

*Dedicated to Christa Deeleman-Reinhold*

## **High species diversity, male-female coevolution, and metaphyly in Southeast Asian pholcid spiders: the case of *Belisana* Thorell 1898 (Araneae, Pholcidae)**

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with 642 figures and 3 appendices

**Abstract:** The species-rich Southeast Asian spider genus *Belisana* Thorell 1898 is revised. Previously, the genus contained only two species. Nine species are transferred from *Spermophora*, and 53 species are newly described. Diagnostic features are small size, six eyes and the lack of characters distinctive for other genera. Thus the genus is presently based on plesiomorphies, and cladistic analysis consistently fails to resolve *Belisana* as a monophylum. *Belisana* is thus explicitly treated as a metaphyletic group and not as a clade. Alternative taxonomic options within the frame of the current International Code of Zoological Nomenclature are discussed but rejected for lack of data, justification, and/or practicability. Geographically, *Belisana* ranges from India to the Pacific Islands, and from Korea to Australia. A tight correlation between the male chelicerae (distance between frontal apophyses) and the female external genitalia (distance between a pair of pockets) is documented in *Belisana*.

**Key words:** Southeast Asia, Pholcidae, *Belisana*, diversity, male-female coevolution, metaphyly

### **Contents**

Introduction .....	2	Discussion .....	117
Materials and Methods.....	3	Acknowledgements .....	118
Relationships .....	4	References .....	118
Taxonomy .....	12	Appendices .....	121

## Introduction

Pholcids, comprising mostly tropical spiders, have attracted much less attention than some of their cousins like orb-weavers, jumping spiders, wolf spiders, or cobweb spiders. Few representatives occur in temperate regions, but some of them, like *Pholcus phalangioides* are relatively well known due to their synanthropic mode of life, relatively large size, and characteristic behaviour when disturbed: they vigorously vibrate their body, resulting in a blurring of the contours that makes it difficult for predators to capture them (Jackson 1990, 1992a, b, Jackson et al. 1990, 1992, 1993, Jackson & Rowe 1992). In recent years, *Pholcus phalangioides* and a few other species have become valued model organisms for experimental research into specific subjects like sexual selection, or evolution of sociality (Eberhard et al. 1993, Huber & Eberhard 1997, Jakob 1991, 1994, 2004, Jakob et al. 2000, Kaster & Jakob 1997, Schäfer & Uhl 2002, Schaefer & Uhl 2003, Uhl 1998, Uhl et al. 2004, Yoward 1998). A series of studies on the functional morphology of the copulatory organs has provided a dataset that is unparalleled in any other group of spiders (Huber 1994, 1995, 1997b, 1998a, 2002, Huber and Eberhard 1997, Uhl et al. 1995).

The family contains some remarkable species that may provide crucial information for topics of general interest. For example, *Metagonia mariguitarensis* from Venezuela is the only known spider with directionally asymmetric genitalia (Huber 2004). The question of why spiders are so symmetrical while insects, for example, have evolved asymmetric genitalia many times independently (Richards 1927, Ludwig 1932, Hebsgaard et al. 2004, Sihvonen 2005), remains largely unanswered. Second, *Mecolaesthus longissimus*, another pholcid from Venezuela, is unique in having males that have on average twice as long opisthosomata than females. Sexual size dimorphism in spiders is usually female-biased, and a unique function of the male opisthosoma in the context of sexual selection has been proposed to explain the reversed size-dimorphism in *M. longissimus* (Huber in press). Third, *Ciboneya antraia* from Cuba is apparently the only known animal with dimorphic female genitalia (Huber & Pérez 2001a, b). Dimorphic genitalia, and female dimorphic genitalia in particular, raise a number of important questions regarding species-specificity and taxonomical practice, sex-role reversal, or functionality of genitalia in the presence of considerable intraspecific variation (Huber 2003d). Fourth, the neotropical *Modisimus culicinus* is the only representative of the large clade Haplogynae that is known to practice gustatorial courtship (Huber 1997a).

Comparative studies on pholcid spiders have equally contributed information to topics of general interest. For example, several studies have indicated that specific genitalic structures that are crucial in the functional mechanics of copulation contain information at high taxonomic levels. This supports the notion that in some sense genitalia evolve slowly rather than rapidly (Huber 1995, 1998a, b, 2000, Huber et al. 2005a, b). Second, pholcid spiders have repeatedly evolved a coupling mechanism where apophyses on the male chelicerae grasp a pair of pockets on the female external genitalia (Kraus 1984, Huber 1999, 2003c, 2005, present study). Thus, they provide an excellent opportunity to study male-female coevolution using a pair of simple linear measures.

Pholcids occupy a wide range of ecosystems and habitats, ranging from deserts to rain forests, from sea level to over 3500 m a.s.l., and from the leaf litter to the canopy (Huber 2000, 2001). In primary tropical forests, up to twelve or thirteen species can be found per locality (unpublished data on recent expeditions to Venezuela and Brazil). In these habitats, they mostly occur in the leaf litter and under logs (tiny short-legged species without or with minimal webs), between buttresses of trees (often large dark species in dome-shaped webs), in dome-shaped webs in the lower vegetation (usually light species), and on the underside of leaves (cryptic greenish spiders that can press their bodies flat against the leaf to become virtually invisible). Many species have been found in caves, and some of these are highly troglomorphic, including the total loss of eyes (e.g. Gertsch 1982, Gertsch & Peck 1992, Pérez & Huber 1999). A large part of pholcid diversity in dry regions like Western Australia or northern Mexico results from pholcids using the protected habitats of caves (Gertsch 1982, Huber 2001). Species richness declines rapidly with human interference: secondary forests usually contain no more than one to four species, and plantations, pastures, and similar unnatural habitats are mostly entirely devoid of pholcid spiders.

In terms of described species numbers, the family is only about tenth among spiders, but recent revisions have almost doubled the number (to over 900) and circumstantial data indicate that only a small percentage (maybe 10-20%) of species have been described (e.g. Huber 2003a, b, c). Any recent intense collecting effort in tropical primary forests has turned up numerous, sometimes dozens of unknown species (e.g. Silva 1996 on Peru, Florez 1996 on Colombia, Huber 2003a, b on Madagascar and East Africa; unpublished data on recent expeditions to Venezuela and Brazil). Museum collections worldwide house at least some hundred undescribed species. The concentration of the family's diversity in primary rainforests means that most species occur in geographic areas and habitats that are severely threatened by human impact. Thus, pholcids represent an evolutionary success story with a high probability of converting into a human-induced disaster long before science has unravelled the evolutionary history and actual diversity of the family.

The genus *Belisana* epitomizes this situation. After its taxonomic creation by Thorell in 1898, it soon was synonymized with *Uthina* Simon 1893 (Simon 1903), and the single poorly known and barely noticed species persisted for many decades within the equally virtually unknown genus *Uthina*. Deeleman-Reinhold (1986) recognised the invalidity of the synonymy, and was the first to direct attention to the high diversity and ubiquity of *Belisana* in Southeast Asia. However, only one further species has been added to the genus, in the context of a revision of Australian pholcid spiders (*B. australis* Huber 2001). Most *Belisana* species occur in Southeast Asia which has the highest relative rate of deforestation of any major tropical region (Sodhi et al. 2004).

The aim of the present paper is twofold. First, to document the morphology, distribution, taxonomy, and phylogeny of *Belisana*; and second, to document the coevolution between male chelicerae and female external genitalia in this genus.

## Materials and Methods

Pholcids resembling *Belisana* and *Spermophora* (tiny, 6 eyes) and potential relatives (*Spermophorides*, *Paramicromerys*) were borrowed from more than 40 institutions and individuals worldwide. The list below covers only those with material actually used in the present paper.

AMNH	American Museum of Natural History, New York
AMS	Australian Museum, Sydney
BPBM	Bernice P. Bishop Museum, Honolulu, Hawaii
CAS	California Academy of Sciences, San Francisco
HNU	Hunan Normal University
HU	Hebei University
IRSB	Institut Royal des Sciences Naturelles de Belgique, Brussels
MACN	Museo Argentino de Ciencias Naturales, Buenos Aires
MHNG	Muséum d'Histoire Naturelle, Genève
MNHN	Muséum National d'Histoire Naturelle, Paris
NSMT	National Science Museum, Tokyo
OMNZ	Otago Museum, Dunedin
QMB	Queensland Museum, Brisbane
RMNH	National Museum of Natural History, Leiden (collection C. L. Deeleman Reinhold)
SMF	Senckenbergmuseum Frankfurt
ZMT	Zoological Museum, Turku
ZFMK	Zoologisches Forschungsmuseum Alexander Koenig, Bonn
ZMUC	Zoological Museum, University of Copenhagen

Methods and terminology are as in Huber (2000). Measurements are in mm ( $\pm$  0.02 mm if two decimals are given) unless otherwise noted. Eye measurements and distances between male cheliceral apophyses and female epigynal pockets are  $\pm$  5  $\mu$ m. In the diagnoses, “tiny” refers to total body length <1.4 mm, “relatively large” to body length >1.8 mm; in “short-legged” species male leg 1 length is <10 mm, in “long-legged” species it is >10 mm. Drawings were done with a camera lucida on a Nikon Labophot-2 compound microscope. Photos were made with a Nikon Coolpix 995 digital camera (1600x1200 pixels) mounted on a Nikon SMZ-U dissecting microscope. For SEM photos, specimens were cleaned ultrasonically, dried in HMDS (Brown 1993), and photographed with a Hitachi S-2460 scanning electron microscope.

The following abbreviations are used in the illustrations: ALS: anterior lateral spinnerets; ba: bulbal apophysis; e: embolus; ep: epigynal pocket; f: membranous flap on procurus; hp: hinged process of procurus; PMS: posterior median spinnerets; pr: procurus; s: scape; to: tarsal organ; tr: trochanter.

The numerical cladistic analysis was done using NONA, version 1.8 (Goloboff 1993). Cladogram analysis was done with Winclada, version 1.00.08+ (Nixon 2002). See Relationships for details of the analysis. Locality coordinates are in regular brackets if the data were copied from the original label or publication, but in square brackets when originating from some other source (usually from Alexandria Digital Library at <http://middleware.alexandria.ucsb.edu/client/gaz/adl/index.jsp>; in some cases from the collectors).

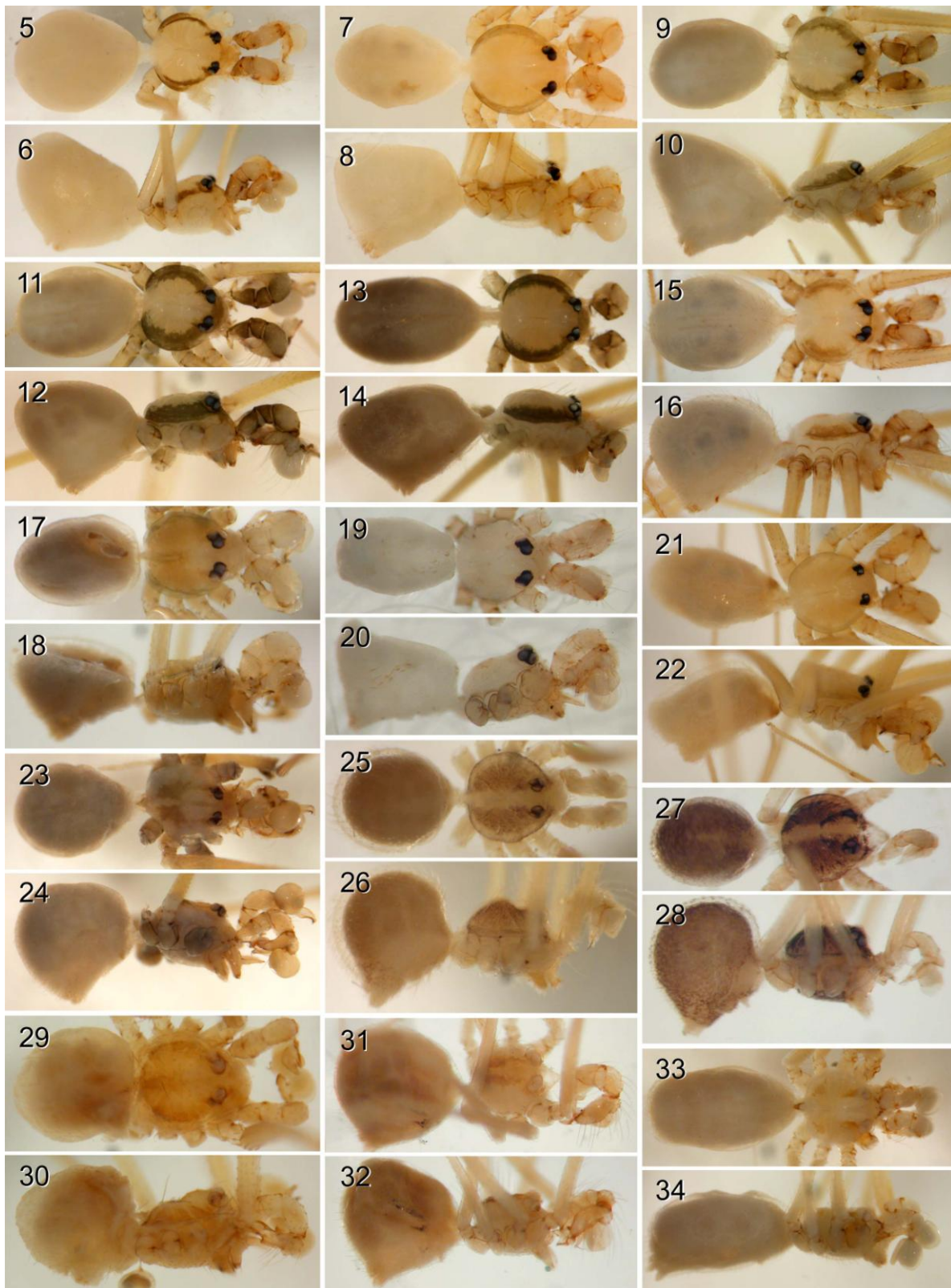
## Relationships

Relationships were analyzed by cladistic analysis, based on the data matrix in Appendix 3. The 71 taxa and 60 characters used for this matrix are listed in Appendices 1 and 2. The matrix is modified from previous matrices (Huber 2003c, 2005) as follows: (1) 17 putative *Belisana* species were added with an emphasis on species for which both sexes were known and for which SEM data were available. (2) Many taxa were deleted, especially New World taxa, holcnemines, and ninetines which were heavily represented in the previous analyses but would not have contributed to the resolution of *Belisana* and its relatives. Only three non-pholcine exemplars remained included as outgroups (Appendix 1), representing each of the other three subfamily-level taxa. In addition, genera that were represented by many species in previous analyses were reduced to five species each. This was justified by the fact that all these genera (*Zatavua*, *Buitinga*, *Paramicromerys*) were monophyletic in the strict consensus trees of preliminary analyses using all species previously included. The five remaining species were chosen to represent both basal and derived species within each genus. This elimination of taxa substantially reduced the number of most parsimonious cladograms and therefore simplified

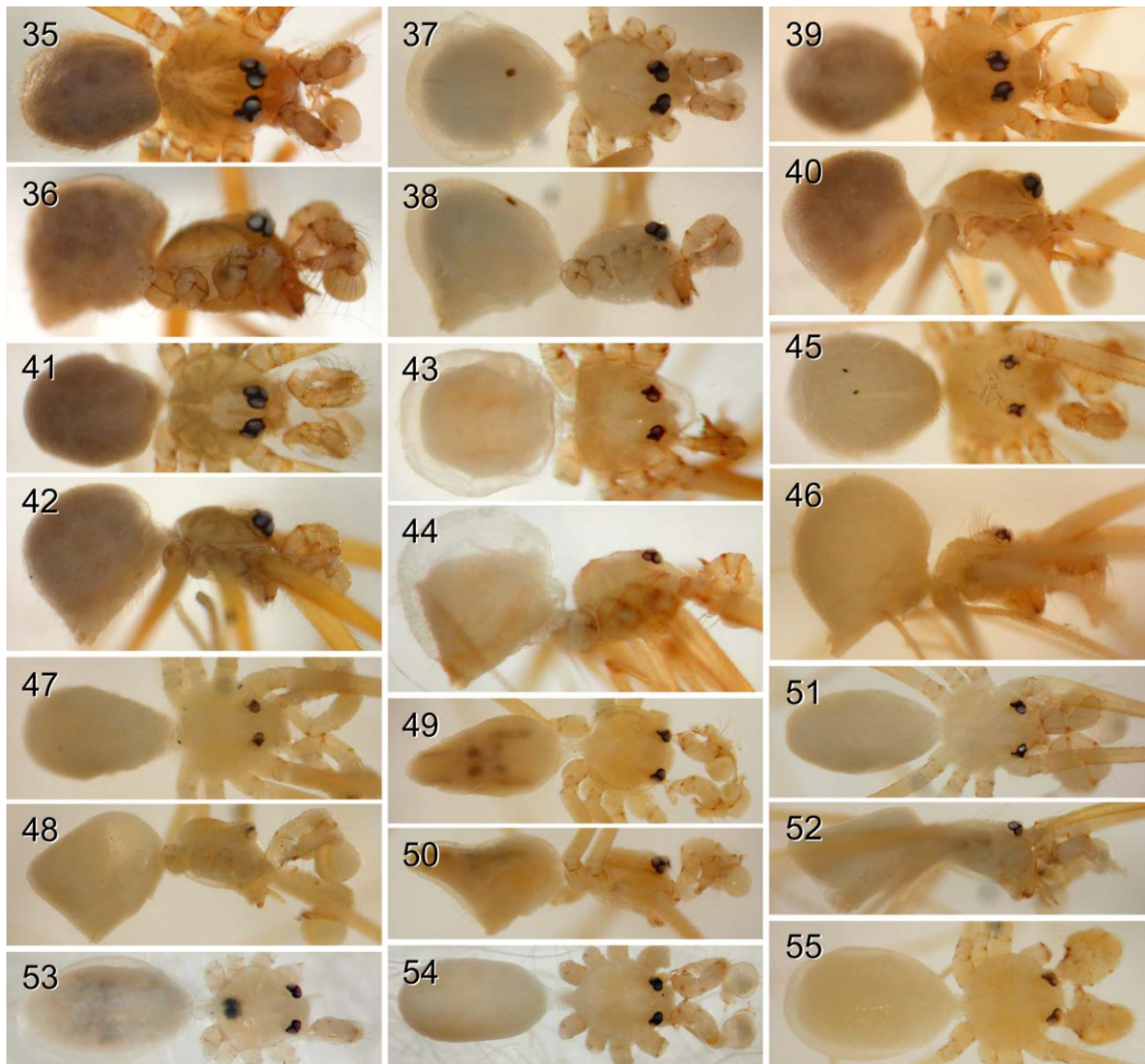


**Figs. 1-4.** *Belisana* habitus, microhabitat, and web. 1. *Belisana sabah*, female with eggsac, in characteristic position on underside of leaf. Photo courtesy Christa L. Deeleman and Paul Zborowsky. 2-4. *Belisana hormigai* webs. Photos courtesy Gustavo Hormiga. The webs in Figs. 2 and 4 were treated with starch to increase visibility of the otherwise barely visible silk lines. Note the spider's position in the upper right in Fig. 2 (directly under the leaf), the regular structure of the web, and the regularly spaced droplets in Fig. 3. A separate publication on these unusual webs is in preparation (G. Hormiga et al.). Scale lines: 3 mm (1), 5 cm (2), 1 cm (3), 3 cm (4).





**Figs. 5-34.** *Belisana* males, dorsal and lateral views, at varying scales. 5, 6. *B. pianma*. 7, 8. *B. nujiang*. 9, 10. *B. scharffi*. 11, 12. *B. inthanon*. 13, 14. *B. hormigai*. 15, 16. *B. akebona*. 17, 18. *B. floreni*. 19, 20. *B. banlakwo*. 21, 22. *B. sabah*. 23, 24. *B. marusiki*. 25, 26. *B. airai*. 27, 28. *B. davao*. 29, 30. *B. wau*. 31, 32. *B. ambengan*. 33, 34. *B. fiji*.



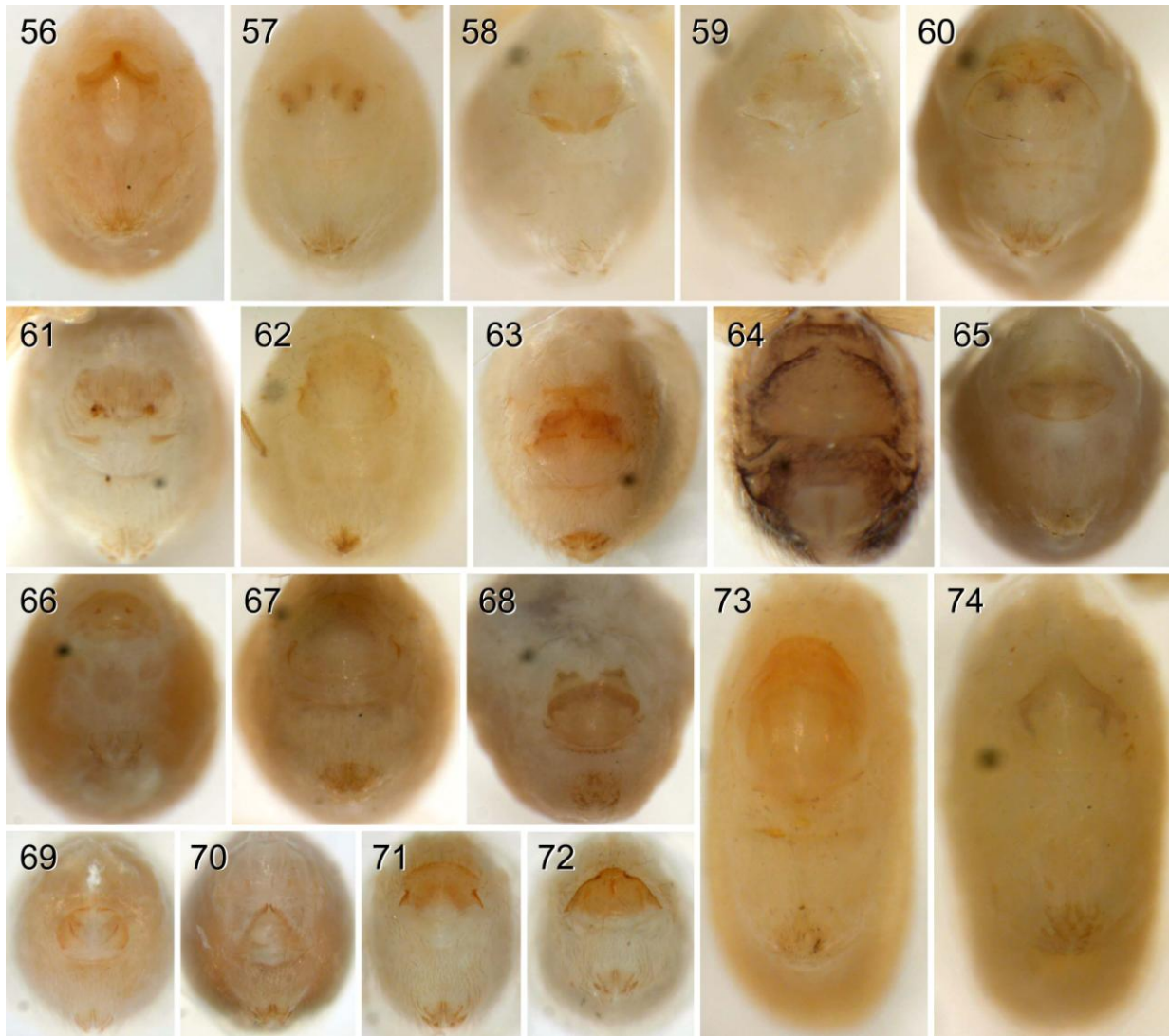
**Figs. 35-55.** *Belisana* males, dorsal and lateral views, at varying scales. 35, 36. *B. leumas*. 37, 38. *B. benjamini*. 39, 40. *B. khieo*. 41, 42. *B. ketambe*. 43, 44. *B. leclerci*. 45, 46. *B. strinatii*. 47, 48. *B. sarika*. 49, 50. *B. apo*. 51, 52. *B. khaosok*. 53. *B. keyti*. 54. *B. tambligan*. 55. *B. jimi*.

cladogram analysis. (3) Three characters were added according to the new taxa included (characters 58-60 in Appendix 2). (4) Several characters were deleted because they were rendered uninformative resulting from the deletion of taxa.

Binary character coding was used as far as possible. Multistate characters were only used when coding as binary characters would not have represented independent evidence in support of a group (characters 3, 14, 31, 43 in Appendix 2). All multistate characters were treated as unordered.

Using NONA with hold/50, mult\*100, and amb- resulted in six most parsimonious cladograms of length 152 (CI = 42; RI = 79). With regard to *Belisana*, there were only two fundamentally different topologies, both of which are shown in Fig. 76. The other four cladograms resulted from two options regarding *Quamtana* (mono- or paraphyletic) and two options regarding relationships among African taxa and *Metagonia*. The most apparent result in the context of the present paper is that *Belisana* was never resolved as a monophyletic group. This was also the case when the data were analyzed using successive weighting. Successive weighting in NONA (with the consistency index as weighting function) resulted in seven most parsimonious cladograms. Stable results were obtained at iteration 2. Figure 77 shows one of these cladograms, together with a variant topology relevant to *Belisana*. All other variation occurred within true *Spermophora*.

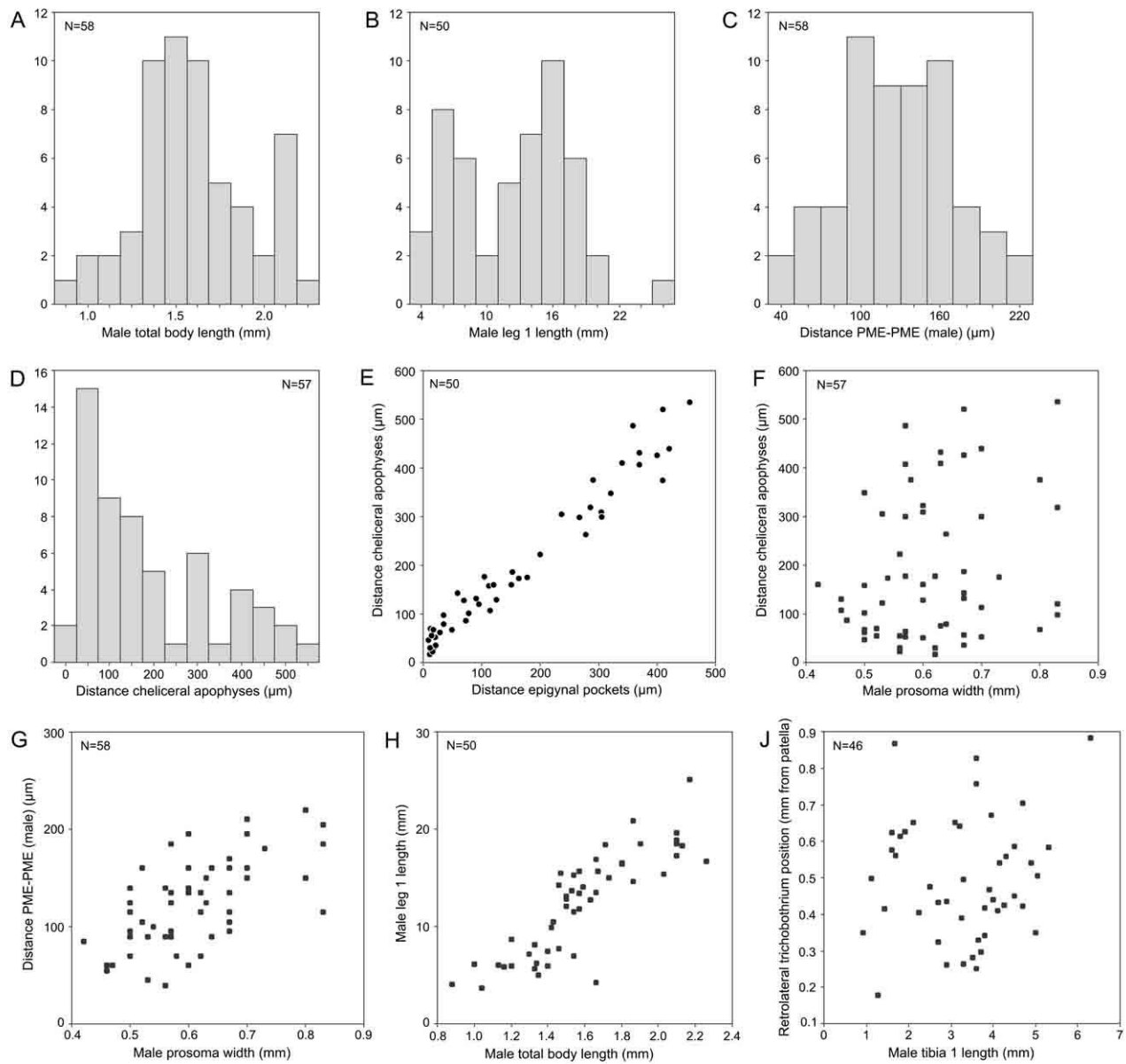




**Figs. 56-74.** *Belisana* female opisthosomata, ventral views, at varying scales. 56. *B. pianma*. 57. *B. nujiang*. 58-59. *B. kaosok*, with and without plug. 60. *B. inthanon*. 61. *B. floreni*. 62. *B. sabah*. 63. *B. akebona*. 64. *B. airai*. 65. *B. scharffi*. 66. *B. aninaj*. 67. *B. hormigai*. 68. *B. marusiki*. 69. *B. fraser*. 70. *B. ranong*. 71. *B. gedeh*. 72. *B. freyae*. 73. *B. flores*. 74. *B. khaoyai*.

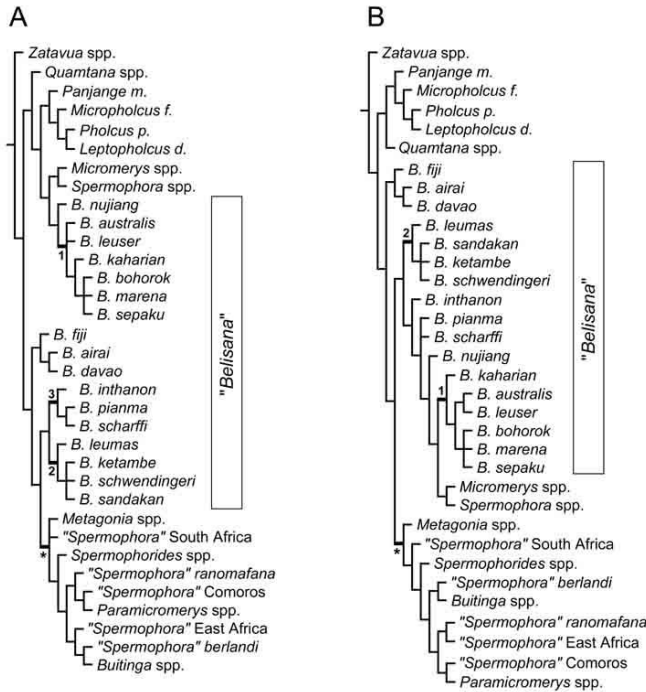
Clade stability was estimated using the Bremer support function in NONA which calculates the number of extra steps required before a clade is lost from the strict consensus of near-minimum length cladograms. Most clades have very low support. Within pholcines, only six clades had a Bremer support of 2 (*Zatavua*; *Belisana airai* + *B. davao*; *Metagonia*; South African '*Spermophora*'; Comoran '*Spermophora*'; *Paramicromerys* + Comoran '*Spermophora*'), true *Spermophora* had 3, *Spermophorides* 4, and *Micromerys* 6; all other clades had a Bremer support of 1. The implications and taxonomic consequences of these results are discussed at the end of this paper, together with a justification for treating *Belisana* as a metaphyletic group.

The possibly closest relative of *Belisana* could not be included in the cladistic analysis for lack of data: *Paraspermophora* Wunderlich 2004, known only from Baltic amber. Two species have been described (Wunderlich 2004; both seen by the author), but numerous important characters cannot be seen in the amber material. In general appearance, *Paraspermophora* is similar to *Spermophorides*, *Spermophora*, and *Belisana*. However, *Paraspermophora* does not share with *Spermophorides* the unusual (dorsal) attachment site of the procurus to the cymbium, and it does not share with *Spermophora* the attachment site of the bulb to the cymbium (dorsal in *Spermophora*). On the other hand, the bulb in *Paraspermophora* is provided with a membranous embolus and a hooked apophysis just as in *Belisana*, and the palpal femur is provided with a proximo-dorsal apophysis like in many *Belisana* species.

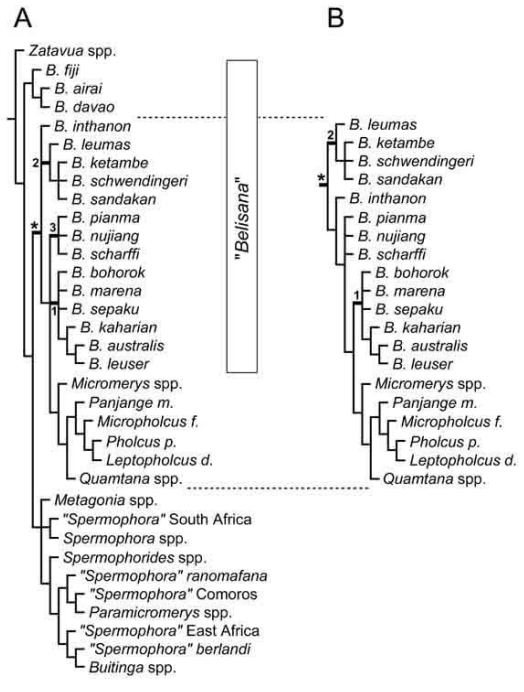


**Fig. 75 A-J.** Histograms and scatter diagrams of some characters in *Belisana*. Each measure represents one species, usually the type specimen. Note the strong correlation between male and female characters in E. None of the characters justifies a delimitation of species groups within the genus. See text for detailed discussion.

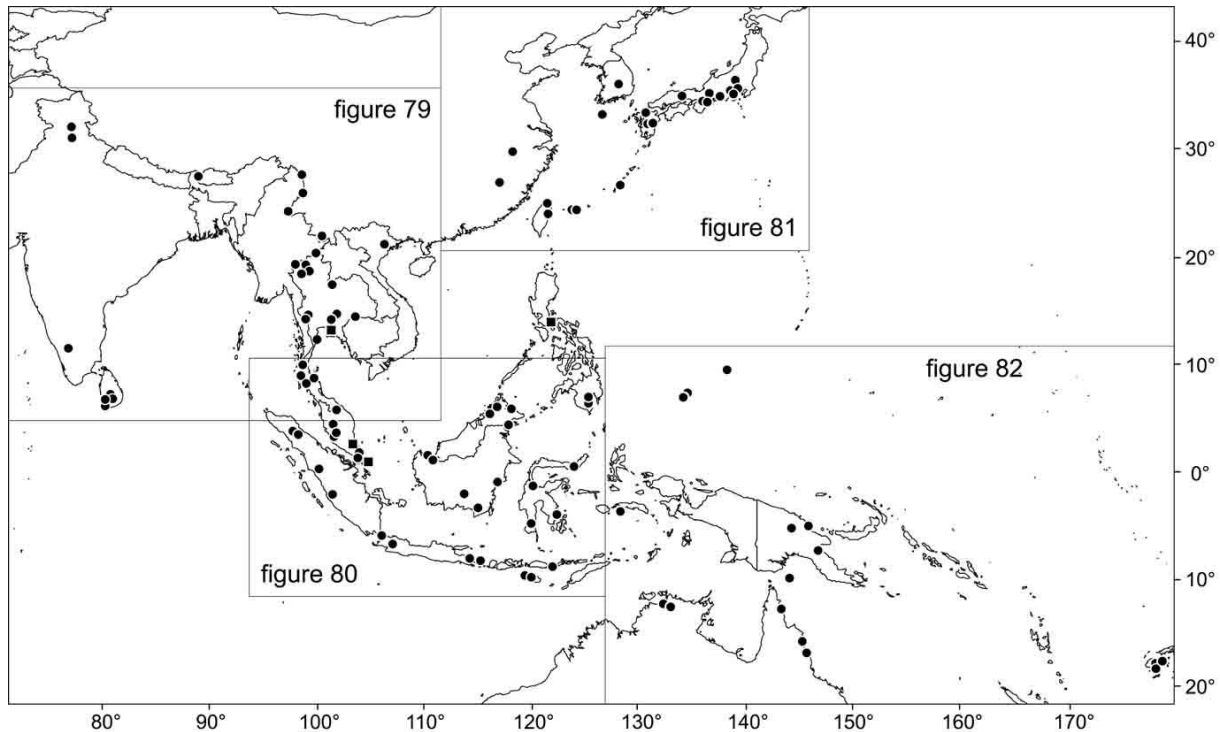
Equally, one potential synapomorphy of the genus or of a species group within *Belisana* could not be included for lack of data: the unique regular web. Deeleman-Reinhold (1986: fig. 1) illustrated such a web for *Belisana* sp. from Sumatra, and generalized this type of web to the entire genus. However, it has not been possible to reconstruct exactly in which species this type of web had been observed (C. L. Deeleman-Reinhold, pers. comm. Nov. 2004). The fact that the same type of web as in the species from Sumatra has been observed in *B. hormigai* from northern Thailand (Fig. 2) indicates that this may in fact be a character uniting a considerable number of species. No such web has ever been described in any other pholcid, indicating that it is most probably apomorphic within pholcids.



**Fig. 76 A, B.** Two of the six most parsimonious cladograms of pholcines obtained by NONA using equal weights of characters. The other four cladograms differed as follows: (1) like A but clade \* like B; (2) like B but *Quamtana* paraphyletic; (3) like B but clade \* like A; (4) like B but *Quamtana* paraphyletic and clade \* like A. Numbered clades are discussed in the text.



**Fig. 77 A, B.** Two of the seven most parsimonious cladograms of pholcines obtained by NONA using successive approximations weighting. The resolution of clade \* was the only difference between these two cladograms. The other cladograms differed only within true *Spermophora*. Numbered clades are discussed in the text.



**Fig. 78.** Known distribution of *Belisana*. All known records are shown. Circles: treated herein; squares: unpublished data.



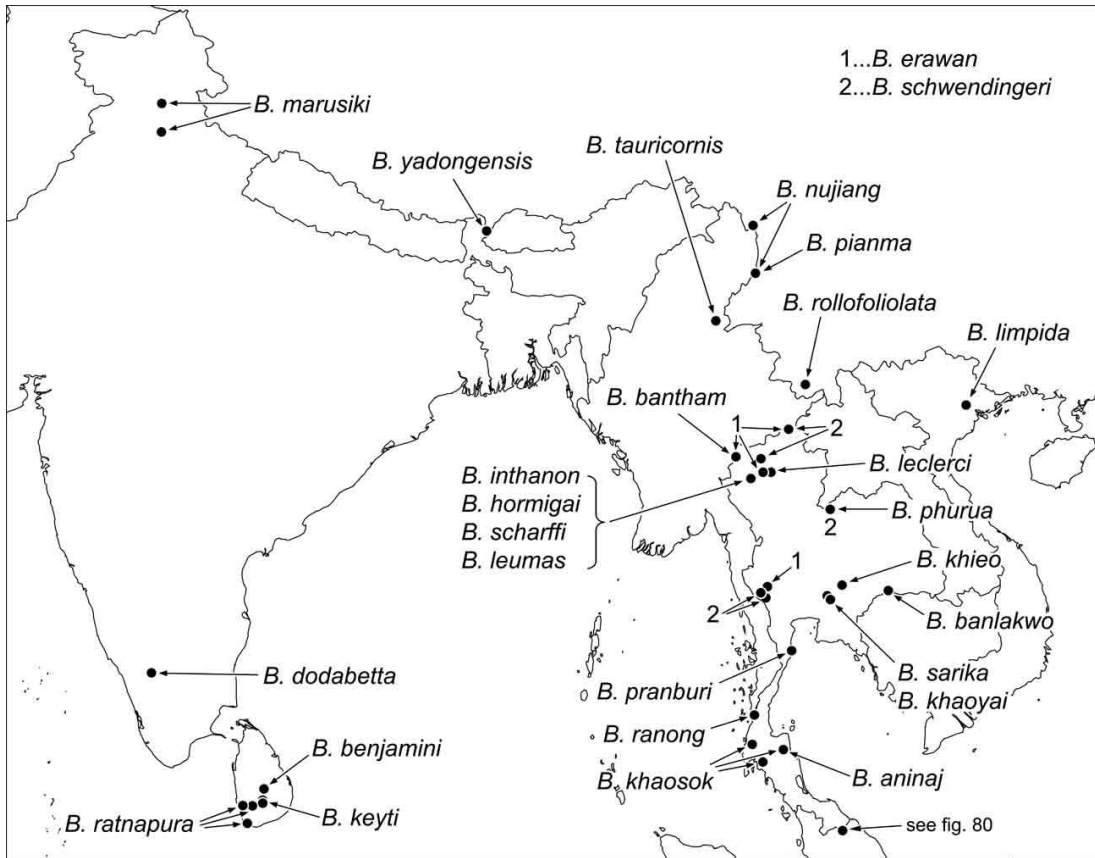


Fig. 79. Known distribution of *Belisana* in India, Sri Lanka, southern China, Myanmar, Thailand, and Vietnam.

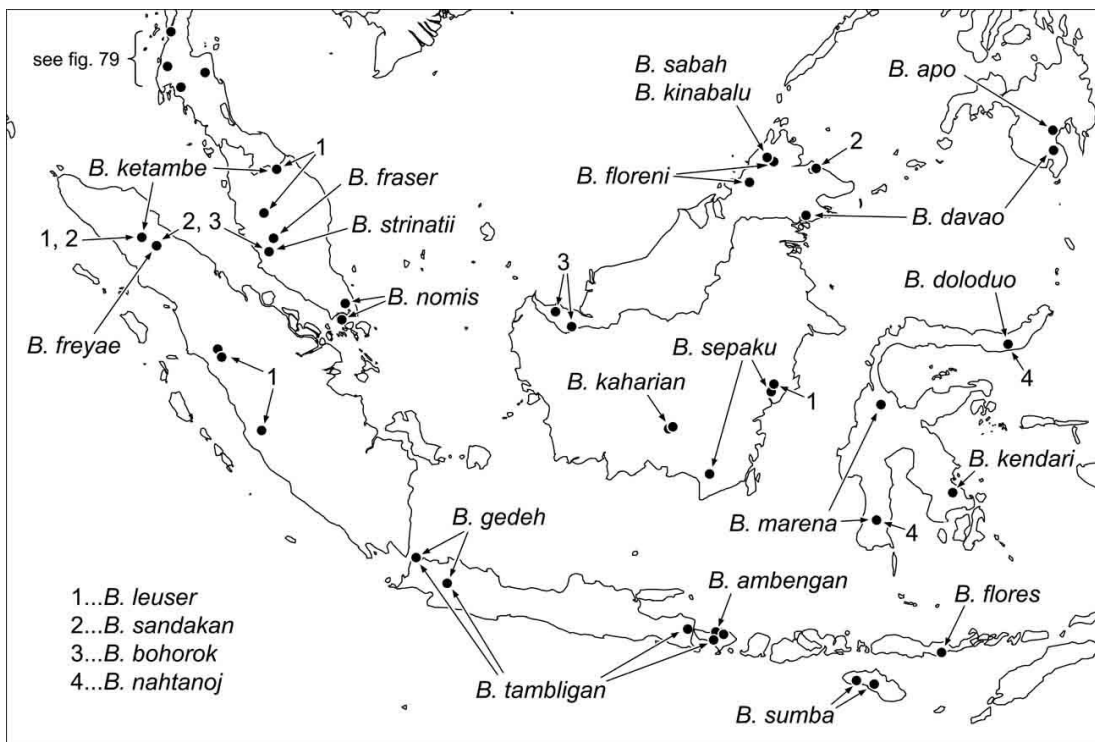


Fig. 80. Known distribution of *Belisana* in Malaysia, Indonesia, and the Philippines.

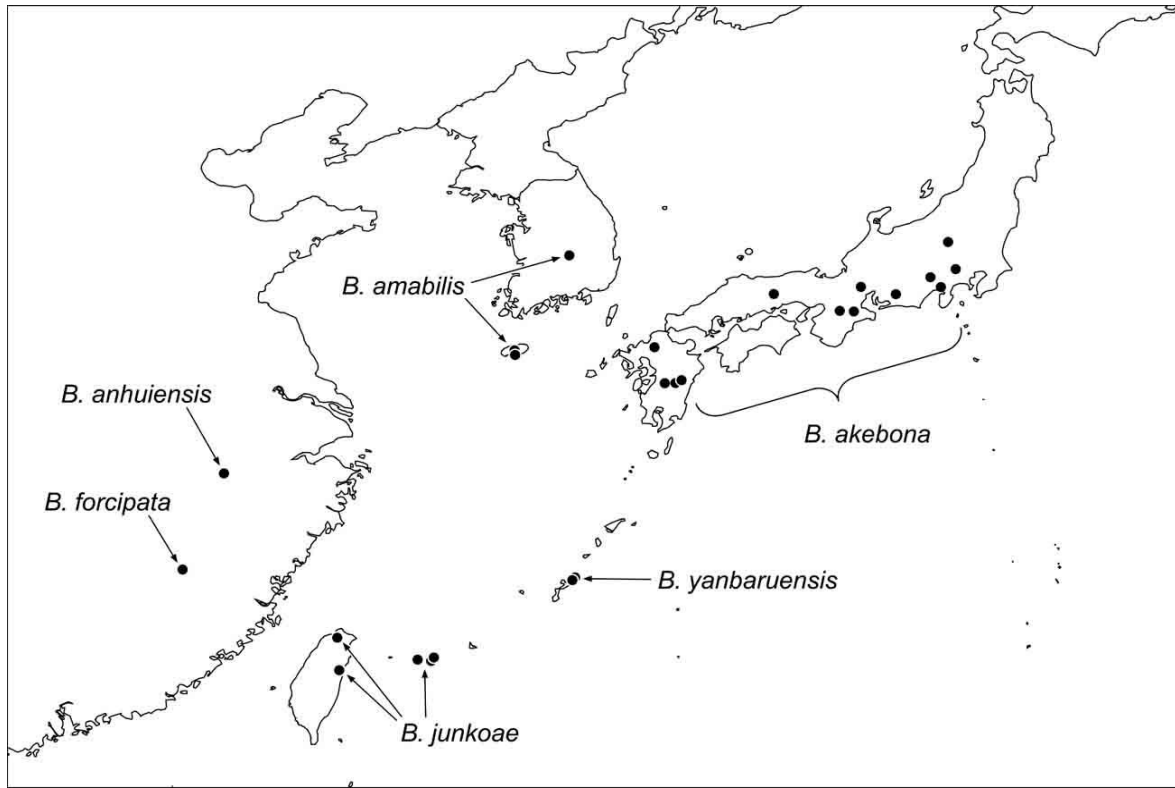


Fig. 81. Known distribution of *Belisana* in eastern China, Taiwan, Korea, and Japan.

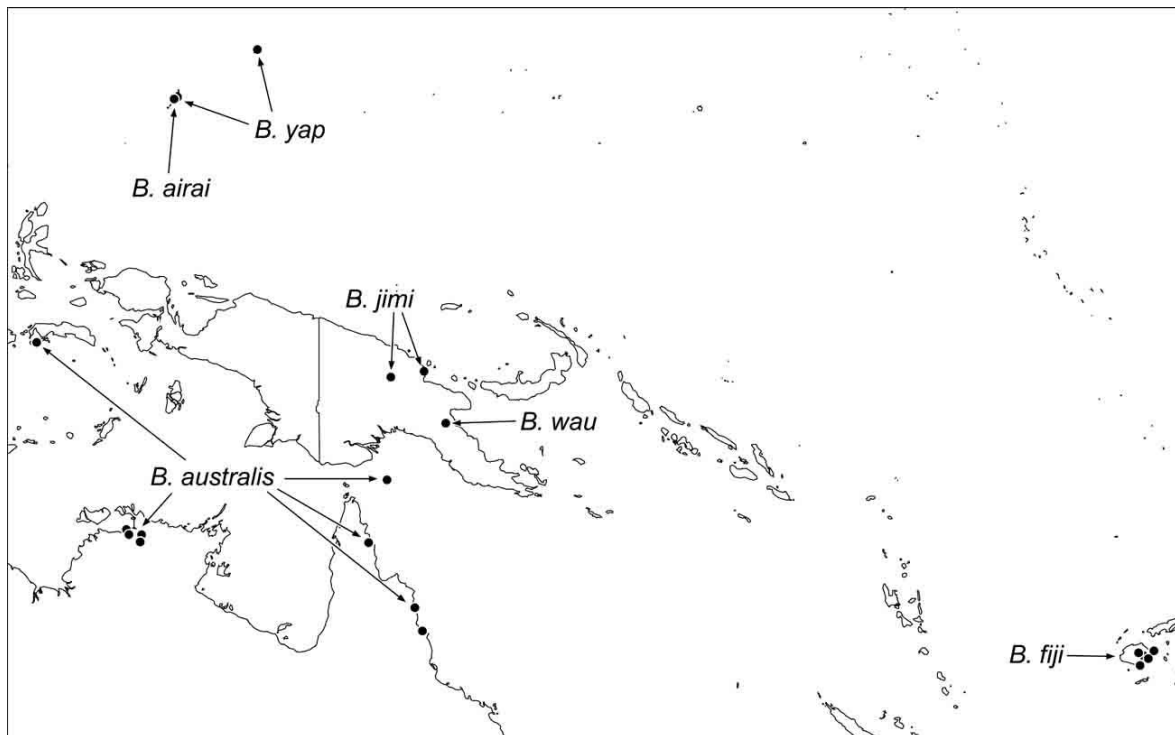


Fig. 82. Known distribution of *Belisana* in Papua New Guinea, Australia, and the Pacific.

## Taxonomy

### *Genus Belisana* Thorell 1898

*Belisana* Thorell 1898: 278. Simon 1903: 988. Simon 1909: 81. Deeleman-Reinhold 1986: 46-48, figs. 1, 5. Huber 2001: 124-126.

**Type species.** *Belisana tauricornis* Thorell 1898, by original designation. The type material was collected in Bhamo, Myanmar (Burma), and is deposited in the Museo Civico di Storia Naturale "Giacomo Doria", Genova, Italy. Repeated loan requests remained unanswered, but Dr. Christa Deeleman-Reinhold has seen the type material (pers. comm., Oct. 2004), and found it to be "in a very bad state, it was almost black and probably had been dry for quite a while". However, judging from the original description, it is obvious that the material treated below is in fact more similar to *B. tauricornis* than to any other Asian pholcid known. This view was also expressed by Dr. Deeleman-Reinhold (pers. comm.) who "could recognize it to be related to the many small species I found in shrub and vegetation ... in SE Asia". Unfortunately, barely any new collections of pholcids from Myanmar seem to exist. However, 'typical' *Belisana* have been collected about 300 km NE (in China) and 500 km SE (in Thailand) of the type locality of *B. tauricornis* (Fig. 79). This is in contrast to *Spermophora*, the only other genus that is similar in overall morphology and shares part of its geographic range with *Belisana*. *Spermophora* is widely distributed between Indonesia, Philippines and Australia, but has never been collected on mainland Southeast Asia (Huber 2005).

The original description of *B. tauricornis* provides few important characters: adult specimens are about 1.5 mm long, eye triads are widely separated, male chelicerae are provided with long apophyses (species name!), legs are thin and long (leg 1 about 9 mm), the opisthosoma is suboval. This description would fit *B. nujiang*, except that Thorell did not mention dark carapace margins for *B. tauricornis*.

**Diagnosis.** Small (0.8-2.3 mm total body length), six-eyed spiders with proximo-lateral apophyses on the male chelicerae. Similar to *Spermophora*, but usually with dorsal apophysis on the male palpal femur, without posterior pockets on the female opisthosoma, without sclerotized ventral flap on the procurus, and without serrated apophysis on the male genital bulb. Distinguished from *Spermophorides* by the absence of pockets on the posterior epigynum plate and by the regular (i.e. not dorsal) attachment site of the procurus on the cymbium. A distinction from the Baltic amber genus *Paraspermophora* is presently not possible.

**Description.** Male. Total length 0.8-2.3 mm, most species about 1.3-1.7 mm (Fig. 75A). Carapace usually without dorsal indentation (only *B. wau* with shallow thoracic furrow), usually monochromous ochre-yellow, sometimes with darker lateral margins (Figs. 5-16) or pair of darker marks (Figs. 23, 25, 27). Six eyes in two triads on barely elevated ocular area. Distance between eye triads very variable (~40-220 µm; Fig. 75C), distance PME-ALE small (~10-20 µm). Sternum never modified, male clypeus sometimes modified (*B. pianma*, *B. kinabalu*, *B. davao*, *B. airai*, *B. yap*, *B. ambengan*; e.g., Figs. 113, 437, 463). Male chelicerae with proximal rounded projections laterally and pair of apophyses distally; distal apophyses always without modified hairs, chelicerae never with stridulatory ridges. Male palpal coxa unmodified, trochanter with retrolateral apophysis and sometimes with ventral apophysis; femur usually with dorsal apophysis proximally, rarely also with ventral projection; procurus usually complex distally, often with membranous ventral flap (e.g., Figs. 97-99) and complex structures with scales and spines (e.g., Figs. 259, 350, 369, 535), in some species with (glandular?) pores (Figs. 258, 441, 444); bulb usually with sclerotized apophysis (often curved or hooked) and membranous embolus (usually rather conical or more complex than tubular). Tarsal organ capsulate (e.g., Fig. 188) or exposed (e.g., Fig. 370). Leg length highly variable (Fig. 75B; leg 1: 4-26 mm; 3-12 x body length; tibia 1 length/diameter [L/d]: 18-89); leg formula 1243 in long-legged species, 1423 in short-legged species. Legs without spines and curved hairs, often with 'vertical' hairs in higher than usual density on metatarsi (e.g., Figs. 101, 169), rarely also seen on tibiae (e.g., *B. ketambe*, *B. airai*); retrolateral trichobothrium of tibia 1 usually at ~10-20%, in very short-legged species up to 50%; prolateral trichobothrium missing on tibia 1, present on other tibiae; tarsus 1 with about 10-20 pseudosegments; tarsus 4 with comb-hairs ventrally: in most species with three rows of branches on each hair (e.g., Figs. 109, 146, 198), in *B. airai* and *B. fiji* apparently simpler with branches closer together (Figs. 477, 639). Opisthosoma globular, oval, or cylindrical, often elevated posteriorly, usually monochromous pale ochre-grey, rarely with darker marks visible through cuticle (Figs. 5-55). Male gonopore with four epiandrous spigots (e.g., Figs. 95, 118, 163), anterior lateral spinnerets (ALS) with widened, pointed, and several cylindrically shaped spigots (e.g., Figs. 105, 106, 149, 166); the latter are absent in some species (e.g., Figs. 264, 265, 517, 518). Posterior median spinnerets (PMS) with two spigots each (e.g., Figs. 105, 130, 265). Posterior lateral spinnerets without spigots.

Sexual dimorphism very slight, females with slightly shorter legs, unmodified chelicerae, with few vertical hairs on metatarsi. Epigynum usually a simple plate with pair of pockets (e.g., Figs. 126, 171, 196) corresponding to male cheliceral apophyses (Fig. 75E), rarely without pockets (*B. bantham*) or with short scape (Figs. 457, 641), never with additional abdominal pockets. In *B. dodabetta*, the pockets appear to be situated on the posterior rather than the anterior epigynal plate. Females of various species had genital plugs (e.g., Figs. 293, 394). Female palpal tarsal organ apparently always capsulate, even in species with exposed male palpal tarsal organs (e.g., *B. leumas*: Figs. 205 and 206).

**Species identification.** In most cases, species identification requires adult male specimens. Without clearing of the female internal genitalia, few species can be identified based on females alone (using geographical information, coloration, and external appearance of the epigynum; e.g., *B. akebona*, *B. fiji*, *B. inthanon*). For males, the first data to consider are geographic origin and the morphology of the chelicerae. This usually reduces the options to less than four species. Further identification requires detachment of one palp (preferably the left one, which is the one illustrated herein) to allow clear observation of the following details: modifications of the trochanter (retrolateral and ventral apophyses), modifications of the femur (dorsal and ventral apophyses), morphology of the procurus and of the bulbous projections. Note that the appearance of the complex procurus and bulb may change dramatically with small changes of the angle at which the object is viewed.

**Phylogeny.** The position of *Belisana* in the pholcines sensu Huber (2000) is strongly supported by the lateral cheliceral apophyses. Within pholcines, *Zatavua* is consistently resolved as the sister taxon to the rest, the latter being defined by the presence of a retrolateral trochanter apophysis on the male palp. Beyond this, the cladograms differ strongly with regard to the position of *Belisana* (Figs. 76, 77; see Relationships above). Agreement exists only with respect to some species groups: the ‘narrow pore plate group’ (clade 1 in Figs. 76, 77) is characterized by narrow pore plates in the female internal genitalia (e.g., Figs. 283, 531, 620); the ‘flat male pto group’ (clade 2 in Figs. 76, 77) is characterized by a flat (exposed) male palpal tarsal organ (e.g., Figs. 205, 227). Some but not all cladograms identify an additional group characterized by dark margins on the carapace (Figs. 5-16), but the species included vary (clades 3 in Figs. 76, 77). Finally, one group is found in all cladograms (*B. fiji*, *B. airai*, *B. davao*), but this clade is only supported by the distance between the PMEs, a character that is both difficult to code unambiguously (Figs. 75C, G) and highly homoplastic.

**Natural History.** Most species have been collected in primary (rarely secondary) tropical forests, either from the leaf litter or from the underside of leaves. Some occur even in fruit plantations (Deeleman-Reinhold 1986), some are found in caves. The web of at least some species consists of a flat, widely and regularly meshed sheet extending between the margins of adjacent leaves (Figs. 2, 4; see also fig. 1 in Deeleman-Reinhold, 1986 of an unidentified species from Sumatra). *Belisana* has been described as “one of the commonest pholcid spiders in [Southeast Asia]” (Deeleman-Reinhold 1986), and quantitative collecting in northern Thailand has shown certain *Belisana* species (*B. hormigai*, *B. scharffi*) to be among the dominant web-building spiders in this region. Representatives of *Belisana* have been collected from close to sea level (e.g., *B. ranong*, *B. airai*, *B. yap*) up to 2500 m a.s.l. (e.g., *B. nujiang*, *B. pianma*, *B. leumas*, *B. dodabetta*).

**Distribution.** *Belisana* is widely distributed between India, Japan, and northern Australia (Figs. 78-82). In the Pacific, it reaches as far east as Fiji. It reaches from about 36°N (in Japan and South Korea) to about 18°S (in Australia and Fiji).

**Composition.** The genus *Belisana* previously contained only two species: *B. tauricornis* and *B. australis*. The former is briefly discussed above, the latter was described in detail by Huber (2001) and is not further treated herein. Nine species are newly transferred from *Spermophora*. Of these, four are redescribed below (*B. akebona*, *B. anhuiensis*, *B. forcipata*, *B. junkoae*); four species are transferred based on published descriptions: *B. amabilis* (Paik 1978) n. comb., *B. rollofoliolata* (Wang 1983) n. comb., *B. yadongensis* (Hu 1985) n. comb., *B. yanbaruensis* (Irie 2002) n. comb. All these species lack the posterior pockets on the female opisthosoma (characteristic for *Spermophora*), and fit the concept of *Belisana* rather than that of any other known genus. The ninth species, *B. limpida* (Simon 1909) n. comb., is only known from the female. I have seen the type material in MNHN (with Simon’s label and vial number 22311). It contains three female specimens and one opisthosoma; the females differ in opisthosoma shape and might well represent two species. The epigyna are extremely simple externally but posterior pockets are missing. Finally, 53 species are newly described below, resulting in a total of 64 described species. This makes *Belisana* the third largest pholcid genus (together with *Anopsicus*), following *Pholcus* (114) and *Metagonia* (79). As in most other pholcid genera, there is clear evidence that the actual diversity is much higher. In the collections studied, I recognized about 30 further species, most

of which were poorly preserved or inadequately labelled. More importantly, the facts that (1) most species seem to have small distributional ranges, (2) some areas that were subjected to intense collecting yielded up to four species, and (3) many areas remain virtually uncollected (e.g., India, Myanmar, Laos, Vietnam, Cambodia, Papua New Guinea), suggest that we must expect many dozens additional species not yet discovered.

**Sequence of descriptions.** Due to the poor resolution of relationships, the species descriptions below are roughly ordered geographically. I start with those species nearest to the type locality of the type species (i.e., species from Yunnan Prov., China, and from northern Thailand), continue with the rest of mainland Southeast Asia, Indonesia, Philippines, Caroline Islands, and Papua New Guinea. Then follow the north-eastern species (Japan, Taiwan, eastern China), the western species (India and Sri Lanka), and finally an unusual species from Fiji.

***Belisana nujiang*, new species**

(Figs. 7, 8, 57, 83-87, 93-111)

*Type.* Male holotype from native forest in Gaoligongshan at 9.5 road km ESE Pianma (25°59'N, 98°40'E), 2500 m a.s.l., Nujiang Pref., Yunnan, China; Oct. 15-18, 1998 (C. Griswold, D. Kavanaugh, C.-L. Long), in CAS.

*Etymology.* The species name is a noun in apposition, taken from the type locality.

*Diagnosis.* Medium-sized, long-legged species with oval or slightly angular opisthosoma and dark margins on prosoma (Fig. 7); distinguished from relatives by the shapes of procurus and bulbal apophyses (Figs. 83, 84), and by the unique female vulval structures (Figs. 86, 87). From *B. pianma* also by the unmodified male clypeus.

*Male (holotype).* Total length 1.5 (1.6 with clypeus), carapace width 0.63. Leg 1: 11.8 (2.9 + 0.3 + 2.9 + 4.4 + 1.3), tibia 2: 2.1, tibia 3: 1.3, tibia 4: 1.8; tibia 1 L/d: 47. Habitus as in Figs. 7 and 8. Carapace pale ochre-yellow, light brown margins laterally, sternum whitish, legs ochre-yellow, without darker rings, opisthosoma ochre-grey, with some slightly darker spots visible through cuticle dorso-laterally. Ocular area not elevated, thoracic furrow absent; distance PME-PME 150 µm; diameter PME 55 µm; distance PME-ALE ~20 µm. Clypeus unmodified. Sternum as long as wide (0.46). Chelicerae as in Fig. 85, with pair of curved apophyses (right angle to paturon in lateral view), tips unmodified (Fig. 93), 415 µm apart. Palps as in Figs. 83 and 84; trochanter with short rounded retrolateral apophysis (more distinct in ventral view), femur with indistinct hump proximo-dorsally, procurus with distinctive curved spine (Figs. 84, 97, 98) and ventral membranous flap with many small scales (Figs. 97, 99), bulb with hooked apophysis (Figs. 83, 98) and embolus with straight spine (Figs. 83, 96). Tarsal organ capsulate (Fig. 94). Retrolateral trichobothrium of tibia 1 at 15%; legs without spines and curved hairs, with vertical hairs proximally on all metatarsi (Fig. 101); tarsus 1 with ~20 pseudosegments, but only about 15 quite distinct distally. Gonopore and ALS as in Figs. 95 and 106.

*Variation.* Tibia 1 in 5 other males: 2.80-3.15 (mean 2.99). Most males with monochromous opisthosoma.

*Female.* In general similar to male. Tibia 1 in 6 females: 2.55-2.70 (mean 2.61). Epigynum simple and flat externally (Figs. 110, 111), with distinctive dark internal structures visible through cuticle (Figs. 57, 86), pockets 340 µm apart. Dorsal view as in Fig. 87.

*Distribution.* Known from two localities in Yunnan Prov., China (Fig. 79).

*Material examined.* CHINA: Yunnan: Nujiang Pref., native forest in Gaoligongshan: male holotype above, together with 4♂3♀ (CAS); Nujiang Pref., Nujiang State Nature Reserve, Qiqi He, 9.9 air km W Gongshan, 2000 m a.s.l. (27°43'N, 98°34'E), July 9-14, 2000 (H.-M. Yan, D. Kavanaugh, C. E. Griswold, H.-B. Liang, D. Ubick, D. Z. Dong), 1♂ in CAS (together with 1♀ that is not conspecific); same collection data but July 13, 2000, 1♀ in CAS.

***Belisana pianma*, new species**

(Figs. 5, 6, 56, 88-92, 112-130)

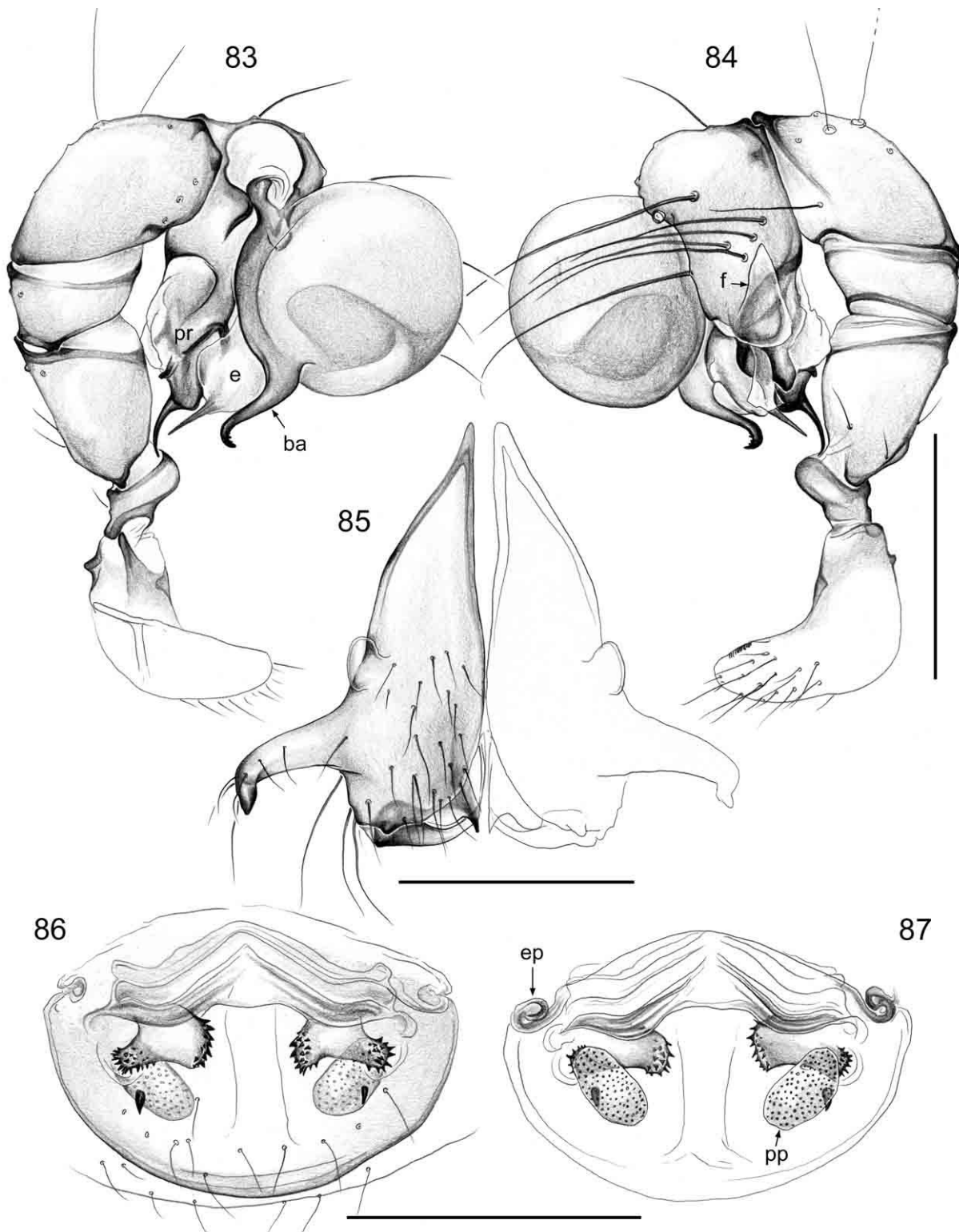
*Type.* Male holotype from native forest in Gaoligongshan at 9.5 road km ESE Pianma (25°59'N, 98°40'E), 2500 m a.s.l., Nujiang Pref., Yunnan, China; Oct. 15-18, 1998 (C. Griswold, D. Kavanaugh, C.-L. Long), in CAS.

*Etymology.* The species name is a noun in apposition, taken from the type locality.

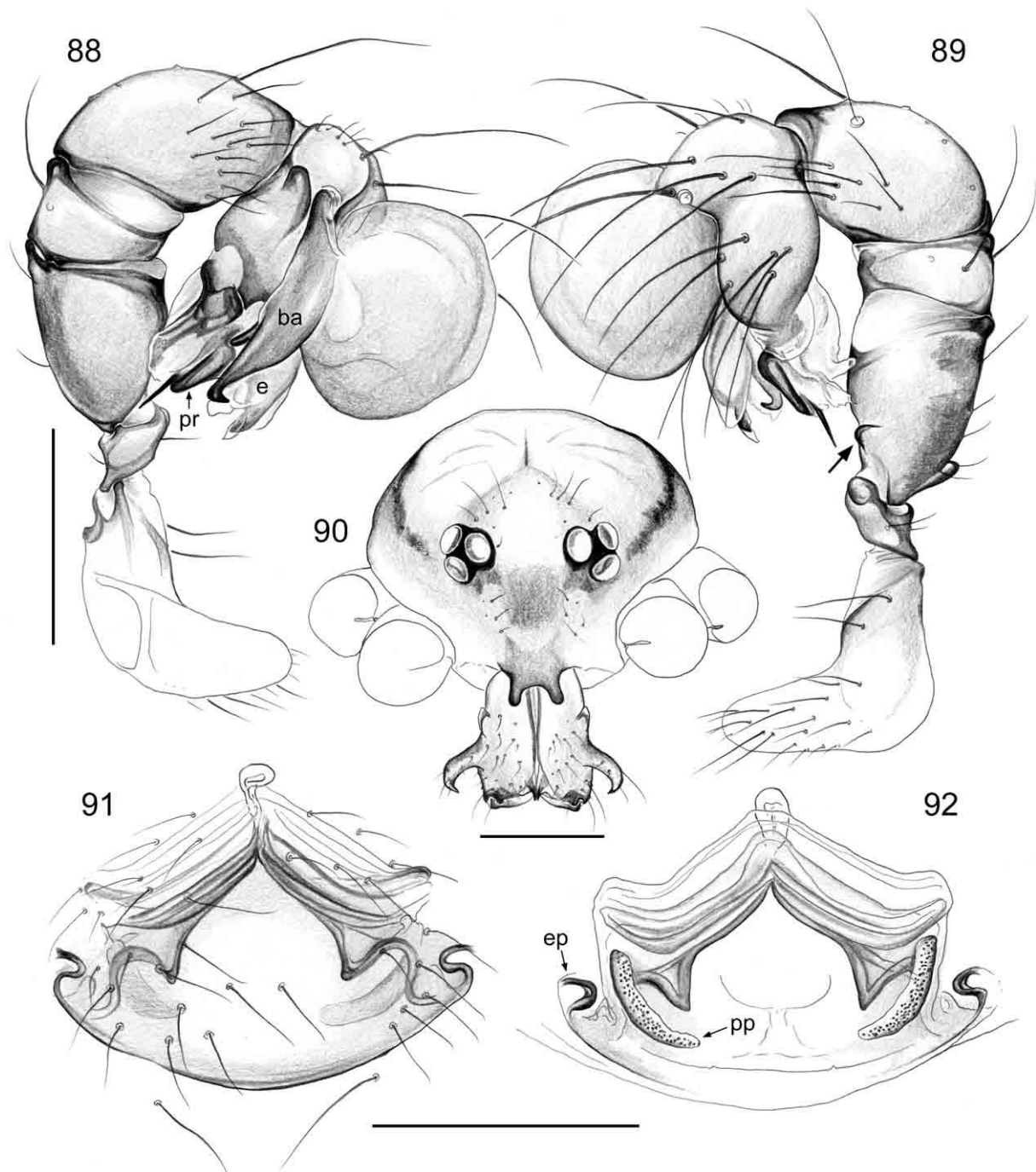
*Diagnosis.* Relatively large, long-legged species with oval opisthosoma and dark margins on prosoma (Fig. 5); easily distinguished from relatives by the male clypeal modification (Figs. 90, 112, 113); also by the shapes of procurus and bulbal apophyses (Figs. 88, 89), and by the ventral femur apophysis (Fig. 89).

