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Source: *Revue suisse de Zoologie*, 131(2) : 319-355

Published By: Muséum d'histoire naturelle, Genève

URL: <https://doi.org/10.35929/RSZ.0128>

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## The genus *Titanidiops* in South-east Asia (Arachnida: Araneae: Idiopidae)

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**Abstract:** Five *Titanidiops* species are described: *T. birmanicus* Schwendinger & Huber, sp. nov. (♂♀) and *T. tenuis* Schwendinger, sp. nov. (♂♀) from Myanmar, *T. sayamensis* Schwendinger & Hongpadharakiree, sp. nov. (♂♀) from Thailand and Myanmar, *T. inermis* Schwendinger, sp. nov. (♂♀) from Thailand, *T. insularis* Schwendinger, sp. nov. (♂♀) from Thailand and Indonesia. A key to the seven *Titanidiops* species known from South-east Asia is provided. *Titanidiops inermis* sp. nov. stands out among its congeners: the males lack a mating clasper, and the females have tiny spicules on coxae I-II and an enlarged heel on the retrolateral-distal corner of coxa IV. A close relationship between *T. inermis* sp. nov. and *T. pylorus* comb. nov. is inferred. Ten species are transferred to *Titanidiops*: *Idiops bombayensis* Siliwal, Molur & Biswas, 2005, *I. bonny* Siliwal, Hippargi, Yadav & Kumar, 2020, *I. crassus* Simon, 1884, *I. joida* Gupta, Das & Siliwal in Gupta *et al.*, 2013, *I. medini* Pratihari & Das in Pratihari *et al.*, 2020, *I. nilagiri* Das & Diksha in Das *et al.*, 2019, *I. oriya* Siliwal in Gupta *et al.*, 2013, *I. pylorus* Schwendinger, 1991, *I. robustus* (Pocock, 1898), *I. vankhede* Siliwal, Hippargi, Yadav & Kumar, 2020. All other Asian species currently under *Idiops* Perty, 1833 presumably also belong to *Titanidiops* Simon, 1903. New localities of *T. pylorus* comb. nov. in Thailand are reported, and the widely disjunct populations of *T. insularis* sp. nov. are discussed. For most species treated here information on biology and on morphological variation is provided.

**Keywords:** Mygalomorphae - trapdoor spiders - morphology - variation - biology - burrow plugs.

## INTRODUCTION

To date only six species of idiopid spiders were reported from South-east Asia: *Idiops crassus* Simon, 1884 from central Myanmar and *I. pylorus* Schwendinger, 1991 from Thailand, both in the subfamily Idiopinae and both here formally transferred to the genus *Titanidiops*. The former species and several others, but surprisingly not *I. pylorus* even though a male and a female paratype were made available, were informally transferred to *Titanidiops* in the comprehensive but unpublished Ph. D. thesis of Flávio U. Yamamoto (2013: 14, 24, 36, 177, 252). The other South-east Asian idiopids are four species in the genus *Prothemenops* Schwendinger, 1991 which occur in Thailand and whose subfamily placement is still unclear; they either belong to the Genysinae (distributed in South Asia, Madagascar and the Neotropics) or to the Arbanitinae (distributed in Australia and New Zealand). For the rest of Asia the idiopid diversity is much higher:

seven species of *Heligmomerus* Simon, 1892 (Idiopinae) occur in India and one in Sri Lanka; fourteen *Idiops* species (Idiopinae) are known from India, one from Pakistan and one from Yemen (all of which presumably belong to *Titanidiops*); two *Titanidiops* species (Idiopinae) are currently known from India; three species of *Scalidognathus* Karsch, 1892 (Genysinae) are recorded for India and another three for Sri Lanka. Only one of the South-east Asian idiopids (*Idiops crassus*) is known from one sex (the female); for the other ten species (including the five new ones presented here) males and females are known. That ratio is quite different for the other thirty-three Asian species: nine are known from both sexes, eight from males only, fourteen from females only, and even one (*Heligmomerus taprobanicus* Simon, 1892) only from a juvenile (World Spider Catalog, 2024). More sampling in Asia is badly needed.

The current study shows that the diversity of Idiopidae in South-east Asia is still poorly known and lags behind that

Manuscript accepted 16.07.2024

DOI: 10.35929/RSZ.0128

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of the Indian Subcontinent, but the geographical range of these obscure and rarely collected spiders extends much further to the south-east than previously known (Fig. 1).

## MATERIAL AND METHODS

**Methods:** Morphological characters were studied, drawn and photographed with a Zeiss SV11 stereomicroscope with a video camera attached. Most photos were stacked with the Automontage©System. All body parts, including copulatory organs, were studied and photographed under 75% ethanol. Gland tissue surrounding the cuticular parts of vulvae was removed by dipping them in cold KOH for about a minute (which makes tissue temporarily transparent) and then tearing most of the tissue (small pieces usually remain) off with an insect pin. Longer exposure of vulvae to chemical solutions often results in the collapse of their receptacular heads. The ventral cuticle of the genital area was cut off with micro-scissors to allow unimpeded view of the vulva. Body measurements are all in millimetres (for other measurements the units are given) and were taken on the dorsal side, between midpoint of anterior and posterior margins. Total body length includes the chelicerae but not the spinnerets. Carapace length was measured with the carapace in a slightly forward-inclined position so that its anterior and posterior margins were at the same focal plane. Eye diameter (especially for AME) refers to the diameter of the cornea and not just to the diameter of the white central area of the eye. Tarsus length was measured from the base of the claws to the proximal margin of the article. Tibia I width of males was measured behind (proximal of) the mating clasper. Leg and palp measurements are given in the following manner: total length (femur + patella + tibia + metatarsus + tarsus). The leg formula is given from the shortest to the longest leg. Counts taken from both sides of the body (e.g., left and right tibia I) are separated by a forward slash whereas fractions are spelled out (e.g., four-fifths instead of 4/5). Terminology of morphological characters generally follows that used in Raven (1985) and Fonseca-Ferreira *et al.* (2021). What we here call “a mating clasper” is called “paired clasping spurs”, “a compound spur of two processes”, “a tibial spur with two hooked processes”, “a double tibial apophysis” etc. by other authors; in Schwendinger (1991) it is called “a twin coupling spur”. We here call the two sperm-storing organs in the vulva “receptacles”, each with its own opening to the genital atrium and separate from the other, and each composed of a basal “stalk” and an apical “head” (Fig. 3H). Short spiniform bristles (in males usually not or only slightly thicker than nearby normal, long bristles) on labium and palpal coxae are here called “spinules” instead of “cuspules” because their apices are pointed instead of blunt or domed. In the paragraph “Variation” only taxonomic characters considered to be relevant are mentioned. Hairs and weak

bristles are not shown in most line drawings of the mating clasper complex of males (except for *T. tenuis* sp. nov.). The locality map (Fig. 1) was created with simplemapp (www.simplemapp.net).

**Museum acronyms:** MHNG - Muséum d'histoire naturelle de Genève, Switzerland; MNHN - Muséum national d'Histoire naturelle, Paris, France; NHML - Natural History Museum, London, UK (formerly British Museum of Natural History); SMF - Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt a. M., Germany; THNHM - Thailand Natural History Museum, Pathumthani, Thailand.

**Other abbreviations used in the text:** ALE - anterior lateral eyes; AME - anterior median eyes; d - dorsal; Distr. - district; MOQ - median ocular quadrangle; p - prolateral; PLE - posterior lateral eyes; PLS - posterior lateral spinnerets; PME - posterior median eyes; PMS - posterior median spinnerets; Prov. - province; r - retrolateral; v - ventral; W.F. - waterfall.

## TAXONOMY

### Family Idiopinae Simon, 1889

### Subfamily Idiopinae Simon, 1889

### Genus *Titanidiops* Simon, 1903

**Type species:** *Idiops compactus* Gerstaecker, 1873, described from the female holotype from “Dafeta” (today called “Taveta”), a town in Kenya, at the border with Tanzania, not from the Zanzibar Archipelago as could be misunderstood from the original publication. Gerstaecker (1873: V-VI, 485) placed the type locality in the “Sansibar-Gebiet (= Zanzibar Region)”, a name then applied to an area that includes the Zanzibar islands and parts of mainland eastern Africa.

**Species included:** In addition to the nine species currently listed under *Titanidiops* (see World Spider Catalog, 2024) we here transfer the following ten species from *Idiops* (see also Discussion): *Titanidiops bombayensis* (Siliwal, Molur & Biswas, 2005) comb. nov.; *T. bonny* (Siliwal, Hippargi, Yadav & Kumar, 2020) comb. nov.; *T. crassus* (Simon, 1884) comb. nov.; *T. joida* (Gupta, Das & Siliwal in Gupta *et al.*, 2013) comb. nov.; *T. medini* (Pratihari & Das in Pratihari *et al.*, 2020) comb. nov.; *T. nilagiri* (Das & Diksha in Das *et al.*, 2019) comb. nov.; *T. oriya* (Siliwal in Gupta *et al.*, 2013) comb. nov.; *T. pylorus* (Schwendinger, 1991) comb. nov.; *T. robustus* (Pocock, 1898) comb. nov.; *T. vankhede* (Siliwal, Hippargi, Yadav & Kumar, 2020) comb. nov.

**Distribution:** Africa (including the Canary Islands), Near East, India, Myanmar, Thailand, Indonesia (newly reported here).

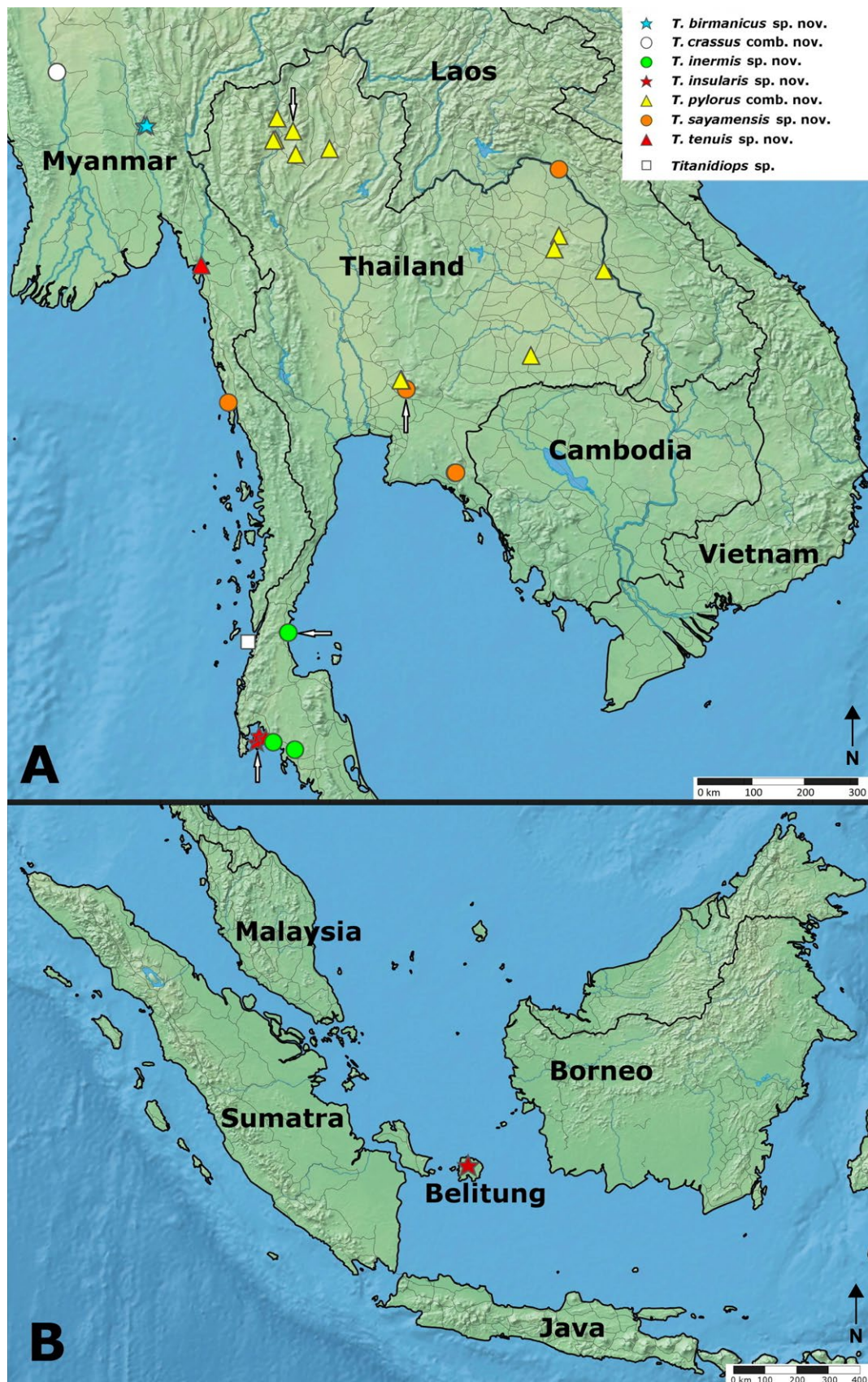


Fig. 1. Localities of *Titanidiops* spp. in South-east Asia. (A) Mainland South-east Asia north of the Thailand-Malaysia border showing most localities. (B) Western part of the Malay Archipelago showing the occurrence of a fourth population of *T. insularis* sp. nov. on Belitung Island in Indonesia. Arrows indicate type localities of species with disjunct populations.



**Diagnosis:** *Titanidiops* is distinguished from the other idiopine genera by possessing a normally developed, membranous opisthosoma (carrying a strongly sclerotized posterior plate in *Galeosoma* Purcell, 1903), a cylindrical tibia III (saddle-shaped, i.e. dorsally concave, in *Heligmomerus*), only two pairs of sternal sigilla (three pairs in *Segregara* Tucker, 1917 and *Gorgyrella* Purcell, 1902), two well developed rows of strong teeth on margins of cheliceral groove [according to Raven (1985: 138) only one row (i.e. the promarginal one) present in *Ctenolophus* Purcell, 1904 (known from

South Africa); according to Dippenaar-Schoeman *et al.* (2021: 5, fig. F) no teeth or only a few small proximal denticles on retromargin in *Ctenolophus*], retromargin of cheliceral groove with a long row of large teeth (see, e.g., Fig. 7C; one or several small denticles, arranged in a row or randomly, confined to the proximal third of the retromargin in *Idiops*, see Fig. 2A, Fonseca-Ferreira *et al.*, 2021: 7, fig. 5, there “prolateral” inadvertently given for “retrolateral” and vice versa).

### Key to the *Titanidiops* species of South-east Asia:

- 1 Males (unknown for *T. crassus* comb. nov.) ..... 2
- Females ..... 7
- 2(1) Mating clasper absent from tibia I (Figs 3A, 12N-T); carapace smooth (Fig. 12A-B); femora of legs and palps dorsally with a longitudinal row of spines; paired tarsal claws with a row of 3-7 denticles; subdistal embolic notch absent (Fig. 12H-M); epiandric spigots spiniform (Fig. 12E) ..... *T. inermis* sp. nov. (Thailand)
- Mating clasper present; carapace smooth or warty; at least palpal femora dorsally without spines; paired claws with a row of 4-6 denticles or with only one large and one small denticle; subdistal embolic notch present or absent; epiandric spigots normally developed ..... 3
- 3(2) Carapace smooth (Fig. 4A-B); leg femora with dorsal spines, palpal femur with long strong bristles instead; paired claws with a row of 4-6 denticles; palpal tibia strongly incrassate (Fig. 4D-E); wart-like tubercle absent from mating clasper complex (Fig. 3B); embolus without subdistal notch or tooth (Fig. 4F) ..... *T. pylorus* comb. nov. (Thailand)
- Carapace covered with wart-like hair bases (Figs 6A, C, 8A, 10A-B, 14A, 15A); all femora without dorsal spines; paired claws with one large denticle and often also with one (rarely two) small denticle(s); palpal tibia moderately incrassate (Figs 6F-G, 8C-D, 10D-E, 14C-D, 15F-G); wart-like tubercle present in mating clasper complex (Fig. 3C-G); embolus with subdistal notch and tooth (Figs 6D-E, 8E-F, 10F-H, 14E-F, 15H-I) ..... 4
- 4(3) Prodorsal-distal process present in tibia I mating clasper complex (Figs 3E-G, 6H, 14H-J, 15B-D) ..... 5
- Prodorsal-distal process absent from tibia I mating clasper complex (Fig. 3C-D) ..... 6
- 5(4) Prodorsal-distal process on tibia I relatively large (Figs 3G, 6H); megaspine of distal mating spur narrow (Figs 3G, 6H) ..... *T. birmanicus* sp. nov. (Myanmar)
- Prodorsal-distal process on tibia I relatively small (Figs 3E-F, 14H-J, 15B-D); megaspine of distal mating spur wide (Figs 3E-F, 14H, 15B) ..... *T. insularis* sp. nov. (Thailand, Indonesia)
- 6(4) Megaspine of distal mating spur directed laterad (Figs 3D, 10M-N); wart-like tubercle of mating clasper complex with a shiny black cap (Figs 3D, 10L-O); hair bases on tibiae only slightly enlarged (Fig. 10I-O) ..... *T. sayamensis* sp. nov. (Thailand, Myanmar)
- Megaspine of distal mating spur directed distad (Figs 3C, 8H); wart-like tubercle of mating clasper complex without a shiny black cap (Figs 3C, 8H-J); hair bases on tibiae distinctly enlarged, wart-like (Figs 3C, 8H-J) ..... *T. tenuis* sp. nov. (Myanmar)
- 7(1) Coxa IV with retrolateral-distal corner enlarged to a distinct heel (Fig. 13C); coxae I-II ventrally with wide bands of spinules (Fig. 13D-E); receptacles widely separated from each other (Fig. 13F-P) ..... *T. inermis* sp. nov. (Thailand)
- Coxa IV with normal retrolateral-distal corner (Figs 7D, 9C, 11C, 16C); coxae I-II ventrally without spinules (Figs 5B, 7B, 9B, 11B, 16B); receptacles widely separated or close to each other ..... 8
- 8(7) Receptacles widely separated from each other (Fig. 5E-O) ..... *T. pylorus* comb. nov. (Thailand)
- Receptacles close to each other (Figs 7F-P, 9D-N, 11F-O, 16E-M, 17) ..... 9
- 9(8) Receptacular head much wider than receptacular stalk (Fig. 3H) ..... *T. crassus* comb. nov. (Myanmar)
- Receptacular head only slightly wider than receptacular stalk (Figs 7F-P, 9D-N, 11F-O, 16E-M, 17) ..... 10
- 10(9) Large-sized spiders (maximum carapace length 11.65) ..... *T. birmanicus* sp. nov. (Myanmar)
- Medium-sized spiders (maximum carapace length 6.70 and 9.21, respectively) ..... *T. insularis* sp. nov. (Thailand, Indonesia) and *T. sayamensis* sp. nov. (Thailand, Myanmar)
- Small spiders (maximum carapace length 5.26) ..... *T. tenuis* sp. nov. (Myanmar)

***Titanidiops crassus* (Simon, 1884) comb. nov.**

Figs 1A, 3H

*Idiops crassus* Simon, 1884: 357-358 (original description of female in Latin).

*Acanthodon crassus* (Simon, 1884): Thorell, 1895: 1-2 (transfer; Latin description of female). – Pocock, 1900: 161-162, fig. 54 (English description and illustration of female).

*Pachyidiops crassus* (Simon, 1884): Simon, 1903: 890 (transfer and listing in French).

*Titanidiops crassus* (Simon, 1884): Yamamoto, 2013: 177-179, fig. 64A-B (informal transfer in unpublished thesis; Portuguese re-description of female holotype and illustration of its vulva).

*Idiops colletti* Pickard-Cambridge, 1889: 37-41, pl. 2, fig. 2a-g (English description and illustration of female).

**Holotype:** MNHN 4189; female (not examined); Myanmar, Magway (= Magwe) Region, Thayet District, Minhla (= Min Hla), 19°58'N, 95°02'E, 50 m; *leg.* J.B. Comotto.

**Remark:** According to the unpublished Ph. D. thesis of Yamamoto (2013: 177) the type specimen is deposited in the MNHN and not in the Museo Civico di Storia Naturale, Genova (Italy) as the title of the original publication (Simon, 1884) indicates.

**Diagnosis:** In the original publication the female holotype is described as a large specimen with 11.5 mm cephalothorax (= carapace) length and 9.6 mm width. The thesis of Yamamoto (2013: 177-179, fig. 64A-B) gives an updated diagnosis and a comprehensive re-description of the holotype (its measurements – carapace length 10.38, width 9.13 – are slightly lower than those given by Simon, 1884), plus illustrations of its vulva in ventral and “frontal” (i.e. anterior) view. The *T. crassus* comb. nov. holotype is roughly of the same size as females of *T. birmanicus* sp. nov. It differs from females of congeneric species examined here by having receptacular heads that are much wider than the corresponding receptacular stalks (Fig. 3H; Yamamoto, 2013: fig. 64A-B).

**Remark:** The fact that the receptacular heads of the holotype are flattened in anterior view is probably an artefact (see, e.g., Fig. 9D-E cf. Fig. 9F-H for *T. tenuis* sp. nov. females) and not a diagnostic character. Receptacular heads often collapse in exuviae, in partly decomposed specimens, or when the vulva is exposed to chemicals for too long [specimens examined by us were cleared by carefully using cold KOH for not longer than one minute, specimens examined by Yamamoto presumably by using Ultrazyme® (Fonseca-Ferreira *et al.*, 2021: 6)].

**Description:** The most recent re-description of the holotype (in Portuguese language) and the first ever illustration of its vulva was given by Yamamoto (2013: 177-179, fig. 64A-B).

**Distribution:** This species is only known from its type locality, south of the town of Magway, west of the Ayeyarwady (= Irrawaddy) River, in the northern part of central Myanmar (Fig. 1A).

***Titanidiops pylorus* (Schwendinger, 1991) comb. nov.**

Figs 1A, 2B-C, 3B, 4-5

*Idiops pylorus* Schwendinger, 1991: 235-239, figs 13, 15, 17-18, 20 (description of males and females in English). – Schwendinger, 1996: 578 (listing). – World Spider Catalog, 2024 (listing).

**Holotype:** MHNG-ARTO-24380; male; Thailand, Chiang Mai Prov., Doi Saket Distr., near Ban Pong Kum, 18°55'N, 99°14'E, 450 m; 9.III.1987; *leg.* P.J. Schwendinger.

**Paratypes:** MHNG-ARTO-24379, MHNG-ARTO-24378; 1 male, 1 female; same locality as for holotype; 9.III.1987, 17.V.1987. – NHML; 1 female; Thailand, Chiang Mai Prov. & Distr., Mae Hia Nai, 18°46'N, 98°55'E, 380 m; 7.III.1986. – MHNG-ARTO-24376, MHNG-ARTO-24377; 2 females; Thailand, Chiang Mai Prov., Mae Taeng Distr., north of Mae Taeng, 19°09'N, 98°57'E, 450 m; 21.I.1987. – NHML; 1 male; Thailand, Tak Prov., Lan Sang, 16°47'N, 99°01'E, 180 m; 25.VII.1987. All *leg.* P.J. Schwendinger.

**New material:** MHNG-ARTO-29051, sample TA-13/10; 1 female; Thailand, Chiang Mai Prov. & Distr., near Ban Pong, 18°45'N, 98°53'E, 300 m; 18.XII.2013. – MHNG-ARTO-29052, sample TH-06/21; 1 female; Thailand, Chiang Mai Prov., Doi Saket Distr., near Ban Pong Kum, 18°55'N, 99°14'E, 460 m (the type locality); 29.XII.2006. – MHNG-ARTO-29053-29054, THNHM; 2 males (both hatched VII.1988, one matured 25.V.1992, the other 25.VI.1992), 1 female; Thailand, Chiang Mai Prov., Mae Taeng Distr., north of Mae Taeng, 19°09'N, 98°57'E, 450 m; 21.I.1987. – MHNG-ARTO-29055; 1 female; Thailand, Lamphun Prov., Mae Tha Distr., Doi Kunthan, 18°30'N, 99°17'E, 950 m; 9.X.1992. – THNHM; 1 male (collected mature); Thailand, Lampang Prov., Ngao Distr., Tham Pa Tai, 18°36'N, 99°53'E, 360 m; 24.VI.2001; *leg.* S. Sonthichai. – MHNG-ARTO-29056-29057; 2 males (one collected mature, the other matured 8.V.1996); Thailand, Sakon Nakhon Prov., Kutbak Distr., Phu Phan, 17°03'N, 103°58'E and 16°49'N, 103°53'E, 280 m and 500 m; 24.XI.1992, 8.XII.1995. – MHNG-ARTO-29058-29059; 1 male (matured 14.VII.1995), 1 female; Thailand, Mukdahan Prov. & Distr., Phu Pha Thoeb, 16°26'N, 104°46'E, 350 m; 7.XII.1994. – MHNG-ARTO-29060-29061, sample TA-13/08; 1 male (matured 26.VIII.2014), 1 female; Thailand, Surin Prov. & Distr., near Ramkhamhaeng University Campus, 14°55'N, 103°28'E, 150 m; 12.XII.2013. – MHNG-

ARTO-29062, sample TH-11/19; 1 female; Thailand, Saraburi Prov., Kaeng Khoi Distr., near Jedkhod Nuea W.F., 14°29'N, 101°10'E, 280 m; 21.XII.2011. – MHNG-ARTO-29063, sample TH-11/20; 1 female; Thailand, Saraburi Prov., Kaeng Khoi Distr., near Sabpawan Reservoir, 14°29'N, 101°09'E, 310 m; 21.XII.2011. All specimens *leg.* P.J. Schwendinger unless otherwise stated.

