



Looks can be deceiving: convergent hair tufts mask a new lineage of Cretaceous mites

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Abstract

The similar morphological traits produced by convergent evolution represent a primary source of taxonomic confusion. The porcupine-like mites from mid-Cretaceous Burmese amber, which can be readily recognized by four tufts of extremely long setae on their backs, have recently been reported by several researchers as members of the family Chyzeriidae Womersley, 1954. However, detailed morphological examination of newly discovered specimens reveals that these similarities are superficial. Some important higher-level taxonomic characters (*e.g.*, retractable gnathosoma, needle-like chelicerae, and two pairs of genital acetabula) of these extinct mites are not clearly presented in reported specimens, obscuring their true phylogenetic position. Here we demonstrate that the hair tufts in these Cretaceous mites represent a case of convergent evolution and that the fossils belong to a previously unrecognized lineage. We revisit 62 new fossils of this group using various imaging technologies, including stereomicroscopy, fluorescence microscopy, and laser confocal scanning microscopy, and we also examined three slide-mounted specimens from three extant families: Chyzeriidae Womersley, 1954, Smarididae Kramer, 1878, and Calyptostomatidae Oudemans, 1923, were also examined for morphological comparison. Newly discovered morphological evidence supports the establishment of a new family Acaro-hystricidae **fam. nov.** to accommodate these extinct Cretaceous mites, which is placed in its own superfamily—Acaro-hystricoidea **superfam. nov.**—distantly related to the extant Chyzeriidae. A new genus and species, *Acaro-hystrix magnifica* **gen. et sp. nov.**, is erected and the genera *Punkochyzeria* Kolesnikov, Turbanov & Vorontsov, 2025 and *Cretachyzeria* Liu, Fan & Ren, 2025 are transferred to this new family. Additionally,

a new species, *Punkochyzeria obtusa* **sp. nov.**, is described and *P. khoyi* Kolesnikov, Turbanov & Vorontsov, 2025 is proposed as a junior synonym of *P. makolae* Kolesnikov, Turbanov & Vorontsov, 2025. A revised diagnosis of *Punkochyzeria* is provided. Furthermore, phylogenetic analyses based on a limited set of morphological characters provide preliminary evidence for a sister-group relationship between Acaro-hystricidae **fam. nov.** and the extant family Calyptostomatidae Oudemans, 1923 within Erythraeina, justifying the establishment of Acaro-hystricoidea **superfam. nov.** We also include the ontogenetic and sexually dimorphic character states within the new family.

Keywords: Cretaceous mites, convergent evolution, Acaro-hystricidae, burmese amber, Parasitengona

Introduction

Convergent evolution can produce strikingly similar morphological traits in distantly related lineages, often obscuring true phylogenetic relationships and complicating taxonomic interpretations (Stayton, 2015; Bittleston *et al.*, 2016). Such deceptive similarities are particularly common in arthropods, where structures related to defence, locomotion or sensory functions may evolve repeatedly under similar ecological pressures (Blanke *et al.*, 2013; Liu *et al.*, 2017). Mites are among the most species-rich and ecologically diverse arthropods, exhibiting remarkable evolutionary plasticity, with nearly 60,000 described species occupying an extraordinary range of terrestrial, marine and freshwater habitats (Walter

& Proctor, 2013; Zhang *et al.*, 2021). Owing to their small body size and high ecological adaptability, similar morphological characters frequently evolve independently across different mite lineages, resulting in a high degree of homoplasy (Perkins *et al.*, 2009; Schäffer *et al.*, 2010; Li *et al.*, 2014). Such homoplastic evolution represents a major source of taxonomic confusion, making it essential to recognize convergent traits in mite systematics.

Recently, several research teams have reported a group of mites from mid-Cretaceous amber, in which clusters of elongated dorsal hairs represent one of the most conspicuous morphological traits and have been treated as important taxonomic characters (Zmudzinski, 2022; Kolesnikov *et al.*, 2025; Liu *et al.*, 2025). On this basis, these fossil mites bearing prominent hair tufts have been associated with extant tuft-bearing lineages of the family Chyzeriidae Womersley, 1954. A review of Burmese amber arachnids also reported a similar fossil mite, but it was classified only as an undescribed member of Acariformes owing to the lack of sufficient morphological information (Selden & Ren, 2017). In addition, a fossil mite with relatively short defensive setae was tentatively identified as *Parachyzeria* sp. in a conference abstract based solely on the presence of two pairs of distinct dorsal tufts of long setae (Zmudzinski, 2022). Liu *et al.* (2025) established a new genus and species, *Cretachyzeria macroseta* Liu, Fan & Ren, based on a single fossil specimen. Meanwhile, Kolesnikov *et al.* (2025), based on detailed morphological observations using laser confocal microscopy, erected the genus *Punkochyzeria* Kolesnikov, Turbanov & Vorontsov, including three species: *Punkochyzeria minaevi*, *P. makolae*, and *P. khoyi*. They further suggested that *Cretachyzeria* might represent a senior synonym of *Punkochyzeria*. Both studies assigned these newly discovered genera to the extant family Chyzeriidae. This classification was primarily based on the presence of conspicuous dorsal hair tufts resembling those observed in the chyzeriid genera *Chyzeria* and *Parachyzeria*. However, both studies overlooked the importance of gnathosomal characters in identifying higher-level taxonomic units and provided no detailed description of the cheliceral morphology.

In this study, through detailed morphological observations and imaging of 62 specimens, we demonstrate that several key morphological features differ markedly from those of Chyzeriidae and even from members of the superfamily Trombidioidea *sensu lato*. The similar dorsal hair tufts shared by these taxa are most likely the result of independent evolution under similar ecological pressures and therefore represent a case of convergent evolution. Based on diagnostic morphological characters, especially those of gnathosoma, and phylogenetic analyses, we establish a new superfamily within Parasitengona, Acaro-hystricoidea **superfam. nov.**, a new family—Acaro-hystricidae **fam. nov.**, a new genus—*Acarohystrix*

gen. nov., and two new species—*Acarohystrix magnifica* **gen. et sp. nov.** and *Punkochyzeria obtusa* **sp. nov.** We transfer the genus *Punkochyzeria* to this new family and provide an updated diagnosis of this genus.

Materials and methods

Material examined

A total of 62 amber specimens containing 67 fossil mites examined here originate from the deposits of Noije Bum near the Hukawng Valley in Kachin State of northern Myanmar. The age of the Burmese amber mine is mid-Cretaceous (upper Albian to lower Cenomanian). Amber pieces were prepared for imaging by trimming with a small electric circular saw, grinding with sandpaper of various grit sizes, and polishing with burnishing powder. All materials are deposited in the Nanjing Institute of Geology and Palaeontology (NIGP) at the Chinese Academy of Sciences, Nanjing, with accession numbers NIGP206770–206799, NIGP206802–206812, and NIGP206814–206835.

Three slide-mounted specimens from three extant families were examined: Chyzeriidae Womersley, 1954, Smarididae Kramer, 1878, and Calyptostomatidae Oudemans, 1923. These extant specimens are deposited in the New Zealand Arthropod Collection (NZAC), Bioeconomy Science Institute, Manaaki Whenua—Landcare Research Group, Auckland, New Zealand. Chyzeriidae: NEW ZEALAND, DN (Dunedin), Rocky Creek, under rock, bark, 14 Oct 1911, No. 10; slide-mounted specimen. Calyptostomatidae: NEW ZEALAND, TO (Taupō), Waiuhi Saddle, litter, moss and rotten wood, 6 Nov 1983, C.F. coll., litter sample 83/112; mounted in Hoyer's medium. Smarididae: USA, Florida, Manatee County, 5 Oct 1972, under bark of the lower stem of *Araucaria cunninghamii*.

Microscopy and imaging

Images of amber specimens under incident and transmitted light were captured using a Zeiss Axio Zoom V16 stereomicroscope, and widefield fluorescence images were taken with a Zeiss Axio Imager 2 light microscope. Confocal images were obtained with a Zeiss LSM 710 confocal laser scanning microscope under the 488 nm argon laser excitation line. Photos of slide-mounted specimens were taken with an interference-phase contrast microscope (Nikon Eclipse 90i). Images were stacked in Helicon Focus 7.0 and figure plates were arranged in Adobe Photoshop 2020.

Phylogenetic analysis

The Cretaceous mite *Acarohystrix magnifica* **gen. et sp. nov.** and 18 representative members of Parasitengona were

scored in a morphological character matrix to clarify the phylogenetic position of Acarohystricidae **fam. nov.** The matrix comprises 17 discrete morphological characters from 13 families, 19 genera, and 19 species (Table 1). The species *Anystis baccharum* was used as an outgroup and phylogenetic analyses were conducted using Maximum Parsimony in TNT 1.5. The strict consensus tree was inferred using unweighted parsimony, whereas extended implied weighting ($k = 12$) was used for exploratory analyses. Heuristic searches were conducted using 1000 random addition sequences followed by SPR branch swapping, with subsequent optimization using TBR. A single most parsimonious tree was recovered. Node support was evaluated using relative Bremer support, jackknife ($P = 36$), bootstrap (1000 replicates), and symmetric resampling ($P = 33$) (Fig. 26). Tree statistics (TL, CI, RI) were calculated in TNT.

Morphological character matrix

TABLE 1. Distribution of morphological characters used for phylogenetic analysis of Acarohystricidae **fam. nov.** Character states scored 0–3, inapplicable (-).

Family	Species	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Anystidae	<i>Anystis baccharum</i> (Meyer & Ueckermann, 1987)	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Smarididae	<i>Fessonia papillosa</i> (Wohltmann, 2010; Costa <i>et al.</i> , 2021)	0	0	1	0	1	1	0	0	0	1	1	1	1	2	0	1	2
	<i>Hirstiosoma ampulligera</i> (Wohltmann, 2010; Costa <i>et al.</i> , 2021)	0	0	1	0	1	1	0	1	0	1	1	1	1	2	0	1	2
Erythraeidae	<i>Phanolphus oedipodarum</i> (von Frauentfeld, 1868)	0	0	0	0	1	1	0	0	0	1	1	0	0	2	0	1	2
	<i>Charletonia rocciai</i> (Treat & Flechtmann, 1979; Costa <i>et al.</i> , 2021)	0	0	0	0	1	1	0	1	0	1	1	0	0	2	0	2	2
	<i>Lasioerythraeus johnstoni</i> (Welbourn & Young, 1987)	0	0	0	0	1	1	0	0	0	1	1	0	0	2	0	2	2
Calyptostomatida	<i>Calyptostoma seemani</i> (Masoumi <i>et al.</i> , 2020)	1	0	1	1	1	0	-	0	0	1	1	1	1	1	0	1	0
Allotanaupodidae	<i>Allotanaupodus winksi</i> (Zhang & Fan, 2007)	1	1	0	0	0	0	-	1	0	0	1	0	1	1	0	1	0
	<i>Nanotanaupodus andrei</i> (Zhang & Fan, 2007)	1	1	0	0	0	0	-	0	0	0	1	0	1	1	0	1	0
Acarohystricidae fam. nov.	<i>Acarohystricix magnifica</i> gen. & sp. nov.	0	0	1	1	1	1	1	0	0	2	0	0	1	1	0	1	1
Chyzeriidae	<i>Parachyzeria indica</i> (Hirst, 1926)	0	0	0	0	0	1	1	0	1	0	1	0	1	0	0	2	0
	<i>Chyzeria novaezealandiae</i> (Hirst, 1924)	0	0	0	0	0	1	1	0	0	0	1	0	1	0	0	2	0
Stygothrombiidae	<i>Stygothrombum garzensis</i> (Li <i>et al.</i> , 2021)	0	1	0	0	1	1	1	2	0	0	1	1	0	0	1	-	0
Hydryphantidae	<i>Austratrombella leprosa</i> (Southcott, 1991; Harvey, 1996)	0	0	0	0	0	0	-	0	0	0	0	1	1	3	0	1	0
Johnstonianidae	<i>Newellia xakriaba</i> (Costa <i>et al.</i> , 2023)	0	0	0	0	0	1	1	0	1	0	0	1	1	0	0	2	2
	<i>Centrotrombidium krenak</i> (Costa <i>et al.</i> , 2023)	1	0	0	0	0	1	-	0	1	0	1	1	1	0	0	2	2
Tanaupodidae	<i>Lassenia lassenii</i> (Newell, 1957)	1	0	0	0	0	1	-	0	0	0	0	0	1	0	0	2	2
Trombellidae	<i>Trombella adelaideae</i> (Womersley, 1954)	1	0	0	0	0	1	-	0	0	0	0	0	1	2	0	2	0
Trombidiidae	<i>Trombidium southcotti</i> (Zhang & Saboori, 1996)	1	0	0	0	0	1	0	0	2	0	0	0	1	0	0	2	2

Character list

0. Anterior prodorsal trichobothria in adult or larva (0 = present, 1 = absent)
1. Posterior prodorsal trichobothria in adult or larva (0 = present, 1 = absent)
2. Eversible armilla connecting gnathosoma and anterior idiosoma (0 = absent; 1 = present)
3. Palp, shape (0 = strong, curved; 1 = slender, straight)
4. Chelicera (0 = non-retractable; 1 = retractable)
5. Crista metopica (0 = absent; 1 = present)
6. Distance between anterior prodorsal trichobothria and posterior prodorsal trichobothria in adults (0 = distant; 1 = close)
7. Number of lateral eyes in adults (0 = two pairs; 1 = one pair; 2 = absent)
8. Eye peduncle (0 = absent; 1 = short peduncle; 2 = long peduncle)
9. Cheliceral digit shape in adults (0 = sickle-like; 1 = short needle-like; 2 = long needle-like)
10. Number of setae on subcapitulum (0 = more than six pairs; 1 = six pairs or fewer)
11. Sejugal furrow (0 = present; 1 = absent)
12. Leg, empodium (0 = present; 1 = absent)
13. Genital acetabula in adults (0 = three pairs; 1 = two pairs; 2 = absent; 3 = more than three pairs)

14. Palp tibia and tarsus (0 = not fused; 1 = fused)
15. Palp thumb-claw complex (0 = absent or nearly absent; 1 = small or tarsus inserted subdistally on tibia; 2 = tarsus inserted on middle to basal tibia)
16. Indication of hysterosomal segments by rows of gland/seta-bearing structures (0 = C–H rows; 1 = C row only; 2 = no rows)

Measurements and terminology

Measurements were recorded using ImageJ and given in micrometres (Tables 2–8). General morphological terminology follows Southcott (1961), Zhang & Fan (2007) and Kolesnikov *et al.* (2025). Abbreviations: ac, anterior margin of crista metopica; al, anterior lens; ap, anal pore; as, anterior sensilla; cd, cheliceral digits; ct, ctenidium; ea, eversible armilla; ga, genital acetabula; gp, genital pore; hs, hypostome; ns, naso; pl, posterior lens; ps, posterior sensilla; sc, sclerite; sf, sejugal furrow; ss, spine-like setae; tc, tibia claw; tr, trichobothrium.

Systematic palaeontology

Phylum Arthropoda von Siebold, 1848

Class Arachnida Lamarck, 1801

Subclass Acari Leach, 1817

Order Trombidiformes Reuter, 1909

Infraorder Anystina van der Hammen, 1972

Parvorder Parasitengonina Oudemans, 1909

Key to the higher taxonomic categories of terrestrial Parasitengonina: Erythraeina (adults and nymphs), referred to Zhang & Fan, 2007

1. Chelicerae or gnathosoma retractable into idiosoma; movable digits of chelicerae long and straightErythraeina.....2
Chelicerae not retractable into idiosoma; movable digits of chelicerae relatively short and often curvedTrombidiina.....4
2. Prodorsum with 1 pair of trichobothria, but without *crista metopica*; entire gnathosoma retractable into idiosoma; adults with 2 pairs of genital acetabula.....
.....Calypstomatoidae (single family Calypstomatidae)
Prodorsum with 2 pairs of trichobothria and a *crista metopica*; chelicerae or gnathosoma retractable into idiosoma; genital acetabula generally absent
.....Erythraeidae.....3
Prodorsum with 2 pairs of trichobothria and an enlarged but weakly sclerotized *crista metopica*; entire gnathosoma retractable into idiosoma; adults with 2 pairs of genital acetabula; exceptionally elongated hypostome with more than ten pairs of setae
..... **Acarohystricoidea**
superfam. nov. (single family **Acarohystricidae** **fam. nov.**)
3. Entire gnathosoma retractable into idiosoma; dorsal setae often broad, flattened, leaf-like and/or serrate Smarididae
Only chelicerae retractable into idiosoma; dorsal setae various in shape, but often simple setiform Erythraeidae
4. Prodorsum without trichobothria; palptarsus inserted ventrally and distally near the base of tibial claw, with a distance from the base of tibia; adults with two pairs of genital acetabulaAllotanaupodoidea (single family Allotanaupodidae)
Prodorsum with one or two pairs of trichobothria; palptarsus inserted more proximally, away from base of tibial claw; adults with three pairs of genital acetabula (if two pairs, then with 1 pair of trichobothria)5

5. Pregenital tubercles present
.....Tanaupodoidea (single family Tanaupodidae)
Pregenital tubercles absent.....6
6. Hysterodorsum with elongate processes densely covered with setae.....
.....Chyzeriidae
Hysterodorsum without elongate finger-like processes densely covered with setae.....
.....Trombidoidea (except Chyzeriidae)

Remarks. The classification of superfamilies follows Costa *et al.* (2024); however, two superfamilies, Amphotrombidoidea Zhang, 1998 and Yurebilloidea Southcott, 1996, are not included (adults and nymphs unknown). A key to the families of Trombidoidea is beyond the scope of this study.

Superfamily Acarohystricoidea superfam. nov.

urn:lsid:zoobank.org:act:18BCADE0-92D3-4D34-8732-ED8C110FCA77

Family Acarohystricidae fam. nov.

urn:lsid:zoobank.org:act:3574E1BB-FF33-48CF-8CCE-B0AFEF5B8F61

Type genus. *Acarohystrix* **gen. nov.** (by present designation)

Included genera. *Acarohystrix* **gen. nov.**

Cretachyzeria Liu, Fan & Ren, 2025; *Punkochyzeria* Kolesnikov, Turbanov & Vorontsov, 2025.

Etymology. Derived from type genus.

Diagnosis. Adults and nymphs. Prodorsum with an enlarged but weakly sclerotized *crista metopica* (Figs 3B, 5, 6). Anterior sensillary area (*ASA*) and posterior sensillary area (*PSA*) on the *crista metopica* adjacent to each other without a distinct boundary; sensillary area bearing two pairs of smooth trichobothria (‘*vi*’ and ‘*si*’ or ‘*PSens*’ and ‘*ASens*’) (Figs 3B, 5, 6, 8C, 12D, 14E, 16D, 17E, 19D, 21E); anterior and posterior regions of sensillary areas with hairless, narrow channels (Figs 5, 6). Naso present (Fig. 5). Eversible armilla connecting gnathosoma and anterior idiosoma present, entire gnathosoma retractable into idiosoma via armilla (Figs 5, 11E, F, 12B, 13E, 16C, F, 19I, 20C, I, 23G). Two pairs of subequal lateral eyes present (Figs 3B, 5C, 6B, 8B, 10D, 12D, 14E, 16D). Posterior part of aspidosoma markedly widened, forming a pair of arched “shoulders” (Figs 2, 4, 7C). Sejugal furrow evident (Fig. 9C).

Opisthosoma with two pairs of dorsal tufts of extremely long setae extending posteriorly beyond terminal opisthosoma, each tuft with about 130–170 setae and inserted into a separate sclerite (Figs 3D, 10E, 12E, 16E, 17C, 18C, 20I, 21D); long tufts including two types of setae: 1) densely ciliated or plumose and 2) rigid, spine-like, without cilia (Figs 3G, 10E, 13D, 15F, 16I, 17C, 18C, 21G). Genital pore with one pair of well-developed genital

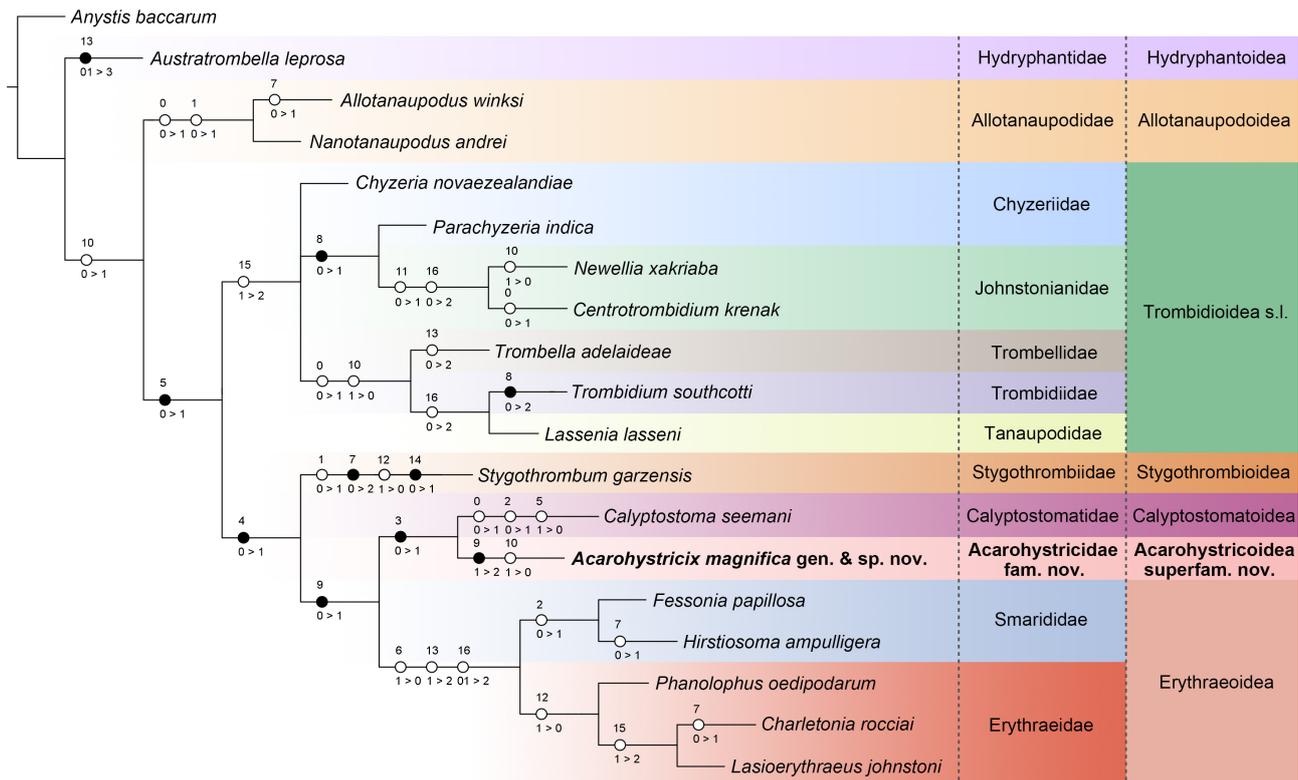


FIGURE 1. Phylogeny of Acaro-hystricidae fam. nov., inferred with unweighted parsimony. Character optimization displays only unambiguous changes. The number above each branch gives the character number, whereas the number below gives the character state changes. The black spots denote homologous characters, while the white spots denote homoplastic characters.

valves (Figs 3E, 8F, 9E, 10F, 11D, 12F, 13E, 15E, 16G, H, 17D, 18G, H, 19F, 20D, J, K), adults with 2 pairs of genital acetabula (Figs 12G, 13C, 20K). Anus with a pair of valves each without setae (Figs 3E, 8F, 9E, 10F, 11D, 12F, 13E, 15E). Posterior margin of opisthosoma bearing relatively long setae posteriorly and laterally (Figs 2, 10F, 12F, 14F, 16I, 20E, 21G). Surface of idiosoma densely covered with short plumose setae.

