

## A new genus of Zalmoxoidea from Colombia (Arachnida: Opiliones: Grassatores)

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**Abstract.** A new genus and species of Neotropical Grassatores, *Hevelia crucis* gen. et sp. nov., is described and illustrated based on material of both sexes from Colombia. After comparison with the greater groups in Zalmoxoidea, especially the putative early derivative families Guasiniidae and Icaleptidae, this new taxon is considered a Zalmoxoidea *incertae sedis*, and seems to be related with *Trypophobica* Cruz-López et al., 2021 (currently in Icaleptidae, but which should be removed from this family) and *Costabrimma* Goodnight & Goodnight, 1983 (currently in Zalmoxoidea *incertae sedis*), both from Central America. Two species currently included in the zalmoxid genus *Stygnoleptes* Banks, 1913 from El Salvador are transferred to *Trypophobica*, creating the new combinations *T. gibbera* (Roewer, 1954) and *T. sellata* (Roewer, 1954). Two morphological structures for Zalmoxoidea are named here: *mons cribellatus* (sexually dimorphic porous prosomal and/or abdominal dorsal hillock) and elbow-spade (lanceolate blade apical in the truncus penis).

**Keywords:** Harvestmen, Laniatores, Neotropics, Central America, rutrum, mons cribellatus.

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<http://zoobank.org/References/230264FE-4943-4600-A6FB-B8B7AE81FB0F>

The Zalmoxoidea is a Pantropical superfamily of Grassatores composed of six families, which is well represented in the Neotropics, with 279 species (Kury et al. 2021). Representatives of Zalmoxoidea are typically inhabitants of soil and leaf litter (Kury & Pérez-González 2002), also dwelling on trees and other forms of tall vegetation.

The families of Zalmoxoidea (Escadabiidae Kury & Pérez-González, 2003, Fissiphalliidae Martens, 1988, Guasiniidae González-Sponga, 1997, Icaleptidae Kury & Pérez-González, 2002, Kimulidae Pérez-González, Kury & Alonso-Zarazaga, 2007, Zalmoxidae Sørensen, 1886) have been defined on the basis of morphological characters, although the current arrangement will most likely change as new taxa and *incertae sedis* names are examined in detail. Later, they were included in molecular analyses with terminals such as “*Icaleptes* sp.”, mostly without verification as to their real identity on morphological grounds (Pérez-González, pers. comm., see below). This led to incorrect conclusions on the composition and position of families such as Icaleptidae, which are of relevance here.

In a recent revision of material from the Tropical Dry Forest of the Caribbean Region of Colombia, we found an interesting new genus and species that we consider belongs to Zalmoxoidea and that are described below. The hypothetical phylogenetic affinities of the new genus are discussed, and we consider this new genus to be arguably closest to *Costabrimma* Goodnight & Goodnight, 1983 from Costa Rica and *Trypophobica* Cruz-López, Monjaraz-Ruedas, Colmenares & Francke, 2021 from Mexico, Guatemala and El Salvador.

### SYSTEMATIC BACKGROUND ON SELECTED ZALMOXOIDS

**Formation and placement of Zalmoxidae/Zalmoxoidea.**—The family Zalmoxidae was created by Sørensen (1886: 63)

based on material from Fiji. This family fell into the synonymy of Epedanidae (Thorell 1889: 674). Roewer (1912: 126) included *Zalmoxis* Sørensen, 1886 as a genus of his Phalangodinae in the immense family Phalangodidae. For eight decades, *Zalmoxis* and related genera remained buried in Phalangodinae while other unlucky arrangements were made regarding the small Grassatores and legions of would-be Zalmoxidae were described under Phalangodinae. Staręga (1989) resurrected Zalmoxidae to include five Palearctic genera (this inclusion was much expanded later by Sharma et al. 2011) and later Kury & Cokendolpher (2000) and Kury (2003) transferred many Neotropical “phalangodids” into Zalmoxidae. An unpublished thesis by Kury (1993) recognized a large superfamily Zalmoxoidea, including Biantidae, Minuidae, Podoctidae, Samoidae, Stygnommatidae and Zalmoxidae, but this name only appeared in press much later (Kury & Cokendolpher 2000: 142). Giribet & Kury (2007) divided this into Zalmoxoidea (Icaleptidae, Guasiniidae, Zalmoxidae + Fissiphalliidae) and Samooidea (Samoidae + Podoctidae + Biantidae + Minuidae + Stygnommatidae). Giribet et al. (2010) included in Zalmoxoidea the same Fissiphalliidae, Guasiniidae, Icaleptidae, and Zalmoxidae, with a paraphyletic Samooidea as the sister group. Sharma & Giribet (2011) augmented Zalmoxoidea, transferring Escadabiidae and Kimulidae into it, resulting in six included families. A similar genital morphology structure shared by all Zalmoxoidea was first demonstrated by Kury & Pérez-González (2002).

**Background on placement of Icaleptidae.**—Kury & Pérez-González (2002) proposed this family based on material from NW South America (Colombia and Ecuador) for species with the plane of leg IV shifted in males (which was later discovered to occur elsewhere as well), but, most importantly, some genital features such as the short stragulum, with both halves fused proximally. The authors originally deemed Icaleptidae to be most closely related to Zalmoxidae and Fissiphalliidae.

