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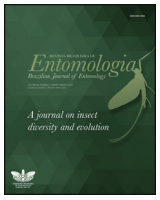

On the identities of Neotropical *Stegana* species (Diptera, Drosophilidae). II. *Stegana acutangula* (Hendel) and *Stegana triseta* (Duda), with descriptions of three new closely related species

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ABSTRACT

Stegana (*Orthostegana*) *acutangula* (Hendel) from Bolivia and *Stegana* (*Steganina*) *triseta* (Duda) from Costa Rica are redescribed based on type specimens, and their identities clarified. A single syntype male of the first species (type species of the subgenus *Orthostegana*) is designated as a lectotype and one male out of the four Costa Rican syntypes (3 males, 1 female) of the latter species was selected as a lectotype of the *Steganina subgenus*. The other three (2 males, 1 female) specimens were designated as paralectotypes. All four males were dissected and their terminalia were photomicrographed. The two male *Stegana triseta* paralectotypes proved to belong to two unknown species closely related to *Stegana acutangula*, described here as *Stegana dudai* sp. nov. and *Stegana turrialba* sp. nov., and another male specimen, collected at Parque Nacional Yasuní, provinces of Napo/Orellana, Ecuador, is described as *Stegana yasuni* sp. nov. Additionally, we have included photomicrographs of the habitus of the type specimens as well as of some nontype specimens from Peru and Costa Rica. Based on the descriptions herein we not only clarified the status of these five species but also propose including all of them in the subgenus *Orthostegana*.

Introduction

During our study of the type material of *Stegana* (*Orthostegana*) *acutangula* (Hendel) and *Stegana* (*Steganina*) *triseta* (Duda), as well as other undetermined specimens of Neotropical *Stegana*, we identified five sibling species among them. In general, the overall morphology of these specimens was not entirely different from the majority of species of the *Stegana* subgenus *Steganina* Wheeler. However, all five of the species described/redescribed here share some special characteristics, especially regarding wing patterns and the complex male terminalia, including the possible presence of a completely membranous and mostly amorphous aedeagus. In our opinion, all of these species are best included in the subgenus *Orthostegana* Hendel .

This is the second of a series of papers that are intended to clarify the identities of species belonging to the Neotropical *Stegana* (Vilela and Bächli, 2020).

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Material and methods

The redescriptions of two species of *Stegana*, one described by Hendel and another by Duda, are based on type specimens on loan from the Naturhistorisches Museum Vienna (NMW), the Hungarian Natural History Museum, Budapest (HNHM), the Zoological Museum Berlin, Germany (ZMB) [now known as the Museum für Naturkunde, Leibniz-Institut], and on undetermined *Stegana* spp. on loan from the Smithsonian Institution, National Museum of Natural History, Washington D.C. (USNM). In addition, specimens are included from the former "Staatliches Museum für Tierkunde Dresden", now Senckenberg collection, Dresden (SMT) as well as from the collection of Michael von Tschirnhaus, housed as a gift in the Drosophilidae collection of the Zoological Museum at the University of Zurich (ZMUZ).

Label data attached to each type specimen are cited in full with a slash [/] indicating a line change and a double slash [//], indicating a label change. Our notes and/or interpretations are included within brackets throughout the text. Specimens loaned from USNM (USNMENT) bear a white label with a QR code printed on the backside.

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The habitus of each specimen was photomicrographed with the rear camera of a Samsung Galaxy S8 smartphone, which was attached to the right eyepiece of a Wild M3 stereomicroscope through a magnetic plate of a clothespin-shaped plastic adapter, as previously shown (Vilela and Bächli, 2020). Objective lenses of 1.6×, and 4× were used, and the camera was set to default or optically zoomed to 2×, 3×, or 4× with the autofocus mode disabled. A series of pictures were taken at consecutively increasing depths of focus for each selected view. The image series were mostly stacked using the "All Methods" algorithm of the open-source software CombineZP (Hadley, 2010), yielding an in focus (Vilela and Prieto, 2018, Vilela and Bächli, 2019, 2020).

Microscope slides preparations were done according to Wheeler and Kambysellis (1966) and Kaneshiro (1969). The abdominal sclerites, including the disarticulated male terminalia, were preserved in glass microvials filled with glycerin and attached by a stopper to the pin of the respective specimen. Further details can also be found in Vilela and Bächli (2000) and Bächli et al. (2004).

Male terminalia were photomicrographed with the same smartphone attached to a Zeiss compound microscope using objective lens of 10×, 16×, 20×, and 25×. The camera was set to default or optically zoomed to 2× and the autofocus mode was disabled. The composite photomicrographs images taken with either the stereomicroscope or compound microscope were edited with Adobe Photoshop Elements software. Unless otherwise indicated, all of the photomicrographs on the same plate were taken and enlarged to the same magnification.

For morphological terminology, measurements and indices see Vilela and Bächli (1990, 2000) and Bächli et al. (2004).

Results and discussion

Stegana Meigen, 1830

Stegana Meigen, 1830: 79 (description).

Type species: *Stegana nigra* Meigen, 1830: 79 (= *Musca furta* Linnaeus, 1767: 991) (des. Zetterstedt, 1847: 2577).

Diagnosis. As proposed by Bächli et al. 2004: 78, but with the following modifications: inner paraphysis absent or present, outer paraphysis greatly reduced (as in all European and Nearctic species), or extremely developed (as in some Neotropical species that are devoid of a sclerotized aedeagus).

Stegana (*Orthostegana*) Hendel, 1913

Orthostegana Hendel, 1913: 631 (description); Duda, 1924: 182 (key); Duda, 1927: 14 (key), 23ff. (description, status); Brues and Melander, 1932: 345 (key).

Stegana (Orthostegana) Hendel: Sturtevant, 1921: 56 (status); Okada, 1971: 89 (status), Wheeler, 1981: 30 (status); Bock, 1982: 28 (status); Sidorenko, 1998: 285 (status); Brake and Bächli, 2008: 293 (affiliation); Zhang et al., 2012: 361ff. (revision); Li et al., 2013: 414 (phylogeny).

Type species: *Orthostegana acutangula* Hendel, 1913 (monotypic).

Diagnosis (modified from Zhang et al., 2012).

Head setae generally thick and long, postocellar setae minute and short. Interfrontals numerous, large. Eye main axis almost vertical. Pleura with or without one upper longitudinal stripe. Tibia of middle leg basally with a posterodorsal row of 3–5 strong, erect setae, followed downwards with a row of posterodorsal smaller setae (see Figs. 2A–D in Zhang et al., 2012). Wings (see Figs. 1C–E in Zhang et al., 2012): generally dark brown, especially along the costa, almost transparent in basal 1/4 and cell m-IV, outside the posterior crossvein a roundish, fully hyaline window may be present; vein R_{2+3} almost straight, slightly curved upwards just before terminating in vein C (obviously referred by the name *Orthostegana*); vein R_{4+5} almost straight in apical half; vein M softly and more or less continuously curved upwards to vein R_{4+5}; costal section IV weak and relatively short, acrocostal (ac) index large (about 8–17 in the nine available descriptions); hb index (describing the length of the costal fringe in costal section III) large, up to 1.00. Abdominal tergites usually dark brown to black except for tergite 1+2, yellowish-brown, and basal and lateral areas paler. Outer paraphysis remarkably developed (embracing gonopore) probably acting as the surrogate intromittent sclerite together with the complex dorsal arch. Inner paraphysis proximally articulated or even fused to posterolateral region of aedeagal apodeme and distally articulated to a complex "dorsal arch". Aedeagus appears absent or, if present, could be represented by a completely membranous, amorphous or condom-shaped component.

Stegana (*Orthostegana*) *acutangula* (Hendel, 1913)
(Figs. 1-16)

Orthostegana acutangula Hendel, 1913: 632 (description, type material, distribution). Malloch, 1924a: 100 (key); Duda, 1924: 182 (key); Duda, 1927: 14, 234ff (description, distribution, key); Wheeler and Takada, 1971: 229 (description, distribution).

Stegana (*Orthostegana*) *acutangula* (Hendel): Malloch, 1924b: 6 (description, distribution); Wheeler, 1960: 110 (description, figures); Wheeler, 1981: 30 (affiliation); Grimaldi, 1990: 16ff. (description, figures, phylogeny); Chen and Wang, 2004: 29 (affiliation); Brake and Bächli, 2008: 293 (affiliation, distribution).

Stegana acutangula (Hendel): Sturtevant, 1921: 114, 133 (affiliation); Wheeler, 1970: 79.6 (distribution); Val et al., 1981: 135 (affiliation); Bächli, 1988: 132 (type material, distribution); Tidon and Almeida, 2016: 739 (distribution).

Type locality. Bolivia, La Paz, Mapiri, Sarampioni 700 m altitude.

Diagnosis.

In general, relatively large, yellowish flies; head setae long and strong; in male front narrower than female, covered with many rather long, unordered interfrontals; pleuron slightly darkened along the upper margin, never with a distinct dark longitudinal stripe; tibia of the middle leg with a row of posterodorsal setae of which uppermost two to four are erect and distinctly prolonged; male abdominal tergites with strong marginal setae which are only present laterally in females; wing transparent in basal fourth, blackish-brown in apical 3/4, becoming somewhat more pale towards hind margin, veins M-III and Cu, as well as posterior crossvein dark, shadowed, remarkably roundish, transparent window in cell m-IV is visible by the naked eye, vein M-IV curved

Figure 1 *Stegana acutangula* (Hendel, 1913), labels of male lectotype #313. For additional labels see "Material examined".

Figure 2 *Stegana acutangula* (Hendel, 1913), male lectotype #313, Sarampioni 700 m, Mapiri, La Paz, Bolivia [NMW], habitus, four views. a) left lateral, b) left oblique dorsal, c) head, thorax and wings dorsal, d) abdomen dorsal. Scale bar = 1 mm.

upwards in apical 1/3, costal section III with 6–9 warts below, vein R_{2+3} almost straight, especially towards the end of the vein C. Cercus dorsally narrow, densely setose, not microtrichose; ventral lobe wide, flattened, medially pointed sharply outwards, distally finger-shaped and curved inwards, bearing a single, long, very thin seta, not microtrichose, not fused to epandrium. Decasternum two-armed, medioventrally keeled. Dorsal arch (connecting decasternum, distal region of hypandrial arms and inner paraphyses) complex, two-sectioned. Aedeagus appears absent or, if present, could be represented by a completely membranous, amorphous component. Inner paraphysis laterally flattened. Outer paraphysis long, rectangle-shaped, bent, laterally flattened; distal margin remarkably serrate bearing ca. 9 similar teeth.

Material examined.

Lectotype male (#313) (by present designation) [dissected] (Fig. 1): "Bolivia-Mapiri / Sarampioni 700m [altitude] // *Orthostegana* / *acutangula* H. [both handwritten] / det. Hendel // SYNTYPUS / *Orthostegana* / *acutangula* H. [both handwritten] G. Bächli det.1985 // TYPUS [red label] // microvial // ♂ // 313 [our unique internal number] || LECTOTYPE [red label] // LECTOTYPE / *Stegana* / *acutangula* Hendel / Vilela & Bächli des." (NMW).

Nontype specimens (18 ♂♂, 15 ♀♀, all from Peru)

2 ♂♂, "Peru. Madre de Dios: / Manu, Erika (near / Salvacion), 550m [altitude], 5-6 / Sept. 1988, AFreidberg // USNMENT // 60 [or 61] [our unique internal numbers] // ♂ [symbol] // Stegana / (Orthostegana) / acutangula (Hendel) / Vilela & Bächli det." (USNM).

2 ♂♂, "Peru. Madre de Dios: / Manu, Rio Manu, 250 m [altitude], / Pakitza, 12º7'S, 70º / 58'W, 9-23 Sep 1988 / Amnon Freidberg // USNMENT // 62 [or 63] [our unique internal numbers] // ♂ [symbol] // Stegana / (Orthostegana) / acutangula (Hendel) / Vilela & Bächli det." (USNM).

1 ♂ [dissected], "Peru. Madre de Dios: / Manu, Erika (near / Salvacion), 550m [altitude], 5-6 / Sept. 1988, AFreidberg // USNMENT / 01372923 [unique number] // 64 [our unique internal number] // ♂ [symbol] // microvial // Stegana / (Orthostegana) / acutangula (Hendel) / Vilela & Bächli det." (USNM).

2 ♂♂, "Peru. Madre de Dios: / Manu, Rio Manu, 250 m [altitude], / Pakitza, 12º7'S, 70º / 58'W, 9-23 Sep 1988 / Amnon Freidberg // USNMENT // 65 [or 66] [our unique internal numbers] // ♂ [symbol] // Stegana / (Orthostegana) / acutangula (Hendel) / Vilela & Bächli det." (USNM).

1 ♂ [dissected], "Peru. Madre de Dios: / Manu, Erika (near / Salvacion), 550m [altitude], 5-6 / Sept. 1988, AFreidberg // USNMENT / 01372923 [unique number] // 67 [our unique internal number] // ♂ [symbol] // microvial // Stegana / (Orthostegana) / acutangula (Hendel) / Vilela & Bächli det." (USNM).

7 ♂♂, "Peru. Madre de Dios: / Manu, Rio Manu, 250 m [altitude], / Pakitza, 12º7'S, 70º / 58'W, 9-23 Sep 1988 / Amnon Freidberg // USNMENT // 68 [–74] [our unique internal numbers] // ♂ [symbol] // Stegana / (Orthostegana) / acutangula (Hendel) / Vilela & Bächli det." (USNM).

1 ♂, "Peru. Madre de Dios: / Manu, Erika (near / Salvacion), 550m [altitude], 5-6 / Sept. 1988, AFreidberg // USNMENT / 01372911 [unique

number] // 124 [our unique internal number] // ♂ [symbol] // Stegana / (Orthostegana) / acutangula (Hendel) / Vilela & Bächli det.“ (USNM).

2 ♂♂, “Peru, Panguana / 9º37’S/74º56’W / 2.ix.-20.x.1981 / Tschirnhaus leg. // X256 / Rio Llulapichis / Prov. Huànaco / roof of tent // 260 [or 261] [our unique internal numbers] // ♂ [symbol] // Stegana / (Orthostegana) / acutangula (Hendel) / Vilela & Bächli det.“ (ZMUZ).

6 ♀♀ [one dissected], “Peru. Madre de Dios: / Manu, Erika (near / Salvacion), 550m [altitude], 5-6 / Sept. 1988, AFreidberg // USNMENT // 75 [–80, 77 dissected] [our unique internal numbers] // ♀ [symbol] // Stegana / (Orthostegana) / acutangula (Hendel) / Vilela & Bächli det.“ (USNM).

2 ♀♀, “Peru. Madre de Dios: / Manu, Erika (near / Salvacion), 550m [altitude], 5-6 / Sept. 1988, AFreidberg // USNMENT // 81 [or 82] [our unique internal numbers] // ♀ [symbol] // Stegana / (Orthostegana) / acutangula (Hendel) / Vilela & Bächli det.“ (USNM).

1 ♀, “Peru. Madre de Dios: / Manu, Erika (near / Salvacion), 550m [altitude], 5-6 / Sept. 1988, AFreidberg // USNMENT / 01372902 [unique number] // 83 [our unique internal number] // ♀ [symbol] // Stegana / (Orthostegana) / acutangula (Hendel) / Vilela & Bächli det.“ (USNM).