**Extended diagnosis:** This is a relatively small species. Its males are distinguished from those of known congeneric species in South-east Asia (the male of *T. crassus* comb. nov. is unknown), except for *T. inermis* sp. nov. which uniquely lacks a mating clasper, by having an essentially smooth carapace with only few indistinct wart-like hair bases in its anterior part (Fig. 4A-B), by having a row of dorsal spines on leg femora

(these less pronounced than in males of *T. inermis* sp. nov. which also have such spines on the palpal femur) and by possessing a row of 4-6 denticles on the paired tarsal claws. Males also lack a wart-like tubercle (see Discussion) in the mating clasper complex (Fig. 3B). Tibia I of males is not incrassate (it is as wide as patella I); the palpal tibia is more strongly incrassate, especially in the median zone (Fig. 4D-E), than in other species treated here (see, e.g., Fig. 6F-G). The embolus apex is spatulate (Fig. 4F), without a notch or tooth. The pseudoscapula (composed of distally bent scopulate hairs with a terminal pore which presumably allows perception of female pheromones; see Foelix *et al.*, 2010: 602, figs 11-13) is very weak in the distal half of leg I, denser in the distal four-fifths of tarsus II and on the entire ventral surface of tarsi III-IV. Females are

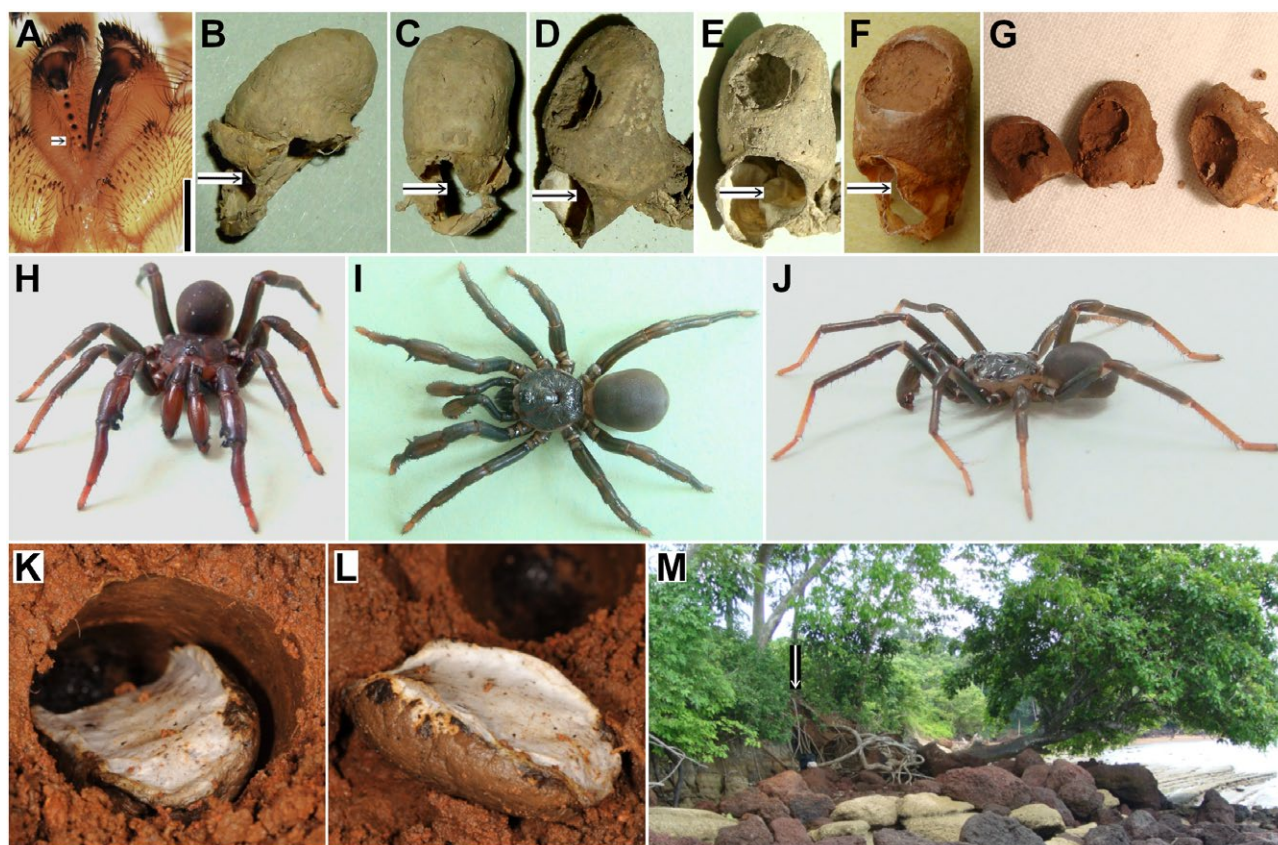


Fig. 2. *Idiops* sp. from Colombia (A), *Titanidiops pylorus* comb. nov. (B-C), *T. inermis* sp. nov. (D-G, J, M), *T. birmanicus* sp. nov. (H, K-L), *T. sayamensis* sp. nov. (I). (A) Chelicerae, labium and palpal coxae of penultimate male, ventral view; short black arrow indicates short proximal row of small teeth on retromargin of cheliceral groove. (B) Soil pellet moulded by spiders and used for burrow plugging, lateral view; long black arrows indicate passage between bottom of soil pellet and attached dense silk lining of burrow wall through which the spider moves; from Surin. (C) Same, frontal view. (D) Soil pellet, lateral view; from Ban Bang Nam Jued. (E) Same, frontal view; from same locality. (F) Same, frontal view; from Ban Laem Pho. (G) Soil pellets from three different burrows at Ban Bang Nam Jued. (H) Habitus of male holotype, frontal view. (I) Habitus of male paratype MHNG-ARTO-28967 from Salika W.F., dorsal view. (J) Habitus of male paratype MHNG-ARTO-29019 from Ban Bang Nam Jued, lateral view. (K) Egg case at bottom of excavated spider burrow. (L) Same, egg case extracted, lying in front of excavated burrow. (M) Unusual habitat on sea shore near Ban Laem Pho; long white arrow indicates place where a burrow was found. Scale line 1.0 mm (A); soil plugs 0.9-1.1 cm long; for lengths of spiders see descriptions.

most similar to those of *T. inermis* sp. nov. by having vulvae with widely separated receptacles (Fig. 5E-O; see also Fig. 13F-P for *T. inermis* sp. nov.), but they differ by the absence of spinules on the ventral side of leg coxae I-II and by the absence of an enlarged retrolateral-distal heel on coxa IV. Macro-spigots are usually (see Variation) present on the PMS and on the proximal article of the PLS of both sexes (Fig. 5C-D) whereas in other species treated here (Figs 7E, 11D-E), except for *T. inermis* sp. nov., macro-spigots are usually absent from these parts.

**Variation:** Carapace lengths of males (n = 9) range 4.00-5.13, carapace widths 3.41-4.45; the largest

female (from Phu Pha Thoeb) has a 5.78 long and 4.81 wide carapace. One of two males from Phu Phan has a straight metatarsus on its right leg I and an abnormally bent metatarsus on its left leg I (Fig. 4I) whereas in the second male from the same locality both metatarsi I display a distinct prolateral knee (Fig. 4H) similar to the metatarsal knees in the holotype (Fig. 4G) and other conspecific males. In the male from Phu Pha Thoeb both metatarsi I have a less pronounced knee than the holotype. All males examined have a row of dorsal spines on all leg femora (these are less conspicuous than in males of *T. inermis* sp. nov.) whereas on the palpal femur they have a dorsal row of long, strong bristles instead. The thin pseudoscapula on tarsus I of males

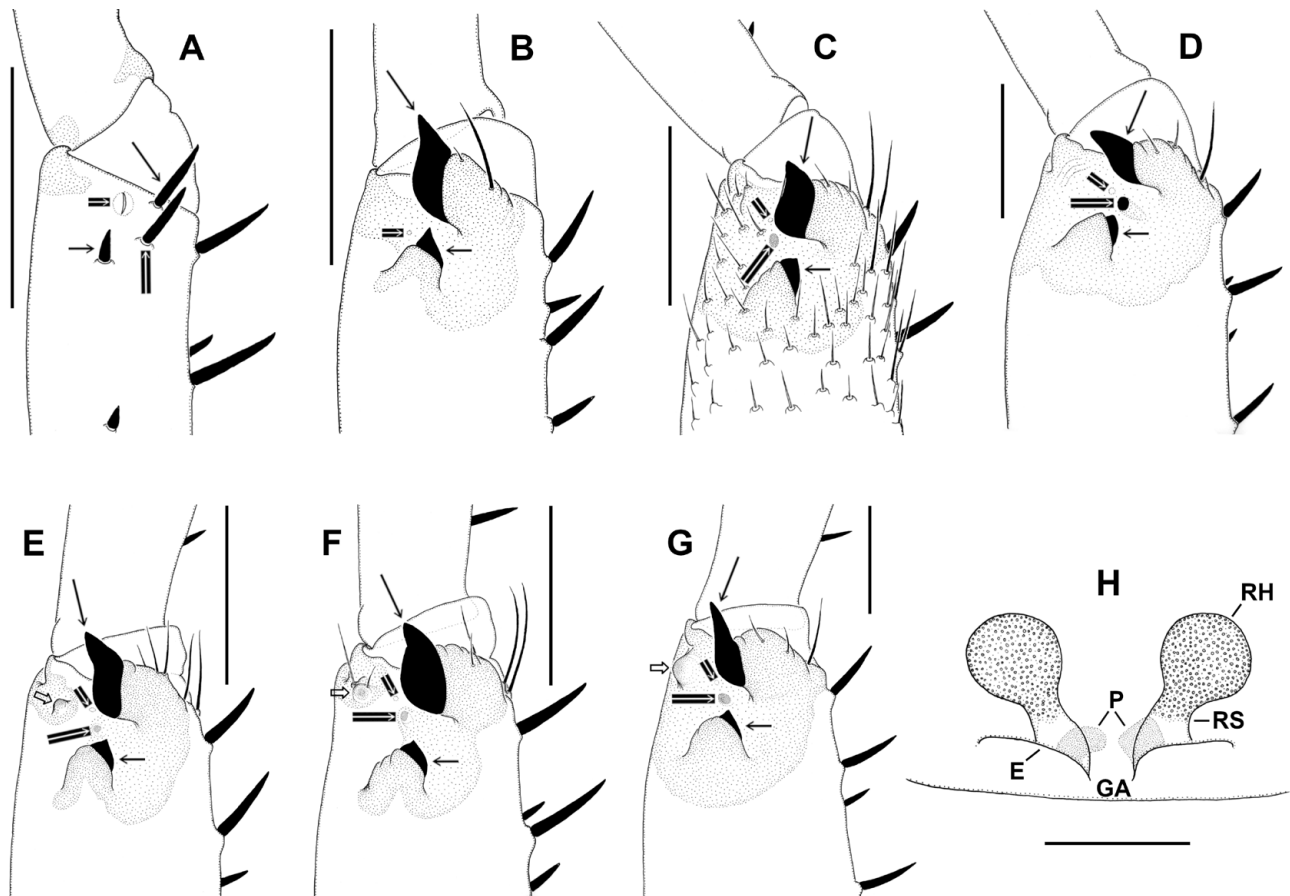


Fig. 3. *Titanidiops* spp.; mirrored drawing of distal part of right tibia I showing spines homologous with components of mating clasper complex, prolateral view (A); drawings of distal part of left tibia I showing mating clasper complex, prolateral view (B-G); drawing of vulva, ventral view (H; re-drawn from Yamamoto, 2013: fig. 64A with permission). (A) *Titanidiops inermis* sp. nov., male holotype. (B) *Titanidiops pylorus* comb. nov., male holotype. (C) *Titanidiops tenuis* sp. nov., male holotype. (D) *Titanidiops sayamenis* sp. nov., male holotype. (E) *Titanidiops insularis* sp. nov., male holotype. (F) *Titanidiops insularis* sp. nov., male MHNG-ARTO-29037 from Belitung Island. (G) *Titanidiops birmanicus* sp. nov., male holotype. (H) *Titanidiops crassus* comb. nov., female holotype. Long black arrows indicate distal spur and megaspine of mating clasper (B-G) and homologous unmodified spine (A); short black arrows indicate subdistal spur and megaspine of mating clasper (B-G) and homologous unmodified spine (A); long white arrows indicate wart-like tubercle (B-G) and homologous unmodified spine (A); short white arrows indicate well-developed slit organ (A) and homologous rudimentary slit organ (B-G); hollow arrows indicate prodorsal-distal process. Abbreviations: E - entrance to receptacle, GA - genital atrium, P - pigmentation, RH - receptacular head, RS - receptacular stalk. Scale lines 1.0 mm (for H as given by Yamamoto, 2013, but more likely corresponding to 0.5 mm).



extends over the distal third to distal half of the article; no relevant variation was found in the expanse of the pseudoscopula of other leg tarsi. Females possess 1-4 strong labial spinules, some of them additionally 1-2 smaller ones; all males lack labial spinules. In most males the AME are slightly or distinctly larger than the PLE (the largest of the remaining eyes; Fig. 4A-B); only in one of two males from Phu Phan (the aberrant one with straight and abnormally bent metatarsi I) AME and PLE are of the same size. In all females examined the AME are slightly smaller than the PLE (Fig. 5A). See also Discussion. Females (males between parentheses) have 1-4 (0-2) macro-spigots on the proximal article of their PLS, 6-11 (2-9) on the median article, 1-2 (0-2) on the distal article; the PMS carry 0-3 (0-2) macro-

spigots. Variation in vulva morphology is shown in Fig. 5G-O.

**Distribution:** This species is widely distributed in northern, north-eastern and central Thailand (Fig. 1A).

**Biology:** *Burrow structure:* The remarkable defence mechanism of this species, which employs a soil pellet (Fig. 2B-C) to plug its burrow, was described and illustrated by Schwendinger (1988: 233-234, fig. 1; 1991: 238, figs 21-23). It was then unique among South-east Asian mygalomorphs, but subsequently very similar burrow plugging devices have been found in Thailand, not only in a congeneric species (in *T. inermis* sp. nov.; Fig. 2D-G), but also in a species belonging to the distantly related family Bemmeridae (i.e. *Damarchus*

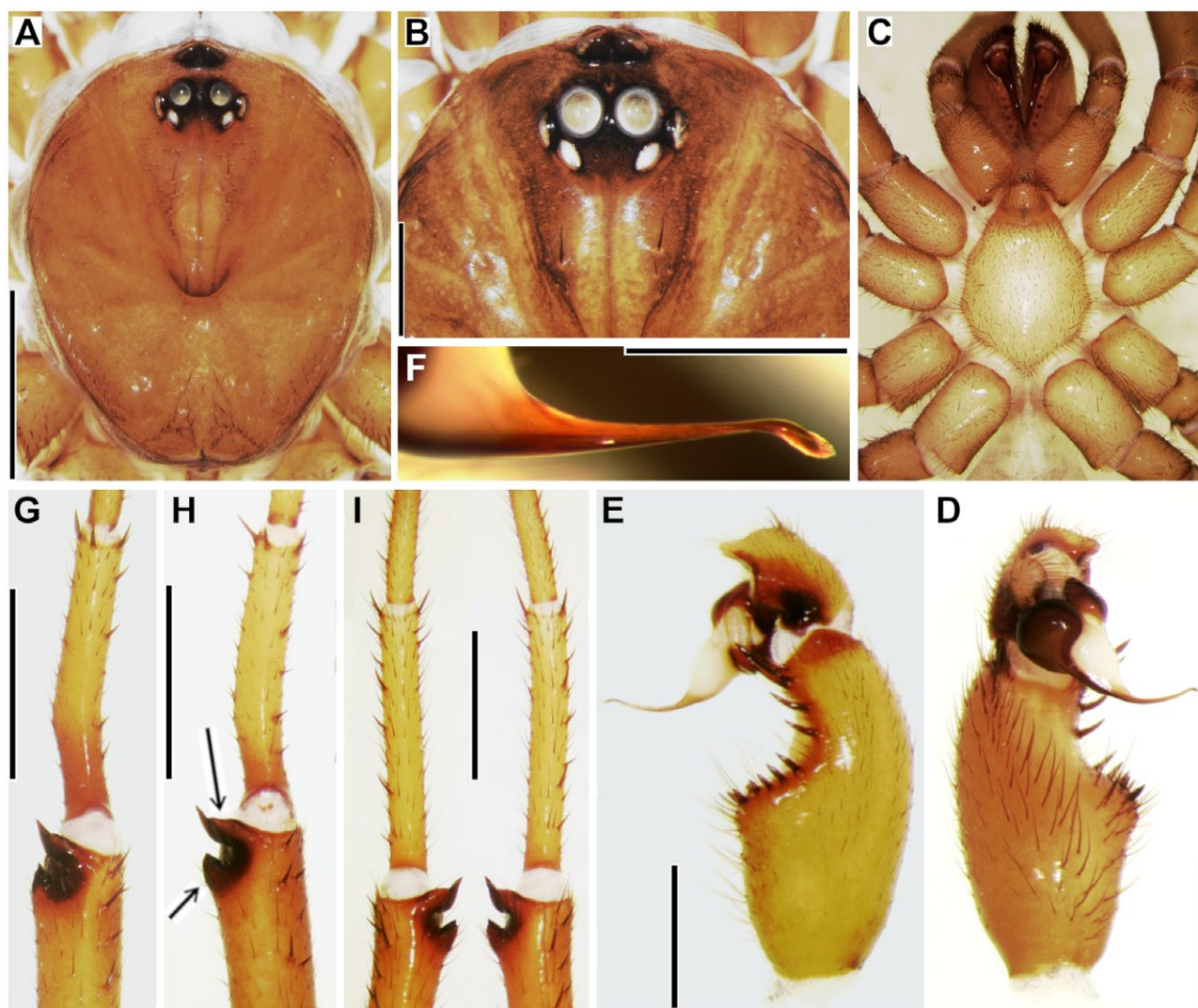


Fig. 4. *Titanidiops pylorus* comb. nov., males; holotype (A, C-G), specimen MHNG-ARTO-29060 from Surin (B), specimen MHNG-ARTO-29057 from Phu Phan showing normally modified metatarsus I (H), aberrant specimen MHNG-ARTO-29056 from Phu Phan showing unmodified right metatarsus I and abnormally modified left metatarsus I (I). (A) Carapace, dorsal view. (B) Anterior part of carapace, dorsal view. (C) Prosoma, ventral view. (D) Distal part of left palp, ventral view. (E) Same, retrolateral view. (F) Apex of left embolus, ventral view. (G-H) Entire metatarsus and distal part of tibia of left leg I, ventral view. (I) Same of left and right leg I, ventral view. Scale lines: 0.5 mm (F), 1.0 mm (B, D-E), 2.0 mm (A, C, G-I).



*pylorus* Schwendinger & Hongpadharakiree, 2023; see Schwendinger & Hongpadharakiree, 2023: 488-489, figs 5A-B, 6). All burrows of *T. pylorus* comb. nov. were equipped with a soil pellet that has a smooth frontal surface (Fig. 2B-C) whereas soil pellets of *T. inermis* sp. nov. have a pronounced circular depression in the frontal surface (Fig. 2D-G). In most soil pellets of *T. pylorus* comb. nov. the dorsal surface (apex) is slightly invaginated (see Schwendinger, 1991: fig. 23)

whereas in soil pellets of male MHNG-ARTO-29056 from Phu Phan and in female MHNG-ARTO-29061 from Surin there is no recognizable invagination (Fig. 2C).

**Phenology:** Males ( $n = 9$ ) matured in captivity between May and November (most of them in June). The late November date is a unique outlier. In captivity it took males almost four years from hatching to maturity. For further information see Schwendinger (1991: 238-239).

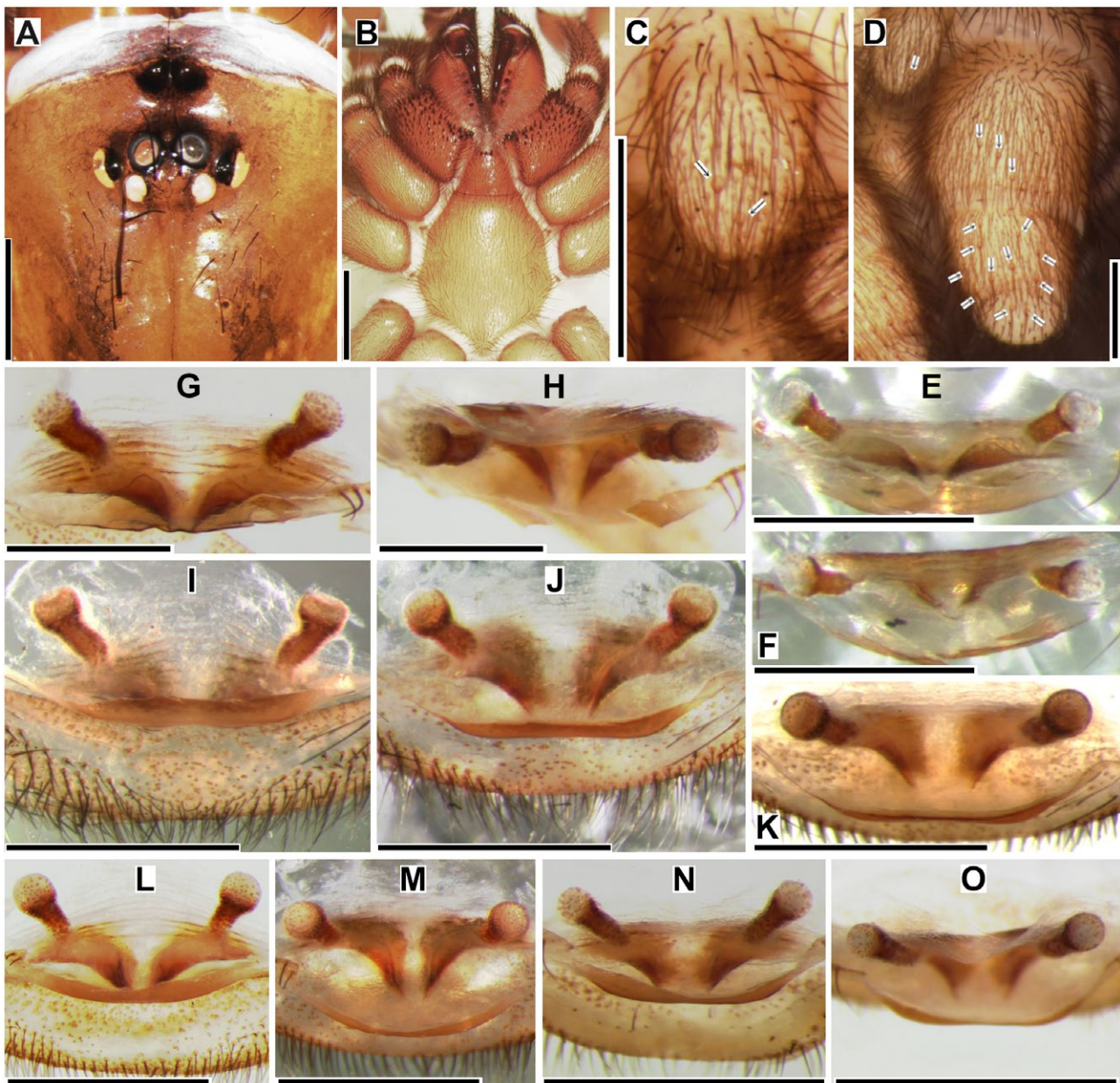


Fig. 5. *Titanidiops pylorus* comb. nov., females; specimen MHNG-ARTO-29061 from Surin (A, I-K), paratype MHNG-ARTO-24377 (B), specimen MHNG-ARTO-29059 from Phu Pha Thoeb (C-D, L-M), paratype MHNG-ARTO-24378 (E-F), paratype MHNG-ARTO-24376 (G-H), specimen MHNG-ARTO-29063 from Sabpawan (N-O). (A) Anterior part of carapace, dorsal view. (B) Prosoma, ventral view. (C) Right PMS, ventral view. (D) Left PMS and PLS, ventral view. (E, G, J, L, N) Vulva, antero-ventral view. (F, H, K, M, O) Vulva, anterior view. (I) Vulva, ventral view. Arrows indicate macro-spigots. Scale lines: 0.5 mm (C-O), 1.0 mm (A), 2.0 mm (B).

***Titanidiops birmanicus* Schwendinger & Huber,  
sp. nov.**

Figs 1A, 2H, K-L, 3G, 6-7

**Holotype:** MHNG-ARTO-28936, sample MT-14/10; male (matured 17.I.2017); Myanmar, Bago Region, Thandaung Lay (= Pathi Village), 19°01'N, 96°35'E, 140 m; 16.VII.2014; *leg.* P.J. Schwendinger & S. Huber.

**Paratypes:** MHNG-ARTO-28937-28943; 7 females (including allotype MHNG-ARTO-28937); collected together with the holotype. – MHNG-ARTO-28944-28946, sample MT-14/09; 3 females; Myanmar, Kayin State, along road from Thandaung Lay to Thandaung Gyi, 19°01'N, 96°38'E, 760 m; 16.VII.2014; *leg.* P.J. Schwendinger & S. Huber. – MHNG-ARTO-28947, sample MT-14/09; 1 female; same locality, 650 m; 16.VII.2014; *leg.* P.J. Schwendinger & S. Huber.

