

## The Goblin Spiders of the New Genus *Volborattella* (Araneae: Oonopidae) from Madagascar

ALMA D. SAUCEDO,<sup>1</sup> DARRELL UBICK,<sup>1</sup> AND CHARLES E. GRISWOLD<sup>1</sup>

### ABSTRACT

A new genus of goblin spider from Madagascar, *Volborattella* Saucedo and Ubick, is proposed and its five included species newly described and illustrated: *V. teresae*, the type species, *V. guenevera*, *V. nasario*, *V. paulyi*, and *V. toliara*. These species differ from other oonopids in several unusual characters, especially the variously modified setae: abdominal scutes having thick recumbent setae with large bases and conspicuous pits; the pedicel region with mats of plumose setae and associated cuticular projections; and anterior metatarsi with prolateral combs. The male palp of *Volborattella* appears to be unique in having a terminal projection (embolar superior prong, ESP) that forms an abrupt spiral and the female a receptaculum with an accessory duct (curved tube). *Volborattella* resemble members of the *Gamasomorpha* complex in lacking leg spines and having a flattened abdomen with complete scutes, but differ genitally. The *Volborattella* female has a receptaculum that is wider than long (as opposed to longer than wide in the *Gamasomorpha* complex) and the male has the embolar region sharply bent (as opposed to evenly curved), which places the genus in the *Pelcinus* complex. The relationship of *Volborattella* to other pelicinoids is not resolved. Although the genus most closely resembles some *Silhouettella* Benoit, *Noideattella* Álvarez-Padilla et al. and *Lionneta* Benoit in various genitalic features, somatically it shares with *Tolegnaro* Álvarez-Padilla et al. and two undescribed Malagasy genera the gamasomorphoid body form and plumose setae. *Volborattella* females are unusual in having antisymmetrical internal genitalia, with the CTs occurring in either a left or right position, and that these differences in handedness (antisymmetry) are evenly distributed. The shape and size of the CT, as examined through light and scanning microscopy, suggest that it is a coupling pocket for the ESP; if so, *Volborattella* females are either righties or lefties in their palpal preference.

<sup>1</sup> Department of Entomology, California Academy of Sciences, San Francisco.

## INTRODUCTION

Madagascar is one of the world's greatest biological hotspots. Its extended geographical isolation has fostered rich endemism and the emergence of unusual biological forms. Continental in origin, Madagascar was enclosed within eastern Gondwana (Wells, 2003), bordered by Africa to the north and west and India to the south and east (Scotese, 1994), and remained attached to India for many millions of years along its eastern margin after splitting from Africa by the end of the Jurassic Period (Wells, 2003). The island has been on a unique evolutionary course since completely separating from its Gondwanan neighbors 80 million (Krause et al., 1997) to 140 million years ago (Rabinowitz et al., 1983).

In contrast to the Malagasy vertebrate fauna (Carlquist, 1965), the spider fauna is not disharmonic (Griswold, 2003). While Madagascar is also home to most spider families found in Africa or Asia, Griswold (2003) notes a particularly strong link to Africa, recording 19 species common to both Africa and Madagascar and 22 genera shared exclusively by Africa and Madagascar at that time. Griswold also notes a weaker affinity to Asia and the Indo-Pacific, with at least nine shared genera not found in Africa (Andriamalala, 2007; Griswold, 1993, 2003). Phylogenetic studies support these associations, particularly to Africa (Griswold, 1990, 1991, 2000, 2001; Griswold et al., 2012; Wood, 2008; Wood et al., 2007). Andriamalala (2007) and Kuntner and Agnarsson (2011a, 2011b) have performed divergence-time estimations through molecular phylogenetics. These studies suggest Cenozoic dispersal of spiders to Madagascar. In contrast, two phylogenetic analyses revealed a biogeographic pattern that may even predate the breakup of Gondwana (Griswold and Ledford, 2001; Wood et al., 2013), and the divergence time estimation by Wood et al. specifically suggests a Mesozoic, Gondwana origin for Malagasy pelican spiders (Archaeidae).

A wide expanse of latitudes (12°–25° S) and a central mountain plateau that stretches the length of the island greatly influence Madagascar's climate and facilitates a wide array of habitats. The wet eastern region is maintained by monsoon cycles and orographic precipitation throughout the year and is historically covered by forest. The western side becomes desiccated during the winter months and is predominated by succulent and scrublike vegetation (Jury, 2003).

The climatic variation coupled with Madagascar's long isolation has cultivated a high proportion of endemic taxa, and spiders are no exception. The endemic spider fauna of Madagascar is represented by 85% of described species, 29% of genera, and even one family (Griswold, 2003). Madagascar is rich in spider diversity, much still undescribed. Although only about 500 species comprising 58 families have been described (Platnick, 2013), it is estimated that over 3000 species may actually occur on the island (Griswold, 2003).

A good example of this underestimated species richness is in the goblin spider family Oonopidae. Goblin spiders occur commonly on all six inhabited continents, yet were among the least known spider families. With the recent focus on oonopids garnered by the goblin spider Planetary Biodiversity Inventory (PBI) project (<http://research.amnh.org/oonopidae/index.php>), the number of described species has increased from about 500 to over 1400, with the total number estimated to be over 2000 species.

Although Millot (1948) first recorded the presence of goblin spiders in Madagascar decades ago, he produced no descriptions or even species identifications, and the true oonopid diversity

is only now being recognized. Thousands of oonopid specimens have become available for study through arthropod surveying expeditions by Vincent and Barbara Roth, Mike Irwin, Rinha Harinhala and Evert Schlinger, Brian Fisher and Charles Griswold, Fernando Álvarez-Padilla, Hannah Wood, Daniela Andriamalala, and the authors, most of which are deposited at the California Academy of Sciences (CAS). These surveys uncovered a rich endemic spider fauna, including over 100 oonopid species, of which 56 have already been described (Ubick and Griswold, 2011a, 2011b; Álvarez-Padilla et al., 2012; Andriamalala and Hormiga, 2013).

Five of these species are described here and placed in the new genus, *Volborattella*. These attractive goblin spiders are easily recognized by the spotty or shimmering abdominal scutes (figs. 22, 93, 112, 139, 156, 180, 198, 217, 243, 256), and can be unambiguously sorted to genus even at lower magnifications (30× or less). Higher magnifications, especially SEM images, show that the unusual appearance of the scutes is due to their uniformly and deeply pitted surface (figs. 30, 31, 124, 144, 185). The arrangement of scutal pits (and their associated flattened setae) seems to be unique, at least among the Malagasy oonopids, and is a possible synapomorphy for the genus. Another spectacular character is the presence of plumose setae and associated papillae at the pedicel region (figs. 16, 18, 27–29, 32, 122, 123, 164–166, 207, 208). Although this combination of structures is uncommon, it is not unique, as similar setae do occur in some other Malagasy genera. The male palp also appears distinctive in having an embolar prong that forms a wide spiral (figs. 67, 127, 169, 224, 271). Similarly curved prongs do occur in some other oonopids, such as *Noideatella* Álvarez-Padilla et al., 2012, and *Lionneta* Benoit, 1979, although these differ in degree of coiling among other features. The female genitalia are unusual in having a broad papillae field that covers the anterior half of the receptacular surface (figs. 99, 145, 186, 232, 268). In most Malagasy oonopids with similar genitalic conformations, the papillae field is smaller and generally restricted to the anterior quarter of the receptaculum (see figs. in Álvarez-Padilla et al., 2012). A broad papillae field is also present in *Silhouettella curieusei* Benoit, 1979 (in his fig. 5G), but there the papillae are distributed longitudinally, running the full length of the receptaculum but absent from the sides (see images on the PBI website: <http://research.amnh.org/oonopidae>). In *Volborattella*, the papillae extend the full width of the receptaculum, but are absent from the posterior half. Another unusual genitalic feature is the presence of an additional curved tube on the receptaculum, which is discussed below.

## RELATIONSHIPS

*Volborattella* have two possible sets of relatives, the *Gamasomorpha* or *Pelcinus* complexes, depending on which characters are examined. Somatically, these oonopids are fully scutate, have broad, flattened abdomens and short, spineless legs. These are all characters shared by *Gamasomorpha* Karsh, 1881, and related genera and suggest that the genus *Volborattella* belongs in this *Gamasomorpha* complex (see discussion in Álvarez-Padilla et al., 2012). A review of the available images of gamasomorphoids, both in published accounts and on the PBI website, turned up only two genera with modified setae at the pedicel, *Grymeus* Harvey, 1987, and *Yumates* Chamberlin, 1924 (including some species currently misplaced in *Gama-*

*somorpha*). In *Grymeus*, these setae are quite different from those in *Volborattella*, being spatulate rather than plumose, lacking associated papillae, and forming a dense mat that completely obscures the book lung covers (see fig. 9 in Harvey, 1987). *Yumates*, on the other hand, closely resemble *Volborattella* in these structures (figs. 284–292), which suggests a possible relationship. However, in *Yumates* the plumose setae occur only on the abdomen (fig. 285), whereas in *Volborattella* they also extend to the adjacent carapace. The two genera have other somatic differences, but their major differences are genitalic (see table 1).

The male palpi of *Yumates* and *Volborattella* have a similar overall morphology, with the embolar complex composed of three main lobes borne upon (and forming) the apical elongation of the bulb. In both, the ventral lobe is attached basally (with the two dorsal lobes separating distally), the embolar opening is located subapically on the retrodorsal lobe, and the prodorsal lobe is sclerotized and bladelike (figs. 67, 289). However, in *Yumates*, the embolar region curves only gradually (without a sharp bend, let alone a spiral), the bulb has a prominent dorsal knob, and the embolar base has a dorsal row of strong tubercles (fig. 289); the latter two features are absent in *Volborattella* (figs. 60, 125, 167). Also, the ventral lobe in *Yumates* is rigid and sclerotized and ends in a single sharp point (fig. 290), but in *Volborattella* it appears more flexible (with conspicuous wrinkles) and terminates in two points (fig. 171). In *Yumates* females, the receptaculum is longer than wide (or at least as long as wide; fig. 292), but in *Volborattella* is clearly wider than long (figs. 99, 145, 186, 232, 268). Also, the two genera differ in the shapes and sizes of the posterior apodemes, which are broadly attached to the receptaculum, appearing batlike in ventral and dorsal views, and being shorter than receptacular length in *Yumates* (figs. 291, 292), but are more narrowly attached and relatively longer in *Volborattella* (figs. 99, 145, 186, 232, 268). These genitalic characters suggest that the two genera are not closely related but belong to different genera complexes, and that the somatic similarity in these genera (including the plumose setae) is from convergence.

In fact, the genitalia of *Volborattella* are most similar to members of another group of oonopids, the *Pellicinus* complex, which have a female receptaculum that is wider than long (as opposed to longer than wide) and a male embolar region sharply bent (as opposed to evenly curved). This group was first recognized by Saaristo (2001) as the *Lionneta* group, discussed by Ubick and Griswold (2011b) and Álvarez-Padilla et al. (2012) as the *Silhouettella* group, and more recently by Platnick et al. (2012b), who renamed the group for its oldest member, *Pellicinus* Simon, 1891. The palp of *Volborattella* most closely resembles that of some species of *Noideattella*, especially *N. tany* (Álvarez-Padilla et al., 2012: figs. 224–230), which also has a long, curved embolar prong, although not forming a complete spiral. Similarly, the female genitalia of *Volborattella* most closely resemble those of *Silhouettella curieusei*, as both have a papillae field that covers much of the receptacular surface (although they differ in the shape of that field) and *S. curieusei* also lacks leg spines. This degree of similarity in the genitalia suggests a close relationship to these genera, and unambiguously places *Volborattella* in the *Pellicinus* complex.

Interestingly, although the genitalic similarities suggest close relations to *Noideattella* and *Silhouettella*, the unusual somatic characters of *Volborattella* are shared by a different group of Malagasy pelicinoids. The two species of *Tolegnaro* Álvarez-Padilla et al. (2012) have similar plumose setae and associated papillae and are also “gamasomorphoid” in body form (Álvarez-

TABLE 1. Comparison of some pelicinoid and gamasomorphoid genera, with the character states of *Volborattella* highlighted. Characters 4–7 are of the pedicel region. Abbreviations: **A1**, posterior apodeme; **abd**, abdomen; **car**, carapace; **ESP**, embolar superior prong; **L**, length; **N**, no; **PME**, posterior median eyes; **Re**, receptaculum; **VP**, embolar ventral process; **Y**, yes.

	Character states	<i>Gamasomorpha</i>	<i>Grymeus</i>	<i>Yumates</i>	<i>Volborattella</i>	new genus A	new genus B	<i>Tolegnaro kepleri</i>	<i>Tolegnaro sagani</i>	<i>Molotra molotra</i>	<i>Noideatella tany</i>	<i>Silhouettella curteusi</i>	new genus C	<i>Lionneta</i>
somatic	1	abd scute: complete, partial, absent	C	C	C	C	C	C	C	C	C	C	CPA	CP
	2	abd shape: depressed, round compressed	D	D	D	D	D	D	D	C	C	D/R	C	C
	3	leg spines: Y, N	N	N	N	N	N	N	Y	Y	Y	N	N	Y
	4	abd plumose setae: Y, N	N	Y	Y	Y	Y	Y	Y	N	N	N	N	N
	5	abd papillae: Y, N	N	N	Y	Y	Y	Y	Y	N	N	N	N	N
	6	car plumose setae: Y, N	N	N	N	Y	Y	Y	Y	N	N	N	N	N
	7	car papillae: Y, N	N	N	N	Y	Y	Y	Y	N	N	N	N	N
	8	PME squared: Y, N	Y		N	Y	Y	Y	Y		N		Y	Y
	9	abd scutes pitted: Y, N	N		N	Y	N/Y	N	N	N	N	N	N	N
	10	abd setae thick: Y, N	N	Y	N	Y	Y	Y	N	N	N	N	N	N
	11	claw inner face comb: Y, N			N	Y		Y	Y		N		N	
	12	legs with cuticular glands: Y, N			Y	Y		Y			Y		Y	Y
	13	cuticular glands anterior notch: Y, N				Y							N	
	14	metatarsal comb: Y, N				Y		Y	N	Y			N	
male	15	cymbium scopula: Y, N	N/Y		N	Y	Y	Y	N	Y	Y		Y	Y
	16	bulb dorsal knob: Y, N	Y	Y	Y	N	Y	N	Y	N	Y	Y	N	N
	17	bulb base extends beyond cymbium	N	N	N	Y	Y	Y	Y	Y	Y	Y	Y	Y
	18	embolar complex: curved, bent, short	C	C	C	B	B	S	B	B	S	B	B	B
	19	ESP curvature: weak, moderate, spiral	W	W	W	S	W	W	W	W	M	W	W	M
	20	VP prongs: 1, 2, 3	1	1	1	2	2		3	2	1	3	2	2
	21	VP texture: smooth, wrinkled	S	S	S	W	W		W	W	W	W	W	W
	22	sternal cavity: pockets, groove	P	G	G	P/G	P		G	G	P	G	P	G
female	23	Re shape: 1, L>W; 2, L=W; 3L<W, 4, absent	1	1-2	1-2	3	3	4	3	3	4	3	3	3
	24	Re papillae field: short, long, wide absent	S	W	L	W	W	A	S	S	S/W	L	S	S
	25	Re size: normal, strongly reduced	N	N	N	N	N	R	N	N	R	N	N	N
	26	A1 L/Re L: A<R; 2 A=R; 3, A>R	1	1	1	3	3	3	3	3	3	2	1	3
					"volborattelloid"									
			gamasomorphoid		pelicinoid									

Padilla et al., 2012: figs. 313–370). Members of *T. kepleri* are more similar to *Volborattella* in lacking leg spines and even having a comb on the inner face of the tarsal claws; those of *T. sagani* have a metatarsal comb on legs I and II, although this species differs in having leg spines. However, both *Tolegnaro* species differ from *Volborattella* genitally in having a male palp with a distinct dorsal knob and a relatively short embolar superior prong (Álvarez-Padilla et al., 2012: figs. 336–341, 365–370) and a female receptaculum with a smaller papillae field that has more densely packed papillae (Álvarez-Padilla et al., 2012: figs. 332–335, 352–356). Two additional species, both undescribed and representing different genera, are also somatically similar to *Volborattella*, even having thick abdominal setae and the metatarsal and tarsal claw combs, but have very different genitalia. These will be described in a subsequent paper.

One of the more unusual features of *Volborattella* is that the female has an additional genitalic structure, a curved tube (CT) at the anterior side of the receptaculum (figs. 99, 145, 186, 232, 268). This is visible as a brownish duct that forms a loop near the GAP and opens externally at a median slit near the gonopore (figs. 230, 261, 276). Although convoluted tubes do occur in some other pelicinoids, such as in *Noideattella tany* (Álvarez-Padilla et al., 2012: figs. 213, 214), in these cases they connect the receptaculum to the opening on the posterior wall of the uterus externus, and so represent the GAP (sense Burger, 2010). The CT is seemingly an additional structure and, as such, is most unusual, although apparently not unique to *Volborattella*. A similar arrangement has been described for *Lionneta* by Burger in his detailed study of these genitalia, and referred to as “tube-like outgrowth” (Burger, 2010: figs. 7C, D, indicated by asterisks). But, unlike the CT in *Volborattella*, which is short and forms a simple arc, the one in *Lionneta* is longer, convoluted and sharply bent.

The function of the CT is not known and was not speculated on by Burger. However, the similarities in size and shape of CT to the long embolic prong (ESP) of the male palpi (in both genera) suggest the obvious possibility that these are coupling structures (figs. 275–283). Morphological details support this: (1) the ESP is flat, bladelike, and compatible with a slitlike CT opening; (2) the blades of the ESP are roughly in a single plane, as is the CT; and (3) a fully inserted ESP would bring the embolar opening close to the main opening into the receptaculum (fig. 278).

Additional support for the “coupling hypothesis” is the asymmetrical position of the CT, which is located either to the left or right of the receptacular midline (fig. 276) and is visible externally through the cuticle (fig. 261). If the CT is actually a coupling pocket, and assuming a uniform mating position in these spiders, it follows that females would be able to copulate with either a right or left male palp, but not both. In *Lionneta*, the CT position is also asymmetrical, which Burger found to be evenly distributed in his population, with five females having the CT on the left side and six on the right (2010: 30). We found a similar distribution in *Volborattella*, and our sample of 43 females (representing all species) contained 22 righties and 21 lefties. This even distribution of right- and left-CT females matches that of left and right male palpi, and is what would be expected if the CT functions as a coupling structure.

Asymmetry represented by left/right handedness, which has been termed “antisymmetry” (for discussion see Agnarsson, 2006), also occurs in another Malagasy oonopid, *Malagiella* Ubick and Griswold, 2011a, but there the antisymmetry is in the orientation of the receptaculum, and not in any additional structures (Ubick and Griswold, 2011a: figs. 228–235). With

these examples of three oonopid genera with antisymmetric genitalia, it is surprising to learn that this phenomenon is quite rare in spiders. A recent survey of arthropod genitalic asymmetry (Huber et al., 2007), documented only three spider genera with female genitalic antisymmetry: two in Pholcidae and one in Theridiidae. Interestingly, the theridiid example, *Asygyna* Agnarsson, 2006, is also from Madagascar, where four of the six known cases of this phenomenon occur! The phylogenetic significance of the CT is not clear. Although it would appear to be a strong synapomorphy for *Volborattella* and *Lionneta*, the many somatic differences between these two genera argue against a close relationship.

In summary, the sister group of *Volborattella* has not been identified, although genitalic evidence (female receptaculum wider than long and male embolar region sharply bent) favors placement in the *Pelcinus* complex. The genus does not seem to be closely related to *Yumates*, despite the presence of similar plumose setae, as the two genera have many somatic and fundamental genitalic differences that point to different placements. And, although *Volborattella* seem to be most closely related to Malagasy taxa, their somatic and genitalic conformations suggest two different sets of possible relatives.

The species of *Volborattella* have numerous somatic differences. The species differ in color, body proportions, eye size and pigmentation, setal pit and base sizes, setal density, plumose setae distribution, scutal ridge presence, and curvature of the dorsal scute. Additionally, the species differ in several sex-related characters. Males show differences in the size and curvature of the embolar superior prong (ESP) and length and shape of the inferior prong (EIP), also in palpal color and pilosity, size of endite projection and anterior sternal cavity form. The female genitalia are less variable, but do differ externally in the shape and thickness of the gonopore opening and internally in receptaculum length, papillae distribution, ridge development, and apodeme shape.

The species seem to fall into three groups. The morphologically most distinct species is *V. nasario*, which differ from the others in several ways, including: an abdomen brown in color and with indistinct spots (fig. 156); abdominal setae with smaller pits and larger bases (fig. 166); male embolus with a longer and narrower superior prong (fig. 169); female genitalia with longer receptaculum and large ventral lobe of the posterior apodemes (figs. 186, 188). The second group contains *V. guenevera* and *V. paulyi*, which differ from the others in having a yellowish abdomen (figs. 112, 139, 243, 256), wide carapace (figs. 107, 134, 238, 251), slightly larger eyes (figs. 110, 137, 241, 251), male embolus with short and broad EIP (figs. 129, 271), and female with a short receptaculum (figs. 145, 262). The third group includes *V. teresae* and *V. toliara* which have an elongate abdomen (figs. 1, 71, 190, 209), a sinuous anterior margin of the dorsal scutum and absence of a wide suprascutal ridge (figs. 25, 96, 201, 220), a male with deeper sternal cavities (figs. 5, 12, 194, 205), smaller endite projections (figs. 21, 206), an EIP longer and apically bent (figs. 67, 224), and a female with receptaculum of intermediate width and pointed A1 (figs. 99, 102, 232, 234).

The relationships between the three groups cannot be fully resolved until the sister group of *Volborattella* is identified. However, as all of the possible relatives of *Volborattella* lack the modified abdominal setae and associated pits, the plesiomorphic state of this character in *Volborattella* would be the one most closely resembling the potential outgroups, namely, the small setal pits of *V. nasario*. As this is the most divergent species in both genitalic and somatic char-

acters, it is regarded as the sister group of the remaining species. Members of the second group, *V. guenevera* and *V. paulyi*, resemble *V. nasario* in several character states, such as a dorsal scutum with evenly curved anterior margin (figs. 115, 142, 246, 259), a wide scutal ridge (figs. 115, 142, although indistinct in *V. paulyi*, figs. 246, 259), a male with shallower sternal cavities (figs. 120, 239), larger endite projections (fig. 121), shorter EIP (figs. 129, 271), and female genitalia with posterior apodeme (A1) not pointed (figs. 147, 268). As the alternate states of the above characters are diagnostic for the third group, *V. teresae* plus *V. toliara*, these are regarded as the most derived *Volborattella*.

### NATURAL HISTORY

*Volborattella* species are somewhat rare and the 326 specimens available for study represent less than 3% of the inventoried Malagasy Oonopidae. Extensive collecting, especially since the 1990s, has produced extensive oonopid collections from most parts of Madagascar (Ubick and Griswold, 2011a, 2011b; Álvarez-Padilla et al., 2012; Andriamalala and Hormiga, 2013), but with relatively few *Volborattella*. Within the genus, only the type species, *V. teresae*, has been commonly collected, and the rarest are *V. nasario*, known from a few localities, and *V. paulyi*, from only one.

*Volborattella* is distributed over most of Madagascar, except the central region, but is primarily concentrated in the humid north and along the western expanse of the island (map 3), which travels a climatic gradient from humid in the northwest to a semidesert in the southwest (Jury, 2003; Wells, 2003). Interestingly, although widespread, the genus is completely absent from the eastern tropical evergreen forests.

With few exceptions, *Volborattella* have been collected from November to April, throughout the island's warm, rainy season (Jury, 2003). This may reflect phenology, or perhaps only the tendency of entomologists to survey during the wet season. While also found in drier habitats, such as dry forest and spiny forest or thicket, this genus tends to prefer moist habitats (e.g., rainforest, gallery forest, littoral forest, montane rainforest) and where moisture is preserved in an otherwise arid environment (e.g., gallery forest and remnant forest). Most commonly found in tropical dry forest, a seasonally dry habitat, they have been collected there only during the wet season and in moist microhabitats. A few specimens of *V. teresae* have been collected from clay or sandy forests of Toamasina in eastern Madagascar. They are primarily extracted from sifted litter, where moisture concentrates and is often insulated as the season progresses into the cooler, dry season from May to September (Jury, 2003). Specifically, they are often found in decaying matter, i.e., leaf mold and rotten wood. A small proportion of specimens have been collected in pitfall traps set in tropical dry forest and spiny forest.

The type species, *V. teresae*, is widely distributed along the coasts of Madagascar (10–925 m elevation), but is most commonly found in the far north and northwest (maps 1, 3). This is the only *Volborattella* species recorded near the central eastern coast. They are found in nearly all recorded *Volborattella* habitat preferences, from humid to arid environments. The most abundant of the species, it accounts for 65% of the known specimens and is sympatric



with each of the other *Volborattella* species, all of which have distinctly more restricted distributions (map 3).

*V. guenevera* is one of the rarest species described here, with only 12 specimens known from eight localities. This species is restricted to the northernmost tip of Madagascar (map 2), in tropical dry forest (10–425 m elevation). A single locality in northwestern Madagascar, Parc National de Namoroka, in which a lone male was recorded, is uncertain due to a suspected labeling error. They are highly sympatric with *V. teresae*, where all but two collection events in which *V. guenevera* were recorded have yielded both species.

*V. nasario* is known from only five localities in northwestern Madagascar (maps 2, 3), occurring in littoral rainforest, tropical deciduous and tropical dry forests (25–250 m elevation). In addition to the sympatric relationship with *V. teresae*, *V. nasario* appears to be parapatric to *V. guenevera*, excluding *V. guenevera*'s questionable occurrence in Parc National de Namoroka. The great majority of specimens (84%) was extracted from a single collection event in Forêt Ambohimanga, in tropical dry forest (250 m elevation). This is highly unusual considering the paucity of *V. nasario* garnered from the remaining collection events and may have been due to several possible factors or perhaps a combination of factors. While the four remaining records do not list a specific microhabitat, this collection may have been the only event that targeted leaf mold and rotten wood, a common microhabitat for this genus. A higher elevation may also be a consideration, where these specimens were collected at 250 m compared with 25 m and 120–130 m elevations. Climate may have played an important role as well. The previous cyclone season was a rather devastating one, with three tropical cyclones in particular greatly contributing to the annual rainfall: Cyclone Cela, Cyclone Elita, and the infamous Cyclone Gafilo (Razafimahazo, 2005). All three cyclones affected the northwest and may have prepared the following seasons for abundance. Ten specimens of *V. teresae* were also collected during this same event. Of course, it is also possible that this species is simply more abundant than current collections suggest, or perhaps it was just serendipity to have happened upon an unusually prolific site.

*V. toliara* is restricted to the decidedly more arid southwest (25–780 m elevation) and is found in a variety of habitats: gallery forest, rainforest, dry forest, tropical dry forest, and spiny forest or thicket. This species is allopatric to *V. nasario* and *V. guenevera* (map 2), but shares at least one known locality with *V. teresae*, in spiny forest or thicket at the southernmost point of the island (map 3). These two species exhibit multiple shared somatic and genitalic similarities to the exclusion of *V. guenevera* and *V. nasario*: typically elongated abdomens with the dorsal scutum anterior margin curved, the lack of a curved scutal ridge above paired ridges in the scutopedicel region, males with deep lateral pouches at sternum anterior margin and a less-pronounced, single toothlike projection on endites anteromedian tips, the long setae on the cymbium prolateral margin more feathery, the embolar inferior prong elongated, and female internal genitalia with triangular anterodorsal lobes on the winglike apodemes and a pair of tiny pits present just posterior to where the apodemes attach to the receptaculum. In addition, these are the only two species found to occur in drier habitats, such as spiny forest or thicket.

*V. paulyi* is known from a single locality, Foulpointe, at the central eastern coast of Madagascar.

## MATERIALS AND METHODS

Specimens were examined using a LEICA M125 and imaged using a LEICA MZ16 stereomicroscope and a LEICA DM4000M compound microscope. Automontage source images were created using a Nikon DXM1200 camera and compiled using software program Automontage Pro Version 5. Female internal genitalia were cleared with Hoyer's medium. Specimens were dissected and prepared for scanning electron microscopy (SEM) primarily according to the protocols in Álvarez-Padilla and Hormiga (2007). Specimen parts prepared for SEM were dehydrated in serial baths of increasing ethanol concentration in order to minimize shriveling. Female genitalia were digested with concentrated contact lens-cleaning solution ReNu® prior to dehydration. Specimens were then critical point dried, sputter coated, mounted on SEM stubs, and imaged with a LEO 1450 VP scanning electron microscope. A total of 326 specimens was examined for this study. Measurements are in mm unless indicated otherwise. All synapomorphies mentioned in this paper are putative.

Setae with long lateral branches are here referred to as “plumose setae,” following the PBI\_OON convention. Other authors (such as Griswold et al., 2005:49) refer to these as “feathery setae” and use “plumose setae” for setae with short branches (which are here called “needlelike setae”).

Species descriptions were generated with the aid of the oonopid PBI descriptive database (<http://research.amnh.org/oonopidae/index.php>). This being a team effort in taxonomy, the new taxa may be hypothesized by different combinations of authors: these attributions are specified in the genus and species descriptions. Species distributions were plotted in Google Earth 5.1 and the maps created using Adobe Photoshop CS. The vegetation map of Madagascar is from Du Puy and Moat (2003) and was obtained online from the GIS Unit of the Royal Botanic Gardens, Kew, and used with permission.

Most of the specimens studied, and unless indicated otherwise, are deposited in CAS, with additional material at the Royal Museum for Central Africa, Tervuren, and the Muséum d'Histoire Naturelle, Genève.

## ABBREVIATIONS

## ANATOMICAL

A1	posterior apodeme
A2	anterior apodeme
GAp	globular appendix of receptaculum (sensu Burger, 2010)
CT	curved tube
DK	dorsal knob of palp
EIP	embolar inferior prong (= E of Ubick and Griswold, 2011b)
EO	embolar opening
ESP	embolar superior prong (= DL of Ubick and Griswold, 2011b)
Op	globular appendix opening (= hole of Burger, 2010)
Pa	papillae of receptaculum
PME	posterior median eyes

PP	posterior median projection of TSc (= nail of Burger, 2010)
Re	receptaculum
TSc	transverse sclerite (= PSc of Burger, 2010; TP of Ubick and Griswold, 2011b)
VL	ventral lobe of A1
VP	ventral process of embolar region (= VL of Ubick and Griswold, 2011b)
VPL	ventral process lobe

#### INSTITUTIONAL

CAS	California Academy of Sciences
MHNG	Muséum d'Histoire Naturelle, Genève
NHMB	Naturhistorisches Museum, Bern
RMCA	Royal Museum for Central Africa

### SYSTEMATICS

#### Oonopidae Simon, 1890

Oonopids are very small (1–3 mm) ecribellate, haplogyne spiders (Ubick, 2005) with two claws (inferior absent) and the typical dysderoid respiratory system with a pair of posterior tracheal spiracles just behind the book lung openings. Recently suggested synapomorphies for the family include tarsal organs that have a proximal longitudinal ridge and that are serially dimorphic from, legs I to IV (Platnick et al., 2012a: 33) and fused testes in the males (Burger and Michalik, 2010). Oonopids have been traditionally classified into two subfamilies based upon the degree of body sclerotization. The Gamasamorphinae (= loricata) are more sclerotized and have abdominal scuta, whereas the soft-bodied Oonopinae (= molles) lack scuta (Roewer, 1942). Recent studies, based primarily on oonopid tarsal organ morphology present a very different classification of three subfamilies. Two of these, Orchestininae and Sulsulinae, contain only soft-bodied species, and the much-enlarged Oonopinae now also includes the loricata species, as well as the remaining molles (Platnick et al., 2012a).

#### *Volborattella* Saucedo and Ubick, new genus

TYPE SPECIES: *Volborattella teresae*, new species.

ETYMOLOGY: The generic name is a contraction of “*volom-borona*,” the Malagasy word for “feather” in reference to the plumose setae in the pedicel area, and *Silhouettella*. It is feminine in gender.

DIAGNOSIS: Members of *Volborattella* are easily recognized by the appearance of the abdomen, which is strikingly spotted or shimmering in alcohol (figs. 22, 23, 93, 94, 112, 113, 139, 140, 156, 157, 180, 182, 198, 199, 217, 218, 243, 244, 256, 257), a condition that has not been previously recorded in the family. These spiders are also unusual in having many types of modified setae, of which these stand out: (1) plumose setae at the pedicel region of both carapace (fig. 16) and abdomen (figs. 122, 123, 164, 207), with associated cuticular projections (figs. 18, 165); (2) feathery setae at the scutal ridges (figs. 29, 122, 123, 208) and on male cymbium (figs.

63, 125, 126, 167, 168, 223, 269); (3) broad, feathery, recumbent scutal setae, with associated wide pits that account for the spotty appearance (figs. 30, 31, 124); (4) setal comb on metatarsi I and II, prolateral ventrodiscal surface (figs. 40, 41); (5) curved modified setae on tibia I, prolateral ventrobasal surface (figs. 34–36); and (6) ventrodiscal setal brush on tibiae III and IV (figs. 45, 46). Additionally, both males and females have claw inner surfaces with a comblike arrangement of numerous tiny teeth, 30–50 on claws I–III (figs. 53–55) and 10–20 on claw IV (figs. 56, 57); comblike teeth also occur in few undescribed Malagasy taxa. The male is recognized by the distinctive embolar region, with the superior (= dorsal) prong forming a prominent spiral (figs. 67, 129, 169, 224, 271). A partial spiral occurs in *Noideatella tany* Álvarez-Padilla et al. (2012: figs. 227–229) and *Lionneta silhouettei* Benoit (Saaristo, 2001: fig.85), although these spiders are very different somatically in having strong leg spines, a compressed abdomen, and in lacking the many types of modified setae as found in *Volborattella*. The female genitalia are of the pelicinoid form, but the receptaculum differs from most others in two ways: (1) The papillae field is broad, covering much of the receptaculum (figs. 99, 145, 186, 232, 268), unlike the narrow field in most pelicinoids (Álvarez-Padilla et al., 2012: figs. 22, 354); a broad field does occur in *Silhouettella curieusei* (Benoit, 1979: fig. 5G) but is in a longitudinal orientation, unlike in *Volborattella*. (2) The receptaculum has an accessory structure, a curved tube (CT), asymmetrically positioned to the left or right of the midline; a similar structure occurs in *Lionneta*, but not in other known pelicinoids.

