

**Madagascar, the real Treasure Island!
Malagasy uncharted diversity of a rare ancient
lineage of armored harvestmen
(Opiliones, Laniatores, Buemarinoidae)**

Willians PORTO & Abel PÉREZ-GONZÁLEZ



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COUVERTURE / *COVER*:

Habitus male of *Flavonuncia vazimba* n. sp.

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ABSTRACT

Buemarinoidae Karaman, 2019 is an ancient lineage of armored harvestmen that comprises six genera with a widely disjunct distribution: *Arbasus* (Simon, 1911) from some caves in France, *Buemarinoa* Roewer, 1956, from some caves in Sardinia, Italy, *Flavonuncia* Lawrence, 1959, endemic to Madagascar, *Fumontana* Shear, 1977, found in the southern Appalachians, United States, *Turonychus* Derkarabetian Prieto & Giribet, 2021, from a cave in Spain and *Phocyx* Porto, Monnod & Pérez-González, 2024, from Australia. The examination of a large series of 375 specimens of Malagasy buemarinoids allows us to redescribe the type species *Flavonuncia pupilla* Lawrence, 1959, and describe four new species: *Flavonuncia ubicki* n. sp., *Flavonuncia mahaka* n. sp., *Flavonuncia vazimba* n. sp. and *Flavonuncia zanahary* n. sp. We found that male genitalia represent key elements in the taxonomy of this group. The genus *Flavonuncia* now comprises five species, making it the sole non-monotypic genus within Buemarinoidae. The Malagasy fauna of *Flavonuncia* represents an interesting and unique opportunity to study the diversification process of an ancient lineage where the majority of the species are extinct and are currently represented by rare relict taxa.

KEY WORDS

Madagascar,
genital morphology,
harvestmen,
insidiatores,
new species.

RÉSUMÉ

Madagascar, la véritable île au trésor! La diversité malgache inexplorée d'une ancienne et rare lignée d'opilions cuirassés (Opiliones, Laniatores, Buemarinoidae).

Les Buemarinoidae Karaman, 2019 représentent une ancienne lignée d'opilions cuirassés qui comprend six genres présentant une répartition largement disjointe : *Arbasus* (Simon, 1911) connu de quelques grottes en France, *Buemarinoa* Roewer, 1956, de quelques grottes en Sardaigne (Italie), *Flavonuncia* Lawrence, 1959, endémique de Madagascar, *Fumontana* Shear, 1977, présent dans le sud des Appalaches, États-Unis, *Turonychus* Derkarabetian Prieto & Giribet, 2021, connu d'une grotte d'Espagne et *Phocyx* Porto, Monnod & Pérez-González, 2024, d'Australie. L'examen d'une grande série de 375 spécimens de buemarinoides malgaches nous permet de redécrire l'espèce type *Flavonuncia pupilla* Lawrence, 1959, et de décrire quatre nouvelles espèces : *Flavonuncia ubicki* n. sp., *Flavonuncia mahaka* n. sp., *Flavonuncia vazimba* n. sp. et *Flavonuncia zanahary* n. sp. Nous avons constaté que les genitalia mâles représentent des éléments clé dans la taxonomie de ce groupe. Le genre *Flavonuncia* compte désormais cinq espèces, ce qui en fait le seul genre non monotypique au sein des Buemarinoidae. La faune malgache de *Flavonuncia* représente une opportunité intéressante et unique d'étudier le processus de diversification d'une lignée ancienne où la majorité des espèces sont éteintes et sont actuellement représentées par des taxons rares relictuels.

MOTS CLÉS

Madagascar,
morphologie génitale,
opilions,
insidiatores,
espèces nouvelles.

INTRODUCTION

The Opiliones superfamily Triaenonychoidea Sørensen, 1886 currently includes four families phylogenetically related as: ((Synthetonychiidae Forster, 1954 + Lomanellidae Mendes & Derkarabetian, 2021) (Triaenonychidae Sørensen, 1886 + Buemarinoidae Karaman, 2019)) (Derkarabetian *et al.* 2021, 2023). Triaenonychidae is the most diverse Triaenonychoidea family with 110 genera and 404 valid species (Kury *et al.* 2022), distributed throughout temperate Gondwana. The sister family Buemarinoidae comprises six genera with a widely disjunct distribution: *Arbasus* (Simon, 1911) from some caves in France, *Buemarinoa* Roewer, 1956, from some caves in Sardinia, *Flavonuncia* Lawrence, 1959, endemic to Madagascar, *Fumontana* Shear, 1977, found in the southern Appalachians, *Turonychus* Derkarabetian Prieto & Giribet, 2021, from a cave in Spain and *Phocyx* Porto, Monnod & Pérez-González, 2024 from Australia (Simon 1911; Roewer 1956; Lawrence 1959; Shear 1977; Karaman 2019, 2023; Derkarabetian *et al.* 2021; Porto *et al.* 2024). The six genera of Buemarinoidae are each currently monotypic and each taxon has a very restricted distribution (three genera are represented by troglobitic species), representing relicts of an ancient hypothesized worldwide distribution (Derkarabetian *et al.* 2021; Porto *et al.* 2024).

The family status of Buemarinoidae was conferred by Derkarabetian *et al.* (2021), by elevating the tribe Buemarinoini Karaman, 2019 (within family Triaenonychidae) to the family rank, relying on UCE data-based phylogenomics including representatives of *Fumontana*, *Turonychus* and *Flavonuncia*. Formerly, the genera now under Buemarinoidae were allocated elsewhere across Cladonychiidae Hadži, 1935, Phalangodidae Simon, 1879, Travuniidae Absolon & Kratochvíl, 1932 and Triaenonychidae, or were unknown to science (Porto *et al.* 2024).

This study focuses on the genus *Flavonuncia*, originally described by Lawrence (1959). We redescribe *Flavonuncia pupilla* Lawrence, 1959 and describe four new species, establishing *Flavonuncia* as the sole non-monotypic genus within this ancient and relictual family. Comprehensive images of

the external and genital morphology of all *Flavonuncia* species are provided, adhering to contemporary standards in harvestmen taxonomy. Finally, we discuss the genital morphology of *Flavonuncia* and the broader Buemarinoidae.

MATERIAL AND METHODS

Specimens were examined using a Leica M205A microscope equipped with a Leica DF295 camera. Male genitalia were dissected, cleared in clove oil, and temporarily mounted on microscope slides as described in Acosta *et al.* (2007). Some genitalia were cleaned with pancreatin prior to mounting on microscope slides. Specimens were examined using an Olympus BH3 microscope equipped with a Nikon DXM 1200 camera and returned to 80% ethanol in microvials kept with their respective specimens. Specimens were cleaned with a fine bristle paintbrush. To remove the most complex particles of dirt we added a few drops of liquid detergent to the vial with alcohol and used ultrasound (Mini ULTRASONIK™ Ney), checking every 15 seconds if the sample is cleaned. For SEM preparations, body parts were dissected, cleaned, and dehydrated via an 80% – 90% – 96% – 100% ethanol series, fixed to aluminum stubs, and gold-palladium coated in a VG Scientific SC 7620 mini sputter-coater. SEM micrographs were taken under a high vacuum with a Philips FEI XL30 TMP. Morphological nomenclature follows Mendes & Kury (2012), Pérez-González & Werneck (2018) and Porto & Pérez-González (2019). Scutum shape outline nomenclature follows Kury & Medrano (2016). Species description structure uses excel sheets proposed by Magalhaes (2019). Images were improved and edited using Adobe Photoshop and Adobe Illustrator, and a map was constructed using shapefiles sourced from Natural Earth data using QGIS (QGIS Project). The specimens studied herein are deposited at the Entomological collection of the California Academy of Sciences (CAS), United States, and the Arachnological collection of the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN-Ar), Argentina.



FIG. 1. — Map showing the geographic distribution of revised material of *Flavonuncia* Lawrence, 1959: **black cross**: *F. zanahary* n. sp.; **red cross**: *F. pupilla* Lawrence, 1959; **black triangle**: *F. ubicki* n. sp.; **black diamond**: *F. vazimba* n. sp.; **white circle with a black cross**: *F. mahaka* n. sp.

ABBREVIATIONS

Institutions

CAS	California Academy of Sciences, San Francisco;
MACN-Ar	Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires;
MNHN	Muséum national d’Histoire naturelle, Paris.

RESULTS

Family BUEMARINOIDAE Karaman, 2019

Genus *Flavonuncia* Lawrence, 1959

Flavonuncia Lawrence, 1959: 20, figs 3a-f, 4a-c. c; 1992: 285. — Karaman 2019: 5.

TYPE SPECIES. — *Flavonuncia pupilla* Lawrence, 1959, by monotypy.

OTHER SPECIES INCLUDED. — *Flavonuncia ubicki* n. sp., *Flavonuncia mahaka* n. sp., *Flavonuncia vazimba* n. sp. and *Flavonuncia zanahary* n. sp.

COMPARATIVE DIAGNOSIS. — Differs from all other Buemarinoidea genera by a combination of its yellow integument color and 3-segmented tarsus on leg I (see Lawrence 1959: 20-22). Characterized by femur I bearing a row of setiferous tubercles, the frontal chelicerae armored. Differs from *Arbasus*, *Buemarinoa* and *Turonychus* because those genera include blind troglobitic species with pedipalps

elongated with thin articles, legs I-II with femur bearing spined tubercles (Shear 1977; Karaman 2019, 2023; Derkarabetian *et al.* 2021), whereas *Flavonuncia* has a developed ocularium and regular raptorial pedipalps. *Flavonuncia* can be separated from *Fumontana* by the morphology of the dorsal scutum because *Fumontana* has large spines on anterior lateral angles (Shear 1977: fig. 1). *Flavonuncia* has smooth chelicerae and pedipalps contrary to the *Phocyx* that has the chelicerae and pedipalps covered by granules and presents microtrichia on some large setae of pedipalps spines.

DISTRIBUTION. — Madagascar.

Flavonuncia pupilla Lawrence, 1959 (Figs 2-5; 23A, F, K)

TYPE MATERIAL. — **Syntypes**. Madagascar • 15 ♂ ♀; Mont Ankaratra, Manjakatempo forest; Elev. 2000 m; R. F. Lawrence 1956; MNHN (not examined).

MATERIAL EXAMINED. — **Madagascar** • 22 ♂, 40 ♀; Toamasina, Ambatovy; Elev. 1075 m; 18°51'3"S, 48°19'17"E; coll. Malagasy ant team; 21.III.2004; EB09 sifted litter (leaf mold, rotten wood) montane rainforest, collection code: BLF10501; CASENT 9072047 • 5 ♂, 6 ♀; same data; MACN-Ar 45997 • 1 ♂; same data; SEM voucher • 22 ♂, 37 ♀; Toamasina, Analamay; Elev. 1068 m; 18°48'22"S, 48°20'13"E; coll. Malagasy ant team; 21.III.2004; EB09 sifted litter (leaf mold, rotten wood) montane rainforest, collection code: BLF10502; CASENT 9072046 • 5 ♂, 6 ♀; same data; MACN-Ar 45998.

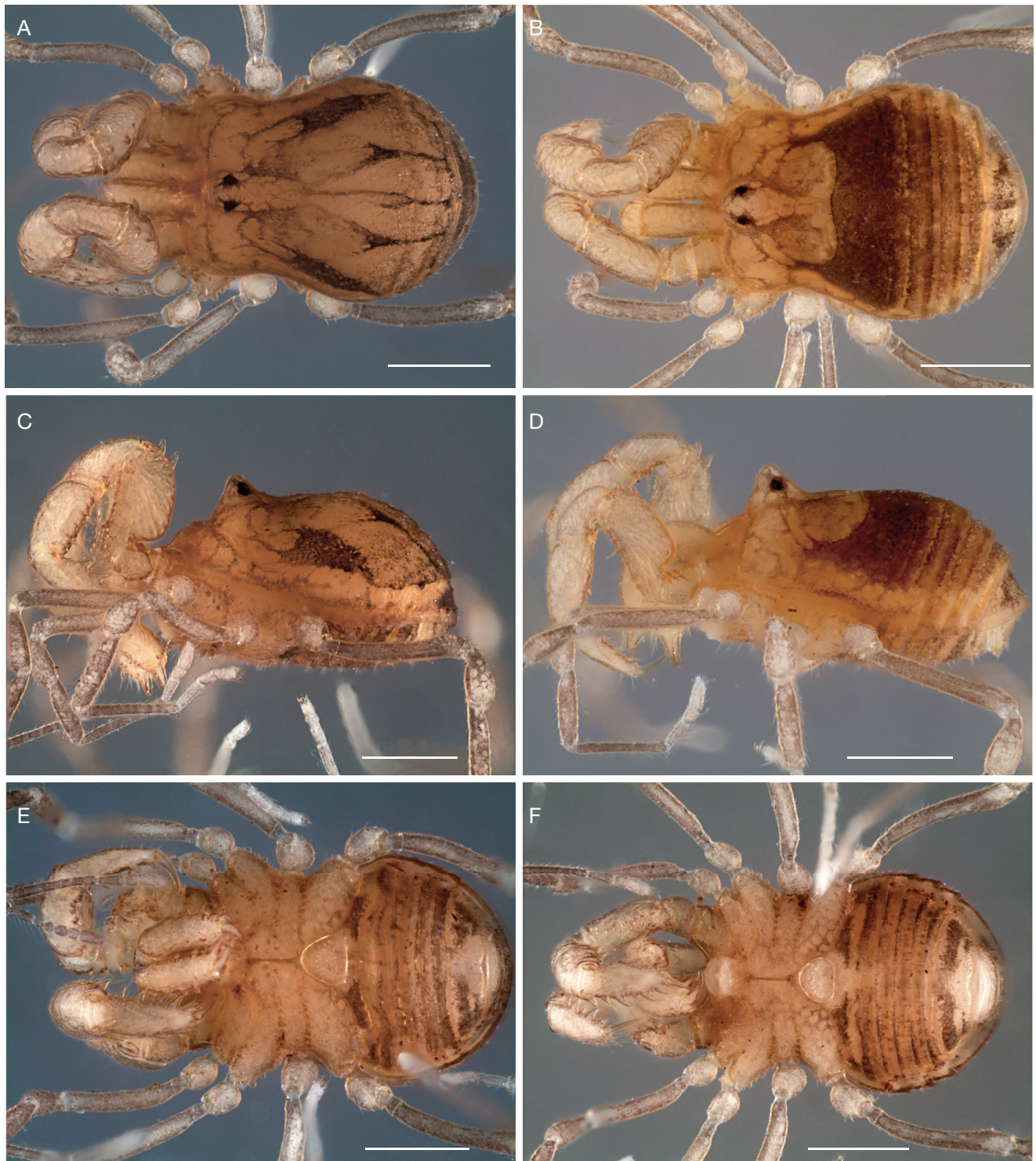


FIG. 2. — *Flavonuncia pupilla* Lawrence, 1959 (CASENT 9072047): **A, C, E**, male; **B, D, F**, female. Scale bars: 1 mm.

