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Original Article

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Systematics of the colour-polymorphic spider genus *Cybaeolus*, with comments on the phylogeny of the family Hahniidae (Araneae)

Agustina Burgo[1], Kefyn Catley[2], Cristian J. Grismado[1], Nadine Dupérré[3], Suresh P. Benjamin[4], Gustavo Hormiga[5], Charles Griswold[6], Leonel Martínez[1], Martín J. Ramírez[1,*]

[1]Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia'—CONICET, Division of Arachnology, Av. Angel Gallardo 470, C1405DJR Buenos Aires, Argentina
[2]Western Carolina University, Cullowhee, NC 28723, United States
[3]Museum of Nature Hamburg, Zoology, Leibniz-Institute for the Analysis of Biodiversity Change (LIB), Center for Taxonomy and Morphology, 20146 Hamburg, Germany
[4]National Institute of Fundamental Studies, Hantana Road, Kandy, Sri Lanka
[5]Department of Biology, The George Washington University, Washington, DC 20052, United States
[6]California Academy of Sciences, Department of Entomology, 55 Music Concourse Drive, San Francisco, CA, 94118, United States

[*]Corresponding author. Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia'—CONICET, Division of Arachnology, Av. Angel Gallardo 470, C1405DJR Buenos Aires, Argentina. E-mail: ramirez@macn.gov.ar

ABSTRACT

We revise the spider genus *Cybaeolus* Simon, 1884, endemic to Chile and Argentina, including three species, *Cybaeolus delfini* (Simon, 1904), *Cybaeolus pusillus* Simon, 1884, and *Cybaeolus rastellus* (Roth, 1967). The genus *Clitistes* Simon, 1902 is synonymized with *Cybaeolus*, and its type species *Clitistes velutinus* Simon, 1902 is synonymized with *Cybaeolus pusillus*. We provide a phylogenetic analysis of *Cybaeolus* and representatives of Hahniidae and outgroups, using molecular markers. Because *Cybaeolus* is nested within Hahniinae, we synonymize the subfamily Cybaeolinae Lehtinen, 1967 with Hahniinae Bertkau, 1878, and provide an updated diagnosis of Hahniidae using characters of the male palp and spinning organs. We trace the evolution of the characteristic transversal arrangement of spinnerets of hahniids; our results indicate that the grouped spinnerets of *Cybaeolus*, as well as the presence of many piriform gland spigots, is a reversion to the ancestral state found in outgroups. The morphology of the male palp of hahniids suggests that the tibial retrolateral apophysis of the male is a functional conductor of the intromittent organ during mating. We document the colour polymorphism of the three species of *Cybaeolus*, which is unrelated to geographic location and time of collection, and similar morphs occur in both sexes of different species.

Keywords: phylogeny; spinning organs; marronoid; RTA clade; South America

INTRODUCTION

Cybaeolus Simon, 1884 is a genus of small spiders that inhabit the forests and shrublands of Chile and adjacent Argentina, which are remarkable in several aspects. They differ from typical members of the family Hahniidae by making webs on foliage (Fig. 1A–E) and are colourful (Figs 1F–J, 2). In contrast, most hahniids make webs on the ground or the leaf litter and are brown with unremarkable coloration patterns. Their morphology is also unusual because they lack the key character diagnostic of hahniids, namely the spinning organs in a transverse row, instead of in a compact group. Because of this arrangement of the spinnerets, the species of *Cybaeolus* were included in disparate families, including Dictynidae, Agelenidae, Cybaeidae, and Linyphiidae.

The genus *Cybaeolus* was first described by Simon (1884) from a single female, in a study of the spiders collected in Cape Horn in Tierra del Fuego in the southernmost extreme of South America. That publication only included short textual descriptions in Latin and illustrations of only some of the described species; additional illustrations of those species were published three years later (Simon 1887); although the description of the type species, *Cybaeolus pusillus* Simon, 1884 was transcribed, the

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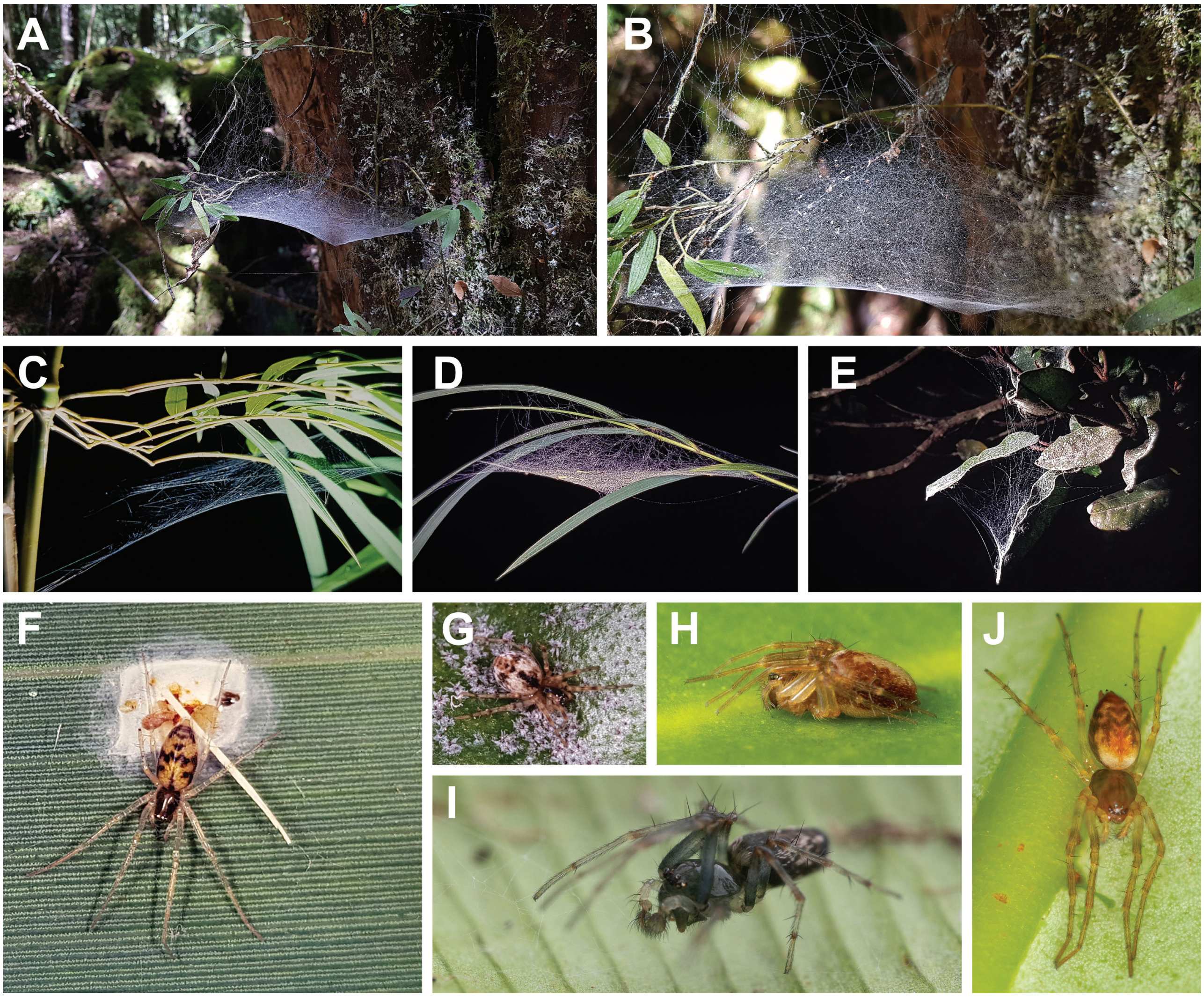

Figure 1. Webs and living specimens of *Cybaeolus*. A, B, web of *C. rastellus* (Roth, 1967) from Argentina, Parque Nacional Nahuel Huapi (MACN-Ar 46683). C, web of *C. pusillus* Simon, 1884 from Chile, Parque Nacional Chiloé (MACN-Ar, slide 466). D, web of *Cybaeolus* sp. from Chile, Monumento Natural Contulmo (MACN-Ar, slide 1020). E, web of *C. delfini* (Simon, 1904) from Chile, Parque Nacional Fray Jorge (AMNH, slide 1299). F, female of *C. pusillus* Simon, 1884 with eggsac, Chile, Parque Nacional Chiloé (MACN-Ar, slide 451). G, female of *C. delfini* (Simon, 1904) (AMNH, slide 1304). H, female of *Cybaeolus* sp. from Chile, Chiloé (photo by Matías Gargiulo). I, male of *Cybaeolus* sp. from Chile, Chiloé (photo by Matías Gargiulo). J, female of *Cybaeolus* sp. from Chile, Chiloé (photo by Matías Gargiulo).

species was not illustrated there. In his subsequent work, Simon (1898) made clear that *Cybaeolus* was included in Cybaeae, currently Cybaeidae. The second species included in *Cybaeolus* was described shortly thereafter, as *Mevianes delfini* Simon, 1904, from a single female from Punta Arenas, in the Strait of Magellan in Chile. In the same work he described a female as *M. wilsoni* Simon, 1904 and a male as *Dictyna fuegiana* Simon, 1904, in all cases without illustrations and listing them in Cryphoeceae (now Cybaeidae) and Dictynidae, respectively. Lehtinen (1967) later synonymized *Mevianes wilsoni* and *Dictyna fuegiana* with *Cybaeolus pusillus* and provided the first illustrations of the genital organs for the two *Cybaeolus* species known at that time.

In the same year, Roth (1967) described a third species, *Mevianes rastellus* Roth, 1967 from Chile near Puerto Montt. He illustrated the three species of the genus, and suggested that *Cybaeolus* and *Mevianes* might be synonyms. However, he was unable to examine the type of *Cybaeolus pusillus* (Roth 1967: 316) and, therefore, made no nomenclatural changes. Such synonymy was consolidated by Lehtinen (1967), who did examine the type. Roth (1967) listed *Mevianes* in Agelenidae, together with other genera that are nowadays included in Agelenidae, Austrochilidae, Cybaeidae, Desidae, Macrobunidae, and Hahniidae. In line with the confusion surrounding *Cybaeolus*, the species *Clitistes velutinus* Simon, 1902 was described from a female from Tierra del Fuego in the family Linyphiidae; the type was recently relocated and illustrated by Dupérré and Harms (2018), transferred to Dictynidae and is here considered a junior synonym of *Cybaeolus pusillus*. As mentioned by Dupérré and Harms (2018), Simon (1902: 21) made a note of the similarity of the tracheal spiracle of *Clitistes velutinus*, which is separated from the spinnerets, as is found in species of *Hahnia*.

Lehtinen (1967) was the first to realize that the genital organs of *Cybaeolus* were characteristically like those of hahniids and transferred them to that family. To reflect

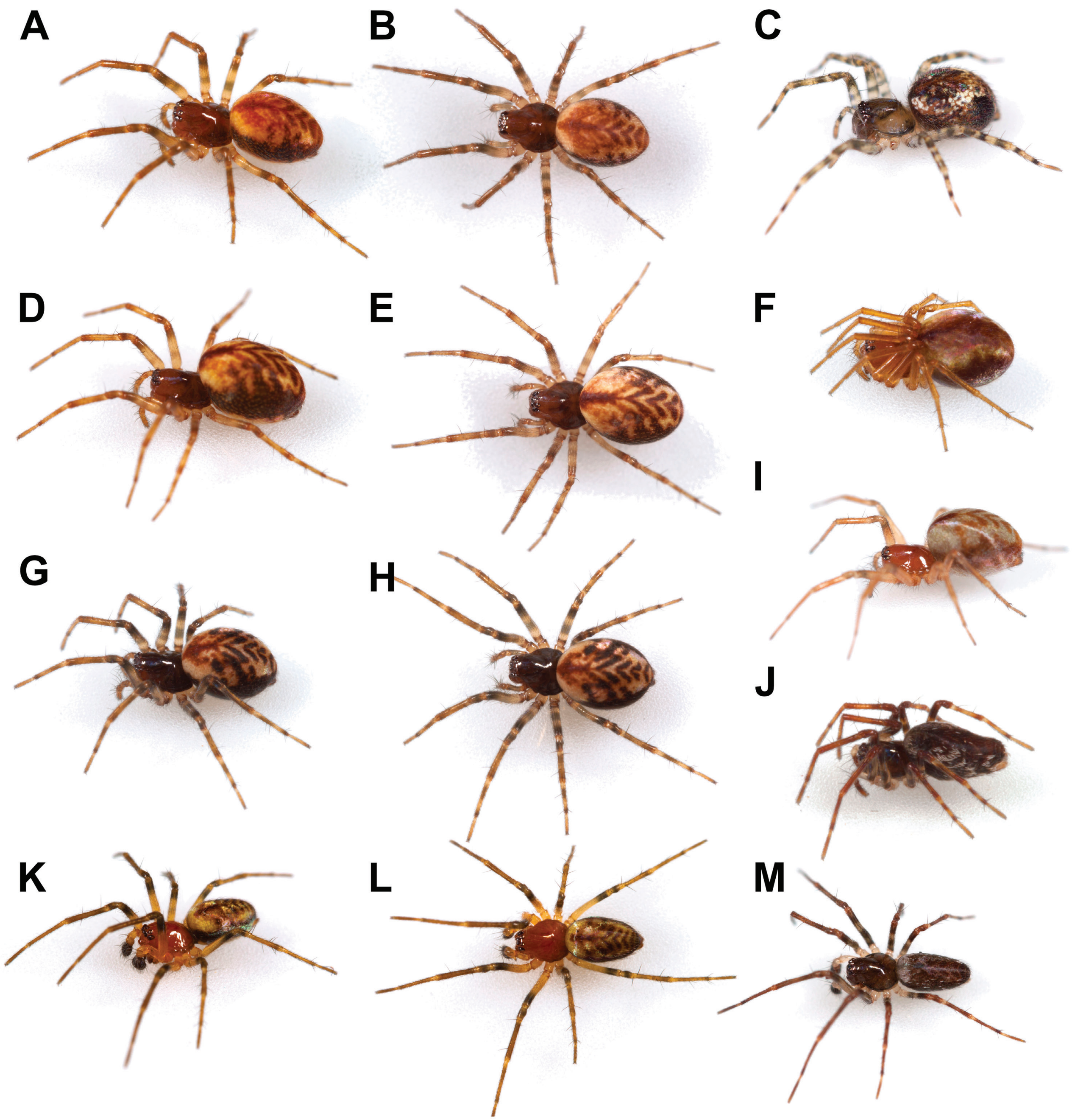

Figure 2. Live specimens of *Cybaeolus*. A, B, female *C. pusillus* Simon, 1884 from Chile, Magallanes (MACN-Ar 43977). C, female *C. pusillus* Simon, 1884 from Argentina, Tierra del Fuego (MACN-Ar MJR-1942). D, E, female *C. pusillus* Simon, 1884 from Chile, Magallanes (MACN-Ar 43976). F, female *C. pusillus* Simon, 1884 from Argentina, Tierra del Fuego (MACN-Ar 46684). G, H, female *C. pusillus* Simon, 1884 from Chile, Magallanes (MACN-Ar 43978). I, female *C. pusillus* Simon, 1884 from Argentina, Tierra del Fuego (MACN-Ar MJR-1789). J, female *C. rastellus* (Roth, 1967) from Argentina, Neuquén (MACN-Ar 46685). K, L, male *C. pusillus* Simon, 1884 from Argentina, Tierra del Fuego (MACN-Ar 46682). M, male *C. rastellus* (Roth, 1967) from Chile, Biobío (MACN-Ar 43342 MJR-2264).

the grouped arrangement of the spinnerets, unlike typical hahniids, Lehtinen created the subfamily Cybaeolinae, including *Cybaeolus* and two genera of uncertain placement (*Austrohahnia* Mello-Leitão, 1942 and *Lizarba* Roth, 1967), although he was unable to examine specimens of the latter two. Along with the typical Hahniinae, including the typical hahniids with well-separated spinnerets, and Cybaeolinae mentioned above, Lehtinen (1967) also included a third subfamily, Cryphoecinae, which is now considered a member of Cybaeidae (Wheeler *et al.* 2017; see also: Castellucci *et al.* 2023, Kulkarni *et al.* 2023). The limits and relationships of Hahniidae and all the closely related families currently grouped in the 'marronoid clade' have a turbulent history that only began to settle with the use of molecular markers (Spagna and Gillespie 2008, Wheeler *et al.* 2017) and, recently, genomic data (Gorneau *et al.* 2023, Kelly *et al.* 2023).

The origin of the transverse aligned spinnerets of hahniids deserves consideration here. The trees based on the molecular phylogenetic studies suggest that the spread spinnerets of the Hahniinae is a derived condition, given that virtually all the families in the marronoid clade, where the hahniids belong, have grouped spinnerets (see: Griswold *et al.* 2005). In a recent study, Castellucci *et al.* (2023) resolved the relationships of three genera with clustered spinnerets that had been placed in Hahniidae at some point (*Mastigusa* Menge, 1854, *Calymmaria* Chamberlin and Ivie, 1937, and *Cryphoeca* Thorell, 1870), and confirmed their placement in the family Cybaeidae. Their analysis also included legacy genetic sequences of two species of *Cybaeolus*, which resulted in them nested within Hahniidae, confirming the previous results of Wheeler *et al.* (2017).

Since *Cybaeolus* have clustered spinnerets, it is interesting to test whether this group represents a phylogenetic intermediate stage in the transformation to aligned spinnerets. This character is of special significance, since the arrangement of the spinnerets is a determinant of the final arrangement of the silk they produce. Wolff *et al.* (2019) showed that the placement of the anterior lateral spinnerets (ALS) at a short distance from each other is important for producing firm anchors of silk threads on the substrate. In contrast, typical hahniids have the ALS widely separated and, consequently, their anchors are weak and separated into two patches (Wolff *et al.* 2021).

Finally, the colourful habitus of *Cybaeolus* specimens is worth mentioning here, because the colour patterns are exceptionally variable within species. Colour polymorphism has been reported in spiders and may be either reversible or genetically determined (Oxford and Gillespie 1998). While the reversible colour changes affect the general darkening of the cuticle or the mobilization of white guanine deposits, those with genetic bases produce the most remarkable colour differences, as in the Hawaiian happy-face spiders (Gillespie and Tabashnik 1989, Oxford and Gillespie 1996), and in other theridiid spiders with similar patterns (Oxford and Reillo 1993, Oxford 2009, Cotoras *et al.* 2017). Colour polymorphism has been rarely reported in the highly diverse marronoid spiders, e.g. for the desid *Ischalea spinipes* L.Koch, 1872, which can vary between green, dark yellow, or brown (Forster and Wilton 1973). In general, the marronoids are not colourful spiders; the clade owes its name to their usually brown coloration (Wheeler *et al.* 2017), although their contrasting patterns might be variable as well. Species of *Cybaeolus*, along with some Dictynidae, are an exception in this regard, as they can have contrasting coloration, including red, white, and black markings.

In this contribution we present a taxonomic revision of the genus *Cybaeolus*, explore the colour polymorphisms in the three species, and present a phylogenetic analysis to clarify their relationships within Hahniidae. Using this phylogeny, we then trace the evolution of the characteristic transversal arrangement of spinnerets in hahniids and test the hypothesis of *Cybaeolus* being an intermediate phylogenetic stage in the transformation from grouped to aligned spinnerets.

MATERIALS AND METHODS

Morphological study

All measurements are in millimeters unless otherwise noted. Incident light images were taken with a Leica DFC 290 digital camera mounted on a Leica M165 C stereo microscope, or with a Leica DFC 295 digital camera on a Leica M205 A stereo microscope. Transmitted light images were taken with a Nikon DXM1200 digital camera mounted on an Olympus BH2 compound microscope. Extended focal range images were assembled with Helicon Focus 5.3. Male and female genitalia were cleared with clove oil in an excavated slide and illustrated using the same Olympus BH2 compound microscope with camera lucida. For the scanning electron micrographs (SEM) the samples were gradually dehydrated to 100% ethanol, critical point dried, and coated with gold-palladium, and examined with a Hitachi SEM s-4700 at the American Museum of Natural History (AMNH), a LEO 1450VP SEM at the California Academy of Sciences (CAS), or a LEO 1430VP at The George Washington University. Female genitalia were digested with pancreatine for SEM examination. To illustrate colour polymorphism, we mainly imaged individuals collected in the field and directly preserved in ethanol 95% and stored at –18°C, since they better maintain their natural coloration. Tracheae were examined after digestion of soft tissues with a KOH solution.

Comparative material examined

Cicurinidae: *Cicurina cicur* (Fabricius, 1793): female from Czech Republic, Zilna (CASENT8082411), male from Austria (CASENT8082413). Cybaeidae: *Calymmaria persica* (Hentz, 1847): USA, Georgia, Rabun Co., Ellicott Rock Wilderness Area (USNM); *Cryphoeca silvicola* (C.L.Koch 1834): Spain, Catalonia, Cadi Mountains, E. de Mas (GWU). Hahniidae: *Hahnia pusilla* (C.L.Koch 1841): Germany, Bayern, Mittelfranken, Feuchtwangen, Thurnhofen (GWU). *Neoantistea magna* (Keyserling, 1887): USA, Maine, Piscataquis Co., WELS 13.8 km. N of Soubunge Mtn. (USNM).

Geo-referencing and distribution maps

Geographical distribution maps were made with the online tool SimpleMappr (Shorthouse 2010) using primarily the coordinates from the original labels of the specimens examined. When coordinates were not specified, localities were geo-referenced using GoogleMaps, and in those cases provided between brackets in the lists of examined material.

Abbreviations

Morphology

AB, accessory bulb of female genitalia (= secondary spermatheca); Ac, aciniform gland spigot; ALE, anterior lateral eye; ALS, anterior lateral spinneret; AME, anterior median eye; AT, anal tubercle; CW, carapace width; Cy, cylindrical gland spigot; CyGv, cymbial groove of male palp; Co, colulus; COp, copulatory opening; E, embolus of male palp; MA, median apophysis of male palp; MAP, major ampullate gland spigot; mAP, minor ampullate gland spigot; N, nubbin (atrophied spigot); PA, patellar retrolateral apophysis of male palp; Pf, pseudoflagelliform gland spigot; Pi, piriform gland spigot; PLE, posterior lateral eye; PLS, posterior lateral spinneret; PME, posterior median eye; PMS, posterior median spinneret; RTA retrolateral tibial apophysis of male palp; RTAGv, groove on the retrolateral tibial apophysis of male palp; TO, tarsal organ; Tp, tartipore; Tr, trichobothria; TS, tracheal spiracle.

Institutions

CASENT, Entomology Collection, California Academy of Sciences, San Francisco, California, USA; AMNH, American

Table 1. Species, voucher numbers, and GenBank accessions for spiders used in the molecular analyses. Identifiers of new sequences start with 'PQ' and are in boldface.

Species	*H3*	*COI*	28S	18S	16S	12S	Voucher identifier
Agelenidae: *Agelena labyrinthica*	KR074077	FN554797	AY633851	AY633862			MH:AB 424, NJNU03002
Agelenidae: *Coelotes terrestris*	KY779284	KY778997	KY791137	KY791439	KY791740	KY792039	ZZ746
Agelenidae: *Eratigena atrica*	KY018086	KY017548	KY016884	KY016266	KY015700	KY015269	ARASP000037
Amaurobiidae: *Amaurobius similis*	KY018089	KY017551	KY016887	KY016269	KY015703	KY015271	ARANS000001
Amaurobiidae: *Pimus iviei*	KY018090	KY017553	KY016889	KY016271	KY015705	KY015273	ARAMH000009
Cicurinidae: *Cicurina brevis*		MF816593					BIOUG19072-G07
Cicurinidae: *Cicurina* sp.	KR074086	KY017744	KR074034	KY016480	KY015900	KY015427	ARAMH000010, ZZ-2016
Cybaeidae: *Blabomma* sp.		JF887146.1	HM576649	HM576633			011Bla, 10-SKBC-0721
Cybaeidae: *Calymmaria* sp.	KY018167	KY017652	KY017004	KY016382	KY015802	KY015350	ARACG000231
Cybaeidae: *Cryphoeca exlineae*		DQ628614	DQ628672	DQ628745			CRYPHOECASP1
Cybaeidae: *Cybaeus giganteus*	KY018168	KY017653	KY017005	KY016383	KY015803	KY015351	ARAMH000017
Cybaeidae: *Dirksia cinctipes*	MN590109	KP646037	MN590085	MN590055			10-SKBC-0676, BIOUG25730
Cybaeidae: *Ethobuella tuonops*	MN590110	KP646037		MN590056			BIOUG07526-D06, BIOUG04718
Cycloctenidae: *Cycloctenus* sp.	KY018169	KY017654	KY017006	KY016384	KY015804	KY015352	ARACG000133
Cycloctenidae: *Orepukia* sp.	KY018174	KY017659	KY017011	KY016389	KY015809	KY015357	ARACG000132
Cycloctenidae: *Pakeha* sp.	KY018175	KY017660	KY017012	KY016390	KY015810		ARACG000169
Cycloctenidae: *Toxopsiella* sp.	KY018177	KY017662	KY017014	KY016392	KY015812		ARACG000134
Desidae: *Amphinecta* sp.	KY018183	KY017672	KY017024	KY016399	KY015821	KY015364	ARACG000187
Desidae: *Badumna longinqua*	KY018185	KY017674	DQ628665	KY016401	KY015823		ARACG000013, BLONGINQUA1
Desidae: *Cambridgea* sp.	KY018188	KY017679	KY017030	KY016406	KY015827	KY015367	ARACG000097
Desidae: *Desis formidabilis*	KY018192	KY017683	KY017034	KY016410	KY015831	KY015371	ARACG000274, ARACG000062
Desidae: *Metaltella* sp.	KY018200	KY017690	KY017042	KY016418	KY015836	KY015379	ARACG000060
Dictynidae: *Argyroneta aquatica*	KY018206	KY017697	KY017051	KY016427	KY015842		ARANS000035
Dictynidae: *Dictyna latens*		KY017698			KY015843	KY015386	ARAGH000080
Dictynidae: *Dictyna major*	MN590120		KY017052	KY016428		KY015387	ARAGH000049, BIOUG14292
Dictynidae: *Mallos pallidus*		KY017700	KY017055	KY016430	KY015844	KY015388	ARAGH000050
Macrobunidae: *Anisacate tigrinum*	KY018091	KY017554	KY016890	KY016272	KY015706	KY015274	ARAMR000066
Macrobunidae: *Callevopsis striata*	KY018092	KY017555	KY016891	KY016273	KY015707		ARAMR000281
Macrobunidae: *Rubrius antarcticus*	KY018096	KY017560	KY016897	KY016280	KY015712	KY015278	ARAMR000067

Table 1. Continued

Species	*H3*	*COI*	28S	18S	16S	12S	Voucher identifier
Stiphidiidae: *Aorangia* sp.	KY018438	KY017931	KY017374	KY016715	KY016125	KY015580	ARACG000199, ARACG000197
Stiphidiidae: *Neoramia setosa*	KY018442	KY017936	KY017378	KY016719	KY016129	KY015584	ARACG000019
Stiphidiidae: *Stiphidion* sp.	KY018447	KY017943	KY017385	KY016726	KY016135	KY015590	ARASP000081
Toxopidae: *Otagoa* sp.	KY018510	KY018017	KY017465	KY016804	KY016203	KY015647	ARACG000235
Toxopidae: *Toxops* sp.		KY018018	KY017466	KY016805	KY016204	KY015648	ARACG000278
Hahniidae sp.	**PQ586898**	**PQ594831, BOLD MSB026**	**PQ590672**		**PQ590682**		MACN-Ar 29751, DLP-4115
Hahniidae sp.		**PQ594833, BOLD MSB059**	**PQ590674**				MACN-Ar 36386, DLP-4185
Hahniidae sp.		**PQ594832, BOLD MSB057**	**PQ590673**		**PQ590683**		MACN-Ar 36389, DLP-4183
Antistea brunnea	MN590134	KM839029	MN590103	MN590079			BIOUG05745-F10
Antistea elegans		MZ610412					ZMUO_000263
Cybaeolus delfini ♂	**PQ586887**	**PQ585713**	**PQ590670**		**PQ590676**		MACN-Ar 43327, AGB-0011
Cybaeolus delfini ♀	**PQ586888**	**PQ585714**	**PQ590671**		**PQ590677**		MACN-Ar 43581, AGB-0013
Cybaeolus delfini ♀		**PQ585704, BOLD SPDCH098**					CASENT 9034004
Cybaeolus delfini ♀		**PQ585705, BOLD SPDCH137**					CASENT 9034055
Cybaeolus delfini ♀		**PQ585706, BOLD SPDCH180**					CASENT 9039052
Cybaeolus delfini ♂	**PQ586886**	**PQ585712, BOLD MSB047**	**PQ590669**				MACN-Ar 36484, DLP-4137
Cybaeolus delfini ♀	**PQ586885**	**PQ585711, BOLD MSB075**	**PQ590668**				MACN-Ar 36425, DLP-4201
Cybaeolus delfini ♂	**PQ586884**	**PQ585710, BOLD MSB084**	**PQ590667**				MACN-Ar 36410, DLP-4210
Cybaeolus delfini ♀	**PQ586882**	**PQ585707, BOLD SPDAR1008**	**PQ590665**		**PQ590675**		MACN-Ar 33729, MLB-4345
Cybaeolus delfini ♂	**PQ586883**	**PQ585708, BOLD SPDAR1009**	**PQ590666**				MACN-Ar 33730, MLB-4346
Cybaeolus delfini ♀		**PQ585709**					MACN-Ar 33731, MLB-4347
Cybaeolus pusillus ♂	**PQ586893**	**PQ585723**			**PQ590680**		MACN-Ar 43386, AGB-0012
Cybaeolus pusillus ♂		**PQ585715, BOLD SPDCH096**					CASENT 9034002

Table 1. Continued

Species	*H3*	*COI*	28S	18S	16S	12S	Voucher identifier
Cybaeolus pusillus ♂		**PQ585716, BOLD SPDCH097**					CASENT 9034003
Cybaeolus pusillus ♀		**PQ585717, BOLD SPDCH179**					CASENT 9039051
Cybaeolus pusillus ♂		**PQ585718, BOLD SPDCH181**					CASENT 9039053
Cybaeolus pusillus ♀		**PQ585719, BOLD SPDCH182**					CASENT 9039054
Cybaeolus pusillus ♀	**PQ586892**	**PQ585722**			**PQ590679**		MACN-Ar 40780, CJG-2039
Cybaeolus pusillus ♂	**PQ586889**	**PQ585720**					MACN-Ar 42865, LNP-4084
Cybaeolus pusillus ♀	**PQ586890**	**PQ585721**			**PQ590678**		MACN-Ar 42876, LNP-4133
Cybaeolus pusillus ♂	**PQ586894**	**PQ585724, BOLD SPDAR1023**					MACN-Ar 29776, MLB-4362
Cybaeolus pusillus ♀	**PQ586891**						MACN-Ar 29776, MLB-4363
Cybaeolus rastellus ♀	KY018252	KY017745	KY017117	KY016481	KY015901		ARAMR000290
Cybaeolus rastellus ♀		**PQ585725, BOLD SPDCH136**					CASENT 9034054
Cybaeolus rastellus ♂	**PQ586895**	**PQ585726**			**PQ590681**		MACN-Ar LNP-4082
Cybaeolus rastellus ♂	**PQ586897**						MACN-Ar 43342, MJR-2264
Cybaeolus rastellus ♀	**PQ586896**	**PQ585727, BOLD SPDAR1068**					MACN-Ar 34362, MLB-4415
Hahnia cinerea	MN590136	KM839424	MN590105	MN590081			BIOUG09408-D11, BIOUG05370
Hahnia clathrata	FJ949043	FJ949005		FJ948881			11_2
Hahnia glacialis		KP656504					BIOUG14298-F10
Hahnia helveola		KX536850					ZSM_B_ARACH_723
Hahnia nava	KY018254	KY269491.1		KY016483	KY015902	KY015428	ARANS000022, ZFMK_TIS_19074
Hahnia ngai	MT445988	MT433973	MT434975	MT437224			RMNH.ARA.18415, RMNH.ARA.18414
Hahnia ononidum	MN590137	KY268726	MN590106	MN590082			ZFMK-TIS-18426, BIOUG13667
Hahnia ovata		ON324519					HNU616
Hahnia petrobia		MT607762					MT607762
Hahnia pusilla		KY270030					ZFMK-TIS-2504873
Hahnia saccata		MT433972		MT437222		MT434903	RMNH.ARA.18412
Hahnia sp.		JN294784					BIOUG_BIOUG00622-A05
Hahnia sp.		KR074066					ZZ-2016
Hahnia zhejiangensis	KR074093		KR074041	KR073991			0

Table 1. Continued

Species	*H3*	*COI*	28S	18S	16S	12S	Voucher identifier
Hexamatia seekhaow	MT445987	MT433971	MT434974	MT437221	MT434972		RMNH.ARA.18411
Intihuatana sp.	**PQ586899**	**PQ585728, BOLD MSB030**					MACN-Ar 29762, DLP-4120
Neoantistea agilis	DQ628644	KP650263	DQ628678	DQ628714			NAGILIS2, BIOUG13542-G05
Neoantistea gosiuta		MF808254					BIOUG14142-A03
Neoantistea magna		MF813777					BIOUG13170-A02
Neoantistea quelpartensis		JN817206	JN816996	JN816788	JN816572		LEGO_26_3
Neohanhia nr. *pristirana*		**PQ585729, BOLD SPIPO256**					FML_SCB1DEL012

Museum of Natural History, New York, USA; GWU, The George Washington University, Washington, DC, USA; MACN-Ar, National Collection of Arachnology, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; MCZ, Museum of Comparative Zoology, Harvard University, Massachusetts, USA; MNHN, Muséum National d'Histoire Naturelle, Paris, France; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; ZMH, Zoological Museum, Centrum für Naturkunde, University of Hamburg, Germany.

Phylogenetic analysis

We obtained sequences from 26 samples of the three known species of *Cybaeolus*, and of five additional species of Hahniidae. To these, we added legacy sequences of *Cybaeolus* and of other genera of Hahniidae, as well as representatives of the remaining families in the marronoid clade. For the new sequences, the extraction and amplification of DNA was made in the Laboratory of Molecular Tools at Museo Argentino de Ciencias Naturales (MACN), from tissues preserved in absolute alcohol at −18°C. We targeted the markers histone 3 (*H3*), cytochrome *c* oxidase subunit I (*COI*), 28S ribosomal RNA (28S), and 16S ribosomal RNA (16S), previously used to estimate relationships of marronoid spiders (Wheeler *et al.* 2017). Details of extraction, primers, and polymerase chain reaction (PCR) protocols are the same as in Magalhaes and Ramírez (2022). Sequencing was outsourced to Macrogen Inc., South Korea. The resulting chromatograms were analysed individually to detect contaminated sequences or ambiguous portions. In addition to these sequences obtained in the laboratory, we combined our data with additional sequences from previous work (Wheeler *et al.* 2017, Rivera-Quiroz *et al.* 2020), using the markers mentioned above plus 12S ribosomal RNA (12S) and 18S ribosomal RNA (18S). For the *COI* marker, additional sequences obtained by the Arachnology Division at MACN and deposited in the BOLDSYSTEMS platform (https://www.boldsystems.org/) were also used. Sequences were aligned with MAFFT online v.7.463 (Katoh and Standley 2013), using the L-INS-I algorithm. See Table 1 for a list of vouchers and sequence identifiers.

