



Research article

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First records and a new genus of comb-tailed spiders (Araneae: Hahniidae) from Thailand with comments on the six-eyed species of this family

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Abstract. The family Hahniidae is reported from Thailand for the first time. The genus *Hexamatia* gen. nov. and two new species, *Hexamatia seekhaow* gen. et sp. nov. and *Hahnia ngai* sp. nov., are described and illustrated. DNA sequences are provided for all the species reported here. The phylogenetic position of the novel genus *Hexamatia* gen. nov. and its relation to *Hahnia* are discussed. Based on these results, a new combination is proposed for *Hexamatia senaria* (Zhang, Li & Zheng, 2011) gen. et comb. nov. = *Hahnia senaria*. Known distribution of the species *Hahnia saccata* Zhang, Li & Zheng, 2011, originally described from China, is expanded. A brief review and notes on the taxonomy of the six-eyed hahniids are included.

Keywords. Thai, Chiang Mai, new species, hahniids, phylogeny.

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Introduction

The family Hahniidae Bertkau, 1878 is relatively easy to identify due to the advanced location of the tracheal spiracle in relation to the spinnerets and the characteristic arrangement of these in more or less one transverse row (at least in the Hahniinae Bertkau, 1878) (Lehtinen 1967; Opell & Beatty 1976). Other members of this family (e.g., *Cicurina* Menge 1871 and *Cybaeolinae* Lehtinen, 1967) do not share this transverse arrangement of the spinnerets (Roth 1967; Wang *et al.* 2019). The Hahniidae currently

includes 351 species in 23 genera distributed worldwide (WSC 2020). The family status of Hahniidae has been confirmed by molecular phylogenies being placed within the RTA clade, closely related to Cybaeidae Banks, 1892 and Dictynidae O. Pickard-Cambridge, 1871 (J.A. Miller *et al.* 2010; Wheeler *et al.* 2017). However, the relations and delimitations of its genera have always been problematic. Only a few local revisions have been done, two for Nearctic species (Gertsch 1934; Opell & Beatty 1976) and one for New Zealand species (Forster 1970). Beside these revisions, Lehtinen (1967) published some comparative tables including diagnostic characters of 17 extant genera (10 currently valid, WSC 2020) and one more from Baltic amber. Presently, two genera, *Cicurina* and *Hahnia* C.L. Koch, 1841, have served as ‘wastebin taxa’ for new species descriptions, having a great morphological heterogeneity and accounting together for almost 70% of all the valid hahniid species (WSC 2020). The great heterogeneity and unclear delimitations in these and other hahniid genera are a recurrent note in new species publications (Forster 1970; Zhang *et al.* 2013; Huang *et al.* 2017).

The Hahniidae have a worldwide distribution, being more diverse in the Americas and Asia but also having a fair number of species described from Europe, Africa and Oceania (WSC 2020). In Asia, eight genera and 93 species have been recorded distributed from the Middle East to Eastern Russia and Japan. In South and Southeast Asia, hahniids have been reported from Hong Kong, Indonesia, Laos, Philippines, Southern China, Sri Lanka, Taiwan and Vietnam (Lehtinen 1967; Bosmans 1992; Barrion & Litsinger 1995; Tang *et al.* 1996; Zhang *et al.* 2011, 2013; Zhang & Zhang 2013; Liu *et al.* 2015; Huang *et al.* 2017). This is the first time the Hahniidae are reported from Thailand. Here we describe a new genus and two new species in this family based on molecular and morphological data. Additionally, we include a brief literature review on the rare six-eyed hahniids.

Material and methods

The hahniid species reported here were collected in the Chiang Mai Province, Thailand, between July 16th and 28th 2018. All the specimens were captured using methods optimized for ground dwelling spiders: leaf litter sifting, Winkler extractors, pitfall traps and direct collecting on ground, among leaf litter and under rocks or logs.

Specimen habitus and other somatic characters were photographed under a Leica MI6SC stereo microscope equipped with a Nikon DS-Ri2 camera. Genitals were photographed using a Leica DM 2500 microscope attached to the same camera. Specimens were observed in ethanol using semi permanent slide preparations (Coddington 1983). Female genitalia were dissected, digested using pancreatine solution (Álvarez-Padilla & Hormiga 2007) and cleared with methyl salicylate.

Four legs were taken from one individual of each species for DNA extraction. Six gene fragments (COI, H3, 12S, 16S, 18S and 28S) were amplified following M.A. Miller *et al.* (2010) and Wheeler *et al.* (2017) protocols; list of primers is provided in the Supplementary material (Supplementary file 1). Sequences were edited in Geneious Prime 2020.0.5. New sequences generated for this study were deposited in GenBank; accession numbers are reported in Table 1. All the specimens used here have been deposited in the collection of the Naturalis Biodiversity Center, Leiden, the Netherlands (RMNH.ARA.18411–RMNH.ARA.18415).

We used sequences from the three species we collected, as well as 15 other species with available sequences in GenBank. We used in total 14 species of Hahniidae, three species of Cybaeidae Banks, 1892, and one species of Agelenidae C.L. Koch, 1837, *Agelena labyrinthica* Walckenaer, 1805, as an outgroup. The sequences used to test the relationships and position of the new species within the Hahniidae are listed in Table 1. We used MAFFT ver. 7.450 online (<https://mafft.cbrc.jp/alignment/server/>) with default parameters to build the alignments. Alignments for 18S were further trimmed manually due to the size difference of some sequences. 16S and 12S were not used due to the low availability of these loci for

Table 1. GenBank accession numbers of DNA sequences used for our analyses. * marks the new sequences generated for the present work.

Family	Species	COI	H3	12S	16S	18S	28S
Agelenidae	<i>Agelena labyrinthica</i>	FN554797	KR074077			AY633862	AY633851
Cybaeidae	<i>Calymmaria</i> sp. 1	DQ628611	DQ628638			DQ628702	DQ628666
Cybaeidae	<i>Cryphoeca exlineae</i>	KM840792.1	MN590107.1			MN590054.1	MN590084.1
Cybaeidae	<i>Cybaeus morosus</i>	FJ263792	DQ628641			DQ628707	DQ628671
Hahniidae	<i>Antistea brunnea</i>	HQ580602.1	MN590134.1			MN590079.1	MN590103.1
Hahniidae	<i>Cybaeolus</i> cf. <i>rastellus</i>	KY017745	KY018252			KY016481	KY017117
Hahniidae	<i>Cybaeolus pusillus</i>		KY018253.1			KY016482.1	KY017118.1
Hahniidae	<i>Hahnia cinerea</i>	GU683831.1	MN590136.1			MN590081.1	MN590105.1
Hahniidae	<i>Hahnia clathrata</i>	FJ949005	FJ949043			FJ948923	
Hahniidae	<i>Hahnia nava</i>	KY270115	KY018254.1			KY016483.1	
Hahniidae	<i>Hahnia ngai</i> sp. nov.	MT433973 *	MT445988 *		MT434973 *	MT437224 *	MT434975 *
Hahniidae	<i>Hahnia ononidum</i>	MG047916.1	MN590137.1			MN590082.1	MN590106.1
Hahniidae	<i>Hahnia saccata</i>	MT433972 *		MT434903 *		MT437222 *	
Hahniidae	<i>Hahnia</i> sp. ZZ-2016 (China)	KR074066	KR074092			KR074014	
Hahniidae	<i>Hahnia zhejiangensis</i>	KR074067.1	KR074093.1			KR073991.1	KR074041.1
Hahniidae	<i>Hexamatia seekhaow</i> sp. nov.	MT433971 *	MT445987 *		MT434972 *	MT437221 *	MT434974 *
Hahniidae	<i>Neoantistea agilis</i>	HQ580773.1	DQ628644.1			DQ628714.1	DQ628678.1
Hahniidae	<i>Neoantistea quelpartensis</i>	JN817206.1				JN816788.1	JN816996.1