3 ♀♀, “Peru. Madre de Dios: / Manu, Erika (near / Salvacion), 550m [altitude], 5-6 / Sept. 1988, AFreidberg // USNMENT // 84 [-86] [our unique internal numbers] // ♀ [symbol] // Stegana / (Orthostegana) / acutangula (Hendel) / Vilela & Bächli det.“ (USNM).

2 ♀♀, “Peru. Madre de Dios: / Manu, Erika (near / Salvacion), 550m [altitude], 5-6 / Sept. 1988, AFreidberg // USNMENT // 89 [or 90] [our unique internal numbers] // ♀ [symbol] // Stegana / (Orthostegana) / acutangula (Hendel) / Vilela & Bächli det.“ (USNM).

1 ♀, “Peru / Pinipini / O.Garlepp // Coll. W. Schnuse // Orthostegana / acutangula [both handwritten] / det. Hendel // 114 // 186 [our unique internal number] // ♀ [symbol] // Stegana / (Orthostegana) / acutangula (Hendel) / Vilela & Bächli det.” (SMT).

Note.

Hendel mentioned two female specimens housed in the “Staatliches Museum für Tierkunde”, Dresden. However, according to Bächli (1988), a syntype is also stored in the Natural History Museum, Vienna (NMW). We have analyzed the latter syntype from the NMW that, fortunately, turned out to be a male. In the event additional syntype specimens are identified, we have decided to designate this NMW specimen as a lectotype. Among the type series of *S. triseta*, we identified two (1 ♂, 1 ♀) *S. acutangula* specimens. Although only two males (#64, #67) and one female (#77), out of the 33 Peruvian nontype specimens mentioned above, were dissected, all of the males share the general characteristics; therefore, the 15 females were also included. Even considering that females of *Stegana* species usually are not identifiable, we have assumed that all of them belong to *Stegana acutangula*.

Description.

♂. (n = 19) [#60 - #74, #124, #260, #261, #313LT] (Figs. 2-6, 8-12). Body length about 3.5 mm.

Figure 3 *Stegana acutangula* (Hendel, 1913), male lectotype #313, Sarampioni 700 m, Mapiri, La Paz, Bolivia [NMW], close-ups, three head views, one of the scutellum: a) frontal, b) dorsal, c) left oblique dorsal, d) prescutellars and scutellum dorsal. Scale bar = 0.5 mm.

Figure 4 *Stegana acutangula* (Hendel, 1913), male lectotype #313, Sarampioni 700 m, Mapiri, La Paz, Bolivia [NMW], mid tibia (a) plus tarsomeres (b, c) and tergites 6, 7 plus external terminalia (d) close-ups: a) left leg dorsal, b) left leg lateral, c) right leg dorsal, d) right oblique posterior. Images in c and d were acquired at the same magnification. Scale bars = 0.5 mm.

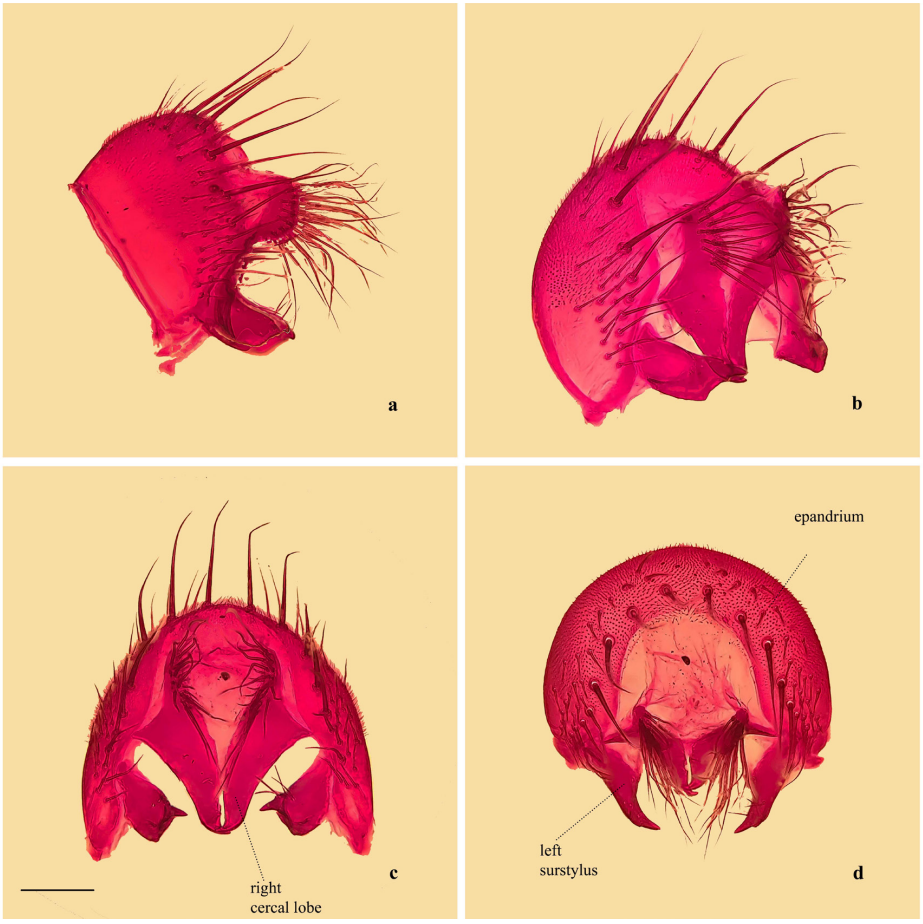

Figure 5 *Stegana acutangula* (Hendel, 1913), male lectotype #313, Sarampioni 700 m, Mapiri, La Paz, Bolivia [NMW], external terminalia, four views: a) left lateral, b) left oblique posterior, c) ventroposterior, d) dorsoposterior. Scale bar = 0.1 mm.

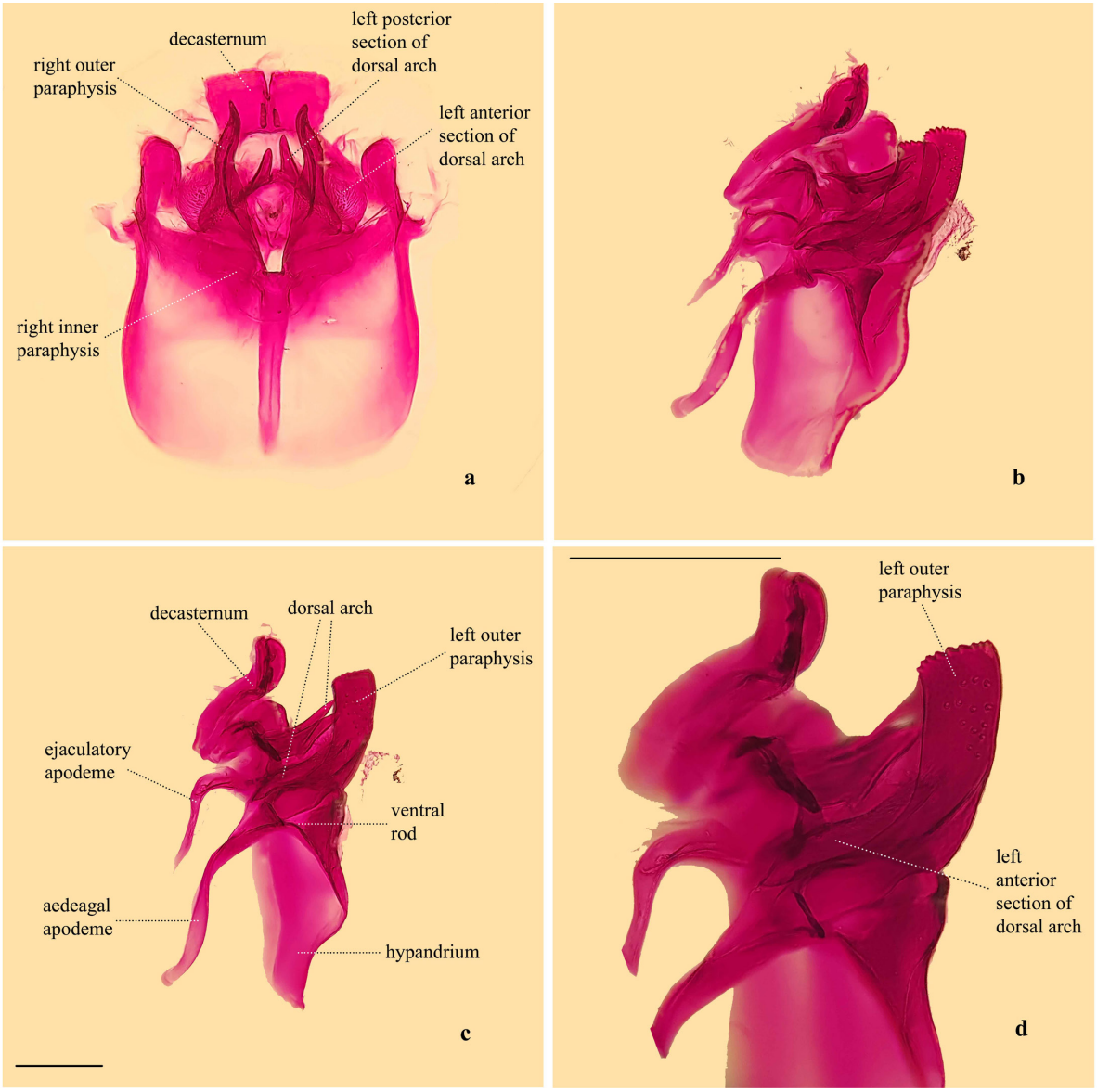

Figure 6 *Stegana acutangula* (Hendel, 1913), male lectotype #313, Sarampioni 700 m, Mapiri, La Paz, Bolivia [NMW], internal terminalia, four views: a) anterior, b) left oblique dorsal, c) left lateral, d) left lateral (close up). Images in a-c and d were acquired at different magnifications. Scale bars = 0.1 mm.

Head (Figs. 3a-c, 9) generally yellowish; all head setae strong, black, but postocellars short, fine. Front narrow, variably yellowish to brownish, usually becoming darker brownish downwards, covered with about 40 distinct interfrontals. Frontal length 0.55 (0.47–0.61) mm. Frontal index about 1.81 (1.61–2.19), top to bottom width ratio about 1.52 (1.37–1.75). Frontal triangle a bit prolonged, black, about 35% of frontal length; ocellar triangle indistinct, about half frontal length. Orbital plates narrow, in apical third slightly diverging from eye margin, about 70% of frontal length. Orbital setae almost in a row, distance of or3 to or2 about 30% of or3 to or1, distance of or2 to or1 about 70% of or3 to or1, distance of or3 to or1 about 125% of or3 to vtm, or1/or3 ratio about 0.90 (0.79–0.97), or2/or1 ratio about 0.79 (0.64–0.96), 2 fine setae outside the orb row; vt index about 1.01 (0.94–1.14), postocellar setae fine, apically crossed, about 30% (16–37%) of frontal length; ocellar setae about 93% (84–107%) of frontal length. Face whitish. Carina short, narrow, flat. Vibrissal index 0.33 (0.25–0.40). Cheek yellowish, index about 23 (17-28). Eye roundish, with main axis almost vertical, index = 1.18 (1.12–1.25), postoculars in a single row. Antenna yellow, Flagellomere 1 index about 1.94 (1.67–2.14). Arista with 5–9 long dorsal, 5–9 long ventral and 5–7 short inner branches, plus short terminal fork. Proboscis and palpus yellow.

Thorax (Figs. 2b-c, 8b-d) length about 2.04 (1.93–2.08) mm. Scutum slightly flattened, brownish, laterally slightly paler; 12, rarely 14 rows of acrostichal setae; 2 (3) postpronotals, h index about 0.69 (0.58–0.77). Transverse distance of dorsocentral setae about 490% of longitudinal distance; dc index about 0.40 (0.24–0.50). Scutellum slightly prolonged, brownish, laterally and apically somewhat more pale, margin rather sharp; distance between apical scutellars about 75% of that of the apical to the basal one; basal ones divergent; scut index about 1.25 (1.15–1.39). Pleura brownish-yellow, slightly darkened along upper margin, but never with a distinct dark longitudinal stripe. Sterno index about 0.93 (0.63–1.11). Halter yellow. Legs yellow, fore femur with 4 strong antero-ventrals and 2–3 weaker postero-ventrals, tarsal joint 1 shorter than joints 2–5 together; middle tibia with an antero-dorsal row of setulae, the uppermost 3 (rarely 4) distinctly prolonged (Figs. 4a, 10c-d); middle tarsus with two rows of strong, cuneiform setulae below, tarsomere 1 about as long as tarsomeres 2–5 together.

Figure 7 *Stegana acutangula* (Hendel, 1913), labels of a male nontype specimen #67, Rio Manu, Madre de Dios, Peru, 250 m [USNM]. For additional labels see "Material Examined".

Wing (Figs. 2c, 8c) in basal 1/4 hyaline, apical 3/4 blackish-brown, becoming somewhat more pale towards hind margin, veins M-III and Cu; posterior crossvein darkened; a kind of roundish window is visible with the naked eye in cell m-IV; vein R_{2+3} almost straight, also at the very end; vein M-IV distinctly curved upwards in apical half, costal section III with 6–9 warts below; in many specimens, in particular those from Peru, the "heavy bristles" fringe do not abruptly stop but seems to become shorter and less visible towards the wing tip. Wing length = 3.37 (3.11–3.78) mm, length to width ratio about 2.18 (2.07–2.34). Indices: C = 2.69 (2.43–3.17), ac = 6 (3–8), hb = 0.96 (0.86–1.00), 4C = 0.77 (0.67–0.85), 4v = 1.51 (1.33–1.65), 5x = 0.89 (0.67–1.10), M = 0.39 (0.33–0.46), prox. X = 0.50 (0.38–0.62).

Abdomen (Figs. 2a,d, 8a,d, 10c) generally blackish-brown, tergite 1+2 yellowish, but laterally and apically more or less darkened. All tergites with strong, long marginal setae, which are more evident in tergite 6 (a conspicuous sexual dimorphism).

Terminalia ♂ (Figs. 5, 6, 11, 12), based on *Stegana acutangula* lectotype #313 (Bolivia, Mapiri), Wien, and two nontype specimens #64 and #67 of *Stegana acutangula* (Peru, Madre de Dios, Manu). Epandrium (Figs. 5, 11)

Figure 8 *Stegana acutangula* (Hendel, 1913), male nontype specimen #67, Rio Manu, Madre de Dios, Peru, 250 m [USNM], habitus, four views: a) left lateral, b) left oblique dorsal, c) head, thorax and wings dorsal, d) abdomen in focus dorsal. Scale bar = 1 mm.

