



## Article

# A Family Affair: Diagnosing and Delimiting Prostygnae (Opiliones: Gonyleptoidea) <sup>†</sup>

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**Abstract:** The former subfamily Prostygnae was recently elevated to family rank, and its phylogenetic relationships were investigated based on molecular data. In this study, we provide a revised morphological diagnosis for the family, focusing on characters from the exomorphology and male genital morphology. Morphological data supporting their inclusion in the MECO clade are provided. Additionally, a key to the genera is presented, and *Prostygna stellatus* **sp. nov.**, a new Ecuadorian species, is described. The geographic distribution of prostygnid species is mapped. An overview of the inclusion and exclusion of genera formerly within Prostygnae, but currently in Gonyleptoidea incertae sedis, is presented, and the following new familial assignments are proposed: *Binamballeus* Roewer, 1952 and *Puna metatarsalis* (Kury, 1994) **comb. nov.** (transferred to Cranidae), *Sclerostygnellus* Roewer, 1943 (transferred to Manaosbiidae) and *Globitarsus* Roewer, 1913, *Lisarea* Roewer, 1943, *Meridanatus* Roewer, 1943, *Micropachylus* Roewer, 1913, *Prostygnaidius* Roewer, 1915, and *Troya* Roewer, 1914 (all transferred to Nomoclastidae). Three subjective synonyms of *Troya* are proposed: *Peladoius* Roewer, 1914 **syn. nov.**, *Prostygnaellus* Roewer, 1914 **syn. nov.**, and *Minyssus* Roewer, 1943 **syn. nov.**, combining their species with *Troya* and, finally, *Prostygnaellus riveti* Roewer, 1914 is considered as a junior secondary homonym of *Troya riveti* Roewer, 1914 **syn. nov.**



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**Keywords:** Ecuador; Cranidae; new species; Peru; Prostygnae; taxonomy

## 1. Introduction

Prostygnae is a micro-diverse family of Grassatores with six species [1] distributed in southern Ecuador and northern Peru. The systematic placement of Prostygnae/Prostygnae within Gonyleptoidea has undergone a series of changes. It transitioned from being nested within Gonyleptidae, to Cranidae, and ultimately emerged as an autonomous family within the unranked clades Carunculata Kury, 2020 (=MECO + Askawachidae Kury & Carvalho, 2020) and MECO Kury & Villarreal, 2015 (formerly Me/Co, =Cosmetidae Koch, 1839 + Metasarcidae Kury, 1994 + Prostygnae Roewer, 1913). The internal composition of this subfamily/family also changed significantly over time.

In the current project, we provide an account of the evolution of the Prostygnae concept, elucidating its taxonomic framework, evolutionary history, and geographical distribution, and we offer a comprehensive genus-level key to facilitate the classification of related taxa. Additionally, we introduce a new species from Ecuador and provide a description thereof. Finally, we propose several family reassignments of species previously affiliated with Prostygnae.

### 1.1. Taxonomic Historical Background of Prostygnaidae

Roewer [2] proposed a reorganization of the family Gonyleptidae, dividing it into numerous subfamilies. One such subfamily was Prostygnae, which was based on the absence of features of the other subfamilies (plesiomorphic states of characters). In Roewer's original classification of Prostygnae, he included six genera, which are now distributed across various families, apart from the type genus, one in Manaosbiidae (*Camelianus* Roewer, 1912), one in Agoristenidae (*Sabanilla* Roewer, 1913), two in Nomoclastidae (*Globitarsus* Roewer, 1913, *Micropachylus* Roewer, 1913), and one peculiar gonyleptoid that remains unplaced as of yet (*Ostracidium* Perty, 1833). This practice of grouping unrelated genera in Prostygnae reached its pinnacle in the work of Soares, Soares, and Jim [3], who listed several genera, mostly monotypic, that currently correspond to various families within Gonyleptoidea.

Over the years, the family Gonyleptidae was splintered, leading to the extraction of several taxa to establish their own distinct families, such as Cryptogeobiidae, Metasarcidae, Stygnidae (Sørensen in [4–6]). Kury [7] introduced the concept of a separate family Cranidae, including Prostygnae. However, it became increasingly evident that Prostygnae was not in the immediate phylogenetic vicinity of the Cranidae.

Kury [8] pointed out that the male genitalia of *Prostygna* Roewer, 1913 bore a stronger resemblance to those of Cosmetidae rather than those of Cranidae. Villarreal and García [9] presented illustrative comparisons between the stylus of *Prostygna* and of a cosmetid species. They highlighted the presence of a wattle in both *Prostygna* and the cosmetid, while noting that both lacked a styler cap, a possible synapomorphy for cranid species.

Morphologically-based phylogenetic analysis of the Cranidae [10] revealed that Prostygnae stood near the unranked MECO clade, which, at that time, encompassed Cosmetidae and Metasarcidae. These findings were subsequently supported by the similarities in the ventral plate microsetae pattern between Prostygnae and the MECO clade, rather than the Cranidae family [11].

Meanwhile, Kury and Carvalho [12] introduced the new Askawachidae family and established the new unranked taxon Carunculata that encompassed Cosmetidae, Metasarcidae, Prostygnae, and Askawachidae. They alluded to the impending cranid paper while taking this step. Medrano et al. [13] concurred with the placement of Prostygnae in MECO as the possible sister-group of Cosmetidae.

Derkarabetian et al. [14], employing UCEs (Ultra-Conserved Elements), provided further validation for the placement of Prostygnae within the MECO clade, as the sister-group of Metasarcidae + Cosmetidae. This corroboration was substantiated by evidence from an entirely distinct dataset, adding an extra layer of molecular confirmation to the earlier morphological findings.

Therefore, all the recent literature places Prostygnae outside Cranidae and nested within MECO. We concur with this placement and, as such, do not need to repeat any testing here, although a few comments on the morphology are given in the "Discussion" section.

