Invertebrate Zoology, 2025, 22(4): 662–717

On encrusted soil and mud: a preliminary phylogenetic analysis of the mud spider family Paratropididae Simon, 1889 (Araneae: Mygalomorphae) brings to light new species and genera

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ABSTRACT: We present the first exploratory morphological phylogeny of the spider family Paratropididae Simon, 1889, offering a critical re-evaluation of its internal systematics. Our analysis reveals seven distinct lineages, recognised here as putative genera, three of which are newly described from Ecuador and Guyana. This study underscores the previously overlooked diagnostic value of both somatic and genitalic characters in genus-level delimitation within the family. In addition to a revised concept of *Paratropis* Simon, 1889, we describe 11 new species based on detailed genital morphology. Two species, *Paratropis pasochoa* Dupérré et Tapia, 2024 and *Anisaspis awa* Sherwood, Brescovit et Lucas, 2023, are transferred to the new genus *Alienus* gen.n., forming the new combinations *Alienus pasochoa* comb.n. and *Alienus awa* comb.n., based on topotypic and type material and their phylogenetic placement. *Stormtropis celiae* (Santos, Gomes, Almeida, de Morais et Bertani, 2025) comb.n. and *Stormtropis manauara* (Santos, Gomes, Almeida, de Morais et Bertani, 2025) comb.n. are transferred to *Stormtropis* from their previously incorrect placement in *Paratropis*. We further propose *Anisaspis* Simon, 1892 and its type species *A. tuberculata* as *nomina dubia* due to the absence of diagnostic adult material. Our findings highlight the importance of using robust morphological datasets to recover natural groups, providing a refined framework for future studies. Additionally, we report the first occurrences of *Stormtropis* Perafán, Galvis et Pérez-Miles, 2019 from Venezuela, describe the first species and a new endemic genus (*Yamaratropis* gen.n.) from an Andean Tepui, and document novel behaviours, including burrow construction and the use of anthropogenic materials (*e.g.*, microplastics). The discovery of burrowing behaviour in several species offers new insight into the behavioural evolution of early Bipectina, suggesting a basal origin for open burrow entrance types. This work establishes a critical morphological baseline for future integrative research.

How to cite this article: Peñaherrera-R. P., Ríos-Tamayo D., León-E. R.J., Drolshagen B., Sherwood D. 2025. On encrusted soil and mud: a preliminary phylogenetic analysis of the mud spider family Paratropididae Simon, 1889 (Araneae: Mygalomorphae) brings to light new species and genera // Invert. Zool. Vol.22. No.4. P.662–717. doi: 10.15298/invertzool.22.4.10

KEY WORDS: Aranei, Andes, Amazonia, cladistics, morphology, Neotropics, taxonomy.

На покрытой коркой почве и грязи: предварительный филогенетический анализ пауков семейства Paratropididae Simon, 1889 (Araneae: Mygalomorphae) выявляет новые виды и роды

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РЕЗЮМЕ: Впервые предложена рабочая морфологическая филогения семейства пауков Paratropididae Simon, 1889, с критической переоценкой системы семейства. Наш анализ выявил семь отчетливых линий, трактуемых здесь как возможные рода, три из которых описаны из Эквадора и Гайаны как новые для науки. Подчеркнута важность некоторых ранее пропущенных соматических признаков и признаков строения гениталий для выделения родов внутри семейства. В дополнение к ревизованной концепции рода *Paratropis* Simon, 1889, на основании морфологии гениталий описано 11 новых для науки видов. На основании изучения топотипов и типового материала два вида, *Paratropis pasochoa* Dupérré et Tapia, 2024 и *Anisaspis awa* Sherwood, Brescovit et Lucas, 2023, перенесены в новый род *Alienus* gen.n., с образованием новых комбинаций *Alienus pasochoa* comb.n. и *Alienus awa* comb.n. *Stormtropis celiae* (Santos, Gomes, Almeida, de Morais et Bertani, 2025) comb.n. и *Stormtropis manauara* (Santos, Gomes, Almeida, de Morais et Bertani, 2025) comb.n. перенесены в род *Stormtropis* вместо исходно ошибочного размещения в составе рода *Paratropis*. Ввиду отсутствия половозрелых особей, пригодных для диагностирования, род *Anisaspis* Simon, 1892 и его типовой вид *A. tuberculata* рассматриваются как *nomina dubia*. Род *Stormtropis*

Perafán, Galvis et Pérez-Miles, 2019 впервые отмечен в фауне Венесуэлы. Дано описано монотипического нового рода (*Yamaratropis* gen.n.) из тепуй (столовых гор) Анд. Отмечены особенности поведения пауков семейства, в т.ч. конструкция нор и использование антропогенных материалов (напр., микропластики). Обнаружение роющего поведения некоторых видов позволяет дать новый взгляд на эволюцию поведения группы Bipectina, предполагая в качестве базального (исходного) варианта новы с открытым входным отверстием. Настоящая работа дает морфологическую основу для дальнейших исследований в области интегративной таксономии.

Как цитировать эту статью: Peñaherrera-R. P., Ríos-Tamayo D., León-E. R.J., Drolshagen B., Sherwood D. 2025. On encrusted soil and mud: a preliminary phylogenetic analysis of the mud spider family Paratropididae Simon, 1889 (Araneae: Mygalomorphae) brings to light new species and genera // Invert. Zool. Vol.22. No.4. P.662–717. doi: 10.15298/invertzool.22.4.10

КЛЮЧЕВЫЕ СЛОВА: Aranei, Анды, Амазония, кладистика, морфология, Неотропика, таксономия.

Introduction

The family Paratropididae Simon, 1889 (Araneae: Mygalomorphae), commonly known as bald-legged or mud spiders, are small to medium sized spiders previously considered to be closely related to the families Barychelidae Simon, 1889 and Theraphosidae Thorell, 1869 (Mori, Bertani, 2020). Generally, members of this cryptic spider family cover their body, entirely or partially, with mud, soil, and small mineral crystals using a modified scaly cuticle (Perafán *et al.*, 2019, Dupérré, Tapia, 2020; PP-R and DS pers. obs.). Paratropididae is currently composed of four genera: *Anisaspis* Simon, 1892 (3 spp.), *Anisaspoides* Pickard-Cambridge, 1896 (1 sp.), *Stormtropis* Perafán, Galvis et Pérez-Miles, 2019 (5 spp.), and *Paratropis* Simon, 1889 (23 spp.), with species in the family known from Brazil, Colombia, Ecuador, French Guiana, Guyana, Mexico, Peru, St. Vincent, and Venezuela (World Spider Catalog, 2025).

Historically, phylogenetic analyses of Mygalomorphae placed Paratropididae between differing families and clades without a definite corroboration of evolutionary relationships to other families. In initial Mygalomorphae phylogenies, Paratropididae was positioned as the sister family of Theraphosidae, within the Theraphosoidina clade (Goloboff, 1993a; Raven, 1985). Nevertheless, the first robust molecular phylogenetic analyses evaluating family-level relationships, suggest Paratropididae to be evolutionarily distant from Theraphosoidina and more closely related to Dipluridae and Hexathelidae. Subsequently, Opatova *et al.* (2020), under an anchored phylogenomic approach, placed Paratropididae as a standalone lineage diverging as sister of the rest of all the Bipectina clade by preferred phylogenetic hypothesis. This same study showed that Paratropididae could be additionally placed as sister group of Nemesoidina by combining both Anchored Hybrid Enrichment and transcriptomic data (Opatova *et al.*, 2020). Most recently, Kulkarni *et al.* (2023) placed the family close to Halonoproctidae and Idiopidae based on ultraconserved elements (UCEs) and six sanger-sequencing-based molecular marker data. Nevertheless, they discuss that incongruent or contrasting Mygalomorphae family placements within the phylogeny could differ by taxon sampling as well the nature of the data classes of each study.

Currently, the taxonomy of Paratropididae still presents challenges in terms of understanding and classifying their morphology, which would help to recognise natural groups i.e., Dupérré & Tapia (2024). For this reason, we propose the first morphologically based phylogenetic analysis that supports and evaluates the proposal of new paratropidid genera. Alongside this analysis, we propose three new genera, 11 new species, and three new combinations regarding the putative placement of each taxon in the preferred phylogenetic hypothesis. Although work does not evaluate inter-relationships between putative closest families and Paratropididae, which previously mentioned seems to be conflictive, the first steps to a clear taxonomy is to provide and recognise valuable diagnostic characters at

Paratropididae generic-level and intrafamilial relationships.

Material and methods

Phylogenetic analysis

The morphological characters for Paratropididae were based on somatic, and female and male sexual structures found during direct examination of specimens, considering also that each character to be used and extracted from the descriptions of the previously known species and genera (Perafán *et al.*, 2019; Almeida, Morais, 2022). This was applied in the case of the newly established *Inpatropis* gen.n. and *Stormtropis* species, with the latter being corroborated by an author of the genus (Carlos Perafán pers. comm. to PP-R). Due to the lack of ecological information, potential behavioural characters were avoided. Cryptic behaviour, often attributed to the scaly cuticle and its particle adhesion, could be inferred in almost all the included taxa based on morphology. Nonetheless, there could be multiple cuticle morphologies or types that may explain particle adhesion within Paratropididae; these can be accessible using fine microscopy techniques (i.e. Scanning Electron Microscope) which represent important future research directions for this family.

For the experimental approach we used two datasets, the first would focus on assessing the phylogeny based on the taxa with the most relevant and complete information possible. In this case, we used research on species that had been examined in person and presented clear and interpretable information with available data entries for both sexes. This meant excluding *Stormtropis* species where only females are known. On the other hand, the second analysis matrix included all examined material and species with information extracted from literature regardless of whether both sexes were known for the taxon (*e.g. Stormtropis* species). See Remarks section of *Paratropis* in relation to Dupérré & Tapia (2024) and Santos *et al*. (2025) species regarding why we exclude them from this dataset, with the exception of *P. cryptica, P. pasochoa,* and *P. celiae* as topotypic or corresponding material were available to PP-R and DS of these species during this research. Additionally, this second dataset included two newly described species, that are temporally considered within *Stormtropis* (see Remarks section on *Stormtropis* below for further explanation), in order to evaluate the influence of this group and the importance of including at least one male and female representative for each genus in the phylogenetic inferences in this study.

The analyses were informed by 64 characters, however, nine of them were excluded (Appendix A) due to their high homoplastic nature (including three multiple-state characters); these increased noise in clade resolution during preliminary analyses. We expect that further research could increase the number of characters used and allow for the consideration of those that were excluded for these phylogenetic analyses (i.e. biogeographic evaluation on the recovered clades in *Paratropis*). We obtained a final list of 55 characters, with 49 discrete characters and 6 multistate characters. On both sets, the genus *Anisaspoides* (see Taxonomy section for further information regarding species composition of this genus) was condensed into a single taxonomic unit due to missing sexes of both herein accepted species. This was done to obtain clearer positioning and dynamics of the characters presented in this peculiar group. For out-group selection, we used the genus *Macrothele* (family Macrothelidae Simon, 1892) as a recent molecular-based phylogeny of Mygalomorphae suggested that Macrothelidae is the sister clade to Bipectina, with Paratropididae representing the earliest diverging lineage within Bipectina, thus showing a close relationship to Macrothelidae (Opatova *et al.*, 2020). Directly examined specimens that are not mentioned within the Taxonomy section are listed in Appendix B.

The character matrix of each set was built and edited in Mesquite 2.74 (Maddison *et al.*, 2023). Unknown states are presented as “?”. Multi-state characters were treated as non-additive (Fitch, 1971, (minimum mutation model). Spermathecal receptacle morphology characters were treated under a nested strategy (Brazeau, 2011) by fragmenting into binary coding of what can be normally considered as multistate characters. With this approach, inapplicable entries could be applied for further step characters on taxa which present the absence or different independent state on the first general character. Following this, inapplicable entries were presented as “-”. Character matrix of each dataset is available at https://morphobank.org/

For both sets, heuristic searches were conducted using TNT 1.6 (Goloboff, Morales, 2023). Under maximum parsimony, each matrix was submitted into implied (IW) and equal weighting (EW) strategies. Trees were collapsed under ‘rule 1’ (Coddington, Scharff, 2005). IW searches followed the proposed methodology by Mirande (2009) by setting varying values of the concavity constant that allowed suitable comparisons among tree searches across a symmetric variation of the mean fit for each extra step that represents relation to a transformation (Mirande, 2009; Machado, Teixeira, 2021). Therefore, under this methodology, we set 13 distortion groups from 50 to 90% of the fit and five hits of searching alongside the rest of the default parameters of the script provided by Mirande (2009). EW searchers followed Hazzi *et al.* (2018), using the command line *hold 1000; mult 30 = tbr drift*. Branch supports were estimated through symmetric resample for IW and jackknife for EW, both under 5000 replicates (Goloboff, 1993b). Character optimisation and the final tree edition were performed with WinClada 1.61 (Nixon, 2021). The preferred phylogenetic hypothesis of each set was submitted under fast transformation (ACCTRAN) character optimisation to study the homoplastic and non-homoplastic characters and each respective character state.

Morphological character polarization

(1) Eyes: eight = 0 (Fig. 13D); six = 1 (Almeida, de Morais, 2022: fig. 7).

(2) Superior tarsal claw: single row of various teeth = 0; only one large tooth on legs I–IV = 1 (Santos *et al.* 2025: fig. 33); only one large tooth on leg IV = 2.

(3) Maxillary lobe: unmodified = 0; anteriorly projected = 1 (Fig. 3).

(4) Eye tubercle: slightly domed = 0; strongly domed = 1 (Fig. 26C; Dupérré, Tapia, 2024: fig. 3).

(5) Cheliceral teeth: one-row arrangement = 0; two rows arrangement = 1 (although some literature states that *Macrothele* (family Macrothelidae) has two rows of teeth on the cheliceral furrow, this is not the case, as shown in several descriptions, (*e.g.* Zhang *et al.*, 2024: fig. 6C).

(6) Cheliceral denticles: absent = 0; present = 1.

(7) Sternum: longer than wide = 0; almost as long as wide = 1.

(8) Spinneret composition: Posterior lateral and median spinnerets present = 0 (Fig. 34F); Posterior lateral spinneret present and posterior median spinnered absent = 1 (Perafán *et al.*, 2019: fig. 1B).

(9) Labial cuspules: few (less than 10) = 0; moderately numerous (less than 70) = 1; numerous (more than 70) = 2.

(10) Coarse spines in tibia I of female: absent = 0; present = 1. Small coarse spines distributed across ventral section of tibia I. These spines are generally covered by soil particles, thus is suggested to gently clean this leg segment using a soft brush.

(11) Posterior lateral spinnerets: long = 0; short = 1 (undoubtedly, the PLS of macrothelids are longer than those in Paratropididae; e.g. (Zhang *et al.*, 2024: fig. 6A).

(12) Preening-combs: absent = 0; present = 1 (incorrectly referenced as “spiny plexus”; e.g. Yang *et al.* (2018: fig. 1O–V), Tang *et al.* (2020, 2022).

(13) Palpal trochanthal lyra: absent = 0; present = 1 (Haupt, 2000: fig. 1).

(14) Midventral rows of bristles on leg tarsi: absent = 0; present = 1 (such bristles are interspersed among the tarsal spines of the legs).

(15) Serrula: present = 0; absent = 1.

(16) Abdominal ventro-basal spinules: absent = 0; present =1. Small resembling spiniform setae, distributed across basal section of abdomen (females and males) on ventral and lateral faces (e.g. Fig. 28E).

(17) Spiky maxillary cuspules: absent = 0; present = 1. Generally elongated cuspules with pointed apex, this type of cuspules constitute exclusively all the maxillary cuspules (Fig. 18H) or in combination of compact and rounded apex cuspules, unmodified cuspules (Fig. 18J).

(18) Femur, patella, and tibia of legs I and II covered with spiniform microtrichium-like scopulae in prolateral, retrolateral, and ventral surfaces (Figs 1, 36A, 38): absent = 0; present = 1.

(19) Coxae dorso-retrolateral and dorso-prolateral surfaces covered with apically dilated multi-layered thin seta: absent = 0; present = 1.

(20) Distal tarsal organ: low and smooth = 0; big and protruding = 1 (Santos *et al.*, 2025: fig. 52).

(21) Apical segment of posterior lateral spinneret: digitiform = 0 (Fig. 13A); domed =1 (Almeida, de Morais, 2022: figs 5, 6).

(22) Male abdominal pattern: absent = 0; present = 1 (Fig. 18A).

(23) Female abdominal pattern: absent = 0; present = 1 (Fig. 26A).

(24) Abdominal setiferous tubercles: absent = 0; presence = 1 (Santos *et al.*, 2025: figs 27, 28, 42, 45).

(25) Dorsal cephalic spinules: absent = 0; present = 1 (Almeida, de Morais, 2022: figs 1, 8).

(26) Fovea: deep without major curvature (regularly with a radial indentation) = 0; shallow and straight = 1; deep and procurved = 2.

(27) Spermathecae, principal branch: shorter (≤1 time the length of oval receptacle or vesicle area) = 0 (Fig. 17F); medium (>1–2 times the length of oval receptacle or vesicle area) = 1 (Fig. 18K–L); elongated (>2 times the length of oval receptacle or vesicle area) = 2 (Fig. 24H).

(28) Spermathecae, principal branch dorsal longitudinal fold: absent = 0; present = 1.

(29) Spermathecae, principal branch ventral longitudinal fold: absent = 0; present = 1.

(30) Spermathecae, principal branch: emerging from wide and rounded bursa copulatrix = 0; emerging from thin and inconspicuous bursa copulatrix = 1.

(31) Spermathecae, receptacle apical concavity: absent = 0; present =1 (Fig. 35F).

(32) Spermathecae, number of receptacles: one = 0; multilobulated (vesicles) = 1.

(33) Spermathecae, simple lobular receptacle: absent = 0; present =1.

(34) Spermathecae, caliciform-shaped receptacle: absent = 0; present =1.

(35) Spermathecae, mushroom-shaped receptacle: absent = 0; present =1.

(36) Spermathecae, digitiform receptacle: absent = 0; present =1.

(37) Spermathecae, dimensionality, one lobule (not applied for vesicles; see character 38): bidimensional = 0; tridimensional = 1.

(38) Spermathecae, dimensionality, multilobular (vesicles): bidimensional = 0; tridimensional = 1.

(39) Spermathecae, receptacle distal concavity: absent = 0; present = 1 (Fig. 17F).

(40) Spermathecae, receptacle width (not applicable for species with vesicles): wider than the width of principal branch = 0; same as principal branch width = 1; thinner than the width of principal branch = 2.

(41) Spermathecae, receptacle or vesicle sclerotisation: constant to the rest of spermathecae = 0; slightly more sclerotised = 1; hypersclerotised = 2.

(42) Spermathecae, principal branch sclerotised neck (constriction): absent = 0; present = 1.

(43) Spermathecae, distal sclerotised ring of principal branch: absent = 0; present = 1.

(44) Spermathecae, wide membranous plate below spermathecae: absent = 0; present = 1.

(45) Palpal bulb, tegulum/embolus length proportion: embolus less than ~5 times tegulum length = 0; embolus more than ~5 times tegulum length = 1.

(46) Palpal bulb, ventral median depression (sensu Sherwood *et al.* (2021): absent = 0; present = 1.

(47) Palpal bulb, dorsal embolic keel: absent = 0; present = 1 (Fig. 33D–E).

(48) Palpal bulb, prolateral embolic keel: absent = 0; present = 1 (Fig. 19C).

(49) Palpal bulb, embolus curvature: absent = 0; median section = 1 (Figs 19, 33); distal section = 2 (*e.g.* Dupérré, Tapia, 2020: figs 5–9, 39–41).

(50) Male tibial apophysis: absent = 0; present = 1 (males of macrothelids do not bear an apophysis, but several isolated spines).

(51) Male tibia I, retrolateral basal process: absent = 0; present = 1 (Dupérré, Tapia, 2024: fig. 29A, C).

(52) Male tibia I, retrolateral cluster of spines (preening brush): absent = 0; present = 1 (Dupérré, Tapia, 2024: fig. 29D).

(53) Retrolateral cymbial apophysis: absent = 0; present = 1 (Fig. 2).

(54) Prolateral teeth row (male and female specimens): continuous = 0 (Fig. 3A); remarkably discontinuous = 1 (Fig. 3B).

(55) Spermathecae, principal branch basal dilatation: absent = 0; present = 1 (Sherwood *et al.*, 2022: fig. 14).

Definition of some new characters

Longitudinal folds (modified from Dupérré & Tapia (2020)): Vertical cuticular folds that generally extend over spermathecae principal branch longitudinal folds and basal section of each spermathecal receptacle. The classification of these folds follows the position in which they develop (dorsal (Dupérré, Tapia, 2020: figs 11–12 or ventral (Fig. 18K)).

Receptacle concavities (proposed herein): Indentations located at the dorsal and apical surface of each spermathecal receptacle. Depending on the position of these indentations each one is classified as distal concavity (dorsal surface of receptacle, distal section of spermathecae) (Figs 17F, 18L, 23F, 24H, 25F, 26F, 28I) and apical concavity (apical surface of receptacle, apical section of spermathecae) (Fig. 35F).

Embolic keels (subapical tooth *sensu* Perafán *et al.* (2019), and embolic tooth *sensu* Sherwood *et al.* (2023): Herein, we propose a new name and follows a new classification concerning what embolus surface this structure develops (prolateral and dorsal surfaces). Thus, prolateral embolic keel and dorsal embolic keel terms are suggested to be used for future studies regarding this family. Generally, the prolateral embolic keel is visible at a dorsal view of the bulb (Fig. 19C) while the dorsal embolic keel is visible at prolateral or retrolateral views (Fig. 33).

Material and species description format

Examined type and non-type material are deposited at the Museo de Zoología, Universidad San Francisco de Quito, Quito, Ecuador (ZSFQ-i); Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito, Ecuador (QCAZ); Natural History Museum, London, United Kingdom (BMNH); Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil (INPA-ARA); Museum of Natural History Karlsruhe, Karlsruhe, Germany (SMNK-ARA); Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina (MACN-Ar); Zoologisches Museum, Berlin, Germany (ZMB).

Specimens deposited at ZSFQ-i were examined and measured under an Olympus SZX16 stereomicroscope with an Olympus DP73 digital camera using Micro Imaging Software CellSens for Olympus. Specimens deposited at QCAZ were examined under a Nikon SMZ745T. Specimens deposited at BMNH were examined and measured under a Leica MZ12.5 stereomicroscope. Specimens deposited at INPA-ARA, SMNK-ARA, MACN, and ZMB were examined and measured under a Leica M205 auto-montage. Chelicerae length is considered in total length. Female genitalia were excised using a syringe tip, soft tissue digested with a solution of 15% potassium hydroxide KOH, washed in distilled water and 75% ethanol. Compound images were obtained by stacking a series of photographs taken at different depths and then processed with the staking software of Helicon Focus and editing tools of Photoshop. Morphological descriptions and terminology follow Sherwood *et al.* (2022), but in a shorter format, notation of spines follows the format of Dupérré & Tapia (2020) and only considers coarse spines present in tarsi, metatarsi, and tibiae if present. This paper was registered in ZooBank prior to publication: urn:lsid:zoobank.org:pub:68E67835-3780-410A-82B2-DDB82A11EA00.

Morphological abbreviations

Legs spination terminology: plv — prolatero-ventral; rlv — retrolatero-ventral.

Somatic: AME — anterior median eyes; ALE — anterior lateral eyes; PME — posterior median eyes; PLE — posterior lateral eyes; PLS — posterior lateral spinnerets; PMS — posterior median spinnerets; ITC

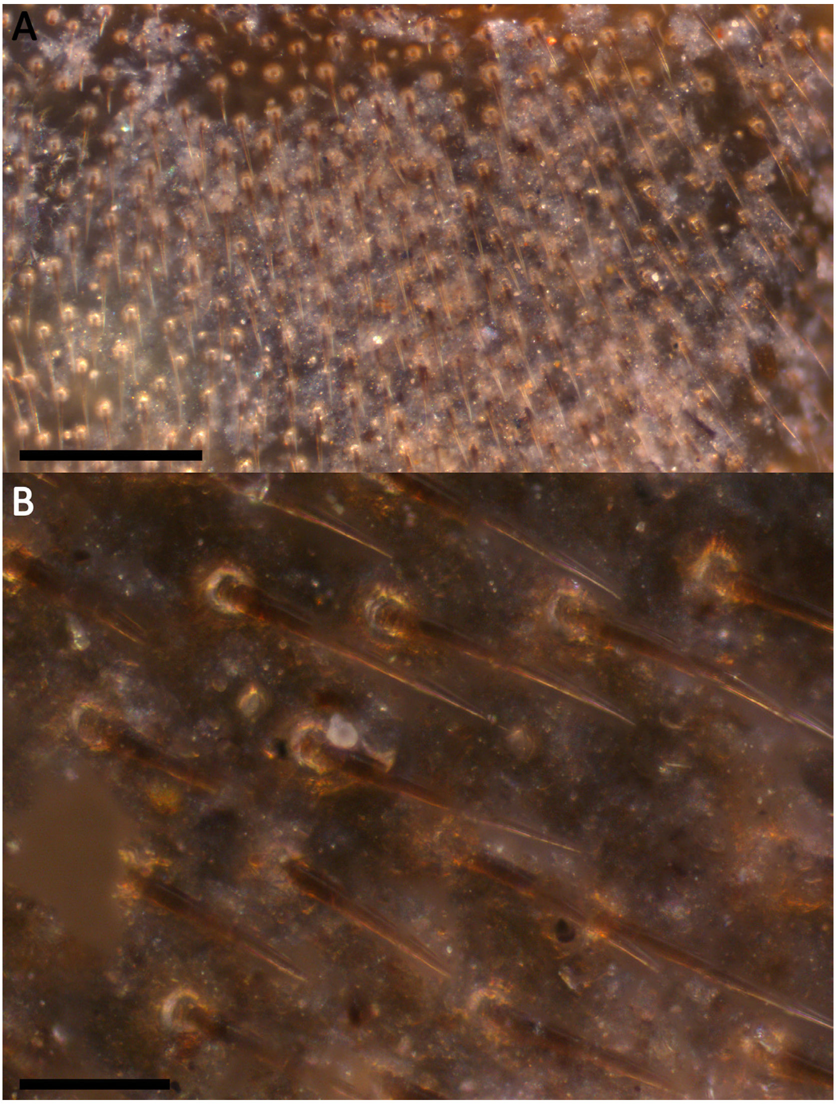

Fig. 1. Spiniform microtrichium-like scopulae of femur I in *Yamaratropis machinaza* sp.n., holotype female (ZSFQ-i20433): A — general view; B — close-up view. Scale bars = 0.07 mm (A); 0.01 mm (B).

— inferior tarsal claw; Sps — multi-layered spatulate seta; Sts — multi-layered thin seta.

Female genitalia: AC — apical concavity; DC — distal concavity; DLF — dorsal longitudinal fold; VE — vesicles; VLF — ventral longitudinal fold.

Male genitalia: PEK — prolateral embolic keel; DEK — dorsal embolic keel.

Results

Morphological phylogeny

Morphological characters in both sets composed 49% of the character entries as general somatic features while 35% were composed of spermathecal morphology and 16% composed of exclusive male tibiae, cymbium, and palpal bulb morphology (51% sexual characters). A total of 21 terminal taxa were evaluated on the first dataset (see Appendix 1), nine of these taxa were scored for both males and females, while ten were scored only from females and two for males. On the second dataset (see Appendix 2), a total of 26 terminal taxa were evaluated, nine of these taxa were scored for both males and females, while twelve were scored only for

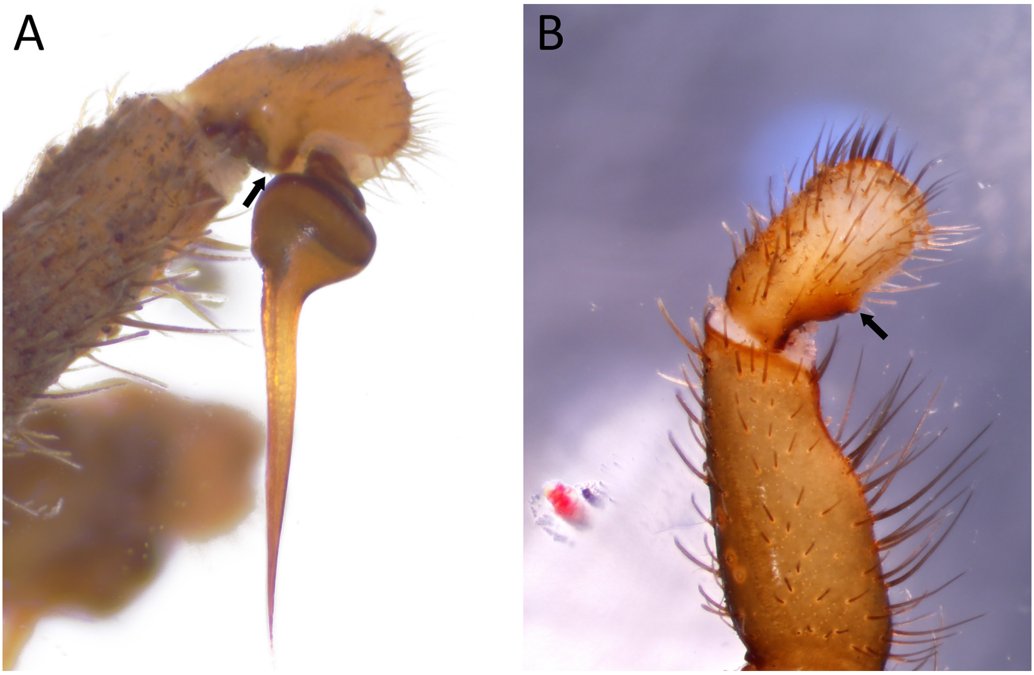

Fig. 2. Retrolateral cymbial apophysis (arrow): A — non-type male of *Paratropis elicioi* (QCAZ I260724); B — paratype male (ZSFQ-i20430) of *Alienus abditus* sp.n.