Subcapitulum with extremely elongated hypostome; hypostome with more than ten pairs of setae (Figs 3H, I, 5A, D, 11G, 12H, 13E, 16C, F, 20C, 23G). Movable digit of chelicerae very long, needle-like (Figs 3I, 5A, B, D, 16C). Palp slender and straight; thumb-claw complex small: palptibia bearing a single sickle-shaped, claw-like seta (odontus); palptarsus long, finger-like, inserted subdistally on tibia (Figs 3J, 5, 8I, 12C, H, 16C, F, 20C, 23G). Each leg terminating in a pair of well-developed claws, without an empodium (Figs 3C, F, 8G, H, 10G). Leg length comparison: Leg I > Leg IV > Leg II and Leg III.

Larvae unknown.

Remarks. The diagnosis of the family is partly based on, and modified from, the generic diagnosis of *Acarohystrix* gen. nov. and *Punkochyzeria* presented by Kolesnikov *et al.* (2025). Several characters described previously are here recognized as important diagnostic

features of the family, such as the position of the sensillary area, the morphology of the hypostome, and the presence of four tufts of extremely long setae. Several additional important characters are provided here, including the morphology of the chelicera, the presence of an eversible armilla (retractable gnathosoma), the number of genital acetabula, and the insertion position of the palptarsus. These characters are crucial for determining the higher-level taxonomic placement of this group.

Included species: *Acarohystrix magnifica* gen. et sp. nov.; *Cretachyzeria macroseta* Liu, Fan & Ren, 2025; *Punkochyzeria minaevi* Kolesnikov, Turbanov & Vorontsov, 2025; *Punkochyzeria makolae* Kolesnikov, Turbanov & Vorontsov, 2025 = *Punkochyzeria khoyi* Kolesnikov, Turbanov & Vorontsov, 2025 **syn. nov.**; *Punkochyzeria obtuse* sp. nov.

Genus *Acarohystrix* gen. nov.

urn:lsid:zoobank.org:act:7F57F666-5D75-4BDE-A3C7-69EC272088CF

Type species. *Acarohystrix magnifica* sp. nov. (by present designation).

Etymology. The generic name combines the Greek prefix “acari-” (meaning mites) and the suffix “-hystrix” (meaning “porcupine” or a spiny animal), referring to the

extinct mites bearing tufts of long setae that resemble the spines of a porcupine. The generic name is feminine in gender.

Diagnosis. Propodosoma distinctly elongated (short in *Punkochyzeria*). Bothridia of two posterior sensilla connected (separated in *Punkochyzeria*). *Crista metopica* oval, with well-defined margins (indistinct or partially defined in *Punkochyzeria*). Anterior and posterior eyes separated, both situated on a single oval sclerite (adjacent and not on a sclerite in *Punkochyzeria*). Two pairs of eyes, positioned laterally to *crista metopica*, posterior to posterior sensilla (eyes parallel to and level with sensilla in *Punkochyzeria*). Tarsus I distinctly shorter than tibia I (longer than or equal to tibia I in *Punkochyzeria*).

***Acarohystrix magnifica* sp. nov.**

urn:lsid:zoobank.org:act:CEBD316E-177E-426C-8AEF-0C4EF373A7E1

(Figs 2, 3)

Type material. Holotype: NIGP206788, subadult [male]. Myanmar, Kachin State, Hukawng Valley, precise locality unknown, mid-Cretaceous (Cenomanian) burmite, deposited in NIGP, Nanjing, China.

Etymology. The species name comes from the Latin “magnificus”, meaning magnificent.

Diagnosis. Bothridia of anterior sensilla (*ASens*) and posterior sensilla (*PSens*) equal in size. Lateral margins of naso distinct. Eversible armilla distinct. Dorsal tufts of long setae slightly exceeding posterior margin of opisthosoma; plumose long setae with very dense cilia, cilia length at least twice the diameter of setal shaft.

Remarks. The holotype is well preserved, with both dorsal and ventral external features clearly visible. The cuticle is translucent, and slender linear structures extending along the leg segments can be observed within the legs, interpreted as possible remnants of internal muscle fibres (Fig. 2). Owing to the translucent cuticle, the needle-like chelicerae are visible through the ventral side of the subcapitulum under CLSM (Fig. 3I). *Acarohystrix magnifica* sp. nov. exhibits dorsal tufts of similar length and plumose long setae of similar morphology to those of *Punkochyzeria minaevi* Kolesnikov, Turbanov & Vorontsov, 2025 (Figs 3D, G, 15E, F).

Description. Idiosoma length 1510, width 820. Posterior margin of idiosoma strongly curved, forming a distinct arcuate outline (Figs 2, 3E); hysterosoma suboval; aspidosoma triangular, projecting anteriorly, gradually narrowing anteriorly (Fig. 3A); posterior part of aspidosoma distinctly widened laterally, forming a pair of arched projections, like shoulders, between propodosoma and metapodosoma (Fig. 3D). Anterior margin of proterosoma with an eversible armilla connecting

gnathosoma and idiosoma; entire gnathosoma retractable into idiosoma via armilla (Fig. 3H).

Gnathosoma elongate, projecting anteriorly (Fig. 3H). Palp slender and straight, covered with sparse setae; femur, genu, tibia and tarsus exposed (Fig. 3H). Femur longest, tibia shortest; femur about twice as long as genu; tibia less than half length of genu; tarsus slightly longer than tibia (Fig. 3J); palptarsus finger-like, distally expanded; tibial claw sickle-shaped, slightly shorter than palptarsus (Fig. 3J); dorsal ctenidium absent or with one spinose seta (Fig. 3J). Hypostome elongate and narrow, tapering anteriorly, extending to base of palpgenu (Fig. 3H); ventral surface with about 10 pairs of long setae (length not exceeding width of hypostome) (Fig. 3H). Chelicerae very long and needle-like, as long as entire hypostome (Fig. 3I).

Aspidosoma densely covered with short barbed setae (Fig. 3A, B). Anterior prodorsum with a narrow tongue-shaped naso, lateral margins distinct, apex with longer setae than those on lateral part (Fig. 3B). *Crista metopica* located above naso, oval, margins distinct (Fig. 3B). A smooth, glabrous longitudinal channel present anterior and posterior to the *crista metopica*. A sensillary area composed of two pairs of trichobothria located at *crista metopica*; bothridia of anterior sensilla (*ASens*) and posterior sensilla (*PSens*) nearly equal in size; anterior pair with separated bothridia, posterior pair with connected bothridia (Fig. 3B). Eversible armilla present anterior to naso, bearing extremely short fine setae (Fig. 3A, B). Two pairs of lateral eyes, equal in size, diameter 50–60; anterior and posterior lenses separated by less than one lens diameter, both located on an oval weakly sclerotized plate; eyes positioned laterally to sensillary area, posterior to bothridia of posterior sensilla (Fig. 3B). Sejugal furrow distinct, length exceeding half idiosoma width (Fig. 3D). Ventral propodosoma densely covered with short barbed setae; median longitudinal ventral furrow distinct (Fig. 3E). Propodosoma and hysterosoma separated by a V-shaped groove, concave toward propodosoma (Fig. 3E).

Anterior hysterosoma with two pairs of dorsal sclerites, median pair rectangular, lateral pair triangular (Fig. 3D). Each sclerite bearing a tuft of extremely long setae extending posteriorly beyond margin of idiosoma, forming four dorsal tufts covering the dorsum of hysterosoma. Two types of long dorsal setae present: (1) numerous, slender, flexible, with dense plumose branches, branch length at least twice diameter of shaft, length about 1000, branch density decreasing toward base; (2) shorter, thicker, rigid, spine-like, lacking branches (Fig. 3G). Posterior margin of hysterosoma bearing relatively long plumose setae directed posteriorly (Fig. 2).

Genital opening located posterior to coxae IV, length about 280 µm; one pair of genital valves present, bearing fine plumose setae shorter than ventral hysterosomal



FIGURE 2. General habitus of *Acarohystrix magnifica* gen. et sp. nov. (NIGP206788), under incident light. **A,** Dorsal view. **B,** Ventral view. Scale bars, 500 μ m.

setae and densely arranged (Fig. 3E). Male genital region surrounded by a sclerotized rhomboid boundary, covered by fine setae (Fig. 3E). Anal opening with one pair of valves, each without setae, length about 80 μ m, positioned above midpoint between posterior margin of genital opening and posterior margin of hysterosoma (Fig. 3E). Genital acetabula not visible.

Leg I longer than other legs; segments of leg I slightly broader than those of other legs (Fig. 3C). Tarsus I distinctly shorter than tibia I, tapering distally, apex pointed, covered with dense setae (Fig. 3C). Tarsi II and III longer than tibiae (Fig. 3F). Tarsus IV nearly equal in length to tibia IV. Each leg terminating in one pair of well-developed claws, without empodium claws of legs II–IV similar in size, claws of leg I about half size of those on other legs (Fig. 3C, F). Leg segments bearing fine short setae.

Genus *Punkochyzeria* Kolesnikov, Turbanov & Vorontsov, 2025

Type species. *Punkochyzeria minaevi* Kolesnikov, Turbanov & Vorontsov, 2025.

Included species. *Punkochyzeria minaevi* Kolesnikov, Turbanov & Vorontsov, 2025; *Punkochyzeria makolae* Kolesnikov, Turbanov & Vorontsov, 2025 = *Punkochyzeria khoi* Kolesnikov, Turbanov & Vorontsov, 2025 **syn. nov.**; *Punkochyzeria obtuse* **sp. nov.**

Diagnosis (emended from Kolesnikov *et al.*, 2025). *Crista metopica* with indistinct margins (Fig. 5 A–C) (present study). Bothridia of two posterior sensilla separated (present study). Anterior and posterior eyes adjacent (present study). Two pairs of eyes situated at the same level as sensillary area (Kolesnikov *et al.*, 2025) (Fig. 6). Dorsal surface of hysterosoma beneath four tufts

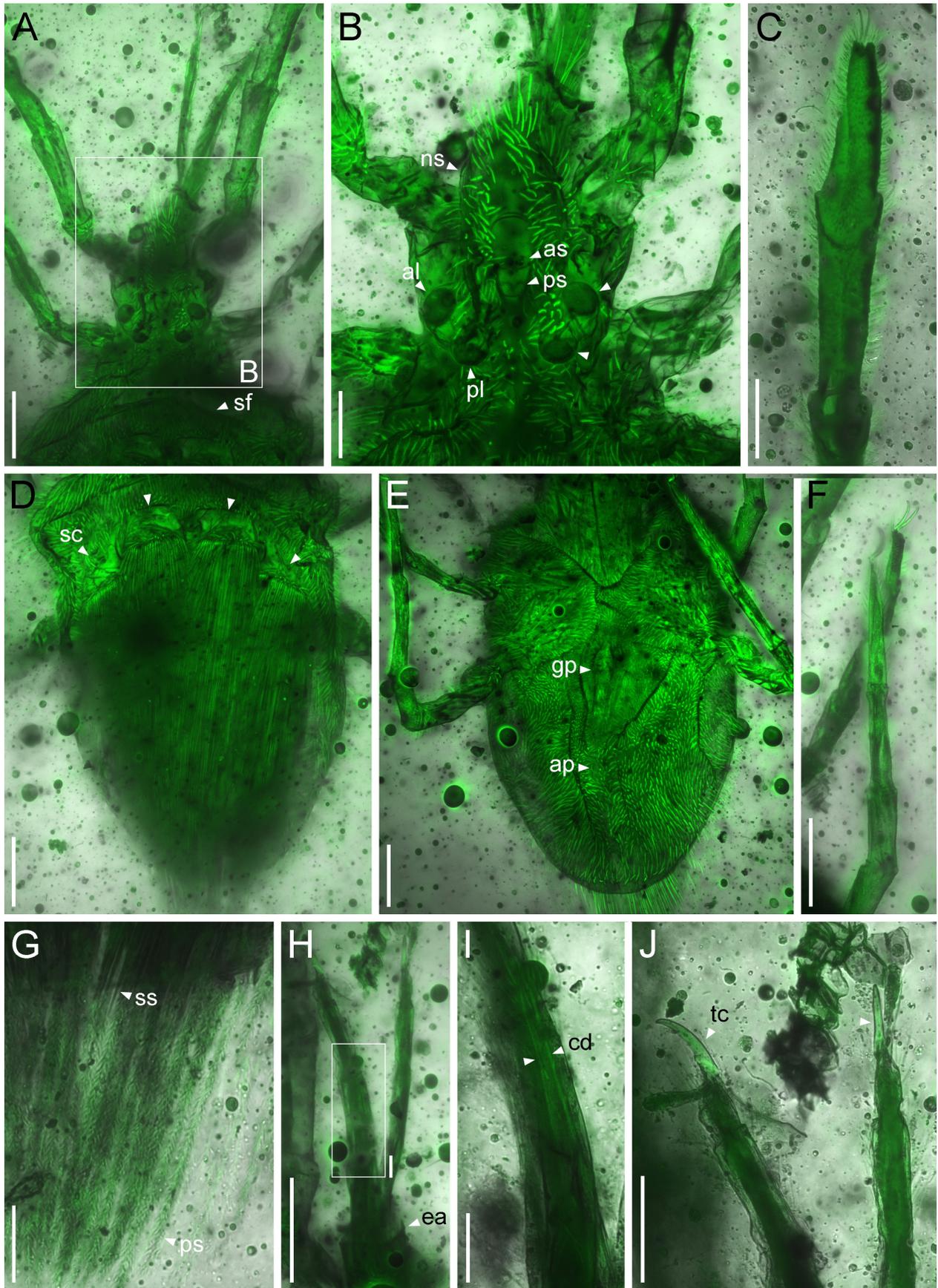


FIGURE 3. Details of *Acarohystrix magnifica* gen. et sp. nov. (NIGP206788), under CLSM. **A**, Proterosoma in dorsal view. **B**, Prodorsum. **C**, Tibia and tarsus of leg I. **D**, Hysterosoma in dorsal view. **E**, Hysterosoma in ventral view. **F**, Tibia and tarsus of legs II and III. **G**, Details of dorsal tufts of long setae. **H**, Gnathosoma. **I**, Hypostome. **J**, Palp. Abbreviations: ps in **B**, posterior sensilla; ps in **G**, plumose setae. Scale bars, 200 μm in **A**, **C**, **D–F**, **H**; 100 μm in **B**, **J**; 50 μm in **I**, **J**.

of long setae without setae, only median longitudinal row of setae present (Kolesnikov *et al.*, 2025). Dorsal cuticle of hysterosoma with reticulate sculpture (Kolesnikov *et al.*, 2025).

Remarks. Kolesnikov *et al.* (2025) suggested that the morphologically similar genus, *Cretachyzeria* Liu, Fan & Ren, 2025 may represent a senior synonym of *Punkochyzeria*. These two genera indeed share numerous characters, including the morphology of the palp (Kolesnikov *et al.*, 2025: fig. 10I; Liu *et al.*, 2025: 245, fig. 2E), the four dorsal tufts of long setae (Kolesnikov *et al.*, 2025: fig. 10A; Liu *et al.*, 2025: 245, fig. 1A), the adjacent anterior and posterior eyes (Kolesnikov *et al.*, 2025: fig. 10E; Liu *et al.*, 2025: 245, fig. 2A), and two pairs of eyes situated at the same level as the sensillary area (Kolesnikov *et al.*, 2025: fig. 10D; Liu *et al.*, 2025: 245, fig. 2A). However, we refrain from treating *Punkochyzeria* as a junior synonym of *Cretachyzeria* without reexamining the holotype of *Cretachyzeria*.

The genera *Punkochyzeria* and *Cretachyzeria* show strong morphological similarities with *Acarohystrix* **gen. nov.**, including the presence of an eversible armilla (Kolesnikov *et al.*, 2025: fig. 10I; Liu *et al.*, 2025: 245, fig. 2 D, E; overlooked in the original papers), an extremely elongated hypostome (Liu *et al.*, 2025: 245, fig. 2 D, E; overlooked in the original paper; Kolesnikov *et al.*, 2025: fig. 10I); two pairs of subequal lateral eyes (Kolesnikov *et al.*, 2025: fig. 10E; Liu *et al.*, 2025: 245, fig. 2 A), a evident sejugal furrow (Liu *et al.*, 2025: 245, fig. 2 D, E; overlooked in the original paper), the presence of arched shoulders (Kolesnikov *et al.*, 2025: fig. 10A; Liu *et al.*, 2025: 245, fig. 1), and four tufts of long dorsal setae (Kolesnikov *et al.*, 2025: fig. 10A; Liu *et al.*, 2025: 245, fig. 1). Despite the lack of information on the sensillary area, chelicera, and the detailed structure of tufts of long setae, these features are sufficient to transfer these taxa into *Acarohystricidae* **fam. nov.**

Based on the characters of the new genus *Acarohystrix* **gen. nov.** and the examined material of *Punkochyzeria*, several characters originally proposed by Kolesnikov *et al.* (2025) as generic diagnostic features are here elevated to family-level characters, including palps slender; palptibia bearing a single claw; *Crista metopica* with two sensillary areas located next to each other; idiosoma widened at the boundary between aspidosoma and opisthosoma; and four dorsal tufts of extremely long setae on the hysterosoma, each tuft inserted into a distinct projection. Conversely, several other characters previously used for generic diagnosis are here regarded as species-level characters, including anterior sensillary area (*ASA*) extended anteriorly, triangular shaped; bothridia of posterior sensilla (*PSens*) larger than those of anterior sensilla (*ASens*). The ontogenetic and sexual dimorphic characters of *Punkochyzeria* are clarified based on

abundant specimens (see Discussion). In addition, we note that the dorsal row of spinose setae (ctenidia) on palptibia may be related to ontogenetic development.

***Punkochyzeria minaei* Kolesnikov, Turbanov & Vorontsov, 2025**
(Figs 4A, B, 7, 8, 9, 10, 11, 15)

Type Material. Holotype, PIN-5608/343a, postlarva [unknown]; paratype IM-1177a, postlarva [unknown]. Myanmar, Kachin State, Hukawng Valley, precise locality unknown, mid-Cretaceous (Cenomanian) burmite, PIN-5608/343a deposited in Borissiak Paleontological Institute, Russian Academy of Sciences; IM-1177a deposited in private collection of Ilya G. Minaev (Ryazan, Russia).

Additional material: Deutonymph: NIGP206782 [sex unknown], 206783 [sex unknown], 206793 [sex unknown], 206798 [female], 206808 [male]. Subadult: 206771 [male], 206796 [female], 206797 [male], 206819 [female], 206823 [female], 206824 [male], 206827 [sex unknown], 206832 [female]. Adult: 206778 [female], 206802 [male], 206803 [sex unknown]. Myanmar, Kachin State, Hukawng Valley, precise locality unknown, mid-Cretaceous (Cenomanian) burmite, deposited in NIGP, China.

Diagnosis (emended from Kolesnikov *et al.*, 2025). Eversible armilla short (Figs 5B, 11E, 15E) (present study). Bothridia of anterior and posterior sensilla (*ASens*, *PSens*) equal in size (present study); distance between bothridia of left and right *ASens* greater than that between bothridia of *PSens* (Figs 5B, 6B, C, D, E) (present study). Anterior margin of *crista metopica* (or sensillary area) broadly arcuate (Figs 5B, 6B, C, D, E) (present study). Dorsal tufts of long setae slightly exceeding posterior margin of opisthosoma (Figs 4A, 9C, 10E, 11C) (present study); plumose long setae with very dense cilia, cilia length at least twice the diameter of setal shaft (Figs 9C, 10E, 15F) (Kolesnikov *et al.*, 2025). Palp tibial claw robust, basal width in lateral projection equal to or wider than width of palptarsus (Fig. 5D) (Kolesnikov *et al.*, 2025). Posterior margin of idiosoma slightly rounded, protruding, lateral margins strongly convergent (Figs 4B, 9B, E, 10C, F, 11D) (present study). Claw of leg I weakly developed, shorter than those of other legs (present study).

