

A new species of scops-owl (Aves, Strigiformes, Strigidae, *Otus*) from Príncipe Island (Gulf of Guinea, Africa) and novel insights into the systematic affinities within *Otus*

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Abstract

A new species of scops-owl (Aves, Strigiformes, Strigidae, *Otus*) is described from Príncipe Island, São Tomé and Príncipe (Gulf of Guinea, Africa). This species was discovered for science in 2016, although suspicions of its occurrence gained traction from 1998, and testimonies from local people suggesting its existence could be traced back to 1928. Morphometrics, plumage colour and pattern, vocalisations, and molecular evidence all support the species status of the scops-owl from Príncipe, which is described here as *Otus bikegila* **sp. nov.** Phylogenetic analyses suggest that this species descended from the first colonisation of the Gulf of Guinea islands, being sister to the clade including the mainland African Scops-Owl *O. senegalensis*, and the island endemics São Tomé Scops-Owl *O. hartlaubi* and Pemba Scops-Owl *O. pembaensis*. The most diagnostic trait in the field is its unique call which, curiously, is most similar to a distantly related *Otus* species, the Sokoke Scops-Owl *O. ireneae*. The new species occurs at low elevations of the old-growth native forest of Príncipe, currently restricted to the south of the island but fully included within Príncipe Obô Natural Park. *Otus bikegila* **sp. nov.** takes the number of single-island endemic bird species of Príncipe to eight, further highlighting the unusually high level of bird endemism for an island of only 139 km².

Resumo

Descrevemos uma nova espécie de mocho-de-orelhas ou kitóli (Strigiformes: Strigidae: *Otus*) da Ilha do Príncipe, São Tomé e Príncipe (Golfo da Guiné, África). Esta espécie foi descoberta para a ciência apenas em 2016, embora suspeitas da sua existência tenham ganho força a partir de 1998, e testemunhos de habitantes locais sobre a sua ocorrência já estarem documentados em 1928. A morfometria, a cor e padrão da plumagem, as vocalizações e dados moleculares demonstram que esta população de mocho no Príncipe é uma espécie nova, que foi batizada de mocho-do-príncipe (lista mundial) ou kitóli-do-príncipe (nome nacional), *Otus bikegila* **sp. nov.** As análises filogenéticas indicam que esta espécie descende da primeira colonização das ilhas do Golfo da Guiné, sendo irmã do clado que inclui o mocho-d'orelhas-africano *O. senegalensis*, do continente, o mocho-de-são-tomé (ou kitóli-de-são-tomé) *O. hartlaubi* e o mocho-de-pemba *O. pembaensis*, ambos endêmicos das ilhas que lhes dão o nome. No campo, a característica mais diagnóstica é o seu canto único que, curiosamente, é mais parecido com o da espécie de *Otus* mais afastada, o mocho-de-sokoke *O. ireneae*. A nova espécie ocorre nas zonas baixas da floresta nativa do Príncipe, atualmente restrita ao sul da ilha, mas totalmente inserida no Parque Natural do Obô do Príncipe. *Otus bikegila* **sp. nov.** eleva o número de espécies de aves endêmicas restritas ao Príncipe para oito, sublinhando ainda mais o nível extremamente elevado de aves endêmicas para uma ilha de apenas 139 km².

Keywords

Biodiversity, endemism, exploration, Gulf of Guinea, integrative taxonomy, *Otus bikegila* sp. nov., Príncipe Scops-Owl, systematics

Palavras-chave

Biodiversidade, endemismo, exploração, Golfo da Guiné, Kitóli-do-príncipe, Mocho-do-príncipe, *Otus bikegila* sp. nov., sistemática, taxonomia integrada

“But I discovered that the very same aggregations or groupings of individuals that the trained zoologist called separate species were called species by the New Guinea natives. I collected 137 species of birds. The natives had 136 names for these birds (...)”

Ernst Mayr - Interview - Omni Magazine, February 1983

Introduction

Species are indeed the face of biodiversity with whom everyone relates to. The discovery of new species consistently makes headlines expressing wonder and joy. And yet, it has been estimated that only ca. 14% of extant species have been described, with invertebrates making most of the undescribed species (Mora et al. 2011). In this age of human-driven extinction (Ceballos et al. 2020), a major global effort should be undertaken to document what may soon not be anymore (Dijkstra 2016). Such new wave of exploration, carried out by professional and amateurs alike, would have the additional benefit of helping to revive a global interest in the natural world and the mysteries it holds. Only by rekindling this link can the current biodiversity crisis be reverted.

The discovery of new species tends to have a higher impact when it occurs in familiar groups like mammals or birds. Birds in particular are likely the best studied animal group, making the discovery of new species more challenging and often restricted to remote locations and/or difficult-to-study groups (e.g., Rheindt et al. 2020; Lane et al. 2021; Milá et al. 2021). This paper illustrates how exploration led to the discovery of a new owl species on the forests of Príncipe Island, Gulf of Guinea, Africa.

Owls (Aves, Strigiformes) are a charismatic bird group that made their way into most human cultures, where they are generally either symbols of wisdom or, on the contrary, omens of bad luck (Marcot and Johnson 2003). This is certainly linked to their nocturnal habits and associated elusiveness, their inquisitive look enhanced by their large eyes facing forward, and their calls heard through the night, which together help in creating an aura of mystery surrounding these species. In many aspects, this mystery has also permeated for a long time the scientific knowledge we have of the group. This is strikingly illustrated by the results of the extensive efforts carried out in recent decades, which through exploration in the field (e.g., Lambert and Rasmussen 1998; Warakagoda and Rasmussen 2004; Sangster et al. 2013) and taxonomic revisions (e.g., Fuchs et al. 2008; Flint et al. 2015; Salter et al. 2020) resulted in the remarkable increase of the number of recognised species of owls from 146 in 1975 (Morony et al. 1975) to up to 230 species in 2021 (Gill et al. 2021). This dramatic increase was supported by the widespread adoption of an integrative taxonomic framework (Padiál et al. 2010; Sangster 2018), which combines the use of multiple lines of evidence, such as genetics, morphology, acoustics, geography and behaviour to reach informed decisions on the species status of a given taxon (see also Cadena and Zapata 2021).

Still, compared to other groups, the current discrepancy in the number of owl species accepted by different authorities highlights the challenges associated with the taxonomy and systematics of this group. This stems from their nocturnal habits, making

them difficult to study, and from being a group where, at the generic level, morphological variation between species can be similar or lower than within-species (Marks et al. 1999). This is because, in owls, the evolution of plumage pattern and colour is driven by the pressure to remain cryptic during daytime as a defence against predators or to avoid being mobbed by other birds, a common occurrence among members of the family (Marks et al. 1999; König et al. 2008). This led to the convergent evolution of similar camouflaged patterns across species, as happens in other nocturnal bird groups like the nightjars (Caprimulgidae: Holyoak 2001). As such, plumage is generally not diagnostic in owls, with distantly related species often being strikingly similar (Marks et al. 1999). This morphological uniformity is especially evident, and taxonomically challenging, in the most speciose genus of the family: *Otus* Pennant, 1769, which includes over 50 recognised species, occurring across Asia, Europe, and Africa (Marks et al. 1999; König et al. 2008; Winkler et al. 2020). Commonly known as scops-owls, these small to medium-sized predators show two main plumage colour types, rufous or grey (or grey-brown) morphs, which often occur in the same populations (Pons et al. 2013).

In contrast to plumage, vocalisations of members of the Strigidae family are species-specific. As with most non-passerines and suboscine passerines, owl songs are not learned (Gahr 2000) and therefore have a strong genetic basis. Additionally, contrarily to the difficulty in observing owls, their vocalisations are conspicuous and easily detected as they play a major role in territorial defence and mate attraction (Marks et al. 1999; König et al. 2008). Vocalisations thus represent the most important trait to differentiate species of owls (e.g., Marshall 1978; Sangster et al. 2013; Flint et al. 2015), and new species are often first discovered through their calls (Melo and Dallimer 2008, 2009; Sangster et al. 2013).

The Gulf of Guinea, Central Africa, has three oceanic islands, Príncipe, São Tomé, and Annobón, in a northeast to southwest line, with São Tomé touching the equator. The rainforests of the islands constitute an independent ecoregion (Gascoigne 2004) characterised by high endemism levels across groups (Jones 1994). Endemism is particularly striking in birds, with the islands having been classified as the third most important in the world for the conservation of forest birds (Buchanan et al. 2011). Relatively to their area, the two larger islands (which together make the Democratic Republic of São Tomé and Príncipe) have by far the highest number of endemic bird species in the world (at least 28 endemic species in 996 km²; Melo et al. 2022).

Although birds are the best-studied group of the Gulf of Guinea islands (Jones and Tye 2006; Melo et al. 2022), the presence of a candidate species of owl on Príncipe Island was only confirmed in 2016 (Ryan 2016; Verbelen et al. 2016), following decades of the accumulation of evidence pointing towards it (Suppl. material 1). In this paper we confirm the distinctiveness of the population of scops-owls from Príncipe using morphometrics, plumage colouration and pattern, song, and mitochondrial and nuclear DNA sequence data. We discuss the origin of this species by placing it within a large-scale phylogeny of the genus *Otus*. Together with the new species, this phylogeny included 14 taxa never previously analysed, providing novel insights on the relationships within the most speciose genus of the Strigidae family.

Materials and methods

Study site

Príncipe Island ($1^{\circ}31.80'N$ – $1^{\circ}43.20'N$, $7^{\circ}19.80'E$ – $7^{\circ}28.20'E$) is located in the Gulf of Guinea, ca. 220 km offshore Gabon (Fig. 1). Part of the Cameroon Line of Volcanoes, its oldest sub-aerial rocks date to the origin of the line at ca. 30 Ma (Burke 2001). With a surface area of 139 km² (ca. 17 km long and 8 km wide), it has a relatively flat low-lying area in the north, contrasting with the rugged central and southern region characterised by high ridges that rise up to 948 m a.s.l. at Pico do Príncipe (Jones and Tye 2006). It has an oceanic equatorial climate, with an annual precipitation that can reach 5,000 mm. Most of the accessible regions of the island were cleared and converted to plantations (Jones and Tye 2006). Some of those areas were abandoned and regenerated into secondary forest (Atkinson et al. 1991; Castanheira-Diniz and Cardoso-de-Matos 2002; Jones and Tye 2006). The remaining area is covered with two types of native forest stratified by altitude: lowland and montane rainforest, the latter being restricted to Pico do Príncipe and the surrounding summits (Exell 1944).

Fieldwork for specimen and tissue sample collection, measurements, and additional bioacoustics recordings took place in May 2017, July 2018, and January 2019. All samples and vocalisation recordings were collected within Príncipe Obô Natural Park (PONP), in the south of Príncipe (Fig. 1). Locality information was recorded using a GPS receiver (Garmin GPS Map 62s; Garmin International Inc., Olathe, Kansas, United States).

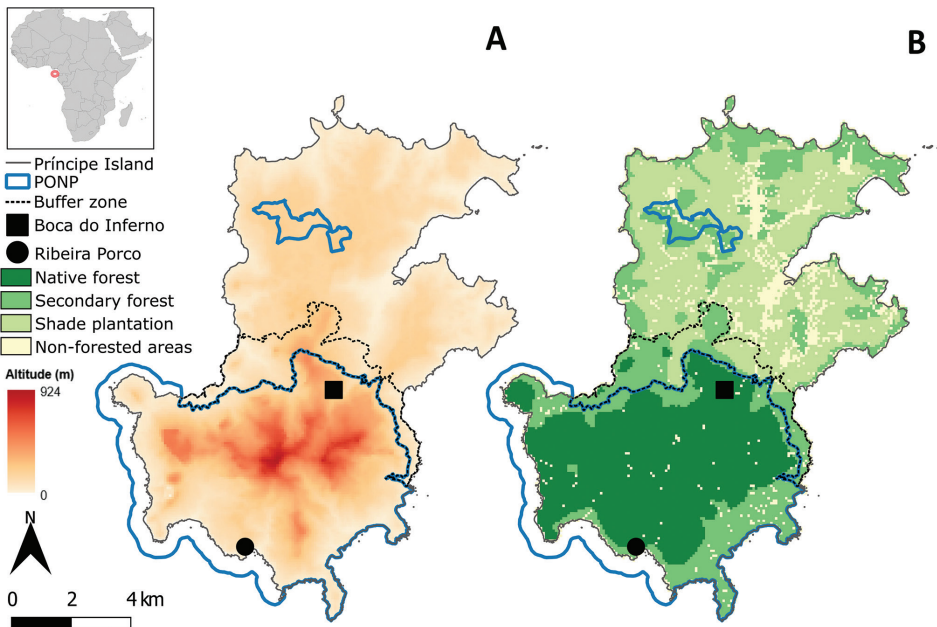


Figure 1. Altitudinal **A** and land use maps **B** of Príncipe Island, with the limits of the Príncipe Obô Natural Park (PONP) and its buffer zone, and the two localities where the four individuals of the candidate species of *Otus* from Príncipe were captured; inset: location of Príncipe in Africa.

Voucher specimen collection

On May 29, 2017, in the Ribeira Porco area (1°33.03'N, 7°22.29'E, Fig. 1), one individual was captured using mist-nets (Fig. 2A), measured and a blood sample collected. This individual was euthanised by inhaling an Isoflurane 1 mL/5 L solution, dissected, fixed with absolute EtOH, and preserved in 80% EtOH. Afterwards, the specimen was prepared as a study skin and spread wing, and the partial skeleton was prepared following a modified procedure (Cataldo 2017) from that described by Davis and Payne (1992) and Baker et al. (2003). Previously to being captured, recordings of its vocalisations and of those of a second bird were obtained using a recorder (Edirol R-09HR, Roland, Japan) and a microphone (MKE 400, Sennheiser, Germany); these were elicited by playing back previously recorded vocalisations of this taxon to attract it into the nets. The voucher specimen was photographed to document life colouration and appearance (Fig. 2A). The voucher was deposited in the ornithological collection of the Natural History and Science Museum of the University of Porto (Table 1).

Taxonomy

In this study, species diagnosis was based upon four lines of evidence: morphometrics, plumage colouration and pattern, song, and DNA sequence data.

Species and subspecies limits of scops-owls are challenging to ascertain, leading to numerous taxonomic arrangements. This study follows the taxonomic arrangement and nomenclature of The Clements Checklist of Birds of the World (Clements et al. 2021). Terminology and description scheme follow Sangster et al. (2013), and the features used for the description are depicted in the Suppl. material 3. Description of colour in life is based on the holotype, with some reference to variation as observed in specimens photographed in the field (Fig. 2).

Morphology

Four scops-owl individuals from Príncipe (including the vouchered specimen) were captured in the field. These were measured together with representatives of four of the five species of the Afro-Palearctic clade (sensu Pons et al. 2013) and *O. brucei obsoletus* (Cabanis, 1875). The latter was included due to the potential affinities of *O. brucei* (Hume, 1872) with African species (Pons et al. 2013). The Arabian Scops-Owl *O. pamelae* Bates, 1937 was not included, but we measured individuals of *O. senegalensis feae* (Salvadori, 1903) from Annobón Island, considered by some authors as a distinct species (Collar and Boesman 2020; Gill et al. 2021). The morphometric dataset includes measurements collected from museum specimens and living individuals measured in the field (Table 1).

Measurements were taken as follows: bill length from the bill tip to where the culmen enter the feathers (**Bilen**); bill length from the anterior end of the nares to the tip (**Binares**); bill width (**Biwid**) and bill depth (**Bidepth**) at the anterior end of nares; head+bill



Figure 2. The candidate species of *Otus* from Príncipe **A** female specimen MHNC-UP-AVE7000, showing colouration in life (available also in the Macaulay library (ML): ML470442301; grey-brown morph) **B** female (left, sample P9-037) and male (right, sample P9-038) grey-brown morphs captured at Boca do Inferno on January 28, 2019 (ML470438621) **C** rufous morph individual photographed at Ribeira Porco area on July 04, 2016 **D** daytime sighting of a grey-brown morph individual between Rio São Tomé and Ribeira Porco on January 19, 2019 (ML470443361, only the rufous upperparts are clearly seen) **E** grey-brown morph individual photographed in the Ribeira Porco area on January 21, 2019 **F** fully developed brood patch of a female rufous morph (sample P8-001) captured in the Ribeira Porco area on January 20, 2019 (ML470440211). ML – Macaulay Library. Photographs: **A** – HP **B, D, F** – MM and BF **C** – PV **E** – Paul van Giersbergen.

Table 1. Morphological measurements of the scops-owls specimens included in the present study with their respective institutional catalogue number (superscript letters, when present, indicate: HT, holotype; F, female; M, male) and sampling locality. All measures are in millimetres. NA – not available; STP – São Tomé and Príncipe; DRC – Democratic Republic of the Congo; EG – Equatorial Guinea. Morphological measurements – Bilen: bill length from bill tip to where culmen enters feathers; Biwid: bill width; Bidepth: bill depth; Binares: bill length from the anterior end of the nares to the tip; Hebi: head+bill, from the tip of the bill to the opposite point on the back of the skull; Midt: middle toe length; Tarlen: tarsus length; Wilen: wing length; Tailen: tail length; Bolen: body length; P10-4: length of primary feathers; Wing formula: sequence of primary feathers ordered by size; * specimens not collected, blood samples codes from the collection of MM at CIBIO-InBIO.

Taxon	Catalogue number followed by tissue sample (if available)	Locality	Bilen	Biwid	Bidepth	Binares	Hebi	Midt	Tarlen	Wilen	Tailen	Bolen	P10	P9	P8	P7	P6	P5	P4	Wing formula
<i>O. bikoégila</i> sp. nov. 1	MHNC-UP-AVE/7000 ^{HT,F} ; P7-04	STP, Príncipe	16.0	9.0	11.3	11.3	38.9	19.9	32.3	147	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
<i>O. bikoégila</i> sp. nov. 2	NA; P8-401 * F	STP, Príncipe	19.0	10.9	10.4	11.7	44.0	NA	34.0	148	85	NA	82	104	116	122	120	119	115	7 > 6>5 > 8>4 > 9>10
<i>O. bikoégila</i> sp. nov. 3	NA; P9-037 * F	STP, Príncipe	19.0	11.8	11.9	12.6	NA	NA	35.1	151	85	205	84	108	118	121	120	119	115	7 > 6>5 > 8>4 > 9>10
<i>O. bikoégila</i> sp. nov. 4	NA; P9-038 * M	STP, Príncipe	17.4	10.9	12.1	11.6	NA	NA	30.5	145	75	192	80	103	114	118	116	113	108	7 > 6>8 > 5>4 > 9>10
<i>O. hartlaubi</i> 1	NA; ST03-294 *	STP, São Tomé	16.1	6.5	9.7	NA	NA	NA	30.8	130	67	NA	NA	NA	NA	NA	NA	NA	NA	NA
<i>O. hartlaubi</i> 2	NA; ST-R16-0202 *	STP, São Tomé	NA	NA	NA	NA	NA	NA	NA	139	67	NA	NA	NA	NA	NA	NA	NA	NA	NA
<i>O. hartlaubi</i> 3	NA; ST10-440 *	STP, São Tomé	15.5	9.8	NA	NA	NA	NA	32.9	132	68	NA	NA	NA	NA	NA	NA	NA	NA	NA
<i>O. hartlaubi</i> 4	NA; ST-R17-0264 *	STP, São Tomé	NA	NA	NA	NA	NA	NA	27.8	134	67	NA	NA	NA	NA	NA	NA	NA	NA	NA
<i>O. hartlaubi</i>	NA; ST15-144 *	STP, São Tomé	16.1	6.3	9.1	10.1	39.0	NA	31.9	135	65	170	74	86	101	107	106	104	100	7 > 6>5 > 8>4 > 9>10
<i>O. hartlaubi</i>	SMD C50544	STP, São Tomé	17.1	6.1	NA	10.6	39.5	17.1	30.6	136	69	174	65	91	102	108	107	104	92	7 > 6>5 > 8>4 > 9>10
<i>O. s. senegalensis</i>	SMF 25448	Gambia	18.3	6.4	9.8	12.5	42.3	17.3	24.2	141	65	175	66	95	96	96	90	89	81	7 = 8>9 > 6>5 > 5>10
<i>O. s. senegalensis</i>	BMNH 1929.2.18.131	Gambia	NA	6.7	NA	NA	41.0	16.5	22.0	140	60	167	81	98	104	106	105	96	87	7 > 6>8 > 9>5 > 4>10
<i>O. s. senegalensis</i>	BMNH 1907.12.26.41	Gambia	17.0	8.0	10.2	9.4	42.0	19.0	23.0	140	60	190	73	92	99	103	100	94	87	7 > 6>8 > 5>9 > 4>10
<i>O. s. senegalensis</i>	BMNH 1955.6.N-20.3927	Cape Verde	17.0	6.0	11.0	9.0	39.0	18.0	22.0	135	60	170	NA	NA	NA	NA	NA	NA	NA	NA
<i>O. s. senegalensis</i>	BMNH 1955.6.N-20.3926	Senegal	15.3	6.5	10.7	8.2	40.0	15.5	23.0	145	65	170	NA	NA	NA	NA	NA	NA	NA	8 > 7>9 > 6>5 > 4>10
<i>O. s. senegalensis</i>	BMNH 1955.6.N-20.3930	West Africa	16.5	6.1	11.7	9.9	40.0	15.5	24.0	135	57	170	80	97	100	98	98	93	87	8 > 7>6 > 9>5 > 4>10
<i>O. s. senegalensis</i>	BMNH 94.8.15.28	Ghana, Accra	17.1	6.1	11.0	10.5	42.0	15.5	23.0	137	58	175	70	87	94	95	89	84	82	7 > 8>6 > 9>5 > 4>10
<i>O. s. senegalensis</i>	BMNH 1930.12.21.13	Ghana, Tamatuku	15.8	6.3	11.0	9.0	40.0	17.5	22.0	135	55	173	NA	NA	NA	NA	NA	NA	NA	NA
<i>O. s. senegalensis</i>	BMNH 1911.12.23.506	Nigeria, Bauchi	17.2	5.2	11.0	9.4	44.0	18.5	20.0	125	58	170	89	94	99	98	94	88	85	8 > 7>6 > 9>10 > 5>4
<i>O. s. senegalensis</i>	BMNH 1909.12.31.43	DRC, Bunkaya	16.4	6.3	11.1	9.2	40.5	21.0	23.0	140	60	165	76	92	103	105	108	98	93	6 > 7>8 > 5>4 > 9>10
<i>O. s. senegalensis</i>	BMNH 1909.12.31.42	DRC, Katanga	15.8	5.0	10.4	8.0	41.5	15.0	23.0	130	57	150	70	90	95	97	93	86	80	7 > 8>6 > 9>5 > 4>10
<i>O. s. senegalensis</i>	BMNH 1957.35.44	Angola, Sumbe	15.5	5.0	10.4	8.5	37.0	15.5	22.0	125	60	165	65	83	90	90	85	80	75	7 = 8>6 > 9>5 > 4>10
<i>O. s. senegalensis</i>	BMNH 1937.12.27.211	Tanzania	16.7	5.8	9.7	9.5	40.0	16.0	22.0	128	50	160	70	82	90	91	90	86	82	7 > 6>8 > 5>4 = 9>10
<i>O. s. senegalensis</i>	BMNH 1936.2.21.479	Djibouti	16.5	6.0	11.0	9.8	42.0	17.0	21.0	137	60	170	72	87	97	99	96	83	83	7 > 8>6 > 9>4 = 5>10
<i>O. s. senegalensis</i>	SMF 10119	Ethiopia, Maki	16.8	6.3	9.3	11.0	36.1	17.2	22.1	128	53	151	72	87	93	96	96	91	NA	NA

Taxon	Catalogue number followed by tissue sample (if available)	Locality	Bilen	Biwid	Bidepth	Binares	Hebi	Midt	Tarlen	Wilen	Tailen	Bolen	P10	P9	P8	P7	P6	P5	P4	Wing formula
<i>O. s. senegalensis</i>	SMF 10121	Somalia, Bardera	16.5	4.8	8.0	10.1	32.7	13.8	21.5	103	40	126	54	65	72	72	74	72	64	$6 > 5=7 > 8 > 9 > 4 > 10$
<i>O. senegalensis faae</i>	BMNH 1911.12.23.4044	EG, Annobón	16.8	6.4	12.0	10.7	40.0	17.5	20.0	135	60	185	84	95	104	106	102	NA	NA	$7 > 8 > 6 > 9 > 10 > 5 > 4$
<i>O. senegalensis faae</i>	SMF 25452	EG, Annobón	16.9	6.8	9.2	10.9	36.6	16.9	24.1	130	55	165	74	87	97	96	94	91	85	$8 > 7 > 6 > 5 > 9 > 4 > 10$
<i>O. penbuensis</i>	BMNH 1937.2.14.1 HT	Tanzania, Pemba	19.0	8.9	NA	12.2	49.0	20.0	28.0	152	73	210	75	97	108	111	104	98	90	$7 > 8 > 6 > 5 > 9 > 4 > 10$
<i>O. penbuensis</i>	BMNH 1937.12.14.2	Tanzania, Pemba	20.5	8.5	NA	12.7	47.0	21.0	30.0	155	75	212	76	100	109	111	102	97	90	$7 > 8 > 6 > 5 > 9 > 4 > 10$
<i>O. penbuensis</i>	BMNH 1937.12.14.3	Tanzania, Pemba	19.0	9.0	NA	12.2	48.0	20.0	28.0	155	78	212	75	98	109	110	107	95	91	$7 > 8 > 6 > 5 > 9 > 4 > 10$
<i>O. penbuensis</i>	BMNH 1937.12.14.4	Tanzania, Pemba	20.0	8.5	13.5	12.1	47.0	21.0	28.0	150	80	212	75	99	111	112	108	101	96	$7 > 8 > 6 > 5 > 9 > 4 > 10$
<i>O. penbuensis</i>	BMNH 1937.12.14.5	Tanzania, Pemba	18.2	7.5	NA	11.2	46.5	20.0	29.0	150	76	210	75	96	103	104	103	97	92	$7 > 8 > 6 > 5 > 9 > 4 > 10$
<i>O. penbuensis</i>	BMNH 1937.12.14.6	Tanzania, Pemba	18.9	8.0	11.5	11.9	47.0	20.0	28.0	150	76	210	75	95	107	114	113	109	103	$7 > 6 > 5 > 9 > 4 > 10$
<i>O. penbuensis</i>	BMNH 1956.29.9	Tanzania, Pemba	NA	NA	NA	NA	NA	NA	NA	152	NA	190	77	98	107	110	107	104	94	$7 > 8 > 6 > 5 > 9 > 4 > 10$
<i>O. scops</i>	BMNH 941.5.30.8805	Spain, Ibiza	16.2	5.7	9.2	9.5	39.0	18.0	22.0	154	65	190	98	113	116	112	106	101	96	$8 > 9 > 7 > 6 > 5 > 10 > 4$
<i>O. scops</i>	BMNH 87.11.11.43	Spain, Seville	15.1	5.8	11.0	9.1	37.0	16.5	23.0	152	70	182	94	109	107	105	98	92	90	$9 > 8 > 7 > 6 > 10 > 5 > 4$
<i>O. scops</i>	BMNH 97.11.10.292	Spain, Malaga	16.8	6.2	11.0	9.8	40.5	14.2	28.0	147	68	170	85	102	109	106	98	87	86	$8 > 7 > 9 > 6 > 5 > 4 > 10$
<i>O. scops</i>	BMNH 1947.4.89	France, Var	16.1	6.8	11.0	9.0	43.0	18.0	28.0	160	70	200	96	114	114	114	101	96	85	$7 = 8 > 9 > 6 > 10 = 5 > 4$
<i>O. scops</i>	BMNH 1934.1.1.1510	Italy, Bibbiena	16.5	7.0	10.5	9.5	43.0	17.0	24.0	157	71	186	100	117	118	115	111	98	96	$8 > 9 > 7 > 6 > 10 > 5 > 4$
<i>O. scops</i>	BMNH 1905.6.28.739	Italy, Naples	16.5	6.8	10.5	10.0	43.5	17.0	26.0	155	68	185	95	106	110	105	102	95	93	$8 > 9 > 7 > 6 > 10 = 5 > 4$
<i>O. scops</i>	BMNH 1905.6.28.740	Italy, Naples	16.9	6.6	11.0	9.7	46.0	16.1	27.0	159	70	200	92	110	113	109	100	92	90	$8 > 9 > 7 > 6 > 10 = 5 > 4$
<i>O. scops</i>	BMNH 1955.6.N.20.3874	Morocco, Tangier	16.7	7.8	NA	11.5	43.0	20.0	22.0	155	65	180	92	104	104	102	99	94	94	$8 = 9 > 7 > 6 > 5 = 4 > 10$
<i>O. scops</i>	BMNH 1919.12.11.8	Morocco, Atlas	15.0	6.5	9.8	10.0	39.5	14.0	22.0	150	80	178	94	107	109	107	92	88	88	$8 > 9 = 7 > 10 > 6 > 5 = 4$
<i>O. scops</i>	BMNH 73.5.28.10	Algeria	18.1	6.5	NA	11.0	42.0	17.0	26.0	154	70	180	91	105	106	106	98	94	87	$8 = 7 > 9 > 6 > 5 > 10 > 4$
<i>O. scops</i>	BMNH 1916.9.20.746	Sudan, Trufikia	15.5	6.7	NA	9.5	45.0	18.5	24.0	163	75	195	100	115	116	111	100	98	98	$8 > 9 > 7 > 10 = 6 > 5 = 4$
<i>O. scops</i>	BMNH 1977.20.227	Liberia, Mt. Nimba	15.0	6.5	11.5	10.0	42.0	17.0	23.0	154	70	185	NA	NA	NA	NA	NA	NA	NA	$7 > 6 > 8 > 5 > 4 > 9 > 10$
<i>O. scops</i>	BMNH 1977.20.229	Liberia, Mt. Nimba	14.0	5.5	10.3	10.3	42.0	19.0	26.5	155	70	195	94	112	112	107	98	96	91	$8 = 9 > 7 > 6 > 5 > 10 > 4$
<i>O. scops</i>	BMNH 1977.20.232	Liberia, Mt. Nimba	17.0	5.5	10.4	10.0	40.2	17.0	27.0	157	72	175	92	104	NA	NA	NA	NA	NA	NA
<i>O. scops</i>	BMNH 1977.20.228	Liberia, Mt. Nimba	17.3	6.0	10.2	9.5	40.0	17.0	23.0	165	73	190	105	115	NA	NA	NA	NA	NA	$8 > 9 > 7 > 6 > 10 > 5 > 4$
<i>O. brucei obsolens</i>	SMF 25430	Uzbekistan	18.5	5.8	8.7	11.5	43.1	16.9	29.6	153	72	186	96	112	112	114	109	100	90	$7 > 8 > 9 > 6 > 5 > 10 > 4$

Abbreviations of institutional collections: BMNH - The Natural History Museum, Tring, UK; MHNC-UP - Museu de História Natural e da Ciência da Universidade do Porto, Portugal; SMD - Senckenberg Museum Dresden, Germany; SMF - Naturmuseum Senckenberg in Frankfurt am Main, Germany

(**Hebi**), from the tip of the bill to the opposite point on the back of the skull; middle toe length (**Midt**); tarsus length (**Tarlen**), from the tibiotarsus joint to the distal end of the tarsometatarsus, when the foot is held to the leg; tail length (**Tailen**), from where the ruler stops at the root of the central pair of rectrices and to the tip of this same pair (by sliding the ruler between the rectrices and the undertail coverts); body length (**Bolen**) from the top of the head to the tip of the central pair of rectrices; wing length (**Wilen**), flattened, from the carpal joint to the tip of the longest primary; wing formula, sequence of primary feathers ordered by size; and length of primary feathers (**P4–P10**, in which **P1** is the closest to the body), which were transformed in shortfall of P4–P10 to tip of longest primary. Body, wing, and tail length were measured with standard wing and tail rulers to the nearest 1.0 mm. The length of the primary feathers was measured to the nearest 1.0 mm with a ruler with a pin at the origin; the pin is inserted between two primary feathers until it touches the skin (Jenni and Winkler 1989). All other measurements were made using a digital calliper (Mitutoyo CD-P15K, Mitutoyo Corporation, Kawasaki, Japan) to the nearest 0.1 mm. All measurements were collected by MM, BF, and RL (Table 1). A constant of one was added to each number to make all shortfalls non-zero. All measurements were log-transformed (base-10) to normalise distributions (McDonald 2014).

The four individuals from Príncipe were sexed with a molecular protocol (Griffiths et al. 1998), and comprised three females and one male (Table 1). For the statistical analyses males and females were treated together due to the low sampling size, and the fact that most museum specimens were not sexed.

Morphometric differences were explored using a Principal Component Analysis (PCA), performed using the FactoMineR package (Lê et al. 2008) and carried out using R v. 3.6 (R Core Team 2017) in RStudio v. 1.1.447 (RStudio Team 2015). Measurements were size-standardised to prevent the dominance of variables involving larger measurement units, thus allowing comparisons between variables. The wing formula was not used in the analyses. Since several individuals had missing data, to maximise the number of analysed specimens of each species only the following variables were used in the PCA: Bilen, Binares, Biwid, Tarlen, Wilen, and Tailen. This dataset included 44 specimens from seven taxa, including three individuals from Príncipe. Welch's ANOVA (recommended for unbalanced designs, different samples sizes, and different standard deviations; McDonald 2014), was used together with Games-Howell post-hoc comparisons to test whether the groups differed from each other.

Plumage description

We used colour standards (Köhler 2012) to describe the plumage of the species of the Afro-Palearctic clade, except for *O. pamela*, but including *O. senegalensis feae* (see Suppl. material 6). The topographic terms of the scops-owl body are detailed in the Suppl. material 3.

Bioacoustic analyses

We compared the calls of the candidate species with the calls of scops-owls from the Afro-Palearctic clade, *O. brucei*, and the Sokoke Scops-Owl *O. ireneae* Ripley, 1966 (Tables 2,

3). *Otus ireneae* is not part of the Afro-Palearctic clade but was included because it has the most similar calls to the ones of the candidate species. Recordings were collected from Xeno-canto (XC; www.xeno-canto.org), Avian Vocalizations Center (AVoCet; <https://avocet.integrativebiology.natsci.msu.edu>), The Internet Bird Collection (www.hbw.com/ibc), the private collection of PV and the collection of vocalisations obtained during fieldwork on Príncipe by co-authors. Newly collected calls were deposited in Xeno-canto (Suppl. material 7). From each independent source, only one recording was used (unless there were only very limited recordings available). In total, 43 recordings from ten taxa were analysed (Suppl. material 7). In most owls, both sexes produce similar calls for territorial defence, mate attraction, and pair-bonding (Marks et al. 1999; König et al. 2008), therefore our analyses included both male and female recordings. Vocalisations of scops-owls are generally made up of a simple primary call composed by the repetition of the same note (Marks et al. 1999). The call of the Cyprus Scops-Owl *O. cyprius* (von Madarász, 1901) is composed by the coupling of one long and one short note (Flint et al. 2015), and both note types were included in the analysis. The candidate species primary call is characterised by a repeated note (Suppl. material 4: Fig. S2A, B), but its repertoire also includes a cat-like “kee-a-u” note (Suppl. material 4: Fig. S2C, D). The latter was not included in the analysis.

Recordings were sampled using a 16-bit accuracy and a sampling rate converted to 12 kHz in Avisoft-SASLab pro v. 4.3 (Avisoft Bioacoustics). The following 16 variables were collected for each note: F1, frequency at start (peak frequency at 0s, Hz); F2, frequency at end (peak frequency at last of four call intervals, Hz); F3, frequency at 25% of total duration (peak frequency at the first interval, Hz); F4, frequency at midpoint (peak frequency at the second interval, Hz); F5, frequency at 75% of total duration (peak frequency at the third interval, Hz); F6, frequency at maximum amplitude (frequency at maximum amplitude of note, Hz); F7, maximum frequency (maximum frequency through the note, Hz); F8, minimum frequency (minimum frequency through the note, Hz); DT1, total duration (duration, s); DT2, time to maximum amplitude (time to maximum amplitude of note, s); DT3, time to maximum frequency (time to maximum frequency of note, s); DT4, internote interval (start time – end time of previous note, s); DF1, frequency drop from start to end (F2-F1, Hz); DF2, frequency range (F7-F8, Hz); DFT1, slope from 25% to 75% of total duration $([F5-F3]/\Delta t, \text{Hz/s})$; DFT2, slope from midpoint to end $([F2-F4]/\Delta t, \text{Hz/s})$. The 16 variables were extracted from the analysis of the spectrograms. We used a Fast Fourier Transformation size of 512 points, a 100% frame size and a temporal resolution overlap of 87.5% (flat top window type), resulting in a frequency resolution of 86 Hz and a temporal resolution of 4.5 ms. Frequencies were analysed between 0.5 Hz (highpass) and 2.25 Hz (lowpass), except for *O. brucei* with the highpass set at 0.0 Hz; the greyscale was set to 30%. When background noise hampered the measurement of the variables, frequencies were filtered and adjusted by shortening the interval between the highpass and the lowpass.

For each recording, variables were measured on six notes and their means (Suppl. material 8) were used as sample points to calculate the ranges, means and standard deviations for each taxon. A constant of 3000 was added to each computed value to ensure that the dataset only included positive numbers. All measurements were log-transformed (base-10) to normalise distributions (McDonald 2014).

Table 2. Measurements (in Hz) of bioacoustic variables (frequency parameters) of *Otus* species of the Afro-Palaearctic clade, *O. brucei* and of *O. ireneae* (the species whose vocalisations are closest to the ones of the candidate species from Principe). *n*: number of individuals. Average $\pm$ standard deviation; (minimum-maximum values). F1: frequency at start; F2: frequency at end; F3: frequency at 25% of total duration; F4: frequency at midpoint; F5: frequency at 75% of total duration; F6: frequency at maximum amplitude; F7: maximum frequency; F8: minimum frequency.

Taxon	<i>n</i>	F1	F2	F3	F4	F5	F6	F7	F8
<i>O. bitorquatus</i> sp. nov. (main call)	5	891.0 $\pm$ 72.9 (781.7–961.7)	967.0 $\pm$ 32.3 (933.3–1020.0)	1012.3 $\pm$ 44.2 (980.0–1090.0)	981.3 $\pm$ 40.2 (950.0–1050.0)	967.7 $\pm$ 35.8 (931.7–1020.0)	1005.7 $\pm$ 47.6 (976.7–1090.0)	1054.0 $\pm$ 30.1 (1035.0–1106.7)	910.3 $\pm$ 43.2 (868.3–973.3)
<i>O. bitorquatus</i> sp. nov. (cat-like call)	2	966.7 $\pm$ 80.1 (910.0–1023.3)	859.2 $\pm$ 27.1 (840.0–878.3)	1180.8 $\pm$ 121.4 (1095.0–1266.7)	1234.2 $\pm$ 62.5 (1190.0–1278.3)	1149.2 $\pm$ 140.2 (1050.0–1248.3)	1220.0 $\pm$ 70.7 (1170.0–1270.0)	1245.0 $\pm$ 77.8 (1190.0–1300.0)	853.3 $\pm$ 4.7 (850.0–856.7)
<i>O. hirtidubius</i>	5	1236.2 $\pm$ 101.5 (1078.3–1360.0)	1220.7 $\pm$ 54.9 (1155.0–1285.0)	1409.7 $\pm$ 65.9 (1330.0–1478.3)	1396.3 $\pm$ 80.0 (1295.0–1483.3)	1340.5 $\pm$ 62.2 (1250.0–1418.3)	1383.2 $\pm$ 62.5 (1331.7–1480.0)	1461.8 $\pm$ 47.2 (1407.5–1526.7)	1178.2 $\pm$ 83.0 (1066.7–1267.5)
<i>O. senegalensis senegalensis</i>	4	1235.0 $\pm$ 184.2 (1071.7–1433.3)	1133.3 $\pm$ 112.7 (1035.0–1260.0)	1092.5 $\pm$ 123.3 (1021.7–1276.7)	1156.7 $\pm$ 60.5 (1095.0–1236.7)	1074.6 $\pm$ 83.9 (1011.7–1198.3)	1134.2 $\pm$ 84.3 (1051.7–1251.7)	1422.5 $\pm$ 341.5 (1126.7–1908.3)	963.3 $\pm$ 70.4 (885.0–1050.0)
<i>O. senegalensis faoi</i>	3	1220.3 $\pm$ 146.6 (1060.0–1347.5)	1189.2 $\pm$ 50.6 (1132.5–1230.0)	1165.3 $\pm$ 76.3 (1120.0–1253.3)	1203.3 $\pm$ 92.5 (1145.0–1310.0)	1143.1 $\pm$ 46.8 (1110.0–1196.7)	1156.9 $\pm$ 75.1 (1107.5–1243.3)	1310.3 $\pm$ 54.9 (1250.0–1357.5)	1098.9 $\pm$ 68.1 (1050.0–1176.7)
<i>O. penhagensis</i>	5	575.3 $\pm$ 47.8 (506.7–636.7)	665.7 $\pm$ 65.3 (613.3–773.3)	693.7 $\pm$ 52.8 (621.7–770.0)	709.7 $\pm$ 52.7 (633.3–780.0)	711.0 $\pm$ 49.1 (651.7–783.3)	702.0 $\pm$ 50.0 (638.3–776.7)	726.0 $\pm$ 48.9 (660.0–790.0)	593.0 $\pm$ 49.5 (530.0–660.0)
<i>O. pamela</i>	5	1116.3 $\pm$ 72.7 (1031.7–1213.3)	1190.0 $\pm$ 55.4 (1111.7–1268.3)	1219.0 $\pm$ 90.5 (1120.0–1363.3)	1241.0 $\pm$ 104.8 (1096.7–1366.7)	1179.7 $\pm$ 75.6 (1083.3–1291.7)	1250.3 $\pm$ 91.5 (1160.0–1403.3)	1349.0 $\pm$ 114.4 (1220.0–1516.7)	1054.3 $\pm$ 40.4 (1020.0–1123.3)
<i>O. seops</i>	5	1505 $\pm$ 137.5 (1335.0–1695.0)	1210.2 $\pm$ 44.1 (1152.5–1275.0)	1203.8 $\pm$ 39.0 (1155.0–1260.0)	1230.1 $\pm$ 34.9 (1200.0–1285.0)	1255.3 $\pm$ 44.7 (1193.3–1318.3)	1255.3 $\pm$ 46.2 (1210.0–1326.7)	1478.6 $\pm$ 121.8 (1336.3–1628.3)	1183.5 $\pm$ 43.4 (1140.0–1253.3)
<i>O. cyprina</i> (long note)	5	1312.6 $\pm$ 60.0 (1236.7–1400.0)	1079.7 $\pm$ 67.1 (1016.7–1193.3)	1084.6 $\pm$ 73.1 (1035.0–1213.3)	1091.0 $\pm$ 71.7 (1035.0–1216.7)	1101.4 $\pm$ 65.1 (1043.4–1213.3)	1139.4 $\pm$ 72.7 (1063.4–1231.7)	1391.1 $\pm$ 85.4 (1291.7–1520.0)	1059.7 $\pm$ 72.2 (996.7–1183.3)
<i>O. cyprina</i> (short note)	5	1128.1 $\pm$ 59.7 (1058.9–1223.3)	1038.5 $\pm$ 57.1 (998.3–1135.0)	1094.8 $\pm$ 132.1 (1015.0–1330.0)	1046.6 $\pm$ 90.6 (976.7–1200.0)	1045.7 $\pm$ 85.5 (960.0–1186.7)	1067.2 $\pm$ 72.9 (1020.0–1196.7)	1212.9 $\pm$ 104.9 (1124.4–1345.0)	1007.9 $\pm$ 75.4 (945.0–1138.3)
<i>O. brucei</i>	4	355.0 $\pm$ 48.8 (285.0–388.3)	358.3 $\pm$ 49.1 (285.0–388.3)	463.8 $\pm$ 75.5 (356.7–530.0)	447.1 $\pm$ 62.0 (356.7–493.3)	390.4 $\pm$ 50.2 (335.0–450.0)	462.1 $\pm$ 63.6 (370.0–510.0)	469.6 $\pm$ 69.5 (400.0–530.0)	336.3 $\pm$ 48.0 (270.0–373.3)
<i>O. ireneae</i>	2	936.7 $\pm$ 99.0 (866.7–1006.7)	919.2 $\pm$ 38.9 (891.7–946.7)	943.3 $\pm$ 75.4 (890.0–996.7)	945.0 $\pm$ 73.1 (893.3–996.7)	926.7 $\pm$ 51.9 (890.0–963.3)	946.7 $\pm$ 61.3 (903.3–990.0)	958.3 $\pm$ 58.9 (916.7–1000.0)	892.5 $\pm$ 43.6 (861.7–923.3)

Table 3. Measurements (in Hz) of bioacoustic variables (temporal parameters) of *Otus* species of the Afro-Palearctic clade, *O. brucei* and of *O. ireneae* (the species whose vocalisations are closest to the ones of the candidate species from Principe). *n*: number of individuals. Average $\pm$ standard deviation; (minimum-maximum values). DT1: total duration; DT2: time to maximum amplitude; DT3: time to maximum frequency; DT4: internote frequency; DT5: time to maximum frequency; DT6: frequency range; DT7: frequency range; DT8: slope from 25% to 75% of total duration; DT9: slope from midpoint to end.