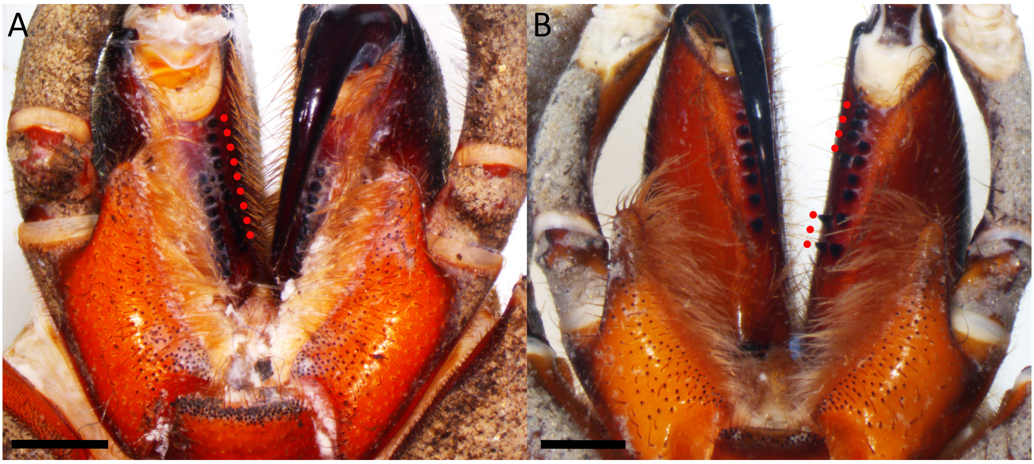

Fig. 3. Prolateral teeth row morphology: A — holotype female (ZSFQ-i20434) of *Paratropis nunka* sp.n., continuous row; B — holotype female (ZSFQ-i20430) of *Yamaratropis machinaza* sp.n., remarkably discontinuous. Scale bars: 2 mm (A); 1 mm (B).

females and five for males. Regarding recent publications related to some species described and placed within *Paratropis* (Almeida, Morais, 2022; Dupérré, Tapia, 2024), the following analyses of both datasets indicated that currently, these species recover *Paratropis* as polyphyletic (i.e., "*P.*" *minuscula* and "*P.*" *pasochoa*). Herein these polyphyletic clades were considered novel genera with the generic placement and naming of each taxon in the analysed phylogenies following the new proposed taxonomic classification within Paratropididae genera (see Taxonomy

Table 1. Results from the phylogenetic inference under implied weighting using second dataset.

Reference	Distortion	*K* value	Steps	Trees	Total fit
K0	50.00	0.57	98	3	11.54
K1	53.33	0.66	98	3	11.19
K2	56.67	0.75	98	3	10.82
K3	60.00	0.86	98	3	10.42
K4	63.33	0.99	98	3	10.00
K5	66.67	1.15	98	3	9.53
K6	70.00	1.34	96	3	9.02
K7	73.33	1.58	96	3	8.43
K8	76.67	1.89	96	3	7.78
K9	80.00	2.30	96	3	7.07
K10	83.33	2.87	96	3	6.28
K11	86.67	3.73	96	3	5.39
K12	90	5.16	96	3	4.38

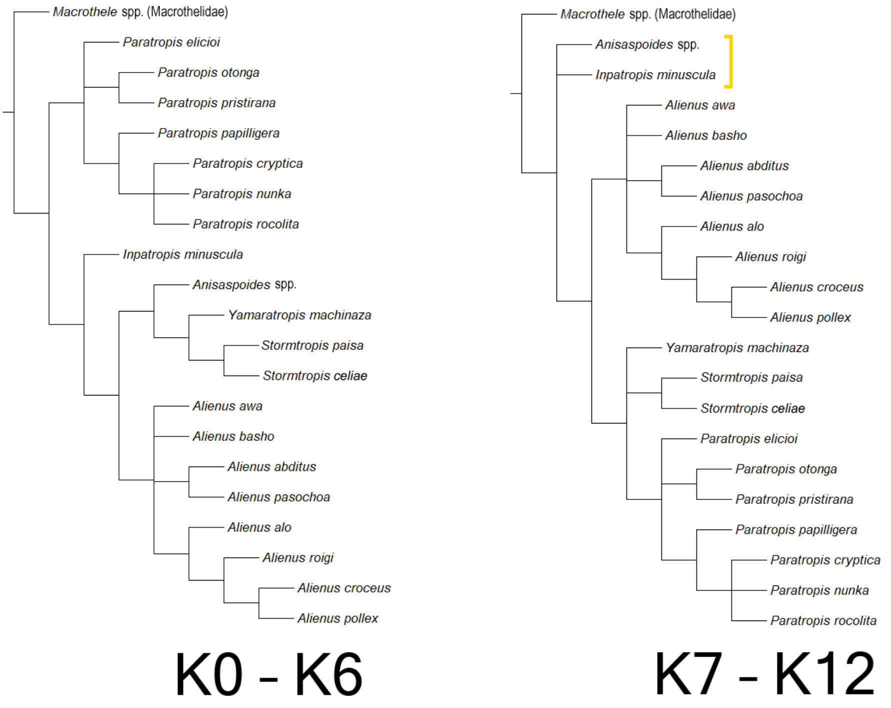

Fig. 4. Strict consensus tree topology patterns of inferred phylogenetic hypothesis of Paratropididae based on implicit weighting strategy under different k-values ranged into two range regimes, first dataset. Yellow band represents unresolved phylogenetic relationships. Abbreviations: K — representation of each K value (see Table 1).

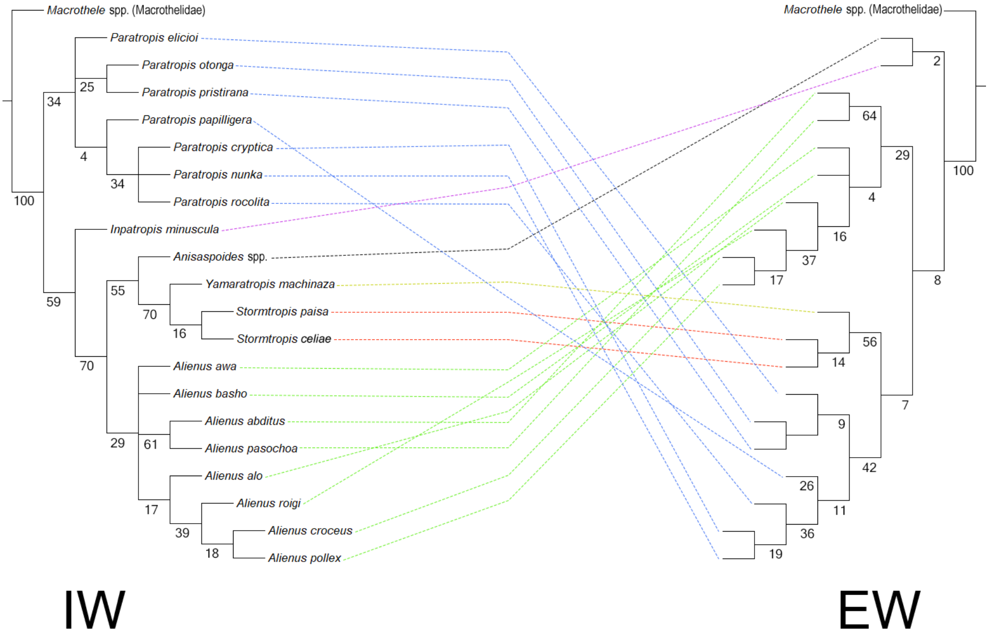

Fig. 5. Strict consensus topologic comparison between preferred IW ($K = 0.861$, 100 steps, CI = 58, RI = 61) and EW (98 steps, CI = 59, RI = 63) analyses from the first dataset. Colour dotted line represents the generic placement of each species and its respective placement between both analyses. Support values for IW (symmetric resampling) and EW (jackknifing) are expressed as GC (Group present/Contradicted). Abbreviations: EW — equal weighting; IW — implicit weighting.

for further information regarding new genera and species, including new combinations and remarks on constrained taxonomic actions for future research).

First dataset analysis

Using the first dataset, implied weight analyses of the 13 distortion groups (Table 1) indicated two general topologies of strict consensus trees alongside the *k*-values ranges of 0.574–1.148 and 1.339 (Fig. 4). The first pattern topology supported the monophyly of all the known genera of Paratropididae: *Alienus* gen.n., *Inpatropis* gen.n., *Paratropis, Stormtropis*, and *Yamaratropis* gen.n. The second topology pattern only supports *Alienus* gen.n., *Paratropis, Stormtropis,* and *Yamaratropis* gen.n. since the placement of *Inpatropis* gen.n. and *Anisaspoides* are unclear as they were recovered as unresolved. Additionally, although grouping clades are consistent within each genus, the most distal clades, *Paratropis*, *Stormtropis*, and *Yamaratropis* gen.n. were collapsed as a trichotomy. In order to further compare the results of this first dataset, we selected a strict consensus tree containing the first pattern since this recovers a better resolution within the studied genera. Specifically, the strict consensus obtained under the *k*-value of 0.861 (100 steps, CI = 58, RI = 61) (Figs 5–6).

In contrast, the equal weight analysis found 63 most parsimonious trees with 98 steps, CI = 59, RI = 63. The strict consensus (Fig. 5) showed a similar topology as the second pattern found in implied weight, nonetheless, results under equal weight recovered all the genera as monophyletic and clearly resolved each phylogenetic relationship. Although this strict consensus indeed shows the best result using these heuristic strategies, results of the implied weight indicated higher support values and were thus decided as the topology with the preferred phylogenetic hypothesis for this dataset. Similarly, this hypothesis

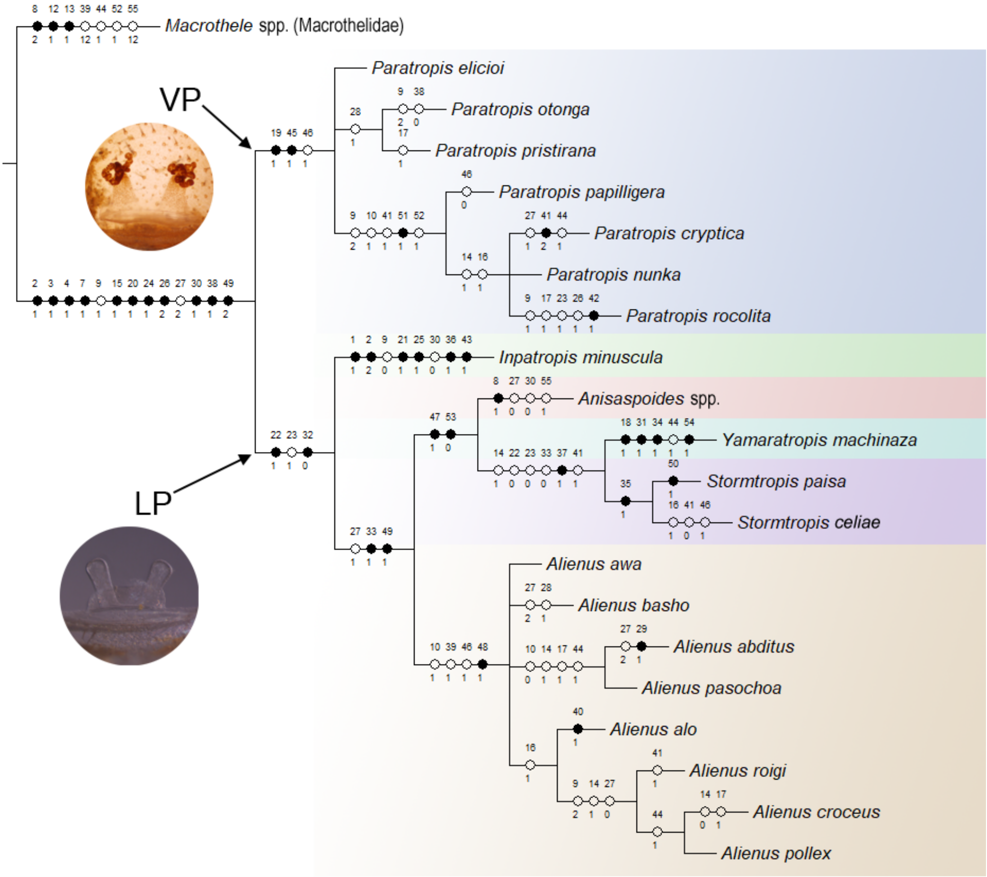

Fig. 6. Preferred phylogenetic hypothesis of Paratropididae using the first dataset. Coloured clade are the herein recognised genera. Black circles, putative synapomorphic characters; white circles, homoplastic characters. Abbreviations: LP — Lobular Paratropids clade; VP — Vesicular Paratropids clade. LP — spermathecae reference of *A. alo* sp.n.; VP — spermathecae reference of *P. cryptica*.

was selected to further the study of delimiting characters in clades of interest.

Following the preferred hypothesis of the first dataset (Fig. 6), Paratropididae is recovered with eight putative synapomorphic characters regarding the closest family (Macrothelidae): the presence of only one large tooth on tarsal claws (Character 2), anteriorly projected maxillary lobe (Character 3), strongly domed eye tubercle (Character 4), cheliceral teeth arranged in two rows (Character 7), absence of serrula (Character 15), big and protruding tarsal organ (Character 20), abdominal setiferous tubercles (Character 24), and remarkable embolus curvature (Character 49). Character 4 and 24 could be considered exempt of homoplasy. Although characters 26, 30, 38 were also optimised as synapomorphies these appear multiple times on other Mygalomorph families. Within Paratropididae two major clades are recognised of which a subfamily status can be considered, nonetheless we expect that future research can firmly confirm this (See Discussion). Herein these clades are referred as “Vesicular Paratropids” (VP) and “Lobular Paratropids” (LP).

The VP clade is only composed of *Paratropis* which is supported and delineates the same genus by two putative synapomorphic characters: the presence of STS setae apically dilated over coxae (Character 19) and the embolus being more than ~5 times tegulum length (Character 45). Within *Paratropis*, two clearly recognised clades are

Table 2. Results from the phylogenetic inference under implied weighting.

Reference	**Distortion**	***K* value**	**Steps**	**Trees**	**Total fit**
K0	50.00	0.67	105	7	11.37
K1	53.33	0.77	105	7	11.02
K2	56.67	0.88	105	7	10.65
K3	60.00	1.00	105	7	10.26
K4	63.33	1.16	105	7	9.83
K5	66.67	1.34	105	7	9.38
K6	70.00	1.57	105	7	8.88
K7	73.33	1.85	103	7	8.36
K8	76.67	2.1	103	7	7.73
K9	80.00	2.69	103	7	7.05
K10	83.33	3.36	103	7	6.29
K11	86.67	4.37	103	7	5.43
K12	90	6.05	103	7	4.43

identified. The first clade contains two northwestern Ecuadorian species, *P. otonga* and *P. pristirana*, and are supported by the homoplastic presence of a dorsal longitudinal fold on principal branch (Character 28). The other clade includes in majority Amazonian species, *P. papilligera, P. cryptica*, *P. nunka* sp.n., and *P. rocolita* sp.n. (northwestern Ecuadorian species). This clade is supported by the presence of a retrolateral basal process (Character 51) as a synapomorphy and the following four homoplastic characters: numerous cuspules (Character 9), presence of coarse spines in female tibia (Character 10), sclerotisation of vesicles constant to the rest of spermathecae (Character 41), presence of a retrolateral cluster of spiniform and elongated setae on male tibia I (Character 52).

The LP clade is composed by *Alienus* gen.n., *Anisaspoides*, *Inpatropis* gen.n., *Stormtropis*, and *Yamaratropis* gen.n., and is supported by the plesiomorphic presence of an abdominal pattern (Character 22) and a single lobule receptacle (Character 32). Additionally, the presence of an abdominal pattern in females (Character 23) is recovered as a homoplastic character for LP. *Inpatropis* gen.n. (monotypic: *I. minuscula* gen. et comb.n.) is recovered as sister to the remaining LP clade genera and is supported by six autapomorphic characters: six eyes (Character 1), loss of the single large tooth in tarsal claw of legs I, III, and IV (Character 2), domed apical segment of posterior lateral spinnerets (Character 21), cephalic spinules (Character 25), digitiform spermathecae receptacle (Character 36), and a distal sclerotised ring of principal branch of spermathecae (Character 43). The genera *Alienus* gen.n., *Anisaspoides*, *Stormtropis*, and *Yamaratropis* gen.n. are separated from *Inpatropis* gen.n. by the plesiomorphic lobular spermathecae receptacle (Character 33) (loss of this character in *Yamaratropis* gen.n. and *Stormtropis*) and the synapomorphic embolus curvature at median section (Character 49).

Subsequently *Anisaspoides*, *Stormtropis*, and *Yamaratropis* gen.n. are recovered grouped within a clade sister of *Alienus* gen.n. Basally to this clade, *Anisaspoides* is positioned and supported by the notorious autapomorphic loss of the posterior median spinnerets (Character 8) and three homoplastic characters: short length of principal branch (Character 27), wide and rounded bursa copulatrix (Character 30) and spermathecae principal branch basal dilatation (Character 55). Meanwhile, *Stormtropis* and *Yamaratropis* gen.n. are recovered as sister genera and are supported by the tridimensionality of spermathecae receptacle (Character 37), here considered as a synapomorphy, and five

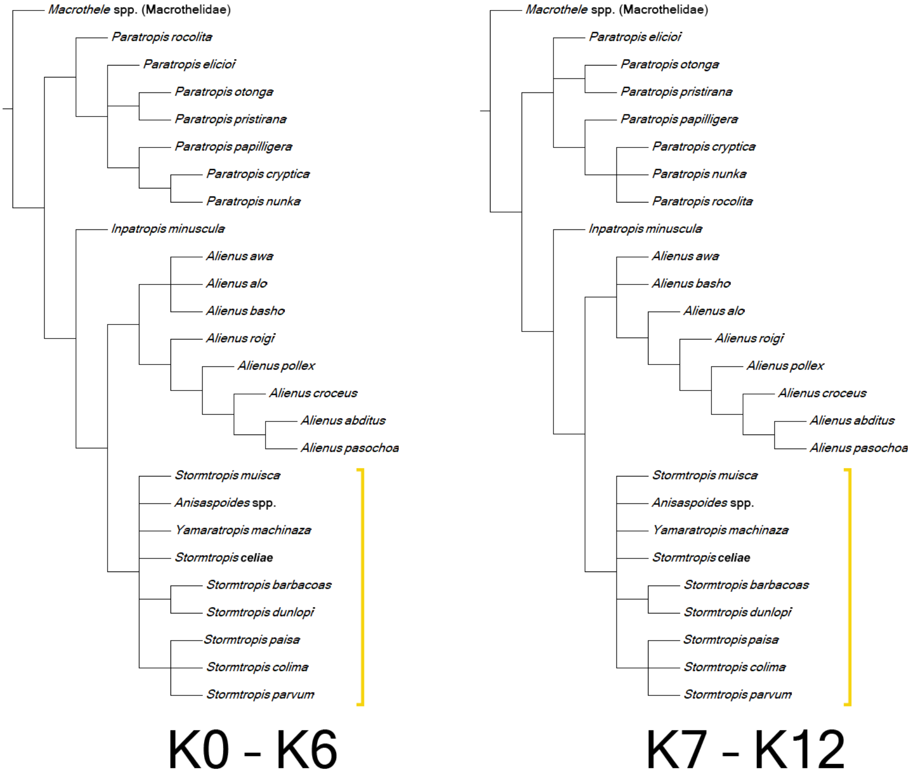

Fig. 7. Strict consensus tree topology patterns of inferred phylogenetic hypothesis of Paratropididae based on implicit weighting strategy under different k-values ranged into two range regimes, second dataset. Yellow band represents unresolved phylogenetic relationships. Abbreviations: K — representation of each K value (see Table 2).

homoplastic characters: coarse spines in tibia I of female (Character 10), absence of abdominal pattern in males and females (Characters 22 and 23), receptacle being not lobular (Character 33), receptacle slightly more sclerotised than branch (Character 41).

Alienus gen.n., the most distant genera, is supported by the synapomorphic presence of a prolateral embolic keel (Character 48) and the following three homoplastic characters: presence of coarse spines in female tibia (Character 10), receptacle distal concavity (Character 39), and a ventral median depression (Character 46). Inside *Alienus* gen.n. two clades are clearly recognised. The first clade is composed by inter-Andean species, *A. abditus* sp.n. and *A. pasochoa* comb.n., and is supported by the following four homoplastic characters: absence of coarse spines in tibia I of female (Character 10), presence of midventral rows of bristles on leg tarsi (Character 14), spiky maxillary cuspules (Character 17), and presence of a wide membranous plate below spermathecae (Character 44).

Second dataset analysis

Using the second dataset, implied weight analyses of the 13 distortion groups (Table 2) indicated two general topologies of strict consensus trees alongside the *k*-values ranges of 0.67–1.57 and 1.85–6.05 (Fig. 7). Both topologies supported the monophyly of *Alienus* gen.n., *Inpatropis* gen.n., and *Paratropis*. While the placement and broader relationships of *Anisaspoides*, *Stormtropis*, and *Yamaratropis* gen.n. were not recovered since these strict consensuses showed a lack of resolution on the distal clades and a

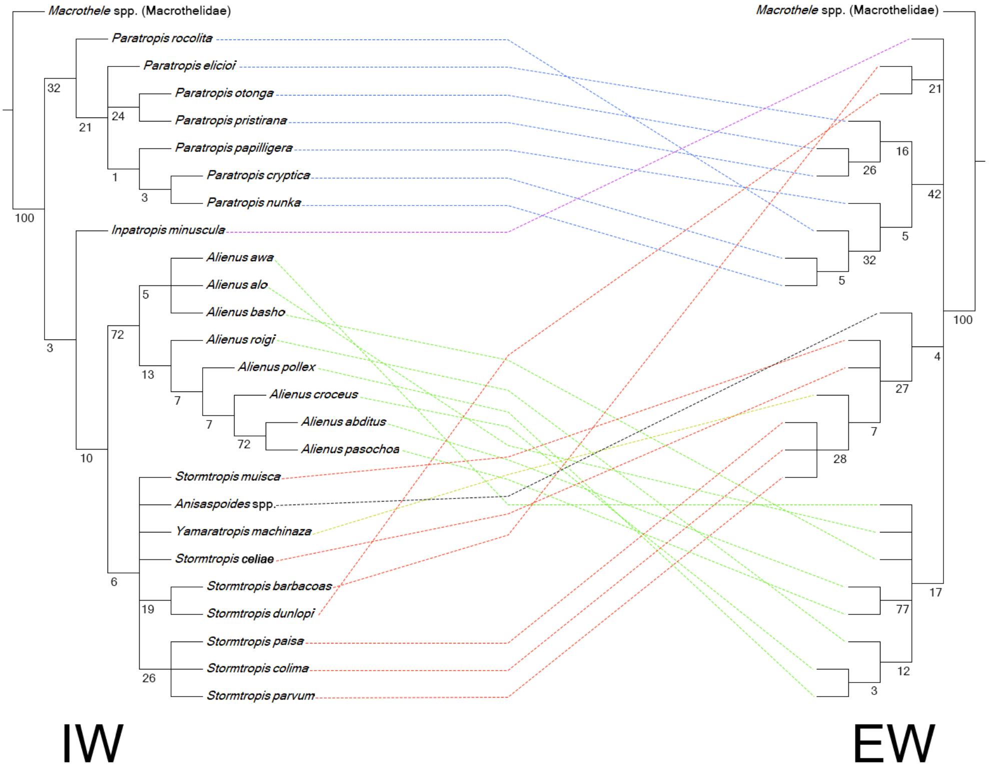

Fig. 8. Strict consensus topologic comparison between preferred IW ($K = 1.57$, 105 steps, CI = 53, RI = 62) and EW (113 steps, CI = 51, RI = 58) analyses from the second dataset. Colour dotted line represents the generic placement of each species and its respective placement between both analyses. Support values for IW (symmetric resampling) and EW (jackknifing) are expressed as GC (Group present/Contradicted). Abbreviations: EW — equal weighting; IW — implicit weighting.

better resolution to basal branches; although two groups of *Stormtropis* were identified (*S. barbacoas* sp.n. + *S. dunlopi* sp.n., herein referred as “A”) and (*S. paisa* + *S. colima* + *S. parvum*, herein referred as clade “B”). Wherein, regarding implied weight analyses we decided to use the most parsimonious (108 steps, CI = 53, RI = 62) and strict consensus (105 steps, CI = 53, RI = 62) trees obtained under the K value of 1.57 for further analysis and comparison between equal weight search (Fig. 8) between results of this dataset.

Equal weight analysis of the second dataset found 300 most parsimonious trees with 113 steps, CI = 51, and RI = 58. The strict consensus (Fig. 8) showed also the monophyly of *Alienus* gen.n., *Inpatropis* gen.n., and *Paratropis*. In comparison with the implied weight strict consensuses trees (Figs 4–5), this strict consensus provided further resolution to the distal clades and recovered *Stormtropis* as paraphyletic, separated by the same identified groups during implied weight analyses (see above). The group B, “basally” positioned, also contained *Anisaspoides*, *Yamaratropis* gen.n., and two unresolved *Stormtropis* (*S. muisca* and *S. celiae* comb.n.) of which could provide taxonomic instability. Although the equal weight analysis provided a better resolution to more Paratropididae genera, particularly regarding *Stormtropis*, wider relationships between genera are not recovered as in the implicit weight (Figs 7–8). By further comparing the obtained strict consensuses trees of both strategies, these trees presented low and mid-range values for branch supports which could be explained due to the low number of spe-

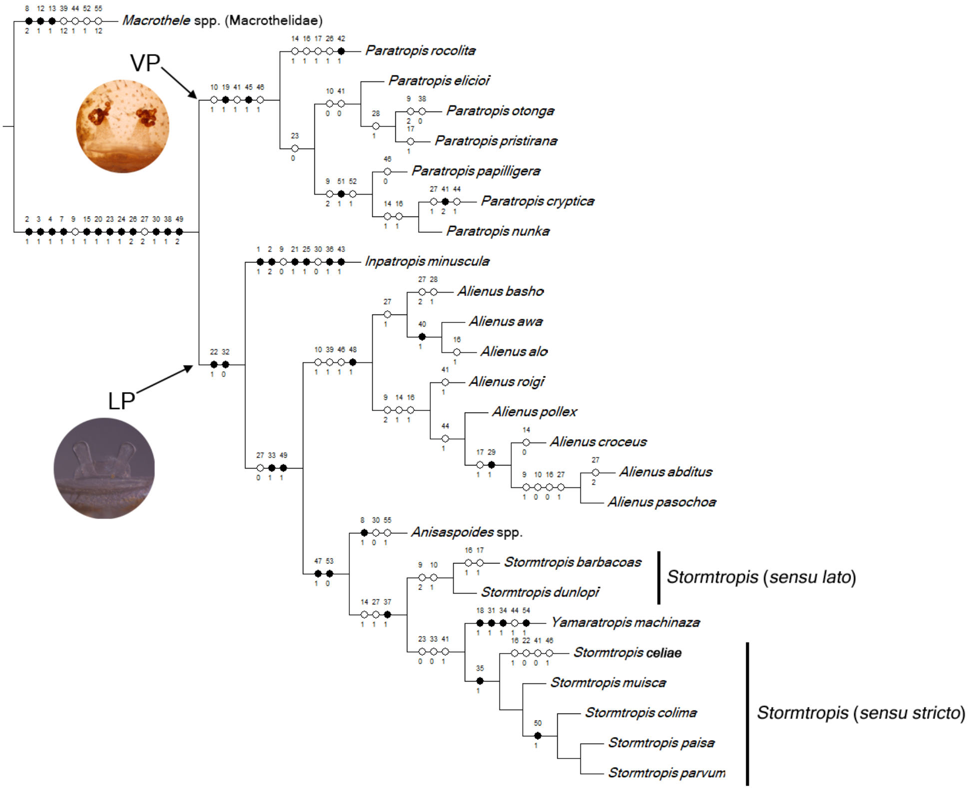

Fig. 9. Most parsimonious topology using IW (*K* = 1.57, 108 steps, CI = 53, RI = 62) for preferred phylogenetic hypothesis of Paratropididae using the second dataset. Coloured clade are the herein recognised genera. Black circles, putative synapomorphic characters; white circles, homoplastic characters. Abbreviations: LP — Lobular Paratropids clade; VP — Vesicular Paratropids clade. LP —spermathecae reference of *A. alo* sp.n.; VP — spermathecae reference of *P. cryptica*.

cies where both sexes' information was available; thus highlighting the need for the discovery of the missing sex of these single-sex-documented species. Robinson-Foulds distances indicated a value of 0.35, which also explains the drifting of some internal nodes of each genus and the changing position of all the studied genera, including groups A and B of *Stormtropis*, but overall, both topologies share 65% of similarity.