**Diagnosis:** Similar to *T. crassus* comb. nov., distinguished by much smaller receptacular heads in females (Fig. 7F-P cf. Fig. 3H and Yamamoto, 2013: fig. 64A-B). Different from other species in South-east Asia by the following combination of characters: Large body size. Males with a distinct but not very dense cover of wart-like hair bases on carapace (Fig. 6A; absent in *T. pylorus* comb. nov., Fig. 4A-B, and in *T. inermis* sp. nov., Fig. 12A-B, very dense in *T. tenuis* sp. nov., Fig. 8A); apex of embolus with a pronounced notch and a laterad- to distad-directed tooth (Fig. 6D-E; no embolic tooth or notch in *T. pylorus* comb. nov., Fig. 4F, no notch and less pronounced proximad-directed tooth in *T. inermis* sp. nov., Fig. 12H-M); tibia I of males incrassate (not incrassate in *T. pylorus* comb. nov. and *T. inermis* sp. nov.); a wart-like tubercle present in mating clasper complex (Fig. 3G; absent in *T. pylorus* comb. nov. and *T. inermis* sp. nov., Fig. 3B and Fig. 3A, respectively) and a relatively large conical process dorso-distally to it [Fig. 3G; equally large in the male syntype of *T. constructor* (Pocock, 1900) from India (see Schwendinger, 1991: fig. 16); distinctly smaller in *T. insularis* sp. nov., Fig. 3E-F; absent in *T. inermis* sp. nov., *T. pylorus* comb. nov., *T. tenuis* sp. nov. and *T. sayamensis* sp. nov., Fig. 3A, 3B, 3C and 3D, respectively]; distal spur of mating clasper stout (much weaker in *T. sayamensis* sp. nov.), its megaspine relatively narrow (wider in all other species) and directed distad (Figs 3G, 6H-J; directed dorsad in *T. sayamensis* sp. nov., Figs 3D, 10I-O); metatarsus I of males with a low, very wide prolateral knee (Fig. 6I-J; with a more prominent knee in *T. sayamensis* sp. nov., Fig. 10I-J, no knee in *T. inermis* sp. nov., Fig. 12N). Females with sperm receptacles close to each other, each with a rather narrow entrance from the genital atrium (Fig. 7F-P; more widely spaced and with wider entrances in *T. pylorus* comb. nov., Fig. 5G-O, and in *T. inermis* sp. nov., Fig. 13F-P).

**Description:** MALE (holotype). *Colour in alcohol* (for living spider see Fig. 2H): Carapace reddish brown; area between eyes almost black (Fig. 6A, C). Chelicerae, palps and legs greyish brown; palpal tibia and leg tibia II dorsally slightly lighter than other articles, metatarsus I and distal part of tibia I slightly darker than other articles. Ventral side of prosoma (including limbs) generally lighter than dorsal side. Leg coxae, labium and sternum light brown; palpal coxae dark orange-coloured in prolateral half, lighter in retrolateral half. Opisthosoma dorsally dark greyish brown, with small light speckles mostly in anterior part, ventrally light greyish brown; genital area, booklung covers and spinnerets light orange-coloured.

**Morphology and measurements:** Body 16.40 long. Carapace 6.28 long, 5.99 wide, covered with relatively small and quite widely spaced wart-like hair bases (Fig. 6A, C). Eight eyes on bipartite mound, with a saddle between ALE and main eye group (AME + PME + PLE); entire eye group 1.11 long, 1.32 wide; ALE and AME separated by 0.33. MOQ 0.60 long, 0.79 wide. Eye diameters: AME 0.39, ALE 0.31, PME 0.16, PLE 0.35. Several transversal wrinkles to left and right of anterior half of eye mound. Posterior zone of pars cephalica with a pronounced boss, slightly lower than eye mound in lateral view. Fovea slightly procurved, 1.16 wide, occupying 20% of carapace width at that point. Proximal article of chelicera 2.11 long, fairly strong; ventral groove with six strong teeth on promargin and 6/7 strong teeth (plus a small denticle on one side) on retromargin; fang claw with sharp, straight proventral keel and with serrate retroventral keel; rastellum on long and narrow process, composed of 10-15 short, thick spines and several weaker and more pointed spines. Palpal coxa 2.40 long, 1.40 wide; with about 10 weak spinules (much shorter but not thicker than nearby bristles) in prolateral half. Labium 0.91 long, 0.74 wide, without spinules. Sternum 3.35 long, 3.10 wide; labio-sternal suture distinct but shallow; two pairs of free sigilla distinct, submarginal (Fig. 6B). Palp 10.95 long (3.97 + 2.11 + 3.88 + 0.99). Tibia moderately incrassate, 1.74 wide, retrolaterally with a curved band of 33/35 spines of various lengths in distal half (Fig. 6G). Tarsus short, distally with two short lobes and 1/2 dorso-distal spines. Palpal organ typical for the genus (Fig. 6F-G); apex of embolus with a distinct, laterad- or distad-directed tooth situated proximal to a distinct notch (Fig. 6D-E).

Legs 3214. Leg I 20.83 long (6.45 + 3.39 + 4.38 + 4.79 + 1.82); leg II 17.32 long (5.41 + 2.73 + 3.64 + 3.97 + 1.57); leg III 14.87 long (4.21 + 2.60 + 2.40 + 3.88 + 1.78); leg IV 21.44 long (6.07 + 3.06 + 4.83 + 5.29 + 2.19). Leg tarsi with a light ventral pseudoscopula: in distal half of tarsus I, in distal three-fifth of tarsus II, in distal two-third of tarsus III, developed as a narrow median band in distal three-fourth of tarsus IV. Leg I: metatarsus slightly curved outward, its prolateral side with a low, very wide knee (Fig. 6I-J); tibia distinctly incrassate (2.02



wide; tibia II in comparison only 1.12 wide), carrying a prolateral-distal mating clasper complex composed of: 1) a stout distal spur carrying a relatively narrow, distad-directed megaspine; 2) a smaller subdistal spur carrying a short, wide, pointed megaspine; 3) a wart-like tubercle (without smooth, shiny surface) between both spurs; 4) a relatively large prodorsal-distal process (Figs 3G, 6H; see also Discussion).

Spines: Palp: femur p2 (one long and one short spine distally); patella, 0; tibia r33/35; tarsus d1/2. Leg I: patella, 0; tibia p2 (megaspines), v7/8; metatarsus p4, r8; tarsus p4, r4/7. Leg II: patella, 0; tibia p0/1, v8/11; metatarsus p7/9, v10/12; tarsus p3/4, r6/7. Leg III: patella d2, p7/8; tibia p7/8, r3, v7/9; metatarsus d10/11, v13/14; tarsus p5, r7/8. Leg IV: patella p12/13; tibia v12 (all weak); metatarsus v12 (all weak); tarsus p12/13, r5, v3. Trichobothria in two curved, distally convergent rows in proximal fourth of tibiae; in a broad band in distal half of metatarsi; in a broad band on entire dorsal side of tarsi. Paired leg claws with one large and usually one (rarely two) small proximal denticle; unpaired leg claws bare.

Opisthosoma oval, 7.77 long, 5.87 wide, densely covered with short dark hairs and with few longer interspersed hairs in posterior zone. PMS 0.50 long, without macrospigots; PLS 1.33 long: proximal article 0.75, without macrospigots; median article 0.27, carrying 5/6 macrospigots; distal article 0.31, with one macrospigot.

FEMALE (allotype). *Colour in alcohol* (darker in living spider): Dorsal side of prosoma uniformly dark brown, ventral side slightly lighter. Leg coxae, labium and sternum mostly reddish brown, except for darker labio-sternal suture and sternal sigilla. Opisthosoma dorsally dark greyish brown, with numerous light speckles, ventrally mostly cream-coloured, except for brown genital area and light brown spinnerets.

*Morphology and measurements*: Body 25.45 long. Carapace 8.39 long, 7.36 wide, smooth, with relatively long black hairs and bristles in front of eye mound and postero-medially on it, along lateral carapace margins and between eye mound and fovea; elsewhere hairs very small and scattered, most distinct in posterior zone of pars thoracica. Entire eye group 1.53 long, 1.74 wide;

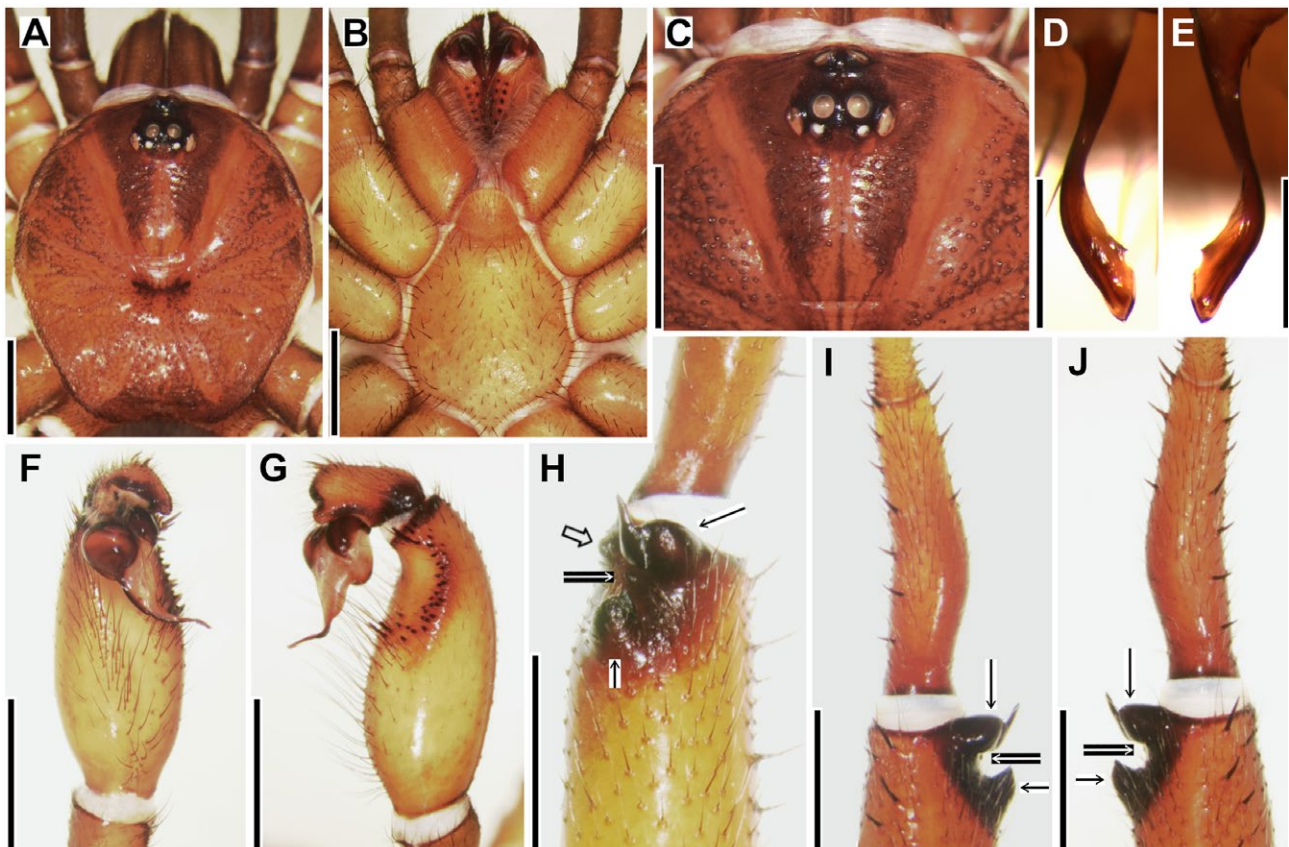


Fig. 6. *Titanidiops birmanicus* sp. nov., male holotype. (A) Prosoma, dorsal view. (B) Prosoma, ventral view. (C) Anterior part of carapace, dorsal view. (D) Apex of right embolus, ventral view. (E) Apex of left embolus, ventral view. (F) Distal part of left palp, ventral view. (G) Same, retrolateral view. (H) Mating clasper complex of left tibia I, prolateral view. (I) Metatarsus and distal part of tibia of right leg I, ventral view. (J) Same of left leg I, ventral view. Long black arrows indicate distal spur and megaspine; short black arrows indicate subdistal spur and megaspine; long white arrows indicate wart-like tubercle; hollow arrow indicates prodorsal-distal process. Scale lines: 0.5 mm (D-E), 2.0 mm (A-C, F-J).



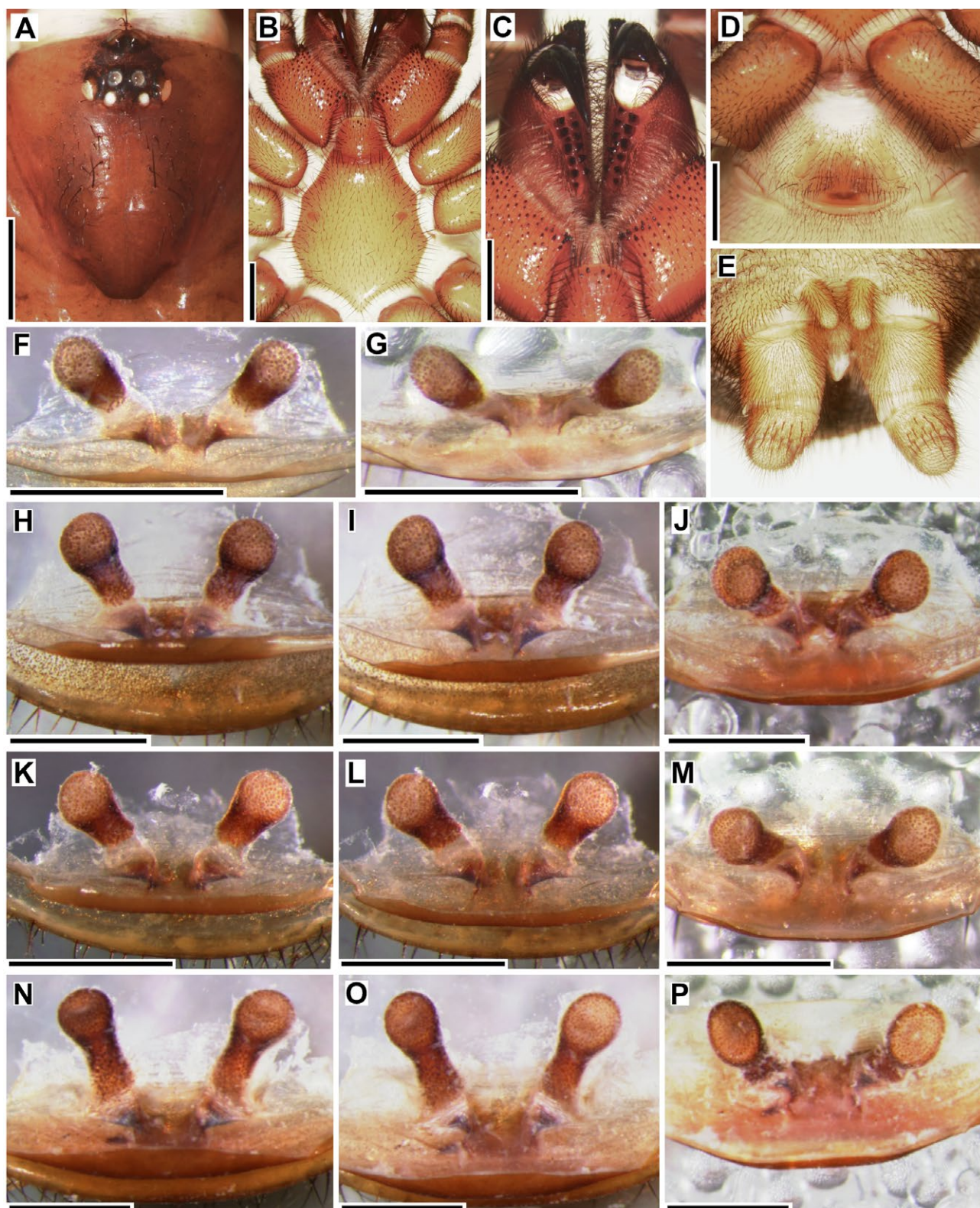


Fig. 7. *Titanidiops birmanicus* sp. nov., females; allotype (A-B, D), paratype MHNG-ARTO-28946 from Thandaung Gyi, 760 m (C, E, N-P), paratype MHNG-ARTO-28943 from Thandaung Lay (F-G), paratype MHNG-ARTO-28938 from Thandaung Lay (H-J), paratype MHNG-ARTO-28947 from Thandaung Gyi, 650 m (K-M). (A) Anterior part of carapace, dorsal view. (B) Prosoma, ventral view. (C) Chelicerae, labium and proximal part of palpal coxae, ventral view. (D) Genital area, ventral view. (E) Spinnerets showing macro-spigots only on medium and distal articles of PLS, ventral view. (H, K, N) Vulva, ventral view. (F, I, L, O) Vulva, antero-ventral view. (G, J, M, P) Vulva, anterior view. Scale lines: 1.0 mm (F-P), 2.0 mm (A-E).

ALE and AME separated by 0.53. MOQ 0.74 long, 0.90 wide. Eye diameters: AME 0.35, ALE 0.39, PME 0.27, PLE 0.43. No wrinkles lateral to eye mound. Posterior zone of pars cephalica with a very prominent boss, clearly higher than eye mound in lateral view. Fovea strongly procurved, with angles between posterior and lateral parts (making it look like a hexagon cut in half; Fig. 7A), 1.44 wide, occupying 21% of carapace width at that point. Proximal article of chelicera 3.31 long, stronger than in male; ventral groove with 6/7 strong teeth on promargin and six strong teeth (plus a small denticle on one side) on retromargin; rastellum on long and narrow process, composed of more than 30 short, thick spines (stronger than in male) and several weaker and more pointed spines. Palpal coxa 3.55 long, 2.36 wide, with about 100 spinules of various sizes (most of them much thicker than nearby bristles) spread over almost entire ventral surface. Labium 1.45 long, 1.65 wide, with six spinules (one of them as thin as nearby setae; Fig. 7C). Sternum 4.88 long, 4.55 wide; labio-sternal suture deeper and sigilla darker than in male (Fig. 7B).

Palp 14.05 long (4.55 + 3.06 + 3.22 + 3.22); tarsus distinctly spindle-shaped; tibia dorsally with a pronounced subdistal pseudosegmentation (see Schwendinger & Hongpadharakiree, 2023: fig. 3J for pseudosegmentation in *Damarchus*).

Legs 2314. Leg I 15.98 long (5.12 + 3.51 + 3.47 + 2.64 + 1.24); leg II 14.54 long (4.63 + 3.14 + 2.81 + 2.56 + 1.40); leg III 14.88 long (4.13 + 3.39 + 2.40 + 3.06 + 1.90); leg IV 20.38 long (5.79 + 4.01 + 4.21 + 4.30 + 2.07). Leg tarsi without pseudoscapula; metatarsus I distinctly, metatarsus II indistinctly spindle-shaped.

Spines: Palp: femur p2 (one long and one short spine distally); patella p1; tibia p26/29, r27/30; tarsus p26/27, r28/29, v3/4. Leg I: patella, 0; tibia p25/31, r35/37; metatarsus p23, r27; tarsus p8/9, r10, v3/4. Leg II: patella, 0; tibia p17/19, r10/15; metatarsus p20/21, r15/17; tarsus p8/10, r5/7, v2/3. Leg III: patella d4, p22/23; tibia p13/14, r12/13, v3/4; metatarsus d26/28, v13/14; tarsus p2, v8/9. Leg IV: patella p37/39; tibia, 0; metatarsus v14; tarsus p4/5, v21/25. A cluster of about 20 spinules dorso-distally on leg tibiae I-II; a cluster of 7/8 spinules at same place on palpal tibia.

Trichobothria mostly as in male; on palpal tarsus arranged as a dorsal band in distal half, but not reaching tip. Paired leg claws with one large and usually one small proximal denticle; unpaired leg claws bare. Palpal claw with one large and 0/1 small denticles.

Opisthosoma oval, 12.81 long, 8.68 wide, long interspersed hairs on dorsal side more numerous than in male. PMS 0.80 long, without macro-spigots; PLS 2.51 long: proximal article 1.24, with 0/1 macro-spigot; median article 0.61, with 11/12 macro-spigots; distal article 0.66, with one macro-spigot.

Vulva (of paratypes; Fig. 7F-P): Receptacles relatively long and relatively close to each other; receptacular heads only moderately wider than receptacular stalks.

**Variation:** The short transversal suture anterior to the fovea of the male holotype (Fig. 6A, C) is an individual deformity, not a species-specific character. Such sutures were also found in several males of other congeners (e.g., in *T. inermis* sp. nov., Fig. 12A versus Fig. 12B). The largest of eleven females examined has an 11.65 mm long and 10.34 wide carapace. This specimen also differs from all other conspecific females by possessing 1/2 macro-spigots on the basal article of the PLS. Two females (including the allotype) have 0/1 macro-spigots there; all other conspecific females lack macro-spigots on the proximal article of the PLS. All specimens have only a single macro-spigot on the distal article of the PLS and lack them on the PMS; on the medium article of the PLS the number of macro-spigots ranges 6-21. The number of spinules on the labium ranges 3-8. In all females, but not in the male holotype, the AME are slightly smaller than the PLE. Leg II is shorter than leg III in all females. Variation in vulva morphology is shown in Fig. 7F-P.

**Distribution:** This species is only known from the type locality and nearby localities east of Toungoo, in central Myanmar (Fig. 1A).

**Biology:** *Habitat:* All spiders were collected from road side banks at the outskirts of a village and from road side banks in an evergreen hill forest.

*Burrow structure:* Burrows were straight and unbranched, without a soil pellet. The male matured (in captivity) in a 3.3 cm long borrow closed by a relatively thick, 1.05 cm long and 1.4 cm wide door. The largest female was extracted from a 10 cm long burrow with a 2.35 cm long and 2.6 cm wide door. All burrows were lined with a dense layer of silk.

*Phenology:* The male holotype matured in captivity in mid-January, about 2.5 years after being captured (thus under unnatural conditions in Europe). When collected in mid-July, four females had egg cases at the bottom of their burrows.

*Egg cases:* These were 2.0-3.15 cm long, 1.4-2.1 cm wide and 1.1-1.3 cm high. Each egg case was shaped like an elongate bowl with its lateral rims slightly turned upward. The lower surface of the egg cases was brownish and plastered with a quite thick layer of soil, its upper surface composed of a tough and relatively thick, white layer of silk devoid of any soil particles (or only with traces of them) (Fig. 2K-L). The egg cases were not suspended at the bottom of the burrow [as are the egg sacs of *T. pylorus* comb. nov. (see Schwendinger, 1991: 238, fig. 24) and many other mygalomorph spiders] and not burrowed under its floor (as in mesothelid spiders), but they were lying on the burrow floor, tightly fitting into the lower half of the cross section of the tube, leaving enough space in the upper half so that the spider can sit on top of the egg case. The four egg cases contained 396, 656, 681 and 795 still pale, bristle- and spineless (second instar) spiderlings.

***Titanidiops tenuis* Schwendinger, sp. nov.**

Figs 1A, 3C, 8-9

**Holotype:** MHNG-ARTO-28948, sample MT-18/06; male (matured 1.V.2013); Myanmar, Mon State, Mottama (= Martaban), near Kyaikkalanbon Pagoda, 16°32'N, 97°36'E, 45-90 m; 18.VI.2012; *leg.* P.J. Schwendinger.

**Paratypes:** MHNG-ARTO-28949-28954, sample MT-18/06; 6 males (matured 6.V.2013; 7.III.2014; 13.III.2014; 14.III.2014; 16.III.2014; 22.III.2014); collected together with the holotype. – MHNG-ARTO-28955-28964; 10 females (including allotype MHNG-ARTO-28955); collected together with the holotype.

**Etymology:** The Latin adjective “tenuis” means “weak, delicate”, referring to the relatively small body size of spiders of this species.

**Diagnosis:** Both sexes are distinguished from those of *T. birmanicus* sp. nov. by their much smaller body size. Males of *T. tenuis* sp. nov. have relatively larger wart-like hair bases on the carapace and on the coxae to the tibiae of legs and palps (Fig. 8A, H-J cf. Fig. 6A, C, H); tibia I is less strongly incrassate; megaspine on distal spur of mating clasper is relatively wider (Figs 3C, 8H cf. Figs 3G, 6H); prolateral knee on metatarsus I is more pronounced (Fig. 8G cf. Fig. 6I-J); no pseudoscopula on tarsus IV. Females of *T. tenuis* sp. nov. are distinguished from those of *T. pylorus* comb. nov. and *T. inermis* sp. nov. by more closely spaced receptacles (Fig. 9D-N cf. Fig. 5E-O, 13F-P).

**Description:** MALE (holotype). *Colour in alcohol* (darker in living spider): Carapace dark reddish brown; area between eyes almost black (Fig. 8A). Dorsal side of chelicerae and legs mostly dark brown, except for slightly lighter coxae, trochanters, tarsi and distal part of metatarsi; palp mostly greyish brown, its tibia dorsally slightly lighter. Ventral side of leg coxae, sternum and labium light brown. Palpal coxa light orange-coloured throughout. Opisthosoma dorsally dark grey, speckled with light spots, with two lighter median patches in anterior half; ventrally mostly light brown, except for cream-coloured genital area and light orange-coloured PLS.

