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A new, montane record of the millipede, *Thrinoxethus verhoeffi* (Kraus, 1956) from the Andes of Peru (Diplopoda: Polydesmida: Aphelidesmidae)

Новая, горная находка вида многоножек-диплопод *Thrinoxethus verhoeffi* (Kraus, 1956) из Анд Перу (Diplopoda: Polydesmida: Aphelidesmidae)

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KEY WORDS: *Thrinoxethus*, taxonomy, description, iconography, distribution, map.

КЛЮЧЕВЫЕ СЛОВА: *Thrinoxethus*, таксономия, описание, иконография, распространение, карта.

ABSTRACT. *Thrinoxethus verhoeffi* (Kraus, 1956) is redescribed and illustrated, based on a record from the Selva Alta in Oxapampa Province (S 10°00′23″, W 75°27′36″, 1550 m a.s.l.), northeastern Peru. This new record seems to come from a presumed source area in the Andes, being both the highest montane and the westernmost in the revealed distribution of that poorly-known species which was previously reported from only two lowland localities in Loreto Department of Peruvian Amazonia.

РЕЗЮМЕ. Переописан и проиллюстрирован вид *Thrinoxethus verhoeffi* (Kraus, 1956), впервые отмеченный в Selva Alta провинции Oxapampa (S 10° 00′23″, W 75°27′36″, на высоте 1550 м, северо-восток Перу). Эта находка, кажется, приурочена к возможному району происхождения в Андах, будучи одновременно и самая западная, и горная в выявленном ареале данного малоизвестного вида, ранее найденного только в двух низинных точках департамента Loreto в перуанской Амазонии.

Introduction

The fairly large Neotropical millipede family Aphelidesmidae presently includes 17 genera and 130+ medium- to large-sized species (40–75 mm long) that range from northeastern Mexico and Tobago in the north to southeastern Peru and north-central Brazil in the south [Enghoff *et al.*, 2015; Almeida *et al.*, 2018, 2021]. The collection of Aphelidesmidae kept in the Zoological Museum, State University of Moscow (ZMUM), Russia, contains not only several species of the genera *Aphelidesmus* Brölemann, 1898, *Haematotropis* Jeekel, 2000 and *Pycnotropis* Carl, 1914 [Golovatch *et al.*, 1998, 2004], all from the Amazonian parts of Peru and/or Brazil, but also a poorly-known species of *Thrinoxethus* Chamberlin, 1941, from the Andes of Peru. The present contribution is devoted to a redescription, a detailed iconography, and a discussion of its distribution.

According to Vohland [1998], the genus *Thrinoxethus* (= *Cyclotropis* Verhoeff, 1941, preoccupied, synonymized by Kraus [1956]) currently comprises the following 15 species:

T. bombonus Chamberlin, 1941 — Peru, Requena Prov., Alto Tapiche, Rio Bombo; based on a ♂ holotype and a ♀ allotype [Chamberlin, 1941].

T. cainarachus Chamberlin, 1941 — Peru, San Martín Prov., La Banda de Shilcayo Distr,, Rio Cainarache, 700–1500 feet a.s.l.; based on a ♀ holotype [Chamberlin, 1941].

T. hermosus Chamberlin, 1941 (the type species) — Peru, Junin Prov., Rio Ucayali, Pampa Hermosa National Sanctuary; based on a ♂ holotype and a ♀ allotype [Chamberlin, 1941].

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T. iquitus Chamberlin, 1941 — Peru, Loreto Dept., Iquitos; based on a ♀ holotype [Chamberlin, 1941]. Vohland [1998] slightly misspelled the name as "*iquitos"*.

T. juani Vohland, 1998 — Peru, San Martín Prov., road Pongo–Terapoto, 800–1000 m a.s.l.; based on a ♂ holotype and four ♀ paratypes [Vohland, 1998].

T. junini Vohland, 1998 — Peru, Junin Prov., 1–3 km SW of Mina Pichito Caluga, 2100 m a.s.l.; based on a ♂ holotype and a ♀ paratype [Vohland, 1998].

T. lamprus Chamberlin, 1941 — Peru, San Martín Prov., Moyobamba, Balsapuerto Trail; based on a ♂ holotype, a ♀ allotype and a juvenile paratype [Chamberlin, 1941].