the Hahniidae in GenBank; Table 1 only reports accession numbers of these markers for our sequences. *Hahnia pusilla* C.L. Koch, 1841, type species of Hahniidae, as well as two more species of *Hahnia* and two of *Iberina* Simon, 1881 had only COI sequences available in GenBank, therefore, they were not used in our final dataset. Matrix was built using COI, H3, 18S and 28S alignments in Sequence Matrix ver. 1.8 (<http://www.ggvaidya.com/taxondna/>); matrix is available in Supplementary file 2. Each locus was treated as a partition and examined with jModelTest2 (Darriba *et al.* 2012) in CIPRES (M.A. Miller *et al.* 2010) to get the best model fit for each; GTR+I+G was selected in all the cases. Our datasets were analyzed using MEGA X (Kumar *et al.* 2018) for maximum parsimony (SPR, default values, bootstrap = 1000), RaXML (Stamatakis 2014) in CIPRES for maximum likelihood (GTR, bootstrap = 1000) and MrBayes ver. 3.2.6 (Ronquist & Huelsenbeck 2003) for windows for the Bayesian inference (GTR+I+G, two independent runs with one cold and three heated chains, mcmc = 1 000 000 gen, samplefreq = 1000, burnin = 2500). The program Tracer ver. 1.7.1 (Rambaut *et al.* 2018) was used to analyze the performance of our BI analyses, and Mega X to estimate the genetic distances (JC model, gamma dist., gamma parameter = 1.00; gaps data treatment = pairwise deletion) for our whole dataset.

Abbreviations (in text and figures)

- A = epigynal atrium
- ALE = anterior lateral eyes
- ALS = anterior lateral spinnerets
- AME = anterior median eyes
- BI = Bayesian inference
- Cd = copulatory duct

CF	=	cymbial furrow
Co	=	copulatory opening
Cy	=	cymbium
E	=	embolus
F	=	femur
Fd	=	fertilization duct
G	=	glands
LE	=	lateral eyes
MA	=	median apophysis
ML	=	maximum likelihood
MP	=	maximum parsimony
P	=	patella
PA	=	patellar retrolateral apophysis
PLE	=	posterior lateral eyes
PLS	=	posterior lateral spinnerets
PME	=	posterior median eyes
PMS	=	posterior median spinnerets
RTA	=	retrolateral tibial apophysis
S	=	spermatheca
Sd	=	spermatic duct
Ss	=	secondary spermatheca
T	=	tibia
Te	=	tegulum

Results

Phylogenetic analyses

Topologies inferred by the three different phylogenetic analyses recovered nearly identical topologies (Fig. 1a–c). The genus *Hahnia* was homogeneously recovered as diphyletic. The clade *Hahnia* 1 was formed by six species of *Hahnia*, and *Hahnia* 2 by *H. ngai* sp. nov. and *H. saccata*, the two species of *Hahnia* we captured in Thailand. The clade *Hahnia* 1 showed high support, although the internal relationships are not fully resolved, having moderate to weak support values in the ML and MP analyses. This clade was found as a sister group to the new genus *Hexamatia* gen. nov. in all our trees. The clade *Hahnia* 2 appears to be more related to *Antistea*+*Neoantistea*. This branch is recovered and highly supported in all the analyses. The cluster formed by *Antistea*+*Neoantistea* is strongly supported although its internal relationships are not resolved and show weak to moderate support in the MP and ML. The three cybaeid representatives form a highly supported group that is consistently recovered as a sister to the monophyletic Hahniidae. Our BI showed an average deviation of split frequencies below 0.003 after 1 000 000 generations. None of the Estimated Sample size parameters fell below the commonly used threshold of 200 suggesting that our BI ran for an adequate length (Drummond *et al.* 2006; Lanfear *et al.* 2016). The trace plot and histograms of both runs are available in Supplementary files 3–4. Pairwise genetic distances for our alignment showed *Hexamatia* gen. nov. to have a wide range of distances with respect to species of *Hahnia*. When compared to species in *Hahnia* 1, this range went from 9.5 to 25% while the distance from *Hahnia* 2 was between 10.7 and 17.8%. In comparison, the distances between *Hexamatia* gen. nov. and *Antistea*+*Neoantistea* were higher and less variable, between 18.0 and 19.2%. See Supplementary file 5 for complete distance matrix.