Maximum likelihood

For the maximum likelihood analyses we used the program IQ-TREE 2.2.0 (Minh *et al.* 2020), partitioning the data by marker, and selecting the best combination of partitions and evolution models by Bayesian information criterion (best-fitting models were TPM2+I+G4 for *H3*, GTR+F+I+G4 for 18S, GTR+F+I+G4 for 16S and 12S together, GTR+F+I+G4 for *COI*, and GTR+F+I+G4 for 28S). Since the relationships of outgroup taxa in the resulting trees were slightly different to that found in recent phylogenomic studies, we used the study of Gorneau *et al.* (2023) based on ultraconserved elements as a backbone topology to constrain our tree search, considering only the taxa in common with our analysis (see Supporting Information, Fig. S1); this means that all the rest of the taxa are free to move anywhere during tree search. Support for groups (branches) was estimated by 1000 cycles of ultrafast bootstrapping. Ten independent runs were performed; of those, six converged into nearly identical log-likelihood values (−57417.7725 to −57417.9604) and identical topologies; the tree with top-ranking log-likelihood is presented in Results, after collapsing branches with bootstrap below 0.5. To estimate the support of an alternative topology with *Cybaeolus* as sister to the rest of the hahniids, we used TNT 1.6 (Goloboff and Morales 2023) to modify the optimal tree placing *Cybaeolus* in such position, and asked for the frequency of the branch of interest (all hahniids except *Cybaeolus*) in the 1000 bootstrapped trees previously saved by IQTREE.

Ancestral character states for the arrangement of spinnerets (grouped; separated in a transversal line) were estimated by maximum likelihood on the optimal tree, using the R packages PHYTOOLS and APE, under the models ER and ARD, and the best-fitting model selected by the Akaike information criterion.

Parsimony

For the parsimony analyses we used TNT 1.6. For the equal weights' analysis, a heuristic search was made using a driven search with the default parameters of the 'new technologies', aiming for 10 independent hits to minimum length. The resulting trees were then submitted to an additional round of tree-bisection reconnection (TBR) branch swapping. These results were compared to a simpler search strategy of 300 random addition sequences, each followed by TBR, which produced 20 hits to minimal length. As both strategies reached the same trees with multiple independent hits, it is likely that the optimal trees were found. Finally, the strict consensus of all the optimal trees was obtained, and on this consensus the support values were calculated by means of 1000 bootstrap pseudoreplicates.

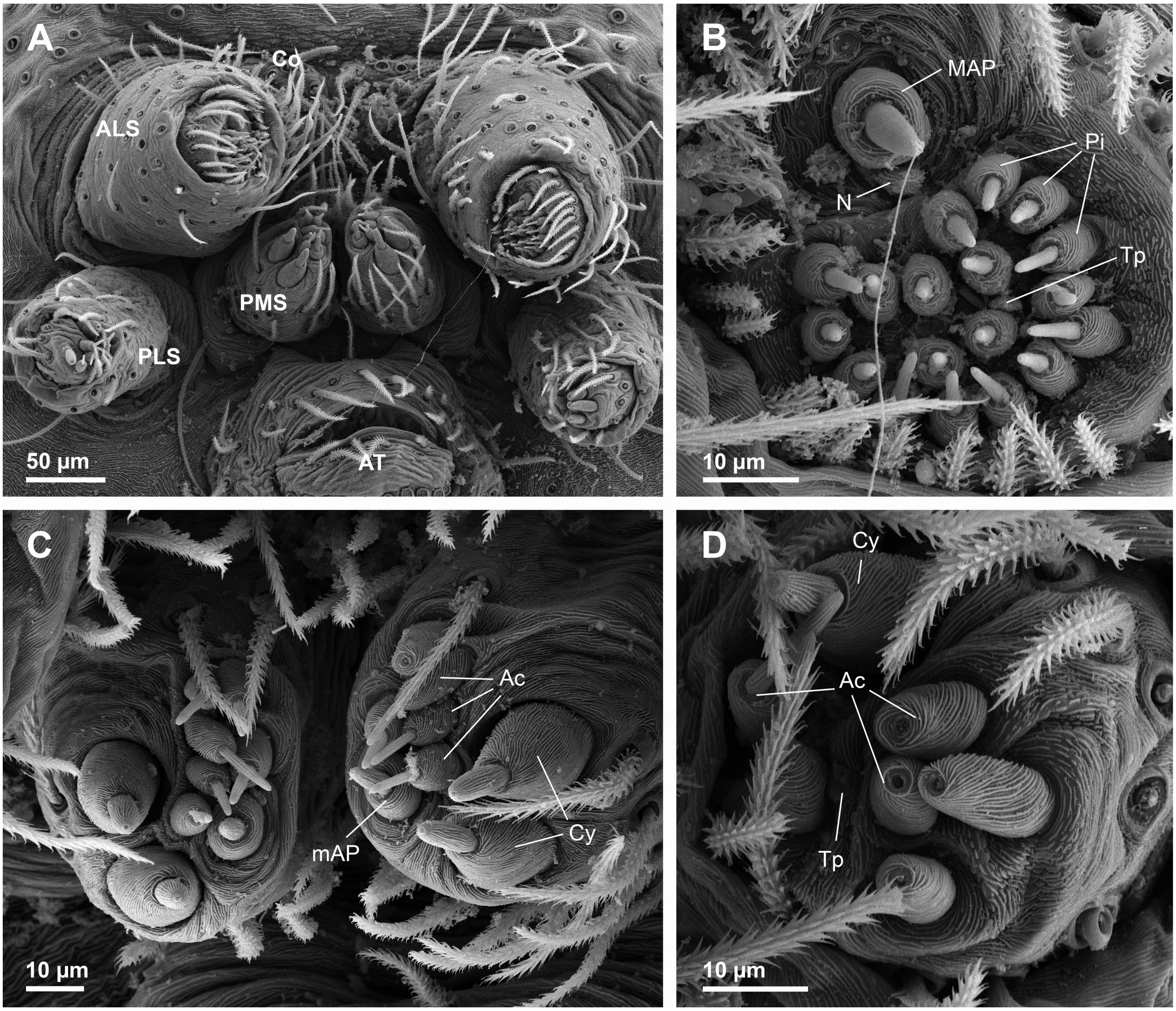

Figure 3. Scanning electron micrographs of spinnerets of *Cybaeolus pusillus* Simon, 1884, female. A, overview. B, ALS left. C, overview of PMS. D, PLS left (several Ac spigot shafts broken). Abbreviations: Ac, aciniform gland spigot; AT, anal tubercle; Cy, cylindrical gland spigot; MAP, major ampullate gland spigot; mAP, minor ampullate gland spigot; N, nubbin (atrophied spigot); Pi, piriform gland spigot; Tp, tartipore.

The implied weighting analysis used the same tree-search strategy; before tree search, a weighing concavity was used such that the weight of the most homoplastic characters is 10% of the weight of the characters without homoplasy, following the guidelines of Goloboff *et al.* (2008); this produced a concavity constant k = 19.394709.

RESULTS

Comparative morphology

Spinning organs

We examined the spinnerets of two species of *Cybaeolus*, two typical Hahniidae, and three representatives of closely related families that were formerly placed in Hahniidae.

Cybaeolus pusillus (Figs 3, 4): The spinnerets are grouped and the colulus is represented as two patches of setae. The ALS (Figs 3B, 4C) have an anterior MAP accompanied by a nubbin, and numerous Pi. The PMS (Figs 3C, 4B) have one mAP gland spigot, three to six Ac, and two Cy in the female. The PLS (Figs 3D, 4D) have four to six Ac, and one Cy in the female. The male epiandrum lacks spigots (Fig. 4E).

Cybaeolus rastellus (Figs 5, 6): The spinnerets are grouped and the colulus is represented as two patches of setae. The ALS (Figs 5B, 6B) have an anterior MAP accompanied by a nubbin, and numerous Pi. The PMS (Figs 5C, 6C) have one mAP gland spigot, three to eight Ac, and two Cy in the female. The PLS (Figs 5D, 6D) have five to eight Ac, and one Cy in the female. The male epiandrum lacks spigots (Fig. 6E).

Hahnia pusilla C.L.Koch 1841—Hahniidae (Figs 7, 8): The spinnerets are in the transverse arrangement typical of Hahniidae; there is no colulus. The ALS have a single central MAP accompanied by a nubbin, and one Pi in the female; the male lacks Pi. The PMS (Figs 7C, D, 8C) have one mAP, four Ac, and two Cy in the female, and two Ac and a mAP in the male. The PLS (Figs 7E, F, 8D) have an elongated distal article, with numerous Ac gland spigots, and one basal Cy in the female. The male epiandrum lacks spigots.

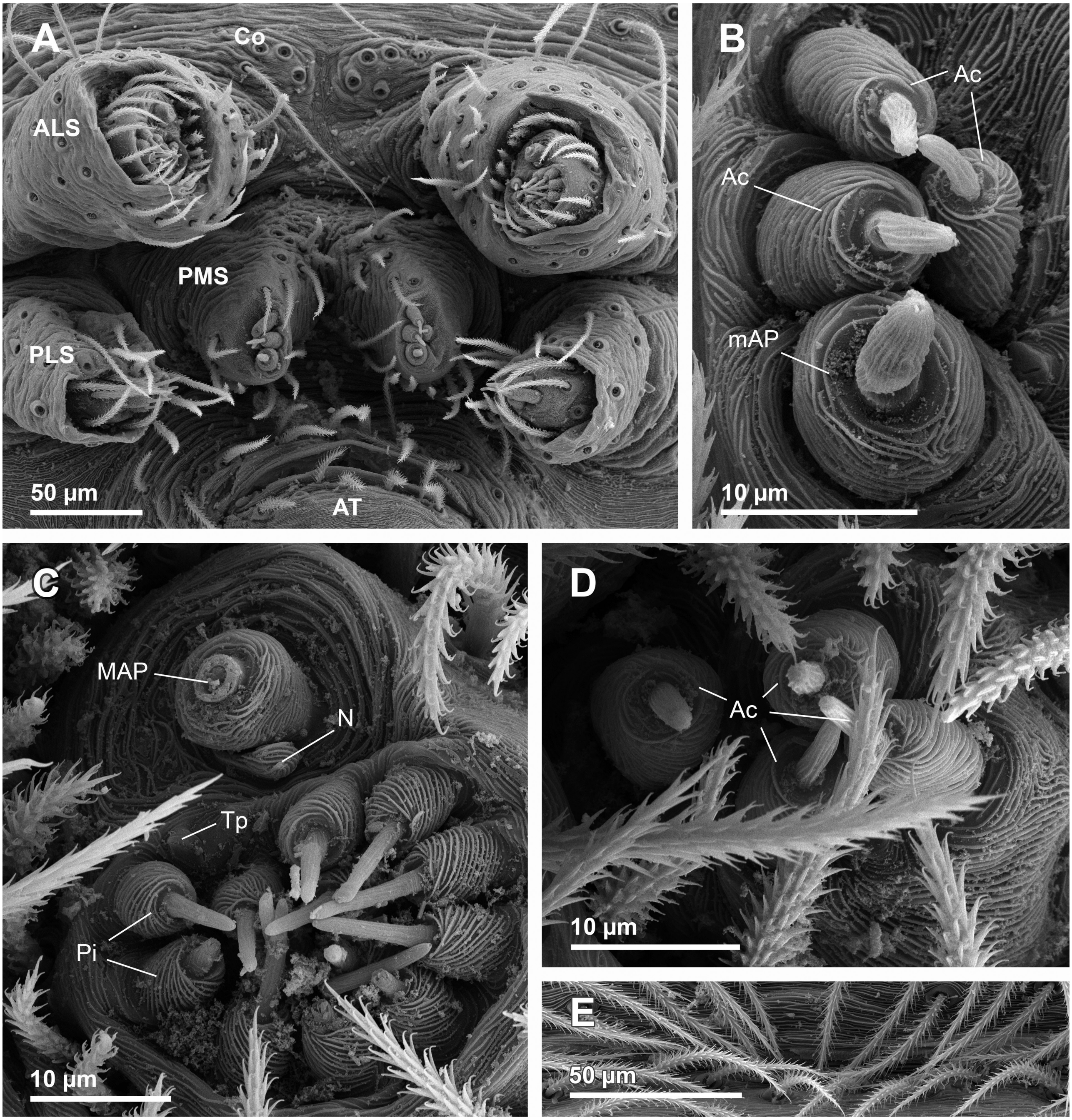

Figure 4. Scanning electron micrographs of spinnerets of *Cybaeolus pusillus* Simon, 1884, male. A, overview. B, PMS left. C, ALS left. D, PLS left. E, epiandrum. Abbreviations: Ac, aciniform gland spigot; AT, anal tubercle; MAP, major ampullate gland spigot; mAP, minor ampullate gland spigot; N, nubbin (atrophied spigot); Pi, piriform gland spigot; Tp, tartipore.

Neoantistea magna (Keyserling, 1887)—Hahniidae (Figs 9, 10): The spinnerets are in the transverse arrangement typical of Hahniidae, with the PMS in-between the ALS; there is no colulus. The ALS have a single MAP accompanied by a nubbin (Figs 9B, 10B), and four Pi in the female; the male lacks Pi. The PMS (Figs 9C, 10C) have numerous Ac, and two Cy in the female; we did not identify any spigot that might be a mAP (mAP of male labelled in Fig. 10C). The PLS (Figs 9D, E, 10D) have an elongated distal article with numerous Ac, and one basal Cy in the female. The male epiandrum lacks spigots.

Cicurina cicur (Fabricius, 1793)—Cicurinidae (Figs 11, 12): The spinnerets are grouped and the colulus is entire. The ALS (Figs 11B, 12B) have a single MAP accompanied by a nubbin (N) and numerous Pi. The PMS (Figs 11C, 12C) have a single mAP, numerous Ac, and three Cy in the female. The PLS (Figs 11D, 12D) have numerous Ac, probably three basal Cy in the female [not seen in our images but illustrated in (Murphy and Roberts, 2015)], and a central large spigot that is atrophied in the male and hence may be a pseudoflagelliform gland spigot.

Calymmaria persica (Hentz, 1847)—Cybaeidae (Fig. 13): The spinnerets are grouped and the colulus is entire. The ALS

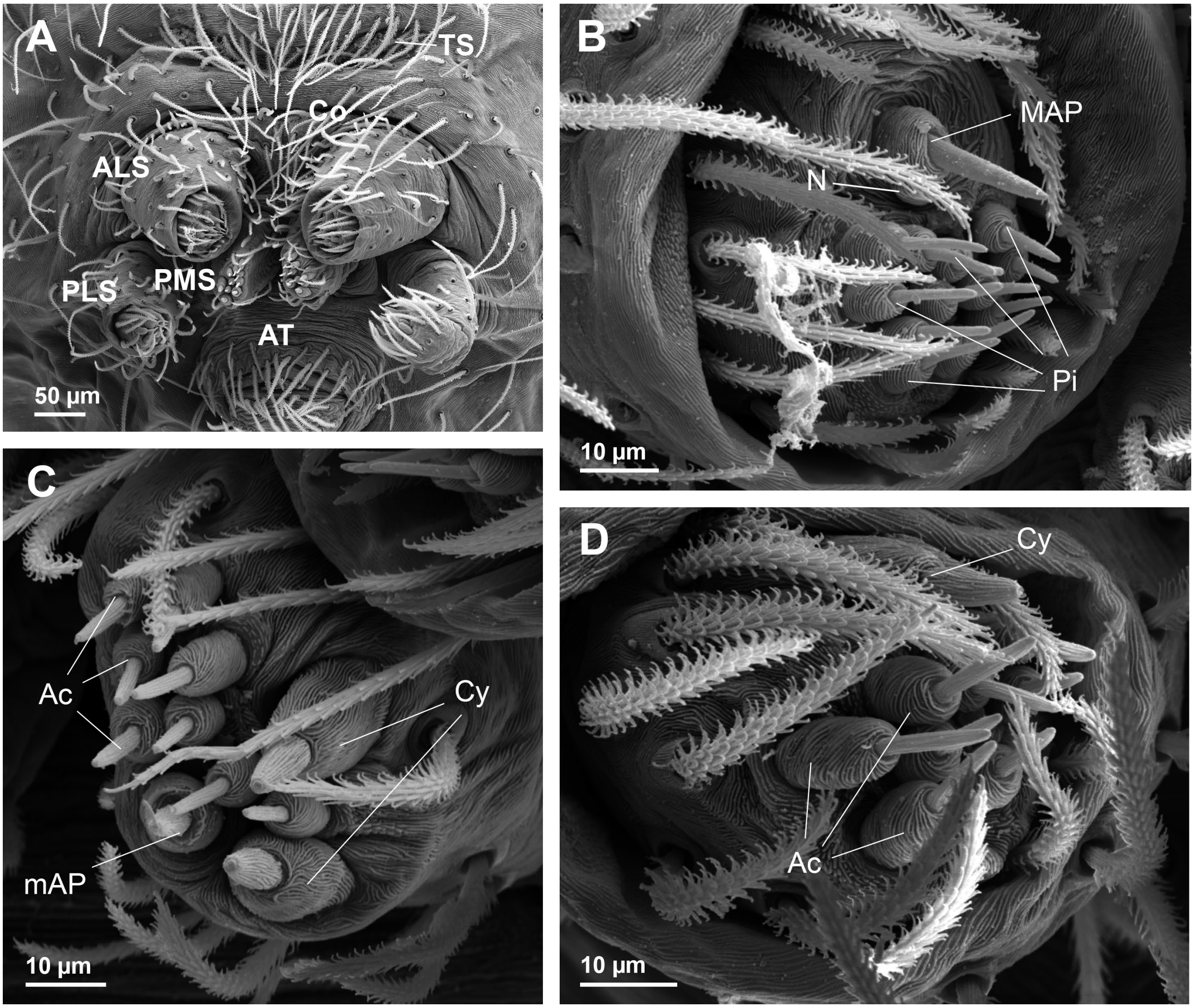

Figure 5. Scanning electron micrographs of spinnerets of *Cybaeolus rastellus* (Roth, 1967), female. A, overview. B, ALS right. C, PMS left. D, PLS right. Abbreviations: Ac, aciniform gland spigot; AT, anal tubercle; Cy, cylindrical gland spigot; MAP, major ampullate gland spigot; mAP, minor ampullate gland spigot; Pi, piriform gland spigot; TS, tracheal spiracle.

(Fig. 13A, E) have a single major ampullate gland spigot (MAP) and numerous piriform gland spigots (Pi). The PMS (Fig. 13C, F) have a single minor ampullate gland spigot (mAP), numerous aciniform gland spigots (Ac), and two cylindrical gland spigots (Cy) in the female. The PLS (Fig. 13B, G) have numerous Ac, and two Cy in the female. The male epiandrum lacks spigots.

Cryphoeca silvicola (C.L.Koch 1834)—Cybaeidae (Fig. 14): The spinnerets are grouped, although the ALS are separated by a diameter, and the PMS are slightly advanced in-between (Fig. 14A, E). The colulus is represented as a pair of patches of hairs [not clear in our images but illustrated in Murphy and Roberts (2015)]. The ALS (Fig. 14B, F) have a single major ampullate gland spigot (MAP) and three or four piriform gland spigots (Pi); the MAP has the same morphology as the Pi, and is identified by the adjacent nubbin and by the strain sensilla of the major ampullate field. The PMS (Fig. 14C, G) have numerous aciniform gland spigots (Ac), and three cylindrical gland spigots (Cy) in the female; there are no evident minor ampullate gland spigots (mAP); given the unremarkable morphology of the MAP in the ALS, it is possible that the mAP are present but not different from the Ac. The PLS (Fig. 14D, H) have numerous Ac, but no Cy in the female.

Male palp

The male palps of the studied hahniid representatives have a relatively simple retrolateral patellar apophysis (Figs 15A, D, G, 16A, D, F). In *Cybaeolus*, this apophysis has several apical thorns (Fig. 15D). The retrolateral tibial apophysis (RTA) is acute and curved, with regularly arranged ridges towards the tip, and a groove from the base to the tip (Figs 15I–L, 16D–H). The retrolateral margin of the cymbium also has a groove leading to the base of the RTA (Figs 15J, K, 16C, E). The copulatory bulb is relatively simple; the embolus is solidly affixed to the tegulum and encircles the bulb clockwise (left palp, ventral view). *Cybaeolus rastellus* and *Hahnia pusilla* have a membranous projection on the tegulum (Figs 15E, H, 16A, C) that we tentatively identify as a median apophysis, but this is absent in *Neoantistea magna* (Fig. 16E). It has been reported for other species that the

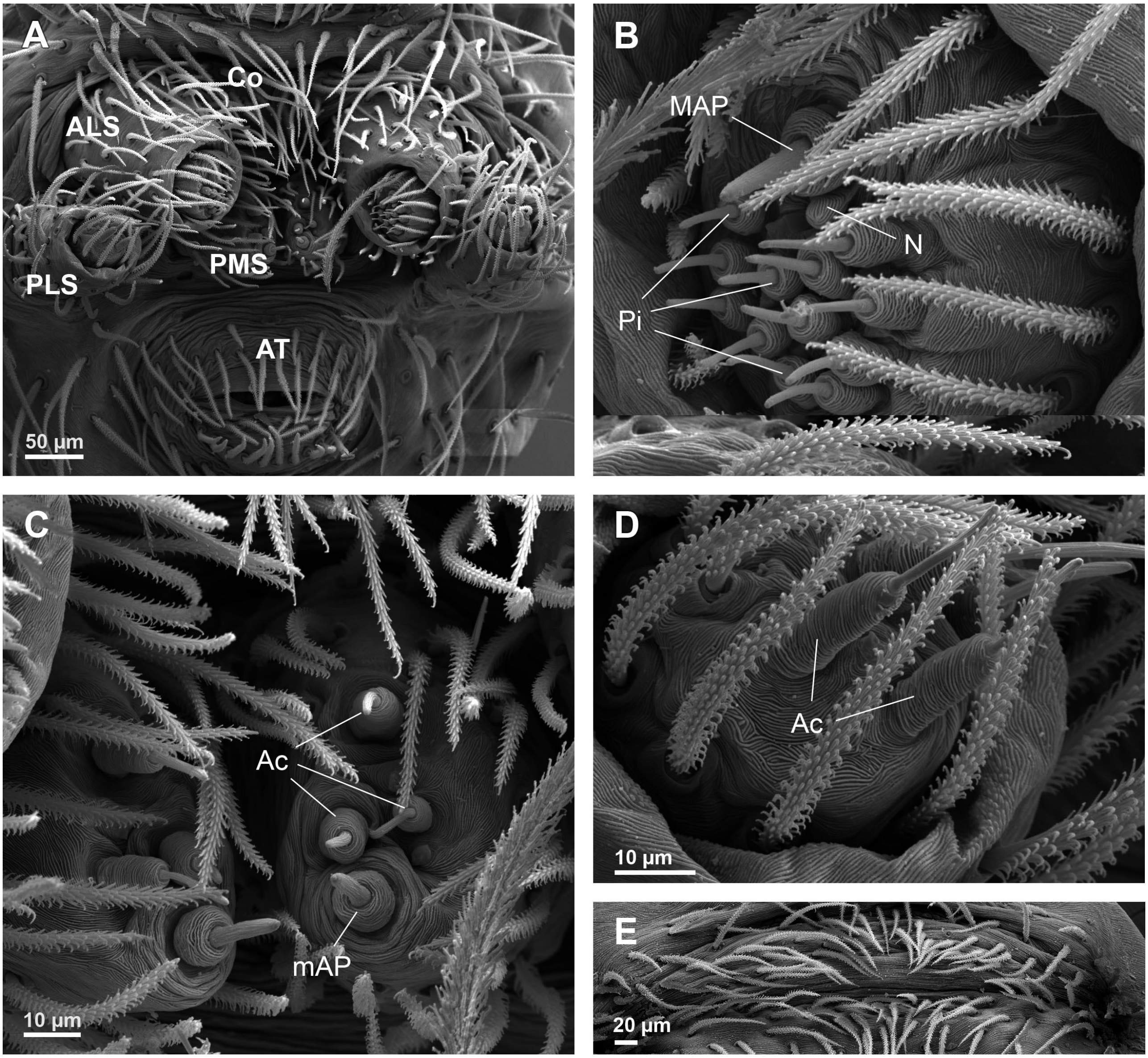

Figure 6. Scanning electron micrographs of spinnerets of *Cybaeolus rastellus* (Roth, 1967), male. A, overview. B, ALS left. C, overview of PMS. D, PLS right. E, epiandrum. Abbreviations: Ac, aciniform gland spigot; AT, anal tubercle; MAP, major ampullate gland spigot; mAP, minor ampullate gland spigot; N, nubbin (atrophied spigot); Pi, piriform gland spigot.

embolus is sometimes found running through the cymbial and RTA grooves, projecting from the tip of the RTA, as illustrated in *Intihuatana antarctica* (Lehtinen 1967: fig. 372) and *Neoantistea inaffecta* (Opell and Beatty 1976: fig. 69).

Taxonomy

Hahniidae Bertkau, 1878

Hahniidae Bertkau 1878: 393 (type genus *Hahnia* C.L.Koch, 1841).

Diagnosis

Members of Hahniidae resemble other entelegyne spiders of the RTA clade by having entelegyne genitalia and a retrolateral tibial apophysis in the male palp, but (except for *Cybaeolus*) differ by having the anterior lateral spinnerets well separated, with the posterior medians advanced in-between them, and the posterior laterals well separated, behind the anterior laterals or, most usually, at their sides, so that all the spinnerets are arranged in a row (Figs 7–10). Additionally, they, including *Cybaeolus*, can be recognized by the male palp with retrolateral tibial apophysis that has a canal, usually curved upwards and with an acute tip bearing regular teeth, a retrolateral patellar apophysis (absent in *Amaloxenops* Schiapelli and Gerschman, 1958 and *Antistea* Simon, 1898), and the simple copulatory bulb with the thin embolus circling clockwise (left palp, ventral view), without conductor, and sometimes with a lightly sclerotized median apophysis as a simple lobe (Figs 15, 16). *Cybaeolus* has grouped spinnerets (Figs 3–6), but the male genitalia have the mentioned diagnostic characters; *Amaloxenops* and *Antistea* lack the patellar apophysis, but the tibial apophysis and the spinnerets are typical of the family.

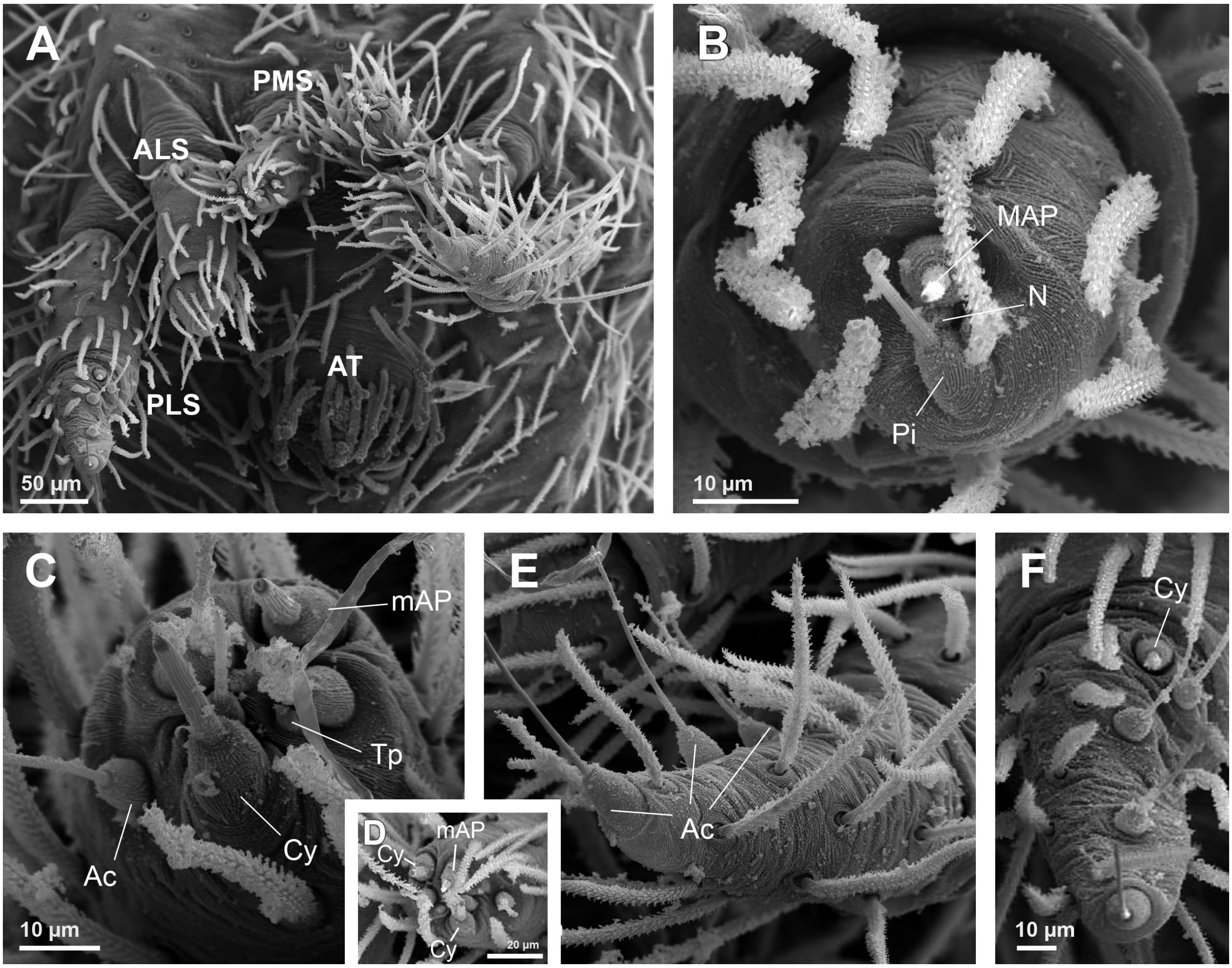

Figure 7. Scanning electron micrographs of spinnerets of *Hahnia pusilla* (C.L.Koch, 1841), female. A, overview. B, ALS left. C, PMS left. D, PMS right. E, PLS left. F, PLS right. Abbreviations: Ac, aciniform gland spigot; AT, anal tubercle; Cy, cylindrical gland spigot; MAP, major ampullate gland spigot; mAP, minor ampullate gland spigot; N, nubbin (atrophied spigot); Pi, piriform gland spigot; Tp, tartipore.

Note

The family Hahniidae traditionally listed only representatives with spinnerets in the characteristic arrangement of a transverse line, until Lehtinen (1967) expanded the family limits to include *Cybaeolus*, with grouped spinnerets, plus several genera now placed in Cybaeidae and Cicurinidae (see: Wheeler *et al.* 2017, Castellucci *et al.* 2023, Gorneau *et al.* 2023). Some hahniids have the posterior lateral spinnerets behind the anterior laterals (e.g. *Lizarba* Roth, 1967, *Paramito* Dupérré and Tapia, 2024), others slightly behind and at the sides (e.g. *Austrohahnia* Mello-Leitão, 1942), and in many the posterior laterals are more at the side of the anterior laterals; this variation forms a continuum. The above diagnosis is provided to reflect those changes.

Hahniinae Bertkau, 1878

Hahniinae Bertkau 1878: 393 (type genus *Hahnia* C.L.Koch, 1841).
Cybaeolinae Lehtinen 1967: 226 (type genus *Cybaeolus* Simon, 1884), synon. nov..

Note

Lehtinen (1967) originally included in Cybaeolinae the genera *Cybaeolus* Simon, 1884, *Lizarba* Roth, 1967, and tentatively *Austrohahnia* Mello-Leitão, 1942. This last genus was tentatively included by Lehtinen (1967: 217) without having seen the type, but he thought that it might be a synonym of *Cybaeolus*. Rubio *et al.* (2014) revised the genus *Austrohahnia* Mello-Leitão, 1942 and transferred it to Hahniinae. Our phylogenetic analysis indicates that *Cybaeolus* is nested within Hahniidae, along with other genera typically considered hahniines, thus we synonymize Cybaeolinae with the older name Hahniinae. For a future revision of the classification of the family, Cybaeolinae remains an available subfamily name.

Cybaeolus Simon, 1884

Cybaeolus Simon 1884: 125 (type species by monotypy *Cybaeolus pusillus* Simon, 1884); 1898: 244.
Mevianes Simon 1904: 110 (type species *M. delfini* Simon, 1904, designated by Petrunkevitch (1928: 93). Synonymized by Lehtinen (1967: 226).
Clitistes Simon 1902: 20 (type species by monotypy *Clitistes velutinus* Simon 1902), synon. nov..

Diagnosis

Species of *Cybaeolus* resemble other hahniids by having a retrolateral hook-shaped tibial process with a groove through

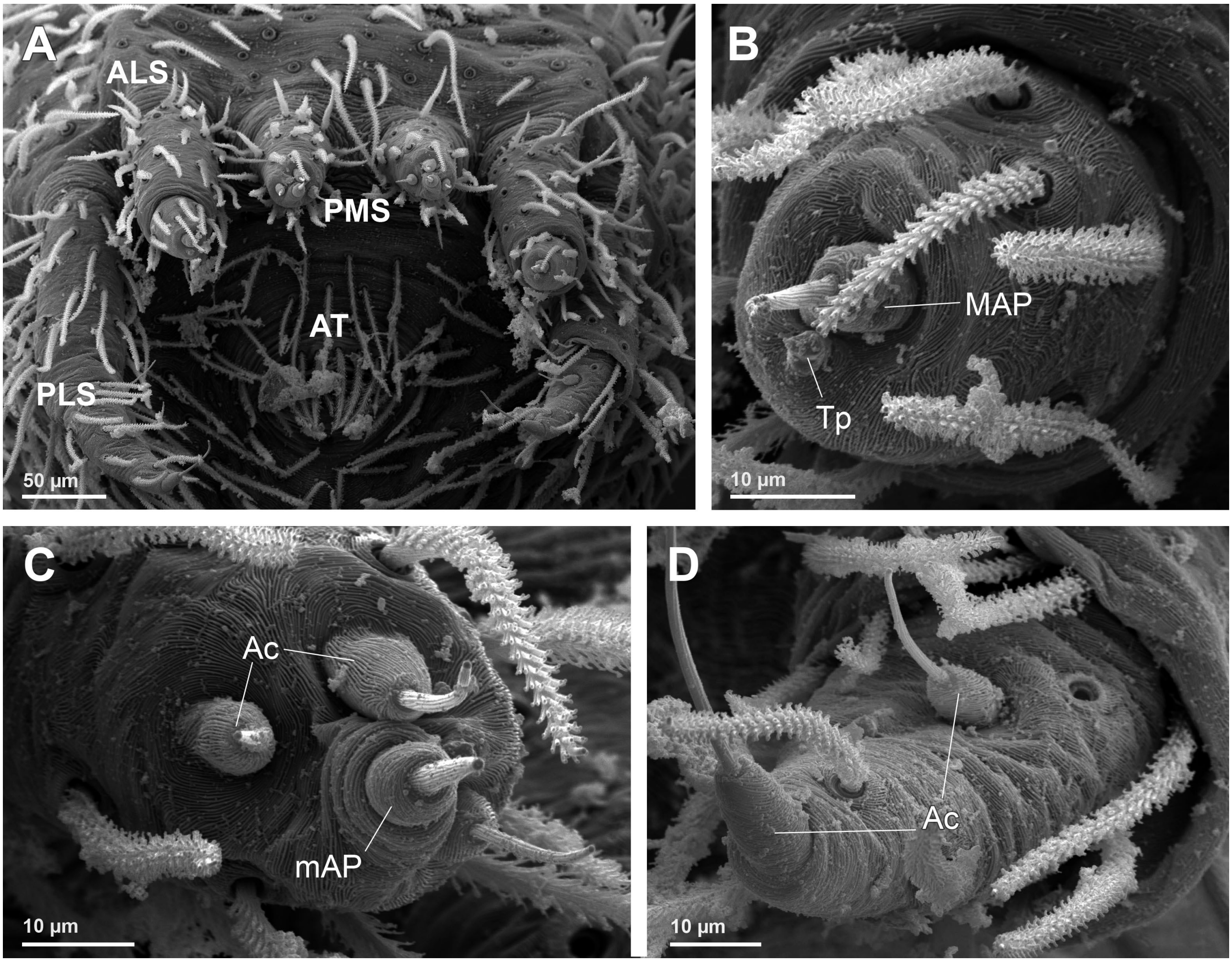

Figure 8. Scanning electron micrographs of spinnerets of *Hahnia pusilla* (C.L.Koch, 1841), male. A, overview. B, ALS left. C, PMS left. D. PLS left. Abbreviations: Ac, aciniform gland spigot; AT, anal tubercle; MAP, major ampullate gland spigot; mAP, minor ampullate gland spigot; Tp, tartipore.

which (presumably) the embolus slides (Fig. 15I–K), but are distinguished by having a retrolateral patellar process with two or more tips (Fig. 15D), and spinnerets arranged in a group with the PMS posterior to the ALS (Figs 3–6), instead of arranged in a line or having the PMS advanced in between the ALS.

