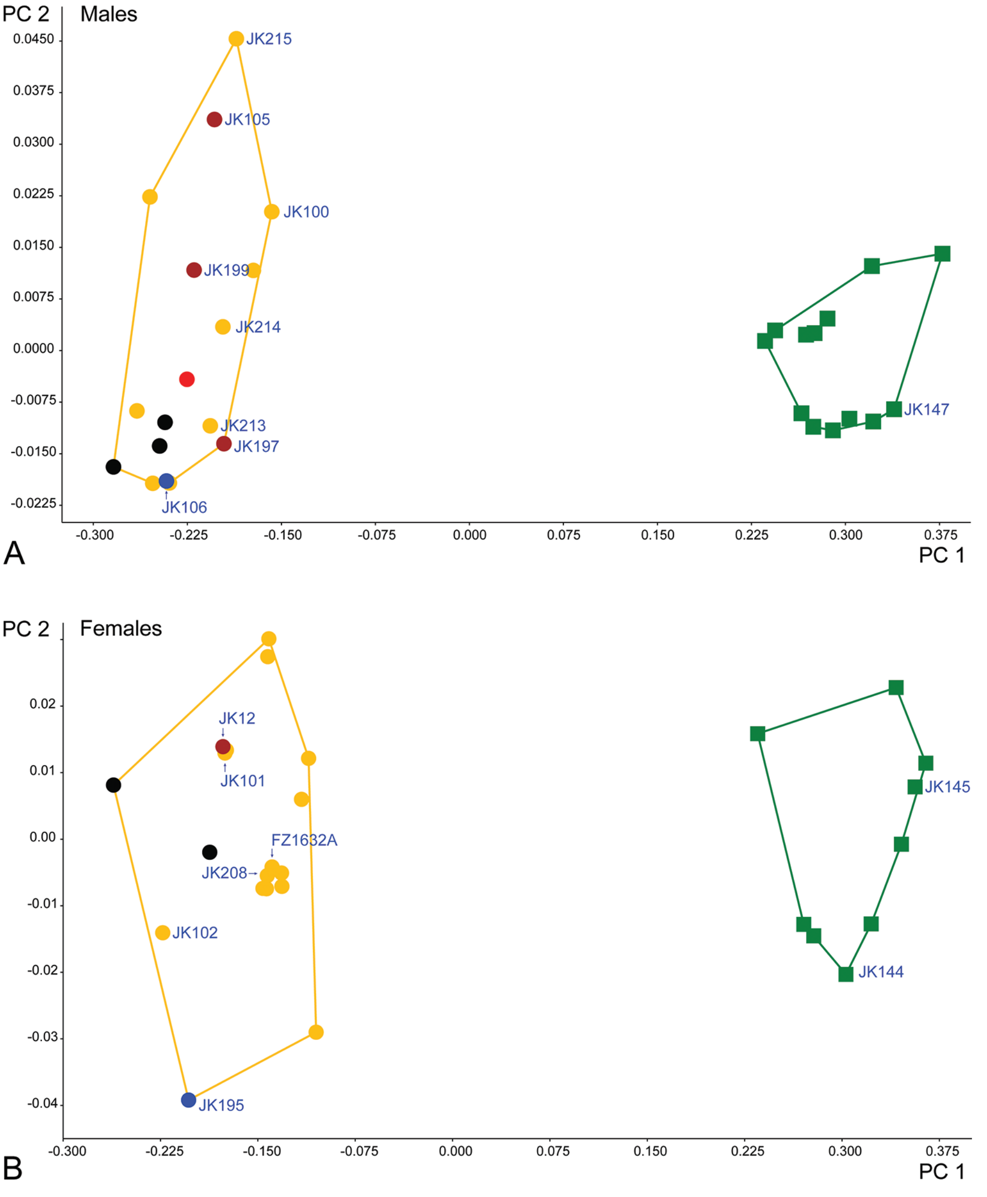

Figure 2. Results of the PCA analysis showing ordination of *Ancyronyx lianlabangorum* sp. nov. and *A. pulcherrimus* Kodada, Jäch & Čiampor specimens along the first two principal components **A** males **B** females. Clusters of *A. pulcherrimus* specimens on left side of plot (yellow lines), clusters of *A. lianlabangorum* sp. nov. on right side (green lines). Yellow circles: *A. pulcherrimus* specimens from Gunung Mulu NP, first lineage; blue circles: *A. pulcherrimus* from Bayur River, second lineage; brown circles: *A. pulcherrimus* from Bayur River, third lineage; black circles: *A. pulcherrimus* from Bayur River, specimens not barcoded, not assignable to the first or second lineage according to morphology; red circle: *A. pulcherrimus* from Brunei; green squares: *A. lianlabangorum* sp. nov. Genetic voucher IDs are included according to Table 1.

Table 3. Loadings onto the principal components for males and females of *Ancyronyx lianlabangorum* sp. nov. and *A. pulcherrimus*. The first and second highest values for each PC are highlighted in bold.

	Males			Females		
	PC 1	PC 2	PC3	PC 1	PC 2	PC3
Explained variance (%)	98.87	0.37	0.34	98.45	0.50	0.46
Loadings of variables:						
BL	0.381	-0.109	-0.270	0.380	0.191	-0.020
EL	**0.420**	-0.630	-0.2981	**0.410**	0.195	-0.327
EW	**0.435**	-0.063	-0.196	**0.445**	0.034	-0.419
PL	0.338	**0.657**	-0.240	0.330	**0.302**	**0.749**
MW	0.354	**0.273**	-0.012	0.342	**0.196**	**0.239**
HW	0.324	0.234	**0.268**	0.323	0.060	-0.244
ID	0.381	-0.160	**0.818**	0.398	-0.889	0.198

Table 4. Metric characters of *Ancyronyx lianlabangorum* sp. nov. and *A. pulcherrimus*, parameters are provided as range and mean ± standard deviation.

	A. lianlabangorum sp. nov.		*A. pulcherrimus* Aggregated data		*A. pulcherrimus* Lineage 1		*A. pulcherrimus* Lineage 2		*A. pulcherrimus* Lineage 3	
	Males $N = 13$	Females $N = 9$	Males $N = 17$	Females $N = 18$	Males $N = 9$	Females $N = 14$	Males $N = 1$	Females $N = 1$	Males $N = 3$	Females $N = 1$
BL: mm	2.54–3.01 2.73 ± 0.12	2.67–3.01 2.86 ± 0.11	1.62–1.84 1.74 ± 0.06	1.70–2.04 1.89 ± 0.09	1.68–1.84 1.76 ± 0.06	1.76–2.04 1.92 ± 0.06	1.70	1.76	1.68–1.76	1.88
EL: mm	**1.86–2.08 1.95 ± 0.07**	**1.90–2.14 2.04 ± 0.08**	**1.12–1.24 1.19 ± 0.04**	**1.18–1.40 1.30 ± 0.06**	**1.12–1.24 1.93 ± 0.04**	**1.18–1.40 1.32 ± 0.05**	**1.20**	**1.20**	**1.14–1.24**	**1.30**
EW: mm	1.26–1.36 1.32 ± 0.04	1.30–1.42 1.37 ± 0.05	0.74–0.82 0.78 ± 0.03	0.78–0.88 0.84 ± 0.02	0.76–0.82 0.79 ± 0.02	0.80–0.88 0.84 ± 0.02	0.74	0.80	0.80–0.82	0.82
BL/EW	**2.02–2.21 2.08 ± 0.05**	**2.04–2.16 2.09 ± 0.03**	**2.10–2.42 2.23 ± 0.08**	**2.09–2.43 2.26 ± 0.07**	**2.17–2.42 2.25 ± 0.08**	**2.20–2.43 2.29 ± 0.06**	**2.30**	**2.20**	**2.10–2.15**	**2.29**
EL/EW	1.44–1.53 1.49 ± 0.02	0.93–1.02 0.97 ± 0.03	1.39–1.63 1.52 ± 0.07	1.47–1.67 1.56 ± 0.05	1.39–1.63 1.52 ± 0.07	1.48–1.67 1.57 ± 0.05	1.62	1.50	1.43–1.51	1.59
PL: mm	**0.78–0.90 0.82 ± 0.03**	**0.78–0.92 0.86 ± 0.05**	**0.50–0.60 0.55 ± 0.03**	**0.54–0.66 0.60 ± 0.03**	**0.52–0.60 0.56 ± 0.03**	**0.56–0.66 0.61 ± 0.03**	**0.52**	**1.58**	**0.54–0.56**	**0.60**
MW: mm	1.02–1.16 1.08 ± 0.04	1.00–1.20 1.11 ± 0.06	0.68–0.76 0.71 ± 0.03	0.70–0.84 0.77 ± 0.04	0.68–0.76 0.72 ± 0.03	0.72–0.84 0.78 ± 0.03	0.70	0.72	0.72–0.76	0.76
PL/MW	**0.70–0.78 0.75 ± 0.02**	**0.74–0.79 0.77 ± 0.02**	**0.74–0.82 0.77 ± 0.03**	**0.73–0.85 0.78 ± 0.03**	**0.74–0.83 0.78 ± 0.03**	**0.73–0.85 0.78 ± 0.03**	**0.74**	**0.81**	**0.74–0.78**	**0.79**
HW: mm	0.60–0.68 0.62 ± 0.02	0.62–0.68 0.65 ± 0.02	0.40–0.46 0.42 ± 0.02	0.42–0.48 0.46 ± 0.02	0.40–0.44 0.42 ± 0.02	0.44–0.48 0.46 ± 0.02	0.42	0.44	0.42–0.46	0.44
ID: mm	**0.34–0.40 0.37 ± 0.01**	**0.34–0.40 0.39 ± 0.02**	**0.22–0.26 0.23 ± 0.01**	**0.22–0.28 0.25 ± 0.01**	**0.22–0.26 0.24 ± 0.01**	**0.24–0.28 0.25 ± 0.01**	**0.24**	**0.26**	**0.22–0.24**	**0.24**

it was strongly correlated with elytral length and width in both sexes. The second principal component (PC 2) explained 0.37% of the variance in males and 0.50% in females, and correlates most strongly with pronotal length and width in both sexes. The analysis revealed two clusters, each representing a different clade/species, distinctly separated along PC 1 axis which strongly correlates with the elytral length and width. The variance revealed by the PCA analysis corresponds to the differences in the actual measurements; body length, elytral length, and elytral width of *A. lianlabangorum* sp. nov. are distinctly greater than in *A. pulcherrimus* (Fig. 2, Table 4). PCA analyses did not confirm the three lineages detected by the phylogenetic analysis of COI nucleotide sequences within the *A. pulcherrimus* clade.

***Ancyronyx lianlabangorum* sp. nov.**
http://zoobank.org/FC6E0E5C-1FE9-431E-BB0B-DF81F5D44FB1

Type locality (Fig. 5A). Pa' Ramudu River (a tributary of Pa' Kelapang River), 3°32'16.2"N, 115°30'22.5"E, ca 900 m a.s.l.; meandering, 7–15 m wide, shallow, slowly flowing through a degraded primary forest; environment of Kampung Ramudu, Kelabit Highlands, Sarawak, Malaysia.

Type material. ***Holotype*** ♂ [JK147] (CFDS): "Malaysia, Sarawak, Miri distr., Ramudu env., 5.03.2019, (No. 51), 3°32'16.2"N, 115°30'22.5"E, ca. 900 m a.s.l., Ramudu riv., J. Kodada & D. Selnekovič lgt.". ***Paratypes*** (CFDS, CKB, NMW): 10 ♂♂ [incl. JK146], 4 ♀♀ [incl. JK144, JK145]: same label data as holotype; 3 ♂♂, 4 ♀♀: "Malaysia, Sarawak, Miri distr., Ramudu env., 5.–6.03.2019, (No.50), Pa' Masia riv., 3°31'57.1"N, 115°30'41.4"E, ca. 970 m a.s.l., J. Kodada & D. Selnekovič lgt."; 1 ♀: "Malaysia, Sarawak, Miri distr., Ramudu env., 28.06.2018, (18) 03°32'50.8"N, 115°29'25.9"E, 920 m a.s.l., Pa' Kasi riv., J. Kodada & D. Selnekovič lgt.".

Diagnosis. *Ancyronyx lianlabangorum* sp. nov. represents one of the largest species characterized by: (1) large size: body length ca 2.5–3.0 mm and elytral width ca 1.3–1.4 mm; (2) comparatively short obovate body form; (3) shiny black head and unicolored yellow pronotum; (4) black-yellowish color pattern of elytra with moderately prevailing black; (5) femora yellowish around middle, lacking dark spot; (6) aedeagus large, with subparallel-sided, apically abruptly narrowed penis; parameres robust, shorter and reaching only up to apical third of penis length, apices wide and emarginate near middle; (7) ovipositor robust, with numerous conspicuous peg-like sensilla; stylus moderately long: ca 0.43× as long as distal portion of coxite; distal part of coxite short and wide: 1.16× as long as wide at middle; longitudinal baculum of paraprocts about twice as long as coxite.

The morphologically most similar *A. pulcherrimus* can be distinguished by: (1) distinctly smaller size: body length ≤2.0 mm and elytral width ≤0.9 mm; (2) subparallel-sided elongate body form; (3) bicolored head and pronotum; (4) black-yellowish color pattern of elytra with moderately prevailing yellow; (5) femora with dark spot near middle; (6) smaller aedeagus with sides of penis subparallel in basal half and gradually tapering in apical half; parameres long, nearly reaching tip of penis, apices subtruncate and wide; (7) ovipositor slender, with fewer conspicuous peg-like sensilla; distal portion of coxite longer and thinner: 1.8× as long as wide at middle; longitudinal baculum of paraprocts ca 1.6× as long as coxite; (8) about 17% divergence of the partial mtDNA for cytochrome c oxidase subunit COI.

Ancyronyx reticulatus, the second similar species, differs from the new species in: (1) distinctly smaller size: body length ≤2.1 mm and elytral width ≤0.9 mm; (2) subparallel-sided elongate body form; (3) bicolored head and pronotum; (4) black-yellowish color pattern of elytra usually with moderately prevailing yellow; (5) surface of elytra and metaventral disc matt, reticulate; (6) smaller aedeagus with sides of penis subparallel along basal half and gradually tapering in apical half; parameres long, nearly reaching tip of penis with apices truncate; (7) ovipositor shorter, with fewer conspicuous peg-like sensilla; stylus longer compared to length of distal portion of coxite; longitudinal baculum of paraprocts ca 1.6× as long as coxite.

Ancyronyx helgeschneideri Freitag & Jäch from Palawan (Philippines) is also quite similar, but differs from the new species in: (1) distinctly smaller size: body length ≤2.0 mm and elytral width up to 0.9 mm; (2) elongate-oval body form; (3) bicolored head and pronotum; (4) elytral color pattern with moderately prevailing dark brown; (5) elytral surface rugulose; (6) distinctly smaller aedeagus with conically tapering penis; parameres long, nearly reaching tip of penis with obliquely truncate apices; (7) ovipositor shorter, stylus and distal portion of coxite relatively longer; longitudinal baculum of paraprocts ca 1.3× as long as coxite.

Description of holotype male. Body form obovate, with rather typical, narrowed "flightless" appearance; elytra strongly convex dorsally, with the highest point at anterior 0.43; BL: 2.97 mm, EW: 1.37 mm, BL/EW: 2.17.

***Coloration* (Fig. 3A).** Labrum black with brownish anterior margin; mandibles dark brown, remaining mouth parts and antennae yellow, except apically darkened terminal antennomere; cranium black dorsally, yellow ventrally; pronotum yellowish; scutellum brownish. Elytra bicolored; anterior half dominantly black with small yellowish spot on humeri and a large central yellowish spot reaching laterally up to the third stria and from anterior fourth up to slightly behind mid-length of the elytra; central spot extending laterad up to margins and posteriad toward apices; thus, the black preapical mark is anchor-shaped. All anepisterna, epimera and lateral portions of metaventrite black; coxae yellow; femora yellowish except small black apical portion; tibiae dark in proximal 0.4 and near articulation with tarsi, yellowish in distal portions; tarsomeres 1–2 darker, tarsomeres 3–5, and claws yellowish brown.

Head. Labrum about as long as clypeus, anterior margin slightly concave, almost straight; bipunctate: larger punctures deeper and with fine setae, smaller punctures dense and very shallow, thus surface appearing microreticulate (visible at a magnification of 160×). Clypeus wide, extremely finely punctate-reticulate on anterior half, smooth and shiny on posterior half. Frons and vertex irregularly punctate, punctation more distinct on central portion, punctures intermixed with flat shiny tubercles; frontoclypeal suture almost straight, extremely finely impressed; surface deeply impressed around antennal insertions. Eyes large, subellipsoidal in lateral view, strongly protruding near middle; ratio of horizontal/vertical eye diameter: 1.36. Antennae 11-segmented, about as long as pronotum; each antennomere with a few scattered trichoid setae; antennomeres 9–11 each with two clusters of peg-like setae near distal margins; terminal segment with additional different sensilla. Ratio of length of antennomeres 1–11: 0.09: 0.09: 0.07: 0.05: 0.05: 0.05: 0.05: 0.07: 0.07: 0.07: 0.17 mm. Gena microsculptured; gula narrow, smooth; gular sutures very fine, but discernible; posterior tentorial pits deep and large. HW: 0.66 mm; ID: 0.38 mm.

Thorax. Pronotum (Fig. 3C) distinctly broader than long, PL/MW: 0.76, PL: 0.87 mm, MW: 1.15 mm, widest near posterior angles; anteriorly attenuate; anterior

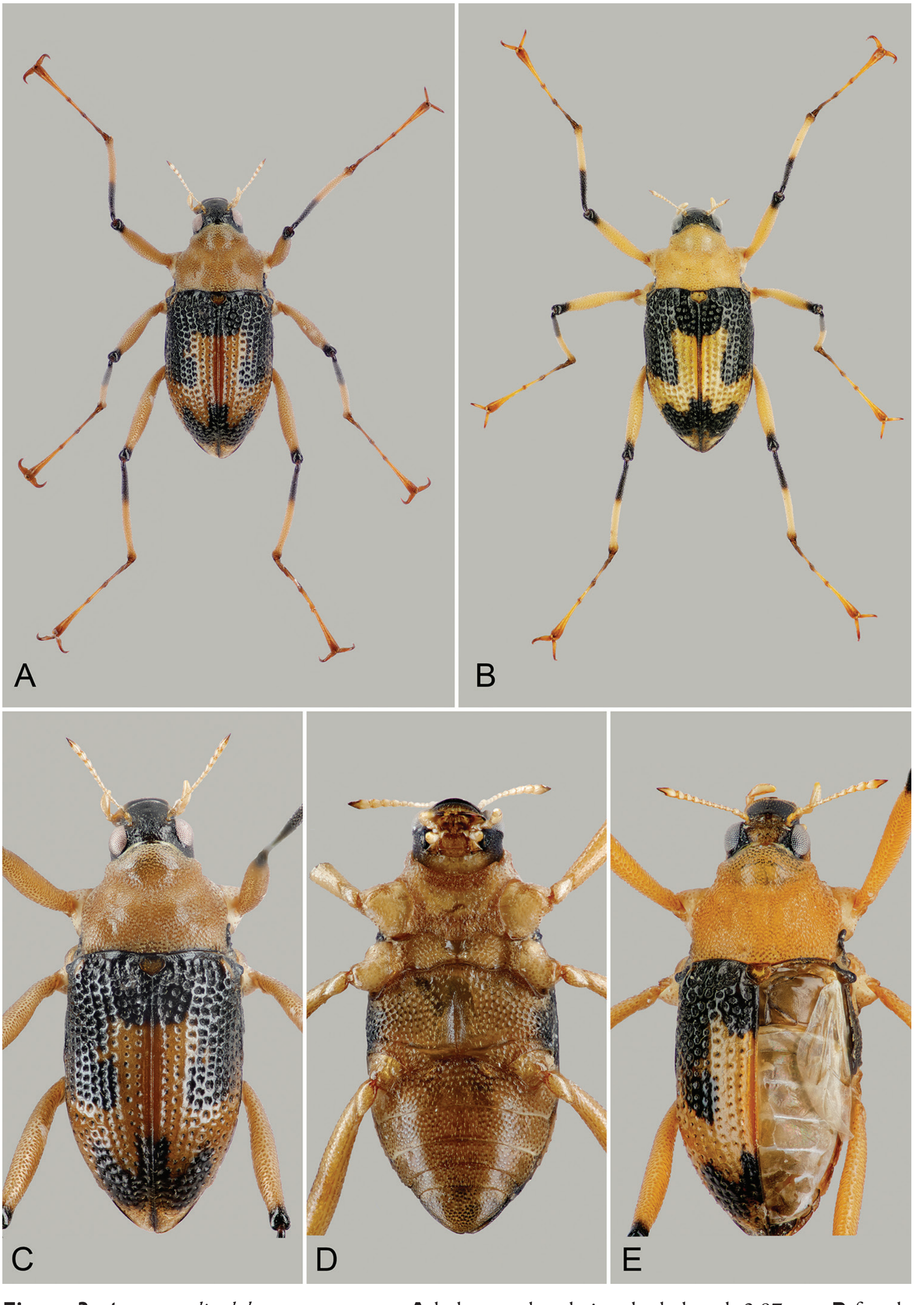

Figure 3. *Ancyronyx lianlabangorum* sp. nov. **A** holotype, dorsal view, body length 2.97 mm **B** female paratype, dorsal view, body length 2.97 mm **C** holotype, dorsal view of body **D** holotype, ventral view of body **E** brachypterous paratype with removed elytron, dorsal view, body length 2.98 mm.

margin strongly arcuate, bordered by narrow protruding translucent edge; hypomeral portion almost entirely visible in dorsal view; anterior transverse groove distinctly impressed, forming a widely open "V"; area posterior of transverse groove strongly gibbous and distinctly higher than anterior portion; mesal longitudinal carina absent; posterolateral oblique grooves shallow, hardly discernible. Pronotal surface with irregularly arranged, flat shiny, sometimes cordiform tubercles, each of which bears a short seta; tubercles in anterior transverse groove dense and coalescent (forming a nearly rasp-like structure), laterad and posteriad gradually smaller and less densely arranged. Prosternum irregularly densely and roughly punctate, very short in front of procoxae; anterior margin strongly concave, unusually thickened; prosternal process distinctly transverse, about as wide as head, depressed near apex, sides slightly sinuate; posterior margin widely rounded, feebly protruding posteriad. Scutellum subpentagonal, smooth and shiny. Elytra (Fig. 3C) moderately elongate and only somewhat wider than pronotum, EL: 2.10 mm, EW: 1.37 mm; convex in lateral view, with highest point at anterior 0.43; lateral sides visible in dorsal view; lateral outline slightly narrowed at level of metacoxae, then gradually convergent towards conjointly rounded apices; elytral punctures forming ten more or less regular rough rows; seven rows between suture and shoulder including accessory scutellary striole (five punctures); punctures large, round to subquadrate and deeply impressed on disc and laterally, smaller and less distinct posteriorly; interstices and intervals very narrow and moderately raised on disc and laterally, posteriorly becoming wider and flatter; surface shiny with sparse short setae and some longer trichoid setae (partly abrased); humeri small but prominent. Lateral rim visible from above, not serrate, finely carinate, positioned at abdominal recess of laterosternites and laterally produced margin of ventrites, very tightly fitted to abdomen. Mesoventrite approximately half as long as prosternum; mesoventral cavity deep and robust; surface strongly and irregularly punctate; without mesoventral discrimen; posterior angles rounded and moderately protruding, raised and partially concealing mesocoxae; mesepimeron small, protruding laterad into short blunt process visible in dorsal view. Metaventrite (Fig. 3D) along midline about as long as combined length of prosternum and mesoventrite; anterior margin arcuate, anterior portion declined; disc with deep wide longitudinal depression mesally, discrimen finely raised, metakatepisternal suture fine; surface densely irregularly roughly punctate, punctures coarser and denser laterally. Hind wing distinctly shorter than elytron, unfunctional, reduced in length and venation (Fig. 3E). Forelegs very long, about 1.73× as long as body; pro- and mesocoxae large and prominent, strongly protruding laterally at least partially visible in dorsal view, bluntly drop-shaped; metacoxae smaller and less protruding laterally. Femora and tibiae with short setae and characteristic pattern of smooth, shiny elongate flat tubercles; tibiae with a few longer setae; distal tarsomeres with several longer setae near apex; claws large, strongly curved, base with three teeth, two larger ones and a smaller one.

Abdomen **(Fig. 3D).** Intercoxal process moderately longer than length of first ventrite posterior of metacoxae, anterior margin very wide, arcuate; anteromedial portion

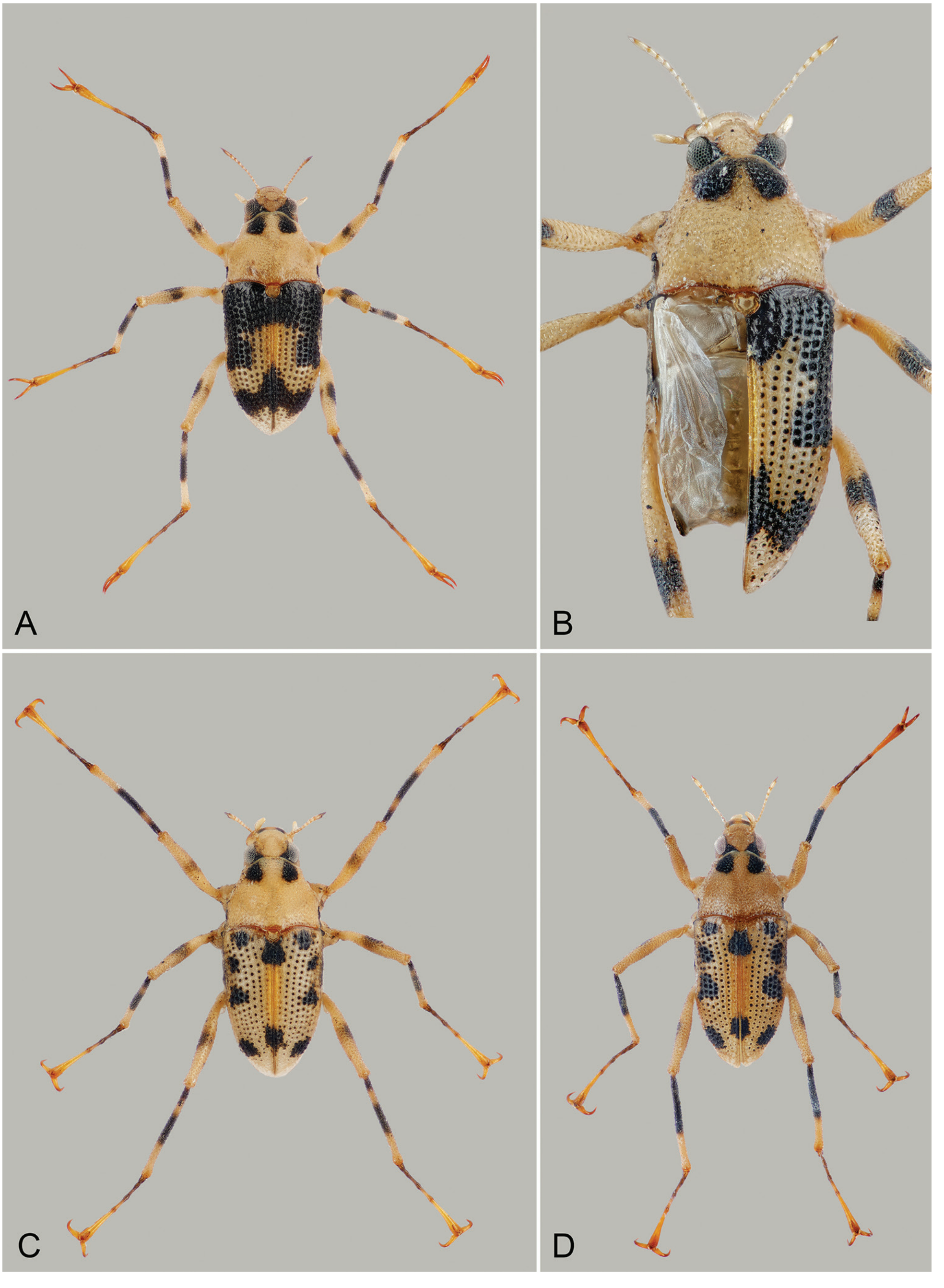

Figure 4. *Ancyronyx pulcherrimus* **A** male from Gunung Mulu NP, body length 1.82 mm **B** brachypterous male from Gunung Mulu NP, dorsal view (left elytron and apical segments of abdomen removed), body length 1.92 mm **C** male from Bayur River, dorsal view, body length 1.70 mm **D** male [JK106] from Bayur River, dorsal view, body length 1.70 mm.

Figure 5. Habitats of *Ancyronyx lianlabangorum* sp. nov. (**A–C**) and *A. pulcherrimus* (**D**) **A** type locality, Pa' Ramudu River **B** Pa' Masia River **C** Pa' Kasi River **D** shaded shallow creek in primary forest, Gunung Mulu NP.

on same level with bottom of metaventral depression; rows of deep punctures arranged along anterior margin; ratio of length of ventrites 1–5: 0.37: 0.23: 0.23: 0.18: 0.30 mm. Surface of ventrites 2–5 with sparse punctures and flat setiferous, almost cordiform tubercles; punctures more distinct on medial area; tubercles more prominent and more conspicuous laterally; fifth ventrite densely tuberculate.

Sternite IX ca 600 μm long and very robust (Fig. 7B); apical margin moderately arcuately emarginate; lateroapical portion with a few moderately long setae and numerous microtrichia; paraprocts not reaching beyond apical margin; ventral strut short and wide. Tergite VIII with complete transverse sinuate ridge dividing anterior and posterior portion, anterior surface with dense microtrichia; sides subparallel along basal half and arcuate in apical half; surface with sparse hair-like setae, which are more robust and longer on sublateral portions than along lateral margins.

Aedeagus (Fig. 6A–C) ca 600 μm long; penis including lateral basal apophyses ca 2.4× as long as phallobase, robust and well sclerotized, sides subparallel, short apical portion abruptly narrowed and moderately curved ventrad (lateral view), dorsolateral portion with numerous shorter setae; apex widely rounded; basal apophyses long; ventral sac large; fibula conspicuous and long, moderately wide; dorsal portion mesally with unusual, more distinctly pigmented/sclerotized longitudinal structure (similar to fibula); surface of endophallus with spinules; corona distinct. Phallobase asymmetrical. Parameres robust and wide, reaching apical third of penis, broadest near base, narrowest near middle; dorsal and ventral outline moderately concave; apices wide, rounded and emarginated in middle, appearing nearly double-peaked (in dorsal/ventral view); apical and lateral surface of parameres with short setae.

Female abdomen and ovipositor. Tergite VIII with strong complete transverse sinuate ridge; anterior portion with dense microtrichia; posterior portion more distinctly pigmented, with two sublateral clusters of strong conspicuous hair-like setae; lateral sides arcuate; apical margin with protruding translucent edge. Sternite VIII robust, median strut short and wide, apex moderately emarginated with more robust hair-like setae (Fig. 7C). Ovipositor (Fig. 7A) 590 μm long; stylus narrow and almost straight, relatively short: ca 0.43× as long as distal portion of coxite. Coxite robust, short and wide, rounded at posterolateral angle; distal portion ca 1.16× as long as wide at middle, slightly bent, with numerous conspicuous stout peg-like setae and with a few thinner peg-like setae, the latter mainly at apical portion; inner margin densely pubescent; proximal portion about as long as distal portion, with several types of peg-like and short fine hair-like setae (omitted in Fig. 7A). Transverse baculum well sclerotized; longitudinal baculum of paraprocts (valvifers) almost twice as long as coxite (measured from the apical margin of coxite to point where it is joining the transverse baculum).

Secondary sexual dimorphism. Females are on average larger and broader than males from the same population, with more elongate ventrite 5, and the longitudinal depression of their metaventrite is broader but shallower.

Variability. The specimens vary moderately in size (Table 4). In contrast to, e.g., *Ancyronyx sarawacensis* and *A. procerus*, the elytral color pattern varies only slightly

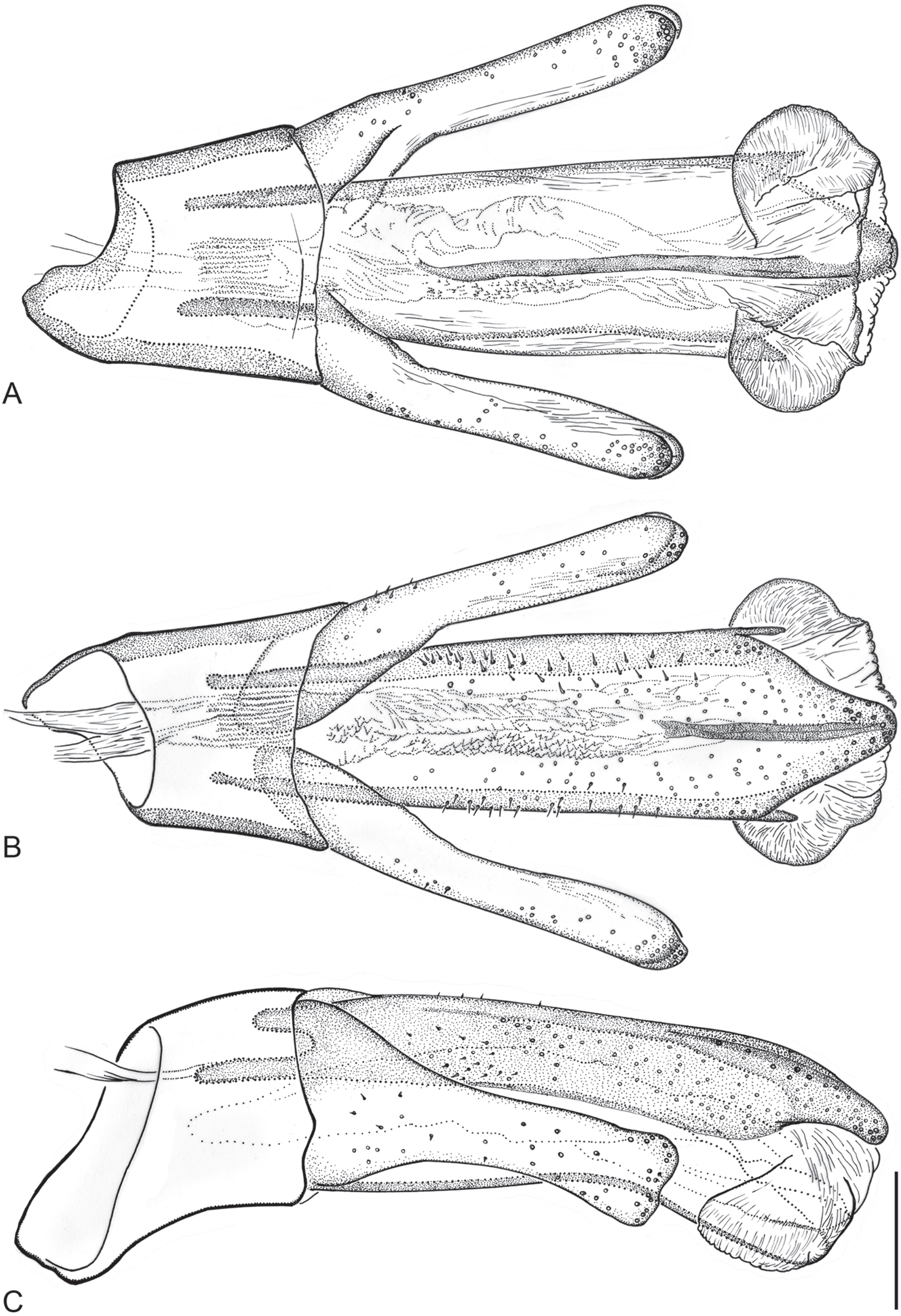

Figure 6. *Ancyronyx lianlabangorum* sp. nov., aedeagus of holotype **A** ventral view **B** dorsal view **C** lateral view. Scale bar: 0.1 mm.

(Fig. 3B). Only a single specimen possesses a bicolored head (Fig. 3E). The surface structure of the head varies moderately in the density of the tubercles and punctures, and most of the specimens lack any trace of the frontoclypeal suture. The shape of the elytra indicates that the specimens have reduced hind wings, in contrast to the apterous 32 specimens of *A. variegatus* examined by Shepard (2019).

Habitat. At the type locality (Pa' Ramudu River), the specimens were sampled from an approximately 200 m long stretch. The river was shallow, moderately meandering, about 7–15 m wide, slowly flowing through a degraded primary forest (data for 5 March 2019). Shallow reaches (10–40 cm) with slow current alternated with deeper pools (50–120 cm); the river was partly shaded by the riparian vegetation including large old trees, dense bamboo groves, shrubs and massive tree ferns (*Cyathea* sp.). The substrate contained gravel, sand, stones and exposed boulders; however, some shallow sections showed bedrock ledge only. Submerged wood, as well as large packs of bamboo roots were present mainly 50–100 m downstream of the connection with the Pa' Masia River. *Ancyronyx lianlabangorum* sp. nov. was collected exclusively from massive, submerged logs in deeper pools with slow current. In contrast, submerged bamboo rootlets and smaller pieces of wood were inhabited only by *Ancyronyx sarawacensis* and *A. acaroides*.

The Pa' Masia River represents a headwater stream in degraded primary forest (Fig. 5B). During our sampling on 6 March 2019, it was about 5–50 cm deep, 3–7 m wide and slowly flowing. Adults inhabited submerged wood in several deeper pools with almost no current.

A single female sampled on 28 June 2018 was found on a large submerged log in a pool of the entirely shaded, shallow Pa' Kasi near the connection with Pa' Kelapang River in the vicinity of Kampung Ramudu (Fig. 5C). The river bottom contained mainly firmly arranged pebbles and rocks.

The altitude of the collection sites ranges from 900 to 970 m a.s.l.

Neither the intensive collection efforts in Pa' Kelapang River near connections with Pa' Ramudu, Pa' Kasi, Pa' Ngaruren and Pa' Buah rivers near Kampung Ramudu revealed any further adults or larvae of *A. lianlabangorum* sp. nov., nor the samplings of the upstream sections of Pa' Kelapang River near Batu Patong, Pa' Mada as well as Pa' Umor. However, in all these habitats we found submerged autochthonous wood inhabited by *Ancyronyx sarawacensis*, *A. procerus*, *A. acaroides*, and several species of *Graphelmis*, *Leptelmis* Sharp, *Elmomorphus* Sharp and *Stenomystax* Kodada, Jäch & Čiampor.

Distribution. This species is known from a few small, slowly flowing tributaries of Pa' Kelapang River near Kampung Ramudu, Kelabit Highlands, Sarawak.

Etymology. We named the species in honor of David Lian Labang ("Uncle David") and his son David Lian Labang Jr from Bareo (Kelabit Highlands, Sarawak). They run Labang Longhouse Lodge in Bareo. Ján Kodada and David Selnekovič have always been happy to take advantage of this fabulous accommodation during several field trips. Uncle David is a retired, well-known employee of the Forest Department Sarawak, who contributed to the knowledge and conservation of Sarawak's nature. We are most grateful to both for many stories and shared information about the terrain, nature, culture, as well as for their endless repertoire of jokes!

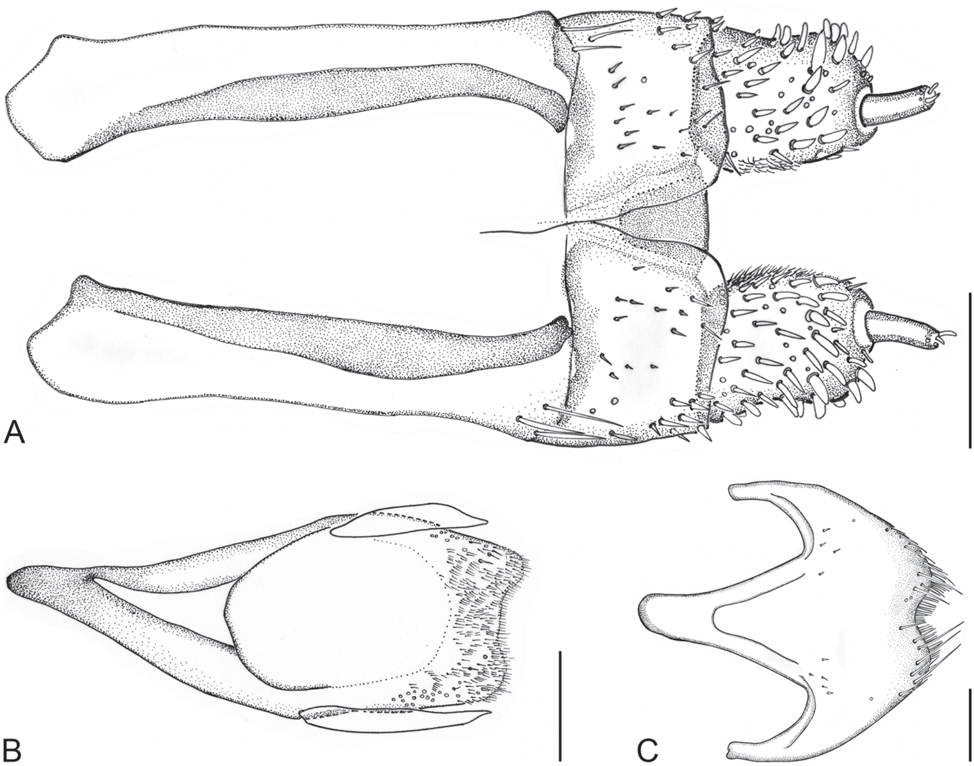

Figure 7. *Ancyronyx lianlabangorum* sp. nov. **A** ovipositor, paratype [JK145], ventral view **B** male sternite IX, holotype, ventral view **C** female sternite VIII, paratype [JK145], ventral view. Scale bars: 0.1 mm.

Ancyronyx pulcherrimus Kodada, Jäch & Čiampor, 2014

Type locality. Ingei River, forest pool, 4°09'15"N, 114°43'04"E, Belait District, Brunei.

Material examined. Type material. ***Holotype*** ♂ (BM): "Brunei: Belait Distr. Sg. Ingei, forest pool near Base Camp, 14.VI.2010 04°09'15"N, 114°43'04"E leg. Mayyer Ling (34)". ***Paratypes*** (NMW, UB): 1 ♂ and 2 ♀♀, same label data as holotype.

Additional material (CCB, CFDS, CKB, NMW, UBDM).

Lineage 1. Sarawak 9 ♂♂ [incl. JK100, JK213, JK214, JK215], 15 ♀♀ [incl. JK101, JK102, JK208, FZ1632]: "Malaysia, Sarawak, Marudi distr., Gunung Mulu NP, 16.10.2018, (40) 04.0267°N, 114.8234°E, 55 m a.s.l., small stream in primary forest, Kodada & Selnekovič lgt.". Brunei 2 ♂♂, 1 ♀ [FR324]: "Brunei: Temburong; small Sungai Peradayan; rivulet, subm. wood; dist. primary forest; c. 25m a.s.l. c. 4°44'25"N, 115°09'50"E 04.11.1997 leg. Mendoza (6f)".

Lineages 2 and 3. Sarawak 5 ♂♂ [incl. JK105, JK106], 1 ♀ [JK12]: "Malaysia, Sarawak, Kuching distr., Bayur riv. near Kampung Bayur, 20.10.2018, 1°14'42.3"N, 110°17'35.3"E 40 m a.s.l., J. Kodada & D. Selnekovič lgt."; 2 ♂♂ [JK197, JK199], 4 ♀♀ [incl. JK193, JK195]: same locality and collectors, but 22.02.2019, (No.43); 1 ♂

[FR344]: "Malaysia: Sarawak, Kg. Bayur 35km SSE Kuching, small hill river Bayur R.; run, subm. wood; second. veget./farmland; c. 50m a.s.l., c.1°14'40"N, 110°17'34"E 12.11.1993 leg. Mendoza (19f)".

Variability. *Ancyronyx pulcherrimus* was represented by three barcode lineages, which are tentatively considered conspecific in the absence of further evidence. The specimens of the first lineage were collected in northern Sarawak and Brunei, while the specimens of the second and third lineages occur sympatrically in southwestern Sarawak. The first lineage is characterized by: (1) elytra predominantly black with a central yellowish, nearly X-shaped pattern and yellowish apices; (2) femora with black band between middle and proximal fourth; and (3) tibiae black on proximal three-quarters (compare Fig. 4 in Kodada et al. 2014). The type specimens are rather uniform in these characters, and all individuals recently collected in Gunung Mulu NP generally agree with them. However, there is some minor variation in the extent of the black coloration of the elytra, pronotum and legs (Fig. 4A, B). The examination of the hind wings of six specimens of the Gunung Mulu population and three specimens from Temburong (Brunei) revealed only short wings not reaching the abdominal apex (Fig. 4B). Macropterous or apterous forms were not detected, and the elytral shape of the remaining specimens suggests that they are flightless too.

The specimens of the second and third lineages differ from the type specimens in the predominantly yellowish elytra, which are provided with several black lateral and sutural spots of variable size. The pronotal spots are usually smaller, and the dark femoral bands are smaller, paler or obsolete (Fig. 4C, D). The examination of their hind wings revealed one macropterous and five brachypterous specimens.

Lineages detected by the analysis of COI nucleotide sequences were not confirmed by PCA analyses of morphometric characters (Fig. 2, Table 4) or corroborated by the genital morphology.

Habitat and syntopic taxa. The stream inhabited by a large population of *A. pulcherrimus* was a small, slowly flowing, very shallow, and entirely shaded meandering creek in Gunung Mulu NP (55 m a.s.l.). It included large amounts of accumulated leaves, and the bottom substrate contained sand and gravel, as well as woody debris (Fig. 5D). The specimens co-occurred with *Ancyronyx sarawacensis* and two new species of Elmidae (*Okalia* Kodada & Čiampor and *Leptelmis*).

The second population was found in a moderately wide (5–8 m) lowland river near Kampung Bayur (Kuching Division); the sampled stretch was shallow and meandering, with sandy/gravelly substrate containing submerged logs, woody debris, and leaves. All specimens were collected exclusively in reaches with stronger current from submerged logs together with *Ancyronyx procerus*, *A. acaroides*, and several other Elmidae (*Leptelmis* sp. and *Graphelmis* spp. of the *G. picta* (Reitter) and *G. marshalli* Hinton species groups).

Distribution. *Ancyronyx pulcherrimus* was so far known only from Brunei (Jäch et al. 2016). The species is here recorded for the first time from Malaysia, where it was collected in Gunung Mulu NP (northern Sarawak) and in the Kuching Division (southwestern Sarawak).

Our recent collecting activities found *A. pulcherrimus* to be less abundant and less widely distributed than *A. sarawacensis*, *A. procerus*, or *A. acaroides*, probably also due to the low dispersal ability of flightless populations.

Discussion

Striking and specific yellowish-black color patterns usually characterize *Ancyronyx* adults (e.g., Jäch 1994, 2004; Kodada et al. 2014). However, the analysis of COI sequences confirmed the existence of intraspecific variability regarding coloration and other morphological characters within populations of *A. sarawacensis* and *A. procerus* (Kodada et al. 2020). All eight *Ancyronyx* species known from Borneo live on submerged wood (woody debris) in running water. They mainly occur in primary or slightly degraded forests, although some specimens were sampled in secondary forests or forest remnants as well. Not any specimen was found in large, polluted rivers or at light traps placed near such rivers in the Kuching Division during our sampling in 2018 and 2019 (Kodada et al. 2020). *Ancyronyx lianlabangorum* sp. nov. and *A. pulcherrimus* represent two obviously rare, flightless species with low dispersal ability. Massive deforestation generally threatens flightless species, which may survive mainly in protected, undisturbed regions. Apparent changes in seasonal patterns affecting precipitation and the intensity and frequency of extreme weather events will strongly impact the populations of these two species.

