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RESEARCH ARTICLE

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The millipede genus *Tetracentrosternus* Pocock, 1895 (Polydesmida, Paradoxosomatidae, Alogolykinae, Alogolykini), with a description of the first, new species from Thailand

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Abstract

The millipede subfamily Alogolykinae and the tribe Alogolykini are recorded in Thailand for the first time, being represented there by *Tetracentrosternus theelorsuensis* **sp. n.** While the new species has characteristics that place it in the genus *Tetracentrosternus*, it also shows a number of unique features that make it necessary to rediagnose this Oriental genus, as well as to key its three currently known species and map their distributions. The tribes Alogolykini and Polydrepanini, as well as the subfamily Alogolykinae are also briefly redefined.

Keywords

Millipede, Alogolykinae, Alogolykini, *Tetracentrosternus*, taxonomy, new species, Thailand

Introduction

The family Paradoxosomatidae has long been known to dominate the millipede fauna of the Oriental realm, including Thailand (Jeekel 1968). Thus, this family accounts for about half of the country's known diplopod species richness (Enghoff 2005). According to our latest estimates, Thailand currently supports 161 nominal species of Diplopoda, of which 71 (about 44%) are paradoxosomatids. They all belong to the nominotypical subfamily Paradoxosomatinae.

All the more interesting is the discovery in Thailand of the first species of the small, purely Oriental subfamily Alogolykinae. This new species, belonging in the small genus *Tetracentrosternus* Pocock, 1895 from the tribe Alogolykini, is described below. Several of its characters are so peculiar that the genus requires a redefinition.

Only two species of *Tetracentrosternus* have hitherto been known: *T. subspinosus* Pocock, 1895, the type species from Myanmar (Pocock 1895, Hoffman 1963, Jeekel 1965), and *T. hoffmani* Golovatch, 2013, from Yunnan, southern China (Golovatch 2013).

Material and methods

The material was collected during a field trip in January 2011 from near Thee Lor Sue Waterfall in the mountains at the frontier between Thailand and Myanmar. Live animals were photographed on the spot. Specimens were preserved in 75% ethanol and studied in the laboratory using an Olympus stereomicroscope. Scanning electron micrographs (SEM) of the right gonopod coated with gold were taken using a JEOL, JSM–5410 LV microscope, returned to alcohol upon examination. Digital images of the specimen were taken in the laboratory and assembled using the "Cell^D" automontage software of the Olympus Soft Imaging Solution GmbH package. In addition, line drawings of the left, completely intact gonopod were also prepared. All material is housed in the Museum of Zoology, Chulalongkorn University (CUMZ), Bangkok, Thailand.

Systematics

Family Paradoxosomatidae Daday, 1889
Subfamily Alogolykinae Hoffman, 1963
Tribe Alogolykini Hoffman, 1963

Genus *Tetracentrosternus* Pocock, 1895

http://species-id.net/wiki/Tetracentrosternus

Diagnosis. Body medium-sized (ca 20–30 mm long, ca 2.0–3.2 mm wide), with 20 segments. Paraterga moderately to strongly developed. Sterna unmodified or with a cone near each coxa. Sternal lobe or cone(s) between ♂ coxae 4 present. First pair of ♂

legs with or without femoral adenostyles. At least some male legs with ventral brushes on tarsi, sometimes also on distal halves of tibiae.

Gonopod with a quite short, subcylindrical, distoventrally densely setose coxite; prefemoral (= setose) part of telopodite short to very short, a quarter or less as long as acropodite, delimited from extremely short femorite by a mesal sulcus, ridge or spine; femorite supporting a long, spiniform, sometimes deeply bipartite femoral process (**fp**) and a similarly long to longer, flagelliform solenomere (**sl**), both more or less clearly sheathed by a mesal fold in basal half of acropodite. The latter suberect to strongly unciform, distal quarter to third with or without evident processes, clearly fimbriate and/or fringed, often phylloid as well.

Type species. *Tetracentrosternus subspinosus* Pocock, 1895; by monotypy.

Other species include *T. hoffmani* Golovatch, 2013 and *T. theelorsuensis* sp. n.

Remarks. Both *Tetracentrosternus* Pocock, 1895 and *T. subspinosus* Pocock, 1895 were originally diagnosed and described too briefly to be readily recognizable. The species was based on a few specimens taken by L. Fea and E. W. Oates at Puepoli (900–1,200 m a.s.l.) and Bia-po, now Carin Cheba (1,000–1,200 m), both in Myanmar (Pocock 1895, Thorell 1895). These two localities lie in the Karin Hills of southeastern Myanmar, in the Tenasserim Mountain Range adjacent to Thailand (Fig. 4).

The sole male of the species, from Puepoli and kept in the British Museum, was redescribed by Hoffman (1963) who designated it as lectotype. Hoffman was the first to provide clear illustrations of its gonopod structure, resulting in the establishment of a new tribe, Alogolykini, to encompass *Tetracentrosternus*, *Alogolykus* Attems, 1936 and *Touranella* Attems, 1937 (Attems 1936, 1937, 1938). Jeekel (1965) redescribed this species in more detail not only from the lectotype, but also from the paralectotypes (from Carin Cheba) still housed in the Genoa Museum. He made new, even more accurate illustrations and a highly detailed redescription, fully accepting the tribe and adding thereto also *Yuennannina* Attems, 1936. A little later, Jeekel (1968) elevated the tribe Alogolykini to the status of a subfamily, Alogolykinae, adding thereto a new tribe, Polydrepanini. Jeekel transferred *Touranella* from Alogolykini to Polydrepanini, because the genus lacks adenostyles on the femora of the male first legs, as do the other constituent genera of the latter tribe.

Tetracentrosternus hoffmani Golovatch, 2013 stems from Mount Gaoligong Shan, western Yunnan, China (Golovatch 2013). Like *T. subspinosus*, it shows adenostyles on male femora 1, a suberect gonopod telopodite with a fringed/fimbriate/spiculate and phylloid apex, and a long, unipartite gonofemoral process.

The new species described below, despite its relative geographical proximity to *T. subspinosus*, shows a number of characters so different that the diagnosis of the genus needs to be refined. Thus, because there are no adenostyles in femora 1 of the male of *T. theelorsuensis* sp. n., this trait can be regarded as only species-specific not only in *Tetracentrosternus*, but in the entire subfamily Alogolykinae. So, following Hoffman (1963), it seems best to return *Touranella* (three species in Vietnam, one in Nepal) to Alogolykini, as its close similarities to *Tetracentrosternus* are apparent. The only meaningful differences lie in gonopod structure, the femoral portion in *Touranella* sometimes being a little longer, the solenomere a little thicker, suberect and rod-shaped rather than flagelliform, while the femoral process when present is considerably shorter (Golovatch 2009a, 2009b). In our opinion, a strong, rod-shaped solenomere versus a thin, flagelliform one remains the basic difference between the tribes Alogolykini and Polydrepanini, respectively. Thereby the subfamily Alogolykinae seems to be best characterized only by the absence of a clear-cut division of the solenophore or solenophore-like structure near/around the solenomere into a membranous *lamina medialis* and/or a similarly membranous *lamina lateralis*, in Polydrepanini often coupled with a twisted, helicoid course of the seminal groove. In addition, the gonofemorite in Alogolykinae is often strongly abbreviated while many species show adenostyles on the male first femora. The latter two traits are also characteristic of the subfamily Australiosomatinae, but the solenophore branch or branches remain free and never sheath a primitively long, strong and rod-like solenomere. A more detailed review of these subfamilies and their tribes (see Jeekel 1968) lies far beyond the scope of the present note.

The gonopod telopodite in *Tetracentrosternus theelorsuensis* sp. n. is strongly elongate and unciform, bearing three evident processes in the distal half, whereas the solenomere is particularly long and nearly as long as the solenophore, while the femoral process is also very long, but deeply bipartite. Besides this, as in *T. subspinosus*, the strongly abbreviated gonofemoral part in the new species is delimited distally by a distinct ridge, as opposed to a strong spine in *T. hoffmani*.

In terms of metatergal structure, *T. theelorsuensis* sp. n. is somewhat intermediate between both congeners, the tegument being only moderately rugulose as opposed to nearly smooth in *T. subspinosus* or rather clearly tuberculate in the rear halves of metaterga in *T. hoffmani*.

There is little doubt that more species of *Tetracentrosternus* await discovery at least in and between eastern Myanmar and southern China, including Thailand (Fig. 4). The same certainly holds true for some other Alogolykini as well, e.g. *Touranella*.

***Tetracentrosternus theelorsuensis* sp. n.**

http://zoobank.org/B30D3F12-C18D-4FFA-A891-46736B54CC7A
http://species-id.net/wiki/Tetracentrosternus_theelorsuensis
Figs 1–3

Holotype ♂ (CUMZ), Thailand, Tak Province, Umphang District, Thee Lor Sue Waterfall, 590 m a.s.l., 15°55'38"N, 98°45'13"E (converted from GPS data), 19.01.2011, leg. N. Likhitrakarn.

Paratypes. ♂ (CUMZ), same District, Mokro Subdistrict, roadside, 1,168 m a.s.l., 16°14'14"N, 98°59'23"E, 20.01.2011, leg. N. Likhitrakarn. 5 ♀, 1 juv. (CUMZ), same District, Pa Wai Waterfall, 804 m a.s.l., 16°34'30"N, 98°50'3"E, 20.01.2011, leg. S. Panha, C. Sutcharit & N. Likhitrakarn.

Name. After Thee Lor Sue Waterfall, the type locality, which is the largest and highest waterfall in Thailand.

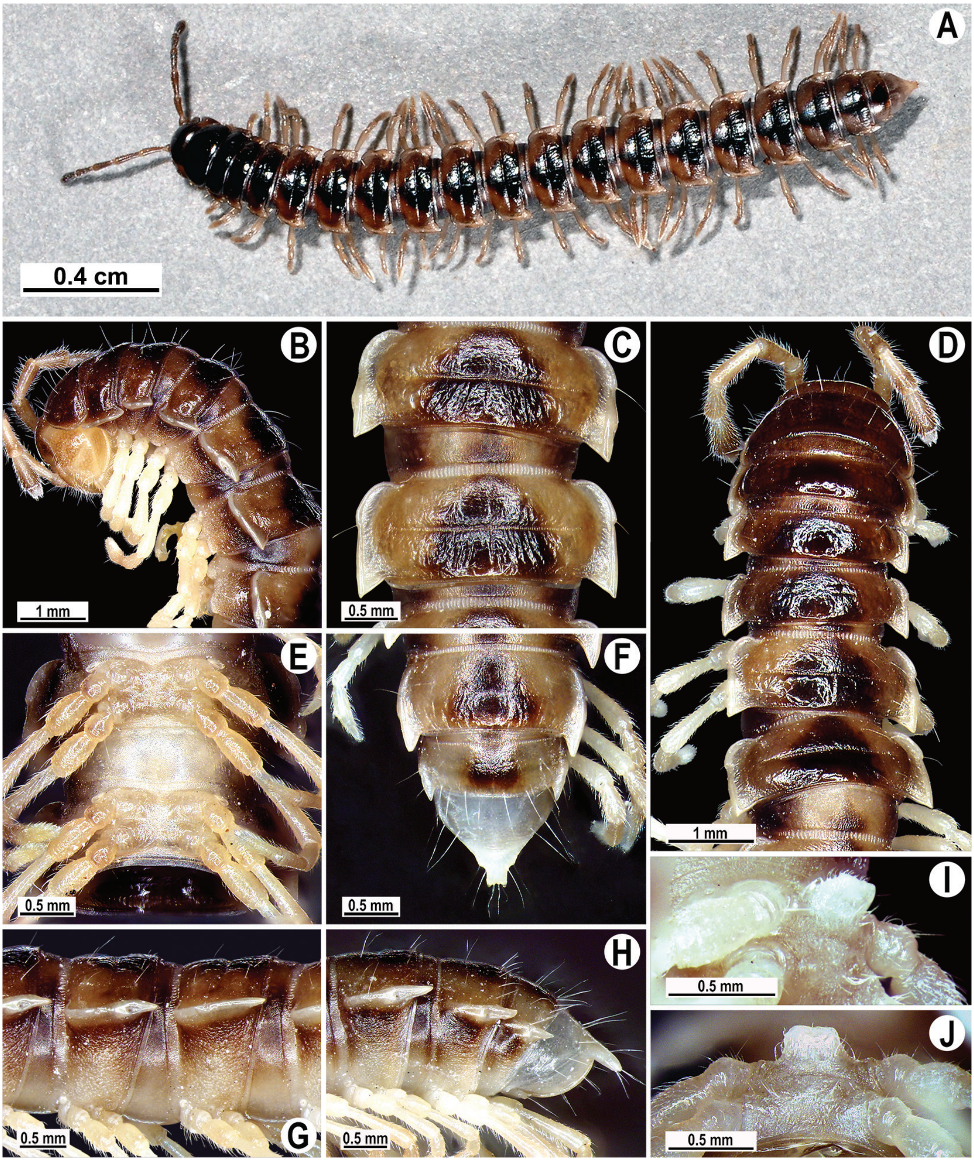

Figure 1. *Tetracentrosternus theelorsuensis* sp. n., ♂ holotype. **A** habitus, live coloration **B, D** anterior part of body, lateral and dorsal views, respectively **C, E, G** segments 10 and 11, dorsal, ventral and lateral views, respectively **F, H** posterior part of body, dorsal and lateral views, respectively **I, J** sternal lobe between coxae 4, sublateral and subcaudal views, respectively.

Diagnosis. Differs from congeners mainly by the first pair of ♂ legs lacking femoral adenostyles, coupled with unmodified sterna and the distal half of the gonopod telopodite being strongly curved, elongate and distally carrying three evident processes. See also Remarks above and Key below.

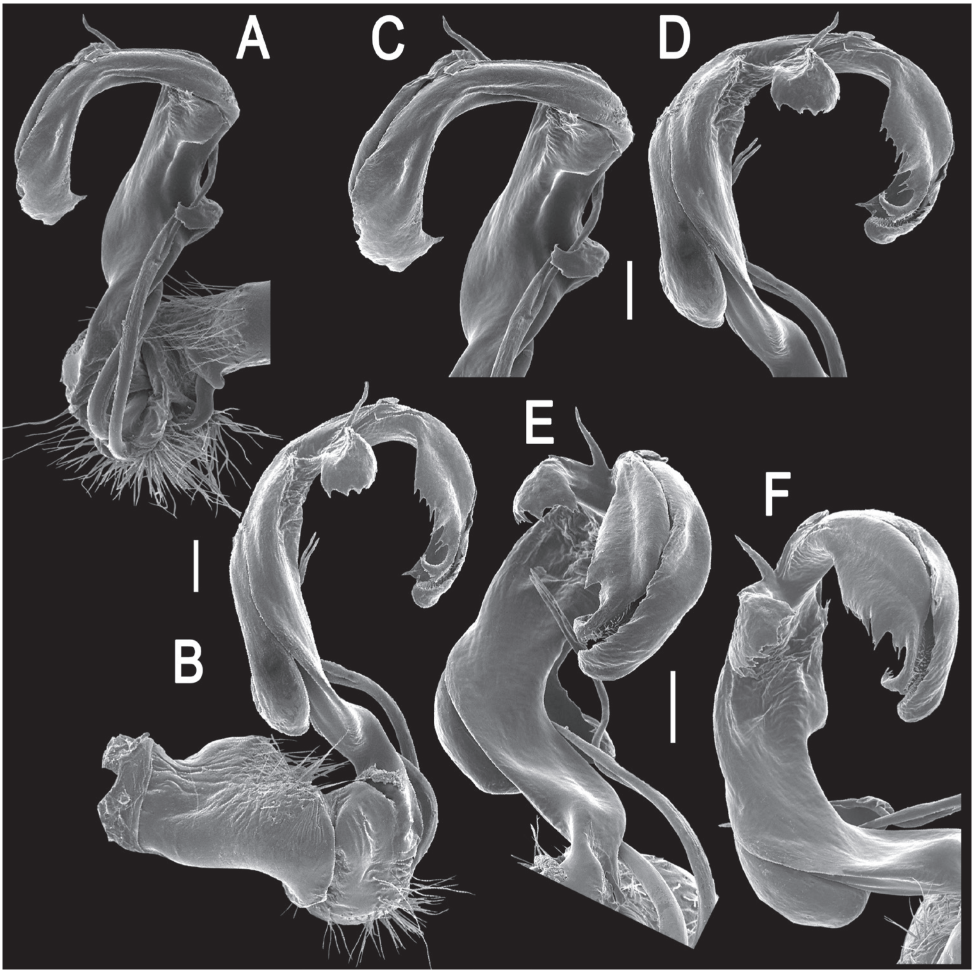

Figure 2. *Tetracentrosternus theelorsuensis* sp. n., ♂ holotype. **A, B** right gonopod (solenomere broken off), mesal and lateral views, respectively **C–F** distal part of right gonopod, mesal, lateral, suboral and subcaudal views, respectively. Scale bar: 0.2 mm.

Description. Length 21–23.5 (♂) or 19.5–22.5 mm (♀), width of midbody pro- and metazona 1.92–1.98 and 2.54–2.75 mm (♂) or 2.07-2.35 and 2.77–3.12 mm (♀), respectively.

Coloration of live animals dark brown (Fig. 1A); paraterga, legs and epiproct light brown, head, collum and metazona 2–4 blackish, following terga with a blackish triangle covering both pro- and metazona; coloration of alcohol material after 2 years of preservation faded to whitish or yellow with a pattern of a contrasting dark brown triangle at posterior edge of pro- and metazona, castaneous brown below paraterga; head and antennomeres 6 and 7 brown to castaneous brown; venter and a few basal

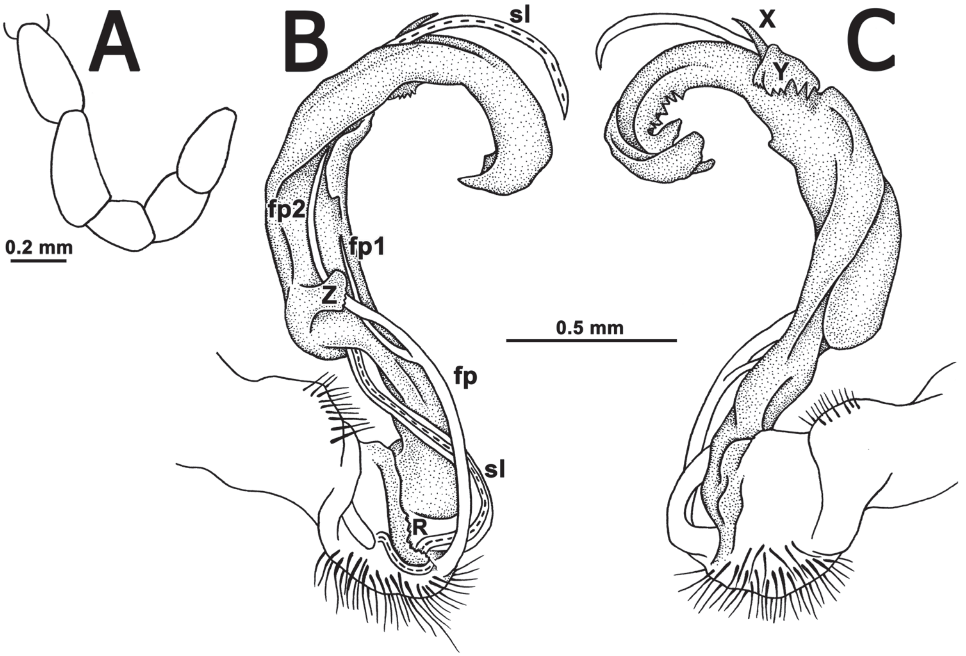

Figure 3. *Tetracentrosternus theelorsuensis* sp. n., ♂ holotype. **A** left first leg **B, C** left gonopod, mesal and lateral views, respectively.

podomeres light brown to yellow-brown, legs growing infuscate (brown) distally; tip of antenna pallid (Fig. 1A–H).

Clypeolabral region and vertex sparsely setose, epicranial suture distinct. Antennae moderately long (Fig. 1A, B), reaching body segment 4 (♂) or 3 (♀) when stretched dorsally. In width, head < collum < segment 3 = 4 < 2 < 5–16 (♂, ♀), thereafter body gently and gradually tapering. Collum with three transverse rows of setae: 5+5 in anterior, 3+3 in intermediate and 4+4 in posterior row; a very faint incision laterally in posterior 1/3; caudal corner of paraterga rounded, slightly declined ventrad, not extending behind rear tergal margin (Fig. 1B, D). Tegument smooth and shining, prozona very finely shagreened, metaterga smooth and delicately rugulose, leathery; surface below paraterga finely microgranulate. Postcollum metaterga with two transverse rows of setae: 2+2 in anterior and 3+3 in posterior row, traceable at least as insertion points when setae broken off. Tergal setae long, strong and slender, about 1/3 of metatergal length. Axial line visible, barely traceable on proterga (♂). Paraterga strongly developed (Fig. 1A–H), especially so in ♂, mostly slightly upturned, lying high (at about upper third of midbody height); caudal corner nearly or fully pointed; either clearly (♂) or only very slightly extending beyond rear tergal margin (♀); paraterga very thin in lateral view, like blunt blades, a little thicker only on pore-bearing segments. Calluses on paraterga 2 delimited by a sulcus both dorsally and ventrally, on following paraterga only dorsally, rather broad on pore-bearing segments. Paraterga 2 broad, anterior edge angular, a little better so in ♀, lateral edge with two small, but evident incisions in anterior half; posterior edge clearly concave (Fig. 1B, D). Anterior edge of paraterga 3–9 clearly convex, of paraterga 10–18 nearly straight and slightly bordered. Lateral edge of paraterga with a slight, but evident incision in anterior 1/3. Posterior edge of paraterga clearly concave, especially strongly so in segments 16–19 (Fig. 1A–D). Ozopores evident, lateral, lying in an ovoid groove at about 1/4 in front of caudal corner. Transverse sulcus usually distinct (Fig. 1C, D, F), slightly incomplete on segments 4, 18 and 19, complete on metaterga 5–17, deep, not reaching bases of paraterga, at most faintly beaded at bottom, a little better developed in ♀. Stricture between pro- and metazona wide, evidently ribbed at bottom down to base of paraterga (Fig. 1B–D, F–H). Pleurosternal carinae complete crests with a sharp caudal tooth in segment 2, a small, caudal, mostly sharp tooth until segment 7 (♂) or 6 (♀) (Fig. 1B, G, H). Epiproct (Fig. 1F, H) conical, flattened dorsoventrally, with two small apical papillae; tip subtruncate; pre-apical papillae small, but visible, lying not too close to tip. Hypoproct roundly subtriangular, setiferous knobs at caudal edge well-separated and evident.

Sterna moderately setose, without modifications; a linguiform, sternal lobe between ♂ coxae 4 (Fig. 1I, J). Adenostyles absent on femur 1 (Fig. 3A). A paramedian pair of evident tubercles in front of gonopod aperture. Legs moderately long and slender, slightly incrassate in ♂, midbody ones ca 1.2–1.3 (♂) or 0.8–1.1 times (♀) as long as midbody height, prefemora without modifications, ♂ tarsal brushes present in all legs.

Gonopods (Figs 2, 3B, C) complex. Coxa a little curved, short, subcylindrical, rather densely setose distoventrally. Prefemur densely setose, length less than 1/4 of femorite + “postfemoral” part. Femorite as usual, very short, delimited distally by a ridge (**R**). Femoral process (**fp**) a slender, distally deeply bipartite flagellum, with branch **fp2** somewhat longer than **fp1**. Acropodite (= solenophore) elongate, clearly unciform, in proximal 1/3 with a small, but distinct, mesal, apically denticulate process (**Z**), in distal 1/4 with a similar, but lateral and more strongly dentate process (**Y**), as well as a spine (**X**) at its base. Solenomere (**sl**) branching off level to **fp**, very long, flagelliform, mostly sheathed by a slightly longer solenophore.

Key to species of *Tetracentrosternus*

1 Paraterga moderately developed, sternal cones present. Myanmar .... ***T. subspinosus***
– Paraterga strongly developed (Fig. 1A, C, D, F), sternal cones absent **2**
2 Gonopod suberect, with a basal gonofemoral tooth and a distally strongly fimbriate/spiculate solenophore, but without evident processes distal to gonofemoral tooth. Southern China ....***T. hoffmani***
– Gonopod strongly elongate and curved distally, supplied with three evident processes distal to femorite (Figs 2, 3). Thailand ...... ***T. theelorsuensis* sp. n.**

Figure 4. Distribution of *Tetracentrosternus* species. **1, 2** *T. subspinosus* (**1** Carin Cheba (= Bia-po) **2** Puepoli) **3** *T. hoffmani* (Mt Gaoligong Shan) **4, 5** *T. theelorsuensis* sp. n. (**4** Thee Lor Sue Waterfall **5** Pa Wai Waterfall).

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RESEARCH ARTICLE

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Beetles that live with ants (Coleoptera, Carabidae, Pseudomorphini): A remarkable new genus and species from Guyane (French Guiana), *Guyanemorpha spectabilis* gen. n., sp. n.

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Abstract

Among the extensive collections currently being made in Guyane (French Guiana), adults of a large and colorful species of pseudomorphine were encountered. The adults present, for the first time in the Western Hemisphere, elytra with a marked color pattern, and in addition a size considerably beyond that of the rest of the members of all other known genera in the Western Hemisphere. Both of these attributes, however, are well known in the Australian pseudomorphine fauna. This new species is described and illustrated and a revised key to the Western Hemisphere genera is included. The type locality of *Guyanemorpha spectabilis* **gen. n.**, **sp. n.** is Guyane, Risquetout, PK20, 4.916°N, 52.516°W, 12m altitude.

Resumen

Entre las colecciones extensivas que actualmente se están conduciendo en Guyane (Guyana Francesa), los adultos de las especies grandes y coloridas de pseudomorfinos fueron encontrados. Los adultos presentan, por primera vez en el hemisferio occidental, élitros con un patrón colorido marcado, además de un tamaño mucho mayor que el resto de los miembros de todos los otros géneros en el hemisferio occidental. Ambos atributos, sin embargo, se conocen bastante bien en la fauna pseudomorfina de Australia. Esta nueva especie se describe e ilustra y una clave revisada para los géneros del hemisferio occidental se incluye. La localidad tipo de *Guyanemorpha spectabilis* **gen. n.**, **sp. n.** es Guyane, Risquetout, PK20, 4.916°N, 52.516°W, altitud de 12m.

Keywords

False-form beetles, identification key, distribution, male genitalia, female ovipositor, Hymenoptera: Formicidae

Palabras clave

Carábidos atípicos, clave de identificación, distribución, genitalia de macho, ovipositor de hembra, Hymenoptera: Formicidae

Introduction

Surprising taxa of Carabidae continue to surface as collections from remote places and new habitats are explored (e.g., Erwin 2000, 2004; Erwin and Geraci 2008). Another such taxon has been discovered in various parts of Guyane during ongoing biotic inventories in reserved areas of Guyane and exploration of that country's insect biodiversity by The Entomological Society Antilles-Guyane (SEAG) (cf. Erwin et al. 2012). The species is remarkable because the adults (Fig. 1) present, for the first time in the Western Hemisphere, elytra with a marked color pattern, and in addition a size considerably beyond that of the rest of members of the other known genera in the Western Hemisphere. Both of these attributes, however, are well known in the Australian pseudomorphine fauna (Baehr 1992, 1997) and it is likely a greater variety of color forms will be found in the future in South America.

Specimens and methods

Included in this study are a total of 4 specimens from other institutions and private collections (Appendix 1). "Methods and species concepts follow those previously described (Ball 1959; Erwin and Kavanaugh 1981; Kavanaugh and Erwin 1991). The species validation and diagnosis format follows as closely as possible that suggested in Erwin and Johnson (2000). Measurements of length (ABL, SBL) and width (TW) follow those of Ball (1972) and Kavanaugh (1979): ABL (apparent body length), measured from apex of labrum to apex of the abdomen; SBL (standardized body length), equals the sum of the lengths of the head (measured from apex of clypeus to a point on midline at level of the posterior edge of compound eyes), PL (pronotal length), measured from apical to basal margin along midline, and LE (elytron length), measured from apex of scutellum to apex of the longer elytron; and TW (total width), measured across both elytra at their widest point with suture closed."

