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Source: Revue suisse de Zoologie, 126(1) : 79-110

Published By: Muséum d'histoire naturelle, Genève

URL: <https://doi.org/10.5281/zenodo.2619524>

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An ancient radiation: Ortholasmatine harvestmen in Asia - a new genus, three new species and a revision of the known species (Arachnida, Opiliones, Nemastomatidae)

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Abstract: The Asian Ortholasmatinae fall into two groups which are attributed to different genera: *Cladolasma* Suzuki, 1963 from Japan and *Asiolasma* gen. nov. The latter is established as a new genus to encompass six mainland Asian species, with a relatively homogeneous male genital morphology, that are different from *Cladolasma* and from all New World ortholasmatines. Seven Asian species are characterized, four of them redescribed: *Cladolasma parvulum* Suzuki, 1963 (Shikoku Is., southern Japan), *Asiolasma angka* (Schwendinger & Gruber, 1992) comb. nov. (northern Thailand), *A. damingshan* (Zhang & Zhang, 2013) comb. nov. (Guangxi, southern China), *A. ailaoshan* (Zhang, Zhao & Zhang, 2018) comb. nov. (southern Yunnan, China). Three species are described as new: *A. juergengruberi* (northern Yunnan, China; male and female), *A. schwendingeri* (northern Vietnam; male and female) and *A. billsheari* (southern Gansu, China; male). All species are illustrated and keyed. Apparently the Ortholasmatinae is a relict group in Asia, represented by morphologically similar and geographically scattered species. A phylogenetic old age is indicated by plesiomorphic character states (poorly developed keel cell network; simple male genitalia with uniform armature; hood at anterior margin of prosoma with lateral apophyses, interconnected by tubercles at the basis of the apophyses which form minute bridges; species restricted to moist forest litter on mountains). It is assumed that ortholasmatines have originated in what is presently Southeast and East Asia where they now represent a relict group; presumably they arrived in the New World later. American species show a number of apomorphic characters which are largely lacking in Asian species. Species in Asia survive in forest formations from tropical (southern China, northern Vietnam, northern Thailand) to subtropical (southern Japan) and to temperate climate conditions (southwestern and northwestern China). Primeval montane forests with a closed canopy and a moist litter layer are important habitat requirements. Except for two species, only single locality records are known.

Keywords: Taxonomy - genital morphology - historical biogeography - relicts - soil fauna - Japan - Thailand - Vietnam - China - New World.

INTRODUCTION

The Ortholasmatinae, family Nemastomatidae, are mostly distributed in the temperate parts of the New World where this group was first discovered. This paper aims at a better characterization of Asian species, of which only few were hitherto described. In addition, it presents not only three new species from northern Vietnam and various parts of central and southern China, but also a new genus to accommodate most of the Asian species. The relationships and historical geography of Asian and American representatives of the subfamily, mainly of the genus *Dendrolasma* Banks, 1894b, is likewise addressed.

TAXONOMIC HISTORY

The bizarre-looking soil-bound ortholasmatine harvestmen are peculiar members of the opilionid faunas of western North and Central America, where a large number of species were documented and well-studied (Shear & Gruber, 1983; Shear, 2010; Cruz-López, 2017). From there the first species were described in 1894 by Banks (1894a, b). He established the genera *Ortholasma* Banks, 1894a and *Dendrolasma* Banks, 1894b, each based on a new species. These were followed by further New World discoveries, altogether 20 valid species currently known from the Americas (Shear & Gruber 1983, 1987; Shear 2006, 2010; Cruz-López, 2017; Cruz-López *et al.*, 2018). The presence of Ortholasmatinae in Asia, however,

remained unknown for a long time and was first documented in 1963 from the island of Shikoku, southern Japan by Suzuki, who named *Cladolasma parvula* (correct: *parvulum*) Suzuki, 1963, and later (Suzuki 1974) placed it in the genus *Dendrolasma*. Nearly 30 years later, Schwendinger & Gruber (1992) presented the first species from mainland Asia: *Dendrolasma angka* Schwendinger & Gruber, 1992 from northern Thailand. While *Ortholasma* and *Dendrolasma* were regarded as New World taxa, the authors mentioned differences between *D. angka* and American *Dendrolasma*, mainly in the structure of the pedipalps and of the dorsal exoskeleton, namely, the free, isolated metapeltidium, and in a specialized male genital conformation. Consequently, Schwendinger & Gruber (1992) placed their new Thai species in *Dendrolasma*, not in the Japanese *Cladolasma*, which then was still in the synonymy of *Dendrolasma*, and followed Suzuki (1974). However they recognized no close relationship between the Thai species and the American *Dendrolasma*. Males of *D. angka* were not available at that time to allow a detailed phylogenetic analysis and an alternative taxonomic placement. Subsequently, Shear (2010) excluded the Thai *D. angka* from *Dendrolasma*, revalidated *Cladolasma* and added *D. angka* to this genus, thus restricting its distribution to Asia. More recently, two additional species were described from China, *C. damingshan* Zhang & Zhang, 2013 from Guangxi Province and *C. ailaoshan* Zhang, Zhao & Zhang, 2018 from Yunnan Province, both correctly assigned to *Cladolasma*, albeit without discussing the characters that would make them congeneric with the quite peculiar *C. parvulum* from Japan.

In the present paper, I characterize (by also including male genital characters) seven species from mainland Asia (Thailand, Vietnam, China) and point out the distinctive features of the sole Japanese ortholasmatine. Obviously, they all belong to two different morphological entities, *C. parvulum* on the one side opposed to all mainland Asian populations on the other side. Strong differences are evident in male genital morphology, which is uniform in the mainland species and markedly different from that of *C. parvulum*. For the mainland Asian species I propose a new genus, the species of which are quite uniform by their external morphology and in details of penis morphology. The mainland Asian species are largely scattered and cover a large area ranging from northern Vietnam and northern Thailand to central China in the Qinling Mountains. The climate in these areas is tropical and subtropical in the southern part and temperate in the northern part. I support the original hypothesis of Shear & Gruber (1983) that ortholasmatine harvestmen might have evolved in what is presently tropical and/or subtropical East Asia, spread to the New World where they underwent a remarkable morphological and ecological radiation, as well as a range expansion. There they occur between near the Alaskan border in the North to México and Honduras in the South, with the greatest diversity

currently known from Central America, represented by several species in four genera (Shear & Gruber, 1983; Shear, 2010; Cruz-López *et al.*, 2018; see Discussion).

MATERIAL AND METHODS

Original line drawings were done with the help of a camera lucida attached to a Carl Zeiss research microscope, whereas the automontage photographs were taken with a Leica Z6 APO A in Admannshagen (J. Schmidt) and in Geneva (P. Schwendinger). Measurements were taken by means of a micrometer disc attached to a Leitz stereo microscope, those of the penis from the original drawings. In addition to the material collected by myself, specimens treated here were handed over to me for study by Peter Schwendinger (Geneva; MNHG), David W. Wrase (Berlin) and Chao Zhang (Baoding; MHBUS). All measurements are given in mm.

Abbreviations of morphological terms

Cx	coxa
do	dorsal
Fe	femur
la	lateral
Mt	metatarsus
Op gen	operculum genitale
Pt	patella
Ta	tarsus
Ti	tibia
Tu oc	tuber oculorum, ocularium
Tr	trochanter
ve	ventral
I, II ... XII	denominate January, February ... December

Museum acronyms

CJM	Working collection of J. Martens, Mainz, Germany
MHBUS	Museum of Hebei University, Baoding, China
MNHG	Muséum d'histoire naturelle de Genève, Switzerland
SMF	Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main, Germany

TAXONOMIC PART

Family Nemastomatidae Simon, 1872

Subfamily Ortholasmatinae Shear & Gruber, 1983

Genus *Cladolasma* Suzuki, 1963

Cladolasma Suzuki, 1963: 40. – Suzuki, 1974: 121 (synonymisation with *Dendrolasma* Banks, 1894b). – Shear, 2010: 16 (revalidation of *Cladolasma*).

Type species: *Cladolasma parvulum* Suzuki, 1963 (by original designation and monotypy).

Remarks: A genus of Nemastomatidae, subfamily Ortholasmatinae, according to the present revision

Key to the currently known Asian Ortholasmatinae species (based on male characters)

- 1A Strongly asymmetric glans penis (in do and la views) with eight strong spines arranged in two narrow rows and a distal chaplet of four slightly smaller spines, stylus not twisted (Figs 6-8), tubercles at posterior opisthosomal margin club-shaped (Figs 2, 5); distributed in southern Japan, Shikoku..... *Cladolasma parvulum*
- 1B Symmetric glans penis with weaker spines arranged in several separated rings (do, ve and la views, Figs 20-22, 38-40, 47-49, 78-83, 94-96, 106-108), tubercles at posterior opisthosomal margin digitiform, tapering towards tip (Figs 17, 19, 26, 31-34, 53-54, 60-61, 63, 65, 88-89, 91-92, 104-105); distributed in mainland Asia 2
- 2A Dorsal apophysis on top of 2nd cheliceral article massive and markedly elevated, ending in a strong pointed hook (Figs 55-56, 72-75, 77, 112-114)..... 3
- 2B Dorsal apophysis of 2nd cheliceral article represented only by a small pointed, not elevated hook (Figs 27, 35, 100)..... 5
- 3A Hook on dorsal apophysis of 2nd cheliceral article directed forward, immediately below the hook an additional blunt low apophysis (Figs 112, 114), a small pointed apophysis prolaterally-distally on pedipalpal patella (Figs 115, 117); known from southern Gansu, China..... *Asiolasma billsheari* sp. nov.
- 3B Hook on dorsal apophysis of 2nd cheliceral article directed more or less downward (Figs 55-56, 72-74), no apophysis on pedipalpal patella (Fig. 58)..... 4
- 4A Hook on a rounded and slightly angular cheliceral apophysis directed downward, more or less parallel to front of 2nd cheliceral article (Figs 55-56), a low apophysis with a short seta on dorsal side of basal cheliceral article (Figs 55-56); known from southern Yunnan..... *Asiolasma ailaoshan*
- 4B Hook of rounded apophysis inclined, forming an obtuse angle against front of 2nd cheliceral article (Figs 72-74, 77), a markedly elevated apophysis carrying a relatively long seta on dorsal side of basal cheliceral article (Figs 72-75); known from northern Yunnan, China..... *Asiolasma juergengruberi* sp. nov.
- 5A Body markedly globular (Fig. 26), dorsal side of scutum with several groups of pointed tubercles (Fig. 26), known from a single mountain in northern Thailand *Asiolasma angka*
- 5B Body of male not globular, flat (Fig. 92), dorsal side of scutum without several groups of pointed tubercles (Fig. 34) 6
- 6A Pedipalp stout, its tibia and tarsus slightly inflated, relatively short (Fig. 37), body small, about 3.1 mm (Fig. 31); known from southern Guangxi, China *Asiolasma damingshan*
- 6B Pedipalp of male slender, tibia and tarsus not inflated, relatively long (Fig. 102), body relatively large, about 3.4-3.6 mm (Fig. 32); known from northern Vietnam *Asiolasma schwendingeri* sp. nov.

comprising one Asian species. The gender of the generic name is neuter.

Extended diagnosis: A genus of Ortholasmatinae with metapeltidium free, neither joined to prosoma nor to opisthosoma; medium-sized species (up to 3.5 mm body length, females larger than males); hood on prosoma short, its lateral apophyses interconnected by bridges at their bases; prosoma with one long apophysis on each side of hood at anterior border; tibia and tarsus of pedipalps with dense cover of clavate setae, not sexually dimorphic, both sexes with ve gland in palpal patella; lattice pattern of interconnected keel cells inconspicuous, the individual anvil-shaped tubercles low, often dorsally rounded and unspecialized. Apophyses at posterior margin of opisthosoma short, slightly inflated at the end, club-shaped. Genital morphology of males: Characterized by rather

unspecialized penis, rather slender, parallel-sided; muscle-containing base of penis relatively long, only slightly inflated, deeply incised, occupying about one fourth of truncus length; truncus in straight continuation of inflated base (in do/ve view). Armature of glans markedly asymmetrical, with strong spicules concentrated on do sides, slightly shorter ones near base of stylus.

Included species: *Cladolasma parvulum* Suzuki, 1963.

Relationships: With regard to genital morphology, *C. parvulum* is separated from all mainland Asian ortholasmatine species. A dorsoventrally asymmetric glans and marked difference in size and arrangement of glans spicules makes this penis different from those of all other Asian and American species. I judge the differences to be strong enough to allot generic ranks to the sole Japanese species and to the presently known six mainland Asian species.

***Cladolasma parvulum* Suzuki, 1963**

Figs 1-15

Cladolasma parvula Suzuki, 1963: 41 (description of juveniles; types not examined). – Shear, 2010: 17 (revalidation of genus, discussion of phylogenetic placement). – Zhang & Zhang, 2013: 450 (comparison with a Chinese species). – Schönhofer, 2013: 24 (species listing).

Dendrolasma parvula (Suzuki, 1963). – Suzuki, 1974: 121 (transfer and redescription of species based on adults; synonymisation of *Cladolasma* with *Dendrolasma*).

Dendrolasma parvulum (Suzuki, 1963). – Shear & Gruber, 1983: 60 (figures, discussion of phylogenetic placement).

Material examined: CJM 2759; 1 male, 1 female; JAPAN, Shikoku, Ehime Pref., Mt Saragamine, beech forest, 1160 m; 33°49' N, 132°46'E; N. Tsurusaki; leg. 7.10.1983.

Remark: The species was correctly described by Suzuki (1963, 1974) and by Shear & Gruber (1983) in many details, but for a comparison with the mainland Asian species an extended description and additional drawings and images created by photo stacking are added here.

Diagnosis: Characterized by male genital morphology (spicules of penis in two groups of similar sizes and arrangement and an additional distal chaplet of four spicules) and by tubercles on dorsal side of scutum

(arranged irregularly, no distinct lattice of keel cells, scanty anvil-shaped tubercles).

Description**MALE**

Body, dorsal side (Figs 2, 4-5): Compared to *Asiolasma* species rather flat, corona analis and sternites markedly extended and causing a slightly inflated and elevated opisthosoma (la view); Tu oc slightly elevated; hood extending from anterior margin of prosoma and including a rather short hood after a short ascent running parallel to prosoma, carrying one distal and five lateral apophyses, the distal one longest, the lateral ones consecutively shorter in direction to basis, interconnected by small anvil-shaped bridges close to the basis of individual apophyses; a pair of long and massive, slightly fusiform apophyses extending from anterior margin of prosoma to about two-thirds of hood length. Posterior margin of opisthosoma with a row of about 15-17 massive tubercles of various lengths, slightly inflated at the apex, longest ones in mid-part of row; all apophyses of hood and rear end of opisthosoma covered with a dense coat of pointed, posteriad-directed denticles.

Lattice cell network of anvil-shaped tubercles inconspicuous (Figs 2, 4-5), formed by low rounded tubercles and only rarely by interconnected anvil-shaped tubercles, most cells not clearly defined, if present irregularly shaped, tubercles forming only dense or loose



Fig. 1. Distributional records of ortholasmatine species in East and Southeast Asia. (1) *Asiolasma billsheari* sp. nov., China, Gansu, Qinling range. (2) *A. juergengruberi* sp. nov., China, Yunnan, above Lugu Hu. (3) Same species as before, China, north of Lijiang. (4) *A. ailaoshan*, China, Yunnan, Ailao Shan. (5) *A. damingshan*, China, Guangxi, Daming Shan. (6) *A. schwendingeri* sp. nov., Vietnam, Mt Ba Vi. (7) *A. angka*, Thailand, Doi Inthanon. (8) *Dendrolasma parvulum*, Japan, Shikoku Island.

agglomerations; on metapeltidium only a transverse row of tubercles, no cells; tubercles slightly darker than surface of prosoma and opisthosoma.

Body, ventral side: Cx front and back side with a row of tubercles, longest on Cx I in front, in addition with dense cover of low rounded tubercles, Op gen with low tubercles, free tergites bent to ventral side, with rear row of low tubercles, most pronounced on corona analis.

Mostly long rounded tubercles on Cx: I 1 pro-la, 1 retro-la, II 1 retro-la especially large, III -, IV 1 pro-la. Tubercles on Tr: I retro-la, II -, III 1 pro-la and retro-la each, IV 1 pro-la.

Chelicera (Fig. 12): Basal article in posterior part dorsally slightly enlarged (la view), do side markedly constricted, saddle-shaped (la view), four strong pointed tubercles on distal part dorso-prolaterally, with few setae laterally and prolaterally, no brush of setae, no obvious glandular tissue. Second article with a strong stumpy apophysis on upper front pointing to ve side. Setae of various sizes, mainly on frontal surface.

Pedipalp (Fig. 14): Tr slender, slightly swollen on do side; three pointed small tubercles on ve side, each with as strong seta; Fe strong and massive, relatively short, continuously widening toward apex, slightly bent downwards, loosely set with few scattered normal hairs except for a group of strong setae mediodistally; Pt slightly enlarged and strongly bulge-like ventrally in central part, glandular tissue recognizable below cuticle in enlarged ve part (outlined in Fig. 14); Ti cylindrical but slender, with indistinct basal stalk, not curved, dense cover of clavate setae concentrated in distal part; Ta slightly more slender than Ti, distinctly stalked, slightly inflated on do side, densely covered with clavate setae all round (mostly omitted in Fig. 14).

Legs: Rather short, all articles cylindrical; Fe widened distally, particular on legs I, III and IV; Tr of all legs set with rounded tubercles of various sizes, largest ones distally, all densely covered with massive microtrichia (Figs 4-5); Fe, Pt and Ti of all legs densely covered with fine microtubercles similar to those on Tr, tubercles with fine microsetae interspersed; Mt and Ta only with fine setae.