*Male (holotype).* Total length 2.0 (2.1 with clypeus), carapace width 0.80. Leg 1: 18.3 (4.6 + 0.4 + 4.5 + 7.0 + 1.8), tibia 2: 3.2, tibia 3: 2.1, tibia 4: 2.7; tibia 1 L/d: 56. Habitus as in Figs. 5 and 6. Carapace pale ochre-yellow, brown margins laterally, sternum whitish, legs ochre-yellow, patellae and tibia-metatarsus joints light brown, opisthosoma ochre-grey, with some large darker spots visible through cuticle dorso-laterally. Ocular area barely elevated, thoracic

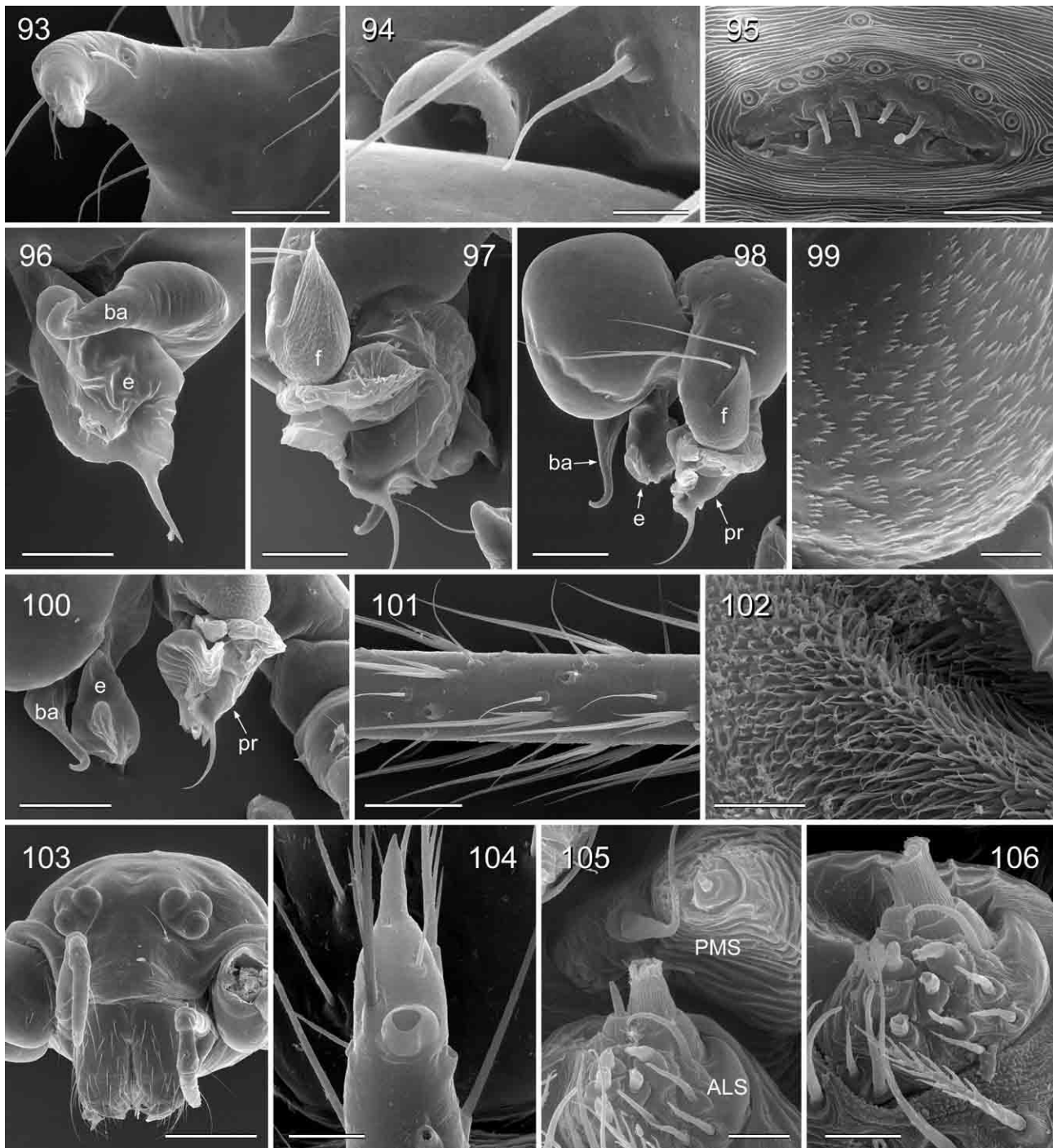




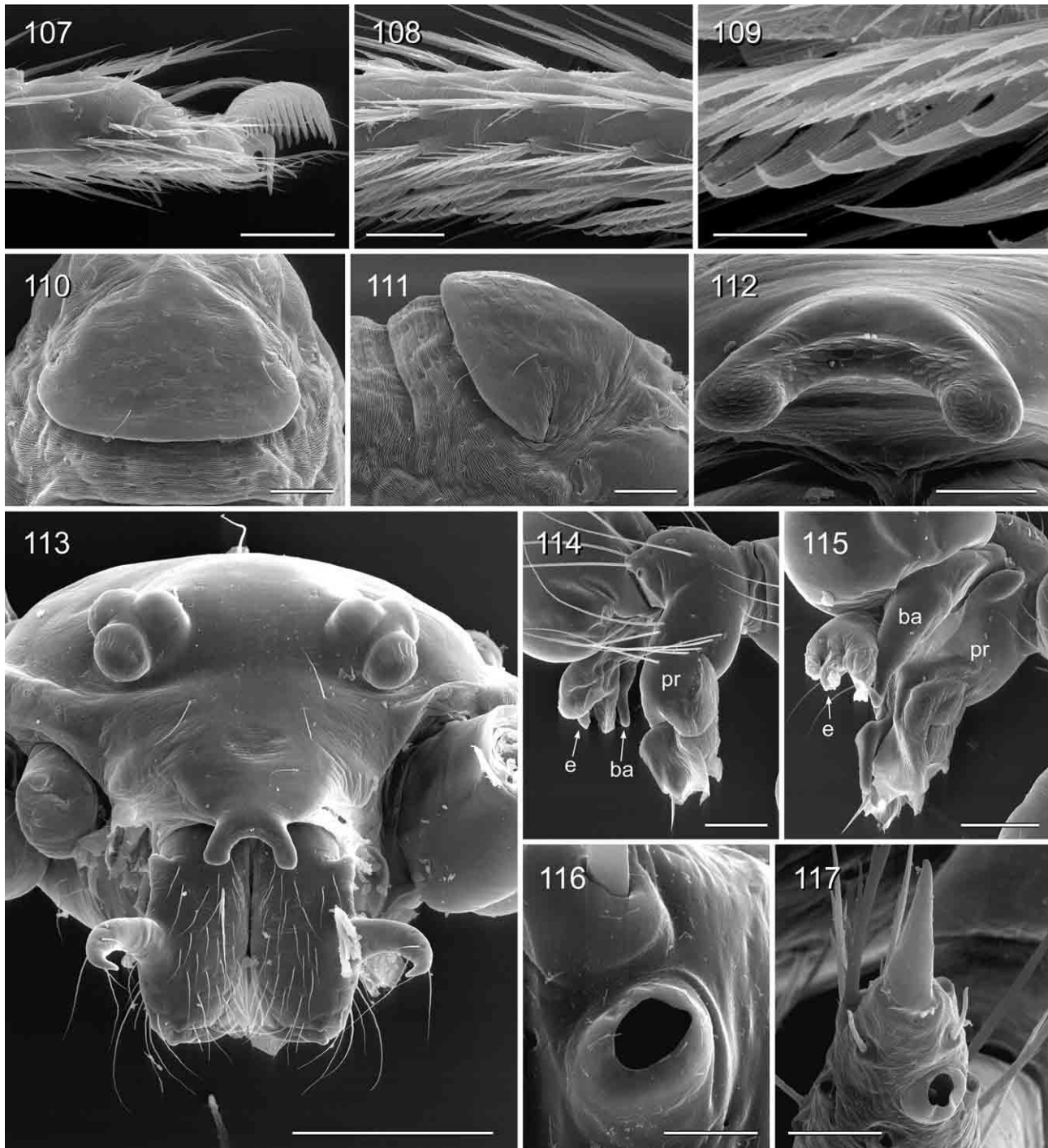
**Figs. 83-87.** *Belisana nujiang*. 83, 84. Left male pedipalp, prolateral (83) and retrolateral (84) views. 85. Male chelicerae, frontal view. 86, 87. Cleared female genitalia, ventral (86) and dorsal (87) views. Scale lines: 0.3 mm (83, 84, 86, 87), 0.2 mm (85).



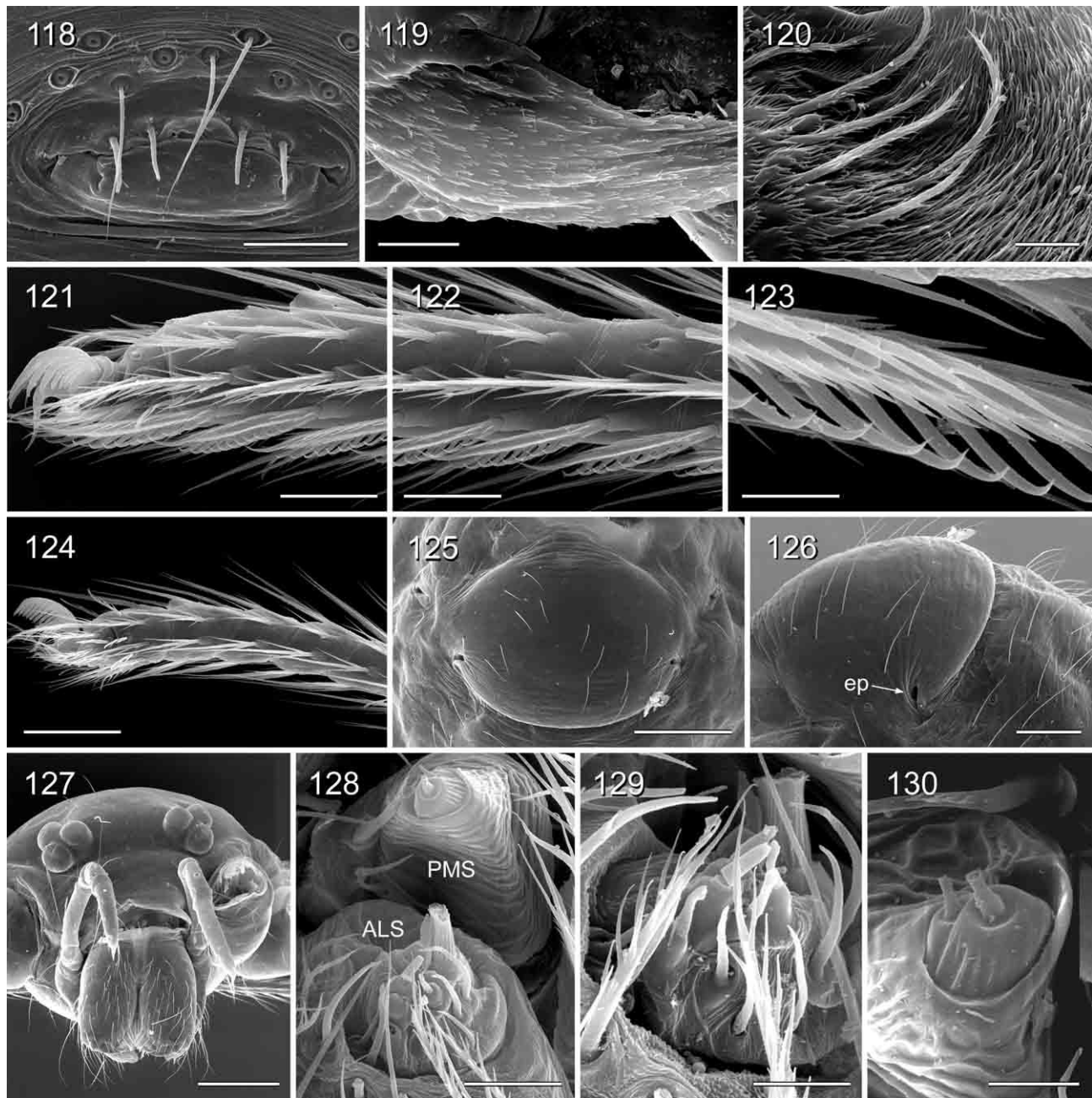
**Figs. 88-92.** *Belisana pianma*. 88, 89. Left male pedipalp, prolateral (88) and retrolateral (89) views (arrow points to distinctive femur apophysis). 90. Male prosoma, frontal view. 91, 92. Cleared female genitalia, ventral (91) and dorsal (92) views. Scale lines: 0.3 mm.



**Figs. 93-106.** *Belisana nujiang*. 93. Right male cheliceral apophysis (note absence of modified hair on tip). 94. Male palpal tarsal organ. 95. Male gonopore with epiandrous spigots. 96. Embolus and bulbal apophysis. 97. Tip of left procurus, retrolatero-ventral view. 98. Left procurus and bulb, retrolateral view. 99. Detail of membranous flap on procurus. 100. Left male palp, tip of procurus and bulbal projections, dorsal view. 101. Hairs on male metatarsus 4 (note 'vertical' hairs). 102. Inside view of male palpal endite. 103. Female prosoma, frontal view. 104. Tip of female palp with tarsal organ, dorsal view. 105. Female ALS and PMS. 106. Male ALS. Scale lines: 10  $\mu$ m (94, 99, 102, 105, 106), 20  $\mu$ m (104), 40  $\mu$ m (93, 95, 101), 50  $\mu$ m (96), 70  $\mu$ m (97), 100  $\mu$ m (98, 100), 200  $\mu$ m (103).



**Figs. 107-117.** *Belisana nujiang* (107-111) and *B. pianma* (112-117). 107. Male tarsus 1 tip. 108. Detail of female tarsus 4, showing comb-hairs. 109. Detail of comb-hair on female tarsus 4. 110. Epigynum, ventral view. 111. Epigynum, lateral view. 112. Male clypeus modification, frontal-ventral view. 113. Male prosoma, frontal view. 114. Left procurus and bulb, retrolateral (slightly distal) view. 115. Right procurus and bulb, prolateral view. 116. Male palpal tarsal organ. 117. Tip of female palp with tarsal organ, dorsal view. Scale lines: 5  $\mu\text{m}$  (109), 10  $\mu\text{m}$  (116), 20  $\mu\text{m}$  (108, 117), 30  $\mu\text{m}$  (107), 40  $\mu\text{m}$  (112), 100  $\mu\text{m}$  (110, 111, 114, 115), 300  $\mu\text{m}$  (113).



**Figs. 118-130.** *Belisana pianma*. 118. Male gonopore with epiandrous spigots. 119. Detail of membranous flap on procurus. 120. Inside view of male palpal endite. 121, 122. Details of female tarsus 4, showing comb-hairs. 123. Detail of comb-hair on female tarsus 4. 124. Female tarsus 1 tip. 125. Epigynum, ventral view. 126. Epigynum, lateral view. 127. Female prosoma, frontal view. 128. Female ALS and PMS. 129. Male ALS. 130. Male PMS. Scale lines: 6  $\mu\text{m}$  (123), 7  $\mu\text{m}$  (130), 10  $\mu\text{m}$  (120, 129), 20  $\mu\text{m}$  (119, 128), 30  $\mu\text{m}$  (121, 122), 40  $\mu\text{m}$  (118), 60  $\mu\text{m}$  (124), 100  $\mu\text{m}$  (126), 200  $\mu\text{m}$  (125, 127).



furrow absent; distance PME-PME 220  $\mu\text{m}$ ; diameter PME 55  $\mu\text{m}$ ; distance PME-ALE  $\sim$ 20  $\mu\text{m}$ . Clypeus with distinctive pair of apophyses (Figs. 90, 112, 113). Sternum wider than long (0.58/0.54). Chelicerae as in Fig. 90, with pair of curved apophyses, tips 375  $\mu\text{m}$  apart. Palps as in Figs. 88 and 89; trochanter with rounded retrolateral apophysis, femur with proximo-dorsal and ventral humps, procurus complex distally, with spine, distinctive dorsal sclerite, ventral membranous flap, and prolateral (hinged?) elements, bulb with hooked apophysis and complex embolus (Figs. 88, 89, 114, 115, 119). Tarsal organ capsulate (Fig. 116). Retrolateral trichobothrium of tibia 1 at 10%; legs without spines and curved hairs, with vertical hairs proximally on all metatarsi; tarsus 1 with  $>$ 20 pseudosegments, but only about 15 quite distinct distally. Gonopore and spinnerets as in Figs. 118, 129, 130.

*Variation.* Tibia 1 in 4 other males: 4.35-4.7. Most males with monochromous opisthosoma.

*Female.* In general similar to male but without clypeal apophyses; marginal bands on carapace less distinct. Tibia 1 in 2 females: 3.6, 4.0. Epigynum simple and flat externally (Figs. 125, 126), valve visible through cuticle (Figs. 56, 91), with pair of lateral pockets 410  $\mu\text{m}$  apart. Dorsal view as in Fig. 92. Palp tip and spinnerets as in Figs. 117 and 128.

*Distribution.* Known from type locality only (Fig. 79).

*Material examined.* CHINA: Yunnan: Nujiang Pref., native forest in Gaoligongshan: type above, together with 4♂3♀ (CAS).

### ***Belisana erawan*, new species**

(Figs. 131-135)

*Type.* Male holotype from Erawan National Park [ $\sim$ 14°38'N, 99°06'E], Kanchanaburi Prov., Thailand; sweeping in evergreen forest, Nov. 16, 1987 (C. L. & P. R. Deeleman), in RMNH.

*Etymology.* The species name is a noun in apposition, taken from the type locality.

*Diagnosis.* Medium-sized, long-legged species with globular opisthosoma; distinguished from relatives by the strong apophysis distally on the procurus (Figs. 131, 132; broad sclerite in ventral view) set with small scales, by the position of the male cheliceral apophyses (Fig. 133), and by the proximo-ventral projection of the palpal femur (Fig. 131).

*Male (holotype).* Total length 1.4 (1.5 with clypeus), carapace width 0.52. Leg 1: 13.1 (3.4 + 0.2 + 3.3 + 5.0 + 1.2), tibia 2: 2.0, tibia 3: 1.2, tibia 4: 1.9; tibia 1 L/d: 57. Habitus similar to *B. kaosok* (cf. Figs. 51, 52). Entire animal pale ochre-grey. Ocular area very flat, not separated from carapace, thoracic furrow absent; distance PME-PME 160  $\mu\text{m}$ ; diameter PME 55  $\mu\text{m}$ ; distance PME-ALE  $\sim$ 15  $\mu\text{m}$ . Clypeus unmodified. Sternum as long as wide (0.38). Chelicerae as in Fig. 133 (shown in slightly dorsal view), tips of apophyses 55  $\mu\text{m}$  apart. Palps as in Figs. 131 and 132; trochanter with short retrolateral apophysis, femur with distinctive proximo-ventral projection, procurus with wide and short proximal part, distally with distinctive toothed apophysis and various membranous elements, bulb with hooked apophysis and simple unsclerotized embolus. Retrolateral trichobothrium of tibia 1 at 15%; legs without spines, curved, and vertical hairs (most hairs missing); tarsus 1 with  $\sim$ 15 pseudosegments, very difficult to see in dissecting microscope.

*Variation.* Tibia 1 in 3 other males: 3.20, 3.25, 3.65.

*Female.* In general similar to male. Tibia 1 in 5 females: 2.1-2.9 (mean 2.63). Epigynum very simple externally, flat and almost invisible, with pair of pockets very close together on posterior projection (Fig. 134; pockets  $\sim$ 15  $\mu\text{m}$  apart), dorsal view as in Fig. 135. ALS apparently with at least 3 spigots in addition to basic set of two.

*Distribution.* Known from four localities in north-western and central-western Thailand (Fig. 79).

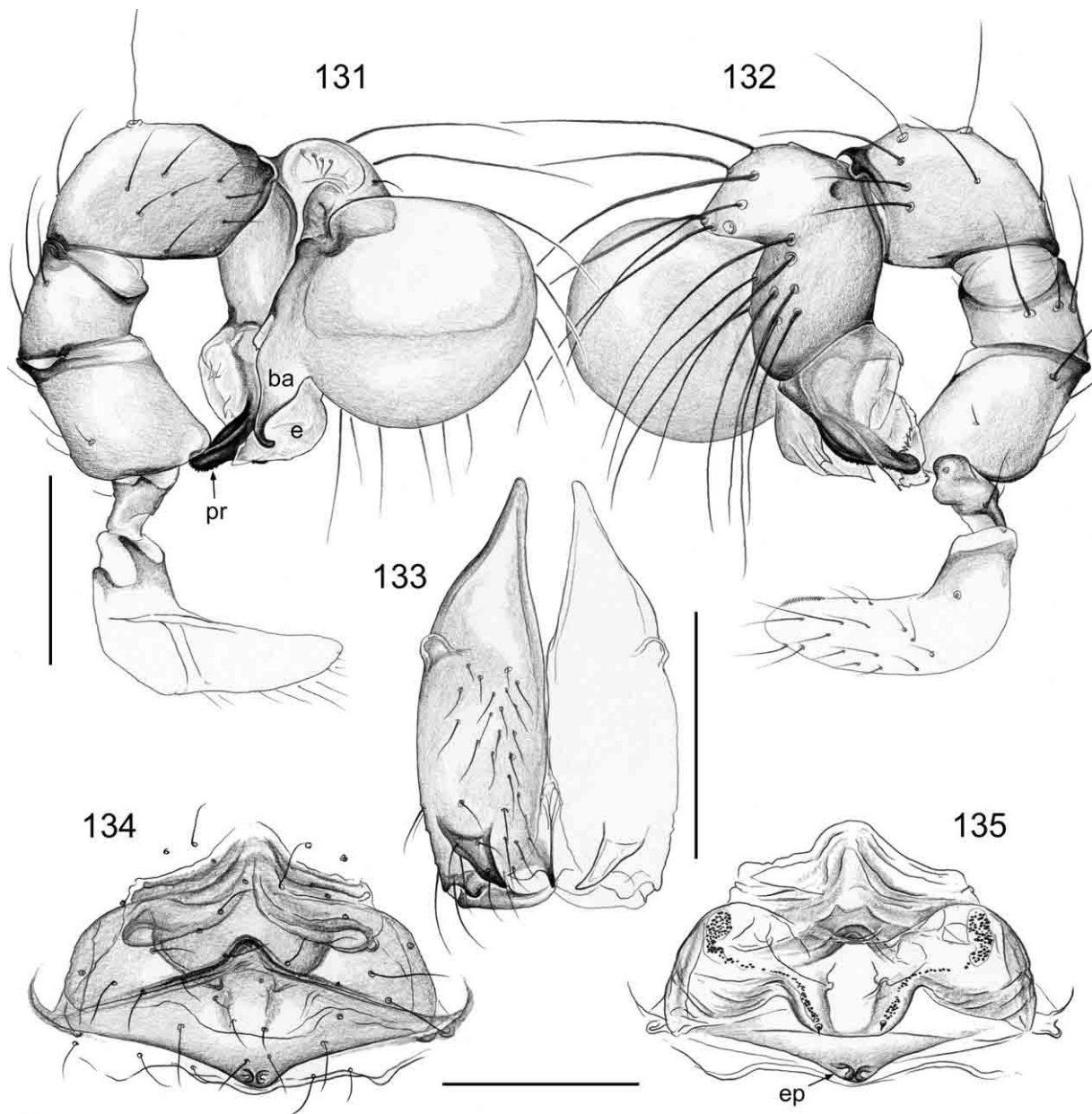
*Material examined.* THAILAND: Kanchanaburi: Erawan N. P.: type above, together with 1♂3♀ (RMNH); Mae Hong Son: Pha Sua waterfall N of Mae Hong Son [ $\sim$ 19°23.5'N, 97°57'E], 420 m a.s.l., Oct. 8, 1990 (P. Schwendinger), 1♂ (MHNG). Chiang Mai: Doi Suthep [ $\sim$ 18°47'N, 98°57'E], jungle, Nov. 16, 1976 (P. Lehtinen), 2♂4♀ 1 juvenile (ZMT, AA3476). Chiang Rai: Mae Sai Distr., Luang Cave (20°22.8'N, 99°52.1'E), 440 m a.s.l., inside limestone cave, Dec. 18, 2003 (P. Schwendinger), 1♂ (MHNG).

### ***Belisana scharffi*, new species**

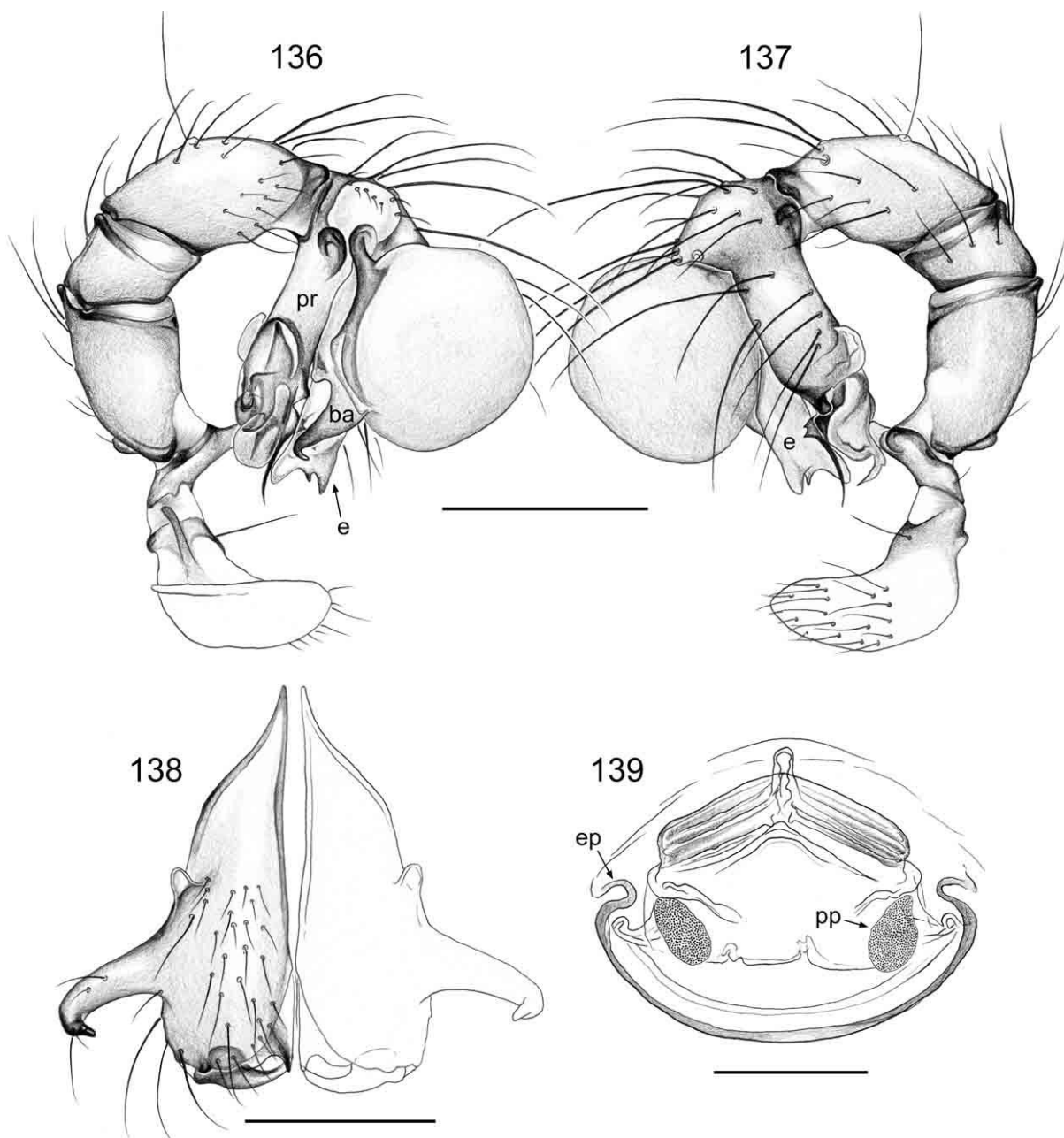
(Figs. 9, 10, 65, 136-153)

*Type.* Male holotype from Doi Inthanon National Park near intersect. rd. to Mae Chaem and checkpoint (18°31.6'N, 98°30.0'E), Chiang Mai Prov., Thailand; wet primary forest,  $\sim$ 1800 m a.s.l., Oct. 3, 2003 (ATOL Expedition 2003), in MACN.

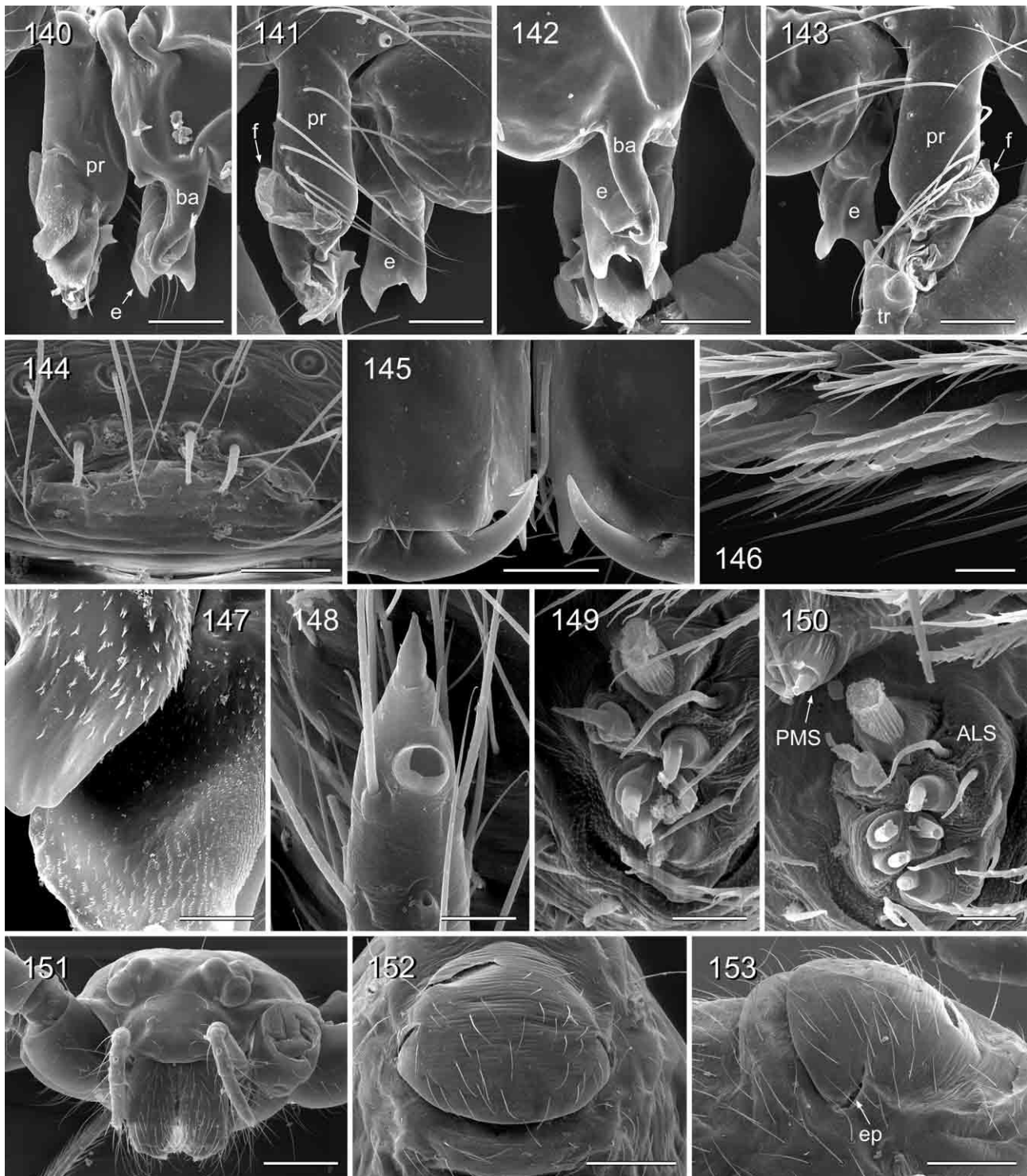
*Etymology.* This species is named for Nikolaj Scharff, leader of the ATOL Expedition 2003 to Thailand.



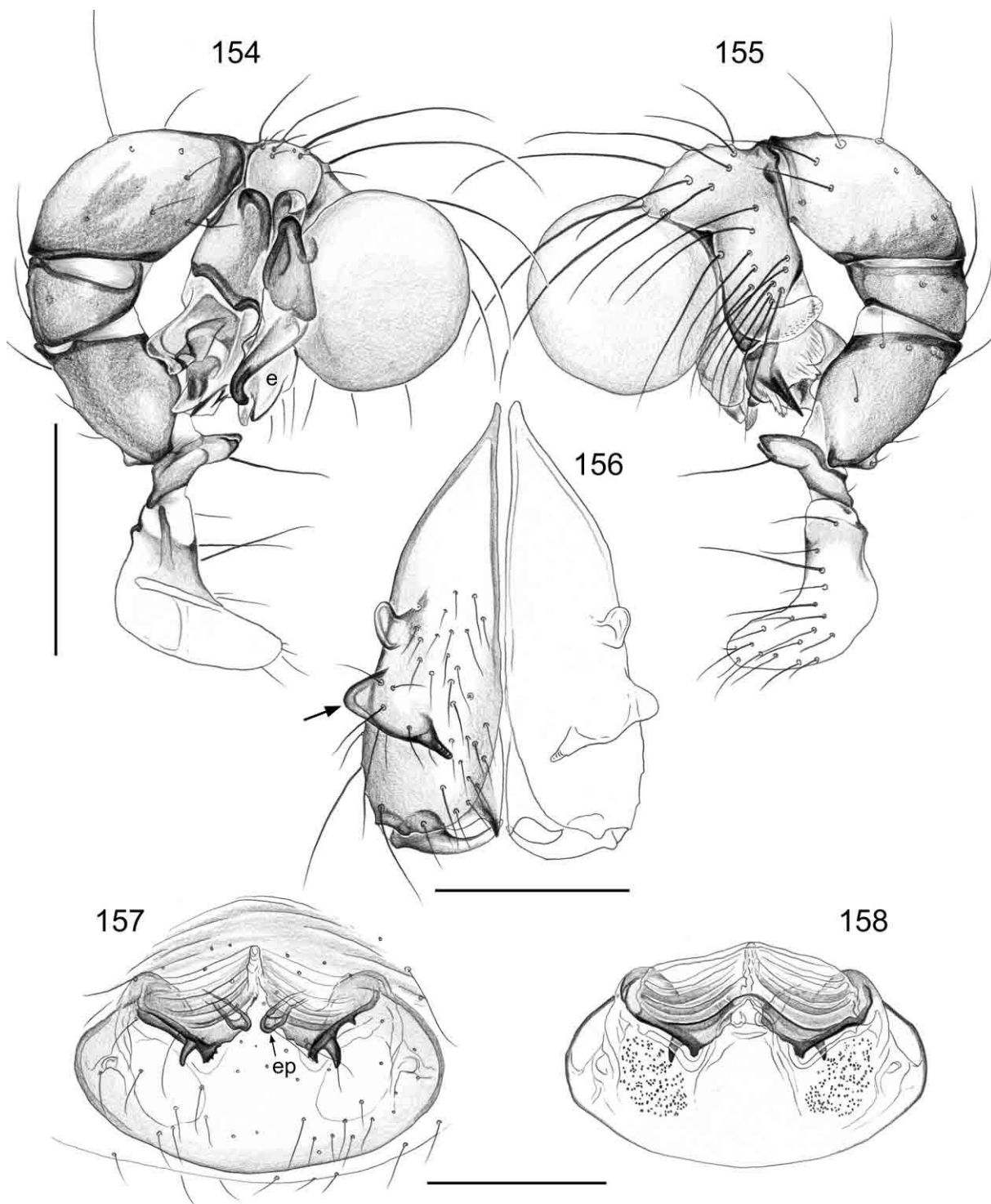
**Figs. 131-135.** *Belisana erawan*. 131, 132. Left male pedipalp, prolateral (131) and retrolateral (132) views. 133. Male chelicerae, frontal view. 134, 135. Cleared female genitalia, ventral (134) and dorsal (135) views. Scale lines: 0.2 mm.



**Figs. 136-139.** *Belisana scharffi*. 136, 137. Left male pedipalp, prolateral (136) and retrolateral (137) views. 138. Male chelicerae, frontal view. 139. Cleared female genitalia, dorsal view. Scale lines: 0.3 mm (136, 137), 0.2 mm (138, 139).



**Figs. 140-153.** *Belisana scharffi*. 140. Left procursus and bulbal projections, prolatero-ventral view. 141. Right procursus and bulb, retrolateral view. 142. Right bulb, prolatateral view. 143. Left procursus, palpal trochanter, and embolus, retrolateral view. 144. Male gonopore with epiandrous spigots. 145. Male chelicerae, posterior view. 146. Comb-hair on male tarsus 4. 147. Distal elements of left procursus, prolatateral view (cf. Fig. 140). 148. Tip of female palp with tarsal organ, dorsal view. 149. Male ALS. 150. Female ALS and PMS. 151. Female prosoma, frontal view. 152. Epigynum, ventral view. 153. Epigynum, lateral view. Scale lines: 10  $\mu$ m (146, 149, 150), 20  $\mu$ m (147, 148), 30  $\mu$ m (144), 40  $\mu$ m (145), 100  $\mu$ m (140-143), 200  $\mu$ m (151-153).



**Figs. 154-158.** *Belisana inthanon*. 154, 155. Left male pedipalp, prolateral (154) and retrolateral (155) views. 156. Male chelicerae, frontal view. 157, 158. Cleared female genitalia, ventral (157) and dorsal (158) views. Scale lines: 0.4 mm (154, 155), 0.2 mm (156), 0.3 mm (157, 158).



**Diagnosis.** Relatively large, long-legged species with oval and dorsally elongated opisthosoma and dark margins on prosoma (Fig. 9); distinguished from similar species with widely spread male cheliceral apophyses (Fig. 138) by the procurus (dorso-distal sclerite: Fig. 137) and the shapes of bulbal apophysis and embolus (Fig. 136).

**Male (holotype).** Total length 1.9 (2.1 with clypeus), carapace width 0.70. Leg 1: 18.9 (4.6 + 0.3 + 4.7 + 7.4 + 1.9), tibia 2: 3.3, tibia 3: 1.9, tibia 4: 2.6; tibia 1 L/d: 76. Habitus as in Figs. 9 and 10. Carapace pale ochre-yellow with darker lateral margins, sternum whitish; legs pale ochre-yellow; opisthosoma pale ochre-grey, with slightly darker spots visible through cuticle dorsally. Ocular area not elevated, thoracic furrow absent; distance PME-PME 150  $\mu$ m; diameter PME 70  $\mu$ m; distance PME-ALE ~20  $\mu$ m. Clypeus unmodified. Sternum about as wide as long (0.50). Chelicerae as in Fig. 138, tips of apophyses 440  $\mu$ m apart. Palps as in Figs. 136 and 137; trochanter with retrolateral and ventral apophyses, femur with small apophysis dorsally, femur and patella darker than other segments, procurus with distinctive distal spine (Figs. 137, 140, 141), transparent membranous flap retrolaterally (Figs. 141, 143), apparently with hinged process, distal elements set with many small scales (Fig. 147); bulb with hooked apophysis and bilobed embolus with small median spine (Figs. 136, 142). Retrolateral trichobothrium of tibia 1 at 15%; legs without spines and curved hairs, with vertical hairs on metatarsi, especially proximally; tarsus 1 with >15 pseudosegments, barely visible. Gonopore and ALS as in Figs. 144, 149.

**Variation.** Tibia 1 in 11 other males: 4.3-5.0 (mean 4.6). Some males with monochromous opisthosoma.

**Female.** In general similar to male; tibia 1 in 13 females: 3.3-4.0 (mean 3.7). Epigynum very simple externally (Figs. 65, 152, 153), with distinctive frontal structure barely visible through cuticle, pockets 420  $\mu$ m apart; dorsal view as in Fig. 139.

**Distribution.** Known from two neighboring localities in Doi Inthanon National Park, Thailand (Fig. 79).

**Material examined.** THAILAND: *Chiang Mai*: Doi Inthanon N. P. at 18°31.6'N, 98°30.0'E, type above, together with 4♂3♀ (MACN); same collection data, 1♀ (MACN); same collection data, three vials with label "MJR 3x03/1-3 web sampled", 2♂3♀ (MACN); Doi Inthanon N. P. at 18°31.8'N, 98°30.2'E, ~500 m from checkpoint at intersect. rd. summit/Mae Chaem, 1 ha inventory, wet primary forest, ~1800 m a.s.l., Oct. 6-7, 2003 (ATOL Expedition 2003), many ♂♂♀♀ (about 120 vials), in MACN.

#### ***Belisana inthanon*, new species**

(Figs. 11, 12, 60, 154-172)

**Type.** Male holotype from Doi Inthanon N. P. at 18°31.8'N, 98°30.2'E, ~500 m from checkpoint at intersect. rd. summit/Mae Chaem, Chiang Mai Prov., Thailand; 1 ha inventory, wet primary forest, ~1800 m a.s.l., Oct. 6-7, 2003 (ATOL Expedition 2003), in MACN.

**Etymology.** The species name is a noun in apposition, taken from the type locality.

**Diagnosis.** Relatively large, long-legged species with oval opisthosoma and dark margins on prosoma (Fig. 11); distinguished from congeners by the lateral projection on the male cheliceral apophyses (Fig. 156), the bifid apophysis on the trochanter (Figs. 154, 155) and the female genitalia (external aspect and internal structures, Figs. 157, 171).

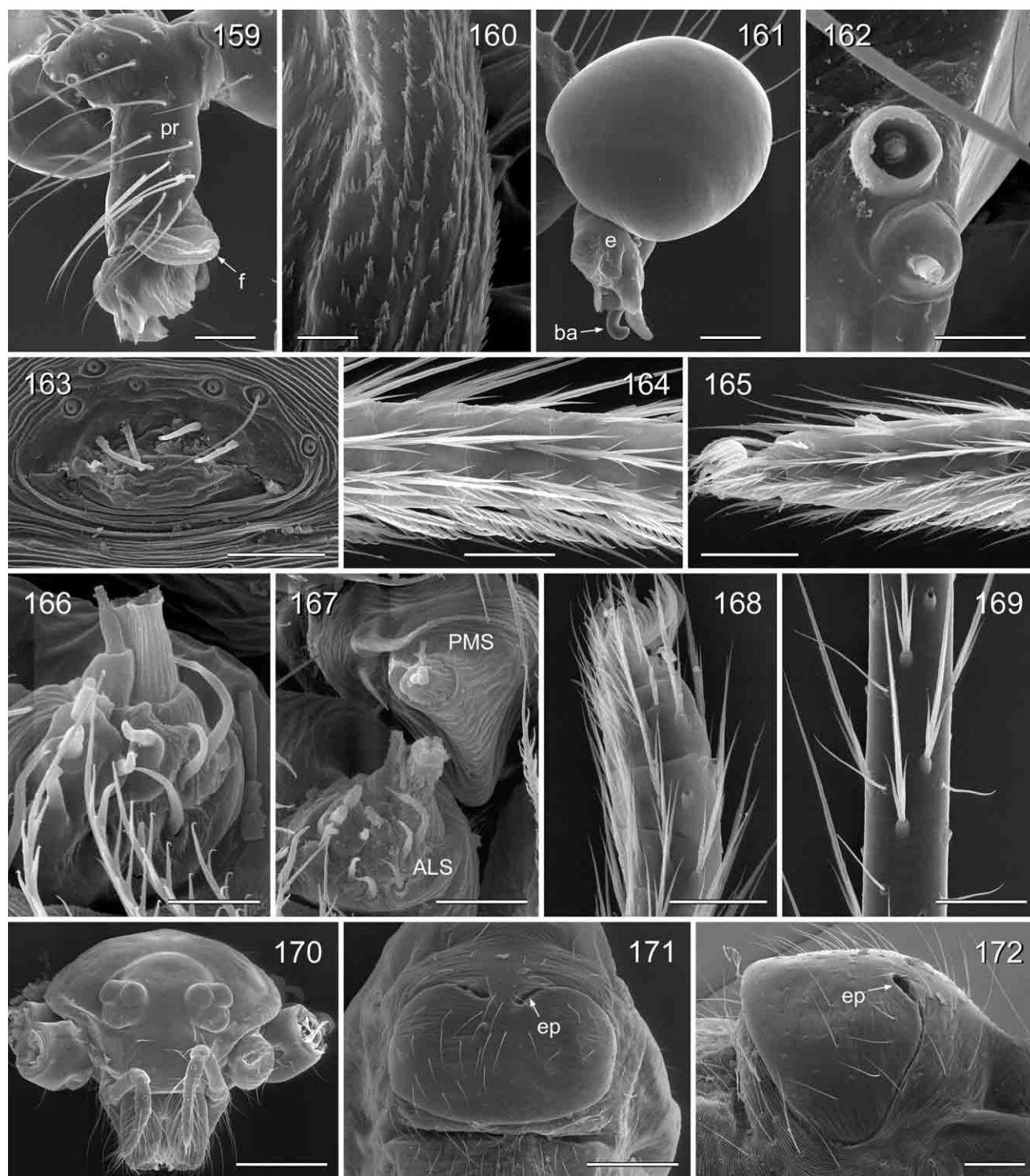
**Male (holotype).** Total length 1.9 (2.1 with clypeus), carapace width 0.83. Leg 1: 18.5 (4.5 + 0.4 + 4.5 + 7.4 + 1.7), tibia 2: 3.1, tibia 3: 2.0, tibia 4: 2.7; tibia 1 L/d: 64. Habitus as in Figs. 11 and 12. Carapace ochre-yellow with wide brown lateral margins, clypeus also brown, sternum pale ochre-yellow; legs ochre-yellow, with brown patellae and tibia-metatarsus joints; opisthosoma ochre-grey, with slightly darker spots visible through cuticle dorsally. Ocular area barely elevated, thoracic furrow absent; distance PME-PME 115  $\mu$ m; diameter PME 90  $\mu$ m; distance PME-ALE ~20  $\mu$ m. Clypeus unmodified. Sternum slightly wider than long (0.56/0.48). Chelicerae as in Fig. 156, with distinctive lateral projections on frontal apophyses, tips 95  $\mu$ m apart. Palps as in Figs. 154 and 155; trochanter with distinctive bifid retrolateral apophysis, femur with small hump dorsally, femur and patella darker than other segments, procurus with straight spine distally, with membranous flap and additional complex structures prolaterally (Figs. 154, 159, 160), bulb with hooked sclerite and bilobed embolus (Figs. 154, 161). Tarsal organ capsulate (Fig. 162). Retrolateral trichobothrium of tibia 1 at 13%; legs without spines and curved hairs, with vertical hairs on metatarsi (Fig. 169), especially frontally; tarsus 1 with >15 pseudosegments, only distally distinct. Gonopore and ALS as in Figs. 163 and 166.

**Variation.** Tibia 1 in 4 other males: 4.5-4.8 (mean 4.68).

**Female.** In general similar to male, but pattern on carapace slightly lighter; tibia 1 in 6 females: 3.3-3.7 (mean 3.55). Epigynum with pockets in anterior position (Figs. 157, 171, 172), 35  $\mu$ m apart, with distinctive internal spine-like structures (Fig. 157); dorsal view as in Fig. 158.

**Distribution.** Known only from type locality (Fig. 79).

**Material examined.** THAILAND: *Chiang Mai*: Doi Inthanon N. P., type above; same collection data, 8 vials with 5♂8♀ (MACN).



**Figs. 159-172.** *Belisana inthanon*. 159. Left procursus, retrolateral view. 160. Detail of membranous flap on procursus. 161. Genital bulb with embolus and hooked bulbal apophysis. 162. Male palpal tarsal organ. 163. Male gonopore with epiandrous spigots. 164. Male tarsus 4 with ventral comb-hairs. 165. Female tarsus 4 tip. 166. Male ALS. 167. Female ALS and PMS. 168. Female tarsus 3 tip. 169. Hairs on male metatarsus 4 (note 'vertical' hairs). 170. Female prosoma, frontal view. 171. Epigynum, ventral view. 172. Epigynum, lateral view. Scale lines: 10  $\mu\text{m}$  (160, 166), 20  $\mu\text{m}$  (162, 167), 30  $\mu\text{m}$  (164), 40  $\mu\text{m}$  (163, 165, 168), 50  $\mu\text{m}$  (169), 100  $\mu\text{m}$  (159, 161, 172), 200  $\mu\text{m}$  (171), 300  $\mu\text{m}$  (170).

***Belisana hormigai*, new species**  
(Figs. 2-4, 13, 14, 67, 173-177, 183-198)

*Type.* Male holotype from Doi Inthanon National Park near intersect. rd. to Mae Chaem and checkpoint (18°31.6'N, 98°30.0'E), Chiang Mai Prov., Thailand; wet primary forest, ~1800 m a.s.l., Oct. 3, 2003 (ATOL Expedition 2003), in MACN.

*Etymology.* Named for Gustavo Hormiga who photographed the web of this species in the field.

*Diagnosis.* Relatively large, long-legged species with oval or slightly angular opisthosoma and dark margins on prosoma (Fig. 13); easily distinguished from congeners by the pair of strong black spines ventrally on the procurus (Figs. 173, 174, 183-185).

*Male (holotype).* Total length 2.0 (2.1 with clypeus), carapace width 0.80. Leg 1: 19.6 (4.8 + 0.3 + 4.9 + 7.9 + 1.7), tibia 2: 3.5, tibia 3: 2.5, tibia 4: 3.2; tibia 1 L/d: 58. Habitus as in Figs. 13 and 14. Prosoma ochre-yellow, carapace with wide black lateral margins, sternum whitish, legs ochre yellow, patellae and tibia-metatarsus joints black; opisthosoma ochre grey with darker spots visible through cuticle dorsally. Ocular area not elevated, thoracic furrow absent; distance PME-PME 150  $\mu$ m; diameter PME 85  $\mu$ m; distance PME-ALE ~20  $\mu$ m. Clypeus unmodified. Sternum slightly wider than long (0.66/0.58). Chelicerae as in Figs. 175 and 190, tips of apophyses unmodified (Fig. 186), 65  $\mu$ m apart. Palps as in Figs. 173 and 174; trochanter with distinct but weakly sclerotized retrolateral apophysis, femur with distinct dorsal apophysis, femur and patella darker than other segments, procurus with three distal sclerites all of which appear hinged, one of these a distinctive pair of spines (Figs. 173, 185); bulb with hooked apophysis and embolus with spine (Figs. 173, 184). Tarsal organ capsulate (Fig. 188). Retrolateral trichobothrium of tibia 1 at 11%; legs without spines and curved hairs, with vertical hairs on all metatarsi (Fig. 195); tarsus 1 with ~20 pseudosegments, fairly distinct. Gonopore and ALS as in Figs. 187, 193.

*Variation.* Tibia 1 in 16 other males: 4.3-5.5 (mean 4.9).

*Female.* In general similar to male, but carapace margins and patellae not as dark as in male; tibia 1 in 12 females: 3.4-3.9 (mean 3.7). Epigynum very simple externally (Fig. 196), with distinctive internal structures visible through cuticle (Figs. 67, 176); with pockets 20  $\mu$ m apart. Dorsal view as in Fig. 177. Palpal tarsal organ and ALS as in Figs. 189 and 192.

*Distribution.* Known from two neighboring localities in Doi Inthanon National Park, Thailand (Fig. 79).

*Material examined.* THAILAND: *Chiang Mai:* Doi Inthanon N. P., type above, together with 8♂ (MACN); same collection data, "Photos 6-16/R2, 17-25/R2, 26-2a/R2" by G. Hormiga, 2♂2♀ (ZMUC); Doi Inthanon N. P. at 18°31.8'N, 98°30.2'E, 1 ha inventory, ~500 m from checkpoint at intersect. rd. summit/Mae Chaem, wet primary forest, ~1800 m a.s.l., Oct. 6-7, 2003 (ATOL Expedition 2003), many ♂♂♀♀ (about 80 vials), in MACN.

***Belisana leumas*, new species**  
(Figs. 35, 36, 178-182, 199-209)

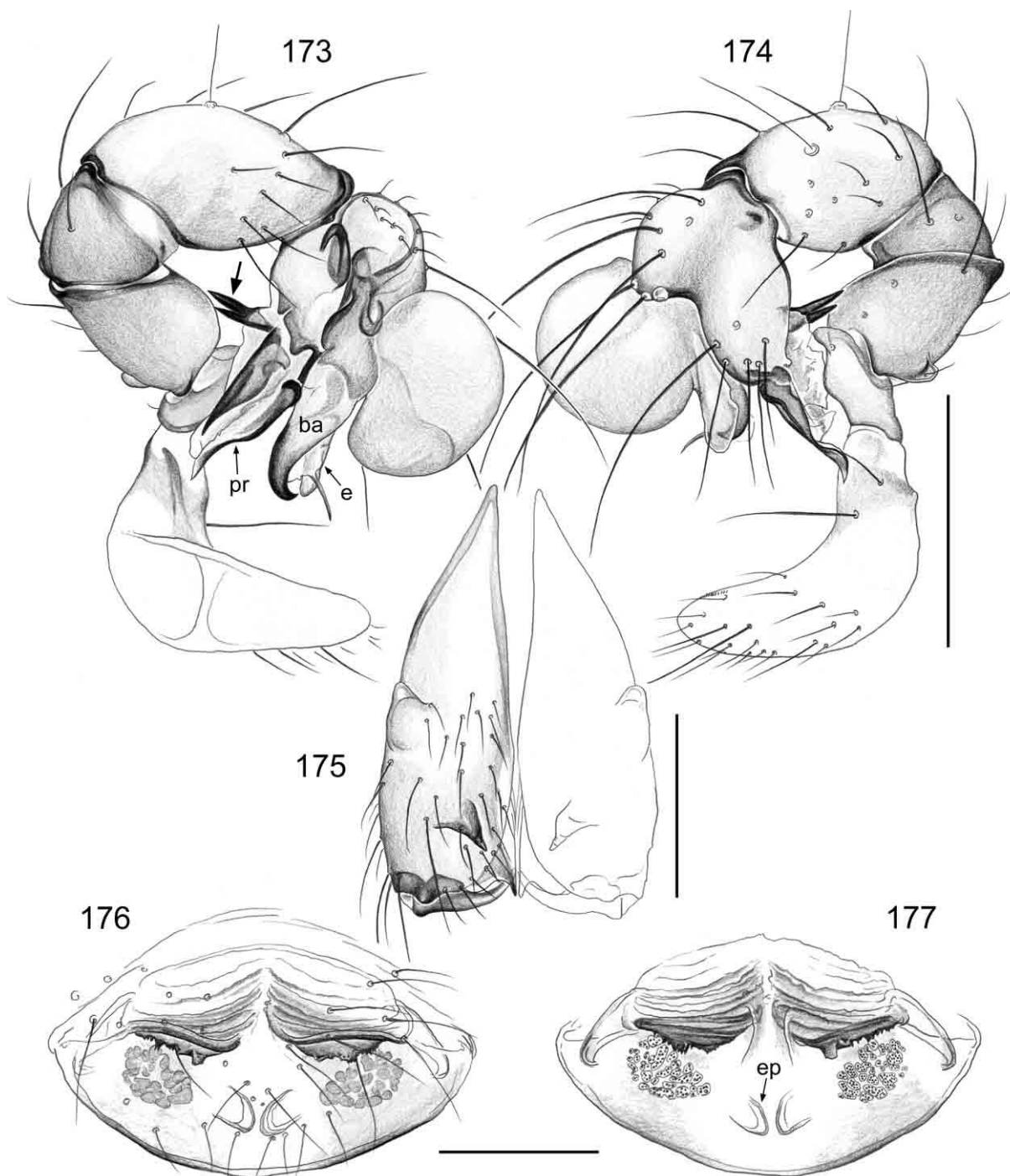
*Type.* Male holotype from Doi Inthanon N. P. at 18°31.8'N, 98°30.2'E, ~500 m from checkpoint at intersect. rd. summit/Mae Chaem, Chiang Mai Prov., Thailand; 1 ha inventory, wet primary forest, ~1800 m a.s.l., Oct. 6-7, 2003 (ATOL Expedition 2003), in MACN.

*Etymology.* The species name is an arbitrary combination of letters, used as a noun in apposition.

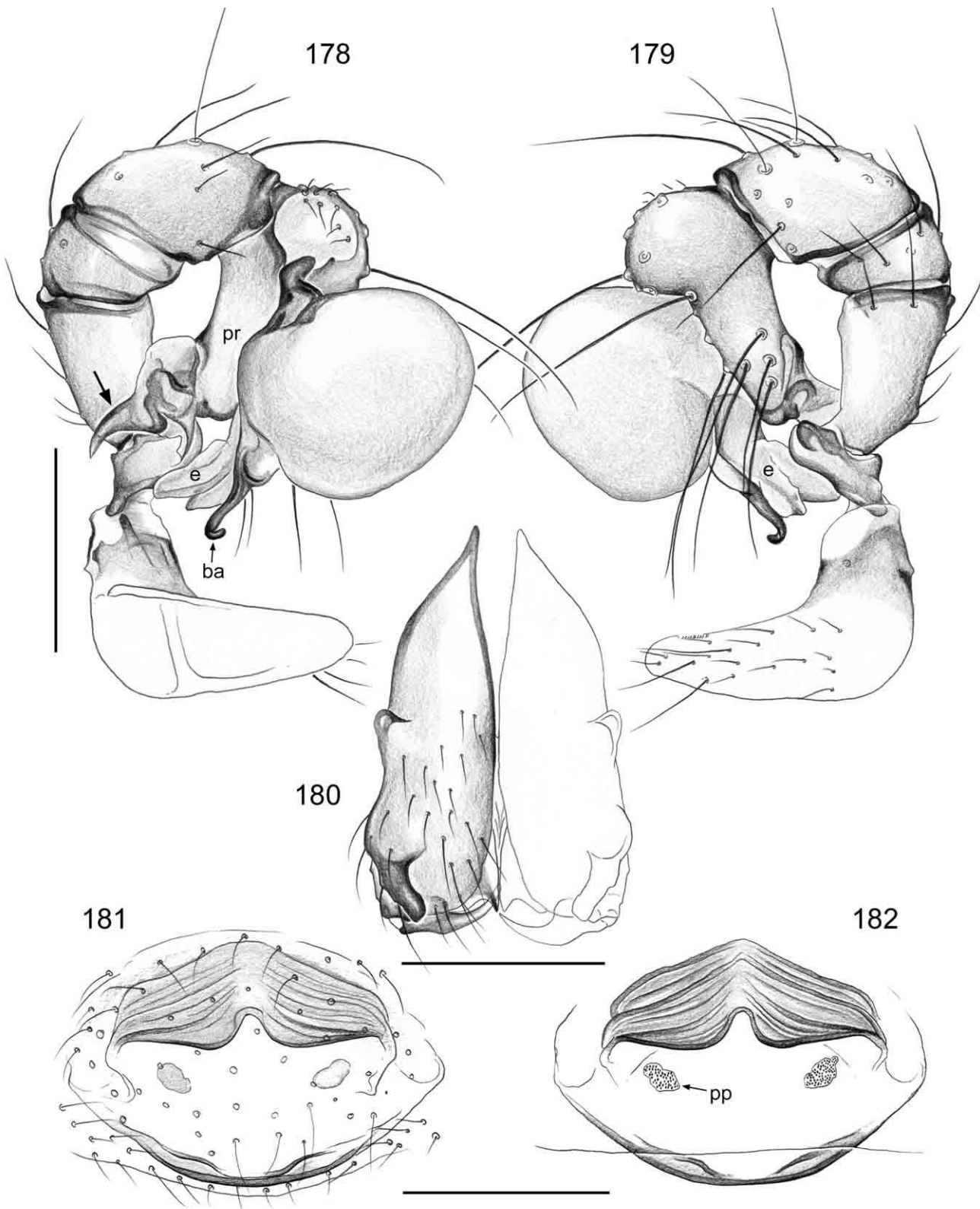
*Diagnosis.* Tiny, short-legged species with globular opisthosoma; easily distinguished from congeners by the distinctive, strong and long apophysis on the procurus (prolateral view, Fig. 178).

*Male (holotype).* Total length 1.2 (1.3 with clypeus), carapace width 0.60. Leg 1: 8.11 (2.00 + 0.27 + 2.10 + 2.77 + 0.97), tibia 2: 1.30, tibia 3: 0.80, tibia 4: 1.27; tibia 1 L/d: 40. Habitus as in Figs. 35 and 36. Carapace ochre-yellow with pair of large darker marks, sternum pale ochre-yellow, legs ochre-yellow; opisthosoma ochre-grey, with large contiguous spots, heart mark and ventral side lighter. Ocular area slightly elevated, thoracic furrow absent; distance PME-PME 60  $\mu$ m; diameter PME 60  $\mu$ m; distance PME-ALE ~15  $\mu$ m. Clypeus unmodified. Sternum slightly wider than long (0.46/0.38). Chelicerae as in Fig. 180, cheliceral apophyses slightly flattened (appear thinner in lateral view), wide tips ~160  $\mu$ m apart. Palps as in Figs. 178 and 179; trochanter with short rounded retrolateral apophysis, femur with indistinct hump dorsally, procurus distally with large flattened (hinged?) sclerite and membranous flap (Figs. 178, 204), bulb with hooked sclerite and bilobed embolus (Figs. 178, 179, 202, 203). Tarsal organ exposed (Fig. 205). Retrolateral trichobothrium of tibia 1 at 31%; legs without spines, curved hairs, and vertical hairs; tarsus 1 with ~13 pseudosegments, fairly distinct.

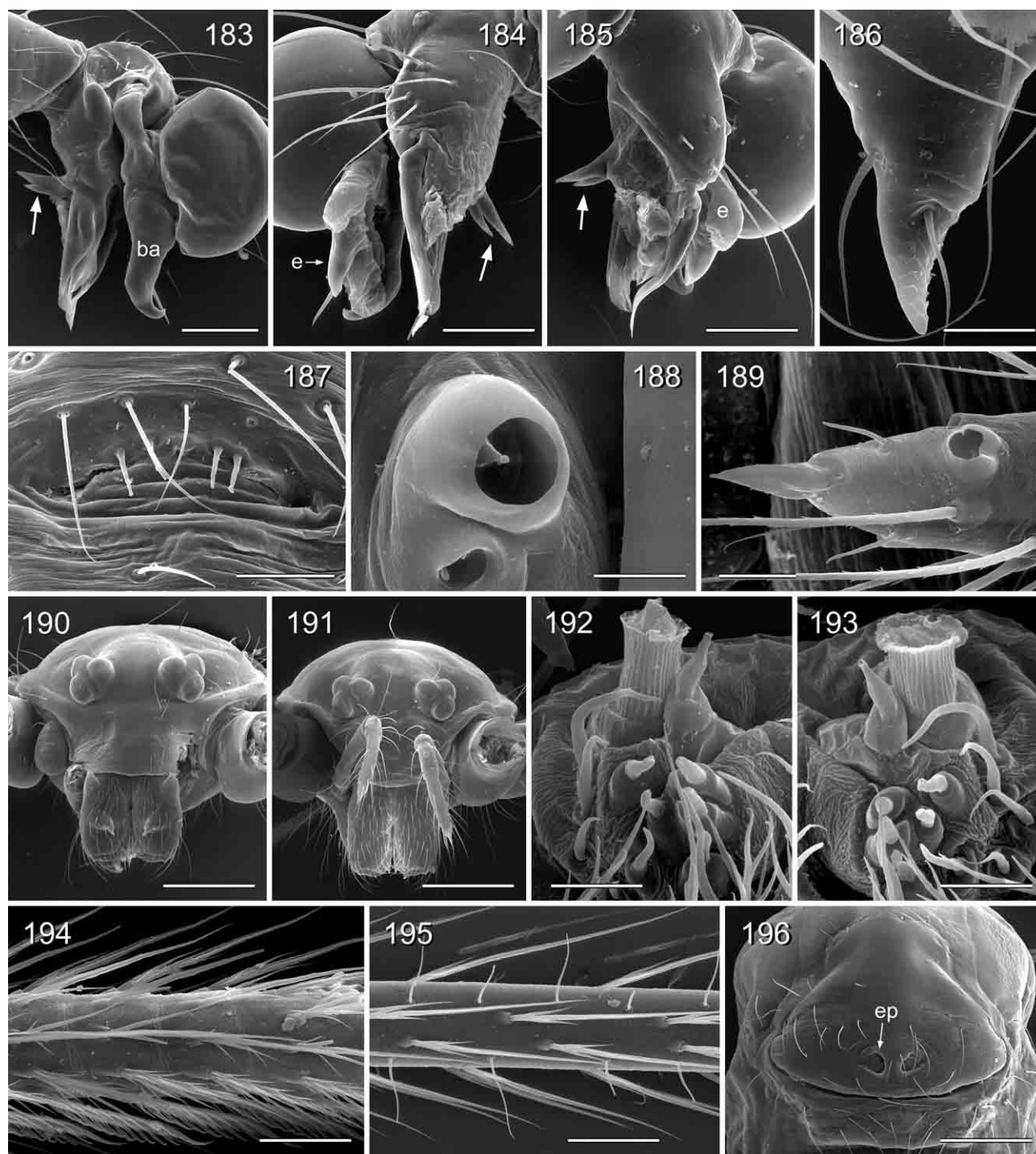
*Variation.* Tibia 1 in 6 other males: 1.93-2.20 (mean 2.08).



**Figs. 173-177.** *Belisana hormigai*. 173, 174. Left male pedipalp, prolateral (173) and retrolateral (174) views (arrow points to distinctive spines on procurus). 175. Male chelicerae, frontal view. 176, 177. Cleared female genitalia, ventral (176) and dorsal (177) views. Scale lines: 0.3 mm (173, 174), 0.2 mm (175-177).

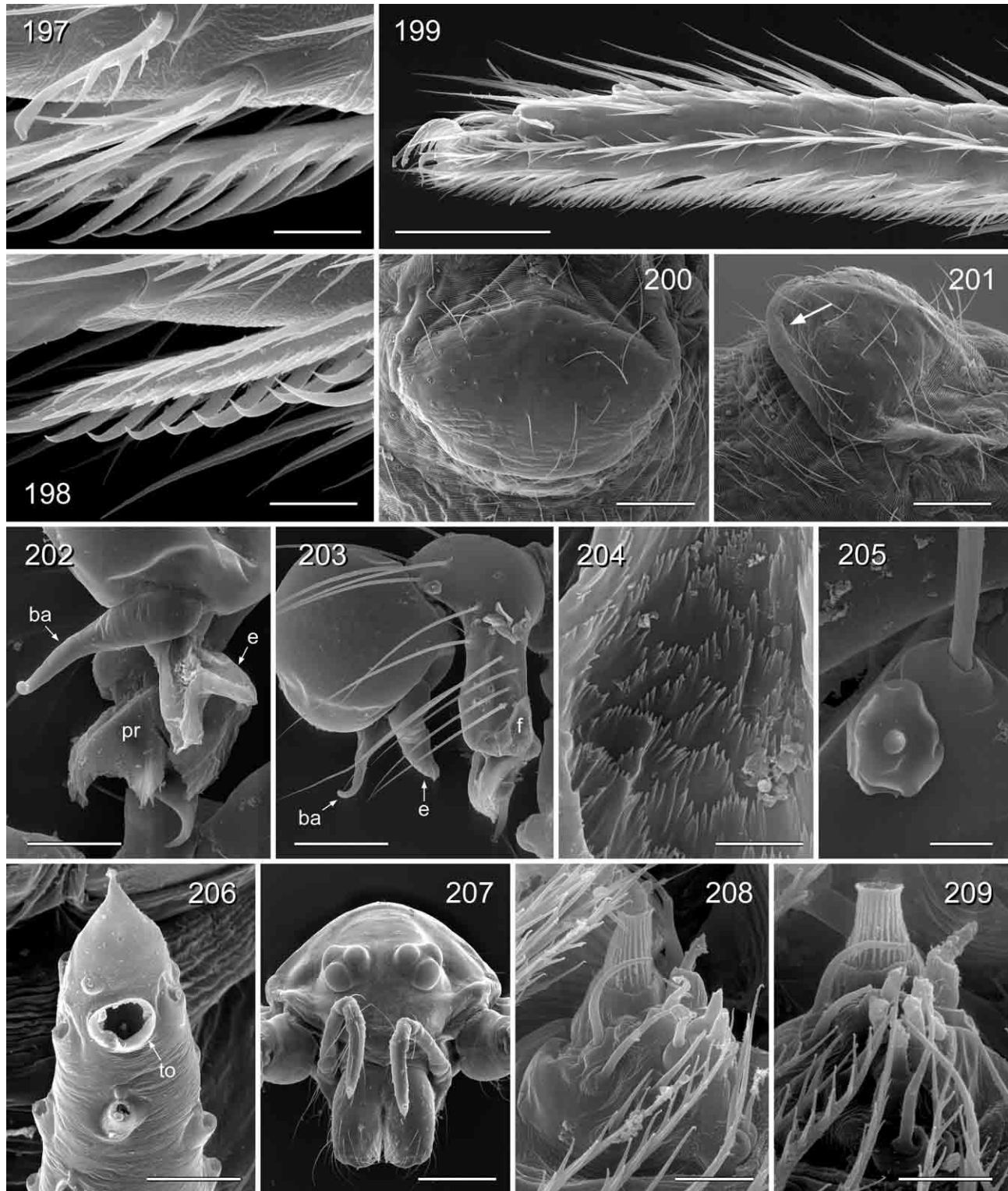


**Figs. 178-182.** *Belisana leumas*. 178, 179. Left male pedipalp, prolateral (178) and retrolateral (179) views (arrow points to distinctive apophysis on procursus). 180. Male chelicerae, frontal view. 181, 182. Cleared female genitalia, ventral (181) and dorsal (182) views. Scale lines: 0.2 mm.



**Figs. 183-196.** *Belisana hormigai*. 183. Left procursus and bulb, prolateral view. 184. Left procursus and bulb, retrolateral (slightly distal) view. 185. Right procursus and bulb, retrolateral view. 186. Male cheliceral apophysis. 187. Male gonopore with epiandrous spigots. 188. Male palpal tarsal organ. 189. Tip of female palp with tarsal organ, dorsal view. 190. Male prosoma, frontal view. 191. Female prosoma, frontal view. 192. Female ALS. 193. Male ALS. 194. Male tarsus 4 with comb-hairs. 195. Hairs on male metatarsus 4 (note 'vertical' hairs). 196. Epigynum, ventral view. Arrows point to distinctive spines on procursus. Scale lines: 10  $\mu\text{m}$  (188, 192, 193), 20  $\mu\text{m}$  (186, 189), 30  $\mu\text{m}$  (194), 40  $\mu\text{m}$  (187), 60  $\mu\text{m}$  (195), 100  $\mu\text{m}$  (183-185), 200  $\mu\text{m}$  (196), 300  $\mu\text{m}$  (190, 191).





**Figs. 197-209.** *Belisana hormigai* (197, 198) and *B. leumas* (199-209). 197, 198. Details of comb-hair on male tarsus 4, retrolateral (197) and prolateral (198) views. 199. Female tarsus 4, distal part, showing pseudosegmentation and comb-hairs. 200. Epigynum, ventral view. 201. Epigynum, lateral view (arrow points to groove-like indentation). 202. Procurus tip and bulbal projections, prolateral view. 203. Left procurus and bulb, retrolateral view. 204. Detail of membranous flap on procurus. 205. Male palpal tarsal organ. 206. Tip of female palp with tarsal organ, dorsal view. 207. Female prosoma, frontal view. 208. Male ALS. 209. Female ALS. Scale lines: 7  $\mu$ m (197, 198, 204), 10  $\mu$ m (205, 208, 209), 20  $\mu$ m (206), 50  $\mu$ m (199), 60  $\mu$ m (202), 70  $\mu$ m (200), 100  $\mu$ m (201, 203), 200  $\mu$ m (207).

*Female.* In general similar to male; tibia 1 in 11 females: 1.37-1.57 (mean 1.44). Epigynum very simple light brown plate (Figs. 200, 201), no pockets but groove-like indentations ~110-130  $\mu\text{m}$  apart (Fig. 181); dorsal view as in Fig. 182.

*Distribution.* Known from several neighboring localities in Doi Inthanon, Thailand (Fig. 79).

*Material examined.* THAILAND: *Chiang Mai:* Doi Inthanon N. P., type above, together with 2♂1♀ (MACN); same collection data, 8 vials with 5♂11♀ (MACN); Doi Inthanon National Park near intersect. rd. to Mae Chaem and checkpoint (18°31.6'N, 98°30.0'E), wet primary forest, ~1800 m a.s.l., Oct. 3, 2003 (ATOL Expedition 2003), 1♂ (MACN); Chom Thong, Doi Inthanon [~18°35'N, 98°29'E], 2590 m a.s.l., June 23, 1986 (P. Leclerc), 1♂ (RMNH); Doi Inthanon, 2530 m a.s.l., April 18-May 23, 1987 (P. Schwendinger) 1♂ (RMNH).

***Belisana bantham*, new species**

(Figs. 210-214)

*Type.* Male holotype from Ban Tham, Tham Plaa [19°18'N, 98°01'E], Mae Hong Son Province, Thailand; June 23, 1986 (P. Leclerc), in RMNH.

*Etymology.* The species name is a noun in apposition, taken from the type locality.

*Diagnosis.* Medium-sized, long-legged species with oval and slightly angular opisthosoma; easily distinguished from relatives by the barely modified male chelicerae (Fig. 212), the long pointed palpal trochanter apophysis (Fig. 211) and the long curved bulbal apophysis (Fig. 210).

*Male (holotype).* Total length 1.4 (1.5 with clypeus), carapace width 0.62. Leg 1: 12.8 (3.3 + 0.3 + 3.2 + 4.7 + 1.3), tibia 2: 2.3, tibia 3: 1.5, tibia 4 missing; tibia 1 L/d: 51. Habitus similar to *B. sarika* (cf. Figs. 47, 48). Entire animal pale ochre-grey. Ocular area very flat, not separated from carapace, thoracic furrow absent; only two eyes present, with well developed lenses and pigment, distance 115  $\mu\text{m}$ ; diameter 60  $\mu\text{m}$ . Clypeus unmodified. Sternum as long as wide (0.41). Chelicerae as in Fig. 212, barely modified. Palps as in Figs. 210 and 211; trochanter with long pointed retrolateral apophysis, procurus rather simple, bulbal apophysis long and curved, with simple embolus that appears attached to bulbal apophysis (Fig. 210). Retrolateral trichobothrium of tibia 1 at 20%; legs without spines, curved, and vertical hairs (most hairs missing); pseudosegments not visible in dissecting microscope.

*Variation.* In the male (and juveniles) from Tham Pha Mon, three lenses are visible on each side, but there is no pigment; chelicerae and genitalia are indistinguishable; tibia 1: 4.0.

*Female.* In general similar to male holotype. Tibia 1: 2.4. Epigynum simple externally (Fig. 213), without pockets; dorsal view as in Fig. 214. ALS with several spigots in addition to basic set of two.

*Distribution.* Known from two neighboring localities in Mae Hong Son Province, Thailand (Fig. 79).

*Material examined.* THAILAND: *Mae Hong Son:* Ban Tham, Tham Plaa: type above, together with 1♀, in RMNH; Ban Sop Pong, Tham Pha Mon [19°17'N, 97°56'E], June 29, 1986 (P. Leclerc), 1♂ 6 juveniles (RMNH).