T. nitens Chamberlin, 1941 — Peru, Requena Prov., Alto Tapiche, Rio Bombo; based on a ♀ holotype [Chamberlin, 1941].

T. paucartambo (Kraus, 1956) — Peru, Cusco Dept., Rio Paucartambo, San Luis Shuaro, montane rainforest at 900 m a.s.l.; originally described in *Pycnotropis* (*Cyclotropis*), based on a ♂ holotype [Kraus, 1956]. Later recorded from a ♂ coming from Tarma Prov., Pan de Azucar, Rio Tarma, Ucayali Basin, 1400 m a.s.l., subtropical rainforest [Kraus, 1959]. Vohland [1998] revised the holotype and provided a few additional details concerning the colouration and gonopodal structure, but she slightly misspelled the name as "*paucartambus*".

T. peruanus (Verhoeff, 1941) — Peru, Huanta Prov., Ayacucho Dept., Sivia, pristine forest at 520 m a.s.l., originally described in *Pycnotropis* (*Cyclotropis*); based on a ♂ and a ♀ (syntypes) [Verhoeff, 1941]. Both are presently housed in the Zoological Institute and Zoological Museum of the Hamburg University, Germany [Weidner, 1960].

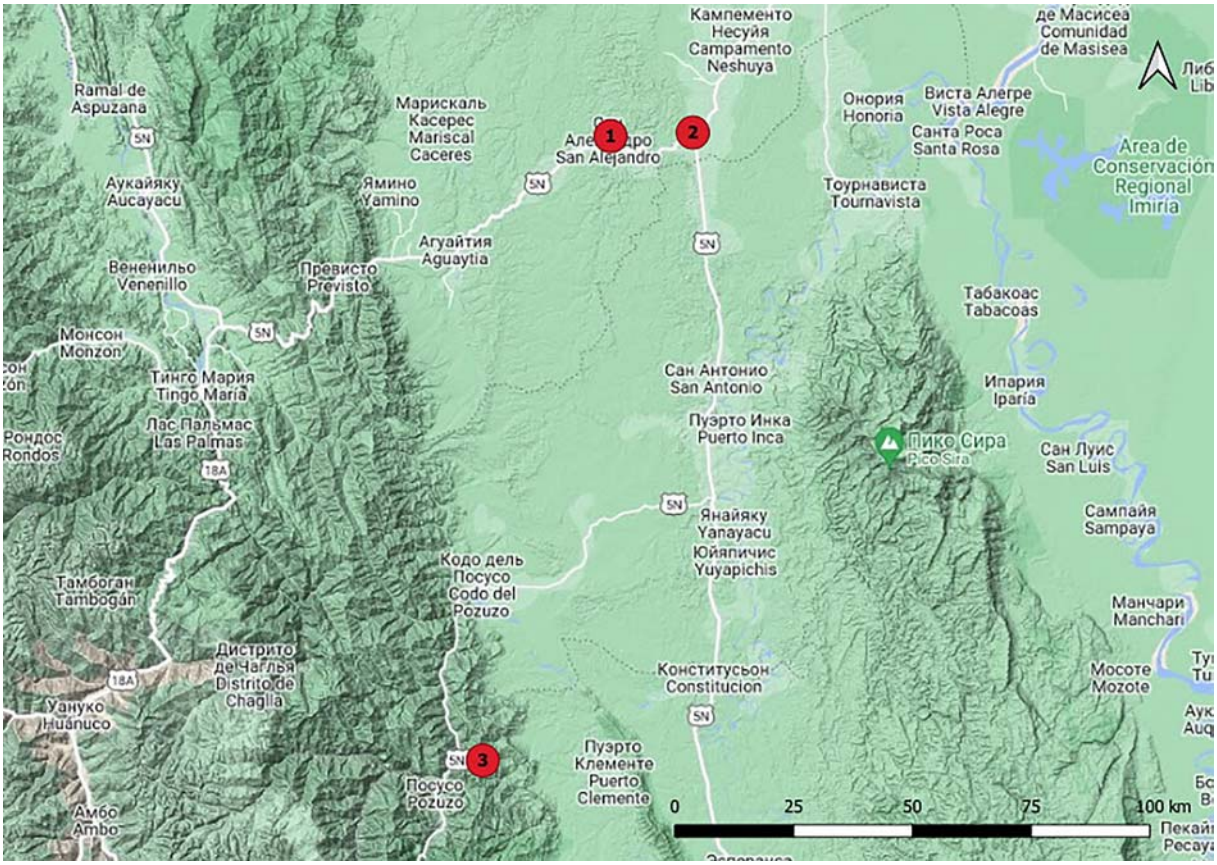
T. phanotypus Chamberlin, 1941 — Peru, Loreto Dept., below Pongo de Manseriche, 550 feet a.s.l.; based on a ♀ holotype [Chamberlin, 1941].

