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Revision of the Genus *Padilla* Peckham and Peckham, 1894 (Araneae: Salticidae) — Convergent Evolution of Secondary Sexual Characters Due to Sexual Selection and Rates of Molecular Evolution in Jumping Spiders

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The horned jumping spider genus *Padilla* Peckham and Peckham is restricted to Madagascar. The genus comprises 15 species, which are herein diagnosed, described, and illustrated in detail. Three synapomorphies of the genus are found. A key to males is provided. Twelve species are new: *P. mazavaloha, P. maingoka, P. manjelatra, P. lavatandroka, P. mitohy, P. griswoldi, P. astina, P. ombimanga, P. mihaingo, P. foty, P. boritandroka,* and *P. ngeroka*. *Padilla javana* is excluded from the genus and considered *incertae sedis* within Salticidae. *Padilla mantis*, *P. glauca*, and *P. lancearea* (Simon 1900) are considered *nomina dubia*. A phylogenetic analysis of 38 morphological characters and two sequenced genes (COI and 28S) exhibit a conflict between the morphological and molecular hypotheses due to convergent evolution of the secondary sex traits such as horn shape. The diversification of cheliceral horns observed in male *Padilla* appears to be sexual selection. The monophyly of the genus has been confirmed both by the Ballinae morphology phylogeny (Benjamin 2004) and the Salticidae 28S phylogeny (Hedin and Maddison 2003). Within Ballinae, *Padilla* is a sister group of the genus *Philates*. Within Salticidae, *Padilla* is a sister group of two balline genera, *Pachyballus* and *Ballus*, with which it forms a monophyletic group that is a sister group to a clade including Marpissoids, Heliophanines, Freyines, Euophryines, and Plexipoids. For the first time, penalized likelihood was used to assess the average rates of molecular evolution of the 28S gene and the ages of the genus and members of the family Salticidae. The ages of *Padilla* (13.06 Mya) and the subfamily Ballinae (23.17 Mya) are too recent for Gondwanan vicariance hypothesis; thus, the stepping stone hypothesis is a better explanation for the distribution.

KEYWORDS: Madagascar, Phylogeny, Horn and life style, convergent evolution, sexual selection, divergence time, Ballinae, Salticidae

The jumping spider family (Salticidae) is represented by more than 5,000 species (Platnick 2006) of varied body forms, behaviors, and ecological relationships. Their unique high-resolution eyes (Land 1985) permit visually mediated predatory behavior (Jackson and Pollard 1996) and complex courtship marked by visual communication, with striking morphological ornamentations (Griswold 1987; Maddison 1988). These secondary sexual characters are proven to be particularly important in jumping spiders, e.g., in the genus *Habronattus*, in which sexual selection for species recognition has played a role in the evolution of male secondary sex traits that are exposed to females during courtship and are known to be associated with prezygotic reproductive isolation and speciation (Griswold 1987; Masta and Maddison 2002).

This study focuses on the genus *Padilla*, an endemic of Madagascar. *Padilla* are small to medium-sized spiders, 4–6 mm in length. Their carapace, which can be low or high, may reflect different life styles documented in jumping spiders by Crane (1949). She recognized "runners" (jumping spiders with low carapace that mostly run and jump only during prey capture) and "hoppers" (refers to jumping spiders with high carapace that mostly jump rather than run). At first sight, *Padilla* resemble pseudoscorpions due to the first pair of legs, which are darker and enlarged compared to the other legs, which are typically pale and slender. The males of this genus display one of the most striking secondary sexual characters: a forward projecting pair of horns on the chelicerae. These horns look like a lance which can be bent near the tip. They have a varying degree of elongation, orientation, and origin in different species.

The genus was described by Peckham and Peckham (1885) based on *Padilla cornuta.* This species was described from a single male specimen from Madagascar and was diagnosed by the presence of straight, stout, and long horns (twice as long as the paturon) originating from the bases of each paturon. After the discovery of six other species, Simon (1900) included *Padilla* within his Bavieae group based on the following characters: (1) depressed cephalothorax, (2) anterior eye row wider than posterior, posterior median eyes closer to anterior laterals, and (3) cephalic region shorter than thoracic. The genus was separated from all other genera within the Bavieae group by (1) a palp short and wider instead of thin and longer, and (2) first legs exaggeratedly thickened. Subsequent tentative placement of the genus has been made by Maddison (1988, 1995) and Benjamin (2004). Both placed the genus within the subfamily Ballinae within the so-called Salticoida group on the basis of two other characters of the male palpi: (1) a well-coiled embolus lying flat on the tegulum, and (2) a tegulum which is divided by a pale, longitudinal furrow. *Padilla*. however, was not represented in their final hypotheses.

Currently, very little is known about the relationship of *Padilla* to other balline genera and nothing is known about the intrageneric relationships. Of seven previously known species, all but one is recorded from Madagascar, *Padilla javana* Simon, 1900, which is recorded from Java. However, the original description is not detailed enough to clarify its position and, unfortunately, the type specimen appears to be lost. This species lacks the extraordinary embellishments present in all male *Padilla* (Prószyński, 2003). Most species *Padilla* are known only from their type specimens, of which only three were located. The aim of this study is to revise the genus, including redescriptions of known species as well as descriptions of new species. A key to species is given and their distributions in Madagascar, correlated with environmental factors, are discussed. The phylogenetic relationships of *Padilla* are examined, and its place within the Salticidae and the Ballinae is assessed for the first time. I have used morphological and molecular data, the latter from two different genic regions (COI, 28S), to generate parsimony and maximum likelihood phylograms.

The nature of these different markers is of value in understanding the behavior of morphological data, such as secondary sexual characters and other somatic characters, contrasted with data from different genic regions in reconstructing phylogeny of *Padilla*. This is the first time that the rates of evolution of the 28S gene in jumping spiders have been documented. Knowledge of the nucleotide sequence rate of evolution inferred from a maximum likelihood tree allowed me to estimate divergence times for this genus and some members of the Salticidae family. I will discuss the biogeographical implications of those results on isolation of *Padilla* in Madagascar.

The presence of horn-like projections on the carapace has already been noted in other spiders (Wanless 1996; Huber et al. 2005). In *Padilla*, the presence of the horns is male biased. They may be used in courtship or male-male combat. The role of sexual selection by female choice in shaping male secondary sex traits has already been documented among insects and other arthropods (Eberhard 1985, 1991; Clark and Uetz 1993; Clark and Morjan 2001; Huber et al. 2005). The diver-

sification of horn, carapace height and body shape observed in *Padilla* may be the result of sexual selection, natural selection, or both. In this paper, I used geospatial and environmental data integrated in ArcGIS 9 and DIVAGIS version 5.2 software as well as a statistical test of correlation among morphological characters and some bioclimatic variables to discuss these alternatives.

Materials and Methods

Conventions.— All anatomical abbreviations are listed in Appendix 2. On the phylograms, nodes that are assigned a letter (e.g., A, B, C, D, B', C') represent a particular group of species or clade. Throughout the discussions of the phylogenetic analysis and relationships among taxa, these letters are used to refer to clades belonging to that node (e.g., clade C, comprising the *Brevis* group, *P. mihaingo, P. mitohy, P. foty,* and *P. maingoka*).

Collections.— Most materials for this study were drawn from a geographically comprehensive collection generated over the last five years from more than 60 sites in Madagascar by the California Academy of Sciences Madagascar Arthropod Survey. Materials from the Muséum National d'Histoire Naturelle in Paris, Royal Museum for Central Africa in Tervuren, and Museum of Comparative Zoology at Harvard University were also examined. In order to assess the diversity of arthropods in Madagascar, the Survey was conducted in sites of varied vegetation, climate, elevation, and geological substrate. Different methods of capture such as Winkler or litter sifting, beating low vegetation, general collecting and pitfall, Malaise traps, light, and yellow pan traps were applied (Fisher 2005). Specimens were preserved in 75% ethanol at room temperature to keep them flexible for morphological work (Martin 1978) and shipped to and deposited in the collections of the Department of Entomology of the California Academy of Sciences.

Description.— I used morphological characters, molecular distances and distributional data to discriminate species. A male and female, if both are known, are described for each species. Species description and illustrations were based on 10 representatives of each species, if possible. Representatives were chosen according to the degree of character variation and site locality to maximize the range of variation and geographic distribution considered. All measurements (Fig. 1) are in millimeters and were taken using an Olympus SZH10 dissecting microscope. The measurements were taken from five males and five females of each species, when possible, and are reported as ranges for each sex. The mean value is also calculated for both sexes. In many species, there were fewer than five individuals of each sex available, or one sex was unknown, so only those numbers are reported (Table 1). Known species are only described to document new information. Examinations of specimens and drawings were made using an Olympus SZH

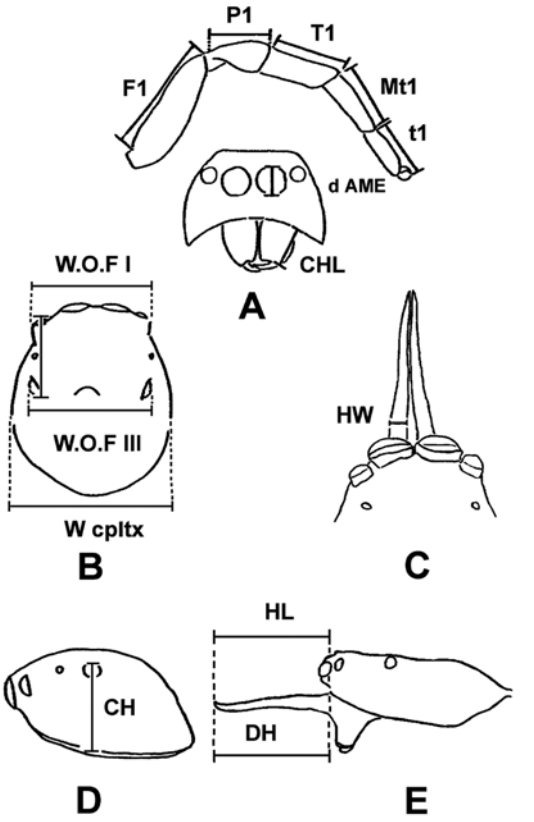

Figure 1. *Padilla* measurements.

TABLE 1. Ratio of the measurements of body, prosoma and legs of *Padilla*.

SPECIES	Number of specimens (♂,♀)	Total L (♂,♀)		Horn L / CL (♂)		CH/ CL (♂,♀)		WOF I/ W cpltx (♂,♀)		W chelic/ CHL (♂,♀)		F1 / WOF II (♂,♀)		F3/ WOF II (♂,♀)		F3/ F4 (♂,♀)		Tb1 / WOF II (♂,♀)	
P. sartor	(1, 0)	5.76	_	0.5	0.31	_	0.70	_	0.80	_	1.36	_	0.82	_	1.12	_	1.20	_
P. mazavaloha	(3, 15)	5.39	0.32	0.41	0.32	0.32	0.76	1.13	0.76	0.94	1.13	1.08	0.69	0.7	1.17	0.83	0.95	0.76
P. maingoka	(2, 0)	6.04		0.38	0.24		0.74		0.80		1.49	_	0.66	_	1.29	_	1.23	_
P. cornuta	(3, 5)	5.14	5.15	0.46	0.31	0.32	0.80	0.90	0.75	0.83	1.28	0.99	0.71	0.6	1.17	0.77	0.96	0.68
P. manjelatra	(2, 1)	5.88	5.76	0.75	0.39	0.4	0.81	0.88	0.64	0.77	1.38	0.97	0.68	0.71	1.38	0.84	1.00	0.70
P. lavatandroka	(13, 10)	5.88	6.67	0.78	0.41	0.38	0.79	0.79	0.62	0.72	1.35	1.16	0.88	0.86	1.11	0.85	0.93	0.83
P. armata	(1, 1)	5.88	5.64	1.63	0.30	0.33	0.70	0.74	0.60	0.73	1.44	0.89	0.85	0.74	1.10	0.86	1.07	0.79
P. griswoldi	(2, 0)	5.4	_	0.53	0.19	_	0.41	_	0.73	_	2.14	_	1.14	_	1.34	_	1.79	_
P. astina	(1, 0)	4.7	_	0.67	0.34	_	0.71	_	0.65	_	1.38	_	0.76	_	1.16	_	1.12	_
P. ombimanga	(1, 0)	5.92	_	0.61	0.30	_	0.69	_	0.70	_	1.38	_	0.75	_	1.21	_	1.21	_
P. boritandroka	(7, 0)	4.55	_	0.04	0.34	_	0.80	_	0.51	_	1.32	_	0.65	_	1.22	_	1.17	_
P. ngeroka	(12, 11)	4.60	4.43	0.22	0.26	0.27	0.81	0.73	0.55	0.88	1.38	0.79	0.62	0.56	1.46	0.73	1.11	0.56
P. mitohy	(0, 9)	_	5.59	_	_	0.27	_	0.82	_	0.87	_	1.09	_	0.69	_	0.76	_	0.82
P. mihaingo	(0, 1)	_	5.53	_	_	0.32	_	0.78	_	0.8	_	1.74	_	1.23	_	0.84	_	1.51
P. foty	(0, 1)	_	4.96	_	_	0.27	_	0.81	_	0.74	_	1.13	_	0.73	_	0.84	_	0.88

Stereo dissecting Microscope equipped with a camera lucida. Photographs of the diagnostic characters were taken using a Nikon DXM1200 digital camera attached to a Leica MZ16 stereomicroscope montaged with the Synchroscopy® Auto montage system pro version 5.01.0005 and were used to generate the final digital images. Female epygina were digested with either KOH under a heat lamp for 3–8 hours, or a proteinase (trypsin or "ReNu": Enzymatic contact lens cleaner, Bausch & Lomb Inc.) overnight. Specimens were soaked overnight in 100% EtOH (transferred from 70% ethanol to absolute ethanol), cleaned with an ultrasonicator, critical point dried with CO_2, sputter coated with AuPd, and scanned with a Leo 1450VP Scanning Electron Microscope (SEM). Automontage and SEM images were saved as TIF files that were edited using Adobe Photoshop. Plates were assembled and labeled using Adobe Photoshop©.

Species distributions were mapped using ArcGIS 9, climatic and ecological conditions were assessed using ArcGIS 9 and DIVAGIS — Worldclim version 3.0.

SPECIES GROUPS.— The new and previously-described species of *Padilla* were divided into four groups based primarily on phenetic similarity in carapace shape (implying a "runner" or "hopper" lifestyle) and male cheliceral horn configuration. For convenience in characterizing and describing species and discussing character distributions, these groups are referred to throughout. I make no *a priori* assumption that these groups represent evolutionary lineages, but test the group monophyly using phylogenetic analysis with morphological and molecular characters, which are discussed below.

armata group
- *P. armata* Peckham and Peckham, 1894
- *P. astina*, new species
- *P. griswoldi*, new species
- *P. ombimanga*, new species

brevis group
- *P. boritandroka*, new species
- *P. ngeroka*, new species

cornuta group
- *P. cornuta* (Peckham and Peckham, 1885)
- *P. lavatandroka*, new species
- *P. manjelatra*, new species

sartor group
- *P. maingoka*, new species
- *P. mazavaloha*, new species
- *P. sartor* Simon, 1900

Unassigned
- *P. foty*, new species
- *P. mihaingo*, new species
- *P. mitohy*, new species

Phylogenetic Analysis

This analysis comprises: (1) a family analysis, (2) a subfamily analysis, and (3) a generic level analysis. First, to test Benjamin's (2004) hypothesis that *Padilla* is a member of Ballinae, I included two species of the genus and one balline genus (*Ballus)* within Hedin and Maddison's (2003) 28S Salticidae tree, which already has one balline genus (*Pachyballus)*, to see if *Padilla* species come out as their sister taxa. Once, the placement of *Padilla* as a Ballinae was confirmed by this analysis, I decided to also add two species of the genus within Benjamin's (2004) Ballinae morphological matrix, since *Padilla* was not included in his sub-family analysis. The intention was (1) to define the placement of *Padilla* within this sub-family, (2) to find its relatives, and (3) to determine the appropriate outgroup taxon. Therefore, characters of the genus were coded according to Benjamin's (2004) matrix and two other characters that are synapomorphies for the genus were added (Appendix 4). These new characters are the path of the sperm duct intermediate between S and C (character 6–1**,** Fig. 2C) and the presence of cheliceral horns (character 42–1). A subfamily analysis was then performed for 42 characters of 18 balline genera including two species of *Padilla*. Once the outgroup was determined by this analysis, generic analyses were performed both for morphology (Appendix 3) and molecular characters in order to assess species relationships within *Padilla*. Finally, a family level analysis was conducted to (1) determine the exact placement of the genus within the family of Salticidae and to (2) assess the probable placement of the sub-family of Ballinae within the Salticidae. My sequences of the 28S gene of all species of *Padilla* were then analyzed along with all the 28S sequences of 84 other salticid genera, including two other balline genera: *Ballus* and *Pachyballus*, which were contributed by Hedin and Maddison (2003).

Outgroup choice.—The subfamily analysis placed the genus *Philates* as the closest relative of *Padilla.* However, within the phylogeny of Ballinae the species of *Padilla* were nested within the genus *Philates.* This raises the possibility that *Padilla* may be merged with the genus *Philates*. Therefore, the genus *Philate*s along with the genus *Ballus* were used as outgroups in the morphological analysis as a test of this hypothesis. *Ballus* was used to root the molecular tree. Even if it is quite distantly related to *Padilla,* its inclusion in this analysis was necessary due to a lack of fresh material of *Philates* for molecular work.

Morphology

Taxa and characters scored.—The characters used in phylogeny inference are assumed to be homologous (Griswold 2001; Hennig 1 966) and are evolving independently of each other (Freeman and Herron 2004). Shared derived characters or synapomorphies are preferred over other characters (Hennig 1966). Special consideration was placed on secondary sexual characters such as the

horns and first leg spination. Those characters are conspicuous and highly differentiated, especially in males. In jumping spiders, those secondary sexual characters are often displayed during courtship (Clark and Morjan 2001; Owens 2003) and may function as species isolating mechanisms (Griswold l 987; Masta 2002). The same attention was accorded to complex and functionally important organs such as the male palp and the female epigynum.

Here I describe the character states scored for each of the taxa included in the morphological phylogenetic analyses and give a matrix as a summary (Appendix 3).

Horns

1. *Presence in males:* (0) absent; (1) present (synapomorphy of all *Padilla).*
2. *Horn curvature:* (0) straight and slightly convergent (*cornuta* group *and brevis* groups; Figs. 3A–G, 4A, 5–8); (1) outward and then inward (*sartor* group; Figs. 9A–C); (2) inward, then outward and finally crossed at tips (*armata* group; Figs. 10A–D).
3. *Horn orientation lateral view:* (0) downward curve (*brevis* group; Figs. 3G–H, 11A–B); (1) almost straight or slightly curved downwards toward the tips (*armata* group; Figs. 3E–F, 12A–B, D*)*; (2) present as double curve, first going down, then going up near tips, but tips not surpassing the clypeus (*cornuta* group; Figs. 3A–B, 13A–D); (3) going upward with tips reaching middle of AME (*sartor* group; Figs. 3C–D, 14A, 15A–C).
4. *Horns tips, dorsal view:* (0) not crossed, separated from each other (*cornuta* group, *brevis* group, *sartor* group (in part, only *P. sartor)*; Figs. 8, 9A, 16, 17); (1) crossing each other (*armata* group, *sartor* group (in part, *P. mazavaloha*, *P. maingoka*); Figs. 9B–C, 10, 18–23).
5. *Horn thickness (horn width/cheliceral width):* (0) slender, mean width<0.15mm (*P. maingoka, P. boritandroka, P. ngeroka*); (1) intermediate, mean width 0.15–0.25mm (*P. sartor, P. cornuta, armata* group); (2) thick, mean width>0.25mm (*P. mazavaloha*, *P. manjelatra, P. lavatandroka*).
6. *Horn length (horn length/carapace length):* (0) horn L/CL< 0.3 (*brevis* group, *P. maingoka*); (1) horn L/CL: 0.3–0.6 (*sartor* group except *P. maingoka, P. cornuta, armata* group); (2) horn L/CL> 0.75 (*P. manjelatra, P. lavatandroaka*).
7. *Horn origin:* (0) from the distal part of the chelicerae near the fangs or CHL/DH<= 0.25 (*brevis* group; Figs. 3G–H); (1) from the proximal part of the chelicerae or CHL/DH>0.5 (all other *Padilla*; Figs. 3B, 3D–F, 12–13, 15).

Leg spination

8. *Femur I midventral spine and bristles:* (0) absent (outgroup taxa); (1) one or two midventral spines and two retromarginal bristles present (all *Padilla*, Figs. 24A–D).
9. *Femur I proximoventral spines:* (0) only one (all *Padilla* except *P. sartor* and *P. ombimanga*); (1) two (*P. sartor, P. ombimanga*; Figs. 16, 21, 25A).

Femur II and III dorsal

10. *Additional promarginal spine:* (0) absent (*P. mihaingo* and *P. mitohy, P. mazavaloha, Ballus*); (1) present (all *sartor* group except *P. mazavaloha, all armata* group, all *cornuta group*, all *brevis* group; Fig. 25D).

Femur IV dorsal

11. *Male patella I spur:* (0) absent (all *Padilla* except *P. manjelatra, P. lavatandroka*); (1) present, proventral (synapomorphic to *P. manjelatra, P. lavatandroka*; Fig. 25B).
12. *Femur and patella I retromarginal setal fringe:* (0) absent (outgroup); (1) present (all *Padilla*).
13. *Tibia I width:* (0) as wide as other leg segments (all other *Padilla*; Figs. 24A–C); (1) clearly broader or wider than femur, patella and metatarsi (*P. boritandroka, P. maingoka; P. mihaingo, P. mitohy, P. ngeroka*; Figs. 24B–C).
14. *Tibial spur:* (0) absent (all *Padilla* except *P. mazavaloha* and *cornuta* group); (1) present (*P. mazavaloha* and *cornuta* group; Fig. 25C).

15. *Tibia I proximoventral distal spine:* (0) larger than the proximals (all *armata* group and *P. sartor*; Fig. 24A); (1) of the same size or smaller than the proximals (Fig. 24D).
16. *Tibia and metatarsus I coloration:* (0) same as other segments; (1) clearly darker than other leg I segments (*P. manjelatra* and *P. lavatandroka*; Fig. 24D).
17. *Tibia and metatarsus I spines:* (0) paired, present both on proventral and retroventral sides of the tibia and metatarsus (all *Padilla* except *P. armata*, *P. astina*, and *P. griswoldi*); (1) not paired, only proventral spines present (all *armata* group except *P. ombimanga* (Fig. 25A).

Carapace

18. *Fovea presence:* (0) absent (*P. foty, P. ngeroka*); (1) present.
19. *Carapace edge:* (0) carapace with lateral whitish bands of scales *(P. astina, P. griswoldi, P. mihaingo; P. mitohy;* Fig. 27A–B); (1) carapace without lateral whitish bands of scales.
20. *Implied Life style (carapace height/carapace length):* (0) "runner" or CH/CL lesser than 0.25 (*brevis* group, *P. maingoka, P. mihaingo, P. foty*; Figs. 28C–D); (1) "intermediate" or CH/CL: 0.30–0.35 (*armata* group, *P. cornuta, P. sartor, P. mazavaloha*; Fig. 28B); (2) "hopper" or CH/CL greater than 0.35 (*P. manjelatra, P. lavatandroka;* Fig. 28A).
21. *Cephalothorax shape:* (0) almost rectangular (*brevis* group, *P. maingoka, P. mitohy, P. mihaingo*; Figs. 17, 23, 27,29A–B); (1) "trapezoidal" interiorly narrowed and enlarged between leg II and III (all other *Padilla* and *Philates*; Figs. 4A–C); (2) nearly square, or cephalothorax width = CL (*Ballus*).

Mouth parts

22. *Clypeus border:* (0) clypeus edge with a fringe of white scales (*P. mihaingo, P. mitohy*, all *Armata* group except *P. ombimanga*; Fig. 14C); (1) clypeus edge without a fringe of white scales (Figs. 14A–B, D–E).
23. *Endite shape:* (0) elongate and parallel sided; (1) enlarged and epically expanded (*Armata group, P. manjelatra, P. lavatandroka;* Fig. 30B).
24. *Endite ridge:* (0) located only along the anterior part of the endites as a serrula (*P. foty*); (1) extending past the serrula, reaching to the lateral bases of endites (all other *Padilla*; Fig. 30D).

Chelicerae

25. *Chelicerae edges:* (0) Sharpened or carinate on both lateral margins (*brevis* group; Figs. 14D–E); (1) normal, not having a sharp longitudinal edge along lateral sides or carinate only on upper outer distal margins (all other *Padilla)*.
26. *Cheliceral dorsum:* (0) flattened dorsally (synapomorphy of the *Brevis group*, Figs. 14D–E); (1) not dorsally flattened.
27. *Cheliceral width:* (0) wider or chelicerae width/chelicerae length>0.60 (*P. lavatandroka*, *P. manjelatra*; Fig. 14B); (1) thinner, chelicerae width/chelicerae length<0.60 (*brevis group*; Figs. 14D–E).
28. *Paturon orientation compared to carapace:* (0) paturons not projected forward but rather at 90° from carapace (Fig. 3B); (1) paturons projected forward much more than 90° from the carapace (*brevis* group; Figs. 3H–11B).

Sternum

29. *Sternum anterior part:* (0) oval, anterior part slightly truncated; (1) almost round, anterior part not truncated (*P. lavatandroka, P. manjelatra*; Fig. 30A); (2) almost round, but anterior part truncated (*P. sartor* and *P. ombimanga*).

Abdomen

30. *Abdomen dorsal:* (0) flattened (*P. astina, P. griswoldi*; Fig. 12B–C); (1) not flattened (Figs. 13B–C, 15A).
31. *Spinneret plate:* (0) spinnerets preceded by large half circle ventral plate; (1) without this plate.

Palp

32. *Embolus fold* (*ef*): (0) present (*brevis* group*, P. mazavaloha*; Figs. 31D–E, 32B–D–E); (1) absent.
33. *Embolus coil tilt*: (0) inclined to the retrolateral side (*brevis* group, *P. mazavaloha*; Figs. 31D, 32A–D); (1) not (all other *Padilla*).
34. *Embolar second loop* (*esl*): (0) thickened (*brevis* group*, P. mazavaloha;* Figs. 31D–E, 32D); (1) not thickened (Fig. 29A–D–G).
35. *Tegular groove* (*tg*): (0) absent (*brevis* group and *sartor* group, *Ballus.* sp; Figs. 31A–D–G, 32E–D); (1) shallow (*cornuta* group except *P. cornuta*; Figs. 29E–H); (2) deep (*armata* group and *P. cornuta*; Figs. 29B, 33B–D–H).
36. *Ventral tegulum posterior knob* (*vk*): (0) absent (all other *Padilla*); (1) present (*armata* group; Figs. 33B–E–G).

Epigynum

37. *Interconnection of copulatory opening (co):* (0) interconnected (*P. mihaingo, P. mazavaloha, P. manjelatra*; Fig. 27D); (1) not interconnected (*P. mitohy, P. foty*; *P. cornuta*; *P. ngeroka;* Figs. 26A–B–E–F, 27C–E).
38. *Sulci (sclerotized tube following copulatory openings):* (0) absent (most *Padilla)*; (1) present (*P. foty*, *P. mitohy*; Figs. 26A–B–E–F, 34E–G).

Cladistic Analysis of Morphological Data

PAUP version 4.0b.10 (Swofford, 2001–2002) was used to perform both the subfamily and the intrageneric phylogenetic analysis. I conducted a heuristic search with a random stepwise addition of 1000 replicates subjected to tree bisection-reconnection (TBR) branch swapping. All characters were unordered and equally weighted. Analyses using successive character weighting (Farris 1969; Carpenter 1998), using the maximum value of the rescaled consistency index was also performed to obtain trees that maximize implied weight across all characters. Only the most parsimonious trees were retained. I used MacClade 3.0 and 4.0 (W.P. Maddison and D.R. Maddison 1992, 2000) to optimize characters on the tree. If optimizations were ambiguous, they are resolved using the ACCTRAN option (Accelerated transformation; Farris optimization), which favors secondary loss over convergence to explain homoplasy and therefore maximizes homology (Hormiga 1994; Griswold et al. 1998; Schuh 2000). Uninformative characters were excluded before the calculation of tree statistics. Character state changes were traced with MacClade version 4.0 (W.P. Maddison and D.R. Maddison 2000).

Molecular Analysis

Genus molecular analysis.— To determine the relationships within the genus *Padilla*, a total of 15 taxa, of which 14 species are from the genus *Padilla*, were included in the analysis (Table 2). Two individuals were sequenced for each species for *P. lavatandroka*, *P. mazavaloha*, *P. cornuta*, *P. manjelatra*, *P. ngeroka*, for a total of 19 individuals from 14 species in the genus *Padilla*. The genus *Ballus* was used as the outgroup taxon to polarize the character states of the ingroup and to establish the position of the root.

Note: *P. armata* was not included in the molecular analysis because of a lack of good DNA material. This species is only known from very old type specimens.

Family level molecular analysis.— The placement of the genus inside the family Salticidae was assessed by combining and analyzing the 28S sequences of the genus with the 28S sequences of 84 other salticid taxa from the molecular phylogeny of Hedin and Maddison (2003).

DNA isolation.— Field collected specimens were placed in 75% EtOH and kept in the museum collection until the time of DNA extraction. Total genomic DNA was isolated by grinding two entire legs in lysis buffer (Buffer ATL and Proteinase K) with a Teflon grinding implement. The

TABLE 2. List of all specimens sequenced for molecular phylogenetic analysis: DNA, collection localities, gene bank accession numbers, museum accession numbers.

Species	Localities	COI	28S	Museum accession No.
Ballus chalybeius	SE Azerbaijan, Lenkoran	EF514383	EF514398	CASENT9021988
***Sartor* group**				
Padilla sartor	Antsiranana, Montagne d'Ambre	EF514373	EF514388	CASENT9021839
Padilla mazavaloha	Fianarantsoa, PN Ranomafana	EF514374	EF514389	CASENT9006891
Padilla maingoka	Fianarantsoa, PN Ranomafana, Talatakely	EF514370	EF514386	CASENT9003506
***Cornuta* group**				
Padilla cornuta	Antananarivo, Andranomay	EF514381	EF514396	CASENT9004193
Padilla lavatandroka	Antsiranana, Montagne d'Ambre	EF514375	EF514390	CASENT9021901
Padilla manjelatra	Antsiranana, R.S Manongarivo	EF514382	EF514397	CASENT9021862
***Armata* group**				
Padilla griswoldi	Fianarantsoa	EF514380	EF514395	CASENT9021858
Padilla astina	Toliara, Ifaty	EF514378	EF514394	CASENT9021860
Padilla ombimanga	Antsiranana, Montagne d'Ambre	EF514372	EF514387	CASENT9023432
***Brevis* group**				
Padilla boritandroka	Mahajanga, PN Tsingy de Bemaraha	EF514371	EF514385	CASENT9009733
Padilla ngeroka	Antananarivo, Andranomay	EF514376	EF514391	CASENT9004188
Unassigned				
Padilla foty	Antsiranana, RNI de Lokobe	EF514369	EF514384	CASENT9021859
Padilla mitohy	Antsiranana, Andavakoera	EF514377	EF514392	CASENT9011933
Padilla mihaingo	Antsiranana, Ampondrabe	EF514379	EF514393	CASENT9011958

homogenate was incubated at 55ºC until tissue dissolved (may take up to 48 hours or more) and then purified using DNeasy™ Tissue Kit (Quiagen Inc., Valencia, CA) following the manufacturer's protocols.

POLYMERASE CHAIN REACTION (PCR) AMPLIFICATION.— For each specimen, a fragment of approximately 500 base pairs in length of mitochondrial gene COI and 800bp in length of nuclear gene 28S was amplified via PCR. Double stranded DNA was amplified, with some volume modifications depending on the specimen, in the following reaction: 25µL volume reaction of 12.88–13.88µL PCR water, 2.5µL of 10X PCR buffer (as supplied by the manufacturer of Taq polymerase) or 5µL of Expand High Fidelity ^{Plus} PCR buffer (as supplied by the manufacturer of Expand High Fidelity ^{Plus} Taq), 2.5µL MgCl2 (10mM), 2.5µL dNTP (10mM), and 1.25µL of each primer, 0.12µL Amplitaq® DNAPolymerase (Applied Biosystems Inc., Foster City, CA) or Expand High Fidelity ^{Plus} Taq (Roche). PCR amplification primers for these fragments are listed in Table 3. All reactions were initially denatured at 94–95ºC for 2–5 minutes in a MJ Dyad Thermal Cycler (MJ Reasearch, Waltham, MA) or a DNA Engine Dyad, Peltier Thermal cycler, then subjected to 35 cycles of 30s denaturation at 94–95ºC, 30s annealing at 49ºC for 28S, 45ºC for COI, and 45s extension at 72ºC per cycle, with a final 10 min extension at 72ºC. Amplified products were cleaned using the UltraClean PCR clean-up Kit (MoBio, Solana Beach, CA) prior to sequencing.

SEQUENCING.— All sequencing was done using dye terminator cycle sequencing following the protocol specified by ABI PRISM™ Dye terminator Cycle Sequencing Ready Reaction Kit (Revision B, August 1995, Perkin-Elmer, Norwalk, CT). Primers used for amplification served as sequencing primers. Additional internal primers were designed for sequencing purposes (Table 3)

TABLE 3. Primer sequences for amplification and sequencing of mitochondrial COI,Nuclear large subunit (28S) rDNA divergent domains D1-D3. Reference listed in Hedin and Maddison 2001a and Simon 1994.

Primer	Sequence	Utility	D. mel REF	Primer citation
C1 - N - 2776	5' -GGA TAA TCA GAA TAT CGT CGA GG- 3'	amplification / sequencing	25351 - 6	Simon et al. (1994)
C1 - J - 2309	5' -TTT ATG CTA TAG TTG GAA TTG G- 3'	amplification / sequencing	25351 - 9	Simon et al. (1994)
28S - C	5' -GGT TCG ATT AGT CTT TCG CC- 3'	amplification / sequencing	25351 - 12	Hedin and Maddison (2001)
28S - 0	5' -GAA ACT GCT CAA AGG TAA ACG G- 3'	amplification / sequencing	25351 - 16	Hedin and Maddison (2001)
28Sint - F	5' -CGG AGC CAT CCT RCG ATT C- 3'	amplification / sequencing	22352403	This study
28Sint - R	5' -GAG TGG GCG GAA TCG YAG- 3'	amplification / sequencing	22352404	This study

to provide overlapping sequence coverage for the entire region of 28S. All samples were sequenced in both the forward and reverse directions by way of an ABI 3100 DNA sequencer using a capillary machine.

SEQUENCE ALIGNMENTS.— Mitochondrial and nuclear gene sequences were analyzed and initially aligned using the computer programs Sequencing Analysis 3.4 (ABI Prism™ 1999) and Sequencher 3.1.1 (GeneCodes 1998), respectively. The conserved regions were identified and aligned, and gaps were assigned to minimize changes using ClustalX 1.9a169 (Thompson et al. 1997). The aligned data set was then further manually aligned using MacClade 4.03 (D.R. Maddison and W.P. Maddison 2001) and PAUP*4.0b10 (Swofford 2001). The same process was performed for the combined 28S aligned sequences of salticid genera (Hedin and Maddison 2003) and *Padilla* 28S sequences.

