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A cladistic analysis of the Stygnicranainae Roewer, 1913 (Arachnida, Opiliones, Cranaidae) – where do longipalp cranaids belong?

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A character survey compiling the morphological information of the subfamily Stygnicranainae was carried out. Two new species of *Stygnicranaus* Roewer, 1913 are described from Colombia and the new genus *Agathocranaus* is described from Ecuador. All known species of the subfamily are included in a matrix of 46 morphological characters. Parsimony analysis under implied weights recovered a monophyletic Stygnicranainae including *Tryferos* Roewer, 1931 plus *Stygnicranaus* and *Agathocranaus*. However, the usage of the four subfamilies of Cranaidae as currently defined is abandoned because the two largest subfamilies of Cranaidae – Cranainae and Prostygninae – represent paraphyletic groups (grades), whereas Heterocranainae is a superfluous subfamily, including only the genus *Heterocranaus* Roewer, 1913.

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ADDITIONAL KEYWORDS: Andes – cladistics – Colombia – Cranainae – Ecuador – Gonyleptoidea – Grassatores – Neotropics – Prostygninae – Venezuela.

INTRODUCTION

The Neotropical family Cranaidae Roewer, 1913 was defined by Kury (1994a) by removing four subfamilies from Gonyleptidae and giving them family status. Kury conserved the traditional concept of each one as defined by Roewer (1913). Two of them – Cranainae and Prostygninae Roewer, 1913 – are larger groups, whereas the two others – Heterocranainae Roewer, 1913 and Stygnicranainae Roewer, 1913 – are specialized offshoots with only a few species each. The Stygnicranainae is an Andean group easily recognizable by the extremely elongate pedipalpi at least in the males, which was suggested as a synapomorphy for them (Kury, 1992a). However, it has been suggested that keeping this subfamily could render the Cranainae paraphyletic (Kury, 1995) because no synapomorphy has been yet detected for the Cranainae. Kury (1995) critically analysed the species included in Stygnicranainae and moved the genera *Cranaostygnus* Caporiacco, 1951 and *Stygnicranella* Caporiacco, 1951 to Cranainae as juveniles of *Santinezia* Roewer, 1923 (which was corroborated by González-Sponga, 2003). Roewer (1913, 1931) recognized two original species, each included in a monotypic genus – *Stygnicranaus* Roewer, 1913 and *Tryferos* Roewer, 1931. Kury (1995) added a second species to *Stygnicranaus* and provided a key to identifying all three Stygnicranainae.

In this paper a fourth and a fifth species from Colombia for *Stygnicranaus* and a new genus with a new species from Ecuador are described in the Stygnicranainae. A parsimony analysis is carried out, including all species of the Stygnicranainae and selected Cranaidae as outgroups.

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MATERIAL AND METHODS

Acronyms of depositories

AMNH, American Museum of Natural History, New York; CAS, California Academy of Sciences, San Francisco; BMNH, The Natural History Museum, London; MACN, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA; MNRJ, Museu Nacional, Universidade Federal do Rio de Janeiro; SMF, Senckenberg Museum, Frankfurt; UNAL, Universidad Nacional de Colombia, Bogotá.

General morphology

All terminology was adapted from Kury (1995, 1996). We found it necessary to redescribe Roewer's species (*Stygnicranaus abnormis* Roewer, 1913 and *Tryferos elegans* Roewer, 1931) because his descriptions do not meet modern standards.

All segments of the specimens were examined with a focus on armature, shape, relative size, etc. The male genitalia were dissected and mounted on microscope slides for genital morphology analysis. Herein we use the new term 'capellum' for a differentiation in the apex of the stylus (marked by an arrow in all male genitalia figures). This term originates from Latin and means 'hat', 'hood'. We have so far found a capellum only in cranaids, and this structure might prove to be taxonomically useful. It can assume a number of shapes such as crescent, shovel, or oval. Even though this structure is present in published drawings (see figures of *Santinezia* species and *Stygnicranaus concolor* Kury, 1995; Pinto-da-Rocha & Kury, 2003), this is the first time, to our knowledge, that it is recognized and named. Colour names use the '267 Color Centroids' of the 'NBS/IBCC Color System' as described in Kury & Orrico (2006). Appendix S1 contains a summary of the colours used.

Choice of terminals

For the ingroup, all three described species of the Stygnicranainae were used as well as the three new ones described here. As outgroups, we tried to assemble a wide morphological representation of diversity in Cranaidae and one stygnid to root the tree. A total of six ingroup and nine outgroup terminals was used (Appendix 1).

Cladistic analysis

All variation found was tabulated into a matrix (Appendix 2) via Nexus Data Editor (NDE; Page, 2000) and then exported to WINCLADA (Nixon, 2002) in preparation for phylogenetic analysis. An annotated list of characters can be found in Appendix 3, as well as a list of additional references (Appendix S2) and a list of external published illustrations (Appendix S2). Parsimony under implied weights (Goloboff, 1993) was used to search the trees via Tree Analysis using New Technology (TNT) (Goloboff, Farris & Nixon, 2008). This method of analysis attributes higher values to characters with better fit (f_i) to the trees. A test run of the matrix under concavity 3 was made with 500 random addition sequences (RAS) + 100 tree bisection reconnection (TBR). All characters were unordered and unweighted. and bootstrap values were calculated using TNT default settings under the 'implicit enumeration' option. Bremer support was calculated with PIWE (Goloboff, 1993). Character states were not ordered because additive series in opilionids are not necessarily correct when analysed under developmental contexts. Species of Pachylinae with a single spine on the ocularium have two spines in younger stages, as seen in *Graphinotus ornatus* Kollar in Koch, 1839 (Orrico & Kury, 2007), so the logical, traditional, additive series of 0-1-2 spines is wrong and the correct (even though counter-intuitive) ordination is 0-2-1. In the absence of a single known developmental series in Cranaidae, these multistates are kept unordered. An equal weights analysis was also performed using implicit enumeration search (default settings except for the memory used – 10 000 trees). As we have a small morphological dataset, we followed the reasoning of Goloboff *et al*. (2008) and in the discussion used only the results of the implied weight analysis. Likewise, the differences found (see Results) were only in two basal outgroups and they do not affect the conclusions.

RESULTS

Phylogenetic analysis

Matrix

The 15 terminals were tabulated against the 46 morphological characters: 43 informative and three autapomorphies (Appendix 2).

Cladogram

The test run yielded a single maximum fit (≈8.17), 116-step tree, which is here used to represent the proposed phylogenetic hypothesis for the Stygnicranainae (Fig. 1). The equal weights analysis yielded two trees of length (L) = 116. One is identical to the tree found under implied weights, and the other is almost identical, but *Yania* and *Heterocranaus* switch places. Therefore, because one of the hypotheses is supported by two different methods, we chose the test run to represent all hypotheses and character

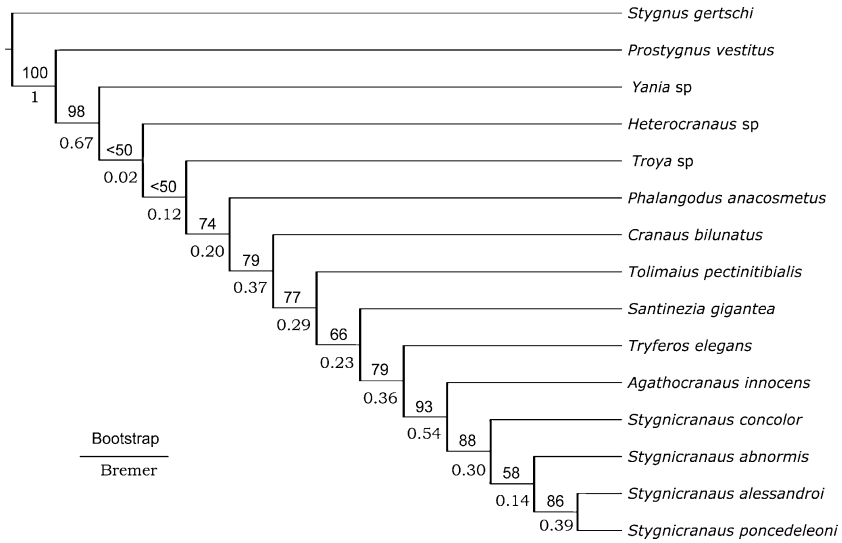


Figure 1. Phylogenetic hypothesis proposal for Stygnicranainae [concavity (k) = 3, congruence or fit (f_i) ≈ 8.17, length (L) = 116]. Number above nodes are bootstrap values and number under nodes, Bremer support (BR). Please note that BR is scaled in fit and not in steps.

Table 1. Tarsal counts for the species of Stygnicranainae

Specimen	I		II		III		IV	
Stygnicranaus poncedeleoni female paratype	8 (3)	9 (3)	19 (3)	20 (3)	8	8	9	9
S. poncedeleoni male paratype	8 (3)	8 (3)	–	18 (3)	8	8	8	–
S. poncedeleoni male holotype	8 (3)	9 (3)	–	19 (3)	8	8	8	9
Agathocranaus innocens male holotype	11 (3)	10 (3)	–	13 (3)	8	8	8	8
Stygnicranaus alessandroi male holotype	8 (3)	9 (3)	18 (3)	17 (3)	9	11	11	10
Stygnicranaus abnormis female holotype	–	–	–	–	8	9	9	9

Table 2. Body measurements of the species of Stygnicranainae

Specimen	CW	CL	AW	AL	SAL	SAW	STD	ST0
Stygnicranaus alessandroi male	4.1	3.0	5.5	6.0	3.4	5.3	1.5	1.3
Stygnicranaus poncedeleoni male	3.5	2.0	4.6	5.0	2.2	2.9	1.5	0.8
S. poncedeleoni female	4.0	2.5	5.8	6.0	2.2	3.7	1.7	0.7
Agathocranaus innocens male	4.2	3.0	6.7	7.0	2.9	4.8	2.4	0.8
Stygnicranaus abnormis female	4.5	3.0	6.0	7.0	2.7	4.7	1.9	0.8

Abbreviations of body measurements: CW, carapace width; CL, carapace length; AW, abdominal scutum width; AL, abdominal scutum length; SAL, stigmatic area length; SAW, stigmatic area width; STD, stigmata distance; ST0, stigma diameter.

optimization. The branching pattern is remarkable because it is completely asymmetrical (pectinate).

TAXONOMY

During the survey for specimens, we found two new species of *Stygnicranaus* and one new species that we believe represents a new genus of Cranaidae. All are described below.

To avoid making the text too repetitive and to ease comparison amongst species, tarsal counts for all species studied are shown together in Table 1, body measurements in Table 2, and appendage measurements in Table 3.

STYGNICRANAUS ROEWER, 1913

Stygnicranaus Roewer, 1913: 423; 1923: 570; Mello-Leitão, 1926: 365; Roewer, 1931: 147; Mello-Leitão,

Table 3. Appendage measurements of the species of Stygnicranainae

Specimen	Cx	Tr	Fe	Pa	Ti	Mt	Ta	Claw
Stygnicranaus alessandroi male								
Leg I ma		1.2	7.5	1.5	4.5	7.8	2.8	
Leg II		1.5	12.8	2.1	10.5	13.1	7.4	
Leg III		1.3	11.6	2.1	5.3	11.3	4.7	
Leg IV		1.5	15.9	2.7	3.0	17.7	5.8	
Pedipalpus	1.3	1.3	7.5	3.5	3.3	–	3.0	3.1
Stygnicranaus poncedeleoni male								
Leg I ma		0.5	6.4	0.9	3.8	6.0	2.2	
Leg II		0.6	12.0	1.4	8.3	9.9	5.7	
Leg III		0.8	7.4	1.4	3.8	7.4	3.0	
Leg IV		1.0	11.6	1.6	5.7	11.9	3.9	
Pedipalpus	1.3	0.8	6.1	3.9	2.1	–	2.2	2.5
S. poncedeleoni female								
Leg I fe		0.7	8.0	1.2	4.5	7.6	2.9	
Leg II		0.9	15.9	1.9	11.3	13.5	7.2	
Leg III		1.2	11.4	2.0	5.3	10.5	3.7	
Leg IV		1.2	16.0	2.5	8.3	16.2	4.7	
Pedipalpus	1.3	0.9	9.1	4.6	3.3	–	2.8	2.8
Agathocranaus innocens male								
Leg I ma		0.9	10.2	1.9	8.3	1.6	4.0	
Leg II		1.0	13.6	2.2	11.5	14.6	5.4	
Leg III		1.2	8.0	2.1	5.1	7.9	4.1	
Leg IV		1.5	10.4	2.3	6.7	9.5	4.7	
Pedipalpus	2.1	1.1	4.9	3.1	3.4	–	2.5	2.1
Stygnicranaus abnormis female								
Leg I fe		0.7	5.7	1.2	3.5	–	–	
Leg II		1.0	12.9	1.6	9.1	11.1	0.0	
Leg III		1.4	8.0	1.7	4.6	8.2	3.3	
Leg IV		1.3	14.4	2.4	8.0	15.1	5.3	
Pedipalpus	1.5	1.4	5.9	3.0	3.2	–	3.2	2.9

KEY TO THE THREE GENERA OF LONGIPALP CRANAIDAE (STYGNICRANAINAE)

1. Ocularium very wide (80% the width of carapace), extremely low (barely elevated from carapace); carapace much shorter than abdominal scutum (Figs 20–21)……*Tryferos*
Ocularium narrow (about 40–50% the width of carapace). moderately high (at least as high as two eye diameters); carapace only slightly shorter than abdominal scutum (Figs 2–3, 6–7, 14–15)……2
2. Ocularium with a pair of minute tubercles; all areas of dorsal scutum entirely unarmed; outline of scutum in dorsal view alpha (subrectangular, with the median laterals bulging, widest at area I–II) (Figs 14–15)…*Agathocranaus*
Ocularium with a pair of strong spines; scutal area III with a pair of stout acuminate spines; outline of scutum in dorsal view pyriform, with widest portion at area IV (Figs 2–3, 6–7)……*Stygnicranaus*

1932: 128; Kury, 1995: 32, 2003: 102 (type species *Stygnicranaus abnormis* Roewer, 1913, by monotypy).