In the case of how to approach the unresolved relationship of *Anisaspoides*, *Stormtropis*, and *Yamaratropis* gen.n. in the second dataset, the implicit weight strategy — specifically under K = 1.57 as the preferred parameter — was considered due to the better capacity to resolve and identify genera relationships and their placement. For the consideration of a preferred phylogenetic hypothesis, one topology was found to be the most congruent, parsimonious, and taxonomically stable tree to discuss character transformation and ingroup relationships (Fig. 9) for Paratropididae. Additionally, this topology coincided with the preferred phylogenetic hypothesis of the first dataset.

Following the preferred hypothesis of the second dataset, Paratropididae was recovered with eight putative synapomorphic characters regarding the closest family (Macrothelidae): the presence of only one large tooth on tarsal claws (Character 2), anteriorly projected maxillary lobe (Character 3), strongly domed eye tubercle (Character 4), cheliceral teeth arranged in two rows (Character 7), absence of serrula (Character 15), big and protruding tarsal organ (Character 20), abdominal setiferous tubercles (Character 24), and remarkable embolus curvature (Character 49)

(Character 4 and 24 could be considered exempt of homoplasy). Within Paratropididae two major clades were recognised that could be considered for subfamily status, nonetheless we considered that future research can firmly confirm this (see Discussion). Herein these clades were referred to as "Vesicular Paratropids" (VP) and "Lobular Paratropids" (LP).

The VP clade was only composed of *Paratropis* which was supported and delineated the same genus by two putative synapomorphic characters: the presence of STS setae apically dilated over coxae (Character 19) and the embolus being more than ~5 times tegulum length (Character 45). Within *Paratropis*, *P. rocolita* sp.n. (northwestern Ecuadorian species) was recovered as sister to all the remaining *Paratropis* and supported by a notable and divergent synapomorphic principal branch sclerotised neck (Character 42). In the remaining *Paratropis*, two clades were recognised and shared the loss of an abdominal pattern [albeit confirmed by females but also inferred in males] (Character 23). The first clade included other northwestern Ecuadorian species, *P. elicioi, P. otonga*, and *P. pristirana*, supported by two homoplastic characters: absence of coarse spines in female tibia I (Character 10) and sclerotization of vesicles constant to the rest of spermathecae (Character 41). The second clade was composed by three Amazonian (Brazil, Colombia, and Ecuador) species, *P. cryptica*, *P. nunka* sp.n., and *P. papilligera*, and were supported by the synapomorphic presence of a retrolateral basal process in male tibia I (Character 51). Also, the numerous cuspules (Character 9), and presence of a retrolateral cluster of spiniform and elongated setae in male tibia I (Character 52) were homoplastic conditions supporting the second clade.

The LP clade, as in the first dataset, was composed by *Alienus* gen.n., *Anisaspoides, Inpatropis* gen.n., *Stormtropis*, and *Yamaratropis* gen.n., and was supported by the plesiomorphic presence of an abdominal pattern [confirmed by males but inferred in females] (Character 22) and a single lobule receptacle (Character 32). *Inpatropis* gen.n. (monotypic) was recovered as sister to the remaining LP clade genera and was supported by six autapomorphic characters: six eyes (Character 1), loss of the single large tooth in tarsal claw of legs I, III, and IV (Character 2), domed apical segment of posterior lateral spinnerets (Character 21), cephalic spinules (Character 25), digitiform spermathecae receptacle (Character 36), and a distal sclerotised ring of principal branch of spermathecae (Character 43). The genera *Alienus* gen.n., *Anisaspoides*, *Stormtropis*, and *Yamaratropis* gen.n. were separated from *Inpatropis* gen.n. by the plesiomorphic lobular spermathecae receptacle (Character 33) (loss of this character in *Yamaratropis* gen.n. and some *Stormtropis*) and the synapomorphic embolus curvature at median section (Character 49).

Alienus gen.n. was recovered as sister of *Anisaspoides*, *Stormtropis*, and *Yamaratropis* gen.n. and was supported by the synapomorphic presence of a prolateral embolic keel (Character 48) and the following three homoplastic characters: presence of coarse spines in female tibia (Character 10), receptacle distal concavity (Character 39), and a ventral median depression (Character 46). Internally two clades were recovered and match geographical distributions. The first clade groups north- and southwestern Ecuadorian species, *A. alo* sp.n., *A. awa* sp.n., and *A. basho* sp.n., and were supported by the homoplastic median length of principal branch (Character 27).

The second clade comprised northwestern, Amazonian, and inter-Andean Ecuadorian species (*A. basho* sp.n. as basal species to this clade, northwestern Ecuador distribution) (*A. croceus* sp.n. and *A. pollex* sp.n., Ecuadorian Amazonia distribution) (*A. abditus* sp.n. and *A. pasochoa* comb.n., inter-Andean distribution). This clade was supported by three homoplastic characters: numerous labial cuspules (Character 9), midventral rows of bristles on tarsi (Character 14), and abdominal ventro-basal spinules (Character 16). The receptacle distal concavity was also present for *Anisaspoides*, we inferred that this spermathecal receptacle structure could be plesiomorphic to the basal genera of this clade (e.g. *Alienus* gen.n. and *Anisaspoides*).

The three aforementioned genera, previously clustered and unresolved using the second dataset in strict consensuses trees, were resolved herein as the most distant clade within the LP clade, supported by the synapomorphic presence of a dorsal embolic keel (Character 47) and the loss of a retrolateral cymbial apophysis (Character 53). Basally to this clade, *Anisaspoides* was positioned and supported by the notorious autapomorphic loss of the posterior median spinnerets (Character 8) and two homoplastic characters: wide and rounded bursa copulatrix (Character 30) and spermathecae principal branch basal

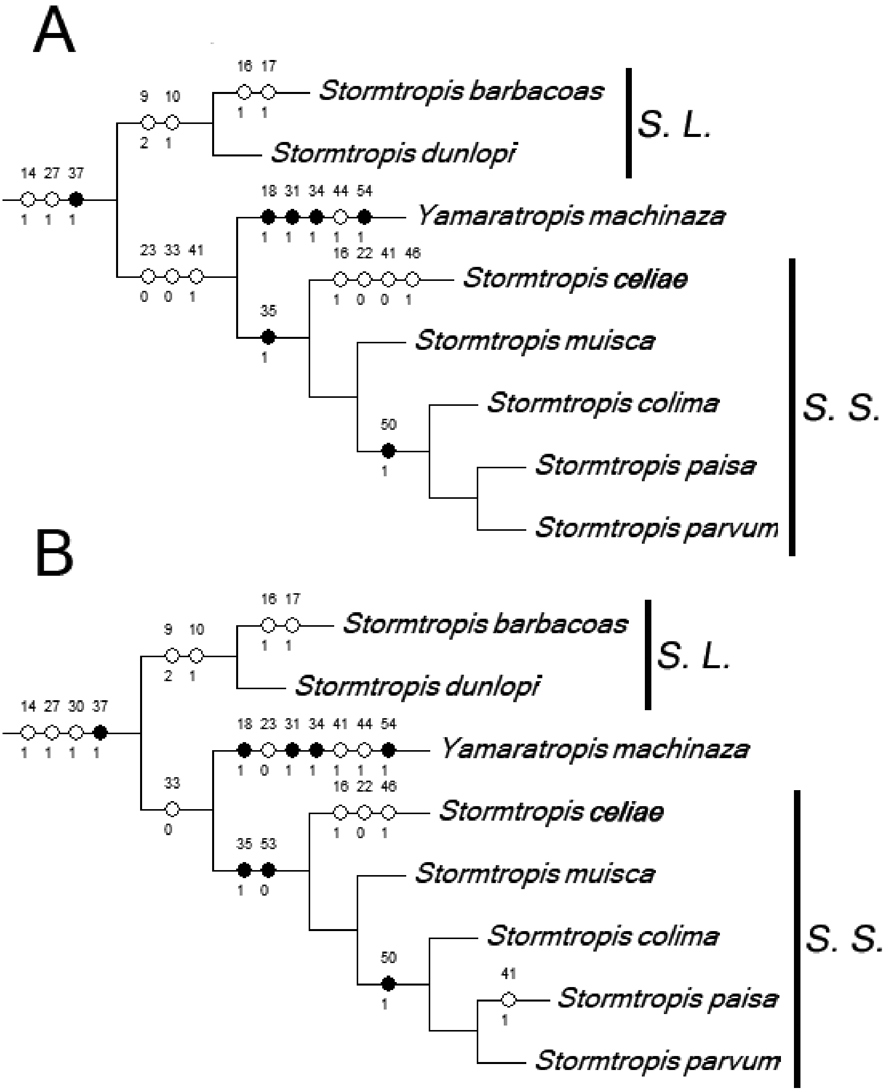

Fig. 10. Preferred phylogenetic hypothesis of Paratropididae using the second dataset, *Stormtropis* character optimisation comparison: A — Fast optimisation (ACCTRAN); B — Slow optimisation (DELTRAN).

dilatation (Character 55). The large clade containing *Stormtropis* and *Yamaratropis* gen.n. was supported by the tridimensionality of the spermathecae receptacle (Character 37), here considered a synapomorphy. Subsequently, *Stormtropis* was still found to be paraphyletic (group A and B), but intersected by *Yamaratropis* gen.n. which is highly supported by four autapomorphic characters: Femur, patella, and tibia of legs I–II with microthrichium-like scopulae (Character 18), receptacle apical concavity (Character 31), caliciform-shaped spermathecae receptacle (Character 34), and prolateral cheliceral teeth row remarkably discontinuous (Character 54). For this reason, we did not consider this large sister clade of *Anisaspoides* as a whole generic unit. Additionally, *Stormtropis sensu lato* was assigned to group A due to the spermathecae morphology affinity to the only known female of previously described species (*S. paisa*).

Importantly, it is in our knowledge that other colleagues are researching the new genus resembling the morphology of group A (see also Taxonomy, *Paratropis* remarks) and we therefore respect their work in not establishing a new genus to house these species (Fernando Pérez-Miles pers. comm. to PP-R). Until their work is published, we considered group A as *Stormtropis sensu lato*, while members of group B are considered as *Stormtropis sensu stricto*. Following this, *Stormtropis sensu lato* was weakly supported by two homoplastic characters: numerous labial cuspules (Character 10) and the presence of coarse spines in female tibia I (Character 10). The absence of non-homoplastic characters could be explained due to the lack of male data entry. Conversely, *Stormtropis sensu stricto* (group B, including also *S. celiae* comb.n. and *S. muisca*) was recovered with only one synapomorphy: mushroom-shaped spermathecae receptacle (Character 35). Interestingly, by also comparing DELTRAN character optimisation, the loss of the retrolateral cymbial apophysis (Character 53) also supported *Stormtropis sensu stricto* as a synapomorphy (Fig. 10); which changed from supporting the whole clade to this genus alone. Internally, *S. colima*, *S. paisa*, and *S. parvum* group together by the synapomorphic presence of a tibial apophysis (Character 50).

Comparison of datasets

By evaluating both datasets we determined that the first dataset was more informative regarding the phylogenetic placement and monophyly of each genus and hence is the recommended phylogenetic organisation and recognition of Paratropididae genera (Fig. 6). Nonetheless, there is still work to be done in order to have a complete understanding on the phylogenetic hypotheses within Paratropididae. We hope that with the addition of upcoming research we can provide more information using the first dataset on the placement of the herein-stated *Stormtropis sensu lato* by adding representatives with data entry of both sexes.

Taxonomy

Paratropididae Simon, 1889

TYPE GENUS: *Paratropis* Simon, 1889 by original designation of Simon (1889).

DIAGNOSIS: Paratropididae can be distinguished from all other spider families by the following set of characters: absence of abdominal sclerites; absence of a serrula; absence of claw tufts; presence of modified setae encrusted with soil arising from symmetrical tubercles on the dorsal abdomen (setiferous tubercles); labium with numerous cuspules (except *Inpatropis* gen.n.), densely covering the anterior edge of the labium; cuticle encrused with mud, and ocular tubercle highly raised.

DISTRIBUTION: North, Central, and South America.

GENERA INCLUDED: *Anisaspoides* F.O. Pickard-Cambridge, 1896; *Alienus* gen.n., *Anisaspis* Simon, 1892 *nomen dubium*; *Inpatropis* gen.n.; *Paratropis* Simon, 1889; *Stormtropis* Perafán, Galvis et Pérez-Miles, 2019; *Yamaratropis* gen.n.

Paratropis Simon, 1889

Paratropis Simon, 1889: 215.

Paratropis: Simon, 1891, 1897, Pickard-Cambridge, 1896, Mello-Leitão, 1923, Caporiacco, 1955, Valdez-Mondragón *et al.*, 2014, Dupérré, 2015, Dupérré, Tapia, 2020, 2024, Sherwood *et al.*, 2023, Santos *et al.*, 2025.

TYPE SPECIES: *Paratropis scruposa* Simon, 1889 by original designation.

DIAGNOSIS: *Paratropis* can be distinguished from all the known Paratropididae genera by the presence of STS setae apically dilated over coxae. Additionally, *Paratropis* differ from *Alienus* gen.n., *Stormtropis*, and *Inpatropis* gen.n. by the absence of an abdominal pattern (except *P. rocolita* sp.n.). Males of *Paratropis* resemble those of *Inpatropis* gen.n. by having an embolus with a distal curvature, absence of embolar keels, and presence of a baso-retrolateral cymbial apophysis. Nonetheless, males of *Paratropis* differ from *Inpatropis* gen.n. by having eight eyes, digitiform apical segment of the posterior lateral spinnerets, embolus more than ~5x the tegulum length, superior tarsal claw with single tooth in legs I–IV, and dorsal cephalic spinules and abdominal pattern absent (six eyes, domed apical segment of the posterior lateral spinnerets, embolus less than ~5x the tegulum length, two anterior abdominal pattern marks, dorsal cephalic spinules present, and superior tarsal claw with single tooth only in leg II in *Inpatropis* gen.n.). Females of *Paratropis* easily differ from all other known genera of Paratropididae by the presence of multilobulated spermathecal receptacle composed of variant shapes of vesicles (unilobulate spermathecal receptacle in the rest of Paratropididae genera).

DISTRIBUTION: Brazil, Colombia, Ecuador, French Guiana, Peru, Mexico, and Venezuela (Fig. 11, 12).

SPECIES INCLUDED: *P. arenosa*, *P. carcosita* (misplaced), *P. cryptica*, *P. elicioi*, *P. esmeraldas* (misplaced), *P. florezi*, *P. kapak* (misplaced), *P. otonga*,

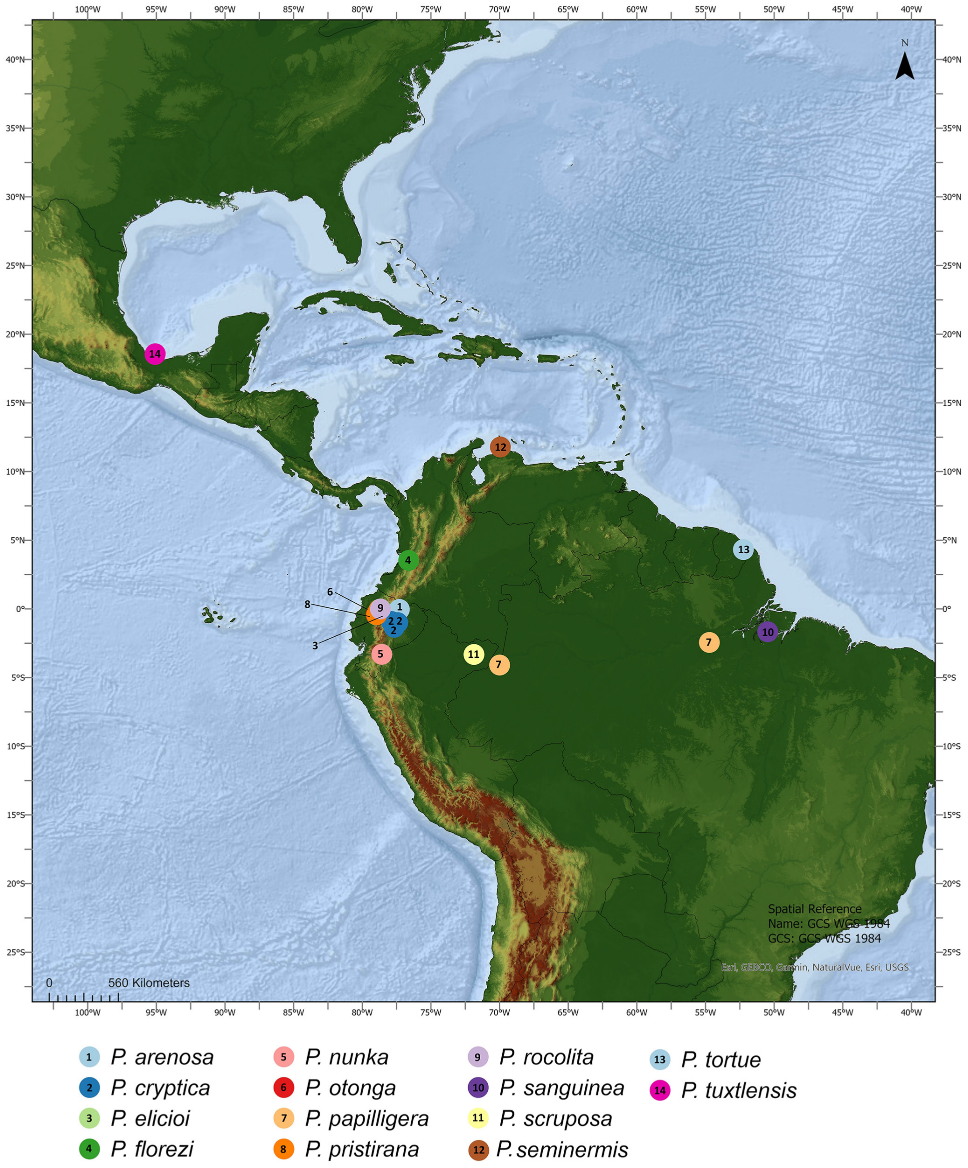

Fig. 11. Map of *Paratropis* distribution.

P. nunka sp.n., *P. papilligera*, *P. pristirana*, *P. pukallucha* (misplaced), *P. rocolita* sp.n., *P. sanguinea*, *P. scruposa*, *P. seminermis*, *P. tortue*, *P. tuxtlensis*, *P. vulcanix* (misplaced).

REMARKS: While searching the type material of *P. scruposa* housed at Muséum National d'Histoire Naturelle, Paris, France, in 2019, DS discovered it could not be found in the collections, possibly having been sent on loan at an unknown time historically. At the time of writing and submitting this article, the specimen was still not available to us for examination. Thus, the detailed morphology of the female genitalia remains unknown on the type species of *Paratropis* along with its relationship to the recovered clades of our morphologic phylogeny. Herein, *Paratropis* is delineated as *sensu lato*, following the characters provided by Valdez-Mondragón *et al.* (2014), Dupérré (2015), Perafán *et al.* (2019), and Dupérré & Tapia

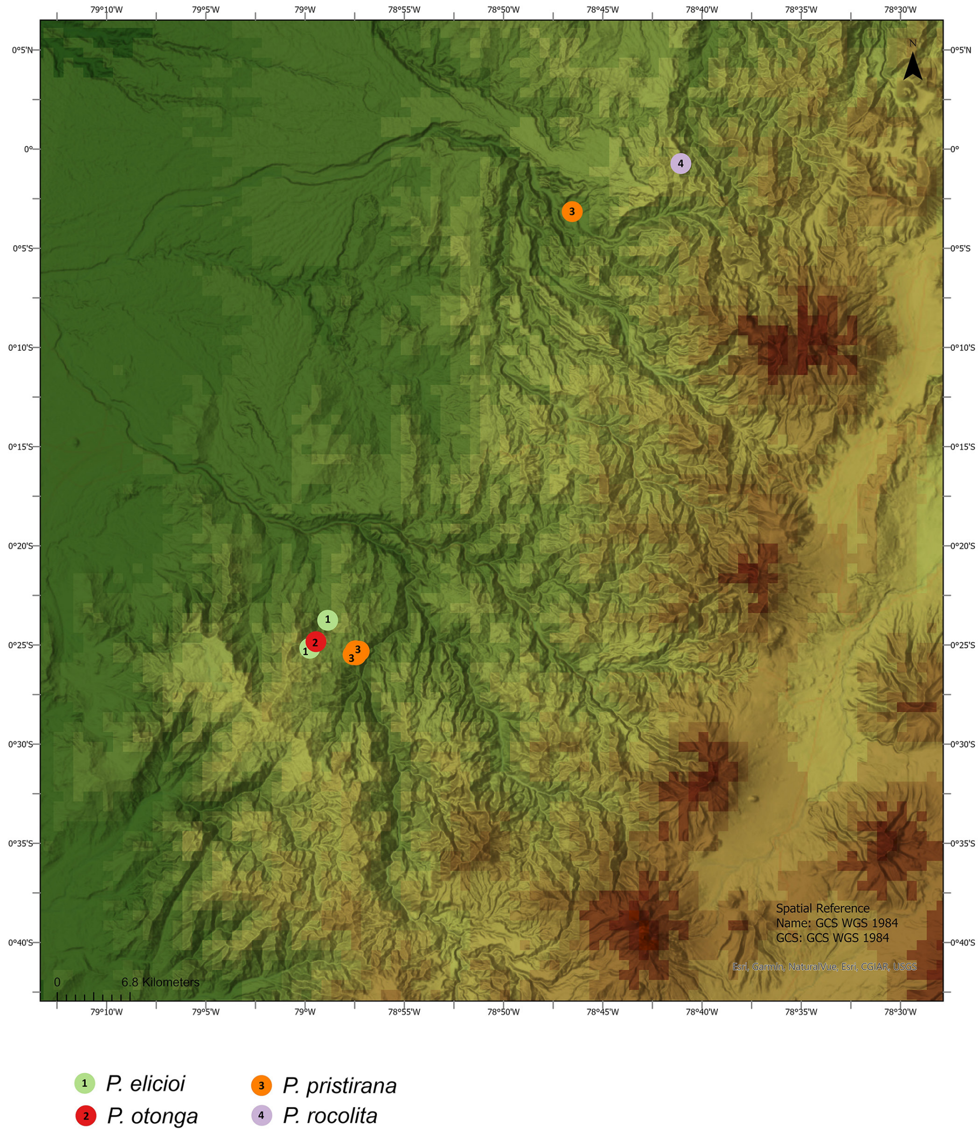

Fig. 12. Close-up map showing species distribution of some sympatric *Paratropis* species.

(2020) and identifying putative synapomorphies recovered from our *Paratropis* clade. Distant clades from this recovered wide *Paratropis* are considered and proposed herein as new genera to keep at systematic resolution of which male and female genitalia morphology as well as some somatic characters had demonstrated its validity on identifying putative natural groups.

Recently, Dupérré & Tapia (2024) described seven new species of *Paratropis* from Ecuador, all but two of which do not agree with the present delimitation of *Paratropis*, therefore we subtly suggest considering them as misplaced in this genus (*P. carcosita*, *P. esmeraldas*, *P. kapak*, *P. pukallucha*) — also for this reason, *Paratropis pasochoa*, after examining topotypic material and testing its phylogenetic placement, is transferred to *Alienus* gen.n. Anecdotally, we know that other colleagues (Fernando Pérez-Miles pers. comm. to PP-R) are working on a new genus of Paratropididae which could correspond to the morphology of the other species of the above-mentioned work. For these reasons, we decided not to take any taxonomic action

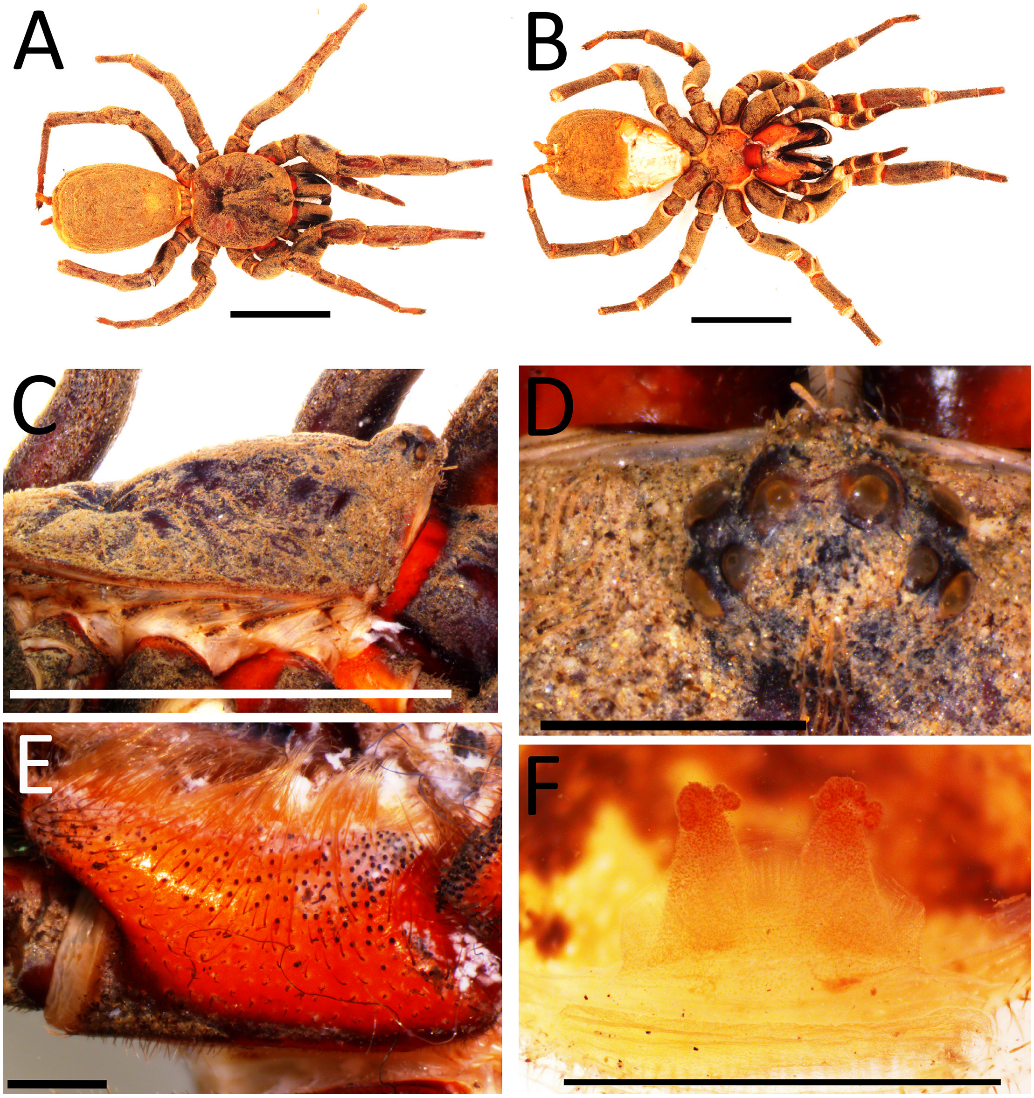

Fig. 13. *Paratropis nunka* sp.n., holotype female (ZSFQ-i20434): A — habitus, dorsal view; B — habitus, ventral view; C — carapace, lateral view; D — eye tubercle; E — left maxilla; F — spermathecae, dorsal view. Scale bars: 10 mm (A–C); 1 mm (D); 0.5 mm (E); 2 mm (F).

for these other species until our colleagues publish their work and when the type material of these species becomes available at QCAZ for our examination (Taryn Ghia pers. comm. to PP-R).

Likewise, Santos *et al.* (2025) recently described three new species of *Paratropis* from Brazil and Colombia. Similar to the case of Dupérré & Tapia (2024), these species do not conform to the present delimitation of *Paratropis* as proposed herein.

Paratropis nunka **Peñaherrera-R., Sherwood, Ríos-Tamayo et Drolshagen sp.n.**

Figs 3A, 13.

TYPE MATERIAL: Holotype ♀ (ZSFQ-i20434), near El Paraiso Reserve, ~10 km NNW from Gualaquiza, parroquia de Amazonas, provincia de Morona Santiago, República del Ecuador (3°18′20.5″S 78°34′24.6″W), 15/10/2022, leg. J. M. Falcón-Reibán.

Table 3. *Paratropis nunka* Peñaherrera-R., Sherwood, Ríos-Tamayo et Drolshagen sp.n. holotype female (ZSFQ-i20434), length of legs and palp.