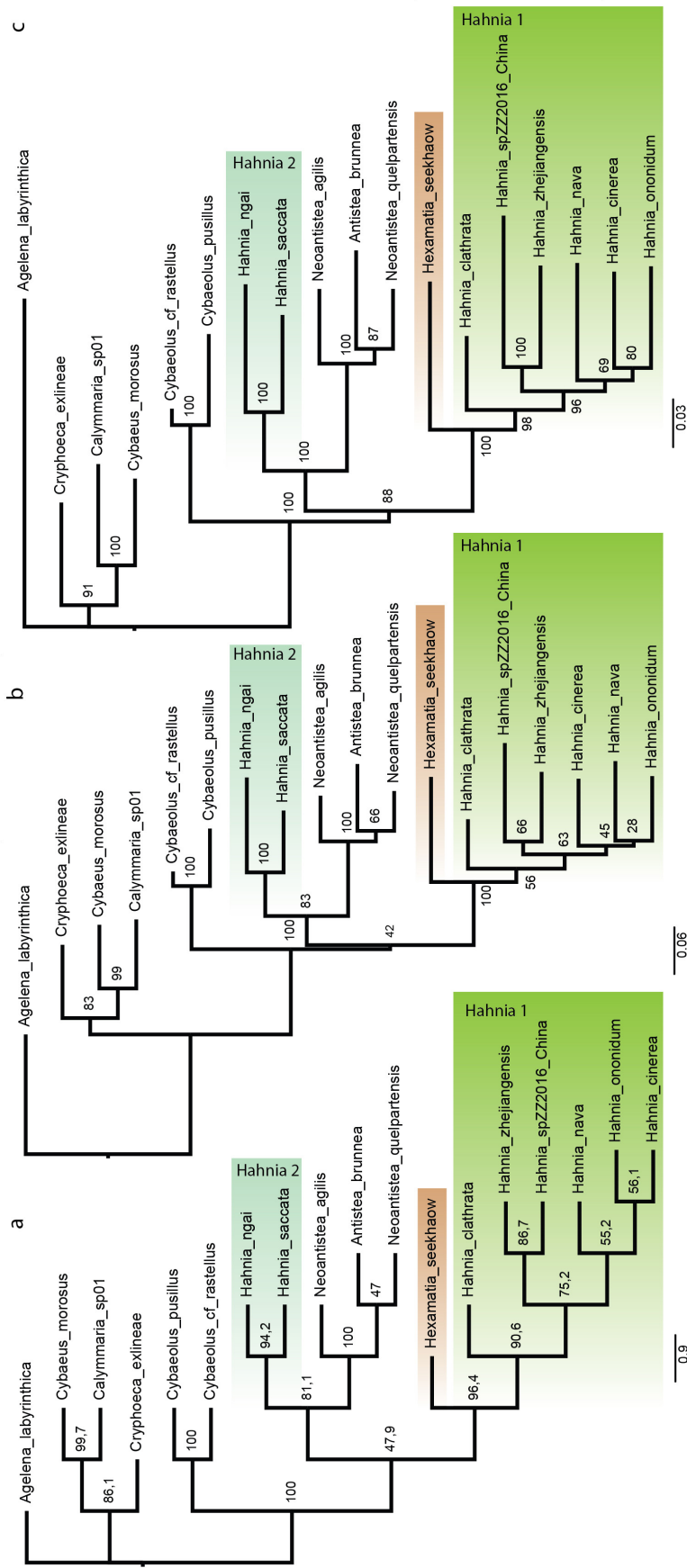


Fig. 1. Tree topologies obtained by different analyses. **a.** Maximum parsimony most parsimonious tree, numbers at nodes indicate bootstrap support. **b.** Maximum likelihood, numbers at nodes indicate bootstrap support. **c.** Bayesian inference, numbers at nodes indicate posterior probabilities. The agelenid *Agelena labyrinthica* Walckenaer, 1805 was used as an outgroup of Cybaeodinae Simon, 1893 and Hahniidae Bertkau, 1878. Fourteen species of Hahniidae and three of Cybaeidae Banks, 1892 were used. Note the diphyly of *Hahnia* C.L. Koch, 1841 and the position of *Hexamaitia* gen. nov. as a sister group to *Hahnia* 1.

Taxonomy

Class Arachnida Lamarck, 1801
Order Araneae Clerck, 1757
Family Hahniidae Bertkau, 1878

Genus *Hexamatia* gen. nov.

urn:lsid:zoobank.org:act:D9504970-17C3-43FF-9231-4D020BC176C7

Type species

Hexamatia seekhaow gen. et sp. nov.

Diagnosis

Hexamatia gen. nov. is distinguished from most hahniid genera by the combination of the following characters: presence of only six eyes, small body size close to 1 mm, and body pale yellow to white, lacking abdominal patterns in males and having faint chevron lines in females (Zhang *et al.* 2011: fig. 23a–b). It can be separated from other six-eyed hahniids by the following combination of characters: from *Amaloxenops* Schiapelli & Gerschman, 1958 by having a backward curved RTA without twists, and presence of PA on the pedipalp patella and MA on the bulb; from *Intihuatana* Lehtinen, 1967 by having an unbifurcated RTA, a shorter and bifurcated PA, and presence of MA; and from *Scotospilus* Zhang, Li & Pham, 2013 by the comparatively short RTA, bifurcated PA and presence of MA.

Etymology

The genus name is formed from two Greek roots: *hexa* (six) and *mati* (eye). It refers to the number of eyes present in this genus, one of its diagnostic characters. The gender is feminine.

Composition

Hexamatia seekhaow gen. et sp. nov. and *Hexamatia senaria* (Zhang, Li & Zheng, 2011) gen. nov., based on the original description and illustrations.

Distribution

Hexamatia seekhaow gen. et sp. nov. is known from Chiang Mai, Thailand; and *Hexamatia senaria* gen. nov. from Yunnan, China (Fig. 8).

Hexamatia seekhaow gen. et sp. nov.

urn:lsid:zoobank.org:act:1D1D0DE7-8A2A-4469-8867-666F9AD6EAEB

Figs 2–3

Diagnosis

Hexamatia seekhaow gen. et sp. nov. greatly resembles *H. senaria* gen. nov. but can be distinguished by the bifurcated PA and having a slightly shorter RTA with a blunter tip (Figs 2f, 3d–e; Zhang *et al.* 2011: figs 21a–d, 22). Another putative difference is the presence of denticles in the distal portion of the RTA; these are not mentioned nor illustrated for *H. senaria* gen. nov.

Etymology

The species epithet is a derivation of the Thai *seekhaow* (white); refers to the lack of color on the body of the holotype of this species.

Type material

Holotype

THAILAND • ♂; Chiang Mai Province, Doi Suthep National Park; 18°48.502' N, 98°53.528' E; 1409 m a.s.l.; 24–28 Jul. 2018; Booppa Petcharad, Jeremy Miller and F. Andrés Rivera-Quiroz leg.; montane evergreen forest with pine; hand coll. among leaf litter; RMNH.ARA.18411 (four legs used for DNA extraction).

Description

Male holotype

Carapace yellowish-white, pale brown in cephalic region (Fig. 2b–c). Legs same color as carapace. Abdomen white without chevron pattern, oval, longer than wide (Fig. 2a–c). Six eyes in two triads,