Genus diagnosis: Dorsal scutum divided into three areas (original area IV completely fused to area III); outline of scutum attenuate pyriform, mesotergal area armed with a pair of high, divergent, straight spiniform processes, pedipalpal femur completely unarmed, much elongated and pedipalpi tarsi and tibia forming subchela.

Included species: Stygnicranaus abnormis Roewer, 1913; *Stygnicranaus concolor* Kury, 1995; *Stygnicranaus alessandroi* sp. nov.; and *Stygnicranaus poncedeleoni* sp. nov.

Remarks: The 'male' holotype of *S. abnormis* is actually a female. In this genus, (known) females are

KEY TO THE SPECIES OF *STYGNICRANAUS*

1. Lateral border of scutum without clearly marked posterior yellow spot; outline of dorsal scutum widest at middle portion; ocularium without pearly tubercles; free tergite II with a pair of robust paramedian spines; dorsoapical apophysis of coxa IV clearly marked.....*S. concolor*

Lateral border of scutum with clearly marked posterior yellow spot; outline of dorsal scutum widest more posteriorly, at area IV; ocularium with pearly tubercles; free tergite II with only a pair of minute granules; dorsoapical apophysis of coxa IV unclear, replaced by group of granules.....2.

2. Cluster of pearly tubercles at the side of the carapace absent; hyaline portion of cheliceral sockets without pearly tubercles.....*S. abnormis*

Cluster of pearly tubercles at the side of the carapace present; hyaline portion of cheliceral sockets with pearly tubercles.....3.

3. Femur IV armed proximally with small spines; anterior border of scutum with two large spines at pedipalpus level; scutum without any whitish spot; scutum densely covered with numerous dark irregular spots.....*S. alessandroi*

Femur IV armed proximally with small pearly tubercles; anterior border of scutum with three small spines at pedipalpus level; scutum with inverted Y-shaped whitish spot formed by smaller independent units; scutum without dark spots.....*S. poncedeleoni*

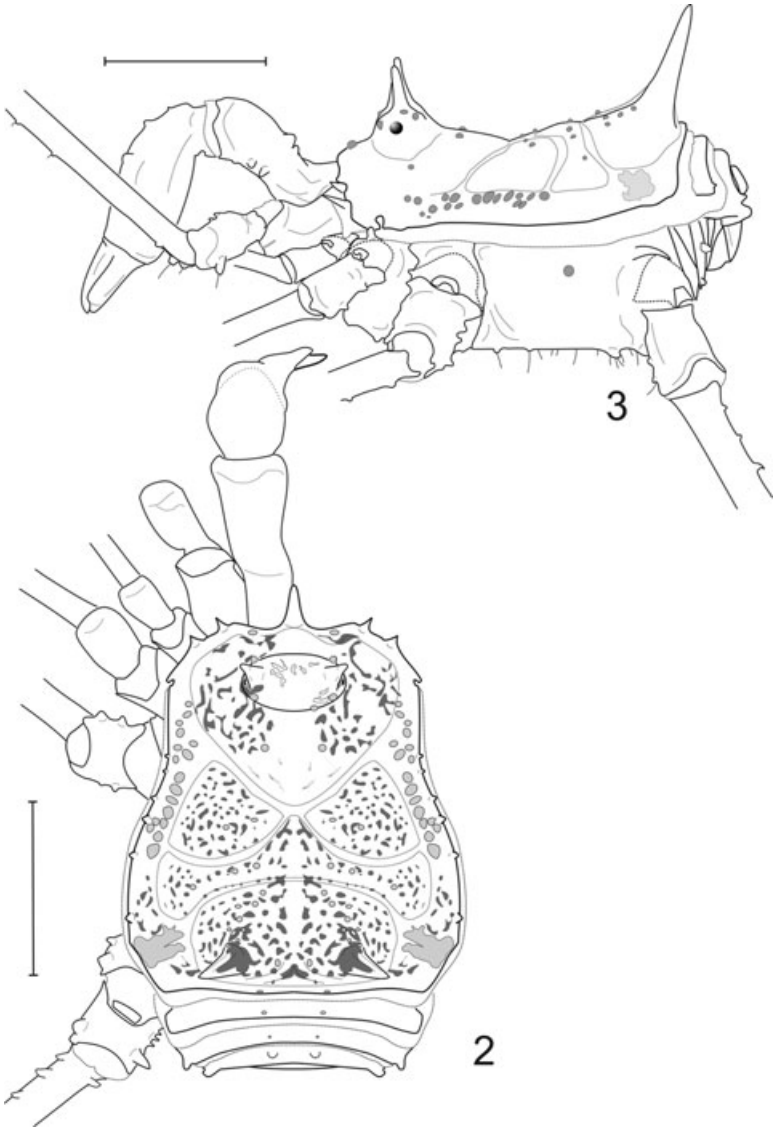
quite similar to males, with analogous armature and just a few dimorphic characters. Pedipalpi for all species within this genus are extremely similar. For the sake of conserving space, illustrations of the pedipalpus are provided only for *S. poncedeleoni*.

STYGNICRANAUS ALESSANDROI SP. NOV. (FIGS 2–5)

Type locality: Colombia, Valle Del Cauca, Dagua. El Salto. World Wildlife Fund (WWF) Ecoregion NT0145 (North-western Andean montane forests).

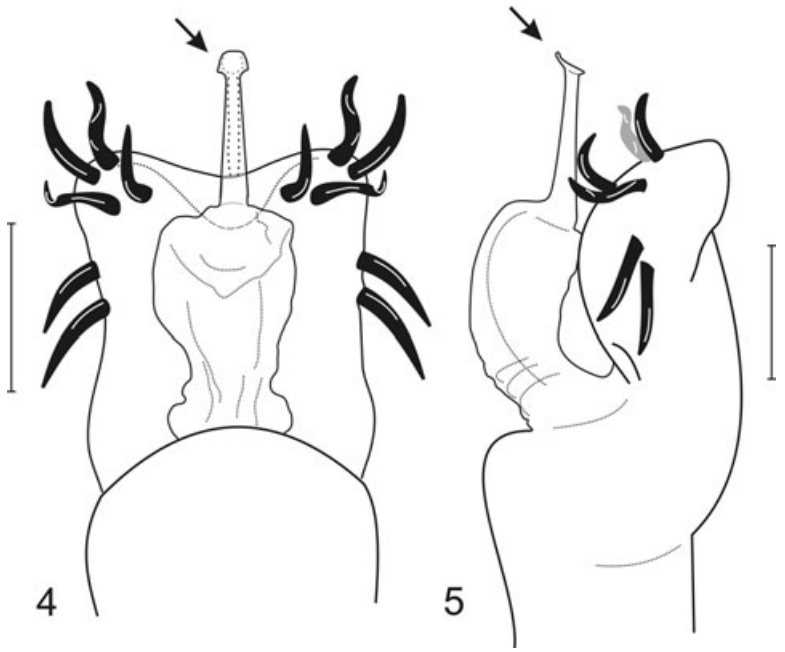
Diagnosis: Stygnicranaus alessandroi differs from *S. concolor* by the presence of white granulation on the scutum, the straight, upward, stout spines in the ocularium (*S. concolor* has curved spines), and for having two small spines in the frontal border of the scute (*S. concolor* has none). It differs from both *S. abnormis* and *S. concolor* in the absence of spines in area I, whereas *S. concolor* and *S. abnormis* both have two small spines. It differs from *S. poncedeleoni* in the presence of small spines instead of the pearly tubercles in coxa IV and by having two and not three teeth at each side of the anterolateral corners of the carapace. It also differs from all other members of Stygnicranainae by the numerous small dark spots on scutum.

Description: Male holotype: Dorsum. (Figs 2–3). Dorsal scutum attenuate pyriform, with carapace only a little smaller than abdominal scutum. Posterior border of scutum straight. Cheliceral sockets shallow with a median tooth. Anterolateral corners of carapace with two teeth each side, one at pedipalpus, the other between it and leg I. Cheliceral sockets with a small pearly tubercle on each side. Posterior corners of scutum with a small tooth on each side. Ocularium elliptical, low, with a pair of stout, paramedian erect (lateral view), slightly divergent (frontal view) spines with blunt point. Surface of ocularium with seven pearly granules concentrated around the base of the spines. Carapace behind ocularium with a pair of rounded pearly setiferous granules. Median third of lateral area with a group of such granules. Posterior part of lateral area of scutum each side with an coalescent island of such tubercles. Grooves of scutum well marked, defining a mesotergum with three areas; original area IV completely fused with area III. A single shallow longitudinal medial groove dividing areas II and III in two halves each. All areas unarmed except for area III armed with a pair of very high acuminate spiniform processes. Scutal area II projecting anteriorly into area I dividing it into left and right halves. Areas I and II each with a transverse row of five to six setiferous tubercles. Area III with clusters of setiferous tubercles anterior to the large spines and reaching their basal part. In the place of area IV a pair of paramedian setiferous tubercles. Single ozopore opening laterally at tip of a dorsolateral low protuberance. Free tergites I–III smooth, except for a pair of paramedian granules each. Corners of tergites I–III each bearing an small acuminate tooth. Venter. Coxae I–III smooth, except for a transverse row of tubercles each. Intercoxal bridges weak. Coxae I–III subrectangular, transverse. Coxa IV the largest, equalling the other three taken together, shaped elongate pentagonal, divergent posteriorly. Coxa IV with one ventral subdistal small tubercle. Stigmatic area long, Y-shaped. Stigmata large, elongate elliptic, clearly apparent, not hidden by any bridges or tubercles, each occupying one third of the area. Maxillary lobes of coxae I–II clearly visible. Free sternites II and III with their corners each bearing an small acuminate process. Chelicera. Basichelicerite long, with bulla attenuate



Figures 2–3. ***Stygnicranaus alessandroi*** **sp. nov.**, male holotype (UNAL) from Colombia. Habitus. Fig. 2. Dorsal view. Fig. 3. Lateral view, spots omitted. Scale bars = 3 mm.

and a medial belt of granules and a mesal subdistal small acuminate tubercle. Hand not swollen, with two frontal rows of setiferous tubercles. Pedipalpus. Much elongate and smooth, with tibia and tarsus forming a subchela. Coxa large, conical, smooth. Trochanter cylindrical with typical sub-basal constriction, and apical dorsomesal tubercles and one ventral setiferous tubercle. Femur longer than dorsal scutum, thicker at distal third, with dorsoapical tubercles and a ventral row of setiferous tubercles. Patella longer than abdominal scutum, thicker at distal third. Tibia as long as patella, cylindrical with four ectal (IiIi) and four mesal (IiIi) spines. Tarsus fusiform, slightly shorter than tibia, with four ectal (IiIi) and six mesal (IiiiIi) spines and two ventral rows of setiferous tubercles. Tarsal claw almost as long as tarsus. Legs. All segments slender and unarmed. Relative length I < III < IV < II. Dorsobasal apophyses of coxae I–II close to the ozopore: coxa I anterior spiniform, posterior small, directed backwards; coxa II anterior spiniform, posterior as a lobe joining coxa III. Coxa IV hidden under dorsal scutum in dorsal view, with prolateral dorsoapical spiniform apophysis and one pearly median prolateral dorsal granule. Trochanters I–IV with basal ventral row of tubercles, interlocking with corresponding tubercles at respective coxae. Trochanter III with a few ventral setiferous tubercles. Trochanter IV with a row of small retrolateral apophyses and a small subdistal prolateral spiniform apophysis. All femora straight. Femora III–IV with a



Figures 4–5. ***Stygnicranaus alessandroi*** **sp. nov.**, male holotype (UNAL) from Colombia. Penis, distal portion. Fig. 4. Dorsal view. Fig. 5. Lateral view. Arrows indicate capellum. Scale bars = 0.1 mm.

pair of small dorsoapical spurs. Femur IV with two rows of granules decreasing in size towards apex. Tarsi III–IV with unpectinated double claws and well-developed tarsal process ('pseudonychium'). Colour. Body background dorsal Brilliant Orange Yellow with numerous Moderate Red small spots. All granules of scutum contrasting Pale Greenish Yellow surrounded by a circular islet of the same colour. In the clusters of lateral margins the islets are coalesced into a larger irregular spot. All appendages more or less the same colour as the scutum, but glossy, darker, and more saturated (background Strong Orange with Deep Orange reticule). Legs growing darker towards the apex. Free tergite III completely Pale Greenish Yellow. Genitalia. (Figs 4–5). Ventral plate subrectangular with shallow lateromedial and anterior constrictions in dorsal view; setae of ventral plate divided in two groups, distal and medial, on each side. Distal group with four helicoidal setae, the innermost hooked and directed distally; the two apical ones directed laterodistally, and the remaining, transverse. Medial group with two substraight, subequal setae directed lateroposteriorly. Follis measuring about two-thirds of the ventral plate maximum length, extending from truncus tip to the base of the distal helicoidal setae with shallow folds in the basal portion. Stylus straight with capellum shovel-like, presenting lateral beaks.