DESCRIPTION: MALE: Total length 1.35–1.65 mm. CEPHALOTHORAX: strongly sclerotized, with setae finely serrate and flattened. Carapace ovoid in most species (figs. 4, 151, 193) to broadly oval in *V. guenevera* and *V. paulyi* (figs. 107, 238); of uniform coloration, light to dark orange-brown; pars cephalica slightly (fig. 195) to more strongly elevated (figs. 109, 127) in lateral view, anteriorly narrowed to at least half its maximum width, without fovea, with rounded posterolateral corners (fig. 4), with surface strongly granulate except on posterior declivity (fig. 9), without pits or spikes, with ventral edge of pars thoracica posterior margin strongly undulate (figs. 8, 16), with setae light-colored and scattered; lateral margin straight (fig. 6) to slightly undulate (fig. 109), strongly rebordered, without denticles, and with marginal setae needlelike, not flattened. Clypeus high (ALE separated from edge of carapace by their radius or more), vertical in lateral view and curved downwards at sides in anterior view, with setae finely serrate, but not flattened (figs. 10, 15, 19). Eyes six, well developed, with squared PME that touch throughout most of their length, with PER slightly recurved in dorsal view, procurved in anterior view (figs. 4, 6, 7, 13–15). Sternum (figs. 5, 11) nearly as wide as long, with uniform coloration, with surface finely punctate (fig. 120), without median concavity or large pits, with radial furrows of tiny pits between coxae (fig. 11), with anterior margin modified (figs. 5, 12, 108, 120, 161, 205), with three pairs of lateral, intercoxal projections (fig. 152), strongly fused to carapace (figs. 5, 6), with posterior margin not extending posteriorly of coxae IV, with infracoxal grooves with anterior and posterior openings at lateral margins (fig. 81, female), without extensions of precoxal triangles, with distances between coxae approximately equal, with setae sparse and evenly scattered. Mouthparts same as sternum in sclerotization. Chelicerae straight, with anterior faces unmodified (fig. 19), with fangs unmodified and directed medially (fig. 20); setae light colored, finely serrate, densest medially, with row of flat-

tened setae on paturon promargins (fig. 89, female), without specialized setae on paturon inner margin. Labium triangular, separate from sternum, with medial indentation at anterior margin, with six or more distal setae, with subdistal setae unmodified (fig. 21). Endites with anteromedian tips strongly pointed with a single toothlike projection (figs. 21, 121, 162, 206), with smooth, slightly spatulate setae at anterior margin (fig. 87, female), with posteromedian parts unmodified, with serrula (fig. 88, female), with palmate setae at anterior margins (fig. 162). PEDICEL REGION: with plumose setae and cup-shaped cuticular outgrowths near posterior margin of pars thoracica (figs. 16, 18, 119) and on anterior of abdomen (fig. 27), with apical branching of plumose setae appearing to form an irregular, latticelike network along surface under plumose setae, with abdominal plumose setae most abundant dorsad and laterad of pedicel, with paired lateral pores in pedicel cavity on cephalothorax (figs. 16, 17), with abdominal pedicel tube short and with small, dorsolateral, triangular extensions (fig. 27), with paired scutal ridges (figs. 25, 27) with pairs of needlelike setae on scutopedicel region on abdomen (figs. 27, 29, 163, 206). ABDOMEN: Ovoid, strongly sclerotized, with scuta strongly rebordered, with interscutal membrane pale yellow (figs. 22–26, 112–116); scutal setae light colored, finely serrate, flattened, uniform, not thickened anteriorly, on anterior margin of small to large, oval to round punctation (figs. 30, 31). Book lung covers small, elliptical, without tubercle on anterolateral edge (fig. 32). Dorsal scutum covering full dorsal surface of abdomen (figs. 22–24), of uniform coloration, with surface punctate (fig. 31), with anterior margin straight to sinuous (figs. 25, 115, 159, 201, 246), strongly rebordered, without projecting denticles on anterior half, and free from epigastric scutum. Epigastric scutum surrounds and extends far dorsad of pedicel, slightly protruding near gonopore (figs. 23–25). Postepigastric scutum only laterally fused to epigastric scutum, not fused near gonopore, without posteriorly directed lateral apodemes visible from exterior, with posterior spiracles connected by groove (figs. 23, 24, 26). Spinneret and supraanal scuta wide, with fringe of setae forming an incomplete ring (figs. 26, 33). Colulus represented only by setae. LEGS: Yellow to whitish, with uniform coloration, with all femora approximately same size, with length of patella plus tibia I shorter than carapace, without leg spines, without ventral scopula on tibiae or metatarsi (figs. 1–3, 34, 42), metatarsi I and II with mesoapical comb (fig. 41), with lyriform slit sensilla near patellar retrolateral base with groove extending distad to patellar margin (figs. 43, 44), with paired rows of small, dorsolateral protuberances flanking distal trichobothria on tibiae (fig. 38), with round to oval cuticular glands with proximal notch on tibiae and metatarsi (fig. 37, female), with prolateral modified setae on tibia I (fig. 35), with patch of modified setae with notched setal pits on ventral apex of tibiae III and IV (figs. 45–47). Superior tarsal claw dentition bidentate, with four lateral teeth on all claws (fig. 55), inner faces with many thin teeth, 20–50 on claws I–III (figs. 53, 55), 10–20 on claw IV (fig. 57), distal teeth fused on claws I and II. Trichobothria with bases rounded, with aperture internal texture gratelike, with hoods covered by numerous low, closely spaced transverse ridges, and with three trichobothria on tibia and one on metatarsus (fig. 48). Tarsal organs teardrop-shaped capsule with the typical number of sensilla, three on legs I and II, two on the other appendages, distal sensilla sometimes bifid, giving the impression of an increased number (fig. 52, female), drop shaped, with two or more sensilla visible. GENITALIA: Sperm pore small, rebordered, and situated in front of anterior spiracles, which are connected by a

deep groove (figs. 69, 124). Palp pale yellow, not strongly sclerotized, with right and left palps symmetrical, with proximal segments all normal size, with femur attaching to patella basally, with three trichobothria on tibia; cymbium ovoid in dorsal view, not fused with bulb or extending beyond distal tip of bulb, with distal patch of setae, with two long setae on prolateral margin near apex (figs. 62, 63), with tarsal organ (fig. 70) near retrolateral margin; bulb stout, spherical, and 1 to 1.5 times as long as cymbium; embolar region with (1) ventral process (VP) that has a secondary lobe (VP2), (2) superior prong (ESP), which originates from the dorsal bulb surface and forms a conspicuous spiral, and (3) inferior prong (EIP), which originates from the retrodorsal surface and contains the embolar duct, which opens (EO) via short tube subapically on the prong (figs. 58–68, 129, 169, 224, 271).

FEMALE: Total length 1.50–1.90 mm. As in male except as noted. CEPHALOTHORAX: Sternum anterior and lateral margins unmodified (figs. 75, 80). Endites without toothlike projection on anteromedian tips (fig. 86). Female palp without spines, with tarsus not swollen, with small protuberances on distal femur, with distal patch of setae on tarsus (figs. 90, 91). ABDOMEN: Book lung covers anterior to book lungs, internally book lungs with digitate extensions (fig. 99). Ventral scuta not fused and epigastric scutum attaching with lateral joints to postepigastric scutum (figs. 94, 95, 98). GENITALIA: External opening slitlike (fig. 98); internally with large receptaculum (Re) composed of domed dorsal sclerite with ventral flexible segment connected to posterior epigastric scutum (fig. 99), with papillae (Pa) in shallow depressions covering anterior half of dorsal receptaculum sclerite (fig. 188), with pair of large, triangular, winglike posterior apodemes (A1) laterally attached to receptaculum (figs. 99, 102), with anterior end of globular appendix (GAP) elevated on stalk projecting from receptaculum to opening at uterus externus (figs. 100, 146, 231), with curved tube at GAP that is asymmetrically positioned, on either the left (figs. 145, 232, 268) or right side (figs. 99, 186), and with T-shaped transverse sclerite (TSc) attached to anterior uterus externus (figs. 100, 146).

SPECIES INCLUDED: *Volborattella paulyi*, *V. teresae*, *V. guenevera*, *V. nasario*, *V. toliara*.

DISTRIBUTION: *Volborattella* is known only from Madagascar.

Key to the Species of *Volborattella*

1. Abdomen color brown or orange, lacking glittery reflections (figs. 93, 156, 198); carapace narrower, with the W / L ratio generally  $\leq 0.82$  (figs. 74, 151, 193); male embolar region with inferior prong tip (EIP) either straight or apically bent (figs. 64, 169, 227); female receptaculum slightly longer (figs. 99, 186, 232).....2
- Abdomen color yellowish or yellow-orange with glittery reflections (figs. 112, 243); carapace wider, with the W/L ratio generally  $\geq 0.85$  (figs. 107, 238); male embolar region with EIP straight (figs. 127, 271); female receptaculum slightly shorter (figs. 145, 262).....4
2. Abdomen color brownish (fig. 156); shape wider, W/L about 0.8; surface finely punctate; setae with small oval pits and large bases (fig. 185); dorsal scute with anterior margin evenly curved (fig. 159); male embolus with superior prong (ESP) long and slender and inferior prong (EIP) short and straight (fig. 169); female genitalia with thicker lower lip of gonopore (fig. 185) and longer receptaculum (fig. 186)..... *V. nasario*

- Abdomen color orangish (figs. 22, 198); shape narrower, W/L about 0.7; surface coarsely punctate; setae with larger round pits and small bases (figs. 30, 31); dorsal scute with anterior margin sinuous (figs. 25, 201); male embolus with ESP shorter and stouter and ISP longer and apically bent (figs. 64, 67, 224, 227); female genitalia with thinner lower lip of gonopore (figs. 98, 229) and shorter receptaculum (figs. 99, 232).....3
- 3. Abdomen with conspicuous pale spots (figs. 22, 23); male embolus with superior prong (ESP) longer, making about a 3/4 turn (fig. 67); female genitalia with receptacular ridge absent and posterior apodemes with large ventral lobe (VL, figs. 99, 102)..... *V. teresae*
- Abdomen without conspicuous pale spots (figs. 198, 199); male embolus with superior prong (ESP) shorter, making about a 1/2 turn (fig. 224); female genitalia with receptacular ridge present and VL strongly reduced (figs. 233, 234)..... *V. toliara*
- 4. Abdomen color yellow-orange, with glittery reflections; shape stouter, W/L from 0.75–0.80 (figs. 112, 139); eyes with black pigment (figs. 110, 137); abdominal setae with pits small, round, and well separated (figs. 124, 144); male embolus with smaller inferior prong (EIP) (fig. 127); female genitalia with larger ventral lobe (VL) of the posterior apodemes (fig. 14) ..... *V. guenevera*
- Abdomen color yellowish, lacking glittery reflections; shape more elongate, W/L from 0.70–0.74 (figs. 243, 256); eyes with gray pigment (figs. 241, 254); abdominal setae with pits large, angular, and contiguous (fig. 261); male embolus with larger inferior prong (EIP) (fig. 271); female genitalia with smaller VL (fig. 268)..... *V. paulyi*

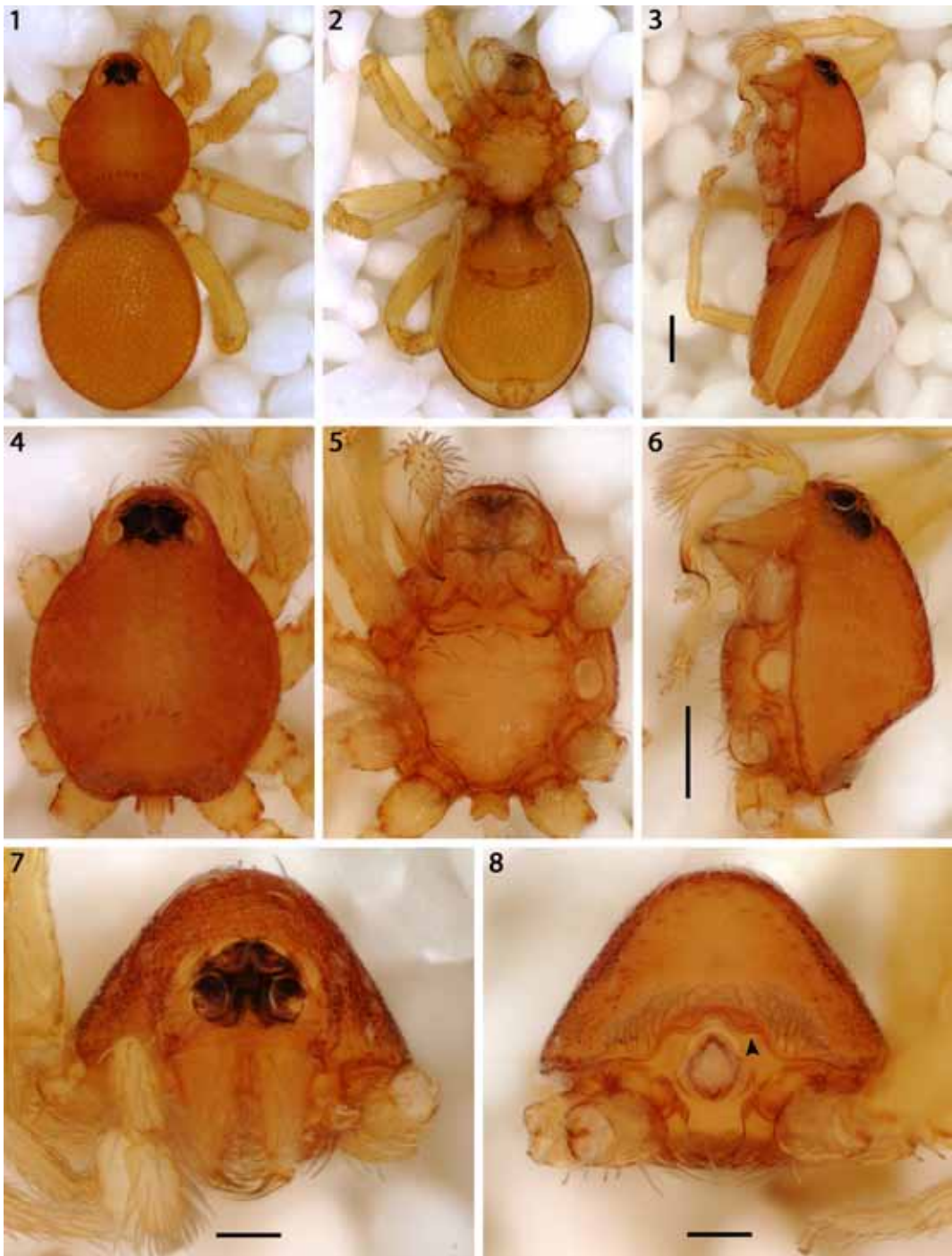
***Volborattella teresae*, new species**

Figures 1–103, 275–283, map 1, 3

**TYPES:** MADAGASCAR: Toliara: Reserve Privé Berenty, Forêt de Bealoka, 14.6 km 329° NW Amboasary, S24.95694°, E46.27138°, elev. 35 m, 3–8 Feb. 2002, gallery forest, sifted litter (leaf mold, rotten wood), collected by Fisher-Griswold Arthropod Team, BLF5316, CASENT 9030856 (PBI\_OON 35756), holotype ♂ and allotype ♀ (deposited in CAS).

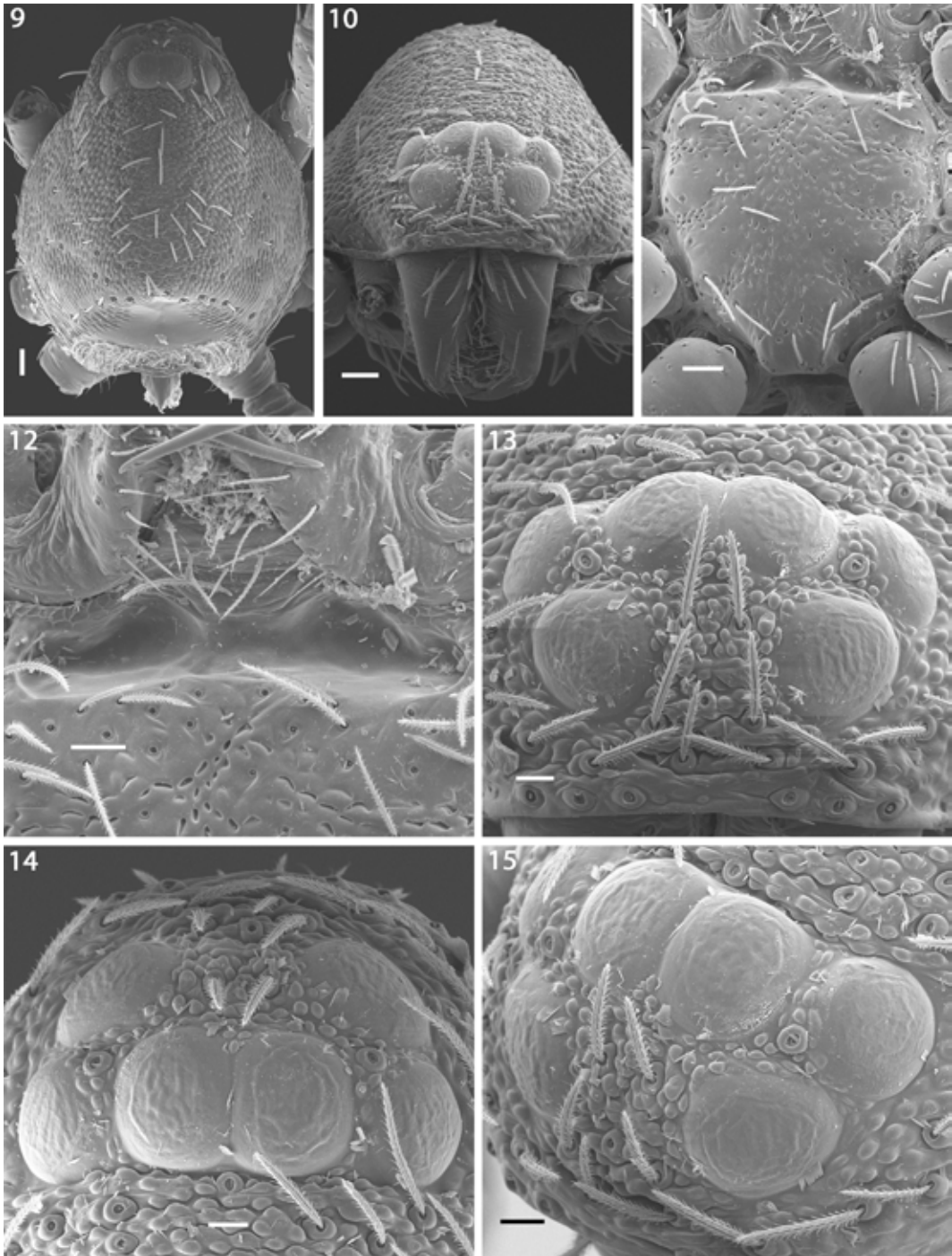
**ETYMOLOGY:** The specific name is in honor of C.E.G.'s friend and spouse, Teresa Meikle.

**DIAGNOSIS:** The orange abdomen covered with pale round spots separates *V. teresae* from other *Volborattella* (figs. 22, 23, 93, 94), as does the combination of large, round setal pits enclosing relatively small setal bases (figs. 30, 31, 98), and abdomen more elongate than in *V. guenevera* and *V. nasario*, and a dorsal scute as in *V. toliara*, with a sinuous anterior margin (figs. 25, 96). The male of *V. teresae* differs from those of *V. guenevera* and *V. nasario* in having a smaller endite projection (figs. 20, 21), deeper sternal cavity (figs. 5, 11, 12), longer embolar inferior prong (EIP) (figs. 64–67), and in lacking a ridge above the scutal ridges (figs. 25, 27). The EIP is slender and apically bent, resembling that in *V. toliara*, from which it differs in having a longer ESP (figs. 64–67, 224–228). The female differs from that of *V. nasario* in having a thinner posterior margin of the gonopore (fig. 98), from *V. nasario* and *V. guenevera* in having pointed (vs. rounded or angular) anterodorsal lobes of the posterior apodemes (A1), from *V. toliara* in having a large ventral lobe of A1 (strongly reduced in *V. toliara*) and in having a weak receptacular ridge (strong in *V. toliara*) (figs. 102, 232–234).

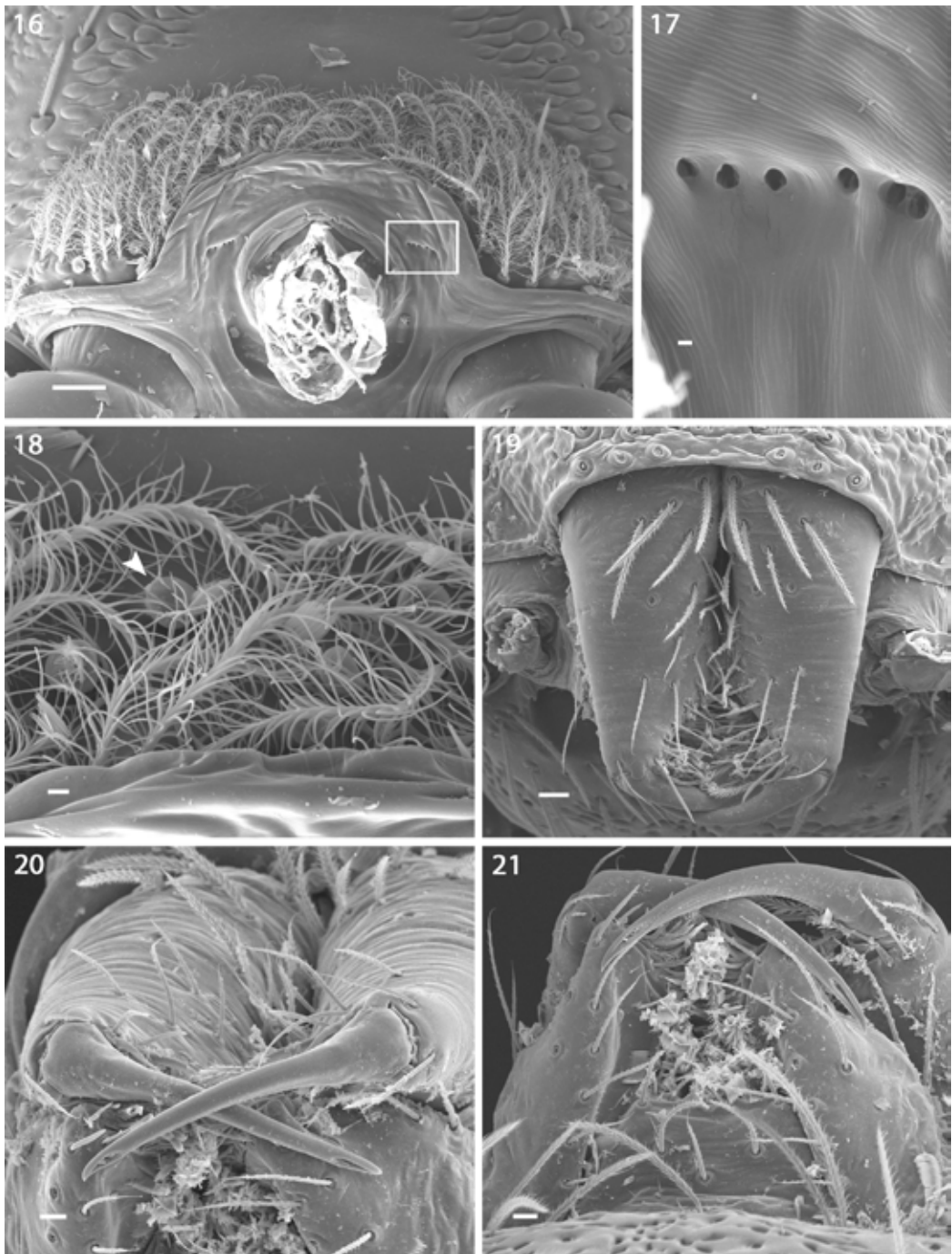


FIGS. 1–8. *Volborattella teresae*, new species, paratype male (PBI\_OON 2006). 1. Habitus, dorsal view. 2. Same, ventral view. 3. Same, lateral view. 4. Prosoma, dorsal view. 5. Same, ventral view. 6. Same, lateral view. 7. Same, anterior view. 8. Same, posterior view, with arrow indicating strong undulation of posterior margin ventral edge. Scale bars: 200  $\mu$ m (3–6), 100  $\mu$ m (7, 8).

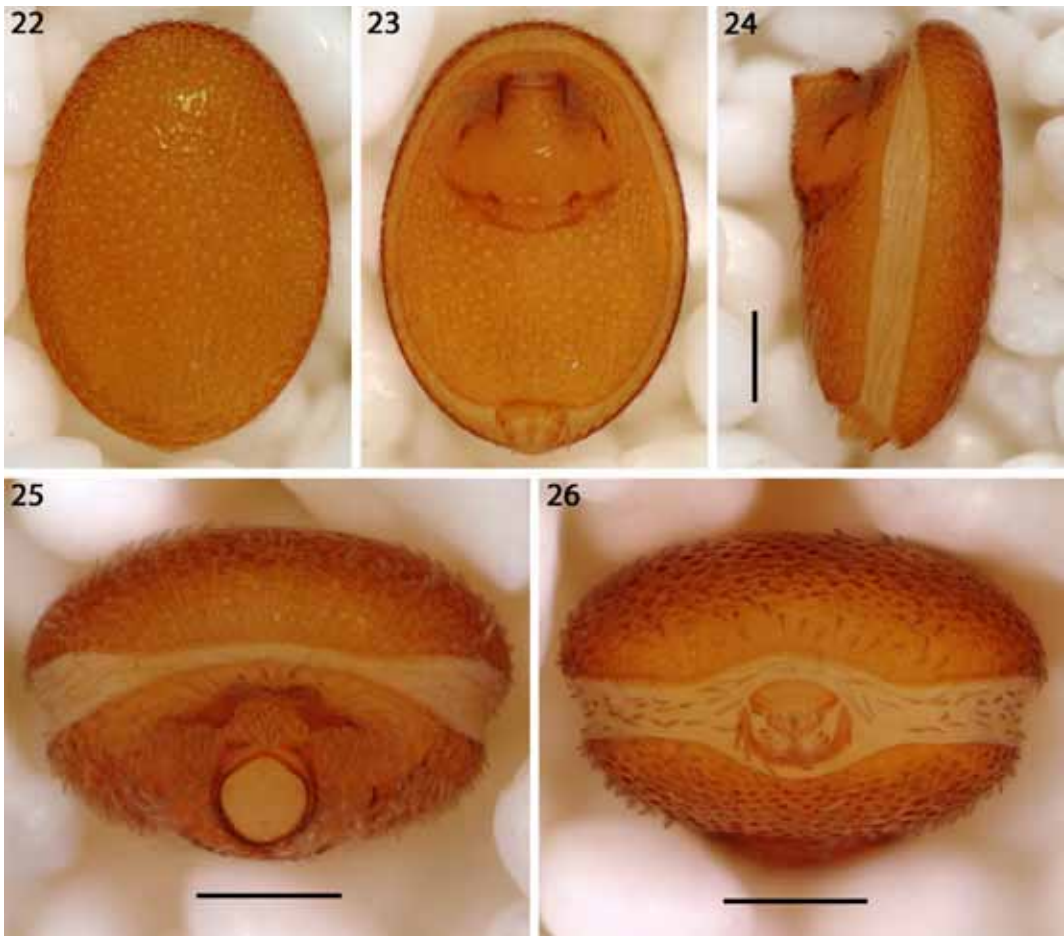




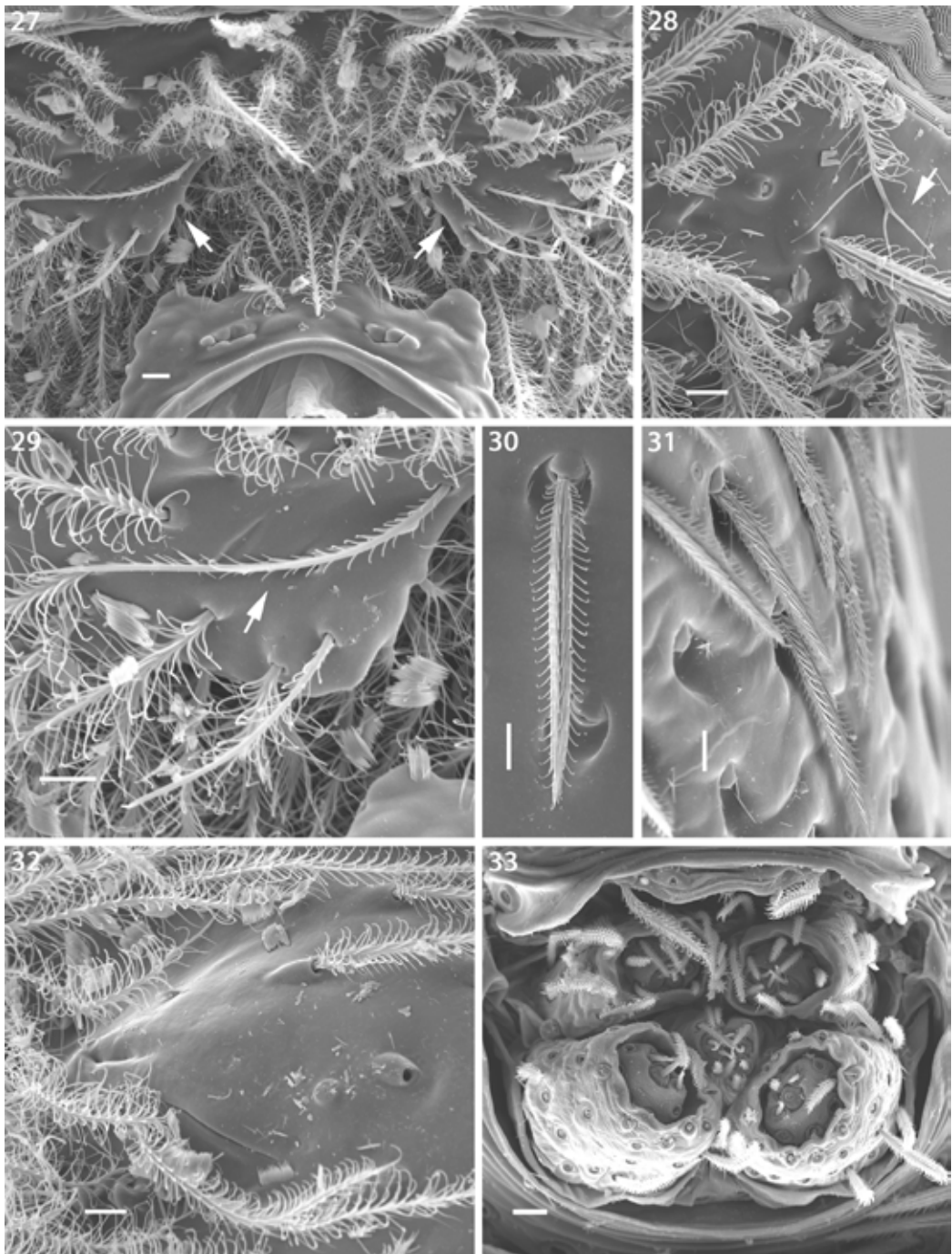
FIGS. 9–15. *Volborattella teresae*, new species, paratype male (PBI\_OON 2006). **9.** Prosoma, dorsal view. **10.** Same, anterior view. **11.** Sternum, ventral view. **12.** Same, anterior margin, ventral view. **13.** Eyes, anterior view. **14.** Same, dorsal view. **15.** Same, anterolateral view. Scale bars: 50  $\mu\text{m}$  (9–11), 30  $\mu\text{m}$  (12), 20  $\mu\text{m}$  (13–15).



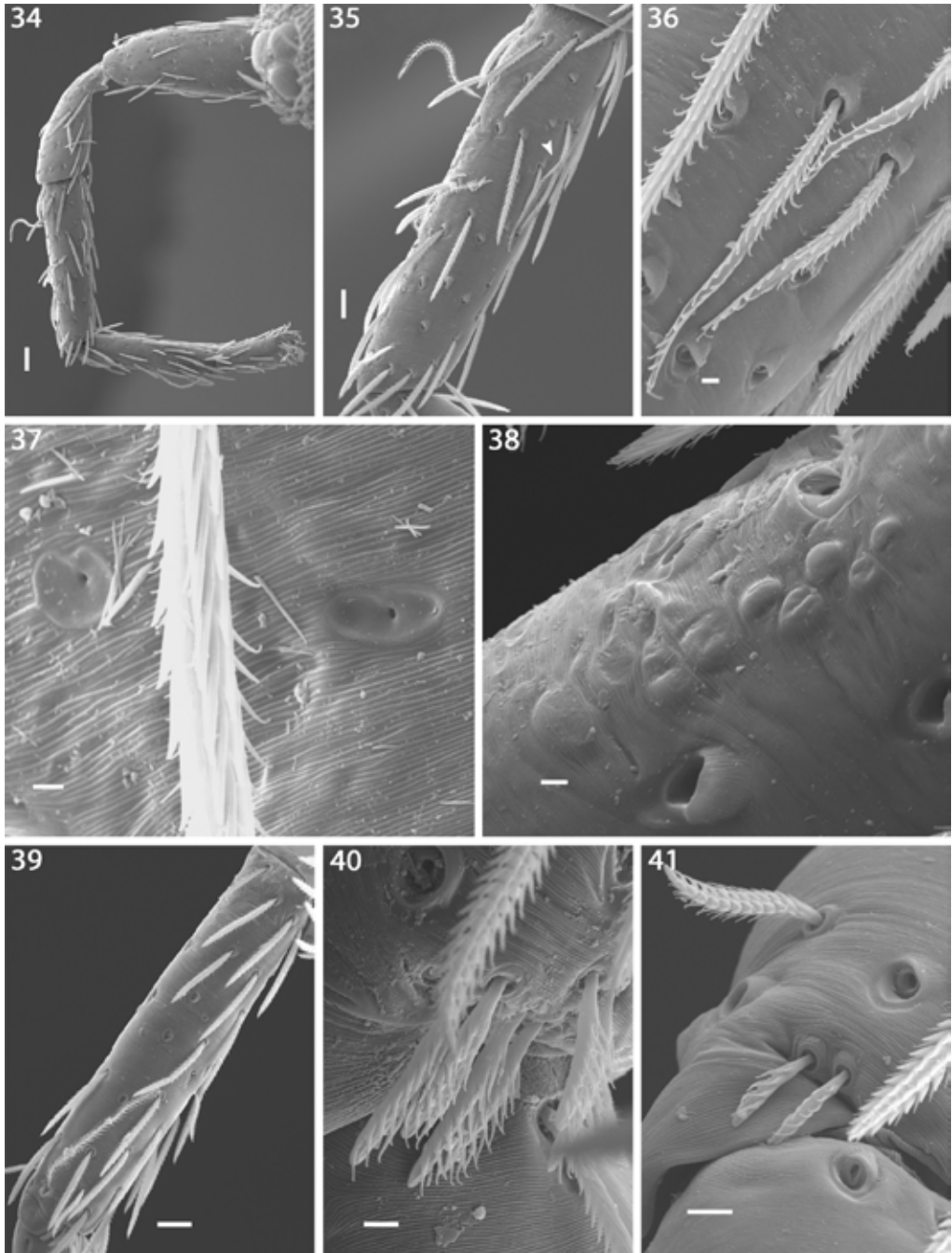
FIGS. 16–21. *Volborattella teresae*, new species, paratype male (PBI\_OON 2006). **16.** Prosoma, posterior view, pedicel region, with box indicating location of pores in pedicel cavity. **17.** Same, pores. **18.** Same, plumose setae, with arrow indicating cup-shaped cuticular outgrowths. **19.** Chelicerae, anterior view. **20.** Fangs, ventral view. **21.** Endites, posterior view. Scale bars: 30  $\mu\text{m}$  (16), 1  $\mu\text{m}$  (17), 3  $\mu\text{m}$  (18), 20  $\mu\text{m}$  (19), 10  $\mu\text{m}$  (20, 21).



FIGS. 22–26. *Volborattella teresae*, new species, paratype male (PBI\_OON 2006), abdomen. 22. Dorsal view. 23. Ventral view. 24. Lateral view. 25. Anterior view. 26. Posterior view. Scale bars: 200  $\mu\text{m}$ .