### 1.2. Composition of Prostygnae/Prostygnaidae

Due to the diagnosis of Prostygnae, as originally conceived by Roewer, to be based on symplesiomorphies, it was likely to gather unrelated genera. It took a significant amount of time for this motley crew to be purged. In Table 1, we present an overview of the inclusion and exclusion of genera within Prostygnae.

**Table 1.** Entries and dismissals of genera in Prostyginae. Destinations marked with the superscript index C mean the genus is being transferred to Cranaidae and index N is being transferred to Nomoclastidae in this paper (see below). Genera marked with the superscript index S signify that the genus is currently under synonymy or being brought under synonymy herein.

| Genus, Author, Year                            | Entered Prostyginae in | Last Assignment before Prostyginae | Removed from Prostyginae in                 | Ultimate Destination (Current)            |
|--|------------------------|------------------------------------|---|---|
| <i>Camelianus</i> Roewer, 1912                 | [2]                    | Gonyleptidae, no subfamily         | [15]  | Manaosbiidae                              |
| <i>Globitarsus</i> Roewer, 1913                | [2]                    | none—then new                      | [16]  | Gonyleptoidea incertae sedis <sup>N</sup> |
| <i>Micropachylus</i> Roewer, 1913              | [2]                    | none—then new                      | [16]  | Gonyleptoidea incertae sedis              |
| <i>Ostracidium</i> Perty, 1833                 | [2]                    | Gonyleptidae, no subfamily         | [17]  | Grassatores incertae sedis                |
| <i>Prostygnum</i> Roewer, 1913                 | [2]                    | none—then new                      | type-genus to which Prostyginae is anchored | Prostygidae                               |
| <i>Sabanilla</i> Roewer, 1913                  | [2]                    | none—then new                      |   | [18]                                      |
| <i>Peladoius</i> Roewer, 1914 <sup>S</sup>     | [19]                   | none—then new                      | [16]  | Gonyleptoidea incertae sedis <sup>N</sup> |
| <i>Prostygnullus</i> Roewer, 1914 <sup>S</sup> | [19]                   | none—then new                      | [16]  | Gonyleptoidea incertae sedis <sup>N</sup> |
| <i>Troya</i> Roewer, 1914                      | [19]                   | none—then new                      | [16]  | Gonyleptoidea incertae sedis <sup>N</sup> |
| <i>Prostygmidius</i> Roewer, 1915              | [20]                   | none—then new                      | [16]  | Gonyleptoidea incertae sedis              |
| <i>Chacoikeontus</i> Roewer, 1929 <sup>S</sup> | [21]                   | none—then new                      | [22]  | Metasarcinae/Metasarcidae                 |
| <i>Chaconatus</i> Roewer, 1929 <sup>S</sup>    | [21]                   | none—then new                      | [5]   | Metasarcinae/Metasarcidae                 |
| <i>Napostygnum</i> Roewer, 1929                | [21]                   | none—then new                      | [23]  | Nomoclastidae                             |
| <i>Nemastygnum</i> Roewer, 1929                | [21]                   | none—then new                      | [24]  | Agoristenidae                             |
| <i>Leptostygnum</i> Mello-Leitão, 1940         | [25]                   | none—then new                      | [18]  | Agoristenidae                             |
| <i>Gonogotus</i> Roewer, 1943                  | [26]                   | none—then new                      | [15]  | Manaosbiidae                              |
| <i>Iquitosa</i> Roewer, 1943                   | [26]                   | none—then new                      | [27]  | Cranaidae                                 |
| <i>Lisarea</i> Roewer, 1943                    | [26]                   | none—then new                      | [16]  | Gonyleptoidea incertae sedis              |
| <i>Meridanatus</i> Roewer, 1943                | [26]                   | none—then new                      | [16]  | Gonyleptoidea incertae sedis <sup>N</sup> |
| <i>Minyssus</i> Roewer, 1943 <sup>S</sup>      | [26]                   | none—then new                      | [16]  | Gonyleptoidea incertae sedis              |
| <i>Poassa</i> Roewer, 1943 <sup>S</sup>        | [26]                   | none—then new                      | [23]  | Nomoclastidae                             |
| <i>Sanvincentia</i> Roewer, 1943               | [26]                   | none—then new                      | [15]  | Manaosbiidae                              |
| <i>Sclerostygnellus</i> Roewer, 1943           | [26]                   | none—then new                      | [16]  | Gonyleptoidea incertae sedis              |
| <i>Binamballeus</i> Roewer, 1952               | [28]                   | none—then new                      | [16]  | Gonyleptoidea incertae sedis <sup>C</sup> |
| <i>Tschaidicancha</i> Roewer, 1957             | [29]                   | none—then new                      | [22]  | Metasarcinae/Metasarcidae                 |
| <i>Cutervolus</i> Roewer, 1957                 | [7]                    | Phalangodidae<br>Tricommatinae     | n/a   | Prostygidae                               |
| <i>Globibunus</i> Roewer, 1912                 | [7]                    | Phalangodidae<br>Tricommatinae     | [30]  | Agoristenidae                             |
| <i>Yania</i> Roewer, 1914                      | [7]                    | Phalangodidae<br>Tricommatinae     | n/a   | Prostygidae                               |
| <i>Llaguena</i> Kury & Pérez-González, 2015    | [31]                   | none—then new                      | n/a   | Prostygidae                               |