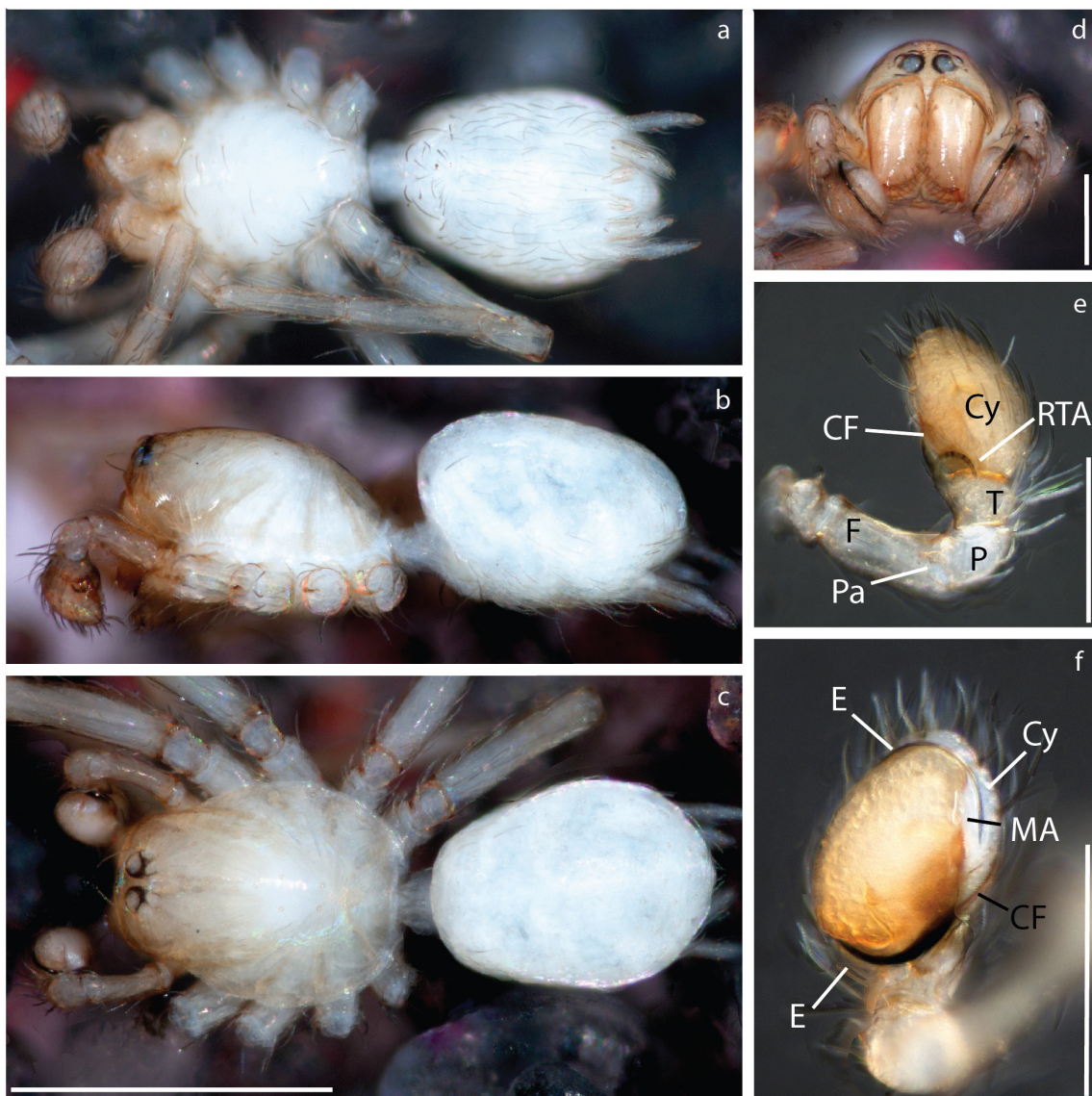


Fig. 2. *Hexamatia seekhaow* gen. et sp. nov., holotype, ♂ (RMNH.ARA.18411). **a–c.** Habitus. **a.** Ventral view. **b.** Lateral view. **c.** Dorsal view. **d.** Prosoma, anterior view. **e–f.** Palp. **e.** Retrolateral view. **f.** Ventral view. Scale bars: a–c = 0.5 mm; d–f = 0.15 mm.

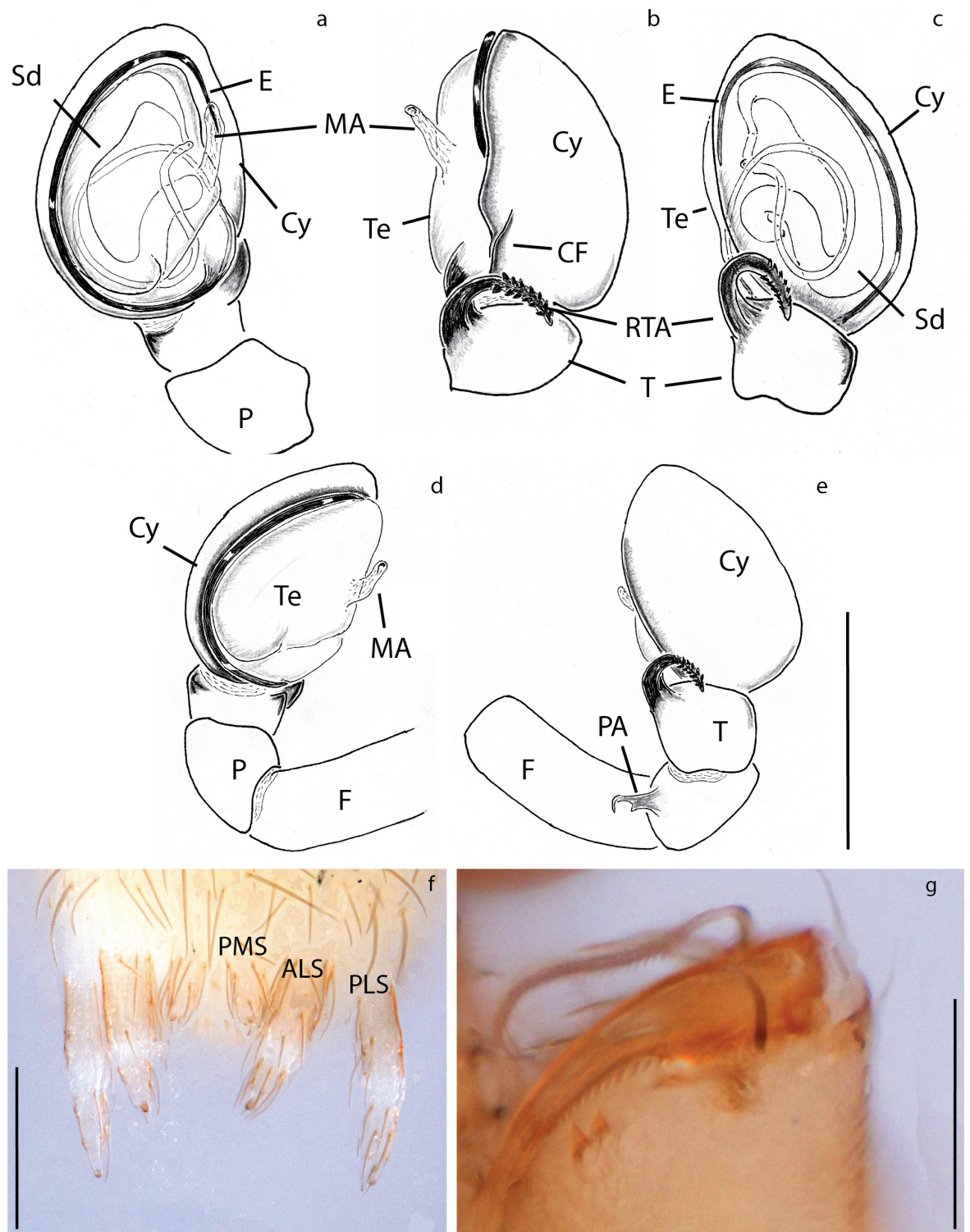


Fig. 3. *Hexamatia seekhaow* gen. et sp. nov., holotype, ♂ (RMNH.ARA.18411). **a–e.** Palp. **a.** Ventral view, cleared. **b.** Retrolateral view. **c.** Dorso-retrolateral view, cleared. **d.** Prolateral view. **e.** Dorso-retrolateral view. **f.** Male spinnerets, ventral view. **g.** Chelicera. Posterior view. Scale bars: a–f = 0.15 mm; g = 0.5 mm.

AME absent ALE 0.04 mm, PME 0.02 mm, PLE 0.02 mm, ALE–ALE 0.02 mm, PME–PME 0.03 mm, PME–PLE contiguous (Fig. 2d). Chelicerae with three promarginal and two retromarginal teeth (Fig. 3g). Tracheal spiracle near middle of abdomen (Fig. 2a).

PALP. Pale brown, same color as cephalic region (Fig. 2c). CF darker, almost as long as RTA (Figs 2e–f, 3b), oval-shaped from ventral view (Figs 2f, 3a). Median apophysis narrow, elongate and transparent (Fig. 3a–b). Embolus filiform, black and long, originating retrolaterally and coiling clockwise around bulb (Figs 2f, 3a–b). RTA spur-like with dark rings. Patellar apophysis short and bifid, with the longer prong hook-shaped (Fig. 3c).

MEASUREMENTS (in mm). Total length 1.1, carapace 0.46 long, 0.33 wide; clypeus 0.01; chelicera 0.2 long, 0.1 wide; pedipalp 0.4 long; palp bulb 0.11 wide; leg I: femur 0.32, patella 0.13, tibia 0.26, metatarsus 0.22, tarsus 0.15; leg II: femur 0.31, patella 0.12, tibia 0.19, metatarsus 0.19, tarsus 0.15; leg III: femur 0.27, patella 0.08, tibia 0.16, metatarsus 0.17, tarsus 0.15; leg IV: femur 0.34, patella 0.11, tibia 0.22, metatarsus 0.21, tarsus 0.16; leg formula IV-I-II-III; abdomen 0.45 long, 0.34 wide.

Distribution

Known from the type locality, Doi Suthep National Park, Chiang Mai, Thailand (Fig. 8).