Genital morphology (Figs 6-11): Penis long and slender, strait, slightly depressed, markedly parallel-sided all over its length (do/ve and la view); basis slightly broadened, deeply split into two parts, containing nearly the entire portion of the two muscles, from there truncus slightly tapering towards glans (do/ve view) and glans towards stylus; glans spindle-shaped and broadened only in la view; stylus short, no helical torsion. Apex of penis with long spindle-like spicules of slightly different sizes and arranged into two groups: i) distally six spicules symmetrically arranged in a chaplet on la, do and ve side, ii) proximally two parallel rows of four larger spicules each, two of them on la side, others on ve side.

FEMALE (Figs 3, 13, 15)

Similar to male; club-shaped tubercles on posterior

margin of opisthosoma shorter than in male (Fig. 3); chelicera (Fig. 13) similar to those of male, including tubercles on basal article, no hook on 2nd article; pedipalp (Fig. 15) as in male, but Fe less bent, less enlarged distally, Pt also enlarged ventrally but less so than in male, glandular tissue also recognizable below cuticle, few clavate setae ventrally. Opisthosoma more arched, giving the impression of a more globular body.

Measurements: Body length of male 3.0 (n=1), female 3.5 (n=1). Leg II length of male, female in parentheses: Fe 2.4 (2.2) Pt 0.7 (0.7) Ti 2.2 (-) Mt 1.5 (-) Ta 1.0 (-). Penis length 1.7.

Variation: Little variation was observed in male genital morphology. All drawings presented by Suzuki (1974), Shear & Gruber (1983) and in this paper, especially concerning spicules on the glans (Figs 6-11), are very similar even in minor details. This may be due to the restricted genepool caused by minute distributional areas of this species. Branches of the hood in some specimens are asymmetrical and uneven on the left and the right side (Figs 2-4), single branches are bent toward the mid-axis. The specimens examined have only few clavate setae on their pedipalpal articles but specimens illustrated in Shear & Gruber (1983: figs 202-203) have many on Fe, Pt and Ti. The latter may be due to abrasion in alcohol-preserved specimens.

Distribution (Fig. 1): This species is confined to Shikoku Island, southern Japan, where the distributional ranges of its populations seem to be rather small. Mt Ishizuchi is mentioned in the original description; N. Tsurusaki provided a series of specimens from Mt Saragamine for study (see photographs and drawings). According to information presented by Suzuki (1963, 1974), the species is confined to moist and cool montane forests, mainly beech (*Fagus crenata*), with a rich understorey of various grass species, roughly between 1200 m and 1500 m altitude.

Genus *Asiolasma* gen. nov.

Type species: *Dendrolasma angka* Schwendinger & Gruber, 1992.

Diagnosis: Asian Ortholasmatinae with free metapeltidium not joined to prosoma or to opisthosoma. Characterized by an unspecialized penis with a rather short, slightly twisted stylus, opening of seminal duct sub-terminal; spicules on apex of penis rather long on do, ve and la sides of glans (rarely on distal part of truncus), in most cases symmetrically arranged in three (rarely four) groups on glans and on distal part of truncus, rather uniform in all known species; network of anvil-shaped denticles on do side of body present, cells not strongly symmetrical, appearing somewhat disorderly, individual cell-forming denticles low in most



Figs 2-5. *Cladolasma parvulum*. (2) Body of male in dorsal view. (3) Body of female in dorsal view. (4) Prosoma of male in dorsal view. (5) Opisthosoma of male in dorsal view. Photographs by J. Schmidt.

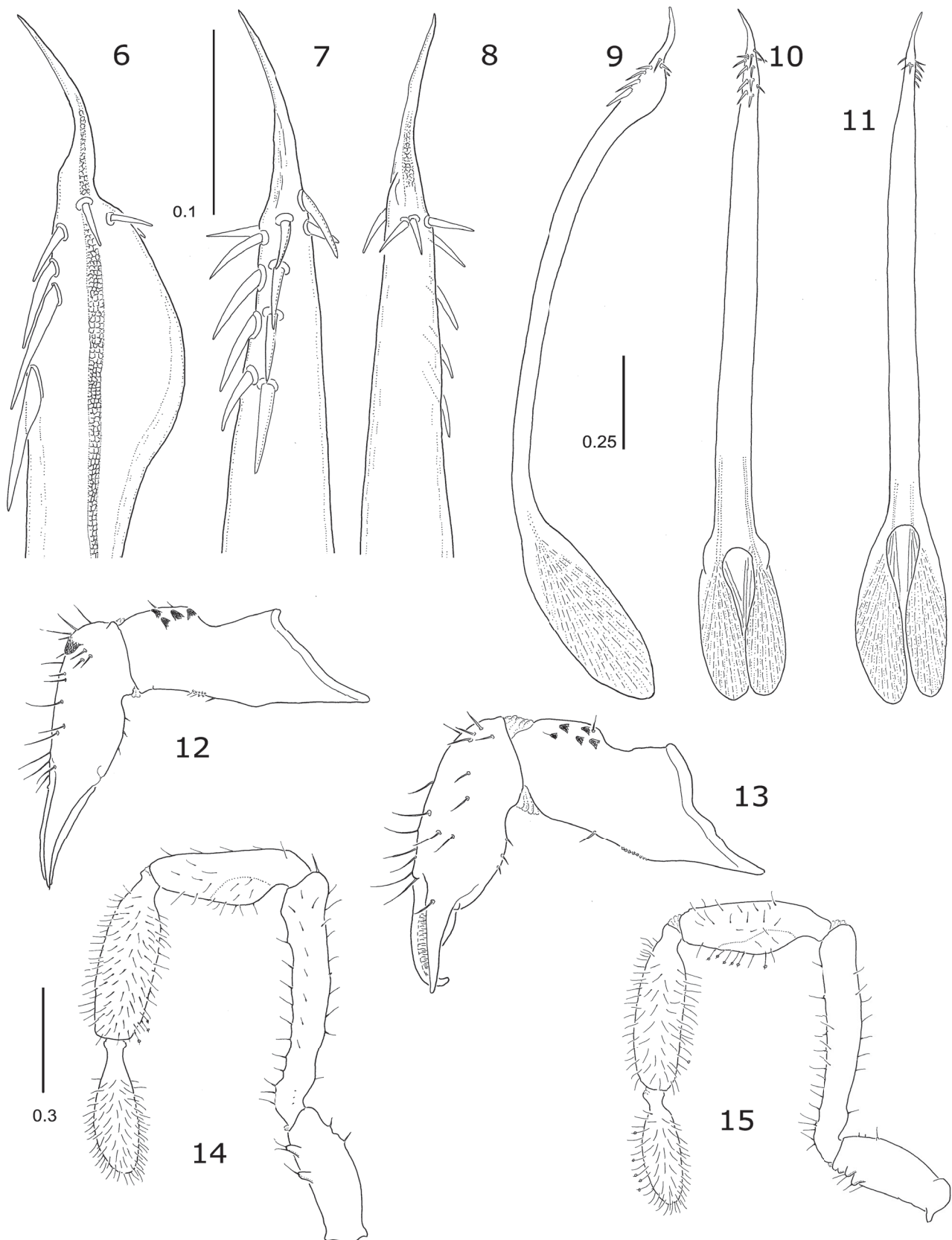
species, thus without marked sculpture on opisthosomal scutum.

Name: It is derived from Asia, the continent where the species of this genus live, and the Greek noun “elasma”, a plate, mainly of metal, referring to the hood on the anterior margin of the prosoma. The name is in analogy of the other generic names of Ortholasmatinae. The gender of the name is neuter.

Distribution (Fig. 1): The six hitherto known species occur in northern Thailand (Doi Inthanon), northern Vietnam, as well as southwestern and southern China (Yunnan, Guangxi and Gansu provinces, respectively). The few available records are highly scattered and span a geographically and climatically large and diverse area from the tropics/subtropics in Vietnam, southern China and northern Thailand to high altitudes of temperate mountain ranges in central southwestern and partly

southern China. According to current knowledge, *Asiolasma* species are confined to mountainous areas between 1200 m and 3300 m in China, 900 m in northern Vietnam, 2400-2500 m in northern Thailand, and the sole *Cladolasma* species has been recorded at 1200-1500 m on Shikoku Island, Japan.

Relationships: Judging from male genital morphology and formation of the hood, all *Asiolasma* gen. nov. species known at present seem to be closely related with each other. These characters seem to be rather uniform, although differences between species are present. Specific distinctions are also found in body shape, body size, equipment of body with a lattice work of anvil-shaped tubercles, size and shape of pedipalps and pattern of setae on pedipalpal articles, presence or absence of pedipalpal glands and shape of apophyses on chelicerae. These need to be carefully identified.



Figs 6-15. *Cladolasma parvulum*, male (6-12, 14), female (13, 15). (6) Glans penis in lateral view. (7) Same in dorsal view. (8) Same in ventral view. (9) Truncus penis in lateral view. (10) Same in dorsal view. (11) Same in ventral view. (12) Right chelicera of male in prolateral view. (13) Same of female. (14) Right pedipalp of male in prolateral view. (15) Same of female. Scales: 0.25 mm (9-11); 0.1 mm (6-8); 0.3 mm (12-15).

The *Asiolasma* gen. nov. species can be divided into two groups. Three of the southern species display only a pointed hook on the upper side of the 2nd cheliceral article (*A. angka* [Fig. 27], *A. damingshan* [Fig. 35], *A. schwendingeri* sp. nov. [Fig. 100]; in the single northern species (*A. billsheari* sp. nov. [Fig. 112] and in two of the southern species this hook is present as well but situated on a massive rounded apophysis (*A. juergengruberi* sp. nov. [Figs 72-74], *A. ailaoshan* [Figs 55-56]). The Japanese *Cladolasma parvulum* stands apart and differs markedly in genital morphology, in a little developed do network of anvil-shaped tubercles and in a small anterior hood (see above).

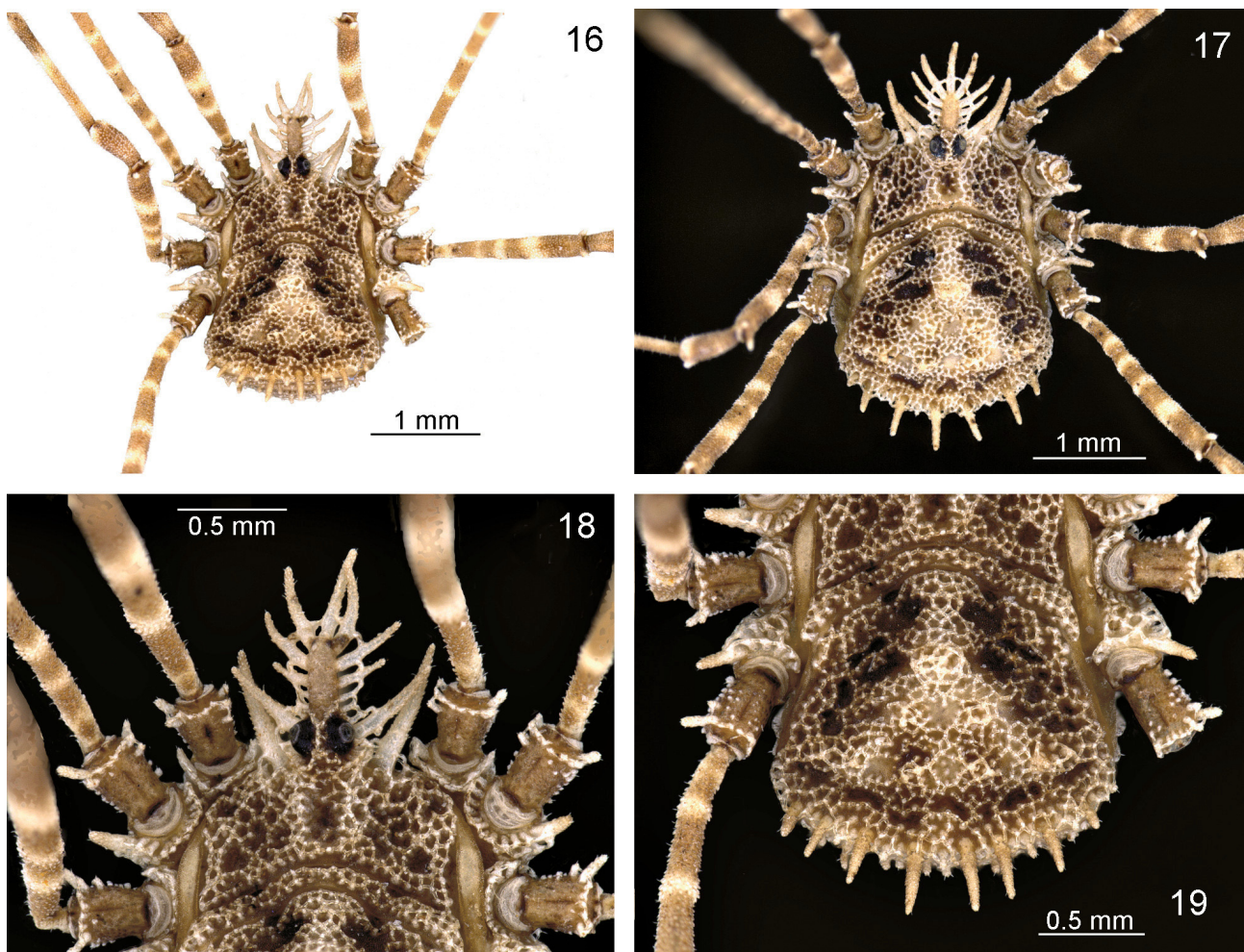
All species of the American ortholasmatine genera *Ortholasma* Banks, 1894a, *Dendrolasma* Banks, 1894b, *Trilasma* Goodnight & Goodnight, 1942, *Martensolasma* Shear, 2006 and *Cryptolasma* Cruz-López, Cruz-Bonilla & Francke, 2018 clearly differ from Asian species by the following characters: i) the penis is much more slender, the inflated base shorter, the stylus formed like a barbed hook (not so in *Dendrolasma*), the armature of the glans

is more diversified and the spicules often of different size and pattern (uniform in *Ortholasma*); ii) many (up to twelve on each side) apophyses are present on the hood, the single distal and all following lateral apophyses of the hood are interconnected by fine bridges only at the distal end of the apophyses (hood lacking in *Martensolasma*); iii) the network of closed keel cells formed by anvil-shaped tubercles on the do scutum is regular, distinctly symmetrical and ornamental, the individual tubercles markedly elevated, resulting in a distinct and elaborate structure of the network (for all characters compare multiple details in Shear & Gruber, 1983 and Shear, 2010).

***Asiolasma angka* (Schwendinger & Gruber, 1992)
comb. nov.**

Figs 1, 16-30

Dendrolasma angka Schwendinger & Gruber, 1992: 57 (description of female).

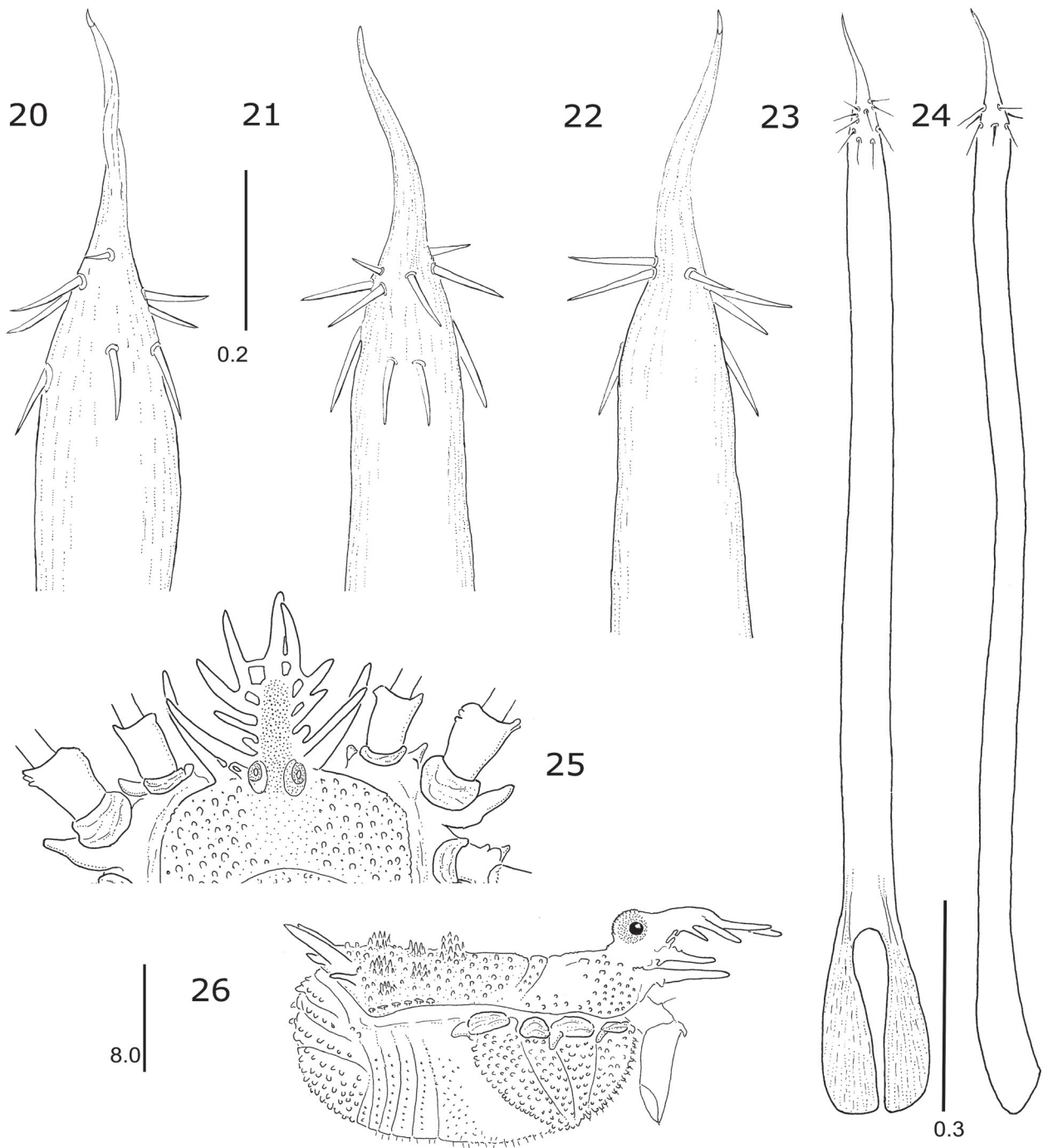


Figs 16-19. *Asiolasma angka*. (16) Body of male in dorsal view. (17) Body of female in dorsal view. (18) Prosoma of male in dorsal view. (19) Opisthosoma of male in dorsal view. Photographs by J. Schmidt.