T. pichitaensis (Kraus, 1959) — Peru, Junin Prov., Mina Pichita Caluga, Rio Casco (affluent of Rio Chanchamayo), montane cloud forest at 2200 m a.s.l.,; originally described in *Pycnotropis* (*Cyclotropis*), based on a ♂ holotype and a ♂ paratype [Kraus, 1959]. Vohland [1998] revised the holotype and slightly refined the original label.

T. siolii Vohland, 1998 — Peru, Loreto Dept., Yurimaguas, "Rio Shanusi" Experimental Station (S 6°56′, W 76°6′), and San Martín Prov., road Pongo — Terapoto (S 6°27′, W 76°17′); based on a ♂ holotype and two paratypes: a ♂ and a ♀ [Vohland, 1998].

T. ucayalus Chamberlin, 1941 — Peru, Loreto Dept., Rio Ucayali, Suhuaya; based on a ♀ holotype [Chamberlin, 1941].

T. verhoeffi (Kraus, 1956) — Peru, Loreto Dept., San Alejandro, 300 m a.s.l.; originally described in *Pycnotropis* (*Cyclotropis*), based on a ♂ holotype [Kraus, 1956]. Later recorded and additionally illustrat-



Map. Distribution of *Thrinoxethus verhoeffi* (Kraus, 1956): 1 — San Alejandro; 2 — Alexander von Humboldt National Park; 3 — Selva Alta.
Карта. Распространение *Thrinoxethus verhoeffi* (Kraus, 1956): 1 — San Alejandro; 2 — Alexander von Humboldt National Park; 3 — Selva Alta.

ed from Peru, Rio Ucayali, Alexander von Humboldt National Park, based on a ♂ [Vohland, 1998].

It is *T. verhoeffi* that will be dealt with below, although is seems very likely to actually represent only a junior synonym of one of Chamberlin's [1941] eight species, five of which remain based on ♀ material alone. Their revision is thus very topical, especially when ♂ topotypes become available for study.

Material and methods

The sample underlying this contribution is housed in the Zoological Museum of the State University of Moscow (ZMUM), Russia. The pictures were taken with a Canon EOS 5D digital camera and stacked using Zerene Stacker software. Final image processing was performed with Adobe Photoshop CC.

Figs 1–5. *Thrinoxethus verhoeffi* (Kraus, 1956), ♂ from near Santa Rosa: 1 — habitus, dorsal view; 2–3 — anterior part of body, dorsal and ventral views, respectively; 4 — middle part of body, dorsal view; 5 — posterior part of body, dorsal view. Photographs by K. Makarov, not taken to scale.

Рис. 1–5. *Thrinoxethus verhoeffi* (Kraus, 1956), ♂ из окрестностей Santa Rosa: 1 — общий вид, сверху; 2–3 — передняя часть тела, соответственно сверху и снизу; 4 — средняя часть тела, сверху; 5 — задняя часть тела, сверху. Фотографии К. Макарова, сняты без масштаба.

Taxonomic part

Thrinoxethus verhoeffi (Kraus, 1956)
Figs 1–27, Map.

Pycnotropis (*Cyclotropis*) *verhoeffi* Kraus, 1956: 146, pl. 19, figs 28–29 (original description).

Thrinoxethus verhoeffi — Jeekel, 1963: 72 (listing); Vohland, 1998: 140, 141, figs 63–70 (taxonomic comments on the holotype and a new record).

MATERIAL. 3 ♂♂, 1 ♀, several juveniles (nearly all fragmented) (ZMUM), Peru, Pasco Region, Oxapampa Prov., ca 5 km W of Santa Rosa, Selva Alta, 1550 m a.s.l., S 10°00′23″, W 75°27′36″, 22–29.XI.2016, I. Melnik leg.

