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***Hirsutisoma grimaldii* sp. nov., a ca. 99-million-year-old ricinuleid (Primoricinulei, Hirsutisomidae) from Cretaceous Burmese amber with a corticolous, scansorial lifestyle**

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Abstract

Ricinulei Thorell, 1876 is an order of Arachnida currently represented in the New and Old Worlds by 103 living species. The order is also represented in the fossil record from the Carboniferous (ca. 305–319 Ma) and the Cretaceous (ca. 99 Ma) periods. In the present contribution, *Hirsutisoma grimaldii* sp. nov., a new extinct species of the suborder Primoricinulei Wunderlich, 2015, is described from a specimen preserved in Cretaceous Burmese amber. The specimen is a well-preserved adult male in which several taxonomically informative structures are visible, allowing the new species to be differentiated from *Hirsutisoma bruckschi* Wunderlich, 2017, the only other congener for which a male is known. This description raises the number of Cretaceous Ricinulei species to six. A comparative table documents morphological differences among the various species of this lineage. Hypotheses concerning the paleoecology and functional morphology of this species and, by extrapolation, other primoricinuleids, are presented. The evidence suggests that Primoricinulei were corticolous, scansorial predators.

Keywords: Arachnida, Ricinulei, Primoricinulei, fossil, Burmese amber, corticolous, scansorial

Introduction

Ricinulei Thorell, 1876, or “hooded tick-spiders,” is an oligodiverse order of Arachnida comprising 103 described living species (Benavides *et al.*, 2021; Botero-Trujillo *et al.*, 2021a, b; Valdez-Mondragón & Cortez-Roldán, 2021). Three extant genera in one family, Ricinoididae Ewing, 1929, are currently recognized. The primarily

South American genus *Cryptocellus* Westwood, 1874, comprising 46 species, is the most speciose, followed by the primarily North and Central American genus *Pseudocellus* Platnick, 1980, with 41 species, and the tropical African genus *Ricinoides* Ewing, 1929, with 16 species.

Ricinulei is an ancient lineage that is well represented in the fossil record, considering the overall rarity of the order. Fossilized specimens have been known for so long that the first Ricinulei to be described was a fossil, *Curculioides ansticii* Buckland, 1837, initially misidentified as a beetle (Selden, 1992).

The oldest fossil ricinuleids date to the Carboniferous (ca. 305–319 Ma) of the U.S.A., Germany, and the U.K. This group of extinct taxa was studied in detail by Selden (1992), who established the suborders Neoricinulei Selden, 1992, for the extant family Ricinoididae, and Palaeoricinulei Selden, 1992, in which the extinct families Curculioididae Cockerell, 1916 and Poliocheridae Scudder, 1884 were accommodated. Curculioididae comprises the genera *Curculioides* Buckland, 1837 and *Amaryxis* Selden, 1992, with eight and three species respectively, whereas Poliocheridae comprises the genera *Poliochera* Scudder, 1884, with three species, and the monotypic *Terpsicroton* Selden, 1992. Since the publication of Selden (1992), only one additional species has been added to the Carboniferous ricinuleid fauna, the recently discovered *Curculioides bohemoni* Whalen & Selden, 2021 from the Pennsylvanian Energy Shale of Illinois, U.S.A. (Whalen & Selden, 2021).

Wunderlich (2012) documented the order from Cretaceous (ca. 99 Ma) Burmese amber deposits,

describing a well-preserved specimen embedded in a piece of amber, as *?Poliochera cretacea* Wunderlich, 2012. Wunderlich (2012) also proposed some rearrangements to the higher classification. Poliocheridae was elevated to the rank of superfamily, as Poliocheroidea, comprising Poliocheridae and Curculioididae. Additionally, the two suborders proposed by Selden (1992), Palaeoricinulei and Neoricinulei, were regarded as superfamilies, and simultaneously considered junior synonyms of Poliocheroidea and Ricinoidoidea, respectively. Shortly thereafter, Wunderlich (2015) described another Cretaceous ricinuleid from Myanmar (Burma), *Primoricinuleus pugio* Wunderlich, 2015, based on a remarkable specimen with unique morphology, assigned to a unique family, Primoricinuleidae Wunderlich, 2015, and suborder, Primoricinulei Wunderlich, 2015. Wunderlich (2015) also proposed the suborder Posteriorricinulei Wunderlich, 2015 to contain all other ricinuleids, extinct and extant (Poliocheroidea and Ricinoidoidea). More recently, Wunderlich (2017) added three species to Primoricinulei, also from Myanmar, placing them in the genus *Hirsutisoma* Wunderlich, 2017 and the monogeneric family Hirsutisomidae Wunderlich, 2017; *Hirsutisoma acutiformis* Wunderlich, 2017; *Hirsutisoma bruckschi* Wunderlich, 2017; and *Hirsutisoma dentata* Wunderlich, 2017. Wunderlich (2017) also described Monooculricinuleidae Wunderlich, 2017, containing the genus *Monooculricinuleus* Wunderlich, 2017, with two species. Monooculricinuleidae have since been determined to be opilionids (Selden & Ren, 2017; Ross, 2019).

In the present contribution, *Hirsutisoma grimaldii*, sp. nov., a new extinct species of the suborder Primoricinulei, is described from a specimen preserved in Cretaceous Burmese amber. The specimen is a well-preserved adult male in which several taxonomically informative structures, including several of the modified leg III, are visible, allowing the new species to be diagnosed from *H. bruckschi*, the only other congener for which a male is known. This description raises the number of Cretaceous Ricinulei species to six. A comparative table documents morphological differences among the various species of this lineage. Hypotheses concerning the paleoecology and functional morphology of this species and, by extrapolation, other primoricinuleids, are presented together with the taxonomic description. The evidence suggests that Primoricinulei were corticolous, scansorial predators.

Material and methods

Material is deposited in the American Museum of Natural

History (AMNH), New York, and the private collection of Jörg Wunderlich (CJW), Hirschberg, Germany.

The classification of fossil and modern ricinuleids is controversial (e.g., Selden, 1992; Harvey, 2003; Prendini, 2011; Wunderlich, 2012, 2015, 2017; Dunlop *et al.*, 2020; Whalen & Selden, 2021). The suprageneric classification applied in the present contribution follows Wunderlich (2017), adopted by Dunlop *et al.* (2020).