Specimens of *Ancyronyx lianlabangorum* sp. nov. were sampled from a morphologically uniform, small population, and also their nucleotide COI sequences showed minimal divergences (Suppl. material 1: Table S1).

Surprisingly, the nucleotide COI divergences among the three lineages of *A. pulcherrimus* showed taxonomic complexity (Suppl. material 2: Table S2). To decide whether they represent one, two, or even three species is challenging and not yet resolved, as there are no standardized procedures to address the taxonomic status of such genetic lineages. However, all specimens were grouped to a single, well-supported but unstructured clade in the tree inferred from amino acid COI sequences (Suppl. material 3: Fig. S1), as all their pairwise distances dropped to 0.00% (Suppl. material 4: Table S3). The very uniform genital and external morphology also supports the homogeneity of the *A. pulcherrimus* clade. Consequently, the differences in the color pattern are considered here as a result of intraspecific variability as reported for other Bornean and Philippine *Ancyronyx* (Kodada et al. 2020; Sabordo et al. in press).

Additionally, the nucleotide sequence divergences among other well-defined *Ancyronyx* species from Borneo were considerably higher, ranging from 9.4% to 20.0% (Table 2). They correspond to unusually deep interspecific divergences detected in a regional survey of 1872 northern European species of Coleoptera as well (Pentisaari et al. 2014). The effectiveness of DNA barcodes in the identification of Coleoptera varies. While barcoding worked quite well when tested for thousands of European beetles (Pentisaari et al. 2014; Hendrich et al. 2015), problems for evolutionary young and radiating species have also been reported (e.g., Hendrich et al. 2010; Balke et al. 2013;

Komarek and Freitag 2020). The higher diversification within the *A. pulcherrimus* clade agrees with a study of Silphidae from Japan, including a meta-analysis of 51 species from 15 families, which revealed a higher genetic differentiation and a higher diversification rate among populations in the flightless lineages than in the flight-capable lineages (Ikeda et al. 2012). Thus, the possibility of the existence of multiple distinct species within the *A. pulcherrimus* clade cannot be ruled out.

Final solutions for the taxonomic status of the three *A. pulcherrimus* lineages require a larger sample size, comprising more localities from a more extensive distributional range. Such an approach should also be combined with the use of nuclear markers.

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Supplementary material 1

Table S1. Pairwise genetic distances (Kimura 2-parameter distance) between nucleotide sequences of *Ancyronyx* and *Graphelmis* species based on the 648 bp barcoding fragment of COI.

Authors: Ján Kodada, Manfred A. Jäch, Hendrik Freitag, Zuzana Čiamporová-Zaťovičová, Katarína Goffová, Dávid Selnekovič, Fedor Čiampor Jr

Data type: DNA data table

Link: https://doi.org/10.3897/zookeys.1003.55541.suppl1

Supplementary material 2

Table S2. DNA barcoding patterns of the variable nucleotide positions in the 648 bp long COI sequence alignment of the *Ancyronyx pulcherrimus* clade.

Authors: Ján Kodada, Manfred A. Jäch, Hendrik Freitag, Zuzana Čiamporová-Zaťovičová, Katarína Goffová, Dávid Selnekovič, Fedor Čiampor Jr

Data type: DNA data table

Link: https://doi.org/10.3897/zookeys.1003.55541.suppl2

Supplementary material 3

Figure S1. Maximum Likelihood tree inferred from aligned COI mtDNA amino acids sequences.

Authors: Ján Kodada, Manfred A. Jäch, Hendrik Freitag, Zuzana Čiamporová-Zaťovičová, Katarína Goffová, Dávid Selnekovič, Fedor Čiampor Jr

Data type: image

Link: https://doi.org/10.3897/zookeys.1003.55541.suppl3

Supplementary material 4

Table S3. Pairwise genetic distances (p-distance) between 29 amino acid sequences (216 positions) of *Ancyronyx* species and the genus *Graphelmis* (outgroup).

Authors: Ján Kodada, Manfred A. Jäch, Hendrik Freitag, Zuzana Čiamporová-Zaťovičová, Katarína Goffová, Dávid Selnekovič, Fedor Čiampor Jr

Data type: DNA data table

Link: https://doi.org/10.3897/zookeys.1003.55541.suppl4

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New and interesting findings of scarab beetles (Coleoptera, Scarabaeoidea) from Tajikistan

Adam Byk[1], Andrzej Matusiak[2], Artur Taszakowski[3], Wojciech T. Szczepański[4], Marcin Walczak[3], Marek Bunalski[5], Lech Karpiński[6]

1 *Department of Forest Protection, Institute of Forest Sciences, Warsaw University of Life Sciences – SGGW, Nowoursynowska 159/34, PL-02-776, Warsaw, Poland* **2** *Odyńca 69/31, PL-02-664, Warsaw, Poland* **3** *Institute of Biology, Biotechnology and Environmental Protection, Faculty of Natural Sciences, University of Silesia in Katowice, Bankowa 9, PL-40-007, Katowice, Poland* **4** *Silesian Entomological Society, Jana III Sobieskiego 2, PL-41-902, Bytom, Poland* **5** *Department of Entomology and Environmental Protection, University of Life Sciences, Dąbrowskiego 159, PL-60-594, Poznań, Poland* **6** *Museum and Institute of Zoology, Polish Academy of Sciences, Wilcza 64, PL-00-679, Warsaw, Poland*

Corresponding author: Lech Karpiński (lkarpinski@miiz.waw.pl)

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Abstract

We report on new findings of nearly 50 species that represent four families of the superfamily Scarabaeoidea, which were collected during an expedition to western Tajikistan that was carried out in June and July 2014. *Rhyssemodes transcaspicus* Rakovič, 1982 is recorded from the country for the first time. Moreover, we describe and illustrate the differences in the external morphology between *Euonthophagus gibbosus* (Scriba, 1790) and *E. koshantschikoffi* (Reitter, 1891), the latter of which has a doubtful systematic position. In the collected material of approximately 1,000 specimens, more than 90% of the species and 95% of the individuals belong to the family Scarabaeidae. The other species represent the families Geotrupidae, Glaphyridae, and Hybosoridae.

Keywords

Euonthophagus koshantschikoffi, Geotrupidae, Glaphyridae, Hybosoridae, new records, *Rhyssemodes transcaspicus*, Scarabaeidae

Introduction

The first comprehensive study that contained information on the scarabaeoid beetle fauna of Tajikistan was presented by Medvedev and Lopatin (1961), who reported on 183 species in the country but provided scant data on habitats, biology, and distribution. More information on the local Scarabaeoidea of the subfamilies Melolonthinae, Rutelinae, and Dynastinae, as well as on the family Glaphyridae, can be found in the earlier monographs of the notable "Fauna SSSR" series (Medvedev 1949, 1951, 1952, 1960) and on the subfamilies Cetoninae and Valginae in the later continuation of this series (Medvedev 1964). These works also contain identification keys to species. Additionally, some information on the scarabaeoid beetles of the subfamily Aphodiinae that occur in Tajikistan was included in the studies of Protzenko (1968), Nikritin (1973), and Nikolajev (1987). Nikolajev (2003) published another work of a great importance for recognising the fauna of the family Geotrupidae; the paper included species of the genus *Lethrus* Scopoli, 1777 (Lethrinae), which constitutes a significant share in the local beetle fauna. Three years later, an extensive monograph containing comprehensive information on the subfamily Scarabaeinae (Scarabaeini, Gymnopleurini, Onthophagini, Onitini) of Russia and adjacent countries, including Tajikistan, was released (Kabakov 2006). According to the latest edition of the Catalogue of Palaearctic Coleoptera, 274 species of scarabaeoid beetles are currently known from Tajikistan (Löbl and Löbl 2016).

The majority of the works on the Scarabaeoidea of Tajikistan were published in the last century. They treat the scarabaeoid Tajik fauna in the context of areas that often reach far beyond the current boundaries of the country, and sometimes even beyond the commonly accepted borders of Central Asia. Consequently, many records have a rather general character without any precise locality data. Therefore, we aim to supplement the current information on the distribution of the taxa of the superfamily Scarabaeoidea in the country. An additional goal of our study is to gather and disseminate information contained in valuable publications that are, however, difficult to access and were usually published exclusively in Russian.

Material and methods

Tajikistan is a relatively small intra-continental country that is situated at the boundary of the subtropical and temperate climatic zones. It is located in the mountain desert zone of the Eurasian continent, in the southern part of Central Asia. In this region, diverse ecosystems such as deserts, steppes, conifer forests, mixed mountain forests, and high-mountain deserts are widely represented. The formation of this unique biological diversity in the country, which counts numerous endemic and relict species, is due to the varied mountain climatic conditions and historical natural processes (Safarov 2003).

An entomological expedition, which consisted of four scientists from the former Department of Zoology, University of Silesia in Katowice (Poland), was undertaken over 25 days from 24 June to 18 July 2014. During the research, several field surveys

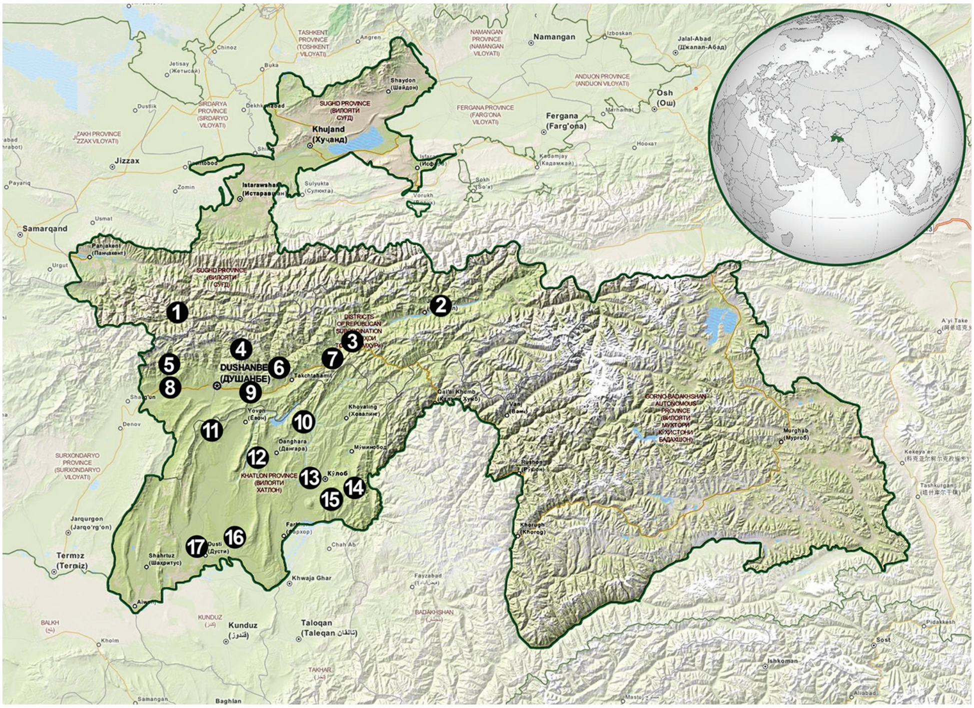

Figure 1. Research plots in the western part of Tajikistan **1** Iskanderkul **2** Tojikobod **3** Gharm **4** Safed Dara (Takob) **5** Kuran, Karatag river valley **6** Romit **7** Komsomolabad and Nurobod **8** Shahrinav **9** Arykboshi **10** Chavrok and Kangurt **11** Dohanaklik **12** Ganchi **13** W of Kulob, Vose–Kulob road **14** Shurroabad **15** Sarichashma **16** Novabad **17** Jilikul (OpenStreetMap contributors).

in various locations in the western part of Tajikistan were conducted (Fig. 1). The most extensive studies were carried out in the central part of the region and in the south-western part of the country along the Afghanistan border. Our investigations were conducted in several research plots including the villages or environs of Arykboshi, Dushanbe, Dohanaklik, Ganchi, Gharm, Iskanderkul, Jilikul, Kangurt, Karatag, Komsomolabad, Kulob, Nurobod, Romit, Sarichashma, Shahrinav, Shurroabad, Takob, Tojikobod, and Vose (Table 1).

The area covered by our study includes several different nature ecosystems such as alpine meadows, mesophilic shrubs, shrub steppes, broad-leaf forests, and tugay, as well as agroecosystems such as gardens, orchards, fields, and pastures (Figs 2, 3). Various field methods were used because scarabaeoid beetles comprise species with a very diverse biology. However, because coprophagy is the main type of feeding behaviour in this group, most of the sampling took place in pastures and semi-desert areas where dung of domestic and wild animals was examined (Fig. 2E). Additionally, beetles were attracted to the artificial light sources during the night.

Beetles were photographed in their habitats with Canon EOS 550D, Canon EOS 600D, and Olympus XZ-1 cameras. Mounted specimens were imaged using a Leica

Table 1. Collection sites of the scarabaeoid beetles in Tajikistan (2014).

No.	Locality	Geographical coordinates	Altitude [m a.s.l.]	Date of collection
1.	Iskanderkul [Искандаркӯл] (Fig. 2A)	39°05'04.1"N, 68°22'03.2"E	2300	18 Jul. 2014
2.	Tojikobod [Тоҷикобод] (Fig. 2B)	39°05'34.1"N, 70°51'45.2"E	2225	13 Jul. 2014
3.	Gharm [Гарм] (Fig. 2C)	39°01'11.1"N, 70°22'07.6"E	1330	14 Jul. 2014
4.	Safed Dara [Сафед Дара] = Takob (Такоб) (Fig. 2D)	38°51'30.7"N, 68°59'58.7"E	2300	27–28 Jun. 2014
		38°49'27.9"N, 68°56'10.4"E	1850	8–10 Jul. 2014
5.	Karatag river valley, near Kuran [Куран] (Fig. 2F)	38°41'44.8"N, 68°22'05.1"E	1060	30 Jun.–1 Jul. 2014
				17 Jul. 2014
6.	Romit [Ромит] (Fig. 2G)	38°46'19.3"N, 69°16'58.5"E	1285	26–27 Jun. 2014
7.	Komsomolabad [Дарбанд] (Fig. 2H)	38°51'50.2"N, 69°56'32.0"E	1160	11–12 Jul. 2014
	Nurobod [Нуробод] (Fig. 3A)	38°47'45.2"N, 69°51'32.6"E	1215	11 Jul. 2014
8.	Shahrinav [Шахринав]	38°36'04.1"N, 68°19'36.0"E	870	1 Jul. 2014
9.	Arykboshi [Арыкбошӣ]	38°34'39.3"N, 69°04'03.7"E	905	28 Jun., 2 Jul. 2014
10.	Kangurt [Кангурт] env.	38°11'57.7"N, 69°33'18.7"E	1065	5 Jul. 2014
	Chavrok [Чаврок], N of Kangurt (Fig. 3B)	38°18'07.9"N, 69°32'51.5"E	1215	5 Jul. 2014
11.	Dohanaklik [Даханакиик] (Fig. 3C)	38°13'50.4"N, 68°40'23.0"E	860	16 Jul. 2014
12.	Ganchi [Сафедсанг]	38°00'08.4"N, 69°09'39.4"E	765	25 Jun. 2014
13.	W of Kulob [Куляб], Vose–Kulob road (Fig. 3D)	37°54'37.0"N, 69°42'41.1"E	525	3 Jul. 2014
		37°54'56.3"N, 69°42'53.6"E	535	3 Jul. 2014
14.	Shurroabad [Ноҳияи Шӯрообод] (Fig. 3E)	37°49'16.1"N, 70°03'20.4"E	2150	4 Jul. 2014
15.	Sarichashma [Сары-Чашма]	37°44'47.6"N, 69°46'19.0"E	920	25 Jun. 2014
15.	Novabad [Новабад] (Fig. 3G)	37°30'14.3"N, 68°53'20.3"E	580	16–17 Jul. 2014
17.	Jilikul [Ҷиликӯл] (Fig. 3H)	37°27'05.5"N, 68°31'16.7"E	330	24 Jun. 2014

M205C stereomicroscope with Leica LED5000 HDI high-diffuse dome illumination and equipped with a Leica DFC495 digital camera. The images that were produced were stacked, aligned, and combined using Leica application suite v. 4.9.0 software. The images selected were cleaned, retouched, and arranged into figures using Adobe Photoshop CS6 software. The geographical coordinates were recorded using a Garmin Oregon 550T 3-Inch Handheld GPS Navigator. For each specimen that was collected, the exact location, altitude, date, and the names of the collectors are given.

All the specimens listed below were collected by Artur Taszakowski (AT), Lech Karpiński (LK), Marcin Walczak (MW), and Wojciech T. Szczepański (WTS). Taxa were identified by Adam Byk (AB), Andrzej Matusiak (AM), and Marek Bunalski (MB). The specimens are preserved in the entomological collection of the Department of Natural History of the Upper Silesian Museum, Bytom, Poland (USMB) and in the collections of the authors. The systematic arrangement and nomenclature were adopted from the Catalogue of Palaearctic Coleoptera (Löbl and Löbl 2016).

Results

As a result of this study, about 950 beetles belonging to 48 species in four families of the superfamily Scarabaeoidea were collected: Geotrupidae (1 sp.), Glaphyridae (2 spp.), Hybosoridae (1 sp.), and Scarabaeidae (44 spp.), including Scarabaeinae (17 spp.), Aphodiinae (12 spp.), Melolonthinae (5 spp.), Cetoniinae (5 spp.), Rutelinae (3 spp.), and Dynastinae (2 spp.). The list of the recorded taxa along with their new localities is presented below.

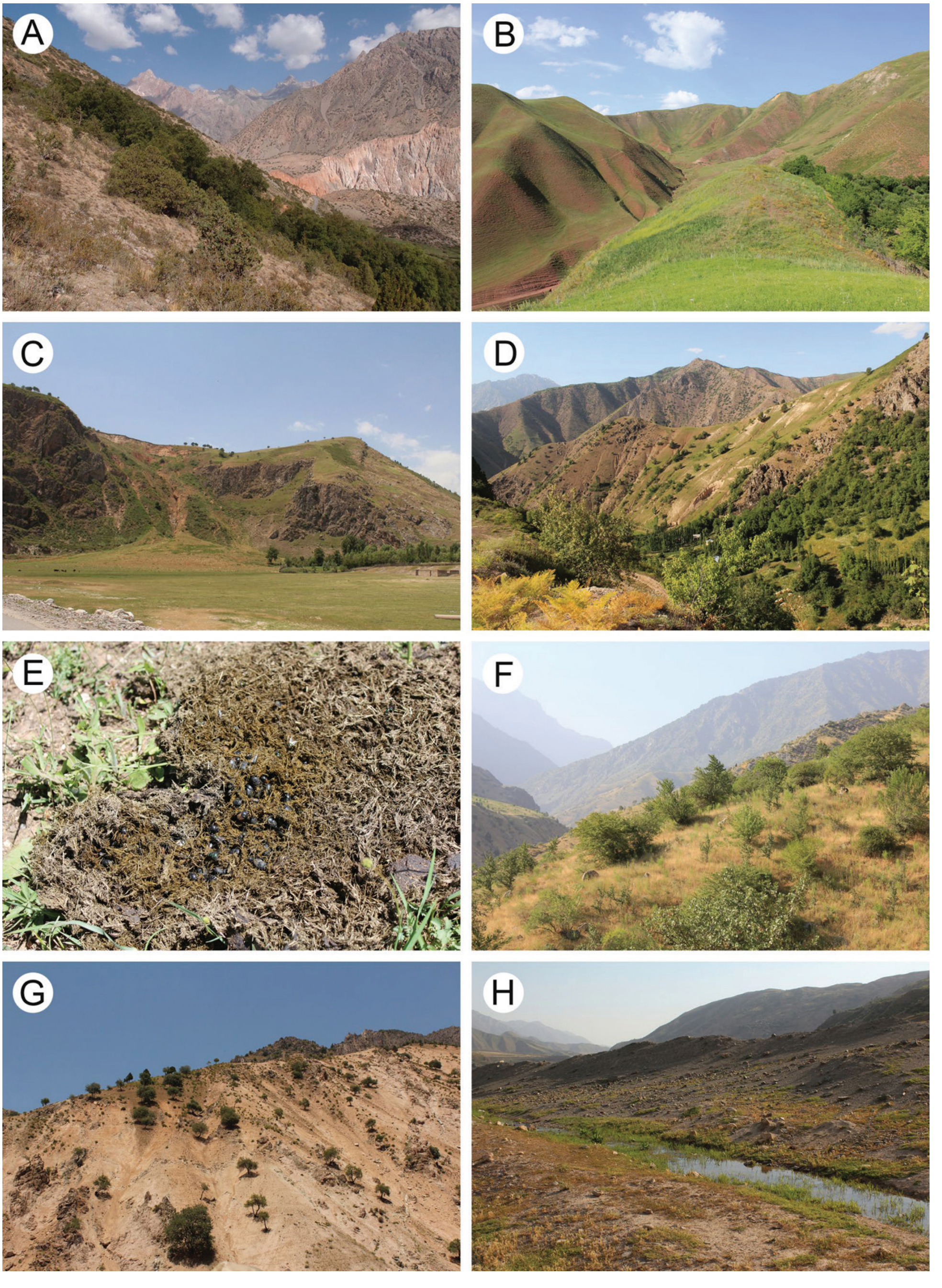

Figure 2. Typical landscapes in Tajikistan, habitats of scarabeoid beetles **A** mountain slope covered with shrubs including *Juniperus* in Iskanderkul environs **B** mountain meadow in Tojikobod environs **C** mountain slopes in Gharm environs **D** mountain meadow overgrown by *Prangos* and *Ferula* in Safed Dara environs **E** swarm of *Onthophagus* beetles in cow dung, Safed Dara environs **F** mountain slope covered with shrubs in Karatag environs **G** steep slope covered with single trees in Romit environs **H** watercourse near a pasture in Komsomolabad environs.

Family Geotrupidae Latreille, 1802
Subfamily Lethrinae Oken, 1843

***Lethrus* (*Mesolethrus*) sp.**

Karatag, 17 Jul. 2014, 1058 m a.s.l., [MW] – 1 ex. (♀);
Shurroabad, 4 Jul. 2014, 2152 m a.s.l., in dung, [WS] – 1 ex. (♀).

Remarks. Three species from the subgenus *Mesolethrus* Nikolajev, 2003 were recorded from Tajikistan, and another two from the neighboring Uzbekistan (Bagaturov and Nikolajev 2015). Females of these species are extremely similar and thus almost unidentifiable. The determination was additionally hindered by significant degree of body damage of our specimens.

Family Hybosoridae Erichson, 1847
Subfamily Hybosorinae Erichson, 1847

***Hybosorus illigeri* Reiche, 1853**

Chavrok, N of Kangurt, 5 Jul. 2014, 1217 m a.s.l., at light, [WS] – 1 ex., [MW] – 2 exx.

Family Glaphyridae Macleay, 1819
Subfamily Amphicominae Blanchard, 1845

***Eulasia* (*Solskiola*) *analis* (Solsky, 1876)**

Romit, 27 Jun. 2014, 1283 m a.s.l., [WS] – 1 ex.;
Takob, 27 Jun. 2014, 2298 m a.s.l., [LK] – 1 ex.

Remarks. This species occurs in Uzbekistan, southern Turkmenistan, northeastern Iran, and northern Afghanistan. In Tajikistan, it was reported from a number of localities: Mumilabad, Kulab, Langar, Darvaz (Medvedev 1960). This is an early spring species, which is usually found from March to May (Medvedev 1960; Medvedev and Lopatin 1961).

We collected it at the end of June in high mountain meadows near Romit and Takob. Two individuals were found on flowers of herbaceous plants.

Subfamily Glaphyrinae W.S. Macleay, 1819

***Glaphyrus* (*Eoglaphyrus*) *turkestanicus* Semenov, 1889**

Shurroabad, 4 Jul. 2014, 2152 m a.s.l., mountain meadows, pastures, [AT] – 1 ex.

Remarks. *Glaphyrus turkestanicus* is distributed in Uzbekistan, Afghanistan (Medvedev 1960), and Tajikistan, where it was recorded mainly from the northern part of the country (Oburdon, Artuch) (Medvedev and Lopatin 1961).

We collected a single male of this species in a mountain meadow near Shurroabad. The beetle was found inside a calyx of *Carduus* sp. (Fig. 3F).

Family Scarabaeidae Latreille, 1802
Subfamily Aphodiinae Leach, 1815

Acanthobodilus immundus (Creutzer, 1799)

W of Kulob, 3 Jul. 2014, 526 m a.s.l., at light, [AT] – 5 exx.;
W of Kulob, 3 Jul. 2014, 537 m a.s.l., at light, [WS] – 1 ex.;
Kangurt, 5 Jul. 2014, 1066 m a.s.l., in dung, [WS] – 1 ex., at light, [AT] – 2 exx., in dung, [MW] – 3 exx.;
Chavrok, N of Kangurt, 5 Jul. 2014, 1217 m a.s.l., at light, [WS] – 4 exx.;
Komsomolabad, 11 Jul. 2014, 1160 m a.s.l., in dung, [WS] – 1 ex.;
Dohanaklik, 16 Jul. 2014, 862 m a.s.l., in dung, [WS] – 3 exx.;
Novabad, 17 Jul. 2014, 580 m a.s.l., desert, semi-desert, in cow dung, [AT] – 1 ex., [MW] – 4 exx.

Acrossus luridus (Fabricius, 1775)

Takob, 28 Jun. 2014, 2300 m a.s.l., [WS] – 2 exx.

Aphodius pedellus De Geer, 1774

Romit, 26 Jun. 2014, 1250 m a.s.l., [WS] – 8 exx.;
Karatag, 17 Jul. 2014, 1058 m a.s.l., in cow dung, [AT] – 1 ex., [MW] – 1 ex.

Bodilus lugens (Creutzer, 1799)

Karatag, 1058 m a.s.l., 30 Jun. 2014, in dung, [MW] – 5 exx., 17 Jul. 2014, in cow dung, [AT] – 3 exx., [MW] – 2 exx., shrubs, [AT] – 1 exx.;
Kangurt, 5 Jul. 2014, 1066 m a.s.l., agrocenoses, at light, [AT] – 2 exx., [MW] – 3 exx.;
Chavrok, N of Kangurt, 5 Jul. 2014, 1217 m a.s.l., at light, [WS] – 2 exx.;
Novabad, 17 Jul. 2014, 580 m a.s.l., desert, semi-desert, in cow dung, [AT] – 1 ex.

Colobopterus erraticus (Linnaeus, 1758)

Romit, 27 Jun. 2014, 1250 m a.s.l., [WS] – 2 exx.;
Karatag, 30 Jun. 2014, 1058 m a.s.l., in dung, [WS] – 1 ex., [MW] – 6 exx.;
Komsomolabad, 11 Jul. 2014, 1160 m a.s.l., in dung, [WS] – 1 ex., [MW] – 1 ex.

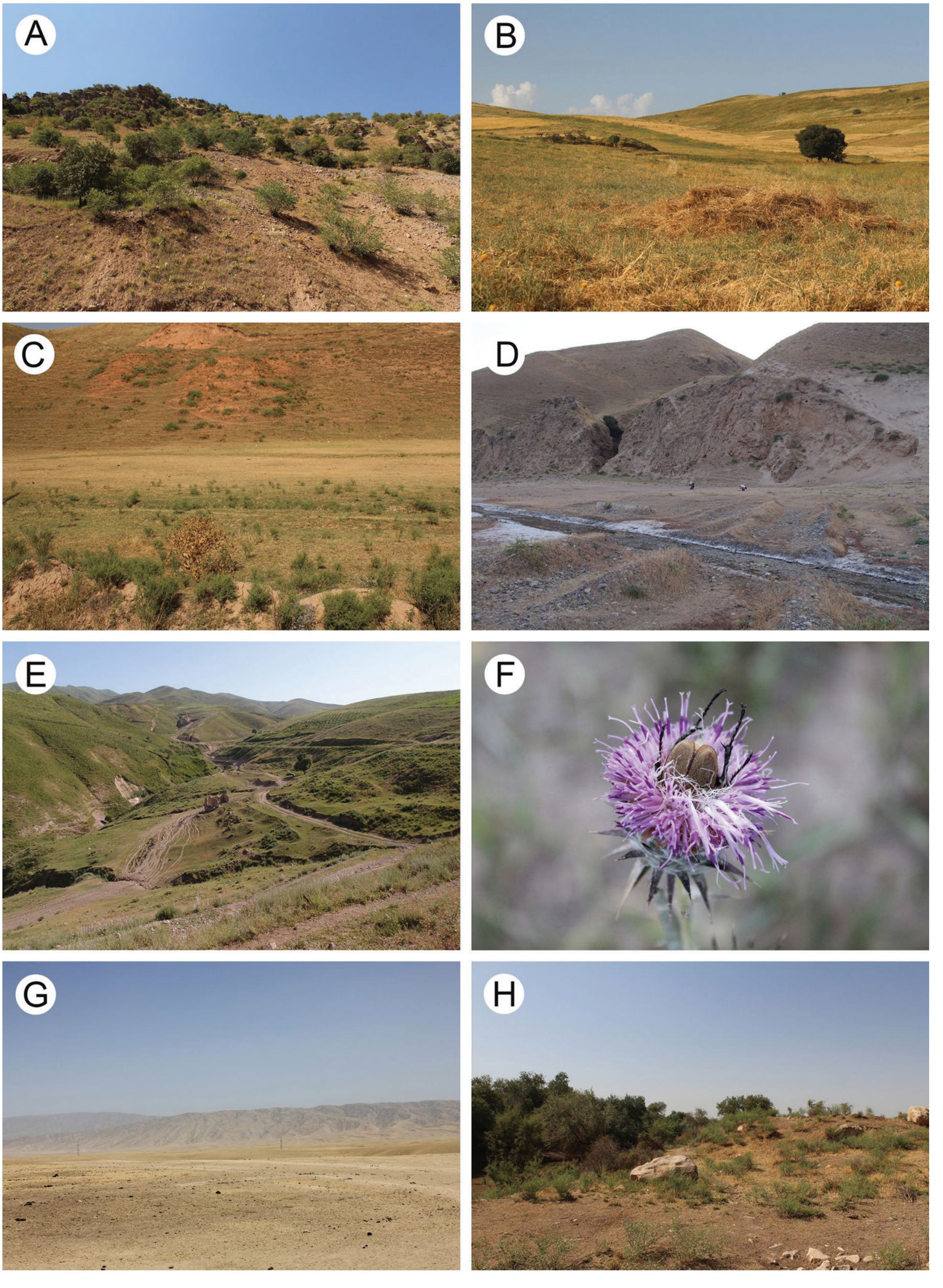

Figure 3. Typical landscapes in Tajikistan, habitats of scarabeoid beetles **A** lush shrub vegetation in Nurobod environs **B** grasslands in Chavrok environs **C** grasslands in Dohanaklik environs **D** grazed slopes in Kulob environs **E** grassy hills in Shurroabad environs **F** *Glaphyrus turkestanicus* feeding in flower cup, Shurroabad environs **G** semi-desert with lots of dung in Novabad environs **H** bank of Vakhsh River overgrown with tamarisk shrubs in Jilikul environs.

***Esymus pusillus pusillus* (Herbst, 1789)**

Takob, 28 Jun. 2014, 2300 m a.s.l., [WS] – 2 exx., [MW] – 3 exx.;
Arykboshi, 2 Jul. 2014, 906 m a.s.l., [WS] – 1 ex., [MW] – 3 exx.

***Eudolus quadriguttatus* (Herbst, 1783)**

Kangurt, 5 Jul. 2014, 1066 m a.s.l., agrocenoses, at light, [AT] – 1 ex.;
Chavrok, N of Kangurt, 5 Jul. 2014, 1217 m a.s.l., at light, [WS] – 3 exx.

***Labarrus lividus* (Olivier, 1789)**

Karatag, 17 Jul. 2014, 1058 m a.s.l., at light, [AT] – 1 ex.;
Kangurt, 5 Jul. 2014, 1066 m a.s.l., agrocenoses, at light, [AT] – 1 ex.;
Chavrok, N of Kangurt, 5 Jul. 2014, 1217 m a.s.l., at light, [WS] – 4 exx.

***Neocalaphodius moestus* (Fabricius, 1801)**
Fig. 4A

Jilikul, 24 Jun. 2014, 332 m a.s.l., at light, [WS] – 5 exx.;
Arykboshi, 2 Jul. 2014, 906 m a.s.l., at light, [WS] – 1 ex., [MW] – 2 exx.;
Karatag, 30 Jun. 2014, 1058 m a.s.l., at light, [AT] – 1 ex., [MW] – 2 exx.;
W of Kulob, 3 Jul. 2014, 526 m a.s.l., at light, [AT] – 5 exx.;
W of Kulob, 3 Jul. 2014, 537 m a.s.l., at light, [WS] – 1 ex.;
Chavrok, N of Kangurt, 5 Jul. 2014, 1217 m a.s.l., at light, [WS] – 1 ex.;
Dohanaklik, 16 Jul. 2014, 862 m a.s.l., in dung, [WS] – 3 exx.;
Novabad, 17 Jul. 2014, 580 m a.s.l., desert, semi-desert, in cow dung, [AT] – 1 ex., [MW] – 1 ex.

***Planolinellus vittatus* (Say, 1825)**

Kangurt, 5 Jul. 2014, 1066 m a.s.l., in dung, [MW] – 2 exx.

***Rhyssemodes transcaspicus* Rakovič, 1982**
Fig. 5

Jilikul, 24 Jun. 2014, 332 m a.s.l., at light, [WS] – 6 exx., [MW] – 1 ex.;
W of Kulob, 3 Jul. 2014, 537 m a.s.l., at light, [WS] – 7 exx., [MW] – 1 ex.;
Chavrok, N of Kangurt, 5 Jul. 2014, 1217 m a.s.l., at light, [WS] – 1 ex.

Remarks. This species has been reported from Uzbekistan and the southern territory of European Russia. According to Rakovič and Král (2015), its presence in Uzbekistan is confirmed by the holotype's label: "Golodnaya Step" (about 120 km southeast

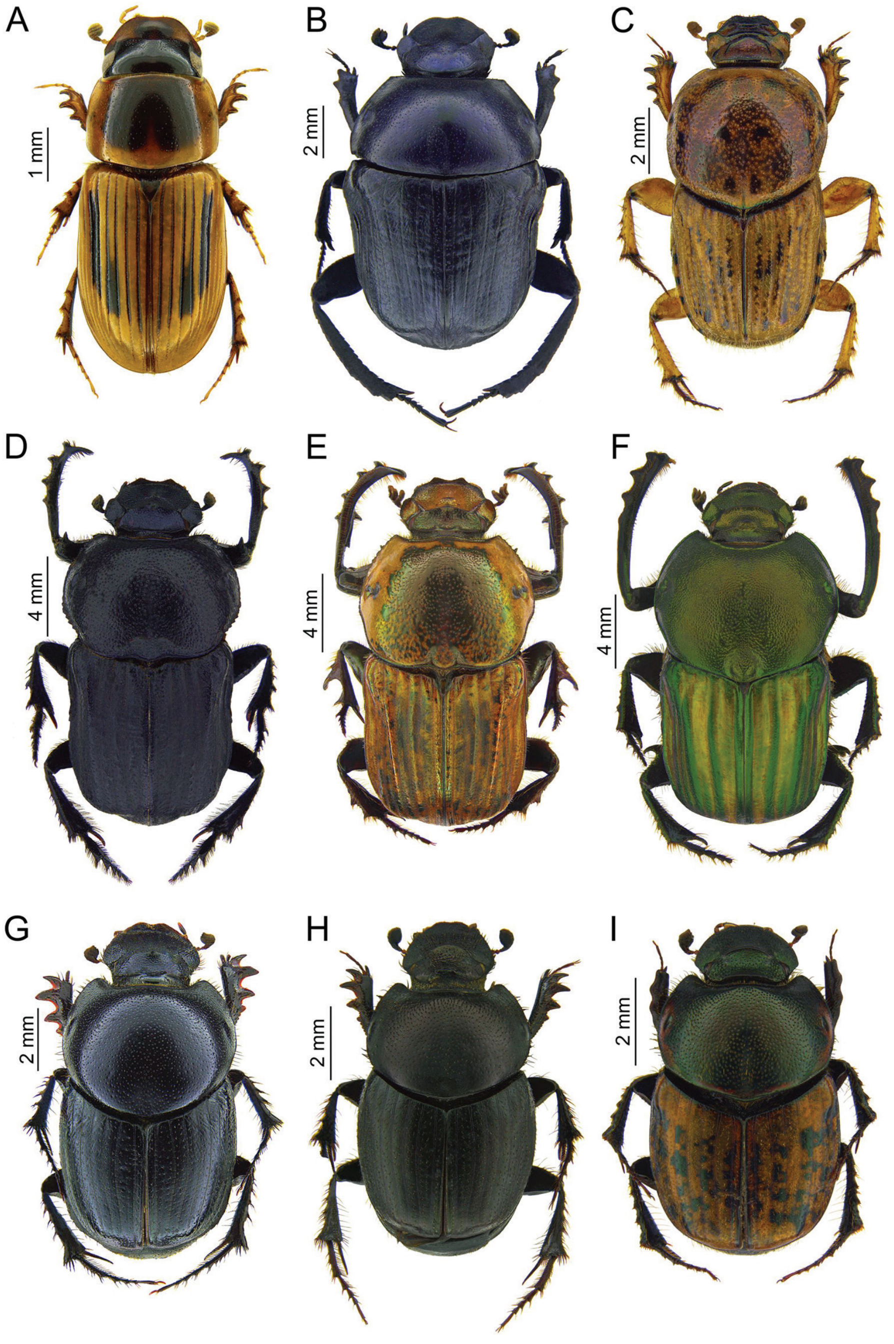

Figure 4. Photos of Scarabaeidae specimens collected during the expedition to Tajikistan in 2014 **A** *Neocalaphodius moestus* **B** *Gymnopleurus aciculatus* **C** *Euoniticellus pallipes* **D** *Cheironitis haroldi*, male **E** *Cheironitis pamphilus*, male **F** *Onitis humerosus*, male **G** *Euonthophagus sulcicollis*, female **H** *Onthophagus sibiricus*, female **I** *Onthophagus haroldi*.

of Tashkent). The presence of *Rh. transcaspicus* in Astrakhan Province and Kalmykia, Russia, was documented by Shokhin (2007) and Shokhin et al. (2014). Although *Rh. transcaspicus* had been synonymised with *Rhyssemodes tenuisculptus* Reitter, 1892 by Nikolajev (1987), it was restored 15 years later by Shokhin (2002).

We collected 16 individuals of *Rh. transcaspicus* at three different sites in the western part of the country, about 300 km south of its type locality. All individuals were found near human settlements with semi-arid (environs of Jilikul) and farmland (environs of Kulob and Chavrok) habitats in the immediate vicinity. In all cases, imagines were attracted to UV light.

This is the first record for Tajikistan. The material was additionally verified by Łukasz Minkina (Poland).

Figure 5. *Rhyssemodes transcaspicus* Rakovič, 1982, species new for the Tajik fauna.

Rhyssemus germanus (Linnaeus, 1767)

W of Kulob, 3 Jul. 2014, 526 m a.s.l., at light, [AT] – 1 ex.;
W of Kulob, 3 Jul. 2014, 537 m a.s.l., at light, [WS] – 1 ex.

Subfamily Scarabaeinae Latreille, 1802

Gymnopleurus aciculatus Gebler, 1841
Fig. 4B

Karatag, 17 Jul. 2014, 1058 m a.s.l., in cow dung, [MW] – 5 exx.;
W of Kulob, 3 Jul. 2014, 526 m a.s.l., in dung, [WS] – 1 ex., [MW] – 5 exx.;
Shurroabad, 4 Jul. 2014, 2152 m a.s.l., in dung, [WS] – 5 exx., [AT] – 10 exx.;
Kangurt, 5 Jul. 2014, 1066 m a.s.l., in dung, [WS] – 3 exx., [MW] – 5 exx.;
Novabad, 17 Jul. 2014, 580 m a.s.l., desert, semi-desert, in cow dung, [MW] – 2 exx.

Euoniticellus fulvus (Goeze, 1777)

Sarichashma, 25 Jun. 2014, 921 m a.s.l., in dung, [WS] – 5 exx.;
Romit, 26 Jun. 2014, 1250 m a.s.l., [WS] – 2 exx.;
Karatag, 30 Jun. 2014, 1058 m a.s.l., in cow dung, [MW] – 6 exx., 17 Jul. 2014, [AT] – 18 exx., [MW] – 14 exx.;
W of Kulob, 3 Jul. 2014, 526 m a.s.l., in dung, [WS] – 2 exx., [MW] – 13 exx., [AT] – 1 ex.;
Shurroabad, 4 Jul. 2014, 2152 m a.s.l., in dung, [WS] – 1 ex., [AT] – 1 ex.;
Komsomolabad, 11 Jul. 2014, 1160 m a.s.l., in dung [WS] – 8 exx., [MW] – 21 exx.;
Gharm, 14 Jul. 2014, in dung, [WS] – 6 exx.;
Dohanaklik, 16 Jul. 2014, 862 m a.s.l., in dung, [WS] – 6 exx., [AT] – 1 ex.;
Novabad, 17 Jul. 2014, 580 m a.s.l., desert, semi-desert, in cow dung, [AT] – 8 exx., [MW] – 3 exx.

Euoniticellus pallipes (Fabricius, 1781)
Fig. 4C

Karatag, 30 Jun. 2014, 1058 m a.s.l., in cow dung, [MW] – 1 ex.;
W of Kulob, 3 Jul. 2014, 526 m a.s.l., in dung, [WS] – 14 exx., [MW] – 2 exx., [AT] – 1 ex.;
Kangurt, 5 Jul. 2014, 1066 m a.s.l., in dung, [WS] – 1 ex.;
Dohanaklik, 16 Jul. 2014, 862 m a.s.l., in dung, [WS] – 3 exx.;
Novabad, 17 Jul. 2014, 580 m a.s.l., [MW] – 1 ex.

Cheironitis haroldi (Ballion, 1871)
Fig. 4D

Karatag, 30 Jun. 2014, 1058 m a.s.l., [MW] – 3 exx., 17 Jul. 2014, [MW] – 4 exx., [AT] – 2 exx.;

W of Kulob, 3 Jul. 2014, 526 m a.s.l., in dung, [MW] – 5 exx.;
Shurroabad, 4 Jul. 2014, 2152 m a.s.l., in dung, [WS] – 16 exx., [AT] – 2 exx.;
Novabad, 16 Jul. 2014, 580 m a.s.l., [MW] – 6 exx.

***Cheironitis pamphilus* (Menetries, 1849)**
Fig. 4E

Karatag, 30 Jun. 2014, 1058 m a.s.l., [AT] – 2 exx.;
W of Kulob, 3 Jul. 2014, 526 m a.s.l., in cow dung, [WS] – 1 ex., [MW] – 1 ex.;
Dohanaklik, 16 Jul. 2014, 862 m a.s.l., [WS] – 6 exx., [AT] – 2 exx.;
Novabad, 16 Jul. 2014, 580 m a.s.l., in horse dung, [WS] – 1 ex., [MW] – 2 exx., [AT] – 2 exx.

Remarks. This is a widely distributed species known from the southern part of the European territory of Russia, Georgia, Armenia, Azerbaijan, Iran, and Afghanistan; it is also widespread in Central Asia: Turkmenistan, Uzbekistan, and Tajikistan. Moreover, it was reported from Syria, Turkey, and Greece (Kabakov 2006), as well as from Cyprus, Lebanon, and Israel (Bezděk 2016c). In Tajikistan, it has been recorded from numerous localities, such as Dushanbe, Gissarskiy Khrebet, Vakhshkiy Khrebet, Khoviling, and Darvaz (Medvedev and Lopatin 1961).

We found most individuals in cow and horse dung in warm and dry meadows at altitudes from 500 to 1050 m a.s.l.

***Onitis humerosus* (Pallas, 1771)**
Fig. 4F

Shurroabad, 4 Jul. 2014, 2152 m a.s.l., in dung, [WS] – 2 exx.

***Euonthophagus amyntas subviolaceus* Ménétriés, 1832**

Takob, 9 Jul. 2014, 1850 m a.s.l., in dung, [WS] – 22 exx., [MW] – 12 exx.;
Arykboshi, 2 Jul. 2014, [MW] – 2 exx.;
Karatag, 30 Jun. 2014, 1058 m a.s.l., [MW] – 3 exx., 17 Jul. 2014, [AT] – 2 exx.;
W of Kulob, 3 Jul. 2014, 526 m a.s.l., in dung, [MW] – 3 exx.;
Shurroabad, 4 Jul. 2014, 2152 m a.s.l., in dung, [WS] – 6 exx., [AT] – 1 ex.

***Euonthophagus koshantschikoffi* (Reitter, 1891)**

Takob, 9 Jul. 2014, 1850 m a.s.l., in dung, [WS] – 21 exx., [MW] – 7 exx.;
Arykboshi, 2 Jul. 2014, [MW] – 2 exx.;
Karatag, 17 Jul. 2014, 1058 m a.s.l., [AT] – 4 exx., [MW] – 8 exx.;
W of Kulob, 3 Jul. 2014, 526 m a.s.l., in dung, [WS] – 3 exx., [MW] – 4 exx.;
Shurroabad, 4 Jul. 2014, 2152 m a.s.l., in dung, [WS] – 3 exx., [AT] – 2 exx.;
Novabad, 16 Jul. 2014, 580 m a.s.l., [MW] – 1 ex.

Table 2. Differences in the external morphology between *Euonthophagus gibbosus* and *E. koshantschikoffi*.

Character	*Euonthophagus gibbosus* (Fig. 6A–C)	*Euonthophagus koshantschikoffi* (Fig. 6D–G)
Head in males	frontal suture arcuately widening towards lateral edges (frontal view), located near clypeus edge (Fig. 6B, C)	frontal suture not widening towards lateral edges (frontal view), located clearly further from clypeus edge, about half of length of head (Fig. 6F, G)
Pronotum	surface matte, rarely with barely noticeable gloss (Fig. 6A)	surface clearly shiny (Fig. 6D, E)
Elytra	surface matte, black, very rarely brown or reddish-brown (in the studied material all of the individuals were uniformly black) (Fig. 6A)	surface slightly shiny, black or reddish-brown (in the studied material approx. 75% of the specimens had a light-coloured elytra) (Fig. 6D, E)
Material examined	64 exx.; Georgia, Armenia, Turkey, Greece, Albania and Spain	55 exx.; Tajikistan (collected in six different localities)

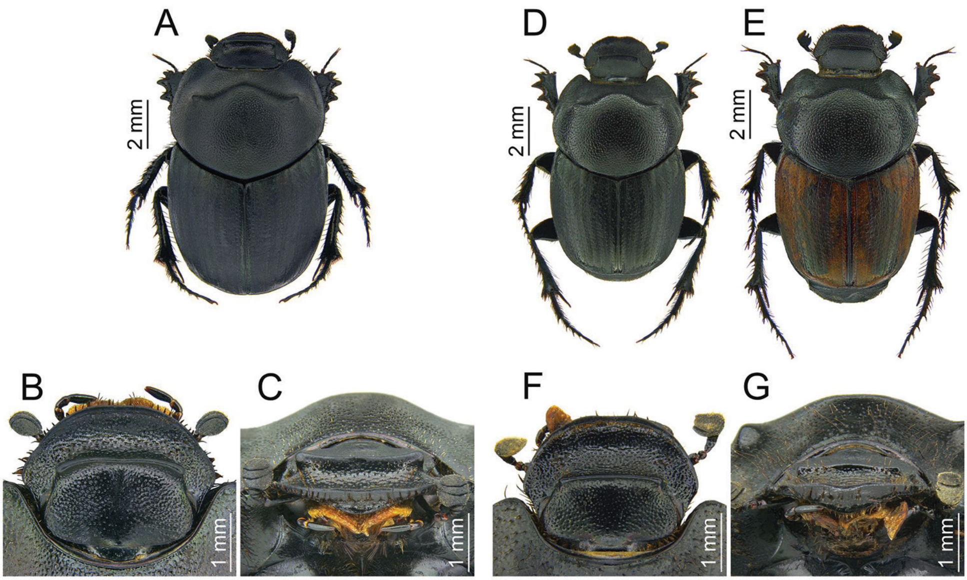

Figure 6. Key characters in two sibling species **A–C** *Euonthophagus gibbosus*: **A** habitus **B** head, dorsal view **C** head, frontal view **D–G** *Euonthophagus koshantschikoffi*: **D, E** habitus **F** head, dorsal view **G** head, frontal view.

