

Original Article

Reassessment of the Saicini phylogeny and evolution of hairy attachment structures on tarsi (Heteroptera: Reduviidae: Emesinae)

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ABSTRACT

Saicini comprise 24 genera and 147 species worldwide. Here, we include additional taxa and characters to the morphological dataset of [Castro-Huertas and Melo \(2023\)](#) into a new one composed of 181 characters, which was analysed cladistically with 63 terminals, comprising 18 genera (75% of the generic diversity), 49 species of Saicini, and 12 outgroups. Saicini was recovered as monophyletic, with *Carayonia orientalis* (Visayanocorini) as its sister-species. Our hypotheses recovered two main clades within Saicini that we recognized as two new subtribes: Saicina subtrib. nov. and Tagalina subtrib. nov.; and the new tribe, Saiciretini trib. nov. of uncertain affinities within Emesinae. Additionally, the morphology and evolution of the scopula is explored. The scopula is a hairy attachment structure on the third tarsomere composed of a set of spatulate setae present on all legs of Saicini and on the meso- and metalegs of a few species of the tribes Emesini and Leistarchini (Emesinae). Scopula presence on all legs had been recovered as synapomorphy of the tribe Saicini. The reconstruction of the ancestral state of the hairy setae shows an emergence of this structure on the ventral region of the third tarsal segment of the protarsus in Saicini and its ancestor without scopula. The arrangement of the scopula is consistent with the recovered clades.

Keywords: phylogeny; morphological characters; scopula; Neotropical region; Afrotropical region; comparative morphology

INTRODUCTION

The largest family of terrestrial predators of Heteroptera are the assassin bugs, the Reduviidae ([Gil-Santana et al. 2015](#)), which have evolved diverse and complex morphological and behavioural adaptations for prey capture ([Forero et al. 2011](#), [Weirauch et al. 2021](#)). Besides locomotion, the legs of reduviids play a key role in hunting performance, and several morphological adaptations on the legs are commonly associated with predatory behaviour, such as raptorial legs (e.g. some Emesinae), prolegs modified into a robust subchela (e.g. Phymatinae), and the presence of various hairy attachment structures ([Weirauch 2007](#), [Zhang et al. 2016](#), [Castro-Huertas et al. 2019](#)). Within Reduviidae, three types of hairy attachment structures are known on the legs: the fossula spongiosa, a modified structure on the apical region of the tibiae, present in several subfamilies of Reduviidae and other Cimicomorpha ([Schuh et al. 2009](#)); an analogous structure to the fossula only present in some immature forms and composed of barbed setae; and the scopula, composed of tenent setae on

the tarsus, which is present only in some tribes within Emesinae ([Weirauch 2005, 2007](#)). The fossula spongiosa is associated with a number of functions, including those related to locomotion, mating behaviour, and prey-capture performance ([Weirauch 2007](#)). Despite [Weirauch and Forero \(2007\)](#) suggesting that the scopula may serve to hold on to smooth plant surfaces, the biological function of the scopula is still unclear.

Within Emesinae, the scopula is formed by a modified set of setae on the third tarsomere of all legs of Saicini (except in *Saicireta* [Melo and Coscarón, 2005](#)), and restricted to the meso- and metalegs of some species of the tribes Emesini (*Ademula peregrina* [Wygodzinsky, 1966](#), *Myiophanes kerzhneri* [Wygodzinsky, 1966](#), *Tridemula* [Horváth, 1914](#), *Pelmatomesa sarophora* [Wygodzinsky, 1966](#), and probably some species of *Empicoris* [Wolff, 1811](#)), and Leistarchini (seven species of *Ploiaria Scopoli, 1786*) ([Wygodzinsky 1966](#), [Weirauch 2007, 2008](#)). The dissimilar presence/absence of the scopula among the tarsi between the tribes raises questions about its biological

function within each group, but the scarce information on their natural history hampers any solid elucidation. Moreover, the homology of ‘scopula’ in Saicini and the other tribes is questionable (Weirauch 2007), and this structure has not been evaluated in a phylogenetic framework.

A recent study with molecular and morphological evidence changed Saicini status from subfamily to tribe within Emesinae, and transferred *Oncerothelus* Stål, 1868 to conform Oncerothelini (Standring *et al.* 2023). Furthermore, a morphological phylogenetic hypothesis emphasizing Saicini taxa suggested that *Saicireta*, the only genus lacking a scopula, cannot be classified as a Saicini (Castro-Huertas and Melo 2023). Saicini currently comprise 24 genera and 147 species worldwide (Castro-Huertas and Melo 2024). Morphologically, it is characterized by the presence of a scopula on the preapical region of all tarsi, the second visible segment of the labium swollen and wider than the other segments, the labium ventrally and the gular region usually with spiniform processes, the anterior region of the anterior pronotal lobe with processes, the apical region of the metanotum with a protruding process, the mcu-an1 crossvein on the forewing in the proximal–distal orientation, and M and CU not fused along the proximal portion of the wing, and the first tarsomere of the protarsus longer than the second (Castro-Huertas and Melo 2023, 2024, Standring *et al.* 2023). *Saicireta*, does not fully align with the set of synapomorphies.

With the aim of elucidating the phylogenetic relationships of the genus *Saicireta* and the evolution of the scopula in Saicini, we modified the morphological matrix proposed by Castro-Huertas and Melo (2023), by improving the taxa representation and adding and re-interpreting characters. We compared scopula ultrastructure using scanning electron microscopy of 12 genera and 37 species of Saicini. We described its morphological features and analysed them using cladistic methods. Characters from Standring *et al.* (2023) were reinterpreted and recoded, and novel characters from the position of the scopula were analysed. The monophyly of the subfamily and its internal generic relationships were tested.

Following the results of the analyses, we propose a redefinition of the newly circumscribed tribe Saicini and we discuss the actual classification of the tribe, including a reconstruction of the scopula trait changes within the group. Two new subtribes are recognized and we give a taxonomic synopsis and key for all the genera of Saicini, including new diagnostic characters. Finally, we also define the position of the genus *Saicireta* within the Emesinae.

MATERIALS AND METHODS

Taxon sampling

To the morphological matrix of Castro-Huertas and Melo (2023), we incorporate three additional genera and eight species of Saicini: *Pristicoris armatus* (Villiers, 1950a), *Tagalis matamorosae* Castro-Huertas and Melo, 2024; *Tagalis pagu* Castro-Huertas and Melo, 2024; *Tolyxopus muizoni* (Villiers, 1950b), *Villiersella agalma* Elkins, 1956, *Villiersella inermis* (Villiers, 1950a), *Villiersella longispinis* Villiers, 1966, and *Villiersella testacea* Villiers, 1967, accounting a total of 18 genera (75% of known genera) and 47 species of Saicini, and 16 taxa as outgroup representing all tribes within Emesinae and one species of Ectrichodiinae to root the resulting trees.

Specimens studied are deposited in the following institutions, abbreviations mostly follow the suggestions of Evenhuis (2017): (JMB) Jean Michel Bérenger, personal collection, France; (MLP) Universidad Nacional de La Plata, Museo de la Plata, La Plata, Argentina; (MNHN) Muséum National d’Histoire Naturelle, Paris, France; (MPUJ) Colección Entomológica, Museo Javeriano de Historia Natural, Pontificia Universidad Javeriana, Bogotá, Colombia; (MUSENUV) Museo de Entomología de la Universidad del Valle, Cali, Colombia; (NMPC) National Museum (Natural History), Prague, Czech Republic; (QCAZ) Pontificia Universidad Católica de Ecuador, Quito, Ecuador; (STRI) Smithsonian Tropical Research Institute, Panama; (TUA) Laboratory of Entomology, Faculty of Agriculture, Tokyo University of Agriculture, Tokyo, Japan; (UNAB) Museo Entomológico Facultad de Agronomía, Universidad Nacional de Colombia, Bogotá, Colombia; and (USNM) National Museum of Natural History, Washington D.C., USA. When citing the examined material, a backslash indicates a separate label. Examined material from the ‘outgroup’ and its host entomological collections is listed in Castro-Huertas and Melo (2023).

Morphological examination, dissections, imaging, and terminology

Using scanning electron microscopy (SEM), we analysed 37 species from 12 genera of Saicini, based on the available material. For cleaning structures for SEM we modified the protocol used by Castro-Huertas *et al.* (2019): male and female left pro- and mesolegs were removed (when available) and cleaned manually with forceps, the structures were kept submerged in soft degrease solution with warm water for 72 h (or more), and rinsed in distilled water. Structures were dehydrated in an ascending series of ethanol in concentrations of 25%, 50%, 70%, and absolute ethanol and dried at room temperature for 24 h before sputter-coated with a palladium–gold alloy (60/40). The hairy attachment ultrastructure was studied using Zeiss Gemini SEM 360 at the Laboratorio de Microscopia Electrónica de Barrido of the Museo Argentino de Ciencias Naturales Bernardino Rivadavia (MACN, Buenos Aires, Argentina). For image editing we used Adobe Photoshop CS6 v.13.1.2. The terminology of leg structures corresponds to Cobben (1978), Weirauch (2005), and Castro-Huertas *et al.* (2019). Genital dissection methods and terminology follow Castro-Huertas and Melo (2023).

Cladistic analyses

A matrix of 181 characters (155 binary, 26 non-additive multistate, 18 not informative, see Supporting Information, Files S1, S2), was constructed from the database of Castro-Huertas and Melo (2023), incorporating five main changes: (i) two male genital characters were included considering the variation found in the additional taxon sampling: the structure of the sternite 8 (S8) surface (#109) and the structure of the dorsolateral angle of the paramere socket in the pygophore (#118); (ii) eight characters from the forewing were reinterpreted and recoded from the phylogenetic hypothesis by Standring *et al.* (2023), characters 13 to 21 from their matrix (here characters #86–93); (iii) two characters from the tenent setae of the scopula arrangement were included (#54 and 56); (iv) characters related to labial segments swelling (#65 and #66) were recodified considering as ‘swollen’ only as conspicuous dorsolateral expansion; and (v)

the length of the setae on the antennae was eliminated from the character matrix (character 2 in [Castro-Huertas and Melo 2023](#)) because the examination of additional material shows that it is a sexually dimorphic character in several genera.

All characters were coded using MESQUITE v.3.81 ([Maddison and Maddison 2023](#)). For the description of characters and its states we follow ([Serenio 2007](#)), although some characters were written as phrases to make the statements clearer. All trees were rooted with *Brontostoma discus* ([Burmeister, 1835](#)) (Ectrichodiinae). Uninformative characters were retained in the matrix because they helped to expand and revise the generic diagnosis. Inapplicable characters (87) were treated following [Goloboff et al. \(2021\)](#) (in some cases, the codification in the root was changed to follow this protocol, because 'absent' must be coded as '0') (see [Supporting Information, File S2](#)).

