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First record of the genus *Pseudopoda* JÄGER 2000 in Laos with description of new species

(Arachnida, Araneae, Sparassidae)

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Abstract

Three new species of the genus *Pseudopoda* are described from Laos: *Pseudopoda confusa* sp. n. (♂, ♀; holotype ♂ in SMF), *Pseudopoda gemina* sp. n. (♀; holotype ♀ in SMF), and *Pseudopoda namkhan* sp. n. (♂, ♀; holotype ♂ in SMF). This is the first time that representatives of this genus have been recorded from Laos. From the morphology of the copulatory organs, these species seem to be closely related to congeners from Nepal, Myanmar, Thailand, China (Yunnan) and Taiwan. Records of the species extend the altitude range to lower altitudes: *P. confusa* sp. n. (580–750 m) for the *diversipunctata* species-group, *P. gemina* sp. n. (260 m) for the whole genus. Mating and copulatory behaviour of *P. namkhan* sp. n. is reported for the first time for the genus.

Key words: Taxonomy, systematics, species group, Heteropodinae, zoogeography, altitude range, Luang Nam Tha Province, Luang Prabang Province, Vientiane Province.

Introduction

Spider diversity of Laos has been poorly investigated, despite its interesting geographical location. Laos is situated in a rather remarkable setting which is significant from a number of aspects contributing to an extremely rich biota. It is the centre of a very rich region in biodiversity (GRESSIT 1970). Two recent expeditions (November 2004, March 2006) were set up by Peter JÄGER, Julia ALTMANN and Vincent VEDEL from the Senckenberg-Museum in Frankfurt am Main, in order to obtain an overview of arachnid richness in this country.

The genus *Pseudopoda*, recently described by JÄGER (2000), is abundant and diverse in Asian mountainous areas (JÄGER 2001). Representatives of this genus were sampled at an altitude range from 300 to 3800 metres from Pakistan to Japan, including the countries neighbouring Laos: China, Thailand, Myanmar and recently Vietnam (JÄGER & VEDEL 2005). Consequently, it was expected that this genus is present at least in northern mountainous parts of Laos (JÄGER 2001: 24). In this paper the first records of this genus from Laos are described.

Material and methods

Specimens were preserved in denatured 70% ethanol. Epigynes were dissected and, afterwards, cleared in 96% lactic

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acid for a few minutes. Examination and drawings were carried out with a Leica MZ 16 stereomicroscope with drawing mirror. When specimens reached maturity, photos were taken in the laboratory, with a Canon EOS 300D (equipped with a Sigma 105 mm macrolens and a Canon ringlite MR 14EX).

For diagnoses and descriptions of family, subfamily and genus and style of description see Jäger (1998, 2001). All measurements are in millimetres. Measurements of appendices are listed as: total length (femur, patella, tibia, metatarsus, tarsus). Projecting point of the embolus is shown by means of the left palp in ventral view. In illustrations, hairs are generally omitted, except for palpal spines.

Abbreviations used:

I–IV	legs I, II, III, IV.
ALE	anterior lateral eyes.
AME	anterior median eyes.
PJ	subsequent number of Sparassidae examined by P. Jäger.
PLE	posterior lateral eyes.
PME	posterior median eyes.
RTA	retrolateral tibal apophysis.
SD	subsequent number of species/DNA-samples (deposited in SMF).
SMF	Senckenberg Museum Frankfurt am Main.

Taxonomy

Family Sparassidae Bertkau 1872

Subfamily Heteropodinae Thorell 1873

Genus ***Pseudopoda*** Jäger 2000

Pseudopoda confusa sp. n.

(Figs. 1–13, 29–32)

Holotype ♂: (PJ 2174), Laos, Luang Nam Tha Province, Luang Nam Tha district, Ban Tavan Mai, 20°58.702' N, 101°28.686' E, 581 m, valley with stream, disturbed primary forest, collected by hand, Jäger & Vedel leg., 9. xi. 2004, found as immature, bred to maturity in laboratory, adult ii. 2005, SD 175, in SMF.

Paratypes (1 ♂, 1 ♀): 1 ♀ (PJ 2173), same data as holotype, SD 180, in SMF. 1 ♂ (PJ 2175), Laos, Luang Nam Tha Province, Muang Sing district, Nam Ha Protected Area (Nam Ha 1 GPS), Road 17, km 46, 745 m, 21°8.075' N, 101°11.991' E, secondary forest, along path, at night, collected by hand, leg. Jäger & Vedel, 16. xi. 2004, as immature, bred to maturity in laboratory, adult ii. 2005, SD 174, in SMF.

Etymology: The specific name is a Latin adjective – confusus, -a, -um – meaning confusing, referring to the complex structures at the tip of the male embolus.

Diagnosis: Medium-sized spiders. The species may be recognized by the following combination of characters:

♂: 1. Short embolus, wide basally, bent at right angles, tip pointing retrolaterad, forming complex twisted structures distally (Figs. 1–3, 6–7). 2. RTA with two short apices and basal bulge in ventral view (Figs. 1–4).