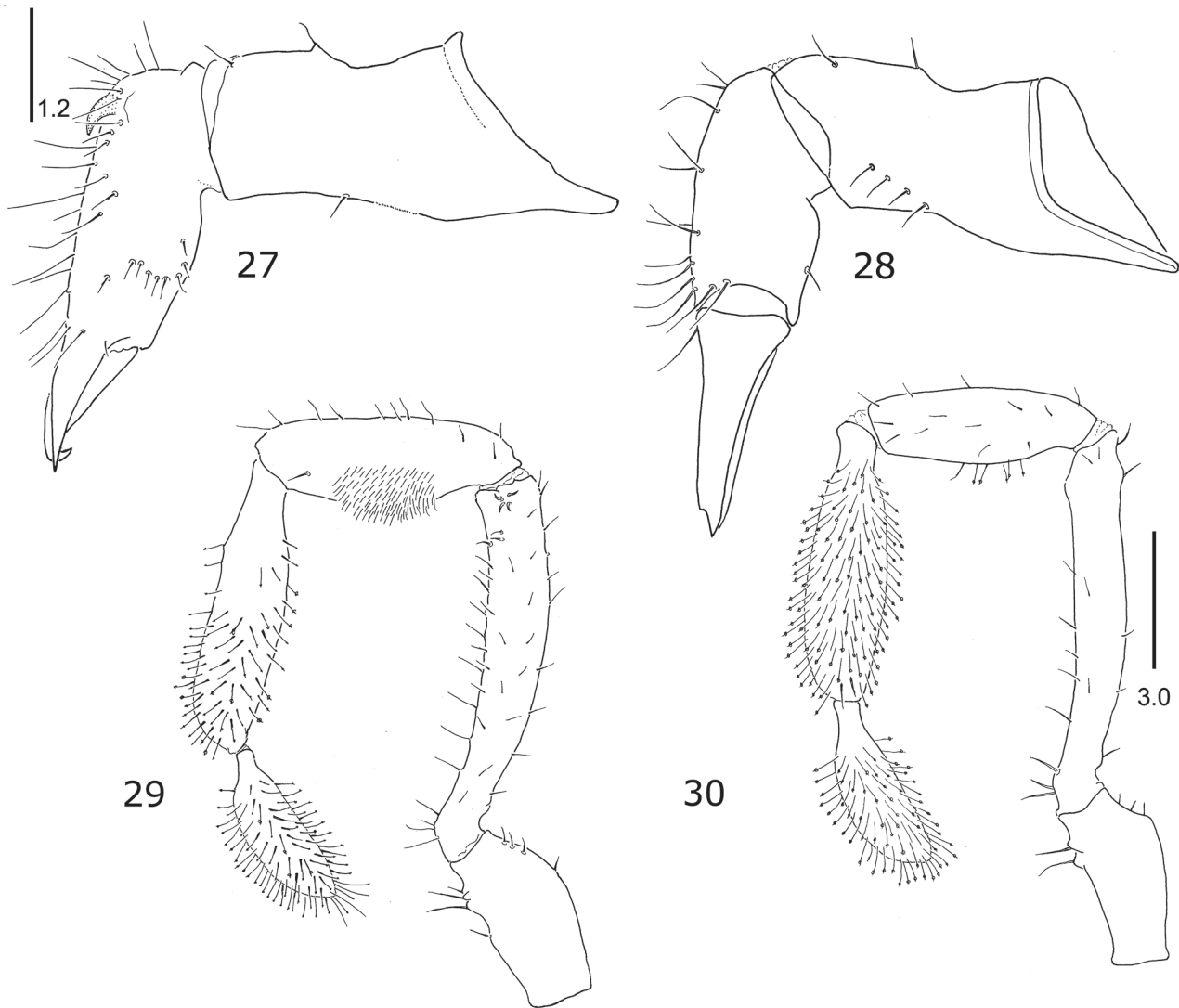
Cladolasma angka (Schwendinger & Gruber, 1992). – Shear, 2010: 17 (transfer). – Schönhofer, 2013: 24 (species listed). – Zhang & Zhang, 2013: 443 (species mentioned). – Zhang, Zhao & Zhang, 2018: 11 (species mentioned).

Material examined: MHNG; female holotype; THAILAND, Chomthong Province, Doi Inthanon

National Park, 2530 m, 28.11.1990. – 2 juvenile paratypes; same locality; 28.11.1990, 19.12.1990. – MHNG; 1 male, 10 juveniles; same locality, 2530 m; 22.2.1992. – MHNG; 1 male, decayed exoskeleton without genitalia, chelicerae and pedipalps; same locality, 2530 m; 22.2.1992. – MHNG; 2 juveniles; same locality, 2530; 13.1.1993. – MHNG, sample



Figs 20-26. *Asiolasma angka*, male. (20) Glans penis in lateral view. (21) Same in ventral view. (22) Same in dorsal view. (23) Truncus penis in ventral view. (24) Same in lateral view. (25) Prosoma in dorsal view. (26) Body in lateral view. Scales: 0.2 mm (20-22); 0.3 mm (23-24); 0.8 mm (25-26).



Figs 27-30. *Asiolasma angka*, male (27, 29), female (28, 30). (27-28) Right chelicera in prolateral view. (29-30) Right pedipalp in prolateral view. Scales: 1.2 mm (27-28); 0.3 mm (29-30).

THMA-01/15; 1 female; same locality (18°35'05.8"N, 98°28'52.3"E), lower montane forest, 2460 m; 26.12.2001. All collected by P. Schwendinger.

Remark: The species was exhaustively described based on a single female and a number of juveniles. Now also males are available and the diagnosis and description are extended accordingly.

Diagnosis: Small species with distinctly globular body; anterior part of prosoma distinctly prolonged, eye mound and projecting hood markedly elevated, rear part of eye mound and hood forming approximately a right angle with prosoma, eyes situated close to anterior margin of prosoma (la view); opisthosoma dorsally with groups of acute processes or smooth cones on areas II-IV; truncus penis straight, parallel-sided, slightly depress, spicules on glans uniform and symmetrically

arranged; male pedipalpal patella with marked proventral brush of small setae.

Description

MALE

Body shape (Figs 16, 18-19, 25-26): Distinctly globular when seen in la view (Fig. 26).

Body, dorsal side (Figs 16, 18-19, 25): Eye mound on anterior margin of prosoma distinctly elevated, projecting into distad-directed hood parallel to do body surface, hood slightly curved (la view); hood bearing one central unpaired and five la (slightly irregularly arranged) paired tubercles, sizes on left and right side different, the basic one longest, followed by a very short one, the remainder continuously prolonged towards tip of hood, all tubercles interconnected by small anvil-shaped bridges; one pair of long apophyses projecting from anterior margin of

prosoma and closely flanking hood, these apophyses longer than all hood tubercles.

Posterior margin of opisthosoma (Figs 16, 19, 26), i.e. area V, with a scattered palisade-like row of eight long and tapering tubercles of various lengths, longest in mid-part of row, between the large tubercles few smaller ones interspersed, all of them densely covered by microdenticles, all tubercles interconnected by low anvil-shaped microtubercles close to basis.

Lattice of keel cells extremely dense, forming dozens of individual cells surrounded by low anvil-shaped tubercles or keels; single larger cells situated behind Tu oc and on 1st, 2nd and 3rd opisthosomal segment laterally, in addition a row of larger cells on 5th opisthosomal segment. All anvil-shaped tubercles low and recognizable only by their light coloration contrasting with the darker cuticle surface; all large cells blackish in colour, all others light brownish. A pair of enlarged median tubercles consisting of minute thin pointed individual tubercles on scutal area II, two median pairs on area III and three pairs on area IV; all are difficult to see from above. No soil incrustation present.

Body, ventral side: Free tergites visible on ve side, each with low tubercles combined with anvil-shaped tubercles, longer tubercles interspersed; corona analis with strong tubercles as well, less so on free sternites. Front and back side of all Cx of legs with a row of tubercles each, all low and inconspicuous, on Cx I larger in front, each tubercle with low seta. Long rounded tubercles on Cx distally: I 1 retro-la, II 1 retro-la, III -, IV 1 pro-la, 1 retro-la. Massive tubercles on Tr: I 1 each pro-la and retro-la, II 1 each pro-la and retro-la, III 1 each pro-la and retro-la, IV 1 each pro-la and 1 retro-la.

Chelicera (Fig. 27): Basal article in posterior part dorsally slightly enlarged (la view), do side markedly constricted, saddle-shaped (la view), one prominent truncate tubercle with one seta on distal margin of saddle, with few setae laterally and prolaterally, no brush of setae, no obvious glandular tissue. Second article with a strong horn-like apophysis on upper side, pointed, bent downward to prolateral side. Setae of various sizes, largest ones mainly on frontal surface.

Pedipalp (Fig. 29): Tr slender, slightly swollen on do side; three small tubercles on ve side, pointed, with a strong seta each; Fe strong and massive, relatively short, continuously enlarged distally, slightly bent downwards, loosely set with few scattered normal hairs except for two groups of strong setae mediolaterally; Pt slightly enlarged and bulge-like ventrally in central part, ventrally and ventro-prolaterally covered with a dense field of short setae, no apparent glandular tissue underneath; Ti cylindrical but slender, with indistinct basal stalk, not curved, with dense cover of clavate hairs concentrated in distal part; Ta more slender than Ti, distinctly stalked, slightly inflated on do side, densely covered with clavate setae all round.

Legs (Figs 16-19): All legs slightly bent ventrally. All

articles round, Fe, Pt, Ti and Ta slightly abraded, few microsetae interspersed; several indistinct white-colored noduli on Fe: in male I 3, II 6, III 3, IV 4; in female I 2, II 6, III 3, IV 4.

Genital morphology (Figs 20-24): Penis long, slender, straight, slightly depressed, almost completely parallel-sided all over its length (do/ve and la views), inconspicuously tapering towards glans, base containing pair of short muscles measuring about less than one fifth of total penis length, only slightly broader than rest of penis, deeply split into two parts (do/ve view); penis in la view slenderer than in do/ve view, parallel-sided except for slightly broadened basis, glans slightly tapering towards stylus; glans spindle-shaped and slightly broadened (only in la view), stylus short, with slight helical torsion (la view). Uniformly long, slightly spindle-like spicules and arranged into two chaplet-like groups around the glans: i) six distal spicules in symmetrically annular group on la, do and ve sides, ii) group of four proximal spicules, two of them on la side, two on ve side; no pair of proximal la spicules on distal part of truncus.

FEMALE: General characters similar to those of male; set of tubercles on posterior opisthosomal margin longer than in male (Fig. 17), eight in male, seven in female, in female distances between tubercles larger, with fewer small tubercles interspersed; ve side of female similar to that of male; chelicera (Fig. 28) similar to those of male in proportions and setation, no hook on 2nd article; pedipalp (Fig. 30) as in male, but Fe less bent, less enlarged distally, Pt only slightly enlarged, with few clavate setae ventrally; do lattice pattern similar to that of male.

Measurements: Body length of males: 3.2 (n=2), of females 3.6-3.7 (n=2). Leg II length of male, of female in parentheses: Fe 3.1 (2.9) Pt 0.8 (0.8) Ti 2.4 (2.7) Mt 1.7 (1.6) Ta 1.4 (1.3). Penis length: 1.7.

Variation: Tubercles of prosomal hood often different in length on left and right side, sometimes deformed; small tubercles on base of hood difficult to see and to count; the large apophyses on prosoma front margin projecting from hood, from margin or from either position on left and right side (observed in one specimen).

Relationships: Within *Asiolasma* the quite isolated position of *A. angka* is defined by a remarkably globular body shape, by the armament of the do side of the opisthosoma with fine peg-like tubercles (or smooth cones) concentrated in groups (Fig. 26), by the placement of the eyes on the prosoma and by a simple male genital morphology with the smallest number of spicules of all known mainland Asian species.

Distribution (Fig. 1): *Asiolasma angka* is recorded only from the Doi Inthanon National Park in northern Thailand. According to current knowledge, the species is restricted to this mountain, the highest in Thailand.

Despite numerous collecting efforts by litter and soil sieving and by setting pitfall traps by P. Schwendinger at various altitudes and in different seasons between 1990 and 2001, he was able to secure only a few juveniles and three adults, one of them a semi-decayed corpse. Apparently the species is rare and ecologically highly specialized, confined to montane forest in a narrow altitudinal corridor between 2460 m and 2530 m. Juveniles were found in XI, I and II, adults in XI and II, all outside the monsoon season when collecting activity is not hindered by constant and heavy rainfall.

***Asiolasma damingshan* (Zhang & Zhang, 2013)
comb. nov.**

Figs 1, 31, 33-46

Dendrolasma damingshan Zhang & Zhang, 2013: 444 (description of male).

Material examined: MHBV Opi-12CZ030; male holotype; CHINA, Guangxi Autonomous Region, Wuming County, Daming Shan National Nature Reserve, 23°30'N, 108°26'E, 1231 m; Chao Zhang leg.; 18.7.2012.

Extended diagnosis: A relatively small species with slightly globular body; prolonged central anterior part of prosoma including eye mound and hood markedly elevated, eyes situated beyond anterior margin of prosoma; central and the two distal pairs of tubercles of hood longest and slender; pedipalps relatively slender, pedipalpal tibia shorter than in the geographically closest species, *A. schwendingeri* sp. nov. from Vietnam.

Description

MALE

Body, dorsal side (Figs 31, 33-34): Body rather flat but less flat than in *A. schwendingeri* sp. nov. when seen in lateral view; eye mound at anterior margin of prosoma markedly elevated, forming a rather steep ascent distinctly elevating the eyes, eye mound smooth, no tubercles on top; eyes strongly displaced distally and integrated into proximal parts of hood, central hood tubercles slightly bent downwards (la view); hood bearing one central unpaired and three lateral paired tubercles, the basic one shortest (less than half size of next one), the following ones consecutively longer, the last one nearly as long as the central unpaired one, tubercles interconnected by small anvil-shaped bridges close to their bases. Lateral to hood at each side one long and massive apophysis projecting from anterior margin of prosoma and closely flanking hood, its top reaching level between 2nd and the 3rd lateral tubercle of hood (Figs 31, 33-34). Posterior margin of opisthosoma with a row of six slender, relatively long tubercles of nearly equal length, slightly tapering towards markedly rounded tip, longest ones in mid-part of row; longer tubercles interspersed by few smaller ones,



Figs. 31-32. *Asiolasma damingshan*, male holotype (31) and *A. schwendingeri* sp. nov., male paratype (32). Body in dorsal view. Scale 1.0 mm. Photographs by P. Schwendinger.

all of them interconnected by low anvil-shaped tubercles close to base. Distinct network of large cells, each of them irregularly surrounded by anvil-shaped elevated tubercles; small and large cells on prosoma, most of them not closed; no cells on metapeltidium but a transverse row of interconnected anvil-shaped tubercles instead; on opisthosoma five rows of cells of various sizes, largest cells in mid-part near posterior margin of opisthosoma.

Body, ventral side: Front and back side of all Cx of legs with row of tubercles, on Cx I pro- and retro-la, Cx II retro-la, Cx III pro- and retro-la, Cx IV retro-la; on Cx I tubercles markedly elevated and anvil-shaped, between the rows of tubercles densely covered with pointed tubercles; Op gen, free sternites, corona analis and free tergites bent to ve side and covered with pointed tubercles, the latter with low tubercles on rough surface and scattered low setae.