Remarks. Kolesnikov *et al.* (2025) treated the relative length of the palptarsus with respect to the tibial claw and the number of spinose setae in the dorsal ctenidium as diagnostic characters at the species level. However, our examination of abundant specimens indicates that the length of palptarsus is correlated with sexual dimorphism (see Discussion). Likewise, the number of spinose setae in the dorsal ctenidium also appears to vary with ontogenetic development (see Discussion). Therefore,



FIGURE 4. Comparison of general morphology between *Punkochyzeria minaevi* and *P. makolae* (NIGP206819 and NIGP206806). **A, C,** Dorsal view. **B, D,** Ventral view. Scale bars, 1 mm in **C, D**; 500 µm in **A, B**.

they should not be regarded as reliable species-level diagnostic features. The length of the dorsal setal tufts represents the most conspicuous character distinguishing *Punkochyzeria minaevi* from *P. makolae*, and this feature does not vary with ontogenetic development (Fig. 24B–D, see Discussion). This difference was not recognized by

Kolesnikov *et al.* (2025), possibly because in some of their specimens the tufts appear spread and therefore cannot be readily compared. Another stable character is the position and size of bothridia of *ASens* and *PSens* Kolesnikov *et al.* (2025) illustrated and described the sensillary area only for *Punkochyzeria khoiyi* **syn. nov.** (= *Punkochyzeria*

makolae). Our examination shows that the sensillary area of *Punkochyzeria minaevi* differs distinctly from that of *P. makolae*. The diagnostic features of the posterior margin of the idiosoma and the claw of leg I distinguish *P. makolae* from *P. obtuse* **sp. nov.**

Examination of two specimens, NIGP206797

and NIGP206802, with the gnathosoma fully exposed revealed two clusters of long barbed setae on the ventral surface of the gnathosomal base (Figs 5D, 11F, H). In most specimens these setae are concealed within the armilla and thus cannot be observed. These structures may function as filtering setae during feeding.

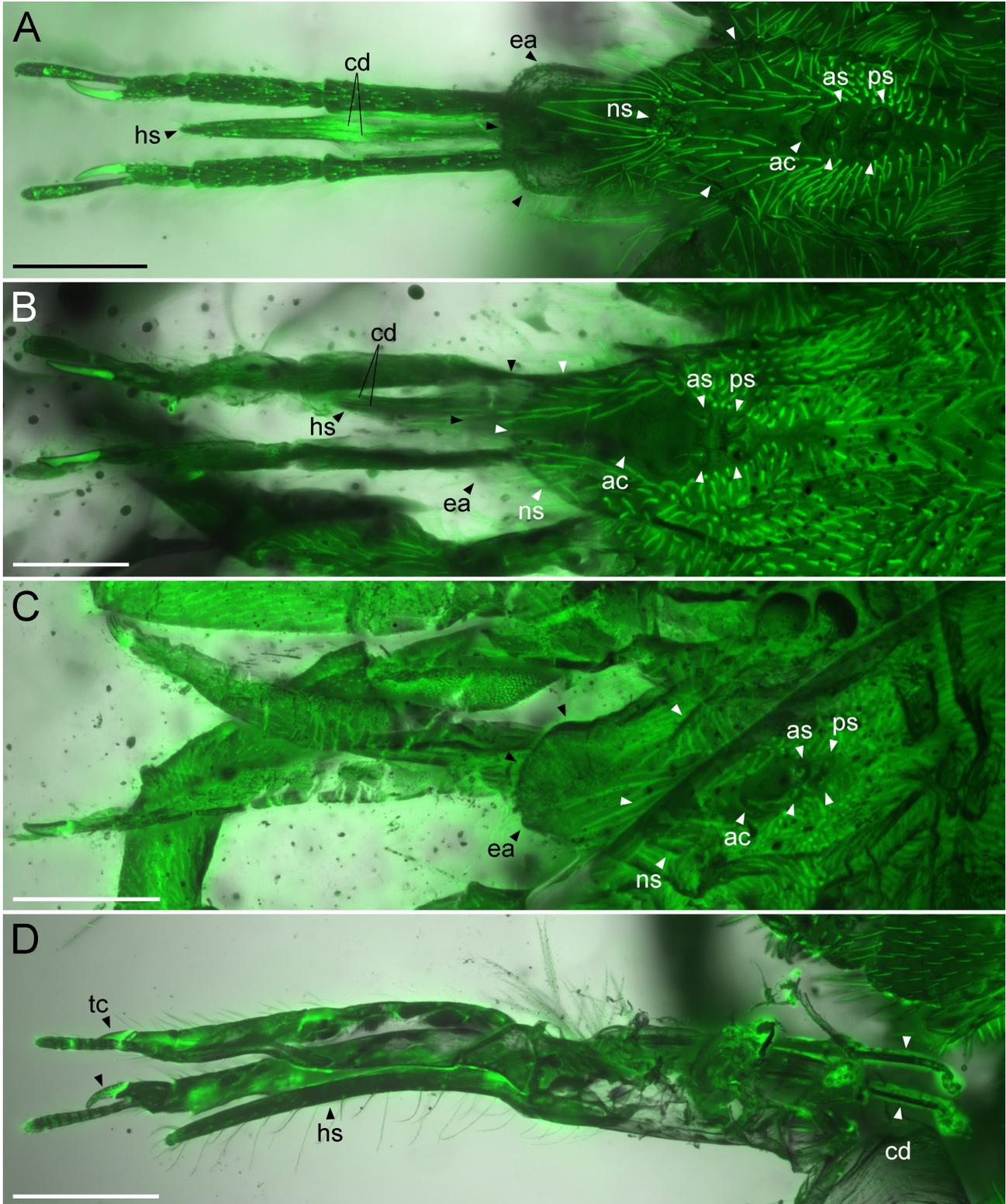


FIGURE 5. Comparative morphological details of gnathosoma and prodorsum of *Punkochyzeria minaevi*, *P. makolae*, and *P. obtuse*. **A.** *P. makolae*, NIGP206806. **B.** *P. minaevi*, NIGP206771. **C.** *P. obtuse*, NIGP206794. **D.** *P. minaevi*, NIGP206797. Scale bars, 200 μ m in **C**, **D**; 100 μ m in **A**, **B**.

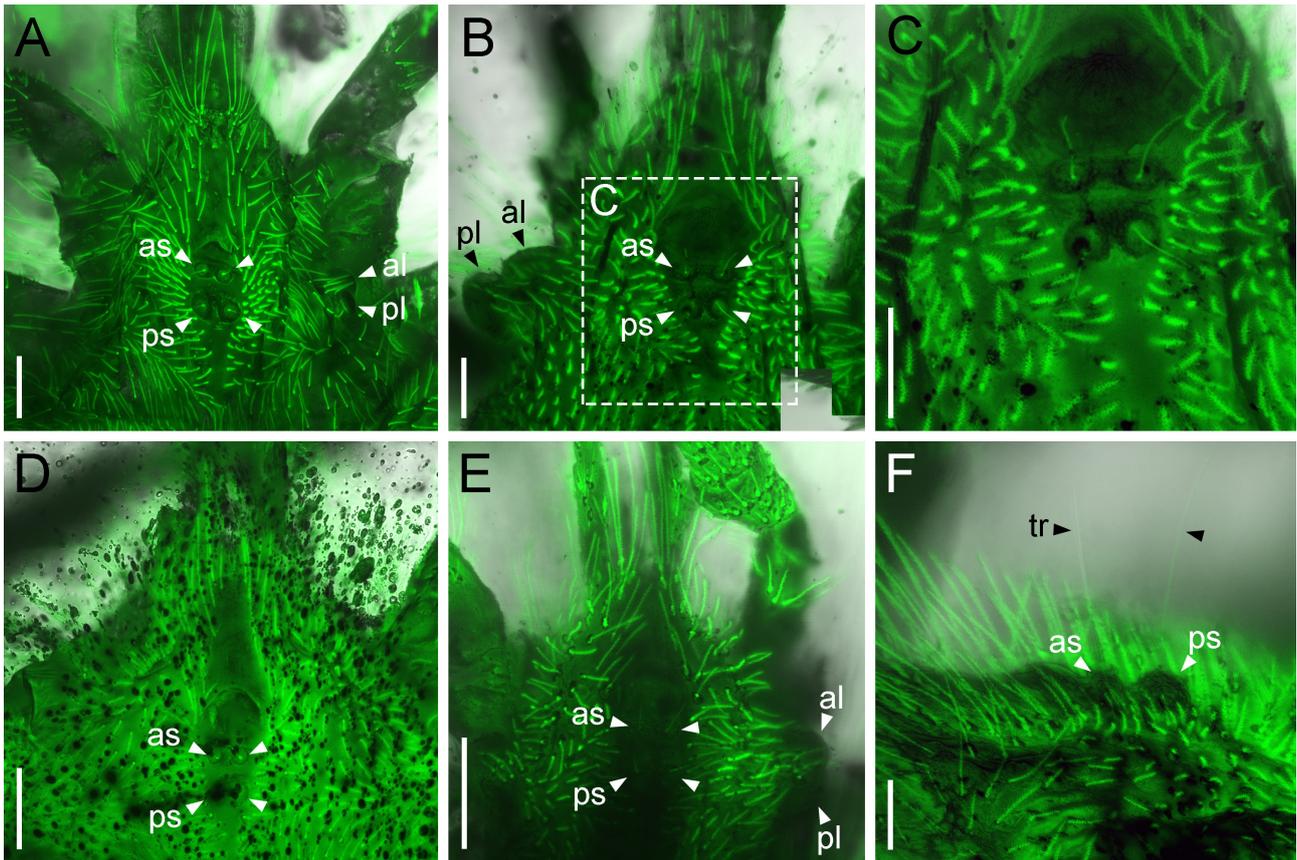


FIGURE 6. Comparative morphological details of sensillary area of *Punkochyzeria minaevi* and *P. makolae*. **A**, *P. makolae*, NIGP206806. **B, C**, *P. minaevi*, NIGP206771. **D**, *P. minaevi*, NIGP206819. **E**, *P. minaevi*, NIGP206798. **F**, *P. makolae*, NIGP206799-3. Scale bars, 100 μ m in **A, D; E**; 50 μ m in **B, C, F**.

***Punkochyzeria makolae* Kolesnikov, Turbanov & Vorontsov, 2025** (= *Punkochyzeria khoyi* Kolesnikov, Turbanov & Vorontsov, 2025 **syn. nov.**)
(Figs 4C, D, 12, 13, 14, 16, 17, 18, 19, 20, 21, 22)

Type Material. Holotype, PIN-5608/344a, postlarva [unknown]; paratype IM-1177a, postlarva [unknown]. Myanmar, Kachin State, Hukawng Valley, precise locality unknown, mid-Cretaceous (Cenomanian) burmite, deposited in the Borissiak Paleontological Institute, Russian Academy of Sciences.

Additional material: Deutonymphs: NIGP206774 [female], 206775 [female], 206777 [male], 206781 [male], 206790 [female], 206791 [female], 206805 [male], 206807 [male], 206809 [female], 206812 [female], 206828 [sex unknown], 206831 [male]. Subadults: NIGP206770 [male], 206771 [male], 206772 [female], 206773 [male], 206776 [male], 206779 [male], 206784 [male], 206787 [female], 206789 [female], 206792 [female], 206796 [female], 206797 [male], 206811 [male], 206814 [sex unknown], 206815 [female], 206816 [male], 206817 [male], 206818 [male], 206819 [female], 206820 [female], 206822 [male], 206823 [female], 206824 [male],

206825 [sex unknown], 206827 [sex unknown], 206832 [female], 206833 [female], 206834 [female]. Adults: NIGP206778 [female], 206780 [female], 206785 [male], 206786 [male], 206802 [male], 206803 [sex unknown], 206806 [male], 206810 [sex unknown], 206821 [female]. Multiple specimens: NIGP206795 [3 deutonymphs: 2 females, 1 male]; NIGP206799 [3 subadults: 2 females, 1 male]; NIGP206830 [2 specimens, ontogenetic stage and sex unknown]; NIGP206835 [3 specimens: 1 male subadult, 2 deutonymph (sex unknown)]. Stage unknown: NIGP206829 [sex unknown]. Myanmar, Kachin State, Hukawng Valley, precise locality unknown, mid-Cretaceous (Cenomanian) burmite: subadult [male], deposited in NIGP, China.

Diagnosis (emended from Kolesnikov *et al.*, 2025). Eversible armilla long (Figs 5A, 12B, 13E, 16C, F, 19I, 23G) (present study). Bothridia of anterior sensilla (*ASens*) smaller than that of posterior sensilla (*PSens*) (present study); distance between bothridia of left and right *ASens* equal to that between bothridia of *PSens* (Figs 5A, 6A, F, 12D, 14E, 16D, 17E, 19D, 21E) (present study). *Crista metopica* (or sensillary area) with acute, narrow anterior margin (present study) (Figs 5A, 6A, 14E, 16D, 17E, 19D).

Dorsal tufts of long setae exceeding far beyond posterior margin of opisthosoma (Figs 4C, D, 12A, 13A, B, 12, 14, 16–22) (present study); plumose long setae with relatively sparse cilia, cilia length at least three times diameter of setal shaft (Figs 16I, 18C, 20E, 21G) (Kolesnikov *et al.*, 2025). Palp tibial claw relatively slender, basal width in lateral projection smaller than width of palptarsus (Fig. 5A) (Kolesnikov *et al.*, 2025).

Remarks. Kolesnikov *et al.* (2025) used the number of comb-like setae on the dorsal side of the palpal claw and the length of the tibial projection bearing the claw as the main characters to distinguish *Punkochyzeria makolae* from *Punkochyzeria khoyi*. It should be noted, however, that the holotype of *P. khoyi* examined in the original study is approximately twice the idiosoma length of the holotype of *P. makolae*, and therefore ontogenetic variation cannot be excluded. Our examination of specimens representing different developmental stages reveals that these characters vary markedly during ontogeny (see Discussion). Lacking more distinct and reliable diagnostic characters, *Punkochyzeria khoyi* Kolesnikov, Turbanov & Vorontsov, 2025 is here regarded as a junior synonym of *Punkochyzeria makolae* Kolesnikov, Turbanov & Vorontsov, 2025.

Another species, *Cretachyzeria macroseta* Liu, Fan & Ren, 2025, shares several diagnostic characters with *Cretachyzeria makolae*, as indicated by the original figures and their captions. These include a long eversible armilla, long dorsal tufts of setae extending far beyond the posterior margin of the opisthosoma, and slender palp tibial claws. However, due to the absence of key diagnostic characters, such as the sensillary area and detailed setal morphology, it is not possible to determine whether they are conspecific, and their synonymy therefore remains uncertain.

The dorsal surface of the hysterosoma lacking setae, except for a median longitudinal row, was previously regarded as a diagnostic feature of *Punkochyzeria minaevi*. However, this character is also observed in one specimen of *P. makolae* (NIGP206820). Therefore, this feature is here suggested to represent a generic character of *Punkochyzeria*.

***Punkochyzeria obtuse* sp. nov.**

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(Figs 7, 8)

Typematerial. Holotype: NIGP206794, subadult [female]. Additional material: NIGP206794, stage unknown [unknown]. Myanmar, Kachin State, Hukawng Valley, precise locality unknown, mid-Cretaceous (Cenomanian) burmite, deposited in NIGP, Nanjing, China.

Etymology. The specific epithet *obtusa* is derived from the Latin *obtusus*, meaning “blunt” or “rounded”, referring to the rounded posterior end of the idiosoma in this species.

Diagnosis. Bothridia of anterior and posterior sensilla (*ASens*, *PSens*) equal in size; distance between bothridia of left and right *ASens* greater than that between bothridia of *PSens* (Fig. 8B, C). *Crista metopica* (or sensillary area) with broadly arcuate, wide anterior margin (Fig. 8C). Dorsal tufts of long setae slightly exceeding posterior margin of opisthosoma; plumose long setae with very dense cilia, cilia length at least twice the diameter of setal shaft (Fig. 8D, F). Palp tibial claw robust, basal width in lateral projection wider than width of palptarsus (Fig. 8I). Claw of leg I well developed, nearly as long as claws of other legs (Fig. 8H). Posterior margin of idiosoma broadly rounded, not protruding, lateral margins weakly convergent (Figs 7, 8F).

Remarks. The new species is most similar to *Punkochyzeria minaevi*, sharing the following characters: bothridia of similar size and position; anterior margin of the sensillary area of similar shape; dorsal tufts of similar length; plumose long setae of similar morphology; and similarly robust palp tibial claws. It differs from *P. minaevi* in having a well-developed claw of leg I and a broadly rounded posterior margin of the idiosoma.

Description. Idiosoma length 1420, width 820. Posterior margin of idiosoma gently curved; hysterosoma approximately rectangular, lateral margins only slightly curved near posterior end (Fig. 8F); aspidosoma triangular, projecting anteriorly and gradually narrowing anteriorly (Fig. 8A); posterior part of aspidosoma distinctly widened laterally, forming a pair of arched projections located between legs II and III, projections densely covered with short setae, setae longer than those on ventral surface of proterosoma (Figs 7, 8A, D). Eversible armilla at anterior end of idiosoma short, bearing sparse setae (Figs 5C, 8B).

Gnathosoma moderately preserved, partly deformed (Fig. 8A). Palp slender and straight, covered with sparse setae; Palp tibial claw robust, slightly curved; palp tarsus slightly longer than tibial claw; dorsal ctenidium with three spinose setae (Fig. 8I). Distal end of tarsus pointed (possibly deformed). Other palpal segments deformed. Hypostome partly visible, bearing sparse setae, extending anteriorly and gradually tapering (Fig. 8A, E). Chelicerae not visible.

Aspidosoma clearly delimited, triangular and projecting anteriorly, densely covered with short barbed setae (Fig. 8A). Lateral margins of naso distinct, apex with longer setae than those on lateral part (Figs 5C, 8B). *Crista metopica* located above naso, oval in shape, with broad, arcuate anterior margin (Fig. 8C). A smooth, glabrous longitudinal channel present anterior and posterior to the

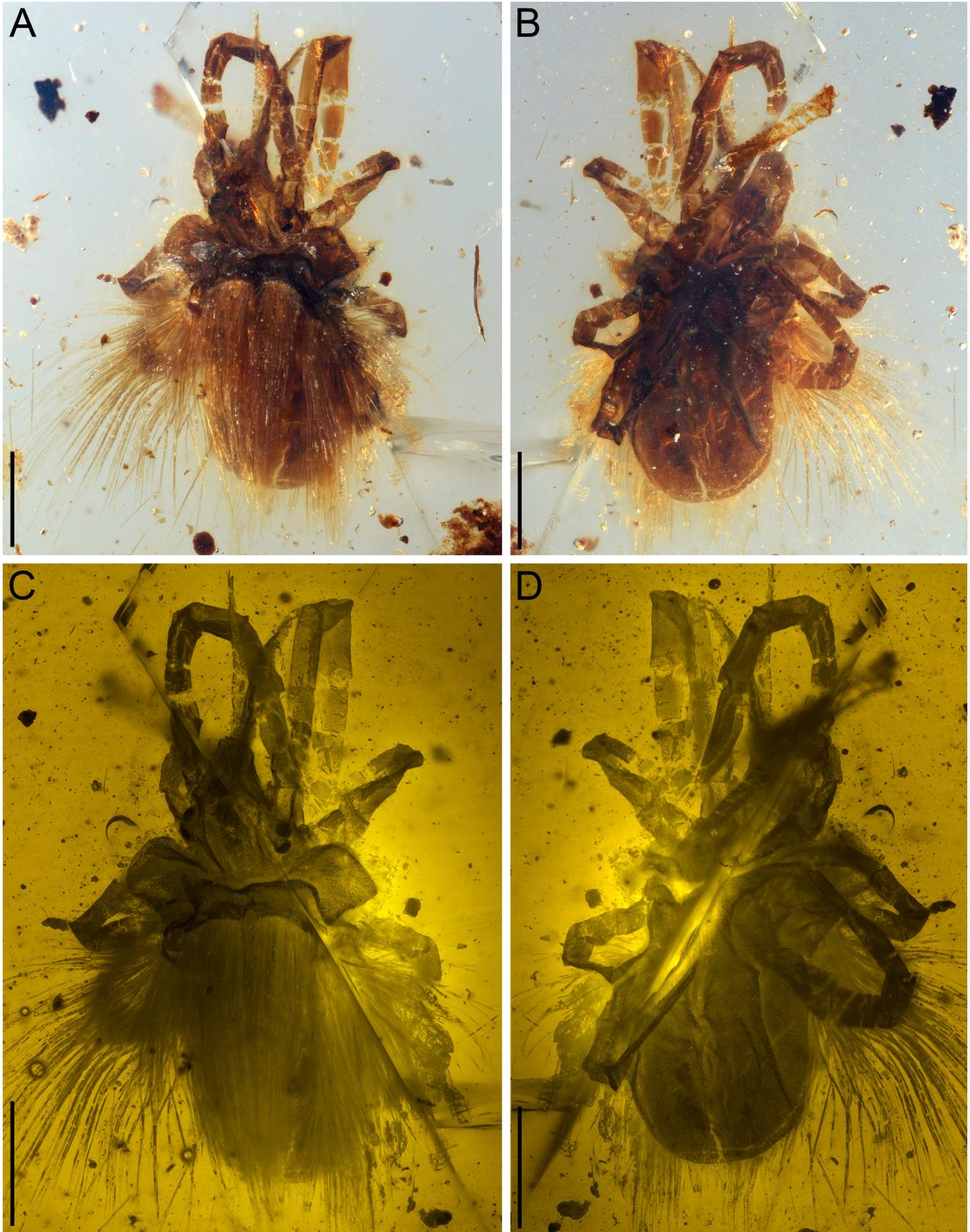


FIGURE 7. General habitus of *Punkochyzeria obtuse* sp. nov. (NIGP206794), under incident light and epifluorescence. A, C, Dorsal view. B, D, Ventral view. Scale bars, 500 μm.