***Belisana schwendingeri*, new species**

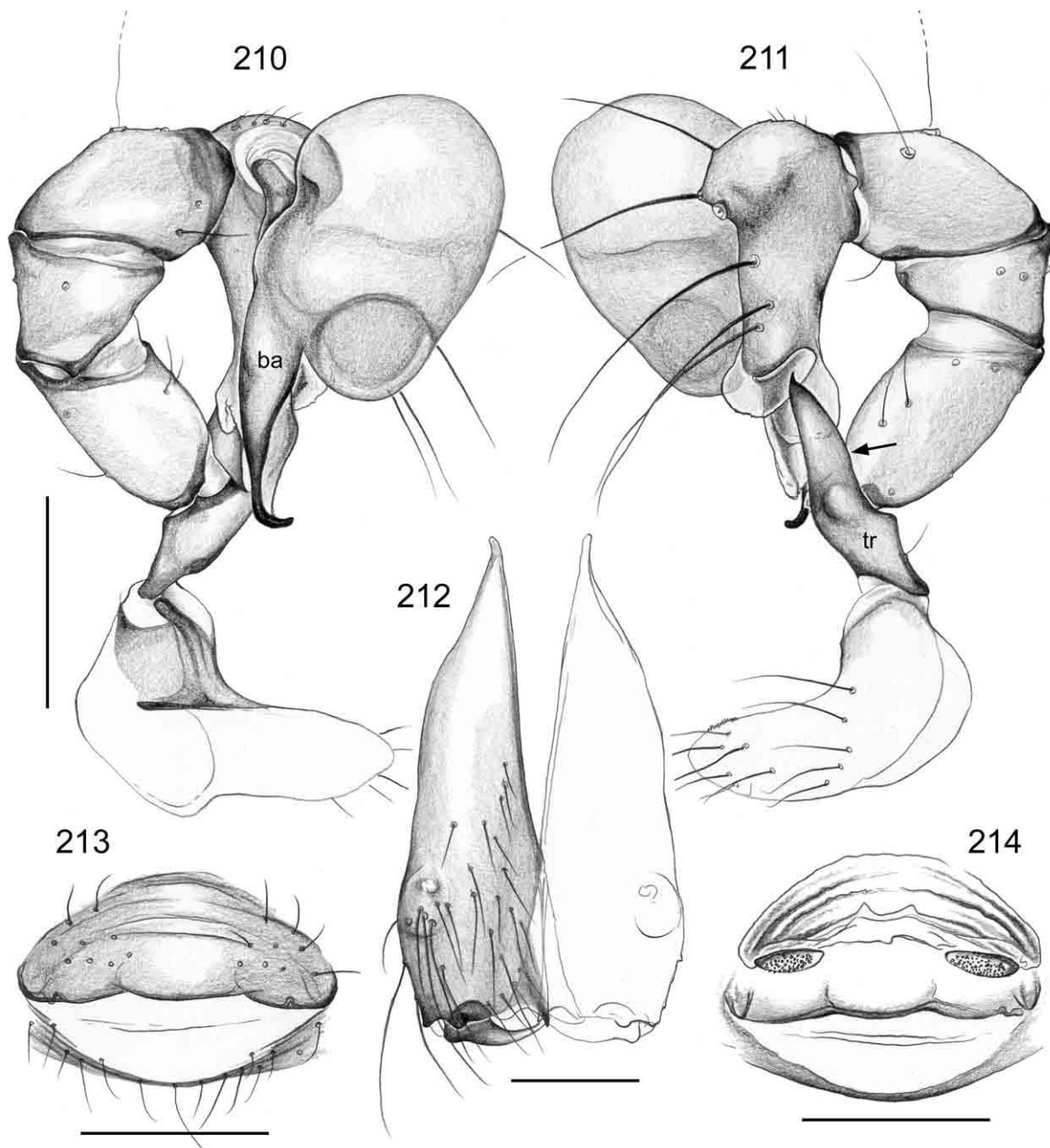
(Figs. 215-227)

*Type.* Male holotype from Doi Chiang Dao [~19°16'N, 98°53'E], Chiang Mai Prov., Thailand; 510 m a.s.l., Aug. 22 – Sept. 22, 1990 (P. Schwendinger), in MHNG.

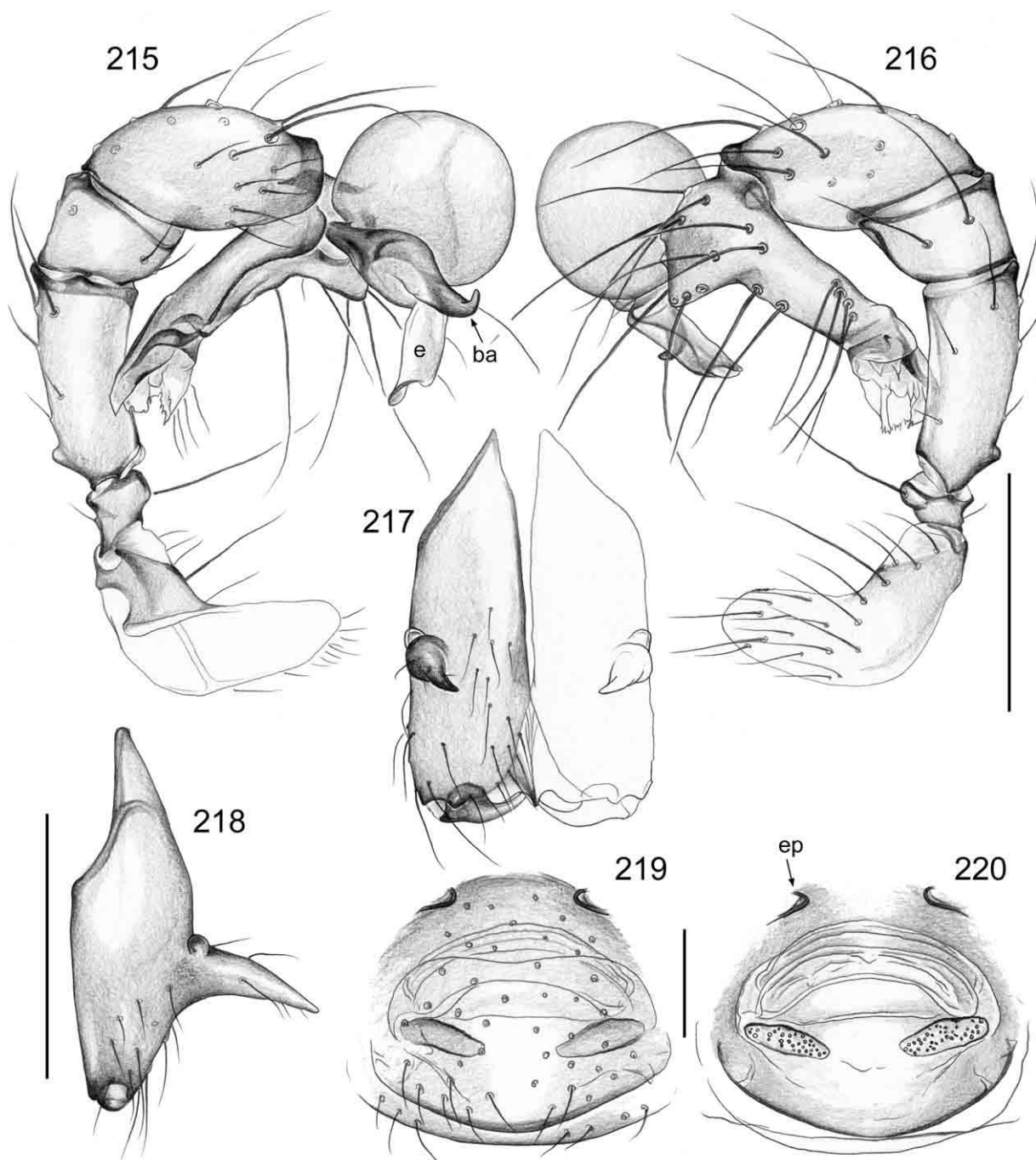
*Etymology.* Named for Peter Schwendinger who provided a large number of specimens for the present study.

*Diagnosis.* Tiny, short-legged species, with globular opisthosoma; distinguished from similar relatives by the shapes of procurus and bulbal apophyses (Figs. 215, 216), and by the position of the cheliceral apophyses (Figs. 217, 218). *Belisana leclerci* has indistinguishable palps, but the cheliceral apophyses face more downward (cf. Fig. 229) and the triads are wider apart (cf. Fig. 43).

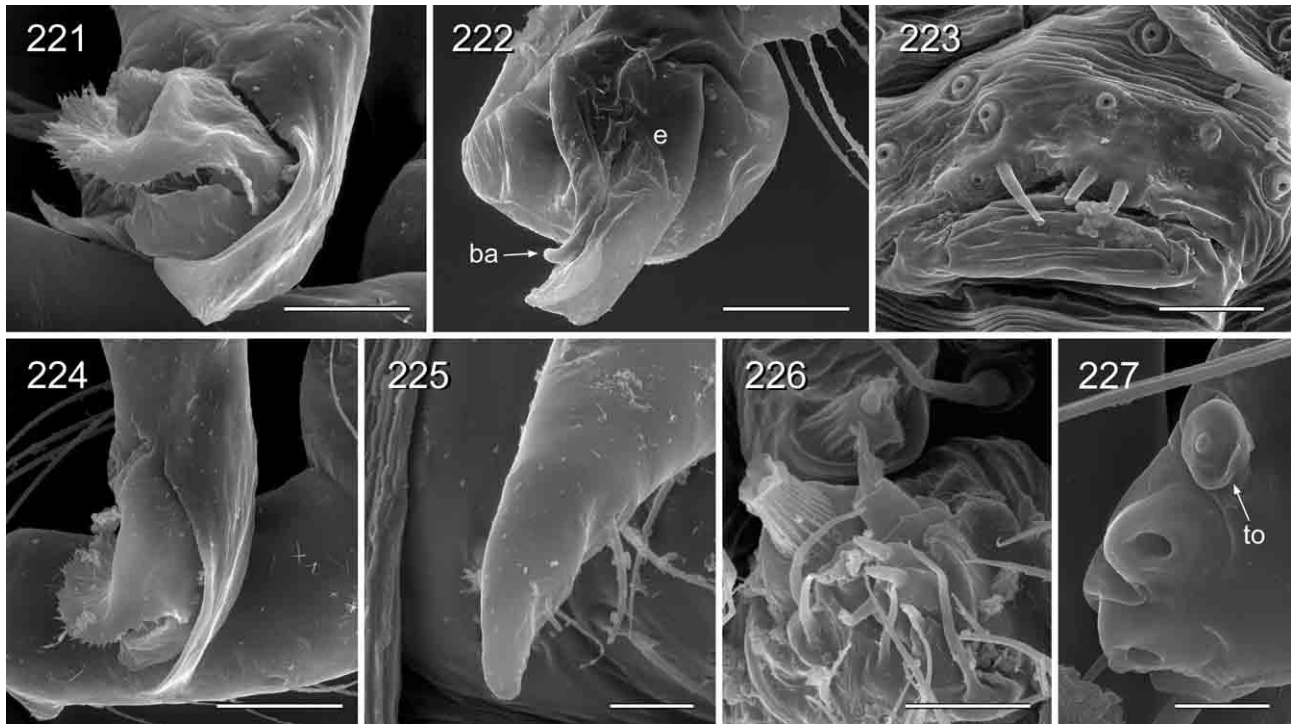
*Male (holotype).* Total length 0.94 (1.04 with clypeus), carapace width 0.46. Leg 1: 3.68 (0.92 + 0.16 + 0.92 + 1.12 + 0.56), tibia 2: 0.60, tibia 3: 0.44, tibia 4 missing; tibia 1 L/d: 19. Habitus similar to *B. ketambe* (cf. Figs. 41, 42). Prosoma and legs ochre-yellow, opisthosoma ochre-grey with slightly darker marks visible through cuticle. Ocular area barely elevated, thoracic furrow absent; distance PME-PME 60  $\mu\text{m}$ ; diameter PME 60  $\mu\text{m}$ ; distance PME-ALE ~20  $\mu\text{m}$ . Clypeus unmodified. Sternum wider than long (0.34/0.30). Chelicerae as in Figs. 217 and 218, with pair of frontal apophyses, tips unmodified (Fig. 225), 105  $\mu\text{m}$  apart, and weakly sclerotized humps at their bases. Palps as in Figs. 215 and 216; trochanter with short retrolateral apophysis, femur with proximo-dorsal hump, procurus complex distally, mostly membranous (Figs. 221, 224), bulb with hooked apophysis and membranous embolus (Figs. 215, 222) (in Fig. 215 the bulbal apophysis is artificially bent away from the embolus). Tarsal organ exposed (Fig. 227). Retrolateral trichobothrium of tibia 1 at 38%; legs without spines, curved hairs, and vertical hairs; tarsus 1 with about 10 indistinct pseudosegments. Gonopore and spinnerets as in Figs. 223 and 226.



**Figs. 210-214.** *Belisana bantham*. 210, 211. Left male pedipalp, prolateral (210) and retrolateral (211) views (arrow points to distinctive trochanter-apophysis). 212. Male chelicerae, frontal view. 213, 214. Cleared female genitalia, ventral (213) and dorsal (214) views. Scale lines: 0.2 mm (210, 211, 213, 214), 0.1 mm (212).



**Figs. 215-220.** *Belisana schwendingeri*. 215, 216. Left male pedipalp, prolateral (215) and retrolateral (216) views. 217, 218. Male chelicerae, frontal and lateral views. 219, 220. Cleared female genitalia, ventral (219) and dorsal (220) views. Scale lines: 0.2 mm (215-218), 0.1 mm (219, 220).



**Figs. 221-227.** *Belisana schwendingeri*. 221. Tip of right procurus, distal view. 222. Bulbal projections. 223. Male gonopore with epiandrous spigots. 224. Right procurus, prolateral view. 225. Tip of male cheliceral apophysis. 226. Male ALS and PMS. 227. Male palpal tarsal organ. Scale lines: 10  $\mu\text{m}$  (225-227), 20  $\mu\text{m}$  (223), 30  $\mu\text{m}$  (221), 50  $\mu\text{m}$  (224), 60  $\mu\text{m}$  (222).

**Variation.** Tibia 1 missing in all other males from Chiang Mai Province. The males from Kanchanaburi Prov. have slightly less curved bulbal apophyses and are therefore assigned tentatively; tibia 1 in one of these males: 1.07 (missing in other male). The male from Tham Kukan (Chiang Rai Province) has even longer legs (tibia 1: 1.63) but identical genitalia.

**Female.** In general similar to male. Tibia 1 in 3 females: 0.76, 0.84, 0.84. Females from Kanchanaburi Prov.: 1.07, 1.10. Epigynum simple externally (Fig. 219), with pair of pockets in very frontal position, 116  $\mu\text{m}$  apart; dorsal view as in Fig. 220. ALS with several spigots in addition to basic two. The female from Phu Rua has a very similar epigynum but the pockets are closer together (90  $\mu\text{m}$ ); it is therefore assigned tentatively.

**Distribution.** Known from five localities in north-western and central-western Thailand (Fig. 79), but specimens from Loei and Kanchanaburi Provinces are assigned tentatively.

**Material examined.** THAILAND: *Chiang Mai*: Doi Chiang Dao: type above, together with 5♂1♀ (MHNG); same locality, Sept. 22-Feb. 23, 1991 (4 vials) (P. Schwendinger), 7♂5♀ (MHNG); *Chiang Rai*: Mae Sai, Ban Tham, Tham Kukan [20°19.5'N, 99°52'E], June 24, 1986 (P. Leclerc), 1♂ (RMNH).

Assigned tentatively: *Loei*: Phu Rua District, Phu Rua [17°27'N, 101°22'E], 1250 m a.s.l., Sept. 5-6, 1992 (P. Schwendinger), 1♀ in MHNG. *Kanchanaburi*: Sai Yok Distr., Wang Badan cave, ~2 km N Sai Yok Noi waterfall (14°14'N, 99°03'E), 250 m a.s.l., inside limestone cave, Dec. 9, 2003 (P. Schwendinger), 1♂2♀ (MHNG); Tham Soi Yok Noi [14°25'N, 98°51'E?], Ban Nam Tok, June 18, 1986 (P. Leclerc), 1♂ (RMNH).

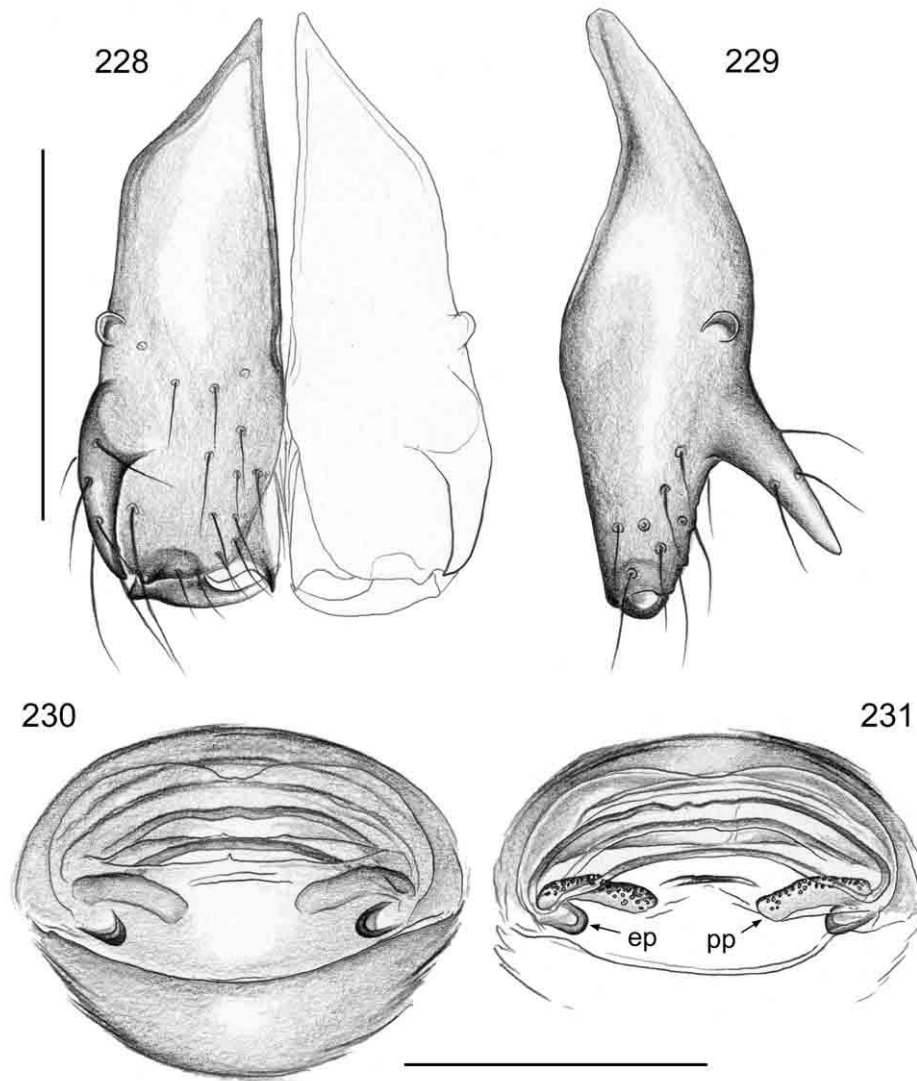
#### ***Belisana leclerci*, new species**

(Figs. 43, 44, 228-231)

**Type.** Male holotype from Ban On Luay [18°47.2'N, 99°14.3'E], Tham Muang Oon, San Kamphaeng Distr., Chiang Mai Prov., Thailand; July 20, 1985 (P. Leclerc), in RMNH.

**Etymology.** Named for Philippe Leclerc who collected several species of *Belisana* in Thailand.

**Diagnosis.** Tiny, short-legged species with globular opisthosoma; closely related to *B. schwendingeri*, with indistinguishable male palps; distinguished by the cheliceral apophyses wider apart and facing down (compare Figs. 229 and 218) and by the position and distance of the epigynal pockets (compare Figs. 230 and 219). In addition, the eyes are smaller in *B. leclerci* and the triads are wider apart (Fig. 43).



**Figs. 228-231.** *Belisana leclerci*. 228, 229. Male chelicerae, frontal and lateral views. 230, 231. Cleared female genitalia, ventral (230) and dorsal (231) views. Scale lines: 0.2 mm.

*Male (holotype)*. Total length 1.2 (1.3 with clypeus), carapace width 0.54. Leg 1: 7.2 (1.9 + 0.2 + 1.9 + 2.4 + 0.8), tibia 2: 1.2, tibia 3: 0.9, tibia 4: 1.4; tibia 1 L/d: 35. Habitus as in Figs. 43 and 44. Prosoma and legs pale ochre-yellow, opisthosoma pale grey. Ocular area very flat, not separated from carapace, thoracic furrow absent; distance PME-PME 100  $\mu$ m; diameter PME 40  $\mu$ m; distance PME-ALE ~15  $\mu$ m. Clypeus unmodified. Sternum as long as wide (0.32). Chelicerae as in Figs. 228 and 229, with pair distinctive apophyses, tips 175  $\mu$ m apart. Palps not distinguishable from those of *B. schwendingeri* (cf. Figs. 215, 216). Retrolateral trichobothrium of tibia 1 not seen; legs without spines, curved, and vertical hairs (most hairs missing); tarsus 1 with ~10 pseudosegments barely visible.

*Female*. In general similar to male. Tibia 1 in 3 females: 1.73-1.90. Epigynum very simple externally (Fig. 230), slightly protruding, with pair of lateral pockets 165  $\mu$ m apart; dorsal view as in Fig. 231. ALS with several spigots in addition to basic set of two.

*Distribution*. Known from type locality only (Fig. 79).

*Material examined*. THAILAND: *Chiang Mai*: type above, together with 3♀ (RMNH).

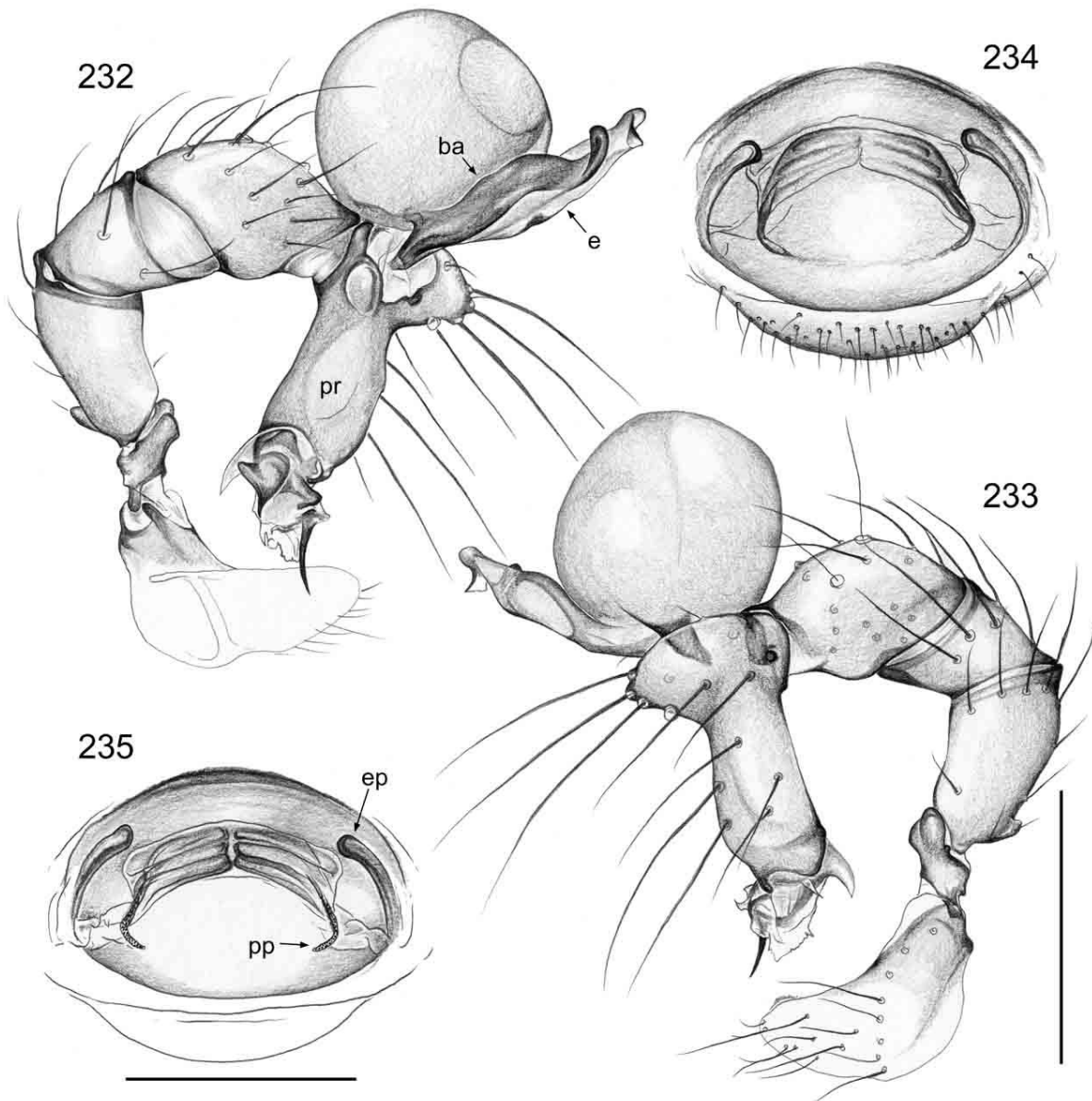
***Belisana phurua*, new species**  
(Figs. 232-235)

*Type.* Male holotype from Phu Rua [17°27'N, 101°22'E], Phu Rua District, Loei Prov., Thailand; 1250 m a.s.l., Sept. 5-6, 1992 (P. Schwendinger), in MHNG.

*Etymology.* The species name is a noun in apposition, taken from the type locality.

*Diagnosis.* Medium-sized, short-legged species with globular opisthosoma; distinguished from relatives by the shapes of procurrus (distal spine, Fig. 232), bulbal projections (Fig. 232), and male chelicerae with widely spread apophyses (cf. *B. gedeh*, Fig. 341).

*Male (holotype).* Total length 1.3 (1.4 with clypeus), carapace width 0.64. Leg 1: 9.9 (2.4 + 0.2 + 2.5 + 3.7 + 1.1), tibia 2: 1.5, tibia 3: 1.0, tibia 4: 1.4; tibia 1 L/d: 47. Habitus similar to *B. ketambe* (cf. Figs. 41, 42). Prosoma and legs pale ochre-yellow, opisthosoma pale ochre-grey. Ocular area very flat, not separated from carapace, thoracic furrow



**Figs. 232-235.** *Belisana phurua*. 232, 233. Left male pedipalp, prolateral (232) and retrolateral (233) views (note that the bulb is artificially rotated out of its normal position). 234, 235. Cleared female genitalia, ventral (234) and dorsal (235) views. Scale lines: 0.3 mm.



absent; distance PME-PME 90  $\mu\text{m}$ ; diameter PME 60  $\mu\text{m}$ ; distance PME-ALE  $\sim 20$   $\mu\text{m}$ . Clypeus unmodified. Sternum as long as wide (0.44). Chelicerae as in *B. gedeh* (cf. Figs. 341, 342), tips of apophyses 265  $\mu\text{m}$  apart. Palps as in Figs. 232 and 233; trochanter with retrolateral apophysis, femur with proximo-dorsal apophysis, procurus complex distally, with distinctive spine, bulb with hooked apophysis, embolus with spine distally. Retrolateral trichobothrium of tibia 1 at 19%; legs without spines, curved, and vertical hairs; tarsus 1 with  $\sim 15$  pseudosegments, fairly distinct distally.

*Female*. In general similar to male. Tibia 1: 2.1. Epigynum simple externally (Fig. 234), with pair of pockets 275  $\mu\text{m}$  apart; dorsal view as in Fig. 235. ALS with several spigots in addition to basic set of two.

*Distribution*. Known from type locality only (Fig. 79).

*Material examined*. THAILAND: *Loei*: Phu Rua: type above, together with 1 ♀ (MHNG).

#### ***Belisana khieo*, new species**

(Figs. 39, 40, 236-239)

*Type*. Male holotype from Khao Yai National Park, Khao Khieo [ $\sim 14^{\circ}42'N$ ,  $101^{\circ}48'E$ ], Nakhon Ratchasima Prov., Thailand; 1150 m a.s.l., Oct. 29, 1997 (P. Schwendinger), in MHNG.

*Etymology*. The species name is a noun in apposition, taken from the type locality.

*Diagnosis*. Tiny, short-legged species with globular opisthosoma; distinguished from relatives by the shapes of procurus and bulbal apophyses (Figs. 236, 237), from some species also by the widely spread male cheliceral apophyses (similar to *B. gedeh*, cf. Fig. 341). A very similar (undescribed) species occurs on Mapur Island (Indonesia) and in Sabah, Malaysia; the palps in that species are almost identical, but the cheliceral apophyses are much longer in lateral view (specimens in MHNG, AMNH, ZMT).

*Male (holotype)*. Total length 1.2 (1.3 with clypeus), carapace width 0.58. Leg 1: 6.21 (1.50 + 0.20 + 1.67 + 1.97 + 0.87), tibia 2: 1.0, tibia 3: 0.77, tibia 4: 1.27; tibia 1 L/d: 27. Habitus as in Figs. 39 and 40. Prosoma and legs ochre-yellow, opisthosoma pale ochre-grey, dorsally slightly darker than ventrally. Ocular area very flat, not separated from carapace, thoracic furrow absent; distance PME-PME 70  $\mu\text{m}$ ; diameter PME 60  $\mu\text{m}$ ; distance PME-ALE  $\sim 20$   $\mu\text{m}$ . Clypeus unmodified. Sternum as long as wide (0.42). Chelicerae similar to *B. gedeh* (cf. Figs. 341, 342), but apophyses more straight forward, tips of apophyses 375  $\mu\text{m}$  apart. Palps as in Figs. 236 and 237; trochanter with short retrolateral apophysis, procurus proximally simple, distal part complex, possibly with hinged sclerites, bulb with hooked apophysis, embolus simple with semicircular sclerite distally (Fig. 236). Retrolateral trichobothrium of tibia 1 at 52%; legs without spines, curved, and vertical hairs (most hairs missing); tarsus 1 with  $\sim 10$  pseudosegments difficult to see in dissecting microscope.

*Female*. In general similar to male. Tibia 1: 1.3. Epigynum simple externally (Fig. 238) with pair of pockets 291  $\mu\text{m}$  apart, dorsal view as in Fig. 239. ALS with several spigots in addition to basic two.

*Distribution*. Known from type locality only (Fig. 79).

*Material examined*. THAILAND: *Nakhon Ratchasima*: Khao Yai N. P.: type above, together with 1 ♀ (MHNG).

#### ***Belisana banlakwo*, new species**

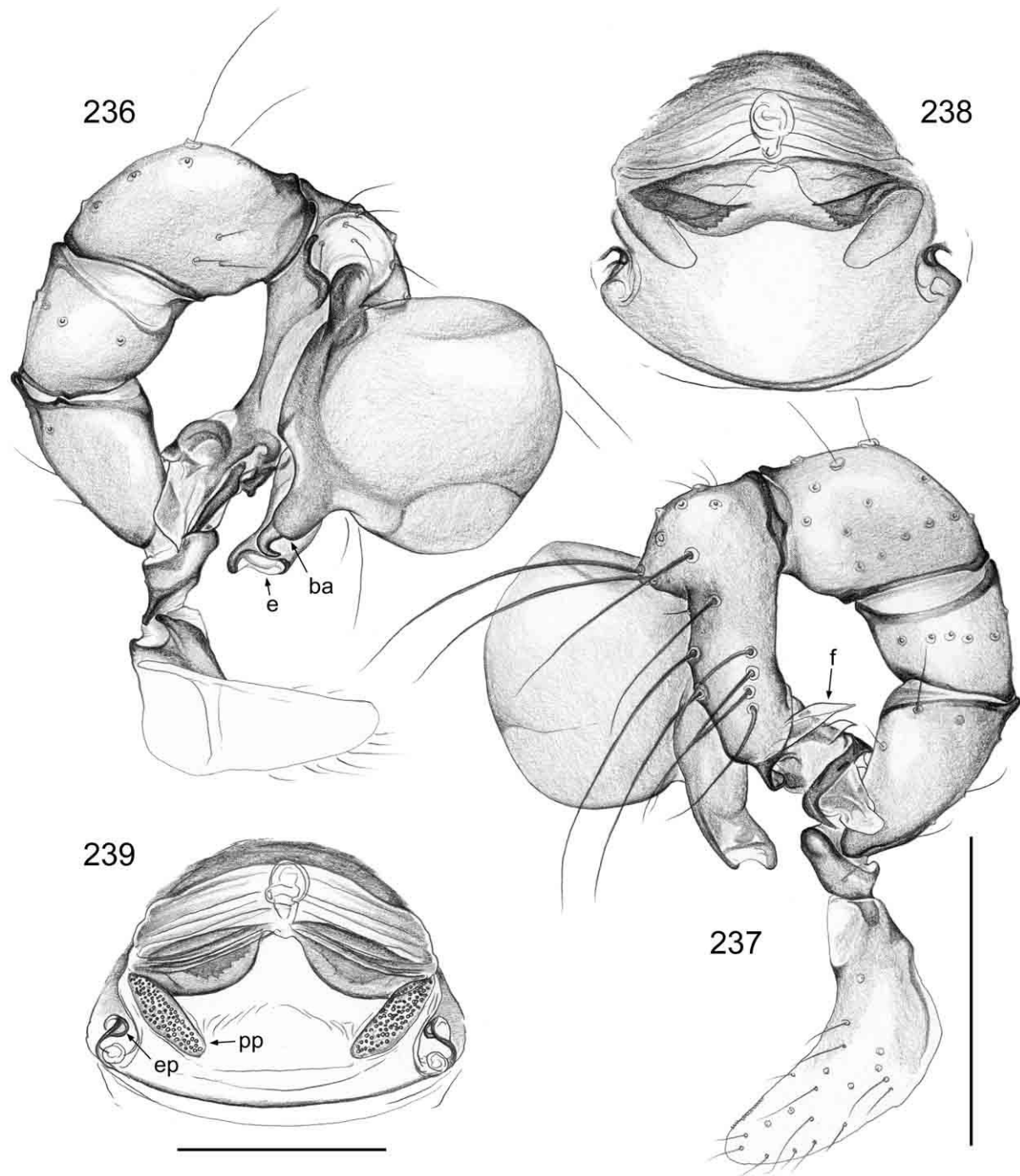
(Figs. 19, 20, 240-245)

*Type*. Male holotype from Ban Lak Wo,  $\sim 5$  km S Surin [ $\sim 14^{\circ}30'N$ ,  $103^{\circ}29'E$ ], Surin District and Province, Thailand; 160 m a.s.l., Nov. 22, 1992 (P. Schwendinger), in MHNG.

*Etymology*. The species name is a noun in apposition, taken from the type locality.

*Diagnosis*. Medium-sized, long-legged species with elongated and slightly angular opisthosoma; distinguished from relatives by the male cheliceral apophyses (Figs. 242, 243) and by the shapes of procurus and bulbal apophysis (Figs. 240, 241).

*Male (holotype)*. Total length 1.5 (1.55 with clypeus), carapace width 0.62. Leg 1: 15.25 (4.0 + 0.25 + 3.95 + 5.85 + 1.2), tibia 2: 2.3, tibia 3: 1.35, tibia 4: 2.15; tibia 1 L/d: 63. Habitus as in Figs. 19 and 20. Prosoma and legs pale ochre-yellow, coxae slightly darker, opisthosoma pale greenish-grey. Ocular area very flat, not separated from carapace, thoracic furrow absent; distance PME-PME 115  $\mu\text{m}$ ; diameter PME 55  $\mu\text{m}$ ; distance PME-ALE  $\sim 20$   $\mu\text{m}$ . Clypeus unmodified. Sternum as long as wide (0.42). Chelicerae as in Figs. 242 and 243, tips of apophyses 175  $\mu\text{m}$  apart. Palps as in Figs. 240 and 241; trochanter with short retrolateral apophysis, patella relatively long, procurus simple except distally, apparently with hinged structure prolatero-distally, bulb with long curved apophysis (appears hooked in Fig. 240 due to angle of view), embolus with spine. Retrolateral trichobothrium of tibia 1 at 17%; legs without spines, curved, and vertical hairs; tarsus 1 with  $> 10$  pseudosegments, distally fairly distinct.

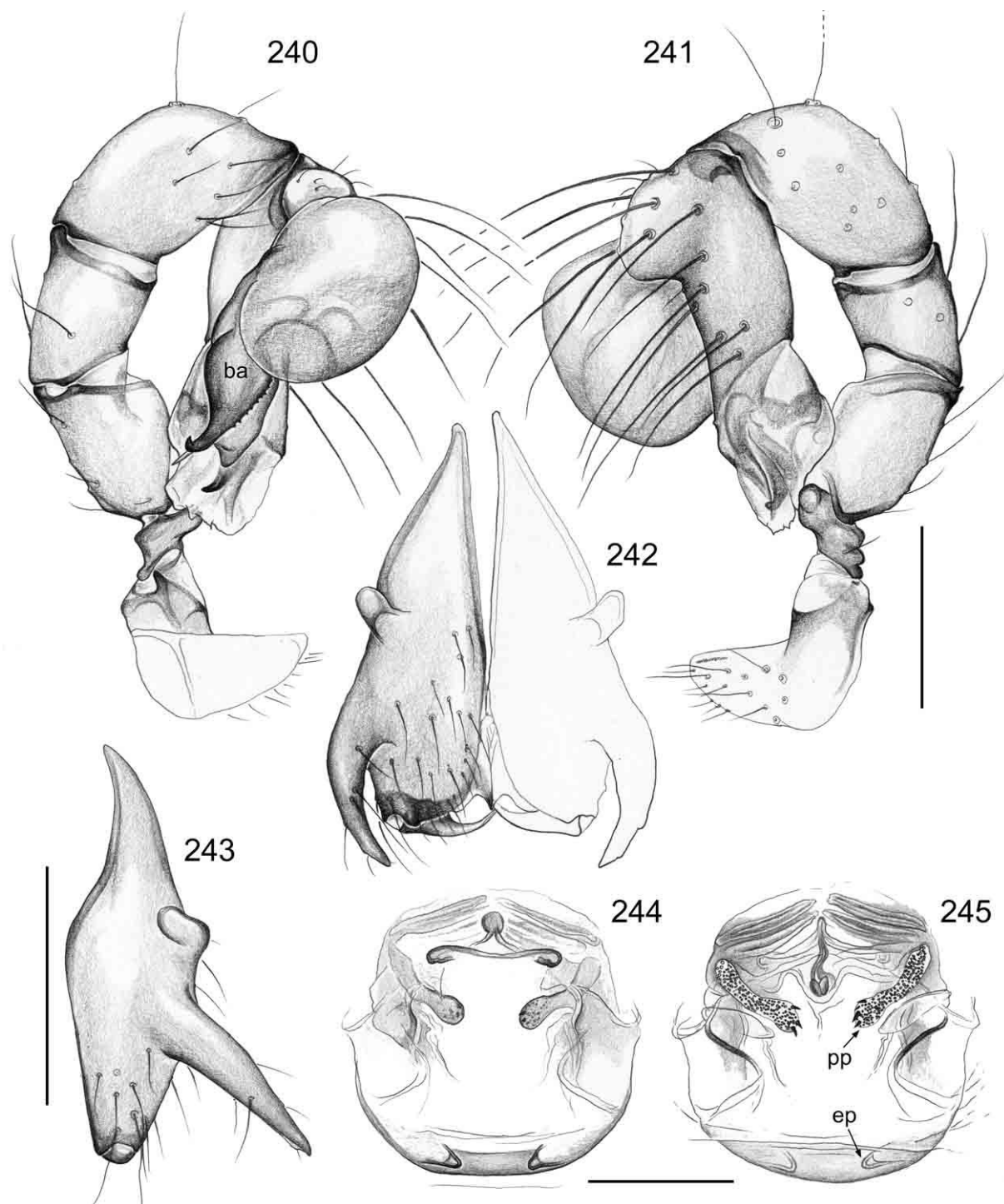


**Figs. 236-239.** *Belisana khieo*. 236, 237. Left male pedipalp, prolateral (236) and retrolateral (237) views. 238, 239. Cleared female genitalia, ventral (238) and dorsal (239) views. Scale lines: 0.3 mm (236, 237), 0.2 mm (238, 239).

*Female.* In general similar to male. Tibia 1 in 4 females: 2.3-3.1. Epigynum very simple externally, not protruding, with pair of pockets 105  $\mu$ m apart (Fig. 244); dorsal view as in Fig. 245, with distinctive spines on pore plates (cf. *B. nujiang*, Fig. 86). ALS with several spigots in addition to basic set of two.

*Distribution.* Known from type locality only (Fig. 79).

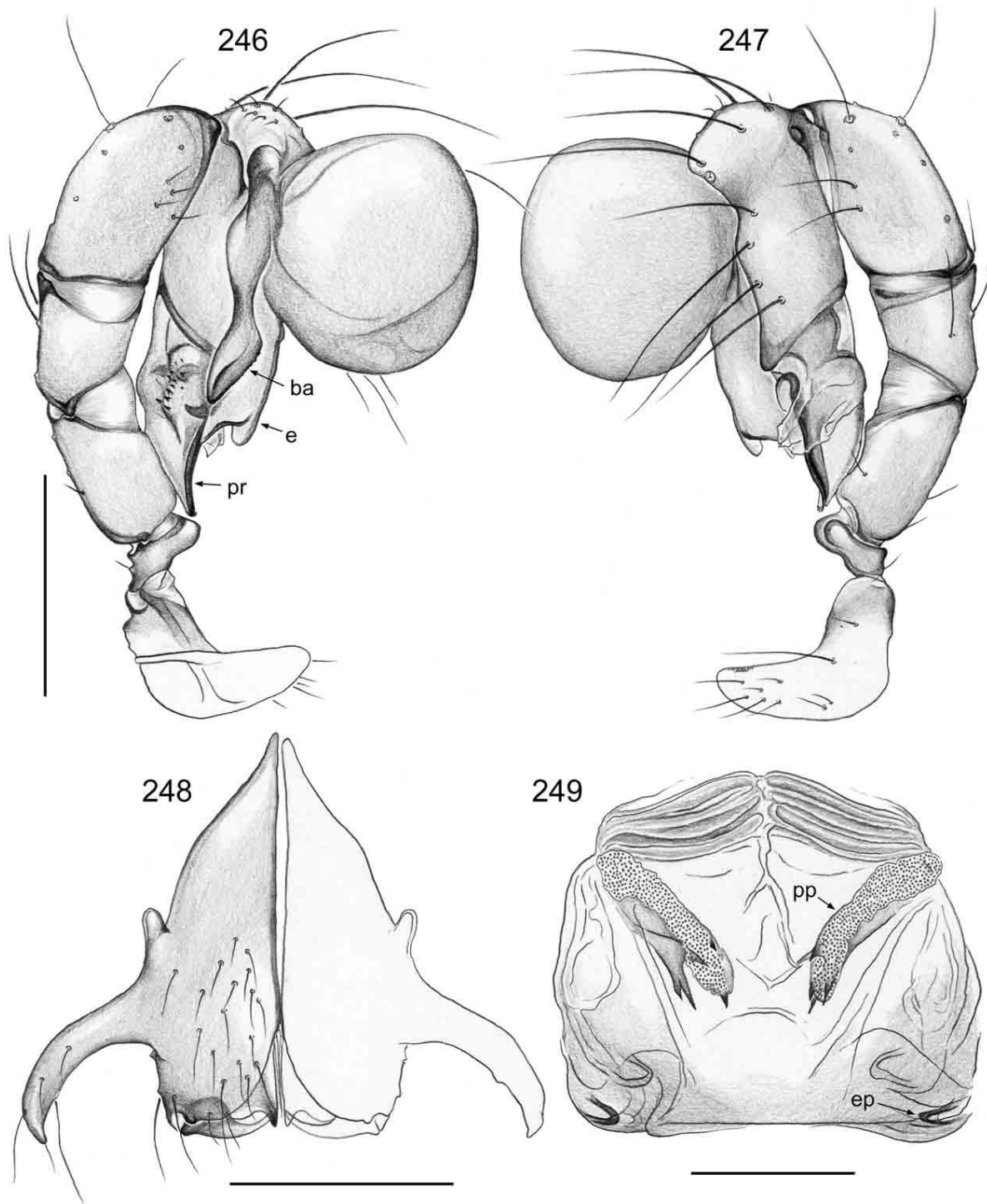
*Material examined.* THAILAND: Surin: Ban Lak Wo: type above, together with 1♂4♀ (MHNG).



**Figs. 240-245.** *Belisana banlakwo*. 240, 241. Left male pedipalp, prolateral (240) and retrolateral (241) views. 242, 243. Male chelicerae, frontal and lateral views. 244, 245. Cleared female genitalia, ventral (244) and dorsal (245) views. Scale lines: 0.2 mm.

***Belisana sarika*, new species**  
(Figs. 47, 48, 246-249)

*Type.* Male holotype from Sarika waterfalls [ $\sim 14^{\circ}17'N$ ,  $101^{\circ}17'E$ ], 110 km NE of Bangkok, Nakhon Nayok Prov., Thailand; from leaves, April 27, 1982 (P. R. Deeleman), in RMNH.



**Figs. 246-249.** *Belisana sarika*. 246, 247. Left male pedipalp, prolateral (246) and retrolateral (247) views. 248. Male chelicerae, frontal view. 249. Cleared female genitalia, dorsal view. Scale lines: 0.3 mm (246, 247), 0.2 mm (248, 249).

*Etymology.* The species name is a noun in apposition, taken from the type locality.

*Diagnosis.* Medium-sized, long-legged species with oval and slightly angular opisthosoma; distinguished from similar relatives by the simple bulbal apophysis (Fig. 246), from many also by the palpal femur without dorsal modification (Figs. 246, 247), and the widely spaced cheliceral apophyses (Fig. 248).

*Male (holotype).* Total length 1.4 (1.5 with clypeus), carapace width 0.63. Leg 1: 12.1 (3.2 + 0.3 + 3.1 + 4.3 + 1.2), tibia 2: 2.0, tibia 3: 1.2, tibia 4: 1.8; tibia 1 L/d: 47. Habitus as in Figs. 47 and 48. Prosoma and legs pale ochre-yellow, sternum whitish, opisthosoma pale ochre-grey. Ocular area barely elevated, thoracic furrow absent; distance PME-PME 125  $\mu$ m; diameter PME 55  $\mu$ m; distance PME-ALE  $\sim$ 20  $\mu$ m. Clypeus unmodified. Sternum about as wide as long (0.42). Chelicerae as in Fig. 248, apophyses pointing slightly downwards (Fig. 248 is in slightly dorsal view), tips 435  $\mu$ m apart. Palps as in Figs. 246 and 247; trochanter with short rounded retrolateral and ventral apophyses, femur small, without dorsal apophysis, tibia unusually long, procurus with strong pointed sclerite distally; bulb with distinctive flattened bulbapophysis and membranous embolus. Retrolateral trichobothrium of tibia 1 at 21%; legs without spines, curved hairs, and vertical hairs; tarsus 1 about 15 pseudosegments, barely visible in dissecting microscope.

*Variation.* Tibia 1 in 3 other males: 2.9, 3.1, 3.7.

*Female.* In general similar to male; tibia 1 in 5 females: 2.45-2.9 (mean 2.63). Epigynum very simple externally, dark internal spines barely visible through cuticle, pockets 370  $\mu$ m apart; dorsal view as in Fig. 249.

*Distribution.* Known from type locality only (Fig. 79).

*Material examined.* THAILAND: *Nakhon Nayok*: Sarika: type above, together with 3♂8♀ (RMNH).

### ***Belisana khaoyai*, new species**

(Figs. 74, 250-267)

*Type.* Male holotype from Khao Yai National Park [ $\sim$ 14°12'N, 101°22'E], Nakhon Nayok Prov., Thailand; 1050 m a.s.l., slope, evergreen forest, from leaf, March 3, 1986 (C. L. & P. R. Deeleman), in RMNH.

*Etymology.* The species name is a noun in apposition, taken from the type locality.

*Diagnosis.* Medium-sized, long-legged species with cylindrical opisthosoma; distinguished from congeners by the shape of the procurus, especially the two distal spines (Figs. 252, 256, 257), and by the unique scaly structures in the female internal genitalia (Fig. 254); from some also by the widely spread male cheliceral apophyses (Fig. 253).

*Male (holotype).* Total length 1.4 (1.5 with clypeus), carapace width 0.50. Leg 1: 11.55 (2.9 + 0.25 + 2.9 + 4.4 + 1.1), tibia 2: 1.8, tibia 3: 1.05, tibia 4: 1.7; tibia 1 L/d: 50. Habitus similar to *B. kaosok* (cf. Figs. 51, 52). Prosoma and legs pale ochre-yellow, sternum whitish, opisthosoma pale ochre-grey. Ocular area barely elevated, thoracic furrow absent; distance PME-PME 140  $\mu$ m; diameter PME 60  $\mu$ m; distance PME-ALE  $\sim$ 20  $\mu$ m. Clypeus unmodified. Sternum about as wide as long (0.40). Chelicerae as in Figs. 253 and 262, apophyses in right angle to paturon, tips 350  $\mu$ m apart. Palps as in Figs. 250 and 251; trochanter with short rounded retrolateral apophysis, femur with dorsal apophysis, procurus complex distally (Figs. 255, 259), with (glandular?) pores (Fig. 258) and two distinctive black spines distally (Figs. 256, 257); bulb with hooked apophysis and membranous embolus. Tarsal organ capsulate (Fig. 260). Retrolateral trichobothrium of tibia 1 at 9%; legs without spines and curved hairs, with vertical hairs on metatarsi (seen on metatarsi 1, 2, 4; most hairs missing); tarsus 1 with about 15 pseudosegments, fairly distinct distally. Gonopore as in Fig. 261, ALS with only two spigots each (Fig. 265).

*Variation.* Tibia 1 in other male: 3.0 (missing in others).

*Female.* In general similar to male; tibia 1 in 11 females: 2.3-2.8 (mean 2.57). Epigynum very simple externally (Fig. 267), with distinctive dark structures visible through cuticle (Fig. 74), pockets 320  $\mu$ m apart; dorsal view as in Fig. 254.

*Distribution.* Known from type locality only (Fig. 79).

*Material examined.* THAILAND: *Nakhon Nayok*: Khao Yai N. P.: type above, together with 5♂10♀ (RMNH); Khao Yai N. P., Oct. 20/25, 1985 (C. L. & P. R. Deeleman), 2♀ (RMNH); Khao Yai N. P., primary forest, slope, Dec. 23, 1988 (C. L. & P. R. Deeleman), 1♀ (RMNH); Khao Yai N. P., near waterfalls, March 4, 1986 (C. L. & P. R. Deeleman), 3♀ (RMNH).

### ***Belisana pranburi*, new species**

(Figs. 268-272, 284-287)

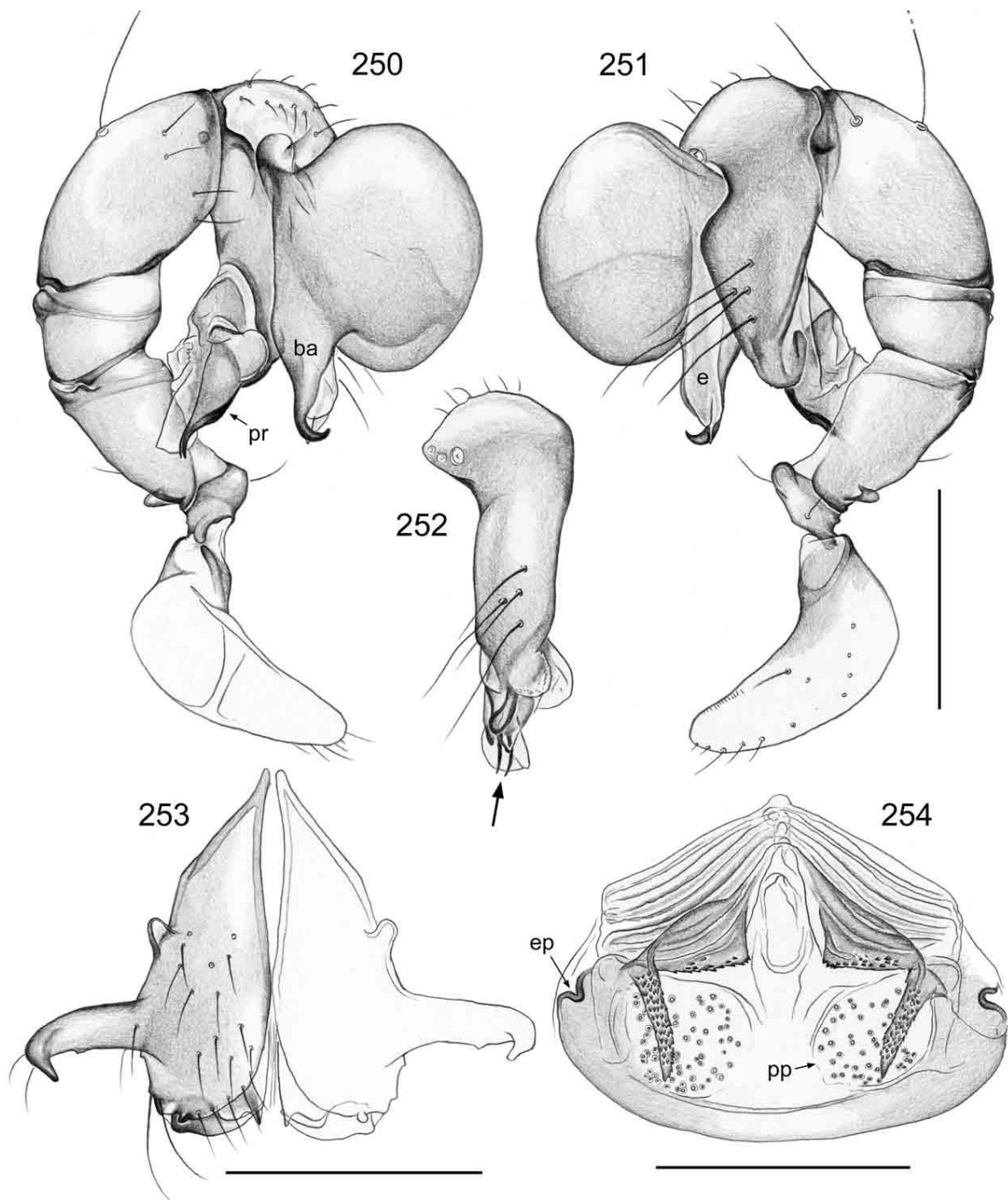
*Type.* Male holotype from Pran Buri [12°20'N, 99°58'E], Sam Roi Yot National Park, Prachuap Khiri Khan Prov., Thailand; leaf litter, Dec. 31, 1988 (C. L. & P. R. Deeleman), in RMNH.

*Etymology.* The species name is a noun in apposition, taken from the type locality.

*Diagnosis.* Tiny, short-legged species with globular opisthosoma; distinguished from relatives by the shapes of procurus, bulb and cheliceral apophyses (Figs. 268-270, 286).

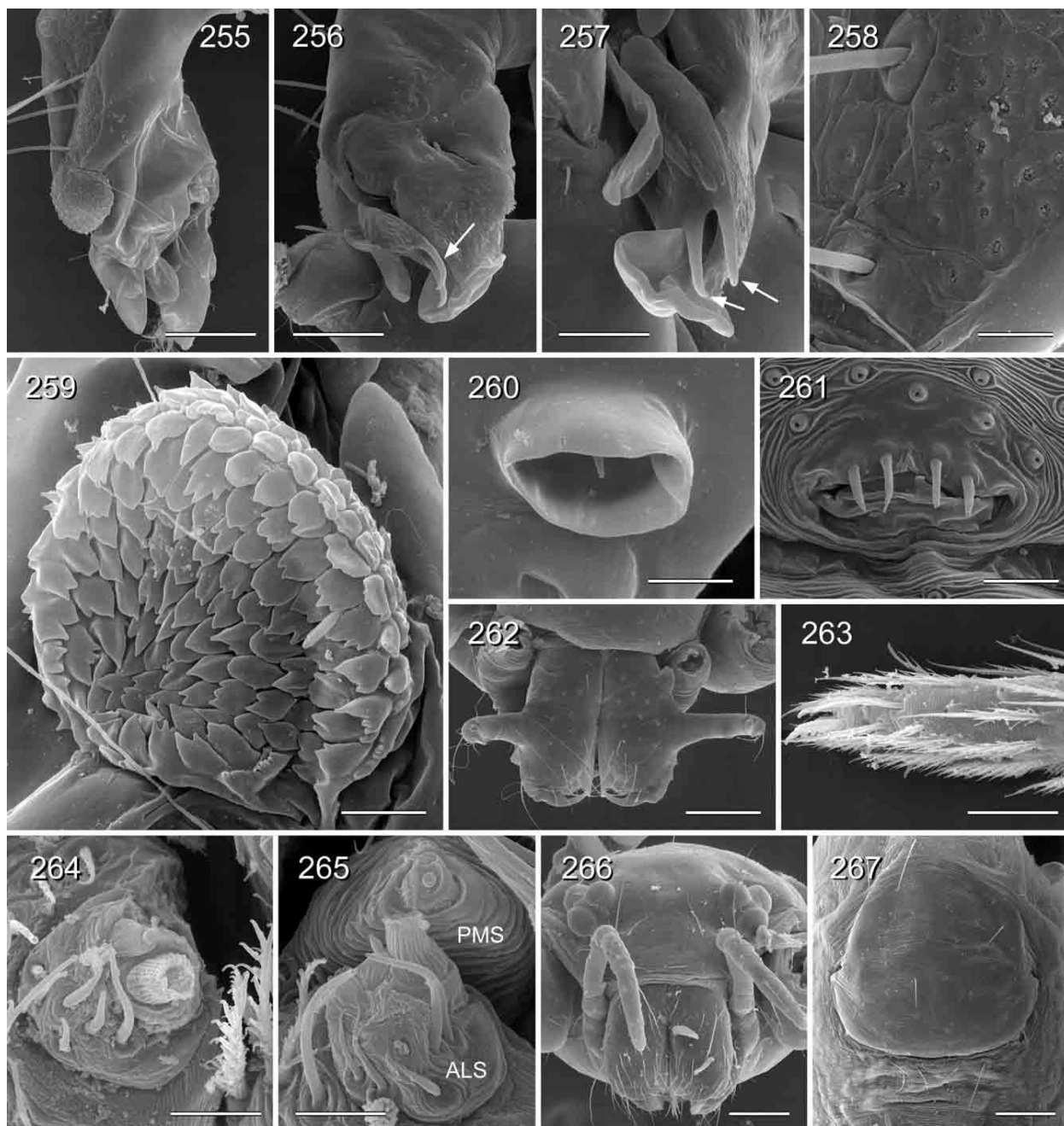
*Male (holotype).* Total length 0.80 (0.88 with clypeus), carapace width 0.42. Leg 1: 4.1 (1.13 + 0.17 + 1.13 + 1.17 + 0.50), tibia 2: 0.63, tibia 3: 0.43, tibia 4: 0.83; tibia 1 L/d: 25. Habitus similar to *B. ketambe* (cf. Figs. 41, 42).





**Figs. 250-254.** *Belisana khaoyai*. 250, 251. Left male pedipalp, prolateral (250) and retrolateral (251) views. 252. Left procurus, dorsal view (arrow points to distinctive spines). 253. Male chelicerae, frontal view. 254. Cleared female genitalia, dorsal view. Scale lines: 0.2 mm.

Prosoma and legs pale ochre-yellow, opisthosoma pale ochre-grey. Ocular area very flat, not separated from carapace, thoracic furrow absent; distance PME-PME 85  $\mu\text{m}$ ; diameter PME 45  $\mu\text{m}$ ; distance PME-ALE  $\sim$ 15  $\mu\text{m}$ . Clypeus unmodified. Sternum as long as wide (0.30). Chelicerae as in Fig. 270, with pair of long curved apophyses, tips 160  $\mu\text{m}$  apart. Palps as in Figs. 268 and 269; trochanter with retrolateral apophysis, procurus simple except distally, with distinctive spine prolaterally, bulb distinctively elongated (Figs. 268, 286), with simple curved apophysis and embolus with unsclerotized spine. Retrolateral trichobothrium of tibia 1 at 44%; legs without spines, curved, and vertical hairs (most hairs missing); pseudosegments not visible in dissecting microscope.



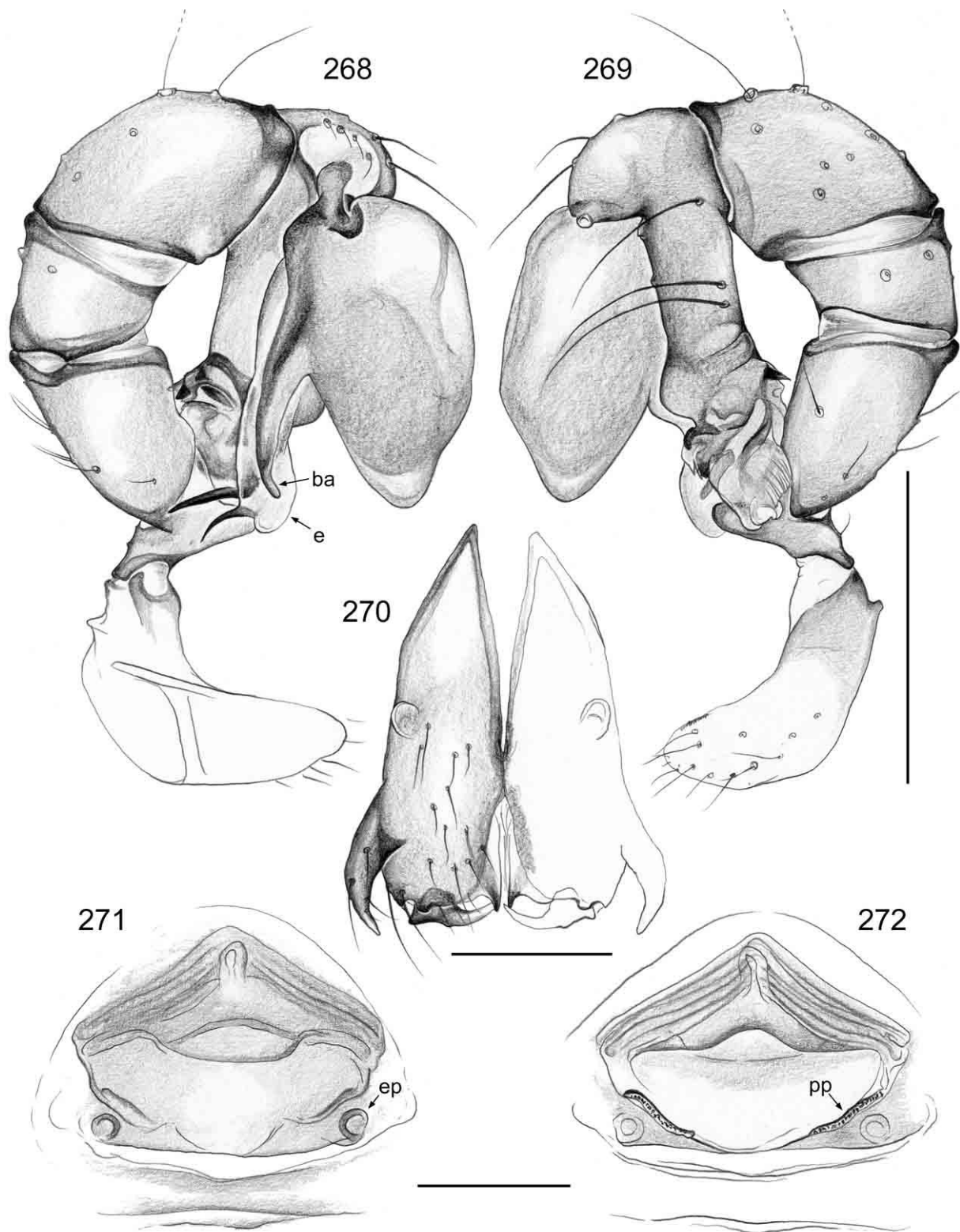
**Figs. 255-267.** *Belisana khaoyai*. 255. Right procursus, dorsal view. 256. Tip of right procursus, prolateral (slightly distal) view. 257. Tip of procursus, showing distinctive pair of spines. 258. Pores on procursus (cf. Fig. 255). 259. Detail of procursus (cf. Fig. 255). 260. Male palpal tarsal organ. 261. Male gonopore with epiandrous spigots. 262. Male chelicerae, frontal view. 263. Female tarsus 4 tip. 264. Female ALS. 265. Male ALS and PMS. 266. Female prosoma, frontal view. 267. Epigynum, ventral view. Arrows point to distinctive spines on procursus. Scale lines: 7  $\mu$ m (260), 10  $\mu$ m (258, 259, 264, 265), 20  $\mu$ m (261), 30  $\mu$ m (257, 263), 50  $\mu$ m (256), 60  $\mu$ m (255), 100  $\mu$ m (262, 266, 267).

*Variation.* Tibia 1 in 3 other males: 1.03-1.20.

*Female.* In general similar to male. Tibia 1 in 10 females: 0.87-1.00 (mean 0.93). Epigynum very simple externally (Fig. 271), almost flat, with pair of lateral pockets 150  $\mu$ m apart; dorsal view as in Fig. 272. ALS as in Fig. 287.

*Distribution.* Known only from type locality (Fig. 79).

*Material examined.* THAILAND: *Prachuap Khiri Khan*: Sam Roi Yot National Park: type above, together with 4♂10♀ (RMNH).



**Figs. 268-272.** *Belisana pranburi*. 268, 269. Left male pedipalp, prolateral (268) and retrolateral (269) views. 270. Male chelicerae, frontal view. 271, 272. Cleared female genitalia, ventral (271) and dorsal (272) views. Scale lines: 0.2 mm (268, 269), 0.1 mm (270-272).

***Belisana ranong*, new species**

(Figs. 70, 273-277)

*Type.* Male holotype from forest outside Ranong [9°58'N, 98°38'E], Ranong District and Province, Thailand; 50 m a.s.l., Sept. 18, 1992 (P. Schwendinger), in MHNG.

*Etymology.* The species name is a noun in apposition, taken from the type locality.

*Diagnosis.* Medium-sized, short-legged species with globular opisthosoma; easily distinguished from relatives by the male cheliceral apophyses (close together, proximal position: Fig. 275), and by the bulbal projections (large flat bulbal apophysis and long, slightly sclerotized embolus: Fig. 273).

*Male (holotype).* Total length 1.44 (1.54 with clypeus), carapace width 0.62. Leg 1: 7.0 (1.8 + 0.2 + 1.8 + 2.3 + 0.9), tibia 2: 1.2, tibia 3: 0.9, tibia 4: 1.3; tibia 1 L/d: 29. Habitus similar to *B. benjamini* (cf. Fig. 37) but with globular opisthosoma like *B. strinatii* (cf. Fig. 46). Prosoma and legs pale ochre-yellow, carapace with light brown median band, opisthosoma pale grey with faint darker marks. Ocular area very flat, not separated from carapace, thoracic furrow absent; distance PME-PME 70 µm; diameter PME 60 µm; distance PME-ALE ~20 µm. Clypeus unmodified. Sternum as long as wide (0.40). Chelicerae as in Fig. 275, apophyses at about 45° angle to paturon, tips of apophyses 30 µm apart. Palps as in Figs. 273 and 274; trochanter with short retrolateral apophysis, femur with indistinct hump proximo-dorsally, procurus rather simple, apparently with hinged structure prolatero-distally, bulb with distinctive flat apophysis, long embolus slightly sclerotized (Fig. 273). Retrolateral trichobothrium of tibia 1 at 34%; legs without spines, curved, and vertical hairs; tarsus 1 with ~10 pseudosegments, difficult to see in dissecting microscope.

*Female.* In general similar to male. Tibia 1 in two females: 1.5, 1.6. Epigynum very simple externally, flat, with pair of pockets in very frontal position (Fig. 276), 15 µm apart; dorsal view as in Fig. 277. ALS with several spigots in addition to basic set of two.

*Distribution.* Known from type locality only (Fig. 79).

*Material examined.* THAILAND: *Ranong*: Ranong: type above, together with 2♀ (MHNG).

***Belisana khaosok*, new species**

(Figs. 51, 52, 58, 59, 278-283, 288-296)

*Type.* Male holotype from Khao Sok National Park, Wing Hin Waterfall Trail (8°55'N, 98°31,7'E), Surat Thani Prov., Thailand; 300 m a.s.l., Oct. 19-20, 2003 (ATOL Expedition), in MACN.

*Etymology.* The species name is a noun in apposition, taken from the type locality.

*Diagnosis.* Medium-sized, long-legged species with elongated and posteriorly elevated opisthosoma; distinguished from similar congeners by the long and downward pointing cheliceral apophyses (Figs. 280, 281), by the ventral apophysis on the male palpal femur (Figs. 278, 279), by the distal elements on the procurus (Fig. 278), and by the bulb without hooked apophysis (Fig. 278).

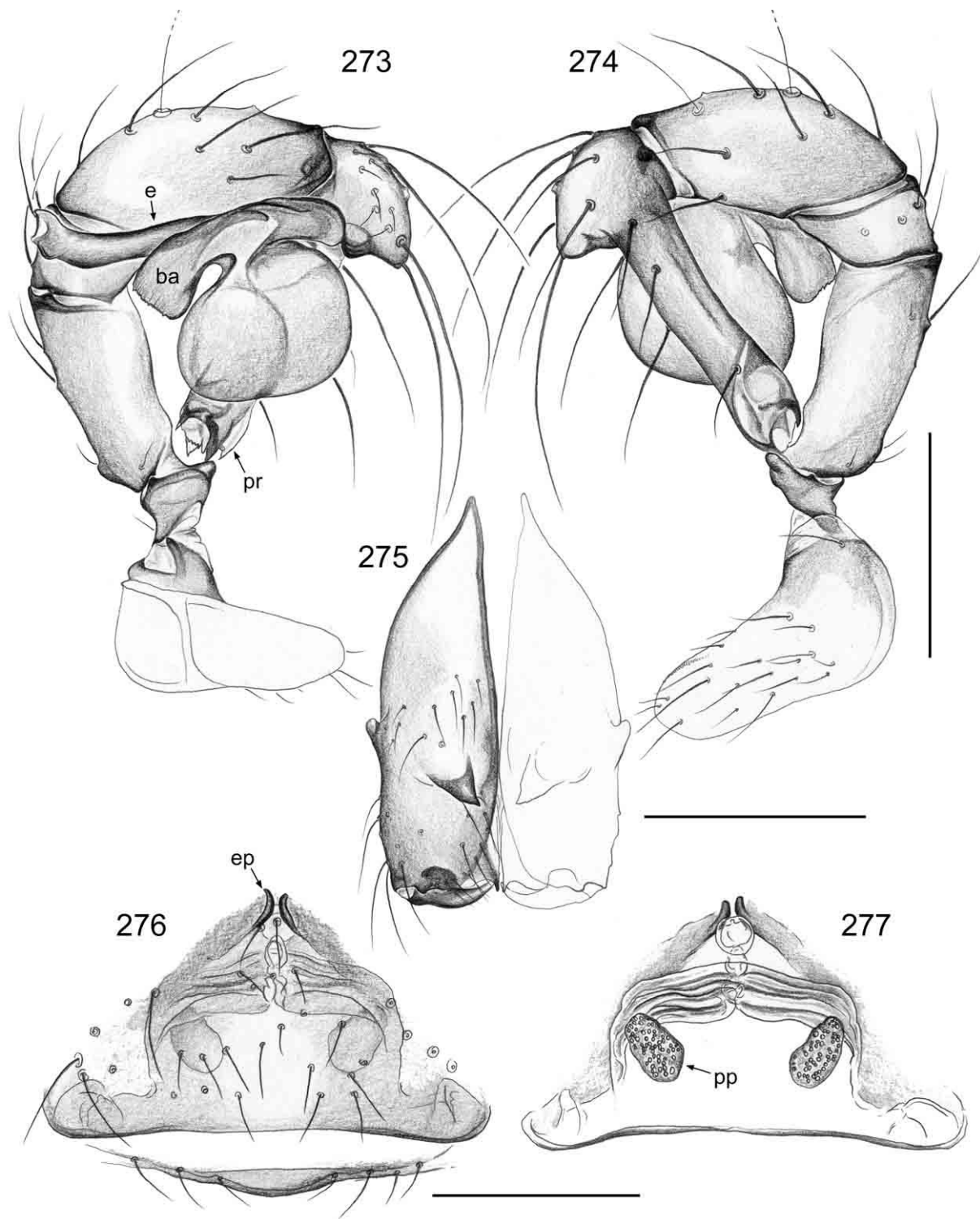
*Male (holotype).* Total length 1.5 (1.6 with clypeus), carapace width 0.57. Leg 1: 13.35 (3.2 + 0.25 + 3.25 + 5.25 + 1.4), tibia 2: 2.0, tibia 3: 1.2, tibia 4: 1.7; tibia 1 L/d: 61. Habitus as in Figs. 51 and 52. Prosoma very pale, almost white, legs pale ochre-yellow, opisthosoma monochromous pale grey. Ocular area not elevated, thoracic furrow absent; distance PME-PME 185 µm; diameter PME 55 µm; distance PME-ALE 20 µm. Clypeus unmodified. Sternum slightly wider than long (0.42/0.38). Chelicerae as in Figs. 280 and 281, with very long frontal apophyses, tips 180 µm apart. Palps as in Figs. 278 and 279; trochanter with small but distinctive retrolateral apophysis, femur with distinctive ventral apophysis and small dorsal apophysis, procurus with distinctive toothed ridge distally (Fig. 278), bulb projections as in Figs. 278 and 279, without apophysis. Retrolateral trichobothrium of tibia 1 at 12%; legs without spines and curved hairs, with more vertical hairs on metatarsi than usual; tarsus 1 with ~15 pseudosegments, distally about 10 fairly distinct.

*Variation.* Tibia 1 in 3 other males: 3.3-3.4. Distance between cheliceral apophyses in male from Khao Luang: 150 µm.

*Female.* In general similar to male; tibia 1 in 9 females: 2.6-2.9 (mean 2.77). There seems to exist considerable variation with regard to epigynum shape, both with respect to the scape (present or absent) and the number of pockets (one or two: Figs. 291, 292); in either case, the pockets do not correspond with the male cheliceral apophyses, so females are assigned with hesitation. Several females had genital plugs (Figs. 58, 293, 294); dorsal view of epigynum as in Fig. 283. Palpal tarsal organ and spinnerets as in Figs. 289 and 290.