Notes

See the Discussion for remarks on six-eyed species.

Genus *Hahnia* C.L. Koch, 1841

Hahnia C.L. Koch, 1841: 61.

Type species

Hahnia pusilla C.L. Koch, 1841.

Hahnia ngai sp. nov.

urn:lsid:zoobank.org:act:F9A7FE4B-77C4-4D9B-AFDB-A2FC6F5E0739

Figs 4, 6a–c

Diagnosis

Hahnia ngai sp. nov. can be easily separated from other members of this genus by the simplified female genitalia. Copulatory ducts show only slightly swollen areas with glandular insertions (Figs 4g, 6b–c) but do not form a receptacle or secondary spermathecae (as seen in Figs 5g, 6e–f).

Etymology

The species epithet is a derivation of the Thai *ngai* (simple), in reference to the relatively simple vulva without the well-formed secondary spermathecae commonly seen in other species of *Hahnia*.

Type material

Holotype

THAILAND • ♀; Chiang Mai Province, Doi Suthep National Park; 18°48.502' N, 98°53.528' E; 1409 m a.s.l.; 24–28 Jul. 2018; Booppa Petcharad, Jeremy Miller and F. Andrés Rivera-Quiroz leg.; montane evergreen forest with pine; Winkler extractor; RMNH.ARA.18415 (four legs used for DNA extraction).

Paratypes

THAILAND • 1 ♀; Chiang Mai Province, Doi Inthanon National Park; 18°35.268' N, 98°29.240' E; 2572 m a.s.l.; 24–28 Jul. 2018; Booppa Petcharad, Jeremy Miller and F. Andrés Rivera-Quiroz leg.; cloud forest; Winkler extractor; RMNH.ARA.18414 • 1 ♀; same collection data as for preceding; hand coll.; RMNH.ARA.18413.

Description

Female

Carapace pear-shaped, reddish-brown, slightly darker in cephalic region; texture smooth (Fig. 4c). AME 0.04 mm, ALE 0.06 mm, PME 0.07 mm, PLE 0.04 mm, AME–AME 0.03 mm, AME–

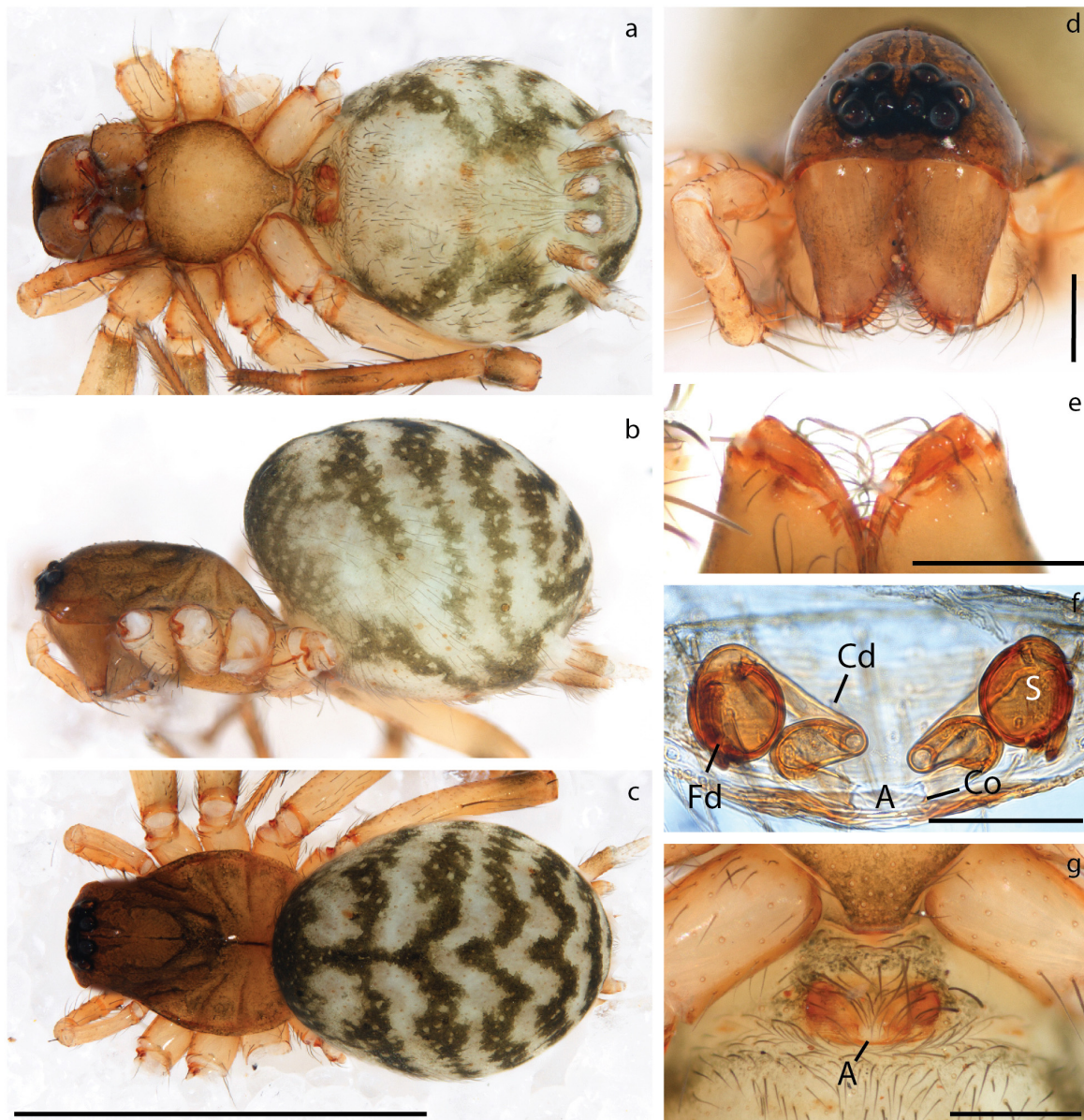


Fig. 4. *Hahnia ngai* sp. nov., holotype, ♀ (RMNH.ARA.18415). **a–c.** Habitus. **a.** Ventral view. **b.** Lateral view. **c.** Dorsal view. **d.** Prosoma, anterior view. **e.** Chelicerae, posterior view. **f–g.** Epigynum. **f.** Dorsal view, cleared. **g.** Ventral view. Scale bars: a–c = 1.0 mm; d–e, g = 0.25 mm; f = 0.1 mm.

ALE 0.02 mm, PME–PME 0.05 mm, PME–PLE 0.03 mm (Fig. 4d). Chelicerae with three promarginal and three retromarginal teeth (Fig. 4e). Legs pale brown, slightly darker on distal segments. Abdomen dark grey with light patches forming five to six chevron bands, oval, longer than wide (Fig. 4c). Tracheal spiracle near middle of abdomen (Fig. 4a).

VULVA. Epigynal plate semitransparent, spermathecae well visible due to transparency. Copulatory openings close together, forming small semi-circular atrium (Figs 4f–g, 6c). Spermatheca sub-spherical with brownish-red coloration (Fig. 4f). Copulatory ducts very simple, slightly swollen centrally (Figs 4f, 6b–c).