## 2. Materials and Methods

The specimens examined for this study are deposited in the Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP-curator: R. Pinto-da-Rocha). The patterns of description follow Villarreal et al. [32,33] with slight modifications. The descriptions of colors use the standard names of the 267 Color Centroids of the NBS/IBCC Color System (online at <http://people.csail.mit.edu/jaffer/Color/Dictionaries#nbs-iscc>) (accessed on 10 October 2023) as described in Kury and Orrico [34]. The terminology for the integumentary ornamentation follows DaSilva and Gnaspini [35], the chaetotaxy of penis ventral plates follows Kury and Villarreal [36], the dorsal scutum outline types follow Kury and Medrano [37], and the penial microsetae follows Kury [11]. The color description refers to specimens preserved in ethyl alcohol. All measurements are in mm unless otherwise noted. Pictures were made using a Sony Cybershot DSC-V1 camera (Rio de Janeiro, Brazil) attached to a stereomicroscope. The multiple images of each species at different focal planes were combined with CombineZP to increase the depth of field and were posteriorly edited in Adobe Photoshop CC 2014 software. Drawings were made using the Inkscape 1.3 and Adobe Illustrator CC 2017 software. Scanning Electron Microscopy (SEM) was carried out with a JEOL JSM-6390LV microscope (Rio de Janeiro, Brazil) at the Center for SEM of the Museu Nacional/UFRJ with an accelerating voltage of 10 kV after sputter-coating with gold-palladium. When listing the examined material, countries are written in bold letters and the first order administrative divisions are written in small caps. The distribution map was made using ESRI ArcGIS 10.4. The colored shapes refer to WWF Terrestrial Ecoregions of the World [38]. The type material of *Prostygnus stellatus* sp. nov. was unfortunately destroyed during the fire at the MNRJ in September 2018 [39], limiting certain aspects of the description of this species. Nonetheless, the information presented is considered sufficient for the accurate diagnosis and future unequivocal identification of the species.

The abbreviation transl. nov. (=translatio nova; new transfer/assignment) is used here for new familial assignments. We avoid the term “attribution” for possible confusion with “Creative Commons Attribution License”.

Morphological abbreviations: DS, dorsal scutum; MS, macrosetae; VP, ventral plate (ventrodiscal setigerous region of penis); macrosetae A1–A3, basal macrosetae of VP; B, ventro-basal macrosetae of VP; C1–C3, distal macrosetae of VP, D1, dorso-lateral subdistal small setae of VP; VP = ventral plate (penis).

## 3. Results

### 3.1. Taxonomic Key to Prostygnae Genera (Males)

|   |                   |
|---|-------------------|
| 1.a.- Mesotergal area III unarmed   | 2                 |
| 1.b.- Mesotergal area III armed with a pair of paramedian spines  | 3                 |
| 2.a.- Without preocular mound; ocularium high, more than five times higher than the ocular diameter; DS with yellow or white spots; MS-C clearly larger than the MS-A | <i>Yania</i>      |
| 2.b.- Preocular mound present; ocularium low, twice the ocular diameter; DS without yellow or white spots; MS-A clearly larger than the MS-C                          | <i>Llaguena</i>   |
| 3.a.- Spines of the scutal area III separated from each other; MS-C located distal on the VP, larger than MS-A  | <i>Prostygnus</i> |
| 3.b.- Spines of the scutal area III arising from a common base, partially fused to each other; MS-C positioned subdistal on the VP, same size of MS-A                 | <i>Cutervolus</i> |

### 3.2. Taxonomy

Order Opiliones Sundevall, 1833

Suborder Laniatores Thorell, 1876

Superfamily Gonyleptoidea Sundevall, 1833

**Family Prostygnae Roewer, 1913**

• Prostygnae (subfamily of Gonyleptidae) Roewer 1913c: 140 (incl. *Camelianus*, *Globitarsus*, *Micropachylus*, *Ostracidium*, *Prostygnus*, *Sabanilla*). Type genus: *Prostygnus* Roewer, 1913 (stem: *Prostygn-*).

Prostygninae (subfamily of Gonyleptidae)—Roewer 1914c: 122 (newly incl. *Peladoius*, *Prostygnellus*, *Troya*); Roewer 1915c: 3 (newly incl. *Prostygnidius*); Roewer 1923: 449 (incl. *Camelianus*, *Globitarsus*, *Micropachylus*, *Ostracidium*, *Peladoius*, *Prostygnellus*, *Prostygnidius*, *Prostygnus*, *Sabanilla*, *Troya*); Roewer 1929f: 273 (newly incl. *Chacoikeontus*, *Chaconatus*, *Napostygnus*, *Nemastygnus*); Mello-Leitão 1930b: 211 (mention); Kästner 1937: 389; Mello-Leitão 1940e: 305 (newly incl. *Leptostygnus*); Roewer 1943: 30 (newly incl. *Gonogotus*, *Iquitosa*, *Lisarea*, *Meridanatus*, *Minyssus*, *Poassa*, *Sanvincenia*, *Sclerostygnellus*); Mello-Leitão 1949: 8 (mention); Roewer 1952c: 57 (newly incl. *Binamballeus*); Roewer 1957a: 80 (newly incl. *Tschaidicancha*); Soares, Soares & Jim 1992: 1 (checkl.); Kury 1992b: 98 (newly incl. *Cutervolus*, *Globibunus*, *Ramonus*, *Yania*).

“Prostigninae” (subfamily of Gonyleptidae): Mello-Leitão 1923c: 132 (incorrect subsequent spelling).

“Prostygninae” (subfamily of Gonyleptidae): Mello-Leitão 1926: 346 (incorrect subsequent spelling (with ligature)).

“Prostygyninae” (subfamily of Gonyleptidae): Roewer 1929f: 181. (incorrect subsequent spelling).

“Prostygninas” (subfamily of Gonyleptidas): Mello-Leitão 1932: 103. (incorrect subsequent spelling (rendered to Portuguese vernacular)).

Prostygninae (subfamily of Cranidae): Kury 1994b: 140 (diagn., compos.) (first use as a subfamily of Cranidae).

Prostygninae (subfamily of Cranidae)—Kury 2003a: 100 (cat.); Kury 2012c: 34 (diagn., incl. *Cutervolus*, *Prostygnus*); Kury 2016: 147 (genit. morph.).

Prostygnidae: Kury & Carvalho 2020: 55 (incl. in MECO) (first use as a family).