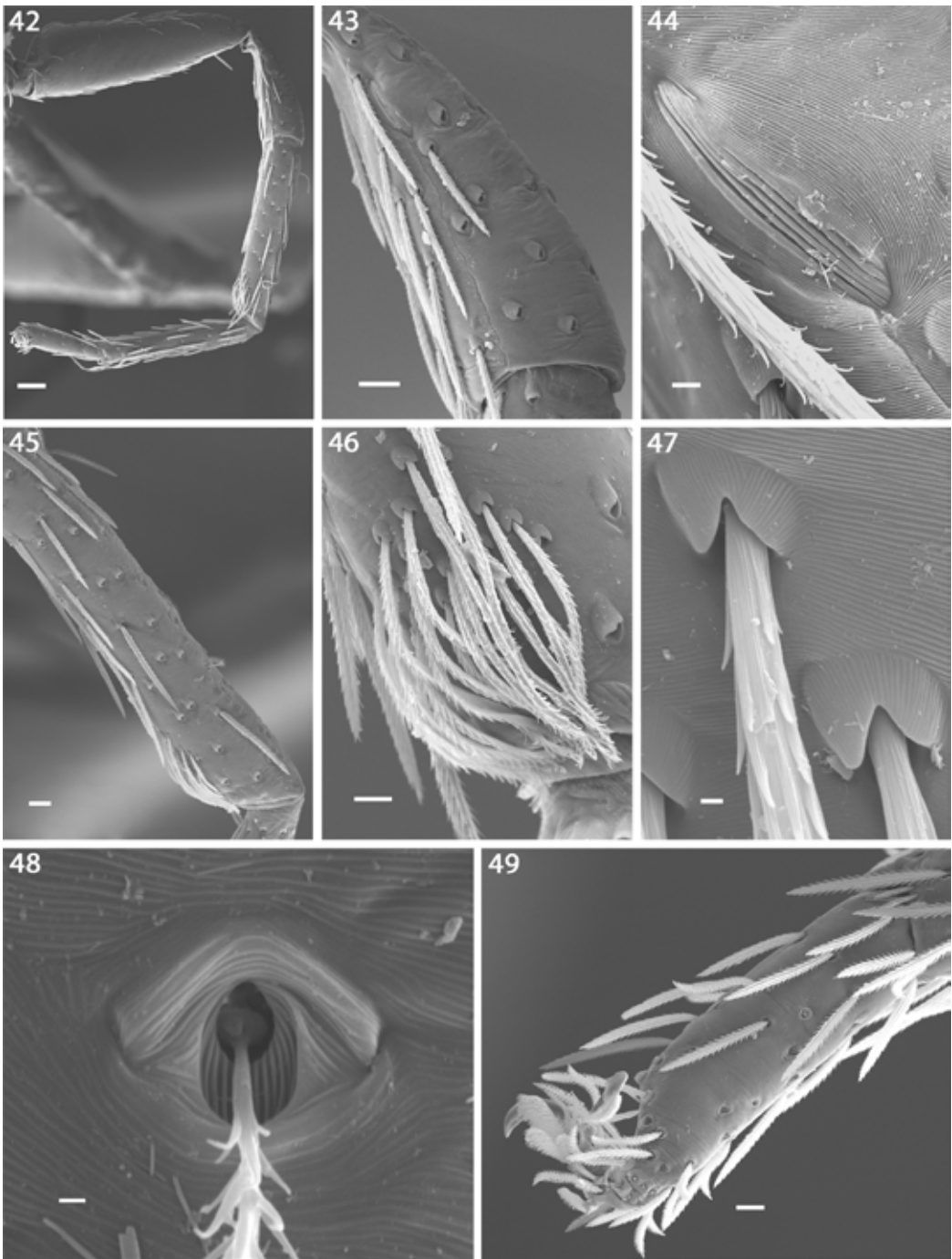


FIGS. 27–33. *Volborattella teresae*, new species, paratypes male and female (PBI\_OON 2006), abdomen. 27. Male, anterior view, scutal ridges (arrows). 28. Female, same, plumose setae showing apical branching (arrow). 29. Male, same, scutal ridge showing needlelike seta (arrow). 30. Female, dorsal scutum, seta, dorsal view. 31. Same, lateral view. 32. Male, book lung cover, ventral view. 33. Female, spinnerets, posterior view. Scale bars: 10  $\mu$ m.

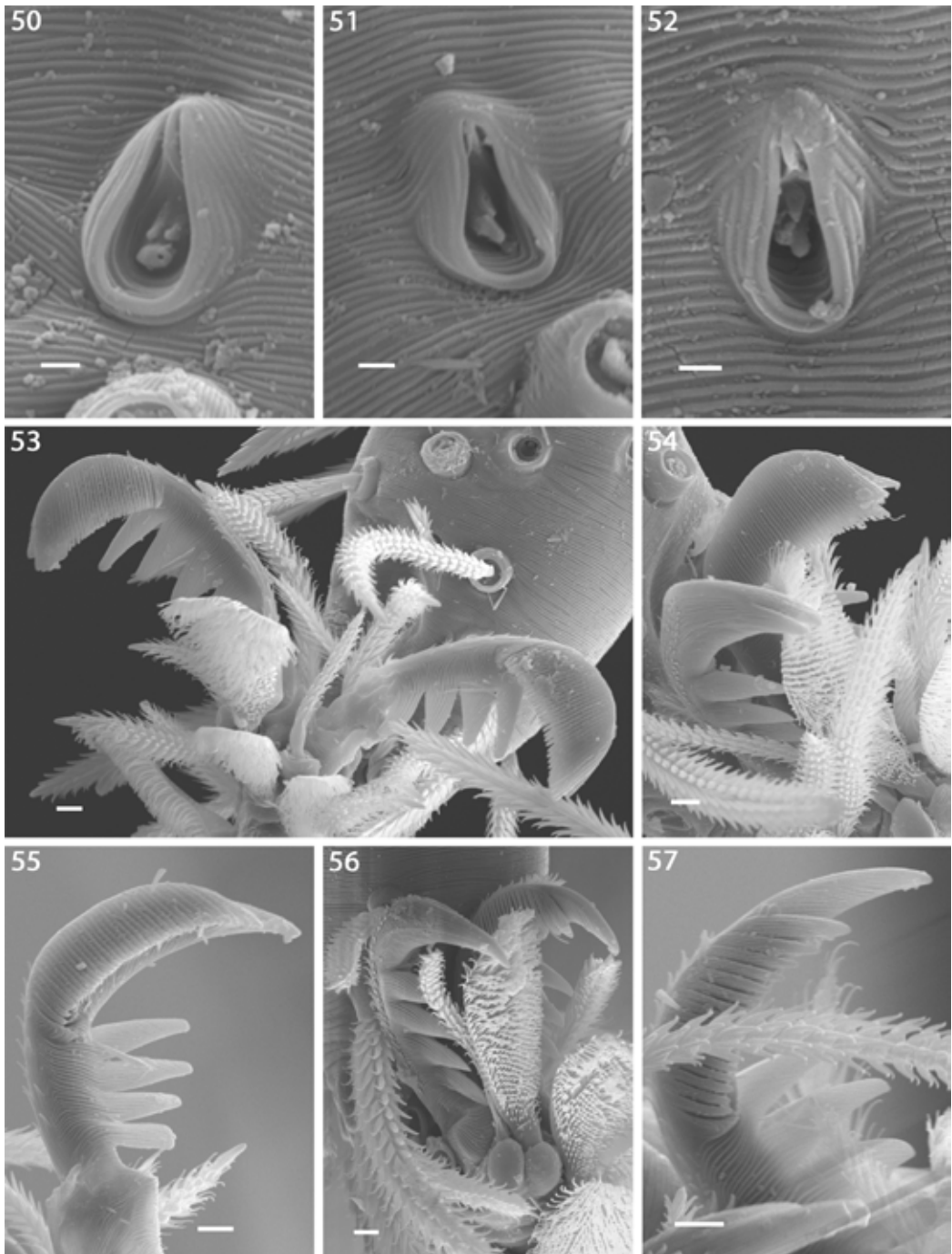


FIGS. 34–41. *Volborattella teresae*, new species, paratypes male and female (PBI\_OON 2006), legs. **34.** Male, leg I, prolateral view. **35.** Male, tibia I, prolateral view, with arrow indicating specialized setae. **36.** Female, same, magnified view. **37.** Female, tibia I, dorsal view showing cuticular glands. **38.** Male, tibia II, dorsal view showing small protrusions. **39.** Male, metatarsus I, prodorsal view. **40.** Female, metatarsus II, prolateral view, comb. **41.** Male, metatarsus III, prolateral view, reduced comb. Scale bars: 40  $\mu\text{m}$  (34), 20  $\mu\text{m}$  (35, 39), 3  $\mu\text{m}$  (36, 38, 40), 2  $\mu\text{m}$  (37), 5  $\mu\text{m}$  (41).

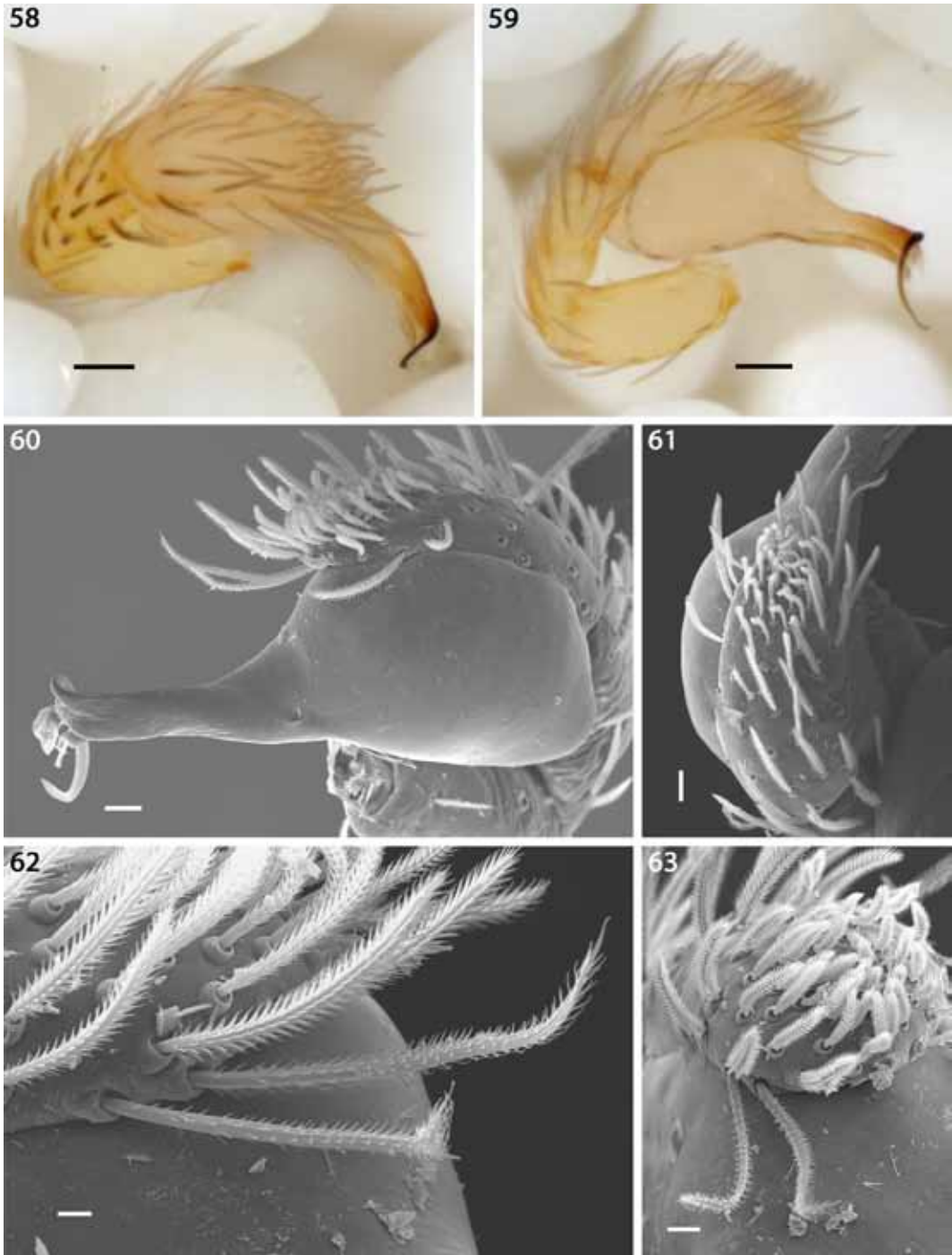




FIGS. 42–49. *Volborattella teresae*, new species, paratypes male and female (PBI\_OON 2006), legs. **42.** Male, leg IV, retrolateral view. **43.** Same, patella IV. **44.** Same, magnified view showing slit sensilla. **45.** Female, tibia IV, retrolateral view. **46.** Same, ventroapical view, specialized setae. **47.** Male, same, showing setal pits. **48.** Same, dorsal view, trichobothria. **49.** Male, tarsus I, prolateral view. Scale bars: 60  $\mu\text{m}$  (42), 20  $\mu\text{m}$  (43, 45), 3  $\mu\text{m}$  (44), 10  $\mu\text{m}$  (46, 49), 1  $\mu\text{m}$  (47, 48).

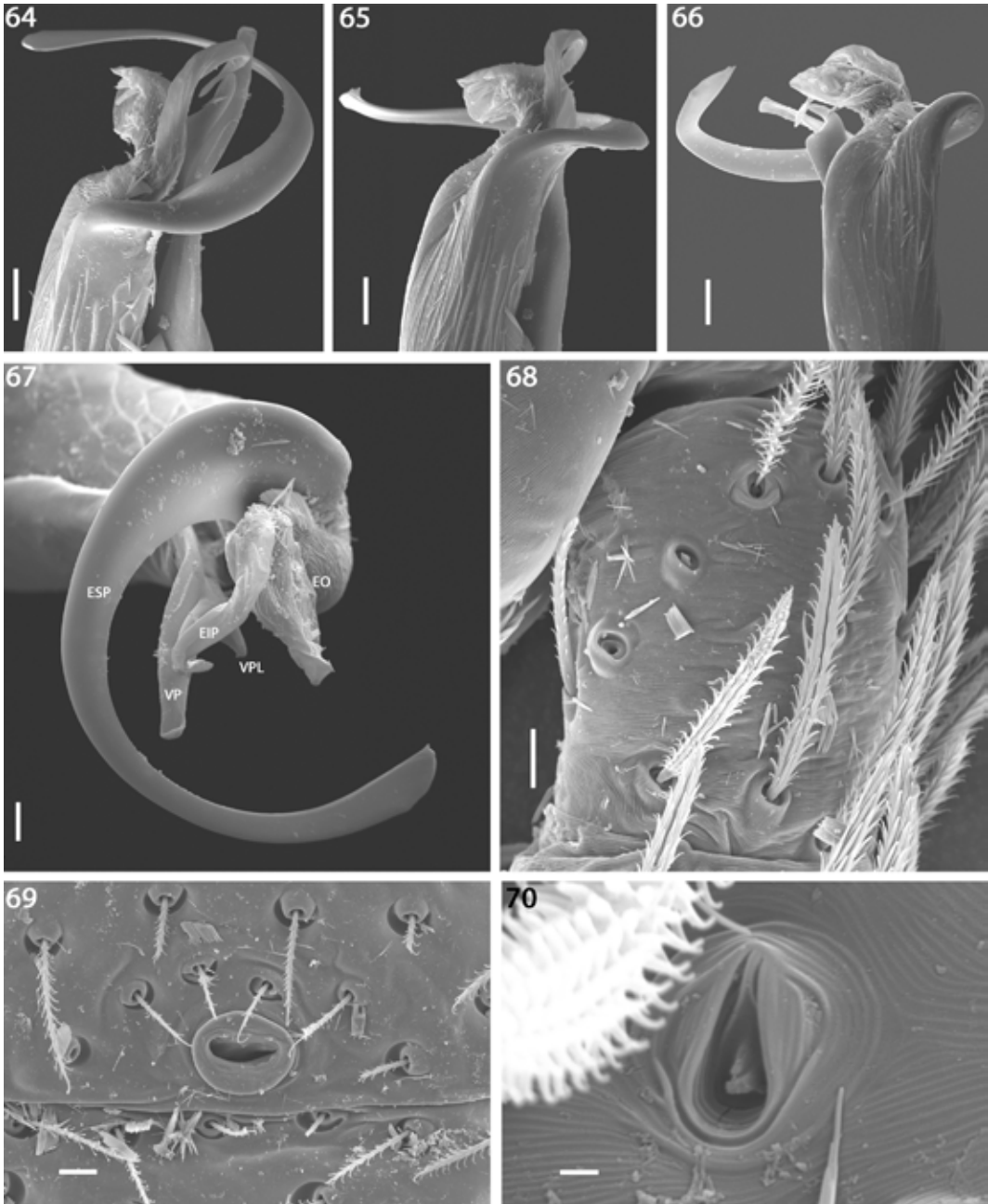


FIGS. 50–57. *Volborattella teresae*, new species, paratypes male and female (PBI\_OON 2006). 50. Female, tarsal organ I, dorsal view. 51. Male, tarsal organ III, dorsal view. 52. Female, tarsal organ IV, dorsal view. 53. Male, claw I, apical view. 54. Female, claw II, retrolateral view. 55. Male, claw III, retrolateral view. 56. Female, claw IV, retrolateral view. 57. Male, same. Scale bars: 1  $\mu\text{m}$  (50–52), 3  $\mu\text{m}$  (53–57).

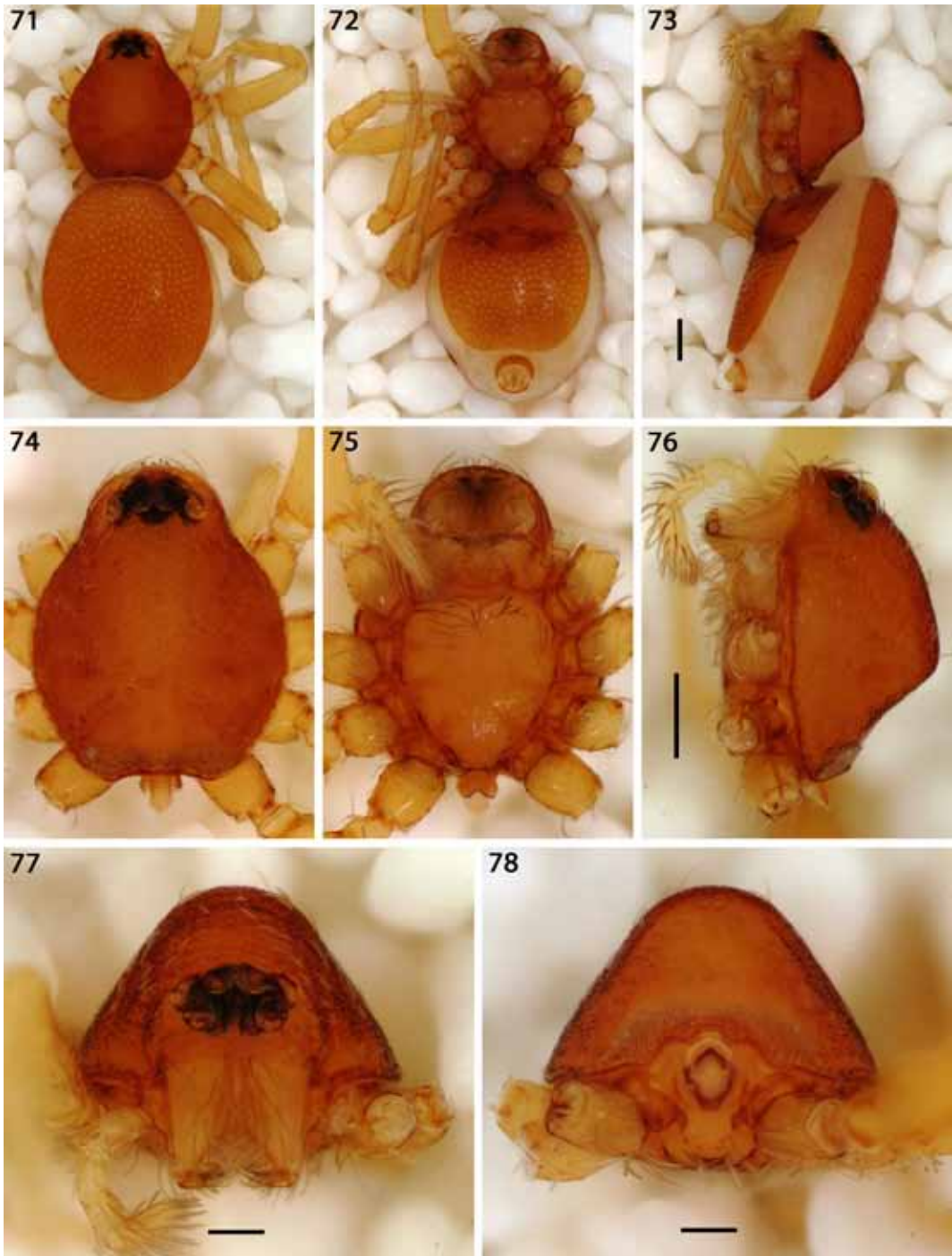


FIGS. 58–63. *Volborattella teresae*, new species, paratype male (PBI\_OON 2006), left palp. **58.** Dorsal view. **59.** Prolateral view. **60.** Bulb, retrolateral view. **61.** Cymbium, dorsal view. **62.** Same, prolateral view, showing long setae. **63.** Same, anterior view. Scale bars: 50  $\mu\text{m}$  (58, 59), 20  $\mu\text{m}$  (60, 61), 6  $\mu\text{m}$  (62), 10  $\mu\text{m}$  (63).

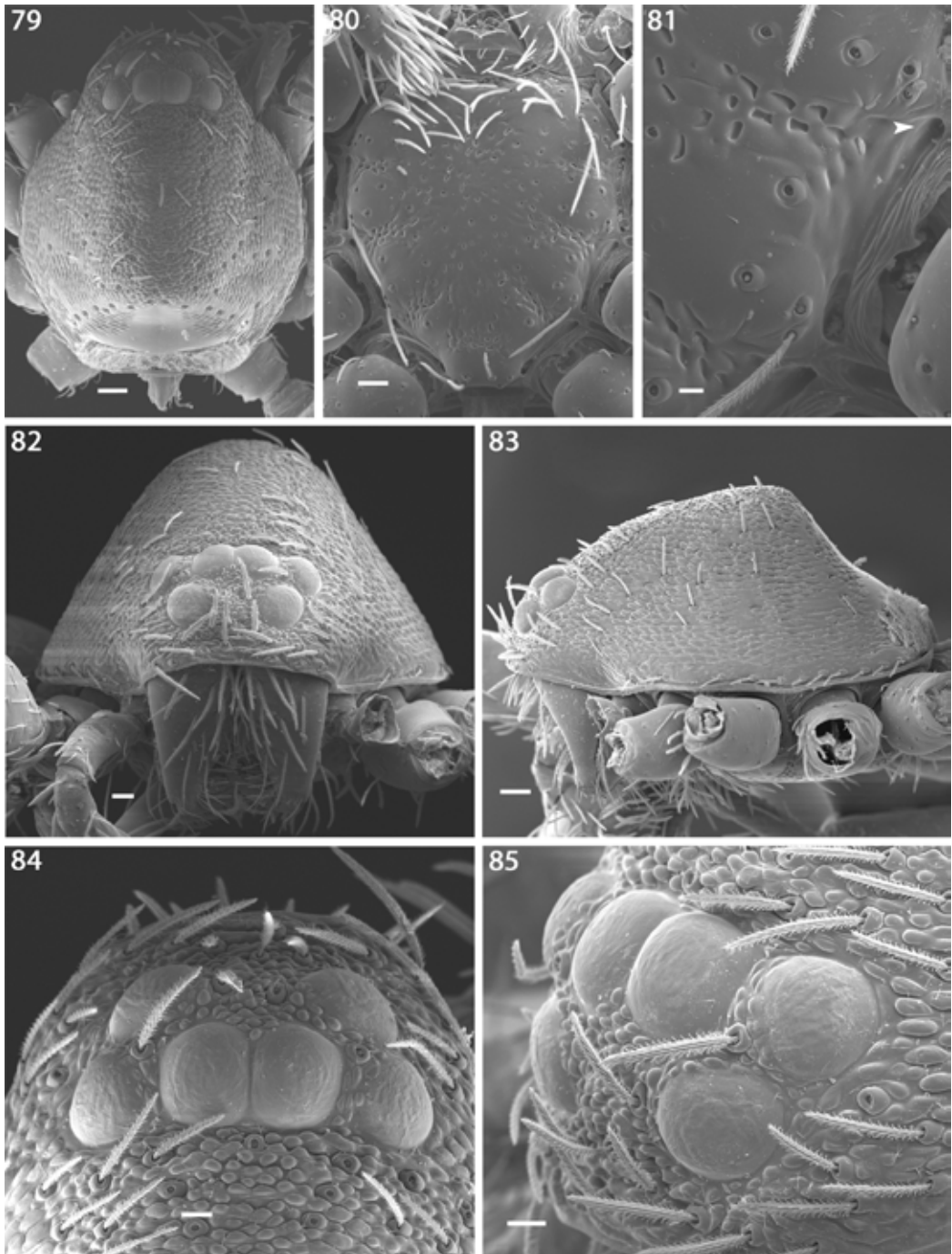




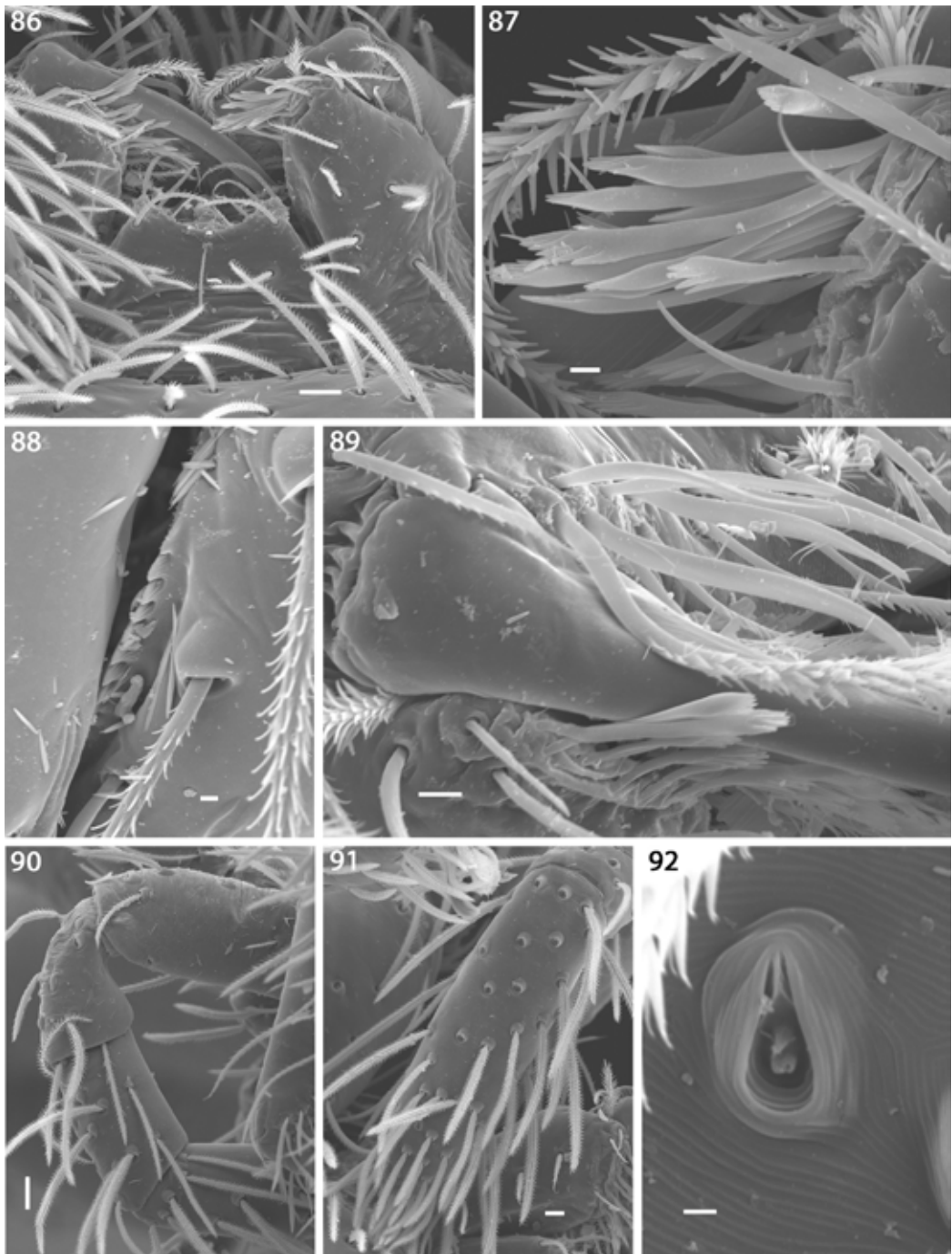
FIGS. 64–70. *Volborattella teresae*, new species, paratype male (PBI\_OON 2006). **64.** Left palp, embolus, prolateral view. **65.** Same, dorsal view. **66.** Same, retrolateral view. **67.** Same, apical view. **68.** Palp, tibia, dorsal view. **69.** Sperm pore, ventral view. **70.** Palp, tarsal organ, dorsal view. Abbreviations: EIP, embolus inferior prong; EO, embolus opening; ESP, embolus superior prong; VP, ventral process; VPL, ventral process lobe. Scale bars: 10  $\mu\text{m}$  (64–66, 68, 69), 6  $\mu\text{m}$  (67), 1  $\mu\text{m}$  (70).



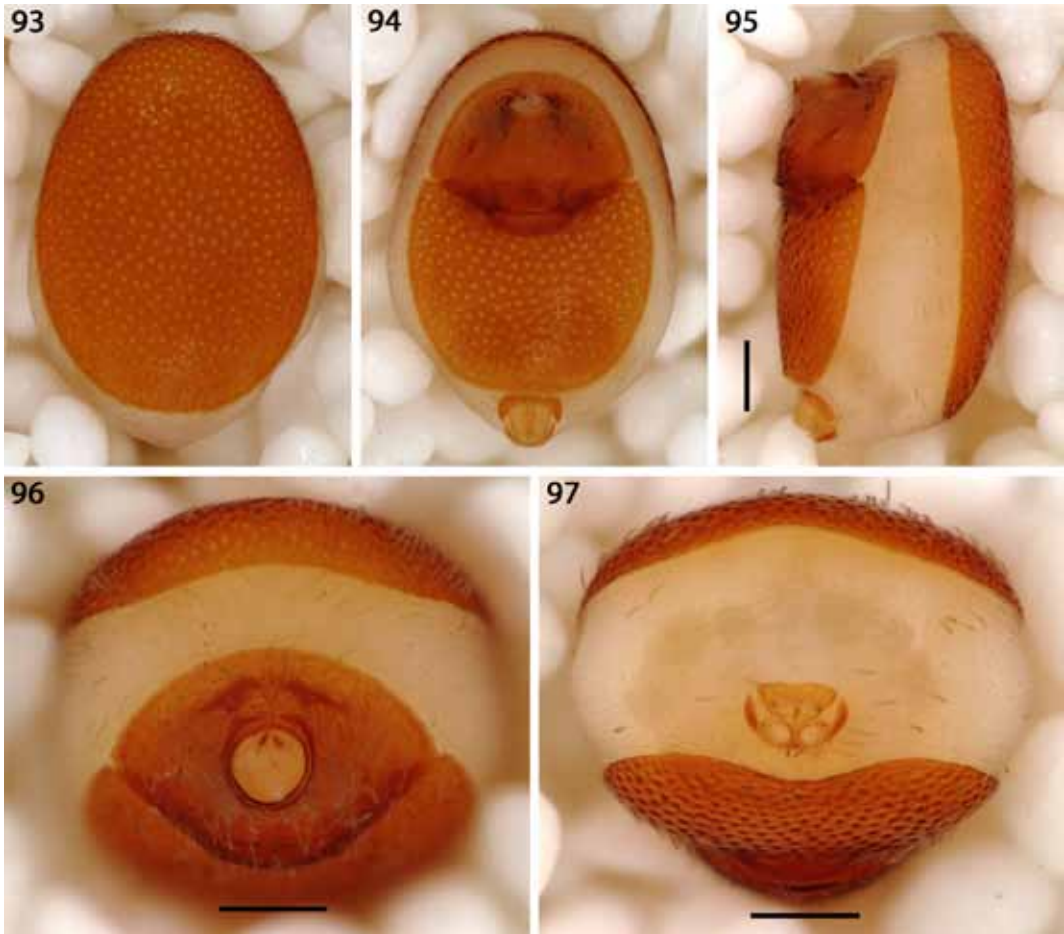
FIGS. 71–78. *Volborattella teresae*, new species, paratype female (PBI\_OON 2006). 71. Habitus, dorsal view. 72. Same, ventral view. 73. Same, lateral view. 74. Prosoma, dorsal view. 75. Same, ventral view. 76. Same, lateral view. 77. Same, anterior view. 78. Same, posterior view. Scale bars: 200  $\mu$ m (73–76), 100  $\mu$ m (77, 78).



FIGS. 79–85. *Volborattella teresae*, new species, paratype female (PBI\_OON 2006). **79.** Prosoma, dorsal view. **80.** Sternum, ventral view. **81.** Same, furrow at lateral margin, with arrow indicating opening in infracoxal groove. **82.** Prosoma, anterior view. **83.** Same, lateral view. **84.** Eyes, dorsal view. **85.** Same, anterolateral view. Scale bars: 60  $\mu\text{m}$  (79), 20  $\mu\text{m}$  (80, 84, 85), 10  $\mu\text{m}$  (81), 30  $\mu\text{m}$  (82), 50  $\mu\text{m}$  (83).