Female: Unknown.

Type material: ♂ holotype, one juvenile. Paratype (UNAL) Colombia, Valle Del Cauca, Dagua. El Salto. August 2006, Giupponi, A. col.

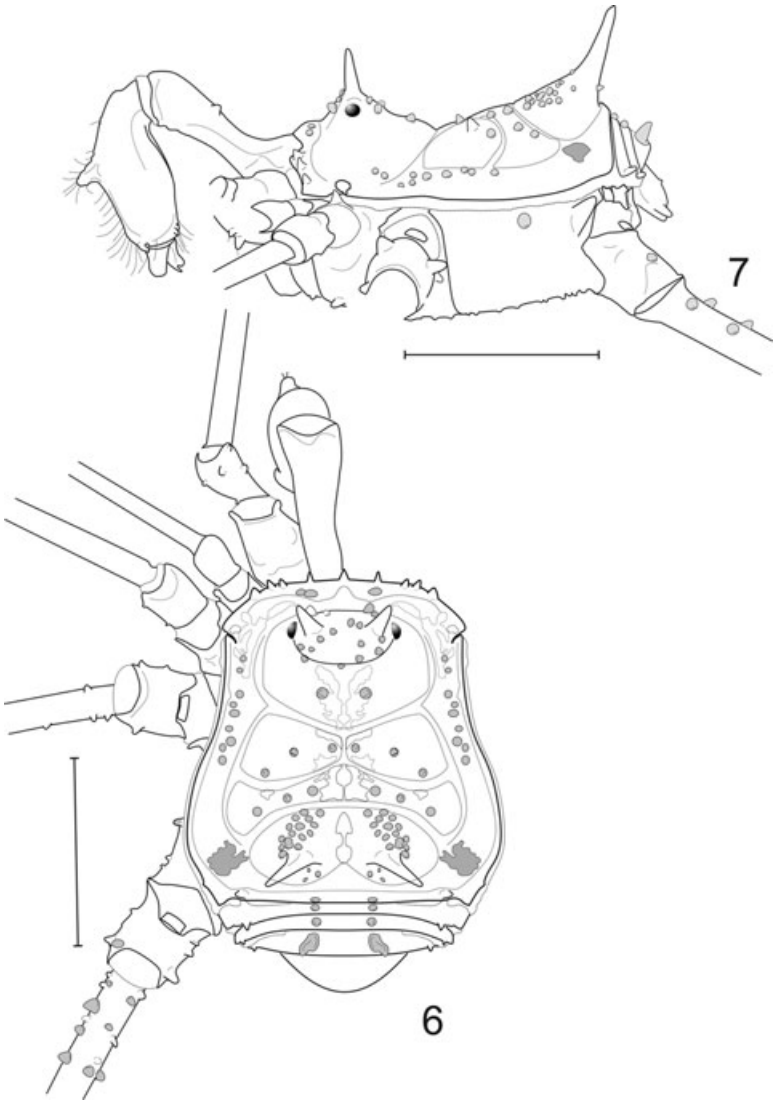
Etymology: The species name honours the collector of the type series, our colleague and friend Alessandro Ponce de Leão Giupponi.

STYGNICRANAUS PONCEDELEONI SP. NOV.
(FIGS 6–11)

Type locality: Colombia, Valle Del Cauca, Dagua. El Salto. WWF Ecoregion NT0145 (North-western Andean montane forests).

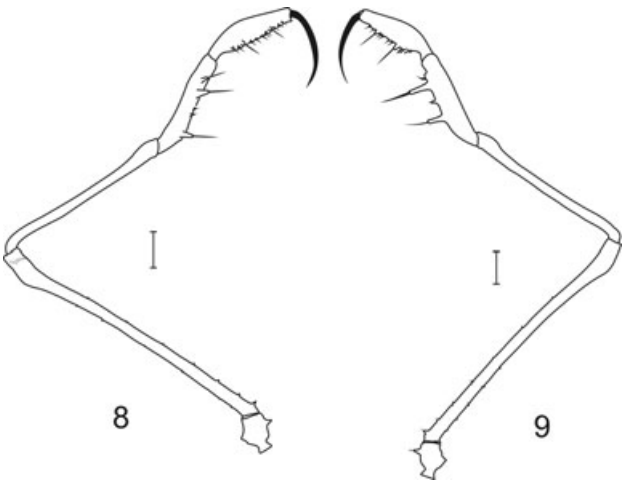
Diagnosis: It is easily distinguished from all other species by the presence of pearly tubercles in coxa IV instead of spines.

Description: Male holotype: Dorsum (Figs 6–7). Dorsal scutum attenuate pyriform, with carapace smaller than abdominal scutum. Posterior border of scutum straight. Cheliceral sockets very shallow with a median tooth. Anterolateral corners of carapace with three teeth on each side, two by the pedipalpus, ectal larger, the third at leg I. Frontal hump with one tubercle each side. Posterior corners of scutum with



Figures 6–7. ***Stygnicranaus poncedeleoni*** **sp. nov.**, male holotype (UNAL) from Colombia. Habitus. Fig. 6. Dorsal view. Fig. 7. Lateral view. Scale bars = 3 mm.

two teeth on each side. Ocularium elliptical, low, with a pair of stout, paramedian erect (lateral view), slightly divergent (frontal view) spines with blunt point. Surface of ocularium with 16 coarse scattered granules. Posterior part of lateral area of scutum each side with an island of such granules. Posterior border of dorsal scutum with two paramedian pearly setiferous tubercles. Carapace behind ocularium with a pair of rounded setiferous tubercles. Anterior half of lateral area with a group of such tubercles. Lateral border of scutum with a irregular row of small scarce tubercles. Grooves of scutum well marked, defining a mesotergum with three areas; original area IV completely fused with area III. A single shallow longitudinal medial groove dividing areas II and III in two halves each. All areas unarmed except for area III armed with a pair of very high acuminate spiniform processes. Scutal area II projecting anteriorly into area I, dividing it in left and right halves. Areas I and II each with a transverse row of six to eight setiferous tubercles. Area III with clusters of setiferous tubercles anterior to the large spines and reaching their basal part. Single V-shaped ozopore opening laterally at the tip of a dorsolateral low protuberance. Free tergites I–II smooth, except for a pair of paramedian pearly granules each, at the same level as the tubercles in the posterior border of the scutum. Free tergite III bearing a paramedian pair of acuminated spiniform tubercules, a lot larger than those in tergites I–II. Their corners each bearing an acuminate small process tooth. Venter. Coxae I–III smooth, except for a transverse row of tubercles in coxa I, two



Figures 8–9. ***Stygnicranaus poncedeleoni*** **sp. nov.**, male holotype (UNAL) from Colombia. Left pedipalpus. Fig. 8. Mesal view. Fig. 9. Ectal view. Scale bars = 1 mm.

rows in II–III. Three irregular rows in coxa IV. Intercoxal bridges weak. Coxae I–III subrectangular, transverse. Coxa IV the largest, almost equalling the other three taken together, shaped lanceolate and pentagonal, divergent posteriorly. Stigmatic area long, Y-shaped. Stigmata large, elongate elliptic, clearly apparent, not hidden by any bridges or tubercles, each occupying one third of the area. Maxillary lobes of coxae II clearly visible. Chelicera. Basichelicerite long, with bulla attenuate, with a medial belt of granules and a mesal subdistal small acuminate tubercle. Hand not swollen, with a frontal medial hooked spine. Pedipalpus (Figs 8–9). Very elongate and smooth, with tibia and tarsus forming a subchela. Coxa large, conical, with a ventral medial row of three setiferous tubercles. Trochanter cylindrical with typical sub-basal constriction, with apical dorsomesal tubercles and a ventral pair of setiferous tubercles, mesal larger than ectal. Femur longer than dorsal scutum, thicker at distal third, with dorsoapical tubercles and a ventral row of setiferous tubercles. Patella longer than abdominal scutum, thicker at distal third. Tibia as long as patella, cylindrical with four ectal (IiIi) and four mesal (IiIi) spines. Tarsus fusiform, slightly shorter than tibia, with 11 ectal (iiIiiiiiIii) and ten mesal (iiIiiiiIii) spines. Tarsal claw almost as long as tarsus. Legs. All segments slender and unarmed. Relative length I < III < IV < II. Dorsobasal apophyses of coxae I–II close to the ozopore: coxa I anterior spiniform, posterior small, directed backwards; coxa II anterior spiniform, posterior as a lobe joining coxa III. Coxa IV hidden under dorsal scutum in dorsal view, with prolateral dorsoapical spiniform apophysis and dorsal granules. Trochanters I–IV with ventrobasal tubercles interlocking with respective coxae. Trochanter II–III with a few prolateral and retrolateral setiferous tubercles. Trochanter IV with a row of small retrolateral apophyses and small subdistal prolateral and retrolateral spiniform apophyses. All femora straight. Femora III–IV with a pair of small dorsoapical spurs, retrolateral larger than prolateral. Femur IV with two rows of granules decreasing in size towards apex. Tarsi III–IV with unpectinated double claws and well-developed tarsal process ('pseudonychium'). Colour. Body and appendage background colour Deep Reddish Orange with strong mottling and spotting in Strong Reddish Orange, especially at scutal grooves. Chelicera by contrast has conspicuous darker reticulation. All granules are Pale Greenish Yellow as well as the inverted Y (from behind the ocularium to lateral of area II) formed by the spots of scutum. Genitalia (Figs 10–11). Ventral plate subrectangular with shallow lateromedial and marked anterior constrictions in dorsal view; setae of ventral plate divided into two groups, distal and medial, on each side. Distal group with four helicoidal setae, the innermost hooked and directed distally; two apical oblique, directed laterodistally, and the remaining one somewhat transverse. Medial group with two substraight, subequal setae directed lateroposteriorly. Follis measuring about two-thirds of the ventral plate maximum length, extending from truncus tip to the base of the distal helicoidal setae with shallow folds in the basal portion. Stylus straight with capellum shovel-like.

Female: Very similar to male, except for the slightly larger size and the absence of the frontal medial hooked spine in the cheliceral hand.

Type material: ♂ holotype (UNAL), one ♂, one ♀ paratypes (MNRJ 17906) Colombia, Valle Del Cauca, Dagua. El Salto. August 2006, Giupponi, A. col.

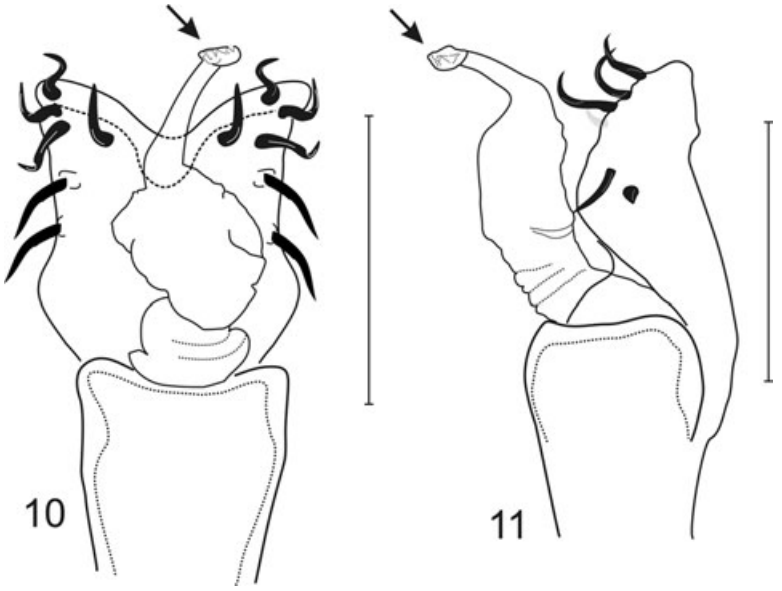
Etymology: The species name also honours the collector of the type series, our colleague and friend Alessandro Ponce de Leão Giupponi.