Icaleptidae was later (Giribet & Kury 2007) assigned to Zalmoxoidea and this placement stayed. Giribet et al. (2010) used an undescribed Icaleptidae MCZ DNA101420 in their phylogeny, and this voucher was examined by Pérez-González, who confirmed its inclusion in the family on morphological grounds. This Icaleptidae resolved as a member of Zalmoxidae, along with a "*Costabrimma* sp." MCZ DNA101428 (from Costa Rica) Giribet et al. (2010, fig. 8). Sharma & Giribet (2011) used again sequences from the voucher MCZ DNA101420 (and in appendix 1 provided provenance data, indicating this specimen was from Nariño, Colombia) and added two more vouchers: "*Icaleptes* sp." MCZ DNA104053 and MCZ DNA104056-1, also from Colombia. All those Icaleptidae resolved as a clade, sister-group of Fissiphallidae + Zalmoxidae Sharma & Giribet (2011, fig. 18). Sharma & Giribet (2012) added two more vouchers named "*Icaleptes* sp." from Guatemala: MCZ DNA104842 and MCZ DNA104845. These five are the only Icaleptidae ever used in molecular analyses so far. Sharma & Giribet (2012, fig. 2) in a paper on the introduction of Zalmoxidae in the Paleotropics, recovered Icaleptidae as comprising all those "*Icaleptes* sp." vouchers + two *Costabrimma*, MCZ DNA105834 and MCZ DNA106164 (both from the same coordinates in Panama, and which resolved as identical).

Kury et al. (2015: 4) warned about the use of potentially "false" members of Icaleptidae: "the accurate familial identification of specimens in those later studies needs to be confirmed using genital characters together with other morphological features".

Pérez-González et al. (2017), in a paper about Kimulidae using the previously published "*Icaleptes* sp." and "*Costabrimma* sp." sequences of Giribet and collaborators, incidentally obtained a polyphyletic Icaleptidae in the Bayesian analysis: (a) the Colombian vouchers grouped as the sister-group of Fissiphallidae + Zalmoxidae, and (b) the Guatemalan vouchers grouped with the Panamanian *Costabrimma*. Based on that, we conclude that "a" are true icaleptids, because they contain the only voucher that was verified, while the "b" were misidentified as *Icaleptes* in the first place. This could be explained by the deficient phylogenetic signal generated by H3 marker in matrices with few genes, which has been demonstrated in other groups of Arthropoda.

Cruz-López et al. (2021) studied *Ethobunus pilosus* (Goodnight & Goodnight, 1953) from Mexico, which they assigned to the new genus *Trypophobica* in Icaleptidae. They added a new sequence of *Trypophobica pilosa*, which was nested in the false icaleptids, concluding that *Trypophobica* should be a member of Icaleptidae, regardless of the total lack of morphological support for this conclusion: "we are aware that the inclusion of *Trypophobica* into Icaleptidae based on our results could contribute to weaken the current morphologically based diagnosis of the family." They included *Trypophobica* in Icaleptidae, but inconsistently left *Costabrimma* as *incertae sedis* (probably owing to the lack of molecular samples). Figures 1 to 3 of Cruz-López et al. (2021) show all Icaleptidae, true and false, grouped in a clade along with *Trypophobica* and *Costabrimma*.

**Background on *Chersobleptes*/*Costabrimma*/*Stygnoleptes*.**—Roewer (1954) created in the Phalangodidae Phalangodinae the two new species *Chersobleptes gibber* Roewer, 1954 and

*Chersobleptes sellatus* Roewer, 1954 from El Salvador in the genus *Chersobleptes* Sørensen in Henriksen, 1932. *Chersobleptes* is nomenclaturally unavailable because it lacks an original type species designation; the subsequent designation of *Chersobleptes crassus* Sørensen, 1932 by Kury (2003) is invalid (ICZN Code Art. 16.1) (Kury & Alonso-Zarazaga 2011: 62). Goodnight & Goodnight (1983: 234) synonymized *Chersobleptes* with *Stygnoleptes* Banks, 1913 also in Phalangodidae Phalangodinae and described the new genus *Costabrimma* Goodnight & Goodnight, 1983, with three new species from Costa Rica. However, 11 years earlier, *Stygnoleptes* was designated as the type of the new subfamily Stygnoleptinae in Gonyleptidae (!) by H. Soares (1972: 68). As the Goodnights did not make any comments about the familial allocation of *Stygnoleptes*, it is quite possible that they simply had overlooked Soares work. Kury (1997: 2) dismantled the Stygnoleptinae and transferred *Stygnoleptes* to Zalmoxidae. Now, both Salvadorian species of Roewer are currently in Zalmoxidae: *Stygnoleptes* (Kury 2003: 251) and the three species described by the Goodnights in *Costabrimma* are in Zalmoxoidea *incertae sedis*. *Costabrimma* appeared as Zalmoxoidea *incertae sedis* in Giribet et al. (2010), while Sharma & Giribet (2012) did not formally include *Costabrimma* in any family, although in the supporting material, the *Costabrimma* vouchers are listed as Icaleptidae. Kury et al. (2015) commented that *Costabrimma* was occasionally considered a member of Icaleptidae but questioned this assignment. Finally, Cruz-López et al. (2021) also left *Costabrimma* as Zalmoxoidea *incertae sedis*.

**Background on Guasiniidae.**—González-Sponga (1997: 53) proposed the new family "Guasiniidae" (with incorrect original stem, corrected later to Guasiniidae by Kury & Pinto-da-Rocha (2002: 354)) for two Venezuelan species, one from Isla Guasina at sea level, another from a tepuy, 1350 m high. He compared it chiefly with Oncopodidae, without proposing any serious phylogenetic discussion. Pinto-da-Rocha & Kury (2003) added a third species from Brazilian Amazonia, and related Guasiniidae with the Zalmoxidae, Fissiphallidae and Icaleptidae, a clade established shortly before (Kury & Pérez-González 2002). Kury (2003: 206) suggested it could be a Zalmoxoidea. Giribet & Kury (2007) formalized its inclusion in Zalmoxoidea.

## METHODS

The types of the new species were photographed with a Leica M205C stereoscope attached to a Leica DFC450 digital camera. All photos were subsequently edited in Photoshop CC 2014 software. Drawings were made with Inkscape v.0.92. and CorelDRAW v.20.0. 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-isc>) as described in Kury & Orrico (2006). All measurements are in mm, unless otherwise noted. Geographic coordinates have been transcribed verbatim from the labels. The distribution map was made using ESRI ArcGIS 10.4.