COMPARATIVE DIAGNOSIS. — Differs from *Flavonuncia ubicki* n. sp. by the absence of tubercles on ocularium and from *Flavonuncia vazimba* n. sp. by the absence of acute ocularium and the yellowish color. Differs from *Flavonuncia mahaka* n. sp. by the shape of the penis, without processes on the top of the ventral plate. Differs from *Flavonuncia zanahary* n. sp. by the smooth granulation of the dorsal scutum. Differs from other Buemarinoidae by the presence of a cheliceral ectal row of four tubercles.

DISTRIBUTION (Fig. 1). — Central region of Madagascar. Lawrence (1959) reported *F. pupilla* from Mont Andohahela (Southeast Madagascar); this record needs confirmation due the short-range endemism shown by species in the genus.

REDESCRIPTION

Male CASENT 9072047

Measurements. See Table 1.

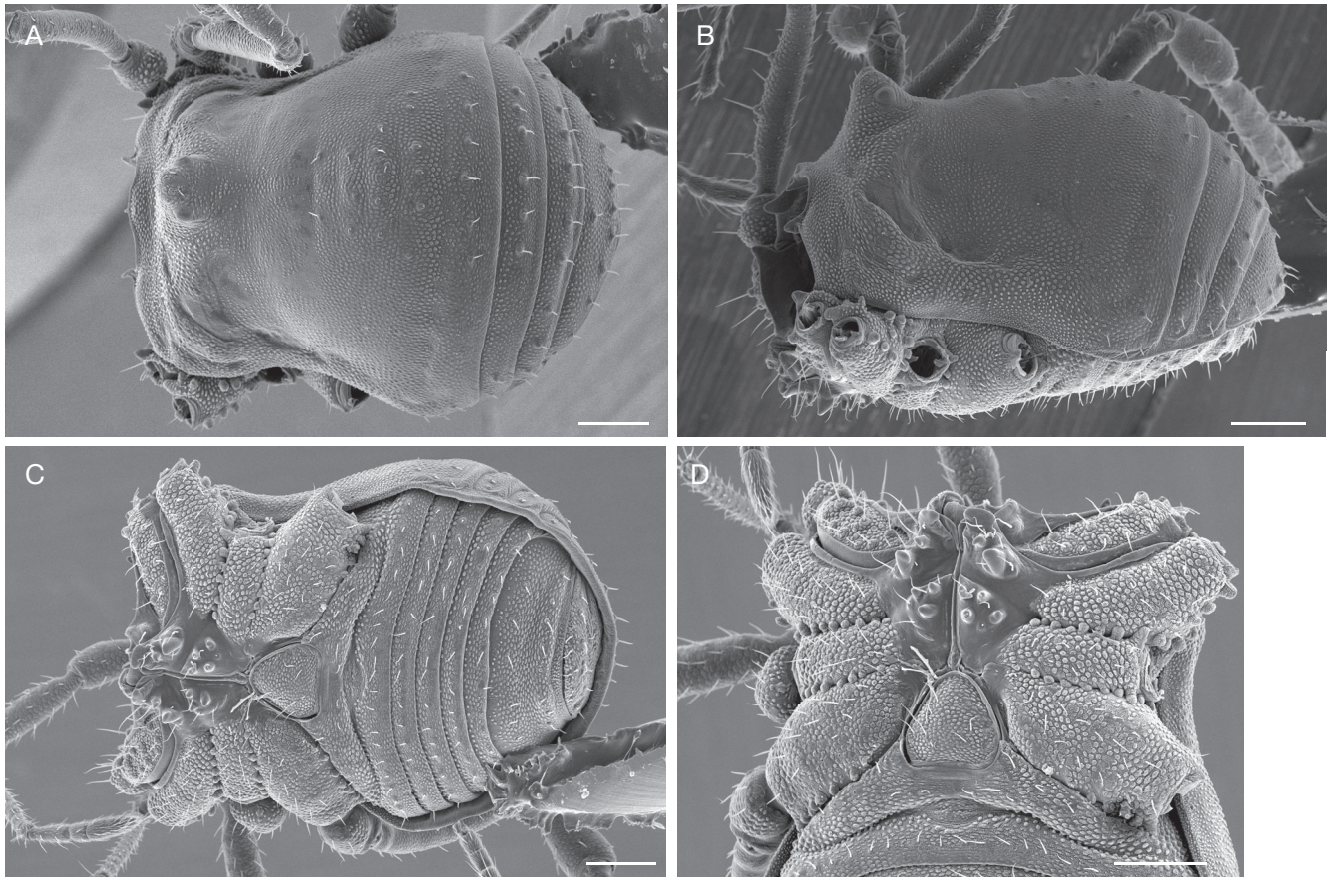


FIG. 3. — *Flavonuncia pupilla* Lawrence, 1959, SEM images of male (MACN-Ar 45996), habitus: **A**, dorsal; **B**, lateral; **C**, **D**, ventral. Scale bars: 200 μ m.

TABLE 1. — Measurement in mm of appendages of *Flavonuncia* Lawrence, 1959 species: **HT**, holotype; **BL**, body length; **CL**, carapace max length; **SL**, scutum max length; **CW**, carapace max width; **SW**, scutum max width; **Tr**, trochanter; **Fe**, femur; **Pa**, patella; **Ti**, tibia; **Ta**, tarsus; **Ca**, claw.

Sspecies	Sex	Voucher	Body						Pedipalp						Leg I					
			BL	CL	SL	CW	SW	Tr	Fe	Pa	Ti	Ta	Ca	Tr	Fe	Pa	Ti	Ta	Ca	
<i>F. mahaka</i> n. sp.	♂ HT	21650	2	0.49	1.4	0.85	1.10	0.26	0.67	0.51	0.64	0.60	0.16	0.21	0.68	0.27	0.40	0.53	0.35	
<i>F. mahaka</i> n. sp.	♀	9072050	1.53	0.49	0.87	0.76	1.00	0.15	0.50	0.30	0.33	0.39	0.19	0.14	0.56	0.25	0.35	0.42	0.34	
<i>F. ubicki</i> n. sp.	♂ HT	21649	2.84	0.69	1.84	1.21	1.42	0.24	1.01	0.66	0.90	0.80	0.30	0.22	0.97	0.38	0.66	0.85	0.50	
<i>F. ubicki</i> n. sp.	♀	9072045	2.32	0.7	1.39	1.06	1.32	0.21	0.75	0.47	0.56	0.64	0.25	0.22	0.88	0.35	0.70	0.88	0.57	
<i>F. vazimba</i> n. sp.	♂ HT	21651	2.18	0.51	1.06	0.79	1.04	0.16	0.63	0.41	0.52	0.50	0.20	0.17	0.70	0.28	0.45	0.50	0.39	
<i>F. vazimba</i> n. sp.	♀	9072147	1.78	0.43	0.93	0.69	0.96	0.13	0.50	0.28	0.41	0.38	0.11	0.14	0.55	0.21	0.56	0.53	0.46	
<i>F. zanahary</i> n. sp.	♂ HT	21652	1.35	0.39	0.83	0.6	0.75	0.10	0.36	0.26	0.30	0.35	0.12	0.10	0.41	0.18	0.32	0.29	0.29	
<i>F. zanahary</i> n. sp.	♀	9072152	1.4	0.44	0.7	0.61	0.80	0.13	0.39	0.24	0.29	0.30	0.10	0.10	0.45	0.21	0.30	0.29	0.29	
<i>F. pupilla</i>	♂	9072047	2.45	0.55	1.16	0.93	1.16	0.18	0.64	0.44	0.53	0.47	0.26	0.20	0.64	0.27	0.41	0.51	0.41	
<i>F. pupilla</i>	♀	9072047	2.38	0.56	0.94	0.82	1.12	0.18	0.62	0.28	0.43	0.48	0.17	0.15	0.64	0.25	0.40	0.47	0.39	

Species	Sex	Voucher	Leg II						Leg III						Leg IV					
			Tr	Fe	Pa	Ti	Ta	Ca	Tr	Fe	Pa	Ti	Ta	Ca	Tr	Fe	Pa	Ti	Ta	Ca
<i>F. mahaka</i> n. sp.	♂ HT	21650	0.21	0.90	0.30	0.67	0.64	0.61	0.20	0.63	0.26	0.54	0.64	0.38	0.20	0.86	0.31	0.60	0.87	0.35
<i>F. mahaka</i> n. sp.	♀	9072050	0.15	0.69	0.31	0.60	0.59	0.61	0.16	0.54	0.23	0.45	0.54	0.37	0.21	0.70	0.30	0.64	0.78	0.47
<i>F. ubicki</i> n. sp.	♂ HT	21649	0.29	1.36	0.50	1.11	1.36	0.95	0.25	1.05	0.35	0.86	1.08	0.56	0.29	1.22	0.50	1.10	1.46	0.79
<i>F. ubicki</i> n. sp.	♀	9072045	0.24	1.03	0.45	0.94	1.07	0.77	0.24	0.84	0.34	0.74	0.93	0.54	0.28	1.12	0.40	0.87	1.22	0.54
<i>F. vazimba</i> n. sp.	♂ HT	21651	0.18	0.73	0.34	0.64	0.64	0.56	0.19	0.68	0.31	0.57	0.64	0.39	0.20	0.83	0.36	0.70	0.96	0.41
<i>F. vazimba</i> n. sp.	♀	9072147	0.15	0.57	0.24	0.46	0.61	0.63	0.13	0.63	0.32	0.55	0.47	0.33	0.15	0.76	0.27	0.60	0.78	0.39
<i>F. zanahary</i> n. sp.	♂ HT	21652	0.12	0.58	0.22	0.43	0.40	0.49	0.13	0.42	0.17	0.35	0.42	0.32	0.14	0.55	0.22	0.46	0.55	0.40
<i>F. zanahary</i> n. sp.	♀	9072152	0.14	0.53	0.26	0.43	0.38	0.51	0.14	0.45	0.18	0.38	0.38	0.34	0.16	0.54	0.18	0.44	0.56	0.37
<i>F. pupilla</i>	♂	9072047	0.20	0.80	0.39	0.63	0.69	0.57	0.19	0.59	0.31	0.52	0.59	0.41	0.20	0.74	0.36	0.61	0.77	0.50
<i>F. pupilla</i>	♀	9072047	0.20	0.79	0.34	0.61	0.66	0.64	0.19	0.66	0.29	0.47	0.61	0.43	0.24	0.82	0.32	0.63	0.87	0.49

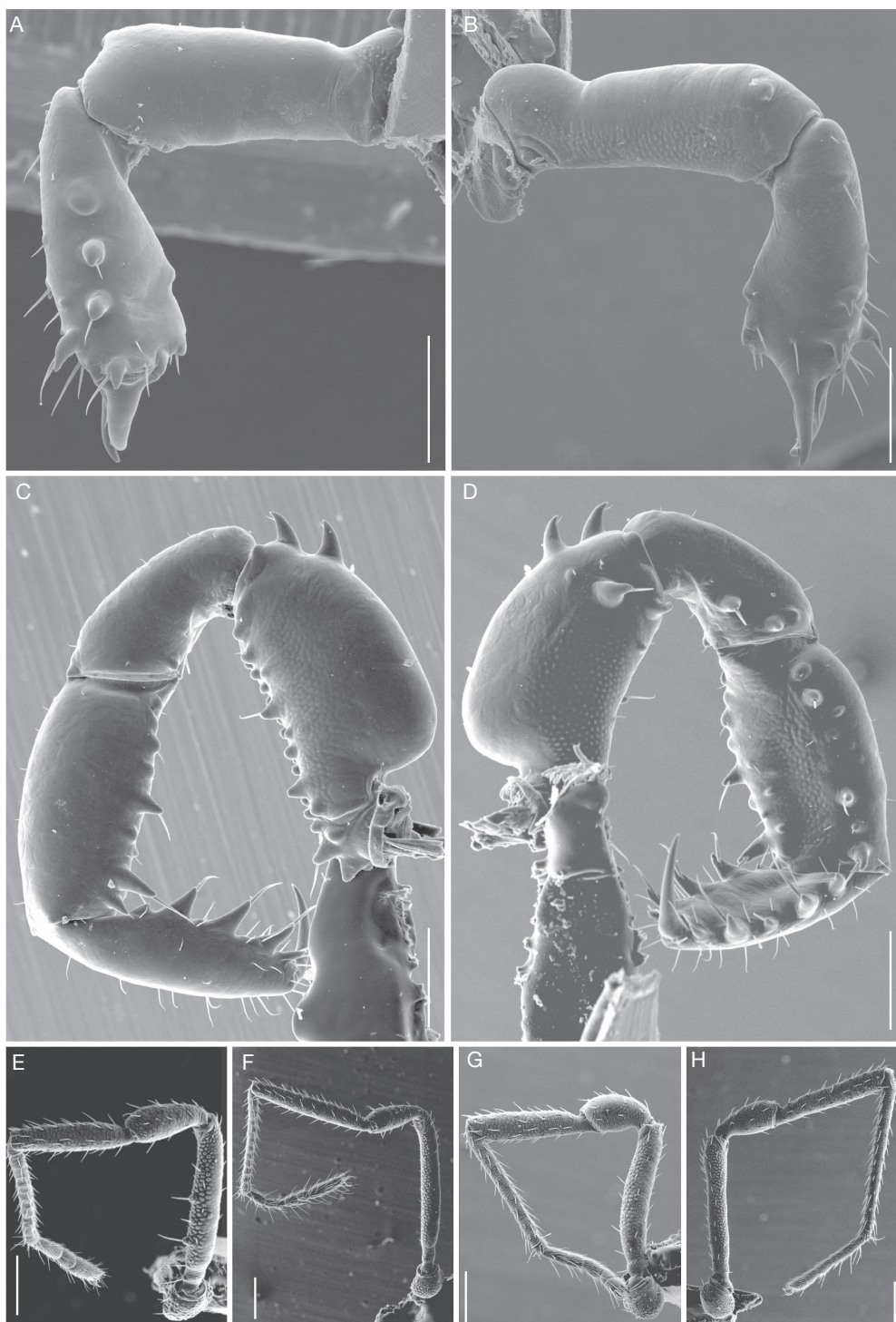


FIG. 4. — *Flavonuncia pupilla* Lawrence, 1959, SEM images of male (MACN-Ar 45996): **A, B**, chelicera, ectal (**A**), mesal (**B**); **C, D**, pedipalp, ectal (**C**), mesal (**D**); **E-H**, legs I (**E**), II (**F**), III (**G**), VI (**H**). Scale bars: 200 µm.