STYGNICRANAUS ABNORMIS ROEWER, 1913 (FIGS 12–13)

Stygnicranaus abnormis Roewer, 1913: 423, fig. 167; 1923: 570, fig. 716; Kury, 2003: 102.

Type locality: Colombia, Maracaibo (Venezuela or Colombia? See discussion below). WWF Ecoregion NT0145 (North-western Andean montane forests).

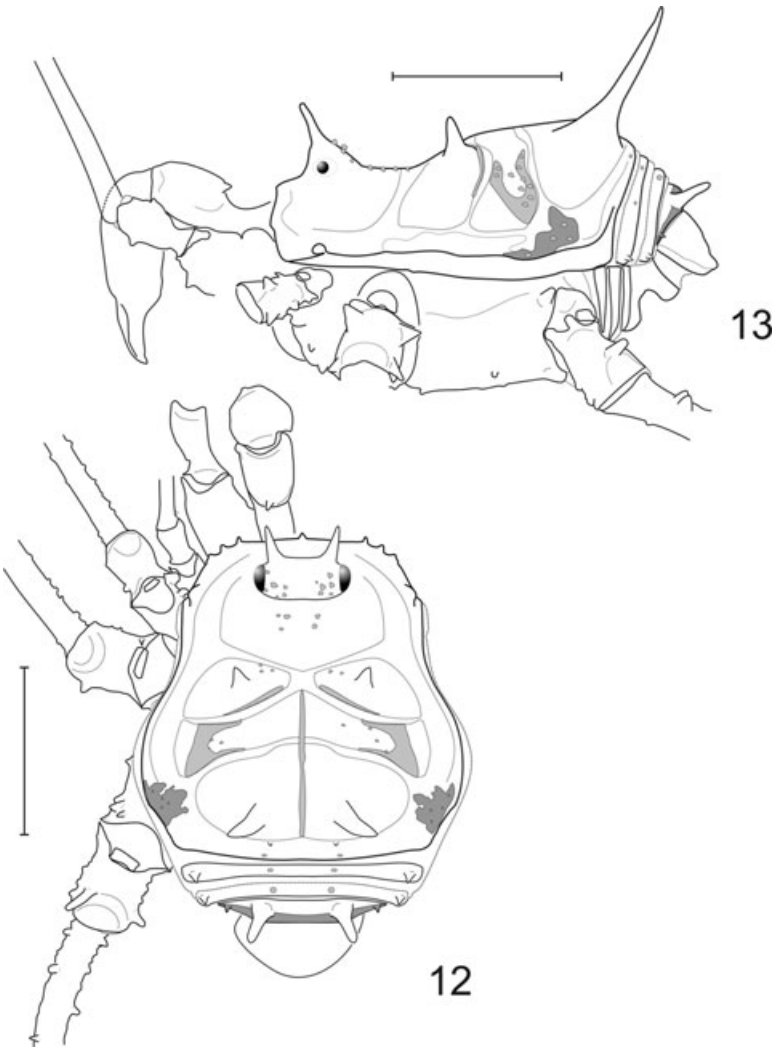
Diagnosis: It is very similar to *S. poncedeleoni*, but does not present pearly rounded granules in femora IV. Also, it is the only species in the genus with a dorsomedial basal small curved spine in the basis of the bulla.



Figures 10–11. ***Stygnicranaus poncedeleoni*** **sp. nov.**, male holotype (UNAL) from Colombia. Penis, distal portion. Fig. 10. Dorsal view. Fig. 11. Lateral view. Arrows indicates capellum. Scale bars = 0.1 mm.

Description: Male: Unknown.

Female holotype: Dorsum (Figs 12–13). Dorsal scutum attenuate pyriform, with carapace smaller than abdominal scutum. Posterior border of scutum straight. Cheliceral sockets very shallow with a median tooth. Anterolateral corners of carapace with three to four small teeth on each side, all at pedipalpus level. Posterior corners of scutum with a setiferous tubercle on each side. Ocularium low, with a pair of stout, paramedian erect (lateral view), slightly divergent (frontal view) spines with blunt point. Surface of ocularium with 14 (seven + seven) coarse scattered granules. Carapace behind ocularium with a few small tubercles. Posterior part of lateral area of scutum with an island of such tubercles on each side. Grooves of scutum well marked, defining a mesotergum with three areas; original area IV completely fused with area III. A single shallow longitudinal medial groove dividing areas II and III into two halves each. All areas armed with a pair of spines except for area II, which is unarmed. Scutal area II projecting anteriorly into area I dividing it partially into left and right halves. Areas I and II each with islands of small white setiferous tubercles. Area III with clusters of setiferous tubercles anterior to the large spines and reaching their basal part. In the place of area IV, a pair of paramedian setiferous tubercles. Single ozopore opening laterally at the tip of a dorsolateral low protuberance. Free tergites I–II smooth, except for a pair of paramedian granules each. Free tergite III with a pair of paramedian strong spines Their corners each bear an acuminate small tooth. Venter. Coxae I–III smooth, except for a transverse row of small tubercles in coxae I and II. Intercoxal bridges weak. Coxae I–III subrectangular, transverse. Coxa IV the largest, almost equalling the other three taken together, shape lanceolate and pentagonal, divergent posteriorly. Stigmatic area long, Y-shaped. Stigmata large, elongate elliptic, oblique, clearly apparent, not hidden by any bridges or tubercles, each occupying one-quarter of the area. Maxillary lobes of coxae II clearly visible. Chelicera. Basichelicerite long, with bulla well marked, and a mesal subdistal small acuminate setiferous tubercle. Median tubercle at posterior rim of bulla. Hand not swollen, with one frontal row of granules. Pedipalpus. Very elongate and smooth, with tibia and tarsus forming a subchela. Coxa large, conical, with a row of ventromedial tubercles. Trochanter cylindrical with typical sub-basal constriction, and apical dorsomesal tubercles and one ventral row of setiferous tubercles. Femur as long as dorsal scutum, slightly thicker at distal third, smooth. Patella longer than abdominal scutum, thicker at distal third. Tibia as long as patella, cylindrical with three ectal (IIi) and three mesal (IIi) spines, dorsally covered with coarse tubercles. Tarsus fusiform, slightly shorter than tibia, with seven ectal (iIiiiIi) and 11 mesal (iiIiiiiiIii) spines and two ventral rows of setiferous tubercles. Tarsal claw almost as long as tarsus. Legs. All segments slender and unarmed. Relative length I < III < IV < II. Dorsobasal apophyses of coxae I–II close to the ozopore: coxa I anterior spiniform, posterior small,



Figures 12–13. *Stygnicranaus abnormis* Roewer, 1913, female holotype (SMF 9800868) from Colombia. Habitus. Fig. 12. Dorsal view. Fig. 13. Lateral view. Scale bars = 3 mm.

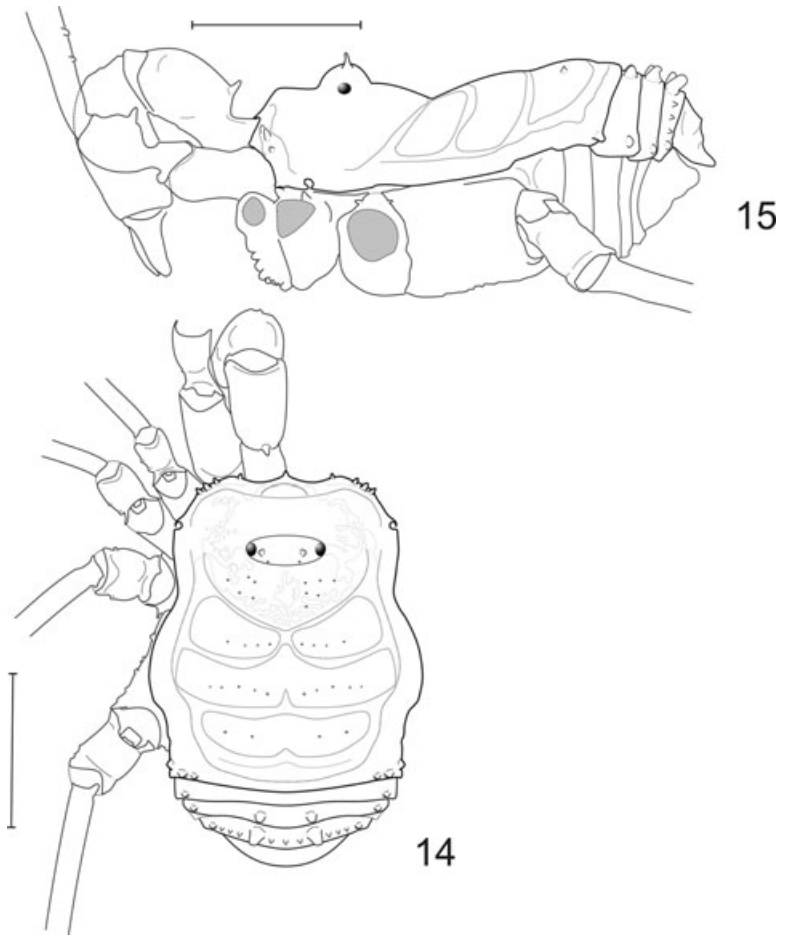
directed backwards; coxa II anterior spiniform, posterior apophysis absent. Coxa IV hidden under dorsal scutum in dorsal view, with two prolateral dorsoapical spiniform apophyses and ventral granules. Trochanters I–IV with ventrobasal tubercles connecting with respective coxae and scattered small setiferous tubercles all over the ventral surface. Trochanter III with a few prolateral and retrolateral setiferous tubercles and distally with anterior and posterior spiniform processes. Trochanter IV with row of retrolateral tubercles, increasing distally and two posterior dorsal subequal spurs. All femora straight (even though the holotype specimen presents curved femora, it is surely a result of the small vial used). Femora III–IV with a pair of small dorsoapical spurs. Femora IV also bear a small basal dorsoretrolateral row of five spines. Tarsi III–IV with unpectinated double claws and well-developed tarsal process ('pseudonychium'). For tarsal counts see Table 1. Colour. Somewhat faded because of conservation in alcohol. Body and appendages background Deep Orange with lighter reticulations. Granules and spots of the scutum Pale Yellow.

Type material (examined): ♀ holotype (and not ♂ as in Roewer, 1913, 1923) – (SMF 9800868 – RI/868-43) – Colombia [or Venezuela?] Maracaibo.

AGATHOCRANAUS GEN. NOV.

Genus diagnosis: As for the single species.

Etymology: From the Greek *agathos* (= good, gentle) + pre-existing genus *Cranaus*. This name is a pun of the closely related *Stygnicranaus*, which means 'mischievous' + *Cranaus*.



Figures 14–15. ***Agathocranaus innocens*** **sp. nov.**, male holotype (AMNH) from Ecuador. Habitus. Fig. 14. Dorsal view. Fig. 15. Lateral view. Scale bars = 3 mm.

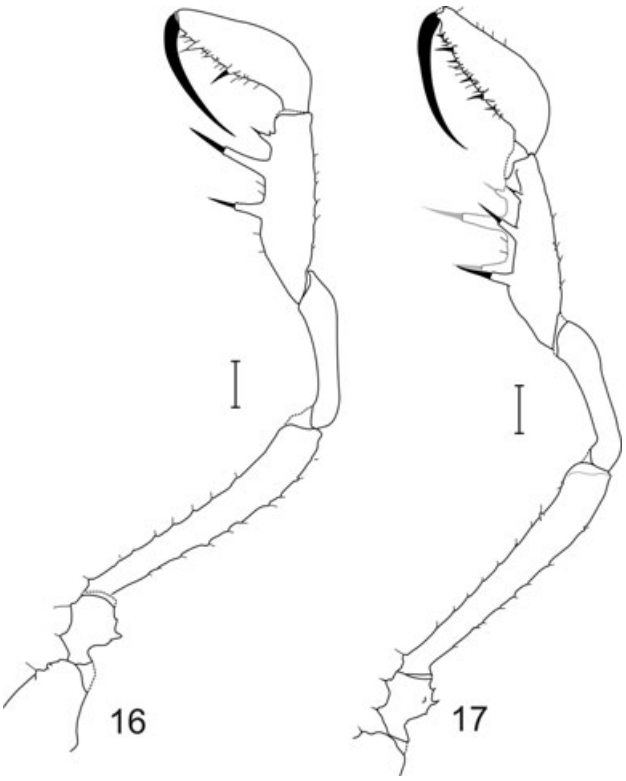
Type species: Agathocranaus innocens sp. nov.