The possibly glandular prosomal structure described by Cruz-López et al. (2021) as a porous elevation either on carapace or on mesotergal area I (or in both) of males is here called *mons cribellatus* (sift-hillock, abbreviated as MC).

Likewise, the lanceolate unarmed apical plate superficially resembling a rutrum, which articulates with the truncus at a straight angle, is herein called **elbow-spade** (abbreviated as El-Sp).

The morphological terminology follows Kury & Medrano (2016) for dorsal scutum shape and Macías-Ordóñez et al. (2010) for male genitalia morphology. Additional abbreviations used: AL = abdominal scutum length, AW = abdominal scutum width, CL = carapace length, CW = carapace width, DS = dorsal scutum, DSL = dorsal scutum length, Tr = trochanter, Fe = femur, Pa = patella, Ti = tibia, Mt = metatarsus, Ta = tarsus.

Abbreviations of the repositories cited are: CBUDC = Colección de Ejemplares Biológicos de la Universidad de Cartagena, Cartagena de Indias, Colombia; ICN = Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia; MNRJ = Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; MUSE-NUV = Museo de Entomología de la Universidad del Valle, Cali, Colombia. Other institutional abbreviation: Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias (INIFAP), Campo Experimental Valles Centrales, Oaxaca, México.

## TAXONOMY

The *mons cribellatus* (glandular prosomal hump) of *Hevelia* gen. nov. could potentially (in spite of being located in different regions of the body) be homologous with similar features in other Zalmoxoidea, as for example in *Costabrimma*, which possesses modified glandular surfaces on the legs, *Minuides* Sørensen, 1932, in the ocularium or on legs (Pérez-González, pers. comm.), and even Pacific Zalmoxidae which show presumably convergent leg glands.

It is tempting to try to relate taxonomically all species with a *mons cribellatus*: (1) *Hevelia* gen. nov., (2) the Salvadorian “*Stygnoleptes*” and (3) *Trypophobica*, also including *Costabrimma* because of the very similar penial morphology. There is no solid evidence so far to ascribe all of them to a taxon without studying many other prospective relatives, especially when there are potential available family-group names for them (Pérez-González, pers. comm.). A proper *mons cribellatus* occurs clearly in the males of all taxa considered, except in *Costabrimma*. The male genitalia of the Salvadorian “*Stygnoleptes*” are unknown; those of *Costabrimma* have a very schematic illustration. It appears that the elbow-spade occurs only in *Hevelia* gen. nov.; both *Costabrimma* (Goodnight & Goodnight 1983, fig. 4) and *T. pilosa* (Cruz-López et al. 2021) have instead a setigerous plate with macrosetae and no articulation, homologous to the rutrum and/or the elbow-spade. It is not known if this was a lapse by the Goodnights, who provided an ultra-simplified drawing (Goodnight & Goodnight 1983, figs. 1–2).

As explained above, *Trypophobica* does not share any special similarities with the Icaleptidae, while the original assignment to this family was due to grouping with probably misidentified “icaleptids”. Likewise, the Salvadorian “*Stygnoleptes*” do not share any special similarities with the typical *Stygnoleptes* and the best course of action right now is to transfer those two species to *Trypophobica*.

## Superfamily Zalmoxoidea Sørensen, 1886

### Genus *Hevelia* gen. nov.

<http://zoobank.org/NomenclaturalActs/E5510ABB-63FE-432D-81C2-2E228608D979>

**Type species.**—*Hevelia crucis* sp. nov.

**Etymology.**—The genus name is in honor our friend and fellow arachnologist Abel Pérez-González (MACN) who is the most outstanding specialist in the world in the difficult superfamilies Samooidea and Zalmoxoidea. Hevel is the biblical Hebrew form of Abel. The gender is feminine.

**Diagnosis.**—Ocularium with a short forward projected conical eminence between the eyes; sternite II with a large triangular process pointing forward in males; sternite III with a pair of conical paramedian medium-sized tubercles. *Mons cribellatus* as a narrow forward-facing projection of scutal area I (as in *T. pilosa*, which, however, has MC widely expanded laterally, and contrasting with *T. llama*, which has MC either on carapace or taking all of carapace + area I). All macrosetae concentrated on the truncus surface, while an articulated apical blade (elbow-spade) remains unarmed, which differentiated *Hevelia* gen. nov. from all other taxa.

### *Hevelia crucis*, sp. nov.

<http://zoobank.org/NomenclaturalActs/6956794F-46FB-4831-B02E-2B3DCF09DD72>

(Figs. 1–4)

**Type material.**—*Holotype male*. COLOMBIA: *Bolívar*: San Jacinto, Corregimiento San Cristóbal, Cerro Capiro, (9.893700°N, 75.241803°W), 260 m, 4–7 December 2019, J.P. Botero, H. Vides, A.F. García, D. Ahumada-C. (ICN-Ao-1977).

*Paratypes*. COLOMBIA: *Bolívar*: 3 ♂, 6 ♀ (MNRJ 701), collected with holotype; 2 ♂, 3 ♀, same locality as holotype, 8–12.xi.2019, M. Cabarcas, D. Ahumada-C. (MNRJ 702); 3 ♂, 3 ♀, same data as previous (CBUDC-ARA 333); 5 ♂, 5 ♀, same data as previous (MNRJ 700); 2 ♂, 3 ♀, same data as previous (MUSENUV-Ar 2101).

**Etymology.**—The species name honors our friend and fellow arachnologist Jesús Cruz-López (INIFAP) who is presently exploring false Neotropical Phalangodidae/Zalmoxidae and has already described the porous hillock in association with Centro-American species. *Crucis* is the genitive of the Latin noun *crux* (cross), which is a literal translation of the Spanish name *Cruz*.