Prostygnidae—Medrano et al. 2021: 590 (phylog. position); Derkarabetian, Lord, Angier, Frigiyik & Giribet 2023: 10 (molec. anal.).

Diagnosis. Medium size (dorsal shield length approximately 4 mm). Outline of DS type kappa (*Prostygnus*) (Figures 1A and 2A) or alpha (*Llaguenia*, *Yania*) (Figure 3A). Dorsal scutum with four well-defined mesotergal areas (Figures 1A,B and 2A,B), area III may have a pair of paramedian spiniform tubercles with a fused (*Cutervolus*), normally separate (*Prostygnus*) (Figures 1A and 2A) or entirely unarmed (*Llaguenia*, *Yania*) (Figure 3A,B). Chelicerae hypertelic in males (Figures 1A,B,D, 2A,B and 3A,B). Pedipalp femur with ventral ornamentation represented by a row of tubercles of equal size and regularly distributed (Figures 1D, 2D, and 3B) (absent in *Llaguenia*). Pedipalp femur without ectal row of tubercles, and without dorso-distal tubercle. Pedipalp tibia, dorsally tuberculated. Legs short. Tibia IV without conspicuous ornamentation like rows of thorns, or any tubercles conspicuously larger than the rest (Figures 1B and 3B). Male genitalia sui generis (Figures 3C,D and 4A,B), with the formation of a ventral plate covered ventrally by type-4 microsetae, distributed in two large lateral areas separated by a central unarmed region (Figure 4C,D). These microsetae can extend and are also present in the lateral areas and slightly up to the most dorsal region at the base of the ventral plate, surrounding the MS-A (Figure 4B,D). Stylus with ventral wattle and thumb-like process (Figures 3E,F and 4A,B,E). Ventral plate without laterobasal projections in the form of spiny sacs (Figure 3C,E) and the distal edge straight or slightly concave without distal cleft (Figures 3D and 4A–C). Large and curved MS-C, larger than MS-A (Figures 3C–F and 4A–D), except *Llaguenia*, where they are clearly smaller; two pairs of MS-A, located basally on the ventral plate, ungrouped from the MS-C; MS-B absent (Figures 3E,F and 4C); MS-D1 present; and MS-D2 absent (Figure 4A,B).

Included taxa. *Cutervolus* Roewer, 1957, *Llaguenia* Kury et Pérez-González, 2015, *Prostygnus* Roewer, 1913, *Yania* Roewer, 1919 **attr. nov.**

Distribution and natural history. Our understanding of family diversity remains limited, with known species mainly stemming from type material. This hampers ecological and biogeographical predictions. Yet, it is notable that all species inhabit high-altitude Andean regions in Ecuador and Peru (Figure 5), primarily between 2260 and 3000 m, except for *Yania flavolimbata*, which reaches up to 4536 m. This species exhibits the highest records (ranging between 3000 and 4536 m). *Cutervolus albopunctatus* has been recorded as cave-dwelling, as well as inhabiting nearby cloud forest environments [24].

**Genus *Prostygnus* Roewer, 1913** *Prostygnus* Roewer 1913c: 141. Type-species by monotypy: *Prostygnus vestitus* Roewer, 1913.

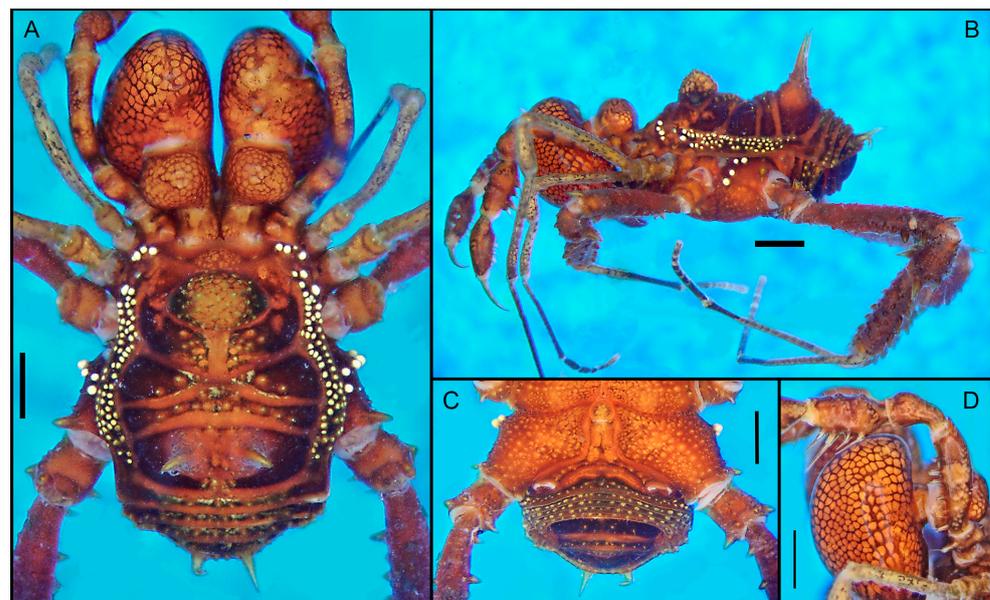
*Prostygnus*—Roewer 1923: 450; Mello-Leitão 1926: 346; Roewer 1929f: 274; Mello-Leitão 1932: 107; Kästner 1937: 389; Soares, Soares & Jim 1992: 10 (checkl.); Kury 2003a: 102 (cat.); Kury 2012c: 35.

Etymology. From Greek πρό (before, forth) + pre-existing genus *Stygnus*. Gender masculine.

Diagnosis. DS outline type kappa. Four scutal areas, area III with a pair of large spines separated from each other. Ocularium domed, high, and tuberculated. DS with yellowish spots on lateral and scutal areas. VP of penis sub-rectangular, with distal border sub-straight or subtle concave, MS-C larger than MS-A.