The data matrix was analysed with implied weighting (IW) using a concave function that weights characters against homoplasy ([Goloboff 1993](#)). The *k*-values used for our analyses were chosen considering the suggestion of [Goloboff \(2022\)](#) for morphological data matrixes, *k*-values ranging 8–12. The number of resultant trees using *k*-values 8 to 10 was 15, and 13 using a *k*-value of 11, all maintaining the main clades but with differences in the position of species within *Villiersella* [Schouteden, 1950](#) and *Tagalis* [Stål, 1860](#). We chose as best result the trees obtained with *k*-value = 12, because the quantity of trees recovered was 3, and it penalizes less strongly for the homoplasy found ([Goloboff et al. 2008](#)). The analyses were conducted in TNT v.1.6 ([Goloboff and Morales 2023](#)) using parsimony as optimality criterion. A heuristic search was carried out holding a maximum of 10 001 trees in memory, with 1000 random addition replications, and 10 trees held per replication. The search strategy considered tree bisection and reconnection (TBR). The search strategy is available as a script ([Supporting Information, File S3](#)). Strict consensus of the resultant trees was calculated and used for synapomorphy mapping and discussion. Tree diagram was generated with Wincladtree script ([Goloboff 2024](#)) and edited in Adobe Photoshop CS6 v.13.1.2. Consistency index (CI) and the retention index (RI) were calculated for each character and the resultant tree. Nodal support was calculated as GC values ([Goloboff et al. 2003](#)) using symmetric resampling with 1000 replicates and expressed as a percentage of the difference between the frequencies of the clades present and those that are contradicted ([Goloboff et al. 2003](#)). Apomorphies were mapped on the tree using the Wincladtree script.

Evolution of the scopula and ancestral state reconstruction

To examine the transformations of the scopula on the tree topology, only two characters were additionally coded for terminal taxa. The first was the structure of the ventral surface of the third tarsal segment of the protarsus, in which flat/with simple setae surface or the presence of scopula condition were coded. The second character was the arrangement of the tenent setae of the scopula, in which covering the entire surface, or denser on apical one-third surface, conditions were coded. For the ancestral state reconstruction, the tree topology of the strict consensus of the three resulting trees of the IW analyses was used. These two characters were coded and optimized with a maximum likelihood approach using the Mk1 model (default), and then mapped in MESQUITE v.3.81.

Taxonomic treatment

Based on the results of the phylogenetic analysis, we recognized two new subtribes and elaborated a taxonomic synopsis for all the genera of Saicini, indicating for each genus the type species and providing a revised diagnosis, including new diagnostic characters. Diagnoses based on the literature are provided for: *Exaeretosoma* [Elkins, 1962](#); *Kiskeyana* [Weirauch and Forero, 2007](#); *Micropolytoxus* [Elkins, 1962](#); and *Quasitagalis* [Gil-Santana et al., 2020](#), which were also included in our analysis; and *Banarocoris* [Miller, 1958](#); *Choreutocoris* [Miller, 1957](#); *Cuernolestes* [Miller, 1953](#); *Madecassosaica* [Villiers, 1957](#); *Spairapeltis* [Miller, 1950](#); and *Vadonocoris* [Villiers, 1957](#), which were not included in our matrix.

Data availability

The data that support the findings of this study are available in the supplementary material of this article.

RESULTS

Cladistic analyses

The IW analysis resulted in three equally most parsimonious trees with a total fit of 26.58225 (CI = 31, RI = 75) ([Supporting Information, File S4](#)). In the strict consensus tree with a total fit of 26.65918 (CI = 31, RI = 75), we recovered incongruence within *Villiersella* clade ([Figs 1, 2](#)). Our analysis is consistent with [Castro-Huertas and Melo \(2023\)](#), with Saicini recovered as a monophyletic group, excluding *Saicireta correntina* [Melo and Coscarón, 2005](#), and supported by seven unambiguous synapomorphies: scopula present in all tarsi (#53-1, #55-1, #57-1), second visible labial segment expanded (#66-1), anterior lobe of pronotum with processes on the anterior and posterior regions (#67-1, 69-1), and forewing with m-cu-an1 (or cu-an1) crossvein located from anterior to posterior margin (#90-1). *Carayonia orientalis* [Ishikawa and Okajima, 2004](#) (Visayanocorini) was inferred as the sister-group of Saicini ([Fig. 1](#)), supported by five unambiguous synapomorphies: stout simple setae on the ventral margin of the maxillary plate (#5-1), the ventral region of second visible labial segment (#24-1), the ventral surface of prothorax (#43-1), the anterolateral dorsal surface of the profemur (#46-1), and on the dorsolateral surface of the protibia (#50-1).

Within Saicini, two main clades were recovered, consistent with the hypotheses of [Castro-Huertas and Melo \(2023\)](#) and [Stranding et al. \(2023\)](#): the 'hairy species' clade' or species without spiniform processes on the prolegs, supported by one unambiguous synapomorphy: ventral surface of the procoxa with stout simple setae (#40-1) ([Fig. 1](#)); and the 'spiny species' clade' or species with several spiniform processes, which it is supported by three unambiguous synapomorphies: spiniform setae present on the ventral margin of the postocular region (#9-1), on the anterodorsal margin of the prosternum (#32-0), and on the anterolateral dorsal surface of the profemur (#45-0).

Micropolytoxus hackeri [Elkins, 1962](#) was recovered as the sister-species of the clade comprising: *Pseudosaica* [Blinn, 1990](#); *Polytoxus* [Spinola, 1850](#); *Tolyxopus* [Villiers, 1969](#); and *Saica* within the 'hairy species' clade'. The aforementioned clade is supported by two unambiguous synapomorphies: the ventral

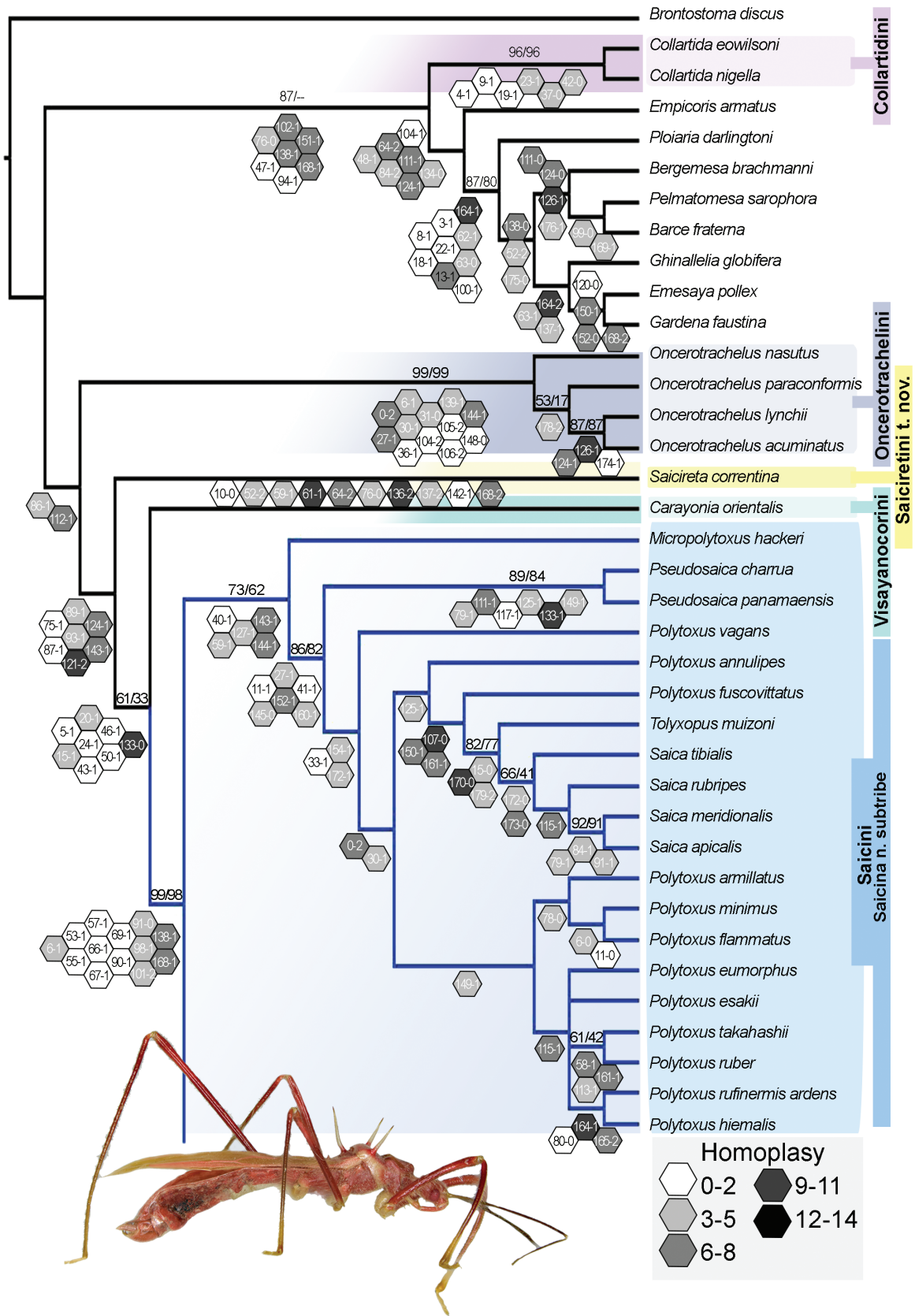


Figure 1. Strict consensus tree recovered with the IW analysis trees under a k -value = 12. First part. Support values in the branches are GC frequencies, only for nodes supported. Homoplasy values corresponding to the difference between the optimized length and the minimum possible length (Goloboff 2024), white means absence or very low homoplasy.