**Diagnosis.**—As for the genus.

**Description.**—Male holotype (ICN-Ao-1977). Measurements (in mm). DSL: 1.11, CL: 0.44, CW: 0.58, AL: 0.66, AW: 0.83; Pedipalp: Tr: 0.036, Fe: 0.075, Pa: 0.035, Ti: 0.046, Ta: 0.040, Claw: 0.022; Leg I: Tr: 0.11, Fe: 0.37, Pa: 0.13, Ti: 0.20, Mt: 0.23, Ta: 0.24; Leg II: Tr: 0.09, Fe: 0.35, Pa: 0.14, Ti: 0.19, Mt: 0.22, Ta: 0.25. Leg III: Tr: 0.10, Fe: 0.32, Pa: 0.13, Ti: 0.26, Mt: 0.31, Ta: 0.27. Leg IV: Tr: 0.14, Fe: 0.70, Pa: 0.39, Ti: 0.53, Mt: 0.73, Ta: 0.36.

*Dorsum*: DS type eta, widest at the level of area III. Anterior margin of carapace with two antero-lateral tubercles each side, cheliceral sockets shallow (Figs. 1A, 2A). Ocularium smooth, with a forward projected conical eminence between the eyes (Figs. 1A, C, D, 2A, B). Mesotergum unarmed, granulated, with four undivided areas; area I trapezoidal, longer than remaining areas, with an anterior coarsely granular rounded

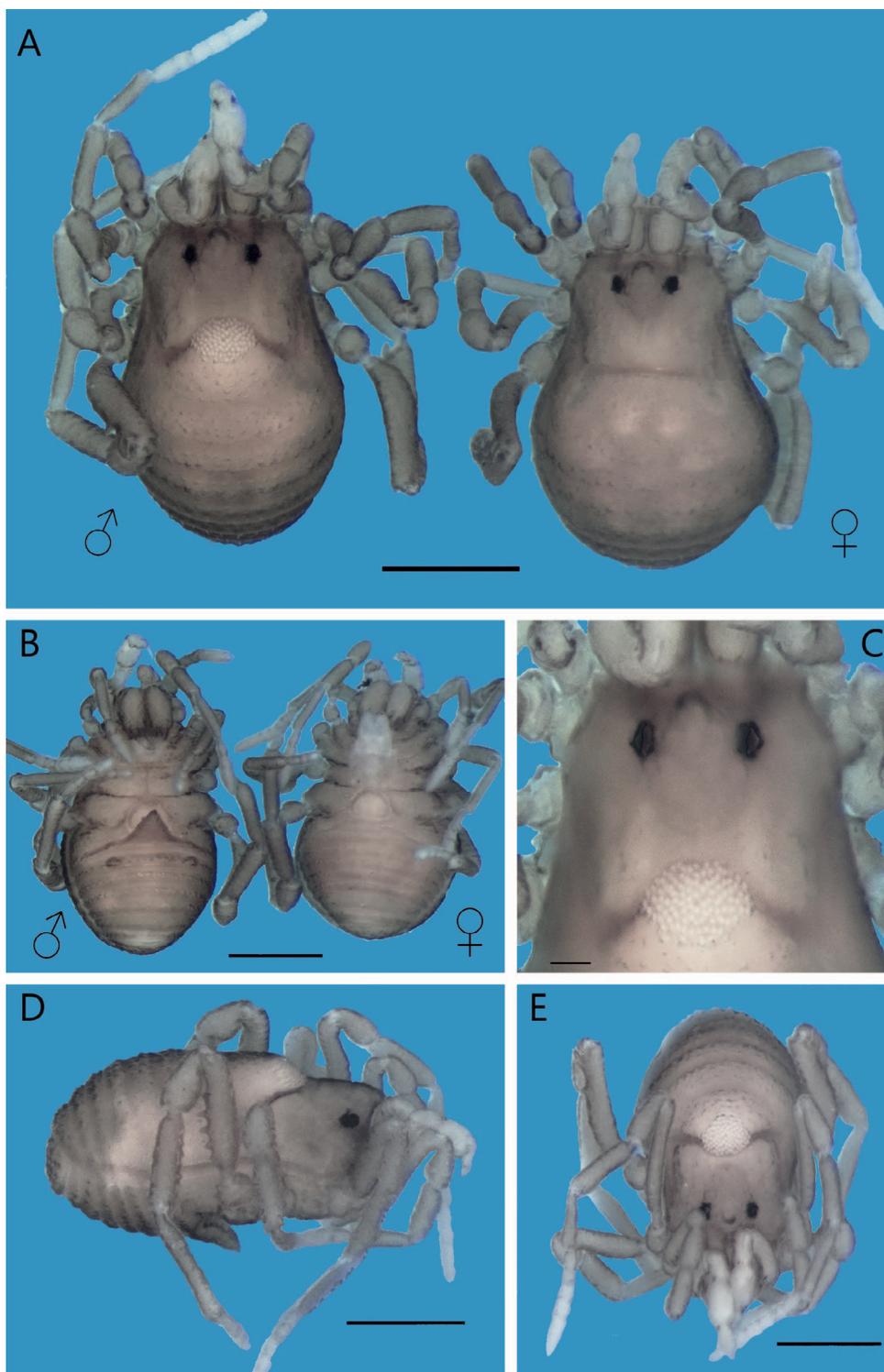


Figure 1.—*Hevelia crucis* sp. nov. A. Male holotype (ICN-Ao-1977) and female paratype (MNRJ 701), dorsal view; B. Same, ventral view; C–E. Male holotype: C. Detail of ocularium and *mons cribellatus* (MC); D. Lateral view; E. Frontal view. Scale bars: 0.5 mm (A, B, D, E); 0.2 mm (C).

protuberance (Figs. 1A, C, E, 2A, B); areas II and III slightly larger at medial region. Lateral margins with some granules. Posterior margin of DS convex and granular. Free tergites each with a transverse row of granules (Figs. 1A, D, E).