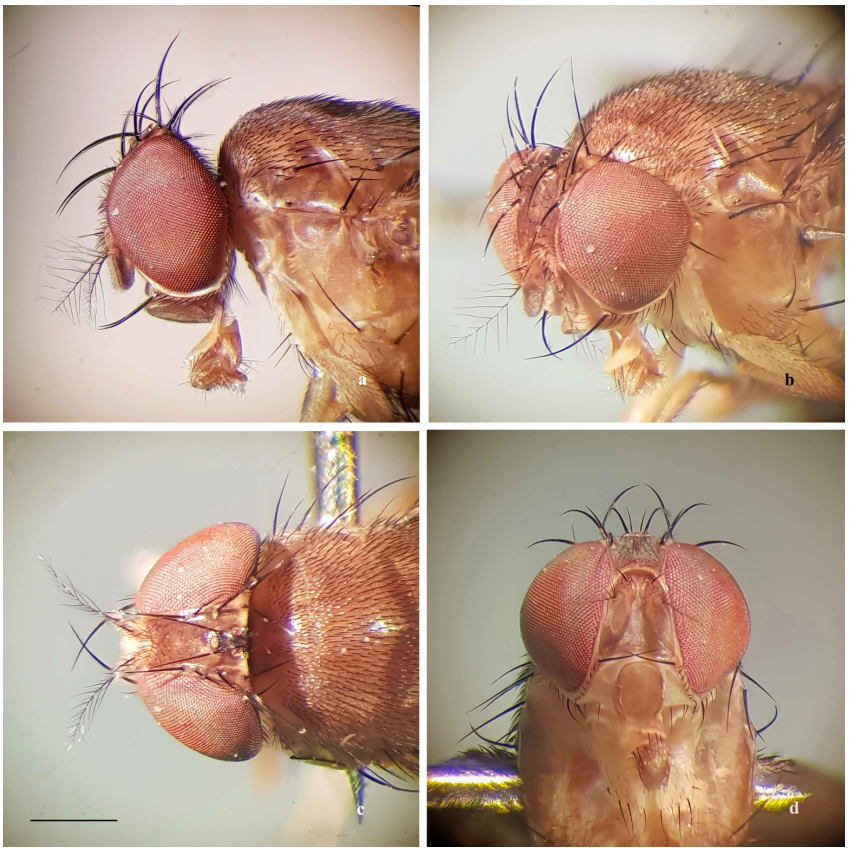

Figure 9 *Stegana acutangula* (Hendel, 1913), male nontype specimen #67, Rio Manu, Madre de Dios, Peru, 250 m [USNM], head close-ups, four views: a) left lateral, b) left oblique dorsal, c) dorsal, d) ventral. Scale bar = 0.5 mm.

Figure 10 *Stegana acutangula* (Hendel, 1913), male nontype specimen #67, Rio Manu, Madre de Dios, Peru, 250 m [USNM], close-ups: a) left katepisternum lateral, b) scutellum dorsal, c) abdomen dorsal, d) left middle tibia and tarsomeres lateral. Scale bar = 1 mm.

Figure 11 *Stegana acutangula* (Hendel, 1913), male nontype specimen #67, Rio Manu, Madre de Dios, Peru, 250 m [USNM], external terminalia, four views: a) left lateral, b) left oblique posterior, c) dorsoposterior, d) oblique anterior. Scale bar = 0.1 mm.

microtrichose, except for a narrow anterior stripe and a ventral area adjacent to surstylus, posteriorly setose, bearing a conspicuous row of long, strong setae adjacent to distal margin (six ventralmost setae gradually reducing in size toward lower area), surrounded by an irregular row of smaller setae; devoid of ventral lobe. Cercus dorsally narrow, densely setose, not microtrichose; ventral lobe long, flattened, medially expanded and sharply pointed outwards, bearing a single, very thin seta, finger-shaped and curved inwards at very tip, not microtrichose, anterolaterally linked to epandrium by membranous tissue. Surstylus somewhat rectangle-shaped, double-walled, dorsodistally bearing a single, strong, terminal projection resembling a large prensiseta (but without socket) on tip of outer surface, ca. 6 long setae along distal margin, and ca. 3 thin setae on distal upper margin of inner surface, not microtrichose, not fused to epandrium. Decasternum distally square-shaped, dorsoventrally flattened, medioventrally keeled, medially incised at distal margin, bearing two lateral arms articulated to hypandrium arms. Hypandrium slightly sinuate in lateral view (Figs. 6c, 12b), as long as wide, anterior margin convex, posterior margin sinuate, medially fused to gonopods; posterior hypandrial process absent; gonopod strongly sclerotized, fused to hypandrium but projected posterad from its mediodistal margin, linked to outer wall of outer paraphysis by membranous tissue. Dorsal arch (see Bächli et al. 2004: 14) remarkably complex, connecting decasternum and hypandrium arms to inner paraphysis, divided into left and right halves (Figs. 6a,c), each two-sectioned; anterior section longitudinally half egg-shaped, weakly sclerotized, mediodistal outer surface covered with long, very thin socketed setulae, anteriorly articulated to distal region of inner paraphysis; posterior section flattened, strongly sclerotized, sharply pointed distally, laid between outer paraphysis, posteriorly articulated to anterior margin of decasternum and laterally connected to distal region of hypandrial arms; the whole sclerite probably display complex movements during the protrusion process. Aedeagus absent or, if present, could be represented by a completely membranous, amorphous component, not acting as an intromittent organ but most probably replaced by both the well-developed pair of outer paraphyses and the pair of sharply pointed anterior sections of dorsal arch. Aedeagal apodeme rod-shaped, ventrodorsally waved, distally bifid. Ventral rod fan-shaped, strongly sclerotized, anteroposteriorly flattened, laterally flanked by inner and outer paraphyses, widely articulated to median area of hypandrium between fused gonopods. Outer paraphysis (Figs. 6, 12) well developed, double-walled, distally rectangle-shaped and serrate with ca. 9 similar teeth at distal margin, medioventrally covered with ca. 13 short socketed setulae in the distal area, medially curved, strongly anteriorly sclerotized and flattened dorsoventrally but narrowed in lateral view, linked to gonopod and laterally to ventral rod by membranous tissue. Inner paraphysis laterally flattened, narrow strip-shaped, anteriorly fused to laterodistal region of aedeagal apodeme, distally articulated to setulose anterior section of dorsal arch. Ejaculatory apodeme relatively long (Figs. 6b-d, 12a, b, d), half as long as aedeagal apodeme and unusually positioned over it, probably because of the putatively short posterior ejaculatory duct that runs from ejaculatory bulb to gonopore.

♀ (Figs. 13-16)

Differences to male: Abdominal tergites only laterally with strong marginal setae. Front generally shorter and broader. Palpus slightly broadened.

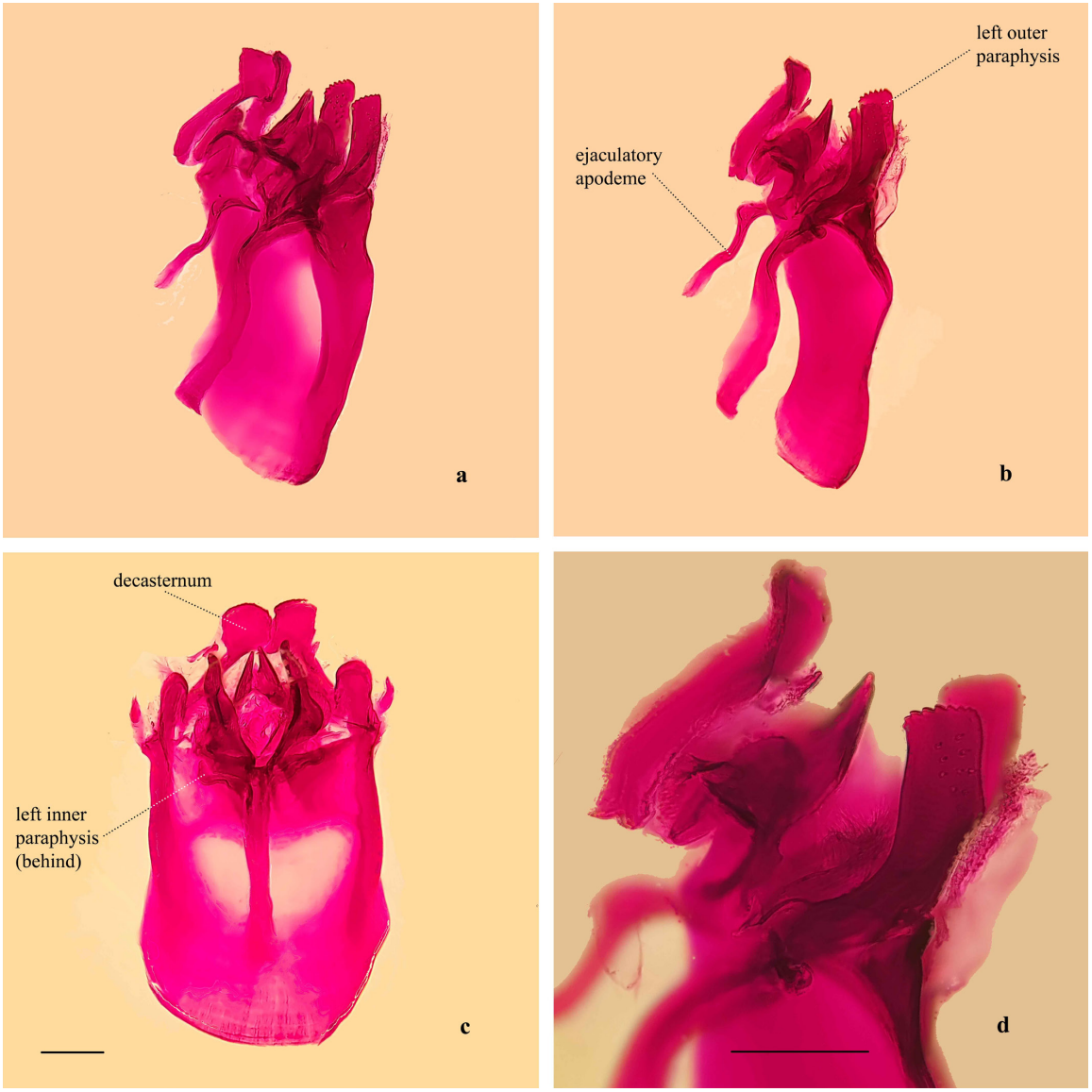

Figure 12 *Stegana acutangula* (Hendel, 1913), male nontype specimen #67, Rio Manu, Madre de Dios, Peru, 250 m [USNM], internal terminalia, four views: a) left oblique anterior, b) left lateral, c) posterior, d) left lateral (close-up). Images in a-c and d were acquired at different magnifications. Scale bars = 0.1 mm.

Figure 13 *Stegana acutangula* (Hendel, 1913), labels of a female nontype specimen #77, Erika (near Salvacion), Manu, Madre de Dios, Peru, 550 m [USNM]. For additional labels see "Material Examined".

Measurements: (n = 15) [#75 - #86, #89, #90, #186]

Frontal length about 0.54 (0.44–0.63) mm, Frontal index about 1.57 (1.37–1.85), top to bottom width ratio about 1.44 (1.33–1.60); or1/or3 ratio about 0.88 (0.76–1.00), or2/or1 ratio about 0.78 (0.67–0.89), postocellar setae about 30 (23-36) % of frontal length, ocellar setae about 0.98 (0.90–1.13) % of frontal length; vt index about 0.99 (0.94–1.06). Vibrissal index 0.33 (0.23–0.39). Cheek index about 25 (19-29). Eye index about 1.16 (1.10–1.21). Flagellomere 1 ratio about 1.98 (1.75–2.38). Thorax length = 2.04 (1.61–2.31) mm. h index about 0.69 (0.48–0.81), dc index about 0.38 (0.32–0.44), scut index about 1.26 (1.16–1.34), sterno index about 0.93 (0.83–1.07). Wing length = 3.69 (3.15–4.27) mm, length to width ratio = 2.20 (1.85–2.63). Indices: C = 2.70 (2.39–3.40), ac = 7 (6-9) M = 0.38 (0.31–0.44), prox. X = 0.46 (0.39–0.55).

♀ Terminalia [#77] (Fig. 16). One pair of finger-shaped cerci inserted beyond and between the epiproct and hypoproct (subanal plate of Laštovka and Máca, 1982). Oviscapt valves absent, sternite 8 (egg guide of Okada, 1971 and Laštovka and Máca, 1982) horizontally positioned, somewhat rectangle-shaped in ventral view, triangle-shaped in profile view, posterior margin with a median shallow notch, and not protruding beyond hypoproct. It is devoid of peg-shaped setae and it

Figure 14 *Stegana acutangula* (Hendel, 1913), female nontype specimen #77, Erika (near Salvacion), Manu, Madre de Dios, Peru, 550 m [USNM], habitus, four views: a) left lateral, b) left oblique dorsal, c) head, thorax, and wings dorsal, d) abdomen dorsal. Scale bar = 1 mm.

Figure 15 *Stegana acutangula* (Hendel, 1913), female nontype specimen #77, Erika (near Salvacion), Manu, Madre de Dios, Peru, 550 m [USNM], head close-ups, four views: a) left lateral, b) left oblique dorsal, c) dorsal, d) frontal. Scale bar = 0.5 mm.

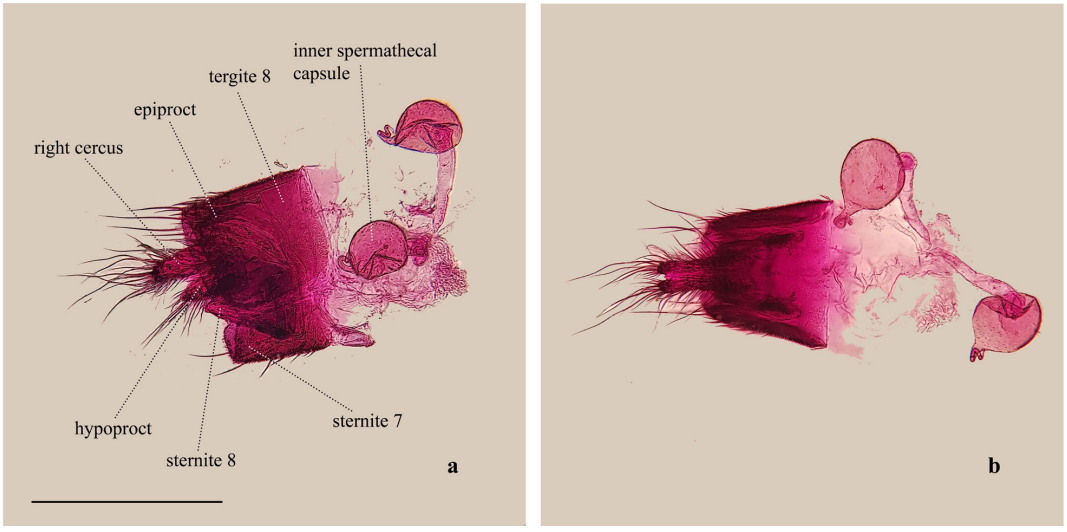

Figure 16 *Stegana acutangula* (Hendel, 1913), female nontype specimen #77, Erika (near Salvacion), Manu, Madre de Dios, Peru, 550 m [USNM], terminalia, two views. a) right lateral, b) ventral. Scale bar = 0.5 mm.

Figure 17 *Stegana triseta* (Duda, 1925), labels of male lectotype #314. For additional labels see "Material Examined".

seems to be similar to those of preceding sternites, except for the distal notch. Inner spermathecal capsule (Fig. 16) somewhat spherical, mostly papillate, bearing a short, slightly spiral-tailed appendage (Laštovka and Máca, 1982), devoid of basal and apical introverts; height slightly shorter than sternite 8.

Distribution.