The terminology of somatic morphology, including leg segments, largely follows publications on extant ricinuleids by the first author (e.g., Botero-Trujillo & Flórez, 2017; Botero-Trujillo *et al.*, 2021a, b). Various novel terms are introduced for structures not previously identified or formally named, including the comb of lamellate projections of the pedipalp, and the lanceolate structure and metatarsal distal expansion of leg III. Similarly, some structures of the fossil species are described by new terms (differing from taxonomic descriptions of extant ricinuleids). This was done for structures that manifest in unique or clearly different configurations (e.g., the sternum, ocelli, and pedipalp tarsus), or when it was impossible to confidently homologize structures with those of extant species (e.g., the horn-shaped and whip-shaped parts of the copulatory apparatus).

Some aspects of the morphology of the fossil species were observed or confirmed with the aid of X-ray microtomography (micro-CT). Micro-CT imaging of the fossil was conducted with the aim of obtaining a quality three-dimensional model of the fossil. Although an adequate model could not be obtained, X-ray imaging proved useful to validate observations conducted under stereomicroscopy and to investigate structures that were obscured (e.g., chelicerae). The specimen was scanned at the AMNH Microscopy and Imaging Facility using a GE v|tome|x s240 with a 180kV X-ray source, with the following scanning parameters: voltage, 90 kV; current, 200 μ A; number of projection images, 2600; image acquisition timing, 750 ms; image averages, 5; diamond target used. Volume reconstruction of raw projections was performed using dataview 2.3.2 and visualized/segmented using 3D Slicer (Fedorov *et al.*, 2012).

Forty-five linear measurements were recorded using a calibrated ocular micrometer, fitted to a Nikon SMZ 1500 stereomicroscope, by smearing the amber piece with a drop of glycerin and covering it with a microscope glass slide coverslip to flatten the image, thus correcting the effect of the surface curvature. Measurements mostly follow Botero-Trujillo *et al.* (2021b).

Digital photomicrographs were taken with a Nikon DS-Ri2 camera fitted to a Nikon SMZ 18 stereomicroscope with a SHR Plan Apo 1 $\times$ Objective, using NIS-Elements Imaging Software, ver. 4.60, at the AMNH Microscopy and Imaging Facility. Glycerin and a glass slide coverslip were used for photography, as described above. Line

drawings were prepared using a camera lucida mounted on the Nikon SMZ 1500 stereomicroscope.

The following specimen, representing the only other species of *Hirsutisoma* known from a male, was examined during the present investigation:

Hirsutisoma bruckschi Wunderlich, 2017. MYANMAR, Holotype ♂ and separate piece of amber from Mid-Cretaceous Burmese amber forest (F2830/BU/CJW; currently in CJW).

Systematic palaeontology

Order Ricinulei Thorell, 1876

†Suborder Primoricinulei Wunderlich, 2015

†Family Hirsutisomidae Wunderlich, 2017

Hirsutisomidae Wunderlich, 2017: 53–55, type genus: *Hirsutisoma* Wunderlich, 2017; Selden & Ren, 2017: 329; Valdez-Mondragón & Francke, 2017: 12; Ross, 2019: 43; Valdez-Mondragón *et al.*, 2018: 114; Dunlop *et al.*, 2020: 125; Valdez-Mondragón *et al.*, 2020: 2; Valdez-Mondragón & Cortez-Roldán, 2021: 2; Valdez-Mondragón & Juárez-Sánchez, 2021: 329.

†*Hirsutisoma* Wunderlich, 2017

Hirsutisoma Wunderlich, 2017: 49, 50, 53–55, 62, 64, 65, type species by original designation: *Hirsutisoma bruckschi* Wunderlich, 2017; Selden & Ren, 2017: 334; Valdez-Mondragón & Francke, 2017: 12; Dunlop *et al.*, 2020: 125.

Included species. *Hirsutisoma acutiformis* Wunderlich, 2017; *Hirsutisoma bruckschi* Wunderlich, 2017; *Hirsutisoma dentata* Wunderlich, 2017; *Hirsutisoma grimaldii* sp. nov.

Locality and horizon. *Hirsutisoma* is exclusively represented in the fossil record of the Mid-Cretaceous (*ca.* 99 Ma) Burmese amber deposits.

†*Hirsutisoma grimaldii* sp. nov.

(Figs 1–4; Tables 1, 2)

Type material. Holotype ♂ (AMNH_IZC 00357137), Myanmar: embedded in an oval piece (18 × 12 × 5 mm) of Cretaceous Burmese amber (*ca.* 99 Ma).

Etymology. The specific epithet is a patronym honoring AMNH Curator, Dr David A. Grimaldi, in recognition of his work on extinct and extant arthropods. Dr Grimaldi's assistance was instrumental in making this fossil available for study.