*Venter*: Coxae I–IV granular. Coxae I and II remarkably more procurved than coxae III–IV; coxa I narrower at proximal region than the other coxae, with two parallel transversal rows of tubercles; coxa III short (almost half of

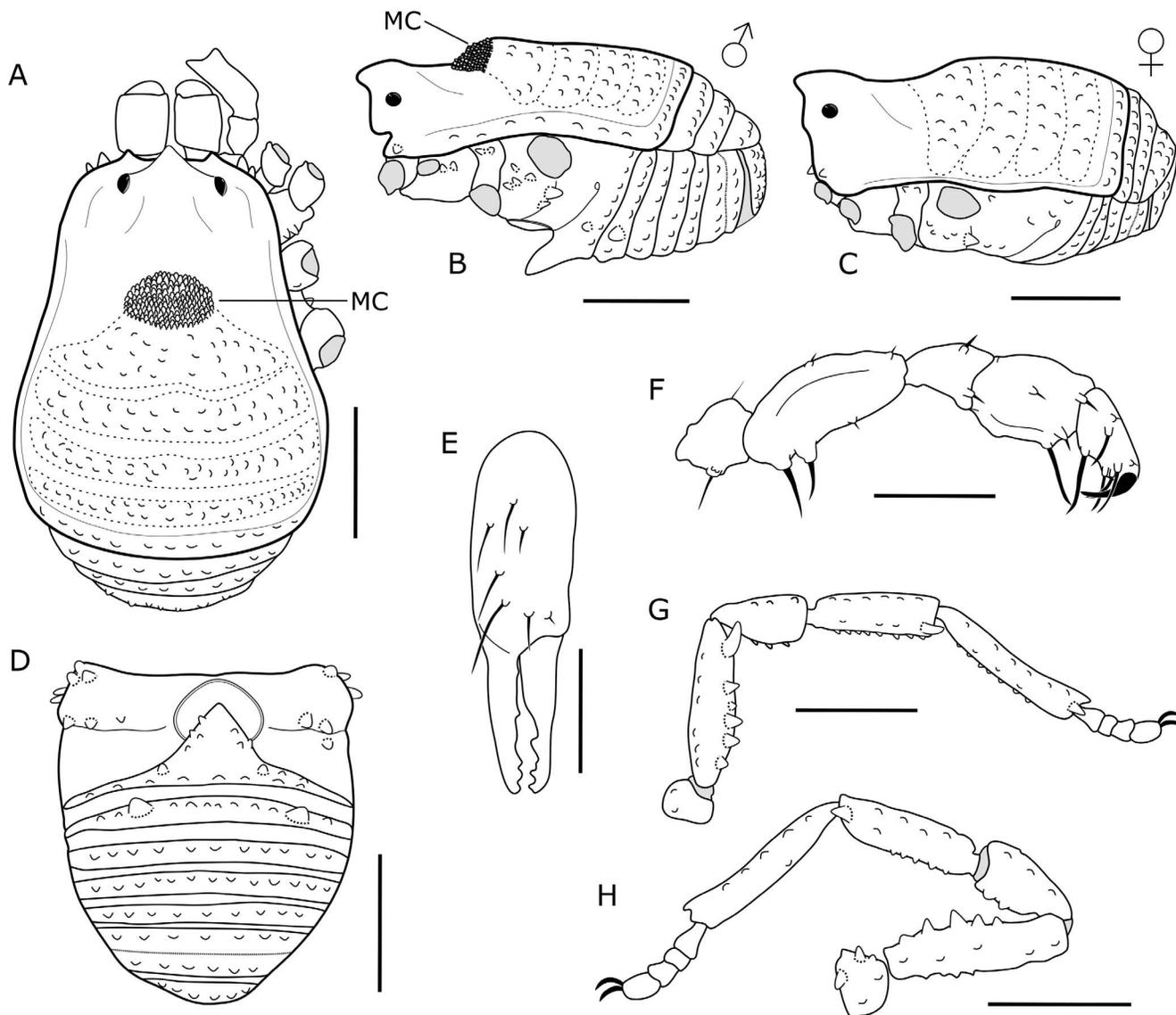


Figure 2.—*Hevelia crucis* sp. nov., schematic. A. Male holotype (ICN-Ao-1977), dorsal view; B. Same, lateral view; C. Female paratype (MNRJ 701), lateral view; D–H. Male holotype: D. Detail of ventral region, showing the genital operculum and the conical projection; E. Chelicera, frontal view; F. Pedipalp, mesal view; G. Leg IV, prolateral view; H. Same, retrolateral view. Abbreviation: MC (*mons cribellatus*). Scale bars: 0.5 mm (A–D, G, H); 50  $\mu$ m (E, F).

coxa II width) and straight (Fig. 1B), with one anteroapical and two posteroapical spines; coxa IV markedly larger than the others, with an incomplete medial transverse suture and some tubercles in anterodistal region (Figs. 1B, 2D). Stigmata extremely reduced or entirely concealed under a fold in the stigmatic area. Free sternites granulate; sternite III with a very large conical process pointing forward (Fig. 2B); sternite IV with a pair of conical paramedian medium-sized tubercles. Anal operculum rounded and granular (Figs. 1B, D, 2B, D).

**Chelicera** (Figs. 2A, E): Basichelicerite unarmed. Cheliceral hand unarmed, not swollen, with several setiferous tubercles on mesal region. Movable and fixed finger each with four rounded teeth.