"Habitus and attribute images of the adult beetles portray most of the character states referred to in the key provided. Male and female genitalic presentations are standard for descriptive taxonomy of carabid beetles, and in this case are digital photo-illustrations (Erwin 2011). The images of the adult and its parts were made with a Visionary Digital™ high resolution imaging system. Figure captions include an ADP number, which is a unique identification number for the specimen that was illustrated or imaged and links the specimen and associated illustrations and/or image to additional information in electronic databases at the NMNH.”

“Geographical data are presented based on all known specimens of each species available at the time of manuscript preparation. Georeferences have been determined from locality information provided on specimen labels. Latitude and longitude are reported in decimal degrees. A distribution map is provided for the species [Fig. 5]. Here, an English vernacular name is proposed, as vernacular names are becoming increasingly needed in conservation and/or agricultural and forestry applications, as well as for the Encyclopedia of Life (www.eol.org),” (Erwin and Amundson in press).

Accounts of taxa

Western Hemisphere genera of Pseudomorphini Newman 1842

Guyanemorpha Erwin, gen. n. Guyane (French Guiana)
Manumorpha Erwin & Geraci, 2008. Brazil, Ecuador, Guyane, Perú
Notopseudomorpha (Baehr, 1997). Middle and South America
Pseudomorpha (s. str.) Kirby, 1825. USA south to Argentina (incl. Caribbean islands)
Samiriamorpha Erwin & Geraci, 2008. Perú
Tuxtlamorpha Erwin & Geraci, 2008. México, Honduras
Yasunimorpha Erwin & Geraci, 2008. Ecuador

Key to the Western Hemisphere genera of Pseudomorphini Newman 1842

1 Mouthparts not visible in dorsal aspect. Preocular lobe absent.................... **2**
1’ Mouthparts visible in dorsal aspect. Preocular lobe present........................ **3**
2(1) Dorsal surface glabrous, markedly shiny... ***Notopseudomorpha* (Baehr, 1997)**
2’ Dorsal surface finely setiferous, not shiny.. ***Samiriamorpha* Erwin & Geraci, 2008**
3(1’) Elytron with only scutellar and ombilicate setae; with elytra markedly tapered to apex.. **4**
3’ Elytron multisetiferous; body form rather broad and subdepressed with elytra not or barely tapered to broadly round apex **5**
4(3’) Body form narrow, somewhat cylindrical .... ***Yasunimorpha* Erwin & Geraci, 2008**
4’ Body form very broad, not cylindrical...................... ***Guyanemorpha* gen. n.**
5(3) Dorsal surface with dense vestiture, of very long thick erect setae equal in length at least to basal 4 antennomeres, but no pubescence; body form subconvex, elytra tapered posteriorly...... ***Manumorpha* Erwin & Geraci, 2008**
5’ Dorsal surface with sparse or no long vestiture, longer setae equal in length only to at most basal 3 antennomeres, also usually with short pubescence; body form subconvex, elytra slightly tapered posteriorly or not.................. **6**

6(5') Major setae of dorsal surface erect or slightly curved posteriorly .... ***Pseudomorpha* Kirby, 1825**

6' Major setae of elytra posteriorly directed and markedly decumbent .... ***Tuxtlamorpha* Erwin & Geraci, 2008**

Pseudomorphini Newman, 1842

http://species-id.net/wiki/Pseudomorphini

Pseudomorphini Newman, 1842:365 (as Pseudomorphites)

Proposed english vernacular name. False-form beetles.

Taxonomy. Stable at the generic level.

Classification. According to Ober and Maddison (2008), Pseudomorphini appears as a branch of the higher Carabidae and associated with Graphipterini and Orthogonini; according to Erwin and Geraci (2008), the adelphotaxon is the tribe Orthogonini. All three tribes are associated in some way with ants or termites. Male genitalia of pseudomorphines have a bonnet-shaped phallobase as in the lebiomorphs, yet their accompanying parameres are large and nearly symmetrical (and in some species the parameres are sparsely setiferous), as in some primitive lineages of the family. Many known lineages of Pseudomorphini have been so highly selected for life with ants (and possibly termites) that external structures do not help much in discovering more normal carabid relatives (cf. Erwin and Amundson, in press).

Taxonomy references. Baehr (1992, 1997); Erwin and Amundson (in press); Erwin and Geraci (2008); Notman (1925), Ogueta (1967).

Larval references. Erwin (1981); Lenko (1972); Liebherr and Kavanaugh (1985), Moore (1964, 1974, 1983).

Guyanemorpha Erwin, gen. n.

http://zoobank.org/66A2E5B7-0831-4E1E-8AD2-ECE683F0AD8D
http://species-id.net/wiki/Guyanemorpha

Type species. *Guyanemorpha spectabilis* Erwin, sp. n.

Proposed english vernacular generic name. Guyane False-form beetles

Adelphotaxon. Probably *Notopseudomorpha* (Baehr, 1997) (see Erwin and Geraci 2008 for phylogeny).

Description. Head (Fig. 2) without supraorbital setigerous punctures, nor any accessory setae; frontal impressions absent. Labrum barely visible with anterior margin shallowly emarginate, quadrisetose; clypeus markedly wide, nearly obscured in dorsal aspect by protruding frons, with obtuse setiferous lateral corners. Eyes slightly convex; small gena with numerous stout setae. Antenna short, just reaching anterior coxa in repose; antennomeres 3-9 slightly wider than 1-3, and appearing slightly flattened. Mandible markedly flattened with a very short and acute apex; outer margin ventral of the scrobe without short stout setae. Maxillary palpi markedly short, 3-segmented, palpomeres slightly depressed, palpomere 3 truncate apically. Labial palpus with short bisetose palpomere 2; palpomere 3 markedly securiform and robust, its distal margin mostly membranous with sensory organs.

Prothorax. Pronotum (Fig. 1) much wider than head, transverse, with narrowly beaded margins; without a pair of setigerous punctures each side, apical, lateral and posterior margins with fringe of short stout setae; hind angles obtuse, broadly rounded. Prosternal process unisetiferous subapically, intercoxal process feebly beaded.

Pterothorax. Metepisternum elongate and markedly narrowed posteriorly, the outer margin about 2 times greater in length than the anterior margin, posterior margin about 0.2 times anterior margin.

Elytra. Elytron (Fig. 1) tapered, markedly narrower apically, width of elytra about equal to that of pronotum at widest point, apical margin truncate with evenly rounded humerus, interneurs and intervals effaced; parascutellar stria absent, scutellum hidden, parascutellar puncture present, marked; without fixed discal setae, surface glabrous. Lateral marginal (umbilical) series of 10 setae, arrayed throughout and widely spaced; lateral margin with fringe of short stout setae.

Hind wings. Macropterous. Venation (Fig. 3).

Legs. Short and depressed, femur posteriorly channeled for reception of tibia in repose; antennal comb notch very shallow; tibial spurs normal; anterior tarsi of male with tarsomeres 2–4 dilated slightly, ventrally each with two laterally placed rows of adhesive articulo-setae.

Abdomen. Abdominal sterna III–VII with patches of short setae and each of IV–VII with a single row of erect ambulatory setae numbering 2 to 8 setae; V and VI in male each with dense row of yellowish robust setae separated medially.

Male genitalia (Fig. 4). Phallobase hooded with small orifice, dorsum not crested; phalloshaft arched throughout its length, diameter sub-rounded to somewhat depressed dorso-ventrally; phalloapex produced, sharp, rounded, markedly depressed dorso-ventrally; endophallus orifice elongate, endophallus with dense patches of microtrichia. Parameres (C) moderately short compared to those of genus *Pseudomorpha*, nearly equal in length, left slightly longer and much broader than right, each apically glabrous. Ring sclerite (E) normal for family.

Female ovipositor and genital tract (Fig. 1). Gonocoxite 2 falcate, base about as long as blade, latter relatively short, pointed distally; margins without ensiform setae; with short preapical nematiform seta.

Guyanemorpha spectabilis Erwin, sp. n.

http://zoobank.org/B86F564C-10FD-43CD-B257-DDE8425CF0D7
http://species-id.net/wiki/Guyanemorpha_spectabilis
Figures 1–5

Holotype. Guyane (French Guiana): Risquetout, PK20, 4.916°N, 52.516°W, 12m, 13 December 2010 (SEAG)(NMNH, held in trust, see below: ADP132101, female). Paratypes are listed below under other specimens examined.

Figure 1. *Guyanemorpha spectabilis* sp. n., female holotype, ADP132101; Risquetout, PK20, Guyane. Habitus and female genital tract glued to card, dorsal aspect, ABL = 13.2mm.

Derivation of specific epithet. The epithet "*spectabilis*" is a Latin adjective describing the very large and colorful beetle species.

Proposed english vernacular name. Spectacular Guyane False-form beetle.

Diagnosis. With the attributes of the genus as described above and color black and rufous with elytral spots (Fig. 1), color tone of head and pronotum uniform black; form broad and stout with tapered elytra; head with preapical lobe prominent but hidden in dorsal aspect beneath the frons, about 2/3 the length of the anterior margin of eye; pronotum (Fig. 1) coequal at base to elytra across humeri; elytron markedly tapered from humerus to narrower truncated apex and without interneurs or intervals, surface glabrous except parascutellar seta and 8 ombilicate setae near lateral margin.

Description. (Figs 1, 2, 3, 4; Appendix 3). Size: Very large for a Western Hemisphere species, ABL = 13.18 to 13.51 mm, SBL = 11.05 to 12.18 mm, TW = 6.36 to 6.86 mm.

2

3

Figure 2–3. 2 *Guyanemorpha spectabilis* sp. n., female holotype, ADP132101; Risquetout, PK20, Guyane. Head, dorsal planar aspect **3** *Guyanemorpha spectabilis* sp. n., female paratype, ADP132105; Nouragues, Saut Pararé, Guyane. Left flight wing, dorsal aspect.

Preocular lobe-eye ratio (L/L): 0.49 to 0.54. Pronotum ratio (L/W): 1.99 to 2.16. Pronotum ratio (W/L): 2.20 to 2.29. As described for genus above and the diagnosis.

Dispersal potential. These beetles are macropterous and have been recorded from flight intercept traps (FITs), hence fully capable of flight; they are likely swift and agile runners as other species in the Tribe. Accordingly, this species may be expected to be more broadly distributed across a wider geographical range than current records indicate.

Way of life. Adults of other pseudomorphines in the Western Hemisphere are found in ant nests and the surrounding vicinity and possibly in termite nests (Ogueta 1967); female adults of species of *Pseudomorpha* are ovoviviparous (Liebherr and Ka-

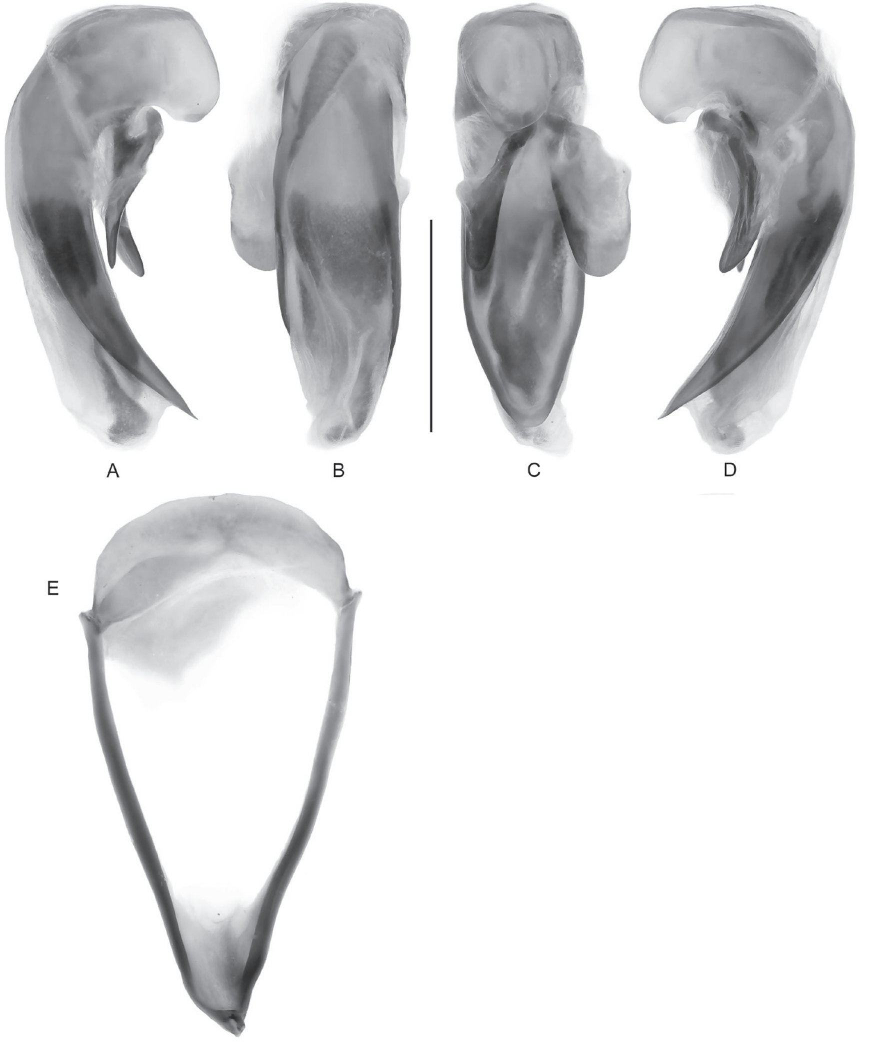

Figure 4. *Guyanemorpha spectabilis* sp. n., male paratype, ADP132103; Risquetout, PK20, Guyane. Male genitalia, median lobe and parameres labeled as in repose in male **A** ventral aspect **B** right lateral aspect **C** left lateral aspect **D** dorsal aspect.

vanaugh 1985); *Pseudomorpha* and *Notopseudomorpha* larvae are ant nest inquilines (Erwin 1981, Lenko 1972). Members of *G. spectabilis* occur at lowland rainforest sites and most likely live with ants. They have been found in July and December.

Other specimens examined. Guyane: Réserve Trésor, 4.610°N, 52.279°W, 225m, 11 July 2009 (S. Brule)(BMNH, ADP124772, male paratype); Risquetout, PK20, 4.916°N, 52.516°W, 12m, 13 December 2010 (J.L. Giuglaris) (MNHP: ADP132103); Nouragues, Saut Pararé, 4.02°N, 52.41°W, 51m, 14 July 2010 (SEAG) (MNHP, ADP132105, female paratype).

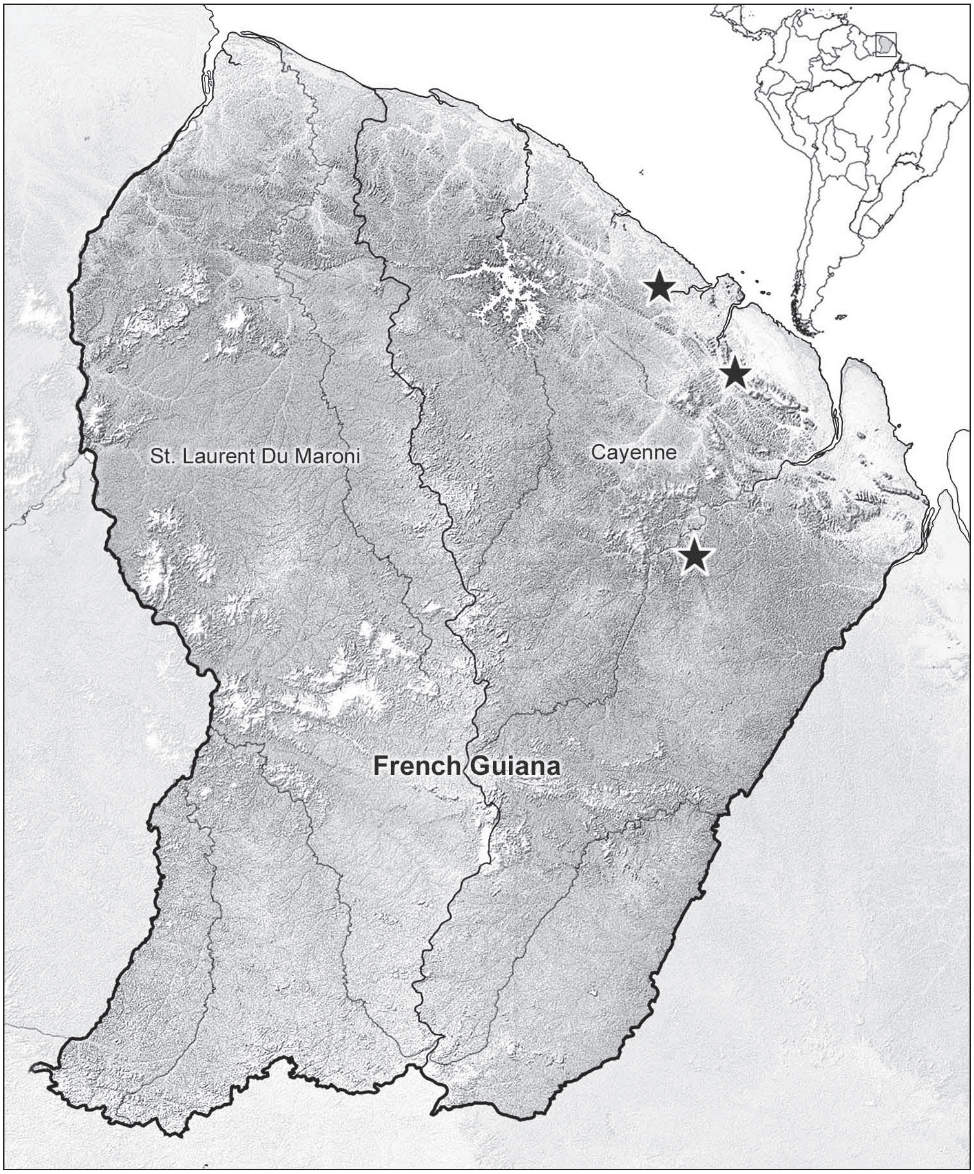

Figure 5. Distribution dot map for known localities of *Guyanemorpha spectabilis* sp. n.

Geographic distribution. (Fig. 5). This species is currently known only from Guyane.

Note. The holotype is currently held in trust at the National Museum of Natural History, Smithsonian Institution, Washington, DC until the planned Natural History Museum of Guyane is established, and at that time the specimen will be transferred there. See details of SEAG carabid collections in Erwin et al. 2012.

Concluding statement

Adults of *Guyanemorpha* share attributes with those of both *Notopseudomorpha* (Baehr) and *Yasunimorpha* Erwin & Geraci. This surprising large and colorful pseudomorphine came as a shock to the author, as all other species of the Tribe in the Western Hemisphere are quite dull fulvous, rufous, or black with no, or little, color contrast on the dorsal surface. Since little in the way of life information is available for the four specimens reported herein except seasonality of adult activity and lowland habitation, only speculation based on fogging samples in Perú and Ecuador can add much to this conclusion. "The pseudomorphines are a very interesting evolutionary off-shoot of the normal carabid morphotype in both form and function and are only just now beginning to be understood in North America. The fact that species of related genera in South America are living with arboreal ants will make learning about them far more difficult. Insecticidal fogging gets adults of these species, but only tearing apart arboreal *Azteca* ant nests while suspended in a tree will produce their larvae, and that is not for carabidologists faint of heart." Erwin and Amundson (in press).

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Appendix 1

Institutions and personnel who loaned specimens for this revision.

BMNH	Maxwell V. L. Barclay, Curator and Collection Manager, Entomology: Coleoptera & Hemiptera, Department of Life Sciences, Natural History Museum, London SW7 5BD
SEAG	S. Brule, J.L. Giuglaris, The Entomological Society Antilles-Guyane, stephanebrule973@hotmail.fr

Appendix 2

Errata: In Erwin and Geraci (2008), Figure captions 13 and 14 are reversed. Fig 13 is *Notopseudomorpha* sp., Costa Rica, and fig. 14 is *Pseudomorpha excrucians* Kirby.

Appendix 3

Table 1. Measurements and ratios for *Guyanemorpha spectabilis* sp. n., all measurements are in millimeters.

Total length (sbl)					
Males			Females		
N	Range	Mean	N	Range	Mean
2	12.079–12.135	12.107	2	11.053–12.185	11.844
Maximum width (tw)					
Males			Females		
N	Range	Mean	N	Range	Mean
2	6.356–6.378	6.367	2	6.41–6.864	6.637
W of head/w of left elytron					
Males			Females		
N	Range	Mean	N	Range	Mean
2	1.041–1.069	1.055	2	0.980–0.991	0.986
Pronotum: width (at widest part)/length					
Males			Females		
N	Range	Mean	N	Range	Mean
2	2.193–2.220	2.207	2	2.253–2.327	2.29
Length of pronotum / length of head					
Males			Females		
N	Range	Mean	N	Range	Mean
2	1.959–2.027	1.993	2	2.040–2.285	2.163
Apparent body length (abl)					
Males			Females		
N	Range	Mean	N	Range	Mean
2	13.510–14.480	13.995	2	13.180–14.180	13.68
Pre-ocular length / eye length					
Males			Females		
N	Range	Mean	N	Range	Mean
2	0.435–0.554	0.494	2	0.520–0.551	0.535

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RESEARCH ARTICLE

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A taxonomic study on the genus *Harpapion* Voss, 1966 from China (Coleoptera, Apionidae)

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Abstract

Harpapion safranum **sp. n.** and *Harpapion borisi* **sp. n.** are described and figured. *Harpapion vietnamense* (Korotyaev, 1987) is recorded as new for China. The genitalia and terminalia of *H. considerandum*, *H. coelebs* and *H. vietnamense* are redescribed and redrawn. The diagnostic characters of *Harpapion* are defined. A key to the known species of the genus *Harpapion* from China is provided. Affinities with the genus *Flavopodapion* Korotyaev, 1987 are discussed.

Keywords

Weevil, *Flavopodapion*, new species, new record, morphology, systematics, key

Introduction

The apionid genus *Harpapion* was erected and initially placed as a subgenus of *Apiotherium* Beguin-Billecocq, 1905 by Voss (1966), and it was later treated as a genus of Apioninae *incertae sedis* by Alonso-Zarazaga and Lyal (1999). Recently, it was considered a member of the tribe Aspidapiini Alonso-Zarazaga, 1990 based on its elongate-triangular scutellum and the genitalia with apparently primitive traits (Alonso-Zarazaga 2011). Moreover, it was recognized as an Afrotropical and Arabian genus (Alonso-Zarazaga and Lyal 1999) until two species, *H. coelebs* (Korotyaev, 1987) and *H. vietnamense* (Korotyaev, 1985), respectively from China and Vietnam were identified as new records of *Harpapion* in Southeast Asia (Alonso-Zarazaga et al. 2011). Wanat (1990) redescribed and figured in detail the Eritrean species *H. dongollanum* (Wagner, 1910), and then Alonso-Zarazaga et al. (2011) pointed out the diagnostic characters of *Harpapion* compared with *Pseudaspidapion* Wanat, 1990.

Recently, we obtained two more specimens of the monotypic species *H. vietnamense*, as well as two series of specimens which are considered to be two new species of the genus *Harpapion* from South China. In describing the new species below, we have also documented and figured the genitalia of *H. considerandum* (type species of *Harpapion*), *H. coelebs* and *H. vietnamense*.

Materials and methods

Materials examined of the new species for this study are to be deposited in the Institute of Zoology, Chinese Academy of Sciences, Beijing (IZCAS) and the Biological Museum, Sun Yat-Sen University, Guangdong (BMSYU). Type and identified specimens were obtained from BMSYU, Natural History Museum (NHM), Zoological Institute (ZIN) on loan or belong to IZCAS.

Descriptions were made and photographs were taken with a Canon EOS 5D mounted on a Nikon SMZ1500. Extended focus images were generated with CombineZM and edited with Adobe Photoshop CS 5.0 when required. Microscopic slides were studied under a Leica DM 2500 microscope and photos were taken with a Nikon CoolPix P7100. Drawings were made from the original photographs by using the software Adobe Illustrator CS5.0, or directly by using a drawing tube attached to the microscope.

Scanning Electron Microscope (SEM) photos were taken with a FEI ESEM Quanta 450 device and the software xT microscope control. Specimens were cleaned by hair pencil and mounted on the mounting card directly.

Nomenclature of the rostral parts follows Alonso-Zarazaga (1989) and that of genitalia follows Alonso-Zarazaga (1990).

The dissecting method used follows Alonso-Zarazaga (1990). Abdomens were put into 10% NaOH for several hours until the inner tissues were digested, and the resultant structures were placed on a temporary microscope slide for examination.

After description, the genitalia and other parts of each specimen were placed in DMHF on an acetate card for long term conservation (Steedman 1958; Bameul 1990).

Labels are described as they are (in Chinese or Cyrillic), with pinyin romanization for Chinese and ISO 9:1995 for Russian, and translations in square brackets; labels are separated by semicolons and lines by slashes. Alternative modern pinyin romanizations are also given in some cases where labels are written using other romanization systems, like Wade-Giles.

Taxonomic treatment

Harpapion Voss, 1966

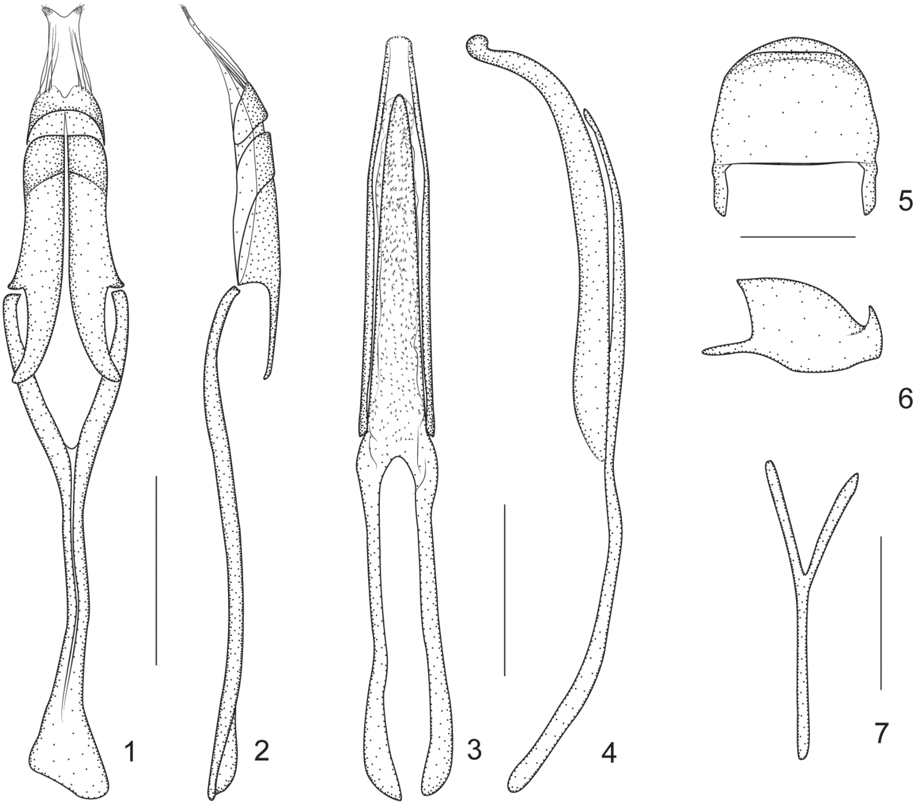
According to species examined, the diagnostic characters of *Harpapion* could be defined as follows: 1) scutellum triangular, distinctly elongate and basally projecting, apically raised (Figure 13); 2) the meso- and metatibial mucros are evidently elongate and bent at their apices (rather than short and straight in *Pseudaspidapion*) (Figures 14, 16); 3) the rostrum is clearly dilated at the antennal insertion and distinctly constricted apicad in dorsal view; 4) the setae fringing the front margin of pronotum are parallel to it; 5) the scales are broad, especially on the meso- and metarostrum, head and propleuron, etc. 6) the 1st elytral stria at base reaches the middle level of the scutellum; 7) the pygidium is of the aspidapionine type, subsemicircular in dorsal view, with the apical flange strongly raised, the transverse sulcus deep but not cutting the sides; 8) the ninth sternite (spiculum gastrale) is Y-shaped, slender and subsymmetrical, not winged; 9) the apex of the penis is moderately to distinctly curved in lateral view, sometimes the pedon is recurved at apex; 10) the tegminal plate is articulated with the free ring, laterally developed, enveloping; the parameroid lobes present a usually well developed apical membranous area with a small apical notch, the basal sclerotized area has a medial sinuation in its front margin and bears 4-7 macrochaetae on each side; the fenestrae are present and variable; the prostegium is bidentate with two lateral projections (absent in *H. coelebs*).