	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
I	8.60	5.10	7.60	5.10	3.00	29.40
II	6.70	3.60	5.30	4.50	2.80	22.90
III	6.00	3.60	4.10	4.70	2.70*	21.10
IV	8.30	3.90	7.40	6.90	4.00	30.50
Palp	4.80	2.50	3.30	–	3.70	14.30

DIAGNOSIS: Females of *Paratropis nunka* sp.n. resemble those of *P. otonga* by having extremely reduced vesicles positioned and arranged vertically towards spermathecal principal branches axis. Nonetheless, *P. nunka* sp.n. differs from *P. otonga* by having a triangular principal branch of spermathecae being ~3 times the length of vesicle area, presence of a wide membranous plate below spermathecae, and absence of a dorsal longitudinal fold (rectangular principal branch of spermathecae being ~4 times the length of vesicle area, presence of a dorsal longitudinal fold and absence of a wide membranous plate below spermathecae in *P. otonga*).

ETYMOLOGY: The specific epithet is a noun in apposition taken from the word *nunka* of the Shuar language, meaning soil, referring to the encrusted soil generally found in members of Paratropididae. This species, like all the known and unknown ones, has the right to inhabit our *núnkar* (our world in Shuar) without the menace of pollutants, destruction of their ecosystems, and smuggling.

DESCRIPTION OF HOLOTYPE FEMALE (ZSFQ-i20434) (Fig. 13): Total length including chelicerae: 29.4. Carapace: length 10.9, width 10.4. Caput: raised. Ocular tubercle: strongly raised. Eyes: ALE > AME > PLE >PME, ALE not projected. Fovea: recurved. Chelicera: length 4.7, width 2.5. Abdomen: length 13.8, width 9.4, short SPS present overal abdomen and small abdominal tubercles; short spinules overal ventro-basal section of abdomen. Maxilla with 180–230 cuspules. Labium: length 2.3, width 2.4, with 150 cuspules. Sternum: length 4.3, width 6.1. Length of legs and palpal segments: see Table 3, leg formula: IV, I, II, III. Trichobothria: tibiae I–IV (8/8/7/5); metatarsi I–IV (11/4/4/4); tarsi I–IV (17/14/missing/12). Spination: tarsi I 14rlv 15plv, II 5rlv 3plv, III [right] 2rlv 6plv, IV 8rlv, 2 plv; metatarsi I 22rlv 20 plv, II 11rlv 14plv, III 9rlv 7plv, IV 7rlv 2plv; tibia I 27rlv 28plv. Tarsi I–IV with ITC. PLS with three segments, basal 1.5, median 0.9, digitiform apical 1.7. PMS present. Spermatheca: with long and triangular principal branches (~3 times length of vesicle area) emerging from thin and inconspicuous bursa copulatrix, each branch with ~7 inconspicuous vesicles. DLF, VLF, and distal concavity absent.

DISTRIBUTION: Known only from the type locality in the valley of the Upano River: near El Paraiso Reserve, ~10 km NNW from Gualaquiza, 1850 m, province of Morona Santiago (Fig. 8). The holotype was collected at a low montane evergreen forest of the Cordillera Real of the Andes of Ecuador, in the Napo biogeographic province Morrone (2014).

Paratropis rocolita Peñaherrera-R., Sherwood, Ríos-Tamayo et Drolshagen sp.n.

Fig. 14.

TYPE MATERIAL: Holotype ♀ (ZSFQ-i20420), near Bellavista Lodge and Tandayapa Cloud Forest Station, parroquia de Nanegalito, provincia de Pichincha, República del Ecuador (0°00′43.5″S 78°41′04.2″W), 26/01/2024, leg. P. Peñaherrera-R.

DIAGNOSIS: Females *of Paratropis rocolita* sp.n. differ from all known species of *Paratropis* by the presence of abdominal pattern and straight and shallow fovea (abdominal pattern absent and recurved and deep fovea in all *Paratropis* species). Additionally, *P. rocolita* sp.n. slightly resembles those of *P. arenosa* by the presence of a spermathecae neck. Nonetheless, *P. rocolita* sp.n. differs from *P. arenosa* by having a triangular principal branch of spermathecae and comparatively having more clustered and shorter vesicles (rectangular principal branch of spermathecae and comparatively having less clustered and elongated vesicles in *P. arenosa*).

ETYMOLOGY: The specific epithet is a noun in apposition in honour of the Ecuadorian band RoCola Bacalao, "la banda mas chimba del Ecuador". This name was chosen in recognition of their distinctive lyrics and rhythms, which author Pedro Peñaherrera-R. has cherished since his teenage years.

DESCRIPTION OF HOLOTYPE FEMALE (ZSFQ-i20420) (Fig. 14): Total length including chelicerae: 10.91. Carapace: length 3.57, width 3.69. Caput: raised. Ocular tubercle: strongly raised. Eyes: ALE > AME > PLE >PME, ALE projected. Fovea: straight and shallow. Chelicera: length 1.86, width 0.93. Abdomen: length 5.48, width 4.22, STS present over numerous developed tubercles, dorso-apical tubercles ~2–3 times the size of the dorsal tubercles [well-developed]; dorso abdominal pattern present. Maxilla with 32–31 cuspules. Labium: length 0.50, width 0.84, with 24 cuspules. Sternum: length 1.84, width 2.09. Length of legs and palpal segments: see

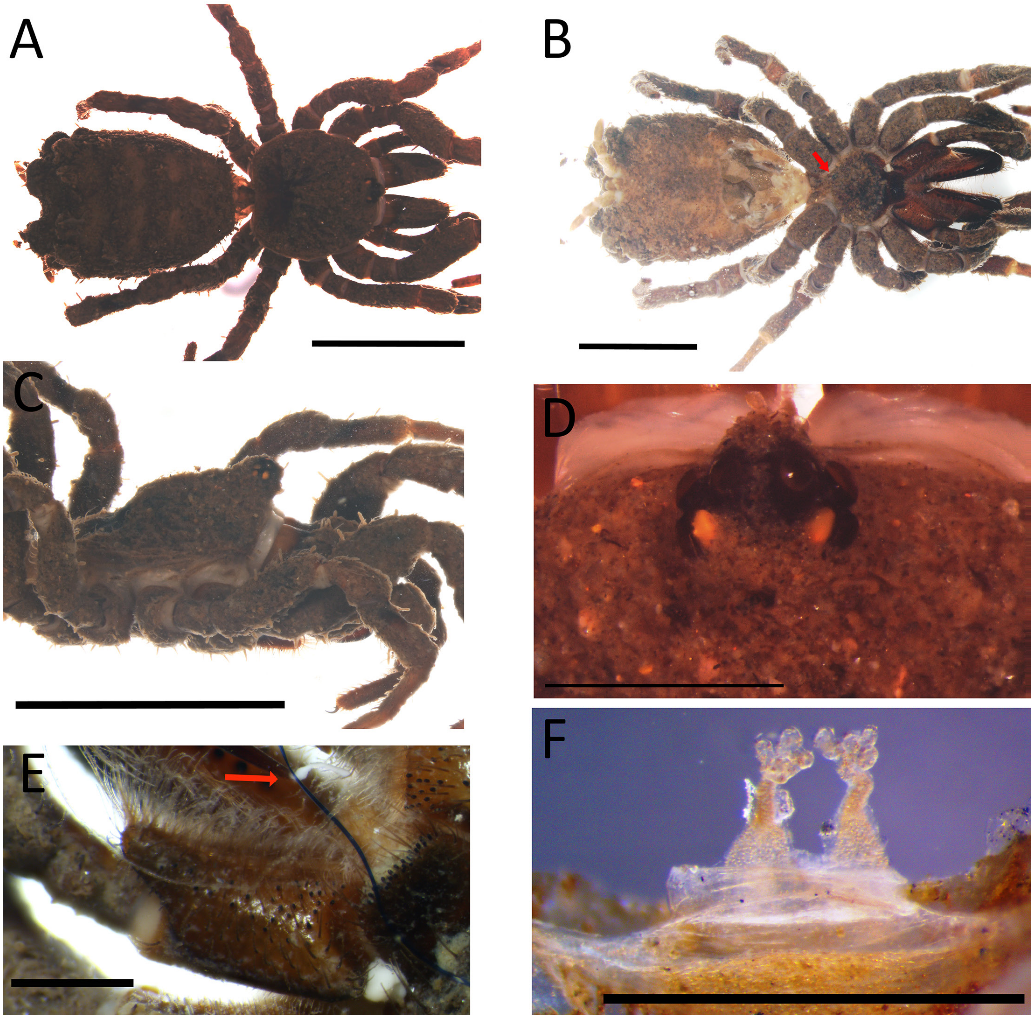

Fig. 14. *Paratropis rocolita* sp.n., holotype female (ZSFQ-i20420): A — habitus, dorsal view; B — habitus, ventral view (arrow, microplastic); C — carapace, lateral view; D — eye tubercle; E — left maxilla (arrow, microplastic); F — spermathecae, dorsal view. Scale bars: 4 mm (A, C); 3 mm (B); 2 mm (D); 1 mm (E); 0.4 mm (F).

Table 4. *Paratropis rocolita* Peñaherrera-R., Sherwood, Ríos-Tamayo et Drolshagen sp.n. holotype female (ZSFQ-i20420), length of legs and palp.

	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
I	2.75	1.48	1.91	1.45	1.08	8.67
II	2.29	1.26	1.46	1.39	0.97	7.37
III	1.35	0.55	1.53	1.30	0.98	5.71
IV	2.79	1.33	2.28	2.15	1.27	9.82
Palp	1.66	0.98	1.01	–	1.15	4.80

Fig. 15. Habitat of *Paratropis rocolita* sp.n. A — overall view; B — close up.

Table 4, leg formula: IV, I, II, III. Trichobothria: tibiae I–IV (4/4/4/4); metatarsi I–IV (2/2/2/2); tarsi I–IV (2/2/2/3). Spination: tarsi I 5rtv 3ptv; metatarsi I 3rtv 2ptv, II 1rtv, III 1rtv 1ptv, IV 1rtv 1ptv. Tarsi I with ITC. PLS with three segments, basal 0.59, median 0.53, digitiform apical 0.66. PMS present. Spermatheca: with long and triangular principal branches (~2 times length of vesicle area) emerging from thin and inconspicuous bursa copulatrix, each branch with a spermathecal neck and ~3 inconspicuous and very sinuous vesicles. DLF, VLF, and distal concavity absent.

DISTRIBUTION AND NATURAL HISTORY: Known only from the type locality in the Tandayapa valley: near Bellavista Lodge and Tandayapa Cloud Forest Station, 3000 m, province of Pichincha (Fig. 15). The holotype was collected at a montane evergreen forest of the Cordillera Occidental of the Andes of Ecuador, in the Northern Andes biogeographic province Morrone (2014) (Fig. 12). Interestingly, during the examination of the holotype female a large microplastic particle was found impregnated over the ventral surface of the cephalothorax (Fig. 14B, E).

Paratropis cryptica Dupérré et Tapia, 2024

Paratropis cryptica Dupérré, Tapia, 2024: 477, figs 23A, 24A–B, 25A–F, 26A–B, 27A–B, 28A–E, 29D.

TYPE MATERIAL: Holotype ♀ (QCAZ, ECFN 7834), Colonso Chalupas Natural Reserve, Comunidad Campos Felices, Tena, provincia de Napo, República del Ecuador (0°54′53.60″S 77°52′41.00″W), leg. E. Tapia, not examined; paratype ♂ same data as holotype but with the following, (QCAZ, ECFN 4861), 21/05/2019, leg. N. Dupérré, A. Tapia, E. Tapia, not examined; paratype ♀ (ZMH-A0003000), Misahualli via Arajuno, provincia de Napo, República del Ecuador (1°05′53.81″S 77°32′59.13″W), 21/05/2019, leg. E. Tapia, not examined.

MATERIAL EXAMINED: 2 ♂ (ZSFQ-i20423, ZSFQ-i20424) 1 ♀ (ZSFQ-i20425) Oglan, parroquia de Arajuno, provincia de Pastaza, República del Ecuador (1°20′37.61″S 77°40′22.37″W), 09/04/2024, leg. J. M. Falcón-Reibán.

DIAGNOSIS: See Dupérré and Tapia (2024).

DISTRIBUTION: This species is known from six localities from the province of Napo and Pastaza, highland Amazonia, at 396–1735 m (Fig. 11). This species can be found in foothill evergreen forest of the Cordillera Real of the Andes of Ecuador, Napo biogeographical province Morrone (2014).

REMARKS: The newly examined specimens represent the first record of *P. cryptica* from the province of Pastaza, extending the species distribution approximately 30 km SSW from the closest locality in the province of Napo and representing the highest record of the species.

Alienus Peñaherrera-R., Sherwood, León-E, Ríos-Tamayo et Drolshagen gen.n.

Paratropis: Dupérré, Tapia, 2024 (in part).

TYPE SPECIES: *Alienus pollex* Peñaherrera-R., Sherwood, Ríos-Tamayo et Drolshagen sp.n. by designation herein.

DIAGNOSIS: Females of *Alienus* gen.n. resemble those of *Anisaspoides* by having a rounded, unilobulate, and bidimensional spermathecal receptacle with a distal receptacle concavity. Nonetheless, females of *Alienus* gen.n. differ from *Anisaspoides* by having posterior median spinnerets, abdominal pattern, and spermathecal principal branches emerging from thin and inconspicuous bursa copulatrix (spermathecal principal branches emerging from wide and rounded bursa copulatrix, posterior median spinnerets and abdominal pattern absent in *Anisaspoides*). Males of *Alienus* gen.n. resemble those of *Stormtropis* by having an embolus less than ~5x the tegulum length, presence of a median embolus curvature, embolar keels, and abdominal pattern. Nonetheless, males of *Alienus* gen.n. differ from *Stormtropis* by having a prolateral embolic keel, retrolateral cymbial apophysis, and absence of a tibial apophysis (dorsal embolic keel, single tibial apophysis with apical cluster of spiniform setae, and retrolateral cymbial apophysis absent in *Stormtropis*). Additionally, males of *Alienus* gen.n. slightly resemble those of *Anisaspoides* by having an embolus less than ~5x the tegulum length, presence of a median embolus curvature, and embolar keels. Nevertheless, *Alienus* gen.n. differs from *Anisaspoides* by having posterior median spinnerets, prolateral embolic keel and abdominal pattern (dorsal embolic keel present and posterior median spinnerets and abdominal pattern absent in *Anisaspoides*).

ETYMOLOGY: The generic epithet (gender: masculine) is a Latin adjective, meaning unconnected or foreign, referring to the disjunct distribution from the inter-Andean valleys down to the Cordillera Oriental and Occidental of the Andes of Ecuador. The gender is masculine.

DISTRIBUTION: Ecuador (Fig. 16).

SPECIES INCLUDED: *A. abditus* sp.n., *A. alo* sp.n., *A. awa* comb.n., *A. basho* sp.n., *A. croceus* sp.n., *A. pasochoa* comb.n., *A. pollex* sp.n., *A. roigi* sp.n.

Alienus pollex Peñaherrera-R., Sherwood, León-E, Ríos-Tamayo et Drolshagen sp.n.
Fig. 17.

TYPE MATERIAL: Holotype ♀ (ZSFQ-i20427) Pachicuntza, parroquia de Pachicuntza, provincia de Zamora Chinchipe, República del Ecuador (3°40′05.30″S 78°36′26.64″W), 03/03/2024, leg. J. M. Falcón-Reibán.

DIAGNOSIS: Females of *A. pollex* sp.n. mostly resemble those of *A. croceus* sp.n. and *A. pasochoa*

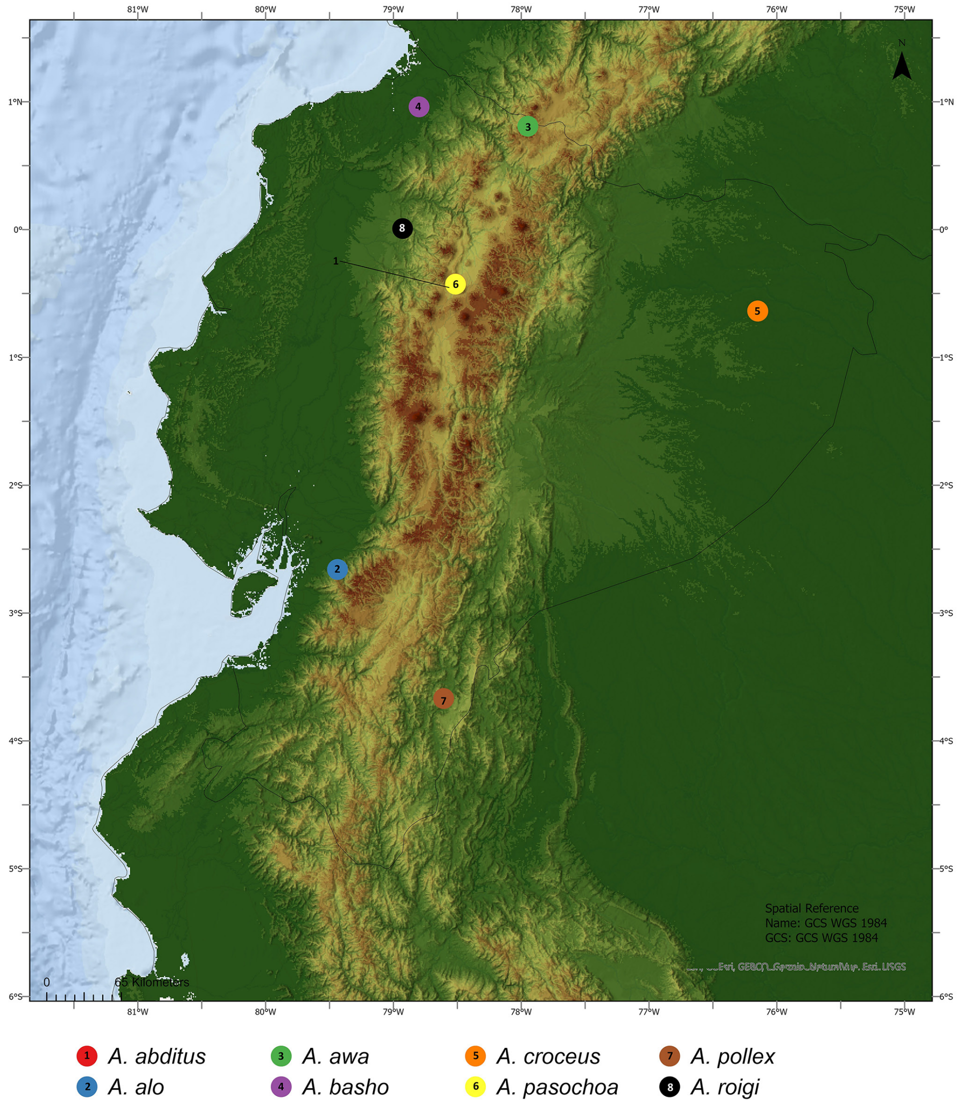

Fig. 16. Map of *Alienus* gen.n. distribution.

comb.n. by having a short length principal branch (1 times the receptacle area) and the absence of longitudinal folds. Nonetheless, females of *A. pollex* sp.n. differ from *A. croceus* sp.n. and *A. pasochoa* comb.n. by having a developed distal concavity, and absence of spiky cuspules and maxillary spinules (weakly developed distal concavity, maxillary spinules present, and spiky cuspules absent in *A. croceus* sp.n.; weakly developed distal concavity, spiky cuspules present, and maxillary spinnules absent in *A. pasochoa* comb.n.).

ETYMOLOGY: The specific epithet is a latin adjective in reference to the similar thumb-shape of the spermathecae of this species.

DESCRIPTION OF HOLOTYPE FEMALE (ZSFQ-i20427) (Fig. 17): Total length including chelicerae: 12.57. Carapace: length 4.18, width 5.57. Caput: raised. Ocular tubercle: raised. Eyes: ALE>AME>PLE>PME. Fovea: straight. Chelicera: length 2.14, width 1.00. Abdomen: length 5.31, width 4.22, SPS and STS present over small abdominal

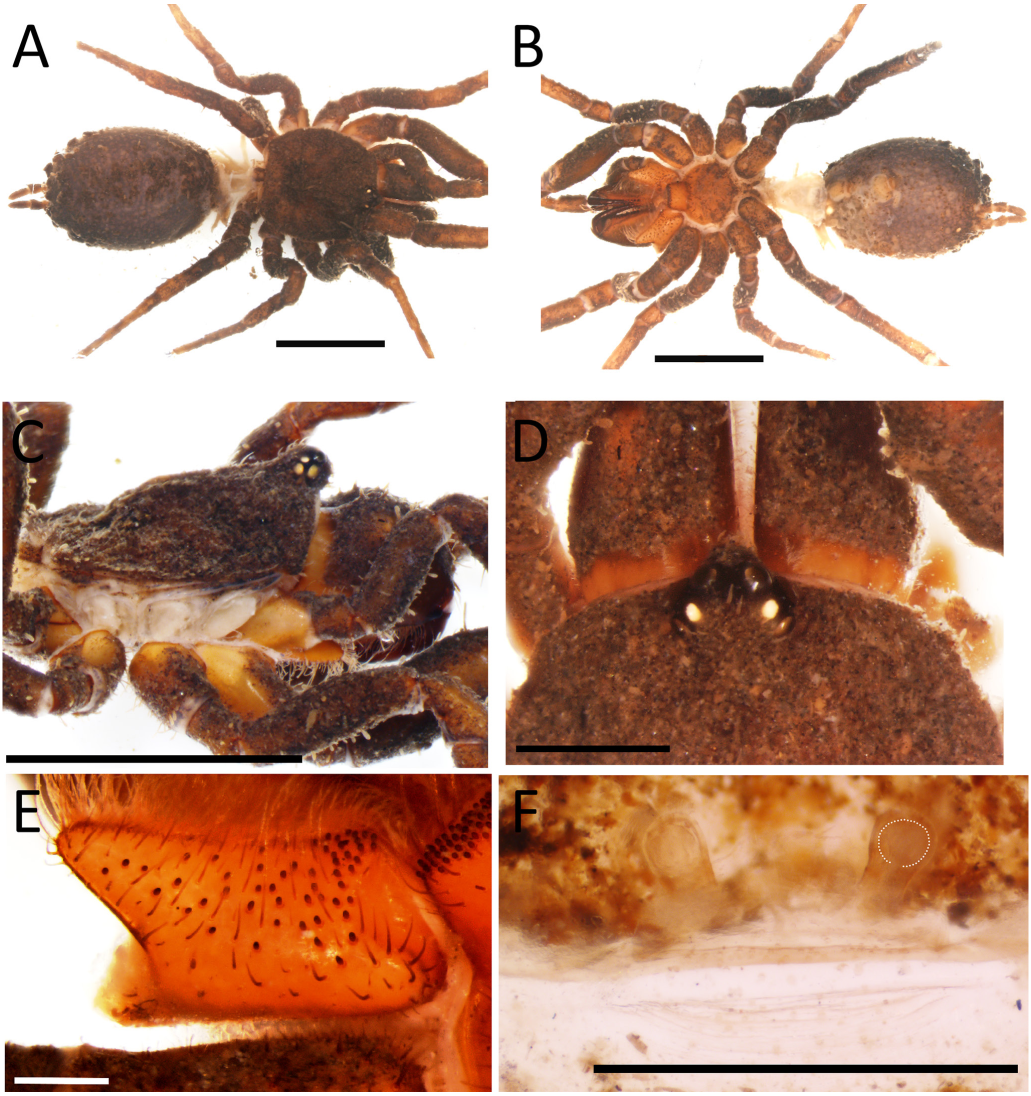

Fig. 17. *Alienus pollex* sp.n., holotype female (ZSFQ-i20427): A — habitus, dorsal view; B — habitus, ventral view; C — carapace, lateral view; D — eye tubercle; E — left maxilla; F — spermathecae, dorsal view. Scale bars: 4 mm (A–C); 1 mm (D), 0.5 mm (E–F).

Table 5. *Alienus pollex* Peñaherrera-R., Sherwood, Ríos-Tamayo et Drolshagen sp.n. holotype female (ZSFQ-i20427), length of legs and palp.

	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
I	3.29	1.68	2.77	2.17	1.27	10.60
II	2.80	1.42	1.62	1.53	1.18	9.43
III	2.20	1.02	1.54	1.74	1.21	8.14
IV	3.03	1.19	2.49	2.53	1.71	10.86
Palp	2.15	0.84	1.12	–	1.13	5.04

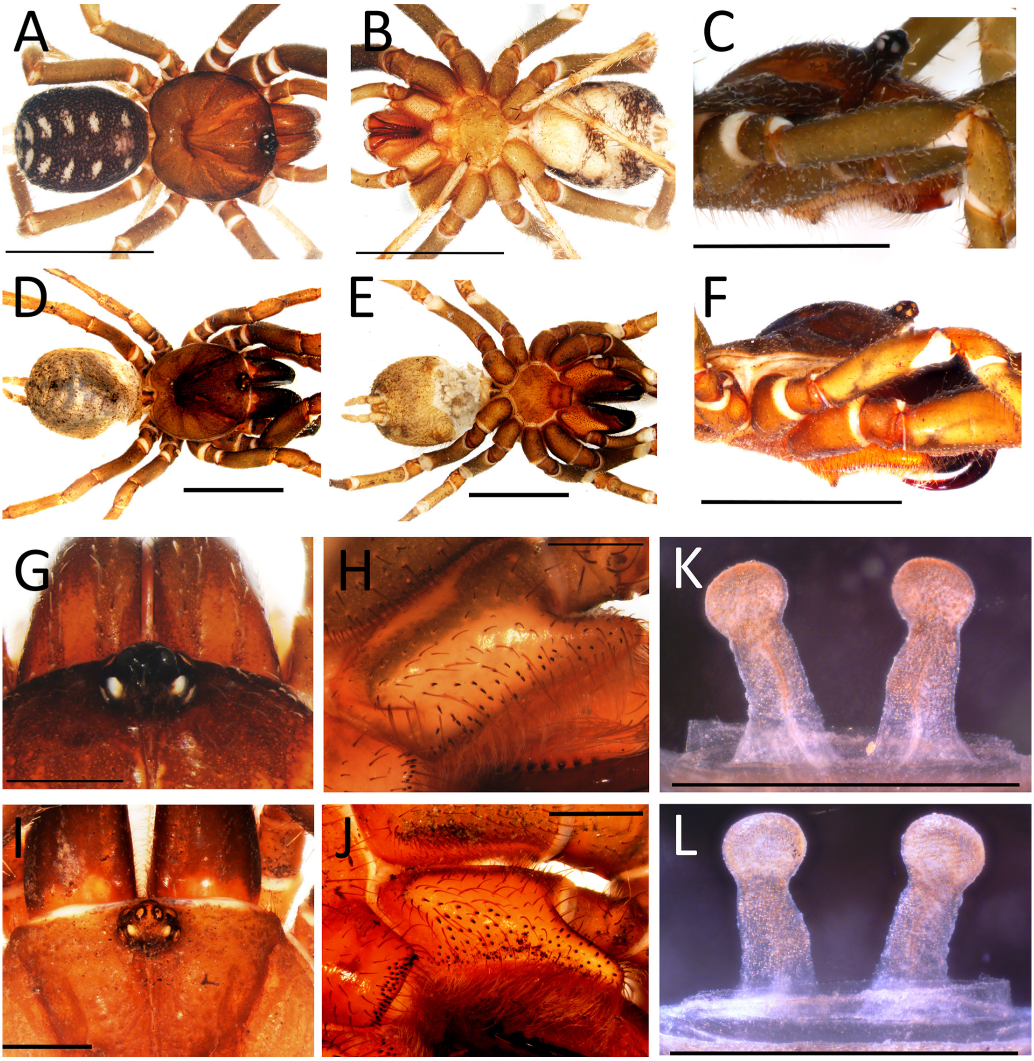

Fig. 18. *Alienus abditus* sp.n., holotype female (ZSFQ-i20429) and paratype male (ZSFQ-i20430): A — male habitus, dorsal view; B — male habitus, ventral view; C — male carapace, lateral view; D — female habitus, dorsal view; E — female habitus, ventral view; F — female carapace, lateral view; G — eye tubercle of male; H — left maxilla of male; H — eye tubercle of female; J — left maxilla of female; F — spermatheca; K — spermathecae, dorsal view; L — spermathecae, ventral view. Scale bars: 5 mm (A–B); 4.5 mm (C); 6 mm (D– F) 1 mm (G); 0.5 mm (H); 1.5 mm (I); 1 mm (J); 0.5 (K–L).

tubercles. Maxilla with 49–52 cuspules. Labium: length 0.66, width 0.94, with 61 cuspules. Sternum: length 1.87, width 1.89. Length of legs and palpal segments: see Table 5, leg formula: IV, I, II, III. Trichobothria: tibiae I–IV (4/4/4/1); metatarsi I–IV (3/4/3/3); tarsi I–IV (6/5/4/5). Spination: Tarsi I 6rtv 5ptv, II 2rtv, 1ptv; Metatarsi I 8rtv 7ptv, II 2rtv 2ptv, III 1rtv, 1ptv, 1ptv. Tarsi I, II, III and IV with ITC. PLS with three segments, basal 0.35, median 0.51, digitiform apical 0.86. PMS present. Spermatheca: unilobed, short principal branch (~1 time the receptacle area) without longitudinal fold; oval receptacle with a developed distal concavity.