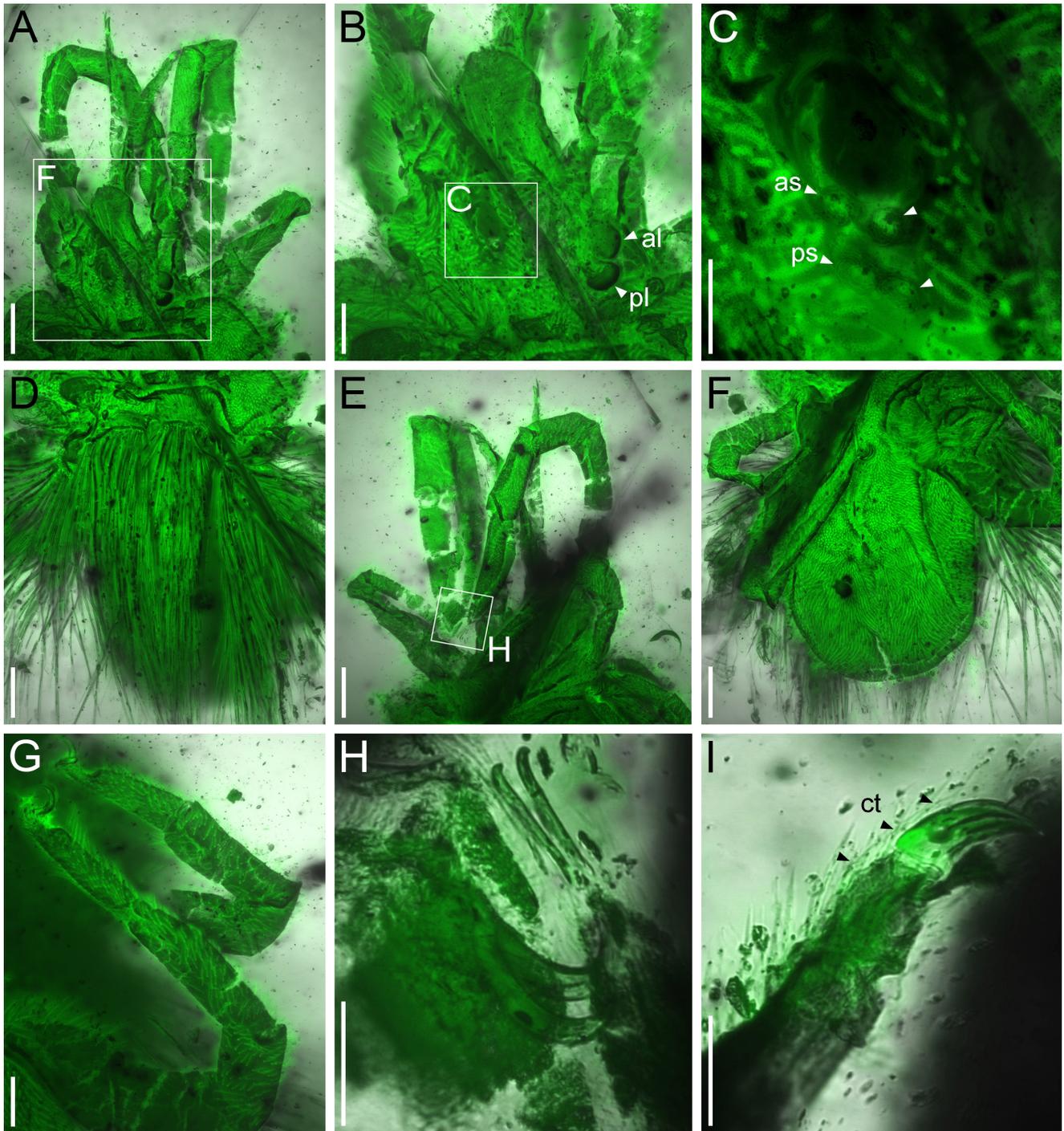


FIGURE 8. Morphological details of *Punkochyzeria obtuse* sp. nov. (NIGP206794), under CLSM. **A**, Proterosoma in dorsal view. **B**, Prodorsum. **C**, sensillary area. **D**, Hysterosoma in dorsal view. **E**, Proterosoma in ventral view. **F**, Hysterosoma in ventral view. **G**, Legs III and IV. **H**, Claws of leg I. **I**, Palp tibial claw and palp tibia. Scale bars, 200 μ m in **A**, **D–F**; 100 μ m in **B**, **G**; 50 μ m in **C**, **H**, **I**.

crista metopica. A sensillary area composed of two pairs of sensilla located at posterior part of *crista metopica*; bothridia of anterior sensilla (*ASens*) and posterior sensilla (*PSens*) nearly equal in size (Fig. 8C). Eversible armilla short with extremely short fine setae (Fig. 8B). Two pairs of lateral eyes, equal in size, diameter 60–70; anterior and posterior lenses adjacent; situated at the same level as

sensillary area (Fig. 8B). Sejugal furrow distinct, nearly as wide as idiosoma (Fig. 8D). Ventral propodosoma densely covered with short barbed setae. V-shaped groove between propodosoma and hysterosoma distinct.

Anterior hysterosoma with two pairs of dorsal sclerites, median pair rectangular, lateral pair not visible. Each sclerite bearing a tuft of extremely long setae

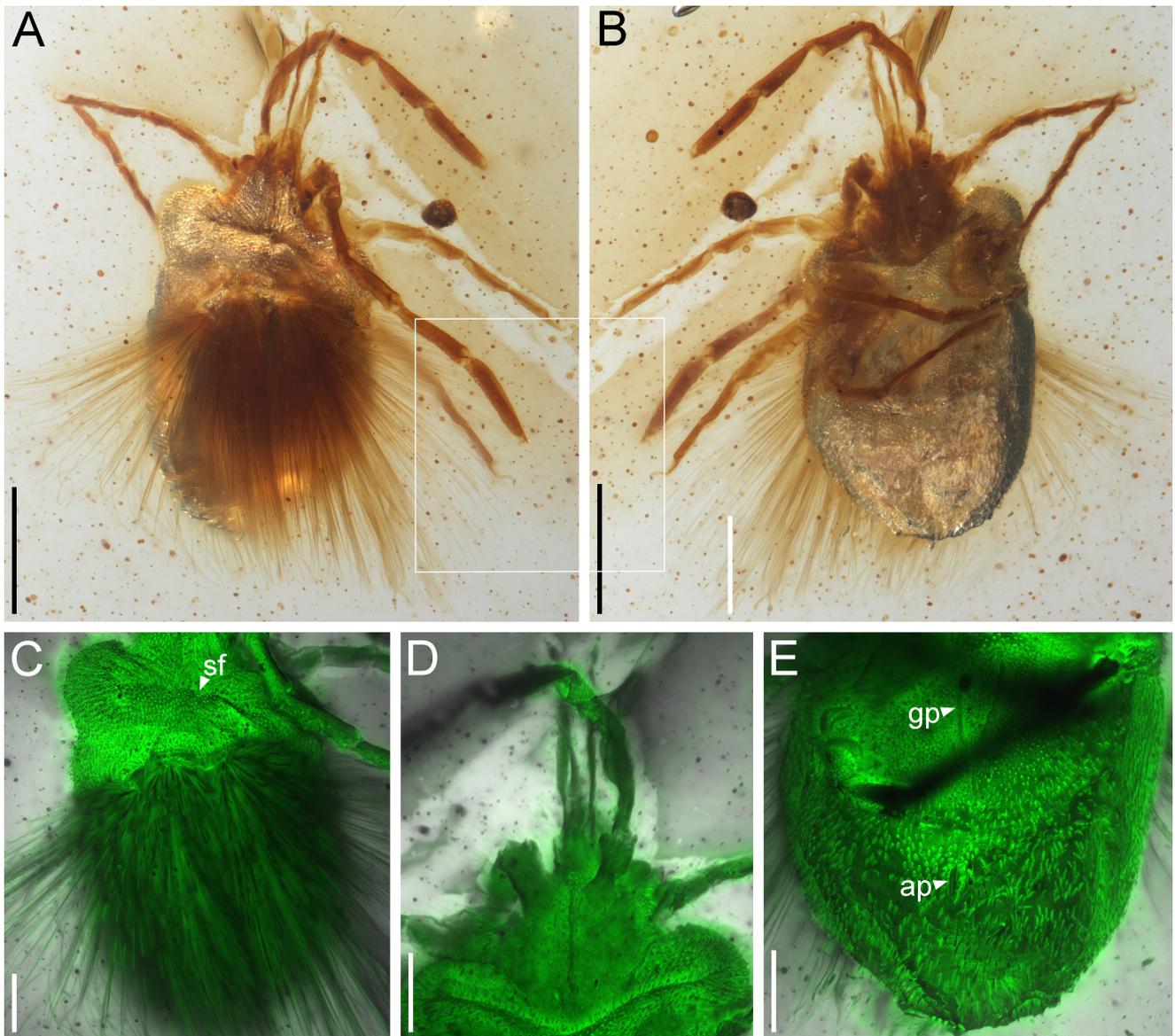


FIGURE 9. General habitus and morphological details of *Punkochyzeria minaevi* (NIGP206771). **A**, General habitus in dorsal view. **B**, General habitus in ventral view. **C**, Hysterosoma in dorsal view. **D**, Proterosoma in ventral view. **E**, Hysterosoma in ventral view. **A**, **B**, under incident light, **C–E**, under CLSM. Scale bars, 500 μm in **A**, **B**; 200 μm in **C–E**.

slightly extending posterior margin of idiosoma, four setal tufts slightly spreading (Fig. 8D). Two types of long dorsal setae present: 1) few, shorter, thicker, rigid, spine-like, lacking branches; 2) numerous, slender, flexible, with dense plumose branches, branch length at least twice diameter of shaft (Fig. 8D, F). Long plumose setae of posterior margin of hysterosoma not observed.

Genital opening located posterior to coxae IV, about 300 μm long; one pair of genital valves present, bearing a few plumose short setae shorter than setae of genital region (Fig. 8F). Anal opening close to genital opening, about 100 μm long, with one pair of anal valves without setae (Fig. 8F).

Tibia and tarsus of leg I more robust than those of

other legs (Fig. 8E). Tarsus I distinctly longer than tibia I, tapering distally, apex pointed (Fig. 8E). Legs with one pair of well-developed claws, empodium absent. Claws of legs II–IV similar in size; claws of leg I nearly as long as those of other legs but slenderer (Fig. 8E, G, H). Leg segments bearing sparse slender setae.

Key to genera and species of Acaro-hystricidae (adults and nymphs)

1. Anterior and posterior eyes separated, both situated on a single oval sclerite; two pairs of eyes posterior to posterior sensilla. Tarsus I distinctly shorter than tibia I.....*Acarohystrix* **gen. nov.**..... (single species *Acarohystrix magnifica* **sp. nov.**) Anterior and posterior eyes adjacent, not on a sclerite; two pairs of eyes parallel to sensilla. Tarsus I longer than or equal to tibia I.....*Punkochyzeria* (*Cretachyzeria*?).....2

2. Eversible armilla long. Dorsal tufts of long setae exceedingly far beyond posterior margin of opisthosoma; Bothridia of *ASens* smaller than that of *PSens*; distance between two bothridia of *ASens* equal to that of *PSens*; *Crista metopica* with acute, narrow anterior margin. Plumose long setae of dorsal tufts with relatively sparse cilia, cilia length at least three times diameter of setal shaft *Punkochyzeria makolae*
Eversible armilla short. Dorsal tufts of long setae slightly exceeding posterior margin of opisthosoma. Bothridia of *ASens* and *PSens* equal in size; distance between two bothridia of *ASens* greater than
3. that of *PSens*; *Crista metopica* with broadly arcuate, wide anterior margin. Plumose long setae of dorsal tufts with very dense cilia, cilia length at least twice the diameter of setal shaft3
Posterior margin of idiosoma slightly rounded, protruding, lateral margins strongly convergent. Claw of leg I weakly developed, shorter than those of other legs *Punkochyzeria minaevi*
Posterior margin of idiosoma broadly rounded, not protruding, lateral margins weakly convergent. Claw of leg I weakly developed, almost as long as those of the other leg.....
..... *Punkochyzeria obtuse* sp. nov.

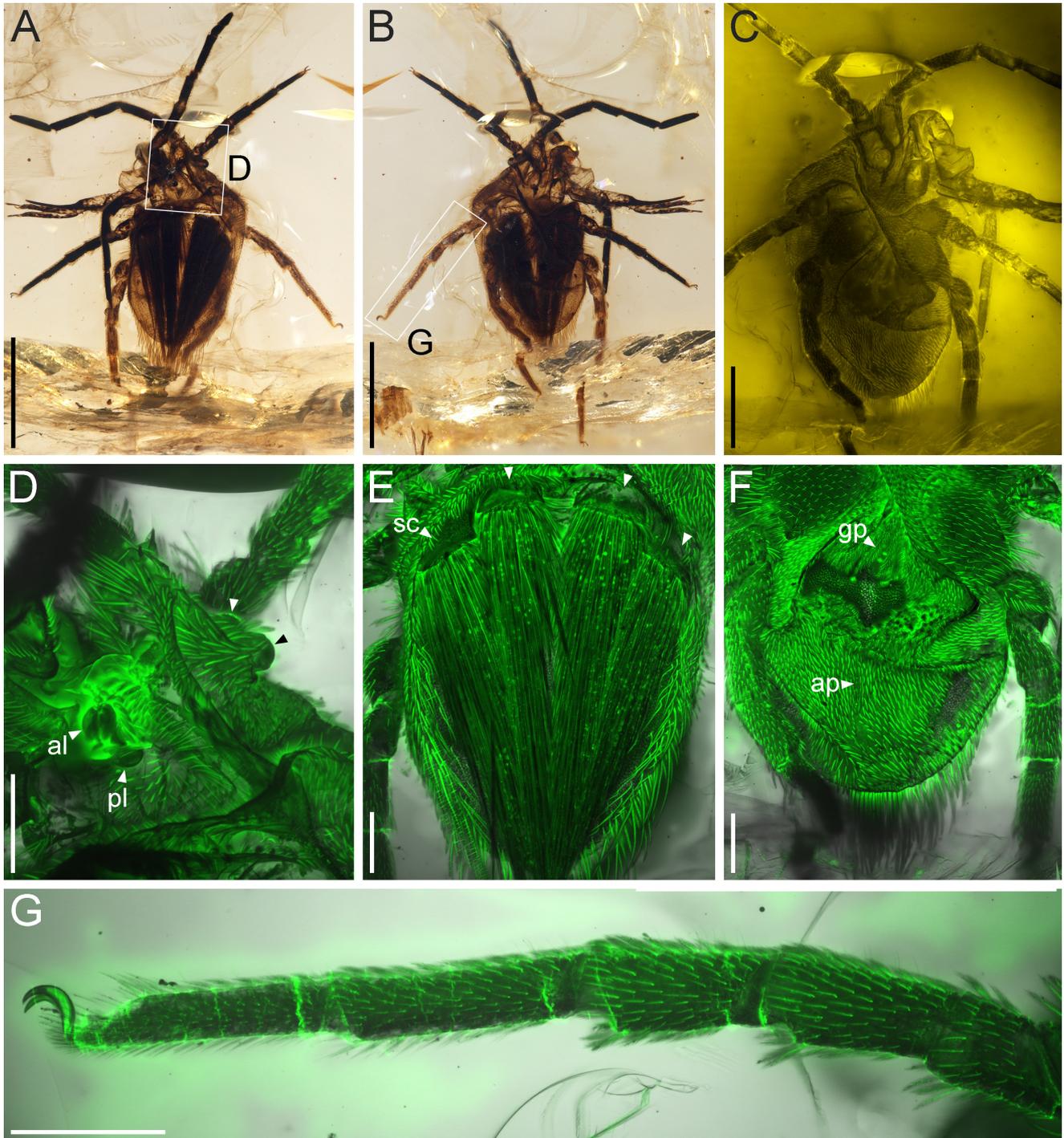


FIGURE 10. General habitus and morphological details of *Punkochyzeria minaevi* (NIGP206797). **A**, General habitus in dorsal view. **B**, **C**, General habitus in ventral view. **D**, Prodorsum in lateral view. **E**, Hysterosoma in dorsal view. **F**, Hysterosoma in ventral view. **G**, Leg III in lateral view. **A**, **B**, under incident light; **C**, under epifluorescence; **D**–**G**, under confocal laser. Scale bars, 1 mm in **A**, **B**; 500 μ m in **C**; 200 μ m in **D**–**G**.

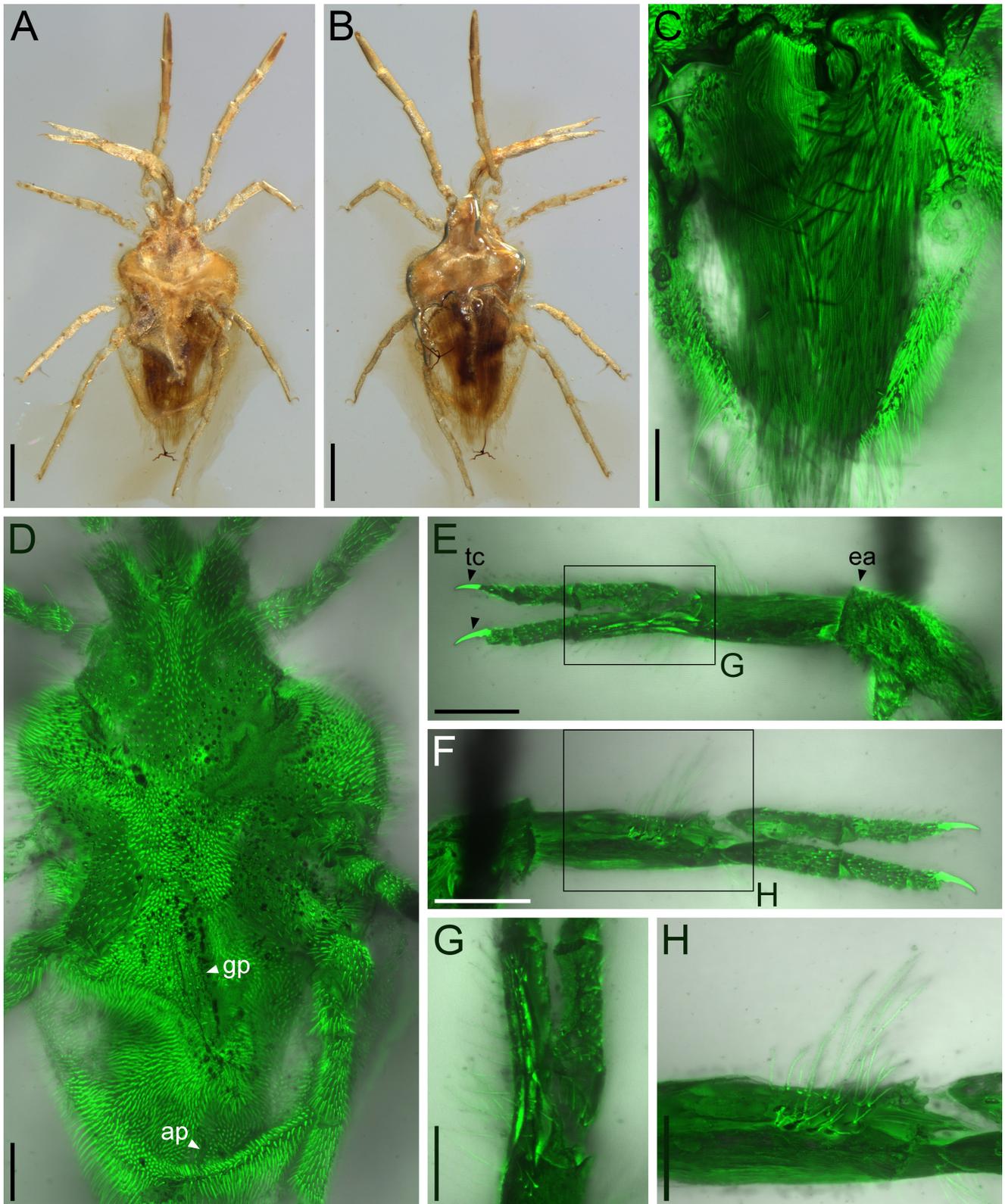


FIGURE 11. General habitus and morphological details of *Punkochyzeria minaevi* (NIGP206802). **A**, General habitus in dorsal view. **B**, General habitus in ventral view. **C**, Hysterosoma in dorsal view. **D**, Idiosoma in ventral view. **E**, **F**, gnathosoma in lateral view. **G**, Hypostome in lateral view. **H**, Base of gnathosoma. **A**, **B**, under incident light; **C–H**, under confocal laser. Scale bars, 500 μm in **A**, **B**; 200 μm in **C–F**; 100 μm in **G**, **H**.

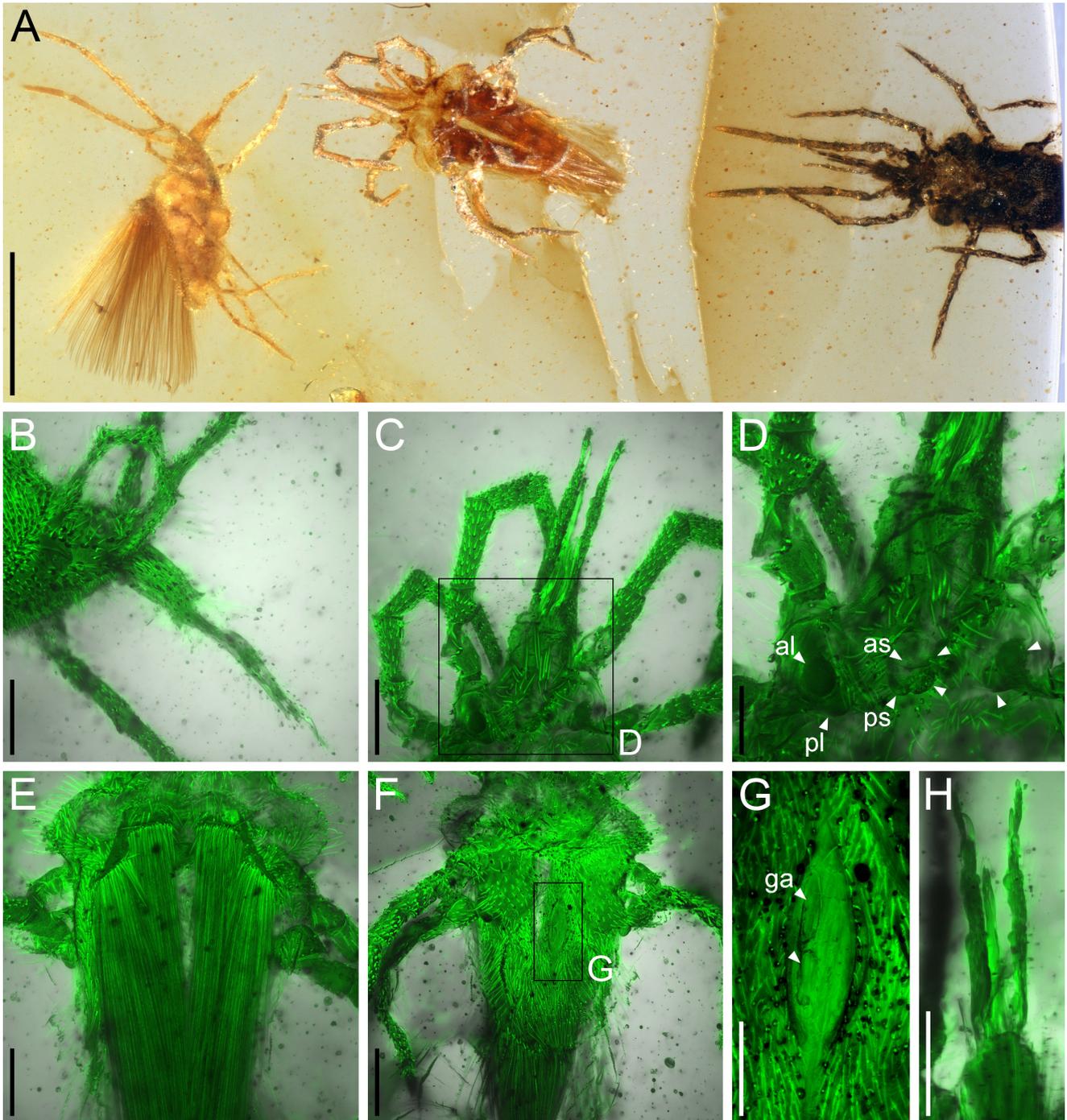


FIGURE 12. General habitus and morphological details of *Punkochyzeria makolae* (NIGP206795). **A**, General habitus of three mites in one single amber, **B**, 206795-1 (left mite). **C–G**, 206795-2 (middle mite). **H**, 206795-3 (right mite). **B**, Detail of proterosoma in lateral view. **C**, Detail of proterosoma in dorsal view. **D**, Detail of propodosoma in dorsal view. **E**, Detail of idiosoma in dorsal view. **F**, Detail of idiosoma in ventral view. **G**, Detail of genital opening. **H**, Detail of gnathosoma in dorsal view. **A**, under incident light, **B–H**, under confocal laser. Scale bars, 1 mm in **A**; 200 μm in **B**, **C**, **E**, **F**, **H**; 100 μm in **D**, **G**.