Bolivia and Peru (new record). Probably widespread in northwestern South America and perhaps in the whole Amazon Forest biome. The male specimen previously recorded from Nicaragua (Wheeler and Takada 1971: 229) proved to belong to the sibling species described below as *Stegana turrialba* sp. nov. The records from Panama (Canal Zone) and perhaps Colombia need to be confirmed.

Comments.

At first sight, we found a certain degree of variability among the 36 studied specimens that we suspected belonged to just one widespread species. However, further analyses of the male terminalia showed the following remarkable details. Although the external male terminalia of the *Stegana acutangula* (# 313) lectotype from Bolivia (Fig. 5) and the one *Stegana triseta* (# 317) paralectotype from Costa Rica (Figs. 40a-c) are very similar, the surface and profile shape of the distal region of the outer paraphysis differ between the two specimens. The Bolivian lectotype has a distally clear-cut square-angled outer paraphysis ornate with a serrate distal margin bearing ca. 9 teeth (Figs. 6b,d), while the Costa Rican *Stegana triseta* paralectotype is ornate with only ca. 3 teeth (Figs. 41a,d) and has a roundish, not square-angled, ventral tip. The latter specimen is described below as *Stegana (Orthostegana) turrialba* n. sp., a Central American species, so far recorded from Nicaragua (and probably from Panama and Colombia) under the binomial *Stegana acutangula* (misidentification).

It should be emphasized that the serrate silhouette of the distal margin of the bent, rectangle-shaped outer paraphysis is one of the most striking features of the internal male terminalia of *Stegana acutangula*. With a rectangle-shaped head silhouette and nine (coincidentally) equal-sized spikes, it resembles the fictional American character Bart Simpson of the animated TV series "The Simpsons Family".

Stegana (*Orthostegana*) *triseta* (Duda, 1925), comb. nov.
(Figs. 17-24)

Oxyphortica triseta Duda, 1925: 160 (description, type material), Duda, 1927: 14, 31 (key, distribution, type material).

Stegana triseta (Duda, 1925): Wheeler, 1970: 79.7 (affiliation, distribution); Bächli, 1984: 258 (type material, distribution).

Stegana (Steganina) triseta Duda: Wheeler, 1981: 31 (affiliation); Brake and Bächli, 2008: 300 (affiliation).

Type locality. Costa Rica, Cartago, La Suiza de Turrialba.

Diagnosis.

Differs from *S. acutangula* in a few details only. In particular, male pleura presents a distinct dark brown longitudinal stripe in upper 1/3 (Fig. 18a), vein R_{2+3} a bit curved up at the very end (Fig. 20c) and distal section of vein M slightly sinuate, bent upwards in the apical third. Cercus lower-positioned, tiny, densely setose, neither microtrichose nor fused to epandrium; ventral lobes not microtrichose, strongly sclerotized and remarkably fused to one another as a huge, rod-shaped, upwards bent structure. Dorsal arch (connecting hypandrium arms)

Figure 18 *Stegana triseta* (Duda, 1925), male lectotype #314, Suiza de Turrialba, Cartago, Costa Rica [HNHM], habitus, four views: a) left lateral (head in ventral view), b) left oblique dorsal (head in left oblique ventral), c) head in left lateral and thorax in dorsal view, d) abdomen dorsal. Scale bar = 1 mm.

Figure 19 *Stegana triseta* (Duda, 1925), male lectotype #314, Suiza de Turrialba, Cartago, Costa Rica [HNHM], head close-ups, four views: a) left lateral, b) frontal, c) dorsal, d) ventral. Scale bar = 1 mm.

Figure 20 *Stegana triseta* (Duda, 1925), male lectotype #314, Suiza de Turrialba, Cartago, Costa Rica [HNHM], three close-ups: a) external terminalia right oblique posterior, b) middle tarsomeres ventral, c) left wing dorsal. Images in a-b and c were acquired at different magnifications. Scale bars = 0.5 mm (a, b), = 1 mm (c).

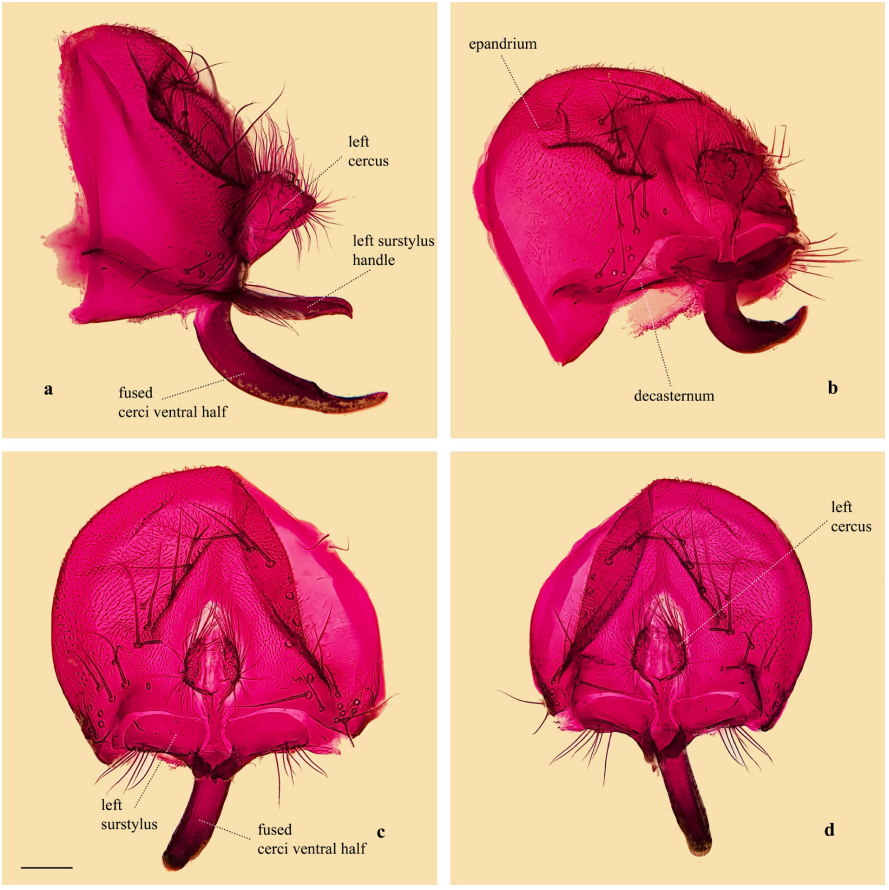

Figure 21 *Stegana triseta* (Duda, 1925), male lectotype #314, Suiza de Turrialba, Cartago, Costa Rica [HNHM], external terminalia, four views: a) left lateral, b) left oblique posterior, c) posterior, d) anterior. Scale bar = 0.1 mm.

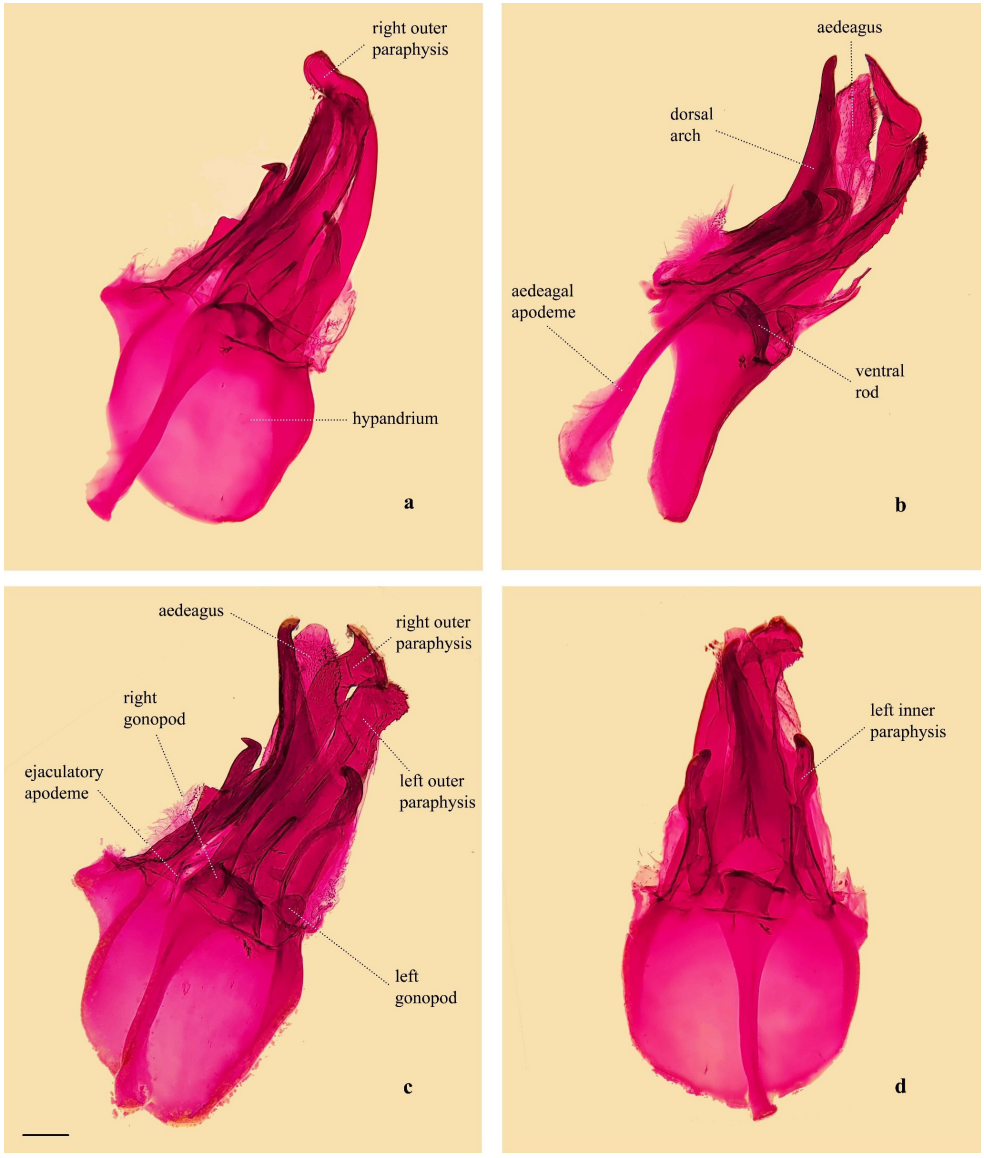

Figure 22 *Stegana triseta* (Duda, 1925), male lectotype #314, Suiza de Turrialba, Cartago, Costa Rica [HNHM], internal terminalia, four views: a) left oblique posterior, b) left lateral, c) left oblique anterior, d) anterior. Scale bar = 0.1 mm.

large, triangle-shaped. Decasternum slightly sinuate. Aedeagus membranous, somewhat tubular (Fig. 22b), mostly microtrichose. Inner paraphysis rod-shaped, distally curved upward, half the length of outer paraphysis, ventrodistally covered with tiny scales. Outer paraphyses long, asymmetric, rectangle-shaped, right one longer and sharply pointed at tip. Ejaculatory apodeme tiny (Fig. 22c), 1/6 length of aedeagal apodeme.

Material examined.

Lectotype male (#314) (by present designation) [dissected] (Figs 17-22): "COSTA RICA / SUIZA DE TURRIALBA // *Oxyphortica* / *triseta* ♂ [symbol] [all handwritten] / DET. DR. O. DUDA // Syn- [handwritten] Typus [red label] // microvial // 314 [our unique internal number] // ♂ [symbol] // LECTOTYPE [red label] // LECTOTYPE / Stegana / *triseta* (Duda) / Vilela & Bächli des." (HNHM).

Paralectotype female (# 316) (by present designation) [dissected] (Figs. 23, 24): "COSTA RICA 1921 / SUIZA DE TURRIALBA // *Ox. triseta* / ♀ [symbol] n. sp. [all handwritten] / DET. DR: O. DUDA // syn- [handwritten] Typus // Zool. Mus. / Berlin // 316 [our unique internal number] // ♀ [symbol] // PARALECTOTYPE [red label] // PARALECTOTYPE / *Stegana* / *triseta* (Duda, 1925) / Vilela & Bächli des." (ZMB).

Comments.

The syntype material from the Budapest Museum contained four specimens (3 ♂♂ and 1 ♀), not three specimens as reported by Duda (1925:161, 1 ♂, 2 ♀♀; 1927:31, 1 ♂, 2 ♀♀ in Budapest, but see Bächli, 1984:258, 2 ♀♀ in Berlin). Only one of them fully fits the description of Duda and was, therefore, selected as a lectotype. The three (2 ♂♂, 1 ♀) other specimens are herein selected as paralectotypes. The latter two males are different from the former and also between each other in several characteristics, and are described below as *Stegana dudai*, sp. nov., and *Stegana turrialba*, sp. nov. The female #316 cannot be associated with any of the three male specimens belonging to the type series. Notably, the pleuron of the female is devoid of a dark brown longitudinal stripe, which is present in the male lectotype. Previously, Brake and Bächli (2008: 300) erroneously mentioned that the Budapest Museum material was lost.

Figure 23 *Stegana triseta* (Duda, 1925), female paralectotype #316, Suiza de Turrialba, Cartago, Costa Rica [ZMB], habitus, four views: a) left lateral (head in left oblique dorsal view), b) left oblique dorsal, c) head right oblique dorsoposterior and thorax dorsal, d) abdomen dorsal. Scale bar = 1 mm.

Description.

♂. (Figs. 18-22)

External characters almost as in *S. acutangula*, but:

Body size about 4 mm.

Front brownish-yellow (Figs. 19b,c), frontal length 0.62 mm; frontal index about 1.38, top to bottom width ratio about 1.27. Frontal triangle indistinct, about 45% frontal length; ocellar triangle mostly blackish, about 30% frontal length. Orbital plates narrow, about 67% frontal length. Distance of or3 to or2 about 30% of or3 to or1, distance of or2 to or1 about 70% of or3 to or1, distance of or3 to or1 about 140% of or3 to vtm, or1/or3 ratio about 1.04, or2/or1 ratio about 8.83, vt index about 1.06, postocellar setae about 31% of frontal length; ocellar setae about 98% of frontal length; vibrissal index about 0.35. Cheek index about 21. Eye index = 1.29. Pedicel slightly brownish. Arista with 7 long dorsal, 5 long ventral and about 8 short inner branches, plus terminal fork.

Thorax (Fig. 18c) brownish-yellow, length about 2.11 mm. h index about 0.30, dc index about 0.28, distance between apical scutellars about 85% of that of the apical to the basal one. Pleura yellowish, with a distinct dark brown longitudinal stripe along dorsal margin (Fig. 18a). Sterno index about 0.97.

Wing (Fig. 20c) length = 3.67 mm, length to width ratio about 2.19. Indices: C = 2.79, ac = 8, hb = 0.42, 4C = 0.65, 4v = 1.27, 5x = 0.75. M = 0.24, prox. X = 0.32.