DESCRIPTION. Body length of complete adults ca 55–57 mm, width of midbody pro- and metazonae 5.0–5.2 and 7.5–8.0 mm, respectively (♂, ♀).

Colouration in alcohol only occasionally brown (Figs 1–5), but mostly dark chocolate brown or dark red-brown to nearly black-brown, largely with contrasting yellowish paraterga (Figs 6–14). Antennae and legs usually dark red-brown (Figs 6–14), but sometimes light yellow-brown (Figs 1–5), usually infuscate distally. Adult body with 20 segments.

Tegument mostly smooth and shining. Head with squarish genae, three central teeth at anterior margin of labrum and a distinct/deep epicranial suture; setae usually compound (= arranged in bundles of individual hairs): 6–9 + 6–9 labral, 2–3 + 2–3 supra-labral, and 1–3 + 1–3 facial (Figs 3, 7); vertex bare. Genal convexities in front of antennal sockets very distinct. Antennae short and robust, *in situ* extending past middle of ring 2 when stretched dorsally (♂, ♀); in length, antennomeres 6>2=3=4=5>1=7, with four apical cones on antennomere 8. Antennomeres 5–7 especially densely setose. Interantennal isthmus about half as large as diameter of antennal socket (Figs 1–3, 6–7, 10–12).

In width, head << collum < 3=15 < ring 2; starting with ring 15, body gradually tapering towards telson (Figs 1–14). Paraterga very strongly developed, broad and wing-shaped, clearly and increasingly arcuate, set low (at about half of midbody height), starting with collum, dorsum strongly and regularly convex; paraterga in lateral view like thin (poreless rings) or thicker (pore-bearing rings) ridges. Paraterga on collum acute triangular to subrectangular, narrowly rounded caudolaterally (Fig. 4). Anterior shoulders of postcollum paraterga infuscate, narrowly bordered and arcuate, laterally turning into strong drop-shaped calluses, increasingly well produced and directed caudolaterad towards telson, narrowly rounded to increasingly pointed; starting with ring 7 or 8, caudolateral corner of paraterga increasingly acute and clearly extending past rear tergal margin, especially well so on rings 16–18, only on ring 19 rather finger-shaped and rounded; caudal margin of paraterga slightly bordered, microdenticulate and increasingly concave (Figs 1–14). Dorsal surface above paraterga very finely areate, areations being polygonal, arranged in three transverse rows, growing more distinct towards and extending onto base of lateral callus, up to nearly or fully obliterate mid-dorsally, each with a traceable insertion point of a seta. Pore formula normal (5, 7, 9, 10, 12, 13, 15–19), ozopores inconspicuous, but quite visible, lateral in position, often traceable dorsally in rings of caudal body half due to lateral margin being slightly sinuate near middle. Stricture between pro- and metazona narrow, shallow and very faintly striolate longitudinally both dorsally and dorsolaterally. Limbus thin and entire, very finely beaded immediately at place of contact to metazonite proper. Pleurosternal carinae traceable only on rings 2–4 as very low subtransverse and denticulate ridges with a roughly granulate surface around (Figs 7, 12). Epiproct spade-shaped, very broad and flat, rounded and sparsely setose at caudal margin, setae again being mostly arranged in bundles of individual hairs (Figs 9, 14). Each paraproct with two bundles of setae borne on distinct tubercles. Hypoproct semi-circular, high and regularly rounded at caudal margin, there with 1+1 bundles of setae, both being well separated.

Sterna basically unmodified, bare or nearly so, only sometimes with traces of a minute knob near each coxa (Figs 3, 7, 12), cross-impressions very distinct, especially so transverse ones; only sternites between ♂ legs 7 considerably broader and slightly excavate to accommodate tips of gonopods (Fig. 7). Each coxa 2 with a small tubercle, round, low and either perforated and bearing a gonopore (♂, Fig. 7) or blunt, slightly elongate and directed ventrocaudally (♀, Fig. 12). Legs robust, setose rather sparsely and mostly ventrally, ca 1.4–1.5 (♂) or 1.2–1.3 times (♀) as long as midbody height; claws simple, slender, slightly curved ventrad, ca 1/3 as long as tarsus (Fig. 15). Many setae on podomeres unusually strong and long (= macrosetae). In length, femur ≥ tarsus > prefemur = postfemur = tibia > coxa (Figs 3, 7, 12, 15).