Taxon	<i>n</i>	DT1	DT2	DT3	DT4	DT5	DT6	DT7	DT8
<i>O. birkigila</i> sp. nov.	5	0.238 $\pm$ 0.007 (0.231–0.248)	0.100 $\pm$ 0.014 (0.078–0.112)	0.057 $\pm$ 0.021 (0.032–0.083)	1.046 $\pm$ 0.053 (0.992–1.121)	76.0 $\pm$ 62.8 (6.7–178.3)	143.7 $\pm$ 25.8 (110–175)	-374.4 $\pm$ 252.1 (-581.5–45.2)	-120.9 $\pm$ 110.2 (-250.3–21.7)
<i>O. birkigila</i> sp. nov. (cat-like call)	2	0.347 $\pm$ 0.009 (0.341–0.354)	0.161 $\pm$ 0.002 (0.160–0.162)	0.138 $\pm$ 0.025 (0.120–0.155)	- -	-107.5 $\pm$ 53.0 (-145.0–70.0)	391.7 $\pm$ 73.1 (340.0–443.3)	-185.7 $\pm$ 117.8 (-268.9–102.4)	-2158.6 $\pm$ 146.7 (-2262.4–2054.9)
<i>O. harti</i>	5	0.292 $\pm$ 0.017 (0.267–0.315)	0.161 $\pm$ 0.054 (0.113–0.241)	0.078 $\pm$ 0.038 (0.030–0.110)	13.899 $\pm$ 2.847 (9.181–15.998)	-15.5 $\pm$ 126.5 (-141.7–186.7)	283.7 $\pm$ 106.5 (140.0–403.3)	-468.4 $\pm$ 348.7 (-773.0–61.0)	-1209.4 $\pm$ 672.6 (-2034.1–312.7)
<i>O. senegalensis senegalensis</i>	4	0.337 $\pm$ 0.150 (0.206–0.476)	0.201 $\pm$ 0.135 (0.091–0.370)	0.058 $\pm$ 0.047 (0.010–0.102)	6.446 $\pm$ 2.426 (4.094–9.131)	-101.7 $\pm$ 72.1 (-173.3–30.0)	459.2 $\pm$ 381.1 (191.7–1023.3)	-155.8 $\pm$ 429.3 (-769.7–230.9)	-240.3 $\pm$ 500.7 (-570.1–503.1)
<i>O. senegalensis fae</i>	3	0.420 $\pm$ 0.019 (0.402–0.441)	0.216 $\pm$ 0.087 (0.121–0.291)	0.119 $\pm$ 0.153 (0.013–0.295)	7.247 $\pm$ 0.201 (7.127–7.479)	-31.1 $\pm$ 107.7 (-142.5–72.5)	211.4 $\pm$ 71.1 (146.7–287.5)	-92.5 $\pm$ 143.8 (-253.2–23.8)	-61.8 $\pm$ 301.4 (-364.3–238.5)
<i>O. penhaensis</i>	5	0.225 $\pm$ 0.017 (0.207–0.246)	0.112 $\pm$ 0.045 (0.061–0.171)	0.112 $\pm$ 0.041 (0.043–0.155)	6.121 $\pm$ 0.916 (5.043–7.570)	90.3 $\pm$ 38.8 (48.3–136.7)	133.0 $\pm$ 7.1 (126.7–145.0)	156.4 $\pm$ 121.3 (-37.3–246.9)	-409.1 $\pm$ 333.4 (-784.9–38.1)
<i>O. pamela</i>	5	0.390 $\pm$ 0.078 (0.281–0.481)	0.160 $\pm$ 0.035 (0.120–0.206)	0.103 $\pm$ 0.034 (0.068–0.157)	5.665 $\pm$ 4.550 (0.444–11.381)	73.7 $\pm$ 59.3 (21.7–158.3)	294.7 $\pm$ 80.7 (200.0–393.3)	-202.1 $\pm$ 130.9 (-407.3–65.4)	-278.6 $\pm$ 443.4 (-588.9–383.5)
<i>O. scops</i>	5	0.248 $\pm$ 0.033 (0.206–0.291)	0.102 $\pm$ 0.050 (0.047–0.169)	0.020 $\pm$ 0.017 (0.010–0.050)	2.608 $\pm$ 0.174 (2.423–2.789)	-294.8 $\pm$ 95.4 (-420.0–182.5)	295.1 $\pm$ 97.6 (178.8–401.7)	430.5 $\pm$ 193.2 (181.5–662.3)	-187.5 $\pm$ 314.0 (-730.4–66.1)
<i>O. cyprina</i> (long note)	5	0.226 $\pm$ 0.014 (0.213–0.245)	0.088 $\pm$ 0.039 (0.049–0.145)	0.019 $\pm$ 0.006 (0.013–0.028)	3.245 $\pm$ 0.236 (3.035–3.643)	-232.8 $\pm$ 49.4 (-283.3–165.0)	331.4 $\pm$ 56.8 (241.7–395.0)	141.9 $\pm$ 160.6 (-32.1–363.9)	-101.0 $\pm$ 114.6 (-211.4–34.0)
<i>O. cyprina</i> (short note)	5	0.124 $\pm$ 0.035 (0.084–0.159)	0.059 $\pm$ 0.024 (0.042–0.100)	0.014 $\pm$ 0.006 (0.008–0.020)	3.344 $\pm$ 0.227 (3.116–3.714)	-89.6 $\pm$ 22.9 (-113.3–58.1)	204.9 $\pm$ 72.7 (129.7–318.3)	-938.8 $\pm$ 1357.8 (-3144.9–2.4)	-357.5 $\pm$ 953.6 (-1438.2–561.9)
<i>O. brucei</i>	4	0.115 $\pm$ 0.021 (0.090–0.133)	0.040 $\pm$ 0.010 (0.032–0.053)	0.032 $\pm$ 0.001 (0.032–0.033)	0.756 $\pm$ 0.140 (0.629–0.922)	3.3 $\pm$ 15.5 (-11.7–25.0)	133.3 $\pm$ 44.5 (100.0–192.3)	-1166.5 $\pm$ 960.3 (-2457.3–377.4)	-1545.8 $\pm$ 115.2 (-1653.0–1387.3)
<i>O. ireneae</i>	2	0.173 $\pm$ 0.026 (0.154–0.192)	0.091 $\pm$ 0.008 (0.085–0.097)	0.063 $\pm$ 0.055 (0.023–0.102)	0.428 $\pm$ 0.027 (0.409–0.447)	-17.5 $\pm$ 60.1 (-60.0–25.0)	65.8 $\pm$ 15.3 (55.0–76.7)	-173.7 $\pm$ 245.7 (-347.5–0.0)	-273.8 $\pm$ 353.7 (-523.9–23.7)

PCA was performed using the FactoMineR package (Lê et al. 2008) using R v. 3.6 (R Core Team 2017) in RStudio v. 1.1.447 (R Studio Team 2015). Measurements were size-standardised to make the variables comparable. Welch's ANOVA and Games-Howell post-hoc comparisons were used to test whether the groups differed from each other (McDonald 2014).

Molecular data

Blood samples were collected non-destructively from the brachial vein of mist-netted individuals and were stored in 96% ethanol for genetic analysis (see molecular dataset: Table 4). Blood samples of the scops-owl from Príncipe were collected at Boca do Inferno (1°36.16'N, 7°24.06'E, ca. 300 m a.s.l.) ($n = 2$) and close to Ribeira Porco (1°33.03'N, 7°22.29'E, ca. 100 m a.s.l.) ($n = 2$), both localities within Príncipe Obô Natural Park (Fig. 1; Suppl. material 9). We obtained four blood samples of *O. hartlaubi* (Giebel, 1872) from São Tomé (Suppl. material 9), and were lent one blood sample of *O. senegalensis feae* (Annobón), and one blood sample of Moheli Scops-Owl *O. moheliensis* Lafontaine & Moolaert 1998. We were lent additional samples from museum specimens, including toe-pad samples for one of each of the two subspecies of the Sandy Scops-Owl, *O. icterorhynchus icterorhynchus* (Shelley, 1873) and *O. i. holerythrus* (Sharpe, 1901), from the American Museum of Natural History, New York (AMNH) (Table 4).

Total genomic DNA was extracted from blood and tissue samples using an overnight Proteinase K digestion (10 mg/ml concentration) followed by a standard high-salt extraction method (Bruford et al. 1992). Before the extraction, blood was removed from the ethanol and left to dry in the incubator. Genomic extractions of toe-pads samples were performed using a specific protocol for museum samples (Dabney et al. 2013).

Mitochondrial and nuclear markers (mtDNA and nuDNA, respectively) were amplified and sequenced for the samples that were available to us. For mtDNA we amplified a fragment of the 12s and 16s ribosomal RNA genes (12S and 16S), ATPase subunit 6 (ATP6), cytochrome oxidase subunit I (COI), cytochrome *b* (CYTB), nicotinamide adenine dinucleotide dehydrogenase subunits 2 and 3 (ND2 and ND3). The nuDNA markers were: leucine-rich repeat and WD repeat-containing protein (KIAA1239), myoglobin intron-2 (MYO2), Recombination Activating Gene 1 (RAG1), saccin (SACS), TGF β 2 intron-5 (TGFB2), and titin (TTN).

Standard polymerase chain reactions (PCR) were performed in a final volume of 25 μ l using 1 μ l of each primer (10 pmol), 0.4 μ l of total dNTPs (10 mM; Promega), 0.1 μ l of 5 U/ml GoTaq Flexi DNA Polymerase (Promega), 5 μ l of 5X Green GoTaq Flexi Buffer (Promega), 4 μ l of MgCl₂ (25 mM; Promega). The first PCR of the fragments amplified using a nested PCR approach (KIAA1239, SACS, TTN) were performed in half total reaction volume (12.5 μ l). Primers and PCR conditions are provided as Suppl. material 10. For the amplification of the toe pads, we amplified shorter fragments of the MYO2, ND2, and ND3 genes. Successfully amplified products were purified and sequenced using dye-labelled dideoxy terminator cycle sequencing on an ABI 3730XL automated sequencer at Macrogen Inc.

Table 4. List of scops-owls (*Otus*) samples and GenBank accession numbers for the gene fragments used in this study. Accession numbers in bold indicate sequences newly produced for this study. STP – São Tomé and Príncipe; EG – Equatorial Guinea; DRC – Democratic Republic of the Congo; CHIMERA – sequences for a given taxon obtained from different individuals.

Taxon	Locality	12S	16S	ATP6	COI	CYTB	ND2	ND3	KIAA	MYO2	RAG1	SACS	TGFB2	TTN
<i>O. bitorquatus</i> sp. nov. 1	STP: Príncipe	OM978880	OM978895	OM913485	OM937282	OM937307	OM937351	ON016156	OM937319	OM937336	ON016107	ON016118	ON016136	ON016141
<i>O. bitorquatus</i> sp. nov. 2	STP: Príncipe	OM978881	OM978896	OM913486	OM937283	OM937308	OM937352	ON016157	–	–	ON016108	ON016119	ON016137	ON016142
<i>O. bitorquatus</i> sp. nov. 3	STP: Príncipe	OM978882	OM978897	–	OM937284	OM937309	OM937353	ON016158	–	OM937337	ON016109	ON016120	ON016139	ON016143
<i>O. bitorquatus</i> sp. nov. 4	STP: Príncipe	OM978883	OM978898	OM913487	OM937285	OM937310	OM937354	ON016159	OM937320	OM937338	ON016110	ON016121	ON016140	ON016144
<i>O. hartlaubii</i> 1	STP: São Tomé	OM978884	OM978899	EU601139	OM937286	EU601108	EU601032	EU600995	OM937321	EU601072	–	ON016122	EU600952	ON016145
<i>O. hartlaubii</i> 2	STP: São Tomé	OM978885	OM978900	–	OM937287	OM937303	OM937349	ON016160	OM937322	OM937329	ON016111	ON016123	ON016130	ON016146
<i>O. hartlaubii</i> 3	STP: São Tomé	OM978886	OM978901	–	OM937288	OM937304	OM937347	ON016161	OM937323	OM937330	ON016112	ON016124	ON016131	ON016147
<i>O. hartlaubii</i> 4	STP: São Tomé	OM978887	OM978902	OM913483	OM937289	OM937305	OM937348	ON016162	OM937324	OM937331	ON016113	ON016125	ON016132	ON016148
<i>O. senegalensis</i>	South Africa	–	–	EU601166	–	EU601127	EU601056	EU601019	–	EU601098	–	–	EU600976	–
<i>O. senegalensis</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>O. senegalensis</i> <i>fae</i>	EG: Annobón	OM978891	OM978908	OM913484	OM937293	OM937306	OM937350	ON016155	OM937327	OM937333	ON016116	ON016128	ON016138	ON016151
<i>O. pambuanensis</i> 1	Tanzania: Pemba	–	–	EU601157	–	EU601123	EU601048	EU601010	–	EU601090	–	–	EU600967	–
<i>O. pambuanensis</i> 2	Tanzania: Pemba	–	–	EU601158	–	EU601124	EU601049	EU601011	–	EU601091	–	–	EU600968	–
<i>O. pamelae</i>	Saudi Arabia	–	–	–	–	–	KC138819	KC138827	–	KC138812	–	–	–	–
<i>O. scops</i> 1	France	–	–	EU601146	–	EU601115	EU601039	EU601001	–	EU601079	–	–	EU600958	–
<i>O. scops</i> 2	France	–	OM978906	–	–	OM937314	–	ON016164	OM937325	OM937334	ON016114	ON016126	ON016135	ON016149
<i>O. scops</i> 3	France	–	OM978907	–	–	OM937313	–	ON016165	OM937326	OM937339	ON016115	ON016127	ON016133	ON016150
<i>O. scops</i> 4	France	OM978890	OM978905	OM913488	OM937292	OM937312	OM937355	ON016163	–	–	–	–	–	–
<i>O. cyprinus</i>	Cyprus	–	–	–	KT803674	OM937311	–	–	–	–	–	–	–	–
<i>O. brucei</i>	CHIMERA– United Arab Emirates: Oman	–	–	–	–	EU348985	KC138817	KC138825	–	KC138811	EU348920	–	–	–
<i>O. longicornis</i>	CHIMERA– Philippines – Isabela, Luzon; Unknown Mindanao; Unknown	U83751	OM978909	EU601151	OM937294	EU601119	OM937356	EU601005	–	EU601084	–	–	EU600962	–
<i>O. mirus</i>	CHIMERA– Philippines: Mindanao; Unknown	U83752	–	–	–	EU601126	EU601057	EU601020	–	EU601099	–	–	EU600978	–
<i>O. elegans</i>	Unknown	–	–	–	AB842985	EU123899	–	–	–	–	–	–	–	–
<i>O. magotensis</i>	Mayotte	–	–	EU601154	–	EU601122	EU601046	EU601008	–	EU601087	–	–	EU600965	–
<i>O. madagascariensis</i>	Madagascar	OM978893	OM978911	OM913489	OM937295	OM937315	OM937357	ON016166	–	EU601082	–	–	EU600960	–
<i>O. rutilus</i>	Madagascar	–	–	EU601135	–	EF198270	EF198304	EU600989	–	EU601066	–	–	EU600946	–
<i>O. capnodes</i>	Comoros: Anjouan	–	–	EU601145	–	EU601114	EU601038	EU601000	–	EU601078	–	–	EU600957	–
<i>O. insularis</i>	Seychelles: Mahé	–	–	EU601128	–	EU601101	EU601022	EU600983	–	EU601059	–	–	EU600940	–
<i>O. sunia</i>	CHIMERA– China x 2; Thailand	OM978894	OM978912	OM913491	ON016106	OM937316	OM937358	ON016167	–	EU601081	EU348927	–	EU600959	–

Taxon	Locality	12S	16S	ATP6	COI	CYTB	ND2	ND3	KIAA	MYO2	RAG1	SACS	TGFB2	TTN
<i>O. socotrinus</i>	Socotra	–	–	–	–	–	KC138824	KC138832	–	KC138816	–	–	KC138810	–
<i>O. pauliani</i>	Comoros: Grande Comore	–	–	–	–	EU601125	EU601058	EU601021	–	EU601100	–	–	EU600979	–
<i>O. mokiensis</i>	Comoros: Moheli	OM978892	OM978910	OM913490	–	OM937317	EU601045	ON016168	OM937328	OM937335	ON016117	ON016129	ON016134	ON016152
<i>O. itersonychnus hololeptinus</i>	CHIMERA–Cameroon: Eftlan; DRC; Kivu	–	–	–	–	OM937318	OM937359	ON016169	–	–	–	–	–	–
<i>O. itersonychnus itersonychnus</i>	Liberia: Lofa County	–	–	–	–	–	OM937360	ON016170	–	OM937332	–	–	–	–
<i>O. bukamaena muruthae</i>	India: Wadi	–	–	–	–	–	OM937340	–	–	–	–	–	–	–
<i>O. lempiji</i>	CHIMERA–Singapore: Indonesia (captiv); Unknown	OM978888	OM978903	OM913481	OM937290	OM937296	OM937341	ON016153	–	EU601076	EU348922	–	EU600981	–
<i>O. letitia</i>	CHIMERA–Russia; China; Laos	–	–	EU601140	GQ482285	EU601109	EU601033	EU600996	–	EU601073	EU348923	–	EU600953	–
<i>O. megalotis</i>	CHIMERA–Philippines–Isabela; Luzon	–	–	EU601133	JQ175645	EU601105	EU601027	EU600988	–	EU601064	–	–	EU600944	–
<i>O. nigrorum</i>	CHIMERA–Philippines: Panay; Unknown	U83755	–	–	–	JN131497	KF792802	–	–	–	EU348924	–	–	–
<i>O. everetti</i>	CHIMERA–Philippines: Mindanao; Unknown	U83754	–	–	U83779	JN131492	JN131480	–	–	–	–	–	–	–
<i>O. semitorques</i>	CHIMERA–Russia; Unknown	AY513588	–	EU601142	AB843645	EU601111	EU601035	EU600998	–	EU601075	–	–	EU600955	–
<i>O. angelinae</i>	Indonesia: Java	–	–	–	–	–	OM937342	–	–	–	–	–	–	–
<i>O. sibiricola</i>	Indonesia: Flores	–	–	–	–	OM937302	–	–	–	–	–	–	–	–
<i>O. spiloecephalus vandewateri</i>	Sumatra	–	–	–	–	OM937297	OM937343	–	–	–	–	–	–	–
<i>O. spiloecephalus vulpes</i>	Malaysia: Perak	–	–	–	–	OM937298	OM937344	–	–	–	–	–	–	–
<i>O. spiloecephalus luciae</i>	Borneo	–	–	–	–	OM937299	–	–	–	–	–	–	–	–
<i>O. spiloecephalus spiloecephalus</i>	CHIMERA–China; Unknown	–	–	EU601147	–	EU601116	EU601040	–	–	EU601080	KJ456094	–	EU600980	–
<i>O. spiloecephalus hambroeki</i>	Taiwan: Hsinshia	–	–	–	–	OM937300	OM937345	–	–	–	–	–	–	–
<i>O. spiloecephalus latouchi</i>	CHIMERA–Laos: China	OM978889	OM978904	OM913482	OM937291	OM937301	OM937346	ON016154	–	–	EU348926	–	–	–
<i>O. irenae</i>	Kenya	–	–	EU601144	–	EU601113	EU601037	EU600999	–	EU601077	–	–	EU600956	–
<i>Bubo bubo</i>	France	–	–	EU601137	–	AJ003969	EU601029	EU600992	–	EU601069	–	–	EU600949	–
<i>Sorex aluco</i>	France	–	–	EU601138	–	EU601107	EU601030	EU600993	–	EU601070	–	–	EU600950	–

PCR amplification of CYTB and ND2 sequences of *O. cyprius*, *O. i. icterorhynchus*, Wallace's Scops-Owl *O. silvicola* (Wallace, 1864), and four subspecies of the Mountain Scops-Owl (Blyth, 1846) [*O. spilocephalus vandewateri* (Robinson & Kloss, 1916), *O. s. vulpes* (Ogilvie-Grant, 1906), *O. s. luciae* (Sharpe, 1888), and *O. s. hambroeki* (Swinhoe, 1870)] was performed in seven fragments of ca. 180–200 bp using custom-made primers (see Suppl. material 10). PCR products were cycle-sequenced in both directions using the Big Dye Terminator v. 3.1. Sequences were read on an ABI 3100 capillary sequencer (Applied Biosystems, Foster City, CA, USA). Samples amplified and sequenced at Muséum national d'Histoire naturelle, Paris (MNHN) (Table 4) followed Pons et al. (2013).

Chromatograms of newly generated sequences were checked by eye, edited and aligned using BioEdit v. 7.0.5.3 (Hall 1999). All newly determined sequences were submitted to GenBank (accession numbers provided in Table 4).

Molecular analyses

Six different datasets were compiled for different purposes, detailed below.

Dataset 1

ND2 sequences of the species belonging to the Afro-Palearctic clade and of *O. brucei*, whose taxonomic affinities are not resolved, although it appears to be closer to African and Indian Ocean islands species than to the Asian species (Pons et al. 2013). This alignment contained 16 sequences belonging to the candidate species from Príncipe, the five species of the Afro-Palearctic clade, including the mainland and Annobón subspecies of *O. senegalensis*, and *O. brucei*. This dataset was used to compute the mean genetic distances matrix (uncorrected p-distance in percentage, using the pairwise deletion option) within and between taxa. Distances were computed using MEGA, v. 7.0.21 (Kumar et al. 2016).

Dataset 2

Molecular dataset used for the phylogenetic and divergence time analyses. This dataset comprised 51 individuals from 39 taxa and a final concatenated sequence alignment of 12,925 bp. This dataset was built with the sequences produced in this study together with previously available sequences. We used homologous sequences of the Tawny Owl *Strix aluco* Linnaeus, 1758 and of the Eurasian Eagle-Owl *Bubo bubo* (Linnaeus, 1758) for outgroup rooting. The input files for phylogenetic inference were prepared in “Pipelogeny” (Muñoz-Pajares et al. 2019). Sequences were automatically aligned using the mafft algorithm (Katoh and Standley 2013). The best model of molecular evolution and the best partition scheme to analyse the molecular dataset was identified using PartitionFinder2 v. 2.1.1 (Lanfear et al. 2012, 2016) using the greedy algorithm and applying the Bayesian Information Criterion (BIC).

Bayesian inference (BI) analyses were computed in MrBayes v. 3.2.6 (Ronquist et al. 2012). Two runs of 100 million generations (starting with random trees) and four

incrementally heated Markov chains were performed, using default heating values and sampling the Markov chains at intervals of 1000 generations. The first 40% of trees were discarded as burn-in, and the remaining trees were retained and summed up to generate a 50%-majority rule consensus tree. Chain mixing, stabilisation and convergence of likelihood values was assessed by examining the standard deviation of split frequencies. PartitionFinder and the partitioned BI analyses were run on the CIPRES gateway server (Miller et al. 2010) on XSEDE. The purpose of this phylogenetic analysis was: 1) to confirm that the representatives of the candidate species form a monophyletic group; 2) to infer the phylogenetic relationships of the candidate species within *Otus*.

We estimated divergence times (one partition per locus) using BEAST 1.10.4 (Drummond et al. 2012). Substitution models for each marker were selected using MEGA X (Kumar et al. 2018) and used default prior distributions for the substitution models parameters. We specified uncorrelated lognormal clock models (Drummond and Rambaut 2007) for the seven mitochondrial loci and strict clock models for six nuclear loci. As calibrations, we used the substitutions rates and corresponding associated uncertainties from Lerner et al. (2011) and specified the following priors: ND2 – normal distribution with mean 0.029 and standard deviation 0.0029; ND3 – normal distribution with mean 0.024 and standard deviation 0.003; ATP6 – normal distribution with mean 0.026 and standard deviation 0.0026; CYTB – normal distribution with mean 0.014 and standard deviation 0.0012. We used uniform distributions for each of the nuclear loci (lower bound: 0.0, upper bound: 0.5). We specified a Birth-Death prior for the tree prior. MCMC chains were run for 50 million iterations with trees and parameters sampled every 1000 iterations. Analyses were run on the CIPRES 3.1 gateway server (Miller et al. 2010). We used Tracer v. 1.7 (Rambaut et al. 2018) to help ensure that the effective sample size for all Bayesian analyses of the underlying posterior distribution was adequate (> 200) for meaningful estimation of parameters.

Datasets 3–6

The alignments of each nuclear gene were analysed separately to obtain evidence for genetic differentiation of lineages from unlinked loci and, hence, to provide further support to their status as distinct species following the criterion of genealogical concordance (Avice and Ball 1990; Avice and Wollenberg 1997). These datasets contained the nuclear markers KIAA1239, MYO2, TGFB2 and TTN. In these four datasets we included all species of the Afro-Palearctic clade (sensu Pons et al. 2013) and, when available, sequences of *O. brucei*. We trimmed all sequences to equal length (KIAA1239: 653 bp, MYO2: 131 bp, TGFB2: 403 bp, and TTN: 706 bp). Sequences were phased using the PHASE algorithm (v. 2.1.1) with default settings (Stephens et al. 2001) as implemented in the software DnaSP (v. 6.12.01; Rozas et al. 2017). PHASE parameters were 1000 iterations, one thinning interval and 100 burn-in iterations and a posterior probability threshold of 0.95 to determine the most probable inferred haplotypes for each nuclear sequence. Analyses were repeated three times with different seed values. Haplotype network reconstruction of phased sequences was performed using the software TCS, v. 1.21 (Clement

et al. 2000). This software applies the method of Templeton et al. (1992) to calculate the minimum number of mutational steps between haplotypes, computing the probability of parsimony for pairwise differences until the probability exceeds 0.95. This analysis was used to detect the occurrence and extent of haplotype sharing in the studied *Otus* species. The resulting networks were plotted using the online tool tcsBU (Múrias dos Santos et al. 2016). We interpreted the lack of haplotype sharing among individuals of different phylogenetic lineages as independent evidence of their evolutionary distinctiveness.

Nomenclature review

This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The LSID (Life Science Identifier) for this publication is: urn:lsid:zoobank.org:pub:0731A37D-B363-43C9-A1AC-69F5E10F6810. The electronic edition of this work was published in a journal with an ISSN, and has been archived and is available from the following digital repositories: <https://zookeys.pensoft.net/>.

Data availability

Molecular data are deposited in GenBank. Photographs and audio recordings are deposited in Macaulay Library and Xeno-canto, respectively. All other datasets underpinning this article are available as supplementary files (Suppl. materials 1–16).

Results

Justification for species delimitation

Following the integration by congruence approach (Padial et al. 2010), we consider independent evolutionary lineages as separate species if two or more independent lines of evidence support their distinctiveness. The candidate species: i) differs in morphology from other *Otus* species (Fig. 3); ii) has a very distinct call (Tables 2, 3; Figs 4, 5); iii) forms a distinct monophyletic group (Fig. 6) that iv) differs from the nearest taxa by a mitochondrial uncorrected pairwise sequence divergence (p -distance) similar or larger than the divergence observed between other currently accepted sister species pairs of the genus *Otus* (Table 5); v) has no haplotype sharing at some of the analysed nuclear markers (Fig. 7). We interpret the concordance between these independent lines of evidence as strong support for its distinctiveness and species status (Avice and Ball 1990; Padial et al. 2010; Sangster 2018). Therefore, we conclude that the candidate species from Príncipe is a distinct species that we describe herein as *Otus bikegila* sp. nov., and for convenience we will use this name throughout the manuscript, anticipating its formal description below.

Morphological differentiation

In the PCA, the first two components presented eigenvalues higher than one (Suppl. material 11), representing 81.7% of the variation. PC1 (60.9% of the variance) was negatively correlated with all variables related with bill, tarsus length and tail length, whereas PC2 (20.8% of the variance) was positively correlated with wing length (Suppl. material 11). *Otus bikegila* sp. nov. is within the variation of *O. pembraensis* and separated from the other species (Fig. 3). All other taxa are separated from each other, except *O. senegalensis feae* that is within the variation of *O. senegalensis senegalensis* (Swainson, 1837).

For the Welch's ANOVAs, *O. brucei obsoletus* was not included due to the small sample size. All variables differed significantly between species ($P < 0.05$), except Bidepth (Suppl. material 12). Games-Howell post-hoc test provided significant values for all the species only for Bilen and Biwid because of missing data from some specimens. This test was used to identify the morphological diagnostic characters detailed in the Diagnosis section.

Bioacoustic differentiation

In the PCA, four components presented eigenvalues higher than one (Suppl. material 13), representing 87.6% of the variation. PC1 (56.8% of the variance) mostly represented frequency characteristics of the note, being positively correlated with the

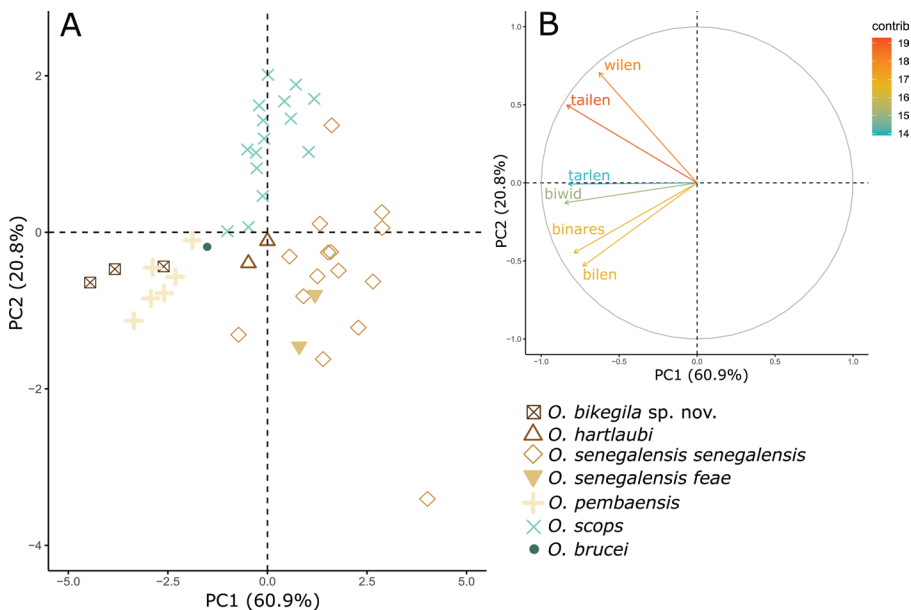


Figure 3. A Principal Component Analysis scatterplot of morphological measurements of *Otus* species and **B** the correlation circle in which ‘contrib’ corresponds to the contribution of the variables in accounting for the variability in the Principal components. Morphological measurement abbreviations – Bilen: bill length from bill tip to where culmen enters feathers; Binares: bill length from the anterior end of the nares to the tip; Biwid: bill width; Tarlen: tarsus length; Tailen: tail length; Wilen: wing length.

frequency variables F1-F8, but also with DT1. PC2 (14.1% of the variance) mostly represented temporal characteristics of the note, being negatively correlated with DT2, DT3, DT4, and DF1. PC3 (9.1% of the variance) was negatively correlated with DFT1 and DFT2, and PC4 (7.6% of the variance) was positively correlated with DF2. Plotting individuals on PC1 versus PC2 (Fig. 5) confirmed our hearing-based assessment that the calls of *O. bikegila* sp. nov. are unique but closest to the ones from *O. ireneae*, both characterised by short notes repeated at a fast rate (Fig. 4). One sample of *O. senegalensis senegalensis*, also came close to those of *O. bikegila* sp. nov. but, otherwise, the calls of the new species are clearly separated from the other species of the Afro-Palearctic clade. Samples of *O. brucei*, *O. pembaensis* and the short note of *O. cyprius* are clearly distinct from all other species. Samples of the long note of *O. cyprius* overlap with samples of *O. scops*. Samples of *O. pamela* and *O. hartlaubi* are contained in the variation of *O. senegalensis senegalensis* and samples of *O. senegalensis feae* and *O. scops* overlap with it.

Means of all bioacoustic variables differed significantly ($P < 0.05$) between species (Suppl. material 14). Low sample size prevented performing the Games-Howell post-hoc test between all taxa pairs. This test identified the bioacoustic diagnostic characters detailed in the Diagnosis section.

Molecular differentiation

The ND2 sequences (Dataset 1; 1037 pb) of the four samples of *Otus bikegila* sp. nov. were identical (Table 5). *Otus bikegila* sp. nov. is a distinct mitochondrial lineage (Dataset 2; Fig. 6), belonging to the Afro-Palearctic clade. The genetic distance between this species and the other taxa included in Dataset 1 ranged between 4.1% (*O. bikegila* sp. nov. vs. *O. hartlaubi* and *O. scops*) and 9.1% (*O. bikegila* sp. nov. vs. *O. brucei obsoletus*). The smallest genetic distances were observed between *O. senegalensis senegalensis* and *O. senegalensis feae* (0.7%), followed by *O. senegalensis feae* and *O. pamela* (3.0%); the highest value was recorded between *O. bikegila* sp. nov and *O. brucei* *O. hartlaubi* (9.1%).

The concatenated sequences of the phylogenetic dataset (Dataset 2; 12,925 bp; Suppl. material 2) were optimally partitioned in seven partitions (Suppl. material 15).

The topology of the majority rule consensus tree (Dataset 2; Fig. 6) is largely in agreement with previously published phylogenies of the genus *Otus* (Fuchs et al. 2008;

Table 5. Genetic divergence, in % base pairs difference, between and within (bold) *Otus* taxa of the Afro-Palearctic clade, estimated from uncorrected pairwise distances of the ND2 fragment (1037 bp). For taxa with a single sample, within-taxon variation could not be calculated (nc).

Taxon		1	2	3	4	5	6	7	8
<i>O. bikegila</i> sp. nov. (n = 4)	1	0.0%							
<i>O. hartlaubi</i> (n = 4)	2	4.1%	0.1%						
<i>O. senegalensis senegalensis</i> (n = 1)	3	4.4%	3.3%	nc					
<i>O. senegalensis feae</i> (n = 1)	4	4.7%	3.6%	0.7%	nc				
<i>O. pembaensis</i> (n = 2)	5	4.5%	3.9%	4.2%	4.5%	0.0%			
<i>O. pamela</i> (n = 1)	6	6.2%	3.6%	3.4%	3.0%	4.5%	nc		
<i>O. scops</i> (n = 2)	7	4.1%	4.7%	4.9%	5.0%	5.3%	3.2%	0.1%	
<i>O. brucei</i> (n = 1)	8	9.1%	7.0%	6.9%	6.5%	7.1%	6.7%	7.7%	nc

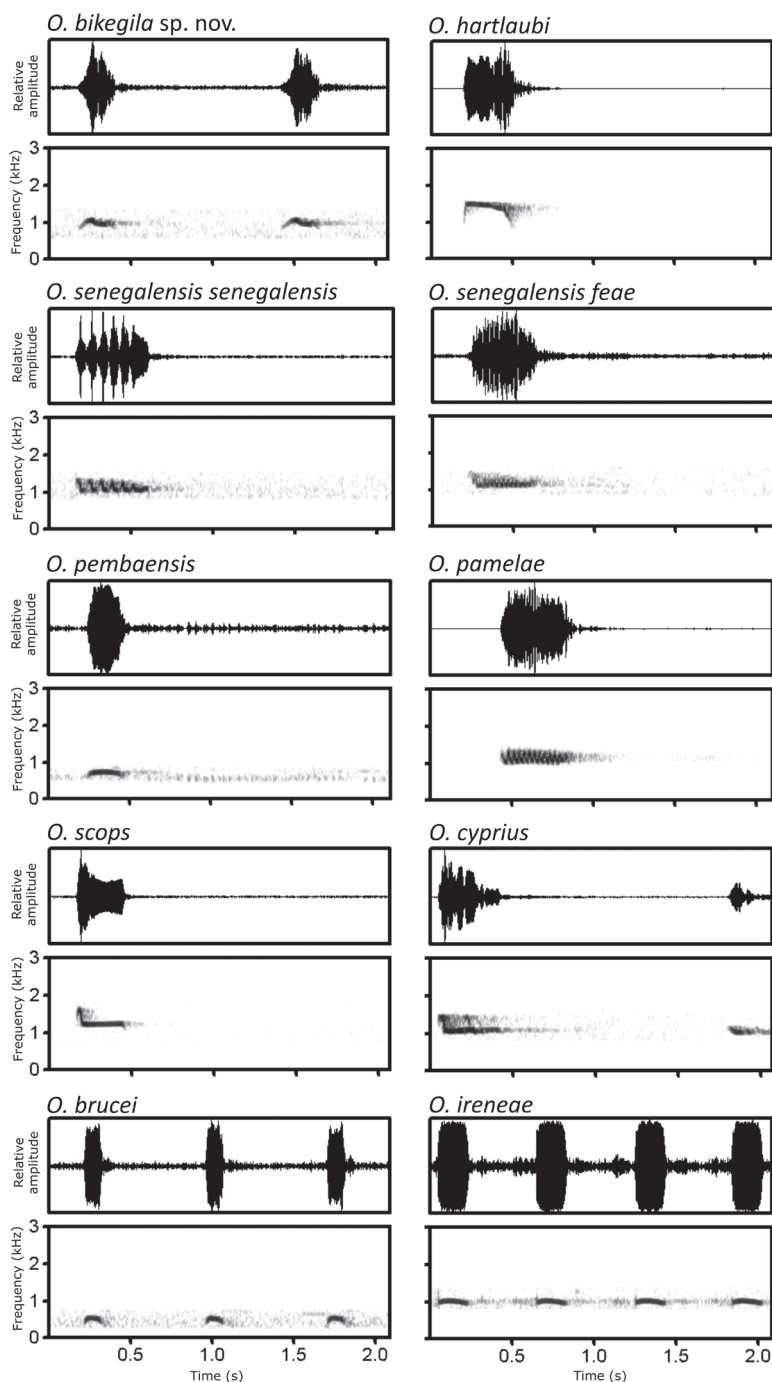


Figure 4. Oscillograms and spectrograms of 2-s sections of the song of *O. bikegila* sp. nov. (XC619448), *O. hartlaubi* (XC673669), *O. senegalensis senegalensis* (XC45502), *O. senegalensis feae* (XC340505), *O. pembraensis* (XC253581), *O. pamela* (XC371431), *O. scopi* (XC383983), *O. cyprus* (XC256102), *O. brucei* (XC158086), and *O. irenae* (XC147630). Each section refers to an individual owl. For more information about the recordings used see Suppl. material 7. Codes from Xeno-canto.org database.

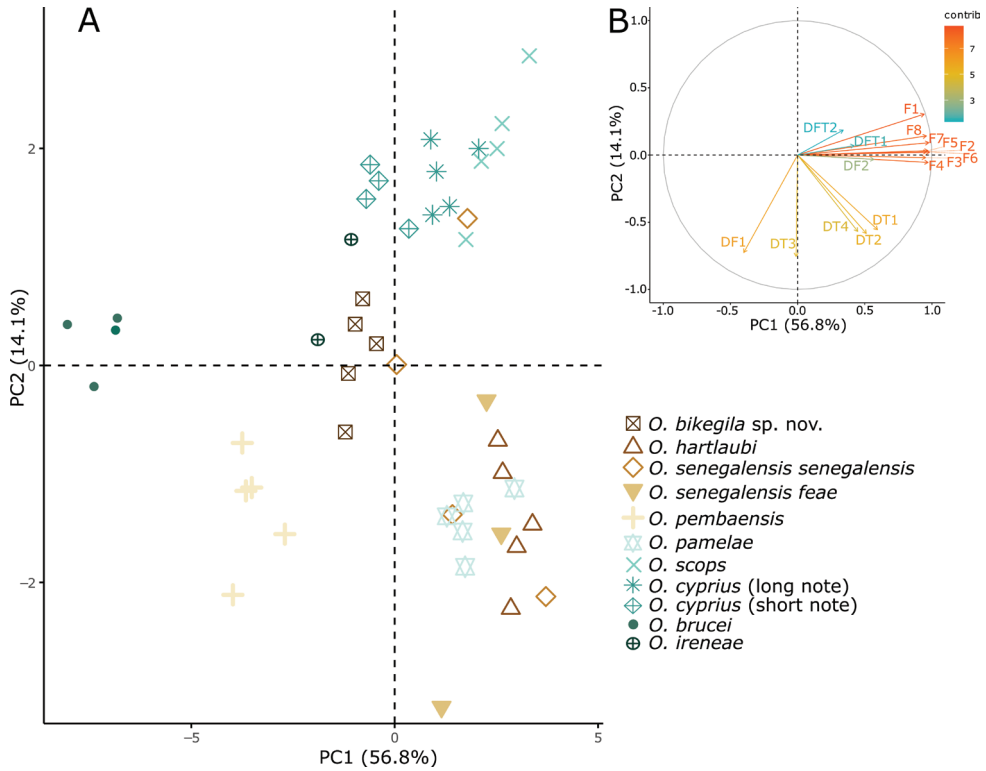


Figure 5. A Principal Component Analysis scatterplot of bioacoustics variables of *Otus* species and **B** the correlation circle in which ‘contrib’ corresponds to the contribution of the variables in accounting for the variability in the Principal components. Bioacoustic parameters – F1: frequency at start; F2: frequency at end; F3: frequency at 25% of total duration; F4: frequency at midpoint; F5: frequency at 75% of total duration; F6: frequency at maximum amplitude; F7: maximum frequency; F8: minimum frequency; DT1: total duration; DT2: time to maximum amplitude; DT3: time to maximum frequency; DT4: internote interval; DF1: frequency drop from start to end; DF2: frequency range; DFT1: slope from 25% to 75% of total duration; DFT2: slope from midpoint to end.

Pons et al. 2013), and increased the resolution of these by resolving some polytomies. An important improvement relatively to Fuchs et al. (2008) and Pons et al. (2013) was the inclusion of 13 additional taxa besides *O. bikegila* sp. nov. *Otus icterorhynchus* was found to represent a relatively basal lineage, sister to the clades containing the Afro-Palearctic and the Indo-Malayan/Indian Ocean species ($PP = 1$), rather than being sister to *O. ireneae*, as often hypothesised. The two subspecies of *O. icterorhynchus* were recovered as sister taxa, albeit with a very high genetic divergence (only one sample per taxon). *Otus brucei* (from the Arabian Peninsula to Asia) was the sister lineage to the Afro-Palearctic clade ($PP = 1$). Other novel insights are detailed in the discussion.

Otus bikegila sp. nov. samples were recovered as monophyletic, and formed a clearly distinct lineage belonging to the Afro-Palearctic clade. It was recovered as the sister lineage ($PP = 1$) of the clade formed by *O. senegalensis senegalensis*, *O. senegalensis feae*, *O. hartlaubi*, and *O. pambaensis* (Fig. 6).

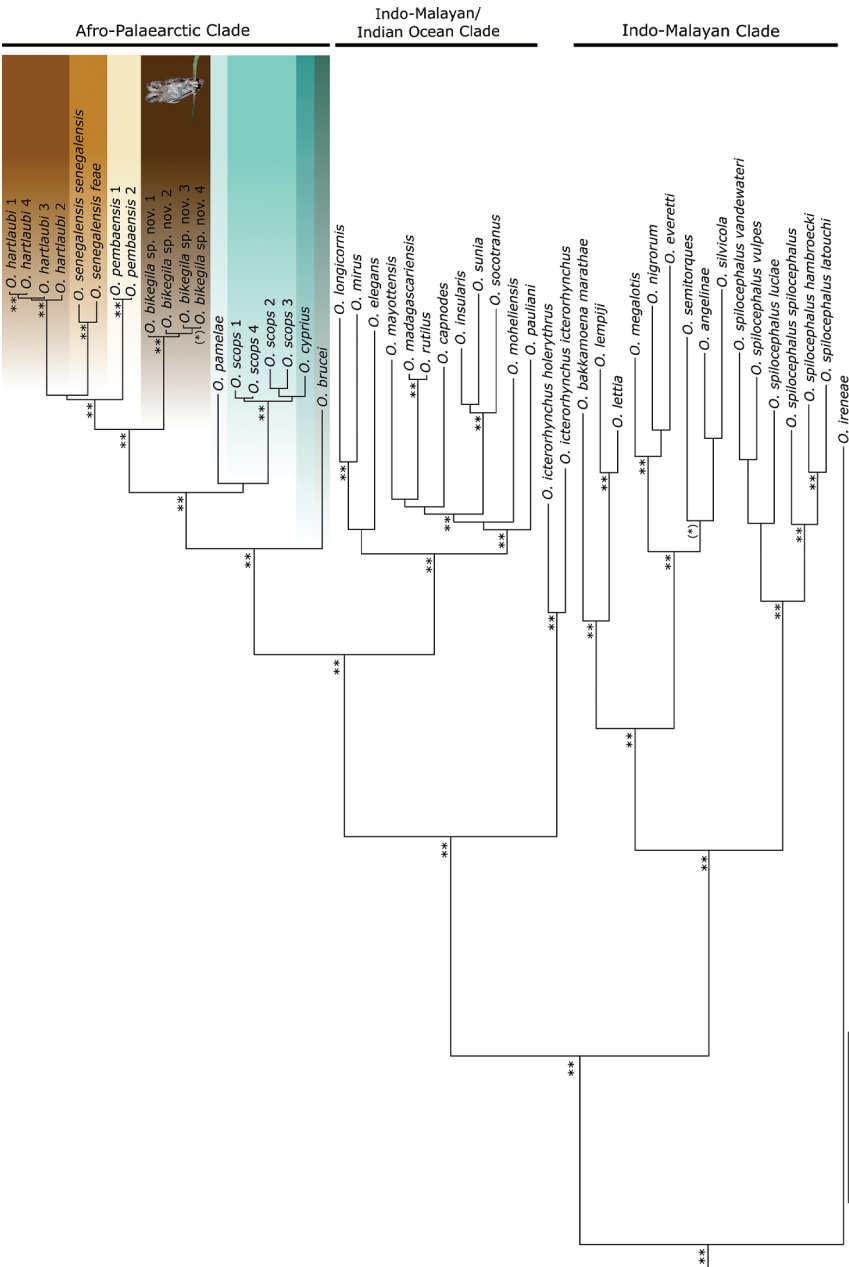


Figure 6. Multi-locus phylogeny of scops-owls (Strigidae: *Otus*). Phylogram (50% majority rule consensus tree) from a Bayesian Inference analysis of the dataset 2, including 12S, 16S, ATP6, COI, CVTB, ND2, ND3, KIAA, MYO2, RAG1, TGF2, and TTN gene fragments. Asterisks denote posterior probabilities values: (*) 0.85–0.94, * 0.95–0.98, ** 0.99–1. Scale bar corresponds to 0.02 substitutions per site. *Strix aluco* was set as outgroups (not shown on the figure).

The best model of sequence evolution for each marker used for the divergence times analyses are listed in the Suppl. material 16. The genus *Otus* started to diversify ca. 7.8 mya (95% high posterior density [HPD]: 6.2–9.6). The two primary clades diverged at ca. 6.3 mya (95% HPD: 5.1–7.7), and went on to diversify at similar times: i) *O. icterorhynchus*/*O. moheliensis*: 4.3 mya (95% HPD: 3.3–5.3), and ii) *O. spilocephalus*/*O. bakkamoena marathae* clade 4.6 mya (95% HPD: 3.7–5.6). *Otus bikegila* sp. nov. diverged from the *O. hartlaubi*/*O. pembraensis*/*O. senegalensis* clade ca. 0.9 mya ago (95% HPD: 0.7–1.1), an estimate similar (e.g., *O. mirus*/*O. longicornis*: 1 mya 95% HPD: 0.7–1.3) or greater (*O. socotranus*/*O. insularis*/*O. sunia*: 0.8 mya 95% HDP: 0.6–1.1) than the divergence estimated between closely related and well accepted species.