Harpapion considerandum (Fåhraeus, 1871)

http://species-id.net/wiki/Harpapion_considerandum
Figures 1–7

Remarks. *Pygidium* subsemicircular in dorsal view, 0.83× as long as wide, apical flange strongly raised, transverse sulcus deep (Figure 5–6).

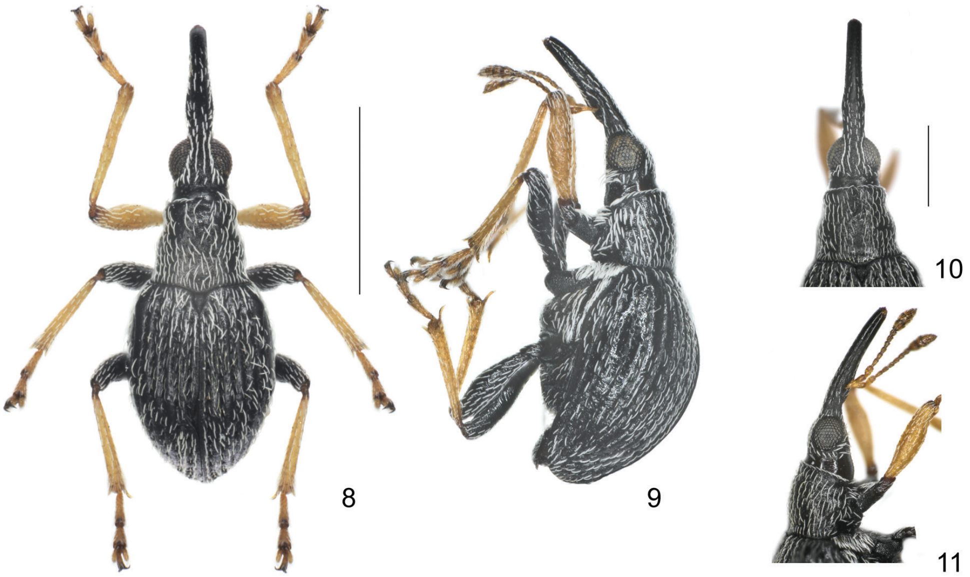
Genitalia and terminalia. Ninth sternite (spiculum gastrale) Y-shaped, slender and nearly symmetrical, not winged, manubrium about 1.21× as long as arms (Figure 7). Penis in dorsal view with pedon gradually and distinctly constricted apicad from apical 1/3, apex rounded, tectum apically constricted; temones moderately elongate, about 0.76× as long as pedon; in side view pedon extremely incurved at apical 1/4, nearly forming a 60° angle, with apical plate slightly recurved at extreme apex, without projections; endophallus with dense tiny spicules (Figures 3–4). Tegminal plate articulated with free ring, laterally developed, enveloping; parameroid lobes with apical membranous area long, bearing two tufts of visible microchaetae apically; basal sclerotized area elongate, front margin weakly sinuate medially, bearing 4 long macrochaetae dorsolaterally on each side; fenestrae large, not separated; linea arquata visible; prostegium bidentate, teeth elongate, curved; median unsclerotized strip elongate and nearly reaching the anterior margin of fenestrae. Manubrial apex asymmetrically broadened (Figures 1–2).



Figures 1–7. *H. considerandum* Fåhraeus, 1871 **1** tegmen, dorsal view **2** tegmen, lateral view **3** penis, dorsal view **4** penis, lateral view **5** pygidium, dorsal view **6** pygidium, lateral view **7** ninth sternite (spiculum gastrale). Scales (mm): **1–2**: 0.2, **3–4**: 0.2, **5–6**: 0.1, 7: 0.1.

Materials. 1♂: (white, printed): Magila / E. Africa / A. V. Legros / 98-190; (white, printed and handwritten): Wagner det. ♂ / considerandum Fåhr.; 1♀: (white, handwritten): X. 1983 / in clove tree / CIEA15888; (white, handwritten): Tanzania / Zanjibar / Kitunda; (white, printed): pres by: Comm Inst Ent B. M. 1984-1. Specimens in the NHM.

Distribution. *Harpapion considerandum* s. str. has been recorded from the following African countries: Guinea, Cameroon, Republic of the Congo, Democratic Republic of the Congo (ex Zaire), Chad, Ethiopia, Kenya, Tanzania, Uganda, Angola, Zimbabwe and South Africa (Eastern Cape, Western Cape and Natal) (Balfour-Browne 1944; Beguin-Billecocq 1910; Fåhraeus 1871; Hoffmann 1968a, 1968b; Hustache 1929, 1939; Marshall 1940; Voss 1959, 1966, 1974; Wagner 1911). Two subspecies, whose status is doubtful, have been recorded as follows: ssp. *circumscriptum* (Hartmann, 1897) from Senegal, Guinea, Mali, Nigeria and Tanzania (Hartmann 1897; Voss 1966); and ssp. *combustum* (Wagner, 1908) from Tanzania and Angola (Marshall 1953; Wagner 1908).



Figures 8–11. *Flavopodapion gilvipes* (Gemminger, 1871) **8** male, dorsal view **9** male, lateral view **10** female, head and rostrum, dorsal view **11** female, head and rostrum, lateral view. Scales (mm): **8–9**: 1.0, **10–11**: 0.5.

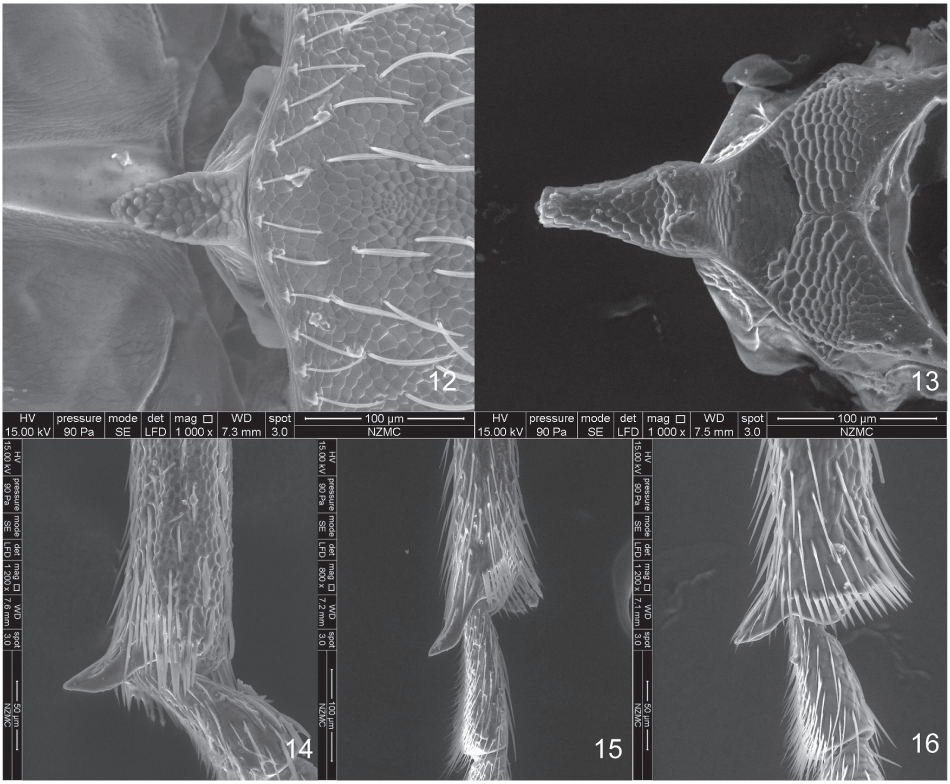
Harpapion coelebs (Korotyaev, 1987)

http://species-id.net/wiki/Harpapion_coelebs

Figures 25–32

Remarks. *Pygidium* subsemicircular in dorsal view, 0.83× as long as wide, apical flange strongly raised, transverse sulcus distinctly depressed and wide, disc with 2–3 rows of punctures between disc and sulcus, pubescent sparse and minute (Figures 29–30).

Genitalia and terminalia. Eighth sternite transverse, with apical edge wide, slightly concave (Figure 31). Ninth sternite (spiculum gastrale) Y-shaped, very weak, almost symmetrical, not winged, manubrium about 1.83× as long as arms (Figure 32). Penis in dorsal view with sides almost parallel, apical plate ogival and distinctly constricted apicad in a short rectangular projection, with 2 subdentiform projections, tectum evidently constricted apicad, in side view, pedon depressed, moderately curved, apical plate slightly incurved; temones slim, about 0.43× as long as pedon; endophallus with markedly dense spicules (Figures 27–28). Tegminal plate articulated with free ring, moderately depressed, slightly enveloping laterally; parameroid lobes with apical membranous area long and tapering apicad, without microchaetae; basal sclerotized area short, front margin widely sinuate in middle, with 6 long macrochaetae and 8-10 sensilla on each side; fenestrae distinctly enlarged, transverse, narrowly separated; linea arquata visible; prostegium extremely concave without any projections; median unsclerotized strip elongate and surpassing fenestrae. Manubrial



Figures 12–16. SEM photos **12–13** scutellum **12** *F. gilvipes* (Gemminger, 1871) **13** *H. safranum* sp. n.**14–16** metatibial mucro **14** *H. safranum* sp. n. **15** *F. gilvipes* (Gemminger, 1871) **16** *Pseudaspidapion botanicum* Alonso-Zarazaga & Wang, 2011.

apex broken when dissected (the apex of manubrium should be tangled inside the thorax) (Figures 25–26).

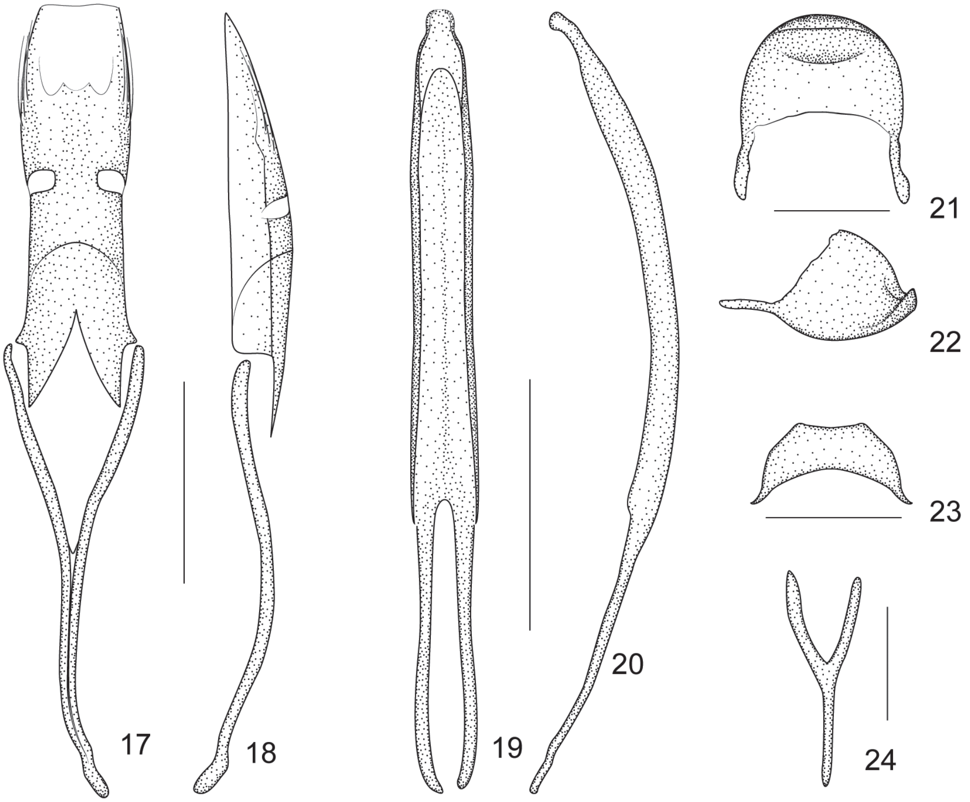
Materials. Paratype: 1♂: (white, printed): 云南景东董家坟 [Yúnnán JǐngDōng Dǒngjiāfén] / 1956.V.28/1250m / leg. 克雷让诺夫斯基 [Kryzhanovsky]; (white, printed): Юньнань, 10 км. N Цзин- [Yúnnán, 10 km north of Jǐng-] / дуна [-Dōng], 1250 м, 28. V. 1956 / Крыжановский [Kryzhanovsky].

Distribution. Yunnan.

Harpapion vietnamense (Korotyaev, 1987)

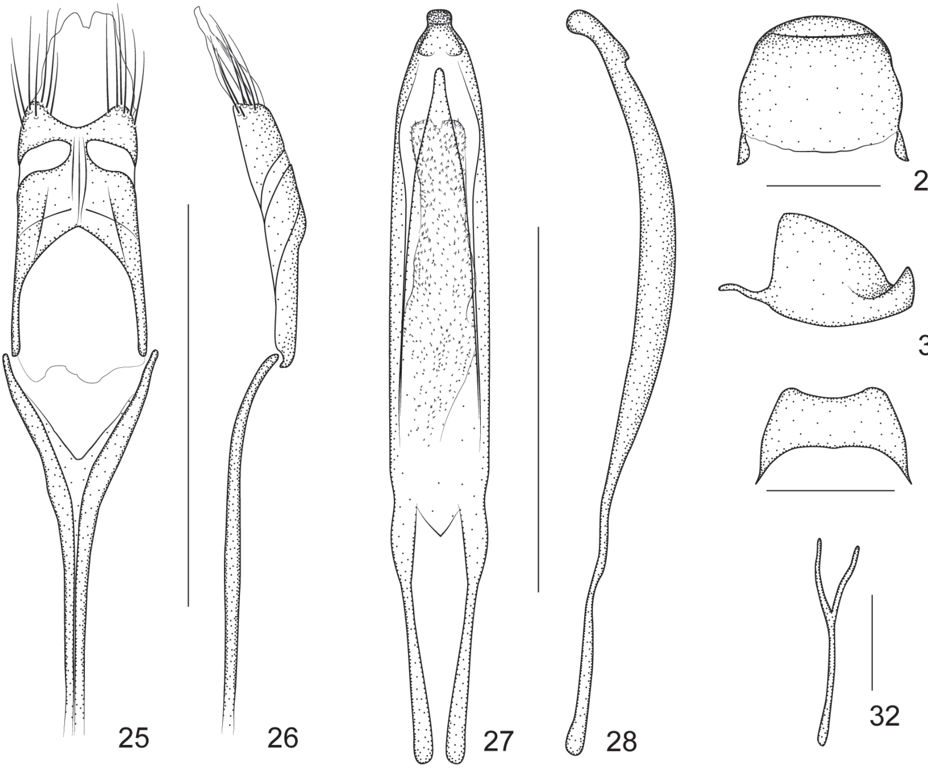
http://species-id.net/wiki/Harpapion_vietnamense
Figures 33–40

Remarks. *Pygidium* subsemicircular in dorsal view, 0.89× as long as wide, apical flange strongly raised, transverse sulcus deep and narrow, disc nearly smooth, without visible punctures or pubescence (Figures 37–38).



Figures 17–24. *Flavopodapion gilvipes* (Gemminger, 1871) **17** tegmen, dorsal view **18** tegmen, lateral view **19** penis, dorsal view **20** penis, lateral view **21** pygidium, dorsal view **22** pygidium, lateral view **23** eighth sternite, dorsal view **24** ninth sternite (spiculum gastrale). Scales (mm): **17–18**: 0.2, **19–20**: 0.2, **21–22**: 0.1, **23**: 0.1, **24**: 0.1.

Genitalia and terminalia. Eighth sternite moderately elongate, apical edge constricted, relatively concave, basal edge with a medial tubercle, sides distinctly extended backwards (Figure 39). Ninth sternite (spiculum gastrale) Y-shaped, symmetrical, not winged, manubrium about 2.25× as long as arms (Figure 40). Penis in dorsal view with pedon sides almost parallel, apically elongate and distinctly constricted halfway, with 2 subdentiform projections, tectum evidently dilated apicad, in lateral view, pedon slightly depressed, apical plate distinctly elongate and gently curved ventrad, extreme apex recurved; temones about 0.74× as long as pedon; endophallus in anterior half with dense spicules and basal half with 2 sclerotized semicylindrical, hollow structures fused at base (Figures 35–36). Tegminal plate articulated with free ring, about 0.94× as long as manubrium, moderately depressed, slightly enveloping laterally; apical membranous area of parameroid lobes developed and extremely tapering apicad, with a minute apical notch, without distinctly visible microchaetae; basal sclerotized area slightly elongated, front margin widely and roundly sinuate, with 5–6 long macrochaetae and 8-10 sensilla on

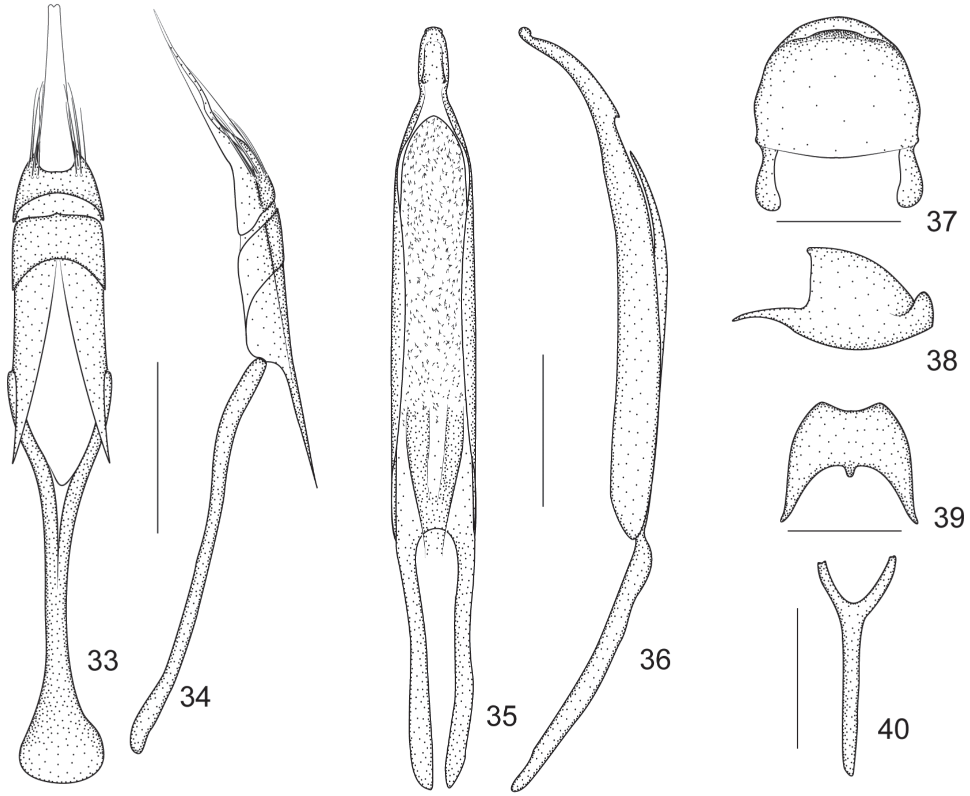


Figures 25–32. *Harpapion coelebs* (Korotyaev, 1987) **25** tegmen, dorsal view **26** tegmen, lateral view **27** penis, dorsal view **28** penis, lateral view **29** pygidium, dorsal view **30** pygidium, lateral view **31** eighth sternite, dorsal view **32** ninth sternite (spiculum gastrale). Scales (mm): **25–26**: 0.5, **27–28**: 0.5, **29–30**: 0.2, **31**: 0.2, **32**: 0.1.

each side; fenestrae tranverse, not separated; linea arquata present; prostegium evidently bidentate, teeth elongate, almost straight, acute; median unsclerotized strip elongate and reaching the linea arquata. Manubrial apex distinctly broadened (Figures 33–34).

Materials. Holotype. ♂ (white, handwritten): Вьетнам, пров. Хашонбинь [V’etnam, prov. Hašonbin’] [Vietnam, prov. Hà Sơn Bình] / 7 км ю.-в. Хоабиня, вторичный тропический лес и кустарник на склоне [7 km û.-v. Hoabinâ, vtoričnyj tropičeskij les i kustarnik na sklone] [7 km SE of Hòa Bình, tropical secondary forest and scrub on the hillside] / 17. X 1976 / leg. Л. Н. Медведев [L. N. Medvedev]; 1♂: 云南景洪勐海县纳板河 [Yúnnán Jĭnghóng Mĕnghăixiàn Nàbănhé] / 保护区过门山（森林） [băohùqū Guòménshān (sēn lín [forest]) / 2009.V.06, 1114m; 22.24644°N, 100.60610°E, 飞阻 [Fēizŭ (flight intercept)] / 采集人：孟令曾 [Căijírén (leg.): Mèng Lìngzēng]; Guomenshan, VI/1D / 06.05.2009/ leg. L. Z. Meng; IOZ(E)1369311; 1♂: 云碧大开河 [Yún Bì Dàkāihé] / 1957.IV.23 / 朱增浩 [leg. Zhū Zēnghào]; IOZ(E)1639312.

Distribution. Yunnan (new record for China), Vietnam.



Figures 33–40. *Harpapion vietnamense* (Korotyaev, 1987) **33** tegmen, dorsal view **34** tegmen, lateral view **35** penis, dorsal view **36** penis, lateral view **37** pygidium, dorsal view **38** pygidium, lateral view **39** eighth sternite, dorsal view **40** ninth sternite (spiculum gastrale). Scales (mm): **33–34**: 0.2, **35–36**: 0.2, **37–38**: 0.2, **39**: 0.2, **40**: 0.2.

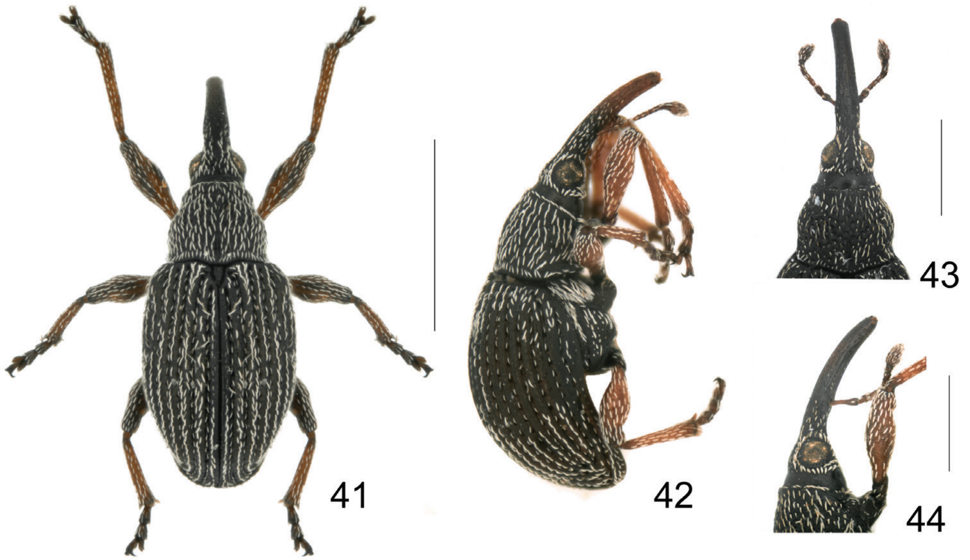
Harpapion safranum Wang & Alonso-Zarazaga, sp. n.

http://zoobank.org/887BB3CE-2FF2-4337-A439-88763EA93AE1
http://species-id.net/wiki/Harpapion_safranum
Figures 13, 14, 41–52

Description (holotype). *Measurements* (in mm): Standard length: 1.84. Rostrum: length: 0.77, maximum width: 0.16. Pronotum: median length: 0.53, maximum width: 0.57. Elytra: median length: 1.33, maximum width: 0.92.

Integument (Figures 41–42) generally piceous, antennae, prorostrum and tarsi dark reddish brown, femora reddish brown, and tibiae pale reddish brown.

Vestiture composed of distinctly whitish, thick, lanceolate scales with acute to rounded apices, rarely truncate (some scales on hind margin of eyes elliptical to nearly rhombic) and grayish acute hairs on antennae, tibiae and tarsomeres. Pronotal vestiture centripetal, scales on apex parallel to margin, but on base perpendicular to margin, pronotal disc with scales distinctly longer and thicker than on legs, reaching base of



Figures 41–44. *Harpapion safranum* sp. n. **41** male, dorsal view **42** male, lateral view **43** female, head and rostrum, dorsal view **44** female, head and rostrum, lateral view. Scales (mm): **41–42**: 1.0, **43–44**: 0.5.

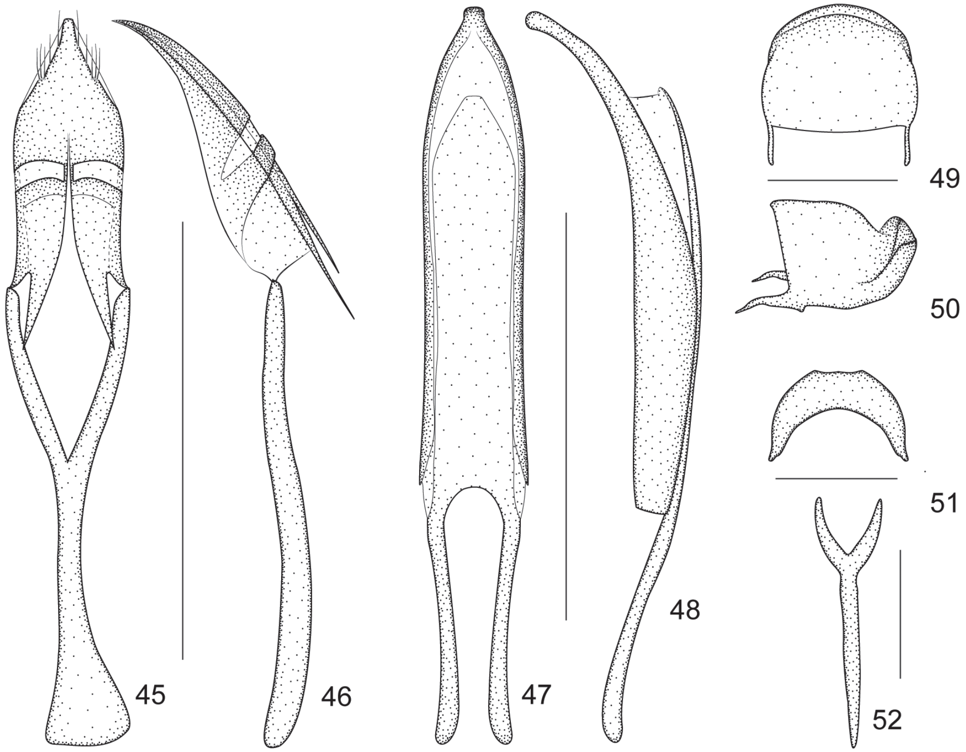
anterior scales. Elytral scales in one row per interstriae, two irregular rows on disc, scales on striae 1/2-2/3 as long as scales on interstriae. One specialized seta on apical region of 9th interstria.

Rostrum cylindrical and moderately robust, in dorsal view 8.25× as long as apical width, 1.45× as long as pronotum in midline, widest at mesorostrum, prorostrum constricted apicad, metarostrum with sides almost parallel, metarostrum with median dorsal area impunctate, dorsal submedial sulci and dorsal submedial keels weak, minutely punctate and pubescent, lateral area of metarostrum and prorostrum with weak oblong confluent punctures, weakly microreticulate, apical third of prorostrum almost impunctate, smooth and shining; in lateral view moderately curved, sides converging to apex, carinae and sulci weak, ventral medial keel fine and complete, ventral sublateral keels with dense line of scales under mesorostrum.