Remarks. We collected a series of individuals belonging to *E. koshantschikoffi*, a taxon with a uncertain systematic position. This species was described from the environs of Tashkent, Uzbekistan, under the name *Onthophagus koshantschikoffi* Reitter, 1891, and its range is limited to Central Asia. In 1972, this species was recognised as a junior synonym of *Onthophagus gibbosus* (Scriba, 1790), a much more widely distributed species which was described from southern Germany (Zunino 1972). Five years later, Kabakov (1977) maintained this synonymisation and added the area of the occurrence of *O. koshantschikoffi* to the distributional range of *O. gibbosus*. Nearly 30 years later, Kabakov (2006) gave this taxon the rank of subspecies—*O. gibbosus koshantschikoffi*—and indicated several morphological characters for distinguishing it; Kabakov (2006) once again demarcated the distributional range of *O. gibbosus koshantschikoffi* while pointing out that it occurs only in the south-eastern part of the species' range. On the other hand, according to Löbl et al. (2006), Shokhin et al. (2014), and Ziani and Bezděk (2016), this taxon is a separate species, as *Euonthophagus koshantschikoffi*, but these authors gave no comments that would justify the restoration of a specific status for this taxon.

In considering the general distribution of these taxa and the differences in their morphology (Table 2), we support the position of Löbl et al. (2006), Shokhin et al. (2014), and Ziani and Bezděk (2016) that *E. koshantschikoffi* is a valid species and recognize as such. We emphasize, however, that the systematic position of these two taxa requires further research, including study of specimens from their contact zone, preferably using molecular methods.

Euonthophagus sulcicollis **(Reitter, 1892)**
Fig. 4G

Karatag, 30 Jun. 2014, 1058 m a.s.l., [MW] – 2 exx.;
W of Kulob, 3 Jul. 2014, 526 m a.s.l., in dung, [WS] – 8 exx., [MW] – 3 exx.;
Dohanaklik, 16 Jul. 2014, 862 m a.s.l., in dung, [AT] – 2 exx.;
Novabad, 16 Jul. 2014, 580 m a.s.l., [WS] – 1 ex., [AT] – 2 exx.

Remarks. The species is widely distributed in Central Asian countries, in Iran and Afghanistan (Kabakov 2006). It was recorded from Kazakhstan, Uzbekistan, Kyrgyzstan, Turkmenistan and Pakistan by Ziani and Bezděk (2016). In Tajikistan, it was noted *inter alia* from Argankun, Vakhshkiy Khrebet, Beshkentskaya Valley, Chiluchor Chashma, Darvaz (Medvedev and Lopatin 1961). This is a rather common species that mainly occurs on loess and sandy soils and it reaches the altitude of 3000 m a.s.l. (Kabakov 2006).

We found 17 individuals in cow dung in rather warm sites in mountain pastures and semi-desert habitats.

Onthophagus **(*Altonthophagus*)** ***sibiricus*** **Harold, 1877**
Fig. 4H

Takob, 28 Jun. 2014, 2300 m a.s.l., [WS] – 1 ex.

Onthophagus **(*Exonthophagus*)** ***haroldi*** **Ballion, 1871**
Fig. 4I

Shurroabad, 4 Jul. 2014, 2152 m a.s.l., in dung, [WS] – 1 ex.

Remarks. *Onthophagus haroldi* is mainly distributed in Central Asia and Kazakhstan, in northeastern Iran, northern Afghanistan, and in the Xinjiang Autonomous Region of China (Kabakov 2006). In Tajikistan, Medvedev and Lopatin (1961) recorded it from the vicinity of Dushanbe, Vakhshkiy Khrebet, Beshkentskaya Valley, and Chiluchor Chashma.

We found a single individual in cow dung on a south-facing grassy slope.

***Onthophagus* (*Onthophagus*) *taurus* (Schreber, 1759)**
Fig. 7A

Takob, 9 Jul. 2014, 1850 m a.s.l., in dung, [MW] – 6 exx.;
Arykboshi, 2 Jul. 2014, [MW] – 9 exx.;
Karatag, 30 Jun. 2014, 1058 m a.s.l., in dung, [WS] – 3 exx., [MW] – 39 exx., [AT] – 5exx., 17 Jul. 2014, in dung, [MW] – 14 exx., [AT] – 41exx.;
W of Kulob, 3 Jul. 2014, 526 m a.s.l., in dung, [WS] – 1 ex., [MW] – 4 exx., [AT] – 2exx.;
Kangurt, 5 Jul. 2014, 1066 m a.s.l., in dung, [WS] – 2 exx., [MW] – 4 exx.;
Komsomolabad, 11 Jul. 2014, 1160 m a.s.l., in dung, [WS] – 5 exx., [MW] – 6 exx.;
Tojikobod, 13 Jul. 2014, 2223 m a.s.l., [AT] – 5 exx.;
Gharm, 14 Jul. 2014, in dung, [WS] – 3 exx.;
Dohanaklik, 16 Jul. 2014, 862 m a.s.l., in dung, [WS] – 7 exx., [AT] – 4exx.;
Novabad, 17 Jul. 2014, 580 m a.s.l., desert, semi-desert, in cow dung, [MW] – 10 exx., [AT] – 28 exx.

***Onthophagus* (*Palaeonthophagus*) *afghanus* Petrovitz, 1961**

Takob, 9 Jul. 2014, 1850 m a.s.l., in dung, [MW] – 1 ex.;
Karatag, 30 Jun. 2014, 1058 m a.s.l., in dung, [MW] – 2 exx.

***Onthophagus* (*Palaeonthophagus*) *basipustulatus* Heyden, 1889**
Fig. 7B

Takob, 9 Jul. 2014, 1850 m a.s.l., in dung, [MW] – 1 ex.;
Karatag, 1058 m a.s.l., 30 Jun. 2014, in dung, [MW] – 2 exx.;
Novabad, 17 Jul. 2014, 580 m a.s.l., [MW] – 1 ex.

Remarks. This species occurs in the southernmost parts of Kazakhstan, Kyrgyzstan, and mountainous regions of Uzbekistan and Tajikistan; it has also been reported from Afghanistan by Kabakov (2006). Although it has been recorded from Syria, Turkey, Armenia, and Azerbaijan (Ziani and Bezděk 2016), these data most probably relate to another species, *O. formaneki* Reitter, 1897 (Kabakov 2006).

We found four individuals of *O. basipustulatus* in cow dung.

***Onthophagus* (*Palaeonthophagus*) *leucostigma* (Steven, 1806)**

Sarichashma, 25 Jun. 2014, 921 m a.s.l., in dung, [WS] – 3 exx.

***Onthophagus* (*Palaeonthophagus*) *pygargus* Motschulsky, 1845**
Fig. 7C

Romit, 26 Jun. 2014, 1250 m a.s.l., [WS] – 1 ex.;

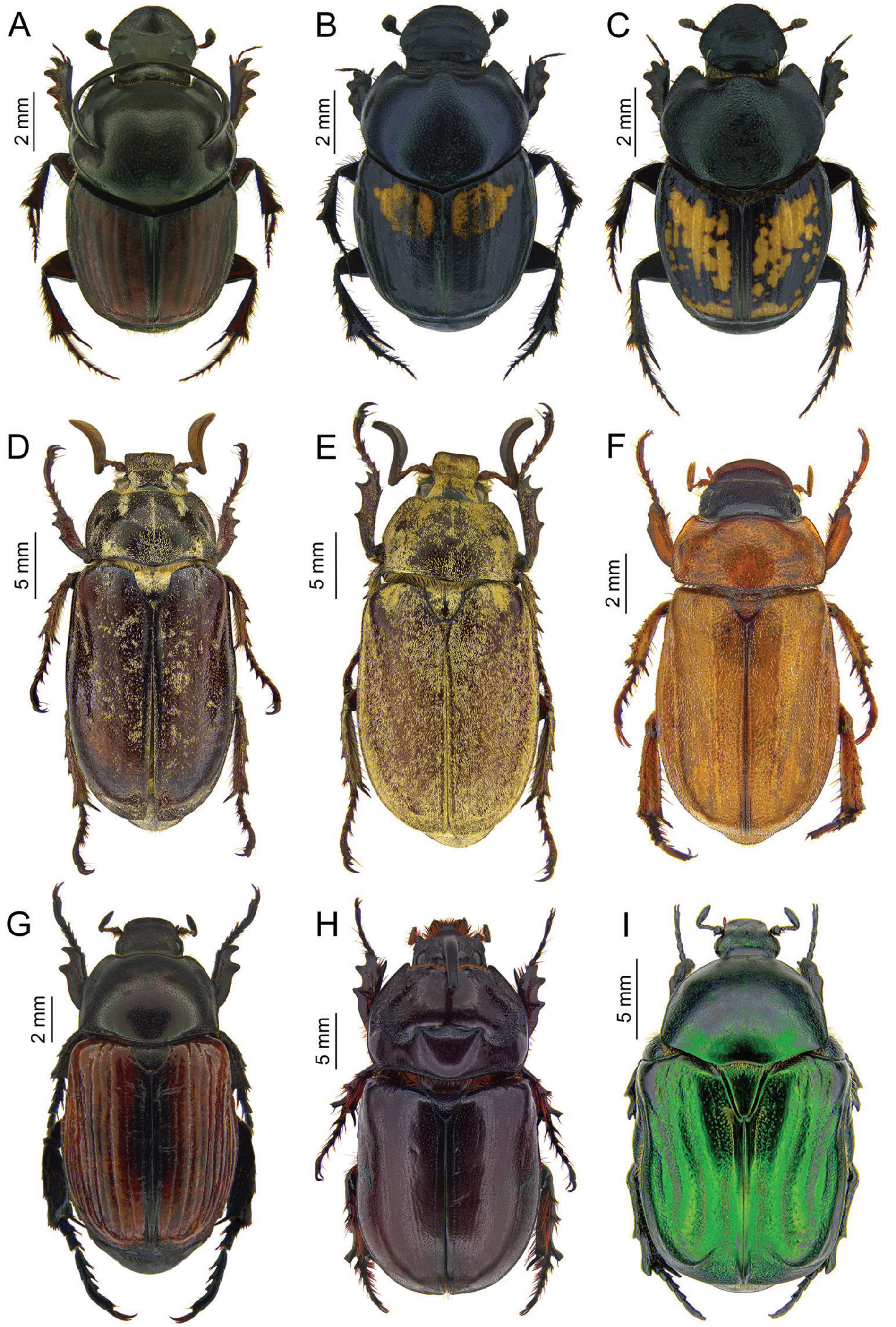

Figure 7. Photos of Scarabaeidae specimens collected during the expedition to Tajikistan in 2014 **A** *Onthophagus taurus*, male **B** *Onthophagus basipustulatus*, female **C** *Onthophagus pygargus*, female **D** *Polyphylla tridentata* **E** *Polyphylla adspersa* **F** *Adoretus nigrifrons* **G** *Cyriopertha glabra* **H** *Oryctes nasicornis turcestanicus* **I** *Protaetia bogdanoffi*.

Takob, 9 Jul. 2014, 1850 m a.s.l., in cow dung, [WS] – 5 exx., [MW] – 6 exx., [AT] – 6 exx.;
Arykboshi, 2 Jul. 2014, [MW] – 3 exx.;
Karatag, 30 Jun. 2014, 1058 m a.s.l., in cow dung, [MW] – 6 exx., 17 Jul. 2014, in dung, [MW] – 5 exx.;
W of Kulob, 3 Jul. 2014, 526 m a.s.l., in sheep dung, [MW] – 28 exx.;
Shurroabad, 4 Jul. 2014, 2152 m a.s.l., in horse dung, [WS] – 30 exx., [AT] – 1 ex.;
Novabad, 17 Jul. 2014, 580 m a.s.l., [MW] – 5 exx.

Remarks. The species is widespread in Central Asia, from Köpet Dag mountain range in Turkmenistan to the Russian–Chinese border. The northern boundary of its distributional range is limited by the foothills of Tian Shan. It also occurs in Armenia, Iran, Afghanistan, and China (Xinjiang) (Kabakov 2006). In Tajikistan, *O. pygargus* is very common and was recorded from numerous localities including Zeravshanskiy Khrebet, near Marguzor Lake, and Gissarskiy Khrebet, Khozretisho (Medvedev and Lopatin 1961).

We found this species to be one of the most frequently occurring dung beetles in our field survey. We collected it in large numbers in many localities, both in mountain and other pastures near highly urbanized areas. It was found in cow, horse, and sheep dung.

Scarabaeus carinatus (Gebler, 1841)

Ganchi, 25 Jun. 2014, 766 m a.s.l., [WS] – 1 ex.;
Kangurt, 5 Jul. 2014, 1066 m a.s.l., in dung, [MW] – 2 exx., [AT] – 1 ex.

Remarks. *Scarabaeus carinatus* inhabits mountains of Central Asia and Afghanistan; it is known from Turkmenistan, Uzbekistan, Tajikistan, and Kyrgyzstan. This species has also been recorded from southern and western Kazakhstan (Kabakov 2006) and Iran (Král and Bezděk 2016). It prefers mountain valleys to 3200 m a.s.l. (Kabakov 2006).

We found four individuals in cow dung in mountain pastures.

Subfamily Melolonthinae Leach, 1819

Polyphylla (*Mesopolyphylla*) *tridentata* (Reitter, 1890)

Fig. 7D

Karatag, 30 Jun. 2014, 1058 m a.s.l., at light, [WS] – 1 ex., 17 Jul. 2014, 1058 m a.s.l., at light, [WS] – 2 exx., [LK] – 1 ex.

Remarks. The species has been reported from southeastern Uzbekistan, northwestern Tajikistan, and western Kyrgyzstan (Medvedev 1951). In Tajikistan, it is known from the Nauskiy region, Gissarskiy Khrebet, from the vicinity of Lake Iskanderkul, and in the village Obigarm (Medvedev and Lopatin 1961).

In the valley of a mountain river in the vicinity of Karatag, four males were attracted to a UV lamp.

***Polyphylla* (*Xerasiobia*) *adspersa* (Motschulsky, 1854)**
Fig. 7E

Jilikul, 11 Jul. 2014, 332 m a.s.l., at light, [LK] – 1 ex.;
Arykboshi, 28 Jun. 2014, 906 m a.s.l., at light, [WS] – 2 exx., [LK] – 2 exx., [MW] – 1ex.;
Shahrinav, 1 Jul. 2014, 868 m a.s.l., at light, [WS] – 3 exx., [AT] – 1 ex.;
W of Kulob, 3 Jul. 2014, 537 m a.s.l., at light, [WS] – 1 ex.;
Chavrok, N of Kangurt, 5 Jul. 2014, 1217 m a.s.l., at light, [WS] – 1 ex., [MW] – 1 ex.;
Komsomolabad, 12 Jul. 2014, 1160 m a.s.l., [LK] – 1 ex.

***Amphimallon solstitiale solstitiale* (Linnaeus, 1758)**

Takob, 8 Jul. 2014, 1850 m a.s.l., [WS] – 5 exx., [MW] – 3 exx.;
Shurroabad, 4 Jul. 2014, 2152 m a.s.l., [WS] – 1 ex.;

***Panotrogus myschenkovi* (Ballion, 1871)**

Kangurt, 5 Jul. 2014, 1066 m a.s.l., at light, [AT] – 1 ex.;
Chavrok, N of Kangurt, 5 Jul. 2014, 1217 m a.s.l., at light, [WS] – 2 exx.;
Tojikobod, 13 Jul. 2014, 2223 m a.s.l., [LK] – 1 ex., [MW] – 1ex.

***Maladera* (*Amaladera*) *euphorbiae* (Burmeister, 1855)**

Jilikul, 24 Jun. 2014, 332 m a.s.l., at light, [AT] – 1 ex.;
Arykboshi, 28 Jun. 2014, 906 m a.s.l., at light, [AT] – 1 ex.;
Karatag, 30 Jun. 2014, 1058 m a.s.l., at light, [LK] – 1 ex.;
Shahrinav, 1 Jul. 2014, 868 m a.s.l., at light [WS] – 1 ex., [AT] – 1 ex. [MW] – 1 ex.

Subfamily Rutelinae Macleay, 1819

***Adoretus* (*Adoretus*) *nigrifrons* (Steven, 1809)**
Fig. 7F

Jilikul, 24 Jun. 2014, 332 m a.s.l., at light, [WS] – 4 exx., [LK] – 2 exx., [AT] – 4 exx., [MW] – 3 exx.;
Arykboshi, 28 Jun. 2014, 906 m a.s.l., at light, [LK] – 3 exx., [AT] – 1ex.;
Karatag, 30 Jun. 2014, 1058 m a.s.l., at light, [LK] – 1 ex., [MW] – 4 exx.;
Shahrinav, 1 Jul. 2014, 868 m a.s.l., at light [WS] – 3 exx.;
W of Kulob, 3 Jul. 2014, 537 m a.s.l., at light, [WS] – 3 exx., [AT] – 1 ex., [MW] – 1 ex.;
Kangurt, 5 Jul. 2014, 1066 m a.s.l., [MW] – 1 exx.;
Chavrok, N of Kangurt, 5 Jul. 2014, 1217 m a.s.l., at light, [WS] – 1 ex., [LK] – 3 exx.;
Gharm, 14 Jul. 2014, meadow, [WS] – 1 ex.

***Anomala oxiana* Semenov, 1891**

Karatag, 17 Jul. 2014, 1058 m a.s.l., at light, [AT] – 1 ex.

***Cyriopertha* (*Cyriopertha*) *glabra* (Gebler, 1841)**
Fig. 7G

W of Kulob, 3 Jul. 2014, 526 m a.s.l., [MW] – 2 exx.;
Tojikobod, 13 Jul. 2014, 2223 m a.s.l., [WS] – 13 exx., [LK] – 1 ex., [MW] – 3 exx. [AT] – 4 exx.

Remarks. This species is distributed in Uzbekistan, northern Tajikistan, southern Kazakhstan, and Kyrgyzstan (Medvedev 1949). It has also been recorded from Eastern Siberia and China (Xinjiang) (Zorn and Bezděk 2016). In Tajikistan, Medvedev and Lopatin (1961) reported it from a number of localities, including Dushanbe, Gissarskiy Khrebet, Fayzabad, Muskinabad, Khozretisho, and Khujand, among others. This species inhabits dry steppes, and it is also often found in farmlands (Medvedev 1949).

We caught this species in mountain meadows, and it was observed in large numbers. Adults were observed flying over the grass and became more active in the evening. It is worth noting that two color forms, the typical brownish form (Fig. 7G) and a melanistic form, were observed sympatrically.

Subfamily Dynastinae Macleay, 1819

***Pentodon bidens bidens* (Pallas, 1771)**

Jilikul, 24 Jun. 2014, 332 m a.s.l., at light, [AT] – 1 ex.;
Romit, 26 Jun. 2014, 1283 m a.s.l., at light, [LK] – 1 ex., [MW] – 3 exx.

***Oryctes nasicornis turcestanicus* Minck, 1914**
Fig. 7H

Romit, 26 Jun. 2014, 1283 m a.s.l., at light, [LK] – 2 exx., [MW] – 1 ex.;
Karatag, 30 Jun. 2014, 1058 m a.s.l., at light, [LK] – 1 ex.;
Kangurt, 5 Jul. 2014, 1066 m a.s.l., [MW] – 3 exx.

Subfamily Cetoniinae Leach, 1815

***Protaetia* (*Netocia*) *bogdanoffi* (Solsky, 1876)**
Fig. 7I

Takob, 8 Jul. 2014, 1850 m a.s.l., [WS] – 1 ex., [AT] – 1 ex.;
Chavrok, N of Kangurt, 5 Jul. 2014, 1217 m a.s.l., at light, [WS] – 1 ex.

Remarks. *Protaetia bogdanoffi* was reported from Uzbekistan, Tajikistan, Kyrgyzstan, and Afghanistan (Medvedev 1964), as well as from Kazakhstan (Bezděk 2016a). In Tajikistan, it has been recorded in Zaalayskiy Khrebet (Trans-Alay Range), Darvaz, Gissarskiy Khrebet, and Khozretisho (Medvedev and Lopatin 1961). This species occurs in open areas, such as steppe and semi-desert habitats, and in river valleys, as well as in higher mountains up to 2500 m a.s.l.

The individuals caught in a mountain meadow in the environs of Takob were collected on flowers, most likely of *Heracleum* or *Prangos*. Another individual, caught at Chavrok, was attracted to a UV lamp near human settlements, in a typical agricultural landscape.

***Protaetia* (*Netocia*) *interruptecostata* (Ballion, 1871)**

Karatag, 30 Jun. 2014, 1058 m a.s.l., [MW] – 1 ex.

***Protaetia* (*Potosia*) *marginicollis* (Ballion, 1871)**

Takob, 8 Jul. 2014, 1875 m a.s.l., herbaceous habitat, [AT] – 1 ex., 10 Jul. 2014, alt. 1880 m, [WS] – 1 ex.
Karatag, 1 Jul. 2014, 1088 m a.s.l., shrubs on the river, [AT] – 2 exx.

***Stalagmosoma albellum* (Pallas, 1781)**

Shurroabad, 4 Jul. 2014, 2152 m a.s.l., mountain meadow, pastures, [AT] – 1 ex.

***Oxythyrea cinctella* (Schaum, 1841)**

Sarichashma, 25 Jun. 2014, 921 m a.s.l., [WS] – 2 exx., [LK] – 4 exx., [AT] – 2 exx.;
Romit, 27 Jun. 2014, 1250 m a.s.l., [WS] – 10 exx., [AT] – 1 ex.;
Takob, 9 Jul. 2014, 1850 m a.s.l., [WS] – 2 exx., [AT] – 2 exx., [MW] – 2 exx.;
Arykboshi, 28 Jun. 2014, 906 m a.s.l., [MW] – 3 exx., [AT] – 1ex.;
Karatag, 30 Jun. 2014, 1058 m a.s.l., [WS] – 2 exx., [AT] – 1ex.;
Kangurt, 5 Jul. 2014, 1066 m a.s.l., [WS] – 3 exx.;
Chavrok, N of Kangurt, 5 Jul. 2014, 1200 m a.s.l., [WS] – 4 exx.;
Nurobod, 11 Jul. 2014, 1215 m a.s.l., [WS] – 2 exx., [AT] – 1ex.;
Tojikobod, 13 Jul. 2014, 2223 m a.s.l., [WS] – 2 exx., [LK] – 1 ex.;
Iskanderkul, 18 Jul. 2014, 2300 m a.s.l., meadow, [WS] – 2 exx., [AT] – 1 ex.

Discussion

Approximately 17% of the scarabaeoid fauna of Tajikistan was recorded during our 25-day survey, which was conducted from 24 June to 18 July 2014. We found one species, *Rhyssemodes transcaspicus*, that has not been previously recorded from the country. The occurrence of three species, *Cheironitis eumenes*, *Onthophagus silus* and *O. ovatus*

(Kabakov 2006), had been omitted in the second edition of the Catalogue of Palaearctic Coleoptera (Löbl and Löbl 2016). Moreover, Nikolajev and Pak (2020) described from Tajikistan a new species of the genus *Trochaloschema* (*T. dubium* Nikolajev & Pak, 2020), and Pak and Gubin (2020) described two new species of the genus *Lethrus* (*L. ahriman* Pak & Gubin, 2020 and *L. asmodeus* Pak & Gubin, 2020). Therefore, with these recent publications and our finding of *R. transcaspicus* in Tajikistan, the number of scarabaeoid species in the country is increased to 281.

The most commonly observed species of pleurostict scarab beetles were *Adoretus nigrifrons* (35 exx.) and *Oxythyrea cinctella* (48 exx.). The laparostict scarabs were dominated by: *Onthophagus taurus* (198 exx.), *O. pygargus* (96 exx.), *Euoniticellus fulvus* (116 exx.), and *Euonthophagus koshantschikoffi* (55 exx.). Nineteen species that are typical for the region of Central Asia were also found: *Lethrus* (*Mesolethrus*) sp., *Eulasia analis*, *Glaphyrus turkestanicus*, *Gymnopleurus aciculatus*, *Euonthophagus sulcicollis*, *E. koshantschikoffi*, *Onthophagus sibiricus*, *O. haroldi*, *O. afghanus*, *O. pygargus*, *Scarabaeus carinatus*, *Polyphylla tridentata*, *Panotrogus myschenkovi*, *Maladera euphorbiae*, *Anomala oxiana*, *Cyriopertha glabra*, *Protaetia bogdanoffi*, *P. interruptecostata*, and *P. marginicollis*, as well as one subspecies, *Oryctes nasicornis turcestanicus*. Most of the coprofagous Scarabaeoidea of Tajikistan are species whose imagines appear in the spring or at the turn of spring and summer, so the relatively small number of taxa collected is undoubtedly due to the rather late period of our study. Species whose adults start to occur in the summertime constitute less than a half of the scarabeoid beetles of Tajikistan (Medvedev and Lopatin 1961).

Most of the field research on the scarabaeoid beetles of Tajikistan was conducted in the middle of the 20th century and almost exclusively by Russian entomologists. This was partly caused by the political isolation of the country and partly by the lack of transport and tourist infrastructure. After its separation from the Soviet Union in 1991 and the introduction of tourism facilities, the intensification of research was possible for both scientists and amateur entomologists. This, in turn, undoubtedly contributed to a better understanding of the local entomofauna and in a relatively short time resulted in the description of new species and newly recorded taxa for this country (Novikov 1999; Gusakov 2003, 2007, 2008; Nikolajev 2008; Ivanova 2012; Ivanova and Pak 2012; Akhmetova and Frolov 2014).

The richness of the scarabaeoid fauna of Tajikistan and the geography of the country clearly indicate the possibility of finding further species of this superfamily, in particular in near the borders with neighbouring countries where numerous other taxa have been recorded, for example *Eremazus cribratus* Semenov, 1893 (Bezděk 2016b), *Acrossus rufipes* (Linnaeus, 1758), and *Rhodaphodius foetens* (Fabricius, 1787) (Dellacasa et al. 2016). These beetles are rather common in Kazakhstan, Kyrgyzstan, Turkmenistan, or Uzbekistan, and there are suitable similar habitats available for them in Tajikistan. Considering the numerous isolated and largely inaccessible biotopes, the presence of as many as 80 endemic species of Scarabaeoidea, and a remarkably few representatives of the subfamily Aphodiinae, it is very likely to expect some new taxa for the local fauna and perhaps even some yet undescribed. Already, this was confirmed by the recent discovery of three new species of Scarabaeoidea, *Trochaloschema dubium*, *Lethrus ahriman*, and *L. asmodeus*, as well as by the results of studies of other groups of beetles (Greń et al. 2016; Kadyrov et al. 2016) and aphids (Depa et al. 2017). Therefore, new expeditions to Tajikistan are highly desirable.

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RESEARCH ARTICLE

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Taxonomic revision of the Afrotropical hover fly genus *Senaspis* Macquart (Diptera, Syrphidae)

Marc De Meyer[1], Georg Goergen[2], Kurt Jordaens[1]

1 *Royal Museum for Central Africa, Invertebrates Section and JEMU, Leuvensesteenweg 13, B3080 Tervuren, Belgium* **2** *International Institute of Tropical Agriculture, Biodiversity Centre, 08 BP 0932 Tri Postal, Cotonou, Benin*

Corresponding author: Marc De Meyer (marc.de.meyer@africamuseum.be)

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Abstract
The representatives of the Afrotropical hover fly genus *Senaspis* Macquart (Diptera) are revised. In total, ten species are recognized. *Senaspis apophysata* (Bezzi) is herewith placed as junior synonym of *S. flaviceps* Macquart, *S. livida* (Bezzi) is herewith placed as junior synonym of *S. dentipes* (Macquart) and *S. griseifacies* (Bezzi) is herewith placed as junior synonym of *S. haemorrhoa* (Gerstaecker). All species are redescribed and an identification key is provided. DNA barcoding analysis (7 species, 64 barcodes) showed that the technique can be used to unambiguously identify the species. The relationships among the different *Senaspis* species are discussed based on morphological and DNA data.

Keywords
Africa, DNA barcoding, Eristalinae, flower fly

Table of contents

Introduction

Hover flies (Diptera, Syrphidae) constitute a diverse family of true flies, comprising ca. 6200 species (Pape et al. 2013). The group is poorly represented in the Afrotropical Region with slightly over 600 species known (Ssymank et al. in press). However, this could be a reflection of the limited surveying and studies conducted on this group in the region (Dirickx 1998). Nevertheless, syrphids most likely play an equally important role as pollinators, predators or decomposers, in a number of ecosystem services, as they do in other biogeographical regions (Inouye et al. 2015). Reviews on the current state are provided by Dirickx (1998), Whittington (2003) and Ssymank et al. (in press) and there is a clear need to improve the general knowledge on this group of flies.

Among the elements hampering an improved knowledge of the Afrotropical syrphid diversity is the lack of identification tools for most genera (Ssymank et al. in press). Eristalines are not an exception to this with relatively recent keys (i.e., published over the last 30 years) available only for the genera *Ceriana* Rafinesque, 1815 (Thompson 2013), *Chasmomma* Bezzi, 1915 (Kassebeer 2000), *Graptomyza* Wiedemann, 1820 (Whittington 1992, 1994), *Megatrigon* Johnson, 1898 (Doczkal et al. 2016), *Syritta* Le Peletier & Audinet-Serville, 1828 (Lyneborg and Barkemeyer 2005) and *Phytomia* Guérin-Méneville, 1834 (De Meyer et al. 2020). Currently, the African fauna of a number of eristaline genera is under revision, aiming to improve our knowledge for this group. This paper presents a taxonomic revision for the Afrotropical representatives of the genus *Senaspis* Macquart, 1850.

Senaspis was described by Macquart in 1850 with type species *Senaspis flaviceps* Macquart, 1850. It is an exclusively Afrotropical genus, although the types of some species were labelled as originating from the Neotropical (*S. nigripennis* (Macquart, 1855), Colombia) or Oriental (*S. dentipes* (Macquart, 1842), Java) Regions (see below under comments under respective species for details). Kertész (1910) made the unjustified emendation of the genus name to *Stenaspis*. As the latter is pre-occupied by *Stenaspis* Audinet-Serville, 1834 (Coleoptera: Cerambycidae), Bezzi (1912) proposed *Protylocera* Bezzi, 1912 as new name. However, Curran (1927a) outlined that the initial change to *Stenaspis* was unnecessary and thus the name *Senaspis* is retained as valid. Loew (1860) suggested using the name *Plagiocera* Macquart, 1842 for *S. maculipennis* (Loew, 1858) and related species, which Loew did not list. The genus *Plagiocera* was proposed by Macquart (1842) for the Nearctic *Milesia cruciger* Wiedemann, 1830. However, the name is preoccupied by *Plagiocera* Klug, 1834 (Hymenoptera: Cimbicidae) (see Evenhuis et al. 2016). Hull (1949) proposed the name *Triatylosus* Hull, 1949 as subgenus for a single species with additional facial tubercles on either side of the medial one: *Xylota dibaphus* Walker, 1849. This subgeneric division was not followed by Smith and Vockeroth (1980) in the Catalogue of Afrotropical Diptera. The latter listed 14 *Senaspis* species, but they recorded *Eristalis cupreus* Macquart, 1842 both under *Senaspis* and under *Eristalinus* Rondani, 1845. Whittington (1993) listed it solely under the genus *Senaspis*. Dirickx (1998) listed *cupreus* Macquart under the genus *Eristalis* Latreille, 1804. The study of the type material of this species (at MNHN) corroborates that it is not a *Senaspis* species but a species of the genus *Eristalinus sensu stricto* and thus, it is excluded from this revision.

Representatives of *Senaspis* are reported from wetlands and riverbanks, especially when visited by domestic or wild mammals, as well as other water bodies (Ssymank et al. in press). Several specimen labels indicate rotting stems of banana stumps or decaying coconut trunk (Harmer 1913) as larval habitat and Copeland et al. (1999) described the larvae of *S. haemorrhoa* (Gerstaecker, 1871) collected from a stump of the cycad *Encephalartos tegulaneus* Melville (Zamiaceae). Furthermore, larvae of *Senaspis* species have been reported from sewage ponds and pig slurry (Curtis and Hawkins 1982; Ssymank et al. in press). Though adult Syrphidae are likely among the most important pollinators within the Diptera (Doyle et al. 2020), literature records of flower visiting *Senaspis* are still scanty (Nilsson et al. 1986) probably due to the unavailability of comprehensive identification keys for the genus.

Recent expeditions by staff members of the Royal Museum for Central Africa and the International Institute of Tropical Agriculture, as well as specimens collected independently by other research groups, have expanded the material available, including specimens suitable for DNA extraction. The main objectives of this manuscript are, therefore, to provide a taxonomic revision of all representatives of the genus *Senaspis*, to present an identification key and to discuss the interrelationships based on morphological and DNA data.

Materials and methods

Material for study was obtained from the following institutions:

AMGS	Albany Museum, Grahamstown, South Africa;
AMNH	American Museum of Natural History, New York, USA;
BMSA	Bloemfontein Museum, Bloemfontein, South Africa;
CDFA	California Department of Food and Agriculture, Sacramento, USA;
CNC	Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Canada;
ICIPE	International Centre of Insect Physiology and Ecology, Nairobi, Kenya;
IITA	International Institute of Tropical Agriculture, Cotonou, Benin;
KBIN	Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels, Belgium;
KMMA	Koninklijk Museum voor Midden-Afrika, Tervuren, Belgium;
MCSNG	Museo Civico di Storia Naturale "Giacomo Doria", Genoa Italy;
MNB	Museum für Naturkunde, Berlin, Germany;
MNHN	Muséum national d'Histoire naturelle, Paris, France;
NHMUK	Natural History Museum, London, UK;
NMSA	KwaZulu-Natal Museum, Pietermaritzburg, South Africa;
NRMS	Naturhistoriska Riksmuseet, Stockholm, Sweden;
MZH	Finnish Museum of Natural History, Zoology unit, Helsinki, Finland;
OBPE	Office Burundais pour la Protection de l'Environnement, Bujumbura, Burundi;
OXUM	Oxford University Museum, Oxford, UK;
ZFMK	Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany.

Morphological terminology largely followed Thompson (1999). Morphological observations were made with a Leica MZ8 stereomicroscope. Digitial images were obtained using the set-up as outlined in Brecko et al. (2014). Stacking was done using the software Zerene Stacker (zerenesystems.com/cms/home). Male genitalia were dissected using forceps and soaked 24–48 hours (depending on time required for sufficient clearance) in a cold 10% KOH solution after which they were transferred to acetic acid for 24 hours. Once sufficiently cleared, they were transferred to glycerine. Digital images were taken with a Leica MZ16 microscope and mounted Leica DFC500 digital camera using Leica Application Suite (LAS) automontage software (version 3.8). Measurements of wing and body lengths were taken by use of a calibrated ocular through the stereomicroscope, and are based on ten specimens (whenever available) randomly chosen, from which minimum and maximum length were selected. Body measurements were taken between the anterior margin of the frons and the posterior end of tergum IV; wing measurements between the tegula and the apex of the wing. For type material, text on identification and location labels is given ad verbatim. Text is indicated in quotation marks (" ") and each line on the label is separated by a double forward slash (//). Text not given on labels (i.e., collection depository) is given in square brackets ([ ]).

Literature references are given for original taxon descriptions under each species. For full bibliographic references, we refer to Dirickx (1998).

Procedures for DNA barcoding followed Jordaens et al. (2015). Briefly, genomic DNA was extracted from a single leg using the NucleoSpin Tissue Kit (Macherey-Nagel, Düren), following the manufacturer's instructions. PCR reactions were undertaken in 25 µl reaction volumes that contained 1.5 mM $MgCl_2$ in 1 × PCR buffer (Invitrogen), 0.2 mM of each dNTP, 0.2 µM of each primer and 0.5 units of Taq polymerase (Invitrogen). The DNA barcode fragment of the mitochondrial cytochrome *c* oxidase subunit I (COI) gene was amplified using primer pair LCO1490 and HCO2198 (Folmer et al. 1994). The PCR profile was an initial denaturation step of 5 min at 95 °C, followed by 35 cycles of 45 s at 95 °C, 45 s at an annealing temperature of 45 °C and 1.5 min at 72 °C, and ending with a final extension step of 5 min at 72 °C. PCR products were purified using the GFX PCR DNA Purification Kit (GE Healthcare) and diluted in 15 µl of sterile water or using the ExoSap protocol (Invitrogen) following the manufacturer's instructions. PCR-products were bidirectionally sequenced using the ABI PRISM BigDye Terminator v3.1 Cycle Sequencing Kit and run on an ABI3130xl Genetic Analyzer. Sequences were assembled in SeqScape v2.5 (Life Technologies) and inconsistencies were checked by eye on the chromatogram.

In total, we obtained 20 new DNA barcodes and complemented this dataset with 21 DNA barcodes of Jordaens et al. (2015) (GenBank accession numbers: KR831198–KR831218), 19 unpublished barcodes obtained by CNC, and four unpublished barcodes from MZH (GenBank Accession numbers MW066957–MW066999, see Suppl. material 2: Table S1). Hence, the total *Senaspis* DNA barcode dataset comprised 64 sequences. *Eristalis tenax* (Linnaeus, 1758) was used to root the topologies. No DNA barcodes could be obtained for *S. melanthysana* (Speiser, 1913), *S. pennata* (Hervé-Bazin, 1914), or *S. xanthorrhoea* (Bezzi, 1912).

A Neighbor-Joining (NJ) tree (Saitou and Nei 1987) was constructed using the K2P model in MEGA v7 (Kumar et al. 2016) (see Suppl. material 1: Fig. S1), and pairwise p-distances (i.e., the proportion of sites at which two sequences differ) within and among species were calculated. Moreover, a NJ and a Maximum Likelihood (ML) topology (Guindon and Gascuel 2003) were constructed after removing identical sequences with DAMBE v.7 (Xia 2018) (Fig. 114). Branch support in the NJ analysis was evaluated using 1,000 bootstrap replicates. For the ML analysis, the dataset was partitioned according to codon position and the Akaike Information criterion in jModelTest v.2 (Guindon and Gascuel 2003; Darriba et al. 2012) was used to select the most appropriate model of evolution. These were the F81+I+G (first position), GTR+I+G (second position), and GTR+G (third position) model, respectively. Then, Garli v.2.01 (Zwickl 2006) was used to perform the ML analysis (two replicates; 500 bootstrap pseudoreplicates) taken into account the most appropriate models of evolution for each of the three codon positions. In each analysis, *Eristalis tenax* was constrained as root. Bootstrap values were considered to be meaningful if ≥ 70% (Hillis and Bull 1993). Specific results of the DNA barcode analysis are discussed in the Comments parts under each taxon of the Taxonomy and systematics section when relevant and in the Discussion.

Taxonomy and systematics

Senaspis Macquart, 1850: 437.

Senaspis Macquart, 1850: 437. Type species: *Senaspis flaviceps* Macquart, 1850 (by monotypy).
Protylocera Bezzi, 1912: 414 [unnecessary replacement name].
Triatylosus Hull, 1949: 398 (as subgenus). Type species: *Xylota dibaphus* Walker, 1849 (by original designation).

Generic diagnosis. *Senaspis* species are morphologically characterized by the combination of the following characters: eyes bare and maculate (less conspicuous in dried specimens), dorsal facets in male usually only slightly larger than ventral facets, more pronounced so in *S. dibapha* (Walker, 1849) and *S. nigrita* (Bigot, 1859); antennal arista bare; frons in lateral view with distinct protuberance; wing with cell r_1 usually closed and petiolate, or narrowly open at most (see Fig. 69) (if distinctly open then hyaline, without dark markings; see *Senaspis pennata*; Fig. 79); vein R_{4+5} strongly sinuate; thorax with triangular (dorsomedial) part of anepimeron bare, katepimeron bare or pilose at least in dorsal part; metatibia with conspicuous pile on at least apical half ventrally (except in *S. flaviceps*).

Key to the Afrotropical species of *Senaspis*

1 Wing hyaline (Fig. 79), without dark markings; cell r_1 open for a distance equal to height of cell. Scutellum not marginate apically (Fig. 63). Metatibia with long (equal in length to width of tibia) and very dense pile on ventral and dorsal margins along its entire length (Fig. 90) ..... ***S. pennata* (Hervé-Bazin)**

– Wing largely dark (Figs 65, 68) or at least with some darker markings (Figs 64, 72–78); cell r_1 usually closed (if open then for distance shorter than height of cell). Scutellum marginate apically (Figs 52–60). Metatibia with short pile along ventral and dorsal margins (Figs 83–84), at most with longer pile (but never as long as width of tibia) on apical half to two-thirds (Figs 80–82, 85–89) **2**

2 Wing hyaline with a distinct dark brown macula on medial part (Figs 64, 73, 78) **3**

– Wing either largely dark (Figs 65, 68) or fumose with darker but less defined areas (Figs 72, 74–77) **5**

3 Postabdomen (terga posterior to tergum IV) and at least part of tergum IV conspicuously orange to orange-red, with pale orange pile (Fig. 95), sometimes all abdominal terga largely yellow to yellow-orange (Fig. 100). Metafemur with two ventral swellings on apical part, the proximal swelling less developed (Fig. 85) **4**

– All abdominal terga dark and with dark pile, sometimes postabdomen reddish but then without pale orange pile (Fig. 91). Metafemur ventrally with a single swelling on apical part (Fig. 80) ..... ***S. dentipes* (Macquart)**

4 All abdominal terga dark yellow to yellow-orange, with pale orange pile except dark pile medially on posterior half of terga II and III (Fig. 100)........... .... ***S. xanthorrhoea* (Bezzi)**

– Abdomen darker, orange colour and pale pile restricted to, at most, posterior margin of tergum III, whole of tergum IV and postabdomen (Fig. 95) .... ***S. haemorrhoa* (Gerstaecker)**

5 Scutellum colour pale yellow, strongly contrasting with dark scutum (Fig. 59). Metafemur ventrally with two distinct swellings in apical part (Fig. 87). Wing veins yellowish basally, slightly darkened in apical fourth (Fig. 75)............... .... ***S. nigrita* (Bigot)**

– Scutellum colour largely concolourous with scutum, at least along the basal half (Figs 53–56, 58, 60–61). Metafemur ventrally with a single swelling in apical part (Figs 84, 86, 88, 89), if there is a weak second swelling basally of major one, then former without dark setae (Fig. 81). Wing veins yellowish or dark (Figs 65, 68, 74, 76) **6**

6 Wing largely dark brown, hyaline area restricted to narrow band along posterior margin or paler area in apical part, distal third of cell br and medial part of cell bm concolourous (Figs 65, 68); lower calypter white to yellow, with pale fringe...**7**

– Wing yellow to pale brown infuscated, with darker area at most restricted to anterior half of wing, distal third of cell br darker coloured than medial part of cell bm (Figs 72, 74, 76); lower calypter black to pale brownish, with dark or pale fringe..**8**

7 Scutum with conspicuous white to yellow long pile (Figs 54, 55), contrasting with dark pile on pleura (Fig. 3). Metafemur thickened, black (Fig. 82). Face dark, with a single medial tubercle (Figs 20, 22) .... ***S. elliotii* Austen**

– Scutum without conspicuous pale pile, with conspicuous black pollinosity along transverse suture (Fig. 53). Metafemur slender, reddish (Fig. 81). Face usually red, rarely brownish, with medial and lateral tubercles (Figs 16, 18) ... . ***S. dibapha* (Walker)**

8 Face and antennae yellow to red (Figs 24–27). Wing lower calypter black with white fringe (Fig. 72). Male metafemur with distinct basoventral tubercle (Fig. 83) .... ***S. flaviceps* Macquart**

– Face and antennae dark (Figs 32–35, 40–45). Wing lower calypter pale brown to brown, with pale or dark fringe (Figs 74, 76, 77). Male metafemur without basal tubercle (Figs 86, 88) **9**

9 All abdominal sterna with long dark pile (Fig. 6). Metafemur moderately thickened, with ventral margin straight or slightly convex (Fig. 86). Wing lower calypter with dark fringe (Fig. 74) .... ***S. melanthysana* (Speiser)**

– Abdominal sterna I–III with long pale pile (Fig. 10), darker in other sterna. Metafemur strongly thickened, with ventral margin concave (Fig. 88). Wing lower calypter with pale fringe (Figs 76, 77)..**10**

10 Abdominal terga with short pale pile on lateral margins (Fig. 98). Scutellum with pale pile .... ***S. umbrifera* (Walker)** (holotype)

– Abdominal terga with short dark pile or intermixed pale and dark pile on lateral margins (Fig. 99). Scutellum usually with dark pile on disc (rarely completely pale pilose)...................................***S.* near *umbrifera* (Walker)** (see comments under *umbrifera* for discussion on the identity of this taxon)

Taxonomic treatments

***Senaspis dentipes* (Macquart, 1842)**
Figs 1, 12–15, 52, 64, 80, 91, 102

Eristalis dentipes Macquart, 1842: 97.
Helophilus aesacus Walker, 1849: 609. Syn. by Smith and Vockeroth (1980).
Plagiocera maculipennis Loew, 1858: 381. Syn. by Austen (1909).
Eristalis latevittatus Bigot, 1858: 365. Syn. by Kertész (1910).
Protylocera aesacus var. *livida* Bezzi, 1912: 421. Syn. nov.

Differential diagnosis. A predominantly subshiny brownish species (Fig. 1), without distinct pilosity. The wing (Fig. 64) is largely hyaline but with a distinct dark brown medial macula. It can be differentiated from other *Senaspis* species with a distinct wing macula (*S. haemorrhoa*, *S. xanthorrhoea*) by the absence of orange pile on the abdominal terga and the presence of a single distinct ventral swelling in the apical fifth of the metafemur (Fig. 80) (two swellings in *S. haemorrhoa* and *S. xanthorrhoea*).

Examined material. *Eristalis dentipes* Macquart: Lectotype (hereby formally designated and published; see comments), male, "N° 1177. // Eristalis // dentipes." "272 // 97" "70" "MNHN, Paris // ED6399" "LECTOTYPE" "TYPE // Vockeroth '69" "LECTOTYPE // Eristalis // dentipes Macq. // Desig. Thompson 1977" [MNHN].