DISTRIBUTION: Known only from the type locality in the valley of the Upano River: Pachicuntza, 940 m, province of Zamora Chinchipe (Fig. 16). The holotype was collected at a foothill evergreen forest of the Cordillera de Kutukú, in the Napo biogeographic province Morrone (2014).

Table 6. *Alienus abditus* Peñaherrera-R., Sherwood, Ríos-Tamayo et Drolshagen sp.n. holotype female (ZSFQ-i20429), length of legs and palp.

	Femur	**Patella**	**Tibia**	**Metatarsus**	**Tarsus**	**Total**
I	5.13	1.76	3.80	2.22	1.48	15.03
II	3.96	2.01	2.49	2.13	1.68	12.54
III	3.15	1.88	2.06	2.32	1.48	10.42
IV	4.50	2.23	3.32	2.98	1.95	14.25
Palp	2.69	1.55	1.65	–	1.44	7.64

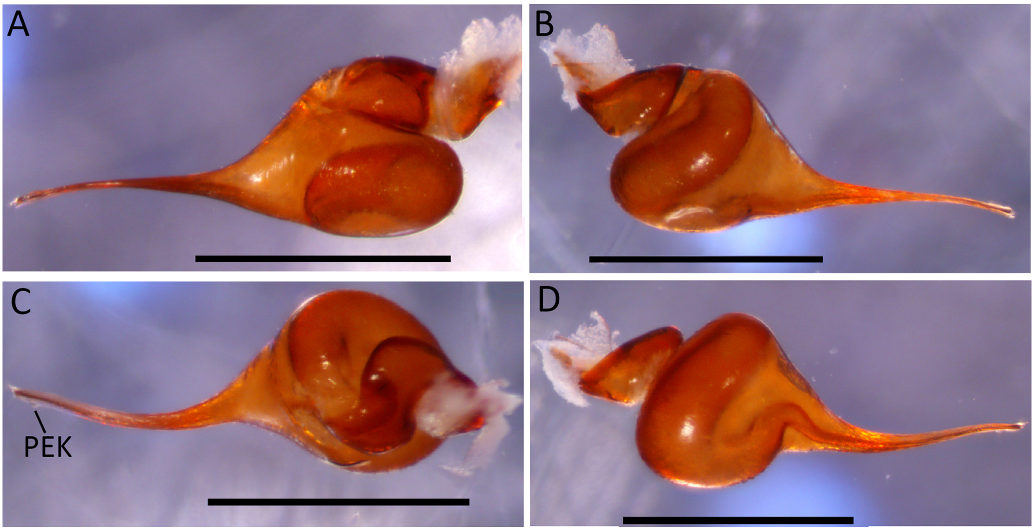

Fig. 19. *Alienus abditus* sp.n., paratype male (ZSFQ-i20430) palpal bulb: A — prolateral view; B — retrolateral view; C — dorsal view; D — ventral view. Scale bars 1 mm (A–D).

Alienus abditus Peñaherrera-R., Sherwood, Ríos-Tamayo et Drolshagen sp.n.

Figs 2B, 18–19, 21–22.

TYPE MATERIAL: Holotype ♀ (ZSFQ-i20429), Refugio de Vida Silvestre Pasochoa, parroquia de Uyumbicho, provincia de Pichincha, República del Ecuador (0°25′30.76″S 78°30′46.17″W), 29/12/2021, leg. P. Peñaherrera-R.; paratype ♂ (ZSFQ-i20430), same data as holotype.

DIAGNOSIS: Females of *A. abditus* sp.n. resemble those of *A. alo* sp.n. by having a median length principal branch (~2 times the receptacle area). Nonetheless, females of *A. abditus* sp.n. differ from *A. alo* sp.n. by having a developed distal concavity, presence of spiky cuspules and ventral longitudinal folds (weakly developed distal concavity, spiky cuspules and ventral longitudinal folds absent in *A. alo* sp.n.). Additionally, females of *A. abditus* sp.n. differ from *A. alo* sp.n. by comparatively having a more developed lobe. Males of *A. abditus* sp.n. easily differ from *A. awa* comb.n. by having a weakly developed prolateral embolic keel (developed prolateral embolic keel in *A. awa* comb.n.).

ETYMOLOGY: The specific epithet is a Latin adjective, meaning hidden, referring to the discovery of a second species from the Pasochoa Volcano. Additionally, referring to the underestimated diversity of this group, the specimens of this species were the ones that inspired author Pedro Peñaherrera-R. to undertake this Paratropididae project three years ago.

DESCRIPTION OF HOLOTYPE FEMALE (ZSFQ-i20429) (Fig. 18): Total length including chelicerae: 14.59. Carapace: length 6.29, width 6.19. Caput: raised. Ocular tubercle: strongly raised. Eyes: ALE>PLE>AME>PME. Fovea: procurved. Chelicera: length 3.52, width 1.67. Abdomen: length 7.50, width 5.62, SPS and STS present over small abdominal tubercles. Maxilla with 68–74 cuspules. Labium: length 1.20, width 1.33, with 44 cuspules. Sternum: length 2.30, width 3.61. Length of legs and palpal segments: see Table 6, leg formula: I, IV, II, III. Trichobothria: tibiae I–IV (6/6/6/4); metatarsi I–IV (4/3/3/3); tarsi I–IV (9/8/7/7). Spination: tarsi I 7rtv 9ptv. Metatarsi I 3rtv 1ptv, II 2rtv 2ptv, III 2rtv, 1ptd, 1ptv; IV 1ptv. Tarsi I with ITC. PLS with three segments, basal 0.85, median 0.75, digitiform apical 1.07. PMS present. Spermatheca: unilobed, median

Table 7. *Alienus abditus* Peñaherrera-R., Sherwood, Ríos-Tamayo et Drolshagen sp.n. paratype male (ZSFQ-i20430), length of legs and palp.

	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
I	3.98	1.98	3.53	2.71	1.61	14.81
II	3.76	1.51	2.54	2.78	1.97	12.08
III	2.72	1.41	1.78	2.28	1.51	9.96
IV	2.99	1.12	2.77	3.07	1.92	12.35
Palp	1.53	1.06	1.48	–	0.65	5.44

Fig. 20. Habitat of *Alienus abditus* sp.n.

principal branch (~2 times the receptacle area) with ventral longitudinal fold; oval receptacle with a developed distal concavity.

DESCRIPTION OF PARATYPE MALE (ZSFQ-i20430) (Figs 18–19): Total length including chelicerae: 10.21. Carapace: length 4.33, width 4.43. Caput: raised. Ocular tubercle: strongly raised. Eyes: AME > ALE > PLE >PME. Fovea: procurved. Chelicera: length 1.66, width 0.94. Abdomen: length 4.57, width 3.50, SPS and STS present over small abdominal tubercles. Maxilla with 39–40 cuspules. Labium: length 0.84, width 1.21, with 33 cuspules. Sternum: length 1.76, width 2.39. Length of legs and palpal segments: see Table 7, leg formula: I, IV, II, III. Trichobothria: tibiae I–IV (5/6/5/4); metatarsi I–IV (4/3/4/4); tarsi I–IV (6/5/6/5). Spination: metatarsi II 2rtv 2ptv. Palpal cymbium with weakly developed retrolateral apophysis. Leg I with absence of tibial apophysis. Tarsi I with ITC. PLS with three segments, basal 0.58, median 0.32, digitiform apical 0.65. PMS present. Palpal bulb: embolus medially curved and twisted retrolaterally, weakly developed prolateral embolic keel.

DISTRIBUTION AND NATURAL HISTORY: Known only from its type locality in the Pasochoa Volcano: Refugio de Vida Silvestre Pasochoa, 2960 m, province of Pichincha (Fig. 20). The holotype and paratype were collected in a sural (forest patches composed only of native bamboo, *Chusquea* cf. *scandens*) of a high montane evergreen forest of the Cordillera Real of the Andes of Ecuador, in the Northern Andes biogeographic province Morrone (2014) (Fig. 16). The female and male holotype were found next to each other below two separate rocks, each burrow was composed of a superficial and wide chamber (~7 cm^2) and a vertical chamber of ~5 cm (Fig. 17). The female had approximately 7 juveniles showing a marked crypsis through detritus adhesion (Figs 21–22).

Fig. 21. Burrow of *Alienus abditus* sp.n. with the holotype female and some juveniles.

Fig. 22. Juvenile of *Alienus abditus* sp.n. (not collected).

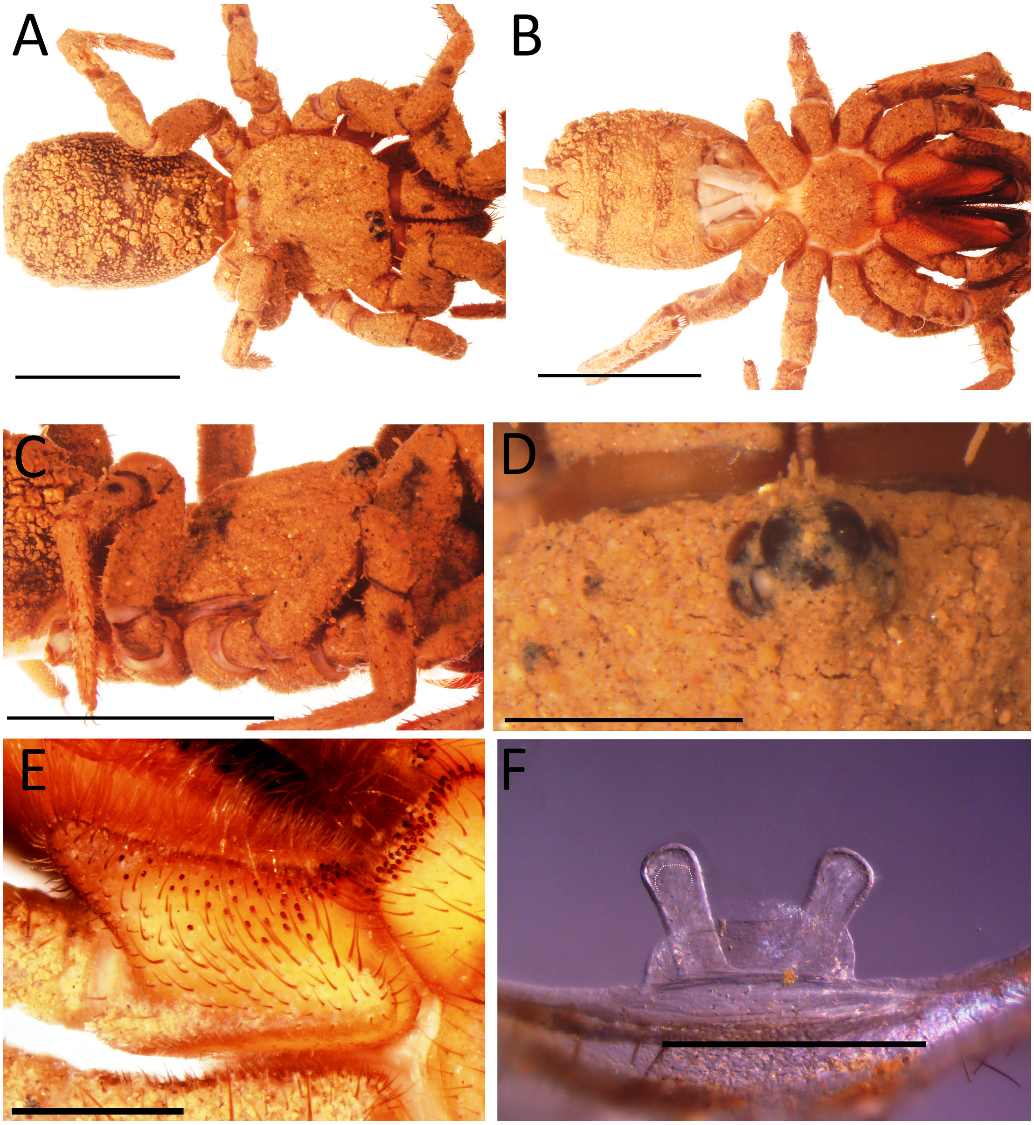

Fig. 23. *Alienus alo* sp.n., holotype female (ZSFQ-i20422): A — habitus, dorsal view; B — habitus, ventral view; C — carapace, lateral view; D — eye tubercle; E — left maxilla; F — spermathecae, dorsal view. Scale bars: 3 mm (A– C); 1 mm (D–E); 0.5 mm (F).

Alienus alo Peñaherrera-R., Sherwood, León-E, Ríos-Tamayo et Drolshagen sp.n.

Fig. 23.

TYPE MATERIAL: Holotype ♀ (ZSFQ-i20422), Corona de Oro, parroquia de Molleturo, provincia de Azuay, República del Ecuador (2°39′31.32″S 79°26′16.41″W), 09/10/2022, leg. P. Peñaherrera-R, A. Guerrero-Campoverde and R.J. León-E.

DIAGNOSIS: Females of *A. alo* sp.n. resemble those of *A. abditus* sp.n. by having a median length principal branch (~2 times the receptacle area). Nonetheless, females of *A. alo* sp.n. differ from *A. abditus* sp.n. by having a weakly developed distal concavity, and spiky cuspules and ventral longitudinal folds absent developed distal concavity, presence of spiky cuspules and ventral longitudinal folds in *A. abditus* sp.n.). Additionally, females of *A. alo* sp.n. differ from *A. abditus* sp.n. by comparatively having a less developed lobe.

ETYMOLOGY: The specific epithet, a noun in apposition, is an expression "aló", usually used by

Table 8. *Alienus alo* Peñaherrera-R., Sherwood, Ríos-Tamayo et Drolshagen sp.n. holotype female (ZSFQ-i20422), length of legs and palp.

	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
I	3.27	1.98	2.58	2.07	1.33	11.23
II	missing					
III	2.17	1.60	1.53	1.58	1.18	8.06
IV	2.83	1.84	2.69	2.72	1,51	11.59
Palp	2.44	1.15	1.36	–	1.70	6.65

the members of the Mygalomorphae Group of the Laboratory of Terrestrial Zoology of the USFQ when they discover things they didn't expect to find (i.e. this species).

DESCRIPTION OF HOLOTYPE FEMALE (ZSFQ-i20422) (Fig. 23): Total length including chelicerae: 12.46. Carapace: length 3.94, width 4.28. Caput: raised. Ocular tubercle: strongly raised. Eyes: ALE>AME>PLE>PME. Fovea: procurved. Chelicera: length 2.80, width 1.01. Abdomen: length 5.72, width 4.17, SPS and STS present over small abdominal tubercles. Maxilla with 48–43 cuspules. Labium: length 0.76, width 1.14, with 40 cuspules. Sternum: length 2.22, width 2.62. Length of legs and palpal segments: see Table 8, leg formula: IV, I, II, III. Trichobothria: tibiae I–IV (6/6/4/3); metatarsi I–IV (4/3/3/3); tarsi I–IV (7/4/4/6). Spination: tarsi I 8rtv 7ptv, II 2rtv, III 3ptv, IV 2ptv; metatarsi I 8rtv 6ptv, II 2rtv 2ptv, III 1rtv 4ptv, IV 1rtv 3ptv; femur 2rtv. Tarsus I with ITC. PLS with three segments, basal 0.61, median 0.41, digitiform apical 0.71. PMS present. Spermatheca: unilobed, short principal branch (~1.2 times the receptacle area) without longitudinal folds; Oval receptacle with a weakly developed distal concavity.

DISTRIBUTION: Known only from the type locality in the western slope of the Cajas Massif: Corona de Oro, 1520 m, province of Azuay. The holotype was collected in a low montane evergreen forest of the Cordillera Occidental of the Andes of Ecuador, in the Northern Andes biogeographic province Morrone (2014).

Alienus awa (Sherwood, Brescovit et Lucas, 2023) comb.n.

Anisaspis awa Sherwood *et al.*, 2023: 769, figs 1–7.

TYPE MATERIAL: Holotype ♂ (NHMUK-014602298), Volcan Chiles, Paramo, 3600 m, 27 July 1999, Melanie de Witt colln., examined.

DIAGNOSIS: Males of *A. awa* comb.n. easily differ from *A. abditus* sp.n. by having a developed prolateral embolic keel (weakly developed prolateral embolic keel in *A. abditus* sp.n.).

DESCRIPTION: See Sherwood *et al.* (2023).

REMARKS: Based on our phylogenetic results (Fig. 6), *Anisaspis awa* is placed within *Alienus* gen.n., for this reason herein we transfer this species to *Alienus* gen.n. and create the new combination: *Alienus awa* comb.n.

Alienus basho Sherwood, Drolshagen, Peñaherrera-R. et Ríos-Tamayo sp.n.

Fig. 24.

TYPE MATERIAL: Holotype ♀ (BMNH 1890.5.15.10–11), Cachari [= Cachabí, Esmeraldas, Ecuador], Purch. of Rosenburg.

DIAGNOSIS: *Alienus basho* sp.n. can be easily distinguished from all the known females of *Alienus* by the elongated principal branch, being 4 times the receptacle area (less than 4 times as long as receptacle area in all other known congeners).

ETYMOLOGY: The specific epithet is an eponym honouring Robbie Basho (1940–1986) the great American musician and troubadour whose music is a constant source of comfort for author Danniella Sherwood.

DESCRIPTION OF HOLOTYPE FEMALE (BMNH 1890.5.15.10-11) (Fig. 24): Total length including chelicerae: 22.5. Carapace: length 9.0, width 7.7. Caput: raised. Ocular tubercle: strongly raised. Eyes: AME > ALE > PLE >PME. Fovea: straight. Chelicera: length 4.5, width 2.2. Abdomen: length 9.00, width 7.30, STS present over small abdominal tubercles. Maxilla with 15 cuspules. Labium: length 1.60, width 2.00, with 80–100 cuspules. Sternum: length 3.60, width 4.50. Length of legs and palpal segments: see Table 9, leg formula: IV, I, II, III. Trichobothria tibia I d9, II d9, III d10, IV d6, palp d9, metatarsus I d5, II d4, III d5, IV d5, tarsus I d15, II d15, III d12, IV d10, palp d11. Spination: tibia I plv15, rlv11, III plv2, rlv1, palp p2, metatarsus I plv13, rlv14, II plv8, rlv9, III plv4, rlv4, IV plv8, rlv2, tarsus I plv8, rlv10, II plv2, rlv4, III plv3, rlv1, IV plv8, rlv7, palp plv5, rlv5. Tarsi I–IV without ITC. PLS with three segments, basal 1.90, median 1.00, digitiform apical 1.60. PMS present. Spermathecae: unilobed, elongated principal branch (~4 times the receptacle area) with dorsal longitudinal fold; ova receptacle with a developed distal concavity.

DISTRIBUTION: Known only from the type locality (Fig. 16). The holotype was collected at a low evergreen forest of the Ecuadorian Chocó, in

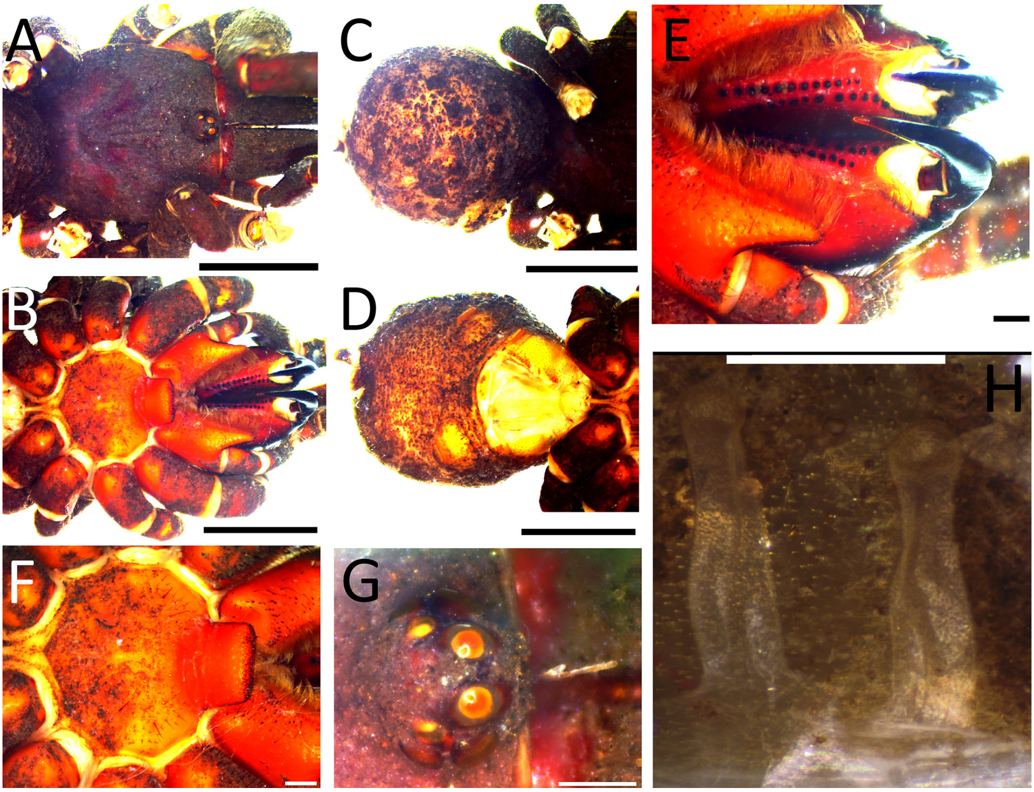

Fig. 24. *Alienus basho* sp.n., holotype female (BMNH 1890.5.15.10–11): A — carapace, dorsal view; B — carapace, ventral view; C — abdomen, dorsal view; D — abdomen, ventral view; E — chelicera, ventral view; F — sternum and maxillae, ventral view; G — eye tubercle; H — spermathecae, dorsal view. Scale bars: 1 mm (A–H).

Table 9. *Alienus basho* Sherwood, Drolshagen, Peñaherrera-R. et *Ríos-Tamayo* sp.n. holotype female (BMNH 1890.5.15.10-11), length of legs and palp.

	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
I	5.9	3	5.3	4.6	2.1	20.9
II	5	2.9	3.4	4	2	17.3
III	4.5	2.4	2.8	3.7	2	15.4
IV	6	3	5.4	5.8	2.4	22.6
Palp	3.5	1.7	2	–	3.5	10.7

the Chocó-Darien biogeographic province Morrone (2014).

REMARKS: The original data label for these specimens carries the text “Purch. of Rosenberg” which refers to the ornithologist William Frederick Henry Rosenberg (1868–1957) who collected many birds, reptiles, and invertebrates from South America, especially NW Ecuador. He was also known to purchase the collections of others, as was common at the time. The inclusion of “Purch.” on that label indicates this material was part of a purchase the BMNH made from Rosenburg. A considerable amount of Ecuadorian arachnid material in the BMNH has data labels that read “Purch. of Rosenberg” (DS pers. obs.). Although the specimen label indicates the locality of “Cachari”, this is a misspelling of Cachabí where many specimens were also collected by Rosemberg (Boulenger, 1898; Hartert, 1898; Brown, 1941; Paynter, 1993; McCarthy *et al.*, 2000) located in the province of Esmeraldas, northwestern Ecuador. As in McCarthy *et al.* (2000), herein we follow Brown (1941) and Paynter (1993) regarding the type locality restriction of Cachabí for

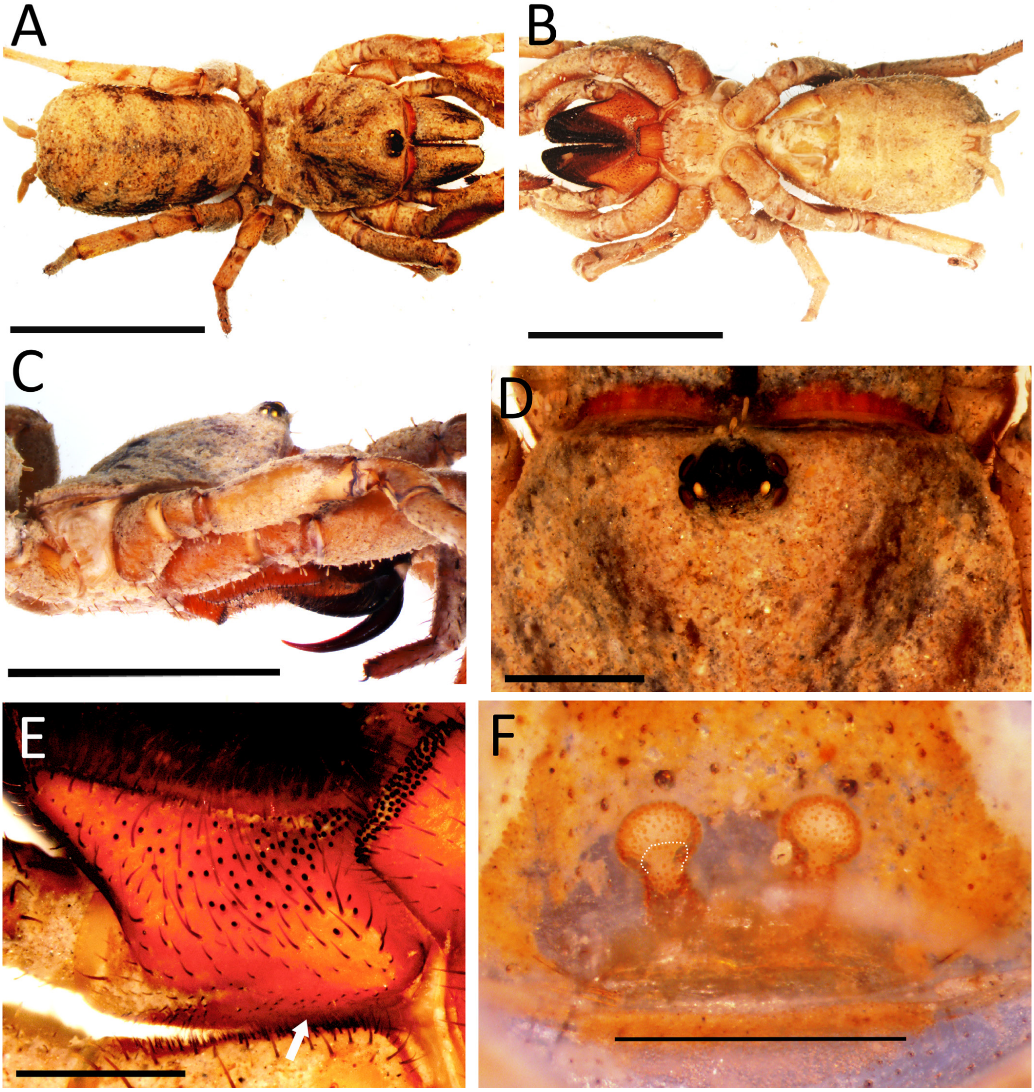

Fig. 25. *Alienus croceus* sp.n., holotype female (ZSFQ-i20412): A — habitus, dorsal view; B — habitus, ventral view; C — carapace, lateral view; D — eye tubercle; E — left maxilla (arrow, maxillary spinules); F — spermathecae, dorsal view (white dotted line indicates the distal concavity). Scale bars: 6 mm (A–C); 1 mm (D–E); 0.5 mm (F).

A. basho sp.n. as follows: Cachabí (approximately 0.96, –78.80), 25 km SE from Concepción, province of Esmeraldas.

Alienus croceus Peñaherrera-R., Sherwood, Ríos-Tamayo et Drolshagen sp.n.

Fig. 25.

TYPE MATERIAL: Holotype ♀ (ZSFQ-i20412), Tiputini Biodiversity Station, provincia de Orellana, República del Ecuador (0°38′16.98″S 76°08′57.65″W), 23/07/2023, leg. Guerrero-Campoverde and M. Vinueza; 2 Paratypes ♀ (ZSFQ-i8251, ZSFQ-i20433), Tiputini Biodiversity Station, provincia de Orellana, República del Ecuador (0°38′12.61″S 76°08′57.90″W), 30/05/2022, leg. P. Peñaherrera-R.

DIAGNOSIS: Females of *A. croceus* sp.n. mostly resemble those of *A. pasochoa* comb.n. by having a short length principal branch (1 times the receptacle area), weakly developed distal concavity, and the absence of longitudinal folds. Nonetheless, *A. croceus* differ from *A. pasochoa* comb.n. by the presence of

Table 10. *Alienus croceus* Peñaherrera-R., Sherwood, Ríos-Tamayo et Drolshagen sp.n. holotype female (ZSFQ-i20412), length of legs and palp.

	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
I	3.43	2.13	3.46	2.64	1.50	16,03
II	3.24	1.36	2.42	2.43	1.25	11.55
III	3.20	1.70	1.88	2.04	1.45	11.01
IV	3.68	1.85	3.38	3.06	1.68	14.28
Palp	2.74	1.41	1.35	–	2.02	7.17

maxillary spinules, coarse spines in female tibia I, and absence of spiky maxillary cuspules (spiky maxillary cuspules present, and maxillary spinules and coarse spines in female tibia I absent in *A. pasochoa* comb.n.).