**Morphology and measurements:** Body 10.73 long. Carapace 4.57 long, 4.03 wide, densely covered with relatively large wart-like hair bases (Fig. 8A); the corresponding hairs tiny; only a single strong short bristle on anterior carapace margin, in front of ALE. Eight eyes on bipartite mound, with a saddle between AME and main eye group; entire eye group 0.89 long, 0.86 wide; ALE and AME separated by 0.22. MOQ 0.47 long, 0.58 wide. Eye diameters: AME 0.27, ALE 0.26, PME 0.20, PLE 0.27. Several fine transversal wrinkles to left and right of anterior half of eye mound. Pars

cephalica slightly and evenly arced, its posterior zone without a boss, at same level as eye mound in lateral view. Fovea slightly procurved, 0.88 wide, occupying 23% of carapace width at that point. Proximal article of chelicera 1.64 long; ventral groove with five strong and two weak teeth on pro- and retromargin; fang claw with sharp, straight proventral keel and with serrate retroventral keel; rastellum on long and narrow process, composed of 11/12 short, thick spines and several weaker and more pointed spines. Palpal coxa 1.67 long, 0.90 wide, without recognizable spinules (but several bristles in prolateral half clearly shorter than others). Labium 0.66 long, 0.88 wide, without spinules (but four bristles shorter than others). Sternum 2.46 long, 2.25 wide; labio-sternal suture and two pairs of free sternal sigilla shallow and rather indistinct (Fig. 8B).

Palp 6.90 long (2.41 + 1.31 + 2.19 + 0.99). Tibia moderately incrassate, 1.01 wide, retrolaterally with a curved band of 33/38 spines of various lengths in distal half (Fig. 8D). Tarsus short, distally with two short lobes and one dorsal spine. Palpal organ typical for the genus (Fig. 8C-D); apex of embolus with a distinct, laterad-directed tooth proximal to a shallow notch (Fig. 8E-F).

Legs 3214. Leg I 13.25 long (4.11 + 2.16 + 2.74 + 3.01 + 1.23); leg II 11.44 long (3.59 + 1.81 + 2.27 + 2.57 + 1.20); leg III 9.77 long (2.74 + 1.70 + 1.56 + 2.46 + 1.31); leg IV 13.95 long (3.92 + 2.00 + 3.07 + 3.37 + 1.59). Leg tarsi with a weak ventral pseudoscopula: in distal half of tarsus I, in distal four-fifth of tarsi II-III, essentially none on tarsus IV (only few scopuliform hairs in an irregular median row in distal three-fourths). Leg I: metatarsus with a distinct prolateral knee (Fig. 8G); tibia incrassate (1.26 wide; tibia II in comparison only 0.74 wide), carrying a prolateral-distal mating clasper complex composed of: 1) a stout distal spur carrying a relatively wide, distad-directed megaspine; 2) a smaller subdistal spur carrying a short, wide, pointed megaspine; 3) a wart-like tubercle without smooth, shiny surface between both spurs. No prodorsal-distal process in mating clasper (Figs 3C, 8H). Leg tarsus II slightly spindle-shaped. Relatively large hair bases dorsally on chelicerae, palpal trochanter to tibia, and on trochanters, femora and tibiae, as well as ventrally on all femora and on tibia I of legs (Fig. 8H); hair bases less pronounced dorsally on leg patellae, indistinct on all metatarsi and tarsi.

Spines: Palp: femur p2 (one long and one short spine distally); patella, 0; tibia r33/38; tarsus d1. Leg I: patella, 0; tibia p2 (megaspines) + 1, r8/9; metatarsus p7, r7/8; tarsus p3, r3/4. Leg II: patella, 0; tibia p4, v6/7; metatarsus p6, r5; tarsus p1/2, r2. Leg III: patella d3, p4/6; tibia p5/7, r3/4, v6/7; metatarsus d9, v8/9; tarsus p0/2, r1/2. Leg IV: patella p7/8; tibia v6/7 (all long and weak); metatarsus v7 (all long and weak); tarsus v10/11.

Trichobothria as in male of previous species. Paired leg claws with one large and rarely one small proximal denticle; unpaired leg claws bare.

Opisthosoma oval, 4.22 long, 3.31 wide, densely covered



with short dark hairs and few longer interspersed hairs in posterior zone of ventral side. PMS 0.38 long, without macro-spigots; PLS 1.12 long: proximal article 0.57, without macro-spigots; median article 0.27, with four macro-spigots; distal article 0.28, with one macro-spigot. FEMALE (allotype): *Colour in alcohol* (darker in living spider): Dorsal side of prosoma uniformly brown, except for slightly darker chelicerae; ventral side of prosoma slightly lighter than dorsal side. Dark pigment around AME and behind ALE and PLE (Fig. 9A). Palpal coxae, labium, sternum and ventral side of chelicerae more reddish than ventral side of legs. Opisthosoma dorsally dark greyish brown, more densely speckled than in male, ventrally lighter greyish, except for darkened epigynal area (Fig. 9C) and light brown spinnerets.

*Morphology and measurements*: Body 16.14 long. Carapace 5.37 long, 4.53 wide, smooth, with few very thin hairs on pars thoracica; slightly stronger ones on lateral

carapace margin; long and strong bristles on, in front and behind eye mound and about half way back to fovea, one pair among them very long. Entire eye group 1.07 long, 1.08 wide; ALE and AME separated by 0.38. MOQ 0.49 long, 0.68 wide. Eye diameters: AME 0.27, ALE 0.24, PME 0.17, PLE 0.29. No wrinkles lateral to eye mound. Posterior zone of pars cephalica with a pronounced boss, clearly higher than eye mound in lateral view. Fovea strongly procurved, with angles between posterior and lateral parts (Fig. 9A), 0.93 wide, occupying 21% of carapace width at that point. Proximal article of chelicera 2.29 long, stronger than in male; ventral groove with 7/8 teeth (mostly strong, two smaller ones on left side) on promargin and 6/8 teeth (most of them strong, one small on left side) on retromargin; rastellum on long and narrow process, composed of 14/15 short, thick spines (stronger than in male) and several weaker and more pointed spines. Palpal coxa 2.02 long, 1.25 wide, with

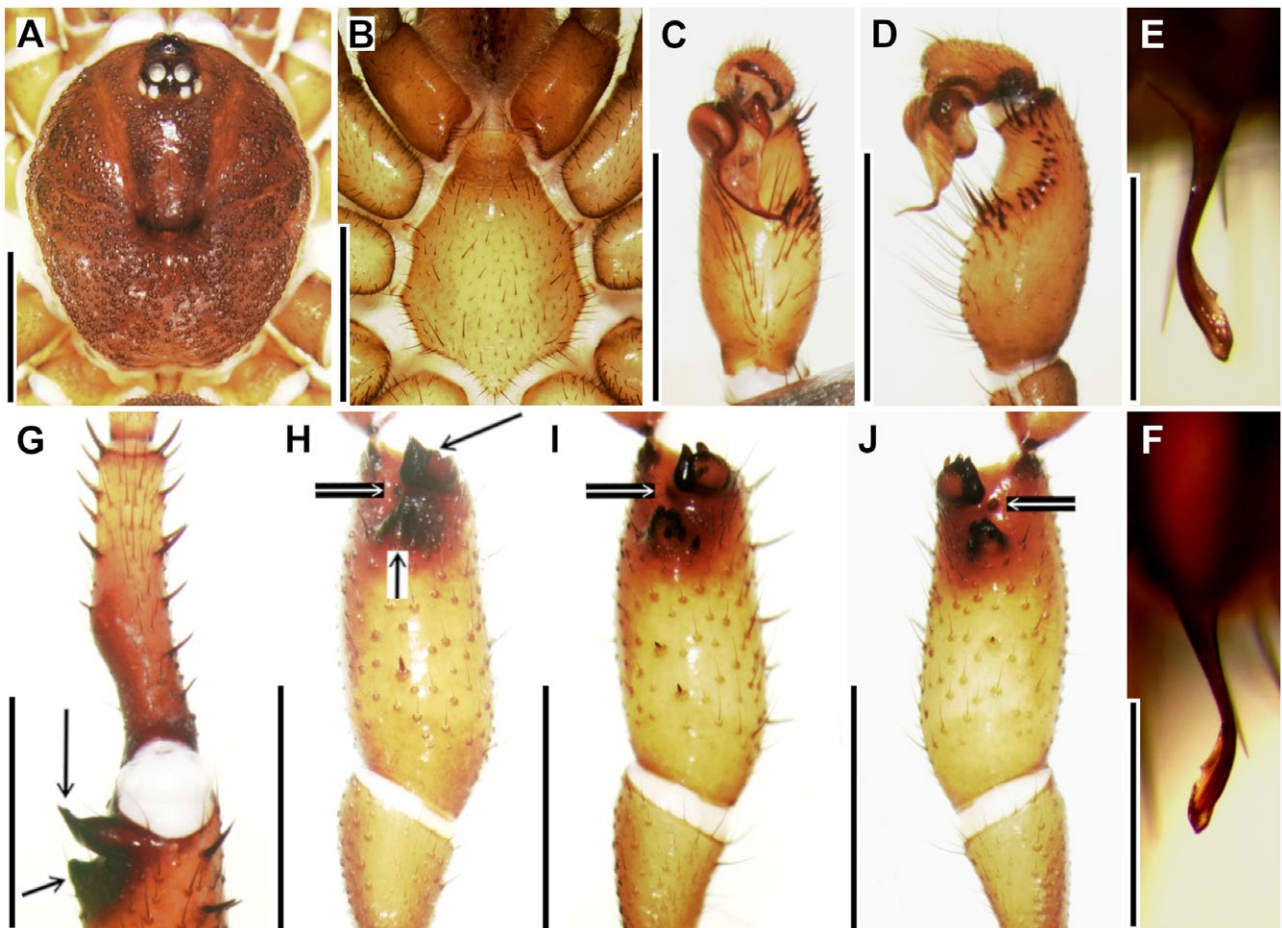


Fig. 8. *Titanidiops tenuis* sp. nov., males; holotype (A-H), aberrant paratype MHNG-ARTO-28949 with surplus megaspines on coupling spurs (I-J). (A) Carapace, dorsal view. (B) Prosoma, ventral view. (C) Distal part of left palp, ventral view. (D) Same, retrolateral view. (E) Apex of right embolus, ventral view. (F) Apex of left embolus, ventral view. (G) Metatarsus and distal part of tibia of left leg I, ventral view. (H-I) Tibia and patella of left leg I, prolateral view. (J) Same of right leg I, prolateral view. Long black arrows indicate distal spur and megaspine; short black arrows indicate subdistal spur and megaspine; long white arrows indicate wart-like tubercle. Scale lines: 0.5 mm (E-F), 2.0 mm (A-D, G-J).



more than 50 spinules of various sizes spread over almost entire ventral surface, the strongest ones in prolateral half. Labium 0.90 long, 1.09 wide, carrying four strong spinules. Sternum 3.11 long, 2.78 wide; labio-sternal suture and sternal sigilla quite inconspicuous, as in male (Fig. 9B).

Palp 8.56 long (2.89 + 1.96 + 1.77 + 1.94); tarsus slightly spindle-shaped; tibia dorsally with a moderately pronounced subdistal pseudosegmentation.

Legs 2314. Leg I 9.98 long (3.22 + 2.18 + 2.13 + 1.58 + 0.87); leg II 8.91 long (2.73 + 1.96 + 1.77 + 1.47 + 0.98); leg III 9.44 long (2.51 + 2.13 + 1.53 + 1.99 + 1.28); leg IV 12.54 long (3.35 + 2.51 + 2.62 + 2.64 + 1.42). Leg tarsi without pseudoscapula; metatarsi I-II not spindle-shaped (unlike in female of *T. birmanicus* sp. nov.).

Spines: Palp: femur p2 (one long and one short spine distally); patella p1; tibia p14/18, r17; tarsus p19, r18/19, v3. Leg I: patella, 0; tibia p15/16, r18/21; metatarsus

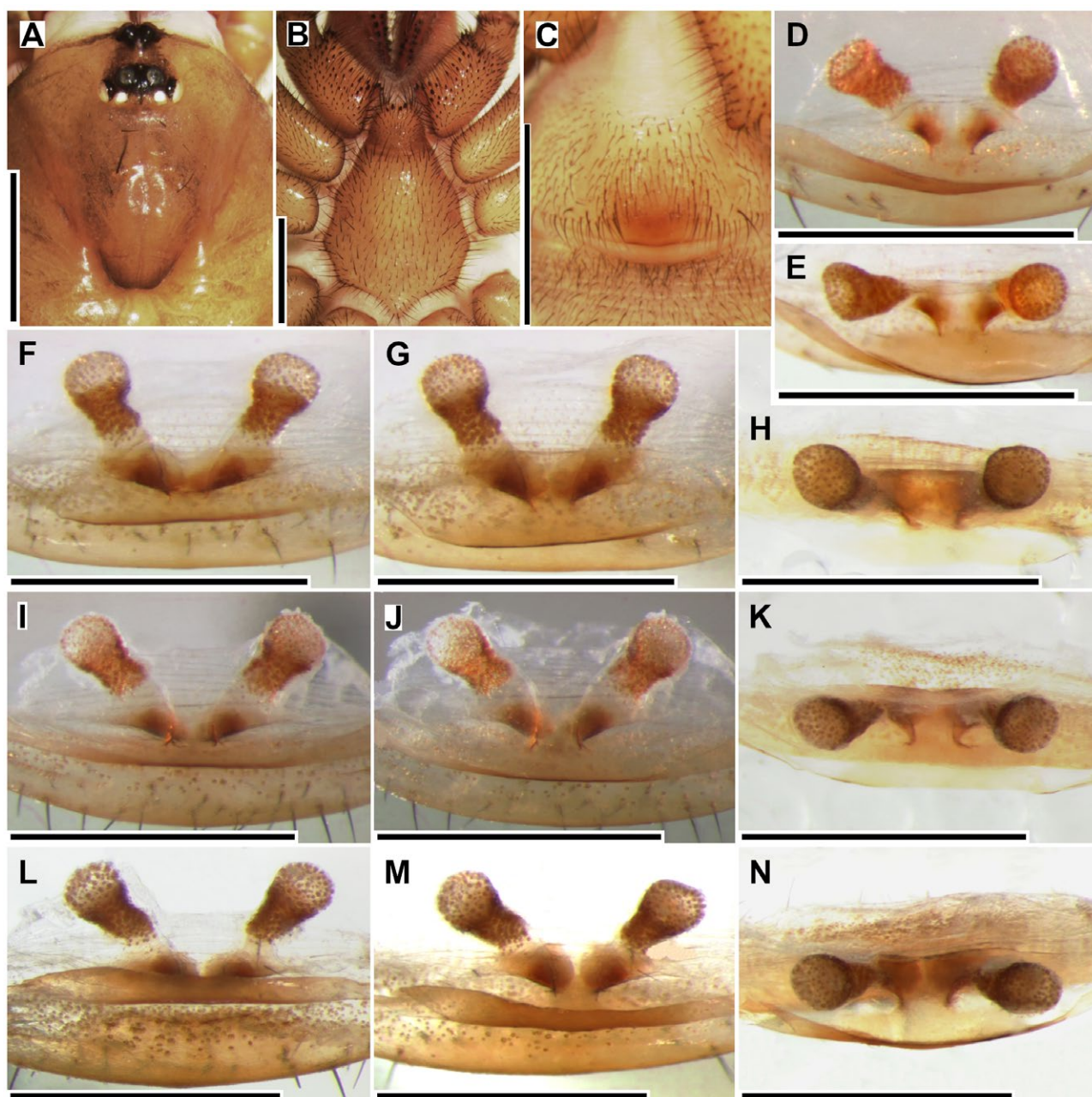


Fig. 9. *Titanidiops tenuis* sp. nov., females; allotype (A-E), paratype MHNG-ARTO-28956 (F-H), paratype MHNG-ARTO-28957 (I-K), paratype MHNG-ARTO-28958 (L-N). (A) Anterior part of carapace, dorsal view. (B) Prosoma, ventral view. (C) Genital area, ventral view. (D-E) Vulva from exuvia. (F-N) Vulvae from specimens. (F, I, L) Vulva, ventral view. (D, G, J, M) Vulva, antero-ventral view. (E, H, K, N) Vulva, anterior view. Scale lines: 1.0 mm (D-N), 2.0 mm (A-C).

p16/17, r15/17; tarsus p7/8, r6, v3. Leg II: patella, 0; tibia p8/10, r10/12; metatarsus p10/14, r9/11; tarsus p6, r4/5, v2/3. Leg III: patella d2/3, p16; tibia p7/8, r4, v3 (quite long and weak); metatarsus d13/17, v4/5; tarsus v2/3. Leg IV: patella p20; tibia v4/5 (quite long and weak); metatarsus v10/11; tarsus v12/14. A cluster of 15/16 spinules dorso-distally on leg tibia I; on tibia II 22/28 spicules in a dorso-distal cluster extending backward in a narrow band and further in a single row to midpoint of article; a dorso-distal cluster of seven spinules on palpal tibia.

Trichobothria as in females of previous species. Paired leg claws with one large subproximal denticle and on some (anterior) legs additionally with one small denticle; unpaired leg claws bare. Palpal claw with one large and one small denticle.

Opisthosoma oval, 7.36 long, 4.96 wide; with several long hairs interspersed between many short hairs, even longer hairs on ventral side. PMS 0.53 long, without macro-spigots; PLS 1.63 long: proximal article 0.83, without macro-spigots; median article 0.41, with six macro-spigots; distal article 0.39, with one macro-spigot. Vulva (of paratypes; Fig. 9D-N): Receptacles relatively long and relatively close to each other; receptacular heads not much wider than receptacular stalks; vulva essentially indistinguishable from vulvae of *T. birmanicus* sp. nov. (see Fig. 7F-P).

**Variation:** In males (n = 7) the carapace length ranges 3.77–4.74, the corresponding width ranges 3.31–4.25. The largest female (n = 10) has a 5.26 long and 4.42 wide carapace; in the smallest reproductive female (with an egg case) it is 4.29 and 3.57, respectively. The subdistal embolic tooth is distinct in five males examined (Fig. 8E–F), rather indistinct in two males. Male paratype MHNG-ARTO-28949 has 2/3 megaspines on the distal spur of the tibia I mating clasper and 4/5 megaspines on the subdistal spur (Fig. 8I–J) whereas all other males have only a single megaspine on each spur (Figs 3C, 8H), as do all males of all other congeneric species examined. Therefore surplus megaspines on the coupling spurs is clearly an aberration. In the smallest male (MHNG-ARTO-28951) both metatarsi I have a more pointed prolateral knee than in other males. Females possess 3–11 pronounced spinules of various sizes on their labium; males have 0–4 more or less distinctly developed labial spinules. The AME are equally large to distinctly larger than the PLE in males (Fig. 8A); in all females the AME are slightly smaller than the PLE (Fig. 9A). In all specimens examined the PMS lacks macro-spigots; so does the proximal article of the PLS, except for a single female which carries a single macro-spigot on one side; the median article of the PLS has 3–7 macro-spigots; the distal article has a single macro-spigot in all specimens examined. The pseudoscapula in males shows little intraspecific variation: covering the distal two-thirds

of tarsus I in four males, the distal half in three males (including the holotype); one male has slightly more scattered scopuliform hairs on tarsus IV than the others. In all females there are two prolateral-distal spines on the palpal femur: one always long and strong, the other always shorter and usually also weaker (as it is the case in all females of *T. birmanicus* sp. nov.); only in the allotype is it as strong as the longer spine. Variation in vulva morphology is shown in Fig. 9D–N.

**Distribution:** The new species is only known from the type locality, close to the Andaman coast of the northern part of southern Myanmar (Fig. 1A).

**Biology:** *Habitat:* All spiders were collected from the steep soil banks of a rural road fringed with planted trees.

*Burrow structure:* Burrows in the field were more or less straight and unbranched, up to 3 cm long (in captivity up to 4 cm), without a soil pellet, closed by a quite thick (slightly cork-shaped) door. In males (all matured in captivity) doors were 0.6–0.8 cm long and 0.7–0.9 cm wide. The largest burrow (of a female) had a door 1.1 cm long and 1.2 cm wide. All burrows were lined with a dense layer of silk.

*Phenology:* Males matured in captivity in early May, about 10.5 months after being captured, and in early to late March, about 21 months after being captured. In mid-June one fresh egg case was extracted from the burrow of a female. Another female laid eggs in its transport vial the day after being captured. These eggs were subsequently eaten by their mother.

*Egg case:* The extracted and preserved egg case is 1.0 cm long, 0.75 cm wide and 0.5 cm high, white on its upper surface, brown elsewhere (as in *T. birmanicus* sp. nov., Fig. 2K–L). It contains 45 undeveloped (and thus newly laid) eggs.

### *Titanidiops sayamensis* Schwendinger & Hongpadharakiree, sp. nov.

Figs 1A, 2I, 3D, 10–11

*Idiops* sp. – Schwendinger, 1996: 578 (mentioned as an additional species occurring in Thailand).

**Holotype:** MHNG-ARTO-28965, sample TH-11/17; male (matured 1.IV.2014); Nakhon Nayok Prov. & Distr., Salika W.F., 14°19'N, 101°15'E, 100 m; 18.XII.2011; *leg.* P.J. Schwendinger & K. Hongpadharakiree.

**Paratypes:** MHNG-ARTO-28966–28968, sample TH-11/17; 3 males (matured 4.III.2014; 3.IV.2014; mid-IV.2014); collected together with the holotype. – MHNG-ARTO-28969–28972, sample TH-11/17; 4 females (including allotype MHNG-ARTO-28969); collected together with the holotype. – THNHM; 1 male (matured 18.XII.2014); collected together with the



holotype. – THNHM; 1 female; Salika W.F.; 2010; *leg.* K. Hongpadharakiree. – MHNG-ARTO-28973-28976, sample TA-22/09; 4 males (matured 8.I.2014; 15.II.2015; 17.II.2015; 27.II.2015); Thailand, Chanthaburi Prov., Khao Khitchakut Distr., near Krathing W.F., 12°50'N, 102°07'E, 45 m; 5.IX.2013; *leg.* P.J. Schwendinger. – MHNG-ARTO-28977-28980, sample TA-22/09; 4 females; same data. – THNHM; 1 female; near Krathing W.F., 12°50'N, 102°08'E, 250 m; 28.X.2010; *leg.* K. Hongpadharakiree. – MHNG-ARTO-28981, MHNG-ARTO-28995-28996, sample TH-09/10; 1 male (matured beginning of I.2009), 2

females; Thailand, Nong Khai Prov., Bung Kla Distr., Phu Wua, 18°14'N, 103°58'E, 390 m, 13./14.VI.2013; *leg.* P.J. Schwendinger. – MHNG-ARTO-28997-28999, sample MT-19/05; 3 males (matured 19.III.2015; 1.IV.2015; 10.V.2015); Myanmar, Tanintharyi Region, Dawei, near Myaw Yit Pagoda, 14°05'N, 98°05'E, 5-20 m; 21.VI.2013; *leg.* P.J. Schwendinger. – MHNG-ARTO-29000-29002, sample MT-19/05; 3 females; same data as for previous specimens.