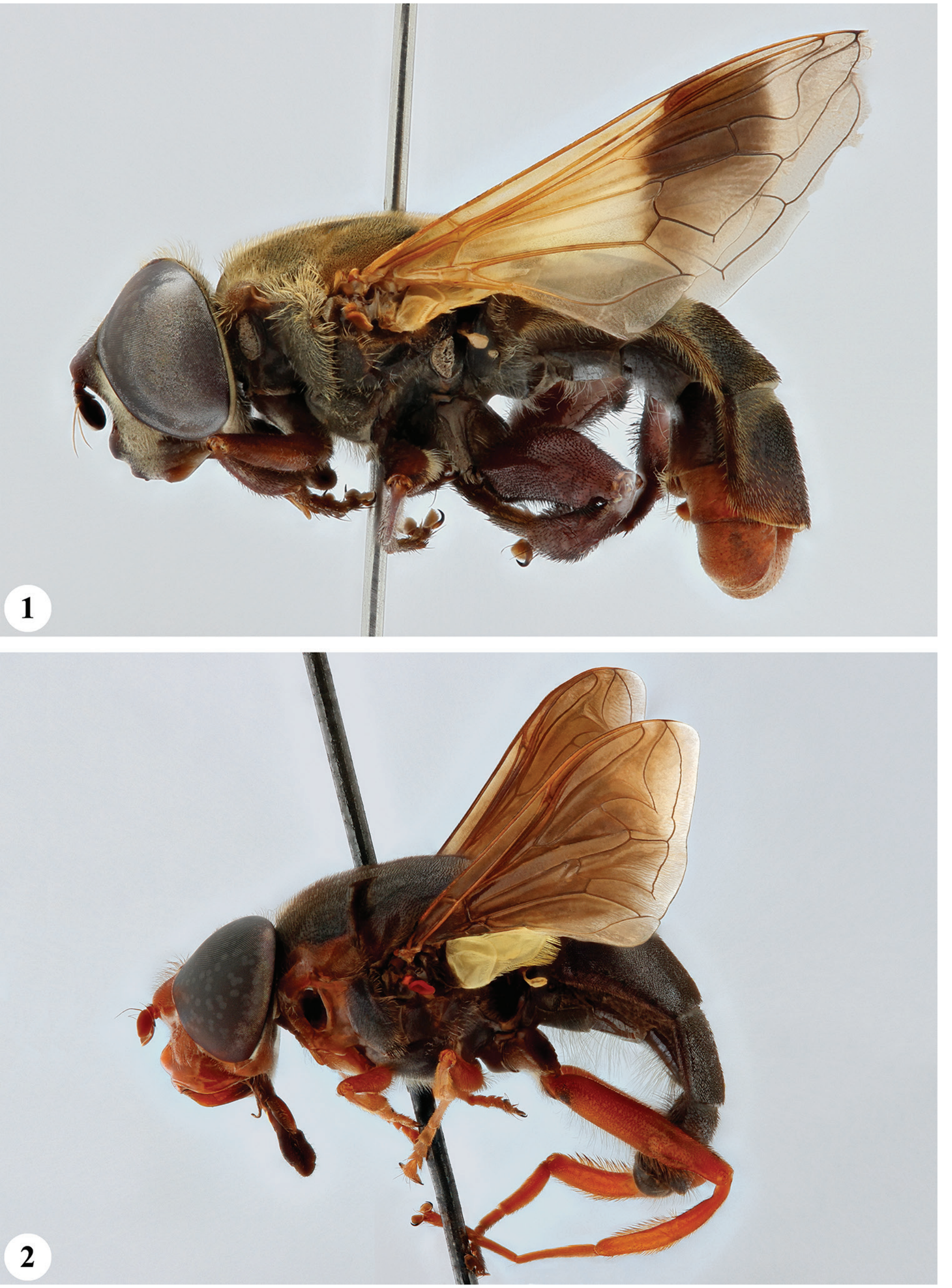
Helophilus aesacus Walker: Holotype, male, "Holo- // type" "Type" "Helophilus // aesacus // Wlk." "Sierra Leone" [NHMUK].

Eristalis latevittatus Bigot: Holotype, female, "2423 // 83" "TYPE" "Eristalis // latevittatus ♀. // n.sp. J. Bigot. // Gabon. // Coll. Thomson." [MNHN].

Protylocera aesacus var. *livida* Bezzi: Lectotype (hereby designated), male "Is. Fernando Poo // Basile // 400–600 m.s.m. // VIII–IX.1901. L. Fea leg.;" "Typus" "SYNTYPUS // Protylocera // aesacus var. // livida Bezzi, 1912" "Protylocera // aesacus Walker // v. livida // det. Bezzi, 1912" "Museo Cvico // di Genova" "Protylocera // aesacus // var. lívida n." "LECTOTYPUS" [MCSNG]. Paralectotype, female, "Is. Fernando Poo // Musola // 500–800 m.s.m. // Ɨ III.1902. L. Fea leg.;" "SYNTYPUS // Protylocera // aesacus // var. lívida" "Protylocera // aesacus Walker // v. livida // det. Bezzi, 1912" "Museo Civico // di Genova" "PARA- // LECTOTYPUS" [MCSNG].

Other material. Angola • 1♀; Congulu, Apr. 1934; K. Jordan leg.; NHMUK • 1♂; 7 mi W Gabela; 16–18 Mar. 1972; NHMUK. Benin • 1♀; Ahozon; Jun. 2005; G. Goergen leg.; IITA • 1♂; Calavi, IITA Station; 4 Apr. 1994; G. Goergen leg.; IITA • 1♀; same collection data as for preceding; 4 Aug. 1995 • 1♀; same collection data as for preceding; 5 Mar. 1997 • 1♂ 1♀; same collection data as for preceding; Jun. 2006

• 1♂; same collection data as for preceding; 18 Apr. 2007 • 4♂♂ 2♀♀; same collection data as for preceding; Jun. 2007 • 1♂; same collection data as for preceding; 16 Nov. 2011; K. Jordaens leg.; KMMA • 11♂♂ 3♀♀; same collection data as for preceding; 8 Dec. 2013 • 1♂; same collection data as for preceding; 16 Dec. 2013 • 3♀♀; Cotonou; 3 Jun. 1914; W.A. Lamborn leg.; NHMUK • 1♂; Cotonou; 24 Sep. 2002; G. Goergen leg.; IITA • 1♀; same collection data as for preceding; May 2006 • 1♀; same collection data as for preceding; 25 Apr. 2012 • 1♀; Dassa; Aug. 2007; G. Goergen leg.; IITA • 1♂; Lama forest; 26 Jul. 1995; G. Goergen leg.; IITA • 1♂; Lokoli; Feb. 2006; G. Goergen leg.; IITA • 1♂; Lokossa; Jan. 2005; G. Goergen leg.; IITA • 2♀♀; same collection data as for preceding; Oct. 2005 • 2♂♂; same collection data as for preceding; Jan. 2006 • 2♂♂; same collection data as for preceding; Mar. 2006 • 1♀; Niaouli; Jun. 2003; G. Goergen leg.; IITA • 1♀; Ouidah; Nov. 2004; G. Goergen leg.; IITA • 2♀♀; same collection data as for preceding; May 2006 • 1♂ 1♀; same collection data as for preceding; 23 Apr. 2009 • 1♂; Pénéssoulou; Jun. 2004; G. Goergen leg.; IITA • 1♂; Porto Novo; Aug. 2006; G. Goergen leg.; IITA • 1♂; Porto Novo; 27 Jan. 2016; K. Jordaens leg.; KMMA • 1♂; Tanougou Waterfalls; 20 Jan. 2020; G. Goergen leg.; IITA • 1♂; Togbin; Dec. 2005; G. Goergen leg.; IITA. Burundi • 1♂; Busoni, Kisenyi; 17 Dec. 1950; F. François leg.; KBIN • 2♂♂ 1♀; Kibira NP, Rwegura; 31 May 2018; E. Sinzinkayo leg.; OBPE • 1♀; same collection data as for preceding; 28 Nov. 2019 • 1♀; Kisenyi; May 1955; F.J. François leg.; KBIN • 1♀; Kitega; 22 Oct. 1950; F. François leg.; KBIN • 1♂; Lake Nyanza; 7 [?] 2013; L. Ndayikeza leg.; OPBE • 1♂; same collection data as for preceding; 23 [?] 2013 • 1♂; Nyakibande, Mumirwa; 27 Jan. 2018; E. Sinzinkayo leg.; OBPE • 1♀; same collection data as for preceding; 16 May 2018 • 1♂; same collection data as for preceding; 24 Apr. 2019 • 2♂♂ 1♀; same collection data as for preceding; 14 Jul. 2019 • 2♀♀; Nyamurembe, Bururi; 7 Mar. 1953; P. Basilewsky leg.; KMMA • 1♀; Rumonge; 1934; A. Lestrade leg.; KMMA • 1♀; Rumonge; 19–20 Jun. 1948; F. François leg.; KBIN • 1♀; same collection data as for preceding; 25 Nov. 1948 • 1♀; same collection data as for preceding; 25 Feb. 1949 • 1♀; same collection data as for preceding; 19 May 1952 • 1♀; Rumonge; 7 Mar. 1953; P. Basilewsky leg.; KMMA • 1♀ Usumbura [= Bujumbura]; G. Pierrard leg.; KMMA. Cameroon • 2♀♀; Bafut Forest, Nguenba; 29 Nov. 1967; de Miré leg.; MHNH • 1♂; Batanga; 24 Jun. 1911; A.I. Good leg.; CNC • 1♀; Ebogo; 9 Jul. 1999; G. Goergen leg.; IITA • 1♀; Kumba-Victoria Rd boundary post; 9 Nov. 1949; H. Oldroyd leg.; NHMUK • 1♀; Lolodorf; 28 Aug. 1915; A.I. Good leg.; CNC • 2♂♂; Mbalmayo; 3 Jul. 1998; G. Goergen leg.; IITA • 1♂; same collection data as for preceding; 2 Aug. 2000 • 1♀; Victoria [= Limbe]; Jun. –Aug. 1917; F.H. Fitz Roy leg.; NHMUK. Democratic republic of the Congo • 1♀; Abok; 1927; Ch. Scops leg.; KMMA • 2♀♀; Albertville [= Kalemie]; 14 Aug. 1953; J. Verbeke leg.; KBIN • 1♂; Bambesa; 30 Oct. 1933; J.V. Leroy leg.; KMMA • 1♂; Bambesa; 6 Jul. 1937; J. Vrydagh leg.; CNC • 1♀; same collection data as for preceding; 2 Oct. 1937; KMMA • 1♀; same collection data as for preceding; 24 Mar. 1939; KBIN • 1♀; same collection data as for preceding; 3 Jun. 1939; KBIN • 1♀; same collection data as for preceding; 11 Nov. 1940; KMMA • 1♀; Barumbu; Aug. 1925; J. Ghesquière leg.;



Figures 1, 2. *Senaspis* species, habitus, lateral view **1** *S. dentipes* (Macquart) (♂) **2** *S. dibapha* (Walker) (♂).

Figures 3, 4. *Senaspis* species, habitus, lateral view **3** *S. elliotii* Austen (♂) **4** *S. flaviceps* Macquart (♂).

KMMA • 1♂; Bafwasende; Nov. 1945; F. François leg.; KMMA • 1♂; Bezali; 3 Oct. 1968; P.M. Elsen leg.; KMMA • 1♀; Boma; R.F. Achille leg.; KMMA • 1♀; Boma; 17 Jun. 1915; Lang and Chapin leg.; KMMA • 1♀; Bomputu, Salonga; Jun. 1936; J. Ghesquière leg.; KBIN • 1♂; Bukama; 2 Apr. 1911; Bequaert leg.; KMMA • 1♀; Bumba; Dec. 1939–Jan. 1940; H. De Saeger leg.; KMMA • 1♀; Coquilhatville [= Mbandaka]; 1946; Ch. Scops leg.; KMMA • 1♂; between Deti and Ibambi; 5 Jul. 1931; F.R. Swift leg.; NHMUK • 1♀; Eala; Mar. 1935; A. Corbisier leg.; KMMA • 1♀; Eala; Mar. 1935; J. Ghesquière leg.; KBIN • 1♀; same collection data as for preceding; 12 Aug. 1935 • 1♀; same collection data as for preceding; 19 Nov. 1935 • 1♂; same collection data as for preceding; 12 Nov. 1936 • 1♀; Elisabethville [= Lubumbashi]; Nov. 1932; C.V. Hirschberg leg.; KBIN • 1♀; Elisabethville [= Lubumbashi]; Nov. 1933; M. Bequaert leg.; KBIN • 1♂; same collection data as for preceding; 22 Apr. 1934 • 1♀; same collection data as for preceding; 3 Mar. 1935 • 1♂; Elisabethville [= Lubumbashi]; 1–6 Sep. 1932; de Loose leg.; KMMA • 1♀; same collection data as for preceding; 24 Nov. 1932 • 1♀; Faradje; 30 Mar. 1912; Lang and Chapin leg.; KMMA • 1♀; same collection data as for preceding; Nov. 1912 • 1♀; Idjwi Island, Kivu; 8 Nov. 1952; J. Verbeke leg.; KBIN • 1♀; Jadotville [= Likasi]; J. Muller leg.; KBIN • 3♂♂; Kadjudju; Feb. 1932; G. Babault leg.; MHNH • 4♂♂ 4♀♀; same collection data as for preceding; May–Jun. 1932 • 2♂♂ 8♀♀; same collection data as for preceding; Aug. 1932 • 2♂♂; same collection data as for preceding; Sep. 1932 • 1♀; Kapanga; Nov. 1932; F.G. Overlaet leg.; KMMA • 2♂♂ 1♀; same collection data as for preceding; Dec. 1932 • 1♀; same collection data as for preceding; Mar. 1933 • 1♀; Kasongo; 10 Sep. 1959; P.L.G. Benoit leg.; KMMA • 1♀; Katoko-Kobe; 10–20 Jan. 1958; Segers leg.; KBIN • 1♀; Katompe; 12 Dec. 1923; M. Bequaert leg.; KMMA • 1♀; Kimuenza; Sep. 1962; M.J. Deheegher leg.; KMMA • 1♀; Kisantu; 1927; P. Vanderyst leg.; KMMA • 1♀; Komi, Sankuru; Dec. 1930; J. Ghesquière leg.; KMMA • 1♀; same collection data as for preceding; CNC • 2♂♂; Kwango; Panzi; 12 Feb. 1939; Mrs Bequaert leg.; KMMA • 1♀; Lubutu; 22 Jan. 1915; J. Bequaert leg.; KMMA • 1♀; Lukolela; 3 Jan. 1931; .P. Chapin leg.; AMNH • 1♂; same collection data as for preceding; 7 Jan. 1931 • 1♀; Luputa, Lomami; Jan. 1935; Bouvier leg.; KMMA • 1♀; same collection data as for preceding; Mar. 1935 • 1♂; same collection data as for preceding; May 1935 • 1♀; Mbandaka; 1 Feb. 1962; A.B. Stam leg.; KMMA • 1♀; Mboga; Jul. 1914; J. Bequaert leg.; KMMA • 1♀; Medje, Ituri; 9–15 Jul. 1910; Lang and Chapin leg.; AMNH • 1♂; Medje, Ituri; 1–7 Sep. 1910; Lang and Chapin leg.; KMMA • 1♂ 2♀♀; Moma, Equateur; Jun. 1925; J. Ghesquière leg.; KMMA • 1♀; N'Guli; 6–9 Oct. 1913; Rodhain leg.; KMMA • 1♀; Niangara, Uelé; Nov. 1910; Lang and Chapin leg.; KMMA • 1♀; Nzali, Ubangi; 3 Feb. 1932; H.J. Brédo leg.; KMMA • 2♀♀; Pawa, Uelé; 1938; A. Dubois leg.; KMMA • 1♀; Poko, Uelé; Aug. 1913; Lang and Chapin leg.; AMNH • 1♀; same collection data as for preceding; KMMA • 1♂; Pweto, Katanga; Oct. 1926; A. Bayet leg.; KMMA • 3♂♂ 1♀; Stanleyville [= Kisangani]; Mar. 1915; Lang and Chapin leg.; AMNH • 1♂; same collection data as for preceding; CNC • 3♂♂ 1♀; same collection data as for preceding; KMMA • 1♀; same collection data as for preceding; 6 Apr. 1915; CNC • 1♀;

same collection data as for preceding; 7 Apr. 1915; KMMA • 1♀; same collection data as for preceding; 14 Apr. 1915 • 1♂; same collection data as for preceding; Apr. 1915 • 1♂; same collection data as for preceding; KBIN • 1♀; Tshibamba, Lulua; Mar. 1932; F.G. Overlaet leg.; KMMA • 4♀♀; Uvira, Kivu; 25 Aug. 1957; P. Basilewsky leg.; KMMA. Equatorial Guinea • 1♂; Fernando Po [= Bioko Island], Basile; Aug. 1901; L. Fea leg.; MCSNG • 1♂; Musola; Jan. 1902 ; L. Fea leg.; MCSNG • 1♀; same collection data as for preceding; Mar. 1902 • 1♀; Punta Frailes; Oct.–Nov. 1901; L. Fea leg.; MCSNG • 1♂ 1♀; San Benito [= Mbini]; 1885; Guiral leg.; MHNH. Ethiopia • 1♂; Arba-Minch, Lake Chano; 19 Oct. 2012; A. Pauly leg.; KMMA. Gabon • 1♂; Ipassa, route de Makokou; 2–17 May 1974; M. Donskoff and J. Le Breton leg.; MHNH. Ghana • 1♀; Accra; 1–20 Jul. 1988; M. Hauser leg.; CDFA • 1♀; Burobu-ro, Kumasi; 4 Jun. 1976; A.B. Stam leg.; KMMA • 1♀; same collection data as for preceding; 12 Jul. 1976 • 1♀; same collection data as for preceding; 17 Jul. 1976 • 1♀; same collection data as for preceding; 28 Jul. 1976 • 1♀; Cape Coast; Dec. 2004; G. Goergen leg.; IITA • 1♂; Obuasi, Ashanti; 8 Aug. 1906; W.M. Graham leg.; NHMUK • 2♂♂ 1♀; same collection data as for preceding; 25 Aug. 1907 • 1♀; Takoradi; 2–6 Jun. 1957; G.H. Heinrich leg.; CNC • 1♂; Tsito; 26 Jan. 1969; O.W. Richards leg.; NHMUK • 2♂♂ 1♀; Wati Waterfalls; Feb. 2003; G. Goergen leg.; IITA • 1♀; Worawora; Mar. 2005; G. Goergen leg.; IITA. Guinea Bissau • 1♂ 2♀♀; Bolama; Jun.–Dec. 1899; L. Fea leg.; MCSNG. 'GUINEA' • 1♀; Westermann leg.; MNB [labeled as type of *maculipennis* considered to originate from Guinea Bissau according Smith and Vockeroth (1980); cf. comments]. Ivory Coast • 1♀; Adiopodoumé; 4 Jul. 1948; Jouer leg.; MHNH • 1♂; Banco National Park; 23 Apr. 1989; J. Londt leg.; NMSA. Kenya • 1♀; Itieni Forest, Nyambene Hills; 16–30 Oct. 2011; R.S. Copeland leg.; ICIPE • 1♂; Kaimosi; Feb. 1949; V.G.L. van Someren leg.; NHMUK • 1♀; Lukusi River, Kakamega Forest; 5 Apr.–26 Jun. 2017; R.S. Copeland leg.; ICIPE • 1♂; Taveta Forest; Aug. 1947; V.G.L. van Someren leg.; NHMUK. Liberia • 1♂; Bendu, Robertsport; 11 Apr. 1943; F.M. Snyder leg.; AMNH • 1♀; Du River camp 3; 1926; J. Bequaert leg.; KMMA • 1♀; Kpaine; 17 Aug. 1953; W. Peters leg.; NHMUK • 1♂; Monrovia; 24 May 1957; G.H. Heinrich leg.; CNC. Malawi • 1♂; Mt Mlanje; 9 Oct. 1913; S.A. Neave leg.; NHMUK. Mozambique • 1♀; East of Mt Mlanje; 21 Nov. 1913; S.A. Neave leg.; NHMUK • 1♂; Kola Valley; 5 Apr. 1913; S.A. Neave leg.; NHMUK • 1♂; Rikatla; H.A. Junod leg.; NMSA. Nigeria • 1♂ 1♀; Afikpo; 2 Jun. 1910; J.J. Simpson leg.; NHMUK • 1♂; Gadau; Jul. 1938; Buxton and Lewis leg.; NHMUK • 2♂♂; Ibadan; 24 Jul. 1947; J.L. Gregory leg.; NHMUK • 1♀; same collection data as for preceding; Jun. 1951; CNC • 1♂; Ibadan, IITA station; 24 Jan. 1997; G. Goergen leg.; IITA • 1♀; same collection data as for preceding; 26 Jan. 1998 • 1♂ 1♀; Ile-Ife; 30 Oct. 1969; J.T. Medler leg.; CNC • 1♀; Jos; Oct.–Dec. 1965; E. Bot Gwong leg.; KMMA • 1♀; Kaduna; Aug. 1952; Nash leg.; NMSA • 2♀♀; Kaduna; 19 Sep. 1962; M.W. Service leg.; NHMUK • 1♀; Olokemeji, Ibadan; AMNH. Republic of the Congo • 1♀; Fernand-Vaz; Sep.–Oct. 1902; L. Fea leg.; MCSNG • 1♂; Haut Ivindu, Ogooué; 1906; J. Gravot leg.; MHNH • 1♂; Lambaréné, Ogooué; 1913; E. Ellenberger leg.; MHNH. Sierra Leone • 1♀; Bomaru; 8 Aug. 1912; J.J.

Figures 5, 6. *Senaspis* species, habitus, lateral view **5** *S. haemorrhoa* (Gerstaecker) (♂) **6** *S. melanthysana* (Speiser) (♂).

Figures 7, 8. *Senaspis* species, habitus, lateral view **7** *S. nigrita* (Bigot) (♂) **8** *S. xanthorrhoea* (Bezzi) (♂).

Simpson leg.; NHMUK • 1♀; Daru; 31 Jul. 1912; J.J. Simpson leg.; NHMUK • 1♀; same collection data as for preceding; 18 Aug. 1912 • 1♀; Ka-Yima; 23 Jun. 1912; J.J. Simpson leg.; NHMUK • 1♀; Lungi; 14 Jul. 1959; C.P. Hoyt leg.; NHMUK. South Africa • 1♂; Dukuduku, between St Lucia and Matubatuba; 7–8 Apr. 1960; B. Stuckenberg leg.; NMSA • 1♀; Empangeni; 15 Apr. 2003; P. Reavell leg.; NMSA • 1♀; False Bay Park Reserve, Mpophomeni Trail area; 2 Jan. 1996; J. and A. Londt leg.; NMSA • 1♂ 1♀; Hazyview, Kruger Park Lodge area; 1–7 Oct. 2010; J. and A. Londt leg.; NMSA • 1♀; Middlekop; 11 Mar. 1979; NMSA • 1♂; Mpenjati Nature Reserve; 20 Mar. 2010; J. and A. Londt leg.; NMSA • 2♂♂ 1♀; same collection data as for preceding; 22–23 Jan. 2011 • 1♂; San Lameer Resort area; 11 Feb. 2012; J. and A. Londt leg.; NMSA. Tanzania • 1♀; Amani; G. Pringle leg.; NHMUK • 1♂; Kibonoto, Kilimanjaro; 29 Apr. 1906; Sjöstedt leg.; MNB • 1♀; Kigoma; 1924; C.R. Steel leg.; NHMUK • 1♂; Lembene, Usambara; 7 Jun. 1916; T.J. Anderson leg.; NHMUK • 3♀♀; Morogoro; J.G. Halcrow leg.; NHMUK • 1♂ 1♀; Morogoro; 16 May 1925; A.H. Ritchie leg.; NHMUK • 1♂ 1♀; same collection data as for preceding; 18 May 1925 • 1♂ 2♀♀; same collection data as for preceding; 20 May 1925 • 2♂♂ 1♀; same collection data as for preceding; 28 Jun. 1925 • 1♀; same collection data as for preceding; 10 Jun. 1925 • 1♀; Morogoro, Uluguru; A.G. Wilkins leg.; NHMUK • 1♀; Moschi; 1904; Alluaud leg.; MHNH. Togo • 1♀; Dzogbégan; 3 Jul. 1997; G. Goergen leg.; IITA • 1♂; Dzogbégan; 24–25 Jan. 2016; K. Jordaens leg.; KMMA • 1♂ 1♀; Kloto; 5 May 1996; G. Goergen leg.; IITA • 1♀; same collection data as for preceding; 3 Jul. 1997 • 1♂; same collection data as for preceding; Mar. 2000 • 6♂♂ 1♀; same collection data as for preceding; Aug. 2003 • 13♂♂ 5♀♀; same collection data as for preceding; Jan. 2004 • 3♂♂; same collection data as for preceding; Feb. 2004 • 31♂♂ 3♀♀; same collection data as for preceding; Mar. 2004 • 5♂♂ 1♀; same collection data as for preceding; Apr. 2004 • 1♂ 1♀; same collection data as for preceding; Jun. 2004 • 2♂♂; same collection data as for preceding; Nov. 2004 • 1♂ 1♀; same collection data as for preceding; Jan. 2005 • 4♂♂; same collection data as for preceding; Feb. 2005 • 3♂♂; same collection data as for preceding; Mar. 2005 • 1♀; same collection data as for preceding; Sep. 2005 • 1♀; same collection data as for preceding; Nov. 2005 • 1♂; same collection data as for preceding; Dec. 2005 • 1♂; same collection data as for preceding; Feb. 2006 • 1♀; same collection data as for preceding; May 2007 • 1♂; same collection data as for preceding; Jun. 2007 • 2♂♂; same collection data as for preceding; Oct. 2007 • 1♂; same collection data as for preceding; Jan. 2008 • 1♀; same collection data as for preceding; Jul. 2008 • 1♂; same collection data as for preceding; Jul. 2015 • 1♀; Kloto Forest; Jun. 2004; G. Goergen leg.; IITA • 1♂; Kuma-Tokpli; 21–24 Jan. 2016; K. Jordaens leg.; KMMA • 1♂; Lokossa; Jun. 2006; G. Goergen leg.; IITA • 1♀; Obé, near Akloa; 22 Apr. 2008; A. Ssymank leg.; MZH. Uganda • 1♀; Ankole; H.B. Johnston leg.; NHMUK • 1♂; Southeast Ankole; 4–8 Oct. 1911; S.A. Neave leg.; NHMUK • 1♂; Western Ankole; 10–14 Oct. 1911; S.A. Neave leg.; NHMUK • 1♀; between Jinja and Busia or Mbwago, E. Busoga; 28 Jul.–1 Aug. 1911; S.A. Neave leg.; NHMUK • 2♀♀; between Lake Kioga SE shore and Kakindu; 22–23 Aug. 1911; S.A. Neave leg.; NHMUK • 1♂; Buamba Forest, Semliki

Valley; 3–7 Nov. 1911; S.A. Neave leg.; NHMUK • 3♂♂ 4♀♀; Budongo Forest, nr Lake Albert; Apr. 1972; E. Babyetagara leg.; CNC • 1♂ 1♀; Busoga; 1903; D. Bruce leg.; NHMUK • 2♂♂; Busoga; Mar. 1906; A. Hodges leg.; NHMUK • 1♂; Entebbe; 12–20 Jan. 1912; S.A. Neave leg.; NHMUK • 3♀♀; Entebbe; 14 Nov. 1912; C.C. Gowdey leg.; NHMUK • 1♂ 1♀; same collection data as for preceding; 18–20 Nov. 1912 • 1♀; same collection data as for preceding; 3–4 Dec. 1912 • 1♂; same collection data as for preceding; 12–13 Dec. 1912 • 1♀; Entebbe; 1 Feb. 1972; H. Falke leg.; CNC • 1♂; same collection data as for preceding; 10 Jun. 1972 • 1♂; same collection data as for preceding; 23–31 Jan. 1973 • 3♂♂; same collection data as for preceding; 25–28 Jan. 1973 • 1♀; same collection data as for preceding; Mar. 1973 • 1♀; Entebbe; 1 May 1973; M.K. Paulus leg.; CNC • 1♂; nr Entebbe; 23–31 Jan. 1973; H. Falke leg.; CNC • 1♂ 1♀; same collection data as for preceding; 1–14 Feb. 1973 • 1♀; south side Lake George; 17–19 Oct. 1911; S.A. Neave leg.; NHMUK • 4♂♂; Ibanda; 23–28 Dec. 1972; H. Falke leg.; CNC • 1♀; Jinja; Sep. 1928; V.G.L. van Someren leg.; NHMUK • 1♀; near Kakindu, Nile banks; 24 Aug. 1911; S.A. Neave leg.; NHMUK • 3♂♂ 2♀♀; Kayonza Forest, Kigezi; Sep. 1972; H. Falke leg.; CNC • 1♂; Kigaloma, Katwe; 2 Feb. 1912; H.B. Owen leg.; NHMUK • 1♀; Kilembe, Ruwenzori Range; Dec. 1934–Jan. 1935; F.W. Edwards leg.; NHMUK • 1♀; Magyo, Buvuma Island, Lake Victoria; Mar. 1968; E. Vertriest leg.; KMMA • 1♀; Masaka, Katera Forest; Nov. 1955; V.G.L. van Someren leg.; NHMUK • 1♀; Mbale-Kimu Road; 15–17 Aug. 1911; S.A. Neave leg.; NHMUK • 1♀; Mt Kokanjero; 7–9 Aug. 1911; S.A. Neave leg.; NHMUK • 1♀; W. Nile; 13 Nov. 1958 NHMUK • 2♂♂; Nkokonjera; 23 Dec. 1910; C.C. Gowdey leg.; NHMUK • 1♂; Nyabushozi, Nyrbthozi County; 21 Jan. 1975; P. Mugabi leg.; CNC • 1♀; Salt Lake to Wawamba Country; 1894; G.F. Scott Elliot leg.; NHMUK • 1♂ 1♀; Siroko River; 12–14 Aug. 1911; S.A. Neave leg.; NHMUK • 4♂♂ Tero Forest, Southeast Buddu; 26–30 Sep. 1911; S.A. Neave leg.; NHMUK • 1♂; Unyoro, Kafu River Valley; 23–28 Dec. 1911; S.A. Neave leg.; NHMUK • 1♂; Wasa River; 11–14 Apr. 1914; R.E. McConnell leg.; NHMUK. Zimbabwe • 1♀; Bomponi; 6 May 1963; D. Cookson leg.; NMSA.

Description. Body length: 10.3–15.9 mm. Wing length: 7.9–12.0 mm.

Male (Fig. 1). Head (Figs 12, 13). Eye bare; holoptic, eye contiguity for distance equal to length of ocellar triangle, facets dorsally slightly larger, at most twice as large in diameter as ventral ones. Frons black to black-brown; largely subshiny, with greyish brown pollinosity in dorsal fifth and along eye margins; with very dispersed, short pale pile. Face black to black-brown; subshiny with pale brownish to greyish pollinosity, in parts more densely so, medial part and ventral margins largely devoid of pollinosity; in parts with dispersed long pale pile; facial tubercle strongly pronounced. Gena colour and pollinosity as ventral lateral margins of face, with short to long pale pile. Occiput black-brown, covered with dull grey pollinosity; with dispersed pale pile. Antennal segments black-brown, basoflagellomere apically slightly paler; arista pale to dark yellow.

Thorax (Fig. 52). Scutum subshiny black; grey pollinose, except on anterior part of scutellum, at transverse suture and along lateral margins where more densely orange-brown pollinose; with short pale pile, anteriorly and on notopleuron somewhat

Figures 9, 10. *Senaspis* species, habitus, lateral view **9** *S. umbrifera* (Walker) (♂ holotype) **10** *S.* nr *umbrifera* (Walker) (♂).

Figure 11. Habitus, lateral view *S. pennata* (Hervé-Bazin) (♀).

longer. Scutellum pale brownish to orange-brown, anterior margin narrowly darker; with short pale pile. Pleura ground colour black-brown, sparsely greyish pollinose; covered with dispersed long pale pile, anterior anepimeron sometimes partially black pilose; pilosity absent on meron, dorsomedial anepimeron, anterior part of katepisternum and anterior anepisternum. Scutellum apical margin weakly rounded, distinctly marginated, 2.5 times as wide as long.

Legs. Brown to black-brown; with short black pile, along posterior margin of pro- and mesofemora with longer pale pile. Metafemur (Fig. 80) distinctly thickened, with one distinct ventral swelling in apical fifth, with dense short stout setae on swelling; metatibia thickened and slightly curved, with pile along ventral margin not distinctly more dense.

Wing (Fig. 64). Faint yellowish brown tinge, towards posterior margin and apex more greyish; with distinct dark brown macula running from anterior margin and covering most of stigma, parts of cell r_1 and r_{2+3}, distal part of cell br and basal part of r_{4+5}, decreasing in colour on anterior part of cell dm; distally of brown macula more hyaline patch. Calypters yellow-white, in medial part more pale brownish; with fringe of yellow-white pile. Cell r_1 variable, usually closed with petiole at most equal to height of base of stigma but usually shorter, sometimes closed but petiole missing; vein R_{4+5} sinuate, usually not appendiculate, rarely with short appendix.

Abdomen (Fig. 91). Subshiny brown to black-brown, postabdomen more reddish brown; with greyish to greyish brown pollinosity, except for anteromedial macula on terga I and II, pair of sublateral maculae on terga I–III and posterior part of tergum IV where more shining; with short dark pile, except tergum I, anterior margin tergum II, and lateral margins of all terga where pale pile. Sterna orange-brown to black-brown, with short dispersed pale pile. Male genitalia as in Fig. 102.

Female. As male except for the following character states: Eye (Figs 14, 15) dichoptic, facets equal to subequal in size. Frons subshiny black to black-brown in ventral protruding part, dorsally with greyish to greyish brown pollinosity. Postabdominal terga often less reddish brown; subshiny maculae sometimes more extensive and more pronounced.

Distribution. Angola, Benin, Burundi, Cameroon, Democratic Republic of the Congo, Equatorial Guinea, Ethiopia, Gabon, Ghana, Guinea Bissau, Ivory Coast, Kenya, Liberia, Malawi, Mozambique, Nigeria, Republic of the Congo, Sierra Leone, South Africa, Tanzania, Togo, Uganda, Zimbabwe. 'Java' as type locality is probably an error.

Comments. The orginal description of *dentipes* Macquart mentioned the geographic origin of the type as "de Java". No label on the lectotype pin indicates a locality or region, and the locality is probably an error. The type specimen of *dentipes* bears a lectotype label with designation by F.C. Thompson in 1977. The original description did not indicate the number of specimens examined by Macquart but only made reference to the fact that the description is based on male only and that material is housed in the 'Muséum' (referring to MNHN). No additional specimens could be traced in the MNHN collection. The lectotype designation (made in accordance with recommendation 73♀ of the ICZN (Thompson pers. comm.)) has not been published elsewhere.

The type of *maculipennis* Loew could not be traced. According to the original description (Loew 1858) as well as the detailed redescription by Loew (1860), this is a male specimen from 'Guinea'. One female specimen in MNB collection (Guinea, Westerm., additional label '843') is indicated as type but this contradicts with the above, and thus appears not be part of the type series. This specimen was also mentioned by Karsch (1887). According to Smith and Vockeroth (1980) 'Guinea' refers to Guinea Bissau.

The taxon *livida* Bezzi was described as a variety of *aesacus* Walker by Bezzi (1912), based on two specimens from Fernando Po [= Bioko Island], which were among a series of specimens identified as *aesacus*. He pointed out the few morphological differences and suggested that they could be just teneral specimens, which did not attain their full colours and wing markings. Smith and Vockeroth (1980) elevated *livida* to species rank. Examination of the type material, however, indicates that Bezzi was correct in considering these as teneral specimens and that there is no morphological evidence for considering *livida* as a distinct species, different from *dentipes*. We, therefore, synonymize *livida* with *dentipes*.

Senaspis dibapha **(Walker, 1849)**

Figs 2, 16–19, 53, 65–67, 81, 92, 103

Xylota dibaphus Walker, 1849: 560.
Eristalis nigripennis Macquart, 1855: 108. Syn. nov.

Eristalomyia rufonasuta Bigot, 1891: 375. Syn. by Bezzi (1912).
Eristalis (*Stenaspis*) *gypseisquama* Speiser, 1910: 123. Syn. by Bezzi (1912).
Eristalis (*Stenapsis*) *gypseisquama* var. *sulfurata* Speiser, 1911: 240. Syn. by Smith and Vockeroth (1980).

Differential diagnosis. The only *Senaspis* species with a pair of lateral facial tubercles in addition to the medial one (Fig. 16) (only single medial tubercle in all other *Senaspis* species). Legs predominantly orange to rufous with slender metafemur (Fig. 81) (thickened in all other *Senaspis* species). The wing is largely brownish without distinct medial macula (Fig. 65).

Examined material. *Xylota dibaphus* Walker: Lectotype (hereby formally designated and published; see comments), female, "Lecto- // type" "Xylota // Type // dibaphus // Walk." "Locality?" "LECTOTYPE of // Xylota // dibaphus Walker // desig. F.C. Thompson 1987" [NHMUK].

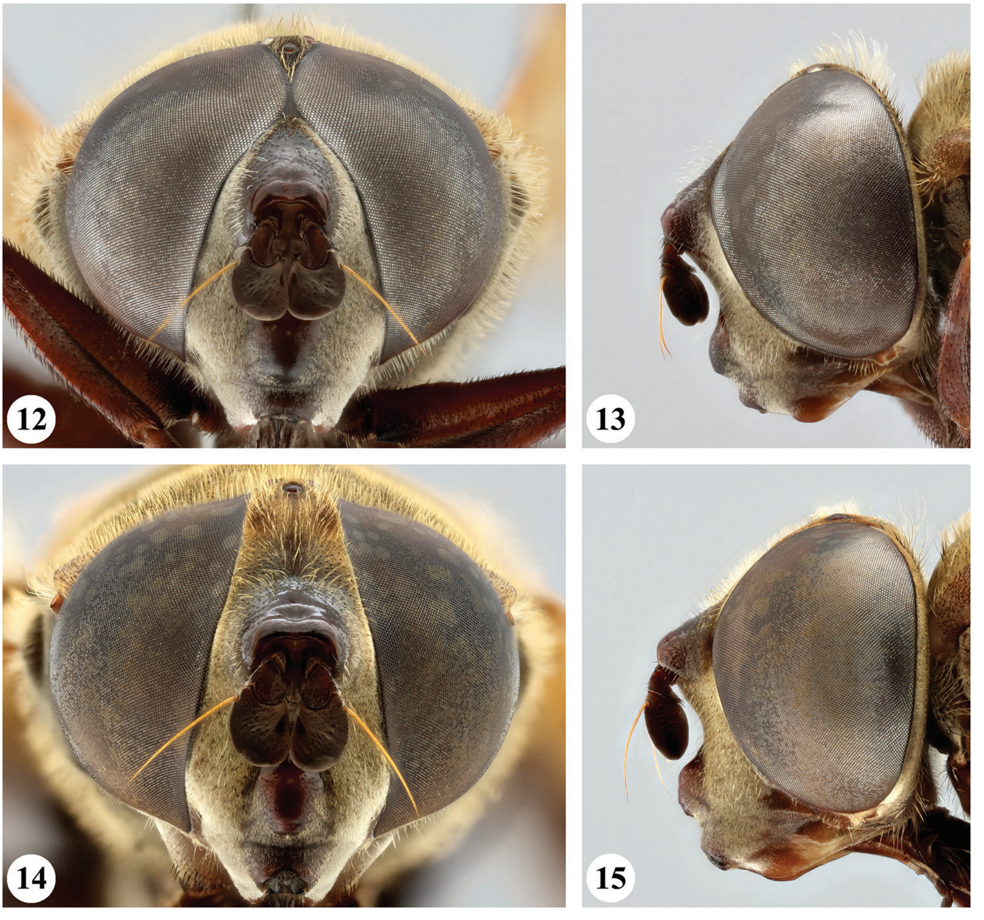
Eristalis nigripennis Macquart: Lectotype (hereby designated), male, "SYN- // TYPE" "ex. coll. Bigot. // Prs. by // G.H. Verrall. // B.M.1901–14." "E. nigripennis ♂. // Columbia Macq." "NHMUK010369880" "LECTOTYPUS" [NHMUK]. Paralectotype, male, "SYN- // TYPE" "COLUMBIA" "ex. coll. Bigot. // Prs. by // G.H. Verrall. // B.M.1901–14." "Eristalis // nigripennis // ♂. Macq." "NHMUK010369879" "PARA- // LECTOTYPUS" [NHMUK].

Eristalomyia rufonasuta Bigot: Holotype, female, "Holo- // type" "Assinie // Afrique oc" "Type // J. Bigot" "Eristalomyia // rufonasuta // ♀" "Assinie, // W. Africa. // Ex coll. // Bigot. // Pres by // G.H. Verrall. // 94.234." "BMNH(E) # // 230784" [NHMUK].

Eristalis (*Stenaspis*) *gypseisquama* Speiser: Holotype, female, "Kilimandj. // Sjöstedt" "Kibonoto // kulturz." "maj" "Eristalis (Dolichom.) // gÿpseisquama // P. Speiser det. // Tÿpe!" "NHRS-BYWS // 000002768" "Loan // 575/99" [NRMS, examined through images].

Eristalis (*Stenapsis*) *gypseisquama* var. *sulfurata* Speiser: Lectotype (hereby designated), male, "Typus" "Kamerun // Barombi-Stat. // Preuss S." "Juli–Oktob. // 1890 Preuss S." "Zool. Mus // Berlin" "LECTOTYPUS" [MNB]. Paralectotype, female, "Typus" "Kamerun // Barombi-Stat. // Preuss S." "Zool. Mus // Berlin" "PARA- // LECTOTYPUS" [MNB]. Paralectotype, female, "Typus" "Kamerun // Barombi-Stat. // Preuss S." "Zool. Mus // Berlin" "PARA- // LECTOTYPUS" [MNB]. Paralectotype, male, "Typus" "S. Kamerun. // Bipindi //IV. 97. //G. Zenker. S°." "Buschwald. // IV. 97." "Eristalis (Stenasp) // gypseisquama m. // P. Speiser det." "Zool. Mus. // Berlin " "PARA- // LECTOTYPUS " [MNB]. Possibly paralectotype (see comments), female: "Sierra Leone // Dr Staudinger V. " "Sierra // Leone // Staudinger" "Zool. Mus. // Berlin " [MNB].

Other material. Angola • 1♂; Camissombo; 4–13 Feb. 1958; G.H. Heinrich leg.; CNC • 1♀; Landana; 1875; Klein leg.; MNHN • 2♂♂ 1♀; 30 km N of Quiculungo; Sep.–Oct. 1957; CNC • 1♀; Texeira de Sousa [= Luau]; Feb. 1965; C.A. Green leg.; NMSA. Benin • 1♀; Bonou; 24 Nov. 2011; G. Goergen leg.; IITA • 3♂♂ 3♀♀; Niaouli; 21 Nov. 2011; G. Goergen leg.; IITA • 1♂; Niaouli; 10 Dec. 2013; K. Jordaens and G. Goergen leg.; KMMA • 3♀♀; Pénéssoulou; Jun. 2014; G. Goergen leg.;



Figures 12–15. Head, frontal and lateral view *S. dentipes* (Macquart) (**12, 13** ♂ **14, 15** ♀).

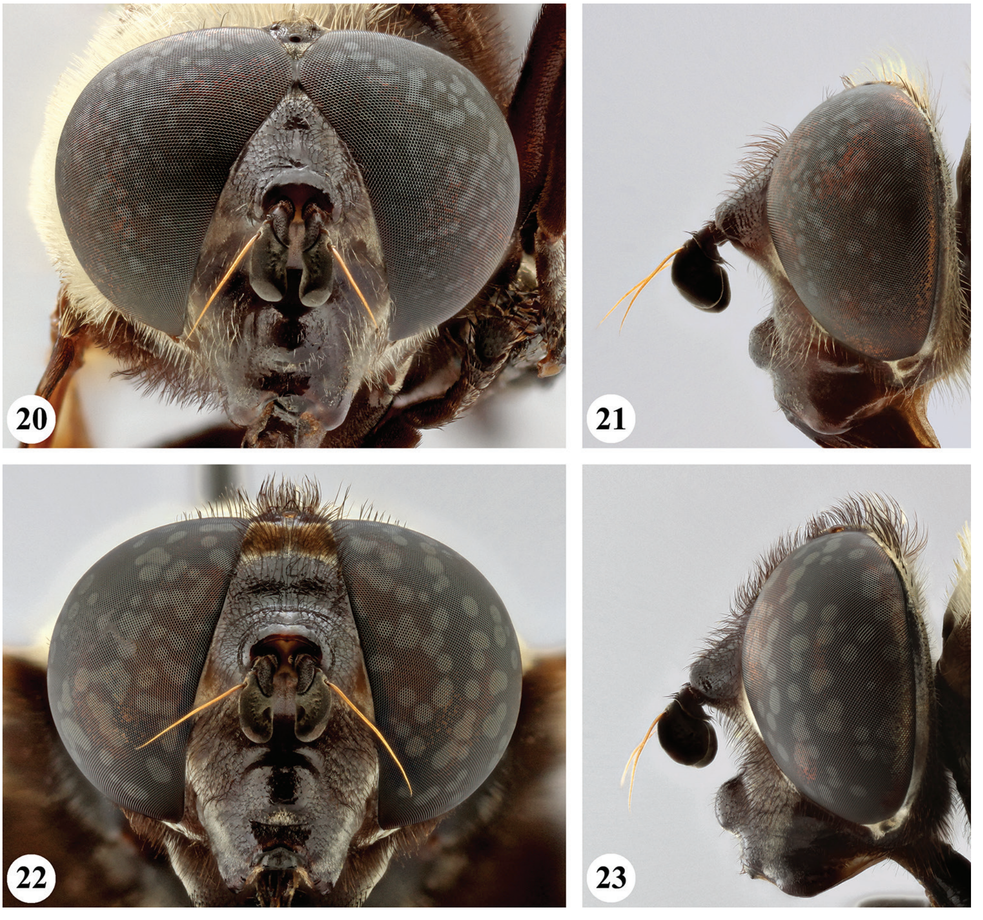
IITA • 1♀; Pobè; 27 Jan. 2016; G. Goergen leg.; IITA • 1♂ 9♀♀; Porto Novo; Aug. 2006; G. Goergen leg.; IITA • 1♂; Sérou; Nov. 2016; G. Goergen leg.; IITA. Burundi • 1♀; Bubanza, Gihanga Hill; 20 Nov. 195[?]; F.J. François leg.; KBIN • 1♀; Kisenyi; 26 Dec. 1952; KBIN • 1♀; Mugina; 21 Jun. 1949; F.J. François leg.; KBIN • 3♂♂ 2♀♀; Murmirwa, Nyakibande; 24 Apr. 2019; E. Sinzinkayo leg.; OBPE • 3♂♂ 1♀; same collection data as for preceding; 14 Jul. 2019 • 1♂; Murmirwa, Nyambuye; 18 Jun. 2019; E. Sinzinkayo leg.; OBPE • 3♀♀; same collection data as for preceding; 18 Sep. 2019 • 4♂♂ 6♀♀; Rwegura, Kibira NP; 31 May 2018; E. Sinzinkayo leg.; OBPE • 1♀; Teza, Kibira NP; 28 May 2018; E. Sinzinkayo leg.; OBPE. Cameroon • 2♀♀; Abong M'bang; 1–30 Apr. 1936; F.G. Merfield leg.; NHMUK • 1♂ 1♀; D'Ja Posten; 1–30 Jul. 1936; F.G. Merfield leg.; NHMUK • 1♂; Lolodorf; 5 Nov. 1913; A.I. Good leg.; CNC • 3♀♀; Mbalmayo; 3 Jul. 1998; G. Goergen leg.; IITA • 2♀♀; same collection data as for preceding; 7 Jul. 1998 • 5♀♀; same collection data as for preceding; 8 Jul. 1998 • 3♀♀; same collection data as for preceding; Sep. 1998 • 1♀; same coll-

Figures 16–19. Head, frontal and lateral view *S. dibapha* (Walker) (**16, 17** ♂ **18, 19** ♀).

ection data as for preceding; Nov. 1998 • 1♂; same collection data as for preceding; May 1999 • 1♀; same collection data as for preceding; 9 Jul. 1999 • 1♀; Metet; 15 Aug. 1919; A.I. Good leg.; CNC • 1♂; N'Tem; 1907; Cottes leg.; MNHN • 1♀; Tokélé; 16 Oct. 1965; B. de Miré leg.; MNHN • 1♀; Yaoundé-Ototomo; 23 Jul. 1965; L. Matile leg.; MNHN • 1♂; Yaoundé-Nkolbisson; 17–21 Oct. 1967; L. Tsacas leg.; MNHN. Central African Republic • 1♂; Bagandou, Lobaye; 14 Sep. 1967; L. Matile leg.; MNHN. Democratic republic of the Congo • 1♀; Abok; Oct. 1935; Ch. Scops leg.; KMMA • 5♂♂ 12♀♀; Akenge, Stanleyville [= Kisangani]; Lang and Chapin leg.; KMMA • 1♀; Akunimbagi; 22 Nov. 1932; H.J. Brédo leg.; KMMA • 1♀; Bafwasende, Stanleyville [= Kisangani]; Nov. 1945; F. François leg.; KMMA • 1♀; same collection data as for preceding; 3 Mar. 1946 • 1♂ 1♀; Bafuwasikuli; 11 Sep. 1912; Christy leg.; KMMA • 1♀; Bamania, Equateur; 1958; P. Hulstaert leg.; KMMA • 1♀; Bamanya, Tshuapa; 1968; P. Hulstaert leg.; KMMA • 1♂ 1♀; Bambesa; 21 Mar. 1938; J. Vrydagh leg.; KBIN • 1♂; same collection data as for preceding; 6–9 Nov.