**Pedipalp** (Fig. 2F): Coxa short and unarmed. Trochanter with one ventroectal setiferous tubercle. Femur dorsally with two small setiferous tubercles, ventrally with two large basal

setiferous tubercles and one small setiferous tubercle at median portion. Patella cylindrical, with two small ectodistal setiferous tubercles. Tibia ventrally with three ectal setiferous tubercles. Tarsus ventrally with three ectal and two mesal setiferous tubercles.

**Legs:** Legs I–IV with some granules; Ti I–IV apically with one retrolateral dorsal and one prolateral dorsal tubercle. Fe I with one ventral row of tubercles reaching the medial region; Pa I with one ventroapical tubercle. Tr IV with two retrolateral tubercles (Fig. 2H); Fe IV half the size of DS length, with one prolateral and retrolateral row of tubercles (the distalmost tubercle of the prolateral row is larger than the others and projected backwards) (Figs. 2G, H); Pa IV with 2 median tubercles in the retrolatero-ventral face (Fig. 2H). Ti IV with one prolateral and retrolateral large tubercle projected backwards at distal portion, and a retrolateral row of five

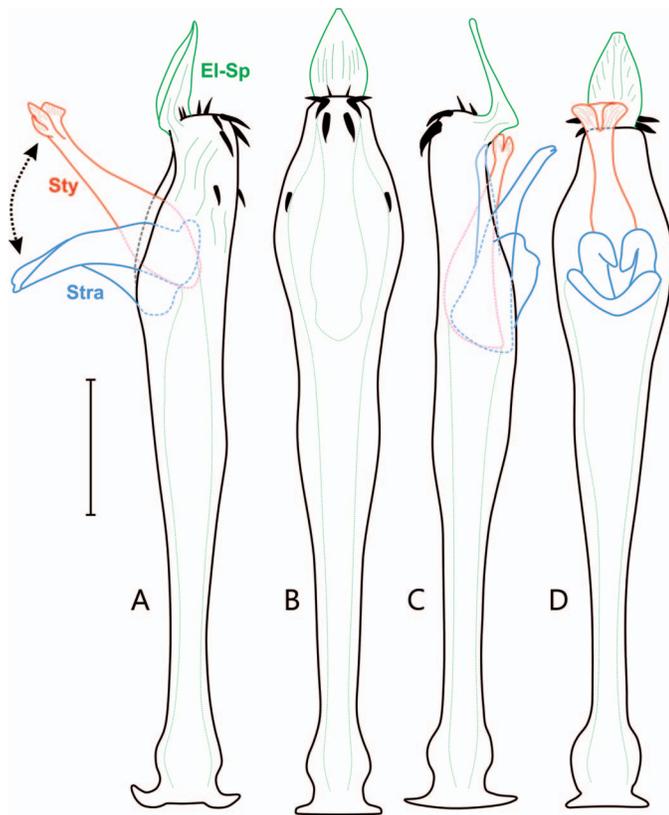


Figure 3.—*Hevelia crucis* sp. nov. (MNRJ 701) paratype, penis: A. Dextralateral view (expanded). B. Ventral view. C. Sinistrolateral view; D. Dorsal view. Abbreviations: El-Sp = elbow-spade; Sty = stylus; Stra = stragulum. Scale bar: 100  $\mu$ m.

small tubercles (Figs. 2G, H). Mt IV with one prolateral large tubercle at distal portion (Fig. 2G). Tarsal formula: 4(2)/5(2)/3/4.

**Male genitalia** (Figs. 3A–D): Truncus cylindrical, elongate, alternating between distinctly thinner/thicker regions. Distal part of truncus expanded laterally (as seen in dorsal/ventral views); apex truncated. There are 3 pairs of proximal macrosetae and 2 pairs of much smaller apical ones. There is a foliar blade (elbow-spade, El-Sp) apically on the truncus which is articulated by means of an elbow-joint. Stragulum as a pair of very long, apically curved, independent rods. Stylus thick at proximal half, apically cleft into two flattened lobes.

**Color** (in alcohol, Fig. 1): DS Dark Yellow (88), Mons cribellatus Moderate Yellow (87), chelicera, pedipalps and legs Grayish Yellow (90).

**Female**. Paratype (MNRJ 701), measurements: DSL: 1.08, CL: 0.42, CW: 0.57, AL: 0.66, AW: 0.89; Pedipalp: Tr: 0.032, Fe: 0.072, Pa: 0.029, Ti: 0.040, Ta: 0.037, Claw: 0.020; Leg I: Tr: 0.05, Fe: 0.35, Pa: 0.17, Ti: 0.21, Mt: 0.22, Ta: 0.24; Leg II: Tr: 0.09, Fe: 0.41, Pa: 0.17, Ti: 0.30, Mt: 0.24, Ta: 0.36. Leg III: Tr: 0.09, Fe: 0.34, Pa: 0.14, Ti: 0.26, Mt: 0.26, Ta: 0.22. Leg IV: Tr: 0.09, Fe: 0.41, Pa: 0.18, Ti: 0.32, Mt: 0.41, Ta: 0.30. Tarsal formula: 3(2)/5(3)/4/5. Similar to male, except for: DS wider at level of areas II–III; lack of anterior rounded granular protuberance on mesotergal area I; leg IV slender and less armed; absence of triangular large process on abdominal sternite III (Figs. 1B, 2C).

**Distribution**.—This species is known only from the type locality (Fig. 4).

*Costabrimma* Goodnight & Goodnight, 1983

*Costabrimma* Goodnight & Goodnight 1983: 203.

**Type species**.—*Costabrimma cruzensis* Goodnight & Goodnight, 1983, by original designation.

**Etymology**.—From the toponym Costa Rica + pre-existing genus *Brimma*. Gender feminine.

**Remarks**.—*Costabrimma* is a heterogeneous assemblage, which is currently being studied (Pio Colmenares, pers. comm.). It was originally described in Phalangodinae but was removed to Grassatores *incertae sedis* by Kury (2003).