Dorsum (Figs 2A, C; 3A, B). Outline hourglass-shaped of Eta (η) type. Ocularium conical, with two small granules bearing setae, eyes situated at the midpoint of the ocularium. Mesotergal scutum without tubercles or apophyses, carapace smaller than mesotergum, mesotergal areas not clearly defined, areas I-II with a row of two small granules, areas III-IV with six, the posterior border with a row of 10 granules. Free tergites bearing a row of granules on each tergite.

Venter (Figs 2E; 3C, D). Coxae ventral surface covered by setae; coxa I bearing 8-9 granules, almost all ventral surface covered by cerotegument, excepted by the proximal coxae II-III; proximal coxa II with a remarkable tubercle with three basal setae and one tubercle with subdistal setae; coxa III with 3-4 tubercles; small bridge present; spiracles not visible. Sternum straight with a drop shape-base.

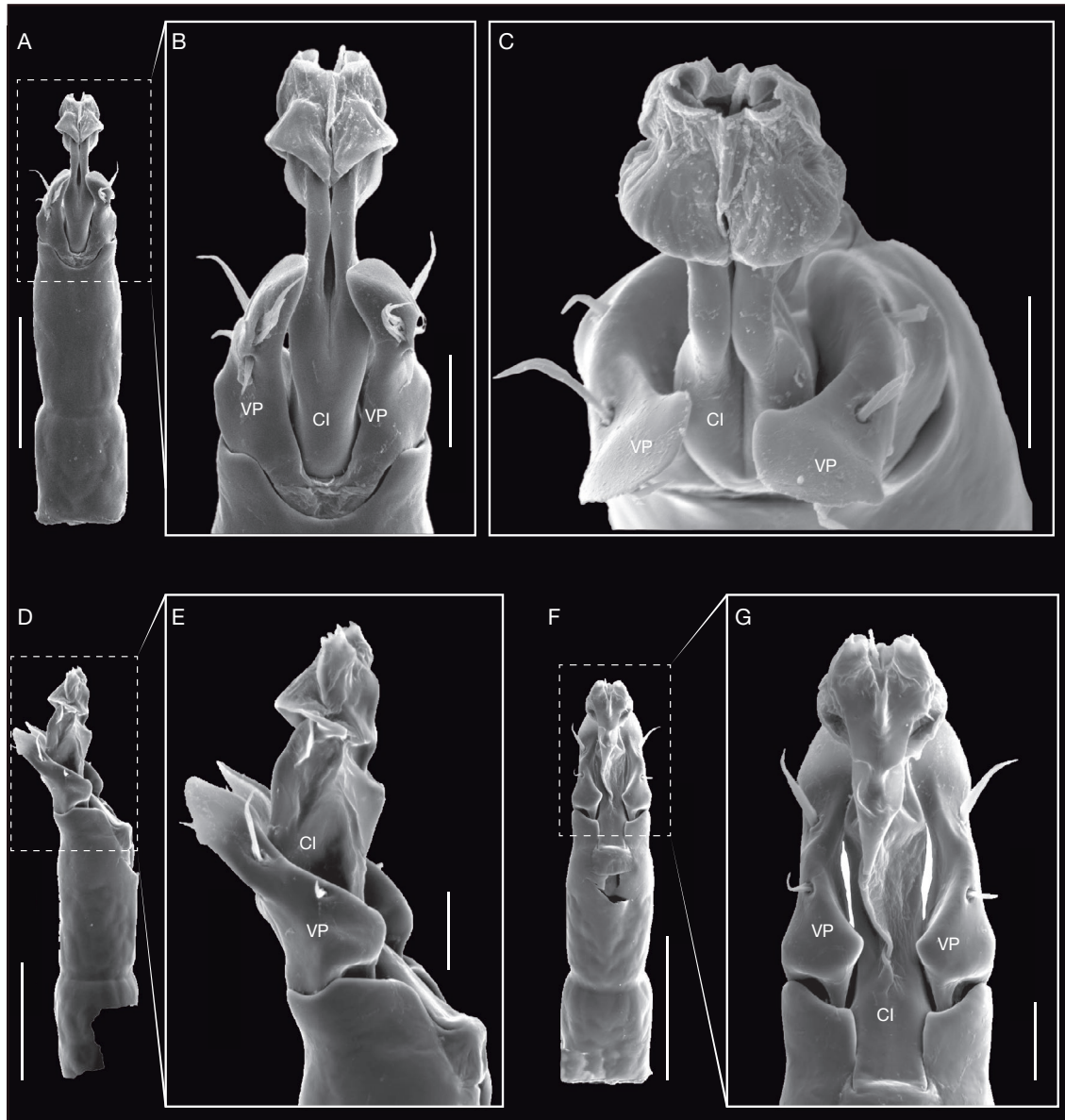


FIG. 5. — *Flavonuncia pupilla* Lawrence, 1959, SEM images of male (MACN-Ar 45996) penis: **A, B**, ventral view; **C**, apical view; **D, E**, lateral view; **F, G**, dorsal view. Abbreviations: **CI**, capsula interna; **VP**, ventral plate. Scale bars: A, D-F, 200 µm; B, C, G, 50 µm.

Chelicerae (Figs 4A, B). Basicheliceritae bearing a small tubercle in the dorsodistal surface, cheliceral hand bearing an ectal row composed of one granular and three tubercles with subdistal setae, four mesal small granular and three frontal tubercles with subdistal setae.

Pedipalps (Figs 4C, D). Trochanter with four ventral tubercles, femur bearing a ventral row of small tubercles and two distal acute tubercles on the distal surface, patella with one ectal and three mesal tubercles, tibia ventral surface bearing sparse small tubercles, with a medial and two apical acute tubercles with subdistal setae, tarsus bearing four ectal and five mesal tubercles with setae.

Legs (Figs 4E, G). Astragalus longer than calcaneus. Tarsal count: 3-6-4-4.

Genitalia (Figs 5; 23A, E, K). *Capsula interna* longer than ventral plate, distally with a complex structure ending in a thin free stylus. Ventral distal part of the *capsula interna* bearing a pentagonal process. Ventral plate with a deep cleft separating into two halves, the apical portion of the ventral plate rectangular arch-shaped, with the upper and lower macrosetae aligned in the dorsal view. In the ventral view, two grouped upper macrosetae and one isolated lower macroseta.

Female (CASENT 9072048)

(Fig. 2B, D, F)

Similar to males, showing dimorphism in coloration, females with a dark brown opisthosoma while males are yellowish with brown stripes. Pedipalps larger in males.



FIG. 6. — *Flavonuncia ubicki* n. sp. (CASENT 9072045), **A, C, E**, male; **B, D, F**, female. Scale bars: A, C, E, 1 mm; B, D, F, 500 μ m.

Flavonuncia ubicki n. sp.
(Figs 6-9; 23B, G, L)

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TYPE MATERIAL. — **Holotype**. Madagascar • ♂; Toamasina,

Analamay-Mantadia, Ambaroharanana; Elev. 1012 m; [18°48'14"S](#), [48°24'18"E](#); coll. Malagasy ant team; 19-21.XII.2012; sifted litter, rainforest, collection code: BLF30324; CASTYPE 21649.

Paratypes. Madagascar • 1 ♀; same data as for holotype; CASENT 9072045 • 1 ♂ SEM voucher; same data; MACN-Ar 45999 • 1 ♀; same data; MACN-Ar 46000.

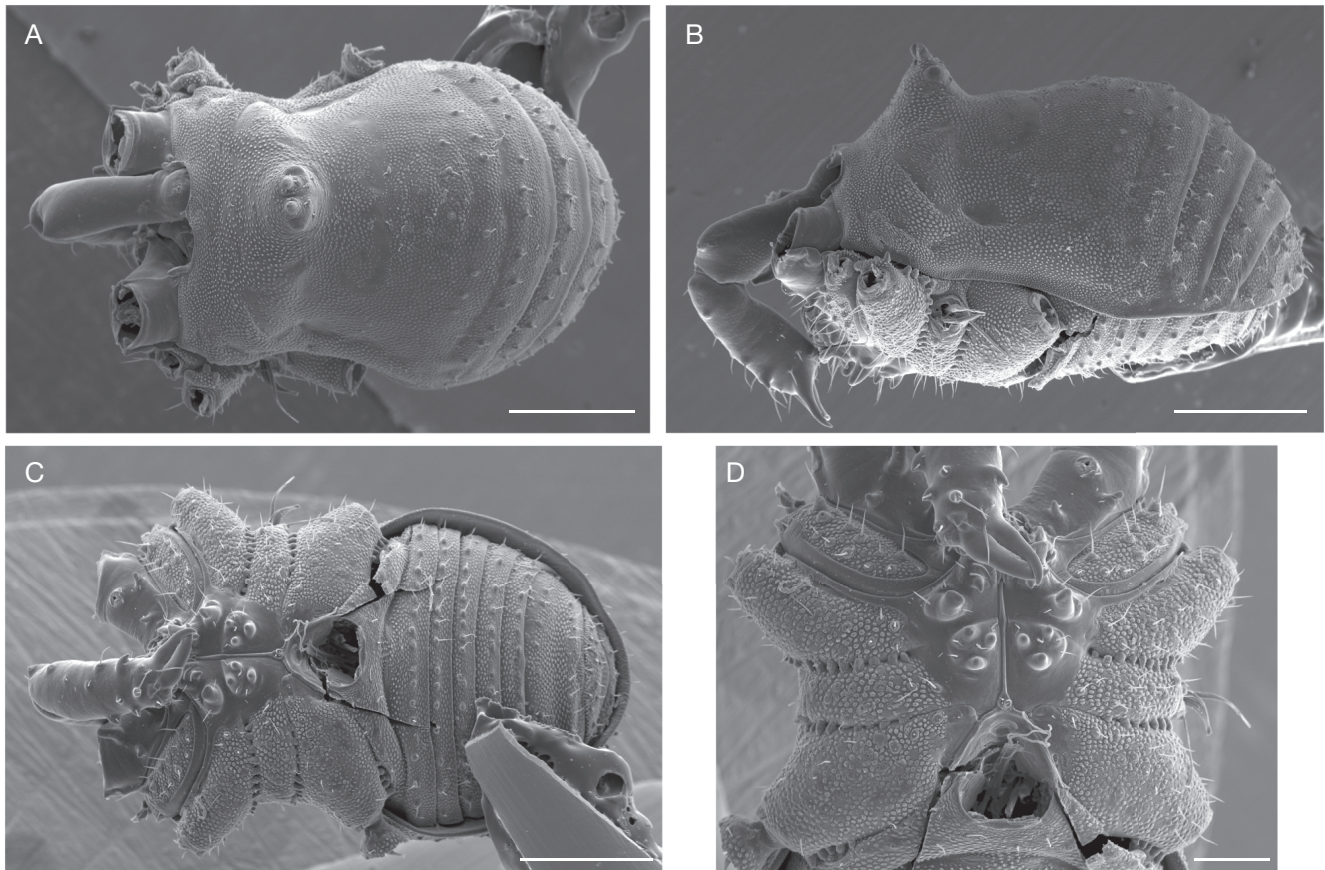


FIG. 7. — *Flavonuncia ubicki* n. sp., SEM images of male paratype (MACN-Ar 45999): **A**, habitus, dorsal; **B**, lateral; **C**, **D**, ventral. Scale bars: A-C, 500 µm; D, 200 µm.

ETYMOLOGY. — Patronymic in honor of the former CAS arachnologist and friend Darrell Ubick, in recognition of his contribution to the advances of arachnology.

COMPARATIVE DIAGNOSIS. — Robust, long legged *Flavonuncia* species, differing from all known *Flavonuncia* species by the pair of apical tubercles present on the top of the ocularium. The penis is similar to *Flavonuncia pupilla*.