Terminalia ♂ (Figs 21, 22). Epandrium (Fig. 21) distally microtrichose, bare at velum-shaped fold of anterior margin and the posteroventral area adjacent to concave margin surrounding surstyli, with a single tiara-shaped, medially positioned row of ca. 19 (8 on each side) long setae ventrally followed by irregular rows of short setae; bearing an inverted Y-shaped, sclerotized area adjacent to cercus. Cercus lower-positioned, tiny, conoid-shaped in lateral view (Fig. 21a,b), densely setose, neither microtrichose nor fused to epandrium; ventral lobes not microtrichose, strongly sclerotized and remarkably fused to one another forming a huge, rod-shaped, upwards bent, spine-shaped component (Fig. 21). Dorsal arch (connecting hypandrium arms) large, triangle-shaped. Surstylus roughly golf club-shaped in lateral view, shaft strongly sclerotized, slightly curved dorsalwards and inwards ending in a sharp tip, double-walled, outer wall lateroventrally bearing a patch of ca. 7 long, thin setae (as long and thin as cerci setae), prensisetae absent on inner margin; surstyli shaft convergent over fused cercal lobes; weakly linked to epandrium by membranous tissue. Decasternum strongly sclerotized, dorsoventrally flattened, proximally abruptly turned inwards, distally fused to ventral margin of surstyli. Dorsal arch strongly sclerotized, somewhat triangle-shaped, projected backwards sheltering aedeagus or even attached to it, distally sinuate in lateral as well in anterior view, medially carinate, medially turned rightwards, distally turned leftwards, linked to posterior hypandrium arms by membranous tissue. Hypandrium somewhat drop-shaped in anterior view (Fig. 22d), distolaterally turned dorsalwards, slightly wider than long, as long as epandrium, anterior margin convex, posterior margin concave, lateral arms strongly sclerotized, close to each other, distally hook-shaped and linked laterally to strongly developed dorsal arch; posterior hypandrial process absent; left gonopod (Fig. 22c) weakly sclerotized, triangle-shaped, apparently linked both to hypandrium posterior margin and to left paraphysis by membranous tissue;

Figure 24 *Stegana triseta* (Duda, 1925), female paralectotype #316, Suiza de Turrialba, Cartago, Costa Rica [ZMB], close-ups, head three views, one katepisternum view: a) dorsal, b) obliquedorsal, c) frontal, d) left katepisternum. Scale bar = 0.5 mm.

right gonopod smaller (Fig. 22d). Aedeagus (Fig. 22b, c) membranous, somewhat tubular, covered with microtrichia which are longer and denser above gonopore, as long as aedeagal apodeme, apparently tightened linked to ventrodistal area of the strongly sclerotized, plate-like dorsal arch, probably acting as the intromittent organ together with the pair of asymmetrical outer paraphyses and rod-shaped inner paraphyses; probably linked to aedeagal apodeme by a narrow membranous tissue. Aedeagal apodeme (Fig. 22b) anteriorly expanded dorsoventrally in lateral view, distally expanded laterally in anterior view. Ventral rod strongly sclerotized anteroposteriorly flattened, bifid at tip, linked to posterior hypandrium margin by membranous tissue. Outer paraphyses strongly sclerotized, conspicuously asymmetric (Fig. 22c); right paraphysis (the longest) devoid of setae, ventromedially serrate, distally twisted and turned to the left, sharply pointed at tip, marginally smooth; left paraphysis anteriorly conspicuously expanded laterally, serrate dorsomarginally at distal half and tip. Inner paraphyses 1/2 the length of outer paraphyses, rod-shaped, flanking aedeagus, distally pointed and turned upwards, left one slightly longer than right one. Ejaculatory apodeme (Fig. 22c) weakly sclerotized, relatively short, 1/6 as long as aedeagal apodeme and unusually positioned over it, probably because of the extremely short posterior ejaculatory duct that runs from ejaculatory bulb to gonopore.

♀. (#316) (Figs. 23, 24). See comments above.

Differences to ♂: relatively broader front, no pleural stripe.

Measurements: Frontal length about 0.51 mm, frontal index about 1.67; top to bottom width ratio about 1.39; or1/or3 ratio about 0.92, or2/or1 ratio about 0.68; postocellar setae about 20% of frontal length, ocellar setae about 0.97% of frontal length; vt index about 0.93. Vibrissal index 0.27. Cheek index about 12. Eye index about 1.21. Flagellomere 1 ratio about 2.00. Thorax length = 1.71 mm. dc index about 0.51, sterno index about 1.00. Wing length = 2.83 mm, length to width ratio = 2.13. Indices: C = 2.41, ac = 7, Chb = 0.64, 4C = 0.73,4V = 1.27,5X = 0.64, M = 0.23, prox. X = 0.43.

Distribution.

Costa Rica

Comments.

Based on the set of common characteristics of all species described here, *S. triseta* Duda should be moved from the subgenus *Oxyphortica* into the subgenus *Orthostegana* (new comb.). Consequently, restricting the subgenus *Oxyphortica* to Oriental species.

Stegana (Orthostegana) dudai sp. nov.
urn:lsid:zoobank.org:act:2EFCB0A7-7DD2-4671-9758-5E17ACEE2610
(Figs. 25-35)

Oxyphortica triseta Duda, 1925: 160 (part, description, misidentification).

Type locality. Costa Rica, Cartago, La Suiza de Turrialba.

Diagnosis. Differing in external morphology from *S. acutangula* in a few details only. Cercus long, narrow, conspicuously sinuate, medially

Figure 25 *Stegana dudai*, sp. nov., labels of male holotype #176. For additional labels see "Material Examined".

expanded laterally, densely setose, not microtrichose or fused to epandrium; ventral lobe conspicuously rod-shaped, devoid of seta and microtrichia, distally curved up and inwards. Dorsal arch (connecting hypandrium arms and inner paraphyses) complex, three-sectioned. Aedeagus membranous, amorphous. Inner paraphysis laterally flattened, narrow strip-shaped, ca. 1/3 length of outer paraphysis. Outer paraphysis long, laterally flattened, rectangle-shaped, narrower at distal 1/4, dorsodistally finger-shaped and sharply pointed.

Material examined.

Holotype male (#176) [dissected] (Figs. 25-30): "COSTA RICA / Turrialba / Nov. 1922 / Pab. Schild // yellow label // ALMelander / Collection / 1961 // USNMENT / 01372854 // ♂ [symbol] // microvial // 176 [our unique internal number] // HOLOTYPE [red label] // HOLOTYPE / *Stegana* / *dudai* spec. nov. / Vilela & Bächli det." (USNM).

Paratype male (#315) [dissected], paralectotype of *Stegana triseta* (Duda) (by present designation) (Figs. 31-35): "COSTA RICA 1921 / SUIZA DE TURRIALBA // *Ox. triseta* / ♀ [[misidentified sex symbol] n. sp. [all handwritten] / DET. DR. O. DUDA // Syn- [handwritten] Typus [red label] // microvial // 315 [our unique internal number] // ♂ [symbol] // PARALECTOTYPE [red label] // PARALECTOTYPE / *Stegana* / *triseta* (Duda, 1925) / Vilela & Bächli des. // PARATYPE [red label] // PARATYPE / *Stegana* / *dudai* spec. nov. / Vilela & Bächli det." (HNHM).

Figure 26 *Stegana dudai*, sp. nov., male holotype #176, Turrialba, Cartago, Costa Rica [USNM], habitus, four views: a) left lateral, b) left oblique dorsal, c) head and thorax dorsal, d) abdomen dorsal. Scale bar = 1 mm.

Figure 27 *Stegana dudai*, sp. nov., male holotype #176, Turrialba, Cartago, Costa Rica [USNM], head close-ups, four views: a) left lateral, b) left oblique dorsal, c) dorsal, d) frontal. Scale bar = 0.5 mm.

Figure 28 *Stegana dudai*, sp. nov., male holotype #176, Turrialba, Cartago, Costa Rica [USNM], close-ups, three views: a) right katepisternum, b) mid tibia and tarsomeres, lateral, c) left wing ventral. Images in a-b and c were acquired at different magnifications. Scale bars = 1 mm.

Description.

♂. (2 ♂♂) (Figs. 26-30, 32- 35)

External characteristics almost as in *S. acutangula*, but body size about 3.5 mm.

Measurements.

Frontal length 0.53–0.61 mm; frontal index about 2.07–2.12, top to bottom width ratio about 1.60–1.65. or1/or3 ratio about 0.8–1.00, or2/or1 ratio about 0.76–0.86, postocellar setae about 23–25% of frontal length; ocellar setae about 50–84% of frontal length; vibrissal index about 0.3–0.42. Cheek index about 16–28. Eye index = 1.22–1.31. Flagellomere 1 ratio about 1.88–2.14. Arista with 6 dorsal, 5 ventral and about 8 short inner branches, plus short terminal fork.

Thorax length about 1.60–1.87 mm; sterno index about 0.93–1.16.

Wing length = 2.80–3.22 mm, length to width ratio about 2.09–2.16. Indices: C = 2.45–2.58, ac = 6–7, hb = 0.58–0.59, 4C = 0.73–0.79, 4v = 1.55–1.77, 5x = 0.75–0.80, M = 0.31–0.32, prox. X = 0.35–0.46.

Terminalia ♂ (Figs. 29, 30, 34, 35). Epandrium dorsodistally microtrichose (Figs. 29a-c, 34a-c), bare at velum-shaped fold of anterior margin (Fig. 34d) and the posteroventral area adjacent to concave margin surrounding surstyli, bearing a single tiara-shaped, adjacent to inner margin, row of ca. 6 thick, long setae on each side, anteroventral margin slightly prolonged ventralwards, devoid of ventral lobe. Cercus (Figs. 29a,b, 34a,b) long, narrow, conspicuously sinuate, not microtrichose, heavily setose, except for a narrow stripe along outer margin of ventral area; lobe bare, narrow, tube-shaped, slightly sinuate, blunt-tipped, devoid of setae; anteriorly linked to epandrium by membranous tissue. Surstylus double-walled, devoid of prensisetae, proximally narrow, mediodistally expanded upwards (Fig. 34b), distally concave (Figs. 34 a, c), bearing a row of ca. 7 tiny setulae, a ventral spine-like projection, and conspicuous, dorsal spine-shaped tip bent inwards; linked to epandrium by membranous tissue. Decasternum (Fig. 35d) well sclerotized, m-shaped in posterior view. Dorsal arch remarkably complex, divided into left and right halves (each one three-sectioned, Figs. 30a, 35a), strongly dorsally sclerotized and fused; anterior section weakly sclerotized, ellipsoid-shaped, bearing many setulae over outer surface, articulate to posterior end of rod-shaped inner paraphysis and median section; median section anteriorly cone-shaped, blunt, distally plaited, sharply pointed and deeply bifid at distal half (Figs. 30b,c, 35b,c), positioned between outer paraphyses; posterior section saddle-shaped (Figs. 30b, 35b), anteriorly articulate to ventral margin of decasternum and posteriorly to median section of dorsal arch. Hypandrium slightly sinuate in lateral view (Figs. 30a, 35a), as long as wide, anterior margin convex, posterior margin sinuate, medially fused to gonopods just above a large, weakly sclerotized elliptical area; posterior hypandrial

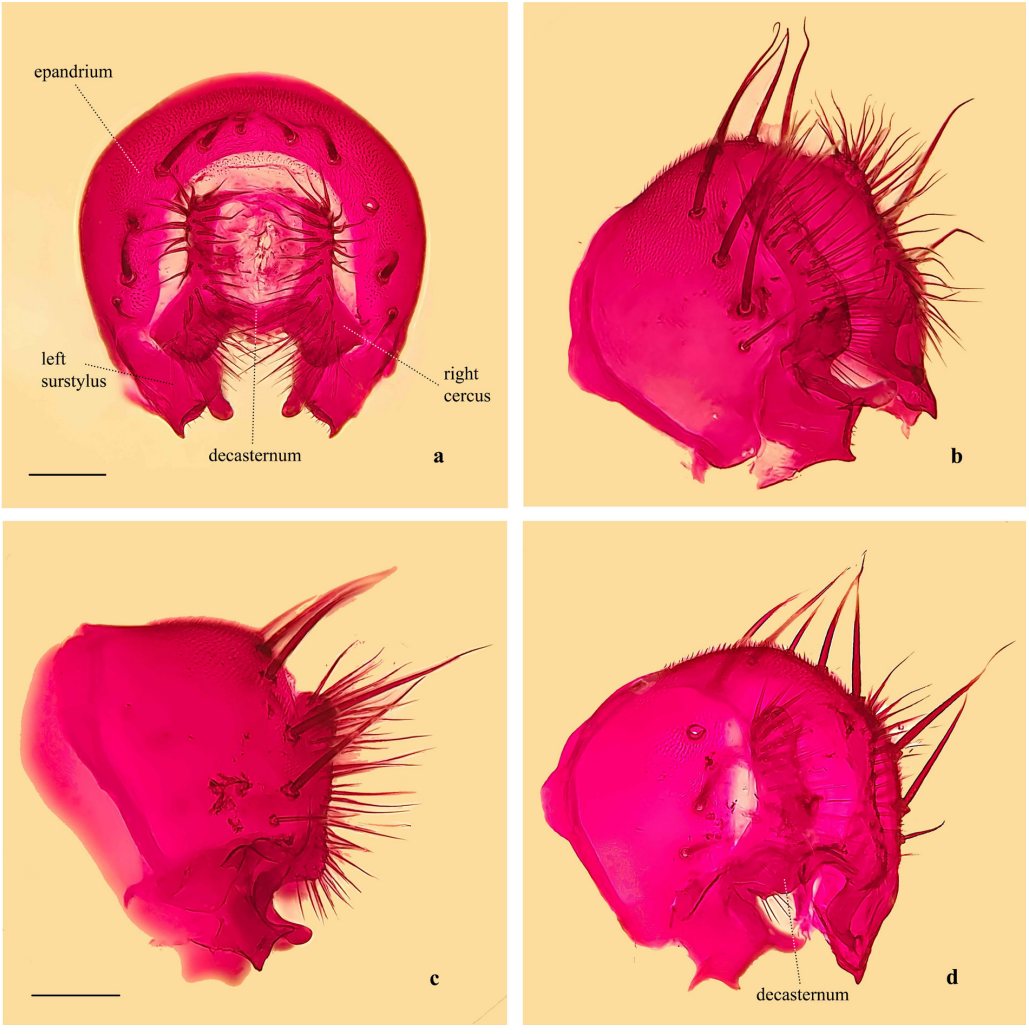

Figure 29 *Stegana dudai*, sp. nov., male holotype #176, Turrialba, Cartago, Costa Rica [USNM], external terminalia, four views: a) posterior, b) left oblique posterior, c) left lateral, d) oblique anterior. Images in a and b-d were acquired at different magnifications. Scale bars = 0.1 mm.