Head transverse, frons very weakly convex, as wide as metarostrum, constricted behind eyes, medial area impunctate and glabrous, lateral areas with irregular rows of punctures and scales, subocular keel not reaching middle of eyes, area between subocular keel flat, microreticulate and impunctate. Eyes round, moderately convex.

Antennae inserted at basal 0.23 of rostral length, scape 3.20× as long as wide, about as long as mesorostral width. Pedicel 2.00× as long as wide, as long as desmomeres 2+3, desmomeres 2–3 1.33× as long as wide, desmomeres 4–5 and 7 1.00× as long as wide, desmomere 6 0.75× as long as wide. Club oval, slightly flattened, 1.88× as long as wide, as long as last 5.5 desmomeres, sutures obsolete.

Pronotum campaniform, 0.93× as long as wide, apical constriction relatively strong, little wider at base than at middle, base 1.39× as wide as apex, bisinuate with rounded



Figures 45–52. *Harpapion safranum* sp. n. **45** tegmen, dorsal view **46** tegmen, lateral view **47** penis, dorsal view **48** penis, lateral view **49** pygidium, dorsal view **50** pygidium, lateral view **51** eighth sternite, dorsal view **52** ninth sternite (spiculum gastrale). Scales (mm): **45–46**: 0.5, **47–48**: 0.5, **49–50**: 0.2, **51**: 0.2, **52**: 0.2.

medial projection towards scutellum, basal flange developed. Prescutellar fovea shallow, very short, about as broad as diameter of one puncture, as long as 2–3 diameters, reaching 1/4 of pronotum. Discal punctures relatively deep, ca. 0.5–1× diameter apart, interspaces moderately convex, microreticulate.

Scutellum elongate, triangular, ca. 2.00× as long as wide, 2 basal tubercles fused at base in front view, apical tubercle rounded, slightly prominent and hardly visible in lateral view (Figure 13).

Elytra elongate, 1.45× as long as wide, 2.51× as long as pronotum, widest almost at middle, humeri moderately developed, striae deep, about as wide as interstriae, punctures elongate, apically connected 1+2+9, 3+4, 5+6, 7+8, interstriae evidently convex with small punctures, surface distinctly wrinkled, not microreticulate, shining.

Ventral areas. Mesocoxae separated by a distance of 0.17× own transverse diameter. Metasternum 0.88× as long as mesocoxae. Mesosternal apophysis more prominent than metasternal apophysis. Anterior metasternal rim present. Abdominal ventrites microreticulate, length ratio along midline: 32-16-4-6-17. Ventrites 1-4 coarsely punctate, Ventrite 5 minutely punctate with median convexity. Suture I marked only on sides, erased in middle, distance from hind margin of metacoxae as long as ventrite 2. Ventrite 5 semicircular, transverse, 0.41× as long as wide. Pygidium subsemicircular, 0.71× as long as wide, apical flange strongly raised with row of punctures and hairs; transverse sulcus deep; disc pubescent and punctured as that of ventrite 5 (Figures 49–50).

Legs. Profemora little larger than metafemora, slightly robust, 3.11× as long as wide, widest at middle, minutely punctate. Protibiae almost straight, 7.05× as long as wide (Figure 33). Protarsomere 1 1.93× as long as wide, protarsomere 2 1.25× as long as wide, protarsomere 3 bilobed, 0.82× as long as wide, lobes narrow, onychium 2.75× as long as wide, projecting from lobes of tarsomere 3 for 0.55× its length. Meso- and metatibial mucrones distinctly elongate and bent at apices (Figure 14), mesotibial mucro ca. 0.50× as long as apical tibial width, metatibial mucro longer than mesotibial one, ca. 0.67× as long as apical tibial width. Tarsal claws with conspicuous obtuse basal teeth.

Genitalia and terminalia. Eighth sternite moderately elongate, constricted to narrow, truncate apical margin, basal margin with sides distinctly extended backward (Figure 51). Ninth sternite (spiculum gastrale) Y-shaped, not winged, manubrium ca. 3.00× as long as arms (Figure 52). Penis in dorsal view with pedon slightly widened at level of ostium, distinctly constricted apicad, apical plate ogival, apex with button-like prong, tectum with sides almost parallel, apically moderately constricted, in lateral view, pedon depressed, moderately curved, apical plate slightly incurved; temones about 0.50× as long as aedeagal tube; endophallus without obvious structures (Figures 47–48). Tegminal plate articulated with free ring, laterally enveloping,; apical membranous area of parameroid lobes undeveloped, only laterally visible, without microchaetae; basal sclerotized area extremely enlarged and extended apicad, triangular-shaped, with 5 short macrochaetae on each lateroapical edge, without sensilla; fenestrae short, transverse, narrowly separated; linea arquata present, very close to basal margin of fenestrae; prostegium bidentate, teeth acute, slightly curved; median unsclerotized strip elongate and surpassing fenestrae. Manubrial apex evidently and asymmetrically broadened (Figures 45–46).

Variation. Male paratypes. Measurements (mm, n=5): Standard length: 1.62–1.90. Rostrum: length: 0.61–0.75, maximum width: 0.14–0.16. Pronotum: median length: 0.47–0.57, maximum width: 0.51–0.60. Elytra: median length: 1.26–1.46, maximum width: 0.72–0.92. Female paratypes (Figures 43–44). Measurements (mm, n=2): Standard length: 1.80-1.86. Rostrum: length: 0.72-0.79, maximum width: 0.16-0.17. Pronotum: median length: 0.51-0.54, maximum width: 0.56-0.58. Elytra: median length: 1.44-1.42, maximum width: 0.90-0.91. Females differ from males by the rostrum entirely black without reddish apex, about 1.41–1.46× longer than pronotum, antennae inserted at basal 0.33 of rostrum, tibiae simple, unarmed. Otherwise practically as in male.

Type-locality. China, Guangdong: Zhongshan City eighth district, 22°30'58.82"N 113°23'36.81"E.

Materials. Holotype: 1♂: 广东中山八区 [Guǎngdōng Zhōngshān Bāqū] / 1957.VII.31; 中国科学院 [zhōngguókēxuéyuàn] / 山坡草地 [shānpōcǎodì] / 46; IOZ(E)1639313; Paratypes: 3♂: Kwangtung [Guǎngdōng] S. China / Loh Fau Shan, [Luófúshān], / Poh-lo [Bóluó] District / April 6–8, 1934 / K. C. Yeung; En-

071380-En-071382; 1♂: Hong Kong: Un-long [Yuánláng], / New Territories / September 19. 1940 / J. Linsley Gressitt; En-071403; 1♂: Hainan I. South China / Ta-hian [probably Dàoxiǎng], Alt. 300 met. / N. side, 5- Finger Mts. [Wúzhǐshān] / VI-12-1935 / L. Gressitt / En-071423; 1♀: Kwangtung [Guǎngdōng], S. China / Ho-yün [Heyun] to Wui-lung [probably Wéilóng] / Ho-yuen [Héyuán] District / Apr. 7, 1940. J. L. / Gressitt & F. K. To; En-071409; 1♀: Kwangtung [Guǎngdōng], S. China. / Sin-fung [Xīnfēng] to Lung-kai [Longgai (probably Lóngjīe which can be found on the modern maps)]. / Sin-fung [Xīnfēng] & Lien-p'ing [Liánpíng] / Dist's, Apr. 12, 1940 / L. Gressitt & F. E. To; En-071367.

Distribution. Guangdong, Hong Kong, Hainan.

Type deposition. Holotype will be deposited in IZCAS, while all paratypes in BMSYU.

Remarks. *Harpapion safranum* sp. n., can be easily recognized from other species from China by its external characters (red colour of entire legs and antennae, etc.) However, it is extremely similar to *H. considerandum* which can be distinguished from the former by genitalia which were described above and illustrated in Figures 1–7.

Etymology. This species is named *safranum* after its testaceous legs. This is a Medieval Latin name of the plant now called *Crocus sativus* L. (saffron) which yields a yellowish-orange dye. It is considered a noun in apposition.

Harpapion borisi Wang & Alonso-Zarazaga, sp. n.

http://zoobank.org/03462889-EF2B-418A-BAE5-394758F1E2DB
http://species-id.net/wiki/Harpapion_borisi
Figures 53–62

Description (holotype). *Measurements* (in mm). Standard length: 1.22. Rostrum: length: 0.44, maximum width: 0.08. Pronotum: median length: 0.36, maximum width: 0.41. Elytra: length: 0.94, maximum width: 0.54.

Integument generally piceous, tibiae and tarsi relatively paler and antennae pale reddish brown (Figures 53–54).

Vestiture composed of whitish to semitransparent, partly thick, lanceolate scales with acute to rounded apices, and semi-transparent acute hairs on antennae, tibiae and tarsomeres. Head, meta- and mesorostrum bearing broader scales with rounded apices, prorostrum nearly glabrous. Pronotal vestiture centripetal, scales on apex parallel to margin, on base perpendicular to margin, pronotal sides with scales distinctly longer and thicker than those on disc and elytra, reaching base of anterior scales. Elytral scales in one regular row per interstria, scales on striae tiny, grayish to transparent. One specialized seta on apical region of 9th interstria.

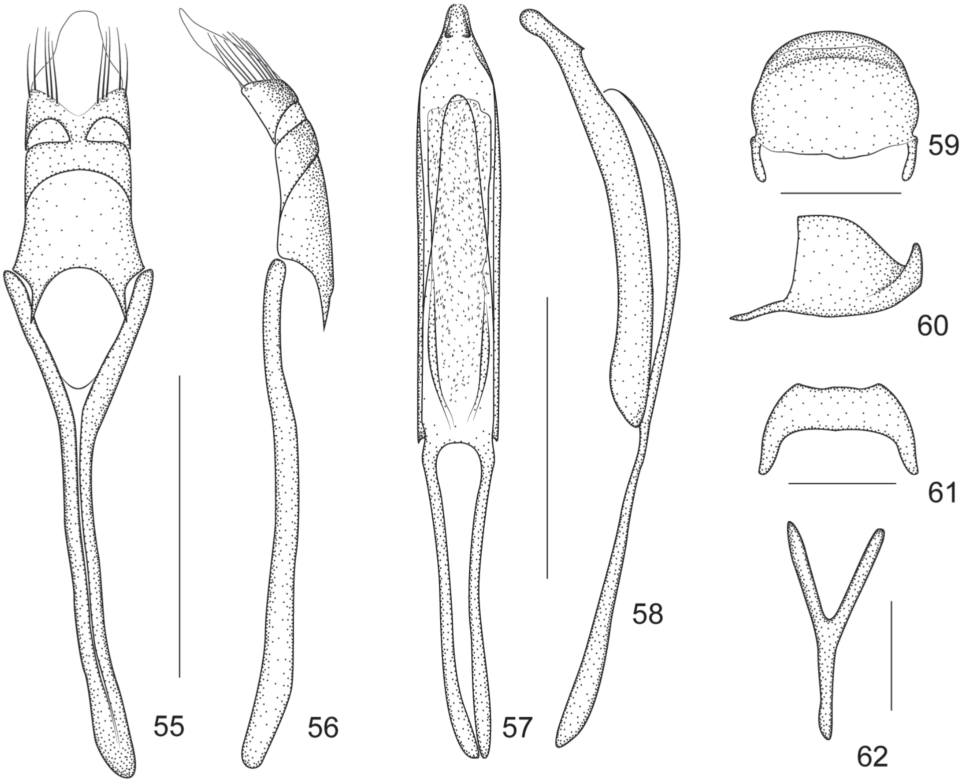
Rostrum cylindrical and moderately robust, in dorsal view 5.71× as long as apical width, 1.22× as long as pronotum in midline, widest at mesorostrum, prorostrum tapering apicad, tube-shaped, metarostrum slightly constricted at rostral base, metarostrum with no distinct sulci, two very shallow and parallel punctate dorsal submedial sulci expanded from mesorostral level to nearly middle of prorostrum,

Figures 53–54. *Harpapion borisi* sp. n. **53** male, dorsal view **54** male, lateral view. Scales (mm): **53–54**: 1.0.

meso- and metarostrum surface microreticulate, matte, prorostrum smooth, shining, almost impunctate; in lateral view weakly curved, almost straight, sides converging to apex, each side with very thin low dorsal sublateral keel running from front margin of eye to upper margin of scrobe and beyond, limiting ventrally dorsal sublateral sulcus.

Head almost as long as wide, frons very weakly convex and slightly narrower than metarostrum, constricted behind eyes, medial area rough, wrinkled, subocular keels curving to meet medially, nearly reaching middle of eyes, area between subocular keel flat, microreticulate and impunctate. Eyes subcircular, distinctly convex.

Antennae inserted at basal 0.22 of rostral length, scape 2.5× as long as wide, about 0.71× as long as mesorostral width. Pedicel 1.75× as long as wide, nearly as long as desmomeres 2+3+4, desmomeres 2 2.0× as long as wide, desmomeres 3–7 ca. 1.00× as long as wide; club oval, slightly flat, 2.0× as long as wide, as long as the last 5.5 desmomeres, sutures obsolete.



Figures 55–62. *Harpapion borisi* sp. n. **55** tegmen, dorsal view **56** tegmen, lateral view **57** penis, dorsal view **58** penis, lateral view **59** pygidium, dorsal view **60** pygidium, lateral view **61** eighth sternite, dorsal view **62** ninth sternite (spiculum gastrale). Scales (mm): **55–56**: 0.2, **57–58**: 0.2, **59–60**: 0.1, **61**: 0.1, **62**: 0.05.

Pronotum campaniform, 0.88× as long as wide, constriction relatively strong, at base nearly as wide as at middle, base 1.25× as wide as apex, bisinuate with rounded medial projection towards scutellum, basal flange developed. Prescutellar fovea shallow, puncture-like, elliptical, about 1.5× as broad as diameter of puncture, as long as 2 diameters. Discal punctures very shallow, weakly visible, ca. 0.5-1× diameter apart, interspaces moderately convex, microreticulate.

Scutellum large, elongate, triangular, ca. 2.5× as long as wide, with two separate basal tubercles, obtuse; apex constricted and slightly raised, moderately visible in lateral view.

Elytra elongate, 1.74× as long as wide, 2.61× as long as pronotum, widest almost at middle, humeri distinct, striae deep, about 0.50× as wide as interstriae, distinctly catenulate-punctate, punctures round to oblong, space between punctures about 2.0–3.0× as long as puncture length, apically connected 1+2+9, 3+4, 5+6, 7+8, interstriae evidently convex with wrinkled surface, not microreticulate, shining.

Ventral areas. Mesocoxae and metacoxae narrowly separated by distance of 0.21× and 0.30× of transverse diameter, respectively. Metaventrite 0.75× as long as mesocoxae. Mesoventral process slightly more prominent than metaventral process. Anterior metasternal rim almost absent. Abdominal ventrites microreticulate, with length ratios along midline: 22-14-4-5-13. Ventrites 1–2 coarsely punctate, 3–5 very sparsely and minutely punctate, ventrite 5 minutely punctate with median convexity. Suture I scarcely visible, distance from hind margin of metacoxae, as long as ventrite 2. Ventrite 5 subsemicircular, transverse, 0.39× as long as wide. Pygidium suboblong, 0.76× as long as wide, apical flange strongly raised with row of punctures and hairs; transverse sulcus distinctly depressed; disc pubescent and punctured as that of ventrite 5 (Figures 59–60).

Legs. Profemora slightly larger than metafemora, slightly robust, 3.07× as long as wide, widest at middle, minutely punctate. Protibiae almost straight, 6.33× as long as wide. Protarsomere 1 2.4× as long as wide, protarsomere 2 0.86× as long as wide, protarsomere 3 bilobed, 0.75× as long as wide, lobes narrow, onychium 2.0× as long as wide, projecting from lobes of tarsomere 3 for 0.50× its length. Meso- and metatibiae similarly mucronate, mucros incurved at apices. Tarsal claws with conspicuous, acute basal teeth.

Genitalia and terminalia. Eighth sternite short, apical edge relatively wide, distinctly concave (Figure 61). Ninth sternite (spiculum gastrale) Y-shaped, not winged, manubrium about as long as arms (Figure 62). Penis in dorsal view, with pedon sides almost parallel, apex distinctly constricted, apical plate subtriangular, with 2 small dentiform projections, tectum evenly constricted apicad; temones about 0.71× as long as aedeagal tube; in lateral view, pedon depressed, moderately curved, apical plate slightly incurved, dentiform projections visible; endophallus with dense minute spicules and basally with 2 elongate incurved structures (Figures 57–58). Tegminal plate articulated with free ring, slightly enveloping in lateral view; not notched apically, apical membranous area of parameroid lobes developed and tapering apicad, without microchaetae; basal sclerotized area short, apical margin deeply sinuate medially, with 5 long macrochaetae on each lateroapical edge, without sensilla; fenestrae short, transverse, narrowly separate; linea arquata present; prostegium bidentate, teeth short, narrow, acute; median unsclerotized strip absent. Manubrial apex moderately broadened near apex (Figures 55–56).

Variation. Male paratype. Measurements: Standard length: 1.20. Rostrum: length: 0.42, maximum width: 0.10. Pronotum: median length: 0.34, maximum width: 0.36. Elytra: median length: 0.96, maximum width: 0.50. Female unknown.

Type-locality. China, Yunnan, Menghai, Nabanhe National Natural Reserve, Guomenshan, N22.24644°, E100.60610°.

Materials. Holotype: 1♂: (white, printed): 云南景洪勐海县纳板河 [Yúnnán Jǐnghóng Měnghǎixiàn Nàbǎnhé] / 保护区过门山（森林） [bǎohùqū Guòménshān (sēn lín [forest])] / 2009.III.16 1114m; 22.24644°N, 100.60610°E飞阻 [Fēizǔ (flight intercept)] / 采集人：孟令曾 [Cǎijírén (leg.): Mèng Lìngzēng]; Guomenshan VI/1D / 16.03.2009 / leg. L. Z. Meng; IOZ(E)1639309; Paratype: 1♂, (white, printed): 云南景洪勐海县纳板河 [Yúnnán Jǐnghóng Měnghǎixiàn Nàbǎnhé] / 保护区过门山（森林） [bǎohùqū Guòménshān (sēn lín [forest])] / 2009.VI.26 1114m ; 22.24644°N, 100.60610°E飞阻 [Fēizǔ (flight intercept)] / 采集人：孟令

曾 [Cǎijírén (leg.): Mèng Lìngzēng]; Guomenshan VI/1D / 26.06.2009 / leg. L. Z. Meng; IOZ(E)1639310.

Distribution. Yunnan.

Type deposition. Both holotype and paratype will be deposited in IZCAS.

Remarks. *Harpapion borisi* sp. n. can be distinguished from other congeners by the following traits: 1) body standard length 1.22–1.24 mm (the others more than 1.5 mm); 2) elytral scales with similar size, in one regular row per interstria; 3) rostral pubescence not surpassing middle of prorostrum, nearly entire prorostrum glabrous; 4) prostegial teeth short and narrow; 5) tegminal median unsclerotized strip absent; 6) spiculum gastrale with manubrium about as long as arms.

Etymology. This species is named after the Russian curculionidologist Boris A. Korotyaev, who has much improved the taxonomy of Apionidae from South China and helped us in many ways.

Key to species of *Harpapion* from China (based on male characters)

1 All legs and antennae reddish brown; apical plate of pedon without dorsal dentiform projections; fenestrae narrowly separated, transverse, rectangular; parameroid lobes with basal sclerotized area extremely enlarged and extended medially, triangular, apical membranous area reduced to lateral strip; median unsclerotized strip elongate and surpassing fenestrae .... ***H. safranum* sp. n.**

– All legs black; apical plate of pedon with 2 dorsal dentiform projections; fenestrae separated or confused, differently shaped; parameroid lobes with basal sclerotized area short and medially sinuate, apical membranous area developed; median unsclerotized strip just or not reaching linea arquata **2**

2 Body larger, standard length more than 2 mm; scales of elytral striae short, tips of anterior scales not or hardly reaching the base of posterior ones; antennal scape at least 3.5× as long as wide; tegmen with prostegium reduced and deeply concave, untoothed .... ***H. coelebs***

– Body smaller, standard length less than 2 mm; scales of elytral striae elongate, tips of anterior scales surpassing base of posterior ones; antennal scape at most 3.1× as long as wide; tegmen with prostegium developed and bidentate **3**

3 Standard length 1.78–1.90 mm; rostral pubescence surpassing middle of prorostrum, only apex glabrous; elytral scales around scutellum distinctly whiter and thicker compared with semitransparent and thin scales on elytral disc; fenestrae fused; prostegium with very long teeth .... ***H. vietnamense***

– Standard length 1.22–1.24 mm; rostral pubescence not surpassing middle of prorostrum, nearly entire prorostrum glabrous; almost all elytral scales with same size and coloration; fenestrae separate; prostegium with short narrow teeth .... ***H. borisi* sp. n.**

Discussion

Some previously considered generic characters of the tegmen like parameroid lobes, fenestrae and prostegium (Alonso-Zarazaga 1983, 1990) show a great amount of variation among the above species. The basal sclerotized area (the dorsal layer of the tegmen (Wanat 2001)) of parameroid lobes of the type species *H. considerandum* is short and medially sinuate, and the apical membranous area (the ventral layer of the tegmen (Wanat 2001)) is well developed and prominent. These characters are also present in *H. vietnamense*, *H. coelebs* and *H. borisi* but not in *H. safranum* which externally resembles *H. considerandum* very much. Also the fenestrae of *H. considerandum* join medially, as in *H. vietnamense*, but they are separated in the other species as well as in *H. dongollanum.* Particularly, the prostegium of *H. coelebs* is extremely retracted and lacks the lateral teeth, which is unique hitherto in this genus. After all, significant similarities of external characters as well as most internal characters let us conclude that they should remain for the time being in *Harpapion*, and the inconsistency mentioned above has to be considered as a specific divergence not having generic value.

Additionally, a close genus, *Flavopodapion* Korotyaev, 1987 (type species *F. gilvipes* (Gemminger, 1871)) (Alonso-Zarazaga et al. 2011) resembles *Harpapion* very much. On one hand, its scutellum seems normally triangular, but two slightly raised basal projections can be found under SEM (Figure 12). On the other hand, its meso- and metatibial mucros show the peculiar bending present in the species of *Harpapion* (Figure 15). Other characters such as the rostrum clearly dilated at antennal insertion, the scale arrangement on the anterior and posterior margins of the pronotum and the apical flange of the pygidium strongly raised, etc. (Figures 8–11) coincide with those of *Harpapion*. However, some characters underline the differences between both genera, namely, in *Flavopodapion*, the relatively slender body, the triangular scutellum not constricted in the apical half and lacking a raised apex and clear basal projections. Moreover, the genitalia and terminalia show more significant differences: the ninth sternite (spiculum gastrale) with the manubrium distinctly shorter than the arms (Figure 24), the parameroid lobes with the basal sclerotized area evidently elongate, laterally extending apicad and leaving a membranous asetose area extending between the lobes and not tapering apicad, so that the apex in a general outline seems truncate, not pointed, the widely separate, reduced, lateral fenestrae, almost round in dorsal view, and the obsolete median unsclerotized strip (Figures 17–18). However, not too many related species are known in detail to allow drawing definite conclusions on the systematics of this particularly complex group of Apionidae.

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RESEARCH ARTICLE

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Permian ancestors of Hymenoptera and Raphidioptera

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Abstract

The origin of Hymenoptera remains controversial. Currently accepted hypotheses consider Hymenoptera as the first side branch of Holometabola or sister-group to Mecopteroidea. In contrast, fossils confirm the idea of Martynov that Hymenoptera are related to Megaloptera and Raphidioptera. Hymenoptera have descended along with Raphidioptera from the earliest Megaloptera, the Permian Parasialidae. A related new family, minute Nanosialidae from the Permian of Russia is supposedly ancestral to Raphidioptera. The fusion of the third ovipositor valvulae is shown to be not a synapomorphy of Neuropteroidea. Parasialids and nanosialids bridge the gap between megalopterans and snakeflies; all can be classified into a single order, Panmegaloptera **nom. n.**, including a new suborder Siarapha for Nanosialidae. The earliest megalopterans and their descendants, Raphidioptera and Hymenoptera, have passed through a "miniaturization bottleneck," likely a common macroevolutionary mechanism.

Keywords

Holometabola, Neuropteroidea, Hymenoptera, Raphidioptera, Permian, miniaturization

> *Wings are the very books in which the identities of many insect groups are written*
> *(Conrad 2013)*

Introduction

The earliest and most primitive Hymenoptera are sawflies (Symphyta) from the Triassic subfamily Archexyelinae of the extant family Xyelidae (Rasnitsyn 1969). Several hypotheses have been proposed regarding their origin: (A) Hymenoptera have descended from an extinct non-holometabolan group—Protoblattoidea (Handlirsch 1906–1908) or Protohymenoptera (now Megasecoptera; Tillyard 1924)—and acquired complete metamorphosis in parallel to other holometabolan groups; such views are now abandoned. (B) Hymenoptera constitute the first side branch of Holometabola, as retaining the unmodified ovipositor (Ross 1965), the view supported by molecular evidence (Wiegmann et al. 2009, Beutel et al. 2011, Trautwein et al. 2012); hymenopterans are derived from the extinct order Miomoptera (Carboniferous–Jurassic), interpreted as the most basal holometabolan group (Rasnitsyn 2002), but no intermediate fossil forms have been found (Miomoptera are supposedly polyphyletic—Shcherbakov 2006, Nel et al. 2012). (C) Hymenoptera constitute a sister-group to Mecopteroidea (Hennig 1969), but the proposed synapomorphies (Kristensen 1975, 1999, Königsmann 1976, Beutel and Vilhelmsen 2007) are inconclusive: eruciform larvae (exceptions: Nannochoristidae and some Trichoptera) with a single pretarsal claw (shared with some Coleoptera; exception: Argidae—Rasnitsyn 1969) and silk produced by the labial glands (shared with Psocoptera); a fully sclerotized floor of the sucking pump in adults (shared with Paraneoptera). (D) Hymenopterans have descended from archaic neuropteroids and show many similarities with Megaloptera and Raphidioptera (Crampton 1924, Martynov 1930, 1937, Ross 1936, 1955).

This latter hypothesis was formulated as follows: "…Hymenoptera evolved from ancestors, somewhat intermediate between Megaloptera, Raphidioptera and Mecoptera" (Martynov 1930). "Not only the number but also the position of these cross-veins [in the hymenopterous wing] is practically the same as in the *Sialis* wing. This similarity seems too great for a simple coincidence and again suggests a close relationship between the Megaloptera and Hymenoptera" (Ross 1936). "All this resemblance in the venation and structure of wings, as well as in other morphological characters, lead us to the conclusion that the whole order Hymenoptera is allied to the order Raphidioptera, and that the venation in the ancestors of Hymenoptera was similar to that in Raphidioptera, but was somewhat simpler. Raphidioptera represent perhaps a conservative side-branch which evolved early from some ancestors closely allied to those of Hymenoptera" (Martynov 1937). "Coleoptera arose from a raphidian-like ancestor… Hymenoptera may have arisen from the same ancestral form as the Coleoptera" (Ross 1955).

The Permian fossils discussed below partly bridge the gaps between megalopterans, snakeflies, and hymenopterans and confirm the neuropteroid nature of the latter.

Like many authors, especially those tracing taxa transforming through time, I follow traditional phylogenetics rather than cladistics and accept both ancestral and terminal taxa (in cladistics, paraphyletic and holophyletic)—these are just two stages in the taxon history, all paraphyletic taxa have once been holophyletic, and *vice versa,* the now holophyletic taxa may eventually turn paraphyletic. As Cavalier-Smith (2010) points out, "Hennigian cladistics emphasizes only lineage splitting, ignoring most other major phylogenetic processes… It has been conceptually confusing and harmed taxonomy, especially in mistakenly opposing ancestral (paraphyletic) taxa" (see also Sharov 1971, Mayr and Bock 2002, Rasnitsyn 2006, Hoerandl and Stuessy 2010, and references therein).