Discussion

Systematics

Although the phylogenetic analysis presented here is based on a relatively limited set of morphological characters and

consequently yields generally low node support values (Fig. 26), it nevertheless provides a tentative framework for assessing the systematic placement of the new family. The low support observed in several nodes is not unexpected in morphology-based analyses of fossil taxa



FIGURE 13. Morphological details of *Punkochyzeria makolae* (NIGP206790). **A**, General habitus in dorsal view. **B**, General habitus in ventral view. **C**, genital opening. **D**, Detail of body in dorsal view. **E**, Detail of body in ventral view. **A**, **B**, under incident light, **C–E**, under confocal laser. Scale bars, 500 μm in **A**, **B**; 400 μm in **D**, **E**; 50 μm in **C**.

and should be interpreted with caution. The parameters are as follows: CI = 50, RI = 68, and TL = 46. Our phylogenetic results should be regarded as exploratory, providing a preliminary hypothesis of relationships.

Despite these limitations, our results provide preliminary support for placing the extinct family Acaroheystricidae **fam. nov.** (Acaroheystricoidea **superfam. nov.**) within Erythraeina, and suggest a potential sister-

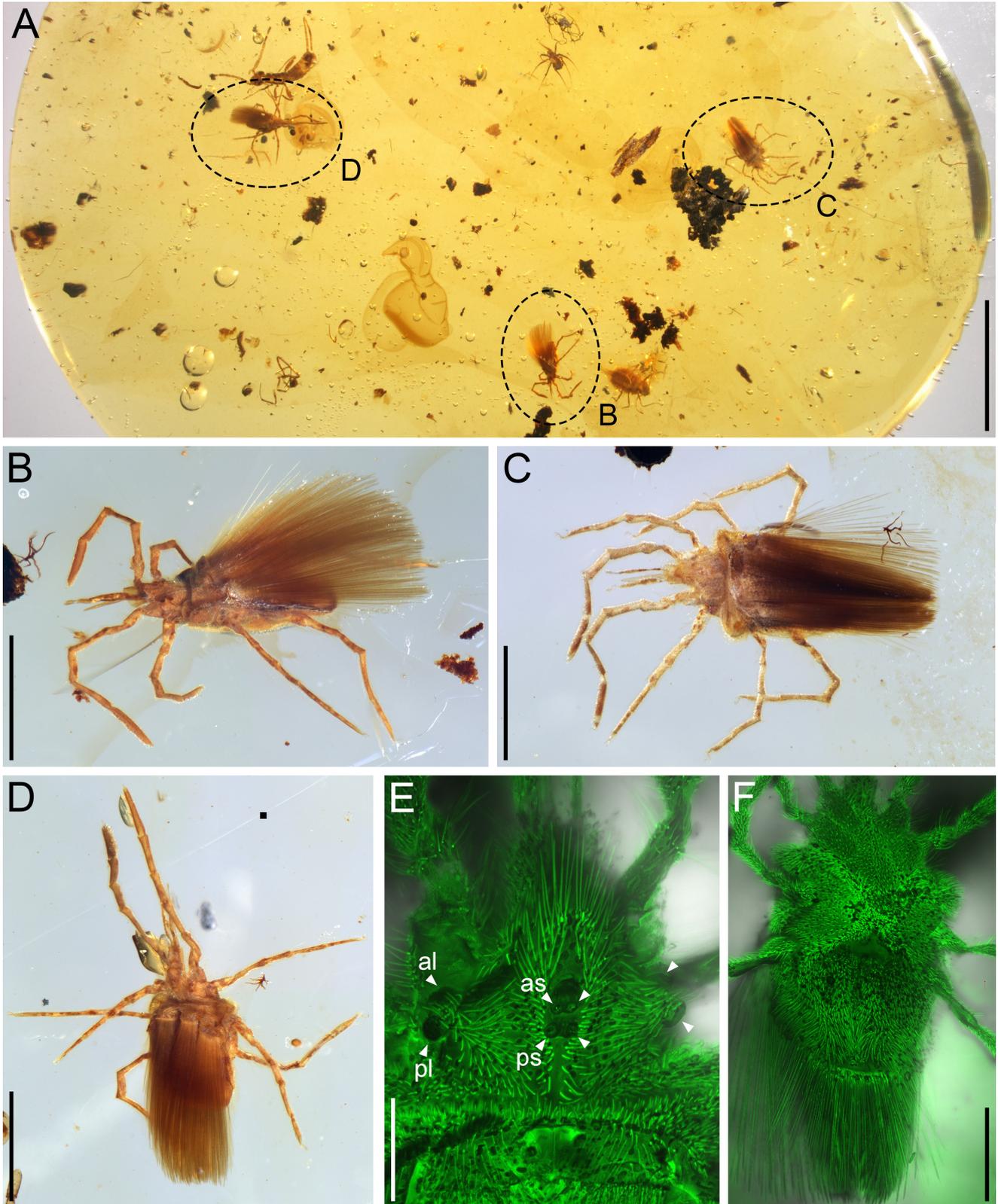


FIGURE 14. General habitus and morphological details of *Punkochyzeria makolae* (NIGP206799). **A**, General habitus of three mites in one single amber, **B**, 206799-1 (middle mite). **C**, **E**, **F**, 206799-2 (right mite). **D**, 206799-3 (left mite). **B**, General habitus in lateral view. **C**, **D**. General habitus in dorsal view. **E**, Detail of prodorsum in dorsal view. **F**, Detail of idiosoma in ventral view. **A–D**, under incident light, **E**, **F**, under confocal laser. Scale bars, 5000 μm in **A**; 1 mm in **B–D**; 500 μm in **F**; 200 μm in **E**.

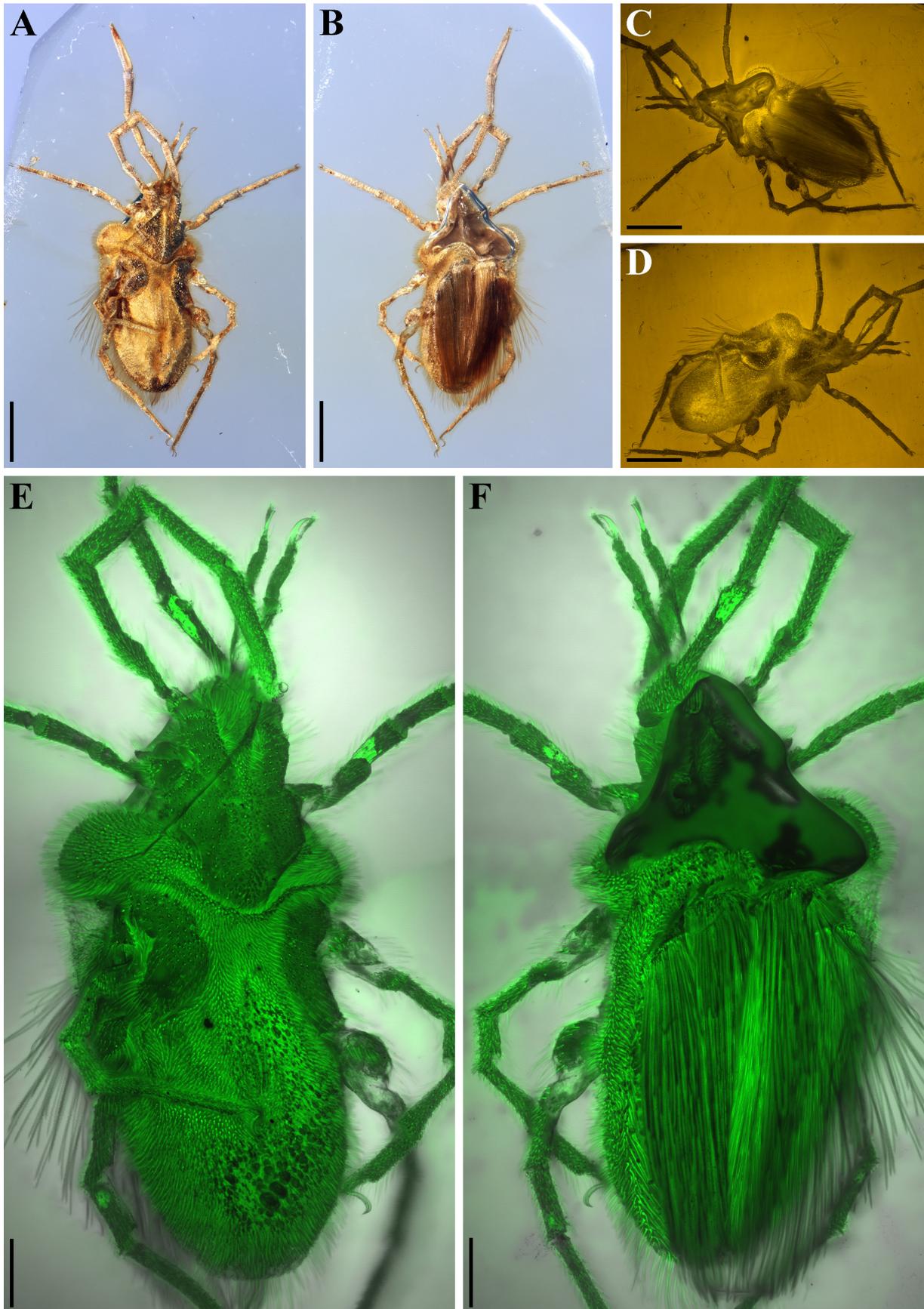


FIGURE 15. General habitus and morphological details of *Punkochyzeria minaei* (NIGP206796). **A, D, E**, ventral view. **B, C, F**, dorsal view. **A, B**, under incident light. **C, D**, under epifluorescence, **E, F**, under confocal laser. Scale bars, 500 μm in **A–D**; 200 μm in **E, F**.

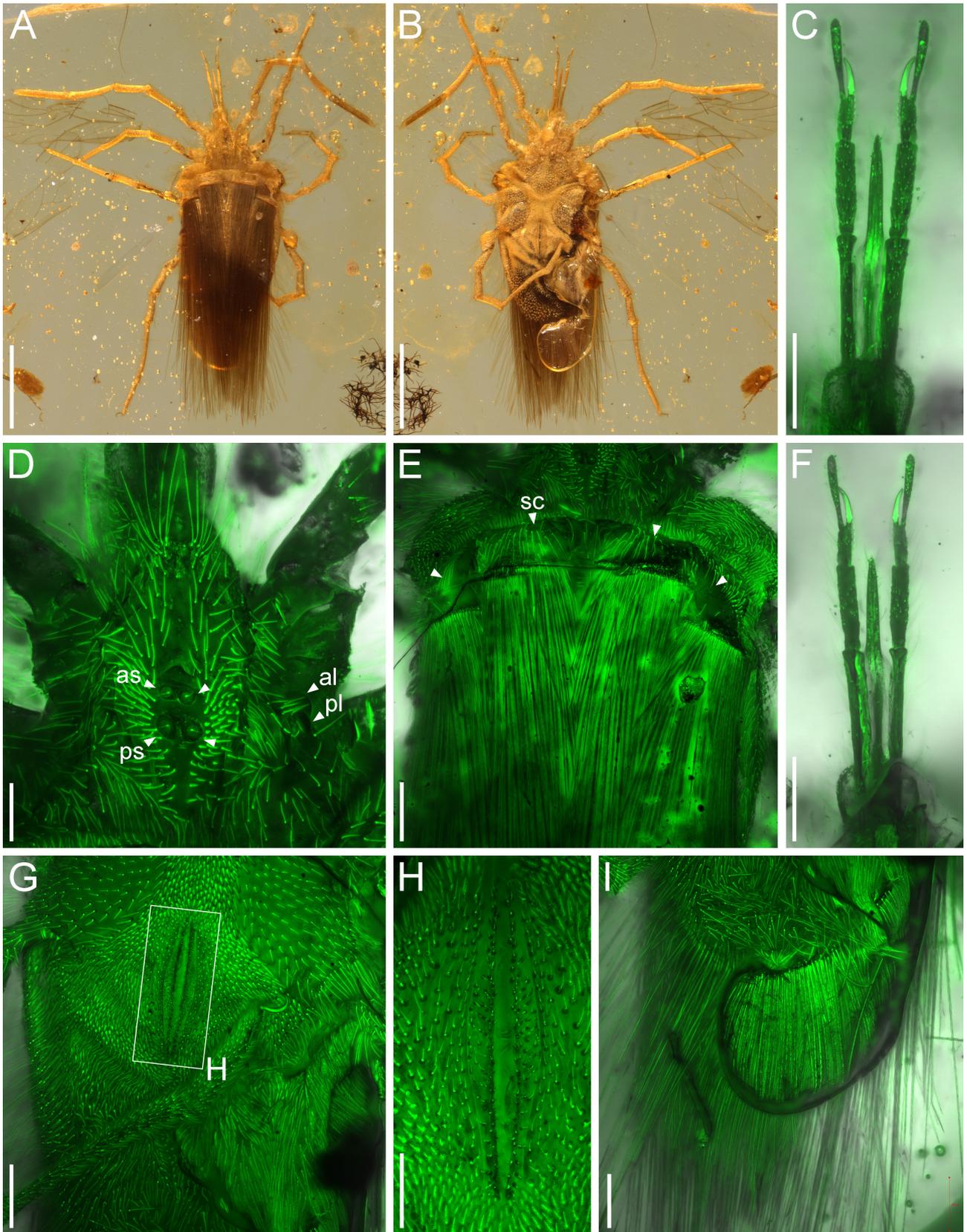


FIGURE 16. General habitus and morphological details of *Punkochyzeria makolae* (NIGP206806). **A**, General habitus in dorsal view. **B**, General habitus in ventral view. **C**, Detail of gnathosoma in dorsal view. **D**, Detail of prodorsum in ventral view. **E**, Detail of propodosoma in dorsal view. **F**, Detail of gnathosoma in ventral view. **G**, Detail of opisthosoma in ventral view. **H**, Detail of genital opening. **I**, Long setae on posterior part of idiosoma. **A**, **B**, under incident light, **C–I**, under confocal laser. Scale bars, 500 μ m in **A**, **B**; 200 μ m in **C**, **E–G**, **I**; 100 μ m in **D**, **H**.

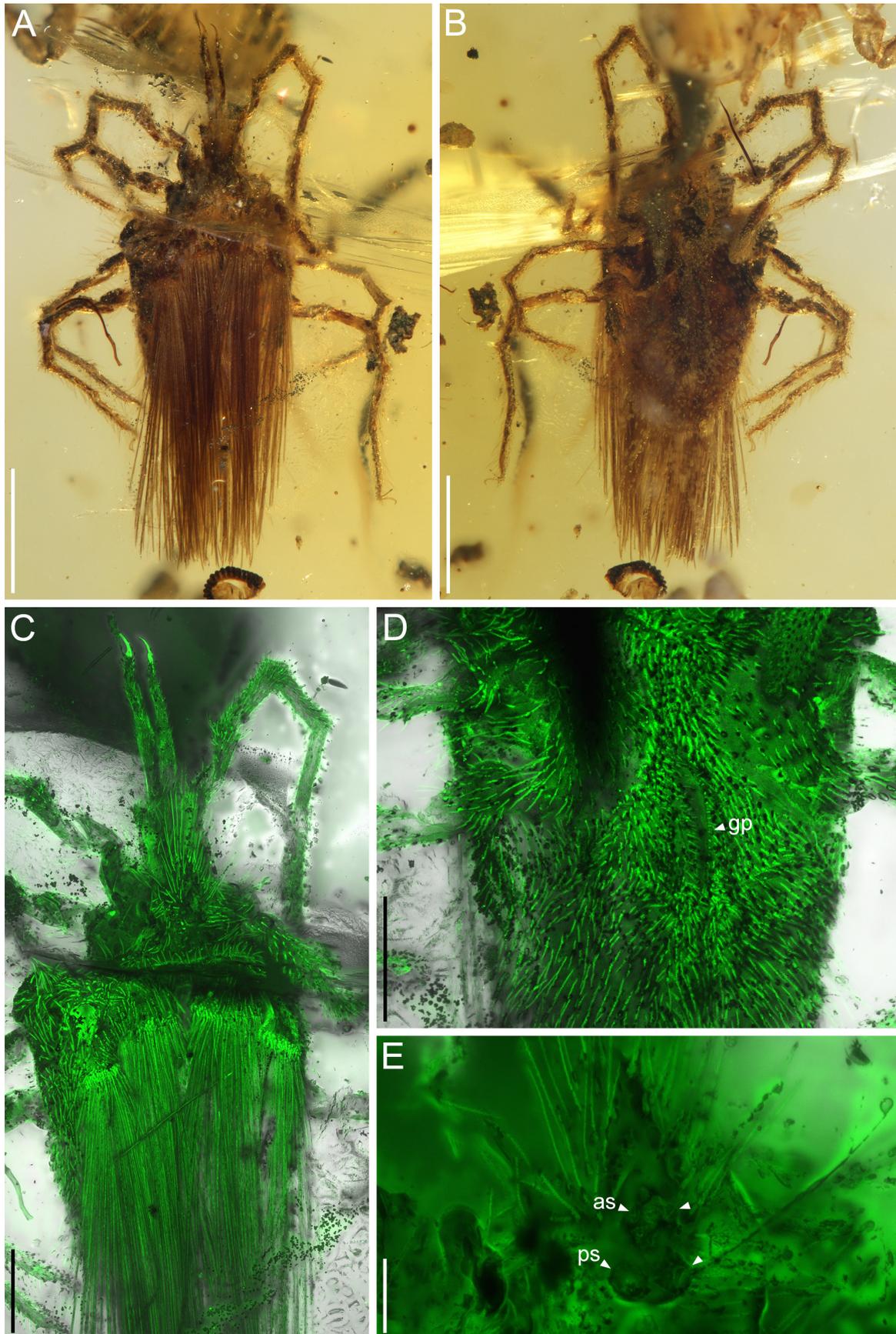


FIGURE 17. General habitus and morphological details of *Punkochyzeria makolae* (NIGP206774). **A**, General habitus in dorsal view. **B**, General habitus in ventral view. **C**, Detail of gnathosoma and idiosoma in dorsal view. **D**, Detail of hysterosoma in ventral view. **E**, Detail of sensillary area. **A**, **B**, under incident light, **C–E**, under confocal laser. Scale bars, 500 μm in **A**, **B**; 200 μm in **C**, **D**; 50 μm in **E**.