PRELIMINARY SEQUENCE ANALYSIS.— Base composition bias was calculated (Irwin et al. 1991) for the entire fragment. A value of zero indicates no bias and a value of one indicates complete bias. A chi square test in PAUP*4.0b10 (Swofford 2001) was used to test for heterogeneity of nucleotide frequencies among taxa.

PHYLOGENETIC ANALYSIS OF MOLECULAR DATA.— Phylogenetic analysis is reconstructed from the sequence data by using parsimony and maximum likelihood. All analyses were performed using PAUP*4.0b10 (Swofford 2001). Data from different genic regions (COI, 28S) were analyzed first separately as different genes are expected to have different evolutionary dynamics. The two data partitions were combined after their phylogenetic congruence was assessed using the incongruence length difference (ILD) test (Farris et al. 1994) implemented in PAUP*. A single analysis combining data from all genes has the advantage of being based on more data than any single analysis and evolutionary history is best assessed by using datasets from distinct sources (Wheeler et al. 1993). Confidences on clade credibility are both based on results from separate and combined analysis.

Parsimony: Search was performed using the random stepwise addition option of the heuristic search for 1,000 replicates with tree bisection-reconnection (TBR) branch swapping, collapse of zero-length branches, and equal weighting of all COI and 28S characters. All ambiguously aligned sites were excluded. Only the mostly parsimonious trees were retained and summarized with a strict consensus tree.

Maximum likelihood: To determine which model best fit, the dataset was subjected to Modeltest 3.06 (Posada and Crandall 1998) and the resulting Akaika information criterion was used. Once the best-fit model of evolution was found, a heuristic search was executed using the initial parameter estimates obtained from a neighbor-joining (NJ) tree generated in PAUP*. The parameters of the better tree found were re-estimated and the search was repeated. This process was continued until a tree converged on the same maximum likelihood tree. For both parsimony and maximum likelihood, I characterized the reliability of each phylogenetic hypothesis by resampling the original dataset 1000 times using the non–parametric bootstrap (Felsenstein 1985; Hillis and Bull 1993).

The maximum likelihood model was also used to determine whether (1) *Padilla* combined 28S and COI sequences and (2) all the 28S Salticidae sequences are evolving at a constant rate and fit a molecular clock (Felsenstein 1 993). I used a procedure proposed by Felsenstein (1993) to test for a molecular clock. This test uses a likelihood ratio test (LRT) to determine if there are significant differences between the likelihood scores obtained from an analysis where the branch lengths are unconstrained as compared to an analysis where the branch lengths are constrained so terminal ends are contemporaneous. The likelihood test statistic was assumed to be approximately equal to an χ^2 distribution with n-2 degrees of freedom, where n equals the number of taxa sampled (Felsenstein 1 981).

Estimation of divergence times and rates of molecular evolution for Salticidae.— The LRT test statistic for the 28S Salticidae data was significant ($2\Delta L = 2[-22284.10856 – (-22636.34008)] = 704.464$, $P<0.001$ ($df = 96$)), meaning that there is rate inconstancy across lineages. In absence of a molecular clock, it is appropriate to use the penalized likelihood (PL) method implemented in the program r8s version 1. 7.0 for estimating divergence times. This method allows rates of evolution to vary substantially across lineages to accommodate branch-length differences in the input likelihood tree; however, it attaches a "penalty" cost to limit rate variations on neighboring branches (Sanderson 2002). The smoothing parameter (λ) governs the degree to which differing rates on neighboring branches are to be penalized. A cross validation criterion was used to select the optimal level of smoothing that best fit the data. A 30 million year old fossil specimen of the genus *Lyssomanes* was used as a minimum age calibration point (Miguel and Penny 2003). The minimum age of 30 million years was then assigned to the node representing the hypothetical common ancestor between *Lyssomanes* and the large clade that includes the Salticoida division. During initial cross validation runs, it was observed that the results were unstable unless a fixed age constraint was placed on the age of the root. Optimization routines in penalized likelihood generally need at least one fixed node (Sanderson 2006 in r8s version 1.7 User's Manual). Based on the analysis of Penney et al. (2003), who assembled data from 830 spider fossils, fossils of the family Salticidae and their relatives were recorded only during the Cenozoic and were all less than 65 million years old (figure 2 in Penney et al. 2003). Thus, fixing the root at 65 million years gives a conservative estimate.

Character mapping.— The "horn curvature" and the "life style" reflected by the carapace height were mapped onto the resulting genus maximum likelihood tree. The carapace height is described as a ratio of the cephalothorax height (CH) divided by the length of the carapace (CL) (Fig. 1). The horn curvature character is divided into the character states: (0) "horn straight and slightly convergent" (Fig. 3A); (1) "horn presenting a simple curve, going outward and then inward" (Fig. 3C); (2) "horn presenting a double curve", going inward, then outward, and finally crossed at tips (Fig. 3E). Crane (1949) defined the "runner" and "hopper" lifestyles in jumping spiders. She suggested a correlation between these lifestyles and carapace height based on the presence of the extensor muscles responsible for the jumping power within the carapace. Those with a high carapace she called "hoppers": these have strong muscles in their carapace that allow them to jump more often. Conversely, those with a low carapace and weaker muscles, these Crane called "runners", run most of their time and jump only during prey capture. For the sake of a hypothesis, here I infer these salticid life styles in *Padilla*, even though nobody has yet made detailed observations on *Padilla* biology. Therefore, if the mean CH/CL of a species is greater than 0.35 and the carapace is greatly enlarged between leg II and III, the "life style" state is assumed to be "hoppers". If the mean CH/CL of a species is between 0.30–0.35 and the carapace is just trapezoidal, the "life style" is assumed to be "intermediate" between "hoppers" and "runners". If the mean CH/CL is less than 0.25 and the carapace is almost rectangular, the "life style" state is assumed to be "runners".

In species of *Padilla* and across the family of Salticidae, I have noticed four kinds of body shape: (1) elongate (*P. cornuta, P foty*; *P. sartor, P. mazavaloha;* Figs. 8A, 9A–B, 34C); (2) beetle like (*Armata* group, Fig. 10); (3) scorpion like (*brevis* group; *P. mihaingo*; *P. maingoka; P. mitohy;* Figs. 9C, 17, 34A–B); (4) high or protruding (*P. manjelatra, P. lavatandroka*; Fig. 8B–C). This character was not included in the phylogenetic analysis because it could not be considered as a phylogenetically independent character. However, in order to investigate whether these four kinds of body shapes are related to species phylogeny or species environmental conditions, I decided also to map them on the resulting molecular tree and correlate them with environmental factors.

Results

Morphological Analyses

Placement of Padilla within Subfamily Ballinae.— The first parsimony analysis of 42 unordered and equally weighted characters of 18 balline taxa, including two species of *Padilla*, produced 26 most parsimonious trees of 85 steps, consistency index of 0.56 (CI), and retention index of 0.64 (RI). Repeated analysis with successive weighting (Farris 1969; Carpenter 1988), using the maximum value of the rescaled consistency index, resulted in three most parsimonious trees. The consensus of these trees (Fig. 35) has a length of 40 steps, a consistency index (CI) of 0.77, and a retention index (RI) of 0.83. This tree is presented as the preferred hypothesis of generic interrelationships within the Ballinae. Within this tree *Padilla* form a well supported monophyletic group (99% bootstrap support) with two synapomorphic characters: path of the sperm duct intermediate between S and C (**6-1**) and cheliceral horns present (**42-1**). The two species of *Padilla* were placed as sister group to *Philates chelifer* based on one synapomorphy: size of translucent septum (sv) small (**19-1**).

Phylogenetic relationships within genus *Padilla*.— The first analysis of 38 equally weighted characters under parsimony produced three most parsimonious trees, with a length of 76 steps, consistency index of 0.61 (CI), and retention index of 0.72 (RI). The analysis was repeated after successive character weighting (Farris 1969; Carpenter 1988), using the maximum value of the rescaled consistency index. This analysis produced three trees (length = 34 steps, CI = 0.82, RI = 0.89), identical in topology to the three most parsimonious trees produced in the unweighted analysis. The consensus of these three trees is considered as the preferred hypothesis of *Padilla* species relationships (Fig. 36).

The monophyly of the genus *Padilla* is resolved at Node D, well supported (97% bootstrap) by three synapomorphies: (1) presence of horns on male chelicera (**1-1**), F1 with one or two midventral spines and two retromarginal bristles (**8-1**), F1 and Pt1 with a retromarginal fringe of setae (**12-1**). The cladistic analysis splits the genus into three major clades A, B, and C.

Clade A: supported by 66% bootstrap includes all *armata* group and *P. sartor*. Within this clade, the monophyly of the *armata* group is well supported (93% bootstrap) by three synapomorphies: horn presenting a double curve on dorsal view (**2-2**), laterally almost straight with tips curving downwards (**3-1**), and palp with a ventral tegulum posterior knob (**36-1**). The group including *P. armata*, *P. griswoldi* and *P. astina* is strongly supported (89%) by two more synapomorphies: Tb1 and Mt1 with unpaired spines (**17-1**), and clypeus border with a fringe of white scales (**22-0**). Likewise, sister grouping between *P. griswoldi* and *P. astina* (87% bootstrap) is supported by two more synapomorphies: carapace edge with lateral whitish bands of scales (**19-0**), and abdomen dorsally flattened (**30-0**).

Clade B: includes *P. mazavaloha* and the *cornuta* group. Within this clade, sister grouping between *P. manjelatra* and *P. lavatandroka* is strongly supported (100% bootstrap) by five synapo-

morphies: horn length implied by the ratio HL/CL>0.75 (**6-2**), presence of male Pt1 proventral spur (**11-1**), Tb1 and Mt1 coloration darker than other leg segment (**16-1**), sternum almost rounded with anterior part not truncated (**29-1**), and palp tegular groove shallow (**35-1**). The monophyly of the *cornuta* group is weakly supported (58% bootstrap) by one synapomorphy: horn laterally presenting a double curve (**3-2**). The placement of *P. mazavaloha* as a sister taxon of the *cornuta* group was weakly supported (61% bootstrap) by the morphological synapomorphy: presence of tibial spur on the first legs (**14-1)**.

Clade C: supported by 70% bootstrap, includes the *brevis* group, *P. maingoka*, *P. mitohy*, *P. mihaingo* and *P. foty*. Within this clade, the monophyly of the *brevis* group is strongly supported (100% bootstrap) by four synapomorphies: horn laterally going downward (**3-0**), horn originating from the distal part of the chelicerae near the fangs or CHL/DH<= 0.25 (**7-0)**, and thinner reflected by the ratio CW/CHL<0.60 (**27-1**); paturon projected forward (**28-1**). Sister grouping between *P. mihaingo* and *P. mitohy* is also strongly supported (95% bootstrap) by three synapomorphies: absence of an additional promarginal spine on F3 and F4 (**10-0**), carapace with lateral whitish bands of scales (**19-0**), and clypeus border with a fringe of white scales (**22-0**).

Note.— The placement of *P. maingoka* within this major clade is unclear. It constitutes the only difference among the three most parsimonious trees which placed it either (1) with the *brevis* group, (2) with the group including *P. mihaingo* and *P. mitohy* or (3) as the sister taxon of the group including these four species. This group of species excluding *P. foty* is supported (87% bootstrap) by three synapomorphies: horn slender, implied by the ratio horn width/cheliceral width<0.15mm (**5-0**), horn length implied by the ratio horn L/CL< 0.3 (**6-0**), Tb1 clearly broader or wider than femur, patella and metatarsi (**13-1**). All members of clade C are united by one more synapomorphic character: cephalothorax almost rectangular (**21-0**).

The cladistic analysis splits all *Padilla* species into three major clades (A, B, C) and confirms the monophyly of all the groupings hypothesized on horn morphology except for the sartor group, whose members are scattered within the three major clades.

Molecular Analysis

Phylogenetic relationships within genus *Padilla*

This study produced a final aligned 1137 base pair (bp) fragment for each taxon, consisting of 759 aligned bp for 28S and 378 aligned bp for COI. The aligned fragment contained 222 sites (115 sites for COI, 107 sites for 28S) that were variable (19.52%) and 129 sites (81 sites for COI, 48 sites for 28S) that were parsimoniously informative (11.34%). Examination of base composition in the entire data set resulted in the following: A: 0.1986; C: 0.2335; G: 0.30054; T: 0.2673. The entire combined data set exhibited 0. 09 base composition bias for all characters and 0.1702 for only variable characters; a Chi-square test for homogeneity of base frequency among taxa was 4.435390 (df = 42) when all characters were included and 30.784074 (df = 42) when constants were excluded, resulting in P values of 1 and 0.899559, respectively. The heterogeneity test suggests that the sequences have roughly the same base composition (are not heterogeneous). The COI data set revealed a base composition bias for only variable characters (0.41). This is mainly due to variation within third positions. However, inspection of the entire COI (0.26) and combined data set (0.09) did not reveal any extreme bias. So this heterogeneity bias does not appear to present a problem for phylogenetic interpretation.

Phylogenetic analysis of COI DNA

The parsimony search found 5 trees of 215 steps, CI = 0.61, RI = 0.58 (Fig. 37A). The maxi-

mum likelihood analysis of the COI data partition using GTR+G+I model of sequence evolution results in one tree with a –ln L= 1614.30907 (Fig. 38A).

Phylogenetic analysis of 28S DNA.— The parsimony search found 2 trees of 165 steps, CI = 0.77, RI = 0.71 (Fig. 37B). The maximum likelihood analysis of the 28S data partition using GTR+G+I model of sequence evolution results in six trees with a –ln L= 1879.24764 (Fig. 38B).

Phylogenetic analyses of combined 28S and COI DNA.— The parsimony analysis of all characters resulted in one tree of 436 steps, CI = 0.64, RI = 0.58 (Fig. 39). The best fit maximum likelihood model for both 28S and COI separately and combined, determined using the Akaika criteria in Modeltest 3.06 (Posada and Crandall 1998) was the General Time Reversible with gamma rates variation and proportion of invariable sites (GTR+G+I). The maximum likelihood search in PAUP using this model resulted in one maximum likelihood tree with a –ln L= 3771.21431 (Fig. 40). Maximum likelihood was also used to test for molecular clock. The likelihood ratio test (LRT) statistic is $2\Delta L = 2[- 3771.21431 – (- 3775.54665)] = 8.6646$, $P = 0.7978 > 0.001$ (df = 13). The molecular clock assumption was not rejected for the combined *Padilla* data set, which indicates that the rate of neutral evolution accumulated in the different sequences was constant over time across the species of *Padilla*. Therefore, branch length for maximum likelihood tree of *Padilla* can be interpreted as divergence times.

Relationships within *Padilla*.— The placement of all taxa did not conflict in the trees obtained from the COI and 28S data, except for the placement of *P. cornuta* which was the sister taxon of *P. ngeroka* in the COI hypothesis (Figs. 37A–38A), whereas it was at the base of the clade including *P. astina* and *P. griswoldi* in the 28S (Fig. 37B). The ILD test for congruence among data partition found a P value greater than 0.01 suggesting that combining the data will improve or at least will not reduce phylogenetic accuracy despite the differences between the COI and the 28S hypotheses (Cunningham 1997).

The combined parsimony and maximum likelihood analysis of 28S and COI data each resulted in one tree. The maximum likelihood analysis (Fig. 40) split *Padilla* species into three major clades A, B‘, C‘. Both parsimony and maximum likelihood analyses agree on clade C‘; but members of clades A and B‘, although grouped in the same order do not form a clade in the parsimony analysis (Fig. 39).

Placement within the Salticidae

The monophyly of the genus *Padilla* within the Salticidae was strongly supported by the parsimony (94% bootstrap) and maximum likelihood tree produced from 832 bp of 28S sequences of 98 salticid taxa (Hedin and Maddison 2003) to which I added 14 species of *Padilla* and one balline genus, *Ballus* (Figs. 41–42). *Padilla* was placed as a sister group of two other balline genera, *Ballus* and *Pachyballus,* with which it forms a monophyletic group that is sister group to the clade including marpissoids, heliophanines, freyines, euophryines, and plexipoids.

Estimation of divergence times and rates of molecular evolution

The cross validation analysis selected $\lambda = 10^{7.5}$ as the optimal value of the smoothing parameters that best fit the data. The divergence time analysis was carried out in the absence of rate constancy across lineages or molecular clock, the average rates of molecular evolution of the 28S genes estimated from the penalized likelihood method is $1.064 \pm 0.104 \times 10^{-8}$ substitutions per sites per years (S/S/Y). A summary of the average rate variation across taxa and the estimated ages of some taxa are given in Table 4.

TABLE 4. Estimated ages and substitution rates of the 28S gene in jumping spiders.

Reconstruction method: Penalized likelihood
Smoothing factor = 31622777
Penalty function = Ancestor-Descendant
Optimization via Truncated-Newton (TN) method with bound constraints
Fossil: Lyssomanes assigned a minimum age of 30Ma
Root fixed-age constraint: 65Ma
Rates are for branches subtending indicated node
Rates are in units of substitutions per site per unit time

Node	Estimated age) (Ma)	Estimated rates (x10-8)/ sites/ year
Unident _ spartaeine - Portia	38.73	1.0219
Salticoida	31.67	1.1571
Ballinae	23.17	1.1750
Padilla	13.06	1.1594
Heliophanines	13.05	1.1378
Freyines	9.77	1.0619
Euophryines	5.74	1.0844
Marpissoids	3.99	1.0183
Plexippoids	3.76	1.0902
Plexippines	2.93	1.0959
Pellenines	1.89	1.0675

Summary of rate variation (substitutions per site per year)

Mean = 1.064×10^{-8}
Std Dev = 0.104×10^{-8}
Min = 0.803×10^{-8}
Max = 1.295×10^{-8}
Range = 0.492×10^{-8} Ratio = 1.613

DISCUSSION

This is the first taxonomic treatment of this genus since Peckham and Peckham (1894) and Simon (1900). This study has recognized 15 species of *Padilla*, twelve of which are newly described; however, many more species are expected to be discovered. This is also the first morphological and molecular study to examine phylogenetic relationships among members of the genus *Padilla*, and the first time the relationships of this genus to members of the subfamily Ballinae and family Salticidae have been phylogenetically analyzed.

Molecular data contrasted with morphology data

Even if the species composition within clades A, B' and C' (Fig. 40) of the maximum likelihood analysis is almost the same as species composition within clades A, B, C (Fig. 36) in the morphology parsimony analysis, the arrangement of taxa inside these major clades is slightly different, e.g.,

Clade A: in the molecular analysis, sister grouping of *P. sartor* and *P. ombimanga* are strongly supported both by parsimony (100% bootstrap) (Fig. 39) and maximum likelihood (100% bootstrap) (Fig. 40). Those taxa share six morphological apomorphies but did not form a clade in the morphology hypothesis (Fig. 36).

Clade B': the *cornuta* group and the *brevis* group each break apart. *P. cornuta* (*cornuta* group) and *P. ngeroka* (*brevis* group) form a strongly supported sister group pair (96% bootstrap support

for parsimony, Fig. 39; 96% for MLE, Fig. 40): these were not associated in the morphology analysis (Fig. 36).

Clade C': *P. foty* and *P. mitohy* are strongly supported sister taxa (74% bootstrap both for parsimony and MLE). *P. mihaingo* is well supported as their sister taxon (100% bootstrap both for parsimony and MLE). *P. boritandroka* (*brevis* group) remained within the same clade and form a well supported clade with these latter (88% bootstrap for both parsimony and MLE).

All the groups based on horn morphology, body shape and implied "life style" were paraphyletic in the molecular hypotheses, except for the sister group relationship between *P. griswoldi* and *P. astina* which remained strongly supported by both parsimony and MLE (100% bootstrap), as did the relationship between *P. manjelatra* and *P. lavatandroka* (100% bootstrap).

Character mapping

When the discrete characters describing, 'horn curvature' and "implied life style" are mapped onto the maximum likelihood tree, it is shown that the double curved horn of the *armata* group (Fig. 3E), simple curved horn of the *sartor* group (Fig. 3C) and straight horn of the *cornuta* and *brevis* groups (Figs. 3A–G) have evolved more than once (Fig. 43). Likewise, implied lifestyle showed homoplasy. Only two "hoppers", *P. manjelatra* and *P. lavatandroka,* formed a natural group (Fig. 44).

The results of the phylogenetic analysis revealed a conflict between the morphological and molecular hypotheses suggesting convergent evolution of the cheliceral horns, carapace height and body shapes, which are the most conspicuous characters differentiating species of *Padilla*. Yet, leg spination has proven to be more efficient in uniting natural groups such as *P. ombimanga* plus *P. sartor*, *P. griswoldi* plus *P. astina,* as well as all members of clade C' (all with enlarged Tb1).

Origin of the diversification of morphological characters

In *Padilla*, secondary sexual characters, somatic characters and the four types of body shape have evolved convergently when mapped into the molecular phylogeny. These different morphological forms may represent an adaptation to local environmental conditions or forms that may promote reproductive success. Variations in these traits could either be the results of natural selection, sexual selection or both. In order to investigate which of these alternatives might be probable in *Padilla*, I use environmental information and environmental niche modeling taken from distribution data of *Padilla* (Worldclim-DIVAGIS version 5.2) (Table 5). These data allowed estimation of some environmental parameters such as the annual temperature and precipitation, mean temperature of the wettest and driest quarter, precipitation of the wettest and driest quarter, altitude, vegetation and ecological niche quality of the localities where each species occurs and correlated these parameters with morphological data. If horn morphology and body shape correlated with specific ecological conditions of the locality, the diversification of those characters seen in *Padilla* could possibly be the result of natural selection. If these characters were uncorrelated with specific ecological conditions of the locality, their evolution may be due to sexual selection.

Sympatric sister species occurring under similar ecological parameters

I noticed two unusual cases of sympatric sister species with different horn morphology, carapace height and body shape collected from localities that have similar ecological conditions: *P. ngeroka* (*brevis* group, "runner") and *P. cornuta* (*cornuta* group, "intermediate") are sister species according to the molecular analyses (Figs. 39, 40). Their distributions overlapped in two sites: in

TABLE 5. Species, characters and bioclimatic variables from DIVAGIS (Worldclim)

Species	Body shape	Horn	Annual mean T° (°C)	Annual P° (mm)	Mean T° of wettest quarter (°C)	Mean T° of driest quarter (°C)	P° of wettest quarter (mm)	P° of driest quarter (mm)
P. sartor	Elongate	Sartor group	20.1917	1367	21.6333	18.9000	815	66
P. mazavaloha	Elongate	Sartor group	21.1833	1351	22.5333	19.9167	821	62
P. mazavaloha	Elongate	Sartor group	18.5250	1610	21.2333	16.8333	862	123
P. mazavaloha	Elongate	Sartor group	24.2667	1829	25.4167	22.2167	1142	48
P. mazavaloha	Elongate	Sartor group	20.0833	1355	21.5500	18.7667	809	65
P. maingoka	Scorpion like	Sartor group	18.5250	1610	21.2333	16.8333	862	123
P. cornuta	Elongate	Cornuta group	17.5792	1323	20.1000	14.1500	800	56
P. cornuta	Elongate	Cornuta group	18.5250	1610	21.2333	16.8333	862	123
P. cornuta	Elongate	Cornuta group	17.4125	1406	19.5000	14.1833	900	18
P. cornuta	Elongate	Cornuta group	17.5792	1323	20.1000	14.1500	800	56
P. cornuta	Elongate	Cornuta group	17.4125	1406	19.5000	14.1833	900	18
P. cornuta	Elongate	Cornuta group	19.7916	1452	22.1667	17.3333	918	195
P. manjelatra	Protruding	Cornuta group	22.7792	1677	24.0500	20.6833	1053	38
P. manjelatra	Protruding	Cornuta group	15.9417	1558	18.2667	13.9167	799	142
P. manjelatra	Protruding	Cornuta group	22.2833	1416	23.7833	20.1667	791	95
P. lavatandroka	Protruding	Cornuta group	20.1917	1367	21.6333	18.9000	815	66
P. lavatandroka	Protruding	Cornuta group	21.1833	1351	22.5333	19.9167	821	62
P. astina	Beetle like	Armata group	23.2667	367	25.6500	20.7667	498	98
P. griswoldi	Beetle like	Armata group	18.9375	1770	21.5167	17.2167	936	139
P. griswoldi	Beetle like	Armata group	16.6625	1310	21.2333	16.8333	862	123
P. ombimanga	Beetle like	Armata group	21.1833	1351	22.5333	19.9167	821	62
P. boritandroka	Scorpion like	Brevis group	24.2667	1829	25.4167	22.2167	1142	48
P. boritandroka	Scorpion like	Brevis group	23.4708	1318	24.7333	22.2667	841	53
P. boritandroka	Scorpion like	Brevis group	23.7625	1437	25.1333	21.7333	808	97
P. boritandroka	Scorpion like	Brevis group	26.3208	1030	28.2167	23.1333	727	7
P. boritandroka	Scorpion like	Brevis group	22.7792	1677	24.0500	20.6833	1053	38
P. boritandroka	Scorpion like	Brevis group	26.4125	1250	27.4333	24.2833	951	7
P. ngeroka	Scorpion like	Brevis group	17.5792	1323	20.1000	14.1500	800	56
P. ngeroka	Scorpion like	Brevis group	17.8375	1503	20.5333	16.1333	802	117
P. ngeroka	Scorpion like	Brevis group	17.6833	1461	21.2333	16.8333	862	123
P. foty	Elongate	Unassigned	25.4000	2024	26.6000	23.5000	1213	86
P. mitohy	Scorpion like	Unassigned	23.8583	1553	24.9500	22.0000	966	56
P. mitohy	Scorpion like	Unassigned	24.3292	1488	25.4500	22.5000	937	58
P. mihaingo	Scorpion like	Unassigned	25.6500	1384	26.9500	24.4167	756	113

the evergreen rain forest of Ranomafana (Central Southeastern region) and in the broadleaf deciduous forest of Andranomay (Central region) (Figs. 45, 46). The average ecological conditions of the points where *P. ngeroka* was collected were not much different from *P. cornuta*'s: mean annual temperature: 17.7°C and 18.05°C respectively; mean annual precipitation: 1431 mm and 1420 mm, respectively; altitude: (900–1410m) and (1000–1300m). Similarly, the molecular analyses (Fig. 39, 40) suggested sister group relationships between another sympatric pair: *P. sartor* (*sartor* group) and *P. ombimanga* (*armata* group). Not much of a difference in ecological conditions was noticed for these sympatric sister species except for the occurrence of *P. sartor* at the forest edge (Fig. 47, 48) (Table 5). There are additional cases of species of disparate morphology occurring together under conditions of similar ecology. Many species exhibiting different horn morphology, carapace height and body shape were found to occur next to each other at 1300 m in the evergreen mountain rainforest of Montagne d'Ambre (Northern region), i.e., *P. sartor* (*sartor* group), *P. ngeroka* (*brevis* group), *P. lavatandroka* (*cornuta* group) and *P. ombimanga* (*armata* group) and at 900m elevation at the same locality in Ranomafana (Central Southeastern region), i.e., *P. cornuta* (*cornuta* group) and *P. maingoka* (*sartor* group).

Species with similar horn shape, carapace height, and body shape were found to occur in very different environmental conditions

The most striking is the case of the *armata* group: *P. griswoldi* and *P. astina* are sister species in all analyses (Fig. 36, 39–40) and share seven morphological features including horn type, carapace height and body shape. Yet, *P. griswoldi* was found in the Eastern central rain forest of Ranomafana at elevation of 1150–1300 m, 17.8ºC mean annual temperature and 1540 mm mean annual precipitation, whereas, *P. astina* occurs in a dry spiny forest of the South, at elevation of 20 m , 24.4°C mean annual temperature, 367 mm mean annual precipitation.

From these observations and a simple statistical test of correlation between horn curvature, body shape and some bioclimatic variables provided by Worldclim version 3.0 (annual temperature and precipitation, mean temperature of the wettest and driest quarter, precipitation of the wettest and driest quarter; Figs. 49–50), horn morphology and body shape appeared to be uncorrelated with ecological conditions such as temperature, precipitation, vegetation type, altitude and niche quality in *Padilla*. Even if there are few cases where species of similar morphology have been found around the same locality, they were not sympatric and therefore their ecological conditions might differ slightly. Consequently, the diversification of the cheliceral horn observed in *Padilla* could be driven by sexual selection. Thus, with respect to the male-biased presence of the horns, I find their presence only on males compelling evidence for sexual selection. Knowing male and female jumping spiders to coexist in the same habitat and therefore, under the same ecological pressure (predators, competitors) and roughly performing the same activity (Alroth 2005); the presence of the horns only among males appears to be in favor of the sexual selection hypothesis and cannot be explained by any other hypothesis such as predation or character displacement. These horns are conspicuous and tactile and might be used both in male fights for mates (contest) or in female choice (Anderson 1 994). Moreover, a case of diversification of cheliceral projections due to female choice has already been observed in pholcid spiders (Huber et al. 2005). Therefore, the most probable explanation for the high rate of diversification of cheliceral horns among *Padilla* species is sexual selection.

However, with regard to the body shape and implied lifestyle, no firm conclusion should be drawn before further study of behavior and ecology and more field work is completed. Even if different body shapes and implied life styles were not related to any environmental conditions that have been investigated (Fig. 50), those characters are observed in both males and females. In addition, the estimation of these environmental factors might be too coarse compared to the size of these spiders to be able to detect fine-scale microhabitat variations that could affect their morphologies (i.e., environmental data estimated from 90 m above ground might be inadequate to depict microhabitat differences that could be important to arthropods). Moreover, inasmuch as carapace height and/or “implied life style” appear to be related to modes of locomotion (Crane 1 949), data on the nature of substrate might be needed.

Evolution of the horns and body shape

The generic molecular clock combined with the phylogenetic hypotheses allow me to infer the evolution of some conspicuous morphological characters through time in *Padilla*. *Padilla* appears to have evolved 13.06 million years ago from an ancestor that did not have a horn and was beetle like. The general tendency observed from the phylogram (Figs. 40, 43) suggests that *Padilla* horns were primitively double curved (basal part of clade A, members of the *armata* group), evolved through a simple curve to become straight and long in the *cornuta* group, remained straight but shortened in part of the *brevis* group, and then evolved to become a simple curve again. Finally, more derived species of *Padilla* have straight and very short horns (*P. boritandroka*). Concerning

body shape and implied life style, *Padilla* appears to have begun as beetle-like spiders with an intermediate life style, evolved into *"hoppers*" and then "runners", with some species reverting to an intermediate lifestyle; however, all more recent species of *Padilla* are "runners" (Figs. 40, 44).

Rates of substitutions and estimated ages of the genus and some members of the Salticidae

This is the first time the rates of substitution of the 28S gene have been reported for jumping spiders. My results seem to be comparable with those of Brower's (1994) estimation of the rate of evolution of mitochondrial DNA (COI) in arthropods (2.3% sequence divergence per million years or $2.3 \times \lambda 10^{-8}$ substitutions per sites per year), because nuclear DNA is known to evolve more slowly than mitochondrial DNA (Caccone et al. 2004). Mean rates based on the penalized likelihood method for the 28S gene in salticids and their relatives was $1.064(\pm 0.104) \times 10^{-8}$ substitutions per sites per year. Note that Brower (1994) used pairwise divergences to calculate their rate, whereas I used penalized likelihood.

Most salticids are recently diverged. The oldest estimated divergence date is 38.73 million years (Table 4) for the node subtending *Unident – spartaeine* and *Portia.* The true salticids (Salticoida division) diverged from this group 31.67 million years ago. The node supporting members of the subfamily Ballinae constitutes the oldest group within the salticoida division (23.17 million years). *Padilla* diverged from this group 13.06 million years ago.

Distribution of *Padilla*

Members of the three different clades are distributed within the remnant rainforest across the northeastern and northwestern Madagascar, but only a few species are recorded from the central regions and from dry areas. The genus seems not to occur in the far south except for *P. astina* (1 specimen). It is unclear if this gap is due to lack of collections or true absence of these spiders in most of this region. But considering the intensive sampling from more than 60 sites, including places located in the far South, absence and rarity are more probable explanations. Of all the 17 localities where species of *Padilla* were collected, the evergreen montane forest of the north (Montagne d'Ambre) is the richest in species and, thus, may be considered as a zone of radiation. Many species are narrowly distributed and are known from a single locality. These localities are identified as areas of endemism for *Padilla* and are of conservation importance. They are Montagne d'Ambre and Ranomafana, both supporting two endemic species, and Lokobe, Daraina – Ampondrabe, and Ifaty, each supporting one endemic species. Members of clade A have a central, southeastern, southwestern and northern distribution. Members of clade B' are distributed along the east coast, through the central region to the far north. They include the most widespread species of *Padilla* and were the only ones found in the central regions where the conditions appear less suitable. Members of clade C'; however, were mostly found in the north and northwestern Madagascar, except *P. maingoka* from the central southeastern region. They are all flattened, scorpion-like spiders with the exception of *P. foty* (Fig. 44).

Biogeography

The balline morphology trees suggested a close relationship between *Padilla* and the genus *Philates* found in Gondwanan plates. *Philates* is known from Africa to Sri Lanka, Indonesia, Philippines, Java, Borneo, and New Guinea (Prószyński, 2006). The distribution of *Padilla* exhibits an eastern and northwestern split with a few species from the central and southern Madagascar

(Fig. 51). This seems to favor a radiation from either the East (India, Sri Lanka, Indonesia) or the northwestern part of Madagascar or northeastern Africa. The ages of *Padilla* (13.06 MYA) and the sub-family Ballinae (23.17 MYA) are too recent for Gondwanan vicariance hypothesis. According to modern understanding of the geological history of the Indian Ocean around this time frame, two other hypotheses are possible: (1) the existence of a land bridge linking Madagascar, Africa, India and the Seychelles Islands (2) transoceanic long distance dispersal. The first hypothesis suggests that as India assumed its current position from the early Eocene through Miocene, global sea levels were dropping, with a marked regression at the Rupellian/Chattian boundary (Haq et al. 1988). At that time, significant portions of the Chagos/Laccadive Plateau (about half way between Africa and Indonesia) and the contiguous Mascarene Plateau (including the Seychelles Bank), could have been emergent, and served as stepping-stones through which terrestrial organisms with low dispersal ability could migrate (Schatz 1996). Some Malagasy plants such as the genus *Pandanus* (Pandanaceae) (Martin et al. 2003), *Dillenia* (Dilleniaceae), *Nepenthes* (Nepenthaceae), Malagasy cichlid fishes (Vences et al. 2001), the gekko genus *Phelsuma***,** as well as mammals, e.g., tenrecs, carnivorans, and rodents (McCalll 1997), have been suggested to have dispersed through this land bridge, also called "Lemurian stepping stones" (Schatz 1996). The second hypothesis or the long distance dispersal during the Miocene, has been suggested for Melastomaceae plants and agamid lizards (Renner 2004; Raxworthy et al. 2002), which also exhibit the same distribution and a recent divergence time as the ancestors of *Padilla*. Those organisms may have reached Madagascar by means of floating on solid materials, or transported by birds, by monsoonal winds, or by the occasional storms and cyclones that occur in the Indian Ocean and between Madagascar and Africa. I found the first hypotheses most probable in the case of *Padilla* because jumping spiders are mostly terrestrial organisms, even if the second hypotheses could also be possible.