Nuclear markers independently supported the evolutionary independence of the taxa of the Afro-Palearctic clade. The taxa included in the analysis shared no haplotypes for markers KIAA1239 and TGFB2; the latter was the most variable of the analysed nuclear markers with a total of 19 haplotypes (Fig. 7). For MYO2, *O. hartlaubi*

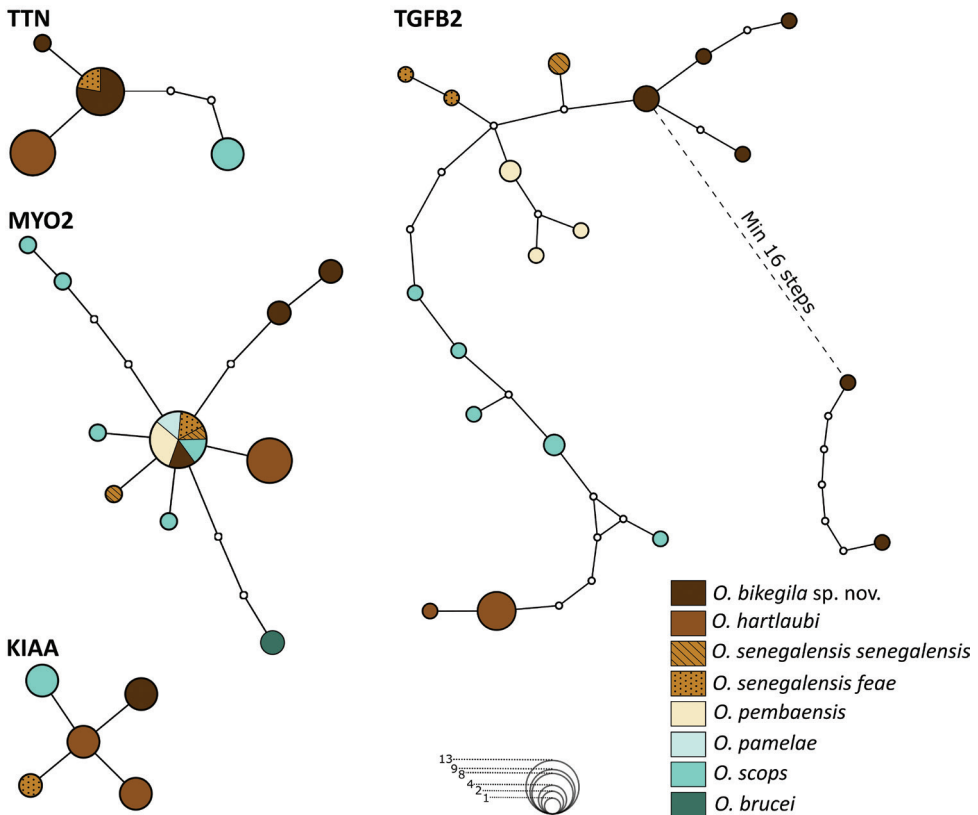


Figure 7. Haplotype network reconstruction for the nuclear KIAA, MYO2, TGFB2, and TTN gene fragments in *Otus bikegila* sp. nov., *O. hartlaubi*, *O. senegalensis senegalensis*, *O. senegalensis feae*, *O. pembraensis*, *O. pamelae*, *O. scops*, and *O. brucei* (when available). Area of circles is proportional to the number of individuals with that haplotype. The smallest circles (white) represent unsampled or extinct haplotypes.

and *O. brucei* had no shared haplotypes, whereas *O. bikegila* sp. nov., *O. scops* and *O. senegalensis* had some unique haplotypes but shared the most common one (Fig. 7). *Otus hartlaubi* and *O. scops* did not share any TTN haplotype, with *O. bikegila* sp. nov. having both one unique haplotype and one shared with *O. senegalensis feae* (Fig. 7).

***Otus bikegila* sp. nov.**

<https://zoobank.org/0731A37D-B363-43C9-A1AC-69F5E10F6810>

Figs 2A, 8

Material. Holotype. MHNC-UP-AVE7000: SÃO TOMÉ and PRÍNCIPE • ♀, adult, moulting; Príncipe Island, South Príncipe, ca. 500 m NW of Ribeira Porco river mouth (Fig. 1); 1°33.03'N, 7°22.29'E; ca. 100 m a.s.l.; 29 May 2017; HP and Ceciliano do Bom Jesus leg.; skin prepared by Vanya Rohwer, skeleton prepared by Vanya Rohwer and Daniele Cataldo; left wing removed for wing mounting, all bones with the exception of the left tarso-metatarsus (tarsus) removed for skeleton preparation; Audio-recorded by HP (Xeno-canto audio: XC619445, XC619447; GenBank: 12S OM978880, 16S OM978895, ATP6 OM913485, COI, OM937282; CYTB, OM937307; ND2, OM937351; ND3, ON016156; KIAA1239, OM937319; MYO2, OM937336; RAG1, ON016107; SACS, ON016118; TGFB2, ON016136 and TTN, ON016141; Gulf of Guinea database of MM: P7-04.

Diagnosis. The new species (Figs 2, 9) is assigned to the genus *Otus* based on genetic and morphological similarities to other known species of this genus. Phylogenetic analyses place it within the Afro-Palearctic clade, making generic placement unambiguous. Placement of the new species in *Otus* is further supported by its morphological characters: small size, distinctive ear-tufts, facial disc, short rounded wings, and short tail. The new species differs from the other described taxa of the Afro-Palearctic *Otus* clade (*O. hartlaubi*, *O. senegalensis*, including *O. s. feae* sometimes treated as a distinct species, *O. pemaensis*, *O. pamela*, *O. scops*, *O. brucei*) by high genetic differentiation (pairwise ND2 distance ranging from 4.1% to 9.1%), by the lack of haplotype sharing at the KIAA1239 and TGFB2 nuclear markers, as well as from a combination of morphological, genetic and natural history (bioacoustics) traits.

We provide here a diagnosis relatively to the closely related species belonging to the Afro-Palearctic clade and also to *O. ireneae* due to the similarity in their calls. The diagnosis is based on the following analysed morphological characters: 1) Biwid; 2) Binaries; 3) Tarlen; 4) Wilen; 5) Tailen; 6) SP10; 7) SP9; 8) SP4; on the following analysed bioacoustics characters: 9) F1; 10) F2; 11) F3; 12) F4; 13) F5; 14) F6; 15) F7; 16) F8; 17) DT1; 18) DT2; 19) DT4; 20) DF1; 21) DF2; 22) DFT1; 23) DFT2; and on the 24) list of diagnostic substitutions identified at the analysed nuclear markers (Tables 1–4; Suppl. materials 12, 14).

In overall appearance, *O. bikegila* sp. nov. is most similar to *O. hartlaubi* from which it differs in one morphological and 10 bioacoustic characters: longer Wilen (145 to 151 mm vs. 130 to 139 mm), lower F1 (781.7 to 961.7 Hz vs. 1078.3 to 1360.0 Hz), lower F2 (933.3 to 1020.0 Hz vs. 1155.0 to 1285.0 Hz), lower F3 (980.0

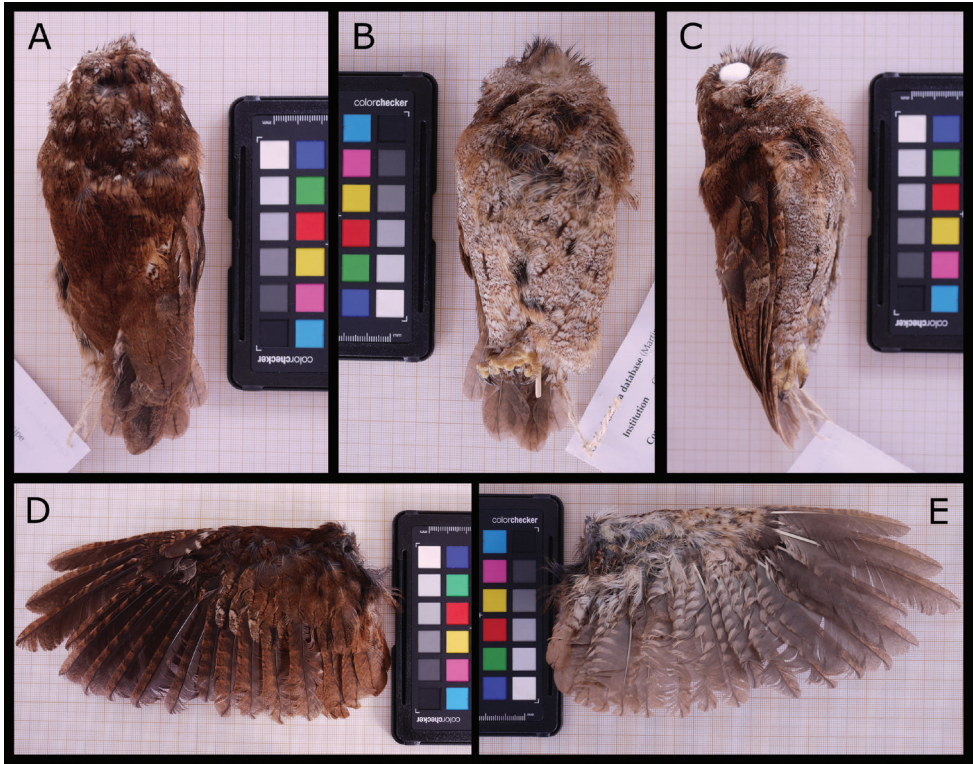


Figure 8. *Otus bikegila* sp. nov., female holotype (MHNC-UP-AVE7000). Views **A** dorsal **B** ventral **C** lateral **D** left wing top and **E** left wing under. Millimetric paper on the background and colour reference plate (Colorchecker, X-Rite Inc.) for size and colour assessment.

to 1090.0 Hz vs. 1330.0 to 1478.3 Hz), lower F4 (950.0 to 1050.0 Hz vs. 1295.0 to 1483.3 Hz), lower F5 (931.7 to 1020.0 Hz vs. 1250.0 to 1418.3 Hz), lower F6 (976.7 to 1090.0 Hz vs. 1331.7 to 1480.0 Hz), lower F7 (1035.0 to 1106.7 Hz vs. 1407.5 to 1526.7 Hz), lower F8 (868.3 to 973.3 Hz vs. 1066.7 to 1267.5 Hz), shorter DT1 (0.231 to 0.248 s vs. 0.267 to 0.315 s), shorter DT4 (0.992 to 1.121 s vs. 9.181 to 15.998 s). *Otus bikegila* sp. nov. differs from *O. hartlaubi* also by the following molecular characters: KIAA (T vs. C in site 347); TTN (G vs. C in site 91); MYO2 (G vs. A in site 2); TGFB2 (C vs. A in site 28, G vs. A in site 33, G vs. T in site 47, T vs. C in site 99, A vs. G in site 178, G vs. T in site 305, C vs. G in site 369).

Otus bikegila sp. nov. differs from *O. senegalensis senegalensis* in seven morphological and one bioacoustic characters: higher Biwid (9.0 to 11.8 mm vs. 4.8 to 8.0 mm), larger Binares (11.3 to 12.6 mm vs. 8.0 to 12.5 mm), longer Tarlen (30.5 to 35.1 mm vs. 20.0 to 24.2 mm), longer Wilen (145 to 151 mm vs. 103 to 145 mm), longer Tailen (75 to 85 mm vs. 40 to 65 mm), longer SP10 (37 to 40 mm vs. 10 to 32 mm), longer SP9 (13 to 18 mm vs. 1 to 16 mm), lower F4 (950.0 to 1050.0 Hz vs. 1095.0 to 1236.7 Hz); and in the following molecular characters: TGFB2 (A vs. G in site 178, T vs. G in site 344).



Figure 9. Principe Scops-Owl *Otus bikegila* sp. nov. from Príncipe Island, Africa. Left: Adult rufous morph in the typical posture. Right: Adult grey-brown morph in a stress posture, when it raises the ear tufts to increase the efficiency of camouflage. Original artwork by MNC.

Otus bikegila sp. nov. differs from *O. senegalensis feae* in one morphological and four bioacoustic characters: larger Biwid (9.0 to 11.8 mm vs. 6.4 to 6.8 mm), lower F2 (933.3 to 1020.0 Hz vs. 1132.5 to 1230.0 Hz), lower F7 (1035.0 to 1106.7 Hz vs. 1250.0 to 1357.5 Hz), shorter DT1 (0.231 to 0.248 s vs. 0.402 to 0.441 s), shorter DT4 (0.992 to 1.121 s vs. 7.127 to 7.479 s); and in the following molecular characters: KIAA (T vs. C in site 347, T vs. C in site 503); TGFB2 (A vs. G in site 178, T vs. C in site 285, G vs. C in site 392).

Otus bikegila sp. nov. differs from *O. pumbaensis* in one morphological and nine bioacoustic characters: shorter SP4 (6 to 9.5 mm vs. 11 to 21 mm), higher F1 (781.7 to 961.7 Hz vs. 506.7 to 636.7 Hz), higher F2 (933.3 to 1020.0 Hz vs. 613.3 to 773.3 Hz), higher F3 (980.0 to 1090.0 Hz vs. 621.7 to 770.0 Hz), higher F4 (950.0 to 1050.0 Hz vs. 633.3 to 780.0 Hz), higher F5 (931.7 to 1020.0 Hz vs. 651.7 to 783.3 Hz), higher F6 (976.7 to 1090.0 Hz vs. 638.3 to 776.7 Hz), higher F7 (1035.0 to 1106.7 Hz vs. 660.0 to 790.0 Hz), higher F8 (868.3 to 973.3 Hz vs. 530.0 to 660.0 Hz), shorter DT4 (0.992 to 1.121 s vs. 5.043 to 7.570 s); and in the following molecular characters: TGFB2 (A vs. G in site 178, T vs. C in site 285, C vs. T in site 345).

Otus bikegila sp. nov. differs from *O. pamela* in seven bioacoustic characters (morphology not analysed): lower F1 (781.7 to 961.7 Hz vs. 1031.7 to 1213.3 Hz), lower F2 (933.3 to 1020.0 Hz vs. 1111.7 to 1268.3 Hz), lower F4 (950.0 to 1050.0 Hz vs. 1096.7 to 1366.7 Hz), lower F5 (931.7 to 1020.0 Hz vs. 1083.3 to 1291.7 Hz), lower F6 (976.7 to 1090.0 Hz vs. 1160.0 to 1403.3 Hz), lower F7 (1035.0 to 1106.7 Hz vs. 1220.0 to 1516.7 Hz), lower F8 (868.3 to 973.3 Hz vs. 1020.0 to 1123.3 Hz).

Otus bikegila sp. nov. differs from *O. scops* in seven morphological and 11 bioacoustic characters: higher Biwid (9.0 to 11.8 mm vs. 5.5 to 7.8 mm), larger Binares (11.3 to 12.6 mm vs. 9.0 to 11.5 mm), longer Tarlen (30.5 to 35.1 mm vs. 22.0 to 28.0 mm), shorter Wilen (145 to 151 mm vs. 147 to 165 mm), longer SP10 (37 to 40 mm vs. 12 to 24 mm), longer SP9 (13 to 18 mm vs. 0 to 7 mm), shorter SP4 (6 to 9.5 mm vs. 10 to 29 mm), lower F1 (781.7 to 961.7 Hz vs. 1335.0 to 1695.0 Hz), lower F2 (933.3 to 1020.0 Hz vs. 1152.5 to 1275.0 Hz), lower F3 (980.0 to 1090.0 Hz vs. 1155.0 to 1260.0 Hz), lower F4 (950.0 to 1050.0 Hz vs. 1200.0 to 1285.0 Hz), lower F5 (931.7 to 1020.0 Hz vs. 1193.3 to 1318.3 Hz), lower F6 (976.7 to 1090.0 Hz vs. 1210.0 to 1326.7 Hz), lower F7 (1035.0 to 1106.7 Hz vs. 1336.3 to 1628.3 Hz), lower F8 (868.3 to 973.3 Hz vs. 1140.0 to 1253.3 Hz), shorter DT4 (0.992 to 1.121 s vs. 2.423 to 2.789 s), higher DF1 (6.7 to 178.3 Hz vs. -420.0 to -182.5 Hz), lower DFT1 (-581.5 to 45.2 Hz/s vs. 181.5 to 662.3 Hz/s); and in the following molecular characters: KIAA (T vs. C in site 347, A vs. G in site 632); TTN (T vs. C in site 535, G vs. A in site 536, G vs. T in site 634); TGFB2 (G vs. A in site 33, G vs. T in site 47, A vs. G in site 178, T vs. C in site 285).

Otus bikegila sp. nov. differs from *O. cyprius* in four bioacoustics characters (morphology and nuclear markers not analysed): presence of a monosyllabic primary song (*O. cyprius* has a distinctive di-syllabic primary song), lower F1 (781.7 to 961.7 Hz vs. 1236.7 to 1400.0 Hz [long note] and 1058.9 to 1223.3 Hz [short note]), shorter DT4 (0.992 to 1.121 s vs. 3.035 to 3.643 s [long note] and 3.116 to 3.714 [short note]), and having a higher DF1 (6.7 to 178.3 Hz vs. -283.3 to -165.0 Hz [long note] and -113.3 to -58.1 [short note]).

Otus bikegila sp. nov. differs from *O. brucei* in 11 bioacoustic characters (morphology not analysed): higher F1 (781.7 to 961.7 Hz vs. 285.0 to 388.3 Hz), higher F2 (933.3 to 1020.0 Hz vs. 891.7 to 946.7 Hz), higher F3 (980.0 to 1090.0 Hz vs. 356.7 to 530.0 Hz), higher F4 (950.0 to 1050.0 Hz vs. 356.7 to 493.3 Hz), higher F5 (931.7 to 1020.0 Hz vs. 335.0 to 450.0 Hz), higher F6 (976.7 to 1090.0 Hz vs. 370.0 to 510.0 Hz), higher F7 (1035.0 to 1106.7 Hz vs. 370.0 to 530.0 Hz), higher F8 (868.3 to 973.3 Hz vs. 270.0 to 373.3 Hz), longer DT1 (0.231 to 0.248 s vs. 0.090 to 0.133 s), longer DT2 (0.078 to 0.112 s vs. 0.032 to 0.053 s), higher DFT2 (-250.3 to 21.7 Hz/s vs. -1653.0 to -1387.3 Hz/s); and in the following molecular characters: MYO2 (T vs. C in site 22; C vs. T in site 118; C vs. T in site 129).

Otus bikegila sp. nov. differs from *O. ireneae* in one bioacoustic character (morphology and nuclear markers not analysed): longer DT4 (0.992 to 1.121 s vs. 0.409 to 0.447 s).

Description of the holotype. Morphological measurements available in Table 1. The topographic terms of the scops-owl body are detailed in the Suppl. material 3.

General colouration: Back, Burnt Amber 48 with Robin Rufous 29 shades; front, Pale Buff 1 feathers with Cinnamon 21 and Dusky Brown 285 markings (forming stripes defined by Dusky Brown 285 lines) with Robin Rufous 29 shades.

Head: Chin feathers Pale Buff 1 with Sayal Brown 41 shading along shaft, ending with a bristle-like barb Sepia 286. Throat feathers Pale Buff 1 with Pale Pinkish Buff 3 and Sepia 286 dots and markings sometimes forming bands; Pale Buff 1 shaft proximally becoming Pale Pinkish Buff 3 and Sepia 286 distally. Feathers of forehead Sepia 286 and few Pale Buff 1 shading. Tip of the head triangle Prout's Brown 47. Triangle outside facial disk with an overall appearance Prout's Brown 47, triangle with feather with Sepia 286 middle stripe along shaft, Prout's Brown 47 and Sepia 286 in their internal portion and Sepia 286 and Pale Buff 1 in the outer portion but always ending with Prout's Brown 47 or Robin Rufous 29 in the distal portion. Triangle delineated by Pale Buff 1/Smoke Grey 266 stripes (the eyebrows). Eyebrows Pale Buff 1/Smoke Grey 266 down to the bill: Pale Buff 1 feathers ending with a thin Cinnamon 21 line followed by a broader Jet Black 300 band; Pale Buff 1 feathers with middle Sepia 286 stripe along shaft and densely vermiculated with Sepia 286 and Cinnamon 21 shades; eyebrows feathers in distal portion are Pale Buff 1 densely vermiculated with Sepia 286 and Cinnamon 21 shades, ending in Prout's Brown 47. Crown feathers Prout's Brown 47 with Sepia 286 middle stripe along shaft, Pale Buff 1 in proximal section and Prout's Brown 47 with Sepia 286 vermiculation along mid and distal portion. Ear tuft not visible in the mounted specimen, but with feathers Pale buff 1 in proximal section becoming Cinnamon 21 with densely Sepia 286 vermiculation and ending with Prout's Brown 47; ear feathers pull up some of the eyebrow feather with Sepia 286 and Cinnamon 21 dense vermiculation. Nape feathers Pale Pinkish Buff 3 with well-defined Sepia 286 irregular stripes, ending with middle Sepia 286 stripe along shaft and Burnt Amber 48. Neck feathers with longer underfeathers (then in nape) with middle Sepia 286 stripe along shaft with Pale Pinkish Buff 3, Pale Buff 1, Pale Pinkish Buff 3 and becoming Pale Buff 1 and Burnt Amber 48 all with Sepia 286 irregular markings. Overall appearance of rictal bristles: Jet Black 300 patches with Cinnamon 21 and Pale Buff 1 shades next to the bill (following with Pale Buff 1/Smoke Grey 266 eyebrows); bristles with terminal Jet Black 300 colour;

bristles closer to the bill Pale Buff 1 in proximal position, changing into Cinnamon 21 and ending in Jet Black 300 or Pale Buff 1 in the proximal section and Jet Black 300 in distal section; bristles closer to the eye Jet Black 300 in proximal position, changing into Cinnamon 21 and ending in Jet Black 300 or only Jet Black 300 (the shortest one). Rim with two narrow Raw Umber 23 bands, one on each side, not extending to the centre; Pale Buff 1 feathers with Sepia 286 irregular markings, becoming Cinnamon 21 (with no Sepia 286 markings), ending with Raw Umber 23. Facial disk feathers Pale Buff 1 with multiple bands of Sepia 286 (generally 3), the terminal Sepia 286 bands is preceded by a thin Robin Rufous 29 band; feather ending with 2 to 5 bristle-like barbs.

Upperparts: Overall colour of mantle (i.e., upper back) and rump: Burnt Amber 48 with Robin Rufous 29 shades. Feathers Sayal Brown 41 with middle Sepia 286 line along shaft, and with irregular Sepia 286 markings in the proximal section. Feathers turning Cinnamon-Rufous 31 with Sepia 286 markings in the distal portion of the feather. Mantle is delimited distally (neck) by a Cinnamon-Rufous 31 band and laterally by a series of 8 feathers that are lighter in colour (Cinnamon-Rufous 31): outer vane Light Buff 2 with Cinnamon-Rufous 31 shades and with a Sepia 286 curve line that defines a Raw Sienna 32 colour close to shaft, one or more Sepia 286 spots on distal outer vane; outer vane ending distally with Raw Sienna 32 with Sepia 286 markings; inner vane is Raw Sienna 32 with Sepia 286 irregular markings. These feathers appear to make a line that delineates the outside of the mantle. Similarly, the feathers of the mantle at the base of the neck form a lighter Cinnamon Rufous 31 line that follows the external side of the folded wings, making a triangle. Scapulars as upperparts. Proximal shaft Pale Buff 1, Vandyke Brown 282 in distal portion; Vandyke Brown 282 middle stripe along shaft. Outer vane is Cinnamon 21 with Sepia 279 markings and inner vane is Sepia 279 with Cinnamon 21 markings.

Underparts: Breast overall Pale Buff 1 with Sepia 286 irregular markings and Robin Rufous 29 shading. Breast feathers Pale Pinkish Buff 3 with Sepia 286 dots and markings proximally and Pale Pinkish Buff 3 shaft, distally Sepia 286 with Pale Pinkish Buff 3 dots and markings forming irregular bands, middle Sepia 286 stripes along shaft. Belly overall similar to breast but with colours more defined and with Light Buff 2 shadings. Belly feathers Pale Pinkish Buff 3 in proximal section followed by a Sepia 286 V stripe. This is followed by a Pale Buff 1 broad band delimited distally with a thin Pale Pinkish Buff 3 line followed by a Sepia 286 line. Distally, these feathers are Pale Buff 1 with irregular spots Sepia 286 and Pale Pinkish Buff 3. Some feathers on the belly and the vent have a marked middle and broad Sepia 286 line along shaft. Vent is similar to breast and belly but with feathers Cinnamon 21 in proximal section followed by a Sepia 286 stripe. This is followed by a Pale Buff 1 broad band delimited distally with a thin Cinnamon 21 followed by a Sepia 286 line. The feather then becomes Pale Buff 1 with a Cinnamon 21 thin band followed by a Sepia 286 line, ending with a Pale Buff 1 colouration with Sepia 286 irregular dots and markings. Flank feathers Pale Buff 1 with Cinnamon 21 shading followed by a broad Cinnamon 21 V stripe followed by a Sepia 286 line, ending with a broad Pale Buff 1 section with Sepia 286 markings only in the very distal portion. Undertail coverts are similar to flanks but with more defined bands. Feathers are Pale Buff 1 followed by a broad Cinnamon 21 band defined distally by a thinner warm Sepia 40 line. This colouration is repeated twice. Feathers end with a broad Pale Buff 1 band fol-

lowed by a Cinnamon 21 band with irregular Warn Sepia 40 markings. Tarsus covered with feathers to base of toes. Feathers overall similar to flank but with less Pale Buff 1 and more Cinnamon 21 shading and one or two Sepia 286 dots in distal section. Tarsus feathers have a larger proportion of Pale Buff 1 close to toes. Tarsus feathers are Pale Buff 1 proximally, followed by Cinnamon 21 shading and Sepia 286 markings distally (approximately 1/4 of the feather distally), no middle stripe along shaft. Toes feathers are Pale Buff 1 with Cinnamon 21 shadings and Sepia 286 markings only in the distal section.

Wing: Overall Prout's Brown 47 with Dark Greyish Brown 284 leopard blotches. Primaries shaft Vandyke Brown 282. Outer vane of primaries with six or seven 'leopard' Dark Greyish Brown 284 spots in Cinnamon 21 background becoming Pale Buff 1 in some instances. Spots interior with a gradient of Cinnamon 21 to Dark Greyish Brown 284 with lighter spots on outer primaries. Spots circumference with Dark Greyish Brown 284 to Jet Black 300. 'Leopard spots' start faint (P1-P2-P3) and become stronger moving outwards. Inner vane of primaries with Dark Greyish Brown 284 with Cinnamon 21 shadings towards the distal section of the feather. Exterior edge makes a Pale Buff 1 line. Under-primaries have a Pale Buff 1 shaft proximally becoming Cinnamon 21 towards the distal portion. Outer vane of under-primaries is proximally Hair Brown 277 with Pale Pinkish Buff 3 irregular triangles, becoming Cinnamon 21 in distal section with Sepia 279 lines delimiting the leopard spots that are fading towards the distal portion of the feather. Inner vane of under-primaries is Hair Brown 277 with Light Buff 2 markings in proximal section and Cinnamon 21 markings in distal section. Secondaries shaft Vandyke Brown 282. Outer vane of secondaries is similar but much less marked pattern than primaries: spots on outer vanes less marked, fading into the background towards S10. Inner vane of secondaries with Sepia 279 with Cinnamon 21 shadings and markings especially towards the distal section of the feather. Under-secondaries have a Pale Buff 1 shaft proximally becoming Cinnamon 21 and later Sepia 279 towards the distal portion. Outer vane of under-secondaries with Hair Brown 277 with Cinnamon 21 markings. Inner vane of under-secondaries with Hair Brown 277 with six to seven Light Buff 2 triangles only on the outer part of the inner vane, which become irregular markings (Cinnamon 21 in colour) towards the distal portion of the feather. Tertiaries shaft like primaries (Vandyke Brown 282). Outer and inner vane of tertiaries similar in colour and similar to the outer vane of the secondaries. Under-tertiaries have Pale Buff 1 shaft proximally becoming Cinnamon 21 and later Sepia 279 towards the distal portion. Outer and inner vanes of under-tertiaries are similar: Cinnamon 21 with irregular Sepia 279 lines in the proximal portion, becoming irregular dots towards the distal section; terminal 1/5 with a Sepia 279 middle stripe along shaft. Primary coverts with Vandyke Brown 282 shafts. Outer vane of primary coverts with Sepia 279 with Cinnamon 21 markings becoming more packed towards the distal portion of the feather. Inner vane of primary coverts is similar to outer but with less packed Cinnamon 21 markings. Secondary coverts are overall Sepia 279 with Cinnamon 21 markings. Shaft is Vandyke Brown 282. Outer vane of secondary coverts with a Pale Buff 1 blotch delimited proximally by a Sepia 279 thin and sharp line. This blotch can have in its inner parts a Cinnamon 21 blotch delimited by a Sepia 279 thin and sharp line. Additional Sepia 279 lines distributed heterogeneously can be found on the outer vane. Inner vane of secondary coverts Sepia 279 with Light

Buff 2 markings in proximal section and Cinnamon 21 markings in the distal portion of the feather. Lesser coverts with shafts Pale Buff 1 proximally and Vandyke Brown 282 in distal portion. Vandyke Brown 282 middle stripe along shaft. Outer vane of lesser coverts Cinnamon 21 with Sepia 279 markings and Pale Pinkish Buff 3 markings delimited irregularly by Sepia 279 dashed lines. Inner vane of lesser coverts Sepia 279 with Cinnamon 21 markings. Coverts in the under-wings with Pale Buff 1 shaft. Outer vane on the coverts from the under-wings is Pale Buff 1 and Light Buff 2 with one Sepia 279 leopard spot and some additional (but rare) Sepia 279 markings. Inner vane of the coverts from the under-wings Pale Buff 1 and Light Buff 2 with Light Neutral Grey 297 colouration that become Sepia 279 distally. Alula shaft is Vandyke Brown 282. Outer vane of alula with five Verona Brown 37 'leopard' spots delimited by Sepia 279 lines which is sharper in distal portion. Leopard spots separated by Pale Pinkish Buff 3 with Cinnamon 21 shadings. Inner vane of alula Sepia 279 with four Light Buff 2 partial bands.

Tail: Verona Brown 37 with Sepia 286 markings that fades towards the distal portion of the feather. Shaft Sepia 286. Outer feathers of the tail have an outer vane Verona Brown 37 with broad Sepia 286 bands, and an inner vane with broad poorly defined Sepia 286 bands intercalated by Light Buff 2, Pale Pinkish Buff 3 and more distally Verona Brown 37 bands.

Bill: Dusky Brown 285 and lower bill Light Buff 2.

Iris: Yellow.

Vocalisations: Call recordings collected at the moment of specimen collection included the call of the holotype and a second individual (XC audios: XC619445, XC619447): one emitted the main call type (the single repetitive note used in the bioacoustic analyses), and the other the cat-like call. We believe that the holotype individual was the one giving the main call, but this was uncertain. Thus, it is not possible to provide bioacoustics parameters specific to the holotype.

Variation: Morphometric variation in *O. bikegila* sp. nov. is based on the analysis of three additional individuals, of which one is a male (Table 1; Fig. 2). The male (P9-038) had shorter tarsus and wing length than the female holotype and the other two females. This result is consistent with the reversed sexual dimorphism in size described for all species of scops-owls (Marks et al. 1999; König et al. 2008). Two colour morphs (rufous and grey-brown) have been documented in the field (Figs 2, 9). Molecular sexing of the four captured individuals has shown that colour morph is not associated with sex. Examples of the grey-brown morph include the holotype (Figs 2A, 8), individuals P9-037 and P9-038 (Fig. 2B), and individuals photographed in the field (Fig. 2D, E); examples of the rufous morph include the first photographed individual of this species (Fig. 2C) and individual P8-001 (Fig. 2F). Plumage pattern and colour of the latter is similar to the holotype, although in the rufous morph the eyebrows are less marked, the underparts are more similar in colour to the upperparts and have more prominent sepia marks and stripes along the feather shafts. In the field, we observed no differences in the rate of occurrence of the two morphs.

Vocalisations were recorded at the type locality by MM in 2002, 2007, 2011, 2018 and 2019 and at Boca do Inferno in 2019, and by PV at the type locality in 2016. The call of *O. bikegila* was described in Melo and Dallimer (2009). Among vocalisations of

Otus species, the primary call of *O. bikegila* sp. nov. is unique in consisting in a short, undulated note emitted at a fast repetition rate, reminiscent of insect calls, of ca. one note per second (Tables 2, 3; Fig. 4; Suppl. material 4: Fig. S2A). Vocalisations were often performed in duet (Suppl. material 4: Fig. S2B), with intercalated or overlapping notes. *Otus bikegila* sp. nov. is able to produce a cat-like “kee-a-u” note, which is emitted both in duets (Suppl. material 4: Fig. S2D) and by single birds (Suppl. material 4: Fig. S2C). We confirmed in the field that the same individual can produce both calls. Bioacoustic parameters (mean $\pm$ standard deviation) of the primary and of the cat-like notes are available in Tables 2, 3.

Etymology. The species name is a patronym honouring Ceciliano do Bom Jesus, known as ‘Bikegila’ (Suppl. material 5). The species epithet name is intentionally defined as an invariable noun in apposition (not a noun in the genitive case) for better pronunciation; no confusion with the species authority is possible because the noun is an oral nickname.

Bikegila, a native of Príncipe Island, began the ‘Príncipe Scops-Owl saga’ in 1998, when he shared with MM reports of two sightings of birds that looked like owls in parrot nests. Since then, Bikegila took part in every field effort that led to the bird’s discovery for science; he also led the capture of all sampled individuals, including the holotype, which required ingenious ways to erect canopy nets. For almost 25 years, Bikegila has put all his resources, including bottomless fieldwork skills and a vast knowledge of Príncipe, towards the successful completion of innumerable research projects in a terrain that the collector José Correia considered to be the “*bad among the bad or the worse among the worse*” [sic] (Diary, 2 September 1928, Archives AMNH, New York). Besides his skills, Bikegila’s “*cheerful temperament, possibly the first requirement for an undertaking in inhospitable regions*” (von Humboldt 1841), coupled with an unbeatable gift for story-telling and an underlying quiet wisdom, contributes as much to making the expeditions he leads memorable and successful. A former parrot harvester, Bikegila became a warden of Príncipe Obô Natural Park soon after its creation; he is now a much sought-after nature guide.

We believe that most field researchers are grateful to the ‘Bikegilas’ with whom they are/were honoured to work with. As such, the name is also in recognition of all the people, around the world, who through their deep relationship with and knowledge of the regions they inhabit, play key roles in the description of new species and of new sites to science.

Common name. We propose the English common name Príncipe Scops-Owl, the name for São Tomé and Príncipe as Kitóli-do-príncipe, and the name for the Portuguese list of the birds of the world as Mocho-do-príncipe. All common names refer to Príncipe Island, from where it is endemic.

Distribution and natural history. All records from *O. bikegila* sp. nov. come from old-growth native lowland rainforest with mid-height (14–20 m) trees (Fig. 10), with the species apparently preferring lower elevations (Melo and Dallimer 2009; Freitas et al. 2022). Its area of occurrence is fully within the limits of Príncipe Obô Natural Park. Detailed surveys have been carried out to determine the area of occupancy of this species, to estimate its population size, ecological requirements, and to propose an IUCN Red List category (Freitas et al. 2022).

The holotype (Figs 2A, 8; female MHNC-UP-AVE7000), collected on 29 May 2017, was undergoing a well-advanced moult, a process that takes place after the

breeding season. The female captured close to Ribeira Porco, in January 2019 (P8-001) had a fully developed brood patch (Fig. 2F), whereas the female captured at Boca do Inferno on the same month (Fig. 2B, left) was growing back the belly feathers, suggesting that she had a recent brood patch. This indicates that breeding takes place in December-January, as with most bird species of the islands of São Tomé and Príncipe (Jones and Tye 2006; Madeira 2018).

Otus bikegila sp. nov. starts calling at dusk and continues throughout the night. Contrarily to the São Tomé Scops-Owl *O. hartlaubi* that regularly vocalises during the day, *O. bikegila* sp. nov. seems to require darkness to sing, although on a single occasion one individual was heard during the day (Melo and Dallimer 2009). Response to the playback of its call was fast and intense at all times of the year we were able to test it, with birds of either sex approaching the speaker. This indicates that *O. bikegila* sp. nov. is territorial all-year round as it is known from most sedentary cavity-nesting owls (Marks et al. 1999; König et al. 2008). During the day it may roost outside of tree cavities, as suggested when we accidentally flushed one bird when taking habitat measurements. In this situation the bird raised its ear tufts, which are otherwise seldom observed (Fig. 2D).

Discussion

Otus bikegila: a new bird species, endemic to Príncipe Island

Multiple lines of evidence were brought together to demonstrate, unambiguously, that the recently discovered population of scops-owls on Príncipe Island makes a well-differentiated species, *Otus bikegila*. Genetic distances, and associated divergence times, to its closest relatives were in the range of those separating currently accepted species (Table 5). Morphological differences, although present, did not stand out (for the human eye at least), whereas vocalisations were unique and clearly distinctive (even for the human ear) and, in fact, it was bioacoustics that led to the discovery of the population of the Príncipe Scops-Owl. Its unique vocalisations were closest to those of *O. ireneae*, an *Otus* species from which it is distantly related, underscoring the value of song in scops-owls to assess taxonomic status but not for inferring taxonomic affinities (Fuchs et al. 2007). Phylogenetic data placed *O. bikegila* as the sister lineage of the clade containing all African scops-owl species of the Afro-Palearctic clade (sensu Pons et al. 2013 and Fig. 6), rather than as the sister species of *O. hartlaubi* endemic to the neighbouring island of São Tomé. This leads to the curious conclusion that Príncipe was likely the first island in the Gulf of Guinea to be colonised by a species of scops-owl, albeit the last species to be discovered and described for science. It also begs the question if an undescribed scops-owl waits to be discovered in the extensive rainforests of Bioko Island, the only island of the Gulf of Guinea without records of a scops-owl. This apparent absence is puzzling as Bioko is a land-bridge island, which has been connected to the mainland in multiple instances in the past (Rohling et al. 1998; Lambert and Chappel 2001), and currently lying at ca. 30 km from Cameroon where *O. icterorhynchus*, a rainforest specialist, is present.



Figure 10. **A** aerial view of the south of Príncipe Island home of *Otus bikegila* sp. nov., and **B** habitat of the type locality at ca. 150 m a.s.l. Photographs: **A** Alexandre Vaz **B** MM.

Although it may seem odd for a bird species to remain undiscovered for science for so long on such a small island, this is by no means an isolated case when it comes to owls. For example, the recently described Rinjani Scops-Owl *O. jolandae* Sangster, King, Verbelen & Trainor, 2013 was found to be a previously undescribed species from Lombok Island, Indonesia (Sangster et al. 2013). Similarly, the Anjouan Scops-Owl *O. capnodes* (Gurney, JH, 1889) was rediscovered in 1992 (Safford 1993), 106 years after its last observation, in an area of primary forest that is smaller and more regularly visited than that of Príncipe, and the Flores Scops-Owl *O. alfredi* (Hartert, E, 1897), rediscovered in 1994, 98 years after the previous report (Widodo et al. 1999).

Novel insights in the phylogenetics of the genus *Otus*

Our phylogenetic analyses confirmed the supported nodes from previous phylogenies (Fuchs et al. 2008; Pons et al. 2013), resolved previously unsupported nodes, and provided novel insights in the affinities of species not previously included.

In relation to African taxa, the most interesting result came from the inclusion of samples from the two subspecies of the only African *Otus* species never sequenced before: the Sandy Scops-Owl *O. icterorhynchus*. Together with *O. ireneae*, this is the only species on the African continent that is a lowland forest specialist (albeit each species occupies very distinct forest types), and the two species were widely hypothesised as being closely related (Marks et al. 1999; König et al. 2008; Holt et al. 2020). Perhaps more surprisingly, *O. icterorhynchus* has been considered to form a superspecies ('yellow-billed scops-owls') with two Asian taxa, the Andaman Scops-Owl *O. balli* (Hume, 1873) and the Sumatran *Otus spilocephalus stresemanni* (Robinson, 1927) (Marshall 1978), although '*stresemanni*' could be an anomalous form of another species and/or a hybrid (Pamela Rasmussen in Holt et al. 2020). Our phylogenetic analyses clarify the affinities of *O. icterorhynchus*, which was found to be sister to the clade containing the Afro-Palearctic and the Indo-Malayan/Indian Ocean clades. Each of its subspecies was available to us by a single individual, but their genetic divergence levels overlap with the levels found between many currently accepted scops-owls sister species pairs.

This study better resolved the branching sequence within the Afro-Palearctic clade, except for the position of *O. pamela* that could not be determined, contra Pons et al. (2013) who recovered it as the sister lineage of this clade. Instead, *O. brucei*, with populations extending from the Arabian Peninsula into Asia, was recovered as the sister lineage of the clade which then branches into African and Eurasian subclades (assuming that *O. pamela* is sister to *O. scops*).

The internodes separating *O. senegalensis* (mainland and Annobón Island), *O. hartlaubi* (São Tomé Island), and *O. pombaensis* (Pemba Island) are very short, indicating that the divergence between these three species (i.e., the colonisation of both islands from their mainland ancestor) occurred almost simultaneously, creating a hard polytomy. Our analyses failed to identify solid lines of evidence for the distinctiveness of *O. senegalensis feae* from *O. senegalensis senegalensis*, although we did identify a diagnostic morphological character (bill length from tip to nares, Suppl. material 12) and three molecular diagnostic characters

at the TGFB2 gene (C vs. T in site 285, T vs. G in site 344, C vs. G in site 392). In a dataset with a wider taxonomic sampling of *O. senegalensis* but fewer sequencing data, the Annobón sample nested within the mainland samples (*unpublished data*). A better sampling of *O. senegalensis senegalensis* from across its range will help to resolve this taxonomic issue.

Our sampling increased considerably the taxon coverage for the centre of the diversity of the *Otus* genus, the Indo-Malayan region (Marks et al. 1999), but has failed to solve most of the many taxonomic pending issues. The Ryukyu Scops-Owl *O. elegans* (Cassin, 1852), a species restricted to small oceanic islands from the northern Philippines to Japan, and included for the first time in a phylogenetic study, was recovered as the fourth Asian representative of the Indo-Malayan/Indian Ocean clade (Fig. 6; sensu Pons et al. 2013), albeit with no statistical support. At this stage, our results mainly highlight the need for using a phylogeographic-level sampling scheme across the region (i.e., multiple samples per site covering all areas of occurrence) to enable a thorough systematic revision of the Indo-Malayan taxa, a crucial step towards reconstructing the diversification history of the genus *Otus*.

Our molecular dataset confirmed the low levels of divergence (well within intraspecific variation) of three taxa pairs that are currently treated either as separate species or subspecies. These pairs are: i) *O. senegalensis senegalensis* (mainland Africa) and *O. s. feae* (Annobón Island), treated as separate species by del Hoyo (2020) and Gill et al. (2021) based on Collar and Boesman (2020); ii) *O. scops* and *O. cyprius*, treated as a distinct species by Gill et al. (2021) and Clements et al. 2021, based on Flint et al. (2015); and iii) the two species from Madagascar, the Malagasy Scops-Owl *O. rutilus* (Pucheran, 1849) and the Torotoroka Scops-Owl *O. madagascariensis* Grandidier, A, 1867, whose specific status was proposed by Rasmussen et al. (2000) and adopted by most authorities (e.g., Clements et al. 2021, del Hoyo 2020, Gill et al. 2021), but contested by Fuchs et al. (2007) using a representative geographic sampling.

Conclusions

The discovery of a new bird species inhabiting the forests of Príncipe Island in 2016 (here formally described as *Otus bikegila*) underscores both the actuality of field-based explorations aiming at describing biodiversity (Dijkstra 2016), and how such curiosity-driven endeavour is more likely to succeed when coupled with local ecological knowledge, the participation of keen amateur naturalists, and persistence.

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Supplementary material I

Timeline

Authors: Martim Melo, Bárbara Freitas, Philippe Verbelen, Sátiro R. da Costa, Hugo Pereira, Jérôme Fuchs, George Sangster, Marco N. Correia, Ricardo F. de Lima, Angelica Crottini

Data type: Text report.

Explanation note: Timeline of the discovery for science of the Principe Scops-Owl *Otus bikegila* sp. nov.

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Link: <https://doi.org/10.3897/zookeys.1126.87635.suppl1>

Supplementary material 2

Alignment

Authors: Martim Melo, Bárbara Freitas, Philippe Verbelen, Sátiro R. da Costa, Hugo Pereira, Jérôme Fuchs, George Sangster, Marco N. Correia, Ricardo F. de Lima, Angelica Crottini

Data type: Docx file.

Explanation note: Concatenated sequences of the phylogenetic dataset.

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Link: <https://doi.org/10.3897/zookeys.1126.87635.suppl2>

Supplementary material 3

Figure S1. Topography Owls

Authors: Martim Melo, Bárbara Freitas, Philippe Verbelen, Sátiro R. da Costa, Hugo Pereira, Jérôme Fuchs, George Sangster, Marco N. Correia, Ricardo F. de Lima, Angelica Crottini

Data type: Image (pdf file).

Explanation note: **Figure S1.** Topography of owls, with the terms used for the description and diagnosis of the Principe Scops-Owl *Otus bikegila* sp. nov. Illustration by MNC.

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Link: <https://doi.org/10.3897/zookeys.1126.87635.suppl3>

Supplementary material 4

Figure S2. Song oscillograms and spectrograms

Authors: Martim Melo, Bárbara Freitas, Philippe Verbelen, Sátiro R. da Costa, Hugo Pereira, Jérôme Fuchs, George Sangster, Marco N. Correia, Ricardo F. de Lima, Angelica Crottini

Data type: Image (pdf file).

Explanation note: **Figure S2.** Oscillograms and spectrograms of 10s sections of the call of *O. bikegila* sp. nov.: (A) primary call of an individual, recorded on January 20, 2019, XC619448; (B) two different individuals duetting, recorded on July 28, 2018, XC619439; (C) cat-like “kee-a-u” call of one individual, recorded on January 15, 2019, XC619443; (D) two different individuals duetting, in which one emits a cat-like “kee-a-u” call, recorded on January 20, 2019, XC619448. Codes from Xeno-canto.org database.

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Link: <https://doi.org/10.3897/zookeys.1126.87635.suppl4>

Supplementary material 5

Figure S3. Bikegila

Authors: Martim Melo, Bárbara Freitas, Philippe Verbelen, Sátiro R. da Costa, Hugo Pereira, Jérôme Fuchs, George Sangster, Marco N. Correia, Ricardo F. de Lima, Angelica Crottini

Data type: Image (pdf file).