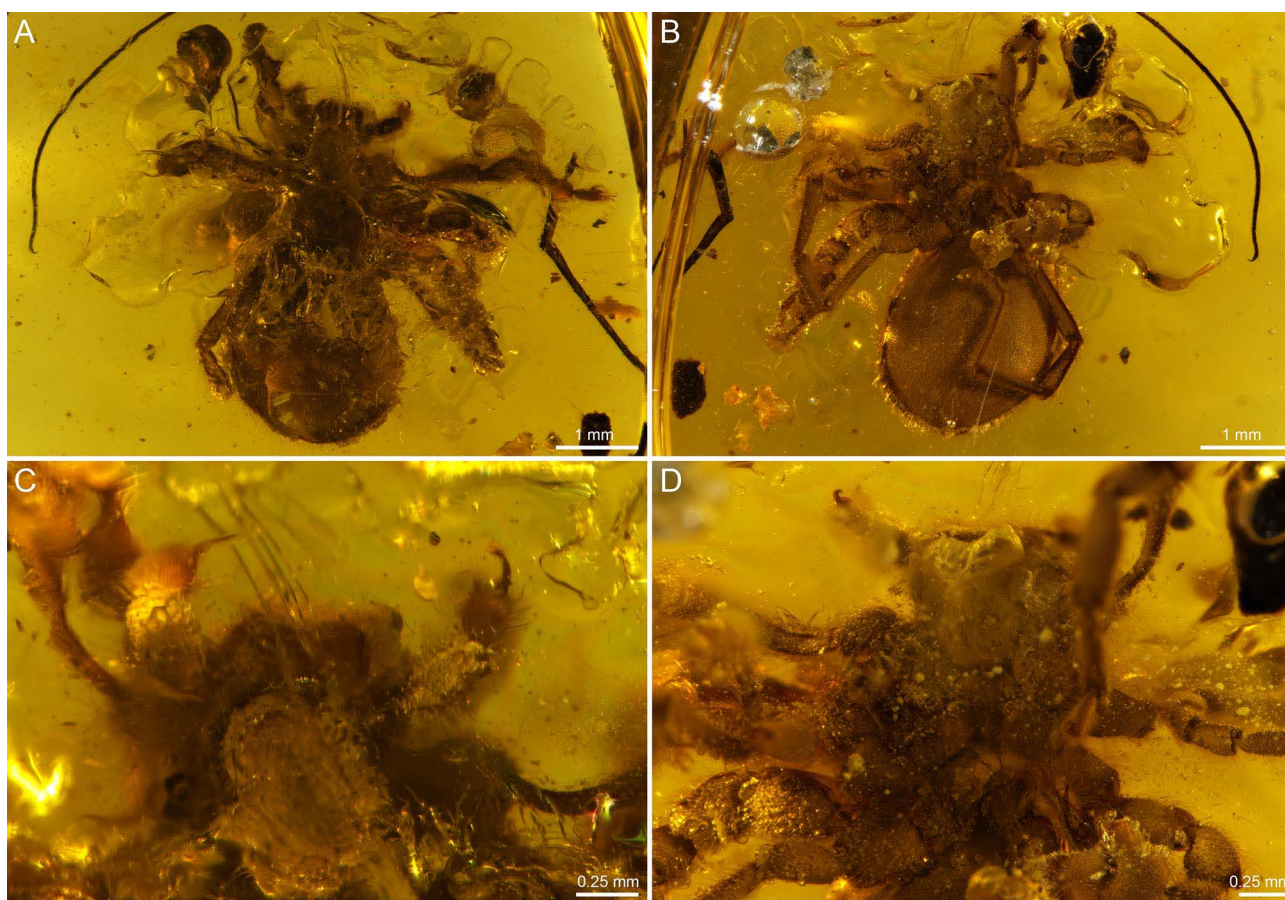


FIGURE 1. *Hirsutisoma grimaldii* sp. nov., holotype ♂ (AMNH_IZC 00357137). **A** and **B**, Habitus, dorsal (**A**) and ventral (**B**) aspects. **C**, Prosoma, anterodorsal aspect. **D**, Coxosternal region.

Diagnosis. *Hirsutisoma grimaldii* may be recognized by the presence of a distinct comb of 8–10 lamellate projections basally on the proventral surface of the pedipalp tarsus (Fig. 3D–F), a structure absent in the type specimens of other congeners. It differs further from *H. bruckschi*, the only other *Hirsutisoma* species for which the adult male is known, in the morphology of the male leg III and copulatory apparatus: in the male of *H. grimaldii*, the prolateral surface of the metatarsus of leg III is sharply expanded distally, the first tarsomere of leg III bears a pronounced longitudinal ridge retrodorsally, and the horn-shaped part of the copulatory apparatus is relatively long, reaching well past the midline of the first tarsomere (Figs 2C, D, 4D). In the male of *H. bruckschi*, the prolateral surface of the metatarsus of leg III is not expanded distally, no ridge is present retrodorsally on the first tarsomere of leg III, and the horn-shaped part of the copulatory apparatus is shorter, reaching to the midline of the first tarsomere.

Description. Male. Based on holotype (AMNH_IZC 00357137).

Measurements. Total length, approximately 3.91 mm (Table 1).

Inclusion. Complete specimen. Ventral aspect completely visible (Fig. 1B), amber matrix without

significant imperfections; pedipalp coxae partially obscured by debris (Fig. 1D). Dorsal aspect of specimen, especially carapace, partly obscured by bubbles (Fig. 1A, C).

Colouration and hardness. Cuticle pale brown, uniformly coloured. Pedipalp tarsus and copulatory apparatus reddish. Colour of specimen and apparent compression of some leg segments (by pressure exerted by amber), suggest cuticle may be not heavily sclerotized.

Setation. Coxosternal region, opisthosoma dorsal surface (posterior half) and, especially, ventral surface covered with short to medium-sized, rather spinose macrosetae. Opisthosoma dorsal surface of anterior one- or two-thirds densely hirsute, long macrosetae (some about half opisthosomal length) obscuring anterior dorsal sclerites (Figs 2A, 3C); unclear whether macrosetae originate along anterodorsal external margin of opisthosoma or from surface of anterior tergites; external border of opisthosoma provisioned along entire length with dense array of medium-sized macrosetae (apparently originating from ventral sclerites). Cucullus and legs covered with bristle-like macrosetae of variable length (Figs 1, 2); leg III, dorsal surface of first tarsomere with brush-like array of brownish macrosetae (apparently clavate) distally (Fig. 2C, D). Pedipalps, setation similar to