1938 • 1♂; Bambesa; 10 Aug. 1933; J.V. Leroy leg.; KMMA • 1♀; same collection data as for preceding; 10 Oct. 1933 • 1♀; same collection data as for preceding; 20 Oct. 1933 • 1♂; same collection data as for preceding; Dec. 1934 • 3♂♂ 1♀; same collection data as for preceding; 15 Oct. 1933; H.J. Brédo leg. • 1♂; same collection data as for preceding; 1 Oct. 1938; J. Vrydagh leg. • 6♂♂ 5♀♀; same collection data as for preceding; Jul. 1943; J. Vrydagh leg. • 1♂; Bangala, Kutu; 18 Jun. 1935; G. Settembrino leg.; KBIN • 1♂; Barumbu; Feb. 1921; J. Ghesquière leg.; KMMA • 1♀; Barumbu; 22 Jun. 1921; Tihou; KMMA • 1♂; Bas Congo; KMMA • 1♀; Basoko; 1911; Bequaert leg.; KMMA • 1♀; Basoko; Oct. 1948; P.L.G. Benoit leg.; KMMA • 1♀; Beni Bendi, Sankuru; Jan. 1895; L. Claetens leg.; KBIN • 1♀; Benzali, Kinshasa; 3 Oct. 1968; P.M. Elsen leg.; KMMA • 1♀; Bokuma, Tshuapa; Jul. 1952; P. Lootens leg.; KMMA • 1♀; same collection data as for preceding; 6 Feb. 1954 • 1♂; Bolingo, Busira River; 23 Jun. 1936; J. Ghesquière leg.; KBIN • 1♀; same collection data as for preceding; 24 Jun. 1936 • 1♀; Bombutu, Salonga; Jun. 1936; J. Ghesquière leg.; KBIN • 1♀; south of Bukavu, Tanganyika; 28 Aug. 1931; NHMUK • 2♀♀; Bumba; Dec. 1939–Jan. 1940; H. De Saeger leg.; KMMA • 1♀; Coquilhatville [= Mbandaka]; 12 May 1927; E. Mestdagh leg.; KBIN • 1♂; Costermansville [= Bukavu]; Jan.–Jun. 1951; H. Bomans leg.; KMMA • 1♀; Dekese, Itunda; Aug. 1959; F.J. François leg.; KBIN • 1♂ 1♀; same collection data as for preceding; Nov. 1959 • 1♀; same collection data as for preceding; Dec. 1959 • 1♂; same collection data as for preceding; 10 Feb. 1960 • 1♂; same collection data as for preceding; 23 Feb. 1960 • 1♀; Dingila, Uelé; 15 Jul. 1933; J.V. Leroy leg.; KMMA • 1♂; Djambi; 23 Dec. 1913; CNC • 1♂; Eala; Apr. 1932; H.J. Brédo leg.; KMMA • 1♂; Eala; 27 Mar. 1935; J. Ghesquière leg.; KBIN • 1♂; same collection data as for preceding; 7 May 1935 • 1♂; same collection data as for preceding; 17 May 1935 • 1♀; same collection data as for preceding; 25 Jun. 1935 • 1♀; same collection data as for preceding; 12 Aug. 1935 • 1♂; same collection data as for preceding; Aug. 1935 • 1♀; same collection data as for preceding; 25 Sep. 1935 • 2♂♂ 1♀; same collection data as for preceding; Sep. 1935 • 1♀; same collection data as for preceding; 25 Oct. 1935 • 1♀; same collection data as for preceding; Oct. 1935 • 1♀; same collection data as for preceding; 20 Nov. 1935 • 1♀; same collection data as for preceding; Nov. 1935 • 1♂; same collection data as for preceding; Jan. 1936 • 1♀; same collection data as for preceding; 6 Feb. 1936 • 2♂♂ 4♀♀; same collection data as for preceding; Mar. 1936 • 1♀; same collection data as for preceding; 19 Aug. 1936 • 1♂; same collection data as for preceding; 28 Sep. 1936 • 1♂ 1♀; same collection data as for preceding; Sep. 1936 • 1♂; same collection data as for preceding; 7 Oct. 1936 • 1♂; same collection data as for preceding; 22 Oct. 1936 • 1♂; same collection data as for preceding; 23 Oct. 1936 • 1♂; same collection data as for preceding; 26 Oct. 1936 • 1♀; same collection data as for preceding; 27 Oct. 1936 • 1♀; same collection data as for preceding; 6 Nov. 1936 • 1♂; same collection data as for preceding; 10 Nov. 1936 • 1♂; same collection data as for preceding; 24 Nov. 1936 • 1♂; Elisabethville [= Lubumbashi]; 26 Feb. 1939; H.J. Brédo leg.; KMMA • 1♂; Etata, Tshuapa; Sep–Oct. 1969; J. Hauwaerts leg.; KMMA • 1♀; Flandria [= Boteka], Tshuapa; Sep. 1946–Aug. 1947; P. Hulstaert leg.; KMMA • 1♀; Gamangui, Ituri; Feb.

1910; Lang and Chapin leg.; KMMA • 1♂; Gandjo, P.N. Albert; 1934; G.F. de Witte; KMMA • 1♀; Goma, Kivu; 10–15 May 1953; J. Verbeke leg.; KBIN • 1♀; Gombari, Uelé; D.J. Rodhain leg.; KMMA • 1♀; Inongo; Aug. 1913; J. Maes leg.; KMMA • 1♀; Irangi, Kivu; Feb. 1986; E. Heiss leg.; CDFA • 1♀; Isangi; May 1949; R.P. Camps leg.; KMMA • 2♂♂ 1♀; Ituri Forest; Jul. 1976; E. Babyetagara leg.; CNC • 1♀; Jenge; Dec. 1931; Putnam leg.; KMMA • 1♀; Jumbi, Mayumbe; 5 May 1926; A. Collart leg.; KMMA • 2♀♀; Kabinda; 1914; J. Schwetz leg.; NHMUK • 3♂♂ 2♀♀; Kadjudju; May–Jun. 1932; G. Babault leg.; MNHN • 4♂♂ 2♀♀; same collection data as for preceding; Aug. 1932 • 1♂ 1♀; Kakanou, Lomami; Jun. 1918; J. Schwetz leg.; KBIN • 1♀; Kalenge, Lulua; Aug. 1932; G.F. Overlaet leg.; KMMA • 3♀♀; same collection data as for preceding; Feb. 1934 • 1♀; Kalonge, P.N. Albert; 23–31 Jul. 1952; P. Vanschuytbroeck and J.Kekenbosch leg.; KMMA • 1♀; same collection data as for preceding; 27–30 Jul. 1952 • 1♀; Kapanga, Lulua; Nov. 1928; Walker leg.; KMMA • 1♀; Kapanga, Lulua; Aug. 1932; G.F. Overlaet leg.; KMMA • 2♀♀; same collection data as for preceding; Nov. 1932 • 1♂; same collection data as for preceding; Jan. 1933 • 1♂ 4♀♀; same collection data as for preceding; Mar. 1933 • 1♂ 1♀; same collection data as for preceding; Nov. 1933 • 1♂; same collection data as for preceding; Nov. 1933; CNC • 1♂; Kelzongo, Ubangi; 1 Feb. 1932; H.J. Brédo leg.; KMMA • 1♀; Keshero, Kivu; 27 Aug. 1953; J. Verbeke leg.; KBIN • 1♀; Kibali, Yindi, Ituri; May 1949; A.E. Bertrand leg.; KMMA • 1♂; Kibombo; 31 Oct. 1910; Bequaert leg.; KMMA • 1♀; Kisantu; 1932; De Wulf leg.; KMMA • 1♀; Kikyo, nr Kalonge, P.N. Albert; 10 Aug. 1952; R.P. Lootens leg.; KMMA • 1♀; Kissenyi, Kivu; 25 Apr. 1923; Van Saceghem leg.; KMMA • 1♀; same collection data as for preceding; 1924 • 1♀; Komi, Sankuru; Dec. 1930; J. Ghesquière leg.; CNC • 1♂; same collection data as for preceding; 8 Apr. 1930; KMMA • 3♀♀; same collection data as for preceding; May 1930 • 2♂♂; same collection data as for preceding; Jun. 1930 • 1♀; same collection data as for preceding; Dec. 1930 • 1♀; Kona; 16 May 2010; P. Grootaert leg.; KMMA • 1♂ 1♀; Kondue, Sankuru, E. Luja leg.; KMMA • 1♂; Lemba, Mayumbe; 1–10 Dec. 1915; R.Mayné leg.; KMMA • 1♀; Leverville [= Lusanga]; 1♂; Jan. 1914; P. Vanderijst leg.; KMMA • 1♀; 1928; J. Tinant leg.; KMMA • 1♂; Lokandu, Biawa Island; Jul. 1939; Vissers leg.; KMMA • 1♂ 1♀; Lubutu; 22 Jan. 1915; J. Bequaert leg.; KMMA • 1♂; Lueba near Baraka, Lake Taganyika; 16 Apr. 1927; R. Bois leg.; NHMUK • 1♂; Luebo; 30 Aug. 1921; H. Schouteden leg.; KMMA • 1♂; Lukolela; Nov. 1934; Ledoux leg.; KMMA • 1♀; Luputa, Lomami; Sep. 1934; Bouvier leg.; KMMA • 3♀♀; same collection data as for preceding; May 1935 • 1♂; Lusambo; 1938; V. Lagae leg.; KMMA • 1♂; Luvungi; Feb. 1916; Rodhain leg.; KMMA • 1♀; Mayumbe; 1917; R. Mayné leg.; KMMA • 1♀; Mbau, North Kivu; 8–21 Dec. 1971; H. Falke leg.; CNC • 1♀; Moanda; KMMA • 1♀; Mobeka, Ubangi; 11 Aug. 1947; M. Poll, leg.; KMMA • 2♀♀; Moma, Equateur; Jun. 1925; J. Ghesquière and Prince Leopold leg.; KMMA • 2♂♂; Mongbwalu, Kilo; 1937; Scheitz leg.; KMMA • 1♀; Mulungu, Kivu; 5 Apr. 1937; H.J. Brédo leg.; KMMA • 1♀; Mulungu, Kivu; Nov. 1951; P. Lefèvre leg.; KMMA • 1♂; Niangara, Uelé; Nov. 1910; Lang and Chapin leg.; KMMA • 1♂; Ouellé, Bouta; A. Dubois leg.; MNHN • 1♀; Poko; Uelé; Aug. 1913; Lang and Chap-



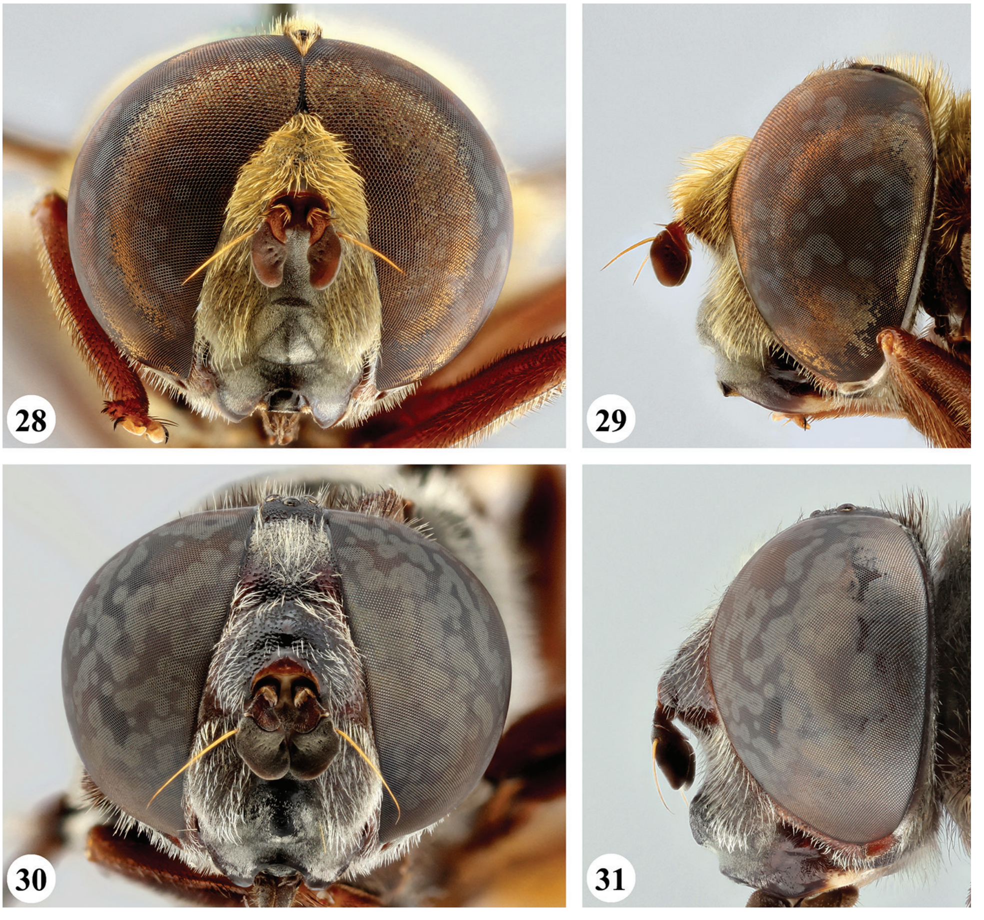
Figures 20–23. Head, frontal and lateral view *S. elliotii* Austen (**20, 21** ♂ **22, 23** ♀).

in leg.; CNC • 13♂♂ 18♀♀; same collection data as for preceding; KMMA • 1♂; Rumangabo, Nyakibanda, P.N. Albert; 11–13 Apr. 1945; G.F. de Witte leg.; KMMA • 1♀; Rutshuru; Jan. 1928; Ch. Seydel leg.; KMMA • 2♀♀; Rutshuru; 24 Nov. 1952; J. Verbeke leg.; KBIN • 1♀; Sake, nr Mutayo River, Kivu; 21 Mar. 1953; J. Verbeke leg.; KBIN • 1♂; Sankuru; 1910; Abrassart leg.; KMMA • 1♂; Shakakombe; 20 Apr. 1959; F.J. François leg.; KBIN • 1♀; Stanleyville [= Kisangani]; Lang and Chapin leg.; CNC • 1♂; same collection data as for preceding; Mar. 1915 • 2♂♂ 3♀♀; same collection data as for preceding; NHMUK • 1♂ 2♀♀; same collection data as for preceding; KMMA • 1♂; Tshibinda, Kivu; Dec. 1927; Ch. Seydel leg.; KMMA • 1♀; Uelé River; Rodhain leg.; KMMA • 2♂♂; Uruwu to Beni; Dec. 1935; F. François leg.; KMMA • 1♀; Uvira; Aug.–Dec. 1949; G. Marlier leg.; KMMA • 1♀; Wamba; 1936; Degotte leg.; KMMA • 1♀; Yahuma; Dec. 1948; P.L.G. Benoit leg.; KMMA • 1♀; Yangangu, Libenge; Oct.–Nov. 1945; C. Henrard leg.; KMMA. Equatorial Guinea • 1♀; Nkolentangan; 17 Nov. 1907; S.G. Tessmann leg.; MNB • 2♂♂ 3♀♀; San Be-

Figures 24–27. Head, frontal and lateral view *S. flaviceps* Macquart (**24, 25** ♂ **26, 27** ♀).

nito [= Mbini]; 1885; Guiral leg.; MNHN. Gabon • 1♀; Lambaréné; 1921; E. Le Moult leg.; MNHN • 1♀; Lastourville; G. Le Testu leg.; MNHN • 2♀♀; Libreville; Aug. 1892; MNB • 1♂; Libreville road, 50 km from Makokou; 8 May 1974; M. Donskoff and J. Le Breton leg.; MNHN • 1♀; Mabilé range; 14 Apr. 2016; G. Goergen leg.; IITA • 1♂; Makokou; Jul. 1970; J. David leg.; MNHN • 1♂; Muni, Mts de Cristal; 15–31 Oct. 1969; A. Villiers leg.; MNHN. Ghana • 1♀; Aburi; 1912–1913; W.H. Patterson leg.; NHMUK • 1♀; Ayona; May 2008; G. Goergen leg.; IITA • 1♀; Buro-Buro, Kumasi; 24 May 1976; A.B. Stam leg.; KMMA • 1♀; Cape Coast; Dec. 2004; G. Goergen leg.; IITA • 1♀; Kade; 3 Apr. 1964; C. Dudley leg.; NMSA • 1♀; Nadia; 1913; A.E. Evans leg.; NHMUK • 1♂; Nyabo, Ashanti; 29 Mar. 1947; J. Bowden leg.; NHMUK • 1♀; Obuasi; 20 Feb. 1906; W.M. Graham leg.; NHMUK • 1♀; same collection data as for preceding; 11 Aug. 1906 • 1♀; same collection data as for preceding; 24 Jul. 1907 • 1♀; same collection data as for preceding; 4 Aug. 1907 • 1♀; same collection data as for preceding; [no date] • 12♂♂ 7♀♀; Wati Waterfalls;

Feb. 2003; G. Goergen leg.; IITA. Guinea Conakry • 3♀♀; Tamara Island, Iles de Los; Jul. 1913; J. Serand leg.; MNHN • 1♀; Yanlé; Jun. 1942; M. Lamotte leg.; MNHN. Ivory Coast • 1♀; Daloa; Dec. 1930–Apr. 1931; Ch. Alluaud and P.A. Chappuis leg.; MNHN • 1♀; Danané; Jan. 1939; L. Chopard leg.; MNHN • 1♀; Duékué; Dec. 1930–Apr. 1931; Ch. Alluaud and P.A. Chappuis leg.; MNHN • 1♀; Koun-Abronso; Sep. 1961; J. Decelle leg.; KMMA • 1♀; Odienne; 1 May 1973; V. Vittard leg.; MNHN. Kenya • 1♀; Bura, Taita; Mar. 1912; Alluaud and Jeannel leg.; MNHN • 1♀; Bwamba; Jul.–Aug. 1946; V.G.L. van Someren leg.; NHMUK • 2♀♀; Ilala, 14 mi E Mumias; 18–21 Jun. 1911; S.A. Neave leg.; NHMUK • 1♀; Kaimosi; Mar.–Apr. 1932; V.G.L. van Someren leg.; NHMUK • 1♀; same collection data as for preceding; Feb. 1949 • 1♂; Kakamega Forest; 18–22 Jan. 1972; C.F. Huggins leg.; NHMUK • 1♂; Mawakota; Jul. 1929; V.G.L. van Someren leg.; NHMUK • 1♀; Nyangnori, West Nandi; Oct. 1904; Alluaud leg.; MNHN • 1♀; Taveta; Aug. 1947; V.G.L. van Someren leg.; NHMUK • 1♂; Yala River, S edge Kakamega Forest; 21–28 May 1911; S.A. Neave leg.; NHMUK. Liberia • 1♀; House Voinjana; 3 Sep. 1959; NHMUK • 1♀; river camp 3; 1926; J. Bequaert leg.; KMMA. Malawi • 1♂; Chintheche; Dec. 1977; R. Jocqué leg.; KMMA • 1♀; Mt Mlanje; 26 Oct. 1912; S.A. Neave leg.; NHMUK • 1♂; same collection data as for preceding; 6 Apr. 1913 • 1♀; Mt Mlanje; Jan.–Feb. 1914; J.B. Davey leg.; NHMUK • 1♂; 10 km W Nkhata Bay; 5–6 Mar. 1987; J. and A. Londt leg.; NMSA. Mozambique • 1♀; Tumbine Mountains, Milange; Apr. 1958; B. Stuckenberg leg.; NMSA. Nigeria • 1♂ 1♀; Aiyangba, N Nigeria; 11 Jan. 1911; T.J. Simpson leg.; NHMUK • 1♂; Ibadan, IITA Centre; Oct. 1997; G. Goergen leg.; IITA • 2♂♂; same collection data as for preceding; Nov. 2001 • 2♀♀; Ile-Ife; 30–31 Dec. 1969; J.T. Medler leg.; CNC • 1♂; S. Nigeria; T.J. Simpson leg.; NHMUK. Republic Of The Congo • 2♀♀; Lambaréné, Ogooué; E. Ellenberger leg.; MNHN • 1♀; same collection data as for preceding; 1911 • 2♀♀; same collection data as for preceding; 1912 • 3♀♀; same collection data as for preceding; 1913 • 2♀♀; N'Kogo, Ogooué; 1901; J. Bouyssou leg.; MNHN • 2♂♂; N'Goko-Sanga Basin, Ouesso; 1906; J. Gravot leg.; MNHN • 1♀; Ubokasanga; 1906; D. Gnavorod leg.; MNHN. Rwanda • 1♀; Ninda, P.N. Albert; 26 Sep. 1934; G.F. de Witte leg.; KBIN • 1♀; Rubona; 17 Jun. 1955; P. Elsen leg.; KMMA • 1♀; Shangugu; 23 Oct.–15 Nov. 1948; F.J. François leg.; KBIN • 1♀; Shangugu; 6 Apr. 1953; P. Basilewsky leg.; KMMA. Tanzania • 1♀; Bukoba; 10 Jun. 1912; C.C Gowdey leg.; NHMUK • 1♀; Amani; G. Pringle leg.; NHMUK • 1♂; Amani; 10 Dec. 1960; CNC • 1♂ 1♀; Morogoro; 6 May 1925; A.H. Ritchie leg.; NHMUK • 1♂ 2♀♀; same collection data as for preceding; 10 May 1925 • 2♂♂; same collection data as for preceding; 16 May 1925. Togo • 2♀♀; Dzogbégan; 9 Jun. 1999; G. Goergen leg.; IITA • 1♂; Kloto; Aug. 2003; G. Goergen leg.; IITA • 1♀; same collection data as for preceding; Dec. 2003 • 30♂♂ 20♀♀; same collection data as for preceding; Jan. 2004 • 35♂♂ 24♀♀; same collection data as for preceding; Feb. 2004 • 7♂♂ 4♀♀; same collection data as for preceding; Mar. 2004 • 3♂♂ 2♀♀; same collection data as for preceding; Apr. 2004 • 1♂; same collection data as for preceding; Jan. 2005 • 12♀; same collection data as for preceding; Oct. 2005 • 1♂ 1♀; same collection data as for preceding; Nov. 2005 • 1♂; same collection data as for preceding; Feb. 2006 • 4♂♂; same collection data as for preceding; Feb. 2007 • 1♂; same collection data as for preceding; Jan. 2008 • 1♂; same collection data as for preceding; Nov. 2015 • 1♀; same collection data as for preceding; 21–24 Jan. 2016 • 1♀; Kloto Forest; Oct. 2005; G. Goergen leg.; IITA • 2♂♂ 1♀; Kuma-Tokpli; 21–24 Jan. 2016; G. Goergen leg.; KMMA. Uganda • 1♀; Ankole, West Uganda; 30 Dec. 1975; M.K. Paulus leg.; CNC • 1♀; Ankole-Toro border, E Lake George; 20–21 Oct. 1911; S.A. Neave leg.; NHMUK • 2♀♀; Buamba Forest, Semliki Valley; 3–7 Nov. 1911; S.A. Neave leg.; NHMUK • 1♂; Budongo Forest, Unyoro; 11–15 Dec. 1911; S.A. Neave leg.; NHMUK • 1♂; Buramba Forest, Toro District; 22 Oct. 1913; R.E. McConnell leg.; NHMUK • 1♂; East Busoga, between Jinja and Busia or Mbwago; 28 Jul–1 Aug. 1911; S.A. Neave leg.; NHMUK • 1♀; Bwamba; 1 Jul. 1976; E. Babyetagara leg.; CNC • 1♂; Bwamba Valley; Jul. 1945; V.G.L. van Someren leg.; CNC • 1♀; Doro or Durro Forest, Toro; 25–29 Oct. 1911; S.A. Neave leg.; NHMUK • 1♂ 1♀; Mount Elgon; 4–8 Dec. 1972; H. Falke leg.; CNC • 1♀; Entebbe; 1–11 Sep. 1911; S.A. Neave leg. • 1♂ 3♀♀; same collection data as for preceding; 18–20 Nov. 1912; C.C. Gowdey leg. • 1♂; same collection data as for preceding; 3–4 Dec. 1912 • 2♂♂; same collection data as for preceding; 12–13 Dec. 1912 • 1♂; same collection data as for preceding; 1959; P.S. Corbet leg. • 1♀; Entebbe; 16 Oct. 1971; H. Falke leg.; CNC • 1♀; same collection data as for preceding; 17 Jun. 1972 • 1♂; same collection data as for preceding; 26 Oct. 1971; ZFMK • 9♀♀; near Entebbe; 1–14 Feb. 1973; H. Falke leg.; CNC • 2♀♀; Gayaza, Ankole; 17 Mar. 1936; H.B. Johnston leg.; NHMUK • 1♂ 3♀♀; Lake George; 17–19 Oct. 1911; S.A. Neave leg.; NHMUK • 1♀; Hoima-Kampala Road; 3 Jan. 1912; S.A. Neave leg.; NHMUK • 1♂ 1♀; Ibanda; 23–28 Dec. 1972; H. Falke leg.; CNC • 2♂♂; same collection data as for preceding; 19–24 Apr. 1973 • 1♂ 1♀; Impenetrable Forest, Ruhiza, Kigezi; 1–10 Jun. 1972; E. Babyetagara leg.; CNC • 1♂; Jinja; Sep. 1928; V.G.L. van Someren leg.; NHMUK • 1♂; same collection data as for preceding; Oct. 1930 • 1♂; Katera Forest, South of Maseka; May 1972; E. Babyetagara leg.; CNC • 2♂♂ 2♀♀; Kayonza Forest, Kigezi; May 1972; E. Babyetagara leg.; CNC • 2♂♂; Mabira Forest, Chagwe; 16–25 Jul. 1911; S.A. Neave leg.; NHMUK • 1♂; Maramagambo Forest, Lutoto, on Lake Edward Road; 1 Feb. 1912; H.B. Edwards leg.; NHMUK • 1♀; Masinda; Feb. 1912; R. Fyffe leg.; NHMUK • 1♀; Mbali; 19 Aug. 1912; C.H. Marshall leg.; NHMUK • 1♀; Mbarara, Ankole; Sep. 1966; M.G. Jefferies leg.; NHMUK • 1♂; Mbuma; 22 May 1910; C.A. Wiggins leg.; NHMUK • 1♀; Mpanga Forest, Toro; 13–23 Nov. 1911; S.A. Neave leg.; NHMUK • 1♂; Nakasongola; 28 Jul. 1911; C.C. Gowdey leg.; NHMUK • 1♂; same collection data as for preceding; 28 Aug. 1912 • 2♀♀; Nkokonjera; 23 Dec. 1910; C.C. Gowdey leg.; NHMUK • 1♀; Nyanza Victoria Northwest shores; 12–15 Sep. 1911; S.A. Neave leg.; NHMUK • 1♂; Nyrbthozi County, Nyabushozi; 21 Jan. 1975; P. Mugabi leg.; CNC • 1♂; Ruwenzori Foothills; 3–8 Jan. 1972; H. Falke leg.; CNC • 1♂; Rumi River; [no date]; J. Fraser leg.; NHMUK • 1♀; same collection data as for preceding; 12 Feb. 1912 • 1♀; Semliki Forest; 18 Feb. 1912; J. Fraser leg. NHMUK. Zimbabwe • 1♀; Bomponi; 16 May 1965; D. Cookson leg.; NMSA • 1♂; same col-



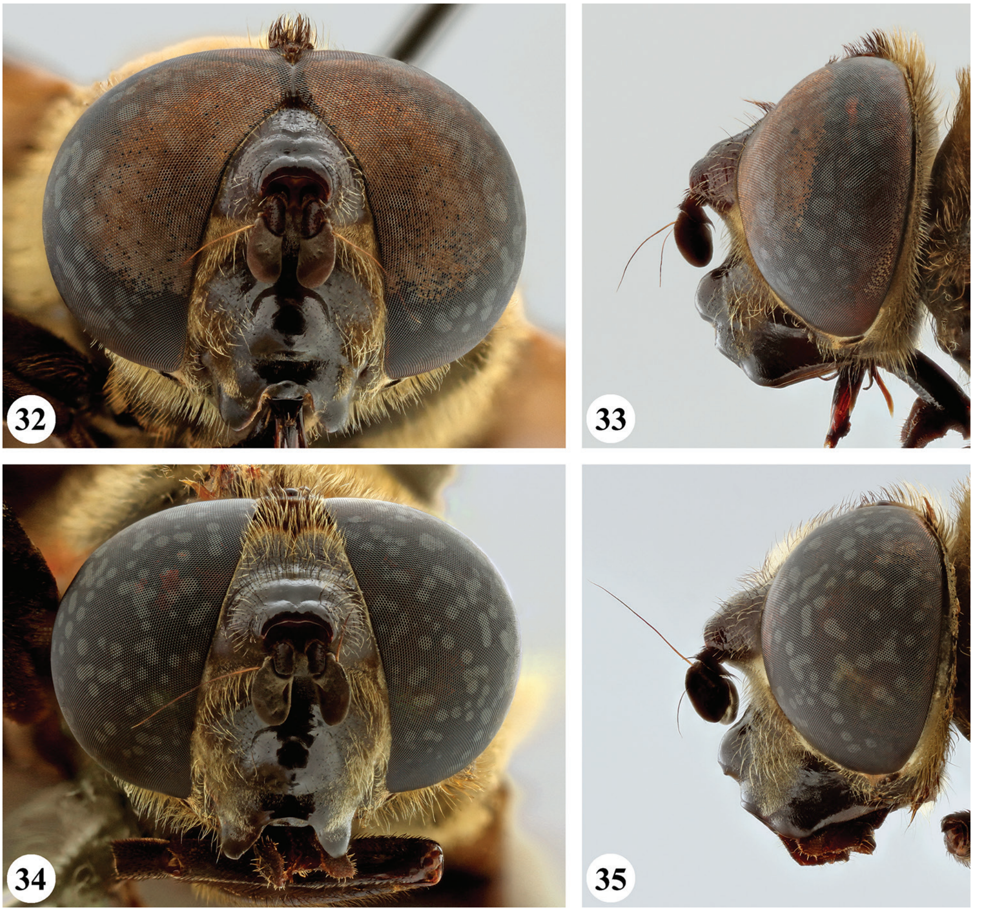
Figures 28–31. Head, frontal and lateral view *S. haemorrhoa* (Gerstaecker) (**28, 29** ♂ **30, 31** ♀).

lection data as for preceding; 24 May 1965 • 1♂; N. Vumba; 7 Apr. 1966; D. Cookson leg.; NMSA • 1♀; Zonwi River bridge; 17 Feb. 1963; A. van Bruggen leg.; NMSA.

Description. Body length: 13.5–18.2 mm. Wing length: 11.0–12.7 mm.

Male (Fig. 2). Head (Figs 16, 17). Eye bare, holoptic; eye contiguity for distance at most 1.5 times length of ocellar triangle, facets slightly enlarged in dorsal half, ca. three times as large in diameter as ventral facets. Frons dark rufous to black-brown; largely subshiny with black pollinosity in dorsal fifth only; dispersed short dark pile, dorsally somewhat longer. Face ground colour rufous (very rarely more black-brown); mainly shining with weak grey pollinosity only below antenna, along eye margin and below lateral facial tubercle; in parts with dispersed short pale pile; facial tubercle strongly pronounced, distinct lateral tubercle present. Gena colour and pollinosity as face; with short to long pale pile. Occiput black-brown, along eye margin more orange, with dispersed pale pile. Antennal segments and arista rufous.

Thorax (Fig. 53). Scutum subshiny black; with very short black pile; postpronotum and notopleuron more orange to rufous and with longer pale or dark pile; trans-



Figures 32–35. Head, frontal and lateral view *S. melanthysana* (Speiser) (**32, 33** ♂ **34, 35** ♀).

verse suture with fascia of black pollinosity. Scutellum clearly marginated, distinctly rounded and at most twice as wide as long; rufous, sometimes darker; with short dark pile, along margins paler pile. Pleura ground colour black to black-brown, along anterior spiracle more orange to rufous, covered with dispersed long dark pile except on meron, dorsomedial anepimeron, ventral part of katepimeron, anterior part of katepisternum and anterior anepisternum.

Legs. Orange to rufous (very rarely more brown), metatarsomeres 3–5 darker; with short pale orange pile, along posterior margin of pro- and mesofemora and ventral margin of metafemur with longer pile, sometimes pile partially dark red. Metaleg (Fig. 81), femur slender, with slight ventral swelling in apical fifth, pile at swelling black and more dense; tibia slightly thickened and curved, pile along ventral margin in apical half to two-thirds longer and more dense.

Wing (Fig. 65). Brownish, except alula and along posterior margin where hyaline; hyaline area not distinctly demarcated. Calypters dull chalk-white to yellow with fringe of silvery white to yellow pile (Figs 66, 67). Cell r_1 closed, petiole usually shorter than height of base of stigma, at most as long as base. Vein R_{4+5} sinuate and short appendiculate, sometimes appendix missing.

Abdomen (Fig. 92). Uniformly subshiny black to black-brown, rarely posteriorly more rufous; with short dark pile except tergum I where silver-grey. Sterna rufous to black-brown; with dispersed long pale pile except for sternum IV and postabdomen where dark. Male genitalia as in Fig. 103.

Female. As male except for the following character states: Eye dichoptic (Figs 18, 19), dorsal facets slightly larger than ventral ones. Frons with rufous to black pollinosity in dorsal part for length equal to ocellar triangle; with short dark pile except dorsal of antennal implant where intermixed with greyish pile. Scutellum usually darker, almost concolourous with medial part of scutum, sometimes more than twice as wide as long.

Distribution. Angola, Benin, Burundi, Cameroon, Central African Republic, Democratic Republic of the Congo, Equatorial Guinea, Gabon, Ghana, Guinea Conakry, Ivory Coast, Kenya, Liberia, Malawi, Mozambique, Nigeria, Republic of the Congo, Rwanda, Sierra Leone, Tanzania, Togo, Uganda, Zimbabwe. Record from Colombia for the type specimen of *nigripennis* is probably an error as the species is not reported from the Neotropical Region (see Comments).

Comments. This species has been described under several names but most of them were synonymized subsequently. No distinct character states could be discerned to confirm the specific status of these taxa, so the different synonymies are confirmed. The description of *S. nigripennis* deviates in some aspects from the morphological character states observed in *S. dibapha*: "face d'un noir brunâtre luisant" [face shiny brownish black]; "Thorax et abdomen… à légers reflets verts" [Thorax and abdomen with light greenish reflections]; "jambes postérieures…. ciliées de noir" [posterior legs… black ciliated]. Other character states correspond with *S. dibapha*. However, the two syntypes of *S. nigripennis* in the NHMUK collection do not correspond with the above mentioned deviations, although one syntype (partially covered in mould) does have a darker facial colour than usually observed and the pilosity of the metatibia is dark reddish (as observed in other specimens). Speiser (1913) also pointed out a slightly different shape of the scutellum in *S. nigripennis*, compared to *S. dibapha*, but this seems to fall within the variability observed in the material examined. In all other aspects they are identical to other material of *S. dibapha* studied, including the type. They are labelled as originating from Colombia, as stated in the original description by Macquart: "De la Colombie". Speiser (1913) already suggested the synonymy, but he did not formally designate it based on the geographical issue. Thompson et al. (1976) in the Neotropical catalogue listed this under the genus *Palpada* Macquart, 1834 as a new combination and indicated Oxford museum as type depository. However, no type specimen could be traced in the OXUM collection (Z. Simmons, pers. comm.). Montoya (2016) did not list *nigripennis* anymore in his catalogue of Syrphidae from Colombia. The Systema Dipterorum website (Evenhuis and Pape 2020) listed it as junior synonym of *S. dibapha*. We consider the type material at NHM as being representative and hence *S. nigripennis* as being synonymous with *S. dibapha*. The type of *S. dibapha* bears a lectotype label by F.C. Thompson, dated 1987, but this lectotype designation does not seem to have been published. Here we thus formally place *nigripennis* Macquart as synonym of *dibapha* Walker.

Speiser (1910) described *gypseisquama* from a number of specimens originating from West (Cameroon and Sierra Leone) and East (Tanzania, Uganda) Africa. Afterwards, Speiser (1911) considered the material from West Africa as a separate variety (*sulfurata*), based on the coloration of the calypters. Of the specimens from West Africa, a number could be traced in the MNB collection (see above type material examined). The material from Uganda (for *gypseisquama*) and part of the material from Barombi, Cameroon and the male specimen from Kondué, Democratic Republic of the Congo (for var. *sulfurata*) could, however, not be traced. The female specimen from Sierra Leone in the MNB collection (apparently received or purchased from Staudinger) could be the type referred to as 'ein angekauftes F aus Sierra Leone' in Speiser (1910). Although the latter is not explicitly mentioned in Speiser (1911) as type of var. *sulfurata*, it is implied under "Alle diese Exemplare haben hell citronengelbe statt weisser Schüppchen, sind aber sonst völlig gleich mit den Ostafrikanern" [All of these specimens have bright lemon yellow instead of white calypters, but are otherwise identical to the East Africans] (in Speiser 1910) and "westafrikanische Form als besondere Varietät mit einem Namen zu belegen" [to assign a name to the West African form as a special variety] (in Speiser 1911).

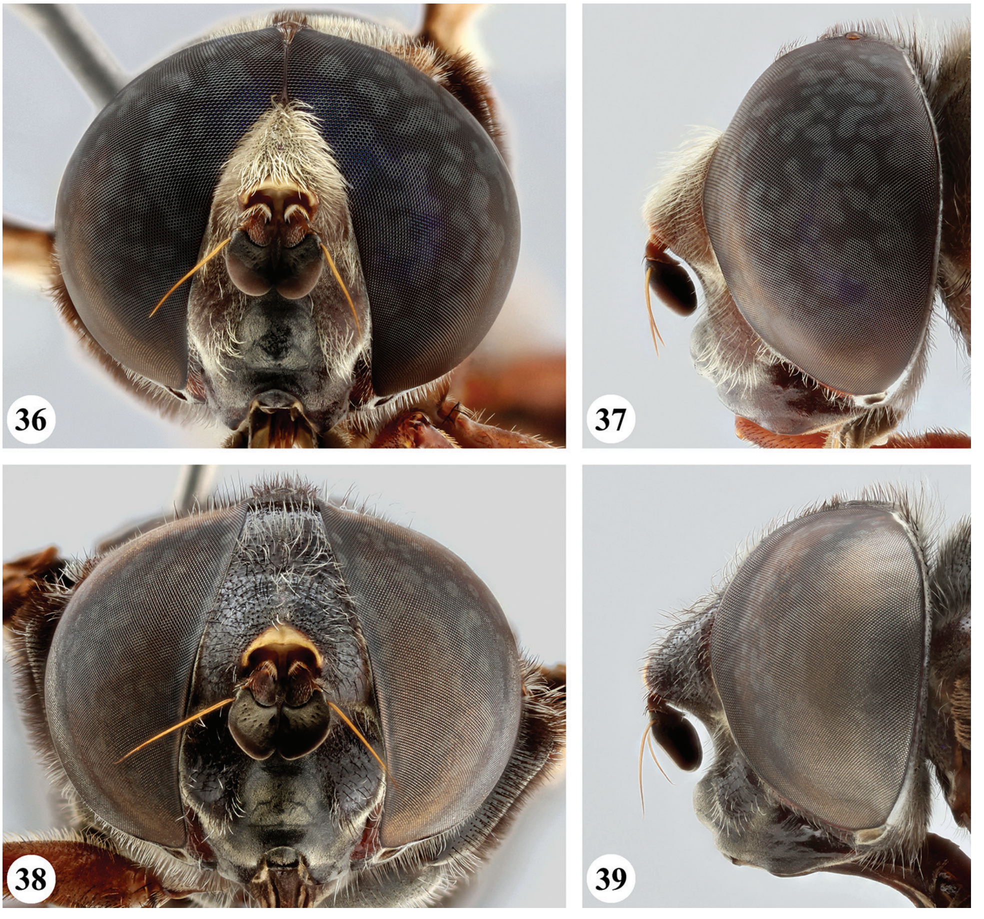
Smith and Vockeroth (1980) listed *sulfurata* as a distinct species but as junior synonym of *dibapha*. As indicated the colour of the lower calypter is variable from yellowish to bright white. Speiser (1911) suggested that there is a geographical separation between *S. gypseisquama sensu stricto* found in eastern Africa, and the variety *sulfurata* found in West and Central Africa. However, we have studied long series throughout the full geographical range and do not confirm this pattern. Both colour forms were found in close by or same locations (Figs 66, 67, material from same locality in the Democratic Republic of the Congo: Dekese, Itunda). DNA barcodes of specimens from West (i.e., Benin, Ghana, Togo), Central (D.R. Congo) and East (Uganda) Africa do not show any separation (Suppl. material 1: Fig. S1). No other correlated characters states could be linked to the color of the lower calypter. Therefore, the character is considered to be variable, not related to geographic distribution and of no taxonomic importance.

Senaspis elliotii **Austen, 1909**

Figs 3, 20–23, 54, 55, 68–71, 82, 93, 104

Senaspis elliotii Austen, 1909: 90.
Eristalis (*Stenaspis*) *ellioti* var. *claricella* Speiser, 1910: 123.

Differential diagnosis. Species differentiated from all other *Senaspis* species by the conspicuous dense white to yellow pile on scutum, contrasting with the black pile on pleura (Fig. 3) (other species with dense pale pilosity on the scutum like *S. melanthysana* and *S. umbrifera*, have the pale pile continued on pleura (Figs 6, 9)). The wing is predominantly dark, except along posterior margin and at the apex where hyaline (Fig. 68).

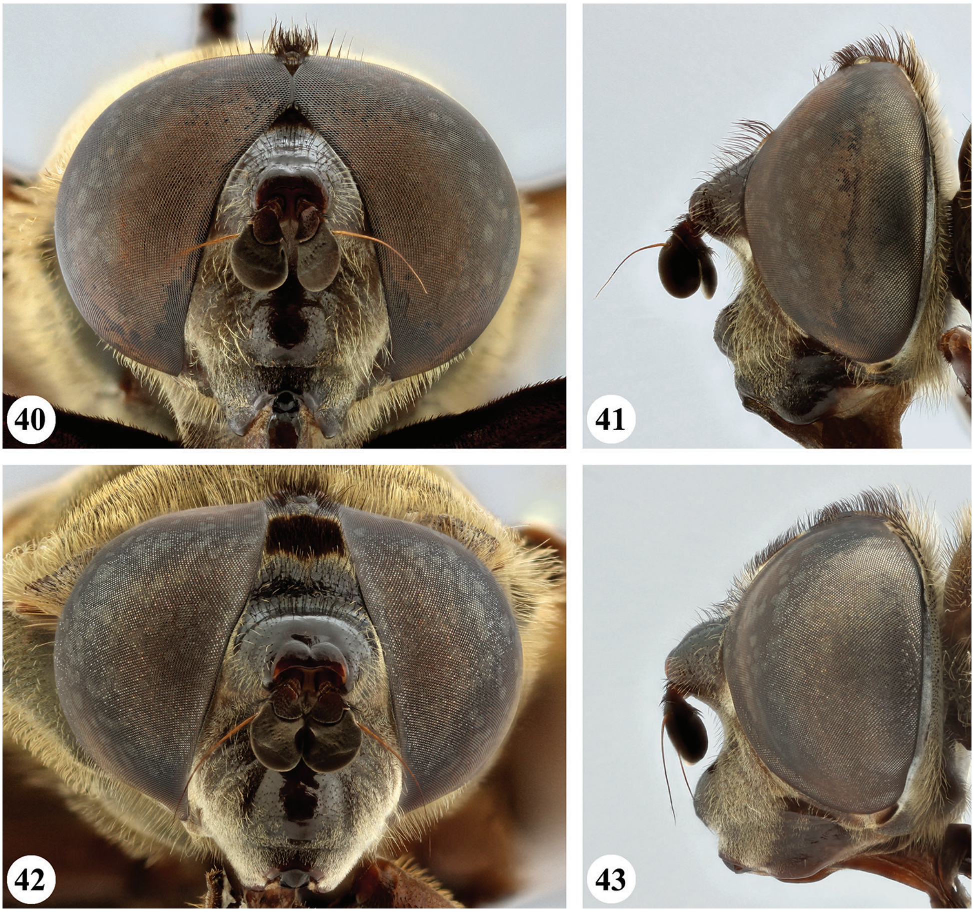


Figures 36–39. Head, frontal and lateral view *S. nigrita* (Bigot) (**36, 37** ♂ **38, 39** ♀).

Examined material. *Senaspis elliotii* Austen: Lectotype (hereby designated), male, "Syn-//type" "Senaspis // Type // elliotti // Austen, ♂" "Ruwenzori, // Scott Elliot.5. // 7–8,000 ft. // 95–41." "LECTOTYPUS" [NHMUK]. Paralectotype, female, "Syn-// type" "Makumbu, // B.E. Africa. // C.S. Betton. // 1900.35 // 6.II–8.III.99." "PARA- // LECTOTYPUS" [NMHUK]. Paralectotype, female, "Syn-//type" "Senaspis // Type // elliotti // Austen, ♀" "Between Salt Lake//& Wawamba Country // Ruwenzori district, // Uganda // 1894. // G.F. Scott Elliot // 95.41" "PARA- // LECTOTYPUS" [NHMUK].

Eristalis (*Stenaspis*) *ellioti* var. *claricella* Speiser: Holotype, male, "Kilimandj. // Sjöstedt" "13 dec." "Obstgarten- // Steppe" "Eristalis (Stenaspis) // ellioti Aust. var. claricella // P. Speiser det. // Typ. der Var." "NHRS-BYWS // 000002772" "Loan // 575/99" [NRMS, examined through images].

Other material. Angola • 1♀; Nova Gaia; 14–21 Dec. 1957; G.H. Heinrich leg.; CNC • 1♀; 30 km N Quiculungo; Sep.–Oct. 1957; CNC. Burundi • 1♂; Bururi; Jun. 1948; F.J. François leg.; KBIN • 1♀; Bururi; May 1960; R.P. Giraudin leg.;



Figures 40–43. Head, frontal and lateral view *S.* nr *umbrifera* (Walker) (**40, 41** ♂ **42, 43** ♀).