♀: 1. Broad U-shaped median septum (Fig. 8). Septum wider than in *Pseudopoda lutea* (Thorell 1895) (Jäger 2002: fig. 184). 2. Epigynal field distinctly trilobate in anterior part (Fig. 8). 3. Internal duct system with spherical structures in anterior half (Figs. 10, 12).

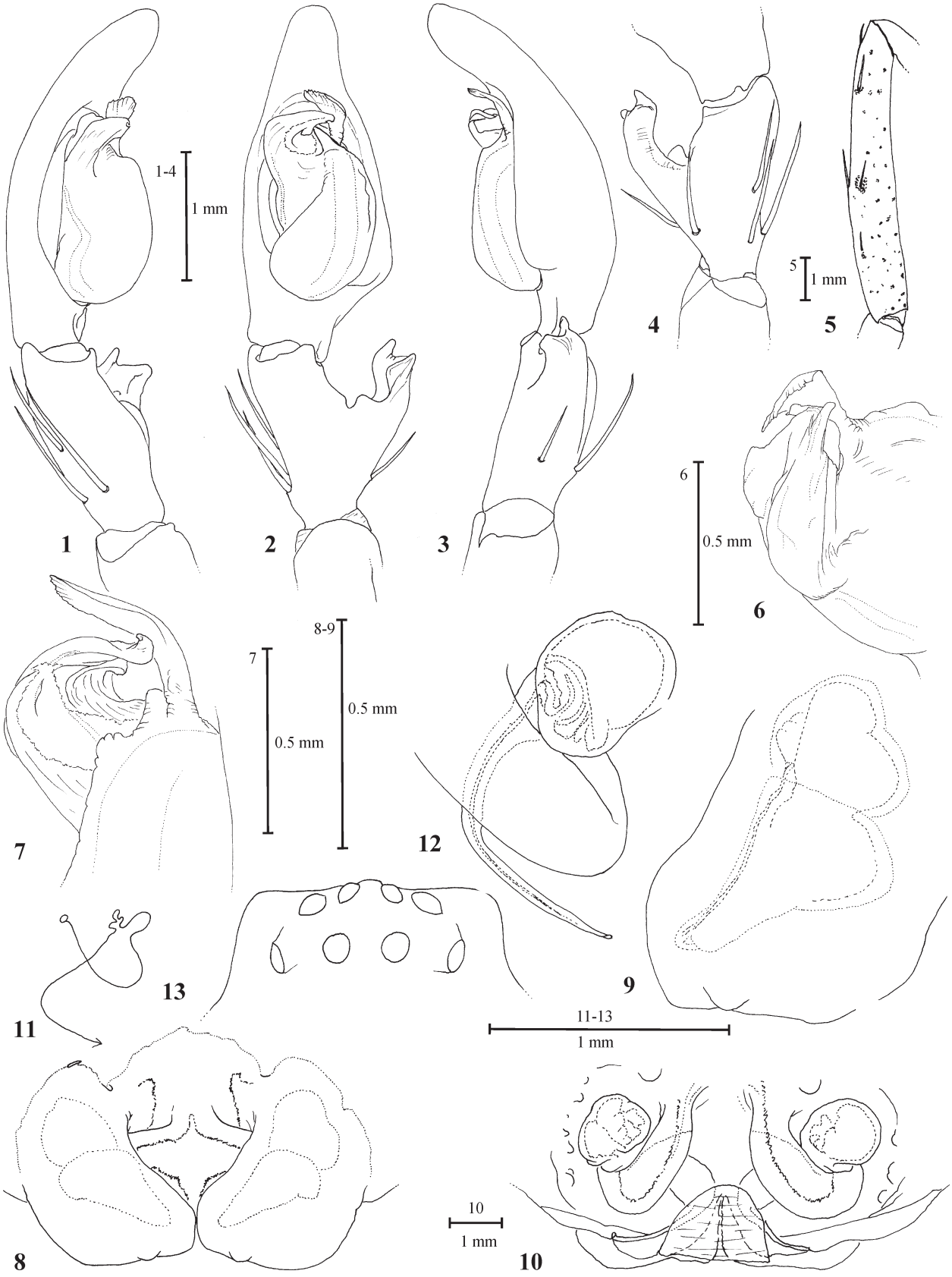
Description

Measurements ♂ (data of holotype first, those of paratype in parentheses): Prosoma length 5.0 (6.0), prosoma width 5.1 (5.3), anterior width of prosoma 2.8 (2.9), height of dorsal shield of prosoma 2.3 (2.8), opisthosoma length 6.3 (7.6), opisthosoma width 4.1 (5.3). Eye diameters: AME 0.23 (0.28), ALE 0.36 (0.38), PME 0.30 (0.31), PLE 0.35 (0.38). Eye interdistances: AME–AME 0.22 (0.25), AME–ALE 0.06 (0.07), PME–PME 0.33 (0.34), PME–PLE 0.37 (0.42), AME–PME 0.32 (0.35), ALE–PLE 0.30 (0.31). Clypeus height at AME 0.27 (0.31), clypeus height at ALE 0.29 (0.30). Leg formula: 2143. Spination pattern: Palp 131, 101, 2101; femur I–III 323, IV 331; patella 101; tibia I–II 2226, III–IV 2126; metatarsus I–II 1014, III 2024, IV 3036. Measurements of palp and legs: Palp 8.2 (8.1) [2.6, 1.1, 1.6, –, 2.9 (2.6, 1.2, 1.5, –, 2.8)], I 29.9 (31.3) [8.0, 2.9, 8.9, 7.6, 2.5 (8.4, 3.2, 9.2, 7.8, 2.7)], II 32.1 (31.6) [8.7, 3.0, 9.6, 8.1, 2.7 (8.5, 3.0, 9.5, 8.0, 2.6)], III 25.1 (24.9) [7.8, 2.3, 7.0, 5.8, 2.2 (7.1, 2.5, 7.0, 6.2, 2.1)], IV 27.5 (27.9) [8.0, 2.4, 7.5, 7.5, 2.1 (8.1, 2.6, 7.4, 7.6, 2.1)].

Palp as in diagnosis. Embolus arising from a 10-o'clock-position on the tegulum. Sperm duct running retrolaterally almost straight and parallel to the tegular margin. RTA arising basally to medially from tibia (Figs. 1–4).

Colour (in ethanol): Yellowish brown with short dark hairs. Dorsal shield of prosoma with fovea and radial bands darker. Sternum, coxae and labium without pattern. Legs with dark spine patches and small spots. Additional white spots, consisting of white hairs, at the insertion points of spines. White band running dorsally from the patella to the tarsus of leg IV (both white patterns only scarcely visible in ethanol). Dorsal opisthosoma with irregular pattern; posterior half with two longitudinal parallel dark bands and two small white round patches (the latter almost invisible in ethanol). Ventral opisthosoma with irregular pattern, two crescent patches in front of epigastric furrow and irregular patch in front of spinnerets. For colouration of living specimens see Figs. 29–30.

Measurements ♀: Prosoma length 5.3, prosoma width 5.2, anterior width of prosoma 3.0, height of dorsal