Explanation note: **Figure S3.** Photograph taken at Boca do Inferno, Príncipe Island, January 27, 2019, showing the Principe Scops-Owl *Otus bikegila* sp. nov., the two first authors of the paper (BF on the left and MM on the right), and Ceciliano do Bom Jesus, known as ‘Bikegila’ (centre), who started the 20-year saga that led to this discovery, and in honour of whom the new species was named (see ‘Etymology’).

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Link: <https://doi.org/10.3897/zookeys.1126.87635.suppl5>

Supplementary material 6

Table S1. Description

Authors: Martim Melo, Bárbara Freitas, Philippe Verbelen, Sátiro R. da Costa, Hugo Pereira, Jérôme Fuchs, George Sangster, Marco N. Correia, Ricardo F. de Lima, Angelica Crottini

Data type: Morphological.

Explanation note: **Table S1.** Plumage colour and pattern description of *O. bikegila* sp. nov., *O. hartlaubi*, *O. scops scops*, *O. senegalensis senegalensis*, *O. senegalensis feae* and *O. pambaensis*. Colour definition follow the colour standards of Köhler (2012). The analysed characters are depicted in the Suppl. material 3: Fig. S1. Abbreviations of institutional collections: BMNH - The Natural History Museum, Tring, UK; MHNC-UP - Museu de História Natural e da Ciência da Universidade do Porto, Portugal; SMD - Senckenberg Museum Dresden, Germany; SMF - Naturmuseum Senckenberg in Frankfurt am Main, Germany.

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Link: <https://doi.org/10.3897/zookeys.1126.87635.suppl6>

Supplementary material 7

Table S2. Details of song recordings

Authors: Martim Melo, Bárbara Freitas, Philippe Verbelen, Sátiro R. da Costa, Hugo Pereira, Jérôme Fuchs, George Sangster, Marco N. Correia, Ricardo F. de Lima, Angelica Crottini

Data type: Database: song recordings

Explanation note: **Table S2.** Details of the recordings used for bioacoustic analyses. Recording codes - XC: Xeno-canto; IBC: The Internet Bird Collection (now under the Macaulay Library); AV: Avian Vocalizations Center (AVoCet). STP: São Tomé and Príncipe.

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Link: <https://doi.org/10.3897/zookeys.1126.87635.suppl7>

Supplementary material 8

Table S3. Song measurements

Authors: Martim Melo, Bárbara Freitas, Philippe Verbelen, Sátiro R. da Costa, Hugo Pereira, Jérôme Fuchs, George Sangster, Marco N. Correia, Ricardo F. de Lima, Angelica Crottini

Data type: Statistics: Bioacoustics.

Explanation note: **Table S3.** Measures taken for the songs in each recording used for bioacoustic analyses. Bioacoustic parameters - F1: frequency at start; F2: frequency at end; F3: frequency at 25% of total duration; F4: frequency at midpoint; F5: frequency at 75% of total duration; F6: frequency at maximum amplitude; F7: maximum frequency; F8: minimum frequency; DT1: total duration; DT2: time to maximum amplitude; DT3: time to maximum frequency; DT4: internote interval; DF1: frequency drop from start to end; DF2: frequency range; DFT1: slope from 25% to 75% of total duration; DFT2: slope from midpoint to end.

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Link: <https://doi.org/10.3897/zookeys.1126.87635.suppl8>

Supplementary material 9

Localities

Authors: Martim Melo, Bárbara Freitas, Philippe Verbelen, Sátiro R. da Costa, Hugo Pereira, Jérôme Fuchs, George Sangster, Marco N. Correia, Ricardo F. de Lima, Angelica Crottini

Data type: excel file.

Explanation note: Coordinates of tissue sampling localities for *Otus bikegila* sp. nov. and *O. hartlaubi*.

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Link: <https://doi.org/10.3897/zookeys.1126.87635.suppl9>

Supplementary material 10

Table S4. Genomic regions, primers and amplification conditions

Authors: Martim Melo, Bárbara Freitas, Philippe Verbelen, Sátiro R. da Costa, Hugo Pereira, Jérôme Fuchs, George Sangster, Marco N. Correia, Ricardo F. de Lima, Angelica Crottini

Data type: Database: Genomic regions and primers.

Explanation note: **Table S4.** Gene name, primer name, sequence, source, and amplification conditions used in the present study. PCR conditions start with temperature (in °C) of each step followed by the time in seconds. * primers used to amplify internal fragments (used for the amplification of DNA from toe-pad extractions). # custom-made primers used to amplify CYTB and ND2 fragments from *Otus cyprius*, *O. i. icterorhynchus*, *O. silvicola*, *O. spilocephalus vandewateri*, *O. s. vulpes*, *O. s. luciae*, and *O. s. hambroeki*.

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Link: <https://doi.org/10.3897/zookeys.1126.87635.suppl10>

Supplementary material 11

Table S5. PCA factor loadings of morphological variables

Authors: Martim Melo, Bárbara Freitas, Philippe Verbelen, Sátiro R. da Costa, Hugo Pereira, Jérôme Fuchs, George Sangster, Marco N. Correia, Ricardo F. de Lima, Angelica Crottini

Data type: Statistics: Morphological.

Explanation note: **Table S5.** Factor loadings of morphological variables on the first two principal components for seven *Otus* taxa (*O. bikegila* sp. nov., *O. hartlaubi*, *O. senegalensis senegalensis*, *O. senegalensis feae*, *O. pambaensis*, *O. scops*, *O. brucei*). Eigenvalues and percentage of variance explained by the respective components are given at the bottom of the table. Morphological measurements – Bilen: bill length from bill tip to where culmen enters feathers; Binares: bill length from the anterior end of the nares to the tip; Biwid: bill width; Tarlen: tarsus length; Wilen: wing length; Tailen: tail length.

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Link: <https://doi.org/10.3897/zookeys.1126.87635.suppl11>

Supplementary material 12

Table S6. Morphological differentiation

Authors: Martim Melo, Bárbara Freitas, Philippe Verbelen, Sátiro R. da Costa, Hugo Pereira, Jérôme Fuchs, George Sangster, Marco N. Correia, Ricardo F. de Lima, Angelica Crottini

Data type: Statistics: Morphology.

Explanation note: **Table S6.** Results of Welch's ANOVA and Games-Howell post-hoc comparisons performed with the morphometric variables of six *Otus* taxa (*O. bikegila* sp. nov., *O. hartlaubi*, *O. senegalensis senegalensis*, *O. senegalensis feae*, *O. pembraensis*, *O. scops*). Superscript values indicate significance levels (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.005$; **** $P < 0.001$) and NA (Not Available, significance level not possible to obtain due to low sample size). Some individuals had missing data, not allowing for the test performance (indicated by -). Morphological measurements – Bilen: bill length from bill tip to where culmen enters feathers; Biwid: bill width; Bidepth: bill depth at the anterior end of nares; Binares: bill length from the anterior end of the nares to the tip; Hebi: head+bill, from the tip of the bill to the opposite point on the back of the skull; Midt: middle toe length; Tarlen: tarsus length; Wilen: wing length; Tailen: tail length; Bolen: body length; SP: shortfall in relation to tip of longest primary (P1 is the closest to the body), SP10: shortfall of P10; SP9: shortfall of P9; SP5: shortfall of P5; SP4: shortfall of P4.

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Link: <https://doi.org/10.3897/zookeys.1126.87635.suppl12>

Supplementary material 13

Table S7. PCA factor loadings of bioacoustic variables

Authors: Martim Melo, Bárbara Freitas, Philippe Verbelen, Sátiro R. da Costa, Hugo Pereira, Jérôme Fuchs, George Sangster, Marco N. Correia, Ricardo F. de Lima, Angelica Crottini

Data type: Statistics: Bioacoustics.

Explanation note: **Table S7.** Factor loadings of bioacoustic variables on the four principal components in 10 *Otus* taxa (*O. bikegila* sp. nov., *O. hartlaubi*, *O. senegalensis senegalensis*, *O. senegalensis feae*, *O. pembaensis*, *O. pamela*, *O. scops*, *O. cyprius*, *O. brucei*, *O. ireneae*). Eigenvalues and percentage of variance explained by the respective components are given at the bottom of the table. Bioacoustic parameters - F1: frequency at start; F2: frequency at end; F3: frequency at 25% of total duration; F4: frequency at midpoint; F5: frequency at 75% of total duration; F6: frequency at maximum amplitude; F7: maximum frequency; F8: minimum frequency; DT1: total duration; DT2: time to maximum amplitude; DT3: time to maximum frequency; DT4: internote interval; DF1: frequency drop from start to end; DF2: frequency range; DFT1: slope from 25% to 75% of total duration; DFT2: slope from midpoint to end.

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Link: <https://doi.org/10.3897/zookeys.1126.87635.suppl13>

Supplementary material 14

Table S8. Bioacoustics differentiation

Authors: Martim Melo, Bárbara Freitas, Philippe Verbelen, Sátiro R. da Costa, Hugo Pereira, Jérôme Fuchs, George Sangster, Marco N. Correia, Ricardo F. de Lima, Angelica Crottini

Data type: Statistics: Bioacoustics.

Explanation note: **Table S8.** Results of Welch's ANOVA and Games-Howell post-hoc comparisons performed with the bioacoustic variables of 10 *Otus* taxa (*O. bikegila* sp. nov., *O. hartlaubi*, *O. senegalensis senegalensis*, *O. senegalensis feae*, *O. pambaensis*, *O. pamela*, *O. scops*, *O. cyprius*, *O. brucei*, *O. ireneae*). Superscript values indicate significance levels that are indicated with asterisks (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.005$; **** $P < 0.001$) and NA (Not Available, significance level not possible to obtain due to low sample size). Bioacoustic parameters - F1: frequency at start; F2: frequency at end; F3: frequency at 25% of total duration; F4: frequency at midpoint; F5: frequency at 75% of total duration; F6: frequency at maximum amplitude; F7: maximum frequency; F8: minimum frequency; DT1: total duration; DT2: time to maximum amplitude; DT3: time to maximum frequency; DT4: internote interval; DF1: frequency drop from start to end; DF2: frequency range; DFT1: slope from 25% to 75% of total duration; DFT2: slope from midpoint to end.

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Link: <https://doi.org/10.3897/zookeys.1126.87635.suppl14>

Supplementary material 15

Table S9. Phylogeny: sequence partition and evolution models

Authors: Martim Melo, Bárbara Freitas, Philippe Verbelen, Sátiro R. da Costa, Hugo Pereira, Jérôme Fuchs, George Sangster, Marco N. Correia, Ricardo F. de Lima, Angelica Crottini

Data type: Analysis: Partitioning scheme and selected models of evolution.

Explanation note: **Table S9.** Best-fitting partitioning scheme, and respective best model of sequence evolution, inferred with PartitionFinder2 for the dataset used to infer the phylogenetic affinities within the genus *Otus* (Suppl. material 2: Dataset 2: 12,925 bp).

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Link: <https://doi.org/10.3897/zookeys.1126.87635.suppl15>

Supplementary material 16

Table S10. Divergence times: sequence evolution models

Authors: Martim Melo, Bárbara Freitas, Philippe Verbelen, Sátiro R. da Costa, Hugo Pereira, Jérôme Fuchs, George Sangster, Marco N. Correia, Ricardo F. de Lima, Angelica Crottini

Data type: Analysis: Selected models of evolution for divergence times.

Explanation note: **Table S10.** Best models of sequence evolution, inferred with MEGA X, for the markers used in divergence time analyses of the genus *Otus*.

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Rhagophthalmidae Olivier, 1907 (Coleoptera, Elateroidea): described genera and species, current problems, and prospects for the bioluminescent and paedomorphic beetle lineage

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Abstract

Rhagophthalmidae are a small beetle family known from the eastern Palearctic and Oriental realms. Rhagophthalmidae are closely related to railroad worms (Phengodidae) and fireflies (Lampyridae) with which they share highly modified paedomorphic females and the ability to emit light. Currently, Rhagophthalmidae include 66 species classified in the following 12 genera: *Bicladodrilus* Pic, 1921 (two spp.), *Bicladum* Pic, 1921 (two spp.), *Diophtoma* Pascoe, 1860 (two spp.), *Diplocladon* Gorham, 1883 (two spp.), *Dodecatoma* Westwood, 1849 (eight spp.), *Falsophrixothrix* Pic, 1937 (six spp.), *Haplocladon* Gorham, 1883 (two spp.), *Menghuoius* Kawashima, 2000 (three spp.), *Mimoochotyra* Pic, 1937 (one sp.), *Monodrilus* Pic, 1921 (two spp. in two subgenera), *Pseudothilmanus* Pic, 1918 (two spp.), and *Rhagophthalmus* Motschulsky, 1854 (34 spp.). The replacement name *Haplocladon gorhami* Kundrata, **nom. nov.** is proposed for *Diplocladon hasseltii* Gorham, 1883b (described in subgenus *Haplocladon*) which is preoccupied by *Diplocladon hasseltii* Gorham, 1883a. The genus *Reductodrilus* Pic, 1943 is tentatively placed in Lampyridae: Otoretinae. Lectotypes are designated for *Pseudothilmanus alatus* Pic, 1918 and *P. marginalis* Pic, 1918. Interestingly, in the eastern part of their distribution, Rhagophthalmidae have remained within the boundaries of the Sunda Shelf and the Philippines demarcated by the Wallace Line, which separates the Oriental and Australasian realms. This study is intended to be a first step towards a comprehensive revision of the group on both genus and species levels. Additionally, critical problems and prospects for rhagophthalmid research are briefly discussed.

Keywords

Catalogue, classification, Drilidae, Lampyridae, neoteny, Oriental Region, Phengodidae

Introduction

Rhagophthalmidae are a small elateroid family distributed in South, East, and South-east Asia (Wittmer 1979; Kawashima et al. 2010; Kundrata and Bocak 2011a; Kazantsev 2012). Soft-bodied males are capable of flight, whereas all known females are strongly paedomorphic and remain larva-like as adults (Fig. 1). Predaceous larvae occur in soil and leaf litter where they feed on millipedes. Both larvae and adults are bioluminescent, although the biology and ecology of most species are unknown (Li and Liang 2008; Kawashima et al. 2010). Rhagophthalmidae have a convoluted history of classification. Most genera were originally placed either in Lampyridae or the widely defined Drilidae (currently Drilini in Elateridae: Agrypninae; Kundrata and Bocak 2011b). The separate family Rhagophthalmidae was proposed by Olivier (1907, 1910) for genera which had antennae with 12 antennomeres and more or less emarginate eyes. However, since their erection, the composition and classification of Rhagophthalmidae have varied greatly, and various authors have recognized 3–11 genera in the group. At various times, the majority of Rhagophthalmidae have been considered either a subgroup of Lampyridae (e.g., McDermott 1964, 1966) or Phengodidae (Crowson 1972; Lawrence and Newton 1995; Bocak 2007), or a separate family close to one of the two above-mentioned families (Olivier 1910; Winkler 1925; Wittmer and Ohba 1994). Recent phylogenomic approaches suggest Rhagophthalmidae are sister to Phengodidae, and both are closely related to Lampyridae, Sinopyrrophoridae, and Elateridae (Zhang et al. 2018; Douglas et al. 2021; Kusy et al. 2021; Cai et al. 2022).

The early history of Rhagophthalmidae systematic research dates back to 1849, when Westwood (1849) described *Dodecatoma* Westwood, 1849 based on a single species from India. Motschulsky (1854) then described *Rhagophthalmus* Motschulsky, 1854 based on one species from China, and Pascoe (1860, 1862) added *Diophtoma* Pascoe, 1860 and *Ochotyra* Pascoe, 1862 from Bangladesh and India, respectively. While *Dodecatoma* was placed in the widely delimited Drilidae, the remaining genera were classified in Lampyridae (e.g., Gemminger 1869). Gorham (1883a, b) described *Diplocladon* Gorham, 1883 and its subgenus *Haplocladon* Gorham, 1883, both from Indonesia, and placed them in Drilidae.

Several new species of *Rhagophthalmus* from Southeast Asia, India, and China were added by Olivier (1885) and Fairmaire (1889, 1896, 1899). Gorham (1895) described the second species of *Dodecatoma* from India, and classified *Diophtoma*, *Diplocladon*, *Dodecatoma*, *Haplocladon* (originally as a subgenus), and *Ochotyra* in Drilinae. He later described a second species of *Haplocladon*, which was collected in India (Gorham 1903). Olivier (1907) erected the family Rhagophthalmidae for *Diophtoma*, *Ochotyra*, and *Rhagophthalmus*. In 1910, he provided the first catalogues for Rhagophthalmidae and Drilidae (Olivier 1910), with the latter including *Diplocladon* (with *Haplocladon* as a

synonym) and *Dodecatoma*. Jakobson (1911) included many soft-bodied groups, including “Rhagophthalmini”, in his “Cantharididae”. Olivier (1912) revised *Rhagophthalmus* and recognized 12 species, five of which were newly described from China and Sri Lanka. Gahan in Morice (1913) reported a new species of *Diophtoma* from Sri Lanka.

Many new taxa currently belonging to Rhagophthalmidae were then described by the French coleopterist Maurice Pic, a person famous for his usually short and uninformative descriptions (e.g., Villiers 1958; Bezdek and Regalin 2015). Pic described the following taxa from Asia: one new species of *Diophtoma* and four species of *Rhagophthalmus* from India, Sri Lanka, China, and Indochina (Pic 1916, 1917, 1925a, b); genus *Pseudothilmanus* Pic, 1918, with its monotypic subgenus *Drilothilmanus* Pic, 1918 from northern India (Pic 1918); genus *Bicladodrilus* Pic, 1921, with two species from the Philippines and Vietnam (Pic 1921a, 1923); genus *Bicladum* Pic, 1921, with two species from Borneo and Sumatra (Pic 1921b, 1930a); a new variety and a new species of *Dodecatoma* from Indonesia and the Philippines, respectively (Pic 1921b, 1924); a new variety of *Diplocladon* from Indonesia (Pic 1921b); a new genus *Monodrilus* Pic, 1921 from Indonesia (Pic 1921b) and subsequently the monotypic subgenus *Dodecatomorpha* Pic, 1928 from Vietnam (Pic 1928); and a monotypic *Mimoochotyra* Pic, 1937 from Indonesia. Pic (1937) also erected *Falsophrixothrix* Pic, 1937 for two species from Indonesia, one of which was already described by Pic in the genus *Phrixothrix* Olivier, 1909 (currently in Phengodidae; Pic 1914).

Later, Wittmer (1939, 1944) added another three species from Indonesia and Singapore to *Falsophrixothrix*, with one being new and two transferred from *Phrixothrix* (Olivier 1911; Pic 1921a). Wittmer (1944) published a comprehensive catalogue of genera and species in Drilidae in which he listed many genera that are currently in Rhagophthalmidae, i.e., *Bicladodrilus*, *Bicladum* (as *Bicladon* [sic!]), *Diplocladon* (with *Haplocladon* as a synonym), *Dodecatoma*, *Falsophrixothrix*, *Mimoochotyra*, *Monodrilus*, and *Pseudothilmanus*. Pic (1951) described an additional species of *Falsophrixothrix* from Vietnam. In his major works on Lampyridae, McDermott (1964, 1966) included *Diophtoma*, *Mimoochotyra* (as *Mimochotyra* [sic!]), *Ochotyra*, and *Rhagophthalmus* in the subfamily Rhagophthalminae.

Crowson (1972) redefined Drilidae to include only a few core genera. Although Crowson excluded the majority of genera from Drilidae, he did not suggest any family placement for many, which left them in an uncertain position. Crowson (1972) also redefined Phengodidae by including *Cydistus* Bourgeois, 1885 as well as genera which are currently in Rhagophthalmidae, i.e., *Diophtoma*, *Diplocladon*, *Falsophrixothrix*, and *Rhagophthalmus*. Lawrence and Newton (1995) distinguished the subfamily Rhagophthalminae within Phengodidae, and included the genera *Cydistus*, *Diophtoma*, *Diplocladon*, *Dodecatoma*, *Falsophrixothrix*, *Mimoochotyra* (as *Mimochotrya* [sic!]), *Ochotyra* (as *Ochotrya* [sic!]), and *Rhagophthalmus*. Other major works on Rhagophthalmidae were those by Walter Wittmer, who described three new species of *Dodecatoma* from Afghanistan, India, and Nepal (Wittmer 1979, 1995), synonymized *Ochotyra* with *Rhagophthalmus* (Wittmer and Ohba 1994), and described eight new species of *Rhagophthalmus* from China, Japan, and Myanmar (Wittmer and Ohba 1994; Wittmer 1997).

Kawashima (1998) described the morphology of a larviform adult female of *Rhagophthalmus*. He also erected *Menghuoius* Kawashima, 2000 for two Chinese species originally classified in *Rhagophthalmus*, and later described the third species of that genus from Myanmar (Kawashima 2000, 2002). Kawashima and Satô (2001) described three species of *Rhagophthalmus* from Myanmar, Taiwan, and Thailand, and Kawashima and Sugaya (2003) added an additional new species from Taiwan. Branham and Wenzel (2003) studied the evolution of bioluminescence in the soft-bodied elateroids (i.e., “cantharoids”) and confirmed that *Rhagophthalmus* is closely related to *Diophtoma* and *Diplocladon*. Li and Liang (2008) described the morphology of a larviform adult female of *Diplocladon* from China. Li et al. (2008a) described two new species of *Rhagophthalmus* from China, provided information on the morphology and distribution for several other species, and provided a distribution map for all species in China and surrounding regions.

In the Rhagophthalmidae chapter of the Handbook of Zoology, Kawashima et al. (2010) included only *Diophtoma*, *Diplocladon*, *Dodecatoma*, *Menghuoius*, *Mimochotyra* (as *Mimochotyra* [sic!]), and *Rhagophthalmus*. Kundera and Bocak (2011a) revised the long-neglected genus *Pseudothilmanus* (with its subgenus *Drilothilmanus*, which they synonymized with *Pseudothilmanus*), added it to Rhagophthalmidae, and also listed *Bicladodrilus*, *Bicladum* (as *Bicladon* [sic!]), *Diophtoma*, *Diplocladon*, *Dodecatoma*, *Falsophrixothrix*, *Mimochotyra* (as *Mimochotyra* [sic!]), *Monodrilus*, *Reductodrilus*, and *Rhagophthalmus* (including *Menghuoius* and *Ochotyra*). Ho et al. (2012) described two new species of *Rhagophthalmus* from Taiwan. Kazantsev (2012) described two species of *Dodecatoma* from India and Nepal. Most recently, Yiu (2017) described a new species of *Diplocladon* and a new species of *Rhagophthalmus* from Hong Kong. Roza (2020) added information on the morphology and distribution of *Pseudothilmanus*.

Besides research on the diversity, systematics, and morphology of Rhagophthalmidae, many studies in the 21st century have focused on their bioluminescence (Ohmiya et al. 2000; Ohba 2004a; Chen et al. 2010; Oba et al. 2011; Oba 2015; Liu et al. 2020) and embryogenesis (Kobayashi et al. 2001, 2002, 2003). Additionally, the rapid development of molecular phylogenetic methods in the last decades has enabled scientists to test the phylogenetic placement of Rhagophthalmidae within Elateroidea using one or several markers (e.g., Suzuki 1997; Bocakova et al. 2007; Sagegami-Oba et al. 2007; Stanger-Hall et al. 2007; Kundera and Bocak 2011b; Kundera et al. 2014; McKenna et al. 2015), mitogenomes (Li et al. 2007; Amaral et al. 2016; Chen et al. 2019), or a phylogenomic approach (Zhang et al. 2018; Amaral et al. 2019; Douglas et al. 2021; Kusy et al. 2021; Cai et al. 2022).

Despite the long history of rhagophthalmid systematic research, we lack a comprehensive study which would summarize all relevant information of all genera and species in the group. Therefore, in this study, we provide an annotated catalogue of genera and species of Rhagophthalmidae, including information on their synonyms, type material, distribution, and bibliography. We believe this study will serve as a robust framework for subsequent taxonomic revisions of all genera in addition to studies devoted to diversity, evolution, nature conservation, and ecology of the group.

Materials and methods

Names of family-, genus-, and species-group taxa are given with the name of the author, and the year and page of publication. The page given is the page where the taxon name and description are printed. The year and page given for the incorrect subsequent spellings are the first year and page in which they are used. Incorrect subsequent spellings not in prevailing usage are unavailable (ICZN 1999, Art. 33.3). Complete data and comments for genus-group names are presented with the lowest-rank name, i.e., subgenus rather than genus, since these criteria follow the Principle of Coordination (ICZN 1999, Art. 36.1 and 43.1).

We provide the type species for each genus-group name, including information on its designation. We follow Recommendation 73F of the Code (ICZN 1999) and provide lectotype designations to fix the species identity for two species of *Pseudothilmanus* Pic, 1918. These species were originally described based on an unknown number of specimens, then redescribed (Kundrata and Bocak 2011a) under the assumption that the original descriptions were based only on holotypes. We do not provide lectotype designations for species in other genera, as they must first be revised in detail. Under each name, the currently valid name is listed first, followed by synonyms in chronological order.

Misspellings and unavailable names are followed by a colon “:”. We list all relevant references known to us for all genera, as well as for the family Rhagophthalmidae, particularly those that include information on systematics, classification, phylogeny, biology, and ecology. Since PhD or any other student theses are not officially published in the sense of the Code (ICZN 1999), we list only the relevant works (i.e., Ho 2002; Jeng 2008; Roza 2022) at the end of the Literature sections under each genus and species. Dates of publications and exact bibliographic references (especially problematic ones, often not cited uniformly by researchers) are taken from the following comprehensive general works: Chandler (2000); Bouchard et al. (2011); Bousquet (2016); and Evenhuis (2020). For the date of publication of F. P. Pascoe’s description of the genus *Dioptoma* (Pascoe 1860), we follow Evenhuis (2020).

Type depositories

ESRI	Endemic Species Research Institute, JiJi, Nantou, Taiwan
ICM	Insect Center, Moscow, Russia
KNHMZ	Kunming Natural History Museum of Zoology, Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming, China
MNHN	Museum National d’Histoire Naturelle, Paris, France
MSNG	Museo Civico di Storia Naturale, Genova, Italy
MZB	Bogor Zoology Museum, Bogor, Indonesia
NHMB	Naturhistorisches Museum, Basel, Switzerland
NHMUK	Natural History Museum, London, The United Kingdom
NKME	Naturkundemuseum Erfurt, Germany

NMNS	National Museum of Natural Science, Taichung, Taiwan
NTU	Department of Entomology, National Taiwan University, Taipei, Taiwan
NWU	Nagoya Women's University, Nagoya, Japan
PCIK	collection of I. Kawashima, Yokosuka-shi, Kanagawa, Japan
RMNH	Naturalis Biodiversity Center, Leiden, The Netherlands
SMNH	Swedish Museum of Natural History, Stockholm, Sweden
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany
TARI	Taiwan Agricultural Research Institute, Taichung, Taiwan
TLES	Insect Museum, Tai Lung Experimental Station, Hong Kong, China
YCM	Yokosuka City Museum, Yokosuka, Japan
ZMM	Zoological Museum of M.V. Lomonosov State University, Moscow, Russia

Systematics

Rhagophthalmidae Olivier, 1907

Rhagophthalmidae E. Olivier, 1907: 63. Type genus. *Rhagophthalmus* Motschulsky, 1854.

Rhagophthalmidae: Junk 1912: 24 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Phagophthalmidae: Blair in Gahan 1925: vi [unavailable name, incorrect subsequent spelling not in prevailing usage].

Rhagophthalmidae: Harvey 1952: 389 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Rhagophthalmidae: Ohba 1998: 2 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Rhagophthammidae: Suzuki and Kobayashi 2009: 31 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Literature. Olivier (1907: 1, 63): catalogue; Lefroy (1909: 327): catalogue; Olivier (1910: 3): catalogue; Jakobson (1911: 662, 687): catalogue [as Rhagophthalmini]; Junk (1912: 24): bibliography [as Rhagophthalmidae [sic!]]; Olivier (1912: 467): revision of *Rhagophthalmus*; Blair (1915a: 411): bioluminescence; Pic (1923: 25): catalogue; Gahan (1925: vi): remark [as Phagophthalmidae [sic!]; attributed to KG Blair]; Handlirsch (1925: 589): catalogue [as Rhagophthalmini]; Winkler (1925: 522): catalogue; Ridley (1934: 58): larval biology and morphology; Pic (1937: 137): genus description; Harvey (1952: 389, 450): remark, bioluminescence [also as Rhagophthalmidae [sic!], also as Rhagophthalminae [sic!]]; Brues et al. (1954: 565): classification; Crowson (1955: 68): remark, morphology [as Rhagophthalminae]; Harvey (1955: 19): checklist, bioluminescence; Raj (1957: 788): larval biology; McDermott (1964: 49): revision [as Rhagophthalminae]; McDermott (1966: preface (unnumbered), 121): catalogue, distribution [as Rhagophthalminae]; Mikšić and Mikšić (1966: 31): remark [as Rhagophthalminae];

Nakane (1968: 3): remark [as Rhagophthalminae]; Crowson (1972: 50): classification, morphology [as Rhagophthalminae]; McElroy et al. (1974: 415): remark [as Rhagophthalmidae [sic!]]; Lawrence (1982: 512): remark; Haneda (1985: 167): bioluminescence [as Rhagophthalmidae [sic!]]; Herring (1987: 158): checklist [as Rhagophthalminae]; LeSage (1991: 424): remark [also as Rhagophthalminae]; Wittmer and Ohba (1994: 341): taxonomy, biology; Lawrence and Newton (1995: 857): catalogue, review [as Rhagophthalminae]; Chen and Ho (1996: 46): distribution; Ohba et al. (1996a: 1): morphology, biology; Ohba (1997a: 5): checklist; Ohba (1997c: 51): breeding; Suzuki (1997: 11, 38): phylogeny, biology [also as Rhagophthalminae]; Wittmer (1997: 257): species descriptions; Chen and Ho (1998: 34): bioluminescence; Ohba (1998: 2): biology [also as Rhagophthalmidae [sic!]]; Costa et al. (1999: 22): remark [as Rhagophthalminae]; Goto and Kawashima (2000: 141): distribution; Jeng et al. (2000: 316): remark; Kawashima (2000: 131): genus description; Kim et al. (2000: 214): molecular phylogeny; Ohmiya et al. (2000: 32): luciferase; Branham and Wenzel (2001: 565): phylogeny [also as Rhagophthalminae and Rhagophthalmidae [sic!]]; Kawashima and Satô (2001: 423): species descriptions; Kobayashi et al. (2001: 1): embryogenesis, morphology [also as Rhagophthalminae]; Hua (2002: 71): catalogue; Kawashima (2002: 487): species description; Kobayashi et al. (2002: 1): embryogenesis, morphology [also as Rhagophthalminae]; Branham and Wenzel (2003: 3): phylogeny; Chen (2003: 52): morphology, bioluminescence; Hayashi and Suzuki (2003: 4): biology, morphology, phylogeny, figure of mating; Kawashima and Sugaya (2003: 353): species description; Kawashima et al. (2003: 255): catalogue; Kobayashi et al. (2003: 19): embryogenesis, morphology; DeCock (2004: 341): bioluminescence; Ohba (2004a: 225): bioluminescence, biology; Lau and Meyer-Rochow (2006: 19): eye morphology; Li et al. (2006: 817): molecular phylogeny; Arnoldi et al. (2007: 2): molecular phylogeny, remark; Bocak (2007: 224): catalogue [as Rhagophthalminae]; Bocakova et al. (2007: 477): molecular phylogeny [also as Rhagophthalminae]; Hunt et al. (2007: 1915): molecular phylogeny; Li et al. (2007: 197): mitochondrial genome, phylogeny [also as Rhagophthalminae]; Sagegami-Oba et al. (2007: 110): molecular phylogeny [also as Rhagophthalminae]; Stanger-Hall et al. (2007: 38): molecular phylogeny; Bocak et al. (2008: 2021): molecular phylogeny; Li and Liang (2008: 109): female morphology; Li et al. (2008a: 259): species descriptions, distribution [also as Rhagophthalminae]; Li et al. (2008b: 494): review [also as Rhagophthalminae]; Bogahawatta et al. (2009: 5): distributional remark [as Rhagophthalminae]; Levkanicova and Bocak (2009: 212): molecular phylogeny; Suzuki and Kobayashi (2009: 30): embryogenesis [also as Rhagophthalminae and Rhagophthamidae [sic!]]; Chen et al. (2010: 196): biology, bioluminescence; Kawashima et al. (2010: 135): book chapter [also as Rhagophthalminae]; Lawrence et al. (2010a: 5): classification; Lawrence et al. (2010b: 165): remark; Bouchard et al. (2011: 326): family-group names catalogue; Kundrata and Bocak (2011a: 57): revision of *Pseudothilmanus*; Kundrata and Bocak (2011b: 364): molecular phylogeny [also as Rhagophthalminae]; Lawrence et al. (2011: 7): phylogeny; Oba et al. (2011: 775): biology, bioluminescence [also as Rhagophthalminae]; Yiu (2011a: 14): remark; Yiu (2011b: 20): bioluminescence, larva; Amaral et al. (2012: 1262): luciferase, phylogeny

[as Rhagophthalmidae]; Ho et al. (2012: 1): species descriptions; Johnson et al. (2012: 178): ICZN case; Kazantsev (2012: 349): species descriptions; Timmermans and Vogler (2012: 299): remark, molecular phylogeny; Kundrata et al. (2013: 201): molecular phylogeny; Yiu (2013: 101): remark, bioluminescence; Amaral et al. (2014: 415): molecular phylogeny; Bocak et al. (2014: 103): molecular phylogeny; Hosoe et al. (2014: 331): biology; ICZN (2014: 195): ICZN case; Kundrata et al. (2014: 163): molecular phylogeny; Li et al. (2015: 269): catalogue; Martin et al. (2015: 516): molecular phylogeny; McKenna et al. (2015: 843): molecular phylogeny [also as Rhagophthalmidae [sic!]]; Oba (2015: 99): bioluminescence; Amaral et al. (2016: 255): molecular phylogeny; Bocak et al. (2016: 2): molecular phylogeny; Kundrata et al. (2016: 293): molecular phylogeny; Lawrence (2016: 17): classification; Wijekoon et al. (2016: 69): checklist [also as Rhagophthalmidae]; Amaral et al. (2017a: 674): mitogenome, phylogeny; Kundrata et al. (2017: 153): molecular phylogeny; Martin et al. (2017: 564): phylogeny; Wang et al. (2017: 1): phylogeny; Yiu (2017: 60): species descriptions, key; Bocak et al. (2018: 2): molecular phylogeny; Fallon et al. (2018: 2, 96): genomes, bioluminescence; Kusy et al. (2018a: 5): molecular phylogeny; Kusy et al. (2018b: 2): molecular phylogeny; Tan (2018: 127, 135): distribution, photographs; Zhang et al. (2018: 3): molecular phylogeny; Amaral et al. (2019: 283): molecular phylogeny [also as Rhagophthalmidae [sic!]]; Chen et al. (2019: 4): molecular phylogeny; Jeng (2019: 8): biofluorescence, biology; Kundrata et al. (2019: 1259): molecular phylogeny; Martin et al. (2019: 2): molecular phylogeny [also as Rhagophthalmidae]; McKenna et al. (2019: 4): molecular phylogeny; Liu et al. (2020: 46): luciferase, phylogeny [also as Rhagophthalmidae]; Rosa et al. (2020: 7): molecular phylogeny; Roza (2020: 421): morphology, distribution; Zhang et al. (2020: 1): molecular phylogeny, bioluminescence; Douglas et al. (2021: 2): molecular phylogeny; Ge et al. (2021: 3): mitogenomic phylogeny; Kusy et al. (2021: 111): molecular phylogeny; Li et al. (2021a: 5): remark; Li et al. (2021b: 1): phylogeny, distribution, morphology; Seri and Rahman (2021: 715): remark; Cai et al. (2022: 6): molecular phylogeny; Ge et al. (2022: 2): mitogenomic phylogeny; Powell et al. (2022: 1): molecular phylogeny, bioluminescence [also as Rhagophthalmidae [sic!]]. In addition to the aforementioned literature, Rhagophthalmidae were mentioned in some student works, e.g., PhD theses by Ho (2002), Jeng (2008), and Roza (2022).

Remarks. As defined here, Rhagophthalmidae include 12 genera (one of them with two subgenera) and 66 species distributed primarily in East, South, and Southeast Asia, with a few species found on the border of South and Central Asia (i.e., Afghanistan). Males can be recognized by antennae with 12 antennomeres, with antennomere III longer than antennomere II. In cases where the antennae are serrate or pectinate, antennomere III is not simple, i.e., the serration or rami begin on antennomere III. Females are more (e.g., *Diplocladon* or *Haplocladon*; see Remarks under these genera) or less (e.g., *Rhagophthalmus*) larviform (for more information, see Kawashima et al. 2010). Known larvae are predators of millipedes, similar to larvae of the closely related Phengodidae. Although Rhagophthalmidae were credited by McDermott (1966) to “Olivier, 1902”, we found no evidence of the publication to which McDermott referred, similar to Lawrence and Newton (1995: 858).

Genus *Bicladodrilus* Pic, 1921

Bicladodrilus Pic, 1921a: 15. Gender: masculine. Type species. *Bicladodrilus bakeri* Pic, 1921; by monotypy.

Bieladodrilus: Pic 1923: 62 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Bicalodrilus: Pic 1930b: 320 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Literature. Pic (1921a: 15): original description; Pic (1923: 62): species description [as *Bieladodrilus* [sic!]]; Pic (1930b: 320): remark [as *Bicalodrilus* [sic!]], key; Wittmer (1941: 197): catalogue, distribution; Wittmer (1944: 211): catalogue; Bocakova et al. (2007: 484): molecular phylogeny; Hunt et al. (2007: suppl.): molecular phylogeny; Bocak et al. (2008: 2019): molecular phylogeny; Levkanicova and Bocak (2009: 214): molecular phylogeny; Costa and Zaragoza-Caballero (2010: 134): remark; Kawashima et al. (2010: 139): book chapter; Kundrata and Bocak (2011a: 57): remark; Kundrata and Bocak (2011b: 370): molecular phylogeny; Kundrata et al. (2013: 202): molecular phylogeny; Kundrata et al. (2014: 167): molecular phylogeny; Bocak et al. (2016: suppl.): molecular phylogeny; Kovalev and Kirejtshuk (2016: 205): remark; Kundrata et al. (2016: 296): molecular phylogeny; Bocak et al. (2018: 4): molecular phylogeny; Kundrata et al. (2019: 1263): molecular phylogeny; Liu et al. (2020: 46): remark. In addition to the aforementioned literature, this genus was included in PhD theses by Jeng (2008) and Roza (2022).

Remarks. This genus currently contains two described species from the Philippines and Vietnam, respectively. The generic assignment of a specimen reported as “*Bicladodrilus* sp.” from China, which was used in the molecular phylogenetic analyses by Bocakova et al. (2007), Bocak et al. (2008, 2018), Levkanicova and Bocak (2009), and other studies, needs a careful re-examination. *Bicladodrilus* is similar to *Bicladum* and *Diplocladon* in having strongly bipectinate antennae and long elytra. This generic complex is in need of revision.

***Bicladodrilus bakeri* Pic, 1921**

Bicladodrilus bakeri Pic, 1921a: 15.

Type depository. Described based on an unknown number of specimens. Syntype, male (MNHN).

Type locality. Philippines: Mindanao.

Distribution. Philippines.

Literature. Pic (1921b: 15): original description; Pic (1923: 63): comparison with *B. laticollis* Pic, 1923; Wittmer (1941: 197): catalogue, distribution; Wittmer (1944: 211): catalogue.

***Bicladodrilus laticollis* Pic, 1923**

Bicladodrilus [sic!] *laticollis* Pic, 1923: 62.

Type depository. Described based on an unknown number of specimens. Syntype, male (MNHN).

Type locality. Vietnam: Lào Cai [Tonkin: Lao-Kay].

Distribution. Vietnam.

Literature. Pic (1923: 62): original description; Wittmer (1944: 211): catalogue.

Genus *Bicladum* Pic, 1921

Bicladum Pic, 1921b: 12. Gender: neuter. Type species. *Bicladum multipunctatum* Pic, 1921; by monotypy.

Bicladon: Pic 1930a: 2 [unavailable name, incorrect subsequent spelling].

Literature. Pic (1921b: 12): original description; Pic (1921a: 15): comparison with *Bicladodrilus*; Pic (1930a: 2): species description [as *Bicladon* [sic!]]; Pic (1930b: 320, 321): remark, key [as *Bicladon* [sic!]]; Wittmer (1944: 211): catalogue [as *Bicladon* [sic!]]; Lawrence et al. (2010b: 175): remark [as *Bicladon* [sic!]]; Kundrata and Bocak (2011a: 57): remark [as *Bicladon* [sic!]]; Janisova and Bocakova (2013: 3): remark [as *Bicladon* [sic!]]; Kovalev and Kirejtshuk (2016: 205): remark [as *Bicladon* [sic!]]. In addition to the aforementioned literature, this genus was included in a PhD thesis by Jeng (2008).

Remarks. This genus currently contains two described species from Borneo and Sumatra, respectively. It is similar to *Bicladodrilus* and *Diplocladon* in having strongly bipectinate antennae and long elytra. This generic complex is in need of revision.

***Bicladum mjobergi* Pic, 1930**

Bicladon [sic!] *mjöbergi* [sic!] Pic, 1930a: 2, 4.

Type depositories. Described based on an unknown number of specimens. One syntype, male (MNHN), two syntypes, males (labelled as “Typus” and “Paratypus”) (SMNH).

Type locality. Indonesia: Sumatra, Medan.

Distribution. Indonesia (Sumatra).

Literature. Pic (1930a: 2, 4): original description; Wittmer (1944: 211): catalogue [as *Bicladon* [sic!]].

Remarks. Pic (1930a: 5) also reported an unnamed variety of *B. mjobergi* based on a specimen from Tjinta Radja. This specimen is deposited in SMNH and bears the label “Typus”; however, based on Article 72.4.1. of the Code (ICZN 1999) it should not be considered a part of the type series.

***Bicladum multipunctatum* Pic, 1921**

Bicladum multipunctatum Pic, 1921b: 12.

Type depository. Described based on an unknown number of specimens. Syntype, male (MNHN).

Type locality. Borneo (without any further data).

Distribution. Borneo (probably northern region).

Literature. Pic (1921b: 12): original description; Pic (1930a: 5): comparison with *B. mjobergi*; Wittmer (1944: 211): catalogue [as *Bicladon* [sic!]].

Genus *Diophtoma* Pascoe, 1860

Fig. 1A, B

Diophtoma Pascoe, 1860: 118. Gender: feminine. Type species. *Diophtoma adamsii* Pascoe, 1860; by monotypy.

Diaphtoma: Wijekoon et al. 2016: 70 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Literature. Pascoe (1860: 118): original description, drawings of male habitus, head, and antenna; Pascoe (1862: 323): comparison with *Ochotyra*; Gerstaecker (1863: 409): remark; Gemminger (1869: 1647): catalogue; Gorham (1880: 66): remark; Gorham (1881: 63): remark; Olivier (1885: 372): remark; Gorham (1890: 550): catalogue; Gorham (1895: 309): redescription; Sharp (1899: 251): remark; Gorham (1903: 330): distributional note; Olivier (1907: 63): catalogue; Gahan (1908a: xlviii): remark; Gahan (1908b: 205): remark; Olivier (1910: 1): catalogue; Olivier (1912: 467): remark; Morice (1913: cxviii): introduction of a new species attributed to Gahan; Green (1913: 718): male and female morphology, bioluminescence, drawing of male habitus; McDermott (1914: 304): remark; Blair (1915a: 413): bioluminescence; Blair (1915b: 191): bioluminescence; Blair (1915c: 37): bioluminescence, morphology; Gravely (1915: 502): remark; Bugnion (1916: 83): remark; Pic (1916: 8): species description; Lucas (1920: 241): catalogue; Bugnion (1929: 4): remark; Brues (1941: 41): remark; Harvey (1952: 392): remark; Harvey (1955: 19): checklist, bioluminescence; Bess (1956: 25): remark; McDermott (1964: 50): revision; McDermott (1966: 122): catalogue; Mikšić and Mikšić (1966: 32): remark; Lloyd (1971: 101): remark, drawing of male habitus with distribution of luminous organs; Crowson (1972: 52): remark; Paulus (1975: 78): remark; Herring (1978: 471): checklist; Lloyd (1978: 252): remark, drawing of male habitus with distribution of luminous organs; Lloyd (1979: 302): remark; Ohba (1980: 14): remark; Crowson (1981: 314): remark, drawing of male habitus with distribution of luminous organs; Sivinski (1981: 168): remark; Lloyd (1983: 136): remark, bioluminescence; Hoffmann (1984: 230): remark; Herring (1987: 158): checklist; Cicero (1988: 148): remark; Viviani and Bechara (1993: 615): remark; Wittmer and

Ohba (1994: 342): remark; Lawrence and Newton (1995: 857): catalogue, remark; Branham (1996: 18): remark; Ohba et al. (1996a: 17): remark; Viviani and Bechara (1997: 389): remark; Sivinski et al. (1998: 29): remark; Kawashima (2000: 131): remark; Branham and Wenzel (2001: 566): phylogeny; O’Keefe (2002: 182): remark; Branham and Wenzel (2003: 5): phylogeny; Li et al. (2008a: 259): remark; Li et al. (2008b: 495): review; Li and Liang (2008: 111): remark; Bogahawatta et al. (2009: 1): remark; Suzuki and Kobayashi (2009: 30): remark; Chen et al. (2010: 196): remark; Kawashima et al. (2010: 135): book chapter; Kandrata and Bocak (2011a: 57): remark; Oba et al. (2011: 777): remark; Wijekoon et al. (2016: 70): checklist [as *Diaptoma* [sic!]]; Liu et al. (2020: 46): remark. In addition to the aforementioned literature, this genus was included in PhD theses by Jeng (2008) and Roza (2022).

Remarks. This genus currently contains two described species from Bangladesh, India, and Sri Lanka. Males are characterized by short antennae and deeply emarginate eyes, each with a smaller upper portion and a larger lower portion (Fig. 1B). Regarding the gender of *Diaptoma*, Pascoe (1860) treated it as feminine and since the name is not a Greek noun, here we follow Pascoe’s decision.

***Diaptoma adamsii* Pascoe, 1860**

Fig. 1A, B

Diaptoma adamsii Pascoe, 1860: 118.

Diaptoma adamsi: Gemminger 1869: 1647 [unavailable name, incorrect subsequent spelling].