Gonopod aperture transversely oval, simple, its caudal rim slightly elevated (Fig. 18). Gonopods (Figs 3, 7, 15–27) with long subcylindrical coxites, both closely adjacent and fused medially at base through a small, central, rudimentary, sternal sclerite; coxites unusually densely setose, setae (= macrosetae) also being unusually long and strong; each coxite with a short, small, simple and unciform cannula, as usual. Telopodites elongate, about twice as long as coxites, simple, directed cephalad and slightly crossing only terminally, each telopodite clearly and deeply bipartite, well delimited against acropodite only laterally; prefemorite (= densely setose part, **pf**) ca 1/3 as long as acropodite, with an inconspicuous vesicle-like structure (**v**) apicomesally at base of solenomere branch (**sl**), the latter the longest and strongest of the two, and a strong, sigmoid, somewhat shorter, more slender, apically acuminate, prefemoral process (**pfp**); **sl** unciform, strongly, but regularly curved mesad, protected by **pfp** on ventral side, branching subapically into a shorter ventral spine and a longer, curved, acuminate, flagelliform solenomere proper. Seminal groove (**sg**) first running mesally on **pf** to twist thereafter ventrolaterally on **pf** before moving through **v** onto **sl**.

REMARKS. Despite as many as five of the congeners being known only from ♀ holotypes [Chamberlin [1941], thus clearly jeopardizing the identity of the younger name *verhoeffi*, we are quite confident that the samples described and illustrated by Kraus [1956] and Vohland [1998] from two lowland parts of Peruvian Amazonia are conspecific. The only size of older material that was published was that of the ♂ holotype: length 60 mm, width 8.3 mm [Kraus, 1956]. This agrees very closely with our data: length 55–57 mm, width 7.5–8.0 mm. The colour was described as uniformly light yellow-brown with orange-yellow calluses on paraterga. One of our ♂♂ also matches this description quite well (Figs 1–5), although most of our samples are dark chocolate brown to dark red-brown with contrasting yellow calluses (Figs 6–14). Minor differences can also be noted in the presence of a small ventral knob near each of coxae 3–6 [Kraus, 1956].

The decisive evidence of conspecificity, however, comes from the gonopodal structure which agrees in every detail, including not only the conformation of the gonotelopodite, but also the abundant macrosetae located on the gonocoxites (Figs 22–24). This latter character, according to the late R.L.

Figs 6–9. *Thrinoxethus verhoeffi* (Kraus, 1956), ♂ from near Santa Rosa: 6–7 — anterior part of body, dorsal and ventral views, respectively; 8 — middle part of body, dorsal view; 9 — posterior part of body, dorsal view. Photographs by K. Makarov, not taken to scale.

Рис. 6–9. *Thrinoxethus* cf. *verhoeffi* (Kraus, 1956), ♂ из окрестностей Santa Rosa: 6–7 — передняя часть тела, соответственно сверху и снизу; 8 — средняя часть тела, сверху; 9 — задняя часть тела, сверху. Фотографии К. Макарова, сняты без масштаба.

Hoffman, is deemed to represent a symplesiomorphy shared, so far as known, only with *T. siolii* (see Vohland [1998]). All minor variations in size, colour, peripheral and gonopodal characters etc. can be regarded as only infraspecific, especially inasmuch as the distribution of *T. verhoeffi* appears to be quite vast (Map).

Now that *T. verhoeffi* has become recorded in a mountainous part of northeastern Peru, the following biogeographic scenario can readily be suggested. The Andean Selva Alta, both the highest montane and the westernmost record, may have served as a source area whence a downstream dispersal into the Ucayali Basin of Amazonia could have occurred, at

least as far east as Alexander von Humboldt National Park in Loreto (Map).

Molecular analyses must definitely be applied to clarify and stabilize the taxonomy of Aphelidesmidae, *Thrinoxethus* included.

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Competing interests. The authors declare no competing interests.

Figs 10–14. *Thrinoxethus verhoeffi* (Kraus, 1956), ♀ from near Santa Rosa: 10 — habitus, dorsal view; 11–12 — anterior part of body, dorsal and ventral views, respectively; 13 — middle part of body, dorsal view; 14 — posterior part of body, dorsal view. Photographs by K. Makarov, not taken to scale.

