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Monograph

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Pseudocetherinae (Hemiptera: Reduviidae) revisited: phylogeny and taxonomy of the lobe-headed bugs

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Abstract. The concept of the previously monogeneric subfamily Pseudocetherinae (Hemiptera: Heteroptera: Reduviidae) is revised and expanded. We here transfer *Gerbelius* Distant, 1903, *Kayanocoris* Miller, 1954, *Microvarus* Jeannel, 1917, *Paragerbelius* Miller, 1958, and *Voconia* Stål, 1866 from Reduviinae to Pseudocetherinae and treat *Kayanocoris*, *Microvarus*, *Paragerbelius*, and *Pseudocethera* Villiers, 1963 as junior synonyms of *Voconia*, resulting in new combinations for *Voconia conradti* (Jeannel, 1917) comb. nov., *V. ifana* (Villiers, 1963) comb. nov., *V. monodi* (Villiers, 1963) comb. nov., *V. motoensis* (Schouteden, 1929) comb. nov., *V. ornata* (Distant, 1903) comb. nov., *V. schoutedeni* (Villiers, 1964) comb. nov., *V. typica* (Miller, 1958) comb. nov., and *V. wegneri* (Miller, 1954) comb. nov. We also describe 23 new species of *Voconia*: *V. bakeri* sp. nov., *V. bracata* sp. nov., *V. brachycephala* sp. nov., *V. chrysoptera* sp. nov., *V. coronata* sp. nov., *V. decorata* sp. nov., *V. dolichocephala* sp. nov., *V. fasciata* sp. nov., *V. grandioculata* sp. nov., *V. hemera* sp. nov., *V. isosceles* sp. nov., *V. laosensis* sp. nov., *V. lasiosoma* sp. nov., *V. lirophleps* sp. nov., *V. loki* sp. nov., *V. mexicana* sp. nov., *V. minima* sp. nov., *V. nyx* sp. nov., *V. smithae* sp. nov., *V. tridens* sp. nov., *V. trinidadensis* sp. nov., *V. tuberculata* sp. nov., and *V. vittata* sp. nov. Lectotypes are designated for *Gerbelius confluens* Distant, 1903, *G. typicus* Distant, 1903, *V. conradti* comb. nov., *V. ornata* comb. nov., and *V. pallidipes* Stål, 1866. A revised diagnosis and description of Pseudocetherinae are provided along with photographs of the species and of the male genitalia of 13 pseudocetherine and five closely related reduviine species. An identification key to the two genera of Pseudocetherinae as well as a key to species of *Voconia* are presented. A phylogenetic hypothesis is proposed for the relationships of Pseudocetherinae using parsimony analyses of 77 morphological characters.

Keywords. Reduviidae, taxonomy, phylogeny, assassin bugs, lobe-headed bugs.

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Introduction

The assassin bugs, or Reduviidae Latreille, 1807 (Hemiptera: Heteroptera), are a large group of mostly predatory true bugs with approximately 7000 described species in 24 subfamilies (Maldonado 1990; Weirauch *et al.* 2014; Forthman & Weirauch 2017). The subfamilial classification, however, is not settled, with multiple analyses finding that the second largest subfamily, the Reduviinae Latreille, 1807 (about 1100 spp.), is polyphyletic and falls into 11–14 separate clades (Weirauch 2008; Weirauch & Munro 2009; Hwang & Weirauch 2012; Zhang *et al.* 2016). Pseudocetherinae Villiers, 1963 have historically been treated either as a subfamily (Maldonado 1990; Weirauch *et al.* 2014) or a tribe within the distantly related Cetherinae Jeannel, 1919 (Putshkov & Putshkov 1985). Hwang & Weirauch (2012) recovered species that we here consider to be part of the expanded concept of Pseudocetherinae within their *Reduvius* clade of the Reduviinae. Prior to this work, Pseudocetherinae comprised only the genus *Pseudocethera* Villiers, 1963 that contained three rarely collected Afrotropical species (Villiers 1963b, 1964): *Ps. monodi* Villiers, 1963 described from a single micropterous female specimen from Belgian Congo (now the Democratic Republic of the Congo), *Ps. ifana* Villiers, 1963 from Sudan based on a macropterous male specimen (Villiers 1963a), and *Ps. schoutedeni* Villiers, 1964 based on a micropterous and a macropterous male from Belgian Congo (Villiers 1964). The natural history of Pseudocetherinae is unknown beyond a reference to the collection site of the holotype of *Ps. ifana* that was recorded as "underneath a piece of dead wood" by Villiers (1963a).

Pseudocetherinae were initially diagnosed by their unique trilobate head formed by the large and anteriad projecting clypeus and maxillary plates, antennal pedicel longer than scape, small or vestigial ocelli, slender labium with (visible) labial segment I long and appressed against the ventral head surface, the proximity of the coxal cavities of fore and mid legs, and the three-segmented tarsi (Villiers 1963b). Additionally, the dorsal abdominal glands on terga IV–VI are absent in Pseudocetherinae in contrast to most other Reduviidae (Weirauch 2006), the prosternum is drawn into an anteriad-directed process, and the apex of the third visible labial segment is bent and slender (Weirauch *et al.* 2014). While this combination of diagnostic characters sets *Pseudocethera* apart from the great majority of reduviid subfamilies, some or all of these features are also observed to varying degrees in five genera that are currently classified as Reduviinae: *Microvarus* Jeannel, 1917 (two Afrotropical species), *Gerbelius* Distant, 1903 (three Oriental species), *Kayanocoris* Miller, 1954 (one Oriental species), *Paragerbelius* Miller, 1958 (one Melanesian species), and *Voconia* Stål, 1866 (one Australian species) (Maldonado 1990). Miller (1954, 1958) was the first to suggest close relationships between three of the Oriental and Australasian genera, noting the resemblance in general habitus among *Gerbelius ornatus* Distant, 1903 and the members of *Kayanocoris* and *Paragerbelius*. Subsequently, a morphology-based cladistic analysis across Reduviidae recovered the reduviine species *G. ornatus* and *Microvarus conradti* Jeannel, 1917 in a well-supported clade with the pseudocetherine *Ps. monodi* (Weirauch 2008), and a molecular phylogenetic analysis using ribosomal data recovered *Voconia loki* sp. nov. (misidentified as *Kayanocoris wegneri* Miller, 1954) as sister to three described and undescribed species of *Gerbelius* (Hwang & Weirauch 2012). Based on this morphological and molecular phylogenetic evidence, a revision of *Pseudocethera* and related taxa that are currently classified as Reduviinae is overdue. In addition, we have located specimens of *Pseudocethera* and putatively related genera in several collections that represent 23 undescribed species. These specimens most closely resemble Afrotropical species currently placed in the genus *Microvarus* but originate not only from the Afrotropical region but also from the Neotropical and Oriental regions. We posit that a phylogenetic hypothesis focused on *Pseudocethera* and related genera, with significant representation of other reduviine genera, will be the most scientifically sound way to (1) evaluate subfamilial and generic concepts and (2) infer the generic classification of existing and new species. Although we attempted to generate molecular data using non-destructive sampling of pinned museum specimens, we failed to produce a workable molecular dataset; we therefore decided to rely on morphology-based phylogenetic analyses to inform the classification of Pseudocetherinae.

The objectives of this study are to: (1) test the monophyly of Pseudocetherinae and putatively related genera currently classified as Reduviinae using 77 morphological characters and 33 ingroup and seven outgroup taxa using parsimony analyses, (2) revise generic and subfamilial concepts of Pseudocetherinae based on phylogenetic relationships, (3) provide redescriptions of *Gerbelius* and *Voconia*, (4) provide nine species redescriptions and 23 new species descriptions for *Voconia*, and (5) provide keys to genera of Pseudocetherinae and species of *Voconia*.

Material and methods

Specimens

Sixty ingroup specimens were physically examined for this revision. Wherever it was not possible to receive type material on loan, we coded from images of the types, original descriptions, and other specimens that had been authoritatively identified where applicable – details are provided for those cases in the remarks section of the species description.

Repositories

Specimens are deposited in the following institutions:

AMNH = American Museum of Natural History, New York, USA
AMS = Australian Museum, Sydney, Australia
ANIC = Australian National Insect Collection, Canberra City, Australia
BMNH = The Natural History Museum, London, United Kingdom
BPBM = Bernice P. Bishop Museum, Honolulu, Hawaii, USA
HNHM = Hungarian Natural History Museum, Budapest, Hungary
INHS = Illinois Natural History Survey, Champaign, Illinois, USA
MNHN = Muséum national d'histoire naturelle, Paris, France
NBCN = Naturalis Biodiversity Centre, Leiden, the Netherlands
NHMUK = The Natural History Museum, London, United Kingdom (alternative for BMNH)
NHMW = Naturhistorisches Museum Wien, Vienna, Austria
NHRS = Swedish Museum of Natural History, Stockholm, Sweden
RMCA = Musée Royal de l'Afrique Centrale, Tervuren, Belgium
RMNH = Rijksmuseum van Natuurlijke Historie Naturalis, Amsterdam, the Netherlands (alternative for NBCN)
UCR = Entomology Research Museum, Department of Entomology, University of California, Riverside, California, USA
ZRC = Lee Kong Chian Natural History Museum, Zoological Reference Collection, National University of Singapore, Singapore
ZSMC = Zoologische Staatssammlung, Munich, Germany

Databasing and maps

All physically examined specimens were databased using the American Museum of Natural History's Arthropod Easy Capture (AEC) instance (https://research.amnh.org/pbi/locality/index.php) of the Planetary Biodiversity Inventory for Plant Bugs project locality database (PBI database). Matrix code labels with unique specimen identifiers (USIs) were attached to all specimens examined directly. The USI numbers (e.g., AMNH_PBI 00094810) comprise an institution and a project code (AMNH_PBI) as well as a unique number (00094810) for each specimen. Distribution maps were plotted with SimpleMappr (http://www.simplemappr.net) and are based on all physically examined specimens as well as records from the literature. To plot the specimens without GPS coordinates, Google Earth ver. 9.140.0.4 (Google, LLC) was used to estimate the coordinates of the locality provided.

Imaging, morphological methods, and measurements

Dorsal and lateral habitus photographs, as well as close-ups of the head and male genitalia were taken on a Leica DFC 450 C Microsystems camera (Leica, Wetzlar, Germany) using a Planapo 2.0× objective and a Leica Application Suite (LAS) ver. 4.3. Stacked images were assembled using LAS. Male genitalia were excised and macerated in heated 10% potassium hydroxide solution for 5–10 minutes and rinsed in distilled water. They were temporarily stored in a 96-well plate containing 100% glycerol for examination and eventually sealed in polyethylene vials containing glycerol and attached to the specimen's pin. The pygophore, eighth abdominal segment, one paramere, and the phallus were removed for examination in glycerol gelatin for imaging for *Gerbelius* sp., *G. typicus*, *V. bakeri* sp. nov., *V. conradti*, *V. grandioculata* sp. nov., *V. lasiosoma* sp. nov., *V. laosensis* sp. nov., *V. mexicana* sp. nov., *V. nyx* sp. nov., *V. pallidipes* Stål, 1866, *V. tridens* sp. nov., *V. tuberculata* sp. nov., *V. typica* (Miller, 1958) and *V. vittata* sp. nov. Scanning electron micrographs (SEMs) were acquired on a Hitachi TM-1000 Tabletop Electron Microscope (Institute for Integrative Genome Biology, UCR) for one male *V. dolichocephala* sp. nov. (AMNH_PBI 00168745) to document details of the head, prothorax, labium, hemelytron, and pygophore. The specimen was not removed from the point or coated making this approach maximally non-destructive.

Measurements of selected morphological features were obtained from photographs using ImageJ2 (Rueden *et al.* 2017) and are provided in Table 1. Body length is recorded in dorsal view along the midline from the clypeal apex to the posteromedial margin of the abdomen. Dorsal head measurements were obtained from images of the head oriented horizontally for better accuracy. This allowed us to record head length from the maxillary plate apex to the posterior margin of the head (defined by the transition of head granulations to smooth neck) since the maxillary plates in most species are slightly longer than the clypeal apex. Head length recorded from the clypeal apex to the posterior margin of the head is recorded in Supp. file 1. The scape, pedicel, and labium were measured from the proximal and distal midpoints.

Terminology

Terminology generally follows Schuh & Weirauch (2020). When referring to the hemelytra we refer to it in an abducted position, meaning away from the midline of the body or perpendicular to the longitudinal axis of the body. We refer to a seta on a protuberance as a setigerous tubercle, large setae as macrosetae, and short, thin macrosetae as pubescence. Abbreviations for wing cells and veins in descriptions and the cladistic analysis are as follows: Cu-An_1 cell, cell between cubital and first anal veins; M-Cu cell, cell between medial and cubital veins; M, medial vein; R, radial vein. We refer to labial segments as: labial segment I, first visible segment; labial segment II, second visible segment; labial segment III, third visible segment. In reduviids the first abdominal tergum is referred to as syntergum I+II. Here, we refer to syntergum I+II individually as tergum I and tergum II since they are clearly identifiable in Pseudocetherinae.

Species descriptions and redescriptions

Descriptions are based on examination of available specimens for a given species, including type material, type images of *Voconia conradti*, *V. pallidipes*, and *V. wegneri*, and the original descriptions of *V. ifana* and *V. monodi*. Descriptions were compiled from a character matrix of 98 discrete characters assembled in Mesquite ver. 3.51 (Maddison & Maddison 2019). This descriptive character matrix was exported as descriptions for each taxon in Mesquite and then punctuation and sentence structure were manually edited. Species descriptions are provided for all species of *Voconia*, including formerly recognized *G. ornatus*, as well as species placed in the genera *Kayanocoris*, *Microvarus*, *Paragerbelius*, and *Pseudocethera* but transferred to *Voconia* in this study. Because the habitus of species of *Gerbelius* resembles that of other small-bodied Reduviinae compared to *Voconia*, we suspect that our survey of

Table 1 (continued on next three pages). Measurements (in mm) of Pseudocetherinae.

Species	Sex	USI or Averages	Total length clypeus to abdomen	Head		Anteocular to maxillary plates	Postocular	Synthlipsis	Eye Width	Ocellus length	Scape length	Pedicel length	Labium length	
				Length clypeus to neck	Width across eyes								Segment I	Segment II dorsal surface
Gerbelius typicus	♂	AMNH_IZC 00321200	7.57	1.07	0.82	0.31	0.37	0.36	0.20	0.08	0.29	0.91	0.62	0.49
Gerbelius sp. 1	♀	UCR_ENT 00052189	7.49	1.21	0.99	0.37	0.49	0.50	0.24	0.08	0.31	1.04	0.69	0.60
Gerbelius sp. 2	♂	UCR_ENT 00073816	7.49	1.16	0.88	0.34	0.45	0.43	0.21	0.10	0.30	1.10	?	?
Gerbelius sp. 3	♀	UCR_ENT 00052219	7.87	1.02	0.85	0.33	0.37	0.42	0.21	0.09	0.30	1.14	0.68	0.59
Voconia bakeri	♂	UCR_ENT 00073810	9.82	?	0.98	0.32	0.40	0.36	0.28	0.11	0.33	1.18	0.87	0.52
Voconia bracata	♂	AMNH_PBI 00170707	10.76	2.06	1.18	0.71	0.76	0.38	0.41	0.14	0.51	2.13	1.86	0.70
Voconia brachycephala	♀	AMNH_PBI 00213935	7.42	1.03	1.00	0.26	0.35	0.39	0.33	0.12	?	1.19	0.86	0.28
Voconia chrysoptera	♀	UCR_ENT 00001551	10.45	1.45	1.21	0.43	0.57	0.49	0.37	0.19	0.41	2.15	1.04	0.68
Voconia conradti	♂	**Mean** (N = 5)	10.87	1.58	1.37	0.51	0.56	0.46	1.20	0.19	0.36	1.76	1.23	0.65
		Min.	10.39	1.47	1.34	0.43	0.46	0.41	0.42	0.17	0.34	1.72	1.16	0.61
		Max.	11.37	1.69	1.41	0.57	0.63	0.49	4.22	0.22	0.38	1.78	1.29	0.67
		Range	0.98	0.22	0.07	0.14	0.17	0.09	3.80	0.05	0.04	0.06	0.13	0.06
	♀	AMNH_PBI 00170693	11.21	1.70	1.32	0.60	0.66	0.57	0.37	0.10	0.29	1.61	0.62	0.40
Voconia coronata	♂	AMNH_PBI 00170706	10.95	1.57	1.27	0.49	0.53	0.37	0.44	0.15	0.44	2.36	1.39	0.67
Voconia decorata	♂	UCR_ENT 00073809	10.02	1.57	1.20	0.45	0.54	0.43	0.38	0.13	0.32	1.61	1.27	0.67
Voconia dolichocephala	♂	AMNH_PBI 00168747	7.11	1.31	0.83	0.45	0.52	0.30	0.25	0.10	0.27	1.09	1.09	0.32
	♂	AMNH_PBI 00168745	7.54	1.17	0.80	0.39	0.46	0.29	0.25	0.13	0.31	1.50	1.07	0.39
	♀	AMNH_PBI 00170709	8.77	1.39	0.96	0.43	0.58	0.32	0.30	0.11	0.36	1.42	1.15	0.39
	♀	AMNH_PBI 00168748	9.01	1.44	0.93	0.49	0.49	0.37	0.26	0.13	0.35	1.62	1.29	0.38
Voconia fasciata	♂	AMNH_PBI 00127097	8.69	1.25	1.18	0.39	0.40	0.49	0.33	0.16	0.34	1.55	1.03	?
Voconia grandioculata	♂	AMNH_PBI 00168749	9.16	1.30	1.37	0.39	0.40	0.43	0.43	0.20	0.35	1.91	1.06	0.37
	♂	AMNH_PBI 00213934	9.67	1.34	1.31	0.35	0.44	0.43	0.42	0.22	0.38	2.15	1.10	0.45
Voconia hemera	♂	UCR_ENT 00073812	9.16	1.12	0.88	0.34	0.37	0.35	0.25	0.13	?	1.32	1.08	0.46
	♂	UCR_ENT 00073813	9.31	1.40	1.11	0.44	0.47	0.43	0.37	0.13	0.35	1.30	1.06	0.53
Voconia isosceles	♂	UCR_ENT 00073814	8.81	1.08	0.85	0.34	0.35	0.46	0.33	0.10	0.24	1.17	1.11	0.66

Table 1 (continued). Measurements (in mm) of Pseudocetherinae.

Species	Sex	USI or Averages	Total length clypeus to abdomen	Head: Length clypeus to neck	Head: Width across eyes	Anteocular to maxillary plates	Postocular	Synthlipsis	Eye Width	Ocellus length	Scape length	Pedicel length	Labium length: Segment I	Labium length: Segment II dorsal surface
Voconia laosensis	♂	UCR_ENT 00001552	9.21	1.38	1.14	0.42	0.40	0.43	0.35	0.14	0.37	1.33	1.04	0.57
Voconia lasiosoma	♂	UCR_ENT 00127826	9.37	1.38	1.03	0.40	0.42	0.36	0.33	0.11	0.32	1.00	1.16	0.54
Voconia lirophleps	♂	AMNH_PBI 00170704	8.94	1.34	1.18	0.42	0.43	0.38	0.39	0.15	0.33	1.32	1.18	0.62
Voconia loki	♂	UCR_ENT 52216	8.29	1.29	1.06	0.39	0.40	0.31	0.38	0.12	0.30	0.94	1.10	0.52
Voconia mexicana	♂	**Mean** (N = 3)	10.63	1.45	1.24	0.50	0.48	0.44	0.39	0.17	0.38	1.94	0.99	0.43
		Min.	10.34	1.28	1.05	0.45	0.44	0.39	0.33	0.14	0.36	1.90	0.77	0.31
		Max.	10.89	1.55	1.35	0.57	0.54	0.48	0.42	0.21	0.39	1.98	1.22	0.55
		Range	0.55	0.27	0.30	0.12	0.09	0.09	0.10	0.07	0.03	0.08	0.46	0.24
	♀	AMNH_PBI 00170701	12.19	1.51	1.34	0.62	0.65	0.51	0.35	0.19	0.43	2.18	1.11	0.46
Voconia minima	♂	UCR_ENT 00073811	8.51	1.40	1.02	0.40	0.48	0.36	0.33	0.13	?	1.20	0.94	0.46
Voconia motoensis	♀	UCR_ENT 00070525	11.59	1.43	1.24	0.36	0.47	0.43	0.40	0.13	0.39	1.85	0.97	0.72
Voconia nyx	♂	AMNH_PBI 00170705	10.04	1.45	1.16	0.46	0.45	0.42	0.34	0.16	0.44	1.35	1.11	0.65
Voconia ornata	♂	AMNH_PBI 00213933	8.04	1.23	0.94	0.41	0.42	0.39	0.26	0.15	0.31	1.34	1.00	0.51
	♂	AMNH_PBI 00170696	8.69	1.28	0.98	0.42	0.46	0.44	0.28	0.15	0.38	1.27	1.12	0.54
	♀	**Mean** (N = 3)	8.15	1.16	0.87	0.36	0.42	0.40	0.23	0.12	0.31	1.48	1.00	0.47
		Min.	7.80	0.93	0.72	0.31	0.33	0.31	0.19	0.11	0.30	1.26	0.95	0.46
		Max.	8.51	1.29	0.96	0.40	0.48	0.45	0.26	0.13	0.33	1.75	1.05	0.48
Voconia pallidipes	♂	**Mean** (N = 3)	10.85	1.69	1.37	0.58	0.60	0.56	0.40	0.18	0.39	2.06	1.26	0.53
		Min.	10.52	1.67	1.33	0.56	0.59	0.55	0.38	0.17	0.36	1.92	1.24	0.50
		Max.	11.32	1.73	1.42	0.60	0.61	0.57	0.42	0.19	0.42	2.20	1.27	0.55
		Range	0.80	0.05	0.08	0.04	0.02	0.02	0.04	0.02	0.06	0.28	0.03	0.05
	♀	AMNH_PBI 00170708	10.72	1.51	1.18	0.53	0.53	0.54	0.30	0.13	0.32	1.80	1.19	0.47
Voconia schoutedeni	♂	UCR_ENT 00070524	6.75	1.20	0.91	0.62	0.31	0.43	0.26	0.05	0.23	0.59	?	?
Voconia smithae	♂	UCR_ENT 00127891	9.76	1.50	1.14	0.53	0.51	0.45	0.33	0.13	0.30	1.67	?	?
	♂	AMNH_PBI 00213936	9.74	1.33	1.11	0.56	0.42	0.47	0.30	0.12	0.31	1.57	?	?

Table 1 (continued). Measurements (in mm) of Pseudocetherinae.

Species	Sex	USI or Averages	Total length clypeus to abdomen	Head		Anteocular to maxillary plates	Postocular	Synthlipsis	Eye Width	Ocellus length	Scape length	Pedicel length	Labium length	
				Length clypeus to neck	Width across eyes								Segment I	Segment II dorsal surface
Voconia tridens	♂	AMNH_PBI 00170712	7.96	1.25	0.97	0.55	0.35	0.45	0.28	0.13	0.26	0.90	?	?
Voconia trinidadensis	♀	AMNH_PBI 00170700	10.08	1.48	1.09	0.53	0.50	0.44	0.32	0.15	0.39	1.42	1.12	0.68
Voconia tuberculata	♂	**Mean** (N = 3)	8.56	1.39	0.98	0.47	0.52	0.35	0.29	0.15	0.36	1.63	1.24	0.36
		Min.	7.93	1.33	0.87	0.41	0.49	0.33	0.24	0.15	0.31	1.43	1.20	0.33
		Max.	8.86	1.42	1.04	0.49	0.56	0.38	0.33	0.16	0.40	1.80	1.28	0.40
		Range	0.93	0.09	0.17	0.08	0.07	0.04	0.09	0.01	0.09	0.37	0.09	0.08
	♀	AMNH_PBI 00168743	8.81	1.33	0.90	0.46	0.50	0.38	0.27	0.12	0.38	1.50	1.13	0.36
	♀	AMNH_PBI 00168744	8.44	1.33	0.92	0.43	0.51	0.34	0.27	0.15	0.29	1.42	1.14	0.35
	?	AMNH_PBI 00168741	8.64	1.38	0.97	0.46	0.51	0.38	0.30	0.17	0.36	2.12	1.21	0.43
Voconia typica	♂	UCR_ENT 00073815	12.39	2.13	1.28	0.78	0.78	0.38	0.44	0.16	0.57	2.37	2.01	0.76
Voconia vittata	♂	AMNH_PBI 00088406	7.15	1.07	0.99	0.28	0.38	0.40	0.28	0.11	?	?	0.83	0.30
Voconia tuberculata	♂	**Mean** (N = 3)	8.56	1.39	0.98	0.47	0.52	0.35	0.29	0.15	0.36	1.63	1.24	0.36
		Min.	7.93	1.33	0.87	0.41	0.49	0.33	0.24	0.15	0.31	1.43	1.20	0.33
		Max.	8.86	1.42	1.04	0.49	0.56	0.38	0.33	0.16	0.40	1.80	1.28	0.40
		Range	0.93	0.09	0.17	0.08	0.07	0.04	0.09	0.01	0.09	0.37	0.09	0.08
	♀	AMNH_PBI 00168743	8.81	1.33	0.90	0.46	0.50	0.38	0.27	0.12	0.38	1.50	1.13	0.36
	♀	AMNH_PBI 00168744	8.44	1.33	0.92	0.43	0.51	0.34	0.27	0.15	0.29	1.42	1.14	0.35
	?	AMNH_PBI 00168741	8.64	1.38	0.97	0.46	0.51	0.38	0.30	0.17	0.36	2.12	1.21	0.43
Voconia typica	♂	UCR_ENT 00073815	12.39	2.13	1.28	0.78	0.78	0.38	0.44	0.16	0.57	2.37	2.01	0.76
Voconia vittata	♂	AMNH_PBI 00088406	7.15	1.07	0.99	0.28	0.38	0.40	0.28	0.11	?	?	0.83	0.30
Voconia wegneri	♂	RMNH.INS1091587	9.08	1.55	1.05	?	0.50	0.39	0.34	0.06	0.29	1.11	1.61	0.37

Gerbelius specimens deposited in various natural history collections has not been comprehensive. We therefore refrain from describing new species of *Gerbelius* as part of the present study and only provide a redescription of the genus. Data interpreted from labels (e.g., interpretation of coordinates or foreign text) in the material citations are distinguished with square brackets and verbatim citations (e.g., archaic geographic names) are encased in double quotation marks.

Cladistic analysis

Forty taxa comprising 33 ingroup species and seven outgroup species were analyzed (Figs 1–2). Outgroup selection was informed by the molecular phylogenies presented in Hwang & Weirauch (2012) and included two *Reduvius* clade taxa (*Reduvius personatus* (Linnaeus, 1758) and *Leogorrus* sp. voucher UCR_ENT 00128936), as well as species representing more distantly related clades of Reduviinae (*Microlestria* clade: *Microlestria* sp. voucher UCR_ENT 00128936; *Nalata* clade: *Nalata* nr. *spinicollis* Champion, 1899 voucher UCR_ENT 00052188; *Velitra* clade: *Velitra rubropicta* (Amyot & Serville, 1843) voucher UCR_ENT 00128938; *Acanthaspis* clade: *Acanthaspis* sp. voucher UCR_ENT 00128937; and *Chryxus tomentosus* Champion, 1898) that based on recent molecular analyses (Knyshov *et al*., unpubl. data) may be closely related to the *Reduvius* clade.

The descriptive matrix was used as the framework for this analysis by first removing non-informative (autapomorphic) characters. The 77 morphologically discrete characters (29 binary, 48 non-additive [unordered] multistate) used in the analysis are listed in the results. Characters are from the head (39), thorax (12), hemelytron (6), legs (6), abdomen (2), and male genitalia (12). We selected nine characters that rely on color patterns that are not highly variable within species given our specimen sampling. Inapplicable characters were treated as missing data and intraspecific variation coded as polymorphic. Gil-Santana *et al.* (2007) was used to code *C. tomentosus*, and male genitalic characters for *Reduvius personatus* are based on Weirauch *et al.* (2015). Since male genitalia across Reduviidae are not well-documented (Forero & Weirauch 2012), the pygophore and phallus dissections of the remaining outgroup taxa are made available. Characters and character states are indicated in the image plates (e.g., 2-0 in Fig. 3 refers to character 2 and state 0 in the results). The character matrix is provided as a text file in Supp. file 2.

The equal weighting (EW) analysis was conducted in TNT ver. 1.5 (Goloboff & Catalano 2016) using New Technology Search with the following parameters: find minimum length 100 times; ratchet (Nixon 1999) with default settings and 200 iterations; tree-drifting with default settings and 200 cycles; tree fusing with default settings. Clade support was evaluated using jackknife with default settings and 200 replicates. Tree length (L), consistency index (CI), and retention index (RI) were also calculated in TNT. The trees were then imported into WinClada ver. 1.00.08 (Nixon 2002) to estimate the strict consensus tree (Fig. 1).

Implied weighting (IW) (Goloboff 1993) analyses were performed in TNT under the same New Technology Search parameters as mentioned above. Several concavity values, which downweigh homoplasious characters, were explored to compare tree length and tree topology under the different weighting schemes: K = 3, K = 6, K = 9, K = 12 (Fig. 2). The lower values penalize homoplasy more strongly, though a value of K = 12 is still relatively strong considering that a value of K = 20 weighs homoplasies "very far from mild" in certain large datasets (Goloboff *et al*. 2008). The matrix was resampled with symmetric resampling (Goloboff *et al.* 2003) under default settings and 200 replicates. The IW tree provided greater resolution for our analysis than the EW tree, with the K = 12 analysis having the best fit. We therefore used the most parsimonious tree derived from the K = 12 analysis to document and discuss character transformations. WinClada was used to illustrate unambiguous changes and treated any additional step as homoplastic (Fig. 2). To avoid local optima, we ran IW analyses with

several random seeds (1, 10, 123, 1234, 12345) and maintained the above-mentioned settings with a concavity of K = 9.

Results

Cladistic analysis

The EW analysis resulted in eight most parsimonious trees (length = 468; CI = 0.353, RI = 0.625). The strict consensus tree collapsed 12 nodes (Fig. 1). The IW analyses with four different concavities recovered one parsimonious tree each, all with the same topology. Increasing the K-values, which decreases the penalty against homoplasious characters, improved the best score and resulted in higher CI and RI values: K = 3 resulted in best score = 33.53464, CI = 0.348, RI = 0.618; K = 6 resulted in best score = 24.58040, CI = 0.349, RI= 0.619; K = 9 resulted in best score = 19.55168, CI = 0.353, RI = 0.625; K = 12 resulted in best score = 16.26989, CI = 0.353, RI = 0.625. Characters and character optimizations are described

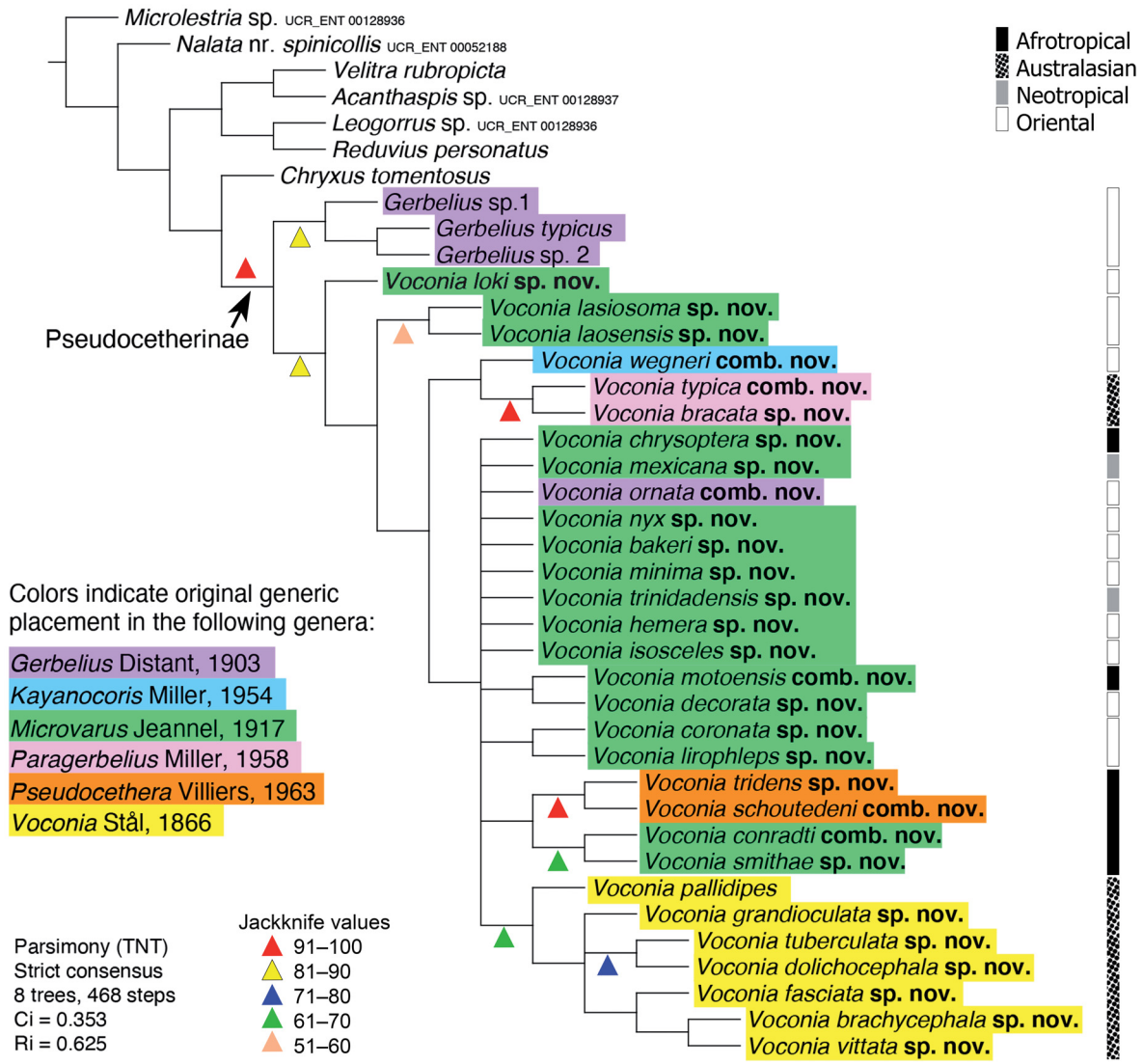

Fig. 1. Strict consensus tree resulting from equal weighting analysis. Jackknife values over 51 are reported for tree one of eight.

and discussed in the section below using the most parsimonious tree derived from the K = 12 IW analysis. Exploring different random seeds for the IW analyses with K = 9 did not result in different tree statistics (best score = 19.55168; CI = 0.353; RI = 0.625) and the topology remained the same.

Our results (Figs 1–2) corroborate prior molecular and morphological evidence that the expanded Pseudocetherinae (i.e., *Pseudocethera* plus five genera currently classified as Reduviinae) are a well-supported (resampling values of ≥ 99) clade with part of *Gerbelius* forming the sister taxon to all other Pseudocetherinae (Weirauch 2008; Hwang & Weirauch 2012; Knyshov *et al*., unpubl. data). We therefore formally transfer *Gerbelius*, *Kayanocoris*, *Microvarus*, *Paragerbelius*, and *Voconia* from

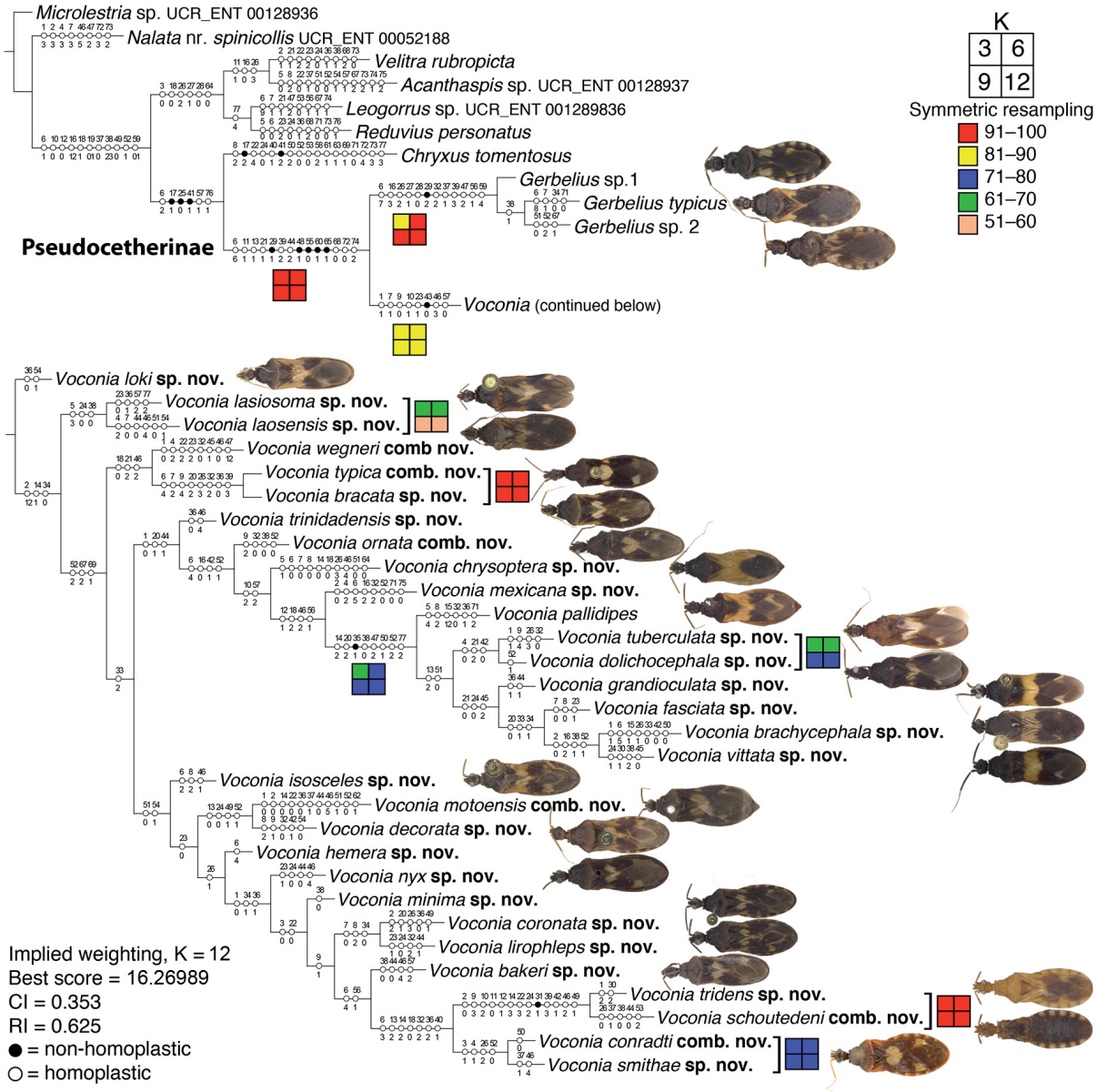

Fig. 2. Tree resulting from implied weighting analysis using K = 12 with characters unambiguously optimized. Symmetric resampling values over 51 are represented for trees obtained with K = 3, K = 6, K = 9, and K = 12 analyses. Characters and character states are described in pp. 11–22. Specimens not to scale.

Reduviinae to Pseudocetherinae in the Taxonomy section below and provide a revised diagnosis for Pseudocetherinae. *Gerbelius typicus* and two undescribed species of *Gerbelius* form a well-supported clade, but *G. ornatus* is nested among species that would be referred to as *Microvarus* under the generic concepts prior to this work. *Gerbelius ornatus* is therefore removed from *Gerbelius*. Within the non-*Gerbelius* pseudocetherine clade, *Pseudocethera* and *Paragerbelius* are highly supported (resampling values of ≥ 99) monophyletic groups, and Australasian species that would be referred to as *Voconia* under the current generic concept (Fig. 1, yellow highlight) form a well-supported (resampling values of 70–75) clade. However, *Microvarus*, as currently diagnosed, is paraphyletic in our analyses. This situation is complicated by the fact that we are here describing 23 new species of Pseudocetherinae, most of which would be classified as *Microvarus* under traditional diagnoses (Fig. 1, green highlight), but we are reluctant to describe new species in a paraphyletic grade. In addition, while we recovered two small, well-supported clades among these new species (*V. laosensis* sp. nov. + *V. lasiosoma* sp. nov. from the Oriental region and *V. conradti* + *V. smithae* sp. nov. from the Afrotropical region), most relationships among non-*Gerbelius* Pseudocetherinae are poorly supported. We therefore decided to synonymize *Microvarus*, *Kayanocoris*, *Paragerbelius*, and *Pseudocethera* under *Voconia*, rather than preserving these generic concepts and describing several small or monotypic new genera that would be difficult to diagnose.