DISTRIBUTION (Fig. 1). — Known only from the type locality.

DESCRIPTION

Male (CASTYPE 21649)

Measurements. See Table 1.

Dorsum (Figs 6A, C; 7A, B). Outline hourglass-shaped of Eta (η) type. Ocularium conical, with a pair of apical tubercles, eyes located on the top of the ocularium. Mesotergal scutum without tubercles or apophyses. Carapace smaller than mesotergum, mesotergal areas not clearly defined, areas I-II with a row of two small setiferous granules, area III with three, area IV with eight, the posterior border with a row of 15 granules. Free tergites bearing a row of granules on each tergite.

Venter (Figs 6E; 7C, D). Coxae ventral surface covered by setae; coxa I bearing 8-9 granules, almost all ventral surface covered by cerotegument, except by the proximal coxa II-III;

proximal coxa II with a remarkable tubercle with three basal setae and one tubercle with subdistal setae; coxa III with three tubercles, small bridge present, spiracles not visible. Sternum straight with a drop shape base.

Chelicerae (Fig. 8A, B). Basicheliceritae bearing a small tubercle on dorso-distal surface, cheliceral hand bearing seven ectal small tubercles with subdistal setae, two mesal small granules, and one mesal tubercle with subdistal setae.

Pedipalps (Fig. 8C, D). With one ventral and two small dorsal tubercles, femur bearing a ventral row of small tubercles and two distal acute tubercles on the distal surface, patella with four mesal tubercles, tibia ventral surface bearing sparse small tubercles, with a medial and 2-3 apical acute tubercles with subdistal setae, tarsus bearing four ectal and five mesal tubercles with setae.

Legs (Fig. 8E-H). Astragalus longer than calcaneus. Tarsal count: 3-6-4-4.

Genitalia (Figs 9; 23B, G, L). Penis proportionally larger than other species of *Flavonuncia*. *Capsula interna* longer than the ventral plate, ventral view with a cleft separating the *capsula interna* into two halves, apical portion of ventral

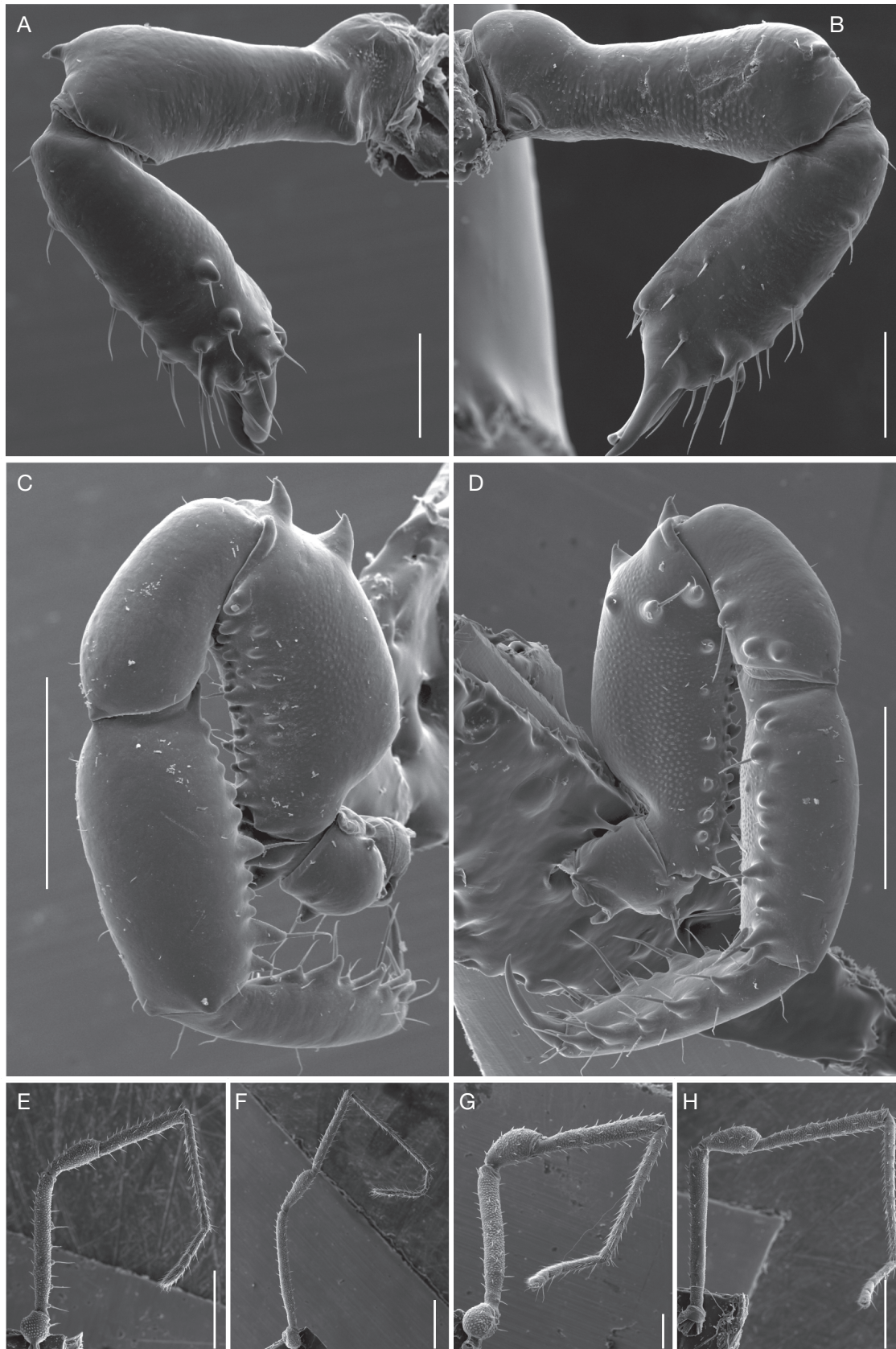


FIG. 8. — *Flavonuncia ubicki* n. sp., SEM images of male paratype (MACN-Ar 45999): **A, B**, chelicera, ectal (**A**); mesal (**B**); **C, D**, pedipalp, ectal (**C**), mesal (**D**); **E, F**, legs, I (**E**), II (**F**), III (**G**), VI (**H**). Scale bars: A, B, G, 200 μ m; D-F, H, 500 μ m.

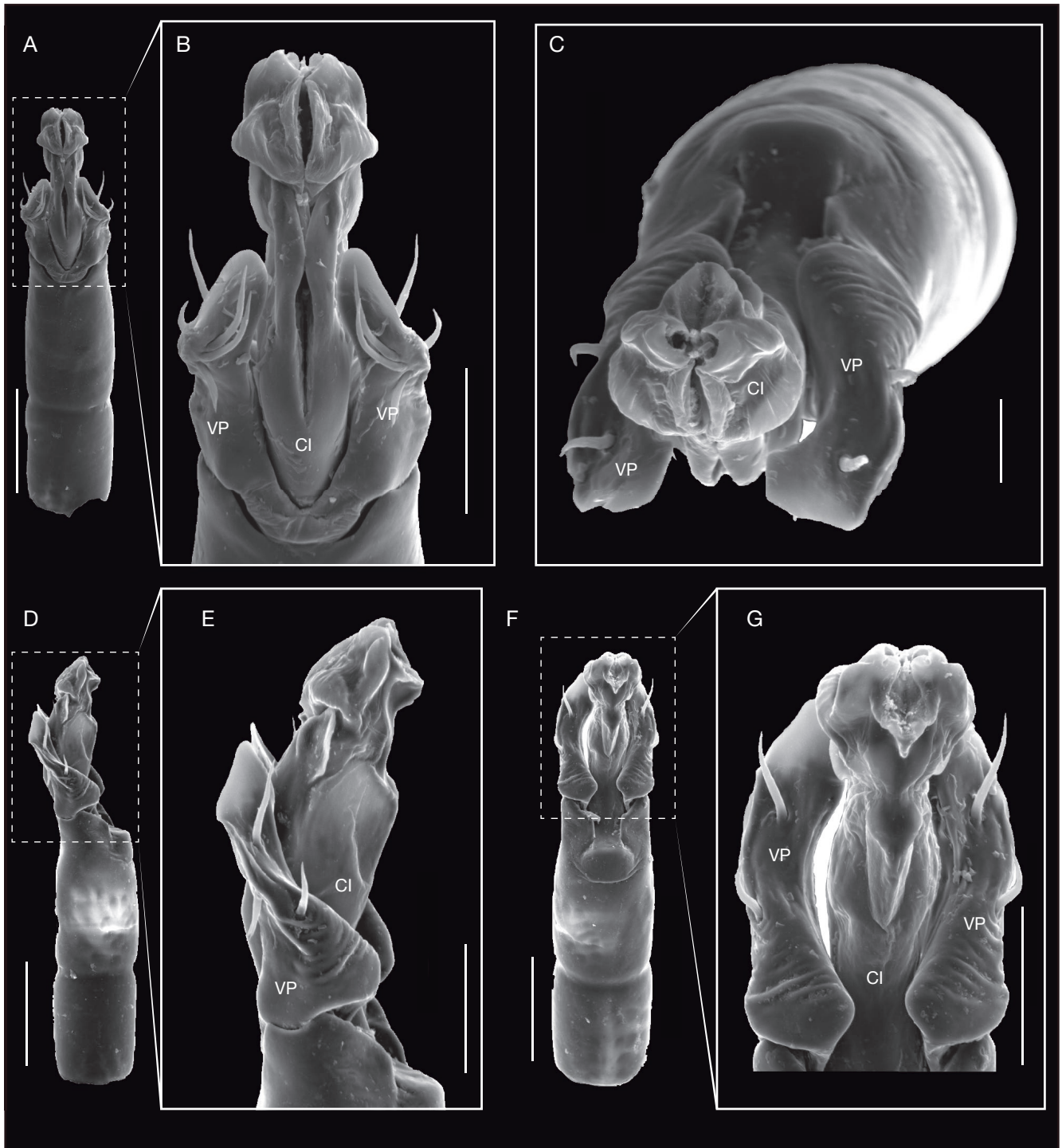


FIG. 9. — *Flavonuncia ubicki* n. sp., SEM images of male paratype (MACN-Ar 45999) penis: **A, B**, ventral view; **C**, apical view; **D, E**, lateral view; **F, G**, dorsal view. Abbreviations: **CI**, capsula interna; **VP**, ventral plate. Scale bars: A, D, F, 200 µm; B, E, G, 100 µm; C, 50 µm.

plate narrow arch-shaped, with upper and lower macrosetae not aligned in dorsal view. Ventral view, with a group of three macrosetae. Distal *capsula interna* with a complex structure ending in a thin free stylus. Ventral distal part of the *capsula interna* bearing a hexagonal process.

Female (CASENT 9072045) (Fig. 6B, D, F)

Similar to male, presenting dimorphism in the body coloration, females having a dark brown opisthosoma while the males are yellowish with brown stripes. Pedipalps larger in males.



FIG. 10. — *Flavonuncia mahaka* n. sp. (CASENT 9072050): **A, C, E**, male, **B, D, F**, female. Scale bars: 500 µm.

Flavonuncia mahaka n. sp.
(Figs 10-14; 23C, H, M)

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TYPE MATERIAL. — **Holotype**. Madagascar • ♂; Toliara, Parc National Andohahela, Col de Tanatana 33.3 km NW Tolagnaro;

Elev. 275 m; 24°45'31"S, 46°51'13"E; coll. B. L. Fisher *et al.*; 22-24. XI.2006; sifted litter (leaf mold, rotten wood) montane rainforest; collection code: BLF15100; CASTYPE 21650.

Paratypes. Madagascar • 5 ♂, 35 ♀; same data as for holotype; CASENT 9072050 • 1 ♂; SEM voucher; same data; MACN-Ar 46001 • 3 ♂, 3 ♀; same data; MACN-Ar 46002.