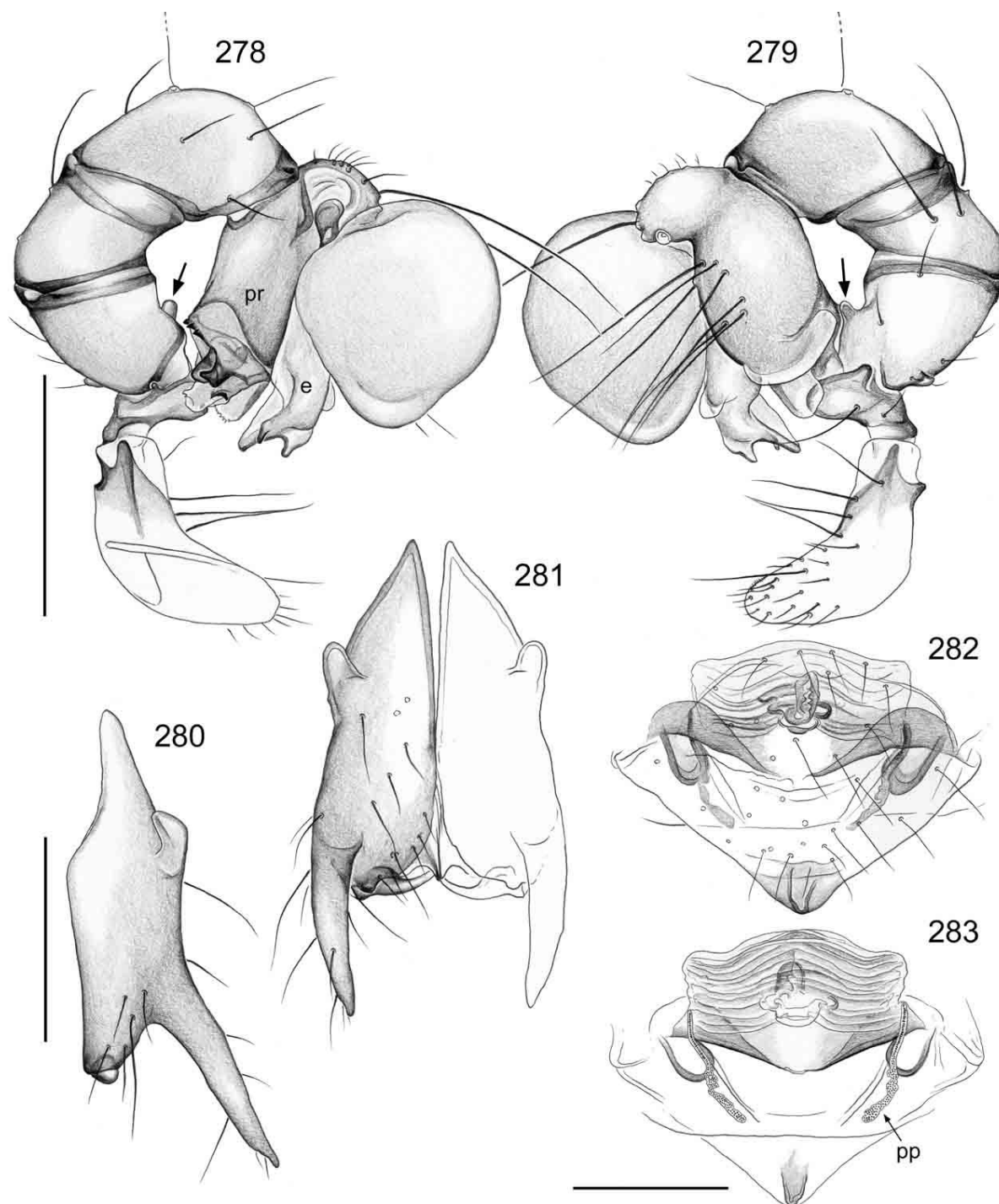
*Distribution.* Known from three neighboring localities in southern Thailand (Fig. 79).

*Material examined.* THAILAND: *Surat Thani*: type above, together with 2♀ (MACN); same collection data, 5♀ 2 juveniles (2 vials) (MACN). *Nakhon Si Thammarat*: Khao Luang National Park (8°43,4'N, 99°40,1'E), 355 m a.s.l.,



**Figs. 273-277.** *Belisana ranong*. 273, 274. Left male pedipalp, prolateral (273) and retrolateral (274) views. 275. Male chelicerae, frontal view. 276, 277. Cleared female genitalia, ventral (276) and dorsal (277) views. Scale lines: 0.2 mm.

Oct. 10-12, 2003 (ATOL Expedition), 2♂6♀ 3 juveniles (2 vials) (MACN). *Krabi*: Khao Phanom Bencha N. P. [8°17'N, 98°56'E], primary forest, Dec. 16, 1990 (C. L. & P. R. Deeleman), 2♂2♀ 2 juveniles (RMNH).



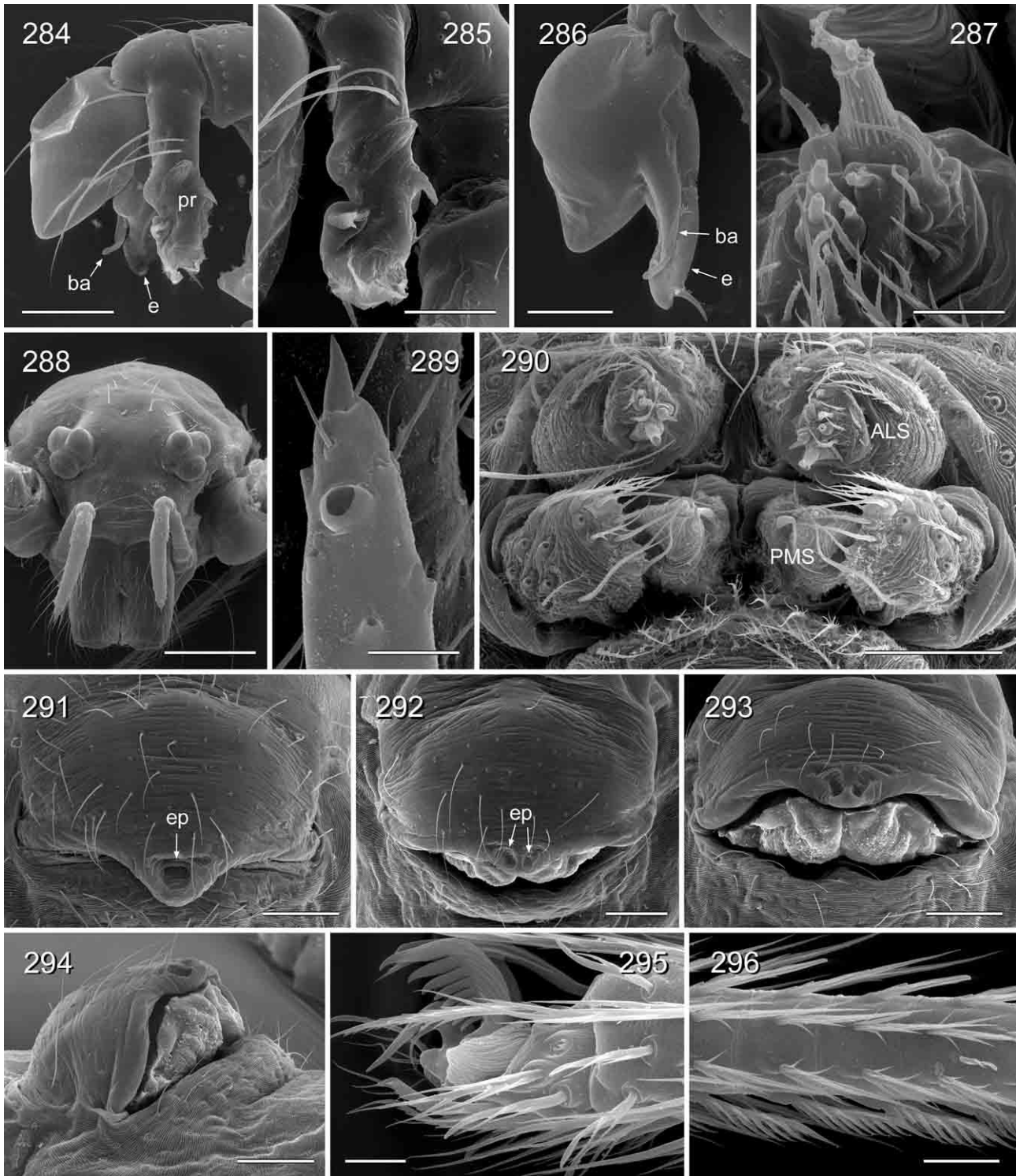
**Figs. 278-283.** *Belisana khaosok*. 278, 279. Left male pedipalp, prolateral (278) and retrolateral (279) views (arrows point to distinctive apophysis on femur). 280, 281. Male chelicerae, lateral and frontal views. 282, 283. Cleared female genitalia, ventral (282) and dorsal (283) views. Scale lines: 0.3 mm (278, 279), 0.2 mm (280-283).

***Belisana aninaj*, new species**

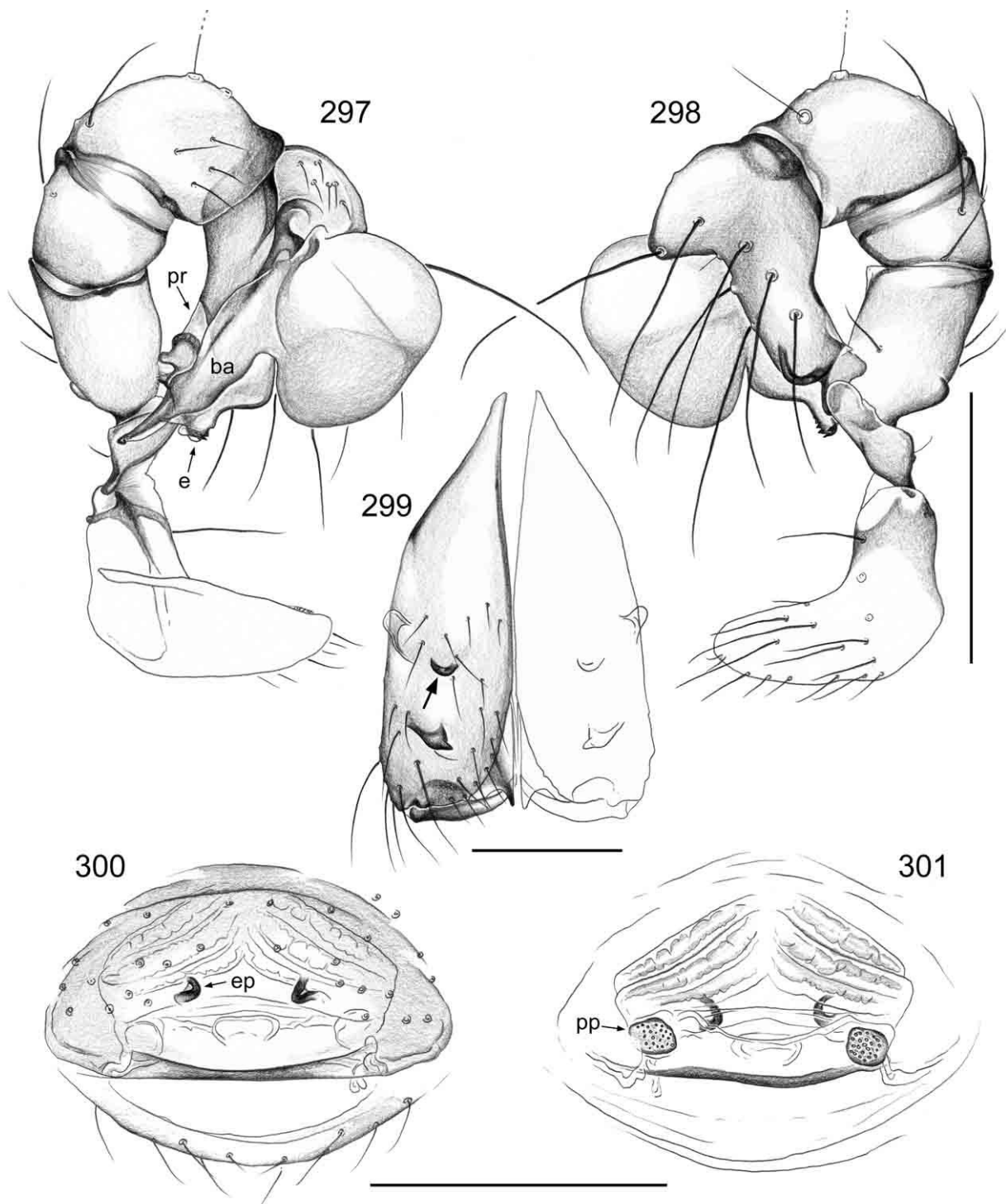
(Figs. 66, 297-301)

*Type.* Male holotype from Khao Luang National Park (8°43,4'N, 99°40,1'E), Nakhon Si Thammarat Prov., Thailand; 355 m a.s.l., Oct. 10-12, 2003 (ATOL Expedition), in MACN.





**Figs. 284-296.** *Belisana pranburi* (284-287) and *B. kaosok* (288-296). 284. Left procurus and bulb, retrolateral view. 285. Left procurus, retrolateral (slightly distal) view. 286. Right bulb, prolateral view. 287. Female ALS. 288. Female prosoma, frontal view. 289. Tip of female palp, dorsal view. 290. Female spinnerets. 291. Epigynum, morphotype with single median pocket. 292-294. Epigynum, morphotype with paired pockets, in ventral, slightly posterior, and lateral views (with genital plug). 295. Tip of female tarsus 3. 296. Detail of female tarsus 4 with ventral comb-hairs. Scale lines: 7  $\mu\text{m}$  (287), 10  $\mu\text{m}$  (295), 20  $\mu\text{m}$  (289, 296), 60  $\mu\text{m}$  (285, 290), 70  $\mu\text{m}$  (286), 100  $\mu\text{m}$  (284, 291-294), 200  $\mu\text{m}$  (288).



**Figs. 297-301.** *Belisana aninaj*. 297, 298. Left male pedipalp, prolateral (297) and retrolateral (298) views. 299. Male chelicerae, frontal view. 300, 301. Cleared female genitalia, ventral (300) and dorsal (301) views. Scale lines: 0.2 mm (297, 298, 300, 301), 0.1 mm (299).

*Etymology.* The species name is an arbitrary combination of letters, used as a noun in apposition.

*Diagnosis.* Tiny, short-legged species with globular opisthosoma; easily distinguished from most congeners by the proximal apophyses on the male chelicerae (Fig. 299; very distinct in lateral view), and by the long bulbal apophysis (Fig. 297).

*Male (holotype).* Total length 1.06 (1.13 with clypeus), carapace width 0.47. Leg 1: 6.0 (1.6 + 0.2 + 1.7 + 2.1 + 0.4), tibia 2: 1.1, tibia 3: 0.7, tibia 4: 1.1; tibia 1 L/d: 34. Habitus similar to *B. ketambe* (cf. Figs. 41, 42). Prosoma and legs pale ochre-yellow, carapace with pair of distinctive light brown marks; opisthosoma pale ochre-grey. Ocular area barely elevated, thoracic furrow absent; distance PME-PME 60  $\mu$ m; diameter PME 55  $\mu$ m; distance PME-ALE ~20  $\mu$ m. Clypeus unmodified. Sternum slightly wider than long (0.38/0.34). Chelicerae as in Fig. 299, tips 85  $\mu$ m apart. Palps as in Figs. 297 and 298; trochanter with simple rounded retrolateral apophysis, femur with indistinct dorsal hump, procurus relatively simple, bulb with long, distally hooked apophysis. Retrolateral trichobothrium of tibia 1 at 33%; legs without spines, curved hairs, and vertical hairs (many hairs missing); tarsus 1 with ~10 pseudosegments.

*Variation.* Tibia 1 in 2 other males: 1.63, 1.83.

*Female.* In general similar to male; tibia 1 in 10 females: 1.33-1.57 (mean 1.46). Epigynum simple light brown oval plate with distinctive pair of dark pockets 75  $\mu$ m apart (Fig. 300); dorsal view as in Fig. 301. ALS with several spigots.

*Distribution.* Known only from type locality (Fig. 79).

*Material examined.* THAILAND: *Nakhon Si Thammarat*: Khao Luang N. P.: type above, together with 2♂~8♀ (MACN); same collection data, 2♀ (MACN).

### ***Belisana ketambe*, new species**

(Figs. 41, 42, 302-319)

*Type.* Male holotype from Ketambe [~3°45'N, 97°45'E], Gunung Leuser N. P., Aceh, Sumatra, Indonesia; March 2-4, 1986 (S. Djojosedharmo), in RMNH.

*Etymology.* The species name is a noun in apposition, taken from the type locality.

*Diagnosis.* Tiny, short-legged species with globular opisthosoma; distinguished from similar relatives by the shapes of procurus and bulbal apophyses (Figs. 302, 303), and by the position of the cheliceral apophyses (Fig. 304). *Belisana sandakan* is very similar but has a shorter bulbal apophysis, a slightly different procurus, and cheliceral apophyses closer together (cf. Figs. 360-362).

*Male (holotype).* Total length 1.3 (1.4 with clypeus), carapace width 0.56. Leg 1: 5.9 (1.4 + 0.2 + 1.6 + 1.9 + 0.8), tibia 2: 0.9, tibia 3: 0.6, tibia 4: 1.1; tibia 1 L/d: 29. Habitus as in Figs. 41 and 42. Prosoma and legs ochre-yellow, opisthosoma pale grey. Ocular area not elevated, not separated from carapace, thoracic furrow absent; distance PME-PME 40  $\mu$ m; diameter PME 60  $\mu$ m; distance PME-ALE ~20  $\mu$ m. Clypeus unmodified. Sternum wider than long (0.40/0.35). Chelicerae as in Fig. 304, tips of frontal apophyses unmodified (Fig. 308), 225  $\mu$ m apart. Palps as in Figs. 302 and 303; trochanter with retrolateral apophysis, femur with very indistinct proximo-dorsal hump, procurus with simple proximal part, more complex and possibly hinged distal part, bulb with hooked apophysis and membranous embolus (Fig. 307). Tarsal organ exposed (Fig. 313). Retrolateral trichobothrium of tibia 1 at 36%; legs without spines and curved hairs, with vertical hairs in several rows on tibiae 1, 2, and 4, and on metatarsi 1 and 2 (Fig. 316); tarsus 1 with about 12 pseudosegments. Spinnerets and gonopore as in Figs. 309 and 311.

*Variation.* Tibia 1 in 20 other males: 1.40-1.68 (mean 1.55). Some males with darker marks visible through abdominal cuticle. Males from Thailand have a procurus that is distally apparently minimally different (membranous structures).

*Female.* In general similar to male. Tibia 1 (N = 30): 1.28-1.52 (mean 1.39). Epigynum as in Figs. 305, 318, 319, with pair of pockets 200  $\mu$ m apart; dorsal view as in Fig. 306. ALS and palpal tarsal organ as in Figs. 310, 312.

*Distribution.* Known from two localities in Sumatra and southern Thailand (Fig. 80).

*Material examined.* INDONESIA: *Sumatra*: Gunung Leuser N.P.: type above, together with 14♂~44♀ (RMNH). THAILAND: *Narathiwat Prov.*: Waeng Distr., Hala Bala W.S., research station (5°47.7'N, 101°50.1'E), 190-200 m a.s.l., Oct. 13-14, 2003 (ATOL Expedition), 7♂10♀ (2 vials) (MACN); same locality, 200 m a.s.l., Jan. 8, 1999 (P. Schwendinger), 1♂1♀ 2 juveniles (MHNG).

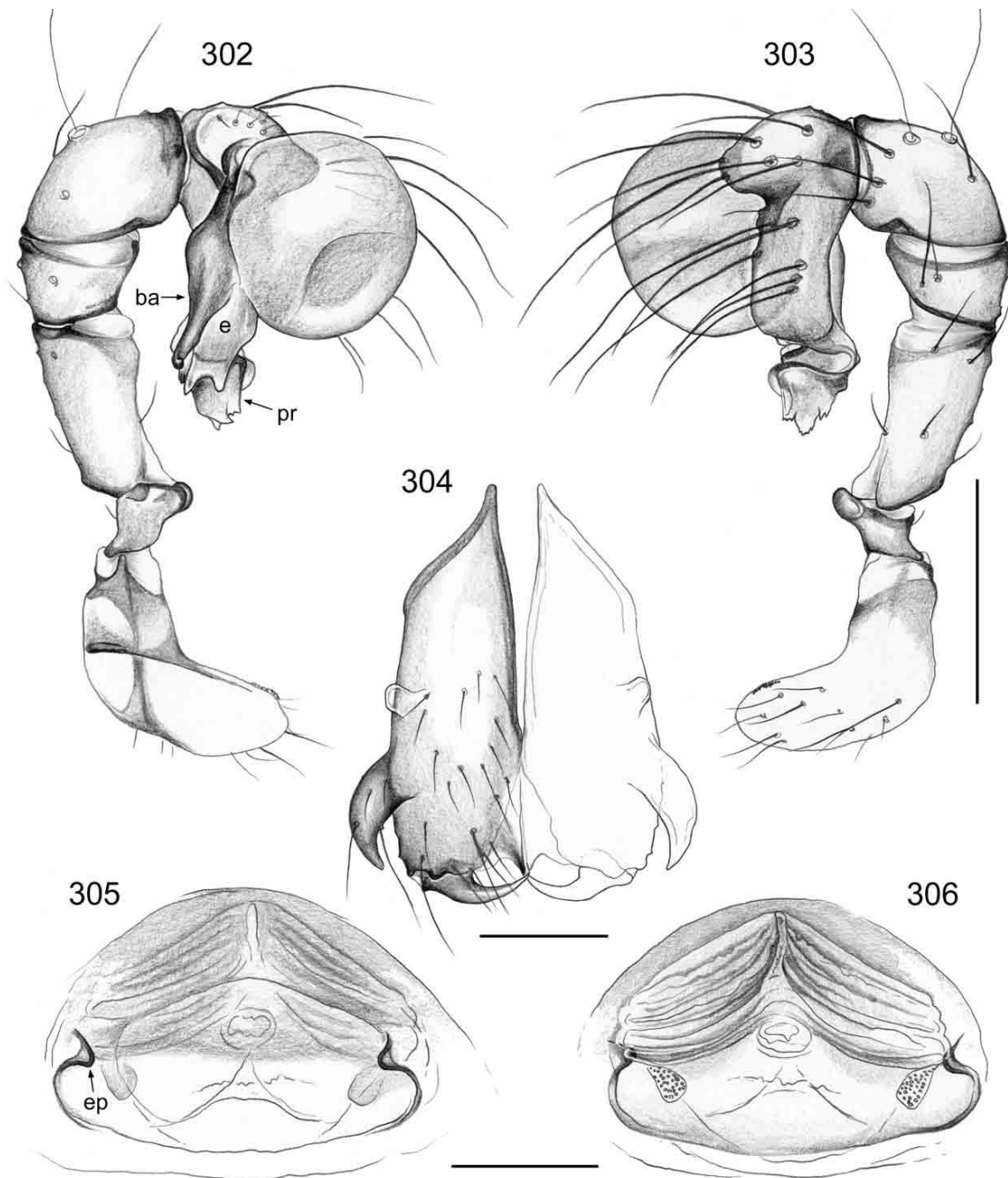
### ***Belisana fraser*, new species**

(Figs. 69, 320-324)

*Type.* Male holotype from Bukit Fraser [Fraser's Hill, 3°43'N, 101°45'E], Malaysia; date and collector unknown, in OMNZ.

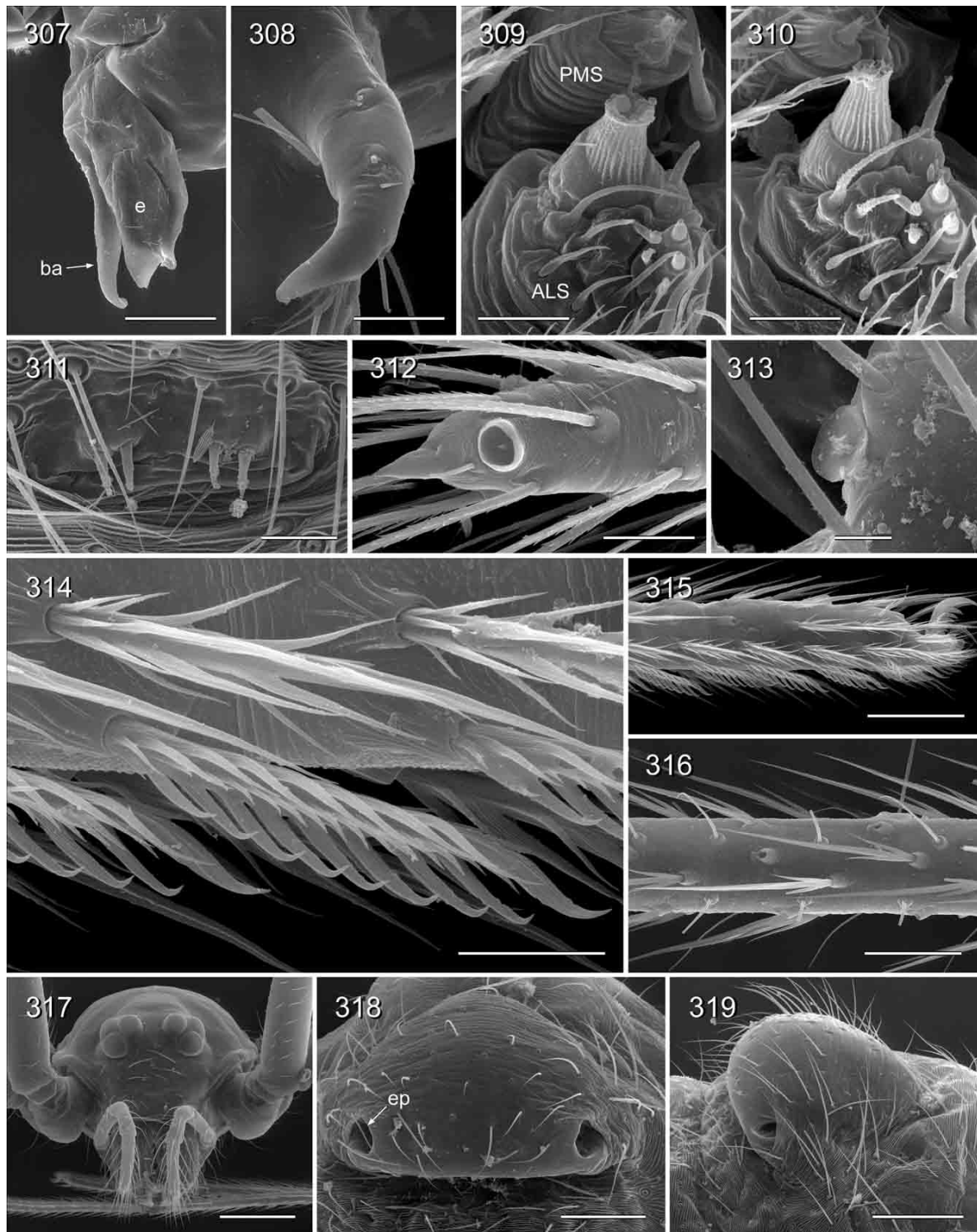
*Etymology.* The species name is a noun in apposition, taken from the type locality.

*Diagnosis.* Tiny, short-legged species with globular opisthosoma; very similar to *B. nomis*, but with thicker cheliceral apophyses (compare Figs. 322 and 330), differently curved bulbal apophysis and relatively smaller bulb (compare Figs. 320 and 328).



**Figs. 302-306.** *Belisana ketambe*. 302, 303. Left male pedipalp, prolateral (302) and retrolateral (303) views. 304. Male chelicerae, frontal view. 305, 306. Cleared female genitalia, ventral (305) and dorsal (306) views. Scale lines: 0.2 mm (302, 303), 0.1 mm (304-306).

*Male (holotype)*. Total length 1.1 (1.2 with clypeus), carapace width 0.50. Leg 1: 5.86 (1.43 + 0.17 + 1.53 + 2.03 + 0.70), tibia 2: 0.87, tibia 3: 0.63, tibia 4: 1.00; tibia 1 L/d: 29. Habitus similar to *B. benjamini* (cf. Figs. 37, 38). Prosoma and legs pale ochre-yellow, opisthosoma pale grey. Ocular area not elevated, thoracic furrow absent; distance PME-PME 95  $\mu$ m; diameter PME 55  $\mu$ m; distance PME-ALE ~10  $\mu$ m. Clypeus unmodified. Sternum slightly wider than long (0.36/0.32). Chelicerae as in Fig. 322, with thick (also in lateral view) frontal apophyses, tips 65  $\mu$ m apart. Palps as in Figs. 320 and 321; trochanter with very short retrolateral projection, femur with indistinct hump dorsally,



**Figs. 307-319.** *Belisana ketambe*. 307. Bulbal projections. 308. Male cheliceral apophysis. 309. Male ALS. 310. Female ALS. 311. Male gono-pore with epiandrous spigots. 312. Tip of female palp with tarsal organ, dorsal view. 313. Male palpal tarsal organ. 314. Comb-hair on female tarsus 4. 315. Female tarsus 4 tip. 316. Hairs on male metatarsus 1 (proximally). 317. Female prosoma, frontal view. 318. Epigynum, ventral view. 319. Epigynum, lateral view. Scale lines: 10  $\mu$ m (309, 310, 313, 314), 20  $\mu$ m (311, 312), 30  $\mu$ m (308), 40  $\mu$ m (315, 316), 60  $\mu$ m (307), 70  $\mu$ m (318), 100  $\mu$ m (319), 200  $\mu$ m (317).

procursus with membranous ventral flap and distal sclerites, bulb with curved apophysis and spine-like projection. Retrolateral trichobothrium of tibia 1 not seen; legs without spines, curved hairs, and vertical hairs; tarsus 1 with ~10 pseudosegments, very indistinct.

*Female.* In general similar to male; tibia 1: 1.33. Epigynum very simple externally, with pockets in relatively anterior position (Fig. 323), 30 µm apart; dorsal view as in Fig. 324. ALS with several spigots.

*Distribution.* Known only from type locality (Fig. 80).

*Material examined.* MALAYSIA: *Pahang*: Bukit Fraser: type above, together with 1♀ (OMNZ).

### ***Belisana strinatii*, new species**

(Figs. 45, 46, 325-327)

*Type.* Male holotype from “Gua Anak Takun (grotte)”, Templer Park [~3°19'N, 101°36'E], Selangor, Malaysia; Feb. 25, 1975 (P. Strinati), in MHNG.

*Etymology.* Named for the collector, Pierre Strinati.

*Diagnosis.* Medium-sized, short-legged species with globular opisthosoma; distinguished from similar congeners by a brush of hairs on the head and the triads far apart (Figs. 45, 46); also by the shapes of procursus and bulbal projections and the position and shape of the cheliceral apophyses (Figs. 325-327).

*Male (holotype).* Total length 1.35 (1.45 with clypeus), carapace width 0.60. Leg 1: 7.7 (1.9 + 0.25 + 1.9 + 2.8 + 0.85), tibia 2: 1.4, tibia 3: 1.0, tibia 4: 1.4; tibia 1 L/d: 31. Habitus as in Figs. 45 and 46. Prosoma and legs pale ochre-yellow, opisthosoma monochromous pale grey. Ocular area slightly elevated and separated from carapace, thoracic furrow absent; distance PME-PME 195 µm; diameter PME 45 µm; distance PME-ALE 10 µm. Clypeus unmodified. Sternum slightly wider than long (0.44/0.38). Chelicerae as in Fig. 327, frontal apophyses close together pointing inwards, tips 50 µm apart. Palps as in Figs. 325 and 326; trochanter with relatively long retrolateral apophysis (appears short in retrolateral view), femur with indistinct dorsal hump, procursus complex distally (mostly membranous), bulb with long, distally hooked sclerite and rather simple embolus. Retrolateral trichobothrium of tibia 1 at 33%; legs without spines and curved hairs, with more vertical hairs on metatarsi than usual; tarsus 1 with >15 pseudosegments, distally fairly distinct.

*Variation.* Opisthosoma in other males darker grey, with some dark spots dorsally; tibia 1 in two other males: 1.85, 1.9.

*Female.* Unknown.

*Distribution.* Known only from type locality (Fig. 80).

*Material examined.* MALAYSIA: *Selangor*: type above, together with 2♂ (MHNG).

### ***Belisana nomis*, new species**

(Figs. 328-333)

*Type.* Male holotype from Labrador (Labrador Nature Reserve) [1°16'N, 103°48'E], Singapore; forest litter, Sept. 6, 1992 (C. L. & P. R. Deeleman), in RMNH.

*Etymology.* The species name is an arbitrary combination of letters, used as a noun in apposition.

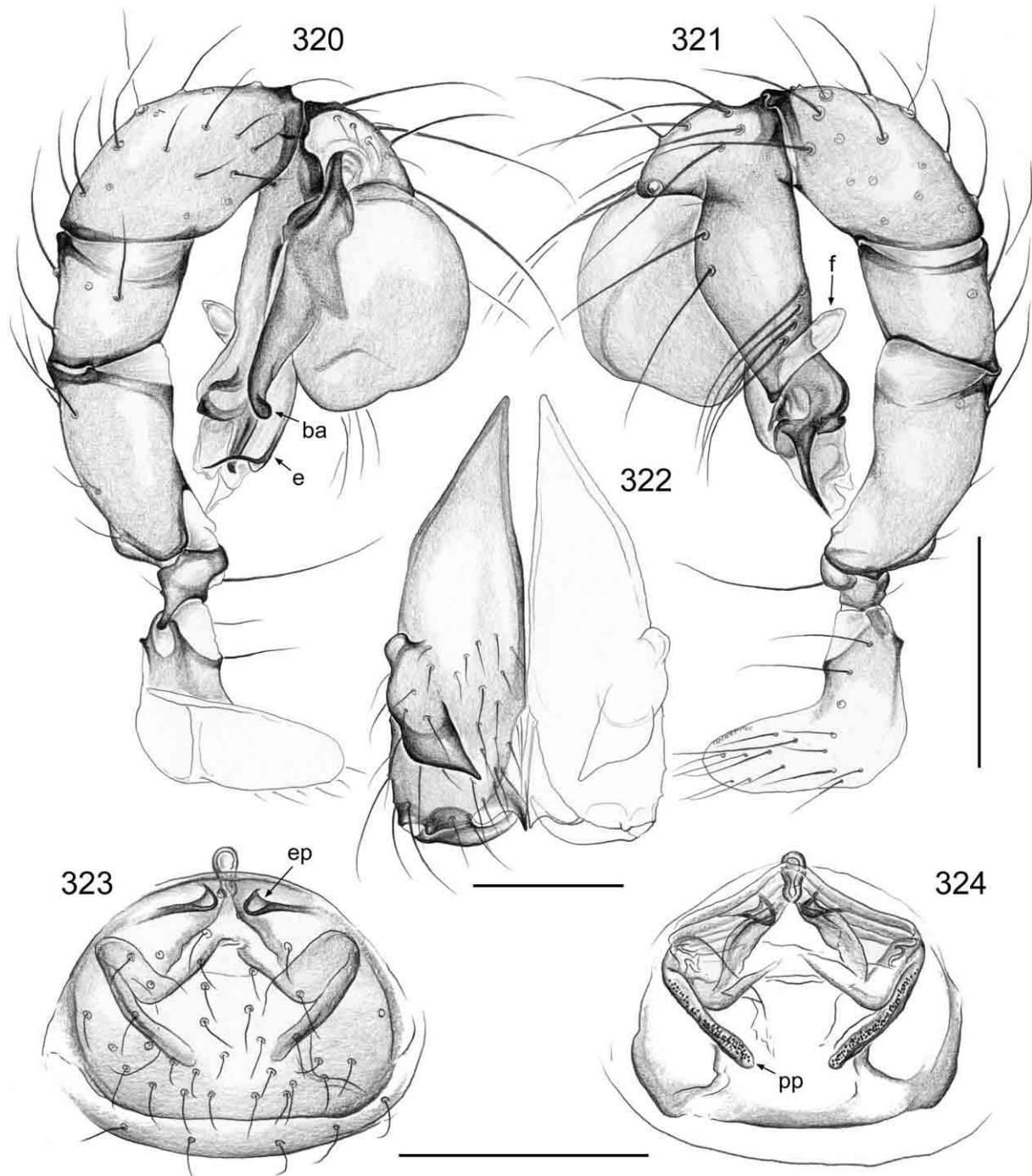
*Diagnosis.* Tiny, short-legged species with globular opisthosoma; distinguished from similar congeners by the shapes of bulbal apophysis (Fig. 328), procursus (Fig. 329), and cheliceral apophyses (Figs. 330, 331).

*Male (holotype).* Total length 1.1 (1.2 with clypeus), carapace width 0.50. Leg 1: 5.9 (1.4 + 0.2 + 1.6 + 1.9 + 0.8), tibia 2: 0.9, tibia 3: 0.7, tibia 4: 1.1; tibia 1 L/d: 30. Habitus similar to *B. ketambe* (cf. Figs. 41, 42). Prosoma and legs pale ochre-yellow, opisthosoma pale grey. Ocular area barely elevated, thoracic furrow absent; distance PME-PME 70 µm; diameter PME 55 µm; distance PME-ALE ~20 µm. Clypeus unmodified. Sternum about as wide as long (0.35). Chelicerae as in Figs. 330 and 331, tips of apophyses 65 µm apart. Palps as in Figs. 328 and 329; trochanter with simple retrolateral apophysis, femur with small dorsal apophysis, procursus complex distally (mostly membranous), bulb with distinctively curved apophysis (Fig. 328). Retrolateral trichobothrium of tibia 1 at 39%; legs without spines, curved hairs, and vertical hairs; tarsus 1 with ~10 pseudosegments, barely visible.

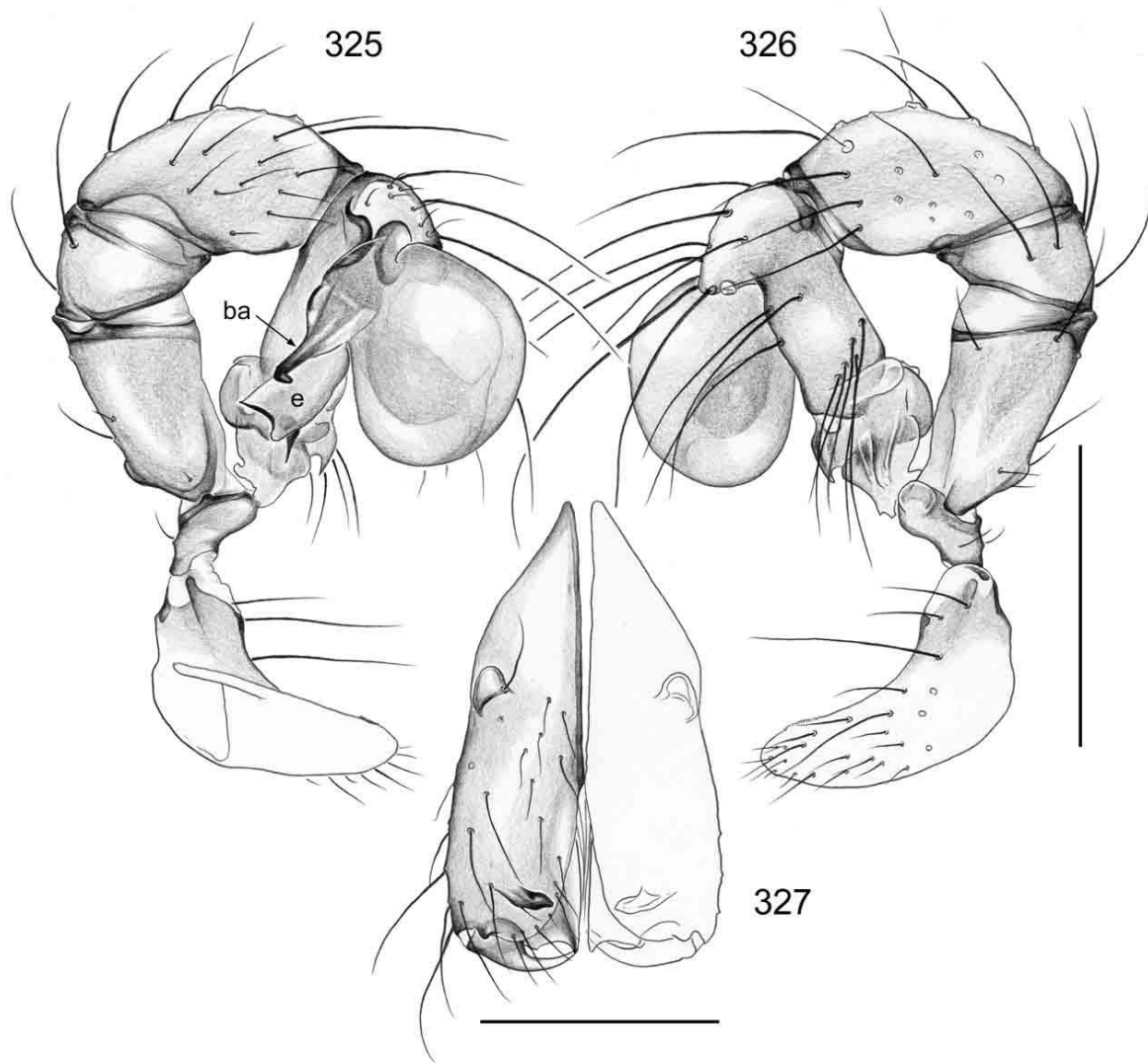
*Variation.* Tibia 1 in other male from type locality: 1.75. The male from Malaysia has identical genitalia but the cheliceral apophyses are wider apart (115 µm); it is therefore assigned tentatively; tibia 1: 2.0.

*Female.* Female from type locality in general similar to male; tibia 1: 1.3. Epigynum simple externally, with pockets in frontal position, 50 µm apart (Fig. 332); dorsal view as in Fig. 333. ALS with several spigots. The females from Malaysia have slightly longer legs, tibia 1: 1.5, 1.6; however, these females may not even be conspecific with the male from that locality, because a very similar second (undescribed) species occurs at the same locality (in RMNH).





**Figs. 320-324.** *Belisana fraser*. 320, 321. Left male pedipalp, prolateral (320) and retrolateral (321) views. 322. Male chelicerae, frontal view. 323, 324. Cleared female genitalia, ventral (323) and dorsal (324) views. Scale lines: 0.2 mm (320, 321, 323, 324), 0.1 mm (322).



**Figs. 325-327.** *Belisana strinatii*. 325, 326. Left male pedipalp, prolateral (325) and retrolateral (326) views. 327. Male chelicerae, frontal view. Scale lines: 0.3 mm (325, 326), 0.2 mm (327).

*Distribution.* Known from two neighboring localities in Singapore and Malaysia (Malaysian specimens assigned tentatively).

*Material examined.* SINGAPORE: Labrador Nature Reserve, type above, together with 1♂1♀ (RMNH).

Assigned tentatively: MALAYSIA: *Johor*: Kota Tinggi, Jalan Lombong, B. F. Station [ $\sim 1^{\circ}45'N$ ,  $103^{\circ}54'E$ ], rain forest, Oct. 31-Nov. 4, 1976 (P. Lehtinen), 1♂2♀ (ZMT, AA3452).

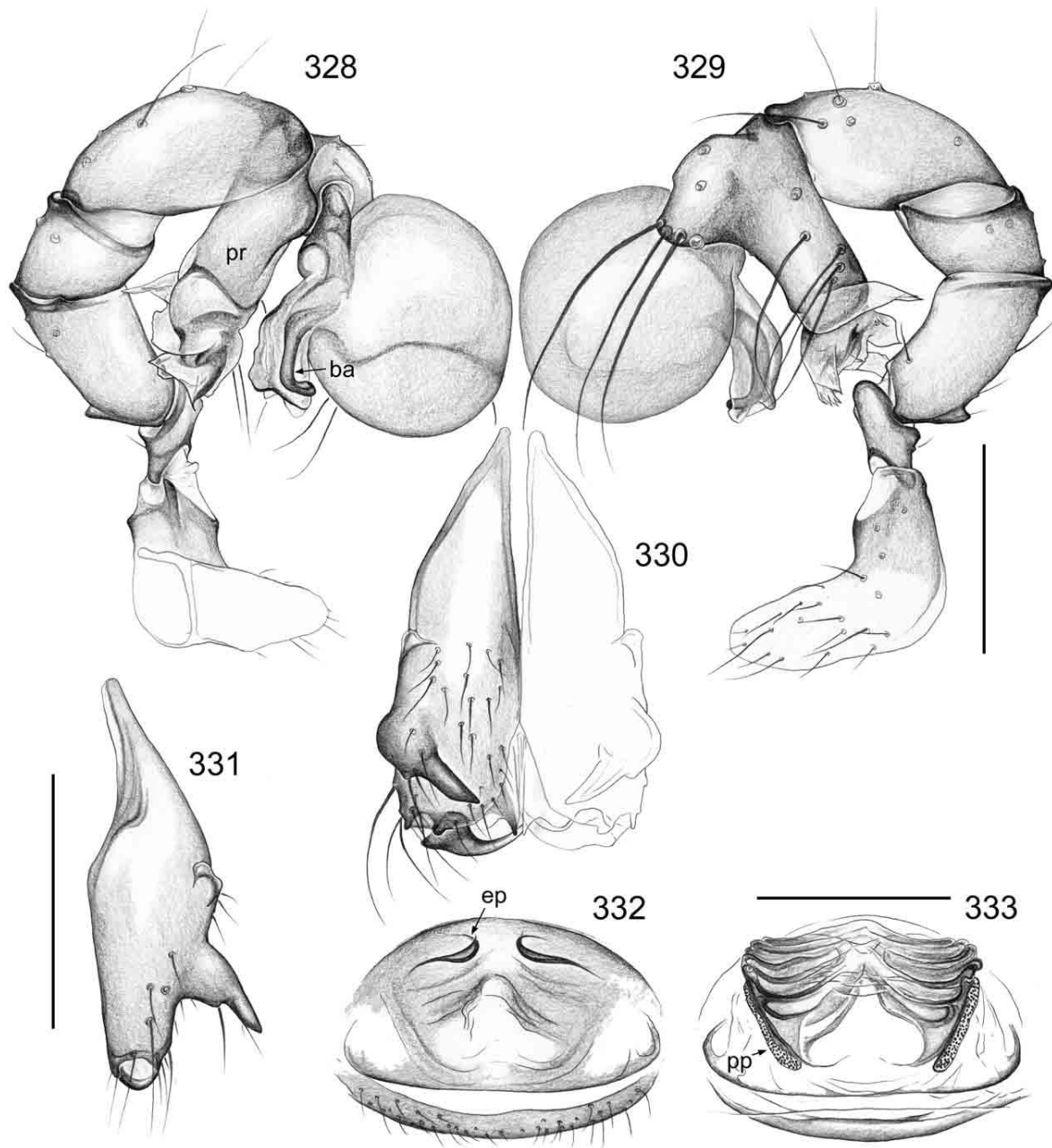
***Belisana freyae*, new species**

(Figs. 72, 334-338)

*Type.* Male holotype from Bohorok [ $\sim 3^{\circ}30'N$ ,  $98^{\circ}12'E$ ], North Sumatra Prov., Sumatra, Indonesia; Dec. 31, 1983 (C. L. & P. R. Deeleman), in RMNH.

*Etymology.* Named for Regina Frey, one of the zoologists who established the Bohorok Centre for Orang-Utans in 1973.

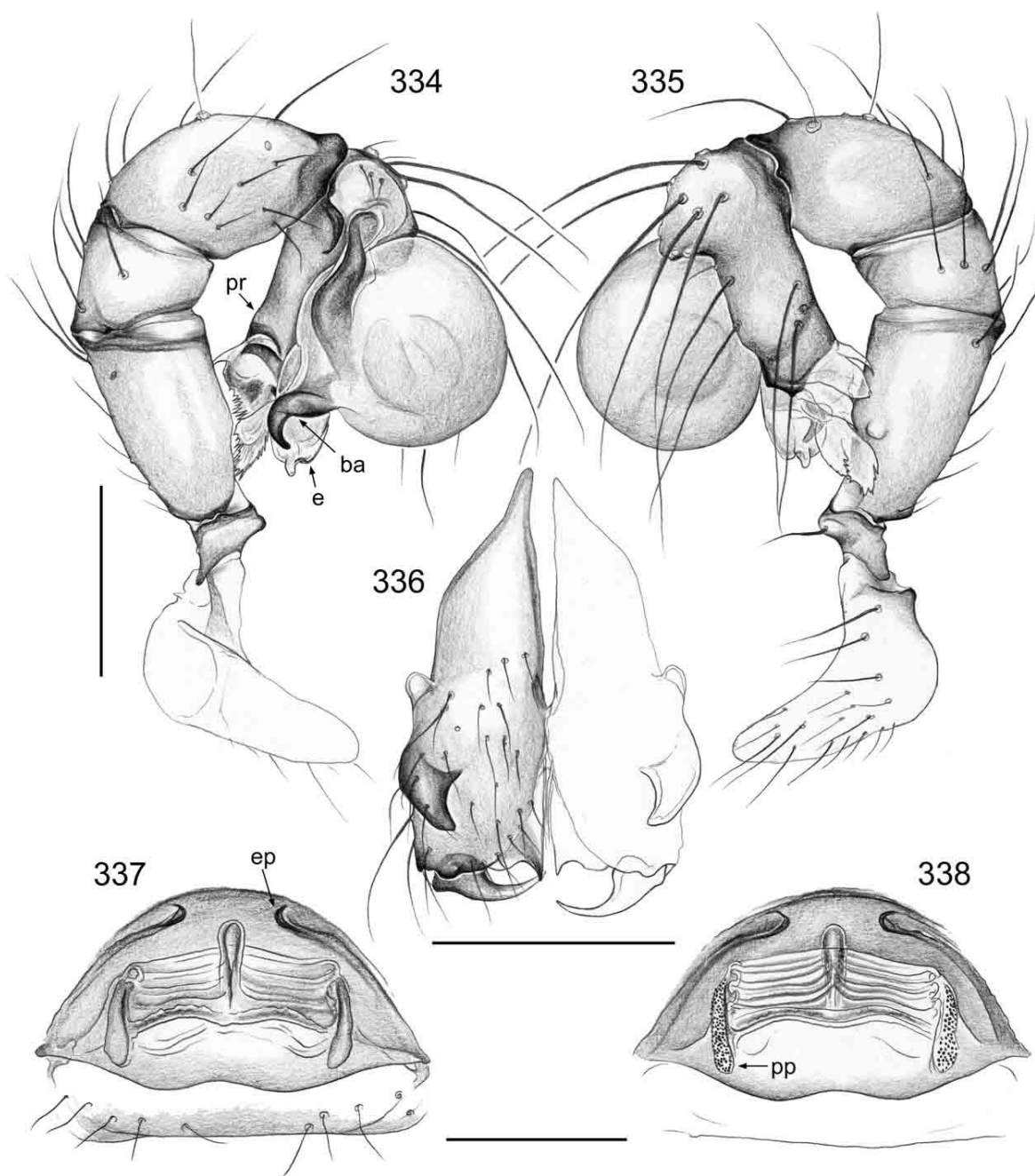
*Diagnosis.* Tiny, short-legged species with globular opisthosoma; distinguished from similar congeners by the shapes of procurus (Fig. 335), bulbal apophysis (Fig. 334), and cheliceral apophyses (Fig. 336).



**Figs. 328-333.** *Belisana nomis*. 328, 329. Left male pedipalp, prolateral (328) and retrolateral (329) views. 330, 331. Male chelicerae, frontal and lateral views. 332, 333. Cleared female genitalia, ventral (332) and dorsal (333) views. Scale lines: 0.2 mm.

*Male (holotype)*. Total length 1.3 (1.4 with clypeus), carapace width 0.50. Leg 1: 7.5 (1.80 + 0.23 + 1.90 + 2.63 + 0.93), tibia 2: 1.23, tibia 3: 0.80, tibia 4: 1.37; tibia 1 L/d: 31. Habitus similar to *B. leumas* (cf. Figs. 35, 36). Entire animal pale ochre-yellow, carapace slightly darker, opisthosoma pale greyish. Ocular area barely elevated, thoracic furrow absent; distance PME-PME 90  $\mu$ m; diameter PME 60  $\mu$ m; distance PME-ALE 20  $\mu$ m. Clypeus unmodified. Sternum slightly wider than long (0.40/0.36). Chelicerae as in Fig. 336, tips of apophyses 160  $\mu$ m apart. Palps as in Figs. 334 and 335; trochanter with simple retrolateral apophysis, femur with distinctive retrolateral hump, without dorsal apophysis, procurus complex distally (mostly membranous), bulb with distinctive hooked apophysis (Fig. 334). Retrolateral trichobothrium of tibia 1 at 29%; legs without spines, curved hairs, and vertical hairs (many hairs missing); tarsus 1 with about 10 pseudosegments, only distally about 5 fairly visible.

*Variation*. Tibia 1 in 3 other males: 1.88, 1.93, 1.93. Some males with large dark spots visible through abdominal cuticle.



**Figs. 334-338.** *Belisana freyae*. 334, 335. Left male pedipalp, prolateral (334) and retrolateral (335) views. 336. Male chelicerae, frontal view. 337, 338. Cleared female genitalia, ventral (337) and dorsal (338) views. Scale lines: 0.2 mm.

*Female.* In general similar to male; opisthosoma mostly with large dark spots visible through cuticle; tibia 1 in 4 females: 1.6-1.7. Epigynum simple externally (Figs. 72, 337), light brown, with dark median internal structure visible through cuticle; pair of pockets 110  $\mu$ m apart; dorsal view as in Fig. 338. ALS with several spigots.

*Distribution.* Known only from Bohorok area, Sumatra (Fig. 80).

*Material examined.* INDONESIA: *Sumatra*: Bohorok: type above, together with 1♀ (RMNH); same locality, May 27, 1983 (C. L. & P. R. Deeleman), 2♂2♀ 2 juveniles (RMNH); Gunung Leuser N. P. at Bohorok, 200-1000 m up from station, "various litters", Aug. 7-10, 1982 (C. L. & P. R. Deeleman), 2♂2♀ 3 juveniles (RMNH).

***Belisana gedeh*, new species**

(Figs. 71, 339-359)

*Type.* Male holotype from Cibodas, Gedeh N. P. [ $\sim 5^{\circ}55'S$ ,  $106^{\circ}03'E?$ ], Java, Indonesia; 1500-1600 m a.s.l., Nov. 1986 (S. Djojosedharmo), in RMNH.

*Etymology.* The species name is a noun in apposition, taken from the type locality.

*Diagnosis.* Tiny, short-legged species with globular opisthosoma; distinguished from similar congeners by the shape of the procurus (Fig. 340), the long bulbal apophysis (Fig. 339), and the widely spread cheliceral apophyses (Fig. 341).

*Male (holotype).* Total length 1.3 (1.4 with clypeus), carapace width 0.53. Leg 1: 7.46 (1.83 + 0.20 + 2.03 + 2.43 + 0.97), tibia 2: 1.17, tibia 3: 0.83, tibia 4: 1.50; tibia 1 L/d: 33. Habitus similar to *B. leumas* (cf. Figs. 35, 36). Prosoma and legs pale ochre-yellow; opisthosoma pale grey. Ocular area barely elevated, thoracic furrow absent; distance PME-PME 45  $\mu\text{m}$ ; diameter PME 60  $\mu\text{m}$ ; distance PME-ALE 20  $\mu\text{m}$ . Clypeus unmodified. Sternum slightly wider than long (0.42/0.36). Chelicerae as in Figs. 341, 342, and 352, tips of apophyses 305  $\mu\text{m}$  apart. Palps as in Figs. 339 and 340; trochanter with retrolateral apophysis, femur with indistinct dorsal hump, procurus complex distally (Figs. 347-350), bulb with long curved apophysis and membranous embolus (Figs. 339, 347). Tarsal organ capsulate (Fig. 351). Retrolateral trichobothrium of tibia 1 at 27%; legs without spines, curved hairs, and vertical hairs; tarsus 1 with over 15 pseudosegments, distally quite distinct. Gonopore and spinnerets as in Figs. 353 and 358.

*Variation.* Tibia 1 in 8 other males: 1.90-2.13 (mean 2.00).

*Female.* In general similar to male; tibia 1 in 17 females: 1.70-1.90 (mean 1.79). Epigynum simple externally (Figs. 354, 355), light brown, strongly protruding in some females; pockets 235  $\mu\text{m}$  apart; dorsal view as in Fig. 344. Spinnerets and palpal tarsal organ as in Figs. 357 and 359.

*Distribution.* Known from two localities in western Java (Fig. 80).

*Material examined.* INDONESIA: *Java*: Cibodas: type above, together with 4♂12♀ (RMNH); Bogor, Puncak Pass [ $6^{\circ}42'S$ ,  $106^{\circ}59'E$ ], 1000 m a.s.l., Aug. 16, 1980 (P. R. & C. L. Deeleman), 1♂4♀ 3 juveniles (RMNH); Bogor, Puncak Pass, Telaga Warna, wet jungle litter, Oct. 6, 1979 (P. Lehtinen), 3♂2♀ (ZMT AA 3458).

***Belisana sandakan*, new species**

(Figs. 360-375)

*Type.* Male holotype from Sandakan [ $5^{\circ}50'N$ ,  $118^{\circ}07'E$ ], Till Hill, Sabah (Borneo), Malaysia; "tanap-forest", Nov. 5, 1979 (P. Lehtinen), in ZMT (AA 3451).

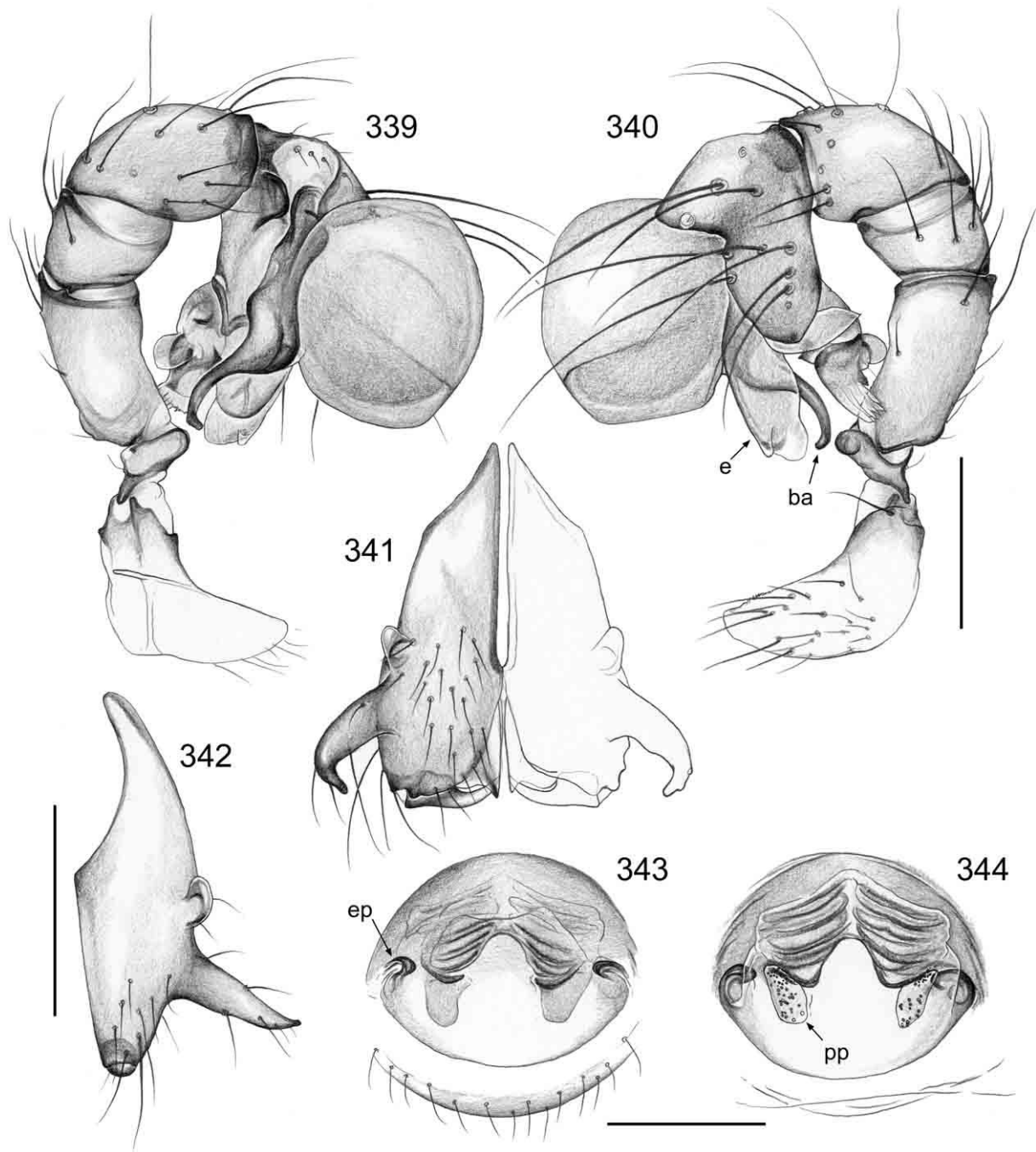
*Etymology.* The species name is a noun in apposition, taken from the type locality.

*Diagnosis.* Tiny, short-legged species with globular opisthosoma; distinguished from similar congeners by the shape of the procurus (Fig. 361), the short bulbal apophysis (Fig. 360), and the shape and position of the cheliceral apophyses (Figs. 362, 363).

*Male (holotype).* Total length 0.92 (1.00 with clypeus), carapace width 0.46. Leg 1: 6.16 (1.50 + 0.20 + 1.63 + 2.40 + 0.43), tibia 2: 0.93, tibia 3: 0.63, tibia 4: 1.13; tibia 1 L/d: 36. Habitus similar to *B. benjamini* (cf. Figs. 37, 38). Prosoma and legs pale ochre-yellow; opisthosoma pale grey. Ocular area slightly elevated, thoracic furrow absent; distance PME-PME 55  $\mu\text{m}$ ; diameter PME 55  $\mu\text{m}$ ; distance PME-ALE  $\sim 10$   $\mu\text{m}$ . Clypeus unmodified. Sternum about as wide as long (0.34). Chelicerae as in Figs. 362 and 363, tips of apophyses 130  $\mu\text{m}$  apart. Palps as in Figs. 360 and 361; trochanter with rounded weakly sclerotized retrolateral apophysis, femur with indistinct hump dorsally, procurus with distinctive dark sclerite distally (Fig. 361) and complex system of membranous structures (Figs. 367, 369), bulb with distinctively short hooked sclerite (Figs. 360, 368). Tarsal organ exposed (Fig. 370). Retrolateral trichobothrium of tibia 1 not seen; legs without spines, curved hairs, and vertical hairs (most hairs missing); pseudosegments not seen. ALS and gonopore as in Figs. 371 and 373.

*Variation.* Tibia 1 in 3 other males from type locality and Selangor: 1.43, 1.57, 1.60. Males from Sumatra have the identical distinctive bulbal apophysis, but their cheliceral apophyses are slightly wider apart and pointing less downwards, and the large ventrodiscal sclerite on the procurus is slightly smaller; they are therefore assigned tentatively; tibia 1 in these males: 1.43, 1.67, 1.77.

*Female.* In general similar to male; tibia 1 in 12 females from type locality and Selangor: 1.27-1.57 (mean 1.41); tibia 1 in female from Sumatra: 1.50. Epigynum very simple externally (Fig. 375), variably protruding, not darker than rest of opisthosoma, pockets 125  $\mu\text{m}$  apart; cleared ventral view as in Fig. 364; pore plates not seen. Spinnerets and palpal tarsal organ as in Figs. 372 and 374.



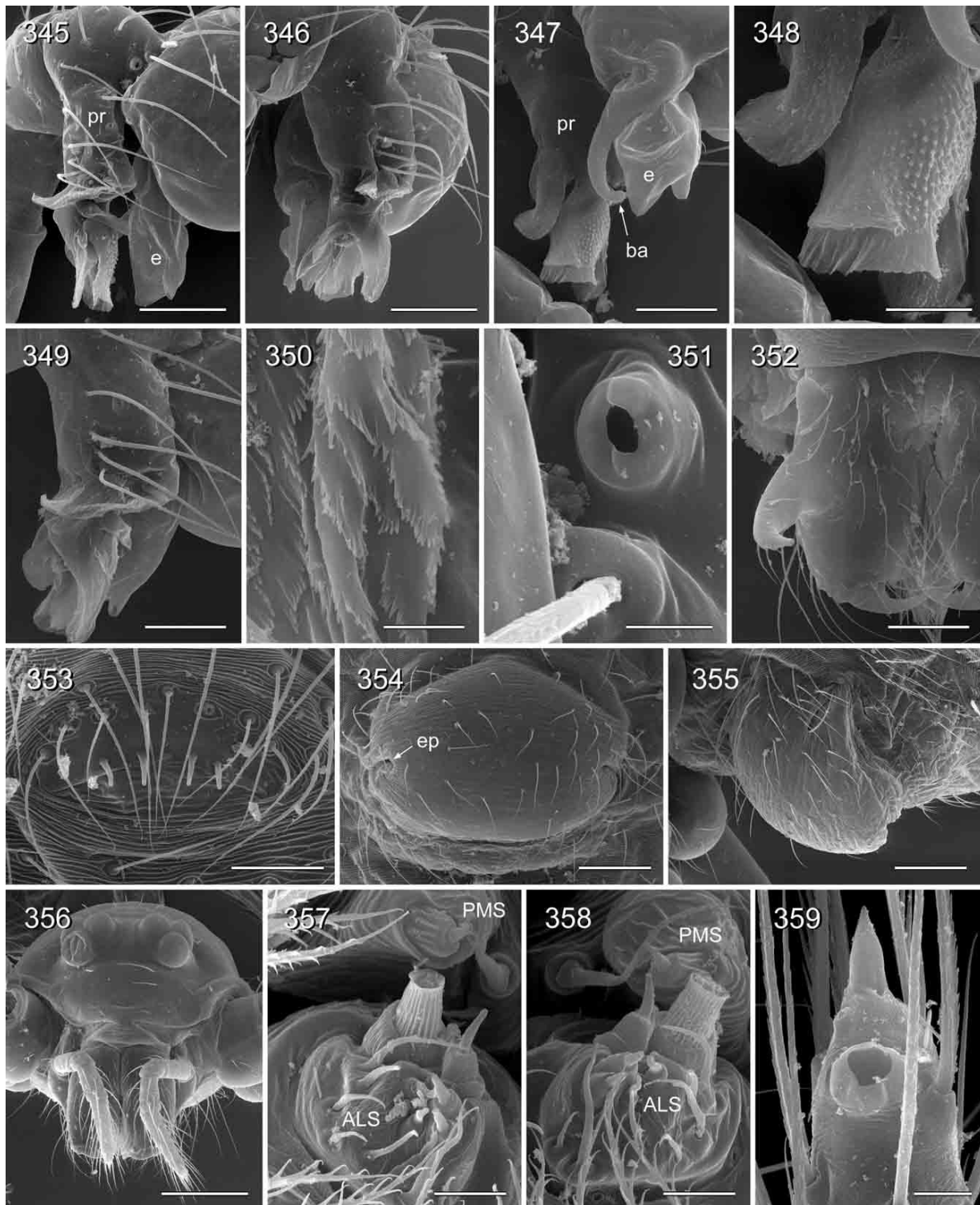
**Figs. 339-344.** *Belisana gedeh*. 339, 340. Left male pedipalp, prolateral (339) and retrolateral (340) views. 341, 342. Male chelicerae, frontal and lateral views. 343, 344. Cleared female genitalia, ventral (343) and dorsal (344) views. Scale lines: 0.2 mm.

*Distribution.* Known from Northern Borneo and mainland Malaysia; specimens from Sumatra are assigned tentatively (Fig. 80).

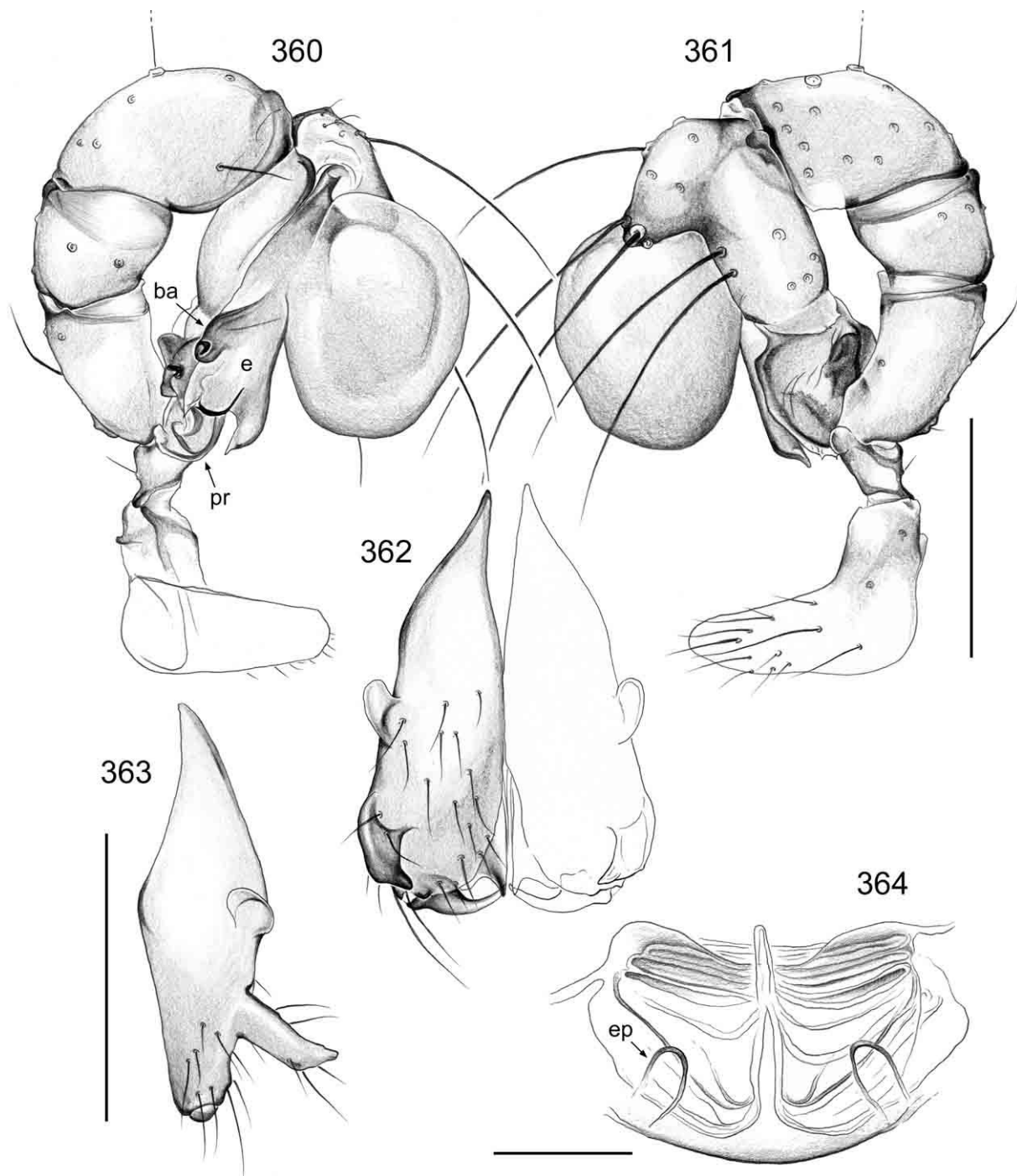
*Material examined.* MALAYSIA: *Sabah*: Sandakan: type above, together with 3♂5♀ (ZMT); *Selangor*: Templer Park [ $\sim 3^{\circ}19'N$ ,  $101^{\circ}36'E$ ], Hutan Simpan, Nov. 20, 1979 (P. T. Lehtinen), 3♂5♀ (ZMT AA 3456); Templer's Park, litter, March 19, 1985 (C. L. & P. R. Deeleman), 1♂4♀ (RMNH).

Assigned tentatively: INDONESIA: *Sumatra*: North Sumatra Prov.: Gunung Leuser, Bohorok [ $\sim 3^{\circ}30'N$ ,  $98^{\circ}12'E$ ], along river, litter on bank, Dec. 30, 1983 (collector not given), 2♂1♀ (RMNH); Gunung Leuser, Ketambe [ $\sim 3^{\circ}45'N$ ,  $97^{\circ}45'E$ ], leaf litter, May-June 1986 (S. Djojodharmo), 1♂ (RMNH).





**Figs. 345-359.** *Belisana gedeh*. 345. Right procurus and bulb, retrolatero-dorsal view. 346. Right procurus and bulb, retrolatero-ventral view. 347. Left procurus and bulbal projections, prolateral (slightly distal) view. 348. Tip of left procurus (cf. Fig. 347). 349. Right procurus, retrolateral view. 350. Detail of membranous flap on procurus. 351. Male palpal tarsal organ. 352. Male chelicera, frontal view. 353. Male gonopore with epiandrous spigots. 354. Epigynum, ventral view. 355. Epigynum, lateral view. 356. Female prosoma, frontal view. 357. Female ALS and PMS. 358. Male ALS and PMS. 359. Tip of female palp with tarsal organ, dorsal view. Scale lines: 7  $\mu$ m (350), 10  $\mu$ m (351, 357-359), 30  $\mu$ m (348), 40  $\mu$ m (353), 70  $\mu$ m (347, 349, 352), 100  $\mu$ m (345, 346, 354, 355), 200  $\mu$ m (356).

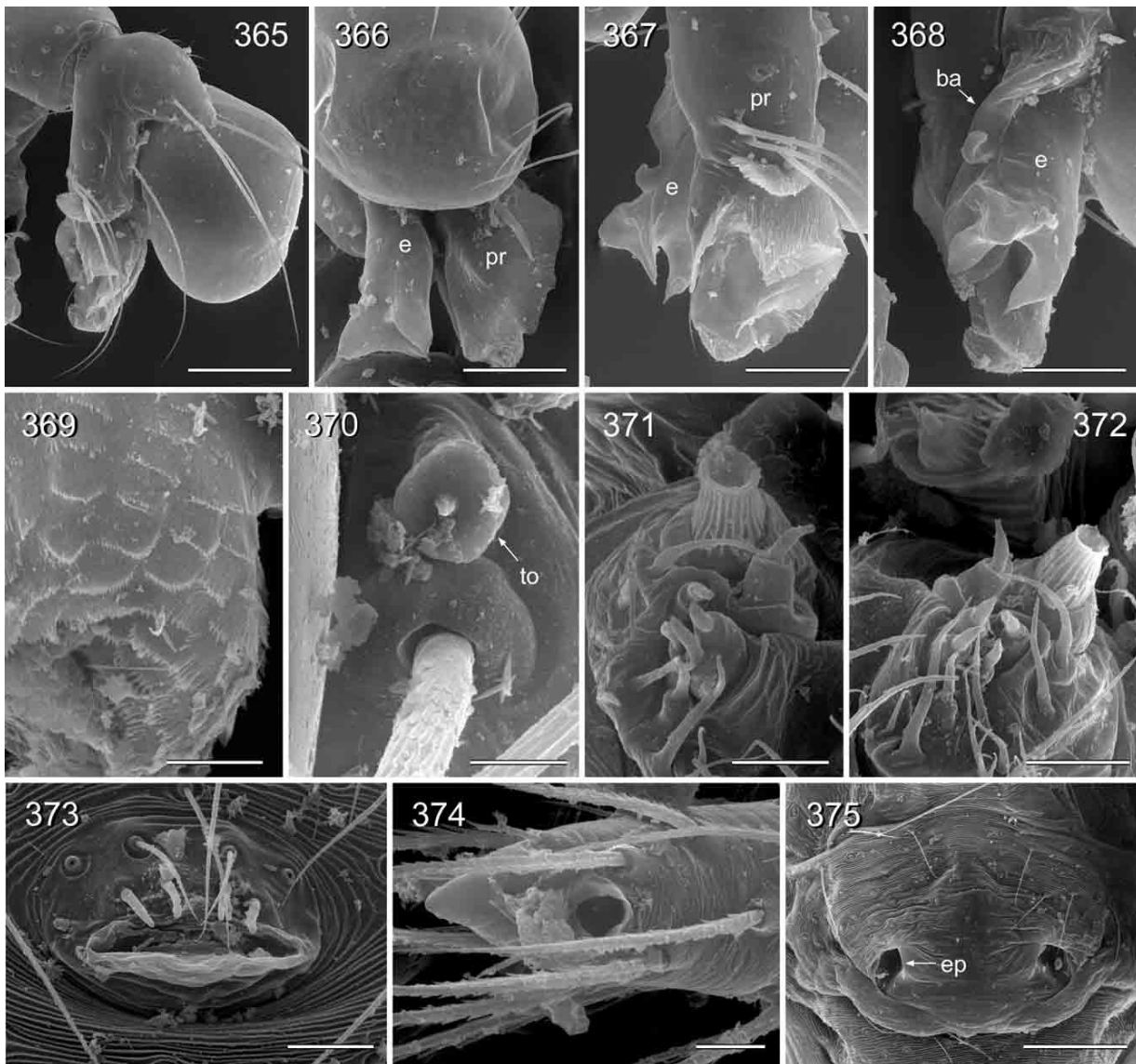


**Figs. 360-364.** *Belisana sandakan*. 360, 361. Left male pedipalp, prolateral (360) and retrolateral (361) views. 362, 363. Male chelicerae, frontal and lateral views. 364. Cleared female genitalia, dorsal view. Scale lines: 0.2 mm (360-363), 0.1 mm (364).