While our phylogenetic hypothesis may not be robust enough to meaningfully infer the historical biogeography of Pseudocetherinae, it is worth pointing out that with the expansion of Pseudocetherinae through the new species and taxa treated in new combinations, this subfamily is now known from the Afrotropical, Australasian, Oriental and Neotropical regions.

Description and documentation of morphological characters with comments on character optimizations (Figs 3–15)

1. **Head, postocular region, coloration medially in dorsal view**: uniform (0), with dark patches adjacent to ocellar margin (1), with red patches adjacent to ocellar margin (2), with dark medial stripe (3). *Voconia tridens* sp. nov. has red patches adjacent to the ocellar margin, while several other pseudocetherines have dark, blackish markings. Most, however, are uniformly colored.

2. **Head, postocular region, coloration laterally in dorsal view**: uniform (0), with paired pale patches adjacent to lateral ocellar margin (Fig. 3C) (1), with a semicircular pale stripe around both ocelli (Fig. 3B) (2), pale with lateral margins dark (3). Shows homoplasy; involves multiple losses or gains of the semicircular pale stripe and yellow patches adjacent to the ocelli within Pseudocetherinae.

3. **Labium, coloration**: as remainder of head (0), lighter than head (Fig. 3G) (1). The labium is lighter than the head in most pseudocetherines and is the same color as the head in two clades: (*V. tridens* sp. nov. + *V. schoutedeni*) and (*V. coronata* sp. nov. + (*V. lirophleps* sp. nov. + (*V. bakeri* sp. nov. + *V. minima* sp. nov.))).

4. **Scutellum, coloration**: uniform (Fig. 4B) (0), dark with contrasting yellow apical spine (Fig. 4A) (1), dark with brown apical spine (2), pale with dark apical spine and pale apex (3). The color of the scutellum varies by species.

5. **Clavus, coloration with hemelytron abducted**: uniformly dark (0), uniformly yellow (1), dark with distal yellow stripe (Fig. 4B) (2), dark with proximal and distal yellow stripes (3), yellow with small, dark medial spot (4). Most pseudocetherines have a distal yellow stripe on the clavus. Proximal and distal yellow stripes are a non-homoplastic synapomorphy for *V. lasiosoma* sp. nov. and *V. laosensis* sp. nov. Uniformly yellow clavi are present in *V. tridens* sp. nov. and *V. chrysoptera* sp. nov. The small, dark medial spot is present in *V. pallidipes*.

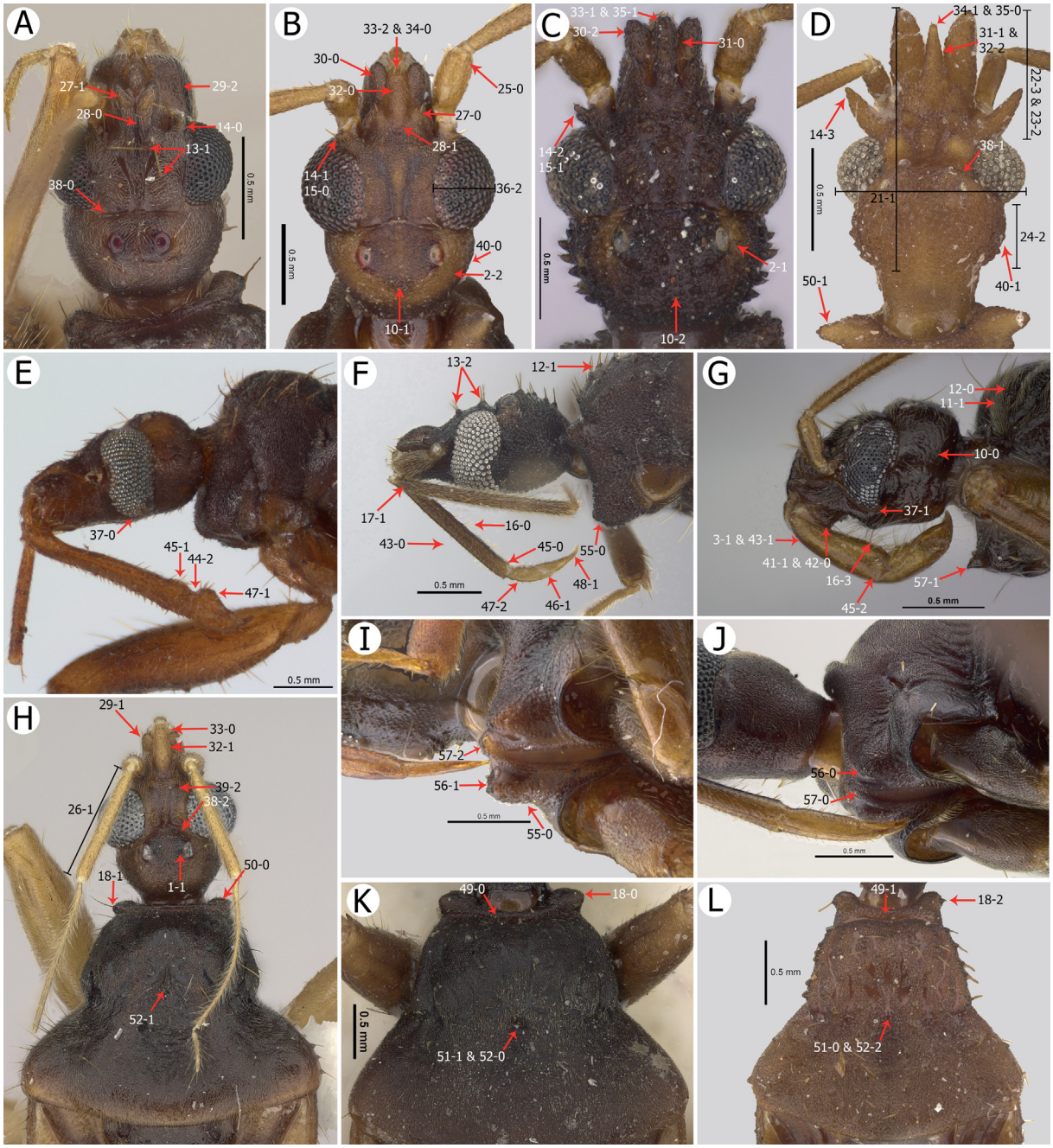

Fig. 3. Morphological characters. **A–D**. Head in dorsal view. **A**. *Gerbelius* nr. *confluens*. **B**. *Voconia decorata* sp. nov. **C**. *Voconia pallidipes* Stål, 1866. **D**. *Voconia schoutedeni* (Villiers, 1964) comb. nov. **E–G**. Head in lateral view. **E**. *Voconia wegneri* (Miller, 1954) comb. nov. **F**. *Voconia dolichocephala* sp. nov. **G**. *Gerbelius typicus* Distant, 1903. **H**. *Voconia loki* sp. nov., head and pronotum in dorsal view. **I–J**. Prosternum in ventrolateral view. **I**. *Voconia mexicana* sp. nov. **J**. *Voconia bracata* sp. nov. **K–L**. Pronotum in dorsal view. **K**. *Voconia conradti* (Jeannel, 1917) comb. nov. **L**. *Voconia tuberculata* sp. nov.

6. **Corium, coloration pattern with hemelytron abducted**: uniformly yellow (0), dark with thick medial yellow stripe (1), proximal half mostly yellow, distal half brown with yellow spot at distal apex (2), dark with proximal, anteromedial, posteromedial, and distal yellow spots (3), dark with anteromedial, posteromedial, and distal yellow spots (Fig. 4C) (4), dark with anteromedial and posteromedial yellow spots (5), dark with anteroproximal yellow stripe and posteromedial and distal yellow spots (Fig. 4B) (6), dark with proximal, anteromedial, and distal yellow spots (7), proximal third yellow, yellow stripe along claval margin (Fig. 4A) (8), dark with posteromedial and distal yellow spots (9), uniformly dark (10), dark with proximal yellow spot and thick medial white stripe (11), dark with thick medial red stripe and red spot at distal apex (12). Corium coloration is highly variable; character state 3 is a non-homoplastic synapomorphy for *V. conradti* and *V. smithae* sp. nov. Character states 9-12 are observed in the outgroups.

7. **Membrane, coloration**: uniformly dark (Fig. 4A) (0), dark, pale V-shaped marking along R and M veins (1), dark, large pale patch between R and M veins (Fig. 4C) (2), dark with pale spotting (3). The pale V-shaped marking along the R and M veins is lost across *Voconia* several times, while a large pale spot between the R and M veins is a synapomorphy for *V. typica* and *V. bracata* sp. nov.

8. **Membranal veins, coloration**: as remainder of membrane (0), R and M veins proximally pale, remainder as membrane (Fig. 4A) (1), veins forming Cu-An_1 and M-Cu cells paler than remainder of membrane (Fig. 4B) (2). Contrasting light colored membranal veins are present in *Voconia decorata* sp. nov. + *Voconia isosceles* sp. nov., *V. coronata* sp. nov., *V. lirophleps* sp. nov., and *Voconia pallidipes*. The membranal veins of most species are proximally pale on the R and M veins. *Voconia chrysoptera* sp. nov. and *V. fasciata* sp. nov. have uniformly dark membranal veins.

9. **Abdomen, dorsal laterotergites, coloration**: uniform (0), dark with yellow spots on anterior margins (Fig. 4B) (1), dark with yellow spots on posterior margins (Fig. 4A) (2), yellow with dark spots posteriorly (Fig. 4D) (3), laterotergites I and II paler than the rest (Fig. 4C) (4). The clade comprising *V. tridens* sp. nov. and *V. schoutedeni* have yellow bodies, and accordingly yellow dorsal laterotergites with dark posterior spots. The remaining pseudocetherines have dark bodies, some with yellow spots on the anterior margin and others on the posterior margin of the dorsal laterotergites.

10. **Head and pronotum, surface**: smooth (0), finely granulose (Fig. 3B) (1), coarsely granulose (Fig. 3C) (2), tuberculate (3). Species of *Gerbelius* have a smooth to corrugated head surface while all species of *Voconia* have granulations on the head and thorax. Course granulation is a synapomorphy for *V. tridens* sp. nov. + *V. schoutedeni* as well as the clade containing *V. chrysoptera* sp. nov., *V. mexicana* sp. nov., and the Australian species of *Voconia* containing *V. pallidipes* and kin.

11. **Head and pronotum, vestiture, pubescence**: glabrous (0), with pubescence (Fig. 3G) (1). Pseudocetherinae have a pubescent head and pronotum with varying densities. The African clade containing *V. tridens* sp. nov. and *V. schoutedeni* are less densely pubescent.

12. **Head and pronotum, vestiture, setal base of macrosetae**: macrosetae without tubercles (Fig. 3G) (0), setigerous tubercles (Fig. 3F) (1). Macrosetae are interspersed among the pubescence in Pseudocetherinae. These macrosetae may be on tubercles as in *V. tridens* sp. nov. + *V. schoutedeni* and the clade containing *V. mexicana* sp. nov. and the Australian species of *Voconia* (*V. pallidipes* and kin).

13. **Head, interocular region, setation**: without prominent, paired macrosetae (0), with two prominent pairs of macrosetae paramedially (Fig. 3A) (1), with two prominent pairs of setigerous tubercles

paramedially (Fig. 3F) (2), with stout setigerous tubercles medially (3). This character is highly homoplastic. The interocular region usually features two paired macrosetae (except in *Voconia motoensis*, *V. decorata* sp. nov., *V. mexicana* sp. nov., *V. pallidipes*, *V. wegneri* comb. nov., and *V. bracata* sp. nov.). A tuberculate setal base is a synapomorphy for *V. tridens* sp. nov., *V. schoutedeni*, and *V. smithae* sp. nov. Both medial and paramedial setigerous tubercles are found in the Australian *V. brachycephala* sp. nov., *V. fasciata* sp. nov., *V. grandioculata* sp. nov., and *V. vittata* sp. nov.

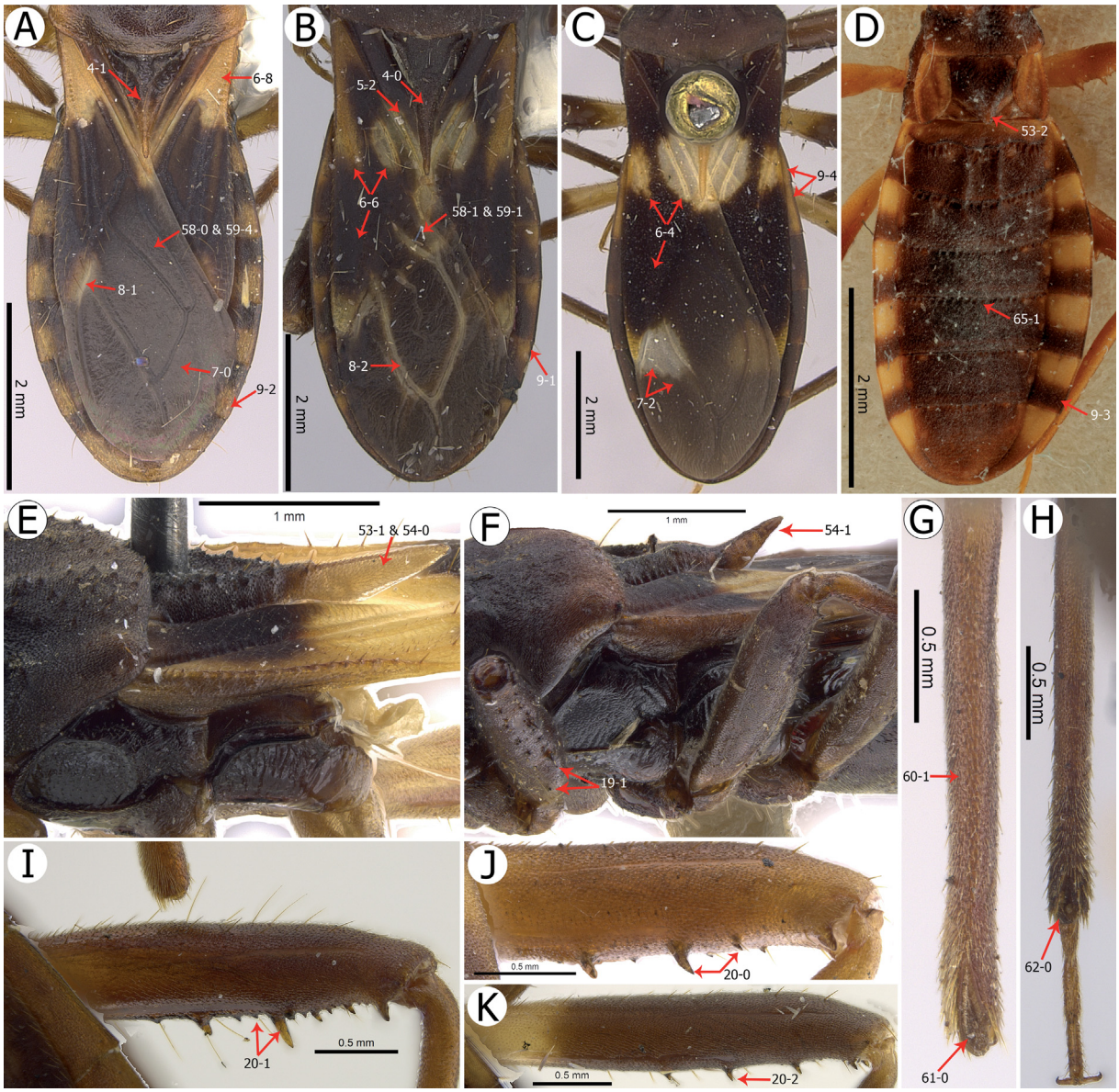

Fig. 4. Morphological characters. **A–D**. Scutellum and hemelytron, dorsal view. **A**. *Gerbelius typicus* Distant, 1903. **B**. *Voconia lirophleps* sp. nov. **C**. *Voconia bracata* sp. nov. **D**. *Voconia schoutedeni* (Villiers, 1964) comb. nov. **E**. *Voconia grandioculata* sp. nov., thorax, lateral view. **F–H**. *Voconia nyx* sp. nov. **F**. Thorax, lateral view. **G**. Fore tibia, ventral view. **H**. Mid tibia and tarsus, ventral view. **I–K**. Hind femur, posterior view. **I**. *Voconia mexicana* sp. nov. **J**. *Voconia decorata* sp. nov. **K**. *Voconia bracata* sp. nov.

14. **Head, antennifer, armature basolaterally**: without lateral protuberance (Fig. 3A) (0), with short lateral setigerous tubercle (Fig. 3B) (1), with long lateral setigerous tubercle (Fig. 3C) (2), with long lateral spine (Fig. 3D) (3). Species of *Gerbelius*, *V. chrysoptera* sp. nov., *V. loki* sp. nov., and *V. motoensis* comb. nov. have a typical, unarmed antennifer. However, in the remaining species of *Voconia* the antennifer has either a laterally projecting setigerous tubercle or a long spine. The long spine is a synapomorphy of *V. tridens* sp. nov., *V. schoutedeni* comb. nov., *V. ifana* comb. nov. and *V. monodi* comb. nov. Although *V. ifana* comb. nov. and *V. monodi* comb. nov. were not included in the phylogenetic analysis, the laterally projecting spine on the antennifer is present in descriptions and illustrations (Villers 1963a, 1963b).

15. **Head, antennifer, lateral setigerous tubercle quantity**: one (Fig. 3B) (0), two (Fig. 3C) (1), three (2). Of those species with a lateral setigerous tubercle on the antennifer, *V. brachycephala* sp. nov., *V. mexicana* sp. nov., and *V. pallidipes* have more than one setigerous tubercle projecting from the antennifer. These tubercles are adjacent to one another.

16. **Labium, labial segment I, morphologically ventral surface, vestiture**: with sparse, short setation (Figs 3F, 6E) (0), with dense, short setation (1), with sparse, long setation (2), with dense, long setation (Fig. 3G) (3), with sparse setigerous tubercles (4). Dense, long setation on the morphologically ventral surface of the labium is a synapomorphy for *Gerbelius*. In *Voconia* the setation is short (Fig. 6E) with varying densities, except in *V. mexicana* sp. nov. where the setation is longer but is sparse, unlike in *Gerbelius*.

17. **Antenna, scape and pedicel, vestiture**: with sparse, long macrosetae (0), with dense, short macrosetae (Fig. 3F) (1), with dense, long macrosetae (2). Dense, short macrosetae on the scape and pedicel is a synapomorphy for Pseudocetherinae.

18. **Pronotal collar, anterolateral angles, setal base**: without macrosetae or setigerous tubercles (Fig. 3K) (0), with macrosetae (Fig. 3H) (1), with setigerous tubercles (Fig. 3L) (2). The anterolateral angles of the pronotal collar in most Pseudocetherinae have macrosetae and are absent in the African clade (*V. schoutedeni* + *V. tridens* sp. nov.) + (*V. smithae* sp. nov. + *V. conradti*)), *V. chrysoptera* sp. nov., and the clade including *V. wegneri*, *V. typica*, and *V. bracata* sp. nov. Setigerous tubercles on the anterolateral angles is a synapomorphy of *V. mexicana* sp. nov. and the Australian clade (*V. pallidipes* and kin).

19. **Legs, all femora, armature**: unarmed (0), ventral surface with anterior and posterior rows of spine-like protuberances with macrosetae at base of protuberance (Fig. 4F) (1), setigerous tubercles (2). Pseudocetherinae have two rows of spine-like protuberances on the ventral surface of all femora (Fig. 4F) with macrosetae at the base of the protuberance (Fig. 4I).

20. **Legs, mid and hind femora, posterior row of spine-like protuberances**: with three large spines on distal half and three or fewer small spines (Fig. 4J) (0), with three large spines on distal half and many small spines (Fig. 4I) (1), with four or more large spines on distal half (Fig. 4K) (2). The number of spines on the femur is species-specific, though Pseudocetherinae typically have three large spines on the distal half of the femur with a variable number of small spines interspersed. In several species, namely *V. bracata* + *V. typica*, *V. dolichocephala* + *V. tuberculata*, *V. grandiocula*, and *V. pallidipes*, the distal half of the femur has four or more large spines.

21. **Head, shape in dorsal view**: globose, about as long as wide (0), elongate, less than 1.5 times as long as wide (Fig. 3D) (1), distinctly elongate, at least 1.5 times as long as wide (2). An elongate head (less than 1.5 times as long as wide) is a homoplastic synapomorphy for Pseudocetherinae. There is intraspecific variation in the head shape of *V. conradti* from globose to elongate. A globose head

shape is a homoplastic synapomorphy for the clade containing *V. grandioculata* sp. nov., *V. fasciata* sp. nov., *V. brachycephala* sp. nov., and *V. vittata* sp. nov. A distinctly elongate head (at least 1.5 times as long as wide) is a homoplastic synapomorphy for the clade containing *V. wegneri*, *V. typica*, and *V. bracata* sp. nov. as well as the clade containing *V. tuberculata* sp. nov. and *V. dolichocephala* sp. nov.

22. **Head, anteocular region, length relative to head**: about one quarter of head length (0), about one third of head length (1), about half of head length (2), two-fifths of head length (Fig. 3D) (3), less than a fifth of head length (4). The anteocular region is about one third the head length in most pseudocetherines but varies interspecifically. An anteocular region that is about two-fifths of the head length is a non-homoplastic synapomorphy for the clade containing *V. tridens* sp. nov. and *V. schoutedeni*.

23. **Head, anteocular region, length relative to postocular region**: shorter than postocular region (0), about as long as postocular region (1), longer than postocular region (Fig. 3D) (2). Anteocular length was recorded to the apex of the clypeus. An anteocular region that is shorter than the postocular region is synapomorphic for *Gerbelius*, though more sampling may challenge our analyses. An anteocular region that is longer than the postocular region is synapomorphic for *V. tridens* sp. nov. + *V. schoutedeni*.

24. **Head, postocular region, length relative to eye**: shorter than eye (0), about as long as eye (1), longer than eye (Fig. 3D) (2). A postocular region that is longer than the eye is synapomorphic for *Gerbelius*, *V. tuberculata* sp. nov. + *V. dolichocephala* sp. nov., *V. tridens* sp. nov. + *V. schoutedeni*, as well as *V. wegneri* + (*V. typica* + *V. bracata* sp. nov.). In *V. conradti* + *V. smithae* sp. nov. a postocular region that is about as long as the eye is a synapomorphy, and for *V. lasiosoma* sp. nov. + *V. laosensis* sp. nov. and *V. motoensis* + *V. decorata* sp. nov. the postocular region is shorter than the eye.

25. **Antenna, scape, length**: apex not reaching or slightly surpassing apex of head (Fig. 3B) (0), greatly surpassing apex of head (1). A relatively short scape is a synapomorphy for Pseudocetherinae.

26. **Antenna, pedicel, length**: 0.5–0.7 times the length of head width (0), 0.8–1.2 times the length of head width (Fig. 3H) (1), 1.3–1.7 times the length of head width (2), 1.8–2.2 times the length of head width (3). These values were separated as shorter than the width of head, roughly the width of head, longer than the width of head, and those with an unusually extra-long pedicel, namely *V. chrysoptera* sp. nov., *V. coronata* sp. nov., *V. typica* + *V. bracata* sp. nov., and *V. tuberculata* sp. nov. Pedicel length, however, varies interspecifically, with *V. schoutedeni* having the shortest pedicel at about 0.6 times the length of the head width.

27. **Mandibular plates, length in dorsal view**: short (barely surpassing antennifer apex) (Fig. 3B) (0), long (distinctly surpassing the antennifer apex) (Fig. 3A) (1). Short mandibular plates are the ancestral condition for Pseudocetherinae and are found in *Voconia*, while long mandibular plates are a synapomorphy for *Gerbelius*.

28. **Mandibular plates, shape in dorsal view**: basal halves adjacent (Fig. 3A) (0), not adjacent medially (Fig. 3B) (1). Non-adjacent mandibular plates are the ancestral condition and are found in *Voconia*, while mandibular plates that join posteromedially is a synapomorphy for *Gerbelius*.

29. **Maxillary plates, shape in dorsal view**: not elongate anteriorly (0), elongate anteriorly forming an ellipsoid projection (Fig. 3H) (1), enlarged laterally forming a flattened projection (Fig. 3A) (2). With this revision, elongate, ellipsoid maxillary plates were diagnostic for Pseudocetherinae (Villiers

1963a). Ellipsoid maxillary plates are diagnostic of *Voconia* and laterally enlarged maxillary plates are a synapomorphy for *Gerbelius*.

30. **Maxillary plates, apex in dorsal view**: directed straight (Fig. 3B) (0), convergent (1), divergent (Fig. 3C) (2). The direction of the maxillary plates converges in *V. vittata* sp. nov. and the clade containing *V. lirophleps* sp. nov., *V. bakeri* sp. nov., and *V. minima* sp. nov. The direction of the maxillary plates varies intraspecifically in *V. mexicana* sp. nov., *V. ornata*, and *V. dolichocephala* sp. nov. being either straight or diverging.

31. **Maxillary plates, position in dorsal view**: adjacent to clypeus (Fig. 3C) (0), not adjacent to clypeus (Fig. 3D) (1). Maxillary plates are typically adjacent to the clypeus in Pseudocetherinae except in the clade containing *V. tridens* sp. nov. and *V. schoutedeni*.

32. **Clypeus, width medially in dorsal view**: about as wide as maxillary plates (Fig. 3B) (0), wider than maxillary plates (Fig. 3H) (1), narrower than maxillary plates (Fig. 3D) (2). Clypeus width varies interspecifically with respect to the width of the maxillary plates. It may be more slender as in *V. schoutedeni* + *V. tridens* sp. nov., which are more of an extreme example and have an acuminate clypeus and thick maxillary plates. The width is taken from the midpoint of both structures for consistency.

33. **Clypeus, length in dorsal view**: surpassing apex of maxillary plates (Fig. 3H) (0), reaching apex of maxillary plates (Fig. 3C) (1), shorter than apex of maxillary plates (Fig. 3B) (2). Clypeus length varies interspecifically but is typically shorter than the ellipsoidal projecting maxillary plates in *Voconia*. The clypeus surpasses the maxillary plate apex in *V. brachycephala* sp. nov., *V. lasiosoma* sp. nov., *V. loki* sp. nov., and *V. wegneri*. A clypeal apex that reaches the apex of the maxillary plates is a homoplastic synapomorphy of *V. bracata* sp. nov. and *V. typica*.

34. **Clypeus, apex, size in dorsal view**: not narrowed (Fig. 3B) (0), narrowed (Fig. 3D) (1). The clypeus narrows in *V. loki* sp. nov. and three *Voconia* clades (*V. bakeri* + *V. minima* sp. nov., *V. nyx* sp. nov. + ((*V. tridens* sp. nov. + *V. schoutedeni*) + (*V. smithae* sp. nov. + *V. conradti*)), *V. fasciata* sp. nov. + (*V. brachycephala* sp. nov. + *V. vittata* sp. nov.)).

35. **Clypeus, apex, shape**: round (Fig. 3D) (0), bifid (Fig. 3C) (1). A bifid clypeus is a non-homoplastic synapomorphy of the Australian *Voconia* clade containing *V. pallidipes* and kin.

36. **Eyes, width in dorsal view**: wider than synthlipsis (0), about as wide as synthlipsis (1), narrower than synthlipsis (Fig. 3B) (2). Reconstructed as eyes narrower than synthlipsis in the most recent common ancestor of Pseudocetherinae with several transitions (Tab. S1).

37. **Eyes, position in lateral view**: reaching ventral head margin (Fig. 3E) (0), not reaching ventral head margin (Fig. 3G) (1). In *Gerbelius*, the eye in lateral view does not reach the ventral head margin, while in most species of *Voconia* the eye reaches the ventral head margin. Exceptions are the African species *V. motoensis*, *V. smithae* sp. nov., and *V. schoutedeni.*

38. **Head, transverse interocular sulcus, shape in dorsal view**: nearly straight (Fig. 3A) (0), curved and smoothly rounded anteriorly (Fig. 3D) (1), sharp triangular bend anteriorly (Fig. 3H) (2), square-bracket shape with opening anteriorly (e.g., *Acanthaspis* sp. voucher UCR_ENT 00128937) (3). Our analyses recovered multiple transitions between the different shapes of the transverse sulcus. Within Pseudocetherinae, a nearly straight transverse interocular sulcus is a synapomorphy for *V. lasiosoma* sp. nov. + *V. laosensis* sp. nov. It was also reconstructed for the most recent common ancestor of the Australian clade, though the sulcus in *V. brachycephala* sp. nov. is rounded and

triangular in *V. vittata* sp. nov. A triangular sulcus is a synapomorphy for *V. typica* + *V. bracata* sp. nov., *V. motoensis* + *V. decorata* sp. nov., as well as for *V. coronata* sp. nov. + *V. lirophleps* sp. nov.

39. **Head, interocular glabrous markings, shape**: single medial line (0), two parallel lines joined paramedially at interocular sulcus (1), two parallel lines, anterolaterally curved, joined paramedially at interocular sulcus (Fig. 3H) (2), V-shaped, joined medially at interocular sulcus (3). Pseudocetherinae have two longitudinal glabrous lines in the interocular region of the head. In most *Voconia* the two lines are parallel and curve anterolaterally. In *Gerbelius*, *V. tridens* sp. nov. + *V. schoutedeni*, *V. typica* + *V. bracata* sp. nov., and *V. dolichochephala* sp. nov. + *V. tuberculata* sp. nov., the glabrous lines are perpendicular and meet at the interocular sulcus.

40. **Head, postocular region, shape in dorsal view**: gently rounded (Fig. 3B) (0), subrectangular (Fig. 3D) (1). The postocular region of most pseudocetherines is gently rounded, except for in the African clade ((*V. tridens* sp. nov. + *V. schoutedeni*) + (*V. smithae* sp. nov. + *V. conradti*)), where it is subrectangularly rounded.

41. **Buccula, shape**: flat (0), with ventrolateral swelling (Fig. 3G) (1), with ventral spine (2). In Pseudocetherinae the buccula is slightly swollen ventrolaterally.

42. **Buccula, anterolateral swelling, shape in lateral view**: flat buccular margin (Fig. 3G) (0), with protrusion surpassing buccular margin (1). The swelling of the buccula is either flat apically or has a protruding bump that overlaps with the labium in lateral view. This protrusion may be a small, rounded bump as in *V. decorata* sp. nov. In *V. tridens* sp. nov. and *V. schoutedeni* this protrusion is large and spine-like with small setigerous tubercles along the margin. In *V. chrysoptera* sp. nov., *V. fasciata* sp. nov., *V. grandioculata* sp. nov., *V. mexicana* sp. nov., and *V. ornata* the protrusion is rounded with setigerous tubercles along the apical margin. *V. pallidipes* has large protruding setigerous tubercles.

43. **Labium, width**: gracile (Fig. 3F) (0), stout (Fig. 3G) (1). A gracile labium was considered diagnostic for Pseudocetherinae (Villiers 1963a). Under the new classification that defines the subfamily more broadly, a gracile labium is a synapomorphy for *Voconia* and a stout labium is diagnostic for *Gerbelius*.

44. **Labium, labial segment I, length in lateral view**: not reaching posteroventral eye margin (0), reaching posteroventral eye margin (1), surpassing posteroventral eye margin (Fig. 3E) (2). The length of labial segment I varies interspecifically, but it is always the longest labial segment in Pseudocetherinae.

45. **Labium, labial segment I, shape in lateral view**: straight (Fig. 3F) (0), swollen subapically on morphologically ventral surface (Fig. 3E) (1), gradually widened apically (Fig. 3G) (2). Labial segment I is typically straight in *Voconia*. In *V. grandioculata* sp. nov., *V. fasciata* sp. nov., *V. brachycephala* sp. nov., and species of *Gerbelius* the labium gradually widens apically. In *V. wegneri* the morphologically ventral surface is swollen subapically.

46. **Labium, morphologically dorsal surface of labial segment II, length relative to segment I**: 0.2 times the length of segment I (0), 0.3 times the length of segment I (Fig. 3F) (1), 0.4 times the length of segment I (2), 0.5 times the length of segment I (3), 0.6 times the length of segment I (4), 0.7 times the length of segment I (5), 0.8 times the length of segment I (6), 0.9 times the length of segment I (7), longer than segment I (8). The length of segment I was recorded from the proximal and distal midpoints, while the length of segment II reported here is recorded from the

morphologically dorsal surface. Measurements were rounded up for values with 0.05 and up. The morphologically ventral surface of segment II is shorter and reported in Supp. file 1. The length of the morphologically dorsal surface of segment II varies interspecifically. However, the length of segment II among members of *Gerbelius* ranges from 0.8–0.9 times the length of segment I and ranges between 0.2–0.7 times the length of segment I in *Voconia*, with *V. wegneri* having the largest disparity between both segments (0.2 times the length of segment I) and *V. motoensis* having the smallest disparity between both segments (0.7 times the length of segment I).

47. **Labium, labial segment II, shape in lateral view**: nearly straight (0), swollen ventrobasally, narrowed apically (Fig. 3E) (1), morphologically dorsal surface convex (Fig. 3F) (2). While most *Voconia* possess a nearly straight labial segment II, the ventrobasal swelling of segment II is uniquely diagnostic for *V. wegneri.* The morphologically dorsal surface of segment II is convex in *V. wegneri*, the Australian clade containing *V. pallidipes* and kin, and *Gerbelius*.

48. **Labium, labial segment III, shape**: gradually narrowing, straight (0), drawn into a bent, slender apex (Fig. 3E–G) (1). Labial segment III is drawn into a bent, slender apex in all Pseudocetherinae, even in *V. wegneri* which has an unusually short labial segment III.

49. **Pronotal collar, length medially in dorsal view**: narrow (Fig. 3K) (0), wide (Fig. 3L) (1). Most pseudocetherines have a narrow pronotal collar, with the exception of *V. motoensis*, *V. decorata* sp. nov., *V. coronata* sp. nov., *V. tuberculata* sp. nov., *V. dolichocephala* sp. nov., *V. fasciata* sp. nov., and *V. vittata* sp. nov., which have a wide pronotal collar.

50. **Pronotal collar, anterolateral angles, shape**: projecting forward (Fig. 3H) (0), flared laterally (Fig. 3D) (1), without projection (2). The anterolateral angles of the pronotal collar in Pseudocetherinae generally project forward, but the shape varies interspecifically. Laterally flared anterolateral angles are most prominently expressed in the clade containing *V. tridens* sp. nov. and *V. schoutedeni* sp. nov.

51. **Pronotum, median apodeme depression, depth**: shallow (Fig. 3L) (0), deep (Fig. 3K) (1). The depth of the pronotal apodeme depression varies. A shallow apodeme depression is a synapomorphy for part of the Australian clade ((*V. tuberculata* sp. nov. + *V. dolichocephala* sp. nov.) + (*V. grandioculata* sp. nov. + (*V. fasciata* sp. nov. + *V. brachycephala* sp. nov. + *V. vittata* sp. nov.))). A shallow apodeme is also present in *V. tridens* sp. nov. + *V. schoutedeni*, *V. decorata* sp. nov., and *V. isosceles* sp. nov. A deep apodeme depression is a synapomorphy for *V. conradti* + *V. smithae* sp. nov. as well as *V. wegneri* + (*V. typica* + *V. bracata* sp. nov.).

52. **Pronotum, median apodeme depression, shape**: circular (Fig. 3K) (0), elongated longitudinally (Fig. 3H) (1), elongated transversely (Fig. 3L) (2). A circular pronotal apodeme depression is present in *V. ornata*, *V. mexicana* sp. nov., and the African species *V. motoensis*, *V. conradti*, and *V. smithae* sp. nov. Longitudinally and transversely elongated apodemes are more common and vary intraspecifically.

53. **Scutellum, apical spine, length**: short (e.g., *Microlestria* sp.) (0), long (Fig. 4E) (1), reduced (Fig. 4D) (2). All macropterous morphs in Pseudocetherinae have a long scutellar spine, while micropterous individuals, such as those of *V. schoutedeni* sp. nov., have a reduced scutellar spine.

54. **Scutellum, apical spine, orientation in lateral view**: subhorizontal (Fig. 4E) (0), raised (Fig. 4F) (1). The orientation of the scutellar spine varies interspecifically, and intraspecifically in *V. mexicana* sp. nov. where the female has a raised scutellar spine but the scutellar spine is subhorizontal in the males.

55. **Prosternum, shape in lateral view**: drawn into anteriad-directed process (Figs 3F, I, 6D) (0), smoothly rounded (1). A prosternum that is drawn into an anteriad-directed process is a synapomorphy for Pseudocetherinae, corroborating previous hypotheses (Weirauch 2008; Weirauch *et al.* 2014).

56. **Prosternum, anteriad-directed process, shape in anterolateral view**: smoothly rounded, without paramedial lobes (Fig. 3J) (0), with paramedial lobes (Fig. 3I) (1). The *Gerbelius* clade, *V. bakeri* sp. nov., the African clade ((*V. conradti* + *V. smithae* sp. nov.) + (*V. tridens* sp. nov. + *V. schoutedeni*)), and the clade containing *V. mexicana* sp. nov. and Australian kin have protrusions on the prosternum that project past the margins of the stridulitrum.

57. **Stridulitrum, anterior margin, shape**: not elongated into protuberance (Fig. 3J) (0), projected into sharp spine (1), projected into small protuberance (Fig. 3I) (2). The stridulitrum of most *Voconia* is not elongated into a protuberance. In *Gerbelius*, *V. grandioculata* sp. nov., and *V. fasciata* sp. nov. the stridulitrum projects anteriorly into a sharp spine. The remaining Australian species in the clade with *V. chrysoptera* sp. nov. and *V. mexicana* sp. nov., along with *V. lasiosoma* sp. nov. and *V. bakeri* sp. nov., have a stridulitrum that protrudes into a small protuberance.

58. **Hemelytron, Cu-An$_1$ cell, relative length**: similar length as M-Cu cell (Fig. 4A) (0), shorter than M-Cu cell (Fig. 4B) (1), absent (2). The Cu-An$_1$ cell is similar in length to the M-Cu cell in *Gerbelius*. A short Cu-An$_1$ cell is a synapomorphy for *Voconia*.

59. **Hemelytron, Cu-An$_1$ cell, shape**: ovate (0), triangular (Fig. 4B) (1), square (2), wedge-shaped (3), slender and tapered apically (Fig. 4A) (4). A triangular Cu-An$_1$ cell is a synapomorphy for *Voconia* and a slender, apically tapered Cu-An$_1$ cell is a synapomorphy for *Gerbelius*.

60. **Legs, tibiae in cross section**: ovate (0), laterally compressed (Fig. 4G–H) (1). Laterally compressed tibiae are a synapomorphy for Pseudocetherinae.

61. **Fore leg, fossula spongiosa (male)**: present (Fig. 4G) (0), absent or vestigial (1). A fossula spongiosa is present on the fore legs of all pseudocetherine males.

62. **Mid leg, fossula spongiosa (male)**: present (Fig. 4H) (0), absent or vestigial (1). A fossula spongiosa is present on the mid legs of most pseudocetherine males, except that it is absent or vestigial in *V. motoensis*.

63. **Fore leg, fossula spongiosa (female)**: present (0), absent or vestigial (1). Due to the scarcity of females, there is a lot of missing data for females, but the fossula spongiosa may be present on the fore legs of all pseudocetherine females.

64. **Mid leg, fossula spongiosa (female)**: present (0), absent or vestigial (1). Due to the scarcity of females, there is a lot of missing data for females, but it appears that the fossula spongiosa is absent on the mid legs of pseudocetherine females, except in *V. chrysoptera* sp. nov. where it is present.

65. **Dorsal abdominal glands**: present (0), absent (Fig. 4D) (1). Dorsal abdominal glands are absent in Pseudocetherinae, corroborating previous hypotheses (Weirauch 2008; Weirauch *et al.* 2014).

66. **Pygophore, transverse bridge, posterior margin shape**: round (Fig. 13; *V. tuberculata* sp. nov.) (0), triangular (Fig. 13; *V. tridens* sp. nov.) (1). The posterior margin of the transverse bridge is round in most of the observed Pseudocetherinae, and triangular in *V. nyx* sp. nov., and the African species *V. tridens* sp. nov. and *V. conradti*.

67. **Pygophore, posterior region of ventral surface, shape in lateral view**: without swelling (Fig. 12; *V. laosensis* sp. nov.) (0), with slight swelling (Fig. 11; *V. conradti*) (1), with large swelling (Fig. 12; *V. mexicana* sp. nov.) (2). The swelling of the pygophore apex varies interspecifically.