Relationships of *Padilla* with other Salticidae

Hedin and Maddison (2003) included one balline genus in his molecular analysis of the family of Salticidae: *Pachyballus*. This genus comes out always as sister group to the genus *Mantisatta*, which in analyses with two of his genes (28S and 16S) were included within the marpissoids. Maddison expressed the concern that members of the Ballinae such as *Ballus*, *Marengo*, and similar salticids may be marpissoids. Here, I have added 15 more balline species and my phylogenetic analysis seems to suggest that members of the Ballinae may form a monophyletic group that is sister group to a large clade including marpissoids, heliophanines, freyines, euophryines, and plexipoids, as in Maddison's combined gene tree (Figs. 41–42).

Conclusion

In this study, the taxonomy and phylogenetic relationships of species of *Padilla* and the placement of this genus within the subfamily Ballinae and the family Salticidae have been assessed for the first time. The study clearly demonstrates the need for contrasting two independent phylogenies (molecular and morphology) in order to detect patterns of morphological homoplasy. For instance, it is shown that the horns, carapace height and body shape evolved convergently in *Padilla*, whereas first leg spines have proven to be more efficient in identifying some of the natural groups. It is also suggested that the most probable explanation of the horn diversification observed in this genus is sexual selection. This can be illustrated (1) by case of unusual sympatric sister species with different horn types occurring at the same locality under similar ecological parameters; (2) cases of sister species with same horn type occurring in ecologically extremely different localities and; (3) absence of correlation between horn shape and any bioclimatic variables; (4) the presence of

horns only on males when males and females have roughly the same activity and live at the same locality, and thus are probably under the same ecological pressure.

Clearly, further collections and research on *Padilla* behavior and ecology are needed to define the mechanisms of sexual selection at work and their influence on the use of horns, the diversification of body shape, and life styles.

The balline subfamily morphology analysis placed *Padilla* as a sister group of *Philates chelifer* and nested within members of the genus *Philates* (Fig. 35). Yet, the generic analysis has proved that *Padilla* was a monophyletic genus. Moreover, a well supported monophyly of the genus within the family of Salticidae has been demonstrated (Figs. 41–42). My study suggests the probable placement of *Padilla* along with other balline genera as a sister group to a large clade, including marpissoids, heliophanines, freyines, euophryines and plexipoids (Figs. 41–42).

The internal classification of the different groups within Salticidae has long been problematic (Hedin and Maddison 2001–2003, Benjamin 2004), especially, within the free embolus groups. Relationships between most of the subfamilies including Ballinae are still unresolved (Hedin and Maddison 2003). This study provides new information about the probable phylogenetic placement of a group of salticids, the subfamily Ballinae, and opens up to further molecular work on this group.

Delimitation of areas of endemism is essential to both studies of historical biogeography and conservation planning. The rarity of species of *Padilla* in tropical dry forest, their near absence in the xerophytic areas of the far south of Madagascar, and the concentration or localized distribution of species in the remaining suitable rainforest of the island, seem to indicate a sensitivity of this genus to desertification. This sensitivity must be seriously considered by those interested in conservation. Recently, due to the consequences of deforestation, the island has experienced rise of temperature and reduced rain fall that could threatened endemic species such as *Padilla* (irinnews.org on December 12, 2006).

Padilla is one of the rare beauties of nature. It is an excellent model for further evolutionary studies because of its different life styles, sexually selected characters, recent and rapid and complex speciation, which seems to be driven both by sexual and natural selection. Discovery of *Padilla* phylogeny is the first step to many phylogenetic based studies and will be of value in understanding copulatory mechanisms, sexual selection, natural selection and speciation in *Padilla* and in jumping spiders in general. Knowledge about the average rates of evolution of the 28S gene in Salticidae will be of value in future investigation of spiders' divergence times and is important in future biogeographical studies for jumping spiders.

TAXONOMY

Key to the Males

(N.B. Key to females is not provided because some species are only known from males.)

1. Horns crossing at tip (Fig. 9B) 2
   Horns not crossing at tip,; nearly straight, slightly converging towards tips, tips not close to each other (*brevis* group, *cornuta* group, Fig. 8, 9A, 7) 8

2(1) Horns basally curved inward, then outward, apically converging and crossing at tips. Distal part of chelicerae depressed. Body very compact and beetle-like (*armata* group, Fig. 10) . . . 3
   Horns basally curved outward, near apex slightly bent inward, so that the tips are close to each other (*sartor* group, Fig. 9). Body not compact and not beetle-like 6

3(2) Horns not touching at their median parts; carapace with median longitudinal light line (Figs. 10B–D). 4

Horns touching for a certain length at their median parts. Carapace lacking median longitudinal line (Fig. 10A–C). 5

4(3) Carapace divided longitudinally by thin white median line, bordered by lateral band of white scale-like setae on each lateral margin. Femur I with one large promarginal spine. Dorsum dark purple, with thin yellowish median reticulation. Body generally dark purple (Fig. 10B) . . . . . *Padilla griswoldi* Andriamalala, sp. nov.
Carapace divided longitudinally by thick white median line formed by scale-like setae, lacking setae on lateral margin. Femur I with two large promarginal spines. Dorsum dark brown with thick longitudinal median band of white scale like hairs. Body generally dark brown (Fig. 10D) . . . . . *Padilla ombimanga* Andriamalala, sp. nov.

5(3) Horns markedly bent near tips (Figs. 3E–10A) . . . . . *Padilla armata* Peckham and Peckham
Horns slightly bent near tips (Fig. 10C) . . . . . *Padilla astina* Andriamalala, sp. nov.

6(2) Tibia of first legs variable in thickness but not hook-like 7
Tibia of first legs enlarged, thick, and hook-like (Fig. 24C). Body and carapace dark brown, with two lateral, longitudinal, thin, black band on each side (Fig. 9C) . . . . . *Padilla maingoka* Andriamalala, sp. nov.

7(6) Carapace with red guanine deposit that includes median white spot (Fig. 3C). Tibia and metatarsus of first legs with paired symmetrical spines (of the same size on proventral and retroventral sides). Femur I with one promarginal enlarged spine. Sternum obviously wider than long. Dorsum yellowish to dark orange with medially aligned red chevrons (Fig. 9B) . . . . . *Padilla mazavaloha* Andriamalala, sp. nov.
Carapace with red guanine deposit, but lacking white median spot. Tibia and metatarsi of first legs with paired, obviously asymmetrical spines (of different size on proventral and retroventral sides). Femur I with two promarginal enlarged spines (Fig. 25A). Sternum obviously longer than wide. Dorsum completely dark brown, with single longitudinal yellowish band (Fig. 9A) . . . . . *Padilla sartor* Andriamalala, sp. nov.

8(1) Horns originating from distal part of paturon near fangs. Body flattened (CHL/ DH< 0.25); brevis group (Figs. 3G–H, 17). 9
Horns originating from proximal part of the paturon away from fangs (CHL/DH>0.50). Body not flattened (CH/ CL>0.25); cornuta group (Figs. 8B–C). 10

9(8) Horn extremely short (tooth-like), somewhat thick, and slightly convergent, originating right near fangs (Fig. 3G). Tibia swollen, with ventral tuft of black setae. Femur II-IV yellowish orange with dark lateral patches (Fig. 24B) . . . . . *Padilla boritandroka* Andriamalala, sp. nov.
Horn as long as one-third of carapace, directed downwards, slender, originating just above fangs (slightly higher than in of *P. boritandroka*; Fig. 3H). Femur II–IV uniformly yellowish orange (Fig. 17B). . . . . *Padilla ngeroka* Andriamalala, sp. nov.

10(8) Carapace dorsally with white, medially constricted guanine deposit. Dorsum of abdomen yellowish, with a pair of thick, lateral, dark bands (Fig. 8A). . . . . *Padilla cornuta* Simon.
Carapace dorsally without white guanine deposit. Dorsum of abdomen rather dark, with sclerotized scutum that may be covered with stripes of green iridescent scales. (Figs. 8B–C) . . 11

11(10) Tibial spur present (Fig. 25B). Carapace and abdomen dark, with horizontal stripes of green iridescent setae. Legs II–IV uniformly yellowish orange (Fig. 8B) . . . . . *Padilla manjelatra* Andriamalala, sp. nov.
Tibial spur absent. Carapace and abdomen mottled dark and light brown, without setal stripes. Abdomen with dark brown scutum which sometimes shows yellowish reticulation. Legs II–IV dark brown, with black horizontal stripes (Fig. 8C) . . . . . *Padilla lavatandroka* Andriamalala, sp. nov.

Genus *Padilla* Peckham and Peckham 1894

Padilla Peckham and Peckham 1894, Proc. Nat. Hist. Soc. Wisconsin 2:130 (type species, by monotypy, *P. armata* Peckham and Peckham 1894, deposited in MCZ, Havard, type number 117, examined). Simon 1900, Ann. Soc. Ent. Belg: 395. Simon 1901, Histoire Naturelle des Araignées 2:472.

The genus *Padilla* is correctly placed within the subfamily Ballinae. All species have the characteristics of this subfamily, as follows:

(1) Embolus laying flat on the tegulum that coils at least 360 degrees (Maddison 1988, 1995; Benjamin 2004). In *Padilla* the embolic coil is always with two spirals (Figs. 29, 31–33).
(2) Tegulum divided by a pale longitudinal furrow and a subtegulum extending posteriorly beyond cymbium (Maddison 1995, 1996; Benjamin, 2004). In *Padilla*, the tegulum division may also be an invagination or an abrupt hole that is generally located quite medially as opposed to laterally, e.g., in *P. griswoldi* (Fig. 33B), on the side of the palp in other balline genera.
(3) Palp simple, lacking pars pendula, conductor and median apophysis (Benjamin 2004).
(4) Epigynum with a narrow septum (ek) and with copulatory openings (co), fertilization ducts (fd) and spermathecae (spc) in a linear arrangement (Fig. 26) as observed in some but not all balline genera (Benjamin 2004).
(5) Femur of the first leg generally enlarged (Benjamin 2004). In *Padilla*, femora of the first legs always enlarged.

Diagnosis.— *Padilla* can be differentiated from other genera of the Ballinae by the following combination of characters:

(1) The presence of a pair of horns or forward projecting processes on the male chelicerae.
(2) Femora of leg III and IV with a linear arrangement of three dorsal spines (1/1/1) (Fig. 25D).
(3) Femur and patella of first legs with a fringe of setae along dorsal side.
(4) Path of the sperm duct intermediate between C and S (rather C or S in other balline genera) (Fig. 2C).

All *Padilla* except *P. foty* are also unique in having a serrula (or endite ridge) extending till the base of the endites (Fig. 30D).

Note.— Possible synapomorphies for the genus are the presence of a pair of horns on the male chelicerae, presence of fringe of setae along the retromarginal dorsal side of femora and patella of leg I, and path of the sperm duct intermediate between C and S.

Relationship with members of subfamily Ballinae.— Within the Ballinae, no known genera have horn like projections on the male chelicerae. Although *Goleta workmani* (Peckham and Peckham 1884) has a short spine-like projection on the male chelicerae that is quite similar to one *Padilla* (*Padilla boritandroka*), it was excluded from the Ballinae due to a lack of the diagnostic characters of this subfamily (Benjamin 2004) and presents a completely different palp structure compared with all the balline genera. Some balline species, such as *Cynapes wrightii, Colaxes nitidiventris* and *C. wanlessi, Ballus segmentatus* and *B. chalybeius*, *Philates chelifer* and *P. grammicus, Indomarengo sarawakensis* and *I. chandra,* and *Sadies fulgida,* share with *Padilla* an embolic coil with one or two spirals. However, the two species of *Indomarengo* have a prosomal protuberance (pp) on the posterior part of their carapace (Benjamin 2004, Fig. 55) and posterior median eyes (PME) larger than anterior lateral eyes (ALE). Those characters are not present in any of the *Padilla*. *Ballus segmentatus*, *B. chalybeius* and *Cynapes wrightii* all have a broader epigynal septum (Figs. 9, 18, 22, 23 in Benjamin 2004). *Ballus segmentatus* also has a different spine arrangement on femur III and IV (Alicata and Cantarella 1987). *Philates* is the closest to *Padilla* morphologically. However, *Philates* lacks the male cheliceral horns and has long and large leaf like scales

on Tb1 which were not observed in any of the *Padilla* (Fig. 52C). In addition, the path of the sperm duct is C instead of intermediate between C and S as in *Padilla* (Fig. 2).

Description.— *Padilla* are small sized salticids with a total length of 4.31–6.93 in ♂, 4.72–6.93 in ♀. A ratio of measurements between various parts of the body and a measure of some parameters are reported in Table 1. The specimens available do not form an adequate statistical sample, but one can obtain at least an idea of intraspecies variation and of the differences and similarities between species.

Padilla are sexually dimorphic. Males and females are quite different , the differences being more or less pronounced depending on the species. For example, in *P. ngeroka* males and females display completely different coloration and markings. The male is completely dark, whereas the females are rather yellowish with two lateral dark bands. Females of *P. manjelatra* and *P. lavatandroka* also have different leg coloration compared with their males. However, males and females of some species, such as *P. mazavaloha* and *P. cornuta,* are very similar except for the presence of secondary sexual traits such as the horns and the tibial spurs, which are absent in females. The dimorphism is expressed more in body coloration and the secondary sex traits such as leg spination and the presence of cheliceral horns, rather than body size. This is often the case in hunting spiders where both male and female exhibit the same feeding activities (Alroth l 995).

The presence of horns originating from the upper (proximal) or lower (apical) part of the male chelicerae is one of the synapomorphies that unite all species of *Padilla*. These horns may range from being as long as the carapace to extremely short as a spine (Fig. 3G). I divided the male *Padilla* in four separate groups according to (1) origin and curvature of these horns and (2) on phenetic similarity in carapace shape (implying "runner" or "hopper" lifestyle): the *sartor* group, *cornuta* group, *armata* group and *brevis* group. The *sartor* group is characterized by horns dorsally presenting a simple curve, as opposed to horns that present a double curve in *armata group* (Figs. 3C–D, 9). Within the *cornuta* group and the *brevis* group, the horns are rather straight and convergent (Figs. 3A–G). In this latter group, the horns originate from the distal part of the chelicerae. Three species that are known only from females were left unassigned. I find these groups very useful for communicating about *Padilla*. [List of these species groups is given in appendix 1 and their monophyly tested with morphology and molecular data in the phylogenetics section above.

Sartor group: males within this group have horns that originate from the proximal part of the chelicerae and which curve first outwards, then inwards, finally crossing each other at their apex (Figs. 3C–D, 9); in *P. sartor* the horns meet but do not cross (Fig. 9A). The tegulum division of the palp is a shallow invagination instead of a groove (Figs. 31D-E-G-H). The species that are included within this group are: *P. sartor, P. mazavaloha,* and *P. maingoka.*

Armata group*:* All males within this group have horns that originate from the proximal part of the chelicerae and which curve first inwards, and may be distant from, close to, or touching each other. The horns then go outwards, and finally curve inwards and cross at their tips (Figs. 3E–F, 10). The palp has a tegulum with a deep groove and a ventral posterior knob (Figs. 33B-D-H). The species that are included within this group are: *P. armata, P. griswoldi, P. astina*, and *P. ombimanga.*

Cornuta group*:* All males within this group have straight and convergent horns that originate from the proximal part of the chelicerae (Figs. 3A–B, 8). The palp has the tegulum with a shallow tegular groove (Figs. 29E–H). The species that are included within this group are: *P. cornuta, P. manjelatra*, and *P. lavatandroka.*

Brevis group*:* All males within this group have horns that originate from the distal part of the chelicerae and which are straight (Figs. 3G–H). The chelicerae project forward and are parallel to the carapace instead of perpendicular to it (Fig. 3H); the paturons are flattened dorsally with pro-

marginal and retromarginal sharpened edges (Figs. 14D–E). The palp has an embolus coil (ec) that is inclined toward the retrolateral side, with embolus second loop (el) thickened and embolus fold (ef) present on the prolateral side. The tegulum division (tg) is a shallow invagination (Fig. 32). The species that are included within this group are: *P. boritandroka* and *P. ngeroka.*

General description of Padilla.— Carapace generally smooth (Figs. 53A–C), with length 1.63–3.1 in ♂, 1.96–3.33 in ♀, and varies in height and width (Figs. 3, 28), with cephalothorax height 1.33–0.44; cephalothorax width 0.88–2.63. The higher the carapace, the wider the region between leg II and III. Carapace almost rectangular (Fig. 9C) in the most flattened species (*P. maingoka*), whereas trapezoidal and greatly enlarged between leg II and III (Figs. 3A, 4A, 8B–C) in males of *P. manjelatra* and *P. lavatandroka*. Top of carapace often decorated with differently colored and shaped guanine deposits (Fig. 3C, 10, 16): usually red in the *sartor* group (except *P. maingoka*) (Fig. 9A–B), orange in some members of the *armata* group (Figs. 10B–C), white with a median constriction in *P. cornuta* (Figs. 5, 8A), and unicolor in some species, i.e., *P. manjelatra* (Figs. 6, 8B), and *P. maingoka* (Figs. 9C, 23). In some species, bands of white scales present on lateral sides of carapace and above clypeus (Figs. 12C, 53B–D); bands particularly thick in *P. mihaingo* (Fig. 27B). Cephalic region shorter than thoracic (Simon l 900). Ocular quadrangle as wide anteriorly as posteriorly, W.O.F I 0.76–2.06, W.O.F II 0.95–1.96. Eyes surrounded by black pigmentation (Fig. 3C-E-F-G), PME twice as large as ALE, PME small, PLE not raised except in *P. lavatandroka* and *P. manjelatra.* Thoracic fovea either point like (3E), or short line (Figs. 3C, 54F), or shallow invagination (3A). Clypeus generally low; chilum present or absent (Fig. 14C). Chelicerae may be strong thick, or elongate, or conspicuous in the ♂ of some species (all *armata* group, all *sartor* group except *P. maingoka,* generally all *cornuta* group) and slender in some other ♂ such as *P. maingoka*, ♂ within *brevis* group and generally in ♀. The edge of paturon either carinate *(brevis* group*,* all male *armata* group*)* or not. Distal part of paturons either depressed (*Armata* group) or not. Fangs generally short and thick (Fig. 14). Promargins of chelicerae usually pluridentate with three to five teeth continued with sharp line, whereas the retromargins vary from fissidentate to pluridentate depending on species (Fig. 30C). The number of teeth or points (for fissidentate) varies from 4 to 6. Endites generally flattened and sometimes sclerotized, elongated and parallel-sided in some species, rather apically expanded in some others (Fig. 30B). Labium generally flattened, longer than wide and sclerotized (Fig. 30B). Sternum either flattened or convex, generally longer than wide, with broad (Fig. 30A), truncated or narrow anterior margin.

Leg formula 1432. First legs longer and larger than other legs. Femora of first legs usually with two or three bristles on dorsal surface, two or three prolateral spines, and one or two proventral spines (Fig. 24, 25A). Tibia of first leg as wide as or wider than femur, with three pairs of spines that may be symmetrical (Figs. 24B–D) or asymmetrical (Figs. 24A–C), with fringe of thick setae on ventral side in some species (*P. boritandroka;* Fig. 24B)*,* either simple or hook-like (*P. maingoka*; Fig. 24C). Metatarsus of first leg without a preening comb; bearing two pairs of spines on ventral surface that may be symmetrical (of the same size on proventral and retroventral surfaces) or not (*armata* group); metatarsus pseudosegmented or curved in a*rmata* group; ventral surface of metatarsus of some species withdark spot that may extend longitudinally between two metatarsal spines. Tarsi with two pectinate claws with different numbers of teeth as in all members of the Salticoida division (Maddison, 2003), e.g., prolateral claw with 23 teeth, retrolateral with 11 teeth; claw tuft usually black, scopulae absent (Fig. 52D–E). Femora of legs III–IV often with row of three dorsal spines (1/1/1), with additional proventral distal spine or retroventral distal spine, or both, depending on species (Fig. 25D). Metatarsus of leg III often with long trichobothrium on dorsal side. Abdomen with scutum in *P. lavatandroka* and *P. boritandroka* (Figs. 7, 55). Some species of *cornuta* and *armata* groups have two or three pairs of dark patches on abdominal dorsum (Figs. 7,

20). Spinnerets may be preceded by plate. Anterolateral spinnerets (ALS) often conical, sometimes cylindrical, and shorter than the posterolaterals (PLS). ALS of ♀ with several pyriform gland spigots and two major ampullate gland spigots (MAP) on mesal margin. ♂ ALS with only one MAP. Both ♂ and ♀ PMS show two classes of spigots: two minor ampullate gland spigots (mAP) located medially, and three aciniform gland spigots (AC). ♀ PLS with with seventeen AC; ♂ PLS with fifteen AC (Fig. 56). Cylindrical gland spigots absent, often the case of spiders that lay eggs within a retreat and cover them with layers of silk threads (Kovoor 1979). Details of male palp and female epigynum discussed above and below in species descriptions.

Natural History.— Nearly all species of *Padilla* for which collection data are available have been collected either by beating low vegetation, from pitfall traps or rarely from Malaise traps in humid tropical high or low altitude forests. The majority of species occur in warm and wet areas where the annual mean temperature varies between 15.9°C and 26.3ºC and the mean annual precipitation is 367–1829 mm (Table 5), however, a few species were collected from tropical dry forest (*P. mihaingo, P. mitohy*). The genus was mostly found along the eastern north and northwestern evergreen forests and central mountain rain forests at 700–1300 m elevation. Species of *Padilla* were located between 10–1300 m elevations, however, the "runners" were mostly found below 780 m in deciduous broadleaf low altitude forest, shrubland or wooded grassland, except *P. maingoka* (900 m). *Padilla* was almost absent in the far South where the vegetation is xerophytic except *P. astina*, which was collected from a dry spiny forest near the beach. Many species were concentrated in the evergreen mountain rain forest of Montagne d'Ambre. Several species are narrowly distributed, e.g., *P. griswoldi, P. astina, P. foty, P. maingoka,* and *P. mihaingo* were only collected from one locality. The genus seems to be very rare. Despite the intensive collecting from more than 60 sites of varied vegetation and altitude across the island, only 107 specimens were collected (including adults and juveniles).

Composition.— Fifteen species are presented here in this study, including the three previously described species, *Padilla armata* Peckham and Peckham, 1894, *P. cornuta* (Peckham and Peckham, 1885), and *P. sartor* Simon, 1900, and twelve newly described.

The types of three other species, *P. mantis* Simon, 1900, *P. glauca* Simon, 1900 and *P. lancearea* Simon, 1900, all described from Madagascar, could not be located and are considered lost. These names are considered *nomina dubia*. I also exclude *P. javana* (Java) from the genus because it lacks the horns on male chelicerae, a diagnostic character of *Padilla*, (Prószyński, 2003 in *Padilla*: <*http://salticidae.org/salticid/diagnost/padilla/padilla.htm*>).

Distribution.— Probably all of Madagascar except the far South (Figs. 51, 57, 58, 59).

Padilla armata Peckham and Peckham, 1894

Figs. 3E, 4B, 10A, 12A, 18.

Padilla armata Peckham and Peckham, 1894:130–132, pl. 13, fig. 1 (Syntypes from Madagascar, no specific locality, deposited in MCZ, Harvard, type number 117, examined). Simon, 1901a: 472, f. 542. Prószyński, 1984a: 95. Wanless and Lubin, 1986: 1211, f. 3A, C. Platnick, 2006.

Material examined.— Syntypes. Madagascar: no specific locality, 1894, Peckham and Peckham, 1♂ 8 juveniles deposited in MCZ, Harvard, type number 117.

Lectotype designation.— The one adult male is here designated as the lectotype.

Diagnosis of the *armata* group.— Distinguished from other male *Padilla* in having (1) horns dorsally presenting a double curve, first going inward, then outward, finally converging and crossed at the tips, about as long as half of the carapace length (horn length/carapace length: 0.51–0.67), originating from the proximal part of the chelicerae, and either distant from, or close

to, or touching each other (Figs. 10B, 12B, 18), (2) tibia of first legs with spines that are only present on proventral surface, retroventral surface without spines (unpaired; Fig. 24A), and consist of one larger distal and two smaller proximals (asymmetrical), (3) body very compact and beetle-like (Figs. 18, 10B), (4) abdomen almost as long as the carapace and (5) lateral margins of the paturons carinate.

Diagnosis.— *P. armata* can be distinguished from all other males within the *armata group* by the following combination of characters: (1) horns sharply bent near the distal end (not sharply bent in *P. astina*), touching each other at their median parts (as in *P. astina*, but different from *P. griswoldi*) (Fig. 3E), (2) abdomen somewhat longer and heavier compared with the cephalothorax (somewhat shorter in *P. astina* and *P. griswoldi*; Fig. 12) and (3) carapace guanine deposit very pale.

Description.— Male (Lectotype, no specific locality): Carapace reddish orange with two dark patches anteriorly, abdomen yellowish orange with an orange scapus, with aligned dark brown patches separated by yellowish white setae in juveniles female. Legs orange, darkened at their promargins; all eyes surrounded by dark pigmentation (Figs. 3E, 4B, 18).

Total length: 5.88. Carapace length: 2.63. Abdomen length: 3.25. Horn length/carapace length: 0.61. Horn width: 0.21. DH: 0.50. DH/CHL: 0.75. Width ocular field I: 1.33. Width ocular field III: 1.36. Height cephalothorax: 0.80. Diameter AME/length chelicerae: 0.61. Height cephalothorax/width cephalothorax: 0.42. Width cephalothorax/width ocular field III: 1.40.

Femur I/width ocular field II: 1.44. Femur III/width ocular field III: 0.85. Femur IV/Femur III: 1.10. Tibia I/width ocular field III: 1.07. Tarsi I/metatarsi I: 0.34.

Promargins of chelicerae pluridentate, with five teeth and continued distally as sharp line; retromargins fissidentate with six points.

Natural history.— Not specified by Peckham and Peckham (1894).

Distribution.— Peckham and Peckham (1894) did not specify where in Madagascar the type specimens of *Padilla armata* were collected.

Padilla griswoldi Andriamalala, sp. nov.

Figures 10B, 12B, 19, 25D, 33A–C, 60–61.

Material examined.— Holotype: Madagascar: **Fianarantsoa Province**: Ranomafana National Park, 1500 m, 21.2554ºS, 47.4552ºE, rainforest, Malaise trap, 12–21 December 1999, E.I. Schlinger and M.E. Irwin, 1♂ (CAS), CASENT 9021858. Other material examined: Madagascar: **Fianarantsoa Province:** Ranomafana National Park, radio tower, 1300 m, 21.25083°S 47.4071713°E, rainforest, Malaise trap, 3 December 2002, Fisher/Griswold Arthropod team, 1♂ (CAS), CASENT9021902.

Etymology.— The species name is a patronym in honor of my advisor, Charles E. Griswold.

Diagnosis.— *Padilla griswoldi* differs from other *Padilla* of the *armata* group in having the following characters: (1) carapace divided by a thin longitudinal white line, (2) horns convergent, close to but not touching each other at their median part (as it is in *P. astina*), then going outward before slightly crossing near tips, bases widely separated (very close to each other in *P. astina*), (3) guanine deposit extending towards the posterior part of the carapace (Figs. 10B,19), (4) horns cylindrical, sharpened and darkened on their margins, with rows of setae on lateral edges, and stridulating lines on dorsal and ventral sides, mostly near the tips and (5) femur III dorsally without additional retromarginal spine (Fig. 25D).

Description.— Male (Holotype from Ranomafana National Park, Fianarantsoa, Madagascar): Carapace brown reddish with red guanine deposit, thin white median line, and one thick lateral band of white scales on each side. Margin of clypeus with fringe of white scales. Abdomen reddish brown with thin yellowish median folium (Fig. 19). Legs brown, darkened on their promarginal and retromarginal sides (Fig. 19).

Total length: 5.39. Carapace length: 2.46. Abdomen length: 2.93. Horn length/carapace length: 0.51. Horn width: 0.18. DH: 0.58. DH/CHL: 0.97. Width ocular field I: 0.76. Width ocular field III: 0.76. Height cephalothorax: 0.44. Diameter AME/length chelicerae: 0.81. Height cephalothorax/width cephalothorax: 0.24. Width cephalothorax/width ocular field III: 2.41.

Femur I/width ocular field III: 2.16. Femur III/width ocular field III: 1.16. Femur IV/Femur III: 1.34. Tibia I/width ocular field III: 1.79. Tarsi I/metatarsi I: 0.51.

Promargins of the chelicerae pluridentate with three teeth. Retromargins fissidentate with five teeth.

Variation.— Male (n=2): carapace length: 2.33–2.46. Abdomen length: 2.93–3.06. Diameter AME: 0.38–0.40. Horn length/ carapace length: 0.51–0.56. Femur I length: 1.64–1.66.

Female: Unknown.

Natural history.— Specimens were collected from rainforest in Malaise traps.

Distribution.— Central Southern Madagascar (Fig. 60, 61).

***Padilla astina* Andriamalala, sp. nov.**

Figures 10C, 12C, 14C, 20, 24A, 33D–F, 60–61.

Material examined.— Holotype: Madagascar: **Toliara Province**: Ifaty 18 km N of Toliara**,** 20 m, 23.1885ºS 43.6239ºE, tropical dry forest, malaise trap, 14 December 1999, E.I. Schlinger, 1♂ (CAS), CASENT9021860.

Etymology.— The species name is taken from Astina, my mother's name.

Diagnosis.— Distinguished from *Padilla griswoldi* in having the following characters: (1) carapace without a longitudinal median white line, (2) guanine deposit not extending towards the posterior part of the carapace, restricted to its anterior parts, (3) horns not sharply bent near the distal end (different from *P. armata)*, convergent, touching each other for a certain distance at their median part, then continuing outwards before conspicuously crossing at their tips, (4) horn bases very close to each other and (5) femur III with an additional distal retromarginal spine (Fig. 10C, 20).

Description.— Male (Holotype from Ifaty, Toliara, Madagascar): Carapace with two anterior dark spots of guanine deposit and thick lateral band of white scales. Clypeal margin with fringe of white scales (Fig. 14C). Abdominal dorsum with two pairs of dark yellowish patches and a wide yellowish median band, followed laterally by narrow reddish brown bands. Spinnerets preceded by thin, wide yellowish plate. Legs brown, darkened on their promarginal and retromarginal sides, same as in *P. griswoldi* (Fig. 20).

Total length: 4.69. Carapace length: 2.13. Abdomen lenght: 2.56. Horn length/carapace length: 0.67. Horn width: 0.18. DH: 0.44. DH/CHL: 0.92. Width ocular field I: 1.16. Width ocular field III: 1.13. Height cephalothorax: 0.71. Diameter AME/length chelicerae: 0.83. Height cephalothorax/width cephalothorax: 0.44. Width cephalothorax/width ocular field III: 1.44.

Femur I/ width ocular field III: 1.38. Femur III/width ocular field III: 0.76. Femur IV/Femur III: 1.16. Tibia I/width ocular field III: 1.12. Tarsi I/metatarsi I: 0.45.

Promargins of the chelicerae pluridentate, with three distal teeth and a proximal sharp line; retromargins fissidentate with four points.

Female: Unknown.

Natural history.— Specimen was collected from tropical dry forest by Malaise trap.

Distribution.— Southern Madagascar (Figs. 60, 61)

***Padilla ombimanga* Andriamalala, sp. nov.**

Fig. 10D, 12D, 21, 33G-H-I, 47, 48.

Material examined.— Holotype: Madagascar: **Antsiranana Province**: Park National Montagne d'Ambre, 1000–1200 m, 12°31′53.5″S; 49º10′36.8″E , tropical rainforest, beating trees, 14-20 December 2005, Hannah Wood and Harisoa Raholiarisendra, 1♂ (CAS), CASENT9023432.

Etymology.— The species name is from the Malagasy "*ombimanga*," which refers to a "black bull."

Diagnosis.— Distinguished from *P. griswoldi* and *P. astina* by the following characters: (1) carapace without a thick band of white scales on lateral sides, (2) femur of leg I with two proventral spines (as in *P. sartor*, Fig. 25A), (3) abdomen with a single median band of thick white scales that is extended horizontally at the posterior part, (4) clypeus without a thick fringe of white scales, (5) horns very close to each other, but not touching and (6) horn bases very close to each other and not widely separated (Figs. 10D, 21).

Description.—Male (Holotype from National Park Montagne d'Ambre, Antsiranana, Madagascar): Carapace dark brown with an orange thin horizontal guanine deposit along the anterior edge. Clypeal margin without a fringe of white scales. Abdominal dorsum dark brown with a single thick longitudinal band of white scales. Three pairs of dark patches are visible on the dorsum. First legs dark brown; all the other legs yellow. Spinnerets not preceded with a plate (Fig. 21).

Total length: 5.92. Carapace length: 2.76. Abdomen length: 3.16. Horn length /carapace length: 0.61. Horn width: 0.23. DH: 0.7. DH/CHL: 0.8. Width ocular field I: 1.5. Width ocular field III: 1.53. Height cephalothorax: 0.84. Diameter AME/length chelicerae: 0.73. Height cephalothorax/width cephalothorax: 0.30. Width cephalothorax/width ocular field III: 1.41.

Femur I/width ocular field III: 1.38. Femur III/width ocular field III: 0.759. Femur IV/Femur III: 1.21. Tibia I/width ocular field III: 1.21. Tarsi I/metatarsi I: 0.446.

Promargins of the chelicerae are pluridentate with five teeth and a distal sharp line. Retromargins are fissidentate with five teeth.

Female: Unknown.

Natural history.— Specimen was collected from tropical dry forest by beating trees.

Distribution.— Northern Madagascar (Figs. 47, 48).

***Padilla sartor* Simon, 1900**

Figs. 9A, 16, 15A, 25A, 31A–C, 47–48.

*Padilla sarto*r Simon, 1900b:393 (type specimen from Madagascar (no specific locality given), not located in MNHN Paris, not examined); Simon, 1901a: 461, f. 539–541 (m); J. Prószyński 2000, Platnick 2006.

Material examined.— Madagascar: **Antsiranana Province**: National Park Montagne d'Ambre, 12.2km 211º SSW of Joffreville, 1300 m, 12º35′47″S, 49º9′34″E, mountain rainforest, beating low vegetation, 2–7 February 2001, Fisher/Griswold Arthropod Survey team, 1♂ (CAS), CASENT 9021839.

Note.— The type specimen of *Padilla sartor* was not located, and seems to be lost. However, the drawings of the diagnostic characters from Simon's 1900 original description (also shown in "Diagnostic, Drawing Library" by Prószyński 2000) correspond to the characteristics of a male specimen collected from Montagne d'Ambre (Northern Madagascar) by the following characters: (1) horn curving outward then inward with tips separated and (2) femur of leg I with two proventral strong spines (Fig. 25A). Even though there are some slight differences between the specimen observed and Simon's descriptions (concerning the abdomen coloration, presence of bands of scales on the margins of the carapace and geographic location), I will consider and describe here this specimen as *Padilla sartor* until the type and additional specimens are observed.