Рис. 10–14. *Thrinoxethus verhoeffi* (Kraus, 1956), ♀ из окрестностей Santa Rosa: 10 — общий вид, сверху; 11–12 — передняя часть тела, соответственно сверху и снизу; 13 — средняя часть тела, сверху; 14 — задняя часть тела, сверху. Фотографии К. Макарова, сняты без масштаба.

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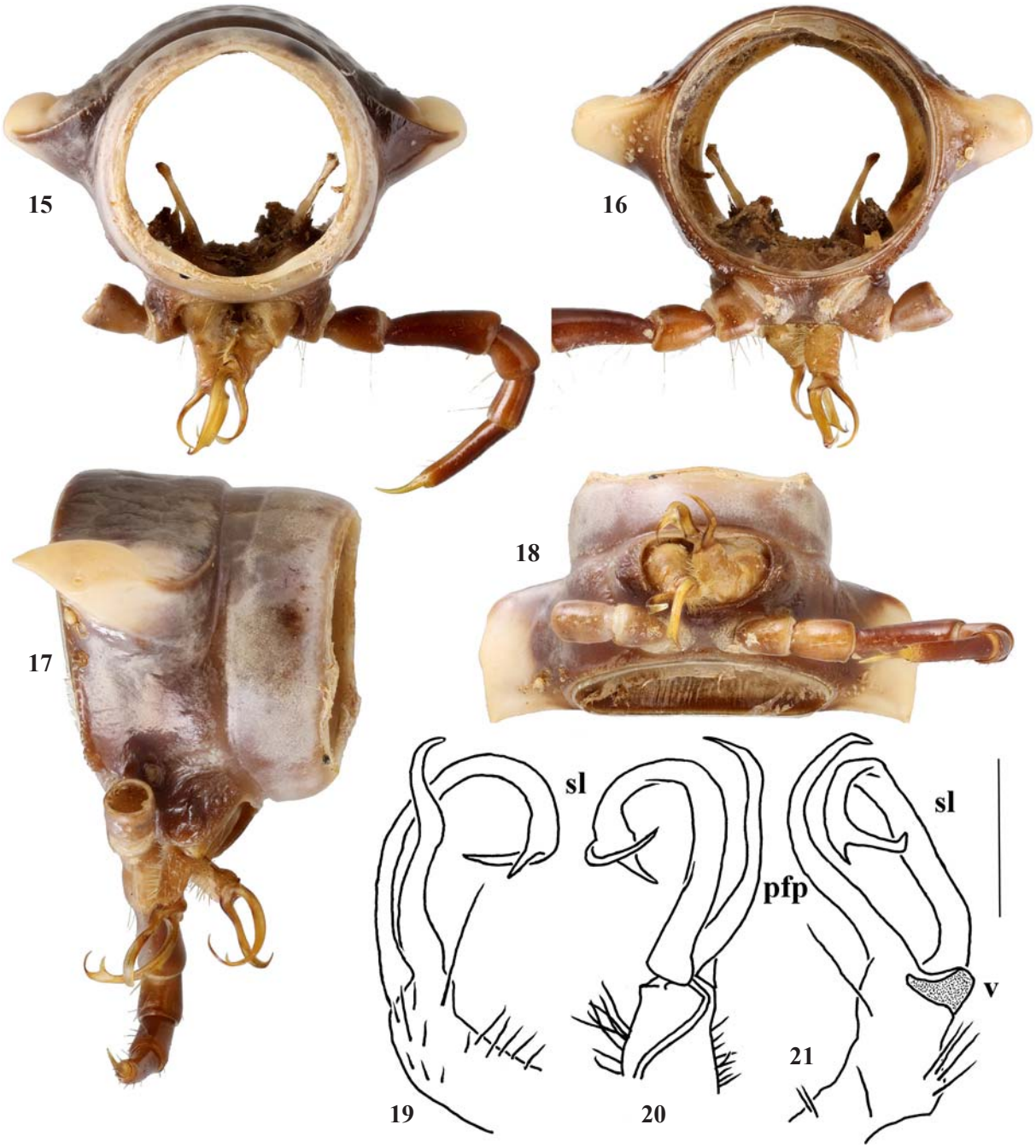
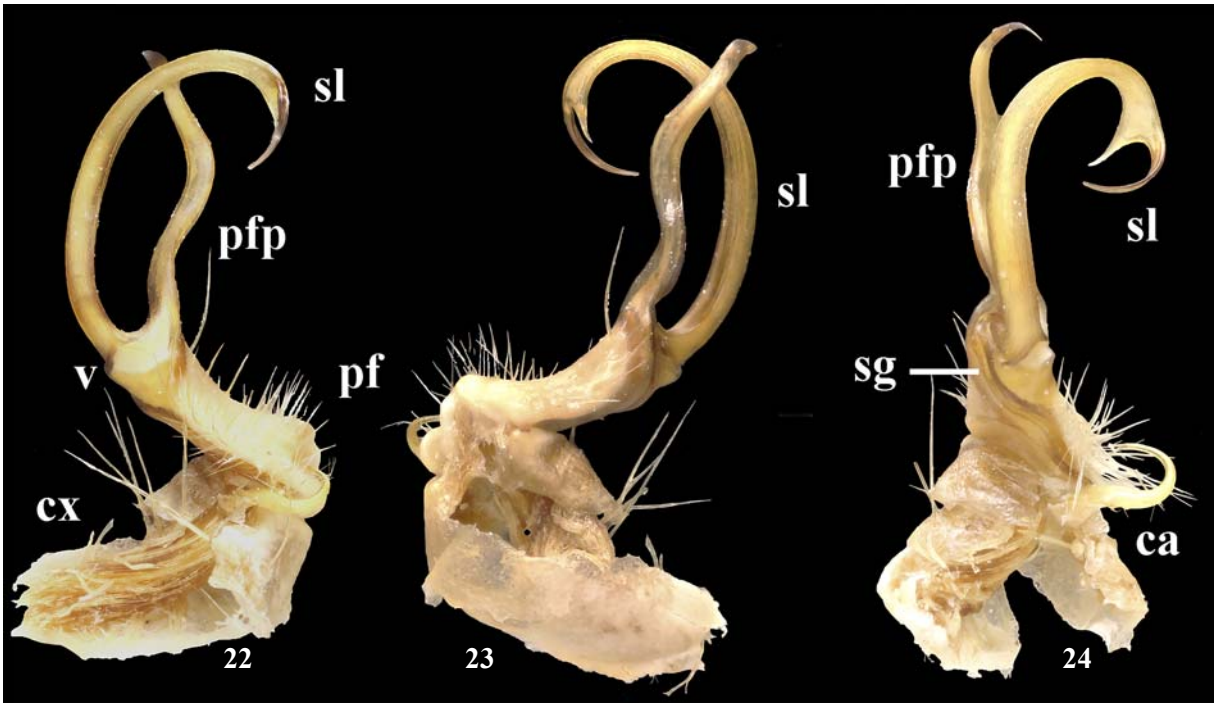