***Belisana leuser*, new species**  
(Figs. 376-394)

*Type.* Male holotype from Ketambe [ $\sim 3^{\circ}45'N$ ,  $97^{\circ}45'E$ ], Gunung Leuser N. P., Aceh, Sumatra; no date and collector, in RMNH.

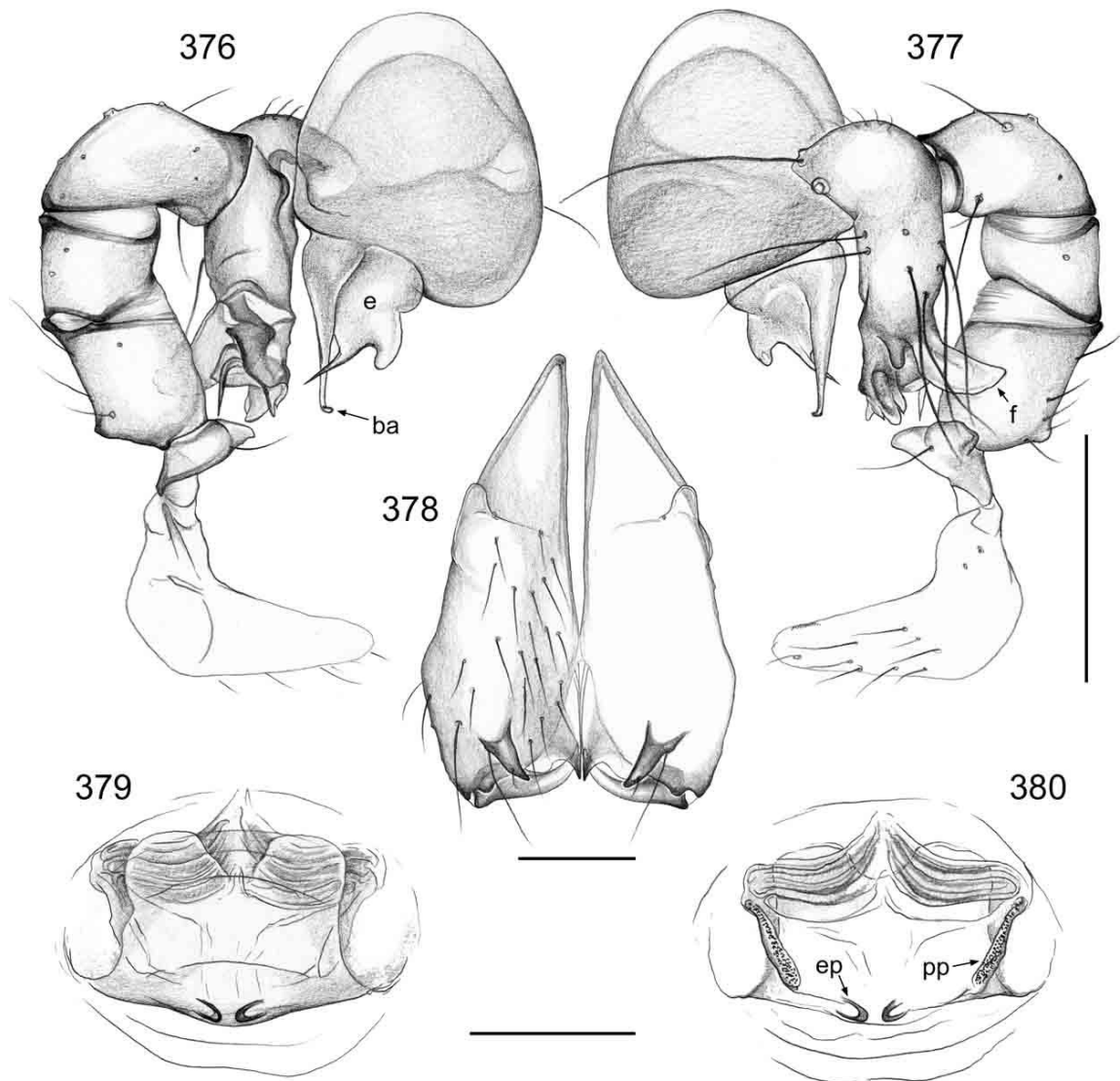
*Etymology.* The species name is a noun in apposition, taken from the type locality.



**Figs. 365-375.** *Belisana sandakan*. 365. Right procurus and bulb, retrolatero-dorsal view. 366. Tip of procurus and bulb, prolatero-dorsal view. 367. Tip of procurus, retrolatero-ventral view. 368. Bulbal projections, prolatero-ventral view. 369. Detail of procurus. 370. Male palpal tarsal organ. 371. Male ALS. 372. Female ALS. 373. Male gonopore with epiandrous spigots. 374. Tip of female palp with tarsal organ, dorsal view. 375. Epigynum, ventral (slightly posterior) view. Scale lines: 7  $\mu$ m (369-371), 10  $\mu$ m (372, 374), 20  $\mu$ m (373), 50  $\mu$ m (368), 60  $\mu$ m (366, 367), 100  $\mu$ m (365, 375).

**Diagnosis.** Medium-sized, long-legged species with elongated and posteriorly elevated opisthosoma; distinguished from similar congeners by the shapes of procurus (Figs. 377, 381) and bulbal apophyses (Figs. 376, 382), and by the position of the cheliceral apophyses (Fig. 378).

**Male (holotype).** Total length 1.6 (1.7 with clypeus), carapace width 0.64. Leg 1: 5.0 + 0.3 + 5.0 + 7.8, tarsus missing, tibia 2: 3.3, tibia 3: 1.8, tibia 4: 2.5; tibia 1 L/d: 89. Habitus similar to *B. kaosok* (cf. Figs. 51, 52). Entire spider pale ochre-yellow. Ocular area barely elevated, not separated from carapace, thoracic furrow absent, carapace very flat; distance PME-PME 160  $\mu$ m; diameter PME 50  $\mu$ m; distance PME-ALE ~20  $\mu$ m. Clypeus unmodified. Sternum as wide as long (0.45). Chelicerae as in Figs. 378 and 385, with pair of simple frontal apophyses, tips unmodified (Fig. 388), 80  $\mu$ m apart. Palps as in Figs. 376 and 377; trochanter with retrolateral and ventral apophyses, femur with small dorsal hump, procurus complex distally, apparently with hinged process prolaterally, with large transparent ventral flap (Figs. 377, 381, 383), bulb with long and slender hooked apophysis and embolus with spine (Figs. 376, 382).



**Figs. 376-380.** *Belisana leuser*. 376, 377. Left male pedipalp, prolateral (376) and retrolateral (377) views. 378. Male chelicerae, frontal view. 379, 380. Cleared female genitalia, ventral (379) and dorsal (380) views. Scale lines: 0.3 mm (376, 377), 0.1 mm (378), 0.2 mm (379, 380).

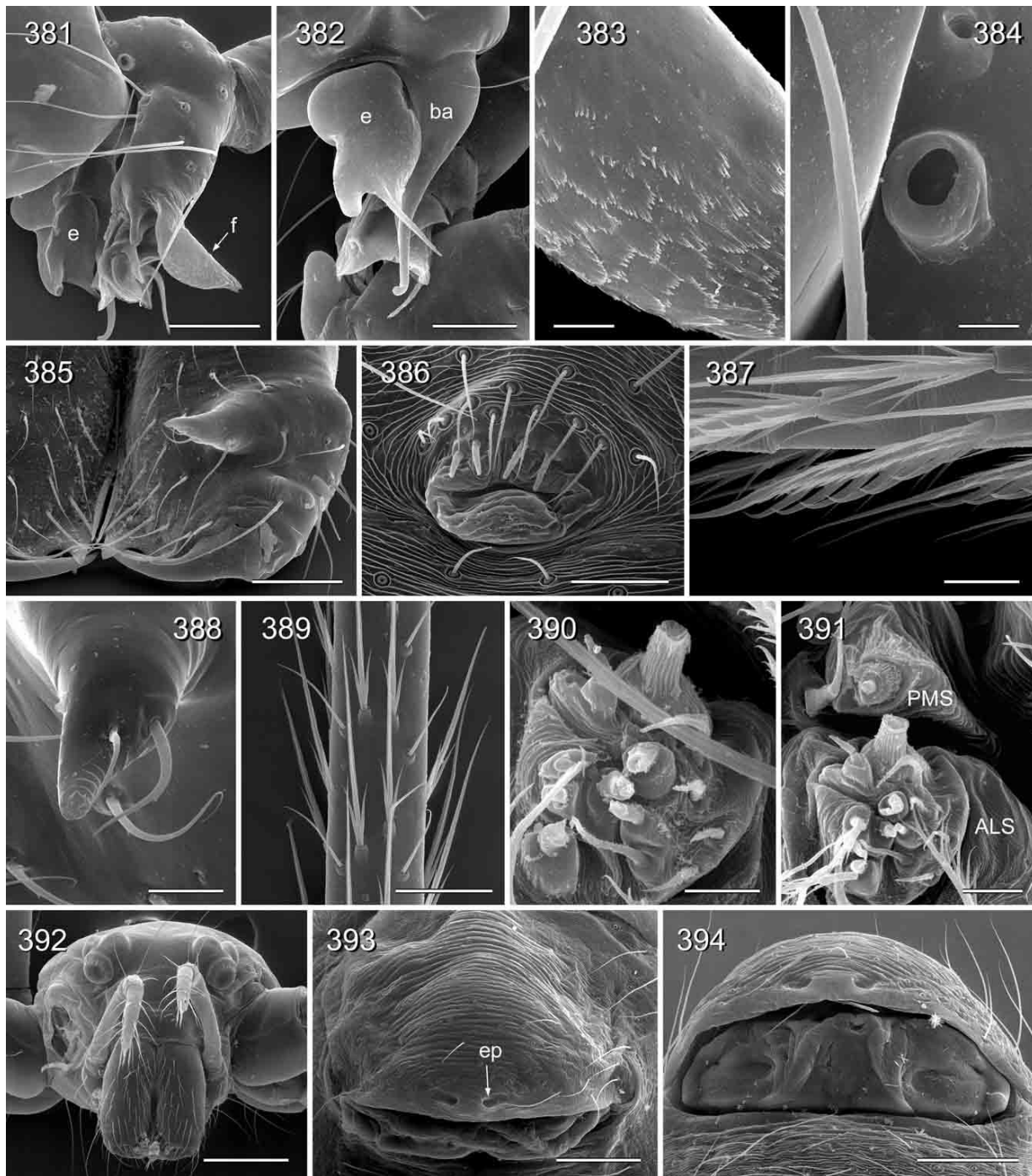
Tarsal organ capsulate (Fig. 384). Retrolateral trichobothrium of tibia 1 at 7%; legs without spines and curved hairs, with vertical hairs on metatarsi (Fig. 389); tarsus 3 with about 11 pseudosegments. Gonopore and spinnerets as in Figs. 386 and 391.

*Variation.* Tibia 1 in 20 other males: 4.2-5.4 (mean 4.79).

*Female.* In general similar to male. Tibia 1 in 20 females: 3.1-3.7 (mean 3.54). Epigynum very simple externally (Fig. 393), with pair of pockets 35  $\mu$ m apart; often with genital plug (Fig. 394); dorsal view as in Fig. 380. ALS as in Fig. 390.

*Distribution.* Known from Sumatra, Malaysia, Southern Thailand, and Kalimantan (Borneo) (Fig. 80).

*Material examined.* INDONESIA: *Sumatra*: Aceh Prov.: Gunung Leuser N.P., Ketambe: type above, together with 32♂>40♀, in RMNH; Ketambe, camp, May 4, 1984 (Suyono), ~30♂30♀ (RMNH); same collection data but Feb. 5, 1985, ~35♂40♀ (RMNH); Ketambe, submontane forest at 1400 m a.s.l., Nov. 28, 1984 (Suyono & Sudiro), 9♂9♀ (RMNH); Ketambe at 1400 m a.s.l., July 17, 1985 (Bugama & Yono), 1♂3♀ (RMNH); West Sumatra Prov.: Mt. Singalang [ $\sim$ 0°08'N, 100°10'E], Anai, 400-520 m a.s.l., from leaves in secondary forest, June 10/22, 1994 (S. Djojosedharmo), >60♂60♀ (RMNH); Rimba Panti Reserve [ $\sim$ 0°22'N, 100°03'E], from leaves in lowland rainfor-



**Figs. 381-394.** *Belisana leuser*. 381. Left procurus and bulb, retrolateral (slightly distal) view. 382. Right embolus and bulbal apophysis, prolateral view. 383. Detail of membranous flap on procurus. 384. Male palpal tarsal organ. 385. Male chelicera, frontal (slightly distal) view. 386. Male gonopore with epiandrous spigots. 387. Comb-hair on male tarsus 4. 388. Male cheliceral apophysis. 389. Hairs on male metatarsus 4. 390. Female ALS. 391. Male ALS and PMS. 392. Female prosoma, frontal view. 393. Epigynum, ventral view. 394. Epigynum, posterior view showing plug. Scale lines: 10  $\mu$ m (383, 384, 387, 388, 390, 391), 40  $\mu$ m (386, 389), 50  $\mu$ m (385), 70  $\mu$ m (382), 100  $\mu$ m (381, 393, 394), 200  $\mu$ m (392).

est, Aug. 3-4, 1982 (P. R. & C. L. Deeleman), 5♂9♀; Jambi Prov.(?): Kerinci National Park [ $\sim$ 2°05'S, 101°23'E?], 800 m a.s.l., from leaves near river, July 20-30, 1988 (S. Djojosedharmo), >200♂200♀ (several vials) (RMNH).

*Kalimantan*: East Kalimantan Prov.: Samarinda, Sanga Sanga [0°30'S, 117°09'E], jungle litter, Oct. 29, 1979 (P. Lehtinen), 1♂ prosoma (ZMT, AA3448). *MALAYSIA*: *Pahang*: Cameron Highlands (4°29'N, 101°27'E), April 14-21, 1990 (V. & B. Roth), 4♂4♀ (CAS). *THAILAND*: *Naratiwat Prov.*: Waeng Distr., Hala Bala W.S., research station (5°47.7'N, 101°50.1'E), 190-200 m a.s.l., Oct. 13-14, 2003 (ATOL Expedition), 5♂4♀ (MACN).

***Belisana bohorok*, new species**

(Figs. 395-398, 403-410)

*Type*. Male holotype from Bohorok [~3°30'N, 98°12'E], North Sumatra Prov., Sumatra, Indonesia; May 30, 1983 (S. Djojosedharmo), in RMNH.

*Etymology*. The species name is a noun in apposition, taken from the type locality.

*Diagnosis*. Medium-sized, long-legged species with cylindrical opisthosoma; distinguished from similar congeners by the shape of the procurus (ventrodiscal rounded sclerite, Fig. 395); from the similar *B. kaharian* by the shorter bulbal apophysis (compare Figs. 395 and 399); from some species also by the position of the male cheliceral apophyses (Fig. 397).

*Male (holotype)*. Total length 1.4 (1.5 with clypeus), carapace width 0.50. Leg 1: 15.45 (3.6 + 0.25 + 3.7 + 6.4 + 1.5), tibia 2: 2.2, tibia 3: 1.3, tibia 4: 2.1; tibia 1 L/d: 70. Habitus similar to *B. tambligan* (cf. Fig. 54). Prosoma and legs pale ochre-yellow, opisthosoma pale ochre-grey. Ocular area barely elevated, thoracic furrow absent; distance PME-PME 125 µm; diameter PME 60 µm; distance PME-ALE ~20 µm. Clypeus unmodified. Sternum about as wide as long (0.38). Chelicerae as in Fig. 397, tips of frontal apophyses 47 µm apart. Palps as in Figs. 395 and 396; trochanter with retrolateral apophysis, femur with dorsal apophysis and small ventral hump, procurus with distinctive flat sclerite with small scales (Figs. 395, 404); bulb with hooked apophysis and membranous embolus (Figs. 395, 404, 405). Tarsal organ capsulate (Fig. 406). Retrolateral trichobothrium of tibia 1 at 8%; legs without spines and curved hairs, vertical hairs seen on metatarsi 1 (probably present on other metatarsi too); tarsus 1 with >15 pseudosegments, fairly distinct distally. Gonopore as in Fig. 407.

*Variation*. Tibia 1 in 9 other males: 3.2-4.3 (mean 3.81). One male without pigment around eyes.

*Female*. In general similar to male; tibia 1 in 24 females: 2.15-3.4 (mean 2.95). Epigynum very simple external-ly (Fig. 409), pockets 10 µm apart; dorsal view as in Fig. 398. Spinnerets as in Fig. 410.

*Distribution*. Known from several localities on Sumatra, mainland Malaysia, and Sarawak (Borneo) (Fig. 80).

*Material examined*. *INDONESIA*: *Sumatra*: Bohorok: type above, together with 3♂8♀ (RMNH); same collection data, 1♂1♀ (RMNH); same locality, April 26, 1983 (S. Djojosedharmo), 6♂18♀ (RMNH); Bohorok, trail 6, Nov. 14, 1983 (S. Djojosedharmo), 2♂7♀ (RMNH). *MALAYSIA*: *Sarawak*: Semengoh Arboretum [1°30'N, 110°15'E], lower track, March 23-April 6, 1985 (C. L. & P. R. Deeleman), 1♂ (RMNH); same locality, beating shrub, April 6, 1985 (C. L. Deeleman), 1♂1♀ (RMNH); Balai Ringin [1°03'N, 110°45'E], 40 km E of Serian, secondary forest, April 7, 1985 (P. R. & C. L. Deeleman), 1♂ (RMNH). *Selangor*: Templers Park nr. Kuala Lumpur [3°19'N, 101°36'E], leaf litter, Dec. 1, 1990 (C. L. & P. R. Deeleman), 1♂ (RMNH).

***Belisana kaharian*, new species**

(Figs. 399-402, 411-416)

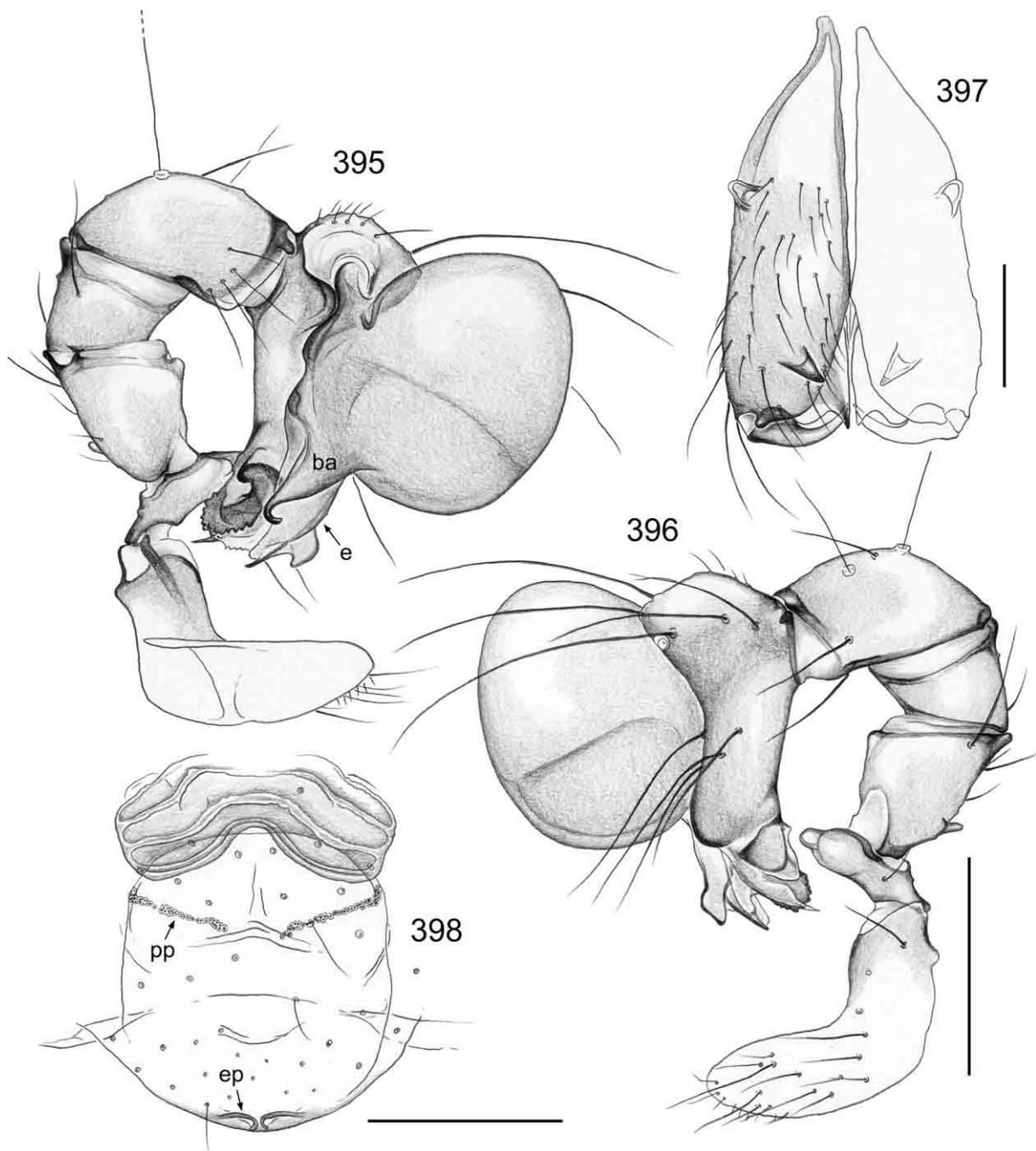
*Type*. Male holotype from Kaharian (2°02'S, 113°40'E), Central Kalimantan (Borneo), Indonesia; in foliage, swampy primary forest, Sept. 2-16, 1985 (S. Djojosedharmo), in RMNH.

*Etymology*. The species name is a noun in apposition, taken from the type locality.

*Diagnosis*. Medium-sized, long-legged species with cylindrical opisthosoma; distinguished from most congeners by the shape of the procurus (ventrodiscal rounded sclerite, Fig. 399); from the similar *B. bohorok* by the longer bulbal apophysis (Fig. 399) and the strong spine distally on the procurus (Fig. 400, 412, 413); from some species also by the position of the male cheliceral apophyses (Fig. 401).

*Male (holotype)*. Total length 1.5 (1.6 with clypeus), carapace width 0.57. Leg 1: 15.65 (3.9 + 0.25 + 3.8 + 6.2 + 1.5), tibia 2: 2.2, tibia 3: 1.2, tibia 4: 2.2; tibia 1 L/d: 66. Habitus similar to *B. tambligan* (cf. Fig. 54). Prosoma and legs pale ochre-yellow, opisthosoma pale ochre-grey. Ocular area barely elevated, thoracic furrow absent; distance PME-PME 135 µm; diameter PME 60 µm; distance PME-ALE ~20 µm. Clypeus unmodified. Sternum about as wide as long (0.40). Chelicerae as in Figs. 401 and 414, tips of frontal apophyses ~50 µm apart (slightly artificially spread in Fig. 401). Palps as in Figs. 399 and 400; trochanter with retrolateral and ventral apophyses (Fig. 412), femur with small dorsal apophysis, without ventral hump, procurus distally with flattened sclerite and strong spine (Figs. 412, 413); bulb large, with hooked apophysis (Fig. 411) and unsclerotized bifid embolus (Figs. 399, 411).





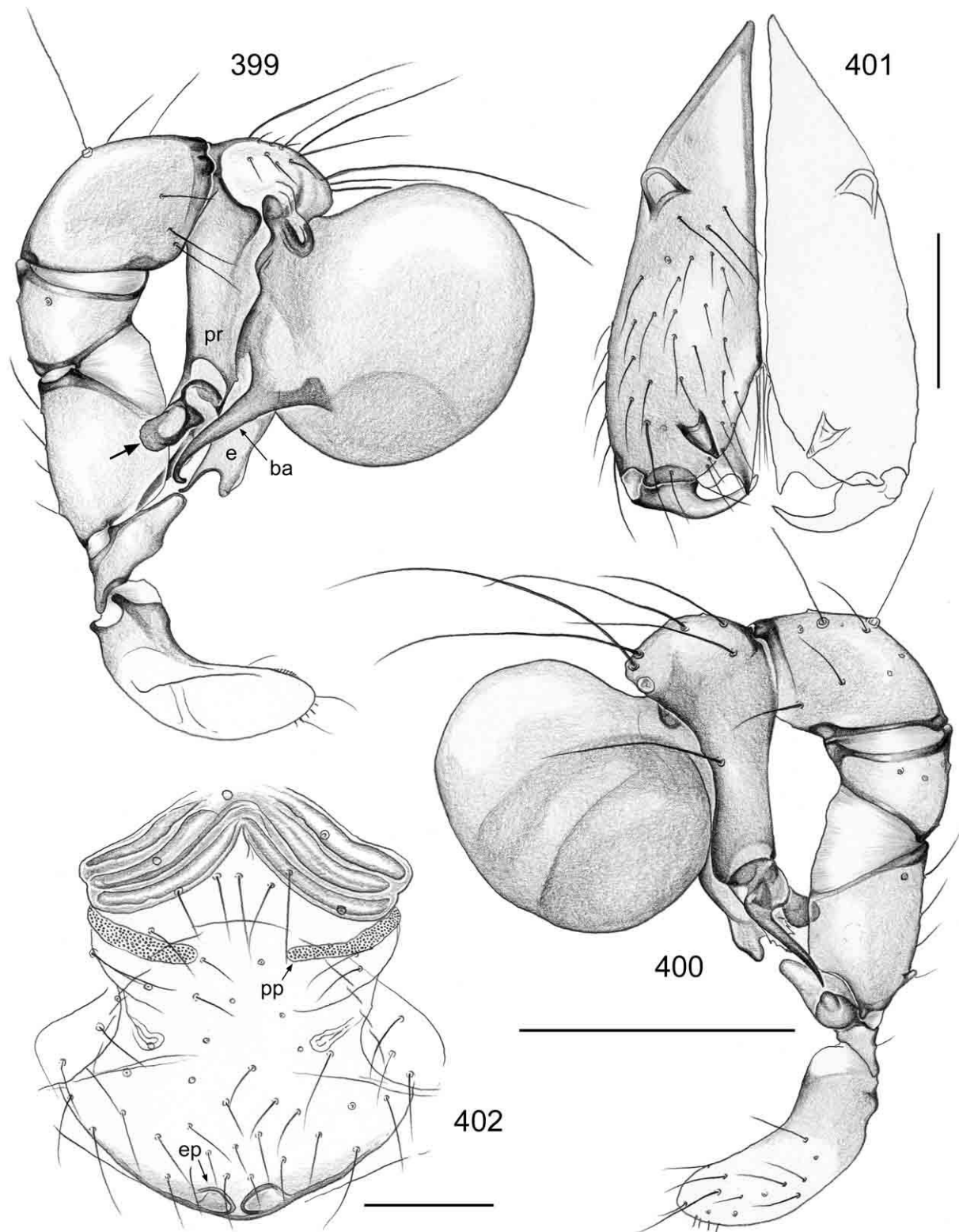
**Figs. 395-398.** *Belisana bohorok*. 395, 396. Left male pedipalp, prolateral (395) and retrolateral (396) views. 397. Male chelicerae, frontal view. 398. Cleared female genitalia, dorsal view. Scale lines: 0.2 mm (395, 396, 398), 0.1 mm (397).

Retrolateral trichobothrium of tibia 1 at 9%; legs without spines and curved hairs, vertical hairs seen on metatarsi 1-3; tarsus 1 with >15 pseudosegments, barely visible in dissecting microscope. Gonopore and spinnerets as in Figs. 415 and 416.

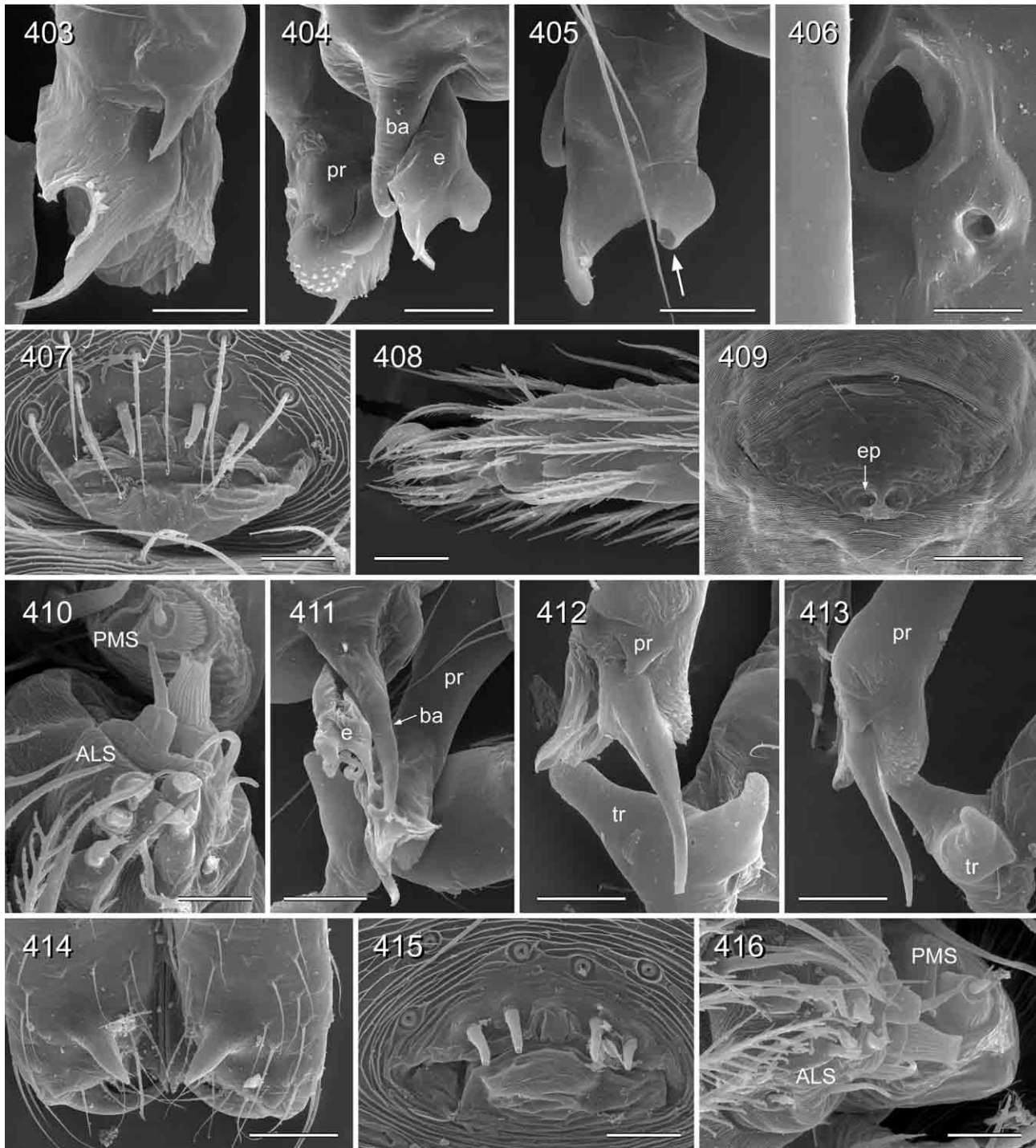
*Variation.* Tibia 1 in 6 other males: 3.4-3.7 (mean 3.53).

*Female.* In general similar to male; tibia 1: 3.3. Epigynum very simple externally, pockets 12  $\mu$ m apart; dorsal view as in Fig. 402.

*Distribution.* Known from two neighboring localities in Kalimantan (Fig. 80).



**Figs. 399-402.** *Belisana kaharian*. 399, 400. Left male pedipalp, prolateral (399) and retrolateral (400) views. 401. Male chelicerae, frontal view. 402. Cleared female genitalia, dorsal view. Scale lines: 0.3 mm (399, 400), 0.1 mm (401, 402).



**Figs. 403-416.** *Belisana bohorok* (403-410) and *B. kaharian* (411-416). 403. Right procurus, retrolateral view. 404. Left procurus and bulbal projections, prolateral view. 405. Embolus, showing opening of sperm duct (arrow). 406. Male palpal tarsal organ. 407. Male gonopore with epiandrous spigots. 408. Female tarsus 4 tip. 409. Epigynum, ventral view. 410. Female ALS and PMS. 411. Right procurus and bulbal projections, prolateral view. 412. Left procurus, retrolatero-dorsal view. 413. Left procurus and palpal trochanter, retrolateral view. 414. Male chelicerae frontal view. 415. Male gonopore with epiandrous spigots. 416. Male ALS and PMS. Scale lines: 10  $\mu\text{m}$  (406, 410, 416), 20  $\mu\text{m}$  (407, 408, 415), 40  $\mu\text{m}$  (403, 405), 50  $\mu\text{m}$  (412, 414), 60  $\mu\text{m}$  (404, 413), 70  $\mu\text{m}$  (411), 100  $\mu\text{m}$  (409).

*Material examined.* INDONESIA: Kalimantan: Kaharian: type above, together with 6♂3♀ (RMNH); 40 km NW of Pelang-Karaya [ $\sim 2^{\circ}00'S$ ,  $113^{\circ}45'E$ ], secondary forest, from leaves, Sept. 1985 (S. Djojosedharmo), 1♂ (RMNH).

***Belisana sabah*, new species**

(Figs. 1, 21, 22, 62, 417-421)

*Type.* Male holotype from Kinabalu National Park, headquarters, ridge [ $\sim 6^{\circ}09'N$ ,  $116^{\circ}39'E$ ], Sabah (Borneo), Malaysia; 1550 m a.s.l., April 5, 1998 (C. L. Deeleman & P. Zborowski), "FOTO 292 25-26", in RMNH.

*Etymology.* The species name is a noun in apposition, taken from the type locality.

*Diagnosis.* Relatively large, long-legged species with elongated and posteriorly slightly elevated opisthosoma; distinguished from similar congeners by the shape of the procurus (large hinged process, Fig. 417); from the similar *B. kinabalu* (cf. Fig. 422) by the widely spread male cheliceral apophyses (Fig. 419) and the internal female genitalia (Fig. 421).

*Male (holotype).* Total length 2.1 (2.25 with clypeus), carapace width 0.83. Leg 1: 16.7 (4.0 + 0.35 + 4.15 + 6.7 + 1.5), tibia 2: 2.9, tibia 3: 1.75, tibia 4: 2.1; tibia 1 L/d: 49. Habitus as in Figs. 1, 21 and 22. Prosoma and legs mostly pale ochre-yellow, carapace laterally slightly darker, sternum whitish, opisthosoma pale ochre-grey. Ocular area barely elevated, thoracic furrow absent; distance PME-PME 205  $\mu\text{m}$ ; diameter PME 70  $\mu\text{m}$ ; distance PME-ALE  $\sim 20$   $\mu\text{m}$ . Clypeus unmodified. Sternum slightly wider than long (0.57/0.53). Chelicerae as in Fig. 419, tips of frontal apophyses 535  $\mu\text{m}$  apart. Palps as in Figs. 417 and 418; trochanter with short sclerotized retrolateral apophysis, femur with distinct dorsal apophysis, procurus wide and large, with distinctive prolateral hinged process with strong curved sclerite (Fig. 417); bulb with strong hooked apophysis and mostly membranous embolus. Retrolateral trichobothrium of tibia 1 at 13%; legs without spines and curved hairs, with vertical hairs in higher density on all metatarsi; tarsus 1 with about 15-20 pseudosegments, distally quite distinct.

*Female.* In general similar to male, including slightly darker lateral bands on carapace; tibia 1: 3.4. Epigynum very simple externally, roughly rectangular (Fig. 62), pockets 455  $\mu\text{m}$  apart (Fig. 420); dorsal view as in Fig. 421. ALS apparently with only two spigots each (dissecting microscope).

*Distribution.* Known from type locality only (Fig. 80).

*Material examined.* MALAYSIA: *Sabah*: Kinabalu N. P.: type above, together with 1 ♀ (RMNH).

***Belisana kinabalu*, new species**

(Figs. 422-426, 437-443)

*Type.* Male holotype from Kinabalu National Park, headquarters [ $\sim 6^{\circ}09'N$ ,  $116^{\circ}39'E$ ], Sabah (Borneo), Malaysia; from the underside of leaves, 1550 m a.s.l., July 21-26, 1980 (P. R. & C. L. Deeleman), in RMNH.

*Etymology.* The species name is a noun in apposition, taken from the type locality.

*Diagnosis.* Relatively large, long-legged species with elongated and posteriorly slightly elevated opisthosoma; distinguished from similar congeners by the shape of the procurus (large hinged process, Fig. 422); from the similar *B. sabah* (cf. Fig. 417) by the male cheliceral apophyses (Fig. 424) and the internal female genitalia (Fig. 426).

*Male (holotype).* Total length 1.7 (1.8 with clypeus), carapace width 0.67. Leg 1: 16.45 (3.9 + 0.25 + 4.0 + 6.8 + 1.5), tibia 2: 2.6, tibia 3: 1.7, tibia 4: 2.3; tibia 1 L/d: 65. Habitus similar to *B. tambligan* (cf. Fig. 54). Prosoma and legs pale ochre-yellow, opisthosoma pale ochre-grey. Ocular area barely elevated, thoracic furrow absent; distance PME-PME 135  $\mu\text{m}$ ; diameter PME 70  $\mu\text{m}$ ; distance PME-ALE  $\sim 20$   $\mu\text{m}$ . Clypeus slightly projecting medially (Fig. 437). Sternum about as wide as long (0.48). Chelicerae as in Figs. 424 and 425, tips of apophyses 145  $\mu\text{m}$  apart. Palps as in Figs. 422 and 423; trochanter with rounded retrolateral apophysis, femur with indistinct dorsal hump, procurus very wide, with (glandular?) pores (Fig. 441), distinctive distal sclerite dorsally (Fig. 423), and hinged sclerite prolatero-ventrally (Figs. 422, 440), bulb with long hooked sclerite and embolus bifid with pointed and rounded branches. Retrolateral trichobothrium of tibia 1 at 11%; legs without spines, curved hairs, and vertical hairs; pseudosegments very indistinct, only about 5 visible in dissecting microscope on tarsus 1. Gonopore and spinnerets as in Figs. 438 and 439.

*Variation.* Tibia 1 in 11 other males: 3.7-4.2 (mean 3.97). Two males with darker spots dorsally on opisthosoma.

*Female.* In general similar to male; tibia 1 in 8 females: 3.1-3.8 (mean 3.33). Epigynum a simple whitish oval protruding area (Fig. 443); pockets 60  $\mu\text{m}$  apart; dorsal view as in Fig. 426.

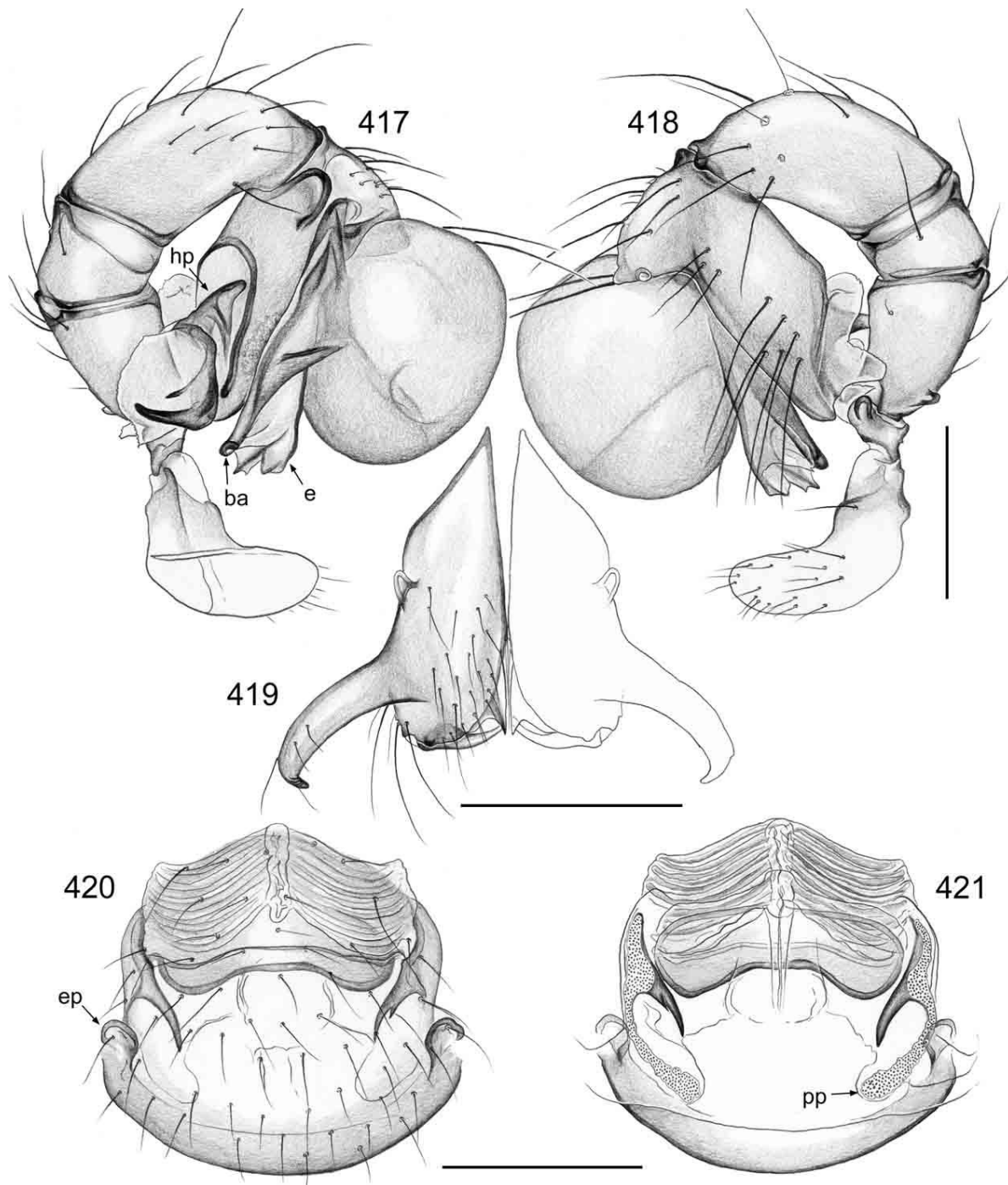
*Distribution.* Known from type locality only (Fig. 80).

*Material examined.* MALAYSIA: *Sabah*: Kinabalu N. P.: type above, together with 13 ♂ 10 ♀; same collection data but June 27, 1979, 1 ♂ (RMNH); same collection data but June 29, 1979, 1 ♂ 2 ♀ (AMNH).

***Belisana floreni*, new species**

(Figs. 17, 18, 61, 427-431)

*Type.* Male holotype from Crocker Range ( $5^{\circ}24'N$ ,  $116^{\circ}05'E$ ), Sabah (Borneo), Malaysia; 50 year old isolated secondary forest, fogging canopy (*Melanopsis*, Euphorbiaceae), Feb. 20, 2001 (A. Floren), in RMNH.

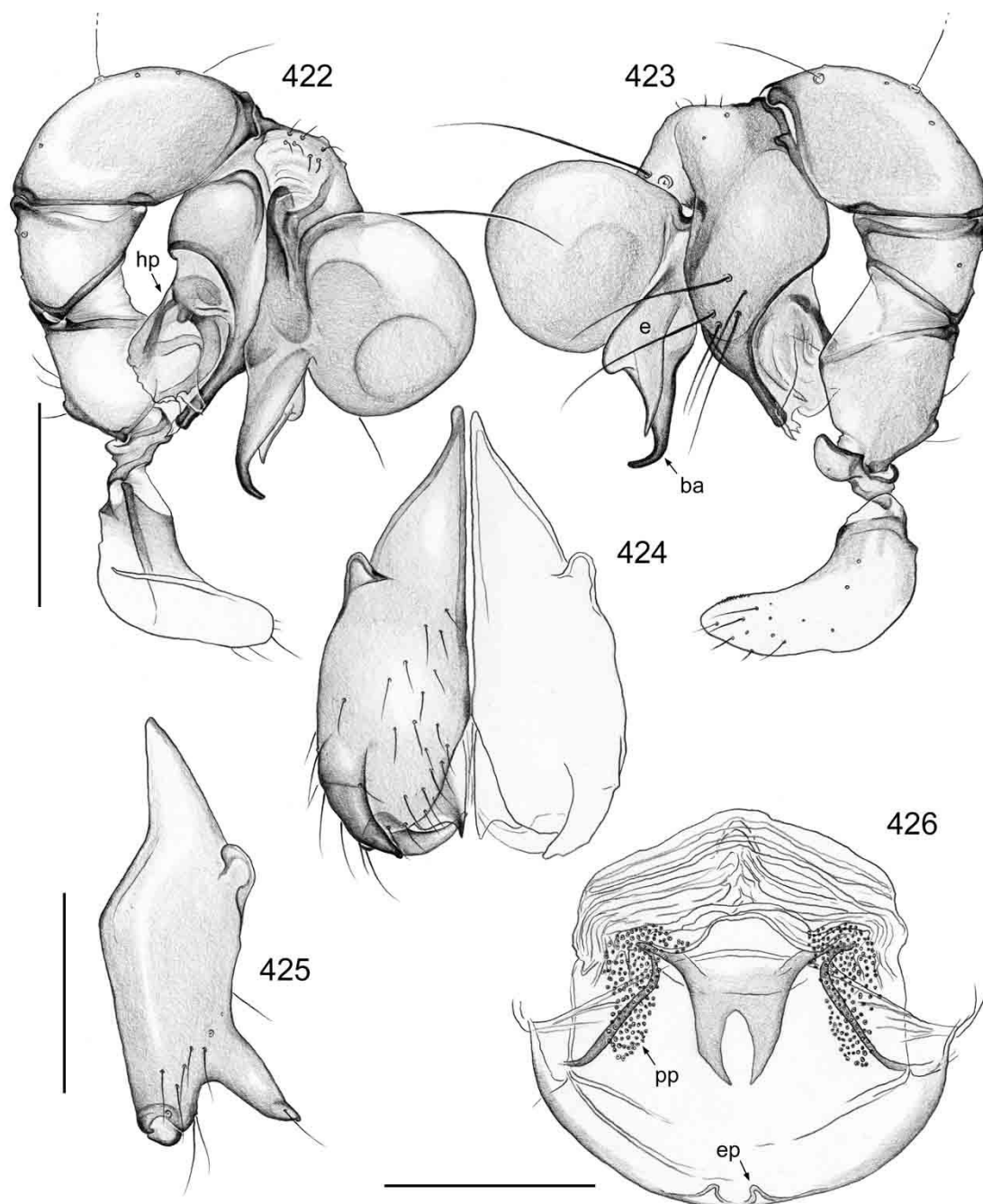


**Figs. 417-421.** *Belisana sabah*. 417, 418. Left male pedipalp, prolateral (417) and retrolateral (418) views. 419. Male chelicerae, frontal view. 420, 421. Cleared female genitalia, ventral (420) and dorsal (421) views. Scale lines: 0.3 mm.

*Etymology.* Named for the collector, Andreas Floren.

*Diagnosis.* Medium-sized, long-legged species with oval opisthosoma; easily distinguished from congeners by the male genital bulb (shapes of projections, elongation of bulb, Fig. 427), and by the shape of the procurus (dorsal protrusion, Fig. 428); from many species also by the widely spread male cheliceral apophyses (Fig. 429).

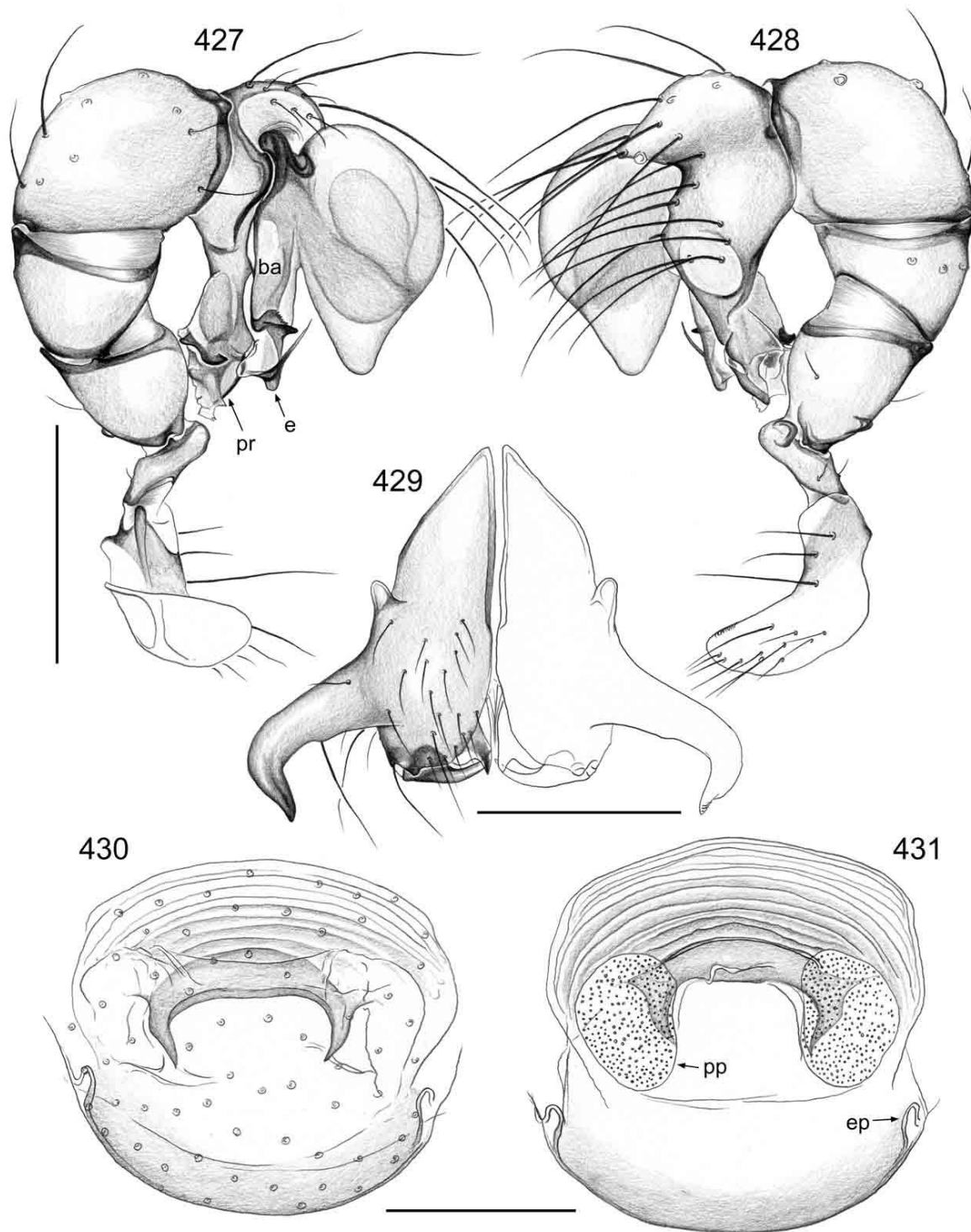
*Male (holotype).* Total length 1.4 (1.5 with clypeus), carapace width 0.57. Leg 1: 2.6 + 0.25 + 2.7 + 3.9, tarsus missing, tibiae 2 and 4 missing, tibia 3: 1.0, tibia 1 L/d: 51. Habitus as in Figs. 17 and 18. Prosoma and legs ochre-



**Figs. 422-426.** *Belisana kinabalu*. 422, 423. Left male pedipalp, prolateral (422) and retrolateral (423) views. 424, 425. Male chelicerae, frontal and lateral views. 426. Cleared female genitalia, dorsal view. Scale lines: 0.3 mm (422, 423, 426), 0.2 mm (424, 425).

yellow, carapace laterally slightly darker, sternum whitish, opisthosoma monochromous pale grey. Ocular area barely elevated, thoracic furrow absent; distance PME-PME 135  $\mu\text{m}$ ; diameter PME 70  $\mu\text{m}$ ; distance PME-ALE  $\sim$ 20  $\mu\text{m}$ . Clypeus unmodified. Sternum about as wide as long (0.42). Chelicerae as in Fig. 429, apophyses in lateral view perpendicular to paturon, tips 410  $\mu\text{m}$  apart. Palps as in Figs. 427 and 428; trochanter with short rounded retrolateral apophysis, femur with small dorsal apophysis, procurus as in Fig. 428, distinctively projecting dorsally, complex dis-





**Figs. 427-431.** *Belisana floreni*. 427, 428. Left male pedipalp, prolateral (427) and retrolateral (428) views. 429. Male chelicerae, frontal view. 430. Cleared female genitalia, ventral (430) and dorsal (431) views. Scale lines: 0.3 mm (427, 428), 0.2 mm (429-431).

tally; bulb with cone-shaped prolongation, distinctive flat serrated sclerite on bulbal apophysis (Fig. 427), embolus with long spine curved in prolateral direction. Retrolateral trichobothrium of tibia 1 at 12%; legs without spines, curved hairs, and vertical hairs.

*Variation.* Tibia 1 in other male: 2.5 (missing in others).

*Female* (Poring Hot Springs). In general similar to male. Epigynum very simple externally (Fig. 61), pockets 370  $\mu\text{m}$  apart (Fig. 430); dorsal view as in Fig. 431.

*Note.* The assignment of the females to the males is tentative. At least two further (undescribed) similar species with widely spaced male cheliceral apophyses and female epigynal pockets occur at the type locality (in RMNH).

*Distribution.* Known from three neighboring localities in Sabah, Northern Borneo (Fig. 80).

*Material examined.* MALAYSIA: *Sabah*: Crocker Range at 5°24'N, 116°05'E, type above, together with 2♀ (possibly not conspecific) (RMNH); Crocker Range at 5°26'N, 116°08'E, 20 year old isolated secondary forest, fogging canopy (*Melanopsis*, Euphorbiaceae), Feb. 18, 2001 (A. Floren), 1♂1♀ (RMNH); Mt. Kinabalu National Park, Poring Hot Springs (6°02'N, 116°50'E), primary forest, 500-700 m a.s.l., fogging *Aglaia* sp. (Meliaceae), March 30, 1998 (A. Floren), 1♂ (RMNH); same data but March 28, 1998, 1♂2♀ 2 juveniles, females probably conspecific (RMNH).

#### ***Belisana sepaku*, new species**

(Figs. 432-436, 444-448)

*Type.* Male holotype from Sepaku [0°55'S, 116°46'E], 40 km NNW of Balikpapan, Kalimantan (Borneo), Indonesia; degraded rain forest, Aug. 5, 1980 (P. R. & C. L. Deeleman), in RMNH.

*Etymology.* The species name is a noun in apposition, taken from the type locality.

*Diagnosis.* Medium-sized, long-legged species with elongated and posteriorly slightly elevated opisthosoma; distinguished from similar congeners by the shapes of procurus, bulbal projections, and cheliceral apophyses (Figs. 432-434).

*Male (holotype).* Total length 1.6 (1.7 with clypeus), carapace width 0.60. Leg 1: 16.9 (4.0 + 0.3 + 4.1 + 7.0 + 1.5), tibia 2: 2.5, tibia 3: 1.4, tibia 4: 2.3; tibia 1 L/d: 62. Habitus similar to *B. tambligan* (cf. Fig. 54). Prosoma and legs ochre-yellow, sternum whitish, opisthosoma pale ochre-grey. Ocular area barely elevated, thoracic furrow absent; distance PME-PME 135  $\mu\text{m}$ ; diameter PME 70  $\mu\text{m}$ ; distance PME-ALE ~20  $\mu\text{m}$ . Clypeus unmodified. Sternum about as wide as long (0.44). Chelicerae as in Fig. 434, tips of frontal apophyses 128  $\mu\text{m}$  apart. Palps as in Figs. 432 and 433; trochanter with wide but short, weakly sclerotized retrolateral apophysis, femur with small dorsal apophysis, procurus with (glandular?) pores (Fig. 444), membranous flap and further distinctive distal elements (Fig. 445); bulb with hooked apophysis and distinctive embolus. Retrolateral trichobothrium of tibia 1 at 10%; legs without spines and curved hairs, with vertical hairs seen on metatarsi 4 only (most hairs missing); tarsus 1 with >15 pseudosegments, barely visible in dissecting microscope. ALS as in Fig. 446.

*Variation.* Tibia 1 in 7 other males: 4.0-4.4 (mean: 4.23).

*Female.* In general similar to male; tibia 1 in 13 females: 3.0-3.7 (mean 3.42). Epigynum very simple externally (Fig. 447), pockets at the ends of long transversal grooves (Fig. 435), 70  $\mu\text{m}$  apart; dorsal view as in Fig. 436.

*Distribution.* Known from two localities in SE Kalimantan, Borneo (Fig. 80).

*Material examined.* INDONESIA: *Kalimantan*: Sepaku: type above, together with 9♂14♀ (RMNH); same collection data but Aug. 3, 1980, 1♂1♀ together on one leaf (RMNH); Rian Kanan [Riam Kanan: 3°24'S, 114°54'E], degraded primary forest, from leaf, July 31, 1980 (P. R. & C. L. Deeleman), 2♂3♀ (RMNH).

#### ***Belisana davao*, new species**

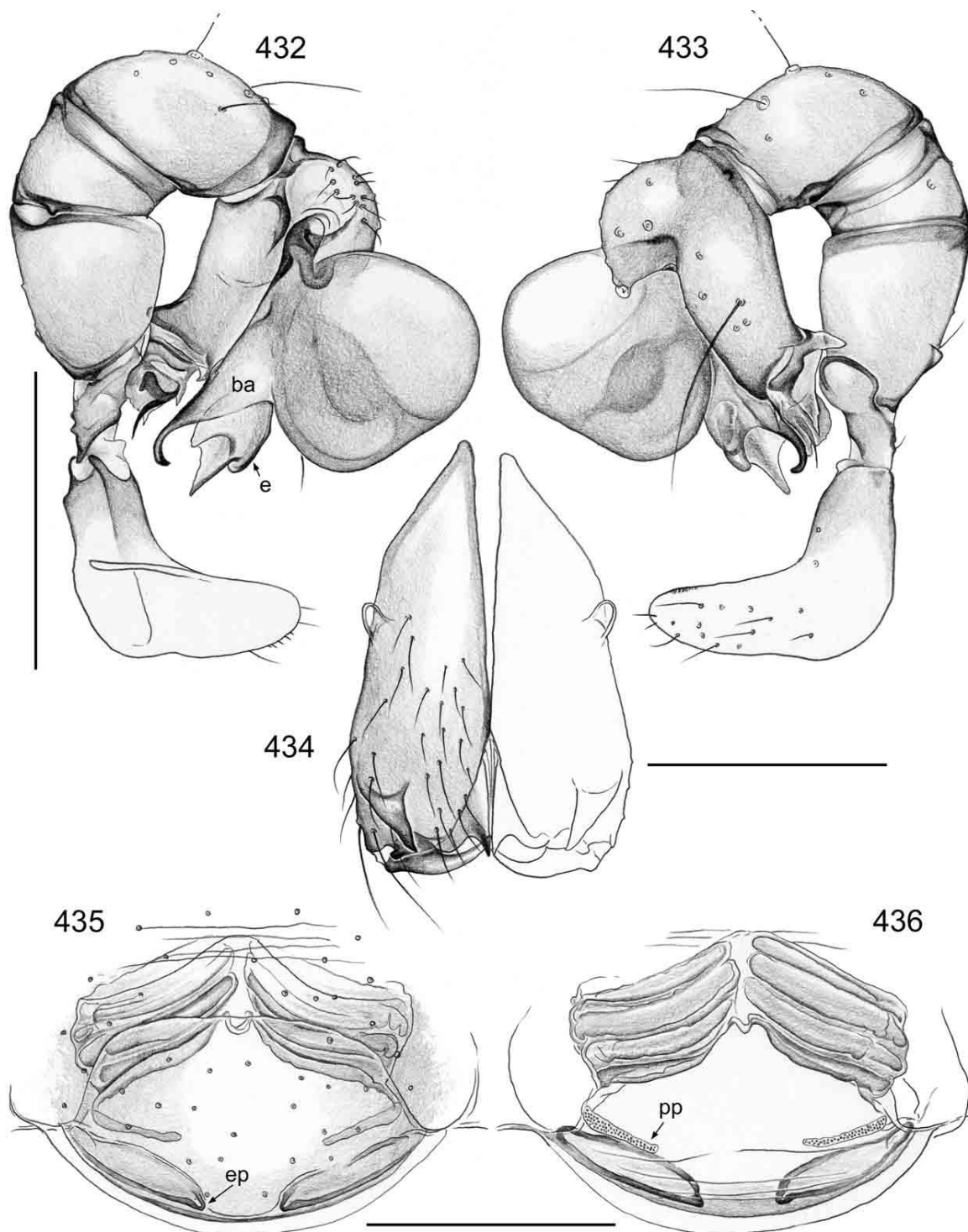
(Figs. 27, 28, 449-462)

*Type.* Male holotype from Eagle Reserve [on Mt. Apo], Davao [~6°59'N, 125°16'E], Mindanao, Philippines; 800 m a.s.l., secondary forest, April 24 & 26, 1982 (C. L. & P. R. Deeleman), in RMNH.

*Etymology.* The species name is a noun in apposition, taken from the type locality.

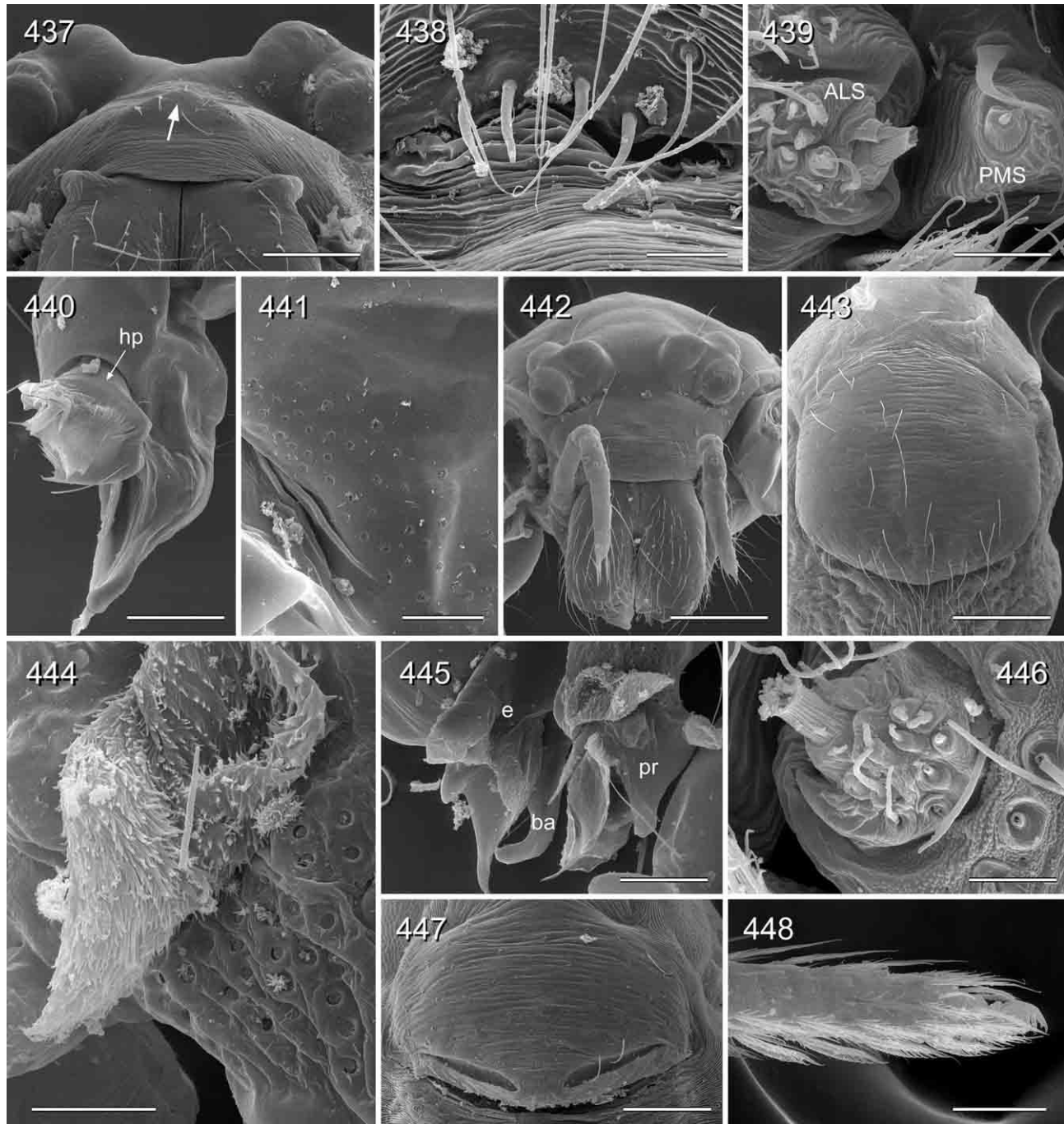
*Diagnosis.* Tiny, short-legged species with globular opisthosoma; easily distinguished from most congeners (except *B. airai*) by the dark pattern on the carapace (Fig. 27) and by the transversal row of thickened hairs on the male clypeus. Distinguished from *B. airai* by the closely spaced male cheliceral apophyses (Fig. 451) and the pockets on the epigynum closely together on a scape-like projection (Figs. 452, 457).

*Male (holotype).* Total length 1.15 (1.35 with clypeus), carapace width 0.56. Leg 1: 5.0 (1.33 + 0.23 + 1.27 + 1.57 + 0.60), tibia 2: 0.9, tibia 3: 0.7, tibia 4: 1.2; tibia 1 L/d: 18. Habitus as in Figs. 27 and 28. Carapace ochre-yellow with dark brown pattern, sternum brown with light speckles. Legs pale ochre-yellow, without rings. Opisthosoma grey with indistinct darker marks. Ocular area slightly elevated, thoracic furrow absent; distance PME-PME 140  $\mu\text{m}$ ; diameter PME 60  $\mu\text{m}$ ; distance PME-ALE ~20  $\mu\text{m}$ . Clypeus projecting with several thickened hairs in a transversal row at rim. Sternum wider than long (0.42/0.34). Chelicerae as in Fig. 451, with pair of small apophyses, tips unmodified, 30  $\mu\text{m}$  apart. Palps as in Figs. 449 and 450; trochanter with simple retrolateral apophysis; procurus rather simple, with



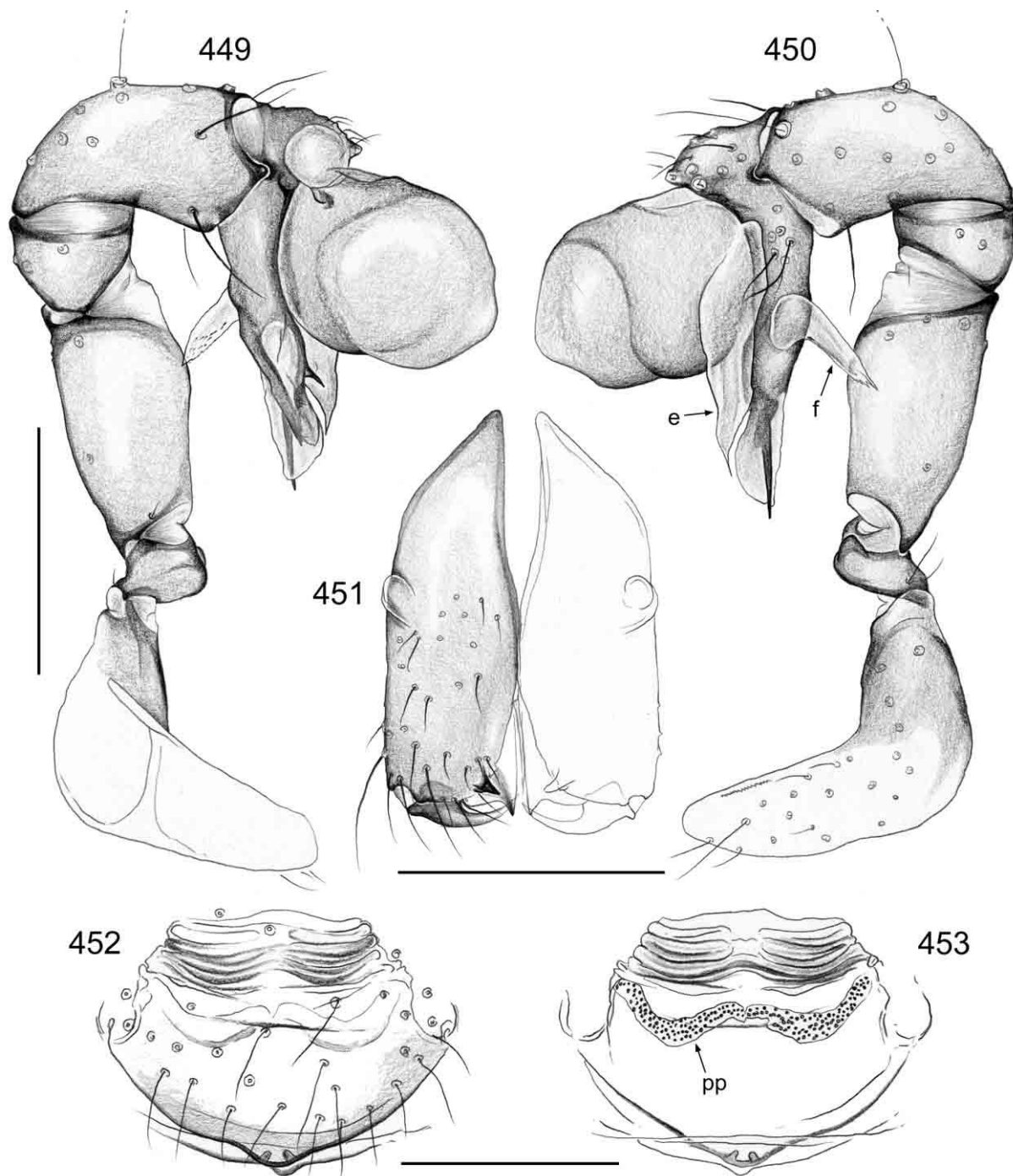
**Figs. 432-436.** *Belisana sepaku*. 432, 433. Left male pedipalp, prolateral (432) and retrolateral (433) views. 434. Male chelicerae, frontal view. 435. Cleared female genitalia, ventral (435) and dorsal (436) views. Scale lines: 0.3 mm (432, 433), 0.2 mm (434-436).

transparent flap ventrally; bulb with single projection (presumably the embolus). Retrolateral trichobothrium of tibia 1 at 14%; legs apparently without spines, curved hairs, and vertical hairs (most hairs missing). Tarsus with ~10 pseudosegments, barely visible in dissecting microscope.



**Figs. 437-448.** *Belisana kinabalu* (437-443) and *B. sepaku* (444-448). 437. Male clypeus with median projection (arrow), slightly ventral view. 438. Male gonopore with epiandrous spigots. 439. Male ALS and PMS. 440. Left procurus, prolateral (slightly distal) view. 441. Pores on male procurus (cf. Fig. 440). 442. Female prosoma, frontal view. 443. Epigynum, ventral view. 444. Membranous flap and pores on procurus. 445. Tip of left procurus and bulbal projections, retrolateral view. 446. Male ALS. 447. Epigynum, ventral view. 448. Female tarsus 4 tip. Scale lines: 10  $\mu$ m (446), 20  $\mu$ m (438, 439, 441, 444), 40  $\mu$ m (448), 60  $\mu$ m (445), 100  $\mu$ m (437, 440, 447), 200  $\mu$ m (442, 443).

*Variation.* The males from Borneo have palps and chelicerae indistinguishable in shape from those of the type, but several differences exist: the males from Borneo are smaller (carapace width: 0.48) but have longer legs (tibia 1: 1.67, 1.70); their clypeus seems to be unmodified, and palps and chelicerae are slightly smaller (distance between tips of cheliceral apophyses: 30  $\mu$ m). These specimens are assigned tentatively.