ETYMOLOGY: The specific epithet is a Latin adjective, meaning yellow, in reference to the yellowish colouration that the encrusted mud has on this species.

DESCRIPTION OF HOLOTYPE FEMALE (ZSFQ-i20412) (Fig. 25): Total length including chelicerae: 17.51. Carapace: length 5.83, width 5.43. Caput: raised. Ocular tubercle: strongly raised. Eyes: AME>ALE>PME>PLE. Fovea: procurved. Chelicera: length 3.29, width 1.38. Abdomen: length 8.59, width 5.46, SPS and STS present over small abdominal tubercles. Maxilla with 63–73 cuspules. Labium: length 1.12, width 1.36, with 77 cuspules. Sternum: length 2.35, width 2.86. Length of legs and palpal segments: see Table 10, leg formula: I, IV, II, III. Trichobothria: tibiae I–IV (6/6/6/4); metatarsi I–IV (4/4/3/3); tarsi I–IV (6/7/5/6). Spination: Tarsi I 8rtv 6ptv, II 2rtv, 1ptv. Metatarsi I 10rtv 8ptv, II 4rtv 2ptv, III 2rtv, 2ptv, 1ptv; IV 5ptv, 2v. Tarsi I, III and IV with ITC. PLS with three segments, basal 0.78, median 0.54, digitiform apical 0.75. PMS present. Spermatheca: unilobed and short length principal branch (1 times the receptacle area) without longitudinal folds; oval receptacle with a weakly developed distal concavity.

DISTRIBUTION AND NATURAL HISTORY: Known only from the type locality in the lowland Amazonia of Ecuador: Tiputini Biodiversity Station (TBS), 220–230 m, province of Orellana. The holotype and paratypes were collected at an old-growth Lowland Evergreen Non-Flooded (Terra Firme) Forest, in the Napo biogeographic province Morrone (2014) (Fig. 16). This species was found inside vertical burrows of ~3–8 cm. The paratypes were found in syntopy with a species of *Bolostromus* (Cyrtaucheniidae) and each individual burrow, at least 4 of them with a distance of 3–10 cm.

Alienus pasochoa **(Dupérré and Tapia, 2024) comb.n.**

Fig. 26.

Paratropis pasochoa Dupérré, Tapia, 2024: 471, figs 18A–B, 19A–C (misplaced; described based on a subadult female).

TYPE MATERIAL: Holotype ♀ (here considered as subadult ♀) (QCAZ 262395), Pasochoa, provincia de Pichincha, (00°25′00″ S 78°27′00″W), 29/06/1989, leg. P. Jimenez, not examined.

MATERIAL EXAMINED: 1 ♀ (ZSFQ-i20428), Refugio de Vida Silvestre Pasochoa, parroquia de Uyumbicho, provincia de Pichincha, República del Ecuador (0°25′34.00″S 78°30′51.56″W), 29/12/2021, leg. P. Peñaherrera-R.

DIAGNOSIS: Females of *A. pasochoa* comb.n. mostly resemble those of *A. croceus* sp.n. by having a short length principal branch (1 times the receptacle area), weakly developed distal concavity, and the absence of longitudinal folds. Nonetheless, *A. croceus* differ from *A. pasochoa* comb.n. by the presence of spiky maxillary cuspules, and the absence of maxillary spinules and coarse spines in female tibia I (presence of maxillary spinules and coarse spines in female tibia I, and absence of spiky maxillary cuspules in *A. croceus* sp.n.).

DESCRIPTION OF NON-TYPE FEMALE (ZSFQ-i20428) (Fig. 26): Total length including chelicerae: 13.45. Carapace: length 4.89, width 5.21. Caput: raised. Ocular tubercle: strongly raised. Eyes: ALE>PLE>AME>PME. Fovea: procurved. Chelicera: length 2.07, width 1.18. Abdomen: length 6.49, width 6.15, SPS and STS present over small abdominal tubercles. Maxilla with 56–95 cuspules. Labium: length 0.84, width 1.30, with 72 cuspules. Sternum: length 2.06, width 3.06. Length of legs and palpal segments: see Table 11, leg formula: I, IV, II, III. Trichobothria: tibiae I–IV (6/6/6/5); metatarsi I–IV (4/5/4/4); tarsi I–IV (7/8/7/7). Spination: tarsi I 6rtv 7ptv. Metatarsi I 4rtv 1ptv, II 2rtv 2ptv, III 2rtv, 2ptv; IV 1rtv, 1ptv. Tarsi I–II with ITC. PLS with three segments, basal 0.45, median 0.40, digitiform apical 0.75. PMS present. Spermatheca: unilobed and short length principal branch (1 times the receptacle area) without longitudinal folds; oval receptacle with a weakly developed distal concavity.

DISTRIBUTION AND NATURAL HISTORY: Known only by two localities in the Pasochoa Volcano: inside the Refugio de Vida Silvestre Pasochoa at 2850 m and at the northern slope of the Pasochoa Volcano at 3000m, both province of Pichincha. The species

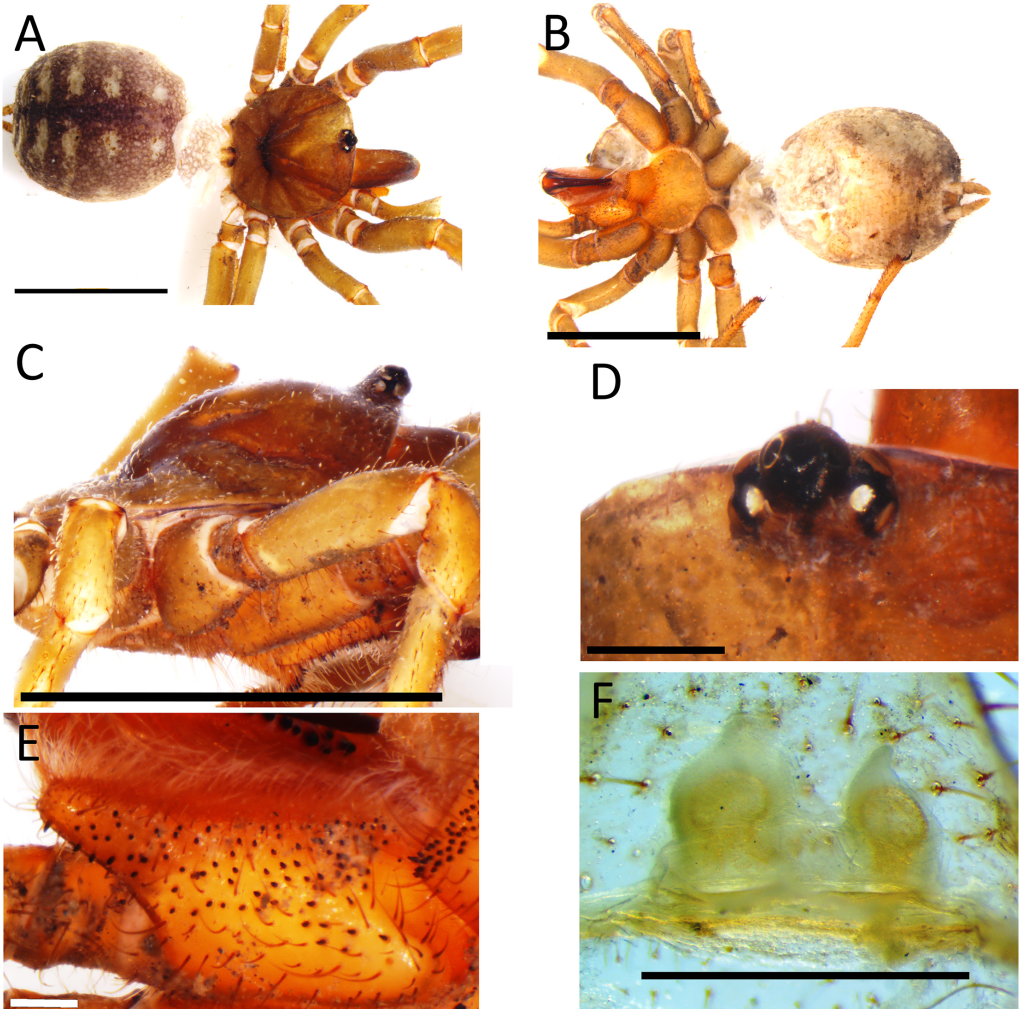

Fig. 26. *Alienus pasochoa* comb.n., non-type female (ZSFQ-i20428): A — habitus, dorsal view; B — habitus, ventral view; C — carapace, lateral view; D — eye tubercle; E — left maxilla; F — spermathecae, ventral view (white dotted line indicates the distal concavity). Scale bars: 5 mm (A– C); 0.5 mm (D–E); 0.2 mm (F).

Table 11. *Alienus pasochoa* (Dupérré et Tapia, 2024) comb.n. non-type holotype female (ZSFQ-i20428), length of legs and palp.

	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
I	3,81	2,02	3,19	2,09	1,4	12,51
II	2,88	1,43	2,22	1,82	1,36	9,71
III	2,38	0,89	1,52	1,61	1,16	7,56
IV	3,62	1,28	2,77	2,87	1,81	12,35
Palp	2,26	1,54	1,18	–	1,52	6,5

can be found in a high montane evergreen forest of the Cordillera Real of the Andes of Ecuador (unknown to inhabit into specific sural patches as in *A. abditus* sp.n.), in the Northern Andes biogeographic province Morrone (2014) (Fig. 27). The examined female was found below a rock with a simple vertical burrow of at least 20 cm.

REMARKS: Dupérré & Tapia (2024) described *A. pasochoa* comb.n. based on a specimen of 7.52 millimetres, which showed the typical paratropidid

Fig. 27. Habitat of *Alienus pasochoa* comb.n.

habitus by having soil particles encrusted on different parts of its body. During the examination of Paratropididae specimens from the Pasochoa Volcano collected by PP-R, a female resembling spermathecae and maxillary cuspule morphology of *A. pasochoa* comb.n. was identified (cf. Fig. 26 vs. Dupérré & Tapia (2024: fig. 19C). Nonetheless, this specimen is almost twice the size of the supposed adult female of this species. Additionally, the examined female does not exhibit the cryptic habitus as Dupérré & Tapia (2024: figs 18–19). As observed in juveniles of *A. abditus* sp.n. is it possible that juvenile and subadult stages of *A. pasochoa* comb.n. are the only ones that exhibit the cryptic habitus. Given the holotype of *A. pasochoa* comb.n. presents a partly developed spermathecae, due to the extremely small size of the spider we consider that the holotype female is in fact a subadult. For this reason, herein we provide a description and illustrations of an adult female of *A. pasochoa* comb.n.

Alienus roigi **Ríos-Tamayo, Sherwood, Peñaherrera-R., León-E. et Drolshagen sp.n.**

Fig. 28.

TYPE MATERIAL: Holotype ♀ (MACN-Ar 46807), 4 km de San Miguel de los Bancos, Bajada al Río Blanco, Pichincha, Ecuador, 26/11/1978, leg. A. Roig; paratypes 2 ♀♀ (MACN-Ar 38339), same data.

DIAGNOSIS: Females of *A. roigi* sp.n. can be easily distinguished from all other known females of *Alienus* by the comparatively enlarged and wide spermathecae receptacle (short and so wide in other known female congeners).

ETYMOLOGY: The specific epithet is an eponym honouring Argentinean entomologist Arturo Roig Alsina, collector of the type specimens.

DESCRIPTION OF HOLOTYPE FEMALE (MACN-Ar 38339) (Fig. 28): Total length including chelicerae: 15.9. Carapace: length 5.8, width 5.1. Caput: raised. Ocular tubercle: raised. Eyes: ALE > AME, PLE > AME, PME > AME. Fovea: procurved. Chelicera: length 3.1, width 2.0. Abdomen: length 8.2, width 6.0, SPS present over weakly developed tubercles. Maxilla: with 75/73 cuspules. Labium: length 1.3, width 2.0, with 82 cuspules. Sternum: length 3.0, width 3.9. Length of legs and palpal segments: see Table 12, leg formula IV, I, II, III. Trichobothria: tibiae I–IV (7/7/8/6); metatarsi I–IV (4/3/3/4); tarsi I–IV (10/9/9/10); palpal tibia (7); palpal tarsus (8). Spination: palpal tibia 1 plv 2 rlv, tarsi 2 plv 5 rlv; leg I (right): tibia 3 plv 3 rlv; metatarsi 13 plv 13 rlv; tarsi 6 plr 5 rlv; leg II: metatarsi 7 plv 4 rlv; tarsi 5 plv 3

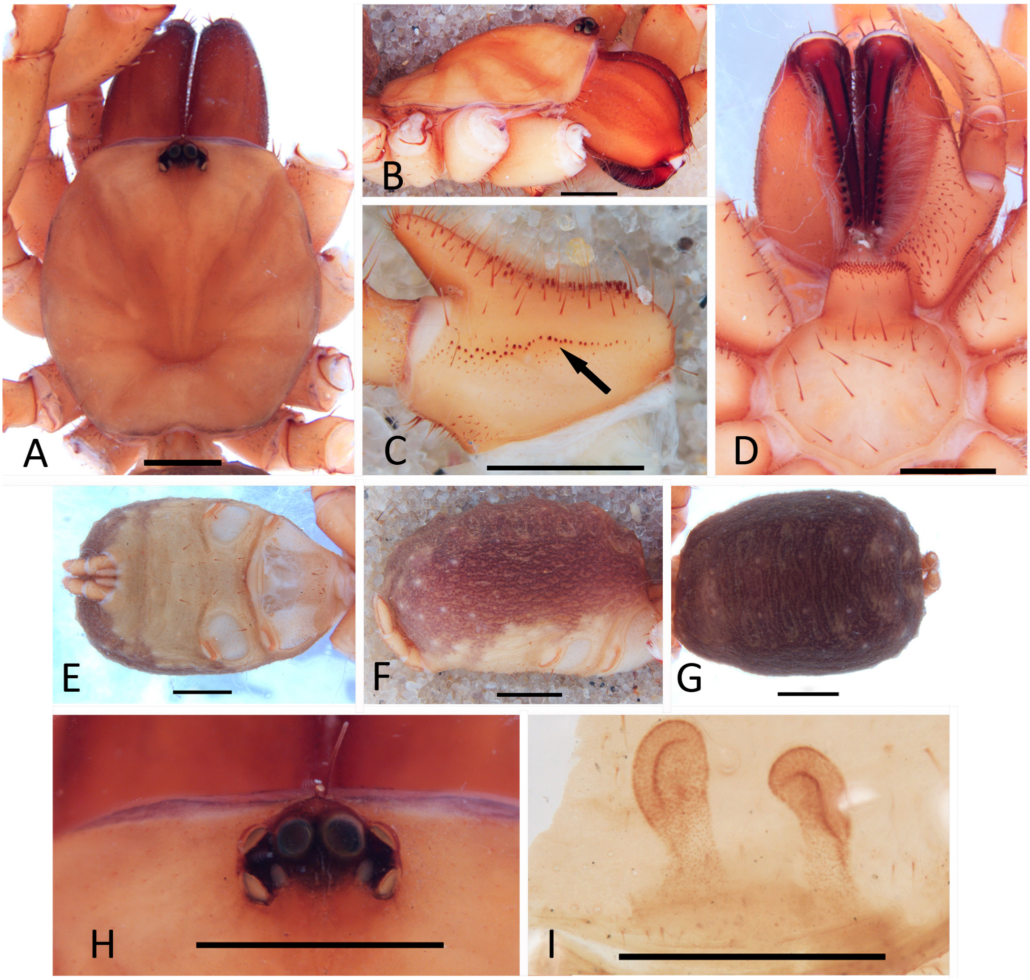

Fig. 28. *Alienus roigi* sp.n., holotype female (MACN-Ar 46807): A — carapace, dorsal view; B — carapace, lateral view; C — left maxilla lateral view; D — sternum and maxillae; E — abdomen, ventral view; F — abdomen, lateral view; G — abdomen, dorsal view; H — eye tubercle; I — spermathecae, dorsal view. Scale bars: 2 mm (A–H); 1 mm (I).

Table 12. *Alienus roigi* Ríos-Tamayo, Sherwood, Peñaherrera-R., León-E. et Drolshagen sp.n. holotype female (MACN-Ar 38339), length of legs and palp.

	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
I	6.5	3.5	4.8	4.4	1.8	21.0
II	5.1	2.9	3.3	3.8	1.8	16.9
III	4.5	2.4	2.6	3.4	1.7	14.6
IV	6.2	2.9	4.8	5.5	2.6	22.0
Palp	3.7	2.2	2.2	–	2.7	10.8

rlv; leg III: metatarsi 7 plv 8 rlv; tarsi 4 plv 2 rlv; leg IV: tibia 1-1 plv; metatarsi 5 plv 3 rlv; tarsi 4 plv 1 rlv. PLS with three segments, basal 0.7, median 0.8, digitiform apical 1.2. PMS present. Spermatheca: unilobed, short principal branch (~1 times the receptacle area) without longitudinal folds; wide oval receptacle with a well-developed distal concavity.

DISTRIBUTION: Known only from the type locality in the Mindo valley: 4 km from San Miguel de los Bancos, surroundings of Rio Blanco, 970 m, province of Pichincha (Fig. 16). The holotype was collected at a foothill evergreen forest of the Cordillera Occidental of the Andes of Ecuador, in the Northern Andes biogeographic province Morrone (2014).

Anisaspis Simon, 1892 *nomen dubium*

Anisaspis Simon, 1897: 549.
Anisaspis: Sherwood *et al.*, 2023.

TYPE SPECIES: *Anisaspis tuberculata* Simon, 1892 *nomen dubium* by original designation.

REMARKS: Recently, the type species of *Anisaspis* has been discussed in two works (Perafán *et al.*, 2019; Sherwood, Brescovit, *et al.*, 2023). However, only in the latter is the type series properly designated and redescribed, whereas Perafán *et al.* (2019) falsely claimed there was a single 'holotype' in BMNH. Regardless, the type material is immature (Perafán *et al.* 2019, Sherwood *et al.*, 2022, DS pers. obs.) and the only character with valuable diagnostic character was the absence of the posterior median spinnerets which is also shared with the genus *Anisaspoides* (type species described from an adult female; see Sherwood *et al.* (2023)). According to Raven (1985), *Anisaspis* have other characters that could be considered informative for genera recognition like the domed apical segment of the posterior lateral spinneret as well as presence of dorsal spines on leg tarsi. Nonetheless, during previous examination of the type material by DS these characters where not found. Since there are no more informative characters to separate both genera the question must be asked whether they are synonymous, nonetheless this cannot be confirmed until adult topotypes are collected and described. Recent fieldwork by arachnologists on Saint Vincent did not find *A. tuberculata* (G. Hormiga pers. comm. to DS) and thus both the genus and type species remain nebulous. A non-type specimen from Saint Vincent, falsely referred to as a "female holotype" by Raven (1985) also exists in Muséum national d'Histoire naturelle, Paris, France (MNHN) but this is also an immature. Therefore, we propose *Anisaspis* and *Anisaspis tuberculata* Simon, 1892 as *nomina dubia* until such time as topotypic adults are described.

Anisaspoides F.O. Pickard-Cambridge, 1896

Anisaspoides F.O. Pickard-Cambridge, 1896: 726.
Anisaspis: Perafán *et al.*, 2019 (in part).
Anisaspoides: Sherwood *et al.*, 2023.

TYPE SPECIES: *Anisaspoides gigantea* F.O. Pickard-Cambridge, 1896 by original designation (F.O. Pickard-Cambridge, 1896).

DIAGNOSIS: *Anisaspoides* can be differentiated from all known genera of Paratropididae by the absence of posterior median spinnerets. Females of *Anisaspoides* resemble those of *Alienus* gen.n. by having a rounded, unilobulate, and bidimensional spermathecal receptacle with a distal receptacle concavity. Nonetheless, females of *Anisaspoides* differ from *Alienus* gen.n. by having spermathecal principal branches emerging from wide and rounded bursa copulatrix and posterior median spinnerets and abdominal pattern absent (presence of posterior median spinnerets, abdominal pattern, and spermathecal principal branches emerging from thin and inconspicuous bursa copulatrix in *Alienus* gen.n.). Males of *Anisaspoides* slightly resemble those of *Alienus* gen.n. by having an embolus less than ~5x the tegulum length, presence of a median embolus curvature, embolar keels, and ITC in leg I. Nevertheless, *Anisaspoides* differs from *Alienus* gen.n. by having a crested dorsal keel and posterior median spinnerets and abdominal pattern absent (presence of posterior median spinnerets, prolateral embolic keel and abdominal pattern in *Alienus* gen.n.).

DISTRIBUTION: Brazil and Colombia.

SPECIES INCLUDED: *A. camarita* (Perafán, Galvis et Pérez-Miles, 2019) comb.n., *A. gigantea* F.O. Pickard-Cambridge, 1896.

REMARKS: The delimitation of the genus *Anisaspoides* consists of *A. gigantea* and the newly transferred *A. camarita*, each species described on the basis of a distinct sex.

Anisaspoides camarita (Perafán, Galvis et Pérez-Miles, 2019) comb.n.

Anisaspis camarita Perafán *et al.*, 2019: 7, figs 1A–F.

TYPE MATERIAL: Holotype ♂ (ICN-Ar 1404) Bosque de Bavaria, departamento de Meta, Colombia (4°10′51.2″N 73°38′52.8″W), 07/10/2005, leg. H.J. Salazar not examined.

REMARKS: *Anisaspoides* is the currently valid genus without posterior median spinnerets (see above); for this reason, *Anisaspis camarita* is herein transferred to *Anisaspoides* until *Anisaspis* is resolved.

Inpatropis Peñaherrera-R., Sherwood, Ríos-Tamayo et Drolshagen gen.n.

Paratropis: Almeida, Morais, 2022 (in part).

TYPE SPECIES: *Inpatropis minuscula* (Almeida et Morais, 2022) comb.n. by designation herein.

DIAGNOSIS: *Inpatropis* gen.n. can be differentiated from all other Paratropididae genera by having six eyes, domed apical segment of the posterior lateral spinnerets, presence of abdominal pattern, and presence of dorsal cephalic spinules. Males of *Inpatropis* gen.n. resemble those of *Paratropis* by having an embolus with a distal curvature, absence of embolar keels, and presence of a baso-retrolateral cymbial apophysis. However, males of *Inpatropis* gen.n. differ from *Paratropis* by having two anterior abdominal marks, dorsal cephalic spinules present, six

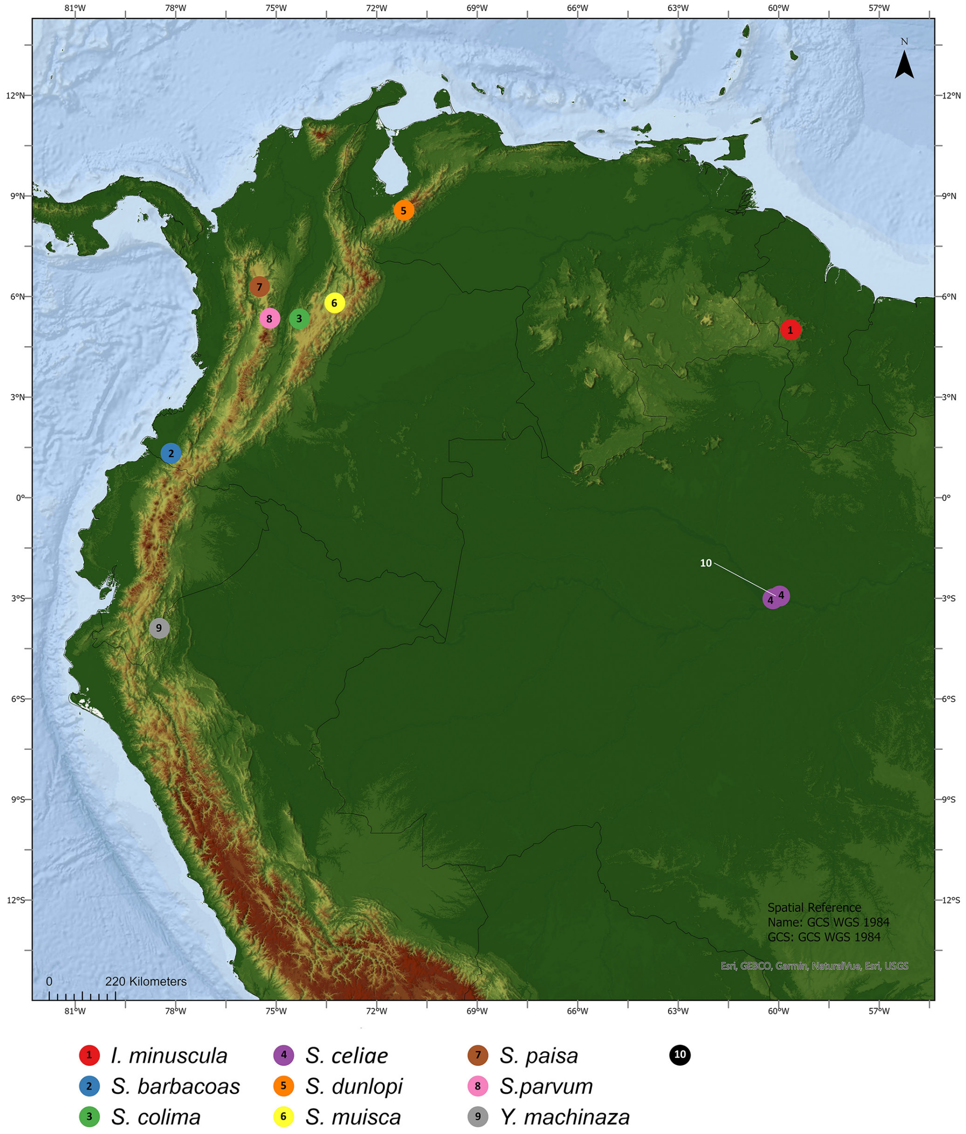

Fig. 29. Distribution of *Inpatropis* gen.n., *Stormtropis*, and *Yamaratropis* gen.n.

eyes, domed apical segment of the posterior lateral spinnerets, embolus less than ~5x the tegulum length, and inferior tarsal claw in all the legs absent (eight eyes, digitiform apical segment of the posterior lateral spinnerets, inferior tarsal claw variant but present at least in one leg, embolus more than ~5x the tegulum length, and dorsal cephalic spinules and abdominal pattern absent in *Paratropis*). Females of *Inpatropis* gen.n. slighly resemble those of *Anisaspoides* by having principal branches emerging from wide and rounded bursa copulatrix. Nonetheless, *Inpatropis* gen.n. differ from *Anisaspoides* and any other know genera by having digitiform spermathecal receptacles, six eyes, domed apical segment of the posterior lateral spinnerets, and presence of dorsal cephalic spinules.

ETYMOLOGY: The generic epithet is a combination of the letters INPA in honour of the Instituto Nacional de Pesquisas da Amazônia, whose researchers Marlus Queiroz Almeida and José Wellington de Morais described the type species, and *-tropis*, as a reference to the genus *Paratropis* where the species was originally described. The gender is feminine.

DISTRIBUTION: Guyana (Fig. 29).

REMARKS: The reduced total size, comparatively more quadrate sternum, and ellipsoid labium in *Inpatropis minuscula* comb.n. could also separate the new genus from all other known Paratropididae taxa, but these characters should be tested if they are constant within more representatives of *Inpatropis* gen.n.

SPECIES INCLUDED: *I. miniscula* comb.n.

Inpatropis minuscula **(Almeida et Morais, 2022) comb.n.**

Paratropis minusculus Almeida et Morais, 2022: figs 1–11.

TYPE MATERIAL: Holotype ♂ (MCZ 47063) Potaro-Siparuni, Bay Camp, 8 km WNW Chenapau, Potaro River, Guyana (5°00′35.06″N 59°38′09.35″W), 12/3/2014, leg. M.G. Branstetter, not examined; paratypes 3♀♀ (MCZ 47061) Potaro-Siparuni, Bay Camp, 8 km WNW Chenapau, Potaro River, Guyana (5°00′43.13″N 59°38′38.22″W), 05/3/2014 leg. M.G. Branstetter, not examined.

DIAGNOSIS: As per genus diagnosis.

REMARKS: Although the male of this species shows an enlarged embolus without keels, resembling those males of *Paratropis*, the absence of the posterior median eyes, cephalic spinules, domed apical section of posterior lateral spinnerets in both sexes and females without spermathecae vesicula or any receptacle morphology does not coincide with any known Paratropididae genera. According to the phylogenetic analyses *I. minuscula* comb.n. conforms a single basal clade of the LP clade, divergent from *Paratropis*. For this reason, this species is now transferred into its own genus for taxonomic stability.

Stormtropis **Perafán, Galvis et Pérez-Miles, 2019**

Stormtropis Perafán *et al.*, 2019: 16.

Paratropis Santos *et al.*, 2025: 235 (in part).

TYPE SPECIES: *Stormtropis parvum* Perafán, Galvis et Pérez-Miles, 2019 by original designation (Perafán *et al.*, 2019).

DISTRIBUTION: Brazil, Colombia, and Venezuela (Fig. 29).

SPECIES INCLUDED: *S. barbacoas* sp.n., *S. colima*, *S. celiae* comb.n., *S. dunlopi* sp.n., *S. manauara* comb.n., *S. muisca*, *S. paisa*, *S. parvum*.