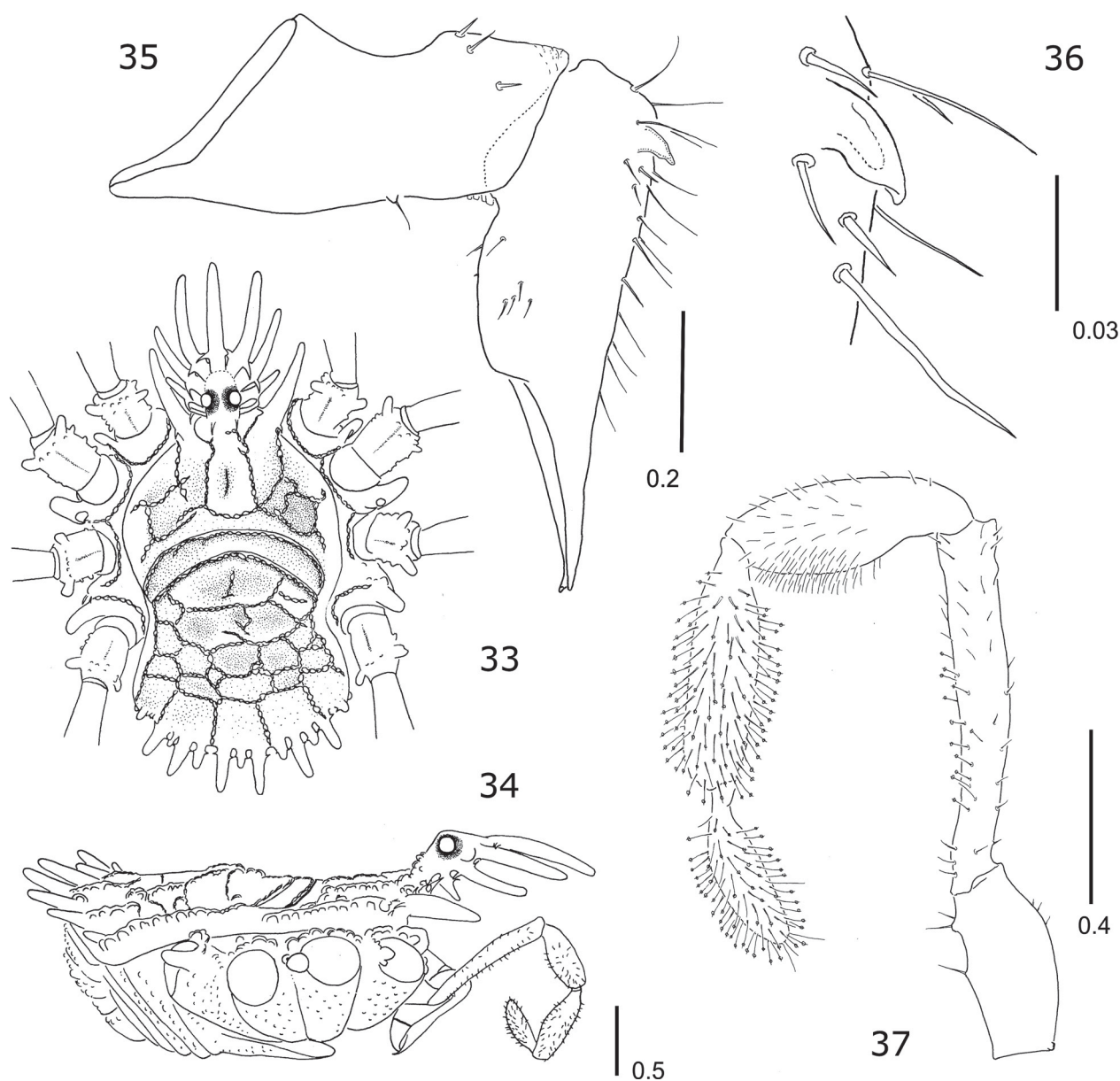
Legs: Light brownish, Mt and Ta contrastingly blackish, slender; Fe I slightly inflated, covered with densely

packed light pointed microtubercles and fine setae; long rounded tubercles on Cx: I retro-la, II 1 retro-la, III -, IV 1 pro-la; number of articles on Ta: leg I 4, II 5, III 6, IV 6. No pseudo-articulations.

Chelicera (Figs 35-36): Basal article in posterior part dorsally slightly invaginated (la view), set with few setae laterally and prolaterally, no brush of setae, no obvious glandular tissue. Second article with a strong apophysis on upper side prolaterally, pointed and slightly twisted at tip, bent downward. Setae of various sizes, mainly on frontal side.

Pedipalp (Fig. 37): Tr slender, slightly swollen on do side;

two small tubercles on ve side, pointed and with strong seta each; Fe long and slender, slightly bent downwards, slightly enlarged distally, set with few scattered setae, ventrally in proximal part with scattered clavate hairs; Pt slightly enlarged and bulge-like ventrally in distal two-thirds, ventrally and prolaterally with a loose field of short setae, no glandular tissue apparent below; Ti cylindrical but slender, with indistinct basal stalk, not curved, dense cover of clavate hairs on all sides; Ta more slender than Ti, distinctly stalked, slightly inflated on do side, densely covered with clavate setae all round, few long fine setae at distal end.

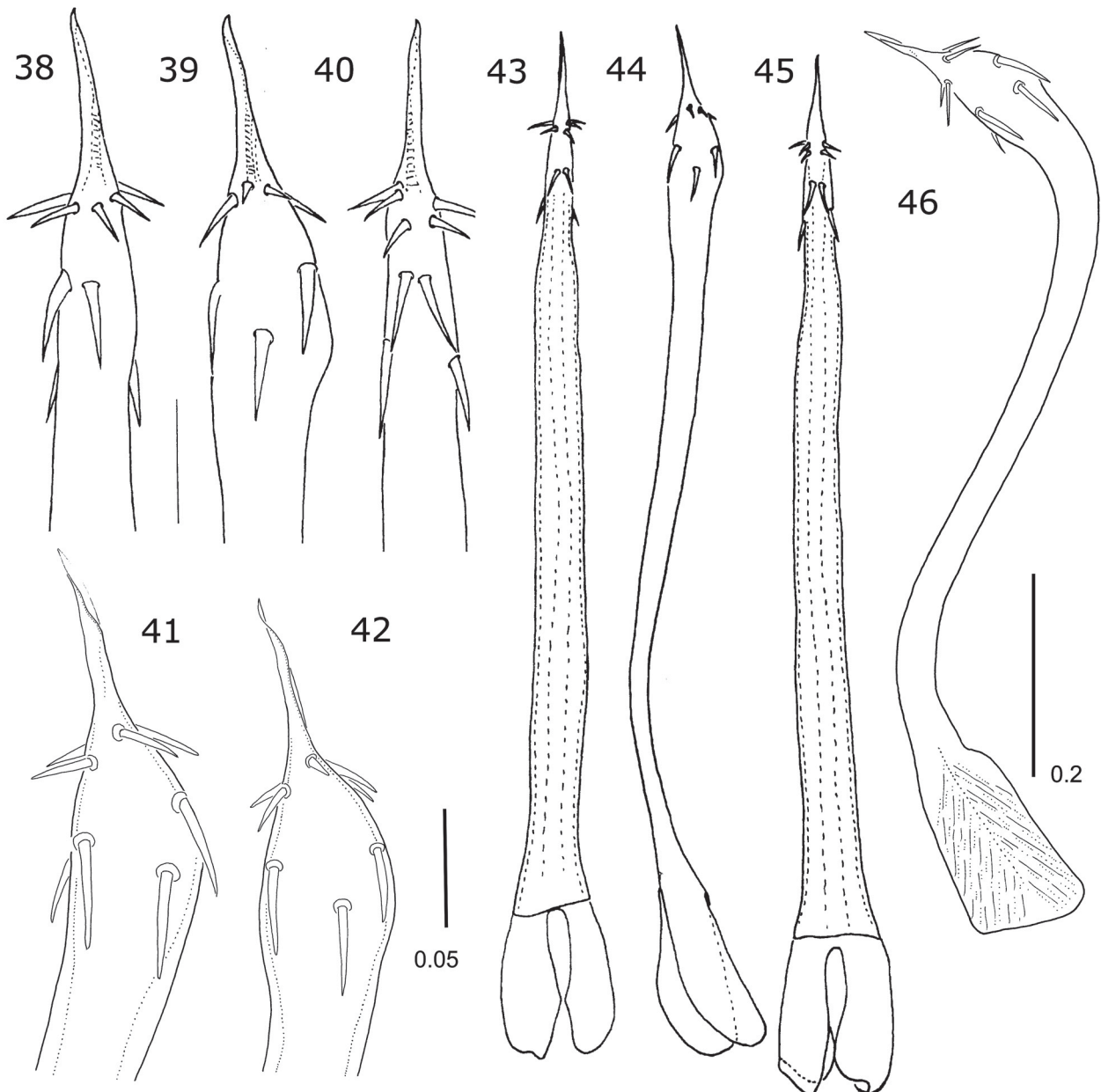


Figs 33-37. *Asiolasma damingshan*, male holotype. (33) Body in dorsal view. (34) Same in lateral view. (35) Chelicera in prolateral view. (36) Apophysis of 2nd cheliceral article in prolateral view. (37) Left pedipalp in retrolateral view. Figs 33-34 reproduced from Zhang & Zhang (2013). Scales: 0.03 mm (36); 0.2 mm (35); 0.4 mm (37); 0.5 mm (33-34).

Genital morphology (Figs 38-46): Penis very long and slender, about two-thirds of body length, base slightly broadened, deeply split into two parts, there two muscles concentrated; truncus moderately slender, slightly depressed, nearly parallel-sided, only slightly tapering toward distal end (ve/do view; Figs 43, 45); penis extremely slender in la view (Figs 44, 46), beyond base parallel-sided, slightly broadened below glans; glans (Figs 38-42) spindle-shaped and broadened (la view); stylus short and in strait continuation of glans, with a slight helical torsion.

Apex of penis with longer (proximal ones) or slightly shorter (distal ones) spindle-shaped spicules, these symmetrical on do and ve side and arranged in three groups from distal to proximal: i) distal group: six spicules in somewhat irregular arrangement on all sides on basis of stylus, ii) central group: four spicules, two of them on do side, the other two on la side, iii) proximal group: one each on la edge of truncus, close to and interconnected with central group of spicules (Figs 39, 42).

FEMALE: Unknown.



Figs 38-46. *Asiolasma damingshan*, male holotype. (38) Glans penis in ventral view. (39, 42) Same in lateral view. (40) Same in dorsal view. (41) Same in slightly different lateral view. (43) Whole penis in ventral view. (44, 46) Same in lateral view. (45) Same in dorsal view. Figs 38-40 and 43-45 reproduced from Zhang & Zhang (2013). Scales: 0.05 mm (38-42); 0.2 mm (43-46).

Measurements: Body length of male holotype: 3.50. Leg II: Tr 0.40, Fe 3.00, Pt 1.00, Ti 2.50, Mt 1.30, Ta 1.48 (data according to Zhang & Zhang, 2013). Penis length 1.25.

Relationships: *A. damingshan* appears closely related to *A. schwendingeri* sp. nov. from northern Vietnam (Figs 32, 88-93). Both species lack a massive cheliceral apophysis on 1st cheliceral article; body size in *A. damingshan* (Fig. 31) smaller, tubercle of anterior hood (absolutely and relatively) shorter, slenderer, thus forming a narrower palmate fan cover above pedipalps and chelicerae than in *A. schwendingeri* sp. nov. Pedipalpal tibia is shorter and slenderer than in the latter species. Armature of glans differs, two proximal spicules in *A. schwendingeri* sp. nov. are more remote from central group of spicules (Figs 38-42 cf. Figs 94-96).

Distribution (Fig. 1): This species is so far only known from a locality in the Daming Shan Natural Reserve in the Chinese province Guangxi. The sole specimen was collected from soil litter in a subtropical rain forest at 1231 m altitude (Zhang & Zhang, 2013).

***Asiolasma ailaoshan* (Zhang, Zhao & Zhang, 2018)
comb. nov.**

Figs 1, 47-59

Cladolasma ailaoshan Zhang, Zhao & Zhang, 2018: 12 (description of male and female).

Material examined: MHBU Opi-20160422; male holotype; CHINA, Yunnan Province, Zhenyuan County, Qianjiazai town, Daming Shan, Ailao Shan Natural Reserve, 24°16'12"N, 101°15'46"E, 2170 m; A. Nakamura leg.; 18.8.2011. – MHBU Opi-20160423; female paratype; collected together with holotype.

Diagnosis: Body rather globular, prolonged anterior part of prosoma including eye mound and hood slightly elevated, distal part of hood slightly bent downward, tubercles of hood markedly fanned, massive apophyses on anterior margin of prosoma flanking hood laterally; marked sexual dimorphism in body size, female much larger than male.

Description

MALE

Body, dorsal side (Fig. 53): Body rather flat but less flat than in *A. schwendingeri* sp. nov. when seen in la view (Fig. 54); Tu oc at anterior margin of prosoma only slightly elevated and forming no marked bend, eyes not distinctly raised on tubercle, displaced beyond anterior margin of prosoma and integrated into proximal part of hood, central hood tubercle slightly bent downwards (la view); hood bearing one central unpaired and four lateral paired tubercles, proximal pair shortest (about half size of following one), next two pairs consecutively longer,

last pair nearly as long as central unpaired tubercle; all hood tubercles interconnected by small anvil-shaped bridges close to their bases. Lateral to hood one long and massive apophysis on each side projecting from anterior margin of prosoma, slightly bent inwards and flanking hood, distinctly shorter than all other appendages in prosoma front area.

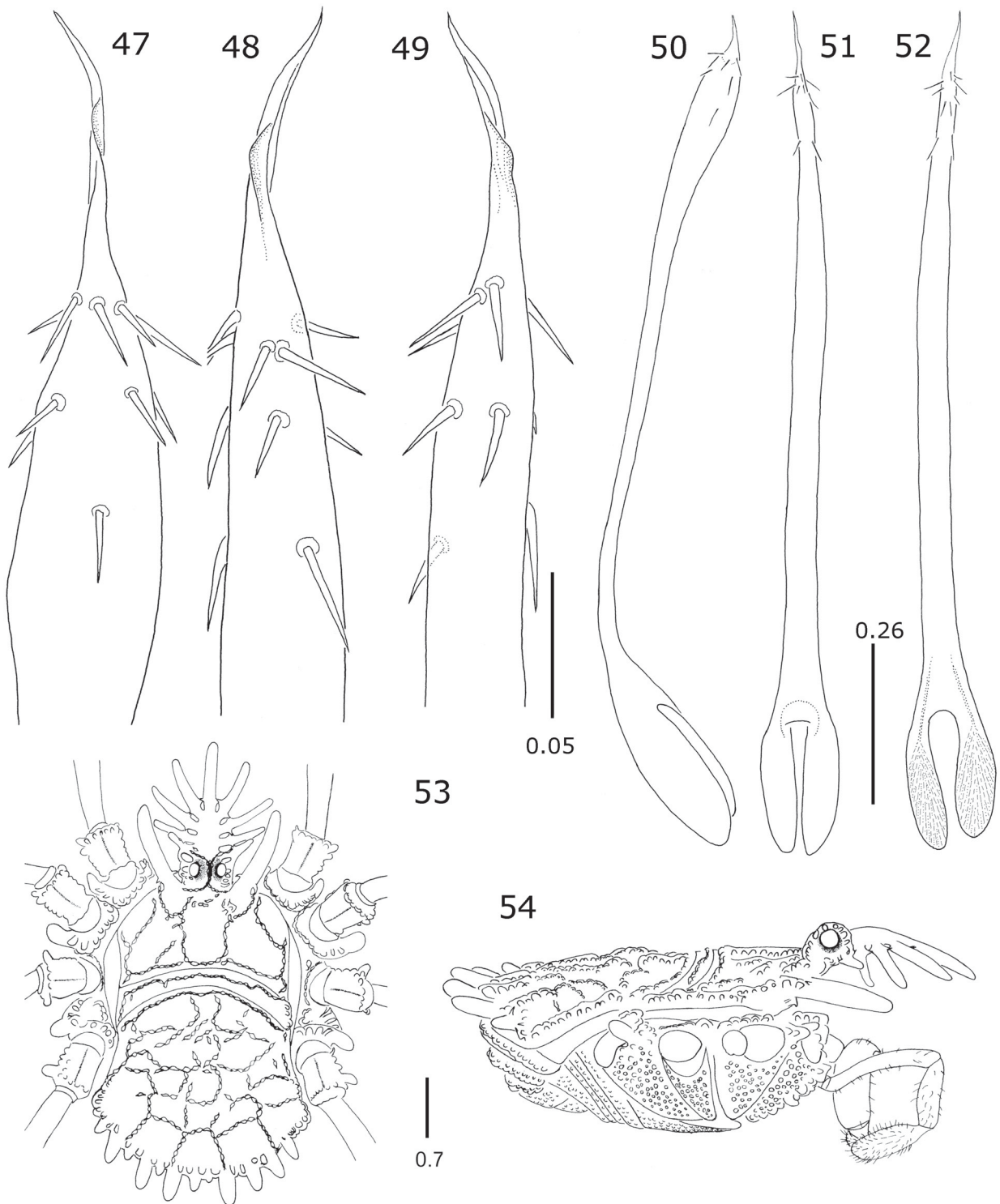
Posterior margin of opisthosoma with a row of six massive truncate tubercles slightly tapering towards rounded tip, longest in mid-part of row (Fig. 53). Network of keel cells loose, most cells not closed and interconnected with neighbouring ones; three large central cells on prosoma, two additional small ones on disto-lateral margin of prosoma; on metapeltidium no cells but a transverse row of anvil-shaped tubercles all over its breadth; on opisthosoma irregular open cells of different sizes, the five largest ones opening towards posterior end of opisthosoma.

Ventral side: Coxae densely set with small setae-bearing tubercles on ventral surfaces and with dorso-distal rows of anvil-shaped tubercles; a row of anvil-shaped tubercles along anterior and posterior margins of coxae II-IV; coxae I and II with distal digitiform processes retrolaterally; coxa IV with similar process prolaterally. Genital operculum short, almost tongue-shaped, surface with irregular tubercles. Sternites with transverse rows of low keels, reduced along midline.