AGATHOCRANAUS INNOCENS **SP. NOV.** (FIGS 14–19)

Type locality: Ecuador (North). WWF Ecoregion unknown.

Diagnosis: Dorsal scutum type alpha with very smooth ornamentation in all scutal areas including ocularium. The pedipalpal tibia forming a subchela and dorsally covered with coarse granulation.

Description: Male holotype: Dorsum (Figs 14–15). Dorsal scutum type alpha of Kury, Villarreal & Costa (2007); carapace only a little smaller than abdominal scutum. Posterior border of scutum substraight. Cheliceral sockets very shallow with a small median tooth. Anterolateral corners of carapace with three teeth on each side, all at pedipalpus level. Frontal border of carapace somewhat swollen. All other borders smooth except for the posterior corners with two small setiferous tubercles on each side. Ocularium low, convex, with a pair of stout, paramedian erect (lateral view), slightly divergent (frontal view), extremely small spines with sharp points, otherwise smooth. Carapace smooth with minute granules behind ocularium. Grooves of scutum well marked, defining a mesotergum with three areas; original area IV completely fused with area III. All areas unarmed with a transverse row of granules. Scutal area II projecting anteriorly into area I dividing it into left and right halves. Area I with a row of four setiferous tubercles each side. Area II with a transverse row of five setiferous tubercles on each side. Area III with two pairs of the same type of tubercle, paramedian, slightly larger than the others found in dorsal scutum, the posterior area bears a row of eight granules that marks what would be area IV. Single ozopore opening laterally at the tip of a dorsolateral low protuberance. Free tergites I–III smooth, except for a pair of paramedian tubercles each that increase from I to III. Free tergite 3 with a row of acuminate



Figures 16–17. ***Agathocranaus innocens*** **sp. nov.**, male holotype (AMNH). Fig. 16. Left pedipalpus, ectal view. Fig. 17. Right pedipalpus, mesal view. Scale bars = 1 mm.

small tubercules, of which the paramedian ones are small blunt spines. Their corners each bear a granule. Venter. Coxa I with a row of blunt tubercles. Coxae II–III smooth, except for a transverse row of setiferous tubercles each. Intercoxal bridges well developed. Coxa III fused by intercoxal bridges to coxa IV. Coxae I–III subrectangular, transverse. Coxa IV the largest, almost equalling the other three taken together, shape lanceolate and pentagonal, divergent posteriorly. Stigmatic area long, Y-shaped. Stigmata moderately large, elongate elliptic, clearly apparent, not hidden by any bridges or tubercles, each occupying one-fifth of the area. Stigmata completely transverse as opposed to the stigmata of the *Stygnicranaus* genus. Maxillary lobes of coxa II clearly visible. Chelicera. Basichelicerite long, with bulla attenuate, with a dorsomedial basal small curved spine in the basis of the bulla. Hand not swollen, with two frontal rows of granules. Pedipalpus (Figs 16–17). Very elongate with tibia and tarsus forming a subchela. Coxa large, conical, with a ventral row of small tubercles. Trochanter cylindrical with typical sub-basal constriction, incrassated with small curved spines and two ventral setiferous tubercles. Femur as long as dorsal scutum, thicker at distal third, with dorsoapical tubercles and a ventromesal subapical row of setiferous tubercles. Patella length about half the femur length, thicker at distal third, with minute dorsal granules. Tibia as long as patella, cylindrical with three ectal (iIi) and three mesal (IIi) spines, dorsally covered with coarse granulation. Tarsus fusiform, slightly shorter than tibia, with six ectal (iIiiIi) and 12 mesal (iIiiiiiiIiii) spines and bearing a ventromesal row of setiferous tubercles. Tarsal claw almost as long as tarsus. Legs. All segments slender and unarmed. Relative length I < III < IV < II. Dorsobasal apophyses of coxae I–II close to the ozopore: coxa I anterior and posterior spiniform, posterior small, directed backwards; coxa II anterior spiniform, posterior as a lobe joining coxa III. Coxa IV hidden under dorsal scutum in dorsal view, with prolateral dorsoapical spiniform apophysis and dorsal granules, also bearing a ventroretrolateral apical apophysis applied against free sternite I. Trochanters I–III with a few prolateral and retrolateral setiferous tubercles. Trochanter IV with scarce setiferous tubercles and no apophyses. All femora straight and without spurs. Tarsi III–IV with unpectinated double claws and well-developed tarsal process ('pseudonychium'). Colour. Body background dorsal Moderate Reddish Orange with varied Brilliant Orange mottling. Carapace and all appendages more or less the same background colour as the scutum, with darker reticulation. Genitalia (Figs 18–19). Ventral plate subrectangular with shallow lateromedial and marked anterior constrictions in dorsal view. Setae of ventral plate divided into two groups, distal and medial, on each side. Distal group with four helicoidal setae, all closely grouped. Medial group with two substraight setae, both directed lateroposteriorly. Follis measuring about two-thirds of the ventral plate maximum length, extending from truncus tip to the anterior border of ventral plate, with shallow folds in the basal portion. Stylus straight with capellum, crescent-shaped, presenting a large, ventral beak.

Type material: ♂ holotype (AMNH) Ecuador (North) September 1977, L. E. Peña col.

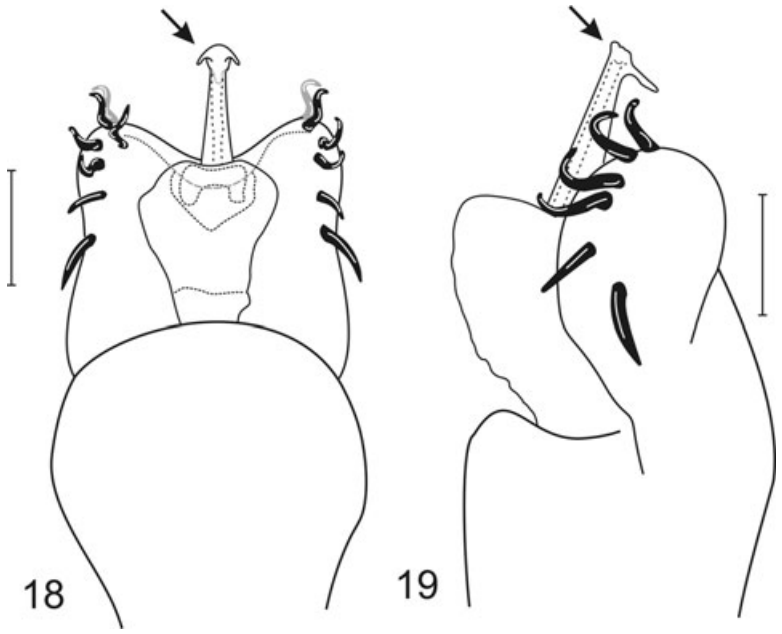
Etymology: From the Latin *innocens* (= harmless), referring to the delicate appearance and lack of the heavy spination typical of its counterpart, *Stygnicranaus* and also consonant with the generic name.

Female: Unknown.

Tryferos Roewer, 1931

Tryferos Roewer, 1931: 147; Kury, 2003: 103.

Genus diagnosis: As for the single species.



Figures 18–19. ***Agathocranaus innocens*** **sp. nov.**, male holotype (AMNH) from Ecuador. Penis, distal portion. Fig. 18. Dorsal view. Fig. 19. Lateral view. Arrows indicate capellum. Scale bars = 0.1 mm.

Type species: Tryferos elegans, Roewer, 1931, by monotypy.

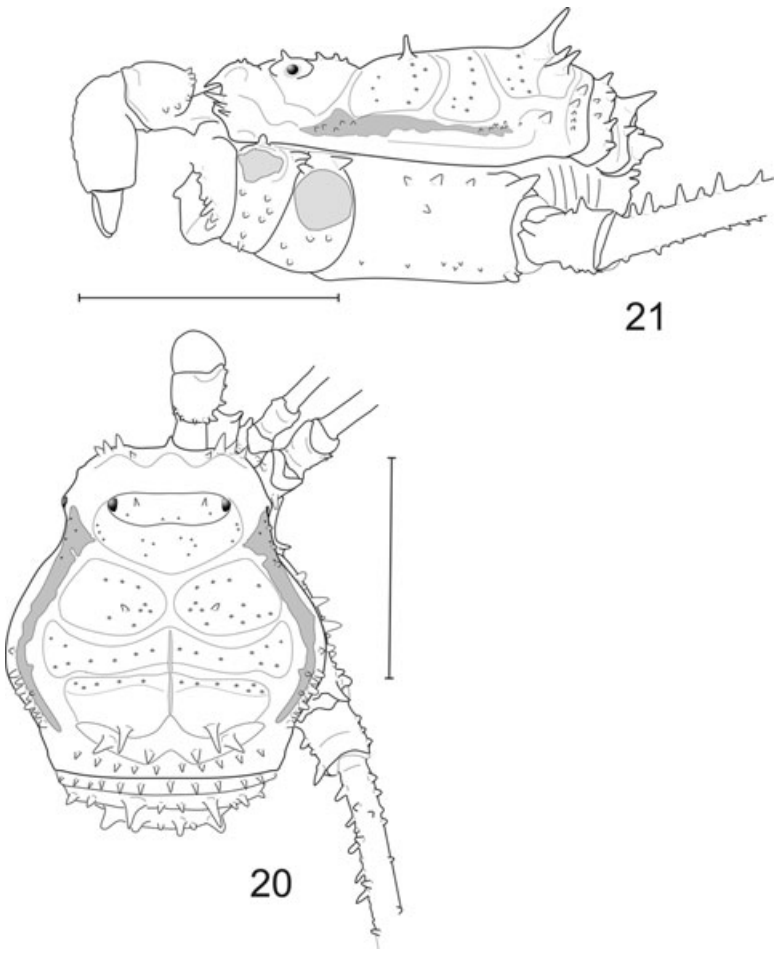
TRYFEROS ELEGANS ROEWER, 1931 (Figs 20–27)

Tryferos elegans Roewer, 1931: 147, fig. 20; Kury, 2003: 103.

Type locality: Ecuador. Guayas. Isla de Puná (2 °50′S, 80 °08′W). WWF Ecoregion NT0214 (Ecuadorian dry forests).

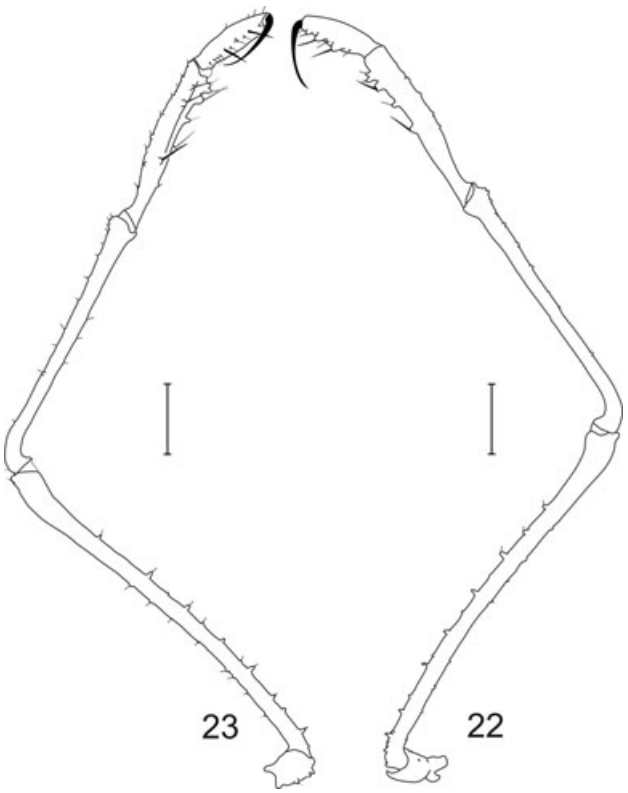
Diagnosis: An unusual species with a very low, wide, and flattened ocularium and carapace much shorter than abdominal scutum The area IV bearing two divergent acuminate spines and a few sharp smaller tubercles and the nearly rounded, not elongated pedipalpal tarsus that does not form a subchela are unique amongst all related genera.