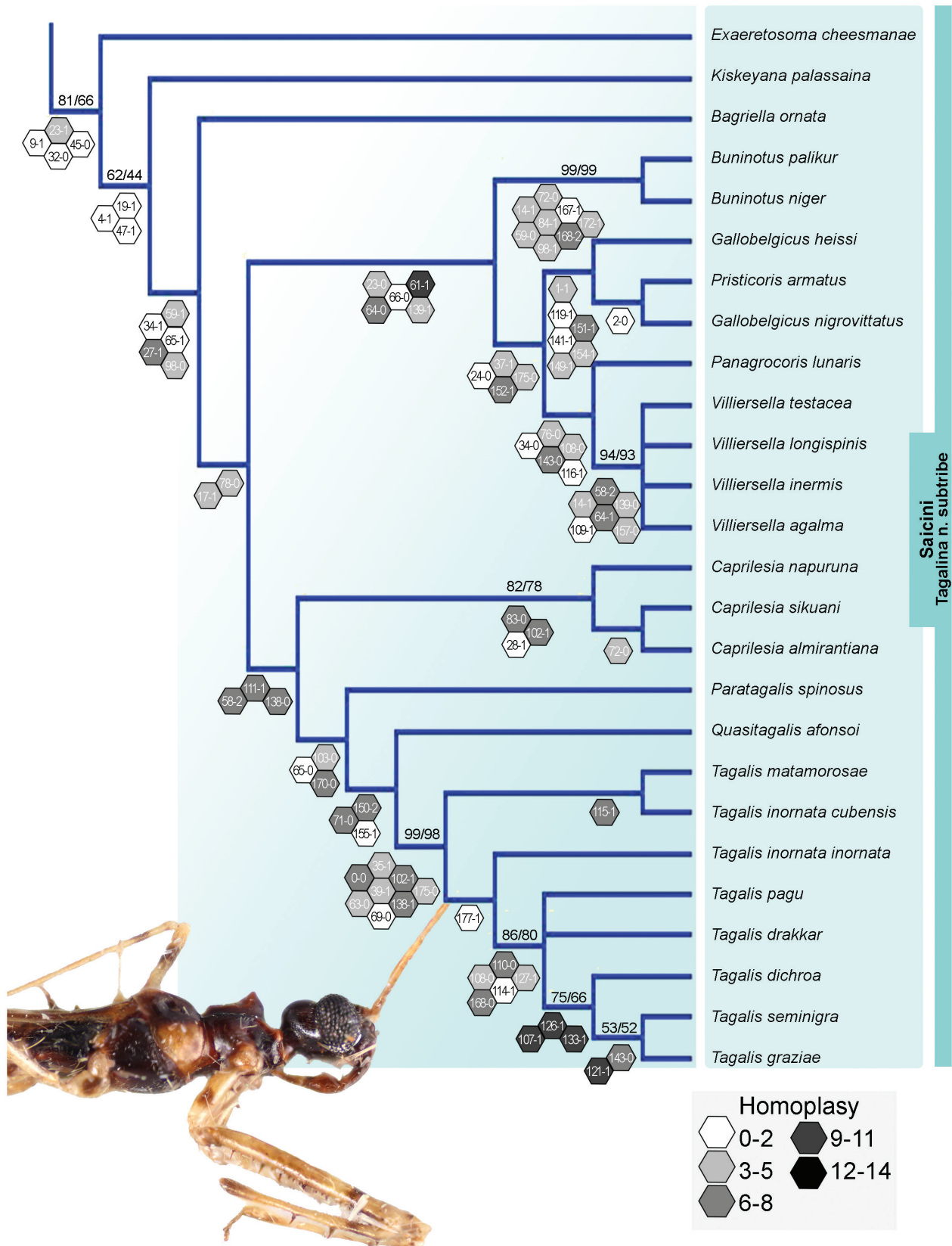


Figure 2. Strict consensus tree recovered with the IW analysis trees under a k -value = 12. Second part. Support values in the branches are GC frequencies, only for nodes supported. Homoplasy values corresponding to the difference between the optimized length and the minimum possible length (Goloboff 2024), white means absence or very low homoplasy.

margin of the postocular region and the ventral surface of the procoxa with simple setae in a tuft (#11-1, 41-1). Two genera were identified as natural groups: *Pseudosaica* is supported by the lateral margins of the paramere socket of the pygophore produced (#117-1), while *Saica* is supported by homoplastic characters.

Exaeretosoma cheesmanae Elkins, 1962 was recovered as sister-species of the genera that constitute the ‘spiny species’ clade’ (Fig. 2). Additionally, two species known only from females and exclusively Neotropical, *Kiskeyana palassaina* and *Bagriella ornata*, were recovered as sister-species of the other genera of the spiny clade. These genera are divided into two main clades: one comprising Asian and African genera, except for *Buninotus* Maldonado Capriles, 1981, and supported by a single unambiguous synapomorphy: the second visible labial segment not expanded (#66-0); the other clade is composed exclusively of Neotropical species and is supported by three homoplastic characters. Four genera were recovered as natural groups: *Caprilesia* Gil-Santana, Marques and Costa, 2006 supported by the third visible labial segment with stout setae ventrally (#28-1); *Buninotus* supported by the subapical posterior region of the tergite 9 with a folding (#167-1); *Tagalis* supported by the posterior region of anterior pronotal lobe flat (#69-0); and *Villiersella* supported by the posteromedial surface of the abdominal sternite 8 with processes (#109-1).

General structure of the scopula in Saicini and its ancestral reconstruction

The third tarsomere is typically rounded and dilated in comparison with the other tarsal segments (Fig. 3B). The scopula is present on the ventral region of the third tarsomere of all legs of Saicini (Figs 3A, B). It is formed by a set of long and spatulate setae distributed over the entire surface (Figs 3C, F), or more densely on the apical third (Fig. 3D, G, H). The ventral surface of the third tarsal segment associated to the scopula is consistently rugose, exhibiting small and rounded protuberances (Fig. 4A, B). In certain genera, such as *Tagalis*, the distal ventral margin is ornamented with conspicuous spiniform processes (Fig. 4A).

Each seta arises from a circular socket (Fig. 4B), and it is always long, exhibiting a smooth to striate longitudinal surface (Fig. 4C, D). Their position can be vertical (Fig. 3G) to curved (Fig. 3E). The apex is spatulate (Figs 3E, 4C–H), dorsally nearly smooth or only basally striate (Fig. 4F–H) and ventrally rugose (Fig. 4C–E). The shape of the apex is variable, with specimens exhibiting an apex contour almost rounded (Fig. 4D), quadrangular (Fig. 4E) or triangular (Fig. 4G), and in a front view almost flat (Fig. 4C) or cup-like shape (Fig. 4D), or a combination of diverse shapes observed in a single specimen not following a pattern. Unfortunately, these shapes were not easy to define in many species and were not possible to codify.

This study did not provide evidence of sexual dimorphism in the scopula. However, slight variations in the shape of the apex of the setae were observed between the pro- and mesotarsus in most species.

Our results show that the last common ancestor of Saicini had the ventral surface of the third tarsal segment of the protarsus flat or with unmodified setae (0.00909676 proportional likelihood) (Fig. 5). The scopula appears in Saicini with two different tenent setae arrangements (0.012841 proportional likelihood): covering

the entire surface in the ‘hairy species’ clade’, and denser on one-third apical surface in the ‘spiny species’ clade’.

Taxonomy

Taxonomic position of Saicireta Melo and Coscarón, 2005

Saicireta was described based on six male and female specimens from Corrientes Province in northern Argentina, for the new species *S. correntina*. The genus was characterized by the ventral region of the head and labium with simple setae (Fig. 6A), the forewing with four closed cells (Fig. 6B), and the metapleura with a tubercle near the coxal cavity (Fig. 6C). Melo and Coscarón (2005) proposed that *Saicireta* could be related to *Pseudosaica*, based on the absence of spiniform processes on the forelegs, and the spined humeral angles, mesonotum and metanotum, and additionally described two remarkable characteristics: the posterior apex of stridulatory sulcus conspicuously acute and projected (Fig. 6D), and the posteromedial process of pygophore nearly triangular with the base elevated (Fig. 6G).

Our results show *Saicireta* as sister-species of the clade comprising the Visayanocorini and Saicini, and that it is markedly distinct from any other Saicini genera, including *Pseudosaica*, with which it is not closely related (Castro-Huertas and Melo 2023, Castro-Huertas and Melo 2024). Our results recover two autapomorphies for *Saicireta correntina*: the ventral margin of the postocular region with thin simple setae (#10-0) (Fig. 6A), and the lateral submedial margin of paramere with a process (#142-1) (Fig. 6F).

In this context, the decision to place *Saicireta* within any current Emesinae tribe became complex. A first strategy we considered was to follow the diagnostic characteristics proposed by Standring *et al.* (2023) for each Emesinae tribe. *Saicireta* shares one character with Leistarchini: the ventral surface of the first and second visible labial segments devoid of setae; and one with Emesini: the ventral surface of protibiae with spiniform setae. However, other diagnostic characteristics, including forewing venation, the cuticular surface of the protrochanter and protibia, and the pretarsal structure of the protarsus, are notably distinct. Consequently, *Saicireta* does not align with any tribe. A second strategy was to use the key to the tribes proposed by Wygodzinsky (1966) as an approach to the old organization of the subfamily. However, this led to contradictory situations related to M-vein insertion and claw structure. Based on the forewing structure only, and the basal spiniferous process of the posteroventral series of the profemur not conspicuously produced, *Saicireta* is barely consistent with Wygodzinsky’s notion of Emesini.

Our phylogenetic hypothesis strongly suggests that this genus may belong to a different tribe, given that it is recovered as a sister-species of the clade composed of the Visayanocorini and Saicini, which have strong evidence as natural groups (Castro-Huertas and Melo 2023, Standring *et al.* 2023). In consequence, we propose a new tribe within Emesinae.

Saiciretini tribe nov.

(Fig. 6A–G)

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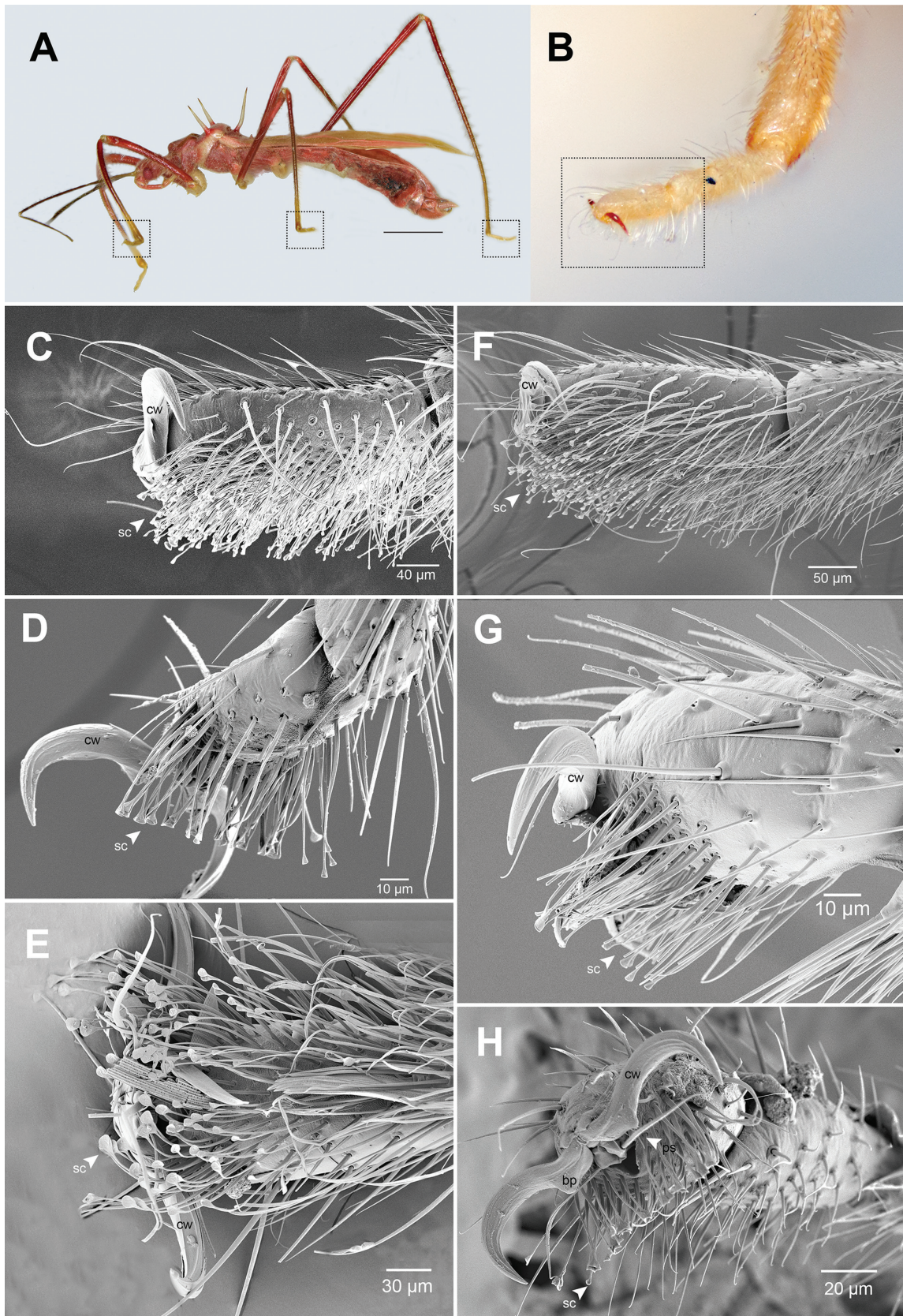


Figure 3. Scopula structure. A, general habitus *Saica tibialis*; B, protarsus, lateral view. C–E, SEM, third tarsomere of protarsus; C, *Polytoxus esaki*, male; D, *Tagalis seminigra*, female; E, *Buninotus niger*, female. F–H, SEM, third tarsomere of mesotarsus; F, *Polytoxus rufinermis ardens*, female; G, *Panagrocis lunaris*, male; H, *Villiersella inermis*, male. Abbreviations: bp, basal protuberance of claw; cl, claw; ps, parempodial setae; sc, scopula. Black dashed square indicating scopula localization.