Diagnosis of the *sartor* group.— Distinguished from other male *Padilla* not included in the *Sartor* group by having (1) a pair of horns projecting forward from the proximal parts of the chelicerae, which, dorsally, first curve outward, and distally slightly bend inward, so that the tips are close to or crossing each other, laterally going upward with tips exceeding the middle of AME (Figs. 3C–D); (2) a red guanine deposit on the ocular area of the carapace, except for *P. maingoka* (Figs. 9, 16, 22, 23) and (3) tegulum division of the palp is a shallow invagination instead of a groove (Figs. 31D–E-G–H).

Diagnosis of *P. sartor*.— Distinguished from all other males within the *Sartor* group by the following combination of characters: (1) horns as long as half of the carapace (horn length/carapace length: 0.5), with the tips not crossed (different from *P. mazavaloha* and *P. maingoka*), (2) femur of leg I with two proventral strong spines (only one in *P. mazavaloha* and *P. maingoka*) (Fig. 25A), (3) abdomen dark with a single longitudinal yellowish band (with longitudinally aligned chevrons in *P. mazavaloha*), (4) guanine deposit only red (red with a white median part in *P. mazavaloha*), (5) tibia I without a promarginal spur (present in *P. mazavaloha*), (6) tibia and metatarsi I with asymmetrical pairs of spines on pro and retroventral sides (spines are of different size on pro and retroventral sides) and (7) male palp with embolus base concave, posterior part of the tegulum visible, and tegulum division a shallow invagination (Figs. 31A–C).

Description.— Male (from Montagne d'Ambre, Antsiranana, Madagascar): Carapace dark brown with red guanine deposit and two black spots on top; abdomen dark brown with a single yellowish longitudinal band; all eyes surrounded by dark pigmentation; first legs dark brown, other legs yellow (Figs. 9A, 16).

Total length: 5.76. Carapace length: 2.60. Abdomen length: 3.16. Horn length/carapace length: 0.50. Horn width: 0.24. DH: 0.40. DH/CHL: 0.66. Width ocular field I: 1.53. Width ocular field III: 1.50. Height cephalothorax: 0.80. Diameter AME/length chelicerae: 0.86. Height cephalothorax/width cephalothorax: 0.53. Width cephalothorax/width ocular field III: 1.44.

Femur I/width ocular field III: 1.36. Femur III/width ocular field III: 0.83. Femur IV/Femur III: 1.13. Tibia I/width ocular field III: 1.20. Tarsi I/metatarsi I: 0.47.

Promargins of chelicerae pluridentate with five teeth and continued distally with a sharp line; retromargins are fissidentate with six points.

Female: Unknown.

Natural history.— A specimen was collected from mountain forest by beating low vegetation.

Distribution.— Northern and eastern Madagascar (Figs. 47–48). The type specimen was collected from Tamatave, Sainte-Marie (Toamasina Province), whereas the one male specimen described above was collected from Montagne d'Ambre (Antsiranana Province).

Padilla mazavaloha Andriamalala, sp. nov.

Figures 3C, 4Ca, 9B, 15B, 22, 31D–F, 52B, 53A.

Material examined.— Male holotype and female paratype: Madagascar: **Antsiranana Province:** National Park Montagne d'Ambre, 3.6 km 235º SW of Joffreville, 925 m, 12º32′4″S, 49º10′46″E, mountain rainforest, beating low vegetation, 20–26 January 2001, Fisher/Griswold Arthropod Survey team, 1♂ 1♀(CAS), CASENT 9006683. Other material examined.— Madagascar: **Antsiranana Province**: National Parc Montagne d'Ambre, 2.79 air km NE of Parc entrance, 1000 m, 12º32′S, 49º10′E, 21–30 May 1993, Fisher/Griswold Arthropod team: 1♂ 3♀ (CAS), CASENT9021899 – 4♀ (CAS), CASENT9020188. National Parc Montagne d'Ambre, 2.79 air km NE of Parc entrance, 1000–1200 m, 12º31′53.5″S, 49º10′36.8″E, 14–20 December 2005, Fisher/Griswold Arthropod team: 1♀ (CAS), CASENT9023433 – 1♀ (CAS), CASENT9023434 – 1♀ (CAS), CASENT9023435. National Park Montagne d'Ambre, 3.6 km 235º

SW Joffreville, 925m, 12º32′4″S, 49º 10′46″E, 20–26 January 2001, L.J. Boutin coll, 1♀ (CAS), CASENT9000755. Reserve Speciale Manongarivo, 10.8 km 229º SW Antanambao, 400 m, 13º577′S, 48º26′E, 8 May 1998, B.L. Fisher, 6♀ (CAS), CASENT9020185. **Fianarantsoa Province:** National Park Ranomafana, radio tower, 1130 m, 21.25083ºS, 47.40717ºE, 3 September 2003, R. Harin'Hala, 1♂(CAS), CASENT 9006891.

Etymology.— The species name is from the Malagasy word "mazava loha," which refers to a dark zebu bull with a clear yellowish head.

Diagnosis.— Distinguished from *P. sartor* and *P. maingoka* by the following combinations of characters: (1) guanine deposit on the ocular area is red, but with a median white spot (Figs. 3C, 4Ca), (2) abdominal dorsum with chevrons on the posteromedian instead of a single yellowish median band (Figs. 9B, 22), (3) tibia I provided with a distal proximoventral spur (same as in *P. cornuta* in Fig. 25C) and (4) tibia and metatarsus I with symmetrical pairs of spines (spines of the same size on pro and retroventral sides). Also, metatarsus I has a ventral black spot extending over space between the two metatarsal spines. Sternum is broader than long.

Description.— Females and males are of the same color (yellowish to orange), but males are a bit darker. Carapace yellowish, slightly darker at the anterolateral regions (dark brown in males and brown orange in the posteromedian); abdomen yellowish, with two dark longitudinal lateral bands and median chevrons in females; dark with median chevrons in males; all eyes surrounded by dark pigmentation; first legs yellowish, and slightly darkened on the pro and retrolateral sides (completely dark, except for the tarsi in males), all other legs yellow (Fig. 22).

Male (Holotype from National Park Montagne d'Ambre, Antsiranana, Madagascar): Total length: 5.22. Carapace length: 2.46. Abdomen length: 2.76. Horn length/carapace length: 0.42. Horn width: 0.32. DH: 0.56. DH/CHL: 0.82. Width ocular field I: 1.46. Width ocular field III: 1.45. Height cephalothorax: 0.76. Diameter AME/length chelicerae: 0.84. Height cephalothorax/width cephalothorax: 0.53. Width cephalothorax/width ocular field III: 1.28.

Femur I/width ocular field III: 0.97. Femur III/width ocular field III: 0.69. Femur IV/Femur III: 1.16. Tibia I/width ocular field III: 0.83. Tarsi I/metatarsi I: 0.51.

Promargins of chelicerae pluridentate with three teeth and a distal sharp line, retromargins fissidentate with six points.

Variation.— Male (n=2): total length: 5.23–5.56. Carapace length: 2.46–2.70. Abdomen length: 2.76–2.86. Femur I length: 1.40–2.02.

Female (Paratype from National Park Montagne d'Ambre, Antsiranana, Madagascar): As male but without promarginal distal spur on tibia I.

Total length: 5.39. Carapace length: 2.26. Cephalothorax width: 1.65. Width ocular field I: 1.40. Width ocular field III: 1.33. Height cephalothorax: 0.72.

Tibia I/width ocular field III: 0.78. Tibia III/tibia IV: 0.64. Patella III/tibia III: 0.96. Femur I/width ocular field III: 1.09. Femur III/width ocular field III: 0.75.

Promargins of chelicerae pluridentate with six teeth, retromargins fissidentate with six points.

Variation.— Female (n=5): total length: 4.72–5.76. Carapace length: 2.16–2.33. Abdomen length: 2.56–3.43. Cephalothorax width: 0.88–1.73. Femur I length: 1.24–1.46. Patella III/tibia III: 0.86–1.25.

Natural history.— Specimens were collected from mountain forest or in rainforest by beating low vegetation between 400–1130 m elevations. The localities where the species were found have an annual mean temperature which varies between 18°C and 24ºC, and a precipitation up to 809–1142 mm during the rainy season, 48–123 mm during about the four months dry season (Worldclim version 1.3).

Distribution.— Widespread in northern and eastern Madagascar.

***Padilla maingoka* Andriamalala, sp. nov.**
Figures 9C, 14A, 15C, 23, 24C, 28C, 31G–I.

Material examined.— Holotype: Madagascar: **Fianarantsoa Province:** Ranomafana National Park, Talatakely, 900 m, 21.25041ºS 47.41945ºE, 10–16 January 2001, D.H Kavanaugh, K.M. Kavanaugh, R. Brett, E. Elsom and F. Vargas, 1♂ (CAS), CASENT 9003529. Other material examined: same locality as holotype, 2–22 January 2001, Fisher/Griswold Arthropod team, 1♂ (CAS), CASENT 9003506.

Etymology.— The species name is from the Malagasy word "Maingoka," which means "scorpion".

Diagnosis.— Differs from all males within the *Sartor* group by the following combination of characters, (1) tibia I hook like (Fig. 24C), (2) body flattened and more convex (protruding for *P. sartor* and *P. mazavaloha*) (Figs. 15C, 28C), (3) horns shorter (horn length/ carapace length: 0.38), tips crossed at the apex, weakly separated from each other, (4) carapace ocular area with a faint yellowish guanine deposit instead of red, or guanine deposit absent and (5) femur III with additional promarginal spine (three dorsal spines only in *P. sartor* and *P. mazavaloha*). Metatarsi without ventral black spot extending over space between the two metatarsal spines.

Description.— Male (Holotype from Talatakely, Ranomafana National Park, Fianarantsoa, Madagasacar): Carapace and abdomen dark brown with two thin dark longitudinal lines on lateral sides; anterior part of carapace ocular area bears a faint horizontal yellowish guanine deposit; all eyes surrounded by dark pigmentation; first legs brown, darker on pro and retrolateral sides, other legs yellowish (Fig. 23).

Total length: 6.09. Carapace length: 2.56. Abdomen length: 3.53. Horn length/carapace length: 0.38. Horn width: 0.12. DH: 0.38. DH/CHL: 0.90. Width ocular field I: 1.28. Width ocular field III: 1.30. Height cephalothorax: 0.66. Diameter AME/length chelicerae: 0.95. Height cephalothorax/width cephalothorax: 0.39. Width cephalothorax/width ocular field III: 1.30.

Femur I/ width ocular field III: 1.46. Femur III/width ocular field III: 0.63. Femur IV/Femur III: 1.36. Tibia I/ width ocular field III: 1.26. Tarsi I/metatarsi I: 0.41.

Promargins of chelicerae with three teeth and a distal sharp line, retromargins fissidentate with five points.

Variation.— Male (n=2): total length: 6.0–6.09. Carapace length: 2.4–2.56. Abdomen length: 3.53–3.60. Femur I length: 1.90–1.92. Tibia I length: 1.52–1.64. Patella length: 0.96–1.10.

Female: Unknown.

Natural history.— Specimens were collected from mixed tropical forest by pitfall traps and by beating low vegetation.

Distribution.— Central southern Madagascar.

***Padilla cornuta* (Peckham and Peckham, 1885)**
Figures 5, 8A, 13A, 25C, 29A–C, 45–46, 62A–B.

Icius cornutus Peckham and Peckham, 1885a:30–32 (syntype male and female from Madagascar, MCZ type 115, examined). *Padilla cornuta* Peckham and Peckham, 1894:130. Prószyński, 1987:74. Platnick 2006.

Material examined.— Madagascar: **Antananarivo Province:** Andranomay, 11.5 km 147° SSE Anjozorobe, 1300 m, 18º28′24″S, 47º57′36″E, 5–13 December 2000, Fisher/Griswold Arthropod team 2♂ (CAS), CASENT9004193 – 2♀ 11 juveniles (CAS), CASENT9021863 – 3♀ 8 juveniles (CAS), CASENT 9003868. Reserve speciale d'Ambohitantely, 20.9 km 72° NE Ankazobe, 1410 m, 18º13′31″S, 47°17′13″E, 17–22 April 2001, Fisher/Griswold Arthropod team, 2♀ (CAS), CASENT 9021861 – 1♂ (CAS), CASENT 9001225. **Toamasina Province**: Montagne d'Anjanaharibe 19.5 km NNE of Ambinanitelo, 1100 m, 15.178333°S, 49.635°E, 12–16 March 2003, Fisher/Griswold Arthropod team, 1♂ (CAS), CASENT9020140.

Fianarantsoa Province: Park National Ranomafana, 900m, 21º15′S, 47º25′E, 5–7 December 1993, C. Griswold, 1♂ (CAS), CASENT 9020186.

Diagnosis of the *cornuta* group.— Distinguished from other male *Padilla* not included within the *Cornuta* group by having: (1) a pair of horns projecting forward from the proximal parts of the chelicerae, dorsally straight and converging near the tips, but neither touching nor crossing each other, laterally presenting a double curve (Figs. 3A–B) (2) tegulum division of the palp is a shallow invagination, except in *P. cornuta* (Figs. 29E–H).

Diagnosis of *P. cornuta*.— Different from other males within the *cornuta* group by the following combinations of characters (1) horns are cylindrical with dark sharp edges and often with pigmentation at their bases, strong and thicker, going upwards till the apex (Figs. 13A), (2) carapace with a white guanine deposit that is constricted by two black spots at its median part (different from *P. manjelatra* and *P. lavatandroka*) (Fig. 8A), (3) tibia with a median proximal spur (Fig. 25C) and (4) abdomen is yellowish with two thick dark lateral bands (Figs. 5, 8A).

Palp with a protuberance (pb) on anterior retrolateral side (Figs. 29A–C), and the basal prolateral of which is divided by a horizontal slit (only on the basal prolateral side in all other male *Cornuta* group; Figs. 29E–H). Tegular division of the palp forming a large longitudinal hole as in the *Armata* group species (Fig. 29B). Retrolateral tibial apophysis relatively long (extending till the mid-length of the cymbium), slightly converging to the cymbium. Velum is absent (Figs. 29A–C).

Description.— Male (from Ankazobe, Ambohitantely, Antananarivo, Madagascar): Carapace and abdomen are dark on lateral sides; a thick yellowish band is present on the median part of the cephalothorax and abdominal dorsum. The abdomen has also one pair of dark patches (Fig. 5).

Total length: 5.92. Carapace length: 2.56. Abdomen length: 3.36. Horn length/carapace length: 0.50. Horn width: 0.22. DH: 0.52. DH/CHL: 0.81. Width ocular field I: 1.43. Width ocular field III: 1.43. Height cephalothorax: 0.80. Diameter AME/length chelicerae: 0.78. Height cephalothorax/width cephalothorax: 0.42. Width cephalothorax/width ocular field III: 1.32.

Femur I/width ocular field III: 1.38. Femur III/width ocular field III: 0.75. Femur IV/Femur III: 1.20. Tibia I/ width ocular field III: 1.09. Tarsi I/ metatarsi I: 0.52.

Promargins of chelicerae are pluridentate with five teeth continued with a sharp line; retromargins are fissidentate with five points.

Variation.— Male (n=3): total length: 4.36–5.92. Carapace length: 1.96–2.56. Abdomen length: 2.4–3.36. Femur I length: 1.06–1.98. Horn length/carapace length: 0.43–0.60. Horn width: 0.14–0.22.

Note.— Males of *Padilla cornuta* exhibit a case of allometry. Larger males have stronger body and horns and dark ventral abdomens, whereas smaller ones are very weak looking and with whitish ventral abdomens. The distribution of those two variants overlapped in the central part of the island.

Female (from, Ankazobe, Ambohitantely, Antananarivo, Madagascar): As male, except that dorsal abdomen provided with one to two pairs of dark yellowish patches (male patches are not very distinct). Ventral abdomen is yellowish with dark round spots around the spinnerets: one dark purple above, and one or two pairs on lateral sides. Also, cervical groove is more obvious in females than in the male.

Total length: 5.49. Carapace length: 2.53. Abdomen length: 2.96. Cephalothorax widths: 1.63. Width ocular field I: 1.40. Width ocular field III: 1.40. Height cephalothorax: 0.70.

Femur I/ width ocular field III: 1.01. Femur III/ width ocular field III: 0.66. Tibia I/ width ocular field III: 0.71. Tibia III/ tibia IV: 0.66. Patella III/ tibia III: 1.08.

Promargins of the chelicerae are pluridentate with three teeth continued with a sharp line; retromargins are fissidentate with five points.

Genitalia with the copulatory openings (co) not interconnected but rather widely separated at their anterior parts. The fertilization ducts (fd) and the spermathecae (spc) form a large coil at the posterior parts of the epigynum (Figs. 62A–B.).

Variation.— Female (n=5): total length: 4.31–5.99. Carapace length: 1.96–2.53. Abdomen length: 2.35–3.66. Cephalothorax width: 1.23–1.63. Femur I length: 1.06–1.42. Patella III/ tibia III: 1–1.083.

Natural history.— Specimens were collected from mountain forest, mixed tropical rainforest by general collecting, and by beating low vegetation.

Distribution.— Central, central southern, eastern, and central western parts of Madagascar (Figs. 45, 46).

***Padilla manjelatra* Andriamalala, sp. nov.**

Figures 3A, 6, 8B, 13C, 24D, 25B, 29D–F, 62C–D.

Material examined.— Male holotype and female paratype: Madagascar: **Antsiranana Province**: Marojejy reserve, 8.4 km NNW of Manantenina, 700m, 14º26′S, 49º45′E, 10–16 November 1993, mountain rainforest, general collecting and beating low vegetation, C. Griswold, J. Coddington, N. Scharff, S. Larcher, and R. Andriamasimanana, 1♂ 1♀ (CAS), CASENT9021900. Other material examined: Madagascar: **Antsiranana Province:** Reserve Speciale de Manongarivo, 12.8 km 228º SW of Antanambao, 780 m, 13º58.6′S, 48º25.4′E, 12 October 1992, 1♂ (CAS), CASENT9021862. Binara forest, 9.4 km 235º SW Daraina, 1100m, 13º14.5′48″S, 49º36′E, 6 December 2003, Fisher/Griswold Arthropod team, 1♂ (CAS), CASENT 9011917.

Etymology.— The species name is from the Malagasy word "manjelatra," which means "brilliant".

Diagnosis.— Distinguished from *P. cornuta* by the following characters: (1) horns very long, almost as long as the carapace (horn length/carapace length: 0.8), thicker (horn width: 0.34), slightly outward at the base, then converging, upturned or touching each other at tips, horns not flattened dorso-ventrally but cylindrical and without a pigment deposit at their bases as in *P. cornuta* (Figs. 3A–B), (2) presence of spur both on tibia I and patella I (Fig. 25B), (3) carapace higher and greatly enlarged between legs II and III, without a white guanine deposit as in *P. cornuta* (Figs. 3A–B), (4) endites have ridges that extend to their bases (same as in Fig. 30D) and (5) palp without a protuberance on the anterior retrolateral side (different from *P. cornuta*) (Figs. 29D-E-F). Body dark, high (CH/CL >0.35), compact and robust compared with *P. cornuta* (Figs. 6, 8B). Legs light orange.

Description.— Male (Holotype from Marojejy, Antsiranana, Madagascar): Carapace and abdomen completely black with horizontal stripes of green iridescent hairs. Those horizontal stripes of scale-like hairs become lighter at the posterior part of the abdomen. All eyes are surrounded with black pigmentation. All legs are yellowish to orange. Tibia and metatarsi of the first legs are black (Figs. 6, 24D).

Total length: 5.72. Carapace length: 2.86. Abdomen length: 2.86. Horn length/carapace length: 0.80. Horn width: 0.34. DH: 0.56. DH/CHL: 0.8. Width ocular field I: 1.93. Width ocular field III: 1.86. Height cephalothorax: 1.16. Diameter AME/length chelicerae: 0.98. Height cephalothorax/width cephalothorax: 0.49. Width cephalothorax/width ocular field III: 1.27.

Femur I/width ocular field III: 1.27. Femur III/width ocular field III: 0.78. Femur IV/Femur III: 1.14. Tibia I/width ocular field III: 0.87. Tarsi I/metatarsi I: 0.56.

Promargins of the chelicerae are pluridentate with three teeth; retromargins are fissidentate with four points.

Retrolateral tibial apophysis is short with rounded tip, curved toward the cymbium.

Variation.— Male (n=3): total length: 5.19–6.53. Carapace length: 2.56–3.03. Abdomen

length: 2.63–3.50. Femur I length: 2.04–3.05. Horn length/carapace length: 0.71–0.80. Horn width: 0.20–0.34.

FEMALE (Paratype from Marojejy, Antsiranana, Madagascar): As male but legs darker with black stripe.

Total length: 5.76. Carapace length: 2.50. Abdomen length: 3.26. Cephalothorax width: 2.06. Width ocular field I: 1.83. Width ocular field III: 1.76. Height cephalothorax: 1.0.

Femur I/ width ocular field III: 0.97. Femur III/ width ocular field III: 0.71. Tibia I/ width ocular field III: 0.70. Tibia III/ tibia IV: 0.76. Patella III/ tibia III: 1.03.

Promargins of the chelicerae are pluridentate with four distal teeth followed by a proximal sharp line; retromargins are fissidentate with four points.

Genitalia sclerotized with the copulatory openings interconnected at the anterior parts of the epigynum (different from *P. cornuta*, Figs. 62C–D).

NATURAL HISTORY.— Specimens were collected from rainforest and mountain forest by general collecting and beating low vegetation.

DISTRIBUTION.— Northern Madagascar.

***Padilla lavatandroka* Andriamalala, sp. nov.**

Figures 2A–C, 4A–a, 7, 8C, 13B, 14B, 28A, 29G–I, 30A–D, 52A, 52D–E, 53B–D, 54A–F, 56A–F, 62E–F.

MATERIAL EXAMINED.— MALE HOLOTYPE AND FEMALE PARATYPE: MADAGASCAR: **Antsiranana Province:** National Parc Montagne d'Ambre**,** 2.79 air km NE of Parc entrance, 1000 m, 12º32′S, 49º10′E, 21–30 November 1993, mountain rainforest, beating low vegetation, C. Griswold, J. Coddington, N. Scharff, S. Larcher, and R. Andriamasimanana, 1♂ 1♀ (CAS), CASENT9020190. OTHER MATERIAL EXAMINED: MADAGASCAR: **Antsiranana Province:** National Parc Montagne d'Ambre, 12.2 km 211º SSW of Joffreville, 1300m, 12º35′47″S, 49º9′34″E, 2–7 February 2001, Fisher/Griswold Arthropod team, 1♂ (CAS), CASENT9006890. National Parc Montagne d'Ambre, 12.2 km 211º SSW of Joffreville, 1000–1200 m, 12º31′53.5″S, 49º10′36.8″E, 14–20 December 2005, Fisher/Griswold Arthropod team, 1♂ (CAS), CASENT9023436. National Parc Montagne d'Ambre, 2.79 air km NE of Parc entrance, 1000m, 12º 32′S, 49º 10′E, 21–30 June 1993, C. Griswold, J. Coddington, N. Scharff, S. Larcher and R. Andriamasimanana, 5♂ 3♀ 1juvenile (CAS). CASENT9021901 – 3♂ 2♀ (CAS), CASENT9020190 – 3♂ 4♀ (CAS), CASENT-9020189. National Parc Montagne d'Ambre**,** 2.79 air km NE of Parc entrance, 1000 m, 12º32′S, 49º10′E, 21–30 November 1993, C. Griswold, J. Coddington, N. Scharff, S. Larcher, and R. Andriamasimanana, 1♂ 2♀ (CAS), CASENT 9025471.

ETYMOLOGY.— The species name is from the Malagasy words "lava tandroka," which means "with long horns."

DIAGNOSIS.— Body, carapace and horns are the same as *P. manjelatra*, but distinguished from it by the following characters: (1) tibia I without a spur (Figs. 7, 8C), (2) abdomen with a dark brown scutum (sclerotized plate) and yellow reticulations instead of *transverse* stripes of iridescent green scale-like hairs, body and legs rather brown, (3) palp is very simple, without any protuberance (same as in *P. manjelatra*, but different from *P. cornuta*) (Figs. 29G–I) and (4) embolus tip is different from all other *Padilla* by being circular.

DESCRIPTION.— MALE (Holotype from National Parc Montagne d'Ambre**,** 2.79 air km NE of Parc entrance, Antsiranana, Madagascar): Carapace, abdomen and legs dark brown. Male may have few iridescent green scales on the abdomen. All legs brownish orange. First legs dark yellow with the tibia and metatarsi darkened as in *P. manjelatra*. The other legs yellowish with horizontal brown chocolate stripes (Fig. 7).

Total length: 6.63. Carapace length: 3.10. Abdomen length: 3.51. Horn length/carapace length: 0.79. Horn width: 0.32. DH: 0.80. DH/CHL: 0.87. Width ocular field I: 1.96. Width ocular field III:

1.80. Height cephalothorax: 1.33. Diameter AME/length chelicerae: 0.69. Height cephalothorax/width cephalothorax: 0.52. Width cephalothorax/width ocular field III: 1.42.

Femur I/width ocular field III: 1.50. Femur III/width ocular field III: 0.90. Femur IV/Femur III: 1.09. Tibia I/width ocular field III: 1.04. Tarsi I/metatarsi I: 0.50.

Promargins of chelicerae pluridentate with four teeth, retromargins fissidentate with five points.

Palp tegular division not a groove, but rather a shallow longitudinal invagination. Posterior part of the tegulum not visible from the ventral side. Velum absent. Retrolateral tibial apophysis short, straight with a round tip (Fig. 29G-H-I).

Variation.— Male (n=5): total length: 5.13–6.63. Carapace length: 2.50–3.10. Abdomen length: 2.63–3.53. Femur I length: 1.88–2.70. Horn length/carapace length: 0.75–0.81. Horn width: 0.28–0.32.

Female (Paratype from National Parc Montagne d'Ambre**,** 2.79 air km NE of Parc entrance, Antsiranana, Madagascar): Carapace brown orange with lines of brilliant white hairs on lateral sides between eyes and edges, slightly longer than wide. Dorsum brown chocolate with yellowish reticulations; bears two pairs of dark patches. Legs as in male but tibia and metatarsi of leg I not darkened.

Total length: 6.42. Carapace length: 3.16. Abdomen length: 3.26. Cephalothorax width: 2.50. Width ocular field I: 2.06. Width ocular field III: 1.96. Height cephalothorax: 1.26.

Femur I/width ocular field III: 1.08. Femur III/width ocular field III: 0.83. Tibia I/width ocular field III: 0.81. Tibia III/tibia IV: 0.73. Patella III/tibia III: 1.09.

Promargins of the chelicerae pluridentate with four distal teeth and a proximal sharp line, retromargins fissidentate with five points.

Genitalia: distinguished from *P. manjelatra* by having the copulatory openings (co) not interconnected at their anterior part (Figs. 62E–F).

Variation.— Female (n=5): Total length: 6.42–6.93. Carapace length: 3.06–3.33. Abdomen length: 3.26–3.73. Cephalothorax width: 2.43–2.63. Femur I length: 2.10–2.38. Patella III/tibia III: 1.07–1.16.

Natural history.— Specimens were collected from mountain forest by beating low vegetation.

Distribution.— Northern Madagascar.

Padilla mitohy Andriamalala, sp. nov.

Figures 27A, 27 C–E, 34A–E.

Material examined.— Holotype: Madagascar: **Antsiranana Province:** Reserve Naturelle Integrale de Lokobe**,** 6.3 km ESE of Hellville, 30 m, 13º25′10″S, 48º19′52″E, 19–24 March 2001, rainforest, general collecting and beating low vegetation, Fisher/Griswold Arthropod survey team, 1♀ (CAS), CASENT 9007991. Other material examined: Madagascar: **Antsiranana Province**: Nosy Be, Reserve Naturelle Integrale de Lokobe, 6.3 km 112º ESE Hellville, 30 m, 13º25′10″S, 48º 19′52″E, 19–24 March 2001, Fisher/Griswold Arthropod team 1♀ (CAS), CASENT9007991 – 1♀ (CAS), CASENT9007992 – 1♀ (CAS), CASENT9003237 – 1♀ (CAS), CASENT9025473. Forêt d'Andavakoera, 21.4 km 75º ENE Ambilobe; 4.6 km 356º N Betsiaka, 425m, 13º07′06″S, 49º13′48″E, 15 December 2003, Fisher/Griswold Arthropod team, 2♀ (CAS), CASENT 9011933. Reserve Special de l'Ankarana, 13.6 km 192º SSW Anivorano Nord, 210 m, 12º51′49″S, 49º13′33″E, 16–20 February 2001, Fisher/Griswold Arthropod team, 3 ♀ (CAS), CASENT 9001478.

Etymology.— The species name is from the Malagasy word "*mitohy*" meaning "continuous."

Diagnosis.— Distinguished from females of *P. manjelatra* and *P. lavatandroka* by the follow-

ing characters: (1) body elongate and not globular (Fig. 34A), (2) carapace shorter than the abdomen, with longitudinal bands of white scales on the lateral sides, (3) abdomen dark brown with a dorsal folium instead of reticulations, (4) tibia of first legs enlarged compared with other leg segments and provided with thick fringe of setae and (5) epigynum anterior part not fully sclerotized (only the part around the two copulatory pockets is sclerotized), copulatory openings not interconnected and continued posteriorly with the sclerotized tube or "sulci" as in *P. foty* (Figs. 27C–E, 34E).

Description.— Female (Holotype from Réserve Naturelle Integrale de Lokobe**,** 6.3 km ESE of Hellville, Antsiranana, Madagascar): Carapace dark brown with lateral thick lines of white scales. Abdomen dark with a median folium and yellowish lateral sides. First legs dark brown except tarsi which are yellow. All the other legs yellow. Metatarsi provided with one dark ventral spot that extended beyond the two metatarsal spines (Figs. 27A, 34A).

Total length: 5.92. Carapace length: 2.16. Abdomen length: 3.76. Cephalothorax width: 1.50. Width ocular field I: 1.16. Width ocular field III: 1.23. Height cephalothorax: 0.63.

Femur I/width ocular field III: 0.96. Femur III/width ocular field III: 0.66. Tibia I/width ocular field III: 0.85. Tibia III/tibia IV: 0.57. Patella III/tibia III: 1.11.

Promargins of the chelicerae pluridentate with two distal teeth and a sharp line. Retromargins pluridentate with six distal small teeth.

Genitalia: Epigynum having the copulatory openings not interconnected, and followed posteriorly by lateral sulci (tube connecting the copulatory openings to the posterior part of the epigynum). Spermathecae narrower.

Variation.— Female (n=5): total length: 5.26–5.92. Carapace length: 2.03–2.16. Abdomen length: 3.1–3.76. Cephalothorax width: 1.36–1.53. Femur I length: 1.18–1.44. Patella III/tibia III: 1.10–1.15.

Male.— Unknown.

Natural history.— Specimens were collected from rainforest by beating low vegetation.

Distribution.— Northern Madagascar.

***Padilla mihaingo* Andriamalala, sp. nov.**

Figures 27B–F, 34B–F.

Material examined.— Holotype: Madagascar: **Antsiranana Province:** Forêt d'Ampondrabe**,** 26.3 km NNE of Daraina, 175 m, 12º58′12″S, 49º42′E, 10 December 2003, tropical dry forest, general collecting by day Fisher/Griswold Arthropod survey team, 1♀ (CAS), CASENT9011958.

Etymology.— The species name is from the Malagasy word "mihaingo," which means "dressed up."

Diagnosis.— Distinguished from other females like *P. mitohy* by the following characters: (1) copulatory openings interconnected at the anterior part of the epigynum and not followed by lateral sulci, spermathecae are broader (Figs. 27D–F), (2) femur III dorsal without an additional promarginal distal spine like in *P. mitohy* and (3) width ocular field III narrower than width ocular field I (contrary to *P. mitohy*).

Description.— Female (Holotype from Forêt d'Ampondrabe**,** 26.3 km NNE of Daraina, Antsiranana, Madagascar): Coloration same as *P. mitohy* (Figs. 27B, 34B).

Total length: 5.52. Carapace length: 2.16. Abdomen length: 3.36. Cephalothorax width: 1.50. Width ocular field I: 1.16. Width ocular field III: 0.70. Height cephalothorax: 0.70.

Femur I/width ocular field III: 1.74. Femur III/width ocular field III: 1.22. Tibia I/width ocular field III: 1.51. Tibia III/tibia IV: 0.57. Patella III/tibia III: 0.91.

Promargins of chelicerae pluridentate with three distal teeth and a proximal sharp line; retromargins fissidentate with six points.

MALE.: Unknown.

NATURAL HISTORY.— Specimen was collected from tropical dry forest by general collecting by day.

DISTRIBUTION.— Northern Madagascar.

***Padilla foty* Andriamalala, sp. nov.**
Figures 34C–G.

MATERIAL EXAMINED.— HOLOTYPE: MADAGASCAR: **Antsiranana Province**: Reserve Integralle Naturelle de Lokobe**,** 6.3 km ESE of Hellville, 30 m, 13º25′10″S, 48º19′52″E, 19–24 March 2001, rainforest, beating low vegetation, J.J. Rafanomezantsoa et al., 1 ♀ (CAS), CASENT 9021859.

ETYMOLOGY.— The species name is from the Malagasy word "*foty,*" which means "white."

DIAGNOSIS.— Distinguished from *P. mitohy* and *P. mihaingo* by the following characters: (1) carapace without bands of white scales on lateral sides, (2) abdominal dorsum yellowish with thin lateral dark bands instead of a folium (Fig. 34C), (3) spinnerets not preceded with a plate, (4) copulatory openings not interconnected, spermathecae narrower, and sulci present (different from *P. mihaingo)* (Fig. 34G) and (5) femur III dorsal with an additional pro-marginal distal spine as *P. mihaingo*.

DESCRIPTION.— FEMALE (Holotype from Reserve Integralle Naturelle de Lokobe**,** 6.3 km ESE of Hellville, Antsiranana, Madagascar): Carapace yellowish white with brown lines on lateral sides. Abdomen dorsum whitish with two dark median lateral bands terminated by horizontal spots at posterior part, venter uniformly whitish. Spinnerets not preceded by a plate (Fig. 34G).

Total length: 4.96. Carapace length: 2.06. Abdomen length: 2.90. Cephalothorax width: 1.46. Width ocular field I: 1.20. Width ocular field III: 1.20. Height cephalothorax: 0.56.

Femur I/width ocular field III: 1.13. Femur III/width ocular field III: 0.73. Tibia I/width ocular field III: 0.88. Tibia III/tibia IV: 0.60. Patella III/tibia III: 0.92.

Retromargins of chelicerae pluridentate with five teeth, promargins pluridentate with three distal teeth and a proximal sharp line

MALE: Unknown.

NATURAL HISTORY.— The type specimen was collected from tropical rainforest by beating low vegetation.

DISTRIBUTION.— Northern Madagascar.