MNHN • 1♀; Bututsi, Mugamba; Jul.–Aug. 1948; F.J. François leg.; KBIN • 1♂; Cankuzo, Ruvubu Park; Jun. 2010; F. Ngendakuriyo leg.; OBPE • 1♀; Kibira Tinyabakwe; 4 Nov. 2010; OBPE • 2♂♂; Makamba; 28–29 May 1948; F.J. François leg.; KBIN • 1♂; same collection data as for preceding; 19 May 1949 • 1♀; Mt Bururi; May 1948; F.J. François leg.; KBIN • 1♂; Muhinga, Michinga Hill, Butezana; 11 May 1952; F.J. François leg.; KBIN • 1♂; Mukungu; 26 [?] 2013; L. Ndayikeza leg.; OBPE • 1♀; Murmera-Umushiha; 2011; OBPE • 1♀; Nyakibande, Mumirwa; 27 Jan. 2018; E. Sinzinkayo leg.; OBPE • 1♀; same collection data as for preceding; 24 Apr. 2019. Democratic Republic Of The Congo • 1♀; Bitale, Kalehe, Kivu; 23 May 1950; G. Marlier leg.; KMMA • 1♀; Boswenda; 22 Oct. 1914; J. Bequaert leg.; KMMA • 1♀; Bulira; Nov. 1932; L. Burgeon leg.; CNC • 2♀♀; same collection data as for preceding; KMMA • 1♀; Elisabethville [= Lubumbashi]; 25 Apr. 1927; M. Bequaert leg.; KMMA • 1♂; same collection data as for preceding; [no date]; KBIN • 1♀; same collection data as for preceding; 7 Sep. 1927 • 1♀; same collection data as for preceding;

10 Feb. 1928 • 1♀; same collection data as for preceding; 30 Sep. 1929 • 1♀; same collection data as for preceding; Mar. 1930; L. Courtois leg.; KMMA • 1♀; 16 Sep. 1932; same collection data as for preceding; De Loose leg. • 1♂ 2♀♀; from Beni to Lesse; Jul. 1911; Murtula leg.; KMMA • 1♀; Ibanda, Ruwenzori Mts; 199; Ch. Alluaud leg.; MNHN • 1♀; Kabare, Shabunda; R. Mayné leg.; KMMA • 5♂♂ 5♀♀; Kadjudju, Kivu; May–Jun. 1932; G. Babault leg.; MNHN • 7♂♂ 11♀♀; same collection data as for preceding; Aug. 1932 • 1♂ 1♀; same collection data as for preceding; Sep. 1932 • 1♂; Kalembelembe, Baraka; Jul. 1918; R. Mayné leg.; KMMA • 2♀♀; Kalimabenge River, Uvira; 23 Mar. 1949; G. Marlier leg.; KMMA • 1♀; Kansenia; Nov.–Dec. 1929; R.P. de Montpellier leg.; KMMA • 1♀; Kapanga; Oct. 1932; F.G. Overlaet leg.; KMMA • 1♂; same collection data as for preceding; Nov. 1933 • 1♂; Kitembo; 1927; G. Babault leg.; MNHN • 1♀; Lubudi; 1947; R. Claire leg.; KMMA • 1♀; Lubumbashi; 23 Jul. 1970; A.B. Stam leg.; KMMA • 1♂ 1♀; Lulenga, Kivu; Dec. 1927; Ch. Seydel leg.; KMMA • 1♀; Mulungu; 19–26 Nov. 1932; L. Burgeon leg.; KMMA • 1♀; Rutshuru, Parc National Albert, Kivu; 15–25 Sep. 1933; G.F. de Witte leg.; KMMA • 1♀; Ruwenzori Mt.; 26 Apr. 1914; AMNH • 1♀; Stanleyville [= Kisangani]; Mar. 1915,; KMMA; Lang and Chapin leg.; KMMA • 1♀; Tshamugussa, Parc National Albert; 8–15 Aug. 1934; G.F. de Witte leg.; KBIN • 1♀; Tshaya; 1932; G. Babault leg.; MNHN • 1♂ 1♀; Tshibinda; Kivu; Nov. 1927; Ch. Seydel leg.; KMMA • 2♀♀; same collection data as for preceding; Dec. 1927. Ethiopia • 2♀♀; Maraquo; 3 May 1914; O. Kovacs leg.; NHMUK • 1♀; Mulata Mts, Harar; 22–25 Oct. 1920; AMNH. Kenya • 1♀; Gatamayu; 5 Feb. 1942; V.G.L. van Someren leg.; NHMUK • 1♀; Ilala, 14 mi E Mumias; 18–21 Jun. 1911; S.A. Neave leg.; NHMUK • 2♀♀; Jomboni Hills; May 1947; V.G.L. van Someren leg.; NHMUK • 1♂ 2♀♀; Kaimosi; Apr. 1922; NHMUK • 1♀; Kijabe; Feb. 1932; V.G.L. van Someren leg.; NHMUK • 1♂ 1♀; Mawakota; Apr. 1925; V.G.L. van Someren leg.; NHMUK • 1♀; same collection data as for preceding; Jul. 1929 • 1♂; Mombasa; Jun. 1926; V.G.L. van Someren leg.; NHMUK • 1♂; same collection data as for preceding; Apr. 1928 • 1♀; Nairobi; Aug. 1904; Ch. Alluaud leg.; MNHN • 2♂♂; Nairobi; Apr. 1927; V.G.L. van Someren leg.; NHMUK • 1♀; same collection data as for preceding; Nov. 1928 • 1♀; same collection data as for preceding; [no date]; F.J. Jackson leg. • 1♂; Ngong; 26 Oct. 1919; A. Loveridge leg.; NHMUK • 1♀; Ngong; Apr. 1934; V.G.L. van Someren leg.; NHMUK • 1♀; Ngong; Feb. 1941; V.G.L. van Someren leg.; NHMUK • 1♂ 1♀; Nyeri; Dec. 1948; V.G.L. van Someren leg.; NHMUK • 1♂; Taita Hills; Aug. 1947; V.G.L. van Someren leg.; NHMUK • 1♀; Tumutumu; Jan. 1939; V.G.L. van Someren leg.; NHMUK • 1♂; same collection data as for preceding; Apr. 1939 • 2♂♂; Yala River, S edge Kakumega Forest; 21–28 May 1911; S.A. Neave leg.; NHMUK. Malawi • 1♀; Blantyre; 1914; J.B. Davey leg.; NHMUK • 2♂♂ 1♀; Cholo; R.C. Wood leg.; NHMUK • 1♀; Fort Anderson [= Mlanje]; 24 Jul. 1908; R. Newstead leg.; NHMUK • 1♀; Fort Johnston [= Mangochi]; Jan. 1910; H.N. Tate leg.; NHMUK • 1♂; Limbe; 25 Sep. 1916; R.C. Wood leg.; NHMUK • 1♀; Maiwale; 12 m E. of Fort Johnston [= Mangochi]; 20 Sep. 1926; W.A. Lamborn leg.; OXUM [image examined only] • 1♂; Mlanje; 7 Dec. 1912; S.A. Neave leg.; NHMUK • 1♀; same collection data as for

preceding; 20 Jan. 1913 • 1♀; same collection data as for preceding; 12 Feb. 1913 • 2♀♀; same collection data as for preceding; 7 May 1913 • 1♀; Zomba; H.S. Stannus leg.; CNC • 4♀♀; Zomba; H.S. Stannus leg.; NHMUK . Mozambique • 1♀; Revoué Valley, env. Andrada; Mar. 1905; G. Vasse leg.; MNHN. Rwanda • 1♂; Kibungu; Oct.–Dec. 1937; R. Verhulst leg.; KMMA • 1♀; Kisenyi; 14 Feb. 1952; A.E. Bertrand leg.; KMMA • 1♀; Rubona; 5 Apr. 1963; G. Pierrard leg.; KMMA • 1♂; Shangugu; 23 Oct.–15 Nov. 1948; F.J. François leg.; KBIN. South Africa • 1♂; Entabeni Forest Station, Zoutpansberg; Jan. 1975; B. Stuckenberg leg.; NMSA • 1♀; Schroutzich, Zoutpansberg District; 29 Mar. 1922; J. Gowdey leg.; NMSA. Tanzania • 1♀; Bunduki; 30 Apr.–2 May 1957; P. Basilewsky and N. Leleup leg.; KMMA • 1♀; Kibonoto; 4 May 1906; Sjöstedt leg.; MNHN • 1♀; Kibonoto; 2 May 1906; Sjöstedt leg.; MNB • 2♀♀; Kilema; Mar. 1912; Alluaud and Jeannel leg.; MNHN • 1♀; Tshihinda; 21–27 Aug. 1931; J. Ogilvie leg.; CNC • 1♀; Ukami; MNHN. Uganda • 1♂; SE Ankole; 4–8 Oct. 1911; S.A. Neave leg.; NHMUK • 2♂♂ 2♀♀; W Ankole; 10–14 Oct. 1911; S.A. Neave leg.; NHMUK • 1♂; Buamba Forest, Semliki Valley; 3–7 Nov. 1911; S.A. Neave leg.; NHMUK • 2♀♀; Budongo Forest, nr Lake Albert; Apr. 1972; E.B. Babyetagara leg.; CNC • 2♂♂; Diamond Trail, Ruwenzori; 6 Dec. 2018; K. Jordaens leg.; KMMA • 1♂ 1♀; Entebbe; 7–9 May 1912; C.C. Gowdey leg.; NHMUK • 1♀; Fort Portal; Jan. 1909; Ch. Alluaud leg.; MNHN • 1♀; Ruhiza, Impenetrable Forest, Kigezi; 1–10 Jun. 1972; E.B. Babyetagara leg.; CNC • 1♀; Jinja; Aug. 1928; V.G.L. van Someren leg.; NHMUK • 1♀; same collection data as for preceding; Sep. 1928 • 1♀; Kayonza Forest, Kigezi District; May 1972; H. Falke leg.; CNC • 2♂♂ 4♀♀; same collection data as for preceding; E.B. Bayetagara leg. • 3♂♂ 4♀♀; Lower Ruwenzori Mountains; 14 Apr. 1973; H. Falke leg.; CNC • 1♀; Masinde; Feb. 1912; R. Fyffe leg.; NHMUK • 1♀; Mpanga Forest; 26 Feb. 1912; J. Fraser leg.; NHMUK • 4♂♂ 5♀♀; Mt Elgon; 4–8 Dec. 1972; H. Falke leg.; CNC • 11♂♂ 17♀♀; Mt Kokanjera, SW of Elgon; 7–9 Aug. 1911; S.A. Neave leg.; NHMUK • 1♀; Namwamba Valley; Dec. 1934–Jan. 1935; F.W. Edwards leg.; NHMUK • 2♀♀; Nkokonjera; 23 Dec. 1910; C.C. Gowdey leg.; NHMUK • 1♂; NW shores Vic. Nyanza; 12–15 Sep. 1911; S.A. Neave leg.; NHMUK • 1♀; Nyabushozi, North Ankole; 21 Jan. 1975; P. Mugabi leg.; CNC • 1♀; North Ruwenzori; 1–2 Nov. 1911; S.A. Neave leg.; NHMUK • 2♂♂ 6♀♀; Ruwenzori Foothills; 3–8 Jan. 1972; H. Falke leg.; CNC • 1♂ 3♀♀; Tero Forest, SE Buddu; 26–30 Sep. 1911; S.A. Neave leg.; NHMUK • 1♂ 1♀; Usuka; 7 Dec. 1910; C.C. Gowdey leg.; NHMUK. Zambia • 1♀; Abercorn; 23 Apr. 1951; F.O. Albrecht leg.; NHMUK. Zimbabwe • 1♂; Bomponi, Vumba; 16 May 1965; D. Cookson leg.; NMSA • 1♂; Cross Kopie, Umtali; 13 Feb. 1964; D. Cookson leg.; NMSA • 1♀; Mt Selinda; 8 Feb. 1954; N.J. Myers leg.; NMSA • 1♀; Salisbury [= Harare]; 1 Jan. 1952; J.M. Brown leg.; NMSA • 1♀; Umtali; 21 Jan. 1952; N.J. Myers leg.; NMSA • 1♂; N. Vumba; 6 Nov. 1965; D. Cookson leg.; NMSA.

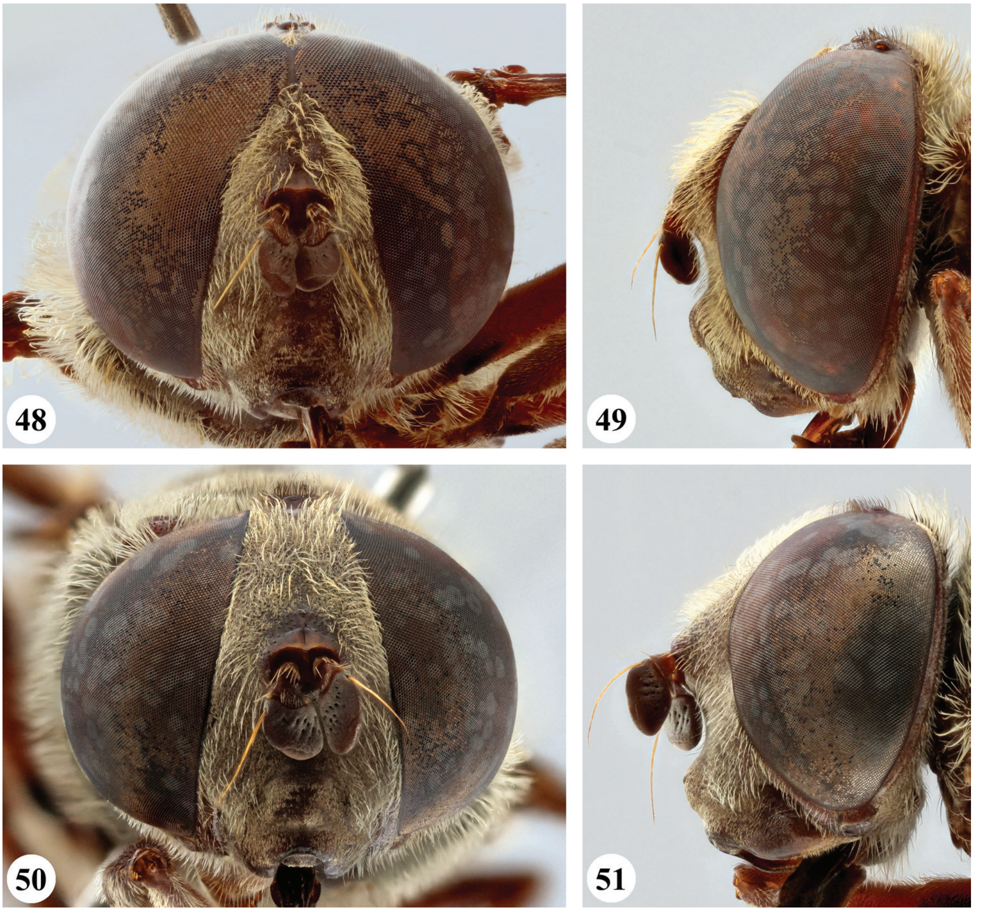
Description. Body length: 11.9–19.0 mm. Wing length: 8.7–13.5 mm.

Male (Fig. 3). Head (Figs 20, 21). Eye bare; narrowly dichoptic, eyes separated for width at most equal to one facet, narrow separation for distance shorter than length of ocellar triangle; facets dorsally slightly larger, at most twice as large in diameter as ventral

Figures 44–47. Head, frontal and lateral view **44, 45** *S. umbrifera* (Walker) (♂ holotype) **46, 47** *S. pennata* (Hervé-Bazin) (♀).

ones. Frons black-brown; largely subshiny with weak greyish pollinosity along dorsal and lateral margins; dispersed short dark pile, dorsally somewhat longer, sometimes pile more pale. Face ground colour black-brown; covered with dense silvery pollinosity except facial tubercle which is bare; in parts with dispersed short pale pile; facial tubercle strongly pronounced. Gena colour and pollinosity as face; with short to long pale pile. Occiput black-brown, covered with dull grey pollinosity; with dispersed pale pile except dorsally where sometimes darker yellow. Antennal segments black-brown to black, arista orange-brown.

Thorax (Figs 54, 55). Scutum and scutellum completely covered by dense pale to orange-yellow pollinosity; furthermore with dense short pile of same colour, pile longer along margins. Scutellum marginated; weakly rounded, 2.5 times wider than long. Pleura ground colour black-brown, covered with dispersed long predominantly dark pile except on meron, dorsomedial anepimeron, ventral part of katepimeron, anterior part of katepisternum and anterior anepisternum.



Figures 48–51. Head, frontal and lateral view *S. xanthorrhoea* (Bezzi) (**48, 49** ♂ **50, 51** ♀).

Legs. Black-brown, sometimes femora more red-brown; with short black pile, along posterior margin of pro- and mesofemora and ventral margin of metafemur with longer pile. Metaleg (Fig. 82), femur thickened, with slight ventral swelling in apical fifth, pile more dense where swollen; tibia thickened and curved, pile along ventral margin in apical half to two-thirds longer and more dense.

Wing (Fig. 68). Brownish throughout, sometimes with purplish shine when viewed from angle; alula hyaline and posterior margin narrowly and apex broadly paler; sometimes slightly paler maculae in centre of wing cells, paler areas not distinctly demarcated and sometimes absent; if present then usually in at least cells cup, dm, r_{4+5}, and r_{2+3} (Figs 69–71) (in type of var. *claricella* wing largely hyaline with slight fumose areas surrounding veins and cross-veins). Calypters dull chalk-white with fringe of silvery white pile; sometimes calypters and fringe more yellow. Cell r_1 open (Fig. 69) or closed, if closed usually not distinctly petiolate (Fig. 70), rarely with very short petiole less than one third of height of stigma (Fig. 71). In type of var.

claricella narrowly open. Vein R_{4+5} sinuate and usually distinctly short appendiculate, rarely without appendix.

Abdomen (Fig. 93). Uniformly subshiny black to black-brown, postabdomen weakly brownish pollinose; with short dark pile except tergum 1 and postabdomen where pale pile. Sterna with long black pile. Male genitalia as in Fig. 104.

Female. As male except for the following character states: Eye dichoptic (Figs 22, 23), facets equal to subequal in size. Frons with brownish pollinose fascia in dorsal part for length equal to ocellar triangle, along dorsal and ventral margin of fascia narrowly greyish pollinose; frons usually with dispersed pale pile throughout, sometimes mixed with darker pile or completely black pile. Wing coloration variable, sometimes more uniformly brownish throughout but with more distinct hyaline maculae in several cells, rarely hyaline margins posteriorly broader. Cell r_1 rarely narrowly open.

Distribution. Angola, Burundi, Democratic Republic of the Congo, Ethiopia, Kenya, Malawi, Mozambique, Rwanda, South Africa, Tanzania, Uganda, Zambia, Zimbabwe.

Comments. The type of the variety *claricella* corresponds with the typical *S. elliotii* in all aspects except for the wing characteristics as described above. The narrowly open cell r_1 was observed in other material. No other specimens with the hyaline maculae were observed in the material examined, although the extension and distinctiveness of hyaline maculae in the wing cells was observed to be variable. We suspect that it concerns a teneral specimen of *S. elliotii*.

Several authors have spelled the name of this species in variant ways, i.e., as *elliottii* (e.g., Smith and Vockeroth 1980), *ellioti* (e.g., Speiser 1910) or *elliotti* (e.g., Curran 1927). In the original description Austen (1909) specifically stated that the species is named after Mr. G.H. Scott Elliot but indicated in the text that the specimens were collected by G.F. Scott Elliot (a Scottish botanist who collected in several African countries). In both cases the name was spelled as Elliot (with single 't') and Austen gave the species name as *elliotii*. This should be considered as the correct original spelling and alternative spellings should be considered as incorrect subsequent spellings according to article 33.4 of the ICZN.

Senaspis flaviceps Macquart, 1850

Figs 4, 24–27, 56, 72, 83, 84, 94, 105

Senaspis flaviceps Macquart, 1850: 438.
Protylocera apophysata Bezzi, 1915: 64. Syn. nov.

Differential diagnosis. A large brown to reddish brown species (Fig. 4) differentiated from all other *Senaspis* species by conspicuous yellow face and frons (Fig. 24) (dark in all other species), and a bare katepimeron (pilose in all other species). The male metafemur bears a prominent basoventral tubercle (Fig. 83) (absent in all other species).

Examined material. *Senaspis flaviceps* Macquart: ***Holotype***, male, "MUSEUM PARIS // MADAGASCAR // GOUDOT 1839" "86 // 39" "Senaspis // flaviceps. ♂.

// Macq. n. g., n. sp." "TYPE" "TYPE // Vockeroth '69" "HOLOTYPE" "MNHN, Paris // ED6772" [MNHN].

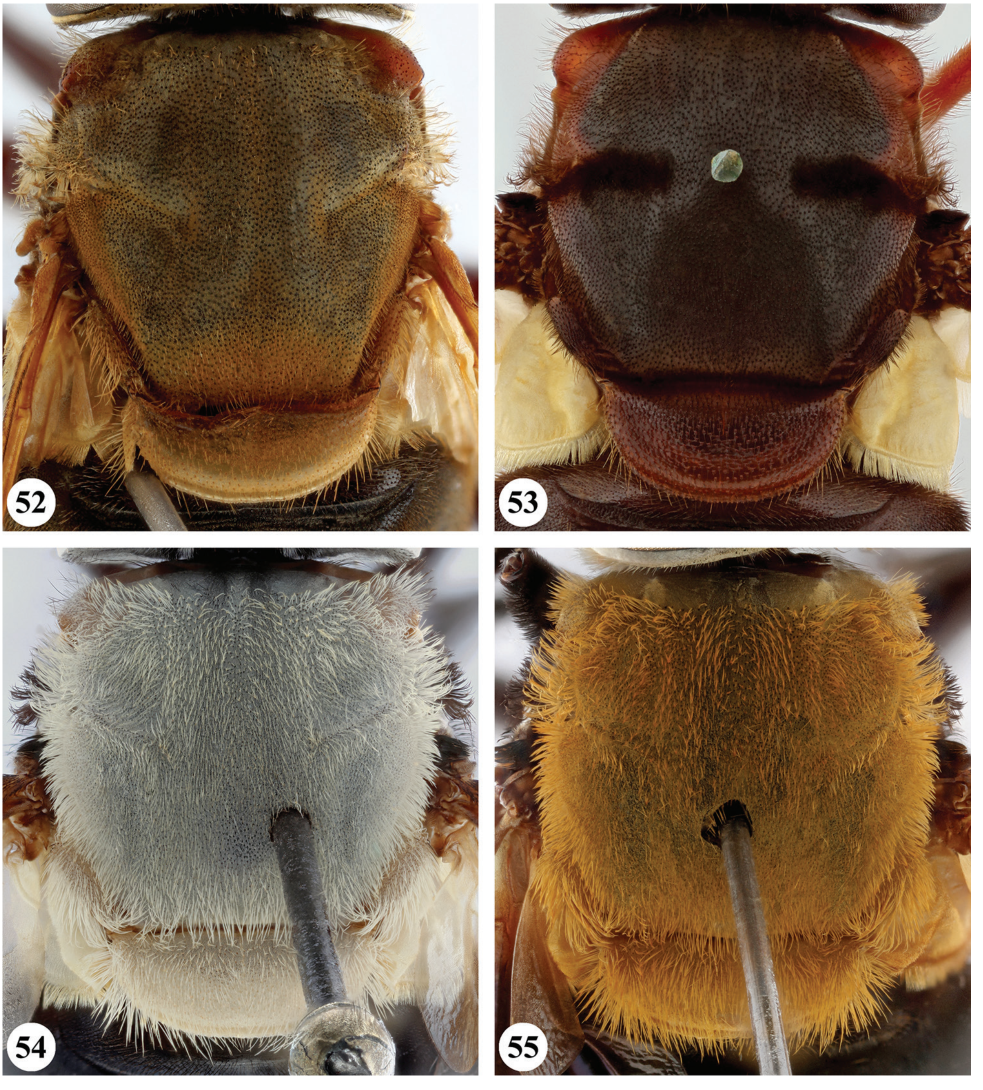
Protylocera apophysata Bezzi: ***Holotype***, male, "Protylocera // Type // apophysata // Bezzi." "Holo- // type" "Betsileo, // Madagascar // Revd. D. Cowan. // 82.30." "Protylocera // apophysata // n. sp." "NHMUK010369877" [NHMUK].

Other material. Madagascar • 1♀; Ahitsitondrona; Dec. 1949; J. Vadon leg.; KMMA • 1♀; Ambatosoratra, Sambava; Nov. 1960 • 2♀♀; Ambodivoangy; Aug. 1961; J. Vadon leg.; KMMA • 1♀; Atsimo, Atsinanana, 50 km S Farafangana; 24 Feb.–3 Mar. 2007; M.E. Irwin and R. Harin'hala leg.; CDFA • 1♀; Fampanambo; Jun. 1960; J. Vadon leg.; KMMA • 1♀; same collection data as for preceding; Jan. 1961 • 1♀; same collection data as for preceding; Mar. 1961 • 2♂♂ 1♀; same collection data as for preceding; 1962 • 1♂ 1♀; Fort Dauphin [= Taolagnara], Mandena; 14–18 Apr. 1968; K.M.G. and P.D. leg.; NHMUK • 1♀; Foulpointe [= Mahavelona]; Jan. 1995; A. Pauly leg.; KMMA • 1♂; same collection data as for preceding; May 1995 • 1♀; same collection data as for preceding; 25 Oct. 1995 • 1♂; Horombe, Vohibasia National Park, Adrefana; Atsimo; 9–15 Feb. 2013; M. Irwin and Rin'ha leg.; CDFA • 1♀; Ivolaina; Feb. 1960; Sigwalt leg.; MNHN • 1♀; same collection data as for preceding; Oct. 1961 • 1♂; Ivondro; Dec. 1938; A. Seyrig leg.; MNHN • 3♂♂; Mananara; Oct. 1963; J. Vadon leg.; KMMA • 1♀; Maroantsetra; J. Vadon leg.; MNHN • 1♀; Miarinarivo; 1919; E. Séguy leg.; MNHN • 1♂; Mus Pragense; CNC • 1♀; Oriental Forest, Moramanga; Jan.–May 1937; C. Lamberton leg.; CNC • 1♂ 1♀; same collection data as for preceding; May–Sep. 1938 • 1♀; Oubanghi-Chari, Fort Sibut; 1968; Breuning leg.; KMMA • 1♀; Ranomafana National Park; 1–10 Dec. 2009; M.E. Irwin and R. Harin'hala leg.; CDFA • 1♀; Ranomafana National Park; 13 Jan. 2014; M. Hauser leg.; CDFA • 1♀; Ranomafana National Park; Rogez leg.; CNC • 2♂♂; Ranomafana National Park; 21 Dec. 2017; Schmid-Egger leg.; CDFA • 1♀; Sorulirano; A. Seyrig leg.; MNHN • 1♂; Tsivory; 1906; Fauchère leg.; MNHN • 1♂ 1♀; no locality; 1937; A. Seyrig leg.; MNHN.

Description. Body length: 17.5–23.8 mm. Wing length: 12.7–17.5 mm.

Male (Fig. 4). Head (Figs 24, 25). Eye bare; holoptic, eye contiguity for distance equal to length of ocellar triangle, facets dorsally only slightly larger, at most twice as large in diameter as ventral facets. Frons yellow; weakly subshiny, largely with yellow pollinosity; dispersed yellow pile, dorsally somewhat longer. Face yellow; subshiny with yellow pollinosity, ventral part mainly yellow-orange subshiny; in parts with dispersed long pale pile; facial tubercle moderately pronounced. Gena colour and pollinosity as ventral lateral margins of face; with short to long pale pile. Occiput orange-brown, covered with orange-brown pollinosity; with dispersed pale pile except dorsally where sometimes more rufous. Antennal segments yellow; arista yellow at base, brown apically.

Thorax (Fig. 56). Scutum subshiny black-brown, postpronotum and lateral margin broadly rufous, narrowly along transverse suture and anterior of scutellum also rufous; with weak grey pollinosity and short rufous pile. Scutellum near to three times as wide as long, apical margin straight, not rounded; rufous; with short rufous pile. Pleura ground colour black-brown, with grey pollinosity, covered with dispersed long dark (more rufous at dorsal margin of posterior anepisternum and anterior anepimeron) pile

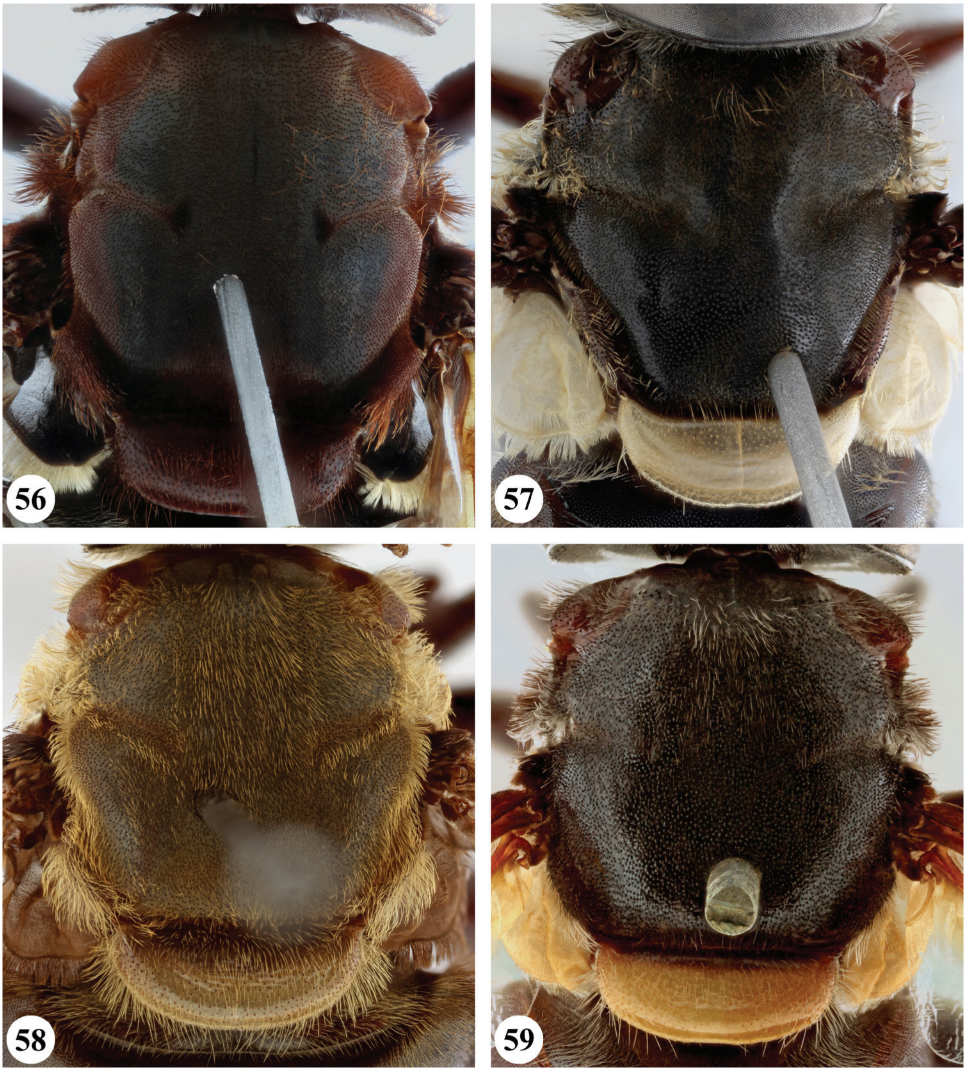


Figures 52–55. *Senaspis* species, thorax, dorsal view **52** *S. dentipes* (Macquart) (♂) **53** *S. dibapha* (Walker) (♂) **54, 55** *S. elliotii* Austen (♂).

except katepimeron, meron, dorsomedial and posterior anepimeron, anterior part of katepisternum and anterior anepisternum.

Legs. Brown to black-brown, femora partly more reddish brown ventrally; with short black pile, along posterior margin of pro- and mesofemora with longer pile. Metaleg (Fig. 83), femur distinctly thickened, with one distinct ventral tubercle in basal fourth to fifth, tubercle with distinct short dark pile; tibia thickened, distinctly bent at base, and only slightly curved, no longer pile along ventral margin.

Wing (Fig. 72). Yellowish brown tinge especially in anterior half, in parts more black-brown; towards posterior margin and apex more hyaline. Calypters black with



Figures 56–59. *Senaspis* species, thorax, dorsal view **56** *S. flaviceps* Macquart (♂) **57** *S. haemorrhoa* (Gerstaecker) (♂) **58** *S. melanthysana* (Speiser) (♂) **59** *S. nigrita* (Bigot) (♂).

fringe of silvery white pile. Cell r_1 closed, petiole at least as long as height of base of stigma. Vein R_{4+5} sinuate but not appendiculate.

Abdomen (Fig. 94). Uniformly subshiny brown to reddish brown, terga IV and V and postabdomen often more rufous; with short dark pile, except tergum I where grey, and postabdomen where more rufous. Sterna dark; with long pale pile. Male genitalia as in Fig. 105.

Female. As male except for the following character states: Eye dichoptic (Figs 26, 27), facets of equal size. Thorax pilosity darker medially. Metafemur (Fig. 84) more slender, without ventral tubercle. Abdominal sterna IV–V with shorter dark pile.

Distribution. Species described from Madagascar. Keiser (1971) also reported the species from the Comoros (Grande Comore).

Comments. The type material of *S. flaviceps* and *S. apophysata* was compared and considered to be conspecific. *Senaspis apophysata* is thus considered as a junior synonym of *S. flaviceps*. This synonymy was already suggested (Ssymank et al. in press, F.C. Thompson pers. comm.) but not formally published. The original description of *S. flaviceps* mentions the type locality as "De l'Afrique. Cap?" but the type specimen bears a label indicating "Madagascar" // "Goudot 1839". All studied material originates from Madagascar and no specimens collected on the African mainland were found. We, therefore, consider the current distribution of this species to be limited to Madagascar (and possibly Comoros; see Keiser 1971). *Senaspis flaviceps* differs from all other species within the genus in some aspects, such as the bare katepimeron (pilose in the rest, albeit weakly so), the presence of a basal tubercle in the male metafemur (absent in all others), the relatively longer petiole (at least as long as height of base of stigma, shorter in all others), and the larger body size (larger than 17 mm and up to 23 mm).

Senaspis haemorrhoa (Gerstaecker, 1871)

Figs 5, 28–31, 57, 73, 85, 95, 106

Plagiocera haemorrhoa Gerstaecker, 1871: 363.
Dolichomerus griseifacies Bezzi, 1908: 381. Syn. nov.

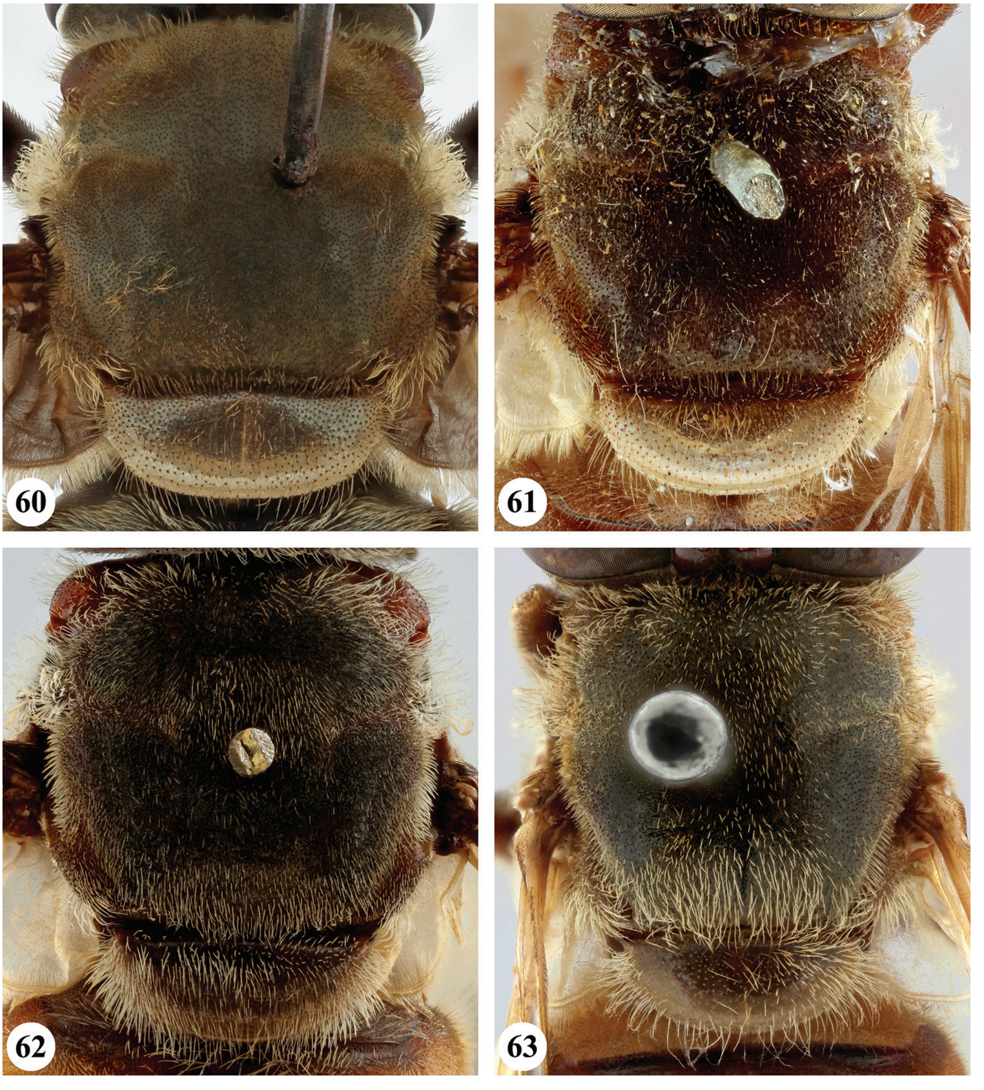
Differential diagnosis. A species with a distinct medial dark brown macula on the wing (Fig. 73). It can be differentiated from other *Senaspis* species with a distinct wing macula by the coloration of the abdomen: largely brown with the posterior terga conspicuously orange to orange-red and with red pile (Fig. 95) (without red pile in *S. dentipes* (Fig. 91); red coloration and pile more extensive in *S. xanthorrhoea* (Fig. 100)).

Type. *Plagiocera haemorrhoa* Gerstaecker: Syntypes, male, female [number unknown], TANZANIA, Wanga [not examined, institutional depository unknown].

Examined material. *Dolichomerus griseifacies* Bezzi: ***Lectotype*** (hereby designated), male, "Senaspis // haemorrhoa / det. C. Kassebeer 1996" "Dolichomerus // griseifacies // ♂ n.sp." "Cf. Ann. Soc. Ent. Belg // Vol. 52 (1908) p. 381" "Ex-typis" "M. Bezzi det., 1908 : // Dolichomerus // griseifascies Bezzi" "Moliro // Mars–Mai 95 //J. Duvivier" "♂" "LECTOTYPUS" [KBIN]. Paralectotype, male, "Cf. Ann. Soc. Ent. Belg // Vol. 52 (1908) p. 381" "Ex-typis" "M. Bezzi det., 1908: // Dolichomerus // griseifascies Bezzi" "Moliro // Mars–Mai 95 //J. Duvivier" "♂" "PARA- // LECTOTYPUS" [KBIN]. Paralectotype, male, "Cf. Ann. Soc. Ent. Belg // Vol. 52 (1908) p. 381" "Ex-typis" "M. Bezzi det., 1908: // Dolichomerus // griseifascies Bezzi" "Moliro // Mars–Mai 95 //J. Duvivier" "♂" "PARA- // LECTOTYPUS" [KBIN].

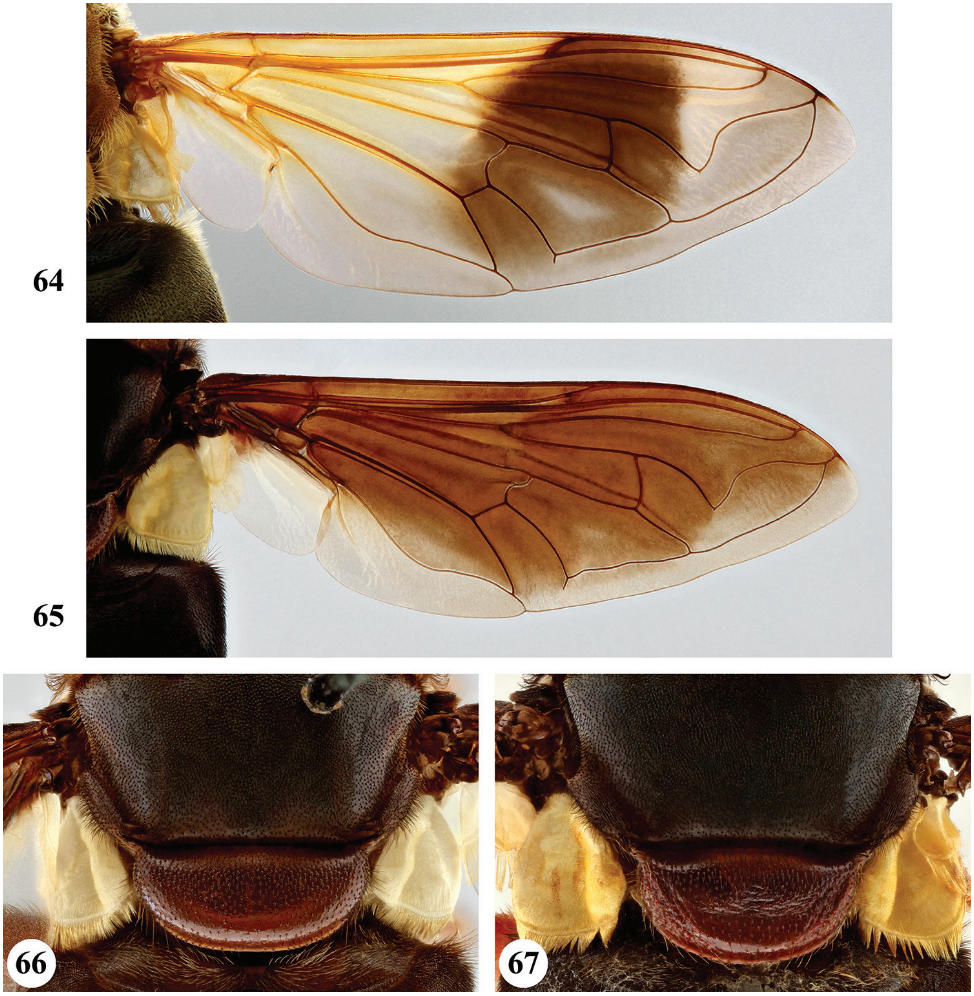
Other material. Angola • 2♂♂; 12 mi SW Luimbale; 20–21 Mar. 1972; NHMUK • 2♀♀; Luanda; Jun. 1957–Jul. 1958; G. Heinrich leg.; CNC • 1♀; Roçada; 30 Feb. 1972; NHMUK. Benin • 1♀; Cotonou; 3 Jun. 1914; W.A. Lamborn leg.; NHMUK

• 7♂♂; Porto Novo; 7 Mar. 2018; K. Jordaens leg.; KMMA • 1♂ 1♀; Sémé; Nov. 2019; G. Goergen leg.; IITA. Botswana • 1♂; 20 km W Chonzi; 28 Aug. 1983; C. Stockmann leg.; NMSA • 1♀; Molepolole District; 3 Mar. 1963; T. Oatley leg.; NMSA • 1♀; Serowe; 14 Apr. 1983; P. Forchhammer leg.; NMSA. Burundi • 2♂♂; Bubanza, Gihanga Hill, Ruzizi; 23 Nov. 1951; F.J. François leg.; KBIN • 1♂; Bujumbura; 26 Feb. 1979; J. Decelle leg.; KMMA • 1♂ 1♀; Bujumbura; 21 Feb. 2017; G. Goergen leg.; IITA • 2♀♀; Kanyinya; Dec. 1947–Jan. 948; Dames de Marie leg.; KMMA • 1♂; Kitega; 3 Dec. 1950; F.J. François leg.; KBIN • 1♂; same collection data as for preceding; 1 May 1952 • 4♂♂ 3♀♀; same collection data as for preceding; 19 May 1955 • 1♀; same collection data as for preceding; 12 Jun. 1957 • 1♀; 11 Dec. 1962; M. Fontaine leg.; KMMA • 1♂; Murehe; 19 [?] 2013; S. Girukwishaka leg.; OBPE • 1♂; Rusizi N P; 26 [?] 2013; S. Girukwishaka leg.; OBPE • 1♀; Musuma, Bututsi; 29 Nov. 1950; F.J. François leg.; KBIN • 1♂ 9♀♀; Nyakibande, Mumirwa; 24 Apr. 2019; E. Sinzinkayo leg.; OBPE • 4♂♂ 9♀♀; same collection data as for preceding; 14 Jul. 2019 • 1♀; Nyambuye; Mumirwa; 18 Mar. 2019; E. Sinzinkayo leg.; OBPE • 1♂ 18; same collection data as for preceding; May 2019 • 6♀♀; same collection data as for preceding; 18 Sep. 2019 • 1♀; Rumonge; 20 Apr. 1948; • 1♀; same collection data as for preceding; 19–20 Jun. 1948 • 1♂; same collection data as for preceding; Jul. 1948 • 1♀; same collection data as for preceding; May 1949 • 1♀; 19 Feb. 1950; all F.J. François leg.; KBIN • 5♂♂ 20♀♀; Rwegura, Kibira NP; 31 May 2018; E. Sinzinkayo leg.; OBPE • 1♀; Rusinga NP, secteur Delta; 18 May 2018; E. Sinzinkayo leg.; OBPE • 2♂♂ 10♀♀; same collection data as for preceding; 19 May 2018 • 1♂; same collection data as for preceding; 20 May 2018 • 1♂ 4♀♀; same collection data as for preceding; 24 May 2018 • 1♀; Usumbura; Sep. 1961; G. Pierrard leg.; KMMA. Comoros • 1♂ 1♀; Le Galawa, Grande Comore; 22 Apr.–5 May 1991; K.M. Guichard leg.; NHMUK • 1♀; M'Vouni, Grande Comore; 23 Apr.–3 May 1991; K.M. Guichard leg.; NHMUK • 1♂ 1♀; Moroni, Grande Comore; Malet leg.; MNHN • 1♀; Grande Comore; 1899; MNHN. Democratic Republic Of The Congo • 3♀♀; Albertville [= Kalemie]; 14 Aug. 1953; J. Verbeke leg.; KBIN • 1♀; same collection data as for preceding; 17 Aug. 1953 • 1♀; same collection data as for preceding; 24 Aug. 1953 • 1♀; same collection data as for preceding; Jul. 1955; H.E. Bomans leg.; KBIN • 1♂; same collection data as for preceding; Dec. 1918; R. Mayné leg.; KMMA • 1♂; same collection data as for preceding; 1–20 Jan. 1919 • 1♂; same collection data as for preceding; 7 Feb. 1933; L. Burgeon leg.; KMMA • 1♀; Bendera; Oct. 1958; N. Leleup leg.; KMMA • 1♀; Baudouinville [= Kirungu]; May 1953; H. Bomans leg.; KMMA • 1♂; Bukama; 18 Apr. 1911; Bequaert leg.; KMMA • 1♂; same collection data as for preceding; 4 Jun. 1911 • 1♀; 3 Aug. 1923; Ch. Seydel leg.; KMMA • 1♀; Buta; 1949; R.F. Hutsebaut leg.; KMMA • 3♂♂; Chamunyonge; Lake Edward; 26 Sep. 1953; F.J. François leg.; KBIN • 2♂♂ 4♀♀; Costermansville [= Bukavu]; 1948; P.H. Vercammen leg.; KMMA • 1♂; Costermansville [= Bukavu]; 13 May 1949; H. Bomans leg.; KMMA • 1♀; Elisabethville [= Lubumbashi]; May 1964; E. Coussement leg.; KBIN • 2♂♂; Elisabethville [= Lubumbashi]; M. Bequaert leg.; KBIN • 1♂; Elisabethville [= Lubumbashi]; Nov. 1919; KMMA • 6♂♂; Elisabethville [= Lubumbashi]; 19 Sep. 1919; J. Ghesquière leg.;



Figures 60–63. *Senaspis* species, thorax, dorsal view **60** *S.* nr *umbrifera* (Walker) (♂) **61** *S. umbrifera* (Walker) (♂ holotype) **62** *S. xanthorrhoea* (Bezzi) (♂) **63** *S. pennata* (Hervé-Bazin) (♀).