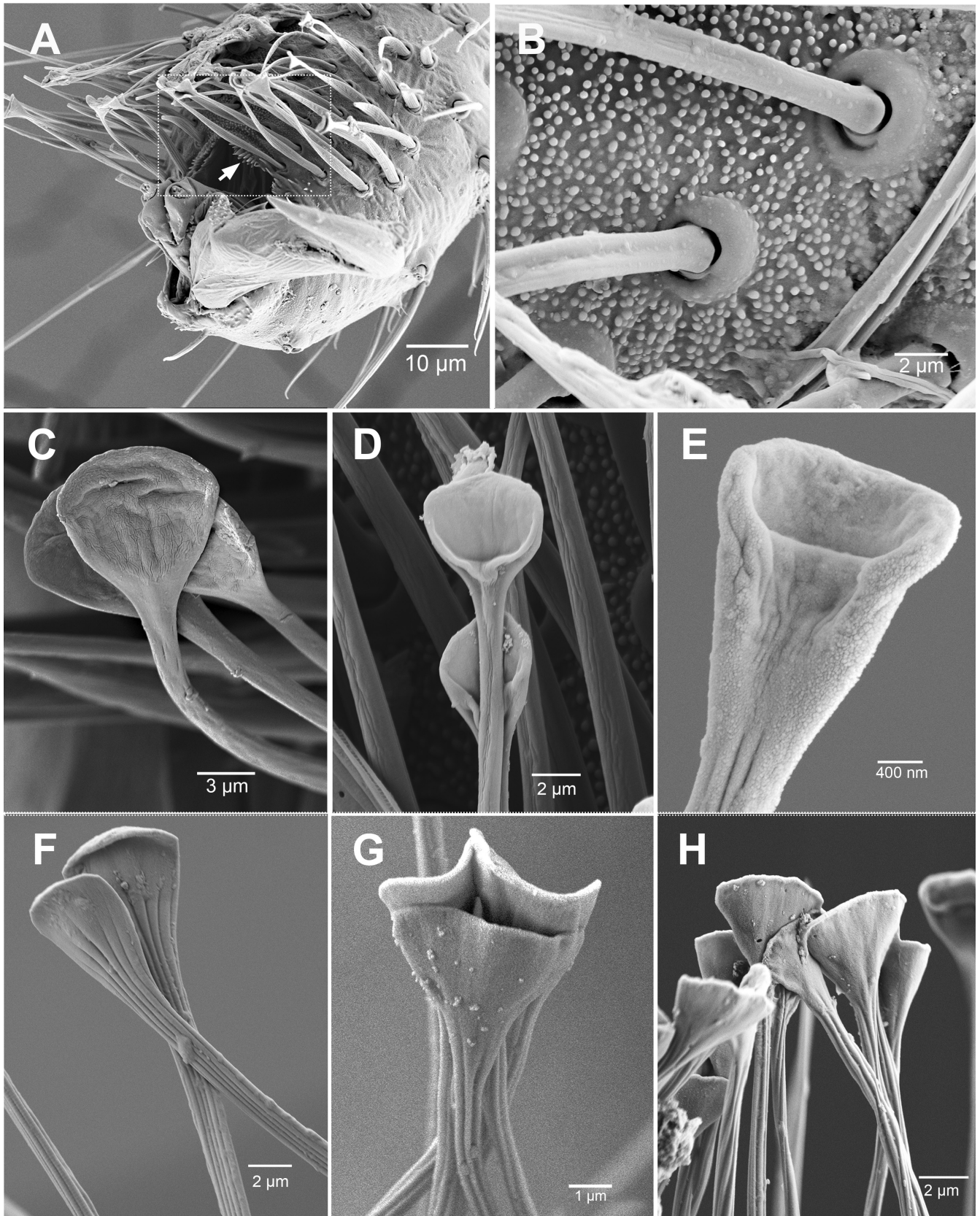


Figure 4. A, B, third tarsomere surface; A, *Tagalis matamorosae*, female; B, *Paratagalis spinosus*. C–H, tenent setae structure; C, *Buninotus niger*, female, ventral; D, *Polytoxus ardens*, male, ventral; E, *Tagalis seminigra*, female, ventral; F, *Polytoxus rufinermis ardens*, male, dorsal; G, *Villiersella inermis*, male, dorsal; H, *Villiersella longispinis*, female, dorsal.

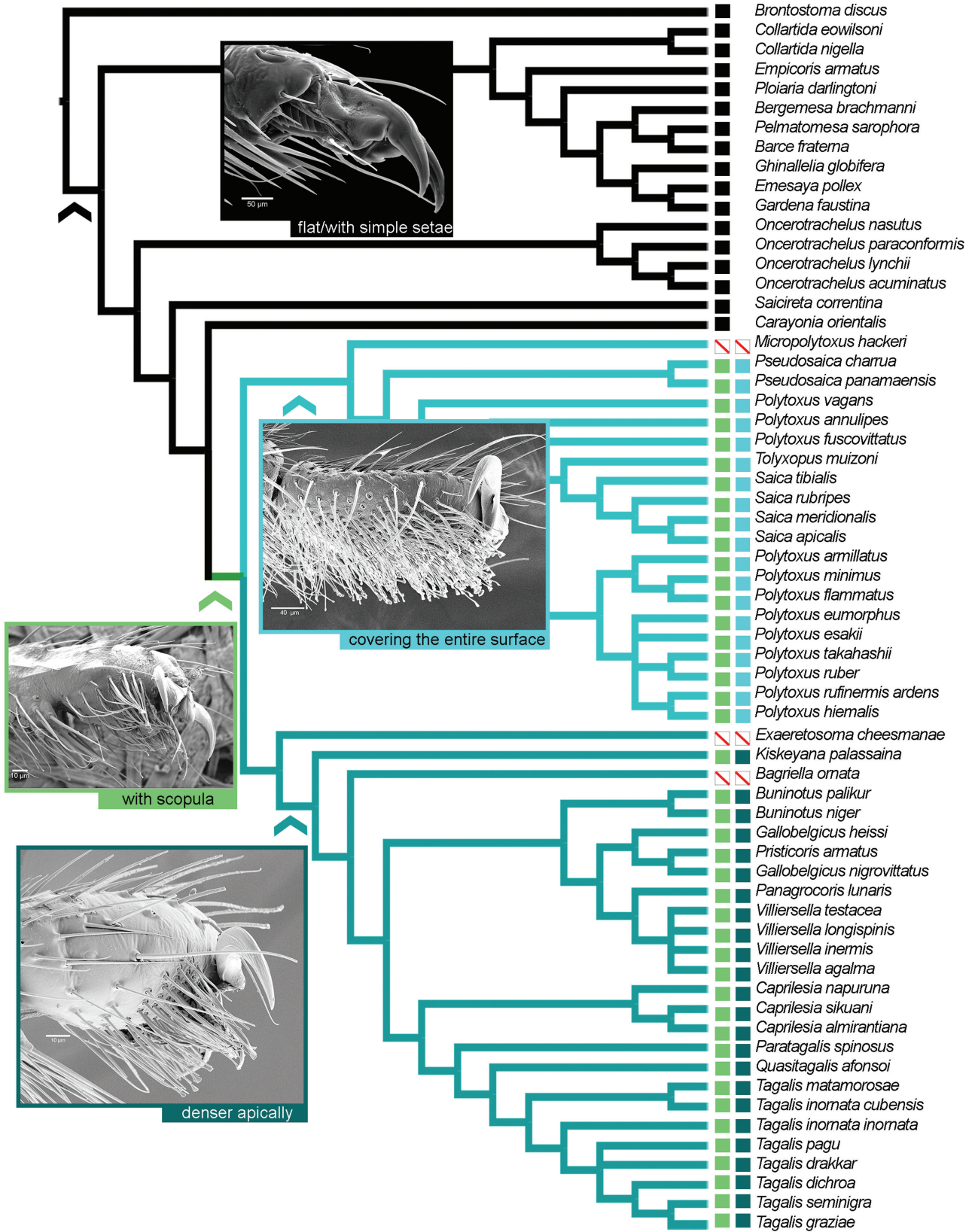


Figure 5. Evolution of the scopula in Saicini. Tree shown is the result of the strict consensus tree recovered with the IW analysis trees under a k -value = 12. Coloured squares next to terminal names indicate character states for protarsal scopula and tenent setae arrangement. Slashed squares indicate missing information.

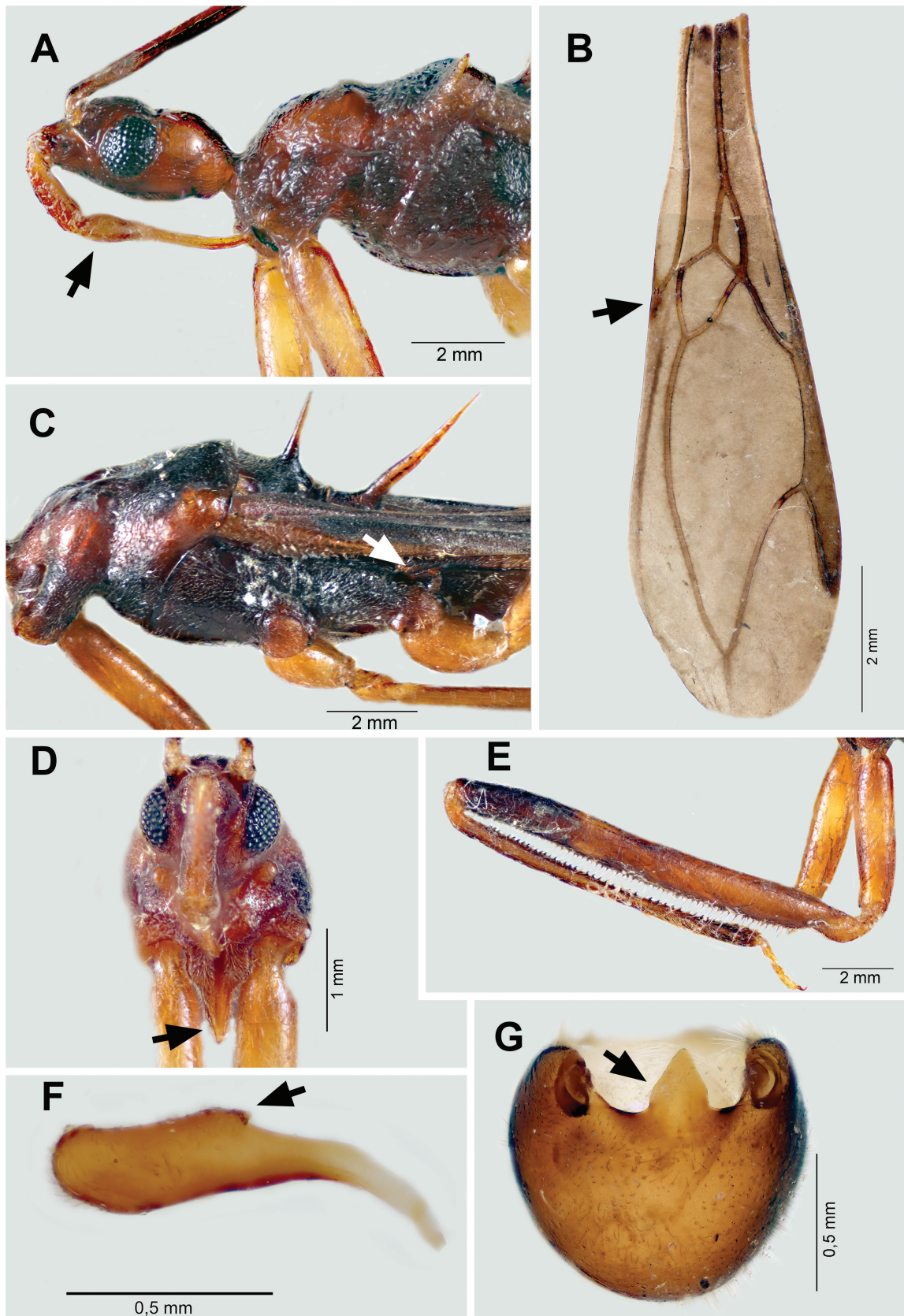


Figure 6. *Saicireta* type genus of Saiciretini trib. nov. A, head and prothorax, lateral view. B, forewing. C, thorax, lateral view. D, head and prothorax, frontal view. E, proleg, lateral view. F, paramere. G, pygophore, caudal view. Arrows indicate diagnostic characters.