Diaptoma greeni Gahan in Morice 1913: cxviii. Synonymized with *D. adamsii* (as a variety) by McDermott (1966: 122). McDermott (1966) attributed the name *D. greeni* to Gahan (1908a: xlviii); however, there is no such name in that publication, and we believe that this name first appeared in 1913.

Diaptoma adamsi: Bogahawatta et al. 2009: 1 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Type depository. Holotype of *D. adamsii*, male (NHMUK). 25 syntypes of *D. greeni* (eight males from Maskeliya, eight males and four females from Dikoya, four males and one female from Bogawantalawa; Fig. 1A) (NHMUK).

Type locality of *D. adamsii*. Bangladesh: Dhaka [“India: Dacca”]. Type localities of *D. greeni*. Sri Lanka: Bogawantalawa, Dikoya, and Maskeliya.

Distribution. Bangladesh, India (Karnataka, Kerala, Tamil Nadu, Uttarakhand), Sri Lanka.

Literature. Pascoe (1860: 118): original description, drawings of male habitus, head, and antenna; Gemminger (1869: 1647): catalogue [as *D. adamsi* [sic!]]; Gorham (1880: 66): remark [as *D. adamsi* [sic!]]; Olivier (1885: 372): remark [as *D. adamsi* [sic!]]; Gorham (1890: 550): catalogue [as *D. adamsi* [sic!]]; Gorham (1895: 310): redescription, distributional note [as *D. adamsi* [sic!]]; Sharp (1899: 251): remark [as



Figure 1. Morphology of Rhagophthalmidae **A** habitus of *Diophtoma adamsii* from Sri Lanka (syntype of *D. greeni*), female, NHMUK, dorsal view **B** head of *Diophtoma adamsii* from Sri Lanka, male, NHMUK, frontal view **C** head and pronotum of *Diplocladon hasseltii hasseltii* from Indonesia, male, SDEI, dorsal view **D** habitus of *Falsophrixothrix* sp. from Indonesia, male, NHMUK, dorsal view **E** head and pronotum of *Rhagophthalmus* sp. from China, male, first author's collection, lateral view **F** habitus of *Rhagophthalmus* sp. from China, male, first author's collection, dorsal view. Scale bars: 5.0 mm (**A, F**); 1.0 mm (**B, E**); 2.0 mm (**C, D**).

D. adamsi [sic!]; Gorham (1903: 330): distributional note [as *D. adamsi* [sic!]]; Olivier (1910: 1): catalogue [as *D. adamsi* [sic!]]; Morice (1913: cxviii): original description of *D. greeni* (attributed to Gahan), remarks on *D. adamsi* [sic!]; Green (1913: 718): male and female morphology, bioluminescence, drawing of male habitus [as *D. adamsi* [sic!]]; McDermott (1914: 304): remark; Blair (1915a: 413): bioluminescence [as *D. adamsi* [sic!]]; Blair (1915b: 191): bioluminescence [as *D. adamsi* [sic!]]; Blair (1915c: 37): bioluminescence, morphology [as *D. adamsi* [sic!]]; Gravely (1915: 502): remark [as *D. adamsi* [sic!]]; Bugnion (1916: 96): remark [as *D. adamsi* [sic!]]; Pic (1916: 8): comparison with *D. atripennis* Pic, 1916 [as *D. adamsi* [sic!]]; Lucas (1920: 241): catalogue [as *D. adamsi* [sic!]]; Brues (1941: 41): remark [as *D. adamsi* [sic!]]; Harvey (1952: 450): remark, bioluminescence [as *D. adamsi* [sic!]]; McDermott (1964: 50): redescription [as *D. adamsi* [sic!]]; McDermott (1966: 122): catalogue, synonymization of *D. greeni* with *D. adamsi* [sic!]; Lloyd (1971: 101): remark, drawing of male habitus with distribution of luminous organs [as *D. adamsi* [sic!]]; Lloyd (1978: 252): remark, drawing of male habitus with distribution of luminous organs [as *D. adamsi* [sic!]]; Lloyd (1979: 302): remark [as *D. adamsi* [sic!]]; Crowson (1981: 314): remark, drawing of male habitus with distribution of luminous organs [as *D. adamsi* [sic!]]; Sivinski (1981: 168): remark [as *D. adamsi* [sic!]]; Lloyd (1983: 136): remark, bioluminescence [as *D. adamsi* [sic!]]; Hoffmann (1984: 230): remark [as *D. adamsi* [sic!]]; Branham (1996: 18): remark [as *D. adamsi* [sic!]]; Ohba et al. (1996a: 17): remark; Sivinski et al. (1998: 29): remark [as *D. adamsi* [sic!]]; Kawashima (2000:

131): remark; Branham and Wenzel (2001: 567): phylogeny [as *D. adamsi* [sic!]]; Branham and Wenzel (2003: 5): phylogeny [as *D. adamsi* [sic!]]; Li et al. (2008b: 496): review [also as *D. adamsi* [sic!]]; Bogahawatta et al. (2009: 1): remark [both *D. adamsi* [sic!] and *D. greeni*]; Kawashima et al. (2010: 135): book chapter [as *D. adamsi* [sic!]]; Wijekoon et al. (2016: 70): catalogue [both *Diaptoma adamsi* [sic!] and *D. greeni*]. In addition to the aforementioned literature, this species was included in PhD theses by Jeng (2008) and Roza (2022).

Remarks. This species was referred to as “*adamsi*” in the majority of publications. The original spelling “*adamsii*” was used only by McDermott (1914), Ohba et al. (1996a), and Kawashima (2000). However, following Article 33.4. of the Code (ICZN 1999), the original spelling should be maintained. It should be noted that the current concept of *D. adamsii* may include several species.

***Diaptoma atripennis* Pic, 1916**

Diaptoma atripennis Pic, 1916: 8.

Type depository. Described based on an unknown number of specimens. Two syntypes, males (MNHN).

Type locality. India: Tamil Nadu, Madurai [Madura].

Distribution. India (Tamil Nadu).

Literature. Pic (1916: 8): original description; McDermott (1966: 122): catalogue; Li et al. (2008b: 496): review.

Genus *Diplocladon* Gorham, 1883

Fig. 1C

Diplocladon Gorham, 1883a: 5. Gender: neuter. Type species. *Diplocladon hasseltii* Gorham, 1883, by monotypy.

Diplocadum: Pic 1921b: 12 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Diplocladum: Pic 1928: 86 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Diplocadon: Viviani and Bechara 1993: 615 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Diploclocladon: Tan 2018: 135 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Literature. Gorham (1883a: 5): original description; Gorham (1883b: 249, 250): comparison with *Haplocladon*; Gorham (1883c: 597): remark; Gorham (1887: 76): catalogue, redescription; Waterhouse (1890: 25): remark, figure of male habitus;

Gorham (1895: 310): remark; Olivier (1910: 8): catalogue; Lucas (1920: 243): catalogue; Rüschkamp (1920: 386): distributional note; Pic (1921b: 12): comparison with *Bicladum* and *Monodrilus* [as *Diplocadum* [sic!]]; Pic (1928: 86): remark [as *Diplocadum* [sic!]]; Pic (1930a: 2): distributional note [as *Diplocadum* [sic!]]; Pic (1930b: 320): remark, key; Ridley (1934: 60): larval biology and morphology; Wittmer (1944: 211): catalogue; Haneda (1950: 2): bioluminescence; Harvey (1952: 451): bioluminescence, drawings of female habitus with position of luminous organs, photographs of male and female habitus; Crowson (1955: 68, 171): remark; Haneda (1955: 364): remark, bioluminescence; Harvey (1955: 19): checklist, bioluminescence; Harvey (1957: 554): remark; McDermott (1964: 50): remark; Nakane (1968: 3): remark; Lloyd (1971: 101): remark, drawing of female habitus with luminous organs; Crowson (1972: 52): remark; Paulus (1972: 49): remark; Halverson et al. (1973: 1332): biology, bioluminescence; McElroy et al. (1974: 417): remark; Paulus (1975: 78): remark; Case and Strause (1978: 332): remark; Herring (1978: 471): checklist; Lloyd (1978: 252): remark, drawing of female habitus with distribution of luminous organs; Ohba (1980: 14): remark; Crowson (1981: 314): remark, drawing of female habitus with distribution of luminous organs; Sivinski (1981: 168): remark; Lloyd (1983: 136): remark, bioluminescence; Hoffmann (1984: 229): remark; Haneda (1985: 167): bioluminescence; Herring (1987: 157): checklist; Cicero (1988: 148): remark; De Keyser (1989: 54): remark; Viviani and Bechara (1993: 615): remark [as *Diplocadon* [sic!]]; Wittmer and Ohba (1994: 350): remark; Lawrence and Newton (1995: 857): catalogue, remark; Branham (1996: 18): remark; Ohba et al. (1996a: 13): remark; Ohba et al. (1996b: 30): remark; Ohba (1997a: 17): remark; Viviani and Bechara (1997: 389): remark [as *Diplocadon* [sic!]]; Branham and Wenzel (2001: 566): phylogeny; O'Keefe (2002: 182): remark; Branham and Wenzel (2003: 3): remark; Li and Liang (2008: 109): remark, female description; Li et al. (2008b: 495): review; Suzuki and Kobayashi (2009: 31): remark; Kawashima et al. (2010: 135): book chapter, figures of male and female habitus, and details of female abdominal segments; Kundrata and Bocak (2011a: 57): remark; Oba et al. (2011: 777): remark; Yiu (2012: 30): catalogue, figures of habitus; Yiu (2013: 113): remark, biology; Kovalev and Kirejtshuk (2016: 205): remark; Yiu (2017: 64): description of a new species, identification key; Tan (2018: 135): possible larva, distribution, figures of larval habitus and bioluminescence [also as *Diplocadon*]; Liu et al. (2020: 46): remark; Lawrence et al. (2021: 456): wing morphology; Li et al. (2021b: 4): remark; Seri and Rahman (2021: 721): remark. In addition to the aforementioned literature, this genus was included in PhD theses by Jeng (2008) and Roza (2022).

Remarks. See more information on *Haplocladon*, which was once considered a subgenus of *Diplocadon* (Gorham 1883b) or even its synonym (e.g., Wittmer 1944), under the genus name *Haplocladon* below. Some authors who mentioned *Diplocadon* were actually probably referring to *Haplocladon* (for more details, see Remarks under *D. hasseltii*). *Diplocadon* currently contains two described species, one from China and one from Indonesia. It is similar to *Bicladodrilus* and *Bicladum* in having strongly bipectinate antennae (Fig. 1C) and long elytra. This generic complex is in need of revision.

***Diplocladon atripenne* Yiu, 2017**

Diplocladon atripennis [sic!] Yiu, 2017: 64.

Type depository. Holotype, male (TLES). Paratype, male (TLES).

Type locality. China: Hong Kong, Lantau, Wo Tin (22.27351°N, 113.98819°E).

Distribution. China (Hong Kong).

Literature. Yiu (2017: 64): original description, figures of male habitus, pregenital segments and genitalia.

***Diplocladon hasseltii hasseltii* Gorham, 1883**

Fig. 1C

Diplocladon hasseltii Gorham, 1883a: 6.

Diplocladon hasselti: Olivier 1910: 8 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Type depository. Described based on two specimens (Gorham 1887). One syntype, male (RMNH); one syntype, male (MNHN).

Type locality. Indonesia: Sumatra, Boenga mas (Palembang).

Distribution. Indonesia (Sumatra, Java).

Literature. Gorham (1883a: 6): original description; Gorham (1887: 76): catalogue, redescription; Waterhouse (1890: 25): remark, figure of male habitus; Olivier (1910: 8): catalogue [as *D. hasselti* [sic!]]; Lucas (1920: 243): catalogue [as *D. hasselti* [sic!]]; Ridley (1934: 60): larval biology and morphology [as *D. hasselti* [sic!]]; Wittmer (1944: 211): catalogue [as *D. hasselti* [sic!]]; Haneda (1950: 2): bioluminescence, drawings of adult male and female, and position of luminous organs; Harvey (1952: 451): bioluminescence, drawings of female habitus with position of luminous organs, photographs of male and female habitus; Haneda (1955: 364): remark, bioluminescence; Lloyd (1971: 101): remark, drawing of female habitus with luminous organs [as *D. hasselti* [sic!]]; Lloyd (1978: 252): remark, drawing of female habitus with distribution of luminous organs [as *D. hasselti* [sic!]]; Crowson (1981: 314): remark, drawing of female habitus with distribution of luminous organs [as *D. hasselti* [sic!]]; Sivinski (1981: 168): remark [as *D. hasselti* [sic!]]; Lloyd (1983: 136): remark, bioluminescence [as *D. hasselti* [sic!]]; Hoffmann (1984: 229): remark [as *D. hasselti* [sic!]]; Haneda (1985: 167): bioluminescence, drawings of adult male and female, and position of luminous organs [as *D. hasselti* [sic!]]; De Keyzer (1989: 54): remark [as *D. hasselti* [sic!]]; Wittmer and Ohba (1994: 350): remark [as *D. hasselti* [sic!]]; Branham (1996: 18): remark [as *D. hasselti* [sic!]]; Ohba et al. (1996a: 13): remark; Ohba et al. (1996b: 30): remark; Ohba (1997a: 17): remark; Li and Liang (2008: 109): remark; Kawashima et al. (2010: 135): book chapter, figures of male and female habitus, and details of female abdominal segments [as *D. hasselti* [sic!]]; Yiu (2017: 64): comparison with *D. atripennis*; Lawrence et al. (2021: 456): wing morphology, figure

of hind wing [as *D. hasselti* [sic!]]. In addition to the aforementioned literature, this species was included in PhD theses by Jeng (2008) and Roza (2022).

Remarks. Based on the available figures, adults of both sexes which were reported by Haneda (1950) from Singapore, and repeatedly mentioned in subsequent studies (e.g., Harvey 1952; Haneda 1955, 1985; Lloyd 1971, 1978; Crowson 1981; Kawashima et al. 2010), are probably members of *Haplocladon*. We are aware of several *Haplocladon* specimens from Singapore (deposited in NHMUK) but no *Diplocladon* are known from that area.

***Diplocladon hasseltii testaceum* Pic, 1921**

Diplocadum [sic!] *hasselti* [sic!] var. *testaceum* Pic, 1921b: 12.

Diplocladum [sic!] *hasselti* [sic!] var. *testaceus* [sic!]: Pic 1930a: 2.

Type depository. Described based on an unknown number of specimens. No type specimen found in MNHN by RK.

Type locality. Indonesia: Sumatra.

Distribution. Indonesia (Sumatra).

Literature. Pic (1921a: 12): original description [as a variety of *Diplocadum* [sic!] *hasselti* [sic!]]; Pic (1930b: 2): distributional note; Wittmer (1944: 211): catalogue.

Remarks. The name “*testaceum*” is deemed to be subspecific according to Article 45.6.4. of the Code (ICZN 1999).

Genus *Dodecatoma* Westwood, 1849

Dodecatoma Westwood, 1849: 1. Gender: feminine. Type species. *Dodecatoma bicolor* Westwood, 1849, by monotypy.

Dodecatomax: Crowson 1955: 171 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Literature. Westwood (1849: 1): original description, drawings of male habitus, head, mouthparts, antenna, and leg; Schaum (1850: 165): morphology, remark; Lacordaire (1857: 377): catalogue, redescription; Motschulsky (1861: 134): comparison with *Pachytarsus* Motschulsky, 1861; Gemminger (1869: 1686): catalogue; Gorham (1895: 309): species description, remark; Olivier (1910: 8): catalogue; Fowler (1912: 138): remark; Lucas (1920: 246): catalogue; Rüschkamp (1920: 386): distributional note; Pic (1921b: 12): species description; Pic (1924: 713): species description, remark; Pic (1930b: 321): remark; Wittmer (1941: 197): catalogue; Wittmer (1944: 211): catalogue; Harvey (1952: 392): remark; Crowson (1955: 68, 171): remark [also as *Dodecatomax* [sic!]]; Goidanich (1957: 565): remark; McDermott (1964: 50): remark; Paulus (1972: 49): remark; Wittmer (1979: 89): species description, drawing of male antenna; Lawrence and Newton (1995: 857): catalogue, remark; Wittmer (1995:

110): species descriptions; Bocak (2007: 225): catalogue; Li et al. (2008b: 495): review; Kawashima et al. (2010: 135): book chapter; Kundera and Bocak (2011a: 58): remark; Oba et al. (2011: 777): remark; Kazantsev (2012: 349): descriptions of new species, identification key; Johnson et al. (2012: 178): ICZN case; ICZN (2014: 195): ICZN case; Kovalev and Kirejtshuk (2016: 205): remark; Liu et al. (2020: 46): remark; Lawrence et al. (2021: 456): wing morphology. In addition to the aforementioned literature, this genus was included in PhD theses by Jeng (2008) and Roza (2022).

Remarks. *Dodecatoma* currently contains eight described species from Afghanistan, India, Nepal, Indonesia, and the Philippines. This genus is in need of revision; taxa from Southeast Asia should be removed from *Dodecatoma*, and the generic assignment of the species with serrate antennae described recently by Kazantsev (2012) needs careful re-examination (the remaining species of *Dodecatoma*, including the type species, have pectinate antennae).

***Dodecatoma bicolor* Westwood, 1849**

Dodecatoma bicolor Westwood, 1849: 1.

Type depository. Described based on an unknown number of specimens. Syntype, male (OUMNH).

Type locality. India: Deccan Plateau (without further details; “North India” on the label of the syntype in OUMNH).

Distribution. India (Karnataka, Maharashtra).

Literature. Westwood (1849: 1): original description, drawings of male habitus and body parts; Schaum (1850: 165): morphology, remark; Gemminger (1869: 1686): catalogue; Gorham (1895: 309): distributional note; Olivier (1910: 8): catalogue; Lucas (1920: 246): catalogue; Pic (1924: 714): comparison with *D. testaceiceps* Pic, 1924; Pic (1930b: 321): remark; Wittmer (1944: 211): catalogue; Lawrence and Newton (1995: 858): catalogue, remark; Bocak (2007: 225): catalogue; Johnson et al. (2012: 178): ICZN case; ICZN (2014: 195): ICZN case; Lawrence et al. (2021: 456): wing morphology, figure of hind wing. In addition to the aforementioned literature, this species was included in PhD theses by Jeng (2008) and Roza (2022).

***Dodecatoma fuscicornis fuscicornis* Gorham, 1895**

Dodecatoma fuscicornis Gorham, 1895: 309.

Type depository. Described based on “several examples” (Gorham 1895: 309). Three syntypes, males (NHMUK). Several specimens from Belgaum deposited in MNHN are potentially syntypes (RK pers. obs.).

Type locality. India: Karnataka, Belgaum.

Distribution. India (Karnataka).

Literature. Gorham (1895: 309): original description; Olivier (1910: 8): catalogue; Wittmer (1944: 211): catalogue; Wittmer (1979: 90): comparison with other species; Johnson et al. (2012: 179): ICZN case.

***Dodecatoma fuscicornis testaceicornis* Pic, 1921**

Dodecatoma fuscicornis var. *testaceicornis* Pic, 1921b: 12.

Type depository. Described based on an unknown number of specimens. Syntype, male (MNHN).

Type locality. Indonesia: Java.

Distribution. Indonesia (Java).

Literature. Pic (1921b: 12): original description; Wittmer (1944: 212): catalogue.

Remarks. The name “*testaceicornis*” is deemed to be subspecific according to Art. 45.6.4. of the Code (ICZN 1999). This taxon is not morphologically similar to *D. fuscicornis* Gorham, 1895 nor to any other species of *Dodecatoma*.

***Dodecatoma gracilis* Wittmer, 1995**

Dodecatoma gracilis Wittmer, 1995: 110.

Type depository. Holotype, male (NHMB). One paratype, male (NHMB).

Type locality. Nepal: near Simra Abhabar, 200 m.

Distribution. Nepal.

Literature. Wittmer (1995: 110): original description, figures of male antenna and genitalia; Bocak (2007: 225): catalogue; Johnson et al. (2012: 179): ICZN case; Kazantsev (2012: 349): comparison with *D. saluki* and *D. schmidtii*, identification key.

***Dodecatoma parvicornis* Wittmer, 1979**

Dodecatoma parvicornis Wittmer, 1979: 89.

Type depository. Holotype, male (NHMB). Two paratypes, males (NHMB).

Type locality. Afghanistan: Nuristan, Baschgultal.

Distribution. Afghanistan, Pakistan.

Literature. Wittmer (1979: 89): original description, drawing of antenna; Bocak (2007: 225): catalogue; Johnson et al. (2012: 179): ICZN case.

***Dodecatoma riedeli* Wittmer, 1995**

Dodecatoma riedeli Wittmer, 1995: 112.

Type depository. Holotype, male (SMNS). Three paratypes, males (NHMB).

Type locality. India: Uttarakhand [“Uttar Pradesh”], Rishikesh.

Distribution. India (Uttarakhand).

Literature. Wittmer (1995: 112): original description, figures of male antenna and genitalia; Bocak (2007: 225): catalogue; Johnson et al. (2012: 179): ICZN case; Kazantsev (2012: 349): comparison with *D. saluki* and *D. schmidtii*, identification key.

***Dodecatoma saluki* Kazantsev, 2012**

Dodecatoma saluki Kazantsev, 2012: 349.

Type depository. Holotype, male (ICM). One paratype, male (NKME).

Type locality. India: Uttarakhand [Uttaranchal], Nainital Distr., 5 km SE Mukteshwar, Satkhol.

Distribution. India (Uttarakhand), Nepal.

Literature. Kazantsev (2012: 349): original description, figures of male habitus, pregenital segments, and genitalia.

***Dodecatoma schmidtii* Kazantsev, 2012**

Dodecatoma schmidtii Kazantsev, 2012: 349.

Type depository. Holotype, male (NKME).

Type locality. Nepal: Kali Gandaki valley, Upper Lete.

Distribution. Nepal.

Literature. Kazantsev (2012: 349): original description, drawings of male basal antennomeres and genitalia.

***Dodecatoma testaceiceps* Pic, 1924**

Dodecatoma testaceiceps Pic, 1924: 713.

Dodecatoma testaceipes: Wittmer 1944: 212 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Type depository. Described based on an unknown number of specimens (but probably only one). One syntype, male (MNHN).

Type locality. Philippines: Luzon, Mt. Maquilang.

Distribution. Philippines.

Literature. Pic (1924: 713): original description; Wittmer (1941: 197): catalogue; Wittmer (1944: 212): catalogue [as *D. testaceipes* [sic!]].

Remarks. This species clearly does not represent a member of Rhagophthalmidae and needs to be transferred into a proper family in a future revision.

Genus *Falsophrixothrix* Pic, 1937

Fig. 1D

Falsophrixothrix Pic, 1937: 138. Gender: feminine. Type species. *Phrixothrix javanus* [sic!] Pic, 1914; by original designation (Pic 1937: 138).

Literature. Olivier (1911: 20): species description [as *Phrixothrix*]; Pic (1914: 13): species description [as *Phrixothrix*]; Pic (1921a: 16): species description [as *Phrixothrix*]; Pic (1937: 138): original generic description; Wittmer (1938: 301): description of an aberration [term used to denote a class of individuals within a species; unavailable name; see Glossary in ICZN (1999)]; Wittmer (1939: 23): species description; Wittmer (1944: 217): catalogue; Pic (1951: 5): species description; Crowson (1972: 52): remark; Paulus (1975: 78): remark; Herring (1978: 471): checklist; Herring (1987: 157): checklist; Viviani and Bechara (1993: 615): remark; Lawrence and Newton (1995: 857): catalogue, remark; Viviani and Bechara (1997: 389): remark; O'Keefe (2002: 182): remark; Li et al. (2008b: 495): review; Kawashima et al. (2010: 139): book chapter; Lawrence et al. (2010b: 175): remark; Kundrata and Bocak (2011a: 57): remark; Oba et al. (2011: 777): remark; Janisova and Bocakova (2013: 3): remark; Kovalev and Kirejtshuk (2016: 205): remark; Kundrata et al. (2019: 1263): molecular phylogeny; Douglas et al. (2021: 2): molecular phylogeny. In addition to the aforementioned literature, this genus was included in PhD theses by Jeng (2008) and Roza (2022).

Remarks. *Falsophrixothrix* currently contains six described and several undescribed species from Southeast Asia. It can be recognized by its small body size, strongly bipectinate antennae (Fig. 1D), and usually shortened elytra which do not cover the entire abdomen. It should be noted that all previous authors treated the gender of *Falsophrixothrix* as masculine; however, *-thrix* (hair in Greek) is feminine.

***Falsophrixothrix costata* Pic, 1951**

Falsophrixothrix costatus [sic!] Pic, 1951: 5.

Type depositary. Described based on an unknown number of specimens. Syntype, male (MNHN).

Type locality. Vietnam: Ho Chi Minh City [Saigon].

Distribution. Vietnam.

Literature. Pic (1951: 5): original description.

***Falsophrixothrix flava* Wittmer, 1939**

Falsophrixothrix flavus [sic!] Wittmer, 1939: 23.

Type depository. Described based on two specimens. Holotype, male (NHMB); para-type, male (?MZB; in Drescher coll. according to the original description).

Type locality. Indonesia: Java, Parahyangan (= Priangan, Preanger), Tangkuban Perahu [G. Tangkoeban Prahoe].

Distribution. Indonesia (Java).

Literature. Wittmer (1939: 23): original description; Wittmer (1944: 217): catalogue.

***Falsophrixothrix humeralis* Pic, 1937**

Falsophrixothrix humeralis Pic, 1937: 138.

Falsophrixothrix humeralis ab. *unicolor* Wittmer, 1938: 301 [unavailable name, ICZN 1999].

Type depository. Described based on an unknown number of specimens. Syntype (labelled as “Holotypus”), male (NHMB).

Type locality. Indonesia: Java, Parahyangan (= Priangan, Preanger), Tangkuban Perahu [G. Tangkoeban Prahoe] [only “Java” in the original description, remaining information taken from the locality label under the syntype].

Distribution. Indonesia (Java).

Literature. Pic (1937: 138): original description; Wittmer (1938: 301): description of *F. humeralis* ab. *unicolor*; Wittmer (1939: 24): comparison with *F. flavus* [sic!]; Wittmer (1944: 217): catalogue; Pic (1951: 5): comparison with *F. costatus* [sic!]. In addition to the aforementioned literature, this species was included in a PhD thesis by Jeng (2008).

Remarks. Wittmer (1938: 301) described the aberration of *F. humeralis* (ab. *unicolor*) from Tangkuban Perahu [“G. Tangkoeban Prahoe”] based on material from the collection of F. C. Drescher (possibly in MZB); however, this name is deemed to be infrasubspecific according to the Code (ICZN 1999, Article 45.6.2.).

***Falsophrixothrix javana* (Pic, 1914)**

Phrixothrix javanus [sic!] Pic, 1914: 13.

Falsophrixothrix javanus [sic!]: Pic 1937: 138.

Type depository. Described based on an unknown number of specimens. Syntype, male (MNHN).

Type locality. Indonesia: Java.

Distribution. Indonesia (Java).

Literature. Pic (1914: 13): original description [as *Phrixothrix*]; Pic (1921a: 16): comparison with *F. punctatus* [sic!] (Pic, 1921) [as *Phrixothrix*]; Pic (1937: 138): comparison with *F. humeralis*; Wittmer (1939: 24): comparison with *F. flavus* [sic!]; Wittmer (1944: 217): catalogue.

***Falsophrixothrix punctata* (Pic, 1921)**

Phrixothrix punctatus [sic!] Pic, 1921a: 16.

Falsophrixothrix punctatus [sic!]: Wittmer 1944: 217.

Type depository. Described based on an unknown number of specimens. Syntype, male (MNHN).

Type locality. Singapore.

Distribution. Singapore.

Literature. Pic (1921a: 16): original description [as *Phrixothrix*]; Wittmer (1944: 217): catalogue.

***Falsophrixothrix pygmaea* (Olivier, 1911)**

Phrixothrix pygmaeus [sic!] E. Olivier, 1911: 19.

Falsophrixothrix pygmaeus [sic!]: Wittmer 1939: 24.

Type depository. Described based on an unknown number of specimens. At least one syntype, male (RMNH). Five additional male specimens in RMNH (originally from the Zoological Museum, Amsterdam, ZMAN) may also be syntypes (RK pers. obs.).

Type locality. Indonesia, Java: Banyuwangi [Banjoewangi].

Distribution. Indonesia (Java).

Literature. Olivier (1911: 19): original description [as *Phrixothrix*]; Wittmer (1939: 24): comparison with *F. flavus* [sic!]; Wittmer (1944: 217): catalogue.

Genus *Haplocladon* Gorham, 1883

Haplocladon Gorham, 1883b: 249 [as a subgenus of *Diplocladon* Gorham, 1883].

Gender: neuter. Type species. *Haplocladon gorhami* Kundrata, 2022, nom. nov. [replacement name for *Diplocladon hasseltii* Gorham, 1883b]; by monotypy.

Literature. Gorham (1883b: 249): original description; Gorham (1895: 310): remark; Gorham (1903: 330): species description; Olivier (1910: 8): catalogue; Wittmer (1944: 211): catalogue; Crowson (1955: 68): remark; Paulus (1972: 49): remark; Li

and Liang (2008: 109): remark [as *D. haplocladon* [sic!]]. In addition to the aforementioned literature, this genus was included in a PhD thesis by Jeng (2008).

Remarks. Gorham (1883b) originally described *Haplocladon* as a subgenus of *Diplocladon* but later treated it as a separate genus (Gorham 1895, 1903). Unfortunately, he named type species of both *Diplocladon* and *Haplocladon* as “*hasseltii*” (Gorham 1883a, b), which probably confused some subsequent authors who treated *Haplocladon* as a synonym of *Diplocladon* (Olivier 1910; Wittmer 1944; Li and Liang 2008). Crowson (1955) and Paulus (1972) again considered *Haplocladon* a separate genus. Since *Haplocladon* differs at first sight from *Diplocladon* by the unipectinate antennae (versus bipectinate in *Diplocladon*), we prefer to keep *Haplocladon* at a generic level. Because *Diplocladon hasseltii* Gorham, 1883a and *Diplocladon hasseltii* Gorham, 1883b (described in subgenus *Haplocladon*) are primary homonyms, the latter junior name is permanently invalid (Art. 57.2 of the Code; ICZN 1999) and should be replaced by a new name (see below). Currently, *Haplocladon* contains two species, one from Indonesia and one from southern India. Based on the available figures, specimens reported by Haneda (1950) from Singapore and identified as *Diplocladon hasseltii*, which were later mentioned by other authors (e.g., Harvey 1952; Haneda 1955; Lloyd 1971; Lloyd 1978; Crowson 1981; Haneda 1985; Kawashima et al. 2010), are probably members of *Haplocladon*.

***Haplocladon gorhami* Kundrata, nom. nov.**

Replacement name for *Diplocladon hasseltii* Gorham, 1883b.

Diplocladon hasseltii Gorham, 1883b: 250 (described in subgenus *Haplocladon*). Preoccupied by *Diplocladon hasseltii* Gorham, 1883a: 6.

Haplocladon haselti: Gorham 1903: 330 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Type depository. Described based on an unknown number of specimens. Two syntypes, males (one from Sumatra, one from Java) (RMNH).

Type locality. Indonesia: Sumatra, Lampung, Soekadana; Java, Batavia.

Distribution. Indonesia (Sumatra, Java).

Literature. Gorham (1883b: 250): original description; Gorham (1903: 330): remark [as *H. haselti* [sic!]]; Olivier (1910: 8): catalogue [as *D. hasselti*]; Wittmer (1944: 211): catalogue [as *D. hasselti*].

Remarks. Gorham (1883b: 250) also reported an unnamed variety of *H. hasseltii* as “var. totum testaceum” (i.e., colour description but not the official name of the variety) from Ardjoeno and Batavia in Java. At least one specimen from Batavia labelled as “var.” is present in MNHN. Two specimens from Ardjoeno and one specimen from Batavia deposited in RMNH bear the label “Type”; however, based on Article 72.4.1. of the Code (ICZN 1999), they should not be considered a part of the type series for *Haplocladon gorhami*.

***Haplocladon indicum* Gorham, 1903**

Haplocladon indicum Gorham, 1903: 330.

Diplocladon indicum: Olivier 1910: 8.

Type depository. Holotype, male (MNHN).

Type locality. India: Nilgiri Hills.

Distribution. India (Nilgiri Hills).

Literature. Gorham (1903: 330): original description; Olivier (1910: 8): catalogue [as *D. indicum*]; Wittmer (1944: 211): remark [as *D. indicum*]; Li and Liang (2008: 109): remark [as *D. haplocladon indicum* [sic!]]; Yiu (2017: 64): comparison with *Diplocladon atripennis* [sic!] [as *D. indicum*].

Genus *Menghuoius* Kawashima, 2000

Menghuoius Kawashima, 2000: 132. Gender: masculine. Type species. *Rhagophthalmus ingens* Fairmaire, 1896, by original designation.

Menghouius: Bocak 2007: 225 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Menhuoius: Li et al. 2008a: 264 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Distribution. China (Anhui, Guangxi, ?Hong Kong, Yunnan, Zhejiang), Myanmar, Vietnam.

Literature. Kawashima (2000: 132): original description; Kawashima (2002: 487): species description, figures of habitus, body parts, and male genitalia; Bocak (2007: 225): catalogue [as *Menghouius* [sic!]]; Li et al. (2008a: 264): distribution, morphology, biology, figures of male antenna and genitalia, and larval and female habitus [as *Menghouius* [sic!]]; Li et al. (2008b: 495): review; Kawashima et al. (2010: 136): book chapter, drawings of head, tarsi, and antenna; Chen et al. (2019: 3): molecular phylogeny; Liu et al. (2020: 46a): luciferase, phylogeny, figures of male and female habitus, and female bioluminescence. In addition to the aforementioned literature, this genus was included in a PhD thesis by Jeng (2008).

Remarks. *Menghuoius* currently contains three described species from China, Myanmar, and Vietnam. It is similar to *Rhagophthalmus* in habitus, short, serrate antennae, and deeply emarginate eyes but differs in the large size and robust mandibles (Kawashima 2000). *Menghuoius* was implicitly considered a junior synonym of *Rhagophthalmus* by Li et al. (2008a) based on the similar morphology of females of both genera. However, since the morphology of highly pedomorphic, larva-like females of Rhagophthalmidae is much less informative than the morphology of adult males, we consider *Menghuoius* a separate genus until a detailed revision of *Rhagophthalmus* and related genera is carried out.

***Menghuoius giganteus* (Fairmaire, 1888)**

Rhagophthalmus giganteus Fairmaire, 1888: 25.

Menghuoius giganteus: Kawashima 2000: 139.

Rhagophthalmus gigantus: Moreira et al. 2022: 7 [unavailable name, incorrect subsequent spelling not in prevailing usage; page number may be changed when the publication is printed].

Type depository. Described based on an unknown number of specimens. Syntype, male (MNHN).

Type locality. China: Yunnan.

Distribution. China (Anhui, Guangxi, Yunnan, Zhejiang).

Literature. Fairmaire (1888: 25): original description [as *R. giganteus*]; Fairmaire (1896: 227): comparison with *R. ingens* [as *R. giganteus*]; Olivier (1902: 88): catalogue [as *R. giganteus*]; Olivier (1910: 1): catalogue [as *R. giganteus*]; Jakobson (1911: 687): catalogue [as *R. giganteus*]; Olivier (1912: 469): revision [as *R. giganteus*]; Winkler (1925: 522): catalogue [as *R. giganteus*]; Wu (1937: 385): catalogue [as *R. giganteus*]; McDermott (1966: 122): catalogue [as *R. giganteus*]; Kawashima (2000: 139): comparison with *R. ingens* [as *R. giganteus*]; Hua (2002: 71): catalogue [as *R. giganteus*]; Bocak (2007: 225): catalogue; Li et al. (2008a: 264): distribution, morphology, biology, figures of male antenna and genitalia, and larval and female habitus [also as *R. giganteus*]; Li et al. (2008b: 496): review [as *R. giganteus*]; Chen et al. (2019: 3): molecular phylogeny; Liu et al. (2020: 46a): luciferase, phylogeny, figures of male and female habitus, and female bioluminescence; Moreira et al. (2022: 7): luciferase, molecular phylogeny [as *R. gigantus* [sic]]. In addition to the aforementioned literature, this species was included in a PhD thesis by Jeng (2008).

***Menghuoius ingens* (Fairmaire, 1896)**

Rhagophthalmus ingens Fairmaire, 1896: 227.

Menghuoius ingens: Kawashima 2000: 134.

Type depository. Described based on an unknown number of specimens. Syntype, male (MNHN).

Type locality. China: probably Hong Kong (Fairmaire 1896).

Distribution. China (?Hong Kong), Vietnam.

Literature. Fairmaire (1896: 227): original description [as *R. ingens*]; Olivier (1902: 88): catalogue [as *R. ingens*]; Olivier (1910: 1): catalogue [as *R. ingens*]; Jakobson (1911: 687): catalogue [as *R. ingens*]; Olivier (1912: 469): revision [as *R. ingens*]; Winkler (1925: 522): catalogue [as *R. ingens*]; Wu (1937: 385): catalogue [as *R. ingens*]; McDermott (1966: 122): catalogue [as *R. ingens*]; Kawashima (2000: 134): redescription; Hua (2002: 71): catalogue [as *R. ingens*]; Kawashima (2002: 491):

comparison with *M. kusakabei*; Bocak (2007: 225): catalogue [also as *R. ingens*]; Li et al. (2008a: 264): remark, distribution [also as *R. ingens*]; Li et al. (2008b: 496): review [as *R. ingens*]; Kawashima et al. (2010: 136): book chapter, drawings of head, tarsi and antenna; Yiu (2017: 60): comparison with *R. motschulskyi* [as *R. ingens*]; Chen et al. (2019: 11): molecular phylogeny; Liu et al. (2020: 47): remark. In addition to the aforementioned literature, this species was included in a PhD thesis by Jeng (2008).

Remarks. Olivier (1912) mentioned that *R. ingens* could be conspecific with *R. giganteus*.

***Menghuoius kusakabei* Kawashima, 2002**

Menghuoius kusakabei Kawashima, 2002: 487.

Type depository. Holotype, male (NWU). Four paratypes, males (PCIK).

Type locality. Myanmar: Chin state, Natma Taung National Park near Kanpetlet, Mt. Victoria, ca. 2000 m.

Distribution. Myanmar.

Literature. Kawashima (2002: 487): original description, figures of habitus, body parts, male genitalia.

Remarks. Jeng (2008) reported a possible female of *M. kusakabei* from Myanmar.

Genus *Mimochotyra* Pic, 1937

Mimochotyra Pic, 1937: 137. Gender: feminine. Type species. *Mimochotyra ocularis* Pic, 1937; by monotypy.

Mimochotyra: McDermott 1964: 11 [unavailable name, incorrect subsequent spelling].

Mimotyra: Herring 1987: 158 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Mimochotyra: Lawrence and Newton 1995: 857 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Literature. Pic (1937: 137): original description; McDermott (1964: 11, 51): revision [as *Mimochotyra* [sic!]]; McDermott (1966: 122): catalogue [as *Mimochotyra* [sic!]]; Mikšić and Mikšić (1966: 32): remark [as *Mimochotyra* [sic!]]; Herring (1987: 158): checklist [as *Mimotyra* [sic!]]; Lawrence and Newton (1995: 857): catalogue [as *Mimochotrya* [sic!]]; Kawashima (2000: 131): remark [as *Mimochotyra* [sic!]]; Bocakova et al. (2007: 484): molecular phylogeny [as *Mimochotyra* [sic!]]; Hunt et al. (2007: suppl.): molecular phylogeny [as *Mimochotyra* [sic!]]; Li et al. (2008a: 259): remark [as *Mimochotyra* [sic!]]; Li et al. (2008b: 495): review [as *Mimochotyra* [sic!]]; Li and Liang (2008: 111): remark [as *Mimochotyra* [sic!]]; Chen et al. (2010: 196): remark [as *Mimochotyra* [sic!]]; Costa and Zaragoza-Caballero (2010: 134): remark [as *Mimochotyra* [sic!]].

[sic!]; Kawashima et al. (2010: 135): book chapter [as *Mimochotyra* [sic!]]; Kandrata and Bocak (2011a: 59): remark [as *Mimochotyra* [sic!]]; Kandrata and Bocak (2011b: 370): molecular phylogeny [as *Mimochotyra* [sic!]]; Oba et al. (2011: 777): remark [as *Mimochotyra* [sic!]]; Kandrata et al. (2013: 202): molecular phylogeny; Kandrata et al. (2014: 167): molecular phylogeny; Bocak et al. (2016: suppl.): molecular phylogeny; Kandrata et al. (2016: 296): molecular phylogeny; Bocak et al. (2018: 4): molecular phylogeny; Kandrata et al. (2019: 1263): molecular phylogeny; Liu et al. (2020: 46): remark [as *Mimochotyra* [sic!]]. In addition to the aforementioned literature, this genus was included in a PhD thesis by Jeng (2008).

Remarks. This genus currently contains a single described species from Java, Indonesia. According to Pic (1937), it is characterized by having serrate antennae with thickened median antennomeres, and relatively long elytra. The specimen identified as *Mimochotyra* [sic!] and used in the molecular phylogenetic analyses by Bocakova et al. (2007) and more recent studies needs serious re-examination, as it was collected in Malaysia.

Mimochotyra ocularis Pic, 1937

Mimochotyra ocularis Pic, 1937: 137.

Type depository. Described based on an unknown number of specimens (probably only one). Syntype, male (NHMB).

Type locality. Indonesia: Java, Gunung Raung [Raoeng], “Bajoekidoel” [detailed data taken from the syntype label; only “Java: Bajoekidoel” [sic!] in original description].

Distribution. Indonesia (Java).

Literature. Pic (1937: 137): original description; McDermott (1964: 51): revision [as *Mimochotyra* [sic!]]; McDermott (1966: 122): catalogue [as *Mimochotyra* [sic!]]; Li et al. (2008b: 496): review [as *Mimochotyra* [sic!]].

Genus *Monodrilus* Pic, 1921

Monodrilus Pic, 1921b: 12. Gender: masculine. Type species. *Monodrilus marginatus* Pic, 1921; by monotypy.

Remarks. *Monodrilus* has more or less serrate antennae and relatively long elytra, and currently contains two species from Indonesia (Java) and Vietnam, respectively, each in a monotypic subgenus. Following Wittmer (1944), we retain the concept of *Monodrilus* with two subgenera; however, Pic (1930b) already suggested *Dodecatomorpha* could be a separate genus. A proper taxonomic revision should be conducted to resolve the status of *Dodecatomorpha*.

Subgenus *Monodrilus* Pic, 1921

Monodrilus Pic, 1921b: 12. Gender: masculine. Type species. *Monodrilus marginatus* Pic, 1921; by monotypy.

Literature. Pic (1921b: 12): original description; Pic (1928: 86): comparison with *Dodecatomorpha* Pic, 1928; Pic (1930b: 321): remark; Wittmer (1944: 212): catalogue; Lawrence et al. (2010b: 175): remark; Kundrata and Bocak (2011a: 57): remark; Janisova and Bocakova (2013: 3): remark. In addition to the aforementioned literature, *Monodrilus* was included in a PhD thesis by Jeng (2008).

Remarks. This subgenus currently contains a single described species from Java, Indonesia.

***Monodrilus marginatus* Pic, 1921**

Monodrilus marginatus Pic, 1921b: 12.

Type depository. Described based on an unknown number of specimens. Syntype, male (MNHN).

Type locality. Indonesia: Java.

Distribution. Indonesia (Java).

Literature. Pic (1921b: 12): original description; Pic (1928: 87): comparison with *Dodecatomorpha roberti* Pic, 1928; Wittmer (1944: 212): catalogue. In addition to the aforementioned literature, this species was included in a PhD thesis by Jeng (2008).

Subgenus *Dodecatomorpha* Pic, 1928

Dodecatomorpha Pic, 1928: 86 [as a subgenus of *Monodrilus* Pic, 1921]. Gender: feminine. Type species. *Monodrilus roberti* Pic, 1928 [in subgenus *Dodecatomorpha*]; by monotypy.

Literature. Pic (1928: 86): original description; Pic (1930b: 321): remark; Wittmer (1944: 212): catalogue.

Remarks. *Dodecatomorpha* currently contains a single described species from Vietnam.

***Monodrilus (Dodecatomorpha) roberti* Pic, 1928**

Monodrilus roberti Pic, 1928: 86 [in subgenus *Dodecatomorpha*].

Type depository. Described based on an unknown number of specimens. Three syntypes, males (MNHN).

Type locality. Vietnam [“Darsa, en Cochinchine”].

Distribution. Vietnam.

Literature. Pic (1928: 86): original description; Pic (1930b: 321): remark; Wittmer (1944: 212): catalogue.

Genus *Pseudothilmanus* Pic, 1918

Pseudothilmanus Pic, 1918: 2. Gender: masculine. Type species: *Pseudothilmanus alatus* Pic, 1918; by monotypy.

Drilothilmanus Pic, 1918: 3. Type species: *Drilothilmanus marginatus*, 1918; by monotypy. Synonymized by Kundrata and Bocak (2011a: 58).

Literature. Pic (1918: 2, 3): original descriptions of *Pseudothilmanus* and *Drilothilmanus*, respectively; Wittmer (1944: 215): catalogue [also as *Drilothilmanus*]; Kundrata and Bocak (2011a: 58): revision, synonymization of *Drilothilmanus*; Liu et al. (2020: 46): remark; Roza (2020: 421): morphology, distribution, figures of male habitus, pronotum, and hind wing [2018 erroneously used as the date of the original description of this genus in figure caption]. In addition to the aforementioned literature, this genus was included in a PhD thesis by Roza (2022).

Remarks. This genus has relatively long, serrate antennae and long elytra. It contains two species distributed in the Himalayas (India, Nepal).

Pseudothilmanus alatus Pic, 1918

Pseudothilmanus alatus Pic, 1918: 2.

Type depository. Described based on an unknown number of specimens. Lectotype by present designation, with the following label data: “Type [red printed label] / Type [handwritten] / Nov. genus India [handwritten] / *Pseudothilmanus alatus* Pic [handwritten]” (treated as the holotype and figured by Kundrata and Bocak 2011a), male (MNHN).

Type locality. India (without any further details).

Distribution. India (Uttarakhand), Nepal.