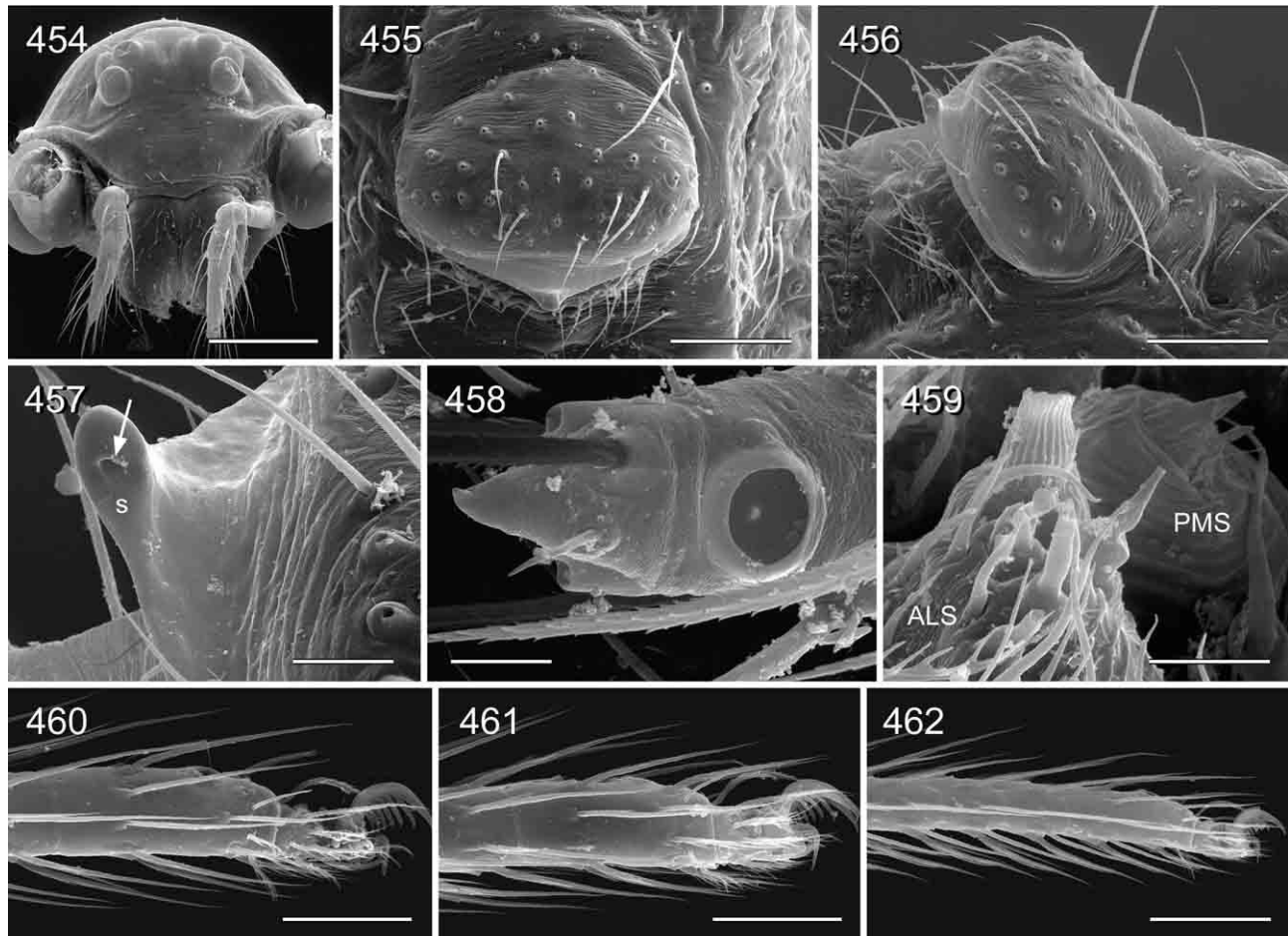


**Figs. 449-453.** *Belisana davao*. 449, 450. Left male pedipalp, prolateral (449) and retrolateral (450) views. 451. Male chelicerae, frontal view. 452, 453. Cleared female genitalia, ventral (452) and dorsal (453) views. Scale lines: 0.2 mm.

*Female.* In general very similar to male, but clypeus unmodified. Tibia 1 in female from Philippines: 1.10; in 4 females from Borneo: 1.53-1.60. Epigynum simple, with short scape-like projection posteriorly provided with pair of pockets 15  $\mu$ m apart (Figs. 455-457); dorsal view as in Fig. 453. Palpal tarsal organ and spinnerets as in Figs. 458 and 459.

*Distribution.* Known from Mindanao and Sabah (Fig. 80).

*Material examined.* PHILIPPINES: *Mindanao*: Davao, Eagle Reserve: type above, together with 1♀.



**Figs. 454-462.** *Belisana davao*. 454. Female prosoma, frontal view. 455. Epigynum, ventral view. 456. Epigynum, lateral (slightly ventral) view. 457. Scape on epigynum with pocket (arrow). 458. Tip of female palp with tarsal organ, dorsal view. 459. Female ALS and PMS. 460. Female tarsus 1 tip. 461. Female tarsus 3 tip. 462. Female tarsus 4 tip. Scale lines: 10  $\mu$ m (458, 459), 20  $\mu$ m (457), 40  $\mu$ m (460, 461), 60  $\mu$ m (462), 100  $\mu$ m (455, 456), 200  $\mu$ m (454).

Assigned tentatively: MALAYSIA: *Sabah*: Tawau district, Bal Estate, Tiger Hill [4°25'N, 117°49'E], jungle litter, Nov. 2, 1979 (P. Lehtinen), 2♂5♀ (ZMT, AA3463).

***Belisana airai*, new species**  
(Figs. 25, 26, 64, 463-480)

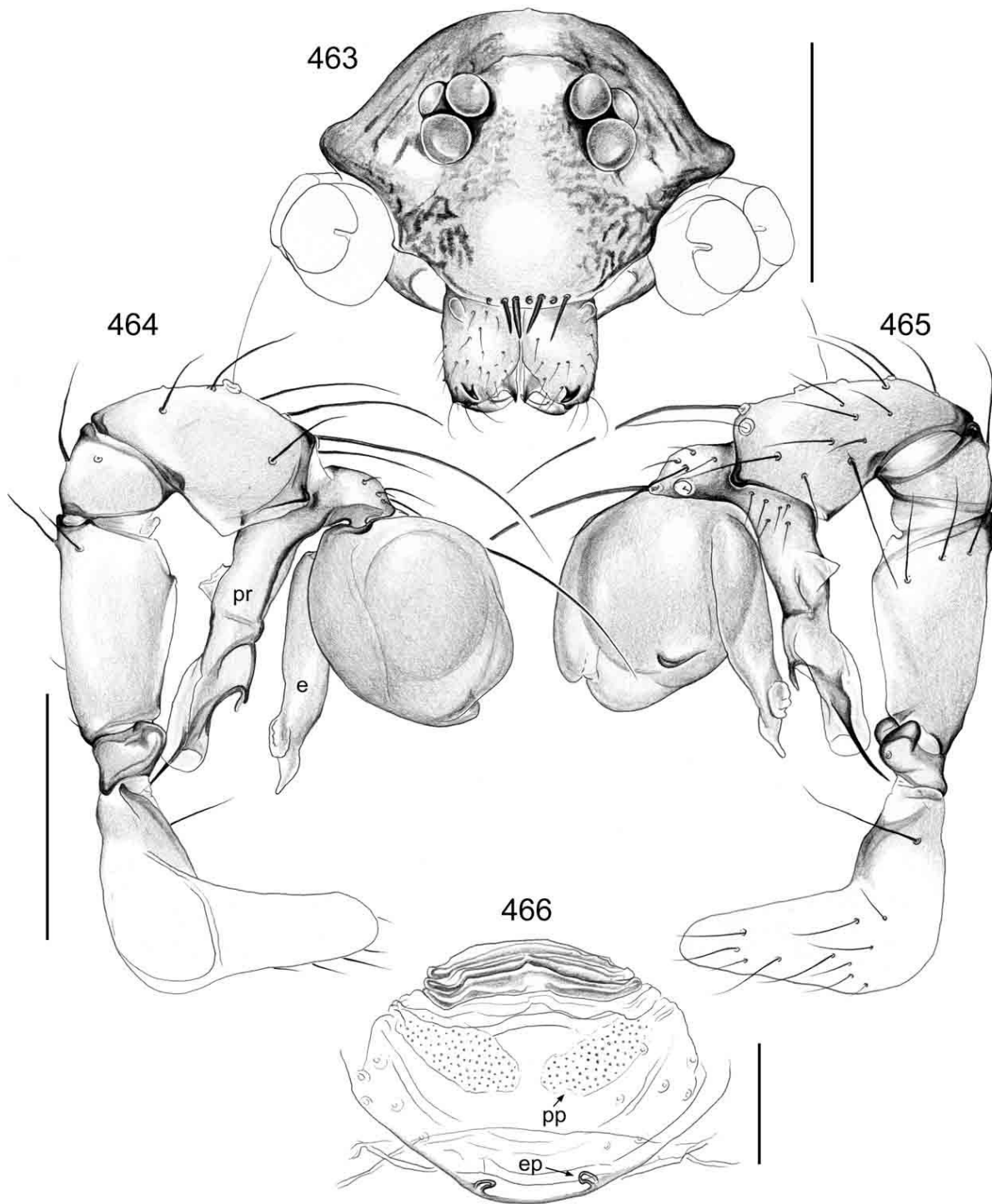
*Type.* Male holotype from Babelthuap Island, Airai [7°22'N, 134°33'E], Caroline Islands, Palau; in mango tree litter, May 5, 1973 (J. W. Berry), in BPBM.

*Etymology.* The species name is a noun in apposition, taken from the type locality.

*Diagnosis.* Tiny, short-legged species with globular opisthosoma; easily distinguished from most congeners (except *B. davao*) by the dark pattern on the carapace (Fig. 25) and by the transversal row of thickened hairs on the male clypeus (Fig. 463). Distinguished from *B. davao* by the more widely spaced male cheliceral apophyses (Fig. 463) and the pockets on the epigynum wider apart (Figs. 466, 479).

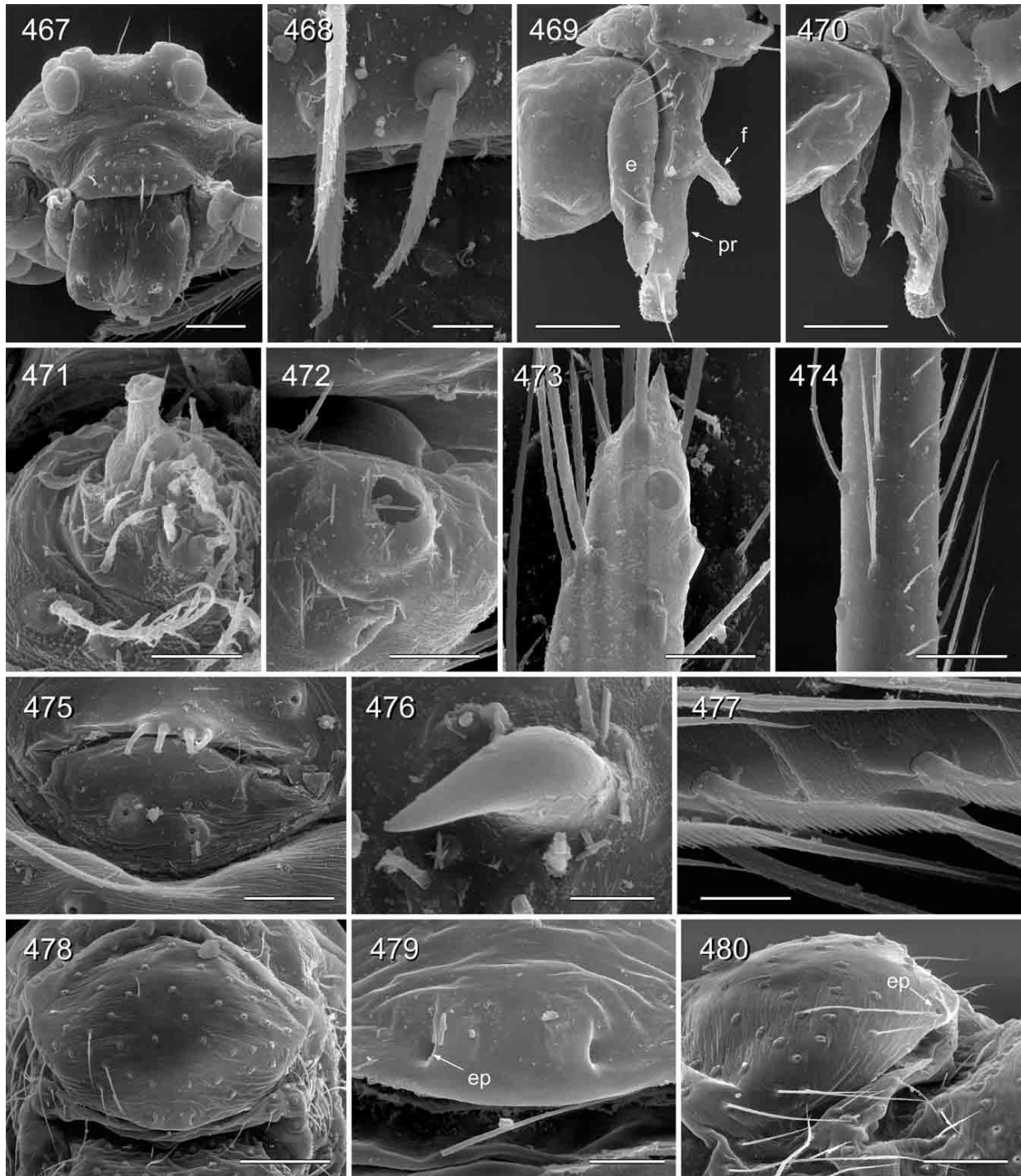
*Male (holotype).* Total length 1.0 (1.1 with clypeus), carapace width 0.50. Leg 1: 4.25 (1.07 + 0.17 + 1.07 + 1.37 + 0.57), tibia 2: 0.76, tibia 3: 0.63, tibia 4: 1.07; tibia 1 L/d: 20. Habitus as in Figs. 25 and 26. Carapace ochre-yellow with brown margins and pair of large brown marks, sternum brown with many light small spots, legs pale ochre-yellow; opisthosoma ochre-grey with barely visible darker spots. Ocular area slightly elevated, thoracic furrow absent; distance PME-PME 115  $\mu$ m; diameter PME 45  $\mu$ m; distance PME-ALE ~10  $\mu$ m. Clypeus with several thickened hairs (Figs. 463, 467, 468). Sternum as long as wide (0.36). Chelicerae as in Fig. 463, with pair of simple frontal apophy-





**Figs. 463-466.** *Belisana airai*. 463. Male prosoma, frontal view. 464, 465. Left male pedipalp, prolateral (464) and retrolateral (465) views. 466. Cleared female genitalia, dorsal view. Scale lines: 0.3 mm (463), 0.2 mm (464, 465), 0.1 mm (466).

ses, tips unmodified (Fig. 476), 100  $\mu$ m apart. Palps as in Figs. 464, 465, 469, 470; very similar to *B. davao* (cf. Figs. 449, 450). Tarsal organ capsulate (Fig. 472). Retrolateral trichobothrium of tibia 1 not seen; legs without spines and



**Figs. 467-480.** *Belisana airai*. 467. Male prosoma, frontal view. 468. Modified hairs on male clypeus (cf. Fig. 467). 469. Left bulb and procurus, retrolateral view. 470. Right bulb and procurus, prolateral view. 471. Male ALS. 472. Male palpal tarsal organ. 473. Tip of female palp with tarsal organ, dorsal view. 474. Male tibia 1, prolateral view. 475. Male gonopore with epiandrous spigots. 476. Male cheliceral apophysis. 477. Comb-hair on female tarsus 4. 478. Epigynum, ventral view. 479. Pockets on epigynum (cf. Fig. 478). 480. Epigynum, lateral view. Scale lines: 7  $\mu$ m (476), 10  $\mu$ m (468, 471, 472, 477), 20  $\mu$ m (473, 475, 479), 50  $\mu$ m (474), 70  $\mu$ m (469, 470, 480), 100  $\mu$ m (467, 478).

curved hairs; with vertical hairs in one prolateral row on tibia 1 (Fig. 474); tarsus 1 with ~7 pseudosegments. ALS and gonopore as in Figs. 471 and 475.

*Variation.* Tibia 1 in 6 other males: 1.10-1.21 (mean 1.15). Males from Koror Island have a longer ventral flap on the procurus.

*Female.* In general similar to male but clypeus unmodified; all females with dark pattern on opisthosoma, in some cases very distinct, but area around spinnerets whitish. Tibia 1 in 21 females: 0.87-1.13 (mean: 0.97). Epigynum simple light plate (Figs. 478, 480), pockets 75  $\mu$ m apart (Fig. 479); dorsal view as in Fig. 466. Palpal tarsal organ as in Fig. 473. ALS with several spigots.

*Distribution.* Known from several islands of Palau, Caroline Islands (Fig. 82).

*Material examined.* REPUBLIC OF PALAU (Caroline Islands): Babelthuap Island: type above, together with 2♂9♀ 3 juveniles (BPBM); same locality, litter in lowland tropical forest N of airstrip, March 27, 1973 (J. A. Beatty, J. W. Berry), 2♂4♀ (BPBM); Koror Island [7°20'N, 134°29'E], litter at edge of Taro Patch #2, April 3, 1973 (J. A. Beatty, J. W. Berry), 2♂1♀ (BPBM); Koror Island, Taro Patch, May 9, 1973 (J. W. Berry, J. A. Beatty), 3♀ (BPBM); Koror Island, banana litter below Entomological Laboratory, Feb. 20, 1973 (J. W. Berry), 1♀ (BPBM); same data but March 9, 1973, 1 juvenile (BPBM); Arakabesan Island (=Ngerekebesang) [7°21'N, 134°27'E], pitfall in mixed tropical forest, 20 ft a.s.l. Feb. 22, 1973 (J. W. Berry), 1♂ (BPBM); same locality at 374 ft a.s.l., dry forest litter, March 1, 1973 (J. W. Berry), 6♀ 3 juveniles (BPBM); Arakabesan Island, litter in mixed lowland forest, 20 ft a.s.l., Feb. 16, 1973 (J. W. Berry), 1♀ (BPBM); Malakal Island [7°20'N, 134°27'E], litter in dry tropical forest, 300 ft a.s.l., March 19, 1973 (J. W. Berry, J. A. Beatty), 2♂ 1 juvenile (BPBM).

#### ***Belisana yap*, new species**

(Figs. 481-485)

*Type.* Male holotype from Wanyaan [9°33'N, 138°12'E], Yap Island, Caroline Islands, Federal States of Micronesia; in litter, April 17, 1980 (J. A. Beatty & J. W. Berry), in BPBM.

*Etymology.* The species name is a noun in apposition, taken from the type locality.

*Diagnosis.* Medium-sized, long-legged species with slightly elongated and angular opisthosoma; distinguished from most congeners by the cone-shaped median projection on the clypeus; also by the shapes of procurus and bulbal projections (Figs. 481, 482), by the dorsally inflated male palpal femur (Fig. 482) and by the scape on the epigynum (Fig. 484). The BPBM has some specimens from Angaur and Babelthuap Islands that have very similar palps and clypeus projections, but very different cheliceral proximal projections (large, situated frontally, not laterally).

*Male (holotype).* Total length 1.4 (1.5 with clypeus), carapace width 0.56. Leg 1: 14.2 (3.5 + 0.3 + 3.6 + 5.4 + 1.4), tibia 2: 2.25, tibia 3: 1.4, tibia 4: 2.0; tibia 1 L/d: 68. Habitus similar to *B. khaosok* (cf. Figs. 51, 52). Prosoma and legs ochre-yellow, opisthosoma light grey. Ocular area flat, triads slightly elevated, thoracic furrow absent; distance PME-PME 90  $\mu$ m; diameter PME 60  $\mu$ m; distance PME-ALE ~10  $\mu$ m. Clypeus with cone-shaped projection above chelicerae. Sternum as long as wide (0.40). Chelicerae as in Fig. 483, tips of apophyses 55  $\mu$ m apart. Palps as in Figs. 481 and 482; trochanter with retrolateral apophysis, femur dorsally inflated, patella relatively long, procurus simple except distally, bulb with simple embolus and hooked apophysis. Retrolateral trichobothrium of tibia 1 at 21%; legs without spines, curved, and vertical hairs; tarsus 1 with ~20 pseudosegments, distally fairly distinct.

*Variation.* Tibia 1 in 4 other males: 3.2-3.9.

*Female.* In general similar to male but clypeus unmodified. Tibia 1 in 5 females: 2.2-3.1 (mean 2.50). Epigynum with distinctive anterior scape-like structure and pair of pockets 10  $\mu$ m apart (Fig. 484); dorsal view as in Fig. 485, with elongated pore plates. Apparently with only two spigots on ALS.

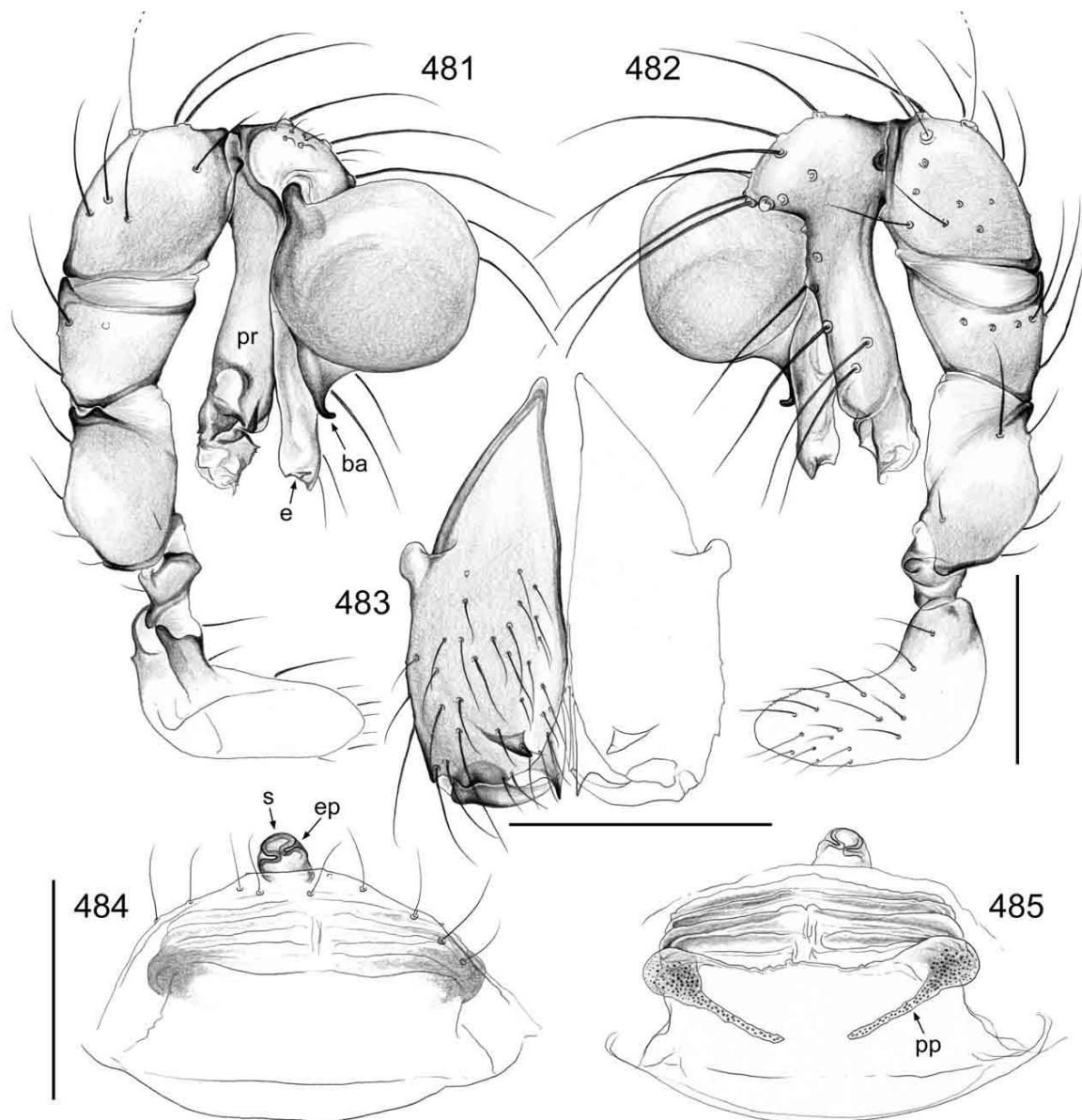
*Distribution.* Known from several of the Caroline Islands (Micronesia and Palau) (Fig. 82).

*Material examined.* MICRONESIA: *Yap Island:* type above, together with 2♂ (BPBM); Road to Fanif, shaken from dead lower banana leaves, May 31, 1973 (J. A. Beatty, J. W. Berry), 2♂ 1 juvenile (BPBM); Gilman Point, litter in coconut grove, May 29, 1973 (J. A. Beatty, J. W. Berry), 1♀ (BPBM); Aringel village, mature forest, Feb. 1, 1980 (J. W. Berry), 1♂1♀ (BPBM); Fedor village, banana leaves, Feb. 1, 1980 (J. W. Berry), 1♂ (BPBM); Fedor village near Taro Patch, March 10, 1980 (J. W. Berry), 1♀ (BPBM). PALAU: *Babelthuap Island:* Airai [7°22'N, 134°33'E], litter in lowland forest near airstrip, March 27, 1973 (J. A. Beatty, J. W. Berry), 1♂3♀ (BPBM); *Koror Island:* Koror village [7°20'N, 134°29'E], tree shaking in vacant lot, March 13, 1973 (J. A. Beatty, J. W. Berry), 2♀ (BPBM); Kayancel Atoll, tree shaking, May 23, 1973 (J. W. Berry), 1♀ (BPBM).

#### ***Belisana apo*, new species**

(Figs. 49, 50, 486-490)

*Type.* Male holotype from Nature Reserve at Mt. Apo [-6°59'N, 125°16'E], Davao, Mindanao, Philippines; secondary forest, 800 m a.s.l., April 26, 1982 (P. R. Deeleman), in RMNH.

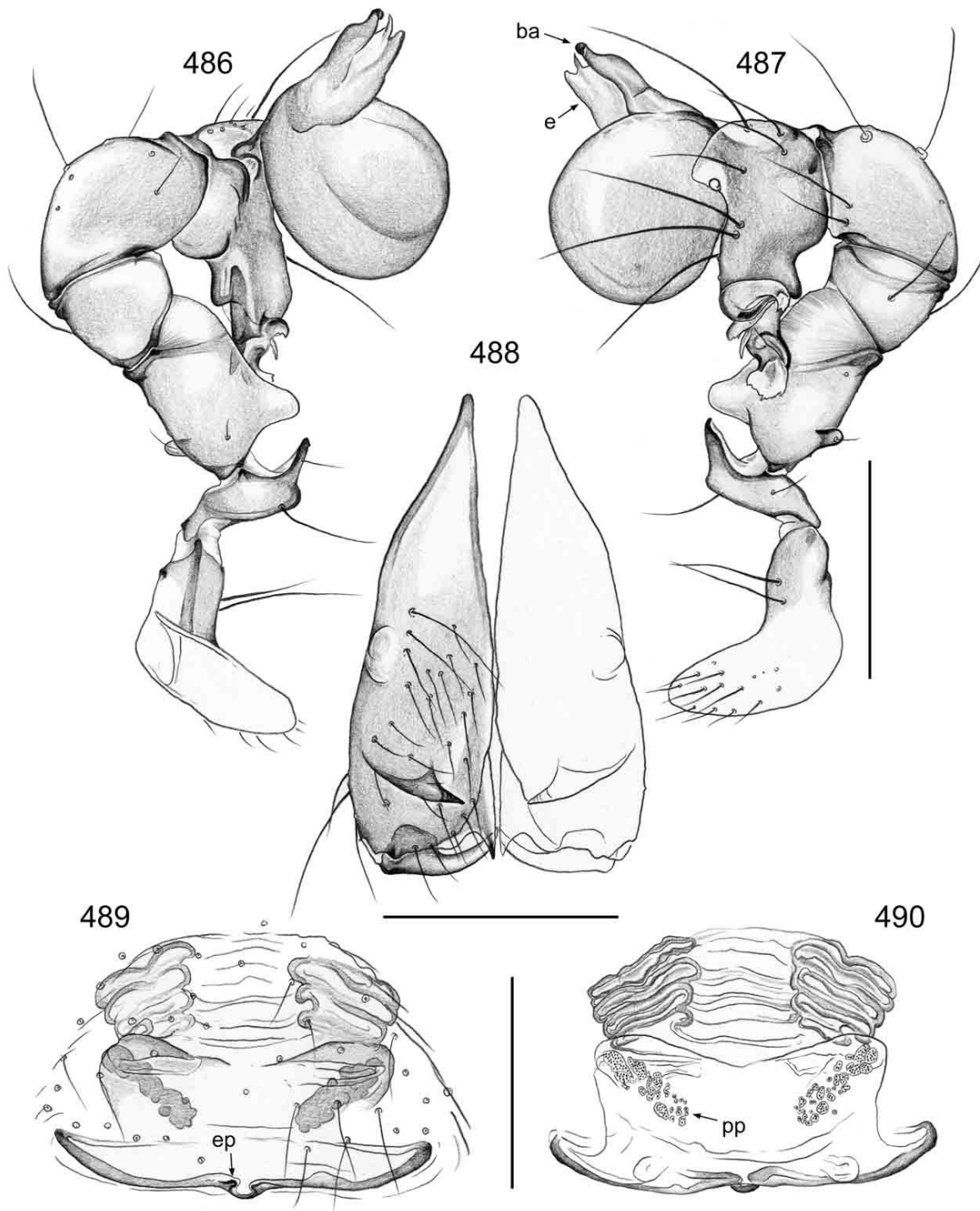


**Figs. 481-485.** *Belisana yap*. 481, 482. Left male pedipalp, prolateral (481) and retrolateral (482) views. 483. Male chelicerae, frontal view. 484, 485. Cleared female genitalia, ventral (484) and dorsal (485) views. Scale lines: 0.2 mm.

*Etymology.* The species name is a noun in apposition, taken from the type locality.

*Diagnosis.* Relatively large, long-legged species with dorsally strongly elongated opisthosoma (Fig. 50); easily distinguished from similar congeners by the shapes of male palpal trochanter and femur (ventral projections, Figs. 486, 487).

*Male (holotype).* Total length 2.0 (2.1 with clypeus), carapace width 0.70. Leg 1: 17.3 (4.3 + 0.3 + 4.3 + 6.8 + 1.6), tibia 2: 2.7, tibia 3: 1.5, tibia 4: 2.3; tibia 1 L/d: 69. Habitus as in Figs. 49 and 50. Prosoma and legs pale ochre-yellow, carapace laterally with slightly darker submarginal lines, opisthosoma pale ochre-grey, with two pairs of round and two pairs of elongated dark marks dorsally. Ocular area barely elevated, thoracic furrow absent; distance PME-PME 210  $\mu$ m; diameter PME 65  $\mu$ m; distance PME-ALE ~20  $\mu$ m. Clypeus unmodified. Sternum slightly wider than long (0.50/0.46). Chelicerae as in Fig. 488, proximal apophyses reduced to indistinct pair of humps, tips of frontal apophyses 50  $\mu$ m apart. Palps as in Figs. 486 and 487; trochanter with distinctive sclerotized retrolateral apophysis (rather ventrally; distally flattened), femur with dorsal (slightly sclerotized) apophysis and distinctive ventral (weakly sclerotized)



**Figs. 486-490.** *Belisana apo*. 486, 487. Left male pedipalp, prolateral (486) and retrolateral (487) views. 488. Male chelicerae, frontal view. 489, 490. Cleared female genitalia, ventral (489) and dorsal (490) views. Scale lines: 0.3 mm (486, 487), 0.2 mm (488-490).

projection, procurus distally complex, apparently with prolateral hinged process; bulbal apophysis hooked at tip, membranous embolus with distal spine. Retrolateral trichobothrium of tibia 1 at 13%; legs without spines and curved hairs, with vertical hairs in higher density on metatarsi (seen on metatarsi 2-4); tarsus 1 with ~15 pseudosegments, indistinct.

*Female.* In general similar to male, including dorsal abdominal pattern and submarginal lines on carapace; tibia 1: 3.2. Epigynum very simple externally, pockets close together, close to posterior rim (Fig. 489), 20  $\mu\text{m}$  apart; dorsal view as in Fig. 490.

*Distribution.* Known from type locality only (Fig. 80).

*Material examined.* PHILIPPINES: *Mindanao*: Mt. Apo Nature Reserve: type above, together with 1 ♀ (RMNH).

***Belisana tambligan*, new species**

(Figs. 54, 491-496, 509-518)

*Type.* Male holotype from Lake Tambligan [ $\sim 8^{\circ}15'S$ ,  $115^{\circ}07'E$ ], Bali, Indonesia; dense secondary forest, from leaves, 1150 m a.s.l., Feb. 9, 1995 (C. L. Deeleman), in RMNH.

*Etymology.* The species name is a noun in apposition, taken from the type locality.

*Diagnosis.* Relatively large, long-legged species with elongated and posteriorly elevated opisthosoma; distinguished from similar congeners by the shape of the procurus (distal elements, Figs. 491, 492); from some species also by the male cheliceral apophyses (Figs. 493, 494).

*Male (holotype).* Total length 2.0 (2.1 with clypeus), carapace width 0.83. Leg 1 missing, tibia 2: 3.6, tibia 3: 2.0, tibia 4: 3.1; tibia 2 L/d: 54. Habitus as in Fig. 54 (the male shown is not the holotype). Prosoma and legs ochre-yellow; opisthosoma pale ochre-grey, some slightly darker large spots dorsally. Ocular area not elevated, thoracic furrow absent; distance PME-PME 185  $\mu\text{m}$ ; diameter PME 60  $\mu\text{m}$ ; distance PME-ALE 20  $\mu\text{m}$ . Clypeus unmodified. Sternum slightly wider than long (0.54/0.50). Chelicerae as in Figs. 493, 494, and 509, tips of apophyses 320  $\mu\text{m}$  apart. Palps as in Figs. 491 and 492; trochanter with short rounded retrolateral apophysis, femur with distinct dorsal projection, procurus with distinctive sclerite distally, bulb with membranous embolus and basally thick apophysis (Fig. 511). Tarsal organ capsulate (Fig. 512). Legs without spines, curved hairs, and vertical hairs (leg 1 and many hairs missing); tarsus 2 with about 15 pseudosegments, fairly visible. Gonopore as in Fig. 513. ALS with only two spigots each (Fig. 518).

*Variation.* In most other males there are no darker spots on the opisthosoma (Fig. 54). Tibia 1 in 15 males from Bali and eastern Java: 5.0-6.0 (mean 5.73). Specimens from western Java are assigned tentatively because their cheliceral and bulbal apophyses are slightly thinner and longer, the dorso-distal procurus apophysis is slightly stronger, and the legs are shorter (at similar body size): tibia 1 in 4 males from western Java: 4.1, 4.3, 4.4, 4.7.

*Female.* In general similar to male; opisthosoma always monochromous; tibia 1 in 12 females: 3.6-4.4 (mean 4.07). Epigynum extremely simple externally (Fig. 515), not pigmented, barely protruding; pockets 285  $\mu\text{m}$  apart (Figs. 495, 515); dorsal view as in Fig. 496. Palpal tarsal organ capsulate (Fig. 516). ALS with only two spigots each (Fig. 517).

*Distribution.* Known from several localities on Bali and eastern Java (Fig. 80); specimens from western Java are assigned tentatively.

*Material examined.* INDONESIA: *Bali*: Lake Tambligan: type above, together with 2 ♂7 ♀ (RMNH); Mekori temple garden, Blimbing [ $8^{\circ}24'S$ ,  $115^{\circ}02'E$ ], Aug. 31, 1992 (C. L. & P. R. Deeleman), 3 ♂7 ♀ (RMNH); Batukau rainforest [ $8^{\circ}20'S$ ,  $115^{\circ}05'E$ ], Aug. 6, 1992 (C. L. & P. R. Deeleman), 2 ♂1 ♀ (RMNH); Kintanami [ $8^{\circ}14'S$ ,  $115^{\circ}19'E$ ], lake, mixed pine, sweeping, Aug. 4, 1992 (C. L. & P. R. Deeleman), 1 ♂1 ♀ (RMNH); *Java*: Mt Ijen Pass [ $\sim 8^{\circ}05'S$ ,  $114^{\circ}15'E$ ], forest at 1135 m a.s.l., from leaves, July 8, 1979 (P. R. & C. L. Deeleman), >40 ♂30 ♀ (RMNH).

Assigned tentatively: *Java*: Cibodas [ $5^{\circ}55'S$ ,  $106^{\circ}03'E?$ ], 1550 m a.s.l., from leaves, Dec. 7-8, 1986 (S. Djojodharmo), 2 ♂ (RMNH); Bogor, Puncak Pass [ $6^{\circ}42'S$ ,  $106^{\circ}59'E$ ], 1000 m a.s.l., from leaves, Aug. 16, 1980 (P. R. & C. L. Deeleman), 2 ♂ (RMNH).

***Belisana ambengan*, new species**

(Figs. 31, 32, 497-499)

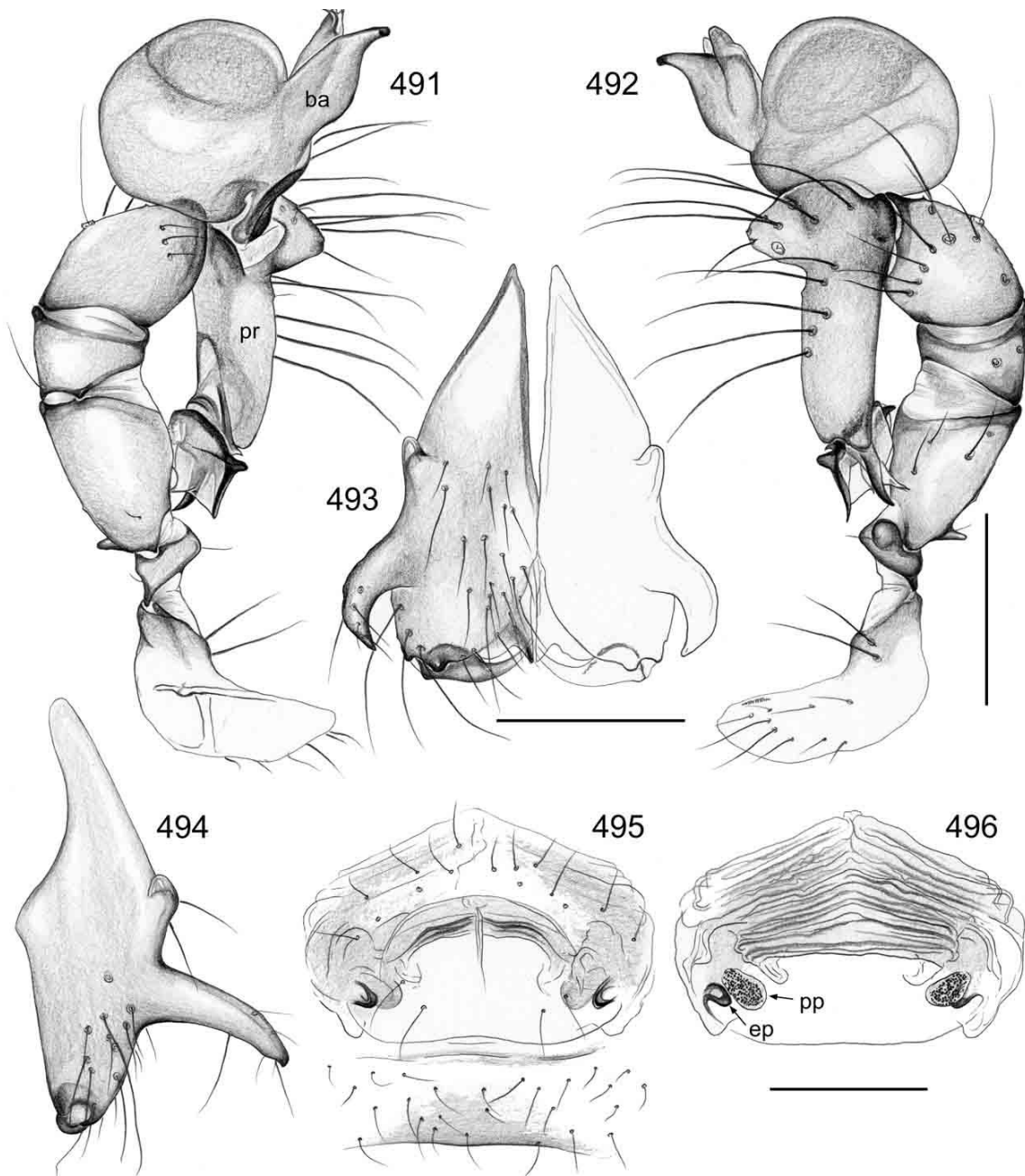
*Type.* Male holotype from Ambengan [ $8^{\circ}10'S$ ,  $115^{\circ}06'E$ ], Bali, Indonesia; secondary forest, from leaves, Jan. 19-31, 1990 (S. Djojodharmo), in RMNH.

*Etymology.* The species name is a noun in apposition, taken from the type locality.

*Diagnosis.* Medium sized species with medium long legs and globular opisthosoma; easily distinguished from congeners by the median apophysis on the male clypeus, the eyes without pigment, and the brown stripes behind the eye triads (Fig. 31); also by the shapes of procurus and chelicerae (Figs. 497-499) and by the bulb without apophysis (only a small projection on prolateral side of embolus: Fig. 497).

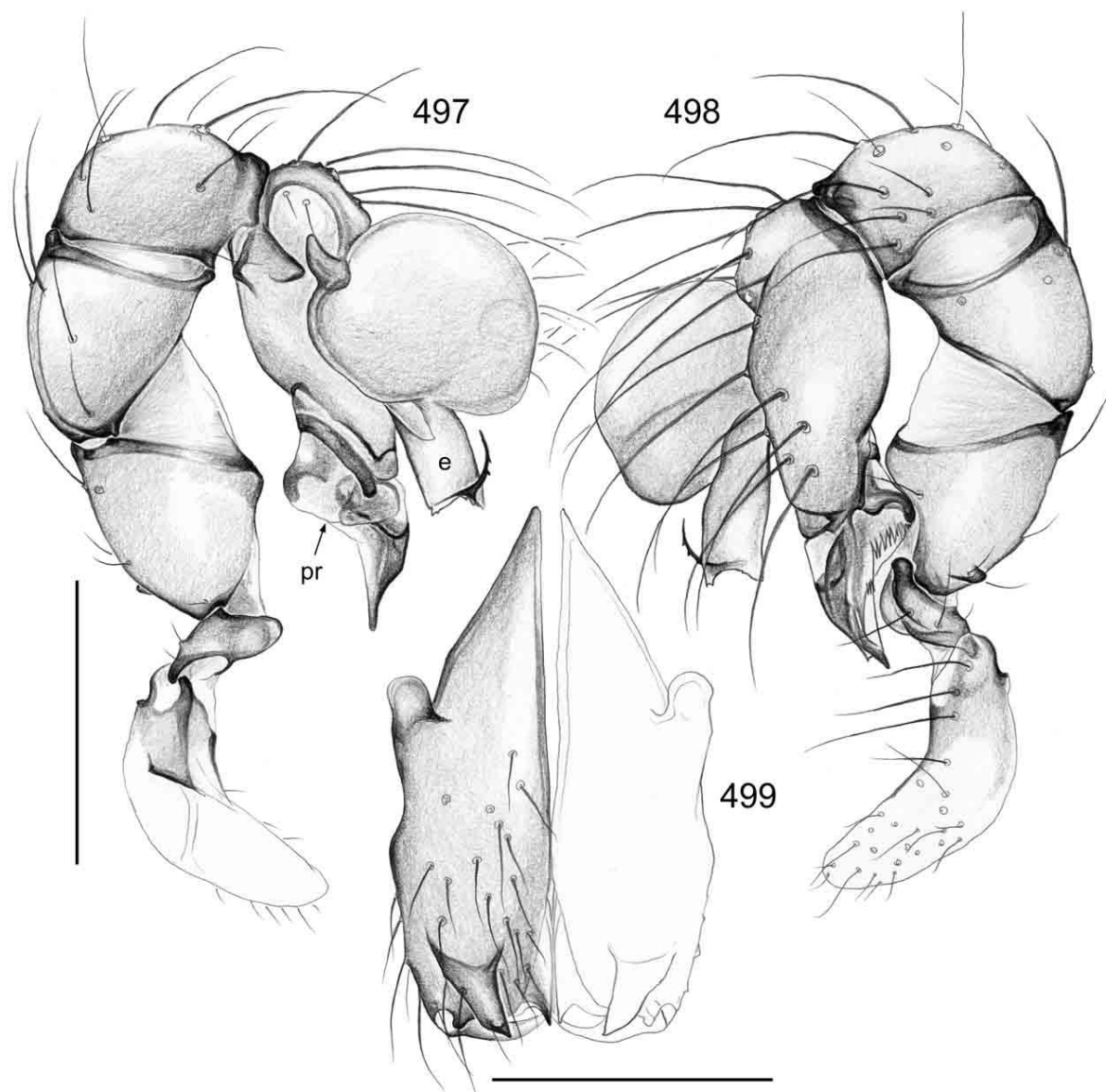
*Male (holotype).* Total length 1.3 (1.4 with clypeus), carapace width 0.57. Leg 1: 10.43 (2.57 + 0.23 + 2.70 + 3.73 + 1.20), tibia 2: 1.70, tibia 3: 1.03, tibia 4: 1.60; tibia 1 L/d: 44. Habitus as in Figs. 31 and 32. Prosoma and legs most-





**Figs. 491-496.** *Belisana tambligan*. 491, 492. Left male pedipalp, prolateral (491) and retrolateral (492) views. 493, 494. Male chelicerae, frontal and lateral views. 495, 496. Cleared female genitalia, ventral (495) and dorsal (496) views. Scale lines: 0.3 mm (491, 492), 0.2 mm (493-496).

ly pale ochre-yellow, carapace with distinctive light brown marks behind eye triads, eyes without any black pigment; opisthosoma ochre-grey, some slightly darker large spots dorsally. Ocular area slightly elevated, thoracic furrow absent; distance PME-PME 95  $\mu$ m; diameter PME 60  $\mu$ m; all eyes seemingly contiguous. Clypeus with distinctive conical median projection, about 90  $\mu$ m long. Sternum slightly wider than long (0.67/0.63). Chelicerae as in Fig. 499, apophyses at about 45° angle to paturon, tips 65  $\mu$ m apart. Palps as in Figs. 497 and 498; trochanter with small but dark retrolateral apophysis, femur with distinct dorsal projection, procurus long with distinctive sclerites distally, bulb with strongly inward-curved spine on embolus. Retrolateral trichobothrium of tibia 1 at 16%; legs without spines, curved hairs, and vertical hairs (many hairs missing); tarsus 1 with about 10 pseudosegments, poorly visible.



**Figs. 497-499.** *Belisana ambengan*. 497, 498. Left male pedipalp, prolateral (497) and retrolateral (498) views. 499. Male chelicerae, frontal view. Scale lines: 0.3 mm (497, 498), 0.2 mm (499).

*Female.* In general similar to male but clypeus unmodified; tibia 1: 2.73. Opisthosoma missing.

*Distribution.* Known only from type locality (Fig. 80).

*Material examined.* INDONESIA: *Bali*: Ambengan: type above, together with 1♀ (prosoma only); the vial includes one additional female that is not conspecific.

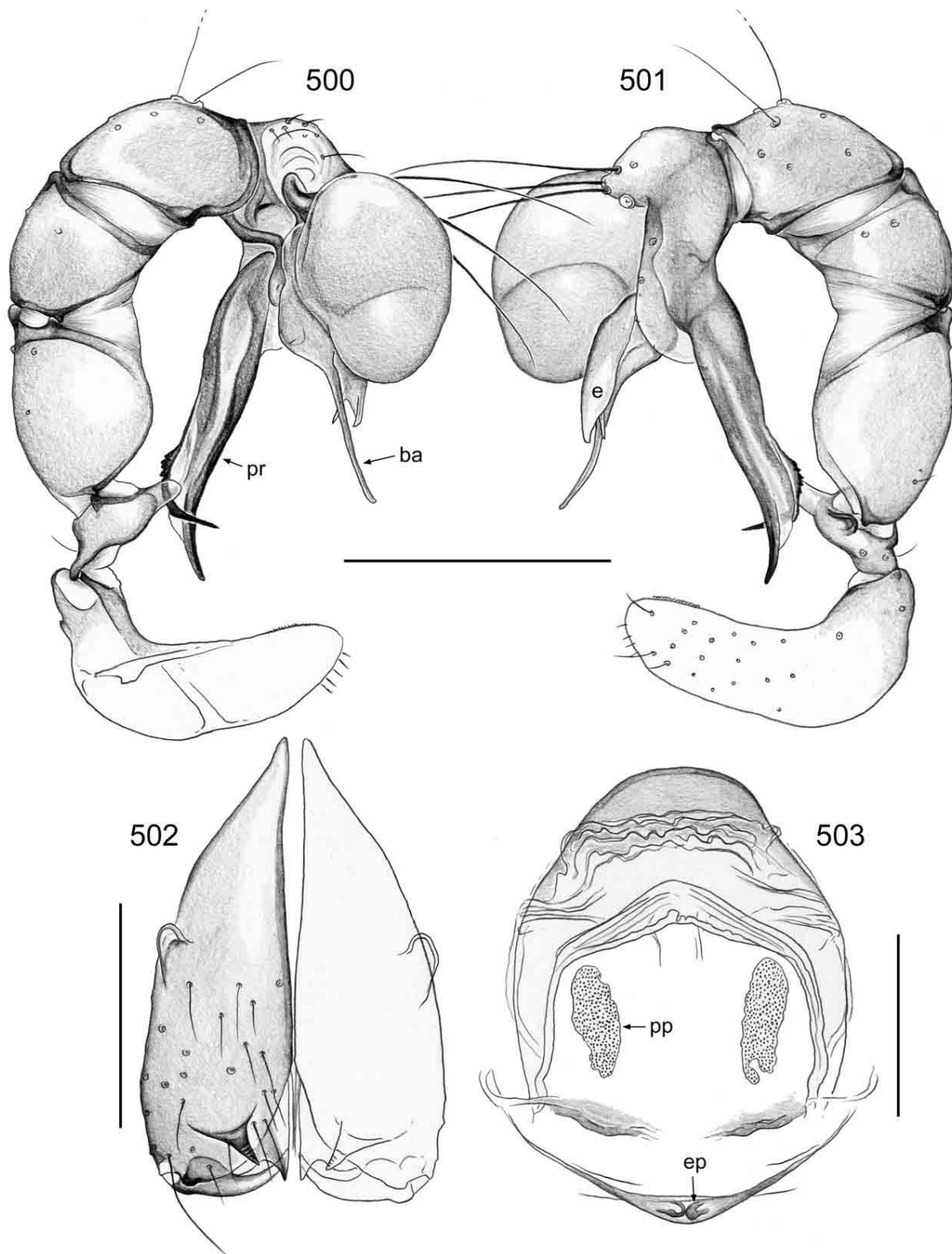
***Belisana flores, new species***

(Figs. 73, 500-503)

*Type.* Male holotype from Kelimoto [=Kelimutu, near Moni; ~8°48'S, 121°55'E], Flores, Indonesia; primary forest, 1400 m a.s.l., Aug. 16, 1992 (C. L. & P. R. Deeleman), in RMNH.

*Etymology.* The species name is a noun in apposition, taken from the type locality.

*Diagnosis.* Relatively large, long-legged species with cylindrical opisthosoma elongated beyond spinnerets; easily distinguished from congeners by the shape of the procurus (long and narrow, with proximally serrated spine, Figs. 500,



**Figs. 500-503.** *Belisana flores*. 500, 501. Left male pedipalp, prolateral (500) and retrolateral (501) views. 502. Male chelicerae, frontal view. 503. Cleared female genitalia, dorsal view. Scale lines: 0.3 mm (500, 501), 0.2 mm (502, 503).

501); also by the bulbal projections (bulbal apophysis transformed to long thin projection, Fig. 500; similar in *B. sumba*), and the femur without dorsal projection (Fig. 501).

*Male (holotype).* Total length 1.9 (2.0 with clypeus), carapace width 0.67. Leg 1 missing, tibia 2: 3.1, tibia 3: 1.85, tibia 4 missing. Habitus similar to *B. tambligan* (Fig. 54). Prosoma and legs mostly pale ochre-yellow, patellae and tibia-metatarsus joints slightly darker, sternum whitish, opisthosoma pale ochre-grey, dorsally slightly darker spots visible through cuticle. Ocular area barely elevated, thoracic furrow absent; distance PME-PME 115  $\mu\text{m}$ ; diameter PME 70  $\mu\text{m}$ ; distance PME-ALE  $\sim$ 20  $\mu\text{m}$ . Clypeus unmodified. Sternum slightly wider than long (0.50/0.46). Chelicerae as in Fig. 502, tips of apophyses 55  $\mu\text{m}$  apart. Palps as in Figs. 500 and 501; trochanter with short sclerotized retrolateral apophysis and longer, weakly sclerotized ventral projection, femur without projections, procurus with very long bifid ventro-distal sclerite, possibly hinged; bulb with distinctive long bulbal apophysis and weakly sclerotized embolus with spine. All hairs on legs missing.

*Female.* In general similar to male; tibia 1 missing. Epigynum longer than wide, simple externally (Fig. 73), with pair of pockets 15  $\mu\text{m}$  apart; dorsal view as in Fig. 503.

*Distribution.* Known from type locality only (Fig. 80).

*Material examined.* INDONESIA: *Flores Island*: Kelimoto: type above, together with 1 $\sigma$  (and one female that is not conspecific), in RMNH.

### ***Belisana sumba, new species***

(Figs. 504-508, 519-522)

*Type.* Male holotype from 10 km W of Lewa [ $\sim$ 9 $^{\circ}$ 45'S, 119 $^{\circ}$ 53'E], Sumba, Indonesia; evergreen forest, sweeping, July 8, 1992 (C. L. & P. R. Deeleman), in RMNH.

*Etymology.* The species name is a noun in apposition, taken from the type locality.

*Diagnosis.* Relatively large, long-legged species with oval opisthosoma; easily distinguished from similar congeners by the shape of the procurus and by the long ventral male palpal trochanter apophysis and the ventral femur apophysis (Fig. 505); also by the bulbal projections (bulbal apophysis transformed to long thin projection, Fig. 504; similar in *B. flores*).

*Male (holotype).* Total length 1.85 (1.90 with clypeus), carapace width 0.63. Leg 1: 18.5 (4.5 + 0.3 + 4.7 + 7.4 + 1.6), tibia 2: 3.0, tibia 3: 1.9, tibia 4: 2.8; tibia 1 L/d: 76. Habitus similar to *B. jimi* (cf. Fig. 55). Prosoma and legs pale ochre-yellow, patellae and tibia-metatarsus joints light brown, opisthosoma pale grey with slightly greenish spots. Ocular area barely elevated, thoracic furrow absent; distance PME-PME 150  $\mu\text{m}$ ; diameter PME 60  $\mu\text{m}$ ; distance PME-ALE  $\sim$ 20  $\mu\text{m}$ . Clypeus unmodified. Sternum about as wide as long (0.44). Chelicerae as in Fig. 506, tips of apophyses 75  $\mu\text{m}$  apart. Palps as in Figs. 504 and 505; trochanter with retrolateral and long ventral apophyses, femur with dorsal hump and distinctive ventral projection, procurus with three terminal structures: long dorsal sclerite, long hinged ventral sclerite and short dorsal sclerite with scales; bulb with long and thin, weakly sclerotized projection and short sclerite with membranous structure (embolus?). Retrolateral trichobothrium of tibia 1 at 9%; legs without spines and curved hairs, with vertical hairs in higher than usual density on metatarsi; tarsus 1 with >15 pseudosegments, barely visible in dissecting microscope.

*Female.* In general similar to male; two females with monochromous opisthosoma, third female with several dark spots on opisthosoma; tibia 1: 3.8 (missing in 2 females). Epigynum very simple externally (Fig. 521), without pockets but with distinctive weakly sclerotized scape (Figs. 507, 521, 522; visible in dissecting microscope only in lateral view); dorsal view as in Fig. 508. ALS as in Fig. 520.

*Distribution.* Known from two localities on Sumba Island (Fig. 80).

*Material examined.* INDONESIA: *Sumba Island*: 10 km W of Lewa: type above, together with 1 $\sigma$  2 juveniles; 10 km W of "Waingabubak" (Waikabubak) [ $\sim$ 9 $^{\circ}$ 38'S, 119 $^{\circ}$ 20'E], mahony and kajuputi, near stream, Feb. 2, 2001 (C. L. Deeleman), 2 $\sigma$  assigned tentatively (RMNH).

### ***Belisana doloduo, new species***

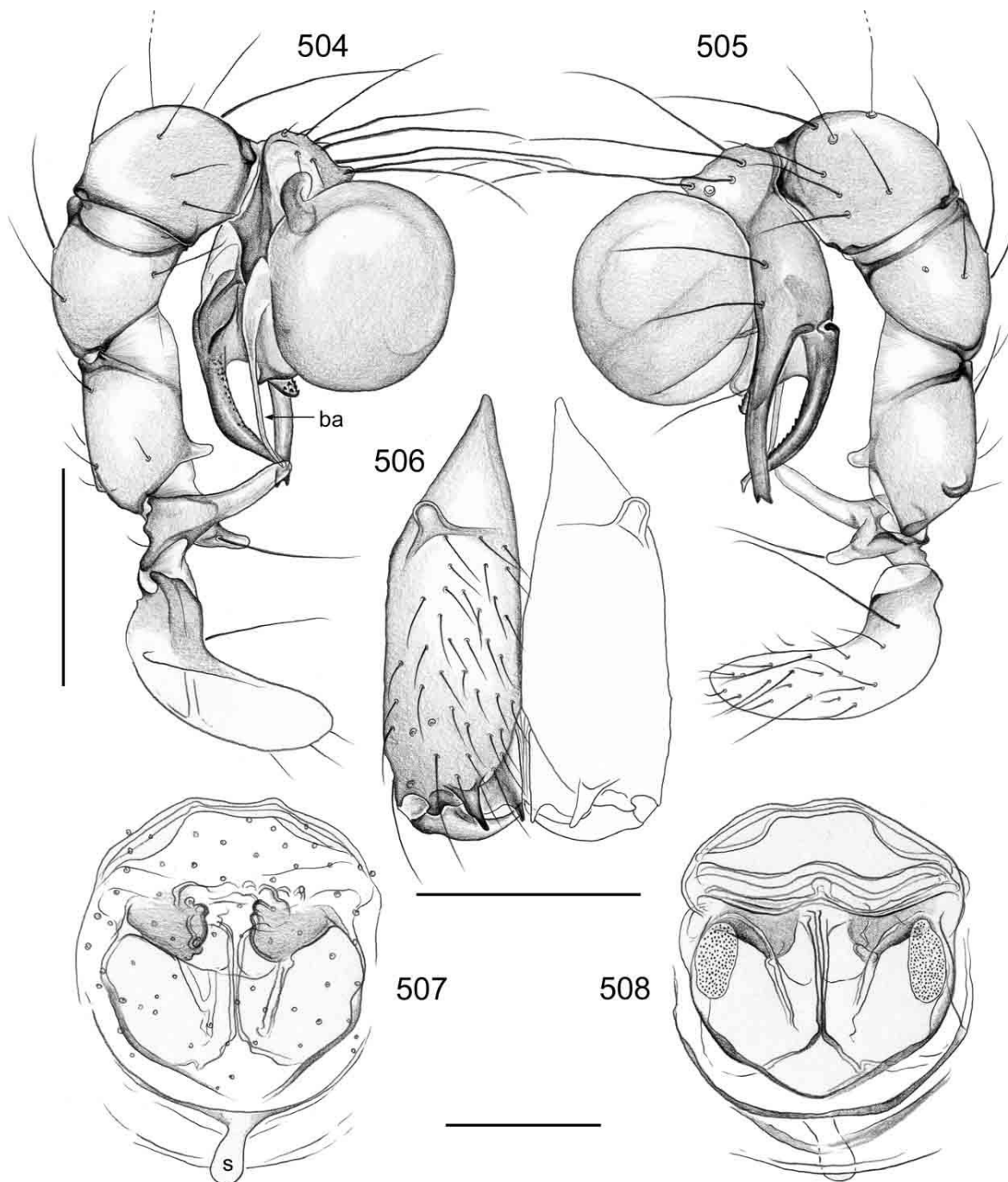
(Figs. 523-526)

*Type.* Male holotype from Dumoga, watershed protection near Doloduo [0 $^{\circ}$ 31'N, 123 $^{\circ}$ 55'E], North Sulawesi, Indonesia; primary forest, July 27-30, 1982 (P. R. & C. L. Deeleman), in RMNH.

*Etymology.* The species name is a noun in apposition, taken from the type locality.

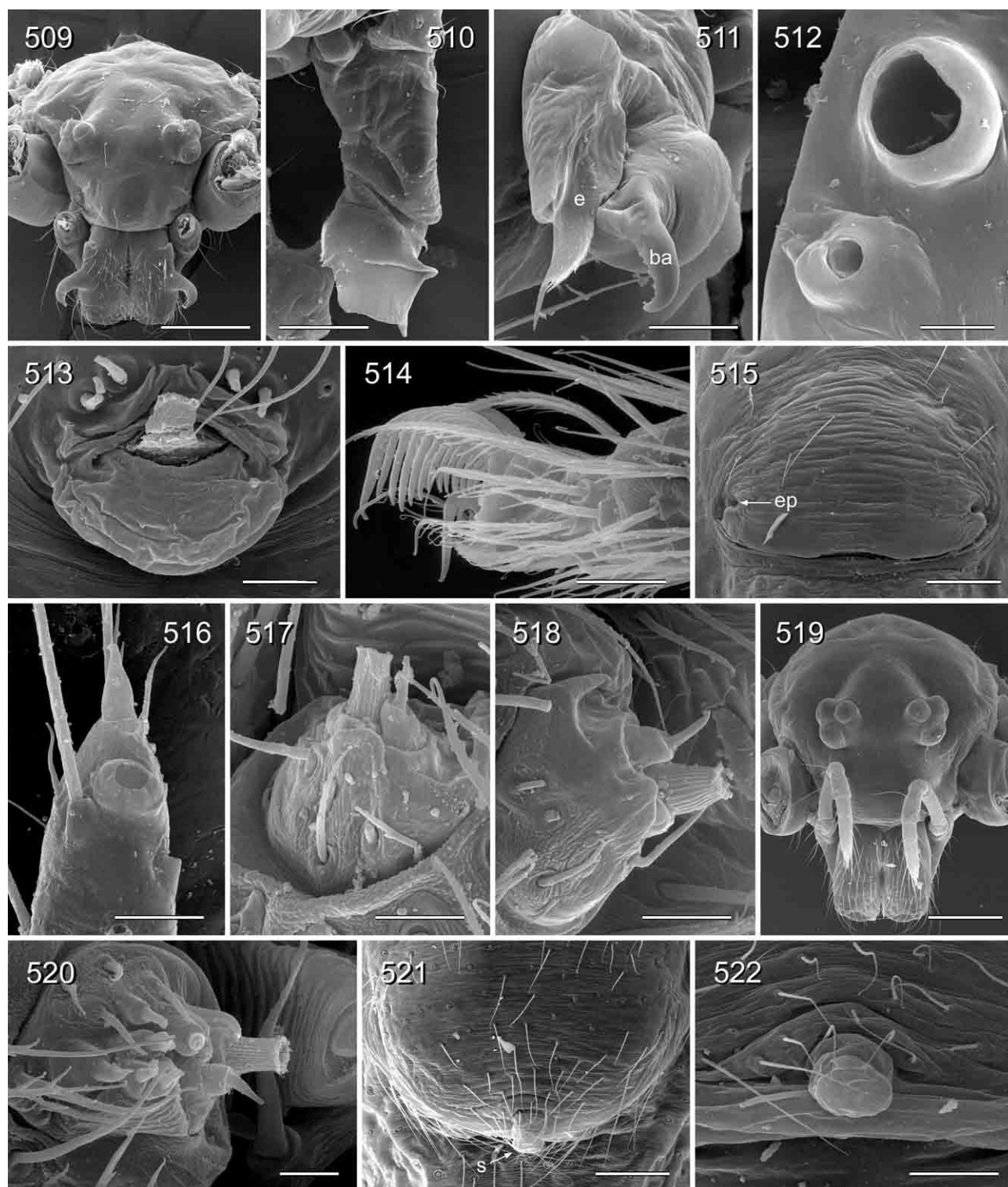
*Diagnosis.* Relatively large, long-legged species with cylindrical opisthosoma; distinguished from similar congeners by the long, widely curved bulbal apophysis (Fig. 523); also by the shapes of procurus (Fig. 524) and male chelicerae (Fig. 525).

*Male (holotype).* Total length 1.7 (1.8 with clypeus), carapace width 0.57. Leg 1: 16.45 (4.2 + 0.3 + 4.25 + 6.7 + 1.0), tibia 2: 2.8, tibia 3: 1.5, tibia 4: 2.5; tibia 1 L/d: 80. Habitus similar to *B. tambligan* (cf. Fig. 54). Prosoma and



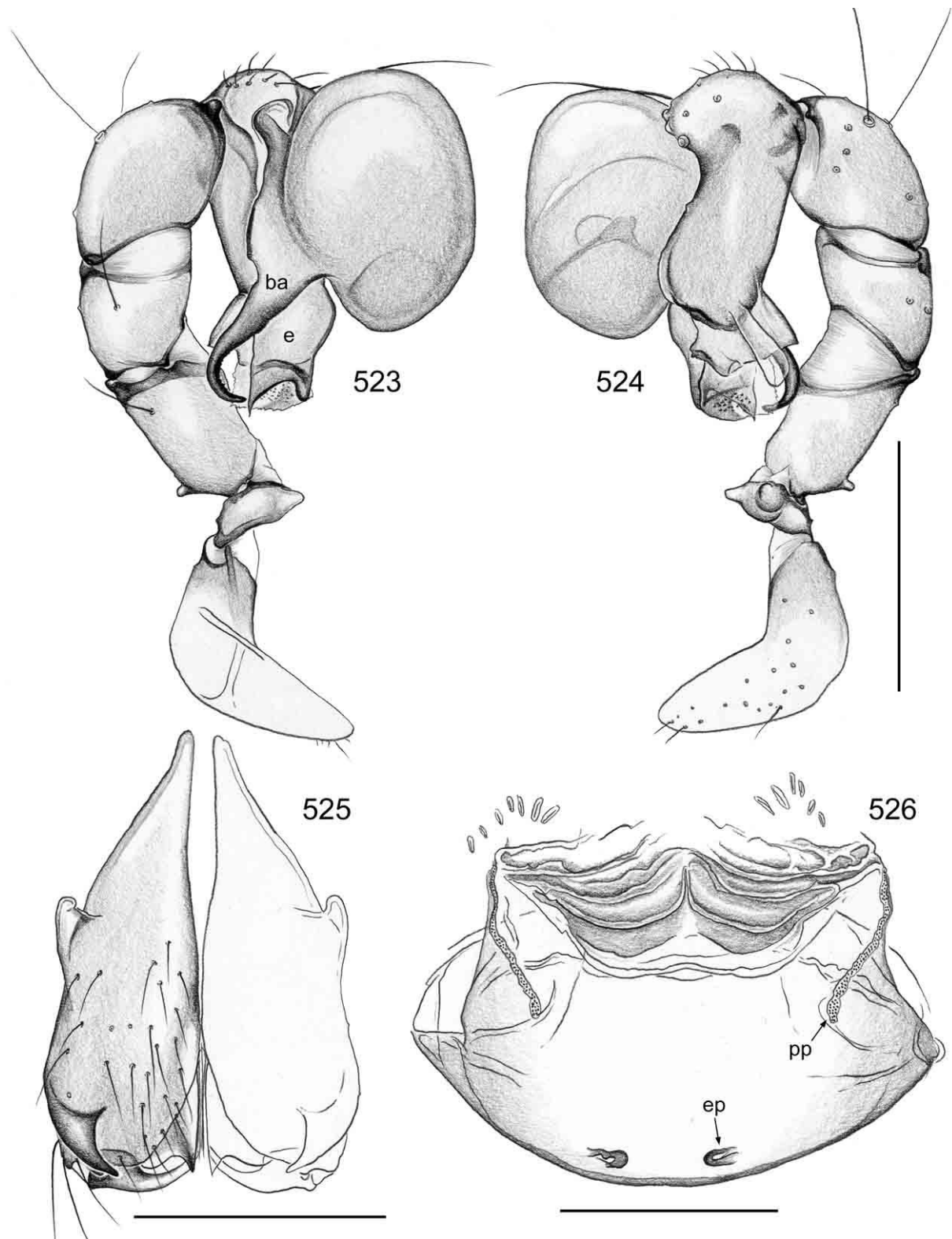
**Figs. 504-508.** *Belisana sumba*. 504, 505. Left male pedipalp, prolateral (504) and retrolateral (505) views. 506. Male chelicerae, frontal view. 507, 508. Cleared female genitalia, ventral (507) and dorsal (508) views. Scale lines: 0.3 mm (504, 505), 0.1 mm (506), 0.2 mm (507, 508).

legs pale ochre-yellow, opisthosoma pale ochre-grey. Ocular area barely elevated, thoracic furrow absent; distance PME-PME 125  $\mu$ m; diameter PME 65  $\mu$ m; distance PME-ALE  $\sim$ 20  $\mu$ m. Clypeus unmodified. Sternum about as wide as long (0.42). Chelicerae as in Fig. 525, tips of frontal apophyses 135  $\mu$ m apart. Palps as in Figs. 523 and 524; trochanter with ventral and longer retrolateral apophyses, femur with distinct dorsal apophysis, procurus with distinctive distal elements; bulb with strong and widely curved apophysis, bifid embolus. Retrolateral trichobothrium of tibia 1 at 10%; legs without spines and curved hairs, with vertical hairs on metatarsi; tarsus 1 with  $\sim$ 20 pseudosegments, fairly distinct distally.



**Figs. 509-522.** *Belisana tambligan* (509-518) and *B. sumba* (519-522). 509. Male prosoma, frontal view. 510. Left procurus, prolateral view. 511. Bulbal apophysis and embolus, distal view. 512. Male palpal tarsal organ. 513. Male gonopore with epiandrous spigots. 514. Male tarsus I tip. 515. Epigynum, ventral view. 516. Tip of female palp with tarsal organ, dorsal view. 517. Female ALS. 518. Male ALS. 519. Female prosoma, frontal view. 520. Female ALS. 521. Epigynum, ventral view. 522. Scape on epigynum. Scale lines: 10  $\mu$ m (512, 517, 518, 520), 20  $\mu$ m (513, 514, 516), 50  $\mu$ m (511, 522), 100  $\mu$ m (510, 515, 521), 200  $\mu$ m (519), 300  $\mu$ m (509).





**Figs. 523-526.** *Belisana doloduo*. 523, 524. Left male pedipalp, prolateral (523) and retrolateral (524) views. 525. Male chelicerae, frontal view. 526. Cleared female genitalia, dorsal view. Scale lines: 0.3 mm (523, 524), 0.2 mm (525, 526).

*Variation.* Tibia 1 in other male: 4.0.

*Female.* In general similar to male; tibia 1: 3.55 (missing in other females). Epigynum very simple externally, pockets 90  $\mu\text{m}$  apart; dorsal view as in Fig. 526.

*Distribution.* Known from type locality only (Fig. 80).

*Material examined.* INDONESIA: *Sulawesi*: Dumoga: type above, together with 3♂4♀ (RMNH).

***Belisana marena*, new species**

(Figs. 527-544)

*Type.* Male holotype from Marena, Lore Lindu Reserve [ $\sim 1^{\circ}18'S$ ,  $120^{\circ}05'E$ ], North Sulawesi, Indonesia; from leaves, July 23-24, 1982 (P. R. & C. L. Deeleman) in RMNH.

*Etymology.* The species name is a noun in apposition, taken from the type locality.

*Diagnosis.* Relatively large, long-legged species with cylindrical opisthosoma; distinguished from similar congeners by the shapes of procurus, bulbal projections (especially the embolus) and the male chelicerae (Figs. 527-530).

*Male (holotype).* Total length 1.8 (1.9 with clypeus), carapace width 0.67. Leg 1: 19.85 (5.0 + 0.3 + 5.05 + 7.5 + 2.0), tibia 2: 3.3, tibia 3: 1.8, tibia 4: 2.75; tibia 1 L/d: 82. Habitus similar to *B. tambligan* (cf. Fig. 54). Prosoma and legs ochre-yellow, opisthosoma pale ochre-grey. Ocular area barely elevated, thoracic furrow absent; distance PME-PME 170  $\mu\text{m}$ ; diameter PME 60  $\mu\text{m}$ ; distance PME-ALE  $\sim 20$   $\mu\text{m}$ . Clypeus unmodified. Sternum slightly wider than long (0.48/0.42). Chelicerae as in Figs. 529, 530, and 536, tips of frontal apophyses 300  $\mu\text{m}$  apart. Palps as in Figs. 527 and 528; trochanter with wide retrolateral apophysis, femur without dorsal apophysis (only barely visible hump retrolatero-dorsally), procurus with distinctive distal sclerite (prolateral view); bulb with slightly curved (not hooked) apophysis (Fig. 533), with distinctive finger-like projection on embolus (probably containing the sperm duct). Retrolateral trichobothrium of tibia 1 at 10%; legs without spines, curved hairs, and vertical hairs; tarsus 1 with  $\sim 25$  pseudosegments, fairly distinct. Gonopore and ALS as in Figs. 537 and 539.

*Variation.* Tibia 1 in 3 other males: 5.0, 5.1, 5.6; distance between tips of cheliceral apophyses: 290, 320, 335  $\mu\text{m}$ . Two males from southern Sulawesi are assigned tentatively: their palps appear identical (both in shape and size) but the cheliceral apophyses are shorter and closer together (distance between tips: 220, 265  $\mu\text{m}$ ), and they are in general smaller and paler; tibia 1 in these males: 4.0, 4.7.

*Female.* In general similar to male; tibia 1 in 5 females: 3.4-4.0 (mean 3.74). Epigynum very simple externally (Fig. 544), pockets barely visible in dissecting microscope, 305  $\mu\text{m}$  apart; dorsal view as in Fig. 531. Palp tip (with tarsal organ) and spinnerets as in Figs. 540 and 541.

*Distribution.* Known from two localities in Sulawesi (Fig. 80; specimens from southern Sulawesi are assigned tentatively).

*Material examined.* INDONESIA: *Sulawesi*: Marena: type above, together with 5♂7♀ (RMNH).

Assigned tentatively: *Sulawesi*: 55 km from Ujungpandang and 23 km from Camba [ $\sim 4^{\circ}47'S$ ,  $119^{\circ}57'E$ ], forest on limestone, Aug. 14, 1980 (P. R. & C. L. Deeleman), 2♂ (RMNH).