Included species. "*Prostygnus*" *calcar* Roewer, 1943; *Prostygnus stellatus* sp. nov.; *Prostygnus vestitus* Roewer, 1913.

Remarks. *Prostygnus calcar* does not exhibit the diagnostic characters of the genus or even the family; rather, it seems to be a member of Nomoclastidae, with its generic assignment appearing to be impossible given the current state of knowledge regarding this species. Consequently, we have chosen to tentatively retain its placement within *Prostygnus*, despite recognizing its lack of affiliation with this group, until specimens of this species can be thoroughly examined.



**Figure 1.** *Prostygnus stellatus* sp. nov. (MZUSP 57274), male holotype: (A) habitus, dorsal view; (B) habitus, lateral view; (C) coxae III-IV, stigmatic area and free sternites, ventral view; (D) left chelicera and pedipalp, ectal view. Scale bars: 1 mm.

***Prostygnus stellatus* sp. nov.**

urn:lsid:zoobank.org:act:DE8A563F-133C-45E8-8E49-8BB2A23338AF  
(Figures 1, 2, 4 and 5)

*Prostygnus* sp. Villarreal & García 2016: 35.

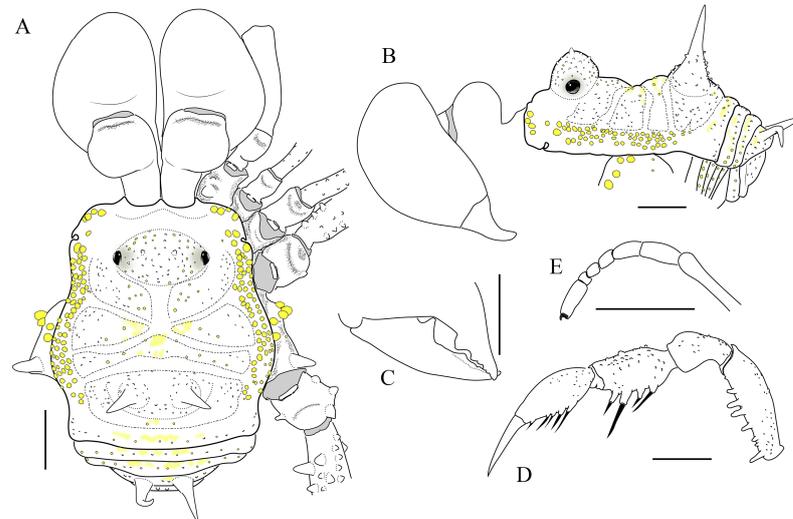
Type material examined. Holotype. Male, ECUADOR, Zamora, S. Francisco, alt. 2.000 m; 2009, barkspray leg. (MZUSP 57274).

Diagnosis. Differs from *P. vestitus* Roewer, 1913 by: (1) the color pattern of the dorsal shield, consisting of a succession of yellow spots in the lateral areas of the dorsal shield (Figures 1A,B and 2A,B) instead of diffuse spots in the lateral zones of the mesotergal areas; (2) size of the paired tubercles of the ocularium, short and not spiniform (Figures 1A,B and 2A,B); and (3) presence of round yellow tubercles on the prolateral side of the coxae IV (Figures 1A–C and 2A,B).

Description. Measurements: dorsal scutum length = 4.5; dorsal scutum width = 4.1; interocular distance = 1.5; pedipalp: coxa = 0.6, trochanter = 0.9, femur = 1.9, patella = 1.0, tibia = 1.4; tarsus = 1.5, tarsal claw = 1.1; total = 8.4; leg IV: femur = 3.2, patella = 1.2, tibia = 1.9, metatarsus = 3.2. Dorsum (Figure 1A,B). Dorsal scutum outline kappa. Anterior margin of prosoma with 3–4 anterolateral yellow tubercles; cheliceral sockets shallow, between two short processes, medial process short. Eyes on a common ocularium, oval and domed, high, three times the ocular diameter; densely covered by tubercles and with a dorsal paramedian pair of large tubercles. Lateral margin with a row of yellow rounded granules. Mesotergum divided into four areas: I divided medially into two triangular halves, with one pair of yellow granules on each side; II unarmed and entire, with a row of yellow tubercles, invading medially area I, but not reaching the carapace; III with a paramedian pair of strong, large, and straight spines and some tubercles on each side. Posterior margin almost straight, with a row of small yellow tubercles. Free tergites I–III with a row of small yellow tubercles, and III with a paramedian pair of acuminate large spines. Venter (Figure 1C). Coxae I–IV with rows of scattered granules. Stigmatic area with a transversal row of granules and stigmata oval and sub-parallel. Chelicerae (Figures 1D and 2B,C). Segment I with the bulla globose and smooth; II swollen and smooth, fixed finger with one medial large tooth and four distal small teeth (iiii); mobile finger with a large basal tooth and with a distal dentate lamella. Pedipalps (Figures 1D and 2D). Coxa dorsally with a proximal low hump. Trochanter with one dorsal, one large ventral, and two ecto-ventral tubercles. Femur ventrally straight and dorsally curved in lateral view, dorsally smooth and ventrally with a row of nine tubercles (liililiii). Patella slightly swollen sub-distally, with tiny dorsal granules, ventrally smooth. Tibia dorsally with abundant tubercles, ventrally smooth; tibia ectal lili. Tarsus dorsally with tiny granules and ventrally smooth; tarsus ectal III\_i. Legs (Figures 1B and 2E). Coxa IV with four prolateral conspicuous and rounded and yellow tubercles, some small uncolored tubercles, and one dorso-distal large spine. Trochanter I–II smooth; III globose, dorsally with scattered tubercles and one conspicuous retrolateral distal tubercle; IV sub-square, with three prodorsal and one proventral tubercle, one retroventral, and one dorsodistal large tubercle. Femur I–II with longitudinal rows of granules; III–IV slightly swollen, with longitudinal row of wide tubercles and presence of dorso-distal large tubercles, III with some large proximal tubercles, and IV with large proventral tubercles. Patella III–IV with longitudinal rows of tubercles, III with retroventral large tubercles, and IV with pro and retroventral large tubercles, and prolateral large distal tubercle. Tibia III–IV with longitudinal row of conspicuous sub-equal tubercles. Tarsal segmentation: 6(3)/7(3)/7(3). Penis (Figure 4). VP sub-rectangular elongate, slightly constricted in the subapical portion, with the apical corners rounded and almost straight distal margin. With three pairs of large and curved MS-C on the latero-distal corners; one pair of subapical MS-D located sub-dorsally. Two pairs of MS-A basally in ventral plate, straight, conical, and shorter than MS-C, located almost dorsally. Two pairs of short MS-E in the apical portion of the VP, close to MS-C; without MS-B. Ventral and lateral surfaces of the VP covered by numerous microsetae of type 4, (except the ventromedial portion). Glans columnar elongate inserted in no podium in apical part of the truncus, with ventral wattle and stylus cylindrical and dorsally curved, with apex compressed, flat crest around the ventral half of the opening, with a few ventro-distal projections. Coloration in alcohol (Figure 1). Dorsal scutum brownish orange with mesotergal areas and postero-lateral of dark brown carapace; ocularium, dark orange, yellow. Free tergites, proximally dark brown and distally brownish orange; paramedian spines, brilliant greenish yellow. Medial zone of area I–II with irregular spots, brilliant greenish yellow; lateral tubercles on the DS, vivid greenish yellow. Chelicerae, brownish orange with reticulate dark brown. Pedipalps, brownish orange with dark brown bands. Legs I–II, brilliant greenish yellow with dark brown irregular spots; metatarsus and tarsus, dark brown. Coxae and trochanter III–IV, deep orange yellow. Femora, patellae, and tibia III–IV, deep brown. Metatarsus III–IV, proximally brilliant greenish yellow and distally dark brown. Female. Unknown.