Literature. Pic (1918: 2): original description; Wittmer (1944: 215): catalogue; Kundrata and Bocak (2011a: 59): revision, figures of male habitus, antenna, pronotum, leg, elytral apex, pregenital segments, and genitalia; Roza (2020: 421): morphology, distribution, figures of male habitus, pronotum, and hind wing [2018 erroneously used as the date of the original description of this species in figure caption]. In addition to the aforementioned literature, this species was included in a PhD thesis by Roza (2022).

Remarks. Roza (2020) listed Uttar Pradesh for the distribution of this species; however, it was based on the specimen from NHMUK mentioned by Kundrata and Bocak (2011a), which was collected in western Almora, Kumaon which lies in Uttarakhand (considered to be part of Uttar Pradesh prior to 2000).

***Pseudothilmanus marginatus* Pic, 1918**

Driloithilmanus [as a subgenus of *Pseudothilmanus*] *marginatus* Pic, 1918: 3.

Pseudothilmanus marginatus: Kundrata and Bocak (2011a: 58).

Type depository. Described based on an unknown number of specimens. Lectotype by present designation, with the following label data: “Type [red printed label] / Type [handwritten] / Darjeeling Juni Fruhstorfer leg. [printed] / *Driloithilmanus marginatus* Pic [handwritten]” (treated as the holotype and figured by Kundrata and Bocak 2011a), male (MNHN).

Type locality. India: West Bengal, Darjeeling.

Distribution. India (West Bengal).

Literature. Pic (1918: 3): original description; Wittmer (1944: 215): catalogue [as *Driloithilmanus*]; Kundrata and Bocak (2011a: 60): revision, figures of male habitus, antenna, pronotum, leg, and genitalia; Roza (2020: 422): morphology, distribution, figures of male habitus, pronotum, and hind wing [2018 erroneously used as the date of the original description of this species in figure caption].

Genus *Rhagophthalmus* Motschulsky, 1854

Fig. 1E, F

Rhagophthalmus Motschulsky, 1854: 45. Gender: masculine. Type species: *Rhagophthalmus scutellatus* Motschulsky, 1854, by monotypy.

Ochotyra Pascoe, 1862: 323. Gender: feminine. Type species: *Ochotyra semiusta* Pascoe, 1862: 323, by monotypy. Synonymized with *Rhagophthalmus* Motschulsky, 1854 by Wittmer in Wittmer and Ohba (1994: 342).

Ochotiza: Bourgeois 1903: 479 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Ochrotyra: Lefroy 1909: 327 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Rhagophthalma: Crowson 1981: 274 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Ochotrya: Lawrence 1988: 15 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Rhagophthalmus: Suzuki 1997: 38 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Ragophthalmus: Viviani et al. 1999: 8274 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Rhagophtha: Chen 2003: 52 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Rhagophthalmus: Stanger-Hall et al. 2007: 38 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Rhagophthalmus: McKenna et al. 2015: 849 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Literature. Motschulsky (1854: 45): original description; Motschulsky (1859: 59): remark; Motschulsky (1861: 134): comparison with *Pachytarsus* Motschulsky, 1861; Pascoe (1862: 323): original description of *Ochotyra*; Gerstaecker (1863: 409): remark [as *Ochotyra*]; Gemminger (1869: 1647, 1655): catalogue [also as *Ochotyra*]; Marschall (1873: 223, 239): remark [also as *Ochotyra*]; Gorham (1881: 63): remark [as *Ochotyra*]; Olivier (1885: 372): species description; Heyden (1886: 286): remark; Fairmaire (1888: 25): species description [currently in *Menghuoius*]; Fairmaire (1889: 352): species description; Gorham (1890: 550): catalogue [as *Ochotyra*]; Bourgeois (1892: 236): distributional note; Cardon (1892: 238): checklist; Gorham (1895: 310): distributional note [also as *Ochotyra*]; Fairmaire (1896: 227): species descriptions [one currently in *Menghuoius*]; Fairmaire (1899: 624): species description; Olivier (1902: 87): catalogue; Bourgeois (1903: 479): distributional note [as *Ochotiza* [sic!]]; Gorham (1903: 330): distributional note [as *Ochotyra*]; Bourgeois (1905: 130): distributional record [as *Ochotyra*]; Olivier (1907: 63): catalogue [also as *Ochotyra*]; Olivier (1908: 17): remark; Lefroy (1909: 327): catalogue [also as *Ochrotyra* [sic!]]; Olivier (1910: 1): catalogue [also as *Ochotyra*]; Jakobson (1911: 687): catalogue; Olivier (1912: 467): revision, key [also as *Ochotyra*]; Pic (1916: 9): species description; Pic (1917: 3): species description; Lucas (1920: 567): catalogue; Pic (1921b: 18): species description [as *Ochotyra*]; Pic (1923: 25): catalogue; Handlirsch (1925: 589): catalogue; Pic (1925a: 17): species description; Pic (1925b: 72): species description; Winkler (1925: 522): catalogue; Pic (1937: 137): comparison of *Ochotyra* with *Mimoochotyra*; Wu (1937: 385): catalogue; Pic (1938: 15): checklist; Harvey (1952: 392): remark [also as *Ochotyra*]; Brues et al. (1954: 565): classification; Raj (1957: 788): larval biology, photograph of larvae; McDermott (1964: 11, 50): revision [also as *Ochotyra*]; McDermott (1966: 121): catalogue [also as *Ochotyra*]; Mikšić and Mikšić (1966: 32): remark [also as *Ochotyra*]; Nakane (1968: 3): remark; Crowson (1972: 52): remark; Herring (1978: 471): checklist; Lloyd (1978: 254): remark; Ohba (1980: 14): remark; Crowson (1981: 274): remark [as *Rhagophthalmus* [sic!]]; Sivinski (1981: 168): bioluminescence; Herring (1987: 157): checklist [also as *Ochotyra*]; Lawrence (1988: 15): remark [also as *Ochotrya* [sic!]]; Wittmer and Ohba (1994: 341): review, synonymy of *Ochotyra* with *Rhagophthalmus*, figures of habitus and body parts; Lawrence and Newton (1995: 857): catalogue, remark [also as *Ochotrya* [sic!]]; Ohba (1995: 13): remark, bioluminescence; Branham (1996: 18): remark; Chen and Ho (1996: 46): distribution, figure of habitus; Ohba et al. (1996a: 1): morphology, biology; Ohba et al. (1996b: 30): remark; Nakane (1997: 36): remark; Ohba (1997a: 5): checklist; Ohba (1997b: 19): remark; Ohba (1997c: 51): breeding; Ohba et al. (1997: 25): remark; Suzuki (1997: 4): phylogeny, biology; Wittmer (1997: 257): species descriptions; Chen and Ho (1998: 34): bioluminescence; Kawashima (1998: 16): female morphology; Ohba (1998: 3): checklist, biology; Costa et al. (1999: 22): remark; Kawashima (1999: 141): remark; Viviani et al. (1999: 8274): remark [as *Ragophthalmus* [sic!]]; Goto and Kawashima (2000: 143): distributional remark; Jeng et al. (2000: 316): remark; Kawashima (2000: 131): taxonomy; Kim et al. (2000:

214): molecular phylogeny; Ohmiya et al. (2000: 32): luciferase; Viviani and Ohmiya (2000: 267): remark [as *Ragophthalmus* [sic!]]; Branham and Wenzel (2001: 565): phylogeny; Kawashima and Satô (2001: 423): species descriptions [also as *Ochotyra*]; Kobayashi et al. (2001: 1): embryogenesis; Viviani et al. (2001: 1287): bioluminescence [as *Ragophthalmus* [sic!]]; Hua (2002: 71): catalogue; Kawashima (2002: 492): remark; Kobayashi et al. (2002: 1): embryogenesis; O'Keefe (2002: 182): remark; Ugarova and Brovko (2002: 322): bioluminescence; Viviani (2002: 1836): remark [as *Ragophthalmus* [sic!]]; Viviani et al. (2002: 538): remark [as *Ragophthalmus* [sic!]]; Branham and Wenzel (2003: 3): phylogeny, remark; Chen (2003: 52): morphology, bioluminescence [also as *Rhagophtha* [sic!]]; Hayashi and Suzuki (2003: 4): morphology, biology, phylogeny; Kawashima and Sugaya (2003: 353): species description, identification key; Kawashima et al. (2003: 255): catalogue [also *Ochotyra*]; Kobayashi et al. (2003: 19): embryogenesis, development; Satô and Kawashima (2003: 9): remark; DeCock (2004: 341): bioluminescence; Ohba (2004a: 226): bioluminescence, biology; Ohba (2004b: 6): bioluminescence, biology; Lau and Meyer-Rochow (2006: 20): morphology; Li et al. (2006: 818): molecular phylogeny; Arnoldi et al. (2007: 2): molecular phylogeny; Bocak (2007: 225): catalogue [also as *Ochotyra*]; Bocakova et al. (2007: 484): molecular phylogeny [as *Ochotyra*]; Geisthardt and Satô (2007: 234): catalogue [species *incertae sedis* in Lampyridae]; Hunt et al. (2007: suppl.): molecular phylogeny [as *Ochotyra*]; Lau et al. (2007: 27): eye morphology; Li et al. (2007: 197): mitochondrial genome, phylogeny; Sagegami-Oba et al. (2007: 105): molecular phylogeny; Stanger-Hall et al. (2007: 38): molecular phylogeny [also as *Rhagophthalmus* [sic!]]; Bocak et al. (2008: 2019): molecular phylogeny [as *Ochotyra*]; Dong et al. (2008: 479): phylogeny; Li and Liang (2008: 109): female morphology; Li et al. (2008a: 259): species descriptions, taxonomy, distribution [also as *Ochotyra*]; Li et al. (2008b: 494): review [also as *Ochotyra*]; Noguchi et al. (2008: 2): luciferase; Sheffield et al. (2008: 2500): mitochondrial genomes; Bogahawatta et al. (2009: 10): remark; Day et al. (2009: 93): remark; Levkanicova and Bocak (2009: 212): molecular phylogeny; Suzuki and Kobayashi (2009: 30): embryogenesis [also as *Ochotyra*]; Chen et al. (2010: 196): biology, bioluminescence; Costa and Zaragoza-Caballero (2010: 134): remark [also as *Ochotyra*]; Kawashima et al. (2010: 135): book chapter [also as *Ochotyra*]; Lawrence et al. (2010b: 173): remark; Bouchard et al. (2011: 326): family-group names catalogue; Kundrata and Bocak (2011a: 57): remark [also as *Ochotyra*]; Kundrata and Bocak (2011b: 370): molecular phylogeny [as *Ochotyra*]; Lawrence et al. (2011: 7): phylogeny; Oba et al. (2011: 777): biology, bioluminescence; Yiu (2011a: 14): remark; Yiu (2011b: 20): biology, bioluminescence; Amaral et al. (2012: 1262): luciferase, phylogeny; Ho et al. (2012: 1): species descriptions; Kazantsev (2012: 352): remark; Timmermans and Vogler (2012: 300): molecular phylogeny; Yiu (2012: 30): catalogue; Kundrata et al. (2013: 202): molecular phylogeny [as *Ochotyra*]; Yiu (2013: 101): biology, bioluminescence; Amaral et al. (2014: 415): molecular phylogeny [also as *Rhagophthalmus* [sic!]]; Hosoe et al. (2014: 331): chemical defence; Kundrata et al. (2014: 167): molecular phylogeny; Li et al. (2015: 269): catalogue;

Martin et al. (2015: 519): molecular phylogeny; McKenna et al. (2015: 843): molecular phylogeny [also as *Rhagophthalmus* [sic!]]; Oba (2015: 99): bioluminescence; Amaral et al. (2016: 254): molecular phylogeny; Bocak et al. (2016: 3): molecular phylogeny; Kovalev and Kirejtshuk (2016: 205): remark; Kundera et al. (2016: 296): molecular phylogeny; Wijekoon et al. (2016: 71): checklist [also as *Ochotyra*]; Amaral et al. (2017a: 674): mitogenome, phylogeny; Amaral et al. (2017b: 84): phylogeny; Amaral et al. (2017c: 157): phylogeny; Martin et al. (2017: 568): molecular phylogeny; Wang et al. (2017: 2): molecular phylogeny, transcriptome; Yiu (2017: 59): species description; Bocak et al. (2018: suppl): molecular phylogeny; Fallon et al. (2018: 8, 96): genomes, bioluminescence; Kusy et al. (2018a: 5): molecular phylogeny; Kusy et al. (2018b: 4): molecular phylogeny; Stanger-Hall et al. (2018: 8): remark; Yiu and Jeng (2018: 72): remark; Zhang et al. (2018: 3): molecular phylogeny; Amaral et al. (2019: 284): molecular phylogeny; Chen et al. (2019: 8): molecular phylogeny; He et al. (2019: 566): molecular phylogeny; Jeng (2019: 13): biofluorescence, biology; Kundera et al. (2019: 1263): molecular phylogeny; Liu et al. (2019: 3183): mitogenomic phylogeny; Martin et al. (2019: 3): molecular phylogeny; Liu et al. (2020: 46): luciferase, phylogeny [also as *Ochotyra*]; Zhang et al. (2020: 5): molecular phylogeny, bioluminescence; Ge et al. (2021: 3): mitogenomic phylogeny; Lawrence et al. (2021: 456): wing morphology; Li et al. (2021b: 2): remark; Cai et al. (2022: 6): molecular phylogeny; Ge et al. (2022: 3): mitogenomic phylogeny; He et al. (2022: 4): mitogenomic phylogeny; Moreira et al. (2022: 7): luciferase, molecular phylogeny. In addition to the aforementioned literature, this genus was included in PhD theses by Ho (2002), Jeng (2008), and Roza (2022).

Remarks. *Rhagophthalmus* is the most speciose genus in the family. It contains 34 species from South, East, and Southeast Asia. This genus is characterized by having deeply emarginate eyes and relatively short antennae (Fig. 1E, F). Wittmer in Wittmer and Ohba (1994) synonymized *Ochotyra* with *Rhagophthalmus*, and we follow this concept until a proper revision of the genus is carried out. On the other hand, *Menghuoius*, which was synonymized with *Rhagophthalmus* by Li et al. (2008a), is considered here a separate genus (see Remarks under *Menghuoius*).

Rhagophthalmus angulatus Wittmer, 1997

Rhagophthalmus angulatus Wittmer, 1997: 258.

Type depositary. Holotype, male (NHMB). One paratype, male (NHMB).

Type locality. China: East Hubei, 30 km NE Macheng, 500 m.

Distribution. China (Hubei).

Literature. Wittmer (1997: 258): original description, figures of male antenna and genitalia; Bocak (2007: 225): catalogue; Li et al. (2008a: 265): distribution; Li et al. (2008b: 496): review.

***Rhagophthalmus beigansis* Ho in Ho et al. 2012**

Rhagophthalmus beigansis Ho in Ho et al. 2012: 4.

Type depository. Holotype, male (TARI). Eight paratypes: four males, four females (ESRI, NMNS).

Type locality. China/Taiwan, Lienchiang County, Beigan.

Distribution. China/Taiwan.

Literature. Ho et al. (2012: 4): original description, figures of male habitus, head, antenna and genitalia, and female habitus, head, and bioluminescence; Yiu (2017: 60): remark.

***Rhagophthalmus brevipennis* Fairmaire, 1896**

Rhagophthalmus brevipennis Fairmaire, 1896: 227.

Type depository. Described based on an unknown number of specimens. Syntype, male (RMNH). Three additional male specimens (on one pin) from MNHN with labels different from the RMNH syntype are also labelled as “Type” but they probably represent a different species.

Type locality. India: Maharashtra, Nagpur.

Distribution. India (Maharashtra).

Literature. Fairmaire (1896: 227): original description; Olivier (1902: 87): catalogue; Lefroy (1909: 327): catalogue; Olivier (1910: 1): catalogue; Olivier (1912: 470): revision; McDermott (1966: 121): catalogue; Li et al. (2008a: 265): distribution; Li et al. (2008b: 496): review.

***Rhagophthalmus burmensis* Wittmer in Wittmer and Ohba 1994**

Rhagophthalmus burmensis Wittmer in Wittmer and Ohba 1994: 349.

Type depository. Holotype, male (NHMB). Seven paratypes, males (NHMB).

Type locality. Myanmar: Kambaiti.

Distribution. Myanmar.

Literature. Wittmer and Ohba (1994: 349): original description, drawings of male genitalia; Li et al. (2008a: 265): distribution; Li et al. (2008b: 496): review.

***Rhagophthalmus confusus* Olivier, 1912**

Rhagophthalmus confusus E. Olivier, 1912: 469, 471.

Rhagophthalmus confuses: Wijekoon et al. 2016: 71 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Type depository. Described based on an unknown number of specimens. One syntype, male (NHMUK). One probable syntype, male (MNHN).

Type locality. Sri Lanka.

Distribution. Sri Lanka.

Literature. Olivier (1912: 469, 471): original description; Pic (1916: 9): comparison with *R. notaticollis*; McDermott (1966: 121): catalogue; Li et al. (2008a: 265): distribution; Li et al. (2008b: 496): review; Ho et al. (2012: 1): remark; Wijekoon et al. (2016: 71): checklist [as *R. confuses* [sic!]]. In addition to the aforementioned literature, this species was included in a PhD thesis by Roza (2022).

***Rhagophthalmus elongatus* Wittmer in Wittmer and Ohba 1994**

Rhagophthalmus elongatus Wittmer in Wittmer and Ohba 1994: 348.

Type depository. Holotype, male (NHMB).

Type locality. China: Guangxi prov., Duyang Shan [“Mts. Toyen-chan”].

Distribution. China (Guangxi).

Literature. Wittmer and Ohba (1994: 348): original description, drawings of male genitalia; Kawashima and Satô (2001: 428, 430): comparison with *R. flavus* and *R. minutus*, respectively; Bocak (2007: 225): catalogue; Li et al. (2008a: 265): distribution; Li et al. (2008b: 496): review.

***Rhagophthalmus filiformis* Olivier, 1912**

Rhagophthalmus filiformis E. Olivier, 1912: 469, 470.

Type depository. Described based on an unknown number of specimens. One syntype, male (NHMUK).

Type locality. Sri Lanka.

Distribution. Sri Lanka.

Literature. Olivier (1912: 469, 470): original description; Pic (1925a: 17): comparison with *R. longipennis*; McDermott (1966: 121): catalogue; Kawashima and Satô (2001: 429): comparison with *R. minutus*; Li et al. (2008a: 265): distribution; Li et al. (2008b: 496): review; Ho et al. (2012: 1): remark; Wijekoon et al. (2016: 74): checklist.

***Rhagophthalmus flavus* Kawashima & Satô, 2001**

Rhagophthalmus flavus Kawashima & Satô, 2001: 424.

Type depository. Holotype, male (NWU). One paratype, male (PCIK).

Type locality. Myanmar: Dawna.

Distribution. Myanmar, Thailand.

Literature. Kawashima and Satô (2001: 424): original description, figures of male habitus, antenna, and genitalia; Li et al. (2008a: 265): distribution; Li et al. (2008b: 496): review; Ho et al. (2012: 9): comparison with *R. giallolateralus*.

***Rhagophthalmus formosanus* Kawashima & Sugaya, 2003**

Rhagophthalmus formosanus Kawashima & Sugaya, 2003: 354.

Type depository. Holotype, male (NMNS). Two paratypes, males (PCIK).

Type locality. China/Taiwan: Nantou Hsien, Meimu.

Distribution. China/Taiwan.

Literature. Kawashima and Sugaya (2003: 354): original description, identification key, figures of male habitus, antenna, and genitalia; Bocak (2007: 225): catalogue; Li et al. (2008a: 265): distribution; Li et al. (2008b: 496): review; Ho et al. (2012: 1): remark.

***Rhagophthalmus fugongensis* Li & Liang in Li et al. 2008**

Rhagophthalmus fugongensis Li & Liang in Li et al. 2008a: 260.

Type depository. Holotype, male, No. 0058739 (KNHMZ). 22 paratypes: eight males and 13 females (KNHMZ), one paratype, male (YCM). Although Li et al. (2008a) stated in the original description that the “holotype and most paratypes are deposited in KIZ [now KNHMZ]; one paratype (male) is deposited in YCM” (Li et al. 2008a: 260), Li et al. (2015) listed only six paratypes (sex not mentioned) from KNHMZ, under the collection numbers 0058740–0058745.

Type locality. China: Yunnan Province, Fugong County, Pihe, Wawa Village, 26.59398°N, 98.90819°E, 1263 m.

Distribution. China (Yunnan).

Literature. Li et al. (2008a: 260): original description; Li et al. (2008b: 496): review; Li et al. (2015: 269): catalogue.

***Rhagophthalmus giallolaratus* Ho in Ho et al. 2012**

Rhagophthalmus giallolaratus Ho in Ho et al. 2012: 9.

Type depository. Holotype, male (TARI). Four paratypes: two males and two females (ESRI, NMNS).

Type locality. China/Taiwan, Lienchiang County, Dongjyu.

Distribution. China/Taiwan.

Literature. Ho et al. (2012: 9): original description, figures of male habitus, head, antenna, and genitalia, and female habitus, head, and luminous organ; Yiu (2017: 60): comparison with *R. motschulskyi*.

***Rhagophthalmus gibbosulus* Fairmaire, 1899**

Rhagophthalmus gibbosulus Fairmaire, 1899: 624.

Type depository. Described based on an unknown number of specimens. No type specimen found in MNHN by RK.

Type locality. Probably China, “Koua-Toun” (Fujian).

Distribution. China (Fujian, ?Guangzhou, Shaanxi, Sichuan).

Literature. Fairmaire (1899: 624): original description; Olivier (1902: 88): catalogue; Olivier (1910: 1): catalogue; Jakobson (1911: 687): catalogue; Olivier (1912: 470): revision; Winkler (1925: 522): catalogue; Wu (1937: 385): catalogue; McDermott (1966: 121): catalogue; Hua (2002: 71): catalogue; Bocak (2007: 225): catalogue; Li et al. (2008a: 263): distribution, description and figures of male genitalia; Li et al. (2008b: 496): review.

***Rhagophthalmus hiemalis* Yiu, 2017**

Rhagophthalmus hiemalis Yiu, 2017: 62.

Type depository. Holotype, male (TLES). 15 paratypes: 10 males, five females (TLES).

Type locality. China: Hong Kong, Tsuen Kam Au, 22.40728°N, 114.10357°E.

Distribution. China (Hong Kong).

Literature. Yiu (2017: 62): original description, figures of male and female habitus and male genitalia.

***Rhagophthalmus jenniferae* Kawashima & Satô, 2001**

Rhagophthalmus jenniferae Kawashima & Satô, 2001: 430.

Rhagophthalmus jeniferae: Bocak 2007: 225 [unavailable name, incorrect subsequent spelling, not in prevailing usage].

Type depository. Holotype, male (NWU). Three paratypes, males (NTU, PCIK).

Type locality. China/Taiwan, Fenchihu, Chiai Hsien.

Distribution. China/Taiwan.

Literature. Kawashima and Satô (2001: 430): original description, figures of male habitus, antenna, and genitalia; Kawashima and Sugaya (2003: 353): remark, key; Bocak (2007: 225): catalogue [as *R. jeniferae* [sic!]]; Li et al. (2008a: 265): distribution; Li et al. (2008b: 496): review; Chen et al. (2010: 197): biology and bioluminescence, figures of male and female habitus, body parts, bioluminescence; Ho et al. (2012: 1): remark; Jeng (2019: 13): biofluorescence, biology, figures of larval and female habitus. In addition to the aforementioned literature, this species was mentioned in a PhD thesis by Ho (2002).

***Rhagophthalmus kiangsuensis* Wittmer in Wittmer and Ohba 1994**

Rhagophthalmus kiangsuensis Wittmer in Wittmer and Ohba 1994: 346.

Rhagophthalmus kinagsuensis: Wittmer in Wittmer and Ohba 1994: 347 [unavailable name, incorrect original spelling (ICZN 1999, Art. 19.3); First Reviser (ICZN 1999, Art. 24.2): Bocak (2007: 225)].

Type depository. Holotype, male (MNHN). One paratype, male (NHMB).

Type locality. China: Jiangsu province (without further data).

Distribution. China (Jiangsu).

Literature. Wittmer and Ohba (1994: 346): original description, drawings of male genitalia; Bocak (2007: 225): catalogue; Li et al. (2008a: 265): distribution; Li et al. (2008b: 496): review.

***Rhagophthalmus laosensis* Pic, 1917**

Rhagophthalmus laosensis Pic, 1917: 3.

Type depository. Described based on an unknown number of specimens. One syntype, male (MNHN).

Type locality. Laos: Thakhek ["Taket"].

Distribution. Laos.

Literature. Pic (1917: 3): original description; Pic (1923: 29): catalogue; McDermott (1966: 122): catalogue; Li et al. (2008a: 265): distribution; Li et al. (2008b: 496): review.

***Rhagophthalmus longipennis* Pic, 1925**

Rhagophthalmus longipennis Pic, 1925a: 17.

Ochotyra longipennis: Bocak 2007: 225.

Type depository. Described based on an unknown number of specimens. Syntype, male (MNHN); syntype, male (NHMUK); four syntypes, males (NHMB).

Type localities. Only “Chine” in the original description (Pic 1925a). More detailed locality data available on the syntype labels: Sichuan, Kangding [“Tatsienlu”] (MNHN), Shaanxi, Qinling [“Kinling” or “Kinlung”] (NHMUK and NHMB, respectively).

Distribution. China (Shaanxi, Sichuan).

Literature. Pic (1925a: 17): original description; Wu (1937: 385): catalogue; McDermott (1966: 122): catalogue; Hua (2002: 71): catalogue; Bocak (2007: 225): catalogue [as *Ochotyra longipennis*]; Li et al. (2008a: 265): distribution; Li et al. (2008b: 496): review; Yiu (2017: 62): comparison with *R. hiemalis*.

Remarks. Some previous authors erroneously considered 1923 as the year of original description of this species (as “Pic 1923: 29”); however, it was described as a new species in 1925 (Pic 1925a).

***Rhagophthalmus lufengensis* Li & Ohba in Li et al. 2008**

Rhagophthalmus lufengensis Li, Ogoh, Ohba, Liang & Ohmiya, 2007: 196 [nomen nudum; published without description, unavailable name according to the ICZN (1999, Art. 13)].

Rhagophthalmus lufengensis Li & Ohba in Li et al. 2008a: 262.

Rhagophthalmus lufengensis: Amaral et al. 2014: 415 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Type depository. Holotype, male, No. 0058746 (KNHMZ). 11 paratypes: eight males and three females (KNHMZ, YCM). Li et al. (2015) listed three paratypes (two males, one female) from KNHMZ, under the collection numbers 0058747–0058749.

Type locality. China: Yunnan Province, Lufeng County, Dajiuzhuang, 25.09774°N, 101.80204°E, 1827 m.

Distribution. China (Yunnan).

Literature. Li et al. (2007: 196): nomen nudum, mitochondrial genome, phylogeny; Arnoldi et al. (2007: 2): remark; Li et al. (2008a: 262): original description, figures of male and female habitus, male antenna, and male genitalia; Li et al. (2008b: 496): review; Sheffield et al. (2008: 2500): mitochondrial genome; Timmermans and Vogler (2012: 300): molecular phylogeny; Amaral et al. (2014: 415): molecular phylogeny [as *R. lufengensis* [sic!]]; Li et al. (2015: 269): catalogue; Amaral et al. (2016: 254): molecular phylogeny; Amaral et al. (2017a: 673): mitogenome, phylogeny [as *R. lufengensis* [sic!]]; Wang et al. (2017: 6): molecular phylogeny; Chen et al. (2019: 8): molecular phylogeny; He et al. (2019: 566): molecular phylogeny; Zhang et al. (2020: 5): molecular phylogeny; He et al. (2022: 4): mitogenomic phylogeny.

***Rhagophthalmus minutus* Kawashima & Satô, 2001**

Rhagophthalmus minutus Kawashima & Satô, 2001: 428.

Type depository. Holotype, male (NWU). Three paratypes, males (two in NWU, one in PCIK).

Type locality. Thailand: Kohn Kaen Province, “near Ban Lon, Lam Chee Yai”.

Distribution. Thailand.

Literature. Kawashima and Satô (2001: 428): original description, figures of male habitus, antenna, and genitalia; Kawashima and Sugaya (2003: 358): comparison with *R. formosanus*; Li et al. (2008a: 265): distribution; Li et al. (2008b: 496): review.

***Rhagophthalmus motschulskyi* Olivier, 1912**

Rhagophthalmus motschulskyi E. Olivier, 1912: 469, 472.

Type depository. Described based on an unknown number of specimens. Syntype, male (NHMUK).

Type locality. China: Hong Kong.

Distribution. China (Hong Kong).

Literature. Olivier (1912: 469, 472): original description; Winkler (1925: 522): catalogue; McDermott (1966: 122): catalogue; Hua (2002: 71): catalogue; Bocak (2007: 225): catalogue; Li et al. (2008a: 265): distribution; Li et al. (2008b: 496): review; Yiu (2011a: 14): remark; Yiu (2011b: 20): biology and bioluminescence, figures of female bioluminescence; Ho et al. (2012: 1): remark; Yiu (2012: 30): catalogue, figures of habitus; Yiu (2013: 101): remark, bioluminescence; Yiu (2017: 60): redescription, figures of larva, pupa, and adults, and male genitalia.

***Rhagophthalmus neoobscurus* Wittmer in Wittmer and Ohba 1994**

Ochotyra obscura Pic, 1921b: 18.

Rhagophthalmus neoobscurus Wittmer in Wittmer and Ohba 1994: 342 (replacement name for *O. obscura* Pic, 1921 (in *Rhagophthalmus*), not *R. obscurus* (Pic, 1917)).

Type depository. Described based on an unknown number of specimens. One syntype, male (MNHN).

Type locality. India (no further data). “Dekan India” written on the syntype label from MNHN.

Distribution. India (no further data).

Literature. Pic (1921b: 18): original description [as *Ochotyra obscura*]; McDermott (1966: 122): remark, catalogue [as *Ochotyra obscura*]; Wittmer and Ohba (1994:

342): taxonomy; Li et al. (2008a: 265): distribution; Li et al. (2008b: 496): review; Wijekoon et al. (2016: 74): checklist [as *Ochotyra obscura*].

Remarks. Wijekoon et al. (2016) erroneously cited “P. Melong” instead of “Pic” as the author of *O. obscura*.

***Rhagophthalmus notaticollis* Pic, 1916**

Rhagophthalmus notaticollis Pic, 1916: 9.

Rhagophthalmus notaticolis: Wijekoon et al. 2016: 74 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Type depository. Described based on an unknown number of specimens. One syntype, male (MNHN).

Type locality. Sri Lanka.

Distribution. Sri Lanka.

Literature. Pic (1916: 9): original description; McDermott (1966: 122): catalogue; Li et al. (2008a: 265): distribution; Li et al. (2008b: 496): review; Ho et al. (2012: 1): remark; Wijekoon et al. (2016: 74): checklist [as *R. notaticolis* [sic!]].

Remarks. Wijekoon et al. (2016) erroneously cited “P. Melong” instead of “Pic” as the author of *R. notaticollis*.

***Rhagophthalmus obscurus* (Pic, 1917)**

Rhagophthalmus tonkineus var. *obscurus* Pic, 1917: 4.

Rhagophthalmus tonkineus var. *obscurus*: Winkler 1925: 522 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Rhagophthalmus tonkinensis var. *obscurus*: McDermott 1966: 122 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Rhagophthalmus tokineus var. *obscurus*: Wittmer in Wittmer and Ohba 1994: 342 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Rhagophthalmus obscurus: Wittmer in Wittmer and Ohba 1994: 342.

Type depository. Described based on an unknown number of specimens. One syntype, male (MNHN).

Type locality. Vietnam: Lào Cai [Tonkin: Lao Kay].

Distribution. Vietnam.

Literature. Pic (1917: 4): original description [as *R. tonkineus* var. *obscurus*]; Pic (1923: 29): catalogue [as *R. tonkineus* var. *obscurus*]; Winkler (1925: 522): catalogue [as *R. tonkineus* var. *obscurus* [sic!]]; McDermott (1966: 122): catalogue [*R. tonkinensis* var. *obscurus* [sic!]]; Wittmer and Ohba (1994: 342): taxonomy, drawings of male genitalia [also as *R. tokineus* var. *obscurus* [sic!]]; Wittmer (1997: 258): remark; Li et al. (2008a: 265): distribution; Li et al. (2008b: 496): review.

***Rhagophthalmus ohbai* Wittmer in Wittmer and Ohba 1994**

Rhagophthalmus ohbai Wittmer in Wittmer and Ohba 1994: 344.

Rhagophthalmus ohba: Branham and Wenzel 2001: 567 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Type depository. Holotype, male (YCM). Three paratypes, sex unknown (YCM), three paratypes, two males and one female (NHMB), two paratypes, sex unknown (NWU).

Type locality. Japan: Okinawa Prefecture, Yaeyama Islands, Iriomote Island, Sonai.

Distribution. Japan (Yaeyama Islands), Taiwan (Chen and Ho 1996, 1998; Ho et al. 2012).

Literature. Wittmer and Ohba (1994: 344): original description, drawings of male and female habitus, male antenna and genitalia; Ohba (1995: 13): remark, bioluminescence; Chen and Ho (1996: 46): distribution, figure of habitus; Ohba et al. (1996a: 1): morphology, biology, figures of habitus, body details, and bioluminescence; Ohba et al. (1996b: 30): remark; Nakane (1997: 36): remark; Ohba (1997a: 5): checklist, biology, figures of larval, male and female habitus, male head, and female bioluminescence; Ohba (1997b: 19): remark; Ohba (1997c: 51): breeding, development, immature stages, figures of habitus; Ohba et al. (1997: 25): remark; Suzuki (1997: 4): phylogeny, biology; Wittmer (1997: 259): comparison with *R. angulatus*; Chen and Ho (1998: 34): bioluminescence; Kawashima (1998: 16): female morphology, drawing of female habitus; Ohba (1998: 3): checklist, biology; Costa et al. (1999: 22): remark; Viviani et al. (1999: 8274): remark [as *Ragophthalmus* [sic!]]; Goto and Kawashima (2000: 143): distribution; Kawashima (2000: 131): remarks; Kim et al. (2000: 214): molecular phylogeny; Ohmiya et al. (2000: 32): luciferase; Viviani and Ohmiya (2000: 267): remark [as *Ragophthalmus* [sic!]]; Branham and Wenzel (2001: 567): phylogeny [also as *R. ohba* [sic!]]; Kawashima and Satô (2001: 432): comparison with *R. jenniferae*; Kobayashi et al. (2001: 1): development, eggs; Viviani et al. (2001: 1287): bioluminescence [as *Ragophthalmus* [sic!]]; Kobayashi et al. (2002: 1): embryogenesis, figures of female habitus and bioluminescence; Ugarova and Brovko (2002: 322): bioluminescence; Viviani (2002: 1836): remark [as *Ragophthalmus* [sic!]]; Viviani et al. (2002: 538): remark [as *Ragophthalmus* [sic!]]; Branham and Wenzel (2003: 5): phylogeny [also as *R. ohba* [sic!]]; Chen (2003: 52): morphology, bioluminescence, figures of adult males and females, larva, and bioluminescence; Hayashi and Suzuki (2003: 4): morphology, biology, figure of mating; Kawashima and Sugaya (2003: 353): remark, identification key; Kawashima et al. (2003: 255): catalogue; Kobayashi et al. (2003: 19): embryogenesis, development; Satô and Kawashima (2003: 9): remark; DeCock (2004: 341): remark; Ohba (2004a: 226): bioluminescence, biology, figures of male and female habitus; Ohba (2004b: 6): bioluminescence, biology, figures of male and female habitus; Lau and Meyer-Rochow (2006: 20): eye morphology, figures of male and female head and eye; Li et al. (2006: 818): molecular phylogeny; Arnoldi et al. (2007: 2): molecular phylogeny; Bocak (2007: 225): catalogue; Geisthardt and Satô (2007: 234): catalogue

[in Lampyridae *incertae sedis*]; Lau et al. (2007: 27): eye morphology of male; Li et al. (2007: 197): mitochondrial genome, phylogeny; Sagegami-Oba et al. (2007: 110): molecular phylogeny; Stanger-Hall et al. (2007: 38): molecular phylogeny [also as *Rhagophthalmus* [sic!]]; Li et al. (2008a: 259): comparison with *R. lufengensis* and *M. giganteus*, distribution; Li et al. (2008b: 496): review; Noguchi et al. (2008: 2): luciferase; Sheffield et al. (2008: 2500): mitochondrial genome; Suzuki and Kobayashi (2009: 30): embryogenesis, figure of egg; Chen et al. (2010: 203): habitus figure showing bioluminescence; Kawashima et al. (2010: 137): book chapter, figures of male and female habitus, and female ovipositor; Lawrence et al. (2011: 7): phylogeny, figure of female abdomen; Oba et al. (2011: 773): biology, bioluminescence, figures of male and female habitus, and female bioluminescence; Amaral et al. (2012: 1262): luciferase, phylogeny; Ho et al. (2012: 1): remarks, comparison with *R. beigensis*; Timmermans and Vogler (2012: 300): molecular phylogeny; Amaral et al. (2014: 415): molecular phylogeny; Hosoe et al. (2014: 331): chemical defence, figures of male and female habitus; Kundera et al. (2014: 167): molecular phylogeny; Martin et al. (2015: 519): molecular phylogeny; Amaral et al. (2016: 254): molecular phylogeny; Bocak et al. (2016: suppl.): molecular phylogeny; Kundera et al. (2016: 296): molecular phylogeny; Amaral et al. (2017a: 674): remark; Amaral et al. (2017b: 84): phylogeny; Amaral et al. (2017c: 157): phylogeny; Martin et al. (2017: 568): molecular phylogeny; Wang et al. (2017: 6): molecular phylogeny; Bocak et al. (2018: suppl.): molecular phylogeny; Fallon et al. (2018: 8): genomes, bioluminescence; Stanger-Hall et al. (2018: 8): remark; Chen et al. (2019: 8): molecular phylogeny; He et al. (2019: 566): molecular phylogeny; Kundera et al. (2019: 1263): molecular phylogeny; Liu et al. (2019: 3183): mitogenomic phylogeny; Martin et al. (2019: 3): molecular phylogeny; Liu et al. (2020: 47): luciferase, phylogeny; Zhang et al. (2020: 5): molecular phylogeny, bioluminescence; Ge et al. (2021: 3): mitogenomic phylogeny; Ge et al. (2022: 3): mitogenomic phylogeny; He et al. (2022: 4): mitogenomic phylogeny; Moreira et al. (2022: 7): luciferase, molecular phylogeny. In addition to the aforementioned literature, this species was included in PhD theses by Ho (2002) and Jeng (2008).

***Rhagophthalmus sausiai* Wittmer, 1997**

Rhagophthalmus sausiai Wittmer, 1997: 257.

Type depository. Holotype, male (NHMB). Two paratypes, males (NHMB).

Type locality. China: Guizhou, 60 km N Kaili, Shibing, Yuntai Shan.

Distribution. China (Guizhou).

Literature. Wittmer (1997: 257): original description, drawings of male antenna and genitalia; Bocak (2007: 225): catalogue; Li et al. (2008a: 265): distribution; Li et al. (2008b: 496): review.

***Rhagophthalmus scutellatus* Motschulsky, 1854**

Rhagophthalmus scutellatus Motschulsky, 1854: 45.

Type depository. Holotype, male (ZMM).

Type locality. China: Beijing.

Distribution. China (Beijing, Fujian, Jiangsu/Shanghai).

Literature. Motschulsky (1854: 45): original description; Motschulsky (1859: 59): remark, drawings of male habitus, lateral head, and leg; Gemminger (1869: 1655): catalogue; Olivier (1885: 372): comparison with *R. sumatrensis*; Heyden (1886: 286): remark; Fairmaire (1888: 25): comparison with *R. giganteus*; Fairmaire (1889: 353): comparison with *R. tonkineus*; Bourgeois (1892: 236): distributional note; Cardon (1892: 238): checklist; Fairmaire (1899: 624): comparison with *R. gibbosulus*; Olivier (1902: 88): catalogue; Olivier (1910: 1): catalogue; Jakobson (1911: 687): catalogue; Olivier (1912: 470): revision; Pic (1916: 9): comparison with *R. notaticollis*; Lucas (1920: 567): catalogue; Winkler (1925: 522): catalogue; Pic (1938: 15): checklist; McDermott (1964: 49): remark; McDermott (1966: 122): catalogue; Wittmer and Ohba (1994: 343): taxonomy, morphology, drawings of male genitalia; Wittmer (1997: 261): taxonomy, morphology, distribution, drawings of male genitalia; Kawashima and Satô (2001: 423): remark, comparison with *R. jenniferae*; Hua (2002: 71): catalogue; Kawashima et al. (2003: 255): remark, catalogue; Kawashima and Sugaya (2003: 358): remark, identification key; Bocak (2007: 225): catalogue; Li et al. (2008a: 264): comparison with *R. gibbosulus*, distribution; Li et al. (2008b: 494): review; Suzuki and Kobayashi (2009: 30): remark; Chen et al. (2010: 196): remark; Lawrence et al. (2011: 7): phylogeny; Yiu (2017: 60): remark, comparison with *R. hiemalis*; Lawrence et al. (2021: 456): wing morphology, figure of hind wing. In addition to the aforementioned literature, this species was included in a PhD thesis by Roza (2022).

***Rhagophthalmus semisulcatus* Wittmer, 1997**

Rhagophthalmus semisulcatus Wittmer, 1997: 259.

Type depository. Holotype, male (NHMB). Five paratypes, males (NHMB). According to the original description (Wittmer 1997), there are only five paratypes; however, there are five additional specimens with different labels designated as paratypes in NHMB.

Type locality. China: Yunnan: Yulong Shan, 27°10'N, 100°13'E, 3900 m.

Distribution. China (Yunnan).

Literature. Wittmer (1997: 259): original description, drawings of male antenna and genitalia; Bocak (2007: 225): catalogue; Li et al. (2008a: 264): distribution, biology, figure of female habitus; Li et al. (2008b: 496): review.

***Rhagophthalmus semiustus* (Pascoe, 1862)**

Ochotyra semiusta Pascoe, 1862: 323.

Rhagophthalmus (*Ochrotyra* [sic!]) *semiusta* [sic!]: Lefroy 1909: 327.

Rhagophthalmus semiustus: Wittmer in Wittmer and Ohba 1994: 342.

Type depository. Holotype, male (NHMUK).

Type locality. India: “Malabar”.

Distribution. India (Karnataka, Kerala, Tamil Nadu) [“Malabar, Coromandel”], Sri Lanka.

Literature. Pascoe (1862: 323): original description, drawing of male habitus [as *Ochotyra*]; Gerstaecker (1863: 409): remark [as *Ochotyra*]; Gemminger (1869: 1647): catalogue [as *Ochotyra*]; Gorham (1890: 550): catalogue; Gorham (1895: 310): distributional note, morphology [as *Ochotyra*]; Bourgeois (1903: 479): distributional note [as *Ochotiza* [sic!]]; Gorham (1903: 330): distributional note [as *Ochotyra*]; Bourgeois (1905: 130): distributional note [as *Ochotyra*]; Lefroy (1909: 327): catalogue [as *Rhagophthalmus* (*Ochrotyra* [sic!]) *semiusta* [sic!]]; Olivier (1910: 1): catalogue [as *Ochotyra*]; Pic (1921b: 18): comparison with *R. neoobscurus* [as *Ochotyra*]; McDermott (1964: 50): revision [as *Ochotyra*]; McDermott (1966: 122): catalogue [as *Ochotyra*]; Wittmer and Ohba (1994: 342): taxonomic remark [as *Ochotyra*]; Bocak (2007: 225): catalogue [as *Ochotyra*]; Li et al. (2008a: 265): distribution [as *R. semiusta* [sic!]]; Li et al. (2008b: 496): review [as *R. semiusta* [sic!]]; Wijekoon et al. (2016: 71): checklist [as *Ochotyra*]. In addition to the aforementioned literature, this species was included in a PhD thesis by Jeng (2008).

***Rhagophthalmus sulcatus* Pic, 1925**

Rhagophthalmus sulcatus Pic, 1925b: 72.

Type depository. Described based on an unknown number of specimens. No type material was found in MNHN by RK.

Type locality. India: West Bengal, Darjeeling.

Distribution. India (West Bengal).

Literature. Pic (1925b: 72): original description; McDermott (1966: 122): catalogue; Wittmer (1997: 261): comparison with other species; Bocak (2007: 225): catalogue; Li et al. (2008a: 265): distribution; Li et al. (2008b: 496): review.

Remarks. This species could be a synonym of *R. sulcicollis* Olivier, 1912 (see Wittmer 1997 for more information).

***Rhagophthalmus sulcicollis sulcicollis* Olivier, 1912**

Rhagophthalmus sulcicollis E. Olivier, 1912: 471.

Type depository. Lectotype, male (NHMUK). Five paralectotypes, males (NHMUK) (although only four paralectotypes were reported by Wittmer 1997: 261). There are also two additional specimens in MNHN bearing the labels “lectotype” and “paralectotype”; however, they have locality label data that differ slightly from the original description.

Type locality. China: Tibet/Xizang, Yalong, over 3000 m.

Distribution. China (Tibet/Xizang).

Literature. Olivier (1912: 471): original description; Winkler (1925: 522): catalogue; Pic (1925b: 72): comparison with *R. sulcatus*; McDermott (1966: 122): catalogue; Wittmer (1997: 261): taxonomy, morphology, drawings of male pronotum and genitalia; Hua (2002: 71): catalogue; Bocak (2007: 225): catalogue; Li et al. (2008a: 265): distribution; Li et al. (2008b: 496): review.

***Rhagophthalmus sulcicollis bhutanensis* Wittmer, 1997**

Rhagophthalmus sulcicollis subsp. *bhutanensis* Wittmer, 1997: 261.

Type depository. Holotype, male (NHMB).

Type locality. Bhutan: Karrumphe, 2700 m.

Distribution. Bhutan.

Literature. Wittmer (1997: 261): original description, drawings of male antenna and pronotum; Bocak (2007: 225): catalogue.

***Rhagophthalmus sumatrensis* Olivier, 1885**

Rhagophthalmus sumatrensis Olivier, 1885: 372.

Type depository. Described based on an unknown number of specimens. Three syntypes, males (MSNG).

Type locality. Indonesia: Sumatra, Mt. Singalang.

Distribution. Indonesia (Sumatra).

Literature. Olivier (1885: 372): original description; Fairmaire (1889: 353): comparison with *R. tonkineus*; Olivier (1902: 88): catalogue; Olivier (1910: 1): catalogue; Olivier (1912: 470): revision, drawings of head, antenna, and tarsus; McDermott (1966: 122): catalogue; Wittmer (1997: 259): comparison with *R. angulatus*; Li et al. (2008a: 265): distribution; Li et al. (2008b: 496): review; Ho et al. (2012: 1): remark.