***Padilla boritandroka* Andriamalala, sp. nov.**
Figures 3G–H, 4A–b, 11A, 14E, 17A, 24B, 28D, 32A-B-C, 55.

MATERIAL EXAMINED.— HOLOTYPE: MADAGASCAR: **Antsiranana Province:** Reserve speciale Manongarivo, 10.8 km SW of Antanambao, 400 m, 13º57.7′S, 48º26′E, 8 November 1998, tropical rainforest, beating low vegetation, B.L. Fisher, 1♂ (CAS), CASENT 9020178. OTHER MATERIAL EXAMINED: MADAGASCAR: **Antsiranana Province:** Forêt d' Antsahabe, 11.4 km 275º W Daraina, 550m, 13º12′42″S, 49º33′24″E, 12 December 2003, Fisher/Griswold Arthropod team, 1♂ (CAS), CASENT9011931. Reserve special d'Ambre, 3.5 km 275º SW Sakaramy, 325 m, 12º28′8″S, 49º14′32″E, 26–31 January 2001, Fisher/Griswold Arthropod team, 1♂ (CAS), CASENT 9006821. Reserve special d'Ambre, 3.5 km 275º SW Sakaramy, 325 m, 12º28′8″S, 49º14′32″E, 26–31 January 2001, Fisher/Griswold Arthropod team, 1♂ (CAS), CASENT 9004544. Reserve special Manongarivo, 10.8 km 229º SW of Antanambao, 780 m, 13º57.7′S, 48º26.0′E, 12 October 1998, Fisher/Griswold Arthropod team, 1♂ (CAS), CASENT9020177. **Mahajanga Province:** Parc National Baie de Baly, 12.4 km 337º NNW of Soalala, 10 m, 16º0′36″S, 45º15′54″E, 26–30 June 2002, Fisher/Griswold

Arthropod team, 1♂ (CAS), CASENT3006885. Parc National Tsingy de Bemaraha, 10.6 km 123º ESE of Antsalova, 150 m, 19º42′34″S, 44º43′5″E, 16–20 June 2001, Fisher/Griswold Arthropod team, 1♂ (CAS), CASENT9009733.

Etymology.— The species name is from the Malagasy words "bory tandroka," which means "with short horns."

Diagnosis of the *Brevis* group.— Species within the *Brevis* group are distinguished from other male *Padilla* by having: (1) short horns that originate from the distal part of the chelicerae and which are straight (Figs. 3G–H, 14D–E), (2) chelicerae projecting forward and parallel to the carapace instead of perpendicular to it (Figs. 3G–H, 4A–b) and (3) paturons flattened dorsally with promarginal and retromarginal sharpened edges (Figs. 14D–E).

Diagnosis of *P. boritandroka*.— Male *P. boritandroka* are distinguished from male *P. ngeroka* by the following characters: (1) horns extremely short (horn length/carapace length: 0.02), more or less thick (horn width/horn length: 0.66), converging to each other, with the tips slightly oriented outward, horns arise from the apex of the chelicerae, near the fangs (Fig. 3G), (2) tibia of the first legs extremely fat and provided with a thick promarginal tuft of black hairs (tibia slightly wider than femur and bearing a proventral sparse fringe of black hairs in *P. ngeroka*), (3) patella and femur retrodistally with thick tuft of hairs and (4) promarginal teeth not very large as in *P. ngeroka*.

Description.— Male (Holotype from Réserve spéciale Manongarivo, 10.8 km SW of Antanambao, Antsiranana, Madagascar): Carapace dark or brown, sometimes with spots of white scales on lateral posterior margins. Top of the carapace brown yellowish, flattened, with two black spots. Abdomen dorsum generally brown to brown yellowish, with one median dark band followed laterally by two other dark lateral stripes. In some specimens the dorsum is covered with a dark scutum (sclerotized plate). Also, one pair of whitish spots or a tuft of white scales are sometimes observed on the anteromedian of the dorsum. First legs greatly enlarged and completely dark brown to black, except tarsi which are whitish. All the other legs whitish with lateral maculae (dark lateral patches) on femora and tarsi. Patella and tibia both with retroventral fringe of black hairs (Fig. 55). Top of the carapace and the abdomen are both flattened. Chelicerae longer than wide, dorsoventrally flattened, with sharpened lateral edges and bases widely separated from each other. Fangs long (14E).

Total length: 5.22. Carapace length: 2.16. Abdomen length: 3.06. Horn length/carapace length: 0.02. Horn width: 0.04. DH: 0.12. DH/CHL: 0.23. Width ocular field I: 1.20. Width ocular field III: 1.16. Height cephalothorax: 1.56. Diameter AME/length chelicerae: 0.95. Height cephalothorax/width cephalothorax: 0.52. Width cephalothorax/width ocular field III: 1.34.

Femur I/width ocular field III: 1.44. Femur III/width ocular field III: 0.70. Femur IV/Femur III: 1.29. Tibia I/width ocular field III: 1.27. Tarsi I/metatarsi I: 0.44.

Variation.— Male (n=5): total length: 4.66–5.22. Carapace length: 1.63–2.16. Abdomen length: 2.23–3.06. Diameter AME: 0.31–0.45. Femur I length: 1.16–1.68. Horn length/carapace length: 0.02–0.08. Horn width: 0.03–0.08.

Female: Unknown.

Natural history.— Specimens were collected from tropical dry forest and tropical rainforest by beating low vegetation and general collecting by day.

Distribution.— Western and northern Madagascar.

Padilla ngeroka Andriamalala, sp. nov.

Figures 3H, 4A–B, 11B, 14D, 17B, 32D–F, 34H, 45–46, 63.

Material examined.— Male holotype and female paratype: Madagascar: **Antananarivo**

Province: Andranomay**,** 11.5 km SSE of Anjozorobe, 1300 m, 18º28′24″S, 47º57′36″E, 5–13 December 2000, mountain rainforest, general collecting, Fisher/Griswold Arthropod survey team, 1♂ 1♀ (CAS), CASENT9004188. OTHER MATERIAL EXAMINED: MADAGASCAR: **Antananarivo Province**: Andranomay, 11.5 km SSE of Anjozorobe, 1300 m, 18º28′S, 47º57′36″E, 5–13 December 2000, Fisher/Griswold Arthropod Survey team, 1♂ (CAS), CASENT9025472. National Park Montagne d'Ambre, 2.79 air km NE of Parc entrance, 1000m, 12º32′S, 49º10′E, 21–30 November 1993, C. Griswold, N. Scharff, J. Coddington, S. Larcher, and R. Andriamasimanana, 5♂ 3♀ 1 juvenile (CAS), CASENT9021901 – 3♂ 2♀ (CAS), CASENT9020190 – 3♂ 4♀ (CAS), CASENT9020189. **Fianarantsoa Province**: National Park Ranomafana, N.P Maharira, below summit herb layer, 8 April 1992, S. Kariko and V. Roth, 1♂ MCZ, MCZ65435. National Park Ranomafana, 2.3 km N of Vohiparara village, 18 April 1998, C. Griswold, D. Kavanaugh, N. Penny, M. Raherilalao, E. Rajeriarison, J. Ranorianarisoa, J. Schweikert, and D. Ubick, 1♀ (CAS), CASENT9021864. National Park Ranomafana, Talatakely, 900 m, 21º15′S, 47º25′E, 5–7 July 1993, C. Griswold, N. Scharff, S. Larcher, and R. Andriamasimanana, 1♂ (CAS), CASENT 9020187.

ETYMOLOGY.— The species name is from the Malagasy expression "mainty ngeroka," which means completely dark or black.

DIAGNOSIS.— Distinguished from male *P. boritandroka* by having (1) the horns cylindrical, directed downwards and slightly longer, as long as one third of the carapace (horn length/carapace length: 0.26) (Figs. 3H, 4A–b, 14D), the horns arise from the distal part of the paturon, just above the fangs (slightly higher compared to *P. boritandroka,* Fig. 3H), (2) serrula not extending to the bases of endites, (3) tibiae of first legs are slightly wider than the femur and bear a sparse retroventral fringe of black hairs (tibiae are greatly enlarged and with a thick tuft of hairs in *P. boritandroka*) likewise femur I retrodistal and patella with sparse hairs (not with thick fringe as in *P. boritandroka)* and (4) promargins of the chelicerae pluridentate with four enormous teeth.

DESCRIPTION.— MALE (Holotype from Andranomay, 11.5 km SSE of Anjozorobe, Antananarivo, Madagascar): Both carapace and abdomen dark brown and flattened. Abdomen sometimes provided with dark sclerotized scutum. First legs completely dark except tarsi, the other legs yellowish (Fig. 63).

Total length: 4.75. Carapace length: 2.02. Abdomen length: 2.73. Horn length/carapace length: 0.26. Horn width: 0.1. DH: 0.12. DH/CHL: 0.26. Width ocular field I: 1.05. Width ocular field III: 1.10. Height cephalothorax: 0.57. Diameter AME/length chelicerae: 0.87.

Femur I/width ocular field III: 1.33. Femur III/width ocular field III: 0.60. Femur IV/Femur III: 1.36. Tibia I/width ocular field III: 1.09. Tarsi I/metatarsi I: 0.38. Height cephalothorax/width cephalothorax: 0.42. Width cephalothorax/width ocular field III: 1.21.

Dentition same as *P. boritandroka,* but promarginal teeth very large.

VARIATION.— MALE (n=3): total length: 4.63–5.06. Carapace length: 1.93–2.06. Abdomen length: 2.70–3. Femur I length: 1.44–1.52. Horn length/carapace length: 0.19–0.26. Horn width: 0.08–0.1.

FEMALE (Paratype from Andranomay**,** 11.5 km SSE of Anjozorobe, Antananarivo, Madagascar**):** Females are quite different from males. Both carapace and abdomen yellowish with dark lateral bands that are interrupted at their posterior parts (different from other female *Padilla*). Carapace flattened on its top and with a white guanine deposit on the anterior region. Female abdomen not flattened, and longer and broader.

Total length: 4.46. Carapace length: 1.73. Abdomen length: 2.73. Cephalothorax width: 1.71. Width ocular field I: 0.95. Width ocular field III: 0.95. Height cephalothorax: 0.46.
Femur I/width ocular field III: 0.76. Femur III/width ocular field III: 0.589. Tibia I/width ocular field III: 0.57. Tibia III/tibia IV: 0.63. Patella III/tibia III: 0.96.

Promargins of chelicerae pluridentate with four teeth and a proximal sharp line, retromargins pluridentate with six teeth.

Genitalia: copulatory openings not interconnected at their anterior part. Septum present. On the posterolateral part, the fertilization ducts are straight, short, parallel, and continued with two small spermathecae (that are close to each other, Fig. 34H).

Variation.— Female (n=5)**:** total length: 6.42–6.93. Carapace length: 3.06–3.33. Abdomen length: 3.26–3.73. Cephalothorax width: 2.43–2.63. Femur I length: 2.10–2.38. Patella III/tibia III: 1.073–1.162.

Natural history.— Specimens were collected from mountain forest by beating low vegetation.

Distribution.— Northern Madagascar (Figs. 45–46).

Nomina dubia

Padilla glauca Simon, 1900: The type could not be located at the Muséum National d'Histoire Naturelle de Paris, and Simon's (1900) description does not provide sufficient detail to recognize this species.

Padilla lancearia Simon, 1900: The type could not be located at the Muséum National d'Histoire Naturelle de Paris, and Simon's (1900) description does not provide sufficient detail to recognize this species.

Padilla mantis Simon, 1900: The type could not be located at the Muséum National d'Histoire Naturelle de Paris, and Simon's (1900) description does not provide sufficient detail to recognize this species.

Excluded species

Padilla javana Simon, 1900: The type could not be located at the Muséum National d'Histoire Naturelle de Paris, and Simon's (1900) description does not provide sufficient detail to recognize this species. Fortunately, Prószyński (2003) has examined other specimens of this southeast Asian species. *Padilla javana* lacks the extraordinary embellishments (horns) that are synapomorphic for all male *Padilla* (Prószyński, 2003), and therefore this species, from Java, is excluded from *Padilla*.

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Illustrations (Figures 2–63) and Appendicies 1–4

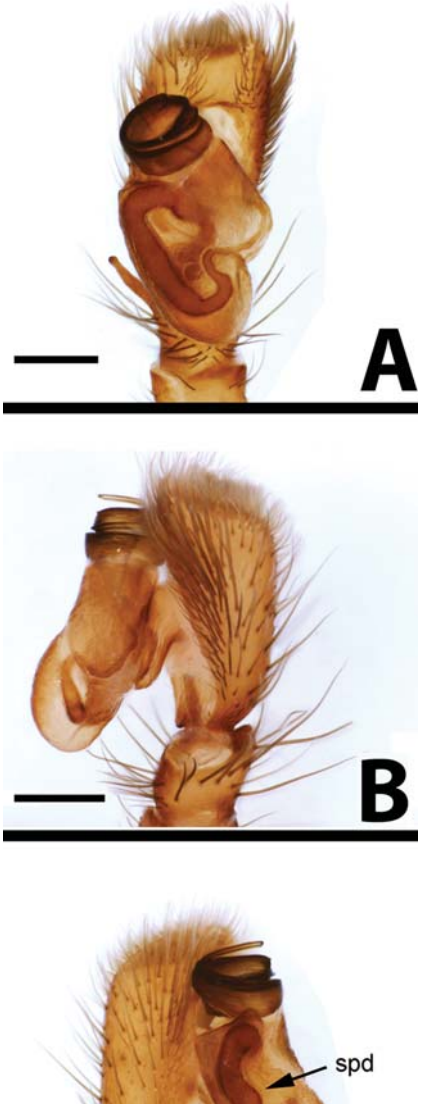


FIGURE 2. *Padilla lavatandroka*, expanded right palp. A. palp, ventral. B. palp, prolateral. C. palp, retrolateral. Scale bars for all = 0.2 mm.

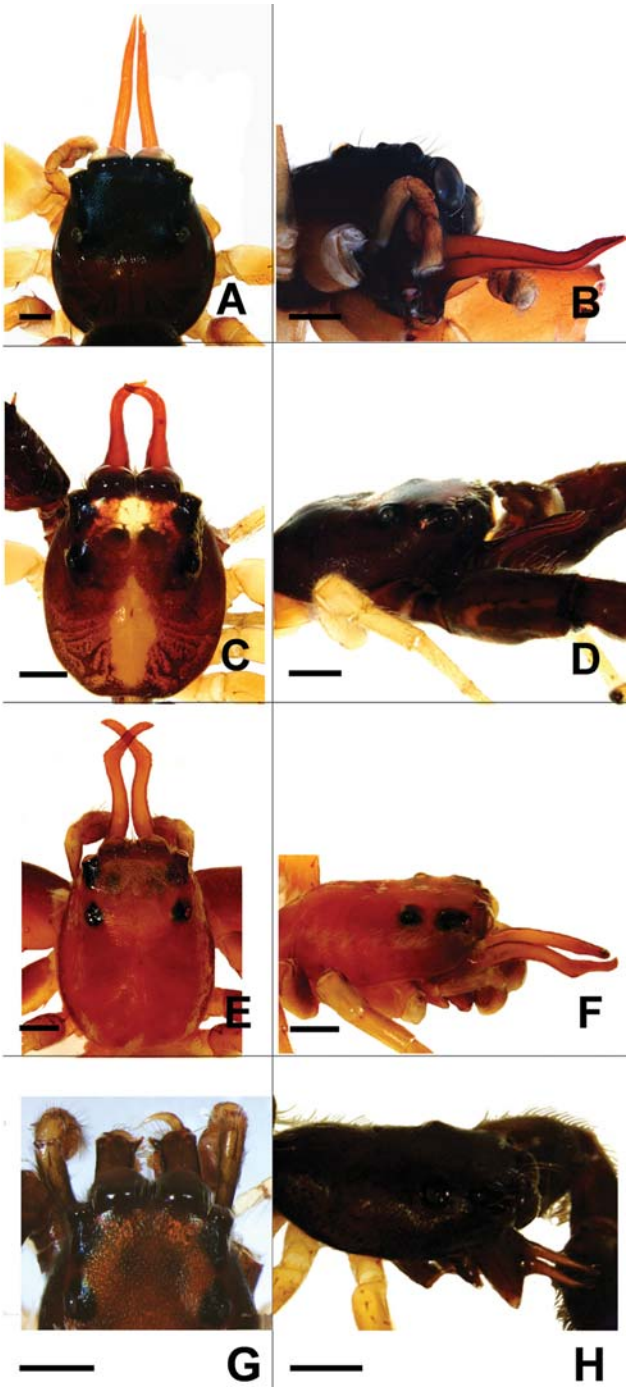


FIGURE 3. Male horn orientation dorsal and lateral view. A. *P. manjelatra*, carapace, dorsal. B. carapace, lateral. C. *P. mazavaloha*, carapace, dorsal. D. carapace, lateral. E. *P. armata* carapace, dorsal. F. carapace lateral. G. *P. boritandroaka* carapace, dorsal. H. *P. ngeroka* carapace, lateral. Scale bars for A, B, C, D, E, F = 0.5 mm.

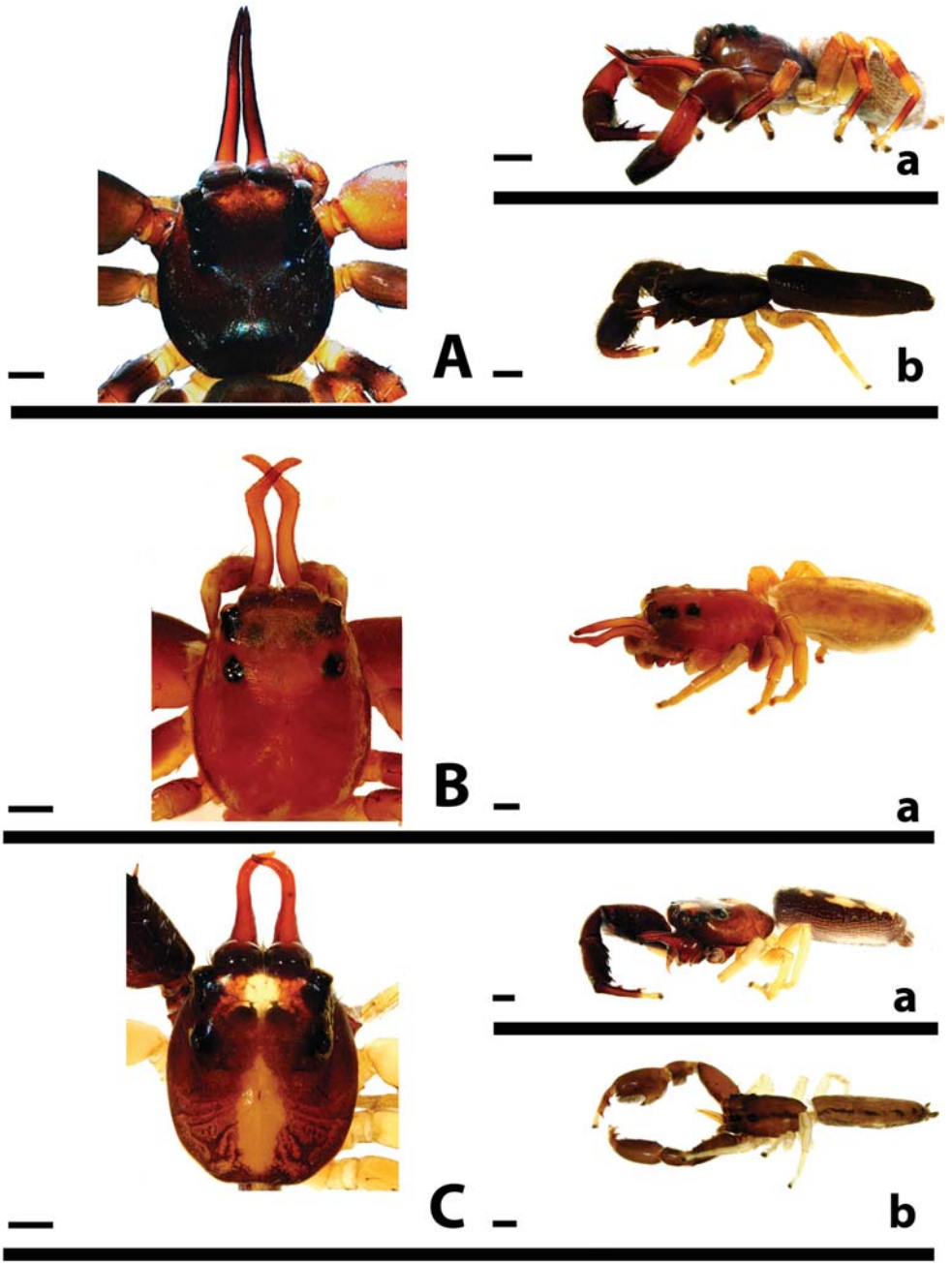


FIGURE 4. *Padilla* horn orientation, body shape. A. *P. lavatandroka*, horn, dorsal, straight. a. laterally is showing a double curve with tips upward; body protruding. b. *P. boritandroka*, laterally going downward; body flattened. B. *P. armata*, horn, dorsal, having a double curve. a. laterally going downward; body intermediate. C. *P. mazavaloha*, horn, dorsal, curving outward, and then inward, with tips crossed to each other. a. *P. mazavaloha*, horn, laterally going upwards with tips surpassing ½ eye diameter; body intermediate. b. *P. maingoka*, horn same orientation, but body flattened. Scale bars for A, B, C = 0.5 mm, all a, b = 0.5 mm.

FIGURE 5. *P. cornuta*, habitus, dorsal. Scale = 1 mm.

FIGURE 6. *P. manjelatra*, habitus, dorsal. Scale = 1 mm.

FIGURE 7. *P. lavatandroka*, habitus, dorsal. Scale = 1 mm.

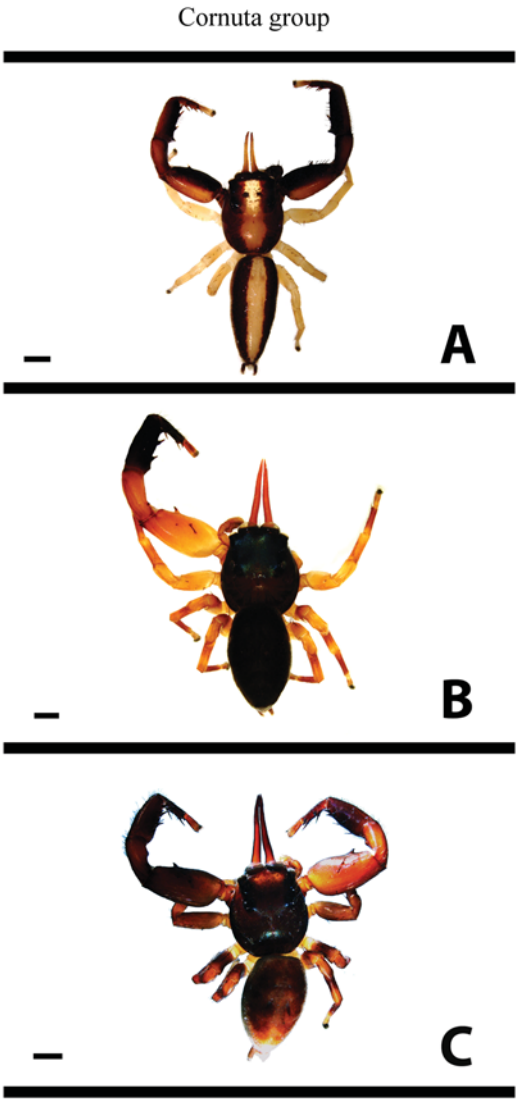


FIGURE 8. *Cornuta* group habitus, dorsal view. A. *P. cornuta*, habitus, dorsal. B. *P. manjelatra,* habitus, dorsal. C. *P. lavatandroka*, habitus, dorsal. Scale bars for A, B, C = 1 mm.

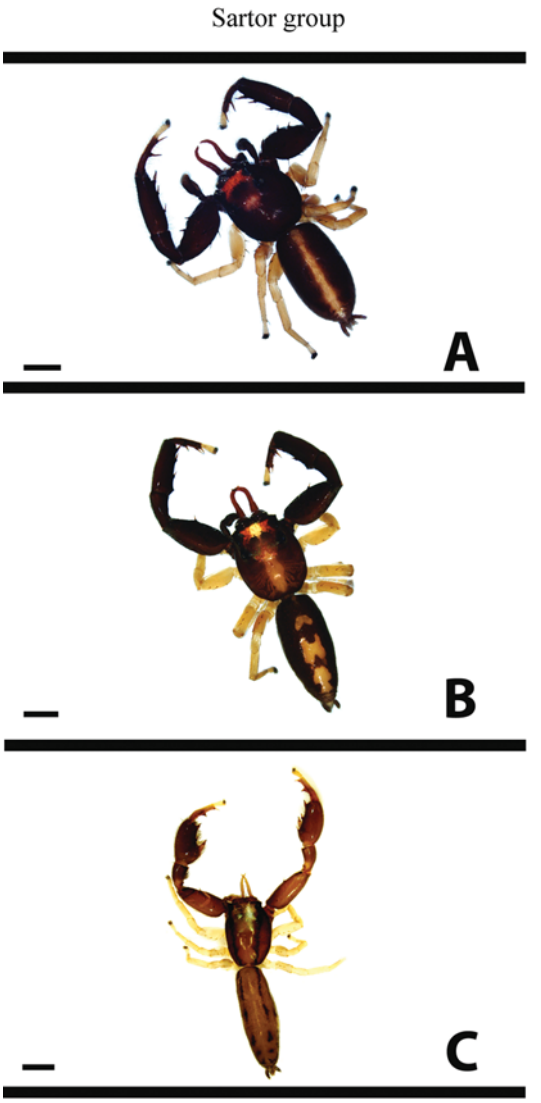


FIGURE 9. *Sartor* group habitus, dorsal view. A. *P. sartor*, habitus, dorsal. B. *P. mazavaloha*, habitus dorsal. C. *P. maingoka*, habitus, dorsal. Scale bars for A, B, C = 1 mm.

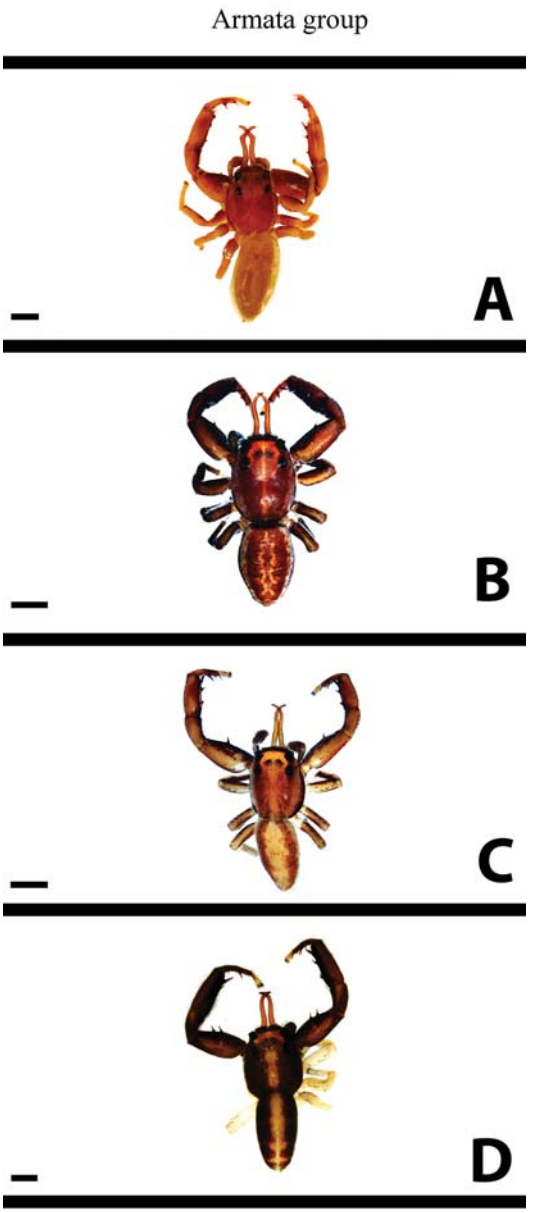


FIGURE 10. *Armata* group habitus, dorsal view. A. *P. armata*, habitus, dorsal. B. *P. griswoldi*, habitus, dorsal. C. *P. astina*, habitus, dorsal. D. *P. ombimanga*, habitus, dorsal. Scale bars for A, B, C, D = 1 mm.

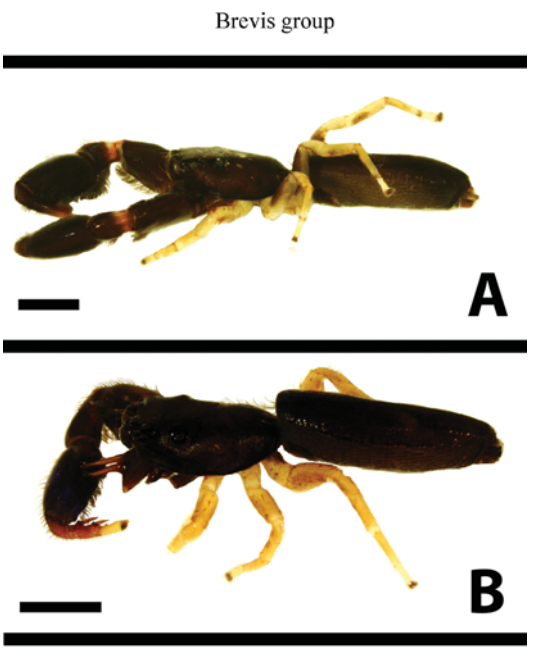


FIGURE 11. *Brevis* group, habitus, lateral view. A. *P. boritandroka*, habitus, lateral. B. *P. ngeroka*, habitus, lateral. Scale bars for A, B = 1 mm.

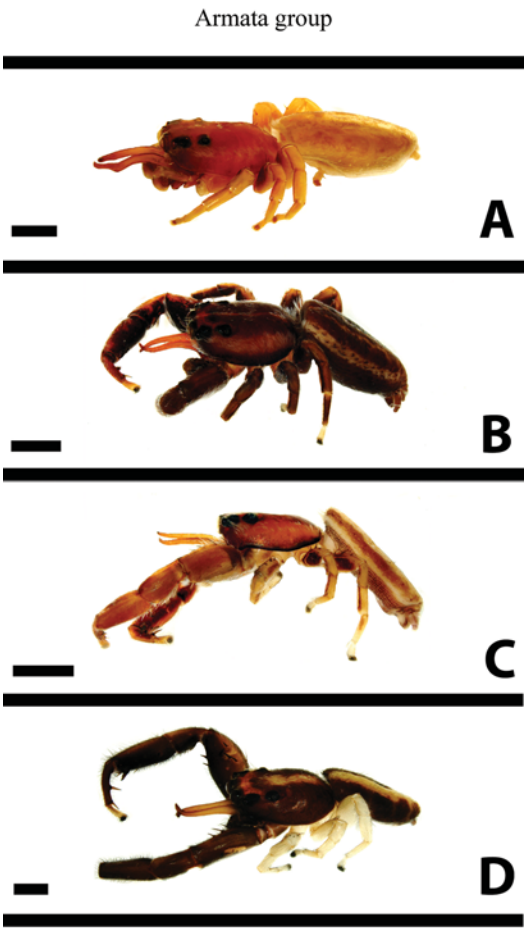


FIGURE 12. *Armata* group, habitus, lateral view. A. *P. armata*, habitus, lateral. B. *P. griswoldi*, habitus, lateral. C. *P. astina*, habitus, lateral. D. *P. ombimanga*, habitus, lateral. Scale bars for A, B, C, D = 1 mm.

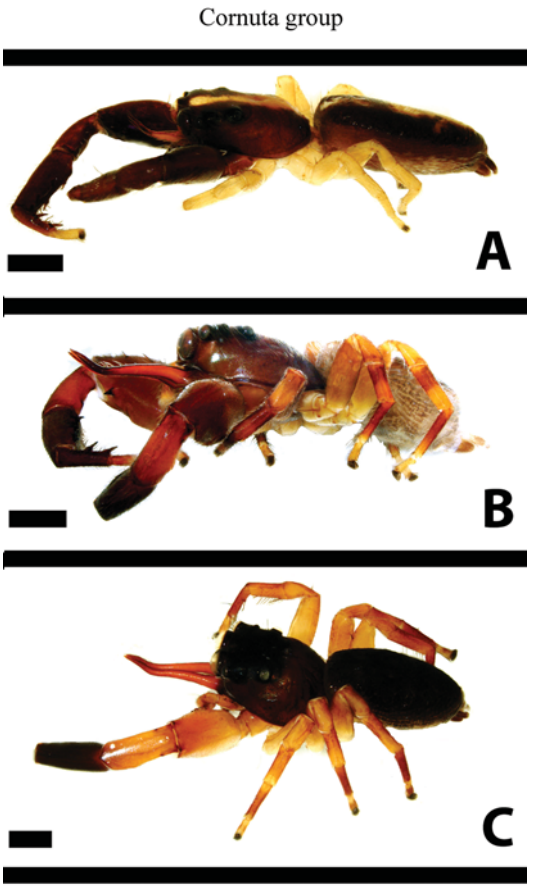


FIGURE 13. *Cornuta* group, habitus, lateral view. A. *P. cornuta*, habitus, lateral. B. *P. lavatandroka*, habitus, lateral. C. *P. manjelatra*, habitus lateral. Scale bars for A, B, C = 1 mm.

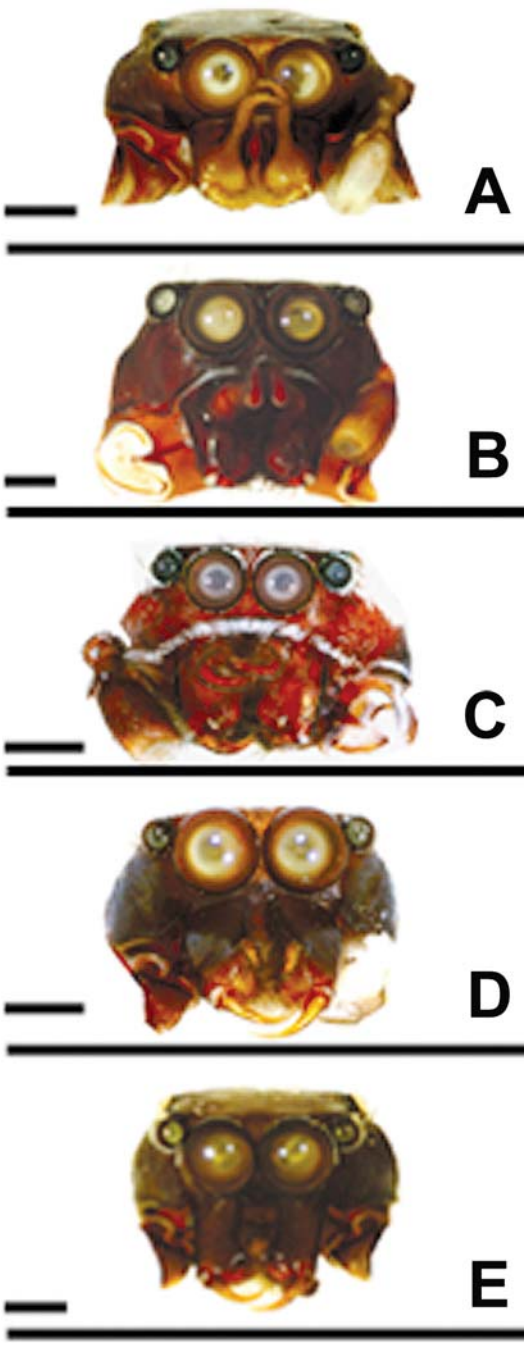


FIGURE 14. Male carapace, front view. A. *P. maingoka*, carapace, front. B. *P. lavatandroka*, carapace, front. C. *P. astina*, carapace, front. D. *P. ngeroka*, carapace, front. E. *P. boritandroka*, carapace, front. Scale bars for A, B, C, D, E = 0.35 mm.