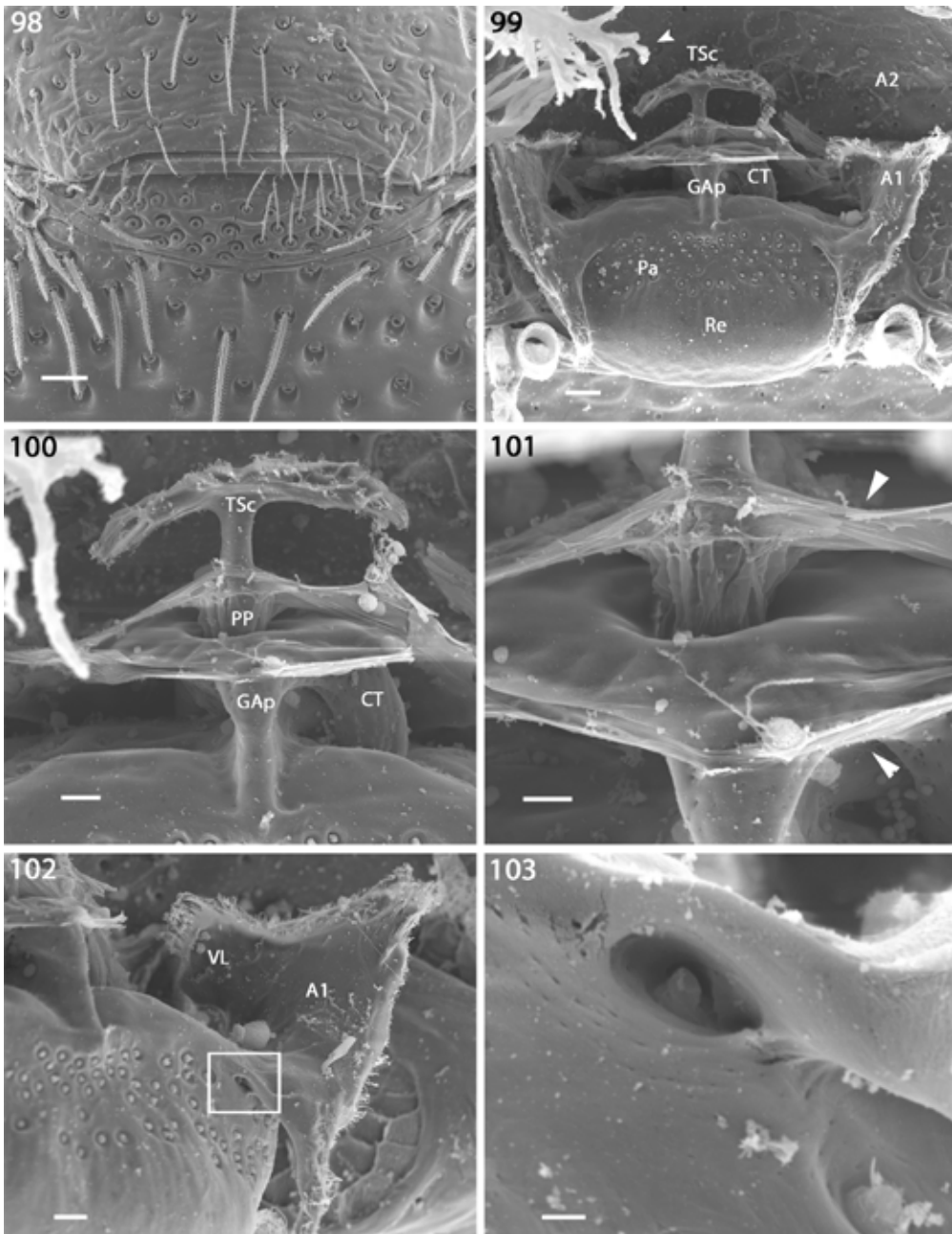


FIGS. 86–92. *Volborattella teresae*, new species, paratype female (PBI\_OON 2006). **86.** Labium and endites, posterior view. **87.** Endites, posterior view showing palmate setae. **88.** Serrula, lateral view. **89.** Chelicerae paturon promargins, ventral view, setae. **90.** Palp, prolateral view. **91.** Same, tarsus, dorsal view. **92.** Same, tarsal organ, dorsal view. Scale bars: 20  $\mu\text{m}$  (86, 90), 3  $\mu\text{m}$  (87), 2  $\mu\text{m}$  (88), 6  $\mu\text{m}$  (89), 10  $\mu\text{m}$  (91), 1  $\mu\text{m}$  (92).



FIGS. 93–97. *Volborattella teresae*, new species, paratype female (PBI\_OON 2006), abdomen. **93.** Dorsal view. **94.** Ventral view. **95.** Lateral view. **96.** Anterior view. **97.** Posterior view. Scale bars: 200  $\mu\text{m}$ .





FIGS. 98–103. *Volborattella teresae*, new species, paratype female (PBI\_OON 2006), genitalia. **98**. Ventral view. **99**. Digested, dorsal view, with arrow to book lung. **100**. Same, uterus externus and associated structures. **101**. Same, showing the anterior and posterior walls of the uterus externus (arrows). **102**. Same, lateral view, showing posterior apodeme (A1) with broad ventral lobe; box shows location of pit. **103**. Same, magnified view of pit. Abbreviations: **A1**, posterior apodeme; **A2**, anterior apodeme; **CT**, curved tube; **GAp**, globular appendix; **Pa**, papillae; **PP**, posterior projection; **Re**, receptaculum; **TSc**, transverse sclerite; **VL**, ventral lobe of A1. Scale bars: 30  $\mu\text{m}$  (98), 20  $\mu\text{m}$  (99), 10  $\mu\text{m}$  (100, 102), 6  $\mu\text{m}$  (101), 2  $\mu\text{m}$  (103).

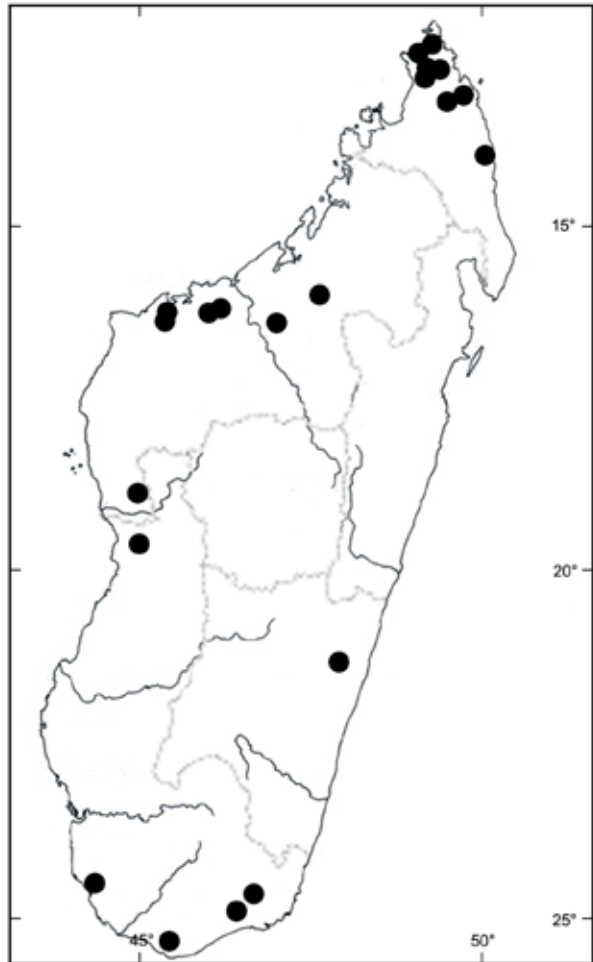
**DESCRIPTION: MALE** (paratype, PBI\_OON 2006): Total length 1.50 mm. **CEPHALOTHORAX:** Orange-brown with setae light colored (figs. 4–8). Carapace with pars cephalica strongly elevated in lateral view (figs. 4, 6, 9) and typically with medium to wide strip of plumose setae and abundant cup-shaped cuticular outgrowths near posterior margin of pars thoracica (figs. 8, 9, 16, 18). Clypeus margin not rebordered (figs. 10, 19). Eyes approximately subequal, ALE and PLE circular, ALE separated by their radius to their diameter, ALE and PLE separated by less than ALE radius, and PLE and PME separated by less than PME radius (figs. 4, 13–15). Sternum with continuous pocket and with a pair of deep lateral pouches at anterior margin (figs. 5, 11, 12), with microsculpture medially and in furrows (figs. 11, and 80, 81 in female), with posterior opening only in infracoxal groove at coxae I. Mouthparts orange-brown (fig. 5). Endites anterior tips with small toothlike projection (figs. 20, 21), much less prominent than in *V. guenevera* and *V. nasario*. **ABDOMEN:** Pedicel region with abundant plumose setae and cuticular outgrowths, along with three pairs of long, needlelike setae on curved scutal ridges (figs. 27–29, 32), which are more feathery than in *V. guenevera* and *V. nasario*. Abdominal scuta orange-brown (figs. 22–26), setae with round pits and small bases (figs. 22, 30, 31). Dorsal scutum anterior margin slightly curved, anterolaterally angular (fig. 25). Postepigastric scutum long, almost semicircular, and covering approximately half to 2/3 of abdomen length (figs. 23, 24). **LEGS:** Yellow-brown (figs. 1–3) and with small mesoapical comb on metatarsus III (fig. 41). Superior tarsal claw dentition with inner faces finely striate on claws I–III (figs. 53–55), with 22 or more distinct medial teeth on claws I–III and 16 medial teeth on claw IV (figs. 56, 57). Tarsal organ I with three sensilla, II with three, distal bifid, III and IV with two, distal broad, palp with two (fig. 51, 70). **GENITALIA:** Sperm pore oval to narrow (figs. 23, 69). Palp yellowish, with darker embolar region and black embolar superior prong (fig. 58, 59), with inferior prong long, folded distally (figs. 64–67), with pair of long setae on cymbium prolateral margin (figs. 60–63), these more feathery than in *V. guenevera* and *V. nasario*.

**FEMALE** (paratype, PBI\_OON 2006): Total length 1.80 mm. As in male except as noted. **CEPHALOTHORAX:** Carapace dark red-brown (figs. 74–78). Eyes with ALE and PLE oval (figs. 74, 77, 79, 82–85). Sternum setae dark colored (fig. 75), coxal groove distinct (figs. 80, 81). **ABDOMEN:** Dorsal scutum anterior margin sinuous (fig. 96). Female palp densely setose (figs. 90–91), tarsal organ with two sensilla (fig. 92). **LEGS:** Light orange (figs. 71–73); tarsal organ I with three sensilla, II with three, distal bifid, IV with two, distal bifid (figs. 50, 52). **GENITALIA:** External opening with anterolateral edge rounded to slightly angular and posterior edge with narrow lip (figs. 94, 98); internally with large oval receptaculum, posterior apodemes (A1) with broadly rectangular ventral lobes, slightly curved medially, and triangular anterodorsal lobes (figs. 99, 102), with pair of tiny pits just posterior to where A1 attach to receptaculum (figs. 102–103), with short stalk (GAp) connecting receptaculum to uterus externus, with additional curved tube (CT) located on the right or left side of GAp, with weak horizontal receptacular ridge (fig. 102), with T-shaped sclerite horizontal bar slightly curved and longer than in *V. guenevera* and *V. toliara*, and with T-shaped sclerite posterior process (PP) columnar (figs. 102–103).

ADDITIONAL MATERIAL EXAMINED: All material was collected from sifted litter by the Fisher-Griswold Arthropod Team, except where noted. MADAGASCAR: **Antsiranana**: Reserve Speciale d'Ambre, 3.5 km 235° SW Sakaramy, S12.46888°, E49.24222°, elev. 325 m, 26–31 Jan. 2001, tropical dry forest, BLF2654, CASENT 9006756 (PBI\_OON 2007), 5♂ 8♀; same, CASENT 9025449 (PBI\_OON 2232), 2♀; Forêt d'Orangea, 3.6 km 128° SE Ramena, S12.25888°, E49.37472°, elev. 90 m, 22 Feb. 2001, littoral forest, BLF3200, CASENT 9025450 (PBI\_OON 2233), 2♂; same, CASENT 9001053 (PBI\_OON 2783), 1♀; same, CASENT 9001047 (PBI\_OON 2790), 1♀; same, remnant dry forest, L.J. Boutin, CASENT 9003173 (PBI\_OON 2779), 1♂; Forêt de Binara, 7.5 km 230° SW Daraina, S13.25500°, E49.61666°, elev. 375 m, 1 Dec. 2003, tropical dry forest (leaf mold, rotten wood), BLF9556, CASENT 9011769 (PBI\_OON 2780), 8♂ 3♀; same, 2 Dec. 2004, tropical dry forest, pitfall trap, B.L. Fisher, BLF9558, CASENT 9023259 (PBI\_OON 2785), 1♂; Forêt de Binara, 9.4 km 235° SW Daraina, S13.26333°, E49.60000°, elev. 1100 m, 5 Dec. 2003, montane rainforest (leaf mold, rotten wood), B.L. Fisher, BLF9800, CASENT 9023256 (PBI\_OON 2789), 1♀; Montagne des Francais, 7.2 km 142° SE Antsiranana (= Diego Suarez), S12.32277°, E49.33805°, elev. 180 m, 23 Feb. 2001, L.J. Boutin, CASENT9000865 (PBI\_OON 2781), 1♂ 3♀; same, 22 Feb. 2001, tropical dry forest, BLF3128, CASENT 9001554 (PBI\_OON 2787), 1♂ 2♀; Forêt Analabe, 30.0 km 72° ENE Daraina, S13.08333°, E49.90833°, elev. 30 m, 27 Nov. 2003, littoral forest (leaf mold, sifted litter), BLF9426, CASENT 9011780 (PBI\_OON 2782), 2♂ 2♀; Reserve Speciale de l'Ankarana, 22.9 km 224° SW Anivorano Nord, S12.90888°, E49.10972°, elev. 80 m, 10 Feb. 2001, tropical dry forest, in tsingy, BLF2972, CASENT 9001440 (PBI\_OON 2784), 10♂ 1♀; same, Camp Anglaise, S12.90888°, E49.10972°, elev. 80 m, 10 Feb. 2001, L.J. Boutin, CASENT 9003713 (PBI\_OON 2791), 1♂ 2♀; Reserve Speciale de l'Ankarana, 13.6 km 192° SSW Anivorano Nord, S12.86361°, E49.22583°, elev. 210 m, 16 Feb. 2001, tropical dry forest, BLF3012, CASENT 9001464 (PBI\_OON 2788), 2♂ 5♀; Parc National Montagne d'Ambre, 3.6 km 235° SW Joffreville, S12.53444°, E49.17944°, elev. 925 m, 20 Jan. 2001, montane rainforest, BLF2564, CASENT 9003775 (PBI\_OON 2786), 1♀; Ambondrobe, 41.1 km 175° SSE Vohemar, S13.71528°, E50.10167°E, elev. 10 m, 29 Nov. 2004, littoral rainforest (leaf mold, rotten wood), BLF11100, CASENT 9038497 (PBI\_OON 35283), 2♀; Makirovana, 14°10'14"S, 49°57'15"E, elev. 225 m, 4–6 May 2011, rainforest, sifted leaf litter, BLF27044, CASENT 9030815 (PBI\_OON 35687), 1♂; **Fianarantsoa**: Forêt Classee Vatovavy, 7.6 km 122° ESE Kianjavato, S21.40000°, E47.94000°, elev. 175 m, 6 Jun. 2005, leaf mold, rotten wood, BLF12296, CASENT 9025451 (PBI\_OON 3457), 1♂; **Mahajanga**: Parc National de Namoroka, 16.9 km 317° NW Vilanandro, S16.40666°, E45.31000°, elev. 100 m, 12 Nov. 2002, tropical dry forest (mold, rotten wood), BLF6582, CASENT 9011501 (PBI\_OON 2227), 2♂ 2♀; Parc National de Namoroka, 17.8 km 329° WNW Vilanandro, S16.37666°, E45.32666°, elev. 100 m, 8 Nov. 2002, tropical dry forest (leaf mold, rotten wood), BLF6506, CASENT 9011667 (PBI\_OON 2236), 7♂ 4♀; same, pitfall trap, BLF6512, CASENT 9011497 (PBI\_OON 2798), 1♂; Parc National Tsingy de Bemaraha, 10.6 km 123° ESE Antsalova, S19.70944°, E44.71805°, elev. 150 m, 16 Nov. 2001, tropical dry forest (leaf mold, rotten wood), BLF4432, CASENT9010318 (PBI\_OON 2228), 12♂ 8♀; same, CASENT 9010357 (PBI\_OON 2230), 7♂ 3♀; Parc National Tsingy de Bemaraha, 2.5 km 62° ENE Bekopaka,



Ankidrodroa River, S19.13222°, E44.81472°, elev. 100 m, 11 Nov. 2001, tropical dry forest (leaf mold, rotten wood), BLF4340, CASENT 9010370 (PBI\_OON 2231), 4♂ 3♀; Parc National d'Ankarafantsika, Ampijoroa Station Forestiere, 5.4 km 331° NW Andranofasika, S16.29888°, E46.81305°, elev. 70 m, 26 Mar. 2001, tropical dry forest, BLF3571, CASENT 9001583 (PBI\_OON 2229), 1♀; Parc National d'Ankarafantsika, Forêt de Tsimaloto, 18.3 km 46° NE de Tsaramandroso, S16.22805°, E46.14361°, elev. 135 m, 2 Apr. 2001, tropical dry forest, BLF3599, CASENT 9001596 (PBI\_OON 2800), 2♂ 5♀; Reserve d'Ankoririka, 10.6 km 13° NE de Tsaramandroso, S16.26722°, E46.04861°, elev. 210 m, 9 Apr. 2001, tropical dry forest, BLF3664, CASENT 9001587 (PBI\_OON 2799), 1♀; Parc National d'Ankarafantsika, 16°18'07.8"S, 46°48'59.5"E, elev. 79m, 23 Apr. 2011, sifting forest litter, Winkler app. extr., MHNG AKF/07/2011 (PBI\_OON 32420), 1♂ 1♀; same, 16°18'47.5"S, 46°48'57.3"E, elev. 78m, 25 Apr. 2011, MHNG AKF/14/2011 (PBI\_OON 32446), 1♂; same, 16°17'32.6"S, 16°17'32.6"S, elev. 88m, 25 Apr. 2012, MHNG AKF/19/2011 (PBI\_OON 32463), 1♀; same, 16°18'46.6"S, 46°48'58.8"E, elev. 89m, 22 Apr. 2011, MHNG AKF/04/2011 (PBI\_OON 35743), 1♂; same, 16°18'47.7"S, 46°48'57.1"E, elev. 89m, 25 Apr. 2011, MHNG AKF/12/2011 (PBI\_OON 35745), 1♀; Forêt Ambohimanga, 26.1 km 314° Mampikony, S15.96278°, E47.43806°, elev. 250 m, 13 Dec. 2004, tropical dry forest (leaf mold, rotten wood), BLF11672, CASENT 9038488 (PBI\_OON 35287), 5♂ 5♀; **Toliara**: Reserve Privé Berenty, Forêt de Bealoka, 14.6 km 329° NW Amboasary, S24.95694°, E46.27138°, elev. 35 m, 3–8 Feb. 2002, gallery forest, sifted litter (leaf mold, rotten wood), collected by Fisher-Griswold Arthropod Team, BLF5316, CASENT 9010278 (PBI\_OON 2006), 4♂ 7♀; Reserve Prive Berenty, Forêt de Malaza, Mandrare River, 8.6 km 314° NW Amboasary, S25.00777°, E46.30611°, elev. 40 m, 6 Feb. 2002, gallery forest (leaf mold, rotten wood), BLF5426, CASENT 9010304 (PBI\_OON 2794), 2♂ 3♀; Reserve Speciale de Cap Sainte Marie, 14.9 km 261° W Marovato, S25.59444°, E45.14694°, elev.



MAP 1. Distribution of *Volborattella teresae*.

160 m, 13 Feb 2002, spiny forest/thicket (leaf mold, rotten wood), BLF5570, CASENT9010312 (PBI\_OON 2792), 1 ♂ 4 ♀; same, pitfall trap, BLF5650, CASENT 9011361 (PBI\_OON 2795), 1 ♂; Reserve Speciale de Cap Sainte Marie, 12.3 km 262° W Marovato, S25.58166°, E45.16833°, elev. 200 m, 11 Feb. 2002, spiny forest/thicket (leaf mold, rotten wood), BLF5500, CASENT 9011377 (PBI\_OON 2796), 1 ♀; Parc National d'Andohahela, Forêt de Manantalinjo, 33.6 km 63° ENE Amboasary, 7.6 km 99° E Hazofotsy, S24.81694°, E46.61000°, elev. 150 m, 12 Jan. 2002, spiny forest/thicket (leaf mold, rotten wood), BLF4810, CASENT 9010270 (PBI\_OON 2793), 1 ♀; Parc National d'Andohahela, Forêt d'Ambohibory, 1.7 km 61° ENE Tsimelahy, 36.1 km 308° NW Tolagnaro, S24.93000°, E46.64556°, elev. 300 m, 16–20 Jan. 2002, tropical dry forest, BLF4984, 9029985 (PBI\_OON 2243), 1 ♂; Parc National Andohahela, Parcelle II, Tsimelahy, 44 km W Tolagnaro, S24.96636°, E46.55469°, elev. 90 m, 28 Dec 2008, primary spiny dry forest, mini-winkler, HW0810, CASENT 9030294 (PBI\_OON 2244), 1 ♀; Mahafaly Plateau, 6.2 km 74° ENE Itampolo, S24.65361°, E43.99666°, elev. 80 m, 21 Feb. 2002, spiny forest/thicket (leaf mold, rotten wood), BLF5758, CASENT 9010330 (PBI\_OON 2797), 1 ♀.

DISTRIBUTION: *V. teresae* is widely distributed around the perimeter of Madagascar, but is most commonly found in the north and along the west coast (map 1).

***Volborattella guenevera*, new species**

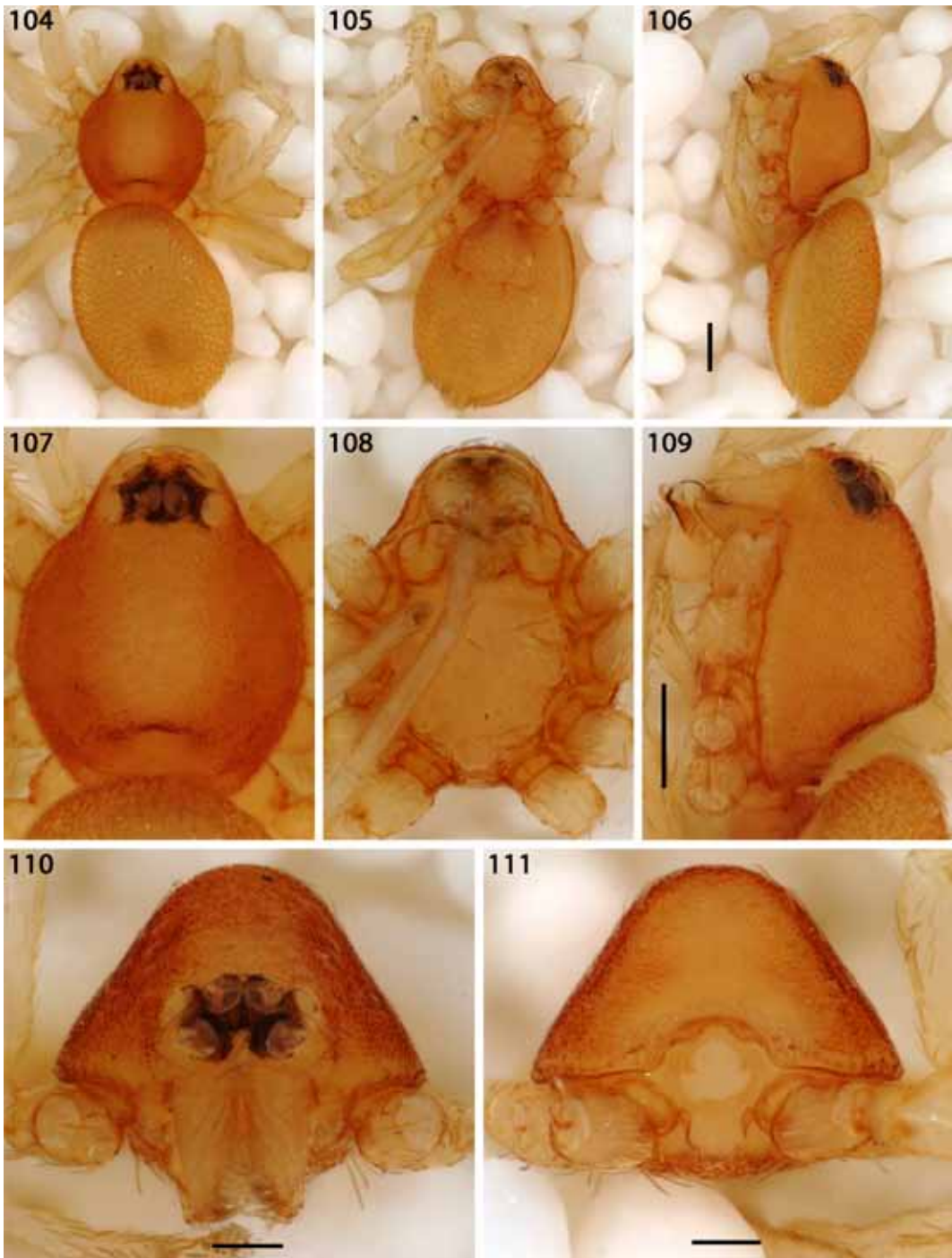
Figures 104–147, maps 2, 3

TYPES: MADAGASCAR: Antsiranana: Forêt d'Analabe, 30.0 km 72° ENE Daraina, S13.08333°, E49.90833°, elev. 30 m, 27 Nov. 2003, littoral rainforest, sifted litter (leaf mold, rotten wood), Fisher-Griswold Arthropod Team, BLF9426, CASENT 9011781 (PBI\_OON 2234), holotype ♂ and allotype ♀ (deposited in CAS).

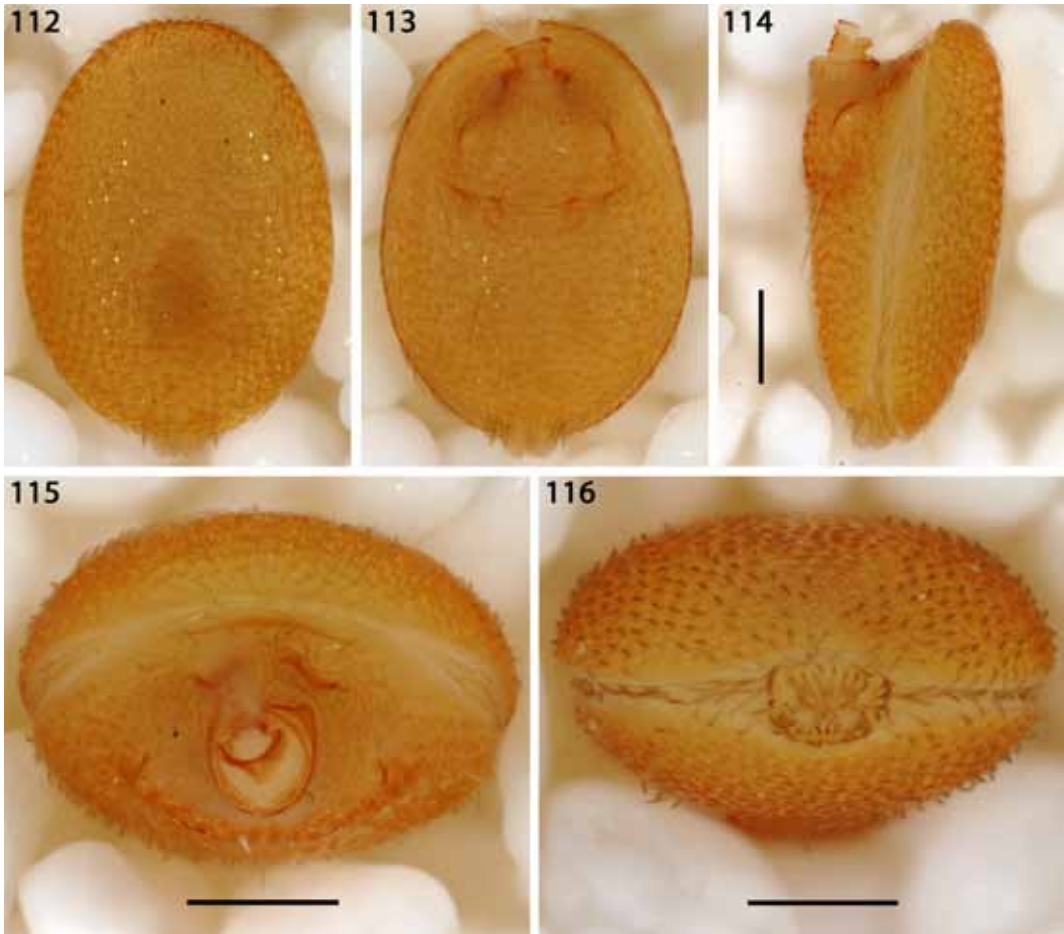
ETYMOLOGY: The specific name is in honor of Jennifer Saucedo; a noun in apposition.

DIAGNOSIS: *V. guenevera* is readily distinguished from other *Volborattella* by its wide abdomen, which is yellowish orange in color and has glittery reflections (figs. 112–114, 139–141). It resembles *V. paulyi* in having large eyes with somewhat reduced pigment (figs. 107, 110, 134–137). The male of *V. guenevera* resembles *V. nasario* in having a prominent endite projection (fig. 121), a shallow pocket at sternum anterior margin (fig. 120), and with a widely curved ridge above the scutal ridges (fig. 115), but differs in having a shorter embolar superior prong and a wider inferior prong (figs. 125–129). The female differs from those of other species in having internal genitalia with posterior apodemes bearing narrow, rectangular, dorsal lobes and small ventral lobes (fig. 147), but most closely resembles *V. paulyi* in having a shorter receptaculum, which lacks a conspicuous receptacular ridge (fig. 145).

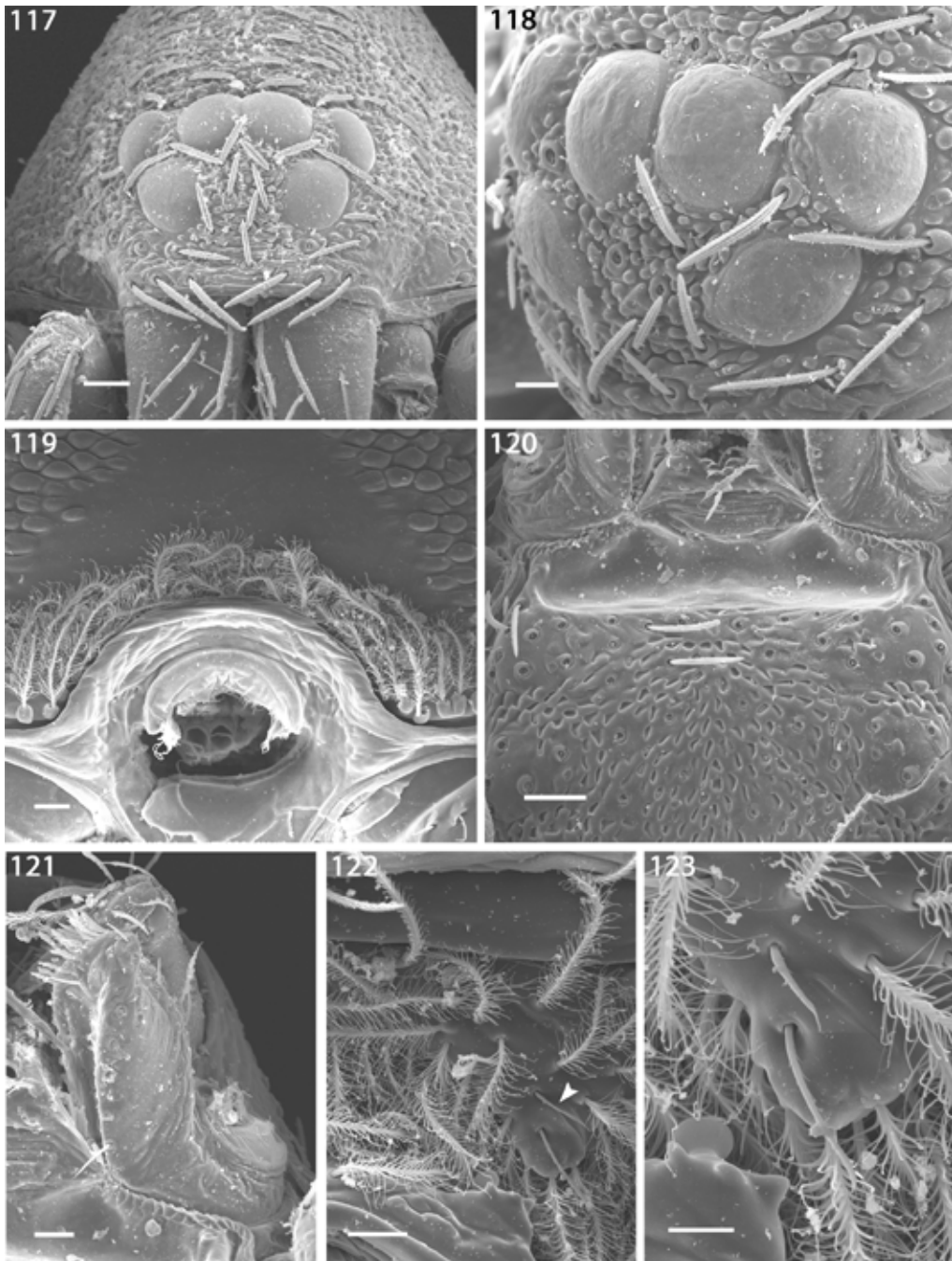
DESCRIPTION: MALE (paratype, PBI\_OON 2224): Total length 1.60 mm. CEPHALOTHORAX: Carapace orange, with pars cephalica strongly elevated in lateral view (figs. 107–111) and typically with narrow to medium strip of plumose setae near posterior margin of pars thoracica (figs. 111, 119). Clypeus margin slightly rebordered, setae light colored (fig. 117, female). Eyes approximately subequal, ALE and PLE oval, ALE separated by more than their diameter, ALE and PLE nearly touching, and PLE and PME separated by less than PME radius (figs. 107, 109, 110, 118). Sternum pale orange, anterior margin with continuous shallow pocket, with micros-



FIGS. 104–111. *Volborattella guenevera*, new species, male (PBI\_OON 2224), habitus. **104.** Dorsal view. **105.** Same, ventral view. **106.** Same, lateral view. **107.** Prosoma, dorsal view. **108.** Same, ventral view. **109.** Same, lateral view. **110.** Same, anterior view. **111.** Same, posterior view. Scale bars: 200  $\mu$ m (106, 109), 100  $\mu$ m (110, 111).

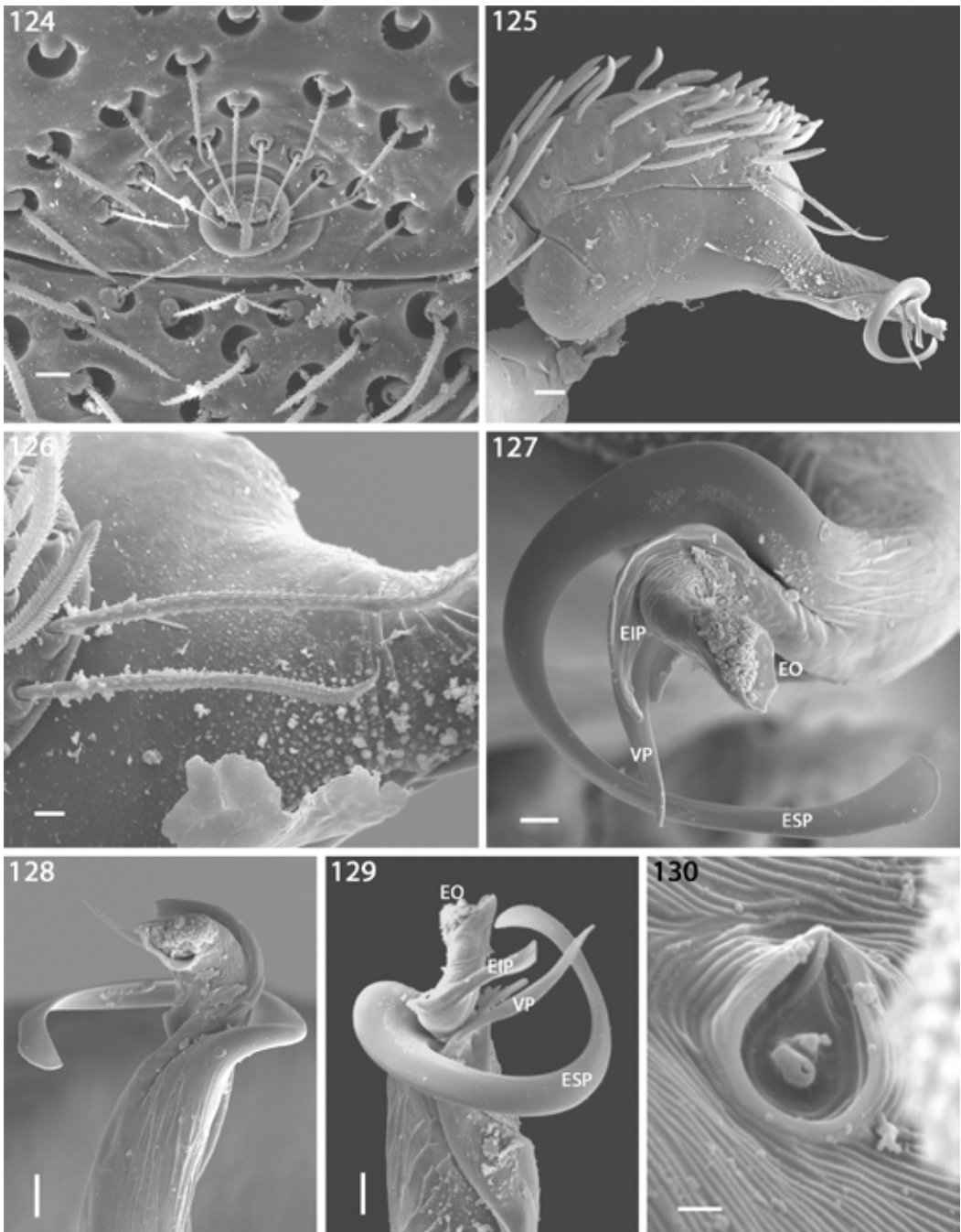


FIGS. 112–116. *Volborattella guenevera*, new species, male (PBI\_OON 2224), abdomen. **112.** Dorsal view. **113.** Ventral view. **114.** Lateral view. **115.** Anterior view. **116.** Posterior view. Scale bars: 200  $\mu\text{m}$ .