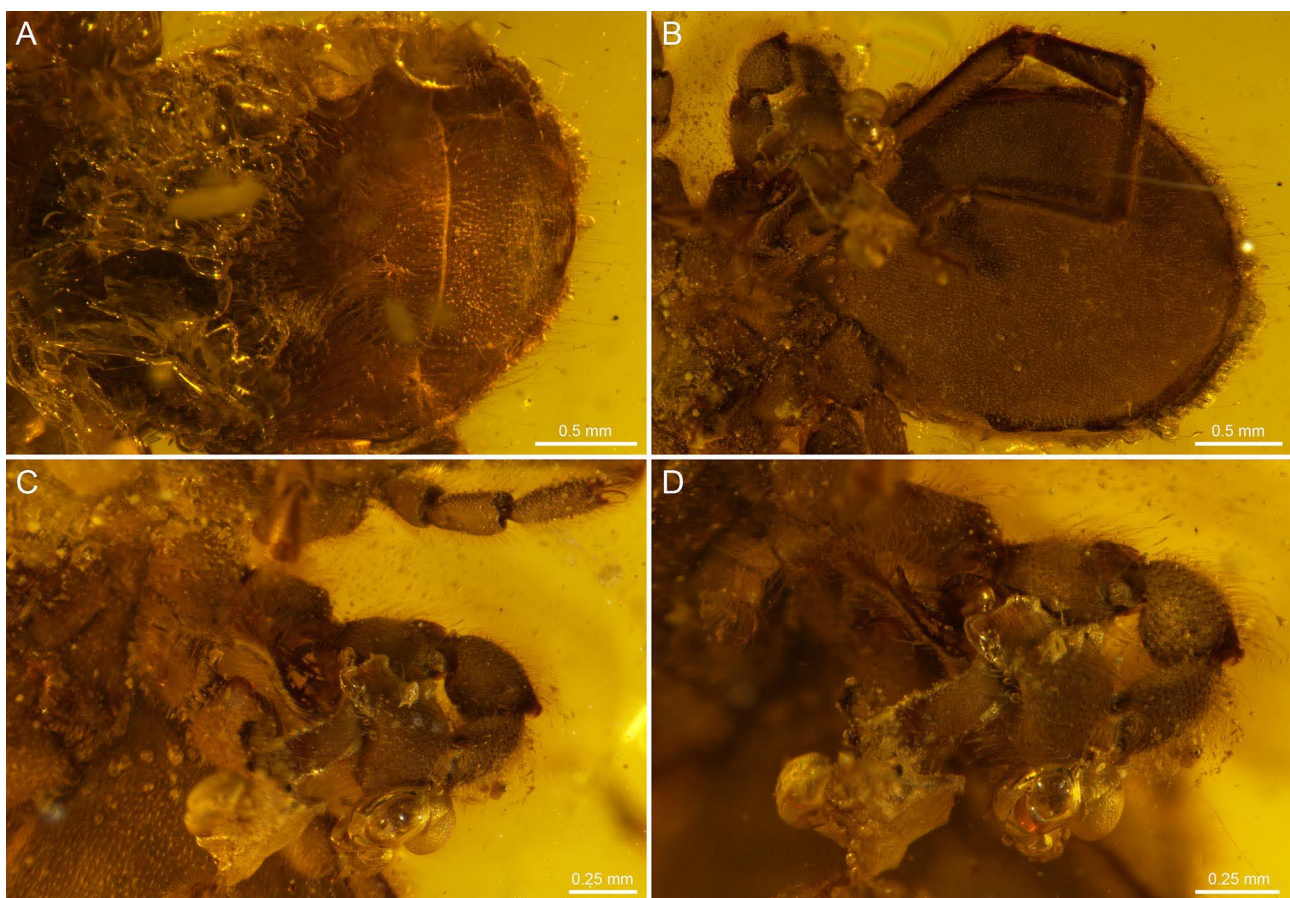


FIGURE 2. *Hirsutisoma grimaldii* sp. nov., holotype ♂ (AMNH_IZC 00357137). A and B, Opisthosoma, dorsal (A) and ventral (B) aspects. C and D, Sinistral leg III, prolateral aspect (C) and closeup (D).

TABLE 1. Measurements (mm) for holotype of *Hirsutisoma grimaldii* **sp. nov.** deposited in the American Museum of Natural History, New York. Abbreviations: L, length; W, width; H, height. Excludes measurements that could not be reliably obtained due to position or preservation of structure. ¹ excludes pygidium or cucullus; ² maximum width; ³ maximum height; ⁴ midline.

			Holotype ♂
Total Body	L ¹		~3.91
Cucullus		W ²	0.58
Carapace		L	~1.25
		W ²	~0.90
Opisthosoma		Total L ¹	2.67
		W ²	1.94
Median Plate	XII	W ²	1.20
Median Plate	XIII	L	0.62
		W ²	1.16
Sternum		L	0.45
		W ²	0.37
Pedipalp		Femur L	~0.26
		Femur H ³	~0.19
		Tibia L	~0.22
		Tarsus (Movable Finger) L	0.15
Leg I		Coxa L	0.41
		Trochanter L	0.32
		Femur L	0.86
		Femur W ⁴	0.09
		Patella L	0.37
		Tibia L	0.54
		Metatarsus L	0.64
		Tarsus L	0.25
Leg II		Coxa L	0.43
		Trochanter L	0.37
		Metatarsus L	0.97
		Tarsus L	~1.25
Leg III		Coxa L	0.43
		Trochanter L	0.32
		Femur L	0.41
		Femur H ⁴	~0.30
		Patella L	0.30
		Tibia L	0.22
		Metatarsus L	~0.43
		Tarsus L	~0.86
Leg IV		Coxa L	0.47
		Trochanter 1 L	0.43
		Trochanter 2 L	0.41
		Femur L	0.84
		Femur W ⁴	~0.15
		Femur H ⁴	0.15
		Patella L	0.69
		Tibia L	0.88
		Metatarsus L	0.69
		Tarsus L	~0.73

legs; tibia prolateral surface with distinct patch of dense, brownish macrosetae (Fig. 1C). Polygonal macrosetae absent.

Tegument surface macrosculpture. Tegument completely smooth, soma and appendages without single visible granule; cuticular pits absent.

Interlocking mechanism. Absent. Prosoma and opisthosoma not interlocked (Fig. 3A); coxae of legs IV unmodified, not hooked to opisthosoma ventrally; opisthosoma dorsal and ventral surfaces visibly oval (Fig. 2A, B), anterior margins not truncate; anterior part

of opisthosoma extending dorsally over posterior part of prosoma, slightly obscuring the latter; exposed pedicel presumably connecting both tagmata (Fig. 3A).

Carapace. Carapace pear-shaped, narrower anteriorly (reminiscent of typical spider carapace), approximately as long as or slightly longer than wide; three pairs of ocelli in two triads laterally (Fig. 3B); sulci, if any, not visible.

Cucullus. Cucullus trapezoidal, slightly wider than long (Figs 1C, 3B); lateral margins slightly diverging ventrally; ventrolateral margins rounded; ventral margin sublinear in ventral aspect, slightly bilobate in anterior