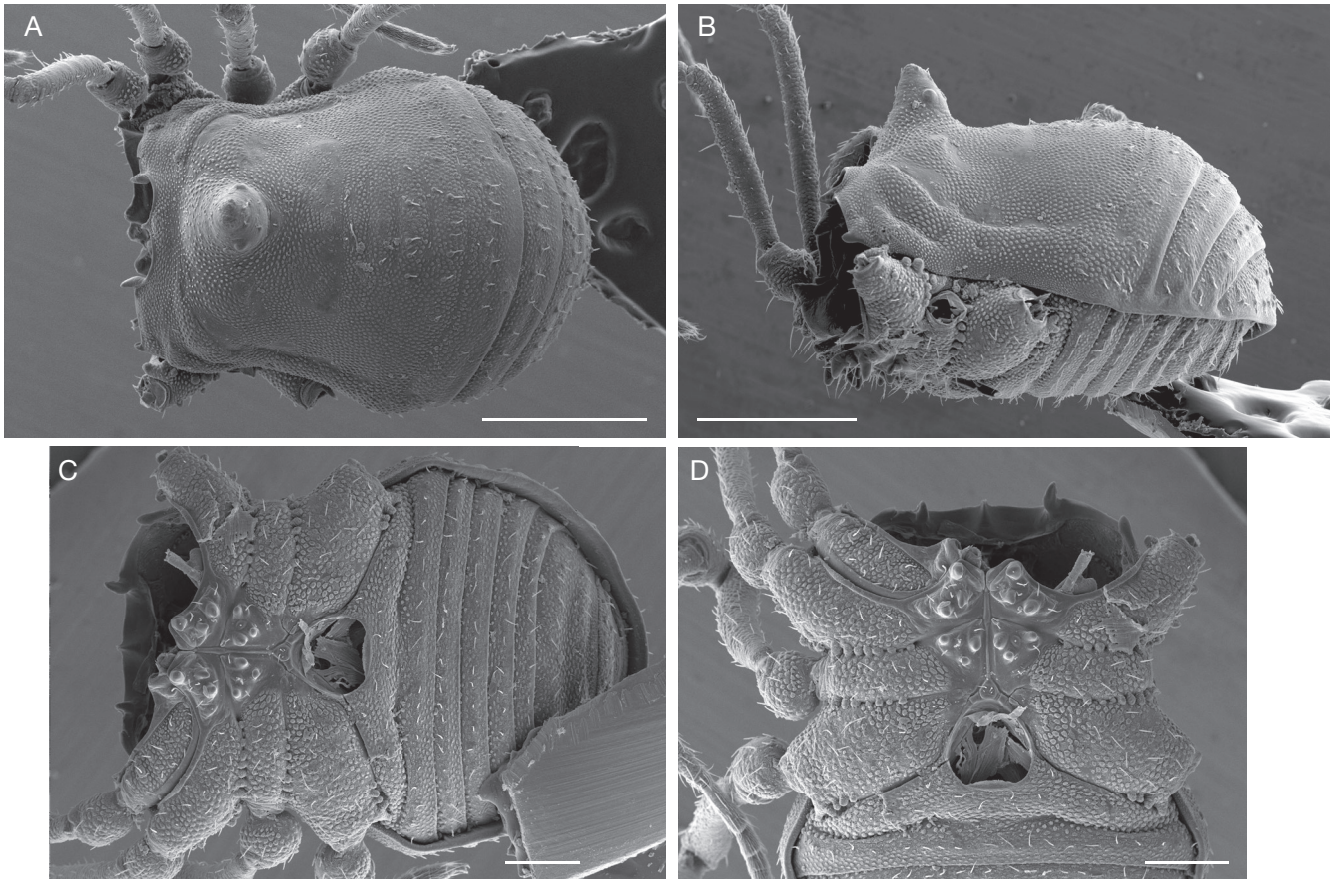


FIG. 11. — *Flavonuncia mahaka* n. sp., SEM images of male paratype (MACN-Ar 46001) habitus: **A**, dorsal; **B**, lateral; **C**, **D**, ventral. Scale bars: A, B, 500 μ m; C, D, 200 μ m.

ETYMOLOGY. — The species epithet, *mahaka*, is a trickster deity of Malagasy mythology. Noun in apposition.

COMPARATIVE DIAGNOSIS. — Differs from all known *Flavonuncia* species by the presence of three tubercles on the dorsal distal femur of the pedipalp and by the penis morphology showing a pair of high sclerotized processes on the ventral plate (Fig. 14).

DISTRIBUTION (Fig. 1). — Known only from the type locality.

DESCRIPTION

Male (holotype CASTYPE 21650)

Measurements. See Table 1.

Dorsum (Figs 10A, C; 11A, B). Outline hourglass-shaped of Eta (η) type. Ocularium conical, eyes situated at ocularium midpoint. Mesotergal scutum without tubercles or apophyses, carapace smaller than mesotergum, mesotergal areas not cleared defined, areas I-II with 1-2 small setiferous granules, area III with five, area IV with eight, the posterior border with a row of *c.* 12 granules. Free tergites bearing a row of granules on each tergite.

Venter (Figs 10E; 11C, D). Coxae ventral surface covered by setae; coxa I bearing 6-7 granules; almost all ventral surface covered by cerotegument, except by the proximal coxae II-III; proximal coxa II with three tubercles bearing basal setae, coxa III with three tubercles, two of those with basal seta; small bridge present, spiracles not visible.

Chelicerae (Fig. 12A, B). Basicheliceritae bearing a small tubercle on dorsal distal surface, cheliceral hand bearing five small ectal tubercles with subdistal setae, three small mesal granules, and four mesal setae.

Pedipalps (Fig. 12C, D). Trochanter with 2-3 ventral and 1-2 small dorsal tubercles, femur bearing a ventral row of small tubercles and three distal acute tubercles, mesal view with three remarkable tubercles, patella with five mesal tubercles, tibia ventral surface bearing sparse small tubercles, with a medial and 2-3 apical acute tubercles with subdistal setae, tarsus bearing four ectal and five mesal tubercles with setae.

Legs (Fig. 12E, H). Astragalus longer than calcaneus. Tarsal count: 3-6-4-4.

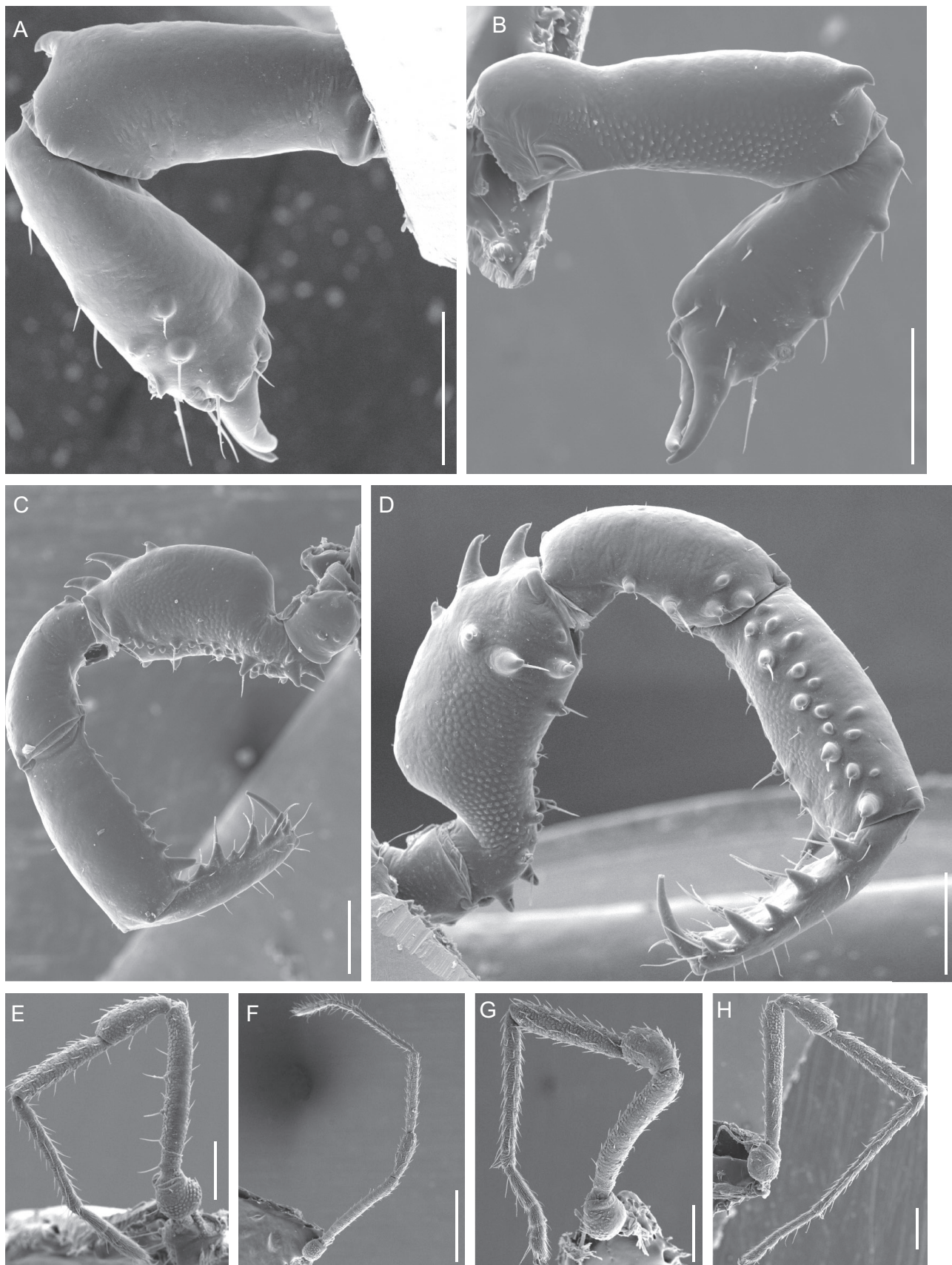


FIG. 12. — *Flavonuncia mahaka* n. sp., SEM images of male paratype (MACN-Ar 46001): **A, B**, chelicera, ectal (**A**), mesal (**B**); **C, D**, pedipalp, ectal (**C**), mesal (**D**); **E-H**, legs I (**E**), II (**F**), III (**G**), VI (**H**). Scale bars: A, B, E-H, 200 µm; C, D, 500 µm.

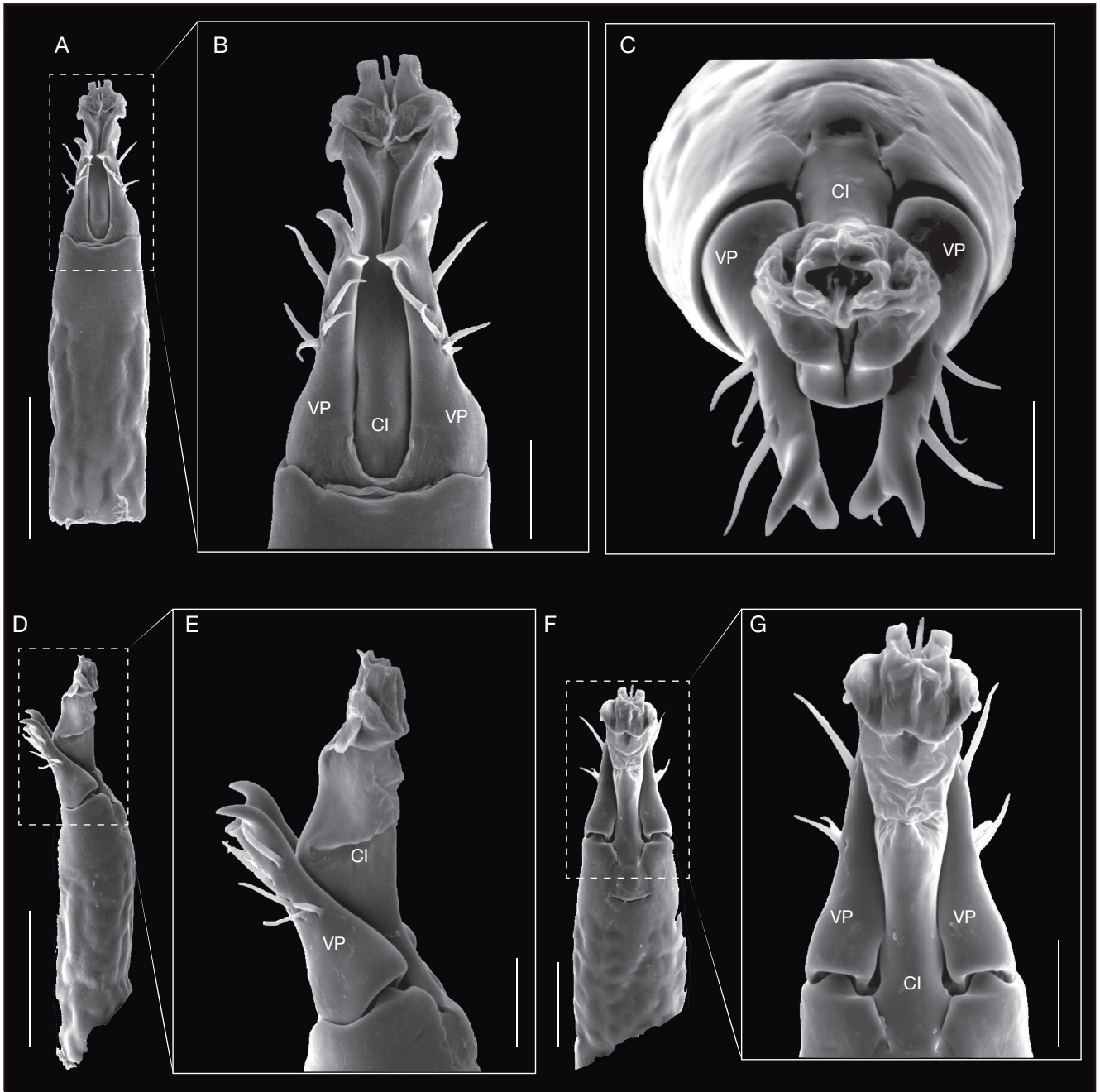


FIG. 13. — *Flavonuncia mahaka* n. sp., SEM images of male paratype (MACN-Ar 46001): **A, B**, chelicera, ectal (**A**), mesal (**B**); **C, D**, pedipalp, ectal (**C**), mesal (**D**); **E, H**, legs I (**E**), II (**F**), III (**G**); VI (**H**). Scale bars: A, B, E-H, 200 μ m, C, D, 500 μ m.

Genitalia (Figs 13; 14; 23C, H, M). Ventral plate bearing five macrosetae in the ventrolateral surface, apical part of the ventral plate acute composing two highly sclerotized processes (Fig. 14). *Capsula interna* longer than the ventral plate, ventral view with a cleft separating the *capsula interna* into two halves, distal *capsula interna* with a complex structure ending in a thin free stylus visible in ventral view.

Female (CASENT 9072050) (Fig. 10B, D, F). Similar to male, showing dimorphism in body coloration, females hav-

ing a dark brown opisthosoma, males yellowish with brown stripes. Pedipalps larger in males.

Flavonuncia vazimba n. sp.
(Figs 15-18; 23D, I, N)

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TYPE MATERIAL. — **Holotype.** Madagascar • ♂; Fianarantsoa, Parc National Befotaka-Midongy Papango 27.7 km S Midongy-Sud.



FIG. 14. — High sclerotized area (arrows) on ventral plate of *Flavonuncia mahaka* n. sp., illustrated in male genitalia (CASENT 9072050), in a temporary microscope slide: **A**, ventral; **B**, lateral view. Not to scale.