Materials and methods

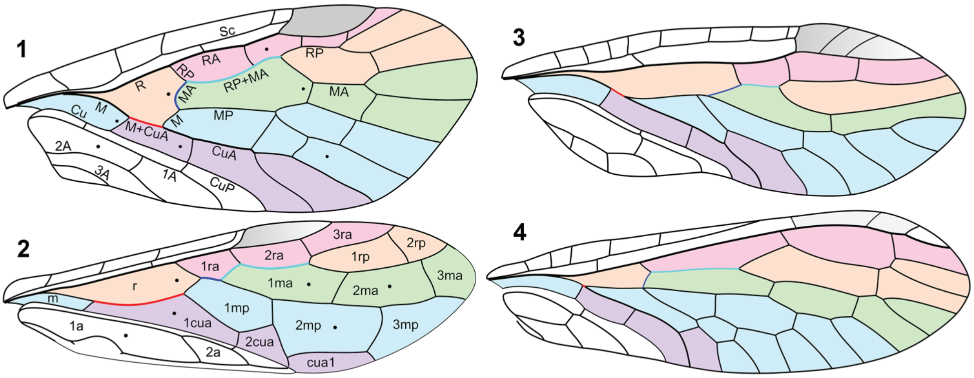
The material on the new taxa described herein is deposited at the Borissiak Paleontological Institute, Russian Academy of Sciences (PIN). The fossils were photographed using a Leica MZ9.5 stereomicroscope and Leica DFC420 camera, and imaged without coating with secondary electron (SE) and backscattered electron (BSE) detectors of a Tescan Vega XMU scanning electron microscope. Images were adjusted with Adobe Photoshop CS3. Line drawings were prepared with Inkscape 0.48.

Results

The only Megaloptera known from the Palaeozoic are Permian Parasialidae (Ponomarenko 1977), singled out into the suborder Archimegaloptera (Engel 2004). Parasialids, sialids, and symphytans possess stable venation patterns with fixed sets of crossveins and cells (often penta- or hexagonal; Figs 1–3, 5, 6, 8, 11), and their veins and wing membrane are evenly covered with short hairs. Parasialids are also similar to symphytans in a well-developed pterostigma, more distal RP origin (RP base crossvein-like), MP only shortly forked, presence of nygmata (enigmatic, likely glandular, dot-like structures found between veins in various primitive Holometabola and some other pterygotes – Stocks 2008), and also in the long M+CuA anastomosis and RP+MA angled at the base of pterostigma in the forewing. Based on this similarity I suggested that Parasialidae are ancestors of Hymenoptera (Shcherbakov 2006). In contrast to hymenopterans, parasialids retained the pterostigma in their hindwings and therefore were functionally four-winged like all neuropteroids.

The only known body fossil of Parasialidae (Fig. 7) is small, short-bodied, somewhat dorsoventrally depressed, with a large, markedly transverse head, and small, very short pronotum, short legs, and rather short abdomen consisting of well sclerotized segments. Its male genitalia are not unlike those of some megalopterans (and symphytans): without prominent genital capsule, with gonocoxites directed caudad and clavate gonostyles directed mediad (Novokshonov 1993). The overall habitus is rather sawfly-like, except for the broader wings, pterostigma in the hind wing, and homonomous pterothorax.

Differences of Hymenoptera from Megaloptera in the forewing structure are all associated with functional two-wingedness acquired by hymenopterans (Tillyard 1924, Ross 1936): (a) RP+M anastomosis (invariably present in all Triassic Hymenoptera, so the free MA base in some Cenozoic Xyelidae and Siricidae should be a reversal); (b)



Figures 1–4. Forewing venation: **1** *Parasialis latipennis* (Parasialidae; veins named) **2** Xyelidae (based mainly on Triassic *Asioxyela paurura* and *Madygenius primitivus;* cells named) **3** *Nanosialis ponomarenkoi* gen. et sp. n. (Nanosialidae) **4** *Grimaldiraphidia* cf. *parvula* (Mesoraphidiidae). Black dots, nygmata. Not to scale.

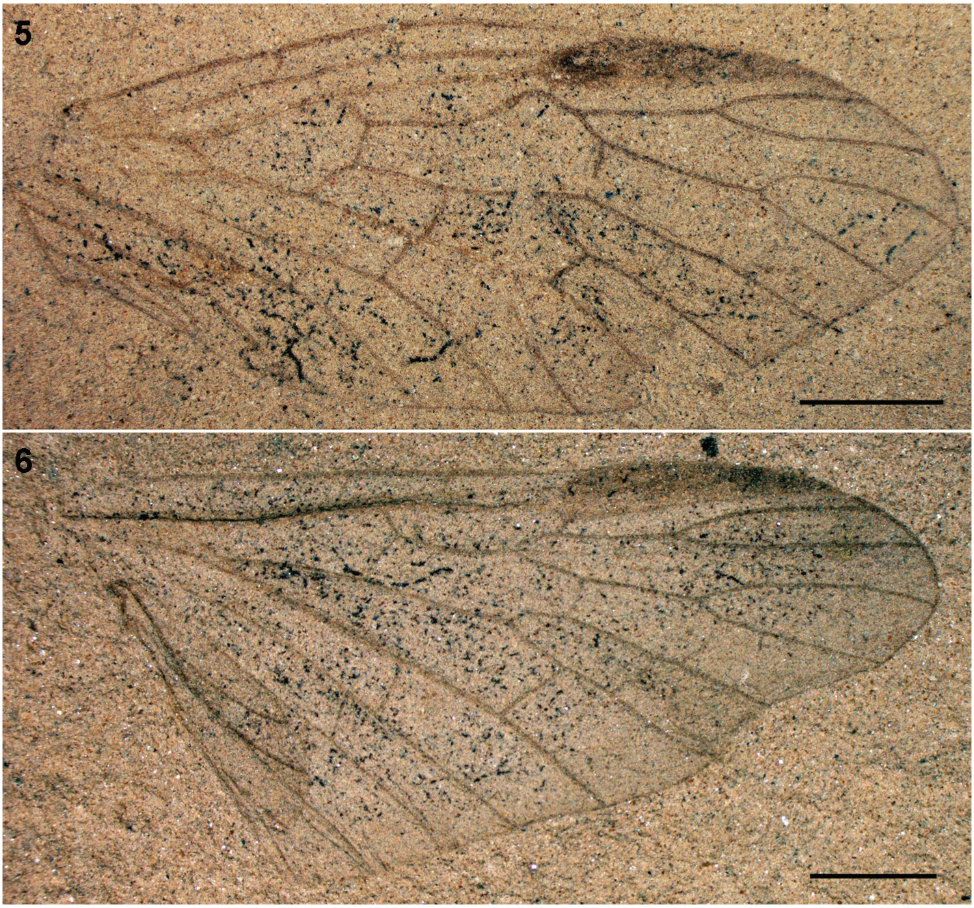
RP+MA two-branched; (c) MP simple; (d) very long M+CuA anastomosis (free CuA base retained in several families of Symphyta—Rasnitsyn 1969); (e) only two free anal veins (the second represents 2A+3A); (f) two braces between zigzagged CuA and anal veins; (g) RP, MA and MP1 shifted anteriorly, with enlargement of medial cells at the expense of radial cells. These characters correlate with narrowing of the forewing (a–e), strengthening of the forewing anal margin coupled in flight to the hind wing hamuli (f), and costalization of the integrated functional wing (g). The hind wing in Hymenoptera is smaller than the forewing (although the hind wing anal area is well-developed in some Symphyta) and lacks the pterostigma, and the metathorax is smaller than the mesothorax.

The metanotum in Symphyta is equipped with cenchri, which are two blister-like lobes, each interlocking with a field of modified microtrichia (spinarea) on the underside of the forewing anal area in repose (Schrott 1986). This wing-locking mechanism is an elaboration of the microtrichial forewing-metanotum coupling occurring in Neuroptera, Raphidioptera, Sialidae (Riek 1967), some Mecoptera (some Nannochoristidae and Meropeidae; in *Merope* the spinarea is displaced to the upper side of the jugal lobe; Hlavac 1974, Kristensen 1989), and Lepidoptera (Common 1969, Kristensen 2003).

In the very rich Late Permian insect fauna from Isady, northern European Russia (Sukhona River, Vologda Region; Severodvinian, correlated to Wuchiapingian, ~258 million years ago; Bashkuev 2011, Aristov et al. 2013), remarkable minute insects related to parasialids have been discovered, described here as a new family.

Order Panmegaloptera nom. n. (=Megaloptera s.l., i.e. *sensu* Latreille, 1802)

Composition. Four suborders: Archimegaloptera, Megaloptera s.str., Siarapha subordo n., Raphidioptera.



Figures 5–6. Parasialidae: **5** *Parasialis dissedens,* holotype forewing (mirror image) **6** gen. indet., hind wing PIN 3353/1073. Scale bars, 2 mm.

Suborder Archimegaloptera Engel, 2004

Diagnosis. As for the family.

Composition. Parasialidae Ponomarenko, 1977

Family Parasialidae Ponomarenko, 1977

http://species-id.net/wiki/Parasialidae

Diagnosis. Medium-sized insects (wings 6.5–17 mm long). Sc joining base of pterostigma; RP origin rather distal; RP and MA deeply forked; rp-ma crossvein present; MP once forked (much beyond R fork). Free base of MA developed as crossvein originating from M stem. Anal area at least 1/2 wing length. In forewing, RP+MA angled forwards at base of pterostigma, M and CuA forming long anastomosis (ending nearly level to R fork), M arched forwards distad of anastomosis, free base of MA just beyond M+CuA fork, and CuA forked. In hind wing (Fig. 6), M and CuA connected by very oblique arculus, CuA simple, and anal area variable (narrow in smaller species and broadened in larger species). Nygmata present. Veins and wing membrane evenly covered with short hairs. Short-bodied, somewhat dorsoventrally depressed. Head large, markedly transverse. Pronotum small, very short; pterothorax homonomous; legs short. Abdomen rather short, with short, well sclerotized segments. Male genitalia without prominent genital capsule, gonocoxites directed caudad, clavate gonostyles directed mediad.

Composition. *Parasialis* Ponomarenko, 1977 (Lower to ?Upper Permian of Eurasia; 4 species; Figs 1, 5, 7, 8), *Sojanasialis* Ponomarenko, 1977 (Middle Permian of Soyana; monobasic).

Remarks. In the wing structure Parasialidae are similar to Sialidae, but in the latter the R and MP forks are more proximal in the forewing, and the nygmata are absent.

The hind wings of Parasialidae differ from the forewings in the basal mcu crossvein (arculus) developed instead of M+CuA anastomosis, and CuA unbranched. The hind wing anal area is expanded, with up to six unbranched anal veins in larger parasialids, but relatively small in the smallest parasialid, *Parasialis rozhkovi* (likewise in Sialidae the extent of the hind wing anal area depends on the body size and abdomen mass, so that e.g. in males of smaller species of *Indosialis* the fore and hind wings have anal areas of equal size).

Suborder Siarapha subordo n.

Diagnosis. As for the family.

Composition. Nanosialidae fam. n.

Family Nanosialidae fam. n.

http://zoobank.org/1CEA1470-7BCD-44C2-AFCA-E9C55CDADE5B
http://species-id.net/wiki/Nanosialidae

Type genus. *Nanosialis* gen. n.

Diagnosis. Minute insects (wings 2.5–4.5 mm long). Sc joining base of large pterostigma. RP origin distal; ir1 crossvein at base of pterostigma. RP and MA simple (sometimes MA with small fork); rp-ma crossvein absent; MP1 with 3–4, MP2 with 2 branches; CuA apparently simple or with terminal fork. MP fork level to, or just before R fork. M and CuA forming X-junction or very short anastomosis much before R fork (M stem arched towards CuA distad of junction). In forewing, RA sometimes with break at base of pterostigma. Free base of MA developed as crossvein originating from base of MP1 (in hind wing sometimes absent). Hind wing similar to forewing, with narrow anal area. Nygmata absent. Veins beset with strong setae; wing membrane bare. Body short. Pterothorax heteronomous: metanotum smaller and much shorter than mesonotum, without scutoscutellar sutures. Abdomen with short segments; 1st tergite with posteromedian notch.

Composition. Two subfamilies.

Remarks. The body structure is known for the type genus only; the degree of pterothoracic heteronomy and first abdominal tergite division may vary among genera, like with modern genera of some neuropteran families.

In the structure of the proximal wing part (especially in the course of M, oblique direction and position of MA, shape of cells) Nanosialidae are similar to Mesoraphidiidae, but in the latter the pterothorax is always homonomous, anal area is much shorter, pterostigma is displaced distally, and RP+MA is usually more branched.

Among isolated wings of Nanosialidae, those having a shorter anal area, narrower costal area, and more delicate membrane are interpreted as the hind wings.

Subfamily Nanosialinae subfam. n.

Diagnosis. Pterostigma lanceolate to triangular, moderately elongate, dark. Anal area ~1/2 wing length, with two anal veins.

Composition. *Nanosialis* gen. n., *Lydasialis* gen. n., *Hymega* gen. n.

Nanosialis gen. n.

http://zoobank.org/50C58857-158A-4870-8C9E-2BF5394D68B0
http://species-id.net/wiki/Nanosialis

Type species. *Nanosialis ponomarenkoi* sp. n.

Diagnosis. Distinct in the long 1mp cell, distal R fork, numerous Sc veinlets, and triangular pterostigma.

Composition. Type species and *N. bashkuevi* sp. n.

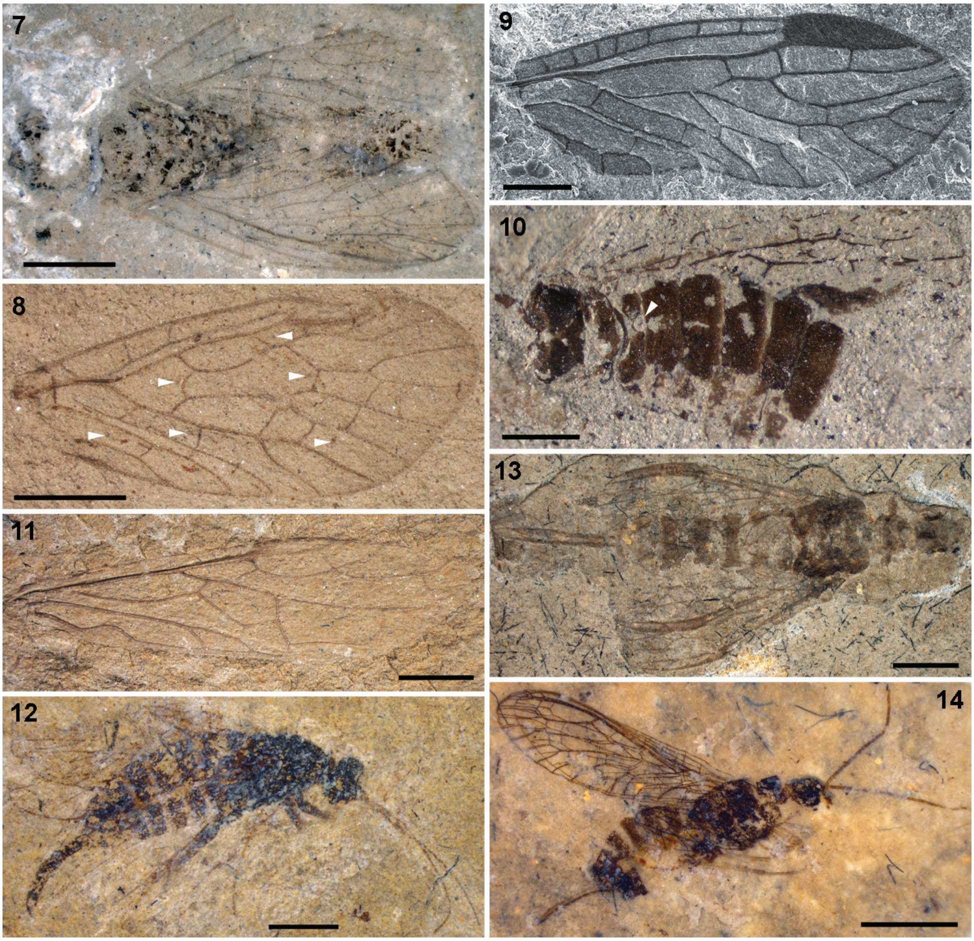
Etymology. Named after Greek *nanos* (dwarf) and *Sialis;* gender feminine.

Remarks. The apparent CuA (probable CuA2) is simple in *N. ponomarenkoi* forewing, but bears a terminal fork in *N. bashkuevi* hind wing. This may be an element of the fore/hind wing heteronomy, like in many mesoraphidiids (*Mesoraphidia inaequalis*, *M. pterostigmalis*, etc.).

Nanosialis ponomarenkoi sp. n.

http://zoobank.org/1E1AC81B-0F3B-45EE-8492-4A94F47DE977
http://species-id.net/wiki/Nanosialis_ponomarenkoi
Figs 3, 9, 10, 15–17, 23, 32, 33

Holotype. Forewing PIN 3840/2603A (part and counterpart).



Figures 7–14. 7–8 Parasialidae: **7** *Parasialis rozhkovi*, holotype male **8** *P. latipennis*, holotype forewing (arrowheads, nygmata) **9–10** Nanosialidae: **9** *Nanosialis ponomarenkoi* gen. et sp. n., holotype forewing PIN 3840/2603A (SEM, SE; mirror image) **10** *N. ?ponomarenkoi,* body with superimposed wings PIN 3840/2604A (counterpart; arrowhead, incision of 1st abdominal tergite) **11–12** Xyelidae: **11** *Asioxyela paurura* (Archexyelinae) forewing PIN 2785/2491 **12** female Xyelinae indet., PIN 2452/582 **13–14** Mesoraphidiidae: **13** female gen. indet., PIN 2997/2662, halves of ovipositor separated **14** female Nanoraphidiini indet., PIN 2784/1127. Permian of Russia (**7–10**), Triassic of Madygen, Kyrgyzstan (**11**), Jurassic of Karatau, Kazakhstan (**12–14**). Scale bars, 2 mm (**7, 8, 11–14**), 500 µm (**9, 10**).

Description. Forewing 3.0 mm long, elongate (2.7:1), narrowly rounded posterior to MA apex; 7 Sc veinlets; pterostigma distally translucent, with 2 veinlets inside; RP base and crossveins ir1, ir2 transverse, not far separated; ir1 at base of pterostigma; mp cell single, rather long; MP1 3-branched, pectinate backwards; MP2 2-branched; CuA simple; anal area 1/2 wing length; two anal veins (2A+3A with 3 branches), delimiting one anal cell.

Adult PIN 3840/2604A (part and counterpart; head, prothorax, legs, right wings, and apex of abdomen beyond 6th segment, missing; left forewing and hind wing plaited and superimposed, as clearly seen in their pterostigmal areas). Tentatively assigned to the same species on account of similar size and reconstructed forewing venation (differing from the holotype in the larger mp cell and more separated ir1 and ir2 crossveins). Hind wing with well-developed pterostigma. Body as preserved ~2 mm long, somewhat depressed dorsoventrally. Mesoscutum 0.7 mm wide, transverse oval (1.9:1), deeply convex; narrow anterior zone laterally cut off by deep grooves; adjacent third steeply sloped, with semicircular median lobe delimited by arched lines; mesoscutellum low triangular, delimited by deep grooves, with posterior margin slightly arched; mesopostnotum rather narrow. Metascutum 0.55 mm wide, ×1.3 narrower and twice shorter than mesoscutum, subtriangular, more flat, with anterior margin concave, area of metascutellum slightly upturned (no scutoscutellar sutures), posterior margin subangulate; metapostnotum very narrow, arched. Abdomen ~0.7 mm wide, well sclerotized; 1st tergite short (especially medially), broadly sinuate anteriorly, with deep semicircular posterior notch nearly dividing it medially; 2–6th tergites longer, transverse (~2.5:1).

Etymology. Named after the paleoentomologist Alexander Ponomarenko.

Nanosialis bashkuevi sp. n.

http://zoobank.org/98E8549D-8C7F-4AF4-A1C9-FEF4892CC044
http://species-id.net/wiki/Nanosialis_bashkuevi
Figs 18, 24

Holotype. Hind wing PIN 3840/2633 (part and counterpart), interpreted as a hind wing due to the delicate, crimpled wing membrane.

Diagnosis. Distinct from the type species in the larger size and more abundant vein branching.

Description. Hind wing ~4.4 mm long, elongate (~3.2:1), acutely rounded at MA apex; 5? Sc veinlets (four preserved); pterostigma rather evenly suffused, without distinct veinlets; MP1 4-branched; CuA with terminal fork.

Etymology. Named after the paleoentomologist Alexei Bashkuev.

Lydasialis gen. n.

http://zoobank.org/E9CAA66F-6B78-49F0-B96A-1EEBA27EE643
http://species-id.net/wiki/Lydasialis

Type species. *Lydasialis micheneri* sp. n.

Diagnosis. Very long 1mp cell; few Sc veinlets; in forewing, RA with a break at nodus, and RP section distal to RP+MA desclerotized.

Composition. Monobasic.

Etymology. Named after *Lyda* and *Sialis;* gender feminine.

Lydasialis micheneri sp. n.

http://zoobank.org/91351955-95EF-402F-8EA2-8A42A49BCFE9
http://species-id.net/wiki/Lydasialis_micheneri
Figs 19, 20, 26, 27

Holotype. Forewing PIN 3840/2602 (the base and most of the anal area missing).

Description. Forewing ~2.8 mm long, broad (~2.4:1), obliquely rounded apically; costal space moderately narrow, with 3 Sc veinlets; pterostigma wide; RA with break at nodus; R fork rather distal; RP base and crossveins ir1, im1, im2, mcu oblique; ir1 at base of pterostigma; RP section between RP+MA and ir1 desclerotized; MA with terminal fork; 1mp cell single, very long; MP1 4-branched, pectinate backwards; MP2 2-branched; CuA with terminal fork beyond mcu.

Hind wing PIN 3840/2601 (base and most of anal area missing, 1A tucked under), interpreted as a hind wing due to the delicate, finely longitudinally wrinkled wing membrane. Tentatively assigned to the same species on account of similar size, few Sc veinlets, a wide pterostigma, and very long 1mp cell. Hind wing ~2.6 mm long, elongate (~2.8:1), narrowly rounded apically; costal space narrower, probably with 3 Sc veinlets; pterostigma wider, rather evenly suffused, without distinct veinlets; no break on RA; only ir1 somewhat oblique; MA simple; MP1 3-branched; MP2 2-branched; CuA with terminal fork.

Etymology. Named after the hymenopterist Charles D. Michener.

Hymega gen. n.

http://zoobank.org/C7797359-A004-4AFD-9EEF-6D1B071632AE
http://species-id.net/wiki/Hymega

Type species. *Hymega rasnitsyni* sp. n.

Diagnosis. Forewing with R fork and ir1 crossvein proximal, costal space wide, 1mp cell very short (apparently more than one mp cell), and two mcu crossveins.

Composition. Monobasic.

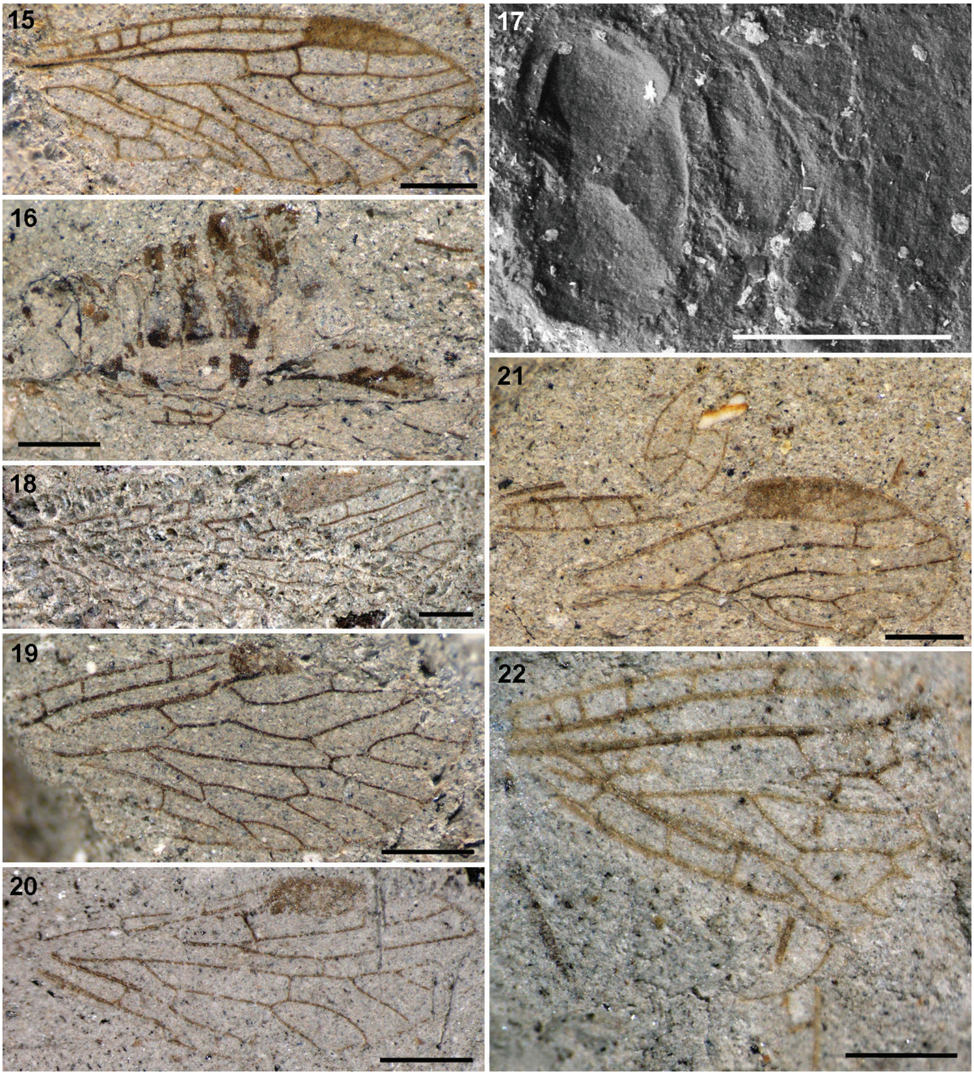
Etymology. Named after Hymenoptera and Megaloptera; gender feminine.

Hymega rasnitsyni sp. n.

http://zoobank.org/0C81D97C-5273-437E-943A-BCC84D2870B6
http://species-id.net/wiki/Hymega_rasnitsyni
Figs 21, 25

Holotype. Forewing PIN 3840/2600 (part and counterpart; costal and mp areas torn off and overturned, base and cubitoanal area missing).

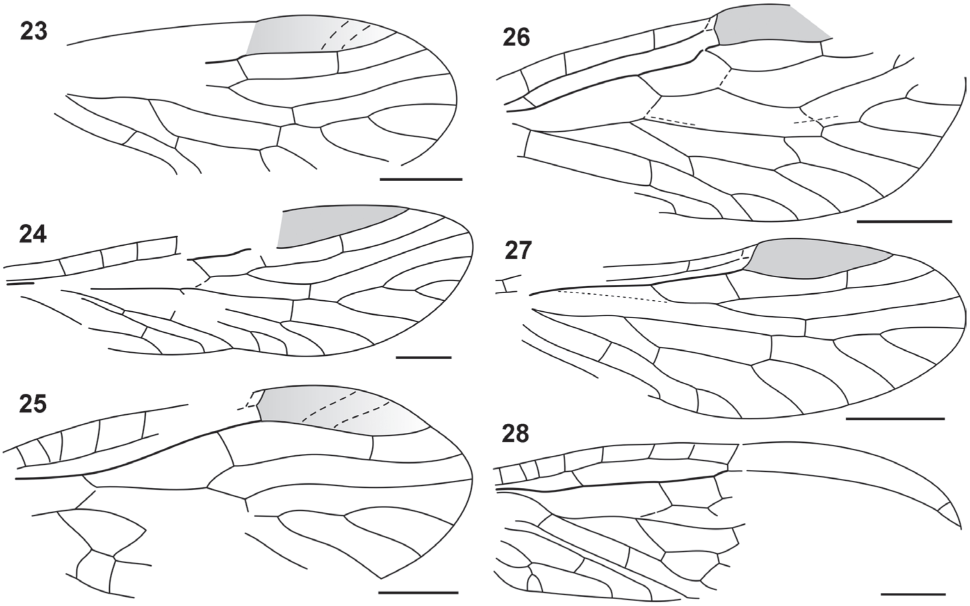
Description. Forewing ~3.4 mm long, broad (~2.5:1); costal space wide, with more than 5 Sc veinlets; pterostigma large, distally translucent, with 2 veinlets in-



Figures 15–22. Nanosialidae: **15** *Nanosialis ponomarenkoi* gen. et sp. n., holotype forewing PIN 3840/2603A (mirror image) **16–17** *N. ?ponomarenkoi* PIN 3840/2604A: **16** body with superimposed wings (part) **17** thorax and base of abdomen (counterpart, SEM, BSE) **18** *N. bashkuevi* sp. n., holotype hind wing PIN 3840/2633 **19** *Lydasialis micheneri* gen. et sp. n., holotype forewing PIN 3840/2602 **20** *L. ?micheneri,* hind wing 3840/2601 **21** *Hymega rasnitsyni* gen. et sp. n., holotype forewing PIN 3840/2600 **22** *Raphisialis martynovi* gen. et sp. n., holotype forewing PIN 3840/2009 (mirror image). Scale bars, 500 µm.

side; R fork proximal; RP base short; ir1 oblique, distant from pterostigma; MP1 4-branched; 1mp cell very short; two crossveins mcu.