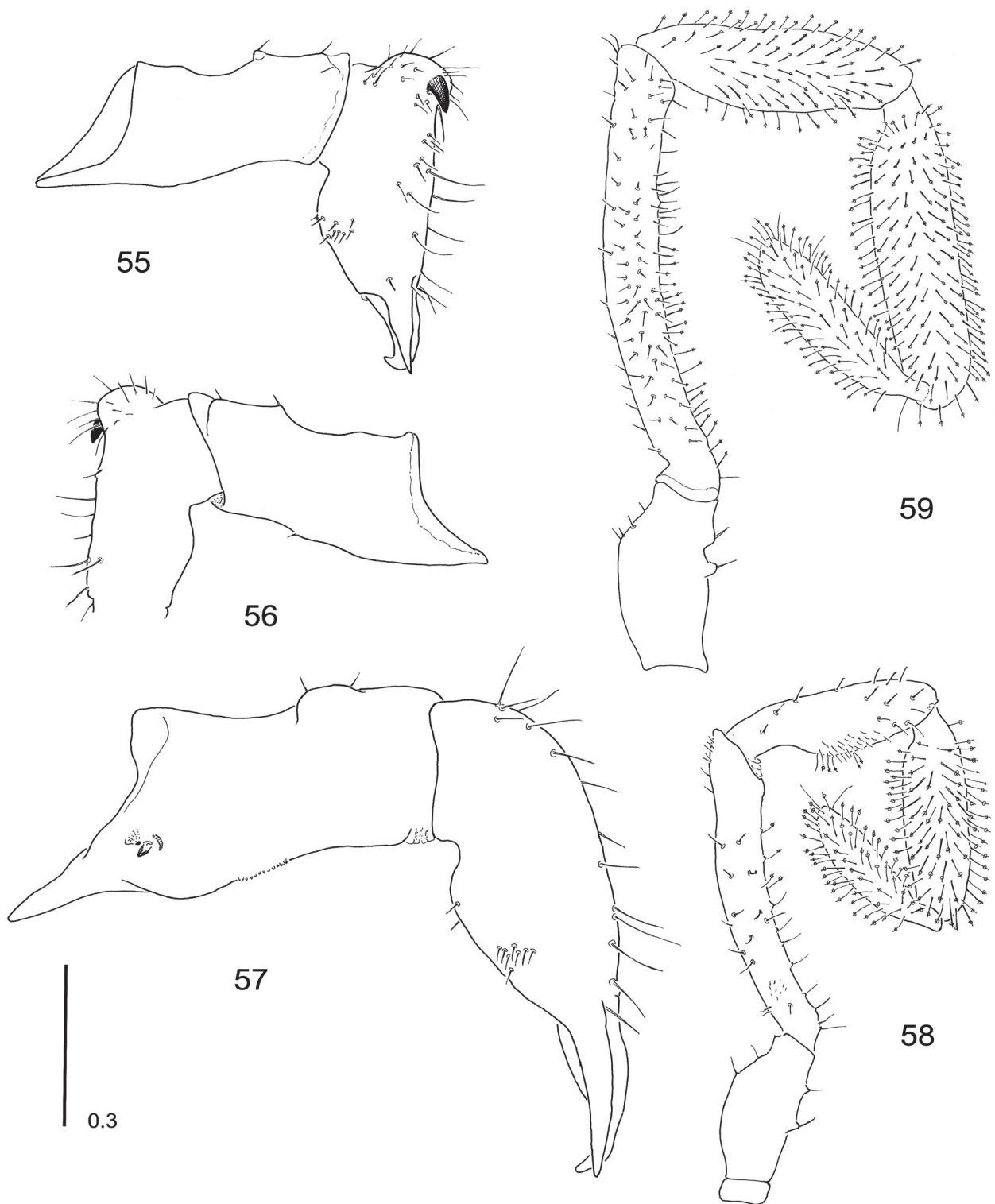
Chelicera (Figs 55-56): Basal article in posterior part dorsally slightly invaginated (la view), in distal part a low apophysis set with a short seta; 2nd article with a massive rounded apophysis on upper side carrying a pointed hook directed downwards and running more or less parallel to front of 2nd article; setae of various sizes, longest on frontal surface, few setae laterally and prolaterally, no brush of setae, no obvious subcuticular glandular tissue.

Pedipalp (Fig. 58): Tr slender, slightly swollen on do side; two small tubercles on ve side, each one pointed and with a small seta; Fe long and slender, slightly bent downwards, slightly enlarged distally, set with few scattered setae, ventrally with scattered clavate hairs, few of those distally; Pt with basal stalk, slightly enlarged and bulge-like ventrally, with a loose field of short setae and only five clavate setae, no apparent glandular tissue below; Ti cylindrical and moderately slender, with indistinct basal stalk, not curved, dense cover of clavate hairs on all sides; Ta slenderer than Ti, distinctly stalked, slightly inflated on do side, densely covered with clavate setae all round, few longer normal setae at distal end.

Genital morphology (Figs 47-52): Penis very long and slender, slightly more than two-thirds of body length, slightly depressed (do/ve view), basis broadened, deeply split into two parts, two muscles concentrated there, from basis slightly tapering towards apex, then parallel-sided up to tip including glans (do/ve view); glans spindle-shaped and broadened (la view); stylus short and in straight continuation of glans, with a slight helical torsion. Armature consisting of uniformly long (proximal



Figs 47-54. *Asiolasma ailaoshan*, male holotype. (47) Glans penis in lateral view. (48) Same in dorsal view. (49) Same in ventral view. (50) Truncus penis in lateral view. (51) Same in ventral view. (52) Same in dorsal view. (53) Body in dorsal view. (54) Same in lateral view. Figs 47-48 reproduced from Zhang *et al.* (2018). Scales: 0.05 mm (47-49); 0.26 mm (50-52); 0.70 mm (53-54).



Figs 55-59. *Asiolasma ailaoshan*, male (55-56, 58), female (57, 59). (55, 57) Right chelicera in proteral view. (56) Same in retrolateral view. (58-59) Left pedipalp in proteral view. Scale: 0.3 mm.

ones) or shorter (distal ones) spindle-shaped spicules, these symmetrical on do and ve side and arranged in three groups from distal to proximal: i) distal group: six spicules in somewhat irregular arrangement, ii) central group: four spicules mainly situated on do and la sides in annular arrangement, iii) proximal group: two spicules distinctly separated from central group on la edges of truncus, one each on la side.

FEMALE: Body much larger than in male; chelicera (Fig. 57) without apophysis on 1st article, generally more slender but much larger than in male; pedipalp (Fig. 59) much larger than in male, general appearance as in male, its Pt less bulged in ve view.

Measurements: Body length of male: 2.8 (n=1), of female 4.6 (n=1). Leg II length of male, of female in parentheses: Fe 2.68 (4.49), Pt 0.88 (1.21), Ti 2.37 (4.09), Mt 1.53 (1.94), Ta 1.33 (1.58) (data according to Zhang *et al.*, 2018). Penis length in strongly curved state 1.05.

Relationships: *Asiolasma ailaoshan* appears closely related to *A. juergengruberi* sp. nov. The latter is much larger (3.0-3.4 mm for male and female) than *A. ailaoshan*. *Asiolasma ailaoshan* is sexually dimorph, the female being much larger than the male (2.8 mm in male, 4.6 mm in female), the apophysis of the male 2nd cheliceral article is less high, more flat, its pointed thorn is directed more downwards and runs parallel to the front side of the article; the proximal pair of spicules of the glans penis is slightly closer to the mid-group spicules than in *A. juergengruberi* sp. nov.

Distribution (Fig. 1): At present this species is only known from the Ailao Shan Natural Reserve in the Chinese province of Yunnan. The two specimens were collected from soil litter in a (sub)tropical rain forest at 2170 m altitude (Zhang *et al.*, 2018).

Asiolasma juergengruberi sp. nov.

Figs 1, 60-87

Holotype: SMF; male; CHINA, northern Yunnan Province, southwest of Lugu Hu (lake), patch of primeval broadleaf forest mixed with scattered pine trees along a road, 3300 m, 27°37' N, 100°49'E; J. Martens leg.; 28.5.2011.

Paratypes: CJM 8143; 1 male, 2 females; collected together with the holotype. – CJM 8144; 2 males; CHINA, northern part of Yunnan Province, Lijiang Naxi, Autonomous County, E of Yulongxue Shan, 30 km N of Lijiang, 2800-2900 m, creek valley, secondary mixed broad leaf and coniferous forest, 27°09.0'N, 100°14.9'E; D.W. Wrase leg.; 13.8.2003.

Diagnosis: A medium-sized, rather globular species with flat Tu oc and hood and with relatively short hood projection; 2nd cheliceral article with pointed hook on

broad elevated apophysis. Penis shaft extremely slender, with short enlarged base, glans/truncus armature containing two proximally dislocated lateral spicules.

Name: This species is dedicated to Dr Jürgen Gruber, an esteemed arachnologist who, together with W.A. Shear, has meticulously studied American and Asian ortholasmatine harvestmen. Name in genitive case.

Description

MALE

Body, dorsal side (Figs 60, 62-63, 65-66): Body dark, nearly black, with dark bluish tinge, slightly elongated (do view), distinctly globular (la view); eye mound on anterior margin of prosoma rather flat and only slightly elevated, projecting into distad-directed hood forming an obtuse angle with do body surface (la view); hood flat, relatively short, bearing one central unpaired and four lateral paired tubercles, the basal one minute and shortest (difficult to see), the distad ones consecutively longer, these tubercles interconnected by robust anvil-shaped bridges in lower half of tubercles. On each side of hood two long apophyses projecting from anterior margin of prosoma and closely flanking hood, the outer ones longer and more massive than the inner ones; all apophyses and tubercles covered by a coat of fine micro tubercles all round.

Posterior margin of opisthosoma (Figs 60, 63, 65) with a row of 12 long and pointed tubercles of various lengths tapering to narrowly ending tip, longest ones in mid-part of row; at bases tubercles interconnected by low anvil-shaped tubercles forming small basal “windows” (Figs 60, 63); dense coat of microtubercles and few short setae all round.

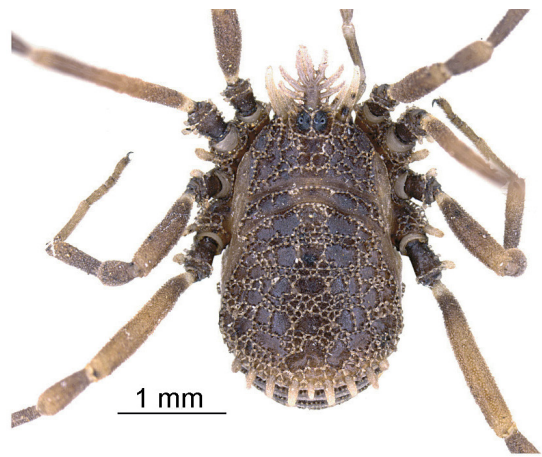
Network of prosomal and opisthosomal keel cells formed by light yellowish anvil-shaped tubercles contrasting with dark smooth cuticle (Figs 60-64); low, well developed, slightly elevated anvil-shaped tubercles (these stronger than in other Asian species) forming many individual small, often open cells all over prosoma, a large one behind Tu oc, on metapeltidium only two minute cells laterally and a row of tubercles on anterior margin; on opisthosoma larger cells in irregular arrangement and of different sizes, largest ones in a para-median row from anterior to posterior and near posterior margin of opisthosoma, in central part and on lateral margin most cells small, only a central large one, always surrounded by low anvil-shaped tubercles.

Body, ventral side: Only on Cx I an indistinct row of large tubercles; other Cx and Op gen with low tubercles, very few of them on free sternites, these bent to ve side, entire ve side with fine incrustation of minute mineral particles. Long, distally rounded tubercles on Cx: I -, II 1 retro-la, III -, IV 1 pro-la. Tubercles on Tr: I 1 very small pro-la and 1 retro-la, II 2 small retro-la, III 1 pro-la, 2 small retro-la, IV 1 pro-la.

Chelicera (Figs 72-75, 77): Basal article on do side with a large, hornlike apophysis slightly bent forward, article



60

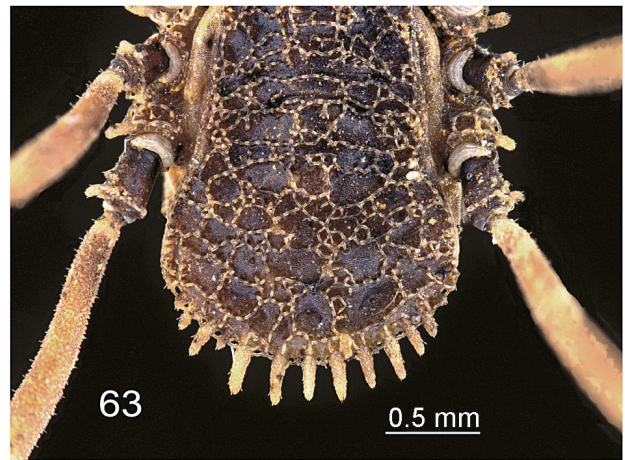


61



62

0.5 mm



63

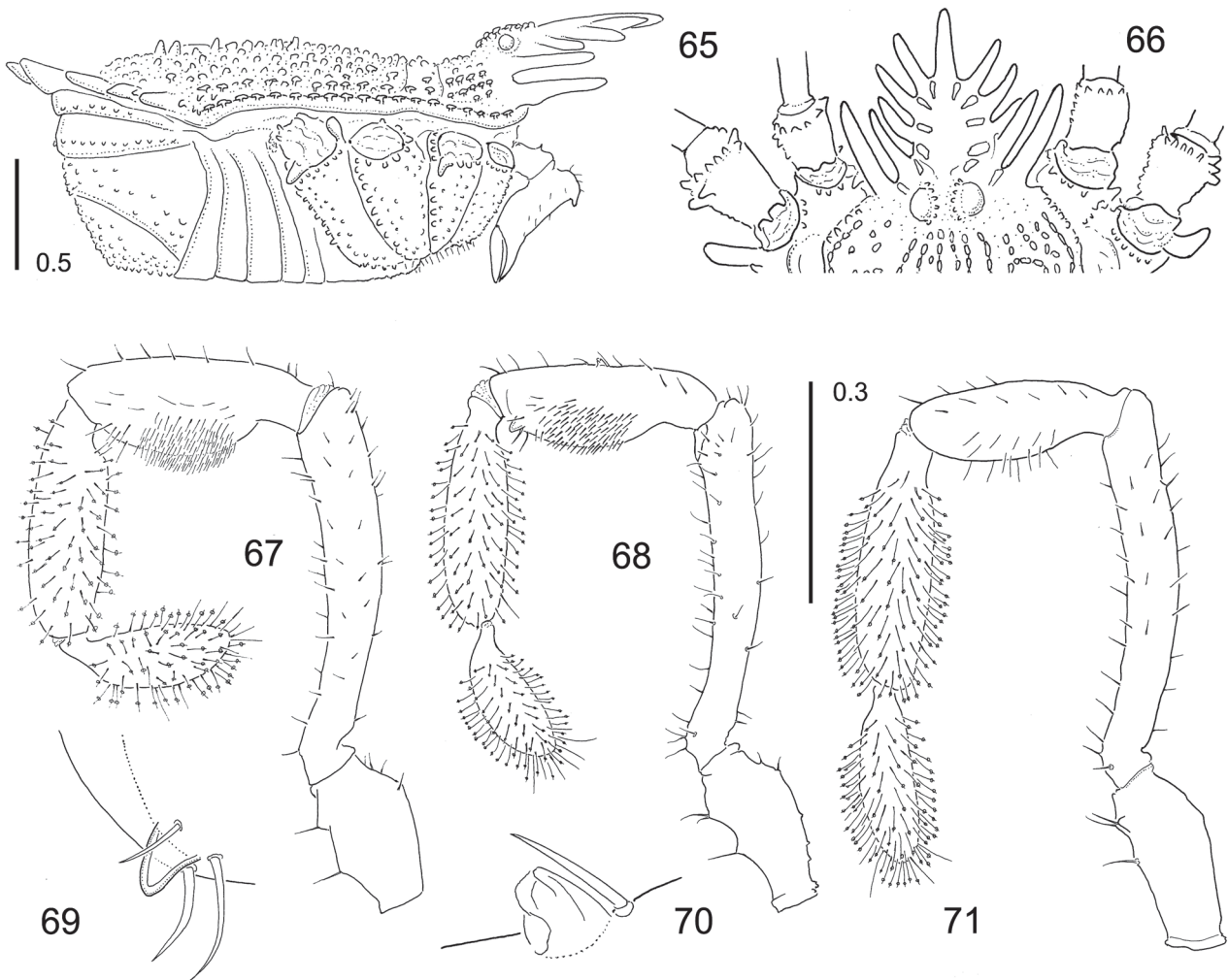
0.5 mm



64

0.5 mm

Figs 60-64. *Asiolasma juergengruberi* sp. nov., male (60, 62-63), female (61, 64). (60-61) Whole body in dorsal view. (62, 64) Prosoma in dorsal view. (63) Opisthosoma in dorsal view. Photographs by J. Schmidt.



Figs 65-71. *Asiolasma juergengruberi* sp. nov., male (65-70), female (71); specimens from Lugu Hu (65-67, 71), specimen from Lijiang area (68-70). (65) Body in lateral view. (66) Prosoma dorsal view. (67-68, 71) Right pedipalp in prolateral view. (69) Apophysis ventrodistally on patella. (70) Same dorsally. Scales: 0.03 mm (67-68, 71); 0.5 mm (65-66); no scale (69-70).

set with few setae laterally and prolaterally, ventrally a row of minute setae, no obvious glandular tissue. Second article on upper side with a large bipartite apophysis with a broad and massive basis extended into a sickle-like pointed apophysis bent forward and slightly to prolateral side. A small field of minute tubercles at basis of sickle-like part of apophysis, best seen from prolateral side.