Etymology. From Latin *stellatus* (with stars), in reference to the high quantity of yellow tubercles that this species has in different parts of the body, which resemble stellar constellations.

Distribution. Only known from the type locality.



**Figure 2.** *Prostygnum stellatus* sp. nov. (MZUSP 57274), male holotype: (A) habitus, dorsal view; (B) habitus, lateral view; (C) right chelicera, frontal view; (D) left pedipalp, ectal view; (E) left tarsomeres I, retrolateral view. Scale bars: 1 mm.

### Genus *Yania* Roewer, 1914

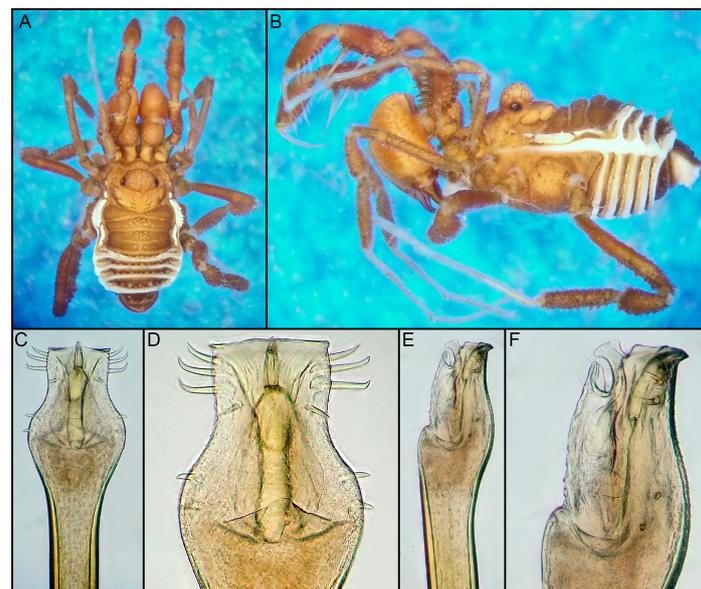
- *Yania* Roewer 1914c: 129. Type-species by monotypy: *Yania flavolimbata* Roewer, 1919.

*Yania*—Roewer 1923: 126; Mello-Leitão 1926: 330; Roewer 1928a: 537; Mello-Leitão 1932: 42; Mello-Leitão 1935e: 93; Kästner 1937: 387; Mello-Leitão 1938: 143; Rambla 1978b: 304; Kury 1994b: 140; Kury 2003a: 102; Kury 2012c: 31.

Etymology. From the toponym Yana Urcu. Gender feminine.

Diagnosis. DS outline type Alpha, with coda almost as wide as the medial bulges. Four scutal areas unarmed. Ocularium domed, high, and tuberculated. DS with yellowish spots on lateral borders. VP of penis amphora-shaped, with distal border straight, MS-C larger than MS-A.

Included species. *Yania flavolimbata* Roewer, 1914



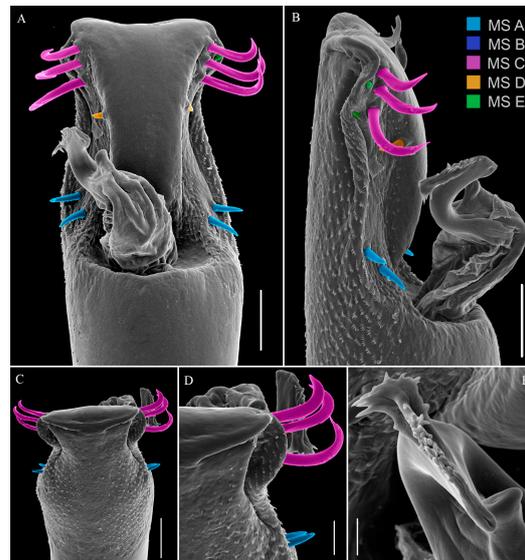
**Figure 3.** *Yania flavolimbata*, male (MZSP 57276). (A) Habitus, dorsal view. (B) Ditto, lateral view. (C) Penis, dorsal view. (D) Ditto, apical portion. (E) Penis, lateral view. (F) Ditto, apical portion. Not scaled figures.