Mount Papango; Elev. 940 m; [23°50'07"S, 46°57'49"E](#); coll. B. L. Fisher *et al.*; 13-15.XI.2006; sifted litter, rainforest, collection code: BLF14776; CASTYPE 21651.

Paratypes. Madagascar • 13 ♂, 22 ♀; same data as for holotype; CASENT 9072147 • 1 ♂; MACN-Ar 46003; SEM voucher; same data • 5 ♂, 5 ♀; same data; MACN-Ar 46004 • 2 ♂, 4 ♀; Fianarantsoa, Parc National Befotaka-Midongy Papango 28.5 km S Midongy-Sud. Mount Papango; Elev. 1250 m; [23°50'27"S, 46°57'27"E](#); coll. B. L. Fisher *et al.*; 17-19.XI.2006, sifted litter, rainforest, collection code: BLF14946; CASENT 9072048.

ETYMOLOGY. — The species epithet, *vazimba*, according to popular belief, were the first inhabitants of Madagascar. While beliefs about the physical appearance of the Vazimba reflect regional variation, they are generally described as smaller in stature than the average person, leading some scientists to speculate that they may have been a pygmy people. Noun in apposition.

COMPARATIVE DIAGNOSIS. — Differs from all known *Flavonuncia* by the light yellow dorsal scutum and the acute shape of ocularium. The ventral distal part of the *capsula interna* of the penis bears a rounded process.

DISTRIBUTION (Fig. 1). — Known only from Parc National Befotaka-Midongy Papango, in Fianarantsoa, Southeast Madagascar.

DESCRIPTION

Male (CASTYPE 21651)

Measurements. See Table 1.

Dorsum (Figs 15A, C; 16A, B). Outline hourglass-shaped of Eta (η) type. Ocularium conical and acute, eyes located in the top half of the ocularium. Mesotergal scutum without tubercles or apophyses, carapace smaller than mesotergum, mesotergal areas smoothly defined, areas I-IV with a row of six, four, seven, and 13 small setiferous granules respectively, the posterior border with a row of *c.* 15 granules. Free tergites bearing a row of granules on each tergite.

Venter (Figs 15E; 16C, D). Coxae ventral surface covered by setae; coxa I bearing 9-11 granules; almost all ventral surface covered by cerotegument, except by the proximal coxa II-III; proximal coxa II with one tubercle bearing basal setae; coxa III with two tubercles and three setae; small bridge present, spiracles not visible.

Chelicerae (Fig. 17A, B). Basicheliceritae bearing a small tubercle on dorso-distal surface, cheliceral hand bearing five

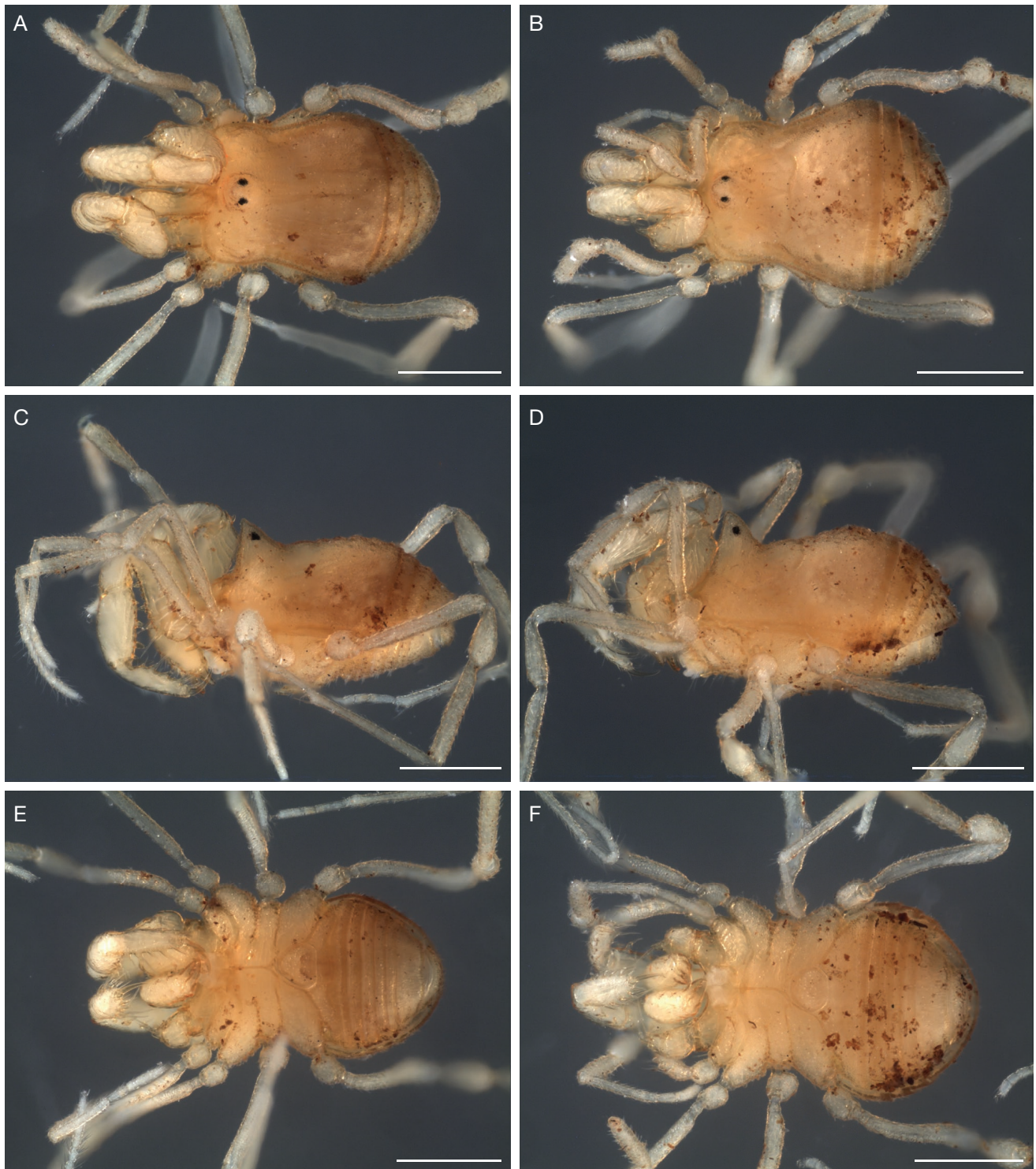


FIG. 15. — *Flavonuncia vazimba* n. sp. habitus (CASENT 9072048): **A, C, E**, male; **B, D, F**, female. Scale bars: 500 μ m.

small ectal tubercles with subdistal setae, two small mesal tubercles, and six mesal setae.

Pedipalps (Fig. 17C, D). Trochanter with four small ventral tubercles, femur bearing a ventral row of small tubercles and

two dorsal distal acute tubercles, mesal view with two tubercles, patella with one ventral ectal and three mesal tubercles, tibia ventral surface bearing sparse small tubercles, with three ectal and mesal acute tubercles with subdistal setae, tarsus bearing four ectal and five mesal tubercles with setae.

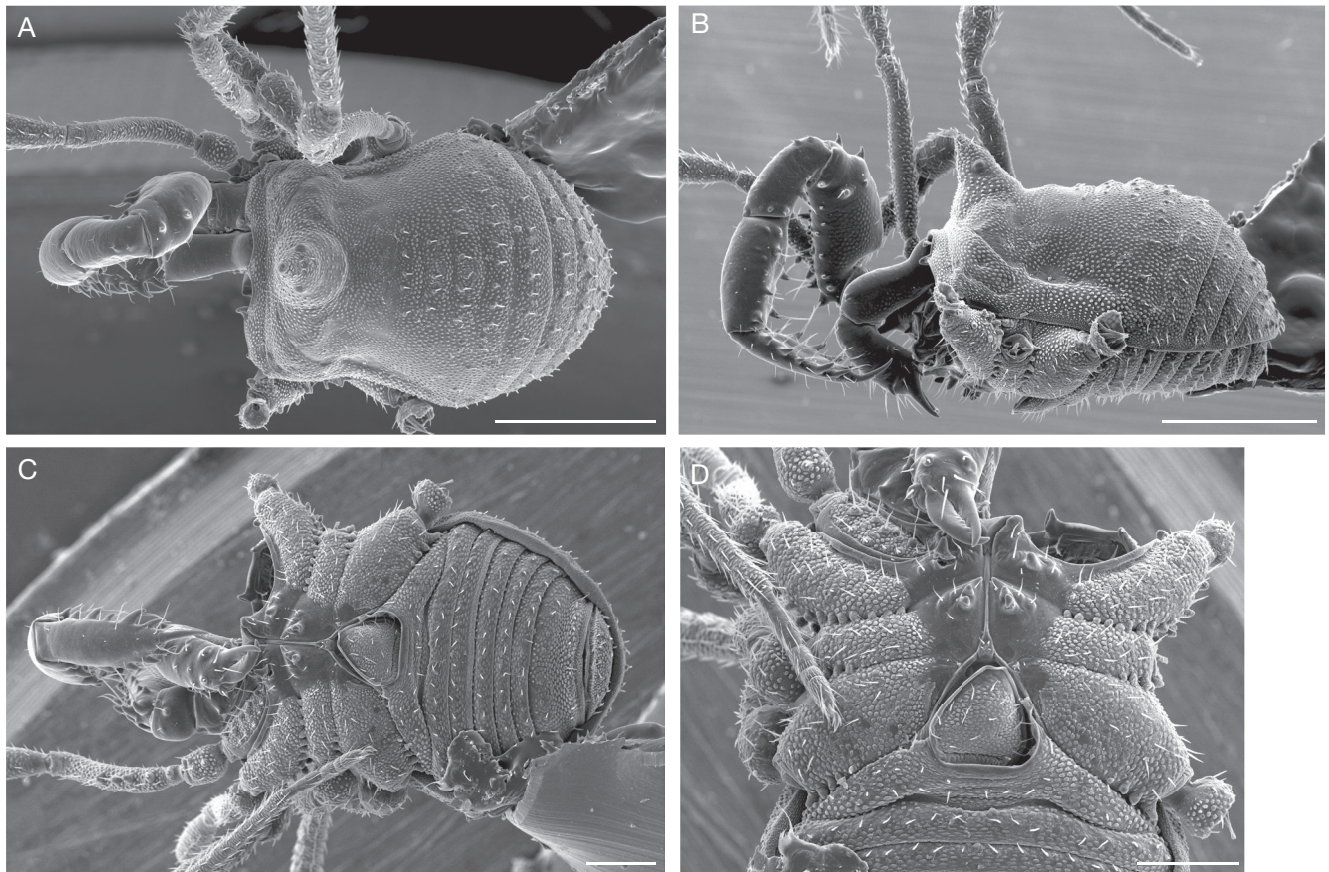


FIG. 16. — *Flavonuncia vazimba* n. sp., SEM images of male paratype (MACN-Ar 46003) habitus: **A**, dorsal; **B**, lateral; **C**, **D**, ventral. Scale bars: A, B, 500 μ m; C, D, 200 μ m.

Legs (Fig. 17E, H). Astragalus longer than calcaneus. Tarsal count: 3-6-4-4.

Genitalia (Figs 18; 23D, I, N). Ventral plate bearing three ventral and two dorsal macrosetae. *Capsula interna* longer than ventral plate, ventral view with a cleft separating *capsula interna* into two halves, apical portion of ventral plate rectangular arch-shaped, with upper and lower macrosetae aligned in dorsal view. In ventral view, two grouped upper macrosetae and one isolated lower macroseta. Distal *capsula interna* with a complex structure ending in a thin free stylus and a pair of fine conductors visible on ventral view. Ventral distal part of the *capsula interna* bearing a rounded process.

Female (CASENT 9072147) (Fig. 15B, D, F)

Very similar to male except for shorter pedipalps.

Flavonuncia zanahary n. sp.
(Figs 19-22; 23E, J, O)

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TYPE MATERIAL. — **Holotype.** Madagascar • ♂; Toamasina, Reserve Speciale Ambatovaky Sandrangato, Elev. 560 m 16°49'03"S,

49°17'42"E; coll. B. L. Fisher *et al.*; 25-27.II.2010; sifted litter, rainforest, collection code: BLF24750; CASTYPE 21652.

Paratypes. Madagascar • 42 ♂, 55 ♀; same data; CASENT 9072152 • ♂; SEM voucher, same data; MACN-Ar 46005 • 15 ♂, 15 ♀; same data; MACN-Ar 46006.

ETYMOLOGY. — The species epithet, *zanahary*, referred to a creator deity of the traditional mythology in Madagascar. Noun in apposition.

COMPARATIVE DIAGNOSIS. — Differs from all *Flavonuncia* species by the grainy dorsal scutum, the femur of pedipalp that is almost squared shape. Ventral distal part of the *capsula interna* without process, bearing a Y-shape groove.

DISTRIBUTION (Fig. 1). — Known only from the type locality.

DESCRIPTION

Male (CASTYPE 21652)

Measurements. See Table 1.

Dorsum (Figs 19A, C; 20A, B). Outline hourglass-shaped of Eta (η) type. Ocularium conical, eyes located on the top of the ocularium. Mesotergal scutum without tubercles or apophyses, carapace smaller than mesotergum, mesotergal areas smoothly defined, areas I-IV with two, three, four, and six small setiferous granules respectively, the posterior border with a row of *c.* 12 granules. Free tergites bearing a row of granules each tergite.