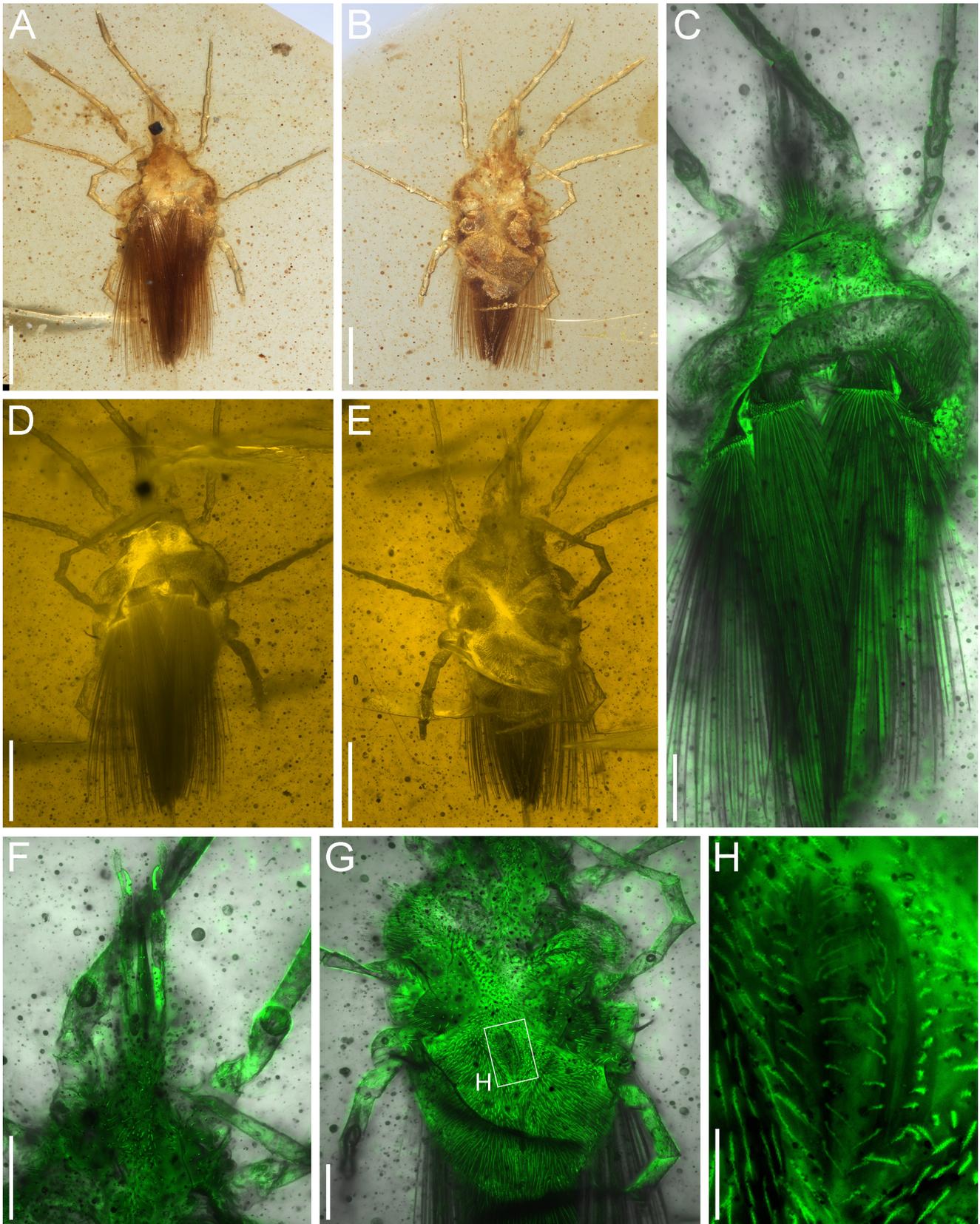


FIGURE 18. General habitus and morphological details of *Punkochyzeria makolae* (NIGP206789). **A, D**, General habitus in dorsal view. **B, E**, General habitus in ventral view. **C**, Detail of gnathosoma and idiosoma in dorsal view. **F**, Detail of gnathosoma and proterosoma in ventral view. **G**, Detail of idiosoma in ventral view. **H**, Detail of genital opening. **A, B**, under incident light. **D, E**, under epifluorescence. **C, F–H**, under confocal laser. Scale bars, 500 μm in **A, B, D, E**; 200 μm in **C, F, G**; 50 μm in **H**.

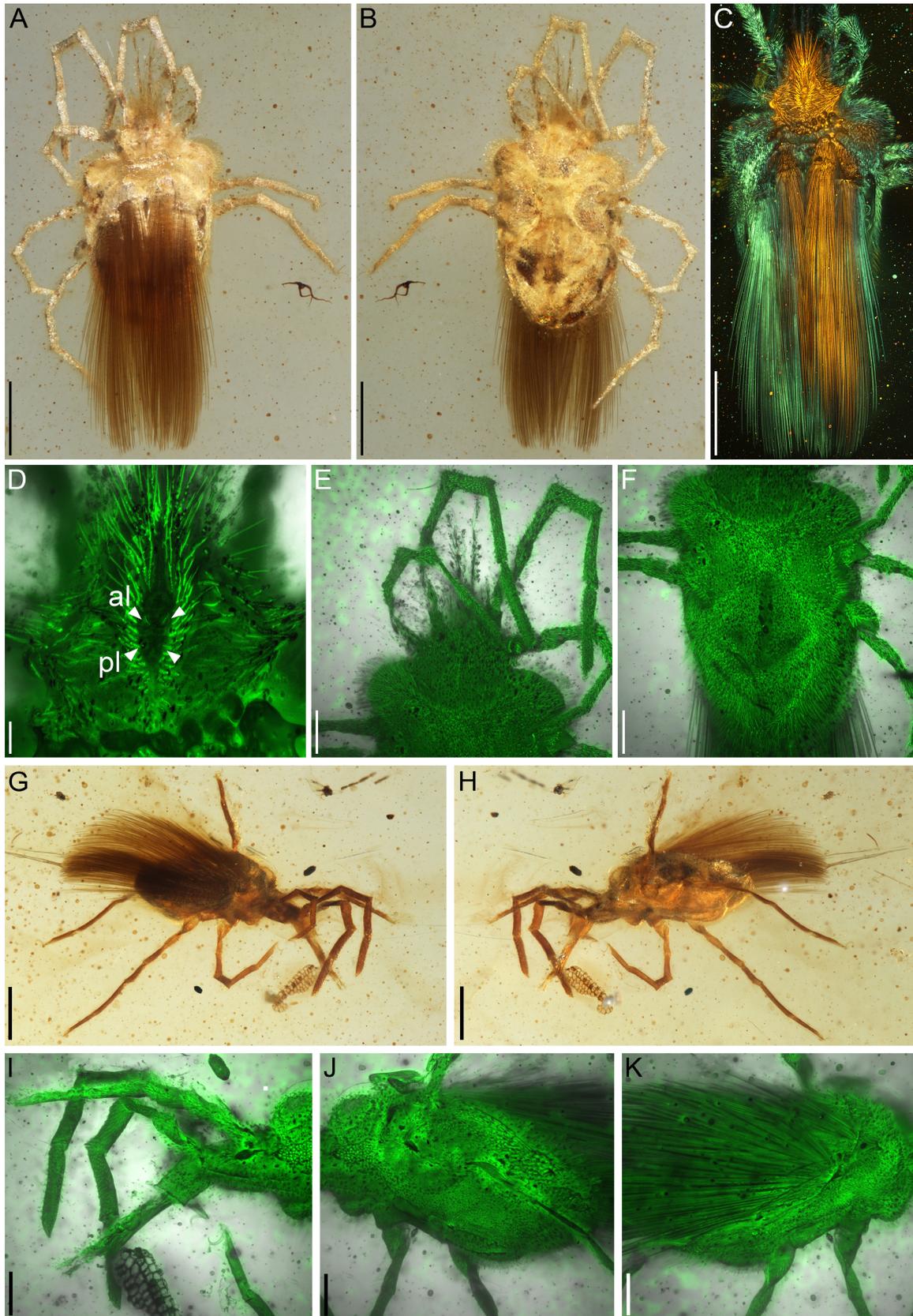


FIGURE 19. General habitus and morphological details of *Punkochyzeria makolae* (NIGP206784 and NIGP206787). **A–F**, NIGP206784; **G–K**, NIGP206787. **A**, General habitus in dorsal view. **B**, General habitus in ventral view. **C**, Detail of idiosoma in dorsal view. **D**, Detail of prodorsum in dorsal view. **E**, Detail of proterosoma in ventral view. **F**, Detail of idiosoma in ventral view. **G, H**, General habitus in lateral view. **I**, Detail of proterosoma in lateral view. **J, K**, Detail of idiosoma in lateral view. **A, B, G, H**, under incident light, **C–F, I–K**, under confocal laser. Scale bars, 500 μm in **A, B, G, H**; 200 μm in **C, E, F, I–K**; 100 μm in **D**.

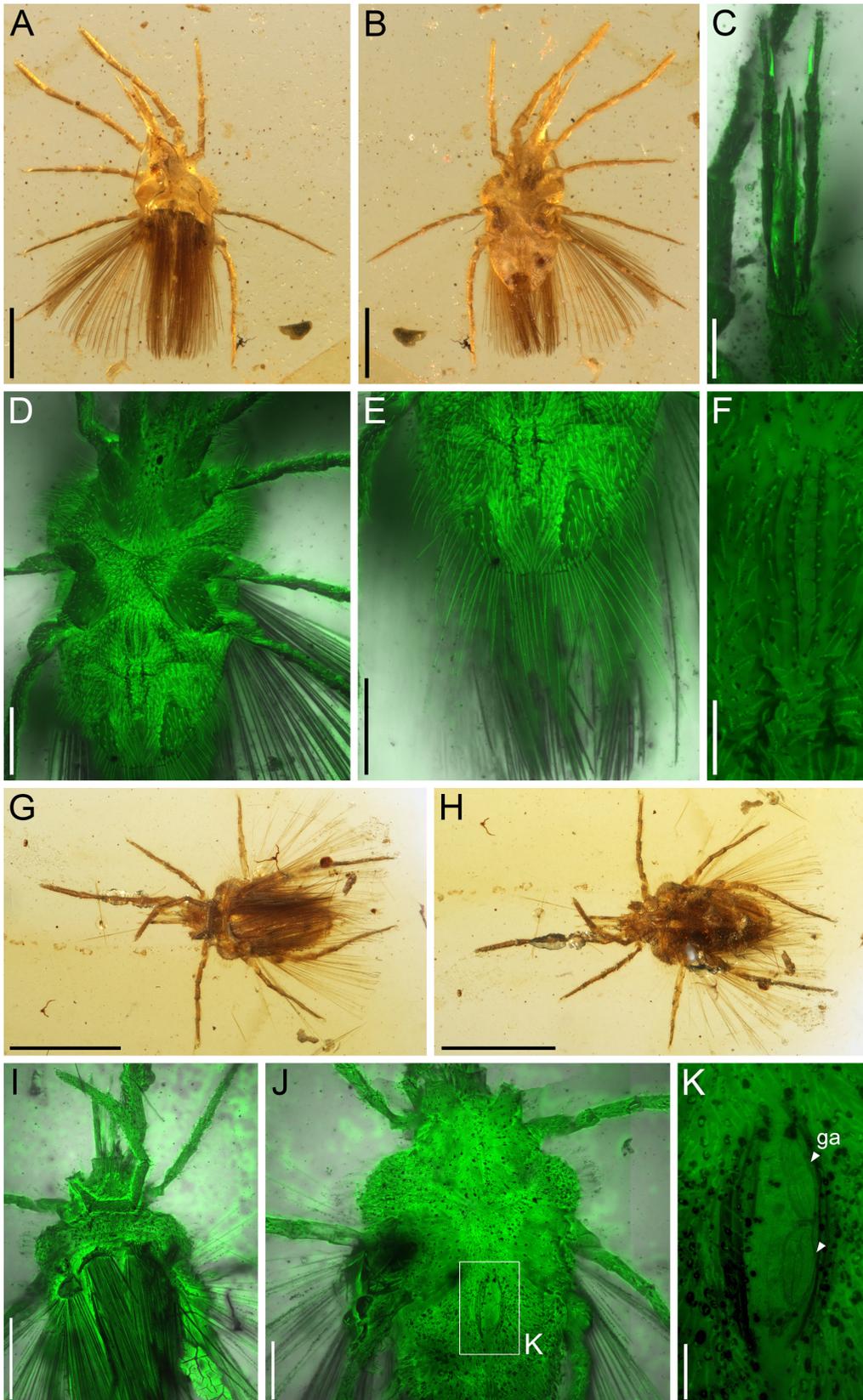


FIGURE 20. General habitus and morphological details of *Punkochyzeria makolae* (NIGP206807 and NIGP206791). **A–F**, NIGP206807; **G–K**, NIGP206791. **A, G**, General habitus in dorsal view. **B, H**, General habitus in ventral view. **C**, Detail of gnathosoma in ventral view. **D**, Detail of idiosoma in ventral view. **E**, Detail of long setae on posterior part of opisthosoma in ventral view. **F**, Detail of genital opening. **I**, Detail of gnathosoma and idiosoma in dorsal view. **J**, Detail of idiosoma in ventral view. **K**, Detail of genital opening. **A, B, G, H**, under incident light, **C–F, I–K**, under confocal laser. Scale bars, 1 mm in **G, H**; 500 μ m in **A, B**; 400 μ m in **I**; 200 μ m in **D, E, J**; 100 μ m in **C, F**; 50 μ m in **K**.

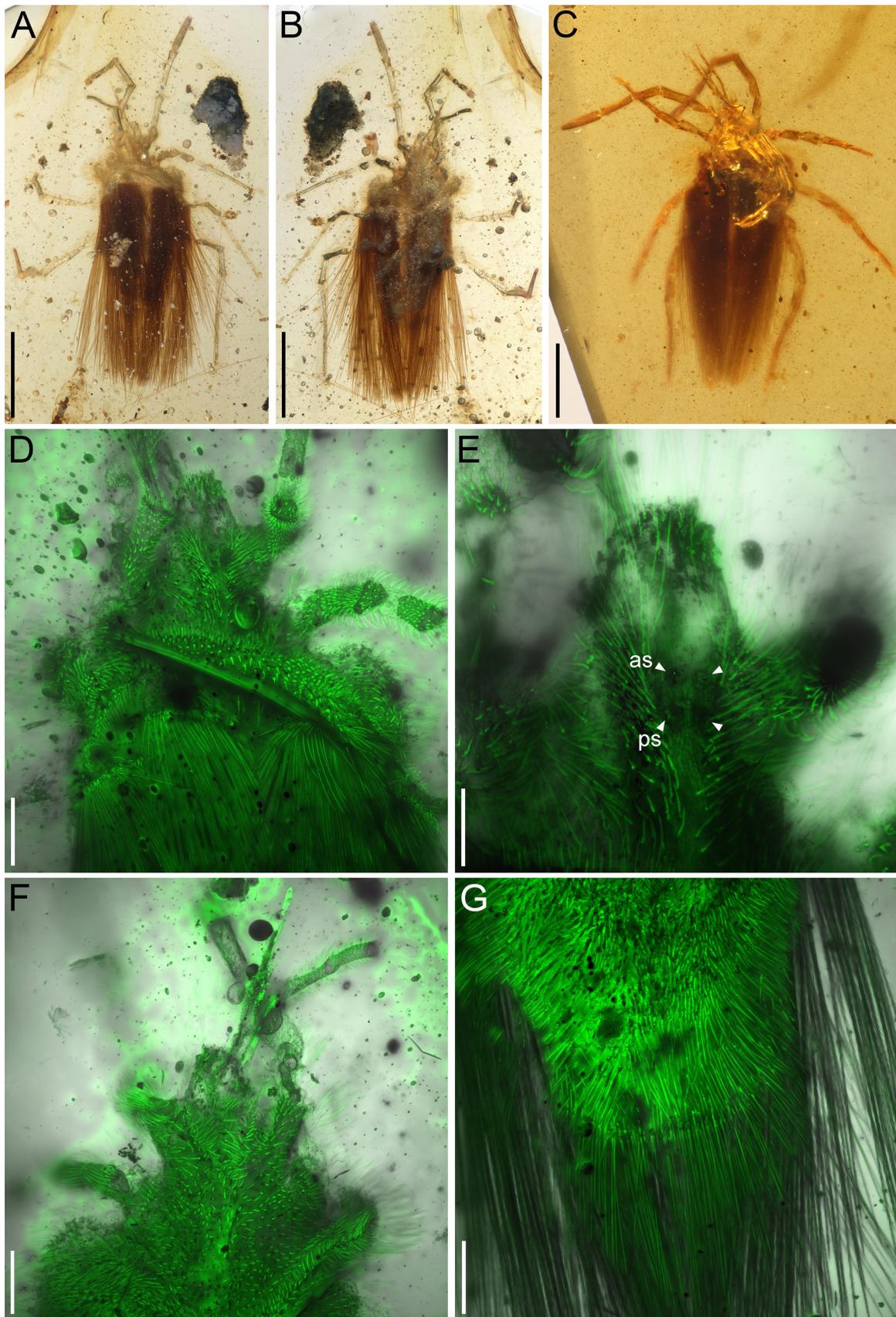


FIGURE 21. General habitus and morphological details of *Punkochyzeria makolae* (NIGP206786 and NIGP206810). **A, B, D–G,** NIGP206786; **C,** NIGP206810. **A, C,** General habitus in dorsal view. **B,** General habitus in ventral view. **D,** Detail of proterosoma in dorsal view. **E,** Detail of prodorsum. **F,** Detail of gnathosoma and proterosoma in ventral view. **G,** Detail of long setae on posterior part of opisthosoma in ventral view. Scale bars, 1 mm in **A–C**; 500 μm in **A, B**; 200 μm in **D, F, G**; 100 μm in **E**.

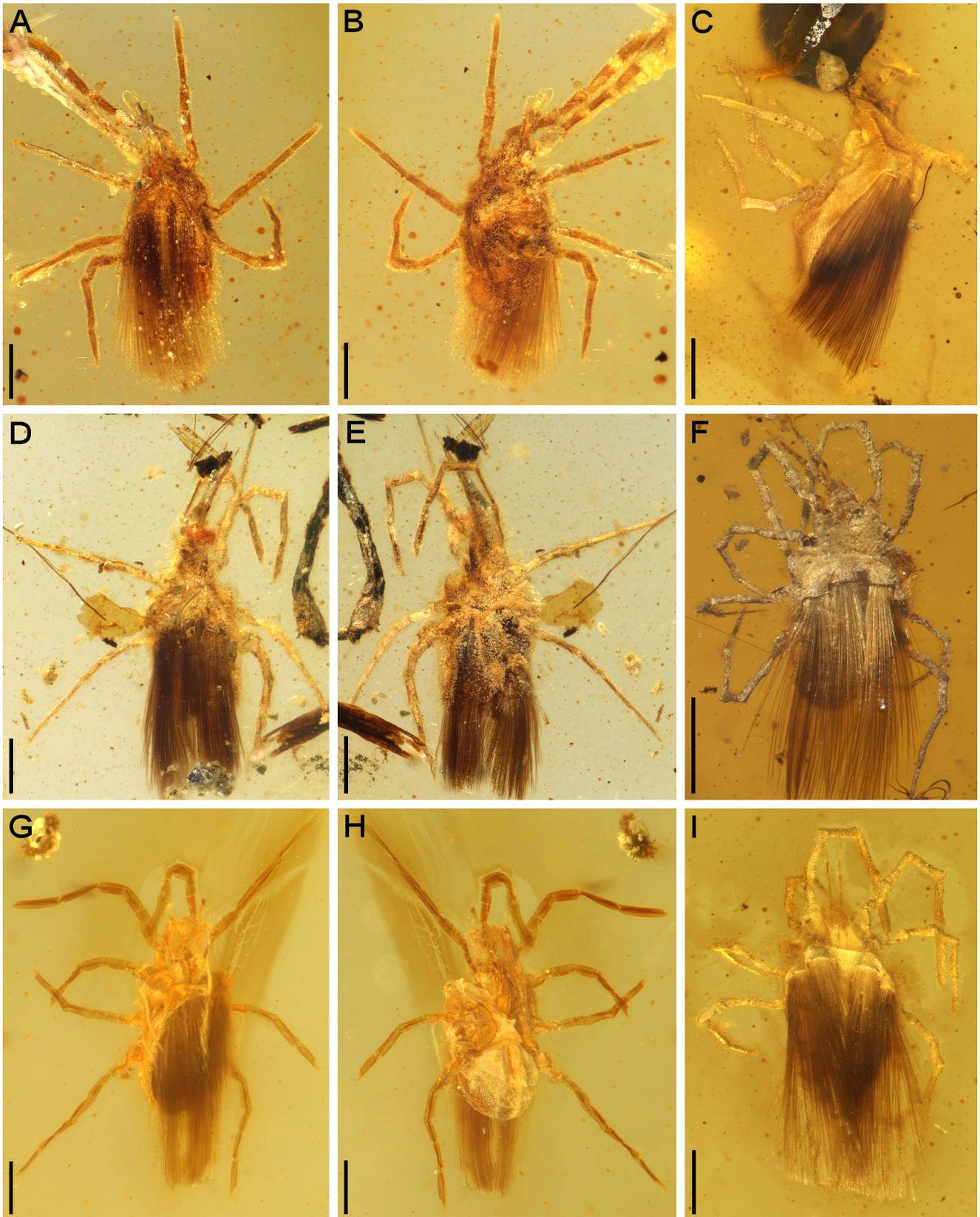


FIGURE 22. General habitus of *Punkochyzeria makolae* (NIGP206815–NIGP206818, NIGP206822, and NIGP206812). **A, B,** NIGP206815. **C,** NIGP206817. **D, E,** NIGP206816. **F,** NIGP206812. **G, H,** NIGP206822. **I,** NIGP206818. **A, D, F, G, I,** General habitus in dorsal view. **B, E, H,** General habitus in ventral view. **C,** General habitus in lateral view. All under incident light. Scale bars, 500 μm in **A, B, F, G**; 200 μm in **D, E, H, I**; 100 μm in **C**.

group relationship between this new superfamily and the extant superfamily Calyptostomatoidea (Fig. 1). This clade is recovered as sister to Erythraeoidea, whereas its relationship to trombidoid lineages appears more distant. This topology is broadly congruent with traditional morphology-based hypotheses, which have long suggested a close affinity between Calyptostomatoidea and Erythraeoidea (Welbourn, 1991; Söller *et al.*, 2001; Zhang & Fan, 2007).

Based on detailed re-investigation of the morphology of the new material, it is clear that these hair tuft-bearing mites share many characters with Erythraeina rather than Trombidiiniina (including Chyzeriidae), such as a retractable gnathosoma and long and straight cheliceral movable digits. The superfamily Acaro-hystricoidea **superfam. nov.** exhibits a mixture of characters shared by superfamilies Calyptostomatoidea and Erythraeoidea. The sister-group relationship between Calyptostomatoidea and Acaro-hystricoidea **superfam. nov.** is supported by the presence of an eversible armilla, two pairs of genital acetabula in adults, a straight and slender palp, and a palptarsus inserted subdistally on the tibia.

The new superfamily may be distinguished from other superfamilies of Erythraeina mites by the following combination of characters: an exceptionally elongated hypostome with more than ten pairs of setae, a very long needle-like cheliceral digit, the presence of a weakly sclerotized *crista metopica*, the presence of a distinct sejugal furrow, and two pairs of extremely long tufts of setae on the dorsal opisthosoma.