Type genus: Saicireta Melo and Coscarón, 2005.

Diagnosis: Postocular region protuberant, and with simple thin setae ventrally (Fig. 6A); anteocular region shorter than postocular region (Fig. 6A); second visible labial segment shorter than third one (Fig. 6A); posterior margin of scutellum entire (Fig. 6C); ventral surface of protibia with both simple and spiniform setae (Fig. 6E); paramere nearly straight, wider at apex, with a process on the lateral submedial margin (Fig. 6F); and gonocoxa 8 rectangular.

Examined material: *Saicireta correntina* Melo and Coscarón, 2005: one male, holotype, ARGENTINA: Corrientes, Ituzaingó, 27°28' S, 56°34' W, Rincón Santa María Reserve, 26.iv.2003/*Saicireta correntina* Melo and Coscarón, 2005/he-10284 (MLP). Four males, one female, paratypes [same data as holotype]/he-10286–10289/he-10285 (MLP).

Redefinition of *Saicini*

Considering the phylogenetic results that help redefine the newly circumscribed Saicini, we use the optimization of the characters from our analyses to complement and modify the diagnosis offered by [Standring et al. \(2023\)](#), propose two new subtribes, and give a diagnosis for each genus. Furthermore, we present for the first time a key to the genera of Saicini of the world.

Saicini Stål, 1859

Type genus: Saica Amyot and Serville, 1843.

Revised diagnosis: With stout, simple or spiniform setae on the ventral margin of the mandibular plates and the postocular region, on the gula, and on all or some labial segments ventrally; second visible labial segment usually swollen; anterior lobe of pronotum with processes on anterior and posterior regions; metanotum with a protruding process apically; forewing with mcu-an1 crossvein with proximal to distal orientation, and M and CU not fused along the proximal portion of the wing; and presence of scopula on the preapical ventral region of all tarsi ([Castro-Huertas and Melo 2023, 2024](#), [Standring et al. 2023](#)). In addition, protibia usually curved; first tarsomere of the protarsus longer than the second; apex of paramere acute; and gonocoxa 8 nearly oval.

Saicina subtribe nov.

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Previously called 'hairy species' clade' because of including species without spiniform processes on the prolegs ([Castro-Huertas and Melo 2023](#), [Standring et al. 2023](#)).

Diagnosis: Recognized by the ventral surface of the procoxa with stout, simple setae; anteocular region usually 0.5 times or shorter than postocular region; posteromedial process of pygophore usually more of three times longer than wide, paramere setae usually restricted to some areas; and basal plate arms of articulatory apparatus longer than the dorsal process of basal plate.

Included genera:

Micropolytoxus Elkins, 1962

Type species: Micropolytoxus hackery Elkins, 1962. By original designation, three species included.

Diagnosis: Humeral angles flat or with minute spines; mesonotum with a short spine, scutellum and metanotum with a well-developed short spine each; males and females macropterous or brachypterous; posteromedial process of pygophore produced and slightly curved ([Elkins 1962](#), [Malipatil and Howarth 1990](#)). In addition, first visible labial segment with thin, simple setae on ventral region; anterior margin of proepisternal supracoxal lobe projected; protuberance of posterior margin of scutellum entire; posteromedial process of pygophore nearly horizontal; and distal portion of endosomal sclerites triangular.

Polytoxus Spinola, 1850

Type species: Acanthothorax sanguineus Costa, 1842. By monotypy, 75 species included.

Polytoxus has been characterized by an unarmed clypeus; the head, labium, profemur and protibia ventrally with tufts of stout setae (but never spiniform setae); anterior pronotal lobe unarmed; humeral angles, meso- and metanotum spined; and forewing with a basal cell ([Rédei and Tsai 2010](#)). Currently, it is composed of 75 species, being the most diverse genus within Saicini. Unfortunately it was not possible to include the type species in our data matrix because of the lack of specimens. Our results show that *Polytoxus* may be paraphyletic, with *P. annulipes* and *P. fuscovittatus* more closely related to *Tolyxopus* and *Saica* than to the other *Polytoxus* species. Interestingly, these results are consistent with [Standring et al. \(2023\)](#), where an unidentified species of *Polytoxus* from India forms a clade with *Tolyxopus* and are sister-group of *Saica* + other *Polytoxus* species. We only had the opportunity to examine 12 species of this genus, mainly from the Oriental Region; we expect that expanding the sampling with more species and from all the known distributional range of the genus would help to clarify the situation of this genus.

Examined material: *Polytoxus annulipes* Miyamoto and Lee, 1966: JAPAN: one male, Komi, Iriomote Is., The Ryukyus, 4.vi.2003, T. Ishikawa leg (TUA); one female, Funaura, Iriomote-jima Is., The Ryukyus, 11.x.2004, T. Ishikawa (TUA). *Polytoxus rufinermis ardens* Ishikawa and Yano, 2002: one male, one female, paratypes, JAPAN: the Ryukyus Okinawa-honto Is., Yona, Yona-ensyurin, 5.xi.1999, Tadashi Ishikawa (TUA). *Polytoxus armillatus* Ishikawa, 1998: one male, one female, paratypes, JAPAN: Chiba Perf. Sakura city, Inba-numa, 9.xi.1997, Koji Toyoda (TUA). *Polytoxus esakii* Ishikawa and Yano, 1999: one male, one female, paratypes, TAIWAN: Shao-Tiengchi, Lan-Yu Is., 24.iii.1998, M. Sakai leg (TUA). *Polytoxus eumorphus* Miller, 1941: JAPAN: one male, Komi, Iriomotejima Is., The Ryukyus, 2.ii.2002, T. Ishikawa leg (TUA); one female, Funaura, Iriomote-jima Is., The Ryukyus, 11.x.2004, T. Ishikawa (TUA). *Polytoxus flammatus* Ishikawa and Yano, 2002: JAPAN: one male, Paratype, The Ryukyus, Iriomote-jima Is., Urauchi, 30.v.1999, Hiroki Mizushima (TUA); one female, The Ryukyus, Iriomote-jima Is., Urauchi, 30.v.1999, T. Ishikawa (TUA). *Polytoxus fuscovittatus* (Stål, 1860): JAPAN: one male, Sumiyoshi, Iriomote Is., the Ryukyus, 18.v.2001, T. Tsuru leg (TUA); one female, Otomi, Iriomote Is., the Ryukyus, 24.v.2003, LT., T. Tsuru leg (TUA). *Polytoxus hiemalis* Ishikawa and Okajima, 2003: one female, Paratype, VIETNAM: Near Tuyen Larn Lake, Ward 3, Da Lat, Lam Dong, 22.xii.2001, T. Ishikawa leg (TUA). *Polytoxus minimus* China, 1940: JAPAN: one male, Ozato, Ishigaki-jima

Is., The Ryūkyūs, 4-5.v.2004, T. Ishikawa (TUA); one female, The Ryukyus, Yonaguni-jima Is., Tarumai, 19.v.2000, Tadashi Ishikawa (TUA). *Polytoxus ruber* Yano, 1998: one male, one female, JAPAN: Maezato, Ishigaki Is., The Ryukyus, 10.vi.2003, T. Ishikawa leg (TUA). *Polytoxus takahashii* Yano, 1998: JAPAN: one male, Maezato, Ishigaki Is., The Ryukyus, 10.vi.2003, T. Ishikawa leg (TUA); one female, Shiramizu, Ishigakijima Is., The Ryukyus, 7.iii.2002, T. Ishikawa leg (TUA). *Polytoxus vagans* Miller, 1940: JAPAN: one male, Ohara, Iriomote-jima Is., The Loochoos, 21.vi.1966, S. Tachikawa leg. / Light trap (TUA); one female, The Ryukyus, Iriomote-jima Is., Urauchi, 22.vi.1998, Chuh Ishikawa (TUA).

Pseudosaica **Blinn, 1990**

Type species: Pseudosaica panamaensis **Blinn, 1990**. By original designation, three species included.

Diagnosis: Humeral angles, mesonotum, and scutellum spined; posteromedial process of pygophore produced, tapering, with an apical keel; posterior margin of abdominal sternite 7 and tergites 8 and 9 slope ventrocephalad; anterior margin of proepisternal supracoxal lobe projected (**Blinn 1990, Castro-Huertas et al. 2023**). In addition, anterior margin of protuberance on scutellum emarginate; transverse bridge of pygophore wide, lateral margin of paramere socket produced, ventral region of pygophore with short dense setae; and dorsal phallosclerite asymmetric.

Examined material: *Pseudosaica panamaensis* **Blinn, 1990**: one male, COLOMBIA: Valle, Cali, 1000 m, domicilio, 17.i.1994, G. Guevara (MUSENUV); one female, PANAMA: Chiriqui, PILA, Jurutungo, 3-5.ix.2017, 1976 m, UTM 17P, 0310426, light trap, 0985320, J.A. Ramírez / BCI 167424 (STRI); one female, ARGENTINA: Chaco, P.N. El Impenetrable, Estación de Campo El Teuco, -25.064561 60.9464903, T. de luz, 10.xii.2021, Melo, M.C. (MLP). *Pseudosaica charrua* **Castro-Huertas, Forero and Melo, 2022**: two males, holotype and paratype, ARGENTINA: Entre Ríos, de Concordia Federación, i.1981, coll. Martínez (MLP).

Saica **Amyot and Serville, 1843**

Type species: Zelus recurvatus **Fabricius, 1803**. By monotypy, 14 species included.

Diagnosis: Head with a tuft of strong setae on mandibular plates and on postocular region ventrally; pedicel subequal to half the length of scape; anterior margin of proepisternal supracoxal lobe produced as an acute to subacute process; thoracic spines always present and of variable length, except on anterior lobe of pronotum; prolegs with simple strong setae; protibiae conspicuously curved; scopula setae dense on ventral surface of all third tarsomere; posteromedial process of pygophore bifid; posterior margin of the abdominal sternite VII of females vertical to subvertical (**Castro-Huertas and Melo 2024**). In addition; gonocoxa 8 with medial margin entire, and with homogeneous setae.