***Rhagophthalmus tienmushanensis* Wittmer in Wittmer and Ohba 1994**

Rhagophthalmus tienmushanensis Wittmer in Wittmer and Ohba 1994: 346.

Type depository. Holotype, male (NHMB).

Type locality. China: Zhejiang, Tianmushan.

Distribution. China (Zhejiang, Shanghai).

Literature. Wittmer and Ohba (1994: 346): original description, drawings of male genitalia; Bocak (2007: 225): catalogue; Li et al. (2008a: 265): distribution; Li et al. (2008b: 496): review.

***Rhagophthalmus tonkineus* Fairmaire, 1889**

Rhagophthalmus tonkineus Fairmaire, 1889: 352.

Rhagophthalmus tonkinensis: McDermott 1966: 122 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Rhagophthalmus tokineus: Wittmer and Ohba 1994: 342 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Type depository. Described based on an unknown number of specimens. No type material was found in MNHN (Wittmer and Ohba 1994; RK, pers. obs.).

Type locality. Vietnam [“Tonkin”].

Distribution. Vietnam, China (Guangxi) (Li et al. 2008a); Laos (Pic 1923).

Literature. Fairmaire (1889: 352): original description; Fairmaire (1896: 228): comparison with *R. brevipennis*; Olivier (1902: 88): catalogue; Olivier (1910: 1): catalogue; Olivier (1912: 470): revision; Pic (1917: 4): comparison with *R. obscurus*; Pic (1923: 29): catalogue, distributional note; Winkler (1925: 522): catalogue; McDermott (1966: 122): catalogue [as *R. tonkinensis* [sic!]]; Wittmer and Ohba (1994: 342): remark, taxonomy [as *R. tokineus* [sic!]]; Li et al. (2008a: 265): distribution [also as *R. tonkinensis* [sic!]]; Li et al. (2008b: 496): review [as *R. tonkinensis* [sic!]].

***Rhagophthalmus xanthogonus* Olivier, 1912**

Rhagophthalmus xanthogonus Olivier, 1912: 469, 471.

Rhagophthalmus xanthogonus: McDermott 1966: 122 [unavailable name, incorrect subsequent spelling not in prevailing usage].

Type depository. Described based on an unknown number of male specimens. No type material was found in MNHN by RK.

Type locality. China (no further data).

Distribution. China (no further data).

Literature. Olivier (1912: 469, 471): original description; Pic (1917: 4): comparison with *R. laosensis*; Winkler (1925: 522): catalogue; McDermott (1966: 122): catalogue [as *R. xanthogenus* [sic!]]; Hua (2002: 71): catalogue [as *R. xanthogenus* [sic!]]; Bocak (2007: 225): catalogue [as *R. xanthogenus* [sic!]]; Li et al. (2008a: 265): distribution [as *R. xanthogenus* [sic!]]; Li et al. (2008b: 496): review [as *R. xanthogenus* [sic!]].

Taxa removed from Rhagophthalmidae

Cydistus Bourgeois, 1885 [Phengodidae: Cydistinae]

Cydistus Bourgeois, 1885: 272. Type species. *Cydistus reitteri* Bourgeois, 1885; by monotypy.

Composition and distribution. Six described species from Asia Minor, the Levant, Iraq, and Iran: *Cydistus chindaaricus* Bolívar y Peltain, 1913, *C. escalerae* Bolívar y Peltain, 1913, *C. nigripennis* Wittmer, 1979, *C. persicus* Bolívar y Peltain, 1913, *C. reitteri* Bourgeois, 1885, and *C. zurcheri* Bourgeois, 1908 (Kundrata et al. 2019).

Remarks. *Cydistus* was originally placed in Drilidae (Olivier 1910; Wittmer 1944). Later, Crowson (1955) hypothesized *Cydistus* might be an intermediate form between Karumiidae (currently a subfamily in Dascillidae) and Phengodidae. Although Paulus (1972) erected Cydistinae within Karumiidae for *Cydistus*, Crowson (1972) transferred this genus into the widely delimited Phengodidae, which also included Rhagophthalmidae. Lawrence and Newton (1995) and Bocak (2007) classified *Cydistus* in Phengodidae: Rhagophthalminae. Lawrence et al. (2010a, b) and Lawrence (2016) considered Cydistinae in Elateriformia *incertae sedis*. Finally, Kundrata et al. (2019) were the first to include Cydistinae in a molecular phylogenetic analysis, and found them sister to the New World Phengodidae, which are only distantly related to Rhagophthalmidae. This placement was confirmed by a morphology-based analysis by Roza (2022).

Luciola antipodum Bourgeois, 1884 [Lampyridae: Luciolinae]

Luciola antipodum Bourgeois, 1884: 285.

Rhagophthalmus antipodum: Olivier 1902: 87; Fauvel, 1904: 140.

Bourgeoisia antipodum: Olivier 1908: 17.

Distribution. New Caledonia, Solomon Islands.

Remarks. This firefly species was originally described in *Luciola* Laporte, 1833 (Bourgeois 1884) and later transferred to *Rhagophthalmus* by Olivier (1902). The same author later placed this species in his new genus *Bourgeoisia* Olivier, 1908, and McDermott (1966) subsequently designated it the type species of this genus. *Bourgeoisia* is currently considered a synonym of *Luciola* (e.g., Ballantyne and Lambkin 2013; Ballantyne et al. 2019). For more information on *L. antipodum* see e.g., McDermott (1966); Ballantyne (1968); Ballantyne and Lambkin (2013); and Ballantyne et al. (2019).

***Reductodrilus* Pic, 1943 [Lampyridae: Ototretinae]**

Reductodrilus Pic, 1943: 9. Type species. *Reductodrilus nigroapicalis* Pic, 1943; by monotypy.

Composition and distribution. Only a single species, *R. nigroapicalis* Pic, 1943 from northern Borneo (Malaysia: Sabah). *Reductodrilus nigroapicalis* var. *latetestaceus* Pic, 1943 should have a subspecific status according to Article 45.6.4. of the Code (ICZN 1999).

Remarks. *Reductodrilus* was initially placed in Drilidae (Pic 1943; Wittmer 1948). After most Drilidae genera were transferred to different families (e.g., Lampyridae, Lycidae, Omethidae, and Rhagophthalmidae) by Crowson (1972), *Reductodrilus* remained in an uncertain position. Kundrata and Bocak (2011a) listed it in Rhagophthalmidae in their revision of *Pseudothilmanus*. Probable syntypes of both subspecies of *R. nigroapicalis* are deposited in MNHN. Here, we tentatively transfer *Reductodrilus* to Lampyridae: Ototretinae based on its suboval and somewhat flattened body, antennae with 11 antennomeres which clearly extend beyond the posterior pronotal margin, head partially covered by pronotum, eyes clearly separated by frons, pronotum transverse, medially elevated, with anterior angles inconspicuous, rounded, and posterior angles projected posteriad (for more details see Janisova and Bocakova 2013). A detailed revision of this genus should improve our understanding of its systematic position.

Discussion

Although Rhagophthalmidae have been known to entomologists for more than a century, their taxonomy and classification are still poorly known. The number of genera included in Rhagophthalmidae and also their placement within Elateroidea classification vary by source (e.g., McDermott 1966; Crowson 1972; Lawrence and Newton 1995; Kawashima et al. 2010; Kundrata and Bocak 2011a). In the last decade, Elateroidea systematic research has accelerated and the classification of the superfamily has experienced many taxonomic changes (e.g., Kundrata et al. 2014, 2019; Bocak et al. 2018; Kusy et al. 2018b, 2021), including the discoveries of two new recent families (Bocak et al. 2016; Rosa et al. 2020) and one new extinct family (Li et al. 2021b). However, only six new species of Rhagophthalmidae were described in three taxonomic papers in the same period (Ho et al. 2012; Kazantsev 2012; Yiu 2017). This is especially striking when compared to the most closely related family of Rhagophthalmidae (i.e., Phengodidae), where numerous taxonomic studies were published (e.g., Constantin 2014, 2016; Zaragoza-Caballero and Hernández 2014; Roza et al. 2017, 2018; Roza and Mermudes 2019, 2020; Vega-Badillo and Zaragoza-Caballero 2019; Vega-Badillo et al. 2020, 2021a, b), including not only descriptions of several new genera and species but also phylogenetic analyses of the group (Zaragoza-Caballero and Zurita-García 2015; Quintino 2017; Kundrata et al. 2019; Roza 2022). In Rhagophthalmidae, the most important research topics include taxonomic limits, phylogenetic relationships, accurate dating of the origin

of the group, the evolution of bioluminescence and pedomorphosis, systematics of all genera (including revisions of already known species as well as descriptions of new taxa), descriptions of pedomorphic females and immature stages for all genera and species, and evaluating the distribution of the group at both generic and family levels.

Phylogenetic relationships, origin, and monophyly of Rhagophthalmidae

The phylogenetic placement of Rhagophthalmidae within Elateroidea has been controversial based on morphology only (Crowson 1972; Lawrence 1988; Branham and Wenzel 2001; Lawrence et al. 2011), and Rhagophthalmidae were often placed either in or close to Lampyridae or Phengodidae. Molecular phylogenetic analyses using various datasets and analytical approaches repeatedly confirmed that Rhagophthalmidae are sister to Phengodidae (Bocakova et al. 2007; Kunderata and Bocak 2011b; Kunderata et al. 2014; Zhang et al. 2018; Douglas et al. 2021; Kusy et al. 2021; Cai et al. 2022). Both families share soft-bodied males with large eyes, often bipectinate antennae with 12 antennomeres, leathery elytra which are usually shortened and narrowed, larviform females, and larvae that possess bioluminescent organs and feed on millipedes (Kawashima et al. 2010; Zaragoza-Caballero and Hernández 2014; Kunderata et al. 2019). Kusy et al. (2021) defined the “lampyroid clade”, which contains Lampyridae, Phengodidae, Rhagophthalmidae, and Sinopyrophoridae. Fossil Cretophengodidae were probably also a part of that clade (Li et al. 2021b).

The date of the origin of Rhagophthalmidae is unclear, as there are no known fossils of the group. Generally, soft-bodied elateroids are rarely found as fossils, and to date, the most informative fossils are inclusions in various ambers. Cretophengodidae were described from mid-Cretaceous amber of northern Myanmar (ca. 99 Mya, Shi et al. 2012; Li et al. 2021b), and Kusy et al. (2021) reported unpublished Phengodidae from the same deposit. Kusy et al. (2021) summarized and reviewed the published molecular dating analyses of the elaterid-lampyroid clade, and showed that median estimates suggest the split of the Lampyridae, Phengodidae, and Rhagophthalmidae clade in the mid-Cretaceous. However, an earlier date is also possible (Kusy et al. 2021).

Another important issue is the monophyly of Rhagophthalmidae. The group was originally proposed only for *Dioptoma*, *Ochotyra*, and *Rhagophthalmus* (Olivier 1907, 1910), and later Pic (1937) added *Mimoochotyra*. This concept was adopted by McDermott (1964, 1966). Crowson (1972) transferred some Asian genera (*Cydistus*, *Diplocladon*, *Falsophrixothrix*) from Drilidae to Phengodidae, and these were later added to Rhagophthalmidae together with *Dodecatoma* (Lawrence and Newton 1995). *Cydistus* was later transferred to Phengodidae (Kunderata et al. 2019). The current concept of Rhagophthalmidae consists of males which have exactly 12 antennomeres, with antennomere III being longer than antennomere II, a telescopic abdomen that is usually narrowed apically, and females which are more or less larva-like. However, the monophyly of this group as currently defined has never been rigorously tested.

Several genera have been included in molecular phylogenetic analyses, including *Bicladodrilus*, *Falsophrixothrix*, *Mimoochotyra*, and *Rhagophthalmus* (incl. *Ochotyra*)

(Bocakova et al. 2007; Kundera et al. 2014, 2019). These genera always formed a monophylum. However, it should be noted that at least the generic placements of specimens identified as *Bicladodrilus* sp. from China and *Mimoochotyra* sp. from Malaysia are dubious. As *Bicladodrilus*, *Bicladum*, and *Diplocladon* are similar in general appearance and possess biflabellate antennae, this generic complex is in need of revision. While there are no described *Bicladodrilus* species in China, a species of *Diplocladon* was recently described from Hong Kong (Yiu 2017). The single described species of *Mimoochotyra* is known from Java (Pic 1937; Wittmer 1944).

In his unpublished PhD thesis, Jeng (2008) focused on systematics and paedomorphosis (neoteny) in Lampyridae. He also included representatives of the rhagophthalmid genera *Dioptoma*, *Diplocladon*, *Dodecatoma*, *Falsophrixothrix*, *Menghuoius*, *Monodrilus*, and *Rhagophthalmus* (incl. *Ochotyra*) in his morphology-based analyses. These genera were monophyletic and sister to Phengodidae. In another unpublished PhD thesis, Roza (2022) focused on phylogenetic relationships of Phengodidae, and included *Bicladodrilus*, *Dioptoma*, *Diplocladon*, *Dodecatoma*, *Falsophrixothrix*, *Pseudothilmanus*, and *Rhagophthalmus* in his morphology-based analyses. These genera formed a monophylum in all analyses performed. A phylogenomic analysis including representatives (ideally type species) of all rhagophthalmid genera would be a valuable assessment of the monophyly of the group.

Bioluminescence and paedomorphosis in Rhagophthalmidae

Within Coleoptera, bioluminescence can be found almost exclusively within the so-called “elaterid-lampyroid clade”, including Elateridae, Lampyridae, Phengodidae, Rhagophthalmidae, and Sinopyrophoridae, and probably the extinct Cretophengodidae (Oba et al. 2011; Fallon et al. 2018; Bi et al. 2019; Li et al. 2021b; Kusy et al. 2021; Powell et al. 2022). In Phengodidae, all known larvae and females are bioluminescent, as are males of some species (Costa and Zaragoza-Caballero 2010). Bioluminescence is hypothesized for lineages in which larvae and females are unknown (e.g., Cydistinae; Kundera et al. 2019). All known larvae and females of Rhagophthalmidae are bioluminescent. Both larvae and females were reported for *Diplocladon* (in fact, it is probably *Haplocladon*; see Remarks under both genera), *Menghuoius*, and *Rhagophthalmus*, whereas only females are known for *Dioptoma* (Green 1913; Gahan 1925; Coblenz and Hughes 1926; Ridley 1934; Haneda 1950; Raj 1957; Lloyd 1971, 1978; Wittmer and Ohba 1994; Ohba et al. 1996a; Kawashima 2000; Jeng 2008; Li and Liang 2008; Li et al. 2008a; Kawashima et al. 2010). Males of at least some genera (e.g., *Dioptoma* and *Rhagophthalmus*) also emit light (Kawashima et al. 2010). At least in some cases, however, there are doubts about the correct genus identification of larvae or females. For example, Jeng (2008) suggested that the giant larviform female from Yunnan, China, identified as *Diplocladon* by Li and Liang (2008) is “likely of *Menghuoius giganteus* or the other related species described from there” (Jeng 2008: 135). The correct identification of larviform females is, however, very important for conclusions on the evolution of morphological modifications

caused by paedomorphosis (e.g., Jeng 2008; Kawashima et al. 2010). This should be possible by e.g., rearing both sexes of the same species from larvae, finding a mating couple, or by the use of DNA barcoding. Information on the life-history and biology of most genera of Rhagophthalmidae is minimal or entirely absent. Further research should be conducted to confirm the presence of bioluminescence in the remaining rhagophthalmid genera.

Elateroid beetles are well-known not only for bioluminescence but also for morphological modifications caused by paedomorphosis (Crowson 1972; Cicero 1988; Bocak et al. 2008; Ferreira and Ivie 2022). In Elateroidea, mainly adult females are more or less modified, with a gradual series of morphological modifications across many families (Elateridae, Jurasaidae, Lampyridae, Lycidae, etc.), ranging from taxa that possess only a slightly softer body cuticle and a more relaxed abdomen through a number of intermediate stages, with variously reduced mouthparts, antennae, elytra, hind wings, and/or parts of the thorax, and a higher number of free abdominal ventrites, to taxa which are highly larviform (Bocakova et al. 2007; Bocak et al. 2008; Ferreira et al. 2019, 2020, 2022; Kundrata and Bocak 2019; Rosa et al. 2020; Ferreira and Ivie 2022). In both Phengodidae and Rhagophthalmidae, all known females are highly paedomorphic, being wingless and larva-like (Costa and Zaragoza-Caballero 2010; Kawashima et al. 2010). In Rhagophthalmidae, females are known only for *Diophtoma*, *Diplocladon* (*Haplocladon*?), *Menghuoius*, and *Rhagophthalmus* (Haneda 1950; Harvey 1952; Ohba 1997c; Kawashima 1998; Chen 2003; Jeng 2008; Li and Liang 2008; Li et al. 2008a); however, only those of *Diplocladon* (*Haplocladon*?) and *Rhagophthalmus* are described in detail (Kawashima et al. 2010). Interestingly, females of both genera exhibit different degrees of paedomorphic modifications, with *Diplocladon* (*Haplocladon*?) being completely larviform (including having stemmata, antennae with three antennomeres, tibiotarsus with a single pretarsal claw, and missing ovipositor) and *Rhagophthalmus* being incompletely larviform (having compound eyes, antennae with six or seven antennomeres, tarsi with five tarsomeres and two pretarsal claws, and ovipositor; Kawashima et al. 2010). Similar cases of different levels of morphological modifications in females of different genera were also reported for e.g., Elateridae (*Drilus* Olivier, 1790 being more paedomorphic than *Omalisus* Geoffroy, 1762 or *Cebrio* Olivier, 1790; Kundrata and Bocak 2019), Jurasaidae (*Jurasai* Rosa et al., 2020 being more paedomorphic than *Tujamita* Rosa et al., 2020; Rosa et al. 2020), and Lampyridae (*Lamprigera* Motschulsky, 1853 or *Stenocladius* Fairmaire, 1878 being more paedomorphic than *Lampyrus* Geoffroy, 1762 or *Lamprohiza* Motschulsky, 1853; Ohba et al. 1997; Dong et al. 2021). It would be, therefore, very interesting to discover and describe in detail the females of all remaining rhagophthalmid genera.

Generic classification and systematics of Rhagophthalmidae

It is clear from the above text that the classification and systematics of Rhagophthalmidae is in a very poor state of knowledge. Species of *Bicladodrilus*, *Bicladum*, *Falsophrixothrix*, *Mimoochotyra*, and *Monodrilus* have not been taxonomically treated since their

descriptions, and their names have usually appeared only in catalogues, if at all. Taxonomic revisions are urgently needed for all genera currently included in Rhagophthalmidae with the exception of *Pseudothilmanus*, which was revised recently (Kundera and Bocak 2011a). Although the most species-rich genus *Rhagophthalmus* received some taxonomic attention in the last decades (e.g., Wittmer and Ohba 1994; Wittmer 1997; Kawashima and Satô 2001; Kawashima and Sugaya 2003; Li et al. 2008a; Ho et al. 2012; Yiu 2017), a comprehensive revision is still needed.

Due to a scarcity of information on the morphology of most rhagophthalmid taxa, an identification key which would help taxonomists to recognize genera and species in collections and subsequently enhance knowledge on their diversity, variability, and distributions, is also missing. Most importantly, it is necessary to delimit generic boundaries in some problematic generic complexes. For example, *Bicladodrilus*, *Bicladum*, and *Diplocladon* share biflabellate antennae and relatively long elytra, and are not clearly distinguished from one other. Detailed taxonomic studies should also be conducted to revise the status of *Ochotyra* (currently a synonym of *Rhagophthalmus*) and *Menghuoius* (currently a separate genus but treated by some authors as a synonym of *Rhagophthalmus*). Some genera contain species which are probably not congeneric with their type species (e.g., some *Dodecatoma* spp. resemble *Pseudothilmanus* more than *D. bicolor*), and e.g., *Dodecatoma testaceiceps* should be removed from Rhagophthalmidae after a detailed revision. Taxonomic attention should be given not only to currently described taxa, but also to numerous undescribed Rhagophthalmidae mainly from Southeast Asia, which are housed in various institutional and personal collections (RK pers. obs.).

Taxonomic revisions are usually hampered by missing, lost, or otherwise unavailable type specimens, especially in long-neglected groups, such as Rhagophthalmidae. However, the vast majority of name-bearing rhagophthalmid type specimens are available in European and Asian museum collections. To date, we have been unable to locate name-bearing type specimens of only five species described by either Pic, Fairmaire, or Olivier, four of which belong to *Rhagophthalmus*. Name-bearing type specimens of species in 10 smaller genera are each deposited in one to three museum collections only; however, those of *Dodecatoma* and *Rhagophthalmus* are in seven and 12 institutions, respectively.

Distribution of Rhagophthalmidae

Rhagophthalmidae are distributed in the Oriental realm and the Palearctic bioregion of East Asia, in the area from Afghanistan and Pakistan, through the Himalayas, Indian Peninsula, Sri Lanka, China, and mainland Southeast Asia, to Sumatra, Java, Bali, Borneo, and the Philippines. The center of genus-level diversity of Rhagophthalmidae lies in Southeast Asia. Nine out of 12 genera have at least one species distributed in Southeast Asia, with five genera (i.e., *Bicladodrilus*, *Bicladum*, *Falsophrixothrix*, *Mimoochotyra*, and *Monodrilus*) being endemic to the region. However, this only accounts for approximately one third of described species. The genera *Dodecatoma* and *Pseudothilmanus* are known only from the Himalayas and surrounding regions (one

species and one subspecies of *Dodecatoma* from Southeast Asia should be removed from that genus), and *Dioptoma* is endemic to the Indian Peninsula and Sri Lanka. Regarding the most species-rich genus *Rhagophthalmus*, only seven out of 34 species are known from Southeast Asia, including only a single species from the Greater Sunda Islands. Another seven species are known from the Indian Peninsula and Sri Lanka, and the remaining majority of species are distributed in mainland China and among the islands of East Asia.

Interestingly, in the eastern part of their distribution, Rhagophthalmidae have remained within the boundaries of the Sunda Shelf and the Philippines, i.e. west of the originally proposed Wallace Line, which was demarcated to separate Indo-Malayan (Oriental) and Austro-Malayan (Australasian) realms (Wallace 1863; Voris 2000; Lohman et al. 2011). The Sunda Shelf is a southward expansion of the continental shelf of Southeast Asia that was intermittently exposed by lowered sea levels during the Pleistocene (Hall 1998; Voris 2000; Lomolino et al. 2017). The Wallace line separates Bali and Borneo on the west from Lombok and Sulawesi on the east. It is a strong dispersal barrier to many terrestrial animals because of deep oceanic trenches (Lomolino et al. 2017). Rhagophthalmidae have a limited dispersal propensity due to their highly modified larviform females and, therefore, it is not surprising that they remained within the boundaries of the continental shelf of Southeast Asia, with a single described species from the Philippines. Additionally, it should be noted that there are no Rhagophthalmidae from east of the Wallace Line among the extensive material of non-type specimens (including numerous new species) that reside in major European museums and several personal collections, which the first author examined for a planned generic revision of the group. A single, unreported rhagophthalmid species from Bali is the closest that the family has been observed to the Wallace Line. A taxonomic revision of Rhagophthalmidae will further improve our knowledge of the distributions of individual genera and their species, some of which are currently known only from a single specimen.

Conclusions

Here we provide the first comprehensive catalogue of the currently defined Rhagophthalmidae. The only catalogues of the group were those of Olivier (1910) and McDermott (1966; Rhagophthalminae as a subfamily of Lampyridae) but they contained only three genera and nine species, and four genera and 21 species, respectively. Here, we recognize 12 genera and 66 species. However, all genera but *Pseudothilmanus* urgently need taxonomic revisions, and numerous new species await formal descriptions. The phylogenetic position of Rhagophthalmidae as a sister group to Phengodidae is now generally accepted; however, interrelationships within the group and generic classification remain poorly known. Although morphology-based analyses in two PhD studies that were focused on related families (Jeng 2008; Roza 2022) confirm the monophyly of currently circumscribed Rhagophthalmidae, molecular analysis including representatives of

all genera would be desirable. Additionally, little information is known of the biology of the group. Although various studies have been published on the ontogeny, biology, and behaviour of the most common genus *Rhagophthalmus*, there is virtually nothing known about the majority of other genera. Because known females in Rhagophthalmidae are highly morphologically modified and remain larviform as adults, they are interesting subjects for researching the evolution of paedomorphosis in Elateroidea. However, only a few have been studied in detail (Kawashima et al. 2010). Additionally, all known larvae and females (and some males) are bioluminescent, and therefore are an important source of information for research on the evolution of bioluminescence in beetles. However, this phenomenon is also understudied in Rhagophthalmidae, as larvae and females are unknown for most genera. Discoveries, field observations, morphological studies, and correct genus and species identifications of larvae and larviform females of Rhagophthalmidae are therefore crucial not only for our improved knowledge of the diversity, systematics, and morphology of the group, but also for a better understanding of the evolution of paedomorphosis and bioluminescence in Elateroidea and beetles in general.

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A new genus *Anamalysia* van Achterberg (Hymenoptera, Braconidae, Alysiinae), six new species, and two new combinations from India, Indonesia, Malaysia, Singapore, Thailand, and Vietnam

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Abstract

A new genus of the tribe Alysiini (Hymenoptera, Braconidae, Alysiinae) is described with specimens from India, Indonesia, Malaysia, Singapore, Thailand, and Vietnam, and six new species are described: *Anamalysia idiaestimorpha* **sp. nov.** (type species), *A. knecosoma* **sp. nov.**, *A. mellipes* **sp. nov.**, *A. transversator* **sp. nov.**, *A. vandervechti* **sp. nov.**, and *A. vanhengstumi* **sp. nov.**. We transfer one species from *Coelalysia* to *Anamalysia*: *A. urbana* (Papp, 1967) **comb. nov.** from Singapore and one species from *Alysiasta* to *Anamalysia*: *A. triangulum* (Fischer, 2006) **comb. nov.** from Malaysia, Laos, Indonesia and Vietnam. A key to the genus of *Anamalysia* is included.

Keywords

Alysiini, identification, key, new combination, Oriental, South Asia, taxonomy

Introduction

Alysiini (Hymenoptera, Braconidae, Alysiinae) is a large tribe with 76 genera and over 1565 valid species (Yu et al. 2016). The Alysiini include mostly koinobiont endoparasitoids of cyclorrhaphous dipteran larvae, which use their mandibles (usually with 3 or 4 teeth or lobes) to break open the puparium of the host (Wharton 1977). In this paper, one new genus *Anamalysis* gen. nov., including six new species (*Anamalysis idiastimorpha* sp. nov. (type species), *A. knekosoma* sp. nov., *A. mellipes* sp. nov., *A. transversator* sp. nov., *A. vandervechti* sp. nov., and *A. vanhengstumi* sp. nov. are described, and two new combinations are reported.

Methods

Specimens from Thailand were collected using a Malaise trap in Nakhon Si Thammarat (Namtok Yong National Park) and Doi Chiangdao (the third highest peak in Thailand). Specimens were preserved in 95% ethyl alcohol and then dehydrated using hexamethyldisilazane (HMDS) as described in Heraty and Hawks (1998) and subsequently card point mounted. The specimens from India were hand-net collected and kept dry before pinned. Specimens from Malaysia, Indonesia, and Vietnam were collected in 70% alcohol with Malaise traps unless otherwise indicated. The specimens were subsequently prepared according to the AXA method (van Achterberg 2009; van Achterberg et al. 2010) and glued on card points.

For the identification of the subfamily Braconidae, see van Achterberg (1990, 1993), for the terminology and measurements used in this paper, see van Achterberg (1988, 1993), and for additional references, see Yu et al. (2016).

Photographs for species plates were produced using a JVC digital camera mounted on a Leica MZ16 microscope and Auto-Montage stacking software. Photos were slightly processed (cropped and background modified) in Photoshop.

COI sequences of *A. knekosoma* sp. nov. and *A. transversator* sp. nov. are deposited in GenBank. For protocols of DNA extraction, PCR, and sequencing, see Yao et al. (2020). Specimens are deposited in the Oberösterreichisches Landesmuseum, Biologiezentrum, Linz (**BZL**); Institute of Ecology and Biological Resources, Vietnam Academy of Science and Technology, Hanoi, Vietnam (**IEBR**); Naturalis Biodiversity Centre, Leiden, the Netherlands (**RMNH**); Texas A&M University, College Station, Texas, USA (**TAMU**); Universiti Kebangsaan Malaysia, Bangi, Selangor, Malaysia (**UKM**); Queen Sirikit Botanic Gardens Entomology Collection, (**QSBG**) Chiang Mai, Thailand.

Results and discussion

Taxonomy

Anamalysisia van Achterberg, gen. nov.

<https://zoobank.org/0A2F1359-EDA4-4A1A-8BC3-31BB43F12139>

Figs 1–8

Type species. *Anamalysisia idiastimorpha* van Achterberg, sp. nov.

Etymology. From “Anamala (or Anaimala) Hills” (the type locality) and the generic name *Alysia* Latreille, 1804. Anamala or Anaimalai Mountains, also known as the Elephant Mountains, are a range of mountains in the southern Western Ghats of central Kerala (India). Gender: feminine.

Diagnosis. Fourth antennal segment 1.1–1.4 times longer than third segment; clypeus rectangularly narrowed ventrally, triangular in dorsal view and with acute ventral apex (Figs 1B, 6B) to round ventral apex (Figs 2B, 3H, 4B, 5F, 8B); area between antennal socket and eye with a narrow groove (Figs 1B, 6B, D, 8B, E); face distinctly sculptured, distinctly transverse and without medio-ventral grooves (Figs 1B, 2B, 4B, 6B, 8B); mandible strongly widened apically and partly sculptured, lateral teeth wide lobe-shaped and second tooth short (Figs 1H, 2E, 3C, G, 4C, 5D, E, 6C, 8G, H); anterior tentorial pits small, far removed from eye; pronope deep and medium-sized to large (Figs 1C, 8D); notauli complete; precoxal sulcus widely crenulate medially and posteriorly narrow or absent; postpectal carina absent; metanotum often distinctly protruding dorsally; vein 2-SR of fore wing 0.9–1.2 times vein 3-SR (for *A. vandervechti*, 2-SR of fore wing 0.5 times vein 3-SR); vein SR1 of fore wing 2.0–2.7 times as long as vein 3-SR (for *A. vandervechti*, vein SR1 of fore wing 0.8 times as long as vein 3-SR); vein r of fore wing much longer than wide; vein m-cu of interstitial or postfurcal; first subdiscal cell of fore wing narrow (Figs 1A, 2D, 3A, 4G, 5A, 8A); vein 3-CU1 of fore wing distinctly longer than vein CU1b (Figs 1A, 2D, 3A, 4G, 5A, 6A, 8A), but slightly shorter in *A. vandervechti* (Fig. 6A); marginal cell of hind wing medium-sized, subparallel-sided; vein 1r-m of hind wing 0.6–0.8 times as long as vein 1-M; vein M+CU of hind wing distinctly longer than vein 1-M; vein m-cu of hind wing distinct, in type species largely sclerotised; tarsal claws rather robust (Figs 1F, 3D); length of first metasomal tergite 1.0–1.4 times its apical width; dorsope present; ovipositor sheath with long erect setae and apically rounded, no apical spine (Figs 1L, 5B), setose part of sheath about 0.4–0.7 times as long as fore wing.

Synonymy. *Alysiasta* Wharton, 1980 sensu Fischer (2006) (partly, not type species); *Coelalysia* Cameron, 1911 sensu Fischer (1988) (partly, not type species).

Biology. Unknown.

Distribution. Oriental.

Notes. The shape of the clypeus is similar to that of the Afrotropical genus *Coelalysia* Cameron, 1911, but *Coelalysia* lacks a complete groove between the antennal socket and the eye, has the dorsope absent or small, the face is largely smooth and strongly

transverse, vein M+CU of the hind wing is distinctly shorter than vein 1-M and vein CU1b of fore wing is about as long as vein 3-CU1 or longer, scutellar sulcus about half as long as scutellum, middle tooth of mandible long and mesosternal sulcus narrowly crenulate posteriorly. *Coelalysia urbana* (Papp, 1967) is excluded from the genus *Coelalysia* and fits well in *Anamalysia*, together with *Alysiasta triangulum* Fischer, 2006 (comb. nov.) and might be the senior synonym of the latter.

Key to species of the genus *Anamalysia* gen. nov.

- 1 Vein SR1 of fore wing about 0.8 times as long as vein 3-SR (Fig. 6A); vein 3-SR of fore wing about twice as long as vein 2-SR; vein 1-R1 of fore wing of ♂ widened medially (♀ unknown); basal fifth of hind tibia whitish; precoxal sulcus present posteriorly; notauli distinctly narrowly crenulate; length of first tergite about 2.4 times its apical width (Fig. 6F); Indonesia (Sumatra).....***A. vandervechti* van Achterberg, sp. nov.**
- Vein SR1 of fore wing 2.0–2.8 times as long as vein 3-SR (Figs 1A, 2D, 3A, 4G, 5A, 8A); vein 3-SR of fore wing 0.8–1.2 times as long as vein 2-SR; vein 1-R1 of fore wing of ♀ narrow medially; basal fifth of hind tibia dark brown or yellowish; precoxal sulcus absent posteriorly (Figs 2F, 4F, 8C); notauli smooth; length of first tergite 1.0–1.3 times its apical width (Figs 1I, 2G, 3F, 4H, 5G, 6F, 8F).....**2**
- 2 Eye in dorsal view 4.2–4.4 times as long as temple and temple narrowed behind eyes (Fig. 3B); middle tooth of mandible free dorsally (Fig. 3C, G); antenna of ♀ with about seven ivory or whitish segments apically; [first tergite 1.4–1.5 times longer than its apical width; hind tibia yellowish brown; lamella above middle tooth of mandible sinuate]; Malaysia.....***A. mellipes* van Achterberg & Yaakop, sp. nov.**
- Eye in dorsal view 1.1–2.6 times as long as temple and temple parallel-sided or widened behind eyes (Figs 1E, 2C, 4E, 8E); middle tooth of mandible connected to curved apical lamella (Figs 1H, 2E, 4C, 5D, E, 8G, H); apical segments of antenna of ♀ black or dark brown (but unknown of *A. urbana*, *A. idiastrimorpha*, *A. vanhengstumi*, and *A. transversator*)**3**
- 3 Eye in dorsal view 1.1 times longer than temple (Fig. 8E); first tergite about 1.4 times longer than its apical width; temples strongly widened behind eyes (Fig. 8E); hind tibia brownish yellow; [head largely yellowish brown laterally]; Vietnam.....***A. vanhengstumi* van Achterberg & Long, sp. nov.**
- Eye in dorsal view 1.6–2.6 times as long as temple (Figs 1E, 2C, 4E); first tergite 1.0–1.2 times as long as its apical width (Figs 1I, 2G, 4H, 5G); temples parallel-sided behind eyes (Figs 1E, 2C, 4E); hind tibia brown or dark brown, rarely paler.....**4**
- 4 Vein r-m of fore wing subvertical (Fig. 1A); eye in dorsal view 1.6–1.8 times as long as temple (Fig. 1E); clypeus slightly narrower and apically more

- acute (Fig. 1B); pterostigma dark brown; [second metasomal tergite blackish dorsally and hardly contrasting with black first tergite; vein 3-SR of fore wing 0.8 times as long as vein 2-SR]; India ***A. idiastimorpha* van Achterberg, sp. nov.**
- Vein r-m of fore wing distinctly inclivous (Figs 2D, 4G, 5A); eye in dorsal view 1.9–3.0 times as long as temple (Figs 2C, 4E); clypeus slightly wider and apically rounded (Figs 2B, 4B, 5F); pterostigma brown **5**
- 5 Width of head 2.1–2.4 times medial length (Figs 2C, 4E); vein m-cu of fore wing subinterstitial (Figs 2D, 4G); vein cu-a of fore wing more postfurcal (Figs 2D, 4G) **6**
- Width of head 1.7–1.9 times medial length; vein m-cu of fore wing less postfurcal (Fig. 5A); vein cu-a of fore wing subinterstitial (Fig. 5A) **7**
- 6 Eye in dorsal view 3.0 times as long as temple (Fig. 4E); propodeum with a complete longitudinal carina, largely smooth anteriorly, except for a short median carina and rugae near it, medially with circular areolate area and posteriorly reticulate, smooth posterior-laterally (Fig. 4D); vein m-cu of hind wing strongly removed from 2-M (Fig. 4G); notauli complete, deep, narrow, and smooth; midpit small and round, connected to notauli (Fig. 4E); length of setose part of ovipositor sheath 0.7 times fore wing and 0.9 times as long as hind tibia (Fig. 4A); length of body 3.5 mm, length of fore wing 3.6 mm ***A. transversator* van Achterberg & Yao, sp. nov.**
- Eye in dorsal view 2.0 times as long as temple (Fig. 2C); propodeum largely smooth and with sparse punctures anteriorly, except for a short median carina with rugae near it, medially with crown-shaped areolate area and bottom carina protuberant, medio-posteriorly densely reticulate, latero-posteriorly smooth with a longitudinal carina respectively (Fig. 2G); vein m-cu of hind wing interstitial (Fig. 2D); notauli complete, deep, and narrow, smooth, without midpit, more depressed in the end of notauli (Fig. 2C, G); length of setose part of ovipositor sheath as long as fore wing and 0.4 times as long as hind tibia (Fig. 2A); length of body 5.0 mm, length of fore wing 4.6 mm ***A. knekosoma* Yao & van Achterberg, sp. nov.**
- 7 Length of setose part of ovipositor sheath about 0.44 times as long as fore wing; hind tibia and tarsus yellowish brown, slightly infuscated; mesosoma brown or reddish brown; vein SR1 of fore wing about 2.2 times as long as vein 3-SR (fig. 25 in Papp 1967); vein m-cu of hind wing subinterstitial; Singapore..... ***A. urbana* (Papp, 1967) comb. nov.**
- Length of setose part of ovipositor sheath 0.37–0.38 times as long as fore wing; hind tibia (except ivory base) and base of tarsus dark brown or infuscate; mesosoma black or dark chestnut brown; vein SR1 of fore wing 2.3–2.4 times as long as vein 3-SR (Fig. 5A); vein m-cu of hind wing usually distinctly antefurcal; Indonesia, Malaysia, Laos, Vietnam..... ***A. triangulum* (Fischer, 2006) comb. nov.**

***Anamalysia idiastimorpha* van Achterberg, sp. nov.**

<https://zoobank.org/839C94E5-28ED-48C2-B96F-CF92048C4DD8>

Fig. 1A–L

Type material. *Holotype*, ♀ (RMNH), SOUTH INDIA, Anaimalai Hills, Cinchona [plantation?], 3500 ft, v.1964, P. Susai Nathan.

Non-type: 1 ♀ (RMNH), INDIA, Kerala, 9–17 km W. Pormudi, 5.xi.1984, B.180, K. Ghorpade.

Description. *Holotype*, ♀, length of body 5.5 mm, length of fore wing 5.0 mm.

Head. Width of head twice its median length, sparsely setose; antenna incomplete, 22+, segments densely setose, length of third segment 0.9 times as long as fourth segment, length of third and fourth segments 3.0 and 4.6 times their width, respectively (Fig. 1G, J); length of maxillary palp 1.2 times height of head; eye in dorsal view 1.8 times as long as temple; temple in dorsal view subparallel-sided behind eyes (Fig. 1E); OOL: diameter of ocellus: POL = 24:7:6 (Fig. 1E); frons flat medially and convex laterally, smooth and with pit between antennal sockets; antennal sockets distinctly protruding; smooth narrow groove between antennal sockets and eye; minimum width of face 0.55 times maximum width of head, densely punctate submedially, more sparsely on remainder of face, with long setae, without crenulate grooves ventrally (Fig. 1B); clypeus narrow, triangular, with long setae and ventrally acute and its surface with a few punctures, moderately convex dorsally, length of malar space 0.1 times basal width of mandible; mandible coarsely rugose medially, strongly widened apically, its medial length 1.4 times its maximum width, upper tooth large and truncate lobe-shaped, with ventral tooth rounded and lobe-shaped, connected to a ventral carina (Fig. 1H).

Mesosoma. Length of mesosoma 1.6 times its height; pronotum dorsally with large deep and round dorsope; side of pronotum with some coarsely crenulate antero-medially, posteriorly finely crenulate and remainder smooth; epicnemial area dorsally punctulate, medially crenulate and ventrally punctate; precoxal sulcus absent posteriorly, remainder very wide and coarsely crenulate; remainder of mesopleuron smooth; episternal scrobe linear; pleural sulcus finely crenulate, but ventrally more coarsely crenulate (Fig. 1K); mesosternal sulcus coarsely crenulate, rather wide posteriorly; metapleuron largely coarsely rugose-punctate; notauli complete, deep and narrow, mainly smooth (Fig. 1C); mesoscutum strongly shiny and largely glabrous, but with long setae near notauli and lateral carina; mesoscutum without a medio- posterior depression; axilla conspicuously setose and lateral carina lamelliform protuberant; scutellar sulcus deep, with one carina and some punctures, 0.3 times as long as scutellum; scutellum rather convex in lateral view; metanotum distinctly lamelliform protruding dorsally in lateral view; surface of propodeum largely smooth antero-laterally, remainder vermiculate- reticulate, without areola and with long irregular median carina; propodeal spiracle round, small and in front of middle of propodeum.

Wings. Pterostigma subelliptical (Fig. 1A), its posterior margin hardly curved; vein r issued distinctly behind middle of pterostigma and distinctly oblique; r:3-SR:SR1 = 5:20:53; 1-SR+M sinuate (left wing) or straight (right wing); SR1 straight; cu-a short

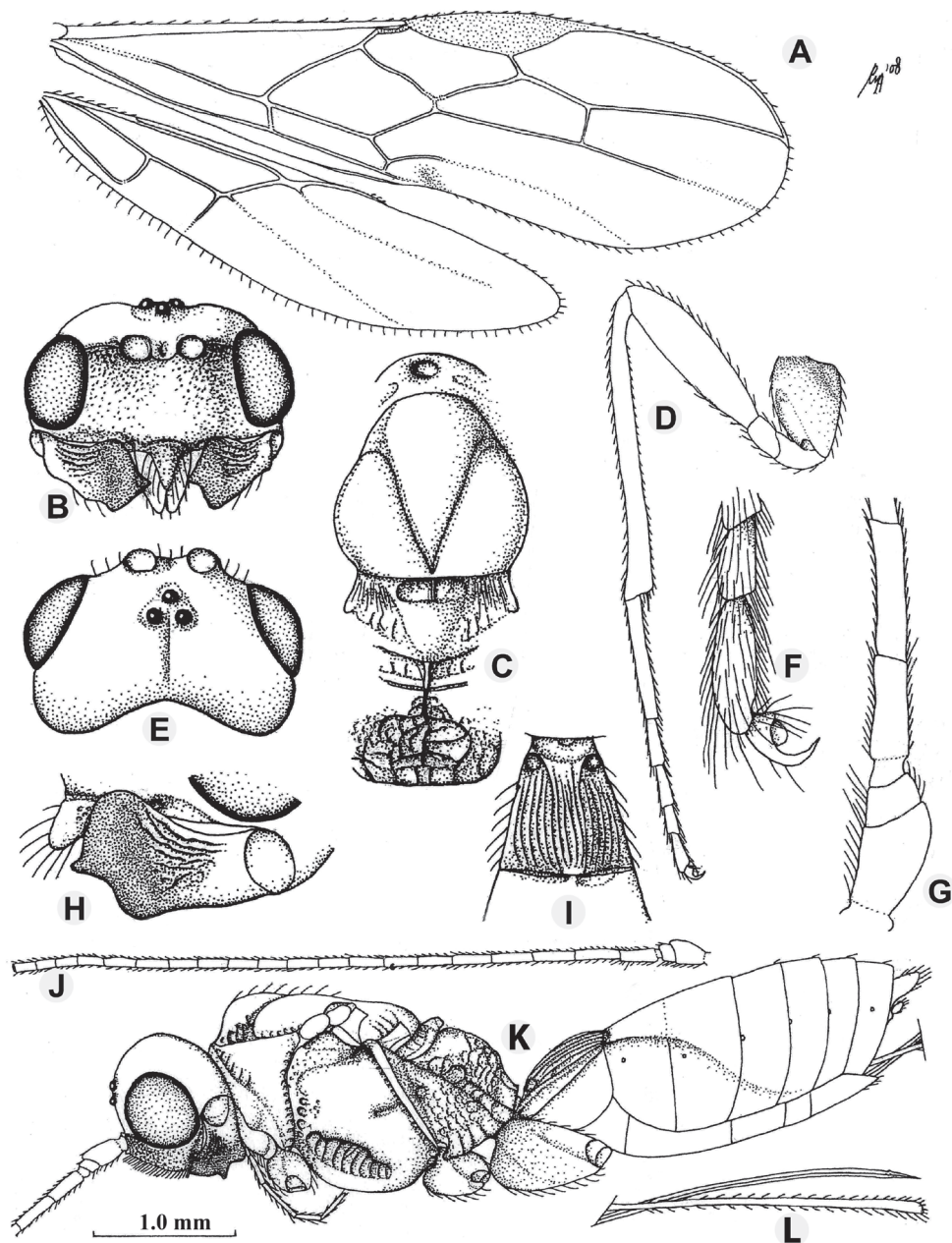


Figure 1. *Anamalsia idiastrimorpha* sp. nov., ♀, holotype **A** wings **B** head, anterior aspect **C** mesosoma, dorsal aspect **D** hind leg **E** head dorsal aspect **F** outer hind claw **G** basal antennal segments **H** mandible full sight on second tooth **I** first metasomal tergite dorsal aspect **J** antenna **K** habitus lateral aspect **L** ovipositor and its sheath. Scale bars: 1.0 mm (**A**, **D**, **J**–**L**); 1.4 mm (**B**, **C**, **E**, **I**); 3.0 mm (**F**, **G**); 4.0 mm (**H**).

and oblique, postfurcal; 1-CU1:2-CU1 = 1:14; 2-SR:3-SR:r-m = 24:20:10; m-cu distinctly postfurcal, slightly converging to 1-M posteriorly; first subdiscal cell 4.7 times as long as wide; CU1b distinctly shorter than 3-CU1 and 3-CU1 oblique. Hind wing: M+CU:1-M:1r-m = 30:22:18; m-cu distinctly developed and removed from 2-M and largely sclerotised (Fig. 1A).