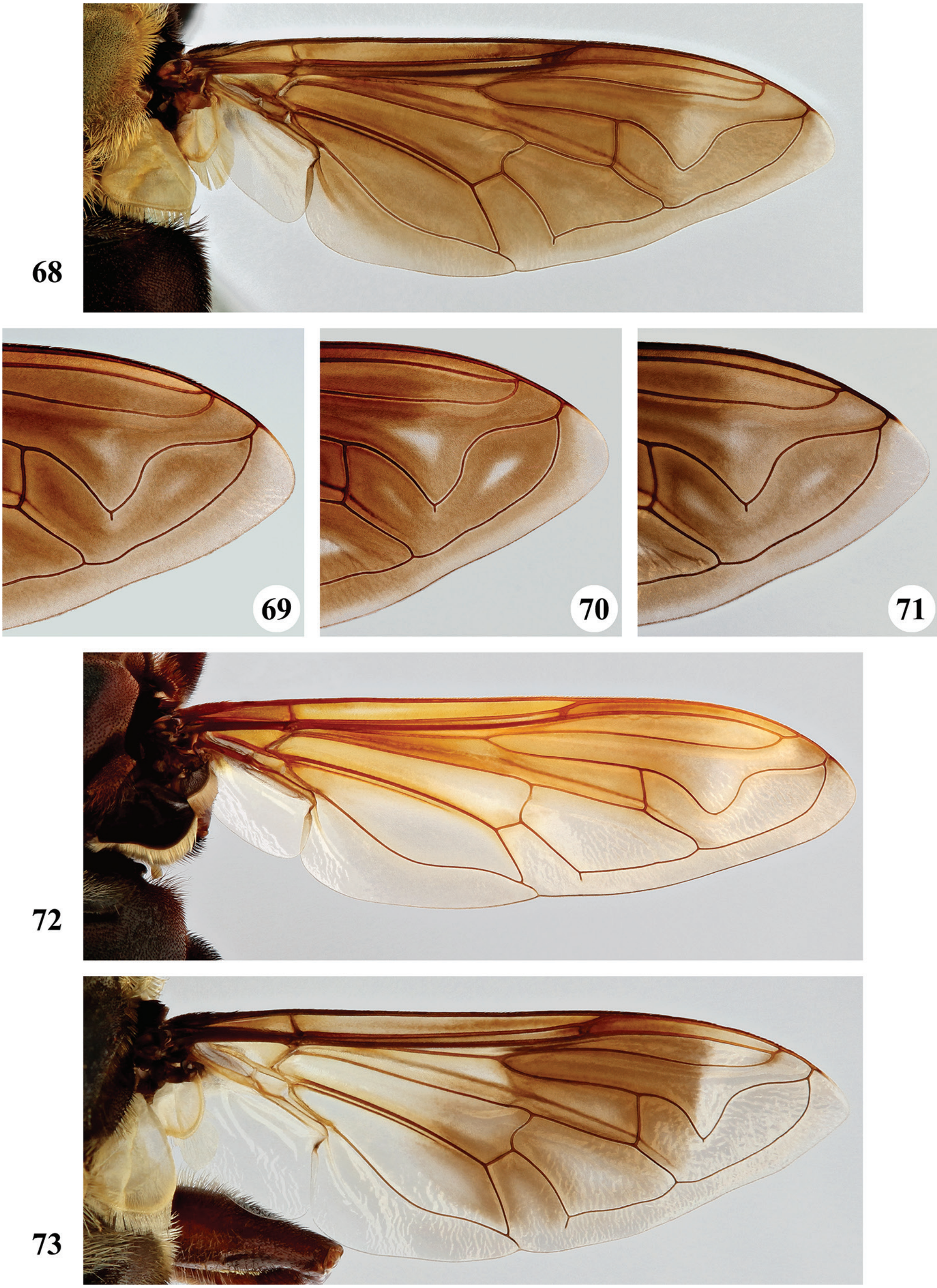
KMMA • 1♀; Elisabethville [= Lubumbashi]; 6 May 1920; M. Bequaert leg.; KMMA • 1♀; same collection data as for preceding; 3 Jun. 1920 • 2♂♂; same collection data as for preceding; 1 Jan. 1921 • 1♀; same collection data as for preceding; 5 Jan. 1921 • 1♂; same collection data as for preceding; 7 Jan. 1921 • 1♀; same collection data as for preceding; 16 Jan. 1921 • 1♂; same collection data as for preceding; 14 Feb. 1921 • 1♂; same collection data as for preceding; 1 Jul. 1923 • 1♂; same collection data as for preceding; 2 May 1923 • 1♀; same collection data as for preceding; Nov. 1929 • 1♀; same collection data as for preceding; Dec. 1939 • 1♀; same collection data as for pre-



Figures 64–67. *Senaspis* species, right wing **64** *S. dentipes* (Macquart) (♂) **65** *S. dibapha* (Walker) (♂) **66, 67** *S. dibapha* (Walker) close-up calypters.

ceding; Dec. 1928; Ch. Seydel leg. • 1♀; 1928–1929; same collection data as for preceding; P. Quarré leg. • 1♂; Elisabethville/Lubumbashi; 5 Jan. 1920; M. Bequaert leg.; NHMUK • 1♂; same collection data as for preceding; 23 Dec. 1920 • 1♀; same collection data as for preceding; 5 Jan. 1921 • 1♀; Goma; 1 May 1953; KBIN • 1♂; Goma; 18 Nov. 1952; J. Verbeke leg.; KBIN • 1♀; same collection data as for preceding; 10–15 May 1953 • 1♀; Ibembo; Uelé; Oct. 1949; R.F. Hutsebaut; KMMA • 1♀; same collection data as for preceding; 20 May 1950 • 1♀; same collection data as for preceding; Apr. 1952 • 1♀; same collection data as for preceding; 1953 • 1♀; Jadotville [= Likasi]; 18 Aug. 1965; E. Coussement leg.; KBIN • 1♀; Jampwe; 1912; Van den Heuvel leg.; KMMA • 1♀; Kabinda, Lomami; KBIN • 1♀; Mt Kabobo, Hte Kiymbi; Sep. 1958; N. Leleup leg.; KMMA • 1♀; Kakanda, Mutaka; 1955; R.P. Th de Caters leg.; KMMA • 1♀; Kamaniola; 1 Feb. 1927; J. Bequaert leg.; KMMA • 1♂; Kambove, Katanga; 11 Jun. 1907; S.A. Neave leg.; NHMUK • 1♀; Kasongo; Sep. 1959; P.L.G. Benoit leg.; KMMA • 4♀♀; Pons leg.; KMMA • 1♀; Kiambi; 27 Apr. 1931; G.F. de Witte leg.; KMMA • 1♂; Kigoma; Jul. 1918; R. Mayné leg.; KMMA • 1♀; same collection data as for preceding; Sep. 1918 • 1♂; Kindu; 15 Nov. 1911; Rodhain leg.; KMMA • 1♀; Kindu (300 km from) Russo; KMMA • 1♂; Kivu; Rodhain leg.; KMMA • 2♂♂ 1♀; Kolwezi; Lualaba; 1–6 Nov. 1952; L. Gilbert leg.; KMMA • 1♀; same collection data as for preceding; 13 Nov. 1952 • 1♀; same collection data as for preceding; 1 Feb. 1953 • 1♀; same collection data as for preceding; 5 Feb. 1953 • 1♀; Kongolo; 6 Feb. 1974; R. Baker leg.; NHMUK • 1♀; Kulu-Mwanza; Katanga; May 1927; A. Bayet leg.; KMMA • 1♀; Kunda; 23 Nov. 1910; Bequaert leg.; KMMA • 1♂; Lubongola; 1939; Hautmann leg.; KMMA • 1♀; same collection data as for preceding; May 1939 • 1♂; Lubumbashi; 5 Jan. 1921; M. Bequaert leg.; KMMA • 1♀; Lubumbashi; 2 Jan. 1968; A.B. Stam leg.; KMMA • 1♂; Lubutu; 22 Jan. 1915; J. Bequaert leg.; KMMA • 1♀; Luluabourg [= Kananga], Kabure; 1937; Soeurs du Carmel leg.; KMMA • 1♀; Luputa, Lomami; Sep. 1934; Bouvier leg.; KMMA • 1♀; same collection data as for preceding; Nov. 1934 • 1♀; same collection data as for preceding; 1935 • 1♀; Lusinga, P.N. Upemba; 10 Apr. 1947; G.F. de Witte leg.; KBIN • 1♀; same collection data as for preceding; 24 Apr. 1947; KMMA • 1♀; same collection data as for preceding; 26 Apr. 1947 • 1♂; Luvungi, North Kivu; 12 Dec. 1932; L. Burgeon leg.; KMMA • 4♂♂; Malondo, Katanga; Ch. Seydel leg.; KMMA • 1♂; Matale; Jul. 1939; Hautmann leg.; KMMA • 1♀; Moba, Tanganyika; Jun. 1931; G.F. de Witte leg.; KMMA • 1♀; Moba, Tanganyika; Jun. 1953; H. Bomans leg.; KMMA • 2♀♀; same collection data as for preceding; Aug.–Oct. 1953 • 2♀♀; Mpala, Tanganyika; H. Bomans leg.; KMMA • 1♀; Nyangwe; 15 Nov. 1910; Bequaert leg.; KMMA • 1♂ 1♀; Nyangwe; Apr.–May 1918; R. Mayné leg.; KMMA • 1♀; Nyonga, Katanga; 18 May 1925; G.F. de Witte leg.; KMMA • 1♀; Paulis; 29 Oct. 1959; M. Fontaine leg.; KMMA • 1♂ 1♀; Stanleyville [= Kisangani]; Apr. 1915; Lang and Chapin leg.; CNC • 1♀; same collection data as for preceding; Feb. 1915; KMMA • 17♂♂ 28♀♀; same collection data as for preceding; Mar. 1915 • 2♀♀; same collection data as for preceding; 1 Apr. 1915 • 1♂ 1♀; same collection data as for preceding; 2 Apr. 1915 • 1♀; same collection data as for preceding; 4 Apr. 1915 • 1♀; same collection data as for preceding; 5 Apr. 1915 • 2♂♂ 1♀; same collection data as for preceding; 6 Apr. 1915 • 2♂♂ 8♀♀; same collection data as for preceding; 7 Apr. 1915 • 4♀♀; same collection data as for preceding; 14 Apr. 1915 • 1♀; same collection data as for preceding; Apr. 1915 • 2♂♂ 3♀♀; same collection data as for preceding; 7 Jul. 1915 • 1♀; same collection data as for preceding; 1915; J. Bequaert leg.; KMMA • 1♀; same collection data as for preceding; 5 May 1926; H. Schouteden leg. • 1♀; same collection data as for preceding; 13 Aug. 1928; A. Collart leg. • 1♀; same collection data as for preceding; 6 Sep. 1928 • 1♂; same collection data as for preceding; 1929; J. Muller leg.; KBIN • 1♀; same collection data as for preceding; 28 Apr. 1932; J. Vrydagh leg.; KMMA • 1♀; Uvira; Jul. 1927; Ch. Seydel leg.; KMMA • 1♀; Uvira; Aug. 1949; G. Marlier leg.; KMMA • 1♀; Vieux-Kasongo; Dec. 1910; Pons leg.; KMMA. Ethiopia • 1♂; Abijata Shala National Park, Oromia; 1–10

Oct. 2012; A. Pauly leg.; KMMA • 1♂ 1♀; Senkele National Park, Oromia; 17 Oct. 2012; A. Pauly leg.; KMMA. Guinea Bissau • 2♀♀; Bolama; Jun.–Dec. 1899; L. Fea leg.; MCSNG. Kenya • 2♀♀; Bungoma, Western Province; 29 Oct. 1968; J. Field leg.; CDFA • 1♀; Funzi Island; 9 Jul. 2012; ICIPE • 1♂; Gede National Park, Malindi; 1 May 1973; H. Falke leg.; CNC • 1♀; Kibwezi; 6 Jan. 1926; W. Feather leg.; NHMUK • 7♀♀; same collection data as for preceding; 24 Dec. 1927 • 4♀♀; same collection data as for preceding; 24 Jan. 1928 • 1♀; same collection data as for preceding; 9 Feb. 1928 • 1♀; Kisumu; Nov. 1932; V.G.L. van Someren leg.; NHMUK • 2♀♀; Lake Mpeketoni near Kipini; 4–5 Mar. 1912; S.A. Neave leg.; NHMUK • 1♀; Loyia Turkana; 20 Aug. 1954; NHMUK • 1♀; Magadi; Jul. 1941; V.G.L. van Someren leg.; NHMUK • 1♀; Mombasa; Jul. 1904; Ch. Alluaud leg.; MNHN • 1♀; Nairobi; 14 Dec. 1951; L.C. Edwards leg.; NHMUK • 1♀; Nanyuki; Jul. 2010; M. Roberts leg.; ICIPE • 1♂; New Runda; 22 Apr. 2012; F. Haas leg.; ICIPE • 2♀♀; Rabai; May 1928; V.G.L. van Someren leg.; NHMUK • 2♂♂; same collection data as for preceding; Jul. 1928 • 1♂; Tsavo East; 6 Jan. 1989; A.u.G. Rautenstrauch leg.; CDFA • 1♀; Uchweni Forest; 1–3 Mar. 1912; S.A. Neave leg.; NHMUK • 1♂ 2♀♀; Ziwani; Aug. 1947; V. G.L. van Someren leg.; NHMUK. Malawi • 1♀; 30 km NW of Dedza; 15 Mar. 1987; J. and A. Londt leg.; NMSA • 3♀♀; Kasungu; 9 Dec. 1980; B. Stuckenberg and J. Londt leg.; NMSA • 1♂; Livingstonia; 3 May 1939; R.C. Wood leg.; NHMUK • 1♀; Mulanje Mountain Forest Reserve; 12–15 Nov. 2016; K. Jordaens leg.; KMMA • 1♂; Ruo; 4 Feb. 1916; R.C. Wood leg.; NHMUK • 1♂ 1♀; Viphya Mountains, Chikangawa; 5–8 Dec. 1980; B. Stuckenberg and J. Londt leg.; NMSA. Mozambique • 1♀; Chiramba, Zambeze; 1929; P. Lesne leg.; MNHN • 1♀; Lourenço Marques [= Maputo]; 1909; J. de O.S. de Azevedo leg.; NHMUK • 2♂♂ 2♀♀; Lourenço Marques [= Maputo]; Sep.–Dec. 1913; H.A. Junod leg.; NHMUK • 1♂; same collection data as for preceding; Jan.–Mar. 1914 • 1♀; Luabo, Lower Zambesi River; Jun.–Jul. 1957; CNC • 1♀; same collection data as for preceding; Aug. 1957 • 2♀♀; Luabo; U. Stuckenberg leg.; NMSA • 2♂♂; Manga, Beira Region; 27 Jul. 1929; P. Lesne leg.; MNHN • 1♂; Revoué Valley, Andrada envir.; Apr.–May 1905; G. Vasse leg.; MNHN • 1♀; Rikatla; H.A. Junod; NMSA • 1♀; Siluwe Hills, W. of Beira; 3 Jun. 1964; D. Cookson leg.; NMSA • 1♀; Tumbine Mountains, Milange District; Apr. 1958; B. and P. Stuckenberg leg.; NMSA. Namibia • 3♀♀; Kombat; 1–6 Apr. 1972; NHMUK • 1♀; between Omaruru and Wilhelmstad; 3 Apr. 1998; F.W. and S.K. Gess leg.; AMGS • 1♀; WNW of Omatjete; 15 Mar. 2004; F.W. and S.K. Gess leg.; AMGS • 1♂; Oranjemund, 28 km from checkpoint on road to Sendelingsdrift; 25 Sep. 1997; F.W. and S.K. Gess leg.; AMGS • 1♀; Rietfontein, 23 mi W SW Grootfontein; 3 Apr. 1972; NHMUK • 1♀; 24 km SE Stampriet, Gross Nabas; 30 Mar. 2000; F.W. and S.K. Gess leg.; AMGS • 1♀; 71 km East Stampriet; 23 Mar. 2000; F.W. and S.K. Gess leg.; AMGS • 1♂; 71 km West Witvlei; 17 Mar. 1984; J. Londt and B. Stuckenberg leg.; NMSA. Nigeria • 1♀; 23 km W Lagos; 11 May 1975; J. Riley leg.; NHMUK. Republic Of The Congo • 1♀; Brazzaville env.; 1907; E. Roubaud and A. Weiss leg.; MNHN. Rwanda • 1♀; Astrida [= Butare]; 22 Feb. 1953; P. Basilewsky leg.; KMMA • 1♀; same collection data as for preceding; 5 Mar. 1955; P. Elsen leg.; • 1♀; same col-



Figures 68–73. *Senaspis* species, right wing **68** *S. elliotii* Austen (♂) **69–71** *S. elliotii* Austen close-up apical end **72** *S. flaviceps* Macquart (♂) **73** *S. haemorrhoa* (Gerstaecker) (♂).

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75
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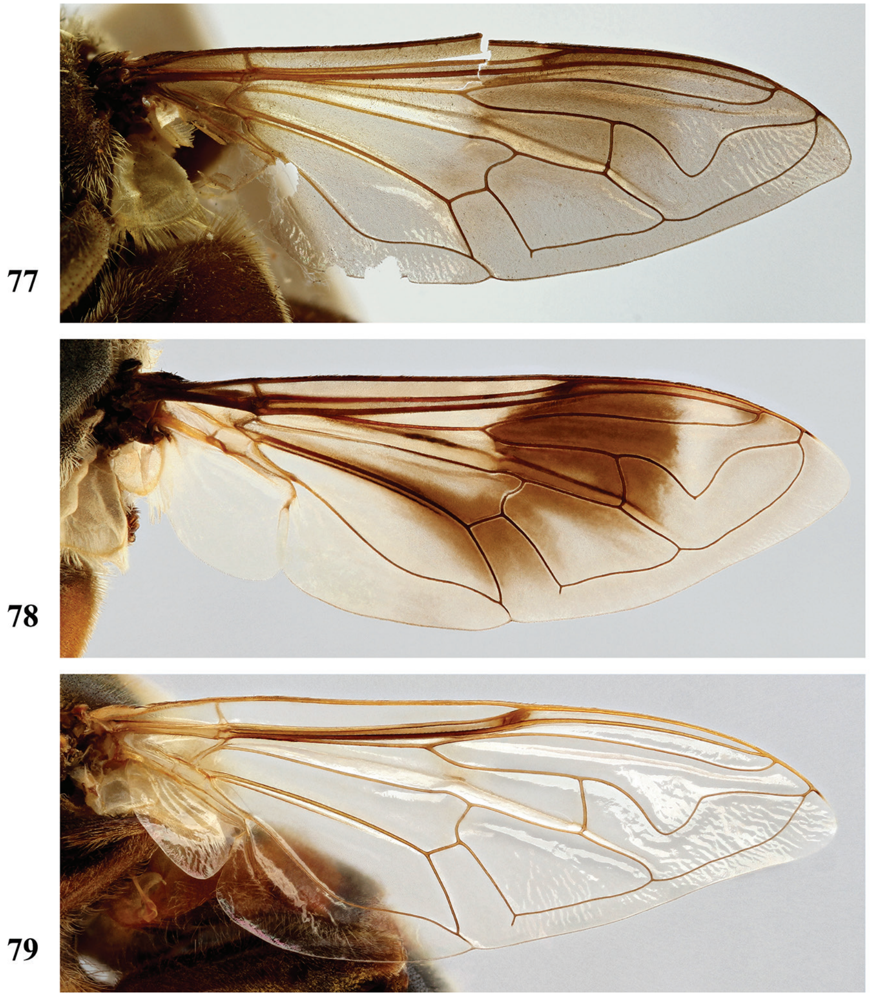
Figures 74–76. *Senaspis* species, right wing **74** *S. melanthysana* (Speiser) (♂) **75** *S. nigrita* (Bigot) (♂) **76** *S.* nr *umbrifera* (Walker) (♂).

lection data as for preceding; 15 Mar. 1955 • 1♀; Karissimbi; Dec. 1925; H. Schouteeden leg.; KMMA. São Tomé and Príncipe • 3♂♂ 2♀♀; São Tomé, Ribeira Palma; Aug. 1900; L. Fea leg.; MCSNG • 3♀♀; Príncipe, Roca Inf. D. Henrique; Mar. 1901; L. Fea leg.; MCSNG • 1♀; 1900; A. Negreiros leg.; MNHN • 1♀; 1919–1921; H.J. Snell leg.; NHMUK • 2♂♂ 1♀; 1920; H. Navel leg.; MNHN • 1♀; 19 Sep. 1921; H.J. Snell leg.; NHMUK • 1♀; no data; H. De Saeger and Prince Leopold leg.; KMMA. Somalia • 1♀; Mogadishu; 20 Feb. 1953; NHMUK. South Africa • 1♀; Amatikulu Nature Reserve; 14 Jun. 2011; J. Londt and T. Dikow leg.; NMSA • 4♀♀; Ben Lavin Nature Reserve; 13 Feb. 2005; J. Londt and T. Dikow leg.; NMSA • 1♂; Bluff, Durban; 8 Mar. 1925; NMSA • 1♀; Blyderivierspoortdam Nature Reserve; 25–26 Oct. 1984; C.D. Eardley leg.; NMSA • 1♀; Empangeni; 7 Apr. 1989; P. Reavell leg.; NMSA

• 1♀; False Bay; 24 Feb.–4 Mar. 1990; A.J. Weaving leg.; NMSA • 1♀; Gillits; 24 Feb. 1957; NMSA • 1♀; Ingwavuma; 10 Dec. 1963; B. and P. Stuckenberg leg.; NMSA • 1♀; Irene; 24 May 1971; C.K. Brain leg.; NMSA • 1♂; Letaba Camp, Kruger National Park; 14–18 Nov. 1961; Vari and Rorke leg.; NMSA • 2♀♀; 37 km N Louis Trichardt, Limpopo; Jan. 1975; B. Stuckenberg leg.; NMSA • 2♂♂ 4♀♀; Mafikeng Game Reserve, Kolobe drinking pond; 16 Mar. 2003; J.Londt leg.; NMSA • 1♀; Mafikeng Game Reserve, Noka picnic site; 17 Mar. 2003; J. Londt leg.; NMSA • 1♀; Malvern; Natal; Jun. 1897; G.A.K. Marshall leg.; NHMUK • 1♀; Mntunzini, Garland Farm, Natal; 1 Aug. 1985; P. Atkinson leg.; NMSA • 1♀; Modimolle, Limpopo; 20 Nov. 2017; A. Vujic and E. Rättel leg.; MZH • 1♂ 2♀♀; Mpenjati Nature Reserve; 22–23 Jan. 2011; J. and A. Londt leg.; NMSA • 1♀; Ndumu Game Reserve, staff house; 15–17 Feb. 2011; J. Londt leg.; NMSA • 1♀; Ndumu Game Reserve, rest camp; 23–29 Nov. 1977; D. Brothers and J. Guillarmod leg.; NMSA • 1♀; Port St John Pondoland; 1–15 Apr. 1924; B.E. Turner leg.; NHMUK • 1♀; 5 km E Sabie, Bergvliet Road; 24 Feb. 1971; B. Stuckenberg leg.; NMSA • 1♂ 1♀; San Lameer resort area; 11–12 Feb. 2012; J. and A. Londt leg.; NMSA • 1♀; Shelly Beach; 29 May 1984; D. Wheeler leg.; NMSA • 1♀; 4 km E Skukuza, Sabie River, Kruger National Park; 4 Jan. 1974; B. and P. Stuckenberg leg.; NMSA • 1♀; Tshifhire, Venda; Jul. 1983; Neluheni leg.; NMSA • 1♀; Umbilo; 21 Mar. 1915; L. Bevis leg.; NMSA • 2♂♂ 1♀; Umtamvuna Nature Reserve; 14 Jan. 1981; J. Londt leg.; NMSA • 1♂; same collection data as for preceding; 29 Oct. 1990; A. Whittington leg. • 1♀; van Reenen's Pass, Ladysmith, Kwa-Zulu Natal; 23 Feb. 2016; G. Ståhls and E. Rättel leg.; MZH • 1♀; Vernon Crookes Nature Reserve; 16 Nov. 2003; G.B.P. Davies leg.; NMSA. Tanzania • 1♀; Amani; 1957; J.G. Halcrow leg.; NHMUK • 1♀; Chenzema, Uluguru Mountains; 2–22 Jul. 1971; L. Berger; N. Leleup and J. Debecker leg.; KMMA • 1♂; Dar es Salaam; Apr. 1961; G. Heinrich leg.; CNC • 1♀; same collection data as for preceding; 12 Sep. 1961 • 1♀; same collection data as for preceding; 14 Sep. 1961 • 11♂♂ 1♀; same collection data as for preceding; Oct. 1961 • 1♂; same collection data as for preceding; 20 Oct. 1961 • 2♂♂; Dodoma; Nov. 2008; G. Goergen leg.; IITA • 2♂♂; same collection data as for preceding; 27 Nov. 2008 • 8♂♂; Iringa-Morogoro; 23 Nov. 2008; G. Goergen leg.; IITA • 1♀; Kunduchi; Jul. 1973; CDFA • 1♀; Lake Manyara; Jun.–Aug. 1937; B. Cooper leg.; NHMUK • 1♀; Matumbi Highlands; 25 Nov. 1989; W.R.B. Hynd leg.; NHMUK • 1♀; Morogoro; 6 May 1925; A.H. Ritchie leg.; NHMUK • 1♂ 1♀; same collection data as for preceding; 20 May 1925 • 2♀♀; same collection data as for preceding; 10 Jun. 1925 • 1♀; nr Morogoro, Uluguru Mountains; Jan. 1962; CNC • 1♂; Mungula Gorge, Bunduki, Uluguru Mts; P. Basilewsky and N. Leleup leg.; KMMA • 1♂; Musoma; 29 Nov. 2008; G. Goergen leg.; IITA • 2♂♂; Mwanza; 30 Nov. 2008; G. Goergen leg.; IITA • 1♂; Njombe; 23 Oct. 1951; W. Peters leg.; NHMUK • 1♀; same collection data as for preceding; 9 Dec. 1952 • 1♂; same collection data as for preceding; 23 Oct. 1957 • 1♂; Old Shinyanga; 26 Mar. 1953; E. Burtt leg.; NHMUK • 1♂; same collection data as for preceding; 28 Mar. 1953 • 1♂; same collection data as for preceding; 10 Apr. 1953 • 1♂; same collection data as for preceding; 11 Apr. 1953 • 1♂; Rukwa Valley; 16 Sep. 1952; NHMUK • 2♀♀; Tanga;

Apr.–May 1950; R.C.H. Sweeney leg.; NHMUK • 3♂♂; Ukara Island; Lake Victoria; 1953; A. Smith leg.; NHMUK • 1♀; Zanzibar; [no date]; ex coll Bigot; NHMUK • 2♀♀; Zanzibar; C. Cooke leg.; CNC • 1♂; Zanzibar; 17 May 1911; W.M. Aders leg.; NHMUK • 1♂; Zanzibar; Jan.–Feb. 1925; H.J. Snell leg.; NHMUK. Togo • 1♂; Kloto; 3 Mar. 2018; K. Jordaens leg.; KMMA. Uganda • 1♂ 1♀; Budongo Forest, nr Lake Albert; 1 Apr. 1972; E.B. Babyetagara leg.; CNC • 1♂ 1♀; Entebbe; May 1906; M. de Rothschild leg.; MNHN • 1♀; Entebbe; 20 Mar. 1911; C.C. Gowdey leg.; NHMUK • 1♀; same collection data as for preceding; 17 Aug. 1911 • 2♂♂ 10♀♀; same collection data as for preceding; 21 Aug. 1911 • 1♀; same collection data as for preceding; 1–11 Sep. 1911 • 2♂♂ 1♀; same collection data as for preceding; 7–9 May 1912 • 1♀; same collection data as for preceding; 27 May 1912 • 5♂♂ 3♀♀; same collection data as for preceding; 3 Sep. 1912 • 2♀♀; same collection data as for preceding; 16 Oct. 1912 • 1♀; same collection data as for preceding; 14 Nov. 1912 • 1♂; same collection data as for preceding; 18–20 Nov. 1912 • 2♀♀; same collection data as for preceding; 3–4 Dec. 1912 • 1♂ 1♀; same collection data as for preceding; 12–13 Dec. 1912 • 1♀; same collection data as for preceding; 31 Dec. 1912 • 1♀; same collection data as for preceding; 20 Mar. 1913 • 5♀♀; same collection data as for preceding; 1913 • 1♀; same collection data as for preceding; 6–13 May 1912; C.A. Wiggins leg. • 1♀; Entebbe; 1 Feb. 1972; H. Falke leg.; CNC • 2♂♂; same collection data as for preceding; 20 Nov. 1972–22 Jan. 1973 • 2♂♂; same collection data as for preceding; 25–28 Jan. 1973 • 1♀; 7 mi N Entebbe; 31 Mar. 1972; H. Falke leg.; CNC • 3♂♂ 3♀♀; near Entebbe; 23–31 Jan. 1973; H. Falke leg.; CNC • 1♂; Kayonza Forst, Kigezi; 1 Sep. 1972; H. Falke leg.; CNC • 1♀; Masindi; Aug. 1945; P.A. Buxton leg.; NHMUK • 1♀; Ruwenzori; 17 May 1911; C.C. Gowdey leg.; NHMUK • 1♀; Sukulu; 26 Jan. 1954; NHMUK • 1♀; Sukulu; 9 Apr. 1961; E. Burtt leg.; NHMUK • 2♂♂ 1♀; same collection data as for preceding; 26 Jan. 1962 • 1♀; same collection data as for preceding; 31 Jan. 1962 • 1♂; Tero; 14 Apr. 1911; C.C. Gowdey leg.; NHMUK • 1♂; Tororo; 30 Jan. 1954; NHMUK. Zambia • 2♂♂; Abercorn; 17 Jan. 1951; F.O. Albrecht leg.; NHMUK • 1♀; same collection data as for preceding; 12 Feb. 1951 • 1♂; same collection data as for preceding; 26 Feb. 1951 • 1♀; Jan. 1966; H. Mathes leg.; KMMA • 1♀; Broken Hill; 1 May 1912; E.A. Copeman leg.; NHMUK • 1♀; same collection data as for preceding; 29 May 1912 • 1♀; Mwinilunga; 9 Apr. 1914; F.V. Bruce Miller leg.; NHMUK • 1♀; Ndola; 31 Jan. 1980; T. Grout leg.; NMSA • 1♀; Nyamkolo; 9 May 1930; A. Loveridge leg.; CNC. Zimbabwe • 1♀; Banket; Dec. 1950; A. Carnegie; NMSA • 1♀; Bazely Bridge, Mutare; 14 Apr. 1964; D. Cookson leg.; NMSA • 1♀; Bomponi; 13 May 1963; D. Cookson leg.; NMSA • 1♂; same collection data as for preceding; 16 Jun. 1965 • 1♀; Chigudu Farm, Mvurwi; 14 Jan. 1985; A.J. Weaving leg.; NMSA • 1♂; Melsetter District; 23 Nov. 1993; E. Bruce-Miller leg.; AMGS • 1♂; Salisbury [= Harare]; 1 Jan. 1952; J.M. Brown leg.; NMSA • 1♀; same collection data as for preceding; 22 Apr. 1978; P.E. Hulley leg. • 1♀; Vumba Mt; March 1938; NHMUK • 1♀; East Vumba; 1 Jun. 1964 • 1♂; North Vumba; 27 Mar. 1964; D. Cookson leg.; NMSA • 1♀; same collection data as for preceding; 16 Nov. 1964.

Description. Body length: 11.0–15.8 mm. Wing length: 8.0–11.0 mm.



Figures 77–79. *Senaspis* species, right wing **77** *S. umbrifera* (Walker) (♂ holotype) **78** *S. xanthorrhoea* (Bezzi) (♂) **79** *S. pennata* (Hervé-Bazin) (♀).

Male (Fig. 5). Head (Figs 28, 29). Eye bare; holoptic, eye contiguity for distance equal to or slightly longer than length of ocellar triangle, facets dorsally slightly larger, at most twice as large in diameter, as ventral ones. Frons black to black-brown; weakly subshiny, with dense greyish pollinosity throughout; with dispersed medium long straw-yellow pile. Face black to black-brown; weakly subshiny, with dense greyish pollinosity, facial tubercle weakly shining black, posterolateral margin of mouth shining brownish; in parts with dispersed long pale pile; facial tubercle strongly pronounced. Gena colour and pollinosity as ventral lateral margin of face; with short to long pale pile. Occiput black-brown, covered with dully grey pollinosity; with dispersed pale pile, except dorsally where pile black adjacent to vertex. Antennal segments black-brown, basoflagellomere apically more brownish, arista pale yellow.

Figures 80–85. *Senaspis* species, hind leg, anterior view **80** *S. dentipes* (Macquart) (♂) **81** *S. dibapha* (Walker) (♂) **82** *S. elliotii* Austen (♂) **83** *S. flaviceps* Macquart (♂) **84** *S. flaviceps* Macquart (♀) **85** *S. haemorrhoa* (Gerstaecker) (♂).

Thorax (Fig. 57). Scutum mainly subshiny black; sparse grey pollinose, more densely so along margins and transverse suture; pilosity variable, usually predominantly pale yellow, sometimes more or less interspersed with short black pile. Scutellum apical margin weakly rounded, distinctly marginated, slightly more than twice as wide as long; pale yellow, anterior margin narrowly black-brown; with short pale pile. Pleura ground colour black-brown, sparsely greyish pollinose; covered with dispersed long pale pile except on meron, dorsomedial anepimeron, ventral part of katepimeron, anterior part of katepisternum and anterior anepisternum.

Legs. Dark brown to reddish brown; with short dark pile, along posterior margin of pro- and mesofemora with longer pale pile except apically, metafemur predominantly long pale pile in basal two-thirds. Metaleg (Fig. 85), femur moderately thickened, with one distinct ventral swelling in apical fifth, a second less developed thickening proximal of this; tibia thickened and slightly curved, pile along ventral margin more dense.

Wing (Fig. 73). Largely hyaline, only with very faint yellowish brown tinge; with distinct dark brown macula running from anterior margin and covering most of stigma, parts of cell r_1 and r_{2+3}, distal part of cell br and basal part of r_{4+5}, decreasing in intensity on anterior part of cell dm, macula well demarcated apically but decreasing gradually in colour basally. Calypters white; with fringe of white pile. Cell r_1 closed, petiole usually approx. equal to height of base of stigma, rarely shorter. Vein R_{4+5} sinuate and short appendiculate, rarely appendix missing.

Abdomen (Fig. 95). Uniformly subshiny brown to reddish brown; tergum IV, postabdomen and sometimes posterior margin of tergum III conspicuously orange to orange-red; with short dark pile, except tergum I completely, anterior half of tergum II and anterior fourth of tergum III with longer silvery to pale yellow pile; lateral margins with pale pile; orange areas with pale orange pile. Male genitalia as in Fig. 106.

Female. As male except for the following character states: Eye dichoptic (Figs 30, 31), facets equal to subequal in size all over. Frons subshiny black to black-brown, in medial part with greyish pollinosity, pilosity shorter and more silvery pale except in front of ocellar triangle where short and black. Thorax, pilosity usually more extensively black, usually as fasciae. Abdomen pale pilosity along lateral margins missing; pale pilosity in tergum II at most in anterior third, tergum III predominantly with black pile. In general, thoracic and abdominal pale pilosity more silvery than in male.

Distribution. Angola, Benin, Botswana, Burundi, Comoros, Democratic Republic of the Congo, Ethiopia, Guinea Bissau, Kenya, Malawi, Mozambique, Namibia, Nigeria, Republic of the Congo, Rwanda, São Tomé and Príncipe, Somalia, South Africa, Tanzania, Togo, Uganda, Zambia and Zimbabwe.

Comments. The type material of *S. haemorrhoa* (both male and female specimens according to the original description) could not be traced.

Senaspis griseifacies was proposed as a species by Bezzi (1908), who provided a short description. Bezzi (1912) included *griseifacies* and *haemorrhoa* Gerstaecker in his key for the genus *Protylocera* (page 416) and provided a more detailed description of *S. griseifacies*. He differentiated the latter from *S. haemorrhoa* mainly on characters of the wing (anterior margin basally more hyaline in *S. griseifacies*, infuscated in *S. haemorrhoa*) and the abdomen (terga II and III along posterior margin yellow in *S. haemorrhoa*, dark in *S. griseifacies*). Examination of long series of *S. haemorrhoa* and of type material of *S. griseifacies* has shown these characters to be variable. In addition, Bezzi (1912) contradicted the abdominal character partially in his detailed redescription where he indicated that in female specimens of *S. griseifacies* the "è spesso rosso anche l'orlo posterior del terzo segment" (partially red along posterior margin of the third segment). Both species are considered conspecific and thus *S. griseifacies* is considered junior synonym of *S. haemorrhoa*. Hervé-Bazin (1914) already alluded to this when indicating that *S. griseifacies* should be considered perhaps as a mere variety of *S. haemorrhoa*. An identification label '*Senaspis haemorrhoa*' of 1996 by C. Kassebeer on one of the types of *S. griseifacies* at the KBIN collection also alludes to the synonymy but apparently was never formally published.

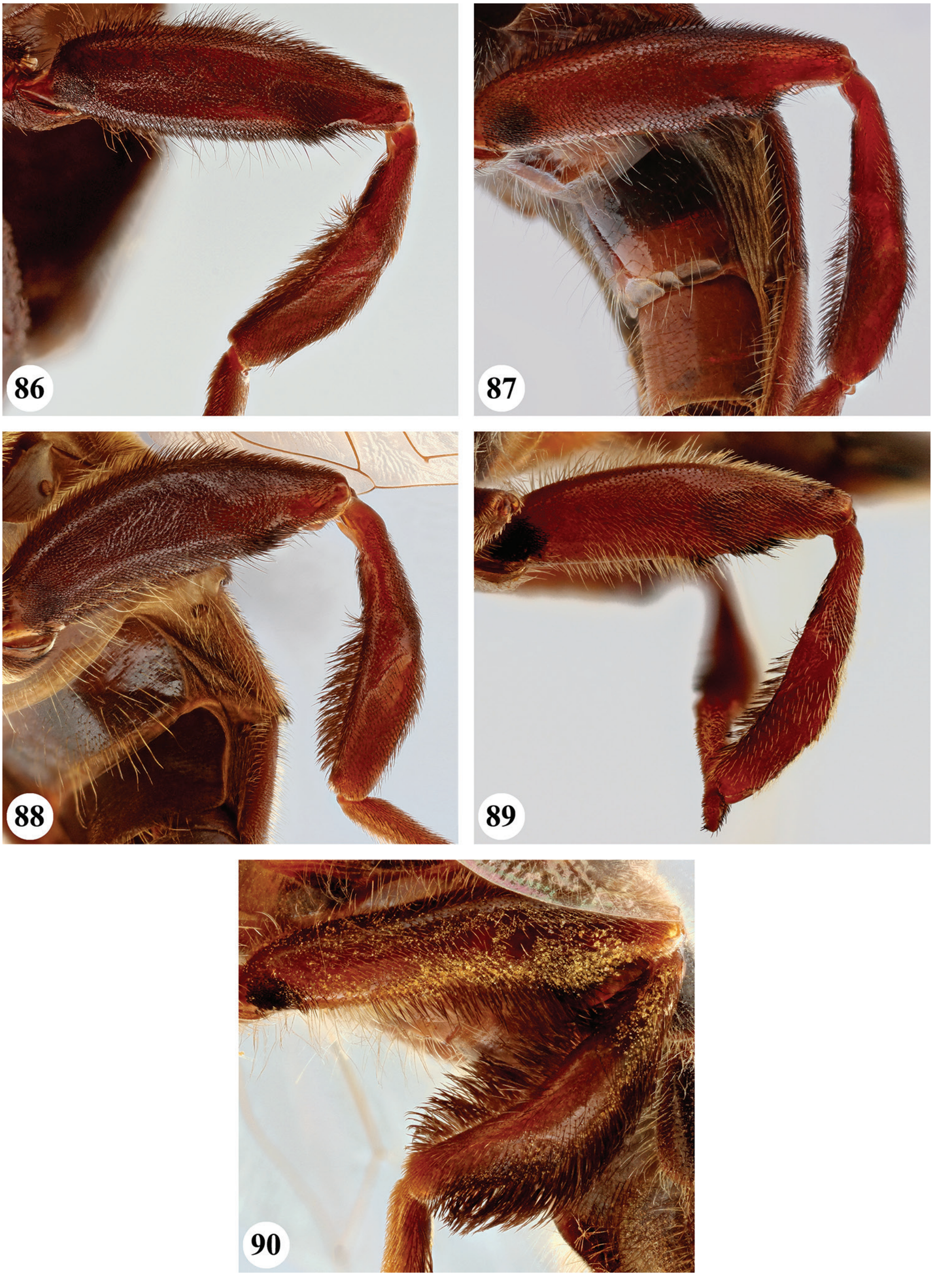
Senaspis melanthysana **(Speiser, 1913)**
Figs 6, 32–35, 58, 74, 86, 96, 108, 109

Protylocera melanthysana Speiser, 1913: 122.

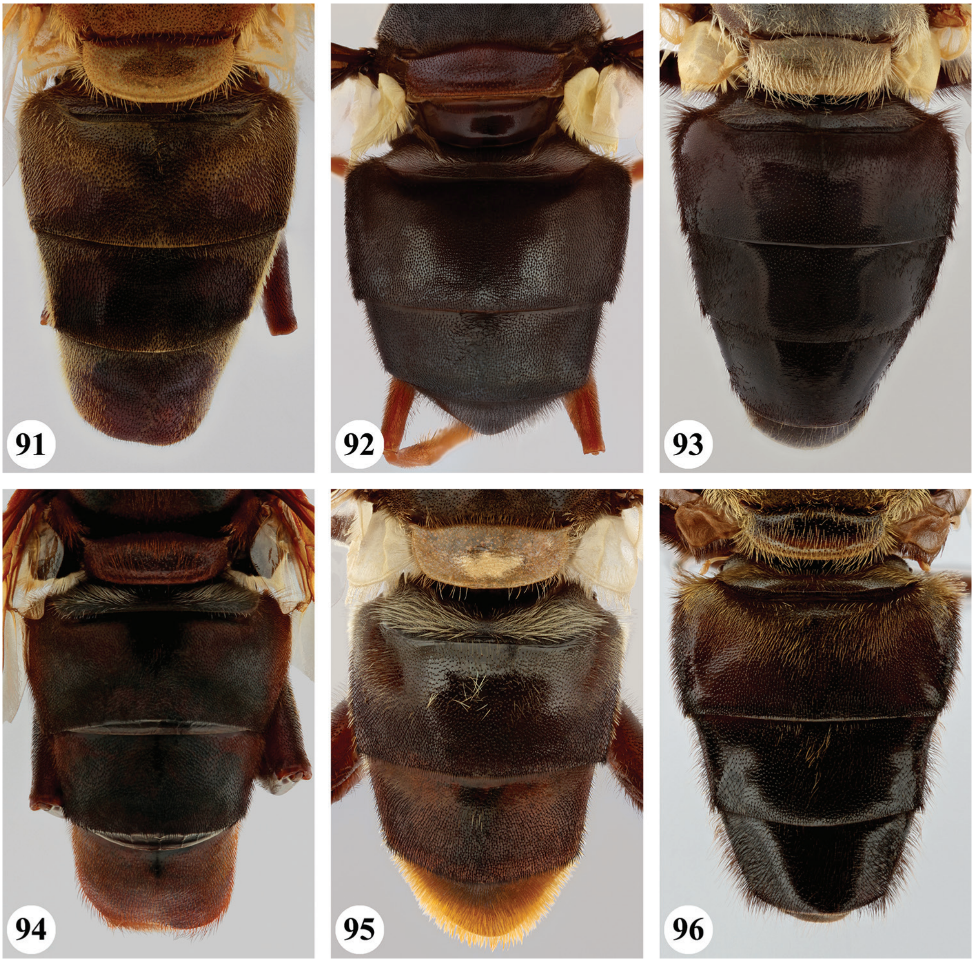
Differential diagnosis. A dark species (Fig. 6) without distinct macula on wing but with darker medial area (Fig. 74). It can be differentiated from *S. nigrita* by the basal half of the scutellum largely concolourous with the scutum (Fig. 58) (scutellum largely yellow, contrasting with dark scutum in *S. nigrita*; Fig. 59). It resembles strongly *S. umbrifera* but can be differentiated by the following characters: metafemur moderately thickened and straight to slight convex ventrally (Fig. 86) (thicker and concave in *S. umbrifera*; Fig. 88); abdomen with long dark pile along lateral margins (Fig. 96) (mixed short pale and dark pile in *S. umbrifera*; Figs 98, 99); long dark pile on all sterna (Fig. 6) (pale pile on sterna II and III in *S. umbrifera*; Fig. 10).

Type. *Protylocera melanthysana* Speiser: Holotype, female, CAMEROON, Soppo am Kamerunberge, von Rothkirch [institutional depository unknown; not examined].

Examined material. Cameroon • 1♀; Yaoundé; Molez leg.; MNHN. Democratic Republic of the Congo • 1♂; Bamania; 11 May 1924; J. Béquaert leg.; KMMA • 1♀; Bayenge, Wamba; 8 Jul. 1956; R. Castelain leg.; KMMA • Eala; 3♂♂; Eala; 29 Jul. 1935; J. Ghesquière leg.; KBIN • 1♂; same collection data as for preceding; 22 Aug. 1935 • 1♂; same collection data as for preceding; Sep. 1935 • 1♂; same collection data as for preceding; 6 Feb. 1936 • 1♀; same collection data as for preceding; Mar. 1936 • 1♂; same collection data as for preceding; Aug. 1936 • 1♀; same collection data as for preceding; Oct. 1936 • 1♀; same collection data as for preceding; Jan. 1935; KMMA • 1♂; same collection data as for preceding; Aug. 1935 • 1♂; Poko; Aug. 1913; NHMUK • 5♂♂ 1♀; Stanleyville [= Kisangani]; Mar. 1915; Lang and Chapin leg.; AMNH • 1♀; same collection data as for preceding; NHMUK • 1♀; same collection data as for preceding; CNC • 6♂♂ 3♀♀; same collection data as for



Figures 86–90. *Senaspis* species, hind leg, anterior view **86** *S. melanthysana* (Speiser) (♂) **87** *S. nigrita* (Bigot) (♂) **88** *S.* nr *umbrifera* (Walker) (♂) **89** *S. xanthorrhoea* (Bezzi) (♂) **90** *S. pennata* (Hervé-Bazin) (♀).



Figures 91–96. *Senaspis* species, abdomen, dorsal view **91** *S. dentipes* (Macquart) (♂) **92** *S. dibapha* (Walker) (♂) **93** *S. elliotii* Austen (♂) **94** *S. flaviceps* Macquart (♂) **95** *S. haemorrhoa* (Gerstaecker) (♂) **96** *S. melanthysana* (Speiser) (♂).

preceding; KMMA • 1♂; same collection data as for preceding; Apr. 1915; AMNH • 1♂; same collection data as for preceding; CNC • 1♀; same collection data as for preceding; 2 Apr. 1915; AMNH • 1♂; same collection data as for preceding; 5 Apr. 1915 • 1♂ 1♀; same collection data as for preceding; 6 Apr. 1915 • 1♀; same collection data as for preceding; 7 Jul. 1915. Kenya • 1♀; Ngong; Apr. 1944; V.G.L. van Someren leg.; NHMUK. Uganda • 1♀; Entebbe; 1–11 Sep. 1911; S.A. Neave leg.; NHMUK • 1♀; same collection data as for preceding; 12–20 Jan. 1912.

Description. Body length: 12.6–19.0 mm. Wing length: 9.5–14.3 mm.

Male (Fig. 6). Head (Figs 32, 33). Eye bare; holoptic, eye contiguity for distance equal to length or 1.5 times length of ocellar triangle, facets dorsally slightly larger, at most twice as large in diameter as ventral ones. Frons black-brown; largely subshiny with black pollinosity in dorsal fifth only, along eye margins narrowly silver-grey pollinose; dispersed short dark pile, dorsally somewhat longer. Face black-brown; subshiny with pale brownish to greyish pollinosity, in parts more densely so, medial part and ventral lateral parts largely devoid of pollinosity; pollinose parts with dispersed long pale pile; facial tubercle strongly pronounced. Gena as pollinose parts of face; with short to long pale pile. Occiput black-brown, covered with dully grey pollinosity; with dispersed pale pile except dorsally where sometimes darker yellow to black. Antennal segments black-brown, arista orange-brown.