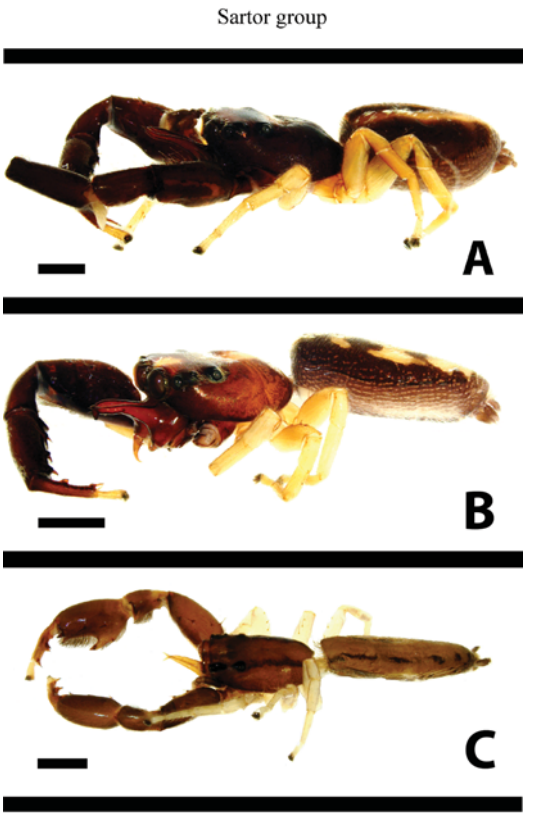


FIGURE 15. *Sartor* group, habitus, lateral view. A. *P. sartor*, habitus, lateral. B. *P. mazavaloha*, habitus, lateral. C. *P. maingoka*, habitus, lateral. Scale bars for A, B, C = 1 mm.

FIGURE 16. *P. sartor*, habitus, dorsal. Scale bar = 1 mm.

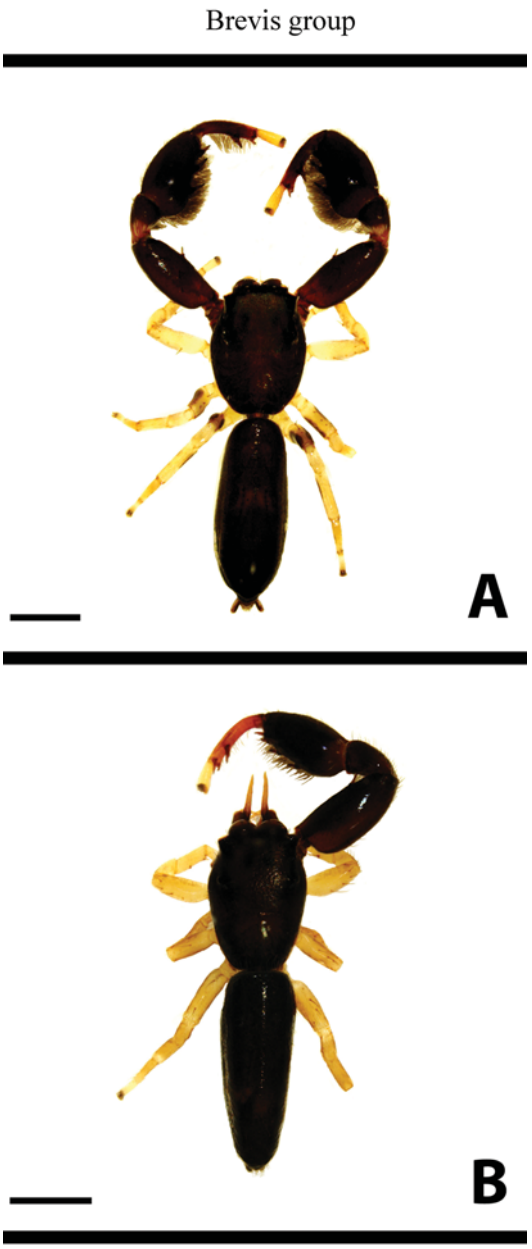


FIGURE 17. *Brevis* group, habitus, dorsal view. A. *P. boritandroka*, habitus, dorsal. B. *P. ngeroka*, habitus, dorsal. Scale bars for A, B = 1 mm.

FIGURE 18. *P. armata,* habitus, dorsal. Scale bar = 1 mm.

FIGURE 19. *P. griswoldi*, habitus, dorsal. Scale bar = 1 mm.

FIGURE 20. *P. astina*, habitus, dorsal. Scale bar = 1 mm.

FIGURE 21. *P. ombimanga*, habitus, dorsal. Scale bar = 1 mm.

FIGURE 22. *P. mazavaloha*, habitus, dorsal. Scale bar = 1 mm.

FIGURE 23. *P. maingoka*, habitus, dorsal. Scale bar = 1 mm.

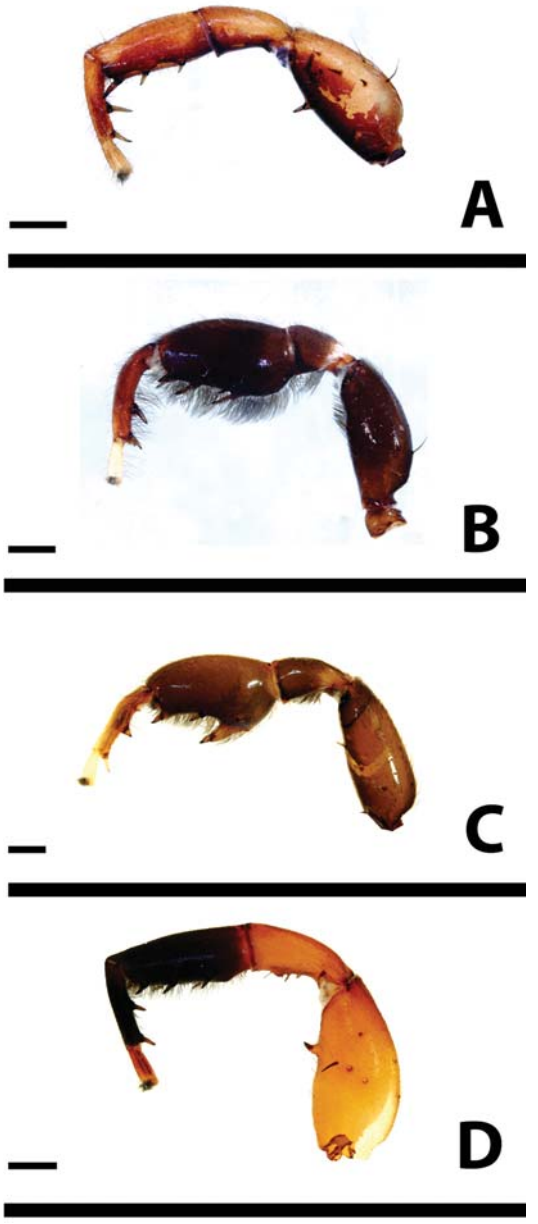


FIGURE 24. *Padilla* front legs, dorsal view. A. *P. astina*, leg I, dorsal. B. *P. boritandroka*, leg I, dorsal. C. *P. maingoka*, leg I, dorsal. D. *P. manjelatra*, leg I, dorsal. Scale bars for all = 0.5 mm.

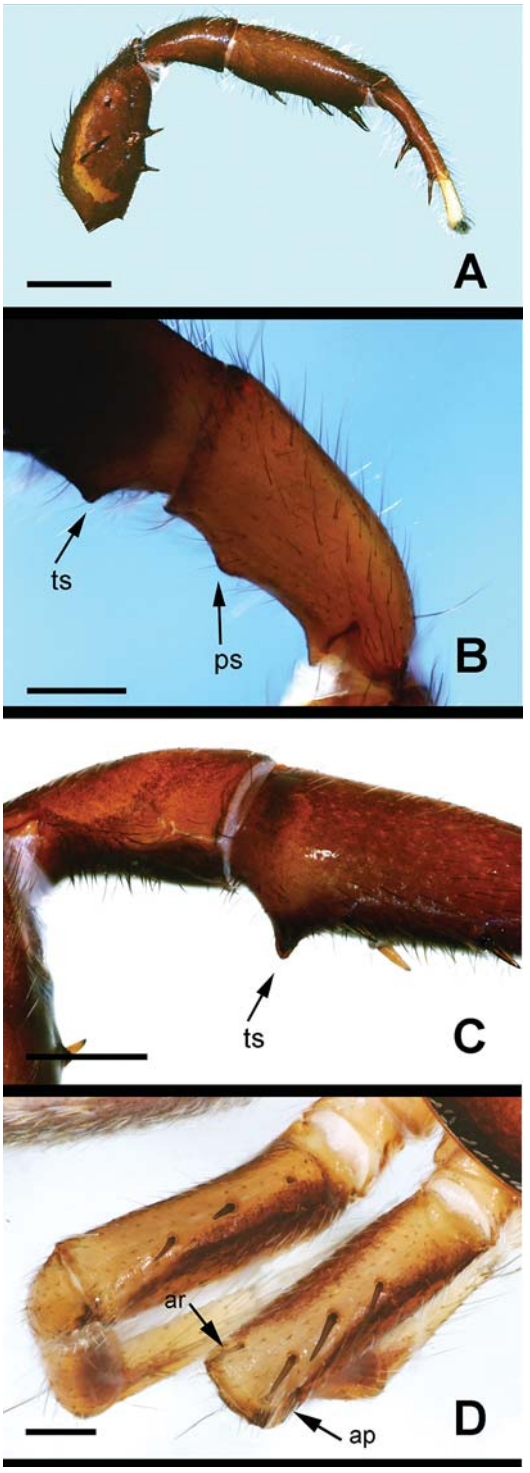


FIGURE 25. *Padilla* leg spinations. A. *P. sartor*, femur I, two proventral spines. B. *P. manjelatra*, Tb1 and Pt1 spurs. C. *P. cornuta*, Tb1 spur. D. *P. griswoldi*, F3 and F4 1/1/1 dorsal spine arrangement, additional promarginal and retromarginal spine. Scale bars for A = 1 mm, B, C = 0.5 mm, D = 0.2 mm.

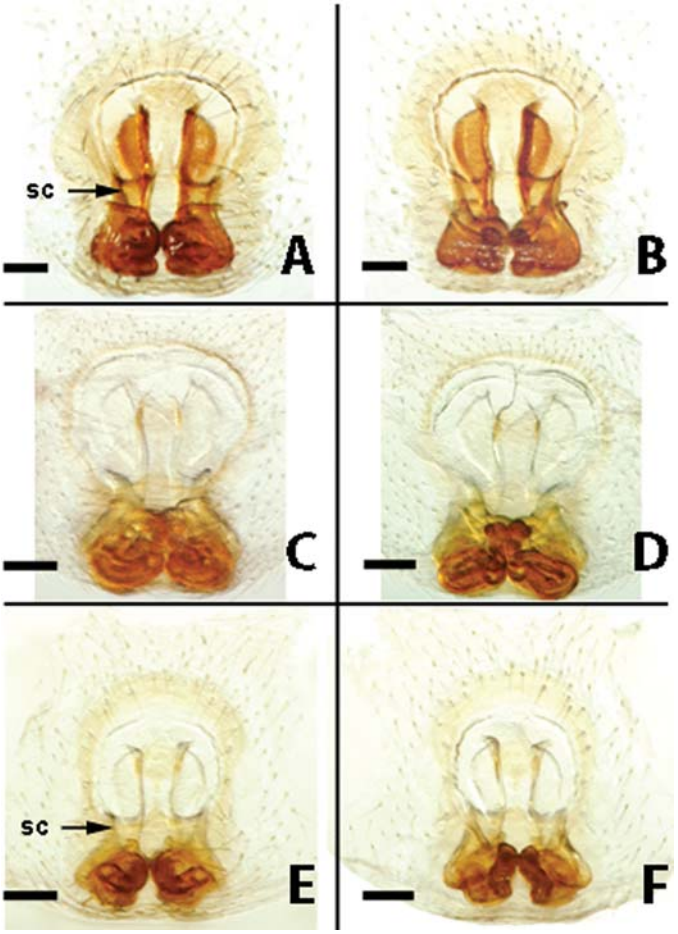


FIGURE 26. *Padilla* female epygina. A. *P. mitohy*, epyginum, ventral. B. epyginum, dorsal. C. *P mihaingo*, epyginum, ventral. D. epyginum, dorsal. E. *P. foty*, epyginum, ventral. F. epyginum, dorsal. Scale bars for A, B, C, D, E, F = 0.2 mm.

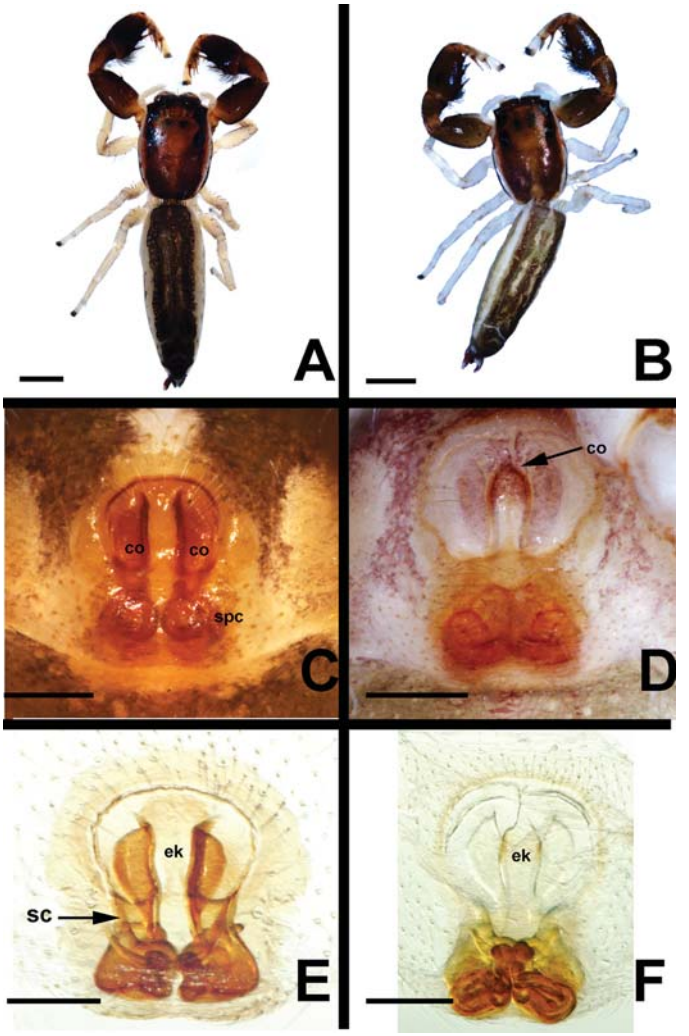


FIGURE 27. *P. mitohy*, *P. mihaingo*, habitus, dorsal, epyginum. A. *P. mitohy*, habitus, dorsal. B. *P. mihaingo*, habitus, dorsal. C. *P. mitohy* epyginum, ventral. D. *P. mihaingo*, epyginum, ventral. E. *P. mitohy*, epyginum, dorsal. F. *P. mihaingo*, epyginum, dorsal. Scale bars for A, B = 1 mm, C, D = 0.3 mm, E, F = 0.2 mm.

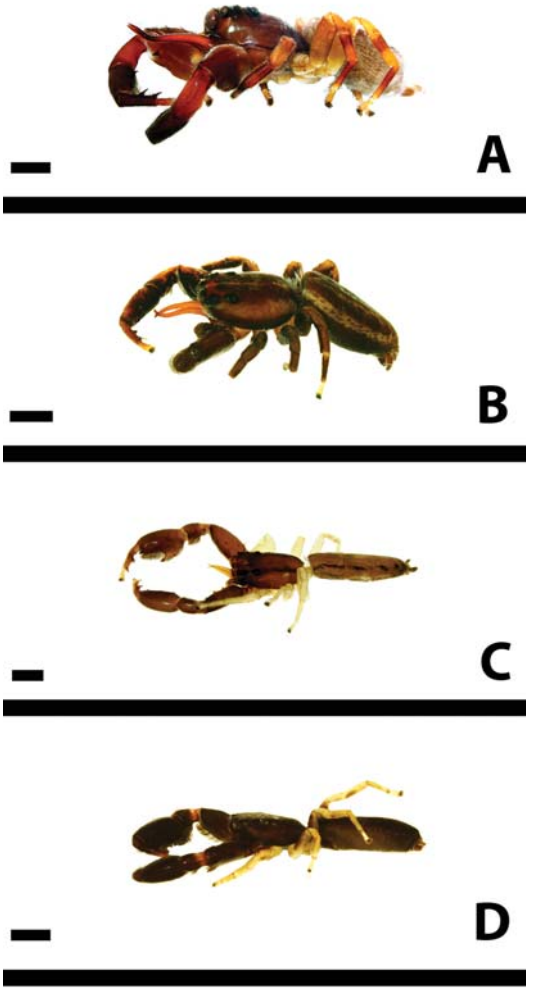


FIGURE 28. Male habitus, lateral view showing the difference in body shape and carapace height. A. *P. lavatandroka*, habitus, lateral ("hopper"). B. *P. griswoldi*, habitus, lateral ("intermediate"). C. *P. maingoka*, habitus, lateral. D. *P. boritandroka*, habitus, lateral (both "runner"). Scale bars for A, B, C, D = 1 mm.

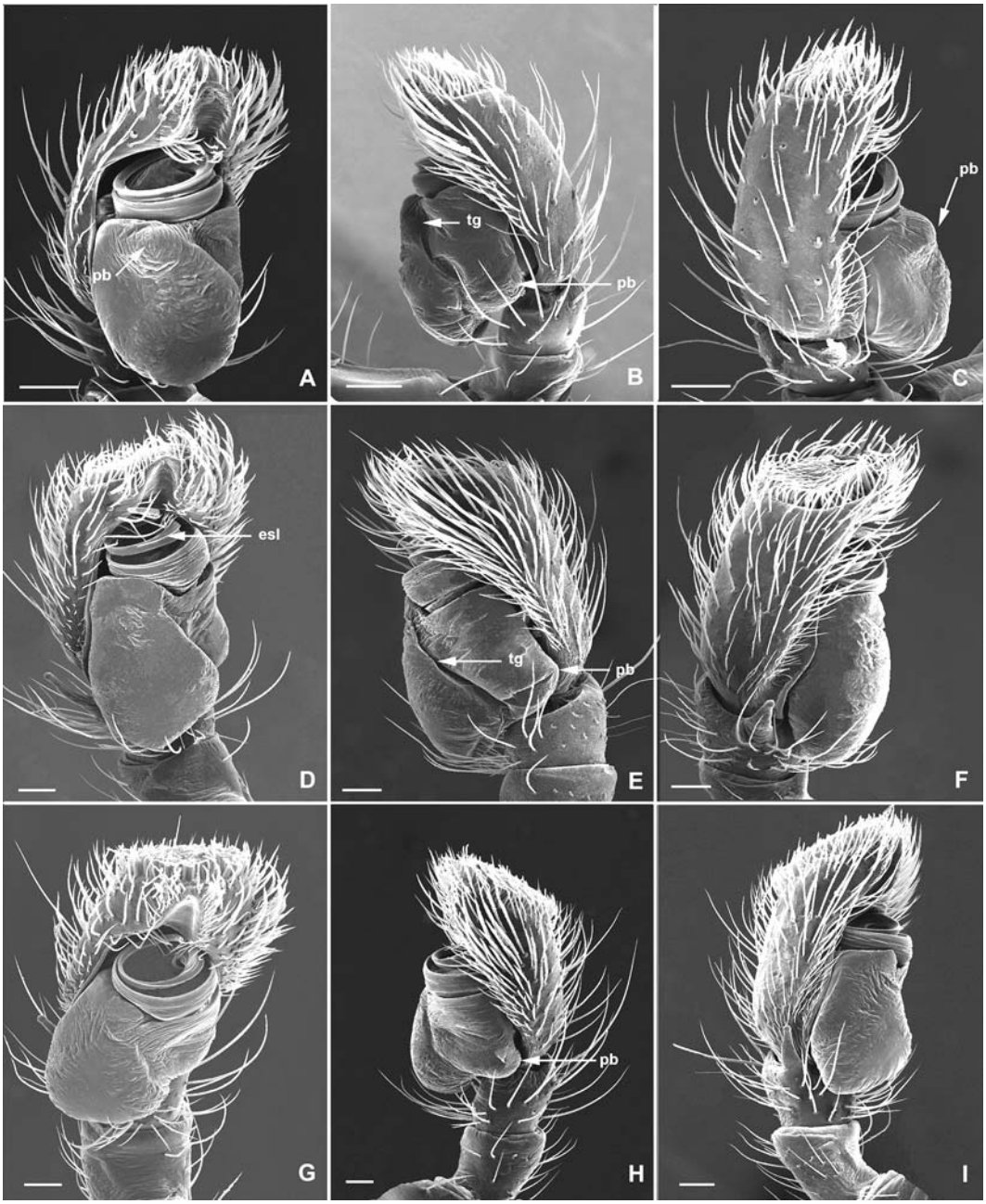


FIGURE 29. *Cornuta* group palps. A. *P. cornuta*, right palp, ventral. B. prolateral. C. retrolateral. D. *P. manjelatra*, right palp, ventral. E. palp, prolateral. F. palp, retrolateral. G. *P. lavatandroka*, right palp, ventral. H. palp, prolateral. I. palp, retrolateral. Scale bars C = 30 µm, A, E, F = 20 µm, B , D, G, H, I = 10 µm.

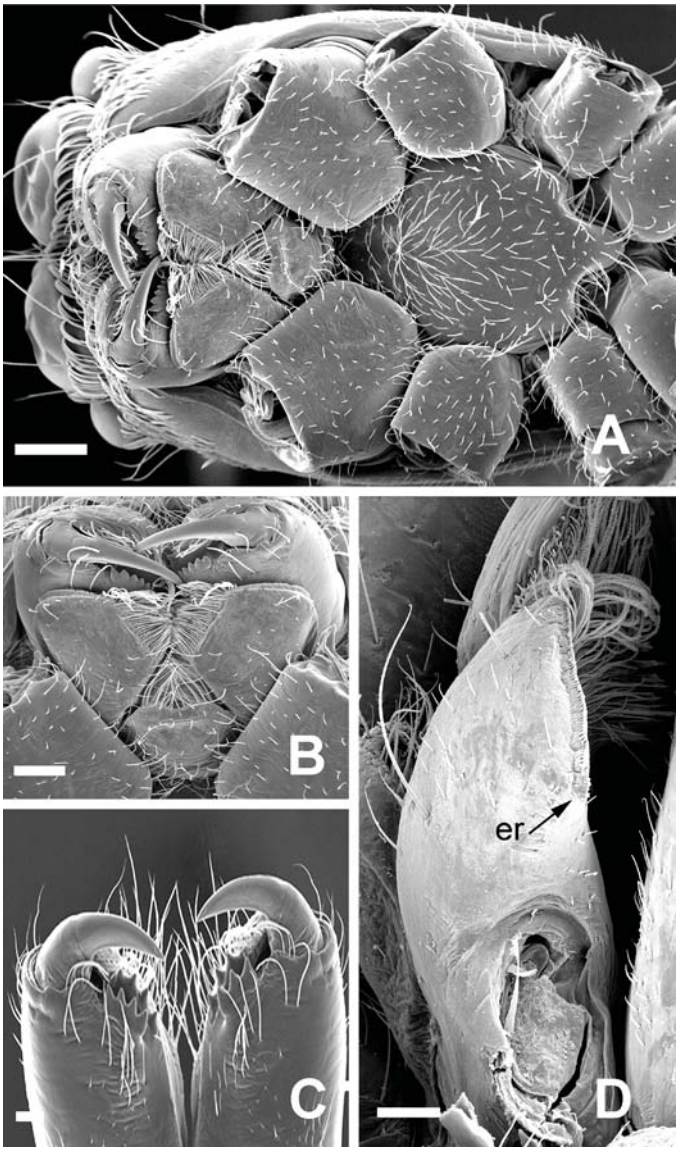


FIGURE 30. *Padilla* mouth parts. A. *P. lavatandroka*, sternum. B. endites, labium, teeth, fangs. C. teeth, fangs, retromargin. D. endite, serrula extending till the base of endite. Scale bars for A = 200 μm, B, C, D = 100 μm.

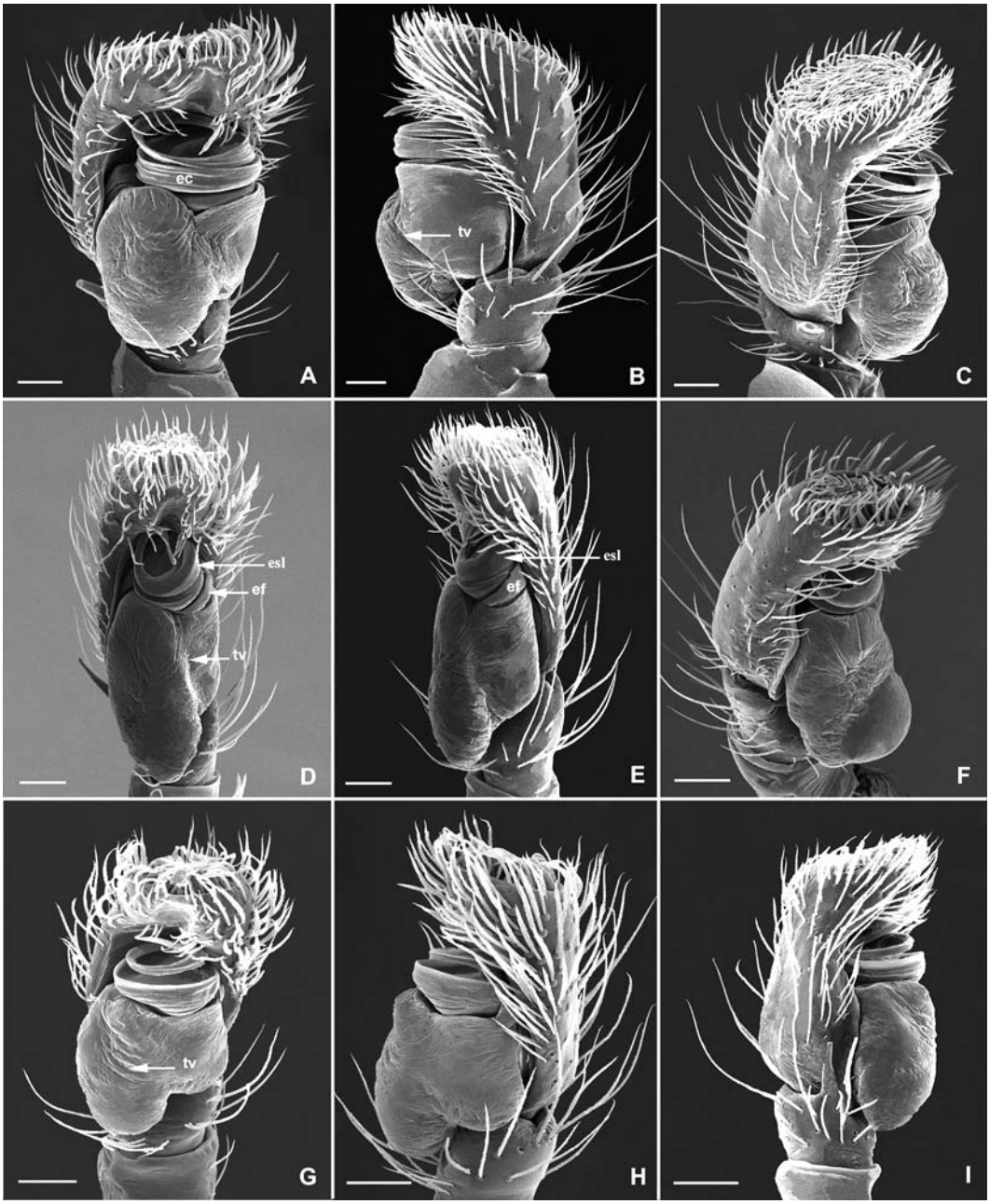


FIGURE 31. *Sartor* group palps. A. *P. sartor*, right palp, ventral. B. prolateral. C. retrolateral. D. *P. mazavaloha*, left palp, ventral. E. prolateral. F. retrolateral. G. *P. maingoka*, right palp, ventral. H. prolateral. I. retrolateral. Scale bars for A, B, C = 100 μm, D, E, F, G, H, I = 30 μm.

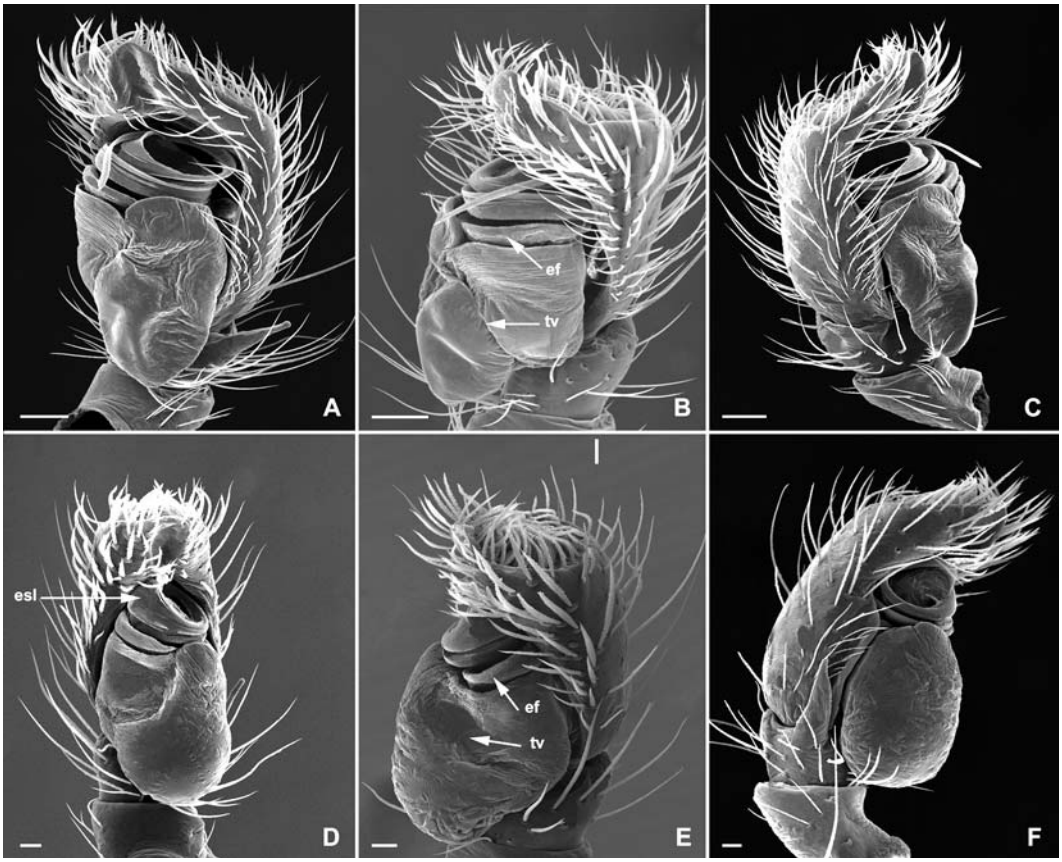


FIGURE 32. *Brevis* group palps. A. *P. boritandroka*, left palp, ventral. B. prolateral. C. retrolateral. D. *P. ngeroka*, left palp, ventral. E. prolateral. F. retrolateral. Scale bars for all = 0.2 mm.

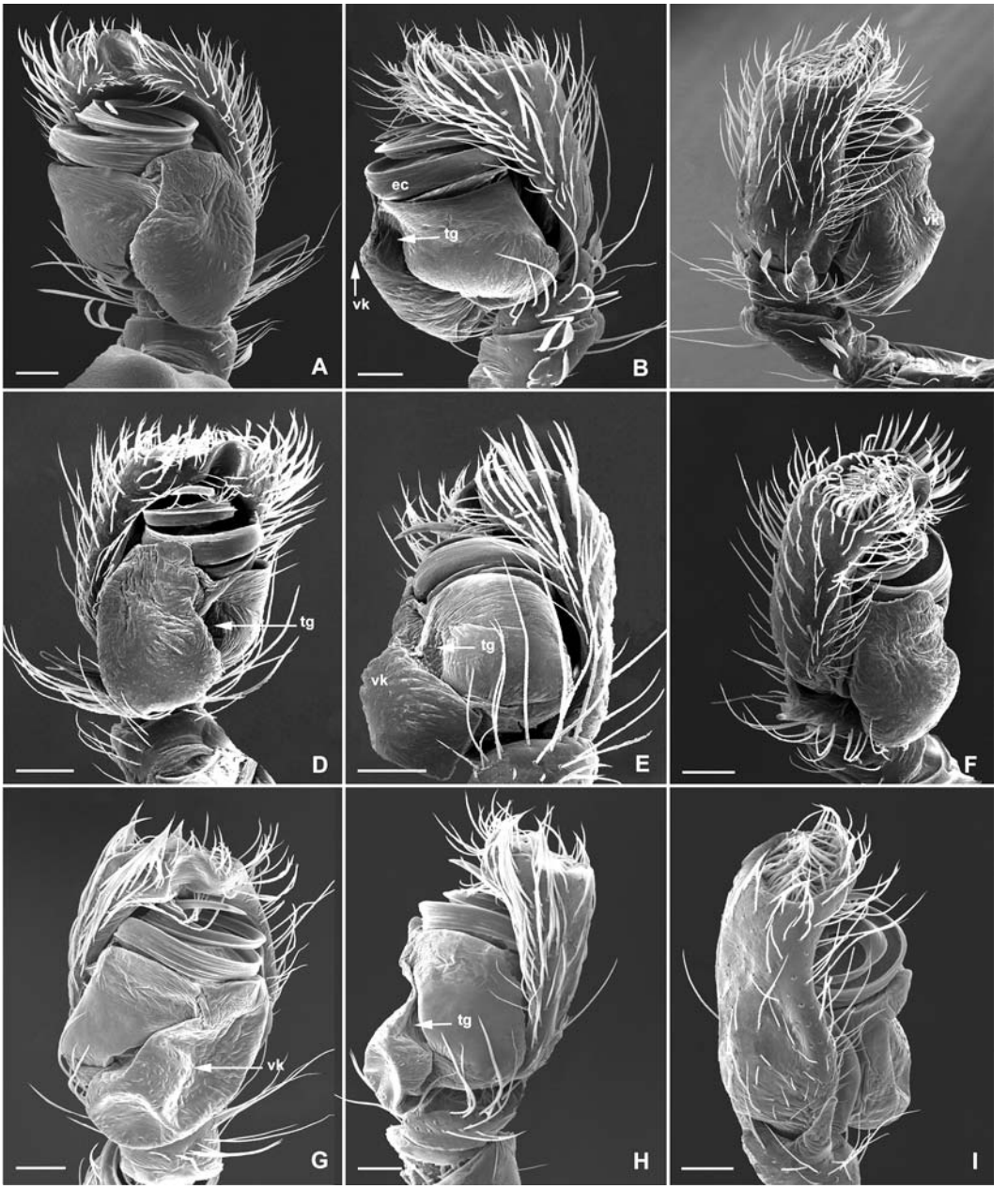


FIGURE 33. *Armata* group palps. A. *P. griswoldi*, right palp, ventral. B. prolateral. C. retrolateral. D. *P. astina*, left palp ventral. E. prolateral. F. retrolateral. G. *P. ombimanga*, right palp, ventral. H. prolateral. I. retrolateral. Scale bars for A, B, C = 30 μm, D, E, F = 20 μm, G, H, I = 10 μm.