68. **Pygophore, median apical process, shape in caudal view**: short spine (Fig. 13; *V. pallidipes*) (0), long spine (Fig. 15; *Nalata* nr. *spinicollis*) (1), short and wide (Fig. 15; *Velitra rubropicta*) (2). A short median apical process on the the pygophore is a synapomorphy for Pseudocetherinae.

69. **Pygophore, median apical process, direction in lateral view**: upright (Fig. 12; *V. laosensis* sp. nov.) (0), sharply bent posteriorly (Fig. 13; *V. pallidipes*) (1). *Gerbelius* sp. 2, *V. lasiosoma* sp. nov., and *V. laosensis* sp. nov. have an upright median apical process. A posteriorly bent median apical process appears to be a putative synapomorphy for most *Voconia* except *V. lasiosoma* sp. nov. and *V. laosensis* sp. nov., where it is upright.

70. **Dorsal pygophore margin, shape in lateral view**: flat (Fig. 11; *Gerbelius* sp. 2) (0), with protuberance (Fig. 11; *V. conradti*) (1). In *Voconia*, the pygophore margin posterior to the paramere socket is raised into a round protuberance.

71. **Posterior pygophore margin, position of macrosetae in caudal view**: on flat margin (Fig. 12; *V. mexicana* sp. nov.) (0), on protuberance (Fig. 11; *Gerbelius* sp. 2) (1), on decline (Fig. 15; *Acanthaspis* sp.) (2). Adjacent to the median apical process are clusters of macrosetae. Some are on a protuberance (e.g., *Gerbelius* sp. 2), a decline (e.g., *Nalata* nr. *spinicollis*), or this posterior margin may be flat (e.g., *V. mexicana* sp. nov.). With the amount of missing data, it appears that the shape of the posterior pygophore might vary interspecifically.

72. **Paramere, shape in dorsal view**: sinusoidal (Fig. 13; *V. pallidipes*) (0), round (Fig. 13; *V. tridens*) (1), hook-shaped (Fig. 15; *Acanthaspis* sp.) (2), sharp bend basally (Fig. 15; *Nalata* nr. *spinicollis*) (3), round with medial protuberance (4). The parameres of Pseudocetherinae are sinusoidal (Fig. 6G), except for *V. tridens* sp. nov., in which they are gently rounded.

73. **Paramere apex, shape**: tapered sharply (Fig. 13; *V. tuberculata* sp. nov.) (0), tapered into squarely rounded tip (Fig. 11; *G. typicus*) (1), expanded (Fig. 15; *Acanthaspis* sp.) (2), round, not sharply tapered or expanded (3). Most Pseudocetherinae have a squarely rounded paramere apex. *V. pallidipes* and *V. tuberculata* sp. nov. have sharply tapered apices, and the paramere apex of *V. grandioculata* sp. nov. does not taper, it is rounded.

74. **Endosoma, armature in lateral view**: without spicules (0), partially covered with spicules (1), almost entirely covered with spicules (Fig. 14; *V. typica*) (2). The endosoma of all Pseudocetherinae is largely covered with spicules.

75. **Dorsal phallothecal sclerites, apex, shape in dorsal view**: round (Fig. 14; *V. mexicana* sp. nov.) (0), tongue-shaped (Fig. 14; *V. lasiosoma* sp. nov.) (1), bifid (Fig. 14; *V. typica*) (2), serrated (Fig. 14; *V. tuberculata* sp. nov.) (3), absent or reduced (Fig. 16; *Microlestria* sp.) (4). Despite the amount of missing data, it appears that the shape of the dorsal phallothecal sclerite apex might vary interspecifically.

76. **Basal plate extension, length in relation to phallotheca**: short (0), long (Fig. 14; *V. mexicana* sp. nov.) (1). A long basal plate extension is a homoplastic synapomorphy of Pseudocetherinae.

77. **Basal plate extension, length**: 1.5–3.9 times as long as wide (0), 4.0–5.4 times as long as wide (Fig. 14; *V. mexicana* sp. nov.) (1), 5.5–6.4 times as long as wide (2), 6.5–8.0 times as long as wide (3), as long as 8.5 times the width (4). Width is recorded from the midpoint. The range for the length to width ratio of the basal plate extension within Pseudocetherinae is between 4.4 and 5.8, with *V. typica* as the exception having a ratio of 7.9. A basal plate extension that is 4.0–5.4 times as long as wide is a synapomorphy of *G. typicus* + *Gerbelius* sp. 2 as well as *V. lasiosoma* sp. nov. + *V. laosensis* sp. nov. A basal plate extension that is 5.5–6.4 times as long as wide is a synapomorphy of the Australian clade containing *V. pallidipes* and kin.

Taxonomy

Class Insecta Linnaeus, 1758
Order Hemiptera Linnaeus, 1758
Suborder Heteroptera Latreille, 1810
Infraorder Cimicomorpha Leston, Pendergrast & Southwood, 1954
Family Reduviidae Latreille, 1807

Subfamily **Pseudocetherinae** Villiers, 1963

Pseudocetherinae Villiers, 1963b: 531. Type genus: *Pseudocethera* Villiers, 1963 (= *Voconia* Stål, 1866).
Reduviinae Latreille, 1807: 126–127 (in part, new concept).

Diagnosis

Distinguished from other Reduviidae by the combination of the following characters: head and pronotum pubescent with interspersed macrosetae or setigerous tubercles; labial segment II straight, as long as remaining segments, and adpressed to head (Fig. 3E–F); apex of the third visible labial segment bent and slender; antennal insertion near eye, medially in lateral view (Fig. 3E–F); pedicel longer than scape; prosternum drawn into an anteriad-directed process (Fig. 6); absence of dorsal abdominal glands on terga IV–VI; ventral surface of all femora with anterior and posterior rows of spine-like protuberances with macrosetae at base of protuberance (Fig. 4F, I); males with fossula spongiosa on fore and mid legs (except in *V. motoensis* sp. nov. where the the fossula spongiosa is absent on the midleg) (Fig. 4G–H); females with fossula spongiosa on fore leg, but fossula spongiosa usually absent or vestigial on mid leg; tibiae laterally compressed (Fig. 4H); three-segmented tarsi (Fig. 4H).

Redescription

Usually macropterous, only micropterous morphs are known in three species and one species includes both micropterous and macropterous morphs.

Body length. 6.7–12.4 mm.

Body. Either robust (Fig. 8, e.g., *V. motoensis* sp. nov.) or slender (Fig. 8, e.g., *V. minima* sp. nov.) with variable color patterns.

Head. Elongate or globose; pubescent with interspersed macrosetae or setigerous tubercles; interocular region with two glabrous lines; scape and pedicel with dense, short macrosetae; scape reaching or slightly surpassing head apex, 0.2–0.3 times length of pedicel; ocelli present in macropterous morphs and minute or absent in micropterous morphs; buccula with ventrolateral swelling; labial segment III drawn into bent, slender apex.

Thorax. Prosternum in lateral view drawn into anteriad-directed process; scutellar spine long, either sub-horizontal or raised.

Hemelytron. In macropterous individuals, Cu-An_1 cell triangular, shorter than M-Cu cell (Fig. 4B) or Cu-An_1 cell similar in length to M-Cu cell, slender and tapered apically (Fig. 4A).

Legs. Fossula spongiosa present on fore tibia, usually present on mid tibia of males; all femora with ventral anterior and posterior rows of spine-like protuberances with macrosetae at base of protuberance (Fig. 4I); tibiae laterally compressed (Fig. 4G–H).

Abdomen. Posterolateral margin of dorsal laterotergites with (Fig. 5, e.g., *Gerbelius* sp. 2) or without single macroseta; anterior margin of terga carinulate; dorsal abdominal glands absent.

Male

Pygophore. Posterior margin with a short median apical process, either straight or bent posteriorly.

Parameres. Sinusoidal or rounded.

Aedeagus. Basal plate extension long in relation to phallotheca; endosoma covered in spicules.

Habitat and collecting method

Pseudocetherinae have been collected using light traps, but records on habitat and collecting methods are scarce on specimen labels.

Distribution (Figs 17–20)

Pseudocetherinae are widespread, with species distributed in the Afrotropical, Neotropical, Oriental, and Australasian regions. The highest diversity occurs in Southeast Asia (Fig. 20) and the lowest in the Neotropics (Fig. 19).

Key to the genera of Pseudocetherinae

1. Cu-An_1 cell of hemelytron of macropterous individuals similar in length to M-Cu cell, slender and tapering apically (Fig. 4A). Maxillary plates enlarged laterally in dorsal view (Fig. 3A). Labium stout, morphologically ventral surface of labial segment I with dense, long macrosetae (Fig. 3G) ..... ***Gerbelius*** Distant, 1903
– Cu-An_1 cell of hemelytron of macropterous individuals shorter than M-Cu cell, triangular (Figs 4B, 6C). Maxillary plates forming ellipsoid projections in dorsal view (Figs 3B, 6B). Labium gracile, morphologically ventral surface of labial segment I with short macrosetae or few long macrosetae (Figs 3E–F, 6E) ..... ***Voconia*** Stål, 1866

Genus ***Gerbelius*** Distant, 1903
Figs 1, 2, 3A, G, 4A, 5, 11, 14, 20

Gerbelius Distant, 1903a: 59. Type species: *Gerbelius typicus* Distant, 1903, by original designation.

Revised diagnosis

Distinguished from the other genus in the subfamily, *Voconia*, by the smooth or corrugated surface of the head and pronotum (Fig. 3G); laterally flattened shape of the maxillary plates (Fig. 3A); long, basally adjacent mandibular plates (Fig. 3A); stout labium densely covered with long macrosetae on the morphologically ventral surface of labial segment I (Fig. 3G); morphologically dorsal surface of labial segment II 0.8–0.9 times length of labial segment I (Fig. 3G); and Cu-An_1 cell slender and tapering apically, similar in size to the M-Cu cell (Fig. 4A).

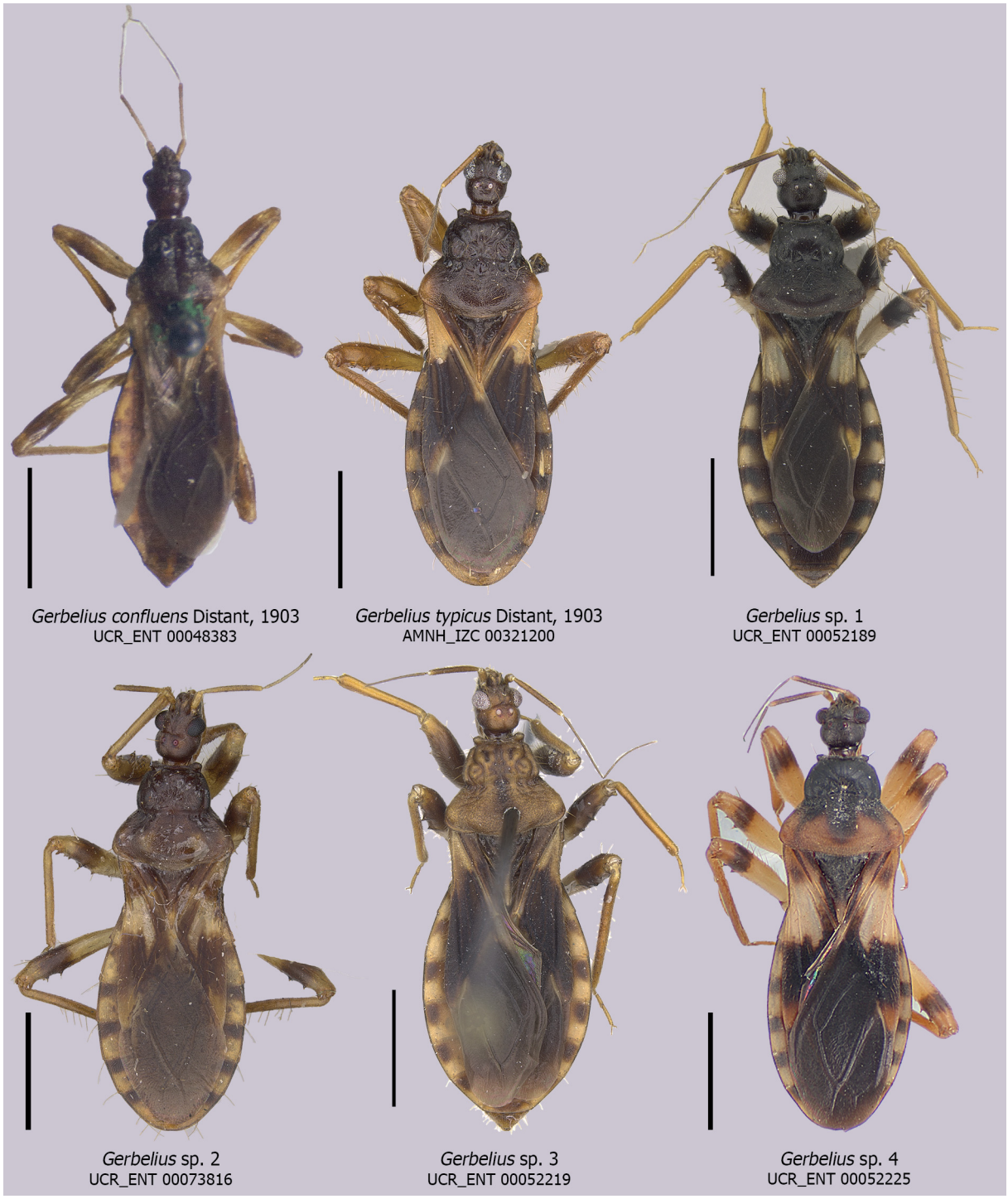

Fig. 5. Dorsal habitus of species of *Gerbelius* Distant, 1903. Scale bars = 2 mm.

Redescription

Body length. 7.0–8.0 mm.

Body. Robust; only macropterous morphs known (Fig. 5).

Coloration. Variable color patterns; scutellum uniform or with contrasting yellow scutellar spine.

Integument and vestiture. Head and pronotum: smooth to corrugated with dense pubescence and sparse, long macrosetae; antennifer with macroseta, without lateral protuberance (Fig. 3A); labium with dense, long macrosetae. Thorax: anterolateral angles of pronotal collar with macrosetae. Hemelytron: corium with dense setation. Legs: posterior row of protuberances on mid and hind femora with three large spines on distal half and three or fewer small spines. Abdomen: ventral surface pubescent with long macrosetae.

Head (Fig. 3A, G). Elongate, 1.2–1.3 times as long as wide; anteocular region about a third of head length and shorter than postocular region (measured to anterior margin of neck); postocular region in dorsal view globose and longer than eye; pedicel 1.1–1.3 times length of head width; mandibular plates in dorsal view long with basal half adjacent; maxillary plates in dorsal view enlarged laterally forming flattened projections, adjacent to clypeus; clypeus width in dorsal view narrower than maxillary plates; interocular glabrous markings V-shaped, joined medially at interocular sulcus; eye width in dorsal view narrower than synthlipsis, eye not reaching ventral head margin in lateral view; ventrolateral swelling of buccula without lateral protrusion that surpasses buccular margin, flat margin; labium stout; second (first visible) labial segment in lateral view surpassing posteroventral eye margin, gradually widened apically; dorsal surface of third (second visible) labial segment convex, 0.8–0.9 times length of second segment; fourth (third visible) labial segment drawn into bent, slender apex.

Thorax. Pronotal collar narrow medially with anterolateral angles short and flared laterally; anterior pronotal lobe lateral margins rounded; scutellum width 0.8 times length; scutellar spine subhorizontal; anteriad-directed process on prosternum with paramedial lobes; anterior margin of stridulitrum projected into sharp spine; proepimeron with obtuse protuberance on posteroventral margin.

Hemelytron (Fig. 4A). Cu-An_1 cell similar in size to M-Cu cell; Cu-An_1 cell slender, tapered apically.

Legs. Fossula spongiosa present on fore and mid legs in males, present on fore but absent or vestigial on mid legs of females.

Abdomen. Anterior margin of terga weakly carinulate; terga II and III with paired, prominent, and longitudinal carinae, almost reaching posterior margin of tergum III.

Pygophore (Fig. 11). Transverse bridge rounded on posterior margin; lateral pygophore margin flat; paramere shape in dorsal view sinusoidal, apex tapered into squarely round tip.

Aedeagus (Fig. 15). Endosoma almost entirely covered with spicules; apex of dorsal phallothecal sclerite rounded in dorsal view; basal plate extension 4.4–4.8 times as long as wide.

Distribution

This genus currently comprises two described species from India and Southeast Asia, and we are aware of at least four undescribed species distributed across India, Laos, Thailand, and Vietnam. *Gerbelius typicus* is the most widespread among them.

Remarks

Photographs of type specimens in their unit trays at the BMNH were used to evaluate species concepts for *G. typicus* and *G. confluens*. This genus previously had a third described species that is now transferred to *Voconia*, *V. ornata*. Molecular phylogenetics recovered a *Gerbelius* clade (*Gerbelius* sp. 3 + [*Gerbelius* sp. 1 + *Gerbelius* sp. 4]) sister to *Voconia wegneri* sp. nov. (Hwang & Weirauch, 2012). We also recovered a well-supported *Gerbelius* clade sister to *Voconia* (Figs 1–2). The pygophore of two specimens were dissected for this study (Figs 11, 14); however, the median apical process of *G. typicus* (AMNH_IZC 00321200) broke off during dissection (Fig. 11). We decided not to describe new species of *Gerbelius* as part of this study. Since species of *Gerbelius* somewhat resemble other small-bodied assassin bugs currently classified as Reduviinae, we suspect that our specimen searches in various natural history collections were not comprehensive for this genus. However, this material should be included in a future revision of this genus.

Gerbelius confluens Distant, 1903

Gerbelius confluens Distant, 1903b: 260, pl. 16 fig. 6, 6a.

Type material

Lectotype (present designation)
MALAYSIA ["SIAMESE MALAY STATES"] • ♀; Terengganu, Bukit Besar; 1903; Annandale and Robinson leg.; USI: UCR_ENT 00048383; BMNH(E) 1255221.

Gerbelius typicus Distant, 1903

Gerbelius typicus Distant, 1903a: 59

Gerbelius typicus – Distant 1904: fig. 175.

Type material

Lectotype (present designation)
MYANMAR ["BIRMANIA"] • ♀; Bhamo; Aug. 1885; L. Fea leg.; Distant coll. 1911-383; USI: UCR_ENT 00048382; BMNH(E) 1255220.

Paralectotype
MYANMAR • 1 ♀; "Palon (Pegu)" [Palon]; Aug.–Sep. "87" [1887]; L. Fea leg.; Distant coll. 1911-383; BMNH.

Additional material examined

INDIA • 1 ♂; Kerala, Trivandrum, Poonmudi Range [Ponmudi]; [8.77° N, 77.12° E]; elev. "3000 ft" [914 m]; Sep. 1971; T.R.S. Nathan leg.; dissected genitalia in vial; USI: AMNH_IZC 00321200.

***Gerbelius* sp. 1**

Material examined

LAOS • 1 ♀; Vientiane Prov., Houayang Nat. Park; 18.09815° N, 102.67535° E; elev. 180 m; 19–20 Jun. 2008; A. Solodovnikov and J. Pedersen leg.; collecting event: LAO08-2G; mostly secondary rainforest; DNA voucher specimen R_CW 0705; USI: UCR_ENT 00052189; UCR.

THAILAND • 1 ♀; Chaiyaphum, Pa Hin Ngam; 15.63553° N, 101.3987° E; elev. 698 m; 11–18 Aug. 2006; Katae Sa-nog and Buakaw Adnafai leg.; collecting event: T444; ecotone between mix deciduous/ dry dipterocarp; DNA voucher specimen R_CW 1185; USI: UCR_ENT 00002541; UCR.

Gerbelius sp. 2

Material examined

VIETNAM • 1 ♂; Gia Lai, 20 km N of Pleiku; [14.15° N, 107.95° E]; elev. 650 m; 9 May 1960; S. Quate leg.; dissected genitalia in vial; USI: UCR_ENT 00073816; BPBM.

Gerbelius sp. 3

Material examined

LAOS • 1 ♀; Vientiane Prov., Phou Khao Khouay; 18.33948° N, 102.80871° E; elev. 750 m; 26–31 May 2008; A. Solodovnikov and J. Pedersen leg.; collecting event: LAO08-7b; DNA voucher specimen R_CW 0704; USI: UCR_ENT 00052219; UCR.

Gerbelius sp. 4

Material examined

THAILAND • 1 ♀; Phetchabun Prov., Nam Nao National Park; 16.728217° N, 101.563933° E; elev. 917 m; 6–13 Nov. 2006; Leng Janteab leg.; collecting event: T1018; malaise trap; DNA voucher specimen R_CW 0552; USI: UCR_ENT 00052225; UCR.

Genus ***Voconia*** Stål, 1866
Figs 1–4, 6–14, 17–20

Voconia Stål, 1866a: 120. Type species: *Voconia pallidipes* Stål, 1866, by subsequent monotypy (Stål 1866b: 165). Gender feminine.

Microvarus Jeannel, 1917: 50. Type species: *Microvarus conradti* Jeannel, 1917, by original designation. **syn. nov.**

Kayanocoris Miller, 1954: 5. Type species: *Kayanocoris wegneri* Miller, 1954, by original designation. **syn. nov.**

Paragerbelius Miller, 1958: 66. Type species: *Paragerbelius typicus* Miller, 1958, by original designation. **syn. nov.**

Pseudocethera Villiers, 1963b: 532. Type species: *Pseudocethera monodi* Villiers, 1963, by original designation. **syn. nov.**

Diagnosis

Distinguished from the other genus in the subfamily, *Gerbelius*, by the granulose integument of the head and pronotum (Fig. 6A, D), ellipsoid shape of the maxillary plates (Fig. 6B, blue), short non-adjacent mandibular plates (Fig. 6B, green), gracile labium with short macrosetae on the morphologically ventral surface of labial segment I (Fig. 6E), and the Cu-An_1 cell of the fore wing shorter than the M-Cu cell and triangular (Fig. 6C).

Redescription

Body length. 6.7–12.4 mm.

Body. Slender or robust; macropterous or micropterous (Figs 7–10).

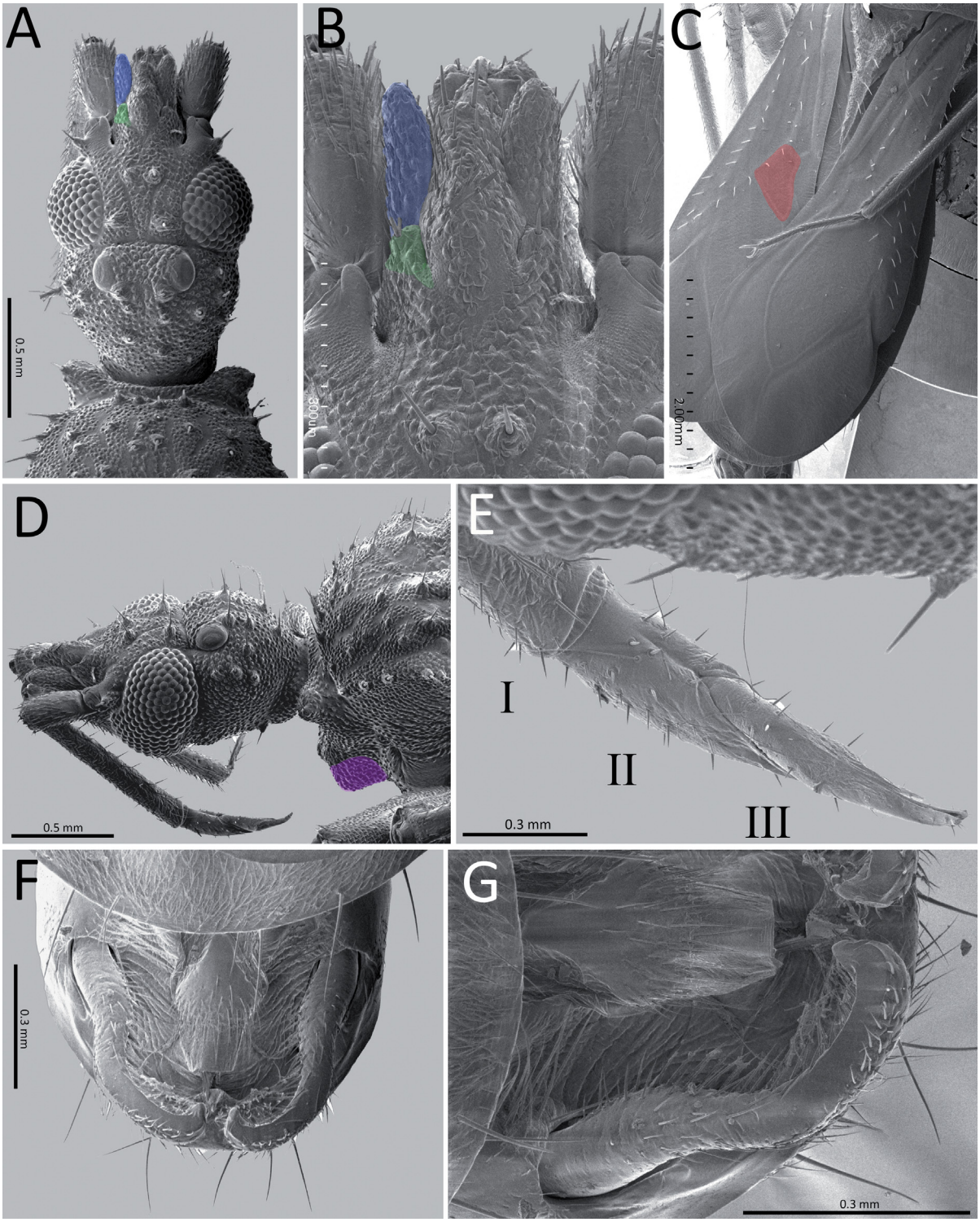

Fig. 6. Diagnostic characters of *Voconia* Stål, 1866 shown on *Voconia dolichocephala* sp. nov. (AMNH_PBI 00168745). **A–B**. Head, dorsal view; maxillary plates = blue, mandibular plates = green. **C**. Hemelytra, Cu-An_1 cell = red. **D**. Head and thorax, lateral view; anteriad directed process = purple; **E**. Labium. **F**. Pygophore, dorsal view. **G**. Paramere.

Coloration. Thorax: scutellum uniform or with contrasting yellow scutellar spine. Hemelytron (abducted): corium with various combinations of yellow spots on the proximal, anteromedial, posteromedial, and distal areas, with medial yellow stripe, or uniformly yellow; membrane uniformly dark or with pale V-shaped marking along R and M veins.

Integument and vestiture. Head and pronotum: granulose with pubescence and interspersed macrosetae or setigerous tubercles; interocular region with two glabrous lines; antennifer with macroseta, with or without lateral protuberance; morphologically ventral surface of labial segment I with short macrosetae or sparse long macrosetae. Thorax: anterolateral angles of pronotal collar armed with macrosetae or setigerous tubercles. Legs: posterior row of spine-like protuberances on all femora well developed, anterior row poorly developed on ventral surface of mid and hind femora. Abdomen: ventral surface pubescent with long macrosetae.

Structure. Head: globose to elongate; mandibular plates in dorsal view short, not adjacent basally; maxillary plates in dorsal view elongate anteriorly, forming ellipsoid projections; pedicel 0.6–1.9 times length of head width; ventrolateral swelling of buccula with or without lateral protrusion that surpasses buccular margin; labium gracile; morphologically dorsal surface of labial segment II 0.2–0.7 times length of segment I; labial segment III drawn into bent, slender apex. Thorax: scutellum width 0.5–0.8 times length; scutellar spine subhorizontal or raised; proepimeron without or with acute protuberance on posteroventral margin. Hemelytron: Cu-An_1 cell triangular, smaller than M-Cu cell. Legs: fossula spongiosa present on fore and mid legs in males, either present on fore and mid legs or absent on mid legs of females.

Distribution

This genus currently comprises nine described species and 23 new species with a circumtropical distribution. The lowest known species diversity is in the Neotropics, and the highest species diversity for this genus is in Southeast Asia across India, Indonesia, Laos, Brunei, and the Philippines.

Remarks

Originally a monotypic genus. It is here expanded to include numerous new species as well as several previously described species formerly placed in Reduviinae.

Key to the species of *Voconia*

1. Corium of macropterous morph entirely yellow [Kenya] ..... ***Voconia chrysoptera*** sp. nov.
– Corium of macropterous morph with various brown and pale patterns (e.g., Fig. 4B–C) or micropterous (Fig. 4D) 2

2. Micropterus; maxillary plates in lateral view about twice the width of scape [Afrotropical] 3
– Macropterous; maxillary plates in lateral view cylindrical, about the width of scape [Circumtropical] 5

3. Maxillary plates toothed at apex; legs yellow [West Africa] .... ***Voconia ifana*** (Villiers, 1963) comb. nov.
– Maxillary plates rounded at apex; legs yellow with distal half of femora brown 4

4. Paired longitudinal carinae on abdominal tergum II not prominent, not reaching posterior margin of segment; ocelli indistinct [West Africa] .....***Voconia monodi*** (Villiers, 1963) comb. nov.
– Paired longitudinal carinae on abdominal tergum II prominent, reaching posterior margin of segment (Fig. 4D); ocelli distinct [Central Africa] ..... ***Voconia schoutedeni*** (Villiers, 1964) comb. nov.

5. Head and pronotum coarsely granulose, with setigerous tubercles (Fig. 3C–D) 6
– Head and pronotum finely granulose, without large setigerous tubercles (Fig. 3B, H) 15

6. Antennifer with large spine-like protuberance (Fig. 3D) [Afrotropical] 7
– Antennifer with setigerous tubercle (Fig. 3C) [New World; Australasia] 8

7. Head and pronotum almost entirely dark brown; scutellar spine slightly raised; hemelytra blackish with pale coloration at base and apex of corium [Central Africa] .... ***Voconia schoutedeni*** (Villiers, 1964) comb. nov.
– Head and pronotum yellow; scutellar spine subhorizontal; hemelytra light brown with proximal half of corium yellow and distal yellow spot [Sudan] ..... ***Voconia tridens*** sp. nov.

8. Clypeus round [Mexico; Honduras] .....***Voconia mexicana*** sp. nov.
– Clypeus bifid (Fig. 3C) [Australia; Papua New Guinea] 9

9. Hemelytron with yellow spots on corium (e.g., Fig. 4B–C) 10
– Hemelytron with a broad yellow band across corium (e.g., Fig. 7, *V. fasciata* sp. nov. and *V. grandioculata* sp. nov.) 12

10. Head globose, about as long as wide [Northern Territory, Australia; Papua New Guinea] ....***Voconia brachycephala*** sp. nov.
– Head elongate, 1.4–1.6 times as long as wide 11

11. Body dark, almost black; males small, body length 7–8 mm [Northern Territory, Australia] ....***Voconia dolichocephala*** sp. nov.
– Body light brown; males larger, body length 8–9 mm [Northern Territory and Queensland, Australia] .....***Voconia tuberculata*** sp. nov.

12. Body longer, 9–11 mm; legs entirely yellow 13
– Body shorter, 7–9 mm; femora dark brown, tibiae and tarsi yellowish-brown 14

13. Eyes as long as ante- and postocular regions in dorsal view; ocelli occupying half-length of postocular region; membranal veins forming Cu-An_1 and M-Cu cells brown; proximal half of corium not entirely yellow; body length 9–10 mm [Western Australia and Queensland, Australia] ....***Voconia grandioculata*** sp. nov.
– Eyes shorter than ante- and postocular regions in dorsal view; ocelli occupying less than half-length of postocular region; membranal veins forming Cu-An_1 and M-Cu cells mostly or entirely yellow; proximal half of corium entirely yellow; body length 10.5–12 mm [New South Wales and Queensland, Australia] ..... ***Voconia pallidipes*** Stål, 1866

14. Corium band is translucent yellow; body length 8–9 mm [Queensland, Australia]..... .....***Voconia fasciata*** sp. nov.
– Corium band is opaque yellow; body length approximately 7 mm [Queensland, Australia] ....***Voconia vittata*** sp. nov.

15. Labial segment I swollen subapically on ventral surface (Fig. 4E); labial segment II swollen ventrobasally and narrowed apically (Fig. 4E); labial segment III stout, 0.2 times length of segment II (Fig. 4E) [Borneo] .....***Voconia wegneri*** (Miller, 1954) comb. nov.
– Labial segments I and II straight; labial segment III elongate, 0.4–0.7 times length of segment II 16

16. Head long, about 1.7 times as long as wide; ventral surface of hind femur with four large spines in posterior row (Fig. 4K); large pale spot between R and M veins (Fig. 4C) 17
– Head elongate, not more than 1.4 times as long as wide; ventral surface of hind femur with three large and 0–3 small spines in posterior row (Fig. 4I–J) 18

17. Mid and hind femora dark, proximal third yellow (Fig. 4K); anterior pronotal lobe convex, strongly curved inward on posterolateral margins; body length about 11 mm [Normanby Island] .... ***Voconia bracata*** sp. nov.
– Legs uniformly dark; anterior pronotal lobe gently rounded, posterolateral margins nearly straight; body length 12–13 mm [New Guinea] ..... ***Voconia typica*** (Miller, 1958) comb. nov.

18. Pronotum dark with contrasting yellow posterior margin; abducted corium dark with antero- and posteroproximal yellow stripes and posteromedial and distal white spots [Trinidad] .... ***Voconia trinidadensis*** sp. nov.
– Color patterns variable but combination not as above [Old World] 19

19. Proepimeron with posteroventral margin rounded [Afrotropical] 20
– Proepimeron with acute protuberance on posteroventral margin [Oriental] 22

20. Fossula spongiosa absent or vestigial on mid leg of males and females; scutellum uniformly brown; abducted corium with an antero- and posteromedial yellow spot; uniformly brown dorsal laterotergites [Central Africa] .....***Voconia motoensis*** (Schouteden, 1929) comb. nov.
– Fossula spongiosa present on mid leg of male; scutellar spine yellow (Fig. 4E); abducted corium with proximal, posteromedial, and distal yellow spots; dorsal laterotergites bicolored 21

21. Body longer, 10–12 mm; dark dorsal laterotergites with strongly contrasting yellow anterior spots; eyes reaching ventral head margin in lateral view; eyes strongly bulging past postocular lateral margins in dorsal view [West and Central Africa] ..... ***Voconia conradti*** (Jeannel, 1917) comb. nov.
– Body shorter, 9–10 mm; light brown dorsal laterotergites with weakly contrasting yellow anterior spots; eyes do not reach ventral head margin in lateral view; eyes do not bulge strongly in dorsal view [Central Africa] .....***Voconia smithae*** sp. nov.

22. Membrane of hemelytra dark; membranal veins forming Cu-An_1 and M-Cu cells paler than remainder of membrane (Fig. 4B) 23
– Membrane of hemelytra dark; membranal veins dark or with R and M veins proximally pale in V-shape 25

23. Body light brown; labium lighter than head, yellow; scutellum dark with contrasting yellow apical spine [Borneo] .....***Voconia decorata*** sp. nov.
– Body dark brown, almost black; labium as dark as head; scutellum uniformly dark [Sumatra]..... 24

24. Head dark with semicircular yellow stripe encircling both ocelli; body longer, about 11 mm; anterior pronotal lobe relatively long, posterior lobe about 1.8 times as long as than anterior lobe .... ***Voconia coronata*** sp. nov.
– Head dark with yellow spots adjacent to lateral ocellar margin; body shorter, about 9 mm; anterior pronotal lobe relatively short, posterior lobe about 2.2 times as long as anterior lobe .... ***Voconia lirophleps*** sp. nov.

25. Legs yellow, distal halves of femora brown [India] .....***Voconia ornata*** comb. nov.
– Femora unicolored [Southeast Asia] 26

26. Legs dark brown 27
– Legs yellow or yellowish-brown 29

27. Dorsal laterotergites dark with yellow spots anteriorly; anterior margin of abducted corium with a small pale spot medially; anteriad-directed process of prosternum with small paramedial lobes; stridulitrum elongated anteriorly into a small protuberance [Philippines] .... ***Voconia bakeri*** sp. nov.
– Dorsal laterotergites uniformly dark; anterior margin of abducted corium with a yellow stripe along proximal half; anteriad-directed process of prosternum smoothly rounded, without paramedial lobes (Fig. 4J); stridulitrum not elongated into an anterior protuberance (Fig. 4J) [Southeast Asia] 28

28. Body length about 10.0 mm; pronotum dark, posterior margin paler [Philippines] .... ***Voconia nyx*** sp. nov.
– Body length about 8.5 mm; pronotum uniformly dark [Philippines] ..... ***Voconia minima*** sp. nov.

29. Anterior margin of abducted corium with medial and distal yellow spots; pronotum and scutellum uniformly dark [Philippines] ..... ***Voconia hemera*** sp. nov.
– Anterior margin of abducted corium with proximal half yellow and distal yellow spot; pronotum dark, posterior margin pale; scutellum dark with contrasting brown or yellow apical spine (Fig. 4E) ... 30

30. Clypeus coloration as rest of head; proximal half of corium entirely yellow, forming a yellow triangle [Philippines] ..... ***Voconia isosceles*** sp. nov.
– Clypeus lighter than rest of head, yellow; proximal half of corium not entirely yellow, with brown markings 31

31. Labial segment I short, not surpassing posteroventral eye margin in lateral view; Cu-An_1 cell elongate, reaching at least half the length of M-Cu cell [Laos] ..... ***Voconia laosensis*** sp. nov.
– Labial segment I long, surpassing posteroventral eye margin in lateral view; Cu-An_1 cell stout, less than half the length of M-Cu cell 32

32. Abducted corium mostly dark with anteroproximal reddish-brown stripe and posteromedial and distal yellow spots; pale posterior margin of pronotum wide, a third of posterior pronotal lobe [Borneo] ..... ***Voconia lasiosoma*** sp. nov.
– Abducted corium with proximal half mostly yellow, distal half dark with distal yellow spot; pale posterior margin of pronotum narrow, a fifth of posterior pronotal lobe [Borneo] .... ***Voconia loki*** sp. nov.

Voconia bakeri sp. nov.
urn:lsid:zoobank.org:act:21FEECCD-754F-4DF8-815B-E18666CE9CE5
Figs 1–2, 7, 9, 11, 14, 20

Diagnosis

This species most closely resembles two other dark-brown Philippine species, *V. minima* sp. nov. and *V. nyx* sp. nov., with yellow posteromedial yellow spots on the abducted corium, but is differentiated by the yellow patches on the dorsal laterotergites, the faint yellow spot on the anteromedial portion of the abducted corium, the presence of small paramedial lobes on the anteriad-directed process of the prosternum, and the stridulitrum being elongated anteriorly into a small protuberance. It specifically differs from *V. minima* sp. nov. by the uniformly dark legs and short labial segment I that does not reach the posteroventral eye margin and from *V. nyx* sp. nov. by the uniformly dark pronotum.

Etymology

Named after Austin Baker, a former colleague at UCR who provided support and insightful comments on this revision.

Type material

Holotype

PHILIPPINES • ♂ (dissected pygophore and aedeagus in vial); Mindanao, Mts Or., Mt Pomalihi, Gingoog City, 21 km W of Gingoog City; [8.81° N, 124.92° E]; elev. 800–1000 m; 16 Oct. 1965; H.M. Torrevillas leg.; light trap; USI: UCR_ENT 00073810; BPBM.

Description

Male (Figs 7, 9)

Body length. About 9.8 mm; macropterous.