Thorax (Fig. 58). Scutum subshiny black, with brownish to brownish grey pollinosity; with short pale pile. Scutellum apical margin rounded, distinctly marginate, ca. 2.5–3 times as wide as long; pale brownish, anterior margin narrowly darker brown; with short pale pile, longer along margin. Pleura ground colour black-brown, greyish pollinose, anepimeron less so; covered with dispersed long pale pile except on meron, dorsomedial anepimeron, ventral part of katepimeron, anterior part of katepisternum and anterior anepisternum, pilosity on posterior anepisternum more conspicuous.

Legs. Mainly black to black-brown; with short black pile, along posterior margin of pro- and mesofemora and along ventral margin of metafemur with longer dark pile, sometimes base of pro- and mesofemora narrowly with more pale brownish pile; along ventral margin of metafemur with longer dark pile, basally with anterodorsal patch of longer dark pile. Metaleg (Fig. 86), femur moderately thickened, with ventral swelling in apical fifth; tibia slightly bent at base, thickened and curved, pile along ventral margin in apical half to two-thirds longer and more dense.

Wing (Fig. 74). Usually distinct fumose yellow-brown tinge, especially in medial part cell r_1, basal part r_{2+3} and distal part R; towards posterior margin and apex more greyish, sometimes posteriorly more hyaline. Calypters dark brown, concolourous with or darker than medial part wing; with fringe of black pile. Cell r_1 closed and petiolate, petiole at most as long as half the height of base of stigma. Vein R_{4+5} sinuate; usually not appendiculate, rarely with short appendix.

Abdomen (Fig. 96). Uniformly subshiny brown to black-brown; with short dark pile, except tergum I, and anterolateral parts of tergum II where pale; pilosity along lateral margins of all terga conspicuous and dense, along tergum IV and postabdomen longer. Postabdomen small. All sterna with dispersed long dark pile. Male genitalia as in Figs 108, 109.

Female. As male except for the following character states: Eye dichoptic (Figs 34, 35), facets equal to subequal in size. Frons with black pollinose fascia in dorsal part for length at least equal to ocellar triangle, bordered by very narrow and less dense greyish-brown fascia. Abdomen, pilosity along lateral margins of all terga short and more dispersed.

Distribution. Cameroon, Democratic Republic of the Congo, Uganda. Also recorded from Kenya (De Meyer et al. 1995) but this needs to be confirmed as the material was unavailable for this study.

Comments. For similarities and differences with *umbrifera*, see comments under the latter. Both species occur sympatrically, like in the Democratic Republic of the Congo

(Kisangani) and Uganda (Entebbe) (see material examined), but *S. umbrifera* has a larger distribution throughout. The holotype could not be found but the original description defines the main diagnostic character states and corresponds with material studied.

Senaspis nigrita **(Bigot, 1859)**

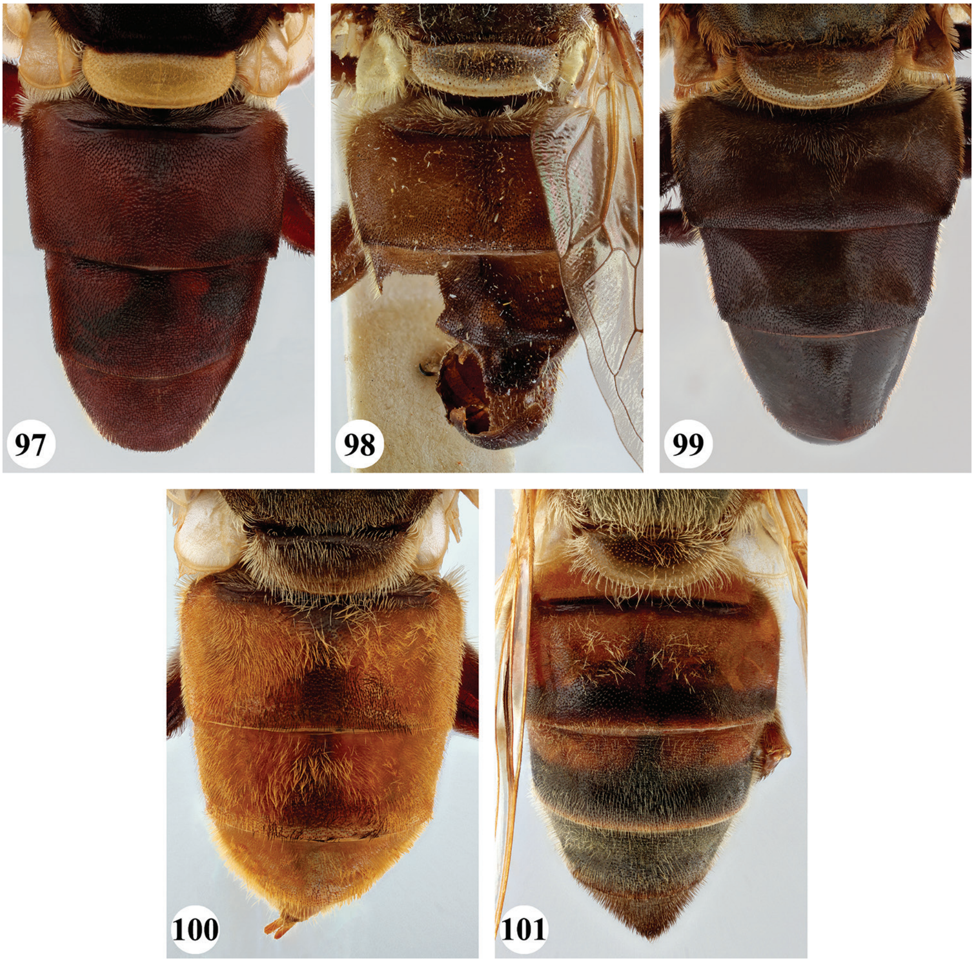
Figs 7, 36–39, 59, 75, 87, 97, 107

Dolichomerus nigritus Bigot, 1859: 431.

Differential diagnosis. A brown to black-brown species (Fig. 7) without distinct macula on wing but with darker medial area (Fig. 75). It can be diferentiated from other *Senaspis* species with dark scutum and similar wing marking (*S. melanthysana*, *S. umbrifera*) by the contrasting yellow scutellum (Fig. 59) (scutellum largely concolourous with scutum, at least along basal half in other species (Figs 58, 61).

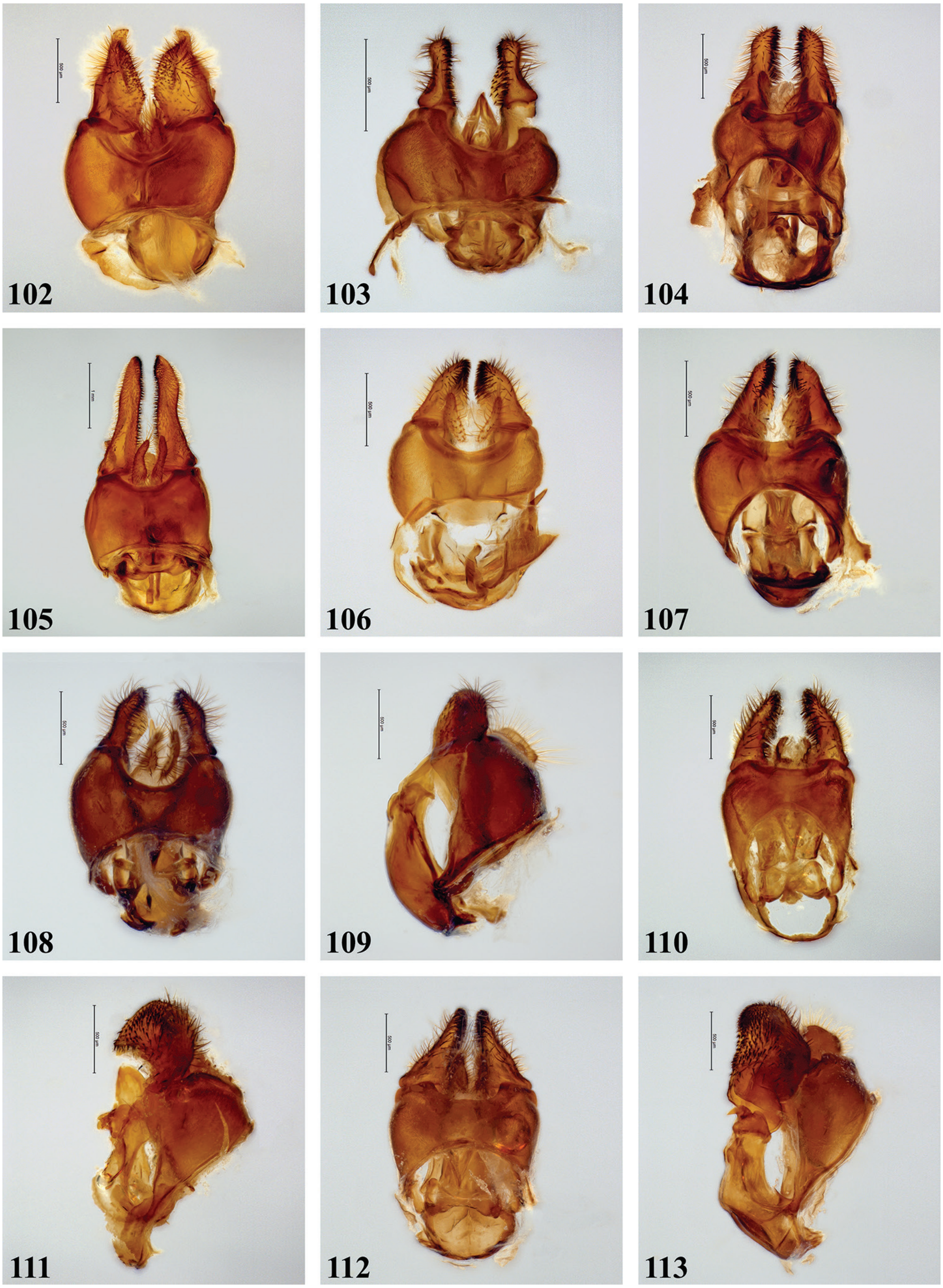
Examined material. *Dolichomerus nigritus* Bigot: ***Lectotype*** (hereby designated), female, "Syn- // type" "ex. coll. Bigot. // Prs. by // G.H. Verrall. // B.M. 1901–14." "SYNTYPE ♀ of // Dolichomerus // nigritus Bigot // MADAGASCAR" "BMNH(E) # // 230785" "NHMUK010369878" "LECTOTYPUS" [NHMUK]. ***Paralectotype***, female, "Syn- / /type" "SYNTYPE ♀ of // Dolichomerus // nigritus Bigot // MADAGASCAR" "ex. coll. Bigot. // Pres. by // G.H. Verrall. // B.M.1901–14." "BMNH(E) # // 230786" "PARA- // LECTOTYPUS" [NHMUK].

Other material. Madagascar • 2♂♂ 1♀; 5 km N Ampotaka, Beloha; 5–15 Mar. 2009; M. Irwin and R. Harin'Hala leg.; CDFA • 1♀; Ambatobevandza; 1919; R. Decary leg.; MNHN • 1♀; Ambatolampy; 1931; Lasère leg.; MNHN • 1♀; Ambatosoratra; Nov. 1960; P. Soga leg.; MNHN • 1♀; Ambodivoangy; Jan. 1967; J. Vadon leg.; KMMA • 1♀; Ambre; Oct. 1902; MNHN • 1♀; Ampassamadinika, Tamatave; 26 Jan. 1992; A. Pauly leg.; KMMA • 1♀; Analmalotra; 1 Nov. 1993; C. Kassebeer leg.; CDFA • 1♀; Andasibe National Park; 17 Dec. 2017; Schmid-Egger leg.; CDFA • 1♀; Andranobe Forest, route d'Andriamena; MNHN • 1♀; Anja Reserve, 10 km SSW Ambalavao; 24 Dec. 2017; Schmid-Egger leg.; CDFA • 1♀; Ankaratra Massif, Manjakatompo; Dec. 1951; Benoist leg.; KMMA • 1♂; Ankaratra Massif, Manjakatompo; Jan. 1958; B. Stuckenberg leg.; NMSA • 1♂; Anosibé; Breuning leg.; KMMA • 1♀; Bekily; Mar. 1930; A. Seyrig leg.; MNHN • 1♂; same collection data as for preceding; May 1933 • 1♂; same collection data as for preceding; Jun. 1933 • 1♂ 5♀♀; Belambo, 20 km NW Boriziny, Mahajanga; 4 Jan. 2007; A.H. Kirk-Spriggs leg.; AMGS • 1♀; Betafo, Ambositra and Miandrivazo regions, Central; 1905; Bouet leg.; MNHN • 1♀; Betsileo; NHMUK • 1♀; Brickaville; Jul. 1959; Sigwalt leg.; MNHN • 2♂♂ 3♀♀; Bevilany, Tulear, 12 Apr. 1968; K.M.G. and P.D. leg.; NHMUK • 1♀; same collection data as for preceding; 14–18 Apr. 1968 • 1♂; Didy; 12 Apr. 1992; A. Pauly leg.; KMMA • 1♂; same collection data as for preceding; 16 Apr. 1992 • 1♀; Fampanambo; 1962; J. Vadon leg.; KMMA • 1♀; Fianarantsoa; A. Bigneux leg.; CNC • 2♀♀; Forest Belt; S. Hutchins leg.; NHMUK • 1♀; Fort Dauphin [= Taolagnaro]; NHMUK • 1♀;



Figures 97–101. *Senaspis* species, abdomen, dorsal view **97** *S. nigrita* (Bigot) (♂) **98** *S. umbrifera* (Walker) (♂ holotype) **99** *S.* nr *umbrifera* (Walker) (♂) **100** *S. xanthorrhoea* (Bezzi) (♀) **101** *S. pennata* (Hervé-Bazin) (♀).

Foulpointe [= Mahavelona]; 12 Nov. 1993; A. Pauly leg.; KMMA • 1♂ 2♀♀; same collection data as for preceding; May 1995 • 1♂ 5♀♀; Imerina, Andrangoloaka Forest; A. Grandidier leg.; MNHN • 1♀; Ivoloina; Mar. 1960; Sigwalt leg.; MNHN • 1♂; Lac Froid, Ambatolampy; 11–15 Dec. 1957; B. Stuckenberg leg.; NMSA • 1♀; 7 km N Joffreville; 20 Mar.–7 Apr. 2001; R. Harin'Hala leg.; CDFA • 1♂ 2♀♀; Mananjara Province; 1910; Goissaud leg.; MNHN • 1♀; Maroantsetra; J. Vadon leg.; MNHN • 1♀; same collection data as for preceding; Nov. 1959; KMMA • 1♀; Montagne d'Ambre; L. Chopard leg.; MNHN • 1♀; Ranomafana National Park; 21 Dec. 2017; Schmid-Egger leg.; CDFA • 1♀; Ranomafana National Park, Radio Tower; 16 Nov. 2001; M.E. Irwin; F.D. Parker and R. Harin'hala leg.; CDFA • 3♀♀; Ranomafana National Park, ValBio Research Centre; 15–17 Jan. 2007; A.H. Kirk-Spriggs leg.; AMGS



Figures 102–113. *Senaspis* species, male terminalia **102–108, 110, 112** dorsal view **109, 111, 113** lateral view **102** *S. dentipes* (Macquart) **103** *S. dibapha* (Walker) **104** *S. elliotii* Austen **105** *S. flaviceps* Macquart **106** *S. haemorrhoa* (Gerstaecker) **107** *S. nigrita* (Bigot) **108, 109** *S. melanthysana* (Speiser) **110, 111** *S. umbrifera* (Walker) (holotype) **112, 113** *S.* nr *umbrifera* (Walker).

• 4♀♀; same collection data as for preceding; 13 Jan. 2014; M. Hauser leg.; CDFA • 3♀♀; Ranomafana National Park, Talatakely; 11 June 2014; A.H. Kirk-Spriggs and R. Harin'Hala leg.; BMSA • 1♀; Sakalava Beach; 7–25 Jun. 2001; R. Harin'Hala leg.; CDFA • 1♀; Tananarive; 1897; E. Dorr leg.; MNHN • 1♂ 5♀♀; same collection data as for preceding; 1914; G. Waterlot leg.; • 1♂ 1♀; same collection data as for preceding; 1916 • 3♀♀; same collection data as for preceding; 1919 • 1♀; same collection data as for preceding; 22 Dec. 1920; R. Decary leg. • 1♂; same collection data as for preceding; 29 Dec. 1920 • 1♀; same collection data as for preceding; 6 Jan. 1921 • 1♀; same collection data as for preceding; 17 Jan. 1921 • 1♀; same collection data as for preceding; 1921 • 1♀; same collection data as for preceding; Jan. 1922 • 1♀; same collection data as for preceding; 1931; Lasère leg. • 2♂♂; Tananarive; Nov. 1952; E.S. Brown leg.; NHMUK • 1♂ 1♀; Tananarive; Jan. 1958; B. Stuckenberg leg.; NMSA • 1♀; Tananarive; 8 Jan. 1971; H May Daly leg.; NHMUK • 1♀; Tananarive; [no date]; MNHN • 1♀; same collection data as for preceding; KMMA • 1♀; Tananarive; [no date]; Le Moult leg.; MNHN • 1♀; same collection data as for preceding; Leray leg. • 1♀; Tsimbazaza, Antanan. Park; 16–22 Oct. 1993; C. Kassebeer leg.; CNC • 2♂♂; Vitambani Forest, 5 km N Ampotaka, Beloha; 12 Aug.–29 Sep. 2009; M. Irwin and Rin'ha leg.; CDFA • 1♂; [no locality]; 1894; P. Camboué leg.; MNHN• 1♀; 1898; Delcroix leg.; MNHN • 1♀; 1906; MNHN • F. Geay leg.; MNHN • 2♂♂ 13♀♀; P. Camboué leg.

Description. Body length: 14.2–18.2 mm. Wing length: 8.7–13.5 mm.

Male (Fig. 7). Head (Figs 36, 37). Eye bare; holoptic, eye contiguity for distance equal to length of ocellar triangle, facets dorsally slightly larger, approx. three times as large in diameter as ventral ones. Frons black-brown; subshiny with brownish pollinosity; long pale yellow pile, especially dorsally and along eye margin. Face black-brown; subshiny with pale brownish to greyish pollinosity, in parts more densely so, ventral lateral margins largely devoid of pollinosity; in parts with dispersed long pale pile; facial tubercle strongly pronounced. Gena colour and pollinosity as ventral lateral margins of face; with short to long pale pile. Occiput black-brown, covered with grey pollinosity; with dispersed pale pile except dorsally where sometimes darker yellow. Antennal segments black-brown, basoflagellomere apically more brown, arista orange-brown.

Thorax (Fig. 59). Scutum subshiny black, weak brownish pollinose; with short pale brown pile in anterior half, posterior part more black pile; postpronotum and notopleuron with longer mixed pale and dark pile. Scutellum apical margin weakly rounded, distinctly marginated, three times as wide as long; pale yellow to straw yellow, anterior margin narrowly black-brown; with short pale pile, along posterior margin somewhat longer. Pleura ground colour black-brown, covered with dispersed long pale or dark pile except on meron, dorsomedial anepimeron, ventral part of katepimeron, anterior part of katepisternum and anterior anepisternum.

Legs. Brown to black-brown, sometimes more rufous; with short black pile, along posterior margin of pro- and mesofemora with longer pale pile, along ventral margin of metafemur with longer dark pile. Metaleg (Fig. 87), femur slightly thickened, with two distinct ventral swellings in apical third, swellings with dispersed short thick setae;

tibia bent at base, thickened and slightly curved, pile along ventral margin in apical half to two-thirds longer and more dense.

Wing (Fig. 75). Faint yellowish tinge, near cross-veins r-m and bm-cu more yellow-brown but no distinct medial macula; distal part of cells r_{2+3} and r_{4+5} more hyaline, as well as along posterior margin, paler areas not distinctly demarcated; alula largely hyaline. Calypters dull straw yellow with fringe of silvery white pile. Cell r_1 closed, petiole very short, at most half height of base of stigma, rarely longer. Vein R_{4+5} sinuate, appendix absent or present.

Abdomen (Fig. 97). Uniformly subshiny brown to black-brown, sometimes more rufous; with short dark pile except tergum I where more densely silver-grey pile; lateral margins intermixed with short pale pile, especially near postabdomen. Terga with dispersed long pale pile. Male genitalia as in Fig. 107.

Female. As male except for the following character states: Eye dichoptic (Figs 38, 39), facets subequal in size. Frons and face pollinosity predominantly greyish; frons with short dark pile dorsally, greyish pile ventrally; with narrow pale fascia dorsally of antennal implant. Thorax dark pile sometimes more extensively so. Leg pilosity sometimes more brownish.

Distribution. Madagascar. Records from Tanzania (Karsch 1888; Smith and Vockeroth 1980) and Uganda (Smith and Vockeroth 1980) could not be confirmed.

Senaspis umbrifera **(Walker, 1849)**

Figs 9, 10, 40–45, 60, 61, 76, 77, 88, 98, 99, 110–113

Merodon umbrifer Walker, 1849: 601.

Differential diagnosis. A dark species (Figs 9, 10) without distinct macula on wing but with darker medial area (Figs 76, 77). It can be differentiated from *S. nigrita* by the basal half of the scutellum largely concolourous with the scutum (Figs 60, 61) (scutellum largely yellow, contrasting with dark scutum in *S. nigrita*; Fig. 59). It resembles strongly *S. melanthysana* but can be differentiated by the following characters: metafemur (Fig. 88) strongly thickened and distinctly concave ventrally (moderately thickened and straight to slight convex ventrally in *S. melanthysana*; Fig. 86); abdomen with mixed short pale and dark pile long lateral margins (Figs 98, 99) (long dark pile in *S. melanthysana*; Fig. 96); long pale pile on sterna, except on sterna IV and V where dark (Fig. 10) (long dark pile on all sterna in *S. melanthysana*; Fig. 6).

Examined material. *Merodon umbrifer* Walker: ***Holotype***, male, “Type” “Holo- // type” “38 // 11. 8 // 292” “HOLOTYPE ♂ of // Merodon // umbrifer Walker // SIERA LEONE // Pres by the Rev. // D.F. Morgan” “merodon // umbrifer. // Wlk.” “NHMUK010369875” [NHMUK].

Other material. (belonging to near *umbrifera*; see Comments). Benin • 1♀; Niaouli; 10 Dec. 2013; K. Jordaens and G. Goergen leg.; KMMA. Central African

Republic • 1♀; Swane de Bébé; 7 Sep. 1970; L. Matile leg.; MNHN. Democratic Republic of the Congo • 1♀; Bamanya; 1–15 Sep. 1963; P. Hulstaert leg.; KMMA • 1♀; Banningville [= Bandundu]; Aug. 1985; A. Fain leg.; KMMA • 1♀; Basankusu; 1949; O.L.V. ten Bunderen leg.; KMMA • 1♂ 1♀; Bokuma; Jul. 1952; P. Lootens leg.; KMMA • 1♂; Eala; Jan. 1935; J. Ghesquière leg.; CNC • 1♂; same collection data as for preceding; 26 Jul. 1935; KBIN • 1♀; same collection data as for preceding; Oct. 1935 • 1♂; same collection data as for preceding; Aug. 1935; KMMA • 2♂♂; Eala, Sep. 1935; KBIN • 1♂; Eala; KMMA • 1♂; Ituri Forest; Jul. 1976; E.B. Babyetagara leg.; CNC • Kavumu to Kabuga road, Kivu; May 1951; H. Bomans leg.; KMMA • 1♀; Kapanga, Lulua; Nov. 1932; F.G. Overlaet leg.; CNC • 1♂; Leopoldville [= Kinshasa]; 1911; Mouchet leg.; KMMA • 1♂ 1♀; Medje; Ituri; Sep. 1910; Lang and Chapin leg.; AMNH • 1♀; same collection data as for preceding; 1–10 Aug. 1910; KMMA • 1♂; same collection data as for preceding; 11–24 Aug. 1910 • 1♂; same collection data as for preceding; 25–30 Aug. 1910 • 1♂; same collection data as for preceding; 26–30 Sep. 1910 • 1♀; same collection data as for preceding; Sep. 1910 • 1♂; Niangara; Nov. 1910; Lang and Chapin leg.; AMNH • 1♂; Poko; Aug. 1913; C.J. Wainwright leg.; NHMUK • 1♀; Rwankwi, N of Lake Kivu; Apr. 1948; J May Leroy leg.; KMMA • 1♀; Shabunda, Lubongola; 1939; Hautmann leg.; KMMA • 1♀; Stanleyville [= Kisangani]; Mar. 1915; Lang and Chapin leg.; AMNH • 2♀♀; same collection data as for preceding; KMMA. Equatorial Guinea • 1♂; Fernando Po [= Bioko Island], Punta Frailes; Oct.–Nov. 1901; L. Fea leg.; MCSNG. Uganda • 1♂; Budongo forest, nr Lake Albert; 1 Apr. 1972; E.B. Babyetagara leg.; CNC • 1♂; Bwindi Impenetrable Forest National Park, Kigezi; 1–10 Jun. 1972; E.B. Babyetagara leg.; CNC; 1♀; Entebbe; 17 Jun. 1972; H. Falke leg.; CNC • 1♀; Entebbe; 1–11 Sep. 1911; S.A. Neave leg.; NHMUK • 1♀; same collection data as for preceding; 12–20 Jan. 1912. • 1♀; Kayonza Forest, Kigezi; May 1972; E.B. Babyetagara leg.; CNC.

Description. Body length: 12.7–17.5 mm (type specimen: 12.7 mm). Wing length: 9.0–12.8 mm (type specimen 9.0 mm).

Male (Figs 9, 10) (based on type of *umbrifera* and non-type material listed above as near *umbrifera*). Head (Figs 40, 41, 44, 45). Eye bare; holoptic, eye contiguity for distance equal to length or 1.5 times length of ocellar triangle, facets dorsally slightly larger, at most twice as large in diameter as ventral ones. Frons black-brown; largely subshiny with black pollinosity in dorsal fifth only, along eye margins narrowly silver-grey pollinose; dispersed short dark pile, dorsally somewhat longer. Face brown to black-brown; subshiny with pale brownish to greyish pollinosity, in parts more densely so, medial part and especially facial tubercle largely devoid of pollinosity; pollinose parts with dispersed long pale pile; facial tubercle strongly pronounced. Gena colour and pollinosity as ventral lateral margins of face; with short to long pale pile. Occiput black-brown, covered with dull grey pollinosity; with dispersed pale pile except dorsally where sometimes darker yellow to black. Antennal segments black-brown, arista orange-brown to brown.

Thorax (Figs 60, 61). Scutum subshiny black, with brownish to brownish grey pollinosity; with short pale pile, usually intermixed with dispersed black pile. Scutellum apical margin weakly rounded, distinctly marginate, three times as wide as long; pale brownish, anterior margin narrowly darker brown; with short pale pile, usually with dark pile on disc (sometimes entirely pale pilose), pilosity along apical margin somewhat longer. Pleura ground colour black-brown, greyish pollinose, anepimeron less so; covered with dispersed long pale pile except on meron, dorsomedial anepimeron, ventral part of katepimeron, anterior part of katepisternum and anterior anepisternum; pilosity on posterior anepisternum more conspicuous.

Legs. Brown to black-brown, sometimes more reddish brown; with short black pile, along posterior margin of pro- and mesofemora with longer pile, sometimes more pale in basal part; along ventral margin of metafemur with longer dark pile, basally with anterodorsal patch of longer pale pile. Metaleg (Fig. 88), femur distinctly thickened and moderately curved, with one distinct ventral swelling in apical fifth, short black pile more dense where swollen; tibia slightly bent at base, thickened and curved, pile along ventral margin in apical half to two-thirds longer and more dense.

Wing (Figs 76, 77). Faint yellowish brown tinge, more pronounced in medial part cell r_1, basal part r_{2+3} and distal part br; towards posterior margin and apex more greyish. Calypters yellow-white to pale brown, with fringe of yellow-white pile. Cell r_1 closed; if petiolate than petiole at most approx. as long as half the height of base of stigma. Vein R_{4+5} sinuate but not appendiculate.

Abdomen (Figs 98, 99). Uniformly subshiny red-brown to black-brown, anterolateral parts of tergum II sometimes less dark; sometimes indistinct black-brown pollinose medial macula along anterior margin of terga II and III; with short dark pile, except tergum 1, and anterolateral parts of tergum II where pale pile; lateral margins usually dark pilose, at most tergum IV partly pale pilose and terga II and III mixed pale and dark pile. Type of *umbrifera* lateral margins completely pale pilose (Fig. 98). Postabdomen conspicuously swollen. Sterna with dispersed long pale pile, on sterna IV and V darker. Male genitalia as in Figs 110–113 (see Comments).

Female (based on material identified as near *umbrifera*). As male except for the following character states. Head (Figs 42, 43), eye dichoptic, facets equal to subequal in size. Frons with black pollinose fascia in dorsal part for length at least equal to ocellar triangle, bordered by very narrow and less dense greyish-brown fascia. Scutellum, dark pile on disc less outspoken, more predominantly paly pilose. Wing, vein R_{4+5} sometimes very short appendiculate. Abdomen with dark pile along lateral margins of all terga.

Distribution. Benin, Central African Republic, Democratic Republic of the Congo, Equatorial Guinea, Sierra Leone, Uganda (but see Comments).

Comments. The type specimen of *S. umbrifera* originates from Sierra Leone. It is in poor condition and the male genitalia were dissected prior to our study; thus, we cannot exclude a mixing of genitalia with another specimen. When comparing the genitalia with some non-type material, some slight differences were observed regarding the shape of the surstyli, the most explicit difference being the shape of the surstyli in lateral view (curved and pointed in the type species (Fig. 111); straight and not pointed in the other material (Fig. 113) and similar to the shape observed in *S. melanthysana*

(Fig. 109). However, no major morphological differences could be observed and except for the differently shaped surstylus the type falls within the observed variability for the characters studied. The only other minor morphological difference observed is that the lateral margin of the abdominal terga of the type is covered with short pale pile while in all other specimens this is black or intermixed black and pale pile. Furthermore, the type is recognized by the entirely pale pile on the scutellum (variable in other specimens); the legs being more red-brown (brown to black-brown in others) and the calypters being yellow-white (yellow-white to pale brown in others). No additional specimens could be obtained from the same region while all non-type male specimens originate from Central Africa (Equatorial Guinea eastwards to Uganda). As the observed differences are very minor, we prefer to take a conservative position by provisionally listing all non-type material under *S. umbrifera* (listed as "*Senaspis* near *umbrifera*"). We consider the morphological differences too minor to warrant describing it as a separate species and propose to await additional material, especially from western Africa before making a formal decision. The only differentiating character (pale pile along lateral margins of abdomen) is, however, incorporated in the identification key. All major structures are also illustrated both for the type specimen and representative non-type specimens.

Senaspis umbrifera resembles *S. melanthysana* in most respect regarding body coloration and pilosity, and wing markings. However, a number of distinct differences could be discerned as pointed out in the key above: the lower calypter has a fringe of pale hairs (dark in *melanthysana*); the abdominal sterna I–III have long pale pile (dark in *melanthysana*), the lateral margins of the abdominal terga have short pale pile along most of their length (long dark pile in *melanthysana*), and the metafemur is strongly thickened and distinctly curved (moderately thickened and straight in *melanthysana*).

Senaspis xanthorrhoea **(Bezzi, 1912)**

Figs 8, 48–51, 62, 78, 89, 100

Protylocera xanthorrhoea Bezzi, 1912: 416.

Differential diagnosis. A species with a distinct medial dark brown macula on the wing (Fig. 78). It can be differentiated from other *Senaspis* species with a distinct wing macula by the coloration of the abdominal terga which is uniformly dark yellow to yellow-orange (Fig. 100) (at least terga I and II completely dark brown in *S. dentipes* (Fig. 91) and *S. haemorrhoa* (Fig. 95)).

Examined material. *Protylocera xanthorrhoea* Bezzi: ***Holotype***, female, "Protylocera // Type // xanthorrhoea // Bezzi." "Holo- // type" "Voi. // 20. VI. to // 21. VII." "B.E. Africa. // C.S. Betton. // 98–12" "Protylocera // xanthorrhoea // n. sp." "NHMUK010369876" [NHMUK].

Other material. Kenya• 1♂ 1♀; Kasigau; Nov. 1938; V.G.L. van Someren leg.; CNC • 1♂ 1♀; Nairobi; 25 Aug. 1951; L.C. Edwards leg.; NHMUK • 2♀♀; same collection data as for preceding; 14. Dec. 1951 • 1♀; same collection data as for preceding; 22 Dec. 1951.

Description. Body length: 12.6–14.3 mm. Wing length: 9.5–10.4 mm. *Male* (Fig. 8). Head (Figs 48, 49). Eye bare; narrowly dichoptic, eyes separated for width equal to 1–2 facets; narrow separation for distance at most equal to length of ocellar triangle; facets dorsally slightly larger, at most twice as large in diameter as ventral ones. Frons black-brown; subshiny, with sparse greyish to greyish brown pollinosity throughout except dorsally of antennal implant; with medium long pale pile. Face black-brown, more reddish brown along buccal cavity; weakly subshiny, with dense greyish to greyish brown pollinosity, only facial tubercle weakly shining black; in parts with dispersed pilosity of long pale pile; facial tubercle strongly pronounced. Gena colour and pollinosity as ventral lateral margins of face; with short to long pale pilosity. Occiput red-brown, covered with dully grey pollinosity; with dispersed pale pile. Antennal segments black-brown, arista pale yellow.

Thorax (Fig. 62). Scutum weakly subshiny black; with dark brown to black pollinosity; with short pale pile; in medial part intermixed with patches of black pile. Scutellum rounded, clearly marginated, slightly more than twice as wide as long; brown, towards posterior margin gradually more yellowish; with short pale pilosity except on disc where black pile, along apical margin longer pile. Pleura ground colour black-brown, sparsely greyish pollinose; covered with dispersed long pale pile except on meron, ventral part of katepimeron, dorsomedial anepimeron, anterior part of katepisternum and anterior anepisternum.

Legs. Reddish brown to orange-brown; with short pale pilosity, along posterior margin of pro- and mesofemora, and dorsal and ventral margin of metafemur with longer pale pile. Metaleg (Fig. 89), femur moderately thickened, with distinct ventral swelling in apical fifth, a second less developed thickening proximal of this, with strong dark setae where swollen; tibia thickened and slightly curved, pile along ventral margin more dense and dark.

Wing (Fig. 78). Largely hyaline, with very faint yellowish brown tinge especially along veins; with distinct dark brown macula running from anterior margin and covering most of stigma, parts of cell r_1 and r_{2+3}, distal part of cell br and basal part of r_{4+5}, decreasing in colour on anterior part of cell dm. Calypters yellow-white; with fringe of yellow-white pile. Cell r_1 closed, petiole variable in length, usually shorter than height of base of stigma. Vein R_{4+5} sinuate, not appendiculate or, at most, with trace of appendix.

Abdomen (as in Fig. 100). Uniformly subshiny dark yellow to yellow-orange, except tergum I and anterior margin of tergum II where darker, in medial part of tergum II dark area extending to halfway tergum; with short pale pilosity, except medially in posterior half of terga II and III where dark pile. Sterna yellow-orange; with long pale pilosity. Male genitalia not dissected.

Female. As male except for the following character states: Eye distinctly dichoptic (Figs 50, 51), facets equal to subequal in size. Frons subshiny black to black-brown, dorsally more red-brown; with greyish brown pollinosity dorsally, more greyish pollinose ventrally. Wing medial macula more extensive with dark streak along posterior half of cell bm and basal part of cell cua_1. Abdomen (Fig. 100), dark area in medial part of tergum II sometimes less extensive.

Distribution. Kenya.

Incertae sedis

Senaspis pennata (Hervé-Bazin, 1914)

Figs 11, 46, 47, 63, 79, 90, 101

Protylocera pennata Hervé-Bazin, 1914: 288.

Differential diagnosis. Different from all other *Senaspis* species by the head in lateral view without distinct protuding frons (Fig. 47); the unmarginated scutellum (Fig. 63), and the completely hyaline wing, with a distinctly open cell r_1 (Fig. 79).

Examined material. *Protylocera pennata* Hervé-Bazin: ***Holotype***, female, "HOLOTYPUS" "MUSÉE DU CONGO // Kalengwe 16.X.1911 // Dr. Bequaert leg.;" "R. DÉT. // M // 69" "Protylocera // pennata // Hervé-B. ♀ // Type" "RMCA ENT // 000016792" [KMMA].

Description. Body length: 15.0 mm. Wing length: 12.2 mm.

Female (Fig. 11). Head (Figs 46, 47). Eye bare; dichoptic, facets equal in size. Frons largely subshiny black-brown in ventral protruding part; dorsally with black pollinosity in front of ocellar triangle for length equal to ocellar triangle, between subshiny and black pollinose part with more dispersed greyish pollinosity continued ventrally narrowly along eye margin; dispersed short dark pile, except for area with greyish pollinosity where pile is pale. Face subshiny brown; with greyish pollinosity, medial part and ventral lateral margins largely devoid of pollinosity; in parts with dispersed long pale pile; facial tubercle weakly pronounced. Gena as pollinose part of face; with short to long pale pilosity. Occiput black-brown, covered with dully grey pollinosity; with dispersed pale pile except dorsally where black. Antennal segments black-brown, arista pale yellow.

Thorax (Fig. 63). Scutum subshiny black, with brownish to brownish grey pollinosity; with short pale brown pile, along lateral margins intermixed with dispersed black pile, pilosity paler posteriorly, pilosity modereately long especially along margins. Scutellum rounded and not marginated, slightly more than twice as wide as long; pale brownish; with pale pilosity except anteriorly on disc where largely orange-brown pile (pile rubbed off in medial part); pilosity moderately long especially along apical margin; Pleura ground colour black-brown, covered with dispersed long pale pile except on meron, dorsomedial anepimeron, anterior part of katepisternum and anterior anepisternum (katepimeron obscured and absence or presence of pilosity not visible).

Legs. Brown to black-brown, pro- and mesofemora more orange-brown posteriorly, tarsal segments yellowish except major part of metabasotarsomere; with short black pilosity, along posterior margin of pro- and mesofemora with longer pale pile, tarsal segments, except major part of metabasotarsomere, with short pale pile; pro- and mesotibiae very dense. Metaleg (Fig. 90), femur moderately thickened, with ventral swelling in apical fifth; tibia thickened and curved, pile on ventral and dorsal margins along entire length, at least as long as width of tibia, and very dense.

Wing (Fig. 79). Completely hyaline. Calypters yellow-white with fringe of yellow-white pile. Cell r_1 distinctly open; vein R_{4+5} sinuate but not appendiculate.

Abdomen (Fig. 101). Subshiny brown to black-brown, weak brownish pollinose; tergum I more yellowish brown; tergum II anterior margin narrowly black, medial anterior half yellowish brown, laterally more extensively so, gradually darkening posteriorly; tergum III with pair of orange-brown fasciae in anterior two-fifths; with short pale pilosity, except tergum V and posterior margin of tergum IV where black pile.

Male. Unknown.

Distribution. Democratic Republic of the Congo.

Comments. The position of this species within the genus *Senaspis* is uncertain. While there are some similarities with other *Senaspis* species (maculate eyes, wing venation except cell r_1 distinctly open, pilosity on metatibia), there are also some distinct differences. For instance, the shape of the head in lateral view (no strongly protruding frons, facial tubercle poorly developed, face extending more ventrally), the scutellum is unmargined, the completely hyaline wing, and the distinctly open cell r_1. As the available material is limited to a single female specimen, we await additional material and/or further revision of other eristaline representatives from the Afrotropical region before proposing any generic assignment.

Discussion

The revised genus *Senaspis* now contains ten valid species, i.e., *S. dentipes* (Macquart), *S. dibapha* (Walker), *S. elliotii* Austen, *S. flaviceps* Macquart, *S. haemorrhoa* (Gerstaecker), *S. nigrita* (Bigot), *S. pennata* (Hervé-Bazin), *S. melanthysana* (Speiser), *S. umbrifera* (Walker), and *S. xanthorrhoea* (Bezzi). We herewith place the following species in synonymy: *Senaspis apophysata* (Bezzi) as junior synonym of *S. flaviceps* Macquart, *S. livida* (Bezzi) as junior synonym of *S. dentipes* (Macquart), *S. nigripennis* (Macquart) as junior synonym of *S. dibapha* (Walker), and *S. griseifacies* (Bezzi) as junior synonym of *S. haemorrhoa* (Gerstaecker). The generic characters, as given above in the generic diagnosis, are representative for all species. However, the closed and petiolate cell r_1 is a variable character with sometimes the petiole missing (see for example *S. dentipes*) or even slightly open (*S. elliotii*). The latter is also the case for *S. pennata*. This species shows a number of morphological differences (see comments listed under the species treatment) with the other species within the genus that makes its placement within this genus uncertain. *Senaspis flaviceps* also is slightly aberrant compared to the other *Senaspis* species: bare katepimeron (pilose in others), presence of a basoventral tubercle in the male metafemur (absent in all others), longer petiole (at least as long as height of base of stigma; shorter in all others) and the larger body size (more than 17 mm; shorter in all others). As *S. flaviceps* is the type species for the genus *Senaspis*, Thompson (pers. comm.) suggested that the generic concept of *Senaspis* should be restricted to *S. flaviceps* and all other taxa placed in a separate genus distinct from *Senaspis*. The available name *Triatylosus* (established as subgenus of *Senaspis* by Hull (1949) with *Xylota dibaphus* Walker as type species) has been proposed to be raised to genus rank and to include all *Senaspis* species except *S. flaviceps*. We, however, propose to wait for more taxonomic revisions for other Afrotropical eristaline groups to have a better understanding of their morphology and their phylogenetic relationships can be ascertained before making changes at generic level.

Besides the position of *S. flaviceps*, no distinct morphological clusters can be recognized among the remaining species although some taxa show morphological similarities. Some *Senaspis* species have a distinct wing marking with a well demarcated dark macula in the medial part (Figs 64, 73, 78). Within this group *S. haemorrhoa* and *S. xanthorrhoea* are similar in appearance with pale pilosity on face and frons (Figs 28–31, 48–51), partial to completely reddish pilosity and coloration of the abdomen (Figs 95, 100), and relatively broadened metafemur with ventrally two subapical swellings (Figs 85, 89). *Senaspis nigrita* shares the latter characteristic with these two taxa (Fig. 87) while the wing marking is similar but with the medial wing marking less pronounced and demarcated (Fig. 75). Also, the male genitalia are similar with the surstyli, in dorsal view, bearing an inner row of stronger setae in the dorsal third (Figs 106, 107). The NJ and ML analysis (Fig. 114) tentatively suggest that *S. haemorrhoa* and *S. nigrita* are sister species (no genetic markers could be obtained for *S. xanthorrhoea*). *Senaspis dentipes* has identical wing markings to *S. haemorrhoa* and *S. xanthorrhoea* but is otherwise morphologically very distinct from both, including differences in male genital structures.

Senaspis melanthysana and *S. umbrifera* are also morphologically very similar to each other. Both species have a very similar appearance and a considerable number of specimens were misidentified in either way. Both have the wing markings more diffused with a general darkish tinge slightly more pronounced in the medial part (Figs 74, 76, 77). The general habitus is very dark, with the dorsal part of the thorax covered by a dense short and predominantly pale pile (Figs 6, 9, 10) continuing on the pleura. Morphological differences between both species are listed above in the taxonomic treatment of the taxa. *Senaspis elliotii* shows some similarities in general appearance (Fig. 3) but is clearly distinct by the dense white to yellow pile on the dorsal part of the thorax, contrasting with the black pile on the pleura, and by the wing coloration which is predominantly dark, except along the posterior margin and at the apex (Fig. 68). Its relationship with the other taxa is unclear.

Senaspis dibapha does not show any morphological similarities with any of the other taxa within *Senaspis*. The general reddish appearance, morphological character states of additional facial tubercles laterally from the medial one (Figs 16, 18), and the slender metafemur (Fig. 81) are unique. The wing (Fig. 65) is largely darkened, except for the posterior margin, and somewhat similar to *S. elliotii* (Fig. 68).

All seven *Senaspis* species for which we obtained DNA barcodes are grouped as such in the NJ topology (Suppl. material 1: Fig. S1; Fig. 114) with a mean interspecific p-distance of 0.075 (range: 0.052–0.130), largely exceeding the mean intraspecific p-distance of 0.0037 (range: 0.002–0.005). The phylogenetic affinities among the species of this genus will be treated elsewhere (Mullens et al. unpublished).

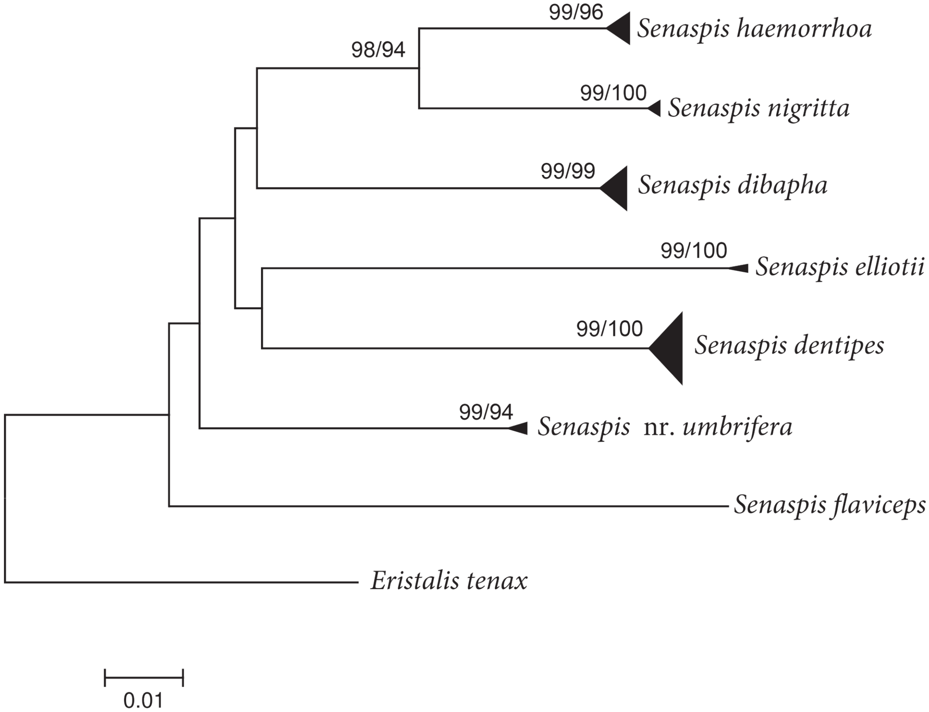


Figure 114. Neighbor-Joining (NJ) and Maximum Likelihood (ML) topology of seven *Senaspis* species and with *Eristalis tenax* as outgroup. Bootstrap values ≥ 70% are presented at the nodes as (NJ/ML).

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Supplementary material 1

Figure S1

Authors: Marc De Meyer, Georg Goergen, Kurt Jordaens

Data type: Neighbor-Joining tree

Explanation note: Neighbor-Joining tree (K2P) of 64 DNA barcodes of seven Afrotropical *Senaspis* species. *Eristalis tenax* was used as outgroup.

Link: https://doi.org/10.3897/zookeys.1003.56557.suppl1

Supplementary material 2

Table S1. Syrphidae collection

Authors: Marc De Meyer, Georg Goergen, Kurt Jordaens

Data type: list of specimens

Explanation note: List of specimens used for Neighbor-Joining tree (K2P) of Figure S1.

Link: https://doi.org/10.3897/zookeys.1003.56557.suppl2