Examined material: *Saica apicalis* **Osborn and Drake, 1915**: COLOMBIA: one male, Nariño, Tumaco, C.I. El Mira, 1°32'59" N 78°11'58" W, 16 m, captura manual, iv.2017, E. Vergara

(UNAB); 1 female, Cundinamarca, Guayabetal, 4°13'40" N 73°48'59" W, 1200 m, 10.iii.1996, F. Munevar (UNAB). *Saica meridionalis* **Fracker and Bruner, 1924**: one female, COLOMBIA: Santander, La Belleza, Ver. Los Naranjos, 21.iii.1997, H. Marín. leg (UNAB). *Saica rubripes* **Champion, 1898**: PANAMA: one male, Panama province, Barro Colorado Is., 30.iv.2015, 9°9'17" N 79°50'53" W, beating, BE-BCI-APR2015-AB, M. Lucas/BCI 11833 (MPUJ); one female, Panama province, Barro Colorado Is., 1.iii.2011, 9°9'17" N 79°50'53" W, light trap LT-ARM1-MAR2011-A, Bobadilla, González, Osorio, Pérez/BCI 37066 (STRI). *Saica tibialis* **Stål, 1862**: COLOMBIA: one male, Cundinamarca, Sasaima, Vda. Nariz Alta, Finca 'El Tapaz' 4°58' N 74°28' W, 1150 m, captura con jama en arbusto, 21.vii.2012, L. Sánchez (UNAB); one female, La Sierra, 07.i.1996, García Parra leg (UNAB).

Tolyxopus **Villiers, 1969**

Type species: Polytoxus muizoni **Villiers, 1950a**. By original designation, two species included.

Diagnosis: Postocular region of head protuberant; protuberance of posterior margin of scutellum anteriorly emarginate; humeral angles flat, meso- and metanotum processes conspicuously reduced, and procoxae nearly two times longer than protrochanters.

Examined material: *Tolyxopus muizoni* (**Villiers, 1950**): one female, CENTRAL AFRICAN REPUBLIC: La Maboke, 25.ix.1967, L. Matile rec (MNHN).

Tagalina **subtribe nov.**

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Previously called 'spiny species' clade' because the species included show several spiniform processes (**Castro-Huertas and Melo 2023, Standing et al. 2023**).

Diagnosis: Recognized by spiniform setae present on the ventral margin of the postocular region, the ventral region of second visible labial segment, the anterodorsal margin of the prosternum, the ventral surface of protrochanter (mixed with simple setae), and on the anterolateral dorsal surface of the profemur.

Included genera:

Bagriella **McAtee and Malloch, 1923**

Type species: Bagriella ornata **McAtee and Malloch, 1923**. Monotypic.

Diagnosis: Head elongate, oval in lateral view; first visible labial segment expanded; gular region with only one pair of spiniform setae; anterior pronotal lobe with short protuberances; humeral angles spined; spines of humeral angles nearly two times longer than its base; and anterodorsal margin of proepisternal supracoxal lobe setose.

Examined material: *Bagriella ornata* **McAtee and Malloch, 1923**: one female (abdomen lost), holotype (high quality images),

PANAMA: Paraiso, CZ, Pan, 17.i.1911, E.A. Schwarz/Type No 51778 U.S.N.M./Holotype *Bagriella ornata* Det. McAtee and Malloch/USNM/Type No 51778 (NMNH).

Banarocoris Miller, 1958

Type species: Banarocoris fuscipennis Miller, 1958. Monotypic.

Diagnosis: Basiflagellomere as long as head, pronotum, and scutellum together; head longer than anterior pronotal lobe, with spiniform setae on the ventral region of mandibular plates, postocular, and gular regions; vertex wider than an eye width; first visible labial segment longer than the other labial segments, with a pair of spiniform setae ventrally; anterior pronotal lobe shorter than posterior lobe, with a pair of short tubercles on anterolateral region; humeral angles spinous; anterodorsal margin of proepisternal supracoal lobe with spiniform setae; profemur, protibia, and protrochanter with spiniform setae.

Buninotus Maldonado Capriles, 1981

Type species: Buninotus niger Maldonado Capriles, 1981. By monotypy, two species included.

Diagnosis: First visible labial segment with a pair of spiniform setae; second visible labial segment with a pair of strong setae; anterior pronotal lobe with four protuberances, a pair on each anterior and posterior regions; humeral angles spined; scutellum with a long, inclined process; procoxae, profemora, and protibiae with long spiniform setae; protibiae curved; meso- and metafemora with a pair of spiniform setae at apex; and forewings with three closed cells (Castro-Huertas *et al.* 2023). In addition, gular region with simple setae; spines of the humeral angles nearly two times longer than its base; subapical posterior region of tergite 9 with a folding; and gonocoxa 8 nearly rectangular, with the medial margin produced.

Examined material: Buninotus niger Maldonado Capriles, 1981: PANAMA: one male, Panama Province, Barro Colorado Is., 14.xi.2012, 9°9'17" N 79°50'53" W, light trap LT-ARM4-Nov2012-A, Bobadilla, Rodríguez, Hernández, Pérez/BCI63328 (STRI); one female, Panama Province, Barro Colorado Is., 20.v.2012, 8°59' N 79°33' W, light trap LT-WHE1-MAY2012-A Bobadilla, Rodríguez, Hernández, Pérez/BCI53469 (STRI); one female, Panama Province, Barro Colorado Is., 14.xi.2012, 9°9'17" N 79°50'53" W, Light trap LT-ARM4-NOV2012-A, Bobadilla, Rodríguez, Hernández, Pérez/BCI63348 (STRI); one female, Panama Province, Barro Colorado Is., 14.xi.2012, 9°9'17" N 79°50'53" W, Light trap LT-ARM3-NOV2012-A, Bobadilla, Rodríguez, Hernández, Pérez/BCI62746 (STRI); one female, Panama Province, Barro Colorado Is., 5-6.ix.2013, 8°59' N 79°33' W, light trap LT-WHE1-SEP2013-B, Bobadilla, Pérez, Bonilla, López/BCI76588 (STRI). *Buninotus palikur* Castro-Huertas, Forero and Melo, 2022: one female, holotype, FRENCH GUIANA: Saül, 1.vii.2008, PL, SEAG magnolia réc/*Buninotus palikur* Castro-Huertas, Forero and Melo 2022 (MNHN); five females, paratypes, FRENCH GUIANA: Kaw, PK 37.5, Malaise, 29.xii.2001, Cerda, J. leg. (MLP); Mt. Chevaux, 11.vii.2009, vitre, SEAG réc (JMB); Mt. des Chevaux, 7.xi.2011, Piège vitre, SEAG réc (JMB); Patawa, PK37, malaise,

3.iv.2002, J. Cerda leg. (JMB); Nouragues I, 23.ii.2011, Vitre Camp, SEAG réc (JMB).

Caprilesia Gil-Santana, Marques and Costa, 2006

Type species: Caprilesia almirantiana Gil-Santana, Marques and Costa, 2006. By monotypy, three species included.

Diagnosis: Postocular region of head subglobose; first and second visible labial segments with a pair of spiniform setae each, and third visible labial segment with one strong seta; humeral angles, mesoscutum and metascutum spined; scutellum with a short protuberance; procoxae, profemora, and protibiae spined; and forewings with two closed cells (Gil-Santana *et al.* 2006, Castro-Huertas *et al.* 2023). In addition, pterostigma of forewing not surpassing the apex of the discal cell, and second tarsomere nearly as long as third tarsomere.

Examined material: Caprilesia sikuanii Castro-Huertas, Forero and Melo, 2022: one male, holotype, COLOMBIA: Meta, Remolinos, Centro Cafam Llanos, 55 km W de Puerto Gaitán, 165 m, 4.274963° N 72.540814° W, 30.iv.2010, A. García *et al.*, Bosque Bavaria, pitfall/MPUJ_ENT 0010541 (MPUJ). *Caprilesia napuruna* Castro-Huertas, Forero and Melo, 2022: one female, holotype, ECUADOR: Napo, Sacha Wagra Lodge, Rio Hollin, 10 km from Archidona, 730 m, 0.96° S 77.75° W, 29.xi.2009, D. Forero [EC09_L4] [fogging]/UCR_ENT 00002682 (QCAZ).

Choreutocoris Miller, 1957

Type species: Gallobelgicus kinabaluensis Miller, 1940. By original designation, three species included.

Diagnosis: Head shorter than pronotum, with spiniform setae on ventral margin of mandibular plate, postocular region, and gular region; first visible labial segment longer than remaining segments together, with spiniform setae; humeral angles spined; anteroventral margin of proepisternal supracoal lobe with a spiniform setae; procoxae about half as long as the profemora, with spiniform setae on inner surface; protibiae, profemora, and protrochanters with spiniform setae; first tarsal segment longer than remaining tarsal segments together; and paramere nearly straight.

Cuernolestes Miller, 1953

Type species: Cuernolestes philippinus Miller, 1953. By monotypy, four species included.

Diagnosis: Clypeus flat; anterior protuberances of anterior pronotal lobe slightly projected; and first protarsal segment as long as second and third segments combined.

Exaeretosoma Elkins, 1962

Type species: Exaeretosoma cheesmanae Elkins, 1962. Monotypic.

Diagnosis: Head with a short but distinct spine behind each antennal insertion; posteromedial process of pygophore produced and basally curved; and paramere wider apically.

***Gallobelgicus* Distant, 1906**

Type species: Gallobelgicus typicus Distant, 1906. By monotypy, six species included.

The genus has been characterized by the clypeus armed with an anteriorly directed spine; head, first visible labial segment, procoxa, protrochanter, profemur, and protibia with large spiniform setae; humeral angles with long spines; and the first tarsal segment subequal to the lengths of the remaining segments combined (Rédei and Tsai 2010). Currently, *Gallobelgicus* consists of six species occurring in the Oriental region. Unfortunately, the type species was not included in our data matrix due to the lack of available specimens. Based on the paramere shape, Miller (1957) proposed a 'Gallobelgicus complex' for the genera *Gallobelgicus*, *Choreutocoris* Miller, 1957, and *Panagrocoris* Miller, 1957. However, this grouping was not recovered in our phylogenetic hypothesis. On the other hand, *Pristicoris* has been previously related to *Gallobelgicus* (Miller, 1952, Rédei and Tsai, 2009), and our results are consistent with this hypothesis. However, we think that the missing data of the matrix (particularly of genitalic characters) have an important effect in the analysis and resulted in the recovery of *Gallobelgicus* as paraphyletic. All *Gallobelgicus* specimens included in the analysis are males, whereas in the case of *Pristicoris* the specimen studied is a female. It is probable that the inclusion of additional male and female specimens for both genera will help to solve their relationship.

Examined material: Gallobelgicus heissi Rédei and Tsai, 2009: one male, THAILAND: Chiang Mai prov., 20 km SW of FANG, 19°49'57"N 99°02'54"E, 11.i. 2006, 1450 m, Lgt. Becar S and Fouqué R (NMPC). *Gallobelgicus nigrovittatus* Ishikawa, 2003: one male, Paratype, THAILAND: Chiang Dao, Pa Kia, 4-6.v.2000, Seidai Nagashima/bv beating from dead leaves (TUA).