Figs. 1–13. *Pseudopoda confusa* sp. n. — Figs. 1–7: ♂ holotype; 1 left palp, prolateral view; 2 left palp, ventral view; 3 left palp, retrolateral view; 4 left palp, tibia, dorsal view; 5 femur I, lateral view; 6 embolus, prolateral view; 7 embolus, retrolateral view. — Figs. 8–13: ♀ paratype; 8 epigyne, ventral view; 9 epigyne, left half, ventral view; 10 vulva cleared, dorsal view; 11 schematic course of female internal duct system, dorsal view; 12 vulva, lateral view; 13 eye arrangement, dorsal view.

shield of prosoma 2.7, opisthosoma length 6.0, opisthosoma width 3.6. Eye diameters: AME 0.31, ALE 0.38, PME 0.30, PLE 0.36. Eye interdistances: AME–AME 0.21, AME–ALE 0.06, PME–PME 0.33, PME–PLE 0.45, AME–PME 0.33, ALE–PLE 0.33. Clypeus height at AME 0.34, clypeus height at ALE 0.31. Leg formula: 2143. Spination pattern: Palp 131, 101, 2121, 1014; femur I–III 323, IV 331; patella 101; tibia 2126; metatarsus I–II 1014, III 2024, IV 3036. Measurements of palp and legs: Palp 7.6 (2.1, 1.2, 1.7, –, 2.6), I 25.7 (7.0, 3.1, 7.4, 6.1, 2.1), II 26.7 (7.5, 3.0, 7.6, 6.5, 2.1), III 21.3 (6.1, 2.3, 6.6, 4.6, 1.7), IV 23.0 (6.9, 2.2, 6.1, 6.0, 1.8).

Epigyne as in diagnosis. Epigynal field wider than long, anterior bands absent. Lateral lobes touching each other at the median line (Fig. 8).

Colour (in ethanol): Same colour and pattern as in ♂, but dorsal shield of prosoma with more dark hairs, i.e. appearing darker. Dorsal opisthosoma in posterior half darker and with large sub-triangular bright white patch. For colouration of living specimen see Figs. 31–32.

Variation: The white pattern situated on the posterior part of the dorsal opisthosoma of the male paratype is represented by three patches, of which the median is sub-triangular and the laterals are roundish (Fig. 30). The three specimens indicate that the shape and size of this patch varies considerably within the species.

Distribution: Northern Laos: Luang Nam Tha Province: Luang Nam Tha district, Muang Sing district.

Pseudopoda gemina sp. n.

(Figs. 14–19, 33–34)

Holotype ♀: (PJ 2212), Laos, Vientiane Province, Vang Vieng district, Ban Phoxay, 260 m, 19°0.731' N, 102°26.766' E, collected on leaves, Jäger & Vedel leg., 17. xi. 2004, SD 187, found as immature, bred to maturity in laboratory, adult iii. 2005, in SMF. — No paratypes.

Etymology: The specific name is a Latin adjective – geminus, -a, -um – meaning twin referring to the unusual double anterior bands of the epigynal field.