**Etymology:** “Sayam” is the Thai word for “Siam”. Latinized adjective.

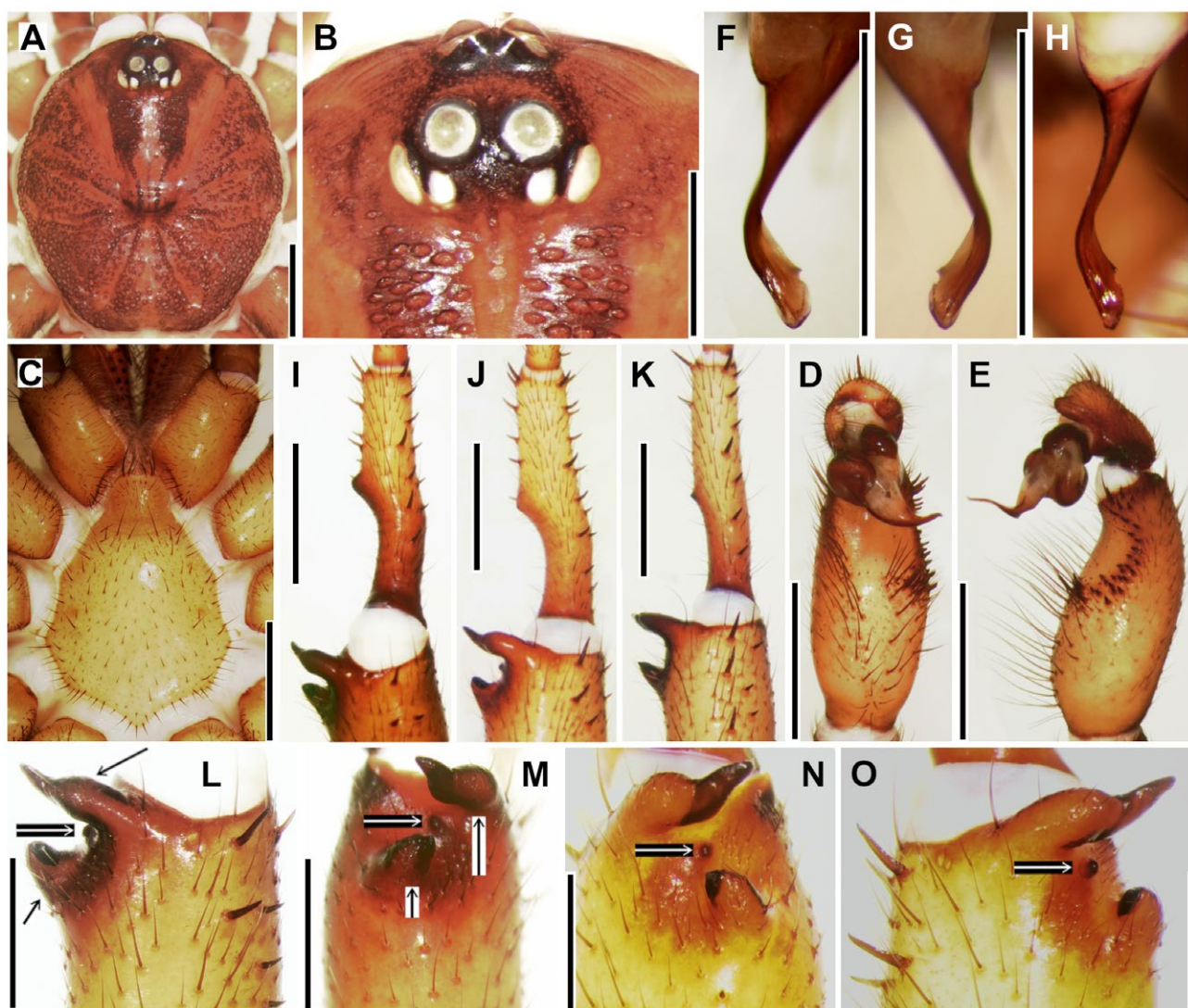


Fig. 10. *Titanidiops sayamensis* sp. nov., males; holotype (A-G, I, L-M), paratype MHNG-ARTO-28966 from Salika W.F. (J, N-O), paratype MHNG-ARTO-28998 from Myaw Yit (H, K). (A) Carapace, dorsal view. (B) Anterior part of carapace, dorsal view. (C) Prosoma, ventral view. (D) Distal part of left palp, ventral view. (E) Same, retrolateral view. (F, H) Apex of right embolus, ventral view. (G) Same of left embolus. (I-K) Metatarsus and distal part of tibia of left leg I, ventral view. (L) Mating clasper complex of left tibia I, ventral view. (M) Same, prolateral view. (N) Mating clasper complex of right tibia I, ventral view. (O) Same, proventral view. Long black arrows indicate distal spur and megaspine; short black arrows indicate subdistal spur and megaspine; long white arrows indicate wart-like tubercle with shiny black cap. Scale lines: 1.0 mm (B, F-H, L-O), 2.0 mm (A, C-E, I-K).



**Diagnosis:** Males are distinct from males of all other species treated here by having a mating clasper complex with a wart-like tubercle carrying a shiny black cap (Figs 3D, 10L-O) and a relatively narrow distal spur carrying a dorsad-directed instead of distad-directed megaspine (Figs 3D, 10I-O); carapace with warty surface (Fig. 10A-B), but warts smaller and more widely spaced than in *T. tenuis* sp. nov. (Fig. 8A); prolateral knee of metatarsus I strongly developed (Fig. 10I-K); embolus with a distinct subdistal notch and tooth (Fig. 10F-H). Females with receptacles

quite close to each other and having rather small heads (Fig. 11F-O); different from those of *T. crassus* comb. nov. (with distinctly larger receptacular heads; Fig. 3H), *T. pylorus* comb. nov. and *T. inermis* sp. nov. (receptacles more widely separated from each other; Fig. 5G-O and Fig. 13F-P), but essentially indistinguishable from receptacles of females of other species treated here.

**Description:** MALE (holotype). *Colour in alcohol* (darker in living spider; see Fig. 2I for male paratype): Carapace reddish brown, with darkened area around

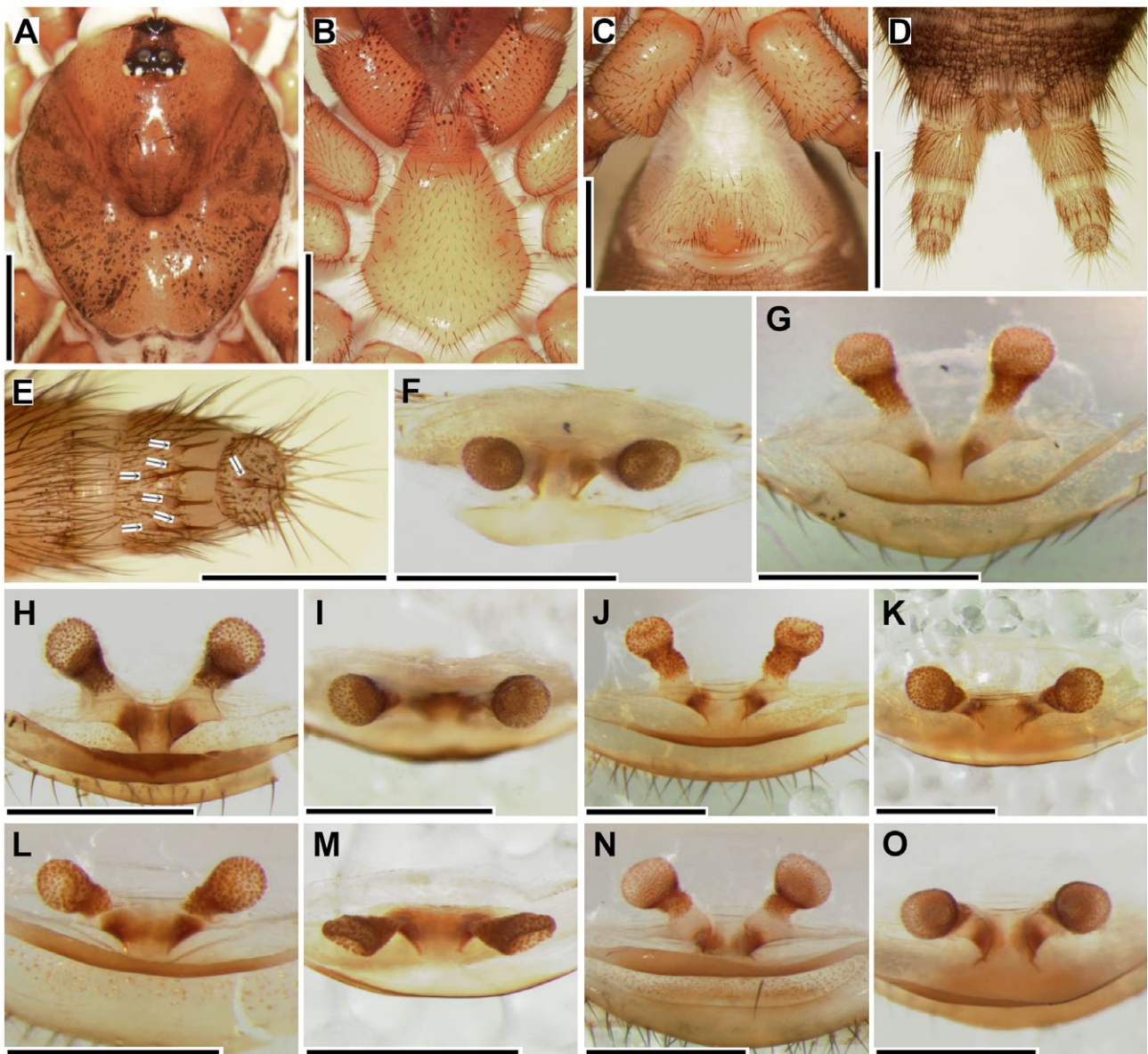


Fig. 11. *Titanidiops sayamensis* sp. nov., females; allotype (A-E), paratype (in THNHM) from Salika W.F. (F-G), paratype MHNG-ARTO-28972 from same locality (H-I), specimen (in THNHM) from Krathing W.F. (J-K), exuvia of specimen MHNG-ARTO-28995 from Phu Wua (L-M), specimen MHNG-ARTO-29001 from Myaw Yit (N-O). (A) Carapace, dorsal view; note dark particles attached to the surface (explained in the paragraph Variation of this species). (B) Prosoma, ventral view. (C) Genital area, ventral view. (D) Spinnerets, ventral view. (E) Left PLS, ventral view. (F, I, K, M, O) Vulva, anterior view. (G-H, J, L, N) Vulva, ventral view. Arrows indicate macro-spigots. Scale lines: 1.0 mm (E-O), 2.0 mm (A-D).



eye mound continuing as two dark parallel, posteriorly narrowing bands back to fovea; areas between ALE and main eye group almost black, both separated by a light transversal band (Fig. 10B). Dorsal side of chelicera, palpal tibia and tarsus, all leg trochanters, tarsus II and metatarsus II, and tarsi III-IV entirely light brown, distal zone of tibia I and proximal half of metatarsus I darkened, other limb articles dorsally light brown, with three dark longitudinal stripes. Leg coxae, labium and sternum light orange-coloured; palpal coxae and ventral side of limbs slightly darker. Fang claw and sclerites of palpal organ dark brown. Opisthosoma dorsally dark grey, densely speckled with light spots, with two lighter median patches in anterior half; ventrally mostly light grey, except for light orange-coloured genital area, booklung covers and spinnerets.

*Morphology and measurements:* Body 15.32 long. Carapace 5.71 long, 5.13 wide, quite densely covered with relatively small wart-like hair bases (Fig. 10A-B); corresponding hairs mostly short and weak, longest and adpressed halfway between eye mound and fovea; only a single strong, short median bristle in front of ALE and three such bristles in front of AME. Eight eyes on bipartite mound, with a saddle between ALE and main eye group; entire eye group 1.12 long, 1.24 wide; ALE and AME separated by 0.28. MOQ 0.61 long, 0.83 wide. Eye diameters: AME 0.38, ALE 0.33, PME 0.22, PLE 0.39. Several fine transversal wrinkles to left and right of anterior half of eye mound. Posterior zone of pars cephalica with a moderate boss, slightly lower than eye mound in lateral view. Fovea slightly procurved, 0.97 wide, occupying 19% of carapace width at that point. Proximal article of chelicera 2.21 long; ventral groove with seven teeth on each margin, 1/2 of them on promargin rather small, one on retromargin small; fang claw with sharp, straight proventral keel and with serrate retroventral keel; rastellum on long and narrow process, composed of 14/16 short, thick spines and several weaker and more pointed spines. Palpal coxa 2.08 long, 1.17 wide, with about 20 very short (shorter than those on labium) spinules, most of them not thicker than nearby bristles. Labium 0.78 long, 1.04 wide, with four short, weak spinules (only little thicker than nearby bristles). Sternum 2.92 long, 2.99 wide; labio-sternal suture distinct and relatively long, it and sigilla of same colour as other parts of sternum (Fig. 10C).

Palp 9.05 long (3.05 + 1.82 + 2.95 + 1.23). Tibia moderately incrassate, 1.36 wide, retrolaterally with a curved band of 31 spines of various lengths in distal half (Fig. 10E). Tarsus short, distally with two short lobes and one dorsal spine. Palpal organ typical for the genus (Fig. 10D-E); apex of embolus with a distinct tooth proximal to a relatively deep notch (Figs 10F-G).

Legs 3214. Leg I 16.36 long (4.94 + 2.86 + 3.21 + 3.86 + 1.49); leg II 14.15 long (4.35 + 2.24 + 2.95 + 3.18 + 1.43); leg III 12.56 long (3.64 + 2.21 + 2.01 + 3.08 + 1.62); leg IV 16.82 long (4.74 + 2.53 + 3.73 + 4.03 + 1.79). Leg tarsi

with a ventral pseudoscapula: in distal half of tarsus I, in distal four-fifth of tarsi II-III, developed as a relatively wide median band in distal two-thirds of tarsus IV. Leg I: metatarsus curved in proximal half, halfway on prolateral side with a pronounced knee (Fig. 10I); tibia distinctly incrassate (1.72 wide; tibia II in comparison only 0.97 wide), carrying a prolateral-distal mating clasper complex composed of: 1) a relatively narrow distal spur carrying a dorsad-directed megaspine; 2) a smaller subdistal spur carrying a short, wide, pointed megaspine; 3) a wart-like tubercle with a black, smooth and shiny cap between both spurs; no prodorsal-distal process present (Figs 3D, 10L-M). Leg tarsus II slightly spindle-shaped; tarsus III indistinctly so. Slightly enlarged hair bases on leg tibiae I-II; these indistinct on other limb articles.

Spines: Palp: femur p2 (one long and one short spine distally); patella, 0; tibia r31; tarsus d1. Leg I: patella, 0; tibia p2 (megaspines) + 1/2, r11; metatarsus p7, r11/13; tarsus p5/6, r4/5. Leg II: patella, 0; tibia p5, r3/4, v5 (plus 3 long, strong bristles); metatarsus p12, r7/9; tarsus p5, r4. Leg III: patella d3, p12; tibia d10/11, v5/7; metatarsus d11/13, p3, v6/9; tarsus p3, r2. Leg IV: patella p17/19; tibia p3, v8/10 (all long and weak); metatarsus p3, v10 (all long and weak); tarsus p2/3, r1/3, v8/10.

Trichobothria as in males of previous species. Paired leg claws with a large subproximal denticle, on anterior legs often additionally with a small denticle; unpaired leg claws bare.

Opisthosoma oval, 6.69 long, 4.81 wide, covered with a mixture of short and medium-sized dark hairs; some even longer bristles on ventral side. PMS 0.49 long, without macro-spigots; PLS 1.45 long: proximal article 0.77, without macro-spigots; median article 0.38, with 5/6 macro-spigots; distal article 0.30, with one macro-spigot. FEMALE (allotype): *Colour in alcohol* (darker in living spider): Dorsal side of prosoma mostly light orange-brown, except for slightly darker chelicerae; area between eyes much darker (Fig. 11A). Ventral side of prosoma mostly light orange-coloured, except for slightly darker labium and palpal coxae, and distinctly darker chelicerae (Fig. 11B). Fang claws dark brown. Three indistinct dark longitudinal stripes on femora and patellae. Opisthosoma dorsally dark greyish brown, densely speckled as in male, with an indistinct light median patch in anterior half; ventrally mostly lighter greyish, except for dark orange-coloured epigynal area and light orange-coloured booklung covers and spinnerets (Fig. 11C-D).

*Morphology and measurements:* Body 18.25 long. Carapace 5.58 long, 4.87 wide, smooth, with few short hairs on lateral margins; stronger (but not longer) bristles in front of ALE, in front of AME and on posterior margin of eye mound; longer bristles between eye mound and fovea, one very long pair at about midway. Entire eye group 1.11 long, 1.19 wide; ALE and AME separated by 0.39. MOQ 0.53 long, 0.74 wide. Eye diameters: AME 0.27, ALE 0.31, PME 0.20, PLE 0.33. No wrinkles lateral to eye mound. Posterior zone of pars cephalica with a

distinct boss, slightly higher than eye mound in lateral view. Fovea distinctly procurved, with indistinct angles between posterior and lateral parts (Fig. 11A), 0.88 wide, occupying 19% of carapace width at that point. Proximal article of chelicera 2.53 long, stronger than in male; ventral groove with 6/8 teeth (most of them strong; one small on right side, three small on left side) on promargin, and 9/10 teeth (most of them strong; four small on right side, three small on left side) on retromargin; rastellum on long and narrow process, composed of 19/20 short, thick spines (stronger than in male) and several weaker and more pointed spines. Palpal coxa 2.21 long, 1.36 wide, with about 60 spinules of various sizes spread over almost entire ventral surface, the strongest ones in prolateral half. Labium 0.91 long, 1.10 wide, carrying three strong plus two weak spinules. Sternum 3.18 long, 2.99 wide; labio-sternal suture and sternal sigilla quite inconspicuous (Fig. 11B).

Palp 9.26 long ( $3.12 + 2.05 + 2.01 + 2.08$ ); tarsus slightly spindle-shaped; tibia dorsally with a weakly pronounced subdistal pseudosegmentation.

Legs 3214. Leg I 10.46 long ( $3.38 + 2.34 + 2.14 + 1.66 + 0.94$ ); leg II 9.68 long ( $3.05 + 2.18 + 1.82 + 1.59 + 1.04$ ); leg III 9.42 long ( $2.50 + 2.05 + 1.46 + 1.98 + 1.43$ ); leg IV 13.48 long ( $3.77 + 2.63 + 2.79 + 2.73 + 1.56$ ). Leg tarsi without pseudoscapula; metatarsi I-II indistinctly spindle-shaped.

Spines: Palp: femur p2 (one long and one short spine distally), patella p1; tibia p19, r16/18; tarsus p17/18, r18/19, v4/5. Leg I: patella, 0; tibia p18/19, r17/19; metatarsus p16/18, r14/15; tarsus p7/8, r7, v3. Leg II: patella, 0; tibia p10, r10/12; metatarsus p13/14, r9/8; tarsus p7/8, r3, v3. Leg III: patella d3, p14/15; tibia d10/16, p1, v2 (quite long and weak); metatarsus d12/14, v6/8; tarsus v5/6. Leg IV: patella p13/15; tibia p1, v4 (quite long and weak); metatarsus v11; tarsus v12. A cluster of 13 spinules dorso-distally on leg tibia I; on tibia II 16/17 spinules in a dorso-distal cluster extending backward in a narrow band in distal fourth of article; a dorso-distal cluster of five spinules on palpal tibia.

Trichobothria as in females of previous species. Paired leg claws with a large subproximal denticle and on some (anterior) legs additionally with a small denticle; unpaired leg claws bare. Palpal claw with one large and one small proximal denticle.

Opisthosoma oval, 8.25 long, 5.23 wide; with a mixture of short and medium-long dark hairs dorsally, ventrally with a few long hairs in genital area and on booklung covers. PMS 0.57 long, without macro-spigots; PLS 1.49 long: proximal article 0.77, without macro-spigots; median article 0.39, with six macro-spigots; distal article 0.33, with one macro-spigot (Fig. 11D-E).

Vulva (of paratypes; Fig. 11F-O): Receptacles relatively long and close to each other; receptacular heads not much wider than receptacular stalks; vulva essentially indistinguishable from vulvae of *T. birmanicus* sp. nov. (Fig. 7F-P) and *T. tenuis* sp. nov. (Fig. 9D-N).

**Variation:** In males ( $n = 10$ ) the carapace length ranges 5.78-6.30, the corresponding width 4.48-5.65. The largest ( $n = 15$ ) conspecific female (in THNHM) has a 9.21 long and 7.76 wide carapace. The dark spots on the carapace of the female allotype (Fig. 11A) are not pigment in the cuticle, but thin particles, shaped like tiny paper shreds, attached to the surface of the cuticle. These particles presumably are fragments of only partly dissolved endocuticle left over from the discarded last exuvia; they can be removed with a brush. The presence of such particles is fairly common: they were also found in nine other *T. sayamensis* sp. nov. females from all localities, in females of at least two other *Titanidiops* species, and in other mygalomorph and mesothelid specimens with a mostly glabrous carapace. Males have up to four weak spinules on their labium; females 3-10 strong spinules. The number of spines on the retrolateral side of the palpal tibia of males ranges 20-40. The prolateral median knee in the metatarsus I of males is expressed either as a spike (Fig. 10K), as an apically pointed cone (Fig. 10J), or as an apically rounded cone (Fig. 10I). All males have a small wart-like tubercle with a shiny black cap in the mating clasper complex, but that is rather difficult to see in specimens where the nearby cuticle is dark (Fig. 10L-M versus Fig. 10N-O). The expanse of the pseudoscapula on leg tarsi of males is quite variable: mostly in the distal half of tarsus I, in a male from Myaw Yit shorter (in distal two-fifths); in distal two-thirds to four-fifths on tarsi II-III; in a quite wide median band in distal two-thirds to three-fourths on tarsus IV. Most specimens lack macro-spigots on the PMS and on the proximal article of the PLS, only the largest female has there 0/1 and 0/3 macro-spigots, respectively; the number of such spigots on the median article of the PLS ranges 3-10; the distal article always carries a single macro-spigot. Variation in vulva morphology is shown in Fig. 11F-O.

**Distribution:** This species has a wide geographical distribution, ranging from southern Myanmar through central and south-eastern to north-eastern Thailand (Fig. 1A).

**Biology:** *Habitat:* Spiders were collected from sloping soil without vegetation beneath tree roots and water pipes in trails, from earth banks on the sides of a footpath, and from the banks of old trenches (at Myaw Yit); all in shady places within forests, never in sun-exposed places.

*Burrow structure:* All burrows inspected were unbranched and more or less straight, up to six centimetres long in females, up to 3.5 cm in males, without a soil pellet, closed by moderately thick doors. In males (all matured in captivity) doors were 0.85-1.25 cm long and 0.9-1.35 cm wide. The largest burrow (belonging to a female) had a door 1.3 cm long and 1.4 cm wide. All burrows were lined with a relatively thin layer of silk; prey remnants were stored at the bottom of the burrows.

**Phenology:** Males matured in captivity between early January and early May; those from Myaw Yit a bit later in the year than males from Thailand, but they were also in captivity for a longer period of time (about 2-3 years versus 0.5-2.5 years in Thai specimens). No egg cases were found in the field or constructed by spiders in captivity.

***Titanidiops inermis* Schwendinger, sp. nov.**

Figs 1A, 2D-G, J, M, 3A, 12-13

**Holotype:** MHNG-ARTO-29018, sample MT-19/01; male (matured 9.IX.2015); Thailand, Chumphon Prov., Lang Suan Distr., Ban Bang Nam Jued, 9°59'N, 99°09'E, 5 m, 13./14.VI.2013; *leg.* P.J. Schwendinger.

**Paratypes:** MHNG-ARTO-29019-29021, sample MT-19/01; 3 males (matured 29.IX.2013; 7.IX.2015; 13.X.2013); collected together with the holotype. – MHNG-ARTO-29022-29029; 8 females; collected together with the holotype. – MHNG-ARTO-29030-29031, sample TH-06/04; 1 male (matured end of IX.2007), 1 female; Thailand, Krabi Prov. & Distr., Ban Laem Pho, near Gastropod Fossil Beach, 8°02'N, 98°53'E, 1 m; 15./17.IX.2006. – MHNG-ARTO-29032-29034, sample TH-08/09; 1 male (matured 8.VIII.2011), 2 females; same locality as for previous specimens; 15./16.VI.2008. – MHNG-ARTO-29035-29036, sample TH-09/04; 1 male (matured 11.VI.2009), 1 female; Thailand, Krabi Prov., Khlong Thom Distr., Khao Phra - Bang Khram, 7°54'N, 99°16'E, 80 m; 2./3.VI.2009. All specimens *leg.* P.J. Schwendinger.

**Other material:** MHNG; 1 juvenile; collected together with the holotype.

**Etymology:** The Latin adjective “inermis” means “unarmed”, referring to the absence of a mating clasper in males of this species.

**Diagnosis:** Males of the new species differ from those of all congeners by lacking a mating clasper on tibia I (Figs 3A, 12N-T); they are further distinguished from congeneric males, except those of *T. pylorus* comb. nov., by having a smooth carapace without wart-like hair bases (Fig. 12A-B), a row of dorsal spines on leg and palp femora, a row of 3-7 denticles on their paired leg claws, and by lacking a subdistal embolic notch (Fig. 12H-M). Females are distinguished from those of other species treated here by having wide bands of tiny spinules on coxae I-II (Fig. 13D-E) and a pronounced heel on the retrolateral-distal corner of their coxa IV (Fig. 13C); they additionally differ from congeneric females, except for those of *T. pylorus* comb. nov., by a vulva with widely spaced receptacles (Fig. 13F-P).

**Description:** MALE (holotype). *Colour in alcohol* (darker in living spider; Fig. 2J): Carapace mostly

brown, slightly more reddish on pars cephalica; irregular dark patches on pars thoracica (but see Variation) and three dark longitudinal bands (narrowing posteriorly) on pars cephalica; black rings around ALE, AME and PLE (Fig. 12A). Chelicerae, palps and legs mostly brown, except for lighter palpal tibia, leg tarsi, entire metatarsi III-IV and distal part of metatarsi I-II, and except for darker lateral parts of palpal tarsus. Ventral side of prosoma (except for chelicerae) mostly slightly lighter than dorsal side; rastellum and fang claw dark brown. Opisthosoma dorsally dark grey-brown, speckled with small light spots, with two indistinct lighter patches in anterior half; ventral side mostly light greyish brown, except for cream-coloured genital area, booklung covers and spinnerets.

**Morphology and measurements:** Body 11.99 long. Carapace (Fig. 12A) 4.38 long, 3.64 wide, smooth, without wart-like hair bases. Few short, strong bristles on and in front of ALE, on lateral carapace margins and on coxal elevations of pars thoracica, many bristles in a triangular area anterior of posterior carapace margin; two longitudinal rows of strong bristles running from eye mound to fovea, one pair in the middle distinctly longer and stronger than others. Eight eyes on bipartite mound, with a saddle between ALE and main eye group; entire eye group 0.96 long, 0.98 wide; ALE and AME separated by 0.23. MOQ 0.60 long, 0.69 wide. Eye diameters: AME 0.35, ALE 0.27, PME 0.20, PLE 0.24. Several fine transversal wrinkles to left and right of anterior half of eye mound. Pars cephalica slightly and evenly arched, its posterior zone without a boss, distinctly lower than eye mound in lateral view. Fovea moderately procurved, 0.71 wide, occupying 21% of carapace width at that point. Proximal article of chelicera 1.43 long; ventral groove with seven teeth (1/2 of them small) on promargin and 5/6 teeth (1/2 of them small) on retromargin; fang claw with sharp, straight proventral keel and with serrate retroventral keel; rastellum on long and narrow process, composed of ten short, thick spines and several weaker and more pointed spines. Palpal coxa 1.53 long, 0.91 wide, without spinules. Labium 0.52 long, 0.78 wide, also without spinules. Sternum 2.47 long, 2.11 wide; labio-sternal suture relatively deep, it and sigilla (two pairs, as in all other congeners) of same colour as other parts of sternum (Fig. 12C).