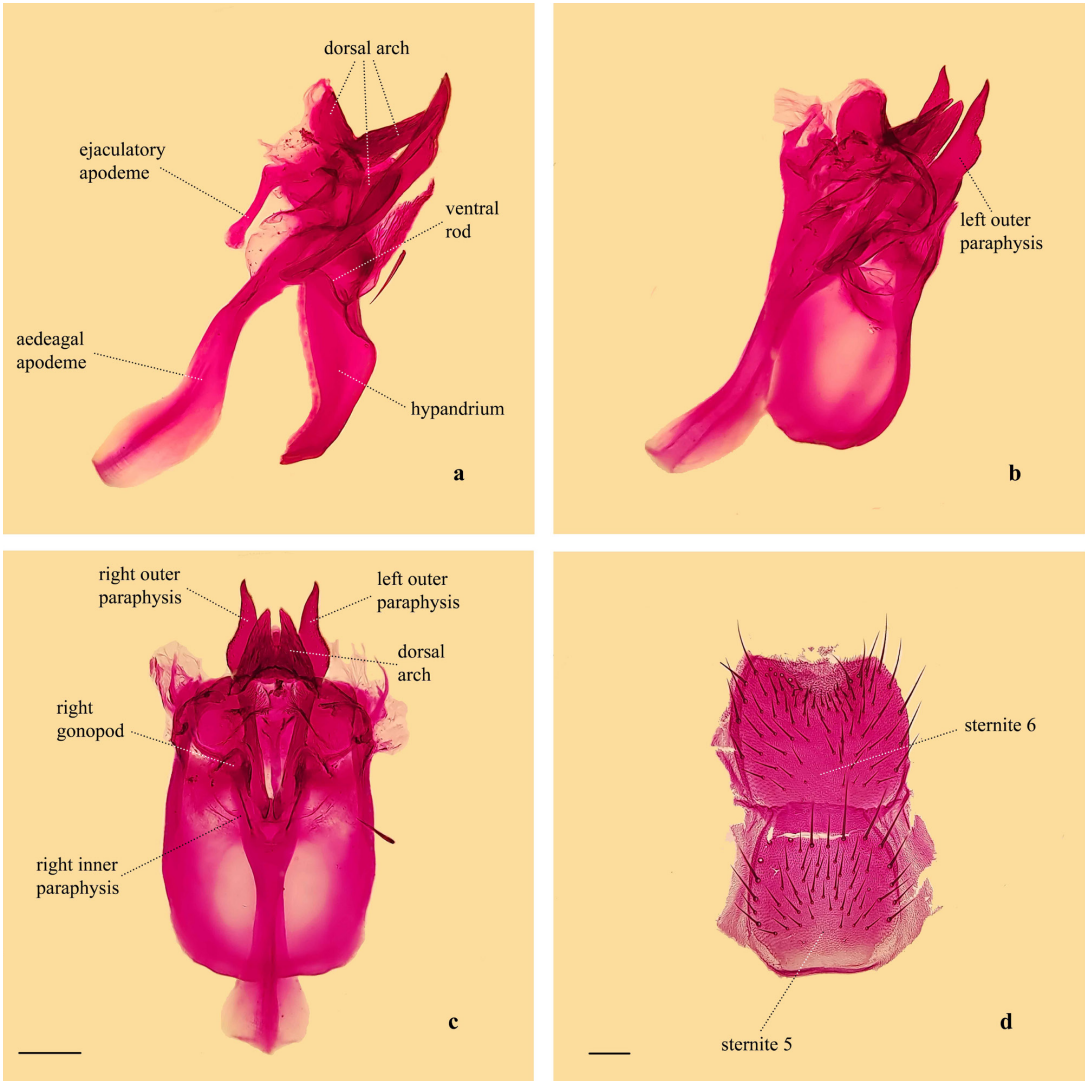

Figure 30 *Stegana dudai*, sp. nov., male holotype #176, Turrialba, Cartago, Costa Rica [USNM], internal terminalia, three views and sternites, one view: a) left lateral, b) left oblique anterior, c) anterior, d) sternites 5 and 6, ventral. Images in a-c and d were acquired at different magnifications. Scale bars = 0.1 mm.

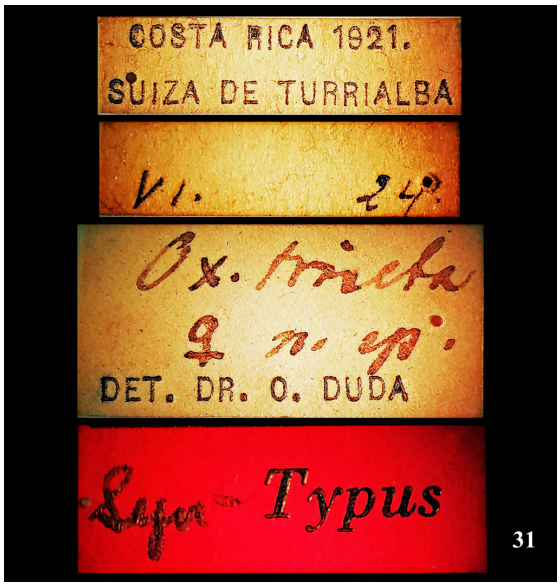

Figure 31 *Stegana dudai*, sp. nov., labels of male paratype # 315 [paralectotype of *Stegana triseta* (Duda, 1925)] [HNHM]. For additional labels see "Material Examined".

process absent; gonopod strongly sclerotized, cone-shaped, fused to hypandrium but posterad projected from mediodistal margin, linked to outer wall of outer paraphysis by membranous tissue. Aedeagus not recognizable, probably membranous and tightly linked to ventrodistal area of the triangle-shaped median branch (Fig. 30a,c) of dorsal arch, acting as the intromittent organ, probably together with outer paraphyses pair. Aedeagal apodeme distally rod-shaped and deeply bifid (Fig. 30c), each branch ca. 1/3 of its total length, proximally dorsoventrally flattened. Ventral rod strongly sclerotized, fan-shaped, anteroposteriorly flattened, laterally flanked by outer paraphyses, widely fused to median area of hypandrium between fused gonopods. Outer paraphysis (Figs. 30a-c, 35a-c) well developed, strongly sclerotized, double-walled, proximally narrow, expanded laterally mediodistally, abruptly narrowed subdistally followed by a sharp tip, distal surface covered with ca. 40 tiny socketed setulae, linked to gonopod and laterally to ventral rod by membranous tissue. Inner paraphysis laterally flattened, narrow strip-shaped, anteriorly fused to laterodistal region of aedeagal apodeme, distally articulated to setulose anterior section of dorsal arch, ca. 1/3 length outer paraphysis. Ejaculatory apodeme short, ca. 1/3 as long as aedeagal apodeme (Fig. 30a,c) and unusually positioned over it, probably because of the extremely short posterior ejaculatory duct that runs from ejaculatory bulb to gonopore.

Figure 32 *Stegana dudai*, sp. nov., male paratype #315 [paralectotype of *Stegana triseta* (Duda, 1925)], Suiza de Turrialba, Cartago, Costa Rica [HNHM], habitus, four views: a) left lateral, b) left oblique dorsal, c) thorax and wings dorsal, d) abdomen dorsal. Scale bar = 1 mm.

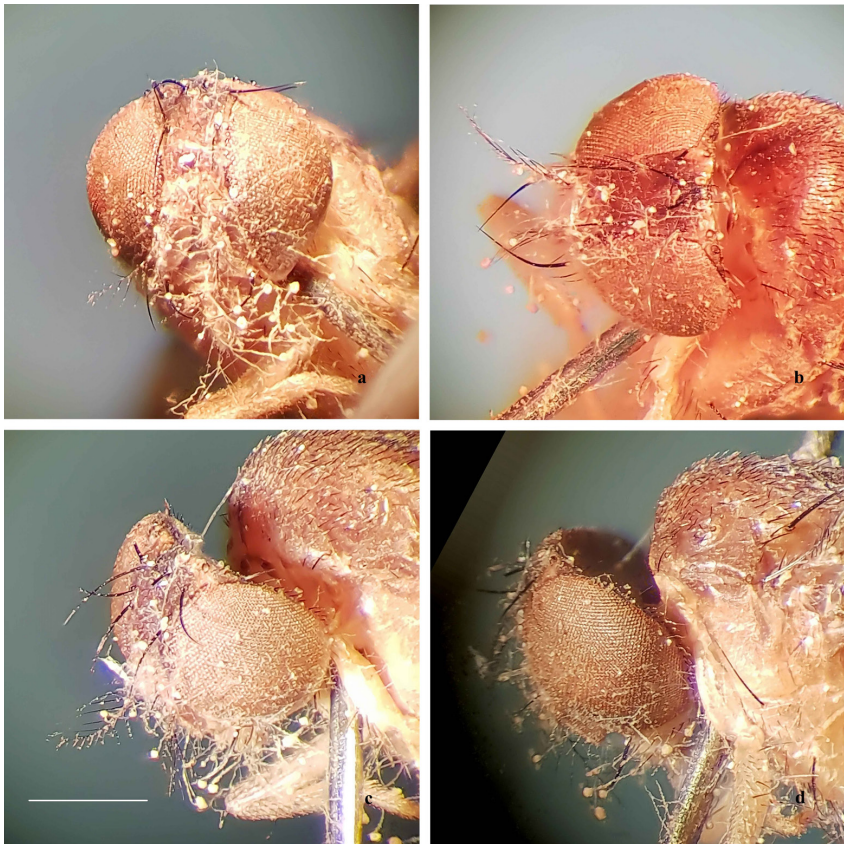

Figure 33 *Stegana dudai*, sp. nov., male paratype #315 [paralectotype of *Stegana triseta* (Duda, 1925)], Suiza de Turrialba, Cartago, Costa Rica [HNHM], head close-ups, four views: a) frontal, b) dorsal, c) left oblique dorsal, d) left lateral. Scale bar = 0.5 mm.

Figure 34 *Stegana dudai*, sp. nov., male paratype #315 [paralectotype of *Stegana triseta* (Duda, 1925)], Suiza de Turrialba, Cartago, Costa Rica [HNHM], external terminalia, four views: a) left oblique posterior, b) posterior, c) left lateral, d) left oblique anterior. Scale bar = 0.1 mm.

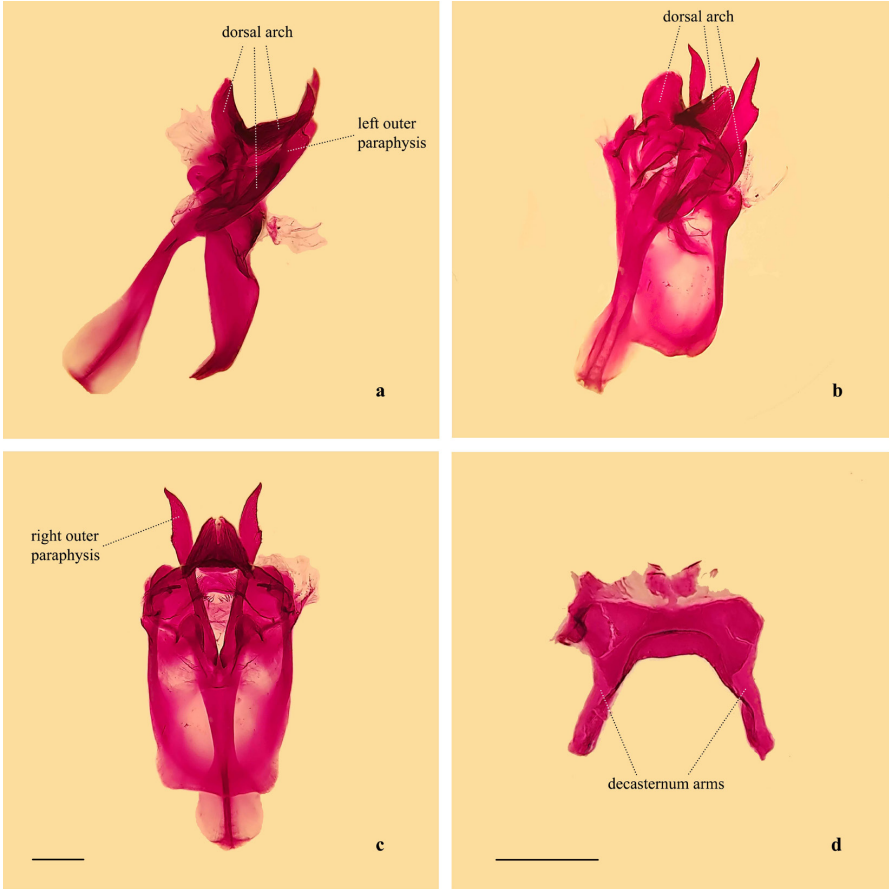

Figure 35 *Stegana dudai*, sp. nov., male paratype #315 [paralectotype of *Stegana triseta* (Duda, 1925)], Suiza de Turrialba, Cartago, Costa Rica [HNHM], internal terminalia, four views: a) left lateral, b) left oblique anterior, c) anterior, d) dorsal arch, posterior section. Images in a-c and d were acquired at different magnifications. Scale bars = 0.1 mm.

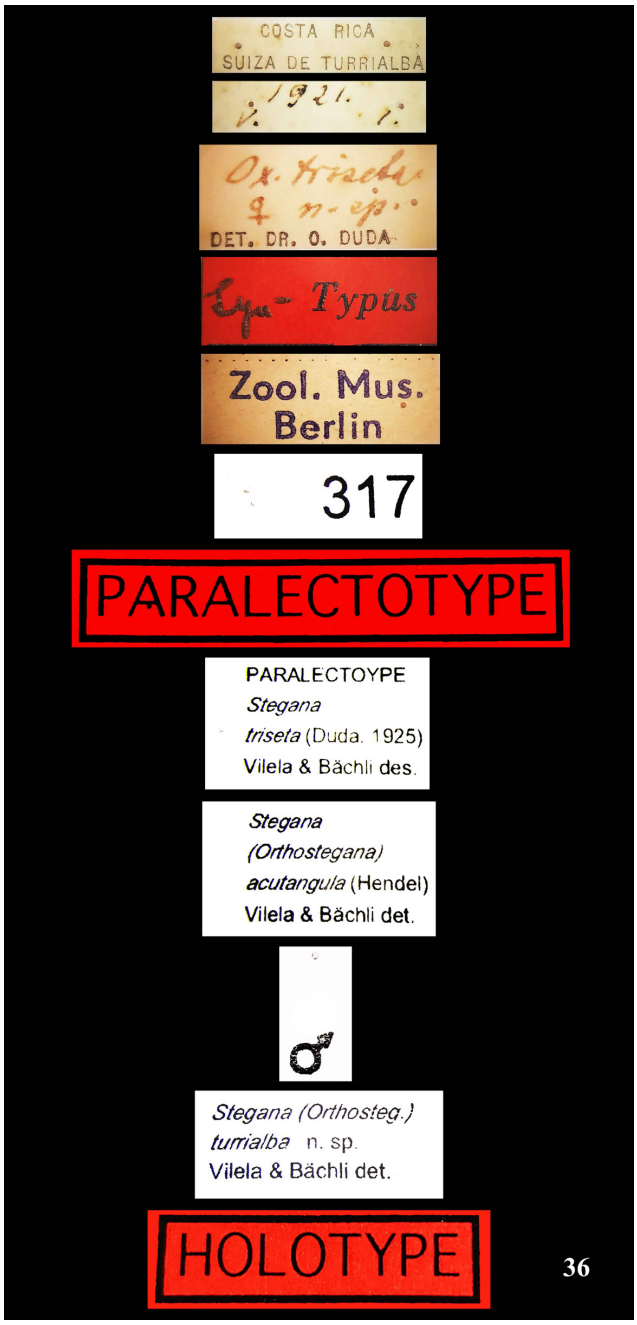

Figure 36 *Stegana turrialba* sp. nov., labels of male holotype #317.

Sternite 6 (Fig. 30d) microtrichose, barrel-shaped, distally shallowly concave, distal and lateral margins bearing a row of medium-sized setae; sternite 5 (Fig. 30d) microtrichose, narrower barrel-shaped.

Female. Unknown.

Distribution.

Costa Rica.

Etymology.