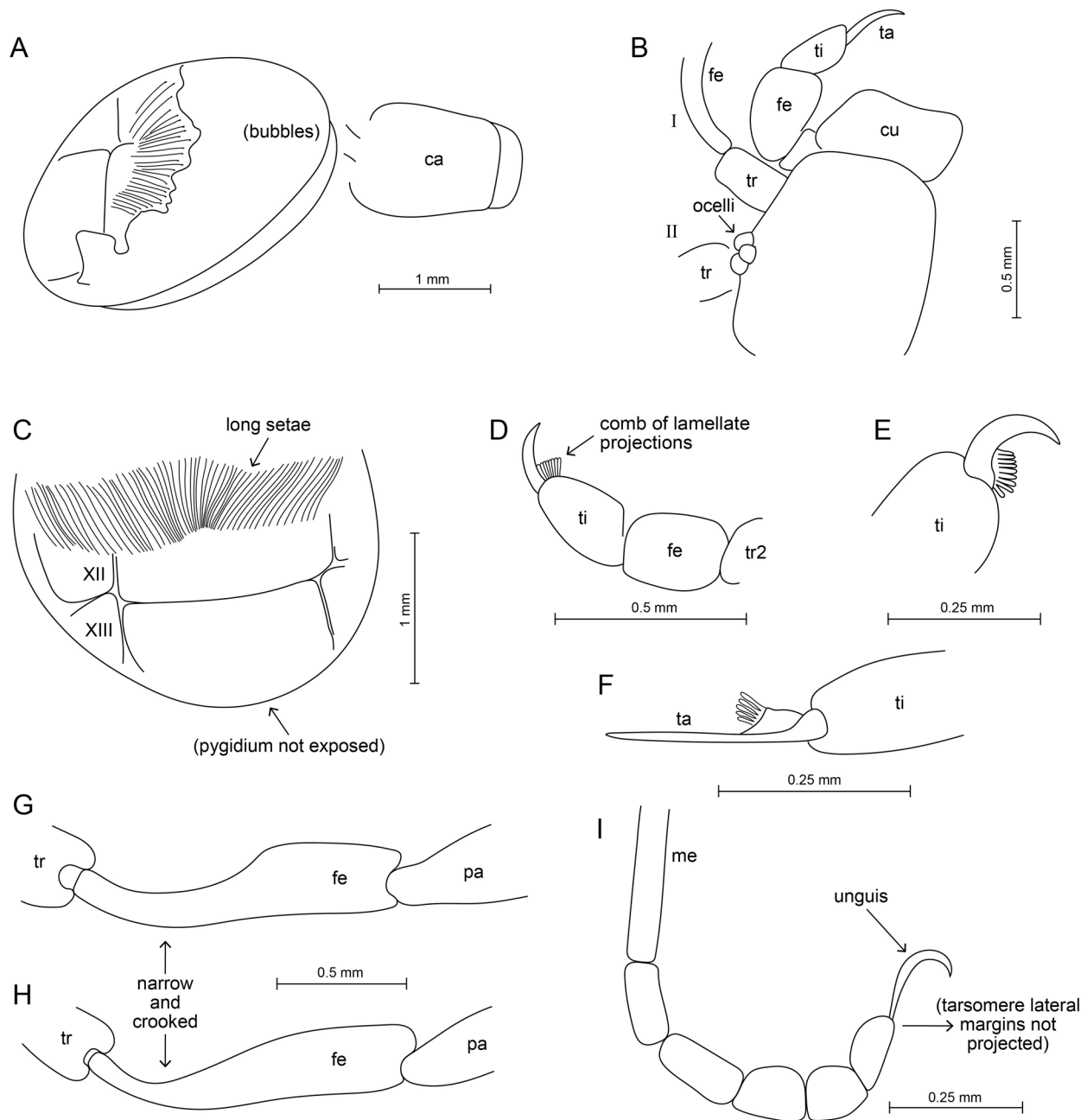


FIGURE 3. *Hirsutisoma grimaldii* sp. nov., holotype ♂ (AMNH_IZC 00357137). **A**, Schematic representation of soma, showing how both tagmata presumably connected by exposed pedicel. **B**, Prosoma, dorsal aspect, showing raptorial pedipalp, and legs I and II. **C**, Opisthosoma, posterior part, dorsal aspect (note median and lateral sclerites of tergites XII and XIII). **D** and **E**, Dextral pedipalp, retroventral aspect (**D**), and closeup of tarsus (movable finger) and lamellate projections (**E**). **F**, Sinistral pedipalp, distal segments, dorsal aspect. **G** and **H**, Dextral leg I femur, dorsal (**G**) and prodorsal (**H**) aspects. **I**, Sinistral leg IV tarsus, prolateral aspect. Abbreviations: ca, carapace; cu, cucullus; fe, femur; me, metatarsus; pa, patella; ta, tarsus (movable finger); ti, tibia; tr, trochanter; tr2, trochanter 2.

aspect; anterior surface slightly concave, almost flat (Fig. 1C), without remarkable structures or modifications; sulci, if any, not visible.

Coxosternal region. Sternum large, situated centrally on prosoma ventral surface (Figs 1D, 4C); drop-shaped, acute posteriorly; coxae of pedipalps and legs arranged concentrically around sternum; coxae of pedipalps

abutting one another, forming floor of preoral cavity; coxae of legs I–IV short, separate from coxae of adjacent legs (*i.e.*, lateral margins not fused along contact zone); sternum and coxae without remarkable structures or modifications.

Chelicerae. Chelicerae retracted into preoral cavity, not visible under light microscopy (micro-CT scanning