Diagnosis: Medium-sized spiders. The species may be recognized by the following combination of characters:

♀: 1. Anterior and median margins of epigynal lateral lobes forming a broad "T" (Fig. 14), which is wider than in *Pseudopoda recta* Jäger & Ono 2001 (Jäger & Ono 2001: fig. 17). 2. Lateral lobes sub-rectangular (Fig. 14). 3. Internal duct system with posterior sub-rectangular indentations in dorsal view (Fig. 15; indentations in *Pseudopoda recta* rounded, larger and visible only in anterior view).

Description

Measurements ♀: Prosoma length 6.5, prosoma width 6.1, anterior width of prosoma 3.7, height of dorsal shield of prosoma 2.2, opisthosoma length 7.3, opisthosoma width 4.0. Eye diameters: AME 0.30, ALE 0.45, PME 0.31, PLE 0.42. Eye interdistances: AME–AME 0.25, AME–ALE 0.09, PME–PME 0.40, PME–PLE 0.52, AME–PME 0.45, ALE–PLE 0.42. Clypeus height at AME 0.47, clypeus height at ALE 0.40. Leg formula: 2143. Spination pattern: Palp 131, 101, 2121, 1014; femur I–III 323, IV 321; patella 101; tibia 2126; metatarsus I–II 1014, III 2024, IV 3036. Measurements of palp and legs: Palp 9.5 (2.7, 1.5, 2.1, –, 3.2), I 29.7 (8.2, 3.4, 8.8, 7.3, 2.0), II 31.3 (8.7, 3.7, 9.1, 7.5, 2.3), III 23.9 (7.5, 2.8, 6.5, 5.3, 1.8), IV 26.7 (8.1, 2.7, 7.0, 6.7, 2.2).

Epigyne as in diagnosis. Epigynal field wider than long, with two anterior lobes laterally; anterior bands short. Anterior margins of lateral lobes straight, median margins in contact along their whole length (Fig. 14).

Colour (in ethanol): Reddish brown to yellowish brown. Dorsal shield of prosoma with fovea slightly darker. Sternum, coxae and labium brighter yellowish brown, without pattern. Legs dorsally reddish brown and ventrally yellowish brown (esp. femora). Femora, especially, with small spots, these being obscure in some parts. White patches situated at the insertion points of spines (almost invisible in ethanol). Opisthosoma without specific pattern except for two pairs of dark muscle sigillae. Ventral opisthosoma with dark patch in front of spinnerets. For colour of living specimen, see Figs. 33–34.

Male: unknown.

Distribution: Only known from the type locality.

Pseudopoda namkhan sp. n.

(Figs. 20–28, 35–40)

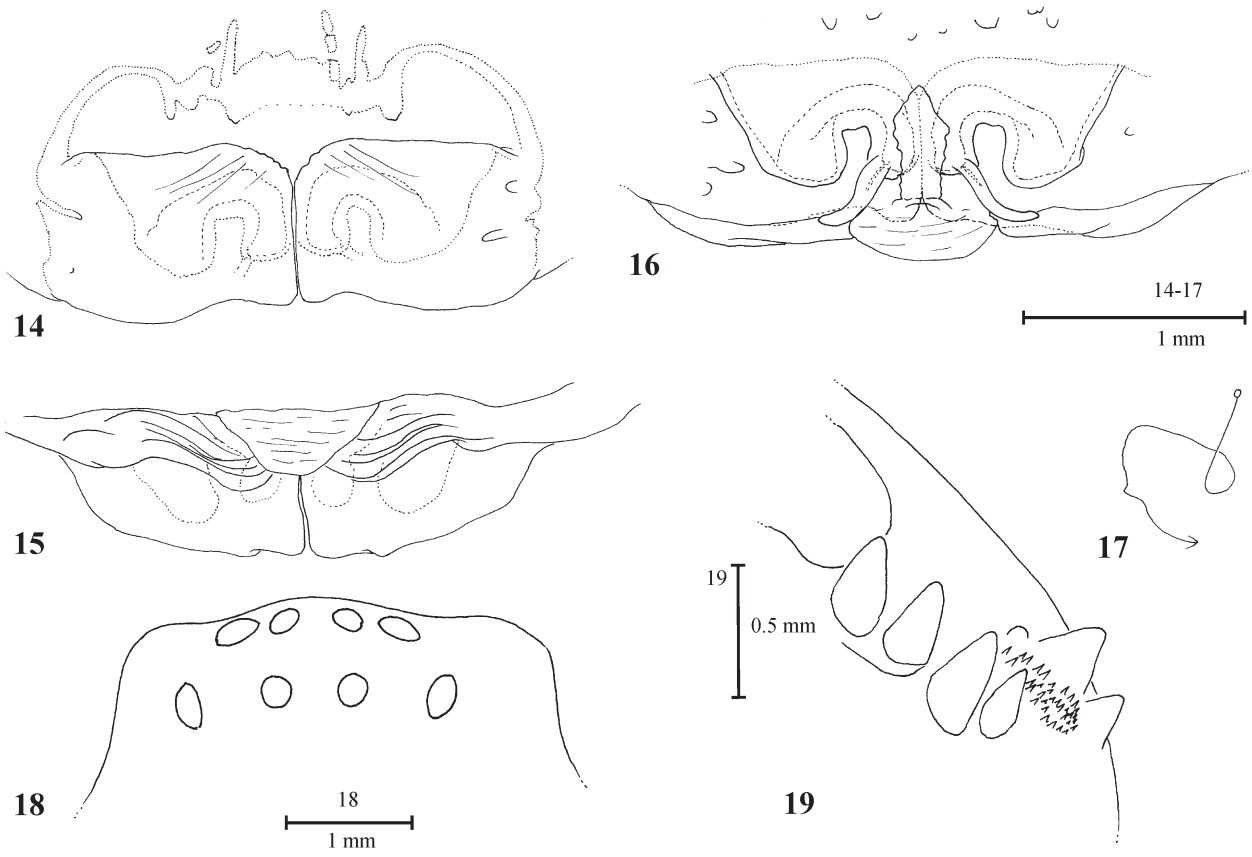
Holotype ♂: (PJ 2471), Laos, Luang Prabang Province, SE Luang Prabang, Nam Khan, Ban Keng Koung, 19°40.963' N, 102°18.442' E, 372 m, along stream, disturbed forest, cultivated land, at night, collected by hand, Jäger & Altmann leg., 8. iii. 2006, in SMF.