Palp 8.08 long (2.86 + 1.30 + 2.95 + 0.97). Tibia moderately incrassate, 1.17 wide, retrolaterally with a curved band of only 9/11 spines of various lengths in distal half (Fig. 12G). Tarsus short, distally with two short lobes and one strong and one weak dorsal spine. Palpal organ typical for the genus (Fig. 12F-G); apex of embolus with a distinct tooth but without a notch (Figs 12H-I).

Legs 3214. Leg I 16.07 long (4.87 + 2.24 + 3.70 + 3.34 + 1.92); leg II 13.06 long (4.03 + 1.82 + 2.66 + 2.86 + 1.69); leg III 11.37 long (2.86 + 1.69 + 1.79 + 3.08 + 1.95); leg IV 16.67 long (4.22 + 2.18 + 3.77 + 4.29 + 2.21). Leg

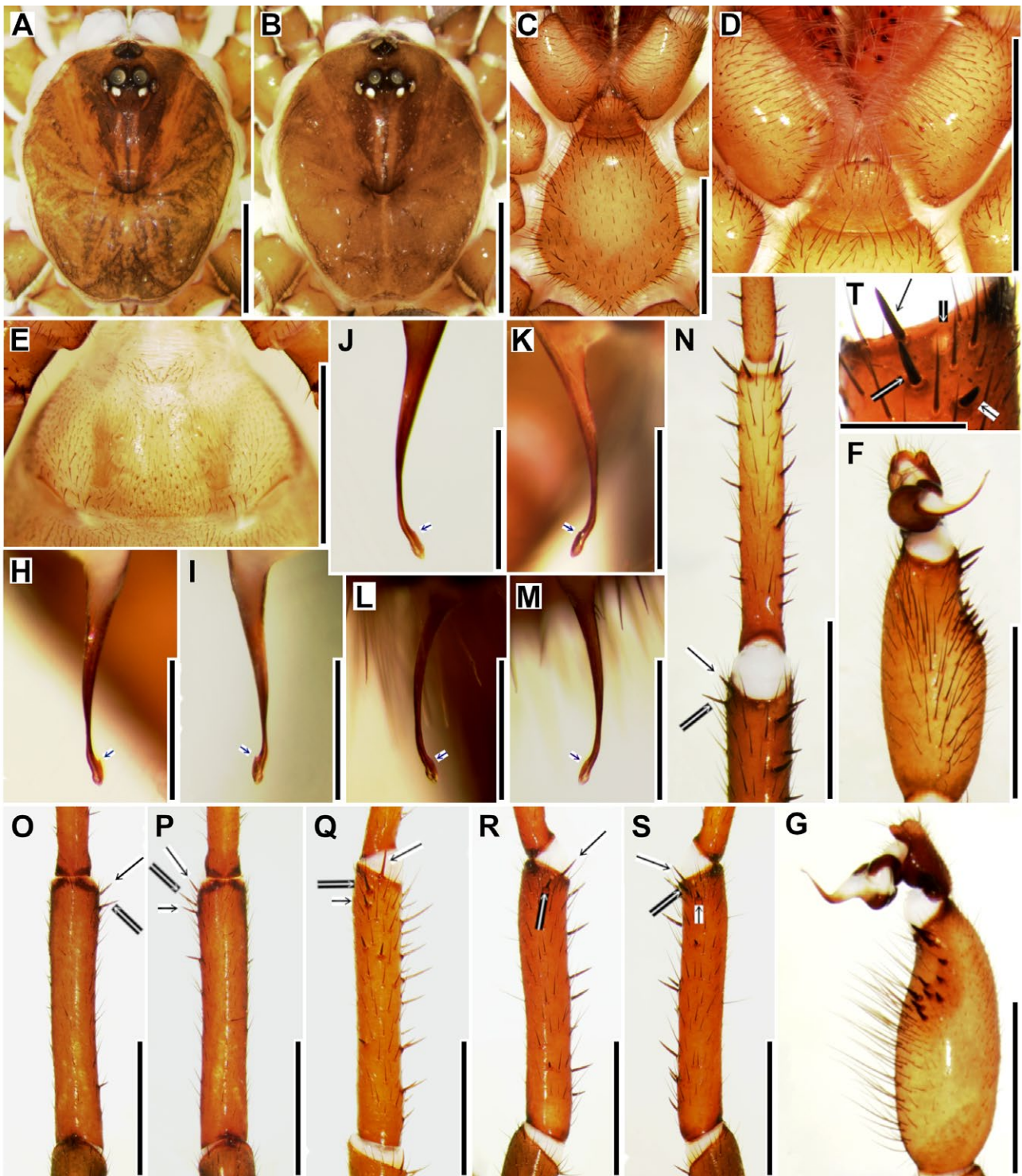


Fig. 12. *Titanidiops inermis* sp. nov., males; holotype (A, C, F-I, N-P, R-T), paratype MHNG-ARTO-29032 from Ban Laem Pho (B, D-E, L-M), paratype MHNG-ARTO-29035 from Khao Phra - Bang Khram (J-K, Q). (A-B) Carapace, dorsal view. (C) Prosoma, ventral view. (D) Labium and palpal coxae, ventral view. (E) Genital area showing spiniform epiandrous spigots, ventral view. (F) Distal part of left palp, ventral view. (G) Same, retrolateral view. (H, J, L) Apex of right embolus, ventral view. (I, K, M) Apex of left embolus, ventral view. (N) Distal part of tibia, entire metatarsus and proximal part of tarsus of left leg I, ventral view. (O) Left tibia I, dorsal view. (P) Right tibia I, dorsal view. (Q) Left tibia I, prolateral view. (R) Left tibia I, prolateral view. (S) Right tibia I, prolateral view. (T) Distal part of right tibia I, prolateral to proventral view. Long black arrows indicate spine that is homologous to distal mating spur and megaspine in other species; short black arrows indicate spine that is homologous to subdistal mating spur and megaspine; long white arrows indicate spine that is homologous to wart-like tubercle; short white arrow indicates well-developed slit organ; very short blue arrows indicate subdistal embolic tooth in various stages of reduction. Scale lines: 0.5 mm (H-M, T), 2.0 mm (A-G, N-S).



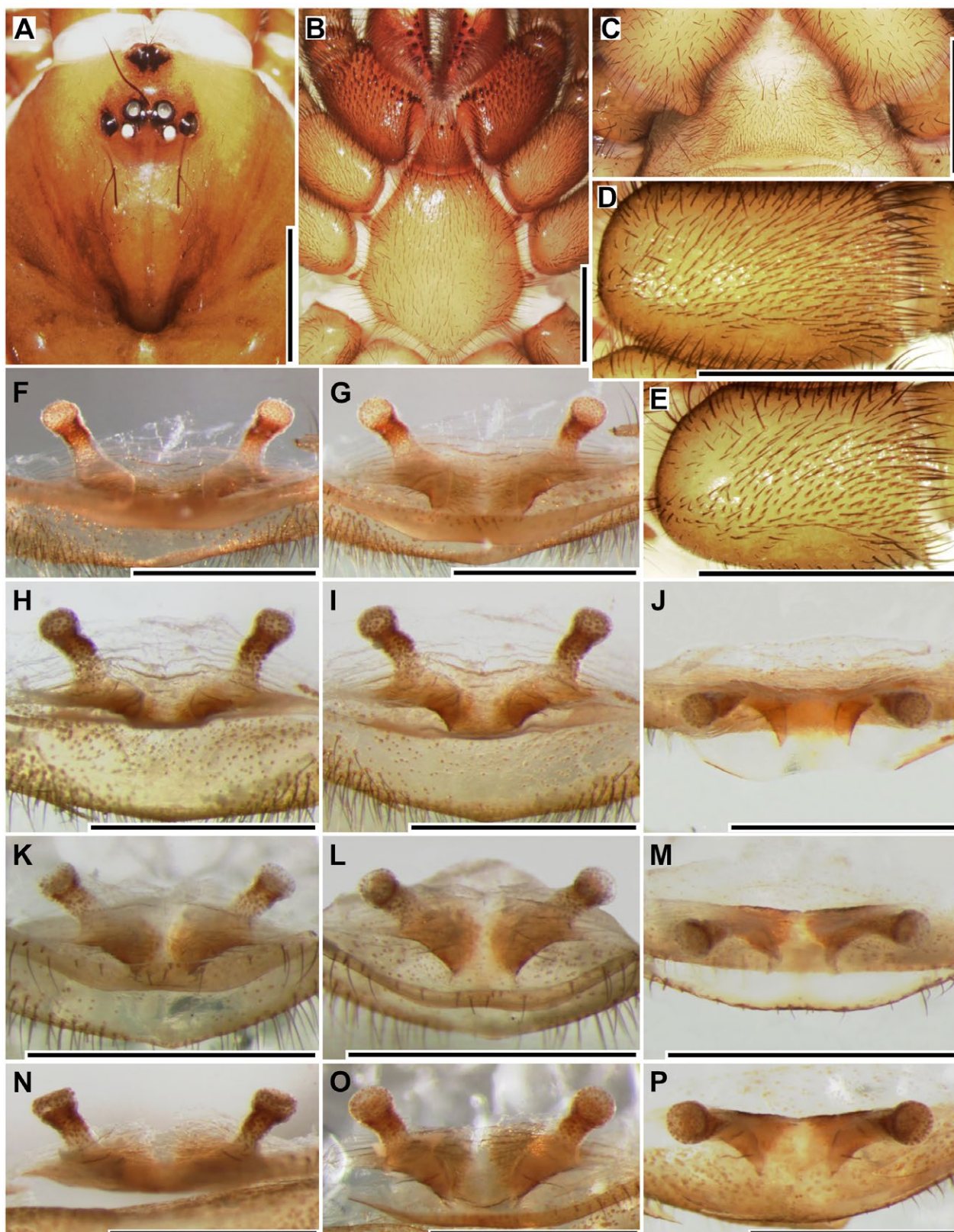


Fig. 13. *Titanidiops inermis* sp. nov., females; allotype (A-E); paratype MHNG-ARTO-29028 from the type locality (F-G), paratype MHNG-ARTO-29024 from the type locality (H-J), paratype MHNG-ARTO-29033 from Ban Laem Pho (K-M), paratype MHNG-ARTO-29036 from Khao Phra - Bang Khram (N-P). (A) Anterior part of carapace, dorsal view. (B) Prosoma, ventral view. (C) Posterior part of coxae IV displaying enlarged retrolateral-distal heels, ventral view. (D) Left coxa I with wide band of spinules, ventral view. (E) Left coxa II with wide band of spinules, ventral view. (F, H, K, N) Vulva, ventral view. (G, I, L, O) Vulva, antero-ventral view. (J, M, P) Vulva, anterior view. Scale lines: 1.0 mm (F-P), 2.0 mm (A-E).

tarsi with a ventral pseudoscapula: very thin in distal two-thirds to three-fourth of tarsus I, thin in distal five-sixth of tarsus II, much denser and covering almost entire ventral side of tarsi III-IV. Leg I: metatarsus unmodified (Fig. 12N); tibia also unmodified and not incrassate (0.71 wide; tibia of shorter leg II in comparison 0.62 wide), without a mating clasper complex but instead with 2/3 prolateral-distal spines (Fig. 12N-P) and with a well-developed prolateral-distal slit organ (Figs 3A, 12T). All leg tarsi slightly spindle-shaped in their proximal half, cylindrical in distal half.

Spines: Palp: femur d1/2; patella, 0; tibia r9/11; tarsus d2 (one of them weak). Leg I: femur d6; patella v2 (long); tibia p3/4 (2/3 of them distally), r3/4, v7/9; metatarsus p4/5, r4/7, v6/8; tarsus p3, r3. Leg II: femur d5/6; patella v2 (long); tibia v8/9; metatarsus p4, v8; tarsus p4, r2/4. Leg III: femur d5/6; patella d3/4, p13/14; tibia p10, r6, v6/8; metatarsus d8/9, p1/2, r1, v9/10; tarsus p4/5, r3. Leg IV: femur d4/5; patella p11/12; tibia v6/7 (long); metatarsus v9; tarsus p5/7, r1/2. Leg coxa II with a broad longitudinal band of minute spinules (less distinct than in conspecific females); spinules on coxa I barely discernible.

Trichobothria as in males of other species. Paired leg claws with a row of 4-7 denticles on legs I-II, 3-5 on legs III-IV; on legs II-IV subproximal denticle usually larger than others; unpaired leg claws bare.

Opisthosoma oval, 5.42 long, 3.57 wide, mostly covered with short dark hairs, in posterior zone and on ventral surface also with longer hairs. Epiandrous spigots weakly spiniform (see Fig. 12E for more strongly spiniform spigots in male paratype). PMS 0.42 long, carrying one macro-spigot; PLS 1.11 long: proximal article 0.61, with one macro-spigot; median article 0.30, with four macro-spigots; distal article 0.20, with one macro-spigot.

FEMALE (allotype): *Colour in alcohol* (darker in living spider): Carapace mostly brown, slightly darkened between ALE and main eye group; black pigment around entire ALE and AME and around most of PLE and PME. Dorsal side of chelicerae, palps and legs slightly darker than carapace. Sternum and coxae I-II brown, coxae III-IV lighter; labium, palpal coxae and ventral side of chelicerae reddish brown; fang claws dark brown. Opisthosoma dorsally dark greyish brown, densely speckled with small light spots, with two light median patches in anterior half; genital area, booklung covers and spinnerets light brown, area between posterior booklung covers light greyish brown, posterior half of ventral side cream-coloured.

*Morphology and measurements*: Body 19.22 long. Carapace 6.46 long, 4.97 wide, smooth, with few very thin but relatively long hairs all over carapace, densest in posterior zone; medium-long bristles in front of ALE and between PME; two pairs of long bristles in anterior half of area between eye mound and fovea; a single very long bristle between AME. Entire eye group 1.27 long, 1.47 wide; ALE and AME separated by 0.60. MOQ 0.55

long, 0.80 wide. Eye diameters: AME 0.28, ALE 0.29, PME 0.22, PLE 0.35. No wrinkles lateral to eye mound. Pars cephalica moderately and evenly arched, its posterior zone at same level as eye mound in lateral view. Fovea distinctly procurved (Fig. 13A), 0.97 wide, occupying 21% of carapace width at that point. Proximal article of chelicera 2.53 long, stronger than in male; ventral groove with 5/6 large plus 1/2 small teeth on promargin and four large plus 1/2 small teeth on retromargin, and with two additional very small teeth between both rows; rastellum on long and narrow process, composed of 16/17 short, thick spines (stronger than in male) and several weaker and more pointed spines. Palpal coxa 2.66 long, 1.49 wide, with about 100 spinules of various sizes spread over almost entire ventral surface, in prolateral half stronger than in retrolateral half, the strongest ones in prolateral-proximal and in prolateral-distal corner (Fig. 13B). Labium 0.97 long, 1.23 wide, carrying two strong spinules. Sternum 3.64 long, 3.25 wide; labio-sternal suture relatively deep, of same colour as indistinct sigilla and as other parts of sternum (Fig. 13B).

Palp 10.53 long (3.51 + 2.21 + 2.34 + 2.47); tarsus slightly spindle-shaped; tibia dorsally with a pronounced, light-coloured subdistal pseudosegmentation.

Legs 3214. Leg I 11.69 long (3.77 + 2.47 + 2.40 + 1.95 + 1.10); leg II 10.62 long (3.64 + 2.27 + 1.92 + 1.69 + 1.10); leg III 10.29 long (2.79 + 2.27 + 1.46 + 2.08 + 1.69); leg IV 13.50 long (3.60 + 2.99 + 2.73 + 2.69 + 1.49).

Leg tarsi without pseudoscapula. Leg coxa IV with a pronounced heel on retrolateral-distal corner (Fig. 13C). Spines: Palp: femur p2; patella p1; tibia p20/21, r18/23; tarsus p24, r23/27, v4. Leg I: patella p2/0; tibia p14, r15/16; metatarsus p19/20, r20; tarsus p8, r9, v3/4. Leg II: patella, 0; tibia p7, r4; metatarsus p17/18, r7; tarsus p6, r3, v3/4. Leg III: patella d2, p17/19, r1/3; tibia p18/20, r13/15, v2 (long and weak); metatarsus p11/13, r9/10, v7/8; tarsus r0/1, v6/7. Leg IV: patella p22/24; tibia v3/4 (long and weak); metatarsus v7; tarsus r1, v14/16. No cluster of spinules dorso-distally on tibiae I-II or on palpal tibia. Leg coxa II with a broad longitudinal band of tiny denticles (as thick as nearby bristles but much shorter) in retrolateral half (Fig. 13E); coxa I equally so, but spinules less distinct (Fig. 13D).

Trichobothria as in females of other species. Palpal claw and paired leg claws with only one large subproximal denticle, on some limbs additionally with a small denticle; unpaired leg claws bare.

Opisthosoma oval, 9.42 long, 6.30 wide; with a mixture of short and medium-long dark hairs dorsally and ventrally. PMS 0.77 long, with one macro-spigot; PLS 1.69 long: proximal article 0.85, with three macro-spigots; median article 0.53, with 5/6 macro-spigots; distal article 0.31, with one macro-spigot.

Vulva (of paratypes see Fig. 13F-P): Receptacles relatively long and widely separated from each other; receptacular heads not much wider than receptacular stalks; essentially indistinguishable from vulva of *T. pylorus* comb. nov. (Fig. 5E-O).

**Variation:** In males ( $n = 7$ ) the carapace length ranges 4.42-4.94, the corresponding width 3.44-4.09. The largest conspecific female ( $n = 12$ ) has a 7.24 long and 5.97 wide carapace. The smallest and the largest male, as well as the largest female examined are all from the type locality. The subdistal embolic tooth is distinct in all males from the type locality (Fig. 12H-I), indistinct (Fig. 12J-K) to absent (Fig. 12L-M) in males from the other two localities; all males lack a subdistal embolic notch. Tibia I and metatarsus I are unmodified in all males (Fig. 12N-S). Instead of a mating clasper there are 1-3 strong spines prolaterally-distally on tibia I of all males: only one spine on both sides in the two males from Ban Laem Pho, 2-3 spines in males from the other two localities (three spines on both sides in the male from Khao Phra - Bang Khram). All males have a row of dorsal spines on the femora of legs and palps; in males from the type locality these spines are slightly more pronounced than in males from the other two localities. The pseudoscapula in males varies in expanse only on tarsus I, covering the distal two-thirds to four-fifths of the ventral side; on other legs there is no variation. All males have a row of 3-7 denticles on their paired tarsal claws. Females possess 1-3 large plus 0-2 small spinules on their labium; most males have no labial spinules, only one male from Ban Laem Pho has two anterior bristles with incrassate bases (i.e. spinules with a filiform apex, these are also present on palpal coxae; Fig. 12D). The AME are clearly larger than the PLE in all males examined; in all females they are distinctly smaller. All females carry a single, very long bristle between their AME. All females have a wide band of tiny spinules on coxae I-II; in females from the type locality these bands are slightly wider than in females from other localities. In all males examined the PMS carry one macro-spigot, in conspecific females 0-2 macro-spigots (one female from Ban Laem Pho with none on one side, one on the other; two females from the type locality and from Khao Phra - Bang Khram with two on both sides). Males have one macro-spigot on the proximal article of the PLS, 3-5 on its median article, and mostly one (one male from the type locality with none on one side) on its distal article. Females have 1-4 macro-spigots on the proximal article of the PLS, 4-8 on its median article, and 1-2 on its distal article. Variation in vulva morphology is shown in Fig. 13F-P.

**Distribution:** This species is known from three localities in southern Thailand: the type locality on the east coast, the other two localities further south, on the west coast (Fig. 1A). The latter two localities are only a few kilometres away from the mainland locality of *T. insularis* sp. nov.

**Biology:** *Habitat:* All spiders were collected from shaded soil banks. Two localities are near the coast: the type locality is an overgrown road side at the foot

of a hill covered with the remnant patch of a primary evergreen forest, about 100 m away from the coast; at Ban Laem Pho the spiders were found right above the rocky shore (Fig. 2M). At Khao Phra - Bang Khram spiders were found on the side of a rural road near a primary forest several kilometres away from the coast.

*Burrow structure:* All burrows were more or less straight and unbranched, up to 8.5 cm long, closed by a moderately thick door, and equipped with a soil pellet about 2 cm below the entrance. In males (all matured in captivity) doors were 0.8-0.9 cm long and 1.0-1.1 cm wide. The largest burrow (of a female) had a door 1.6 cm long and 1.9 cm wide. Some burrows at the type locality (but not elsewhere) had a small knob (like a door knob) in the centre of the outer side of their door. The largest soil pellet was 1.4 cm long, 1.4 cm wide and 1.9 cm high. Soil pellets from all three localities had the same overall shape as soil pellets of *T. pylorus* comb. nov. (see Fig. 2B-C), but are distinguished from them by a more or less wide, circular depression in the upper part of the frontal side (see Fig. 2D-G). This depression was usually uncovered, except for a single case in which a fine sheet of silk, with a central hole, was spun over the depression. *Phenology:* Males matured in captivity between early June and mid-October. One male matured (on 11.VI.) only eight days after being captured; the male that matured in mid-October was collected four months earlier. The presence of an empty egg case in the field at the beginning of June, but none in mid-June and in mid-September, suggests that mating starts in June and eggs are laid after mid-September; the spiderlings hatch and leave the burrow of the mother before June.

*Egg cases:* At the beginning of June an old empty egg case was found in the burrow of a female at Khao Phra - Bang Khram. It was 2.5 cm long, 1.5 cm wide and 0.7 cm high, of the same shape and colouration as in *T. birmanicus* sp. nov. (Fig. 2K-L).

### *Titanidiops insularis* Schwendinger, sp. nov.

Figs 1, 3E-F, 14-17

**Holotype:** MHNG-ARTO-29003, sample TH-07/11; male (matured end of IV.2008); Thailand, Phang Nga Prov., Ko Yao Distr., Ko Yao Yai, west of Ban Hin Kong, 8°02'N, 98°35'E, 60 m; 18.VII.2007; *leg.* P.J. Schwendinger.

**Paratypes:** MHNG-ARTO-29004-29006, sample TH-07/11; 3 males (matured 9.IV.2009; 8.VII.2009; 3.IV.2010); collected together with the holotype. – MHNG-ARTO-29007-29010, sample TH-07/11; 4 females; collected together with the holotype. – THNHM, sample TH-06/10; 1 male (matured 19.IV.2007); from the type locality; 25.IX.2006. – MHNG-ARTO-29011-29014; 4 females (including allotype MHNG-ARTO-29011; same data as for previous specimen. – MHNG-ARTO-29015, sample TH-06/08; 1 male (matured beginning of IV.2007);



Thailand, Phang Nga Prov., Ko Yao Distr., Ko Yao Noi, 8°09'N, 98°38'E, 60 m; 22.IX.2006. – MHNG-ARTO-29016, sample TH-09/06; 1 male (matured 18.III.2010); Thailand, Krabi Prov. & Distr., Thab Khaek - Hang Nak Hill Nature Trail, 80 m; 6.VI.2009. – MHNG-ARTO-29017, sample TH-08/07; 1 female; Thailand, Krabi Prov. & Distr., Thab Khaek - Hang Nak Hill Nature Trail, 8°06'N, 98°45'E, 50-80 m; 13./19. VI.2008. All specimens *leg.* P.J. Schwendinger.

**Other material examined:** MHNG-ARTO-29037-29042, sample IND-08/02; 6 males (matured 29.X.2009; 2.XI.2009; 10.XI.2009; 18.XI.2009; 5.I.2010; 10.I.2010); Indonesia, Bangka Belitung Island Prov., Pulau Belitung, Gunung Tajam, near Gurok Beraye W.F., 2°47'S, 107°52'E, 150 m; 20.IX.2008. – MHNG-ARTO-29043-29047, sample IND-08/02; 5 females; same locality and date as for previous specimens. – MHNG; 1 juvenile male; same data. All specimens *leg.* P.J. Schwendinger.

**Etymology:** The epithet is a Latin adjective (*insularis* = of or from an island) that refers to the occurrence of this species on islands.