Etymology. Named after the paleoentomologist Alexander Rasnitsyn.



Figures 23–28. Nanosialidae venation: **23** *N. ?ponomarenkoi,* forewing, reconstructed **24** *N. bashkuevi* sp. n., hind wing **25** *Hymega rasnitsyni* gen. et sp. n., forewing PIN 3840/2604A, reconstructed **26** *Lydasialis micheneri* gen. et sp. n., forewing **27** *L. ?micheneri,* hind wing PIN 3840/2601 **28** *Raphisialis martynovi* gen. et sp. n., forewing, reconstructed. Scale bars, 500 µm.

Subfamily Raphisialinae subfam. n.

Type genus. *Raphisialis* gen. n.

Diagnosis. Pterostigma sickle-shaped, very elongate. Anal area shorter than 1/2 wing length, with three anal veins.

Composition. Monobasic.

Raphisialis gen. n.

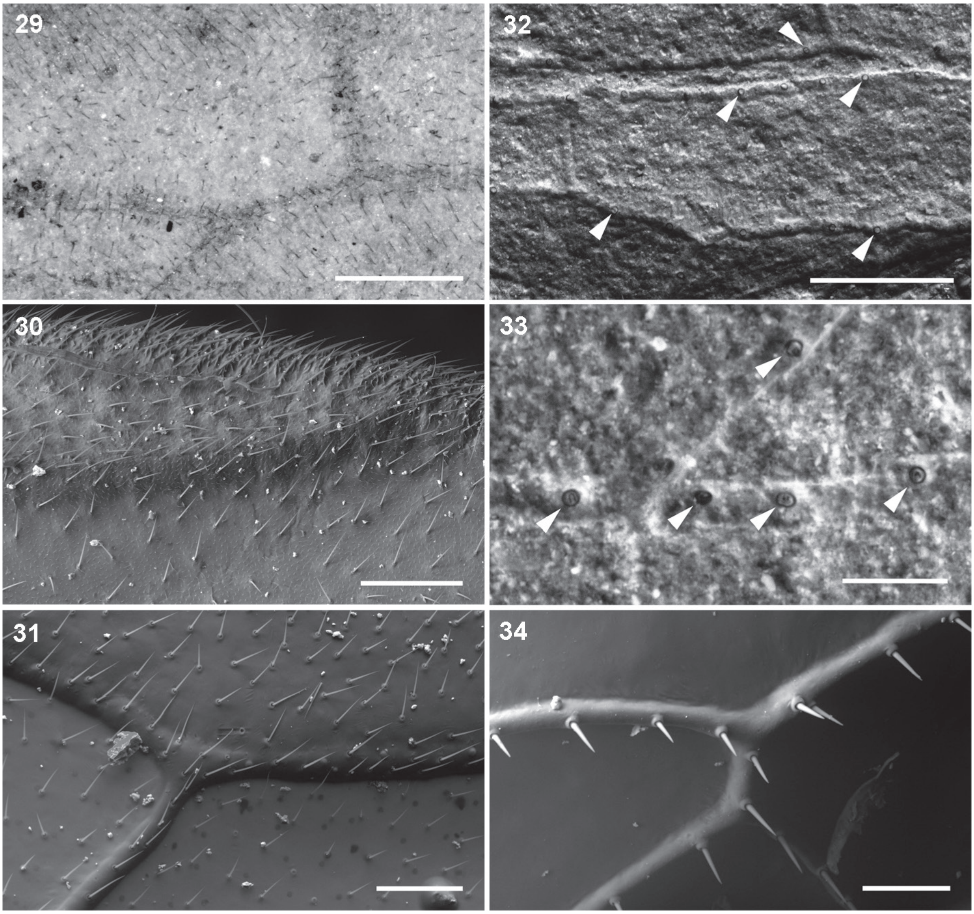
http://zoobank.org/24742579-4E20-4D18-8BDE-587C52231CDD
http://species-id.net/wiki/Raphisialis

Type species. *Raphisialis martynovi* sp. n.

Diagnosis. Forewing with cell 1mp short (apparently several mp cells) and two mcu crossveins.

Composition. Monobasic.

Etymology. Named after *Raphidia* and *Sialis;* gender feminine.



Figures 29–34. Hairs and setae on forewings: **29–31** uniform hair cover on veins and membrane: **29** Parasialidae, *Parasialis rozhkovi* holotype **30** Sialidae, *Sialis* sp. **31** Xyelidae, *Pleroneura coniferarum* **32–34** strong setae on veins only: **32–33** Nanosialidae, *Nanosialis ponomarenkoi* gen. et sp. n., holotype (arrowheads, bases of strong setae on veins) **34** Raphidiidae, *Raphidia* sp., strong erect setae on veins. Recent (**30, 31, 34**); SEM, BSE (**30–34**). Scale bars, 200 µm (**29, 30, 32**), 100 µm (**31, 34**), 50 µm (**33**).

Raphisialis martynovi **sp. n.**

http://zoobank.org/F829E139-1436-4496-8F46-D465BA24BFF3
http://species-id.net/wiki/Raphisialis_martynovi
Figs 22, 28

Holotype. Forewing PIN 3840/2009 (part and counterpart; anal area and incomplete distal part tucked under).

Description. Forewing ~3.9 mm long, elongate (~3.2:1); costal space moderately narrow, with 7 Sc veinlets; pterostigma long, narrow, sickle-shaped, unpigmented;

RA with small fork beyond it; R fork distal; ir1 at base of pterostigma; 1mp cell short (apparently at least three mp cells); two crossveins mcu; anal area shorter than 1/2 wing length; three anal veins (3A with terminal fork), delimiting two anal cells.

Etymology. Named after the paleoentomologist Andrey Martynov.

Discussion

I consider Nanosialidae derivatives of Parasialidae, not *vice versa,* because of simplified venation, heteronomous pterothorax, the lack of nygmata (so far as known, never restored after being lost), and the M stem arched towards CuA after short M+CuA junction (interpreted as remnants of a longer anastomosis like in parasialids). *Lydasialis* shows a pronounced transverse flexion at the base of the forewing pterostigma, RA having a break (articulation) there (Figs 19, 26), the condition broadly similar to that shared by Parasialidae and Symphyta, which have RP+MA angled there instead. The only known nanosialid body fossil (tentatively assigned to *N. ponomarenkoi;* Figs 10, 16, 17) resembles parasialids in having a short body and the hind wings retaining the pterostigma, but its metanotum is narrower and much shorter than mesonotum and lacks scutoscutellar sutures, and the first tergite of abdomen is divided medially.

Nanosialids share several characters with hymenopterans: RP+MA two-branched (occasionally MA with short fork, e.g. in aberrant specimens); rp-ma crossvein absent (restored in some Xyelidae: Triassic *Madygenius* and recent *Macroxyela* – Rasnitsyn 1969, Smith and Schiff 1998); very distal RP origin with ir1 crossvein at base of pterostigma; two anal veins; pterothorax heteronomous; 1st abdominal tergite divided. At first glance, Nanosialidae appear even more sawfly-like than Parasialidae, a kind of long-awaited missing link between Megaloptera and Hymenoptera. However, the situation is not so straightforward.

Nanosialidae are distinct from Parasialidae + Hymenoptera and similar to Mesoraphidiidae (Jurassic–Cretaceous; Fig. 4) and other primitive snakeflies in the structure of the proximal wing part (especially in the course of M, position and oblique direction of MA), MP forked proximally (more branched than RP+MA, whereas in hymenopterans MP is simple and RP+MA forked), shape and number of cells, absence of nygmata, and also in the short, stiff, erect setae along veins, and bare wing membrane. Secondary shortening of the M+CuA anastomosis in Nanosialidae and Raphidioptera is associated with shortening of the M stem itself, bringing the MP fork close to MA base; the evidence of a formerly longer anastomosis is the M stem arched close to CuA beyond the M+CuA in Nanosialidae.

The genus *Raphisialis* (Raphisialinae; Figs 22, 28) is additionally similar to mesoraphidiids in the rather short anal area and long, sickle-shaped pterostigma (unpigmented, as in several *Mesoraphidia* spp.). This incompletely known genus is not separated at the family level because the gap between it and *Nanosialis* is partly filled with *Hymega* (Figs 21, 25) having a short 1mp cell (probably several mp cells) and two mcu crossveins like in *Raphisialis*.

Despite these similarities, Nanosialidae are distinct from Raphidioptera in the longer anal area, more proximal position of pterostigma, less branched RP+MA, and, most importantly, the heteronomous pterothorax, so they cannot be assigned to this order as currently understood. This Permian family is likely to be ancestral to snakeflies, which are still unknown from the Triassic. The striking resemblance between Nanosialidae and Mesoraphidiidae casts doubt on the primitiveness of Jurassic Priscaenigmatidae, considered to be the most basal Raphidioptera (Engel 2002). As evidenced by the pupal tracheation, the CuA1 of Raphidiidae coalesces with MP2 for a distance (Withycombe 1923), so that the apparent CuA is in fact CuA2; this is probably also true of other snakeflies and nanosialids as well.

The aforementioned venation features shared by hymenopterans and nanosialids but not parasialids seem to be associated with miniaturization and likely are homoplasies appearing in closely related lineages, i.e. "underlying synapomorphies" (Saether 1979). Two additional probable homoplasies of Nanosialidae and Hymenoptera are the heteronomous pterothorax (also developed in some functionally four-winged Neuroptera, e.g. Coniopterygidae and Ascalaphidae – Riek 1967) and the first abdominal tergite divided medially (a shallower notch is found also e.g. in Mantispidae – Ferris 1940).

Minute nanosialids, with their veins beset with stiff, erect setae and the wing membrane bare, both like in snakeflies (Figs 32–34), were surely terrestrial. In Parasialidae, the wing membrane and veins are densely covered with short decumbent hairs (Fig. 29). Such a uniform hair cover occurs on the wings of both amphibiotic Megaloptera and terrestrial Hymenoptera (Figs 30, 31) and gives no clue to the life mode of parasialids.

Female genitalia of nanosialids and parasialids are unknown. If Parasialidae were amphibiotic, like the present-day Megaloptera, their ovipositor is likely to have been more or less reduced, suggesting a subsequent restoration of ovipositor in Hymenoptera, Raphidioptera, and possibly in Nanosialidae.

The ovipositor, transformed into a very long, unpaired organ (1st valvulae fused, 3rd valvulae fused dorsally) in living snakeflies, was much more generalized in Mesozoic Mesoraphidiidae, which are sometimes preserved with the left and right halves of the ovipositor separated (in *Siboptera fornicata* (Ren, 1994) and various mesoraphidiids from Karatau, Fig. 13). Therefore, the fusion of the third ovipositor valvulae, previously considered to be a synapomorphy of Neuropteroidea (Mickoleit 1973), was in fact acquired in parallel by some neuropterans and higher snakeflies.

Small Jurassic mesoraphidiids have the ovipositor much shorter than the abdomen, in lateral aspect relatively wide and downcurved (like in some *Xyela* spp. – *Xyela* is from Greek *xyēlē,* curved knife). These small Jurassic snakeflies are short-bodied, with the subquadrate head and short pronotum and abdomen, and look remarkably similar to xyelid sawflies (Figs 12, 14). There are some other notable similarities between snakefies and hymenopterans, including the wasp-like colour pattern in some snakeflies, and the late pupa (in fact, pharate adult) capable of locomotion and with functional mandibles in Xyelidae (Yates and Smith 2009) and Raphidioptera. However, venation differences indicate that the above features have been acquired by snakeflies and sawflies in parallel or inherited from megalopteran ancestors.

Are Parasialidae, the oldest known megalopterans, also the most primitive ones? Megaloptera are still unknown from the Triassic: the only Triassic find ascribed to Megaloptera (Riek 1974) possibly belongs to Polyneoptera (Ansorge 2001). They are rare in the fossil record, likely due to their association with lotic waters, unfavorable for fossil preservation. The two extant megalopteran lineages, Sialoidea and Corydaloidea, are known since the Jurassic (Ansorge 2001, Liu et al. 2012). Sialids and corydalids differ from parasialids in having the vein branching more abundant, which can be interpreted as evidence that the most basal megalopterans are corydalids (because sialids lack nygmata). However, it was suggested (Ponomarenko 1977, 2002) that the early Megaloptera were oligoneurous and that the vein polymerization in Corydalidae is secondary. The discovery of parasialid relatives, oligoneurous Nanosialidae, that are presumably ancestral to the more polyneurous Raphidioptera, further strengthens this hypothesis. Our observations agree with the supposition (Engel and Grimaldi 2008) that Parasialidae may not necessarily have had aquatic larvae and are ancestral to the remaining Megaloptera and Raphidioptera. They furthermore demonstrate that parasialids are ancestral to hymenopterans as well (Fig. 35), placing Hymenoptera among neuropteroid orders.

Parasialidae and Nanosialidae bridge the gap between Megaloptera and Raphidioptera and demonstrate that these two orders can be treated as one. Such was the original concept of Megaloptera (Latreille 1802), but since the currently accepted concept excludes snakeflies, a new name in G. Crampton's style is proposed here to avoid confusion—Panmegaloptera nom. n. The placement of both amphibiotic insects with a reduced ovipositor and terrestrial insects with a long ovipositor into one order may seem unnatural, but such divergent forms are also found in the closely related order Neuroptera. Nanosialidae, which share several characters with Raphidioptera s.str., are better treated as a new suborder, Siarapha, in Panmegaloptera. Living alderflies, dobsonflies, and snakeflies presumably represent only remnants of the past diversity of archaic neuropteroids with chewing larval mouthparts. It is likely that the extinct panmegalopterans were even more diverse in their life modes, and some of them may have shifted, like sawflies, to palyno- or phytophagy.

The larvae of the most basal hymenopterans supposedly developed in staminate cones of gymnosperms, and their females used their long ovipositors to lay eggs into the cones, like many xyelid sawflies still do (Rasnitsyn 1969). The same life style is reconstructed for the most basal hemipterans, Permian Archescytinidae: their females laid eggs into cones, and nymphs dwelt between the scales (Becker-Migdisova 1985). Indeed, the long, modified ovipositors of some archescytinids have closer analogues among hymenopterans, rather than other hemipterans, suggesting that archescytinids have been ecological predecessors of the earliest hymenopterans (Shcherbakov and Popov 2002). Hymenoptera enter the record in the mid-Triassic, at least 10 Myr after the extinction of Archescytinidae about the Permian–Triassic boundary.

Parasialids and nanosialids are found only in the richest Permian fossil insect sites of Eurasia, being rare in all of them: Chekarda (Lower Permian, Urals)—one *Parasialis rozhkovi* specimen per ~7,000 total insects; Tyulkino (Lower Permian, Urals)—one *Parasialis* specimen per ~550 insects; Soyana (Middle Permian, northern European

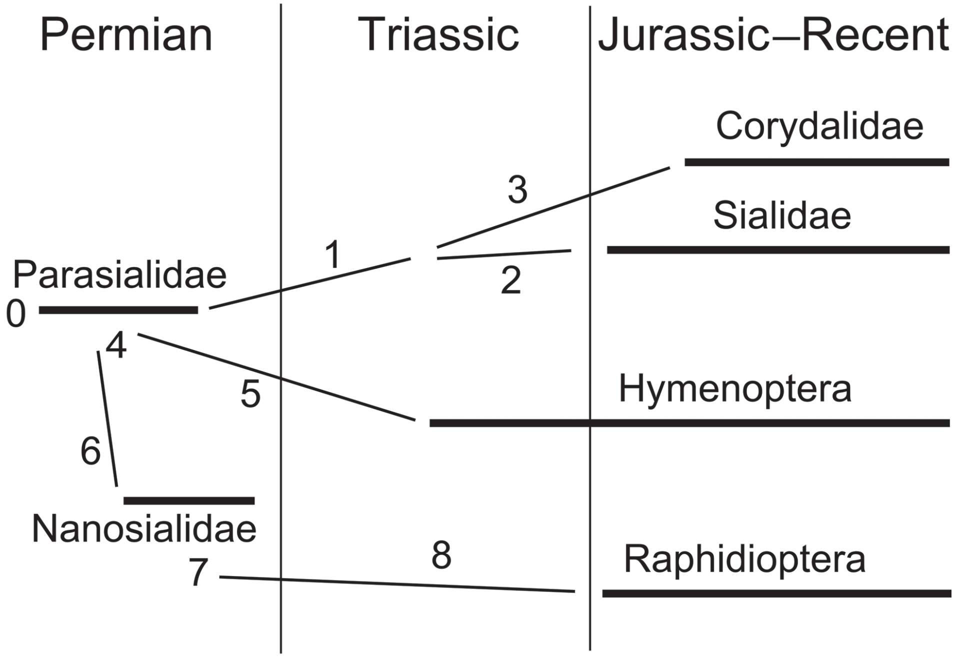


Figure 35. Phylogenetic diagram of Panmegaloptera and Hymenoptera (for characters see Appendix).

Russia)—14 Parasialidae specimens (3 species in 2 genera) per ~4,000 insects; Bor Tolgoy (Upper? Permian, southern Mongolia)—two *Parasialis ovata* specimens (Ponomarenko 2000) per ~900 insects, Isady (Upper Permian, northern European Russia)—11 Nanosialidae specimens (5 species in 4 genera) per ~3,500 insects. In the Permian, all of these sites were situated within zones of semiarid or warm temperate climate (Shcherbakov 2008). Why no nanosialids have yet been recorded in other rich Upper Permian entomofaunas? A possible explanation is that these minute terrestrial neuropteroids preyed upon plant lice, like present-day Raphidiidae and various Neuroptera. Indeed, the Isady insect fauna is exceptionally rich with diverse psyllomorphous hemipterans (Aristov et al. 2013).

Miniaturization can be an important source of morphological novelty, in some cases resulting in the origin of higher taxa (Hanken and Wake 1993). The origins of Hymenoptera, of their ancestors Megaloptera, and their close relatives Raphidioptera were likely associated with a "miniaturization bottleneck." The earliest members of these lineages first underwent reduction in size, leading to incomplete development of many structures (e.g. distal vein branches); later with disappearance of the former size constraints due to changes in the environment or life mode they followed new evolutionary trajectories, regaining some of the lost structures in a highly modified form and evolving new body plans. Naturally, such shifts make tracing the ancestry especially difficult, which can partly explain why the origin of Hymenoptera has long remained a mystery. This mechanism was also responsible for the origin of some other insect orders (e.g. Hemiptera). Still other groups (e.g. Thysanoptera) originated *via* miniaturization but never increased in size again.

After my paper was submitted, an article was published by Nel et al. (2013), likewise stressing the importance of miniaturization in the origin of Hymenoptera and the whole Holometabola plus Paraneoptera. These authors follow the hypothesis B (Hymenoptera are the most basal branch of Holometabola), date the origin of stem hymenopterids at the latest Early Carboniferous (~325 million years ago, Serpukhovian; see their fig. 3) and describe the putative stem hymenopterid *Avioxyela* from the Late Carboniferous (~310 million years ago, Moscovian). The affinities of this fossil, known from fragmentary wings, are highly debatable, it is much more likely to belong to some polyneopteran group (as discussed by Nel et al. 2013 in the supplementary information), and its venation is misinterpreted (the presumed posterior margin of the larger wing is in fact the strengthened costal margin—see their extended data fig. 2). Likewise, other putative Carboniferous paraneopterans and holometabolans described by Nel et al. (2013) may belong elsewhere. For example, *Westphalopsocus,* assigned to Psocodea, is likely to be a nymphal wing pad of a protorthopteran. The data published by Nel et al. (2013) do not affect the conclusions of my paper.

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Appendix

List of characters:

0. Characters of Parasialidae:

wings homonomous; fore and hind wing not coupled in flight;
pterostigma well developed, oval to lanceolate;
R fork rather distal; RP base crossvein-like;
MP forked distally, with 2 branches;
free MA base crossvein-like, connecting RP and M near bases;
RP+MA twice forked, dichotomous (4-branched);
one or two rp-ma crossveins;
nygmata present;
membrane and veins uniformly covered with short hairs;
forewing:
RP+MA angled at base of pterostigma (pronounced nodal flexion);
M+CuA anastomosis moderately long (its apex about level of R fork);
CuA once forked;
Cu base continued with CuP;
anal area reaching ~1/2 wing length;
at least three free anal veins;
hind wing anal area enlarged (in larger species) or not;
pterothorax homonomous;
presumably also: forewing-metanotum microtrichial coupling.

1. Synapomorphies of Sialidae + Corydalidae:

forewing R and MP forks shifted proximad;
ovipositor reduced.

2. Apomorphy of Sialidae:

nygmata lost.

3. Apomorphies of Corydalidae:

RP+MA pectinate;
forewing:
M+CuA anastomosis replaced with crossvein;
Cu base continued with CuA.

4. Homoplasies (underlying synapomorphies) of Hymenoptera and Nanosialidae + Raphidioptera:

forewing:
R fork shifted distad; crossvein ir1 near base of pterostigma;
RP+MA once forked;

rp-ma crossvein absent;
two free anal veins (2A and 3A fused at least proximally);
pterothorax heteronomous;
1st abdominal tergite with deep posteromedian notch.

5. Apomorphies of Hymenoptera:
wings heteronomous; hind wing without pterostigma, coupled to forewing in flight;
M+CuA anastomosis very long;
forewing:
free MA base replaced with RP+M anastomosis;
RP+MA fork shifted distad (to near ir2);
MP simple;
CuA1 shifted posteriad, CuA2 transverse, CuA fork narrow;
two cubitoanal braces between zigzagged CuA and anal veins: crossveins cua-cup and cup-a shifted distad and aligned across reduced distal CuP; CuA2 joining apically fused 1A and 2A+3A;
pterothorax markedly heteronomous;
microtrichial areas of metanotum modified into cenchri.

6. Synapomorphies of Nanosialidae + Raphidioptera:
pterostigma enlarged;
nygmata absent;
membrane bare; short, stiff, erect setae along veins;
M+CuA anastomosis much shortened or replaced with x-junction;
MP fork shifted proximad, MP with 5–6 branches (more branched than RP+MA);
free MA base connecting RP near base and MP near fork;
CuA1 anastomosing to MP2;
short free 3A sometimes restored (Raphisialinae, Inocelliidae);
hind wing anal area always small.

7. Synapomorphies of Raphisialinae + Raphidioptera:
pterostigma sickle-shaped, elongate;
anal area somewhat shortened.

8. Apomorphies of Raphidioptera:
RP+MA usually twice forked, dichotomous (no less than 4, rarely 3 branches);
at least one rp-ma crossvein;
pterostigma shifted distad;
anal area much shortened;
pterothorax always homonomous.

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RESEARCH ARTICLE

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A new species of *Neocarus* Chamberlin & Mulaik, 1942 (Opilioacarida, Opilioacaridae) from Brazil, with remarks on its postlarval development

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Abstract

Neocarus proteus **sp. n.**, is described from caves and the surrounding epigean environment of ferruginous outcrops (Cangas) in Minas Gerais, Brazil. In addition, some notes about development in this species are presented. *Neocarus proteus* is the only species in the genus that has smooth or barbed genital setae and that carries coronidia on the basitarsi, tibiae and genua of legs II–III. Females carry additional setae with rounded tips on the subcapitulum, and are, on average, larger than males. This distinct sexual dimorphism appears in the tritonymphal instar and is maintained in the adults.

Keywords

Acari, Parasitiformes, growth, sexual dimorphism, Neotropical

Introduction

Opilioacarida is one of the orders of mites (Lindquist et al. 2009), but has a very small number of described species. It currently contains one family (Opilioacaridae) with a total of 11 genera (*Adenacarus* Hammen, 1969*, Caribeacarus* Vázquez & Klompen, 2009*, Indiacarus* Das & Bastawade, 2007*, Neocarus* Chamberlin & Mulaik, 1942*, Opilioacarus* With, 1904*, Paracarus* Redikorzev, 1937*, Panchaetes* André, 1947*, Phalangiacarus* Naudo, 1963*, Salfacarus* Hammen, 1977*, Siamacarus* Leclerc, 1989 and *Vanderhammenacarus* Leclerc, 1989), comprising 34 extant and 2 fossil species. Even with this small number of described species, the geographical distribution of these mites is wide, extending to all the continents, except Antarctica. They have been reported from a total of 25 countries (United States, Mexico, Cuba, Puerto Rico, Nicaragua, Costa Rica, Panama, Venezuela, Brazil, Argentina, Uruguay, Italy, Greece, Algeria, Angola, Gabon, Madagascar, Ivory Coast, Tanzania, South Africa, Yemen, Kazakhstan, India, Thailand and Australia (Walter and Proctor 1998, Vázquez and Klompen 2002, Walter and Harvey 2009, Vázquez and Klompen 2009, Vázquez and Klompen 2010, Bernardi et al. 2012).

Nine of the 11 known genera of Opilioacaridae are present in the Old World, but it is the New World that has the largest number of described species, with a total of 15, belonging to the genera *Neocarus* (11 spp.) and *Caribeacarus* (4 spp.). In Brazil, research on these mites is still in its initial phase, and only three species are currently known, two belonging to the genus *Neocarus* (Hammen 1969, Bernardi et al. 2012), and one to *Caribeacarus* (Bernardi et al. 2013).

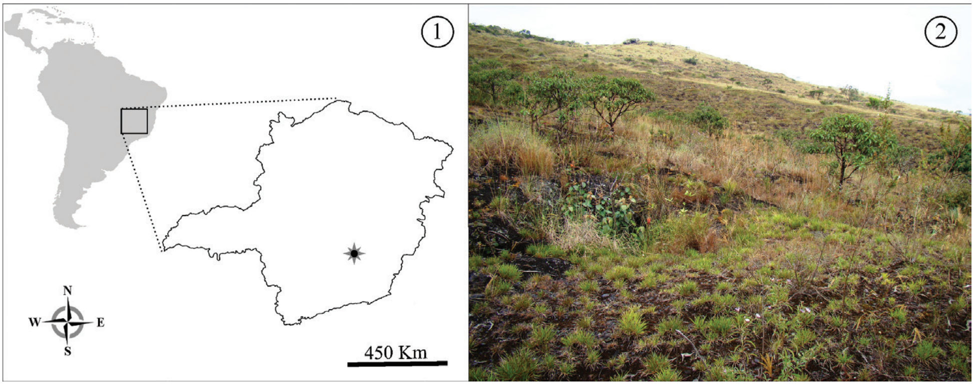
Even though Opilioacarida are considered a primitive group and hence of importance for understanding phylogenetic relationships among mites, current knowledge of Opilioacarida consists mainly of taxonomic descriptions, while studies on behavior, development and other aspects of their biology are rare (Grandjean 1936, Coineau and Legendre 1975, Hoffmann and Vázquez 1986, Vázquez and Palacios-Vargas 1988, Walter and Proctor 1998, Walter and Harvey 2009, Klompen 2000). The objective of this study is to add to the knowledge of both their taxonomy and development by describing a new species of Opilioacaridae found in Brazil, and providing notes on postembryonic development.