Paratypes (5 ♀♀): 1 ♀ (PJ 2480), same data as holotype. 1 ♀ (PJ 2478), same data as holotype except for SD 531. 1 ♀ (PJ 2473), same data as holotype except for 7. iii. 2006, SD 525. 1 ♀ (PJ 2474), same data as holotype except for 7. iii. 2006. 1 ♀ (PJ 2472), Laos, Luang Prabang Province, S Luang Prabang, Nam Khan, Ban Ean, That Se, 19°50.562' N, 102°13.118' E, 304 m, waterfall, along stream, secondary forest, at night, collected by hand, Jäger & Altmann leg., 5. iii. 2006, SD 524. — All in SMF.

Etymology: The specific name refers to the type locality, the Nam Khan river valley, in the Southeast of Luang Prabang; noun in apposition.

Diagnosis: Medium-sized spiders. The species may be recognized by the following combination of characters:

♂: 1. Tip of embolus sickle-shaped, at its base various teeth and one prolate cavity (Figs. 21, 24). 2. RTA with large and broad dorsal part (Figs. 22–23).



Figs. 14–19. *Pseudopoda gemina* sp. n., ♀ holotype. 14 epigyne, ventral view; 15 epigyne, posterior view; 16 vulva cleared, dorsal view; 17 schematic course of female internal duct system, dorsal view; 18 eye arrangement, dorsal view; 19 chelicera, ventral view.

♀: 1. Median and anterior margins of lateral lobes forming a short 'T' (Fig. 25). 2. Internal duct system with loops close to median line (Figs. 25) similar to those in *P. signata* Jäger 2001 or *P. prompta* (O. P. Cambridge 1885), but anterior margins of lateral lobes of the latter two species running latero-anteriorad (Jäger 2001: figs. 22a, 29h). 3. Functionally last part of fertilisation ducts broad and strongly sclerotised.