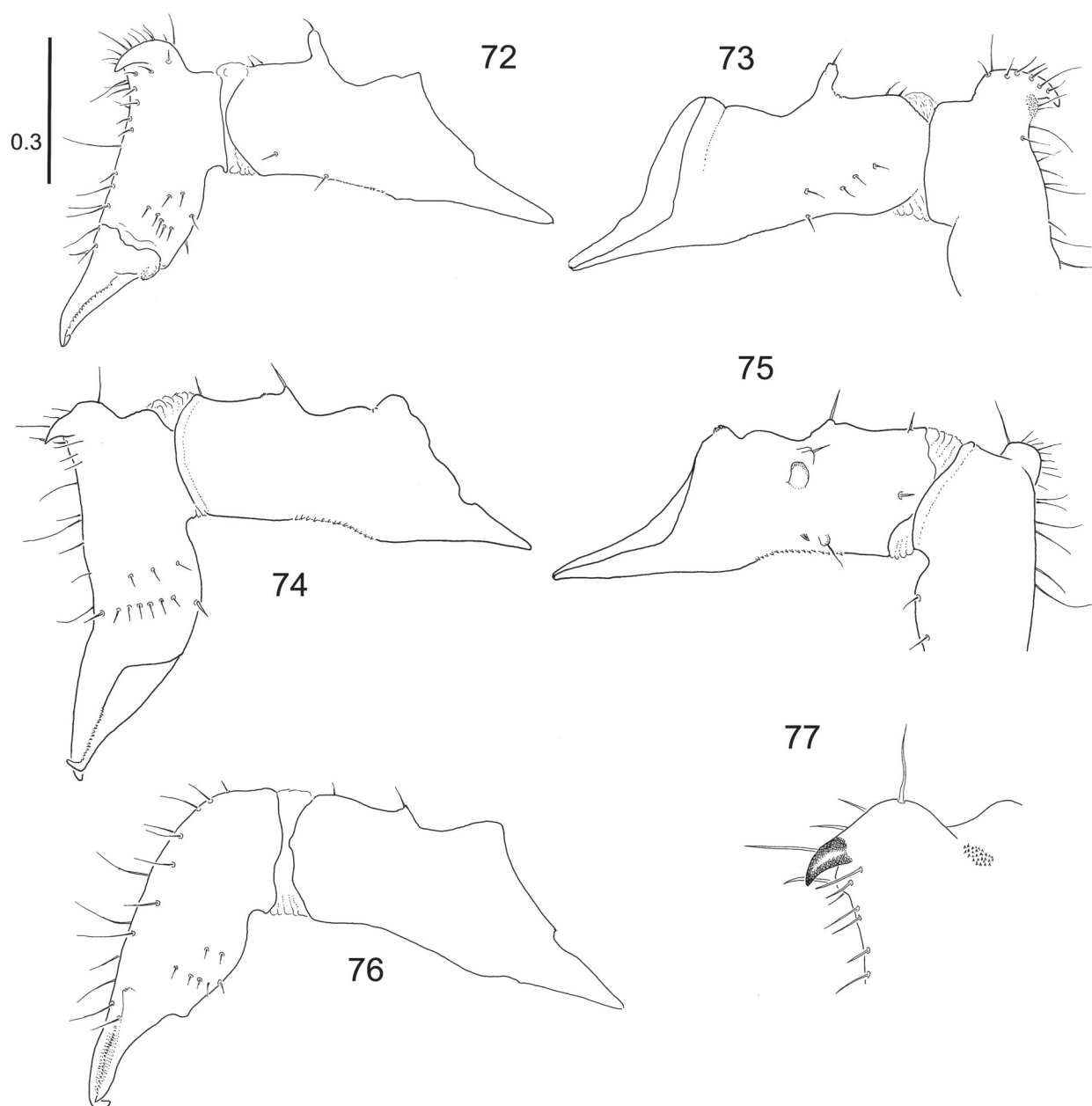
Pedipalp (Figs 67-70): Tr slender, slightly swollen on do side, ventrally with two low tubercles carrying a seta each; Fe slender, slightly club-shaped, bent ventrally and enlarged distally, set with few scattered normal hairs, no clavate hairs; Pt strongly bulge-like and enlarged ventrally, covered ventrally and prolaterally with a field of short setae with glandular tissue below, otherwise few scattered setae on all sides; Ti cylindrical and moderately thick, with basal stalk, inconspicuously curved, clavate hairs on all sides; Ta oval, stalked, slightly inflated on do side, covered with clavate setae all round.

Legs (Figs 60, 62-63): Short, robust, dark brown to

blackish; Fe I and III slightly inflated, covered with minute fine texture of microtubercles and interspersed with minute setae; no pseudo-articulations.

Genital morphology (Figs 78-87): Penis very long and slender, more than two-thirds of body length, basis broadened, deeply split into two parts, two muscles concentrated there; penis above basis slender, parallel-sided (ve/do and la views); glans parallel-sided in do/ve view, slightly tapering toward stylus (do/ve view), spindle-shaped and broadened in la view; stylus short, with a slight helical torsion. Armature with long uniform spindle-shaped spicules, symmetrical on do and ve side and arranged in three groups, these from distal to proximal position: i) six spicules: two each on ve and do side, one on each la side (the latter longest), ii) four, two of them on ve and two on do side, and iii) two spicules on each la sides, the latter on distal part of truncus and distinctly separated from groups i and ii.

FEMALE: Chelicera (Fig. 76) as in male, but do



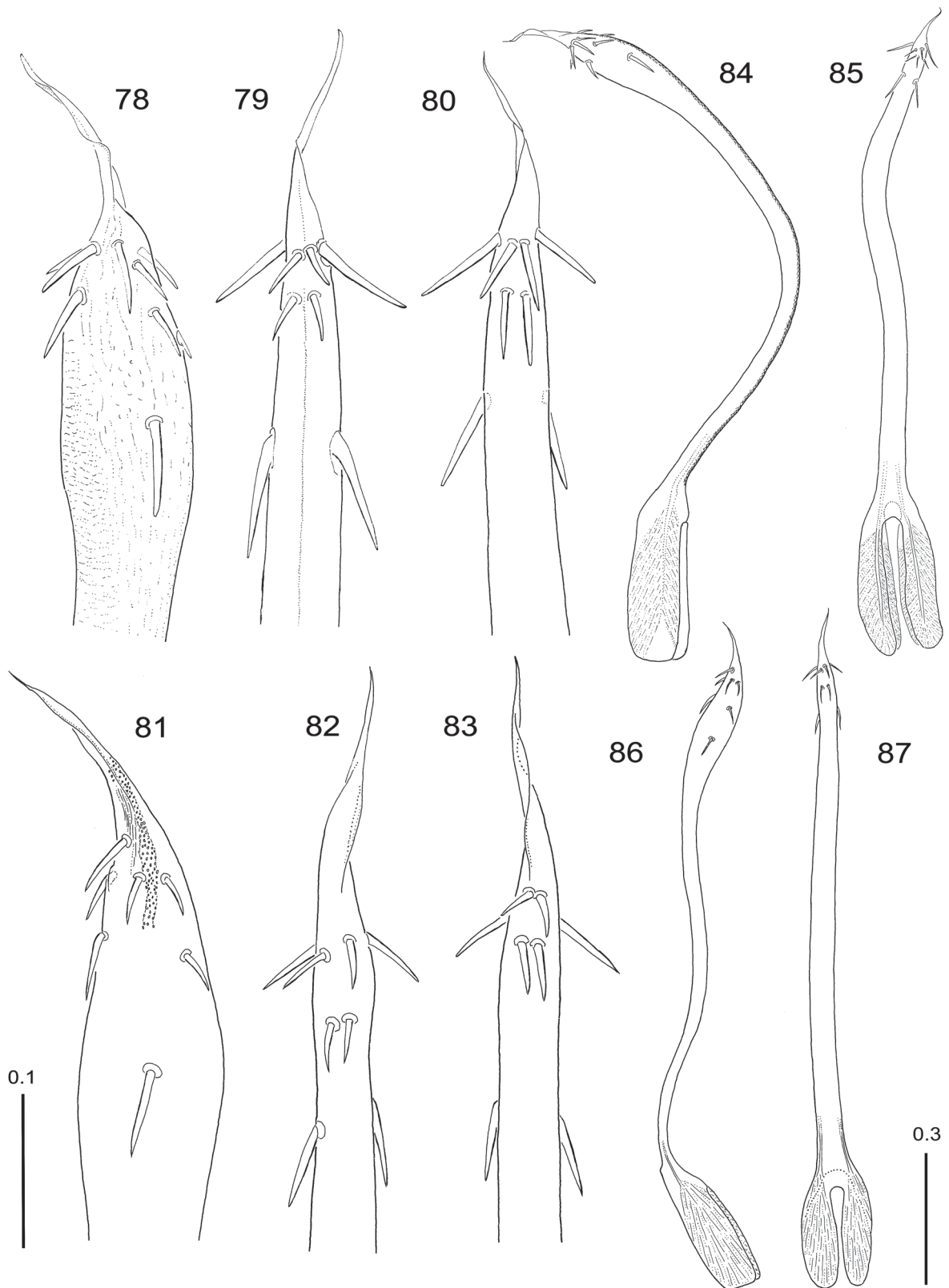
Figs 72-77. *Asiolasma juergengruberi* sp. nov.; male (72-75, 77), female (76). (72, 74, 76) Right chelicera in prolateral view. (73, 75) Same in retrolateral view. (77) Apophysis of 1st cheliceral article. (72-73, 76-77) specimen from Lugu Hu. (74-75) specimen from Lijiang. Scale: 0.3 mm (72-76); no scale (77).

apophysis on basal article smaller, no apophysis on 2nd article; pedipalp (Fig. 71) as in male, but Pt less inflated, no brush of setae on medio-ventral side, only with a few scattered longer setae; keel network on do side of body slightly different (Figs 61, 64), also among specimens; on metapeltidium only one keel cell laterally; nine tubercles on posterior margin of opisthosoma, these shorter than in male and thus more massive.

Measurements: Body length of males 3.0-3.3 (n=3), of females 3.2-3.4 (n=2). Leg II of male, of female in

parentheses: Fe 2.3 (2.2), Pt 0.8 (0.8), Ti 1.9 (1.8), Mt 1.7 (1.6), Ta 1.5 (1.3). Penis length 1.7.

Variation: In specimens from the Lijiang area of Yunnan the basal article of the chelicera has on its do side a slightly smaller hornlike apophysis than in the specimens from Lugu Hu, and the do hook on the 2nd article is lower, less prominent. The differences between the cheliceral hooks visible in Figs 73 and 75 are due to different angles of view. Little variation was observed in penis morphology; the penis of the Lijiang



Figs 78-87. *Asiolasma juergengruberi* sp. nov., genital morphology of male from Lugu Hu (78-80, 84-85) and of male from Lijiang (81-83, 86-87). (78, 81) Glans penis in lateral view. (79, 82) Same in ventral view. (80, 83) Same in dorsal view. (84, 86) Whole penis in lateral view. (85, 87) Same in dorsal view. In Fig. 81 subdistal opening of sperm duct is indicated, end of sperm duct is filled with sperm. Scales: 0.1 mm (78-83); 0.3 mm (84-87).

specimen appears slenderer than the penes of the Lugu Lake specimens (la view), it is narrowest above base, then continuously but slightly widens towards glans. The armature of glans in the Lijiang male examined is as in the Lugu Lake specimens, but the spicules of group i are slightly irregular (Figs 81-83). The pedipalp of the Lijiang specimen is with a small rounded apico-prolateral apophysis and with a smaller truncate apophysis on the do side of the Pt (Figs 68-70), which lack in other males examined.

Relationships: With respect to male genital morphology, *A. juergengruberi* sp. nov. is closest to *A. billsheari* sp. nov. In both species the penial spicules of groups ii and iii are widely separated, and the latter ones are situated in the distal part of the truncus. Both species have in common that the hook of the 2nd cheliceral article is placed on a solid elevated apophysis. The latter character is present also in the tropical species *A. ailaoshan*, though being less prominent there. The prosomal hood is short in *A. juergengruberi* sp. nov. and *A. billsheari* sp. nov.; in *A. ailaoshan* it is considerably longer.

Distribution (Fig. 1): According to present information, the species is confined to mountainous areas in northern Yunnan, China. The two localities known to date, Lugu Lake and close to Lijiang, are about 70 km apart in NE-SW direction. Primeval mixed broadleaf and coniferous forests prevail there. The localities are at 3300 m (Lugu Hu) and 2800-2900 m (Lijiang area) altitude.

Asiolasma schwendingeri sp. nov.

Figs 1, 32, 88-103

Holotype: MHNG; male; VIETNAM, Ha Noi Province, Ba Vi District, Mt Ba Vi (21°04'12"N, 105°21'55"E), 900 m, evergreen forest; A. Schulz leg.; 17.5.2012 [sample VN-12/17].

Paratypes: MHNG, 2 males, 2 females; CJM 8145, 1 male, Mt Ba Vi (21°03'35"N, 105°22'02"E), 1000-1070 m, evergreen forest; P. Schwendinger & A. Schulz leg.; 16.-18.5.2012 [sample VN-12/05c].

Non-types: MHNG; 2 juveniles; Mt Ba Vi (21°03'35"N, 105°22'02"E), 1000-1070 m, evergreen forest; P. Schwendinger & A. Schulz leg.; 16.-18.5.2012 [sample VN-12/05c].

Diagnosis: Largest and most long-legged of all *Asiolasma* species, with rather flat body, anterior part of prosoma including eye mound and hood slightly elevated (la view), visual impression of body massive caused by short hood but slender and fanned tubercles of hood (Figs 88-93); conspicuously long and slender pedipalps only in this species; pedipalpal tibia and tarsus together longer than femur (in both sexes).

Name: The species is dedicated to Dr Peter Schwendinger, esteemed arachnologist, who extensively collected arachnids in Southeast Asia, including specimens of this species and of *A. angka*. Name in genitive case.

Description

MALE

Body, dorsal side (Figs 88-89, 91-93): Body (Fig. 92) rather flat when seen in la view; Tu oc on anterior margin of prosoma markedly elevated and continuing into short hood; central and distal tubercles of hood parallel to surface of prosoma (la view); hood bearing one central unpaired and three lateral paired tubercles, the basic one shortest, the following ones consecutively longer, the unpaired one longest, all neighbouring ones interconnected by small anvil-shaped bridges close to their bases; tubercles slender, markedly spread, forming an open symmetric palmate fan; on each side of hood one long apophysis projecting from anterior margin of prosoma and closely flanking hood, its tip on a level between 2nd and 3rd tubercle of hood.

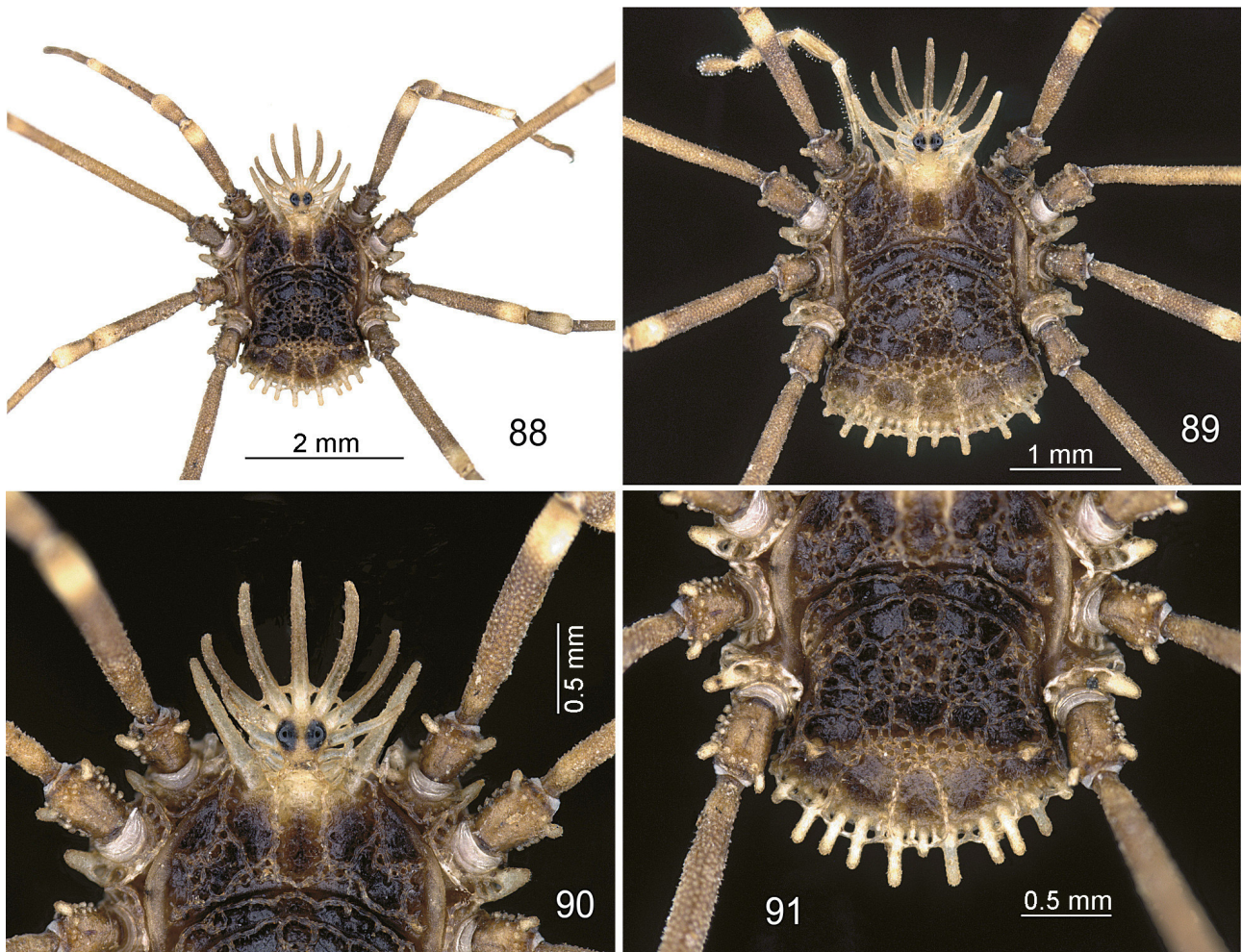
Posterior margin of opisthosoma with a row of eight long tubercles of various lengths, parallel-sided and slightly rounded at tips, longest ones in mid-part of row; tubercles close to basis interconnected by bridges of short lateral-basal denticles resulting in small "windows" (Figs 89, 91); fine texture of microtubercles all round.

Network of prosomal and opisthosomal keel cells made of anvil-shaped tubercles low, forming few large cells in anterior part of prosoma, largest ones behind Tu oc, in parts of metapeltidium no closed cells but an irregular double row of tubercles; on opisthosoma large cells on anterior and posterior margin and on lateral sides, in central part of opisthosoma most cells small except for a large central one, always bounded by low anvil shaped tubercles. All cells blackish in color, slightly lighter keels contrasting with dark smooth cuticle.