Materials and methods

Study area

All of the specimens used in the present work come from collections conducted in 2011 in caves and the epigean environment of ferruginous outcrops locally known as “Cangas”, in the Municipal district of Mariana, Minas Gerais, Brazil (Figs 1 and 2).

The Cangas represent an ancient terrain, with restricted distribution, and are composed of important iron ore deposits. In spite of being located inside the Atlantic



Figures 1–2. Collection site of *Neocarus proteus* sp. n. **1** Location in Minas Gerais, Brazil (star) **2** Detail of the canga environment.

Forest, the vegetation is different from that typically found in this biome, consisting mostly of open grasslands, herbaceous plants and sparsely distributed trees (Jacobi et al. 2007, Jacobi and Carmo 2008).

Floristic and subterranean biodiversity surveys conducted in this area suggest high species richness and a great number of endemic species. Unfortunately, the Cangas are increasingly targeted for intense mineral exploration that puts this biodiversity at risk, because the entire environment is modified during the ore extraction process (Ferreira 2005, Jacobi et al. 2007, Jacobi and Carmo 2008).

Methods

Two different methods were used to collect specimens. The first involved active collection of specimens in the field, searching under stones, in organic matter accumulations and cracks in the soil. The second method was extraction from litter and soil using Berlese-Tullgren funnels (run time 72 hours, heat from a 25 watt bulb). All the specimens collected were stored in 80% ethanol in vials.

Most material was studied as slide-mounted specimens. For this purpose, specimens were dissected, cleared in Nesbitt's solution and mounted on slides using Hoyer's medium (Walter and Krantz 2009).

Specimens were studied with the aid of a Leica DMLS microscope and a Zeiss Axioscope 3 phase contrast microscope, equipped with a drawing tube. Photographs were made with the aid of Nikon Eclipse 90i automated DIC microscope with an integrated digital camera. Measurements were taken using an ocular micrometer and are presented as ranges in micrometers (μm). The nomenclature of setae and other morphological characters follows Grandjean (1936), Hammen (1969, 1977) and Vázquez and Klompen (2002, 2009). The terminology used for the sternal setae (*St1*, *St2*, *St3* and *St5*) follows an attempt to unify setal nomenclature for all Parasitiformes (H. Klompen and M. M. Vázquez, in prep.).

To recognized the instars, we used the criteria for Opilioacaridae provided by Coineau and Hammen (1974), as confirmed by Klompen (unpublished data). These characteristics are: protonymph with 2 pairs of stigma, no acrotarsus on legs II–IV, only 3 pairs of setae on sternal area; deutonymphs with 3 pairs of stigma, acrotarsus present on legs II–IV, usually with more than 3 pairs of setae on sternal region; tritonymphs with 4 pairs of stigma, a divided trochanter, but no sexual organs (ovopositor and male sexual gland absent) are present; in adults sexual organs are present.

Instar abbreviations used: **PN** = protonymph; **DN** = deutonymph; **TN** = tritonymph; **F** = female; **M** = male.

Collection sites of the specimens examined were georeferenced using coordinates in degrees, minutes and seconds with the South American Datum (SAD 69) geodesic system.

Specimens are deposited at the Mite Reference Collection, Department of Entomology and Acarology, Escola Superior de Agricultura "Luiz de Queiroz" (**MZLQ**), Universidade de São Paulo, Piracicaba–SP, Brazil; Collection of Subterrean Invertebrates (**ISLA**), Section of Zoology de Zoologia, Department of Biology, Universidade Federal de Lavras, Lavras–MG, Brazil; and Ohio State University Acarology Collection (**OSAL**), Museum of Biological Diversity, Columbus, OH, USA.

Statistical analysis

To determine the presence of the sexual dimorphism in size for tritonymphs and adults we conducted a series of generalized linear models (GLMs) based on total length of legs I–IV. These analyses were conducted using R PROGRAM (R Development Core Team 2010).

Results

Taxonomy

Family Opilioacaridae With, 1904
Genus *Neocarus* Chamberlin & Mulaik, 1942

Neocarus proteus sp. n.

http://zoobank.org/A94A5CD4-8833-4692-807C-572DD71ECF28
http://species-id.net/wiki/Neocarus_proteus

Type material. Holotype female. Brazil: Minas Gerais: Mariana municipality, 20°20'49.3"S, 43°26'50.8"W, epigean, coll. Pellegrini TG, Souza MFVR, Silva MS, Pompeu DC and Ferreira RL, 21.XII.2011 (**MZLQ**).

Paratypes: Brazil: Minas Gerais: Mariana municipality, 20°20'57.1"S, 43°26'37.5"W, coll. Pellegrini TG, Souza MFVR, Silva MS, Pompeu DC and Ferreira RL, 17.XI.2011, 2M (**ISLA**); same locality and collectors: 20°20'57.1"S, 43°26'37.5"W,

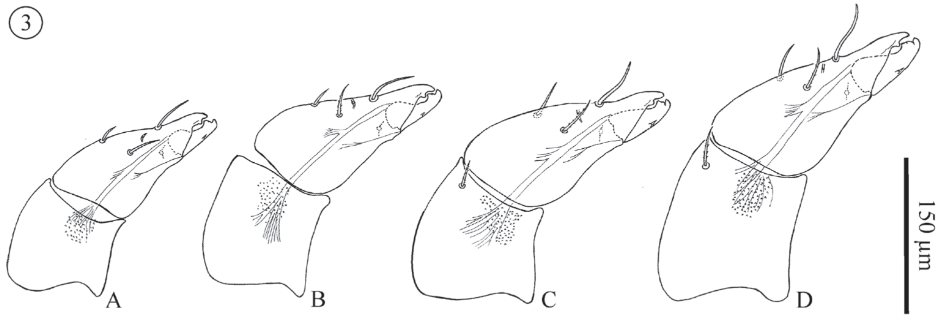
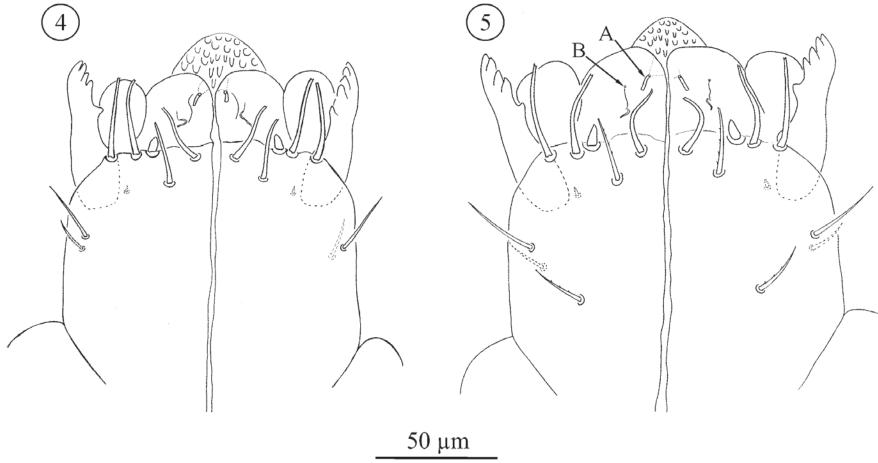


Figure 3. *Neocarus proteus* sp. n. Lateral view of chelicerae. **A** protonymph **B** deutonymph **C** tritonymph **D** adult female.

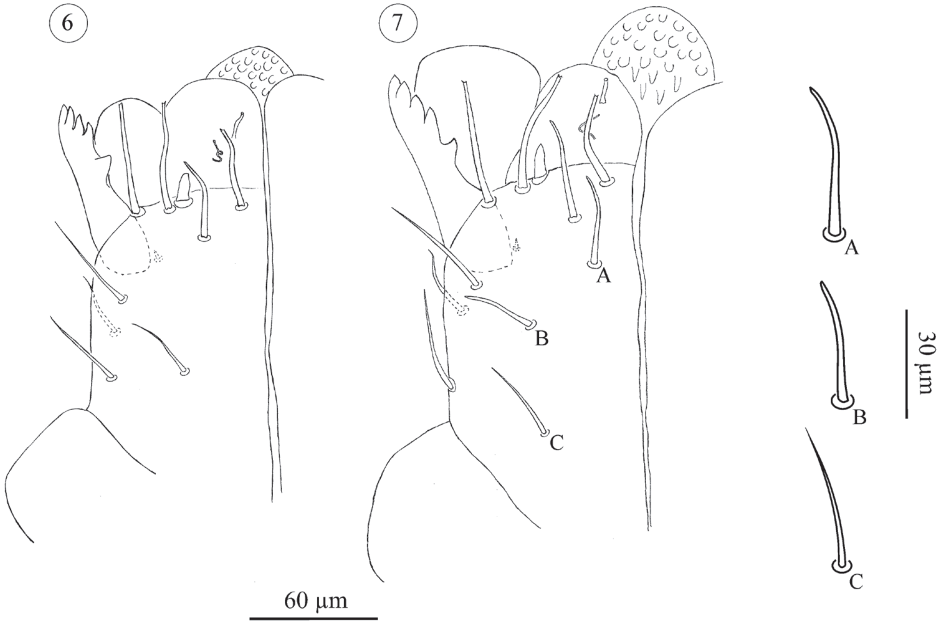


Figures 4–5. *Neocarus proteus* sp. n. Ventral view of subcapitulum. **4** protonymph **5** deutonymph. Arrows indicate the labial glands, **A**: *ogl1* and **B**: *ogl2.*

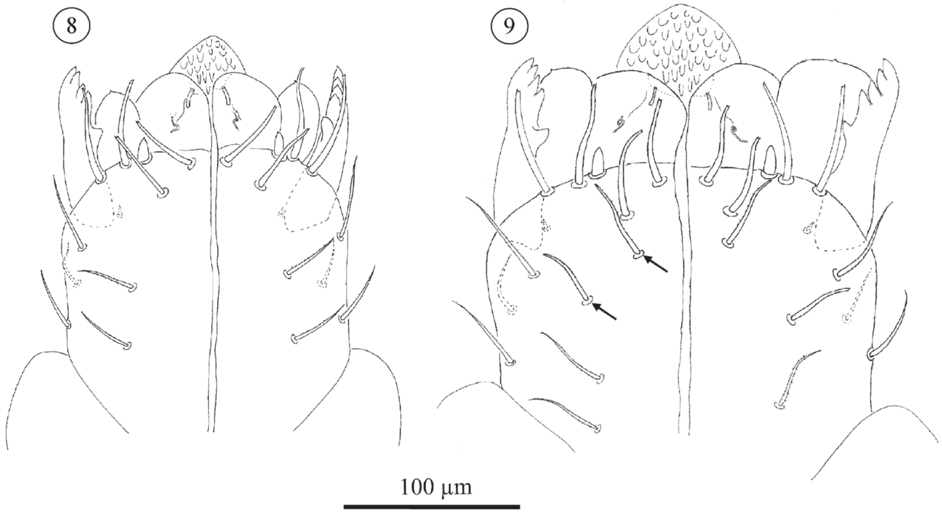
Table 1. Records of *Neocarus proteus* sp. n. in Mariana, Minas Gerais State, Brazil.

Stages	Mariana – Minas Gerais locality		
	20°20'57.1"S, 43°26'37.5"W	20°20'49.3"S, 43°26'50.8"W	20°20'53.6"S, 43°26'47.6"W
PN	3	–	–
DN	8	–	1
TN	12	–	1
♀	10	2	2
♂	24	–	1

14.XI.2011, 1TN, 2F, 6M (**OSAL**); 20°20'53.6"S, 43°26'47.6"W, 18.XI.2011, 1DN, 1TN, 2F, 1M (**MZLQ**); 20°20'57.3"S, 43°26'32.7"W, 19.XI.2011, 1PN, 2DN, 1F, 2M (**OSAL**); 20°20'49.3"S, 43°26'50.8"W, 21.XII.2011, 1F (**ISLA**); 20°20'57.5"S, 43°26'37.2"W, 25.XI.2011, 2PN, 6DN, 10TN, 5F, 6M (**ISLA**); 20°20'57.1"S, 43°26'37.5"W, 14.XII.2011, 2F, 7M, 1TN (**ISLA**) (Table 1).



Figures 6–7. *Neocarus proteus* sp. n. Ventral view of subcapitulum. **6** male tritonymph **7** female tritonymph. **A** and **B**: subcapitular setae with rounded tip; **C**: subcapitular setae with fine tip.



Figures 8–9. *Neocarus proteus* sp. n. Ventral view of subcapitulum. Arrows indicate the setae present in female tritonymphs and female adults only. **8** adult male **9** adult female.

Differential diagnosis. The presence of setae on the female pregenital area may be unique for the South American species of *Neocarus*, *N. platensis* (Silvestri, 1905), *N. potiguar* Bernardi et al., 2012, and *N. proteus*. The female genital area is nude in all *Ne-*

ocarus described from the USA, Mexico and Cuba. Unfortunately, the description of *Neocarus ojastii* Lehtinen, 1980 did not include details on the sternal or genital regions.

Neocarus proteus is the first species in the genus that is known to have the genital setae in the female adult variable, between weakly barbed and smooth. Furthermore, the present species is exceptional in carrying coronidia on the basitarsus, tibia and genu of legs II–III, and on the basitarsus and tibia of leg IV. In *N. potiguar* the genital setae are smooth and the coronidia are limited to basitarsi II–IV. In *N. platensis*, as redescribed by Hammen (1969), the genital setae appear smooth, with coronidia limited to the basitarsus and tibia of legs III (data on legs II and IV were not presented). The presence of coronidia on the tibiae and genua is unusual for *Neocarus*: in most species coronidia are restricted to basitarsi II–IV. Notably, in differentiating the genus *Panchaetes* from *Salfacarus,* Hammen (1977) listed the presence of coronidia on tibiae II–IV as unique to *Panchaetes*. Because this character is no longer restricted to *Panchaetes*, its separation from *Salfacarus* (the other African genus with numerous opisthosomal setae), may need to be revaluated.

The presence of six foliate (*d-type*) setae on the palp tarsus of most adults of *N. proteus* (83.5% of females, 50% of males; N=20) is uncommon within *Neocarus*. Two males have 5 setae on one palp and 6 on other palp. Of the 13 species of *Neocarus* currently described, only four; *N. proteus* sp. n., *N. nicaraguensis* Vázquez & Klompen, 2002, *N. platensis* and *N. potiguar*, carry five or six *d*-type setae on the palp tarsus; the other nine species carry only four or five.

Identifications of *Neocarus* species generally requires consideration of multiple characters simultaneously. Table 2 summarizes this type of comparative data.

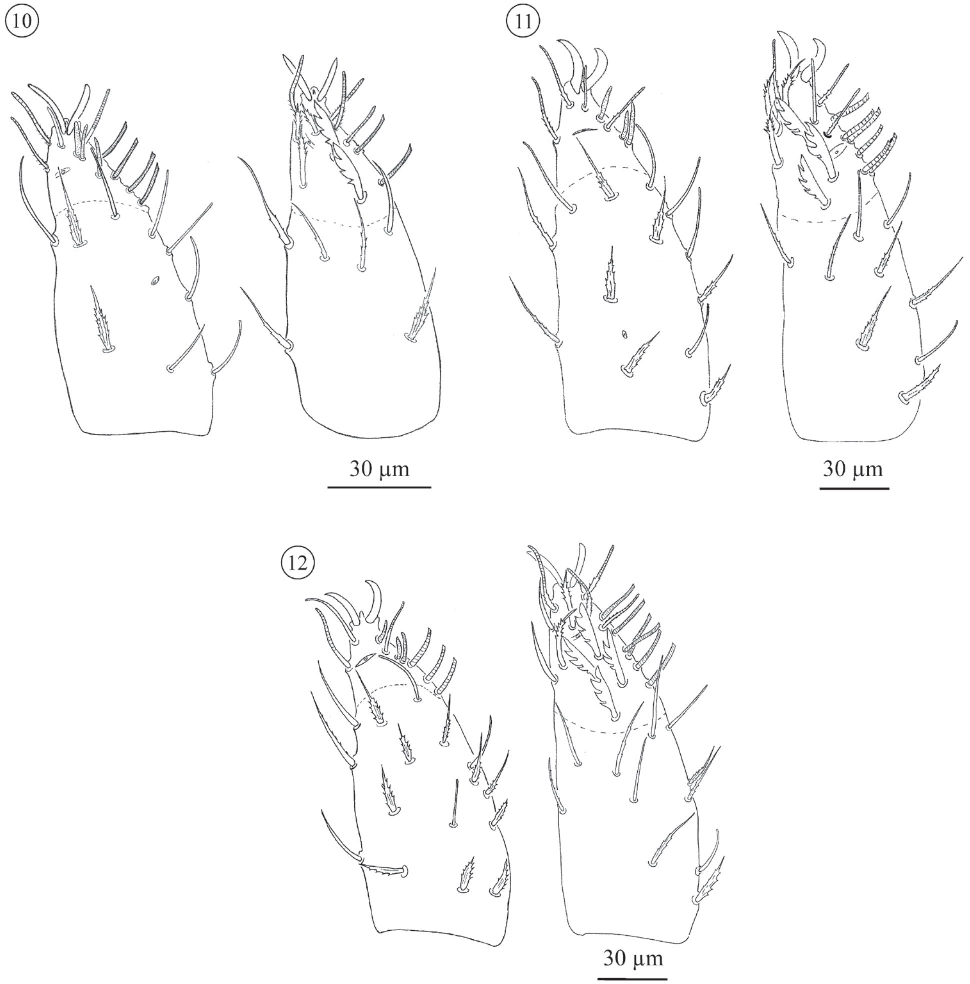
Description. *Chelicera* (Fig. 3); Movable digit (PN 36.9–42.5; DN 45.8–50; TN 45.3–65.9; M 59–64.7; F 63–76.7), digit part of fixed digit (PN 33.6–40.1; DN 40.5–46.8; TN 45.3–61.3; M 45–52.2; F 52–67.5;) and entire fixed digit (segment) (PN 117–118.8; DN 141.5–156.3; TN 153.6–197.6; M 182–202.9; F 195.3–220). Basal segment without setae in all proto- and deutonymphs. One weakly barbed dorsal seta added in all adults and most tritonymphs (one specimen without setae and another 3 with a single seta on one of the two cheliceral bases). Fixed digits each with 2 smooth and 1 barbed seta in all instars (barbs on barbed setae more distinct in later instars). Dorsal and antiaxial lyrifissures present. Rounded and distinct teeth on the fixed digit, one large and distinct tooth with a small medial groove on movable digit. Both digits with a well developed terminal hook. Movable digit with one small denticle on its ventral margin in all instars, more distinct in later instars.

Subcapitulum (Figs 4–9); All stages studied with 4 paralabial setae: *pl1* small, conical; With's organ (*pl2*) membranous, discoid; rutellum (*pl3*) with 1 row of 5 teeth, inserted dorso-laterally; *pl4* small but distinct, inserted dorsal on subcapitulum. Lateral lips with two distinct canals, *ogl1* thicker and shorter than *ogl2* (Fig. 5). All instars also carry at least four circumbuccal setae, somewhat rod-like and with rounded tips. Female tritonymphs and females carry an additional two subcapitular setae resembling circumbuccal setae (Figs 7, 9), one smaller and smooth, the other bigger and weakly barbed, but both with a blunt, slightly rounded or bifurcate tip. These setae are either

Table 2. Comparative setal patterns for the pregenital and genital region of *Neocarus* adults.

Occurence	Species/Subspecies	Female		Male		Palp	
		Pregenital region	Genital region	Pregenital region	Genital region		
		No. and type of setae	No. and type of setae	No. and type of setae	No. and type of setae	*ch*-type	*d*-type
North America							
USA	*N. texanus*	2 st/r	0	4–5 st/r	8–9 sh	14(21[a])	5
Mexico	*N. nohbecanus*	0	0	4-5 st/r	5-7st/r	17-19	4
Mexico	*N. siankaanensis*	0	0	2 st/r	4 st/r	14-15	5
Mexico	*N. bajacalifornicus bajacalifornicus*	2 st/r	0	5–8(13[a]) st/r	7–8(11[a]) st/r	14-18 (21[a])	5
Mexico	*N. bajacalifornicus chamelaensis*	2–3 st/r	0	4–5 st/r	4–6 st/r	16	5
Mexico	*N. calakmulensis*	2–3 st/r	0	2–6 st/r	3–8 st/r	17	5
Mexico	*N. veracruzensis*	2 st/r	0	6–8 st/r , 0–1 s	6–8 st/r	13	5
Central America							
Nicaragua	*N. nicaraguensis*	2–5 st/r	0	2–7 st/r	3–6 st/r	18-22	5 or 6
Cuba	*N. orghidani*	0	0	4–5 st/r	5–7 st/r	20-24	4
South America							
Venezuela	*N. ojastii*	0	0	6–9 ?	13 st/r	-	-
Brazil	*N. proteus*	2–5 st/r	4–6 wb	2–5 st/r	3–5 sh	12 or 13	5 or 6
Brazil	*N. potiguar*	1 tp/r	4–8 sh	5 st/r	7–10 st/r	25-27	5 or 6
Brazil/Argentina/Uruguay	*N. platensis*	0–2 st/r	6–9 sh	6–10 st/r	5–10 sh	14	5 or 6

[a] - number of setae in super adults; sh: smooth setae; st/r - stout and ribbed setae; tp/r: tapering and ribbed setae; wb: weakly barbed setae.

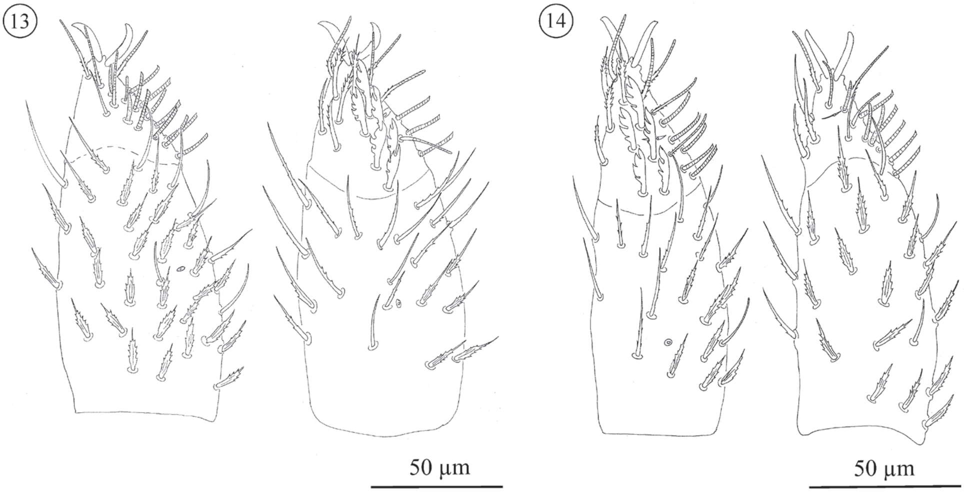


Figures 10–12. *Neocarus proteus* sp. n. Palp, ventral (left) and dorsal (right) view. **10** protonymph **11** deutonymph **12** tritonymph.

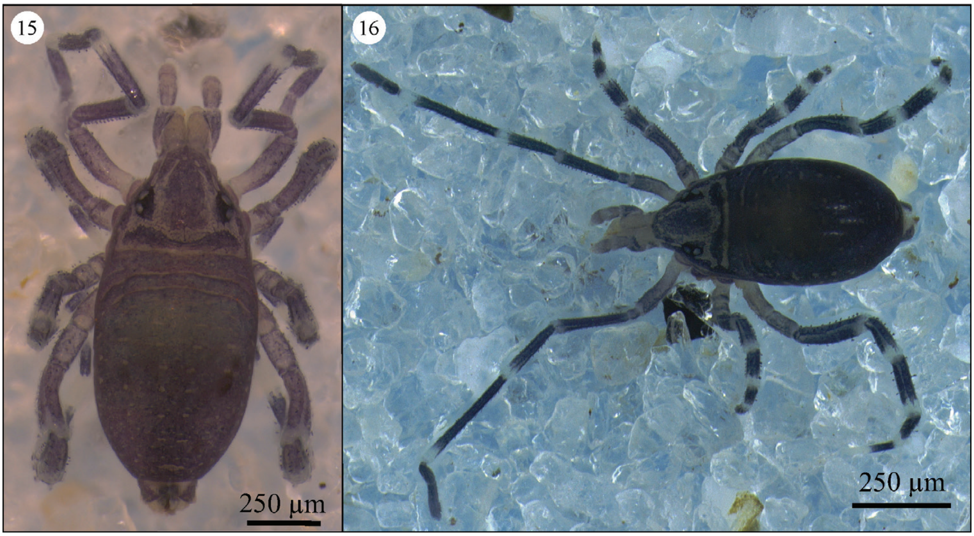
absent or more hair-like, smooth, tapering, and with a fine tip, in male tritonymphs and males. In those instars they resemble the remaining subcapitular setae.

The number of remaining subcapitular setae increases over ontogeny. All instars carry a single dorsal seta, smooth, tapering and with a fine tip. Ventrally, protonymphs, deutonymphs, male tritonymphs, and adult males carry, respectively, 1, 1–2, 2–4, and 4–6 similar fine-tipped setae (Figs 4–6, 8). Female tritonymphs and females carry 3–5 and 4–6 fine-tipped setae ventrally (Figs 7 and 9).

Palp (Figs 10 and 14). Adult trochanter with 3 to 4 ribbed, tapering (= r-type) setae; femur with 6–10 papilliform (= p-type) and 6–13 r-type setae; genu with 1–4 p-type and 27–45 r-type setae. Tibia and tarsus partially fused. Tibia with 6 smooth (= s-type) and 26–34 r-type setae. Palp tarsus with lyrifissures *iπ* and *iα*. Setation

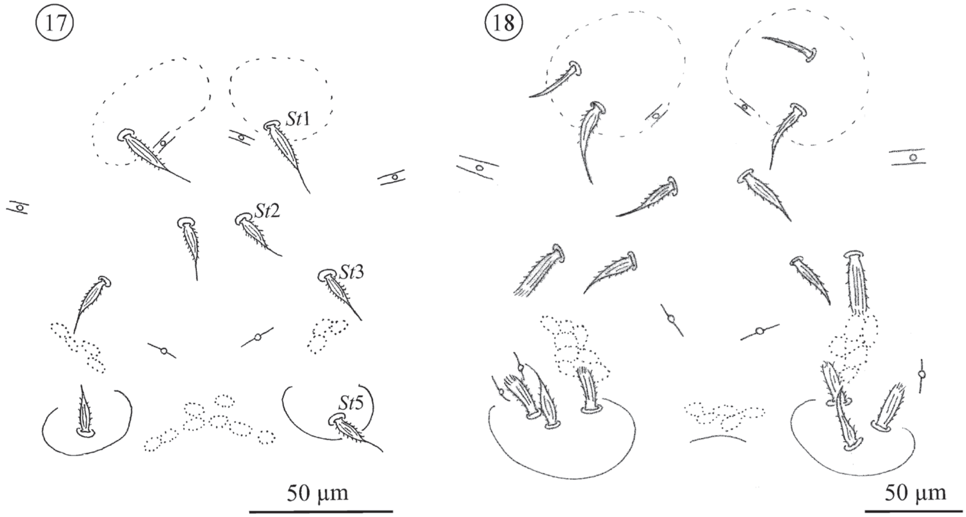


Figures 13–14. *Neocarus proteus* sp. n. Palp, ventral (left) and dorsal (right) view. **13** female **14** male.