REMARKS: During 2024, PP-R visited the collection of ICN where the type material of the previously described species of *Stormtropis* by Perafán *et al.* (2019) were supposed to be deposited, but after searching the collection no such specimens were found. The same year, PP-R also visited the FCE-MY thinking that the material may have been kept there because Carlos Perafán studied under Fernando Pérez-Miles laboratory who is based in Uruguay (Carlos Perafán pers. comm. to PP-R), but unfortunately, the material was not found in this collection either. Because no one knows where this material is, it is possible that they have all been lost.

Santos *et al*. (2025) recently described three new species of *Paratropis* from Colombia and Brazil. The Colombian species (*P. vulcanix*; see *Paratropis* species account) is still considered misplaced within *Paratropis*, but no further taxonomic action is proposed at this time. The Brazilian species (*S. celiae* comb.n. and *S. manauara* comb.n.) are herein transferred to *Stormtropis* based on our phylogenetic results and the optimised diagnostic characters for this genus, such as the absence of receptacle concavities, mushroom-shaped spermathecae receptacle, embolus medial curvature present, dorsal embolic keel present, loss of retrolateral cymbial apophysis, embolus less than ~5 times tegulum length, and absence of STS setae apically dilated over coxae.

Stormtropis barbacoas **Ríos-Tamayo, Sherwood, Peñaherrera-R. et Drolshagen sp.n.**

Fig. 30.

TYPE MATERIAL: Holotype ♀ (SMNK-ARA 19576), Barbacoas, Junin, Nariño, Colombia, 1075 m.a.s.l, MP VII (Leist 3), 20/12/1972–09/09/1973, leg. N. Leist; paratype ♀ (SMNK-ARA 19575), same data.

DIAGNOSIS: Females of *S. barbacoas* sp.n. resemble those of *S. dunlopi* sp.n. by comparatively having smaller receptacles. Nonetheless, females of *S. barbacoas* sp.n. differ from *S. barbacoas* sp.n. by having a short length principal branch (~1 time the receptacle area), maxillary spinules, and coarse spines in tibia I (elongate principal branch being ~2.5 times the receptacle area and maxillary spinules and coarse spines in tibia I absent in *S. dunlopi* sp.n.).

ETYMOLOGY: The species epithet is a noun in apposition taken from the type locality.

DESCRIPTION OF HOLOTYPE FEMALE (SMNK-ARA 19576) (Fig. 30)**:** Total length including chelicerae: 22.6. Carapace: length 8.3, width 7.9. Caput: raised. Ocular tubercle: raised. Eyes: ALE > AME, PLE > AME, PME > AME. Fovea: recurved. Chelicerae: length 4.3, width 2.6. Abdomen: length 10.0, width 7.5, presence of tubercles without multilayered setae. Maxilla with 58/54 cuspules. Labium: length 1.4, width 2.2, with 97 cuspules. Sternum: length 3.2, width 4.7. Length of legs and palpal segments: see Table 13, leg formula IV, I, II, III. Trichobothria: tibiae I–IV (7/6/6/5); metatarsi I–IV (4/4/3/4); tarsi I–IV (9/8/7/8); palpal tibia (6); palpal tarsus (8). Spination: palpal: tibia 4 rlv 1 plv; tarsi 3 plv 5 rlv 1 p; leg I: tibia 14 rlv 8 plv; metatarsi 15 plv 20 rlv; tarsi 6 plv 5 rlv; leg II: tibia 3 rlv; metatarsi 4 plv 5 rlv 2

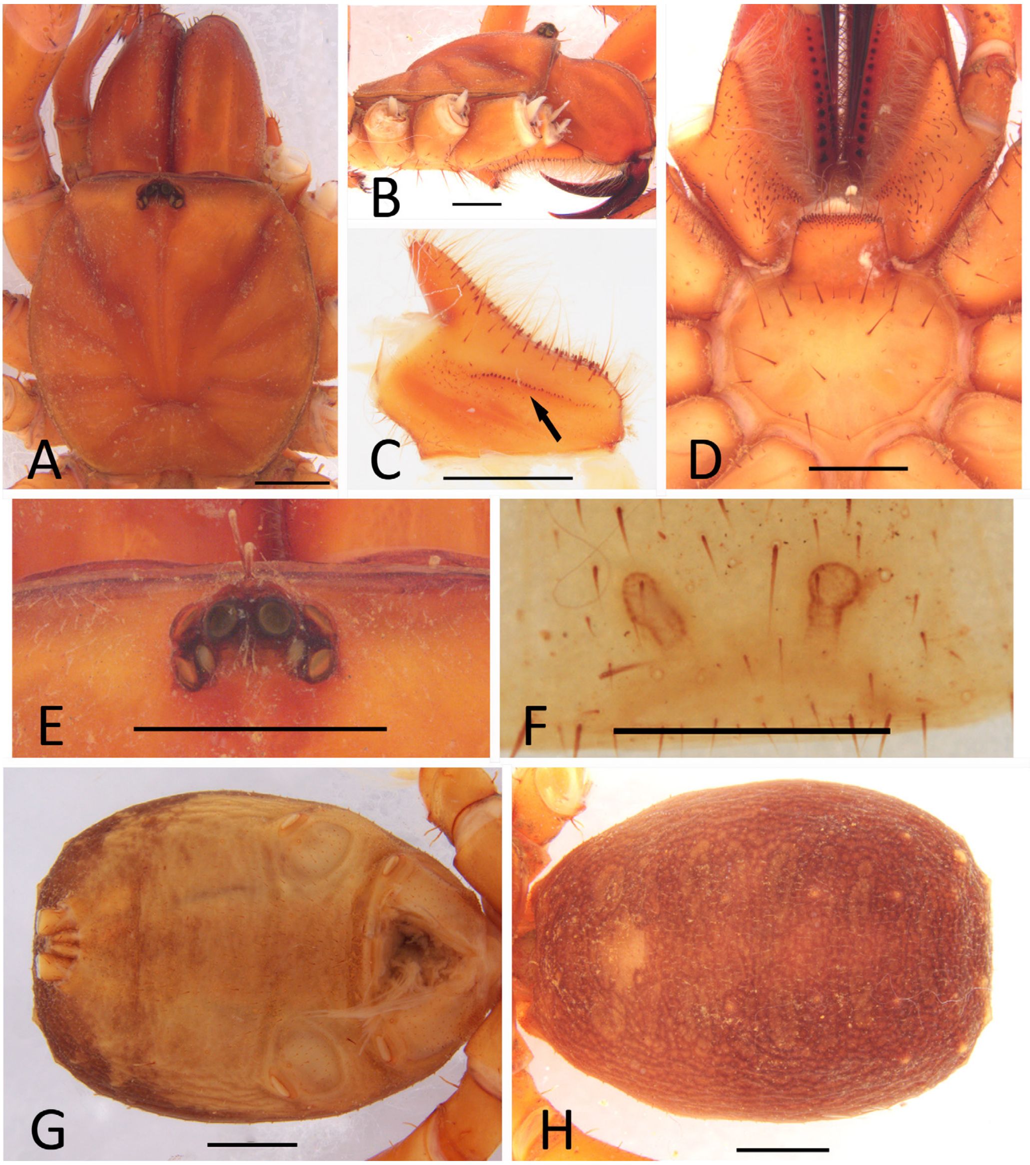

Fig. 30. *Stormtropis barbacoas* sp.n., holotype female (SMNK-ARA 19576): A — carapace, dorsal view; B — carapace, lateral view; C — left maxilla, lateral view (arrow, maxillary spinules); D — sternum and maxillae; E — eye tubercle; F — spermathecae, dorsal view; G — abdomen, ventral view; H — abdomen, dorsal view. Scale bars: 2 mm (A–E, G–H); 1 mm (F).

Table 13. *Stormtropis barbacoas* Ríos-Tamayo, Sherwood, Peñaherrera-R., et Drolshagen sp.n. holotype female (SMNK-ARA 19576), length of legs and palp.

	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
I	7.3	3.7	5.7	5.0	2.1	23.8
II	5.8	3.0	3.9	4.3	2.0	19.0
III	5.0	2.8	3.0	4.0	2.0	16.8
IV	6.9	3.2	5.5	6.2	2.8	24.6
Palp	3.9	2.3	2.4	–	3.0	11.6

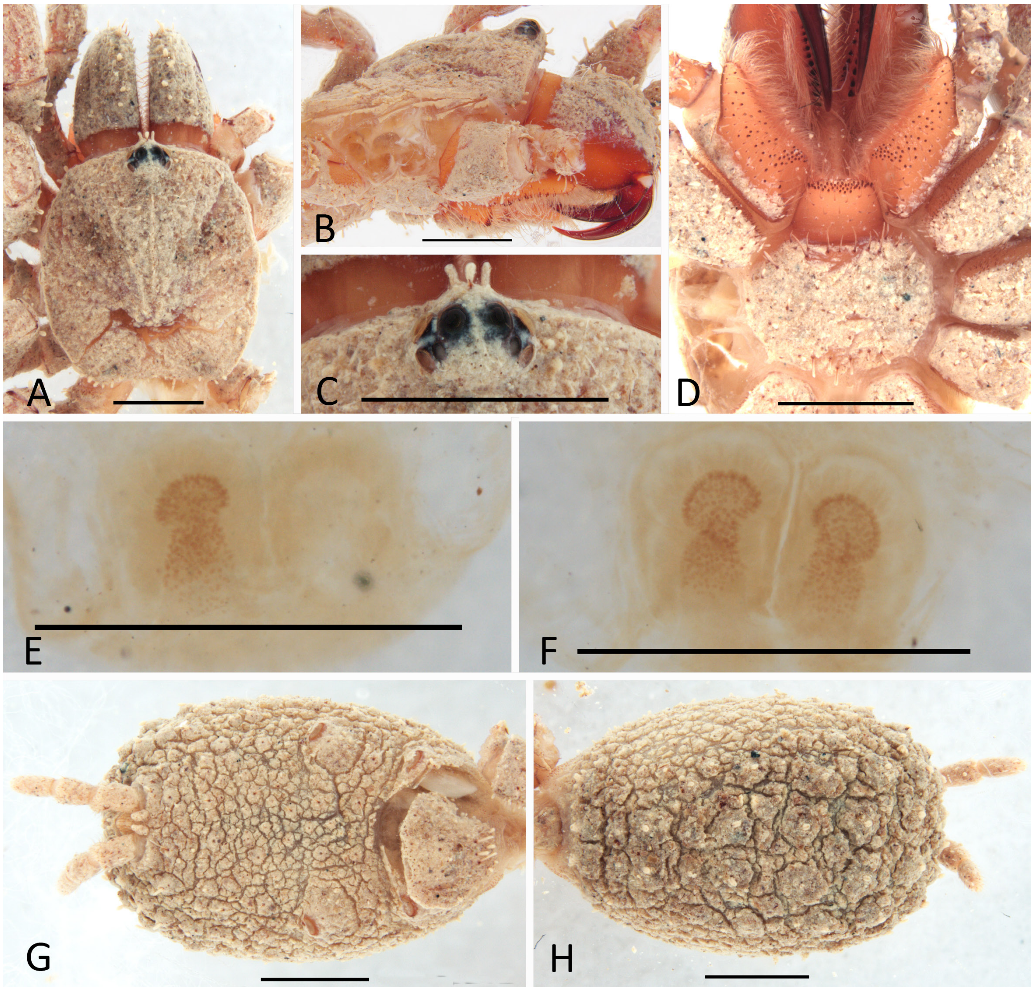

Fig. 31. *Stormtropis celiae* comb.n., non-type female (INPA-ARA 008806): A — carapace, dorsal view; B — carapace, lateral view; C — eye tubercle; D — sternum and maxillae; E — spermathecae (SMNK-ARA 19596), dorsal view; F — spermathecae (INPA-ARA 008806), dorsal view; G — abdomen, ventral view; H — abdomen, dorsal view. Scale bars: 2 mm (A–D, G–H); 1 mm (E–F).

p; tarsi 3 plv 3rlv; leg III: tibia 3 plv 1 rlv, metatarsi 4 plv 4 rlv 1 p; tarsi 3 plv 2 rlv; leg IV: tibia 3 plv; metatarsi 4 plv, 2 rlv; tarsi 5 plv, 2 rlv. Spinnerets: PLS with three segments, basal 0.9, median and apical [missing]. PMS present. Spermathecae with two receptacles, each with a single apical lobe and near absent neck constriction, left lobe ill-defined, right lobe rounded, receptacles almost as long as length of lobe, left receptacle medially sinuous, receptacles thinner than lobes (Fig. 22F). Colour (in alcohol): carapace and legs orange-yellow, abdomen dorsally brown and ventrally light brown. Affinities: most of body and legs with little soil, sternum encrusted.

DISTRIBUTION: Known only from the type locality (Fig. 29).

Stormtropis celiae (Santos, Gomes, Almeida, de Morais et Bertani 2025) comb.n.

Figs 31–33.

Paratropis celiae Santos *et al.*, 2025: 236, figs 1–53.

TYPE MATERIAL: Holotype ♂ (INPA-ARA 9115), Barranco/Plato, Acariquara, Manaus, Amazonas, Brazil (3°4′52.40″S 59°57′30.67″W), 17/04/2018, leg. M. Almeida, not examined; Paratypes 1 ♀ (INPA-ARA 9115) 1 ♂ 3 ♀ (INPA-ARA 9115) same data as holotype but 9/03/2018, not examined.

MATERIAL EXAMINED: 1 ♀ (INPA-ARA 008806), Reserva Ducke, Manaus, Amazonas, Brazil (2°55′52.77″S 59°58′28.54″W), RD E4, collection method: pitfall trap, 17/02/1992, leg. H. Höfer and

Table 14. *Stormtropis celiae* (Santos, Gomes, Almeida, de Morais et Bertani 2025) comb.n. non-type female (INPA-ARA 008806), length of legs and palp.

	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
I	3.9	2.1	3.2	2.7	1.3	13.2
II	3.2	1.7	2.3	2.3	1.3	10.8
III	2.7	1.5	1.8	2.2	1.4	9.6
IV	4.0	1.8	3.4	3.4	2.1	14.7
Palp	2.5	1.3	1.5	–	1.7	7.0

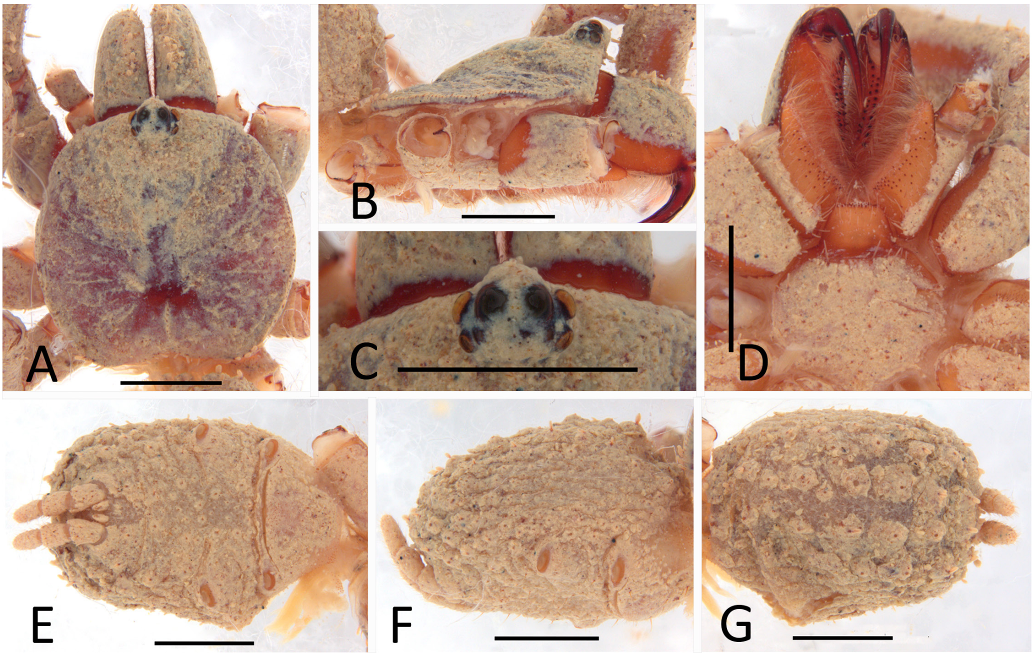

Fig. 32. *Stormtropis celiae* comb.n., non-type male (INPA-ARA 008805): A — carapace, dorsal view; B — carapace, lateral view; C — eye tubercle; D — sternum and maxillae; E — abdomen, ventral view; F — abdomen, lateral view; G — abdomen, dorsal view. Scale bars: 2 mm (A–G).

T. Gasnier; 1 ♂ (INPA-ARA 008805), same data and collector as Holotype, 23/03/1992; 1 ♀ (SMNK-ARA 19596), same data as holotype, collection method: manual, 30/12/1965, leg. L. Beck; 1 ♂ (SMNK-ARA 19606), Manaus, Taruma Mirim, Brazil (3° 0'53.03"S 60°10'21.36"W), TM capoeira E 10 K, collection method: ground eclector, 20/04/1982, leg. J. Adis; 1 ♂ (INPA-ARA 008807), Amazonas, Manaus, Reserva Ducke, Brasil (2°55′52.77″S 59°58′28.54″W), RD E2; collection method: ground eclector, 11/03/1992, leg. H. Höfer and T. Gasnier; 1 ♀ (INPA-ARA 008808), same data and collector, RD E2; collection method: ground eclector, 13/04/1992; 1 ♀ (INPA-ARA 008809), same data and collector, D Q-area 2 Bof N-11; collection method: pitfall trap, 23/03/1992.

DIAGNOSIS: Females of *S. celiae* comb.n. resemble those of *S. paisa* by comparatively having wider and more protruding receptacles. Nonetheless, females of *S. celiae* comb.n. differ from *S. paisa* by having semi-triangular principal branch of spermathecae being ~2.3 times the receptacle area, neck constriction, and having a constant spermathecae sclerotisation (rectangular principal branch being ~2 times the receptacle area, receptacle more sclerotised than principal branch, and neck constriction absentin *S. paisa*). Males of *S. celiae* comb.n. resemble those of *S. muisca* by the absence of a tibial apophysis. Nevertheless, *S. celiae* comb.n. differ from *S. muisca* by having a developed dorsal embolic keel (weakly developed dorsal embolic keel in *S. muisca*).

DESCRIPTION. **Non-type female** (INPA-ARA 008806) (Fig. 31): Total length including chelicerae: 15.68. Carapace: length: 5.35, width: 4.96. Caput: raised. Ocular tubercle: strongly raised. Eyes: AME > PME > PLE > ALE. Fovea: procurved. Chelicerae: length 2.69, width 2.3. Abdomen: length: 7.64, width:

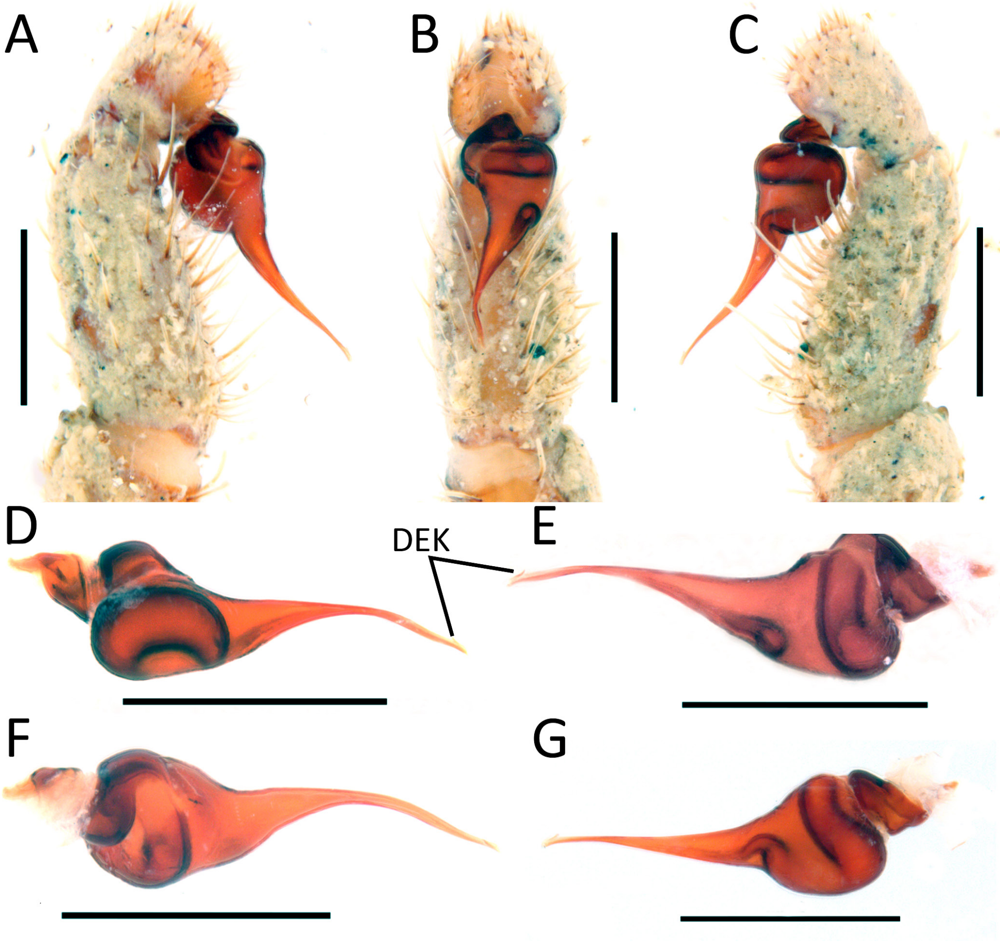

Fig. 33. *Stormtropis celiae* comb.n., non-type male (INPA-ARA 008805): A — palp, prolateral view; B — palp, ventral view; C — palp, retrolateral view; D — bulb, prolateral view; E — bulb, retrolareral view; F — bulb, dorsal view; G — bulb, ventral view. Scale bars: 1 mm (A–G).

5.07, SPS present over numerous weakly developed tubercles; abdominal pattern uninterpretable. Maxilla with 52/54 cuspules. Labium: length: 0.89, width: 1.42, with 37 cuspules. Sternum: length: 2.05, width: 2.88. Length of legs and palpal segments: see Table 14, leg formula IV, I, II, III. Trichobothria: tibiae I–IV (6/6/6/5); metatarsi I–IV (3/3/3/3); tarsi I-IV (6/6/4/4). Spination: palpal: tarsi 1 plv 2 rlv; leg I: metatarsi 4 plv 4rlv, tarsi 6 plr 6 rlv; legs II–III: metatarsi 2 plv 2 rlv; leg IV: metatarsi 4 v, tarsi 1 plv. Tarsi I with ITC. PLS with three segments, basal 0.89, median 0.71, digitiform apical 0.78. PMS present. Spermathecae: with median principal branches emerging from thin and inconspicuous bursa copulatrix, mushroom-shaped receptacles; apical and distal concavity absent.

Non-type male (INPA-ARA 008807) (Figs 32–33): Total length including chelicerae: 12.86. Carapace: length: 5.10, width: 5.17. Caput: raised. Ocular tubercle: strongly raised. Eyes: PME > PLE > AME > ALE. Fovea: procurved. Chelicerae: length 2.10, width 1.17. Abdomen: length: 5.59, width: 3.99, SPS present over numerous weakly developed tubercles; abdominal pattern uninterpretable. Maxilla with 38/41 cuspules. Labium: length: 0.74, width: 1.26, with 25 cuspules. Sternum: length: 2.23, width: 2.84. Length of legs and palpal segments: see Table 15, leg formula IV, I, II, III. Trichobothria: tibiae I–IV (6/6/5/4); metatarsi I–IV (5/4/3/3); tarsi I–IV (5/5/5/5) Spination: metatarsi III 2 plv; IV 1plv. Palpal cymbium without weakly developed retrolateral apophysis. Leg I without tibial apophysis. Tarsi I with ITC. PLS with three segments, basal 0.72, median 0.62, digitiform apical 0.71. PMS present. Palpal bulb: embolus medially curved and twisted retrolaterally, developed dorsal embolic keel.

Table 15. *Stormtropis celiae* (Santos, Gomes, Almeida, de Morais et Bertani 2025) non-type male (INPA-ARA 008807), length of legs and palp.

	Femur	**Patella**	**Tibia**	**Metatarsus**	**Tarsus**	**Total**
I	4.7	2.3	3.9	3.6	1.6	16.1
II	4.4	1.8	3.7	4.1	1.8	15.8
III	3.8	1.8	2.7	3.2	1.5	13.0
IV	4.3	1.8	3.6	4.3	1.9	15.9
Palp	2.1	1.4	1.5	–	1.0	6.0

DISTRIBUTION: Known from the city and surroundings of Manaus (Fig. 29).

REMARKS: Santos *et al.* (2025) provided a clear morphological description of this species, nonetheless, due the expansion of new morphological characters herein we provide a re-description including these characters as well as standarised male palpal bulb views that allow proper comparison of embolus curvatures and structures based on a large number of specimens from Reserva Ducke and Taruma Marim, approximately 16 km NNW and 25 WNW from the type locality in the city of Manaus, respectively. Based on our phylogenetic results (Fig. 6), *Paratropis celiae* is placed within *Stormtropis*, for this reason herein we transfer this species and create the new combination *Stormtropis celiae* comb.n.

***Stormtropis manauara* (Santos, Gomes, Almeida, de Morais et Bertani, 2025) comb.n.**

Paratropis manauara Santos *et al.*, 2025: 240, figs 54–76.

TYPE MATERIAL: Holotype ♂ (INPA-ARA 9116), UFAM, Manaus, Amazonas, Brazil (–3.040082, –059.376535), 30/01/2018, leg. M. Almeida, not examined; paratype ♀ (INPA-ARA 9116), same data, not examined.

REMARKS: Non-type material of this species was examined for another work where full details will be presented (Sherwood *et al.*, in prep.). Based on this, and examination of the photographs of the type material, it is clear based on the morphology of the genitalia that this species belongs to *Stormtropis*, therefore we transfer this species and create the new combination *Stormtropis manauara* comb.n.

***Stormtropis dunlopi* Ríos-Tamayo, Sherwood, Peñaherrera-R. et Drolshagen sp.n.**

Fig. 34.

TYPE MATERIAL: Holotype ♀ (ZMB 30784), Merída, Venezuela, date and collector not stated; paratype 1 ♀ (ZMB-Arach 56379), same data as holotype (abdomen missing).

DIAGNOSIS: Females of *S. dunlopi* sp.n. resemble those of *S. barbacoas* sp.n. by comparatively having smaller receptacles. Nonetheless, females of *S. dunlopi* sp.n. differ from *S. barbacoas* sp.n. by having an elongated principal branch (~2.5 times the receptacle area) and the absence of maxillary spinules and coarse spines in tibia I (short principal branch being ~1 time the receptacle area and maxillary spinules and coarse spines in tibia I present in *S. barbacoas* sp.n.).

ETYMOLOGY: The specific epithet is an eponym in honour of our colleague and friend Jason Dunlop (Museum für Naturkunde, Berlin) in recognition of his decades of work in arachnid palaeontology and as Curator of Arachnida and Myriapoda at one of Germany's foremost natural history collections.

DESCRIPTION OF HOLOTYPE FEMALE (ZMB 30784) (Fig. 34): Total length including chelicerae: 22.9. Carapace: length 9.4, width 9.1. Caput: raised. Ocular tubercle: highly raised. Eyes: ALE > PME > PME > AME. Fovea: procurved. Chelicera: length 3.3, width 2.5. Abdomen: length 10.1, width 7.6, presence of tubercles without multi-layered setae. Maxillae: with 92/88 cuspules. Labium: length 1.9, width 2.6, with 104 cuspules. Sternum: length 4.6, width 5.5. Length of legs and palpal segments: see Table 16, leg formula I, IV, II, III. Trichobothria: tibiae I–IV (7/8/8/6); metatarsi I–IV (5/6/7/7); tarsi I–IV (10/9/10/10); palpal tibia (7); palpal tarsus (12). Spination: palpal: tarsi 1 plv 2 rlv; leg I: metatarsi 9 plv 16 rlv, tarsi 11 plr 10 rlv; leg II: metatarsi 1 plv 3 rlv; tarsi 1 rlv; III: metatarsi 2 plv 2 rlv; tarsi 2plv 2 rlv; leg IV: metatarsi 1 plv; tarsi 2 plv 1 rlv. Spinnerets: PLS with three segments, basal 1.4 (bifurcate), median 1.2, digitiform apical 1.5. PMS present. Spermathecae with two receptacles, each with a single lobe, neck with moderate constriction, lobes rounded, receptacles elongate (>2 times length of lobe).

DISTRIBUTION: Known only from the type locality (Fig. 29).

***Yamaratropis* Peñaherrera-R., Sherwood, León-E., Ríos-Tamayo et Drolshagen gen.n.**

TYPE SPECIES: *Yamaratropis machinaza* sp.n. by monotypy.