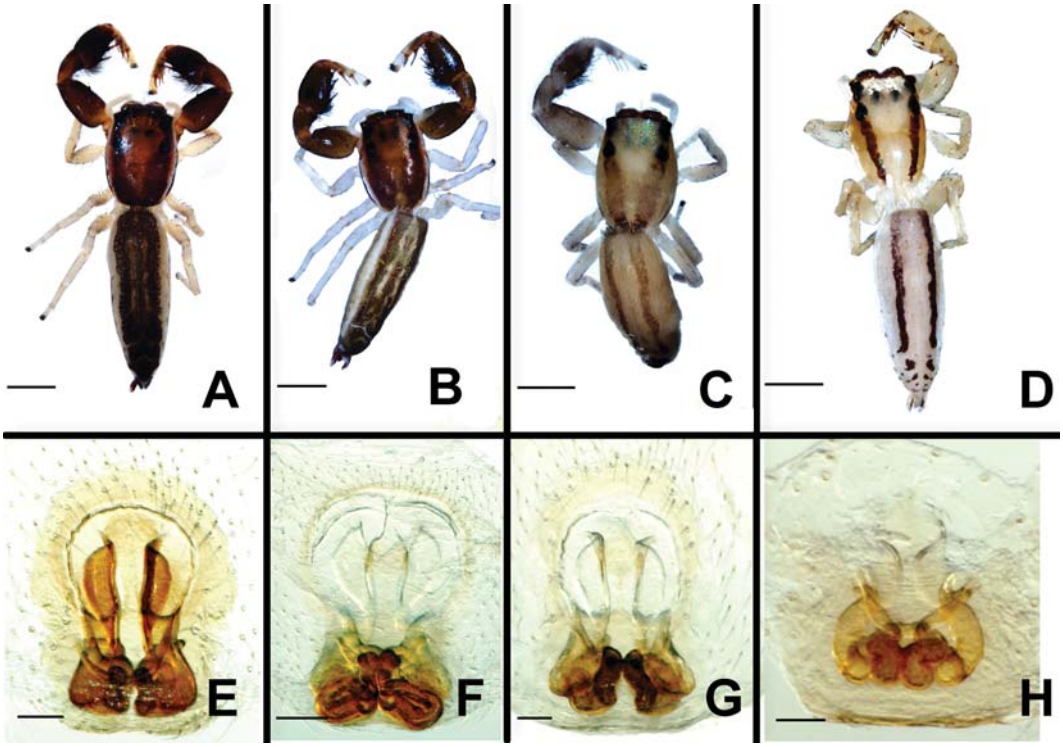


FIGURE 34. Female *Padilla* habitus, dorsal view, epygina dorsal view. A. *P. mitohy*, habitus dorsal. E. epyginum, dorsal. B. *P. mihaingo*, habitus, dorsal. F. epyginum, dorsal. C. *P. foty*, habitus dorsal. G. epyginum, dorsal. D. *P. ngeroka*, habitus dorsal. H. epyginum, dorsal. Scale bars for A, B, C = 1 mm, D, E, F, G, H = 0.2 mm.

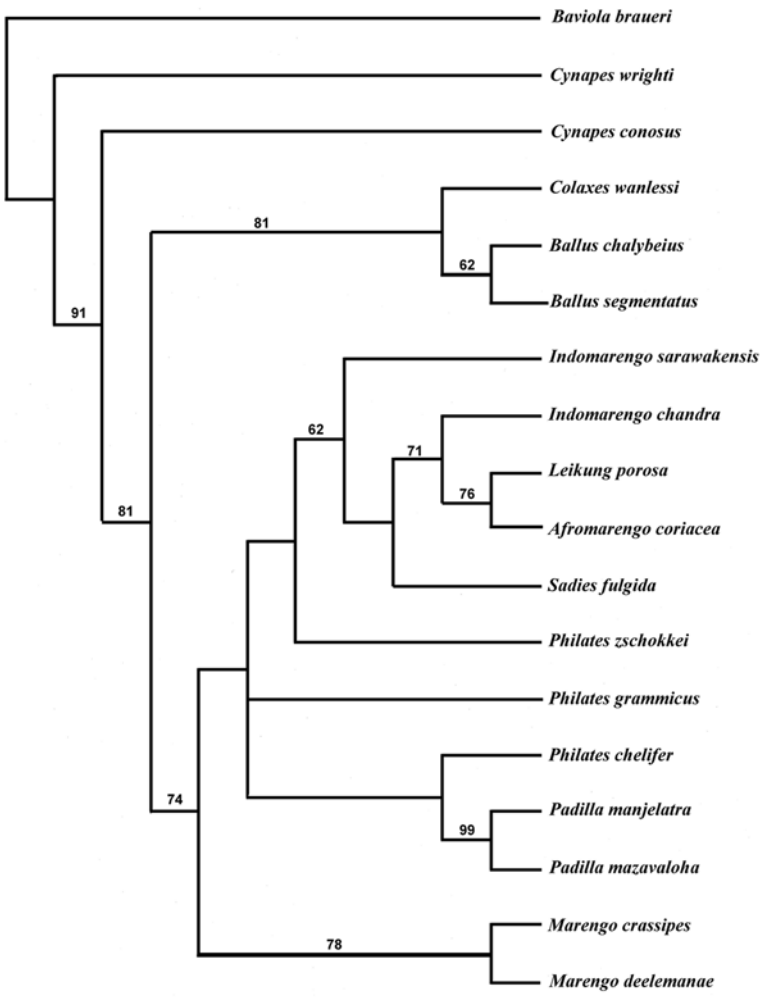


FIGURE 35. Placements of *Padilla* within the Ballinae morphology cladogram (Benjamin, 2004) based on parsimony analysis of 42 morphological characters. Strict consensus of 3 most parsimonious trees, L = 40.68, CI = 0.77, RI = 0.83, HI= 0.22.

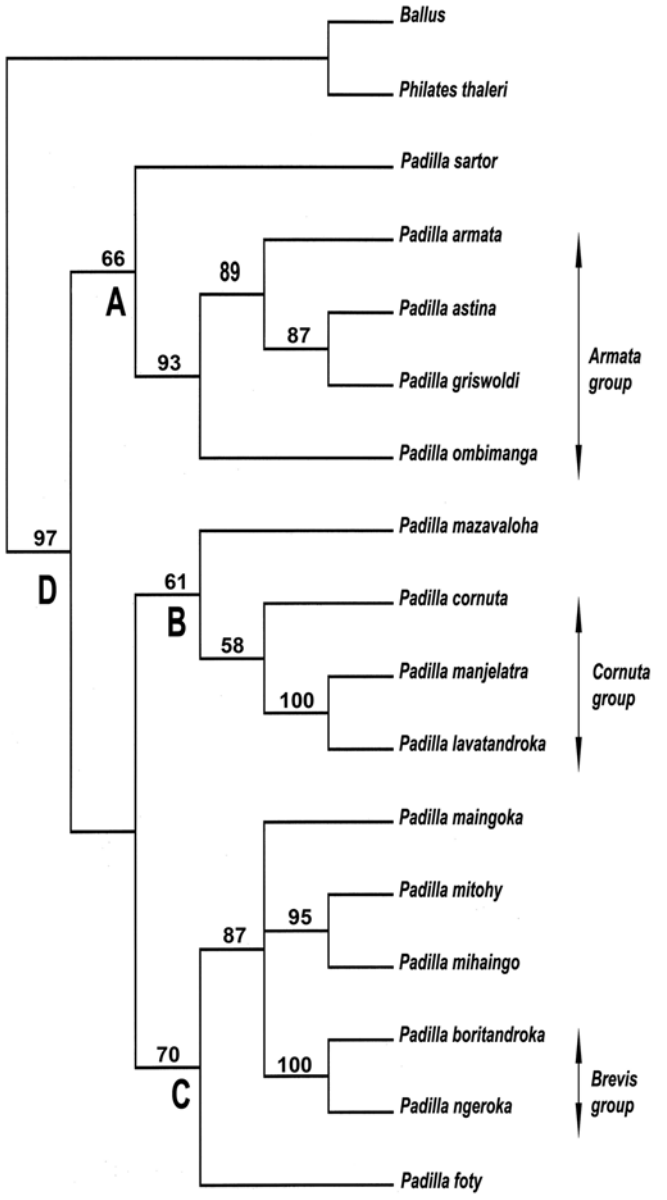


FIGURE 36. Phylogenetic relationships among *Padilla* species based on parsimony analysis of 38 morphological characters. Strict consensus of 3 most parsimonious trees, L = 33.74, CI = 0.82, RI = 0.89, HI = 0.17. Bootstrap values are shown in bold below branches on the cladogram.

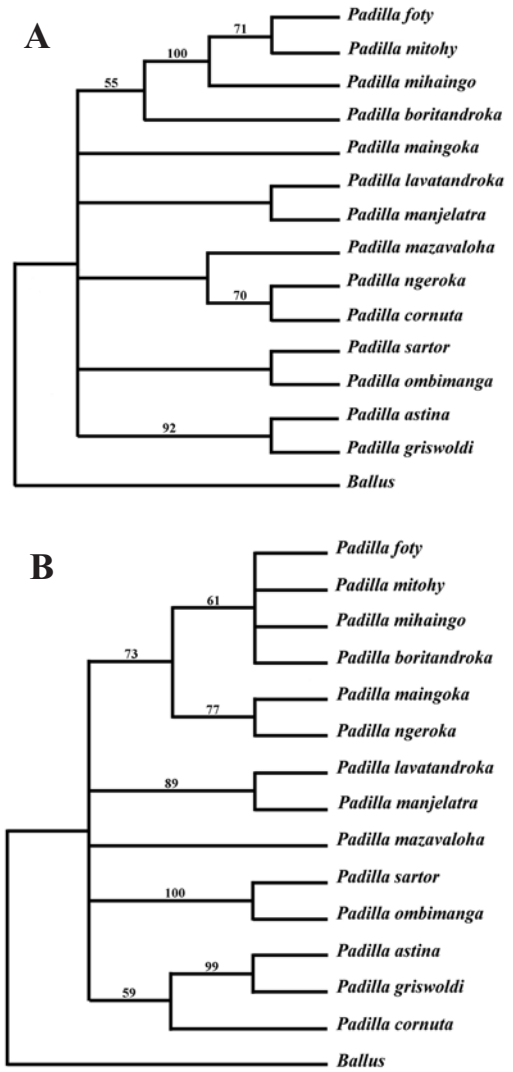


FIGURE 37. Phylogenetic relationships among *Padilla* species based on parsimony. A. analysis of 378 bp of COI gene. Strict consensus of 5 most parsimonious trees, L= 215, CI = 0.61, RI = 0.58. B. analysis of 759 bp of 28S gene. Strict consensus of 2 most parsimonious trees, L= 165, CI = 0.77, RI = 0.71. Bootstrap values are shown in bold below branches on the cladogram.

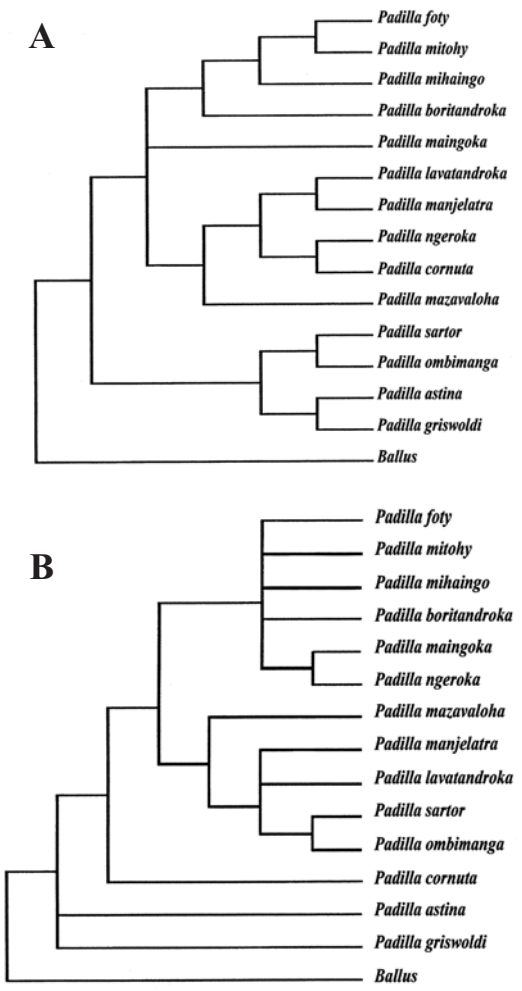


FIGURE 38. Phylogenetic relationships among *Padilla* species based on maximum likelihood analysis using GTR+I+G model, phylogeny from: A. COI gene, 1 tree, –ln L= 1614.30907. B. 28S gene, strict consensus of 6 trees, –ln L= 1879.24764

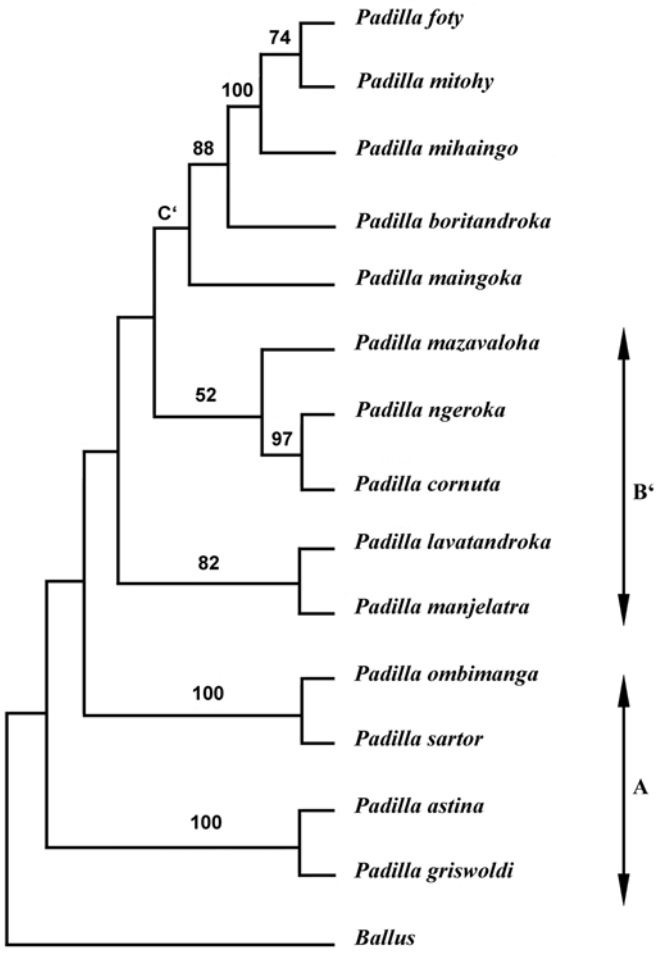


FIGURE 39. Phylogenetic relationships among *Padilla* species based on parsimony analysis of the combained 1137 bp of COI and 28S genes. One tree of L= 436, CI= 0.64, RI= 0.58.

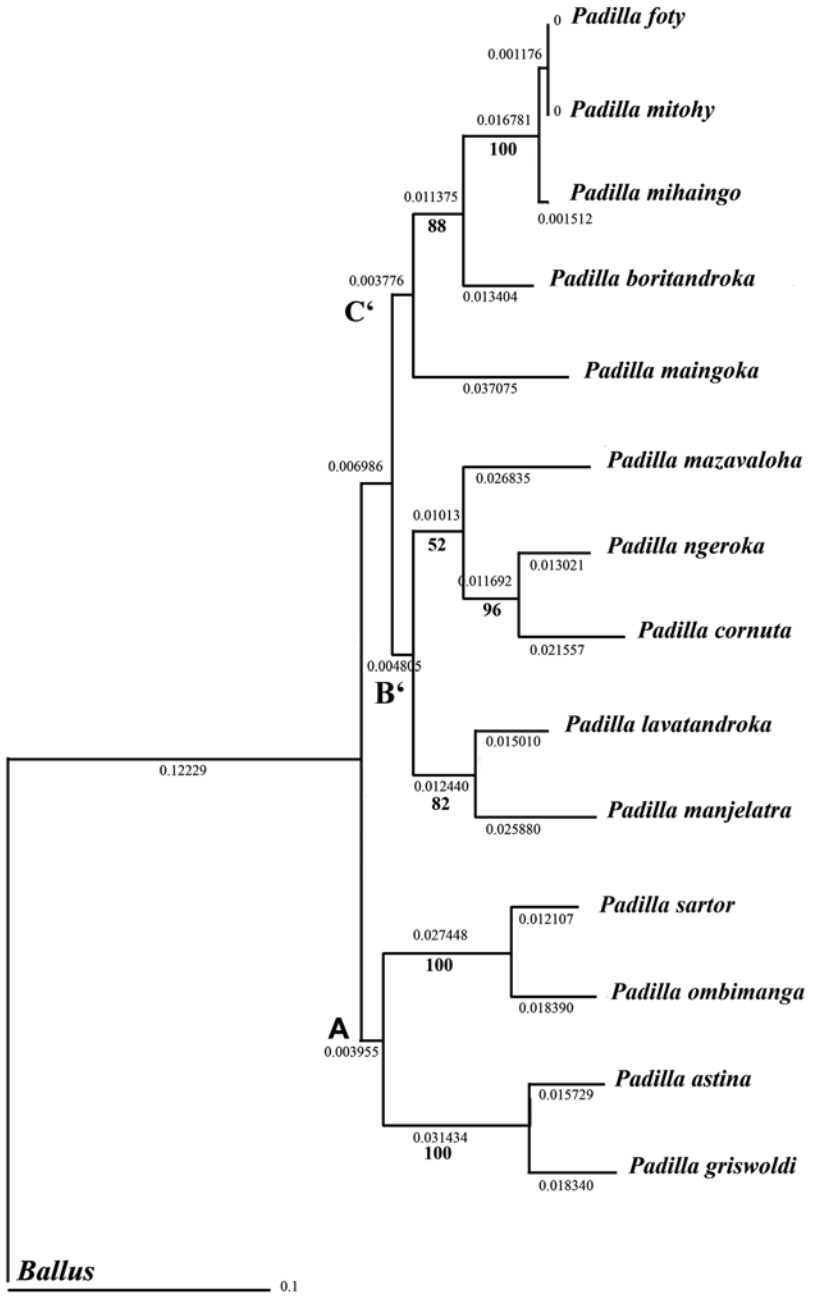


FIGURE 40. Phylogenetic relationships among *Padilla* species based on maximum likelihood analysis using GTR+I+G model, phylogeny from the combained 1137 bp of COI and 28 genes. One tree, -ln L = 3771.21431.

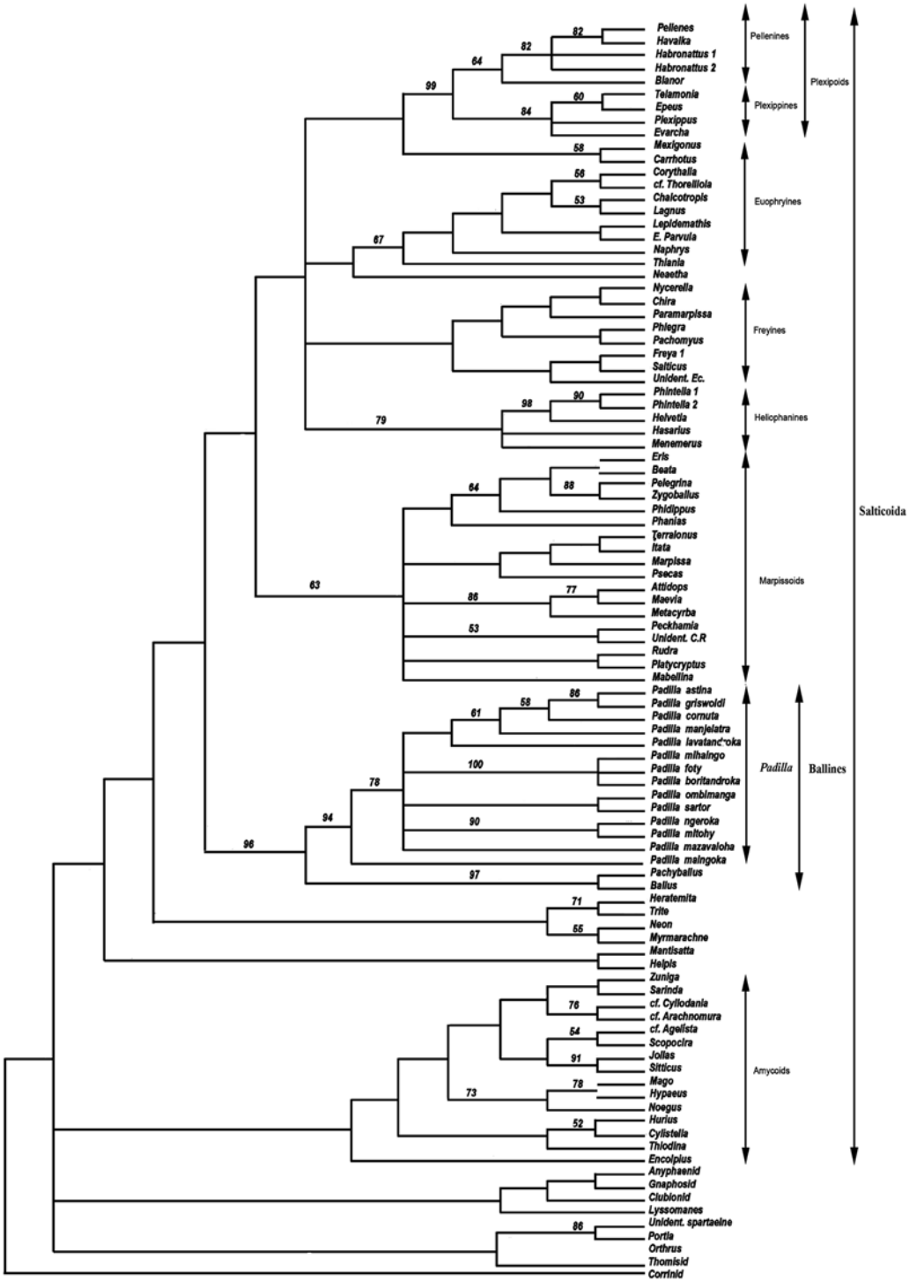


FIGURE 41. Placement of *Padilla* within the 28S Salticidae phylogeny (Hedin and Maddison 2003). Analysis based on parsimony, 35 most parsimonious trees, L= 5222.

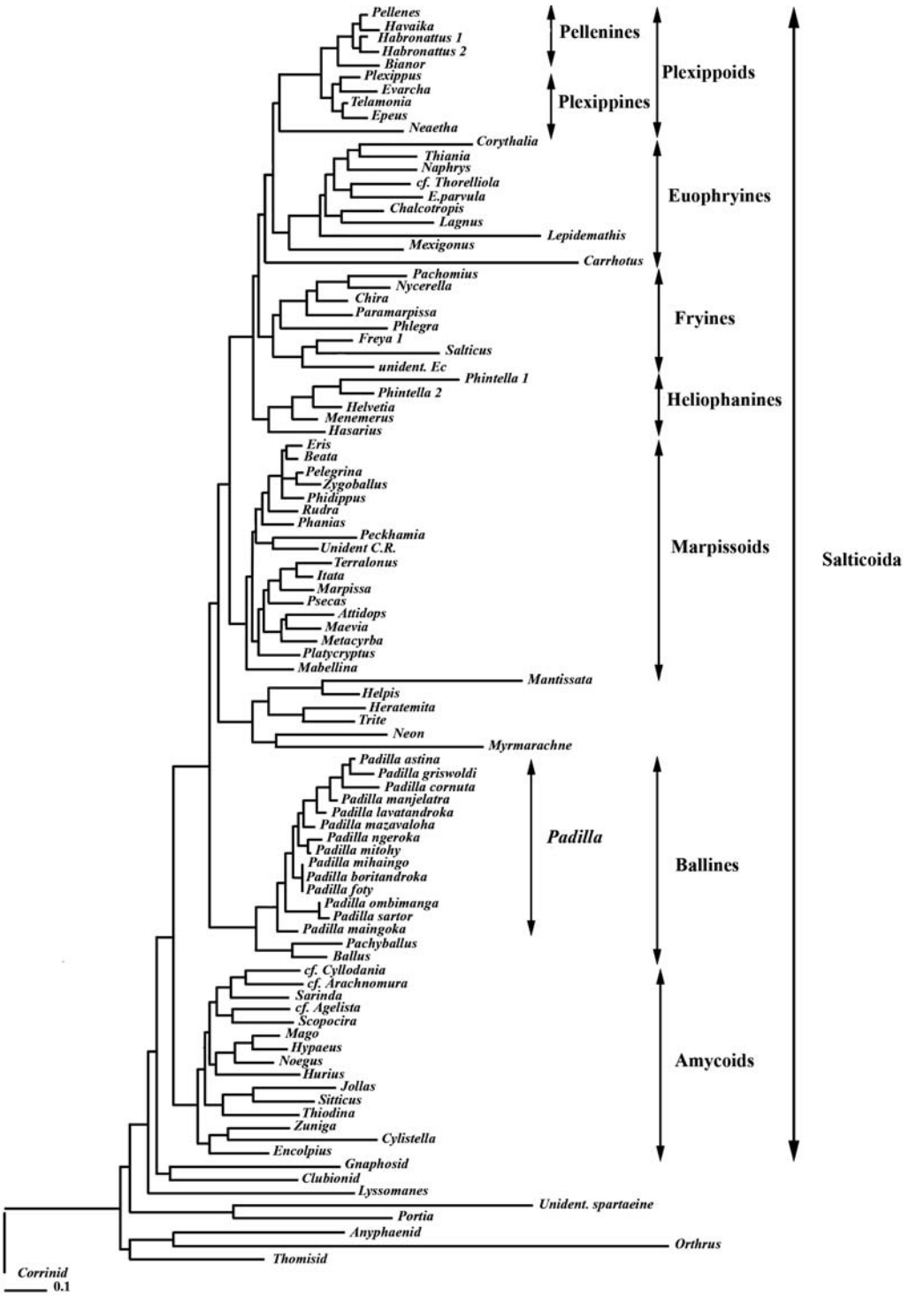


FIGURE 42. Placement of *Padilla* within the 28S Salticidae phylogeny (Hedin and Maddison 2003). Analysis based on maximum likelihood using GTR+G+I model. 1 tree, -ln L = 22284.10856.

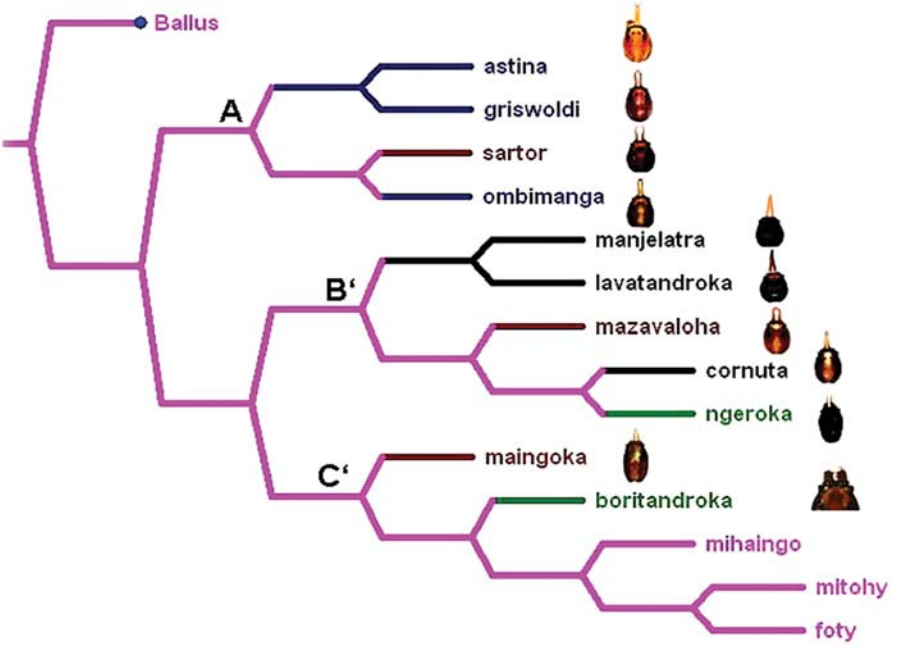


FIGURE 43. Horn curvature mapped on the combained COI and 28S maximum likelihood phylogeny. Convergent evolution of the horn in *Padilla.* Key: Armata group, blue; Sartor group, red; Cornuta group, black; Brevis group, green; unassigned and outgroup, purple.

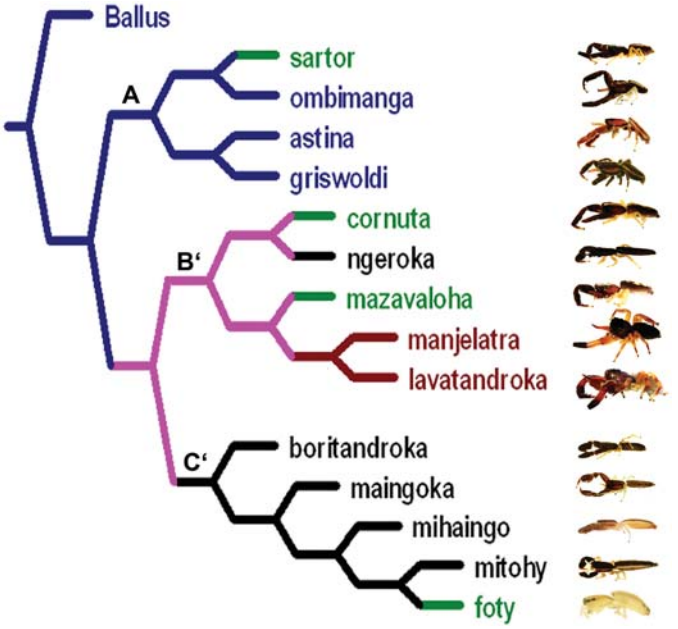


FIGURE 44. Body shape and life styles mapped on the combained COI and 28S maximum likelihood phylogeny. Convergent evolution of the body shape in *Padilla.* Key: elongate-intermediate, green; beetle-like intermediate, blue; scorpion-like runners, black; protruding hoppers, red.

Sympatric Sister Species

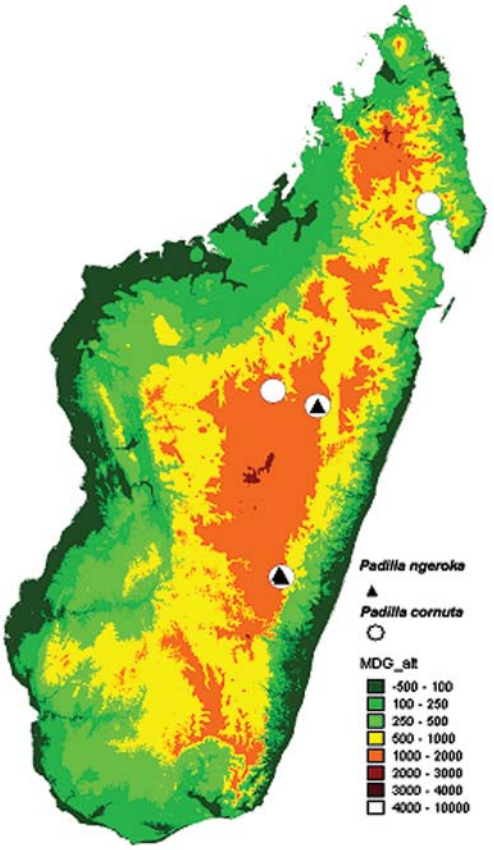


FIGURE 45. Altitudinal distribution map for *P. cornuta* and *P. ngeroka* clade.

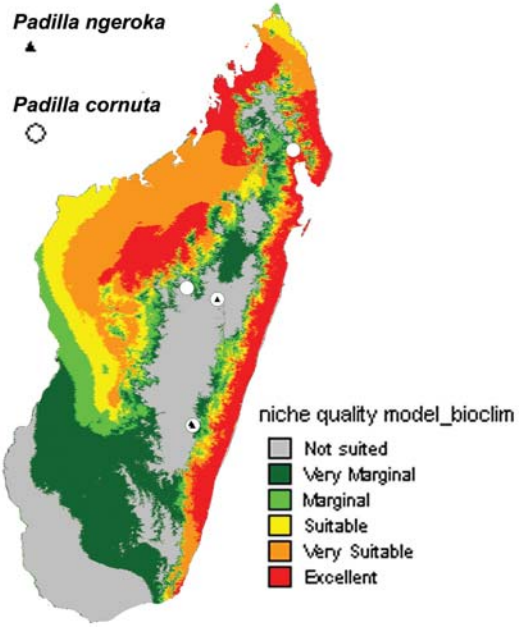


FIGURE 46. *P. ngeroka, P. cornuta* niche quality map.

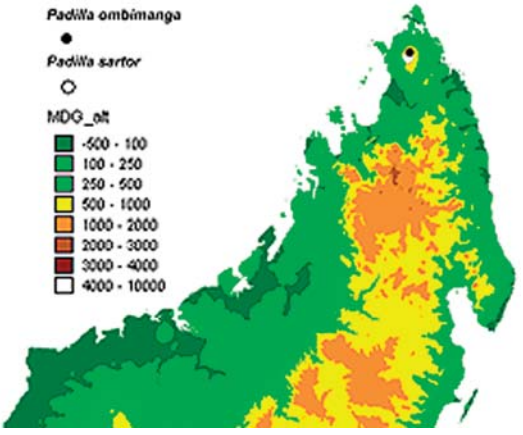


FIGURE 47. Altitudinal distribution map for *P. sartor* and *P. ombimanga* clade.