***Belisana kendari*, new species**

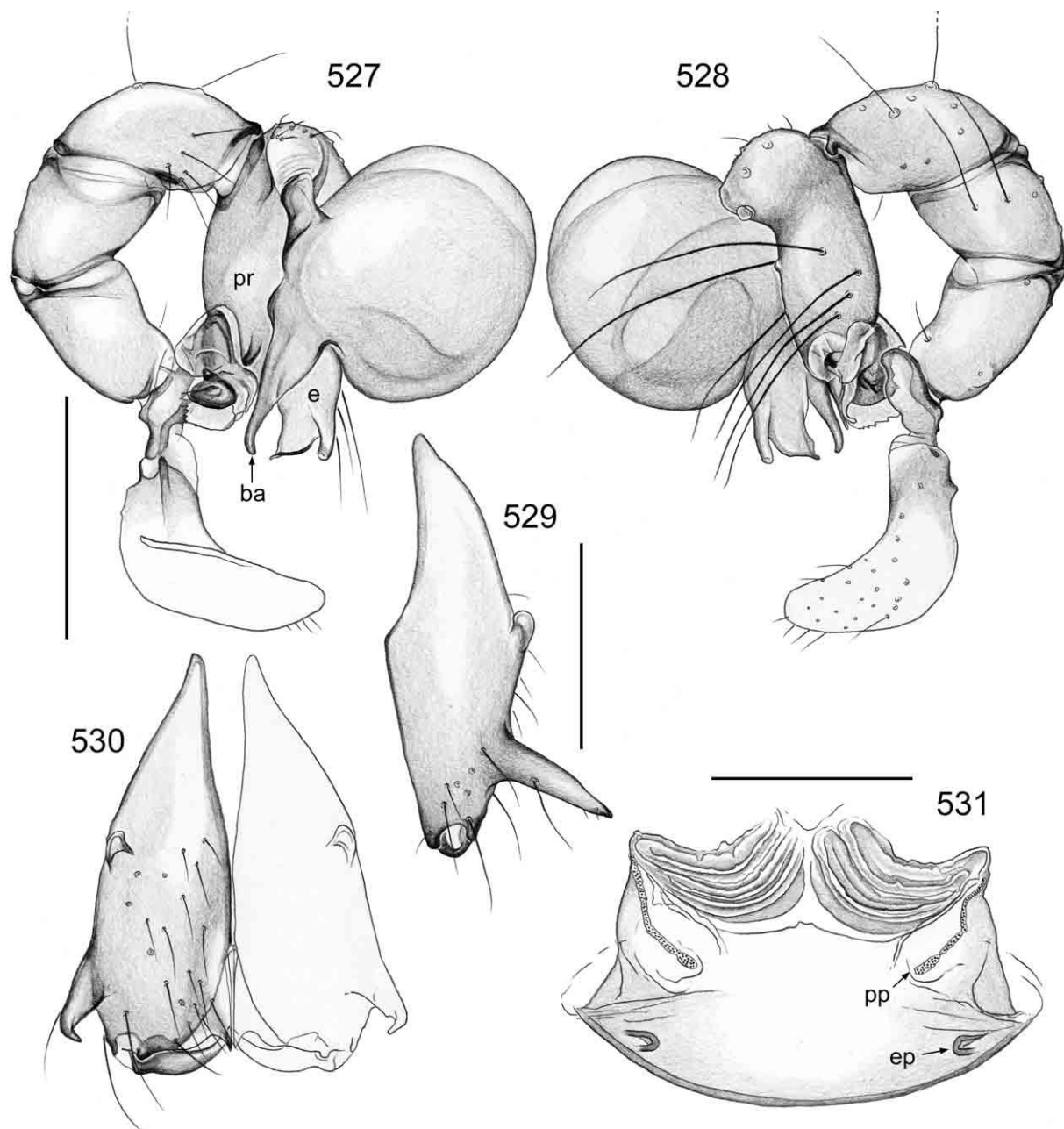
(Figs. 545-549, 554-560)

*Type.* Male holotype from forest 40 km W of Kendari [ $\sim 3^{\circ}58'S$ ,  $122^{\circ}15'E$ ], Sulawesi; Aug. 12, 1980 (P. R. & C. L. Deeleman), in RMNH.

*Etymology.* The species name is a noun in apposition, taken from the type locality.

*Diagnosis.* Relatively large, long-legged species with cylindrical opisthosoma; distinguished from similar congeners by the shapes of procurus and bulbal apophyses (Figs. 545, 546); from many also by the unmodified male palpal femur and the male chelicerae (apophyses close together, Fig. 547).

*Male (holotype).* Total length 1.8 (1.9 with clypeus), carapace width 0.67. Leg 1: 20.85 (5.15 + 0.3 + 5.3 + 8.4 + 1.7), tibia 2: 3.3, tibia 3 missing, tibia 4: 2.9; tibia 1 L/d: 80. Habitus similar to *B. tambligan* (cf. Fig. 54). Prosoma and legs pale ochre-yellow, sternum whitish, opisthosoma pale ochre-grey. Ocular area barely elevated, thoracic furrow absent; distance PME-PME 160  $\mu\text{m}$ ; diameter PME 65  $\mu\text{m}$ ; distance PME-ALE  $\sim 20$   $\mu\text{m}$ . Clypeus unmodified. Sternum about as wide as long (0.46). Chelicerae as in Fig. 547, tips of frontal apophyses 35  $\mu\text{m}$  apart. Palps as in Figs. 545 and 546; trochanter with rounded retrolateral and ventral apophyses, femur without dorsal apophysis, procurus very short, with complex distal elements (Figs. 554, 555, 558) bent ventrally (Figs. 546, 554); bulb with long curved apophysis and membranous embolus (Fig. 555). Tarsal organ capsulate (Fig. 556). Retrolateral trichobothrium of



**Figs. 527-531.** *Belisana marena*. 527, 528. Left male pedipalp, prolateral (527) and retrolateral (528) views. 529, 530. Male chelicerae, lateral and frontal views. 531. Cleared female genitalia, dorsal view. Scale lines: 0.3 mm (527, 528), 0.2 mm (529-531).

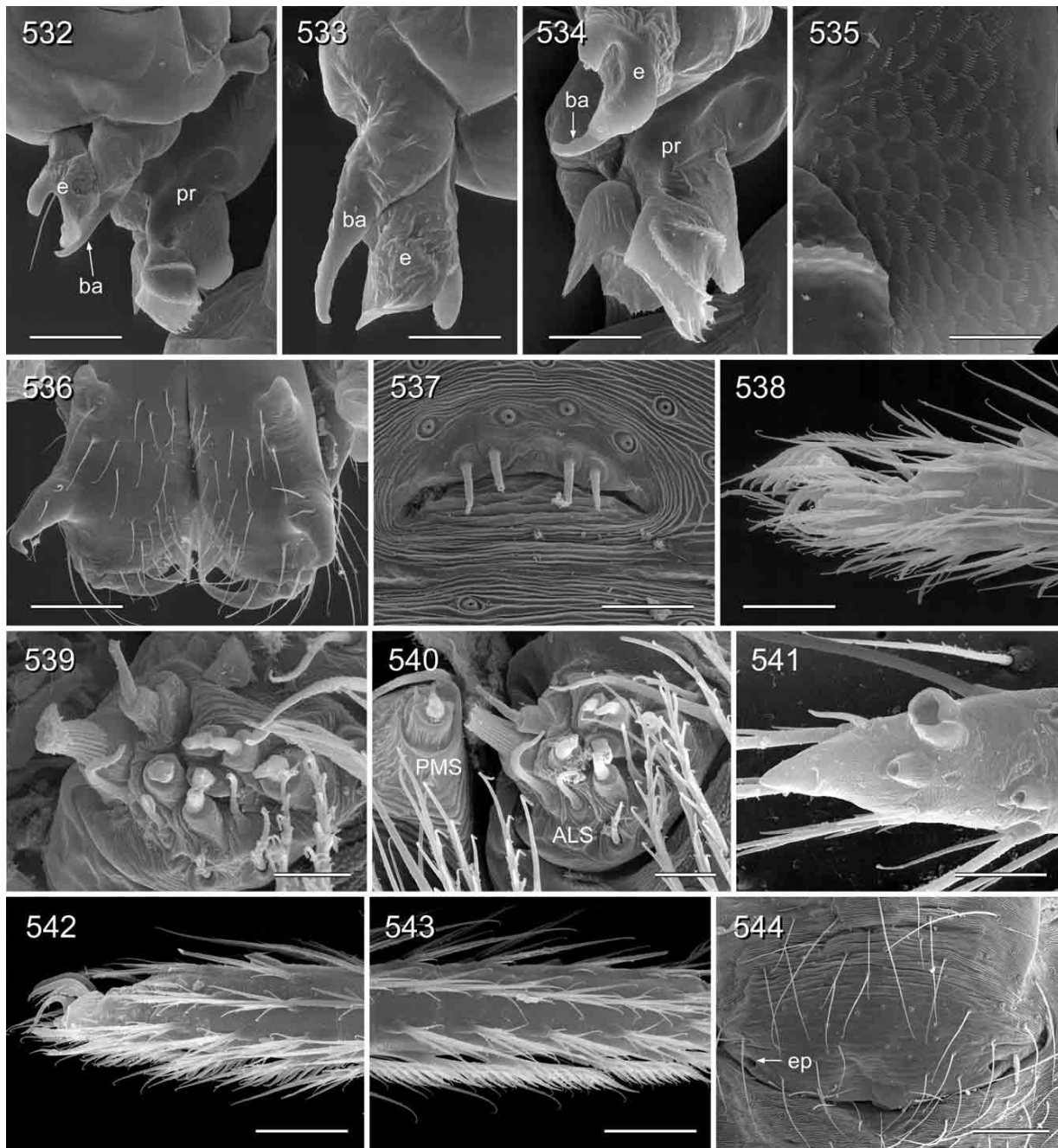
tibia 1 at 11%; legs without spines, curved hairs, and vertical hairs (most hairs missing); pseudosegments not visible in dissecting microscope. Spinnerets and gonopore as in Figs. 557 and 559.

*Variation.* Tibia 1 in 5 other males: 4.5-4.8 (mean 4.66).

*Female.* In general similar to male; tibia 1 in 6 females: 3.2-3.6 (mean 3.52). Epigynum very simple externally (Fig. 560), pockets barely visible in dissecting microscope, 20  $\mu$ m apart (Fig. 548); dorsal view as in Fig. 549.

*Distribution.* Known from type locality only (Fig. 80).

*Material examined.* INDONESIA: Sulawesi: 40 km W Kendari: type above, together with 5♂9♀, in RMNH.

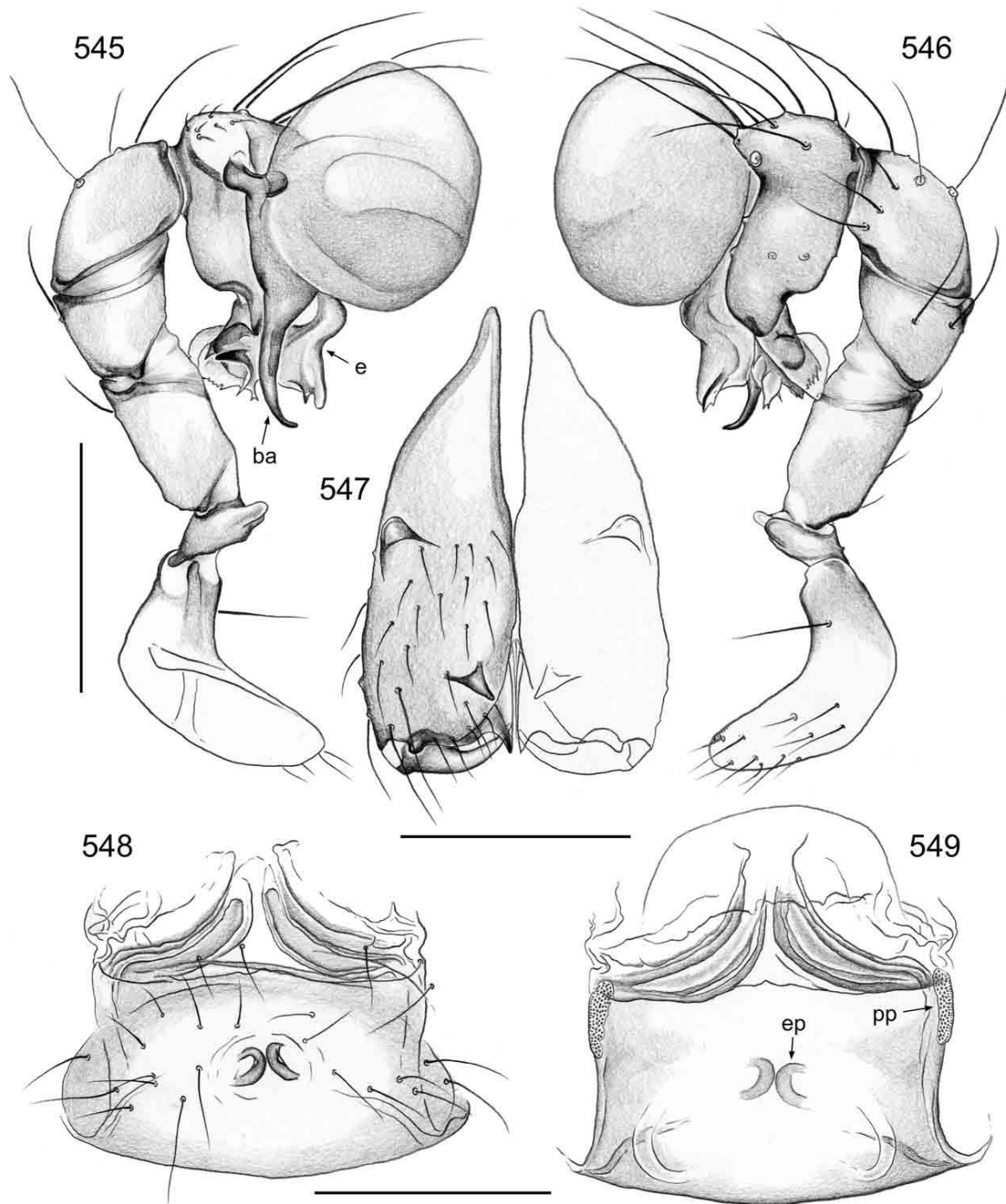


**Figs. 532-544.** *Belisana marena*. 532. Procursus and bulb, prolateral view. 533. Projections of left genital bulb, prolateral view. 534. Right procurus and bulbal projections, prolatero-dorsal (slightly distal) view. 535. Detail of procurus (cf. Fig. 532). 536. Male chelicerae, frontal view. 537. Male gonopore with epiandrous spigots. 538. Male tarsus 1 tip. 539. Male ALS. 540. Female ALS and PMS. 541. Tip of female palp with tarsal organ, dorso-lateral view. 542. Female tarsus 4 tip. 543. Detail of female tarsus 4 with comb-hairs. 544. Epigynum, ventral view. Scale lines: 10  $\mu$ m (539, 540), 20  $\mu$ m (535, 541), 30  $\mu$ m (537, 538, 542, 543), 60  $\mu$ m (533, 534), 100  $\mu$ m (532, 536, 544).

***Belisana nahtanoj*, new species**

(Figs. 550-553, 561-567)

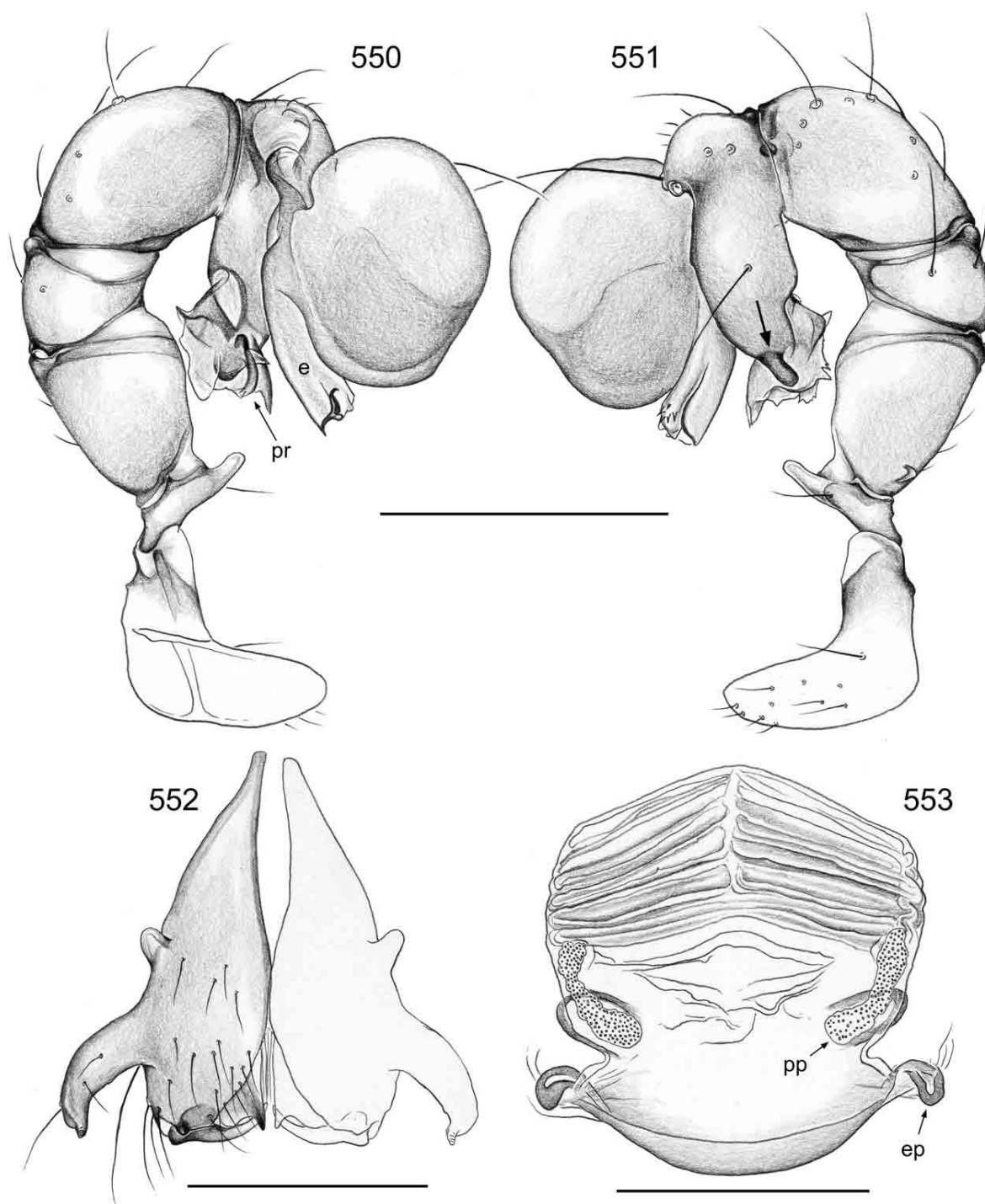
*Type.* Male holotype from forest on limestone, 55 km from Ujungpandang and 23 km from Camba [ $\sim 4^{\circ}47'S$ ,  $119^{\circ}57'E$ ], Sulawesi, Indonesia; Aug. 14, 1980 (P. R. & C. L. Deeleman), in RMNH.



**Figs. 545-549.** *Belisana kendari*. 545, 546. Left male pedipalp, prolateral (545) and retrolateral (546) views. 547. Male chelicerae, frontal view. 548, 549. Cleared female genitalia, ventral (548) and dorsal (549) views. Scale lines: 0.3 mm (545, 546), 0.2 mm (547-549).

*Etymology.* The species name is an arbitrary combination of letters, used as a noun in apposition.

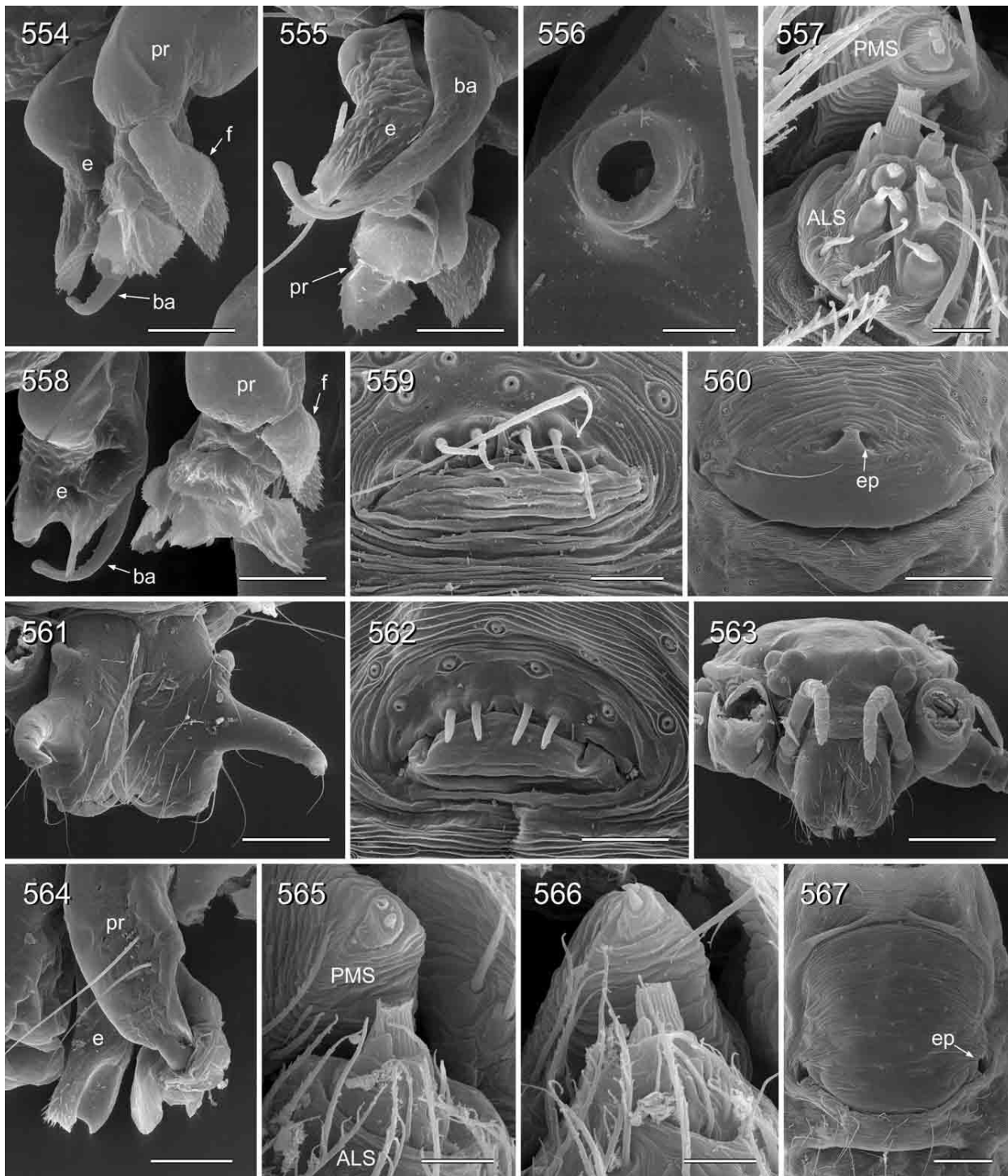
*Diagnosis.* Medium-sized, long-legged, very pale species with cylindrical opisthosoma; distinguished from similar congeners by the shape of the procurus (dark rounded sclerite retrolaterally, Figs. 551, 564; similar to *B. jimi*, cf. Fig. 569), the bulbal projections (no hooked or curved sclerite, Figs. 550, 551); from many also by the widely spread male cheliceral apophyses (Fig. 552).



**Figs. 550-553.** *Belisana nahtanoj*. 550, 551. Left male pedipalp, prolateral (550) and retrolateral (551) views. 552. Male chelicerae, frontal view. 553. Cleared female genitalia, dorsal view. Scale lines: 0.3 mm (550, 551), 0.2 mm (552, 553).

*Male (holotype)*. Total length 1.5 (1.6 with clypeus), carapace width 0.60. Leg 1: 12.7 (3.3 + 0.2 + 3.3 + 4.8 + 1.1), tibia 2: 2.1, tibia 3: 1.1, tibia 4 missing; tibia 1 L/d: 62. Habitus similar to *B. tambligan* (cf. Fig. 54), but with abdominal spots (three pairs of distinct brown spots dorsally). Prosoma and legs very pale ochre-yellow, sternum whitish. Ocular area barely elevated, thoracic furrow absent; distance PME-PME 160  $\mu$ m; diameter PME 45  $\mu$ m; distance





**Figs. 554-567.** *Belisana kendari* (554-560) and *B. nahtanoj* (561-567). 554. Left procursus tip and bulbal projections, retrolateral view. 555. Right procursus tip and bulbal projections, prolateral (slightly distal) view. 556. Male palpal tarsal organ. 557. Female ALS and PMS. 558. Left procursus tip and bulbal projections, dorsal view. 559. Male gonopore with epiandrous spigots. 560. Epigynum, ventral view. 561. Male chelicerae, frontal view. 562. Male gonopore with epiandrous spigots. 563. Female prosoma, frontal view. 564. Left procursus and embolus, retrolateral view. 565. Male ALS and PMS. 566. Female ALS and PMS. 567. Epigynum, ventral view. Scale lines: 10  $\mu\text{m}$  (556, 557, 565, 566), 20  $\mu\text{m}$  (559), 30  $\mu\text{m}$  (562), 50  $\mu\text{m}$  (555, 558), 60  $\mu\text{m}$  (554), 70  $\mu\text{m}$  (564), 100  $\mu\text{m}$  (560, 561, 567), 200  $\mu\text{m}$  (563).

PME-ALE ~20  $\mu\text{m}$ . Clypeus unmodified. Sternum about as wide as long (0.40). Chelicerae as in Figs. 552 and 561, apophyses in lateral view approximately perpendicular to paturon, tips of apophyses 310  $\mu\text{m}$  apart. Palps as in Figs. 550 and 551; trochanter with short retrolateral and longer ventral, weakly sclerotized, finger-like apophysis, femur with small dorsal apophysis, procurus with distinctive sclerite retrolaterally, complex membranous tip (Fig. 564); bulb without hooked apophysis, with dark spine distally on embolus (Fig. 550). Retrolateral trichobothrium of tibia 1 at 8%; legs without spines, curved hairs, and vertical hairs; pseudosegments not seen in dissecting microscope. Gonopore as in Fig. 562. ALS with only two spigots each (Fig. 565).

*Variation.* Tibia 1 in 8 other males: 3.3-3.6 (mean 3.48); abdominal spots variably distinct. The male (together with 4 females) from Dumoga is assigned tentatively to this species: palps and chelicerae are very similar, only the tips of procurus and bulbal projections differ slightly, but the ventral trochanter apophysis is shorter, and the opisthosoma has no spots; tibia 1 in this male: 3.3; distance between cheliceral apophyses: 290  $\mu\text{m}$ .

*Female.* In general similar to male, including abdominal spots; tibia 1 in 12 females from type locality: 2.8-3.1 (mean 2.89). Epigynum very simple externally (Fig. 567), pore plates visible through cuticle, pockets 305  $\mu\text{m}$  apart; dorsal view as in Fig. 553. ALS with only two spigots each (Fig. 566). Tibia 1 in 4 females from Dumoga: 2.7-2.9.

*Distribution.* Known from two localities on Sulawesi (Fig. 80; the specimens from northern Sulawesi are assigned tentatively).

*Material examined.* INDONESIA: *Sulawesi*: 55 km from Ujungpandang and 23 km from Camba: type above, together with 10♂14♀ (RMNH).

Assigned tentatively: *Sulawesi*: Dumoga, watershed protection near Doloduo [0°31'N, 123°55'E], primary forest, July 27-30, 1982 (P. R. & C. L. Deeleman), 1♂4♀ (RMNH).

#### ***Belisana jimi*, new species**

(Figs. 55, 568-570)

*Type.* Male holotype from Jimi River Valley [5°16'S, 144°14'E], Western Highlands Province, Papua New Guinea; under bark, upper stem, *Araucaria hunsteinii*, July 20, 1972 (B. Gray), in AMS (KS 13043).

*Etymology.* The species name is a noun in apposition, taken from the type locality.

*Diagnosis.* Medium-sized, long-legged species with oval opisthosoma; distinguished from similar congeners by the shape of the procurus (dark rounded sclerite retrolaterally, Fig. 569; similar to *B. nahtanoj*), and by the shape of the embolus (Figs. 568, 569); from many species also by the widely spaced male cheliceral apophyses (Fig. 570).

*Male (holotype).* Total length 1.6 (1.7 with clypeus), carapace width 0.60. Leg 1: 13.45 (3.5 + 0.25 + 3.6 + 4.9 + 1.2), tibia 2: 2.3, tibia 3: 1.2, tibia 4: 2.3; tibia 1 L/d: 68. Habitus as in Fig. 55. Prosoma and legs pale ochre-yellow, opisthosoma pale grey. Ocular area not elevated, thoracic furrow absent; distance PME-PME 140  $\mu\text{m}$ ; diameter PME 60  $\mu\text{m}$ ; distance PME-ALE 15  $\mu\text{m}$ . Clypeus unmodified. Sternum slightly wider than long (0.44/0.40). Chelicerae as in Fig. 570, frontal apophyses in lateral view slightly pointing downwards, tips 320  $\mu\text{m}$  apart. Palps as in Figs. 568 and 569; trochanter with very short rounded retrolateral apophysis, femur with small dorsal apophysis, procurus with distinctive retrolateral sclerite and large hinged sclerite distally, bulb large, embolus with strong distal spine. Retrolateral trichobothrium of tibia 1 at 7%; legs without spines, curved hairs, and vertical hairs (possibly more vertical hairs on metatarsi than usual, many hairs missing); tarsus 1 with >15 pseudosegments, distally fairly distinct.

*Variation.* One male with large black spots on opisthosoma visible through cuticle dorsally; one male with distal hinged sclerite on procurus directed ventrally; tibia 1 missing in other males.

*Female.* Unknown.

*Distribution.* Known from two localities in northern Papua New Guinea (Fig. 82).

*Material examined.* PAPUA NEW GUINEA: *Western Highlands*: type above; *Madang*: Baiteta forest [5°01'S, 145°45'E], June 9, 1995 (O. Missa), fogging of *Sarcocephalus* sp. (Rubiaceae), 1♂ (AR 13) (IRSB); same locality, April 18, 1996 (O. Missa), canopy fogging, 1♂ (AR 44) (IRSB).

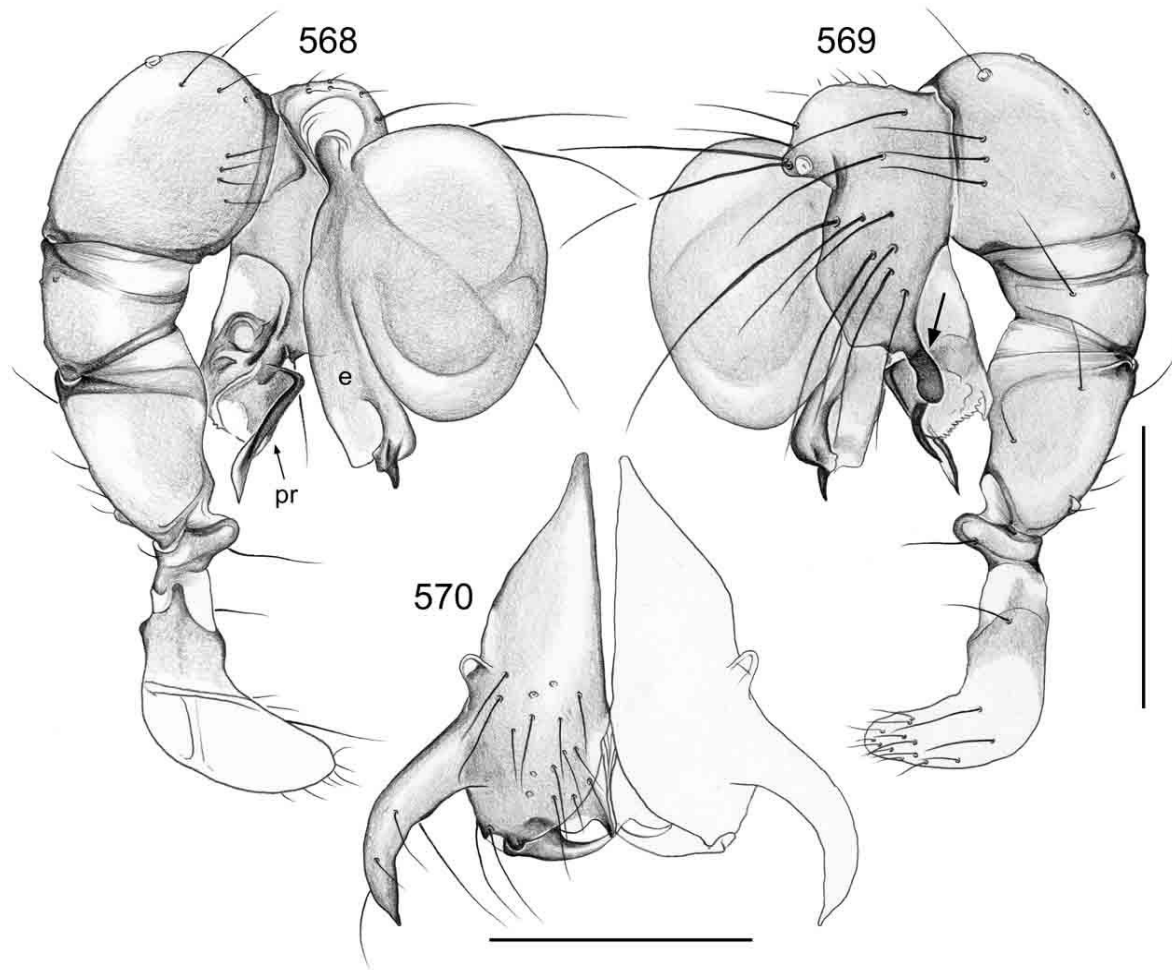
#### ***Belisana wau*, new species**

(Figs. 29, 30, 571-574)

*Type.* Male holotype from Wau [7°20'S, 146°43'E], Morobe Province, Papua New Guinea; under bark, lower stem, *Araucaria cunninghamii*, Sept. 22, 1970 (B. Gray), in AMS (KS 13255).

*Etymology.* The species name is a noun in apposition, taken from the type locality.

*Diagnosis.* Tiny, short-legged species with globular opisthosoma; easily distinguished from similar congeners by the male chelicerae with widely spaced apophyses and additional pair of small frontal cones (Fig. 573), by the shape



**Figs. 568-570.** *Belisana jimi*. 568, 569. Left male pedipalp, prolateral (568) and retrolateral (569) views (arrow points to distinctive sclerite on procurus). 570. Male chelicerae, frontal view. Scale lines: 0.3 mm (568, 569), 0.2 mm (570).

of the procurus (Fig. 572), and by the bulbal projections (large flat apophysis and embolus with subdistal spine, Fig. 571).

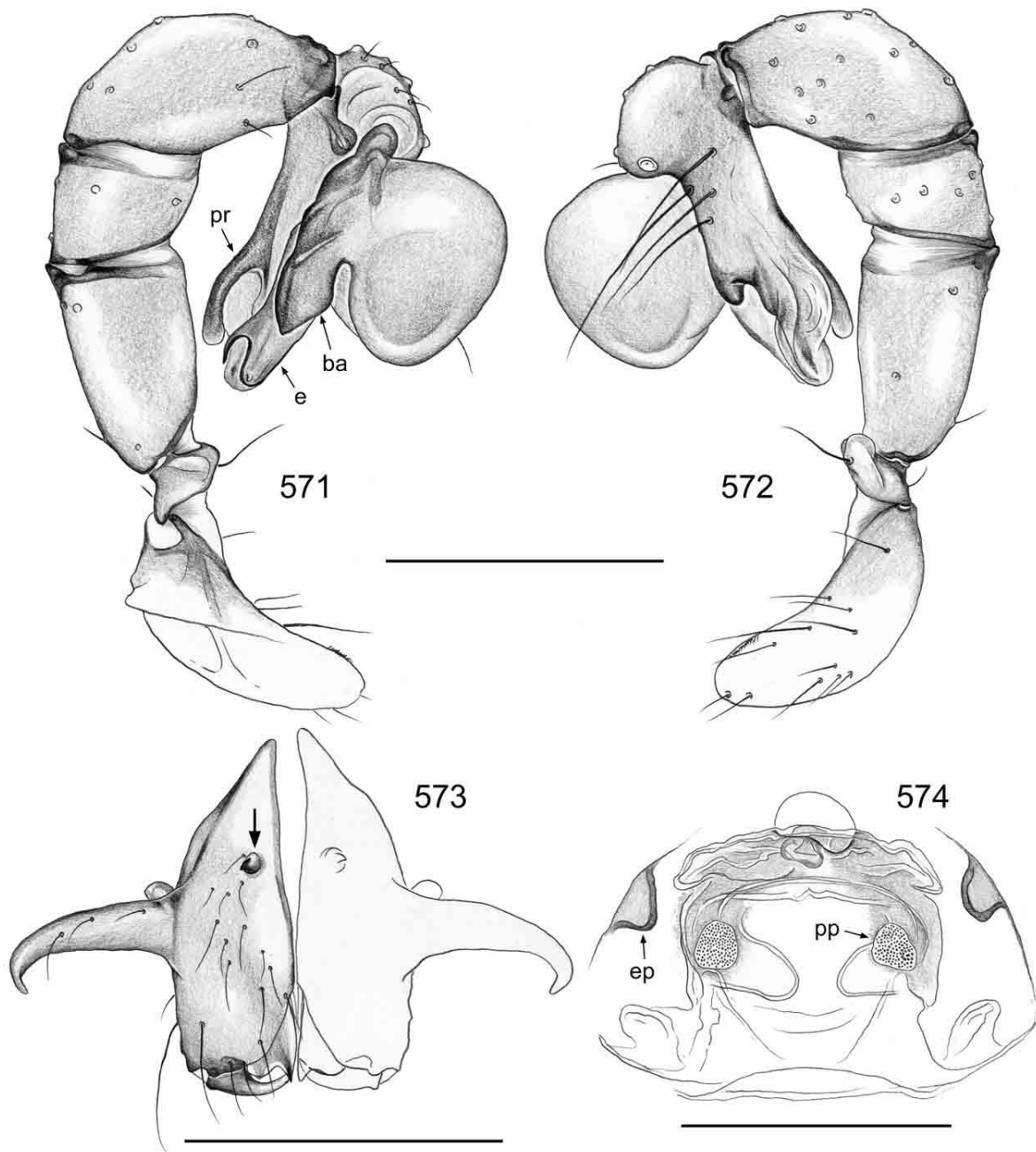
*Male (holotype)*. Total length 1.2 (1.3 with clypeus), carapace width 0.57. Leg 1: 5.69 (1.50 + 0.23 + 1.43 + 1.70 + 0.83), tibia 2 missing, tibia 3: 0.73, tibia 4: 1.07; tibia 1 L/d: 25. Habitus as in Figs. 29 and 30. Carapace ochre-yellow, medially and laterally light brown, sternum and legs pale ochre-yellow, opisthosoma ochre-grey. Ocular area distinctly elevated, thoracic furrow shallow but distinct; distance PME-PME 90  $\mu$ m; diameter PME 70  $\mu$ m; distance PME-ALE 10  $\mu$ m. Clypeus unmodified. Sternum slightly wider than long (0.40/0.36). Chelicerae as in Fig. 573, with distinctive pair of small pointed frontal apophyses proximally, tips of widely spaced apophyses 485  $\mu$ m apart. Palps as in Figs. 571 and 572; trochanter with short rounded retrolateral apophysis, femur without dorsal hump, procurus with distinctive dorsal projection and ventral curved sclerite, bulb with distinctive flat sclerite and embolus with subdistal spine. Retrolateral trichobothrium of tibia 1 at 29%; legs without spines, curved hairs, and vertical hairs; tarsus 1 with ~10 pseudosegments, barely visible.

*Variation*. Tibia 1 in 2 other males: 1.40, 1.43.

*Female*. In general similar to male; tibia 1: 1.40. Epigynum large simple plate, pair of pockets 360  $\mu$ m apart (the epigynum in Fig. 574 was cleared too strongly, so the distance may not be accurate); frontally with darker internal round structure; dorsal view as in Fig. 574. ALS spigots not seen.

*Distribution*. Known only from type locality (Fig. 82).

*Material examined*. PAPUA NEW GUINEA: *Morobe*: Wau: type above; same collection data, 1♂ (AMS KS 13247); same collection data but lowest stem, 1♂1♀ (AMS KS 13246).

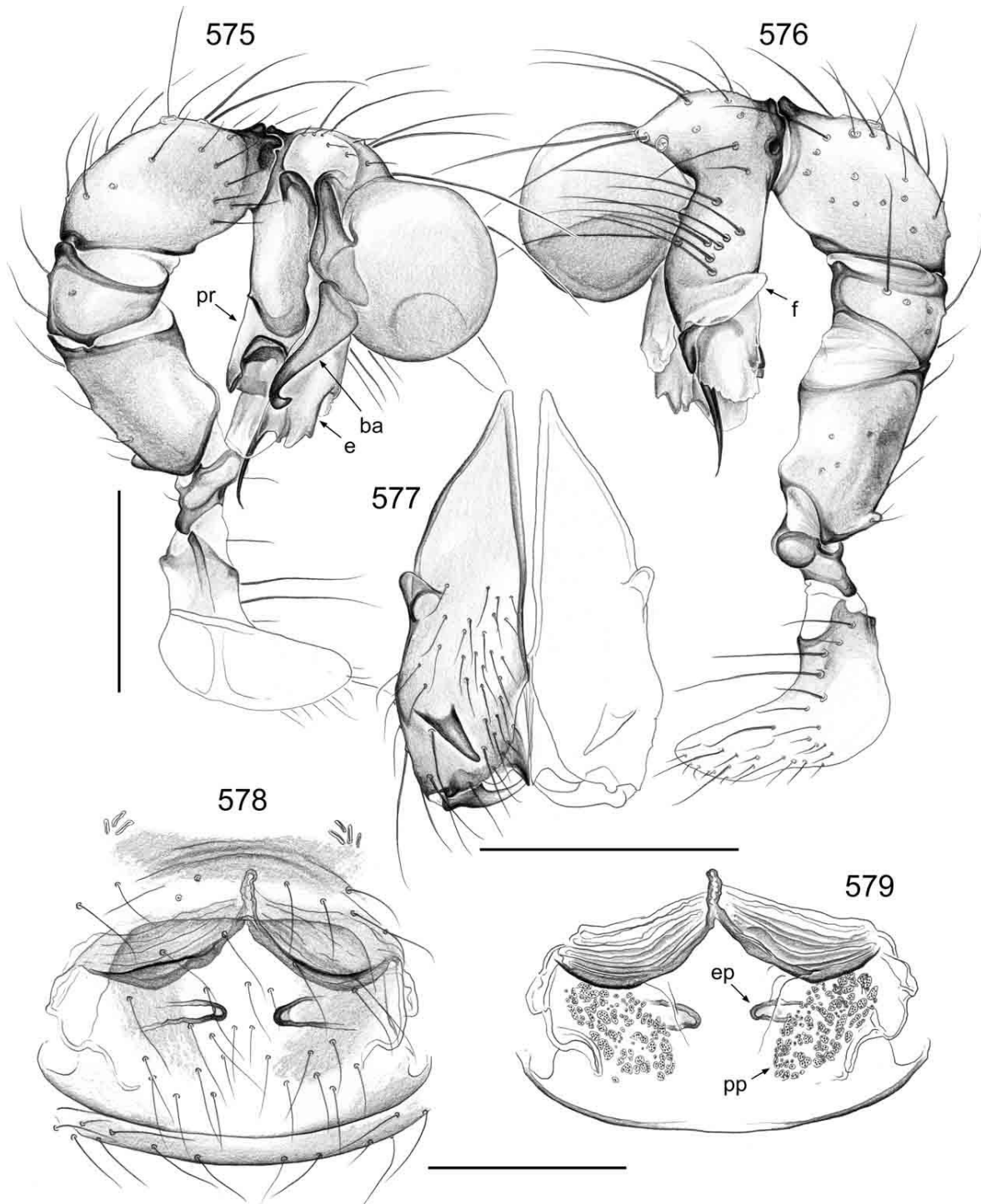


**Figs. 571-574.** *Belisana wau*. 571, 572. Left male pedipalp, prolateral (571) and retrolateral (572) views. 573. Male chelicerae, frontal view (arrow points to distinctive proximal cone-shaped apophysis). 574. Cleared female genitalia, dorsal view. Scale lines: 0.3 mm.

***Belisana akebona* (Komatsu 1961), n. comb.**  
(Figs. 15, 16, 63, 575-579)

*Spermophora akebona* Komatsu 1961: 27-29, 46, pl. 4, figs. 15a-i, 17a-e; Shinkai 1969: 11, figs. 6-12 (not seen); Yaginuma 1970: 646; Yaginuma 1972: 289-290, fig. 15; Yaginuma 1986: 29, fig. 17.6p (figure copied from Yaginuma 1972); Irie 1989: 33-38, figs. 1-14; Chikuni 1989: 27, fig. 1.

*Types.* 1♂3♀ syntypes from Yôzawa-dô, Kamiyôzawa, Itsukaichi-chô (35°44'N, 139°13'E), Tokyo Prefecture, Japan; August 6, 1952 (T. Komatsu), not examined (not found in NSMT, H. Ono, pers. comm.).



**Figs. 575-579.** *Belisana akebona*. 575, 576. Left male pedipalp, prolateral (575) and retrolateral (576) views. 577. Male chelicerae, frontal view. 578, 579. Cleared female genitalia, ventral (578) and dorsal (579) views. Scale lines: 0.3 mm.

*Notes.* This species has been fairly well studied. Komatsu (1961) found it inside two lava caves (Tokyo Prefecture), but not outside. He noted some variation between specimens of the two caves, but considered these to be insufficient to justify creation of an additional species name. The web was described as dome-like, similar to *Pholcus* but with an extremely compact mesh.

Yaginuma (1972) reported on extensive collections around Mt. Fuji-san (Yamanashi and Shizuoka Prefectures) and other Prefectures on Honshu Island. He found the species both in caves and “in shady fields”, and gave a more detailed account of the supposed intraspecific variation.

Irie (1989) found the species on Kyushu Island and gave detailed illustrations of the genitalia of topotypical and newly collected material. His illustrations of the female genitalia suggest that the pockets are closer together in topotypical females than in females from Kyushu, which might indicate reproductive isolation. However, I have seen only a small percentage of the material available in Japanese collections, and have to leave this interesting problem to future, more detailed studies.

Finally, it should be noted that *B. amabilis* (Paik 1978) might be a synonym of *B. akebona*. Only the female of *B. amabilis* is known, but Paik's (1978) figure 3 of the internal female genitalia shows some suggestive similarities to Fig. 578 herein.

*Diagnosis.* Relatively large, long-legged species with oval opisthosoma; distinguished from relatives by the combination of procurus shape (with long spine), hooked bulbal apophysis, and short frontal cheliceral apophyses (Figs. 575-577).

*Male (Sakurai-shi).* Total length 2.0 (2.15 with clypeus), carapace width 0.83. Leg 1: 25.1 (6.0 + 0.4 + 6.3 + 10.3 + 2.1), tibia 2: 4.0, tibia 3: 2.4, tibia 4: 3.3, tibia 1 L/d: 89. Habitus as in Figs. 15 and 16. Carapace pale ochre-yellow, laterally light brown, sternum whitish, legs ochre-yellow, patellae and tibia-metatarsus joints brown, opisthosoma grey, few large darker marks visible through cuticle. Ocular area not elevated, barely separated from carapace, thoracic furrow absent; distance PME-PME 115  $\mu$ m; diameter PME 80  $\mu$ m; distance PME-ALE ~20  $\mu$ m. Clypeus unmodified. Sternum wider than long (0.62/0.56). Chelicerae as in Fig. 577, with pair of short frontal apophyses, tips 120  $\mu$ m apart. Palps as in Figs. 575 and 576; trochanter with rounded retrolateral apophysis, femur with proximo-dorsal hump, procurus with transparent retrolateral flap and long distal spine; bulb with hooked apophysis and relatively complex membranous embolus. Retrolateral trichobothrium of tibia 1 at 14%; legs without spines, curved hairs, and vertical hairs; tarsus 1 with >20 pseudosegments, only about 15 quite distinct distally.

*Variation.* The male described herein is from Sakurai-shi (about 300 km from the type locality) because the only specimen from the type locality (Yôzawa-dô) available to me (see below) was in extremely bad shape. However, there are some slight differences that will have to be reconsidered when more material is available (see also Notes above): the males from Yôzawa-dô have shorter spines on the procurus, a subdistal tooth on the bulbal apophysis (see fig. 4 in Irie 1989), and the bulbal apophysis is more strongly bent (see fig. 4 in Irie 1989). The male from Higashi-awakura-mura has the spine on the procurus even shorter, rounded at the tip and curved in a different direction. The male from Tsuzurase-dô (and probably also the males from Shiratake-dô, all of which are in very poor condition) has the cheliceral apophyses stronger and slightly more lateral (see fig. 5 in Irie 1989). For similar reports on variability that might turn out to represent inter-specific variation, see Irie (1989) and Yaginuma (1972).

*Female (Higashi-awakura-mura).* In general similar to male. Tibia 1 missing. Epigynum very simple externally, pockets 95  $\mu$ m apart (Fig. 578); dorsal view as in Fig. 579. ALS apparently with several spigots.

*Distribution.* Known from several localities on Honshu and Kyushu, Japan (Fig. 81).

*Material examined.* JAPAN: **Honshu:** *Tokyo Prefecture:* Yôzawa-shoyundô, Itsukaichi-machi, Nov. 27, 1988 (E. Shinkai), 2♂ (NSMT Ar4736); *Okayama Prefecture:* Higashi-awakura-mura, Nov. 14, 1992 (K. Nojima), 1♂1♀ (ZFMK); *Nara Prefecture:* Sakurai-shi [34°31'N, 135°53'E], Sept. 26, 2002 (K. Nojima), 1♂ (ZFMK); **Kyushu:** *Kumamoto Prefecture:* Tsuzurase-dô, Itsuki-mura [32°25'N, 130°52'E], Kumagun, Oct. 1, 1988 (T. Irie), 1♂1♀ (NSMT Ar4733); *Shiratake-dô, Yamae-mura* [33°28'N, 130°34'E], Kumagun, Oct. 10, 1988 (T. Irie), 3♂ (NSMT Ar4732); *Miyazaki Prefecture:* Matsuginari-no-ana, Shiba-son, Higashi-usuki-gun [32°30'N, 131°20'E], Sept. 18, 1988 and May 6, 1978 (T. Irie), 4♀ (NSMT Ar4734-5).

***Belisana junkoae* (Irie 1997), n. comb.**

(Figs. 580-584)

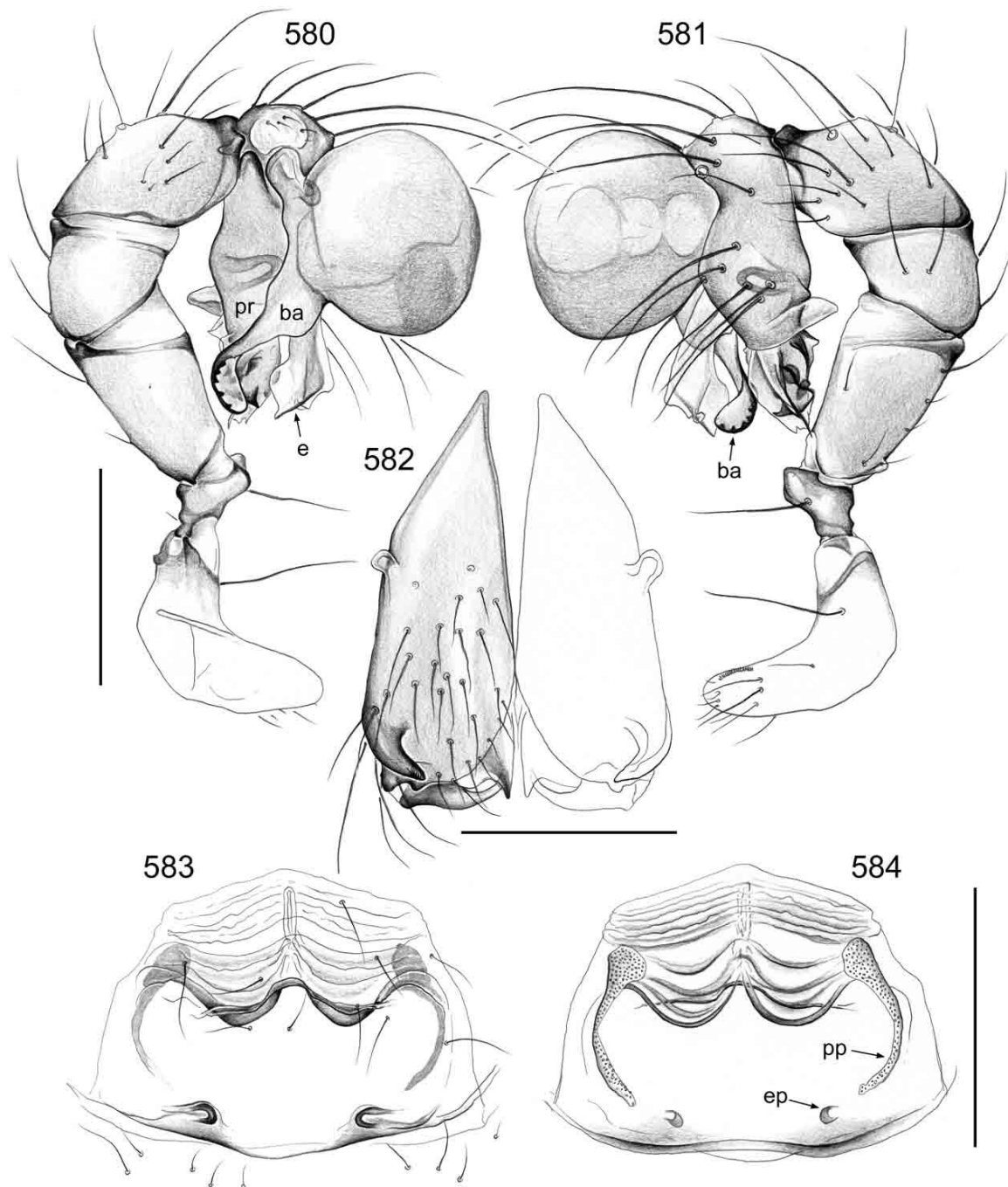
*Spermophora junkoae* Irie 1997: 136-137, figs. 8-11.

*Types.* Male holotype from Sonai-dake [24°23'N, 123°45'E], Iriomotejima, Okinawa Prefecture, Japan; July 30, 1991 (T. & J. Irie), in NSMT (Ar3568), examined. For other type material see below and Irie (1997).

*Diagnosis.* Relatively large, long-legged species with elongated and posteriorly elevated opisthosoma; easily distinguished from relatives by the unique shape of the bulbal apophysis (Fig. 580); also by the shape of the procurus (Fig. 581) and by the shape and position of the cheliceral apophyses (Fig. 582).

*Male* (paratype from Omoto-dake, Ishigaki). Total length 1.9 (2.0 with clypeus), carapace width 0.73. Leg 1: 15.4 (3.7 + 0.3 + 3.8 + 6.1 + 1.5), tibia 2: 2.55, tibia 3: 1.5, tibia 4: 2.1, tibia 1 L/d: 57. Habitus similar to *B. tambligan*





**Figs. 580-584.** *Belisana junkoae*. 580, 581. Left male pedipalp, prolateral (580) and retrolateral (581) views. 582. Male chelicerae, frontal view. 583, 584. Cleared female genitalia, ventral (583) and dorsal (584) views. Scale lines: 0.3 mm (580, 581, 583, 584), 0.2 mm (582).

(cf. Fig. 54). Prosoma and legs very pale ochre-yellow, sternum and opisthosoma pale whitish. Ocular area not elevated, not separated from carapace, thoracic furrow absent; distance PME-PME 180  $\mu$ m; diameter PME 55  $\mu$ m; distance PME-ALE  $\sim$ 20  $\mu$ m. Clypeus unmodified. Sternum as wide as long (0.48). Chelicerae as in Fig. 582, with pair of short, curved frontal apophyses, tips 175  $\mu$ m apart. Palps as in Figs. 580 and 581; trochanter with short retrolateral apophysis, procurus complex distally but difficult to resolve, bulb with distinctive spoon-shaped apophysis with small black cones and membranous embolus. Retrolateral trichobothrium of tibia 1 at 11%; legs without spines, curved and vertical hairs, tarsus 1 with about 15 pseudosegments, distally quite distinct.

*Variation.* Tibia 1 in 8 other males from Japan: 4.15-4.9 (mean 4.42); 4 males from Taiwan: 3.83-4.17. The very bleached holotype is from a different island than the paratype described above, but direct comparison of palps and chelicerae revealed no difference. The males from Taiwan have minimally smaller palps.

*Female.* In general similar to male. Tibia 1 in 6 females from Japan: 3.2-3.75 (mean: 3.51); 6 females from Taiwan: 3.2-3.6 (mean: 3.36). Epigynum flat and very simple externally, with pair of pockets 175  $\mu\text{m}$  apart (Fig. 583); dorsal view as in Fig. 584. ALS with several spigots in addition to basic set of two.

*Distribution.* Known from Ishigakishima and Iriomotejima, Japan, and from Taiwan (Fig. 81).

*Material examined.* JAPAN: *Iriomotejima*: male holotype above; *Ishigakishima*: Banna-dake [24°22'N, 124°09'E], July 11, 1994 (T. Irie), 1♀ ('allotype') (NSMT-Ar3569); Omoto-dake [24°25'N, 124°11'E], July 10, 1994 (T. Irie), 7♂5♀ paratypes (NSMT-Ar4737); Arakawa, July 11, 1994 (T. Irie), 2♂1♀ paratypes (NSMT-Ar4739). TAIWAN: T'ai-pei (Taipei) and environs [25°01'N, 121°27'E], Oct. 1957 (T. Maa), 1♂1♀ (BPBM); "Wushei Nanto Hsien" [24°04'N, 121°30'E?], Oct. 1957 (T. Maa), 8♂~14♀ (mostly in poor condition) (BPBM).

***Belisana anhuiensis* (Xu & Wang 1984), n. comb.**

(Figs. 585-588)

*Spermophora anhuiensis* Xu & Wang 1984: 51-53, figs. 1a-h; Song 1987: 110-111, figs. 73a-d (figures copied from Xu & Wang 1984).

*Types.* Female holotype, male 'allotype', 5♂10♀ paratypes from Mt. Qiyun, Xiuning County [~29°47'N, 118°11'E], Anhui Province, China; Oct. 24, 1983 (Y. Xu, J. Wang), in HNU.

*Diagnosis.* Tiny, short-legged species with globular to slightly oval opisthosoma; distinguished from relatives by the combination of procurus shape (without spine), short curved bulbal apophysis, and short frontal cheliceral apophyses (Figs. 585-588).

*Male (paratype).* Total length 1.2 (1.3 with clypeus), carapace width 0.53. Leg 1 missing, tibia 2: 1.23, tibia 3: 0.93, tibia 4: 1.27. Prosoma and legs ochre-yellow, opisthosoma ochre-grey with some faint darker pattern dorsally. Ocular area barely elevated, not separated from carapace, thoracic furrow indicated by dark line but no indentation; distance PME-PME 90  $\mu\text{m}$ ; diameter PME 45  $\mu\text{m}$ ; distance PME-ALE ~20  $\mu\text{m}$ . Clypeus unmodified. Sternum wider than long (0.40/0.32). Chelicerae as in Figs. 587 and 588, with pair of short, hooked frontal apophyses, tips 125  $\mu\text{m}$  apart. Palps as in Figs. 585 and 586; trochanter with retrolateral apophysis (longer than appears in Fig. 586), procurus without spine but with possibly hinged distal structures, bulb with distinctive curved apophysis and simple embolus. Most hairs on legs missing.

*Female* (not examined). Epigynum simple and flat externally (Xu & Wang 1984: figs. 1b-d). Pockets not shown in original illustrations.

*Distribution.* Known from type locality only (Fig. 81).

*Material examined.* CHINA: *Anhui*: Mt. Qiyun: 1♂ paratype above.

***Belisana forcipata* (Tu 1994), n. comb.**

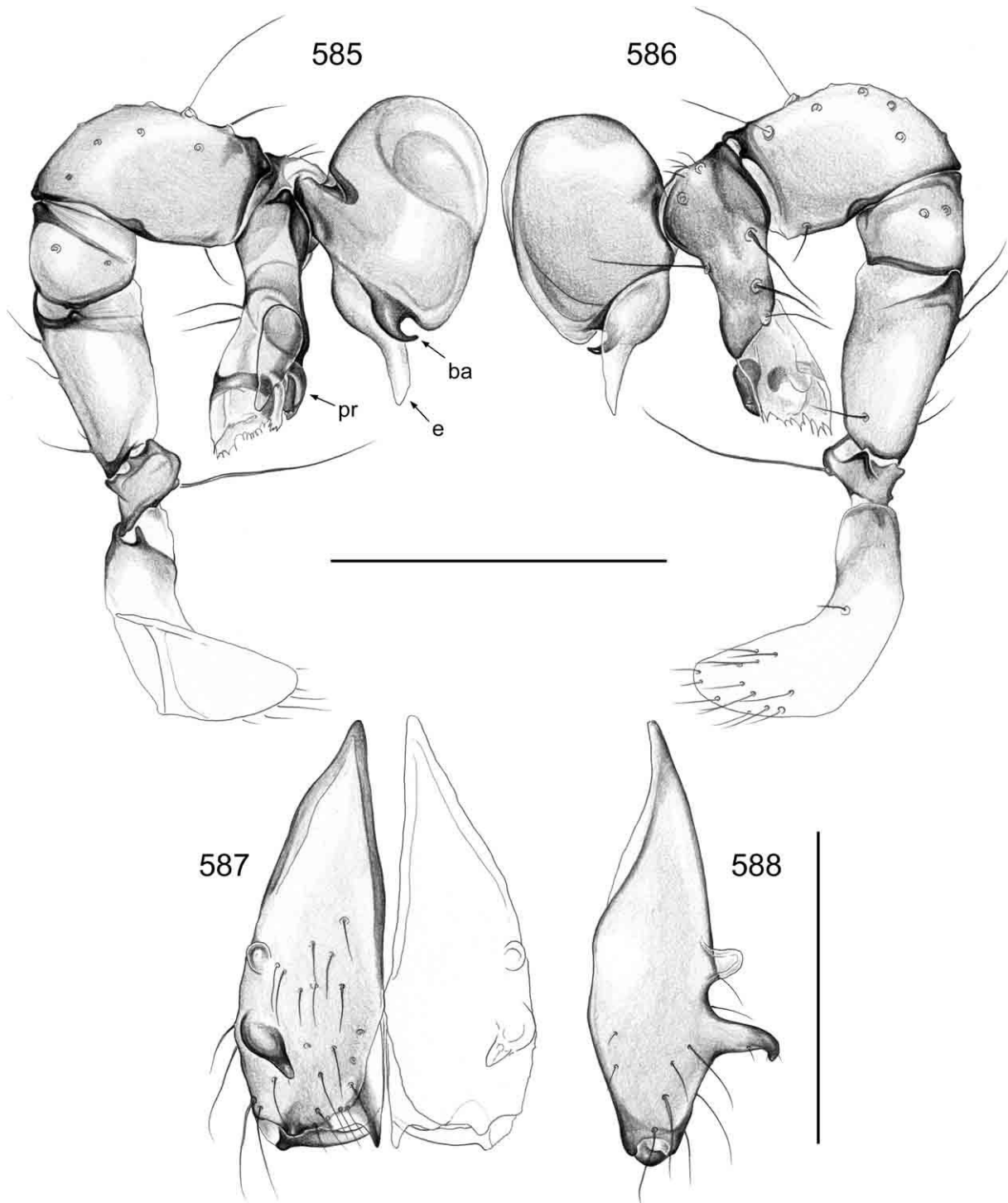
(Figs. 589-591)

*Spermophora forcipata* Tu 1994: 419-421, figs. 1-6; Song et al. 1999: 65, figs. 26x-z, a' (all information copied from Tu 1994).

*Types.* Female holotype, male 'allotype', 3♂2♀ paratypes from Mt. Wuyi [~27°N, 117°E], Fujian Province, China; July 14, 1986 (M.-S. Zhu), in HU (#86014).

*Diagnosis.* Relatively large, long-legged species with oval to cylindrical opisthosoma; distinguished from relatives by the shape of the procurus (spine and dorso-distal element) and by the strong bulbal apophysis (Figs. 589, 590).

*Male (paratype).* Total length 1.8 (1.9 with clypeus), carapace width 0.70. Leg 1: 14.6 (3.7 + 0.35 + 3.65 + 5.6 + 1.3), tibia 2: 2.2, tibia 3: 1.25, tibia 4: 2.1; tibia 1 L/d: 51. Habitus similar to *B. tambligan* (cf. Fig. 54). Prosoma and legs ochre-yellow (the marginal dark spots on the carapace described by Tu 1994 have apparently been lost), opisthosoma ochre-grey. Ocular area barely elevated, thoracic furrow absent; distance PME-PME 195  $\mu\text{m}$ ; diameter PME 55  $\mu\text{m}$ ; distance PME-ALE ~20  $\mu\text{m}$ . Clypeus unmodified. Sternum about as wide as long (0.40). Chelicerae as in Fig. 591, with pair of short frontal apophyses, tips 115  $\mu\text{m}$  apart. Palps as in Figs. 589 and 590; trochanter with retrolateral-ventral apophysis, femur with small retrolateral apophysis, procurus with distinctive dorso-distal sclerite and curved spine (Fig. 590), bulb with strong hooked apophysis and relatively complex embolus (Fig. 589). Retrolateral trichobothrium of tibia 1 at 9%; legs without spines, curved hairs, and vertical hairs (most hairs missing); tarsus 1 with >10 pseudosegments, very indistinct except a few distally.



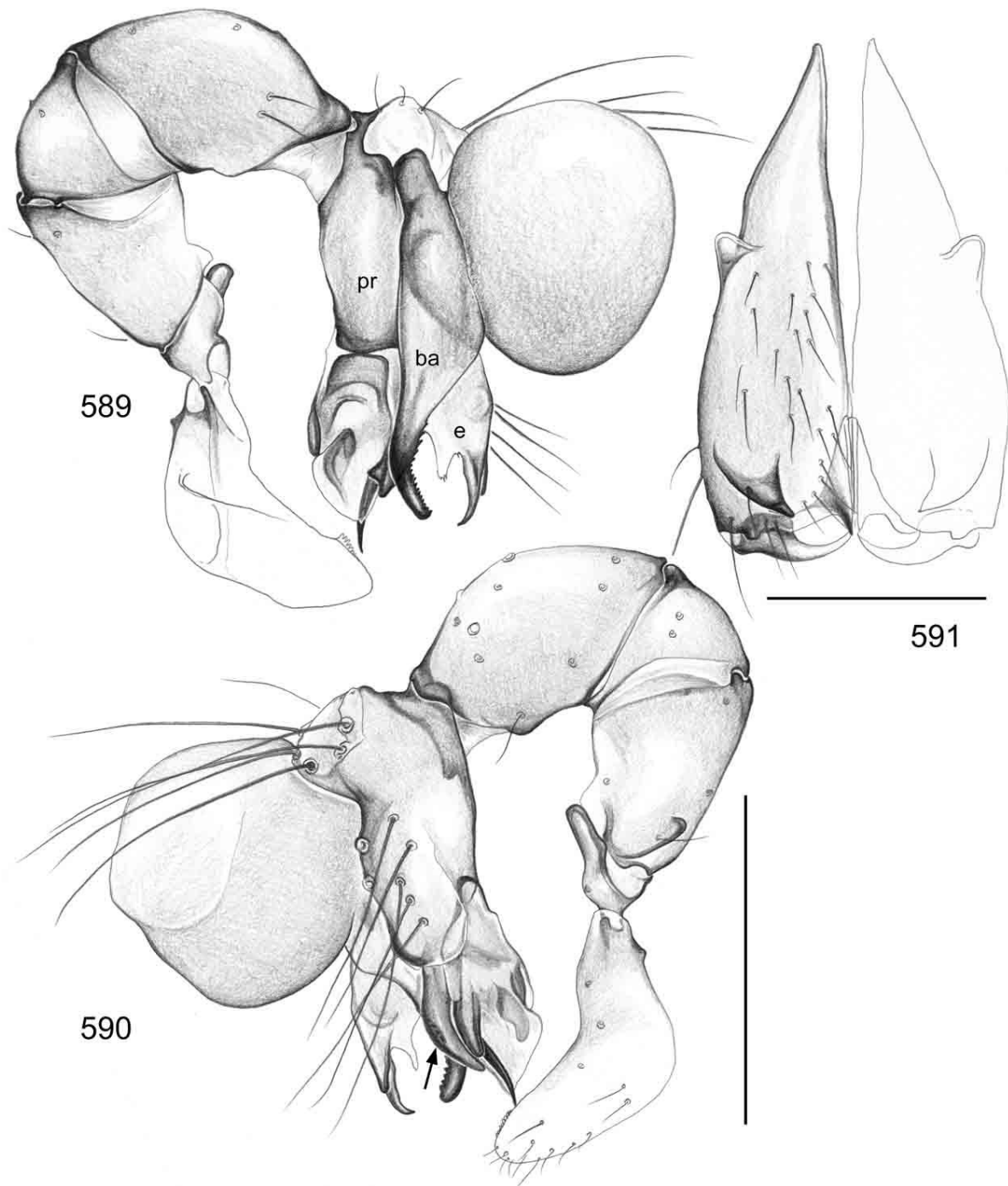
**Figs. 585-588.** *Belisana anhuiensis*. 585, 586. Left male pedipalp, prolateral (585) and retrolateral (586) views. 587, 588. Male chelicerae, frontal and lateral views. Scale lines: 0.3 mm (585, 586), 0.2 mm (587, 588).

*Variation.* Two paratypes with some dark marks dorsally on opisthosoma. Tibia 1 in other male: 4.0.

*Female* (not examined). Epigynum simple and flat externally (Tu 1994: figs. 1-3).

*Distribution.* Known from type locality only (Fig. 81).

*Material examined.* CHINA: Fujian: Mt. Wuyi: 3♂ paratypes above (both palps missing in one male).

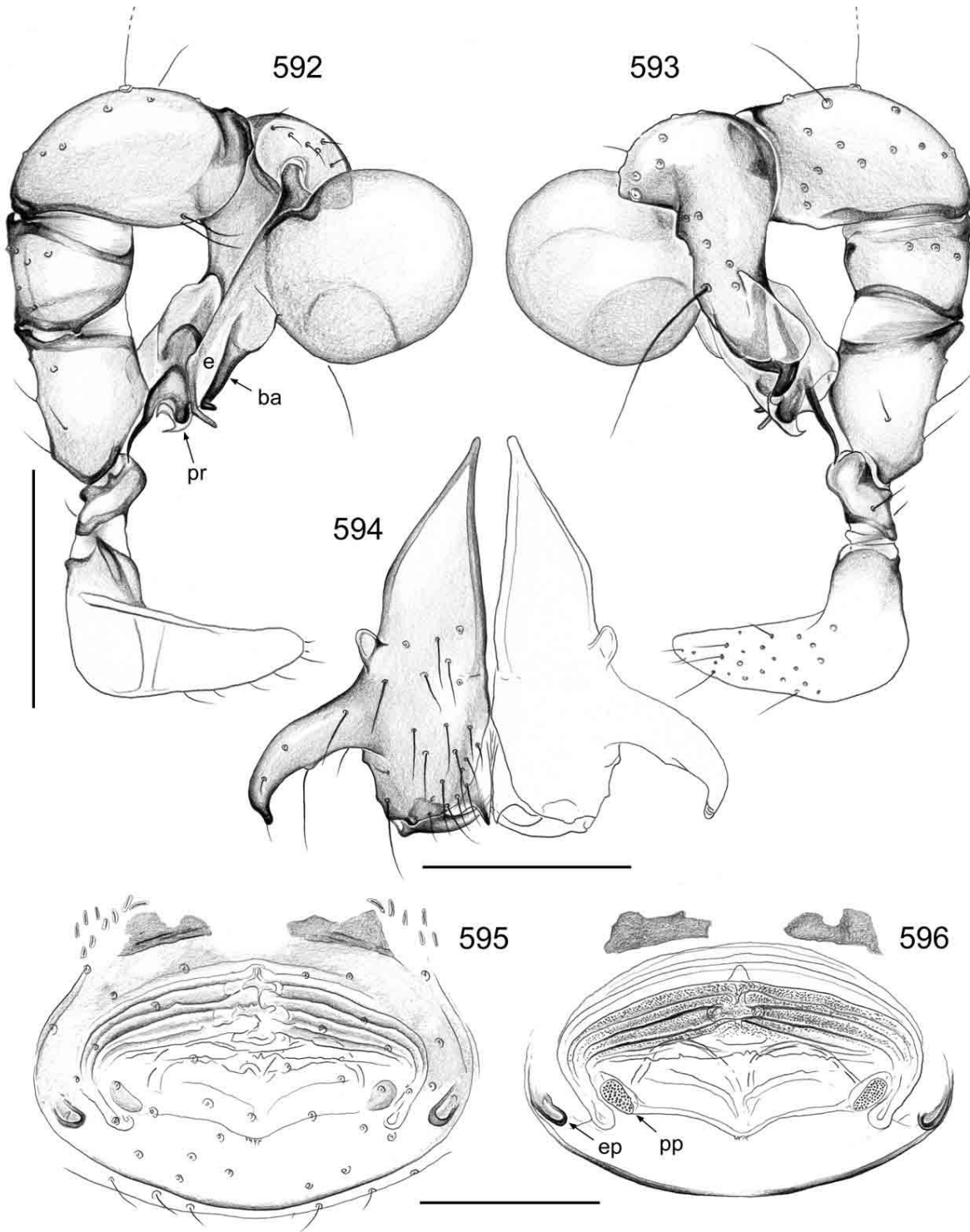


**Figs. 589-591.** *Belisana focipata*. 589, 590. Left male pedipalp, prolateral (589) and retrolateral (590) views. 591. Male chelicerae, frontal view. Scale lines: 0.4 mm (589, 590), 0.2 mm (591).

***Belisana marusiki*, new species**  
(Figs. 23, 24, 68, 592-596)

*Type.* Male holotype from Patlikuhl Town (32°07.4'N, 77°08.8'E), Himachal Pradesh, India; 1200 m a.s.l., June 17-23, 1999 (Y. M. Marusik), in SMF.

*Etymology.* Named for the collector, Yuri Marusik.



**Figs. 592-596.** *Belisana marusiki*. 592, 593. Left male pedipalp, prolateral (592) and retrolateral (593) views. 594. Male chelicerae, frontal view. 595, 596. Cleared female genitalia, ventral (595) and dorsal (596) views. Scale lines: 0.3 mm (592, 593), 0.2 mm (594-596).

*Diagnosis.* Medium-sized species with globular opisthosoma; easily distinguished from most known congeners by the pair of brown marks on the carapace (Fig. 23); also by the shapes of procurcus and bulbal projections (Figs. 592, 593); from many species also by the widely spaced male cheliceral apophyses.

*Male (holotype).* Total length 1.65 (1.75 with clypeus), carapace width 0.67. Legs 1 and 2 missing, tibia 3: 1.8, tibia 4: 2.2. Habitus as in Figs. 23 and 24. Entire animal pale ochre-grey except for distinctive pair of brown marks on carapace and median line on ocular area. Ocular area not elevated, thoracic furrow absent; distance PME-PME 105  $\mu$ m; diameter PME 60  $\mu$ m; distance PME-ALE  $\sim$ 20  $\mu$ m. Clypeus unmodified. Sternum wider than long (0.52/0.44). Chelicerae with long apophyses (Fig. 594), lateral view as in *B. gedeh* (cf. Fig. 342), tips of apophyses 425  $\mu$ m apart. Palps as in Figs. 592 and 593; trochanter with rounded slightly sclerotized retrolateral apophysis, femur with indistinct hump dorsally, procurus with distinctive sclerite distally, bulbal apophysis curved inwards at tip; legs apparently without spines, curved hairs, and vertical hairs (most hairs missing).