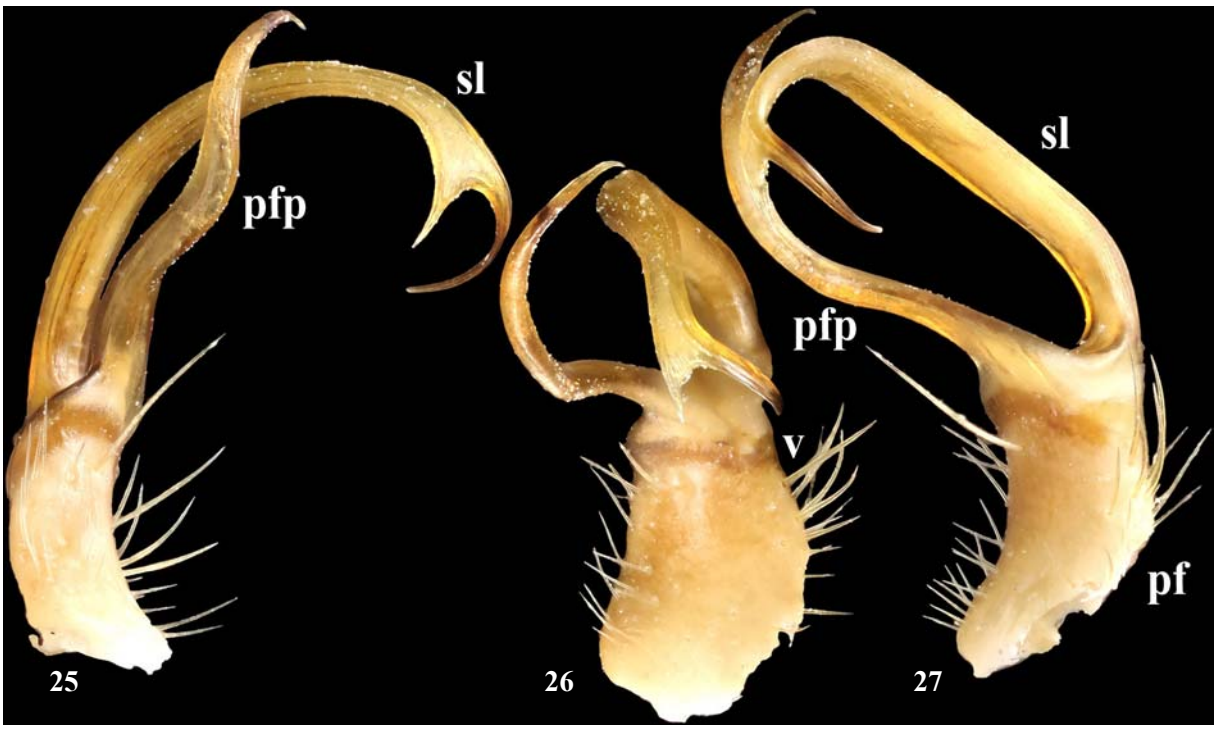
Figs 15–21. *Thrinoxethus verhoeffi* (Kraus, 1956), ♂ from near Santa Rosa: 15–18 — body ring 7 with intact gonopods, anterior, posterior, lateral and ventral views, respectively; 19–21 — right gonopodal telopodite, sublateral, submesal and mesal views, respectively. Abbreviations: pfp — prefemoral process; sl — solenomere; v — vesicle-like structure. Photographs by K. Makarov (15–18), not taken to scale; scale bar: 1.0 mm (19–21).