Description

Small spiders (1.50–3.50) with eight eyes (Fig. 15A), anterior eye row slightly procurved in anterior view, posterior row slightly procurved to straight in dorsal view, AME normally developed, PME separated by one diameter of PME, clypeus no greater than 2.5× diameter of AME. Colour patterns of prosoma, and especially of opisthosoma, extremely polymorphic (Figs. 21A, 22, 23A, 24, 25D, 26E, 27). Carapace light brown, with or without thoracic markings, without foveal furrow. Opisthosoma oval or elongate, it can be dark, pale, orange, or brown, mottled, with or without chevrons. Chelicerae with three or four promarginal and three retromarginal teeth, male with or without stridulatory file made of minute bumps, rastellum (a row of rake setae with thickened bases; Fig. 18C) present in females of *C. delfini* and *C. rastellus*, absent in *C. pusillus*. Endites not convergent, serrula in a transverse line (Fig. 18B), posterior external margin variably inflated or projecting in males. Labium slightly wider than long, anterior edge straight, posterior slightly convex. Sternum shield-shaped, weakly concave anteriorly at base of labium. Male palp with simple retrolateral patellar apophysis with two or more distal thorns (Fig. 15D), RTA acute, curved, furrowed, tip with regular teeth pointing backwards (Figs 15I–K); a swollen area near the RTA base bears several thick setae. Cymbium oval, with retrolateral furrow leading to RTA (Fig. 17J). Copulatory bulb with disc-shaped tegulum, with a membranous patch where the fleshy median apophysis arises in *C. delfini* and *C. rastellus;* only the membranous patch present in *C. pusillus*. Embolus arising proximally from tegulum, rotating clockwise (left palp, ventral view).

Epigyne with paired copulatory openings, usually blocked with mating plugs (Figs 17H, 18G). Copulatory ducts long, leading to spherical spermathecae, fertilization ducts short, on posterior margin; accessory bulb unremarkable, restricted to small bump with gland ducts near the copulatory opening (observed only in *C. rastellus*; Fig. 18I). Spinnerets (Figs 3–6) in relatively compact group, PLS 70–80° from ALS, PMS 40–50° from ALS. ALS conical with wide base, PLS and PMS cylindrical, PLS equal in length to ALS, distal segment of ALS very short; distal

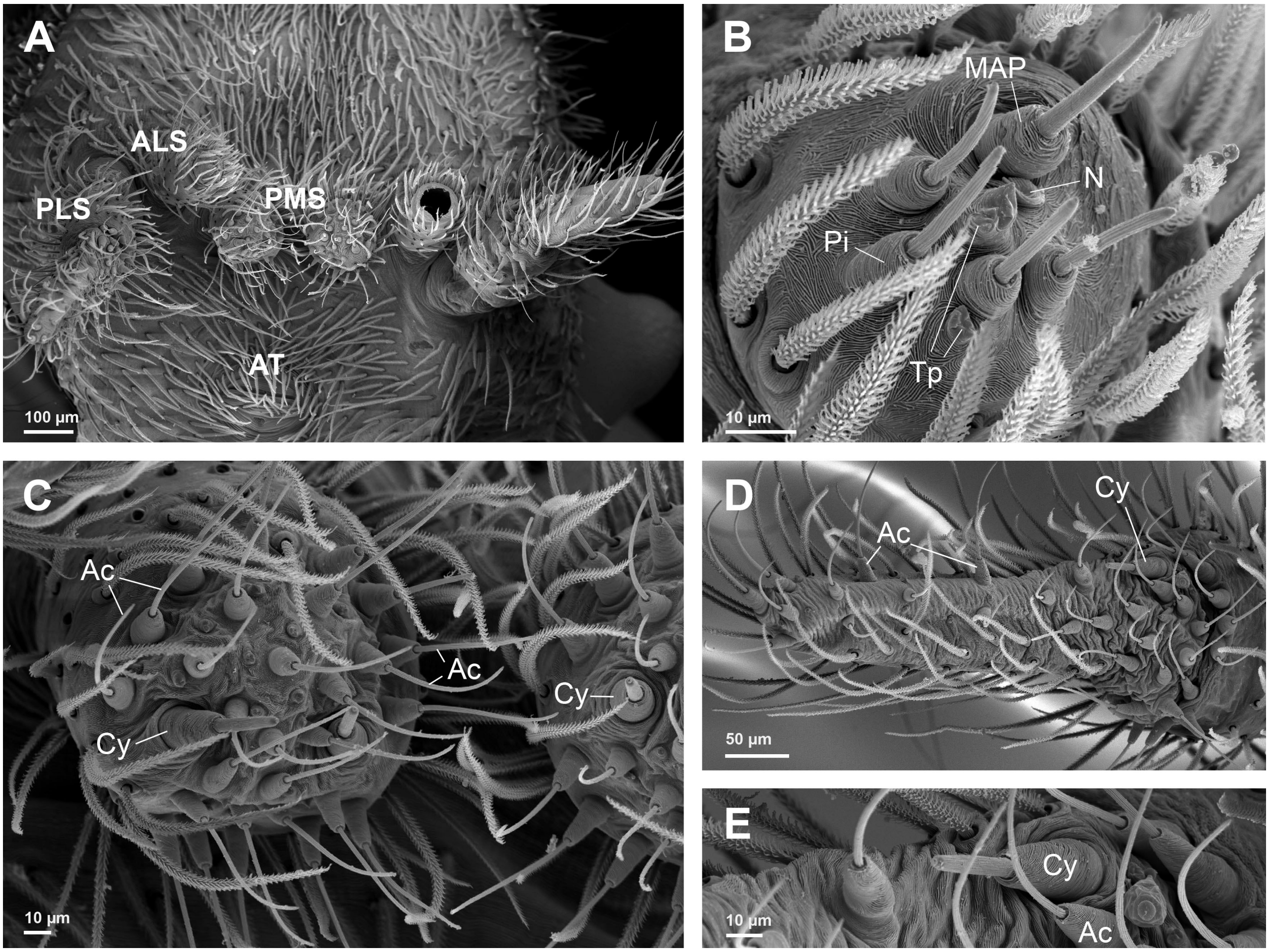

Figure 9. Scanning electron micrographs of spinnerets of *Neoantistea magna* (Keyserling, 1887), female. A, overview. B, ALS right. C, PMS right. D, PLS right. E, same, detail. Abbreviations: Ac, aciniform gland spigot; AT, anal tubercle; Cy, cylindrical gland spigot; MAP, major ampullate gland spigot; mAP, minor ampullate gland spigot; N, nubbin (atrophied spigot); Pi, Piriform gland spigot; Tp, tartipore.

segment of PLS very short, PLS not extended, length equal to or smaller than ALS. Colulus as two patches of setae. Spigot morphology (examined with SEM in adults of *C. pusillus* and *C. rastellus*): ALS with one major ampullate gland spigot flanked by a nubbin, and 10–18 piriform gland spigots. PMS with one minor ampullate gland spigot, two cylindrical gland spigots in female, from five to eight aciniform gland spigots. PLS with one cylindrical gland spigot in female, from six to 11 aciniform gland spigots. Tracheal spiracle wide, slightly separated from spinnerets, leading to two thick trunks, each ramifying in three bundles of tracheoles, all limited to opisthosoma (observed from dissection of *C. rastellus*; Fig. 18E). Leg formula 1243. Spination: femora I with dorsal and prolateral spines, patellae with two dorsal spines, tibiae I and II with dorsal and prolateral spines, tibiae II and IV with dorsal, prolateral, ventral, and retrolateral spines, metatarsi III and IV with prolateral, retrolateral, and ventral spines. Trichobothria with longitudinal fingerprint striae on proximal plate (Fig. 17F), arranged on tarsi d0-1-0 or d0-1-1-0 (Figs 17D, 18D), metatarsi d0-1-0 and tibiae d0-1-0. Tarsal organ a simple keyhole (Fig. 17G).

Composition

Three species: *Cybaeolus pusillus*, *Cybaeolus rastellus*, and *Cybaeolus delfini*.

Distribution

In temperate forests and shrublands of Chile, from Región de Antofagasta to Región de Magallanes, and adjacent Argentina, from Neuquén province to Tierra del Fuego province.

Cybaeolus pusillus Simon, 1884

(Figs 1C, F, 2A–I, K, L, 3, 4, 17, 19A–C, 20A, B, 21, 22, 28A)

Cybaeolus pusillus Simon 1884: 125 [female holotype from Bahía Orange (Isla Hoste, *c.* –55.531, –68.04), Magallanes, Chile, in MNHN, examined]; 1887: E17. Roth 1967: 315, pl. 50, figs 4–6. Lehtinen 1967: 226, fig. 353. Wheeler *et al.* 2017: fig. 5 (voucher ARASP17).

Dictyna fuegiana Simon 1895: 168 [female type from Tierra del Fuego, M.C. Bachkausen, in MNHN, examined by Lehtinen (1967)]. Simon 1904: 84. Synonymized by Lehtinen (1967: 226).

Clitistes velutinus Simon 1902: 20 [female lectotype designated by Dupérré and Harms (2018), from Chile, Magallanes, Isla Navarino, Puerto Toro, *c.* –55.0827, –67.0741, Wald, 19.XII.1892, col. Michaelsen, in ZMH-A0000761, not re-examined]. Miller 2007: 269 (nomen dubium); Dupérré and Harms 2018: 8, fig. 5A–C (female redescribed, removed from nomen dubium), synon. nov..

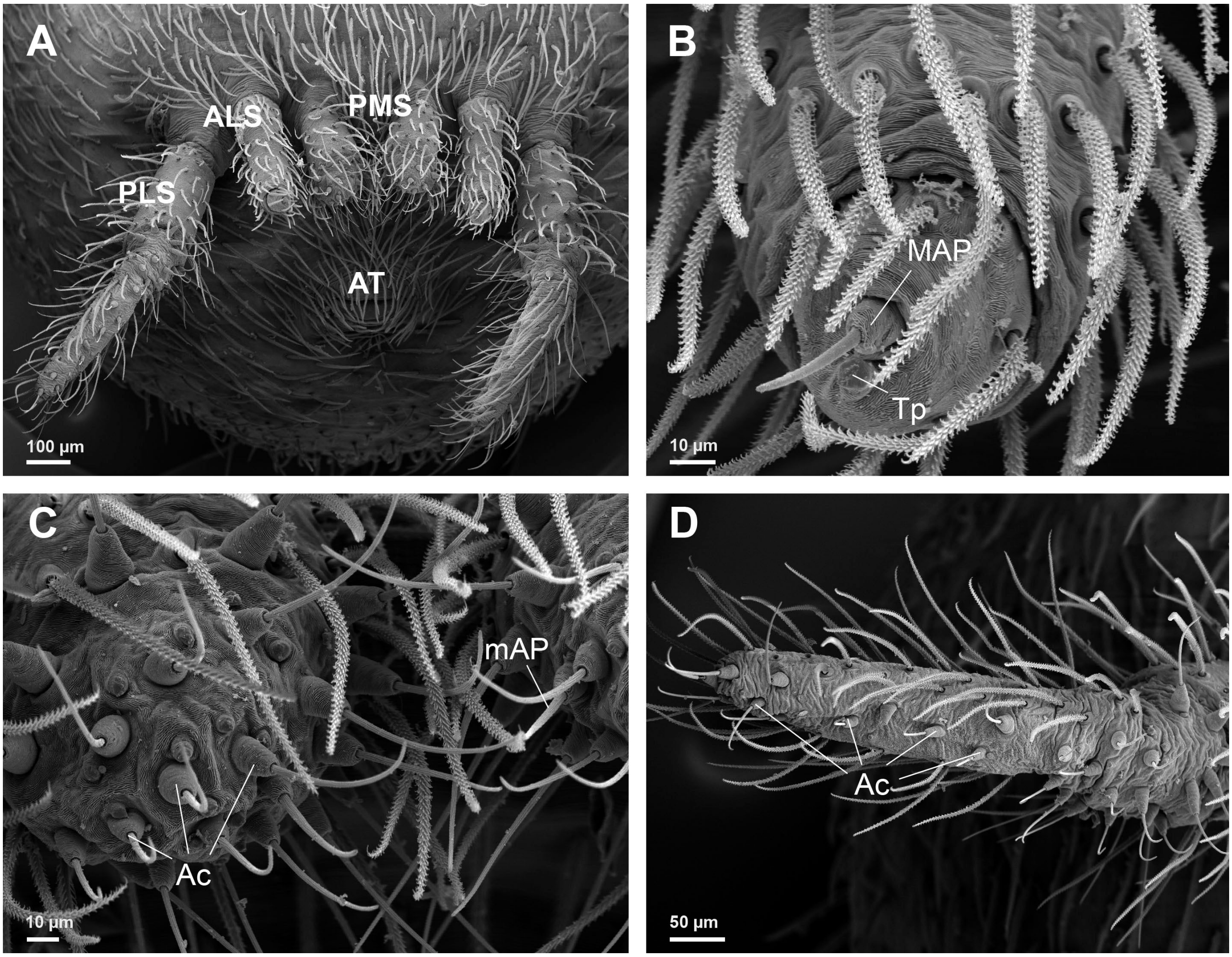

Figure 10. Scanning electron micrographs of spinnerets of *Neoantistea magna* (Keyserling, 1887), male. A, overview. B, ALS left. C, PMS right. D, PLS left. Abbreviations: Ac, aciniform gland spigot; AT, anal tubercle; MAP, major ampullate gland spigot; mAP, minor ampullate gland spigot; Tp, tartipore.

Mevianes wilsoni, Simon 1904: 111 [female holotype from Chile, Magallanes, Bahía Allen Gardiner, *c.* −55.409, −68.301, B. Wilson, in MNHN 22122, examined by Roth (1967) and, Lehtinen (1967)]. Synonymized by Lehtinen (1967: 226).

Diagnosis

Males and females differ from those of other *Cybaeolus* species by lacking a rastellum of thick setae on the cheliceral promargin (Fig. 17B). In addition, males are similar to those of *C. rastellus* by having a dorsally curved retrolateral patellar process with three to five acute tips (Fig. 19A–C), but differ by the lack a median apophysis in the tegulum (Fig. 19A, B), which is found in males of *C. rastellus* (Fig. 19D, E) and *C. delfini* (Fig. 19G, H). Females are similar to those of *C. rastellus* by having the copulatory openings anteriorly in the epigyne but can be distinguished by the copulatory ducts describing complete loops around the spermathecae, visible in ventral view (Figs 20A, 21B, D). In comparison, in *C. rastellus* the loops are restricted to the mesal margins of the spermathecae (Figs 20C, D, 23B–D). The copulatory openings are usually closer to each other than in *C. rastellus*, but this is variable across specimens (Fig. 21D–F).

Description

Male (from Región del Maule, Talca Prov., Alto Vilches, 14–15 Nov. 1993, elev. 1180 m, 35° 36′ S, 71° 04′ W, N.I. Platnick, K.M. Catley, M.J. Ramírez, and R.T. Allen, AMNH; complemented with SEM images from other specimens). Total length 2.36. Carapace 1.00 long, 0.85 wide. Abdomen 1.46 long, 0.86 wide. Eye diameters and interdistances AME 0.05, ALE 0.08, PME 0.07, PLE 0.07, PLE 0.08; AME–AME 0.04, AME–ALE 0.03, PME–PME 0.07, PME–PLE 0.06, ALE–PLE contiguous; MOQ length 0.18, anterior width 0.14, posterior width 0.21. Clypeus height 0.14 (2.8× diameter of AME), orange-brown without marks. Carapace bright orange-brown, thoracic marks extremely faint. Chelicerae length 0.39, ratio 0.45, orange brown, external-posterior side with subtle stridulatory file. Endites orange-brown, not projecting posteriorly. Labium yellow-brown. Sternum slightly wider than long, length 0.57, width 0.64, orange-brown, darker towards edges. Abdomen dorsum mottled white with brick-red stripe over cardiac region extending posteriorly to four indistinct chevrons, laterally dark grey; venter silvery white with dusky median area, broad brick-red band around spinnerets. Pedipalp femur, patella and tibia light-yellow,

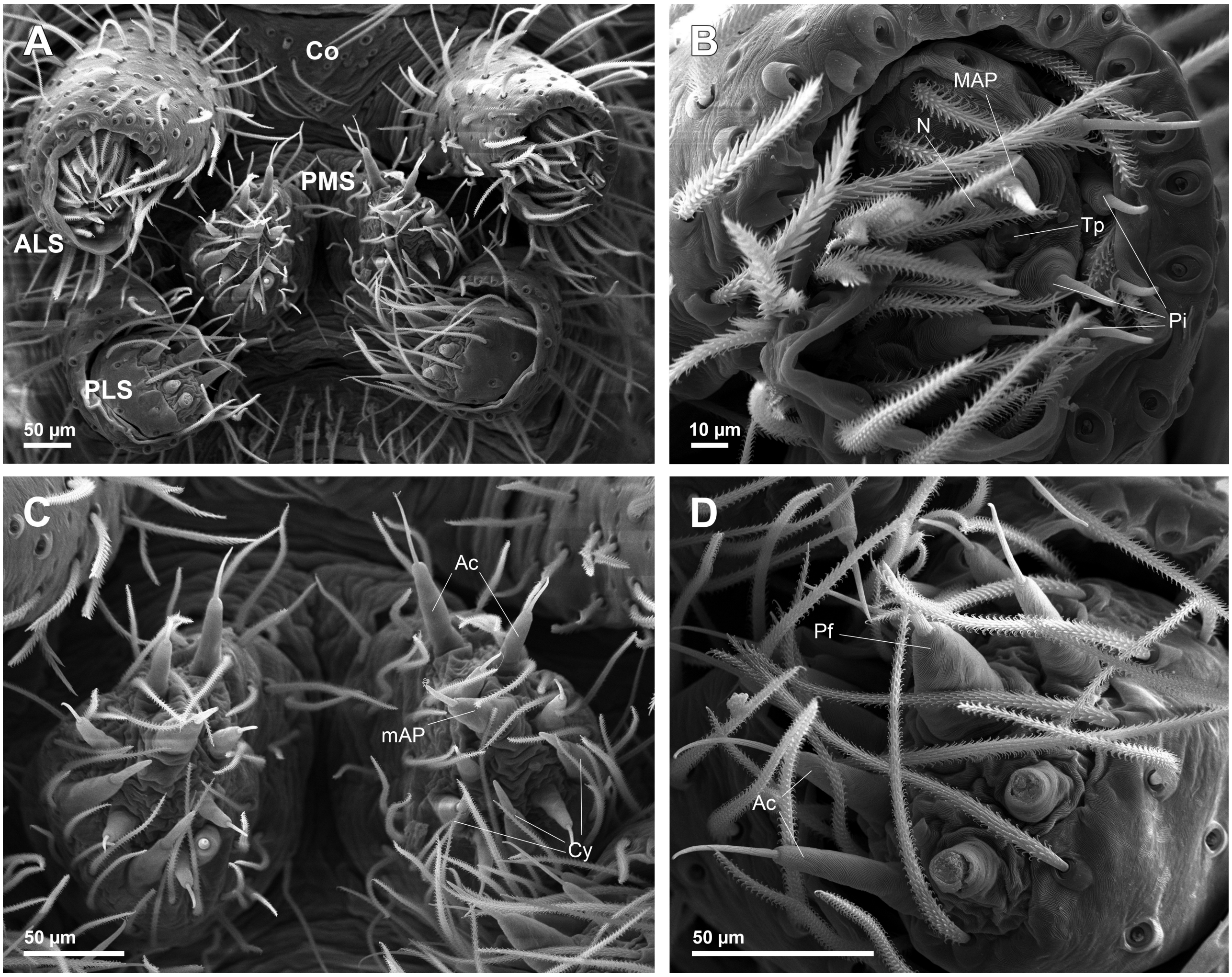

Figure 11. Scanning electron micrographs of spinnerets of *Cicurina cicur* (Fabricius, 1793), female. A, overview. B, ALS left. C, overview of PMS. D, PLS left. Abbreviations: Ac, aciniform gland spigot; Cy, cylindrical gland spigot; MAP, major ampullate gland spigot; mAP, minor ampullate gland spigot; N, nubbin (atrophied spigot); Pf, pseudoflagelliform gland spigot; Pi, piriform gland spigot; Tp, tartipore.

cymbium dark brown. Pedipalp cymbium distinctly rounded, median apophysis absent, only a pale unsclerotized patch in its place (Fig. 19B); tibial apophysis long and procurved, patellar apophysis recumbent on retrolateral surface armed with three or four teeth (Fig. 19B, C). Spinnerets in relatively compact group (Fig. 4A), pigmented, dusky-yellow with distal segments darker. Proximal segment of ALS 3.8× length of distal segment; distal segment of PLS 0.26× length of proximal segment, PLS length equal to ALS. ALS total length 0.19; basal width 0.09, distal segment length 0.05, proximal segment length 0.14. PMS length 0.12, PLS total length 0.19; distal segment length 0.04, proximal segment 0.15. Spigot morphology: ALS with one major ampullate gland spigot flanked by nubbin, and 12 piriform gland spigots (Fig. 4C). PMS with one minor ampullate gland spigot and three aciniform gland spigots, one slightly larger (Fig. 4B). PLS with four aciniform gland spigots (Fig. 4D). Epiandrous spigots absent (Fig. 4E). Legs all light yellow-brown, femora with black annulations distally, tibiae and metatarsi with faint markings. Leg measurements (formula 1243): leg I (total 3.62) femur 0.89, patella 0.31, tibia 0.89, metatarsus 0.90, tarsus 0.54; leg II (3.55) 0.99, 0.28, 0.86, 0.85, 0.57; leg III (2.91) 0.85, 0.28, 0.67, 0.66, 0.45; leg IV (3.29) 0.97, 0.27, 0.73, 0.81, 0.51; palp (1.02) 0.34, 0.21, 0.14, -, 0.33.

Female (holotype, Fig. 21G–J, complemented with SEM data from other specimens). Total length 2.38. Carapace 1.00 long, 0.80 wide. Abdomen 1.46 long, 0.99 wide. Eye diameters and spacing: AME 0.05, ALE 0.07, PME 0.07, PLE 0.07; AME–AME 0.04, AME–ALE 0.06, PME–PME 0.07, PME–PLE 0.09, ALE–PLE virtually contiguous; MOQ length 0.19, anterior width 0.14, posterior width 0.21. Anterior eye row slightly procurved in anterior view, posterior row slightly procurved in dorsal view. Clypeus height 0.11 (2.2× diameter of AME). Carapace pale-yellow, with no thoracic markings, with only a trace of black border to Carapace. Chelicerae without rastellum (Fig. 17B). Endites yellow-brown, as long as wide, posterior lateral edge rounded. Sternum yellow-brown with no markings, slightly wider than long. Abdomen dorsum mottled white over entire surface, anterior mid-dorsal aspect with darker line; venter white mottled blotches. Epigyne flat, centrally rugous, copulatory ducts open medially and anteriorly (Figs 17H, I, 20A, B, 21B, D, G, H), beginning with a lateral loop that passes dorsally to the spermatheca and continues in a second ventral loop that

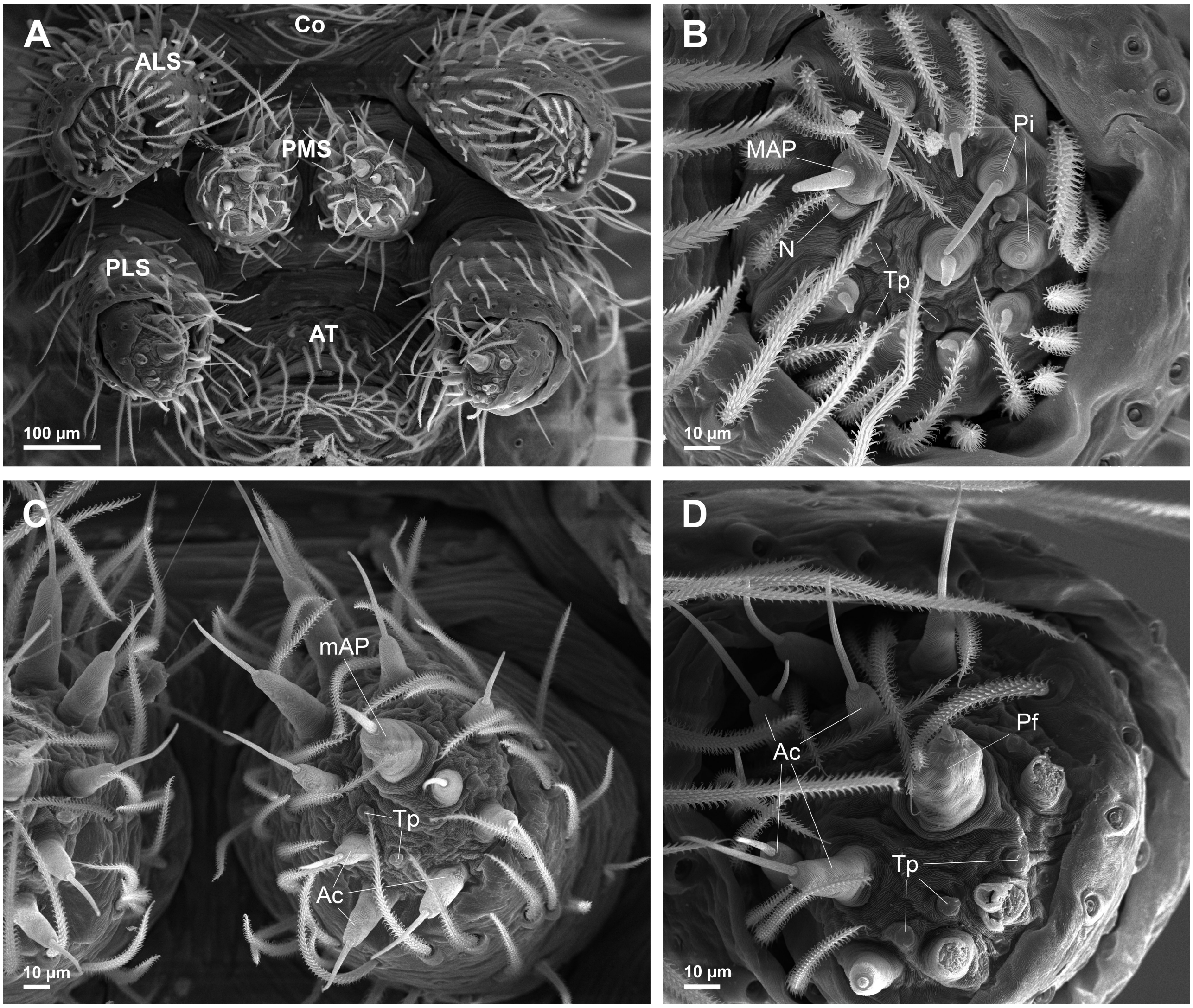

Figure 12. Scanning electron micrographs of spinnerets of *Cicurina cicur* (Fabricius, 1793), male. A, overview. B, ALS left. C, PMS left. D, PLS left. Abbreviations: Ac, aciniform gland spigot; AT, anal tubercle; MAP, major ampullate gland spigot; mAP, minor ampullate gland spigot; N, nubbin (atrophied spigot); Pf, atrophied pseudoflagelliform gland spigot; Pi, piriform gland spigot; Tp, tartipore.

surrounds it; spermathecae large, spherical. Spinnerets in relatively compact group (Fig. 3A), yellow-brown. ALS conical with wide base, PLS and PMS cylindrical, proximal segment of ALS 8× length of distal segment; distal segment of PLS 0.25× length of proximal segment, PLS smaller than ALS. ALS total length 0.18; basal width 0.13, distal segment length 0.2, proximal segment length 0.16. PMS length (not accessible); PLS total length 0.15; distal segment length 0.03, proximal segment length 0.12. Spigot morphology (Fig. 3): ALS with major ampullate gland spigot flanked by nubbin, and 12 piriform gland spigots (Fig. 3B). PMS with one minor ampullate gland spigot, one cylindrical gland spigot, and five to six aciniform gland spigots, one slightly larger (Fig. 3C). PLS with one cylindrical gland spigot, six aciniform gland spigots (Fig. 3D). Legs all pale straw-colour with no markings. Leg measurements (formula 2143): leg I (total 2.96) femur 0.83, patella 0.29, tibia 0.67, metatarsus 0.73, tarsus 0.46; leg II (3.07) 0.82, 0.28, 0.71, 0.78 0.48; leg III (2.55) 0.76, 0.28, 0.51, 0.61, 0.39; leg IV (2.89) 0.76, 0.27, 0.72, 0.74, 0.40; palp (1.06) 0.34, 0.18, 0.21, -, 0.33. Pattern of spines: (most spines missing) pedipalp tarsi p1-1-1, r1-1-1. Femora: I p0-0-1 0-1. Tibiae: I d1-0-1; IV d1-0-1, v0-1-0. Metatarsi: III p0-1-1, v0-1-2, r0-0-1; IV p0-1-1, v0-1-2, r0-0-1.

Variability and colour polymorphism

The male endites may be clearly projecting posteriorly (MACN-Ar 46682 MJR-2828) or swollen and slightly projecting (MACN-Ar 29776). The female copulatory openings are usually close to each other (Fig. 21B, D), but they may be more separated in some specimens (Fig. 21E, F). The body coloration is extremely variable (Figs 2A–I, K, L, 22), even among specimens from the same locality and collection event (Fig. 22A, K).

Natural history

Specimens were found in webs on foliage of *Chusquea* bamboo (Fig. 1C) and other trees and shrubs. The eggsacs are affixed to the underside of a leaf and guarded by the female (Fig. 1F).

Distribution

Known from forests in Chile from Parque Nacional Nahuelbuta, in Región de La Araucanía, to Isla Hoste, in Región de

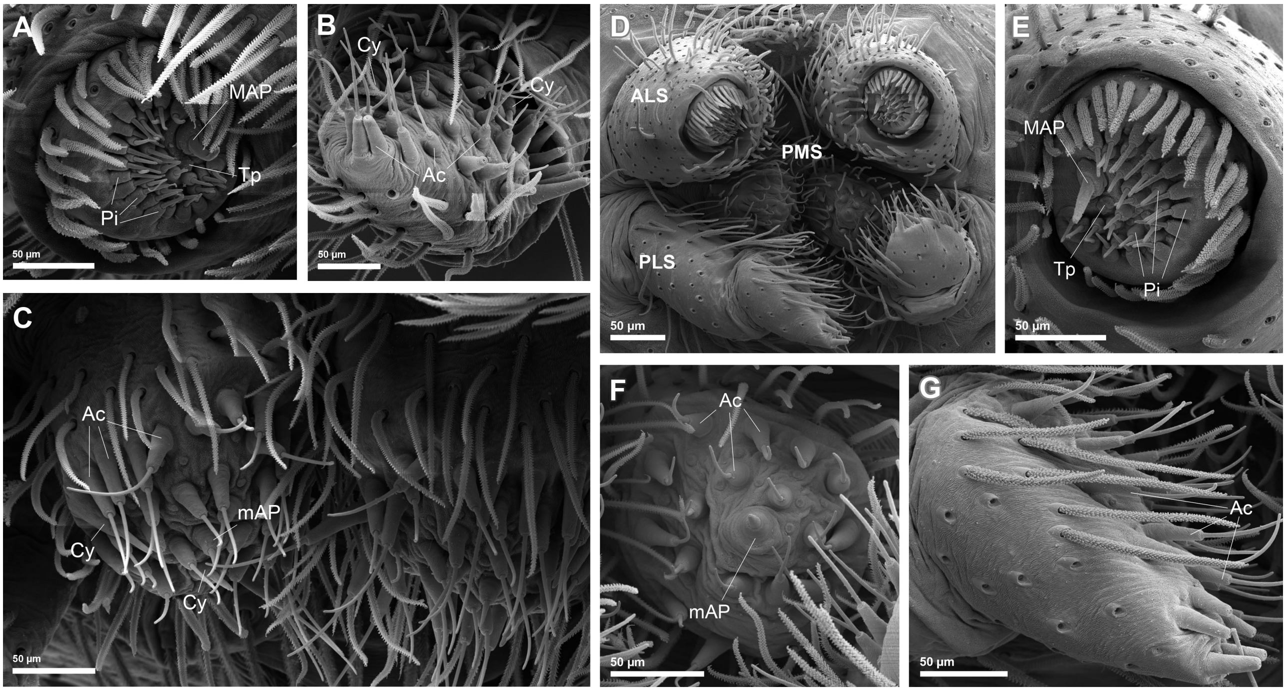

Figure 13. Scanning electron micrographs of spinnerets of *Calymmaria persica* (Hentz, 1847). A–C, female, D–G, male. A, ALS right. B, PLS left. C, overview of PMS. D, overview. E, ALS left. F, PMS left. G, PLS right. Abbreviations: Ac, aciniform gland spigot; Cy, cylindrical gland spigot; MAP, major ampullate gland spigot; mAP, minor ampullate gland spigot; Pi, piriform gland spigot; Tp, tartipore.

Magallanes, and in adjacent Argentina, from Parque Nacional Lanín, in Neuquén Province, to Tierra del Fuego province (Fig. 28A). The gap without records between Parque Nacional Río Simpson in Región de Aysén, and Cueva del Milodón in Región de Magallanes may be due to low sampling effort in the area.