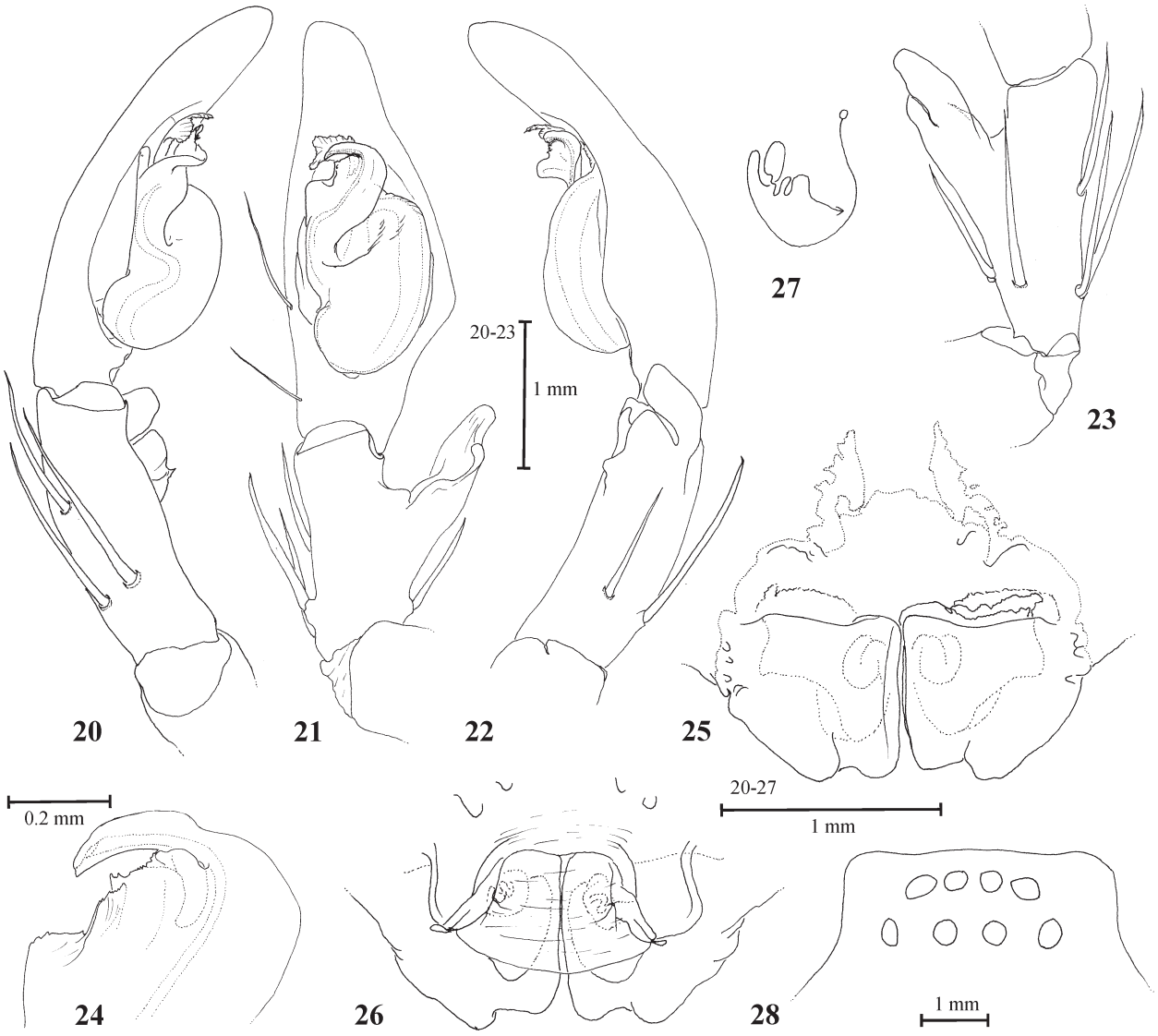
Description

Measurements ♂ (holotype): Prosoma length 6.9, prosoma width 6.1, anterior width of prosoma 3.1, opisthosoma length 6.0, opisthosoma width 3.4. Eye diameters: AME 0.36, ALE 0.46, PME 0.35, PLE 0.43. Eye interdistances: AME–AME 0.17, AME–ALE 0.06, PME–PME 0.29, PME–PLE 0.44, AME–PME 0.40, ALE–PLE 0.35. Clypeus height at AME 0.60, clypeus height at ALE 0.53. Leg formula: 2143. Spination pattern: Palp 131, 101, 2111; femur I–III 323, IV 322; patella 101; tibia I 2226, II 22(1)26, III 2226, IV 2126; metatarsus I 1(2)014, II 1014, III 2(1)024, IV 3036. Measurements of palp and legs: Palp 9.7 (3.2, 1.5, 2.0, –, 3.0), I 35.2 (9.2, 3.6, 10.1, 9.3, 3.0), II 37.7 (10.2, 3.7, 11.1, 9.7, 3.0), III 28.0 (8.3, 2.9, 7.9, 6.9, 2.0), IV 31.2 (9.5, 2.7, 8.5, 8.9, 2.6).

Palp as in diagnosis. Embolus broad and flat, arising from a 9.30-o'clock-position on the tegulum. Sperm duct running retrolaterally almost straight and parallel to the tegular margin, prolaterally distinctly s-shaped. RTA arising basally to medially from tibia, its dorsal and ventral part large in retrolateral view (Figs. 20–24).

Colour (in ethanol): Yellowish brown. Dorsal shield of prosoma with median part darker and irregular, slightly brighter lateral bands. Sternum, coxae and labium bright yellowish brown, without pattern. Legs with dark spine patches and small spots only indistinct. Additional small white spots, consisting of white hairs, at the insertion points of spines. White line running dorsally on tibia and two third of metatarsus of leg IV (white patterns only scarcely visible in ethanol). Dorsal and ventral opisthosoma with irregular pattern; posterior half with white patch. For colouration of specimen see Figs. 35–37 (i.e. more reddish brown).

Measurements ♀ (based on all paratypes): Prosoma length 6.5–8.2, prosoma width 6.1–7.1, anterior width of prosoma 3.5–4.0, opisthosoma length 7.6–11.3, opisthosoma width 5.2–7.2. Eye diameters (PJ 2480):



Figs. 20–28. *Pseudopoda namkhan* sp. n. — Figs. 20–24: ♂ holotype; 20 left palp, prolateral view; 21 left palp, ventral view; 22 left palp, retrolateral view; 23 left palp, tibia, dorsal view; 24 embolus, ventral view. — Figs. 25–28: ♀ paratype; 25 epigyne, ventral view; 26 vulva cleared, dorsal view; 27 schematic course of female internal duct system, dorsal view; 28 eye arrangement, dorsal view.