Рис. 15–21. *Thrinoxethus verhoeffi* (Kraus, 1956), ♂ из окрестностей Santa Rosa: 15–18 — туловищный сегмент 7 с нетронутыми гоноподами, соответственно спереди, сзади, сбоку и снизу anterior, 19–21 — телоподит правого гонопода, соответственно почти сбоку, почти изнутри и изнутри. Обозначения: pfp — префеморальный отросток; sl — соленомер; v — похожая на пузырек структура. Фотографии К. Макарова (15–18), сняты без масштаба; масштаб: 1,0 мм (19–21).



Figs 22–24. *Thrinoxethus verhoeffi* (Kraus, 1956), ♂ from near Santa Rosa, entire left gonopod, mesal, lateral and ventromesal views, respectively. Photographs by A. Korotaeva, not taken to scale. Abbreviations: ca — cannula; pf — prefemorite; pfp — prefemoral process; sg — seminal groove; sl — solenomere; v — vesicle-like structure.

Рис. 22–24. *Thrinoxethus verhoeffi* (Kraus, 1956), ♂ из окрестностей Santa Rosa, левый гонопод целиком, соответственно изнутри, сбоку, одновременно почти снизу и изнутри. Фотографии К. Макарова, сняты без масштаба. Обозначения: ca — канюля; pf — префеморит; pfp — префеморальный отросток; sg — семенная бороздка; sl — соленомер; v — похожая на пузырек структура.



Figs 25–27. *Thrinoxethus verhoeffi* (Kraus, 1956), ♂ from near Santa Rosa, right gonopodal telopodite, sublateral, submesal and mesal views, respectively. Photographs by K. Makarov, not taken to scale. Abbreviations: pf — prefemorite; pfp — prefemoral process; sl — solenomere; v — vesicle-like structure.

Рис. 25–27. *Thrinoxethus verhoeffi* (Kraus, 1956), ♂ из окрестностей Santa Rosa, телоподит правого гонопода, соответственно почти сбоку, почти изнутри и изнутри. Фотографии К. Макарова, сняты без масштаба. Обозначения: pf — префеморит; pfp — префеморальный отросток; sl — соленомер; v — похожая на пузырек структура.

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