*Costabrimma cruzensis* Goodnight & Goodnight, 1983

*Costabrimma cruzensis* Goodnight & Goodnight 1983: 203, figs. 1–7.

**Type material**.—*Holotype male*. COSTA RICA: Puntarenas: Las Cruces, near San Vito (AMNH).

*Paratypes*. COSTA RICA: Puntarenas: ♂♂, ♀♀, collected with holotype (AMNH).

**Records**. COSTA RICA, Limón, Siquirres (1 ♀, original description, non-type).

*Costabrimma nicoyensis* Goodnight & Goodnight, 1983

*Costabrimma nicoyensis* Goodnight & Goodnight 1983: 205, figs. 8–15.

**Type material**.—*Holotype male*. COSTA RICA: Puntarenas: Nicoya Peninsula: Jabilla (AMNH).

*Paratypes*. COSTA RICA: Puntarenas: ♂♂, ♀♀, collected with holotype (AMNH).

**Records**.—COSTA RICA, Guanacaste, Santa Rosa National Park. Puntarenas, Nicoya Peninsula: Reserve near Cabuya; Tambor; Manuel Antonio National Park (♂♂, ♀♀, original description, non-types).

*Costabrimma terrena* Goodnight & Goodnight, 1983

*Costabrimma terrena* Goodnight & Goodnight 1983: 206, figs. 16–21.

**Type material**.—*Holotype male*. COSTA RICA: Heredia: La Selva (AMNH).

*Paratypes*. COSTA RICA: Heredia: 3 ♀, collected with holotype (AMNH)

**Records**. COSTA RICA, Puntarenas, Coto; Osa Peninsula: Llorona Ridge Trail (Goodnight & Goodnight 1983).

*Trypophobica* Cruz-López, Monjaraz-Ruedas, Colmenares & Francke, 2021  
(Fig. 4)

*Trypophobica* Cruz-López, Monjaraz-Ruedas, Colmenares & Francke 2021: 499.

**Type species**.—*Ethobunus pilosus* Goodnight & Goodnight, 1953, by original designation.

**Included species**.—*Trypophobica pilosa* (Goodnight & Goodnight, 1953), *Trypophobica llama* Cruz-López, Monjar-

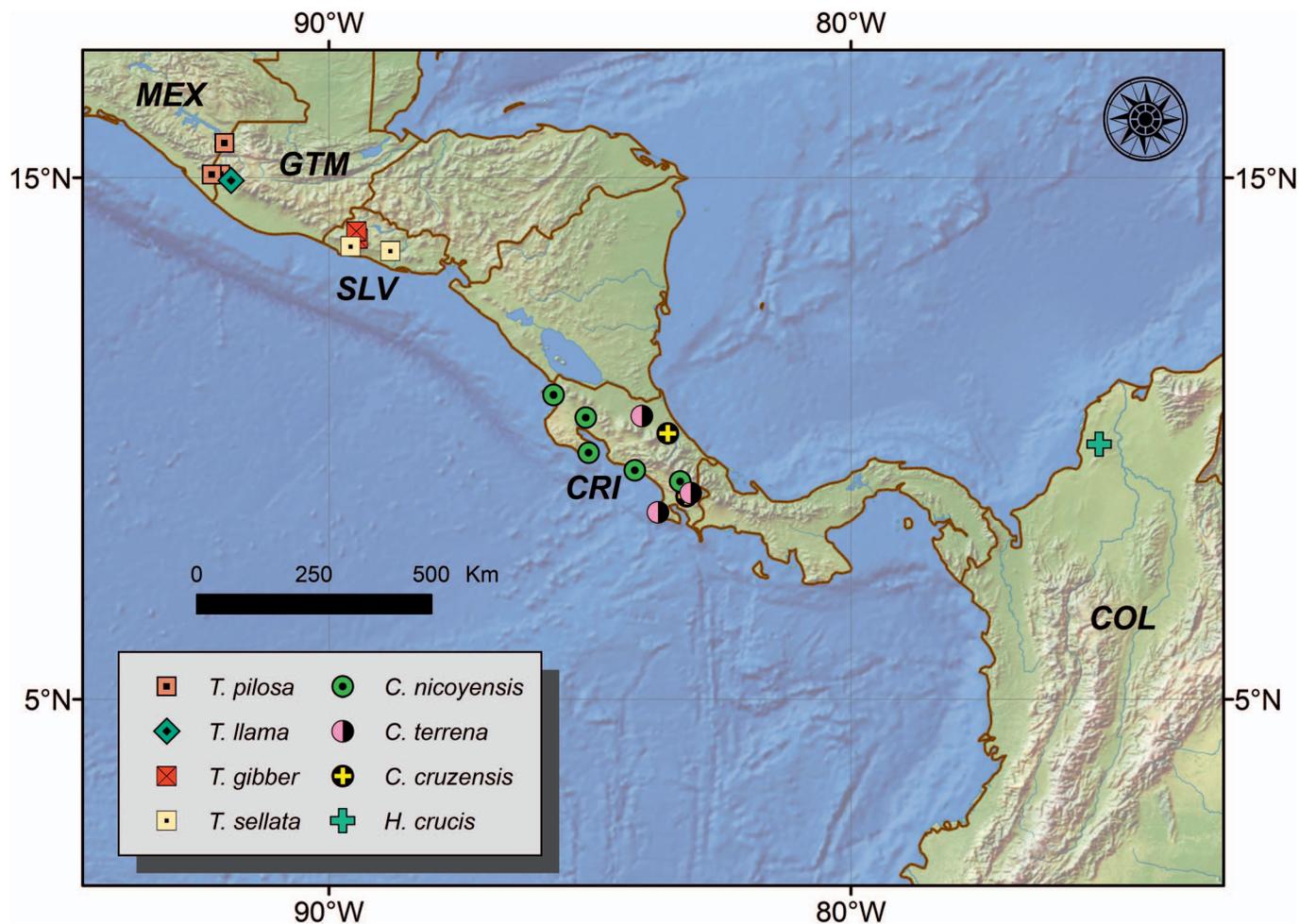


Figure 4.—Central Neotropics, showing the distribution of *Trypophobica*, *Costabrimma*, and *Hevelia* gen. nov. Abbreviations of the countries are: COL = Colombia, CRI = Costa Rica, GTM = Guatemala, SLV = El Salvador and MEX = Mexico.

az-Ruedas, Colmenares & Francke, 2021, *Trypophobica gibbera* (Roewer, 1954), comb. nov. and *Trypophobica sellata* (Roewer, 1954), comb. nov.