MEASUREMENTS (in mm). Total length 2.8, carapace 1.25 long, 0.91 wide; clypeus 0.09; chelicera 0.45 long, 0.25 wide; leg I: femur 0.95, patella 0.37, tibia 0.71, metatarsus 0.72, tarsus 0.55; leg II: femur 0.94, patella 0.34, tibia 0.72, metatarsus 0.68, tarsus 0.55; leg III: femur 0.89, patella 0.33, tibia 0.63, metatarsus 0.71, tarsus 0.51; leg IV: femur 1.12, patella 0.34, tibia 0.93, metatarsus 1.01, tarsus 0.62; leg formula IV-I-II-III; abdomen 1.65 long, 1.23 wide.

Distribution

Known from two localities in Chiang Mai, Thailand (Fig. 8): Doi Suthep National Park (type locality), and the neighboring Doi Inthanon National Park.

Hahnia saccata Zhang, Li & Zheng, 2011
Figs 5, 6d–f

Hahnia saccata Zhang, Li & Zheng, 2011: 16, figs 14a–e, 15a–h, 16a–g.

Material examined

THAILAND • 2 ♀♀; Chiang Mai Province, Doi Suthep National Park; 18°48.780' N, 98°55.928' E; 643 m a.s.l.; 25–28 Jul. 2018; Booppa Petcharad, Jeremy Miller and F. Andrés Rivera-Quiroz leg.; *Dipterocarpus* forest; hand coll.; RMNH.ARA.18412 (four legs of one specimen used for DNA extraction).

Description

Female

Carapace pear-shaped, reddish-brown, slightly darker in cephalic region; texture smooth (Fig. 5c). AME 0.06 mm, ALE 0.11 mm, PME 0.08 mm, PLE 0.05 mm, AME–AME 0.02 mm, AME–ALE 0.01 mm, PME–PME 0.06 mm, PME–PLE 0.04 mm (Fig. 5d). Chelicerae with three promarginal and seven retromarginal teeth (Fig. 5e). Legs same color as carapace, darker on proximal and distal part of each segment. Abdomen dark grey with light patches forming five to six chevron bands, oval, longer than wide (Fig. 5c). Tracheal spiracle near middle of abdomen (Fig. 5a).

VULVA. Epigynal plate dark. Copulatory openings close together but not forming an atrium (Figs 5g, 6f). Spermatheca sub-spherical with brown coloration (Fig. 5f). Copulatory ducts forming secondary spermatheca (Figs 5f, 6e–f).

MEASUREMENTS (in mm). Total length 3.20, carapace 1.45 long, 1.04 wide; clypeus 0.10; chelicera 0.70 long, 0.33 wide; leg I: femur 1.22, patella 0.46, tibia 1.13, metatarsus 0.92, tarsus 0.63; leg II: femur 1.12, patella 0.45, tibia 0.90, metatarsus 0.81, tarsus 0.61; leg III: femur 0.98, patella 0.41, tibia 0.75, metatarsus 0.80, tarsus 0.49; leg IV: femur 1.31, patella 0.45, tibia 1.12, metatarsus 1.03, tarsus 0.65; leg formula IV-I-II-III; abdomen 1.73 long, 1.20 wide.

Distribution

Known from the Menglun Nature Reserve, Yunnan, China (type locality), and Doi Suthep National Park, Chiang Mai, Thailand (present work) (Fig. 8).

Discussion

The Hahniidae, especially the Hahniinae, have traditionally been seen as an easily diagnosable group in part due to the transversal comb-shaped position of the spinnerets. Nevertheless, their position as a family has changed overtime, being initially considered a subfamily of the Agelenidae (Simon 1875;

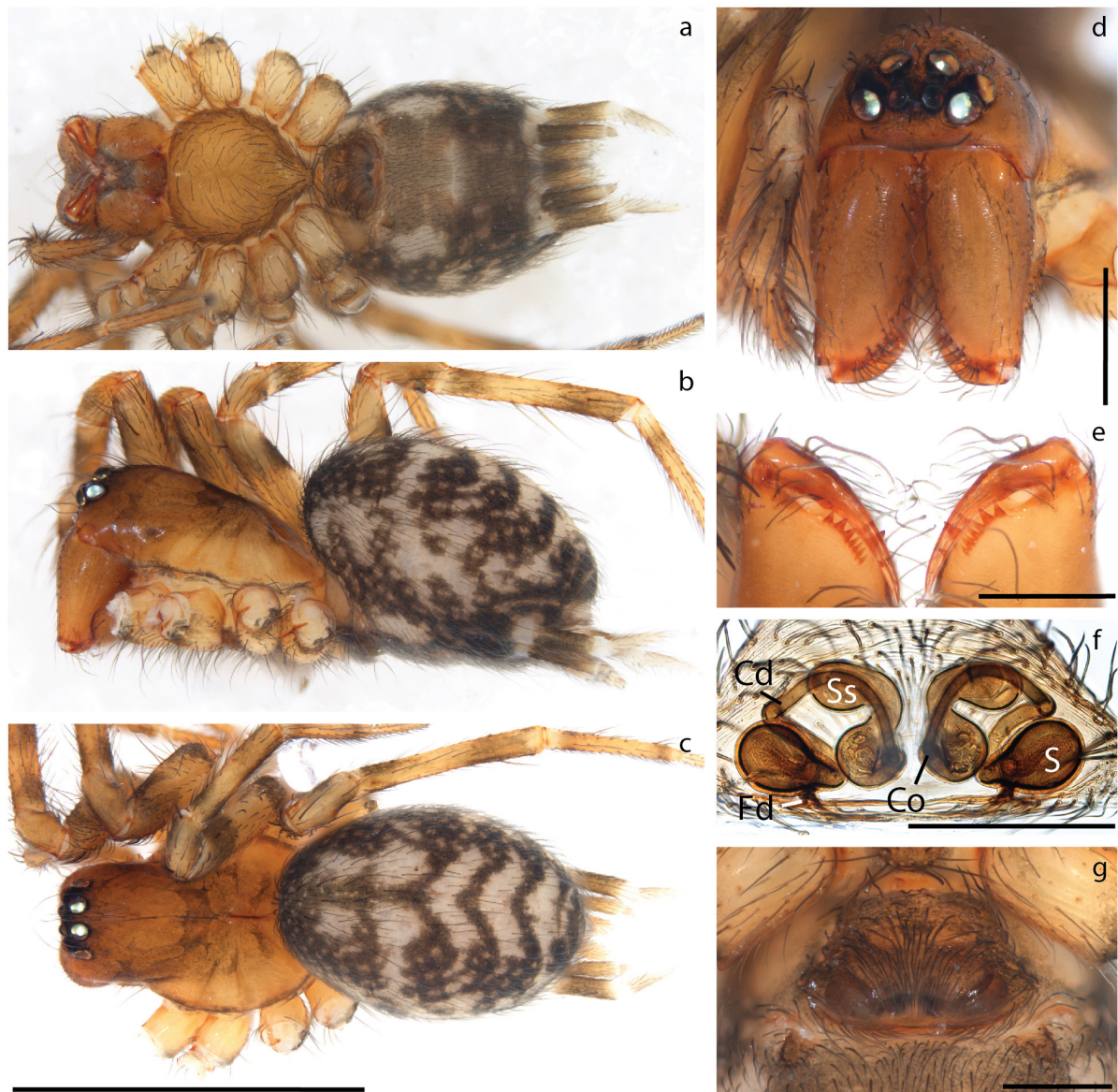


Fig. 5. *Hahnia saccata* Zhang, Li & Zheng, 2011, ♀ (RMNH.ARA.18412). **a–c.** Habitus. **a.** Ventral view. **b.** Lateral view. **c.** Dorsal view. **d.** Prosoma, anterior view. **e.** Chelicerae, posterior view. **f–g.** Epigynum. **f.** Dorsal view, cleared. **g.** Ventral view. Scale bars: a–c = 1.0 mm; d = 0.50 mm; e–g = 0.25 mm.