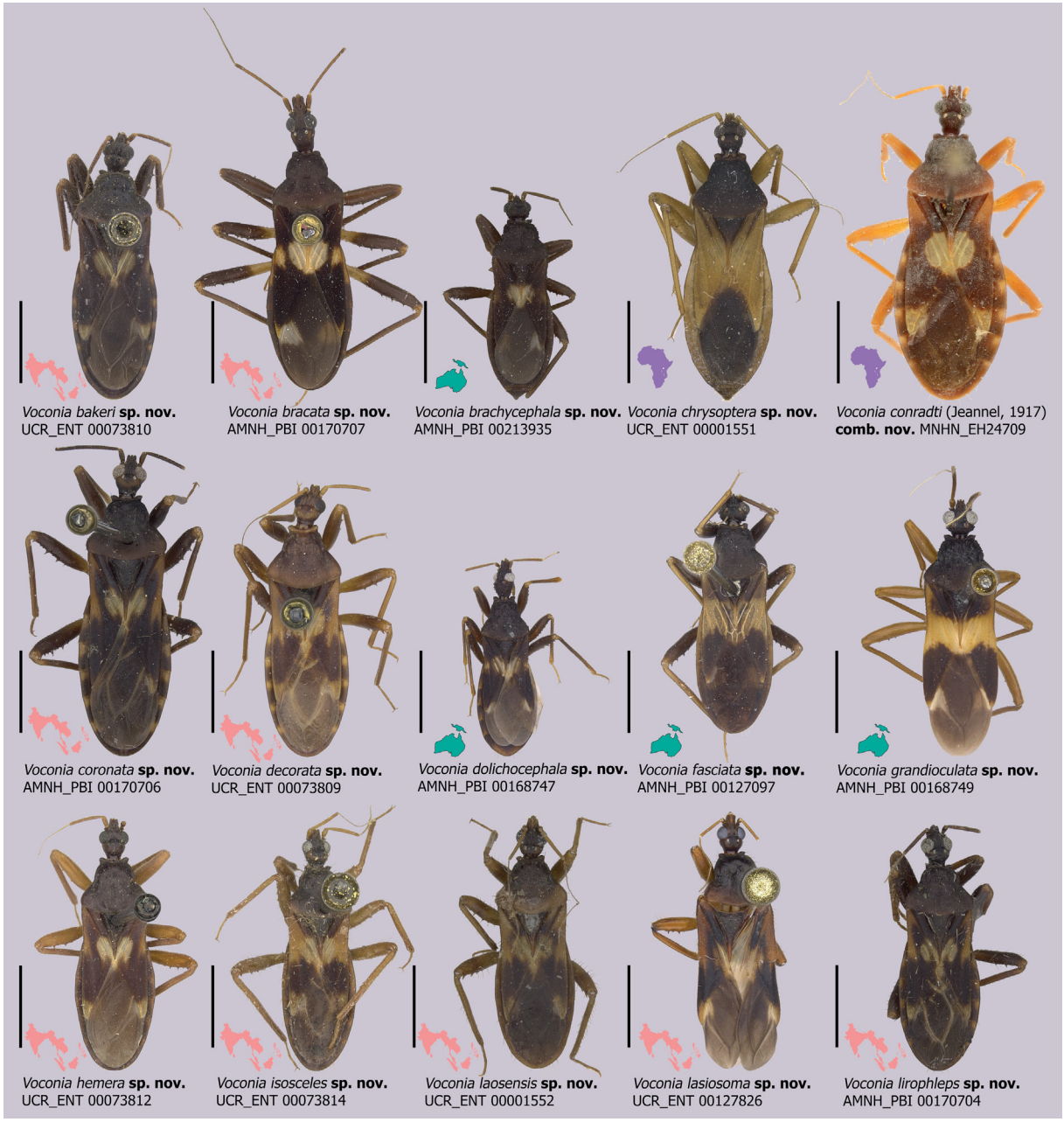

Fig. 7. Dorsal habitus of holotypes of *Voconia* Stål, 1866 species with distribution: purple = Afrotropical region, green = Australasian region, pink = Oriental region. Scale bars = 3 mm.

Coloration. Head: dark brown with paired pale patches adjacent to lateral ocellar margin; labium nearly as dark as head. Thorax: coloration as head; scutellum uniformly dark brown. Hemelytron (abducted): clavus dark reddish-brown, distal half yellow; corium dark reddish-brown with anteromedial, posteromedial, and distal yellow spots; membrane dark with pale V-shaped marking along R and M veins; membranal veins R and M proximally pale, remainder as membrane. Legs: dark brown. Abdomen: dark reddish-brown, almost black; dorsal laterotergites dark with yellow spots anteriorly.

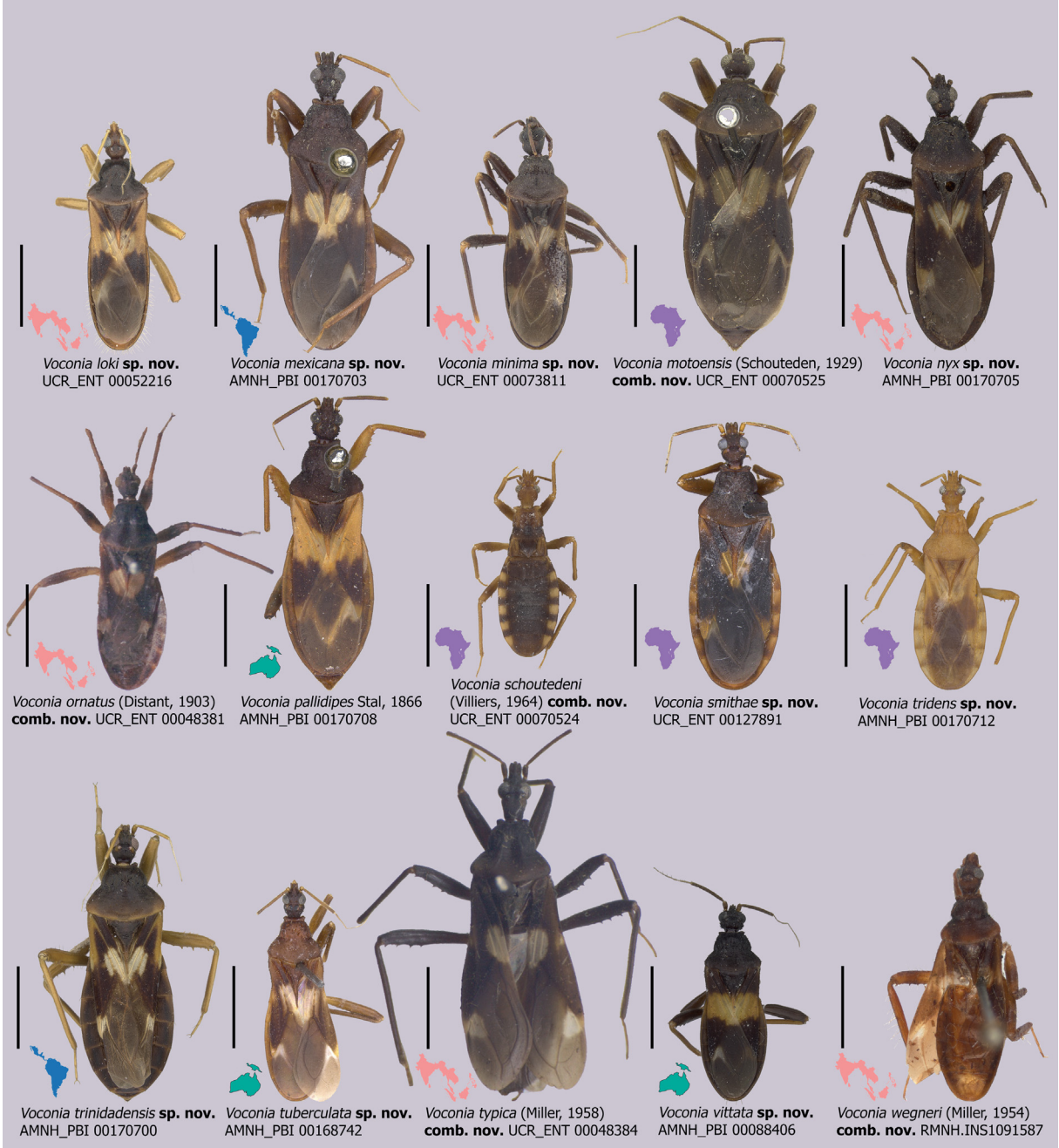

Fig. 8. Dorsal habitus of holotypes of *Voconia* Stål, 1866 species with distribution: purple = Afrotropical region, green = Australasian region, blue = Neotropical region, pink = Oriental region. Scale bars = 3 mm.

Integument and vestiture. Head and pronotum: finely granulose with dense, long macrosetae interspersed among dense pubescence; interocular region with two pairs of macrosetae paramedially; antennifer with macroseta, base without lateral protuberance; morphologically ventral surface of labium with sparse, short macrosetae. Thorax: anterolateral angles of pronotal collar with macrosetae; scutellar lateral carinae with long setation. Hemelytron: corium with sparse long setation. Legs: posterior row of protuberances on mid and hind femora with three large and two small spines on distal half. Abdomen: ventral surface pubescent.

Structure. Head: elongate, about 1.2 times as long as wide; anteocular region about one quarter of head length, shorter than postocular region (measured to anterior margin of neck); postocular region in dorsal view about as long as eye, lateral margins in dorsal view gently rounded; pedicel about 1.2 times length of head width; maxillary plates ellipsoidal, adjacent to and longer than clypeus; apices of maxillary plates in dorsal view converging; clypeus in dorsal view wider than maxillary plates; clypeal apex round, narrowed; interocular glabrous markings anterolaterally curved, joined at interocular sulcus paramedially; interocular sulcus in dorsal view nearly straight; eye width in dorsal view about as wide as synthlipsis; eye reaching ventral head margin in lateral view; ventrolateral swelling of buccula without lateral protrusion that surpasses buccular margin, flat margin; labial segment I in lateral view straight, not reaching posteroventral eye margin; morphologically dorsal surface of labial segment II nearly straight, about 0.6 times length of segment I. Thorax: pronotal collar narrow medially with anterolateral angles short and flared laterally; anterior pronotal lobe about 0.7 times length of posterior pronotal lobe, lateral margins rounded; glabrous markings on pronotum thin and not deeply depressed; median apodeme depression of pronotum deep, elongated longitudinally; scutellar spine long, raised; anteriad-directed process of prosternum with paramedial lobes; anterior margin of stridulitrum projected into small protuberance; proepimeron with acute protuberance on posteroventral margin. Legs: fossula spongiosa present on fore and mid legs. Abdomen: anterior margin of terga weakly carinulate; terga II and III with paired prominent longitudinal carinae, reaching about two-thirds of tergum III. Pygophore (Fig. 11): transverse bridge with rounded posterior margin; posterior region of ventral surface of pygophore in lateral view straight, not swollen; lateral pygophore margin with protuberance; posterior pygophore margin with clustered macrosetae on protuberance; parameres sinusoidal, apex tapered into squarely rounded tip. Aedeagus (Fig. 14): endosoma almost entirely covered with spicules; apex of dorsal phallothecal sclerite tongue-shaped in dorsal view; basal plate extension about 4.3 times as long as wide.

Female

Unknown.

Distribution (Fig. 20)

This species is only known from the type locality in the Philippines. Based on the record of a Miridae Hahn, 1831 specimen with the same collection event, Mt Pomalihi is presumably in Mt Balatukan Range Natural Park. The type locality is also shared with *V. isosceles* sp. nov.

Remarks

The median apical process broke off during dissection (Fig. 11). It was presumably short as is the case in all Pseudocetherinae, but it was not possible to determine if it was upright or bent posteriorly.

Voconia bracata sp. nov.
urn:lsid:zoobank.org:act:32D3A427-888D-4D48-B0C3-5EB69CB43B1A
Figs 1, 2, 3J, 4C, K, 7, 9, 18

Diagnosis

Distinguished from other species of the genus *Voconia* by its long, slender body (about 10.8 mm), long head (about 1.7 times as long as wide), hind leg with four large spines in the posterior row, a large pale spot

between R and M veins, and dorsal laterotergites I and II yellow, the remainder dark brown. This species is most similar to *V. typica*, but is differentiated by the yellow proximal third of the mid and hind femora as well as the anterior pronotal lobe, which is convex, strongly curved inward on the posterolateral margins.

Etymology

The specific epithet is the Latin adjective '*bracatus*, *-a*, *-um*', meaning 'wearing trousers'. It refers to the yellow coloration of the proximal half of the femora.

Type material

Holotype

PAPUA NEW GUINEA • ♂; Milne Bay Province, Waikaiuna, Normanby Island; [10.06° S, 150.97° E]; elev. 0–50 m; 14 Apr. 1956; L.J. Brass leg.; Fifth Archibold Exped. to New Guinea; USI: AMNH_PBI 00170707; AMNH.

Description

Male (Figs 7, 9)

Body length. About 10.8 mm; macropterous.

Coloration. Head: dark brown; postocular region with dark patches adjacent to medial ocellar margin and paired pale patches adjacent to lateral ocellar margin; labial segments II and III lighter than head. Thorax: coloration as head; scutellum dark with contrasting yellow apical spine. Hemelytron (abducted): clavus dark reddish-brown with distal half yellow; corium dark reddish-brown with anteromedial, posteromedial, and distal yellow spots; membrane dark, large pale spot between R and M veins; membranal veins R and M proximally pale, remainder as membrane. Legs (Fig. 4K): dark brown with yellow mid and hind coxae, trochanter, and proximal third of femora. Abdomen (Fig. 4C): dark reddish-brown; dorsal laterotergites I and II yellow.

Integument and vestiture. Head and pronotum: finely granulose with sparse, short macrosetae interspersed among dense pubescence; antennifer with short lateral setigerous tubercle; morphologically ventral surface of labium with dense, short macrosetae; anterolateral angles of pronotal collar without macrosetae or setigerous tubercles. Legs (Fig. 4K): posterior row of protuberances on mid and hind femora with four large spines on distal half. Abdomen: ventral surface pubescent with long macrosetae.

Structure. Head: elongate, about 1.7 times as long as wide; anteocular region about one third of head length, subequal in length to postocular region (measured to anterior margin of neck); postocular region in dorsal view longer than eye, lateral margins gently rounded; pedicel about 1.8 times length of head width; maxillary plates ellipsoidal, adjacent to and reaching apex of clypeus; apex of maxillary plates in dorsal view directed straight; clypeus in dorsal view slightly narrower than maxillary plates; clypeal apex round, not narrowed; interocular glabrous markings V-shaped, joined medially at interocular sulcus; interocular sulcus in dorsal view slightly bent anteromedially, subtriangular; eye width in dorsal view wider than synthlipsis; eye reaching ventral head margin in lateral view; ventrolateral swelling of buccula without lateral protrusion that surpasses buccular margin, flat margin; labial segment I in lateral view straight, surpassing posteroventral eye margin; morphologically dorsal surface of labial segment II slightly curving apically, about 0.4 times length of segment I. Thorax: pronotal collar narrow medially with anterolateral angles short, projected forward; anterior pronotal lobe subequal in length to posterior pronotal lobe, lateral margins rounded; glabrous markings on pronotum thin and not deeply depressed; median apodeme depression of pronotum deep and elongated transversely; scutellar spine long and subhorizontal; anteriad-directed process of prosternum smoothly rounded, without paramedial lobes (Fig. 3J); anterior margin of stridulitrum not elongated into protuberance (Fig. 3J); proepimeron with smoothly rounded posteroventral margin. Legs: fossula spongiosa present on fore and mid legs.

Female
Unknown.

Distribution (Fig. 18)

This species is only known from the type locality of Normanby Island off of Papua New Guinea, where no other Pseudocetherinae species are known.

Remarks

This species forms a well-supported clade with another species from Papua New Guinea, *V. typica* (Figs 1–2).

Voconia brachycephala sp. nov.
urn:lsid:zoobank.org:act:AB497C37-1CBA-4270-AAE0-DDA9ADDCAB25
Figs 1–2, 7, 9, 18

Voconia pallidipes (non Stål, 1866) – Swanson 2015: 268–269, fig. 10. Misidentification.

Diagnosis

Recognized by its Australasian distribution, small size (about 7.4 mm), globose head (about as long as wide), labial segment II swollen ventromedially, and coarsely granulose, tuberculate head and pronotum. Most closely resembles *V. dolichocephala* sp. nov. in size and hemelytral coloration but *V. dolichocephala* sp. nov. has a conspicuously elongate head.

Etymology

The specific epithet is the latinized Greek adjective '*brachycephalus*, *-a*, *-um*', formed from the prefix '*brachy-*' (meaning 'short') and the noun '*cephale*' (meaning 'head'), referring to the fact that this species has the shortest head among species of *Voconia*.

Type material

Holotype
PAPUA NEW GUINEA ["N. GUINEA"] • ♀; Madang Province, Erima; [5.42° S, 145.73° E]; 1896; L. Bíró leg.; "Astrolabe B."; USI: AMNH_PBI 00213935; HNHM.

Material examined from literature

AUSTRALIA • 1 ♀; Northern Territory, 2 km E of Saddle Creek; 15.95694° S, 129.56167° E; elev. 75 m; 27 Sep. 1983; E.L. Schlinger and M.E. Irwin leg.; INHS 914,917.

Description

Female (Figs 7, 9)
Body length. About 7.4 mm; macropterous.

Coloration. Head: dark brown, postocular region with dark patches adjacent to medial ocellar margin; labium lighter than head. Thorax: coloration as head; scutellum dark with contrasting yellow apical spine. Hemelytron (abducted): clavus reddish-brown with distal yellow stripe; corium reddish-brown with anteromedial and posteromedial yellow spots; membrane dark with pale V-shaped marking along R and M veins; membranal veins R and M proximally pale, remainder as membrane. Legs: dark yellowish-brown. Abdomen: dark brown; dorsal laterotergites uniformly dark.

Integument and vestiture. Head and pronotum: coarsely granulose, with dense, short setigerous tubercles interspersed among sparse pubescence; interocular region with two pairs of stout setigerous tubercles paramedially and one medially; antennifer with two adjacent lateral setigerous tubercles; morphologically ventral surface of labium with sparse, long macrosetae. Thorax: anterolateral angles of pronotal collar with setigerous tubercles; scutellar lateral carinae with short macrosetae on setigerous tubercles. Legs: posterior row of protuberances on mid and hind femora with three large spines on distal half and three or fewer small spines. Abdomen: ventral surface pubescent with long macrosetae.

Structure. Head: globose, about as long as wide; anteocular region about one quarter of head length, shorter than postocular region (measured to anterior margin of neck); postocular region in dorsal view shorter than eye, lateral margins gently rounded; pedicel about 1.2 times length of head width; maxillary plates ellipsoidal, adjacent to and shorter than clypeus; apices of maxillary plates in dorsal view diverging; clypeus in dorsal view wider than maxillary plates; clypeal apex bifid, narrowed; interocular glabrous markings anterolaterally curved, joined at interocular sulcus paramedially; interocular sulcus in dorsal view curved and smoothly rounded anteriorly; eye width in dorsal view narrower than synthlipsis; eye reaching ventral head margin in lateral view; ventrolateral swelling of buccula without lateral protrusion that surpasses buccular margin, flat margin; labial segment I in lateral view gradually thickens distally,

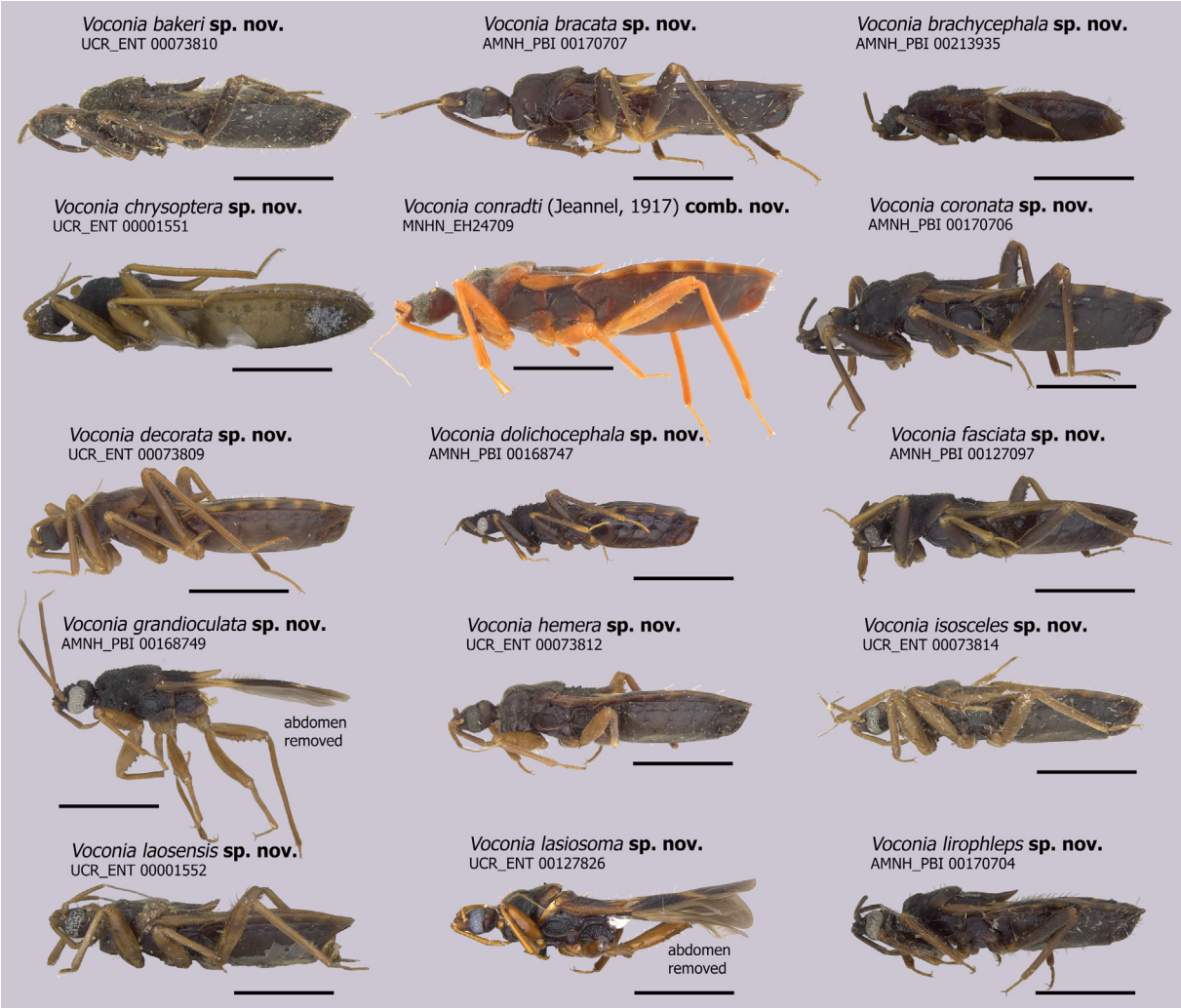

Fig. 9. Lateral habitus of species of *Voconia* Stål, 1866. Scale bars = 3 mm.

surpassing posteroventral eye margin; labial segment II swollen ventromedially; morphologically dorsal surface of labial segment II curves ventrally, about 0.3 times length of segment I. Thorax: pronotal collar narrow medially with anterolateral angles short, projected forward; anterior pronotal lobe about 0.7 times length of posterior pronotal lobe, lateral margins almost straight; glabrous markings on pronotum conspicuous and not depressed; median apodeme depression of pronotum shallow, elongated longitudinally; scutellar spine long and raised; anteriad-directed process of prosternum with paramedial lobes; anterior margin of stridulitrum projected into small protuberance; proepimeron with smoothly rounded posteroventral margin. Legs: fossula spongiosa of fore leg present.

Male

Unknown.

Distribution (Fig. 18)

This species has a disjunct distribution. It is known from Erima in Papua New Guinea (type locality) and the Northern Territory of Australia (Swanson 2015: 268, as *V. pallidipes*).

Remarks

There is little doubt that the specimen figured by Swanson (2015: 269, fig. 10) as *V. pallidipes* pertains to *V. brachycephala* sp. nov. Although the size of the specimen in concern is unknown, its coloration and the short, tuberculate head do not seem to differ from the condition seen in the new species. Since the specimen could not be re-examined, it is, however, not included in the type material of the new species.

Voconia chrysoptera sp. nov.
urn:lsid:zoobank.org:act:79E22180-F528-4166-8D25-02AD3BA726BE
Figs 1–2, 7, 9, 17

Diagnosis

Recognized from other African *Voconia* species by the unique coloration of the corium, abdomen, and legs which are entirely yellow. Additionally, the posterior row of spines on the mid and hind femora have three large and many small spines, and the antennifer lacks a lateral protuberance. Females possess a fossula spongiosa on the mid leg.

Etymology

The specific epithet is the Latin adjective '*chrysopterus*, *-a*, *-um*', meaning 'golden-winged', referring to the entirely yellow corium.

Type material

Holotype

KENYA • ♀; Eastern Province, Mwingi, Nguni; 7 Apr. 2004; M. Snizek leg.; USI: UCR_ENT 00001551; NHMW.

Description

Female (Figs 7, 9)

Body length. 10.5 mm; macropterous.

Coloration. Head: dark brown, maxillary plates lighter; postocular region dark brown with paired pale patches adjacent to lateral ocellar margin; labium lighter than head, yellow. Thorax: coloration as head, with posterior pronotal lobe lighter than anterior lobe; scutellum dark with contrasting yellow apical spine. Hemelytron (abducted): clavus and corium uniformly yellow; membrane uniformly dark;

membranal veins as remainder of membrane. Legs: yellow. Abdomen: ventral surface and dorsal laterotergites yellow.

Integument and vestiture. Head and pronotum: coarsely granulose with sparse pubescence and sparse, short macrosetae; interocular region with two pairs of macrosetae paramedially; antennifer without lateral projection; labium with dense, short macrosetae. Thorax: anterolateral angles of pronotal collar without macrosetae or setigerous tubercles; scutellar lateral carinae with short macrosetae. Hemelytron: corium with dense short setation. Legs: posterior row of protuberances on mid and hind femora with three large spines on distal half and many small spines. Abdomen: ventral surface pubescent.

Structure. Head: elongate, 1.3 times as long as wide; anteocular region about one third of head length, shorter than postocular region (measured to anterior margin of neck); postocular region in dorsal view longer than eye, lateral margins gently rounded; pedicel about 1.8 times length of head width; maxillary plates ellipsoidal, adjacent to and longer than clypeus; apices of maxillary plates in dorsal view diverging; clypeus in dorsal view wider than maxillary plates, apex rounded, not narrowed; interocular glabrous markings curved anterolaterally, joined at interocular sulcus paramedially; interocular sulcus in

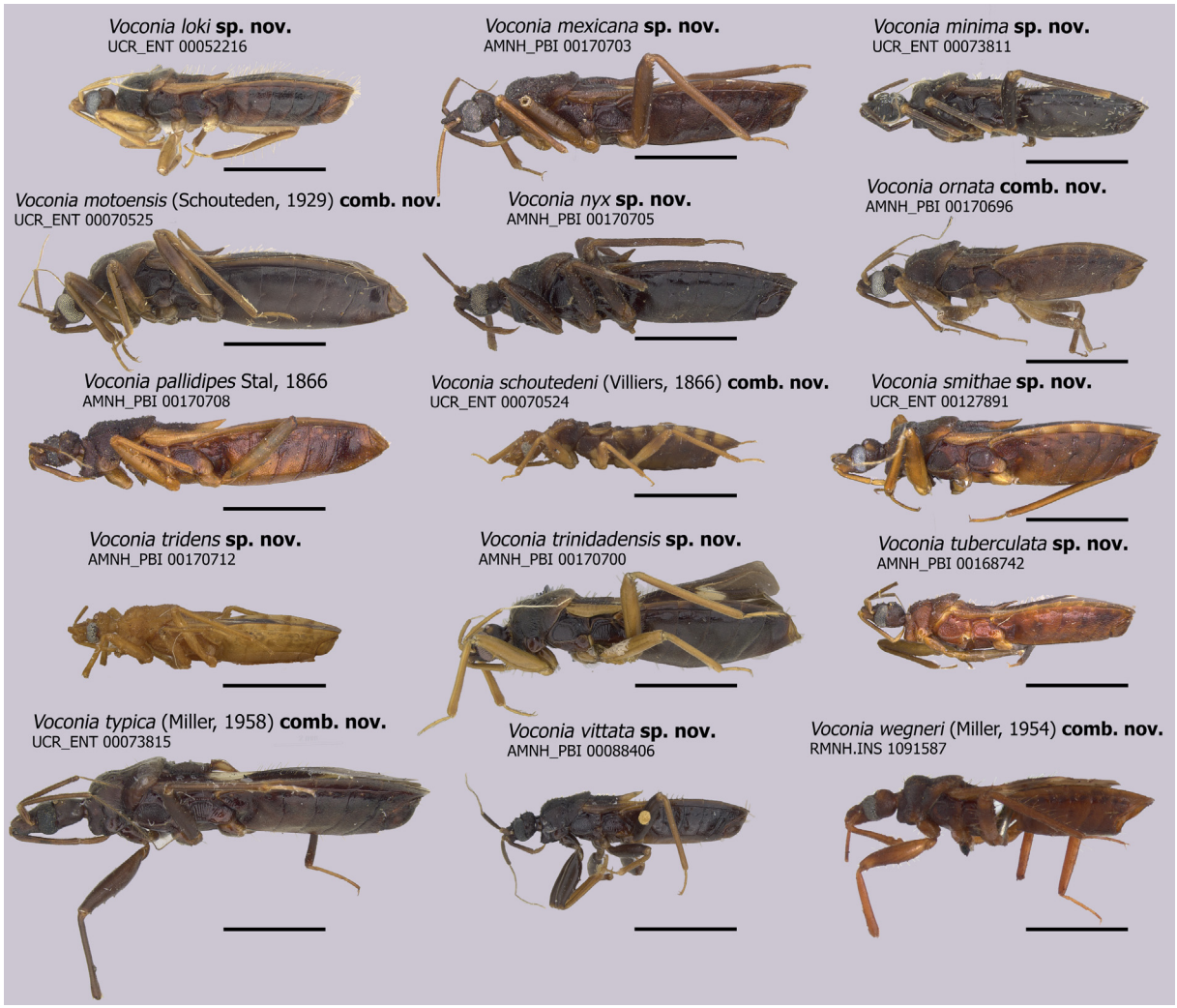

Fig. 10. Lateral habitus of species of *Voconia* Stål, 1866. Scale bars = 3 mm.

dorsal view curved and smoothly rounded anteriorly; eye width in dorsal view narrower than synthlipsis, reaching ventral head margin in lateral view; ventrolateral swelling of buccula with lateral protrusion that surpasses buccular margin, setigerous tubercles along apical margin; labial segment I in lateral view straight, reaching posteroventral eye margin; morphologically dorsal surface of labial segment II nearly straight, about 0.6 times length of segment I. Thorax: with pronotal collar narrow medially with anterolateral angles short, projected forward; anterior pronotal lobe about 0.5 times length of posterior pronotal lobe, lateral margins rounded, glabrous markings not depressed; median apodeme depression of pronotum shallow and elongated longitudinally; scutellar spine long and raised; anteriad-directed process of prosternum smoothly rounded without paramedial lobes; anterior margin of stridulitrum projecting into a small protuberance. Legs: fossula spongiosa present on fore and mid legs.

Male

Unknown.

Distribution (Fig. 17)

This species is only known from the type locality in Mwingi, Kenya. It is the easternmost Afrotropical species.

Remarks

This is the only female in the subfamily with fossula spongiosa present on the mid leg.

Voconia conradti (Jeannel, 1917) comb. nov.
Figs 1–2, 7, 9, 11, 17

Microvarus conradti Jeannel, 1917: 51.
Microvarus achteni Schouteden, 1929: 252. Synonymized by Villiers (1948: 280).

Diagnosis

Distinguished from other species in *Voconia* by its Afrotropical distribution and stout body. This species most closely resembles *V. motoensis* and *V. smithae* sp. nov. It differs from *V. motoensis* by its distinct coloration: yellow scutellar spine, corium with a proximal and distal yellow spot, and contrasting yellow anterior spots on dark dorsal laterotergites. Despite the strong superficial resemblance to *V. smithae* sp. nov. due to its coloration and stoutness, closer examination reveals that *V. conradti* is distinguishable by the longer body (10.4–11.4 mm), dark dorsal laterotergites with strongly contrasting yellow anterior spots, finely granulose head, antennifer with short or absent laterally projecting setigerous tubercle, lack of paired interocular setigerous tubercles, maxillary plates with medial margins diverging, shorter anteocular region than postocular region (measured to where the posterior margin of the granulations meet the anterior margin of the smooth neck), buccula without lateral protrusion, and strongly bulging eyes that greatly surpass the postocular lateral margin in dorsal view and reach the ventral head margin in lateral view.

Type material

Lectotype (present designation)

EQUATORIAL GUINEA • ♂; "Fernando-Po" [Bioko Island]; 1901; L. Conradt leg.; MNHN_EH24709.

Additional material examined

CAMEROON • 1 ♀; N Kolbisson; [3.87° N, 11.45° E]; 27 Jun. 1966; B. de Mire leg.; USI: AMNH_PBI 00170693; AMNH • 1 ♂; same collection data as for preceding; 31 Mar. 1971; USI: AMNH_PBI 00170694; AMNH.

IVORY COAST • 1 ♂; Foro Foro; [7.98° N, 5.06° W]; 13 Oct. 1971; D. Duviard leg.; USI: AMNH_PBI 00170691; AMNH • 1 ♂; same locality as for preceding; 25–28 Sep. 1973; R. Linnavuori leg.; dissected pygophore in vial (Fig. 11), aedeagus lost; USI: AMNH_PBI 00170695; AMNH.

NIGERIA • 1 ♂; W State, Ife; [7.47° N, 4.56° E]; 7 Jul.–14 Aug. 1973; R. Linnavuori leg.; USI: AMNH_PBI 00170692; AMNH.

Redescription

Male (Figs 7, 9)

Body length. 10.4–11.4 mm; macropterous.

Coloration. Head: dark brown; postocular region with dark patches adjacent to medial ocellar margin and pale patches adjacent to lateral ocellar margin; labium lighter than head. Thorax: coloration as head; pronotum uniformly dark (Fig. 3K) or posterior pronotal lobe lighter than anterior lobe; scutellum dark with contrasting yellow apical spine. Hemelytron (abducted): clavus dark reddish-brown with distal yellow stripe; corium dark reddish-brown with proximal, anteromedial, posteromedial, and distal yellow spots; membrane dark with pale V-shaped marking along R and M veins; membranal veins R and M proximally pale. Legs: completely yellow or yellow with distal half of femur dark brown. Abdomen: dark brown, dorsal laterotergites with yellow spots anteriorly.

Integument and vestiture. Head and pronotum: finely granulose with sparse, short macrosetae interspersed among sparse pubescence; interocular region with two pairs of macrosetae paramedially; antennifer with short lateral setigerous tubercle; morphologically ventral surface of labium with sparse, short macrosetae. Thorax (Fig. 3K): anterolateral angles of pronotal collar without macrosetae or setigerous tubercles. Hemelytron: corium with dense long setation. Legs: posterior row of protuberances on mid and hind femora with three large spines on distal half. Abdomen: ventral surface pubescent.

Structure. Head: elongate, 1.1–1.4 times as long as wide; anteocular region about one quarter of head length, shorter than postocular region (measured to anterior margin of neck); postocular region in dorsal view about as long as eye or shorter, lateral margins subrectangular; pedicel about 1.3 times length of head width; maxillary plates ellipsoidal, adjacent to and longer than clypeus; apices of maxillary plates in dorsal view with medial margins diverging; clypeus in dorsal view narrower than maxillary plates; clypeal apex round, narrowed; interocular glabrous markings anterolaterally curved, joined at interocular sulcus paramedially; interocular sulcus in dorsal view curved and smoothly rounded anteriorly; eye width in dorsal view either wider or narrower than synthlipsis; eye reaching ventral head margin in lateral view; ventrolateral swelling of buccula without lateral protrusion that surpasses buccular margin, flat margin; labial segment I in lateral view straight, reaching posteroventral eye margin; morphologically dorsal surface of labial segment II nearly straight, about 0.5 times length of segment I. Thorax (Fig. 3K): pronotal collar in dorsal view narrow medially, with anterolateral angles short, projected forward; anterior pronotal lobe 0.5–0.6 times length of posterior pronotal lobe, lateral margins almost straight; glabrous markings on pronotum slightly depressed; median apodeme depression of pronotum deep, circular; scutellar spine long, raised; anteriad-directed process of prosternum with paramedial lobes; anterior margin of stridulitrum not elongated into protuberance; proepimeron with smoothly rounded posteroventral margin. Legs: fossula spongiosa present on fore and mid legs. Abdomen: anterior margin of terga weakly carinulate; terga II and III with paired prominent longitudinal carinae reaching about one-third of tergum III. Pygophore (Fig. 11): transverse bridge with triangular posterior margin; posterior region of ventral surface of pygophore in lateral view with slight swelling; median apical process in caudal view short; direction of median apical process in lateral view sharply bent posteriorly; lateral pygophore margin with protuberance; posterior pygophore margin with clustered macrosetae on protuberance; parameres sinusoidal, apex tapered into squarely rounded tip.

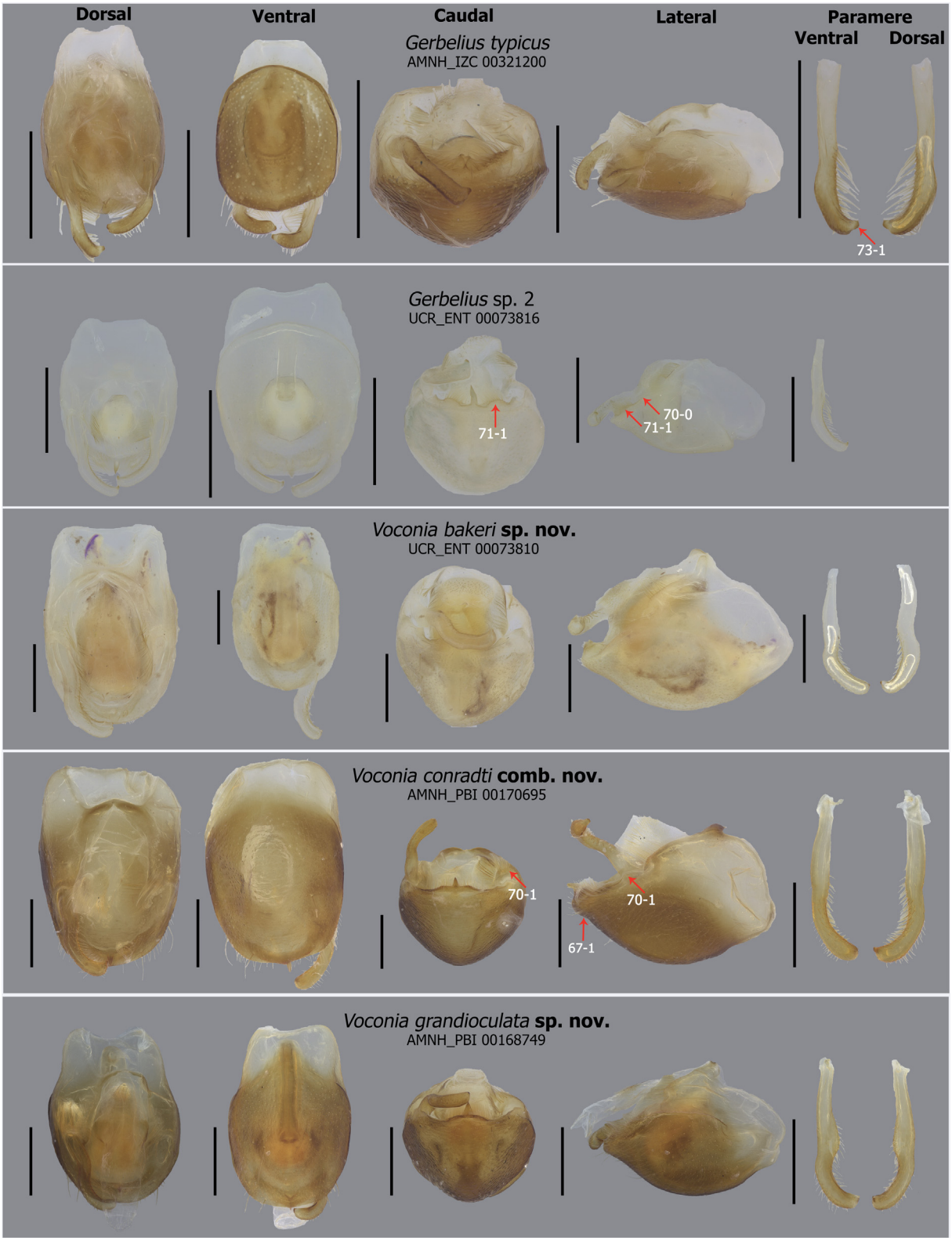

Fig. 11. Pygophore of species of *Gerbelius* Distant, 1903 and *Voconia* Stål, 1866. Median apical process of *Gerbelius typicus* Distant, 1903 and *V. bakeri* sp. nov. damaged/missing. Scale bars = 0.5 mm.

Female

Mostly as male but differs from males by the following. Body length: about 11.2 mm. Head: elongate, about 1.4 times as long as wide; pedicel about 1.2 times length of head width; ocelli minute, occupying 0.15 times length of postocular region. Legs: fossula absent or vestigial on mid leg.

Distribution (Fig. 17)

This species is distributed in Western Africa. The type locality is from Bioko, an island off the west coast, north of Equatorial Guinea.