**Remarks.**—*Trypophobica* was originally included in the family Icaleptidae, although herewith we reject this allocation, leaving this genus as *Zalmoxoidea incertae sedis*. This was a group that possibly fell into Icaleptidae by artifacts, and would be less controversial and problematic if it is removed from that family. It was a very tricky decision from Cruz-López and collaborators.

***Trypophobica gibbera*** (Roewer, 1954), comb. nov.

*Chersobleptes gibber* Roewer 1954: 64, pl. 9, fig. 2.

*Stygnoleptes gibber* (Roewer): Goodnight & Goodnight 1983: 234.

**Type material.**—*Holotype male*. EL SALVADOR: *La Libertad*: Canton La Joya, S Ciudad Arce, 400 m (SMF 8037).

*Paratypes*. EL SALVADOR: *Santa Ana*: 1 ♂, 1 ♀, San Jacinto, km 9.5 road Santa Ana-Metapán, 550–600 m (SMF 8036).

***Trypophobica sellata*** (Roewer, 1954), comb. nov.

*Chersobleptes sellatus* Roewer 1954: 65, pl. 9, fig. 3.

*Stygnoleptes sellatus* (Roewer): Goodnight & Goodnight 1983: 234.

**Type material.**—*Holotype male*. EL SALVADOR: *San Vicente*: E slope of San Vicente volcano, Finca El Carmen, 1300 m (SMF 8039).

*Paratypes*. EL SALVADOR: *San Vicente*: 1 ♂, 7 ♀, collected with holotype (SMF 8040); *Santa Ana*: 1 ♀, Finca San Jorge, near Santa Ana, 1000 m (SMF 8038).

## DISCUSSION

**Comparison of *Hevelia* with other *Zalmoxoidea*.**—The Samooidea have an eversible *capsula interna* with a pair of conductors which may be fused to the stylus (Pérez-González 2006). In contrast, all *Zalmoxoidea* have a non-eversible *capsula interna* and a *capsula externa* clearly visible, well developed and modified into a *stragulum*, that, when expanded, opens as a jackknife, which is a synapomorphy for the superfamily (e.g., Kury & Pérez-González 2002). *Hevelia* gen. nov. possesses the same structures, which allows us to place it confidently in the *Zalmoxoidea*.

Both Fissiphalliidae and *Zalmoxidae* have a *pergula* and a *rutrum* (Kury & Pérez-González 2007) and the two halves of

the *stragulum* are basically fused to a great extent, leaving only the apical portion cleft. The *stragulum* in Zalmoxidae is mostly short (as in *Gjellerupia* Roewer, 1913, *Minuides*, *Zalmoxis*). The Fissiphalliidae possess severe allometry, with both stragulum and rutrum extremely elongate, and all the rest of penis compressed as a short proximal stub (e.g., Martens 1988; Tourinho & Pérez-González 2006). *Phalangodella* was left in Zalmoxoidea *incertae sedis* by Kury & Pérez-González (2015). It probably forms an early branch of a clade which would also include Zalmoxidae and Fissiphalliidae: it has a rudimentary proto-pergula (projected distal ring) and proto-rutrum (thick mushroom-shaped apical process), and furthermore the long stragulum retains the primitive condition of being divided into left and right halves (Kury & Pérez-González, 2015).

The Icaleptidae possess a zalmoxid-like stragulum, fused half-way, and the macrosetae of truncus in two clear-cut shape-size classes, in the same way as Guasiniidae (Kury & Pérez-González 2002) and *Hevelia* gen. nov. A significant difference between the false icaleptids (*Hevelia* and *Trypophobica*) is that *Trypophobica* possess a foliar stragulum that almost surrounds the pars distalis. The Guasiniidae possess a long stragulum, with both prongs entirely independent (Pinto-da-Rocha & Kury 2003) similar to the condition in *Hevelia* gen. nov., although nothing else points to the inclusion of *Hevelia* gen. nov. in this family. The most striking difference between Guasiniidae and *Hevelia* gen. nov. seems to be the apical part of truncus penis, which in the former forms a funnel-shaped calyx and in the latter a very thin elbow-jointed lanceolate plate.

It is uncertain if the elbow-spade is homologous with the rutrum of Zalmoxidae, although both structures, plus the calyx in Guasiniidae, and specially the truncus apex in *Phalangodella*, could share the same developmental origin. There are two main distinctions: (1) the rutrum bears macrosetae, while the macrosetae in *Hevelia* gen. nov. are in the truncus; (2) the rutrum is a direct continuation of the truncus in Zalmoxidae, while in *Hevelia* gen. nov. the elbow-spade is connected to it by a complex articulation. In view of the structural variability of the rutrum and the stragulum in zalmoxids, one cannot discard *Hevelia* gen. nov., as a member of the *Phalangodella*-Fissiphalliidae-Zalmoxidae clade. That said, and even accounting for the wild variation of morphology of rutrum and stragulum in Zalmoxidae, the best decision at the moment is not to include *Hevelia* in the Zalmoxidae, leaving the genus as Zalmoxoidea *incertae sedis*.

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