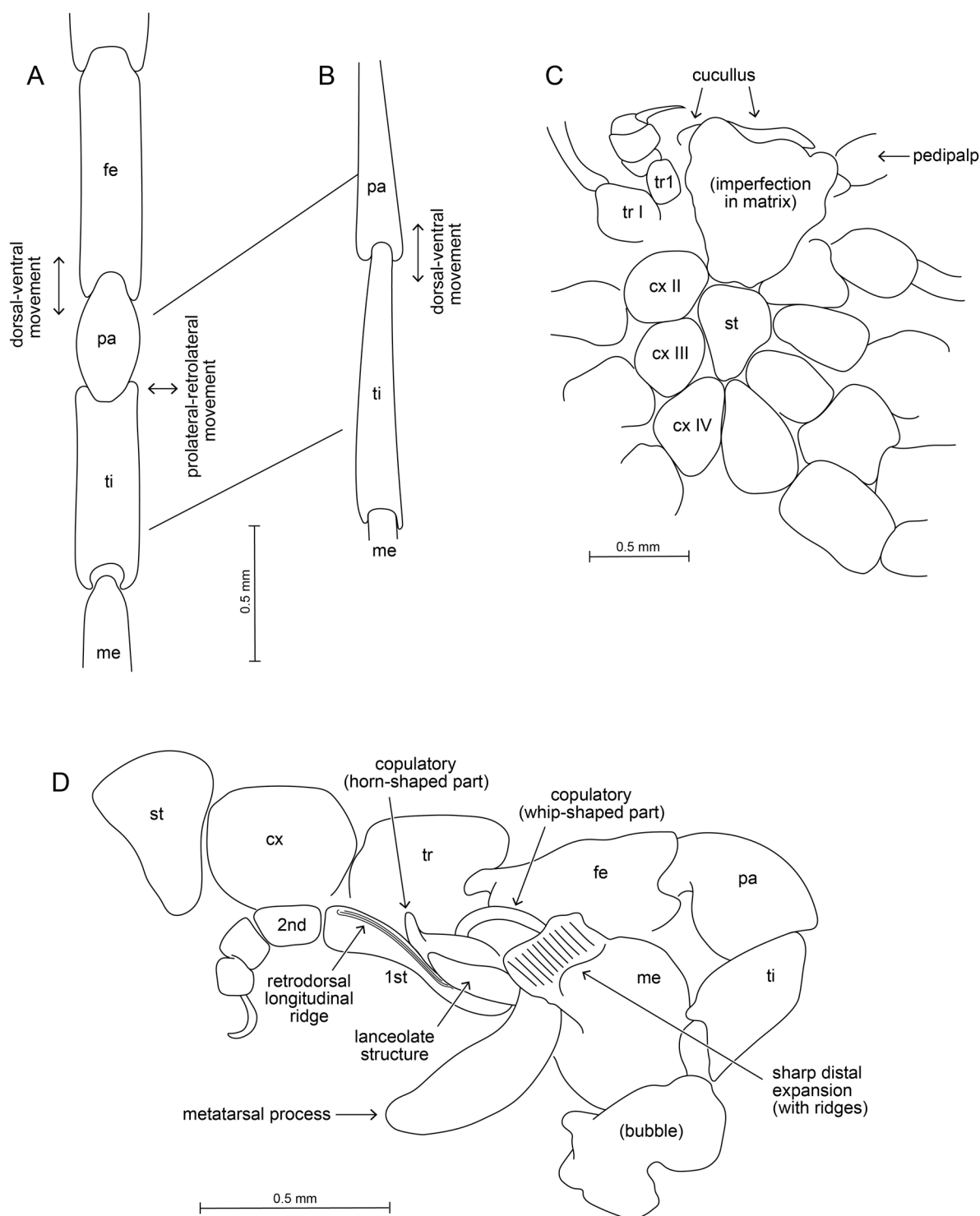


FIGURE 4. Legs and coxosternal region. **A** and **B**, Legs, dorsal aspect, of modern ricinuleid (Ricinoididae Ewing, 1929, schematic representation) (**A**) and *Hirsutisoma grimaldii* **sp. nov.**, holotype ♂ (AMNH_IZC 00357137), dextral leg IV (**B**). **C** and **D**, *Hirsutisoma grimaldii* **sp. nov.**, holotype ♂ (AMNH_IZC 00357137), coxosternal region (**C**) (legs identified by Roman numerals); sinistral leg III, prolateral aspect (**D**) (note modified first tarsomere and unmodified second tarsomere). Abbreviations: cx, coxa; fe, femur; me, metatarsus; pa, patella; st, sternum; ti, tibia; tr, trochanter; tr1, trochanter 1; first and second, proximal tarsomeres.

revealed that fixed and movable fingers are long and similar in length, reminiscent of cheliceral fingers of Solifugae; finger dentition, if any, obscured; manus seemingly unmodified.

Pedipalps. Pedipalps positioned anteriad (Figs 1C, 3B); consisting of coxa, trochanters 1 and 2, femur, tibia, and tarsus; femur slightly longer than deep or wide; tibia length at most twice its maximum diameter, without fixed

finger (not chelate); tarsus (movable finger) long and curved (Fig. 3D–F), about as long as tibia and at least half length of cucullo-carapacial commissure, laterally compressed, with sharp dorsal and ventral edges, basally with comb of 8–10 lamellate projections on proventral surface. Pedipalps without other remarkable structures or modifications.

Legs. Legs comprising seven segments (coxa, one trochanter, femur, patella, tibia, metatarsus, and tarsus), except leg IV with eight (*i.e.*, two trochanters). Plane of flexion of tibia similar to (aligned with) plane of flexion of patella (Fig. 4B), axis of flexion at articulation of tibia and patella slightly rotated or not rotated. Leg femora unmodified. Leg I femur very narrow proximally, longitudinal axis crooked (Figs 1C, D, 3B, G, H); tarsus without dorsomedian lobe. Leg II longest; tarsus comprising five tarsomeres, all longer than wide and similar in length (Fig. 2C); laterodistal margins of first to fourth tarsomeres not overlapping adjacent tarsomere; fifth tarsomere without dorsomedian lobe. Leg III femur, patella, tibia, and metatarsus short and subspherical (Figs 2C, D, 4D); metatarsus prolateral surface with sharp, flat, glabrous expansion distally (Fig. 4D); metatarsal process forming curved, concave flap situated apically on metatarsus, near to and opposing tarsus; tarsus comprising four tarsomeres; first tarsomere markedly elongate, about four times longer than other tarsomeres, sinuous in dorsal aspect, shaped to accommodate copulatory apparatus that originates from its base, with pronounced retrodorsal longitudinal ridge; tarsomeres 2–4 short (each about as long as deep), similar in length and unmodified. Leg IV without remarkable structures or modifications; tarsus comprising five tarsomeres (Fig. 3I). Legs III and IV, terminal tarsomere apex margins not projected, unguis completely exposed in dorsal and lateral aspects (Figs 3I, 4D); dorsomedian lobe absent. Unguis acuminate and sharp on all legs, longer on III and IV.

Copulatory apparatus and associated structures. Comprising two parts not closely associated with one another (other components may be not visible) (Figs 2C, D, 4D); one part short, horn-shaped, lying prodorsally on first tarsomere; adjacent, in retrolateral position, hyaline, laterally compressed, lanceolate structure, apparently originating on metatarsus; other part, about twice length, narrower, and whip-shaped, curling around distal part of metatarsus. Based on morphology of modified leg III, horn-shaped part of copulatory apparatus presumably protected by various structures: ventrally by modified first tarsomere, dorsally by metatarsal process, prolaterally by metatarsal distal expansion, and retrolaterally by metatarsal(?) lanceolate structure.

Opisthosoma. Opisthosoma oval, longer than wide (Table 1), broadest at tergite XII. Dorsal surface divided transversally into separate tergites (Figs 1A, 2A,

3C); tergites without submedian depressions. Tergite X not visible, obscured by long macrosetae and matrix imperfections, segmentation unclear; XI–XIII each comprising median and lateral sclerites (visible for XII and XIII, revealed by micro-CT scanning for XI) (Fig. 3C); median sclerite of tergite XII only partially visible; of XIII cup-shaped, markedly wider than long (Table 1), lateral margins parallel. Sternites XI–XIII entirely fused, forming uniform ventral sternal plate without irregularities (Fig. 2B); submedian depressions absent. Pygidium not exposed (Fig. 2A, B), completely sheltered between dorsal and ventral opisthosomal sclerites, presumably retractile.

Female. Unknown.

Discussion

Remarks on holotypes of Primoricinulei

Wunderlich (2017: 57) reported the holotype of *H. acutiformis* as a female and provided photos of the ventral aspect of the body and the lateral aspect of leg III (Wunderlich, 2017: 336, photos 19, 20 respectively) which indicate that the ventral plate of the opisthosoma is divided transversally, in a manner similar to that observed in juveniles of extant species, and unlike the opisthosoma of the adult male of *H. grimaldii* where this body part is clearly undivided. The tarsus of leg III is clearly four-segmented, a character common to deutonymphs, tritonymphs, and adults of extant species (Platnick, 2002). Based on these observations, it is possible that the holotype of *H. acutiformis* could be a tritonymph, possibly female, based on the slender leg III, and not an adult.