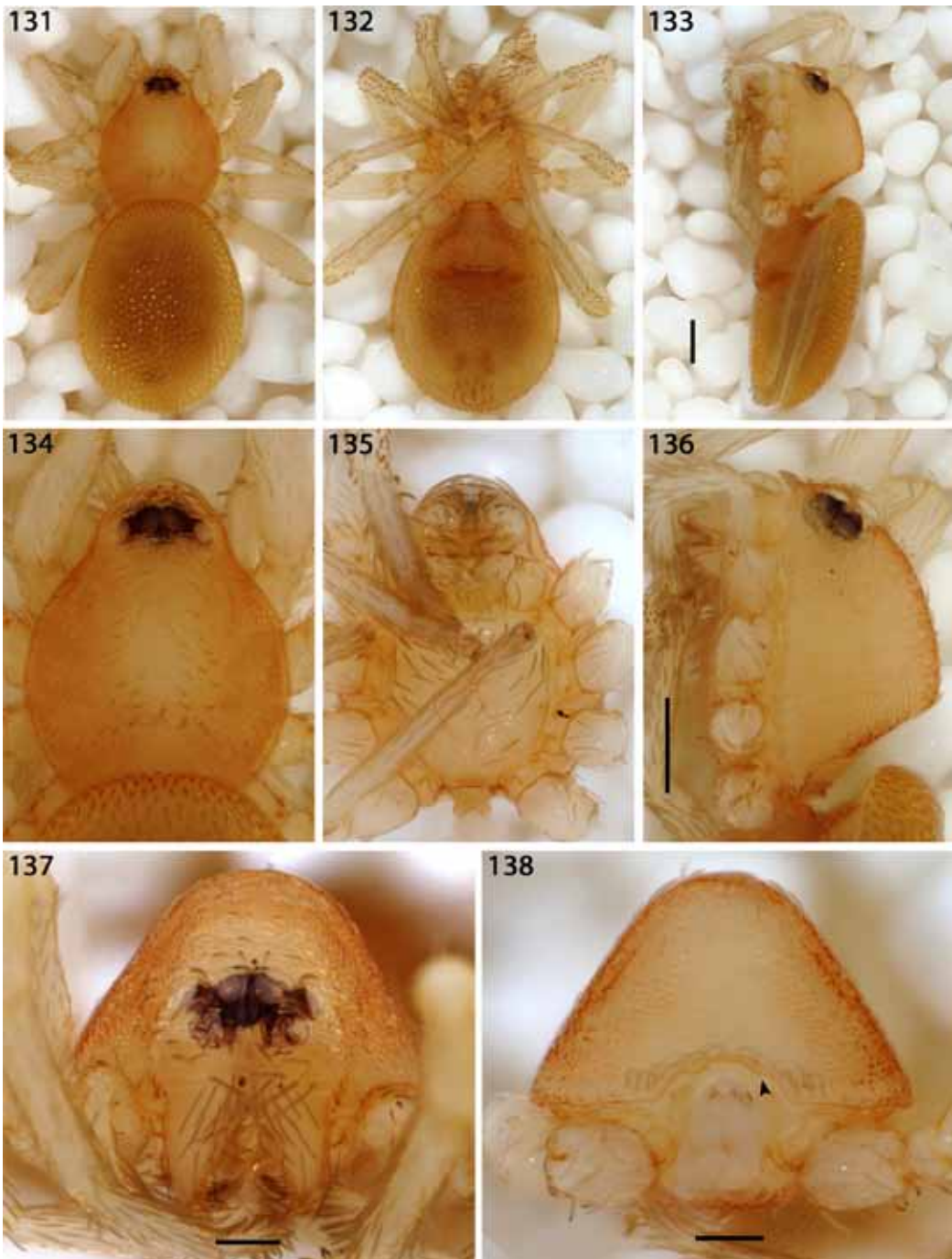


FIGS. 117–123. *Volborattella guenevera*, new species, male (PBI\_OON 2224) and female (PBI\_OON 2770). **117.** Female, prosoma, anterior view. **118.** Male, eyes, anterolateral view. **119.** Male, prosoma, pedicel region, posterior view showing plumose setae. **120.** Male, sternum, ventral view. **121.** Male, endite, ventral view. **122.** Female, abdomen, anterior view, scutal ridges with arrow indicating needlelike seta. **123.** Same, magnified view showing needlelike setae. Scale bars: 40  $\mu\text{m}$  (117, 120), 20  $\mu\text{m}$  (118, 119, 122), 10  $\mu\text{m}$  (123).

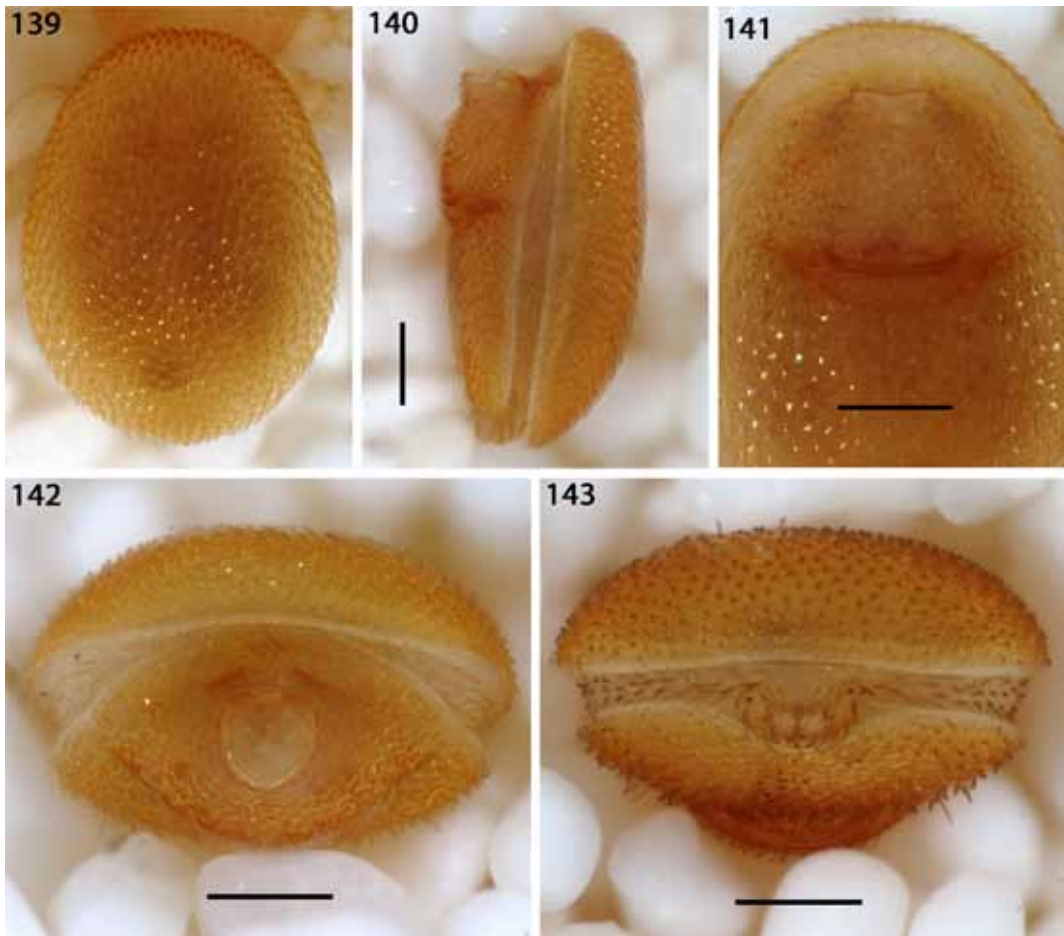




FIGS. 124–130. *Volborattella guenevera*, new species, male (PBI\_OON 2224). **124.** Gonopore, ventral view. **125.** Right palp, prolateral view. **126.** Same, showing long cymbial setae. **127.** Embolar region, apical view. **128.** Same, retrolateral view. **129.** Same, prolateral view. **130.** Palpal tarsal organ, dorsal view. Abbreviations: **EIP**, embolus inferior prong; **EO**, embolus opening; **ESP**, embolus superior prong; **VP**, ventral process. Scale bars: 10  $\mu\text{m}$  (124, 128, 129), 20  $\mu\text{m}$  (125), 6  $\mu\text{m}$  (126, 127), 1  $\mu\text{m}$  (130).



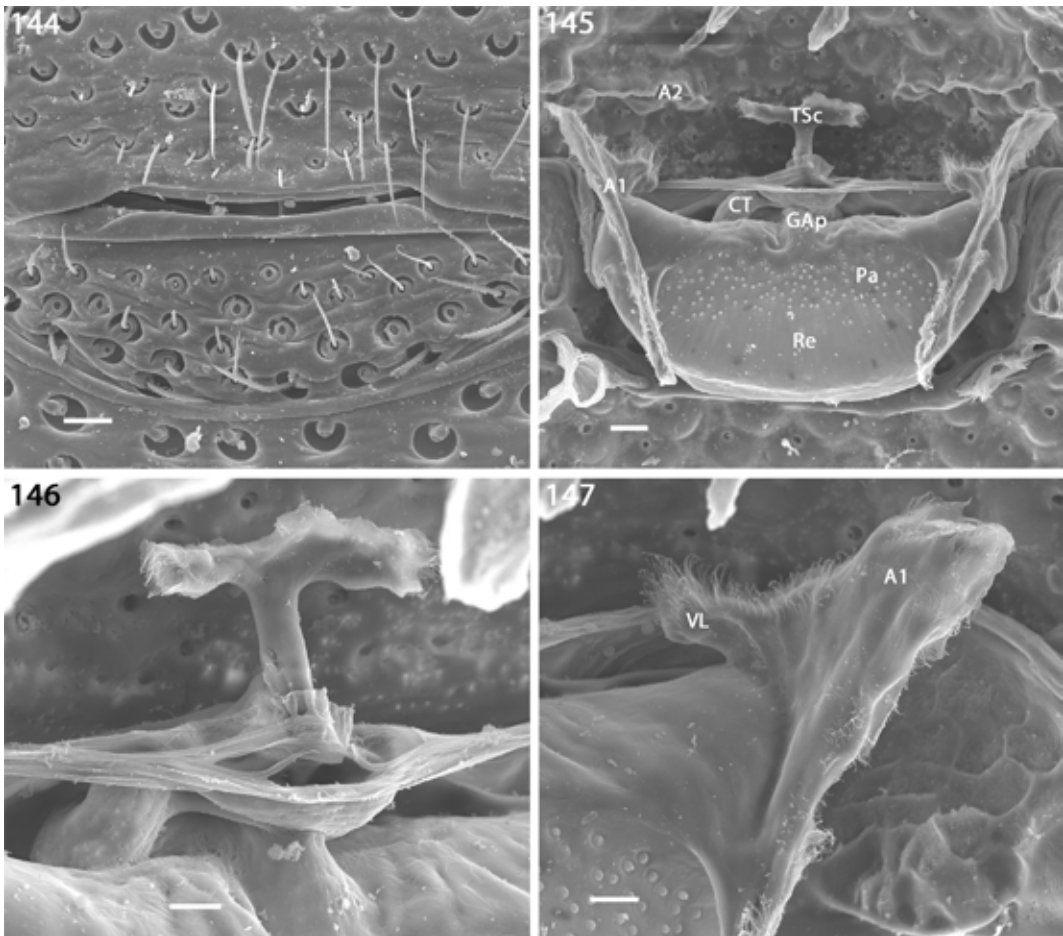
FIGS. 131–138. *Volborattella guenevera*, new species, female (PBI\_OON 2770). **131.** Habitus, dorsal view. **132.** Same, ventral view. **133.** Same, lateral view. **134.** Prosoma, dorsal view. **135.** Same, ventral view. **136.** Same, lateral view. **137.** Same, anterior view. **138.** Same, posterior view, with arrow indicating undulation of posterior margin ventral edge. Scale bars: 200  $\mu\text{m}$  (133, 136), 100  $\mu\text{m}$  (137, 138).



FIGS. 139–143. *Volborattella guenevera*, new species, female (PBI\_OON 2770), abdomen. **139.** Dorsal view. **140.** Lateral view. **141.** Ventral view. **142.** Anterior view. **143.** Posterior view. Scale bars: 200  $\mu\text{m}$  (140, 142, 143) 100  $\mu\text{m}$  (141).

culpture medially and in furrows, with posterior opening only in infracoxal groove at coxae I, and with setae dark colored (figs. 108, 120). Mouthparts pale orange. Endites anterior tips with prominent toothlike projection (fig. 121), more pronounced than in *V. teresae* and *V. toliara*. ABDOMEN: Pedicel region with wide ridge above scutal ridges (fig. 115), more prominent than in female (fig. 142), with three pairs of needlelike setae on scutal ridges (figs. 122–123, female). Abdominal scuta pale orange (figs. 112–116), with sparkling reflections (figs. 112–113), with round setal pits and small setal bases (fig. 124). Dorsal scutum anterior margin evenly curved (fig. 115). Postepigastric scutum almost semicircular and covering approximately half of abdomen total length (figs. 113–114). LEGS: Pale yellow (figs. 104–106). Tarsal organ IV with two sensilla. GENITALIA: Sperm pore circular to oval (figs. 113, 124); palp yellow, cymbium with pair of long prolateral setae (figs. 125, 126), less plumose than in *V. teresae* and *V. toliara*; tarsal organ with two sensilla (fig. 130); embolus superior prong basally broad, apically spatulate, inferior prong short and slightly curved (figs. 125, 127–129).





FIGS. 144–147. *Volborattella guenevera*, new species, female (PBI\_OON 2224, except for 144 = PBI\_OON 2770), epigynum. **144.** Ventral view. **145.** Digested, dorsal view. **146.** Same, T-shaped sclerite. **147.** Same, lateral view, winglike apodeme. Abbreviations: **A1**, posterior apodeme; **A2**, anterior apodeme; **CT**, curved tube; **GAp**, globular appendix; **Pa**, papillae; **Re**, receptaculum; **TSc**, transverse sclerite; **VL**, ventral lobe of A1. Scale bars: 20  $\mu$ m (144, 145), 10  $\mu$ m (146, 147).

**FEMALE** (paratype, PBI\_OON 2770): Total length 1.60 mm. As in male except as noted. **CEPHALOTHORAX:** Carapace yellow-brown, pars cephalica strongly elevated in lateral view (figs. 133, 136). Clypeus setae dark colored. Eyes with ALE circular and separated by their radius to their diameter (figs. 117, 134, 137). Mouthparts with dark-colored setae. Female palp tarsal organ with two sensilla. **ABDOMEN:** Pedicel region with epigastric scutum not extending far dorsal of pedicel (fig. 141). **LEGS** (figs. 131–133): Tarsal organ I with three sensilla, distal bifid, IV with two sensilla, distal bifid. **GENITALIA:** Externally with anterolateral edge angular, posterior edge with narrow lip (figs. 141, 144); internally (based on different female, PBI\_OON 2224) with posterior apodemes (A1), winglike, ventral lobes narrow, rectangular, medially directed, anterodorsal lobes broadly rectangular (fig. 147), receptaculum without conspicuous ridge between globular appendix (GAp) and papillae (fig. 145), GAp represented by



MAP 2. Distribution of *Volborattella* species: triangles, *V. nasario*; squares, *V. guenevera*; diamond, *V. paulyi*; circles, *V. toliara*.

short stalk connecting receptaculum to uterus externus (fig. 146), curved tube (CT) on left side of genitalia in this specimen (but on the right side in female PBI\_OON 2770), T-shaped sclerite with relatively short transverse bar (fig. 146).

ADDITIONAL MATERIAL EXAMINED:

All material was collected by the Fisher-Griswold Arthropod Team from sifted litter, except where noted. MADAGASCAR: *Antsiranana*: Reserve Speciale d'Ambre, 3.5 km 235° SW Sakaramy, S12.46888°, E49.24222°, elev. 325 m, 26–31 Jan. 2001, tropical dry forest, BLF2654, CASENT 9006760 (PBI\_OON 2224), 1 ♂ 1 ♀; Forêt d'Andavakoera, 21.4 km 75° ENE Ambilobe, S13.11833°; E49.23000°, elev. 425 m, 15 Dec. 2003, rainforest (leaf mold, rotten wood), BLF10260, CASENT 9023319 (PBI\_OON 2235), 1 ♀; Reserve Speciale de l'Ankarana, 22.9 km 224° SW Anivorano Nord, S12.90888°, E49.10972°, elev. 80 m, 10–16 Feb. 2001, tropical dry forest (in tsingy), BLF2972, CASENT9001443 (PBI\_OON 2770), 1 ♀; Forêt de Binara, 7.5 km 230° SW Daraina, S13.25500°, E49.61666°, elev. 375 m, 1 Dec. 2003, tropical dry forest (leaf mold, rotten wood), BLF9556, CASENT9011770 (PBI\_OON

2771), 1 ♀; Forêt Ambato, 26.6 km 33° NE Ambanja, S13.46444°, E48.55166, elev. 150 m, 8 Dec. 2004, rainforest (leaf mold, rotten wood), B.L. Fisher, BLF11520, CASENT9036065 (PBI\_OON 35270), 1 ♂ 1 ♀; Ambondrobe, 41.1 km from Vohemar, S13.71527°, E50.10166°, elev. 10 m, 29 Nov. 2004, littoral rainforest (leaf mold, rotten wood), B.L. Fisher, BLF11100, CASENT9038495 (PBI\_OON 35284), 1 ♂; *Mahajanga Prov.*: Parc National de Namoroka, 17.8 km 329° WNW Vilanandro, S16.37666°, E45.32666°, elev. 100 m, 8 Nov 2002, tropical dry forest (leaf mold, rotten wood), Fisher-Griswold Arthropod Team, BLF6506, CASENT 9025447 (PBI\_OON 2237), 1 ♂.

DISTRIBUTION: *V. guenevera* is found in the northern tip of Madagascar (map 2). The single locality in central-western Madagascar, Parc National de Namoroka, is uncertain and a sus-

pected labeling error (indicated as “?” on maps 2, 3).

***Volborattella nasario*,**  
new species

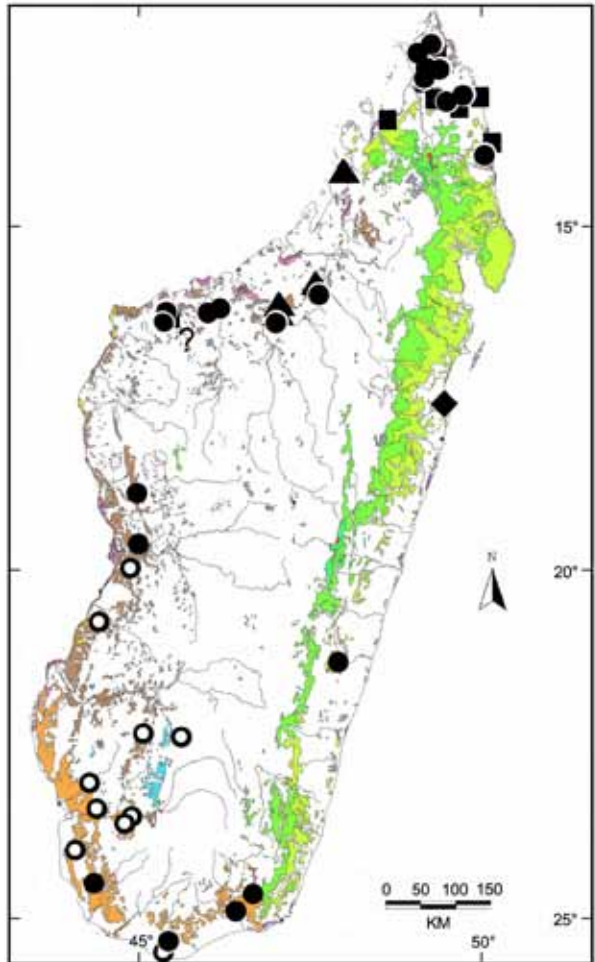
Figures 148–189, maps 2, 3

**TYPES:** MADAGASCAR: Mahajanga: Parc National d’Ankarafantsika, 40 km 306° NW Andranofasika, S16.32083°, E46.81055°, elev. 130 m, 26 Mar.–1 Apr. 2001, tropical dry forest, sifted litter, Fisher-Griswold Arthropod Team, BLF3522, CASENT 9001602, (PBI\_OON 2768), holotype ♂ and allotype ♀, and 1 ♂ and 2 ♀ paratypes (deposited in CAS).

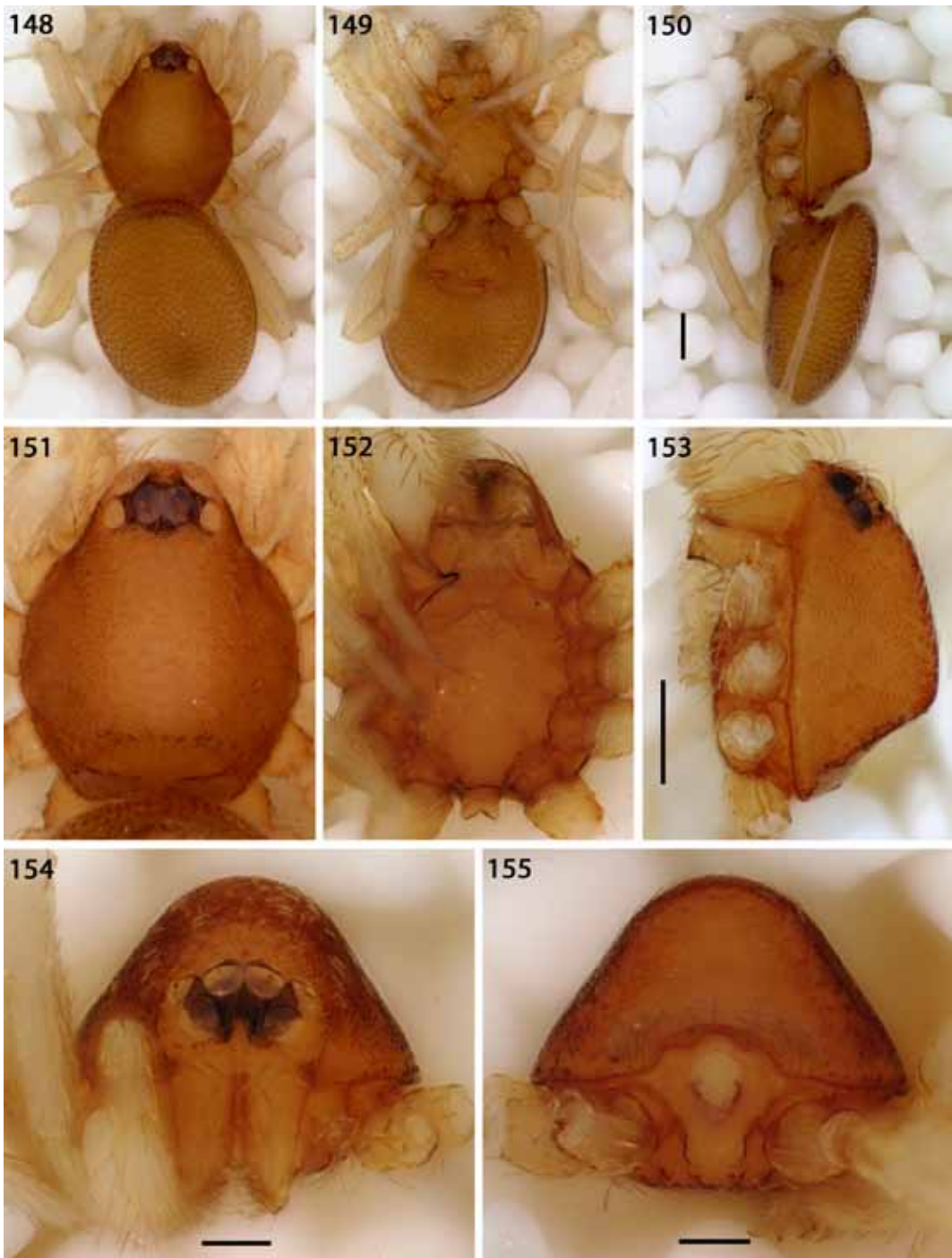
**ETYMOLOGY:** The specific name is in honor of Nasario Mejia; a noun in apposition.

**DIAGNOSIS:** *V. nasario* differs from other *Volborattella* species in having a wide, brownish abdomen with indistinct spots (figs. 156–158, 180–182) and abdominal setae with small, oval pits and large bases (fig. 166). The male of *V. nasario* has an embolus with the superior prong slightly longer and narrower than in other *Volborattella* species, an inferior prong short and slender (figs. 167–171), and the sternal cavity represented by two shallow pockets (figs. 152, 161). It resembles *V. guenevera* in having prominent endite projections (fig. 162), a wide and slightly curved ridge above the scutal ridges (fig. 159), and a straight (opposed to bent) embolar inferior prong (figs. 169–171). The female genitalia differ from those of other species in having a somewhat longer receptaculum (fig. 186), rounded anterodorsal lobes of A1 (fig. 188), and, externally, a thicker posterior margin of the gonopore (fig. 185). The receptaculum resembles that of *V. toliara* in having a strong horizontal ridge (fig. 187).

**DESCRIPTION:** MALE (paratype, PBI\_OON 2225): Total length 1.40 mm. **CEPHALOTHORAX:** Brown and with setae light colored. Carapace with pars cephalica strongly elevated in lateral view (figs. 150, 153), with medium to wide strip of plumose setae (fig. 155) and abundant cup-shaped cuticular outgrowths near posterior margin of pars thoracica. Clypeus margin not rebordered. Endites anterior tips with prominent toothlike projection (fig. 162), larger than in *V. teresae* and *V. toliara*. Eyes with ALE and PME

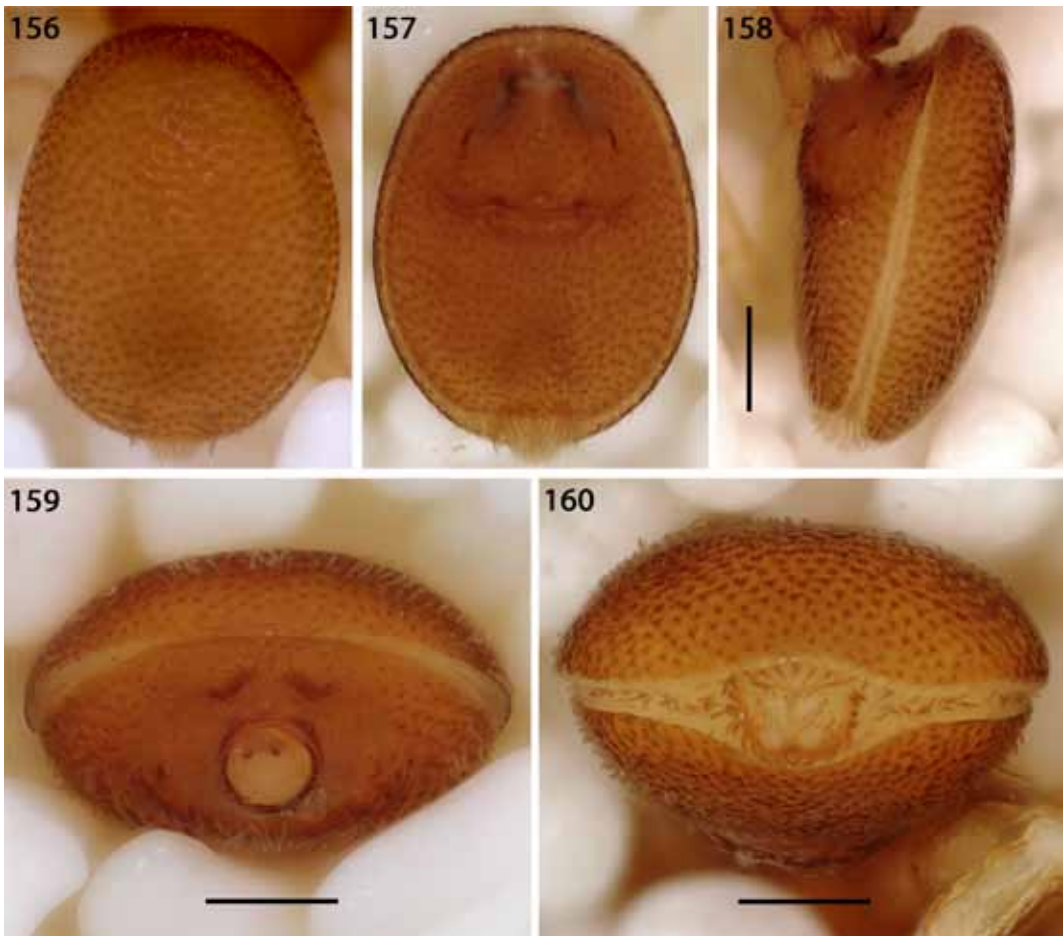


MAP 3. Distribution of *Volborattella* species on vegetation map of Madagascar.



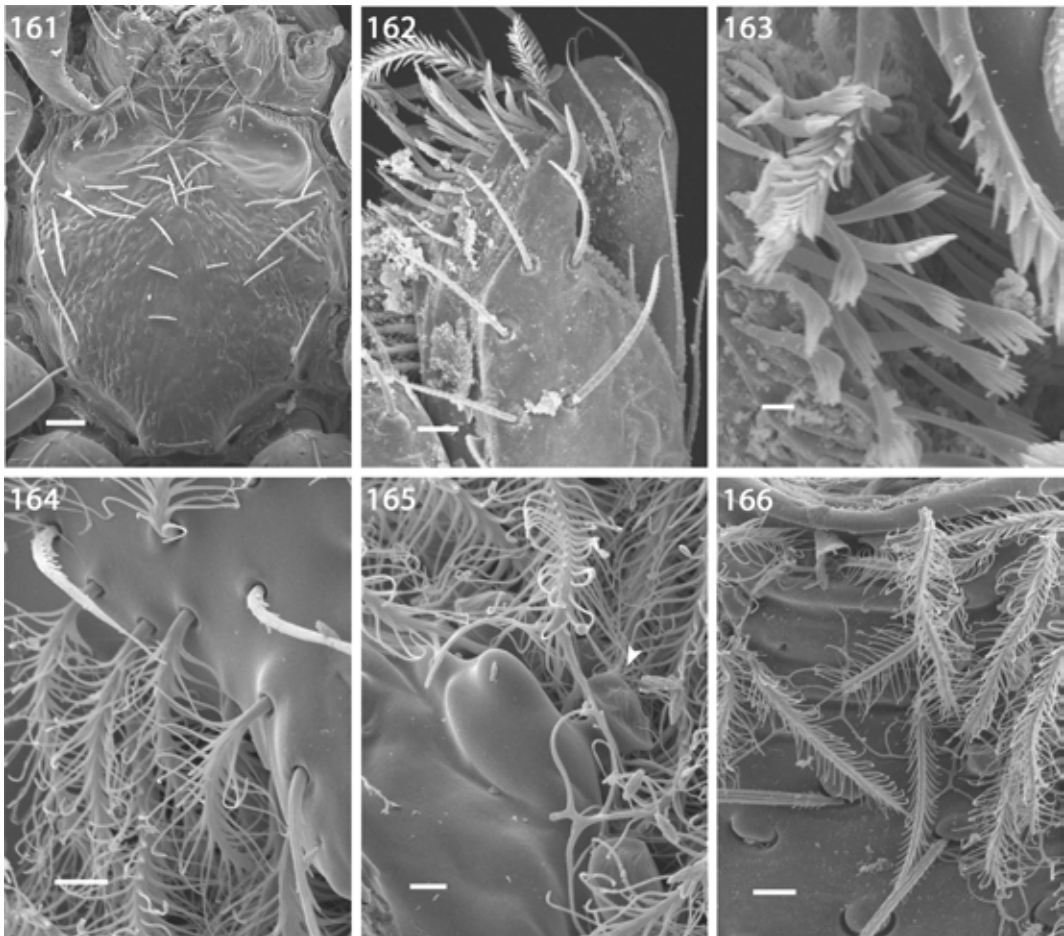
FIGS. 148–155. *Volborattella nasario*, new species, male (PBI\_OON 2225). 148. Habitus, dorsal view. 149. Same, ventral view. 150. Same, lateral view. 151. Prosoma, dorsal view. 152. Same, ventral view. 153. Same, lateral view. 154. Same, anterior view. 155. Same, posterior view. Scale bars: 200  $\mu\text{m}$  (150, 153), 100  $\mu\text{m}$  (154, 155).





FIGS. 156–160. *Volborattella nasario*, new species, male (PBI\_OON 2225), abdomen. **156.** Dorsal view. **157.** Ventral view. **158.** Lateral view. **159.** Anterior view. **160.** Posterior view. Scale bars: 200  $\mu$ m.