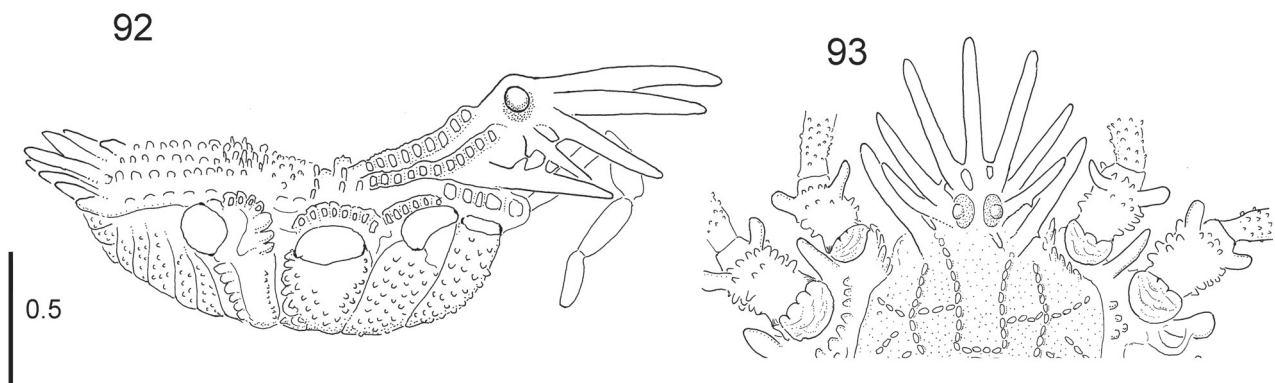
Body, ventral side: Front and back side of all Cx of legs with row of tubercles, on Cx I pro- and retro-la, Cx II retro-la, Cx III pro- and retro-la, Cx IV retro-la; on Cx I tubercles markedly elevated and anvil-shaped, space between rows of tubercles densely covered with minute pointed denticles; free sternites, corona analis and free tergites bent to ve side, covered with low tubercles and fine microtexture, scattered low setae in between.

Tubercles on Tr: I 1 each pro-la and retro-la, II 1 pro-la, 1 retro-la, III 1 pro-la and 1 retro-la, IV 1 pro-la, 1 retro-la.

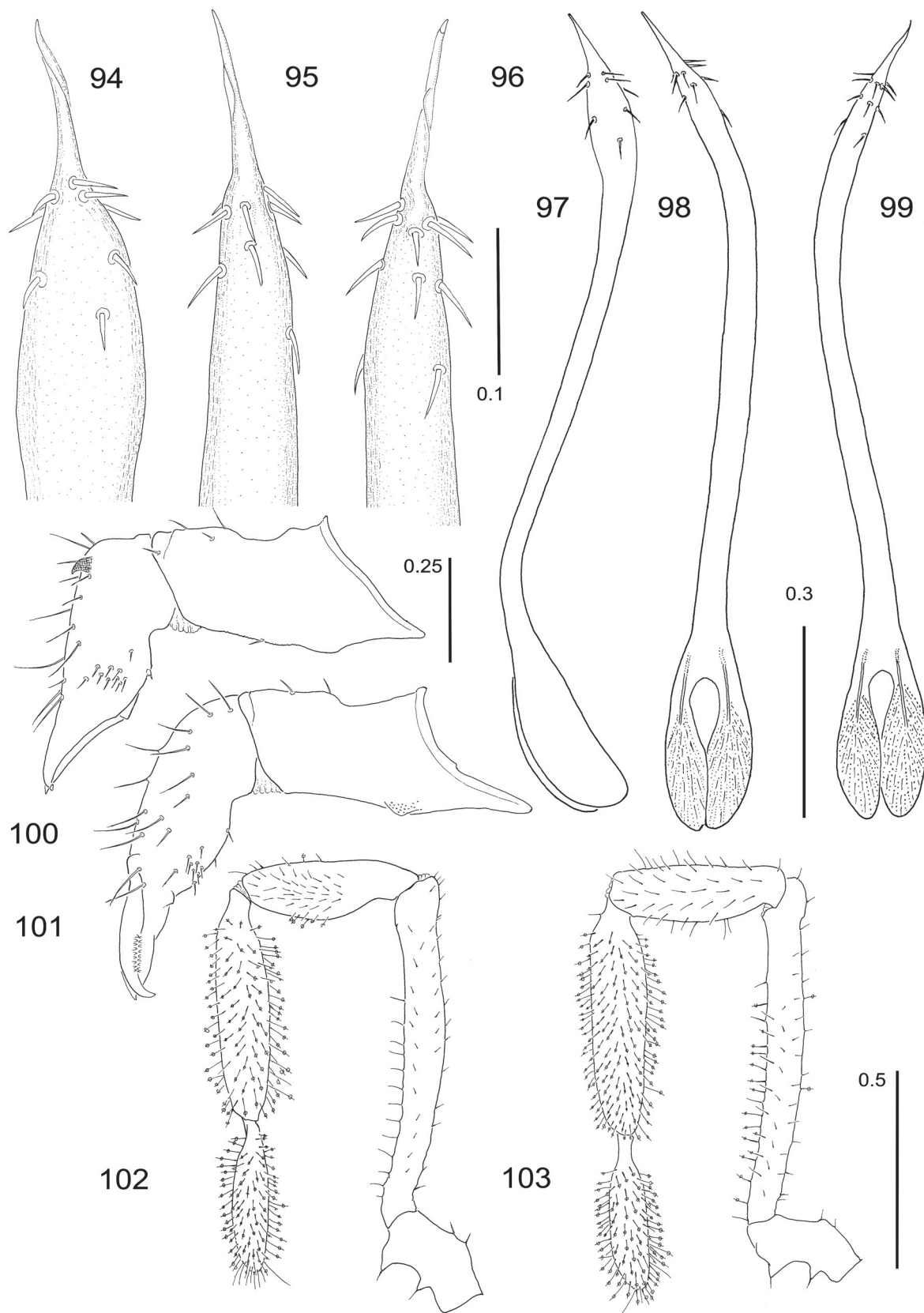
Legs (Figs 88-89, 91): Light brownish, Mt and Ta contrastingly blackish, conspicuously long and slender, no article inflated, covered with densely packed light tubercles and fine setae; long apically rounded tubercles on Cx: I retro-la, II 1 retro-la, III -, IV 1 pro-la, 1 retro-la; articles of Ta (male, female in parenthesis; hyphen separating numbers of different individuals, forward slash indicating difference between right and left side of one individual): leg I 5 (5/4), II 5-6 (4/6), III 6 (7), IV 7 (7).



Figs 88-91. *Asiolasma schwendingeri* sp. nov., dorsal view of male paratype (88, 90-91) and of female paratype (89). (88-89) Entire body. (90) Prosoma. (91) Opisthosoma. Photographs by J. Schmidt.



Figs 92-93. *Asiolasma schwendingeri* sp. nov., male holotype. (92) Entire body in lateral view. (93) Prosoma in dorsal view. Scale: 0.5 mm (92-93).



Figs 94-103. *Asiolasma schwendingeri* sp. nov., male holotype (94-100, 102), female paratype (101, 103). (94) Glans penis in lateral view. (95) Same in ventral view. (96) Same in dorsal view. (97) Whole penis in lateral view. (98) Same in ventral view. (99) Same in dorsal view. (100-101) Right chelicera in prolateral view. (102-103) Right pedipalp in prolateral view. Scales: 0.1 mm (94-96); 0.3 mm (100-101); 0.25 mm (97-99); 0.5 mm (102-103).

Chelicera (Fig. 100): Basal article slightly tapering distally (la view), dorsally slightly constricted, set with few setae dorsally and prolaterally, no brush of setae, no obvious glandular tissue. Second article with a strong apophysis on upper front, pointed, bent downward. Short to long setae on various parts, mainly on 2nd article.

Pedipalp (Fig. 102): Tr slender, slightly swollen on do side, with two marked tubercles on ve side, each pointed and carrying a strong seta; Fe extremely long and slender, slightly curved downwards, slightly enlarged distally and inflated near insertion of Pt, set with few scattered normal hairs; Pt slightly enlarged and bulge-like ventrally, with a loose field of short setae prolaterally, few clavate setae ventrally, no apparent glandular tissue below; Ti cylindrical and slender, with basal stalk, not curved, clavate hairs on all sides; Ta more slender than Ti, stalked, not inflated on do side, densely covered with clavate setae all round, few long and thin hairs at apex.

Genital morphology (Figs 94-99): Penis very long and slender, about two-thirds of body length, slightly curved, basis slightly broadened, deeply split into two parts, two muscles concentrated there; truncus slender, slightly compressed, parallel-sided (ve/do view), slightly broadened from base (la view) towards glans and further towards stylus (do/ve view), glans spindle-shaped and broadened (la view), stylus short and in strait continuation of glans, with slight helical torsion. Armature of glans with uniformly long spindle-shaped spicules arranged in three groups from distal to proximal: i) six in somewhat irregular annular arrangement, symmetrical on do and ve side, ii) four spicules arranged in a ring, one each on do, ve and la sides, iii) two spicules distinctly separated from group ii, one on each la side.

FEMALE (Fig. 90): Similar to male in general appearance of body, anterior hood and opisthosomal tubercles. Chelicera (Fig. 101) without pointed tubercles on 2nd article; pedipalpal Fe (Fig. 103) with scattered clavate setae ventrally but not in distal quarter; Pt less enlarged than in male, other articles as in male. Tubercles at posterior end of opisthosoma (Fig. 89) shorter than in male and slightly thicker.

Measurements: Body length of individual males: 3.4, 3.4, 3.6 (n=3), of females: 3.7, 3.7 (n=2). Leg II: male, female in parentheses: Fe 3.4 (3.1), Pt 1.0 (0.9), Ti 2.9 (2.9), Mt 1.8. (1.7), Ta 2.0 (1.3). Penis length: 1.3.

Variation: Somatic morphology quite homogeneous, but slight variation in lattice keel network of do side of prosoma discernible.

Relationships: Most similar and geographically closest is *A. damingshan* from the southern Chinese province of Guangxi. *Asiolasma schwendingeri* sp. nov. and *A. damingshan* clearly differ in body size, form of anterior hood, proportions and size of male and female pedipalp, pattern of do keel cells and genital morphology, especially armature of glans penis.

Distribution (Fig. 1): Until now this species is known only from a sole locality in Vietnam, Mt Ba Vi, Ba Vi District, Ha Noi Province. The specimens examined were collected in an evergreen forest between 900 m and 1070 m. Adults as well as small juveniles were found in mid May at the beginning of the southwest monsoon when collecting activity is not yet hindered by heavy rainfall. The distance to the type locality of *A. damingshan* in Guangxi Province, China, is approximately 425 km in northeast direction.

Asiolasma billsheari sp. nov.

Figs 1, 104-117

Holotype: SMF; male; CHINA, Gansu Province, western part of Qinling Mountains, 125 km northwest of Longnan, southern side of Lazikou pass, Zhuli valley, 2260 m, 34°07'57"N, 103°56'15"E, north slope, mixed oak/pine forest near creek, moss and litter sifted; D.W. Wrase leg.; 3.8.2012.

Paratype: CJM 8146; 1 male; collected together with holotype.

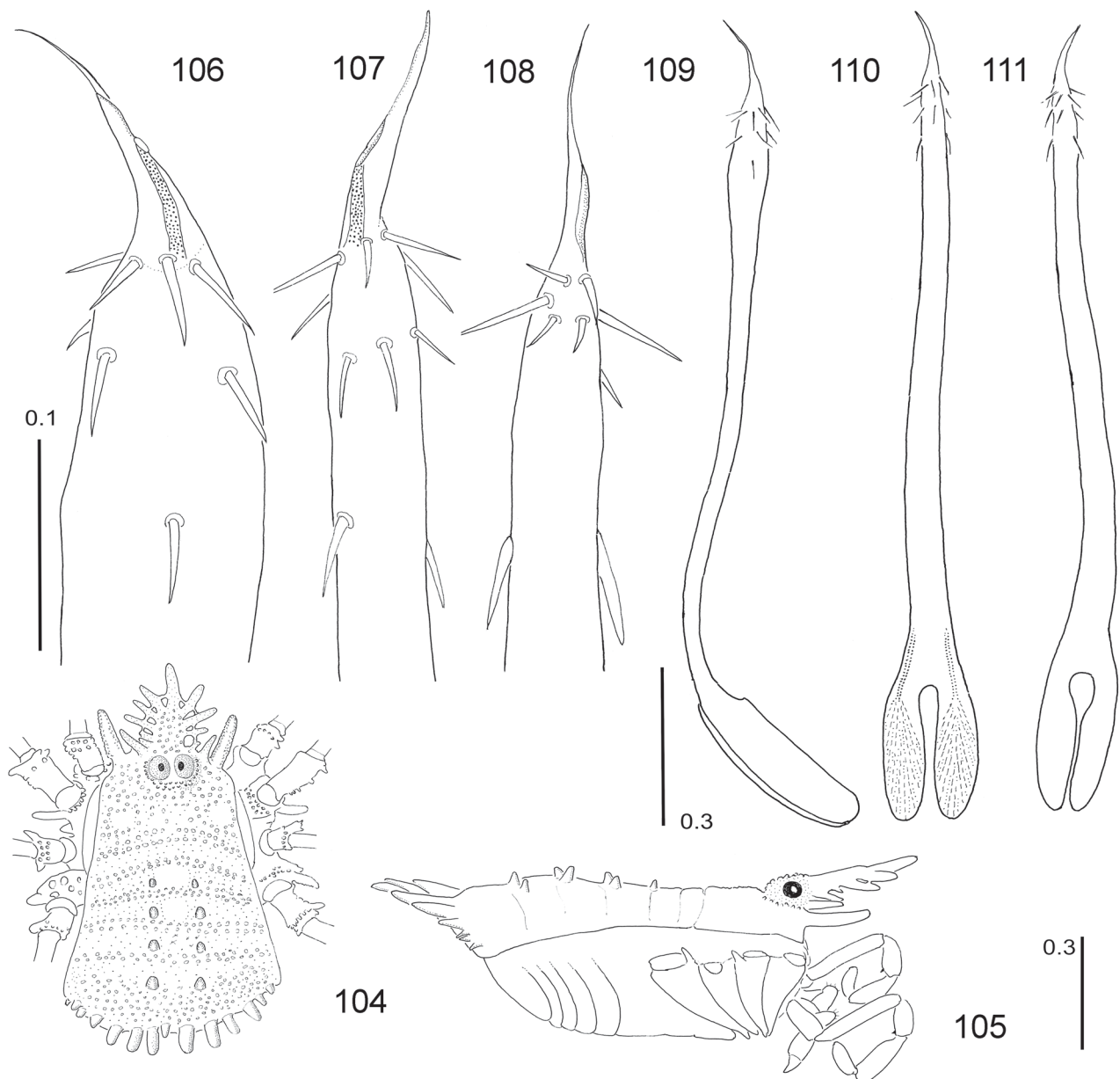
Diagnosis: A relatively small species with rather flat body and short hood; only prolonged anterior part of prosoma with eye mound and hood slightly elevated, similar to geographically close species *A. juergengruberi* sp. nov. from northern Yunnan; body less massive than in *A. schwendingeri* sp. nov. from northern Vietnam, caused by smaller hood processes. Pt of pedipalp with a bent and pointed medio-distal apophysis; areae I-IV of opisthosoma with one paramedian pair of low tubercles.

Name: The species is dedicated to William A. Shear, an esteemed arachnologist and myriapodologist who, together with Jürgen Gruber, meticulously studied New World ortholasmatine harvestmen. Name in genitive case.

Description

MALE

Body, dorsal side (Fig. 104-105): Body rather flat but less so than in *A. schwendingeri* sp. nov. (la view); Tu oc on anterior margin of prosoma only slightly elevated, with a rather low ascent and only slightly elevating eyes; these close to anterior margin of prosoma and hardly integrated into proximal portion of hood, central hood tubercle slightly bent upwards (la view); hood bearing one central unpaired and four or five (unequal on left and right side) lateral paired tubercles, basic one shortest (less than half size of next one or nearly equal size of following one; number of tubercles different on left and right side of hood; Fig. 104), the following ones consecutively longer, last one shorter than central unpaired one; all tubercles interconnected by small anvil-shaped bridges close to their bases; on both sides of hood one short and one long



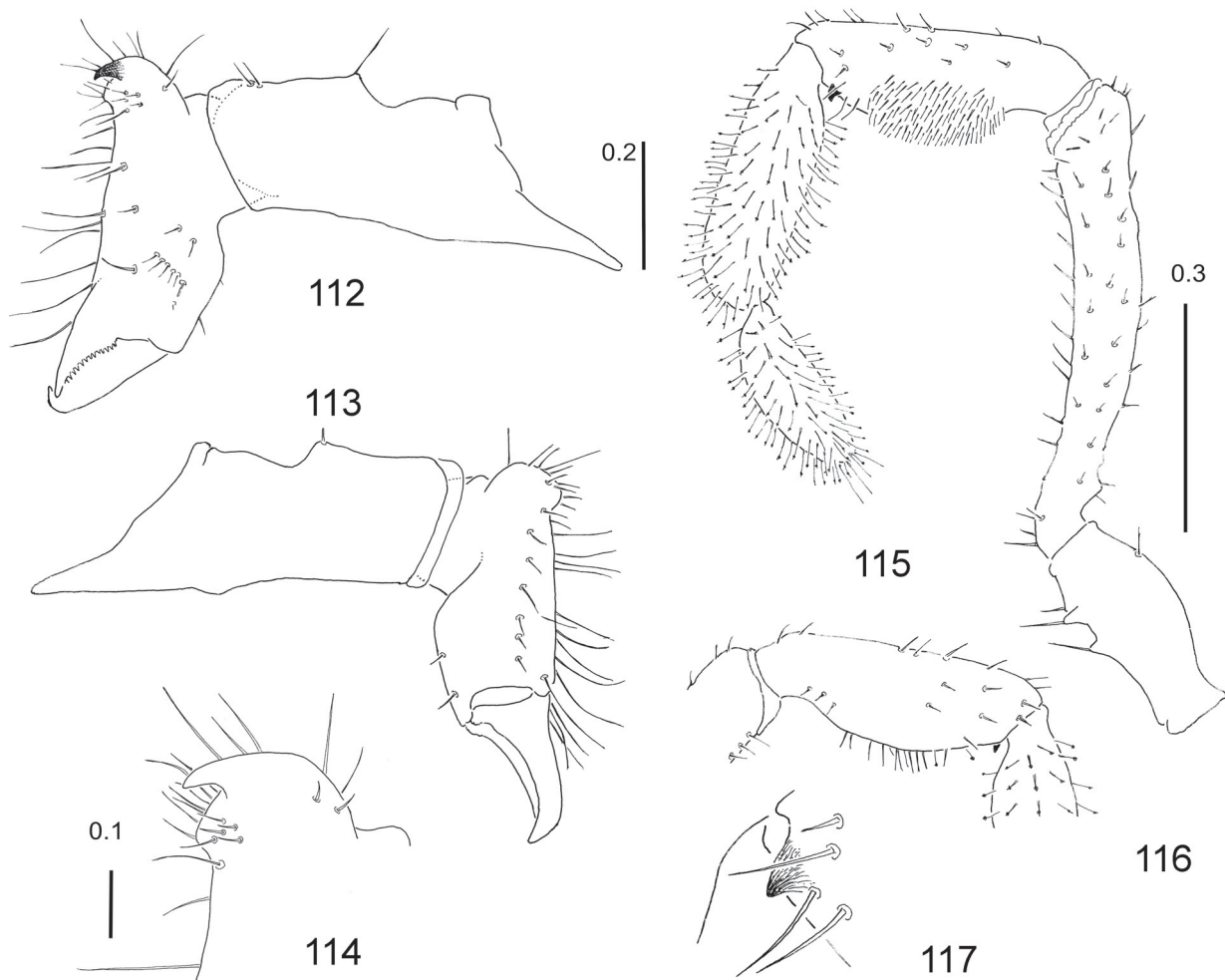
Figs 104-111. *Asiolasma billsheari* sp. nov., male holotype (104, 106-111), male paratype (105). (104) Entire body dorsal view. (105) Same lateral view. (106) Glans penis in lateral view. (107) Same in ventral view. (108) Same in dorsal view. (109) Truncus penis in lateral view. (110) Same in dorsal view. (111) Same in ventral view. In Figs 106-108 subdistal opening of sperm duct is indicated, end of sperm duct is filled with sperm. In Fig. 105 armament with low tubercles on do and ve side of body not shown. Scales: 0.1 mm (106-108); 0.3 mm (104-105, 109-111).

apophysis projecting from anterior margin of prosoma and closely flanking hood, these apophyses thick and massive, covered by small warts. Posterior margin of opisthosoma with a row of 14 tubercles of different lengths, slightly tapering towards markedly rounded tips, longest tubercles in centre and in right part of row. Areae I-IV of opisthosoma with one para-median pair of low indistinct pegs, distal pair shortest, all others of about equal size (do/la view).