Gertsch 1934; Lehtinen 1967, among others) and Dictynidae (Lehtinen 1967; Paquin & Dupérré 2009; Wang *et al.* 2019, among others). Currently, the monophyly of the family is largely recognized, and its relations have been indirectly tested as a part of broad scoped phylogenetic studies (J.A. Miller *et al.* 2010; Wheeler *et al.* 2017). However, the relations between its genera have never been phylogenetically tested. Although our data did not include representatives of all the known hahniid genera, we found some consistent and well supported results with the 14 hahniid species and four loci we analyzed. The position of the new genus *Hexamatia* gen. nov. as a sister group to the core species of *Hahnia* in our study is confidently recovered in all our topologies. We consider that this plus the

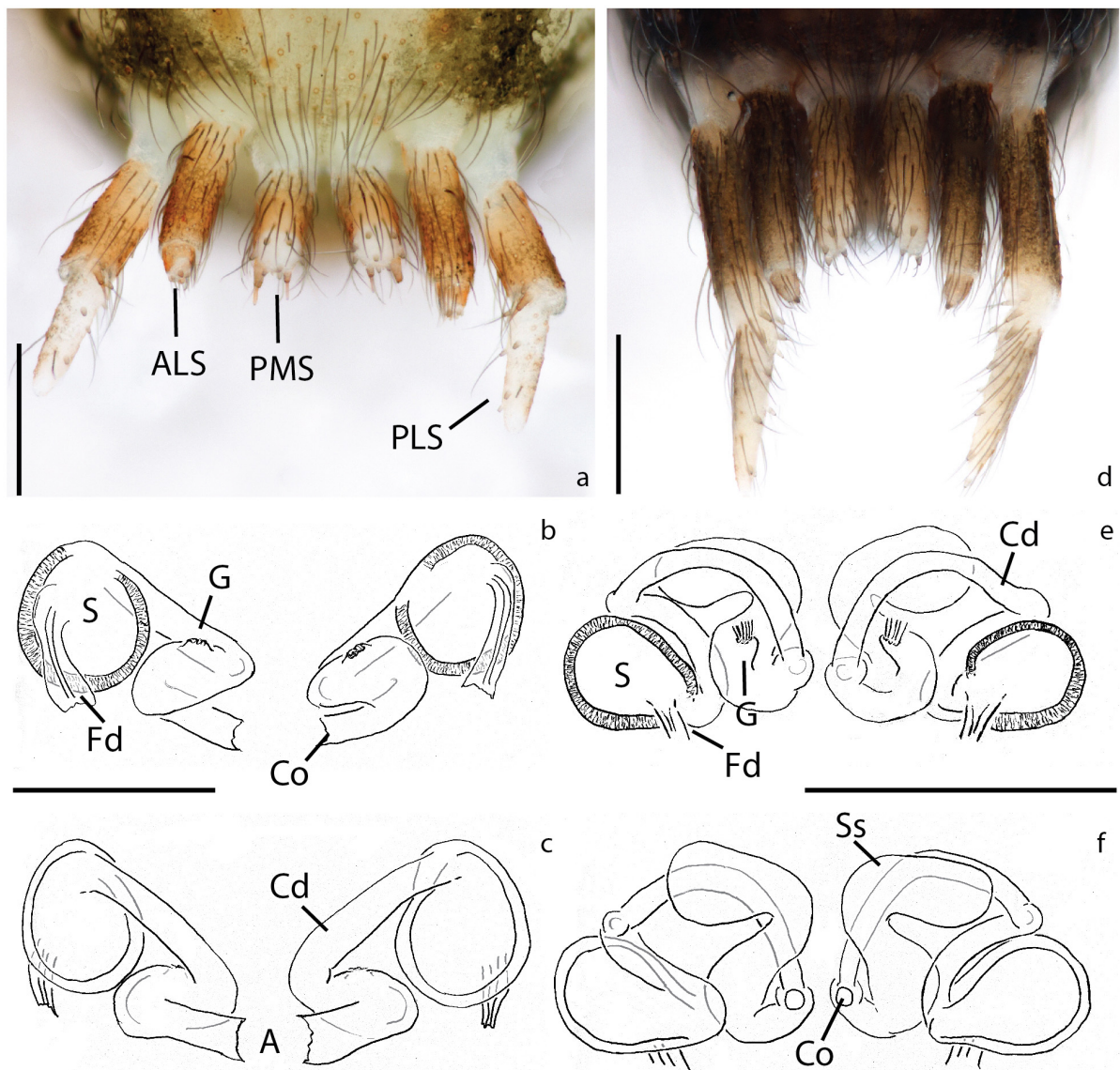


Fig. 6. Female spinnerets and genitals. **a–c.** *Hahnia ngai* sp. nov., holotype (RMNH.ARA.18415). **a.** Spinnerets, ventral view. **b.** Epigynum, cleared, dorsal view. **c.** Ventral view. **d–f.** *Hahnia saccata* Zhang, Li & Zheng, 2011 (RMNH.ARA.18412). **d.** Spinnerets, ventral view. **e.** Epigynum, cleared, dorsal view. **f.** Ventral view. Scale bars: a, d–f = 0.25 mm; b–c = 0.1 mm.