Remarks

Originally described as *Microvarus conradti* based on several specimens which are to be treated as syntypes (Jeannel 1917). The type material of *M. conradti* is deposited at the MNHN under loan restrictions; habitus photographs of one of the syntypes (Fig. 7; USI: MNHN_EH24709) were used to evaluate this species concept and this specimen is designated as the lectotype. The synonymy of *M. achteni* proposed by Villiers (1948) is accepted here without re-examining the type material of Schouteden (1929). This species is transferred to *Voconia* based on the cladistic analysis conducted in this study. Based on the phylogeny, *V. conradti* and *V. smithae* sp. nov. form a well-supported clade (Figs 1–2).

Voconia coronata sp. nov.
urn:lsid:zoobank.org:act:13ED6C82-C06A-4DE4-92E3-EAD71C9B8D71
Figs 1–2, 7, 9, 20

Diagnosis

Distinguished from most species of *Voconia* by the semicircular yellow stripe encircling both ocelli, membranal veins forming Cu-An_1 and M-Cu cells paler than remainder of membrane, and proepimeron with protuberance on posteroventral margin. This species is most similar to two other Oriental species, *V. decorata* sp. nov. and *V. lirophleps* sp. nov. It is distinguishable from *V. decorata* sp. nov. by its distribution in Sumatra and the dark brown, almost black coloration of the body. Despite the holotypes of *V. coronata* sp. nov. and *V. lirophleps* sp. nov. being collected within about 106 km of each other, there are several differences, particularly in size. Among our larger series, conspecific *Voconia* males do not vary more than about ± 1 mm from each other, and *V. coronata* sp. nov. is about 2 mm longer than *V. lirophleps* sp. nov. It is distinguishable by the slightly more elongate head (about 1.3 times as long as wide), the pedicel is much longer (about 1.9 times length of head width), maxillary plates directed straight in dorsal view, postocular region is about as long as the eye, labial segment I is long, almost reaching posterior margin of head, wide pronotal collar, long anterior pronotal lobe relative to posterior pronotal lobe (posterior lobe about 1.8 times as long as anterior lobe), scutellum dark with brown apical spine, inconspicuous distal yellow spot on the corium, and the presence of three large spines and many small spines on the posterior row of spines of the hind leg.

Etymology

The specific epithet is the Latin adjective '*coronatus*, *-a*, *-um*', meaning 'crowned' or 'encircled', referring to the yellow ring around the postocular region of the head.

Type material

Holotype

INDONESIA • ♀; Sumatra, "Central Atjeh" [Aceh], Ketambe; [3.68° N, 97.66° E]; elev. 400 m; 26–27 Jan. 1974; E.W. Diehl leg.; USI: AMNH_PBI 00170706; AMNH.

Description

Male (Figs 7, 9)

Body length. About 11.0 mm; macropterous.

Coloration. Head: dark brown; postocular region dark with a semicircular pale stripe encircling both ocelli; labium nearly as dark as head. Thorax: coloration as head; posterior pronotal lobe lighter than anterior lobe; scutellum dark with brown apical spine. Hemelytron (abducted): clavus dark with distal yellow stripe; corium dark with anteroproximal yellow stripe, posteromedial and small distal yellow spots; membrane uniformly dark; membranal veins forming Cu-An_1 and M-Cu cells paler than remainder of membrane. Legs: dark brown, femora darker. Abdomen: almost black, dorsal laterotergites dark with yellow spots anteriorly.

Integument and vestiture. Head and pronotum: finely granulose with sparse, short macrosetae interspersed among sparse pubescence; interocular region with two pairs of macrosetae paramedially; antennifer with short lateral setigerous tubercle; morphologically ventral surface of labium with sparse, long macrosetae. Thorax: anterolateral angles of pronotal collar with macrosetae; scutellar lateral carinae with long setation. Hemelytron: corium with sparse long setation. Legs: posterior row of protuberances on mid and hind femora with three large spines on distal half and more than three small spines. Abdomen: ventral surface pubescent.

Structure. Head: elongate, 1.3 times as long as wide; anteocular region about one quarter of head length, shorter than postocular region (measured to anterior margin of neck); postocular region in dorsal view about as long as eye, lateral margins gently rounded; pedicel about 1.9 times length of head width; maxillary plates ellipsoidal, adjacent to and surpassing clypeal apex; apices of maxillary plates in dorsal view directed straight; clypeus in dorsal view wider than maxillary plates; clypeal apex round, not narrowed; interocular glabrous markings anterolaterally curved, joined at interocular sulcus paramedially; interocular sulcus in dorsal view bent anteromedially, subtriangular; eye width in dorsal view wider than synthlipsis; eye reaching ventral head margin in lateral view; ventrolateral swelling of buccula without lateral protrusion that surpasses buccular margin, flat margin; labial segment I in lateral view straight, surpassing posteroventral eye margin; morphologically dorsal surface of labial segment II nearly straight, about 0.5 times length of segment I. Thorax: pronotal collar in dorsal view wide medially with anterolateral angles short and flared laterally; anterior pronotal lobe about 0.6 times length of posterior pronotal lobe, lateral margins rounded; glabrous markings on pronotum deeply depressed; median apodeme depression of pronotum shallow, elongated transversely; scutellar spine long, raised; anteriad-directed process of prosternum smoothly rounded, without paramedial lobes; anterior margin of stridulitrum not elongated into protuberance; proepimeron with acute protuberance on posteroventral margin. Legs: fossula spongiosa present on fore and mid legs.

Female

Unknown.

Distribution (Fig. 20)

This species is only known from the type locality of Ketambe in the northernmost province of Sumatra, Aceh.

Remarks

The phylogenetic placement of *V. coronata* sp. nov. is uncertain (Figs 1–2).

Voconia decorata sp. nov.
urn:lsid:zoobank.org:act:93BE46E2-210B-45C7-8FD6-2C38EC62B2D9
Figs 1–2, 3B, 4J, 7, 9, 20

Diagnosis

Distinguished from most other species of *Voconia* by the yellow ring around the postocular region, membranal veins forming Cu-An_1 and M-Cu cells paler than remainder of membrane, and proepimeron with protuberance on posteroventral margin. This species is most similar to two other Oriental species, *V. coronata* sp. nov. and *V. lirophleps* sp. nov. It is distinguishable from these species by its distribution in the Malaysian state of Sabah in Borneo, the light brown coloration of the body, the labium being lighter than the head, and the dark scutellum with a contrasting yellow apical spine.

Etymology

The specific epithet is the Latin adjective '*decoratus*, *-a*, *-um*', meaning 'decorated, elegant', referring to its light brown coloration and yellow markings on the hemelytron and dorsal laterotergites that gives it a flashier and more elegant look.

Type material

Holotype

MALAYSIA ["NORTH BORNEO"] • ♀; Sabah, Tawau, Quoin Hill, Cocoa Res. Stn, [4.42° N, 118.02° E]; elev. 225 m; 16 Sep. 1962; K.J. Kuncheria leg.; USI: UCR_ENT 00073809; BPBM.

Description

Male (Figs 7, 9)

Body length. About 10.0 mm; macropterous.

Coloration. Head (Fig. 3B): light brown, yellowish; postocular region with dark patches adjacent to medial ocellar margin, semicircular pale stripe encircling both ocelli; labium lighter than head. Thorax: coloration as head; posterior margin of posterior pronotal lobe lighter; scutellum dark with contrasting yellow apical spine. Hemelytron (abducted): clavus reddish-brown with distal yellow stripe; corium reddish-brown with anteroproximal yellow stripe, posteromedial and distal yellow spots; membrane light brown with pale V-shaped marking along R and M veins; membranal veins forming Cu-An_1 and M-Cu cells paler than remainder of membrane. Legs: yellowish-brown, distal half of femora darker. Abdomen: yellowish-brown, dorsal laterotergites with yellow spots anteriorly.

Integument and vestiture. Head (Fig. 3B) and pronotum: finely granulose with sparse, short macrosetae interspersed among sparse pubescence; antennifer with short lateral setigerous tubercle; morphologically ventral surface of labium with dense, short macrosetae. Thorax: anterolateral angles of pronotal collar with macrosetae. Hemelytron: corium with sparse, long setation. Legs (Fig. 4J): posterior row of protuberances on mid and hind femora with three large spines on distal half and one small spine. Abdomen: ventral surface pubescent.

Structure. Head (Fig. 3B): elongate, 1.3 times as long as wide; anteocular region about one third of head length, shorter than postocular region (measured to anterior margin of neck); postocular region in dorsal view shorter than eye, lateral margins gently rounded; pedicel about 1.3 times length of head width; maxillary plates ellipsoidal, adjacent to and as long as clypeus; apices of maxillary plates in dorsal view directed straight; clypeus in dorsal view about as wide as maxillary plates; clypeal apex round, not narrowed; interocular glabrous markings anterolaterally curved, joined at interocular sulcus paramedially; interocular sulcus in dorsal view bent anteromedially, subtriangular; eye width in dorsal

view narrower than synthlipsis; eye reaching ventral head margin in lateral view; ventrolateral swelling of buccula with lateral protrusion that surpasses buccular margin; labial segment I in lateral view straight, surpassing posteroventral eye margin; morphologically dorsal surface of labial segment II nearly straight, about 0.5 times length of segment I. Thorax: pronotal collar in dorsal view wide medially with anterolateral angles short, projected forward; anterior pronotal lobe about 0.7 times length of posterior pronotal lobe, lateral margins almost straight; glabrous markings on pronotum deeply depressed; median apodeme depression of pronotum shallow, elongated longitudinally; scutellar spine long, subhorizontal; anteriad-directed process of prosternum smoothly rounded, without paramedial lobes; anterior margin of stridulitrum not elongated into protuberance; proepimeron with acute protuberance on posteroventral margin. Legs: fossula spongiosa present on fore and mid legs.

Female

Unknown.

Distribution (Fig. 20)

This species is only known from the type locality of Quoin Hill in the Malaysian state of Sabah on the island of Borneo.

Remarks

The phylogenetic placement of *V. decorata* sp. nov. is uncertain (Figs 1–2).

Voconia dolichocephala sp. nov.
urn:lsid:zoobank.org:act:7528828E-ADAD-49A4-BA42-98BCE32BF011
Figs 1–2, 6–7, 9, 18

Diagnosis

Distinguished from most other species of *Voconia* by its tuberculate and coarsely granulose head and pronotum. This species most closely resembles another Australian species, *V. tuberculata* sp. nov. These two species are recognized from other Australian species by the acute protuberance on the posteroventral margin of the proepimeron, long macrosetae of the setigerous tubercles, elongate head (1.4–1.6 times as long as wide), and yellow spots antero- and posteromedially on the abducted corium. *Voconia dolichocephala* sp. nov. differs from *V. tuberculata* sp. nov. by its overall dark brown, almost black coloration, dorsal laterotergites uniformly dark or with yellow spots posteriorly, and males are smaller than about 7.5 mm. Females slightly surpass the high-end range for female length of *V. tuberculata* sp. nov. (8.4–8.8 mm).

Etymology

The specific epithet is the latinized Greek adjective '*dolichocephalus*, *-a*, *-um*', formed from the prefix '*dolicho-*' (meaning 'long') and the noun '*cephale*' (meaning 'head'), referring to the long head of the type specimen, which is about a fifth of the body length.

Type material

Holotype

AUSTRALIA • ♀; Northern Territory, Tindal; [14.52° S, 132.38° E]; 1–20 Dec. 1967; W. Vestjens leg.; at light; USI: AMNH_PBI 00168747; ANIC.

Paratypes

AUSTRALIA • 1 ♀; Northern Territory, Kakadu NP, S Alligator River, Gungaree Rainforest; [12.65° S, 132.47° E]; 17 Dec. 1993; S. and J. Peck leg.; coll. S. and J Peck 93-131; at light; USI: AMNH_PBI

00170709; deposited in AMNH • 1 ♀; same collection data as for holotype; USI: AMNH_PBI 00168748; AMNH • 1 ♂; same collection data as for holotype; USI: AMNH_PBI 00168745; AMNH.

Description

Male (Figs 7, 9)

Body length. 7.1–7.5 mm; macropterous.

Coloration. Head (Fig. 3F): dark brown; postocular region uniformly dark with pale patches adjacent to lateral ocellar margin; labial segment I nearly as dark as head, segments II and III lighter than head. Thorax: coloration as head; scutellum uniformly dark brown. Hemelytron (abducted): clavus dark brown with distal yellow stripe; corium dark brown with anteromedial, posteromedial, and distal yellow spots; membrane dark with pale V-shaped marking along R and M veins; membranal veins R and M proximally pale. Legs: dark brown, tarsi yellow. Abdomen: dark brown; dorsal laterotergites uniformly dark or dark with yellow spots posteriorly.

Integument and vestiture. Head (Fig. 3F) and pronotum: coarsely granulose with sparse, long setigerous tubercles interspersed among sparse pubescence; interocular region with two pairs of stout setigerous tubercles paramedially; antennifer with long lateral setigerous tubercle; morphologically ventral surface of labium with sparse, short macrosetae. Thorax: anterolateral angles of pronotal collar with setigerous tubercles; scutellar lateral carinae with setigerous tubercles with long macrosetae. Hemelytron: corium with dense long setation. Legs: posterior row of protuberances on mid and hind femora with four large spines on distal half. Abdomen: ventral surface pubescent, long macrosetae interspersed.

Structure. Head (Fig. 3F): elongate, 1.5–1.6 times as long as wide; anteocular region about one third of head length, shorter than postocular region (measured to anterior margin of neck); postocular region in dorsal view as long as eye, lateral margins gently rounded; pedicel 1.3–1.5 times length of head width; maxillary plates ellipsoidal, adjacent to and as long as clypeus; apices of maxillary plates in dorsal view with medial margins diverging; clypeus in dorsal view wider than maxillary plates; clypeal apex bifid, not narrowed; interocular glabrous markings V-shaped, joined medially at interocular sulcus; interocular sulcus in dorsal view nearly straight; eye width in dorsal view narrower than synthlipsis; eye reaching ventral head margin in lateral view; ventrolateral swelling of buccula without lateral protrusion that surpasses buccular margin, flat margin; labial segment I in lateral view straight, surpassing posteroventral eye margin; morphologically dorsal surface of labial segment II curves ventrally, 0.3–0.4 times length of segment I. Thorax: pronotal collar in dorsal view wide medially with anterolateral angles long, flared laterally; anterior pronotal lobe 0.7–0.8 times length of posterior pronotal lobe, lateral margins almost straight; glabrous markings on pronotum conspicuous and not depressed; median apodeme depression of pronotum shallow, elongated longitudinally; scutellar spine long, subhorizontal; anteriad-directed process of prosternum with paramedial lobes; anterior margin of stridulitrum projected into small protuberance; proepimeron with acute protuberance on posteroventral margin. Legs: fossula spongiosa present on fore and mid legs. Abdomen: anterior margin of terga weakly carinulate, terga II and III with deeper and longer carinules; terga II and III with paired prominent longitudinal carinae, reaching about two-thirds of tergum III.

Female

Mostly as male, distinguished from males by the following. Body length: 8.8–9.0 mm. Head: elongate, 1.5–1.6 times as long as wide; pedicel about 1.5–1.7 times length of head width. Legs: fossula spongiosa absent or vestigial on mid leg.

Distribution (Fig. 18)

This species is only known from the Northern Territory of Australia. The nearest species of *Voconia* is *V. tuberculata* sp. nov., known from about 100 km southeast of the three specimens collected in Tindal.

Remarks

Voconia dolichocephala sp. nov. is nested among the Australian clade. According to the phylogeny (Figs 1–2), it is the sister taxon to *V. tuberculata* sp. nov.

Voconia fasciata sp. nov.
urn:lsid:zoobank.org:act:22FAB401-5B52-4866-86CD-0ED8B980A3A5
Figs 1–2, 7, 9, 18

Diagnosis

Distinguished from most other species of *Voconia* by its tuberculate and coarsely granulose head and pronotum, lateral protrusion of the buccula, and dorsally projecting mandibular plates. This species most closely resembles three other Australian species, *V. grandioculata* sp. nov., *V. pallidipes*, and *V. vittata* sp. nov. This species, *V. grandioculata* sp. nov., and *V. vittata* sp. nov. have a similar yellow stripe across the corium; however, the stripe in *V. fasciata* sp. nov. is pale, almost translucent and the body is larger, total length is about 8.7 mm long. It is easily distinguished from *V. pallidipes* by its smaller size and coloration, i.e., the membranal veins are not yellow, the proximal half of the corium is not entirely yellow, and the legs are not completely yellow as described above.

Etymology

The specific epithet is the Latin adjective '*fasciatus*, *-a*, *-um*', meaning 'banded', referring to the pale yellow band that crosses the middle of the corium and scutellar spine.

Type material

Holotype
AUSTRALIA • ♂; Queensland, Einasleigh River, 33 km W of Mt Surprise; [18.13° S, 143.99° E]; 10–11 Jun. 1993; M. and B. Baehr leg.; USI: AMNH_PBI 00127097; ZSMC.

Description

Male (Figs 7, 9)
Body length. About 8.7 mm; macropterous.

Coloration. Dark brown, maxillary plates lighter; postocular dark with pale patches adjacent to lateral ocellar margin; labium lighter than head. Thorax: coloration as head; posterior pronotal lobe with yellow posterolateral margins; scutellum dark with contrasting yellow apical spine. Hemelytron (abducted): clavus dark brown with distal yellow stripe; corium dark brown with thick medial yellow stripe; membrane and membranal veins uniformly dark. Legs: femora dark brown, tibiae and tarsi yellowish-brown. Abdomen: ventral surface light brown medially, dark brown laterally; dorsal laterotergites I and II paler than remainder.

Integument and vestiture. Head and pronotum: coarsely granulose with dense, short setigerous tubercles interspersed among sparse pubescence; interocular region with setigerous tubercles medially and two pairs paramedially; antennifer with long lateral setigerous tubercle; morphologically ventral surface of labium with sparse, short macrosetae. Thorax: anterolateral angles of pronotal collar with setigerous tubercles; scutellar lateral carinae with short macrosetae on setigerous tubercles. Hemelytron:

corium with dense, long macrosetae. Legs: posterior row of protuberances on mid and hind femora with four spines on distal half. Abdomen: ventral surface pubescent, long macrosetae interspersed.

Structure. Head: globose, about as long as wide; anteocular region about one third of head length, about as long as postocular region (measured to anterior margin of neck); postocular region in dorsal view shorter than eye, lateral margins gently rounded; pedicel about 1.3 times length of head width; mandibular plates in anterior view projecting dorsolaterally; maxillary plates ellipsoidal, adjacent to and reaching apex of clypeus; apices of maxillary plates in dorsal view diverging; clypeus in dorsal view wider than maxillary plates; clypeal apex bifid, narrowed; interocular glabrous markings anterolaterally curved, joined at interocular sulcus paramedially; interocular sulcus in dorsal view nearly straight; eye width in dorsal view narrower than synthlipsis; eye reaching ventral head margin in lateral view; ventrolateral swelling of buccula with lateral protrusion that surpasses buccular margin, setigerous tubercles along apical margin; labial segment I in lateral view gradually thickens distally, surpassing posteroventral eye margin; morphologically dorsal surface of labial segment II curves ventrally, about 0.3 times length of segment I. Thorax: pronotal collar in dorsal view wide medially with anterolateral angles short, flared laterally; anterior pronotal lobe about 0.7 times length of posterior pronotal lobe, lateral margins almost straight; glabrous markings on pronotum depressed near posterolateral margins; median apodeme depression of pronotum shallow, elongated transversely; scutellar spine long, subhorizontal; anteriad-directed process of prosternum with paramedial lobes; anterior margin of stridulitrum projected into sharp spine; proepimeron with smoothly rounded posteroventral margin. Legs: fossula spongiosa present on fore and mid legs.

Female

Unknown.

Distribution (Fig. 18)

This species is only known from the type locality of Einasleigh River in Queensland, Australia.

Remarks

Voconia fasciata sp. nov. is nested within the Australian clade (Figs 1–2). Though poorly supported, it forms the sister taxon to *V. brachycephala* sp. nov. and *V. vittata* sp. nov.

Voconia grandioculata sp. nov.
urn:lsid:zoobank.org:act:23167BBE-77C8-434F-9574-B9F59130EAAB
Figs 1–2, 4E, 7, 9, 11, 14, 18

Diagnosis

Distinguished from most other species of *Voconia* by its tuberculate and coarsely granulose head and pronotum, the lateral protrusion of the buccula, and notably the large ocelli that occupy half the length of the postocular region. Due to the yellow stripe across the corium, this species resembles two other Australian species, *V. fasciata* sp. nov. and *V. vittata* sp. nov. However, the yellow stripe of this species is bright and opaque, unlike that of *V. fasciata* sp. nov. Additionally, the legs are entirely yellow, and the corium has a small proximal yellow spot. It is easily distinguished from *V. pallidipes* by the brown membranal veins, the proximal half of the corium being not entirely yellow, and its globose head.

Etymology

The specific epithet is the Latin adjective '*grandioculatus*, *-a*, *-um*', formed from the prefix '*grandi-*' (meaning 'large') combined with the adjective '*oculatus*, *-a*, *-um*' (meaning 'possessing eyes'), referring to the large ocelli of this species, occupying half the length of the postocular region.

Type material

Holotype

AUSTRALIA • ♂ (dissected pygophore and aedeagus in vial); Queensland, 3 km NE of Mt Webb; [15.05° S, 145.15° E]; 30 Apr.–3 May 1981; A. Calder leg.; at light; USI: AMNH_PBI 00168749; ANIC.

Paratype

AUSTRALIA • 1 ♂; Western Australia, East York; USI: AMNH_PBI 00213934; HNHM.

Description

Male (Figs 7, 9)

Body length. 9.2–9.7 mm; macropterous.

Coloration. Head: dark brown; postocular region with pale patches adjacent to lateral ocellar margin; labial segment I yellowish brown, segments II and III yellow. Thorax (Fig. 4E): coloration as head; scutellum dark with contrasting yellow apical spine. Hemelytron (abducted): clavus dark brown with distal yellow stripe; corium proximal half mostly yellow, distal half dark brown with yellow spot at distal apex; membrane dark with pale V-shaped marking along R and M veins; membranal veins R and M proximally pale. Legs: yellow. Abdomen: dark brown; dorsal laterotergites uniformly colored.

Integument and vestiture. Head and pronotum: coarsely granulose with dense, short setigerous tubercles interspersed among sparse pubescence; interocular region with setigerous tubercles medially and two pairs paramedially; antennifer with long lateral setigerous tubercle; morphologically ventral surface of labium with sparse, short macrosetae. Thorax: anterolateral angles of pronotal collar with setigerous tubercles; scutellar lateral carinae with short macrosetae on setigerous tubercles. Hemelytron: corium with dense, long macrosetae. Legs: posterior row of protuberances on mid and hind femora with four spines on distal half. Abdomen: ventral surface pubescent.

Structure. Head: globose, about as long as wide; anteocular region about one quarter of head length, shorter than postocular region (measured to anterior margin of neck); postocular region in dorsal view shorter than eye, lateral margins gently rounded; pedicel 1.4–1.6 times length of head width; maxillary plates ellipsoidal, adjacent to and as long as clypeus; apices of maxillary plates in dorsal view diverging; clypeus in dorsal view wider than maxillary plates; clypeal apex bifid, not narrowed; interocular glabrous markings anterolaterally curved, joined at interocular sulcus paramedially; interocular sulcus in dorsal view nearly straight; eye width in dorsal view about as wide as synthlipsis; eye reaching ventral head margin in lateral view; ocelli large, occupying half-length of postocular region; ventrolateral swelling of buccula with lateral protrusion that surpasses buccular margin, setigerous tubercles along apical margin; labial segment I in lateral view gradually thickens distally, reaching posteroventral eye margin; morphologically dorsal surface of labial segment II curves ventrally, about 0.4 times length of segment I. Thorax: pronotal collar in dorsal view narrow medially with anterolateral angles short, flared laterally; anterior pronotal lobe 0.6–0.7 times length of posterior pronotal lobe, lateral margins almost straight; glabrous markings on pronotum depressed near posterolateral margins; median apodeme depression of pronotum shallow, elongated transversely; scutellar spine long, raised (Fig. 4E); anteriad-directed process of prosternum with paramedial lobes; anterior margin of stridulitrum projected into sharp spine; proepimeron with smoothly rounded posteroventral margin. Legs: fossula spongiosa present on fore and mid legs. Abdomen: anterior margin of tergum III weakly carinulate, remaining terga not carinulate; terga II and III with paired prominent longitudinal carinae, reaching about one-third of tergum III. Pygophore (Fig. 11): transverse bridge with rounded posterior margin; posterior region of ventral surface of pygophore in lateral view with slight swelling; median apical process short, sharply bent posteriorly in

lateral view; lateral pygophore margin with protuberance; posterior pygophore margin with clustered macrosetae on protuberance; parameres sinusoidal, apex round, not sharply tapered or expanded. Aedeagus (Fig. 14): endosoma almost entirely covered with spicules; apex of dorsal phallothecal sclerite tongue-shaped in dorsal view; basal plate extension about 5.7 times as long as wide.

Female

Unknown.

Distribution (Fig. 18)

This species is known from Queensland and Western Australia.

Remarks

The phylogenetic placement of *V. grandioculata* sp. nov. within the Australian clade is uncertain (Figs 1–2). The abdomen of the holotype was extracted, but we did not get sufficient DNA in our NGS library for Illumina sequencing.

Voconia hemera sp. nov.
urn:lsid:zoobank.org:act:A6B29189-616B-4489-BAE0-4A1F5F055DEA
Figs 1–2, 7, 9, 20

Diagnosis

This species is most similar to other Southeast Asian *Voconia* species with a finely granulose head and pronotum and yellow spots on the anteromedial, posteromedial, and distal apex of the abducted corium. *Voconia hemera* sp. nov. is larger than *V. minima* sp. nov. (9.2–9.3 mm). It is distinguished from *V. ornata*, *V. nyx* sp. nov., and *V. bakeri* sp. nov. by its uniformly yellow legs and antenna as well as its uniformly brown scutellum and dorsal laterotergites.

Etymology

Named after the Greek primordial goddess of the day, Hemera. Refers to the yellow legs and antennae of this species, which differs from a similar yet darker species, *V. nyx* sp. nov., named after the goddess of night. A proper noun in apposition.

Type material

Holotype

PHILIPPINES • ♂; Laguna, Los Baños; [14.17° N, 121.18° E]; 1925; Pemberton leg.; USI: UCR_ENT 00073812; BPBM.

Paratype

PHILIPPINES • 1 ♂; Luzon, Camarines Sur, Mt Isarog, Pili; [13.66° N, 123.37° E]; elev. 800 m; 25 Apr. 1965; H.M. Torrevillas leg.; light trap; USI: UCR_ENT 00073813; BPBM.

Description

Male (Figs 1–2)

Body length. 9.2–9.3 mm; macropterous.

Coloration. Head: dark brown; postocular region with dark patches adjacent to medial ocellar margin, semicircular pale stripe encircling both ocelli; labium lighter than head, brownish yellow. Thorax: as head; scutellum uniformly dark brown. Hemelytron (abducted): clavus reddish-brown with distal yellow stripe; corium reddish-brown with anteromedial, posteromedial, and distal yellow spots; membrane dark

with pale V-shaped marking along R and M veins; membranal veins R and M proximally pale. Legs: yellowish-brown. Abdomen: dark brown.

Integument and vestiture. Head and pronotum: finely granulose with dense, long macrosetae interspersed among dense pubescence; interocular region with two pairs of macrosetae paramedially; antennifer with short lateral setigerous tubercle; morphologically ventral surface of labium with dense, short macrosetae. Thorax: anterolateral angles of pronotal collar with macrosetae; scutellar lateral carinae with long setation. Hemelytron: corium with sparse long setation. Legs: posterior row of protuberances on mid and hind femora with three large and two small spines. Abdomen: ventral surface pubescent.

Structure. Head: elongate, about 1.3 times as long as wide; anteocular region about one third of head length, shorter than postocular region (measured to anterior margin of neck); postocular region in dorsal view about as long as eye, lateral margins gently rounded; pedicel about 1.2 times length of head width; maxillary plates ellipsoidal, adjacent to and as long as clypeus; apices of maxillary plates in dorsal view directed straight; clypeus in dorsal view wider than maxillary plates; clypeal apex round, not narrowed; interocular glabrous markings anterolaterally curved, joined at interocular sulcus paramedially; interocular sulcus in dorsal view bent anteromedially, subtriangular; eye width in dorsal view narrower than synthlipsis; eye reaching ventral head margin in lateral view; ventrolateral swelling of buccula without lateral protrusion that surpasses buccular margin, flat margin; labial segment I in lateral view straight, surpassing posteroventral eye margin; morphologically dorsal surface of labial segment II nearly straight, about 0.5 times length of segment I. Thorax: pronotal collar in dorsal view narrow medially, projected forward; anterior pronotal lobe about 0.8 times length of posterior pronotal lobe, lateral margins rounded; glabrous markings on pronotum thin, gently depressed; median apodeme depression of pronotum shallow, elongated transversely; scutellar spine long, raised; anteriad-directed process of prosternum smoothly rounded, without paramedial lobes; anterior margin of stridulitrum not elongated into protuberance; proepimeron with acute protuberance on posteroventral margin. Legs: fossula spongiosa present on fore and mid legs.

Female

Unknown.

Distribution

This species is only known from the type locality on the Philippine island of Luzon.

Remarks

The holotype locality of Los Baños is about 10 km from the holotype locality of *V. nyx* sp. nov. at Mt Maquiling.

Voconia ifana (Villiers, 1963) comb. nov.
Fig. 17

Pseudocethera ifana Villiers, 1963a: 989, fig. 11.

Revised diagnosis

Distinguished from other species of *Voconia* by the following combination of characters: short body length (about 6.5 mm); coarsely granulose head and pronotum; maxillary plates are not adjacent to and far surpass clypeal apex; maxillary plates in lateral view are wide, about twice the width of scape; antennifer with long lateral spine; eyes do not reach ventral head margin in lateral view. It is recognized from micropterous individuals of *V. schoutedeni* and *V. monodi* by the toothed apex of the maxillary plates.

Type material

Holotype

SENEGAL • ♂; "Forêt classée de Tobor" [Tobor Forest]; 21 Nov. 1961; "Mission IFAN" [Institut Fondamental d'Afrique Noire exped.]; "sous un morceau de bois mort" [under a piece of dead wood]; MNHN.

Description

Male

Body length. About 6.5 mm; micropterous.

Coloration. As described for *V. monodi*, except legs testaceous.

Integument and vestiture. Head and pronotum: coarsely granulose with setigerous tubercles; interocular region with two pairs of large setigerous tubercles paramedially.

Structure. Head: scape not reaching head apex; antennifer with long lateral spine; postocular region in dorsal view as long as eye, lateral margins subrectangular; maxillary plates in lateral view about twice the width of scape and apex toothed; eye not reaching ventral head margin in lateral view; ventrolateral swelling of buccula with lateral protrusion that surpasses buccular margin; labial segment I in lateral view straight, surpassing posteroventral eye margin. Thorax: scutellar spine reduced, subhorizontal. Abdomen: anterior margin of terga carinulate; tergum II with paired prominent longitudinal carinae reaching posterior margin of segment.

Female

Unknown.

Distribution (Fig. 17)

This species is known from Northwest Africa.

Remarks

The holotype was on loan and not available for study at the time we requested it. Consequently, this description is based on the interpretation of the short differential diagnosis and illustration of the head in lateral view provided by Villiers (1963a). Due to the limited data that we were able to obtain, it was excluded from cladistic analyses, but we are confident that it likely forms a clade with *V. schoutedeni* and *V. tridens* sp. nov. because of the unique head morphology, micropterу, and Afrotropical distribution.

Voconia isosceles sp. nov.
urn:lsid:zoobank.org:act:826EFBC8-FA03-42DA-8E5E-E0D4F29A5B66
Figs 1–2, 7, 9, 20

Diagnosis

This species most closely resembles another Southeast Asian species, *V. loki* sp. nov., due to the finely granulose head and pronotum, yellow legs and antennae, dark pronotum with contrasting yellow posterior margin, and the proximal half of the corium being entirely yellow, distal half dark with small distal yellow spot. *Voconia isosceles* sp. nov. is slightly larger (about 8.8 mm long), the membranal veins forming the Cu-An_1 and M-Cu cells are paler than the remainder of the membrane, and the postocular region is dark with a semicircular pale stripe encircling both ocelli.

Etymology

The specific epithet is the Latin adjective '*isosceles*, -, -', which has the same meaning as its equivalent geometric term used in English for a triangle having at least two sides of equal length (also known as a golden triangle). Refers to the yellow or golden isosceles triangle on the proximal half of the corium.

Type material

Holotype

PHILIPPINES • ♂; Mindanao, Gingoog City**,** Mts Or., Mt Pomalihi, 21 km W of Gingoog City; [8.81° N, 124.92° E]; elev. 800–1000 m; 16–18 Oct. 1965; H.M. Torrevillas leg.; light trap; USI: UCR_ENT 00073814; BPBM.

Description

Male (Figs 7, 9)

Body length. About 8.8 mm; macropterous.

Coloration. Head: dark brown; postocular region with dark patches adjacent to medial ocellar margin, semicircular pale stripe encircling both ocelli; labium lighter than head, yellow. Thorax: as head; posterior pronotal lobe with posterior margin lighter, yellow; scutellum dark with contrasting yellow apical spine. Hemelytron (abducted): clavus reddish-brown with distal yellow stripe; corium proximal half yellow, distal half reddish-brown with yellow spot at distal apex; membrane brown with pale V-shaped marking along R and M veins; membranal veins forming Cu-An_1 and M-Cu cells paler than remainder of membrane. Legs: yellow. Abdomen: dark brown ventrally; laterotergites light brown.

Integument and vestiture. Head and pronotum: finely granulose with dense, long macrosetae interspersed among dense pubescence; interocular region with two pairs of macrosetae paramedially; antennifer with short lateral setigerous tubercle; morphologically ventral surface of labium with dense, short macrosetae. Thorax: anterolateral angles of pronotal collar with macrosetae; scutellar lateral carinae with long setation. Hemelytron: corium with dense long setation. Legs: posterior row of protuberances on mid and hind femora with three large spines on distal half. Abdomen: ventral surface pubescent, long macrosetae interspersed.

Structure. Head: elongate, about 1.3 times as long as wide; anteocular region about one third of head length, about as long as postocular region (measured to anterior margin of neck); postocular region in dorsal view about as long as eye, lateral margins gently rounded; pedicel about 1.4 times length of head width; maxillary plates ellipsoidal, adjacent to and as long as clypeus; apices of maxillary plates in dorsal view directed straight; clypeus in dorsal view wider than maxillary plates; clypeal apex round, not narrowed; interocular glabrous markings anterolaterally curved, joined at interocular sulcus paramedially; interocular sulcus in dorsal view bent anteromedially, subtriangular; eye width in dorsal view narrower than synthlipsis; eye reaching ventral head margin in lateral view; ventrolateral swelling of buccula without lateral protrusion that surpasses buccular margin, flat margin; labial segment I in lateral view straight, surpassing posteroventral eye margin; morphologically dorsal surface of labial segment II nearly straight, about 0.3 times length of segment I. Thorax: pronotal collar in dorsal view narrow medially with anterolateral angles short, projected forward; anterior pronotal lobe about 0.6 times length of posterior pronotal lobe, lateral margins rounded; glabrous markings on pronotum conspicuous and not depressed; median apodeme depression of pronotum shallow, elongated transversely; scutellar spine long, raised; anteriad-directed process of prosternum smoothly rounded, without paramedial lobes; anterior margin of stridulitrum not elongated into protuberance; proepimeron with acute protuberance on posteroventral margin. Legs: fossula spongiosa present on fore and mid legs. Abdomen: anterior

margin of terga prominently carinulate; terga II and III with paired prominent longitudinal carinae, almost reaching posterior margin of tergum III.

Female

Unknown.

Distribution (Fig. 20)

This species is only known from the type locality in the Philippines.

Remarks

Based on the record of a Miridae specimen from the same collection event as the holotype, Mt Pomalihi is presumably in Mt Balatukan Range Natural Park. The type locality is also shared with *V. bakeri* sp. nov. Though *V. isosceles* sp. nov. and *V. loki* sp. nov. closely resemble each other, we are treating them as separate species because they were not recovered as closely related taxa in our analyses (Figs 1–2). This hypothesis should be further tested with additional material.

Voconia laosensis sp. nov.
urn:lsid:zoobank.org:act:D92E888A-8436-42C2-8316-881775941725
Figs 1–2, 7, 9, 12, 14, 20

Diagnosis

This species is distinguishable by the elongate Cu-An_1 cell (reaching at least half the length of M-Cu cell) and short labial segment I (not surpassing ventral eye margin in lateral view). This species most closely resembles three other Southeast Asian species, *V. isosceles* sp. nov., *V. lasiosoma* sp. nov., and *V. loki* sp. nov., due to the finely granulose head and pronotum, long setation of the body, semicircular pale stripe encircling both ocelli, and the dark pronotum with contrasting pale posterior margin. However, in *V. laosensis* sp. nov. this pale posterior margin occupies almost the entire posterior pronotal lobe.

Etymology

A proper noun with the Latin adjectival suffix '-*ensis*' meaning 'belonging to', referring to the country of the type locality, Laos. To be treated as an adjective.

Type material

Holotype

LAOS • ♂ (dissected pygophore and aedeagus in vial); Khammouan Prov., Ban Khoun Ngeun; 18.11666° N, 104.48333° E; elev. 250 m; 4–16 Nov. 2000; E. Jendek and P. Pacholátko leg.; USI: UCR_ENT 00001552; NHMW.

Description

Male (Figs 7, 9)

Body length. About 9.2 mm; macropterous.

Coloration. Head: dark brown, maxillary plates and clypeus lighter; postocular region with dark patches adjacent to medial ocellar margin, semicircular pale stripe encircling both ocelli; labium lighter than head, yellow. Thorax: as head; posterior pronotal lobe lighter than anterior lobe; scutellum dark with brown apical spine. Hemelytron (abducted): clavus dark reddish-brown with proximal and distal yellow stripe; corium dark reddish-brown with anteroproximal yellow stripe, posteromedial and distal yellow spots; membrane uniformly dark; pale V-shaped marking along R and M veins. Legs: yellowish-brown. Abdomen: dark brown, laterotergites light brown.

Integument and vestiture. Head and pronotum: finely granulose with sparse, long macrosetae interspersed among sparse pubescence; interocular region with two pairs of macrosetae paramedially; antennifer with short lateral setigerous tubercle; morphologically ventral surface of labium with dense, short macrosetae. Thorax: anterolateral angles of pronotal collar with macrosetae; scutellar lateral carinae with long setation. Hemelytron: corium with sparse long setation. Legs: posterior row of protuberances on mid and hind femora with three large and one small spines on distal half. Abdomen: ventral surface pubescent.

Structure. Head: elongate, about 1.2 times as long as wide; anteocular region about one third of head length, about as long as postocular region (measured to anterior margin of neck); postocular region in dorsal view shorter than eye, lateral margins gently rounded; pedicel about 1.2 times length of head width; maxillary plates ellipsoidal, adjacent to and reaching apex of clypeus; apices of maxillary plates in dorsal view directed straight; clypeus in dorsal view wider than maxillary plates; clypeal apex round, not narrowed; interocular glabrous markings anterolaterally curved, joined at interocular sulcus paramedially; interocular sulcus in dorsal view nearly straight; eye width in dorsal view narrower than synthlipsis; eye reaching ventral head margin in lateral view; ventrolateral swelling of buccula without lateral protrusion that surpasses buccular margin, flat margin; labial segment I in lateral view straight, not reaching posteroventral eye margin; morphologically dorsal surface of labial segment II nearly straight, about 0.6 times length of segment I. Thorax: pronotal collar in dorsal view narrow medially, anterolateral angles short, flared laterally; anterior pronotal lobe about 0.5 times length of posterior pronotal lobe, lateral margins rounded; glabrous markings on pronotum thin and not deeply depressed; median apodeme depression of pronotum shallow, elongated longitudinally; scutellar spine long, raised; anteriad-directed process of prosternum smoothly rounded, without paramedial lobes; anterior margin of stridulitrum not elongated into protuberance. Hemelytron: Cu-An_1 cell elongate, reaching at least half the length of M-Cu cell. Legs: fossula spongiosa present on fore and mid legs. Pygophore (Fig. 12): transverse bridge with rounded posterior margin; posterior region of ventral surface of pygophore in lateral view straight, not swollen; short median apical process upright in lateral view; lateral pygophore margin with protuberance; posterior pygophore margin with clustered macrosetae on protuberance; parameres sinusoidal, apex tapered into squarely rounded tip. Aedeagus (Fig. 14): endosoma almost entirely covered with spicules; apex of dorsal phallothecal sclerite tongue-shaped in dorsal view; basal plate extension 4.4 times as long as wide.

Female

Unknown.