**Diagnosis:** Similar to *T. tenuis* sp. nov., different in larger body size. Males distinguished from those of *T. tenuis* sp. nov. by wart-like hair bases on pars cephalica of carapace relatively smaller and more widely spaced (Figs 14A, 15A cf. Fig. 8A); hair bases on tibiae less distinctly wart-like; a prolateral distal spine present on femora I-II of some males (absent in all *T. tenuis* sp. nov. males); tibia I with a small prodorsal-distal process near mating clasper (Figs 3E-F, 14H-J, 15B-D; absent in *T. tenuis* sp. nov., Figs 3C, 8H-J); prolateral knee of metatarsus I less pronounced (Figs 14G, 15E cf. Fig. 8G). Vulvae of females different from vulva of holotype of *T. crassus* comb. nov. by having distinctly smaller receptacular heads (Figs 16E-M, 17 cf. Fig. 3H), and from vulvae of *T. pylorus* comb. nov. and *T. inermis* sp. nov. by receptacles closer to each

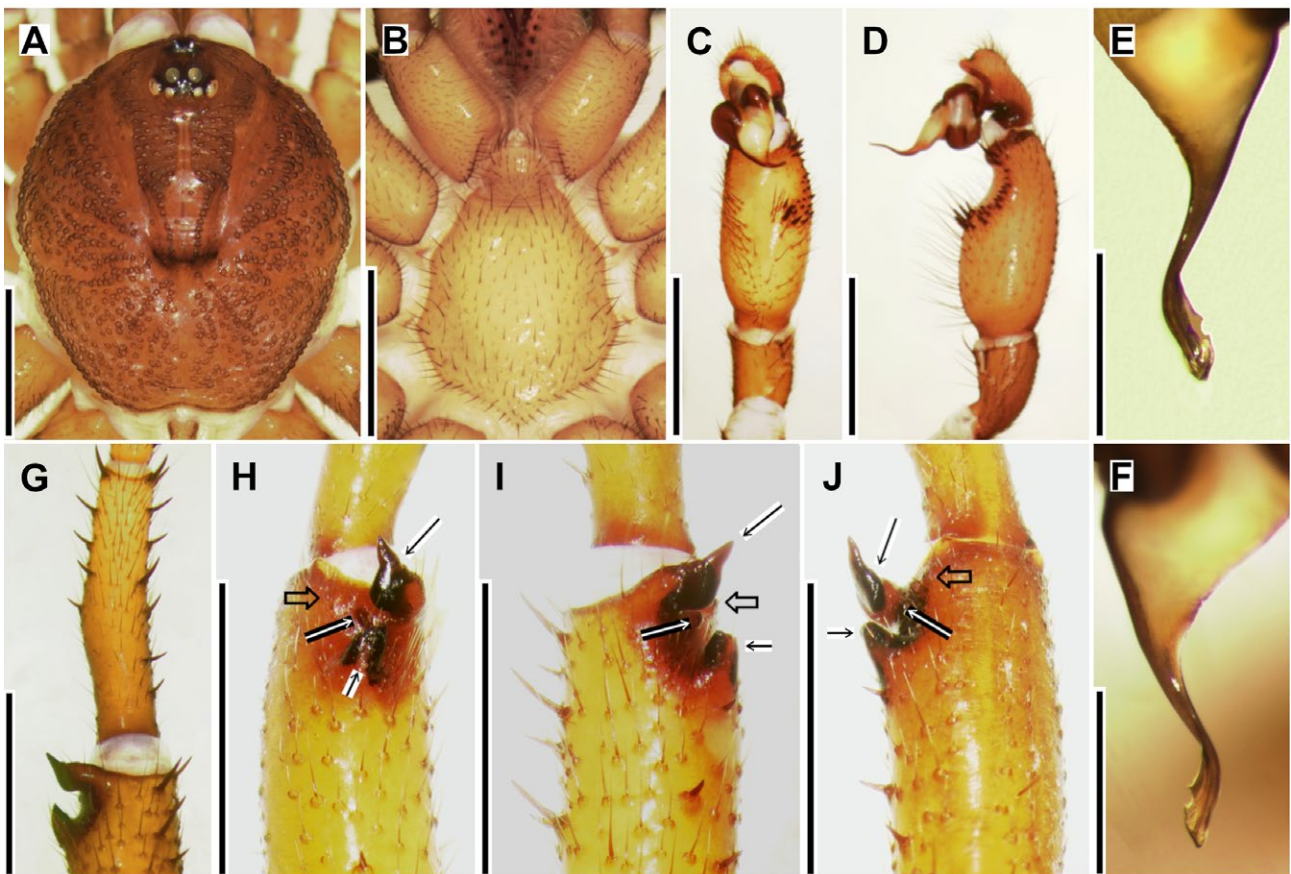


Fig. 14. *Titanidiops insularis* sp. nov., male holotype. (A) Carapace, dorsal view. (B) Prosoma, ventral view. (C) Distal part of left palp, ventral view. (D) Same, retrolateral view. (E) Apex of right embolus, ventral view. (F) Apex of left embolus, ventral view. (G) Metatarsus and distal part of tibia of left leg I, ventral view. (H) Mating clasper complex of left tibia I, prolateral view. (I) Mating clasper complex of right tibia I, proventral view. (J) Same, prodorsal view. Long black arrows indicate distal spur and megaspine; short black arrows indicate subdistal spur and megaspine; long white arrows indicate wart-like tubercle; hollow arrows indicate prodorsal-distal process. Scale lines: 0.5 mm (E-F), 2.0 mm (A-D, G-J).

other (Figs 16E-M, 17 cf. Figs 5E-O and 13F-P), but indistinguishable from females of other species treated here.

**Description:** MALE (holotype). *Colour in alcohol* (darker in living spider): Carapace reddish brown, with darkened area around eye mound continuing as two dark parallel, posteriorly narrowing bands back to fovea; areas between ALE and other eyes almost black (Fig. 14A). Chelicerae, palps and legs mostly brown, except for slightly darker femur to tibia I and proximal three-fourth of metatarsus I, and except for light brown distal half of metatarsi II-IV and entire tarsi II-IV. Ventral side of prosoma (including limbs) slightly lighter than dorsal side. Opisthosoma dorsally dark grey-brown, speckled with light spots, with two faint lighter patches in anterior half; ventrally uniformly light brown.

*Morphology and measurements:* Body 12.92 long. Carapace 4.71 long, 4.35 wide, covered with relatively small wart-like hair bases (Fig. 14A); corresponding hairs mostly short and weak, longest and adpressed halfway between eye mound and fovea. Eight eyes on bipartite mound, with a saddle between ALE and main

eye group; entire eye group 0.83 long, 0.90 wide; ALE and AME separated by 0.22. MOQ 0.42 long, 0.55 wide. Eye diameters: AME 0.26, ALE 0.24, PME 0.15, PLE 0.25. Several fine transversal wrinkles to left and right of anterior half of eye mound. Posterior zone of pars cephalica with a low boss, at same level as eye mound in lateral view. Fovea slightly procurved, 0.75 wide, occupying 18% of carapace width at that point. Proximal article of chelicera 1.82 long; ventral groove with 5/6 teeth on promargin and five teeth (plus two small ones one side) on retromargin; fang claw with sharp, straight proventral keel and with serrate retroventral keel; rastellum on long and narrow process, composed of 8/9 short, thick spines and several weaker and more pointed spines. Palpal coxa 1.69 long, 1.04 wide, with about 30 very short spinules, most of them not thicker than nearby bristles. Labium 0.58 long, 0.84 wide, with three weak spinules (not thicker than nearby bristles). Sternum 2.60 long, 2.34 wide; labio-sternal suture shallow and inconspicuous, it and sigilla of same colour as other parts of sternum (Fig. 14B).

Palp 7.68 long (2.67 + 1.43 + 2.44 + 1.14). Tibia moderately incrassate, 1.14 wide, retrolaterally with a curved band of 30/31 spines of various lengths in distal

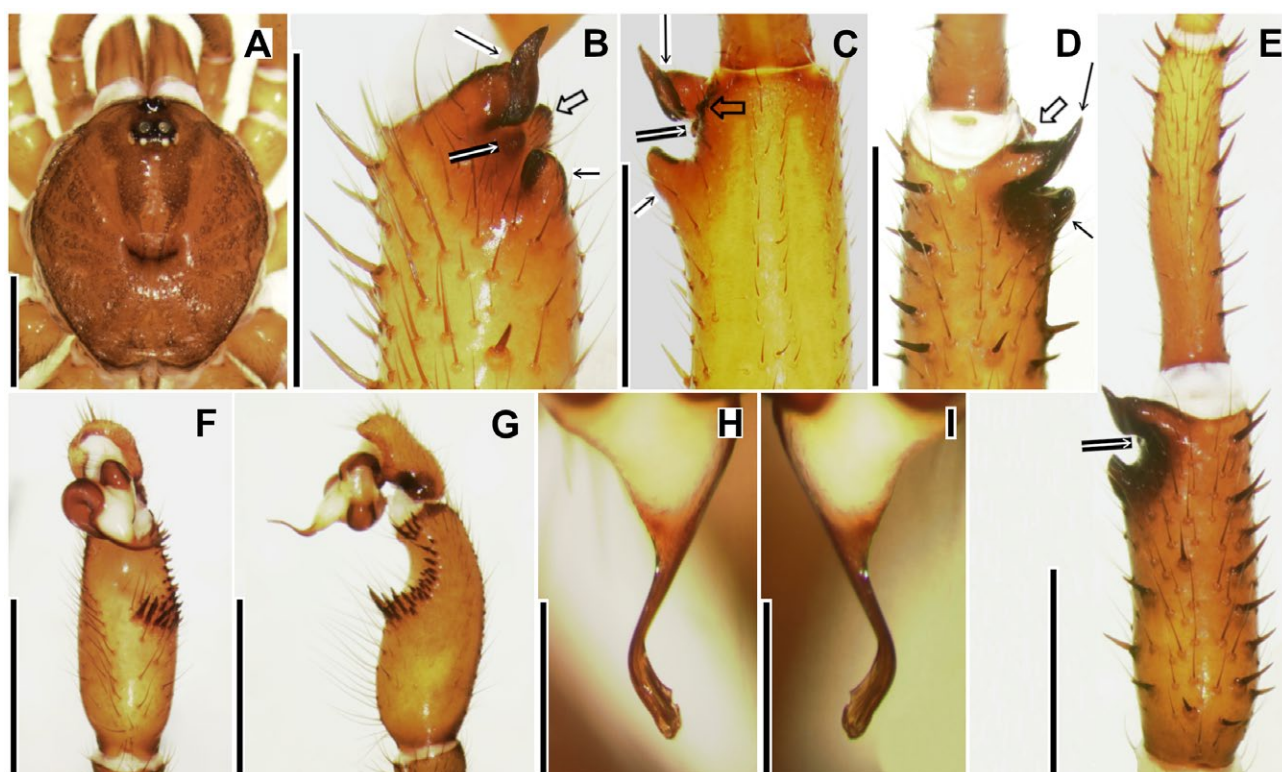


Fig. 15. *Titanidiops insularis* sp. nov., males from Belitung Island; specimen MHNG-ARTO-29040 (A, D-I), specimen MHNG-ARTO-29037 (B-C). (A) Prosoma, dorsal view. (B) Mating clasper complex of right tibia I, proventral view. (C) Same, dorsal view. (D) Same, ventral view. (E) Tibia and metatarsus of left leg I, ventral view. (F) Distal part of left palp, ventral view. (G) Same, retrolateral view. (H) Apex of right embolus, ventral view. (I) Apex of left embolus, ventral view. Long black arrows indicate distal spur and megaspine; short black arrows indicate subdistal spur and megaspine; long white arrows indicate wart-like tubercle; hollow arrows indicate prodorsal-distal process. Scale lines: 0.5 mm (H-I), 2.0 mm (A-G).



half (Fig. 14D). Tarsus short, distally with two short lobes and one dorsal spine. Palpal organ typical for the genus (Fig. 14C-D); apex of embolus with a distinct tooth proximal to a relatively deep notch (Figs 14E-F).

Legs 3214. Leg I 14.48 long ( $4.55 + 2.37 + 3.02 + 3.21 + 1.33$ ); leg II 12.70 long ( $4.03 + 1.95 + 2.63 + 2.76 + 1.33$ ); leg III 10.88 long ( $3.02 + 1.88 + 1.82 + 2.73 + 1.43$ ); leg IV 15.73 long ( $4.45 + 2.31 + 3.51 + 3.77 +$

1.69). Leg tarsi with a ventral pseudoscapula: in distal half of tarsus I, in distal four-fifth of tarsus II, in distal two thirds to three-fourths of tarsus III, essentially absent from tarsus IV (only a few scattered scopuliform hairs in distal four-fifths). Leg I: metatarsus slightly bent outward, on prolateral side with an indistinct knee below midpoint (Fig. 14G); tibia moderately incrassate (1.17 wide; tibia II in comparison only 0.78 wide), carrying

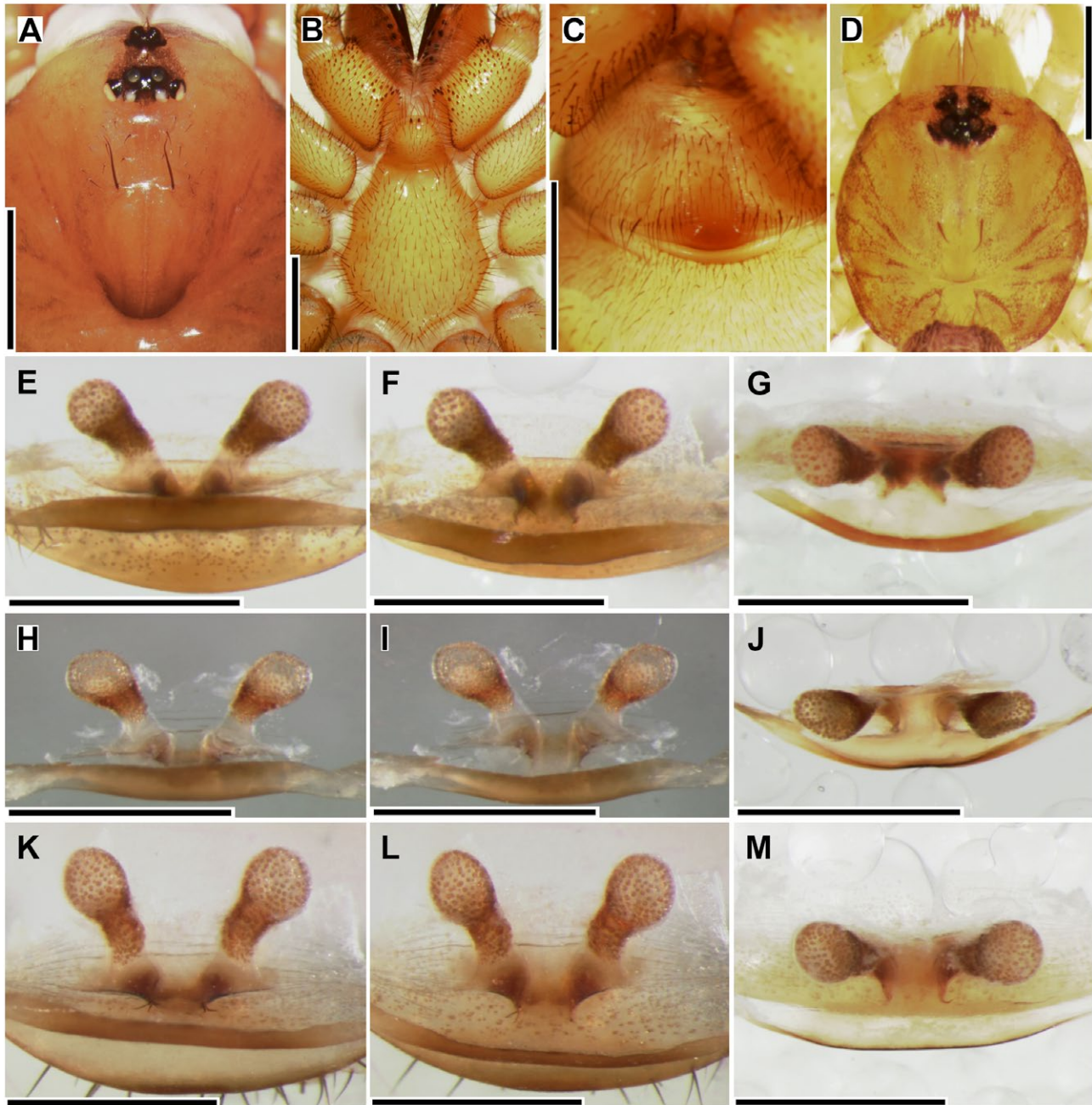


Fig. 16. *Titanidiops insularis* sp. nov., females and juvenile from Thailand; allotype (A-C), juvenile of female MHNG-ARTO-29008 (D); paratype MHNG-ARTO-29009 from Ko Yao Yai (E-G), paratype MHNG-ARTO-29013 from Ko Yao Yai (H-J), paratype MHNG-ARTO-29017 from Thab Khaek - Hang Nak Hill (K-M). (A) Anterior part of carapace, dorsal view. (B) Prosoma, ventral view. (C) Genital area, ventral view. (D) Prosoma, dorsal view. (E, H, K) Vulva, ventral view. (F, I, L) Vulva, antero-ventral view. (G, J, M) Vulva, anterior view. Scale lines: 0.5 mm (D), 1.0 mm (E-M), 2.0 mm (A-C).



a prolateral-distal mating clasper complex composed of: 1) a stout distal spur carrying a wide, distad-directed megaspine; 2) a smaller subdistal spur carrying a short, wide megaspine; 3) a small, dark, wart-like tubercle with same surface texture as nearby cuticle; 4) a small, conical prodorsal-distal process (Figs 3E, 14H-J). Leg tarsus II indistinctly spindle-shaped. Slightly enlarged hair bases (not as much as in males of *T. tenuis* sp. nov.) on tibiae of palps and legs, but not on other articles.

Spines: Palp: femur p1; patella, 0; tibia r30/31; tarsus d1. Leg I: patella v3; tibia p2 (megaspines) + 1/4, v9/11; metatarsus p5/6, r8; tarsus p3/4, r3. Leg II: patella v3/4 (weaker than on patella I); tibia p3/5, r4/5, v8; metatarsus p6/7, r7, v2; tarsus p3, r5/7. Leg III: patella d3, p10/11, v1/2; tibia p8/9, r3, v6/9; metatarsus d9/10, p3, v10; tarsus p3, r3. Leg IV: femur p1 (distally); patella p15/16; tibia v7/8; metatarsus v7/8; tarsus p3, v8/9.

Trichobothria as in males of other species. Paired leg claws with a large subproximal denticle, on anterior legs often additionally with a small denticle; unpaired leg claws bare.

Opisthosoma oval, 5.26 long, 3.77 wide, mostly covered with short dark hairs, in posterior zone additionally with longer hairs. PMS 0.42 long, without macro-spigots; PLS 1.29 long: proximal article 0.65, without macro-spigots; median article 0.33, with five macro-spigots; distal article 0.31, with one macro-spigot.

**FEMALE (allotype):** *Colour in alcohol* (darker in living spider): Dorsal side of prosoma mostly light orange-brown, except for slightly darker carapace and chelicerae; eye mound mostly darkened, black between eyes (Fig. 16A). Ventral side of prosoma slightly lighter than dorsal side; on chelicerae orange-coloured, on labium and sternum light reddish brown (Fig. 16B); rastellum and fang claw dark brown. Opisthosoma dorsally dark greyish brown, densely speckled with small light spots, with two light median patches in anterior half; ventrally mostly cream-coloured, except for darker epigynal area (Fig. 16C).

**Morphology and measurements:** Body 17.14 long. Carapace 5.94 long, 5.32 wide, smooth, with few short hairs on lateral margins and on both sides of eyes; bristles in front of ALE and of AME; longer bristles only in anterior part of area between eye mound and fovea, posterior-most pair very long. Entire eye group 1.05 long, 1.14 wide; ALE and AME separated by 0.36. MOQ 0.47 long, 0.61 wide. Eye diameters: AME 0.24, ALE 0.26, PME 0.19, PLE 0.28. No wrinkles lateral to eye mound. Posterior zone of pars cephalica with a pronounced boss, slightly higher than eye mound in lateral view. Fovea strongly procurved (Fig. 16A); angles between posterior and lateral parts less distinct than in females of other congeners treated here, 1.23 wide, occupying 24% of carapace width at that point. Proximal article of chelicera 2.92 long, stronger than in male; ventral groove with five strong teeth on pro- and retromargin; rastellum on long and narrow process, composed of 17/20 short,

thick spines (stronger than in male) and several weaker and more pointed spines. Palpal coxa 2.27 long, 1.40 wide, with about 70 spinules of various sizes spread over almost entire ventral surface, the strongest ones in prolateral half. Labium 1.04 long, 1.23 wide, carrying two strong spinules. Sternum 3.44 long, 3.05 wide; labio-sternal suture relatively long and deep, of same colour as indistinct sigilla and other parts of sternum (Fig. 16B). Palp 9.60 long (3.18 + 2.14 + 2.14 + 2.14); tarsus slightly spindle-shaped; tibia dorsally with a weakly pronounced subdistal pseudosegmentation.

Legs 2314. Leg I 10.97 long (3.51 + 2.47 + 2.27 + 1.75 + 0.97); leg II 9.81 long (2.99 + 2.21 + 1.95 + 1.62 + 1.04); leg III 10.33 long (2.79 + 2.34 + 1.62 + 2.18 + 1.40); leg IV 14.00 long (3.90 + 2.79 + 2.89 + 2.86 + 1.56). Leg tarsi without pseudoscopula; metatarsus I indistinctly, metatarsus II very indistinctly spindle-shaped.

Spines: Palp: femur p1; patella p1, r1 (weak); tibia p20, r21/23; tarsus p18/21, r21, v2. Leg I: patella, 0; tibia p16, r22/24; metatarsus p14/15, r19/20; tarsus p6/8, r7/8, v3. Leg II: patella, 0; tibia p9, r13/16; metatarsus p13, r9/12; tarsus p7/8, r4, v3. Leg III: patella d3, p13/14; tibia p11/12, r3/4, v2 (long and weak); metatarsus d11/12, v4; tarsus p1/2, v5/6. Leg IV: patella p18/20; tibia v4 (long and weak); metatarsus v8; tarsus r1, v12/13. A cluster of 10/11 spinules dorso-distally on leg tibia I; 16/17 spicules on tibia II; a dorso-distal cluster of four spinules on palpal tibia.

Trichobothria as in females of other species. Paired leg claws and unpaired palpal claw all with only one large subproximal denticle; unpaired leg claws bare.

Opisthosoma oval, 7.92 long, 5.65 wide; with a mixture of short and medium-long dark hairs dorsally, the longest ones in posterior zone; ventrally with many short hairs and a few long bristles in genital area. PMS 0.68 long, without macro-spigots; PLS 1.65 long: proximal article 0.88, without macro-spigots; median article 0.39, with 6/7 macro-spigots; distal article 0.38, with one macro-spigot.

Vulva (of paratypes see Fig. 16E-M, of females from Belitung Island see Fig. 17): Receptacles relatively long and close to each other; receptacular heads not much wider than receptacular stalks; essentially indistinguishable from vulvae of *T. birmanicus* sp. nov. (Fig. 7F-P), *T. tenuis* sp. nov. (Fig. 9D-N) and *T. sayamensis* sp. nov. (Fig. 11F-O).