Description: Male syntype SMF: Dorsum (Figs 20–21). In dorsal view, lateral margins of dorsal scutum convex in the middle and narrower at carapace and posterior quarter, with carapace much smaller than abdominal scutum. Posterior border of scutum straight. Cheliceral sockets very shallow with a median tooth. Anterolateral corners of carapace with three strong acuminate teeth on each side, at pedipalpus and leg I coxae level. Frontal hump very low and unarmed. Ocularium very low, wide, and flattened with a few scattered acuminated granules posteriorly and a pair of paramedian small acuminate tubercles. Carapace behind ocularium with a few scattered setiferous tubercles. Lateral areas of scutum with an irregular row of small setiferous tubercles clustered posterior to area II. Posterior margin of scutum with a transverse row of acuminate setiferous tubercles. Grooves of scutum well marked, defining a mesotergum with four areas. Area I very large, divided into left and right halves with a pair of acuminate, paramedian tubercles and many scattered granules. Area II projecting a little into area I with a transverse row of granules. Area III subelliptical with a pair of high, sharp, parallel spines and many irregularly arranged granules. A single shallow longitudinal medial groove divides areas II and III into two halves each. Area IV crescent-shaped, very small, and embedded into area III with two divergent acuminate spines and a few sharp smaller tubercles. Single ozopore opening laterally at the tip of a dorsolateral low protuberance. Free tergites I–III each with a transverse row of pointed tubercles of which the paramedian pair is larger on tergite II and III. Venter. Coxae I–IV densely granular, I and II each with a transverse row of setiferous tubercles, much stouter in coxa I. Intercoxal bridges weak, virtually absent. Coxae I–III subrectangular, transverse. Coxa IV the largest, equalling the other three taken together, shape lanceolate and pentagonal, divergent posteriorly. Stigmatic area long, Y-shaped. Stigmata small, elliptic, clearly apparent, not hidden by any bridges or tubercles, each occupying one-tenth of the area.

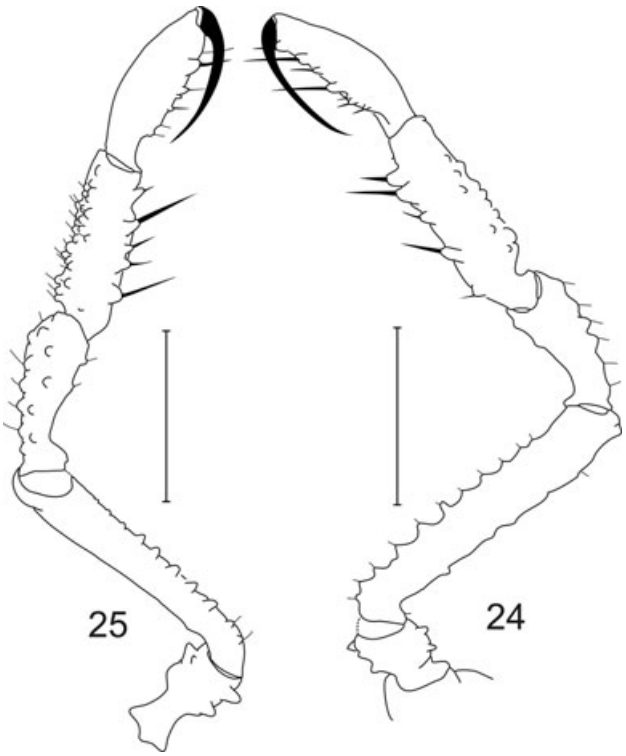


Figures 20–21. *Tryferos elegans* Roewer, 1931, male syntype (SMF 9901458 – RII/1458/43) Ecuador. Guayas. Isla de Puná. Habitus. Fig. 20. Dorsal view. Fig. 21. Lateral view. Scale bars = 3 mm.

Maxillary lobes of coxae I–II clearly visible. Free sternites each with a transverse row of granules growing larger laterally. Dorsal and ventral anal opercles each with a few scattered tubercles. Chelicera. Basichelicerite short, with well-marked bulla. Posterior and lateral margins of bulla with a rim of pointed tubercles. Hand weak, densely covered with small granules. Pedipalpus (Figs 22–25). Very elongate and smooth, with tibia and tarsus not forming a subchela. Coxa very short, cylindrical. Trochanter short, cylindrical with typical sub-basal constriction, with two ventral setiferous tubercles. Femur slender, a little shorter than dorsal scutum, bent in the apex with dorsal and ventral longitudinal rows of short setiferous tubercles, ventral stouter. Patella elongate, only a little shorter than femur, thicker at the apex. Tibia elongate, shorter than patella, ventrally flattened, thinner at basal third, with five ectal (IiIv) and five mesal (IiiIi) spines. Dorsum of patella (distally) and of tibia (entirely) covered with coarse granulation. Tarsus ventrally flattened, much shorter than tibia, with four ectal (IiIi) and four mesal (IiIi) spines and scattered minute setiferous tubercles. Tarsal claw almost as long as tarsus. Legs. All segments slender and unarmed except for femurs I–III covered with a ventral row of setiferous tubercles and coxa, trochanter, and femur IV. Coxa IV with dorsoapical spiniform apophysis. Relative length I < III < IV < II (from Roewer's data, 1931, legs III missing in SMF male). Dorsobasal apophyses of coxae I–II close to the ozopore: coxa I anterior spiniform, posterior small, directed backwards; coxa II anterior spiniform, posterior as a lobe joining coxa III. Coxa IV almost completely hidden under dorsal scutum in dorsal view, with prolateral dorsoapical spiniform apophysis and dorsolateral acuminate tubercles. Trochanters I–IV with ventrobasal tubercles interlocking with respective coxae. Trochanter III with a few prolateral and retrolateral setiferous tubercles. Trochanter IV with row of small retrolateral apophyses and a small subdistal prolateral spiniform apophysis. All femora straight. Femora III–IV with a pair of small



Figures 22–23. *Tryferos elegans* Roewer, 1931, male syntype (SMF 1458). Left pedipalpus. Fig. 22. Ectal view. Fig. 23. Mesal view. Scale bars = 1 mm.



Figures 24–25. *Tryferos elegans* Roewer, 1931. Fig. 24. Male syntype (SMF 1458). Left pedipalpus, ectal view. Fig. 25. Female syntype (SMF 1458). Left pedipalpus, mesal view. Scale bars = 1 mm.

dorsoapical spurs. Femur IV with diverse rows of acuminate tubercles and large prolateral distal hooked spine. Tarsi III–IV with unpectinated double claws and clear tarsal process ('pseudonychium'). Colour. Body background dorsal Strong Orange with numerous small Brilliant Orange Yellow spots. Larger stripes at lateral margin of scutum and area IV Yellowish White. All appendages more or less the same colour as the scutum. Genitalia (Figs 26–27). Ventral plate subrectangular with marked lateromedial and anterior constrictions in dorsal view; all setae of ventral plate clustered in the anterior portion of the ventral plate. Two larger helicoidal setae and four smaller straight setae. Follis as long as the ventral plate maximum length, extending from truncus tip over the anterior border of ventral plate, with shallow folds in the basal portion. Stylus straight with capellum, oval, foliolate, presenting a small apical beak.

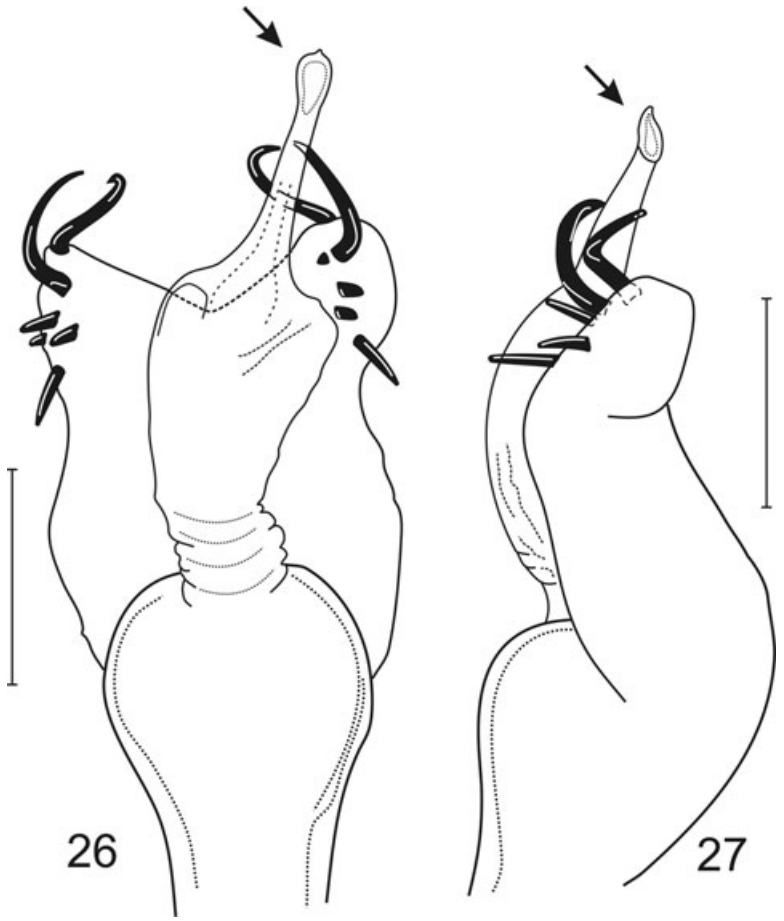
Female: Very similar to male in general proportions and body aspects, except for the metatarsus I not swollen, basal segments of leg IV entirely unarmed, and pedipalpus short instead of elongated as male's (see Figs 24–25). Also, armature of legs much subdued.

Type material: One ♂, two ♀ syntypes (BNHM not examined), One ♂, two ♀ syntypes (SMF 9901458 – RII/1458/43, examined) Ecuador. Isla de Puná.

DISCUSSION

The systematic position of the Stygnicranainae

The conspicuous elongate pedipalpi, combined with the hidden coxa IV of males, were the key features to suggest inclusion of species of Neotropical Laniatores in the Stygnicranainae by most 20th century authors. Because of these features, some Sodreaninae from the Brazilian Atlantic Forest were at some time included in this group: *Gertia* Soares & Soares, 1946 (originally in Stygnicranainae, removed to Sodreaninae by Soares & Soares, 1985); *Stygnobates* Mello-Leitão, 1927 [originally in Mitobatinae, removed to Stygnicranainae by Mello-Leitão, 1932, to Progonyleptoidellinae by Kury, 1992a, and to Sodreaninae by R. Pinto-da-Rocha (pers. comm., 1999)]; *Zortalia* Mello-Leitão, 1936 (originally in Gonyleptinae, transferred to Stygnicranainae by Mello-Leitão, 1939 and to Sodreaninae by Soares & Soares, 1985). Juveniles of laniatorids often have very elongate pedipalpi and



Figures 26–27. *Tryferos elegans* Roewer, 1931 – male syntype (SMF 9901458 – RII/1458/43) Ecuador. Guayas. Isla de Puná. Penis, distal portion. Fig. 26. Dorsal view. Fig. 27. Lateral view. Arrows indicate capellum. Scale bars = 0.1 mm.

some large juvenile cranaines have been wrongly referred to the Stygnicranainae for this reason (see Kury, 1995). The elongation of the pedipalpal segments, most notably the femur and patella, while the tibia/tarsus form a subchela, is widely distributed among the Laniatores. This feature is currently deemed to have originated independently several times, although it is very hard to notice any morphological differences amongst species groups (Kury, 1995). Lineages with elongate raptorial subchelate pedipalpi include the Sodreaninae (Gonyleptidae), Dibuninae (Epedanidae), *Metibalonius* Roewer, 1912 (Podoctidae), *Roewerania* Lawrence, 1934 (Triaenonychidae), some Biantidae, and some Stygnidae. In the adult Cranaidae this may have happened twice: (1) in *Tryferos*, which has very long femur, patella, and tibia only in males (an autapomorphy); and (2) in *Agathocranaus* + *Stygnicranaus*, which have very long coxa and femur in both sexes, which are synapomorphic at this level. Of these, the species of *Stygnicranaus* further developed a very long patella, whereas it is relatively short in *Agathocranaus*. In addition, the general trend towards elongation is perceived as a transformation series; first some segments elongate only in males, then more segments elongate in both males and females.