Distribution (Fig. 20)

This species is only known from the type locality in Laos. This is the only known species of *Voconia* on mainland Southeast Asia.

Remarks

The pygophore was dissected from this pinned holotype and used to extract DNA, for which we acquired the lowest DNA concentration (0.124 ng/µL) and did not sequence.

Voconia lasiosoma sp. nov.
urn:lsid:zoobank.org:act:C5495703-AEE2-49FC-8B08-099ED0F398D3
Figs 1–2, 7, 9, 12, 14, 20

Diagnosis

Recognized from other *Voconia* by the densely long setation on the pronotum, corium, legs, and abdomen. This species most closely resembles two other Southeast Asian species, *V. isosceles* sp. nov. and *V. loki* sp. nov. due to the finely granulose head and pronotum and dark pronotum with contrasting pale posterior margin. While *V. loki* sp. nov. is also hairy, *V. lasiosoma* sp. nov. is larger (about 9.4 mm) than these

two species; legs, antennae, and corium are dark yellowish-brown rather than yellow; dark portions of corium and clavus are black rather than reddish-brown; Cu-An_1 cell stout (less than half the length of M-Cu cell); and proximal half of corium not entirely yellow (abducted corium with anteroproximal yellowish-brown stripe and posteromedial yellow spot).

Etymology

Derived from the Latinized Greek prefix '*lasio-*' meaning 'hairy' combined with the Latinized Greek noun '*-soma*' meaning 'body'. Refers to the long macrosetae covering the body and hemelytra. A noun in apposition.

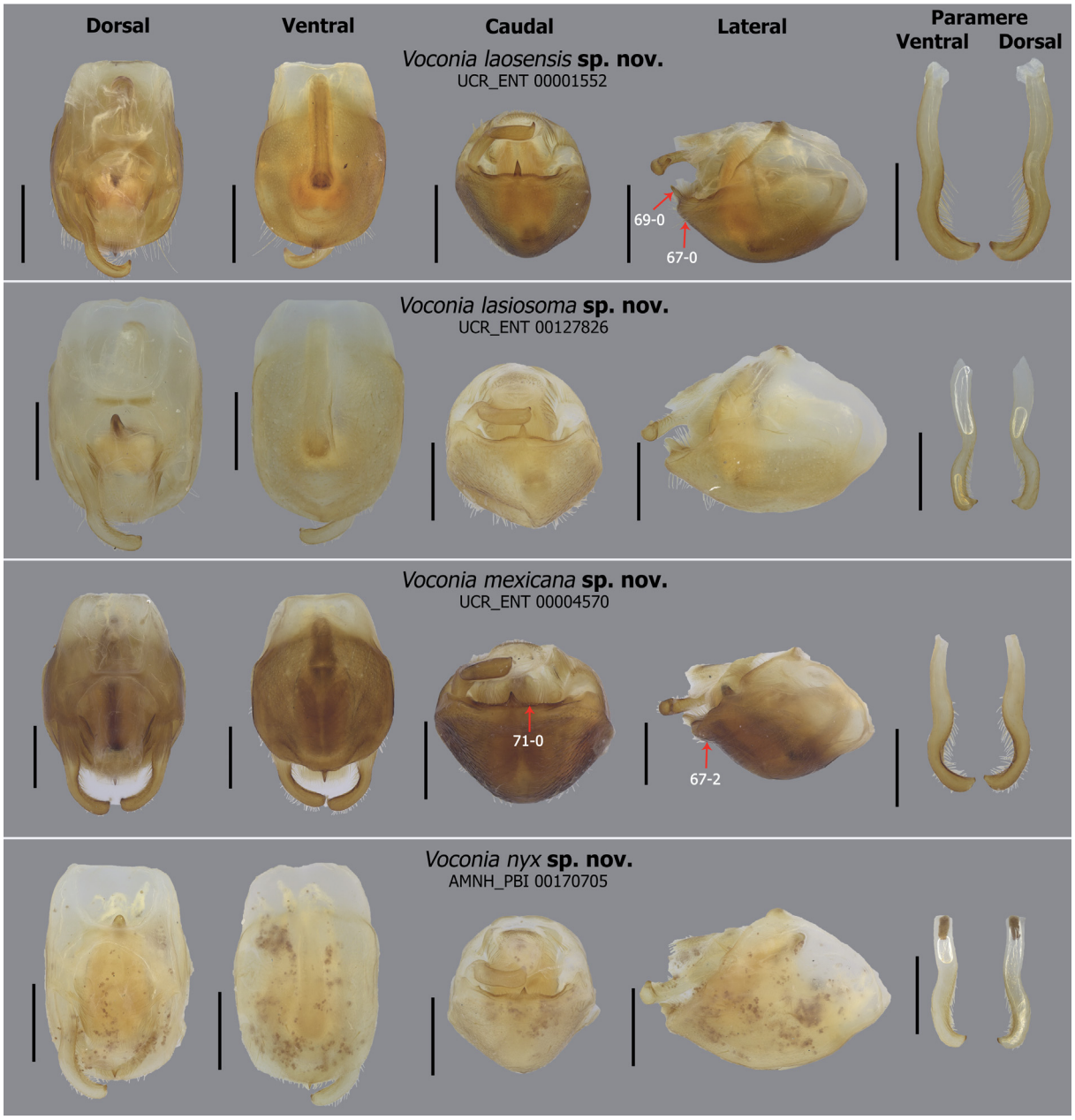

Fig. 12. Pygophore of species of *Voconia* Stål, 1866. Scale bars = 0.5 mm.

Type material

Holotype

MALAYSIA • ♂ (dissected pygophore and aedeagus in vial); Sarawak, Lanjak Entimau Wildlife Sanctuary; [1.55° N, 110.36° E]; [elev. 3 m]; 9–10 Oct. 2017; W. Hwang *et al*. leg.; collecting event: SW17_L_27; MV light trap in dipterocarp forest; DNA voucher R_CW 5472; USI: UCR_ENT 00127826; ZRC.

Description

Male (Figs 7, 9)

Body length. About 9.4 mm; macropterous.

Coloration. Head: dark brown; postocular region with dark patches adjacent to medial ocellar margin, semicircular pale stripe encircling both ocelli; labium lighter than head, yellow. Thorax: anterior pronotal lobe darker than head and posterior pronotal lobe; posterior pronotal lobe with dark yellowish-brown gradient; scutellum dark with contrasting dark yellowish-brown apical spine. Hemelytron (abducted): clavus black with proximal dark yellowish-brown spot and distal yellow stripe; corium black with anteroproximal dark yellowish-brown stripe, posteromedial and distal yellow spots; membrane mostly dark with pale stripe along most of M vein; membranal veins R and M proximally pale. Legs: yellowish-brown. Abdomen: dark brown.

Integument and vestiture. Head and pronotum: finely granulose with dense, long macrosetae interspersed among sparse pubescence; interocular region with two pairs of macrosetae paramedially; antennifer with short lateral setigerous tubercle; morphologically ventral surface of labium with dense, short macrosetae. Thorax: anterolateral angles of pronotal collar with macrosetae; scutellar lateral carinae with long setation. Hemelytron: corium with dense long setation. Legs: posterior row of protuberances on mid and hind femora with three large and three small spines on distal half. Abdomen: ventral surface pubescent, long macrosetae interspersed.

Structure. Head: elongate, about 1.3 times as long as wide; anteocular region about one third of head length, shorter than postocular region (measured to anterior margin of neck); postocular region in dorsal view shorter than eye, lateral margins gently rounded; length of pedicel subequal to head width; maxillary plates ellipsoidal, adjacent to and shorter than clypeus; apices of maxillary plates in dorsal view directed straight; clypeus in dorsal view wider than maxillary plates; clypeal apex round, not narrowed; interocular glabrous markings anterolaterally curved, joined at interocular sulcus paramedially; interocular sulcus in dorsal view nearly straight; eye width in dorsal view about as wide as synthlipsis; eye reaching ventral head margin in lateral view; ventrolateral swelling of buccula without lateral protrusion that surpasses buccular margin, flat margin; labial segment I in lateral view straight, surpassing posteroventral eye margin; morphologically dorsal surface of labial segment II nearly straight, about 0.5 times length of segment I. Thorax: pronotal collar in dorsal view narrow medially, with anterolateral angles short, flared laterally; anterior pronotal lobe about 0.7 times length of posterior pronotal lobe, lateral margins rounded; glabrous markings on pronotum conspicuous and not depressed; median apodeme depression of pronotum deep, elongated longitudinally; scutellar spine long, subhorizontal; anteriad-directed process of prosternum smoothly rounded, without paramedial lobes; anterior margin of stridulitrum projected into small protuberance; proepimeron with acute protuberance on posteroventral margin. Legs: fossula spongiosa present on fore and mid legs. Abdomen: anterior margin of terga prominently carinulate; terga II and III with paired prominent longitudinal carinae, reaching posterior margin of tergum III. Pygophore (Fig. 12): transverse bridge with rounded posterior margin; posterior region of ventral surface of pygophore in lateral view straight, not swollen; short median apical process, upright in lateral view; lateral pygophore margin with protuberance; posterior pygophore margin with clustered macrosetae on protuberance; parameres sinusoidal, apex tapered into squarely rounded tip. Aedeagus

(Fig. 14): endosoma almost entirely covered with spicules; apex of dorsal phallothecal sclerite tongue-shaped in dorsal view; basal plate extension 5.6 times as long as wide.

Female

Unknown.

Distribution (Fig. 20)

This species is only known from the type locality in Sarawak, Malaysia.

Remarks

The holotype was preserved in ethanol when the abdomen was dissected for DNA extraction. We acquired sufficient DNA in our NGS library for Illumina sequencing for future phylogenomic studies, referred to as DNA voucher R_CW 5472.

Voconia lirophleps sp. nov.
urn:lsid:zoobank.org:act:66547E0B-D2F8-46E0-B1F7-CC2DD12BFC2A
Figs 1–2, 4B, 7, 9, 20

Diagnosis

Distinguished from most species of *Voconia* by the pale membranal veins. This species is most similar to two other Oriental species, *V. decorata* sp. nov. and *V. coronata* sp. nov. It is distinguishable from *V. decorata* sp. nov. by its distribution in Sumatra; the dark brown, almost black coloration of the body; and uniformly brown scutellum. *V. lirophleps* sp. nov. is about 2 mm shorter than *V. coronata* sp. nov. It is also distinguishable by the yellow spots adjacent to the lateral ocellar margin; slightly more globose head (about 1.2 times as long as wide); pedicel much shorter (about 1.1 times length of head width); maxillary plates converge in dorsal view, postocular region is shorter than eye; narrow pronotal collar; short anterior pronotal lobe relative to posterior pronotal lobe (about 2.2 times shorter than posterior lobe); conspicuous distal yellow spot on the corium; and only three large spines and two small spines on the posterior row of spines of the hind leg.

Etymology

Derived from the Latinized Greek prefix '*liro-*' meaning 'pale' combined with the Latinized Greek noun '*phleps*' meaning 'vein'. Refers to the prominent pale coloration of the membranal veins. To be treated as a noun in apposition, ending not to be changed.

Type material

Holotype

INDONESIA • ♂; Sumatra, Djulu, Rajeu, 250 km N of Medan; elev. 50 m; E.W. Diehl leg.; USI: AMNH_PBI 00170704; AMNH.

Description

Male (Figs 7, 9)

Body length. About 8.9 mm; macropterous.

Coloration. Head: dark brown; postocular region uniformly dark with pale patches adjacent to lateral ocellar margin; labium nearly as dark as head. Thorax: coloration as head; scutellum uniformly dark brown. Hemelytron (Fig. 4B; abducted): clavus dark reddish-brown with distal yellow stripe; corium dark reddish-brown with anteroproximal yellow stripe, posteromedial and distal yellow spots; membrane uniformly dark;

membranal veins forming Cu-An_1 and M-Cu cells paler than remainder of membrane. Legs: dark brown, femora darker. Abdomen (Fig. 4B): dark brown; dorsal laterotergites dark with yellow spots anteriorly.

Integument and vestiture. Head and pronotum: finely granulose with sparse, short macrosetae interspersed among sparse pubescence; interocular region with two pairs of macrosetae paramedially; antennifer with short lateral setigerous tubercle; morphologically ventral surface of labium with sparse, long macrosetae. Thorax: anterolateral angles of pronotal collar with macrosetae; scutellar lateral carinae with long setation. Hemelytron: corium with sparse long setation. Legs: posterior row of protuberances on mid and hind femora with three large and three small spines on distal half. Abdomen: ventral surface pubescent.

Structure. Head: elongate, 1.2 times as long as wide; anteocular region about one quarter of head length, about as long as postocular region (measured to anterior margin of neck); postocular region in dorsal view shorter than eye, lateral margins gently rounded; pedicel about 1.1 times length of head width; maxillary plates ellipsoidal, adjacent to and as long as clypeus; apices of maxillary plates in dorsal view converging; clypeus in dorsal view narrower than maxillary plates; clypeal apex round, not narrowed; interocular glabrous markings anterolaterally curved, joined at interocular sulcus paramedially; interocular sulcus in dorsal view bent anteromedially, subtriangular; eye width in dorsal view about as wide as synthlipsis; eye reaching ventral head margin in lateral view; ventrolateral swelling of buccula without lateral protrusion that surpasses buccular margin, flat margin; labial segment I in lateral view straight, reaching posteroventral eye margin; morphologically dorsal surface of labial segment II nearly straight, about 0.5 times length of segment I. Thorax: pronotal collar in dorsal view narrow medially with anterolateral angles short, projected forward; anterior pronotal lobe about 0.5 times length of posterior pronotal lobe, lateral margins rounded; glabrous markings on pronotum deeply depressed; median apodeme depression of pronotum shallow, elongated longitudinally; scutellar spine long, raised; anteriad-directed process of prosternum smoothly rounded, without paramedial lobes; anterior margin of stridulitrum not elongated into protuberance; proepimeron with acute protuberance on posteroventral margin. Legs: fossula spongiosa present on fore and mid legs.

Female

Unknown.

Distribution (Fig. 20)

This species is only known from the type locality in North Sumatra.

Remarks

Despite the holotypes of *V. coronata* sp. nov. and *V. lirophleps* sp. nov. being collected within about 106 km of each other, there are several differences, particularly in size. Among our larger series, conspecific *Voconia* males do not vary much in size, and *V. lirophleps* sp. nov. is about 2 mm shorter than *V. coronata* sp. nov.; thus, we are keeping them as separate species.

Voconia loki sp. nov.
urn:lsid:zoobank.org:act:BBC757E0-8E3F-4CCC-9B5F-8E7FA5FAB7A2
Figs 1–2, 3H, 8, 10, 20

Diagnosis

This species most closely resembles two other Southeast Asian species, *V. isosceles* sp. nov. and *V. lasiosoma* sp. nov., due to the finely granulose head and pronotum; legs and antennae yellow; pronotum dark with contrasting yellow posterior margin; and relatively denser and longer setation. *Voconia loki* sp. nov. is smaller (about 8.3 mm long) than these two species. It is also recognized from *V. isosceles* sp. nov. by the stout Cu-An_1 cell (less than half the length of the M-Cu cell), brown membranal veins

that form the Cu-An_1 and M-Cu cells, and the postocular region brown having dark patches adjacent to the medial ocellar margin. Apart from its smaller size, this species is distinguished from *V. lasiosoma* sp. nov. by the almost entirely yellow proximal half of the corium, reddish-brown distal half of the corium instead of black, and yellow legs instead of a darker yellowish-brown.

Etymology

Named after the cunning trickster from Norse mythology and from the Marvel Comics' character, Loki, since this specimen deceived and tricked authors in a previous study (Hwang & Weirauch 2012) who misidentified it as "*Kayanocoris wegneri*" (*V. wegneri* comb. nov.). A proper noun in apposition.

Type material

Holotype

BRUNEI • ♂; Belait District, 21.5 km N of Labi on Labi Rd, Karanga Forest; 4.58244° N, 114.50508° E; elev. 40 m; 28 Jun. 2010; C. Weirauch and W. Hwang leg.; collecting event: BR10_L18; hand collected; low-elevation dipterocarp forest; DNA voucher R_CW 1590; USI: UCR_ENT 00052216; UCR.

Description

Male (Figs 8, 10)

Body length. About 8.3 mm; macropterous.

Coloration. Head (Fig. 3H): light brown; clypeus yellow; postocular region with dark patches adjacent to medial ocellar margin; labium lighter than head, yellow. Thorax: pronotum darker than head; posterior pronotal lobe with posterior margin lighter; scutellum dark with contrasting yellow apical spine. Hemelytron (abducted): clavus reddish-brown with distal yellow stripe; proximal half of corium mostly yellow with small black spot, distal half reddish-brown with distal yellow spot; membrane dark with proximally pale V-shaped marking along R and M veins; membranal veins R and M proximally pale, veins forming Cu-An_1 cell pale. Legs: yellow. Abdomen: dark brown; dorsal laterotergites yellow.

Integument and vestiture. Head and pronotum (Fig. 3H): finely granulose with dense, long macrosetae interspersed among sparse pubescence; interocular region with two pairs of macrosetae paramedially; antennifer with strong macroseta, base not protruded laterally; morphologically ventral surface of labium with dense, short macrosetae. Thorax: anterolateral angles of pronotal collar with macrosetae; scutellar lateral carinae with long setation. Hemelytron: corium with dense long setation. Legs: posterior row of protuberances on mid and hind femora with three large and three small spines on distal half. Abdomen: ventral surface pubescent, long macrosetae interspersed.

Structure. Head (Fig. 3H): elongate, about 1.2 times as long as wide; anteocular region about one third of head length, about as long as postocular region (measured to anterior margin of neck); postocular region in dorsal view as long as eye, lateral margins gently rounded; pedicel about 0.9 times length of head width; maxillary plates ellipsoidal, adjacent to and shorter than clypeus; apices of maxillary plates in dorsal view directed straight; clypeus in dorsal view wider than maxillary plates; clypeal apex round, narrowed; interocular glabrous markings anterolaterally curved, joined at interocular sulcus paramedially; interocular sulcus in dorsal view bent anteromedially, subtriangular; eye width in dorsal view wider than synthlipsis; eye reaching ventral head margin in lateral view; ventrolateral swelling of buccula without lateral protrusion that surpasses buccular margin, flat margin; labial segment I in lateral view straight, surpassing posteroventral eye margin; morphologically dorsal surface of labial segment II nearly straight, about 0.5 times length of segment I. Thorax: pronotal collar in dorsal view narrow medially with anterolateral angles short, projected forward; anterior pronotal lobe about 0.7 times length of posterior pronotal lobe, lateral margins almost straight; glabrous markings on pronotum conspicuous

and not depressed; median apodeme depression of pronotum deep, elongated longitudinally; scutellar spine long, raised; anteriad-directed process of prosternum smoothly rounded, without paramedial lobes; anterior margin of stridulitrum not elongated into protuberance; proepimeron with acute protuberance on posteroventral margin. Legs: fossula spongiosa present on fore and mid legs.

Female

Unknown.

Distribution (Fig. 20)

This species is only known from the type locality in Brunei on the island of Borneo.

Remarks

The holotype is referred to as *Kayanocoris wegneri* R_CW 1590 in Hwang & Weirauch's (2012) molecular phylogeny, where it is recovered as the sister taxon to all other species of *Gerbelius*.

Voconia mexicana sp. nov.
urn:lsid:zoobank.org:act:2FAEA443-4F17-4ABE-9F77-C28792F7D5D0
Figs 1–2, 3I, 4I, 8, 10, 12, 14, 19

Diagnosis

One of two New World species of *Voconia*. Recognized by the coarsely granulose head and prothorax; wide anteocular region; morphologically ventral surface of labium with sparsely long macrosetae; buccula with lateral tubercles protruding past buccular margin; and yellow antero- and posteromedial spots on the abducted corium.

Etymology

The specific epithet is the Latin adjective '*mexicanus*, *-a*, *-um*', meaning 'from or pertaining to Mexico', referring to the country of the type locality.

Type material

Holotype

MEXICO • ♂ (dissected pygophore and aedeagus in vial); Veracruz, 4 mi N of "Cardale" [José Cardel]; 30 Oct. 1982; G. Gordh leg.; DNA voucher R_CW 2768; USI: UCR_ENT 00004570; UCR.

Paratypes

HONDURAS • 1 ♀; El Paraíso, 13 km NW of El Zamorano; [14.15° N, 86.47° W]; 27 Jul. 1977; C.W. and L.B. O'Brien and Marshall leg.; USI: AMNH_PBI 00170701; AMNH.

MEXICO • 1 ♂; Oaxaca, Tehuantepec; [16.33° N, 95.23° W]; 11 Jun. 1964; J.C. and D. Pallister leg.; USI: AMNH_PBI 00170702; AMNH. • 1 ♂; same collection data as for preceding; USI: AMNH_PBI 00170703; AMNH.

Description

Male (Figs 8, 10)

Body length. 10.3–10.9 mm; macropterous.

Coloration. Head: uniformly dark brown; labium lighter than head, yellow brown. Thorax: as head; posterior pronotal lobe with posterior margin lighter; scutellum dark with brown apical spine. Hemelytron (abducted): clavus dark reddish-brown with distal yellow stripe; corium dark reddish-

brown with anteromedial and posteromedial yellow spots; membrane dark with pale V-shaped marking along R and M veins; membranal veins R, M, and An_1 proximally pale. Legs: dark brown. Abdomen: dark brown, laterotergites light brown.

Integument and vestiture. Head and pronotum: coarsely granulose with sparse pubescence on setigerous tubercles; interocular region unarmed with macrosetae; antennifer with 1–3 short lateral setigerous tubercles; morphologically ventral surface of labium with sparse, long macrosetae. Thorax: anterolateral angles of pronotal collar with setigerous tubercles. Hemelytron: corium with dense, short setation. Legs: posterior row of protuberances on mid and hind femora with three large spines on distal half and two to five small spines. Abdomen: ventral surface pubescent.

Structure. Head: elongate, 1.2–1.3 times as long as wide; anteocular region about one third of head length, longer than postocular region (measured to anterior margin of neck); postocular region in dorsal view about as long as eye, lateral margins gently rounded; pedicel 1.4–1.9 times length of head width; maxillary plates ellipsoidal, adjacent to and longer than clypeus; apices of maxillary plates in dorsal view directed straight or diverging; clypeus in dorsal view narrower than maxillary plates; clypeal apex round, not narrowed; interocular glabrous markings anterolaterally curved, joined at interocular sulcus paramedially; interocular sulcus in dorsal view curved and smoothly rounded anteriorly; eye width in dorsal view narrower than synthlipsis; eye reaching ventral head margin in lateral view; ventrolateral swelling of buccula with lateral protrusion that surpasses buccular margin; labial segment I in lateral view straight, reaching or slightly shorter than posteroventral eye margin; morphologically dorsal surface of labial segment II nearly straight, about 0.4 times length of segment I. Thorax: pronotal collar in dorsal view narrow medially with anterolateral angles short, projected forward; anterior pronotal lobe about 0.5–0.6 times length of posterior pronotal lobe, lateral margins rounded; glabrous markings on pronotum thin and gently depressed; median apodeme depression of pronotum deep, circular; scutellar spine long, subhorizontal or raised; anteriad-directed process of prosternum with paramedial lobes (Fig. 3I); anterior margin of stridulitrum projected into small protuberance (Fig. 3I); proepimeron with acute protuberance on posteroventral margin. Legs: fossula spongiosa present on fore and mid legs. Abdomen: anterior margin of terga weakly carinulate; terga II and III with paired prominent longitudinal carinae, reaching about one-third of tergum III. Pygophore (Fig. 12): transverse bridge with rounded posterior margin; posterior region of ventral surface of pygophore in lateral view with large swelling; short median apical process sharply bent posteriorly in lateral view; lateral pygophore margin with protuberance; posterior pygophore margin with clustered macrosetae on flat margin; parameres sinusoidal, apex tapered into squarely rounded tip. Aedeagus (Fig. 14): endosoma almost entirely covered with spicules; apex of dorsal phallothecal sclerite rounded in dorsal view; basal plate extension about 4.3 times as long as wide.

Female

Distinguished from males by the following. Body length: about 12.2 mm. Head: elongate, about 1.2 times as long as wide; anteocular region shorter than postocular region (measured to anterior margin of neck); with sparse, short macrosetae on setigerous tubercles and sparse pubescence on setigerous tubercles; pedicel about 1.6 times length of head width; apices of maxillary plates in dorsal view directed straight; labium lighter than head, brown; labial segment I in lateral view surpassing posteroventral eye margin. Thorax: pronotal collar in dorsal view narrow, almost absent medially; anterolateral angles of pronotum long, projected forward. Hemelytron: corium dark with thick medial yellow stripe; with dense, long macrosetae. Legs: posterior row of protuberances on mid and hind femora with three large spines on distal half and many small spines (Fig. 4I); fossula spongiosa absent or vestigial on mid leg.

Distribution (Fig. 19)

This species is distributed in Southern Mexico and Honduras.

Remarks

The female from Honduras is considerably different from the males from Mexico as the description states above. We keep them as a single species until this hypothesis can be further tested with additional material. Specimen voucher UCR_ENT 00004570 was mis-labelled as collected "4 mi N of Cardale", though it should be "4 mi N of José Cardel" as recorded by other collectors on the same trip.

Voconia minima sp. nov.
urn:lsid:zoobank.org:act:CFBDCF33-C855-47F0-9945-98BE6E37A338
Figs 1–2, 8, 10, 20

Diagnosis

This species is recognized from other Philippine species such as *V. bakeri* sp. nov. and *V. nyx* sp. nov. by its short body length (about 8.5 mm long); dark tibiae with proximal and distal ends yellow; and abducted corium with yellow stripe occupying half of the anteroproximal margin and expanding medially to become adjacent to posteromedial yellow spot.

Etymology

The specific epithet is the Latin adjective '*minimus*, *-a*, *-um*', meaning 'smallest'. Refers to the fact that this is among the smallest species of *Voconia*.

Type material

Holotype

PHILIPPINES • ♂; Mindanao, Zamboanga del Sur, Lemesahan; [7.84° N, 123.30° E]; elev. 600 m; 7 Sep. 1958; H.E. Milliron leg.; tight trap; USI: UCR_ENT 00073811; BPBM.

Description

Male (Figs 8, 10)

Body length. About 8.5 mm; macropterous.

Coloration. Head: dark brown; postocular region with pale patches adjacent to lateral ocellar margin; labium nearly as dark as head. Thorax: as head; scutellum dark, tip of apical spine contrasting yellow. Hemelytron (abducted): clavus dark reddish-brown with distal yellow stripe; corium dark reddish-brown with anteroproximal yellow stripe, posteromedial and distal yellow spots; membrane dark with pale V-shaped marking along R and M veins; membranal veins R and M proximally pale. Legs: dark brown, proximal and distal ends of tibiae and tarsi yellow. Abdomen: dark brown.

Integument and vestiture. Head and pronotum: finely granulose with sparse, long macrosetae interspersed among dense pubescence; interocular region with two pairs of macrosetae paramedially; antennifer with short lateral setigerous tubercle; morphologically ventral surface of labium with dense, short macrosetae. Thorax: anterolateral angles of pronotal collar with macrosetae; scutellar lateral carinae with long setation. Hemelytron: corium with sparse, long setation. Legs: posterior row of protuberances on mid and hind femora with three large and two small spines on distal half. Abdomen: ventral surface pubescent.

Structure. Head: elongate, about 1.4 times as long as wide; anteocular region about one quarter of head length, shorter than postocular region (measured to anterior margin of neck); postocular region in dorsal view about as long as eye, lateral margins gently rounded; pedicel about 1.2 times length of head width; maxillary plates ellipsoidal, adjacent to and longer than clypeus; apices of maxillary plates in dorsal view converging; clypeus in dorsal view about as wide as maxillary plates; clypeal apex

round, narrowed; interocular glabrous markings anterolaterally curved, joined at interocular sulcus paramedially; interocular sulcus in dorsal view nearly straight; eye width in dorsal view about as wide as synthlipsis; eye reaching ventral head margin in lateral view; ventrolateral swelling of buccula without lateral protrusion that surpasses buccular margin, flat margin; labial segment I in lateral view straight, surpassing posteroventral eye margin; morphologically dorsal surface of labial segment II nearly straight, about 0.5 times length of segment I. Thorax: pronotal collar in dorsal view narrow medially with anterolateral angles short, projected forward; anterior pronotal lobe about 0.6 times length of posterior pronotal lobe, lateral margins rounded; glabrous markings on pronotum thin and not deeply depressed; median apodeme depression of pronotum shallow, elongated transversely; scutellar spine long, raised; anteriad-directed process of prosternum smoothly rounded, without paramedial lobes; anterior margin of stridulitrum not elongated into protuberance; proepimeron with acute protuberance on posteroventral margin. Legs: fossula spongiosa present on fore and mid legs.

Female

Unknown.

Distribution (Fig. 8)

This species is only known from the type locality on the Philippine island of Mindanao.

Remarks

The carinules on the dorsal surface of the abdomen were not examined in order to prevent damage to the holotype.

Voconia monodi (Villiers, 1963) comb. nov.
Fig. 17

Pseudocethera monodi Villiers, 1963b: 532, figs 14–15.

Revised diagnosis

Distinguished from other species of *Voconia* by the following combination of characters: short body length (about 7.0 mm long); coarsely granulose head and pronotum; maxillary plates not adjacent to and far surpass clypeal apex; maxillary plates in lateral view wide, about twice the width of the scape and not toothed apically; antennifer with long lateral spine. It is recognized from the micropterous *V. schoutedeni* by the paired, short, and not prominent longitudinal carinae on tergum II, not reaching the posterior margin of the segment; reliefs of the anterior lobe of the pronotum less strong, effaced in front; and indistinct ocelli.

Type material

Holotype

GUINEA • ♀; "Région du Mont Nimba" [Mount Richard-Molard region], "Camp du Gouan" [Guinea camp]; 5 Apr. 1957; L.A.V. leg.; prairie; MNHN.

Redescription

Female

Body length. About 7.0 mm; micropterous.

Coloration. Head: yellowish brown. Thorax: Pronotum yellowish in front and on the sides, brown on the rest of the surface; scutellum brown. Micropterous wing: yellowish. Legs: brown with proximal and

distal part of femur and tarsus testaceous. Abdomen: dark brown, dorsal laterotergites with anterior half yellow.

Integument and vestiture. Head and pronotum: coarsely granulose with setigerous tubercles; interocular region with two pairs of large setigerous tubercles paramedially; antennifer with long lateral spine. Legs: posterior row of protuberances on mid and hind femora with three or four spines.

Structure. Head: scape not reaching head apex and longer than clypeus; apices of maxillary plates in dorsal view directed straight; clypeus in dorsal view narrower than maxillary plates; clypeal apex round, narrowed; eye width in dorsal view narrower than synthlipsis; ocelli absent; postocular region in dorsal view longer than eye, lateral margins subrectangular; labial segment I in lateral view straight, surpassing posteroventral eye margin; pronotal anterolateral angles long, flared laterally; scutellar spine reduced, slightly raised. Abdomen: anterior margin of terga carinulate; tergum II with paired, short, and not prominent longitudinal carinae.

Male

Unknown.

Distribution (Fig. 17)

This species is known from Northwest Africa.

Remarks

Specimens were on loan and not available for this study. Consequently, this description and localities were inferred from the French description, illustrations, and key provided by Villiers (Villiers 1963b, 1964). Villiers (1963b) includes an additional specimen from Guinea that was not treated as type material that we could not examine and have limited information for. We therefore refrain from including it. A drawer image of two specimens from the BMNH in 2011 suggests that this species may be distributed in Sierra Leone (collection event: 11 May 1926) and Nigeria, but their identification is difficult to confirm without better images and without the holotype.

Voconia motoensis (Schouteden, 1929) comb. nov.
Figs 1–2, 8, 10, 17

Microvarus motoensis Schouteden, 1929: 252.
Microvarus inermiceps Villiers, 1964: 107, fig. 27. Synonymized by Villiers (1976: 171).

Revised diagnosis

Distinguished from other species in *Voconia* by its finely granulose head; short labial segment I that does not reach posteroventral eye margin; anterior margin of buccula with dense, long macrosetae; and stout body. This species most closely resembles *V. conradti* and *V. smithae* sp. nov. in its stout body plan and Afrotropical distribution. It is easily recognized from these two species by the absent or vestigial fossula spongiosa on the midleg and its distinct coloration: uniformly brown scutellum, abducted corium with an anteromedial yellow spot, and uniformly brown dorsal laterotergites.

Type material

Holotype

DEMOCRATIC REPUBLIC OF THE CONGO • ♀; Haut-Uélé, Moto; [2.90556° N, 29.415° E]; [elev. 898 m]; 1920; L. Burgeon leg.; USI: UCR_ENT 00070525; RMCA ENT 000018004.

Redescription

Female (Figs 8, 10)

Body length. About 11.6 mm; macropterous.

Coloration. Head: dark brown; labium nearly as dark as head. Thorax: coloration as head; posterior pronotal lobe with posterior margin lighter; scutellum uniformly dark brown. Hemelytron (abducted): clavus dark reddish-brown with distal yellow stripe; corium dark reddish-brown with anteromedial and posteromedial yellow spots; membrane dark with pale V-shaped marking along R and M veins; membranal veins proximally pale. Legs: yellowish-brown with distal half of femora dark brown. Abdomen: dark brown; dorsal laterotergites uniformly dark brown.

Integument and vestiture. Head and pronotum: finely granulose with sparse, short macrosetae interspersed among dense pubescence; antennifer with macroseta, base not protruded; morphologically ventral surface of labium with dense, short macrosetae. Thorax: anterolateral angles of pronotal collar with macrosetae. Hemelytron: corium with sparse long setation. Legs: posterior row of protuberances on mid and hind femora with three large spines on distal half, middle spine much longer. Abdomen: ventral surface pubescent.

Structure. Head: elongate, about 1.2 times as long as wide; anteocular region about one quarter of head length, shorter than postocular region (measured to anterior margin of neck); postocular region in dorsal view shorter than eye, lateral margins gently rounded; pedicel about 1.5 times length of head width; maxillary plates ellipsoidal, adjacent to and longer than clypeus; apices of maxillary plates in dorsal view directed straight; clypeus in dorsal view wider than maxillary plates; clypeal apex round, not narrowed; interocular glabrous markings anterolaterally curved, joined at interocular sulcus paramedially; interocular sulcus in dorsal view bent anteromedially, subtriangular; eye width in dorsal view wider than synthlipsis, eye not reaching ventral head margin in lateral view; ventrolateral swelling of buccula without lateral protrusion that surpasses buccular margin, flat margin; labial segment I in lateral view straight, not reaching posteroventral eye margin; morphologically dorsal surface of labial segment II nearly straight, about 0.7 times length of segment I. Thorax: pronotal collar wide medially with anterolateral angles short, projected forward; anterior pronotal lobe about 0.7 times length of posterior pronotal lobe, lateral margins almost straight; glabrous markings on pronotum thin and not deeply depressed; median apodeme depression of pronotum deep, circular; scutellar spine long, raised; anteriad-directed process of prosternum smoothly rounded, without paramedial lobes; anterior margin of stridulitrum not elongated into protuberance; proepimeron with smoothly rounded posteroventral margin. Legs: fossula spongiosa present on fore leg, absent or vestigial on mid leg.

Male

Unknown.

Distribution (Fig. 17)

Only known from Moto and Garamba National Park (Villiers 1964) in the Haut-Uélé province of the Democratic Republic of the Congo.

Remarks

The carinules on the dorsal surface of the abdomen were not examined to prevent damage to the holotype. The synonymy of *Microvarus inermiceps* proposed by Villiers (1976: 171) was accepted without a re-examination of the type material.

Voconia nyx sp. nov.
urn:lsid:zoobank.org:act:374635C1-1613-483F-A653-17F63F0C9545
Figs 1–2, 4F–H, 8, 10, 12, 14, 20

Diagnosis

This species is most similar to other Southeast Asian species of *Voconia* with a finely granulose head and pronotum and abducted corium with yellow spots on the posteromedial and distal apex. Despite the similarity in color, *V. nyx* sp. nov. is larger than *V. minima* sp. nov. (about 10.0 mm long) and has uniformly brown legs. It is distinguished from *V. bakeri* sp. nov. by its uniformly brown dorsal laterotergites, pale stripe along the posterior margin of the pronotum, and the abducted corium with an anteroproximal yellowish-brown stripe.

Etymology

Named after the Greek primordial goddess of the night, Nyx. Refers to the dark legs and antennae of this species, which differ from those of a similar yet lighter colored species, *Voconia hemera* sp. nov., named after the goddess of day. A proper noun in apposition.

Type material

Holotype

PHILIPPINES • ♂ (dissected pygophore and aedeagus in vial); Laguna, Mt Maquiling; [14.13° N, 121.20° E]; elev. 100 m; 28 Feb. 1949; A.E. Bigornia leg.; USI: AMNH_PBI 00170705; AMNH.

Description

Male (Figs 8, 10)

Body length. About 10.0 mm; macropterous.

Coloration. Head: dark brown; postocular region with pale patches adjacent to lateral ocellar margin; labium lighter than head, brown. Thorax (Fig. 4F): as head; posterior pronotal lobe with posterior margin lighter; scutellum uniformly dark brown. Hemelytron (abducted): clavus dark reddish-brown with distal yellow stripe; corium dark reddish-brown with yellowish-brown stripe on anteroproximal margin, posteromedial and distal yellow spots; membrane dark with pale V-shaped marking along R and M veins; membranal veins R and M pale. Legs: dark reddish-brown. Abdomen: dark reddish-brown; dorsal laterotergites dark brown.

Integument and vestiture. Head and pronotum: finely granulose with sparse, long macrosetae interspersed among dense pubescence; interocular region with two pairs of macrosetae paramedially; antennifer with short lateral setigerous tubercle; morphologically ventral surface of labium with sparse, long macrosetae. Thorax: anterolateral angles of pronotal collar with macrosetae; scutellar lateral carinae with long setation. Legs: posterior row of protuberances on mid and hind femora with three large spines on distal half and three or fewer small spines. Abdomen: ventral surface pubescent.

Structure. Head: elongate, about 1.3 times as long as wide; anteocular region about one third of head length, about as long as postocular region (measured to anterior margin of neck); postocular region in dorsal view shorter than eye, lateral margins gently rounded; pedicel about 1.2 times length of head width; maxillary plates ellipsoidal, adjacent to and longer than clypeus; apices of maxillary plates in dorsal view directed straight; clypeus in dorsal view about as wide as maxillary plates; clypeal apex round, narrowed; interocular glabrous markings anterolaterally curved, joined at interocular sulcus paramedially; interocular sulcus in dorsal view bent anteromedially, subtriangular; eye width in dorsal view about as wide as synthlipsis; eye reaching ventral head margin in lateral view; ventrolateral swelling

of buccula without lateral protrusion that surpasses buccular margin, flat margin; labial segment I in lateral view straight, not reaching posteroventral eye margin; morphologically dorsal surface of labial segment II nearly straight, about 0.6 times length of segment I. Thorax: pronotal collar in dorsal view narrow medially with anterolateral angles short, projected forward; anterior pronotal lobe about 0.6 times length of posterior pronotal lobe, lateral margins rounded; glabrous markings on pronotum thin and not deeply depressed; median apodeme depression of pronotum shallow, elongated transversely; scutellar spine long, raised (Fig. 4F); anteriad-directed process of prosternum smoothly rounded, without paramedial lobes; anterior margin of stridulitrum not elongated into protuberance; proepimeron with acute protuberance on posteroventral margin. Legs (Fig. 4G–H): fossula spongiosa present on fore and mid legs. Pygophore (Fig. 12): transverse bridge with triangular posterior margin; posterior region of ventral surface of pygophore in lateral view with large swelling; short median apical process bent posteriorly in lateral view; lateral pygophore margin with protuberance; posterior pygophore margin with clustered macrosetae on protuberance; parameres sinusoidal, apex tapered into squarely rounded tip. Aedeagus (Fig. 14): endosoma almost entirely covered with spicules; apex of dorsal phallothecal sclerite tongue-shaped in dorsal view; basal plate extension 4.6 times as long as wide.

Female

Unknown.

Distribution (Fig. 17)

This species is only known from the type locality on the Philippine island of Luzon.

Remarks

The holotype locality of Mt Maquiling is about 10 km from the holotype locality of *V. hemera* sp. nov. at Los Baños.

Voconia ornata (Distant, 1903) comb. nov.
Figs 1–2, 8, 10, 20

Gerbelius ornatus Distant, 1903a: 59.

Diagnosis

Distinguished from other species of *Voconia* by the following combination of characters: slender and short body (~7.8–8.7 mm long); proepimeron with protuberance on posteroventral margin; legs yellow with distal half of femora brown; scutellum dark with contrasting yellow apical spine; and dark abducted corium with anteromedial, posteromedial, and distal yellow spots.