However, our results differ from recent molecular phylogenetic analyses, which instead recover Calyptostomatoidea as the sister group to Hydrachnidia, with this combined clade forming the sister lineage to the remaining terrestrial Parasitengona (Costa *et al.*, 2024). Under that framework, several morphological characters previously regarded as evidence for a close relationship between Calyptostomatoidea and Erythraeoidea, such as a retractable gnathosoma and styliform (needle-like) cheliceral digits (Krantz & Walter, 2009), are interpreted as homoplastic rather than synapomorphic. These traits are known to occur independently in multiple lineages, including Erythraeoidea (*e.g.*, Smarididae), Stygothrombioidea, and even within Hydrachnidia (Harvey, 1998; Li *et al.*, 2021; Costa *et al.*, 2021).

Although the phylogenetic significance of gnathosomal characters at higher taxonomic levels (superfamily and above) remains debated, these features remain reliable for distinguishing the Cretaceous mites described herein from members of Chyzeriidae, thereby supporting the validity of the new family.

Morphology

The chelicerae are usually difficult to observe because

they are largely enclosed by the hypostome. In studies of extant taxa, the morphology of the chelicerae is therefore typically examined through dissection or clearing of tissue before slide-mounting. Such options are obviously impossible in fossil specimens.

Fortunately, in one specimen (NIGP206797) the chelicerae are naturally exposed, clearly showing that the movable digit of the chelicera is needle-like (Fig. 5D). In several other specimens, portions of the needle-like chelicerae can also be observed from the dorsal or lateral side of the subcapitulum (Figs 5A, B, 23G), including those illustrated in previously published specimens (Kolesnikov *et al.*, 2025: 468, fig. 10I). In addition, the specimens preserve different positions of the gnathosoma within the armilla, ranging from a fully extended to a retracted condition within the idiosoma.

For comparison, we examined representatives of three extant families: Chyzeriidae Womersley, 1954 (Trombidiina), and Smarididae Kramer, 1878 and Calyptostomatidae Oudemans, 1923 (both belonging to Erythraeina). In Chyzeriidae, the gnathosoma is fixed at the anterior margin of the body and cannot be retracted into the idiosoma; the cheliceral movable digits are relatively short and robust (Fig. 23A, C). This condition is characteristic of Trombidiina. In the examined specimen of Calyptostomatidae, the chelicerae were dissected and clearly show needle-like movable digits with a bifurcated base, a condition consistent with that observed in the amber fossil (Fig. 5A, 23D). We also examined Smarididae, the only family within Erythraeoidea in which the gnathosoma can be retracted into the idiosoma. In this specimen, the gnathosomal morphology is clearly visible, including the needle-like movable digits of chelicerae and an eversible armilla, which closely resembles that observed in Acaro-hystricidae **fam. nov.** (Fig. 23E–G). These observations further support the hypothesis that the new family is more closely related to erythraeine mites than to trombidiine mites such as Chyzeriidae.

Sexual dimorphism

In adult and subadult individuals of acaro-hystricid mites, sexual dimorphism is evident. Specimens NIGP206795 and NIGP206799 each contain three mites of *Punkochyzeria makolae* at the same developmental stage from the same population, which provides an opportunity to reveal sexual dimorphism in Acaro-hystricidae **fam. nov.** The morphology of genital pores differs distinctly between the sexes, similar to certain trombidiid mites (Feider, 1959). Females possess prominent genital acetabula and thin genital valves with fewer than 20 setae (Figs 9E, 11D, 12G, 13C, 15E, 17D, 18H, 20K), whereas males have concealed genital acetabula and thick genital valves bearing over 40 setae (Figs 3E, 10F, 16H). In addition, in males the coxae of legs III and IV extend medially, forming a rhomboid-shaped genital area (Figs 3E, 10F,

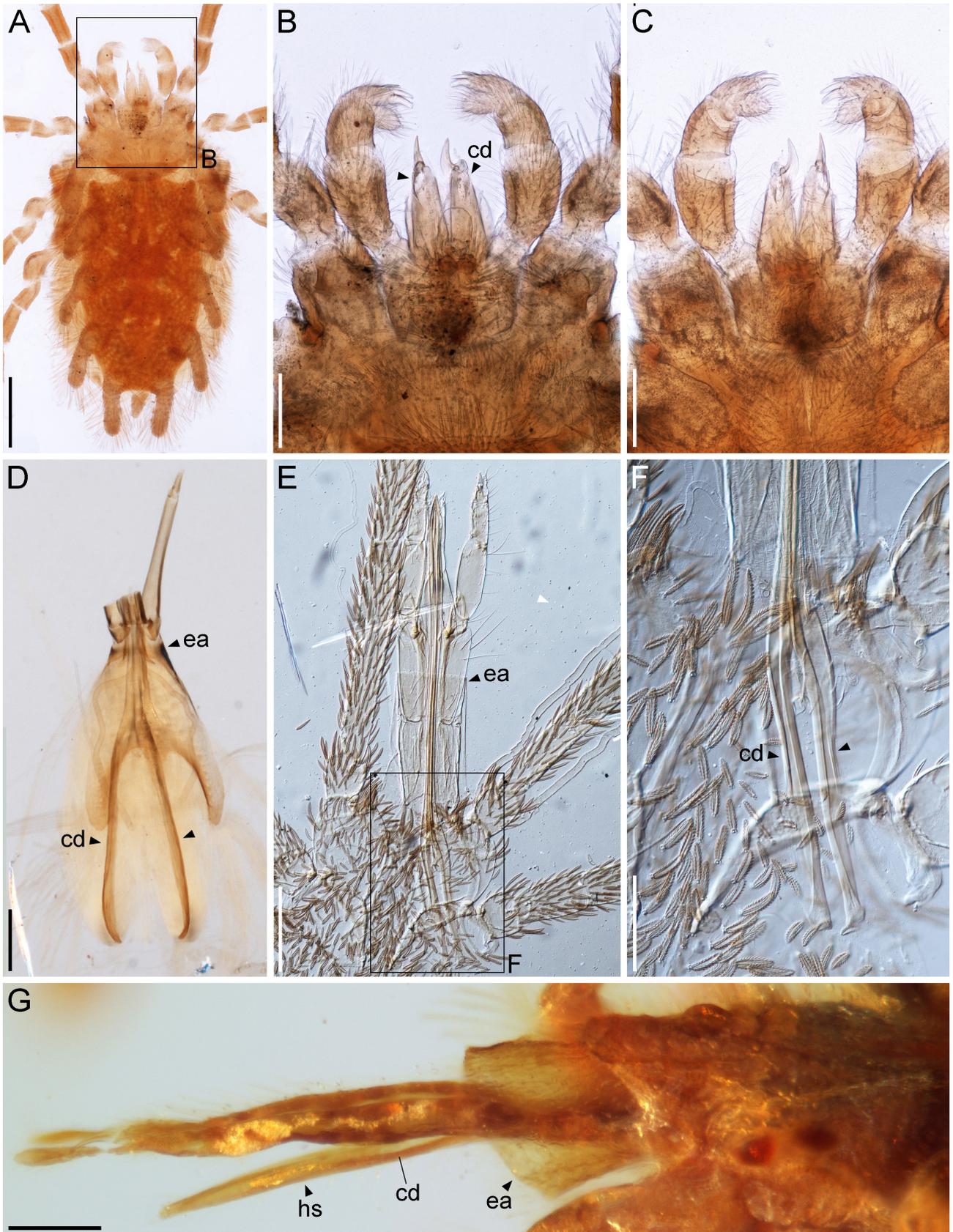


FIGURE 23. Extant mites from Chyzeriidae Womersley, 1954, Calyptostomatidae Oudemans, 1923, and Smarididae Kramer, 1878 and *Punkochyzeria makolae* (NIGP206799-1). **A–C**, *Chyzeria* sp. **D**, Calyptostomatidae sp. **E, F**, Smarididae sp. **G**, *Punkochyzeria makolae*. **A**, General morphology in dorsal view. **B**, gnathosoma in dorsal view. **C**, gnathosoma in ventral view. **D**, Eversible armilla and movable digits of chelicerae. **E**, Gnathosoma in dorsal view. **F**, base of movable digits of chelicerae. **G**, Gnathosoma in lateral view, *P. makolae*. Scale bars, 500 μm in **A**; 200 μm in **B–E**; 100 μm in **F, G**.

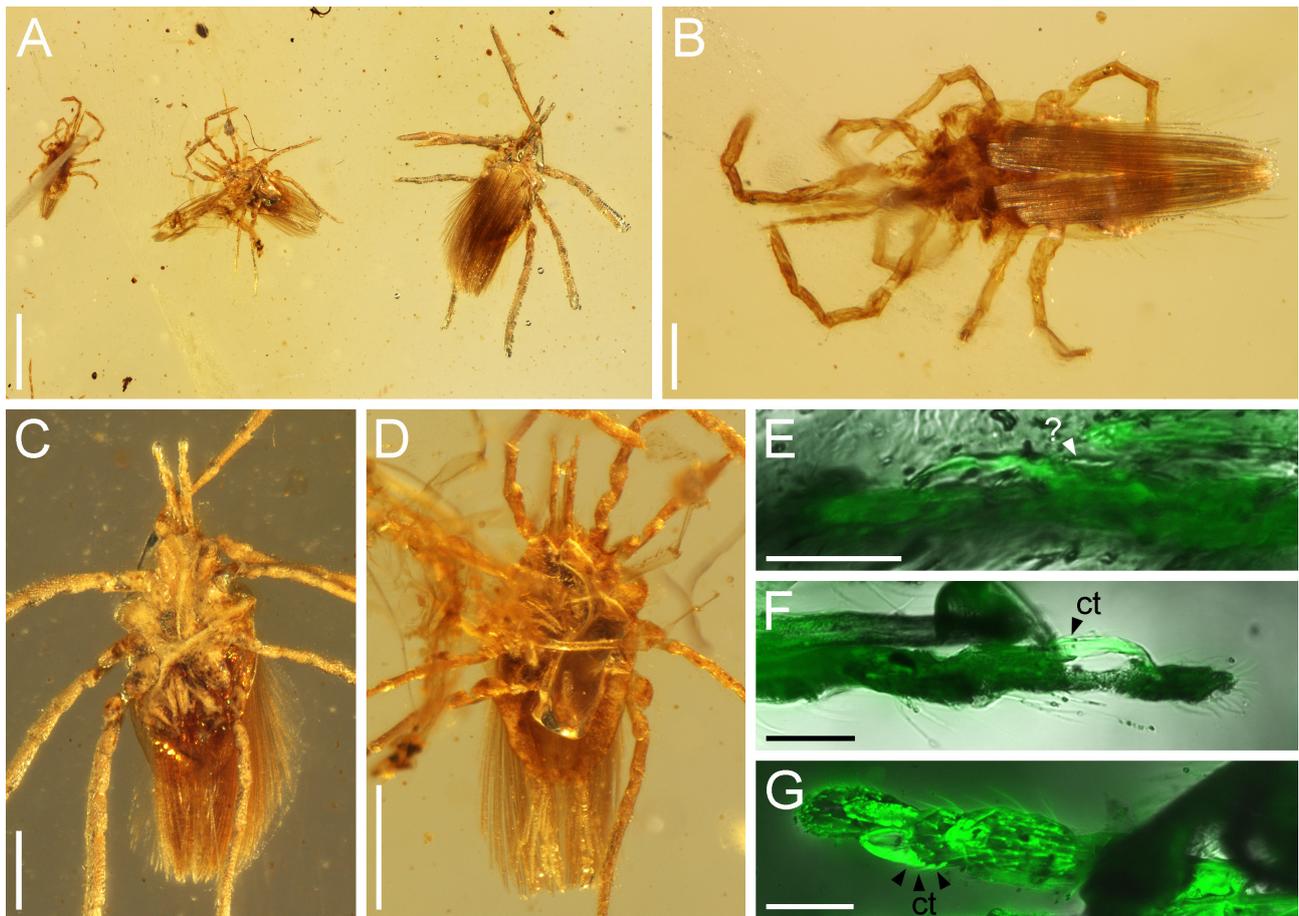


FIGURE 24. General habitus and morphological details of three mites at different developmental stages (NIGP206835). **A**, General habitus in dorsal view. **B**, Deutonymph (206835-3) in dorsal view. **C**, Subadult (206835-1) in ventral view. **D**, Deutonymph (206835-2) in ventral view. **E–G**, Palp thumb-claw complex. **E**, 206835-3. **F**, 206835-2. **G**, 206835-1. Scale bars, 1 mm in **A**; 500 μm in **C**, **D**; 200 μm in **B**; 100 μm in **G**; 50 μm in **E**, **F**.

16G, 19F). Males also have a palptarsus that extends significantly beyond the tibial claw, longer than those of females (Fig. 12C, H).

Ontogenetic development

During specimen examination, we observed that the relative lengths of the tibia and tarsus of leg IV appear to change with increasing body size in this group of mites. To investigate this pattern, measurement data from *Punkochyzeria minaevi* (10 specimens) and *Punkochyzeria makolae* (32 specimens) were compiled and analyzed to explore the potential relationship between these variables (Tables 1–7). The ratio of the tibial length to the tarsal length of leg IV (Ti IV/Ta IV) was plotted against idiosomal length (IL) (Fig. 25).

According to the line chart, the Ti IV/Ta IV ratio in *P. makolae* shows a clear change during ontogenetic development and can be roughly divided into three phases. When the idiosomal length (IL) is less than 1.2 mm, the Ti IV/Ta IV ratio mainly ranges between 0.8 and 1.2. When the idiosomal length ranges from 1.3 to 1.8

mm, the ratio increases to approximately 1.2–1.4. When the idiosomal length exceeds 2.0 mm, the ratio further increases to values above 1.6. The progressive increase of this ratio with body growth (number of molts) indicates a clear allometric growth relationship between the tibia and tarsus of leg IV during ontogeny in this species. The life cycle of most Parasitengona typically comprises seven stages: egg, calyptostatic pre-larva, parasitic (often heteromorphic) larva, calyptostatic protonymph, active predatory deutonymph, calyptostatic tritonymph, and active predatory adult (Zhang, 1998). Molting during the adult stage (post-imaginal molting) is rare but has been documented in Parasitengona (e.g. Trombididae and Arrenuridae) (Krantz & Walter, 2009). Based on this pattern, the three groups of mites observed above may correspond to different developmental stages of *P. makolae*, namely the deutonymph (0.7–1.2 mm), subadult (1.3–1.8 mm), and adult (>2.0 mm) stages.

In contrast, the Ti IV/Ta IV ratio in *P. minaevi* does not show a significant change during ontogenetic development. The ratio remains relatively stable within

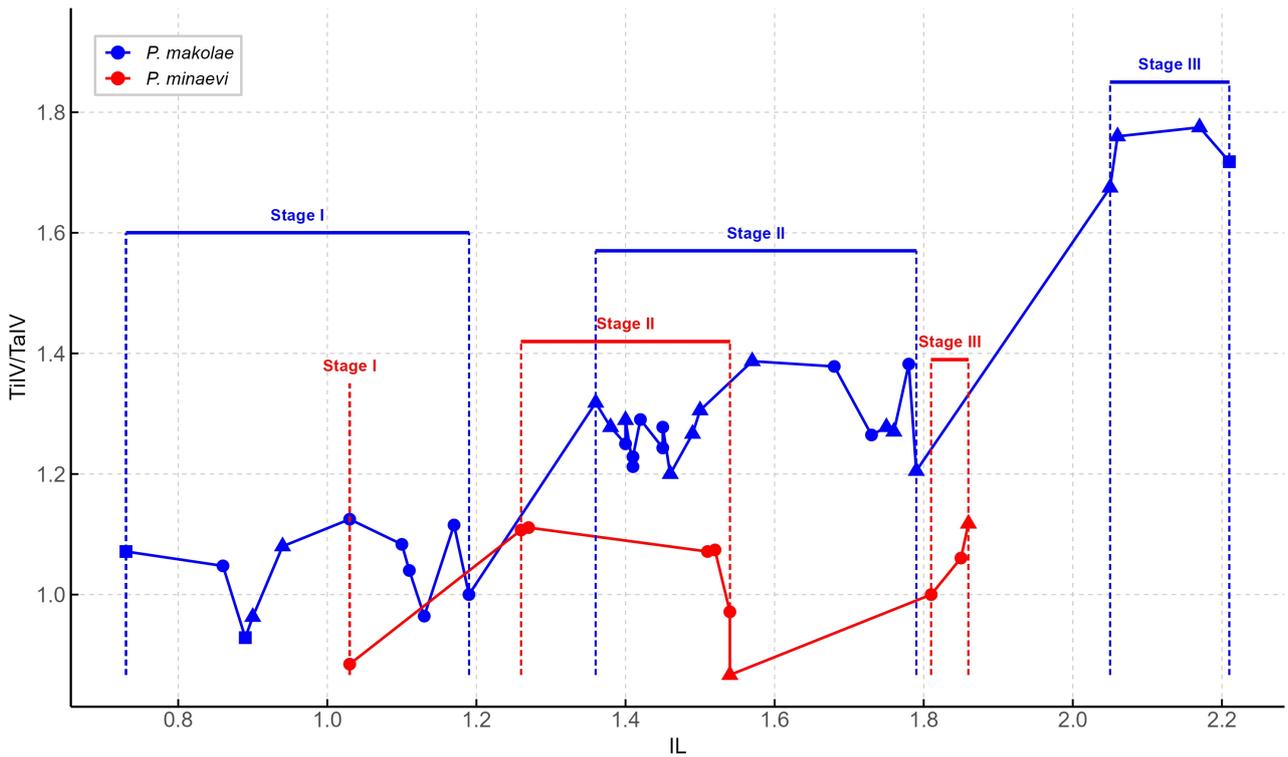


FIGURE 25. Ontogenetic variation of the Ti IV/Ta IV ratio relative to idiosomal length (IL) in *Punkochyzeria minaevi* and *P. makolae*. Circles represent females, triangles represent males, and squares represent specimens of unknown sex.

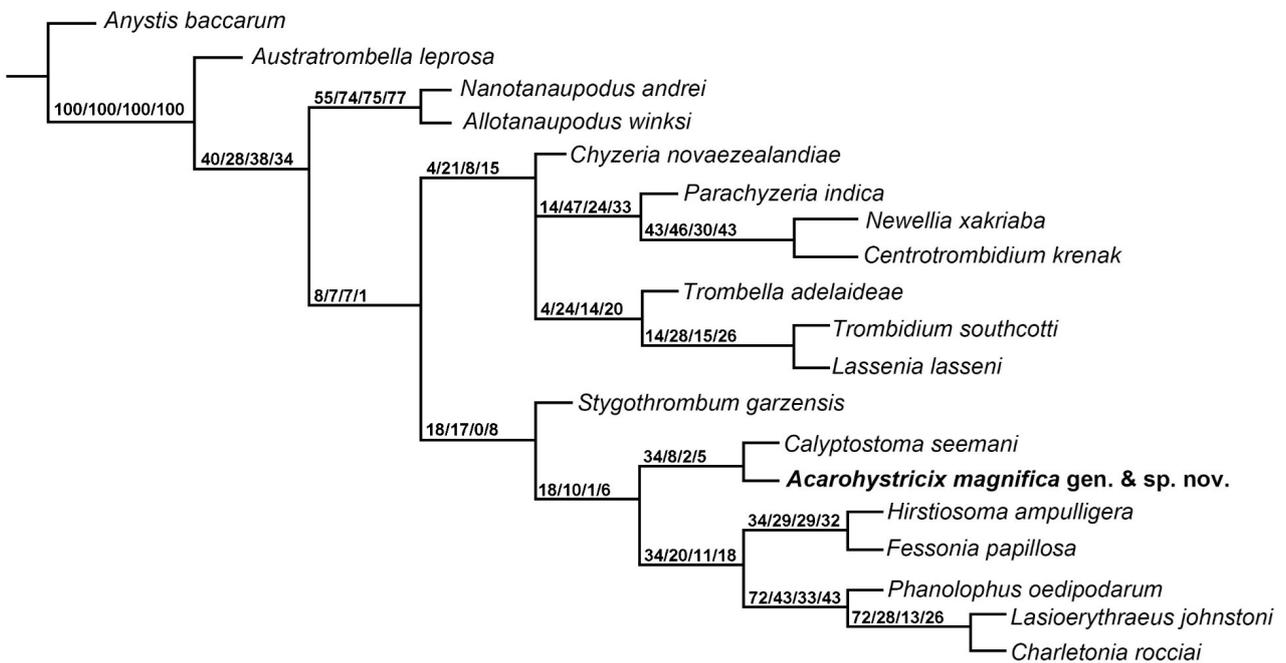


FIGURE 26. The strict consensus tree with node supports. The numbers above bars show relative Bremer, jackknife, bootstrap, and symmetric resampling support value.

a range of approximately 0.8–1.2 across specimens of different body sizes, suggesting that the tibia and tarsus of leg IV may exhibit near-isometric growth in this species. Because the ratio remains relatively constant across body-

length intervals, the developmental stages of *P. minaevi* were primarily inferred based on differences in idiosomal length, corresponding to the deutonymph (Stage I), subadult (Stage II), and adult (Stage III) stages.

Overall, the two species of *Punkochyzeria* exhibit different ontogenetic growth patterns in the proportional relationship between the tibia and tarsus of leg IV. *P. makolae* shows clear allometric growth, whereas *P. minaevi* largely maintains isometric growth. This ontogenetically related proportional change not only reflects differences in growth patterns between the two species but may also serve as an important morphological character for distinguishing them.

Several features vary during ontogeny. Specimen NIGP206835 contains three postnymphal individuals of *P. makolae* at different developmental stages from the same population (Fig. 24): subadult (206835-1) and deutonymphs (206835-2 and 206835-3). Although the two mite specimens are assigned to the deutonymph stage, specimen 206835-3 is smaller (0.73 mm) than specimen 206835-2 (0.89 mm), likely representing an earlier phase within the same instar. It is evident that the length of the dorsal setal tufts relative to the idiosoma remains constant during ontogeny. In addition, the number of spinose setae in the dorsal ctenidium of the palp tibia increases during ontogenetic development. The early deutonymph (206835-3) shows a weakly developed dorsal ctenidium without evident spinose setae (Fig. 24E); the late deutonymph (206835-2) bears one spinose seta in the dorsal ctenidium (Fig. 24F); and the subadult (206835-1) bears three spinose setae in the dorsal ctenidium (Fig. 24G). Adult specimens with an idiosomal length exceeding 2.0 mm (NIGP206806) possess five or six spinose setae in the dorsal ctenidium (Fig. 5A). Likewise, the length of the tibial projection increases during ontogeny. As noted above, these two structures are therefore not reliable species-level diagnostic characters. Kolesnikov *et al.* (2025) distinguished *Punkochyzeria khoyi* (2.15 mm, adult) from *P. makolae* (1.05 mm, deutonymph) primarily based on differences in these characters. However, these differences are most likely attributable to ontogenetic variation rather than true species-level distinctions. Consequently, *Punkochyzeria khoyi* is here treated as a junior synonym of *P. makolae*.