The epithet *dudai* is genitive and refers to the Dipterist Oswald Duda who was one of the pioneers of drosophilid taxonomy.

Comments. During dissection, the ejaculatory apodeme can sometimes be detached from the internal terminalia, which occurred with the paratype.

Stegana (Orthostegana) turrialba sp. nov.
urn:lsid:zoobank.org:act:DBF360D0-78C6-4590-BB8E-78B4CDCA0EC6
(Figs. 36-41)

Oxyphortica triseta Duda, 1925: 160 (part, description, misidentification).

Type locality. Costa Rica, Cartago, La Suiza de Turrialba.

Diagnosis.

Differing in external morphology and terminalia from *S. acutangula* in a few details only. Cercus dorsally narrow and posteriorly setose, not microtrichose; ventral lobe wide, flattened, medially sharply pointed outwards, finger-shaped and curved inwards at the very ventral tip, not microtrichose, not fused to epandrium. Surstylus somewhat triangle-shaped in profile view. Dorsal arch complex, two-sectioned, roughly a quatrefoil window in posterior view, encircles posterior ejaculatory duct and/or gonopore anteriorly. Aedeagus absent or, if present, could be represented by a membranous, amorphous component. Inner paraphysis strip-shaped, laterally sinuate. Outer paraphysis long, longitudinally sinuate, bent, somewhat rectangle-shaped but very ventrodistal end roundish, not straight-angled, outer surface dorsodistally covered with ca. 40 tiny scales, distal margin serrate with ca. 3 teeth at dorsal segment.

Material examined.

Holotype male [rather teneral specimen, dissected] (#317), paralectotype of *Stegana triseta* (Duda) (by present designation): "COSTA RICA / SUIZA DE TURRIALBA // *Ox. triseta* / ♀ [misidentified sex symbol] n. sp. [all handwritten] / DET: DR: O: DUDA // Syn- [handwritten] Typus [red label] // microvial // 317 [our internal number] // ♂ [symbol] n. sp./ DET. DR. O. Duda // Syn- [handwritten] Typus // PARALECTOTYPE [red label] // PARALECTOYPE [misspelled, PARALECTOTYPE] / Stegana / triseta (Duda, 1925) / Vilela & Bächli des. // HOLOTYPE [red label] // *Stegana* (*Orthosteg.*) / *turrialba* n. sp. / Vilela & Bächli det." (ZMB).

Description.

♂

External characters (Figs. 37-39) almost as in *S. acutangula*.

Measurements

Body size about 3.2 mm. Frontal length about 0.49 mm, frontal index about 2.07, top to bottom width ratio about 1.57, or1/or3 ratio about 0.876, or2/or1 ratio about 0.84, vt index about 0.92, postocellar setae about 17% of frontal length, ocellar setae about 86% of frontal length; vibrissal index about 0.41, cheek index about 11, eye index about 1.18. Thorax length about 1.61 mm, h index about 0.67, dc index about 0.43, scut index about 1.21. Wing length about 2.87 mm, length to width ratio about 2.22. Indices: C about 2.61, ac about 4.50, hb about 0.83, 4C about 0.75, 4v about 1.50, 5x about 0.73, M about 0.33, prox. X about 0.50.

Terminalia (Figs. 40, 41). Extremely similar to that of *Stegana acutangula*, except for some subtle but clear-cut non-overlapping differences mainly regarding surstylus (Figs. 40a-c) and outer paraphysis (Figs. 40d, 41). Surstylus somewhat triangle-shaped in profile view (somewhat rectangle-shaped in *S. acutangula*), dorsodistally (Fig. 40b) finger-shaped (sharply pointed (Figs. 5, 11) in *S. acutangula*), ventrodistally pointed

Figure 37 *Stegana turrialba* sp. nov., male holotype #317 [paralectotype of *Stegana triseta*; previously misidentified by us as *Stegana acutangula*], Suiza de Turrialba, Cartago, Costa Rica [ZMB], habitus, four views: a) left lateral, b) left oblique dorsal, c) head thorax and wings dorsal, d) abdomen dorsal. Scale bar = 1 mm.

Figure 38 *Stegana turrialba* sp. nov., male holotype #317 [paralectotype of *Stegana triseta*; previously misidentified by us as *Stegana acutangula*], Suiza de Turrialba, Cartago, Costa Rica [ZMB], head, close-ups, four views: a) left lateral, b) left oblique dorsal [ptilinum incompletely withdrawn into the head], c) dorsal, d) frontal. Scale bar = 0.5 mm.

Figure 39 *Stegana turrialba* sp. nov., male holotype #317 [paralectotype of *Stegana triseta*; previously misidentified by us as *Stegana acutangula*], Suiza de Turrialba, Cartago, Costa Rica [ZMB], close-ups: a) scutellum dorsal, b) head left oblique anterior, c) right wing dorsal. Images in a-b and c were acquired at different magnifications. Scale bars = 0.5 mm (a, b), = 1 mm (c).

Figure 40 *Stegana turrialba* sp. nov., male holotype #317 [paralectotype of *Stegana triseta*; previously misidentified by us as *Stegana acutangula*], Suiza de Turrialba, Cartago, Costa Rica [ZMB], external terminalia (a-c), three views (including the posterior fragment of decasternum) and internal terminalia (d), close-up, one view: a) posterior, b) left oblique posterior, c) left lateral, d) left oblique posterior. Images in a-c and d were acquired at different magnifications. Scale bars = 0.1 mm.

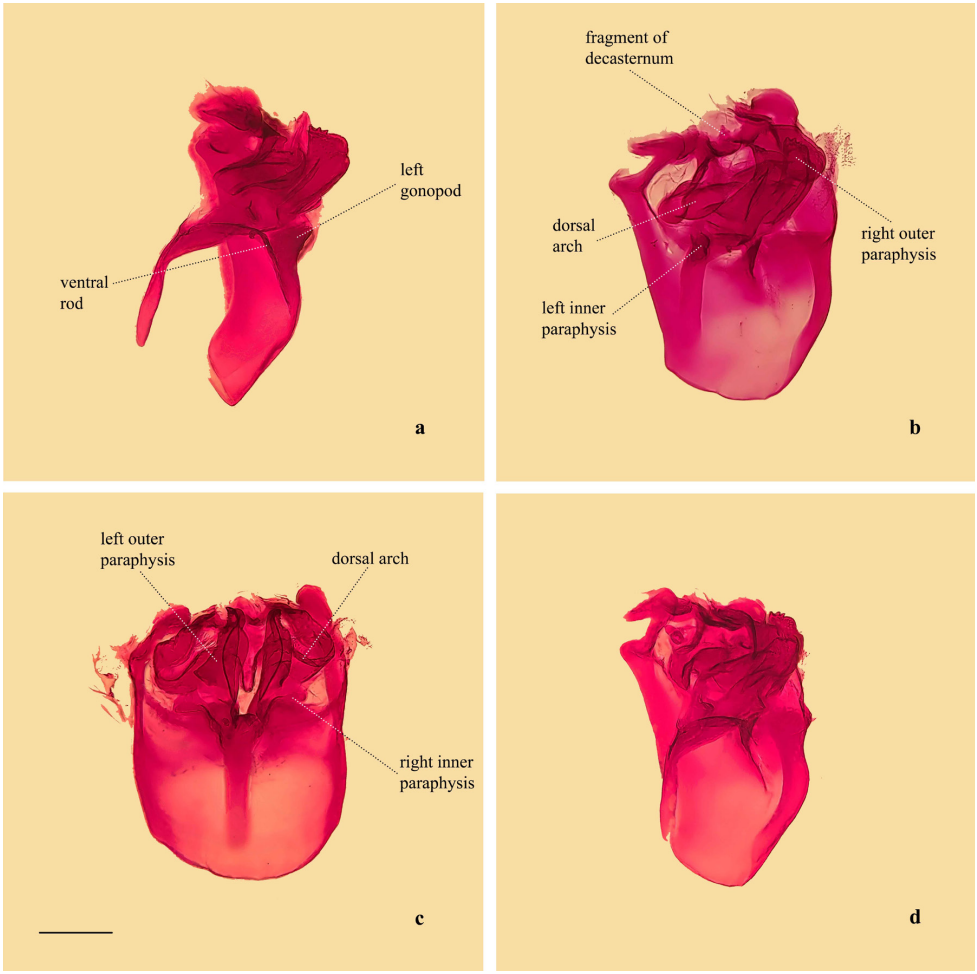

Figure 41 *Stegana turrialba* sp. nov., male holotype #317 [paralectotype of *Stegana triseta*; previously misidentified by us as *Stegana acutangula*], Suiza de Turrialba, Cartago, Costa Rica [ZMB], internal terminalia, four views: a) left lateral, b) left oblique posterior, c) posterior, d) left oblique anterior. Scale bar = 0.1 mm.

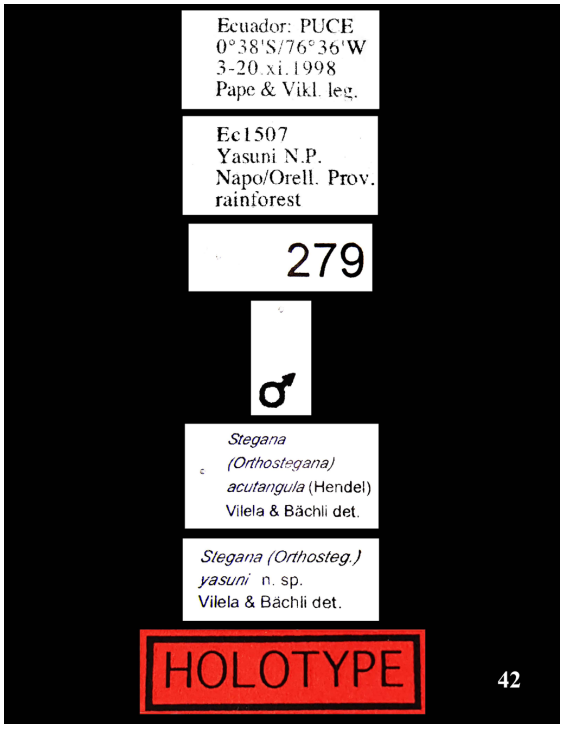

Figure 42 *Stegana yasuni* sp. nov., labels of male holotype #279.

backwards (square-angled in *S. acutangula*), distal margin shallow but widely (Figs 40a-c) concave (mostly straight in *S. acutangula*). In both species, the surstylus is devoid of peg-shaped, socketed prensisetae. Dorsal arch complex, roughly a quatrefoil window in posterior view (Fig. 41c), encircling posterior ejaculatory duct and/or gonopore anteriorly (complex, but not a clearly quatrefoil window as in *S. acutangula*). Outer paraphysis mediodistally concave (straight in *S. acutangula*), dorsodistally square-angled and bearing ca. 3 teeth (adjacent to dorsal corner (Figs. 40d, 41a,b,d), remarkably double-rounded and smooth distoventrally (distally rectangle-shaped with serrate posterior margin bearing ca. 9 even-spaced teeth (Figs. 6b,d, 12a,b,d) in *S. acutangula*); outer surface dorsodistally covered with ca. 40 tiny scales (mediodistally with ca. 13 short socketed setulae in *S. acutangula*).

Female. Unknown.

Distribution.

Costa Rica.

Etymology.

The epithet is a noun in apposition referring to the type locality.

Stegana (*Orthostegana*) *yasuni* sp. nov.
urn:lsid:zoobank.org:act:DDCC232F-6092-42C0-9F78-C1457E902346
(Figs. 42-47)

Figure 43 *Stegana yasuni* sp. nov., male holotype #279 [previously misidentified by us as *Stegana acutangula*], Parque Nacional Yasuni, Province of Napo, Ecuador [ZMUZ], habitus, four views: a) left lateral, b) left oblique dorsal, c) head and thorax dorsal, d) abdomen dorsal. Scale bar = 1 mm.

Type locality. Ecuador, Provinces of Napo/Orellana, Parque Nacional Yasuní.

Diagnosis. Differing in external morphology from *Stegana acutangula* and *S. turrialba* sp. nov. in a few details only. Cercus and dorsal arch virtually identical to those of *Stegana acutangula* and *S. turrialba* sp. nov. Cercal ventral lobe bearing a vertical row of three very thin, long setae. Surstylus somewhat square-shaped, devoid of socketed prensiseta; dorsal inner corner remarkably bilobulated. Aedeagus absent or, if present, could be represented by a membranous, amorphous component. Inner paraphysis sinuate strip-shaped apparently articulated anteriorly to subdistal region of aedeagal apodeme. Outer paraphysis long, subdistal half as narrow as anterior part in lateral view, longitudinally sinuate, bent, roughly rectangle-shaped with distal margin dorsally serrate bearing ca. 3 teeth; very ventrodistal end roundish, not straight-angled; outer surface bare.

Material examined.

Holotype ♂ (#279) [dissected]: "Ecuador: PUCE [Pontificia Universidad Católica del Ecuador; Estación Científica Yasuní] / 0º38'S/76º36'W / 3-20 xi.1998 / Pape+Vikl.leg // Ec1507 [The Michael von Tschirnhaus insect collection code number] / Yasuni N.P. / Napo/Orell. [Orellana] Prov. [Provinces] / rainforest // 279 [our unique internal number] // ♂ [symbol] // *Stegana* / (*Orthostegana*) / *acutangula* (Hendel) [misdentification] / Vilela & Bächli det. // HOLOTYPE [red label] // *Stegana* (*Orthosteg.* [*Orthostegana*]) / *yasuni* n. sp. / Vilela & Bächli det. " [ZMUZ].

Description.

♂ (#279)

External characters (Figs 43, 44, 47c) almost as in *S. acutangula* and *S. turrialba* sp. nov.

Measurements.

Body length about 3.5 mm.

Frontal length about 0.6 mm; frontal index about 2.19; top to bottom width ratio about 1.75. Frontal triangle about 40% of frontal length; ocellar triangle about 35% of frontal length. Orbital plates about 67% of frontal length, distance of or3 to or1 about 200% of or3 to vtm, or1/or3 ratio about 0.96, or2/or1 ratio about 0.77, vt index about 1.00, postocellar setae about 26% of frontal length, ocellar setae about 91% of frontal length, vibrissal index about 0.33. Cheek index about 17. Eye index about 1.18. Arista with 8 dorsal, 6 ventral and about 8 short inner branches, plus short terminal fork.

Thorax length about 1.87 mm. h index about 0.73. dc index about 0.42, distance between apical scutellars about 80% of that of the apical to the basal one; scut index about 1.24.

Figure 44 *Stegana yasuni* sp. nov., male holotype #279 [previously misidentified by us as *Stegana acutangula*], Parque Nacional Yasuni, Province of Napo, Ecuador [ZMUZ], head, close-ups, four views: a) left lateral, b) left oblique dorsal, c) dorsal, d) frontal. Scale bar = 1 mm.

Wing length about 3.22 mm, length to width ratio about 2.19. Indices: C about 2.90, ac about 3, hb about 0.90, 4C about 0.77, 4v about 1.54, 5x about 0.90, M about 0.35, prox. X about 0.50.