The subfamilial divisions in Cranaidae

The Stygnicranainae *sensu* Roewer (i.e. *Stygnicranaus* + *Tryferos* together with *Agathocranaus*) form a monophyletic Stygnicranainae. However, recognizing the Stygnicranainae would render the subfamily Cranainae paraphyletic. Despite searches for synapomorphies of the family Cranaidae, only unconvincing characters have been proposed (Kury, 1992b, 1994a). In the present study, again the Cranaidae as a whole is weakly supported, and most of the less inclusive nodes are well supported by unambiguous synapomorphies. *Prostygnus* lies at the base without any evident connection with the other Cranaidae as already shown in Kury (1992b). However, in Kury's (1992b) results, Prostygninae is polytomic with Cranaidae and a clade is formed

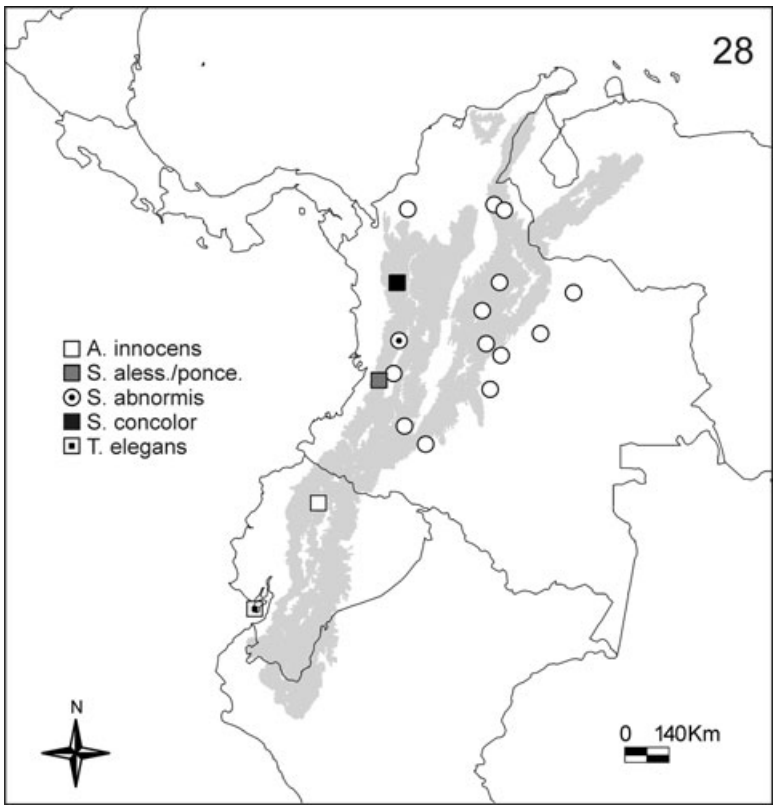


Figure 28. North-western South America showing distribution of the species associated with the name Stygnicranainae. Symbols for each species are in the map, open circles are localities named 'Maracaibo', the one chosen as the possible type locality for *Stygnicranaus abnormis* is marked with a central dot. Grey shade represents World Wildlife Fund Ecoregion NT0145.

by Stygnidae + [Cosmetidae + Gonyleptidae], whereas herein we recovered a closer relationship of some Stygninae with other Cranaidae. Unfortunately, Kury (1992b), as was then current, used subfamilies as terminals and did not provide a list of the material examined. The monophyly of *Prostygnus* + other cranaids is at best uncertain, pending a more rigorous test. The non-*Prostygnus* Cranaidae are much better supported. The arrangement of the terminals of Cranaidae used here (see Fig. 1) is remarkably asymmetrical, and of the four traditional subfamilies, two (Cranainae and Prostygninae) are paraphyletic (i.e. grades) and one (Heterocranainae) is monogeneric (therefore superfluous). The traditional recognition of four subfamilies is a poor rendering of this phylogeny into a classification. Although the present analysis is not intended to test the monophyly of the Cranaidae, in the face of such asymmetry keeping the traditional usage would be unwarranted. As an alternative approach, more craniad terminals could be included in the analysis. This would probably lead to an incredible multiplication of very small subfamilies of low information content. We therefore suggest dropping altogether the subfamilial divisions of the Cranaidae, with the division in genera better reflecting the branching structure of the phylogenetic tree.

THE TYPE LOCALITY OF *STYGNICRANAUS ABNORMIS*

The type locality of *S. abnormis* was questioned by Kury (1995) when he stated that '[the type locality] is almost certainly not Maracaibo, Colombia.' and assumed that Maracaibo, Zulia state, in Venezuela was a better candidate because it is a well-known (type) locality for a number of opilionids and 'Roewer (1913, 1923) was inconsistent in recording the country for Maracaibo and for other localities in Venezuela'. However, there are 11 places called 'Maracaibo' in Colombia. Two of them are in the same WWF ecoregion, Northern Andean montane forests (WWF, 2006), but only one is in the western Andean ridge where all the related species (treated in this paper) are found (Fig. 28). Indeed, this Maracaibo is located between the type (and only known) localities of *S. concolor* and the two *Stygnicranaus* described herein. Even though we understand that the WWF ecore-

gions are categorical data, we also understand that they represent similar environments under the same ecoregion code, so a determined ecoregion may help predict the associated fauna.

CONCLUSIONS

1. The Stygnicranainae *sensu* Roewer (= *Stygnicranaus* + *Tryferos*), which is the current usage, is monophyletic.
2. The genus *Stygnicranaus* in the current sense (= *S. abnormis* + *S. concolor*) constitutes a monophyletic group also including the two new species *S. alessandroi* and *S. poncedeleoni*.
3. The new monotypic genus *Agathocranaus* is the sister group of *Stygnicranaus*, and could have been included in it to avoid creating a monotypic genus, but as there is a clear morphological gap, we decided to treat it as a separate generic entity.
4. A revised Stygnicranainae (including *Agathocranaus* + *Tryferos* + *Stygnicranaus*) would be a monophyletic group. However, keeping this subfamily in the classification creates the problem of rendering the Cranainae paraphyletic. One possible solution could be to synonymize both subfamilies, but this is not the solution we favour, as shown below.
5. Prostygninae is also a nonmonophyletic group, and its core, containing the genus *Prostygnus* (plus a few very closely related genera) is only loosely attached to the Cranaidae.
6. Heterocranainae is monogeneric, containing only *Heterocranaus* and its few species.
7. The current division of the family Cranaidae into four subfamilies does not reflect the phylogeny proposed for the group and includes one monogeneric and two paraphyletic units. We propose herewith to abandon all those subfamilies in favour of dealing only with genera.

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APPENDIX 1

List of terminals and material examined. OG, outgroup taxon:

OG Stygnidae *Stygnus gertschi* (Roewer, 1963) – 1 ♂ – MNRJ 17933 – Colombia. Meta. Villavicencio: Finca La Loma. viii.2006 Alessandro Giupponi col.

OG Heterocranainae *Heterocranaus* sp. – 1 ♂ – MACN AK 009 – Ecuador. Cotopaxi. Páramo de Cotopaxi, Bosque de pinos. 9.ii.1983 Arturo Roig-Alsina col.

OG Prostygninae *Prostygnus vestitus* Roewer, 1913 – 1 ♂ holotype – SMF – 'Colombia, Maracaibo'.

OG Prostygninae *Yania* sp. 4 ♂ 1 ♀. – MACN – Ecuador. Pichincha. 5 km N de Nanegalito, 1500 m. 1.iv.1984 Arturo Roig-Alsina col.

OG Prostygninae *Troya* sp. 1 ♂ – MACN – Ecuador. Azuay. Sayausí, near Cuenca. 6.ix.1978 Arturo Roig-Alsina col.

OG Cranainae *Phalangodus anacosmetus* Gervais, 1842 – 1 ♂ – CAS AK 019 – Colombia. Cundinamarca. Finca Bella Vista, near Sasaima, collected at night on low foliage. 13.v.1965 P. R. & D. L. Craig col.

OG Cranainae *Santinezia gigantea* (Roewer, 1913) – 1 ♂ – AMNH – Ecuador.

OG Cranainae *Cranaus bilunatus* Roewer, 1923 – 1 ♂, 3 ♀ – Ecuador. Pichincha. Puente sobre Río Blanco, ca. San Miguel de los Bancos (0.0166667–78.8833333) 26.xi.1978 Arturo Roig-Alsina col.

OG Cranainae *Tolimaius pectinitibialis* Roewer, 1914 – 1 ♂ 2 ♀. MCZ. Colombia. Huila 10 km east Stadt Leticia, Finca Meremberg 2300 m elev., iii.1979 W. Eberhard col.

Stygnicranaus abnormis Roewer, 1913 – ♀ holotype – (SMF 9800868 – RI/868-43) – Colombia [or Venezuela?] 'Maracaibo'.

Stygnicranaus alessandroi sp. nov. – ♂ holotype, 1 juv. paratype (UNAL) Colombia, Valle Del Cauca, Dagua. El Salto. viii.2006, Giupponi, A. col.

Stygnicranaus poncedeleoni sp. nov. – ♂ holotype (UNAL), 1 ♂, 1 ♀ paratypes (MNRJ 17906) Colombia, Valle Del Cauca, Dagua. El Salto. viii.2006, Giupponi, A. col.

Stygnicranaus concolor Kury, 1995 – 1 ♂ holotype, 1 ♀ paratype – MCZ – Colombia. Antioquia. Urrao, Parque das Orquideas (6 °20′N, 76 °11′W) vii.1985 Marcos Serna col.

Tryferos elegans Roewer, 1931 – 1 ♂ 2 ♀ syntypes – SMF 9901458 – RII/1458/43 – 43. Ecuador. Guayas. Isla de Puná (2 °50′S, 80 °08′W).

Agathocranaus innocens sp. nov. – ♂ holotype, 1 juv. paratype – AMNH Ecuador (North) ix.1977 L. E. Peña col.

APPENDIX 2

Matrix of morphological characters used in this phylogenetic analysis:

Stygnus gertschi	0---00000002000000000?0?0000100000000000001000
Prostygnus vestitus	10101000040200000000010100000110000100000000010

Troya sp	10101000010010000020120000002003010011100010 20
Yania sp	10101000000010000010120000002131000011100011 20
Heterocranaus sp	11101000000210000010220100001001100011100101 20
Tryferos elegans	11210010001311001031002110002022010011200111 01
Phalangodus anacosmetus	10001010011010000020220000000004010011000111 30
Tolimaius pectinitibialis	10020010021210000020100100011021001011110112 41
Cranaus bilunatus	10121010021110000020100000011121010111100111 20
Santinezia gigantea	10020110021101001020000000010021010011100113 41
Agathocranaus innocens	10010010011211211132001001110001120011100111 01
Stygnicranaus abnormis	10020111131210111132002001110 20??????10011301
Stygnicranaus alessandroi	10020111031211131132001001110201010011311113 01
Stygnicranaus poncedeleoni	10020111131211131132002001110301010011111113 01
Stygnicranaus concolor	10020010131210121132002001110201010011100113 01

APPENDIX 3

Annotated list of characters:

In this list, comments are made about the usage of some of the features used herein as characters. Additional external illustrations are listed in Appendix S2. The group+ notation follows Amorim (1982). Additional information can be found in the subsequent appendices. Optimization, length (L), consistency index (CI), and retention index (RI) are mapped on the tree obtained under $k = 3$.

- **1. Common ocularium, presence**
  - Traditional character widely used in the laniatorid taxonomy. Its absence has been a long-established character of the Stygnidae family and proposed as a synapomorphy as char. 8 in Kury (1992b).
  - Here it appears as an uninformative character separating the prime outgroup from the rest.
  - 0 absent; 1 present
- **2. Common ocularium, width relative to carapace**
  - In our analysis the wide ocularium appears as independent acquisitions for both *Heterocranaus* sp. and *Tryferos elegans*. L = 2, CI = 50, RI = 50.
  - 0 narrow; 1 wide.
- **3. Common ocularium, supraocular part, height relative to diameter of cornea**
  - The decreasing height of the ocularium is a synapomorphy for the *Phalangodus anacosmetus* + group (= Cranainae + Stygnicranainae), with a further autapomorphic decrease (state 2) for *T. elegans*. L = 3, CI = 66, RI = 75.
  - 0 around 1 diameter; 1 obviously more than 1 diameter; 2 less than 0.5 diameter.
- **4. Common ocularium, armature**
  - Traditional character widely used in the laniatorid taxonomy in a variety of character states. Used by Kury (1994a: 139) to support the clade Stygnicranainae + Cranainae.
  - The unarmed condition is here plesiomorphic, changing to high spines in *Cranaus bilunatus*+, changing further to tubercles independently in *T. elegans* and *Agathocranaus innocens*.
  - 0 unarmed; 1 a pair of paramedian tubercles; 2 a pair of paramedian high spines.
- **5. Carapace, outline in lateral view**
  - State 1 occurs in Cranaidae, then reverts to zero in *Tolimaius pectinitibialis*+. L = 2, CI = 50, RI = 80.
  - 0 flattened; 1 bison-like, thick, advancing over area I in lateral view.
- **6. Outline of dorsal scutum**
  - The posterior shift of the widest part occurs twice, one as an autapomorphy of *Santinezia gigantea*, the other in *S. abnormis*+. L = 2, CI = 50, RI = 66.
  - 0 widest at middle portion; 1 widest more posteriorly, at area IV.
- **7. Carapace, sexual dimorphism**
  - State 1 is a synapomorphy for the *P. anacosmetus* + group (=Cranainae + Stygnicranainae). L = 1, CI = 100, RI = 100.
  - 0 in male, much larger than in female, invading area I; 1 absent, carapace equal in both sexes.
- **8. Lateral border of scutum, markings**
  - Presence of this spot is a synapomorphy for *S. abnormis*+. L = 1, CI = 100, RI = 100.
  - 0 without posterior spot; 1 with posterior yellow clearly marked spot.