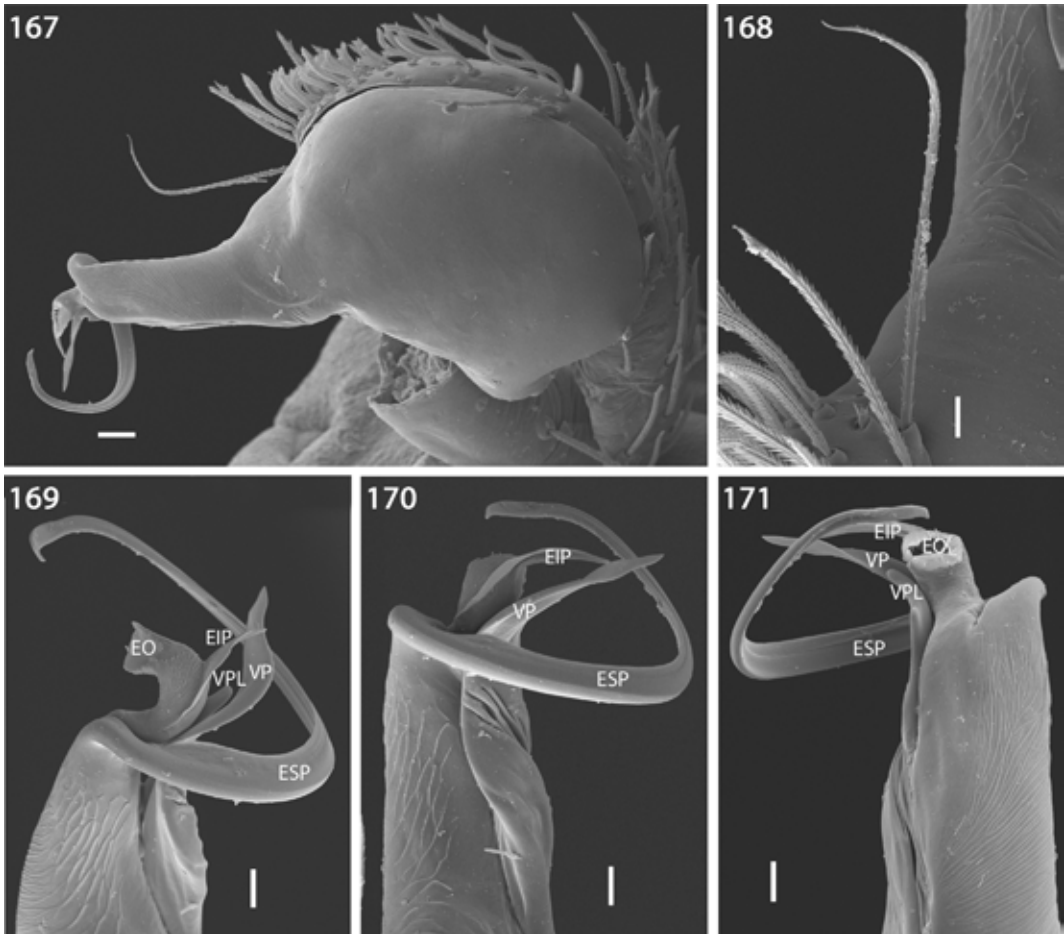
subequal and larger than PLE, ALE and PLE circular, ALE separated by their radius to their diameter, ALE and PLE separated by less than ALE radius, and PLE and PME separated by less than PME radius (figs. 151, 153, 154). Sternum with pair of shallow lateral pouches at anterior margin, with microsculpture anteriorly and in furrows, and with posterior opening only in infracoxal groove at coxae I (figs. 152, 161). Mouthparts orange-brown. ABDOMEN: Pedicel region with a wide and slightly curved ridge above paired curved ridges in scutopedicel area (fig. 159), with cuticular outgrowths very abundant and with three pairs of long, needlelike setae on scutal ridges (fig. 164, female). Abdominal scuta brown, broad (figs. 156–160), setae with oval pits and large bases (fig. 166, female). Dorsal scutum anterior margin evenly curved (fig. 159). Postepigastric scutum almost semicircular, covering approximately half of abdomen length (figs. 157, 158). LEGS: Yellowish (148–150), tarsus IV superior claws with 11 medial teeth. Tarsal organ I with three sensilla, distal bifid. GENITALIA: Sperm pore circular to oval (fig. 157); palp yellowish



FIGS. 161–166. *Volborattella nasario*, new species, male and female (PBI\_OON 2225). **161.** Male, sternum, ventral view. **162.** Male, endite, posterior view. **163.** Same, magnified view showing palmate setae. **164.** Female, abdomen, anterolateral view showing scutal ridge with needlelike setae. **165.** Same, pedicel tube showing apical branching of plumose setae, with arrow at cup-shaped cuticular outgrowth. **166.** Female, abdomen, pedicel tube, ventral view showing latticelike arrangement of setae. Scale bars: 20 μm (161), 10 μm (162, 166), 3 μm (163), 6 μm (164), 4 μm (165).

(figs. 149, 150), cymbium with pair of long prolateral setae (fig. 168) less plumose than in *V. teresae* and *V. toliara*; palpal tarsal organ with two sensilla; embolus superior prong long, slender, tip bent, inferior prong short, straight (fig. 169–171).

**FEMALE** (paratype, PBI\_OON 2225): Total length 1.70 mm. As in male except as noted. **CEPHALOTHORAX:** Carapace dark red-brown (figs. 175–179). Eyes approximately subequal, ALE separated by more than their diameter (figs. 175, 177, 178). Sternum orange-brown, with microsculpture laterally and in furrows, and with setae dark colored (fig. 176). Mouthparts with dark-colored setae. Female palp tarsal organ with two sensilla. **LEGS:** (figs. 172–174) Tarsal organ I with three sensilla. **GENITALIA:** Externally with anterior edge rounded and posterior with wide lip (figs. 182, 185); internally (based on different female,

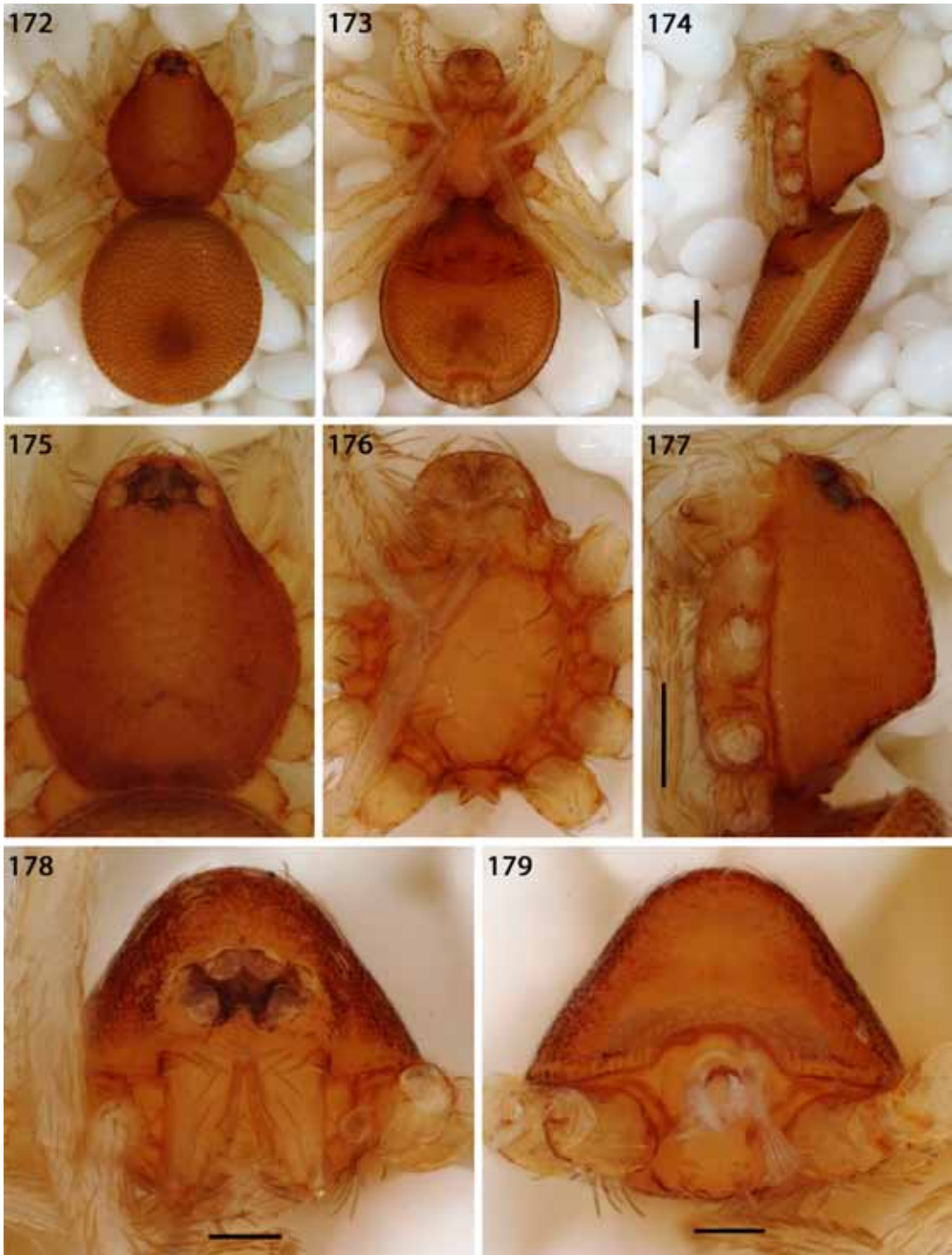


FIGS. 167–171. *Volborattella nasario*, new species, male (PBI\_OON 2225), left palp. **167**. Retrolateral view. **168**. Cymbium, prolateral view, showing long setae. **169**. Embolus, dorsal view. **170**. Same, prolateral view. **171**. Same, retrolateral view. Abbreviations: **EIP**, embolar inferior prong; **EO**, embolar opening; **ESP**, embolar superior prong; **VP**, ventral process; **VPL**, ventral process lobe. Scale bars: 20  $\mu$ m (167), 10  $\mu$ m (168–171).

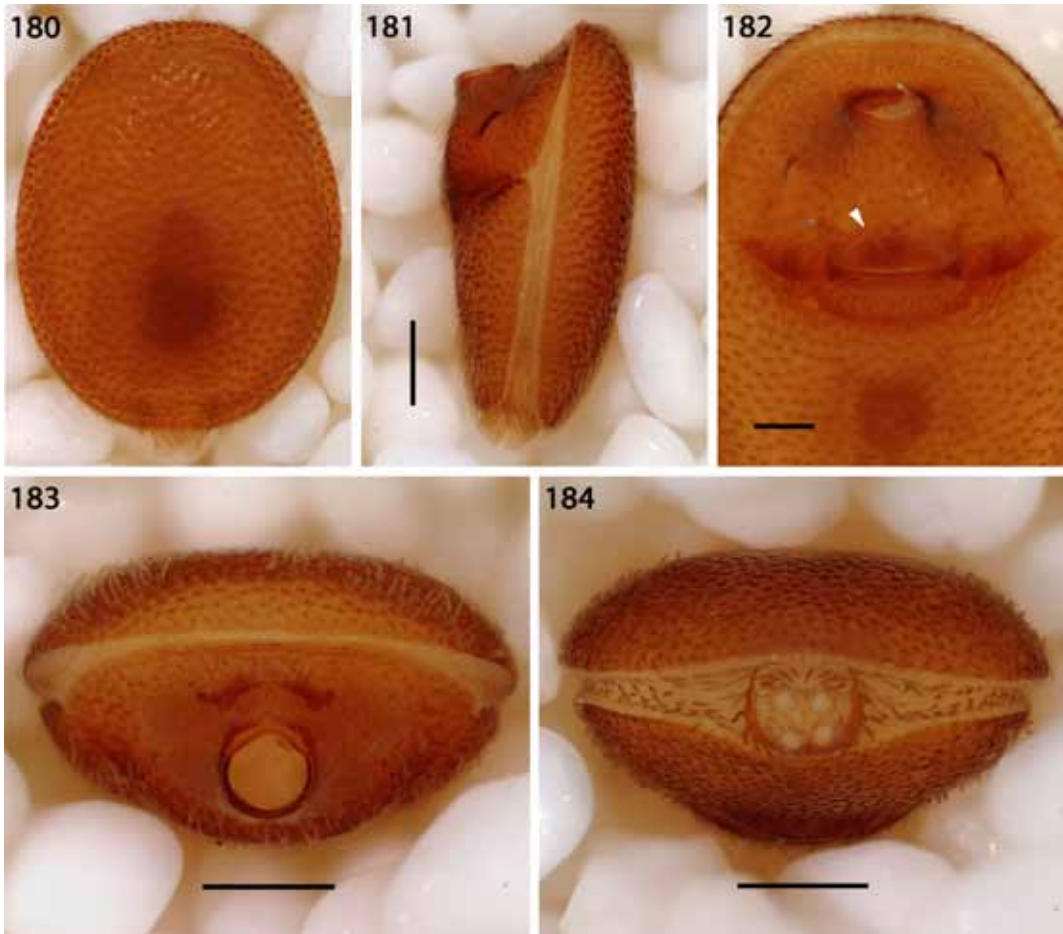
PBI\_OON 2768) posterior apodemes (A1) with ventral lobes of moderate size, rectangular, slightly curved medially, anterodorsal lobes not prominent, rounded (fig. 188); receptaculum with strong horizontal receptacular ridge between globular appendix (GAp) and papillae (fig. 186), CT on right side in this specimen and in female PBI\_OON 2225 (figs. 182, 186, 187), also occurs on the left side of other females, T-shaped sclerite horizontal bar (fig. 187) longer than in *V. guenevera* and *V. toliara*.

ADDITIONAL MATERIAL EXAMINED: MADAGASCAR: ***Antsiranana***: Forêt d'Anabohazo, 21.6 km 247° WSW Maromandia, S14.30888°, E47.91444°, elev. 120 m, 11–16 Mar. 2001, tropical dry forest, sifted litter, Fisher-Griswold Arthropod Team, BLF3338, CASENT 9007435, (PBI\_OON 2225), 1♂ 1♀; Forêt d'Ampombofofo, S12.09944°, E49.33861°, elev. 25 m, 21–22 Nov. 2007, littoral forest, sifted litter, BLF18541, CASENT 9038453 (PBI\_OON 36102), 1♀; ***Mahajanga***: Parc National Ankarafantsika, 27.51 km SSE Marovoay,



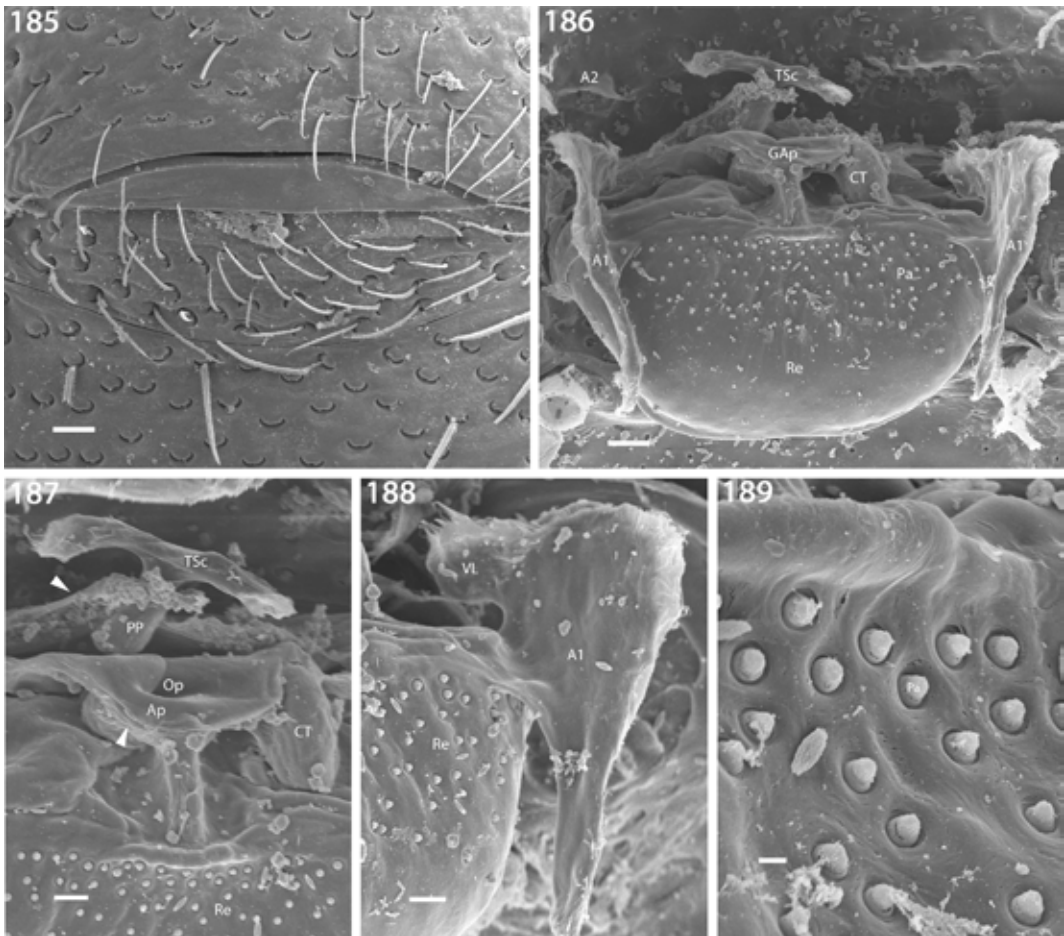


FIGS. 172–179. *Volborattella nasario*, new species, female (PBI\_OON 2225). 172. Habitus, dorsal view. 173. Same, ventral view. 174. Same, lateral view. 175. Prosoma, dorsal view. 176. Same, ventral view. 177. Same, lateral view. 178. Same, anterior view. 179. Same, posterior view. Scale bars: 200  $\mu$ m (174, 177), 100  $\mu$ m (178, 179).



FIGS. 180–184. *Volborattella nasario*, new species, female (PBI\_OON 2225), abdomen. **180.** Dorsal view. **181.** Lateral view. **182.** Ventral view. **183.** Anterior view. **184.** Posterior view. Scale bars: 200  $\mu\text{m}$  (181, 183, 184), 100  $\mu\text{m}$  (182).

S16.29746°, E46.81391°, elev. 126 m, 27 Jan. 2009, primary tropical deciduous forest, winker trap, C. Griswold et al., DANDR09, CASENT 9025446, (PBI\_OON 35157), 1 ♀; Forêt Ambohimanga, 26.1 km 314°NW Mampikony, S15.96277°, E47.43805°, elev. 250 m, 13 Dec. 2004, tropical dry forest, sifted litter (leaf mold, rotten wood), B.L. Fisher, BLF11672, CASENT 9038485, (PBI\_OON 35292), 26 ♂ 21 ♀; Parc National Ankarafantsika, 16°18'10.7"S, 46°48'47.1"E, elev. 81m, 23 Apr. 2011, sifting forest litter, Winkler app. extr., MHNG AKF/08/2011 (PBI\_OON 32407), 2 ♂ 1 ♀; same, 16°18'46.6"S, 46°48'58.8"E, elev. 89m, 22 Apr. 2011, MHNG AKF/04/2011 (PBI\_OON 32416), 3 ♂ 4 ♀; same, 16°18'9.0"S, 46°48'55.6"E, elev. 83m, 24 Apr. 2011, MHNG AKF/11/2011 (PBI\_OON 32426), 4 ♂ 3 ♀; same, 16°18'47.0"S, 46°48'57.1"E, elev. 79m, 25 Apr. 2011, MHNG AKF/13/2011 (PBI\_OON 32434), 2 ♀; same, 16°17'32.4"S, 46°48'35.7"E, elev. 61m, 25 Apr. 2011, MHNG AKF/16/2011 (PBI\_OON 32452), 2 ♀; same, 16°18'46.7"S, 46°48'57.9"E, elev. 88m, 25 Apr. 2011, MHNG AKF/15/2011 (PBI\_OON 32454), 3 ♂, 2 ♀; same, 16°18'10.7"S, 46°48'47.1"E,



FIGS. 185–189. *Volborattella nasario*, new species, female (PBI\_OON 2768, except for 185 = PBI\_OON 2225), epigynum. **185**. Ventral view. **186**. Digested, dorsal view. **187**. Same, magnified view showing open uterus externus (arrows) and associated structures. **188**. Same, lateral view, showing posterior apodeme and receptaculum. **189**. Same, papillae. Abbreviations: **A1**, posterior apodeme; **A2**, anterior apodeme; **CT**, curved tube; **GAp**, globular appendix; **Op**, opening; **Pa**, papillae; **PP**, posterior projection; **Re**, receptaculum; **TSc**, transverse sclerite; **VL**, ventral lobe of A1. Scale bars: 20  $\mu\text{m}$  (185, 186), 10  $\mu\text{m}$  (187, 188), 2  $\mu\text{m}$  (189).

elev. 81m, 23 Apr. 2011, MHNG AKF/08/2011 (PBI\_OON 32459), 1 ♂, 1 ♀; same, 16°18'47.7"S, 46°48'57.1"E, elev. 89m, 25 Apr. 2011, MHNG AKF/12/2011 (PBI\_OON 32467), 2 ♂, 1 ♀; same, 16°18'5.1"S, 46°49'8.3"E, elev. 89m, 23 Apr, 2011, MHNG AKF/05/2011 (PBI\_OON 32468), 1 ♂.

**DISTRIBUTION:** *V. nasario* occurs in western Madagascar (maps 2, 3).

***Volborattella toliara*, new species**

Figures 190–234, maps 2, 3

**TYPES:** MADAGASCAR: Toliara: Beza-Mahafaly, 27 km E Betioky, S23.65000°, E44.63333°, elev. 135 m, 23 Apr. 1997, rainforest, sifted litter, B.L. Fisher, BLF1476, CASENT 9025696 (PBI\_OON 2043), holotype ♂ and allotype ♀, and 3♂, 6♀ paratypes (deposited in CAS).

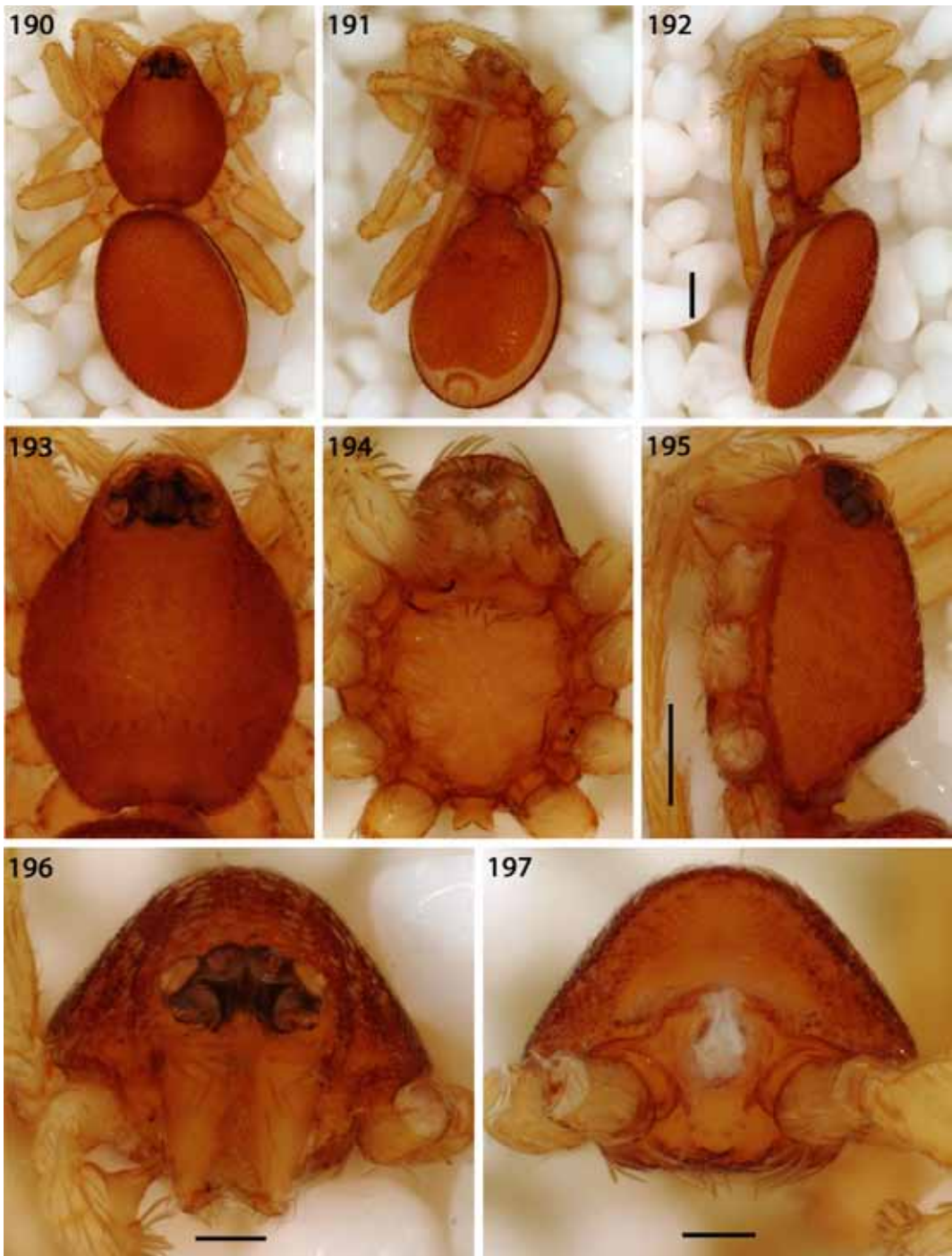
**ETYMOLOGY:** The specific name refers to the known distribution of the species.

**DIAGNOSIS:** *V. toliara* may be recognized by the orange brown abdomen with small spots (figs. 198–200, 217–219), and abdominal setae with round, medium-sized pits and medium to large bases (fig. 229). It resembles *V. teresae* in its more elongate abdomen (figs. 198, 217) and a dorsal scute with a sinuous anterior margin (figs. 201, 220), but differs in having a narrower band of plumose setae at pars thoracica (figs. 197, 216). The male of *V. toliara* most closely resembles that of *V. teresae* in having a long and apically bent embolar inferior prong (figs. 224, 227), deep sternal pockets (fig. 205), small endite projections (fig. 206), and in lacking the wide ridge above the scutal ridges (fig. 210), but differs from that species in having a shorter embolar superior prong (figs. 224, 225). The female genitalia have a sharply defined receptacular ridge (fig. 232) and posterior apodemes lacking ventral lobes (fig. 234), but otherwise closely resemble those of *V. teresae*.

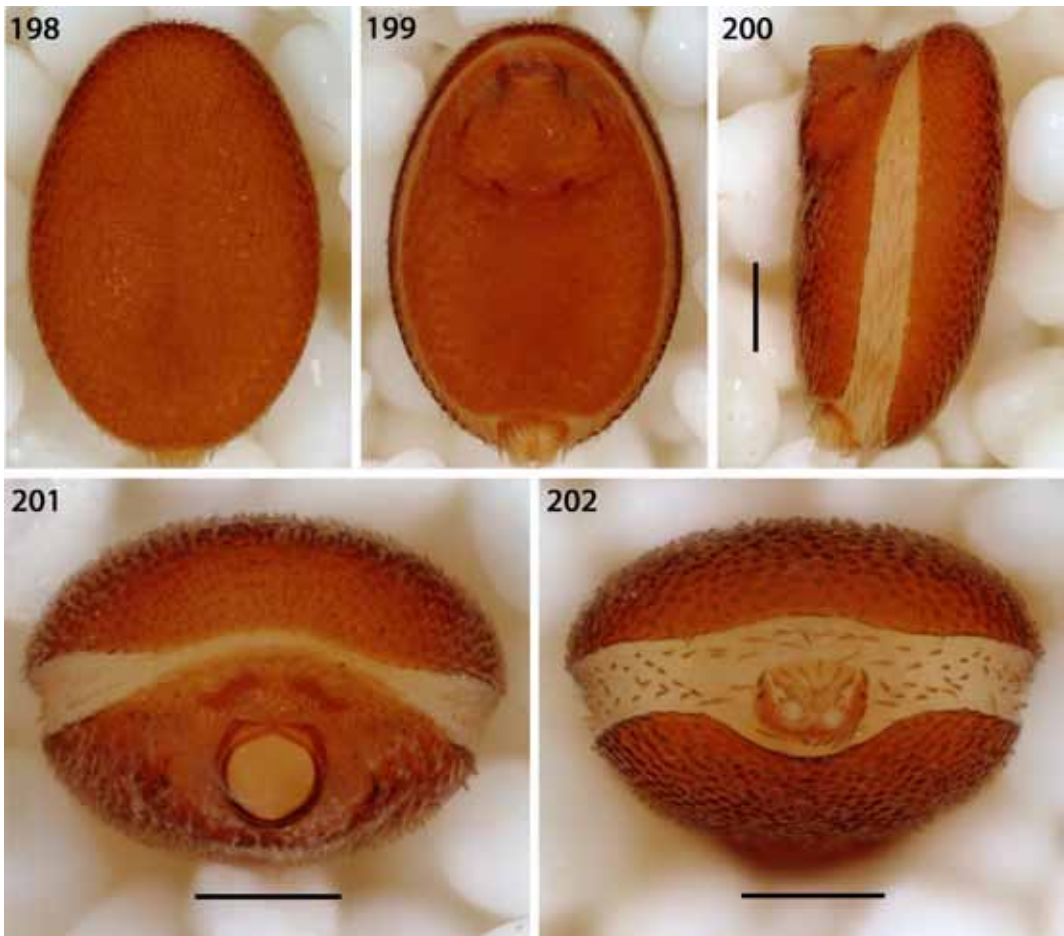
**DESCRIPTION:** MALE (paratype, PBI\_OON 2043): Total length is 1.60 mm. CEPHALOTHORAX: Carapace dark red-brown, ovoid to broadly oval in dorsal view, pars cephalica elevated in lateral view (figs. 193–197), with medium to narrow strip of plumose setae near posterior margin of pars thoracica (fig. 197). Clypeus margin not rebordered, setae dark colored. Eyes with ALE and PME subequal and larger than PLE, ALE and PLE circular, ALE separated by their radius to their diameter, ALE and PLE touching, and PLE and PME touching (figs. 193, 195, 196, 203). Sternum orange-brown, with pair of deep lateral pouches at anterior margin, with microsculpture medially and in furrows, and with light colored setae (figs. 194, 205). Mouthparts orange-brown. Endites anterior tips with small toothlike projection (fig. 206). ABDOMEN: Pedicel region with two pairs of needlelike, bristly setae on scutal ridges (figs. 207, 208). Abdominal scuta red-brown, narrow (figs. 198–200), setae with round pits and medium to large bases. Dorsal scutum anterior margin strongly curved and anterolaterally angular (fig. 201). Postepigastric scutum long, almost semicircular, covering approximately half to 2/3 of abdomen length (figs. 199, 200). LEGS: Dark yellow-brown (figs. 190–192). GENITALIA: Sperm pore circular to oval (fig. 199); palp yellow-brown (figs. 194), cymbium with pair of long prolateral setae, somewhat feathery (figs. 222, 223), embolus superior prong short, forming ca. 180° arc (figs. 224–228), inferior prong long, apically bent (figs. 224, 227).

FEMALE (paratype, PBI\_OON 2043): Total length 1.70 mm. As in male except as noted. CEPHALOTHORAX: Orange-brown (figs. 212–216). Eyes approximately subequal, PME oval, touching less than half their length (figs. 212, 214, 215). Sternum with microsculpture faint, with posterior opening only in infracoxal groove at coxae I, with setae dark colored (figs. 204, 213). Female palp tarsal organ with two sensilla, distal bifid. ABDOMEN: Abdominal scuta orange-brown, epigastric scutum not extending far dorsad of pedicel (figs. 198–200). Dorsal scutum anterior margin only slightly sinuous (fig. 220). LEGS: Light brown (figs. 209–211):



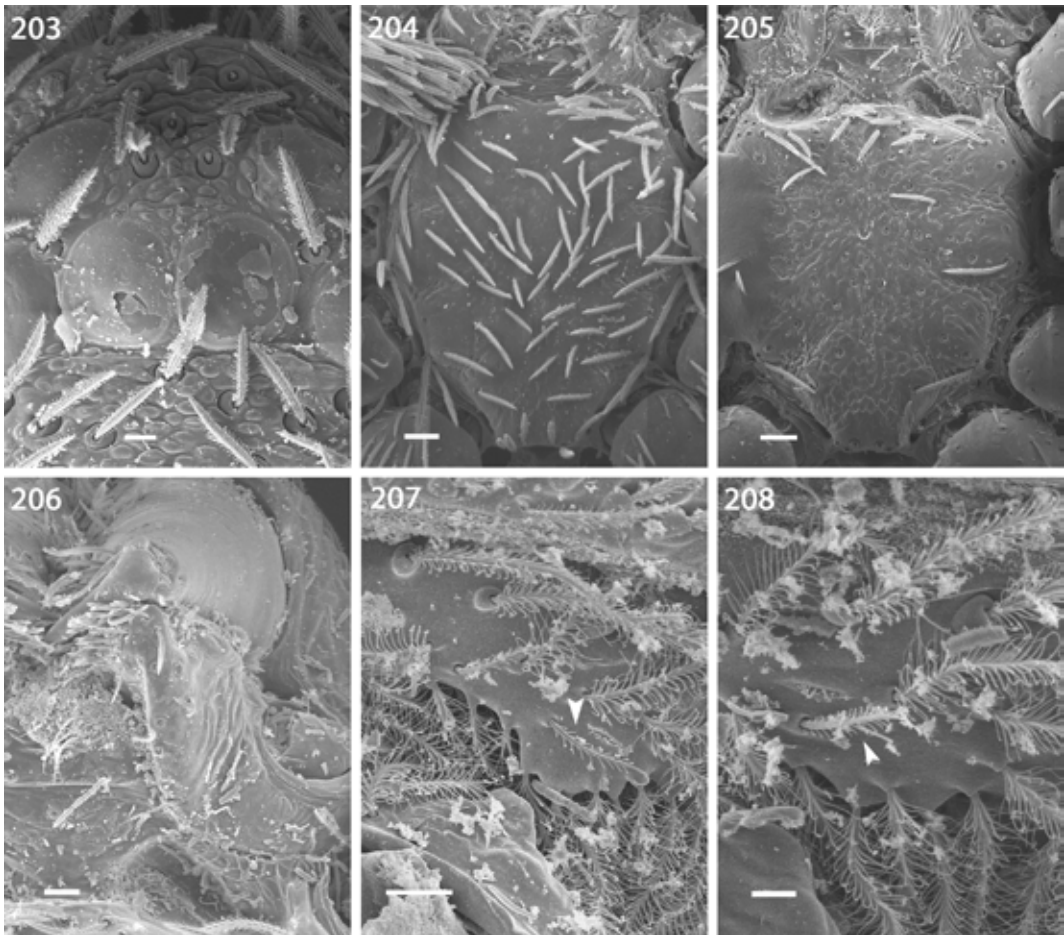


FIGS. 190–197. *Volborattella toliara*, new species, paratype male (PBI\_OON 2043). **190.** Habitus, dorsal view. **191.** Same, ventral view. **192.** Same, lateral view. **193.** Prosoma, dorsal view. **194.** Same, ventral view. **195.** Same, lateral view. **196.** Same, anterior view. **197.** Same, posterior view. Scale bars: 200  $\mu\text{m}$  (192–195), 100  $\mu\text{m}$  (196, 197).