AME 0.36, ALE 0.50, PME 0.37, PLE 0.45. Eye interdistances: AME–AME 0.25, AME–ALE 0.10, PME–PME 0.39, PME–PLE 0.52, AME–PME 0.45, ALE–PLE 0.39. Clypeus height at AME 0.70, clypeus height at ALE 0.67. Leg formula: 2143. Spination pattern: Palp 131, 101, 2121, 1014; femur I–III 323, IV 321; patella 101; tibia I 22(1)26, II 2226, III–IV 2126; metatarsus I–II 1014, III 2024, IV 3036. Measurements of palp and legs: Palp 11.2 (3.2, 1.8, 2.5, –, 3.7), I 34.4 (9.6, 4.1, 9.7, 8.5, 2.5), II 36.1 (10.2, 4.2, 10.3, 8.7, 2.7), III 28.0 (8.6, 3.2, 7.8, 6.3, 2.1), IV 30.7 (9.6, 3.1, 7.7., 8.0, 2.3). Palpal claw with 5–6 teeth.

Epigyne as in diagnosis. Epigynal field slightly wider than long, its anterior bands pointed and with irregular margins. Lateral lobes with a number of small pits at their lateral sides and with a posterior hump on each side (Fig. 25).

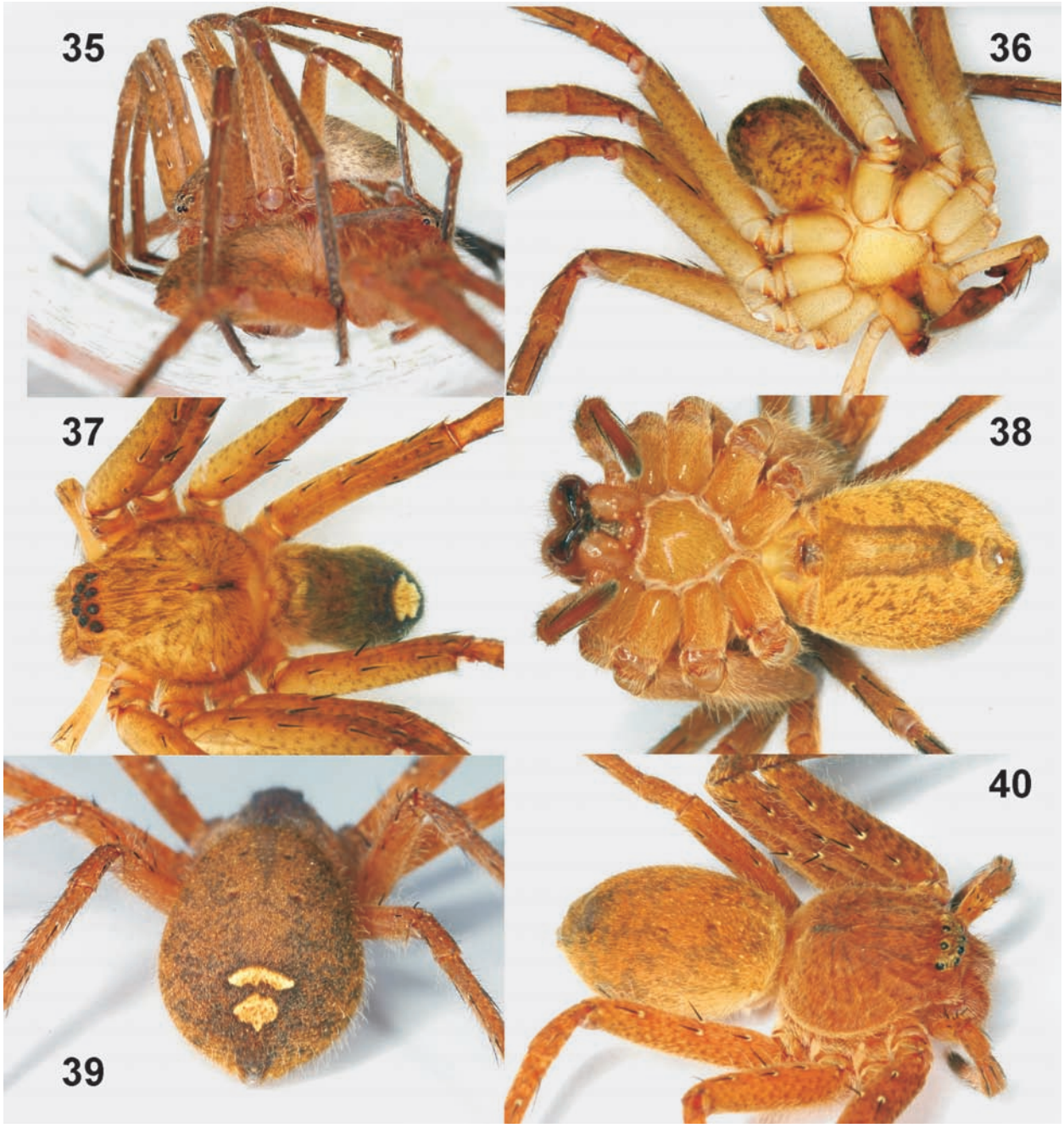
Colour (in ethanol): Same colour and pattern as in male. For colouration of living specimens see Figs. 38–40 (i.e. more reddish brown).