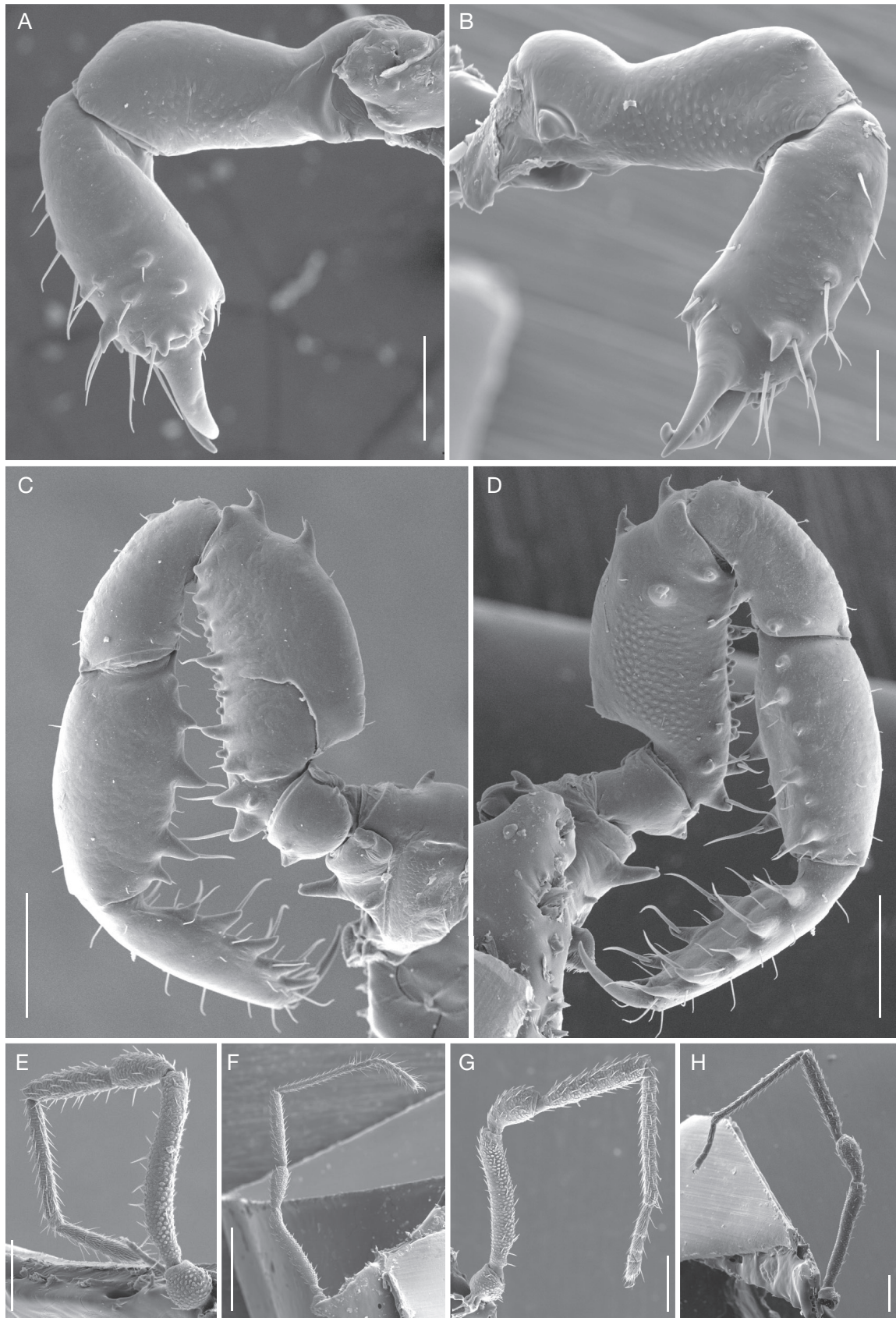


FIG. 17. — *Flavonuncia vazimba* n. sp., SEM images of male paratype (MACN-Ar 46003): **A, B**, chelicera, ectal (**A**), mesal (**B**); **C, D**, pedipalp, ectal (**C**), mesal (**D**); **E-H**, legs I (**E**), II (**F**), III (**G**), VI (**H**). Scale bars: A, B, 100 μ m; C-H, 200 μ m.



FIG. 18. — *Flavonuncia vazimba* n. sp., SEM images of male paratype (MACN-Ar 46003) penis: **A, B**, ventral view; **C**, apical view; **D, E**, lateral view, **F, G**, dorsal view. Abbreviations: **CI**, capsula interna; **VP**, ventral plate. Scale bars: A, D, F, 200 µm; B, C, E, G, 50 µm.

Venter (Figs 19E; 20C, D). Coxae ventral surface covered by setae; coxa I bearing 4-6 granules, almost all ventral surface covered by cerotegument, except by the proximal coxae II-III; proximal coxa II with two tubercles bearing three basal setae, coxa III with two tubercles the first one with 1-2 basal setae, small bridge present, spiracles not visible.

Chelicerae (Fig. 21A, B). Basicheliceritae smooth, chelical hand bearing seven ectal tubercles with subdistal setae, two small mesal tubercles, and five mesal setae.

Pedipalps (Fig. 21C, D). Trochanter with one dorsal and two ventral small tubercles, femur bearing a ventral row of small tubercles and two dorsal distal acute tubercles, mesal



FIG. 19. — *Flavonuncia zanahary* n. sp. habitus (CASENT 9072152): **A, C, E**, male; **B, D, F**, female. Scale bars: 500 μ m.

view with three tubercles, patella with one ventral ectal and three mesal tubercles, tibia ventral surface bearing sparse small tubercles, with three ectal and mesal acute tubercles with subdistal setae, tarsus bearing four ectal and five mesal tubercles with setae.

Legs (Fig. 21E, H). Astragalus longer than calcaneus. Tarsal count: 3-6-4-4.

Genitalia (Figs 22; 23E, J, O). Apical portion of ventral plate rounded triangular-shaped, with the upper and lower mac-

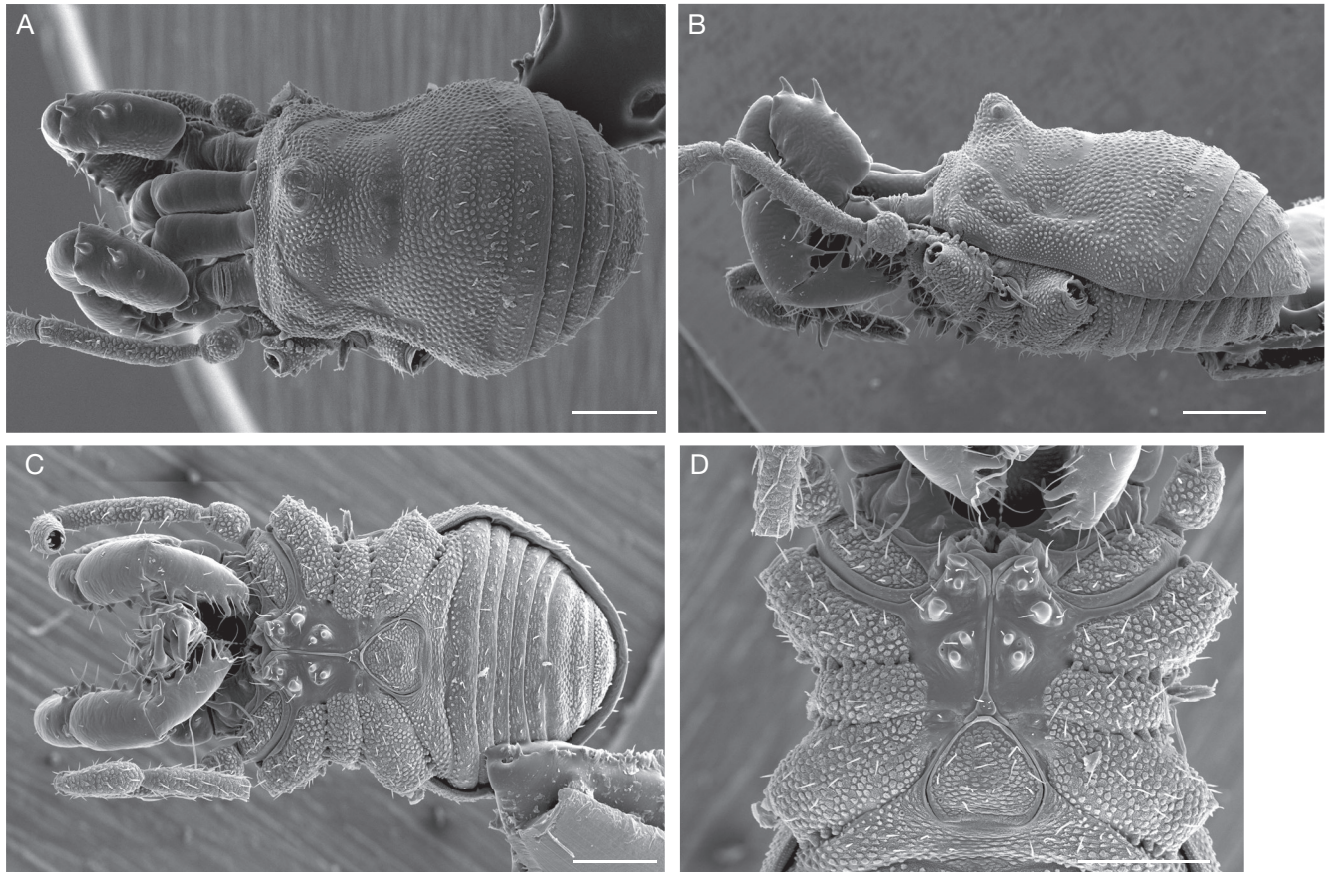


FIG. 20. — *Flavonuncia zanahary* n. sp., SEM images of male paratype (MACN-Ar 46005) habitus: **A**, dorsal; **B**, lateral; **C**, **D**, ventral (**C**, **D**). Scale bars: 200 µm.

rosetae aligned in dorsal view. In ventral view, two grouped upper macrosetae and one isolated lower macroseta. Distal *capsula interna* with a complex structure ending in a thin free stylus. Ventral distal part of *capsula interna* without process, bearing a Y-shape groove.

Female (CASENT 9072152) (Fig. 19B, D, F)

Similar to male, presenting dimorphism in body coloration, females with a dark brown opisthosoma. Males yellowish with brown stripes. Pedipalps larger in males.

DISCUSSION

Until now, all Buemarinoidae genera were represented by a single species. The presence of five different living species of *Flavonuncia* in Madagascar, in addition to being a surprise, is a unique opportunity to explore interspecific variability within a buemarinoid genus. In general, the five species of *Flavonuncia* are quite similar and confirm to the morphological stasis for this ancient group. The small size and slight external morphological differentiation challenge species identifications based only on external features. Conversely, genital morphology exhibits a considerable amount of variability and becomes a key character in this group at different taxonomic levels.

Besides slight differences in the morphology of the ocularium, granulation of dorsum, size and morphology of the penis, the marked sexual dimorphism in color and stripes is one of the most interesting morphological features of *Flavonuncia* species (e.g. Fig. 2A-D). Only *Flavonuncia vazimba* n. sp. does not show this dimorphism, with males and females showing a light-yellow color in both sexes (Fig. 15). All the species of *Flavonuncia* have very similar penis morphology, but some morphological differences can be used as diagnostic characters. The main penial differences are located in the total size and in the morphology of the ventral plate, especially the position of the macrosetae and in the apical outline of the lamellas (Fig. 23, yellow structures). Additionally, fine details of the *capsula interna*, mainly at the apical portion, can be used to differentiate species (Fig. 23).

A comparison among the genitalia of all Buemarinoidae genera, *Arbasus*, *Buemarinoa*, *Flavonuncia*, *Fumontana*, *Phocyx* and *Turonychus*, reveals the great similarity in the bauplan of the penises, but some morphological details seem to connect geographically close genera. The European buemarinoids, *Arbasus*, *Buemarinoa* and *Turonychus* (Fig. 24) are the closest geographically (France, Italy, and Spain). These taxa show almost the same size of the penis, a large ventral plate in comparison to the *capsula interna*, macrosetae distributed in rows and located on the distal part of each lamella, and general morphology of