***Kiskeyana* Weirauch and Forero, 2007**

Type species: Kiskeya palassaina Weirauch and Forero, 2007. Monotypic.

Diagnosis: Spiniform setae on ventral region of mandibular plates, postocular region, and anterodorsal margin of proepisternal supracoxal lobe; anterior pronotal lobe with low paired protuberances anteriorly; humeral angles spined; mesoscutum with one long, erect spine; metanotum large and elongate with one low tubercular spine close to the posterior margin; profemora with two rows of five or six stout and long spines; protibiae with a row of spiniform setae on inner dorsal surface (Weirauch and Forero 2007). In addition, clypeus with a process; gular region glabrous; dorsolateral surface of protibiae with only simple setae; prosternal process with the posterior apex produced; posterior margin of scutellum entire; females brachypterous; second tarsomere as long as third tarsomere; gonocoxa 8 nearly rectangular; and gonoplac compose by one sclerite (fused) with the posteromedial margin produced.

***Madecassosaica* Villiers, 1957**

Type species: Madecassosaica ornata Villiers, 1957. Monotypic.

Diagnosis: Head with spiniform setae on ventral margin of mandibular plate, and postocular and gular regions; anterior region of anterior pronotal lobe with a pair of conspicuous spiniform processes.

***Panagrocoris* Miller, 1957**

Type species: Panagrocoris agilis Miller, 1957. By original designation, three species included.

Diagnosis: Clypeus flat; profemur with very short spiniform setae between long spiniform setae (Miller 1957, Ishikawa 2002). In addition, profemora with antero- and posteroventral series of spiniform setae; first visible labial segment as long as second visible segment; R and M veins of forewing separated, and without r-m crossveins; anterior region of acetabula of proleg with an opening; second tarsomere as long as third tarsomere; posteromedial margin of pygophore flat; paramere extremely curved and slightly wider at base; dorsal region of phallosoma membranous; and tergite 9 near as long as wide.

Examined material: Panagrocoris lunaris Ishikawa, 2002: THAILAND: one male, paratype, Mae Sa, 400–500 m, Mae Rim, Chiang Mai, 3.viii.2001, T. Ishikawa. leg. (TUA); one female, paratype, Mae Sa, 400–500 m, Mae Rim, Chiang Mai, 1.viii.2001, Seidai Nagashima (TUA).

***Paratagalis* Monte (1943a)**

Type species: Paratagalis spinosus Monte, 1943a. By monotypy, two species included.

Diagnosis: Basiflagellomere long, almost three times the length of distiflagellomere; anterior pronotal lobe with four long spines; posterior pronotal lobe with two spines; procoxae spined; profemora and protibiae straight; profemora with a double series of spiniform setae of two lengths intermixed; protibiae with three long spiniform setae; mesonotum and metanotum spined (Monte 1943b, Gil-Santana and Costa 2009). In addition, clypeus usually spined; anterior margin of proepisternal supracoxal lobe projected; apex of profemora with a pair of processes; paramere nearly straight; arms of basal plate of articular apparatus longer than dorsal process of basal plate; ventral region of phallosoma with microtrichia; posteromedial margin of tergite 8 produced; tergite 9 longer than wide, with posteromedial margin tapering and with a process; gonocoxa 8 near triangular; and the gonoplac compose by a pair of sclerites, with the apex tapering and its lateral external margins straight.

Examined material: Paratagalis spinosus Monte, 1943: one male, PARAGUAY: Encarnación, x.1999, CDC, Carpintero (MLP); one female, ARGENTINA: Corrientes, Ituzaingó, Reserva Santa María, x.2003, trampa de luz (MLP); one female, COLOMBIA: Caldas, Norcasia, xi.2013, C. Llano (MPUJ).

***Pristicoris* Miller, 1952**

Type species: Pristicoris bellicosus Miller, 1952. Monotypic.

Diagnosis: Clypeus with a short median tubercle; postocular region globose, longer than antecular region; spiniform setae on ventral margin of mandibular plates and postocular region; gular region with a pair of spiniform setae; first visible labial segment longer than second segment, with a pair of spiniform setae ventrally; second visible labial segment moderately wider medially; third visible labial segment as long as second segment; anterior pronotal lobe nearly quadrangular; humeral angles spined; anterodorsal and ventral margins of proepisternal supracoxal lobe with spiniform setae; meso- and metanotum spined; posterior margin of scutellum entire; procoxae with simple and spiniform intermixed setae; and dorsolateral surface of protibiae with more than three spiniform setae.

Examined material: *Pristicoris armatus* (Villiers, 1950): two females, N. NIGERIA: Nr. Kafanchan, Kagoro Forest, 14.x.1979, J. Deeming. (MNHN).

Quasitagalis Gil-Santana, Oliveira and Zampaulo, 2020

Type species: *Quasitagalis afonsoi* Gil-Santana, Oliveira and Zampaulo, 2020. Monotypic.

Diagnosis: Mesonotum flat; protibial inner surface with a simple (male) or double (female) longitudinal median row of numerous short spiniform setae (Gil-Santana *et al.* 2020). In addition, proepisternal supracoxal lobe anterodorsally glabrous; ventral surface of profemora with spiniform setae in antero- and posteroventral series; protibia curved, with more than three spiniform processes on dorsolateral surface, and both simple and spiniform setae on ventral surface; second visible labial segment as long as third visible labial segment; transverse bridge of pygophore narrow; apex of paramere with a protruding process; and basal plate bridge of the articulatory apparatus absent.

Spairapeltis Miller, 1950

Type species: *Spairapeltis sericea* Miller, 1950. By monotypy, two species included.

Diagnosis: Humeral angles flat; scutellum with a spine apically and two club-like processes posteromedially; paramere apically wide like a spatula.

Tagalis Stål, 1860

Type species: *Tagalis inornata* Stål, 1860. By monotypy, 13 species included.

Diagnosis: First visible labial segment as long as the second one; first and second visible labial segments with a pair of spiniform processes; posterior region of anterior pronotal lobe nearly flat; scutellum with a spine apically; procoxae elongate; humeral angles flat; profemora with spines ventrally and on the upper margin of inner surface; protibiae with three or four spines; second tarsomere as long as the third one; third tarsomere slender and just slightly dilated (Castro-Huertas and Melo 2023, 2024). In addition, head glabrous; anteroventral margin of the proepisternal supracoxal lobe with a simple seta; ventral surface

of procoxae with only simple setae; apex of paramere acute; and gonoplac composed by one sclerite (by fusion).

Examined material: *Tagalis dichroa* Castro-Huertas and Forero, 2014: one male, PANAMA: Panama province, Barro Colorado Is, 17–18.v.2015, 9°9'17"N 79°50'53"W), light trap, LT ARM3-MAY2015-A, A. Bobadilla *et al.* / BCI 1114426 (MPUJ). *Tagalis drakkar* Varela and Melo, 2017: one male, paratype, ARGENTINA: Misiones, Caraguata[y], i.[19]98 (MLP). *Tagalis graziae* Castro-Huertas and Forero, 2021: one male, holotype, COLOMBIA: Risaralda, Pueblo Rico, Montezuma Ecolodge, 5.9 km de Puerto Rico, 05.23016° N 76.08364° W, 1336 m, 2–7.ix.2018, D. Forero/Bosque húmedo [Trampa de luz UV]/MPUJ_ENT 0065075 (MPUJ). *Tagalis inornata inornata* Stål, 1862: one male, PERU: Ucayali, Kirigueti (Luz), ii.[20]04, J. Williams, 73°07'08" W 11°38'13" S. (MLP); one female, ARGENTINA: Misiones, Puerto Iguazú, 4.x.1947, Col. Duret. (MLP). *Tagalis inornata cubensis* McAtee and Malloch, 1923: one male, PARAGUAY: Canindeyú, Res. Mbaracayú, Aguarañu (luz), xii.2003, O. Di lorio (MLP); one male, MEXICO: Veracruz, Los Tuxtlas, Estación de Biología, 22.iv.1985, C. Mayorga (MLP). *Tagalis matamorosae* Castro-Huertas and Melo, 2024: PANAMA: 1 male, Paratype, Panama Province, Barro Colorado Is., 3–4.xi.2016, light trap, LT-ARM4-NOV2016-B, Bobadilla, López, Ramírez/BCI144906 (MLP); one female, paratype, Panama Oeste Province, Barro Colorado Is., 27–28.xi.2019, light trap, LT-ZET1-NOV2016-B, Bobadilla, López, Ramírez/BCI171879 (STRI). *Tagalis pagu* Castro-Huertas and Melo, 2024: one female, paratype, BRASIL: Rio Grande do Sul, Santiago, 1.i.2013, Brusa, F. leg./*Tagalis pagu* Castro-Huertas and Melo, 2024 (MLP). *Tagalis seminigra* Champion, 1898: PANAMA: one male, Panama Province, Barro Colorado Is., 16–17.iii.2018, 9°9'17" N 79°50'53" W, light trap, LT DRAMAR2018-A, A. Bobadilla *et al.* / BCI162391 (STRI); one male, Panama Province, Barro Colorado Is., 8–9.iii.2019, 9°9'17" N 79°50'53" W, light trap, LT ARM-MAR2019-A, A. Bobadilla *et al.* / BCI168278 (STRI); PERU: one male, Ucayali, Kirigueti (luz), vii.2004, J. Williams, 73°07'08" W 11°38'13" S (MLP); one female, Cuzco, Pagoreni (luz), vii.2004 Williams, 72°54'07" W, 11°42'22" S (MLP).

Vadonocoris Villiers, 1957

Type species: *Vadonocoris striatus* Villiers, 1957. Monotypic.

Diagnosis: Anterior pronotal lobe longer than wide; paramere long and longitudinally curved; posteromedial process of pygophore long, curved and apically with a caudal short projection (Villiers 1957, 1979).

Villiersella Schouteden, 1950

Type species: *Polytoxus inermis* Villiers, 1950a. By original designation, four species included.

Diagnosis: Humeral angles flat; parameres long; posterolateral margin of pygophore usually with a protruding process on each side (Elkins 1956, Villiers 1969). In addition, head rounded, gular region with simple setae; second visible labial segment as

long as third visible labial segment; posteromedial surface of the abdominal sternite 8 with processes; apex of paramere flat; and distal portion of endosoma membranous.

Examined material: *Villiersella agalma* Elkins, 1956: one male, GHANA: Tafo, 2.v.1966, Leston / U.V. trap (MNHN). *Villiersella*

inermis (Villiers): one male, GHANA: Tafo, 26.iv.1966, Leston / U.V. trap (MNHN). *Villiersella longispinis* Villiers, 1966: one female, GHANA: Tafo, 4.v.1966, Leston / U.V. trap (MNHN). *Villiersella testacea* Villiers, 1967: one male, GHANA: Tafo, 28.iv.1966, Leston/U.V. trap (MNHN).