Wunderlich (2017: 57) also reported the holotype of *H. dentata* as a female and noted that the legs are “slender, except III apparently quite similar to *H. bruckschei* [sic].” The holotype of *H. bruckschi*, unquestionably an adult male, has leg III similar in general morphology to that of *H. grimaldii*. This includes the short, subspherical femur, patella, tibia, and metatarsus, which give the leg a distinctly robust appearance, also observed in another male belonging to an unidentified *Hirsutisoma* species documented by Wunderlich (2017: 336, 337, photos 23, 24). Conversely, in female or immature specimens of *Hirsutisoma*, in which leg III is visible, *i.e.*, *H. acutiformis* (Wunderlich, 2017: 336, photos 18, 19), leg III is as slender as the other legs. This raises the possibility that the holotype of *H. dentata* could be a male (adult or tritonymph) and not a female.

Wunderlich (2015: 418) reported the holotype of *P. pugio* as a nymph, probably a deutonymph (reported as “nymph 2”). An illustration and photograph of the ventral aspect of the holotype (Wunderlich, 2015: 422, 508, fig. 2, photo 178) indicate that the ventral plate of the opisthosoma

is undivided, which Wunderlich (2015: 419) described as “Opisthosoma... dorsally and ventrally completely covered with an entire scutum.” The description of this body part matches adult specimens of *Hirsutisoma* (e.g., the holotypes of *H. bruckschi* and *H. grimaldii*) and adults of extant species. Photographs also reveal that leg III is unmodified in this specimen (Wunderlich, 2015: 508, photos 177, 178), indicating that it is not an adult male. Another character of this specimen is the five-segmented tarsus of leg IV, illustrated by Wunderlich (2015: 423, fig. 7), a character that is only common to tritonymphs and adults of extant ricinuleids (Platnick, 2002). Taken together, the evidence suggests that the holotype of *P. pugio* is most likely an adult female and not a juvenile.

Paleoecology and functional morphology of Primoricinulei

The holotype of *Hirsutisoma grimaldii* is remarkably well-preserved. The preservation of the coxosternal region and legs, and especially leg III, which carries many of the most important structures for the systematics of Ricinulei, makes this fossil very important for the systematics and evolutionary morphology of the order. Additionally, the clarity with which some structures may be viewed through the fossilized resin, allows the formulation of hypotheses regarding how this species and, by extrapolation, other members of suborder Primoricinulei might have lived, including the niche they might have inhabited. Some structures are evidently related to behaviors common to all life stages, such as hunting, whereas other structures that are sexually dimorphic would be involved in courtship, mating, or fighting for mates. Table 2 presents a list of some of the modifications of *H. grimaldii* and their possible occurrence in other species of Primoricinulei. Where possible, and as far as the fossil record permits, modifications that appear to occur in both sexes and/or in juveniles as well as in adults, are noted.

In addressing the paleoecology of a Posteriorricinulei, *Curculioides bohemoni*, Whalen & Selden (2021: 610) stated:

“All modern ricinuleids occupy one of two overarching niches—terricolous species (living beneath the rainforest floor and into the subsoil), and cavernicolous species (living in the complete darkness of subterranean caverns) (Selden, 1992; Adis *et al.*, 1999). It appears however that the ancestral niche of the order [Ricinulei] is not reflected in these modern ecologies. The recently discovered Cretaceous ricinuleids are preserved in amber, suggesting that they may have exhibited a scansorial lifestyle or at least frequented the bases of tree trunks—an unusual setting for modern ricinuleids (Cooke, 1967; Wunderlich, 2015).”

The morphology of *H. grimaldii*, including characters of the adult male that are also visible in the type of *H.*

bruckschi, appears to support the hypothesis that the habitat and lifestyle of the Cretaceous species, specifically Primoricinulei (i.e., *Hirsutisoma* and *Primoricinuleus* Wunderlich, 2015) differed from that of extant species. Firstly, the prosoma and opisthosoma of *H. grimaldii* are visibly separate, not connected by a coupling mechanism as in other ricinuleids, the Posteriorricinulei of Wunderlich (2017), or the Neoricinulei and Palaeoricinulei of Selden (1992). Also characteristic of this fossil, and the lineage to which it belongs, is the central position of the sternum on the prosoma, with the legs and pedipalps positioned concentrically around it. This results in a markedly different gross morphology, compared to other ricinuleids, which may have been more conducive for other habitats like vegetation. The coxosternal region of *H. grimaldii* suggests that the leg coxae were all separate and not fused to contiguous coxae, unlike extant ricinuleids in which the coxae of legs II are fused to those of legs I and III. This would have granted the animal greater agility with respect to leg movement and perhaps enhanced mobility. The legs, in which the flexion plane of the tibia is aligned with that of the patella, probably allowed the animal to raise its body above the substrate, whereas the unmodified (i.e., not projected) lateral margins of the distal tarsomere of legs III and IV presumably improved adherence to the substrate by the exposed, projecting unguis. The presence of six, laterally-situated ocelli in two triads that protrude from the carapace, more clearly visible in the holotype of *H. bruckschi*, suggests the visual system was relatively well-developed, as in some other predatory arachnids (e.g., spiders, scorpions, and harvestmen). The raptorial pedipalps and markedly modified femur of leg I, which might have assisted with grabbing prey, lend credence to the hypothesis that Primoricinulei may have been active predators.

One of the most distinctive aspects of *Hirsutisoma* (and Hirsutisomidae), is the dense vestiture of long macrosetae covering the anterior part of the opisthosoma. Although the function of this dense setation is unknown, it must have been evolutionarily advantageous, perhaps providing protection (e.g., trapping moisture or repelling parasites) or camouflage (e.g., trapping soil particles), as in extant arachnids.

The unique morphological characters of Primoricinulei suggest a corticolous lifestyle on the trunks and branches of trees, where they are presumed to have been active predators, consistent with the scansorial lifestyle for Cretaceous Ricinulei hypothesized by Whalen & Selden (2021). Interestingly, although Ricinulei appear to have been quite diverse and abundant in the Cretaceous period of Myanmar, not a single extant species of Ricinulei occurs in Asia. With the extinction of the Cretaceous ricinuleids, these morphologically distinct forms were eradicated and

TABLE 2. Taxonomic distribution of selected characters by sex and life stage in species of Primorcinulei Wunderlich, 2015; *Hirsutisoma acutiformis* Wunderlich, 2017; *Hirsutisoma bruckschi* Wunderlich, 2017; *Hirsutisoma dentata* Wunderlich, 2017; *Hirsutisoma grimaldii* sp. nov.; *Primorcinuleus pugio* Wunderlich, 2015. Observations based on literature and published images (Wunderlich, 2015, 2017), except for *H. bruckschi* and *H. grimaldii*, the holotypes of which were examined. Abbreviations: j, juvenile; N, no; Y, yes.