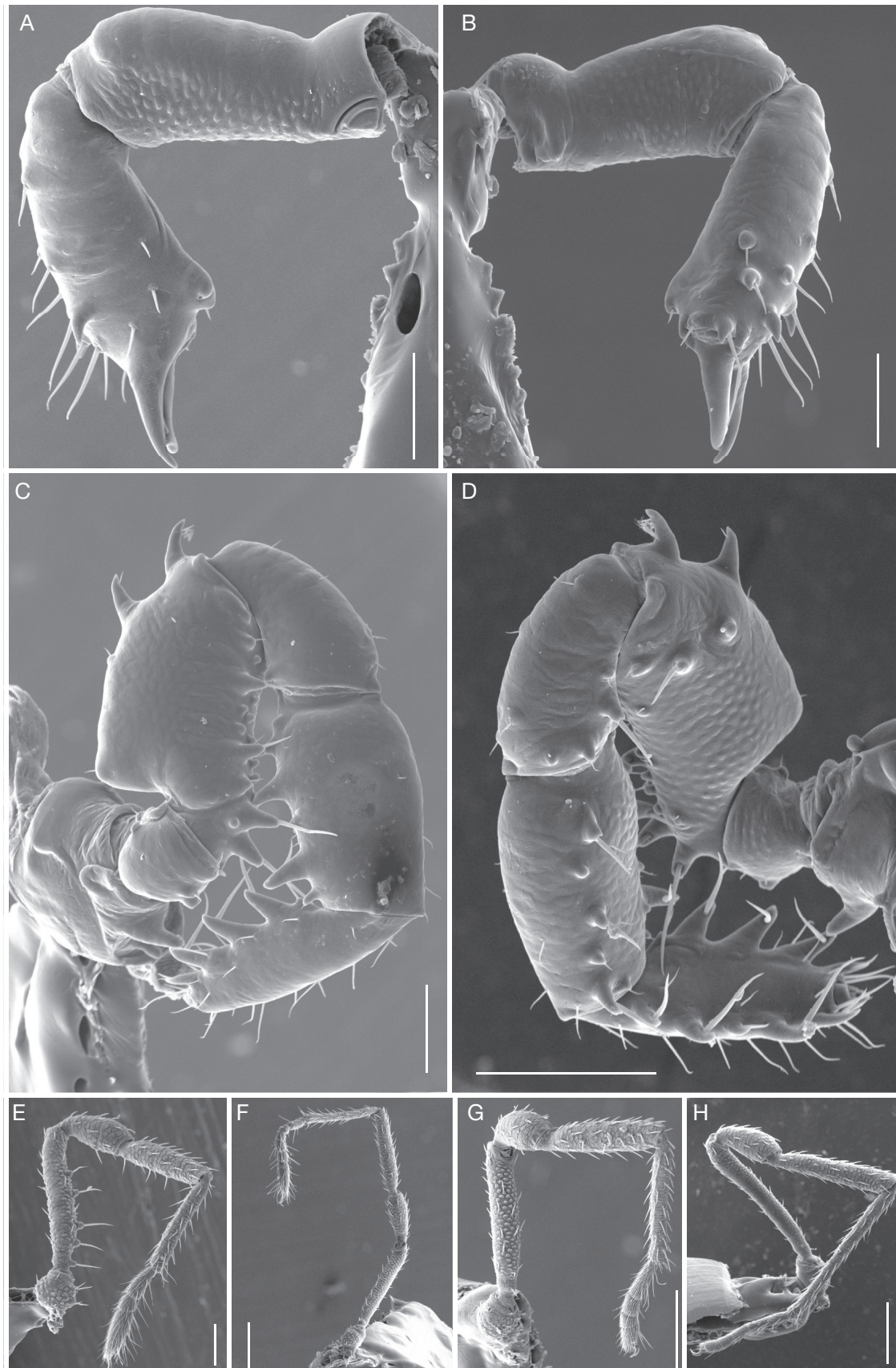


FIG. 21. — *Flavonuncia zanahary* n. sp., SEM images of male paratype (MACN-Ar 46005): **A, B**, chelicera, ectal (**A**), mesal (**B**); **C, D**, pedipalp, mesal (**C**), ectal (**D**); **E-H**, legs I (**E**), II (**F**), III (**G**), VI (**H**). Scale bars: A-C, E, 100 μ m, D, F-H, 200 μ m.

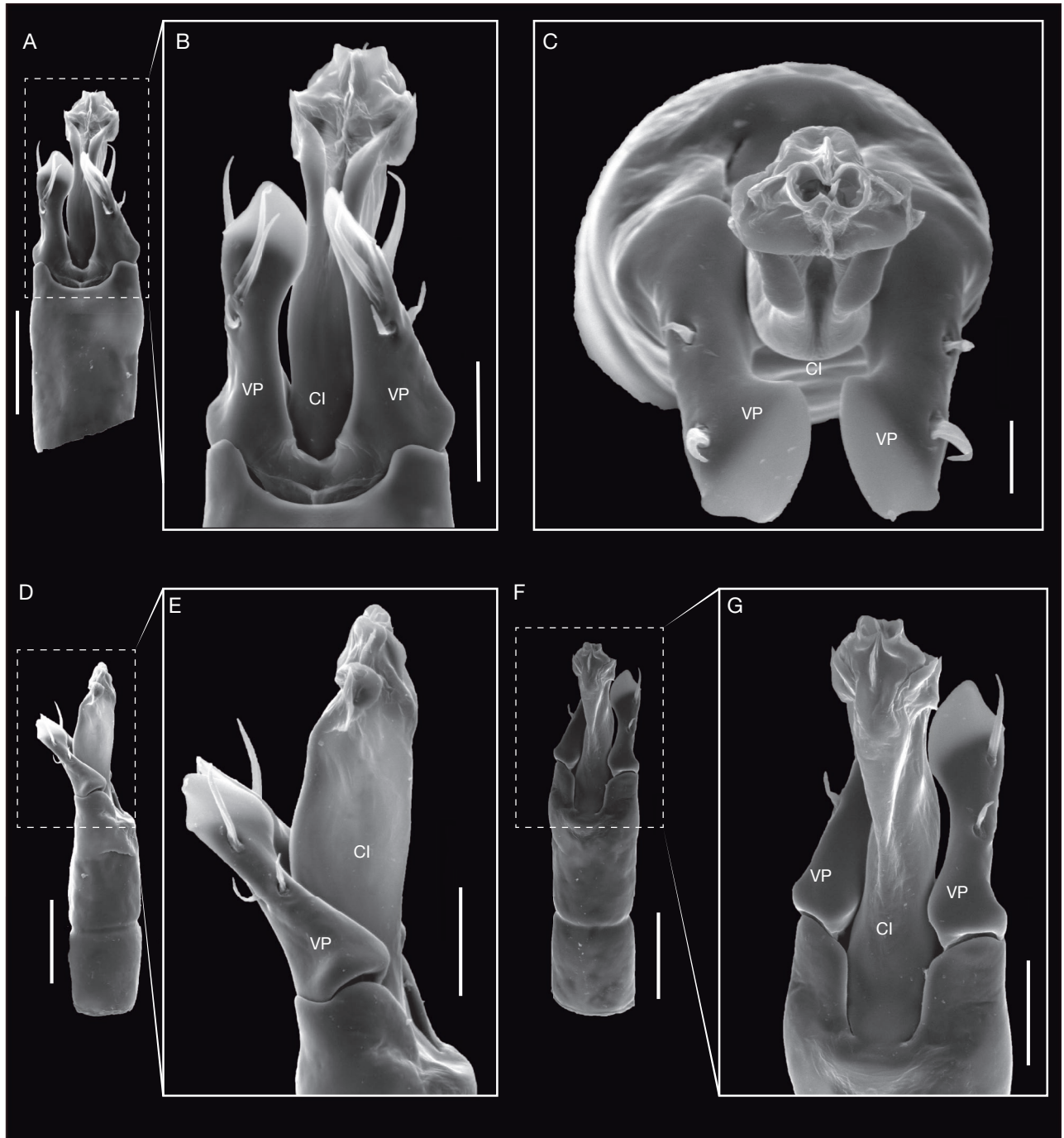


FIG. 22. — *Flavonuncia zanahary* n. sp., SEM images of male paratype (MACN-Ar 46005) penis: **A, B**, ventral view; **C**, apical view; **D, E**, lateral view; **F, G**, dorsal view. Abbreviations: **VP**, ventral plate; **CI**, *capsula interna*. Scale bars: A, D, F, 100 µm; B, E, G, 50 µm; C, 20, µm.

the distal *capsula interna*. It is hard to fully compare the male genital morphology of *Buemarinoa* and *Turonychus* with *Arbasus* because the known drawing of this latter species was based on a penis everted and the twisted lamella make comparisons difficult. *Fumontana* has a more similar *capsula interna* with other genera of the northern hemisphere, despite differences in the shape of the ventral plate. *Flavonuncia* and *Phocyx*, from the southern hemisphere exhibit great similarity in the morphology of the apical region of the *capsula interna* (Fig. 24).

At the family level, male genital morphology is essential to identification within Opiliones. There are two kinds of penises in Laniatores: the hydraulic functioning penis is characteristic of Grassatores, where the glans are everted by hydraulic pressure. On the contrary, Insidiatores bears a muscular functioning penis, where muscles and tendons are responsible for the movement of the glans structures (Macías-Ordóñez *et al.* 2010; Pérez-González & Werneck 2018). Buemoarinoidea is representative of the muscular functioning male genital

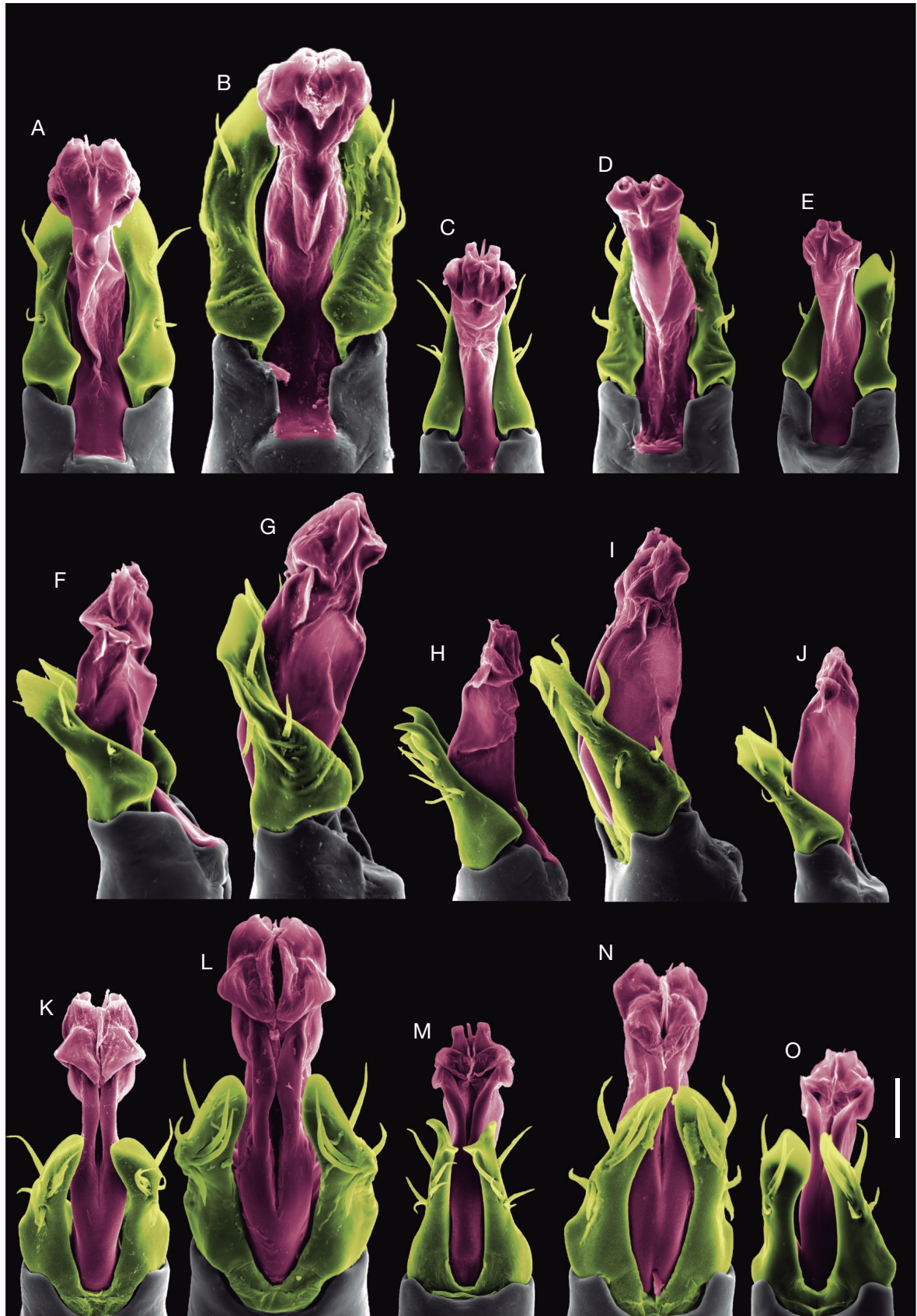


FIG. 23. — SEM images comparing the penis shape and size of : **A, F, K**, *Flavonuncia pupilla* Lawrence, 1959; **B, G, L**, *Flavonuncia ubicki* n. sp.; **C, H, M**, *Flavonuncia mahaka* n. sp.; **D, I, N**, *Flavonuncia vazimba* n. sp.; **E, J, O**, *Flavonuncia zanahary* n. sp.; dorsal view (**A-E**); lateral view (**F-J**); ventral view (**K-O**). Colored structures: ventral plate (yellow), capsula interna (magenta). Scale bars: 50 μ m.



FIG. 24. — Visual depiction of the distribution of *Flavonuncia* Lawrence, 1959, also showing the genital morphology and global distribution. Penis representations are adaptations of Thomas & Hedin (2006), Karaman (2019, 2023), and Derkarabetian *et al.* (2021). Colored structures: ventral plate (yellow), capsula interna (magenta). Scale bar: 100 µm.

morphology. The penis bauplan of Buemarinoidae exhibits a typical ventral plate formed by two independent lamellas (with or without a very weak common base). Each lamella bears five pairs of macrosetae, two dorsal and three ventral (Shear 1977; Thomas & Hedin 2006 and herein; Karaman 2019; Derkarabetian *et al.* 2021). This kind of simple penis with bilamellar ventral plate and lamella that can move independently is a putative synapomorphy for Buemarinoidae, differentiating them from Triaenonychidae. In the latter, the base of the ventral plate is massive, strong, and common to the apical lamella (divided or not), not allowing an independent lamellar movement. Also, the buemarinoid penis shows a remarkable absence of *capsula externa*, having only the *capsula interna*. The absence of *capsula externa* is also present in basal Triaenonychidae (e.g. *Hendea* Roewer, 1931, but this needs further comparisons). However in the majority of Triaenonychidae the glans has a *capsula externa* on the dorsal surface, including species with an elongated *stylus*, exhibited in some groups with male genitalia that are extremely complex both in form and function (see Hunt & Maury 1993; Pérez-González & Werneck 2018; Porto *et al.* 2022). Other kinds of simplified penises are found in representatives of other Insidiatores groups: Lomanellidae Mendes & Derkarabetian, 2021, Synthetonychiidae Forster, 1954, and Travunioidea Absolon & Kratochvíl, 1932 (Derkarabetian *et al.* 2021), but these groups lack a differentiated ventral plate which seems to be a putative synapomorphy for Buemarinoidae + Triaenonychidae.

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