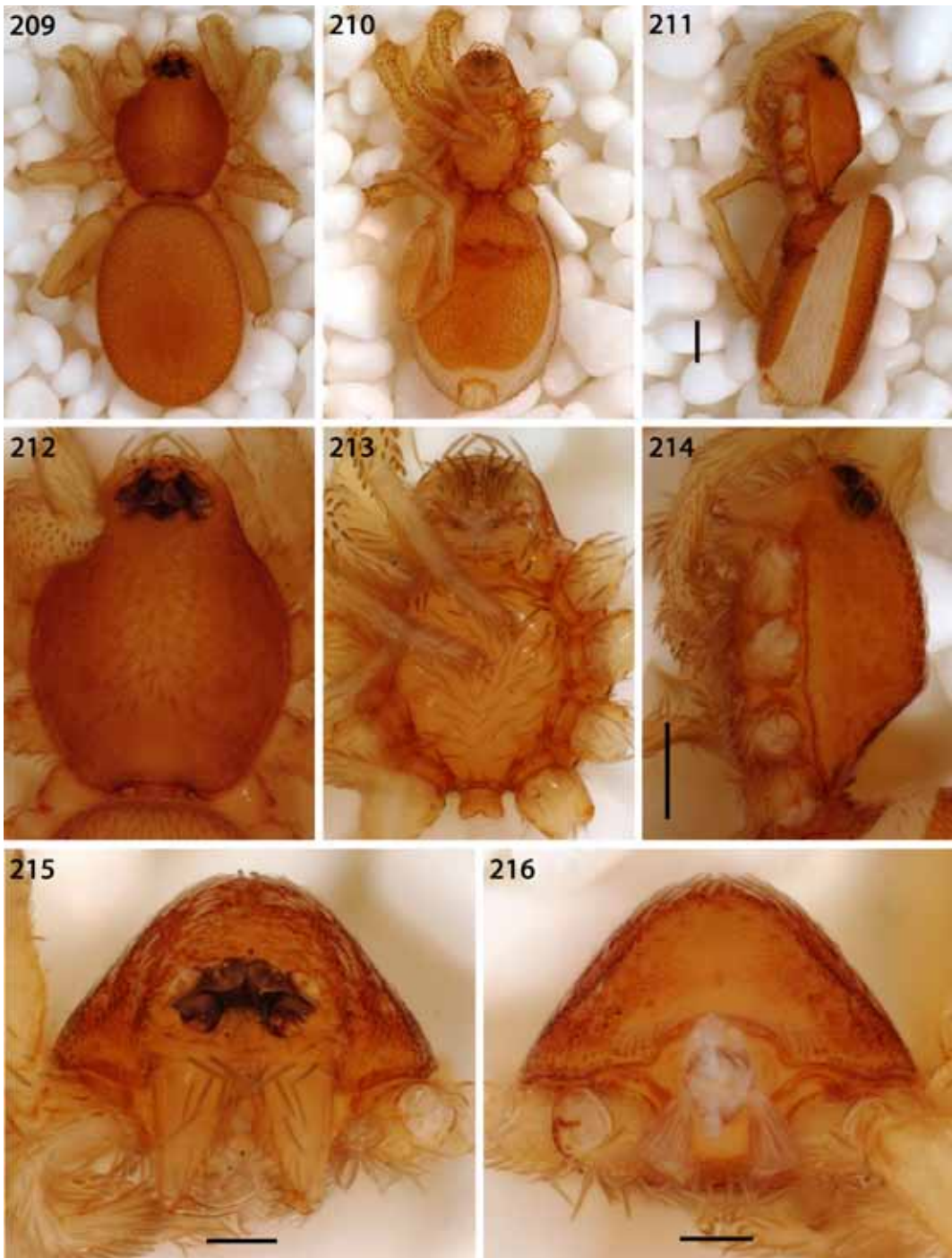


FIGS. 198–202. *Volborattella toliara*, new species, paratype male (PBI\_OON 2043), abdomen. **198.** Dorsal view. **199.** Ventral view. **200.** Lateral view. **201.** Anterior view. **202.** Posterior view. Scale bars: 200  $\mu\text{m}$ .

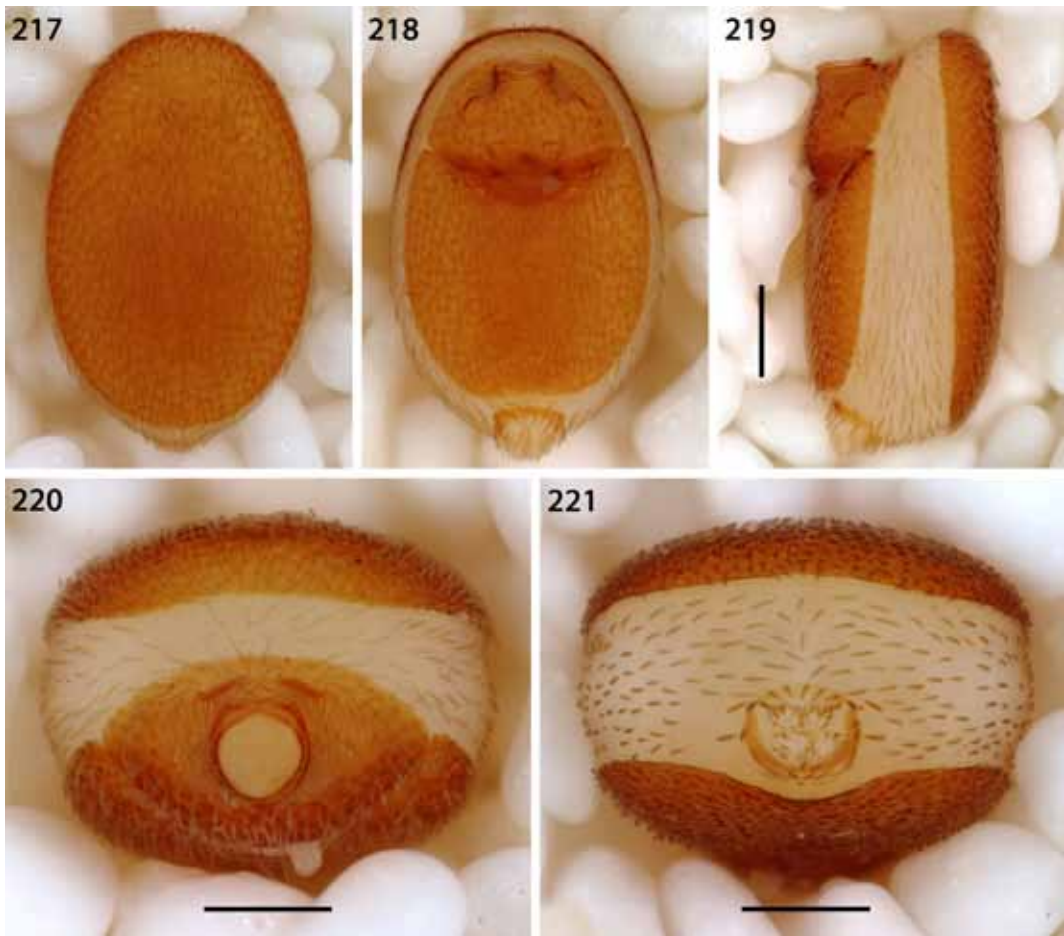




FIGS. 203–208. *Volborattella toliara*, new species, paratypes male and female (PBI\_OON 2043). **203.** Female, PME, dorsal view. **204.** Female, sternum, ventral view. **205.** Male, sternum, ventral view. **206.** Male, left endite, ventral view. **207.** Male, abdomen, anterior view, scutal ridges, with arrow to needlelike seta. **208.** Female, same, with arrow to needlelike seta. Scale bars: 15  $\mu\text{m}$  (203), 40  $\mu\text{m}$  (204, 205), 20  $\mu\text{m}$  (207), 10  $\mu\text{m}$  (208).



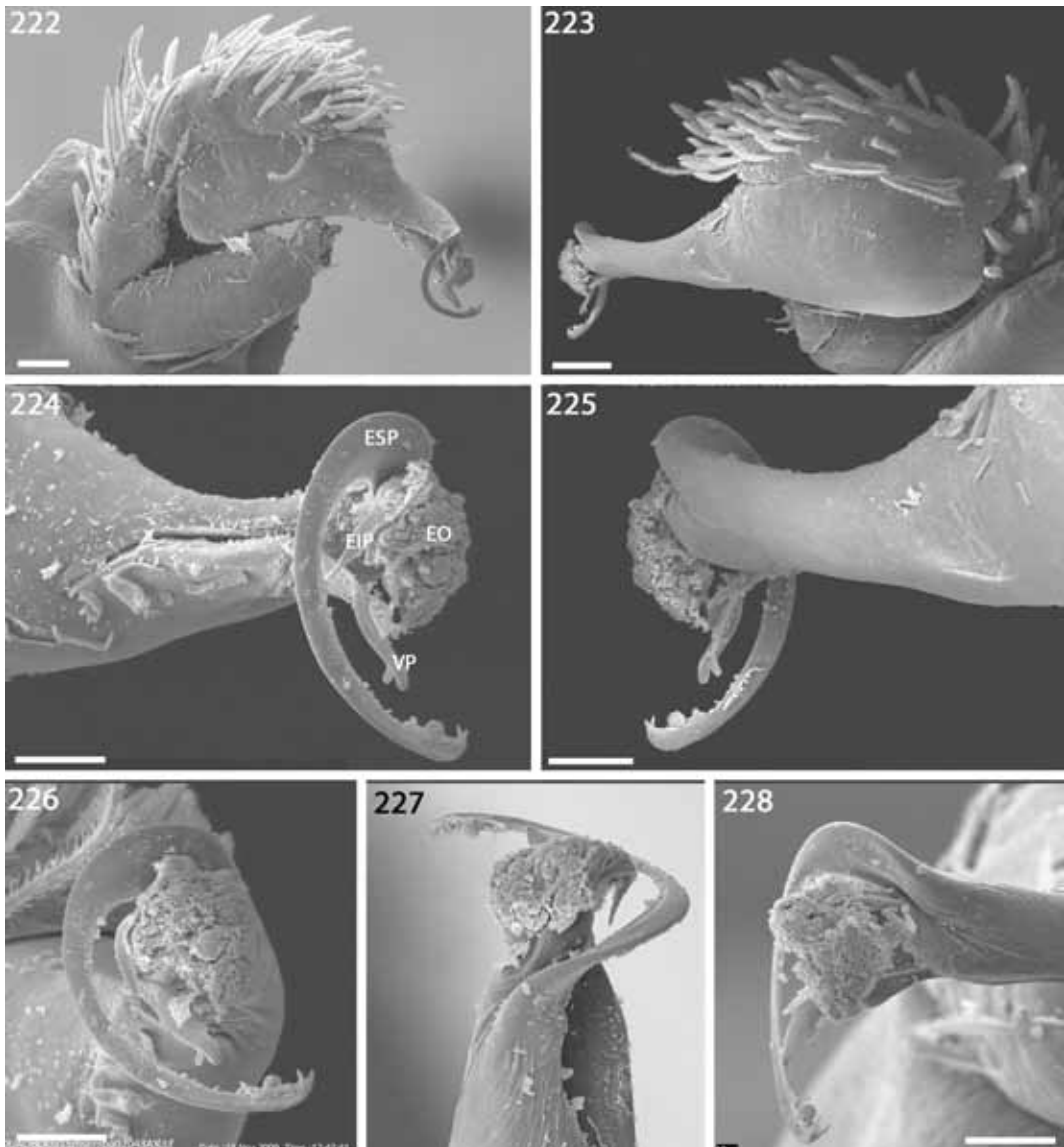
FIGS. 209–216. *Volborattella toliara*, new species, paratype female (PBI\_OON 2043). **209.** Habitus, dorsal view. **210.** Same, ventral view. **211.** Same, lateral view. **212.** Prosoma, dorsal view. **213.** Same, ventral view. **214.** Same, lateral view. **215.** Same, anterior view. **216.** Same, posterior view. Scale bars: 200  $\mu\text{m}$  (211–214), 100  $\mu\text{m}$  (215, 216).



FIGS. 217–221. *Volborattella toliara*, new species, paratype female (PBI\_OON 2043), abdomen. **217.** Dorsal view. **218.** Ventral view. **219.** Lateral view. **220.** Anterior view. **221.** Posterior view. Scale bars: 200  $\mu$ m.

Superior tarsal claw dentition claw I with 40 or more medial teeth, claw IV with ten. Tarsal organ I with three sensilla, distal bifid, IV with two. GENITALIA: Externally with anterior edge rounded to slightly angular, posterior with narrow lip (fig. 229); internally posterior apodemes (A1) reduced, ventral lobes absent, anterodorsal lobes triangular (figs. 232, 234), with a pair of tiny pits (fig. 234) just posterior to posterior apodeme attachment (as in *V. teresae*, figs. 102, 103); receptaculum with strong peaked ridge between globular appendix (GAp) and papillae, curved tube (CT) on left side of specimen (on the right side in other females), T-shaped sclerite with horizontal bar short and medially enlarged (fig. 232).

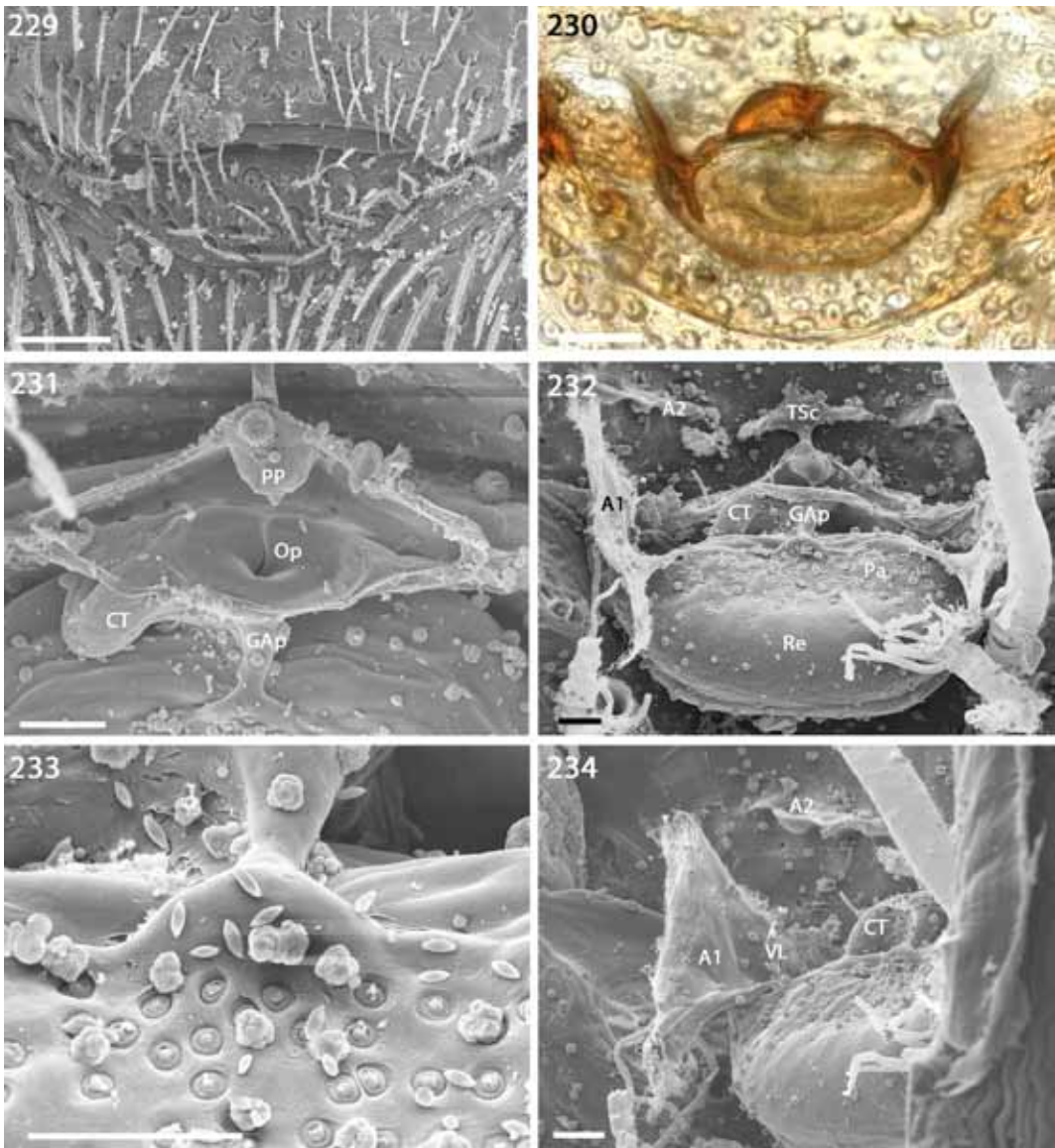
ADDITIONAL MATERIAL EXAMINED: All material was collected by Fisher-Griswold Arthropod Team from sifted litter, except as noted. MADAGASCAR: *Fianarantsoa*: Parc National d'Isalo, 9.1 km 354° N Ranohira, S22.48166°, E45.46166°, elev. 725 m, 27 Jan. 2003, gallery forest (leaf mold, rotten wood), BLF7300, CASENT 9011528 (PBI\_OON 2775), 1 ♂; *Toliara*: Vohibasia Forest, 59 km NE Sakaraha, S22.46666°, E44.85000°, elev. 780 m, 13 Jan. 1996, dry



FIGS. 222–228. *Volborattella toliara*, new species, paratype male (PBI\_OON 2043), genitalia. 222. Male, palp, prolateral view. 223. Same, retrolateral view. 224. Same, embolar region, prolateral view. 225. Same, retrolateral view. 226. Same, apical view. 227. Same, dorsal view. 228. Same, retroapical view. Abbreviations: **EIP**, embolar inferior prong; **EO**, embolar opening; **ESP**, embolar superior prong; **VP**, ventral process. Scale bars: 40  $\mu$ m (222, 223), 20  $\mu$ m (others).

forest, B.L. Fisher, BLF1310, CASENT 9025448 (PBI\_OON 2226), 2♂ 2♀; Manderano, S23.52416°, E44.09277°, elev. 75 m, 29 May 2002, gallery forest (leaf mold, rotten wood), Frontier Project, MGF033, CASENT 9011392 (PBI\_OON 2769), 1♀; Forêt de Mite, 20.7 km 29° WNW Tongobory, S23.52416°, E44.12138°, elev. 75 m, 27 Feb. 2002, gallery forest (leaf mold, rotten wood), BLF5850, CASENT 9010325 (PBI\_OON 2772), 1♂; Reserve Speciale de Cap





FIGS. 229–234. *Volborattella toliara*, new species, paratype female (PBI\_OON 2043), genitalia. **229.** Epigynum, ventral view. **230.** Same, dorsal view. **231.** Same, interior with uterus externus open showing the “nail” (PP) and “hole” (Op). **232.** Same, internal genitalia, dorsal view. **233.** Same, magnified view of receptaculum showing papillae. **234.** Same, anterolateral view, posterior apodeme (A1) showing strongly reduced VL. Abbreviations: **A1**, posterior apodeme; **A2**, anterior apodeme; **CT**, curved tube; **GAp**, globular appendix; **Op**, opening; **Pa**, papillae; **PP**, posterior projection; **Re**, receptaculum; **TSc**, transverse sclerite; **VL**, ventral lobe of A1. Scale bars: 50  $\mu$ m (229, 230), 20  $\mu$ m (231–234).

Sainte Marie, 14.9 km 261° W Marovato, S25.59444°, E45.14694°, elev. 160 m, 13 Feb. 2002, spiny forest/thicket (leaf mold, rotten wood), BLF5570, CASENT 9010311 (PBI\_OON 2773), 2♂ 1♀; Parc National de Tsimanampetsotsa, 6.7 km 130° SE Efoetse, 23 km 175° S Beheloka, S24.10055°, E43.76000°, elev. 25 m, 18 Mar. 2002, spiny forest/thicket (leaf mold, rotten wood),

BLF6160, CASENT 9010293 (PBI\_OON 2774), 1 ♀; Forêt de Kirindy, 15.5 km 64° ENE Marofandilia, S20.04500°, E44.66222°, elev. 100 m, 28 Nov. 2001, tropical dry forest (leaf mold, rotten wood), BLF4605, CASENT 9010348 (PBI\_OON 2776), 1 ♂ 2 ♀; Fiherenana, S23.17694°, E43.96083°, elev. 100 m, 21 Oct. 2002, gallery forest (leaf mold, rotten wood), Frontier Project, MGF040, CASENT 9011405 (PBI\_OON 2777), 1 ♀; Parc National de Kirindy Mite, 16.3 km 127° SE Belo sur Mer, S20.79527°, E44.14694°, elev. 80 m, 6 Dec. 2001, tropical dry forest (leaf mold, rotten wood), BLF4726, CASENT 9011372 (PBI\_OON 2778), 1 ♂; Beza-Mahafaly, 21.67 km ENE Betioky, S23.69700°, E44.59141°, elev. 168 m, 18 Jan. 2009, spiny forest, pitfall trap, Griswold et al., DANDR06, CASENT 9025445, (PBI\_OON 2254), 1 ♂; Beza-Mahafaly, 27 km E Betioky, S23.65000°, E44.63333°, elev. 135 m, 23 Apr. 1997, rainforest, B.L. Fisher, BLF1476, CASENT9030629 (PBI\_OON 3718), 1 ♂.

DISTRIBUTION: *V. toliara* is distributed in southwestern Madagascar (maps 2, 3).

### *Volborattella paulyi*, new species

Figures 235–274, maps 2, 3

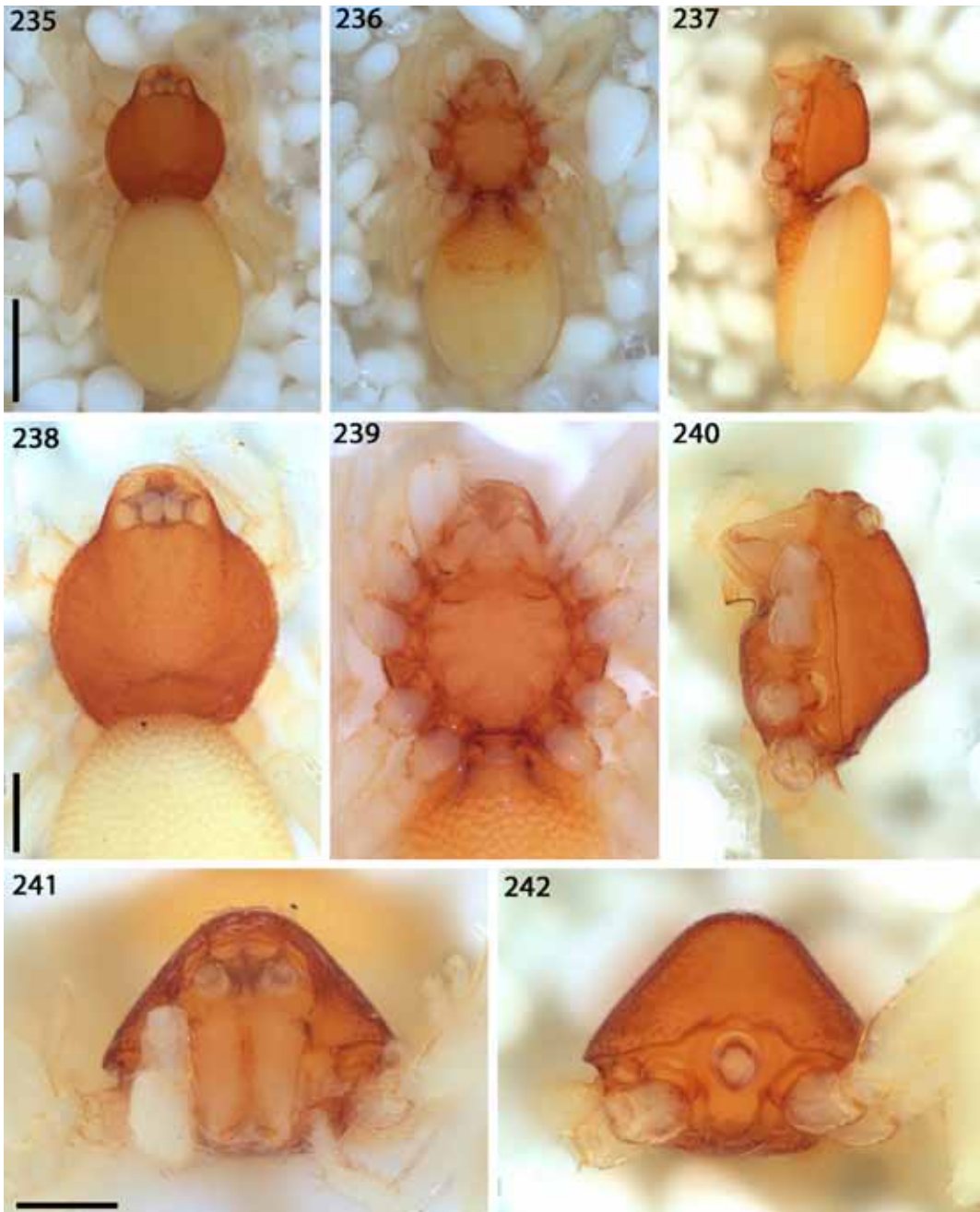
TYPES: MADAGASCAR: Toamasina: Foulpointe [S17.68333°, E49.50000°], Sep. 1994, forest on clay soil, collected by A. Pauly, RMCA 220088 (PBI\_OON 8026), holotype ♂; same data but collected on 2 Dec. 1993 from forest on sandy soil, RMCA 200347 (PBI\_OON 8031), allotype female (deposited in RMCA).

ETYMOLOGY: The specific name is a patronym in honor of Alain Pauly, the sole collector of this species.

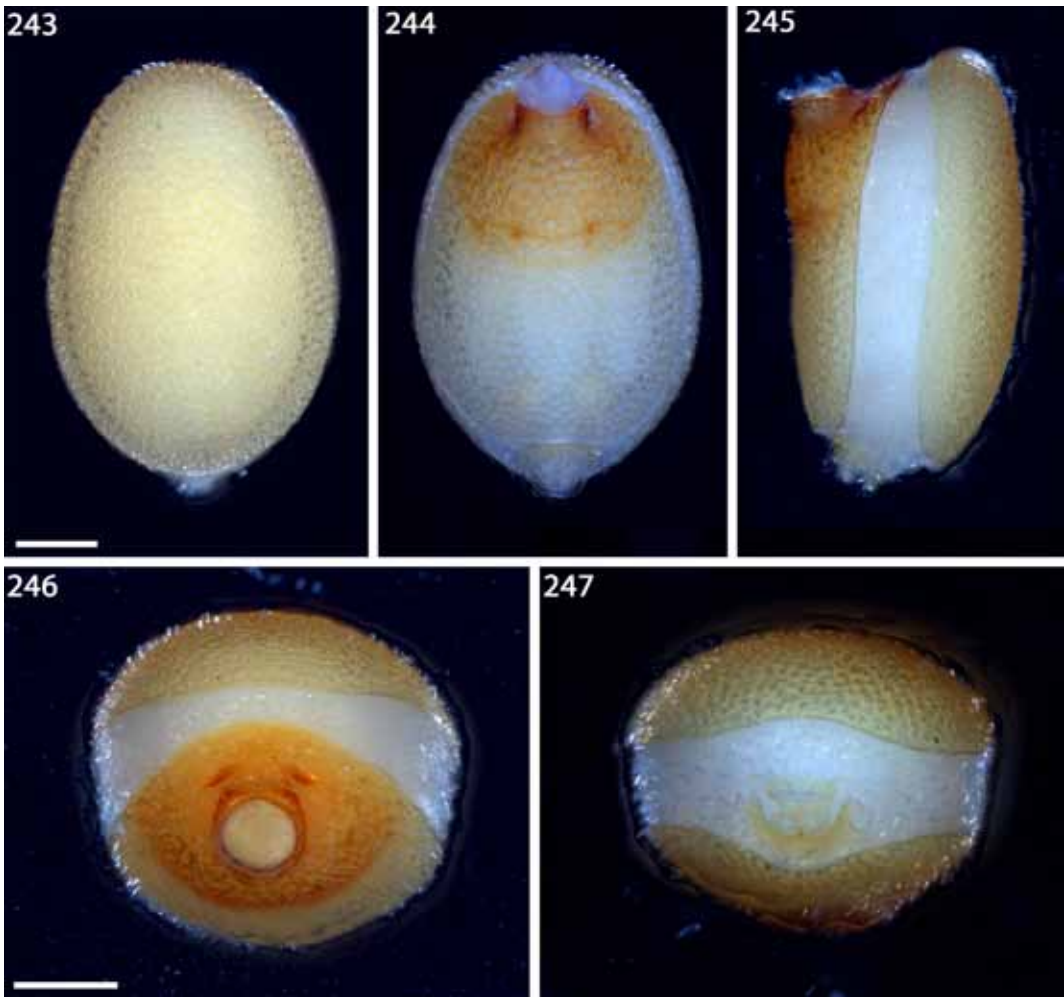
DIAGNOSIS: *V. paulyi* is most easily distinguished from other *Volborattella* species by its pale coloration, with depigmented legs and the abdomen yellowish with pale spots (figs. 243–247, 256–260), and abdominal setae with large, contiguous pits forming honeycomb pattern (figs. 261, 262). It resembles *V. guenevera* in having large, depigmented eyes (figs. 238, 240, 251, 253) and *V. teresae* and *V. toliara* in having a relatively narrow abdomen (figs. 235–237, 248–250). The male differs from those of other *Volborattella* in having a palp with a reddish embolar superior prong and a long, broad inferior prong (figs. 263–266, 271), and the female in having a very short receptaculum (fig. 268) and a transverse sclerite with short, pointed prongs (fig. 262).

DESCRIPTION: MALE (paratype, PBI\_OON 8027): Total length 1.66 mm. CEPHALOTHORAX: Carapace orange-brown, ovoid to broadly oval in dorsal view (fig. 238), pars cephalica slightly to strongly elevated in lateral view (figs. 240, 242), with narrow strip of plumose setae at posterior margin of pars thoracica (figs. 238, 240, 242). Clypeus margin not rebordered, setae light colored (fig. 241). Eyes subequal, ALE and PLE circular, ALE separated by almost their diameter, ALE, PLE, and PME touching, PME squared, touching for about half their length (figs. 238, 240, 241). Sternum orange-brown, with a pair of lateral pouches at anterior margin, with microsculpture mostly in furrows, with light colored setae (fig. 239). Mouthparts light orange-brown. Endites with anterior toothlike projection present (fig. 239). ABDOMEN: Pedicel region with plumose setae and cuticular projections (figs. 242, 245, 246). Abdominal scuta yellowish with pale spots, setae with bases small, pits large and densely packed giving honey-

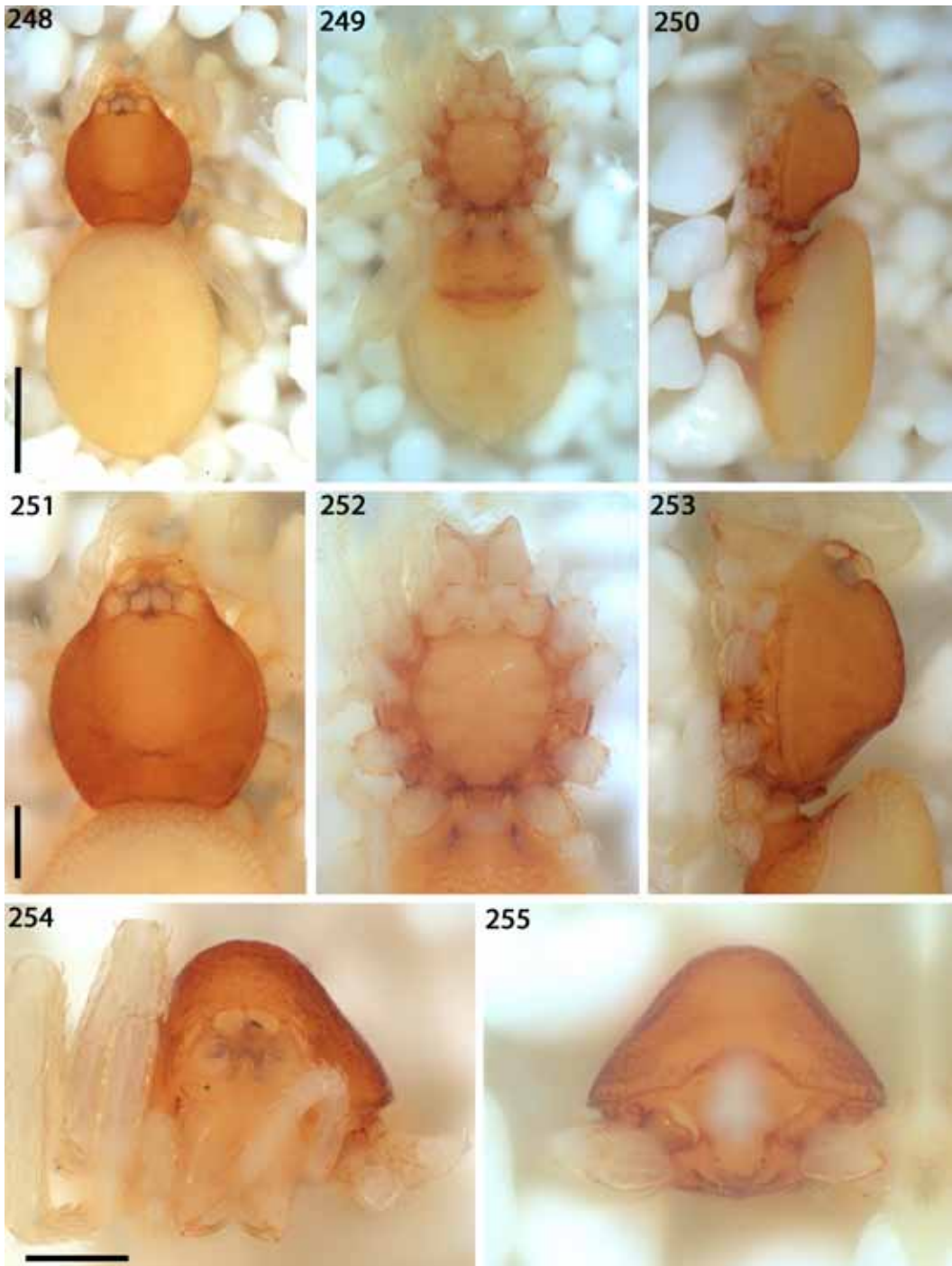




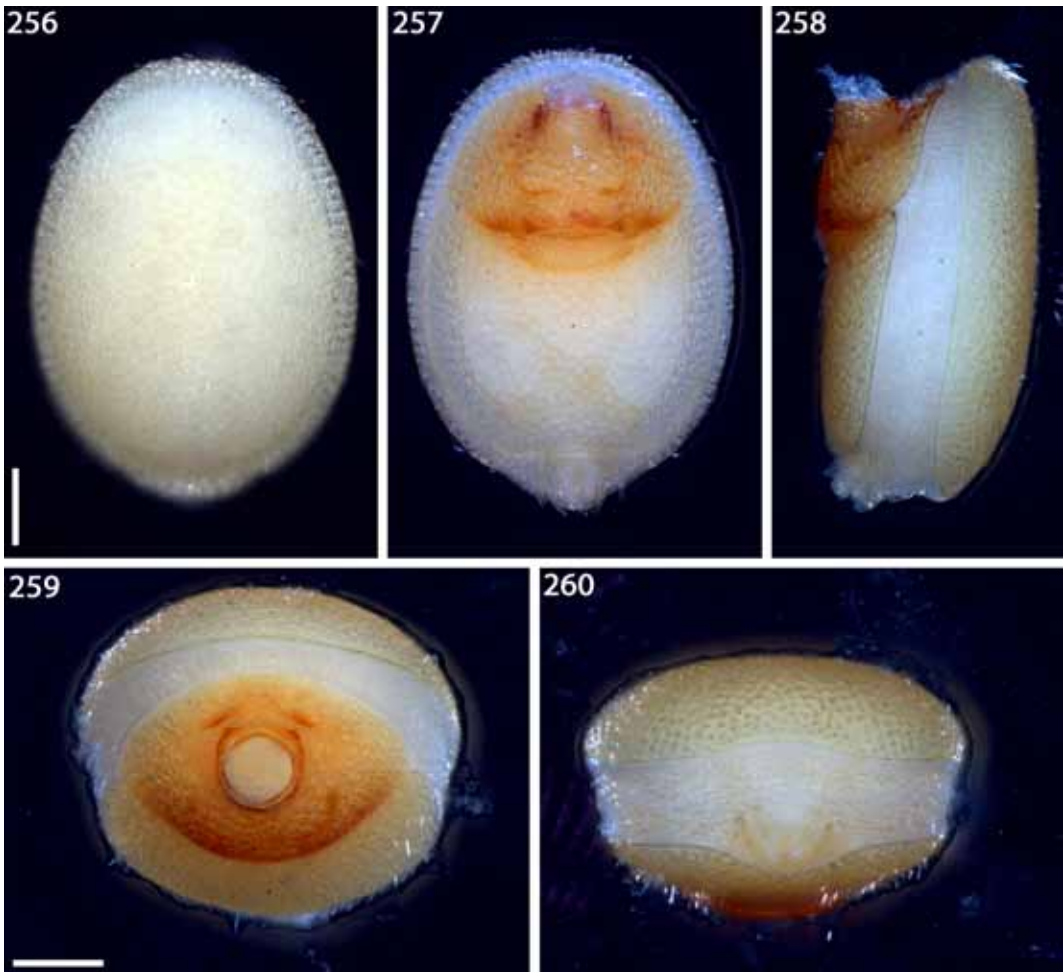
FIGS. 235–242. *Volborattella paulyi*, new species, paratype male (PBI\_OON 8027). 235. Habitus, dorsal view. 236. Same, ventral view. 237. Same, lateral view. 238. Cephalothorax, dorsal view. 239. Same, ventral view. 240. Same, lateral view. 241. Same, anterior view. 242. Same, posterior view. Scale bars: 500  $\mu\text{m}$  (235–237), 200  $\mu\text{m}$  (238–242).