Conclusion

Based on detailed morphological examination and phylogenetic analysis, we reclassified the porcupine-like mites from mid-Cretaceous Burmese amber, characterized by four tufts of extremely long dorsal setae. The superficial similarity of these hair tufts to those of the extant family Chyzeriidae is shown to result from convergent evolution. Several key diagnostic characters, particularly the retractable gnathosoma with needle-like chelicerae, an exceptionally elongated hypostome, a

prodorsum bearing 2 pairs of trichobothria, and adults possessing 2 pairs of genital acetabula support the establishment of a new superfamily, Acaro-hystricoidea **superfam. nov.**, and a new family, Acaro-hystricidae **fam. nov.**, within Erythraeina. This lineage is phylogenetically recovered as a sister group to the extant superfamily Calyptostomatoidea.

This study also clarifies the taxonomic status of previously described genera by transferring *Punkochyzeria* and *Cretachyzeria* to the new family. In addition, new taxa are described, and ontogenetic and sexually dimorphic characters within Acaro-hystricidae are documented.

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APPENDIX: Measurements

TABLE 2. Measurements (μm) for new specimens of Acarohystricidae **fam. nov.**, in the collections of the Nanjing Institute of Geology and Palaeontology (NGIP206770–206779). Abbreviations as follows: IL: idiosoma length; IW: idiosoma width; PaL: palp length (exposed part); Ta: tarsus length; Ti: tibia length; Ge: genu length; Tfe: telofemur length; Bfe: basifemur length; Tr: trochanter length; TL: total length.

No.	206770	206771	206772	206773	206774	206775	206776	206777	206778	206779
Species	<i>P. makolae</i>	<i>P. minaevi</i>	<i>P. makolae</i>	<i>P. minaevi</i>	<i>P. makolae</i>					
Sex	M	F	F	M	F	F	M	M	-	M
IL	1570	1520	1410	-	1100	1190	1760	900	1810	1750
IW	900	890	760	750	660	850	1030	-	1000	940
PaL	590	520	610	460	470	500	-	470	560	500
Ta I	440	380	-	460	330	330	500	320	400	400
Ti I	410	330	-	400	300	310	460	250	330	340
Ge I	340	280	-	330	230	250	380	210	260	270
Tfe I	320	280	-	320	230	250	380	190	280	280
Bfe I	210	280	-	210	160	200	210	170	240	230
Tr I	100	130	80	90	90	130	-	90	-	120
Leg I TL	1820	1680	-	1810	1340	1470	-	1230	-	1640
Ta II	320	250	320	300	300	290	260	250	220	310
Ti II	310	220	300	300	-	250	260	210	200	300
Ge II	210	170	220	210	-	190	250	140	180	190
Tfe II	210	170	210	190	190	190	200	130	190	220
Bfe II	210	180	210	210	210	180	200	130	-	220
Tr II	110	110	110	110	100	110	-	90	-	120
Leg II TL	1370	1100	1370	1320	-	1210	-	950	-	1360
Ta III	340	220	340	330	280	270	370	180	250	280
Ti III	320	220	320	340	220	250	330	190	250	310
Ge III	210	170	220	230	160	200	250	160	170	290
Tfe III	210	160	220	230	160	180	270	140	170	270
Bfe III	220	160	210	240	170	170	210	130	160	250
Tr III	150	110	130	120	110	110	150	120	110	110
Leg III TL	1450	1040	1440	1490	1100	1180	1580	920	1110	1510
Ta IV	310	270	330	-	240	320	370	270	280	360
Ti IV	430	290	400	-	260	320	470	260	280	460
Ge IV	270	220	270	280	190	200	330	170	260	320
Tfe IV	280	230	240	230	180	200	300	190	240	260
Bfe IV	220	190	220	230	190	220	240	140	240	240
Tr IV	160	140	150	170	100	120	160	110	160	150
Leg IV TL	1670	1340	1610	-	1160	1380	1870	1140	1460	1790
Ti IV/Ta IV	1.39	1.07	1.21	-	1.08	1.00	1.27	0.96	1.00	1.28

TABLE 3. Measurements (μm) for new specimens of Acarohystricidae **fam. nov.**, in the collections of the Nanjing Institute of Geology and Palaeontology (NGIP206780–206789). Abbreviations as follows: IL: idiosoma length; IW: idiosoma width; PaL: palp length (exposed part); Ta: tarsus length; Ti: tibia length; Ge: genu length; Tfe: telofemur length; Bfe: basifemur length; Tr: trochanter length; TL: total length.

No.	206780	206781	206782	206783	206784	206785	206786	206787	206788	206789
Species	<i>P. makolae</i>	<i>P. makolae</i>	<i>P. minaevi</i>	<i>P. minaevi</i>	<i>P. makolae</i>	<i>P. makolae</i>	<i>P. makolae</i>	<i>P. makolae</i>	<i>P. obtuse</i>	<i>P. makolae</i>
Sex	F	M	-	-	M	M	M	F	M	F
IL	2130	1790	-	1150	1360	2060	2050	1410	1510	1780
IW	1300	-	-	-	860	1290	-	750	820	1130
PaL	980	530	620	-	440	560	630	600	580	570
Ta I	650	-	330	-	430	620	-	410	250	450
Ti I	560	-	320	-	380	500	560	360	280	420
Ge I	400	-	310	-	240	360	430	290	290	330
Tfe I	450	-	350	-	290	410	450	270	260	340
Bfe I	320	-	-	-	210	340	-	270	200	260
Tr I	210	-	-	-	130	160	-	120	100	110
Leg I TL	2590	-	-	-	1680	2390	-	1720	1380	1910
Ta II	420	-	260	-	300	360	390	310	240	320
Ti II	410	-	270	-	280	420	420	300	190	330
Ge II	220	-	230	-	210	260	220	220	180	260
Tfe II	230	-	150	-	190	290	-	200	170	250
Bfe II	210	-	150	-	160	230	-	210	-	190
Tr II	160	-	110	-	140	170	170	120	-	120
Leg II TL	1650	-	1170	-	1280	1730	-	1360	-	1470
Ta III	360	330	210	-	260	340	370	320	270	320
Ti III	-	350	200	-	300	470	470	330	230	410
Ge III	-	-	190	-	220	280	250	220	190	270
Tfe III	-	230	200	-	200	310	-	210	170	270
Bfe III	-	-	150	-	160	240	-	220	150	250
Tr III	-	-	-	-	110	220	-	140	-	130
Leg III TL	-	-	-	-	1250	1860	-	1440	-	1650
Ta IV	-	390	320	-	220	370	400	350	300	340
Ti IV	-	470	-	-	290	650	670	430	310	470
Ge IV	250	230	-	-	250	240	280	260	200	270
Tfe IV	310	250	-	-	220	280	290	260	-	260
Bfe IV	250	-	-	-	220	220	240	220	-	210
Tr IV	180	-	-	-	140	180	200	170	-	170
Leg IV TL	-	-	-	-	1340	1940	2080	1690	-	1720
Ti IV/Ta IV	-	1.21	-	-	1.32	1.76	1.68	1.23	1.03	1.38

TABLE 4. Measurements (μm) for new specimens of Acarohystricidae **fam. nov.**, in the collections of the Nanjing Institute of Geology and Palaeontology (NGIP206790–206797). Abbreviations as follows: IL: idiosoma length; IW: idiosoma width; PaL: palp length (exposed part); Ta: tarsus length; Ti: tibia length; Ge: genu length; Tfe: telofemur length; Bfe: basifemur length; Tr: trochanter length; TL: total length.

No.	206790	206791	206792	206793	206794	206795-1	206795-2	206795-3	206796	206797
Species	<i>P. makolae</i>	<i>P. makolae</i>	<i>P. makolae</i>	<i>P. minaevi</i>	<i>A. magnifica</i>	<i>P. makolae</i>	<i>P. makolae</i>	<i>P. makolae</i>	<i>P. minaevi</i>	<i>P. minaevi</i>
Sex	F	F	F	-	F	F	F	M	F	M
IL	860	1170	1730	-	1420	1130	1110	-	1540	1570
IW	580	720	-	-	820	-	690	630	-	1040
PaL	400	430	-	-	700	520	520	490	520	660
Ta I	270	380	410	330	450	340	350	340	410	400
Ti I	210	330	380	320	360	300	260	240	340	350
Ge I	170	240	330	-	270	270	220	250	300	310
Tfe I	170	230	-	-	-	210	250	260	290	310
Bfe I	160	190	-	-	-	210	200	200	230	240
Tr I	110	110	-	-	-	110	110	110	110	120
Leg I TL	1090	1480	-	-	-	1440	1390	1400	1680	1730
Ta II	240	230	290	220	-	260	240	250	290	310
Ti II	150	190	260	210	-	190	200	220	240	290
Ge II	130	160	190	-	-	150	160	180	180	220
Tfe II	170	160	-	-	-	150	150	170	180	200
Bfe II	130	150	-	-	-	-	140	160	200	190
Tr II	120	100	-	-	-	-	120	120	120	130
Leg II TL	940	990	-	-	-	-	1010	1100	1210	1340
Ta III	190	220	260	-	250	240	250	230	280	290
Ti III	170	210	270	230	290	200	220	220	230	260
Ge III	130	160	-	180	-	180	180	160	190	210
Tfe III	120	160	-	-	-	-	180	160	170	200
Bfe III	140	150	-	-	-	-	150	140	160	190
Tr III	120	120	-	-	-	-	120	120	130	160
Leg III TL	870	1020	-	-	-	-	1100	1030	1160	1310
Ta IV	210	260	-	300	290	280	250	280	350	380
Ti IV	220	290	-	330	330	270	260	300	340	-
Ge IV	150	180	-	220	-	190	190	180	220	260
Tfe IV	140	200	-	-	-	-	170	160	200	260
Bfe IV	160	160	-	-	-	-	160	140	210	220
Tr IV	120	130	-	-	-	-	120	110	160	160
Leg IV TL	1000	1220	-	-	-	-	1150	1170	1480	-
Ti IV/Ta IV	1.05	1.12	-	1.10	1.14	0.96	1.04	1.07	0.97	-

TABLE 5. Measurements (μm) for new specimens of Acarohystricidae **fam. nov.**, in the collections of the Nanjing Institute of Geology and Palaeontology (NGIP206798–206799, 206802–206808). Abbreviations as follows: IL: idiosoma length; IW: idiosoma width; PaL: palp length (exposed part); Ta: tarsus length; Ti: tibia length; Ge: genu length; Tfe: telofemur length; Bfe: basifemur length; Tr: trochanter length; TL: total length.

No.	206798	206799-1	206799-2	206799-3	206802	206803	206804	206805	206806	206807	206808
Species	<i>P. minaevi</i>	<i>P. makolae</i>	<i>P. makolae</i>	<i>P. makolae</i>	<i>P. minaevi</i>	<i>P. minaevi</i>	<i>P. makolae</i>	<i>P. makolae</i>	<i>P. makolae</i>	<i>P. makolae</i>	<i>P. minaevi</i>
Sex	F	F	M	F	M	-	-	M	M	M	F
IL	1030	1400	1460	1450	1860	-	-	1100	2170	940	1260
IW	620	-	920	-	1080	-	-	530	1230	540	800
PaL	380	600	510	560	910	-	-	390	860	500	500
Ta I	230	470	470	460	430	-	-	260	670	310	-
Ti I	240	350	360	350	380	-	-	200	540	220	-
Ge I	210	320	290	280	330	-	-	170	410	200	-
Tfe I	200	300	320	320	290	-	-	150	460	210	-
Bfe I	150	230	230	200	270	-	-	140	340	140	-
Tr I	100	120	140	140	120	-	-	-	200	100	-
Leg I TL	1130	1790	1810	1750	1820	-	-	-	2620	1180	-
Ta II	190	330	320	-	290	-	-	170	370	220	240
Ti II	200	280	300	-	240	-	-	160	420	180	230
Ge II	-	230	210	-	180	-	-	100	280	160	160
Tfe II	120	210	200	-	160	-	-	-	290	140	120
Bfe II	110	190	190	-	140	-	-	-	230	110	100
Tr II	100	130	130	-	120	-	-	-	190	100	90
Leg II TL	-	1370	1350	-	1130	-	-	-	1780	910	940
Ta III	190	330	310	320	290	-	-	-	350	220	290
Ti III	150	360	310	340	260	-	-	-	470	200	240
Ge III	130	240	240	230	200	-	-	-	310	130	180
Tfe III	140	230	240	220	200	-	-	-	330	120	180
Bfe III	120	200	190	-	150	-	-	-	240	110	140
Tr III	100	160	150	-	120	-	-	-	190	70	120
Leg III TL	830	1520	1440	-	1220	-	-	-	1890	850	1150
Ta IV	260	320	350	370	340	-	-	-	400	250	280
Ti IV	230	400	420	460	380	-	-	-	710	270	310
Ge IV	160	240	240	250	270	-	-	-	340	180	210
Tfe IV	170	270	260	290	230	-	-	-	340	160	210
Bfe IV	150	-	220	-	180	-	-	-	240	130	160
Tr IV	120	-	200	-	150	-	-	-	200	120	120
Leg IV TL	1090	-	1690	-	1550	-	-	-	2230	1110	1290
Ti IV/Ta IV	0.88	1.25	1.20	1.24	1.12	-	-	-	1.78	1.08	1.11

TABLE 6. Measurements (μm) for new specimens of Acarohystricidae **fam. nov.**, in the collections of the Nanjing Institute of Geology and Palaeontology (NGIP206809–206812, 206814–206819). Abbreviations as follows: IL: idiosoma length; IW: idiosoma width; PaL: palp length (exposed part); Ta: tarsus length; Ti: tibia length; Ge: genu length; Tfe: telofemur length; Bfe: basifemur length; Tr: trochanter length; TL: total length.

No.	206809	206810	206811	206812	206814	206815	206816	206817	206818	206819
Species	<i>P. makolae</i>	<i>P. minaevi</i>								
Sex	F	-	M	F	-	F	M	M	M	F
IL	1200	2210	1400	1030	1610	1420	-	1430	1490	1510
IW	-	1330	760	640	-	-	860	-	900	880
PaL	-	800	630	500	-	-	740	-	500	-
Ta I	-	630	510	310	480	370	460	-	510	460
Ti I	-	490	450	230	390	370	400	-	420	370
Ge I	-	400	340	180	320	320	270	-	300	340
Tfe I	-	420	390	-	330	290	370	-	300	350
Bfe I	-	300	230	150	-	230	-	-	230	-
Tr I	-	230	140	90	-	-	-	-	-	-
Leg I TL	-	2470	2060	-	-	-	-	-	-	-
Ta II	-	-	340	240	-	310	340	-	270	270
Ti II	-	-	340	210	-	280	340	-	310	250
Ge II	-	-	250	140	-	250	200	-	210	250
Tfe II	-	-	250	150	-	210	240	-	170	160
Bfe II	-	-	130	-	-	170	200	-	130	-
Tr II	-	-	100	90	-	100	150	-	100	-
Leg II TL	-	-	1410	-	-	1320	1470	-	1190	-
Ta III	-	380	320	-	-	320	270	-	290	290
Ti III	-	460	390	220	-	320	260	-	310	250
Ge III	-	300	260	150	-	200	190	-	210	200
Tfe III	-	310	250	150	-	190	170	-	210	210
Bfe III	-	230	150	-	-	120	150	-	130	-
Tr III	-	-	150	-	-	-	120	-	110	-
Leg III TL	-	-	1520	-	-	-	1160	-	1260	-
Ta IV	-	390	380	240	-	310	330	-	300	280
Ti IV	-	670	490	270	-	400	420	-	380	300
Ge IV	-	380	290	180	-	240	250	-	230	230
Tfe IV	-	400	230	-	-	200	250	-	-	220
Bfe IV	-	-	200	-	-	120	180	-	-	130
Tr IV	-	-	170	-	-	110	130	-	-	-
Leg IV TL	-	-	1760	-	-	1380	1560	-	--	-
Ti IV/Ta IV	-	1.72	1.29	1.13	-	1.29	1.27	-	1.27	1.07

TABLE 7. Measurements (μm) for new specimens of Acarohystricidae **fam. nov.**, in the collections of the Nanjing Institute of Geology and Palaeontology (NGIP206820–206829). Abbreviations as follows: IL: idiosoma length; IW: idiosoma width; PaL: palp length (exposed part); Ta: tarsus length; Ti: tibia length; Ge: genu length; Tfe: telofemur length; Bfe: basifemur length; Tr: trochanter length; TL: total length.

No.	206820	206821	206822	206823	206824	206825	206826	206827	206828	206829
Species	<i>P. makolae</i>	<i>P. minaevi</i>	<i>P. makolae</i>	<i>P. minaevi</i>	<i>P. minaevi</i>	<i>P. makolae</i>	<i>P. obtuse</i>	<i>P. minaevi</i>	<i>P. makolae</i>	<i>P. makolae</i>
Sex	F	F	M	F	M	-	-	F	-	-
IL	1680	1850	1500	1560	1540	1750	-	-	1130	-
IW	1070	960	850	960	740	1090	-	-	600	-
PaL	610	-	-	-	-	-	-	520	480	-
Ta I	510	-	480	-	370	-	-	310	360	-
Ti I	370	-	380	-	250	-	-	260	-	-
Ge I	340	-	290	-	210	-	-	240	-	-
Tfe I	300	-	370	-	250	-	-	200	-	-
Bfe I	-	-	-	-	150	-	-	130	-	-
Tr I	-	-	-	-	110	-	-	100	-	-
Leg I TL	-	-	-	-	1340	-	-	1240	-	-
Ta II	350	-	270	-	220	-	-	230	320	-
Ti II	330	-	230	-	180	-	-	170	-	-
Ge II	250	-	230	-	150	-	-	130	-	-
Tfe II	210	-	-	-	140	-	-	160	-	-
Bfe II	180	-	-	-	-	-	-	-	-	-
Tr II	130	-	-	-	-	-	-	-	-	-
Leg II TL	1450	-	-	-	-	-	-	-	-	-
Ta III	360	-	300	-	180	-	-	-	270	-
Ti III	390	-	310	-	180	-	-	-	280	-
Ge III	290	-	240	-	190	-	-	-	-	-
Tfe III	250	-	220	-	160	-	-	-	-	-
Bfe III	170	-	120	-	100	-	-	-	-	-
Tr III	120	-	120	-	-	-	-	-	-	-
Leg III TL	1580	-	1310	-	-	-	-	-	-	-
Ta IV	370	330	360	-	300	-	-	-	-	-
Ti IV	510	350	470	-	260	-	-	-	-	-
Ge IV	310	260	270	-	190	-	-	-	-	-
Tfe IV	310	-	280	-	160	-	-	-	-	-
Bfe IV	200	-	-	-	120	-	-	-	-	-
Tr IV	120	-	-	-	130	-	-	-	-	-
Leg IV TL	1820	940	1380	-	1160	-	-	-	-	-
Ti IV/Ta IV	1.38	1.06	1.31	-	0.87	-	-	-	-	-

TABLE 8. Measurements (μm) for new specimens of Acarohystricidae **fam. nov.**, in the collections of the Nanjing Institute of Geology and Palaeontology (NGIP206820–206829). Abbreviations as follows: IL: idiosoma length; IW: idiosoma width; PaL: palp length (exposed part); Ta: tarsus length; Ti: tibia length; Ge: genu length; Tfe: telofemur length; Bfe: basifemur length; Tr: trochanter length; TL: total length.

No.	206830-1	206830-2	206831	206832	206833	206834	206835-1	206835-2	206835-3
Species	<i>P. makolae</i>	<i>P. makolae</i>	<i>P. makolae</i>	<i>P. minaevi</i>	<i>P. makolae</i>				
Sex	-	-	M	F	F	F	M	-	-
IL	-	-	1210	1270	1450	1730	1380	890	730
IW	-	-	-	760	820	-	820	620	400
PaL	-	-	530	640	420	560	590	370	370
Ta I	-	-	-	360	490	430	480	250	210
Ti I	-	-	280	360	420	370	360	200	150
Ge I	-	-	-	220	330	300	290	210	150
Tfe I	-	-	-	-	330	280	280	180	140
Bfe I	-	-	-	-	220	-	180	140	-
Tr I	-	-	-	-	140	-	-	110	-
Leg I TL	-	-	-	-	1930	-	-	1090	-
Ta II	-	-	390	280	350	300	430	260	160
Ti II	-	-	290	270	330	310	360	190	150
Ge II	-	-	210	170	250	220	250	160	100
Tfe II	-	-	300	-	250	230	220	130	-
Bfe II	-	-	-	-	180	150	180	90	-
Tr II	-	-	-	-	140	-	120	90	-
Leg II TL	-	-	-	-	1500	-	1560	920	-
Ta III	-	-	270	270	340	270	370	230	160
Ti III	-	-	260	270	340	320	360	190	160
Ge III	-	-	230	210	230	210	240	130	100
Tfe III	-	-	-	190	240	210	220	110	100
Bfe III	-	-	-	140	200	-	160	110	-
Tr III	-	-	-	130	140	-	150	100	-
Leg III TL	-	-	-	1210	1490	-	1500	870	-
Ta IV	-	-	-	270	360	340	360	280	140
Ti IV	-	-	-	300	460	430	460	260	150
Ge IV	-	-	-	200	280	270	290	200	140
Tfe IV	-	-	-	220	240	-	250	170	130
Bfe IV	-	-	-	160	220	-	220	150	90
Tr IV	-	-	-	-	-	-	160	100	80
Leg IV TL	-	-	-	-	-	-	1740	1160	730
Ti IV/Ta IV	-	-	-	1.11	1.28	1.26	1.28	0.93	1.07