KEY TO THE GENERA OF SAICINI OF THE WORLD

(Based on: Miller 1957, Elkins 1962, Malipatil and Howarth 1990, Rédei and Tsai 2010, Gil-Santana *et al.* 2020)

1. Head with strong simple setae, usually in a tuft, ventrally on mandibular plates and postocular region; profemur without spiniform setae, at most with strong erect setae, protibia with simple setae *Saicina* subtribe nov. 2
- 1'. Head with spiniform setae ventrally on mandibular plate, postocular and gular regions; profemur with two or three rows of spines, protibia either with simple setae or spiniform setae *Tagalina* subtribe nov. 7
2. Neotropical and Nearctic distribution 3
- 2'. Palearctic, Afrotropical, Oriental, or Australasian distribution 4
3. Pedicel approximately half as long as scape; medial process of male pygophore bifurcate; posterior margin of seventh abdominal sternite in females vertical or subvertical *Saica* Amyot and Serville
- 3'. Pedicel approximately three-quarters as long as scape; medial process of male pygophore as a single, erect spine; posterior margin of seventh abdominal sternite in females sloping ventrocephalad *Pseudosaica* Blinn
4. Pronotum with a long acute spine near each humeral angle; posterior medial process of pygophore as a hooked spine *Polytoxus* Costa
- 4'. Pronotum without spine or at most with a minute spine near each humeral angle; posterior medial process of pygophore different 5
5. Metanotum with a spine apically and two club-like processes medially; paramere apically wide, spatulate *Spairapeltis* Miller
- 5'. Metanotum without medial processes; paramere different 6
6. Meso- and metanotal processes as short spines, humeral angles with very short spines or flat *Micropolytoxus* Elkins
- 6'. Meso- and metanotal processes as very short tubercles, humeral angles always flat *Tolyxopus* Villiers
7. Neotropical and Nearctic distribution 8
- 7'. Palearctic, Afrotropical, Oriental, or Australasian distribution 14
8. Humeral angles of pronotum without processes, flat 9
- 8'. Humeral angles of pronotum with spine-like processes 10
9. Protibia with a three or four (*T. femorata*) stronger spiniform setae on external border of inner dorsal surface *Tagalis* Stål
- 9'. Protibia with a single or double longitudinal row of numerous short spiniform setae on median part of inner surface *Quasitagalis* Gil-Santana, Oliveira and Zampaulo
10. Procoxae without spiniform setae; anterior pronotal lobe nearly flat *Bagriella* McAtee and Malloch
- 10'. Procoxae with spiniform setae, anterior pronotal lobe with four processes (spines or protuberances) 11
11. Anterior lobe of pronotum with four spines *Paratagalis* Monte
- 11'. Anterior lobe of pronotum with four protuberances 12
12. First visible labial segment with a pair of spiniform setae, second visible labial segment with a pair of strong setae *Buninotus* Maldonado
- 12'. First and second visible labial segments with spiniform setae 13
13. Third visible labial segment without strong setae; only apterous females known *Kiskeyana* Weirauch and Forero
- 13'. Third visible labial segment with a pair of strong setae; macropterous females *Caprilesia* Gil-Santana, Marques and Costa
14. Clypeus armed with a short conspicuous spine *Gallobelgicus* Distant
- 14'. Clypeus with a short tubercle or glabrous 15
15. Clypeus with a short tubercle; anterior pronotal lobe nearly quadrangular *Pristicoris* Miller
- 15'. Clypeus flat; anterior pronotal lobe quadrangular or not. 16
16. Anterior pronotal lobe longer than wide; posteromedial process of pygophore curved *Vadonocoris* Villiers
- 16'. Anterior pronotal lobe as long as wide, nearly quadrangular; posteromedial process of pygophore different as above 17
17. Anterior pronotal lobe with conspicuous tubercles or spiniform processes anteriorly 18
- 17'. Anterior pronotal lobe without processes, nearly flat 19
18. Anterior pronotal lobe with short spines anteriorly *Madecassosaica* Villiers
- 18'. Anterior pronotal lobe with a pair of tubercles anteriorly *Banarocoris* Miller
19. Head with a short but distinct spiniform process behind each antennal insertion *Exaeretosoma* Elkins
- 19'. Head without spiniform processes behind antennal insertions 20
20. Humeral angles flat; paramere very long *Villiersella* Shouteden

20'. Humeral angles with conspicuous spiniform processes, paramere not conspicuously long.....	21
21. First protarsal segment as long as second and third segments combined.....	<i>Cuernolestes</i> Miller
21'. First protarsal segment longer than second and third segments combined	22
22. Profemur with short and long spiniform setae	<i>Panagrocoris</i> Miller
22'. Profemur with only long spiniform setae	<i>Choreutocoris</i> Miller

DISCUSSION

Saicini new definition and taxonomic implications within Emesinae

Our findings are consistent with the most recent hypotheses proposing Saicini as a monophyletic group, as well as the internal clade composition and its closer related groups (Castro-Huertas and Melo 2023, Standring *et al.* 2023). We confirmed that Saicini is currently composed of 23 genera and 146 species (excluding the genus *Saicireta*), and its monophyly is supported, among other characters, by the presence of scopula on the third tarsal segment of all legs.

Of the seven synapomorphies recovered by Standring *et al.* (2023) for Saicini, most are consistent with our results, except for the M-Cu veins not fused at the proximal portion, because some *Saica* species show the proximal portion of the M-Cu veins fused conforming a cell (e.g. *S. apicalis* and *S. meridionalis*). In addition, the second visible labial segment swollen is recovered as a synapomorphy of Saicini, but the examined species of *Buninotus*, *Gallobelgicus*, *Panagrocoris*, *Pristicoris*, and *Villiersella* have the second visible labial sub-basally rounded but not conspicuously expanded. The first labial segment can be expanded in the 'spiny clade' (Standring *et al.* 2023), except for *Exaeretosoma*, *Kiskeyana*, and the clade *Paratagalis* + *Quasitagalis* + *Tagalis*.

The consistency of the two main clades within Saicini, the 'hairy' and 'spiny' clades, recovered previously by Castro-Huertas and Melo (2023) and Standring *et al.* (2023), and in this analysis, provides substantial evidence in support of the establishment of the two new subtribes: Saicina and Tagalina. Although we were not able to analyse some genera, considering the generic original diagnoses, and in agreement with most of Standring *et al.* (2023) predictions except for the genus *Banarocoris*; we are confident with the inclusion of *Spairapeltis* in Saicina subtribe nov.; and *Banarocoris*, *Choreutocoris*, *Cuernolestes*, *Madecassosaica*, and *Vadonocoris* in Tagalina subtribe nov.

It has been challenging to ascertain which taxonomic decision is better to solve the situation of *Saicireta*: establishing a new tribe with a monotypic genus or including an additional genus in the already known tribes. This last option, would involve a partial coincidence with the diagnostic characters recovered in the classification proposed by Standring *et al.* (2023). We believe that the phylogenetic hypothesis proposed here provides substantial evidence in support of the establishment of the new tribe Saiciretini, nevertheless a further phylogenetic analysis with additional Emesinae taxa sampling would be important to evaluate more thoroughly the position of the genus among the other tribes.

Saicini scopula evolution

Mobility and attachment to different types of substrates and surfaces are critical adaptive needs for most terrestrial animals.

In response, several strategies and morphological adaptations have evolved, including specialized structures that allow movement and support. Hexapods in particular have developed two different mechanisms on different parts of the legs to facilitate the attachment to a substrate: smooth pads and hairy surfaces (Beutel and Gorb 2001). Both structures not only increase the contact area and make grasping easier, but in predatory terrestrial insects some of these structures may play an important role in catching prey (e.g. fossula spongiosa; Weirauch 2007). Hairy attachment structures are a morphological feature that has evolved independently several times within arthropods (Beutel and Gorb 2001). For example, walking spiders (those that do not produce silk or build webs) have hairy attachment structures relatively similar in its general structure to Emesinae, which is called scopula too, located on the tarsus and metatarsus enabling spiders to climb smooth, steep surfaces. In several families, they are used for capturing, securing, and handling prey as an alternative mechanism to silk use (Niederegger 2013, Wolff *et al.* 2013). There are several hypotheses on the mechanisms of adhesion of the scopula in spiders (e.g. Niederegger and Gorb 2006, Wolff and Gorb 2013, Wohlfart *et al.* 2014, Pérez-Miles *et al.* 2015), but the biomechanical differences between scopulae with different structure and setae arrangement remain unclear.

Two general traits, observed in Saicini scopula, are consistent with hairy attachment structures previously documented in other arthropods: its localization, and the cuticular surface associated with the scopula. The scopula can be found on various regions of the legs, including claws, pretarsus, tarsal apex, tarsomeres, and tibia (Beutel and Gorb 2001, 2006, Wolff and Gorb 2012). The second most common location is on the tarsomeres, as occurs in Saicini. Moreover, the ventral surface of the third tarsomere associated to the scopula shows conspicuous short protuberances in all species examined. Similar structures have been described in spiders too, which are thought to be sensory cells that degenerate during development in the trichoid complex (Beutel and Gorb 2001).

The evolutionary mechanisms behind the emergence of hairy attachment structures remain unknown, at least within the Reduviidae, and in the particular case of the Emesinae it is intriguing because the scopula, the only hairy attachment structure known, has been recorded on all legs in the Saicini and restricted to the meso- and metatarsi in five genera of Emesini and seven species of *Ploiaria* in the Leistarchini (Wygodzinsky 1966, Weirauch 2007, 2008). Within Emesinae, the scopula emergence seems to be multiple and independent, because the taxa with scopula are not necessarily closely related. Most of the Emesini genera exhibit prolegs typically raptorial, which is notable in contrast to their cursorial meso- and metalegs. Additionally, their pretarsal structures are often markedly modified, featuring asymmetrical claws or cuticular processes (Wygodzinsky 1966, Castro-Huertas *et al.* 2019). On the other hand, the genera

within Oncerotrachelini and Visayanocorini exhibit uniformity in the morphology of their legs (Weirauch 2007), with no modifications of the pretarsal structures. Additional taxa and information on the structure of the tarsus in other tribes could help to test a possible correlation between the presence of the scopula and the highly modified pretarsal structures on the proleg.

The scopula in Saicini is relatively simpler than in other arthropods. The setae in Saicini are consistent with the ‘adhesive setae’ category based on their spatulate shape, enlarged and apically wide [AS, in Wolff and Gorb (2012)]. However, in Saicini the surface of the setae is smooth or slightly grooved longitudinally, lacking ‘setulae’ or cuticular projections, and only exhibiting a rugose surface on the ventral surface of the apical spatula. Furthermore, tarsal hairy attachment in Saicini lacks additional setae or setae pads in other regions of the pretarsus or other tarsomeres.

Another significant aspect is the limited variation observed in the scopula of Saicini. In contrast to other taxa (Foelix *et al.* 1984, Wolff *et al.* 2013), Saicini exhibits minimal variation in the arrangement or ultrastructure of the scopula, both between and within species. The presence of sexual dimorphism, conspicuous structural differences between taxa, or differences between protarsus and mesotarsus were not observed, except for the density and arrangement of tenent setae, which exhibited two distinct conditions: a densely and uniformly distributed pattern on the ventral surface of the third tarsal segment, or a denser distribution only on the apical region. These patterns are congruent with the two main clades of Saicini recovered in our phylogenetic hypothesis.

When considering only the comparative morphology evidence, our results do not support the hypothesis that the scopula performs a different role beyond locomotion and substrate attachment. Nevertheless, further studies into the correlation between the different structures of the legs and the potential role of the scopula in prey catching should be conducted through the use of natural history observations and prey capture performance studies.

SUPPLEMENTARY DATA

Supplementary data are available at *Zoological Journal of the Linnean Society* online.

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CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest in relation to this work.

DATA AVAILABILITY

Morphological matrix and scripts are available in [Supporting Information, Files S2 and S3](#).

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