FIGS. 243–247. *Volborattella paulyi*, new species, paratype male (PBI\_OON 8027). **243.** Abdomen, dorsal view. **244.** Same, ventral view. **245.** Same, lateral view. **246.** Same, anterior view. **247.** Same, posterior view. Scale bars: 200  $\mu\text{m}$ .

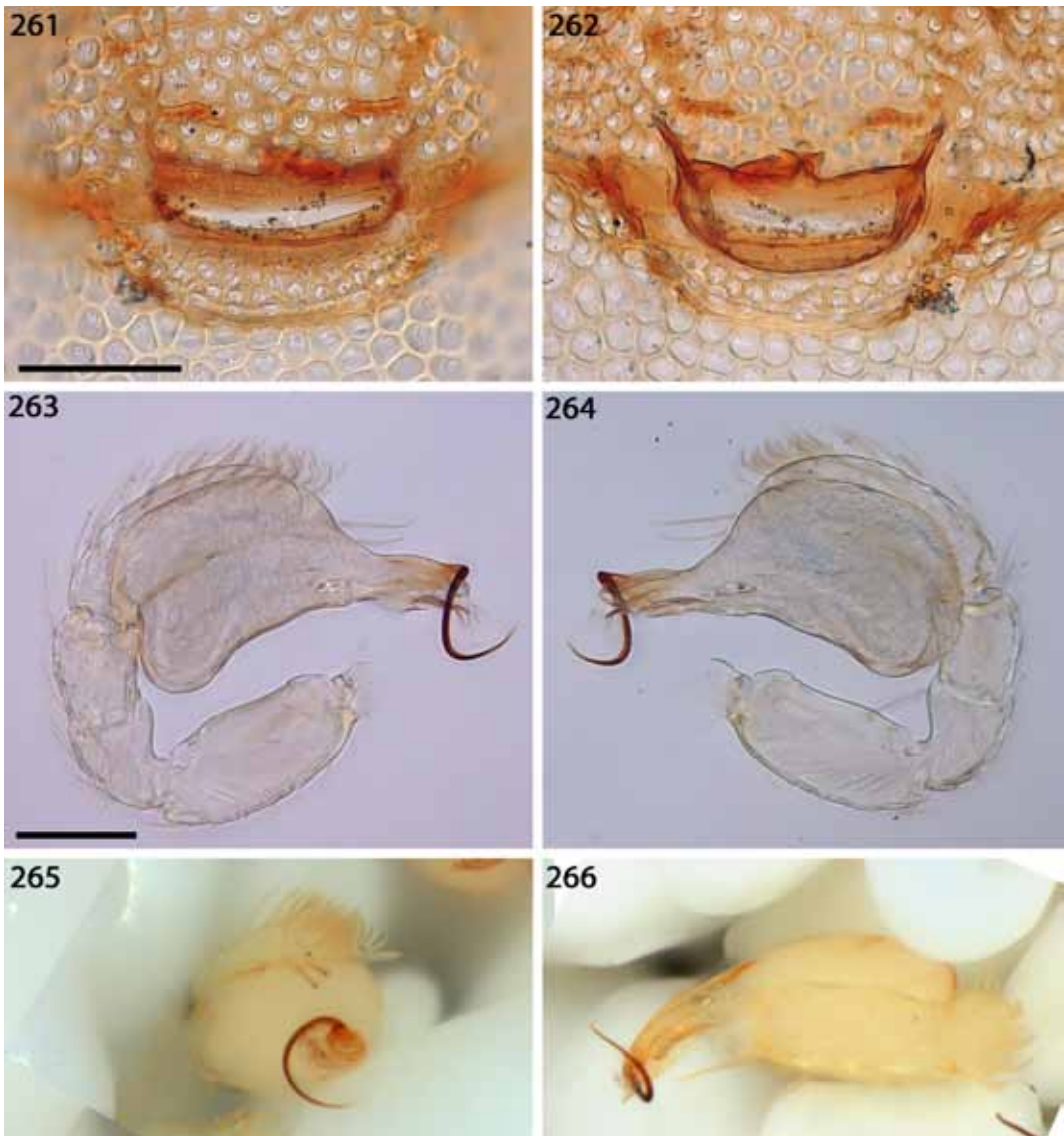


FIGS. 248–255. *Volborattella paulyi*, new species, paratype female (PBI\_OON 8032). 248. Habitus, dorsal view. 249. Same, ventral view. 250. Same, lateral view. 251. Cephalothorax, dorsal view. 252. Same, ventral view. 253. Same, lateral view. 254. Same, anterior view. 255. Same, posterior view. Scale bars: 500  $\mu\text{m}$  (248–250), 200  $\mu\text{m}$  (251–255).

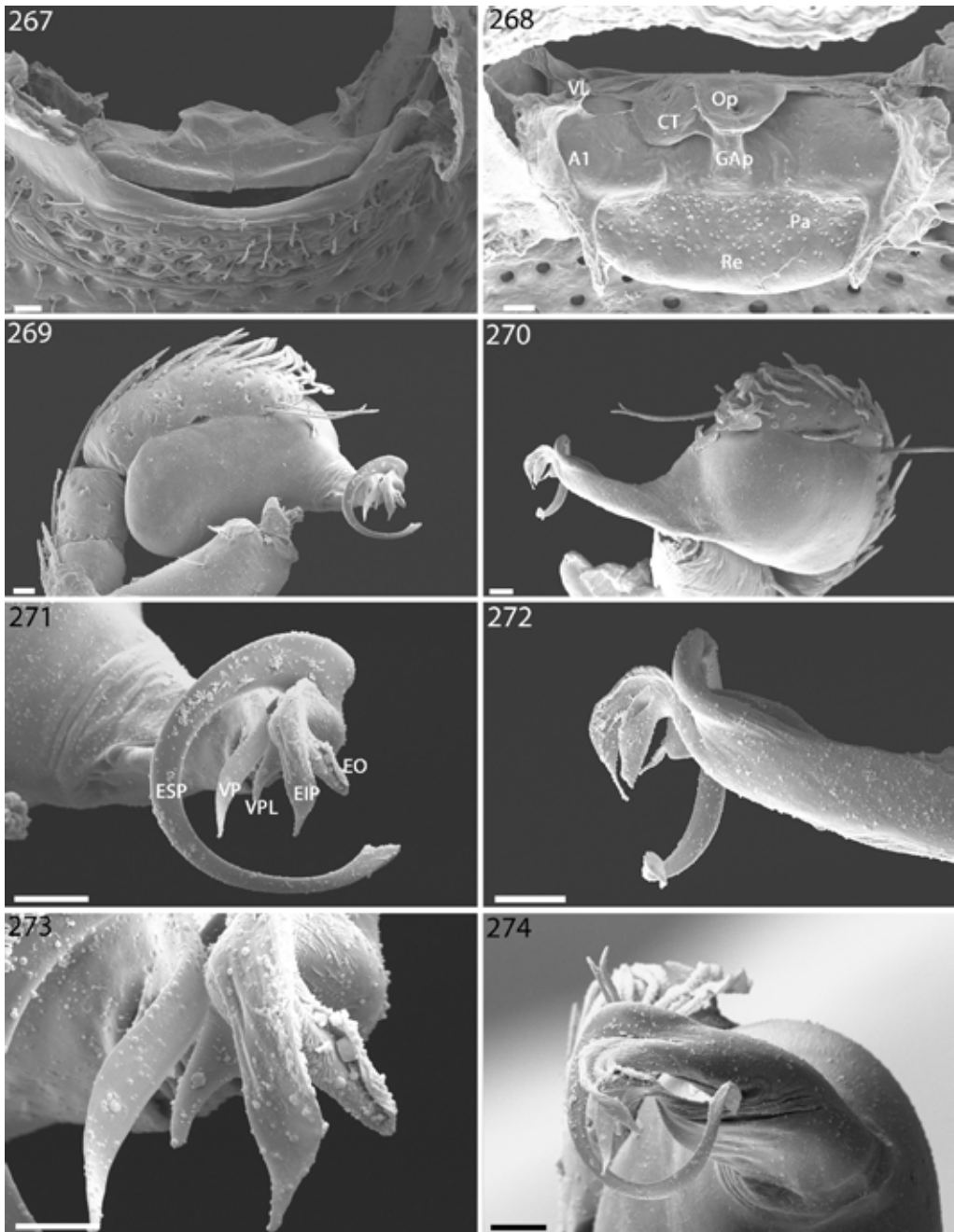


FIGS. 256–260. *Volborattella paulyi*, new species, paratype female (PBI\_OON 8032). **256.** Abdomen, dorsal view. **257.** Same, ventral view. **258.** Same, lateral view. **259.** Same, anterior view. **260.** Same, posterior view. Scale bars: 200  $\mu\text{m}$ .



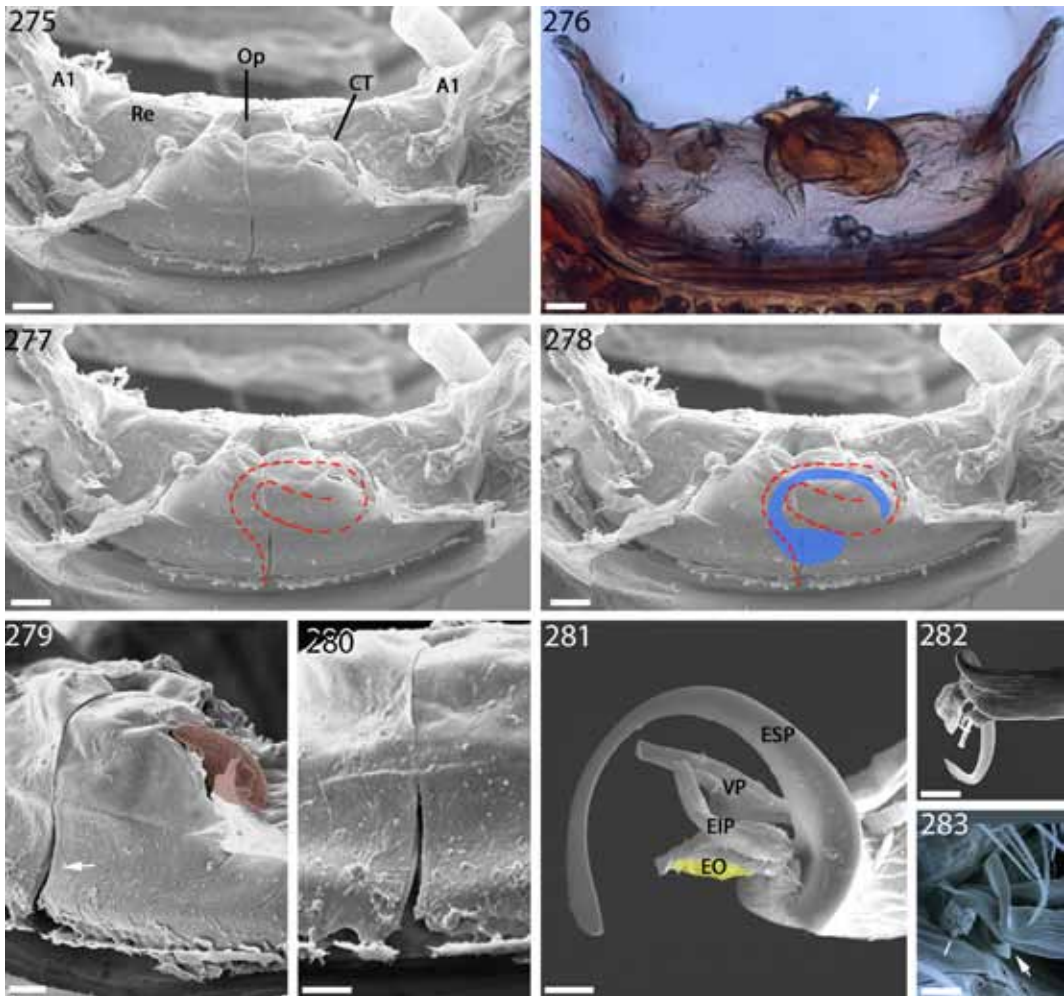


FIGS. 261–266. *Volborattella paulyi*, new species, paratypes male (PBI\_OON 8027) and female (PBI\_OON 8025). **261.** Female, genitalia, ventral view. **262.** Same, dorsal view. **263.** Male, palp, prolateral view. **264.** Same, retrolateral view. **265.** Same, apical view. **266.** Same, ventral view. Scale bars: 200  $\mu$ m.



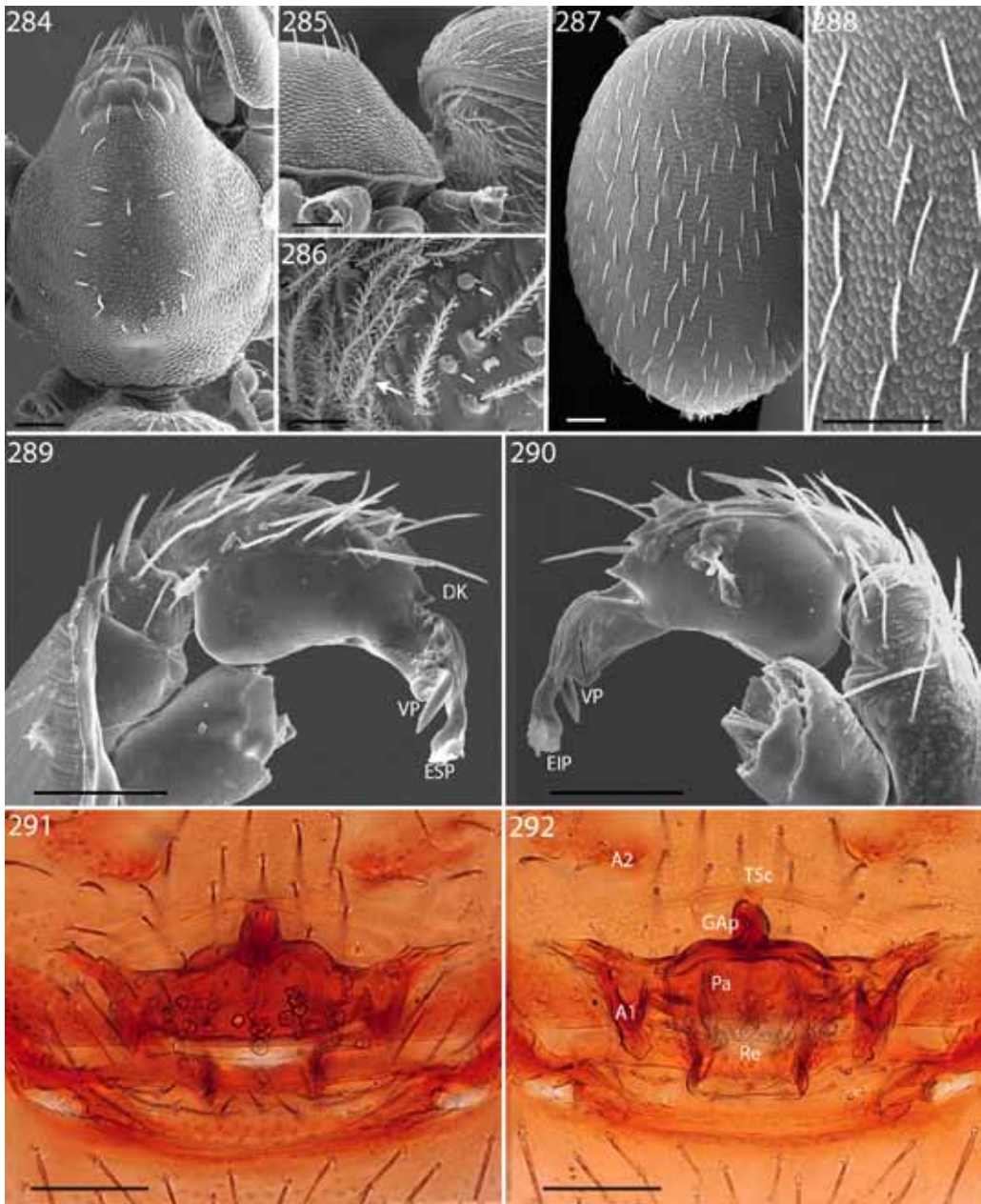
FIGS. 267–274. *Volborattella paulyi*, new species, paratypes male (PBI\_OON 8027) and female (PBI\_OON 8029). **267.** Female, genitalia, posterior part, ventral view. **268.** Same, dorsal view. **269.** Male, palp, prolateral view. **270.** Same, retrolateral view. **271.** Embolar region, prolateral view. **272.** Same, retrolateral view. **273.** Same, magnified view. **274.** Same, retroapical view. Abbreviations: **A1**, posterior apodeme; **CT**, curved tube; **EIP**, embolar inferior prong; **EO**, embolar opening; **ESP**, embolar superior prong; **GAp**, globular appendix; **Op**, opening; **Pa**, papillae; **Re**, receptaculum; **VL**, ventral lobe of A1; **VP**, ventral process; **VPL**, ventral process lobe. Scale bars: 10  $\mu\text{m}$  (273), 20  $\mu\text{m}$  (others).





FIGS. 275–283. *Volborattella teresae*, new species, paratypes female (PBI\_OON 2228) and male (PBI\_OON 2006). 275. Female, posterior genitalia, anteroventral view. 276. Same, through compound microscope with arrow showing CT, anteroventral view. 277. Same, micrograph with CT indicated by dashed line. 278. Same, with left male ESP in blue showing hypothesized coupling. 279. Same, with exposed part of CT highlighted and arrow to ventral slit, sublateral view. 280. Same, magnified view showing ventral slit. 281. Male, embolar region with embolar opening highlighted, retroapical view, same magnification as previous fig. 282. Same, retrolateral view. 283. Same, at rest in sternal cavity, showing secretion at embolar opening (dash) and ESP contracted, forming complete circle (arrow). Abbreviations: A1, posterior apodemes; CT, curved tube; EIP, embolar inferior prong; EO, embolar opening; ESP, embolar superior prong; Op, opening to Re; Re, receptaculum; VP, ventral process. Scale bars: 20  $\mu$ m (275–278, 282, 283), 10  $\mu$ m (279–281).

comb appearance (figs. 243 and 261, female). Dorsal scutum anterior margin evenly curved, not anterolaterally angular (fig. 246). Postepigastric scutum long, almost semicircular, extending to spinneret scutum (figs. 244, 245). LEGS: pale, whitish (figs. 235–237). GENITALIA: Sperm pore circular to oval (fig. 244); palp light yellowish, embolar complex orangish, superior prong (ESP) black with a reddish tint (figs. 263–266), ESP of moderate length, enscripting 2/3 circle, inferior prong straight and broad, with abruptly pointed tip (figs. 269–274).



FIGS. 284–292. *Yumates nesophila* Chamberlin, male and female (284–290; PBI\_OON 2189) and *Yumates* species, female (291, 292; PBI\_OON 35685). **284**. Male carapace, dorsal view. **285**. Same, pedicel region, lateral view. **286**. Same, magnified view showing plumose setae (arrow) and cuticular projections (dashes). **287**. Female abdomen, dorsal view. **288**. Same, magnified view showing setae and scutal texture. **289**. Male palp, prolateral view. **290**. Same, retrolateral view. **291**. Female genitalia, ventral view. **292**. Same, dorsal view. Abbreviations: **A1**, posterior apodeme; **A2**, anterior apodeme; **GAp**, globular appendix; **DK**, dorsal knob; **EIP**, embolar inferior prong; **ESP**, embolar superior prong; **Pa**, papillae; **Re**, receptaculum; **TSc**, transverse sclerite; **VP**, ventral process. Scale bars: 20  $\mu\text{m}$  (229); 100  $\mu\text{m}$  (others).

FEMALE (paratype, PBI\_OON 8032): Total length 1.80 mm. As in male except as noted. CEPHALOTHORAX: Orange-brown (figs. 251–255). Eyes approximately subequal, PME squared, touching for less than half their length (figs. 251, 253, 254). Sternum with microsculpture faint, setae light colored (fig. 252). ABDOMEN: Abdominal scuta yellowish with pale spots (fig. 256), epigastric scutum orange-brown, extending dorsad about one pedicel diameter (figs. 249, 250). Dorsal scutum anterior margin evenly curved (fig. 259). LEGS: Whitish (figs. 248–250). GENITALIA (scans are of a different female, PBI\_OON 8029): Externally with posterior edge a narrow lip (fig. 267); internally, posterior apodemes (A1) with ventral lobes small, rounded, anterodorsal lobes angular (fig. 268), receptaculum with ridge not evident, globular appendix short and thick, curved tube on left side of genitalia, T-shaped sclerite horizontal bar short and pointed (fig. 262).

VARIATION: Although the CT of both the imaged females is left sided, in some other females it is right sided.

ADDITIONAL MATERIAL EXAMINED: MADAGASCAR: *Toamasina*: Foulpointe [S17.68333°, E49.50000°: coordinates not given on label], Nov. 1994, red earth forest litter, A. Pauly, RMCA 220-040 (PBI\_OON 8025), same, 10 Nov. 1993, sandy forest with *Pandanus* marsh, RMCA 200-141 (PBI\_OON 8027), 1 ♂; same, Oct. 1994, clay forest, RMCA 206-413 (PBI\_OON 8029), 1 ♂ 1 ♀; same, 17 Nov. 1993, sandy forest, RMCA 220-090 (PBI\_OON 8030), 1 ♂ 1 ♀; same, Dec. 1993, *Asplenium* forest, RMCA 177-894 (PBI\_OON 8032), 1 ♀; same, Jul. 1994, clay forest, RMCA 220-087 (PBI\_OON 8034), 1 subadult ♂.

DISTRIBUTION: *V. paulyi* is known only from Foulpointe, in eastern Madagascar (maps 2, 3).

#### ACKNOWLEDGMENTS

Funding for this project came from the Research/Education Divisions at California Academy of Sciences (CAS), the Exline-Frizzell and Lindsay Funds (CAS), the Schlinger Foundation and the U.S. National Science Foundation (NSF). C.E.G. acknowledges NSF grants DEB-9296271: “Systematics and Biogeography of Afromontane Spiders” and DEB-0613775 “PBI: Collaborative Research: The Megadiverse, Microdistributed Spider Family Oonopidae,” to C.E.G.; DEB-0072713: “Terrestrial Arthropod Inventory of Madagascar” (to Brian Fisher and C.E.G.); and EAR-0228699: “Assembling the Tree of Life: Phylogeny of Spiders” (W. Wheeler, PI).

We are most grateful to Brian Fisher and the Malagasy Ant Team and to members of the Fisher/Griswold Arthropod Survey team, who were responsible for collecting and processing many of the specimens studied: Daniela Andriamalala, Lantoniaina Andriamampianina, Dylan Berge, Lisa Joy Boutin, Alison Cameron, Randriambololona Tantely Nirina, Brian Fisher, Jennifer Jacobs, Joel Ledford, Gary Ouellette, Pascal Rabeson, Jean-Jacques Rafanomezantsoa, Maminiaina Rajaonarivo, Balsama Rajemison, Jean Claude Rakotonirina, Chrislain Ranaivo, Nicole Rasoamanana, Hanitriniana Rasoazanamavo, Helian Ratsirarson, Domoina Razafindrindra, Diana Silva, Corrie Moreau, and Brinda Vavy. We thank Benjamin Andriamihaja, Directeur Général of the Madagascar Institut pour la Conservation des Ecosystèmes Tropicaux

(MICET) for help with logistics and especially Harin'Hala Hasinjaka (Rin'ha) of that institute and Balsama Rajemison for arranging the permits.

Many thanks go to Norm Platnick for making available the Malagasy material from both the AMNH and MNHN, to Rudy Jocqué and Wouter Fannes (RMCA) for the valuable material from Foulpointe, and to Yvonne Kranz-Baltensperger (NHMB) for making available the material from MNHG; all much appreciated. Many thanks to Anthea Carmichael for help in databasing and image uploading. Appreciation for the interesting discussions goes to the entire PBI group, but especially to Fernando Álvarez-Padilla and Tamás Szûts.

Appreciation goes to the good folks at the GIS Unit of the Royal Botanic Gardens Kew: Justin Moat, Patricia Malcolm-Tompkins, and Aaron P. Davis, for their helpful assistance and permission to use their Map of Remaining Madagascar Primary Vegetation.

Finally, A.D.S especially thanks her M.Sc. thesis committee at San Francisco State University, Greg Spicer, and John Hafernik, the Oonopidae PBI steering committee and project team, the CAS Arachnology lab, particularly, Joel Ledford, Anthea Carmichael, and Tamás Szûts, and warmly thanks Nasario Mejia for his unwavering support and patience. C.E.G. and A.D.S. are grateful to MICET and Renoir, our Malagasy driver, and other members of the Madagascar 2008–2009 expedition team: Gustavo Hormiga, Nikolaj Scharff, Fernando Álvarez-Padilla, Hannah Wood, and Daniela Andriamalala. We are all grateful to Fernando Álvarez-Padilla for his guidance, patience, insight, and ever-present sense of humor.

## REFERENCES

- Agnarsson, I. 2006. Asymmetric female genitalia and other remarkable morphology in a new genus of cobweb spiders (Theridiidae, Araneae) from Madagascar. *Biological Journal of the Linnean Society* 87: 211–232.
- Álvarez-Padilla, F., and G. Hormiga. 2007. A protocol for digesting internal soft tissue and mounting spiders for scanning electron microscopy. *Journal of Arachnology* 35 (3): 538–542.
- Álvarez-Padilla, F., D. Ubick, and C.E. Griswold. 2012. *Noideattella* and *Tolegnaro*, two new genera of goblin spiders from Madagascar, with comments on the Gamasomorphoid and Silhouetteloid oonopids (Araneae, Oonopidae). *American Museum Novitates* 3745: 1–76.
- Andriamalala, D. 2007. Revision of the genus *Padilla* Peckham & Peckham, 1894 (Araneae, Salticidae). Convergent evolution of secondary sexual characters due to sexual selection and rates of molecular evolution in jumping spiders. *Proceedings of the California Academy of Sciences* 58 (13): 243–330.
- Andriamalala, D., and G. Hormiga. 2013. Systematics of the goblin spider genus *Opopaea* (Araneae, Oonopidae) in Madagascar. *Bulletin of the American Museum of Natural History* 380: 1–156.
- Benoit, P.L.G. 1979. Contributions à l'étude de la faune terrestre des îles granitiques de l'archipel des Séchelles (Mission P.L.G. Benoit–J.J. Van Mol 1972). Oonopidae (Araneae). *Revue de Zoologie Africaine* 93: 185–222.
- Burger, M. 2010. Complex female genitalia indicate sperm dumping in armored goblin spiders (Arachnida, Araneae, Oonopidae). *Zoology* 113: 19–32.
- Burger, M., and P. Michalik. 2010. The male genital system of goblin spiders: evidence for the monophyly of Oonopidae (Arachnida: Araneae). *American Museum Novitates* 3675: 1–13.

- Carlquist, S. 1965. *Island life: a natural history of the islands of the world*. New York: Natural History Press, 451 pp.
- Chamberlin, R.V. 1924. The spider fauna of the shores and islands of the Gulf of California. *Proceedings of the California Academy of Sciences* 12: 561–694.
- Du Puy, D.J., and J. Moat. 2003. Using geological substrate to identify and map primary vegetation types in Madagascar and the implications for planning biodiversity conservation. *In* S. Goodman and J. Benstead (editors), *The natural history of Madagascar*: 51–67. Chicago: University of Chicago Press, 1709 pp.
- Griswold, C.E. 1990. A revision and phylogenetic analysis of the spider subfamily Phyxelidinae (Araneae, Amaurobiidae). *Bulletin of the American Museum of Natural History* 196: 1–206.
- Griswold, C.E. 1991. Cladistic biogeography of Afrotropical spiders. *Australian Systematic Botany* 4 (1): 73–89.
- Griswold, C.E. 1993. Investigations into the phylogeny of the Lycosoid spiders and their kin (Arachnida, Araneae, Lycosoidea). *Smithsonian Contributions to Zoology* 539: 1–39.
- Griswold, C.E. 2000. Afrotropical spiders in Madagascar (Araneae, Araneomorphae: Cyatholipidae, Phyxelididae, Zorocratidae). *In* W.R. Lourenço and S.M. Goodman (editors), *Diversity and endemism in Madagascar*: 345–354. Paris: Société de Biogéographie.
- Griswold, C.E. 2001. A monograph of the living world genera and Afrotropical species of cyatholipid spiders (Araneae, Orbiculariae, Cyatholipidae). *Memoirs of the California Academy of Sciences* 26: 1–251.
- Griswold, C.E. 2003. Araneae, spiders. *In* S. Goodman and J. Benstead (editors), *The natural history of Madagascar*: 579–587. Chicago: University of Chicago Press.
- Griswold, C.E., and J. Ledford. 2001. A monograph of the migid trap-door spiders of Madagascar, with a phylogeny of world genera (Araneae, Mygalomorphae, Migidae). *Occasional Papers of the California Academy of Sciences* 151: 1–120.
- Griswold, C.E., M.J. Ramírez, J.A. Coddington, and N.I. Platnick. 2005. Atlas of phylogenetic data for entelegyne spiders (Araneae: Araneomorphae: Entelegynae) with comments on their phylogeny. *Proceedings of the California Academy of Sciences* 56: 1–324.
- Griswold, C.E., H.M. Wood, and A. Carmichael. 2012. The lace web spiders (Araneae, Phyxelididae) of Madagascar: phylogeny, biogeography and taxonomy. *Zoological Journal of the Linnean Society* 164: 728–810.
- Harvey, M.S. 1987. *Grymeus*, a new genus of pouched oonopid spider from Australia (Chelicerata: Araneae). *Memoirs of the Museum of Victoria* 48 (2): 123–130.
- Huber, B.A., B.J. Sinclair, and M. Schmitt. 2007. The evolution of asymmetric genitalia in spiders and insects. *Biological Reviews* 82: 647–698.
- Jury, M.R. 2003. The climate of Madagascar. *In* S. Goodman and J. Benstead (editors), *The natural history of Madagascar*: 75–87. Chicago: University of Chicago Press.
- Karsch, E. 1881. Diagnoses arachnoidarum japonicae. *Berliner Entomologische Zeitschrift* 25: 35–40.
- Krause, D.W., G.V.R. Prasad, W. von Koenigswald, A. Sahni, and F.E. Grine. 1997. Cosmopolitanism among Gondwanan Late Cretaceous mammals. *Nature* 390: 504–507.
- Kuntner, M., and I. Agnarsson. 2011a. Biogeography and diversification of hermit spiders on Indian Ocean islands (Nephilidae: *Nephilengys*). *Molecular Phylogenetics and Evolution* 59: 477–488.
- Kuntner, M., and I. Agnarsson. 2011b. Phylogeography of a successful aerial disperser: the golden orb spider *Nephila* on Indian Ocean islands. *BMC Evolutionary Biology* 11: 119–129.

- Millot, J. 1948. Revue générale des arachnides de Madagascar. Mémoires de l'Institut Scientifique de Madagascar 1 (série A1): 137–155.
- Platnick, N.I. 2013. The world spider catalog, version 14.0. American Museum of Natural History. Online resource (<http://research.amnh.org/iz/spiders/catalog>).
- Platnick, N.I., et al. 2012a. Tarsal organ morphology and the phylogeny of goblin spiders (Araneae, Oonopidae), with notes on basal genera. American Museum Novitates 3736: 1–52.
- Platnick, N.I., N. Dupérré, R. Ott, B.C. Baehr, and Y. Kranz-Baltensperger. 2012b. The goblin spider genus *Pellicinus* (Araneae, Oonopidae), Part 1. American Museum Novitates 3741: 1–43.
- Rabinowitz, P.D., M.F. Coffin, and D. Falvey. 1983. The separation of Madagascar and Africa. Science 220: 67–69.
- Razafimahazo, A.S. 2005. R.A.I. Tropical cyclone committee for the South-West Indian Ocean, Seventeenth Session. World Meteorological Organization. Online resource (<http://www.wmo.int/pages/prog/www/tcp/documents/RAITCC-17En.pdf>), accessed 17 December 2012.
- Roewer, C.F. 1942. Katalog der Araneae von 1758 bis 1940. Bremen 1: 275–290.
- Saaristo, M.I. 2001. Dwarf hunting spiders or Oonopidae (Arachnida, Araneae) of the Seychelles. Insect Systematics and Evolution 32: 307–358.
- Scotese, C.R. 1994. Pangea: paleoclimate, tectonics, and sedimentation during accretion, zenith, and breakup of a supercontinent. Geological Society of America Special Paper 288: 5–9.
- Simon, E. 1891. On the spiders of the island of St. Vincent.—Part 1. Proceedings of the Zoological Society of London 1891: 549–575.
- Ubick, D. 2005. Oonopidae. In D. Ubick, P. Paquin, P.E. Cushing, and V. Roth (editors), Spiders of North America: 185–188. [Poughkeepsie, N.Y.]: American Arachnological Society.
- Ubick, D., and C.E. Griswold. 2011a. The Malagasy goblin spiders of the new genus *Malagiella*. Bulletin of the American Museum of Natural History 356: 1–86.
- Ubick, D., and C.E. Griswold. 2011b. The Malagasy goblin spiders of the new genus *Molotra*. American Museum Novitates 3729: 1–69.
- Wells, N.A. 2003. Some hypotheses on the Mesozoic and Cenozoic paleoenvironmental history of Madagascar. In S. Goodman and J. Benstead (editors), The natural history of Madagascar: 16–34. Chicago: University of Chicago Press.
- Wood, H.M. 2008. A revision of the assassin spiders of the *Eriauchenius gracilicollis* group, a clade of spiders endemic to Madagascar (Araneae, Archaeidae). Zoological Journal of the Linnean Society 152: 255–296.
- Wood, H.M., C.E. Griswold, and G.S. Spicer. 2007. Phylogenetic relationships within an endemic group of Malagasy ‘assassin spiders’ (Araneae, Archaeidae): ancestral character reconstruction, convergent evolution and biogeography. Molecular Phylogenetics and Evolution 45: 612–619.
- Wood, H.M., N. Matzke, R. Gillespie, and C.E. Griswold. 2013. Treating fossils as terminal taxa in divergence time estimation reveals ancient vicariance patterns in the palpimanoid spiders. Systematic Biology 62 (2): 264–284.



All issues of *Novitates* and *Bulletin* are available on the web (<http://digitallibrary.amnh.org/dspace>). Order printed copies on the web from:

<http://shop.amnh.org/a701/shop-by-category/books/scientific-publications.html>

or via standard mail from:

American Museum of Natural History—Scientific Publications  
Central Park West at 79th Street  
New York, NY 10024

Ⓢ This paper meets the requirements of ANSI/NISO Z39.48-1992 (permanence of paper).