DIAGNOSIS: Females of *Yamaratropis* gen.n. are easily differentiated from all known genera of Paratropididae by having an apical receptacle concavity creating a caliciform-shaped receptacle and the presence of spiniform microtrichium-like setae over

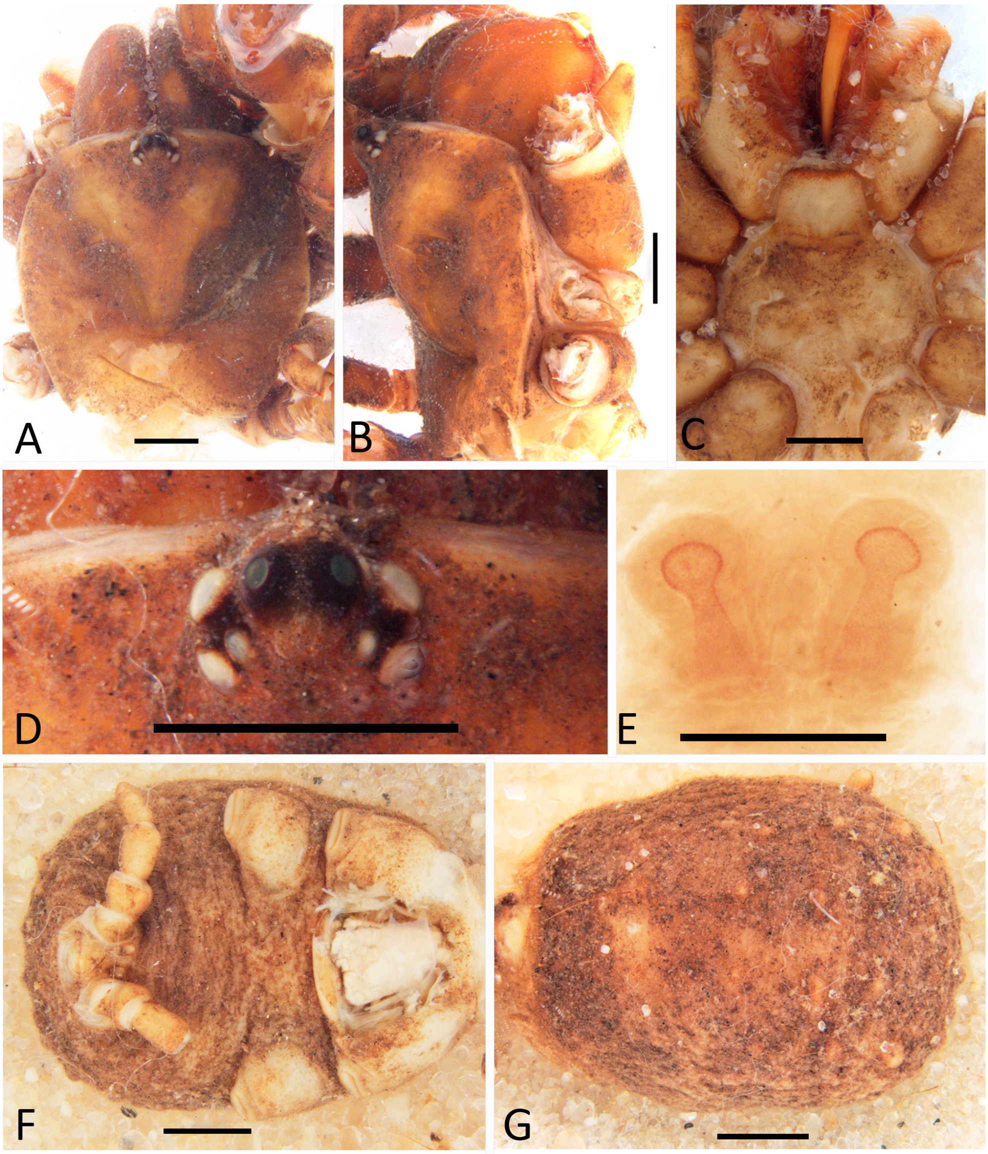

Fig. 34. *Stormtropis dunlopi* sp.n., holotype female (ZMB 30784): A — carapace, dorsal view; B — carapace, lateral view; C — sternum and maxillae; D — eye tubercle; E — spermathecae, dorsal view; F — abdomen, ventral view; G — abdomen, dorsal view. Scale bars: 2 mm (A–D, F–G); 1 mm (E).

Table 16. *Stormtropis dunlopi* Ríos-Tamayo, Sherwood, Peñaherrera-R., León-E. et Drolshagen sp.n. holotype female (ZMB 30784), length of legs and palp.

	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
I	7.0	4.1	5.4	4.6	1.9	23.0
II	5.5	3.3	3.5	3.8	1.9	18.0
III	4.7	2.9	2.7	3.4	1.9	15.6
IV	6.6	3.3	4.9	5.3	2.3	22.4
Palp	4.2	2.6	2.6	–	2.9	12.3

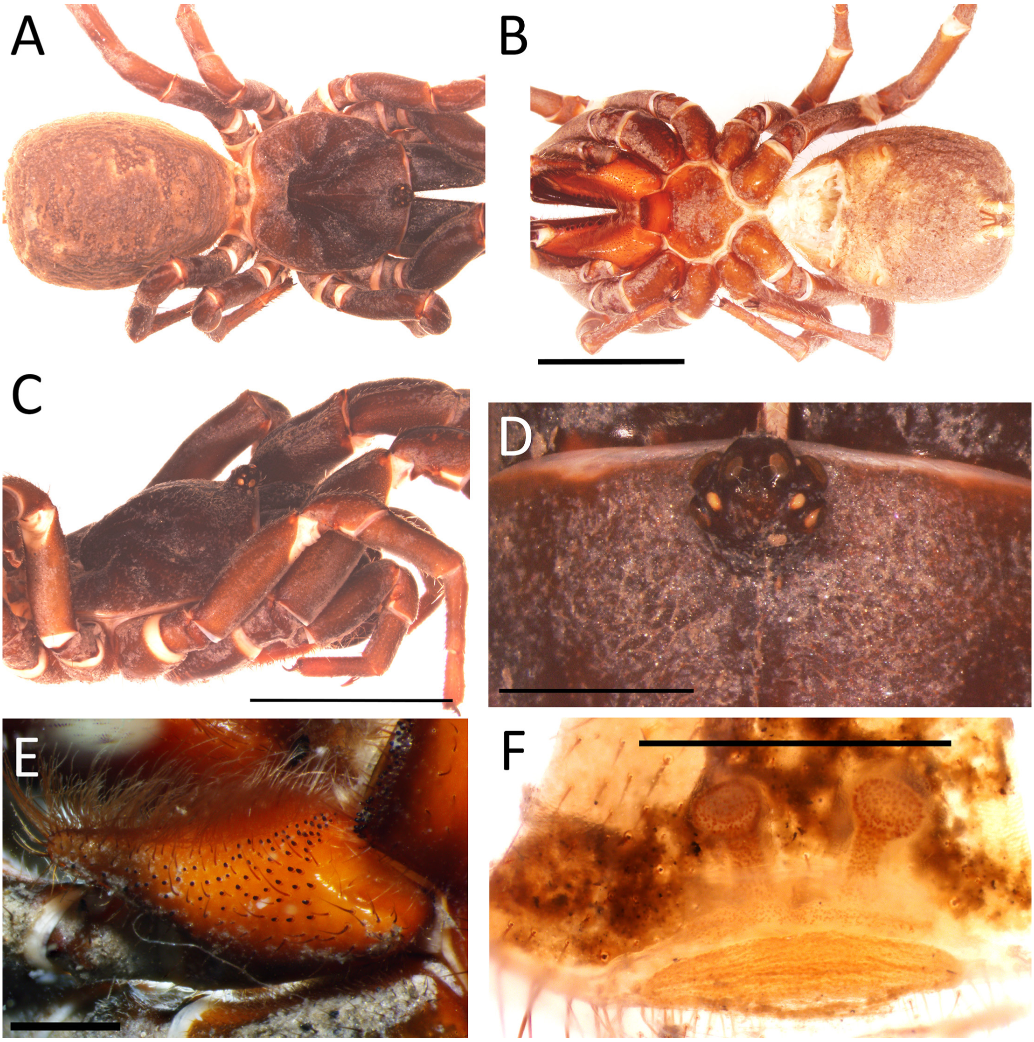

Fig. 35. *Yamaratropis machinaza* sp.n., holotype female (ZSFQ-i20433): A — habitus, dorsal view; B — habitus, ventral view; C — carapace, lateral view; D — eye tubercle; E — left maxilla; F — spermathecae, dorsal view. Scale bars: 8 mm (A–C); 2 mm (D); 1 mm (E); 4 mm (F).

femur, patella, and tibia of legs I–II (apical receptacle concavity and microthrichium-like setae absent in all known genera; rounded unilobulate and bidimensional receptacle in *Alienus* gen.n. and *Anisaspis*, bidimensional unperceptible lobule in *Inpatropis* gen.n., multilobulated [vesicles] in *Paratropis*, mushroom-shaped receptacle in *Stormtropis*).

ETYMOLOGY: The generic epithet is a combination of the Shuar-Chicham word *Yámaram* (new) and the ending *tropis* derived from the related genus *Paratropis*. The gender is feminine.

DISTRIBUTION: Ecuador (Fig. 29).

SPECIES INCLUDED: *Y. machinaza* sp.n.

***Yamaratropis machinaza* Peñaherrera-R., Sherwood, León-E., Ríos-Tamayo et Drolshagen sp.n.**

Figs 1, 3B, 35–36, 38.

TYPE MATERIAL: Holotype ♀ (ZSFQ-i20433), Second plateau, Cerro Machinaza, parroquia de Paquisha, provincia de Zamora Chinchipe, República del Ecuador (3°53′36.95″S 78°29′10.68″W), 15/10/2023, leg. P. Peñaherrera-R.

ADDITIONAL MATERIAL EXAMINED: 1 imm. (ZSFQ-i20432), non-type, same data as holotype.

DIAGNOSIS: As per genus diagnosis.

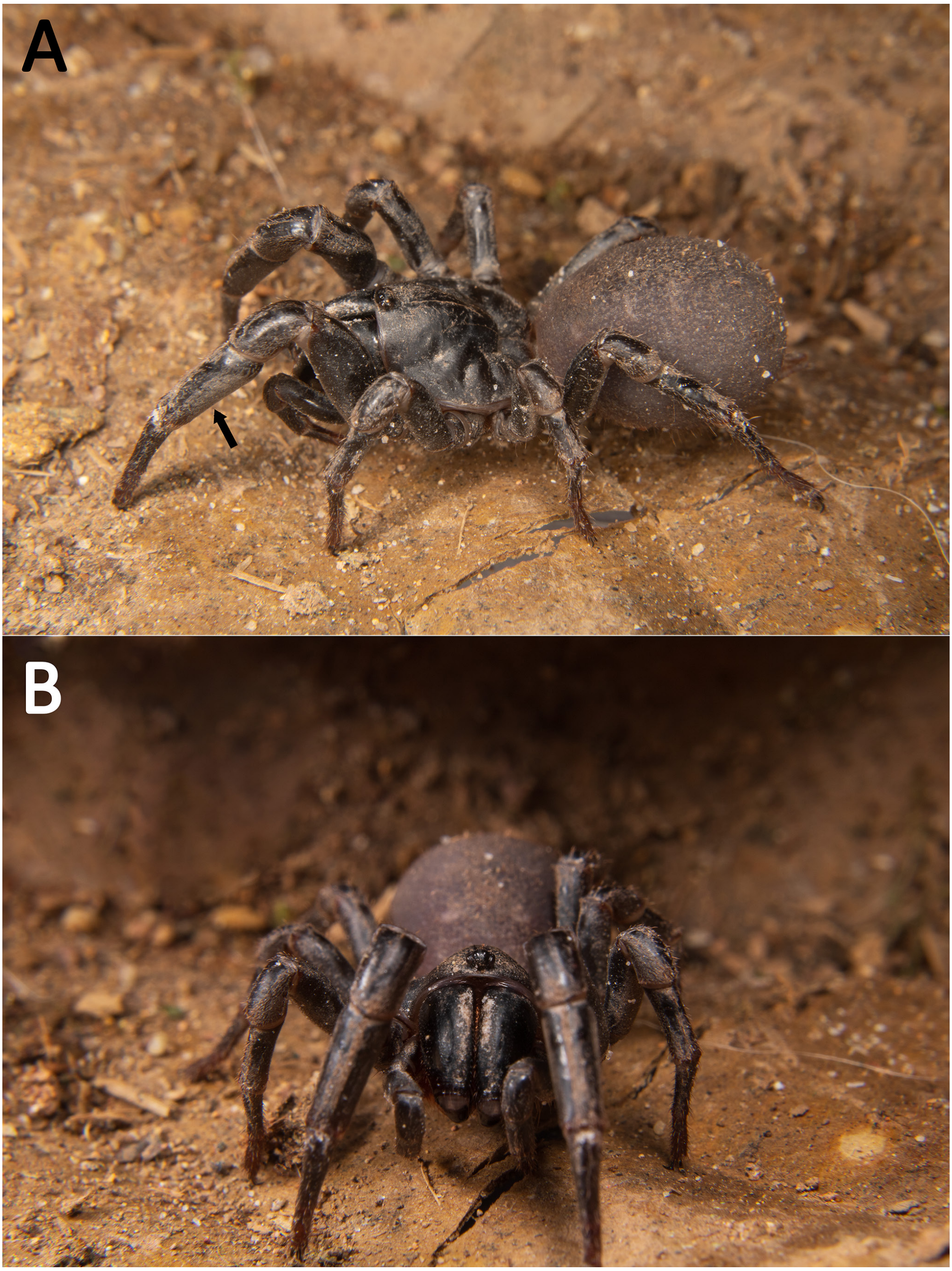

Fig. 36. *Yamaratropis machinaza* sp.n., holotype female (ZSFQ-i20433) habitus *in vivo*: A — lateral view (arrow, spiniform microtrichium-like scopulae); B — frontal view.

Table 17. *Yamaratropis machinaza* Peñaherrera-R., Sherwood, Ríos-Tamayo et Drolshagen sp.n. holotype female (ZSFQ-i20433), length of legs and palp.

	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
I	5.70	3.40	4.50	3.20	1.60	18.40
II	4.50	2.20	3.30	2.50	1.50	14.00
III	3.60	1.90	1.70	2.00	1.40	10.60
IV	4.80	2.60	3.60	3.50	2.00	16.50
Palp	2.90	1.50	1.60	–	2.10	8.10

Fig. 37. Habitat of *Yamaratropis machinaza* sp.n.: A — general view; B — close-up. Photo credits: David Brito-Zapata.

ETYMOLOGY: The specific epithet is an apposition taken from the type locality.

DESCRIPTION OF HOLOTYPE FEMALE (ZSFQ-i20433) (Figs 35–36): Total length including chelicerae: 29.4. Carapace: length 6.2, width 6.6. Caput: strongly raised. Ocular tubercle: strongly raised. Eyes: ALE > AME >PLE >PME. Fovea: recurved. Chelicera: length 3.7, width 1.7. Abdomen: length 9.52, width 7.32, short STS present overall abdomen, abdominal tubercles weakly developed. Maxilla with 73–78 cuspules. Labium: length 1.3, width 1.5, with 44 cuspules. Sternum: length 3.2, width 4.2. Length of legs and palpal segments: see Table 17, leg formula: I, IV, II, III; retrolateral, prolateral and ventral surface

Fig. 38. *Yamaratropis machinaza* sp.n., juvenile (ZSFQ-i20432) habitus *in vivo*. Arrow indicates the spiniform microtrichium-like scopulae.

of femur, patella, and tibia of legs I–II covered with spiniform microtrichium-like setae. Trichobothria: tibiae I–IV (6/6/6/4); metatarsi I–IV (4/4/3/3); tarsi I–IV (8/7/5/7). Spination: tarsi I 4rtv 2ptv; metatarsi I 2rtv, III 1rtv. Tarsi I–II with ITC. PLS with three segments, basal 0.7, median 0.6, digitiform apical 0.8. PMS present. Spermathecae with short principal branches emerging from thin and inconspicuous bursa copulatrix, apical concavity well developed creating a wide caliciform receptacle. Posterior internal fold of epigastric furrow with wide sclerotised plate. DLF and VLF absent.

DISTRIBUTION AND NATURAL HISTORY: Known only from the type locality in the Cordillera del Cóndor, Machinaza Andean Tepuy: Second plateau, Cerro Machinaza, 2390 m, province of Zamora Chinchipe (Fig. 29). The holotype was collected at a montane evergreen forest of the sandstone plateau of the Cordillera del Cóndor, in the Northern Andes biogeographic province Morrone (2014) (Fig. 37). The holotype and juvenile specimen were found in burrows near sandbanks and flagstones, these burrows were simple vertical chambers of ~3–5 cm (Fig. 38).

Discussion

The systematic history of the family Paratropididae Simon, 1889 was summarized by Valdez-Mondragón *et al.* (2014). Since then, the results of the prior total evidence phylogenetic analysis by Bond *et al.* (2012) were mostly supported by the results of a molecular analysis presented by Opatova *et al.* (2020). Paratropididae (based on two species of *Paratropis*) was found to be the most plesiomorphic taxon in the clade formed by Bipectina Goloboff, 1993 plus Atracidae Hogg, 1901 and Dipluridae Simon, 1889 (minus Euagridae Raven, 1979 and the genus *Microhexura* Crosby et Bishop, 1925, which lately were elevated to nominate family level). The new position of the family allows for the interpretation and first comparison of some morphological characters traditionally used for cladistic analyses. According to Goloboff (1993) the following character states may support the monophyly of the Paratropididae as now recognised: 1) the presence of a single strong tooth on the superior tarsal claws (also found in *Myrmekiaphila* Atkinson, 1886, *Heteromigas* Hogg, 1902, *Calathotarsus* Simon, 1903, *Actinopus* Perty, 1833, *Plesiolena* Goloboff et Platnick, 1987, *Idiops* Perty, 1833, *Neocteniza* Pocock, 1895, *Arbanitis* L. Koch, 1874 [as *Misgolas* Karsch, 1878 in Goloboff (1993)] and *Ummidia* Thorell, 1875; 2) an anteriorly produced maxillary lobe (also found in Theraphosidae Thorell, 1869 incl. *Melloina* Brignoli, 1985); 3) the presence of many labial cuspules (also found in *Scotinoecus* Simon, 1892, *Hexathele* Ausserer, 1871, *Porrhothele* Simon, 1892, *Atrax* O. Pickard-Cambridge, 1877 and theraphosids [incl. *Melloina*], but also *Macrothele* Ausserer, 1871; pers. obs.); 4) two rows of teeth on the cheliceral furrow (also found *in Atrax*, *Ischnothele*, *Myrmekiaphila*, *Heteromigas*, *Calathotarsus*, *Actinopus*, *Plesiolena*, *Idiops*, *Neocteniza*, *Arbanitis* [as *Misgolas*] and *Ummidia*, but not *Porrhothele*, contra Goloboff 1993; pers. obs.); 5) a low and domed tarsal organ (also found in *Melloina*, *Ixamatus* Simon, 1887, *Xenonemesia* Goloboff, 1989 and *Microstigmata* Strand, 1932); and 6) a large, quadrate and very inclined labium (also found in *Melloina*). The steeply elevated eye tubercle, as well as the presence of clubbed shaped setae on the opisthosoma further support the monophyly of Paratropididae and, considering only a few of the aforementioned characters might be plesiomorphies, we suspect the grouping to be stable based on the molecular support of previous studies. Despite many of the characters mentioned above not having evolved earlier, similar, or even same states may be found in Bipectina, possibly lowering the stability of clades within Paratropididae if considered in a larger context.

Until now, no detailed evaluation of morphological character dynamics has been proposed that might support the systematics within the family Paratropididae. 39 years ago, Raven (1985) provided for the first time contemporaneous information inferring intrafamilial relationships and supposedly true information on informative characters of which each paratropidid genus known at the name (*Anisaspis, Anisaspoides*, and *Paratropis*) can be delineated. Nonetheless, much of the provided information by Raven (1985) is now invalid because many of the characters presented in that work are variable or do not exist in the mentioned taxa by Raven (1985). For example, the cheliceral teeth curvature pattern was found to be only arranged as juxtaposed in all Paratropididae while in Raven (1985), lately followed by Dupérré (2015) for her Paratropididae key, was supposedly to be a juxtaposed pattern in *Paratropis* and *Anisaspoides* while in *Anisaspis* both teeth should converge at a point that creates a diagonally opposed pattern (Sherwood *et al.*, 2023). It should be noted that additional interest in the family seemed to be too rare to even question the characters presented in Raven (1985) (see Remarks of *Anisaspis* for further examples); except for the inferior tarsal claw which has been largely proven to be variable between species of the different genera (Valdez-Mondragón *et al.*, 2014; Dupérré, 2015; Dupérré, Tapia, 2024).

One of the exceptions where genitalic and somatic characters were taken into account (although noted by Valdez-Mondragón *et al.* (2014) for new lineage recognition was the rise of *Stormtropis* by Perafán *et al.* (2019), which was based on remarkable sexual morphology, contrasting to that of *Paratropis*. Nevertheless, this was the only case, if we had continued with the current taxonomic approach, many genera proposed here would be considered under *Paratropis* due to the broad delimitation of this genus (Almeida, Morais, 2022; Dupérré, Tapia, 2024). Although *Paratropis* delimitation seemed to be continuous and logical until Almeida and Morais (2022), the inclusion of the misplaced *Paratropis* by Dupérré & Tapia (2024) has extremely broadened and simplified the weight of diagnostic characters within Paratropididae by stating that *Paratropis* present few consistent morphological characteristics and broadly diagnosticating this genus even at the point of seeing no differentiation to those of *Stormtropis*. Nonetheless, through this first phylogenetic analysis, we can easily recognise and separate putative natural groups. Further supporting the idea of identifying somatic and genitalic characters for lineage identification through morphological phylogenies, as observed in other studies of Araneae (*e.g.* Bond, Opell, 2002; Oliveira, Brescovit, 2021; Ferretti *et al.*, 2023; Huber *et al.*, 2024; Sánchez-Ruiz, Bonaldo, 2024).

As mentioned by Dupérré & Tapia (2024), primary diagnostic characters for delimiting species of Paratropididae depend on a combination of genitalic and somatic characters. Herein some of them were discarded from our phylogenetic analysis due to their high homoplastic nature, nonetheless, these are useful for delimiting species albeit if they are sex-independent somatic characters should be taken as supportive characters while genitalic characters must be taken as primary diagnostic characters due to its high value in Mygalomorphae taxonomy whenever they can be interpreted and not minimised.

Interestingly, the recovered topology of internal clades in *Paratropis* and *Alienus* gen.n.

appears to align with a logical biogeographical pattern using both datasets; however, this intriguing result is currently under investigation in our ongoing research (Peñaherrera-R. *et al.* in prep.). We further conclude this exploratory work as a new opportunity for this family and researchers since the provided morphological data, phylogenetic approaches, and even distribution records represent a great baseline for new research. We should stress that we are not absolved from what the molecular data may reflect on the internal phylogenetic organisation of this family. Molecular work is ongoing, and we expect at some point to compare the present results with future molecular phylogenies.

Lastly, this work not only expands on the knowledge on the internal systematics of the family Paratropididae but also provides previously unreported natural history data for the family such as the construction of burrows from some sub-Andean, Andean, and Amazonian species and the use of anthropogenic material (use of microplastics in *P. rocolita* sp.n.) for their cryptic habitat. The discovery of burrowing behaviour in Paratropididae additionally provides the argument for a behavioural homoplasy present within the most plesiomorphic clade of Bipectina. Nonetheless, this open-hole entrance type suggests that this is the most basal record of this type of burrow in Bipectina while the rest of the early Bipectina clades indicate a trapdoor entrance type (Wilson *et al.*, 2023). Although the burrow records are scarce, the only species of Paratropididae that were recorded present additional structure or modifications like maxillary spinules and spiky cuspules that intuitively could be linked to this behaviour. Also, we provide the first records of *Stormtropis* from Venezuela and Brazil as well as the first species and endemic genus (*Yamaratropis* gen.n.) of an Andean Tepui. Further, *P. nunka* sp.n. with almost 30 mm of total length is to the best of our knowledge the largest known paratropidid in the world.

Compliance with ethical standards

CONFLICTS OF INTEREST: The authors declare that they have no conflicts of interest.

Acknowledgments

We warmly thank Jan Beccaloni (BMNH), Martín Ramírez and Cristian Grismado (MACN-AR), Dimitri Forero and Luis Carlos Lavado Mora (ICN-Ar), Taryn Ghia, Rafael E. Cárdenas, and Fernanda Salazar-Buenaño (all QCAZ I), Joachim Holstein (SMNK-ARA), and Emilia Peñaherrera-Romero, Margarita López, and Jorge Montalvo (all ZSFQ) for access to the collections and loan of material. DS also thanks Christine Rollard and Elise-Anne Legiun (MNHN) for hospitality during her research visits to the museum in Paris; Maeve McLaughlin and Dana Perry (BMNH) for allowing the use of facilities in the Light Microscopy Facility; and Sylvia Lucas (Instituto Butantan, São Paulo, Brazil) for insightful discussions over coffee about the placement of Brazilian taxa. Two anonymous reviewers, and the editor, whose comments improved the manuscript, are duly thanked. Specimens deposited at ZSFQ-i were collected under the following specimen collection authorisations: MAAE-ARSFC-2021-1151, MAAE-ARSFC-2022-2195, MAATE-ARSFC-2023-3378, MAAE-ARSFC-2023-0163, and MAATE-ARSF Nª01430. Universidad San Francisco de Quito USFQ supported the work of PP-R at the ZSFQ laboratory through research and outreach funds assigned to the Instituto de Biodiversidad Tropical IBIOTROP and Colegio de Ciencias Biológicas y Ambientales COCIBA. The description of *A. alo* sp.n. was an unexpected discovery during an expedition by PP-R in 2022 funded by the Vincent Roth Fund for Systematics Research of The American Arachnological Society; we express our gratitude to all the people who have supported the formation and administration of this grant. PP-R's visits to ICN and FCE-MY collections have been supported by Carmen Beatriz Romero Palacios and Emilia Peñaherrera-Romero. PP-R also thanks Carlos Perafán (Universidad de Caldas, Colombia) and Fernando Pérez-Miles (Universidad de la República, Uruguay) for information regarding some species of *Stormtropis* and for sharing additional information on upcoming work describing a new genus, respectively. PP-R and RJL-E would like to thank Jose Manuel Falcón-Reibán for his friendship and allowing us to revise and use his specimens.

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Responsible editor K.G. Mikhailov

Appendix A

Homoplastic characters discarded from the phylogeny (for abbreviations, see material and methods)

(1) ITC on males: absent = 0; leg I = 1; legs I–IV = 2; legs I–II = 3;. (until now, state 3 is unknown but here is suggested for future research).

(2) ITC on females: absent = 0; leg I = 1; legs I–II = 2; I–IV = 3.

(3) Multi-layered setae type of abdominal setiferous tubercles: absent = 0; SPS = 1; STS = 2; SPS and STS = 3.

(4) Coarse spines in tarsi of female: absent = 0; tarsus I = 1; tarsus I–II = 2; tarsus II–III = 3; tarsus I–IV = 4; tarsus I–III = 5. (until now, state 5 is unknown but here is suggested for future research)

(5) Coarse spines in metatarsi of female: absent = 0; metatarsus I = 1; metatarsus I–II = 2; metatarsus II–III = 3; metatarsus I–IV = 4; metatarsus I–III = 5; metatarsus II = 6 (until now, state 6 is unknown but here is suggested for future research).

(6) Maxillary spinules: absent = 0; present = 1.

(7) Abdominal setiferous tubercle size: weakly developed = 0; developed = 1; de-veloped and a pair of posterior well-developed tubercles = 2.

(8) Male Leg formula: IV, I, II, III = 0; I, IV, II, III = 1.

(9) Female Leg formula: IV, I, II, III = 0; I, IV, II, III = 1.

Appendix B

Additional type and non-type material examined for further information, comparative diagnoses and/or phylogenetic analyses

Lectotype imm. (BMNH 1894.10.17.1–3) and paralectotype imm. (BMNH 1894.10.17.1–3), *Anisaspis tuberculata*, Saint Vincent, Lesser Antilles. Holotype ♀ (BMNH 1896.12.13.71), *Anisaspoides gigantea*, Breves, Brazil. Holotype ♂ (QCAZ I3230) and paratype ♀ (QCAZ I3231) *Paratropis elicioi*, Otonga Biological Reserve, Ecuador; non-type 15 ♂ and 2 ♀ (all QCAZ I260724), *Paratropis elicioi*, Pristirana Natural Reserve, Ecuador. Holotype ♀ (QCAZ I260733) *Paratropis otonga*, Otonga Biological Reserve, Ecuador. Holotype ♂ (QCAZ I260716), allotype ♀ (QCAZ I20720), and 4 paratypes ♂ (all QCAZ I260721) *Paratropis pristirana*, Pristirana Natural Reserve, Ecuador. Holotype ♂ (IBSP 276617) and paratype ♂ (IBSP 290140), *Paratropis tortue*, Montagnes Tortue Biological Reserve, French Guiana.