Other material examined

ARGENTINA: Chubut: *Parque Nacional Los Alerces:* Lago Verde [–42.718°, –71.736°], Jan. 1990, M. Ramírez, 3♂ 3♀ (MACN); Lago Verde reaching Río Rivadavia [–42.709°, –71.724°], Feb. 1986, M. Ramírez, 5♂ 20♀ (MACN); Río Menéndez [–42.729°, –71.747°], Jan. 1990, M. Ramírez, 1♀ (MACN). **Neuquén:** *Parque Nacional Lanín:* Lago Hermoso [–40.351°, –71.554°], 15 Jan. 1985, M. Ramírez, 1♂ (MACN). *Parque Nacional Nahuel Huapi:* Lago Espejo Chico, trail to Cerro La Mona, 40.57593 ºS, 71.70100ºW, 860–1060 m elev., 3 Dec. 2023, mainly *Chusquea*, manual collecting, A. Pérez-González, L. Martínez, M. Ramírez, and W. Porto, 1♂ (MACN-Ar 46821); Lago Ortiz Basualdo [–40.983°, –71.864°], Jan. 1990, M. Ramírez, 3♀ (MACN); Puerto Blest, [–41.033436, –71.816678], 7 Jan. 2000, beating, L. Lopardo and A. Quiaglino, 1♀ (MACN-Ar 42790); Puerto Blest, trail to Laguna Los Cántaros, 41.013754º S, 71.822738º W, 820–890 m elev., 28 Dec. 2010, wet forest, M. Ramírez, V. Werenkraut, and S. Aisen, 1♀ (MACN-Ar 33576); 1♀ (MACN-Ar 33592); 1♀ (MACN-Ar 33598); Puerto Blest, Sendero de la Bahía, 41.02583º S 71.82250º W, 789 m elev., 4 Dec. 2024, secondary forest, manual collecting, A. Pérez-González, L. Martínez, M. Ramírez, and W. Porto, 1♂, 2♀ (MACN-Ar 46817); Río Frías [incorrect label as PN Los Alerces] [–41.11°, –71.8°], Feb. 1986, M. Ramírez, 3♀ (MACN). **Río Negro:** *Parque Nacional Nahuel Huapi:* Seccional Villegas, in front of camping La Pasarela de El Manso, 23 km W Río Villegas (air), 41.564945 S, 71.771917 W, 464 m elev., 8–9 Dec. 2021, beating, Pacheco, M. Pacheco, L. Piacentini, and E. Soto, 3♂ (MACN-Ar 43386 AGB-0012). **Tierra del Fuego:** Lago Roca, N margin, 1.3 km SE Chilean border, 54.81699 S, 68.58022 W, 40 m elev., 12 Dec. 2023, mixed forest, beating, M.J. Ramírez, F. Sola, V. Lencinas, and G. Sancho, 1♀ (MACN-Ar 46684 MJR-2827); 1♂ (MACN-Ar MJR-2828). *Isla de los Estados:* Bahía Franklin, Caleta Lacroix [–54.84°, –64.68°], 26 Nov. 2013, on *Berberis ilicifolia*, 2♀ (MACN-Ar 34106). Puerto Cook, S 54.77970, W 64.05944, 13 m elev., 28–30 Nov. 2014, peat with shrubs, beating, I.L.F. Magalhaes and A.O. Porta, 5♂ 8♀ (MACN-Ar 35866); 19♂ 18♀ (MACN-Ar 35877); Puerto Hoppner, S 54.78344, W064.41387, 13 m elev., 25 Nov. 2014, shrubby forest of *Nothofagus betuloides* near coast, beating, I.L.F. Magalhaes and A.O. Porta, 4♂ 7♀ (MACN-Ar 35871); Puerto Hoppner, 4 km (air) NW Puerto Parry, 54.78091 S, 64.40683 W, 10 m elev., 8–9 Mar. 2017, wet coastal forest, mosses, canelo (*Drymis winteri*) and guindo (*Nothofagus betuloides*), M. Ramírez, 1♀, (MACN-Ar MJR-1789); Puerto Parry, 54.81319º S, 64.37043 W, 2 m elev., 26–27 Nov. 2014, forest of *Nothofagus betuloides*, beating, I.L.F. Magalhaes and A.O. Porta, 5♂ 10♀ (MACN-Ar 35824); San Juan de Salvamento, at the end of bay, 54.75294 S, 063.88901 W, 31 m elev., 1 Dec. 2014, forest of *Nothofagus betuloides*, beating, I.L.F. Magalhaes and A.O. Porta, 14♂ 24♀ (MACN-Ar 35838). *Parque Nacional Tierra del Fuego:* road to Cascada Río Pipo 9 km (air) W Ushuaia, 54.82008º S, 68.47024º W, 89 m elev., 4 Dec. 2012, manual collecting and beating, M. Ramírez, C. Grismado, A. Ojanguren, and E.M. Soto, 1♂ (MACN-Ar 29791); E margin of Lago Roca 15 km (air), W Ushuaia, 54.82581 S, 68.56300 W, 11 m elev., 4 Dec. 2012, mixed forest, manual collecting, M. Ramírez, C. Grismado, A. Ojanguren, and E.M. Soto, 1♂ (MACN-Ar 29748); 1♂ 1♀

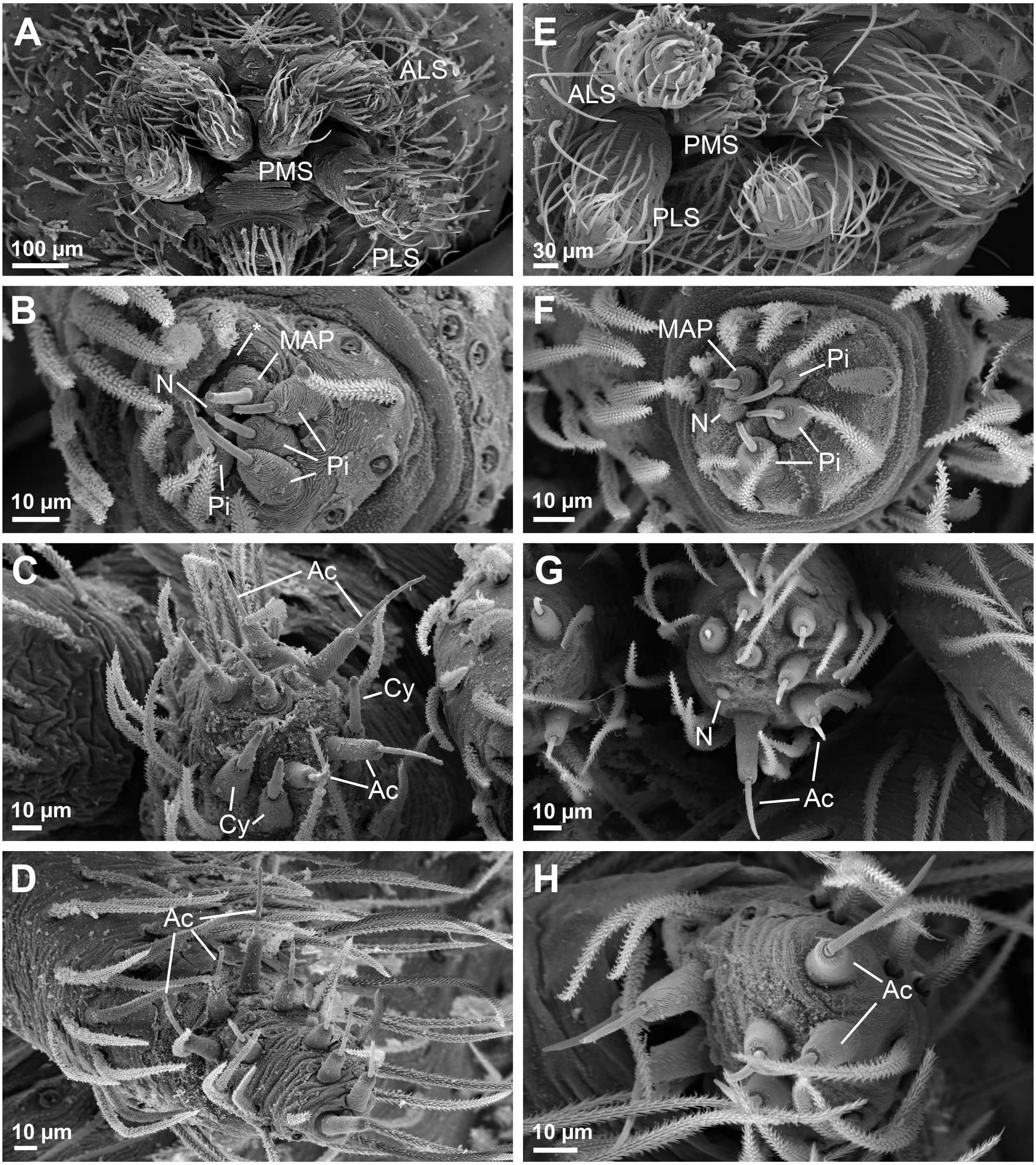

Figure 14. Scanning electron micrographs of spinnerets of *Cryphoeca silvicola* (C.L.Koch, 1834). A–D, female, E–H, male. A, overview. B, ALS left (asterisk to strain sensilla of the major ampullate field). C, PMS left. D, PLS left. E, overview. F, ALS left. G, PMS left. H, PLS right. Abbreviations: Ac, aciniform gland spigot; Cy, cylindrical gland spigot; MAP, major ampullate gland spigot; N, nubbin (atrophied spigot); Pi, piriform gland spigot.

(MACN-Ar 29776 male MLB-04362, female MLB-04363); 4♂ 2♀ (MACN-Ar 29781). Península Mitre, Bahía Buen Suceso, 54.79355 S, 065.2623 W, 15 m elev., 23 Nov. 2014, forest of *Nothofagus*, near coast, beating, I.L.F. Magalhaes and A.O. Porta, 2♂ 1♀ (MACN-Ar 35875). Puerto Español, Península Mitre, 148 km (air) E Ushuaia, 54.90635 S, 65.99230 W, 5 m elev., 5 Mar. 2017, forest with guindo (*Nothofagus betuloides*) and canelo (*Drymis winteri*), M. Ramírez, 1♀, (MACN-Ar MJR-1789). Pta. Aguirre [−54.91°, −66°], 16 Nov. 1949, E.J. Nuñez, 4♀ (MACN-Ar 43426). Ruta B Estancia despedida, 44 km (air) WSW Rio Grande, 53.92318º S, 68.34422º W, 90 m elev., 6 Dec. 2012, forest of ñire (*Nothofagus anctartica*), manual collecting, M. Ramírez, C. Grismado, A. Ojanguren, and E.M. Soto, 2♂ 1♀ (MACN-Ar 29857). **CHILE: Región de Aysén:** Parque

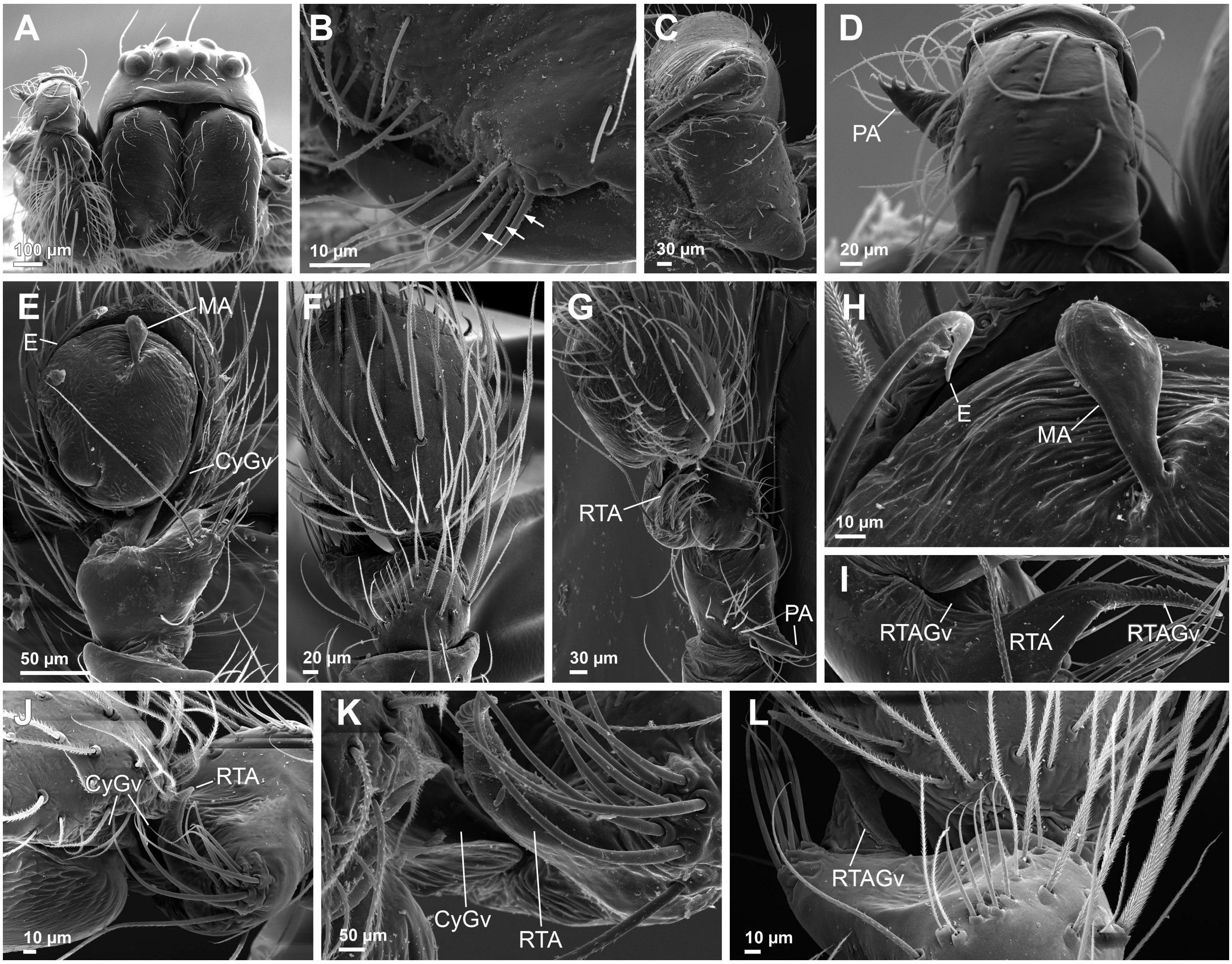

Figure 15. Scanning electron micrographs of male *Cybaeolus rastellus* (Roth, 1967). A, prosoma in anterior view. B, detail of left chelicera in anterior view, showing rake setae with slightly expanded bases. C, left endite, showing posterior lateral edge protruding. D, right palpal patella in dorsal view showing patellar apophysis. E, left palp in ventral view. F, same in dorsal view. G, same in retrolateral view. H, detail of copulatory bulb in ventral view. I, detail of tibial retrolateral apophysis in retrolateral view. J, detail of male palp in retrolateral view. K, same, closeup showing the cymbial groove. L, same, dorsal view, closeup showing the groove on the RTA. Abbreviations: CyGv, cymbial groove of male palp; E, embolus of male palp; MA, median apophysis of male palp; PA, male palpal patellar retrolateral apophysis; RTA retrolateral tibial apophysis of male palp; RTAGv, groove on the retrolateral tibial apophysis of male palp.

Nacional Río Simpson, S margin of Río Simpson [−45.562°, −72.325°], 17 Feb. 1991, M. Ramírez, 2♂ (MACN). **Región de La Araucanía:** Estero Molco [−38.822°, −73.071°], 3 Feb. 1988, T. Cekalovic, 1♀ (AMNH). Cabañas Ruiz, 20.5 km W Angol (air), 37.81290º S, 72.93690º W, 1023 m elev., 11 Jan. 2020, M. Ramírez, E. Soto, J. Wilson, and D. Poy, 1♀ (MACN-Ar 42791). *Monumento Natural Contulmo:* [−38.013°, −73.188°], 300 m elev., 11–12 Feb. 1992, N. Platnick, P. Goloboff, and M. Ramírez, 1♀ (AMNH); [−38.027°, −73.203°], 12 Jan. 1989, M.A. Ramírez, 2♀ (MACN); 38.01314º S, 73.18648º W, 341 m elev., 9 Jan. 2020, M. Ramírez, E. Soto, J. Wilson, and D. Poy, 3♂ 1♀ (MACN-Ar 41386); 38º00′46.2″ S, 73º11′15.4″ O, 360 m elev., 12–13 Jul. 2012, manual night collecting, A. Ojangueren, L. Piacentini, E. Soto, and D. Valdivia, 1♂ (MACN-Ar 42874 LNP-4084); beating, A. Ojangueren, L. Piacentini, E. Soto, and D. Valdivia, 1♀ 1♂ (MACN-Ar 42879); 38º00′46.8″S, 73º11′15.4″ W, 360 m elev., 10–11 Feb. 2005, M. Ramírez and F. Labarque, 1♂ 1♀ (MACN-Ar 42794); Berlese, 1♀ (MACN-Ar 42786). *Parque Nacional Huerquehue:* near Laguna Toro, NE Pucón, 39.14320º S, 71.71238º W, 1225 m elev., 13 Feb. 2012, forest with *Nothofagus, Araucaria, Chusquea*, general collecting, M. Ramírez, M. Izquierdo, P. Michalik, C. Wirkner, and K. Huckstorf, 2♂ 3♀ (MACN-Ar 35138); 1♀ (MACN-Ar 35142 MAI-1866); 1♂ (MACN-Ar 35144 MAI-1868; 1♀ (MACN-Ar 35149); Laguna Toro, 39º08′18.7" S, 71º42′30.9" W, 995 m elev., 7 Feb. 2005, forest with *Nothofagus, Araucaria, Chusquea*, M. Ramírez and F. Labarque, 1♂ (MACN-Ar 33702 MLB-4320); 4♂ 2♀ (MACN-Ar 42793). *Parque Nacional Nahuelbuta:* 37º49′39″ S, 73º 00′ 32.2″ W, 1100 m elev., 15 Feb. 2005, forest with *Nothofagus*, *Araucaria*, M. Ramírez and F. Labarque, 2♂ (MACN-Ar 33658 MLB-4307); 40 km W Angol [−37.82°, −73.01°], 1120 m elev., 13 Feb. 1992, N. Platnick, P. Goloboff, and M. Ramírez, 5♂ 6♀ (AMNH); Pichinahuel, 37º47′ S, 73º0′ W, 1200 m elev., 22 Nov. 2004, T., fogging s/*Araucaria araucana*,

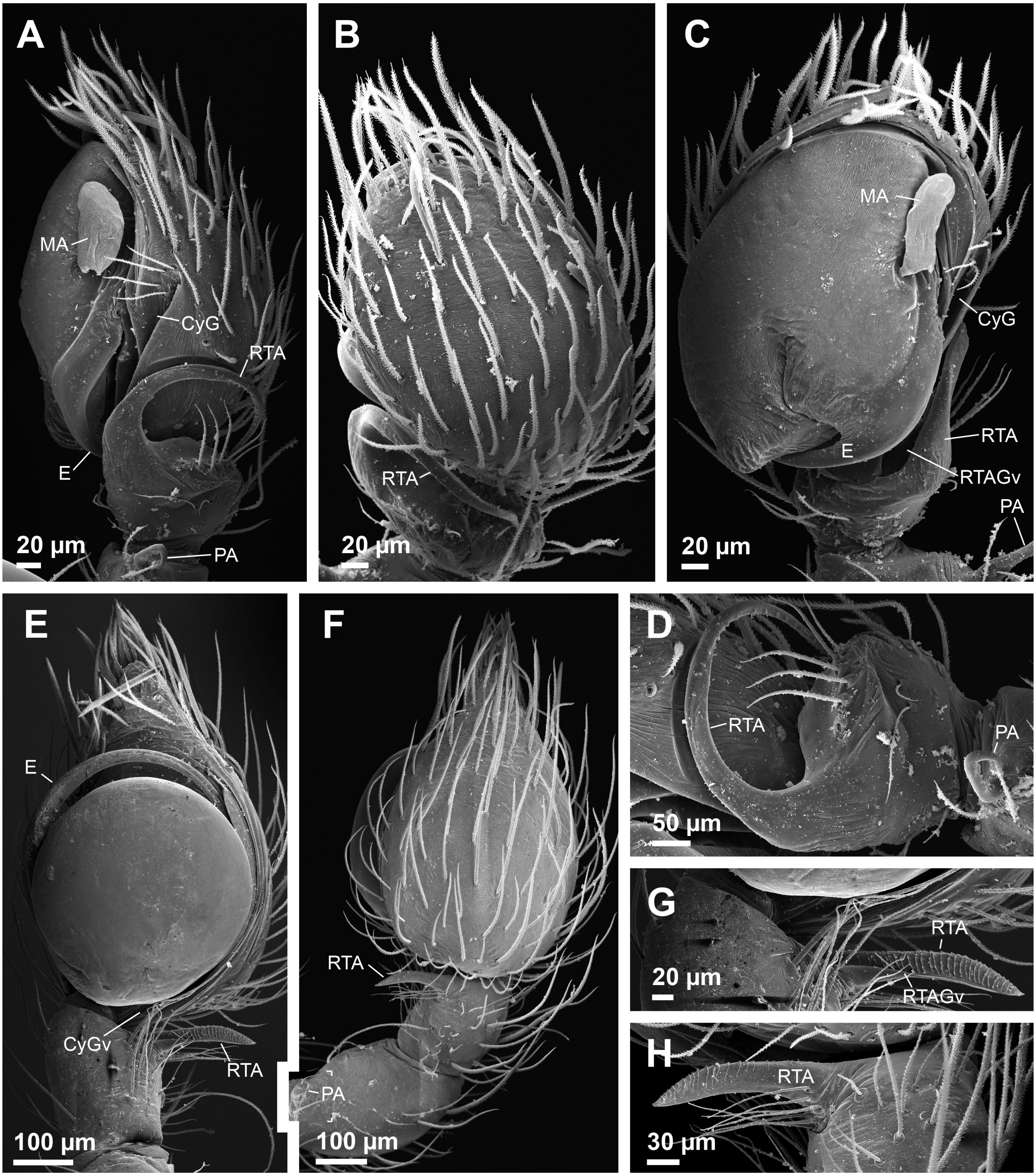

Figure 16. Scanning electron micrographs of left male palps of *Hahnia pusilla* (C.L.Koch, 1841) (A–D) and *Neoantistea magna* (Keyserling, 1887) (E–H). A, retrolateral view. B, dorsal view. C, ventral view. D, tibia and patella in retrolateral view. E, ventral view. F, dorsal view. G, detail of tibial retroleral apophysis in ventral view. H, same, detail in dorsal view. Abbreviations: CyGv, cymbial groove of male palp; E, embolus of male palp; MA, median apophysis of male palp; PA, patellar retrolateral apophysis of male palp; RTA retrolateral tibial apophysis of male palp; RTAGv, groove on the retrolateral tibial apophysis of male palp.

N. dombeyi, J.E. Barriga, 13♂ 11♀ (MACN-Ar 42781 AGB-0018); sector Piedra del Aguila, 29 km W Angol (air), 37.82241° S, 73.03518° W, 1400 m elev., 12 Jan. 2020, M. Ramírez, E. Soto, J. Wilson. and D. Poy, 1♀ (MACN-Ar 42789); 37°47′ S, 73°00′ W, 1200 m elev., 12 Feb. 2005, fogging *Nothofagus antarctica*, J.E. Barriga, 1♂ (MACN-Ar 42787); 1♀ (MACN-Ar 43235); 2♂ 2♀ (MACN-Ar 43237); 3♂ 14♀ (MACN-Ar 43238); 1♀ (MACN-Ar 43242 AGB-0009); 3♂ 4♀ (MACN-Ar 42795). Río Pedregoso, Fundo Nueva Pomeramia [−39.17°, −72.3°], 19 Feb. 1994, T. Cekalovic, 1♂ 3♀ (AMNH). Tolhuaca [−38.23°,

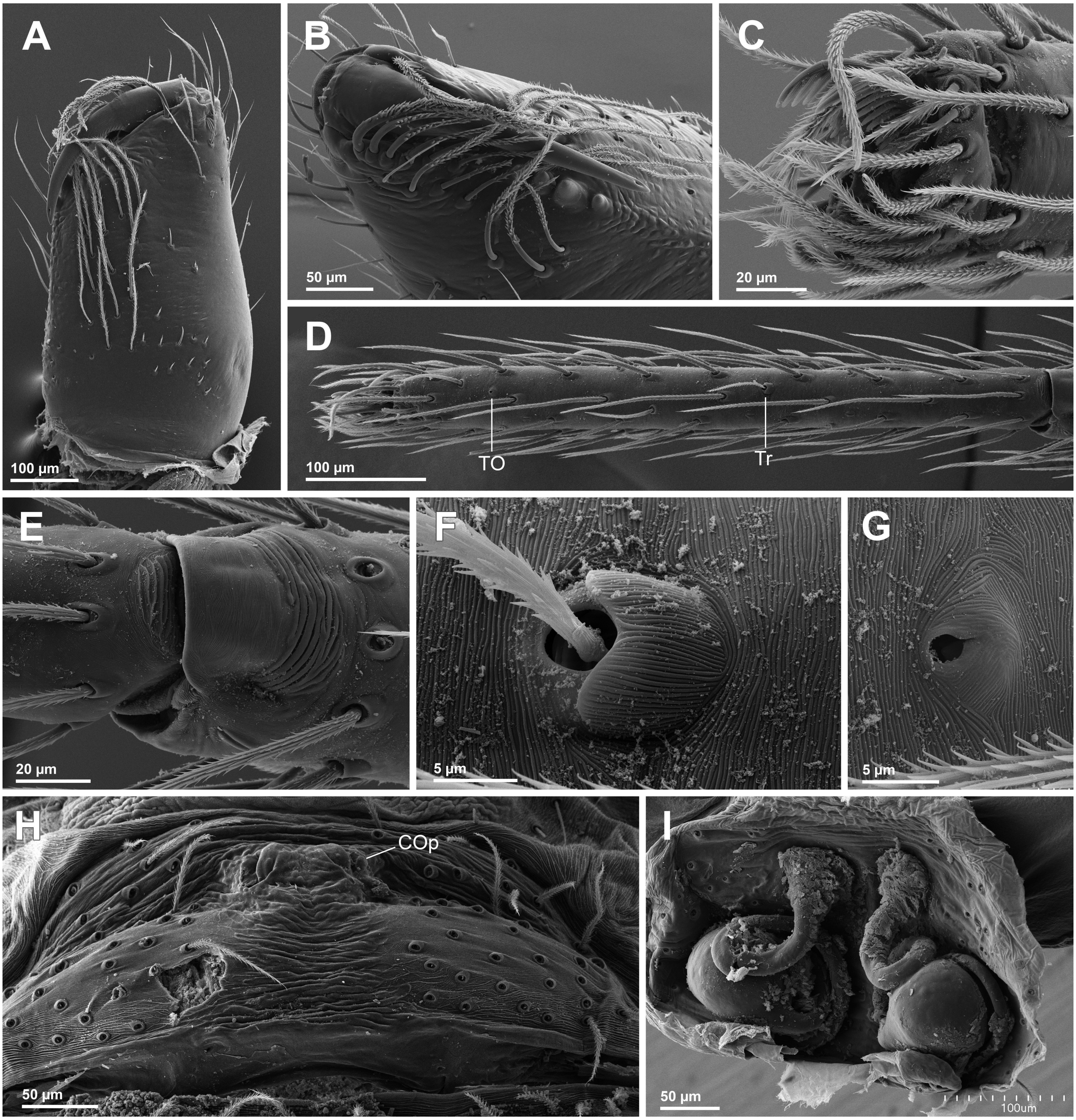

Figure 17. Scanning electron micrographs of female *Cybaeolus pusillus* Simon, 1884. A, left chelicera, posterior view. B, same, detail of promargin and fang, ventral view. C, claws of left leg I. D, tarsus I, dorsal view. E, metatarsal sensory organ of left leg I. F, trichobothrium of tarsus I. G, tarsal organ I. H, epigyne, note copulatory openings obstructed by mating plugs. I, vulva, dorsal view. Abbreviations: COp, copulatory opening; TO, tarsal organ; Tr, trichobothria.

–71.73°], 15–23,Mar. 1986, L. Peña, 7♂ 3♀ (AMNH). **Región de Los Lagos:** Abtao 5 km N Pargua [–41.776°, –73.422°], 7 Feb. 1988, T. Cekalovic, 1♀ (AMNH). Caleta La Arena [–41.681°, –72.654°], 30 Jan. 1990, M. Ramírez, 1♀ (MACN). Chaitén, road side, at night [–42.92°, –72.7°], 10 m elev., 16 Jan. 1986, N. Platnick, P. Goloboff, and R. Schuh, 3♀ (AMNH). Chiloé, Isla Lemuy, Aldachildo [–42.583°, –73.61°], 20 Feb. 1996, T. Cekalovic, 1♀ (AMNH). Chiloé, Isla Lemuy, Ichuac [–42.617°, –73.717°], 20 Feb. 1993, T. Cekalovic, 1♀ (AMNH); Feb. 9, 1993, T. Cekalovic, 1♂ 3♀ (AMNH). Chiloé, Isla Lemuy, Puerto Haro [–42.63°, –73.66°], 24 May 2000, T. Cekalovic, 3♂ 10♀ (AMNH). Chiloé, Isla Quinchao, Curaco de Velez [–42.44°, –73.6°], 10 Feb. 1994, T. Cekalovic, 4♂ 11♀ (AMNH). Chiloé, Isla Quinchao, 3.5 km from Curaco de Velez [–42.44°, –73.6°], 6 Feb. 1988, T. Cekalovic, 2♀ (AMNH). Chiloé, Isla Quinchao, Hullar Alto [–42.407°, –73.573°], 10 Feb. 1994, T. Cekalovic, 19♀ (AMNH); 17 Feb. 1996, T. Cekalovic, 10♀ (AMNH). Chiloé, Isla Quinchao, Hullar Bajo [–42.39°, –73.56°], 10 Feb. 1994, T. Cekalovic, 2♂ 7♀ (AMNH); Feb. 16, 1996, T. Cekalovic, 1♀ (AMNH). Chiloé, Isla Quinchao, Quetro

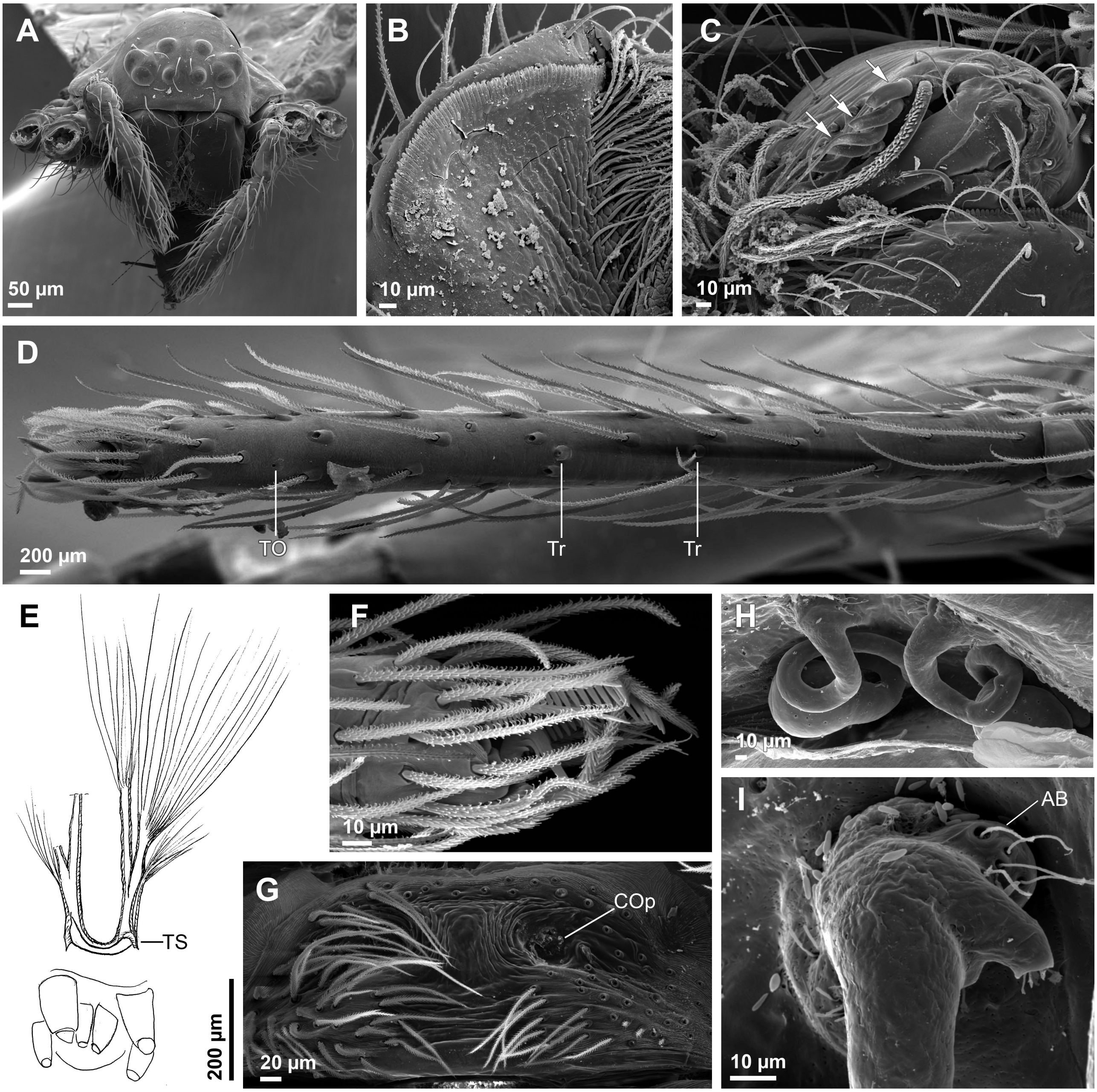

Figure 18. Scanning electron micrographs of female *Cybaeolus rastellus* (Roth, 1967). A, prosoma, anterior view. B, detail of endite showing the serrula, dorsal view. C, left chelicera, ventral view, arrow to expanded bases of rake setae making the rastellum. D, right tarsus I, dorsal view. E, tracheal system. F, claws of right leg I, retrolateral view. G, epigyne, note copulatory opening obstructed by mating plug. H, vulva, anterior-dorsal view. I, same, detail of start of copulatory duct showing small accessory bulb and gland ducts. Abbreviations: AB, accessory bulb; COp, copulatory opening; TO, tarsal organ; Tr, trichobothria.