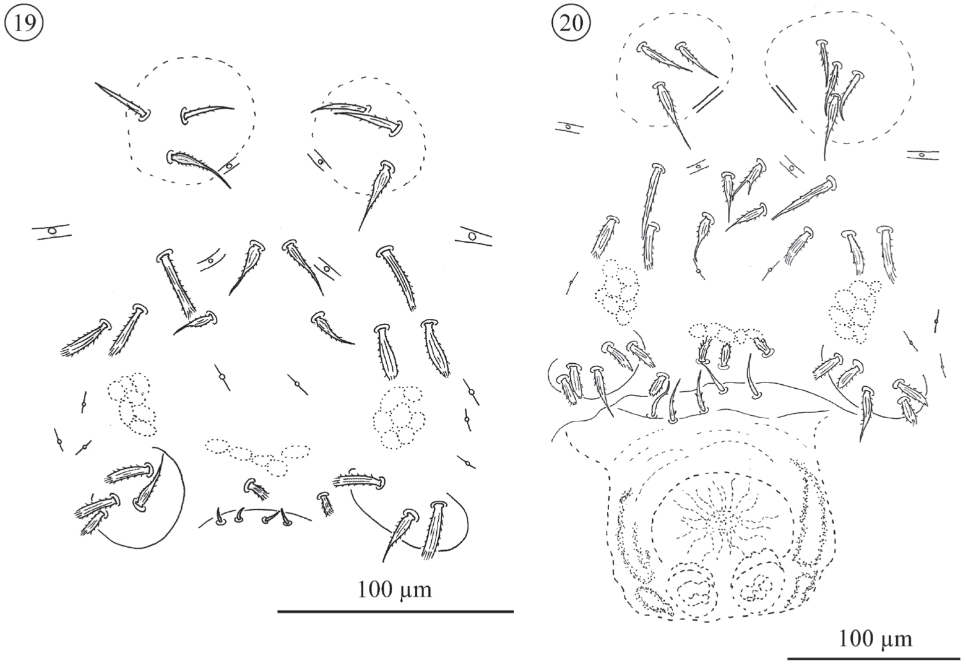


Figures 15–16. *Neocarus proteus* sp. n., adult female. Dorsal view.

includes 3 *s*, 5 or 6 *d*, 6 *v*, 17 *ch*, and 10–11 *sm* setae. The *sm3*-type seta is not present on the male palp. Pretarsus with a pair of well developed sessile claws. No distinct sexual differentiation observed; males generally with fewer trochanteral setae, but ranges overlap. Palp setation of immatures: trochanter: PN 0; DN 0–1; TN 2–3; femur: PN 5 r- and 1 p-type seta; DN 2–6 r plus 1–2 p; TN 4–9 r plus 3–5 p; genu: PN 6 r-type; DN 6–9 r- plus 0–1 p-type; TN 13–21 r- plus 1–2 p. Tarsi of proto-, deuto-, and tritonymphs with, respectively, 2, 3, and 4 *d* setae. Setation of tibiae not scored for immatures.

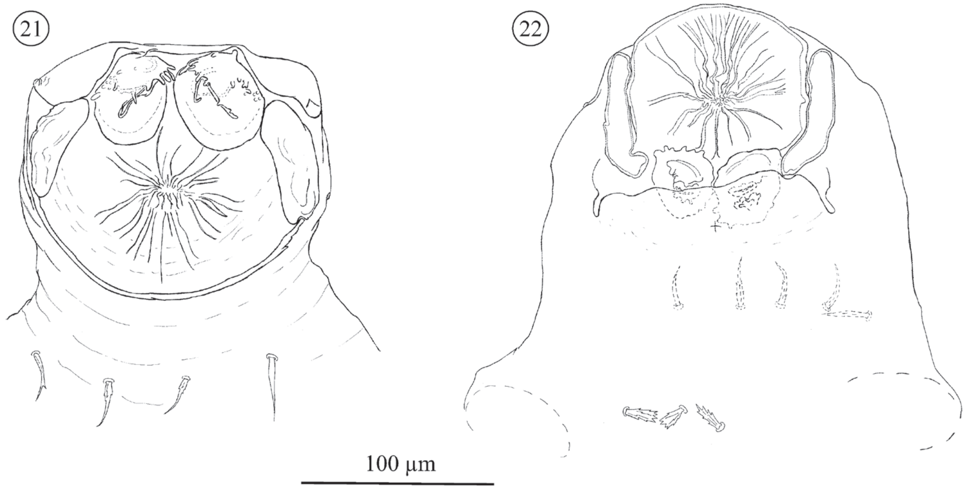


Figures 17–18. *Neocarus proteus* sp. n., sternogenital region. **17** protonymph **18** deutonymph.



Figures 19–20. *Neocarus proteus* sp. n., sternogenital region **19** tritonymph **20** adult female.

Idiosoma (Figs 15 and 16). Adults with body longer (1230–1310 µm) than wide (450–630 µm), oval-shaped. Color light with dark blue patches. Body sometimes with a brownish background resulting from ingested food. Leg segments with strong violet banding.



Figures 21–22. *Neocarus proteus* sp. n., Ovopositor. **21** invagined **22** evaginated.

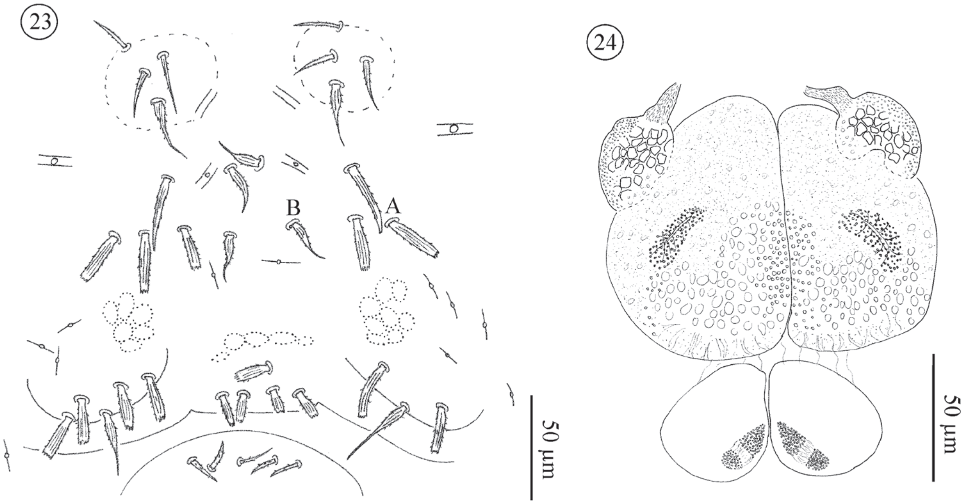
Dorsum: Anterior dorsal shield in all stages with two pairs of eyes, and stout, ribbed setae. Dorsal idiosoma, between the shield and preanal segment, without setae, but with numerous lyrifissures arranged in transverse rows. Preanal segment with 1 dorsal and 2 ventrolateral stout, ribbed setae; anal plates in adults each with 10–15 stout, ribbed setae. Anal plates of PN, DN and TN each with, respectively, 1–2, 3–7 and 4–12 setae.

Sternapophyses: all stages studied with two setae, one small seta at the tip and one long, barbed seta positioned more basally.

Sternogenital region in protonymphs (Figs 17 and 26): sternal area with one pair of verrucae, each carrying one barbed, tapering seta (*St1*). Remaining sternal area with two pairs of small setae, both barbed and tapering (*St2*, *St3*). Pregenital area with one pair of pregenital capsule, each carrying one barbed, tapering seta (*St5*). Genital opening absent. With three pairs of lyrifissures, two pairs large, the third smaller, resembling the lyrifissures on the opisthosoma.

Sternogenital region in deutonymphs (Figs 18 and 26): sternal area with one pair of verrucae, each carrying one barbed, tapering seta (*St1*) and 0–1 barbed, fine setae. Remaining sternal area with two pairs of barbed, tapering setae (*St2*, *St3*), and 0–2 pairs of stout, ribbed and barbed setae usually positioned more laterally. Pregenital area with one pair of capsules, each carrying one barbed, tapering (*St5*) and 0–2 stout, ribbed and barbed setae. Genital opening present or absent, when present very small and poorly visible.

Sternogenital region in tritonymphs (Figs 19 and 26). Sternal verrucae each with one barbed, tapering seta (*St1*) and 1–2 shorter, barbed, fine setae. Sternal area with two pairs of barbed, tapering (*St2*, *St3*) and 1–3 pairs of stout, ribbed and barbed seta. Each pregenital capsules with one barbed, tapering (*St5*) and 1–3 stout, ribbed and barbed setae. Pregenital area between capsules with 0 to 2 stout, ribbed and barbed setae. Genital opening present or absent. The genital area carries 0–4 small and fine setae.



Figures 23–24. *Neocarus proteus* sp. n., adult male **23** sternogenital region **24** male genital glands. **A** and **B** indicate setae illustrated in Fig. 25.

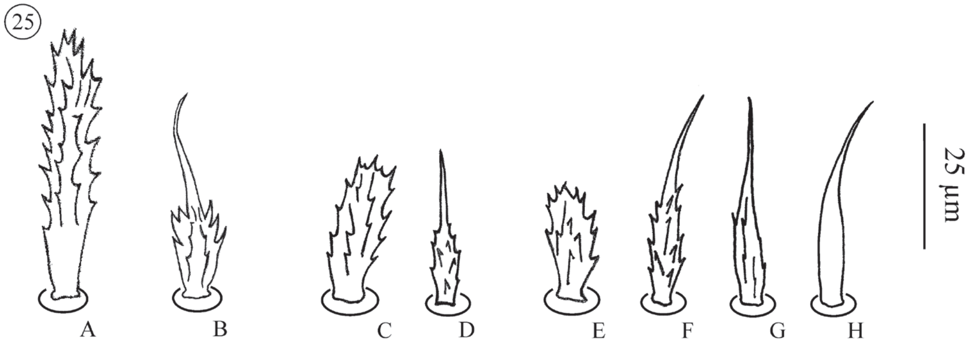


Figure 25. *Neocarus proteus* sp. n., details of shape of sternal and genital setae **A** stout and ribbed seta (sternogenital region) (see Fig. 23: **A**) **B** barbed and tapering seta (*St*3) (see Fig. 23: **B**) **C** stout and ribbed seta (male pre-genital region) **D** barbed and tapering seta (male genital region) **E** stout and ribbed seta (female pre-genital region) **F** and **G** barbed and tapering setae (female genital region) **H** smooth and tapering seta (female genital region).

Sternal region in adults (Figs 20–26). Sternal verrucae each with one long barbed, tapering (*St*1) and 2–4 smaller, barbed, fine setae. Remaining sternal area with two pairs of barbed, tapering (*St*2 and *St*3) and 2–5 pairs of stout, ribbed and barbed setae usually positioned more laterally.

Pregenital and genital area of the female (Figs 20–22 and 26). Each pregenital capsule with one barbed, tapering (*St*5) and 2–5 stout, ribbed and barbed setae. Pregenital area with 2–5 setae of different shapes: stout, ribbed and barbed or smooth. Genital setae with a fine tip, but variable in shape, smooth to barbed at the base and positioned in an invagination, hidden in most of the specimens examined. They are exposed only

Table 3. Mean length and standard deviation (μm) of the legs and palp in all instars of *Neocarus proteus* (4 PN, 9 DN, 6 TN♂, 18 males, 7 TN♀ and 13 females).

Stages	Leg I	Leg II	Leg III	Leg IV	Palp
PN	1080 (± 35)	654 (± 14)	634 (± 18)	1012 (± 52)	288 (± 23)
DN	1423 (± 37)	790 (± 42)	816 (± 42)	1235 (± 45)	359 (± 20)
TN ♂	1762 (± 130)	996 (± 90)	993 (± 136)	1465 (± 182)	384 (±13)
Adult ♂	2282 (± 163)	1303 (± 73)	1331 (± 84)	2063 (± 182)	511 (± 27)
TN ♀	1905 (± 243)	1069(± 88)	10889(± 82)	1704 (± 136)	431 (± 37)
Adult ♀	2397 (± 105)	1410 (± 104)	1416 (± 94)	2246 (± 103)	533 (± 16)

Table 4. Number and position of coronidia on legs II–IV in *Neocarus proteus* (N = 4 PN, 9 DN, 6 TN♂, 18 ♂, 7 TN♀ and 13 ♀).

Stage	Leg II			Leg III			Leg IV	
	Basitarsus	Tibia	Genu	Basitarsus	Tibia	Genu	Basitarsus	Tibia
PN	2	0	0	2	0	0	2–3	0
DN	2	1–2	0	2–3	1–2	0	3–6	1–3
TN	2–4	2–6	0–2	2–4	3–6	0–2	4–9	0–7
Adult	4–8	4–8	1–4	4–9	4–8	1–4	7–15	5–10

during partial or total evagination of the ovipositor (N=3), when they can be observed at the base of that structure (none present at tip). Ovipositor has a tube-like shape, with two rounded structures, similar to glands, and three membranes positioned at tip. In the invaginated ovipositor these membranes remain folded, but in the evaginated ovipositor they are expanded as lobes.

Pregenital and genital area of male (Figs 23–26). Pregenital capsule with one barbed, tapering (*St*5) and 2–4 stout, ribbed and barbed setae. Pregenital area with 4–7 (rarely 2) stout, ribbed and barbed setae. Genital area with 2–5 small, tapering and barbed setae. Accessory glands in males include a pair of large anterior and a pair of small posterior glands. Large glands each with a small canal-like protuberance.

Legs (Figs 27–33, Tables 3 and 4). Leg I longer than others in all instars. Acrotarsi legs II–IV differentiated in all adults, all female tritonymphs, and a few male tritonymphs. Acrotarsal differentiation absent in other male tritonymphs, deutonymphs and protonymphs.

Leg I: Studies of legs I are often difficult, because these legs are fragile and often lost during collection. The results presented are based on three TN♂, three TN♀, six adult females and eight adult males. They show a type of sexual dimorphism that has not previously been recorded for Opilioacaridae. Males carry a number of smooth setae on the tibia (ranging from 29–59), genu (10–22), femur (6–21), and occasionally the trochanter (one smooth setae present in just two specimens). These setae were not observed in females. In tritonymphs this type of setae was observed in just one male tritonymph, placed on the anterior portion of the tibia.

Telotarsus I has a highly modified group of dorsal setae located in the apical portion, close to the tarsal claws, homologous to the Haller's organ of ticks (Moraza 2005).

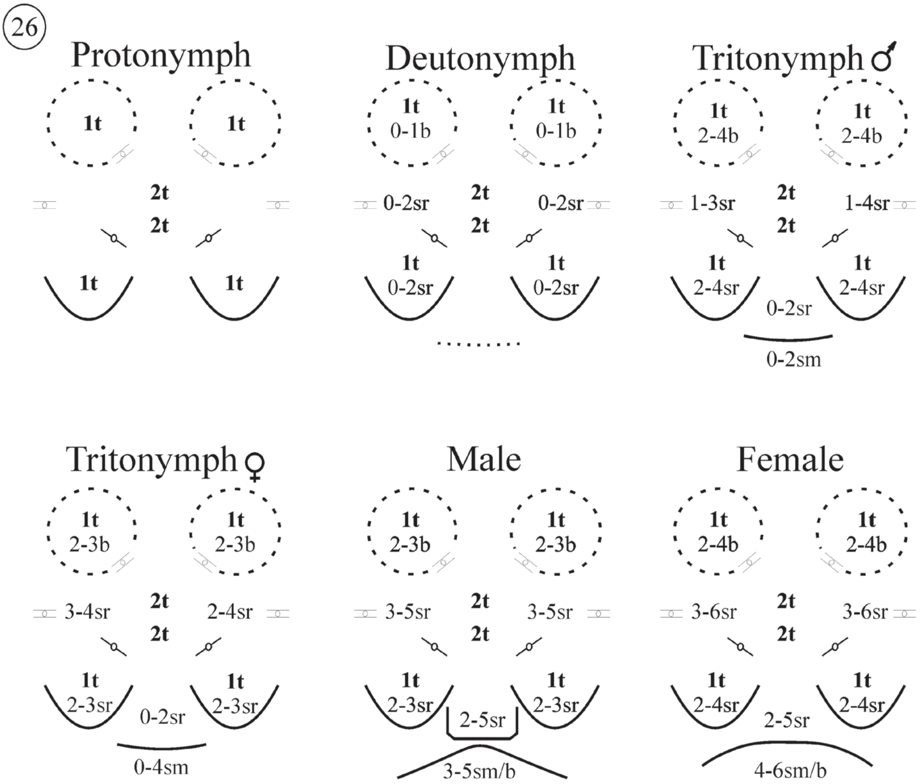


Figure 26. *Neocarus proteus* sp. n., schematic representation of the variation in the numbers of setae observed in the sternogenital area of nymphs and adults; sr, stout and ribbed setae; t, tapering and ribbed setae; b, tapering and barbed; sm: smooth.

Figure 27. *Neocarus proteus* sp. n., anterior portion of tarsus I. Sensillum with "crown-like" tip arrowed.

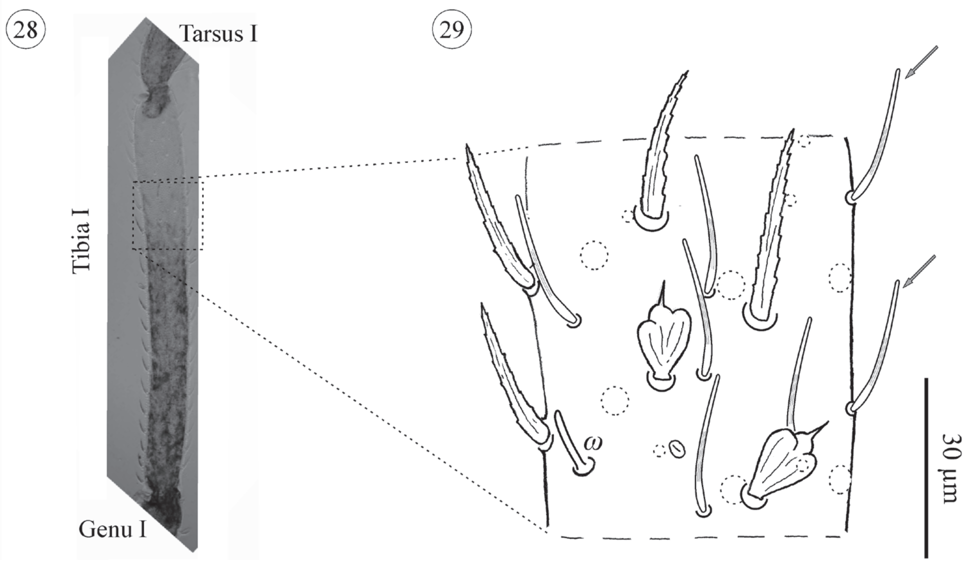


Figure 28–29. *Neocarus proteus* sp. n., tibia I of adult male. **28** General aspect of tibia I **29** details showing solenidion and smooth setae. Arrows indicate smooth setae.

Basitarsus I carries just two types of setae, only smooth setae in the distal half, and a mixture of smooth and tapering, barbed setae in the basal half. All other leg segments carry three types of setae arranged in distal to basal rows: 1) tapering and barbed, 2) papilliform and 3) smooth setae.

One solenidion is present on basitarsus I in all instars. On tibia I solenidia were not observed in the proto- and deutonymphs, appearing in the tritonymph (1–3) and adults (3–5). One caveat: the number of proto- (N=2) and deutonymphs (N=3) with leg I in the correct position to observe the solenidia was quite small. More specimens are needed to confirm this addition sequence.

Legs II–IV in adults: dorsal portion of acrotarsus II with a ribbed and bifurcate seta, one small solenidion, and one long and smooth sensillum (probably also a solenidion). Legs III and IV carry on the dorsal portion only 3 long and barbed setae. Additionally, acrotarsi II–IV present 3 pairs of smooth ventral setae, 1 pair of lightly barbed ventrolateral setae (positioned distally), 2 pairs of smooth lateral setae, and 1 pair of smooth laterodorsal setae (positioned distally). Pretarsi in all instars with one pair of claws and 2 pairs of setae, one pair long and curved, the other small and straight. Pretarsal ambulacrum rounded and smooth.

Coronidia (Figs 32 and 33, arrow) are present in all instars studied, but their number and distribution expands from protonymphs to adults. In protonymphs coronidia are restricted to basitarsi II–IV. In the deutonymphs coronidia appear also on tibiae II–IV. In tritonymphs and adults the distribution of coronidia extends to the genua of legs II–III. The number of the coronidia, and their position is indicated in Figures 32–33 and in Table 4. Coronidia are short and smooth, characteristics that make them similar to the

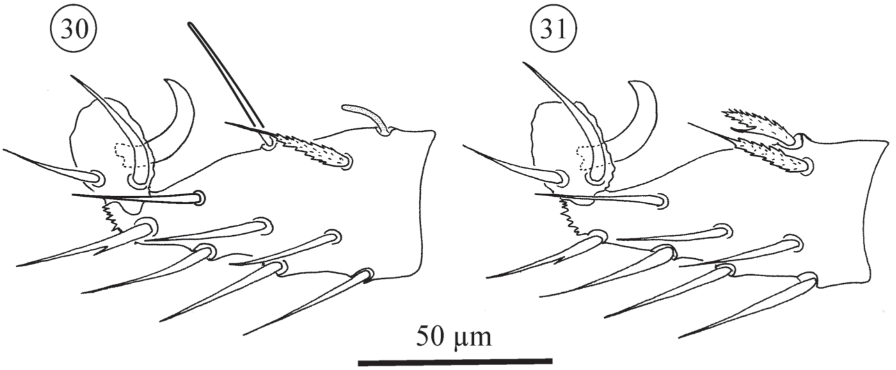
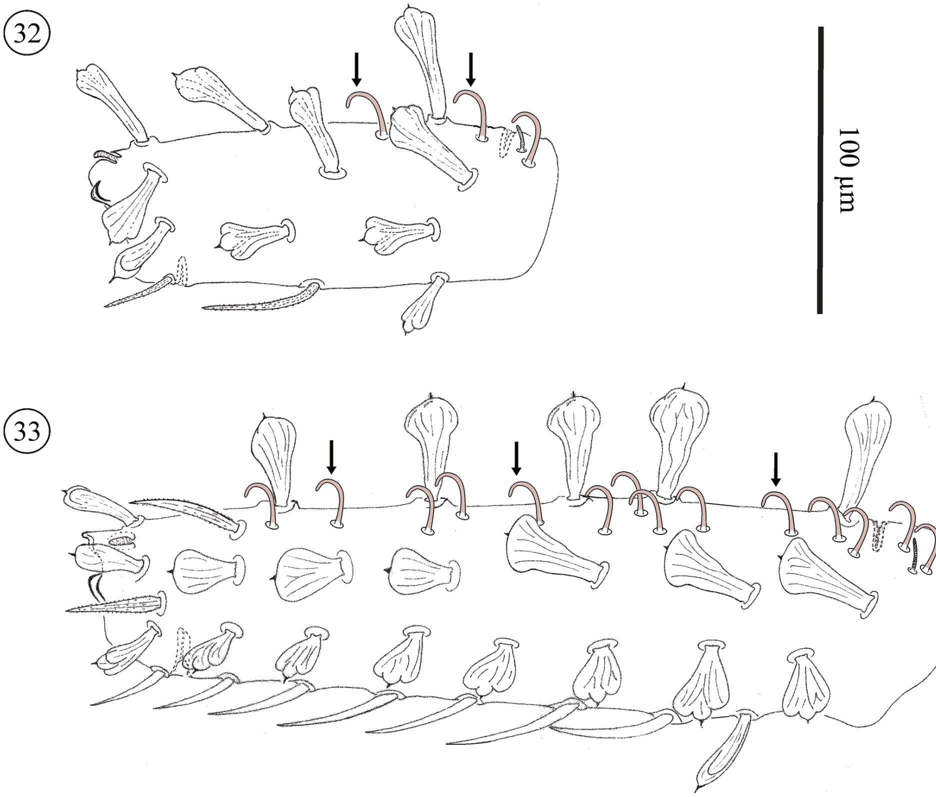


Figure 30–31. *Neocarus proteus* sp. n., adult female, acrotarsus II. **30** anterolateral view **31** posterolateral view.



Figures 32–33. *Neocarus proteus* sp. n., anterolateral view of basitarsus IV. **32** protonymph **33** adult female. Arrows indicate some of the coronidia.

setae present on legs I of the male (see above). However, coronidia in the strict sense are strongly curved middorsally, whereas the smooth setae on legs I are straight. Coronidia s.st. occur solely on legs II–IV, while the smooth setae are limited to legs I of the male.

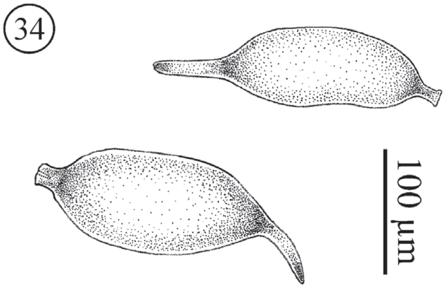


Figure 34. *Neocarus proteus* sp. n., eggs inside female.

Eggs (Figs 34); During dissection of 4 females we observed eggs inside the body. The eggs present varying sizes, suggesting different stages of maturation. The number of eggs observed inside the females was 4, 4, 5 and 6. All eggs observed in *N. proteus* are similar to *N. texanus* eggs, as described by Hammen (1966). They are oval, elongated and whitish in color, two different processes, one blunt and other elongated, were observed at opposite ends of the egg. The blunt process contains an invagination, but the canal described by Hammen (1966) was not observed. Notably, the processes are absent after oviposition (Klompen 2000).

Etymology. Proteus comes from the adjective Greek "protean", meaning versatile, mutable, capable of assuming many forms.

Discussion

Sexual differentiation was not observed in the proto- and deutonymphal instars, but such differentiation was noted in tritonymphs. One of the most consistent secondary sexual dimorphisms appears to be the presence (or absence) of additional subcapitular setae with rounded tips (present in female tritonymphs and females). This traids is present in more than 12 undescribed Brazilian species and, despite not being mentioned in the original descriptions, is also present in *N. potiguar* and *C. brasiliensis*. Notably, this character is quite different from those listed by Hammen (1969) and Coineau and Hammen (1979). For example, Hammen (1969) suggested sexual differentiation in the tritonymph of *N. platensis*, based on the pattern of pregenital setae (present in males, absent in females). This is unlikely to be valid for *N. proteus* as setae may or may not be present in the pregenital area in tritonymphs of both sexes (they are present in that area in all adults). That character therefore has limited use for sexual differentiation of tritonymphs in *N. proteus*.

The difference in the number of specific subcapitular setae is not the only type of sexual dimorphism expressed in tritonymphs and adults. Different patterns in the size of body parts could also be documented. Legs IV and the palps in female tritonymphs are significantly longer than in male tritonymphs (leg IV, F= 5.55, p= 0.04628; palp, F=9, p=0.01). This difference is due to differences in growth rate. When comparing the average size of all legs, those of female tritonymphs are 25% to 28% larger than

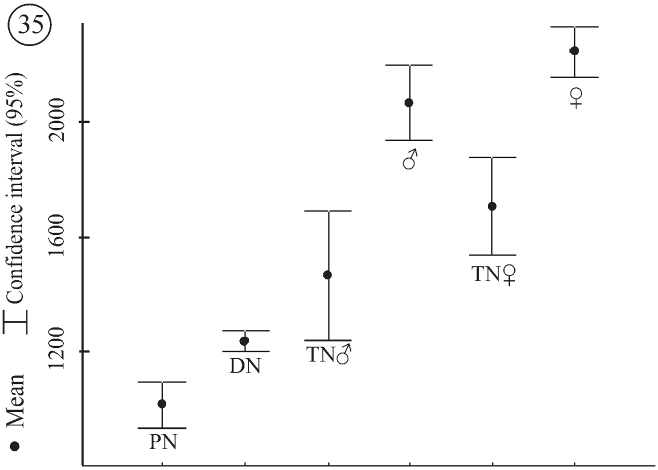


Figure 35. *Neocarus proteus* sp. n., length of leg IV in all instars studied.

those of deutonymphs, whereas legs of male tritonymphs are just 19% to 20% larger. These growth rate differences in tritonymphs reflect size differences for legs II–IV of males and females (data for legs I are insufficient). Legs II–IV in adult females are significantly larger than in adult males (leg II: F=7.5, p=0.01; leg III, F=4.55, p=0.046; leg IV F=5.22, p=0.034; palp F=4.84, p=0.039) (Fig. 35).

Overall size increase of the legs from protonymph to adult is about 2–2.5×. This resembles the growth pattern observed in the acariform mite families Trombiculidae and Histiostomatidae (Jones 1954), in which adults about 2.5× larger than protonymphs.

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