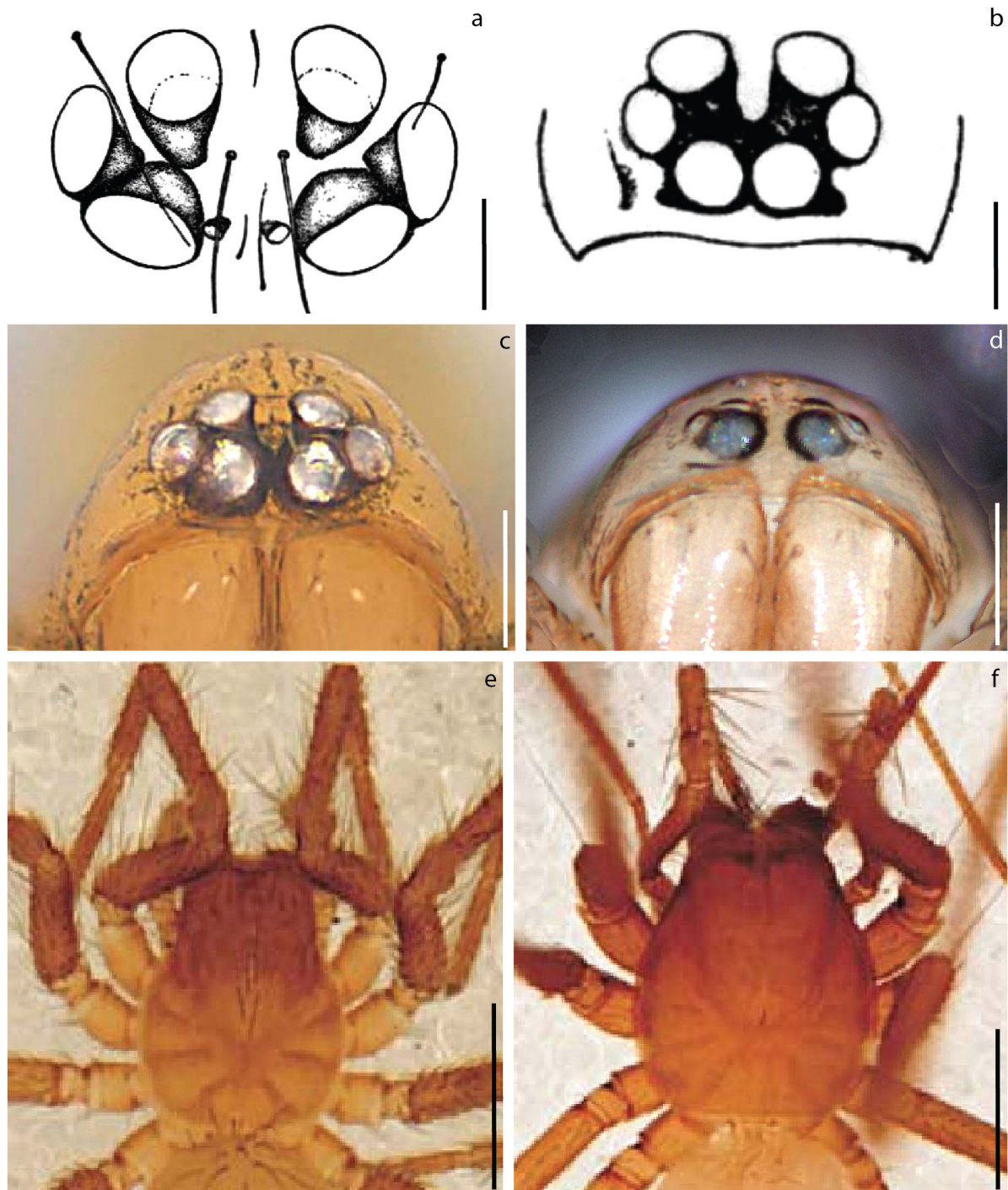


Fig. 7. Examples of eye reduction in the Hahniidae Bertkau, 1878. **a.** Eight eyes with minute AME, *Alistra myops* (Simon, 1898); modified from Schiapelli & Gerschman de P. 1959. **b–d.** Six eyes. **b.** *Amaloxenops vianai* Schiapelli & Gerschman, 1958; modified from Schiapelli & Gerschman de P. 1958. **c.** *Scotospilus longus* Zhang, Li & Pham, 2013; modified from Zhang *et al.* 2013. **d.** *Hexamatia seekhaow* gen. et sp. nov. **e–f.** No eyes, *Iberina mazarredo* Simon, 1881; modified from Fernández-Pérez *et al.* 2014. Scale bars: a–d = 0.1 mm; e–f = 0.5 mm.

morphological differences between the new genus and *Hahnia* (presence of six eyes, small size close to 1 mm and almost complete lack of coloration and abdominal patterns) are sufficient to consider it outside of the *Hahnia* 1 group, and as a genus of its own. We also propose a new combination for *Hexamatia senaria* gen. nov. Although we were not able to test the relationships between *Hexamatia* gen. nov. and other six-eyed hahniids like *Amaloxenops* (Lehtinen 1967; Schiapelli & Gerschman de P. 1958), *Intihuatana antarctica* (Simon, 1902) (Dupérré & Harms 2018) and *Scotospilus* (Zhang *et al.* 2013), clear morphological differences could be observed in somatic and genital characters like body size, coloration, size and shape of RTA and PA, and the presence of MA (see the diagnosis of *Hexamatia* gen. nov.).

The clade *Hahnia* 2 formed by *H. saccata* and *H. ngai* sp. nov. was found to be closely related to *Antistea*+*Neoantistea* in our analyses (Fig. 1a–c), suggesting that these species might be misplaced in *Hahnia*. However, these and many other Asian hahniids require a broader revision and more comprehensive phylogeny to fully resolve their relations within this family. Therefore, *H. ngai* sp. nov. and *H. saccata* remain in *Hahnia*; in the case of the later, as it was originally described by Zhang *et al.* (2011).



Fig. 8. Map of mainland Southeast Asia, showing the collecting sites of Zhang *et al.* (2011) (*Hahnia saccata* Zhang, Li & Zheng, 2011 and *Hexamatia senaria* (Zhang, Li & Zheng, 2011) gen. et comb. nov.), circle; and our new hahniid specimens (*Hexamatia seekhaow* gen. et sp. nov., *Hahnia ngai* sp. nov. and *Hahnia saccata*), square.

Eye reduction in the Hahniidae

This phenomenon appears to be rare in hahniid spiders. Most known species of this family have eight eyes; still, some instances of eye reduction have been documented in at least six genera. The modifications of eyes range from size reduction of AME and lack of AME, to complete absence of eyes (Lehtinen 1967). The evolution of this phenomenon in this family has never been studied, and the relations of the species with reduced eyes are largely unknown. Even their taxonomy has been constantly a subject of debate (Lehtinen 1967; Schiapelli & Gerschman de P. 1959; Catley 1999; Dupérré & Harms 2018).

Size reduction of the AME (Fig. 7a) is relatively common being observed in several species of the following genera: *Alistra* Thorell, 1894 (Lehtinen 1967; Forster 1970; Ledoux 2004), *Amaloxenops* (Schiapelli & Gerschman de P. 1959; Catley 1999; Dupérré & Harms 2018), *Hahnia* (Lehtinen 1967; Ubick *et al.* 2005, among others) and *Neohahnia* Mello-Leitão, 1917 (Mello-Leitão 1917; Lehtinen 1967; Heimer & Müller 1988). Reduction in number of eyes (Fig. 7b–d) is much rarer being documented only in a few species: *Amaloxenops vianai* Schiapelli & Gerschman, 1958 (Schiapelli & Gerschman de P. 1958; Lehtinen 1967), *Hexamatia senaria* gen. nov. (Zhang *et al.* 2011), *Hexamatia seekhaow* gen. et sp. nov., *Intihuatana antarctica* (Dupérré & Harms 2018), *Scotospilus longus* Zhang, Li & Pham, 2013 (Zhang *et al.* 2013), and two unpublished species documented in a revision of South American hahniids (Catley 1999); a quick examination of the illustrations and descriptions of these species suggest that they are not closely related. Finally, complete lack of eyes (Fig. 7e–f) has only been reported in the genus *Iberina* (Fernández-Pérez *et al.* 2014; Ledoux 2014). This wide range in the degree of eye reduction and broad geographical spread of this phenomenon suggest that eyes are a very plastic character and the loss or reduction might have evolved independently several times within this family. Nevertheless, a more comprehensive phylogeny of the Hahniidae is necessary to test this hypothesis.

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Supplementary material

Supplementary file 1. List of primers used in this study. <https://doi.org/10.5852/ejt.2020.724.1157.3141>

Supplementary file 2. Aligned matrix in nexus format. <https://doi.org/10.5852/ejt.2020.724.1157.3143>

Supplementary file 3. Results of the BI analysis shown in a trace plot using the program Tracer ver. 1.7.1 (Rambaut *et al.* 2018). <https://doi.org/10.5852/ejt.2020.724.1157.3145>

Supplementary file 4. Results of the BI analysis shown in a histogram using the program Tracer ver. 1.7.1 (Rambaut *et al.* 2018). <https://doi.org/10.5852/ejt.2020.724.1157.3147>

Supplementary file 5. Pairwise genetic distance for our data set obtained using MEGA X (Kumar *et al.* 2018). <https://doi.org/10.5852/ejt.2020.724.1157.3149>