[–42.418°, –73.58°], 16 Feb. 1996, T. Cekalovic, 2♀ (AMNH); 19 Feb. 1997, T. Cekalovic, 1♂ 36♀ (AMNH); 1♀ (AMNH); 22 Jun. 2000, T. Cekalovic, 1♂ 1♀ (AMNH). *Isla Chiloé:* 15 km S Chepu [–42.044°, –73.968°], 3 Feb. 1991, M. Ramírez, 1♀ (MACN); Chepu [–42.04°, –73.97°], 12 Feb. 1994, T. Cekalovic, 1♂ 1♀ (AMNH); 19 Feb. 1991, T. Cekalovic, 1♀ (AMNH); 21 Feb. 1997, T. Cekalovic, 2♀ (AMNH); 75 m elev., 21 Nov. 1981, N. Platnick and R. Schuh, 2♀ (AMNH); Chepu, NW coast Chiloé Island [–42.04°, –73.97°], 75 m elev., 21 Feb. 1992, N. Platnick, P. Goloboff, and M. Ramírez, 1♀ (AMNH); Cucao, Tepual [–42.649°, –74°], 2 Feb. 1991, M. Ramírez, 2♂ 3♀ (MACN); El Pozuelo (km 1.5 NE Butalcura) [–42.242°, –73.723°], 2 Feb. 2001, T. Cekalovic, 1♂ ♀ (AMNH); km 11 N Castro [–42.38°, –73.76°], 19 Feb. 1997, T. Cekalovic, 5♀ (AMNH); 1♀ (AMNH). Km 2 Puente Río Pudeto [–41.867°, –73.768°], 18 May 1998, T. Cekalovic, 1♀ (AMNH); km 5 SW Chonchi [–42.64°, –73.81°], 2 Feb. 2001, T. Cekalovic, 2♀ (AMNH); 20 Feb. 1997, T. Cekalovic, 2♂ 4♀ (AMNH); 22 Feb. 1997, T. Cekalovic, 2♂ 4♀ (AMNH); 1♀ (AMNH); Mellico, 11 Feb. 1994, T. Cekalovic, 3♀ (AMNH); Pid-Pid [–42.4°, –73.78°], 17 Feb. 1997, T. Cekalovic, 8♀ (AMNH); Pindapulli [–42.3°, –73.62°], 7 Feb. 2001, T. Cekalovic, 9♀

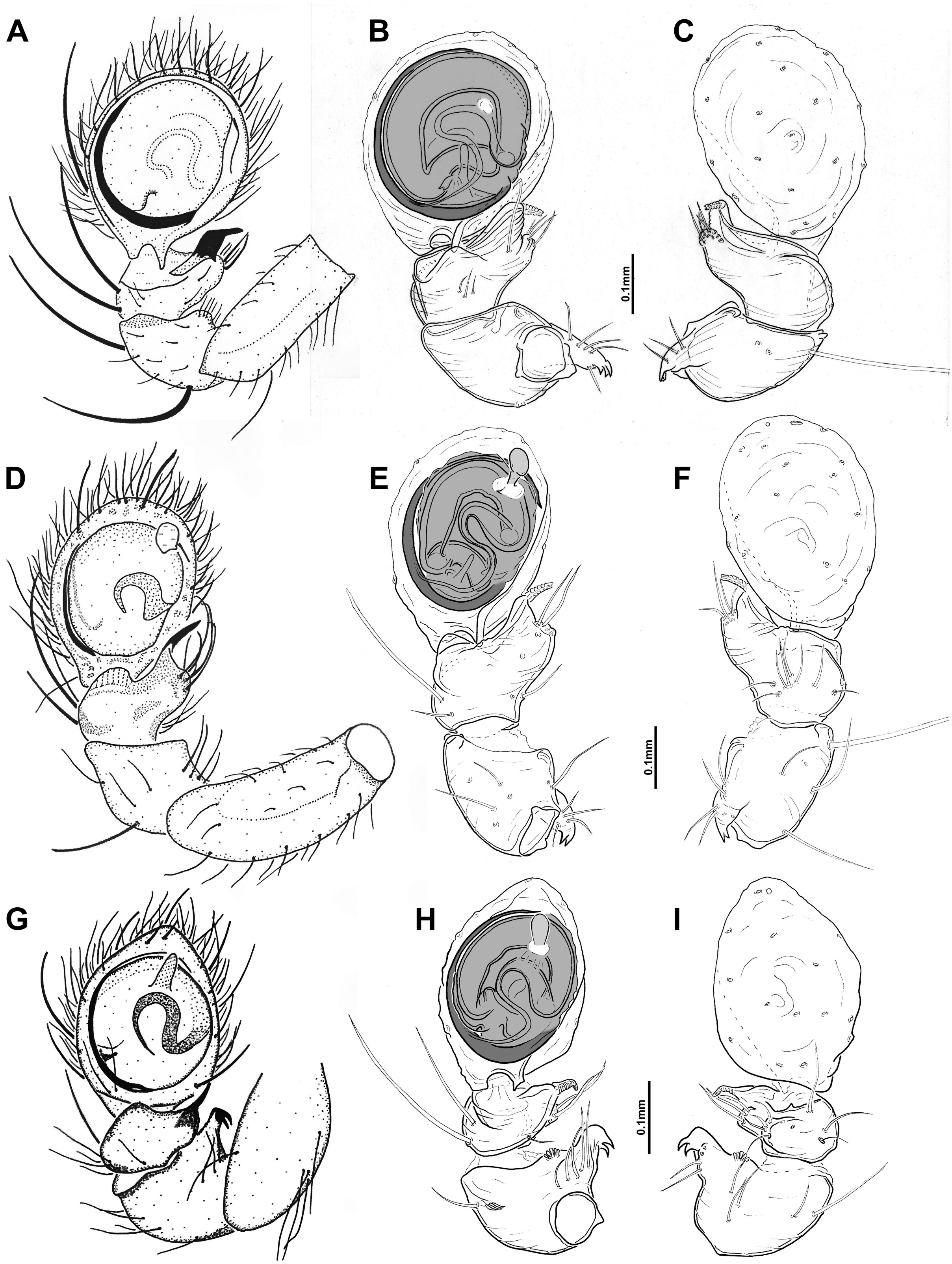

Figure 19. Cleared palps of *Cybaeolus* males. A, *Cybaeolus pusillus* Simon, 1884, ventral view. B, ventral view, cleared (MACN-Ar 42781), C, the same, dorsal view. D, *Cybaeolus rastellus* (Roth, 1967), ventral view. E, ventral view, cleared (MACN-Ar 42802), ventral. F, the same, dorsal view. G, *Cybaeolus delfini*, ventral view. H, ventral view, cleared (MACN-Ar 42773). I, the same, dorsal view.

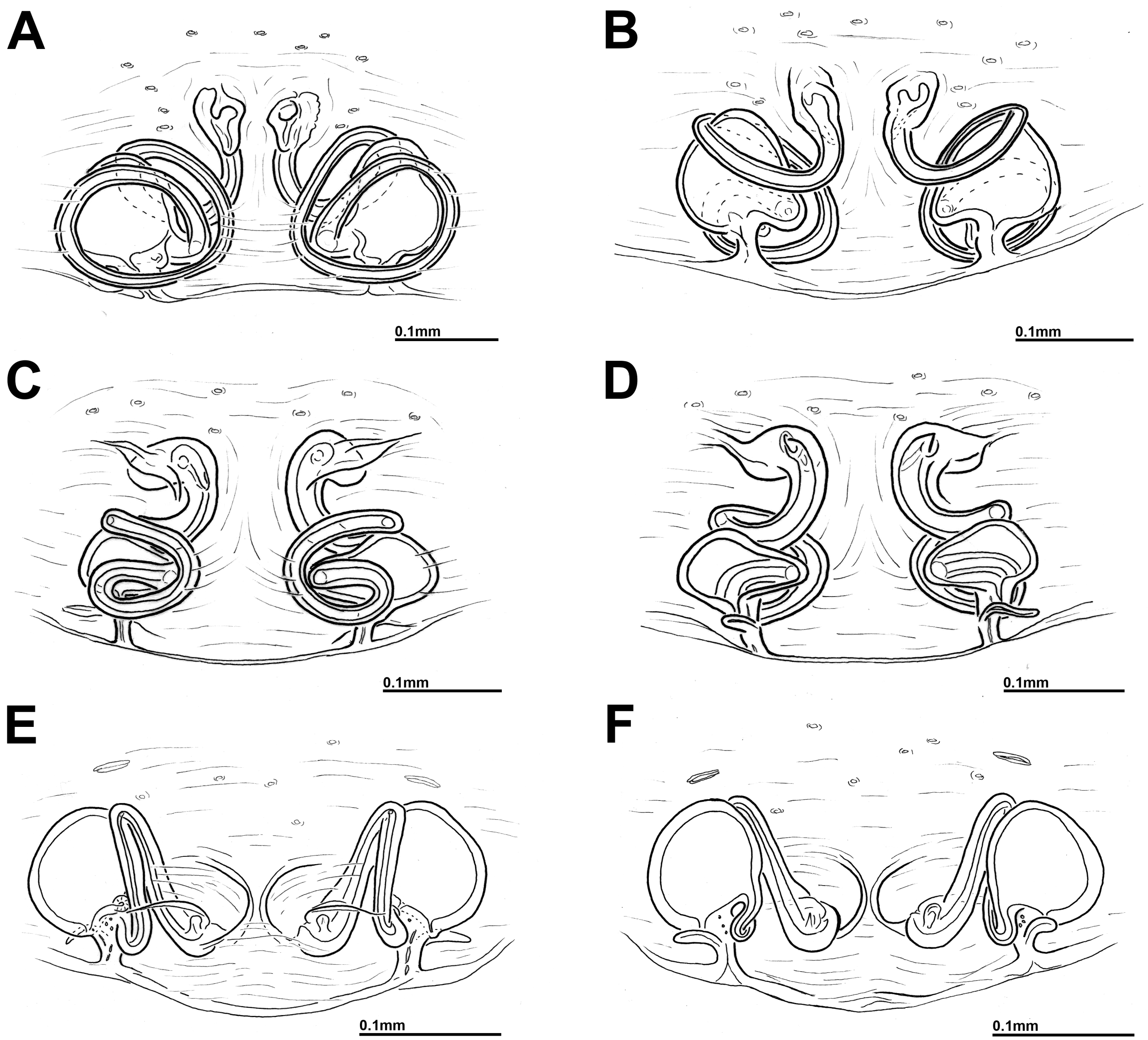

Figure 20. Cleared epigynes of *Cybaeolus* females. A, *Cybaeolus pusillus* Simon, 1884 (MACN-Ar 43242), ventral. B, the same, dorsal. C, *Cybaeolus rastellus* (Roth, 1967) (MACN-Ar 42822), ventral. D, the same, dorsal. E, *Cybaeolus delfini* (Simon 1904) (MACN-Ar 42750), ventral. F, the same, dorsal.

(AMNH). Pío-Pío [–42.814°, –73.584°], 10–12 Mar. 1987, L. Peña, 5♀ (together with 2 immatures) (AMNH); Piruquina [–42.38°, –73.79°], 11 Feb. 1993, T. Cekalovic, 4♀ (AMNH); 10 Feb. 1983, 1♂ 1♀ (AMNH); 1♀ (AMNH); 16 Feb. 1995, 2♂ 3♀ (AMNH); 7 Feb. 1998, 4♂ ♀ (AMNH); 15 Feb. 1996, 3♀ (AMNH); 18 Feb. 1997, 4♀ (AMNH); 9 Feb. 1993, 1♀ (AMNH); 1♂ 4♀ (AMNH); Río Dongo [–42.603°, –73.876°], 19 May 2000, T. Cekalovic, 1♂ 2♀ (AMNH); San Juan de Chadmo [–42.97°, –73.58°], 20 Feb. 1997, T. Cekalovic, 1♀ (AMNH); Vilupulli [–42.605°, –73.788°], 14 Feb. 1996, T. Cekalovic, 5♂ 4♀ (AMNH); native forest totally destroyed, T. Cekalovic, 1♀ (AMNH). Hills S Maicolpue [–40.62°, –73.74°], 50 m elev., 19 Feb. 1992, N. Platnick, P. Goloboff, and M. Ramírez, 2♂ ♀ (AMNH); 1♂ ♀ (AMNH); 2♀ (AMNH). Lago Calafquen, Casa de Piedra, 7 Feb. 1993, T. Cekalovic 1♂ ♀ (AMNH). NW shore Lago Chapo, 41°27′ S, 72°30′ W, 250 m elev., 13 Nov. 1966, M.E. Irwin and E.I. Schlinger, 1♂1♀ (CAS). Osorno [–40.58°, –73.11°], 24 Jan. 1952, Ross Michelbacher, 1♂ 4♀ (CAS). *Parque Nacional Alerce Andino:* sector Sargazo, between start of sendero Los Ulmos and sendero Laguna Sargazo, 41.509747° S, 72.616501° W, 347 m elev., 3–4 Jan. 2023, M. Pacheco, L. Piacentini, and E. Soto,1♂ 3♀ (MACN-Ar 43952); sector Sargazo, sendero Laguna Sargazo, 41.51613° S, 72.604081° W, 382 m elev., 3 Jan. 2023, M. Pacheco, L. Piacentini, and E. Soto, 1♀ (MACN-Ar 43957); sector Sargazo, sendero Los Ulmos, 41.507524° S, 72.619967° W, 382 m elev., 3 Jan. 2023, M. Pacheco, L. Piacentini, and E. Soto, 1♂ ♀ (MACN-Ar 43967); sector Sargazo, sendero 'Rodal Alerce', wet forest, 41°30′35.8″ S, 72°36′44.6″ W, 340 m elev., 4 Feb. 2005, M. Ramírez and F. Labarque, 1♂ 5♀ (MACN-Ar 42779); trail to Saltos del Río

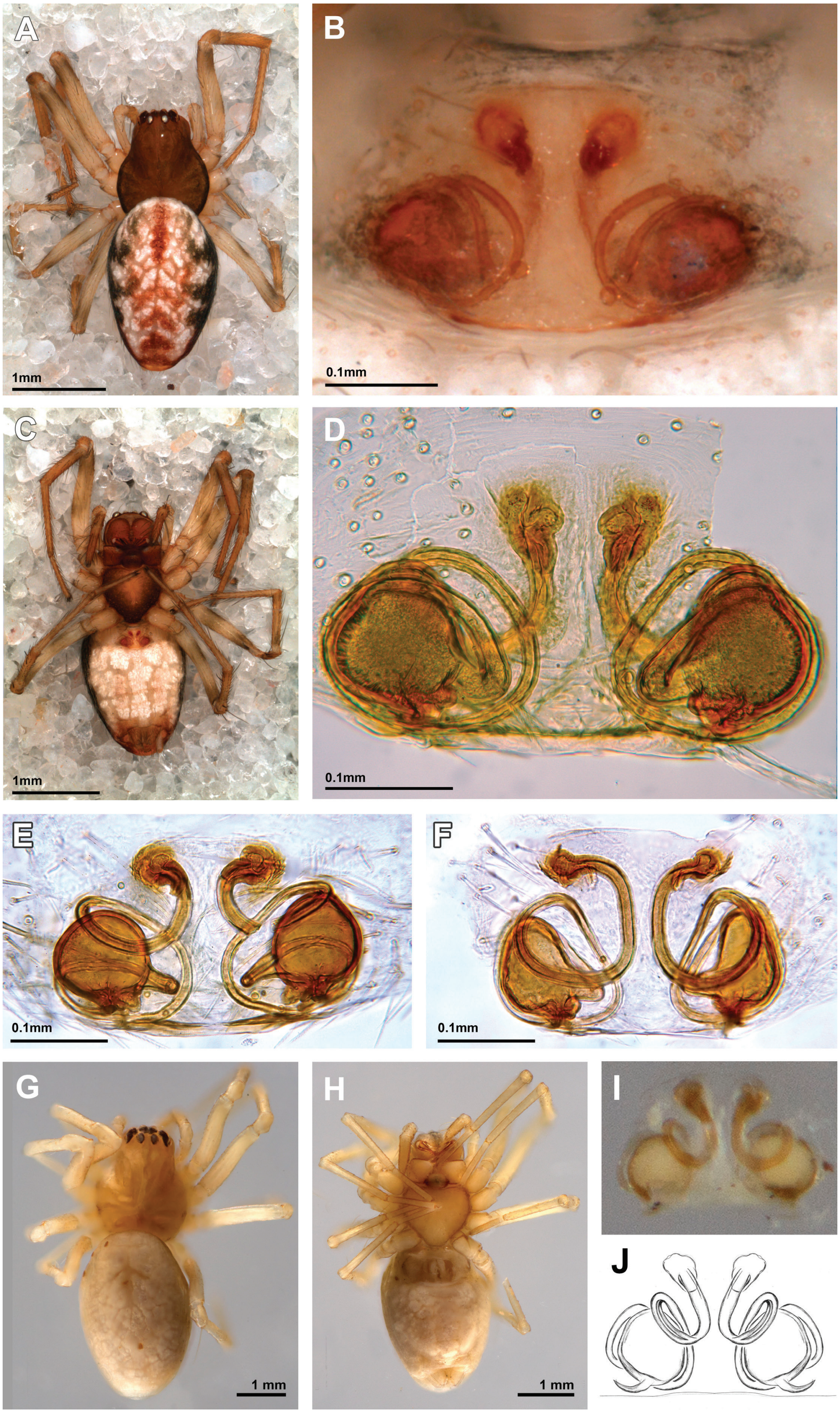

Figure 21. *Cybaeolus pusillus* Simon, 1884, female. A, dorsal habitus. B, epigyne, ventral view. C, ventral habitus (A–C, CASENT 9039051). D, epigyne cleared, ventral view (MACN-Ar 43242). E, epigyne cleared, dorsal view, variant with copulatory openings separated (MACN-Ar 29766). F, epigyne cleared, dorsal view, extreme variant with copulatory openings well separated (MACN-Ar 41386). G, female holotype, dorsal habitus. H, same, ventral habitus. I, same, dissected epigyne, dorsal view. J, same, epigyne cleared, dorsal view.

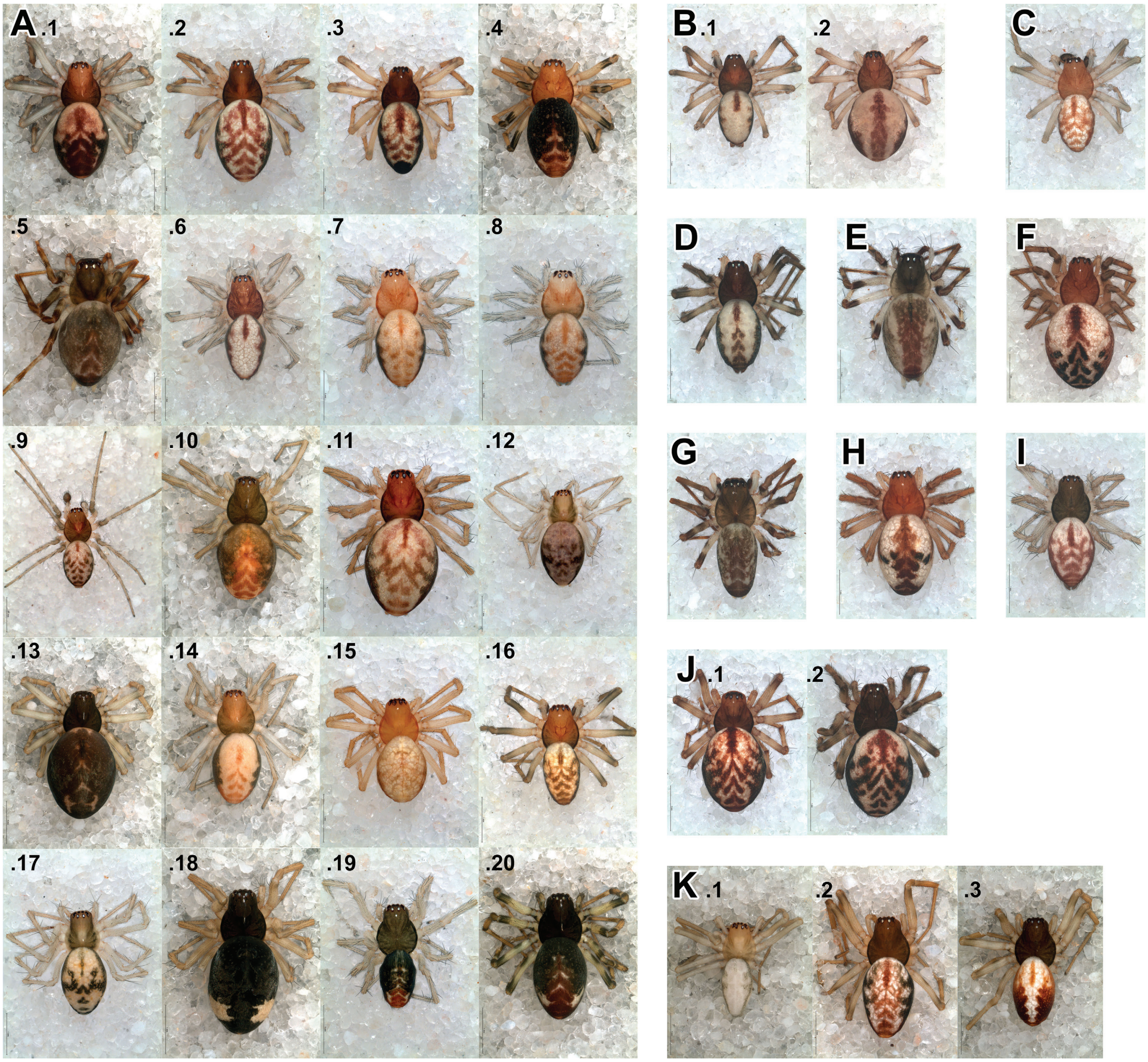

Figure 22. Colour polymorphism in *Cybaeolus pusillus* Simon, 1884, grouped by locality and collection event. A, Chile, Los Lagos, Parque Nacional Puyehue (MACN-Ar 43965). B, Chile, Los Lagos, Parque Nacional Alerce Andino (MACN-Ar 43952). C, Argentina, Río Negro, Parque Nacional Nahuel Huapi (MACN-Ar 43386). D, Chile, Los Lagos, Parque Nacional Puyehue (MACN-Ar 43971). E, Chile, Los Lagos, Parque Nacional (MACN-Ar 43970). F, Chile, Magallanes, Punta Arenas (MACN-Ar 43980). G, Chile, Los Lagos, Alerce Andino (MACN-Ar 43967). H, Chile, Los Lagos, Alerce Andino (MACN-Ar 43957). I, Chile, Los Ríos, Alerce Costero (MACN-Ar 43961). J, Chile, Magallanes, Cueva del Milodón (MACN-Ar 43976, MACN-Ar 43978). K, Chile, Los Ríos, Reserva Costera Valdiviana (CASENT 9039051, CASENT 9039054, CASENT 9034002).

Chaica 7–10 km NE Lenca, 41°34′41.9″ S, 72°33′24.2″ W, 205 m elev., 2 Feb. 2005, M. Ramírez and F. Labarque, 2♀ (MACN-Ar 42780). *Parque Nacional Chiloé:* 15 km S Chepu [–42.14°, –74.05°], 3 Feb. 1991, M. Ramírez, 2♂ 2♀ (MACN-Ar 42792); Arroyo Cole Cole 25 km N Cucao [–42.406°, –74.108°], 8–11 Feb. 1991, M. Ramírez, 1♂ 1♀ (MACN); Cucao, sendero El Tepual, 42.61766° S, 74.10120° W, 15 m elev., 15 Feb. 2012, wet forest of *Tepualia stipularis*, M. Ramírez, M. Izquierdo, P. Michalik, C. Wirkner, and K. Huckstorf, 1♀ (MACN-Ar 42877). *Parque Nacional Puyehue:* 4.1 km E Anticura [–40.66°, –72.19°], 430 m elev., 19–26 Dec. 1982, trap site 662, Valdivian rain forest, A. Newton and M. Thayer, 5♂ ♀ (AMNH); Aguas Calientes [–40.733°, –72.3°], 600 m elev., 18 Dec. to 8 Feb. 1985, *Nothofagus* forest, S. and J. Peck, 1♀ (AMNH); 6♂ 18♀ (MACN-Ar 21092); Antillanca road [–40.776°, –72.209°], 470–720 m elev., 18–24 Dec. 1982, screen-sweeping at dusk, Valdivian rain forest, A. Newton and M. Thayer, 5♂ 8♀ (AMNH); sector Aguas Calientes, sendero Berlin, 40.741952° S, 72.299176° W, 490 m elev., 10 Jan. 2023, M.P. Pacheco, L. Piacentini, and E.M. Soto, 3♂ 19♀ (MACN-Ar 43965); sector Aguas Calientes, sendero El Recodo, 40°44′17.1″ S, 72°18′25.6″ W, 367 m elev., 10 Jul. 2010, Beating, A. Ojangueren, L. Piacentini, and E.Soto, 1♂ (MACN-Ar 42863); 1♀ (MACN-Ar 42876 LNP-4133); sector Aguas Calientes, sendero Los Pioneros, 40.73794° S, 72.311679°

W, 572 m elev., 9 Jan. 2023, M.P. Pacheco, L. Piacentini, and E.M. Soto, 1♂ 2♀ (MACN-Ar 43970); sector Aguas Calientes, sendero Recoba, 40.735181° S, 72.30985° W, 474 m elev., 10 Jan. 2023, M.P. Pacheco, L. Piacentini, and E.M. Soto, 1♂ 1♀ (MACN-Ar 43955); sector Anticura, sendero Pudú, 39º44′08.2″ S, 71º40′13″W, 396 m elev., 8 Jul. 2010, under logs, A. Ojanguren, L. Piacentini, and E. Soto, 1♂ (MACN-Ar 42866); beating, 3♀ (MACN-Ar 42869); 1♀ (MACN-Ar 42881 LNP-4140); manual night collecting, 1♂ (MACN-Ar 42871); sector Anticura, sendero Salto del Indio, 40.663337° S, 72.17616° W, 358 m elev., 11 Jan. 2023, M.P. Pacheco, L. Piacentini, and E.M. Soto, 2♂ ♀ (MACN-Ar 43963); sector Anticura, sendero Salto del Pudú, 40.675656° S, 72.164139° W, 480 m elev., 11 Jan. 2023, M.P. Pacheco, L. Piacentini, and E.M. Soto, 2♂ ♀ (MACN-Ar 43971). *Parque Nacional Villarrica:* 10 km S Pucón [–39.359°, –71.964°], 900 m elev., 15 Dec. 1984 to 10 Feb. 1985, *Nothofagus* forest, S. and J. Peck, 1♂ 1♀ (AMNH); road to Coñaripe, near sector Quetrupillén, 39.45314º S, 71.80915º W, 925 m elev., 13 Feb. 2012, M. Ramírez, M. Izquierdo, P. Michalik, C. Wirkner, and K. Huckstorf, 2♀ (MACN-Ar 42864 AGB-0017); Laguna Quillehue, sendero Fauna, S Curarrehue, S39.55426, W71.53685, 1119 m elev., 12 Feb. 2012, forest with *Nothofagus, Chusquea*, M. Ramírez, M. Izquierdo, P. Michalik, C. Wirkner, and K. Huckstorf, 1♀ (MACN-Ar 29286); sector Quetrupillén, 39º27′42.1″S, 71º50′44.2″W, 1280 m elev., 8 Feb. 2005, forest with *Araucaria, Nothofagus, Chusquea*, M. Ramírez and F. Labarque, 1♀ (MACN-Ar 42782). Puerto Montt, Río Blanco [–41.45°, –72.888°], 24–29 Jan. 1983, G. Arriagada, 8♀ (MACN). Puerto Montt, sector Chapo Rio Blanco [–41.45°, –72.888°], 30 Jan. 30 to 15 Feb. 1983, G. Arriagada, 1♂ (MACN); 2♀ (MACN). Puyehue [–39.669°, –72.286°], 700 m elev., 9 Dec. 1994, L. Peña, 2♂ 2♀ (AMNH). Termas de Puyehue [–40.736°, –72.308°], 180 m elev., 24 Nov. 1981, forest, N. Platnick and R. Schuh, 1♂ ♀ (AMNH). 10 km E Puyehue [–40.72°, –72.45°], 24 Jan. 1951, beating, Valdivian rainforest, Ross Michelbacher, 3♂ 2♀ (CAS). **Región de Los Ríos:** La Herradura, 6km E Niebla [–39.85°, –73.33°], 20 m elev., 16 Feb. 1992, N. Platnick, P. Goloboff, and M. Ramírez, 2♀ (AMNH). Ñancul, Fundo El Lingue [–39.74°, –72.44°], Feb. 8, 1993, T. Cekalovic, 1♀ (AMNH); 4♀ (AMNH). *Parque Nacional Alerce Costero*: sendero Los Melíes, 39.951827° S, 73.55019° W, 32 m elev., 5 Jan. 2023, M.P. Pacheco, L. Piacentini, and E.M. Soto, 1♀ (MACN-Ar 43961). *Parque Oncol:* intersection Tepual trail to Río Cruces [–39.7°, –73.355°], 8 May 2001, T. Cekalovic, 11♀ (AMNH); km 1 before instersection of Cariñanco to Parque Oncol [–39.7°, –73.355°], 13 May 2001, T. Cekalovic, 1♀ (AMNH); rd intersection from Ronoval Canelos to Los Tepuales [–39.7°, –73.32°], 12 May 2001, T. Cekalovic, 3♀ (AMNH); road intersection to Tepual trail [–39.7°, –73.32°], 19 May 2001, T. Cekalovic, 11♀ (AMNH); Sendero Oncol, 13 km NNW Valdivia (air), 39.68806º S, 73.30408º W, 590 m elev., 14 Jan. 2020, M. Ramírez, E. Soto, J. Wilson, and D. Poy, 1♀ (MACN-Ar 42788 AGB-0015); Quitaqui trail [–39.7°, –73.32°], 19 May 2001, T. Cekalovic, 4♂ 13♀ (AMNH). Las Lajas, W La Unión, 13–15 May 1990, L. Peña, 1♀ (AMNH); 1♀ (AMNH); May 9–13 May 1990, L. Peña, 1♂ 4♀ (AMNH). Las Trancas, W La Unión, 500 m elev., 6–10 Feb. 1988, L. Peña, 3♀ (AMNH); May 1990, L. Peña, 1♂ ♀ (AMNH). 36 km W La Unión [–40.18°, –73.46°], 600 m elev., 25–28 Mar. 1981, L. Peña, 3♀ (AMNH). 45 km W La Unión [–40.13°, –73.56°], 900 m elev., 1–2 Mar. 1987, L. Peña, 1♂ 2♀ (AMNH). *Reserva Costera Valdiviana:* Chaihuin, Las Garzas, 39º 59.687′ S, 73º 35.227′W, 26 Feb. 2008, Fogging 150cc/l N. nitida, Arias *et al.* 1♀ (CASENT 9039051 JMA-0094); 1♂ (CASENT 9039053 JMA-0220); 1♀ (CASENT 9039054 JMA-0102); 27 Feb. 2008, 1♂ (CASENT 9034002 JMA-0161); 1♂ (CASENT 9034003 JMA-0100). Río Llancahue, km 3 S Coñaripe [–39.58°, –71.92°], 7 Feb. 1993, T. Cekalovic, 1♀ (AMNH). **Región de Magallanes:** *Monumento Natural Cueva del Milodón*: sector Silla del Diablo [–51.57630°, –72.59473°], 140 m elev., 24 Jan. 2023, forest of ñire (*Nothofagus anctartica*), general collecting, M. Ramírez, G. Sancho, and M.V. Lencinas, 1♀ (MACN-Ar 43976 MJR2700); 1♀ (MACN-Ar 43977 MJR2702); 1♀ (MACN-Ar 43978 MJR2704); 1♀ (MACN-Ar 43979). Punta Arenas, Puerto de Hambre [–53.60985º, –70.93426º], 18 m elev., 26 Jan. 2023, forest of Guindo (*Nothofagus betuloides*) and peat with ñire (*Nothofagus anctartica*), general collecting, M. Ramírez, G. Sancho, M.V. Lencinas, 1♀ (MACN-Ar 43980). **Chile: Región de Ñuble:** Puente Marchant 1300m, 36º 53.5′ S, 71º32.5′ W, 1130 m elev., 20 Feb. 2005, fogging s/*Nothofagus dombeyi*, J. E. Barriga-Tuñón, 1♀ (MACN-Ar 42783 AGB-0016); 2♂ 1♀ (MACN-Ar 42784); 12♂ 9♀ (MACN-Ar 42785). **Región del Maule:** *Parque Nacional Gil de Vilches*: [–35.6°, –71.04°], 1200 m elev., 8 Feb. 1992, N. Platnick, P. Goloboff, and M. Ramírez, 1♂ 1♀ (AMNH). *Reserva Nacional Los Ruiles*: 35º50′02.6″ S, 72º30′35.7″W, 174 m elev., 17 Jul. 2010, manual night collecting, A. Ojangueren, L.Piacentini, E.Soto, D. Valdivia, and J. Pizarro Araya, 1♀ (MACN-Ar 42868).

Cybaeolus rastellus (Roth, 1967)

(Figs 1A, B, 2J, M, 5, 6, 15, 18, 19D–F, 20C, D, 23, 24, 28B)

Mevianes rastellus Roth 1967: 308 pl. 50, figs 7, 8 [male holotype, two males, and five female paratypes from Región de Los Lagos, Llanquihue Prov., Isla Calbuco, *c.* 42° 0′ S, 73° 30′ W (*c.* –41.79°, –73.15°) 21–28 Feb. 1963, H.J. McMillin and A. Archer, in AMNH, examined].
Cybaeolus rastellus, Lehtinen 1967: 226.
Cybaeolus cf. *rastellus,* Wheeler *et al.* 2017: fig. 5 (sequenced, voucher ARAMR-290, reexamined).

Diagnosis

Both sexes are similar to *C. delfini* by having a rastellum of thick setae on the cheliceral promargin (although sometimes with thinner setae, see Fig. 15B). Males of this species are also similar to those of *C. delfini* by having a fleshy median apophysis in the copulatory bulb (Figs 15E, H, 19D, E) and a two-pointed retrolateral patellar process. In *C. rastellus* the median apophysis is distally wider, and the patellar process is directed posteriorly (Fig. 19E, F), instead of anteriorly as in *C. delfini* (Fig. 19H, I). Females are similar to those of *C. pusillus* by having the copulatory openings anteriorly in the epigyne (Figs 20C, D, 23B–D) but can be distinguished by these being further apart from each other, the shorter and thicker copulatory ducts, describing a closer loop on the mesal margin of the spermathecae, six-shaped in ventral view, and the smaller spermathecae.