*Female.* In general similar to male; tibia 1 in 2 females from type locality: 2.67, 3.47. Epigynum very simple externally, light brown (Fig. 68), pockets 400  $\mu$ m apart (Fig. 595); dorsal view as in Fig. 596. ALS with several spigots. The four females from Shimla City below are assigned tentatively because of a different (much less distinct) pattern on the carapace, and the slightly longer legs (tibia 1: 3.77-3.93).

*Distribution.* Known from two neighboring localities in Himachal Pradesh, India (Fig. 79; specimens from the southern locality are assigned tentatively).

*Material examined.* INDIA: *Himachal Pradesh*: Patlikuhl Town: type above, together with 2♀ (SMF).

Assigned tentatively: *Himachal Pradesh*: Shimla City, University Campus (31°06.8'N, 77°08.5'E), 2000-2200 m a.s.l., May 25-27, 1999 (Y. M. Marusik), 4♀ (SMF).

#### ***Belisana dodabetta*, new species**

(Figs. 597-601)

*Type.* Male holotype from NE slope of Dodabetta Peak [ $\sim$ 11°30'N, 76°45'E], Tamil Nadu, India; 2475 m a.s.l., March 11, 1962 (E. S. Ross, D. Q. Cavagnaro), in CAS.

*Etymology.* The species name is a noun in apposition, taken from the type locality.

*Diagnosis.* Medium-sized, long-legged species with slightly elongated and angular opisthosoma; distinguished from relatives by the shapes of procurus and bulbal apophyses (Figs. 597, 598), and by the widely spread male cheliceral apophyses (Fig. 599).

*Male (holotype).* Total length 1.6 (1.7 with clypeus), carapace width 0.67. Leg 1: 15.7 (3.8 + 0.3 + 3.9 + 6.1 + 2.3), tibia 2: 2.8, tibia 3: 1.6, tibia 4: 2.3; tibia 1 L/d: 59. Prosoma and legs ochre-yellow, opisthosoma ochre-grey, with some slightly darker spots visible through cuticle dorsally. Ocular area very flat, not separated from carapace, thoracic furrow absent; distance PME-PME 160  $\mu$ m; diameter PME 60  $\mu$ m; distance PME-ALE  $\sim$ 20  $\mu$ m. Clypeus unmodified. Sternum as long as wide (0.50). Chelicerae as in Fig. 599, with pair of long curved apophyses, tips 520  $\mu$ m apart (tips appear wider apart in Fig. 599 because the apophyses were slightly pressed by the cover slide). Palps as in Figs. 597 and 598; trochanter with large rounded retrolateral apophysis, femur with small hump proximo-dorsally, patella unusually long, procurus with distinctive straight dorsal spine and strong prolateral apophysis, bulb with hooked apophysis and distally widened embolus. Retrolateral trichobothrium of tibia 1 at 12%; legs without spines, curved, and vertical hairs; tarsus 1 with  $\sim$ 20 pseudosegments, but only about 10 quite distinct distally.

*Female.* In general similar to male. Tibia 1 in 3 females: 3.0. Epigynum simple and flat externally (Fig. 600), with pair of lateral pockets 410  $\mu$ m apart apparently on posterior epigynal sclerite; dorsal view as in Fig. 601. ALS with five spigots in addition to basic set of two.

*Distribution.* Known from type locality only (Fig. 79).

*Material examined.* INDIA: *Tamil Nadu*: Dodabetta Peak, type above, together with 3♀ (CAS).

#### ***Belisana ratnapura*, new species**

(Figs. 602-616)

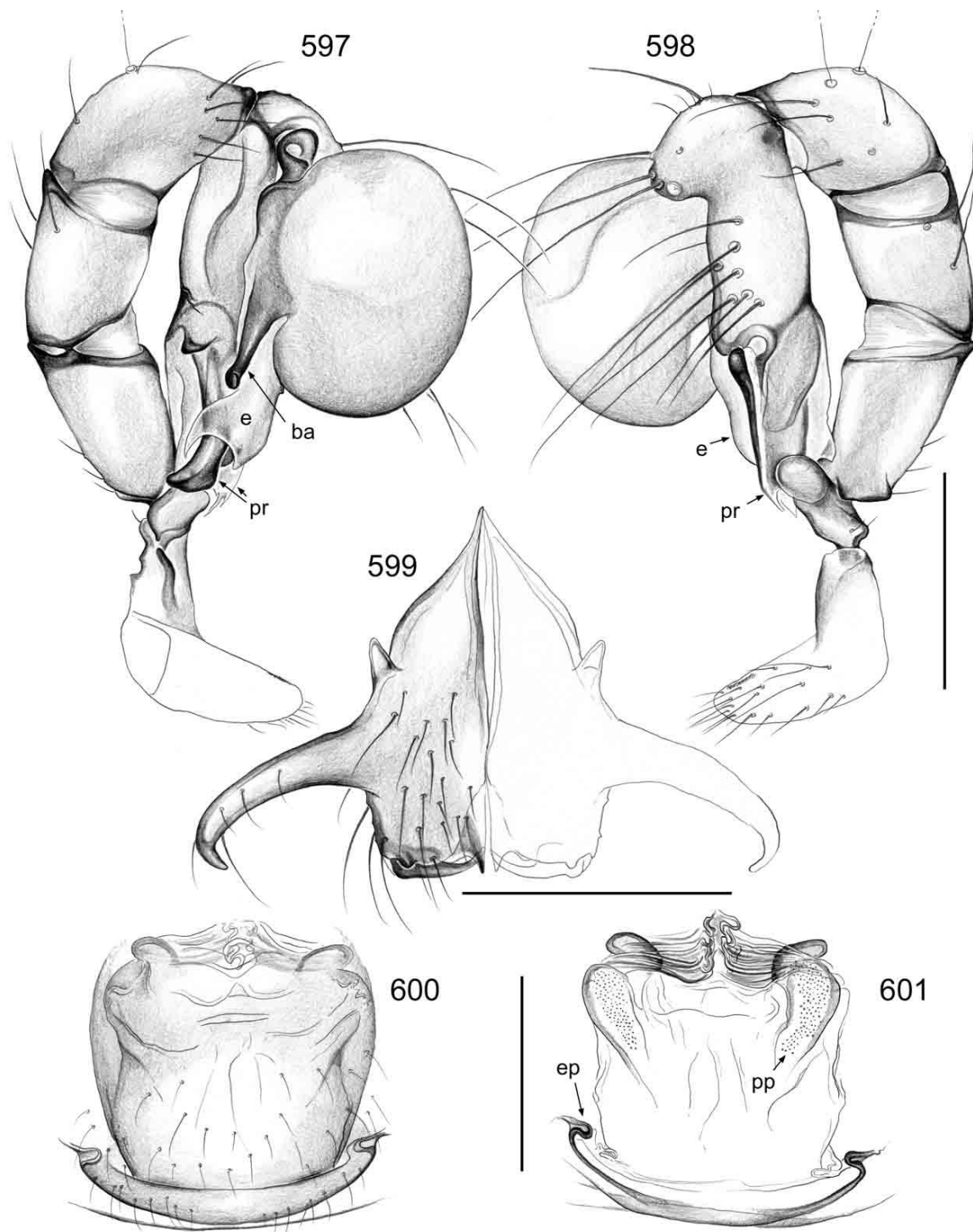
*Type.* Male holotype from Ratnapura [ $6^{\circ}41'N$ ,  $80^{\circ}24'E$ ], Sabaragamuwa Prov., Sri Lanka; forest below tennis club, Aug. 21-22, 1981 (P. R. & C. L. Deeleman), in RMNH.

*Etymology.* The species name is a noun in apposition, taken from the type locality.

*Diagnosis.* Medium-sized, long-legged species with elongated and posteriorly elevated opisthosoma; distinguished from relatives by the small cheliceral apophyses close together (Fig. 604) and the long ventral flap on the procurus (Figs. 603, 606, 609). The RMNH has a very similar species from Kandy, which has a smaller palp, the dorsal sclerite of the procurus more clearly separated from the ventral portion by a membranous area, the distal elements on the procurus slightly different, and the chelicerae slightly larger but very similar in shape.

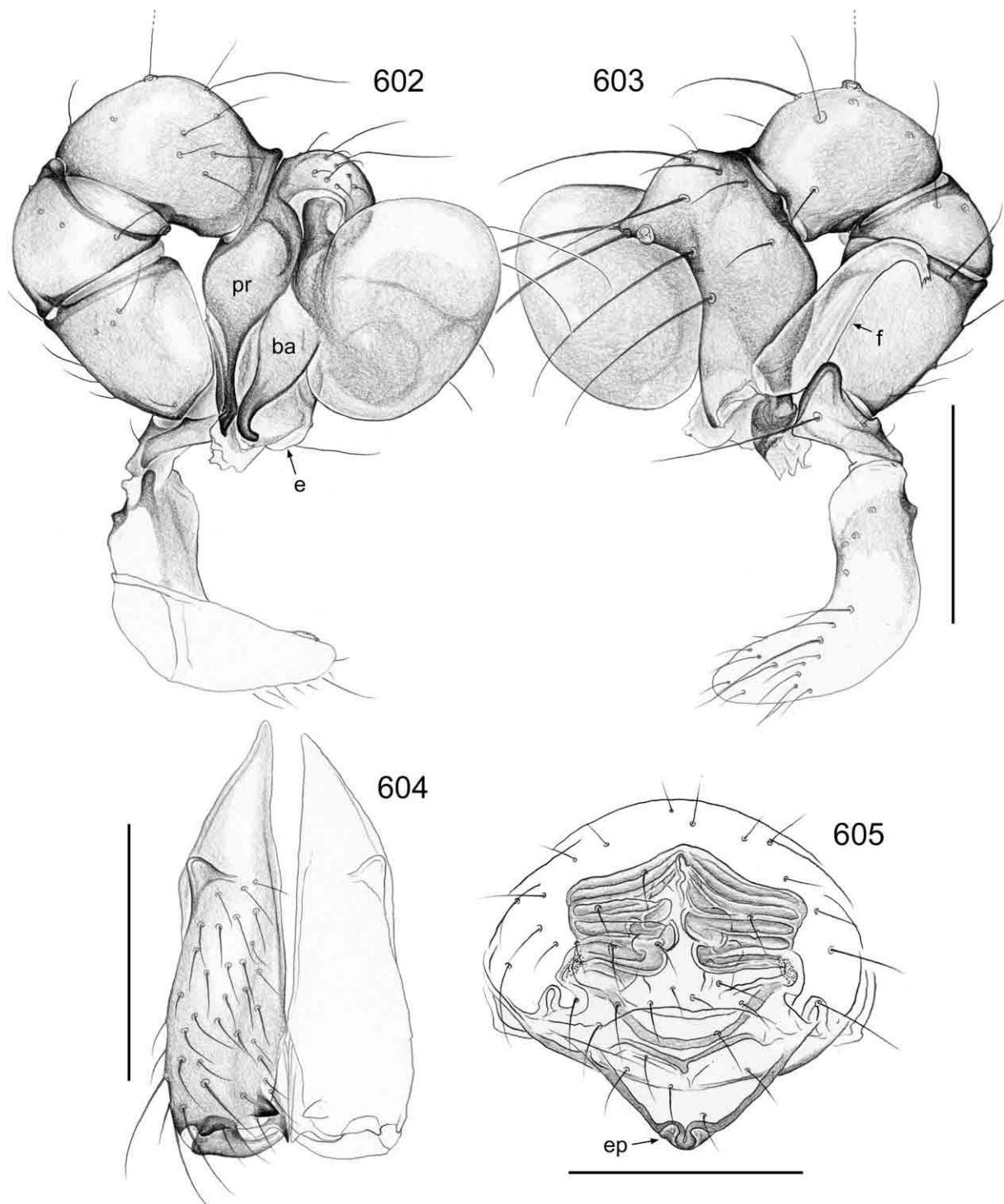
*Male (holotype).* Total length 1.45 (1.6 with clypeus), carapace width 0.62. Leg 1: 14.1 (3.4 + 0.3 + 3.5 + 5.5 + 1.4), tibia 2: 2.2, tibia 3: 1.3, tibia 4: 1.9; tibia 1 L/d: 66. Habitus similar to *B. sabah* (cf. Figs. 21, 22). Entire spider





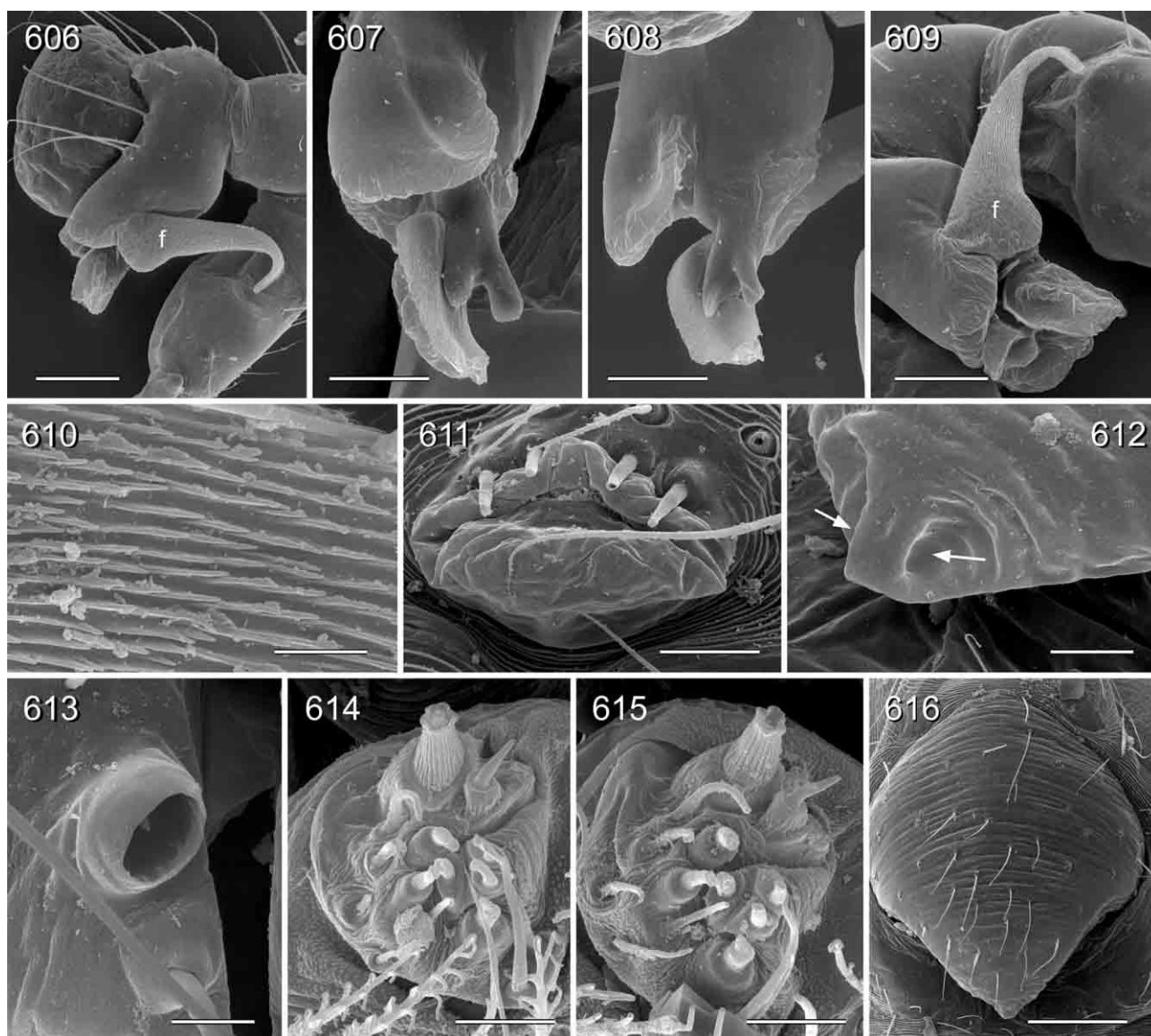
**Figs. 597-601.** *Belisana dodabetta*. 597, 598. Left male pedipalp, prolatral (597) and retrolateral (598) views. 599. Male chelicerae, frontal view. 600, 601. Cleared female genitalia, ventral (600) and dorsal (601) views. Scale lines: 0.3 mm.

pale ochre-yellow to ochre-grey. Ocular area very flat, not separated from carapace, thoracic furrow absent; distance PME-PME 135  $\mu$ m; diameter PME 45  $\mu$ m; distance PME-ALE ~20  $\mu$ m. Clypeus unmodified. Sternum as long as wide (0.40). Chelicerae as in Fig. 604, with pair of small apophyses close together, distance between tips of cheliceral



**Figs. 602-605.** *Belisana ratnapura*. 602, 603. Left male pedipalp, prolateral (602) and retrolateral (603) views. 604. Male chelicerae, frontal view. 605. Cleared female genitalia, dorsal view. Scale lines: 0.2 mm.

apophyses 15  $\mu$ m. Palps as in Figs. 602 and 603; trochanter with retrolateral apophysis, procurus with distinctive membranous ventral flap and bifid distal sclerite (Figs. 606-609), bulb with hooked apophysis and membranous embolus (Fig. 602). Tarsal organ capsulate (Fig. 613). Retrolateral trichobothrium of tibia 1 at 8%; legs without spines, curved, and vertical hairs; tarsus 1 with >15 pseudosegments, distally fairly distinct. Gonopore and ALS as in Figs. 611 and 614.



**Figs. 606-616.** *Belisana ratnapura*. 606. Left procursus, retrolateral view. 607. Right procursus, dorsal view. 608. Right procursus, prolateral view. 609. Membranous flap on left procursus. 610. Detail of membranous flap on procursus. 611. Male gonopore with epiandrous spigots. 612. Pockets (arrows) on epigynum. 613. Male palpal tarsal organ. 614. Male ALS. 615. Female ALS. 616. Epigynum, ventral view. Scale lines: 7  $\mu\text{m}$  (610), 10  $\mu\text{m}$  (613-615), 20  $\mu\text{m}$  (611, 612), 50  $\mu\text{m}$  (607), 60  $\mu\text{m}$  (608), 70  $\mu\text{m}$  (609), 100  $\mu\text{m}$  (606, 616).

*Variation.* Tibia 1 in 26 other males: 3.0-3.7 (mean 3.45).

*Female.* In general similar to male; one female with large dark spots on opisthosoma; tibia 1 in 31 females: 2.8-3.5 (mean: 3.19); epigynum very simple externally (Fig. 616), often with plug, no sclerotized structure; pockets close together on posterior elongation (Figs. 605, 612), about 10  $\mu\text{m}$  apart. ALS as in Fig. 615.

*Distribution.* Known from several localities in SW Sri Lanka (Fig. 79).

*Material examined.* SRI LANKA: *Sabaragamuwa*: Ratnapura: type above, together with 11♂23♀; Sinharadja Forest (S of Ratnapura), small stand of forest in buffer zone, under leaves, Aug. 20, 1981 (P. R. & C. L. Deeleman), 16♂14♀ (RMNH); same locality and collectors, reserve near forest house, Aug. 23, 1981, 3♂ 2 juveniles (RMNH). *Western Prov.*: Bodinagala-Horane [near Horana, 6°43'N, 80°04'E], July 19, 1996 (S. P. Benjamin), 1♂ (MHNG). *Southern Prov.*: Kannaliya [near Galle, 6°02'N, 80°13'E], waterside vegetation, Oct. 14, 1982 (F. Wanless), 1♂ (RMNH); same collection data but rain forest, under leaves, 2♂~5♀ (RMNH).

Undetermined locality: "Kollawa", wet evergreen forest, on leaves, Oct. 15, 1982 (F. Wanless), 1♂2♀ (RMNH).

***Belisana keyti*, new species**

(Figs. 53, 617-620)

*Type.* Male holotype from Hakgala Gardens [6°54'N, 80°48'E], Nuwara Eliya Distr., Central Prov., Sri Lanka; Oct. 21, 1982 (F. Wanless), shrubs, in RMNH.

*Etymology.* Named for George Keyt (1901-1993), one of the most outstanding Sri Lankan painters. The eternal theme of devine and human love is the thread that runs unbroken throughout his prolific artistic career.

*Diagnosis.* Medium-sized, long-legged species with elongated and posteriorly strongly elevated opisthosoma; distinguished from most relatives by the curved procurus (Fig. 618), from *B. benjamini* by the widely spaced male cheliceral apophyses (similar to *B. ketambe*, cf. Fig. 304) and the large flattened bulbal apophysis (Fig. 617).

*Male (holotype).* Total length 1.65 (1.75 with clypeus), carapace width 0.70. Legs 1: 15.0 (3.7 + 0.3 + 3.8 + 5.7 + 1.5), leg 2 missing, tibia 3: 1.5, tibia 4: 2.2; tibia 1 L/d: 61. Habitus as in Fig. 53, but without dark spot on carapace (the male shown is not the holotype). Entire spider pale whitish to ochre-grey. Ocular area very flat, not separated from carapace, thoracic furrow absent; distance PME-PME 160 µm; diameter PME 55 µm; distance PME-ALE ~20 µm. Clypeus unmodified. Sternum as long as wide (0.48). Chelicerae as in *B. ketambe* (cf. Fig. 304), distance between tips of cheliceral apophyses 300 µm. Palps as in Figs. 617 and 618; trochanter with short retrolateral apophysis, femur with small apophysis proximo-dorsally, procurus distinctively curved, only distally complex, bulb with distinctive flattened apophysis and embolus with long distal spine. Legs without spines, curved and vertical hairs; retrolateral trichobothrium of tibia 1 at 15%; pseudosegments barely visible in dissecting microscope.

*Variation.* Tibia 1 in other males from Hakgala: 3.25 (missing in other male), distance between tips of cheliceral apophyses 300, 305 µm. One of these males has a dark spot posteriorly on the prosoma (Fig. 53). The specimens from Horton Plains are assigned tentatively: the males have apparently identical procuri and chelicerae, but the flattened bulbal sclerite has a slightly different shape; tibia 1 in these males: 3.9, 4.0.

*Female.* In general similar to male. Tibia 1 in female from Hakgala: 2.9. Epigynum very simple externally, with pair of lateral pockets 265 µm apart (Fig. 619); dorsal view as in Fig. 620. ALS with several spigots in addition to basic set of two. Tibia 1 in 4 females from Horton Plains: 3.1-3.4.

*Distribution.* Known from two localities in Nuwara Eliya District, Sri Lanka (Fig. 79).

*Material examined.* SRI LANKA: Central Prov.: Nuwara Eliya Distr.: Hakgala Gardens: type above, together with 1 juvenile; Hakgala Forest, July 27, 1996 (S. P. Benjamin), 1♂1♀ 1 juvenile (MHNG); same collection data but July 12, 1996, 1♂ (MHNG).

Assigned tentatively: Nuwara Eliya Distr.: Horton Plains [6°48'N, 80°48'E], 2200 m a.s.l., forest, from leaves, Aug. 13-15, 1981 (P. R. & C. L. Deeleman), 2♂4♀ (RMNH).

***Belisana benjamini*, new species**

(Figs. 37, 38, 621-625)

*Type.* Male holotype from Knuckles Range, Deenston [~7°19'N, 80°51'E], Kandy Distr., Central Prov., Sri Lanka; March 10, 1998 (S. P. Benjamin), in MHNG.

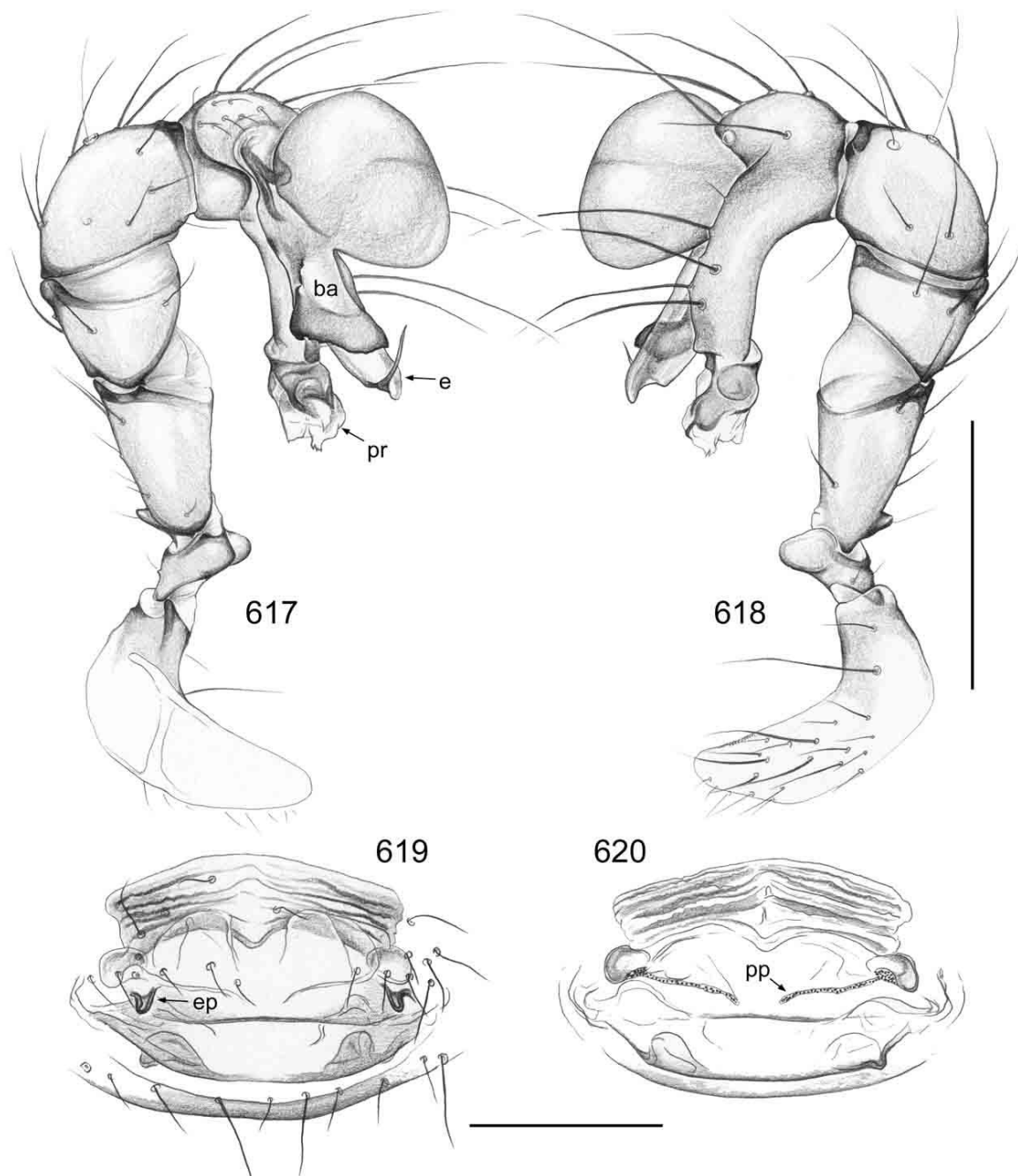
*Etymology.* Named for the collector, Suresh Benjamin.

*Diagnosis.* Medium-sized, long-legged species with oval and posteriorly elevated opisthosoma; distinguished from relatives by the curved procurus (Fig. 622), from *B. keyti* by the male cheliceral apophyses much closer together (Fig. 623) and the bulbal projections (Fig. 621).

*Male (holotype).* Total length 1.45 (1.55 with clypeus), carapace width 0.67. Leg 1: 13.7 (3.5 + 0.3 + 3.6 + 4.9 + 1.3), tibia 2: 2.1, tibia 3: 1.3, tibia 4: 2.0; tibia 1 L/d: 68. Habitus as in Figs. 37 and 38. Prosoma and legs pale ochre-yellow, carapace laterally slightly darker, opisthosoma pale grey. Ocular area very flat, not separated from carapace, thoracic furrow absent; distance PME-PME 95 µm; diameter PME 70 µm; distance PME-ALE ~15 µm. Clypeus unmodified. Sternum as long as wide (0.46). Chelicerae as in Fig. 623, with pair of short apophyses, tips 185 µm apart. Palps as in Figs. 621 and 622; trochanter with large rounded retrolateral apophysis, femur with small hump proximo-dorsally, procurus distinctively curved, only distally rather complex, embolus with long distal spine. Retrolateral trichobothrium of tibia 1 at 23%; legs without spines, curved, and vertical hairs; tarsus 1 with ~10 pseudosegments, poorly visible in dissecting microscope.

*Female.* In general similar to male. Tibia 1 in 11 females: 2.10-2.55 (mean 2.27). Epigynum simple externally, barely protruding, with pair of lateral pockets 155 µm apart (Fig. 624); dorsal view as in Fig. 625. ALS with 6 spigots in addition to basic set of two.

*Distribution.* Known from type locality only (Fig. 79).

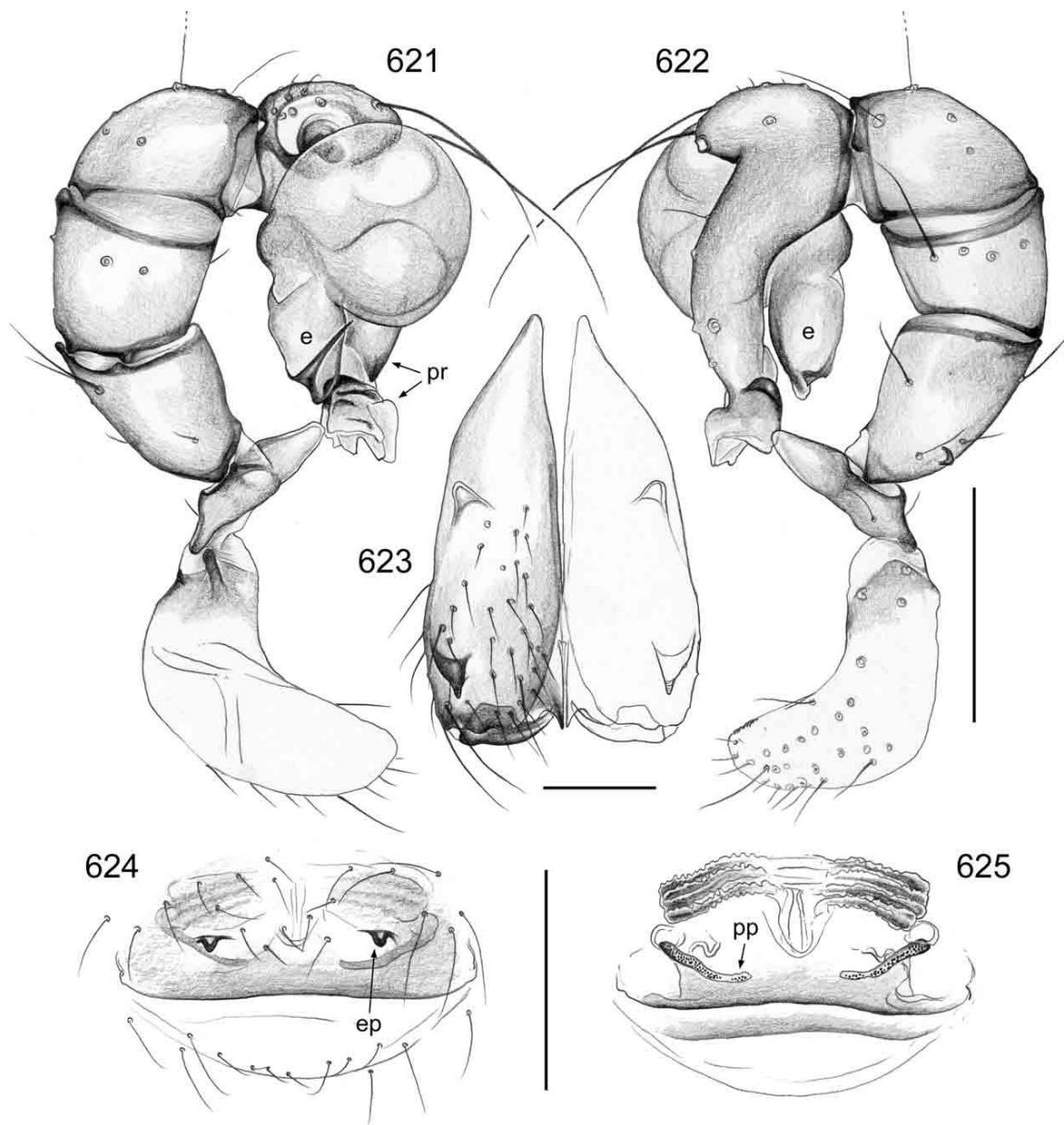


**Figs. 617-620.** *Belisana keyti*. 617, 618. Left male pedipalp, prolateral (617) and retrolateral (618) views. 619, 620. Cleared female genitalia, ventral (619) and dorsal (620) views. Scale lines: 0.3 mm (617, 618), 0.2 mm (619, 620).

*Material examined.* SRI LANKA: *Central Prov.*: Kandy Distr.: Knuckles Range: type above, together with 2♂♀ 4 juveniles (MNHG); same data but March 11, 1998, 2♂6♀ 3 juveniles (MHNG).

***Belisana fiji*, new species**  
(Figs. 33, 34, 626-642)

*Type.* Male holotype from ~3 mi S of Serea [ $\sim 17^{\circ}53'S$ ,  $178^{\circ}18'E$ ], Lomaivuna District, Viti Levu, Fiji; picked from forest tree, May 30, 1987 (J. W. & E. R. Berry), in BPBM.



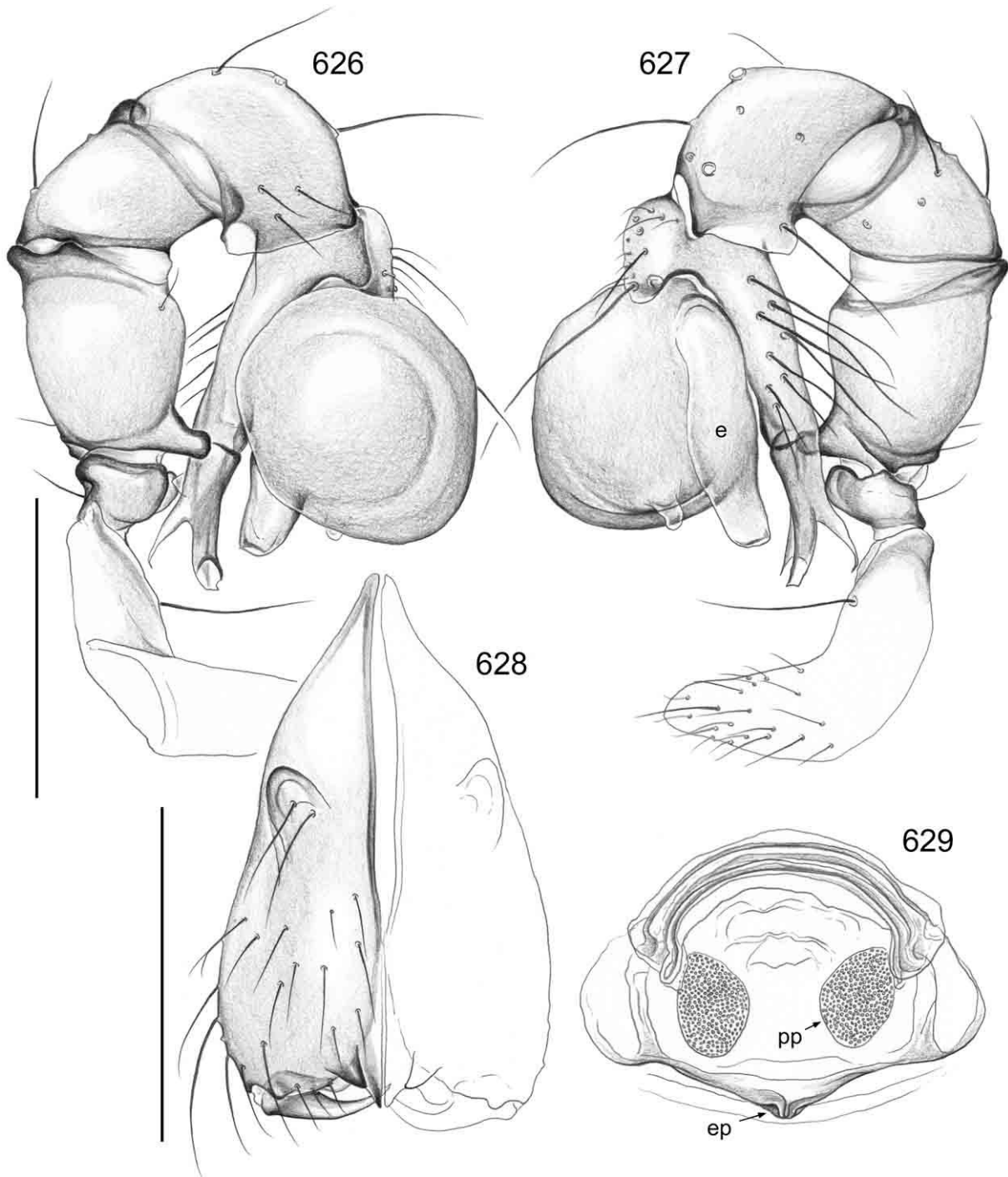
**Figs. 621-625.** *Belisana benjamini*. 621, 622. Left male pedipalp, prolateral (621) and retrolateral (622) views. 623. Male chelicerae, frontal view. 624, 625. Cleared female genitalia, ventral (624) and dorsal (625) views. Scale lines: 0.2 mm (621, 622, 624, 625), 0.1 mm (623).

*Etymology.* The species name is a noun in apposition, taken from the type locality.

*Diagnosis.* Medium-sized, long-legged species with cylindrical opisthosoma; easily distinguished from congeners by pigment-less eyes (Fig. 33), the ventral projection on the male palpal femur (Fig. 626), and the shape of the procurus (Fig. 627).

*Male (holotype).* Total length 1.65 (1.7 with clypeus), carapace width 0.56. Leg 1: 18.4 (4.6 + 0.3 + 4.5 + 7.4 + 1.6), tibia 2: 2.6, tibia 3: 1.5, tibia 4: 2.7; tibia 1 L/d: 68. Habitus as in Figs. 33 and 34. Entire spider pale ochre-yellow except for pair of distinctive brown marks on clypeus and patellae and tibia-metatarsus joints darkened; eyes almost without pigment. Ocular area flat, thoracic furrow absent; distance PME-PME 140  $\mu$ m; diameter PME 60  $\mu$ m; distance PME-ALE ~10  $\mu$ m. Clypeus unmodified. Sternum slightly wider than long (0.50/0.45). Chelicerae as in Fig. 628, proximal projections large, rather frontal than lateral, tips of distal apophyses unmodified (Fig. 635), about 20  $\mu$ m apart. Palps as in Figs. 626, 627, and 630; trochanter with retrolateral apophysis (longer than appears on draw-

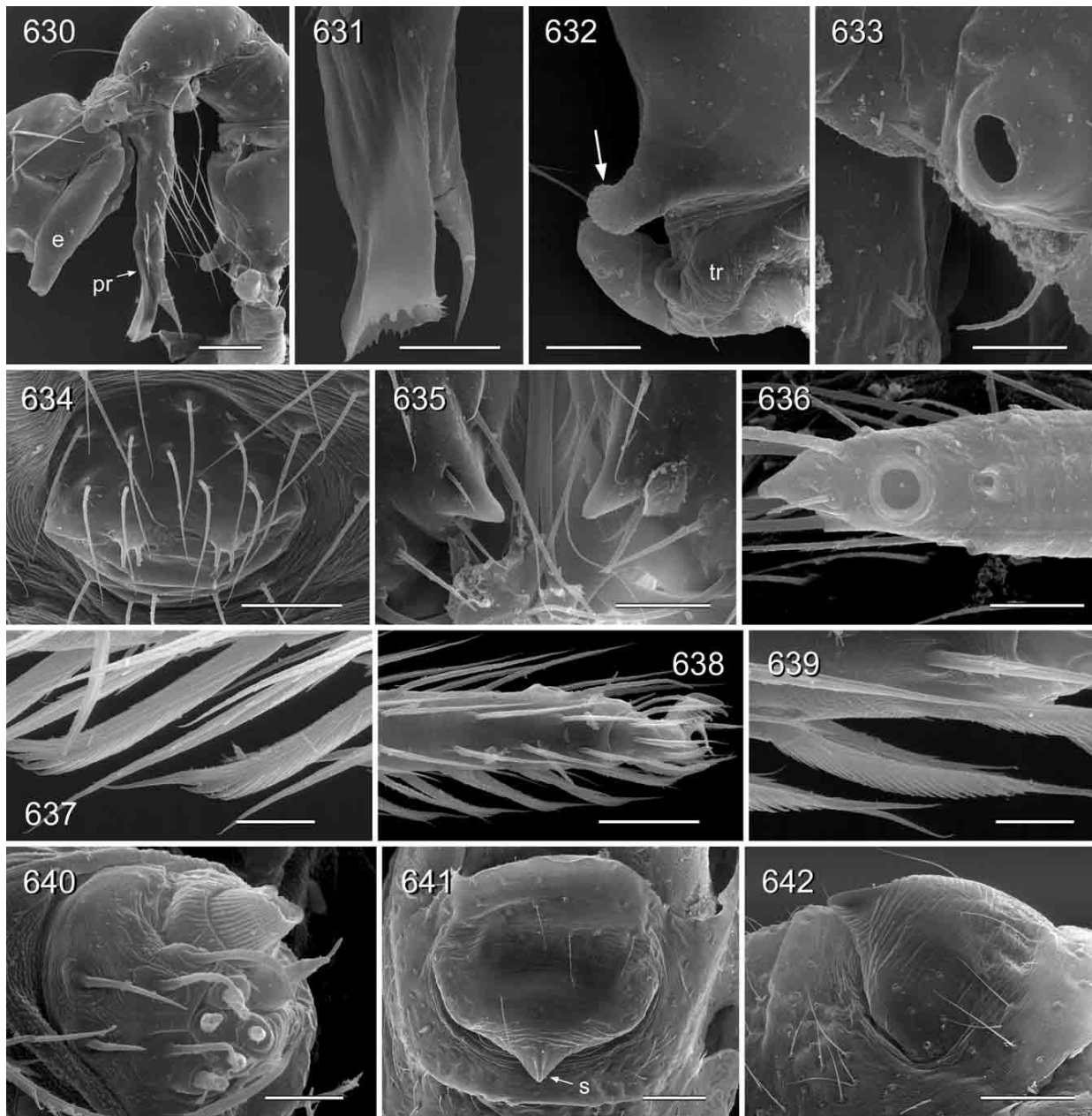




**Figs. 626-629.** *Belisana fiji*. 626, 627. Left male pedipalp, prolateral (626) and retrolateral (627) views. 628. Male chelicerae, frontal view. 629. Cleared female genitalia, dorsal view. Scale lines: 0.3 mm (626, 627), 0.2 mm (628).

ing), femur with distinctive apophysis proximo-ventrally (Fig. 632), procursus simple with transparent ventral projection (Fig. 631), bulb with simple embolus and small additional projection (barely visible in dissecting microscope). Tarsal organ capsulate (Fig. 633). Retrolateral trichobothrium of tibia 1 not seen; legs without spines, curved, and vertical hairs; tarsus 1 with ~15 pseudosegments, distally fairly distinct. Gonopore as in Fig. 634.

*Variation.* Tibia 1 in 17 other males: 3.75-4.90 (mean 4.44).



**Figs. 630-642.** *Belisana fiji*. 630. Left palp, retrolateral view. 631. Tip of right procurus, prolateral (slightly distal) view. 632. Apophyses on male palpal femur (arrow) and trochanter. 633. Male palpal tarsal organ. 634. Male gonopore with epiandrous spigots. 635. Male cheliceral apophyses. 636. Tip of female palp with tarsal organ, dorsal view. 637. Comb-hairs on male tarsus 4. 638. Female tarsus 4 tip. 639. Comb-hairs on female tarsus 4. 640. Female ALS. 641. Epigynum, ventral view. 642. Epigynum, lateral view. Scale lines: 10  $\mu$ m (633, 637, 639, 640), 20  $\mu$ m (635, 636), 40  $\mu$ m (631, 634, 638), 50  $\mu$ m (632), 100  $\mu$ m (630, 641, 642).

*Female.* In general similar to male. Tibia 1 in 17 females: 3.00-3.75 (mean 3.42). Epigynum very simple externally (Figs. 641, 642), with short scape provided with pair of pockets 15  $\mu$ m apart; dorsal view as in Fig. 629. Several spigots on ALS (Fig. 640).

*Distribution.* Known from several localities on Viti Levu and Ovalau Islands, Fiji (Fig. 82).

*Material examined.* FIJI: *Viti Levu*: 3 mi S Serea: type above, together with 9♂2♀ 7 juveniles (BPBM); Nausori, Koronovia Research Station, shaken from trees, May 18, 1987 (J. W. & E. R. Berry), 5♂7♀ 3 juveniles (BPBM); Colo-I-Suva Forest Reserve, ~10 mi N Nausori, dense ridgetop forest, May 20, 1980 (J. A. Beatty), 1♀ (BPBM);

Nausori Highlands, Leweitoko Block, ~1500 ft a.s.l., "shaking", May 27, 1987 (J. W. & E. R. Berry), 1♂2♀ (BPBM); Nausori Highlands, 600 m a.s.l., "Pyrethrum, trees and logs", July 13, 1987 (G. Monteith), 2♀ (QMB S50352); Loma I Vuna District, ~3 km N Nagali, tree shaking in pine woods, May 30, 1987, (J. W. & E. R. Berry), 1♂2♀ 1 juvenile BPBM); Namosi Road, 3 km N Queens Road, tree shaking in forest, May 7, 1987 (J. W. & E. R. Berry, J. A. Beatty), 1♂ (BPBM); 22.4 km W Suva, sweeping and shaking in forest, May 5, 1987 (J. W. & E. R. Berry), 5♀ (BPBM); Sawani, near Suva [~18°01'S, 178°28'E], from epiphytes, July 19, 1956 (R. R. Forster), 1♂ (BPBM); sweeping mangrove near Namuka Harbor [18°20'S, 178°08'E], May 2, 1987 (J. W. & E. R. Berry), 1♀ (BPBM); Nagelewai village (17°43'N, 178°05'E), 260 m a.s.l., vegetation beating, Nov. 28, 2002 (D. Gruner), 1♂ (BPBM); 3 km E Monasavu Dam [17°46'N, 178°03'E], 1000 m a.s.l., "Pyrethrum, trees and logs", July 26, 1987 (Monteith & Cook), 1♂1♀(?) (QMB); *Ovalau Island*: Lovoni track behind Levulca [17°40'S, 178°47'E], Nov. 13, 1988 (R. Raven), 1♂ (QMB).

## Discussion

### 1. Male-female covariance

Previous studies have shown that the sexually modified chelicerae of male pholcid spiders contact the female external genitalia during copulation (review in Huber & Eberhard 1997). In some genera, a simple functional correlation between a pair of apophyses on the male chelicerae and a pair of pockets on the female external genitalia has been suggested previously, based on the obvious covariation among species between distances of apophyses and pockets (e.g. Kraus 1984; Huber 1999). However, only one study has verified this functional correlation by direct observation (Huber 1994). In a revision of South African pholcid spiders (Huber 2003c), this correlation was quantified for a larger group of species in the genus *Quamtana*. The result was an almost exact correlation between the measures (Pearson's Correlation Coefficient  $r = 0.99$ ;  $P < 0.001$ ), with male measures being slightly higher than female measures. The result in the present study, using a much larger number of species, is almost identical ( $r = 0.98$ ;  $P < 0.001$ ). The higher male than female measures found in both studies probably reflect the fact that the basal segments of male pholcid chelicerae are able to perform slight movements against each other (to grip the female), even though they are fused medially (Huber 2002).

It might be argued that such correlations could simply reflect size variation among species, with larger species having higher measures. However, scatter diagrams clearly indicate that this is neither the case in *Quamtana* (Huber 2003c: fig. 260) nor in *Belisana* (Fig. 75F). None of the two genera shows a correlation between prosoma width as an indicator of body size and distance between the cheliceral apophyses. In both cases, the range of variation of the two measures is significantly different. In *Belisana*, the coefficient of variation is 16.3 for prosoma width, but 77.9 for the distance between the cheliceral apophyses.

Technically, calculating correlation coefficients for the data above is inappropriate because the data (species) are not independent but linked by a phylogeny (Harvey & Pagel 1991). However, considering the ease of measurement of the structures involved, and the apparently multiple occurrence of the phenomenon in different pholcid genera, correlation analysis is here used as a preliminary descriptive technique to suggest pholcids as a potentially well suited group to study male-female coevolution.

### 2. Metaphyly

There is a wide consensus that monophyletic genera defined by synapomorphies are a major aim of any taxonomic revision within the frame of the current rank-based Linnean system. However, with the data at hand this is currently unattainable in the present case. *Belisana* fits the concept of a 'metaphyletic' group, with metaphyly being used here in a general meaning to describe unresolved relationships among taxa (cf. Dayrat & Gosliner 2005). A number of potential solutions have been proposed (review in Dayrat & Gosliner 2005) but our current binomial species nomenclature offers no key to handle the problem. Splitting '*Belisana*' into several genera following the cladograms would not only result in a number of poorly supported and partly monotypic genera, but would also depend on arbitrary cladogram choice (note the low support values for most of the nodes). One potential solution would be to identify the position

of the type species and to consider the species closest to it as *Belisana* 'sensu strictu'. All other species could then be added tentatively to *Belisana*, pending new discoveries and final placement. This would avoid the creation of poorly supported taxa, but it presupposes that the type species is adequately known. Unfortunately, this is not the case in *Belisana* (see above for data on type species). From what is known, the type species *B. tauricornis* could belong to almost any of the monophyletic taxa identified within 'Belisana', or it could even be just another terminal branch originating from the paraphyletic system. This leaves only one option that combines stability, practicability, and agreement with the current version of the ICZN with a minimum of phylogenetic misinformation contained in the binomials: to treat 'Belisana' as a para- or even polyphyletic group, aware of the fact that similarity alone is the basis for this preliminary taxonomic construct. Delaying publication until the problem is solved (e.g., by including molecular data and/or the type species) is no alternative.

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**Appendix 1.** Taxa used in the cladistic analysis, with geographic origin and depository of specimens studied.**Outgroups**

<i>Ninetis subtilissima</i> Simon	Yemen: Ja'ar (AMNH)
<i>Ciboneya nuriae</i> Huber & Pérez González	Cuba: Pinar del Rio (IES)
<i>Physocyclus globosus</i> (Taczanowski)	Costa Rica: San José (UCR)

**Pholcines**

<i>Metagonia argentinensis</i> Mello-Leitão	Brazil: Rio Grande do Sul (MCN)
<i>Metagonia rica</i> Gertsch	Costa Rica: San José Prov. (UCR)
<i>Metagonia delicata</i> (O. Pickard-Cambridge)	Nicaragua: Bluefields (UCR)
<i>Metagonia globulosa</i> Huber	Peru: Loreto (MUSM)
<i>Pholcus phalangioides</i> (Fuesslin)	USA: San Francisco (AMNH)
<i>Leptopholcus delicatulus</i> Franganillo	Cuba: Oriente (AMNH)
<i>Micropholcus fauroti</i> (Simon)	USA: Texas (AMNH)
<i>Spermophora senoculata</i> (Dugès)	USA: New York City (AMNH)
<i>Spermophora yao</i> Huber	Australia: Queensland (QMB)
<i>Spermophora palau</i> Huber	Micronesia: Ponape Island (BPBM)
<i>Spermophora tumbang</i> Huber	Indonesia: Kalimantan (RMNH)
<i>Spermophora estebani</i> Simon	Philippines: Luzon (RMNH)
" <i>Spermophora</i> " <i>ranomafana</i> Huber	Madagascar: Fianarantsoa (CAS)
" <i>Spermophora</i> " <i>berlandi</i> (Fage)	Kenya: Rift Valley (MNHN)
" <i>Spermophora</i> " <i>sangarawe</i> Huber	Tanzania: Tanga (ZMUC)
" <i>Spermophora</i> " <i>morogoro</i> Huber	Tanzania: Morogoro (ZMUC)
" <i>Spermophora</i> " <i>masisiwe</i> Huber	Tanzania: Iringa (USNM)
" <i>Spermophora</i> " <i>usambara</i> Huber	Tanzania: Tanga (ZMUC)
" <i>Spermophora</i> " <i>lambilloni</i> Huber	Comoros: Grande Comore (MRAC)
" <i>Spermophora</i> " <i>jocquei</i> Huber	Comoros: Mayotte (MRAC)
" <i>Spermophora</i> " <i>peninsulae</i> Lawrence	South Africa: Western Cape (CAS)
" <i>Spermophora</i> " <i>schoemanae</i> Huber	South Africa: Western Cape (NCP)
<i>Micromerys gracilis</i> Bradley	Australia: Northern Territory (QMB)
<i>Micromerys daviesae</i> Deeleman-Reinhold	Australia: Queensland (QMB)
<i>Panjange mirabilis</i> Deeleman-Reinhold	Australia: Queensland (QMB)
<i>Zatavua vohiparara</i> Huber	Madagascar: Fianarantsoa (CAS)
<i>Zatavua tamatave</i> Huber	Madagascar: Toamasina (MRAC)
<i>Zatavua madagascariensis</i> (Fage)	Madagascar: Toliara (MNHN)
<i>Zatavua griswoldi</i> Huber	Madagascar: Antsiranana (CAS)
<i>Zatavua voahangyae</i> Huber	Madagascar: Fianarantsoa (CAS)
<i>Paramicromerys nampoinai</i> Huber	Madagascar: Antsiranana (CAS)
<i>Paramicromerys mananteina</i> Huber	Madagascar: Antsiranana (CAS)
<i>Paramicromerys scharffi</i> Huber	Madagascar: Fianarantsoa (CAS)
<i>Paramicromerys rothorum</i> Huber	Madagascar: Antsiranana (CAS)
<i>Paramicromerys coddingtoni</i> Huber	Madagascar: Antsiranana (CAS)
<i>Spermophorides</i> sp. 1	Canary Islands: Lanzarote, leg. Wunderlich (ZFMK)
<i>Spermophorides</i> sp. 2	Mallorca, leg. Hillyard, Dec. 21, 1980 (BMNH)
<i>Buitinga uzungwa</i> Huber	Tanzania: Iringa (ZMUC)
<i>Buitinga safura</i> Huber	Tanzania: Iringa (USNM)
<i>Buitinga kadogo</i> Huber	Tanzania: Tanga (CAS)
<i>Buitinga lakilingo</i> Huber	Tanzania: Tanga (CAS)
<i>Buitinga mazumbai</i> Huber	Tanzania: Tanga (CAS)
<i>Quamtana bonamanzi</i> Huber	South Africa: KwaZulu-Natal (NCP, ZFMK)
<i>Quamtana merwei</i> Huber	South Africa: KwaZulu-Natal (NCP)
<i>Quamtana vidal</i> Huber	South Africa: KwaZulu-Natal (NCP, ZFMK)
<i>Quamtana entabeni</i> Huber	South Africa: Limpopo (CAS)
<i>Quamtana ciliata</i> (Lawrence)	South Africa: KwaZulu-Natal (NCP)
<i>Quamtana hectori</i> Huber	South Africa: Gauteng and NW Prov. (CAS, NCP)
<i>Quamtana mabusai</i> Huber	South Africa: Mpumalanga (AMNH)

<i>Quamtana embuleni</i> Huber	South Africa: Mpumalanga (NCP, ZFMK)
<i>Quamtana oku</i> Huber	Cameroon: NW Prov. (CAS, USNM)
<i>Belisana fiji</i> n. sp.	Fiji (BPBM)
<i>Belisana airai</i> n. sp.	Palau (BPBM)
<i>Belisana davao</i> n. sp.	Philippines: Mindanao (RMNH)
<i>Belisana australis</i> Huber	Australia: Northern Territory (QMB)
<i>Belisana leuser</i> n. sp.	Indonesia: Sumatra (RMNH)
<i>Belisana bohorok</i> n. sp.	Indonesia: Sumatra (RMNH)
<i>Belisana marena</i> n. sp.	Indonesia: Sulawesi (RMNH)
<i>Belisana kaharian</i> n. sp.	Indonesia: Kalimantan (RMNH)
<i>Belisana sepaku</i> n. sp.	Indonesia: Kalimantan (RMNH)
<i>Belisana pianma</i> n. sp.	China: Yunnan (CAS)
<i>Belisana nujiang</i> n. sp.	China: Yunnan (CAS)
<i>Belisana scharffi</i> n. sp.	Thailand: Chiang Mai (MACN)
<i>Belisana inthanon</i> n. sp.	Thailand: Chiang Mai (MACN)
<i>Belisana ketambe</i> n. sp.	Indonesia: Sumatra (RMNH)
<i>Belisana schwendingeri</i> n. sp.	Thailand: Chiang Mai (MHNG)
<i>Belisana leumas</i> n. sp.	Thailand: Chiang Mai (MACN)
<i>Belisana sandakan</i> n. sp.	Malaysia: Sabah (ZMT)

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**Appendix 2.** Characters scored for the cladistic analysis. For further discussion of characters see Huber (2000, 2001, 2003b, c, 2005)

1. Eye number: (0) eight; (1) six. All known *Belisana* species have six eyes.
2. Distance between posterior median eyes (PME): (0) >1.75 x diameter of PME; (1) <1.75 x diameter of PME. Considering the histogram in Fig. 75C and the scatter in Fig. 75G, the phylogenetic value of this character appears very difficult to assess.
3. Sculpture of carapace: (0) without median indentation; (1) with median groove; (2) with roughly circular indentation behind ocular area. Most known *Belisana* species have a flat carapace (exception: *B. wau*).
4. Conical median elevation on female carapace: (0) absent; (1) present. Always absent in *Belisana*.
5. Paired modification on male clypeus: (0) absent; (1) present. Several convergent origins within pholcids; in *Belisana* only in *B. pianma*.
6. Unpaired clypeus projection: (0) absent; (1) present. Several convergent origins within pholcids, possibly even within *Belisana*.
7. Epiandrous spigots: (0) absent; (1) present. Epiandrous spigots seem to be present in all pholcines except in *Spermophorides*.
8. Spigots on anterior lateral spinnerets (ALS): (0) about 5-8 spigots present; (1) only basic set of two spigots present. Reduction of the spigots to the basic set of two has convergently occurred several times in pholcids, at least once within *Belisana*.
9. Pseudoentegyny: (0) absent; (1) present. State 1 (in which the spermatheca is provided with two ducts, in analogy to the insemination and fertilization ducts of entelegyne spiders – see Huber 1997b) occurs in *Metagonia* only (Huber 2000).
10. Epigynum with knob-shaped apophysis: (0) absent; (1) present.
11. Epigynum scape without pocket: (0) absent; (1) present. Several *Belisana* species have a scape, but this is always provided with a pair of pockets.
12. Long folded scape on epigynum: (0) absent; (1) present.
13. Position of (pocket-less) scape: (0) in front of epigynum; (1) close to posterior rim.
14. Scape morphology (referring to pocket-less scape only): (0) coiled up; (1) pointing straight back; (2) pointing to the front and turning around.
15. Pockets on posterior epigynum plate: (0) absent; (1) present. Absent in *Belisana*, possibly except *B. dodabetta*.
16. Posterior pocket on female opisthosoma: (0) absent; (1) present between epigynum and spinnerets.
17. Female internal genitalia: (0) symmetric; (1) asymmetric.
18. Leg length: (0) short-legged: male tibia 1 up to 2.5 x carapace width; (1) long-legged: male tibia 1 longer than 2.5 x carapace width. Both short-legged and long-legged species occur within *Belisana*.
19. Spines (macrosetae) in single row ventrally on male femora: (0) absent; (1) present.
20. Relative length of tibia 1 and tibia 4: (0) about same length; (1) tibia 1 >1.15 x tibia 4. Most *Belisana* species have state 1, only some short-legged species (*B. davao*, *B. airai*, possibly *B. schwendingeri*) have relatively long tibiae 4.
21. Prolateral trichobothrium on tibia 1: (0) present; (1) absent. Absent in all pholcines except in *Micromerys*.
22. Position of retrolateral trichobothrium on tibia: (0) distal (after 45% of tibia length); (1) proximal (before 45% of tibia length). Proximal in most *Belisana* species; distal in *B. khieo*. Variation among species appears to be continuous. Note that this character is autocorrelated with leg length.
23. Tarsal pseudosegments: (0) absent; (1) present. Pseudosegments are a synapomorphy of Pholcidae, and have secondarily been reduced in *Micromerys* (Huber 2001).
24. Number of tarsal pseudosegments on male tarsi 1: (0) up to 10; (1) more than 10.
25. Proximolateral apophyses on male chelicerae: (0) absent; (1) present. These apophyses are present in all pholcines except in *Metagonia*.
26. Direction of proximolateral cheliceral apophyses: (0) pointing upwards (1) pointing backwards. State 0 is usual in pholcines, only *Zatavua* has state 1.
27. Stridulatory files laterally on male chelicerae: (0) absent; (1) present. Cheliceral stridulation is not known in pholcines with the exception of some *Metagonia* species (Huber 2000).
28. Proximal frontal projections on chelicerae: (0) absent; (1) present.
29. Pair of teeth on proximal rounded projections: (0) absent; (1) present.
30. Spines (macrosetae) proximally on male chelicerae: (0) absent; (1) present.
31. Globular or conical hairs on male chelicerae: (0) absent; (1) spread over surface; (2) 1-3 imbedded in apophysis (if 3, then tip rounded); (3) 3-5 and more imbedded in apophysis (if 3, then tip pointed).
32. Deep grooves on male cheliceral modified hairs: (0) absent; (1) present.

33. Pair of long modified hairs on tip of male cheliceral apophyses: (0) absent; (1) present.
  34. Sclerotized cone accompanying modified hairs on male cheliceral apophyses: (0) absent; (1) present.
  35. Ventral apophysis distally on male palpal coxa: (0) absent; (1) present.
  36. Retrolateral apophysis on male palpal trochanter: (0) absent; (1) present. This apophysis is present in most pholcines with the exception of *Zatavua* (also absent in some species that are not represented in the data matrix, e.g. *Paramicromerys marojezy* and *Spermophora sumbawa*).
  37. Finger-like apophysis on male palpal trochanter: (0) absent; (1) present.
  38. Ventral concavity on male palpal trochanter: (0) absent; (1) present.
  39. Proximodorsal apophysis on male palpal femur: (0) absent or pointing distad; (1) present, pointing proximad.
  40. Male palpal patella: (0) ventrally shorter than diameter; (1) ventrally as long as or longer than diameter.
  41. Palpal tibia spindle-shaped: (0) no; (1) yes. Never spindle-shaped in *Belisana*.
  42. Position of the dorsal male palpal trichobothrium: (0) regular, i.e. not extremely distal; (1) extremely distal.
  43. Rotation of male palpal tibia-cymbium joints: (0) absent; (1) prolateral joint shifted to ventral position, retrolateral joint shifted to dorsal position (2) prolateral joint shifted to dorsal position, retrolateral joint shifted to ventral position. State 1 is a synapomorphy of *Zatavua*, state 2 is a synapomorphy of *Paramicromerys*.
  44. Retrolateral notch on cymbium: (0) absent; (1) present. A notch retrolaterally on the cymbium is a synapomorphy of a species group within *Zatavua*.
  45. Procursus attachment site on cymbium: (0) straight or ventral; (1) dorsal. State 1 is a synapomorphy of *Spermophorides*.
  46. “*Spermophora* flap”: (0) absent; (1) present (a ventral, unhinged, serrated process of the procurus; see Huber 2001). The membranous flap of *Belisana* is not considered homologous to the sclerotized structure in *Spermophora*.
  47. Hinged process on procurus: (0) absent; (1) present. Present in several *Belisana* species, but in many representatives of the genus this character is very difficult to assess.
  48. Procurus strongly bent ventrally: (0) no; (1) yes.
  49. Process winding around procurus ventrally: (0) absent; (1) present.
  50. Dorsal knob on procurus: (0) absent; (1) present.
  51. Palpal tarsal organ position: (0) proximal; (1) distal. A distal tarsal organ is the synapomorphy of a clade within *Zatavua*.
  52. Male palpal tarsal organ shape: (0) flat/exposed; (1) cup-shaped/capsulate. Most pholcines have capsulate tarsal organs. In one clade within *Belisana* (clade 2 in Figs. 76, 77) males have exposed tarsal organs.
  53. Bulbal attachment site: (0) lateral; (1) dorsal. Always lateral in *Belisana* (some apparent exceptions result from artificially rotated bulbs; e.g. Figs. 215, 232, 486, 491).
  54. Proximal bulbal sclerite: (0) absent or invisible; (1) prominent. Prominent in most *Belisana* species (except *B. airai*, *B. davao*, *B. fiji*).
  55. Embolus: (0) tubular membranous; (1) reduced.
  56. Distal or subdistal spine on embolus: (0) absent; (1) present. Both character states are represented in *Belisana*.
  57. Serrate apophysis on bulb: (0) absent; (1) present. This apophysis has long been known as uncus in *Pholcus* and *Leptopholcus*. A similar serrate structure occurs in some “true” *Spermophora* species and in *Micromerys*.
  58. Dark margin on carapace: (0) absent; (1) present. Dark lateral margins on the carapace may be a synapomorphy of a species group within *Belisana* (clades 3 in Fig. 76A and 77A).
  59. Pore plate in internal female genitalia: (0) oval or round; (1) very narrow. Very narrow pore plates may be a synapomorphy of a species group within *Belisana* (clades 1 in Figs. 76, 77).
  60. Row of spines on male clypeus: (0) absent; (1) present. Spines on the clypeus are a synapomorphy of *B. airai* + *B. davao*.
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## Appendix 3. Data matrix used for cladistic analysis.

	10	20	30	40	50	60
<b>Outgroups</b>						
1. <i>Ninetis subtilissima</i>	0100001000	0---000000	10100-00-0	0-0-000000	0100000000	01001-0000
2. <i>Physocyclus globosus</i>	0121000000	0---000101	01110-10-0	0-0-000000	1000000000	01001-0000
3. <i>Ciboneya nuriae</i>	0110000100	0---000100	11110-00-0	0---000000	0020000000	00001-0000
<b>Pholcines</b>						
4. <i>Metagonia argentinensis</i>	11001010?0	0---001101	?1110-00-0	11--010000	0000001000	0110010000
5. <i>Metagonia rica</i>	1100101010	0---001101	11110-00-0	11--010000	0000001000	0110010000
6. <i>Metagonia delicata</i>	1000001110	0---001101	11110-00-0	110-010000	0000001000	0110010000
7. <i>Metagonia globulosa</i>	111001?0?0	0---001001	?1100-10-0	0---010000	0000001000	01?0010000
8. <i>Pholcus phalangioides</i>	0000001001	0---000101	111?100??0	210-010000	1000000000	0101001000
9. <i>Leptopholcus delicatulus</i>	0000001001	0---000101	11111000-0	210-010000	1000000000	0101001000
10. <i>Micropholcus fauroti</i>	0000001001	0---000101	1111100?-0	210-010000	1000000000	01011-0000
11. <i>Spermophora senoculata</i>	1000001000	0---010101	11111000-0	210-010000	1000011000	0110011000
12. <i>Spermophora yao</i>	1000001000	0---010101	?1111000-0	0-0-010000	?00011000	0110011100
13. <i>Spermophora palau</i>	1000001000	0---010101	11111000-0	0-0-010000	1000011000	01100110?0
14. <i>Spermophora tumbang</i>	100000?000	0---010100	11111000-0	0-0-010000	1000011000	0110011100
15. <i>Spermophora estebani</i>	100000?000	0---010101	??1000-0	0-0-010000	1000011100	0110001100
16. " <i>Spermophora</i> " <i>ranomafana</i>	1010001100	0---010101	11111000-0	0-0-010000	?000001000	0110000110
17. " <i>Spermophora</i> " <i>berlandi</i>	1010001100	11100?0101	11111000-0	300-?10000	0000011000	0110000000
18. " <i>Spermophora</i> " <i>sangarawe</i>	101000?100	0---000111	11111000-0	300-011000	0000101100	?010000100
19. " <i>Spermophora</i> " <i>morogoro</i>	1010001100	0---010111	11111000-0	300-011000	0000001100	0110000100
20. " <i>Spermophora</i> " <i>masisiwe</i>	1010001100	0---010111	11111000-0	300-011000	?000001100	0110000100
21. " <i>Spermophora</i> " <i>usambara</i>	1010001100	0---010101	11111000-0	300-01?000	0000001100	?010000000
22. " <i>Spermophora</i> " <i>lambilloni</i>	1010001100	0---000101	11111000-0	2?0-010100	0000001001	?000000100
23. " <i>Spermophora</i> " <i>jocquei</i>	101000????	??????11?	11111000-0	2?0-010100	0000001001	0100000?0?
24. " <i>Spermophora</i> " <i>peninsulae</i>	1100001000	0---000101	11111000-0	200-010000	0000011000	0110000000
25. " <i>Spermophora</i> " <i>schoemanae</i>	1100001000	0---000101	11111000-0	200-010000	?100011000	0110000000
26. <i>Micromerys gracilis</i>	10000011?0	0---000100	010-1000-0	0---010000	1000001000	01011-1000
27. <i>Micromerys daviesae</i>	10000011?0	0---000100	010-1000-0	0---010000	1000001000	01011-1000
28. <i>Panjange mirabilis</i>	100000?001	101100010?	?1???000-0	0-0-010001	10?0000000	0101000000
29. <i>Zatavua vohiparara</i>	110110?00?	1011000101	11111100-0	0-0-000000	1011000000	1?000?0000
30. <i>Zatavua tamatave</i>	110110?000	0---000101	11111100-0	0-0-000000	1011000000	1?000?0000
31. <i>Zatavua madagascariensis</i>	111000?000	0---00010?	?1111100-0	0-0-000000	1011000000	?000?0000
32. <i>Zatavua griswoldi</i>	1101101000	0---000101	11111100-0	0-0-000000	1011000000	11000?0000
33. <i>Zatavua voahangyae</i>	1100001000	0---000101	11111100-0	0-0-000000	101?000000	11000?0000
34. <i>Paramicromerys nampoinai</i>	101000?100	0---000111	11111000-0	210-110110	0-20001000	?000000100
35. <i>Paramicromerys mananteina</i>	1010001100	0---00011?	11111000-0	210-110110	0-20001000	0100000000
36. <i>Paramicromerys scharffi</i>	101000?100	0---000111	11111000-0	0-0-010110	0-20001000	?000000000
37. <i>Paramicromerys rothorum</i>	101000?100	0---000101	11111000-0	0-0-010100	0-20001000	?000000100
38. <i>Paramicromerys coddingtoni</i>	1010001100	0---000111	11111000-0	0-0-010100	0-20001000	0100010100
39. <i>Spermophorides</i> sp. 1	1110000100	0---100101	11111000-0	0-0-010000	0000101000	0110000000
40. <i>Spermophorides</i> sp. 2	1110000100	0---100101	11111000-0	0-0-010000	0000101000	0110000000
41. <i>Buitinga uzungwa</i>	1010001100	1100000101	11111000-1	300-110001	0100001010	0110000000
42. <i>Buitinga safura</i>	1010001100	1110000101	1111100101	300-110000	0100000000	0110?00100
43. <i>Buitinga kadogo</i>	1010001100	1112000111	1111100110	300-110000	0100000000	0010000100
44. <i>Buitinga lakilingo</i>	111000?100	1112000111	1111100110	300-110000	0100000000	0110000000
45. <i>Buitinga mazumbai</i>	101000?100	1112000111	1111100110	300-110000	010000?000	0110000100
46. <i>Quamtana bonamanzi</i>	0100001000	0---000101	11111000-0	0111010000	1020000000	0101000000
47. <i>Quamtana merwei</i>	0100001000	0---000101	11111000-0	0111010000	1020000000	0101000000
48. <i>Quamtana vidal</i>	1100001000	0---000101	11111000-0	0?1?010000	1000000000	0101000000
49. <i>Quamtana entabeni</i>	0000011000	0---000101	11111000-0	0110010000	1000000000	0101000000
50. <i>Quamtana ciliata</i>	0000011000	0---000101	11111000-0	0110010000	1000000000	0101000000
51. <i>Quamtana hectori</i>	1100001000	0---000101	11111000-0	0110010000	1000000000	0101000000
52. <i>Quamtana mabusai</i>	0100001000	0---000101	11111000-0	0110010000	1000000000	0101000000
53. <i>Quamtana embuleni</i>	0100001000	0---000101	11111000-0	0111010000	1000000000	0101000000
54. <i>Quamtana oku</i>	0100001000	0---000101	11111000-0	0110010001	?000000000	0101000000
55. <i>Belisana fiji</i>	1000001000	0---000101	?111000-0	0-0-010000	0000000000	0100000000
56. <i>Belisana airai</i>	1000001000	0---000000	?101000-0	0-0-010000	0000000000	0100000001
57. <i>Belisana davao</i>	1000001000	0---000000	?11?1000-0	0-0-010000	0000000000	0100000001
58. <i>Belisana australis</i>	1100001000	0---000101	?1111000-0	0-0-010000	0000000000	0101010010
59. <i>Belisana leuser</i>	1000001000	0---000101	11111000-0	0-0-010000	0000000000	0101010010
60. <i>Belisana bohorok</i>	1000001000	0---000101	?1111000-0	0-0-010000	000000?000	0101000010

61. <i>Belisana marena</i>	1000001000	0---000101	?1111000-0	0-0-010000	0000001000	0101000010
62. <i>Belisana kaharian</i>	1000001000	0---000101	?1111000-0	0-0-010000	0000001000	0101010010
63. <i>Belisana sepaku</i>	1000001000	0---000101	?1111000-0	0-0-010000	0000001000	0101000010
64. <i>Belisana pianma</i>	1000101000	0---000101	11111000-0	0-0-010000	0000001000	0101000100
65. <i>Belisana nujiang</i>	1000001000	0---000101	11111000-0	0-0-010000	0000000000	0101010100
66. <i>Belisana scharffi</i>	1000001000	0---000101	11111000-0	0-0-010000	0000001000	0101000100
67. <i>Belisana inthanon</i>	1100001000	0---000101	11111000-0	0-0-010000	0000001000	0101000100
68. <i>Belisana ketambe</i>	1100001000	0---000101	11111000-0	0-0-010000	0000000000	0001000000
69. <i>Belisana schwendingeri</i>	1100001000	0---00000?	11111000-0	0-0-010000	0000000000	0001000000
70. <i>Belisana leumas</i>	1100001000	0---000101	11111000-0	0-0-010000	0100001000	0001000000
71. <i>Belisana sandakan</i>	1100001000	0---000101	???'1000-0	0-0-010000	0000000000	0001010000

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