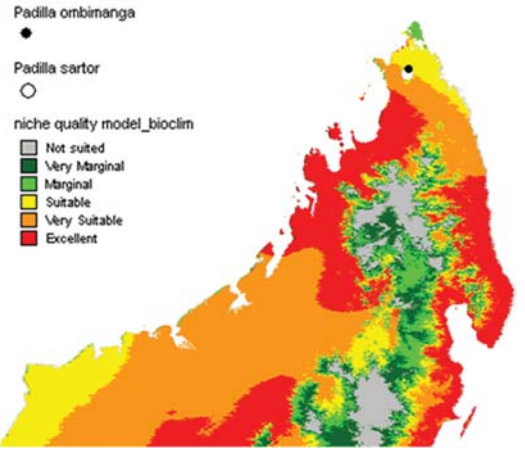


FIGURE 48. *P. sartor*, *P. ombimanga* niche quality map.

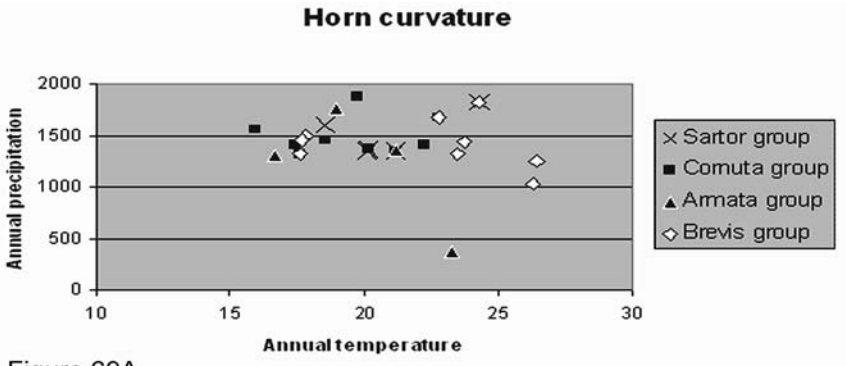


Figure 69A

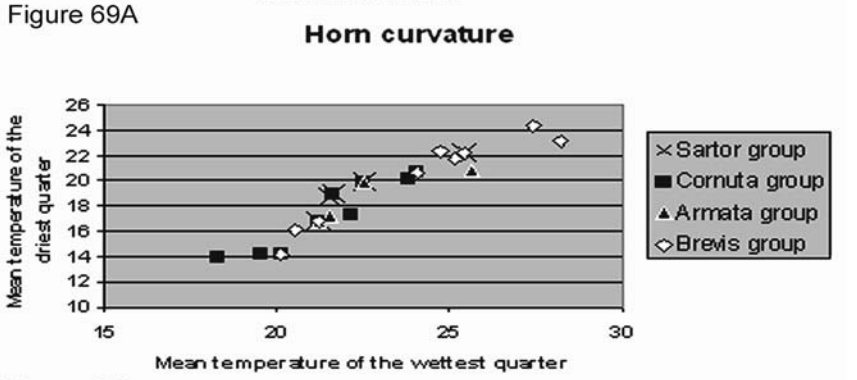


Figure 69B

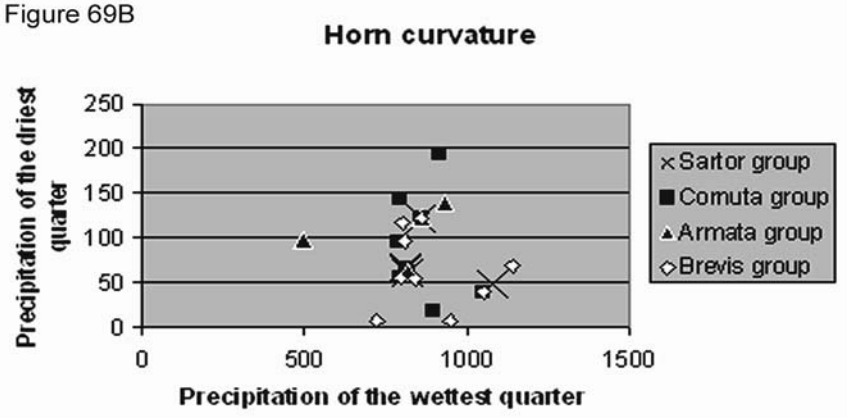


FIGURE 49. Correlation of "horn curvature", temperature and precipitation. A. Horn curvature, annual temperature, annual precipitation. B. Horn curvature, mean temperature of the wettest quarter, mean temperature of the driest quarter. C. Precipitation of the wettest quarter, precipitation of the driest quarter.

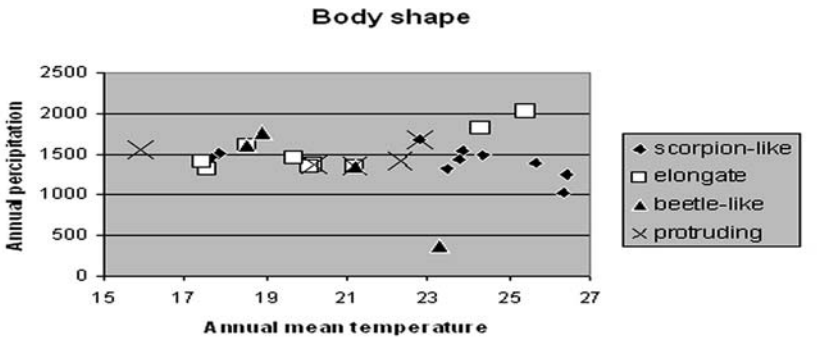


Figure 70A

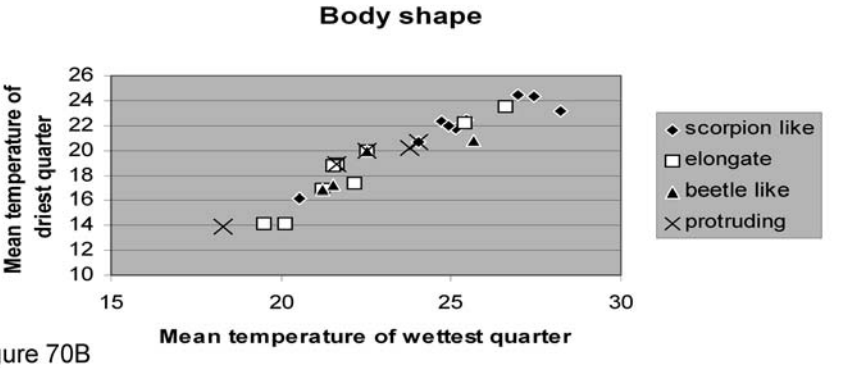


Figure 70B

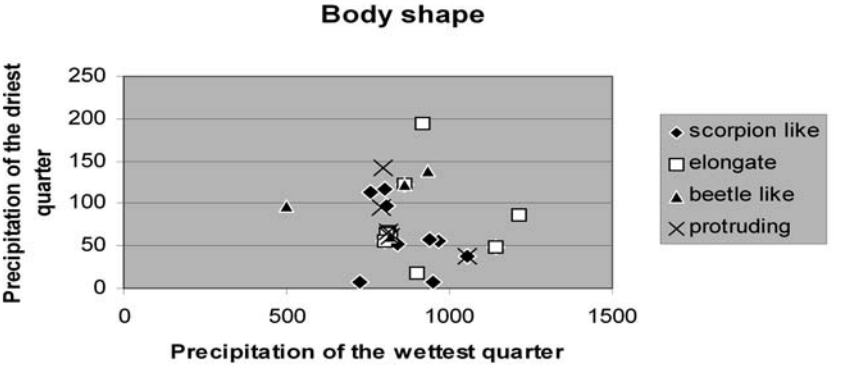


FIGURE 50. Correlation of "body shape", temperature and precipitation. A. Body shape, annual temperature, annual precipitation. B. Body shape, mean temperature of the wettest quarter, mean temperature of the driest quarter. C. Body shape, precipitation of the wettest quarter, precipitation of the driest quarter.

FIGURE 51. Distribution map for *Padilla* species in Madagascar. The dots represent places were species were found.

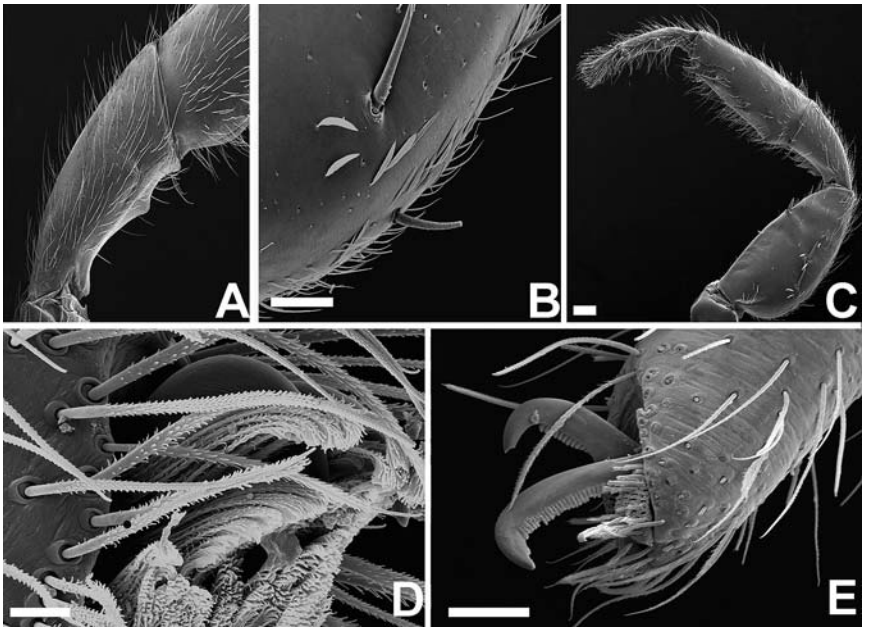


FIGURE 52. *Padilla* first leg SEM. A. *P. lavatandroka*, patella, spur. D. claw tuft. E. claws, prolateral. B. *P. mazavaloha*, femur, scales. C. leg I, proventral. Scale bars for A = 0.5 mm, B = 100 µm, C = 1 mm, D = 30 µm, E = 100 µm.

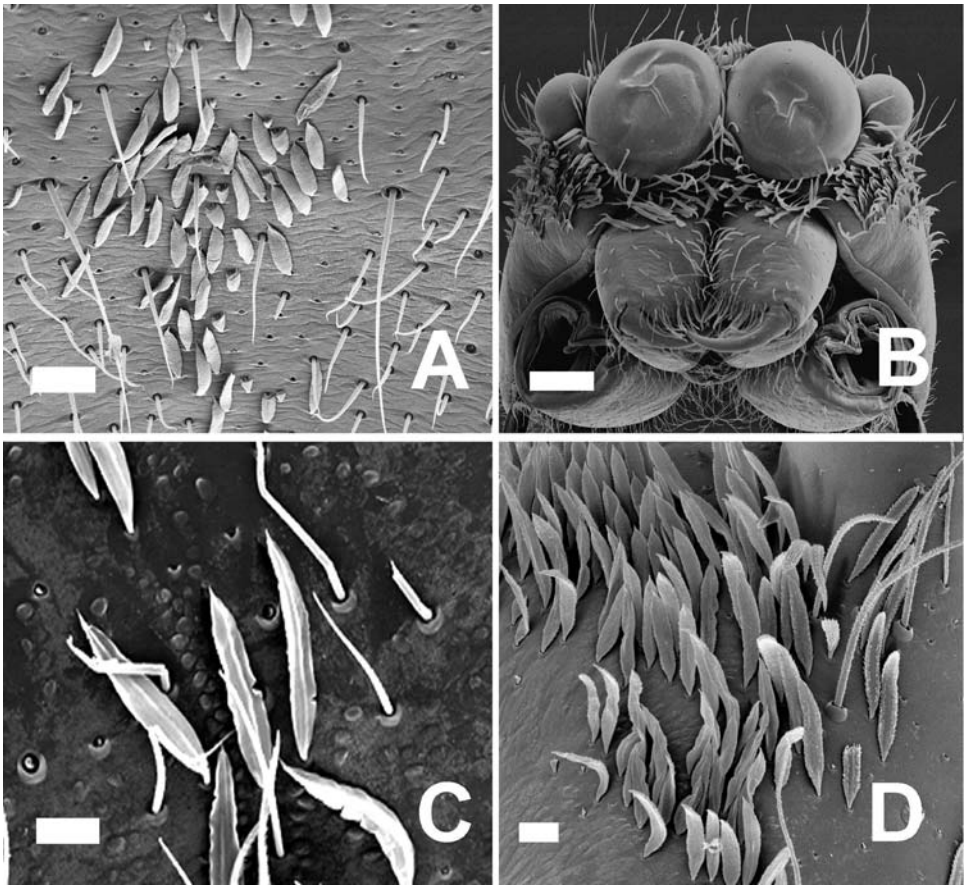


FIGURE 53 (above). *Padilla* carapace texture, scales. A. *P. mazavaloha*, carapace texture, scales. B. *P. lavatandroka*, female, carapace, front view showing scales above clypeus. C. *P.* lavatandroka, carapace texture, scales. D. scales around lateral eyes and on lateral margins of carapace. Scale bar for A = 20 μm, B = 200 μm, C = 10, D = 30μm.

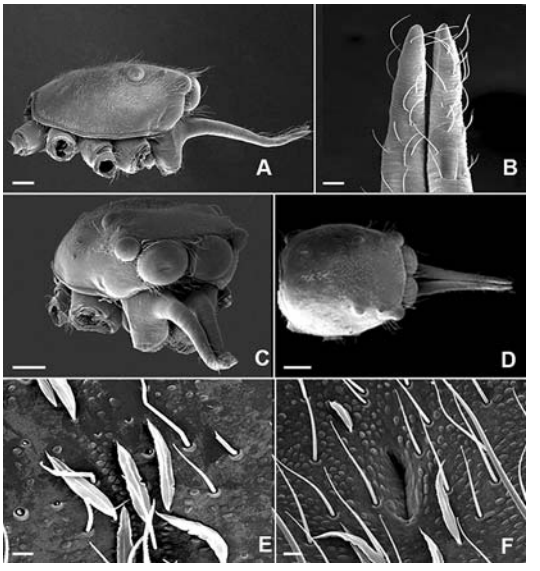
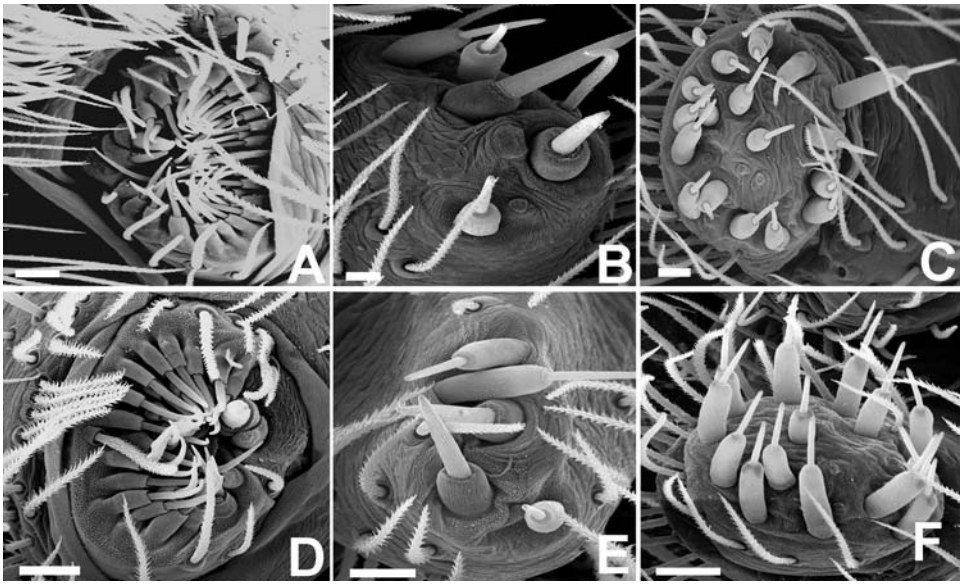
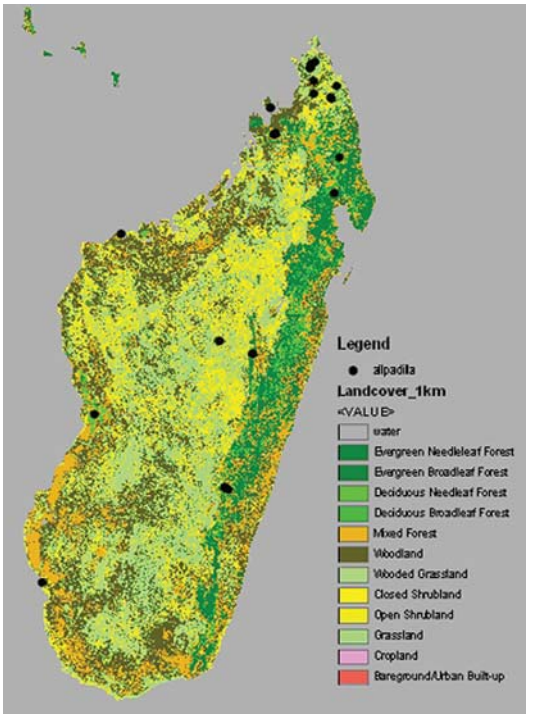


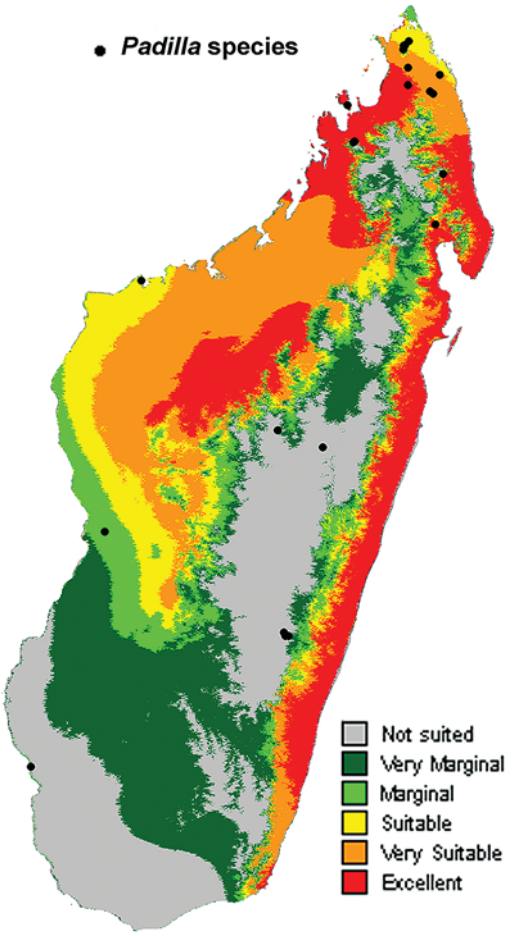
FIGURE 54 (right). *Padilla* horn, horn tips, carapace scales, fovea. A. *P. lavatandroka,* carapace, lateral. B. carapace, dorsal. C. carapace, front. D. Horn tips dorsal, showing hairs and stridulating files. E. carapace scales near fovea. F. fovea. Scale bars for A, B. C = 30μm, D = 20 μm, E, F = 10 μm .

FIGURE 55 (right). *P. boritandroka*, habitus, dorsal. Scale bar = 1 mm.

FIGURE 56 (below). *Padilla* spinning organs. *P. lavatandroka*: A. left ALS. B. left, PMS. C. right, PLS. *P. lavatandroka*: D. right ALS. E. left, PMS. F. right, PLS. Scale bars for all 20 µm.







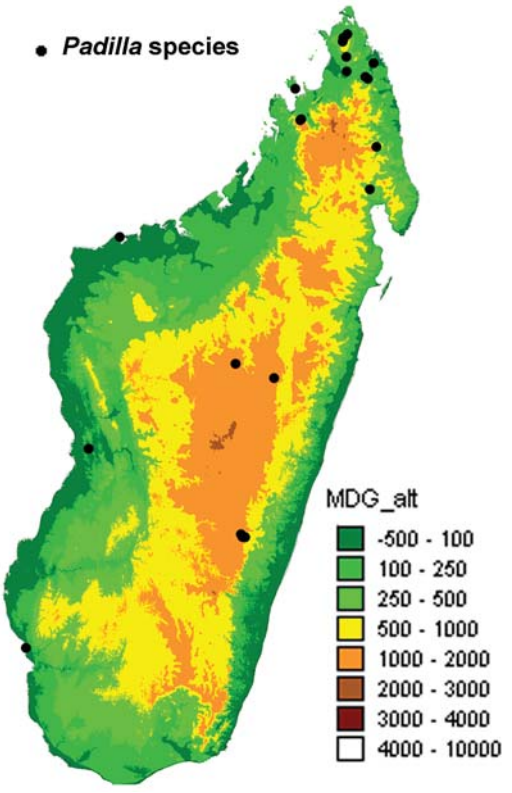


FIGURE 57 (upper left). Vegetation distribution map for all members of the genus *Padilla* in Madagascar.

FIGURE 58 (lower left). Altitudinal distribution map for *Padilla* species.

FIGURE 59 (upper right). Suitable area for the members of the genus *Padilla*.

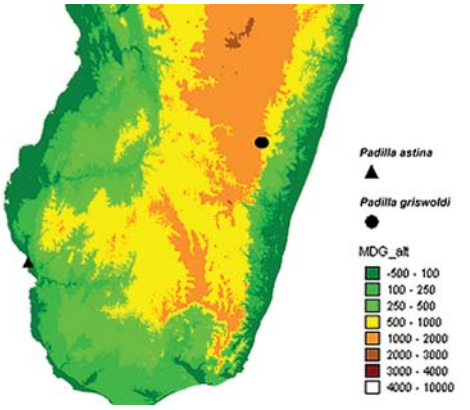


FIGURE 60. Altitudinal distribution map for *P. griswoldi* and *P. astina* clade.

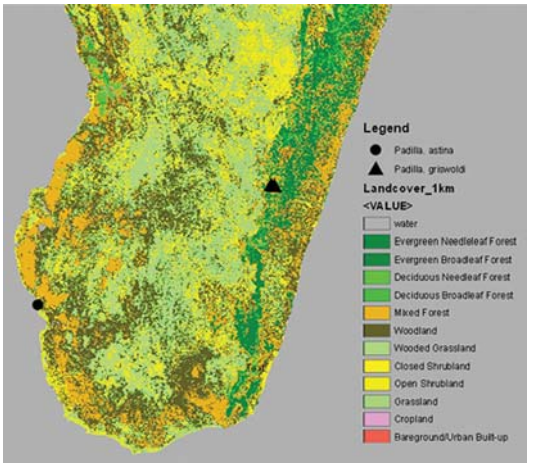


FIGURE 61. *P. griswoldi, P. astina* clade vegetation map.

FIGURE 62 (right). *Cornuta* group female epygina. A. *P. cornuta*, epyginum, ventral. B. epyginum, dorsal. C. *P. manjelatra*, epyginum, ventral. D. epyginum, dorsal. E. *P. lavatandroka*, epyginum, ventral. F. epyginum, dorsal. Scale bars for all = 0.2 mm.

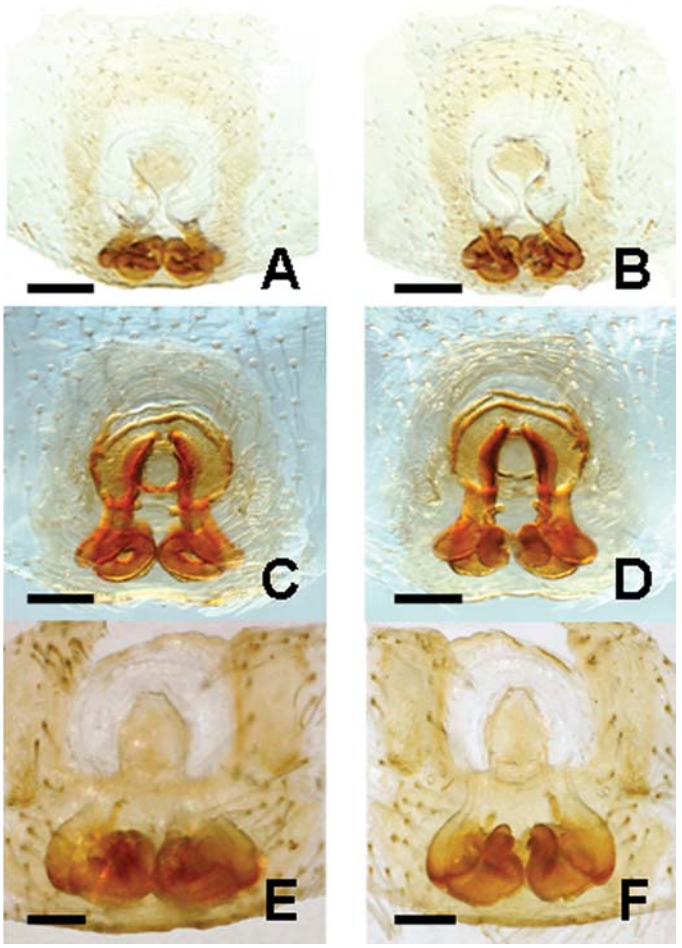


FIGURE 63. *P. ngeroka*, habitus, dorsal. Scale bar = 1 mm.

Appendix. 1. Species groups:

Armata group
- *P. armata* Peckham and Peckham, 1894
- P. ASTINA, new species
- *P. griswoldi,* new species
- *P. ombimanga,* new species

Brevis group
- *P. boritandroka*, new species
- *P. ngeroka*, new species

Cornuta group
- *P. cornuta* (Peckham and Peckham, 1885)

Discussion).
- *P. lavatandroka*, new species
- *P. manjelatra*, new species

Sartor group
- *P. maingoka*, new species
- *P. mazavaloha*, new species
- *P. sartor* Simon, 1900

Unassigned
P. foty, new species
- *P. mihaingo*, new species
- *P. mitohy*, new species

Appendix 2. Anatomical and Institutional abbreviations

Abd L	abdomen length
AC	aciniform gland spigot
ALS	anterior lateral spinnerets
ALE-PME	distance between anterior lateral eyes and posterior median eyes
ap	additional promarginal spine
ar	additional retromarginal spine
CL	carapace length
cpltxL	cephalothorax length
CH	height cephalothorax
CHL	cheliceral length
co	copulatory openings
CW	chelicerae width
dAME	diameter of the anterior median eyes
DH	distal origin of the horns
ec	embolus coil
ef	embolus fold
el	embolus second loop
ek	transluscent septum
er	endite ridge
esl	embolar second loop
F1	femur I length
F3	femur III length
F4	femur IV length
fd	fertilization ducts
H clyp	height clypeus
HL	horn length
HL/ CL	horn length/ Carapace length
HW	horn width
HW/ HL	horn width/ Horn length
L.O.F	length Ocular Field
MAP	major Ampulate
mAP	minor Ampulate
MLE	maximum likelihood
Mt 1	metatarsus I length
Mt 3	metatarsus III length
Mt 4	metatarsus IV length

Institutional abbreviations

CAS	California Academy of Sciences, San Francisco, California
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts

Appendix. 3. Distribution of characters for 16 taxa: 15 *Padilla* species and one outgroup taxon. Character states are scored 0 - 3, "?" for unknown, "_" for unapplicable. Outgroup taxa is bold.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Ballus chalybeius	0	_	_	_	_	_	_	0	0	0	0	0	0	0	1	0	0	0	1
Philates thaleri	0	_	_	_	_	_	_	0	_	1	0	0	0	0	1	0	0	1	0
P. sartor	1	1	3	0	1	1	1	1	1	1	0	1	0	0	0	0	0	1	1
P. mazavaloha	1	1	3	1	2	1	1	1	0	0	0	1	0	1	1	0	0	1	1
P. maingoka	1	1	3	1	0	0	1	1	0	1	0	1	1	0	1	0	0	1	1
P. cornuta	1	0	2	0	1	1	1	1	0	1	0	1	0	1	1	0	0	1	1
P. manjelatra	1	0	2	0	2	2	1	1	0	1	1	1	0	1	1	1	0	1	1
P. lavatandroka	1	0	2	0	2	2	1	1	0	1	1	1	0	1	1	1	0	1	1
P. mitohy	1	_	_	_	_	_	_	1	0	0	0	1	1	0	1	0	0	1	0
P. foty	1	_	_	_	_	_	_	1	0	1	0	1	0	0	1	0	0	0	1
P. mihaingo	1	_	_	_	_	_	_	1	0	0	0	1	1	0	1	0	0	1	0
P. armata	1	2	1	1	1	1	1	1	0	1	0	1	0	0	0	0	1	1	1
P. astina	1	2	1	1	1	1	1	1	0	1	0	1	0	0	0	0	1	1	0
P. griswoldi	1	2	1	1	1	1	1	1	0	1	0	1	0	0	0	0	1	1	0
P. ombimanga	1	2	1	1	1	1	1	1	1	1	0	1	0	0	0	0	0	1	1
P. boritandroka	1	0	0	0	0	0	0	1	0	1	0	1	1	0	1	0	0	1	1
P. ngeroka	1	0	0	0	0	0	0	1	0	1	0	1	1	0	1	0	0	0	1

	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
Ballus chalybeius	2	2	1	1	0	1	1	0	0	0	1	1	1	1	1	0	0	1	0
Philates thaleri	1	1	1	1	1	0	0	0	0	0	0	1	1	1	0	0	0	1	1
P. sartor	1	1	1	1	1	1	1	0	0	2	1	0	1	1	1	0	0	_	0
P. mazavaloha	1	1	1	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0
P. maingoka	0	0	1	0	1	1	1	0	0	0	1	0	1	1	1	0	0	_	0
P. cornuta	1	1	1	0	1	1	1	0	0	0	1	1	1	1	1	2	0	1	0
P. manjelatra	2	1	1	1	1	1	1	0	0	1	1	0	1	1	1	1	0	0	0
P. lavatandroka	2	1	1	1	1	1	1	0	0	1	1	0	1	1	1	1	0	1	0
P. mitohy	0	0	0	0	1	1	1	0	0	0	1	0	_	_	_	_	_	1	1
P. foty	1	0	1	0	0	1	1	0	0	0	1	0	_	_	_	_	_	1	1
P. mihaingo	0	0	0	0	1	1	1	0	0	0	1	0	_	_	_	_	_	0	0
P. armata	1	1	0	1	1	1	1	0	0	0	1	0	1	1	1	2	1	_	0
P. astina	1	1	0	1	1	1	1	0	0	0	0	0	1	1	1	2	1	_	0
P. griswoldi	1	1	0	1	1	1	1	0	0	0	0	0	1	1	1	2	1	_	0
P. ombimanga	1	1	1	1	1	1	1	0	0	2	1	0	1	1	1	2	1	_	0
P. boritandroka	0	0	1	0	1	0	0	1	1	0	1	0	0	0	0	0	0	_	0
P. ngeroka	0	0	1	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0

Appendix. 4. Distribution of characters for 18 Ballinae species. This matrix is a reproduction of Benjamin (2004) ballinae matrix in which we added two *Padilla* species and two other characters that are judged to be synapomorphic to the genus. Character states are scored 0 - 2, "?" for unknown, "-" for unapplicable. Outgroup taxon is bold.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Baviola braueri	0	0	_	0	0	0	0	0	0	1	0	0	0	0	0	0	_	0	_	0	0
Cynapes wrighti	0	1	?	1	1	0	0	0	0	1	0	0	0	0	0	0	_	0	_	0	0
C. conosus	1	1	?	1	1	0	?	0	0	1	1	0	0	0	0	0	_	1	0	0	0
Colaxes wanlessi	1	1	0	1	1	0	0	0	0	1	1	0	0	0	0	0	_	1	0	1	0
Ballus chalybeius	1	1	1	1	1	0	0	0	0	1	1	0	0	0	0	0	_	1	2	1	1
B. segmentatus	1	1	0	1	1	0	1	0	0	1	1	0	0	0	0	0	_	1	0	1	1
Indomarengo sarawakensis	1	1	1	1	1	1	0	1	0	1	1	0	0	0	0	1	1	1	0	1	0
I. chandra	1	1	1	1	1	1	0	1	1	?	?	?	?	?	?	?	?	?	?	1	0
Leikung porosa	1	1	2	1	2	1	0	0	0	0	_	0	1	1	1	1	1	0	_	1	0
Afromarengo coriacea	1	1	1	1	2	1	0	0	0	0	_	0	1	0	1	1	1	0	_	1	0
Philates grammicus	1	1	?	1	1	2	?	0	0	1	1	1	0	0	0	1	1	1	0	1	0
P. zschokkei	1	1	1	1	1	2	1	1	0	1	1	0	0	0	0	1	1	1	0	1	0
Marengo crassipes	1	1	0	1	1	2	0	0	0	1	1	0	0	0	0	0	_	1	0	1	0
M. deelemanae	1	1	1	1	1	2	0	0	0	1	1	0	0	0	0	0	_	1	0	1	0
Philates chelifer	1	1	1	1	1	2	1	0	0	1	1	0	0	0	0	1	_	1	1	1	0
Sadies fulgida	1	1	2	1	1	2	0	0	0	1	1	0	0	0	1	1	0	0	_	1	0
Padilla manjelatra	1	1	2	1	1	1	1	0	1	1	1	0	0	0	0	1	1	0	1	0	0
Padilla mazavaloha	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	1	1	0	1	1	0

	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
Baviola braueri	0	0	0	0	0	0	0	0	0	0	0	0	_	1	1	0	0	0	0	0	0
Cynapes wrighti	0	0	0	1	0	1	0	0	1	0	0	0	_	1	0	1	0	0	0	0	0
C. conosus	0	0	0	0	0	1	0	0	1	0	0	0	_	1	0	1	0	0	1	0	0
Colaxes wanlessi	0	0	0	1	0	0	0	0	1	1	0	0	_	0	1	0	0	0	0	0	0
Ballus chalybeius	0	0	0	0	0	1	0	0	1	1	0	0	_	0	1	0	0	0	0	0	0
B. segmentatus	0	0	0	0	1	1	0	0	1	0	0	0	_	0	1	0	0	0	0	0	0
Indomarengo sarawakensis	0	0	1	0	0	1	1	0	1	1	0	1	2	1	0	0	0	0	0	0	0
I. chandra	0	0	1	0	0	1	1	0	1	1	0	1	2	1	1	?	0	1	0	0	0
Leikung porosa	0	0	1	0	0	1	1	1	1	1	0	1	2	2	0	0	1	1	0	0	0
Afromarengo coriacea	1	0	1	0	0	1	1	0	1	1	1	1	1	1	0	0	0	1	0	0	0
Philates grammicus	1	0	0	0	0	1	0	0	1	1	0	1	?	1	?	?	0	0	0	0	0
P. zschokkei	1	0	1	0	0	1	0	0	1	1	0	1	0	1	?	?	0	0	0	0	0
Marengo crassipes	1	1	0	0	0	1	0	0	1	1	0	1	1	1	0	0	0	0	0	1	0
M. deelemanae	1	1	0	0	0	1	0	0	1	1	0	1	0	1	?	?	0	0	0	1	0
Philates chelifer	0	1	0	0	0	1	0	0	0	1	0	1	0	1	1	0	0	0	0	0	0
Sadies fulgida	1	0	1	0	0	1	1	0	1	0	0	0	_	1	0	1	0	0	0	0	0
Padilla manjelatra	1	0	0	0	1	1	0	1	1	1	0	0	_	1	0	1	0	0	0	1	1
Padilla mazavaloha	1	0	0	0	0	0	0	0	1	1	0	0	_	1	0	1	0	0	0	1	1