Terminalia (Figs 45-47b). Extremely similar to that of *Stegana turrialba* sp. nov., except for some subtle but clear-cut non-overlapping differences mainly regarding cercus ventral lobe and surstylus (Fig. 45), as well as outer paraphysis (Figs 46-47b). Cercus ventral lobe (Fig. 45b-d) bearing a vertical row of three very thin, long setae (one single seta in *S. turrialba* sp. nov.). Surstylus (Fig. 45a-c) somewhat rectangle-shaped in profile view (somewhat triangle-shaped in *S. turrialba* sp. nov.), devoid of peg-shaped, socketed prensiseta in both species; distal margin (Fig. 45b) shallowly concave (deeply concave in *S. turrialba* sp. nov.); dorsal inner corner (Fig. 45c,d) bilobulated (monolobulated in *S. turrialba* sp. nov.). Decasternum anterodorsal surface densely covered with long, very thin socketed setulae similar to those on outer surface of anterior section of dorsal arch (apparently only some setulae on the anterocentral region of dorsal surface in *S. turrialba* sp. nov.). Dorsal arch complex, roughly a quatrefoil window in posterior view (Fig. 46a), encircling posterior ejaculatory duct and/or gonopore anteriorly (as in *S. turrialba* sp. nov.). Outer paraphysis proximally twice as wide as distally in profile view (Fig. 46b) (distally widened and projected distal wards as a lobule in *S. turrialba* sp. nov.); outer surface (Fig. 46b) bare (dorsodistally covered with ca. 40 tiny scales in *S. turrialba* sp. nov.).

Female. Unknown.

Distribution. So far only known from the holotype collected in the Amazonian region of Ecuador. This is the first record of a *Stegana* species occurring in Ecuador (see Brake and Bächli, 2008) and in the Yasuní National Park (see Acurio and Rafael, 2009).

Etymology.

The epithet is a noun in apposition referring to the type locality.

Discussion

In comparison with the current diagnosis of the subgenus *Oxyphortica* (Wang et al., 2017), the external characteristics of species of the subgenera *Orthostegana* and *Oxyphortica* are extremely similar and in some cases overlap. In species of *Oxyphortica*, the M vein of the wing is less curved, but this trait provides little definitive evidence because of intra- and interspecific variations. Herein, we compared the wing vein characteristics of all 40 known *Oxyphortica* species and found that costal section IV is much longer, thus reducing the ac index to about 4–7. It should be pointed out that costal section IV is weak and usually not flattened in this subgenus, which could lead to errors in the ac index measurement. Additionally, the number of erected posterodorsal setae on the middle tibia is variable but does not discriminate between the two subgenera, and a row of posterodorsal setae on the middle tibia, with a few of the upper ones being stout and erect, has been observed in a variety of *Stegana* species belonging to other subgenera as well.

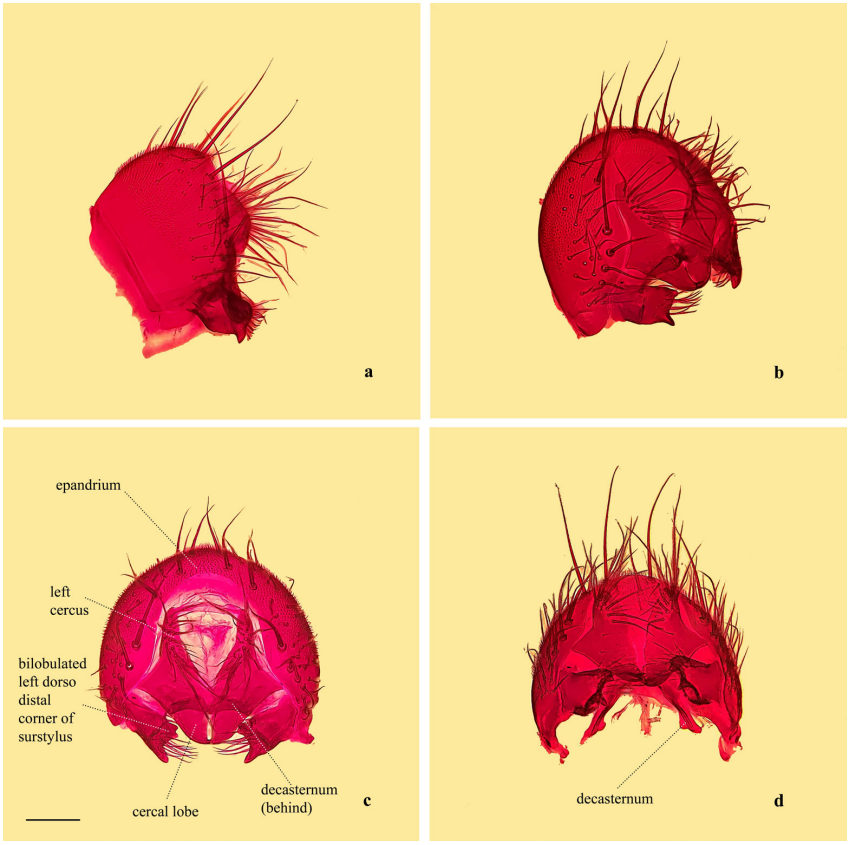

Figure 45 *Stegana yasuni* sp. nov., male holotype #279 [previously misidentified by us as *Stegana acutangula*], Parque Nacional Yasuni, Province of Napo, Ecuador [ZMUZ], external terminalia, four views: a) left lateral, b) left oblique posterior, c) posterior, d) posterior oblique ventral. Scale bar = 0.1 mm.

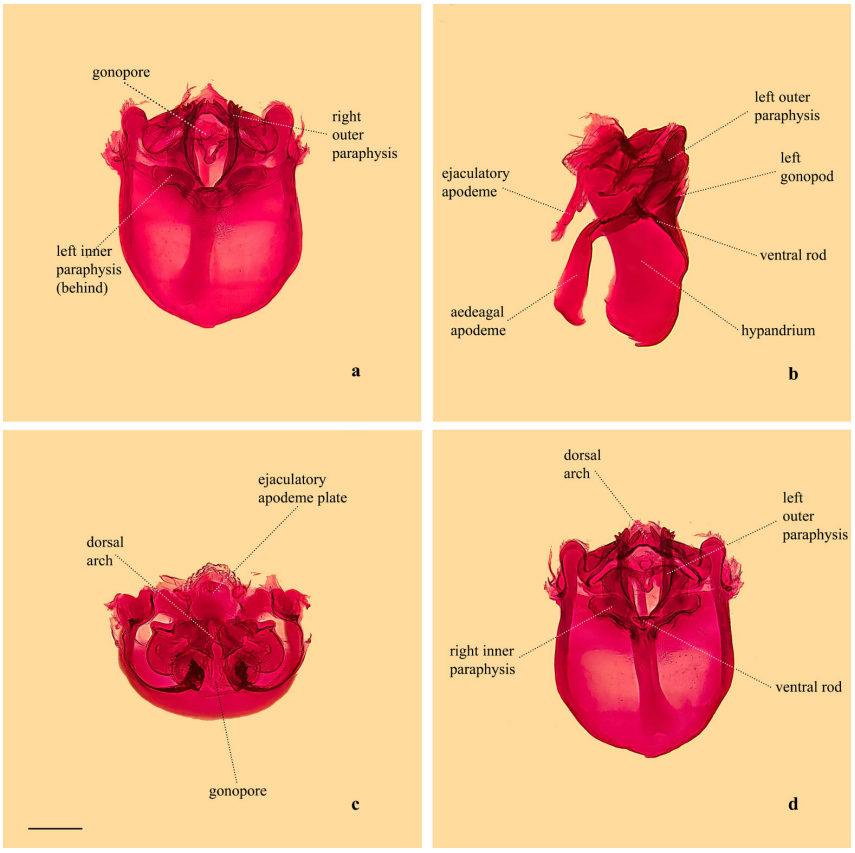

Figure 46 *Stegana yasuni* sp. nov., male holotype #279 [previously misidentified by us as *Stegana acutangula*], Parque Nacional Yasuni, Province of Napo, Ecuador [ZMUZ], internal terminalia, four views: a) posterior, b) left lateral, c) dorsal, d) anterior. Scale bar = 0.1 mm.

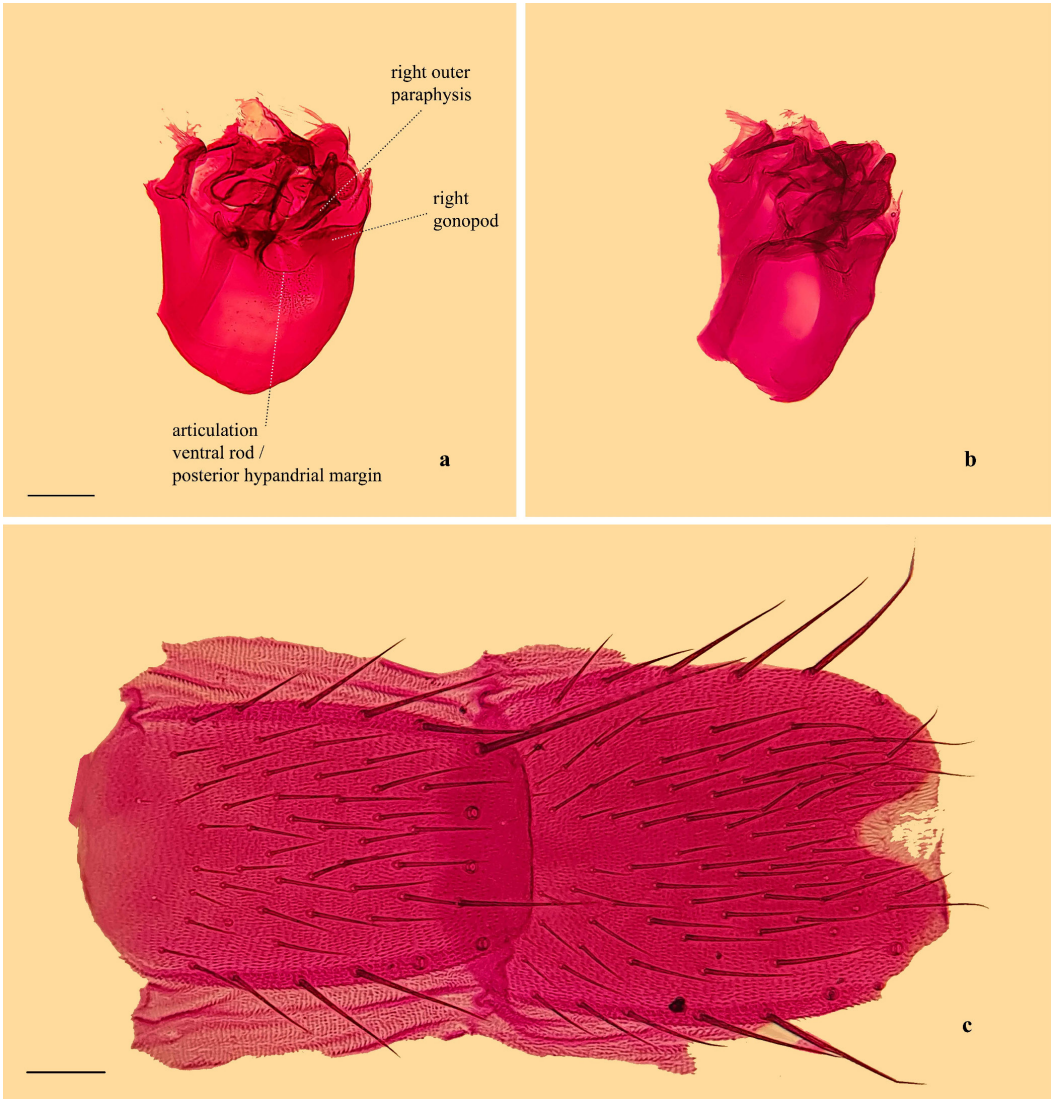

Figure 47 *Stegana yasuni* sp. nov., male holotype #279 [previously misidentified by us as *Stegana acutangula*], Parque Nacional Yasuni, Province of Napo, Ecuador [ZMUZ], internal terminalia (a,b), two views, and two last sternites (c), one view: a) left oblique posterior, b) left oblique anterior, c) ventral. Images in a-b and c were acquired at different magnifications. Scale bars = 0.1 mm.

The descriptions and illustrations of the six Asian species of *Orthostegana* reveal that all exhibit a distinct, sclerotized aedeagus (Sidorenko, 1990; Chen and Wang, 2004; Zhang et al. 2012; Li et al. 2013), a common feature of the *Oxyphortica* subgenus (for further details, see Wang et al., 2017). On the other hand, in *Stegana acutangula*, type species of the subgenus *Orthostegana*, this structure is amorphous (membranous).

Since the external characteristics of all 40 species of the subgenus *Oxyphortica* were recorded in Asia and many details, including a completely dissimilarity shaped aedeagus, overlap with these six Asian species of the *Orthostegana* subgenus. Thus, we propose that the Asian *Orthostegana* species should be included in *Oxyphortica*, consequently making *Orthostegana* an endemic American subgenus.

Previously, Bächli et al. (2004: 14) proposed that the structure designated as the "dorsal arch" of the hypandrium in Steganinae probably originated from the gonocoxite. In the present study, we compared the ribbon-shaped process described by Bächli et al. 2004: 203, Figs 499, 500) that is responsible for the hypandrium arm-inner paraphysis connection in species of *obscura* group of *Drosophila*, to the "dorsal arch" described in the five *Stegana* sibling species (Figs. 6a-c, 22b, 30a,c, 35a,b, 46c,d) cited above. We found that the inner paraphysis of the latter five species clearly articulates distally with the "dorsal arch", and proximally to both the hypandrium arm and distal end of aedeagal apodeme. The similar role of the "ribbon-shaped process" of the *obscura* group of *Drosophila* and the complex two-sectioned "dorsal arch" of the five species of *Stegana* analyzed above, indicates that both structures must be homologous and probably originated from the gonostylus, the distal arm of the primitively two-segmented gonopod (McAlpine 1981: 45), together with the distal region of the decasternum, and not the gonocoxite as previously proposed by Bächli et al. 2004. Moreover, in the species of the subgenus *Drosophila*, the single pair of paraphyses connects the distal end of aedeagal apodeme to the gonopod, which most likely originated from the basal arm (gonocoxite) of the primitively two-segmented gonopod and the apparently absent pair of primitive inner paraphyses is probably fused anterodorsally to the aedeagus.

Conclusions

After describing and/or redescribing five species of the *Stegana* subgenus *Orthostegana*, we propose that the following six species,

Stegana curvinervis (Hendel, 1914), *Stegana singularis* Sidorenko, 1990, *Stegana flavicauda* Zhang and Chen, 2014, *Stegana hirsutina* Zhang and Chen, 2014, *Stegana hylecoeta* Zhang and Chen, 2014, and *Stegana multicardua* Zhang and Chen, 2014 all be transferred from the *Stegana* subgenus *Orthostegana* Hendel to the *Stegana* subgenus *Oxyphortica* Duda (new comb.) and that the species *Oxyphortica triseta* Duda, in the subgenus *Steganina* Wheeler, be transferred to the subgenus *Orthostegana* Hendel (new comb.).

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Conflicts of interest

The authors declare no conflicts of interest.

Author contribution statement

GB, CRV conceived and designed the study; GB intermediated the facilities offered by the Universität Zürich-Irchel, requested the specimens, and made the external morphology descriptions; CRV dissected the flies, prepared the microscope slides, took the photomicrographs, stacked the images and made the internal morphology descriptions. Both authors wrote the manuscript and approved the final version.

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