Body region	Character	Sex/Stage	<i>H. acuti.</i> ¹	<i>H. bruck.</i>	<i>H. dent.</i> ¹	<i>H. grim.</i>	<i>P. pugio</i> ¹
			(♂)			(♂)	
Soma	interlocking mechanism absent between prosoma and opisthosoma, both tagmata connected by exposed pedicel	♂♀j	Y	Y	Y	Y	Y
	body, especially prosoma, noticeably compressed	♂♀j? (a)	?	N	?	N	Y
Carapace	six ocelli in two triads	♂♀j	Y	Y	?	Y	N ²
Cucullus	anterior surface slightly concave, almost flat	♂ (b)	Y	?	?	Y	?
	ventral margin slightly bilobate in anterior aspect	♂ (b)	?	Y	?	Y?	?
Coxosternal region	sternum large, situated centrally on prosoma, with coxae of legs and pedipalps positioned concentrically around it	♂♀j	Y	Y	?	Y	Y
	coxae of legs I–IV separate from coxae of adjacent legs (<i>i.e.</i> , lateral margins not fused along contact area)	♂♀j	?	?	?	Y	?
Chelicerae	fixed finger long, approximately as much as movable finger	♂ (c)	?	?	Y?	Y ⁹	?
	positioned anteriorly	♂♀j	Y?	Y	Y	Y	Y
Pedipalps	femur and tibia medium-sized, similar in length	♂♀j	Y	Y	Y	Y	Y
	tibia without fixed finger (not chelate)	♂♀ (♂♀j)	Y	Y	Y	Y	Y ⁸
	tarsus (movable finger) very long and sharp / pedipalps clearly raptorial	♂♀j	Y	Y	Y	Y	Y
	tarsus (movable finger) with comb of 8–10 lamellate projections basally on proventral surface	♂ (b)	N	N	N	Y	N
	tibia prolateral surface with distinct patch of dense macrosetae	♂ (b)	Y?	Y	Y?	Y	Y?
Opisthosoma	tergites and sternites XI–XIII without submedian depressions	♂ (c)	?	Y?	?	Y	?
	dorsal surface divided transversally into separate tergites	♂♀j	Y ⁶	Y ⁶	?	Y ^{6,9}	N
	dorsal surface with abundant, very long macrosetae	♂♀j	Y	Y	Y	Y	N
	ventral surface with three pairs of structures of unknown function	♂♀j? (a)	N	N?	?	N	Y
	pygidium presumably retractile into opisthosoma	♂♀j	?	Y ⁷	?	Y ⁷	?
Legs (all)	patello-tibial articulation slightly rotated (≤ 30 –40 degrees) or not rotated relative to femoro-patellar articulation	♂♀j	Y?	Y	?	Y	Y?
Leg I	femur very narrow proximally, longitudinal axis crooked	♂♀j	Y	Y	?	Y	Y
	only one trochanter present	♂ (d)	?	Y?	?	Y ⁹	N?
	femur, patella, tibia, and metatarsus short and subspherical	♂	?	Y ⁴	?	Y	?
	metatarsus prolateral surface with flat, glabrous, and sharp expansion distally	♂	?	N	?	Y	?
	metatarsal distal end (or possibly first tarsomere) with hyaline, laterally compressed, lanceolate structure retrolaterally	♂	?	Y	?	Y	?
	metatarsal process (♂) situated apically on metatarsus, near to and opposing tarsus	♂	–	Y	–	Y	–
	metatarsal process (♂) in form of curved, concave flap	♂	–	Y	–	Y	–
	first tarsomere (♂) modified, markedly elongate, sinuous in dorsal aspect, shaped to allow fit of copulatory apparatus	♂	–	Y ³	–	Y ⁹	–
	first tarsomere (♂) with pronounced retrodorsal longitudinal ridge	♂	–	N	–	Y	–
	second tarsomere (♂) unmodified, similar to third tarsomere and without <i>lamina cyathiformis</i>	♂	–	Y ³	–	Y	–
	copulatory apparatus (♂) presumably protected by fit of first tarsomere, metatarsal process, expansion of metatarsus (the latter only in <i>H. grimaldii</i>), and metatarsal(?) lanceolate structure	♂	–	Y ⁵	–	Y	–
	legs III and IV distal tarsomere with lateral margins unmodified, not projected (unlike legs I or II), such that ungues completely exposed in lateral aspect as much as in dorsal aspect	♂ (e)	Y	?	?	Y	Y?
	consisting of horn-shaped part lying prodorsally on first tarsomere, and long and whip-shaped part curling around metatarsus	♂	–	Y	–	Y	–

^a Present at least in female or juvenile, possibly also in male.

^b Present at least in adult male, may be sexually dimorphic.

^c Present at least in male, presumably also in female and juvenile.

^d Present at least in adult male, presumably also in female.

¹ Assessed in female or juvenile.

² Four ocelli in two diads.

³ The morphology of the tarsus of leg III of the male was inaccurately described in the original description. Wunderlich's (2017: 68) fig. 7 suggests the second tarsomere is elongate, whereas examination of the holotype revealed the first tarsomere to be modified. Similarly, although three unmodified tarsomeres are visible in the fossil (second to fourth), only two were illustrated in the description.

⁴ Unlike in the holotype, the femur, patella, and tibia are not clearly subspherical in the illustrations that accompany the original description (Wunderlich, 2017: 68, figs. 7, 8).

⁵ The metatarsal(?) lanceolate structure was not described or illustrated in the original description (Wunderlich, 2017).

⁶ Tergites XII and XIII are separated from one another. Tergites X, XI, and XII may be fused (*i.e.*, no transverse divisional membrane), forming only two dorsal plates (*i.e.*, X–XII + XIII); see *H. acutiformis* in Wunderlich (2017: 336, photo 18).

⁷ Pygidium sheltered in the opisthosoma, presumed to be retractile.

⁸ Wunderlich (2015: 417, 419) reported that the fixed finger is “strongly reduced or even absent.” Selden & Ren (2017: 334) noted that the specimen has a fixed finger on the right pedipalp. Although *P. pugio* was not examined during the present investigation, photographs in Wunderlich (2015: 508, photos 177–180), some of which illustrate the pedipalp, suggest the alleged fixed finger could be a misinterpretation, and that the tibia does indeed lack a fixed finger as in other Primorcinulei.

⁹ Verified with micro-CT scanning.

with them, a corticolous, scansorial lifestyle and hunting strategy unique among Ricinulei.

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