Network of keel cells indistinct, only few closed ones on prosoma laterally; on prosoma scattered anvil-shaped

tubercles also in curved transverse rows; on metapeltidium one transverse row of tubercles; on opisthosoma keel cells nearly lacking, no closed cells except for few small ones near lateral margins and additional smaller ones on area V of scute near posterior margin, these cells not always closed; 1-2 transverse rows of anvil-shaped tubercles on areae I-IV of scute partly interrupted.

Body, ventral side: Cx with longitudinal rows of low light tubercles, similar tubercles on Op gen, free sternites and corona analis; free tergites bent to ve side, with transverse rows of tubercles as well.



Figs 112-117. *Asiolasma billsheari* sp. nov., male holotype. (112) Right chelicera in prolateral view. (113) Same in retrolateral view. (114) Apophysis of 2nd cheliceral article in prolateral view. (115) Pedipalp in prolateral view. (116) Distal part of pedipalpal femur, whole patella and proximal part of tibia in retrolateral view. (117) Apophysis on ventro-distal part of pedipalpal patella in prolateral view. Scales: 0.1 mm (114); 0.2 mm (112-113); 0.3 mm (115-116); no scale (117).

Legs: Short, brownish, without darker marks; Fe I and F II slightly swollen, Fe II with slight shallow constrictions; fine microtexture on all articles except Mt and Ta, the latter with fine setae. Tarsal articles of legs I-IV of holotype, of male paratype in parenthesis; in Ta I different numbers on right and left side: I 6 (5/6), II 9 (9), III 6 (6), IV 6 (6).

Chelicera (Figs 112-114): Posterior part of basal article markedly invaginated dorsally (la view), set with one long elevated seta dorsally and few small setae dorso-distally; 2nd article with a strong massive apophysis on upper side, ending in a pointed hook, bent in anterior direction; rounded rather flat apophysis-like edge below hook (la view). Setae of various sizes situated on hook, otherwise mainly on frontal and prolateral sides of article. Only broad apophysis, not pointed hook visible in la view: no brush of setae present and no obvious glandular tissue.

Pedipalp (Figs 115-117): Tr slender, slightly swollen on do side; two small tubercles distally on ve side, each

pointed and carrying a strong seta; Fe long and slender, slightly bent downwards, slightly enlarged distally, set with few scattered normal hairs, no clavate hairs; Pt markedly enlarged and bulge-like ventrally except for basal part, ventrally and partly prolaterally with a dense field of short setae, no apparent glandular tissue below this brush-like field, a small pointed ventro-prolateral hook close to distal margin of article; Ti cylindrical and slender, with indistinct basal stalk, not curved, with loose cover of clavate hairs on all sides; Ta slenderer than Ti, distinctly stalked, slightly inflated on do side, densely covered with clavate setae all round, distally few long and thin setae interspersed.

Genital morphology (Figs 106-111): Penis very long and slender, more than two-thirds of body length, slightly curved, short basis deeply split into two parts, two muscles concentrated there, penis shaft partly parallel-sided, partly continuously tapering to level of proximal pair of spicules and slightly depressed (ve/la view); penis

(la view) markedly broadened at base and extremely slender above, only slightly enlarged towards glans; glans spindle-shaped and broadened (la view); stylus short and in straight continuation of glans, with slight helical torsion, opening of sperm duct subdistal, sperm in distal end of sperm duct.

Spicules of glans nearly uniform in size and spindle-shaped, arranged in four groups between distal portion of glans and distal part of truncus: i) two spicules on do side, ii) six spicules forming ring on ve, la and do sides, iii) two spicules on each lateral side, iv) one spicule on each lateral side on truncus well below glans armature.

FEMALE: Unknown.

Variation: The armature of the glans is the same in both specimens available. Otherwise no data can be given due to the lack of sufficient material.

Relationships: This species occupies a rather isolated position, but it appears to be closely related to the other species with a massively elevated apophysis of the 2nd cheliceral article, *A. ailaoshan* and *A. juergengruberi* sp. nov. *Asiolasma ailaoshan* is strikingly different in its sexual dimorphism, i.e. the sole known female is much larger than the corresponding male. This dimorphism may also be revealed when the unknown female of *A. billsheari* is discovered. The apophysis of the hood is (absolutely and relatively) shorter in *A. billsheari* sp. nov., thus forming a less broader and less palmate fan cover for pedipalps and chelicerae than in *A. schwendingeri* sp. nov. The minute pegs on the do side of the opisthosoma are absent in *A. ailaoshan* and *A. schwendingeri* sp. nov.

Measurements: Body length (including hood and opisthosomal tubercles) of males: 3.0-3.05 (n=2). Leg II: Tr 0.3, Fe 2.6, Pt 0.8, Ti 2.0, Mt 2.0, Ta 1.6. Pedipalp: Tr 0.3, Fe 0.7, Pt 0.4, Ti 0.45, Ta 0.8. Penis length: 1.7.

Distribution (Fig. 1): The species is only known from the type locality in the Chinese Gansu Province at about 34°N and represents the northernmost known locality of ortholasmatines on mainland Asia (and in Asia in general including the Japanese records of *Cladolasma parvulum*). The two specimens were collected from soil litter in a pine and oak forest at 2260 m altitude.

DISCUSSION

The Nemastomatidae is mainly a Holarctic family of ground-living Dyspnoan harvestmen. According to Shear & Gruber (1983), they are separated into the following two subfamilies: Nemastomatinae Simon, 1872 with a primarily West Palaearctic distribution, and Ortholasmatinae with a strong Nearctic affiliation. While no native nemastomatine species are known from the New World, there are a few ortholasmatines in the Old World, but since first being recorded from southern Japan

(Suzuki, 1963, 1974) species numbers in Asia remained low. Two additional species have recently been discovered in southern China (Zhang & Zhang, 2013; Zhang *et al.*, 2018), and a further three are presented in this paper. This is still a small number despite numerous surveys of the soil fauna in the Himalayas and in Southeast Asia for several decades and, more recently, in China by a number of European and Chinese institutions. Although more species will most likely be discovered in the future, “a wealth of new species to arise from ongoing exploration” of (sub)tropical Asia (Shear & Gruber, 1983; Shear, 2010) is not yet in sight. Consequently, there is a discrepancy between the species-rich ortholasmatine fauna of the Americas with at least 20 species (Shear & Gruber, 1983, 1987; Shear, 2010; Cruz-López, 2017; Cruz-López *et al.*, 2018) and only seven in Asia.

Cruz-López *et al.* (2018) tried to elucidate the phylogenetic relationships within the Ortholasmatinae in a molecular phylogenetic analysis of several of New World and one Asian species, *Cladolasma parvulum*. Their results, based on seven species and one specimen each, are not yet convincing. Their phylogenetic trees establish the only Asian species analyzed as sister to an unidentified *Ortholasma* species (CO1 gene; maximum likelihood) or as sister of *Dendrolasma mirabile* (18S gene; bootstrap). Presently, statistical support for both combinations is low and the molecular phylogenetic relationships of Asian and New World species are still open to question.

Historical biogeography of ortholasmatines: This subject was discussed by Shear & Gruber (1983) and Shear (2010), albeit without a satisfying conclusion achieved. Shear & Gruber (1983) primarily proposed an origin of the subfamily in Asia, with a later dispersal to America, but Shear & Gruber (1983) and Shear (2010) also discussed an alternative scenario and placed the origin of ortholasmatines in the New World, namely, in the central Mexican highlands, or Transverse Volcanic belt, with subsequent dispersal to the northern parts of America, especially to the western coastal areas and southwards to the southern parts of México and even Honduras. Only subsequently did the ortholasmatines enter East Asia. In the light of newly available material the latter scenario is neither very plausible nor convincing and I strongly favour the hypothesis of an Asian origin of the Ortholasmatinae. There are a number of arguments to justify and extend the original hypothesis of Shear & Gruber (1983).

The most prospering group of Nemastomatidae is the nominate subfamily which presently encompasses about 120 species in 18 genera (Schönhöfer, 2013). They are confined to the western Palaearctic, with a few outlying species in Central Asia and China (the genera *Starengovia* Snegovaya, 2010 and *Sinostoma* Martens, 2016, comprising three and one presumed relict species, respectively). Regarding the high diversity of Nemastomatidae in western Eurasia, one may assume

that also the ortholasmatines have originated in Asia, not in its montane nor boreal parts, but in its tropical to subtropical parts like present-day southern China and adjacent areas of northern Thailand and northern Vietnam. I further assume that stem ortholasmatines, in accordance with one of the hypotheses of Shear & Gruber (1983), later reached the New World where they underwent a strong radiation into various morphological and ecological lines. This went hand in hand with a considerable geographical range extension from near the Alaskan border, a boreal area, to the Honduran tropics (Shear, 2010). This radiation led to diversification into five genera in the Americas (Shear, 2010; Schönhofer, 2013; Cruz-López *et al.*, 2018).

The Asian ortholasmatine species show a number of plesiomorphic morphological characters, which indicates that they all still live in their ancestral homeland and are not the descendants of American species. My four main reasons for the Old World origin of ortholasmatines are as follows.

1. *Dorsal latticework*: It appears irregular in Asian species, often not arranged into clearly defined cells, and the anvil-shaped tubercles forming the cells are mostly low, sometimes even difficult to recognize (especially so in *Cladolasma parvulum*). I judge this to be a plesiomorphic character state. In the majority of American species there is a regular symmetrical network of keel cells made of interconnected anvil-shaped tubercles with the individual tubercle markedly elevated and forming an astonishingly regular and distinct dorsal sculpture, presumably a derived character state. Anvil-shaped tubercles are exceedingly developed in *Cryptolasma* where they are present also on the dorsal side of the hood. The individual tubercles are fragmented into many minute branches which are spread in various directions.

2. *Male genital morphology*: The penes of Asian ortholasmatines are quite simple and regarded here as plesiomorphic. The muscle-bearing base of the penis is relatively large, occupying about one fifth of the whole penis. The glans bears uniform and relatively large spicules in a regular arrangement of 2-4 chaplets from below the stylus to the distal part of the truncus (some species do not have spicules on the truncus). The stylus is short, slightly twisted, the opening of the sperm duct is subdistal. The Japanese *Cladolasma parvulum* is an exception in displaying a rather complicated armature of the glans, a presumably derived state.

In the American species the penis is more complicated and apparently derived. The muscle-bearing base is smaller and shorter, the truncus relatively longer (about six times as long as base). The armature of the glans is rather elaborate, with different forms of spicules, larger and smaller ones, even some pointing to the tip of the penis (more uniform in *Ortholasma*). The stylus appears to be extended and it is much longer than the glans, its end recurved, the opening of the sperm duct situated at

the end of a recurved stylus but the top of the stylus is spirally twisted in *Dendrolasma*.

3. *Hood of prosoma*: This is a highly derived character that occurs only in few other dyspnoan families (Trogulidae, Dicranolasmatidae), although details differ considerably (Martens, 1976). In Asian and American ortholasmatine genera the hood is clearly different. In the Asian ones the lateral tubercles of the hood project freely for most of their length, only at their bases are they interconnected by small thorns which stabilize the hood. In American species the often long and delicate tubercles are interlinked by similar projecting thorns, but these are situated at the end of the tubercles, thus giving the hood more stability. The resulting fine net-like structure allows for further forward extension of the hood, and this state is found only in American species (for many details see Gruber & Shear, 1983; Shear, 2010). The more complex hood of American ortholasmatines is regarded as apomorphic.

The hood is completely lacking in Mexican *Martensolasma* species, and this character state is probably apomorphic since it is confined to two species only. This genus has been difficult to include in the Ortholasmatinae by using only morphological characters (Cruz-López *et al.*, 2018) and the molecular phylogenetic analysis is not yet unambiguous. Cruz-López *et al.* (2018) point out that also the monophyly of *Trilasma*, as based on its current diagnosis, is questionable and more separate lineages may be involved. An additional species of Mexican ortholasmatine with an unusual morphology awaits formal description and will render American ortholasmatines even more complex than they look at present (Cruz-López *et al.*, 2018).

The morphological richness of somatic characters, as well as male genital features, is quite poorly developed in Asian species. At present only two lineages, represented by *C. parvulum* on one hand and all hitherto known species of *Asiolasma* gen. nov. on the other, can be recognized. This points towards two old evolutionary lineages represented by scattered relicts. In the Americas the diversity (indeed also with regard to the number of known species) is much higher, indicating a more recent radiation and geographic expansion.

4. *Ecological requirements*: They are quite uniform in the Asian species. All live in humid litter or under pieces of dead wood in primeval forests, montane broadleaf forests, coniferous forests and (sub)tropical evergreen forests, with a closed canopy. This is considered a plesiotypic state and corresponds to that of the majority of nemastomatines which all live in moist soil or litter, sometimes even close to running water (*Paranemastoma bicuspidatum* ([C. L. Koch, 1835] in the European Alps; Martens, 1978). Only one species of nemastomatines is known to climb herbs or low bushes, but only in a moist habitat close to the Georgian Black Sea coast (*Paranemastoma superbum* Redikorzev, 1936; see Martens, 2006). Apparently Asian ortholasmatines do

not inhabit degraded forests with an open canopy and a dry sunlit forest floor. In the Americas the ecological spectrum of ortholasmatines is much larger and includes a number of dry habitats, besides moist habitats in tropical rainforest (Shear & Gruber, 1983; Shear, 2010; Cruz-López *et al.*, 2018). This larger ecological plasticity, as compared to that of Asian ortholasmatines, is considered here as being atypical.

I conclude that ortholasmatines have probably evolved in the Old World, in what is presently the Southeast Asian tropics, and spread only little into the temperate mountains northwards, like the Qinling Range in southern Gansu. Their ancestors could have entered the New World at a presently undefined moment in time and through unknown routes, "...but this points far into the past, certainly previously to the opening of the present Atlantic..." (Shear & Gruber, 1983). There they developed a considerable diversity of morphological traits, resulting in a larger number of species and five presently accepted genera. They enlarged their ecological spectrum to settle also in dry areas and several extant species do no longer require humid soil litter. Ortholasmatines in the area of their origin have remained few, at least as far as currently known. Their morphological diversity, including genitalic traits, is low and on the basis of morphology only two lineages ranking as different genera are presently recognizable. The Asian clades appear to represent relicts even if more species will be discovered in the future. I thus consider the Asian ortholasmatines as the result of an old radiation, and ancestral emigrants led to an extensive, more recent radiation in the Americas.

ACKNOWLEDGEMENTS

Peter Schwendinger put the collections under his care at my disposal and carefully edited various manuscript versions and worked on some of the colour images. Joachim Schmidt kindly provided most of the stacked-automontage images, Peter Schwendinger the remainder of the set (Figs 31-32). Jürgen Gruber helped by commenting on an earlier version of the manuscript and by providing valuable additional information and constructive criticism. Important material from China was provided by David W. Wrase. Together with Sun Yue-Hua (Chinese Academy of Sciences, Beijing) I had the privilege to visit a great number of forested mountainous areas in various parts of China for zoological research. He even made it possible for me to visit remote areas. Zhang Chao (College of Life Sciences, Baoding) kindly loaned the type specimens of *Dendrolasma damingshan* and *D. ailaoshan*. Nobuo Tsurusaki (Tottori University, Japan) provided specimens of *Cladolasma parvulum*. Sergei I. Golovatch (Moscow, Russia) kindly checked and improved an earlier draft of the manuscript. The

Feldbausch-Stiftung and the Wagner-Stiftung at the Fachbereich Biologie of Mainz University granted financial aid for field research in Asia. I heartily thank all friends, colleagues and institutions for their generous help and encouragement.

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