Variation: The white pattern situated on the posterior part of the dorsal opisthosoma varies considerably within the species (Figs. 37, 39–40).

Distribution: Luang Prabang Province: Nam Khan river valley, S to SE Luang Prabang: Ban Keng Koung, Ban Ean (That Se).

Biology: Spiders of this new species were found at night in a small valley close to a stream, sitting on leafs in a distance of about 30–150 cm above the ground and ambushing for prey. In Ban Keng Koung all specimens

Figs. 29–32. *Pseudopoda confusa* sp. n. 29 ♂ holotype, dorsal view; 30 ♂ paratype, opisthosoma, dorsal view, showing tripartite white patch and white lines on leg IV; 31 ♀ paratype, opisthosoma, dorsal view, showing subtriangular white patch; 32 ♀ paratype, ventral view, showing ventral pattern of opisthosoma. — Figs. 33–34. *Pseudopoda gemina* sp. n., ♀ holotype. 33 frontodorsal view, showing pattern of legs with dark spots and white spine patches; 34 ventral view, showing ventral pattern of opisthosoma.



Figs. 35–40. *Pseudopoda namkhan* sp. n. 35 ♂ holotype and female paratype (PJ 2480) in copula, lateral view; 36–37 ♂ holotype (36 ventral view, 37 dorsal view, showing pattern of prosoma and white patch on opisthosoma); 38–40 ♀ paratypes (38, 40 PJ 2472, 39 PJ 2478; 38 ventral view, showing ventral pattern of opisthosoma, 39 opisthosoma, caudal view, showing two white patches; 40 dorsal view.

were collected from small plants growing on the forest floor, one specimen from That Se was sitting on an overhanging branch of a bigger tree. Therefore it cannot be exluded that this species inhabits also higher strata.

The mating behaviour and subsequent copulation could be observed in the laboratory: after a short period of mating the male jumped onto the female's body in a reverse direction (Fig. 35) and remained there, chewing and cleaning its palps. The ♀ showed no activity except for walking around sometime. The ♂ inserted its palps alternating (left palp on right side of ♀ opisthosoma, right palp on right side). One insertion took one to 3 minutes with spines erect only in the time immediately before the palp was removed.

Discussion

According to the morphology of copulatory organs (for details see JÄGER 2001, 2002, JÄGER & ONO 2001) *P. confusa* sp. n. belongs to the *diversipunctata* species-group, which, up to now, was comprised of five species: *Pseudopoda diversipunctata* JÄGER 2001 from Nepal, *P. intermedia* JÄGER 2001 and *P. lutea* (THORELL 1895) both from Myanmar, *P. marsupia* (WANG 1991) from Thailand and China (Yunnan Prov.) and *P. serrata* JÄGER & ONO 2001 from Taiwan. The special appendage on the distal embolus present in both *P. diversipunctata* and *P. marsupia*, a character which grouped both species closely together within this species-group, is missing in *P. confusa* sp. n.

The striking white line present on legs IV of *Pseudopoda confusa* sp. n. can be used for species identification only in combination with other characters. Indeed, several specimens from Sichuan Province (China) belonging to the same genus but to different species exhibit the same feature (JÄGER, unpubl.).

The record of the new species fits in the geographical range so far known for this species-group, i.e. in the more southern part of the distribution range of *Pseudopoda*. The altitudinal distribution of the species-group (1000–2700 m; JÄGER 2001: fig. 74) is extended to considerably lower elevations by the records from northern Laos (580–750 m).

P. gemina sp. n. can be grouped with *P. recta* from Taiwan, by virtue of the rectangular-shaped lateral lobes of the female epigyne (JÄGER & ONO 2001). ♂♂ of both species are unknown, but they are necessary before making statements on their systematic position within the genus. The holotype of *P. gemina* sp. n. was found at an altitude of 260 m. So far *P. virgata* (FOX 1936) represented the record with the lowest proven altitude (300 m from Sichuan Prov., China) for the whole genus.

The third species described here, *P. namkhan* sp. n., cannot clearly be grouped within the genus. The flat and broad embolus and the derived state of the internal duct system as well as the special occurrence of the lateral lobes (JÄGER 2001: figs. 82–83) let them appear as close relatives to representatives of the *martensi* JÄGER 2001 or *latembola* JÄGER 2001 species-group, known from Nepal, Myanmar and China. The altitude at which the specimens of *P. namkhan* sp. n. were collected is distinctly lower than that found in the latter two species-groups.

Mating and copulatory behaviour of *P. namkhan* sp. n. is similar to that of other family members (*Micrommata virescens* (CLERCK 1757), *Holconia immanis* (L. KOCH 1867), *Heteropoda venatoria* (LINNAEUS 1767), *Heteropoda tetrica* THORELL 1897) (JÄGER unpubl.). Common behavioural traits within the Sparassidae are: ♂ jumps onto the female's body, ♀ carries ♂ around, ♂ inserts its palps alternating. Only length of insertion periods for one palp varies considerably: from one minute or so in *Heteropoda* or *Micrommata* up to 11 hours in *Holconia*. Further, detailed analyses should give descriptions on mating modules, involved body parts and a precise time scheme of copulations.

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