**Variation:** In males (n = 13) the carapace length ranges 4.48-5.45, the corresponding width is 4.09-5.06. The largest conspecific female (from the type locality; out of 14 females examined) has a 6.70 long and 5.71 wide carapace; in the smallest reproductive female (from Belitung Island) it is only 3.96 and 3.38, respectively. There is a wide overlap in measurements of specimens from localities in Thailand and from the locality on Belitung Island. The subdistal embolic tooth and notch are distinct in all males examined (Figs 14E-F, 15H-

I). In most males from Thailand the metatarsus I has a weak but distinct prolateral knee (Fig. 14G); in one male from Thailand (from Ko Yao Noi) and in all males from Belitung Island that knee is indistinct (Fig. 15E). The subdistal coupling spur carries a short megaspine that ranges in shape from widely arced to triangular, the latter with a widely to acutely pointed apex. In addition to two coupling spurs with megaspines and a wart-like tubercle without a shiny black cap, all males examined also have a small conical prodorsal-distal process on tibia I (Figs 3E-F, 14H-J, 15B-D). The expanse of the ventral pseudoscapula on leg tarsi I-III of males is

quite variable: covering a fourth to half of tarsus I; half to four-fifths of tarsus II; two-fifths to three-fifths of tarsus III; all males lack a pseudoscapula on tarsus IV. Five males from Thailand have one short prolateral spine distally on femur I, all other males have none. Females possess 2-4 large plus 0-4 small spinules on their labium; males have 0-4 weak labial spinules. The AME are equally large to distinctly larger than the PLE (Fig. 14A) in males from Thailand, slightly smaller to slightly larger (Fig. 15A) in males from Belitung Island; in all females examined the AME are slightly to distinctly smaller than the PLE (Fig. 16A). The PMS

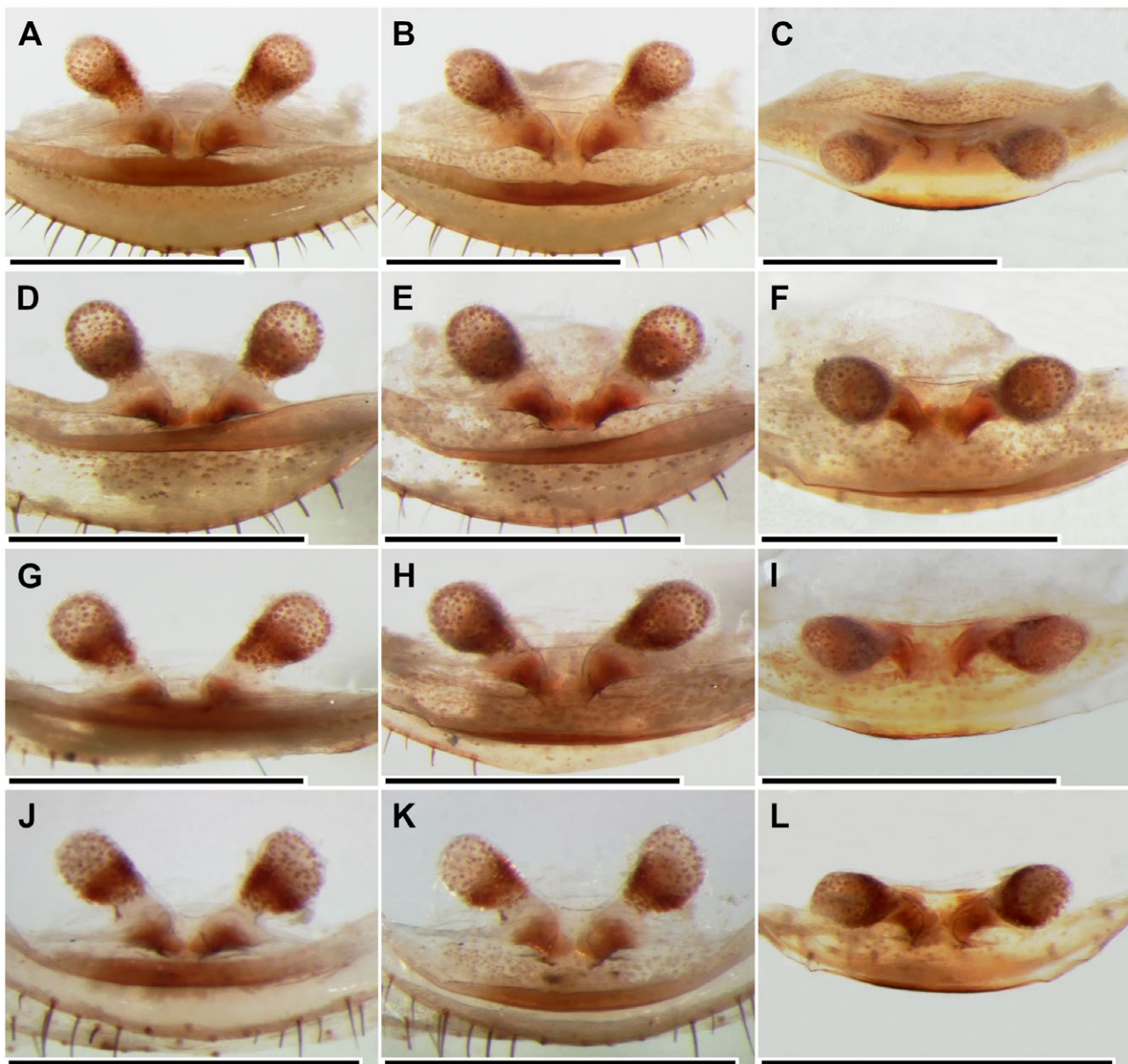


Fig. 17. *Titanidiops insularis* sp. nov., females from Belitung Island; specimen MHNG-ARTO-29045 (A-C), specimen MHNG-ARTO-29047 (D-F), specimen MHNG-ARTO-29046 (G-I), specimen MHNG-ARTO-29044 (J-L). (A, D, G, J) Vulva, ventral view. (B, E, H, K) Vulva, antero-ventral view. (C, F, I, L) Vulva, anterior view. Scale lines: 1.0 mm.

and the proximal article of the PLS always lack macro-spigots; the median article of the PLS has 3-11 (mostly 4-7) macro-spigots; the distal PLS article always has a single macro-spigot. There is no clear gap in the genital morphology of females from Thailand and Indonesia: in most females from Belitung Island the receptacles are relatively shorter (Fig. 17D-L) than in females from Thailand (Fig. 16E-M), but not so in specimen MHNG-ARTO-29045 (Fig. 17A-C).

**Distribution:** This species is known from three localities on the west coast of southern Thailand (two on islands in the Phang Nga Bay and one on the nearby mainland; Fig. 1A), as well as from a locality on the Indonesian island of Belitung (Fig. 1B). The Thai and Indonesian localities are separated by about 1500 km (see also Discussion - The *T. insularis* sp. nov. disjunction). The mainland locality in Thailand is only a few kilometres away from one of the localities of *T. inermis* sp. nov.

**Biology:** *Habitat:* Spiders were collected from earth banks on the sides of a dirt road, of a footpath and of a stream, all in shady places within primary forests or rubber tree plantations.

*Burrow structure:* All burrows inspected were straight and unbranched, up to five centimetres long, without a soil pellet, closed by a moderately thick door. In males (all matured in captivity) doors were 0.75-0.95 cm long and 0.85-1.1 cm wide. The largest burrow (of a female) had a door 1.3 cm long and 1.5 cm wide.

*Phenology:* Males from Thailand matured mostly in April, one male in early July; males from Belitung Island matured between late October and early January. In Thailand two egg cases containing second and third instar spiderlings were found in the field in mid-July, and one egg case containing third instar spiderlings in late September; a fourth female from Thailand built an egg case undetected in captivity and third instar spiderlings emerged from it in early January. On Belitung Island two egg cases containing second and third instar spiderlings were found in the field in late September. The populations in Thailand and in Indonesia have different phenologies.

*Egg cases:* These were 1.1-1.7 cm long, 0.8-1.1 cm wide and 0.5-0.8 cm high, of the same shape and colour as in *T. birmanicus* sp. nov. (Fig. 2K-L). They contained 26, 61, 69, 91, 104 and 129 spiderlings.

*Juveniles:* As in other congeneric species treated here, second instar spiderlings are pale, without bristles or spines. They move about clumsily and remain in the egg case. Third instar juveniles are well pigmented, furnished with bristles and weak spines, with the ALE on the anterior carapace margin (Fig. 16D), but not as close to each other as in larger spiders. These spiderlings are agile, remain in the egg case for a few days and then emerge from it to disperse and build their own tiny burrows. No attempts to perform ballooning have been observed.

### *Titanidiops* sp.

**Remarks:** Three females (MHNG-ARTO-29048-29050) were collected by P.J. Schwendinger on Ko Chang [9°49'N, 98°26'E; Thailand, Ranong Prov. (Fig. 1A); different from the larger and better-known Ko Chang in Trat Prov.] which cannot be unequivocally placed in any of the species treated above. The corresponding male is still unknown. Most *Titanidiops* species in South-east Asia (except for *T. pylorus* comb. nov. and *T. inermis* sp. nov., to which these three females clearly do not belong; they also do not construct soil pellets) are difficult to distinguish on the basis of female specimens only. Genital morphology (not illustrated here) and body size indicate that these three females likely belong to *T. sayamensis* sp. nov.

### *Idiops* sp. or *Ctenolophus* sp.

The SMF houses a single male (SMF 85a; partly desiccated, with three legs detached) which is labelled "Batu-Höhle, leg. Klingel, 15.XI.1961 oder Penang Insel, leg. Klingel, 1.X.1961". The specimen was found in the collection of Hans Klingel (1932-2019), in a vial together with liphistiid spiders, labelled as originating from either the Batu Caves or from Penang Island. Surprisingly the specimen has a short proximal row of small retromarginal teeth on its cheliceral groove and therefore it either belongs to *Idiops* (occurring in the Neotropics) or to *Ctenolophus* (occurring in South Africa), not to *Titanidiops*. This specimen differs from all *Idiops* males illustrated in Yamamoto (2013) and in Fonseca-Ferreira *et al.* (2021) by possessing an unusually long, sigmoid distal coupling spur and a strongly reduced (to a small tubercle without an apical spine) subdistal coupling spur, and by having the prolateral knee of metatarsus I developed as a transversal ridge instead of a cone or mound. Therefore this male presumably belongs to an undescribed species, and we strongly doubt that the ambiguous locality data are correct. If correct, this would be the only known locality of an idiopid species in Peninsular Malaysia, which would not be a big surprise considering the presence of a population of *T. insularis* sp. nov. on Belitung Island, Indonesia. It would also be the only confirmed occurrence of the genus *Idiops* or of the genus *Ctenolophus* in Asia, and that would be a big surprise. However, we strongly believe that this specimen was placed in the wrong vial and was actually collected in the Neotropics, or, more likely, in Africa where Klingel has carried out extensive field work on mammals.

## DISCUSSION

***Titanidiops* and *Idiops*:** Our study of South-east Asian *Titanidiops* species shows that the relative size of the AME is clearly unsuitable for a distinction between



*Idiops* and *Titanidiops* as proposed by Simon (1892: 89-90, figs 90-91) [this distinction was actually between *Idiops* and *Acanthodon* Guérin-Ménéville, 1838, but he had *Acanthodon* (now a synonym of *Idiops*) represented by *A. compactus* (originally *I. compactus*) which later became the type species of *Titanidiops*]. The same author (Simon, 1903: 888) later recognized that his earlier distinction was based on a sexually dimorphic character. That is confirmed here. Most (but not all) males examined in the present study have AME that are clearly larger than the remaining eyes (see, e.g., Fig. 4B) and thus they would belong to *Idiops*. The conspecific females, however, have all eight eyes more or less equal in size (see, e.g., Fig. 5A) and they therefore belong to *Titanidiops*. We here follow the recent distinction of both nominal genera given by Yamamoto (2013: 91-92, fig. 6A-D) and by Fonseca-Ferreira *et al.* (2021: 7, fig. 5A-C). It states that *Idiops* has unequal rows of promarginal and retromarginal teeth on the cheliceral groove: the retromarginal row being much shorter and consisting of much smaller teeth than the promarginal row (Fig. 2A) whereas *Titanidiops* has equally long rows of more or less equally large cheliceral teeth (see, e.g., Fig. 7C). Although Simon based his initial distinction of both genera on an unsuitable character (i.e. relative size of the AME), his assumption that *Idiops* is a New World genus and *Titanidiops* an Old World genus (Simon, 1903: 888) appears to be correct. The generic placement of all Asian and African species currently under *Idiops* needs to be re-evaluated. Ten species which are at present listed under *Idiops* (World Spider Catalog, 2024), but according to available (in the case of Yamamoto, 2013 unpublished) information clearly belong to *Titanidiops*, are here formally transferred. The names of these species, and between brackets the literature or new illustrations on which our decision is based, are given below:

*Titanidiops bombayensis* (Siliwal, Molur & Biswas, 2005) comb. nov. [see Mirza & Sanap, 2012: 88, fig. 11]

*Titanidiops bonny* (Siliwal, Hippargi, Yadav & Kumar, 2020) comb. nov. [see Siliwal *et al.*, 2020: 16782, fig. 15]

*Titanidiops crassus* (Simon, 1884) comb. nov. [see Yamamoto, 2013: 36, 171, 178; he has examined the female holotype deposited in the MNHN]

*Titanidiops joida* (Gupta, Das & Siliwal in Gupta *et al.*, 2013) comb. nov. [see Gupta *et al.*, 2013: 241, fig. 2D]

*Titanidiops medini* (Pratiharihar & Das in Pratiharihar *et al.*, 2020) comb. nov. [see Pratiharihar *et al.*, 2020: 210, fig. 5]

*Titanidiops nilagiri* (Das & Diksha in Das *et al.*, 2019) comb. nov. [see Das *et al.*, 2019: 680, fig. 2D-E]

*Titanidiops oriya* (Siliwal in Gupta *et al.*, 2013) comb. nov. [see Gupta *et al.*, 2013: 247, fig. 4C-D]

*Titanidiops pylorus* (Schwendinger, 1991) comb. nov. [see Figs 4C, 5B; types in MHNG examined]

*Titanidiops robustus* (Pocock, 1898) comb. nov. [see Yamamoto, 2013: 36, 182; he has examined the female holotype deposited in the NHML]

*Titanidiops vankhede* (Siliwal, Hippargi, Yadav & Kumar, 2020) comb. nov. [see Siliwal *et al.*, 2020: 16792-16793, figs 29-30, 42]

All new species described here also possess a long row of large retromarginal cheliceral teeth and therefore correspond to the current diagnosis of the genus *Titanidiops*. We have no information on the cheliceral teeth of the remaining Asian species that at present are placed in *Idiops*. They all need to be revised, and we predict that they also belong to the genus *Titanidiops*. This view is shared by Rafael Fonseca-Ferreira (personal communication) who is currently working on a genomics-based revision of the family Idiopidae.

**Macro-spigots:** A conspicuous character of all *Titanidiops* specimens examined are macro-spigots, situated among normally developed spigots on the ventral side of the four spinnerets (Figs 5C-D, 7E, 11D-E). Macro-spigots were also found in true *Idiops* (specimens in MHNG examined), in *Heligmomerus* (see Siliwal *et al.*, 2010: image 8, fig. 9) and in several genera of trapdoor spiders in other families: *Cteniza* (see Decae *et al.*, 2019: 504, figs 21-22), *Ummidia* (see Decae, 2010: 333, 336), *Conothele* (see Decae *et al.*, 2021: 303, figs 5E, 7E), *Latouchia* (see Decae & Caranhac, 2020: 564, figs 10, 25; Decae *et al.*, 2021: 314, figs 9D, 11D), *Nemesia* (see Decae, 2005: 148; Decae & Di Franco, 2005: 137, fig. 9), *Iberesia* (see Luis de la Iglesia, 2019: 160, fig. 14B; Luis de la Iglesia *et al.*, 2021: 171, figs 15, 28). Macro-spigots are also present, although less pronounced than in *Titanidiops*, in *Prothemenops*, the other idiopid genus known from South-east Asia. The number and distribution of macro-spigots on the spinnerets is quite variable, therefore this character is of only limited value for species identification and distinction. Nevertheless, it can be stated that *T. pylorus* comb. nov. and *T. inermis* sp. nov. stand apart from all other species examined by having most of their specimens furnished with macro-spigots on the PMS and on all three articles of the PLS, often with two macro-spigots on the distal PLS article (Fig. 5C-D). In most specimens of other congeners examined the PMS and the proximal article of the PLS lack macro-spigots, and the distal article of the PLS carries only a single macro-spigot (Figs 7E, 11D-E).

**Mating clasper complex:** Most *Idiops* and *Titanidiops* males (except those of *T. inermis* sp. nov. and *Idiops germaini* Simon, 1892) have their tibia I armed with a prolateral-distal clasping apparatus with which they hold females in position during mating (Schwendinger, 1991: fig. 25). This mating clasper is composed of: 1) Two more or less distinctly developed spurs (the distal one always larger than the subdistal one), each normally carrying a single megaspine (in only one abnormal specimen multiple megaspines were found; Fig. 8I-J).

2) A small wart-like tubercle (e.g., Fig. 3C-G), which is called a “tubérculo prolateral asociado à apófise tibial” by Yamamoto (2013: 85-86, fig. 26C, E) and a “putative slit organ” by Fonseca-Ferreira *et al.* (2021: 9, fig. 6G-I). In males of *T. sayamensis* sp. nov. this tubercle is composed of a very short crater-like base covered by a low cap or dome with a shiny black surface (Figs 3D, 10L-O). This shiny black cap was not found on the wart-like tubercles of males of *T. birmanicus* sp. nov., *T. tenuis* sp. nov. and *T. insularis* sp. nov.; males of *T. pylorus* comb. nov. and *T. inermis* sp. nov. have no wart-like tubercle.

3) In *T. birmanicus* sp. nov. and *T. insularis* sp. nov. there is a domed or conical process slightly dorso-distally to the wart-like tubercle (Figs 3E-G, 6H, 14H-J, 15B-D). The male syntype of *T. constructor* from south-eastern India also has such a process (Schwendinger, 1991: fig. 16).

4) In *T. inermis* sp. nov. (without a mating clasper) a well-developed and clearly visible slit organ can be found prolaterally-distally on tibia I of males (Figs 3A, 12T). In males of other species treated here (all with a mating clasper) this slit organ is not obvious, but instead a tiny light spot can be found at the same position (Fig. 3B-G). Our interpretation of these structures is as follows:

Ad 1) The distal and subdistal spurs and megaspine on tibia I of males of most *Titanidiops* species are modifications of spine bases (developed into spurs) and of the corresponding long slender spines (developed into short thick megaspines). In males of *T. inermis* sp. nov. there are no spurs and megaspines (Figs 2J, 3A, 12N-T); in males of *I. germaini* two prolateral-distal spines are enlarged and sit on slightly raised bases (Fonseca-Ferreira *et al.*, 2021: fig. 18G-H). These two cases could be plesiomorphic, or – more likely – they could be autapomorphic reversions, as Fonseca-Ferreira *et al.* (2021: 33) postulate for *I. germaini*. A similar situation exists in the genus *Prothemenops*. Males of three species in the southern part of central Thailand lack a mating clasper (Schwendinger & Hongpadharakiree, 2014: figs 2I-J, 5I-J, 8J-K) whereas males of the type species (Schwendinger, 1991: figs 8-9) and more than ten as yet undescribed species from more northern parts of Thailand, from Cambodia and Laos, possess a mating clasper that is quite similar to the one in *Titanidiops*, being composed of two spurs carrying megaspines.

Ad 2) We believe that the wart-like tubercle is not a slit organ, but another modification of a spine and its base. In males of *T. sayamensis* sp. nov. the basic structure is still discernible: the short crater-like base is not different from bases of normal spines on tibia I, and the domed cap has a shiny black surface like the shafts of normal spines. We interpret this structure as a strongly reduced spine. Males of *T. birmanicus* sp. nov., *T. tenuis* sp. nov. and *T. insularis* sp. nov., as well as those of many other congeners have lost the rudimentary spine, but its base is still present, modified to a wart-like tubercle with the same surface texture as, but usually darker than, the

surrounding cuticle (Figs 3C, E-G, 6H-J, 8H-J, 14G-J, 15B-E). Males of *T. pylorus* comb. nov. have lost even that remnant (Figs 3B, 4G-I).

Ad 3) The conical process close to the wart-like tubercle may also have developed from a spine base, but, unlike in the wart-like tubercle, we see no indication for this. It may be a completely new structure.

Ad 4) Since the tiny light spot (Fig. 3B-G; not visible in our photos) next to the wart-like tubercle in males of most *Titanidiops* species is in the same position as the well-developed prolateral-distal slit organ in males of *T. inermis* sp. nov. (Figs 3A, 12T), we assume that these are homologous. The light spot appears to be a reduced slit organ.

**The relationships of *T. inermis* sp. nov.:** Since we did not carry out a phylogenetic analysis, the relationships between the species examined are currently unclear. Nevertheless, we here allow ourselves to speculate about the relationships of *T. inermis* sp. nov., which is the most striking of these species and which seems to occupy an isolated phylogenetic position. Some of its morphological characters are unique and therefore do not tell us anything about relationships. These are: 1) the lack of a mating clasper complex in males (Figs 3A, 12N-T); 2) an unmodified metatarsus I in males (Fig. 12N; elsewhere only found in one deviant male of *T. pylorus* comb. nov., Fig. 4I); 3) spiniform epiandrous spigots in males; 4) enlarged heels on the retrolateral-distal corner of coxae IV in females (Fig. 13C); 5) a band of spinules on the ventral side of leg coxae I-II in females (Fig. 13D-E). The latter character was not found in females of the other *Titanidiops* species examined, or in the female holotype of *T. crassus* comb. nov. (Yamamoto, 2013: 287, annex 1); nor is it known from any other *Titanidiops* species. Females of *T. compactus* and *T. robustus* comb. nov. have such spinules on coxa III (Yamamoto, 2013: 288, annex 1), and females of a few Indian species (e.g., *T. vankhede* comb. nov., see Siliwal *et al.*, 2020: 16793, fig. 41) have them on coxa IV. Among the Idiopinae only a few *Gorgyrella* species (e.g., *G. hirschhorni* Hewitt, 1919; see Hewitt, 1919: 205) in southern Africa possess spinules on any or all of coxae I-III.

Other morphological characters are shared only between *T. inermis* sp. nov. and *T. pylorus* comb. nov. but no other congeners in South-east Asia, indicating a close relationship between these two species. These characters are: 1) a smooth carapace in males (Fig. 12A-B and Fig. 4A-B); 2) a longitudinal row of dorsal spines on all leg femora of males; 3) comb-like paired tarsal claws in males; 4) a pseudoscopula covering almost the entire ventral side of tarsus IV in males; 5) widely separated receptacles in females (Fig. 13F-P and Fig. 5G-O); 6) the presence of macro-spigots on the posterior median spinnerets and on all three articles of the posterior lateral spinnerets in males and females (Fig. 5C-D).

The strongest indication of a close relationship between *T. inermis* sp. nov. and *T. pylorus* comb. nov., however, comes from a behavioural character, i.e. both species construct elaborate soil pellets of very similar shapes as part of a complex defence mechanism in their burrows (Fig. 2D-G and Fig. 2B-C). No such soil pellets are known from other idiopid spiders. A parallel case exists in the genus *Euoplos* Rainbow, 1914 (Idiopidae, Arbanitinae): four species in eastern Australia, which all build unusual palisade burrow entrances, were found to form a monophyletic group (Wilson *et al.*, 2019). If the presumed close relationship between *T. inermis* sp. nov. and *T. pylorus* comb. nov. is proven true in a phylogenetic analysis in the future, then the lack of a mating clasper in males of *T. inermis* sp. nov. is a reversion.

**The *T. insularis* sp. nov. disjunction:** On the basis of morphology the Thai and Indonesian populations of this species cannot be distinguished as two distinct species. All minor differences that we found between them (e.g., generally longer receptacles in females from Thailand; Fig. 16E-M cf. Fig. 17) overlap. However, these populations are about 1500 km from each other, without a continuous land connection and without any other known *Titanidiops* localities between them (Fig. 1; the *Idiops* sp. or *Ctenolophus* sp. record from Peninsular Malaysia is extremely doubtful), which is unusual for trapdoor spiders. Comparably large geographical ranges were reported for *Idiops* spp. in Brazil (Fonseca-Ferreira *et al.*, 2021: figs 3B, 4C; Fonseca-Ferreira *et al.*, 2023: fig. 1), but these are all on the same landmass. Several scenarios could explain this striking disjunction: 1) *Titanidiops insularis* sp. nov. was introduced to Belitung Island by man, e.g., in the soil between roots of planted trees. This is unlikely since the first author found the spiders in the last remaining patch of pristine rainforest but nowhere else on the island. 2) Ballooning is a possibility discussed for widely distributed *Idiops* species in Brazil by Fonseca-Ferreira *et al.* (2021: 66). For Idiopidae this mode of potential long-distance transportation has so far only been observed in *Neocteniza toba* Goloboff, 1987, a species widely distributed in Argentina, Paraguay and Brazil (Rossi *et al.*, 2021: 472-473, fig. 19). We think that ballooning – if performed by *T. insularis* sp. nov. – over such a distance is quite unlikely. The early instar spiderlings, which had just emerged from the egg container, would have to be transported by wind currents over 1500 km, quite high up in the atmosphere where it is too cold and for most of the time also too dry for them to survive for longer than a few hours. 3) Another option is overland migration from southern Thailand to Peninsular Malaysia, and from there by oversea island hopping to Sumatra, to Bangka Island and finally to Belitung Island on flotsam or rafts (e.g., uprooted trees washed into the sea). This also is an unlikely scenario, because *Titanidiops* was never

found burrowing in dead wood (as the halonoproctid *Conothele* repeatedly was; observations by the first author), and because we have no reliable records of *Titanidiops* (or any other idiopids) in the intervening area, especially not from Peninsular Malaysia (only a most doubtful *Idiops* sp. or *Ctenolophus* sp. record; see above). 4) The Belitung Island population could be the remnant of a once continuous geographical range from the time when Sundaland (= the Sunda Shelf) was permanently above sea level. About 400,000 years ago Sundaland began to subside and become partially flooded, with temporary, relatively short (in geological terms) re-exposures during glaciation events in the Quaternary (Sarr *et al.*, 2019). Flooding of most of the area between Sumatra and Borneo could have left a *T. insularis* sp. nov. population on Belitung Island. Other conspecific populations between southern Thailand and Belitung Island may have become extinct, or simply have not been discovered yet. 5) The populations in Thailand and the widely disjunct population in Indonesia could represent two cryptic species. Cryptic species complexes are assumed for *Idiops* in the Neotropics by Fonseca-Ferreira *et al.* (2021: 66). An analysis of genomic data would be the most suitable way to solve this mystery. At this stage we believe that a combination of the last two scenarios is the most probable explanation for this disjunction. We assume that both *T. insularis* sp. nov. populations are actually distinct but very closely related species, or different subspecies of the same species, which have been geographically and reproductively separated from each other for up to 400,000 years.

## ACKNOWLEDGEMENTS

The Biology Department of Chiang Mai University provided research facilities for the first author. The National Research Council of Thailand granted him a scholarship, and the Forestry Department of Thailand permitted collecting spiders in protected areas. Saowapha Sonthichai (Chiang Mai University, Thailand) donated a male specimen of *T. pylorus* comb. nov. and organized field trips in northern Thailand. Andreas Schulz (Leverkusen, Germany) accompanied the first author to Belitung Island. Flávio U. Yamamoto (formerly Instituto Butantan, São Paulo, Brazil) kindly allowed us to use information from his unpublished thesis. Rafael Fonseca-Ferreira (Instituto Butantan, São Paulo, Brazil) shared information, pointed out additional publications, reviewed the manuscript and greatly helped to improve it. John Hollier (MHNG) edited the manuscript and checked the text for linguistic shortcomings. Christina Lehmann-Graber scanned the line drawings, and Lionel Monod (both in MHNG) provided additional help with the discussion and with graphics. Peter Jäger (SMF) sent us an *Idiops* sp. or *Ctenolophus* sp. male, which was allegedly collected in Malaysia, for examination.



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