- **9. Mesotergal area I, armature**
  - Armature of mesotergal areas has long been used to diagnose genera (e.g. Roewer, 1923).
  - Presence of high spines in area I is a synapomorphy of *Stygnicranaus*, with a reversal in *S. alessandroi*. L = 2, CI = 50, RI = 50.
  - 0 unarmed or with paired small tubercles; 1 with pair of high erect spines.
- **10. Mesotergal area III, armature**
  - States changed many times with independent reversals. L = 6, CI = 66, RI = 71.
  - 0 with pair of acuminate tubercles; 1 unarmed; 2 with pair of parallel spines in mid line of area III; 3 with pair of immense divergent spines behind the mid line of area III; 4 with pair of columnar erect spines in mid line of area III.
- **11. Invasion of mesotergal area I by projection of area II**
  - Used by Kury (1992b: 98) and Kury (1994a: 139) as a synapomorphy for Cranainae + Stygnicranainae.
  - State 1 is a synapomorphy for the *P. anacosmetus* + group (=Cranainae + Stygnicranainae). L = 1, CI = 100, RI = 100.
  - 0 absent; 1 present.
- **12. Free tergites II and III, armature**
  - State 2 is widespread throughout the tree with all acquisitions being autapomorphic. It could be an artefact of outgroup choice, pending wider terminal sampling. L = 6, CI = 50, RI = 0.
  - 0 unarmed; 1 pair of high acuminate tubercles II > III; 2 pair of low tubercles III acuminate > II rounded; 3 pair of subequal acuminate tubercles.
- **13. Interlocking coxal bridges, development**
  - The reduction of the intercoxal bridges has been proposed as a synapomorphy of Cranaidae by Kury (1993).
  - This analysis concurs with his view (with a reversal in *S. gigantea*). L = 2, CI = 50, RI = 50.
  - 0 well developed; 1 much reduced.
- **14. Orientation of stigmata relative to stigmatic area and free sternites**
  - A synapomorphy of *S. gigantea* + with two reversions in *S. concolor* and *S. abnormis*. L = 3, CI = 33, RI = 50.
  - 0 parallel; 1 oblique.
- **15. Basichelicerite of male, elongation**
  - States 1 and 2 are synapomorphies for *Stygnicranaus* and *Agathocranaus*, respectively. L = 2, CI = 100, RI = 100.
  - 0 short; 1 very elongate and slender with bulla attenuate; 2 long, but not slender and with very strong bulla.
- **16. Basichelicerite, armature**
  - State 1 is a synapomorphy for Stygnicranainae changing throughout taxonomic distribution. L = 3, CI = 100, RI = 100.
  - 0 rim of two to three ectal spines followed by one to two small on posterior border; 1 only one median spine on posterior border; 2 absent; 3 with a rim of small tubercles on the posterior border extending to both sides.
- **17. Cheliceral hand, swelling**
  - Character 7 of Kury (1992b: 98) and 3 of Kury (1994b: 345), used in connection with other Gonyleptoidea.
  - Here it is a synapomorphy for *S. gigantea*+. L = 1, CI = 100, RI = 100.
  - 0 swollen in male; 1 weak in both sexes.
- **18. Pedipalpal coxa**
  - The elongate pedipalpus was used as the only original diagnostic character for Stygnicranainae. Herein we split this into four independent characters.
  - Elongation of pedipalpal coxa is a synapomorphy for *A. innocens*+. L = 1, CI = 100, RI = 100.
  - 0 very short [less than 55% lateral of carapace (cpx) length]; 1 very long (more than 70% lateral of cpx length).
- **19. Pedipalpal trochanter dorsal, armature**
  - State 3 is a synapomorphy for Stygnicranainae. L = 3, CI = 100, RI = 100.
  - 0 unarmed; 1 with mesoapical strong apophysis; 2 with a pair of median subequal spines on median bulla; 3 with a pair of median small tubercles on median bulla, external larger.
- **20. Sexual dimorphism of pedipalpal femur length**
  - The male elongate pedipalpus is a synapomorphy for Stygnicranainae, females also acquiring this feature in *A. innocens*+. L = 2, CI = 100, RI = 100.

- 0 short in both sexes; 1 extremely elongate only in male; 2 extremely elongate in both sexes.

- **21. Pedipalpal femur dorsally, shape**
  - The drastic modification in the structure of pedipalpal femur occurs in *Yania* sp.+ (with some extra changes appearing as autapomorphies) and is reversed in *S. gigantea*+. L = 4, CI = 50, RI = 50.
  - 0 unarmed; 1 with powerful spiny keel; 2 with pseudo carena dorsal and ventral.
- **22. Pedipalpal femur ventrally, armature**
  - State 0 is plesiomorphic, changed to 1 in *Prostygnus* as an autapomorphy and to 2 in the other Cranaidae (*Yania* sp.+) reversing to 0 in *Cranaus bilunatus*+. L = 3, CI = 66, RI = 66.
  - 0 unarmed; 1 with row of strong subequal spines evenly spaced; 2 with row of four to six spines, basal ones more clustered and larger.
- **23. Pedipalpal patella, length**
  - Maximal elongation of patella of pedipalpus is synapomorphic for Stygnicranainae, changing to intermediate state in two of its terminals.
  - 0 clearly shorter than carapace; 1 intermediate, comparable to carapace length; 2 longer than carapace.
- **24. Pedipalpal patella and tibia dorsal, sculpture**
  - This character has already been used by Kury (1994a: 139) to support the monophyly of the Cranaidae.
  - Here it appears independently in different lineages of Cranaidae with no synapomorphic content. L = 4, CI = 25, RI = 0.
  - 0 smooth; 1 with coarse granulation.
- **25. Pedipalpal tibia of male, length**
  - This is an autapomorphy for *Tryferos elegans*. L = 1.
  - 0 as long as tarsus; 1 very elongate, much longer than tarsus.
- **26. Pedipalpal tarsus, shape**
  - This is a synapomorphy for *A. innocens*+. L = 1, CI = 100, RI = 100.
  - 0 flattened, not forming subchela with tibia; 1 rounded, forming a subchela with tibia.
- **27. Ventral surface of pedipalpal tarsus, sculpture**
  - This is a synapomorphy for *A. innocens*+. L = 1, CI = 100, RI = 100.
  - 0 smooth; 1 with two longitudinal rows of small spines.
- **28. Legs I-IV, overall length and shape**
  - Elongation is synapomorphic for *C. bilunatus*+ with a reversal in *T. elegans*. L = 2, CI = 50, RI = 83.
  - 0 short, slightly curved; 1 long, substraight.
- **29. Distal portion of metatarsus I of male, swelling**
  - States 1–2 occur independently each in different terminals. L = 6, CI = 33, RI = 0.
  - 0 not swollen; 1 swollen: distal part is thicker; 2 spindle-like, distal part is almost globous.
- **30. Femur IV, serial armature prolateral and retrolateral**
  - State 0 is synapomorphic for *Heterocranaus* sp+, changing to 2 in *Stygnicranaus* and two further autapomorphies. L = 4, CI = 75, RI = 80.
  - 0 unarmed; 1 with rows of large spines; 2 with rows of small spines; 3 with rows of well marked tubercles.
- **31. Spur of femur IV**
  - State 0 changes to 2 in *C. bilunatus*+ and back to 0 in *A. innocens*+. 3 is autapomorphic for *Yania* sp. L = 4, CI = 75, RI = 66.
  - 0 absent; 1 prolateral dorsoapical; 2 subdistal ventroprolateral; 3 retrolateral dorsoapical.
- **32. Number of distal helicoidal setae of penis ventral plate**
  - Transition from 3 to 4–5 is synapomorphic for Cranaidae *sensu stricto* (*Yania* sp+), acquisition of higher numbers is autapomorphic for two terminals. L = 4, CI = 100, RI = 100.
  - 0 three; 1 four; 2 five; 3 eight; 4 eleven.
- **33. Medial dorsal beak of apex of stylus, presence**
  - The presence is independently acquired in *Heterocranaus* sp. and *A. innocens*. L = 2, CI = 50, RI = 0.
  - 0 absent; 1 present.
- **34. Lateral paired beaks of apex of stylus, presence, shape**
  - The presence can be understood as a synapomorphy for *Troya* sp+, with a reversal in *T. pectinitibialis*. The pointed condition is autapomorphic for *A. innocens*. L = 3, CI = 66, RI = 75.
  - 0 absent; 1 present, short, rounded; 2 present, long, pointed.
- **35. Lateral paired beaks subdistal to stylus, presence**

- Uninformative. Presence is autapomorphic to *T. pectinitibialis*.

○ 0 absent; 1 present.

- **36. Spiniform apophysis in mid-length of stylus, presence**
  - Presence is independently acquired in *Prostygnus vestitus* and *C. bilunatus*. L = 2, CI = 50, RI = 0.

○ 0 absent; 1 present.

- **37. Plane of ventral plate relative to truncus penis, angle**
  - A synapomorphy for *Yania* sp+. L = 1, CI = 100, RI = 100.

○ 0 same; 1 oblique.

- **38. Dorsal process of glans penis, presence**
  - Character 2 of Kury (1992b: 98) and 8 of Kury (1994b: 345), used in connection with other Gonyleptoidea.
  - Here it is a synapomorphy for *Yania* sp+. L = 1, CI = 100, RI = 100.

○ 0 present; 1 absent.

- **39. Frontal surface of carapace, armature**
  - A synapomorphy for *Yania* sp+. A independent reversal occurs in *Phalangodus anacosmetus* and states 2 and 3 are autapomorphic for *T. elegans* and *S. alessandroi*, respectively. L = 4, CI = 75, RI = 50.

○ 0 unarmed; 1 with two to three teeth; 2 with three immense spines; 3 with two immense spines.

- **40. Cluster of pearly tubercles at the side of the carapace**
  - A synapomorphy for *S. alessandroi* + *S. poncedeleoni* with an independent acquirement in *T. pectinitibialis*. L = 2, CI = 50, RI = 50.

○ 0 absent; 1 present.

- **41. Pearly tubercles in the hyaline portion of the cheliceral socket**
  - A synapomorphy for *S. alessandroi* + *S. poncedeleoni*. L = 1, CI = 100, RI = 100.

○ 0 absent; 1 present.

- **42. Femur IV of male, shape and armature**
  - Appendage form and armature has long been used for taxonomic purposes in opilionids.
  - This character optimizes ambiguously between *Heterocranaus* sp. and *Troya* sp. L = 2, CI = 50, RI = 66.

○ 0 short, sinuous and armed with rows of spines; 1 long, substraight, only with scattered spurs.

- **43. Apical apophysis of male coxa IV, shape**
  - The blunt triangle seems to have been independently acquired in *P. vestitus* and *Heterocranaus* sp. L = 2, CI = 50, RI = 0.

○ 0 blunt triangle; 1 sharp curved spine.

- **44. Position of emergency of coxa IV posterior border**
  - State 1 is a synapomorphy for *Yania* sp+, state 3 being a synapomorphy of *Stygnicranaus* homoplastic in *S. gigantea.* State 3 is an autapomorphy of *T. pectinitibialis*, and an independent reversal to state 0 occurs in *Troya* sp. L = 5, CI = 60, RI = 66.

○ 0 at area II; 1 at areas III/IV; 2 at areas IV/V; 3 at free tergite I–II.

- **45. Ventral armature of pedipalpal femur**
  - A decreasing transformation series of 2-4-0 (with an autapomorphy of *P. anacosmetus*) can be seen. L = 5, CI = 80, RI = 75.

○ 0 unarmed; 1 pectinate with six subequal spines all along the femur; 2 three stout basal spines and none in the distal half; 3 one basal immense spine; 4 with one row of coarse granules.

- **46. Shape of femur I**
  - A synapomorphy of *T. pectinitibialis*+. L = 1, CI = 100, RI = 100.

○ 0 thick, sinuous; 1 straight, thin.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Summary of colour centroids (from the NBS/IBCC Color System) used in this paper.
Appendix S2. List of external published illustrations available for character understanding.
Appendix S3. List of synapomorphies for nodes of cladogram obtained under $k = 3$. (Node numbers refer to Fig. S1).
Figure S1. Cladogram with the phylogenetic hypothesis for the Stygnicranainae showing the numbered nodes. This is the same tree as in Fig. 1.

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