Type material

Lectotype (present designation)

SRI LANKA • ♂; "Ceylon" [Sri Lanka]; E.E. Green leg.; Distant coll. 1911–383; USI: UCR_ENT 00048381; BMNH.

Additional material examined

INDIA – **Madhya Pradesh** • 1 ♀; Jahalpur; elev. "1600 ft" [488 m]; Oct. 1957; P.S. Nathan leg.; dissected abdomen in vial; USI: AMNH_PBI 00170698; AMNH • 1 ♀; same collection data as for preceding; Susai Nathan leg.; dissected abdomen in vial; USI: AMNH_PBI 00170697; AMNH. – **Tamil Nadu** • 1 ♀; Tranquebar, Madras; 30 Mar. 1969; K. Krishna leg.; USI: AMNH_PBI 00170699; AMNH. – **Uttar Pradesh** • 1 ♂; Maldevta, Dehra Dun; elev. "3500 ft" [1067 m]; 15 Apr. 1942; Jai K. Uniyal leg.; USI: AMNH_PBI 00170696; AMNH.

UNKNOWN COUNTRY • 1 ♂; "832-13"; USI: AMNH_PBI 00213933; HNHM.

Description

Male (Figs 8, 10)

Body length. 8.0–9.0 mm; macropterous.

Coloration. Head: light brown; postocular region with pale patches adjacent to lateral ocellar margin; labium lighter than head, brown to yellow. Thorax: as head; scutellum dark with contrasting yellow apical spine. Hemelytron (abducted): clavus reddish-brown with distal yellow stripe; corium reddish-brown with anteromedial, posteromedial, and distal yellow spots; membrane dark with pale V-shaped marking along R and M veins; membranal veins R and M proximally pale. Legs: yellow, distal half of femora brown. Abdomen: light brown; dorsal laterotergites dark brown with faint pale bands on posterior margins.

Integument and vestiture. Head and pronotum: finely granulose with dense, short macrosetae interspersed among dense pubescence; interocular region with two pairs of macrosetae paramedially; antennifer with short lateral setigerous tubercle; morphologically ventral surface of labium with sparse, short macrosetae. Thorax: anterolateral angles of pronotal collar with macrosetae. Hemelytron: corium with dense, long macrosetae. Legs: posterior row of protuberances on mid and hind femora with three large spines on distal half and many small spines. Abdomen: ventral surface pubescent.

Structure. Head: elongate, about 1.3 times as long as wide; anteocular region about one third of head length, about as long as postocular region (measured to anterior margin of neck); postocular region in dorsal view about as long as eye, lateral margins gently rounded; pedicel 1.3–1.4 times length of head width; maxillary plates ellipsoidal, adjacent to and longer than clypeus; apices of maxillary plates in dorsal view directed straight or diverging; clypeus in dorsal view about as wide as maxillary plates; clypeal apex round, not narrowed; interocular glabrous markings anterolaterally curved, joined at interocular sulcus paramedially; interocular sulcus in dorsal view nearly straight; eye width in dorsal view narrower than synthlipsis; eye reaching ventral head margin in lateral view; ventrolateral swelling of buccula with lateral protrusion that surpasses buccular margin, setigerous tubercles along apical margin; labial segment I in lateral view straight, reaching posteroventral eye margin; morphologically dorsal surface of labial segment II nearly straight, about 0.5 times length of segment I. Thorax: pronotal collar in dorsal view narrow medially with anterolateral angles short, projected forward; anterior pronotal lobe 0.7–0.8 times length of posterior pronotal lobe, lateral margins almost straight; glabrous markings on pronotum thin and deeply depressed; median apodeme depression of pronotum deep, circular; scutellar spine long, subhorizontal; anteriad-directed process of prosternum smoothly rounded, without paramedial lobes; anterior margin of stridulitrum not elongated into protuberance; proepimeron with acute protuberance on posteroventral margin. Legs: fossula spongiosa present on fore and mid legs.

Female

Mostly as male, distinguished from males by the following. Body length: 7.8–8.5 mm. Head: elongate, 1.3–1.4 times as long as wide; pedicel 1.3–1.5 times length of head width. Legs: fossula spongiosa absent or vestigial on mid leg.

Distribution (Fig. 20)

Distributed in India and Sri Lanka.

Remarks

Originally described as *Gerbelius ornatus* based on an unspecified number of specimens (syntypes) from Sri Lanka (Distant 1903a). Cladistic analyses (Weirauch 2008; present study: Figs 1–2) confirm that this

species is nested within *Voconia*, and hence it is hereby transferred to the latter genus. The abdomen of pinned specimen USI: AMNH_PBI 00170697 was removed for DNA extraction, but insufficient DNA was acquired in the NGS library for Illumina sequencing.

A single male pertaining to the type series (Fig. 8), here designated as the lectotype, was examined from a unit tray image at the BMNH, along with six other specimens for which we can only distinguish the locality for one specimen as Halwaldi, India and is not included in our distribution map nor material examined (Fig. 20). While the locality and date for the lectotype are not specified, we are confident that this specimen was studied by Distant. Kirby (1891) notes that the collector E.E. Green shared his collection of Hemiptera with the BMNH, most of which were collected at Pundaloya and could be inferred as the locality where no locality is mentioned. Less likely localities include Nitagala, Nawalapitya, Kandy, Colombo, or other.

Voconia pallidipes Stål, 1866
Figs 1–2, 3C, 8, 10, 13–14, 18

Voconia pallidipes Stål, 1866b: 165.

Diagnosis

Distinguished from most other species of *Voconia* by the tuberculate and coarsely granulose head and pronotum, tuberculate lateral protrusion of the buccula, the anterolateral angles of the pronotal collar with many (more than two) setigerous tubercles, and the abducted corium with the proximal half entirely yellow and distal half dark with distal yellow spot. This species resembles another Australian species, *V. grandioculata* sp. nov., in coloration but is easily distinguished by its larger size (10.5–11.3 mm long), smaller eyes and ocelli (ocellus does not occupy half-length of postocular region), M-Cu cell partially or entirely yellow, membranal veins forming Cu-An_1 and M-Cu cells mostly or entirely yellow, and yellow clavus with a dark medial spot.

Type material

Lectotype (present designation)
AUSTRALIA • 1 ♀; Queensland, Moreton Bay; Stevens leg.; NHRS-GULI000007827.

Additional material examined:

AUSTRALIA – **New South Wales** • 1 ♀; Inverell; [29.78° S, 151.12° E]; Armstrong leg.; USI: AMNH_PBI 00170708; AMNH. — **Queensland** • 1 ♂; Clermont; [22.82° S, 147.64° E]; Jul. 1928; K.K. Spence leg.; USI: AMNH_PBI 00088008; AMS K 156495 • 1 ♂; Condamine River, 10 km WSW of Dalby; [27.21° S, 151.18° E]; 5 Nov. 1990; M. Baehr leg.; USI: AMNH_PBI 00127094; ZSMC • 1 ♂; Mackenzie River Fitzroy Developmental Road; [22.94° S, 148.92° E]; 11 Nov. 1990; M. Müller leg.; USI: AMNH_PBI 00127093; ZSMC.

Description

Male (Figs 8, 10)
Body length. 10.5–11.3 mm; macropterous.

Coloration. Head (Fig. 3C): dark brown; postocular region with pale patches adjacent to lateral ocellar margin; labium lighter than head, yellow. Thorax: as head; scutellum dark with contrasting yellow apical spine. Hemelytron (abducted): clavus yellow with dark medial spot; corium proximal half yellow, distal half dark reddish-brown with yellow spot at distal apex; membrane dark with pale V-shaped marking along R and M veins, M-Cu cell entirely or partially yellow; membranal veins forming Cu-An_1 and M-Cu cells mostly or entirely yellow. Legs: yellow. Abdomen: light brown, laterotergites uniformly yellow.

Integument and vestiture. Head (Fig. 3C) and pronotum: coarsely granulose with dense, short setigerous tubercles interspersed among sparse pubescence; antennifer with long and 1–2 adjacent short lateral setigerous tubercles; morphologically ventral surface of labium with sparse, short macrosetae. Thorax: anterolateral angles of pronotal collar with setigerous tubercles; scutellar lateral carinae with short macrosetae on setigerous tubercles. Hemelytron: corium with short macrosetae. Legs: posterior row of protuberances on mid and hind femora with four or more large spines on distal half. Abdomen: ventral surface pubescent.

Structure. Head (Fig. 3C): elongate, 1.2–1.3 times as long as wide; anteocular region about one third of head length, about as long as postocular region (measured to anterior margin of neck); postocular region in dorsal view longer than eye, lateral margins gently rounded; pedicel 1.4–1.6 times length of head width; maxillary plates ellipsoidal, adjacent to and longer than clypeus; apices of maxillary plates in dorsal view diverging; clypeus in dorsal view about as wide as maxillary plates; clypeal apex bifid, not narrowed; interocular glabrous markings anterolaterally curved, joined at interocular sulcus paramedially; interocular sulcus in dorsal view nearly straight; eye width in dorsal view about as wide as synthlipsis; ventral eye margin surpassed by setigerous tubercles in lateral view; ventrolateral swelling of buccula with large lateral setigerous tubercles that surpass buccular margin; labial segment I in lateral view straight, surpassing posteroventral eye margin; morphologically dorsal surface of labial segment II curves ventrally, about 0.4 times length of segment I. Thorax: pronotal collar in dorsal view narrow medially with anterolateral angles short, flared laterally; anterior pronotal lobe about 0.8 times length of posterior pronotal lobe, lateral margins rounded; glabrous markings on anterior pronotal lobe depressed near posterolateral margins of pronotum; median apodeme depression of pronotum deep, elongated transversely; scutellar spine long, subhorizontal; anteriad-directed process of prosternum with paramedial lobes; anterior margin of stridulitrum projected into small protuberance; proepimeron with smoothly rounded posteroventral margin. Legs: fossula spongiosa present on fore and mid legs. Abdomen: anterior margin of terga weakly carinulate, tergum II without carinules laterally; terga II and III with paired prominent longitudinal carinae, reaching about one-third of tergum III. Pygophore (Fig. 13): transverse bridge with rounded posterior margin; posterior region of ventral surface of pygophore in lateral view with large swelling; short median apical process, bent posteriorly in lateral view; lateral pygophore margin with protuberance; posterior pygophore margin with clustered macrosetae on decline; parameres sinusoidal, apex tapered sharply. Aedeagus (Fig. 14): endosoma almost entirely covered with spicules; apex of dorsal phallothecal sclerite bifid in dorsal view; basal plate extension about 5.8 times as long as wide.

Female

As male. Body length: about 10.7 mm. Head: elongate, about 1.3 times as long as wide; pedicel about 1.5 times length of head width. Legs: fossula spongiosa absent or vestigial on mid leg.

Distribution

Only known from Eastern Australia.

Remarks

We were unable to physically examine the type material of *Voconia pallidipes* (photographs available on the NHRS website) and we thus based our redescription and character coding on a specimen deposited at the AMNH that was identified as *V. pallidipes* (USI: AMNH_PBI 00170708) by P. Wygodzinsky and that matches the diagnostic features visible in the type photographs. The specimen in the NHRS photographs is the only specimen in the series and thus designated as the lectotype. Characters of the dorsal part of the abdomen (i.e., carinules and carinae), pygophore, and aedeagus are based on a single specimen (USI: AMNH_PBI 00127093), to limit damage to specimens. This species is nested within the well supported Australian clade (Figs 1–2). The record and illustration of *V. pallidipes* by Swanson

(2015: 268–269, fig. 10) is based on misidentification and pertains to *V. brachycephala* sp. nov. (see under the latter species).

Voconia schoutedeni (Villiers, 1964) comb. nov.
Figs 1–2, 3D, 4D, 8, 10, 17

Pseudocethera schoutedeni Villiers, 1964: 112, fig. 31.
Pseudocethera schoutedeni forme *alata* Villiers, 1964: 112, fig. 32; infrasubspecific, permanently unavailable under ICZN Article 45.6.3.

Diagnosis

Distinguished from other species of *Voconia* by the following combination of characters: coarsely granulose head and pronotum; maxillary plates not adjacent to and far surpassing clypeal apex; maxillary plates in lateral view wide, about twice the width of the scape and not toothed apically; antennifer with long lateral spine; eyes in lateral view do not reach ventral head margin; pedicel short, about 0.6 times length of head width. The macropterous morph is recognized from *V. tridens* sp. nov. by the almost entirely dark brown head and pronotum, the scutellar spine is slightly raised, and the hemelytra are blackish with pale coloration at the base and apex of the corium.

Type material

Holotype
DEMOCRATIC REPUBLIC OF THE CONGO • 1 ♂; "P. N. G." [Garamba National Park], "Aka-Gar/4" [confluence of rivers Aka and Garamba south of Mt Bawezi, locality no. 4]; [3.88° N, 29.21° E]; 2 Feb. 1951; Miss. H. De Saeger and J. Verschuren leg.; No. 1195; USI: UCR_ENT 00070524; RMCA-ENT-000018003.

Paratype
DEMOCRATIC REPUBLIC OF THE CONGO • 1 ♀; Garamba National Park; 1952; Miss. H. De Saeger leg.; No. 3283; MNHN.

Material examined from original description

DEMOCRATIC REPUBLIC OF THE CONGO • 1 ♂; Garamba National Park; No. 1281; repository not specified in description.

Redescription

Male (Figs 8, 10)
Body length. About 6.7 mm, micropterous; about 6.7 mm, macropterous.

Coloration. Head (Fig. 3D): yellow; labium as remainder of head (micropterous); almost entirely dark brown (macropterous). Thorax: as head; posterior pronotal lobe darker than anterior lobe; scutellum brown with darker lateral margins. Wing stumps: yellow with brown posterior margins. Hemelytra: blackish, slightly cleared up at the base and apex of corium. Legs: yellow, distal third of femora dark brown. Abdomen (Fig. 4D): dark brown, dorsal laterotergites with anterior half yellow.

Integument and vestiture. Head (Fig. 3D) and pronotum: coarsely granulose with dense, short macrosetae on setigerous tubercles; interocular region with two pairs of large setigerous tubercles paramedially; antennifer with long lateral spine; morphologically ventral surface of labium with sparse, short macrosetae. Thorax: anterolateral angles of pronotal collar without macrosetae or setigerous tubercles; scutellar lateral carinae with pubescent tubercles. Legs: posterior row of protuberances on

mid and hind femora with three large spines on distal half and three or fewer small spines. Abdomen (Fig. 4D): ventral surface pubescent.

Structure. Head (Fig. 3D): elongate, about 1.4 times as long as wide, narrower in macropterous morph; anteocular region two-fifths of head length, longer than postocular region (measured to anterior margin of neck); postocular region in dorsal view longer than eye, lateral margins subrectangular; scape not reaching apex of head, about 0.4 times length of pedicel; pedicel about 0.6 times length of head width; maxillary plates conical, not adjacent to or longer than clypeus; apices of maxillary plates in dorsal view directed straight; clypeus in dorsal view narrower than maxillary plates; clypeal apex round, narrowed; interocular glabrous markings V-shaped, joined medially at interocular sulcus; interocular sulcus in

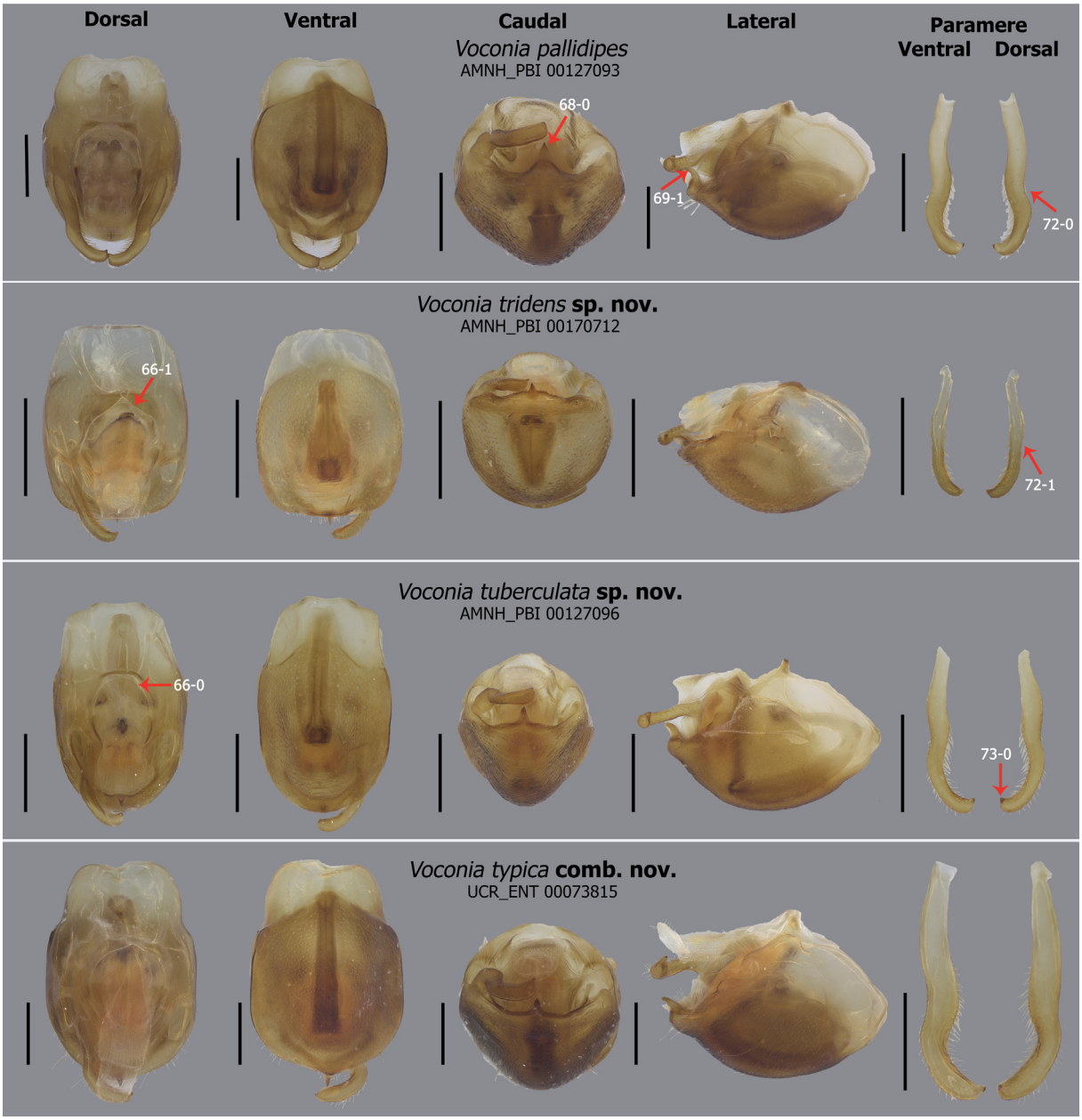

Fig. 13. Pygophore of species of *Voconia* Stål, 1866. Scale bars = 0.5 mm.

dorsal view nearly straight; eye width in dorsal view narrower than synthlipsis in micropterous morph, eyes considerably larger in macropterous morph; eye not reaching ventral head margin in lateral view; ocelli minute, occupying about 0.16 times length of postocular region in micropterous morph, ocelli considerably larger in macropterous morph; ventrolateral swelling of buccula with acute protrusion surpassing buccular margin, small setigerous tubercles along margin of protrusion; labial segment I in lateral view straight, not reaching posteroventral eye margin; morphologically dorsal surface of labial segment II nearly straight, about 0.4 times length of segment I. Thorax: pronotal collar in dorsal view wide medially with anterolateral angles long, flared laterally; anterior pronotal lobe about 1.3 times length of posterior pronotal lobe, lateral margins rounded in micropterous morph; anterior pronotal lobe shorter than posterior pronotal lobe in macropterous morph; glabrous markings on pronotum deeply depressed; median apodeme depression of pronotum shallow, elongated longitudinally; scutellar spine reduced and subhorizontal in micropterous morph; scutellum about 2 times as long as wide at base, with

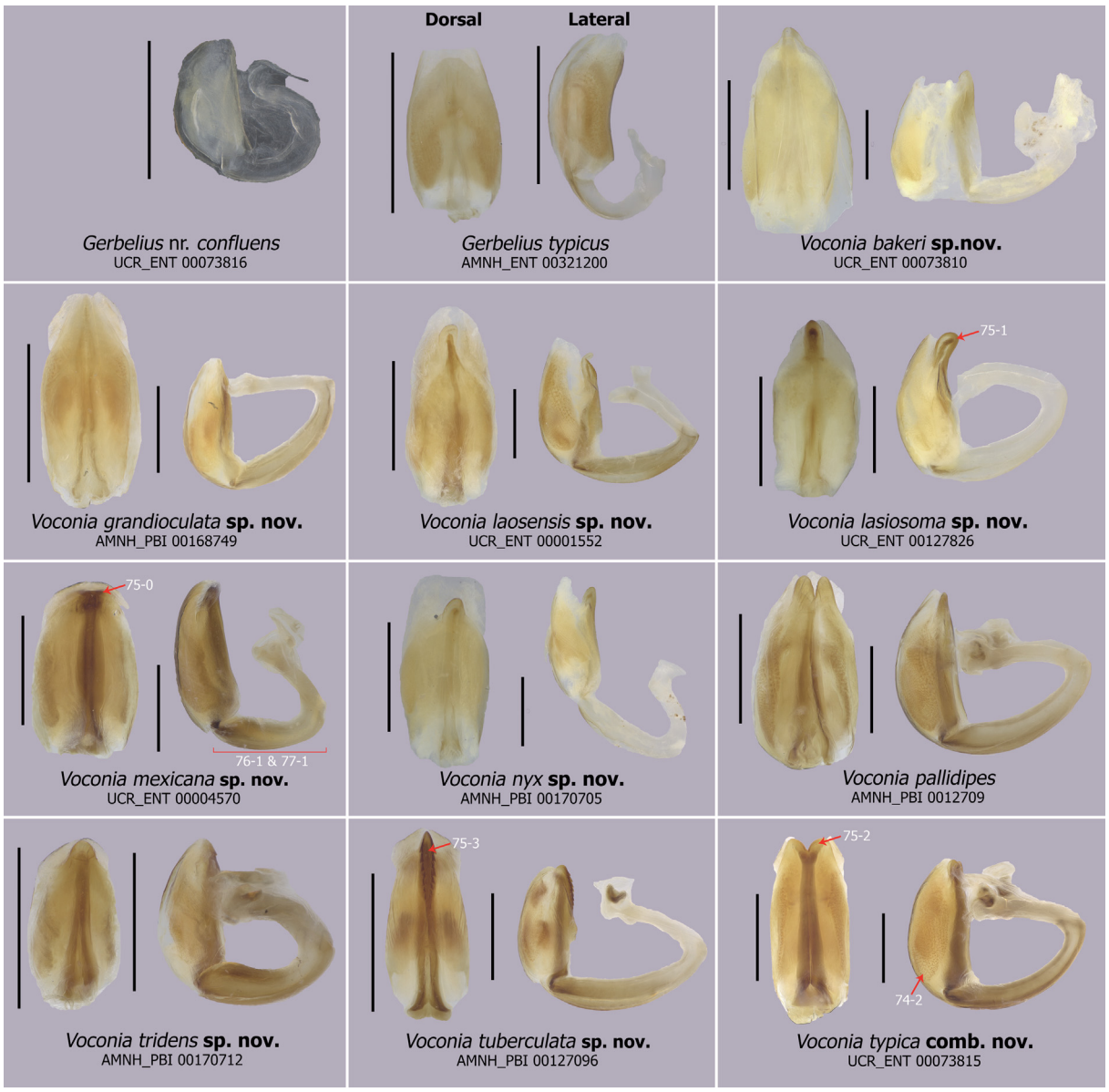

Fig. 14. Aedeagus of species of *Gerbelius* Distant, 1903 and *Voconia* Stål, 1866. Scale bars = 0.5 mm.

long slightly raised scutellar spine in macropterous morph; anteriad-directed process of prosternum with paramedial lobes; anterior margin of stridulitrum not elongated into protuberance; proepimeron with smoothly rounded posteroventral margin. Legs: fossula spongiosa present on fore and mid legs. Abdomen (Fig. 4D): anterior margin of terga prominently carinulate, terga II and III with deeper and longer carinules; terga II with paired prominent longitudinal carinae reaching posterior margin of segment.

Female

As micropterous male. Body length: about 7.0 mm.

Distribution

Distributed in Garamba National Park in the Democratic Republic of the Congo.

Remarks

This description of *V. schoutedeni* is based on the micropterous male holotype (UCR_ENT 00070524), which was the only type specimen available for examination. Any descriptive information of the micropterous female or macropterous form is taken directly from the original description by Villiers (1964). A lectotype was also designated for the macropterous morph, *Pseudocethera schoutedeni* forme *alata* Villiers, 1964. However, this infrasubspecific name is permanently unavailable under ICZN Article 45.6.3, therefore this specimen (referred to as No. 1281 by Villiers) has no type status. A drawer image of specimens at the BMNH in 2011 suggests that the macropterous morph may be distributed as far north as Sierra Leone, but this specimen and the macropterous paratype need to be properly examined.

Voconia smithae sp. nov.
urn:lsid:zoobank.org:act:6E950EB8-E03F-4F9F-B422-BD1D7A1A1594
Figs 12, 14

Diagnosis

Distinguished from other species in *Voconia* by its Afrotropical distribution and stout body. This species most closely resembles *V. motoensis* and *V. conradti. Voconia smithae* sp. nov. differs from *V. motoensis* by its distinct coloration: yellow scutellar spine; abducted corium with a yellow spot at proximal and distal apex, and brown dorsal laterotergites with contrasting yellow anterior spots. Despite the strong superficial resemblance to *V. conradti* due its to coloration and stoutness, closer examination reveals that *V. smithae* sp. nov. is distinguishable by the following: shorter body (9.7–9.8 mm long); light brown dorsal laterotergites with weakly contrasting yellow anterior spots; antennifer with long, laterally projecting setigerous tubercle; paired interocular setigerous tubercles; maxillary plates globular, directed straight anteriorly; longer anteocular region than postocular region (measured to where the posterior margin of the granulations meet the anterior margin of the smooth neck); and eyes do not bulge strongly laterally in dorsal view and do not reach ventral head margin in lateral view.

Etymology

Named after one of the collectors of the holotype and colleague from the Weirauch lab, Samantha Smith.

Type material

Holotype

GABON • ♂; Ogooué-Ivindo, Ipassa Reserve; 0.51167° N, 12.80306° E; elev. 516 m; 3–6 Feb. 2019; S. Smith, Y. Pacheco, S. Bybee, G. Svenson and G. Powell leg.; collecting event: GA19_L8_H; light trap; lowland forest; DNA voucher R_CW 5801; USI: UCR_ENT 00127891; UCR.

Paratypes

REPUBLIC OF THE CONGO • 1 ♂; Sibiti; [3.68° S, 13.35° E]; 25 Nov. 1963; Endrody-Younga leg.; Soil-Zoological Exped.; lamplight; USI: AMNH_PB 00213936; HNHM.

Description

Male (Figs 8, 10)

Body length. 9.7–9.8 mm; macropterous.

Coloration. Head: dark brown; postocular region with dark patches adjacent to medial ocellar margin, pale patches adjacent to lateral ocellar margin; labium lighter than head. Thorax: coloration as head, posterior margin of posterior pronotal lobe lighter; scutellum dark with contrasting yellow apical spine. Hemelytron (abducted): clavus brown with distal yellow stripe; corium dark or light brown with proximal, anteromedial, posteromedial, and distal yellow spots; membrane dark with pale V-shaped marking along R and M veins; membranal veins R and M proximally pale. Legs: yellowish-brown. Abdomen: yellowish-brown; dorsal laterotergites light brown with yellow spots anteriorly.

Integument and vestiture. Head and pronotum: coarsely granulose with sparse, short macrosetae interspersed among sparse pubescence; interocular region with two pairs of stout setigerous tubercles paramedially; antennifer with long lateral setigerous tubercle; morphologically ventral surface of labium with sparse, short macrosetae. Thorax: anterolateral angles of pronotal collar without macrosetae or setigerous tubercles. Hemelytron: corium with dense long setation. Legs: posterior row of protuberances on mid and hind femora with three large spines on distal half and three or fewer small spines. Abdomen: ventral surface pubescent.

Structure. Head: elongate, 1.3–1.4 times as long as wide; anteocular region about one third of head length, longer than postocular region (measured to anterior margin of neck); postocular region in dorsal view about as long as eye, lateral margins gently rounded and subrectangular; pedicel 1.4–1.5 times length of head width; maxillary plates ellipsoidal, adjacent to and longer than clypeus; apices of maxillary plates in dorsal view directed straight; clypeus in dorsal view narrower than maxillary plates; clypeal apex round, narrowed; interocular glabrous markings anterolaterally curved, joined at interocular sulcus paramedially; interocular sulcus in dorsal view curved and smoothly rounded anteriorly; eye width in dorsal view narrower than synthlipsis; eye not reaching ventral head margin in lateral view; ventrolateral swelling of buccula with tuberculate protrusion that surpasses buccular margin; labial segment I in lateral view straight, reaching posteroventral eye margin; morphologically dorsal surface of labial segment II nearly straight, about 0.6 times length of segment I. Thorax: pronotal collar narrow medially with anterolateral angles short and flared laterally; anterior pronotal lobe about 0.6 times length of posterior pronotal lobe, lateral margins almost straight; glabrous markings on pronotum slightly depressed; median apodeme depression of pronotum deep, circular; scutellar spine long, subhorizontal; anteriad-directed process of prosternum with paramedial lobes; anterior margin of stridulitrum not elongated into protuberance; proepimeron with smoothly rounded posteroventral margin. Legs: fossula spongiosa present on fore and mid legs. Abdomen: anterior margin of terga weakly carinulate; terga II and III with paired prominent longitudinal carinae, reaching about one-third of tergum III.

Female

Unknown.

Distribution (Fig. 17)

Only known from Congo and Gabon in Africa.

Remarks

The male paratype varies from the holotype in the following: head and pronotum finely granulose, postocular region subrectangular, buccula without lateral tuberculate protrusion. The holotype was preserved in ethanol when the mid and hind legs were dissected for DNA extraction but was not Illumina sequenced.

Voconia tridens sp. nov.
urn:lsid:zoobank.org:act:82E67D5A-E019-40EE-A019-E3BCD5E781DA
Figs 1–2, 8, 10, 13–14, 17

Diagnosis

Distinguished from other species of *Voconia* by the following combination of characters: coarsely granulose head and pronotum; maxillary plates not adjacent to and far surpass clypeal apex; and antennifers with a long, lateral spine. This species is recognized from the macropterous morph of *V. schoutedeni* by the yellow head and pronotum; the maxillary plates in lateral view are not wide, about the width of the scape; scutellar spine is subhorizontal; and the hemelytra is not blackish, it is a light brown with pale coloration at the base and apex of the corium.

Etymology

The specific epithet is the Latin adjective '*tridens*, -, -', meaning 'three-toothed, three-pronged', derived from the prefix '*tri*-' combined with the Latin noun '*dens*', referring to the elongated and separated maxillary plates and clypeus that form three prongs.

Type material

Holotype

SUDAN • ♂ (dissected pygophore and aedeagus in vial); Blue Nile, Abu Hashim-Galegu; [12.25° N, 34.69° E]; 23–24 Nov. 1962; R. Linnavuori leg.; USI: AMNH_PBI 00170712; AMNH.

Description

Male (Figs 8, 10)

Body length. About 8.0 mm; macropterous.

Coloration. Head: yellow; postocular region with red patches adjacent to medial ocellar margin; labium as head. Thorax: uniformly yellow; scutellum yellow. Hemelytron (abducted): clavus uniformly yellow; corium proximal half mostly yellow, distal half brown with yellow spot at distal apex; membrane dark with pale V-shaped marking along R and M veins. Legs: yellow. Abdomen: yellow, dorsal laterotergites with a pale brown stripe on posterior margin.

Integument and vestiture. Head and pronotum: coarsely granulose with dense, short setigerous tubercles; interocular region with two pairs of stout setigerous tubercles paramedially; antennifer with long lateral spine; morphologically ventral surface of labium with sparse, short macrosetae. Thorax: anterolateral angles of pronotal collar without macrosetae or setigerous tubercles; scutellar lateral carinae with pubescent tubercles. Hemelytron: corium with short macrosetae. Legs: posterior row of protuberances on mid and hind femora with three large spines on distal half. Abdomen: ventral surface pubescent.

Structure. Head: elongate, about 1.3 times as long as wide; anteocular region two-fifths of head length, longer than postocular region (measured to anterior margin of neck); postocular region in dorsal view longer than eye, lateral margins subrectangular; scape not reaching head apex; pedicel about 0.9 times length of head width; maxillary plates ellipsoidal, not adjacent to or longer than clypeus;

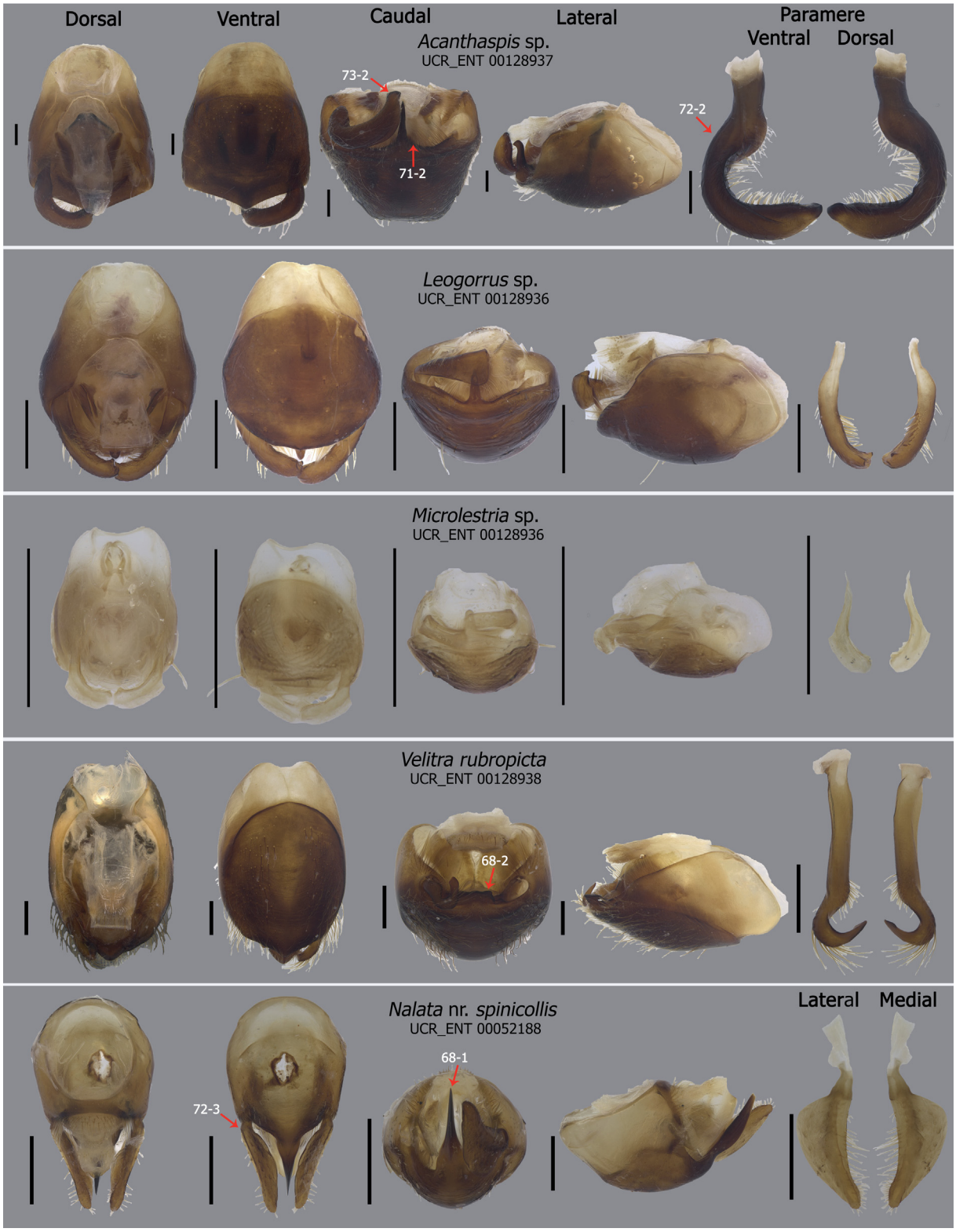

Fig. 15. Pygophore of outgroup species. Scale bars = 0.5 mm.

apices of maxillary plates in dorsal view diverging; clypeus in dorsal view narrower than maxillary plates; clypeal apex round, narrowed; interocular glabrous markings V-shaped, joined medially at interocular sulcus; interocular sulcus in dorsal view curved and smoothly rounded anteriorly; eye width in dorsal view narrower than synthlipsis; eye reaching ventral head margin in lateral view; ventrolateral swelling of buccula with acute protrusion surpassing buccular margin, small setigerous tubercles along margin of protrusion; labial segment I in lateral view straight, surpassing posteroventral eye margin; morphologically dorsal surface of labial segment II nearly straight, about 0.4 times length of segment I. Thorax: pronotal collar in dorsal view wide medially with anterolateral angles long, flared laterally; anterior pronotal lobe about 0.7 times length of posterior pronotal lobe, lateral margins almost straight; glabrous markings on pronotum deeply depressed; median apodeme depression of pronotum shallow, elongated longitudinally; scutellar spine long, subhorizontal; anteriad-directed process of prosternum with paramedial lobes; anterior margin of stridulitrum not elongated into protuberance; proepimeron with smoothly rounded posteroventral margin. Legs: fossula spongiosa present on fore and mid legs. Pygophore (Fig. 13): transverse bridge with triangular posterior margin; posterior region of ventral surface of pygophore in lateral view straight, not swollen; short median apical process sharply bent posteriorly in lateral view; lateral pygophore margin with protuberance; posterior pygophore margin with clustered macrosetae on protuberance; parameres round, apex tapered into squarely rounded tip. Aedeagus: endosoma almost entirely covered with spicules; apex of dorsal phallothecal sclerite tongue-shaped in dorsal view; basal plate extension about 4.6 times as long as wide.

Female

Unknown.

Distribution (Fig. 17)

Only known from the type locality in Northeastern Africa, Sudan.

Remarks

The antennifer spine on the right side of the head of the holotype is absent. We assume it was damaged since three species, *V. schoutedeni*, *V. monodi*, and *V. ifana*, have similar long spines that are paired. The pygophore of specimen AMNH_PBI 00170712 was used for DNA extraction, but we did not get sufficient DNA in our NGS library for Illumina sequencing.

Voconia trinidadensis sp. nov.
urn:lsid:zoobank.org:act:F5E8C8C5-6BD2-4544-A81D-0F31F846EF2E
Figs 1–2, 8, 10, 19

Diagnosis

One of two New World species of *Voconia*. Recognized by the finely granulose head and prothorax; proepimeron with protuberance on posteroventral margin; pronotum dark with contrasting yellow posterior margin; corium dark with anteroproximal yellow stripe, posteromedial and distal white spots; labial segment I in lateral view not surpassing posteroventral eye margin.

Etymology

Named after the collecting locality of the holotype in Trinidad. A proper noun with the Latin adjectival suffix '-*ensis*' meaning 'belonging to'. To be treated as an adjective.

Type material

Holotype

TRINIDAD AND TOBAGO • ♀; Trinidad; J.W. Chapman leg.; USI: AMNH_PBI 00170700; AMNH.

Description

Female (Figs 8, 10)

Body length. 10.5 mm; macropterous.

Coloration. Head: dark brown; maxillary plates light brown; postocular region with pale patches adjacent to lateral ocellar margin; labium lighter than head, yellow. Thorax: as head; posterior pronotal lobe with posterior margin lighter; scutellum dark with contrasting yellow apical spine. Hemelytron (abducted): clavus reddish-brown with distal white stripe; corium reddish-brown with anteroproximal yellow stripe, posteromedial and distal white spots; membrane dark with white V-shaped marking along R and M veins; membranal veins R and M proximally white. Legs: yellow. Abdomen: dark brown, dorsal laterotergites brown medially, with black stripe adjacent to yellow lateral margin.

Integument and vestiture. Head and pronotum: finely granulose with sparse, long macrosetae interspersed among dense pubescence; interocular region with two pairs of macrosetae paramedially; antennifer with short lateral setigerous tubercle; morphologically ventral surface of labium with dense, short macrosetae. Thorax: anterolateral angles of pronotal collar with macrosetae; scutellar lateral carinae with long setation. Hemelytron: corium with sparse, long setation. Legs: posterior row of protuberances on mid and hind femora with three large spines on distal half and many small spines. Abdomen: ventral surface pubescent.