***Yania flavolimbata* Roewer, 1914**

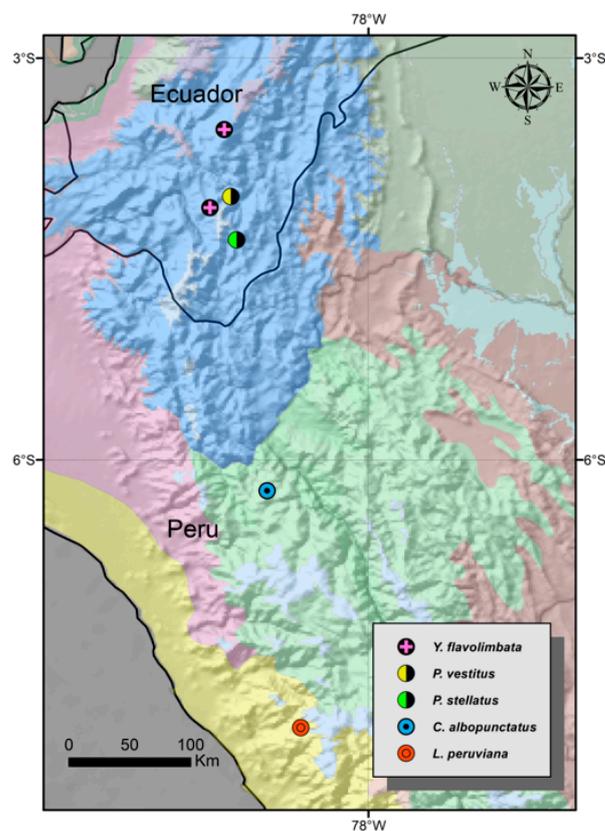
(Figures 3 and 5)

• *Yania flavolimbata* Roewer 1914c: 130, pl. 13, figure 6.*Yania flavolimbata*—Roewer 1923: 126, figure 132; Kury 2003a: 102.

Material examined. Male, ECUADOR, Loja, Cajanuma, páramo, alt. 3000 m; 29 September 2008; J. Schmid leg. (MZUSP 57276).



**Figure 4.** *Prostygnum stellatus* sp. nov. (MZUSP 57274), penis, distal portion: (A) dorsal view; (B) lateral view; (C) ventral view; (D) laterodistal corner, detail in ventral view; (E) stylus, apical view. Scale bars: A, B, C = 50  $\mu$ m; D = 20  $\mu$ m; E = 10  $\mu$ m.



**Figure 5.** Geographical distribution of the family Prostygniidae.

### 3.3. New Familial Assignments

Superfamily Gonyleptoidea

**Family Manaosbiidae Roewer, 1943**

**Genus *Sclerostygnellus* Roewer, 1943 transl. nov.**

- *Sclerostygnellus* Roewer 1943: 35. Type-species by monotypy: *Sclerostygnellus rotundus* Roewer, 1943.

Taxonomy. *Sclerostygnellus rotundus* is documented based on a female specimen (which was incorrectly identified as male by Roewer). There is no positive evidence to establish a connection between *Sclerostygnellus rotundus* and Cranaiidae. Conversely, the scutum outline, area armature, and pedipalp shape all exhibit strong congruence with the characteristics observed in Manaosbiidae.

**Family Cranaiidae Roewer, 1913.**

***Binamballeus* Roewer, 1952 transl. nov.**

- *Binamballeus* Roewer 1952: 145. Type-species by original designation: *Binamballeus metatarsalis* Roewer 1952.

Taxonomy. DS outline type possibly gamma, pedipalpal morphology and dorsal ornamentation, scutal areas, and legs ornamentation are all consistent with Cranaiidae.

***Puna* Roewer, 1925**

- *Puna festae* Roewer 1925: 29, figure 22a-b. Type-species by original designation: *Puna festae* Roewer 1925.
- *Puna festae*—Roewer 1932: 319, Figure 34; Soares & Soares 1948b: 615; Kury 2003: 97.

**“*Puna*” *metatarsalis* (Kury, 1994) comb. nov.**

- *Yania metatarsalis* Kury 1994: 141, figures 2–6.
- *Yania metatarsalis*—Kury 2003a: 102.

Taxonomy. The observed pedipalpal morphology, characterized by a dorsal keel on femora, patellae, and tibiae dorsally tuberculated; the scutal area pattern; and the leg IV ornamentation with a subdistal spine are suggestive of belonging to the Cranaiidae family. Particularly, the alpha outline of the DS, the relatively short legs, high and domed ocularium, and dorsal keel on the pedipalp align it with a subgroup of Cranainae genera, including *Puna*. Despite the ongoing ambiguity surrounding Cranaiidae’s taxonomy and generic boundaries, we tentatively place this species within *Puna*.

**Family Nomoclastidae Roewer, 1943**

**Genus *Globitarsus* Roewer, 1913 transl. nov.**

- *Globitarsus* Roewer 1913a: 145. Type-species by monotypy: *Globitarsus angustus* Roewer, 1913.

Taxonomy. DS outline type zeta, the number of scutal areas, morphology of pedipalps without dorsal ornamentation and ocularium, scutal areas, and legs ornamentation are all consistent with Nomoclastinae (*Nomoclastes*-like) and not with Cranaiidae or Prostygnaidae.

**Genus *Lisarea* Roewer, 1943 transl. nov.**

- *Lisarea* Roewer 1943: 33, figure 29. Type-species by monotypy: *Lisarea ferruginea* Roewer, 1943.