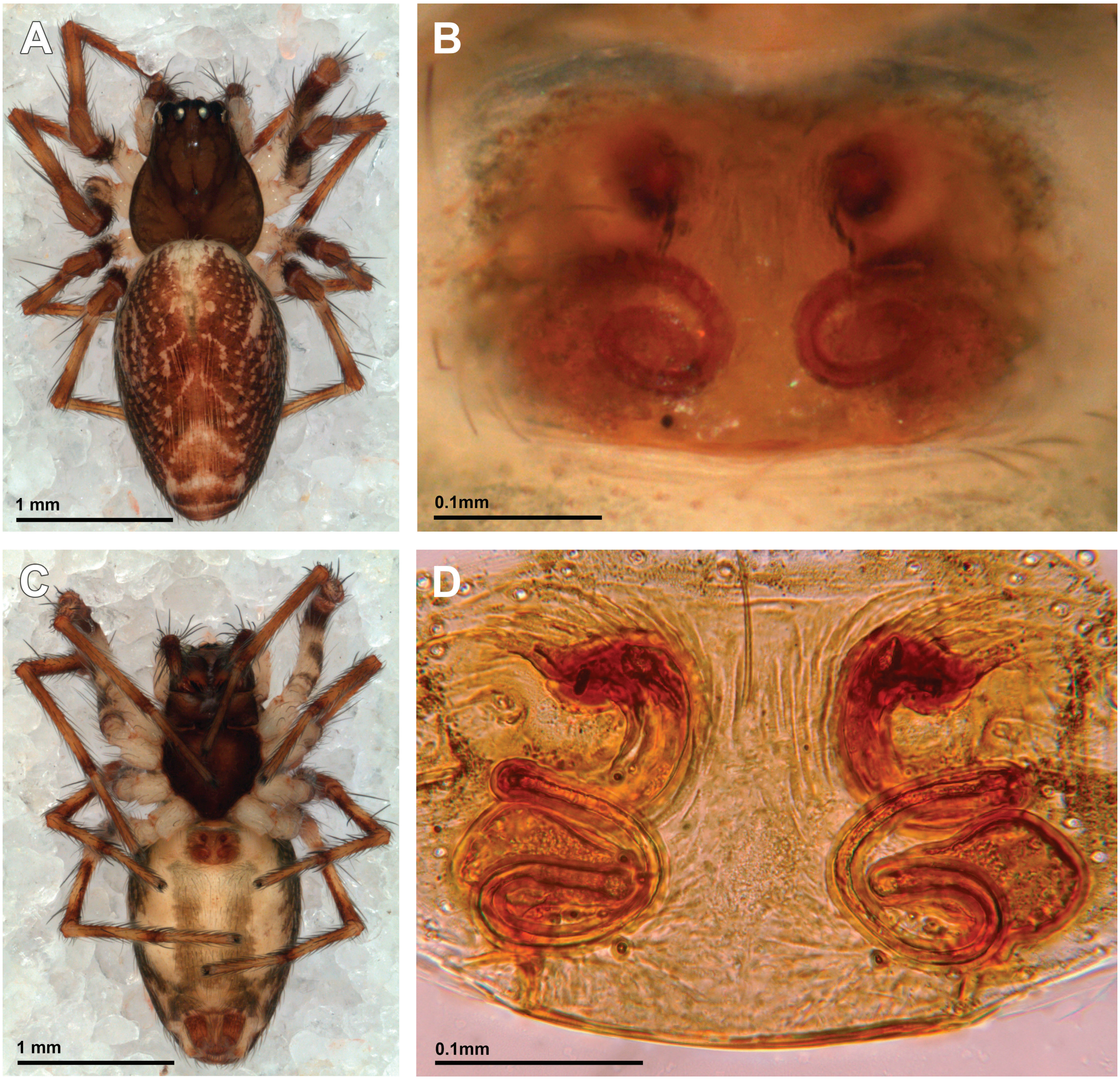

Figure 23. *Cybaeolus rastellus* (Roth, 1967), female. A, dorsal habitus. B, epigyne, ventral view. C, ventral habitus. D, epigyne cleared, ventral view.

Description

Male (holotype, complemented with data from other specimens when not visible in the holotype). Total length 2.63. Carapace 1.06 long, 0.92 wide. Abdomen 1.64 long, 0.80 wide. Eye diameters and interdistances AME 0.05, ALE 0.08, PME 0.07, PLE 0.08; AME–AME 0.05, AME–ALE 0.06, PME–PME 0.10, PME–PLE 0.09, ALE–PLE 0.02; MOQ length 0.16, anterior width 0.15, posterior width 0.24. Anterior eye row slightly procurved in anterior view, posterior row straight in dorsal view. Clypeus height 0.12 (2.4× diameter of AME). Carapace castaneous with indistinct darker border, darker thoracic V-shaped mark, cephalic region weakly setose. Chelicerae orange-brown, without visible stridulatory file (weak stridulatory file observed in some specimens, on external-posterior side). Endites yellow-brown, longer than wide, posterior lateral edge strongly protruding (Fig. 15C). Labium light brown. Sternum castaneous, as wide as long. Opisthosoma distinctly elongated, dorsum: whitish-grey with three to four sepia chevrons posteriorly, mottled laterally, without setae expect on anterior dorsum; venter: mottled greyish-white with two indistinct longitudinal marks extending from epigastric furrow to base of spinnerets, darker around spinnerets. Palpal cymbium oval, copulatory bulb with small median apophysis (Fig. 15E, H), tibial apophysis long and procurved with several long, strong, upwardly curved setae at base, patellar apophysis recumbent on retrolateral side, with two or three teeth (Figs 15D, 19E, F). Spinnerets in relatively compact group (Fig. 6A), ALS pigmented, PLS and PMS unpigmented. Proximal segment of ALS 2.4× length of distal segment; distal segment of PLS 0.24× length of proximal segment. PLS 1.1× length of ALS. ALS total length 0.24; basal width 0.12, distal segment length

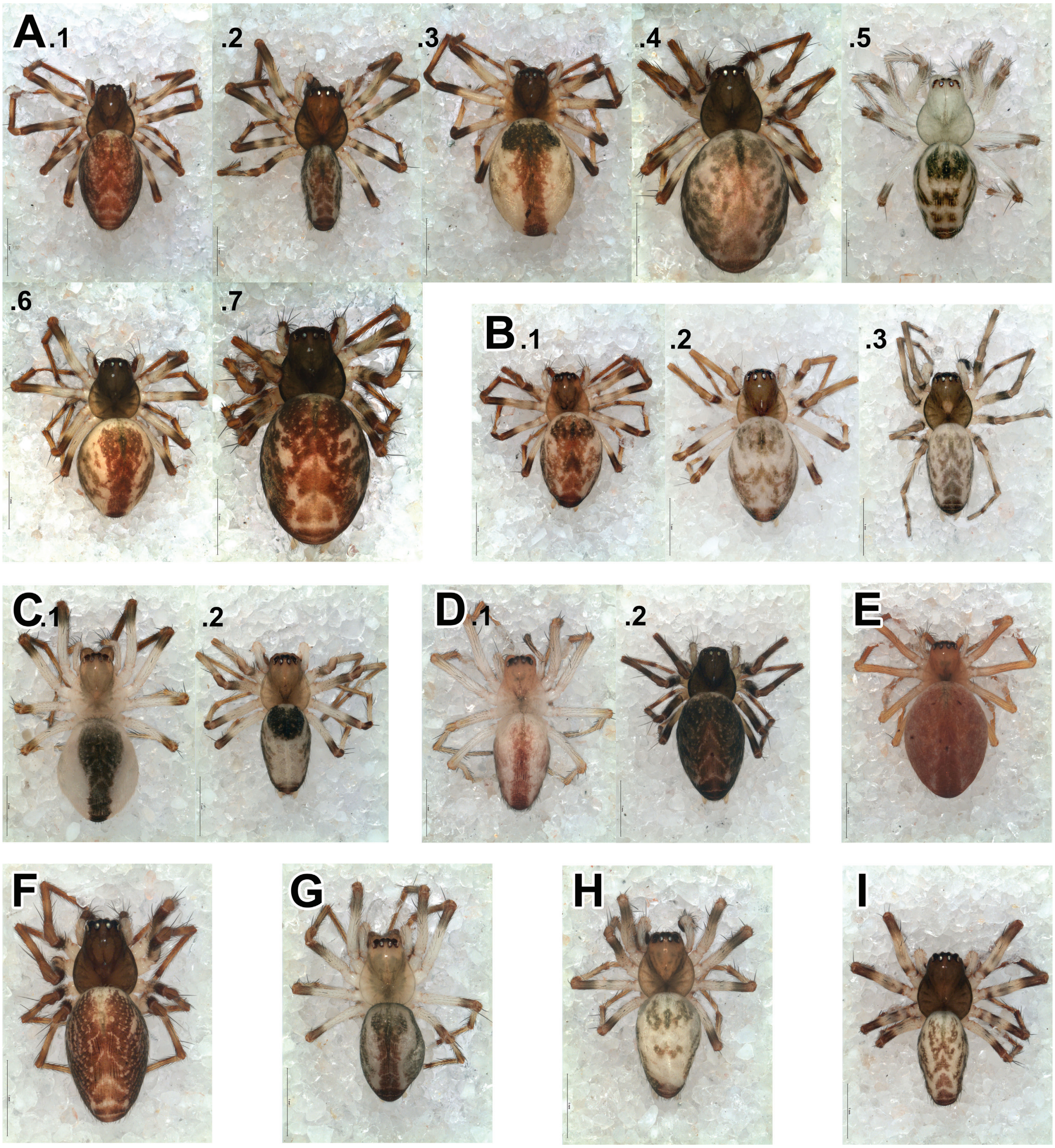

Figure 24. Colour polymorphism in *Cybaeolus rastellus* (Roth, 1967) in Chile, grouped by locality and collection event. A, Los Lagos, Parque Nacional Puyehue (MACN-Ar 43969). B, Los Lagos, Parque Nacional Puyehue (MACN-Ar 43966). C, Los Lagos, Parque Nacional Alerce Andino (MACN-Ar 43968). D, Los Lagos, Parque Nacional Puyehue (MACN-Ar 43954). E, Los Lagos, Parque Nacional Alerce (MACN-Ar 43958). F, Los Lagos, Parque Nacional Puyehue (MACN-Ar 43973). G, Los Lagos, Parque Nacional Alerce Andino (MACN-Ar 43953). H, Los Lagos, Parque Nacional Alerce Andino (MACN-Ar 43959). I, CLos Ríos, Parque Nacional Alerce Costero (MACN-Ar 43962).

0.07, proximal segment length 0.17. PMS total length 0.13. PLS total length 0.26; distal segment length 0.05, proximal segment length 0.21. Spigot morphology: ALS with one major ampullate gland spigot flanked by nubbin, and 12 piriform gland spigots (Fig. 6B). PMS with one minor ampullate gland spigot and three aciniform gland spigots (Fig. 6C). PLS with five aciniform gland spigots (Fig. 6D). Epiandrous spigots absent (Fig. 6E). Legs orange-brown, all articles strongly annulated, lightly spined. Leg measurements (formula 1243): leg I (total 4.13) femur 1.19, patella 0.32, tibia 1.00, metatarsus 0.99, tarsus 0.63; leg II (4.07) 1.15, 0.35, 1.04, 0.92, 0.62; leg III (3.06) 1.04, 0.28, 0.68, 0.61, 0.45, leg IV (3.45) 1.05, 0.32, 0.81, 0.77, 0.48, palp (1.30) 0.44, 0.25, 0.22, -, 0.39. Leg formula 1243. Pattern of spines: Femora: I d0-1-0, p0-0-1; II d0-1-1 (or 0-1-0), p0-0-1 (or p0-1-1-0); III d0-0-1, p0-0-1. Patellae: I d1-0-1; II d1-0-1; III d1-0-1; IV d1-0-1. Tibia: I d1-0-1, p0-0-1; II d1-0-1, p0-1-1; III d1-0-1, p0-0-1, v0-1-1; IV d1-0-1, v0-1-1. Metatarsus: III p0-1-1, v0-0-2, r0-0-1; IV p0-1-1, v0-2-2, r0-0-1.

Female (paratype). Total length 3.63. Carapace 1.13 long, 0.92 wide. Abdomen 2.28 long, 1.42 wide. Eye diameters and spacing: AME 0.05, ALE 0.07, PME 0.06, PLE 0.08; AME–AME 0.06, AME–ALE 0.06, PME–PME 0.09, PME–PLE 0.06, ALE–PLE 0.02; MOQ length 0.21, anterior width 0.16, posterior width 0.21. Clypeus height 0.13 (2.6× diameter of AME). Carapace cephalic region castaneous, shading to orange-brown laterally and posteriorly very faint radiating thoracic marks, weakly setose in cephalic region. Chelicerae length 0.47, ratio: 0.51, dark orange-brown, with prominent rastellum near base of fang. Endites short, as wide as long, without the posterior lateral extension of the male. Labium dusky. Sternum orange-brown, about as long as wide. Abdomen dorsum grey mottled with white, dark purplish-brown mark over cardiac region, dark band around posterior tip of abdomen, venter; without markings, sparsely setose along midline. Epigyne rugose, copulatory openings on shallow elevations (Fig. 18G), copulatory duct begins with a loop anterior to the spermatheca, continues with a second loop, and connects through the ventral part of the spermatheca (Figs 18H, 20C, D, 23B–D); accessory bulb as a small bump with gland ducts near the copulatory opening (Fig. 18I). Spinnerets in relatively compact group (Fig. 5A), ALS conical with wide base, distal segment of PLS very short, proximal segment of ALS 5.5× length of distal segment; distal segment of PLS 0.19× length of proximal segment: PLS 1.2× length of ALS. ALS total length 0.26; basal width 0.15, distal segment length 0.04, proximal segment length 0.22. PMS total length 0.20. PLS total length 0.31; distal segment length 0.05, proximal segment length 0.26. Spigot morphology: ALS with one major ampullate gland spigot flanked by a nubbin and 13 piriform gland spigots (Fig. 5B). PMS with one minor ampullate gland spigot, two cylindrical gland spigots, and eight aciniform gland spigots (Fig. 5C). PLS with one cylindrical gland spigot and 11 aciniform gland spigots (Fig. 5D). Spinneret topology PLS 70° from ALS; PMS 45–50° anterior to ALS. Legs orange-brown, without distinct annulations but with dusky patches ventrally on femora and distally on metatarsus, pedipalp tarsi and tibiae dark orange-brown with patellae and femora a sharply contrasting light straw colour. Legs measurements: leg I (total 3.84), femur 1.11, patella 0.31, tibia 0.95, metatarsus 0.83, tarsus 0.64; leg II (3.86) 1.10, 0.37, 0.94, 0.90, 0.55; leg III (2.91) 0.90, 0.29, 0.64, 0.67, 0.41, leg IV (3.57) 1.06, 0.30, 0.86, 0.82, 0.53, palp (1.18), 0.33, 0.20, 0.27, -, 0.38. Pattern of spines: pedipalp patellae: d1-0-1; tibiae: d1-0-0, p0-0-1; tarsi: d1-0-0, p1-1-1, v0-0-2, r1-1-1. Femora: I d0-0-1, p0-0-1 (or 2); II d0-0-1. Patellae all with: d1-0-1. Tibiae: I d1-0-1, p0-0-1; II d1-0-1, p0-0-1; III d1-0-1, p0-0-1, vO1-1; IV d1-0-1, v0-1-1. Metatarsi: III and IV as male. Trichobothrial distribution tibiae: d1-2, metatarsi: d0-0-1, tarsi: d0-1-0 or 0-1-1-0 (Fig. 18D).

Variability and colour polymorphism

Some males have a weak stridulatory file on the external-posterior side of the chelicerae which is difficult to see.The cheliceral rastellum may have less conspicuous setae in some specimens. The body coloration is extremely variable (Figs 2J, M, 24), even among specimens from the same locality and collection event (Fig. 24A, D).

Natural history

Specimens were found in webs on foliage of trees, bamboo and shrubs in humid forests (Fig. 1A, B).

Distribution

Known from forests in Chile from Región de Ñuble to Parque Nacional Río Simpson, in Región de Aysén, and in wet forests of adjacent Argentina in Parque Nacional Nahuel Huapi in Neuquén Province, and Parque Nacional Los Alerces in Chubut province (Fig. 28B).

Other material examined

ARGENTINA: Chubut: *Parque Nacional Los Alerces*: Lago Futalaufquen [–42.845°, –71.705°], Jan. 1990, M. Ramírez, 1♂ (MACN); Lago Menéndez, Pto Sagrario [–42.611°, –71.892°], 29 Nov. 1996, wet forest with alerce (*Fitzroya cupressoides*), M. Ramírez, 2♀ (MACN-Ar 42799). **Neuquén:** *Parque Nacional Nahuel Huapi:* Puerto Blest, Sendero de la Bahía, S 41.02583, W 71.82250, 789 m elev., 4 Dec. 2024, secondary forest, beating, A. Pérez-González, L.A. Martínez, M.J. Ramírez, and W.L. Porto, 1♀ (MACN-Ar 46685 MJR-2798); Lago Ortiz Basualdo [–40.983°, –71.864°], Jan. 1990, M. Ramírez, 1♂ 1♀ (MACN); Puerto Blest [–41.033436, –71.816678], 10 Jan. 1998, M. Ramírez, 3♀ (MACN-Ar 21086); Puerto Blest [–41.033436, –71.816678], 7 Jan. 2000, L. Lopardo and A. Quiaglino, 1♂ (MACN-Ar 21087); Puerto Blest, Sendero de la Bahía, 41.02583º S 71.82250º W, 789 m elev., 4 Dec. 2024, secondary forest, manual collecting, A. Pérez-González, L. Martínez, M. Ramírez, and W. Porto, 2♂, 2♀ (MACN-Ar 46861); Puerto Blest, trail to Laguna Los Cántaros, 41.013754º S, 71.822738º W, 820–890 m elev., 28 Dec. 2010, wet forest, M. Ramírez, V. Werenkraut, and S. Aisen, 1♂ (MACN-Ar 33597). **Río Negro:** *Parque Nacional Nahuel Huapi:* Lago Frías superior [–41.044°, –71.8°], 1 Feb. 1990, M. Ramírez, 1♂ 2♀ (MACN); Puerto Blest, sector Lago Frías, trail before reaching Puerto Frías, 41.04056º S, 71.80083º W, 754 m elev., 5 Dec. 2023, secondary forest, beating, A. Pérez-González, L.A. Martínez, M.J. Ramírez, and W.L. Porto, 1♀ (MACN-Ar 46683 MJR-2794); trail to Co. La Mona, near Lago Espejo Chico, 40.580069º S, 71.702972º W, 890–940 m elev., 5 Jan. 2011, forest with *Nothofagus dombeyi*, *Chusquea*, M. Ramírez and V. Werenkraut, 1♀1 (MACN-Ar 34362 MLB-0942). **CHILE: Región de Aysén:** *Parque Nacional Río Simpson:* 22 km E Aisén [–45.562°, –72.325°], 300 m elev., 5 Feb. 1985, wet forest, N. Platnick and O. Francke, 1♀ (AMNH); S margin of Río Simpson [–45.562°, –72.325°], 17 Feb. 1991, M. Ramírez, 2♂ 5♀ (MACN). 15 km S Las Islas Juntas, 30 km Puyuhuapi [–44.09°, –72.446°], 100 m elev., 30 Dec. 1984 to 28 Jan. 1985, *Nothofagus* forest, S. and J. Peck, 5♂ 1♀ (AMNH). 16 km W Cisnes Medio, Río Grande [–44.685°, –71.968°], 200 m elev., 30 Dec. 1984 to 28 Jan. 1985, mature beech forest, S. and J. Peck, 1♂ ♀ (AMNH). **Región de La Araucanía:** *Parque Nacional Nahuelbuta:* 37º47′ S, 73º00′ W, 1200 m elev., 12 Feb. 2005, fogging *Nothofagus antarctica*, J.E. Barriga, 1♂ (MACN-Ar 43239); 1♂ (MACN-Ar 43240). *Parque Nacional Ñielol:* nr. Temuco [–38.723°, –72.587°], 250 m elev., 14–30 Dec. 1982, pyrethrin fogging tree bark, forest remnant/*Nothofagus*, A. Newton and M. Thayer, 1♀ (AMNH). 15 km NE Villarrica, Flor del Lago [–39.2°, –72.16°], 300 m elev., 14 Dec. 1984 to 10 Feb. 1985, *Nothofagus* forest, S. and J. Peck, 1♂ 2♀ (AMNH). 17 km W Angol [–37.8°, –72.96°], 800 m elev., 8 Dec. 1984 to 16 Feb. 1985, *Nothofagus* forest, S. and J. Peck, 1♂ 1♀ (AMNH). 21 km NE Pucón, Lago Caburga [–39.18°, –71.81°], 600 m elev., 15 Dec. 1984 to 10 Feb. 1985, mixed forest remnant, S. and J. Peck, 2♂ ♀ (AMNH). *Monumento Natural Contulmo:* 38.01314º S, 73.18648º W, 341 m elev., 9 Jan. 2020, M. Ramírez, E. Soto, J. Wilson, and D. Poy, 1♀ (MACN-Ar 41385); 1♂ 2♀ (MACN-Ar 41388); 38º00′46.8″ S, 73º11′15.4″ W, 360 m elev., 10–11 Feb. 2005, M. Ramírez and F. Labarque, 1♀ (MACN-Ar 33625 MLB-4285); 3♀ (MACN-Ar 42801); 4♀ (MACN-Ar 42803); 3♀ (MACN-Ar 42805); Berlese funnel, 1♀ (MACN-Ar 43427); [–38.013°, –73.188°], 300 m elev., 11–12 Feb. 1992, N. Platnick, P. Goloboff, and M. Ramírez, 3♂ 5♀ (AMNH); 2♂ 1♀ (AMNH); 38º00′46.2″ S, 73º11′15.4″ W, 360 m elev., 12–13 Jul. 2010, manual night collecting, A. Ojangueren, L. Piacentini, E. Soto, and D. Valdivia, 1♀ (MACN-Ar 42822 AGB-0010); 1♂ (MACN-Ar 42865 LNP-4082); 1♀ (MACN-Ar 42873); 1♀ (MACN-Ar 42880 LNP-4077); general collecting, 2♀ (MACN-Ar 42872); [–38.014321, –73.180069], 17–21 Dec. 1998, M. Ramírez, L. Compagnucci, C. Grismado, and L. Lopardo, 1♀ (MACN-Ar 21090); 2♂ 2♀ (MACN-Ar 21088); [–38.027°, –73.203°], 12 Jan. 1989, M. Ramírez, 1♂ 5♀ (MACN); sendero Lemu Mau, 38.01314º S, 73.18648º W, 341 m elev., 9 Feb. 2012, manual night collecting, M. Ramírez, M. Izquierdo, P. Michalik, C. Wirkner, and K. Huckstorf, 1♀ (MACN-Ar 35134). **Región de Los Lagos:** *Chiloé, Isla Quinchao:* 3.5 km from Curaco de Velez [–42.44°, –73.6°], 6 Feb. 1988, T. Cekalovic, 1♀ (AMNH); Quetro [–42.418°, –73.58°], 16 Feb. 1996, T. Cekalovic, 1♀ (AMNH). *Isla Chiloé:* Chepu [–42.04°, –73.97°], 17 m elev., 29 Nov. 1981, N. Platnick and R. Schuh, 1♂ ♀ (AMNH); Chepu, NW coast Chiloé Island [–42.04°, –73.97°], 75 m elev., 21 Feb. 1992, N. Platnick, P. Goloboff, and M. Ramírez, 3♀ (AMNH); km 1 N Puente Río Pudeto [–41.867°, –73.768°], 17 Feb. 1996, T. Cekalovic, 1♀ (AMNH); km 1 W Huillinco [–42.68°, –73.91°], 24 May 1998, T. Cekalovic, 1♀ (AMNH); Lago Huillinco, N margin, 4.6 km (air) ESE Cucao, 42.64117º S, 74.04763º W, 12 m elev., 16 Feb. 2012, wet forest, M. Ramírez, M. Izquierdo, P. Michalik, C. Wirkner, and K. Huckstorf, 3♂ 1♀ (MACN-Ar 34138); Pío-Pío [–42.814°, –73.584°], 10–12 Mar. 1987, L. Peña, 2♀ (AMNH); Piruquina [–42.38°, –73.79°], 19 Feb. 1983, T. Cekalovic, 1♀ (AMNH); Río Cipresal, 42º 35.181′ S, 74º 05.576′ W, 2 Mar. 2008, Fogging 150cc/l N. nitida, 1♀ (CASENT 9034054 JMA-0223). *Parque Nacional Chiloé:* 15 km al S Chepu [–42.14°, –74.05°], 3 Feb. 1991, M. Ramírez, 3♂ 7♀ (MACN-Ar 21085); Arroyo Cole Cole 25 km N Cucao [–42.406°, –74.108°], 8–11 Feb. 1991, M. Ramírez, 4♂ 8♀ (MACN). Llanquihue, Caleta La Arena [–41.681°, –72.654°], 30 Jan. 1990, M. Ramírez, 1♀ (MACN). Llanquihue, Ensenada [–41.179°, –72.553°], 50 m elev., 16 Mar. 1965, H.W. Levi, 1♂ (MCZ). *Parque Nacional Alerce Andino:* 22–24 Jan. 1997, L. Compagnucci, 1♂ 3♀ (together with one immature) (MACN-Ar 21084); sector Sargazo, between start sendero Los Ulmos and sendero Laguna Sargazo, 41.509747° S, 72.616501° W, 347 m elev., 3–4 Jan. 2023, M.P. Pacheco, L. Piacentini, and E.M. Soto, 1♂ ♀ (MACN-Ar 43953); sector Sargazo, sendero Laguna Sargazo, 41.51613° S, 72.604081° W, 382 m elev., 3 Jan. 2023, M.P. Pacheco, L. Piacentini, and E.M. Soto, 1♀ (MACN-Ar 43958); sector Sargazo, sendero Los Ulmos, 41.507524° S, 72.619967° W, 382 m elev., 3 Jan. 2023, M.P. Pacheco, L. Piacentini, and E.M. Soto, 3♂ 2♀ (MACN-Ar 43968); sendero Rodal del Alerce, 41.510801° S, 72.609275° W, 388 m elev., 4 Jan. 2023, M.P. Pacheco, L. Piacentini, and E.M. Soto, 1♂ ♀ (MACN-Ar 43959); sendero 'Rodal Alerce', 41º30′35.8″ S, 72º36′44.6″ W, 340 m elev., 4 Feb. 2005, wet forest, M. Ramírez and F. Labarque, 1♀ (MACN-Ar 33406); 1♀ (MACN-Ar 33407 MLB-4273); 5♂ 18♀ (MACN-Ar 42800); sector Correntoso, sendero 'Huillifoten', wet forest, 41º27′53″ S, 72º38′43.4″ W, 135 m elev., 3 Feb. 2005, M. Ramírez and F. Labarque, 1♀ (MACN-Ar 33382 MLB-4252); 1♀ (MACN-Ar 42797 ARAMR000290); 1♂ 3♀ (MACN-Ar 42809); 1♀ (MACN-Ar 42807); trail to Saltos del Río Chaica 7–10 km NE Lenca, 41º34′41.9″ S, 72º33′24.2″ W, 205 m elev., 2 Feb. 2005, M. Ramírez and F. Labarque, 1♂ 1♀ (MACN-Ar 33393 male MLB-4261, female MLB-4262); 1♀ (MACN-Ar 10836); 1♀ (MACN-Ar 42798 ARAMR000291); 6♂ 14♀ (MACN-Ar 42802 AGB-0019); 1♀ (MACN-Ar 42804 ARAMR000292); 3♀ (MACN-Ar 42806). *Parque Nacional Puyehue:* 600 m elev., 12–20 Feb. 1979, L. Peña, 1♀ (AMNH); 4.1 km E Anticura [–40.66°, –72.19°], 430 m elev., 19–26 Dec. 1982, trap site 662, Valdivian rain forest, A. Newton and M. Thayer, 18♀ (AMNH); 26 Dec. 1982, Valdivian rain forest, A. Newton and M. Thayer, 1♀ (AMNH); 8–26 Dec. 1982, 6♂ ♀ (AMNH); Aguas Calientes, 40°44′ S, 72°18′ W, 500 m elev., 16 Jan. 1995, N. Platnick, K. Catley and D. Silva, 3♂ 6♀ (AMNH); [–40.733°, –72.3°], 600 m elev., 18 Dec. 1984 to 8 Feb. 1985, malaise, *Nothofagus* forest, S. and J. Peck, 2♂ ♀ (AMNH); 40°44′ S, 75°18′45″ W, 450 m elev., J. Miller, I. Agnarsson, F. Alvarez, J. Coddington, and G. Hormiga, 12 Nov. 2000 to 2 Jan. 2001, 1♂ 1♀ (USNM); 500 m elev., 2–5 Jan. 1982, L. Peña, 1♂ 1♀ (AMNH); 450 m elev., 27 Jan. 1986, wet forest, N. Platnick and R. Schuh, 1♀ (together with one immature) (AMNH); 430 m elev., 28 Jan. 28, 1986, primary forest, N. Platnick and R. Schuh, 1♀ (AMNH); 1♂ 1♀ (AMNH); 425 m elev., 31 Jan. 1985, Valdivian forest, N. Platnick, and O. Francke, 2♀ (AMNH); 13–17 Dec. 1998, M. Ramírez, L. Compagnucci, C. Grismado, and L. Lopardo, 1♂ (MACN-Ar 21091); 7♂ 12♀ (MACN-Ar 42796); Aguas Calientes, Derumbes forest trail [–40.733°, –72.3°], 500 m elev., 20 Dec. 1984 to 8 Feb. 1985, S. and J. Peck, 5♂ ♀ (AMNH); Anticura, 40º39′58.6″ S, 72º10′24″ W, 355 m elev., 5 Feb. 2005, M. Ramírez and F. Labarque, 5♀ (MACN-Ar 42808); Antillanca road [–40.776°, –72.209°], 470–720 m elev., 18–24 Dec. 1982, pyrethrin fogging mossy log: 655 m, Valdivian rain forest, A. Newton and M. Thayer, 1♀ (AMNH); sector Aguas Calientes, sendero Berlin, 40.741952° S, 72.299176° W, 490 m elev., 10 Jan. 2023, M.P. Pacheco, L. Piacentini, and E.M. Soto, 1♂ 2♀ (MACN-Ar 43966); sector Aguas Calientes, sendero El Recodo, 40º44′17.1″ S, 72º18′25.6″ W, 367 m elev., 10 Jul. 2010, Beating, A. Ojangueren, L.Piacentini and E.Soto, 1♀ (MACN-Ar 42820 LNP-4131); beating, 1♂ (MACN-Ar 42821 LNP-4132); 1♀ (MACN-Ar 42823); 2♀ (MACN-Ar 42870); sector Aguas Calientes, sendero Los Pioneros, 40.73794° S, 72.311679° W, 572 m elev., 9 Jan. 2023, M.P. Pacheco, L. Piacentini, and E.M. Soto, 1♂ 6♀ (MACN-Ar 43969); sector Aguas Calientes, sendero Recoba, 40.735181° S, 72.30985° W, 474 m elev., 10 Jan. 2023, M.P. Pacheco, L. Piacentini, and E.M. Soto, 1♂ 2♀ (MACN-Ar 43954); sector Anticura, sendero Chile, 40.670723° S, 72.163633° W, 457 m elev., 11 Jan. 2023, M.P. Pacheco, L. Piacentini, and E.M. Soto, 1♂ ♀ (MACN-Ar 43960); sector Anticura, sendero Pudú, 39°44′08.2″S, 71°40′13″ E, 396 m elev., 8 Jul. 2010, under logs, A. Ojanguren, L. Piacentini, and E. Soto, 1♀ (MACN-Ar 42867 LNP-4141); manual night collecting, 1♀ (MACN-Ar 42878); sector Anticura, sendero Salto del Indio, 40.663337° S, 72.17616° W, 358 m elev., 11 Jan. 2023, M.P. Pacheco, L. Piacentini, and E.M. Soto, 3♂ ♀ (MACN-Ar 43964); sector Anticura, sendero Salto del Pudú, 40.675656° S, 72.164139° W, 480 m elev., 11 Jan. 2023, M.P. Pacheco, L. Piacentini, and E.M. Soto, 1♂ 1♀ (MACN-Ar 43973). 1 km E Termas de Puyehue [−40.66°, −72.2°], 305 m elev., 31 Jan. 1985, wet forest, N. Platnick and O. Francke, 1♀ (AMNH). 25–27 km N Chaitén [−42.72°, −72.8°], 40 m elev., 17 Jan. 1986, wet virgin forest, N. Platnick, P. Goloboff and R. Schuh, 1♀ (AMNH). 36 km W La Unión [−40.18°, −73.46°], 600 m elev., 25–28 Mar. 1981, L. Peña, 2♀ (AMNH). 4.5 km W La Unión, E El Mirador [−40.3°, −73.14°], 300 m elev., 1–2 Mar. 1987, L. Peña, 1♂ 1♀ (AMNH). 70 km S Chaitén [−43.42°, −72.36°], 500 m elev., 16 Jan. 1986, wet streambank, N. Platnick, P. Goloboff, and R. Schuh, 1♀ (AMNH). Anticura, E of Puyehue [−40.658°, −72.253°], 26–31 Aug. and 1–5 Sep. 1983, L. Peña, 1♀ (AMNH). Hills S Maicolpue [−40.62°, −73.74°], 50 m elev., 19 Feb. 1992, N. Platnick, P. Goloboff, and M. Ramírez, 3♀ (AMNH). Lago Chapo, 34 km E Puerto Montt [−41.42°, −72.56°], 300 m elev., 24 Dec. 1984 to 2 Feb. 1985, 2nd grow *Nothofagus*, S. and J. Peck, 4♂ 2♀ (AMNH). Pucatrihue coast [−40.54°, −73.71°], 1–10 Feb. 1990, L. Peña, 1♀ (AMNH). Termas de Puyehue [−40.736°, −72.308°], 240 m elev., 14 Mar. 1965, beach vegetation, H.W. Levi, 1♀ (MCZ); 180 m elev., 24 Nov. 1981, forest, N. Platnick and R. Schuh, 1♀ (AMNH); 460 m elev., 25 Nov. 1981, litter from moss and forest floor, N. Platnick and R. Schuh, 2♀ (AMNH). **Región de Los Ríos:** *Parque Nacional Alerce Costero:* sendero Los Melies, 39.951827° S, 73.55019° W, 32 m elev., 5 Jan. 2023, M.P. Pacheco, L. Piacentini, and E.M. Soto, 1♂ ♀ (MACN-Ar 43962). 34 km WNW La Unión [−40.21°, −73.45°], 17 Dec. 1984 to 7 Feb. 1985, mixed evergreen forest, S. and J. Peck, 1♀ (AMNH). 1 before intersection of Cariñanco to Parque Oncol [−39.7°, −73.355°], 12 May 2001, T. Cekalovic, 1♂ ♀ (AMNH). Las Lajas, W La Unión, 9–13 May 1990, L. Peña, 4♀ (AMNH); Las Trancas, W La Unión, Jun. 1990, L. Peña, 1♂ ♀ (AMNH); 500 m elev., 6–10 Feb. 1988, L. Peña, 1♂ 3♀ (AMNH). *Parque Oncol:* Quitaqui trail [−39.7°, −73.32°], 19 May 2001, T. Cekalovic, 2♂ 1♀ (AMNH). **Región de Ñuble:** 9 km W San Fabian de Alico [−36.53°, −71.61°], 24 Feb. 1992, N. Platnick, P. Goloboff, and M. Ramírez, 1♀ (AMNH). **Región del Biobío:** Arauco, Hualpén [−36.798°, −73.163°], 11 Jan. 1989, M. Ramírez, 1♀ (MACN). Bosque de Ramuntcho [−36.752°, −73.185°], 14–16 Nov. 1961, A.F. Archer, 1♀ (AMNH). Caramávida [−37.692°, −73.353°], 1–10 Jan. 1954, L.E. Pena, 3♀ (CAS). Curiman [−36.95°, −73.13°], 29 Dec. 1994, T. Cekalovic, 1♀ (AMNH). Estero Nonguén [−36.87°, −72.98°], 10 Oct. 1996, T. Cekalovic, 1♀ (AMNH); 11 Dec. 1977, 1♀ (AMNH). Lomas Coloradas [−36.9°, −73.12°], 27 May 1988, T. Cekalovic, 1♂ ♀ (AMNH). Pata de Gallina [−38.07°, −73.23°], 560 m elev., 11 Feb. 1992, N. Platnick, P. Goloboff, and M. Ramírez, 1♂ 1♀ (AMNH); 2♀ (AMNH). Quebrada Caramávida, San Alfonso, reserva Arauco, 20 km ESE Antiguala, 37.70942° S, 73.17107° W, 750 m elev., 15 Jan. 2018, forest with *Araucaria*, general collecting, M. Ramírez, A. Ojanguren, A. Pérez Gonzalez, G. Azevedo, and W. Porto, 1♂ (MACN-Ar 43342 MJR-2264).