Structure. Head: elongate, about 1.4 times as long as wide; anteocular region about one third of head length, about as long as postocular region (measured to anterior margin of neck); postocular region in dorsal view about as long as eye, lateral margins gently rounded; pedicel about 1.3 times length of head width; maxillary plates ellipsoidal, adjacent to and longer than clypeus; apices of maxillary plates in dorsal view directed straight; clypeus in dorsal view wider than maxillary plates; clypeal apex round, not narrowed; interocular glabrous markings anterolaterally curved, joined at interocular sulcus paramedially; interocular sulcus in dorsal view curved and smoothly rounded anteriorly; eye width in dorsal view wider than synthlipsis; eye reaching ventral head margin in lateral view; ventrolateral swelling of buccula without lateral protrusion that surpasses buccular margin, flat margin; labial segment I in lateral view straight, reaching posteroventral eye margin; morphologically dorsal surface of labial segment II nearly straight, about 0.6 times length of segment I. Thorax: pronotal collar in dorsal view narrow medially with anterolateral angles short, projected forward; anterior pronotal lobe about 0.5 times length of posterior pronotal lobe, lateral margins almost straight; glabrous markings on pronotum thin, not deeply depressed; median apodeme depression of pronotum deep, elongated transversely; scutellar spine long, subhorizontal; anteriad-directed process of prosternum smoothly rounded, without paramedial lobes; anterior margin of stridulitrum not elongated into protuberance; proepimeron with acute protuberance on posteroventral margin. Legs: fossula spongiosa of fore leg present, absent or vestigial on mid leg. Abdomen: anterior margin of terga prominently carinulate, posterior margin of terga III–VI weakly carinulate; terga II and III with paired prominent longitudinal carinae, reaching about two-thirds of tergum III; medial region between carinae on tergum II coarsely granulose.

Distribution (Fig. 19)

This species is only known from the type locality, Trinidad.

Voconia tuberculata sp. nov.
urn:lsid:zoobank.org:act:B50D3ECC-82C1-431B-95C1-6C8326049678
Figs 12, 14, 17–18

Diagnosis

Distinguished from most species of *Voconia* by its tuberculate and coarsely granulose head and pronotum. This species most closely resembles another Australian species, *V. dolichocephala* sp. nov. These two

species are recognized from other Australian species by the acute protuberance on the posteroventral margin of the proepimeron, the long macrosetae of the setigerous tubercles, the elongate head (1.4–1.6 times as long as wide), and the yellow spots antero- and posteromedially on the abducted corium. *Voconia tuberculata* sp. nov. differs from *V. dolichocephala* sp. nov. by its overall light brown coloration and males are as long as about 7.9 mm. Females are smaller than the examined *V. dolichocephala* sp. nov. females (about 8.8 and 9.0 mm).

Etymology

The specific epithet is the Latin adjective '*tuberculatus*, *-a*, *-um*', meaning 'warty' or 'tuberculate'. Refers to the densely tuberculate surfaces of the body.

Type material

Holotype

AUSTRALIA • ♂ (dissected pygophore and aedeagus in vial); Northern Territory, 17 km NE of Willeroo; [15.23° S, 131.67° E]; 8–9 Nov. 1984; M. and B. Baehr leg.; USI: AMNH_PBI 00127096; ZSMC.

Paratypes

AUSTRALIA – **Northern Territory** • 1 ♂; same collection data as for holotype; USI: AMNH_PBI 00127095; ZSMC • 1 adult sex unknown (abdomen missing); 30 km ESE of Victoria R. Downs; 16.19° S, 131.17° E; 18 Jun. 1969; M. Mendum leg.; USI: AMNH_PBI 00168741; ANIC • 1 ♂; Elsey Ck, 19 km SSE of Mataranka; 15.05° S, 133.07° E; 15 Oct. 1972; Upton and Barrett leg.; USI: AMNH_PBI 00168742; ANIC. — **Queensland** • 1 ♀; Burketown, site of old Broom Hotel: [17.85° S, 139.62° E]; 18 May 1931; T.G. Campbell leg.; light trap; USI: AMNH_PBI 00168743; ANIC • 1 ♀; same collection data as for preceding; USI: AMNH_PBI 00168744; ANIC • 1 ♂; Kunkulla Station, Gregory River; 25 May 1931; I.M. Mackerras leg.; USI: AMNH_PBI 00168746; ANIC.

Description

Male (Figs 8, 10)

Body length. 7.9–8.9 mm; macropterous.

Coloration. Head: dark brown; postocular region with dark patches adjacent to medial ocellar margin and pale patches adjacent to lateral ocellar margin; labium lighter than head. Thorax: coloration as head; scutellum uniformly brown. Hemelytron (abducted): clavus reddish-brown with distal yellow stripe; corium reddish-brown with anteromedial, posteromedial, and distal yellow spots; membrane dark with pale V-shaped marking along R and M veins; membranal veins R and M proximally pale. Legs: yellowish-brown. Abdomen: light brown, dorsal laterotergites I and II paler than remainder.

Integument and vestiture. Head and pronotum: coarsely granulose with sparse, long setigerous tubercles interspersed among sparse pubescence; interocular region with two pairs of stout setigerous tubercles paramedially; antennifer with long lateral setigerous tubercle; morphologically ventral surface of labium with sparse, short macrosetae. Thorax (Fig. 3L): anterolateral angles of pronotal collar with setigerous tubercles; scutellar lateral carinae with setigerous tubercles with long macrosetae. Hemelytron: corium with dense long setation. Legs: posterior row of protuberances on mid and hind femora with four or more large spines on distal half. Abdomen: ventral surface pubescent, long macrosetae interspersed.

Structure. Head: elongate, 1.4–1.6 times as long as wide; anteocular region about one third of head length, shorter than postocular region (measured to anterior margin of neck); postocular region in dorsal view longer than eye, lateral margins gently rounded; pedicel about 1.5–2.2 times length of head width; maxillary plates ellipsoidal, adjacent to and longer than clypeus; apices of maxillary plates in dorsal view diverging; clypeus in dorsal view about as wide as maxillary plates; clypeal apex bifid, not narrowed;

interocular glabrous markings anterolaterally curved, joined at interocular sulcus paramedially or medially forming a V-shaped marking; interocular sulcus in dorsal view nearly straight; eye width in dorsal view narrower than synthlipsis; eye reaching ventral head margin in lateral view; ventrolateral swelling of buccula without lateral protrusion that surpasses buccular margin, flat margin; labial segment I in lateral view straight, surpassing posteroventral eye margin; morphologically dorsal surface of labial segment II curves ventrally, about 0.3 times length of segment I. Thorax (Fig. 3L): pronotal collar in dorsal view wide medially with anterolateral angles long, flared laterally; anterior pronotal lobe 0.6–0.8 times length of posterior pronotal lobe, lateral margins almost straight; glabrous markings on pronotum conspicuous, not depressed; median apodeme depression of pronotum shallow, elongated transversely; scutellar spine long, raised; anteriad-directed process of prosternum with paramedial lobes; anterior margin of stridulitrum projected into small protuberance; proepimeron with acute protuberance on posteroventral margin. Legs: fossula spongiosa present on fore and mid legs. Abdomen: anterior margin of terga weakly carinulate, terga II and III with deeper and longer carinules; terga II and III with paired prominent longitudinal carinae, reaching about two-thirds of tergum III. Pygophore (Fig. 13): transverse bridge with rounded posterior margin; posterior region of ventral surface of pygophore in lateral view with large swelling; short median apical process, sharply bent posteriorly in lateral view; lateral pygophore margin with protuberance; posterior pygophore margin with clustered macrosetae on protuberance; parameres sinusoidal, apex tapered sharply. Aedeagus (Fig. 14): endosoma almost entirely covered with spicules; apex of dorsal phallothecal sclerite serrated; basal plate extension about 5.7 times as long as wide.

Female

Mostly as male, distinguished from males by the following. Body length: 8.4–8.8 mm. Head: elongate, 1.5 times as long as wide; pedicel about 1.5–1.7 times length of head width. Legs: fossula spongiosa present on fore leg, absent or vestigial on mid leg.

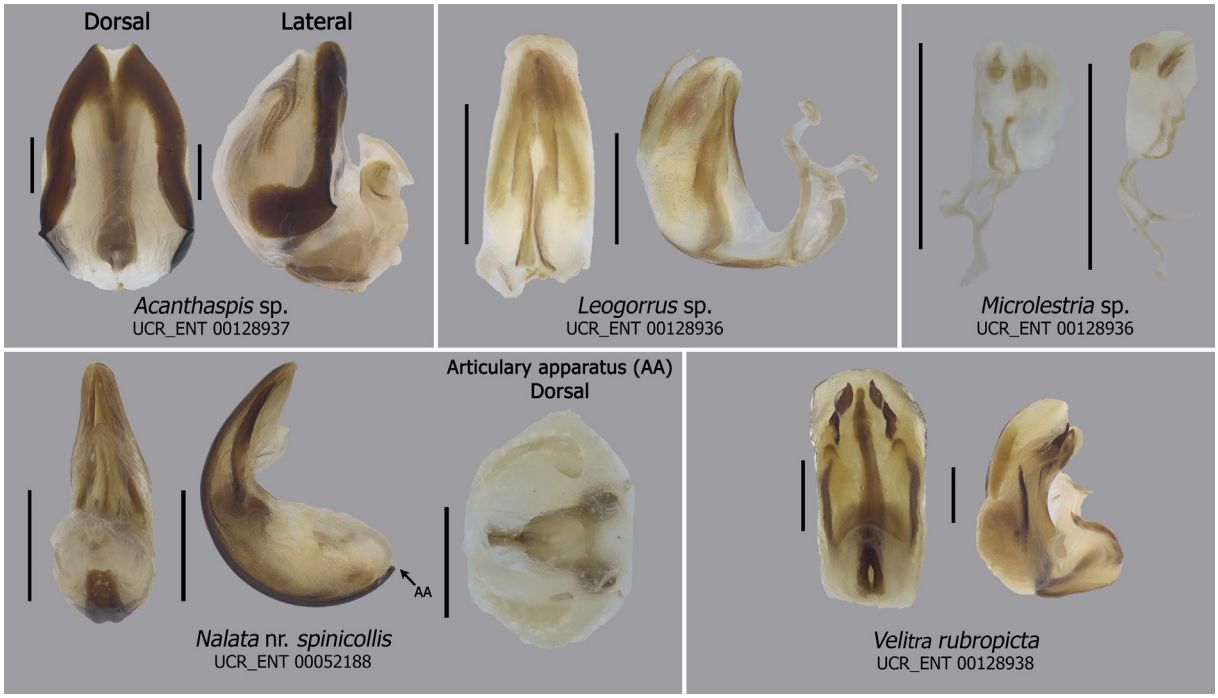

Fig. 16. Aedeagus of outgroup species. Scale bars = 0.5 mm.

Distribution (Fig. 18)

This species is distributed across Northern Territory and Queensland in Australia. The nearest *Voconia* species is *V. dolichocephala* sp. nov., found about 100 km northwest of specimen AMNH_PBI 00168742.

Remarks

The direction of the maxillary plates in dorsal view varies from nearly straight or parallel (e.g., AMNH_PBI 00168741) to strongly diverging (e.g., AMNH_PBI 00168746). *Voconia tuberculata* sp. nov. is nested within the Australian clade. According to our phylogeny (Figs 1–2), *V. tuberculata* sp. nov. was recovered as the sister taxon to *V. dolichocephala* sp. nov. The abdomen of specimen AMNH_PBI 00127096 was used for DNA extraction, but we did not get sufficient DNA in our NGS library for Illumina sequencing.

Voconia typica (Miller, 1958) comb. nov.
Figs 1–2, 8, 10, 13–14, 18

Paragerbelius typicus Miller, 1958: 66, figs 88–92.

Revised diagnosis

This species is most similar to *V. bracata* sp. nov. They are distinguished from other species of the genus *Voconia* by the slender body, long head (1.7 times as long as wide), the ventral surface of the hind leg with four large spines in the posterior row, the large pale spot between the R and M veins, and the dorsal laterotergites I and II being yellow, the remainder dark brown. The following differentiate *V. typica*: largest species of *Voconia* (12.4–12.7 mm long); uniformly brown legs; anterior pronotal lobe is gently rounded, posterolateral margins nearly straight.

Type material

Holotype

INDONESIA • ♂; "North New Guinea" [Papua], Jayapura Co., Cyclops Mts, Sabron camp; [2.50° N, 140.42° E]; elev. "2200 ft" [671 m]; Jun. 1936; L.E.C. leg.; coll. B.M. 1936-271; USI: UCR_ENT 00048384; NHMUK 013588138 (previously BMNH(E) 1255222).

Paratype

INDONESIA • 1 ♂; same collection data as for holotype; BMNH.

Additional material examined:

INDONESIA • 1 ♂; "West New Guinea" [Papua], Central Mountains, Archbold Lake; [3.41° S, 138.53° E]; elev. 760 m; 26 Nov.–3 Dec. 1961; S. Quate and L. Quate leg.; dissected pygophore and aedeagus in vial; USI: UCR_ENT 00073815; BPBM.

Redescription

Male (Figs 8, 10)

Body length. 12.4–12.7 mm; macropterous.

Coloration. Head: dark brown; postocular region with dark patches adjacent to medial ocellar margin and pale patches adjacent to lateral ocellar margin; labium lighter than head, light brown. Thorax: as head; pronotum uniformly coloured; scutellum dark with contrasting yellow apical spine. Hemelytron (abducted): clavus dark reddish-brown with distal yellow stripe; corium reddish-brown with anteromedial, posteromedial, and distal yellow spots; membrane dark with large pale spot between R and M veins;

membranal veins R and M proximally pale, remainder as membrane. Legs: dark brown. Abdomen: dark brown, dorsal laterotergites I and II yellow.

Integument and vestiture. Head and pronotum: finely granulose with sparse, short macrosetae interspersed among dense pubescence; interocular region with two paired macrosetae; antennifer with short lateral setigerous tubercle; morphologically ventral surface of labium with dense, short macrosetae. Thorax: anterolateral angles of pronotal collar without macrosetae or setigerous tubercles. Hemelytron: corium with sparse, long setation. Legs: posterior row of protuberances on mid and hind femora with four large spines on distal half. Abdomen: ventral surface pubescent.

Structure. Head: elongate, about 1.7 times as long as wide; anteocular region about one third of head length, about as long as postocular region (measured to anterior margin of neck); postocular region in dorsal view longer than eye, lateral margins gently rounded; pedicel about 1.8 times length of head width; maxillary plates ellipsoidal, adjacent to and reaching apex of clypeus; apices of maxillary plates in dorsal view directed straight; clypeus in dorsal view narrower than maxillary plates; clypeal apex round, not narrowed; interocular glabrous markings V-shaped, joined medially at interocular sulcus; interocular

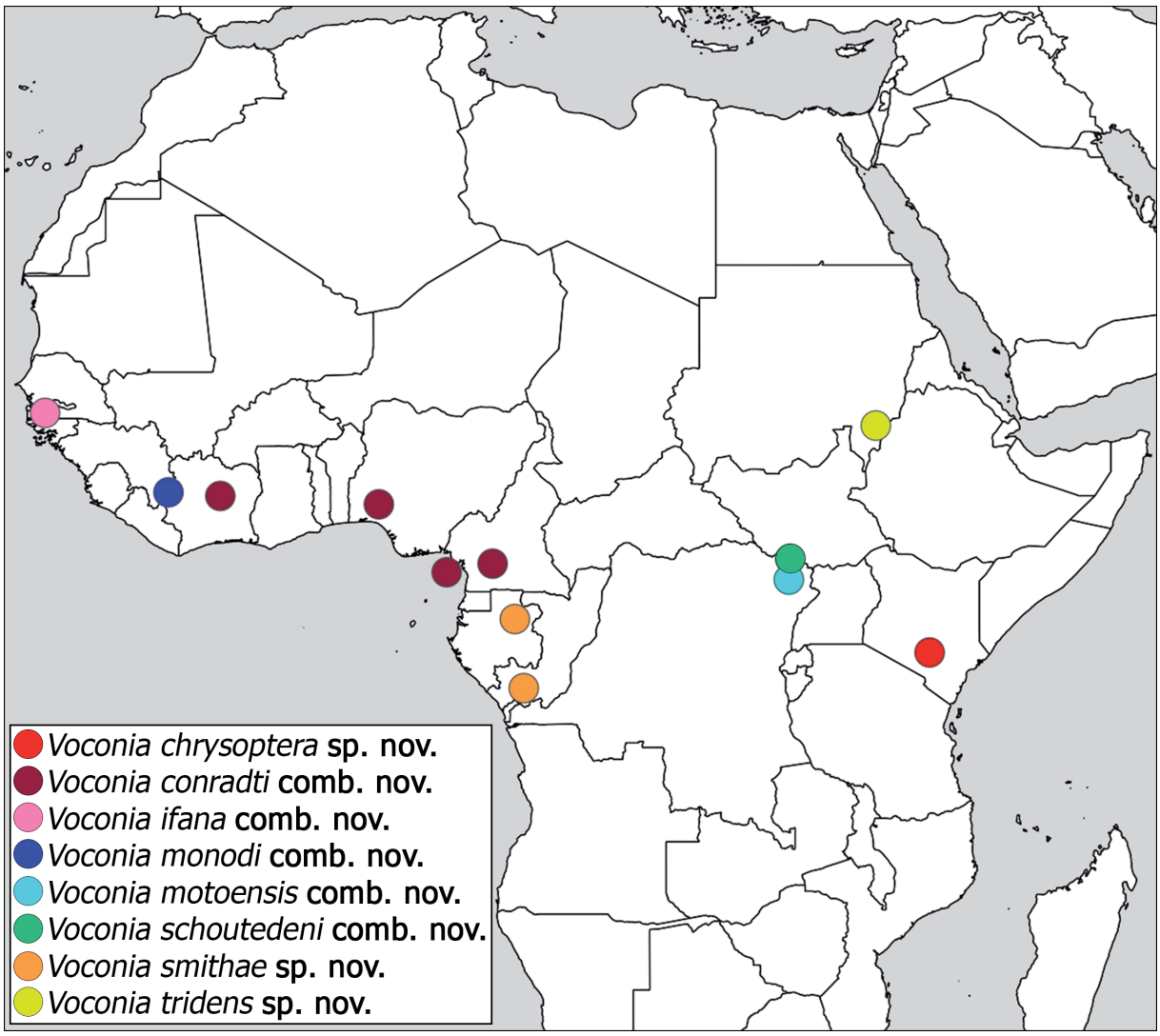

Fig. 17. The distribution of species of *Voconia* Stål, 1866 in Africa.

sulcus in dorsal view bent anteromedially, subtriangular; eye width in dorsal view wider than synthlipsis; eye reaching ventral head margin in lateral view; ventrolateral swelling of buccula without lateral protrusion that surpasses buccular margin, flat margin; labial segment I in lateral view straight, surpassing posteroventral eye margin; morphologically dorsal surface of labial segment II nearly straight, about 0.4 times length of segment I. Thorax: pronotal collar in dorsal view narrow medially with anterolateral angles short, projected forward; anterior pronotal lobe subequal in length to posterior pronotal lobe, lateral margins almost straight; glabrous markings on pronotum thin and deeply depressed; median apodeme depression of pronotum deep and elongated transversely; scutellar spine long, subhorizontal; anteriad-directed process of prosternum smoothly rounded, without paramedial lobes; anterior margin of stridulitrum not elongated into protuberance; proepimeron with smoothly rounded posteroventral margin. Legs: fossula spongiosa present on fore and mid legs. Abdomen: anterior margin of terga weakly carinulate, tergum II without carinules laterally; terga II and III with paired prominent longitudinal carinae, almost reaching posterior margin of tergum III. Pygophore (Fig. 13): transverse bridge with rounded posterior margin; posterior region of ventral surface of pygophore in lateral view with large swelling; short median apical process sharply bent posteriorly in lateral view; lateral pygophore margin with protuberance; posterior pygophore margin with clustered macrosetae on decline; parameres sinusoidal, apex tapered into squarely rounded tip. Aedeagus (Fig. 14): endosoma almost entirely covered with spicules; apex of dorsal phallothecal sclerite bifid in dorsal view; basal plate extension about 7.9 times as long as wide.

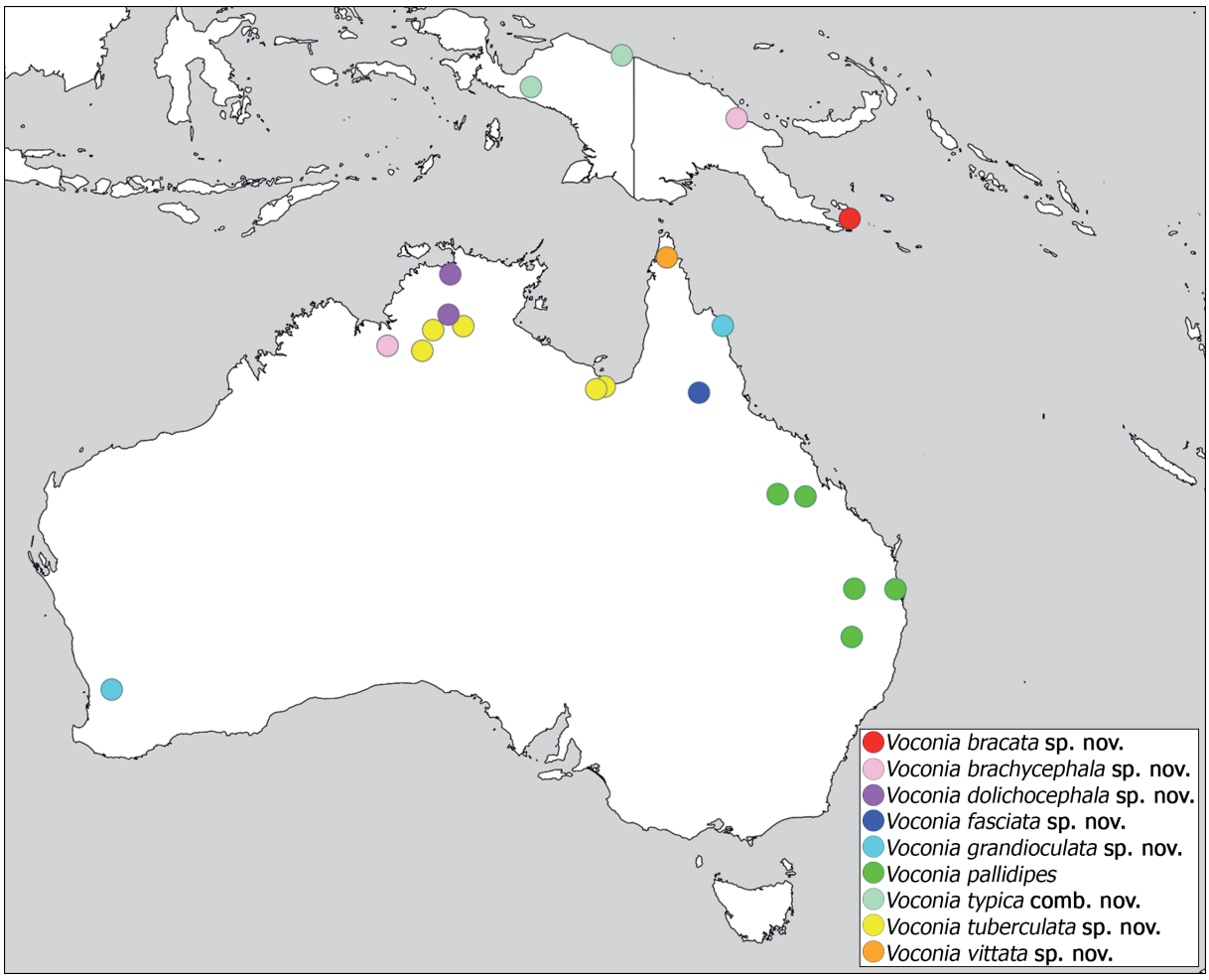

Fig. 18. The distribution of species of *Voconia* Stål, 1866 in the Australasian region.

Female

Unknown.

Distribution (Fig. 18)

This species is distributed on the island of New Guinea, in Papua.

Remarks

This description is based largely on UCR_ENT 00073815, since the holotype (Fig. 8) and paratype remain at the BMNH. Images of the types in their unit trays at the BMNH were used to evaluate this species concept. The abdomen of specimen UCR_ENT 00073815 was used for DNA extraction, but we did not get sufficient DNA in our NGS library for Illumina sequencing.

Voconia vittata sp. nov.
urn:lsid:zoobank.org:act:772BEB7A-1101-4AD1-91C0-8EED38AE4516
Figs 1–2, 8, 10, 12, 14, 18

Diagnosis

Distinguished from other species of *Voconia* by the following combination of characters: short body length (about 7.1 mm long); globose head; tuberculate and coarsely granulose head and pronotum; interocular region with two setigerous tubercles medially; apex of clypeus bifid; corium dark with thick medial yellow stripe; and dark brown femora with contrasting yellowish-brown tibiae and tarsi. This species most closely resembles another Australian species, *V. fasciata* sp. nov., but *V. vittata* sp. nov. is about 1.6 mm shorter and the yellow medial stripe on the corium is opaque.

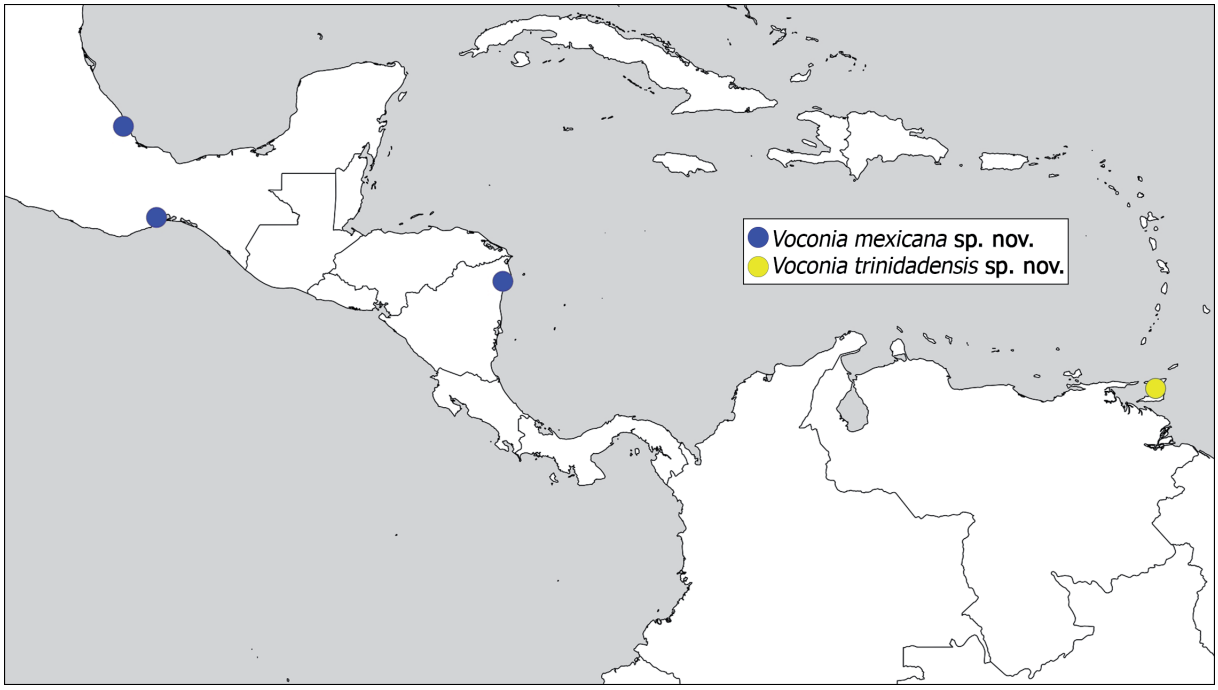

Fig. 19. The distribution of species of *Voconia* Stål, 1866 in Central America.

Etymology

The specific epithet is the Latin adjective '*vittatus*, *-a*, *-um*', meaning 'banded'. Refers to the yellow band or color pattern that crosses the middle of the corium and scutellar spine.

Type material

Holotype

AUSTRALIA • ♂; Queensland, Cape York Peninsula, Dulhunty Rd; 11.86666° S, 142.5° E; 22 Mar. 1992; G. Cassis leg.; at light; USI: AMNH_PBI 00088406; AMS K 156496.

Description

Male (Figs 8, 10)

Body length. About 7.1 mm; macropterous.

Coloration. Head: uniformly dark brown; labium lighter than head, labial segment I brown, II and III yellowish-brown. Thorax: as head; scutellum dark with contrasting yellow apical spine. Hemelytron (abducted): clavus dark reddish-brown with distal yellow stripe; corium dark reddish-brown with thick medial yellow stripe; membrane dark with pale V-shaped marking along R and M veins; membranal veins An_1 and R proximally pale. Legs: femora dark brown, tibiae and tarsi yellowish-brown. Abdomen: yellowish-brown medially, dark reddish-brown laterally; dorsal laterotergites I and II paler than remainder.

Integument and vestiture. Head and pronotum: coarsely granulose with dense, short setigerous tubercles interspersed among sparse pubescence; interocular region with two pairs of stout setigerous tubercles paramedially and two medially; antennifer with long lateral setigerous tubercle; morphologically ventral surface of labium with sparse, long macrosetae. Thorax: anterolateral angles of pronotal collar with setigerous tubercles; scutellar lateral carinae with short macrosetae on setigerous tubercles. Hemelytron:

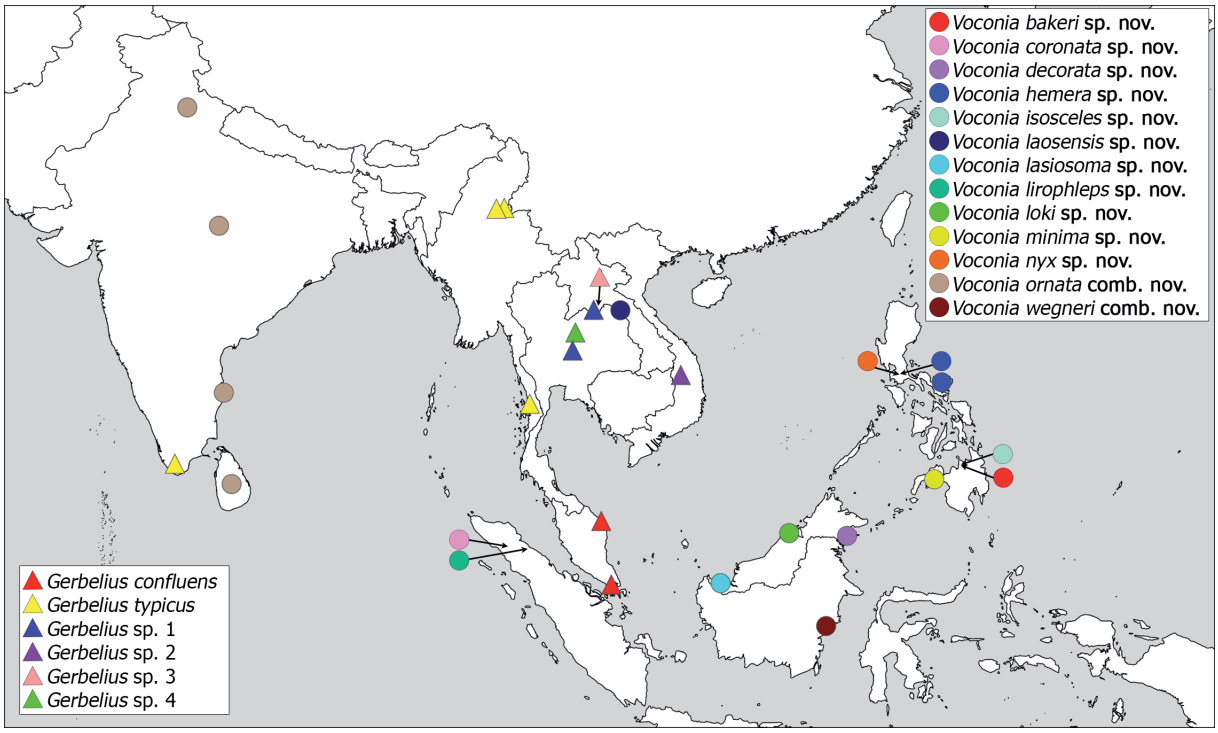

Fig. 20. The distribution of species of *Gerbelius* Distant, 1903 and *Voconia* Stål, 1866 in Southeast Asia.

corium with dense, long macrosetae. Legs: posterior row of protuberances on mid and hind femora with three or four spines on distal half. Abdomen: ventral surface pubescent, long macrosetae interspersed.

Structure. Head: globose, about as long as wide; anteocular region about one quarter of head length, shorter than postocular region (measured to anterior margin of neck); postocular region in dorsal view about as long as eye, lateral margins gently rounded; pedicel about 1.4 times length of head width; maxillary plates ellipsoidal, adjacent to and reaching apex of clypeus; apices of maxillary plates in dorsal view converging; clypeus in dorsal view wider than maxillary plates; clypeal apex bifid, narrowed; interocular glabrous markings anterolaterally curved, joined at interocular sulcus paramedially; interocular sulcus in dorsal view bent anteromedially, subtriangular; eye width in dorsal view narrower than synthlipsis; eye reaching ventral head margin in lateral view; ventrolateral swelling of buccula with lateral protrusion that surpasses buccular margin; labial segment I in lateral view straight, surpassing posteroventral eye margin; morphologically dorsal surface of labial segment II curves ventrally, about 0.4 times length of segment I. Thorax: pronotal collar in dorsal view wide medially with anterolateral angles short, flared laterally; anterior pronotal lobe about 0.9 times length of posterior pronotal lobe, lateral margins almost straight; glabrous markings on pronotum conspicuous and not depressed; median apodeme depression of pronotum shallow, elongated longitudinally; scutellar spine long, raised; anteriad-directed process of prosternum with paramedial lobes; anterior margin of stridulitrum projected into small protuberance; proepimeron with smoothly rounded posteroventral margin. Legs: fossula spongiosa present on fore and mid legs.

Female

Unknown.

Distribution (Fig. 18)

This species is only known from the type locality in Northern Australia.

Remarks

Nested within the well supported Australian clade (Figs 1–2).

Voconia wegneri (Miller, 1954) comb. nov.
Figs 1–2, 3E, 8, 10, 20

Kayanocoris wegneri Miller, 1954: 6, fig. 3.

Revised diagnosis

Distinguished from other species of *Voconia* by the minute ocelli, occupying 0.12 times length of postocular region; labial segment I swollen subapically on ventral surface; labial segment II swollen ventrobasally and narrowed apically; labial segment III very short (about 0.14 mm long), about 0.2 times length of segment II.

Type material

Holotype

INDONESIA • ♂; E Borneo, Balikpapan, Mentawir River; [1.04° S, 116.75° E]; elev. 50 m; 14 Oct. 1950; A.M.R. Wegner leg.; USI: RMNH.INS 1091587; NBCN (previously RMNH).

Redescription

Male (Figs 8, 10)

Body length. ~9.1 mm; macropterous.

Coloration. Head: dark brown with a semicircular pale stripe encircling both ocelli; labium lighter than head, brown. Thorax: as head; scutellum dark with brown apical spine. Hemelytron (abducted): clavus dark with distal yellow stripe; corium dark with anteroproximal yellow stripe, posteromedial and distal yellow spots; membrane dark with pale V-shaped marking along R and M veins; membranal veins R and M proximally pale. Legs: dark brown. Abdomen: dark brown; dorsal laterotergites dark brown.

Integument and vestiture. Head and pronotum: finely granulose with dense, long macrosetae interspersed among dense pubescence; antennifer with short lateral setigerous tubercle; morphologically ventral surface of labium with dense, short macrosetae. Thorax: anterolateral angles of pronotal collar without macrosetae or setigerous tubercles. Legs: posterior row of protuberances on mid and hind femora with four spines on distal half. Abdomen: ventral surface pubescent.

Structure. Head (Fig. 3E): elongate, about 1.5 times as long as wide; anteocular region about half of head length, longer than postocular region (measured to anterior margin of neck); postocular region in dorsal view longer than eye, lateral margins gently rounded; pedicel about 1.1 times length of head width; maxillary plates ellipsoidal, adjacent to and shorter than clypeus; apices of maxillary plates in dorsal view directed straight; clypeus in dorsal view about as wide as maxillary plates; clypeal apex round, not narrowed; interocular glabrous markings anterolaterally curved, joined at interocular sulcus paramedially; interocular sulcus in dorsal view curved and smoothly rounded anteriorly; eye width in dorsal view narrower than synthlipsis; eye reaching ventral head margin in lateral view; ocelli minute, occupying 0.12 times length of postocular region; ventrolateral swelling of buccula without lateral protrusion that surpasses buccular margin, flat margin; labial segment I swollen subapically on ventral surface, surpassing posteroventral eye margin; labial segment II swollen ventrobasally, narrowed apically; morphologically dorsal surface of labial segment II curves ventrally, ~0.2 times length of segment I; labial segment III short, ~0.2 times length of segment II. Thorax: pronotal collar in dorsal view narrow medially with anterolateral angles short, projected forward; anterior pronotal lobe ~0.8 times length of posterior pronotal lobe; glabrous markings on pronotum thin and not deeply depressed; median apodeme depression of pronotum deep, elongated transversely; scutellar spine long, subhorizontal; anteriad-directed process of prosternum smoothly rounded, without paramedial lobes; anterior margin of stridulitrum not elongated into protuberance; proepimeron with smoothly rounded posteroventral margin. Legs: fossula spongiosa present on fore legs, unknown on mid legs.

Female

Unknown.

Distribution (Fig. 20)

This species is only known from the type locality in Eastern Borneo.

Remarks

The holotype remains at the NBCN under loan restrictions; habitus photographs were used to evaluate this species concept. Most closely resembles the two species from New Guinea, *V. bracata* sp. nov. and *V. typica.* These three species form a poorly supported clade in our analyses (Figs 1–2). This hypothesis should be further tested with additional material and molecular data.

Discussion

Pseudocetherinae was originally described based on *Pseudocethera* (3 spp. from Africa) as having a short, tri-lobed head with the antennal pedicel longer than the scape, small or vestigial ocelli, slender labium with labial segment I long and adpressed against the ventral head surface, the close proximity

of the coxal cavities of fore and mid legs, and the three-segmented tarsi. We expand this concept of Pseudocetherinae by transferring in five genera from Reduviinae: *Gerbelius* (three spp. from the Oriental region), *Kayanocoris* (one sp. from Borneo), *Microvarus* (two spp. from Africa), *Paragerbelius* (one sp. from Papua), and *Voconia* (one spp. from Australia). As part of this revision, *Kayanocoris*, *Microvarus*, *Paragerbelius*, and *Pseudocethera* are synonymized with *Voconia*. As pointed out in the results section of the cladistic analysis, *Gerbelius* in the traditional sense is polyphyletic with respect to *G. ornatus*. Members of *Gerbelius* share laterally flattened maxillary plates; long prominent mandibular plates; a stout labium; and the Cu-An_1 cell is slender, tapers apically, and is similar in length to the M-Cu cell. Together, *G. confluens* and *G. typicus*, with two undescribed species, are part of the sister group of all remaining Pseudocetherinae (Figs 1–2). In contrast, *G. ornatus* not only closely resembles species of *Voconia* (anteriorly elongate maxillary plates, gracile labium, and short, triangular Cu-An_1 cell, among other characters) but based on our analyses is nested among them. Therefore, we transfer *G. ornatus* to *Voconia* and maintain *G. confluens* and *G. typicus* as the only two valid species of *Gerbelius*, the second genus of Pseudocetherinae.

Though the transfer of *Gerbelius* into Pseudocetherinae requires significant expansion of the original description, morphological (present study, Figs 1–2; Weirauch 2008), ribosomal (Weirauch 2008; Hwang & Weirauch 2012), and genomic analyses (Knyshov *et al.* unpubl. data) strongly support *Gerbelius* and *Voconia* as sister taxa. The bent apex of the third visible labial segment, anteriad-directed process of the prosternum, absence of dorsal abdominal glands on terga IV–VI, femora with ventral anterior and posterior rows of spine-like protuberances with macrosetae at the base of the protuberance, and laterally compressed tibiae unite Pseudocetherinae and form part of the new description.

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Supplementary material

Supp. file 1. Comprehensive measurements (in mm) of Pseudocetherinae Villiers, 1963. https://doi.org/10.5852/ejt.2022.788.1625.5795

Supp. file 2. Character matrix for phylogenetic analysis. https://doi.org/10.5852/ejt.2022.788.1625.5797

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