Taxonomy. DS outline type zeta, the number and ornamentation of scutal areas, and morphology of pedipalps and ocularium, and legs length and ornamentation are all consistent with Nomoclastinae (*Nomoclastes*-like) and not with Cranaiidae or Prostygnaidae.

**Genus *Meridanatus* Roewer, 1943 transl. nov.**

- *Meridanatus* Roewer 1943: 34. Type-species by monotypy: *Meridanatus berlandi* Roewer, 1943.

Taxonomy. DS outline type beta, the number of mesotergal areas, morphology of pedipalps, ocularium, and legs ornamentation are all consistent with Nomoclastinae (*Quindina*-like) and not with Cranaiidae or Prostygnaidae.

**Genus *Micropachylus* Roewer, 1913 transl. nov.**

- *Micropachylus* Roewer 1913a: 147. Type-species by monotypy: *Micropachylus metatarsalis* Roewer, 1913.

Taxonomy. DS outline type zeta, the number of mesotergal areas, morphology of pedipalps and ocularium, and legs length and ornamentation are all consistent with Nomoclastidae (*Nomoclastes*-like) and not with Cranaidae or Prostygnaidae.

**Genus *Prostygnidius* Roewer, 1915 transl. nov.**

- *Prostygnidius* Roewer 1915: 103. Type-species by monotypy: *Prostygnidius pustulatus* Roewer, 1915.

Taxonomy. DS outline type zeta, the number of mesotergal areas, morphology of pedipalps without dorsal ornamentation, and shape of the femora, ocularium, and legs length and ornamentation are all consistent with Nomoclastidae (*Nomoclastes*-like) and not with Cranaidae or Prostygnaidae.

**Genus *Troya* Roewer, 1914 transl. nov.**

- *Troya* Roewer 1914: 133. Type-species by monotypy: *Troya riveti* Roewer, 1914.
- *Peladoius* Roewer 1914: 135. Type-species by monotypy: *Peladoius riveti* Roewer, 1914. **Syn. nov.**
- *Prostygnellus* Roewer 1914: 137. Type-species by monotypy: *Prostygnellus riveti* Roewer, 1914. **Syn. nov.**
- *Prostygnidius* Roewer 1915: 103. Type-species by monotypy: *Prostygnidius pustulatus* Roewer, 1915. **Syn. nov.**
- *Minyssus* Roewer 1943: 30. Junior subjective synonym of *Prostygnellus* Roewer, 1914 by Soares, Soares & Jim (1992: 10). Type-species by monotypy: *Minyssus isabellinus* Roewer, 1943. **Syn. nov.**

Taxonomy. DS outline type zeta, the number of mesotergal areas, morphology of pedipalps and ocularium, and legs length and ornamentation are all consistent with Nomoclastidae (*Nomoclastes*-like) and not with Cranaidae or Prostygnaidae.

***Troya isabellina* (Roewer, 1943) comb. nov.**

- *Minyssus isabellinus* Roewer 1943: 32, pl. 3, figure 26.
- *Prostygnellus isabellinus*: Soares, Soares & Jim 1992: 10.

***Troya pustulata* (Roewer, 1915) comb. nov.**

- *Prostygnidius pustulatus* Roewer 1915: 103, figure 56.

***Troya riveti* Roewer, 1914**

- *Troya riveti* Roewer 1914: 133, pl. 13, figures 8–8a.
- *Prostygnellus riveti* Roewer 1914: 137, pl. 13, figures 10–10b [junior secondary homonym of *Troya riveti* Roewer, 1914]. **Syn. nov.**
- *Peladoius riveti* Roewer 1914: 134, pl. 13, figs 9–9a [junior secondary homonym of *Troya riveti* Roewer, 1914]. **Syn. nov.**

**4. Discussion**

Even though the composition of Prostygnaidae has undergone drastic changes over time and its definition has been mostly incomplete, for the past few years, this family has been unequivocally placed in the immediate vicinity of Cosmetidae. Furthermore, it is no longer considered to be closely related to or nested within Cranaidae, as was initially believed since the conception of the family [7].

A recent molecular study using UCEs confirms its position inside the clade that includes Metasarcidae and Cosmetidae (MECO) [14] (figure 2), as was initially suggested by Villarreal and García [9] and supported in the topology of the phylogenetic trees obtained by Kury [6] (figure 6), Villarreal [10] (figure 1), Medrano et al. [13] (figure 7).

The shape of the VP; the structure of the macrosetae and microsetae; and, especially, the presence of a wattle ventrally on the stylus firmly place *Prostygnus* and allies in MECO. However, the internal relationships within MECO are still uncertain. The more recent morphological analysis by Medrano et al. [13] proposed Prostygnaidae as the sister group

of Cosmetidae, with Metasarcidae outside, whereas the molecular analysis proposed by Derkarabetian et al. [14] inverted this relation, with Prostygnaidae being the sister-group of Cosmetidae + Metasarcidae.

The presence of lateral spiny sacs on VP is a synapomorphy for the species of Metasarcidae [27] and are, therefore, absent in Prostygnaidae, and the pedipalpal shape, with a compressed femur and foliar patella and tibia, is also a synapomorphy for the species of Cosmetidae. The pedipalps of Prostygnaidae are usually strong, with dorsal ornamentation on the patella and tibia (tuberculated), which initially led to the hypothesis of their relationship with Cranidae. The type and distribution of microsetae on the VP in *Prostygna* are reminiscent of those of Cosmetidae and not the typical pattern of Cranidae, as shown in Kury [11]. The strongly dimorphic chelicerae and carapace, and the DS outline shape of Prostygnaidae with a relatively long coda and well-marked lateral constrictions, resemble the conditions found in some early derivative Cosmetidae, such as Metergininae. Given the comparative morphology of several cosmetid styli, as presented in Medrano and Kury [40], the prostygnid wattle resembles that of *Flirtea picta* (Perty, 1833) more closely, by starting midway along the stylus and without stylar barbs.

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