Cybaeolus delfini (Simon, 1904)

(Figs 1E, G, 19G–I, 20E, F, 25–27, 28C)

Mevianes delfini Simon 1904: 111 [female holotype from Región de Magallanes, Magallanes, Punta Arenas (*c.* S 53.11° W 71.90°), in MNHN, examined]. Roth 1967: 307.
Cybaeolus delfini, Lehtinen 1967: 226.

Diagnosis

Males of *C. delfini* are similar to those of *C. rastellus* by having a fleshy median apophysis in the copulatory bulb and a two-pointed retrolateral patellar process (Fig. 19G–I) but can be distinguished by the patellar process projected anteriorly and then curving abruptly, with its two apical thorns pointing posteriorly, and the median apophysis slightly narrower at the end. In *C. rastellus* (Fig. 19E, F) the patellar apophysis projects posteriorly, and the median apophysis is distally expanded. Females differ from those of the other species by having the copulatory openings in a central position between the spermathecae, on depressions separated by median septum, and copulatory ducts not forming loops (Figs 20E, F, 25E, G, 26A–D, G, H) while the other species have the copulatory openings more advanced (Fig. 20B, D).

Description

Male (MACN-Ar 42819): Total length 1.93. Carapace 0.83 long, 0.70 wide. Abdomen 1.10 long and 0.83 wide. Eye diameters and spacing: AME 0.05, ALE 0.08, PME 0.07, PLE 0.07; AME–AME 0.03, AME–ALE 0,02, PME–PME 0,05, PME–PLE 0,03, ALE–PLE virtually contiguous; MOQ length 0.15, front width 0.12, rear width 0.18. Clypeus height 0.08. Carapace light brown, darker lines radiating from the central region, darker well-defined border, anterior region with setae. Chelicerae length 0.28, ratio 0.38. Endites yellowish-brown, as long as wide, posterior lateral edge rounded. Labium darker anteriorly. Sternum wider than long, length 0.45, width 0.55, dark brown, dark edge, lighter medially. Abdomen with grey, brown, and white mottling dorsally, four to five reddish posterior chevrons. Ventral grey mottling in longitudinal stripes. Pedipalp cymbium oval, slightly pointed distally, copulatory bulb with fleshy median apophysis; tibial apophysis short and recurved, patellar apophysis erect on dorsolateral surface, with two teeth (Fig. 19G–I). Spinnerets in relatively compact group, with similar pigmentation, darker at the basal part and lighter distally. ALS total length 0.13; basal width 0.08. PMS total length 0.10. PLS total length 0.17. Legs light castaneous-yellow with arrows in the proximal segment of the femur, metatarsus and tarsus, dark in the distal segment

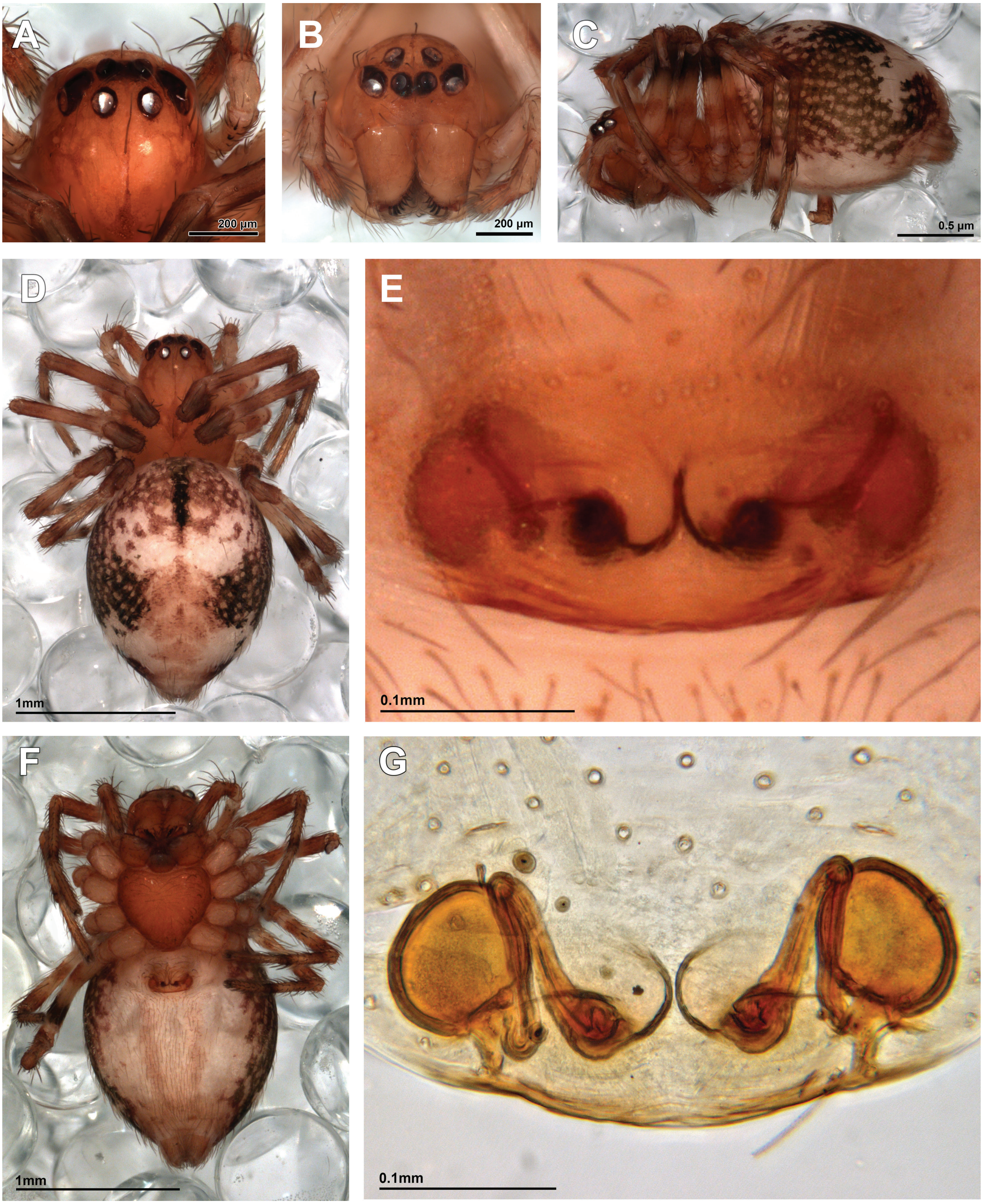

Figure 25. *Cybaeolus delfini* (Simon 1904), female (A–E, MACN-Ar 42819. G, MACN-Ar 42750). A, eyes, dorsal view. B, prosoma, anterior view. C, habitus lateral. D, habitus dorsal. E, epigyne, ventral view. F, habitus ventral. G, epigyne cleared, ventral view.

of femur and patella. Leg measurements (formula 1243): leg I (total 2.66) femur 0.67, patella 0.25, tibia 0.47, metatarsus 0.75, tarsus 0.48 leg II (2.63) 0.75, 0.25, 0.67, 0.60, 0.36; leg III (2.21) 0.62, 0.22, 0.45, 0.55, 0.37; leg IV (2.58) 0.73, 0.25, 0.62, 0.65, 0.33; palp (0.86) 0.27, 0.20, 0.12, -, 0.27. Leg formula 1243. Pattern of spines: Femora: I d0-0-1. Patella: I d1-0-1, II d1-0-1, III d1- 0-1, IV d1-0-1. Tibia: I d1-0-1, p0-0-1, II d1-0-1, p0-0-1, III d1-1-0, p0-0-1, v0-1-0, r0-0-1, IV d1-1-0, p0-0-1, v0-1-0,

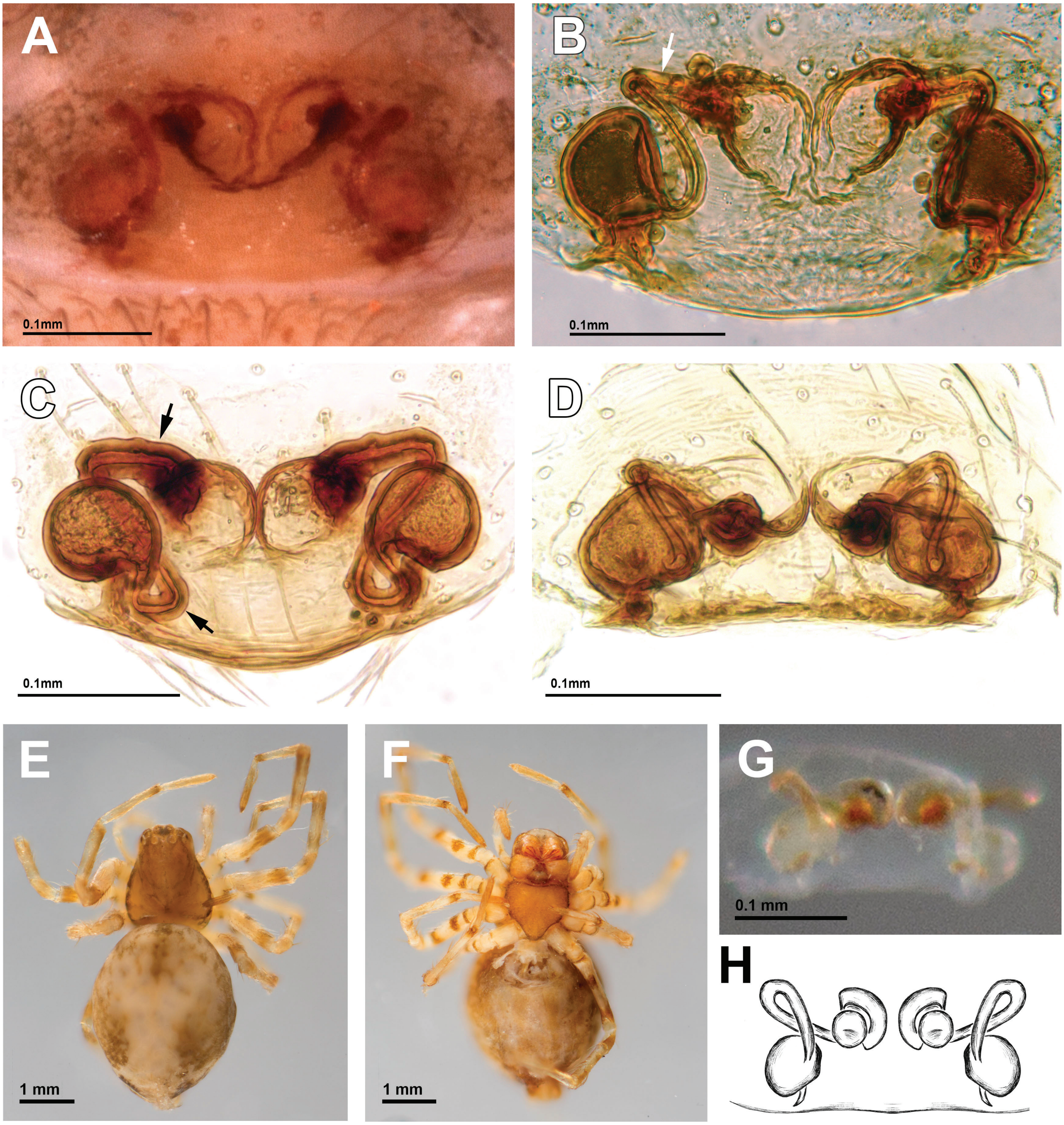

Figure 26. *Cybaeolus delfini* (Simon, 1904), female. A, epigyne from variant with transversal proximal copulatory ducts, ventral view (MACN-Ar 43232). B, same, cleared, ventral view, arrow to proximal copulatory duct. C, genitalia of variant with transversal proximal copulatory duct and longer posterior loop (arrows; AMNH LAM-0559). D, genitalia of intermediate variant (AMNH, LAM-0558). E, holotype, dorsal habitus. F, same, ventral habitus. G, same, epigyne cleared, dorsal view. E, same, schematic drawing.

r0-0-1. Metatarsus: III p0-0-1, v0-1-1, r0-0-1; IV p0-0-1, v0-1-1, r0-0-1. Trichobothria on all tarsi d0-1-0; all metatarsi d0-1-0; all tibiae d0-1-0.

Female (MACN-Ar 42819). Total length 2.27. Carapace 0.90 long, 0.75 wide. Abdomen 1.50 long and 1.18 wide. Eye diameters and spacing: AME 0.07, ALE 0.08, PME 0.07, PLE 0.08; AME–AME 0.03, AME–ALE 0,02, PME–PME 0,07, PME–PLE 0,03, ALE–PLE virtually contiguous; MOQ length 0.18, front width 0.15, rear width 0.20. Anterior eye row slightly procurved in anterior view, posterior row slightly procurved in dorsal view. AME spaced less than their diameter. Clypeus unmarked, 0.12 high. Carapace light brown, slightly darker edges and darker thoracic V-shaped mark. Chelicerae short, with rastellum of five thick setae (Fig. 25B). Endites about as long as wide, rounded posteriorly. Labium wider than long, darker anteriorly. Sternum yellowish brown, wider than long, width 0.58, length 0.50, edge thin brown. Dorsum of abdomen mottled, dark brown in the anterior central line and posterior laterals, mottled light brown in the anterior and posterior part, beige midzone. Epigyne (Figs 20E, F, 25E–G) with two depressions bearing the copulatory

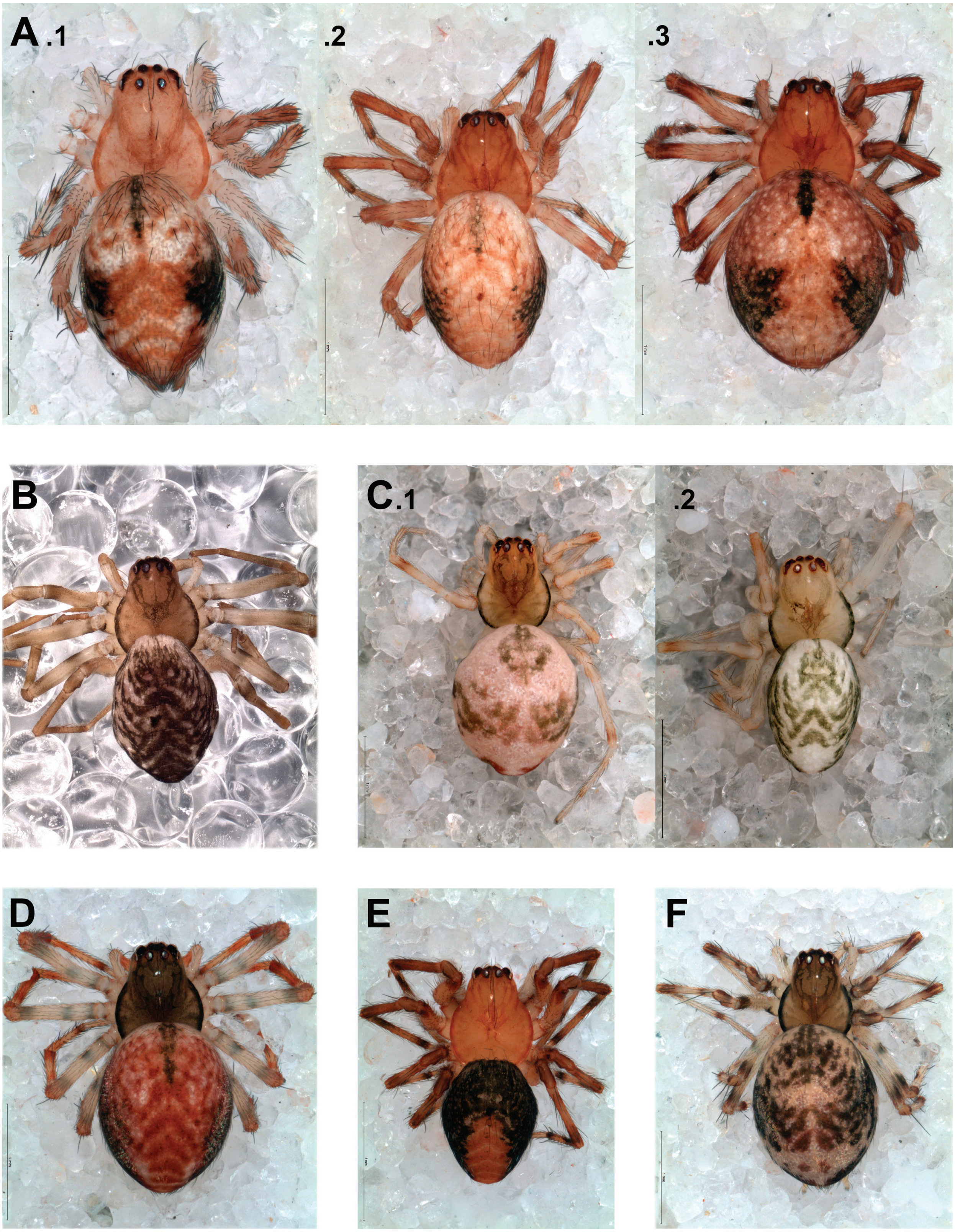

Figure 27. Colour polymorphism in *Cybaeolus delfini* (Simon, 1904), grouped by locality and collection event. A, Argentina, Neuquén: Parque Nacional Lanín (MACN-Ar 43581). B, Chile, La Araucanía, Parque Nacional Nahuelbuta (MACN-Ar 43232). C, Chile, Los Ríos, Reserva Costera Valdiviana, (CASENT 9039052, CASENT 9034004). D, Argentina, Santa Cruz, Chaltén (MACN-Ar 43327). E, Argentina, Neuquén, Parque Nacional Lanín (MACN-Ar 43343). F, Chile, Los Lagos, Parque Nacional Puyehue (MACN-Ar 43972).

openings, separated by median septum. Copulatory ducts relatively short, leading to spherical spermathecae. Spinnerets in relatively compact group, ALS separated by less than a diameter. Legs brownish, with darker pigmentation in the form of rings. Leg measurements (formula 1243): leg I (total 3.00) femur 0.83, patella 0.30, tibia 0.67, metatarsus 0.73, tarsus 0.47 leg II (2.97) 0.83, 0.32, 0.67, 0.70, 0.45; leg III (2.32) 0.70, 0.30, 0.47, 0.55, 0.30; leg IV (2.83) 0.80, 0.28, 0.65, 0.68, 0.42; palp (1.02) 0.33, 0.17, 0.22, -, 0.30. Pattern of spines: Femora: I p0-1. Patella: I d1-0-1, II d1-0-0, III d1-0-1, IV d1-0-1. Tibia: I d1-0-1 v1-0-1, II d0-0-1, III d1-1-0 r0-0-1 p0-0-1, IV d1-1-0 r0-0-1 p0-0-1. Metatarsus: III p0-1-1 r0-0-2 v0-1-0. Holotype female, measurements and spines: Total length 2.63. Carapace 1.00 long, 0.83 wide. Abdomen 1.65 long, 1.40 wide. Eye diameters and interdistances AME 0.05, ALE 0.07, PME 0.07, PLE 0.08; AME–AME 0.06, AME–ALE 0.06, PME–PME 0.09, PME–PLE 0.06, ALE–PLE virtually contiguous; MOQ length 0.20, anterior width 0.16, posterior width 0.23. Clypeus 0.13 (2.6× diameter AME). Chelicerae length 0.37, ratio 0.44. Sternum width 0.62, length 0.55. Leg measurements (formula 1423): leg I (total 3.07) femur 0.86, patella 0.28, tibia 0.63, metatarsus 0.76, tarsus 0.54; leg II (2.94) 0.81, 0.22, 0.62, 0.76, 0.53; leg III (2.54) 0.67, 0.29, 0.50, 0.62, 0.46; leg IV (3.01) 0.78, 0.28, 0.71, 0.75, 0.49; palp (1.00), 0.26, 0.15, 0.22, -, 0.37, 1.00. Leg formula 1423. Spines: (numerous spines broken, metatarsus and tarsus of leg II missing); pedipalp: patella d1-0-1; tibiae: p1-0-1; tarsi: d1-0-0, p1-1-1, r1-1-1. Femora: no spines. Patellae: I d1-0-1; II d1-0-1; III d1-0-1; IV d1-0-1. Tibiae: I d1-0-1; II d1-0-1; III d1-0-1, p1-0-1, v0-1-0, r1-0-1; IV d1-0-1, p1-0-1, v0-1-0, r1-0-1. Metatarsi: III p0-0-1, v0-1-2, r0-0-1; IV p0-0-1, v0-1-0, r0-0-1.

Variability and colour polymorphism:

The copulatory openings are most frequently found medially in the epigyne, on the posterior margins of the paired depressions, and the first stretch of the copulatory duct is diagonal upwards (Fig. 25E, F). Some rare specimens have the copulatory openings in a more anterior position, on the external margins of the paired depressions, and the first stretch of the copulatory duct is transverse (Fig. 26A–C) or slightly diagonal (Fig. 26D, G, H). The copulatory duct may rarely describe a loop on the posterior margin, before entering the spermatheca (bottom arrow in Fig. 26C). We did not detect a geographical pattern of these infrequent morphologies, which are scattered across the species' distribution in Chile, in Coquimbo (AMNH, LAM-0558), Araucanía (MACN-Ar 43231, 43232), Los Lagos (AMNH, LAM-0559), and Magallanes (holotype). The body coloration is extremely variable (Figs 1G, 27). The phylogenetic analysis resulted in two groups of specimens (marked in shades of red on Fig. 29), one from coastal localities in Chile (Chiloé and Reserva Costera Valdiviana), the other from localities close to the Andes in Chile and Argentina, in Araucanía, Neuquén, Río Negro, and Santa Cruz. The minimum inter-group divergence of the *COI* marker was 4.7%, much larger than the maximum divergences intra-group, of 2.3% and 2.0% in the coastal and Andean groups, respectively (maximum likelihood distances, Kimura 2-parameter). We were unable to detect any morphological pattern related with these genetic differences, which could be indicative of cryptic species.

Distribution

Known from forests and shrublands in Chile from Parque Nacional Pan de Azúcar, in Región de Atacama, to Punta Arenas in Región de Magallanes, and in adjacent Argentina, from Parque Nacional Lanín, in Neuquén Province, to El Chaltén, in Santa Cruz province (Fig. 28C).

Other material examined

ARGENTINA: Chubut: Lago Escondido [−41.7°, −71.61°], 19 Nov. 1961, A. Kovács, 1♀ (AMNH). *Parque Nacional Los Alerces:* Lago Futalaufquen [−42.845°, −71.705°], 1 Feb. 1986, M. Ramírez, 1♀ (MACN). **Neuquén:** Lago Hermoso [−40.351°, −71.554°], 15 Jan. 1985, M. Ramírez, 1♂ 2♀ (MACN). *Parque Nacional Nahuel Huapi:* Puerto Blest, trail to Laguna Los Cántaros, 41.013754º S, 71.822738º W, 820–890 m elev., 28 Dec. 2010, M. Ramírez, V. Werenkraut, and S. Aisen, 1♂ (MACN-Ar 34359 MAI-1770, MLB-4412). *Parque Nacional Lanín:* Puerto Canoas and Lago Curilaufquen [−39.815°, −71.606°], 8 Jan. 1985, M. Ramírez, 1♂ (MACN); Seccional Puerto Canoa, mouth of Arroyo Raquithue, 40 km NW Junín de los Andes (air), 39.745306º S, 71.478861º W, 906 m elev., 7 Dec. 2021, beating, M.P. Pacheco, L. Piacentini, and E.M. Soto, 1♂ (MACN-Ar 43343); Seccional Puerto Canoa, mouth of Arroyo Raquithue, 40 km NW Junín de los Andes (air), 39.745306º S, 71.478861º W, 906 m elev., 7 Dec. 2021, beating, M.P. Pacheco, L. Piacentini, and E.M. Soto, 5♀ (MACN-Ar 43581 AGB-0013). **Río Negro:** *Parque Nacional Nahuel Huapi:* near Puerto Alegre, Lago Frías, 41.04394º S, 71.79962º W, 811 m elev., 29 Dec. 2010, M. Ramírez, V. Werenkraut, and S. Aisen, 2♀ (MACN-Ar 43241); trail to Co. La Mona, near Lago Espejo Chico, 40.58546º S, 71.70412º W, 832 m elev., 5 Jan. 2011, M. Ramírez and V. Werenkraut, 1♀ (MACN-Ar 33729 MLB-4345); 1♂ (MACN-Ar 36484 DLP-4137); 1♂ (MACN-Ar 33730 MLB-4346); 40.590821º S, 71.704036º W, 815–840 m elev., 5 Jan. 2011, M. Ramírez and V. Werenkraut, 1♀ (MACN-Ar 43234); 1♀ (MACN-Ar 33731 MLB-4347); trail between Los Rápidos del Río Manso and Lago Los Moscos, 41.349315º S, 71.600526º W, 792 m elev., 13 Sep. 2010, M. Ramírez and V. Werenkraut, 4♀ (MACN-Ar 33791); 1♂ (MACN-Ar 33804); 1♀ (MACN-Ar 33807); 2♀ (together with 1 immature) (MACN-Ar 33822); 1♂ 1♀ (MACN-Ar 42819 AGB-0006). El Bolsón [−41.96°, −71.53°], 13 Mar. 1961, A. Kovács, 1♀ (AMNH). **Santa Cruz:** bike trail to Chorrillo del Salto, 2 km N El Chalten [−49.30836º, −72.89956º], 406 m elev., 12 Jan. 2022, shrubs and forest, beating, P. Pacheco, 2♂ 4♀ (MACN-Ar 43327 AGB-0011). **CHILE: Región de Atacama:** *Parque Nacional Pan de Azúcar:* Las Lomitas, 26.7 km (air) N Chañaral, 26.00979º S, 70.60601º W, 823 m elev., 26 Oct. 2011, M. Ramírez, A. Ojanguren, and J. Pizarro *et al.*, 6♂ 5♀ (MACN-Ar 34237). **Región de Aysén:** Río Emperador Guillermo [−45.285°, −72.123°], 19 Feb. 1984, T. Cekalovic, 1♀ (together with six immatures) (AMNH). *Parque Nacional Laguna San Rafael:* [−46.86°, −73.53°], 16–24 May 1990, L. Peña, 2♀ (AMNH). **Región de Coquimbo:** *Parque Nacional Fray Jorge:* 30°40′ S, 71°41′ W, 580 m elev., 10 Nov. 1993, N. Platnick, K. Catley, M. Ramírez, and Allen, 1♀ (AMNH); 17♀ (AMNH); 1♀ (AMNH LAM-0558). **Región de La Araucanía:** Alto Caledonia, 42 km E Mulchen [−37.78°, −71.69°], 740 m elev., 14 Feb. 1992, N. Platnick, P. Goloboff, and

M. Ramírez, 3♀ (AMNH). *Parque Nacional Villarrica:* road to Coñaripe, near sector Quetrupillén, 39.45314º S, 71.80915º W, 925 m elev., 13 Feb. 2012, M. Ramírez, M. Izquierdo, P. Michalik, C. Wirkner, and K. Huckstorf, 1♂ (MACN-Ar 36410 DLP-4210); 1♀ (MACN-Ar 36425 DLP-4201). Coicoicura, 5 Dec. 1992, T. Cekalovic, 1♀ (AMNH). Estereo Molco [–38.822°, –73.071°], 18 Feb. 1991, T. Cekalovic, 2♀ (AMNH). Malalcahuello [–38.471°, –71.572°], 1570 m elev., 13–31 Dec. 1982, 649 window trap, *Nothofagus pumilio, Araucaria* forest, A. Newton and M. Thayer, 3♀ (AMNH). *Monumento Natural Contulmo:* 38.01314º S, 73.18648º W, 341 m elev., 9 Jan. 2020, M. Ramírez, E. Soto, J. Wilson, and D. Poy, 1♀ (MACN-Ar 41387); 38º00′46.8″ S, 73º11′15.4″ W, 360 m elev., 10–11 Feb. 2005, Berlese, M. Ramírez, and F. Labarque, 1♀ (MACN-Ar 42817). Nahuelbuta, 37º48′09″ S, 73º0′37″ W, 1316 m elev., 20 Feb. 2002, *Nothofagus dombeyi*, J.E. Barriga, 5♂ 14♀ (MACN-Ar 42773 AGB-0040); 1♀ (MACN-Ar 42774 AGB-0001); 1♀ (MACN-Ar 42775 AGB-0002); 1♀ (MACN-Ar 42776 AGB-0003); 1♀ (MACN-Ar 42777 AGB-0004); 1♂ (MACN-Ar 42778 AGB-0005). Parque Nacional Nahuelbuta: Pichinahuel, 37º47′ S, 73º0′ W, 1200 m elev., 22 Nov. 2004, T., fogging s/*Araucaria araucana*, *Nothofagus dombeyi*, J.E. Barriga, 2♀ (MACN-Ar 42812); 1♀ (MACN-Ar 42814); sector Piedra del Aguila, 29 km W Angol (air), 37.82241º S, 73.03518º W, 1400 m elev., 12 Jan. 2020, M. Ramírez, E. Soto, J. Wilson, and D. Poy, 1♀ (MACN-Ar 42813); sector Quetrupillén, 39º27′42.1″ S, 71º50′44.2″ W, 1280 m elev., 8 Feb. 2005, forest with *Araucaria*, *Nothofagus*, *Chusquea*, M. Ramírez and F. Labarque, 1♂ (MACN-Ar 42818); 37º47′ S, 73º00′ W, 1200 m elev., 12 Feb. 2005, fogging *Nothofagus dombeyi*, J.E. Barriga, 1♀ (MACN-Ar 42810); 1♀ (MACN-Ar 42811); fogging *Nothofagus obliqua*, J.E. Barriga, 1♂ (MACN-Ar 42816); fogging *Nothofagus antarctica*, J.E. Barriga, 1♀ (MACN-Ar 43231 AGB-0008); 1♀ (MACN-Ar 43232 AGB-0007); 1♂ (MACN-Ar 43233); 1♂ 1♀ (MACN-Ar 43236); [–37.783°, –73°], 1300 m elev., 1–6 Feb. 1979, L. Peña, 1♀ (AMNH); 37° 49′ 39″ S, 73° 00′ 32.2″ W, 110 m elev., 12 Feb. 2005, forest with *Nothofagus*, *Araucaria*, M. Ramírez and F. Labarque, 1♂ 3♀ (MACN-Ar 42750 AGB-0014). Reserva Nacional Villarrica, sendero Laguna Verde, S39.201466°, O71.820053°, 618 m elev., 6–7 Jan. 2023, M.P. Pacheco, L. Piacentini, and E.M. Soto, 1♂ ♀ (MACN-Ar 43956). Tolten (coastal town), Vilupulli [–39.21°, –73.22°], 27 Feb. 1979, L. Peña, 1♀ (AMNH). **Región de Los Lagos:** 10 km E Puyehue [–39.669°, –72.286°], 24 Jan. 1951, Ross, Michelbacher, 1♀ (CAS). *Parque Nacional Chiloé:* 15 km S Chepu [–42.14°, –74.05°], 3 Feb. 3, 1991, M. Ramírez, 1♀ (MACN-Ar 42815); Arroyo Cole Cole 25 km N Cucao [–42.406°, –74.108°], 8–11 Feb. 1991, M. Ramírez, 1♀ (MACN). *Isla Chiloé:* 5 km SW Chonchi [–42.65°, –73.83°], 2 Feb. 2001, T. Cekalovic, 1♀ (AMNH); 2♂ 2♀ (AMNH); 2♀ (AMNH); Dalcahue NE Castro [–42.37°, –73.65°], 1 Feb. 1981, L. Peña, 1♀ (AMNH); El Pulpito [–42.773°, –73.786°], 21 Jun. 2000, T. Cekalovic, 1♂ 1♀ (AMNH); Cucao [–42.649°, –74°], 12 Feb. 1991, M. Ramírez, 1♂ (MACN); km 2 Puente Río Pudeto [–41.867°, –73.768°], 18 May 1998, T. Cekalovic, 1♀ (AMNH); 2♂ 20♀ (AMNH); km 5 S Compu [–43.14°, –73.63°], Feb. 10, 1999, T. Cekalovic, 1♂ 4♀ (AMNH); Lago Tarahuin [–42.72°, –73.74°], 18 Feb. 1998, T. Cekalovic, 2♀ (AMNH); Loncomilla [–42.167°, –73.625°], 7 Feb. 1988, T. Cekalovic, 3♀ (together with 13 immatures) (AMNH); Mocopulli [–42.33°, –73.7°], 20 Feb. 1986, T. Cekalovic, 1♀ (AMNH); Piruquina [–42.38°, –73.79°], 10 Feb. 1993, T. Cekalovic, 1♀ (AMNH); 16 Feb. 1989, T. Cekalovic, 4♀ (AMNH); 22 Feb. 1991, T. Cekalovic, 2♀ (AMNH); 16 Feb. 1993, T. Cekalovic, 8♀ (AMNH); 7 Feb. 1994, T. Cekalovic, 4♀ (AMNH); Puente Trainel [–42.675°, –73.799°], 9 Feb. 1993, T. Cekalovic, 1♀ (AMNH); Río Cipresal, 42º 35.181′ S, 74º 05.576′ W, 2 Mar. 2008, fogging 150 cc/l *Nothofagus nitida*, Arias *et al.*, 1♀ (CASENT 9034055 JMA-0205); San Juan de Chadmo [–42.971°, –73.581°], 10 Feb. 1999, T. Cekalovic, 1♂ 4♀ (AMNH). Isla Chiloé [no specific locality], 11 Feb. 1993, T. Cekalovic, 3♂ 1♀ (AMNH); 21 Feb. 1991, T. Cekalovic, 2♀ (AMNH). *Chiloé, Isla Quinchao:* 3.5 km from Curaco de Velez [–42.44°, –73.6°], 6 Feb. 1988, T. Cekalovic, 2♀ (AMNH); Curaco [–42.44°, –73.6°], 10 Feb. 1994, T. Cekalovic, 2♀ (AMNH); Lago Poluz [–42.4°, –73.5°], 6 Feb. 1988, T. Cekalovic, 1♀ (AMNH); Laguna Pulol [–42.408°, –73.61°], 7 Feb. 2001, T. Cekalovic, 2♀ (AMNH); Hullar Alto [–42.407°, –73.573°], 17 Feb. 1995, T. Cekalovic, 1♀ (AMNH). *Chiloé, Isla Lemuy, Ichuac:* [–42.617°, –73.717°], 9 Feb. 1993, T. Cekalovic, 2♀ (AMNH). Llanquihue, E slope Volcán Osorno, above Petrohué [–41.145°, –72.411°], 400–1000 m elev., 21 Mar. 1965, H.W. Levi, 1♀ (MCZ). Hills S Maicolpue [–40.62°, –73.74°], 50 m elev., 19 Feb. 1992, N. Platnick, P. Goloboff, and M. Ramírez, 3♀ (AMNH); 1♀ (AMNH). 1 km from road intersection from Osorno to Pucatrihue, 6 Mar. 2001, T. Cekalovic, 1♀ (AMNH). Parque Nacional Puyehue, sector Anticura, sendero Salto del Pudú, 40.675656° S, 72.164139° W, 480 m elev., 11 Jan. 2023, M.P. Pacheco, L. Piacentini, and E.M. Soto, 1♀ (MACN-Ar 43972). Termas de Puyehue [–40.736°, –72.308°], 180 m elev., 24 Nov. 1981, N. Platnick and R. Schuh, 1♀ (AMNH LAM-0557). *Parque Nacional Puyehue:* Volcán Casablanca [–40.779, –72.192], 12 Feb. 1992, M. Ramírez, N. Platnick, and P. Goloboff, 1♀ (AMNH LAM-0559). **Región de Los Ríos:** 34 km WNW La Unión [–40.21°, –73.45°], 700 m elev., 17 Dec. 1984 to 7 Feb. 1985, Fit trap, mixed evergreen forest, S. and J. Peck, 1♀ (AMNH). *Reserva Costera Valdiviana:* Chaihuin, Las Garzas, 39º 59.687′ S, 73º 35.227′ W, 26 Feb. 2008, Fogging 150 cc/l *Nohofagus nitida*, Arias *et al.*, 1♀ (CASENT 9039052 JMA-0165); 1♀ (CASENT 9034004 JMA-0207). Las Lajas, W La Unión, 9–13 Jun. 1990, L. Peña, 1♀ (together with one immature) (AMNH). Las Trancas, W La Unión, 19–20 Nov. 1990, L. Peña, 1♂ 3♀ (AMNH). Neltume [–39.851°, –71.948°], Feb. 1987, T. Cekalovic, 1♂ 1♀ (AMNH). **Región de Valparaíso:** Quebrada El Tigre, 2.5 km E Zapallar, 32.55143º S, 71.43278º W, 357 m elev., 12 Feb. 2011, M. Ramírez, E. Soto, and J. Pizarro, 4♀ (MACN-Ar 33785); 1♀ (MACN-Ar 35160 MAI-4201); 1♀ (MACN-Ar 35162 MAI-4192); 1♀ (MACN-Ar 35169). Zapallar [–32.553°, –71.469°], 27 Nov. 1950, Ross, Michelbacher, 1♀ (CAS). Reserva Parque El Boldo, Zapallar, 300m NNE de ruta costera, 32.54593º S, 71.45179º W, 114 m elev., 12 Feb. 2011, M. Ramírez, E. Soto, and J. Pizarro, 1♂ 1♀ (MACN-Ar 35175). **Región del Biobío:** km 10 N Curanilahue [–37.38°, –73.34°], 21 Nov. 1992, T. Cekalovic, 1♀ (together with one immature) (AMNH). Quebrada Caramávida, 'sector 9', reserva Arauco, 15 km (air) E Antiguala, 37.66839º S, 73.22683º W, 800 m elev., 16 Jan. 2018, M. Ramírez, A. Ojanguren, A. Pérez González, G. Azevedo, and W. Porto, 2♂ 3♀ (MACN-Ar 41274).

Phylogenetic analysis

Identification of legacy sequences

We tested the taxonomic identity of sequences from *Cybaeolus* sp. 11-01 from Miller *et al.* (2010). These legacy sequences matched our new sequences of an unidentified Hahniidae sp. from Chile, Chiloé (MACN-Ar 36389; *COI* divergence 0.2%), and thus are regarded as misidentified.

Maximum likelihood

The 10 analyses under maximum likelihood using the genomic backbone tree produced nine topologies, from which the one with the best fit (larger likelihood) was chosen (Fig. 29). For comparison, the analysis of the data without the genomic constraints produced a tree with very similar topology, except for some relationships of the outgroup taxa (Supporting Information, Fig. S2). Hahniidae appear monophyletic with moderate to high support (bootstrap 81 in the constrained analysis, 98 in unconstrained one); the genus *Cybaeolus* is well supported and nested within the hahniids. The three species of *Cybaeolus* appear as monophyletic, confirming the male–female matching of the Taxonomy section. The analysis of the arrangement of spinnerets produced a better fit for the simplest model (ER). The linear arrangement of the spinnerets is optimized as a synapomorphy of Hahniidae, with a reversal to the grouped state in *Cybaeolus* (Fig. 29). Since the two consecutive groups where *Cybaeolus* is nested have relatively low support (0.59 and 0.77), we further tested if a position of *Cybaeolus* as sister to the rest of the hahniids received any support in the 1000 bootstrap pseudoreplicates; that resolution had a frequency of zero, meaning that such a placement is strongly contradicted by our data.

Maximum parsimony

In the analysis under equal weights using the genomic constraint, *Cybaeolus* is monophyletic with high support values (bootstrap 99), as is each of the species within this genus (Supporting Information, Fig. S3). For the rest of the tree the supports are low, although the optimal topology is similar in general to the one from the maximum likelihood analysis. The low support values may be attributed to the many terminals with sequences from only a single marker. In the implied weighting analysis using the genomic constraint (Supporting Information, Fig. S4), the groups are also similar as in the previous analyses, but the support values are slightly higher than in the equal weights' analysis. In both analyses, the parsimony optimization of the spinnerets' arrangement is the same as in the maximum likelihood analysis.

Colour polymorphism

The three species show remarkable colour polymorphism, which seems unrelated to geographic location and time of collection, since many morphs were collected at the same time in the same locality (Figs 22, 24, 27). There are also coincidences on the same morphs in different species. For example, (i) reddish chevrons, dark cardiac area, dark sides: *C. pusillus* (Fig. 22A.2, A.3, A.11, 1, J, K.2) and *C. delfini* (Fig. 27D); (ii) black with posterior red blotch: *C. pusillus* (Fig. 22A.4, A.19) and *C. delfini* (Fig. 27E); (iii) dark grey: *C. pusillus* (Figs. 22A.5, A.13) and *C. rastellus* (Fig. 24D.2); (iv) dark band on pale background: *C. pusillus* (Fig. 22E) and *C. rastellus* (Fig. 24C.1, G). The examples above also show that similar colour morphs occur irrespective of sex.

DISCUSSION

The phylogenetic analyses corroborate the monophyly of the genus *Cybaeolus* with good support, as well as the monophyly of the family Hahniidae (Fig. 29). Both maximum likelihood and parsimony analyses agree in placing *Cybaeolus* well-nested within hahniids; therefore, we refute the hypothesis that *Cybaeolus* is the sister-group of the rest of the hahniids, as suggested by the morphology of the spinnerets. In this regard, the ancestral state reconstruction of the spinneret's disposition (Fig. 29) implies that the clustered arrangement in *Cybaeolus* is a reversal of the aligned disposition typical of other hahniids. This result is remarkable, as it also involves a complete re-acquisition of a field of numerous piriform gland spigots in the usual arrangement of most araneomorph spiders, i.e. marginal to the major ampullate gland spigots (see: Griswold *et al.* 2005). The anterior spinnerets of the typical hahniids (*Hahnia pusilla* Figs 7, 8 and *Neoantistea magna,* Figs 9, 10; see also: Dupérré and Tapia 2024) have a low number of piriform gland spigots, even totally absent in the males, while in *Cybaeolus* there are numerous piriform gland spigots in both sexes (Figs 3–6). If the reversion to the ancestral condition was the actual evolutionary path, then *Cybaeolus* may have also re-acquired the ability to produce effective attachment disks, which are determined by the position of the spinnerets and the presence of piriform gland spigots (Wolff *et al.* 2019, 2021). Attachment disks are probably important for the building of aerial webs by *Cybaeolus*, thus the position of the ALS spinnerets close to each other, and numerous piriform gland spigots, may produce attachment disks of higher mechanical performance (see: Wolff *et al.* 2019, 2021). In contrast, it has been shown that the aligned spinnerets typical of hahniids results in loosely organized, divided attachment disks with little piriform glue (Wolff *et al.* 2021); strong attachments are probably not essential for the simpler webs built by most other hahniids, which are laid over the substrate (Eberhard 2018). An alternative explanation for the low number of piriform gland spigots in typical hahniids is miniaturization, as most hahniids are very small, while *Cybaeolus* species are relatively large and, consequently, have more of those spigots. Some support for this hypothesis comes from the reports of low number of piriform gland spigots in their first instars of many spider species (Townley and Tillinghast 2009, Alfaro *et al.* 2018), although this is not always the case (e.g. Hajer 1991). However, virtually all miniaturized spider species still have the typical arrangement of a field of several piriform gland spigots at the side of the major ampullate gland spigot field (e.g. Lopardo and Hormiga 2015). Studying the ontogeny of the spinning organs of hahniids will probably clarify some of these questions.

Within *Cybaeolus*, the genetic sequences, especially of the mitochondrial marker *COI*, which had a denser coverage, confirmed the matching of males and females in the three species

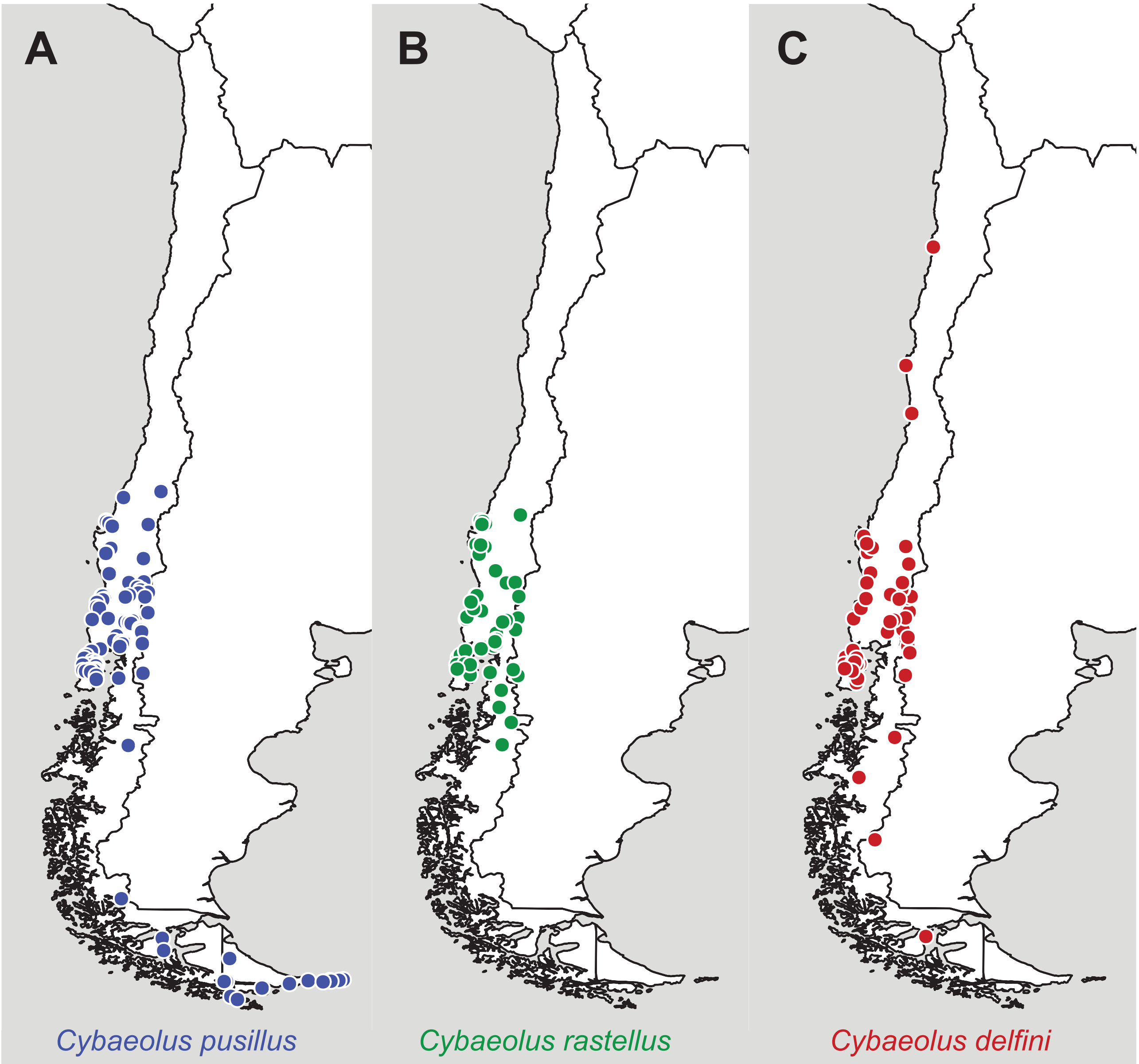

Figure 28. Geographical records of species of *Cybaeolus*. A, *Cybaeolus pusillus* Simon, 1884. B, *Cybaeolus rastellus* (Roth, 1967), C, *Cybaeolus delfini* (Simon, 1904).

(Fig. 29; see Table 1). Within the species *Cybaeolus delfini* we found two genetic clusters divided by a 4.7% divergence of the marker *COI*, although we were not able to find corresponding morphological differences. Additional sampling in intermediate localities, especially in further coastal areas of Chile, may help resolve whether this pattern of divergences is indicative of cryptic species.

Our phylogenetic analysis, although not designed to resolve the relationships of the entire diversity of Hahniidae, confirms that the genus *Hahnia* is polyphyletic as currently circumscribed, as anticipated by previous studies (see: Rivera-Quiroz *et al.* 2020); while a group of species appears closely related to the type species *Hahnia pusilla*, two other species (*Hahnia ngai* Rivera-Quiroz *et al.*, 2020 and *Hahnia glacialis* Sørensen, 1898) are nested in another group, more closely related to *Antistea*, *Neoantistea*, and *Neohanhia* Mello-Leitão, 1917. Furthermore, the recently proposed genus *Hexamatia* Rivera-Quiroz *et al.*, 2020 is nested within *Hahnia*. These preliminary findings will be useful for future research on the delimitation of genera in Hahniidae.

We provide evidence of extensive colour polymorphism in the three species of *Cybaeolus* and discard the hypothesis of a strict association of colour morphs with geographical distribution, because highly divergent colour morphs were sampled at the same date in the same locality. At the same time, the coincidence of the same colour morphs across species suggests that those may be determined by similar genetic basis in the different species (Oxford and Gillespie 1996, 2001). The concurrence of the same colour morphs in males and females is also suggestive of an autosomal determination of the colour morphs. The ecology of *Cybaeolus* species probably involves a selective pressure maintaining the colour polymorphisms, as they are unusual

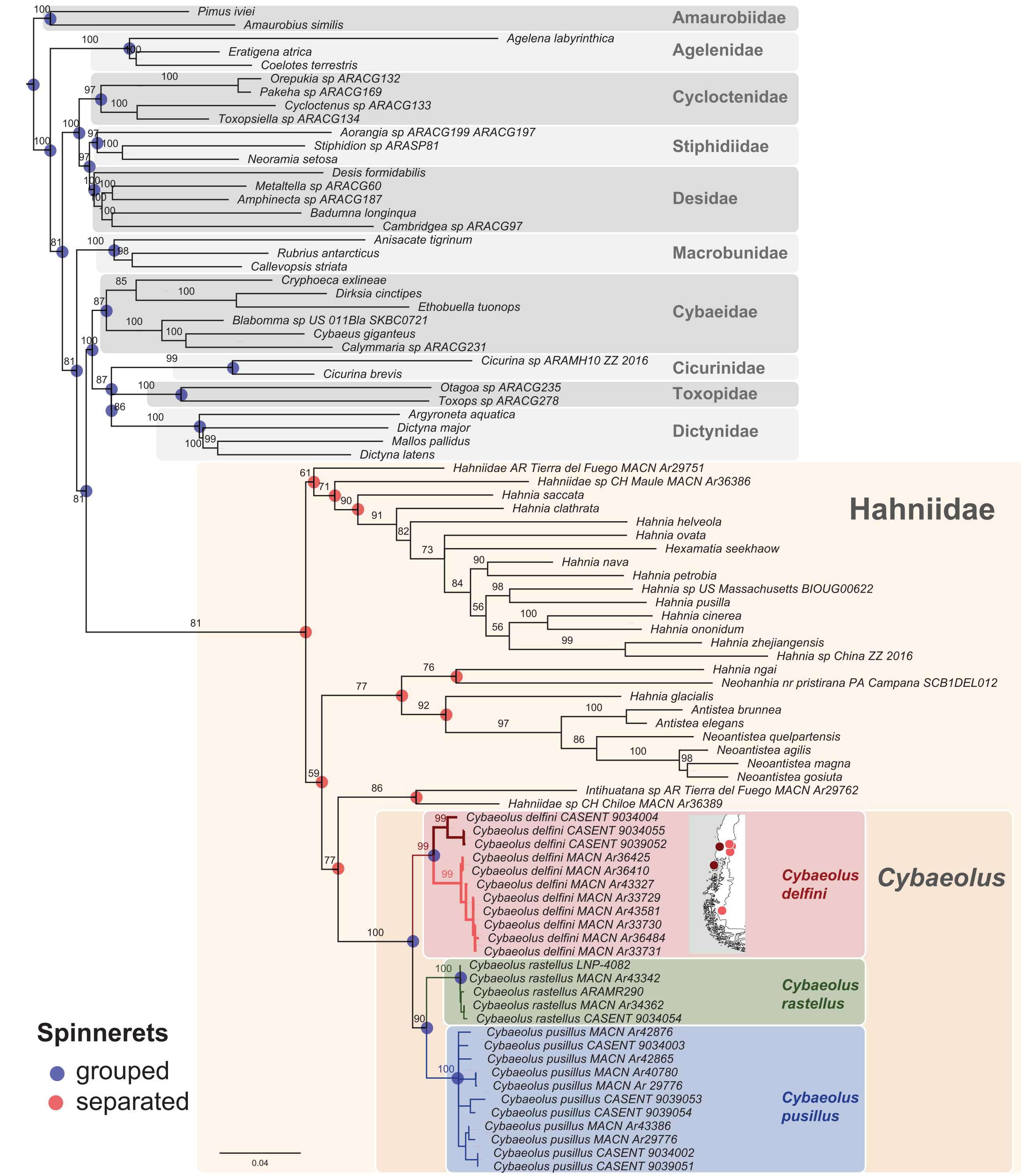

Figure 29. Maximum likelihood tree obtained from the concatenated dataset using a topological constraint from previous genomic analysis of Gorneau *et al.* (2023). Numbers on branches are ultrafast bootstrap percentages. Main nodes are marked with the ancestral state for the disposition of spinnerets. The two genetic *COI* groups of *Cybaeolus delfini* are marked in tones of red, with their geographic origin on the map.

among hahniids in building aerial webs and resting on the underside of leaves, exposed to visual predators. The colour morphs are evidently neither cryptic nor aposematic. This is consistent with apostatic selection of visual predators training to prey on frequent colour morphs, thus maintaining the less frequent colour morphs that are less predated upon until they increase in frequency (Allen 1988, Oxford and Gillespie 1998).

Some characters of the male copulatory organs that are distinctive of hahniids deserve a functional consideration. During mating, the basic functional working of the genital organs in spiders of the RTA clade initiates with the locking of the retrolateral tibial apophysis of the male in a pocket in the female epigyne. Second, once the bulb expansion occurs, the intromittent structure (the embolus) is guided by a male furrowed structure into the copulatory opening of the female (Huber 1995). Very often the furrowed male structure is the conductor, which is absent in Hahniidae. One could argue that the structure that we identified as the median apophysis is in fact a relictual conductor; this may be the case, but still, it lacks a furrow to guide the embolus. Considering the absence of a functional conductor in the male copulatory bulb of hahniids, it is likely that the furrows in the cymbium and in the RTA play the role of guiding the embolus into the copulatory opening of the female. Lehtinen (1967: 368) also pointed out that the cymbial groove of hahniids must work as a functional conductor, and the occasional finding of partially expanded palps with the embolus running through these grooves and projecting from the tip of the RTA, supports this hypothesis. In addition, some hahniid species with extremely large tibial apophyses have correspondingly large copulatory ducts (e.g. *Scotospilus longus* Zhang *et al.*, 2013). It has been already shown that the furrowed RTA of anyphaenid spiders of the genus *Aysha* guide the embolus during mating (Poy *et al.* 2023), and it seems that hahniids may have developed the same strategy. Behavioural experiments would be needed to test this hypothesis.

SUPPLEMENTARY DATA

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

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CONFLICT OF INTEREST

None declared.

DATA AVAILABILITY

The original images, phylogenetic datasets and resulting trees are deposited in the repository of CONICET (http://hdl.handle.net/11336/248075); phylogenetic datasets and resulting trees are also available in Zenodo (DOI: 10.5281/zenodo.14079899).

REFERENCES

Alfaro RE, Griswold CE, Miller KB. The ontogeny of the spinning apparatus of *Tengella perfuga* (Araneae: Zoropsidae). *Invertebrate Biology* 2018;**137**:187–204. https://doi.org/10.1111/ivb.12219

Allen JA. Frequency-dependent selection by predators. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* 1988;**319**:485–503. https://doi.org/10.1098/rstb.1988.0061

Bertkau P. Versuch einer natürlichen Anordnung der Spinnen, nebst Bemerkungen zu einzelnen Gattungen. *Archiv für Naturgeschichte* 1878;**44**:351–410.

Castellucci F, Scharff N, Luchetti A. Molecular systematics and phylogenetics of the spider genus *Mastigusa* Menge, 1854 (Araneae, Cybaeidae). *Molecular Phylogenetics and Evolution* 2023;**186**:107833–9. https://doi.org/10.1016/j.ympev.2023.107833

Chamberlin RV, Ivie W. New spiders of the family Agelenidae from western North America. *Annals of the Entomological Society of America* 1937;**30**:211–41. https://doi.org/10.1093/aesa/30.2.211

Cotoras DD, Brewer MS, Croucher PJ *et al.* Convergent evolution in the colour polymorphism of Selkirkiella spiders (Theridiidae) from the South American temperate rainforest. *Biological Journal of the Linnean Society* 2017;**120**:649–63.

Dupérré N, Harms D. Raising the dead: rediscovery and redescription of some lost spider types (Araneae) described by Eugène Simon. *Evolutionary Systematics* 2018;**2**:1–20. https://doi.org/10.3897/evolsyst.2.24122

Dupérré N, Tapia E. First record of the family Hahniidae in Ecuador with description of thirteen new species and three new genera (Araneae: Hahniidae). *Taxonomy* 2024;**4**:53–111. https://doi.org/10.3390/taxonomy4010005

Eberhard WG. The webs of Neoantistea riparia (Araneae: Hahniidae): are dew drops helpful in prey capture? *Arachnology* 2018;**17**:485–90. https://doi.org/10.13156/arac.2018.17.9.485

Fabricius JC. Entomologiae systematica emendata et aucta, secundum classes, ordines, genera, species adjectis synonimis, locis, observationibus, descriptionibus. *Tome II. Hafniae: Christian Gottlieb Proft*, 1793, 1–519.

Forster RR, Wilton CL. The spiders of New Zealand. Part IV. *Otago Museum Bulletin* 1973;**4**:1–309.

Gillespie RG, Tabashnik BE. What makes a happy face? Determinants of colour pattern in the Hawaiian happy face spider *Theridion grallator* (Araneae, Theridiidae). *Heredity* 1989;**62**:355–63. https://doi.org/10.1038/hdy.1989.50

Goloboff PA, Morales ME. TNT v.1.6, with a graphical interface for MacOS and Linux, including new routines in parallel. *Cladistics* 2023;**39**:144–53. https://doi.org/10.1111/cla.12524

Goloboff PA, Carpenter JM, Arias JS *et al.* Weighting against homoplasy improves phylogenetic analysis of morphological data sets. *Cladistics* 2008;**24**:758–73. https://doi.org/10.1111/j.1096-0031.2008.00209.x

Gorneau JA, Crews SC, Cala-Riquelme F *et al.* Webs of intrigue: museum genomics elucidate relationships of the marronoid spider clade (Araneae). *Insect Systematics and Diversity* 2023;**7**:1–18.

Griswold CE, Ramírez MJ, Coddington JA *et al.* Atlas of phylogenetic data for entelegyne spiders (Araneae: Araneomorphae: Entelegynae) with comments on their phylogeny. *Proceedings of the California Academy of Sciences* 2005;**56 (Suppl. II)**:1–324.

Hajer J. Notes on the spinning apparatus of the spiders *Hyptiotes paratloxus* C. L.K., 1834, and *Uloborus walckenaerius* Latr., 1806 (Araneae: Uloboridae). *Bulletin de la Société des Sciences Naturelles de Neuchâtel* 1991;**116**:99–103.

Hentz NM. Descriptions and figures of the araneides of the United States. *Boston Journal of Natural History* 1847;**4**:54–7. https://doi.org/10.5962/bhl.part.16996

Huber BA. The retrolateral tibial apophysis in spiders-shaped by sexual selection? *Zoological Journal of the Linnean Society* 1995;**113**:151–63. https://doi.org/10.1111/j.1096-3642.1995.tb00931.x

Katoh K, Standley DM. MAFFT multiple sequence alignment software v.7: improvements in performance and usability. *Molecular Biology and Evolution* 2013;**30**:772–80. https://doi.org/10.1093/molbev/mst010

Kelly MB, Khan K, Wierucka K *et al.* Dynamic evolution of locomotor performance independent of changes in extended phenotype use in spiders. *Proceedings of the Royal Society B: Biological Sciences* 2023;**290**:1–8.

Keyserling E. Neue Spinnen aus America. VII. *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien* 1887;**37**:421–90.

Koch CL. Arachniden. In: Herrich-Schäffer GAW (ed.), *Deutschlands Insecten.* Regensburg, Heft: Friedrich Pustet, 1834, 122–6.

Koch CL. Die Arachniden. *Nürnberg Achter Band: C. H. Zeh'sche Buchhandlung*, 1841, 41–131.

Koch L. Die Arachniden Australiens, nach der Natur beschrieben und abgebildet [Erster Theil, Lieferung 3–7]. Nürnberg: Bauer and Raspe, 1872, 105–368.

Kulkarni S, Wood HM, Hormiga G. Advances in the reconstruction of the spider tree of life: a roadmap for spider systematics and comparative studies. *Cladistics* 2023;**39**:479–532. https://doi.org/10.1111/cla.12557

Lehtinen PT. Classification of the cribellate spiders and some allied families, with notes on the evolution of the suborder Araneomorpha. *Annales Zoologici Fennici* 1967;**4**:199–468.

Lopardo L, Hormiga G. Out of the twilight zone: phylogeny and evolutionary morphology of the orb-weaving spider family Mysmenidae, with a focus on spinneret spigot morphology in symphytognathoids (Araneae, Araneoidea). *Zoological Journal of the Linnean Society* 2015;**173**:527–786. https://doi.org/10.1111/zoj.12199

Magalhaes IL, Ramírez MJ. Phylogeny and biogeography of the ancient spider family Filistatidae (Araneae) is consistent both with long-distance dispersal and vicariance following continental drift. *Cladistics* 2022;**38**:538–62.

Mello-Leitão CF. Generos e especies novas de araneidos. *Archivos da Escola Superior de Agricultura e Medicina Veterinaria, Rio de Janeiro* 1917;**1**:3–19.

Mello-Leitão CF. Arañas del Chaco y Santiago del Estero. *Revista del Museo de La Plata (nueva serie, Zoología)* 1942;**2**:381–426.

Menge A. Die im Bernstein befindlichen Myriapoden, Arachniden und Apteren der Vorwelt. In: Koch CL, Berendt GC (eds), *Die in Bernstein Befindlichen Organischen Reste der Vorwelt Gesammelt in Verbindung Mit Mehreren Bearbeitetet und Herausgegeben 1.* Nicolai: Berlin, 1854, 1–124.

Miller JA. Review of erigonine spider genera in the Neotropics (Araneae: Linyphiidae, Erigoninae). *Zoological Journal of the Linnean Society* 2007;**149**:1–263. https://doi.org/10.1111/j.1096-3642.2007.00233.x

Miller JA, Carmichael A, Ramírez MJ *et al.* Phylogeny of entelegyne spiders: affinities of the family Penestomidae (new rank), generic phylogeny of Eresidae, and asymmetric rates of change in spinning organ evolution (Araneae, Araneoidea, Entelegynae). *Molecular Phylogenetics and Evolution* 2010;**55**:786–804. https://doi.org/10.1016/j.ympev.2010.02.021

Minh BQ, Schmidt HA, Chernomor O *et al.* IQ-TREE 2: new models and efficient methods for phylogenetic inference in the genomic era. *Molecular Biology and Evolution* 2020;**37**:1530–4. https://doi.org/10.1093/molbev/msaa015

Murphy JA, Roberts MJ. Spider families of the world and their spinnerets. York: British Arachnological Society, 2015, 1–553.

Oxford GS. An exuberant, undescribed colour polymorphism in *Theridion californicum* (Araneae, Theridiidae): implications for a theridiid pattern ground plan and the convergent evolution of visible morphs. *Biological Journal of the Linnean Society* 2009;**96**:23–34. https://doi.org/10.1111/j.1095-8312.2008.01117.x

Oxford GS, Gillespie RG. Genetics of a colour polymorphism in *Theridion grallator* (Araneae: Theridiidae), the Hawaiian happy-face spider, from Greater Maui. *Heredity* 1996;**76**:238–48. https://doi.org/10.1038/hdy.1996.37

Oxford GS, Gillespie RG. Evolution and ecology of spider coloration. *Annual Review of Entomology* 1998;**43**:619–43. https://doi.org/10.1146/annurev.ento.43.1.619

Oxford GS, Gillespie RG. Portraits of evolution: studies of coloration in Hawaiian spiders: the discrete color polymorphisms in spiders allow the study of evolution 'in action'. *BioScience* 2001;**51**:521–8. https://doi.org/10.1641/0006-3568(2001)051[0521:poesoc]2.0.co;2

Oxford GS, Reillo PR. Trans-continental visible morph-frequency variation at homologous loci in two species of spider, *Enoplognatha ovata* ss and *E. latimana*. *Biological Journal of the Linnean Society* 1993;**50**:235–53.

Petrunkevitch A. Systema Aranearum. *Transactions of the Connecticut Academy of Arts and Sciences* 1928;**29**:1–270.

Poy D, Piacentini LN, Michalik P *et al.* MicroCT analysis unveils the role of inflatable female genitalia and male tibial complex in the genital coupling in the spider genus Aysha (Anyphaenidae, Araneae). *Journal of Morphology* 2023;**284**:1–9.

Rivera-Quiroz FA, Petcharad B, Miller JA. First records and a new genus of comb-tailed spiders (Araneae: Hahniidae) from Thailand with comments on the six-eyed species of this family. *European Journal of Taxonomy* 2020;**724**:51–69.

Roth VD. A review of the South American spiders of the family Agelenidae (Arachnida, Araneae). *Bulletin of the American Museum of Natural History* 1967;**134**:297–345.

Rubio GD, Lo-Man-Hung NF, Iuri HA. A revision of the Neotropical genus *Austrohahnia* Mello-Leitão (Araneae, Hahniidae). *Zootaxa* 2014;**3894**:106–16. http://dx.doi.org/10.11646/zootaxa.3894.1.8

Schiapelli RD, Gerschman BS. Arañas argentinas III. Arañas de Misiones. *Revista del Museo Argentino de Ciencias Naturales Bernardino Rivadavia* 1958;**3**:187–231.

Shorthouse DP. *SimpleMappr, an Online Tool to Produce Publication-Quality Point Maps.* 2010. https://www.simplemappr.net (June 5, 2023, date last accessed).

Simon E. Arachnides recueillis par la Mission du Cap Horn en 1882–1883. *Bulletin de la Société Zoologique de France* 1884;**9**:117–44.

Simon E. Arachnides. In: *Mission Scientifique du Cap Horn, 1882–1883.* Paris: Ministère de la marine et Ministère de l'éducation nationale, 1887, E1–E42.

Simon E. Arachnides recueillis a la Terre-de-feu par M. Carlos Backhausen. *Anales del Museo Nacional de Buenos Aires* 1895;**4**:167–72.

Simon E. *Histoire Naturelle des Araignées. Deuxième Édition, Tome Second.* Paris: Roret, 1898, 193–380.

Simon E. Arachnoideen, excl. Acariden und Gonyleptiden. In: *Ergebnisse der Hamburger Magalhaensischen Sammelreise 1892/1893. Band Arthropoden*, Vol. **6**. Hamburg: Naturhistorisches Museum zu Hamburg, L. Friederichsen and Co., 1902, 1–47.

Simon E. Etude sur les arachnides du Chili recueillis en 1900, 1901 et 1902, par MM. C. Porter, Dr Delfin, Barcey Wilson et Edwards. *Annales de la Société Entomologique de Belgique* 1904;**48**:83–114.

Sørensen W. Arachnida Groenlandica (Acaris exceptis). *Videnskabelige Meddelelser fra den Naturhistoriske Forening i Kjøbenhavn* 1898;**1898**:176–235.

Spagna JC, Gillespie RG. More data, fewer shifts: molecular insights into the evolution of the spinning apparatus in non-orb-weaving spiders. *Molecular Phylogenetics and Evolution* 2008;**46**:347–68. https://doi.org/10.1016/j.ympev.2007.08.008

Thorell T. On European spiders. Review of the European genera of spiders, preceded by some observations on zoological nomenclature [second part]. *Nova Acta Regiae Societatis Scientiarum Upsaliensis* 1870;**7**:109–242.

Townley MA, Tillinghast EK. Developmental changes in spider spinning fields: a comparison between *Mimetus* and *Araneus* (Araneae: Mimetidae, Araneidae). *Biological Journal of the Linnean Society* 2009;**98**:343–83. https://doi.org/10.1111/j.1095-8312.2009.01297.x

Wheeler WC, Coddington JA, Crowley LM *et al*. The spider tree of life: phylogeny of Araneae based on target-gene analyses from an extensive taxon sampling. *Cladistics* 2017;**33**:574–616.

Wolff JO, Paterno GB, Liprandi D *et al*. Evolution of aerial spider webs coincided with repeated structural optimization of silk anchorages. *Evolution* 2019;**73**:2122–34.

Wolff JO, Michalik P, Ravelo AM *et al*. Evolution of silk anchor structure as the joint effect of spinning behavior and spinneret morphology. *Integrative and Comparative Biology* 2021;**61**:1411–31. https://doi.org/10.1093/icb/icab003

Zhang ZS, Li SQ, Pham DS. First description of comb-tailed spiders (Araneae: Hahniidae) from Vietnam. *Zootaxa* 2013;**3613**:343–56. https://doi.org/10.11646/zootaxa.3613.4.2