Legs. Outer side of hind coxa finely punctate and densely setose, dorsally smooth; middle coxa strongly protruding forwards ventrally, less so of hind coxa; tarsal claws moderately robust; length of femur, tibia, and basitarsus of hind leg 3.7, 11.7, and 7.5 times their width, respectively; hind tibia and basitarsus rather short and adpressed bristly setose (Fig. 1D, F).

Metasoma. Length of first tergite equal to its apical width, its surface regularly costate-striate, its dorsal carinae complete (Fig. 1I); laterope absent; dorsope large and deep; remainder of metasoma smooth and rather depressed; ovipositor with minute dorsal notch and some ventral teeth; length of setose part of ovipositor sheath 0.39 times fore wing and nearly as long as hind tibia; apex of ovipositor sheath subtruncate and no apical spine (Fig. 1L); hypopygium medium-sized and apically acute in lateral view (Fig. 1K).

Colour. Black; scapus, pedicellus, and tegulae more or less chestnut brown; palpi pale yellowish; metasoma (except black first tergite and dark parts of second and third tergites) and apically femur and tibia of fore leg brownish yellow; remainder of antenna (as far as present) and of legs, mandible, second tergite dorsally and middle of third tergite, ovipositor sheath, pterostigma (but apex paler brown), and most veins dark brown; wing membrane slightly infuscate.

Variation. The specimen from Kerala is very similar but has the pterostigma narrower, third antennal segment comparatively slender (3.5 times longer than wide and about as wide as fourth segment) and vein m-cu of hind wing unsclerotised. It has 46 antennal segments, 1.8 times as long as fore wing and its apical half completely black; length of fore wing 4.2 mm and of body 4.6 mm; eye in dorsal view 1.7 times as long as temple; length of setose part of ovipositor sheath 0.37 times fore wing.

Distribution. South India (Anamalai Hills).

Etymology. Named after the generic name *Idiasta* Foerster, 1863 because of its morphological similarity.

Anamalysia knekosoma van Achterberg & Yao, sp. nov.

<https://zoobank.org/9E4DD0CE-ED51-42B1-9A15-5BC0FF97B55E>

Fig. 2A–G

Type material. *Holotype*, ♀ (QSBG), THAILAND, Chiang Mai, Doi Chiangdao NP Headquarters 19°24.3'N, 98°55.3'E, 491 m, Malaise trap 16–23.xi.2007, S. Jugsu & A. Watwanich leg. T5713, GenBank accession number MG912777 (COI).

Description. *Holotype*, ♀, length of body 5.0 mm, length of fore wing 4.6 mm.

Head. Width of head 2.4 times its median length, sparsely setose and strongly shiny; antenna complete (Fig. 2A), 47-segmented, segments densely setose, length of third

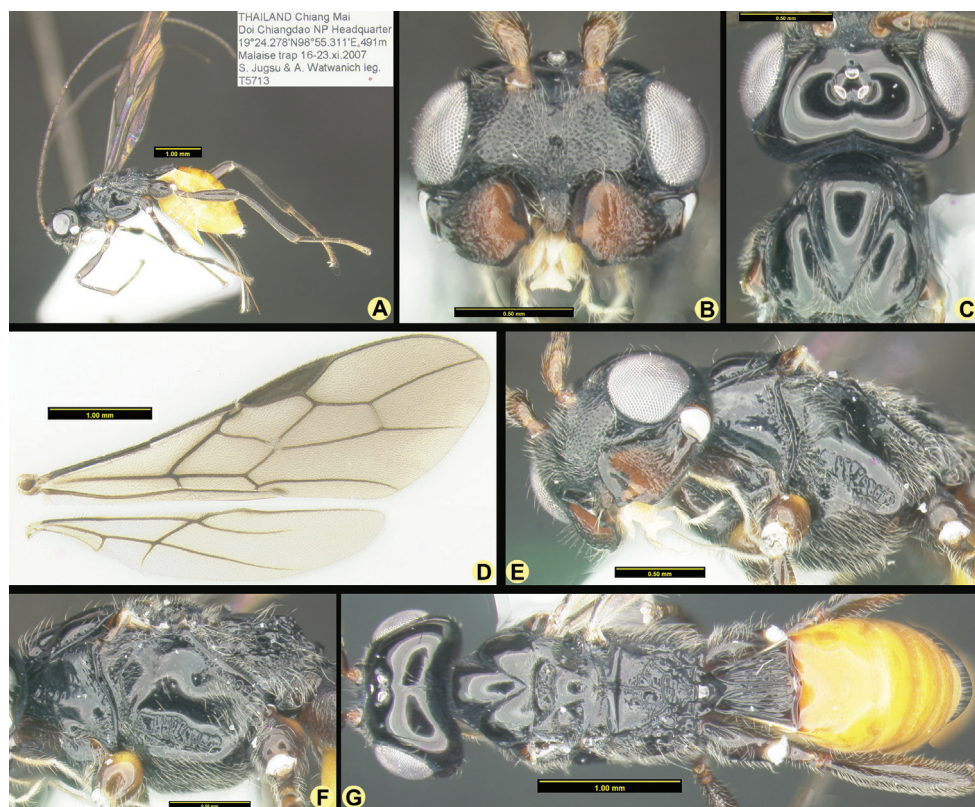


Figure 2. *Anamalsia knecosoma* sp. nov., ♀, holotype **A** habitus lateral aspect **B** head anterior aspect **C** head and mesoscutum dorsal aspect **D** wings **E** mandible and ventrolateral aspect of head and mesosoma **F** mesosoma lateral aspect **G** habitus, dorsal aspect.

segment 0.7 times as long as fourth segment, length of third and fourth segments 3.8 and 6.5 times their width, respectively; length of maxillary palp 1.5 times height of head; eye in dorsal view 2.0 times as long as temple; temple in dorsal view subparallel-sided behind eyes (Fig. 2C); OOL: diameter of ocellus: POL = 14:6:11; frons flat medially (except an incomplete median groove, anteriorly half deep groove and posteriorly half with groove trace) and convex laterally, smooth; antennal sockets distinctly protruding; with a smooth, narrow and superficial groove between antennal sockets and eye; minimum width of face 0.35 times maximum width of head, densely rugulose-punctate, with a Y-shaped carina medially (from antenna sockets to clypeus), medio-posteriorly with fine reticulate, with rather dense and long setae (Fig. 2B); clypeus wide, triangle, width 1.1 times its length, with long setae and ventrally rounded and its surface largely smooth except a few punctures (Fig. 2B); length of malar space 0.1 times basal width of mandible; mandible sparsely rugose medially except teeth part smooth, strongly widened dorsally, its medial length 1.8 times its maximum width, upper tooth large and truncate lobe-shaped, with ventral tooth rather small, rounded and lobe-shaped, connected to a carina (Fig. 2E).

Mesosoma. Length of mesosoma 1.6 times its height; pronotum dorsally with large deep and round dorsope; side of pronotum with some coarse crenulate anteriorly, posteriorly finely crenulate and remainder smooth (Fig. 2F); epicnemial area dorsally smooth, medially crenulate and ventrally punctate-rugose; precoxal sulcus anterior 1/5 smooth and remainder crenulate, widely crenulate anteriorly, narrowed after its middle and absent posteriorly (Fig. 2F); remainder of mesopleuron smooth; episternal scrobe round, deep; pleural sulcus anteriorly smooth and punctulate, with dense setae, posteriorly coarsely crenulate; mesosternal sulcus coarsely crenulate, rather wide posteriorly; metapleuron largely smooth and punctulate, with fine reticulate ventrally; notauli complete, deep and narrow, smooth, without midpit, more depressed in the end of notauli (Fig. 2G); mesoscutum strongly shiny and largely glabrous, but with some long setae near notauli and lateral carina and medial lobe protuberant; mesoscutum without a separate medio-posterior depression (Fig. 2G); axilla rather setose and lateral carina moderately protuberant; scutellar sulcus deep, with one carina and coarsely rugae, without punctures, 0.2 times as long as scutellum; scutellum rather convex in lateral view; metanotum distinctly lamelliform protruding posteriorly in lateral view; propodeum largely smooth and with sparse punctures anteriorly, except for a short median carina with rugae near it, medially with crown-shaped areolate area and bottom carina protuberant, medio-posteriorly densely reticulate, latero-posteriorly smooth with a longitudinal carina respectively (Fig. 2G); propodeal spiracle round, small and medially at propodeum.

Wings. Pterostigma subelliptical, its posterior margin hardly curved; vein r issued distinctly behind middle of pterostigma and distinctly oblique; $r:3-SR:SR1 = 7:22:50$; $1-SR+M$ rather sinuate; $SR1$ straight, slightly curved posteriorly; $cu-a$ short and oblique, strongly postfurcal; $2-SR:3-SR:r-m = 38:36:19$, vein $r-m$ of fore wing distinctly inclivous; $m-cu$ slightly postfurcal, slightly converging to $1-M$ posteriorly; first subdiscal cell 5.0 times as long as wide; $3-CU1:CU1b = 3.2$ and $3-CU1$ oblique. Hind wing: $M+CU:1-M:1r-m = 83:53:45$; $m-cu$ distinctly developed and interstitial (Fig. 2D).

Legs. Outer side of hind coxa largely smooth, punctulate and moderately setose, dorsally shiny and smooth; middle coxa strongly protruding forwards ventrally, hind coxa gradually narrowed; tarsal claws moderately robust; length of femur, tibia and basitarsus of hind leg 3.9, 10.0, and 6.9 times their width, respectively; middle tibia and basitarsus rather short and adpressed setose (Fig. 2A).

Metasoma. Length of first tergite 1.1 times its apical width, its surface regularly costate-striate, its dorsal carinae complete and united submedially (Fig. 2G); laterope absent; dorsope large and deep; remainder of metasoma smooth and rather depressed; ovipositor with minute dorsal notch and some ventral teeth; setose part of ovipositor sheath as long as fore wing and 0.4 times as long as hind tibia (Fig. 2A); apex of ovipositor sheath subtruncate and no apical spine; hypopygium medium-sized and apically acute in lateral view (Fig. 2A).

Colour. Black; head and first tergite apically chestnut brown; scapus, pedicellus, and mandible apically brownish yellow; tegulae brown, but dorsal half brownish yellow; fore leg light brown (except coxa brownish yellow with yellow spot basally,

trochanter, trochantellus with dark yellow spot apically, tibia basally and tarsus apically darkened yellow); middle leg light chestnut brown (but coxa brown with dark yellow spot basally, trochanter, trochantellus with dark yellow spot apically, tarsus apically light brown); hind leg chestnut brown as head (but coxa with brown spot basally, trochanter, trochantellus similar as middle leg, tarsus apically light brown); palpi pale yellowish; remainder of antenna, mandible basally, ovipositor sheath dark brown, metasoma (except blackish first tergite) yellowish brown dorsally, apical segment and metasoma ventrally and laterally yellow (Fig. 2I); pterostigma and most veins brown; wing membrane subhyaline.

Distribution. Thailand.

Etymology. Named after the mainly conspicuously yellow metasoma of the holotype; “knekos” is Greek for yellow and “soma” is Greek for body.

***Anamalsia mellipes* van Achterberg & Yaakop, sp. nov.**

<https://zoobank.org/50584F60-BECC-4E9D-A6CF-2ECB4A7F2B6F>

Fig. 3A–H

Type material. *Holotype*, ♀ (RMNH), MALAYSIA, SW Sabah, near Long Pa Sia (West), c. 1050 m, 25.xi–8.xii.1987, Mal. trap 3, C. v. Achterberg, RMNH’87, DNA voucher number “94”. *Paratypes* (5 ♀): 1 ♀ (TAMU), INDONESIA, West Kalimantan, Gunung Palung Nat. Park, 15.vi–15.viii.1991, Darling, Sutrisno & Rosichon, IIS 910122; Cabang Panti Res. Station, 1° [= primary] rainforest, 100–400 m, alluvial-light gap, 1°15’S, 110°5’E, Malaise trap, head; 1 ♀ (UKM), Malaysia, N. Sembilan, Pasoh Forest Reserve, 24.x.2002, (50 ha plot), Ng, Y.F. & Ruslan, DNA voucher number “84”; 1 ♀ (UKM), [West Malaysia], Johor: Endau-Rompin Selai, 25.ix–1.x.2004, Shah, Roslan, Fauzi, DNA voucher number “59”; 1 ♀ (RMNH), W. Malaysia, Johor, Endau Rompin, Kampung Peta, ix.2007, Mal. trap, Ruslan, Fauzi & Norlie; 1 ♀ (RMNH), W. Malaysia, Pahang, Hutan Kuala Lompat, 29.xii.2006–13.i.2007, Mal. Tr., Ruslan, Fauzi & Norlie, DNA voucher number “73”.

Description. *Holotype*, ♀, length of body 3.6 mm, length of fore wing 3.1 mm.

Head. Width of head 1.7 times its median length, sparsely setose and strongly shiny; antenna incomplete, 24+, segments densely setose, length of third segment 0.9 times as long as fourth segment, length of third and fourth segments 4.0 and 4.3 times their width, respectively (Fig. 3E); length of maxillary palp of paratypes 1.4 times height of head (missing in holotype); eye in dorsal view 4.4 times as long as temple; temple in dorsal view subparallel-sided behind eyes (Fig. 3B); OOL: diameter of ocellus: POL = 11:4:3; frons flat medially (except a complete median groove) and convex laterally, smooth and no pit between antennal sockets; antennal sockets distinctly protruding; with a smooth, narrow and superficial groove between antennal sockets and eye; minimum width of face 0.5 times maximum width of head, densely rugulose-punctate submedially, more sparsely on remainder of face and transversely rugose ventrally and smooth medially, with rather long setae, without crenulate grooves

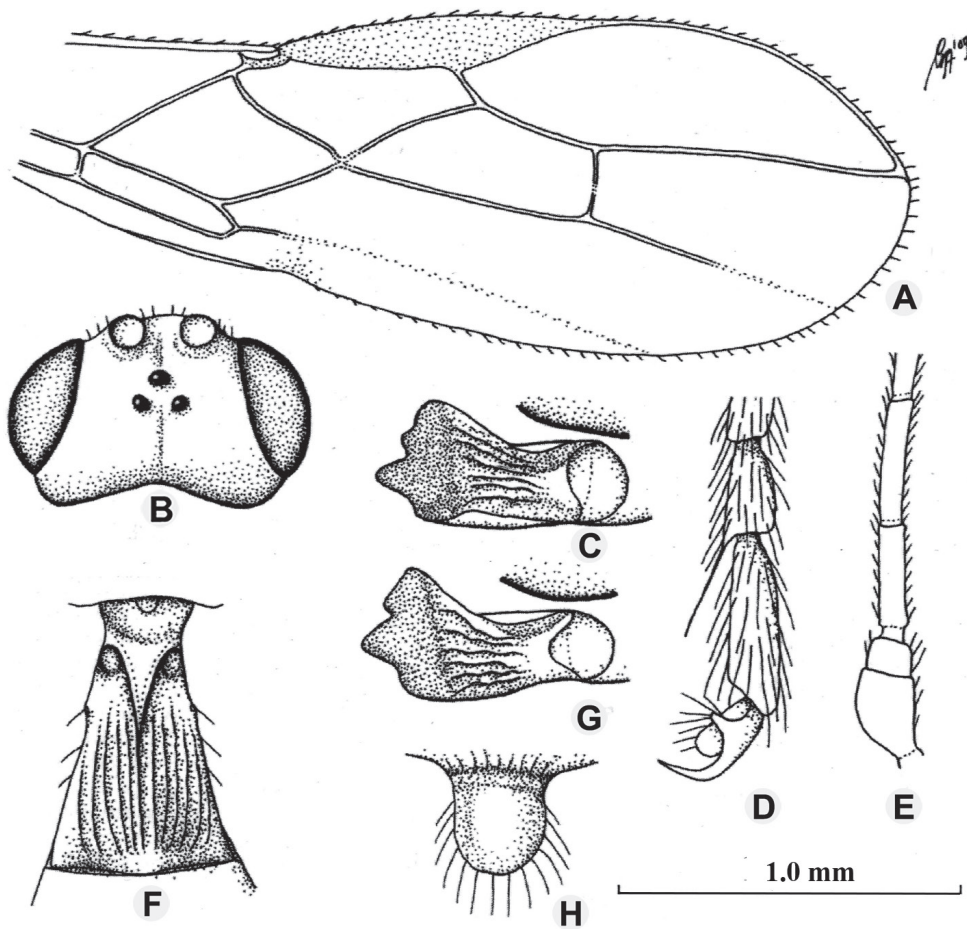


Figure 3. *Anamalysisia mellipes* sp. nov., ♀, holotype **A** fore wing **B** head, dorsal aspect **C** mandible, full sight on first tooth **D** outer hind claw **E** basal antennal segments **F** first metasomal tergite, dorsal aspect **G** mandible, full sight on third tooth **H** clypeus. Scale bars: 1.0 mm (**A**, **B**); 1.5 mm (**C**, **E–G**); 2.5 mm (**D**, **H**).

ventrally; clypeus narrow, nearly parallel-sided, with long setae and ventrally rounded and its surface largely smooth except a few punctures (Fig. 3H); length of malar space 0.1 times basal width of mandible; mandible rugose medially, strongly widened dorsally, its medial length 1.5 times its maximum width, upper tooth large and truncate lobe-shaped, with ventral tooth rather small, rounded and lobe-shaped, connected to a carina (Fig. 3C, G).

Mesosoma. Length of mesosoma 1.5 times its height; pronotum dorsally with large deep and round dorsope; side of pronotum with some coarse crenulae anteriorly and medially, posteriorly finely crenulate and remainder smooth; epicnemial area dorsally smooth, medially crenulate and ventrally punctate-rugose; precoxal sulcus widely crenulate anteriorly, narrowed after its middle and absent posteriorly; remainder of mesopleuron smooth; episternal scrobe round, deep; pleural sulcus coarsely crenulate;

mesosternal sulcus coarsely crenulate, rather wide posteriorly; metapleuron largely smooth, with some rugae ventrally; notauli complete, deep, narrow, and smooth; mesoscutum strongly shiny and largely glabrous, but with some long setae near notauli and lateral carina and medial lobe protuberant; mesoscutum without a separate medio-posterior depression; axilla rather setose and lateral carina moderately protuberant; scutellar sulcus deep, with one carina and no punctures, 0.4 times as long as scutellum; scutellum rather convex in lateral view; metanotum distinctly lamelliform protruding posteriorly in lateral view; surface of propodeum largely smooth anteriorly, except for a short median carina, medially with wide triangular areolate area and posteriorly reticulate; propodeal spiracle round, small and submedially at propodeum.

Wings. Pterostigma subelliptical (Fig. 3A), its posterior margin hardly curved; vein r issued distinctly behind middle of pterostigma and distinctly oblique; $r:3\text{-SR:SR1} = 5:21:53$; 1-SR+M rather sinuate; SR1 straight; cu-a short and oblique, interstitial; $2\text{-SR:3-SR:r-m} = 25:21:13$; m- cu slightly postfurcal, slightly converging to 1-M posteriorly; first subdiscal cell 6.5 times as long as wide; CU1b distinctly shorter than 3-CU1 and 3-CU1 oblique. Hind wing: $M+CU:1\text{-M}:1r\text{-m} = 30:35:13$; m-cu distinctly developed and removed from 2-M.

Legs. Outer side of hind coxa largely smooth, punctulate and moderately setose, dorsally shiny and smooth; middle coxa strongly protruding forwards ventrally, hind coxa gradually narrowed; tarsal claws moderately robust (Fig. 3D); length of femur, tibia, and basitarsus of hind leg 4.2, 14.0, and 10.3 times their width, respectively; hind tibia and basitarsus rather short and adpressed setose.

Metasoma. Length of first tergite 1.4 times its apical width, its surface regularly costate-striate, its dorsal carinae nearly complete and united submedially (Fig. 3F); laterope absent; dorsope large and deep (Fig. 3F); remainder of metasoma smooth and rather depressed; ovipositor with minute dorsal notch and some ventral teeth; length of setose part of ovipositor sheath 0.34 times fore wing and 0.8 times as long as hind tibia; apex of ovipositor sheath subtruncate and no apical spine; hypopygium medium-sized and apically acute in lateral view.

Colour. Dark chestnut brown; scapus, pedicellus, and tegulae more or less brown; palpi pale yellowish; metasoma (except first tergite and base of second tergite), remainder of antenna (as far as present), mandible, coxae (but paler apically) and ovipositor sheath brown; two basal segments of hind tarsus darkened; remainder of legs brownish yellow; pterostigma and most veins pale brown; wing membrane subhyaline.

Variation. Length of fore wing 2.8–3.1 mm and of body 3.3–3.6 mm; antenna of ♀ with 36 (1) segments, 1.9 times as long as fore wing and seven or eight apical segments white or ivory; vein SR1 of fore wing 2.5–3.1 times vein 3-SR; length of first tergite 1.4–1.5 times its apical width; eye in dorsal view 4.2–4.4 times as long as temple; length of setose part of ovipositor sheath 0.32–0.35 times fore wing.

Distribution. Malaysia (East Malaysia: Sabah; West Malaysia: Johor, Pahang, Sembilan).

Etymology. Named after its largely brownish yellow legs; “mel, mellis” is Latin for honey, and “pes, pedus” is Latin for leg.

***Anamalysia transversator* Yao & van Achterberg, sp. nov.**

<https://zoobank.org/F99CC0C6-2493-4D43-8EC8-E211FF121F00>

Fig. 4A–I

Type material. *Holotype*, ♀ (QSBG), THAILAND, Nakhon Si Thammarat, Namtok Yong NP TV aerial, 8°14.3'N, 99°48.3'E, 952 m, Malaise trap, 26.i–2.ii.2009, Paiboon leg. T4307, Genbank accession number MG912720 (COI).

Description. *Holotype*, ♀, length of body 3.5 mm, length of fore wing 3.6 mm.

Head. Width of head 2.1 times its median length, sparsely setose and strongly shiny; antenna incomplete, 26+, however, longer than body (Fig. 4A), segments densely setose, length of third segment 0.7 times as long as fourth segment, length of third and fourth segments 4.3 and 8.0 times their width, respectively; length of maxillary palp 1.5 times height of head; eye in dorsal view 3.0 times as long as temple; temple in dorsal view subparallel-sided behind eyes (Fig. 4E); OOL: diameter of ocellus: POL = 27:6:7; frons flat medially (except an incomplete median groove, anterior half with deep groove and posterior half with groove trace) and convex laterally, smooth; antennal sockets distinctly protruding; with a smooth, narrow, and superficial groove between antennal sockets and eye; minimum width of face 0.6 times maximum width of head, densely rugulose-punctate, with a Y-shaped carina medially (from antenna sockets to clypeus), anterior 2/3 (between and along Y-shaped carina) medially smooth, with rather dense and long setae (Fig. 4B); clypeus wide, triangular, width 2.0 times its length, with long setae and ventrally rounded and its surface largely smooth except a few punctures (Fig. 4B); length of malar space 0.1 times basal width of mandible; mandible sparsely rugose medially except teeth part smooth, strongly widened dorsally, its medial length 2.0 times its maximum width, upper tooth large and truncate lobe-shaped, with ventral tooth rather small, rounded and lobe-shaped, connected to a carina (Fig. 4C).

Mesosoma. Length of mesosoma 1.3 times its height; pronotum dorsally with large deep and round dorsople (Fig. 4E); side of pronotum with some coarse crenulate anteriorly, posteriorly finely crenulate and remainder smooth; epicnemial area dorsally smooth, medially crenulate and ventrally punctate-rugose; precoxal sulcus anterior 1/5 smooth and remainder crenulate, widely crenulate anteriorly, narrowed after its middle and absent posteriorly (Fig. 4F); remainder of mesopleuron smooth; episternal scrobe round, deep; pleural sulcus anteriorly smooth and punctulate, with dense setae, posteriorly coarsely crenulate; mesosternal sulcus coarsely crenulate, rather wide posteriorly; metapleuron largely smooth, with some rugae dorsally and ventrally; notauli complete, deep, narrow. and smooth; midpit small and round, connected to notauli (Fig. 4D, E); mesoscutum strongly shiny and largely glabrous, but with some long setae near notauli and lateral carina and medial lobe protuberant; mesoscutum without a separate medio-posterior depression; axilla rather setose and lateral carina moderately protuberant; scutellar sulcus deep, with one carina and coarsely rugae, without punctures, 0.4 times as long as scutellum (Fig. 4D, E); scutellum rather convex in lateral view; metanotum distinctly lamelliform protruding posteriorly in lateral view; propodeum with a complete longitudinal carina, largely smooth anteriorly, except for a short median carina and rugae near it, medially with circular areolate area and posteriorly

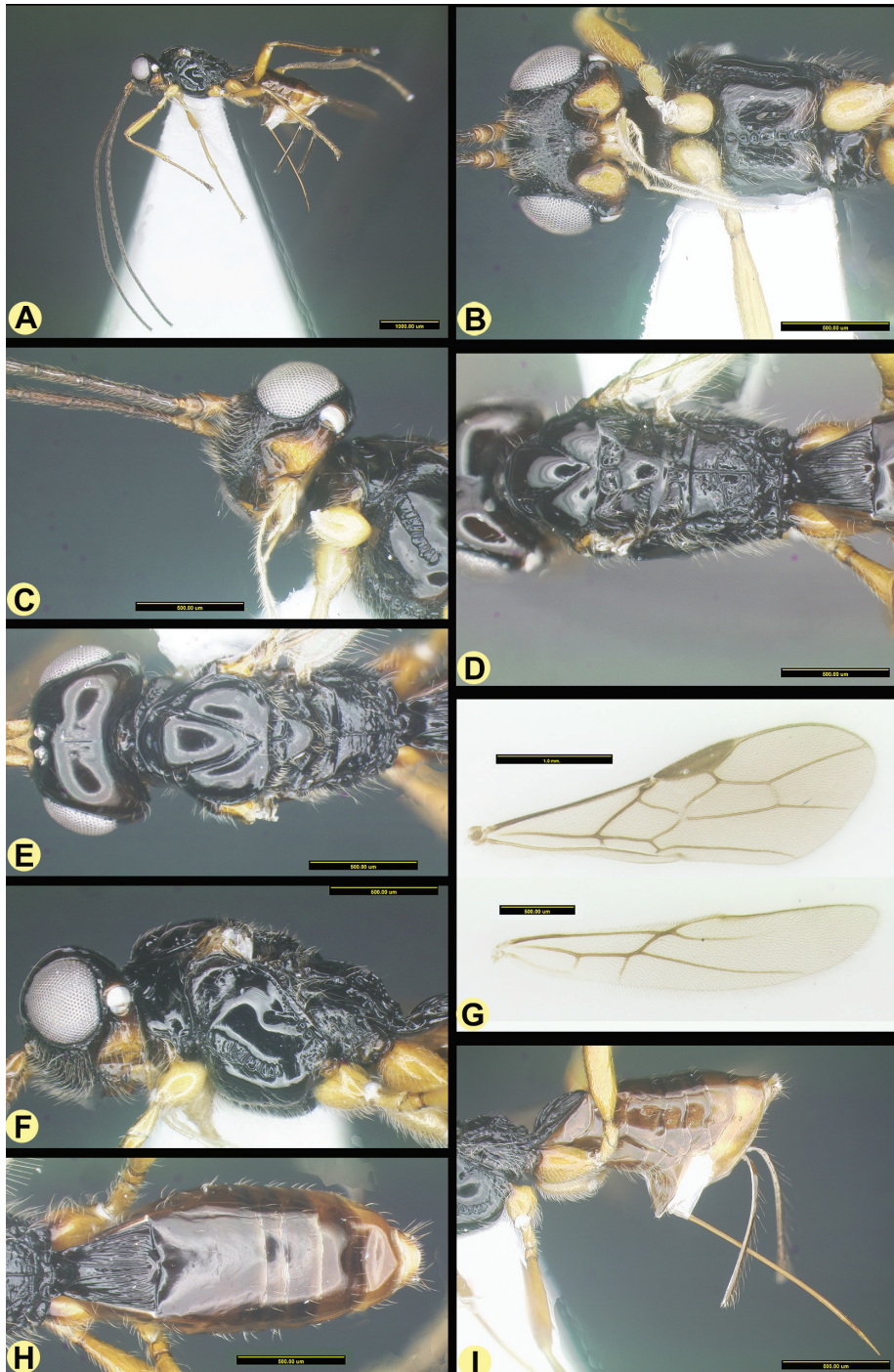


Figure 4. *Anamalysis transversator* sp. nov., ♀, holotype **A** habitus, lateral aspect **B** head anterior aspect and mesosoma ventrally **C** mandible full sight on first tooth **D** mesosoma full sight on propodeum and first tergite dorsally **E** head and mesosoma dorsal aspect **F** mesosoma lateral aspect **G** wings **H** metasoma dorsal aspect **I** propodeum and metasoma lateral aspect.

reticulate, smooth latero-posteriorly (Fig. 4D, E); propodeal spiracle round, small and medially at propodeum.

Wings. Pterostigma subelliptical (Fig. 4G), its posterior margin hardly curved; vein r issued distinctly behind middle of pterostigma and distinctly oblique; $r:3\text{-SR}:SR1 = 14:49:103$; $1\text{-SR}+M$ rather sinuate; SR1 straight, slightly curved posteriorly; cu-a short and oblique, strongly postfurcal; $2\text{-SR}:3\text{-SR}:r\text{-m} = 30:29:14$, vein r-m of fore wing distinctly inclivous; m-cu slightly postfurcal, slightly converging to 1-M posteriorly; first subdiscal cell 3.8 times as long as wide; $3\text{-CU}1:CU1b = 3.2$ and 3-CU1 oblique. Hind wing: $M+CU:1\text{-M}:1r\text{-m} = 29:23:10$; m-cu distinctly developed and removed from 1r-m.

Legs. Outer side of hind coxa largely smooth, punctulate and moderately setose, dorsally shiny and smooth; middle coxa strongly protruding forwards ventrally, hind coxa gradually narrowed; tarsal claws moderately robust; length of femur, tibia, and basitarsus of hind leg 4.3, 10.0, and 8.7 times their width, respectively; middle tibia and basitarsus rather short and adpressed setose (Fig. 4A).

Metasoma. Length of first tergite 1.0 times its apical width, its surface regularly costate-striate, its dorsal carinae nearly complete and united submedially (Fig. 4H); laterope absent; dorsope large and deep (Fig. 4H); remainder of metasoma smooth and rather depressed; ovipositor with minute dorsal notch and some ventral teeth; length of setose part of ovipositor sheath 0.7 times fore wing and 0.9 times as long as hind tibia; apex of ovipositor sheath subtruncate and no apical spine; hypopygium medium-sized and apically acute in lateral view (Fig. 4I).

Colour. Black; head and first tergite chestnut brown; remainder of metasoma yellow; scapus, pedicellus, mandible apically, tegulae, and middle and hind legs (except tibia and tarsus brown, three apical tarsus lightened) brownish yellow; palpi pale yellowish; fore leg yellow (but apical tarsus more or less brown); remainder of antenna (as far as present), mandible basally and ovipositor sheath dark brown; pterostigma and most veins brown; wing membrane subhyaline.

Distribution. Thailand.

Etymology. Named after the comparatively transverse head in dorsal view (Fig. 4E).

Anamalysia triangulum (Fischer, 2006) comb. nov.

Fig. 5A–G

Alysiasta triangulum Fischer, 2006: 612–613.

Type material. *Holotype*, ♀ (BZL), MALAYSIA, Pahang, 30 km NE Raub, ~ 300 m, Lata Lembik, iv–v.2002, ET [electric grid trap], $3^{\circ}56'N$, $101^{\circ}38'E$, E. Jendek & O. Šauša leg., “Holotype, ♀ *Alysiasta triangulum* sp. n., det. Fischer, 2005”.

Additional material. 2 ♀ (TAMU, RMNH), INDONESIA, Sumatra, Aceh, Gunung Leuser Nat. Park, Ketambe Res. Station, 1–30.xi.1989, per D.C. Darling, IIS 890010, 1° [= primary] rainforest, young forest, terrace 3, closed canopy, 350 m, $3^{\circ}41'N$, $97^{\circ}39'E$, Malaise trap w/ pans; 1 ♀ (RMNH), MALAYSIA, SW Sabah, near Long Pa

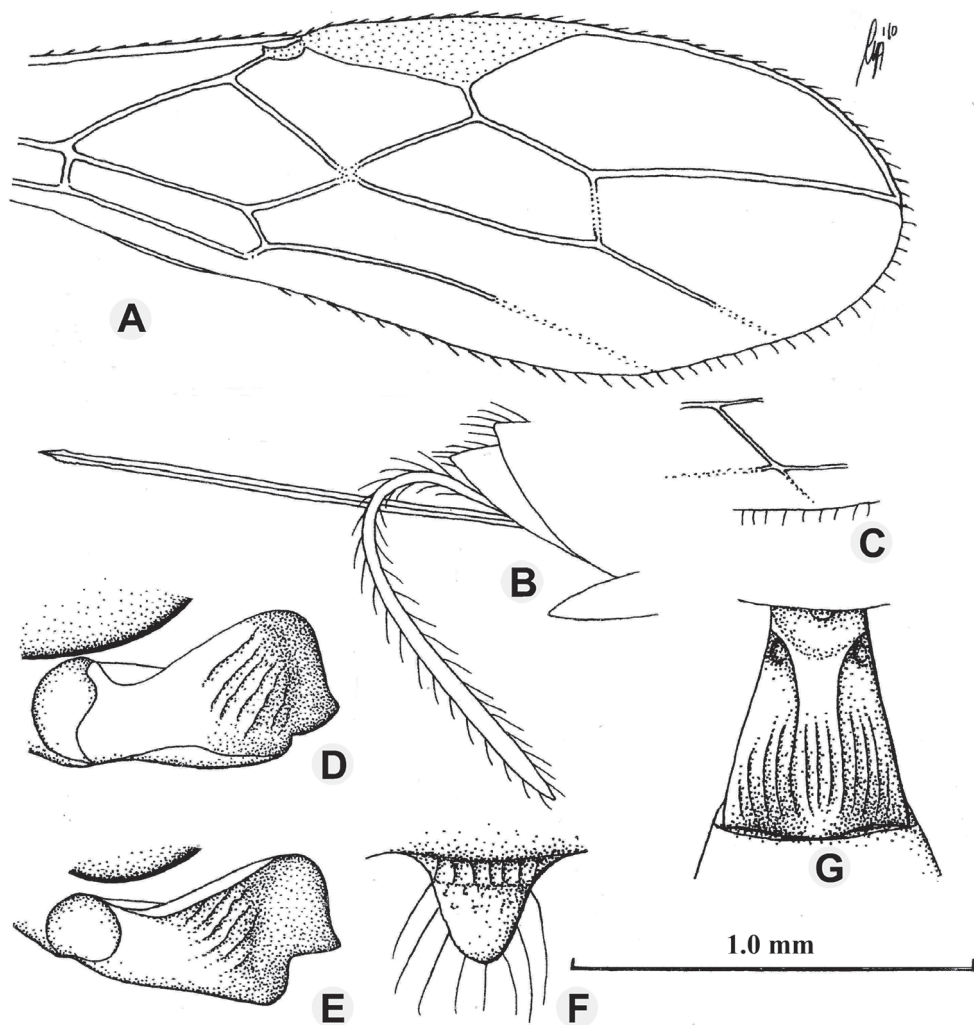


Figure 5. *Anamalsia triangulum* (Fischer), ♀, holotype **A** fore wing **B** ovipositor and its sheath **C** detail of vein m-cu of hind wing **D** mandible full sight on first tooth **E** mandible full sight on third tooth **F** clypeus **G** first metasomal tergite dorsal aspect. Scale bars: 1.0 mm (**A–C**); 1.5 mm (**D, E**); 1.8 mm (**F**); 1.2 mm (**G**).

Sia (West), c. 1020 m, 25.xi– 8.xii.1987, Mal. trap 2, C. v. Achterberg, RMNH'87, DNA voucher number "63"; 1 ♂ (RMNH), "13", INDONESIA, Sumatra, Fort de Kock [= Bukittinggi], x.1913, Edw. Jacobson; 1 ♀ (IEBR), "Alysi. 029", VN [= Vietnam], Ninh Binh, Cuc Phuong N.P., 7–9 v.2002, Kh.D. Long".

Notes. Length of the hind femur of the holotype is four times its width, not five times as indicated in the original description; length of the first metasomal tergite 1.1 times its apical width (Fig. 5G), not 1.3 times as mentioned in the original description; the eye in dorsal view 1.9 times as long as the temple; the hind tibia (except ivory base)

and base of the hind tarsus dark brown; vein SR1 of the fore wing 2.4 times as long as vein 3-SR (Fig. 5A). Colour of head and of mesosoma varies from nearly black to chestnut brown. The male from Sumatra and the female from Sabah have the metasoma dark brown and vein m-cu of hind wing unsclerotised basally (as in holotype).

Distribution. Malaysia (West), Laos, Indonesia, Vietnam. The latter two are new country records for this species.

***Anamalysia urbana* (Papp, 1967) comb. nov.**

Phaenocarpa urbana Papp, 1967: 152–154.

Coelalysia urbana; Fischer, 1988: 116–118 (redescription).

Distribution. Singapore.

Notes. The two existing descriptions are rather confusing. In the original description the first tergite is 1.1 times longer than its apical width, but according to the redescription by Fischer (1988), it is 1.2 times (in the text) or 1.3–1.4 times (in his fig. 39). Vein r-m of fore wing is strongly inclivous according to the original description (Papp 1967: fig. 25) and only moderately so in Fischer (1988: fig. 38). If the original description is accepted then *A. urbana* is hardly separable from *A. triangulum* and the latter might be well a junior synonym of *A. urbana* when more specimens become available. The difference in colour may be the result of ageing and exposure to sunlight.

***Anamalysia vandervehti* van Achterberg & Yaakop, sp. nov.**

<https://zoobank.org/6B584A68-F8EB-4810-B91A-2221A3AF557A>

Fig. 6 A–F

Type material. *Holotype*, ♂ (RMNH), Museum Leiden, [Indonesia], N.O. Sumatra, Deli, Sibolangit, 4.i.1955, J. v. d. Vecht.

Description. *Holotype*, ♂, length of body 4.1 mm, length of fore wing 3.5 mm.

Head. Width of head 1.9 times its median length, largely glabrous dorsally; antenna incomplete, with short adpressed setae and six basal strongly shiny, length of third segment 0.8 times as long as fourth segment, length of third and fourth segments 4.7 and 6.0 times their width, respectively (Fig. 6E); length of maxillary palp 1.3 times height of head; eye in dorsal view 1.5 times as long as temple; temple in dorsal view subparallel-sided (Fig. 6D); OOL: diameter of ocellus: POL = 14:3:4 (Fig. 6D); minimum width of face 0.6 times maximum width of head and 1.7 times its height, coarsely punctate, weakly convex, with long setae and medio-ventrally densely rugose; with oblique groove from antennal socket to eye (Fig. 6B); clypeus elongate and narrow (Fig. 6B), sparsely punctate; vertex strongly shiny, weakly convex, and depressed near stemmaticum; anterior tentorial pit small, round, and far from eye (Fig. 6B); length of malar space 0.1 times basal width of mandible; mandible strongly widened, 1.4 times as long as wide,

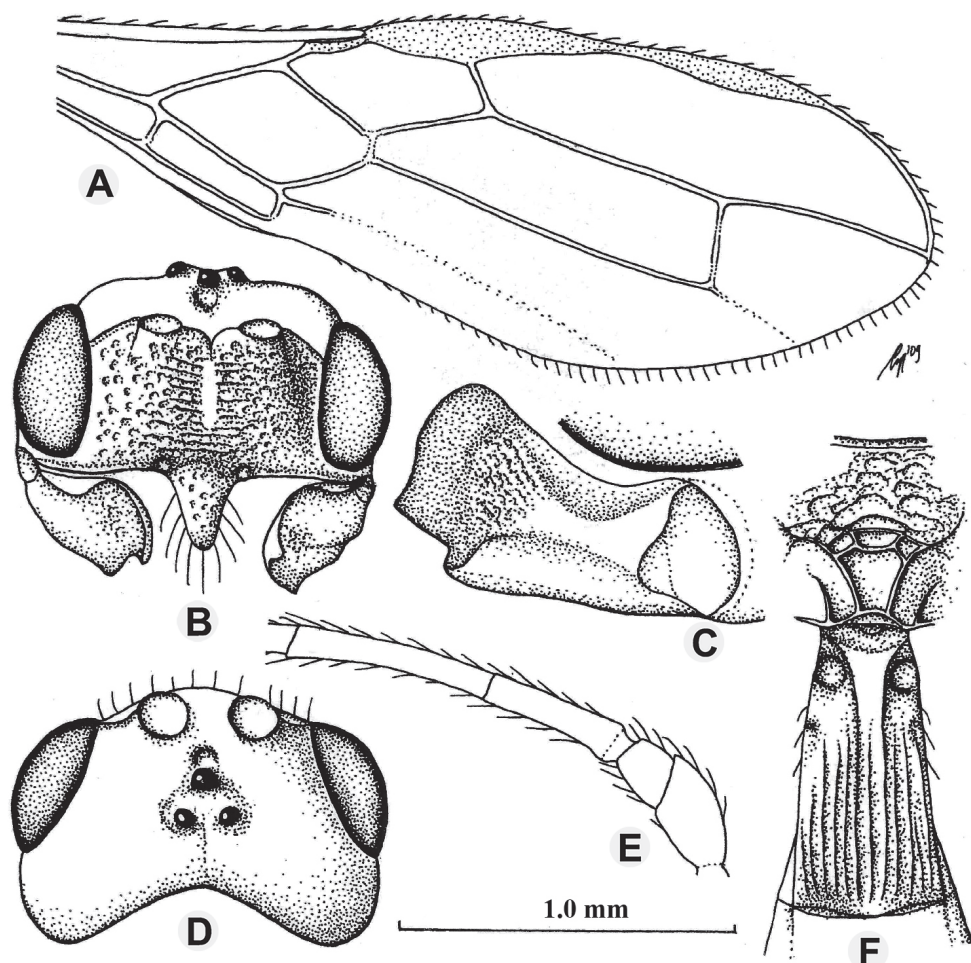


Figure 6. *Anamalsia vandervechti* sp. nov., ♂, holotype **A** fore wing **B** head, anterior aspect **C** mandible, full sight on first tooth **D** head, dorsal aspect **E** basal antennal segment **F** propodeum and first metasomal tergite, dorsal aspect. Scale bars: 1.0 mm (**A**); 1.2 mm (**B**, **D**, **F**); 1.8 mm (**C**, **E**).

subapically partly coarsely punctate-rugose, first tooth broadly lobe-shaped, and continuous with minute tooth and separated from third medium-sized tooth (Fig. 6C).

Mesosoma. Length of mesosoma 1.5 times its height; pronotum with medium-sized pronope; antescutal depression absent; side of pronotum largely crenulate medially; epicnemial area distinctly crenulate; precoxal sulcus complete, wide and coarsely crenulate; remainder of mesopleuron smooth; episternal scrobe large, deep, and round; pleural sulcus largely smooth dorsally and distinctly crenulate ventrally; mesosternal sulcus wide and coarsely crenulate posteriorly and narrowed anteriorly; metapleuron coarsely reticulate; notauli complete, deeply impressed, rather narrow but distinctly crenulate; medio-posterior depression absent; mesoscutum smooth, glabrous, and its

lateral carina interrupted in front of tegulae; scutellar sulcus deep, about twice as wide as long, with one carina, 0.3 times as long as scutellum; scutellum convex, smooth except a few punctures; metanotum with complete median carina but not protruding dorsally; propodeum smooth antero-laterally, reticulate medially and areolate posteriorly, with wide irregular pentagonal areola medially (Fig. 6F); propodeal spiracle round, small and submedially in propodeum.

Wings. Pterostigma elongate subtriangular, its posterior margin straight or slightly convex; vein r issued near middle of pterostigma and oblique; only known species with basal half of 1-R1 distinctly widened; $r:3\text{-SR}:SR1 = 8:41:34$; 1-SR+M narrow and straight; SR1 straight; cu-a medium-sized, postfurcal; $1\text{-CU}1:2\text{-CU}1 = 1:11$; $2\text{-SR}:3\text{-SR}:r\text{-m} = 19:41:14$; m-cu postfurcal and slightly curved, subparallel to 1-M; 3-CU1 slightly shorter than CU1b and widened (Fig. 6A). Hind wing: M+CU:1-M (up to m-cu):1r-m = $20:17:10$; m-cu distinct, largely unsclerotised and distantly antefurcal.

Legs. Hind coxa smooth and baso-ventrally wide rectangular and not protruding; fore tarsal claws rather robust (other missing); length of femur, tibia, and basitarsus of hind leg 5.5, 12.2, and 10.4 times their width, respectively; hind tibia and basitarsus with rather long setae, hind tibia densely setose, comb at inner apex of tibia absent; fore tarsus 1.5 times as long as fore tibia.

Metasoma. Length of first tergite 2.4 times its apical width, its surface longitudinally costate, its dorsal carinae nearly complete (Fig. 6F); laterope absent; dorsope large and deep, pointed dorsally (Fig. 6F); remainder of metasoma smooth and depressed; hypopygium medium-sized and slightly concave posteriorly; parameres large.

Colour. Blackish chestnut brown; scapus, pedicellus, mandible, legs (but middle and hind coxae, hind tibia, except basally, and hind tarsus dark brown) yellowish brown; palpi (but basally brownish), basal fifth of fore and middle tibiae, and basal 0.4 of hind tibia whitish or pale yellowish; tegulae, remainder of antenna, pterostigma and veins more or less dark brown; wing membrane faintly brownish.

Distribution. Indonesia (Sumatra).

Etymology. Named after the collector of the holotype, the hymenopterist Prof. Dr Jacobus van der Vecht (1906–1992) for his excellent contributions to our knowledge of Hymenoptera (van Achterberg 1992).

Anamalysia vanhengstumi van Achterberg, sp. nov.

<https://zoobank.org/74022A0F-DE25-42EB-811D-E60E50365907>

Figs 7A, B, 8A–I

Type material. *Holotype*, ♂ (RMNH), “Alysi. 070”, VN [= Vietnam], Ha Giang, Vi Xuyen, Cao Bo Rung TS, 400 m, 10.v.2007, K.D. Long.

Description. *Holotype*, ♂, length of body 3.9 mm, length of fore wing 3.3 mm.

Head. Width of head 2.4 times its median length, deeply depressed medially and largely glabrous dorsally; antenna incomplete, with 29+ segments, setae short and adpressed and seven basal segments strongly shiny, length of third segment 0.9 times as long

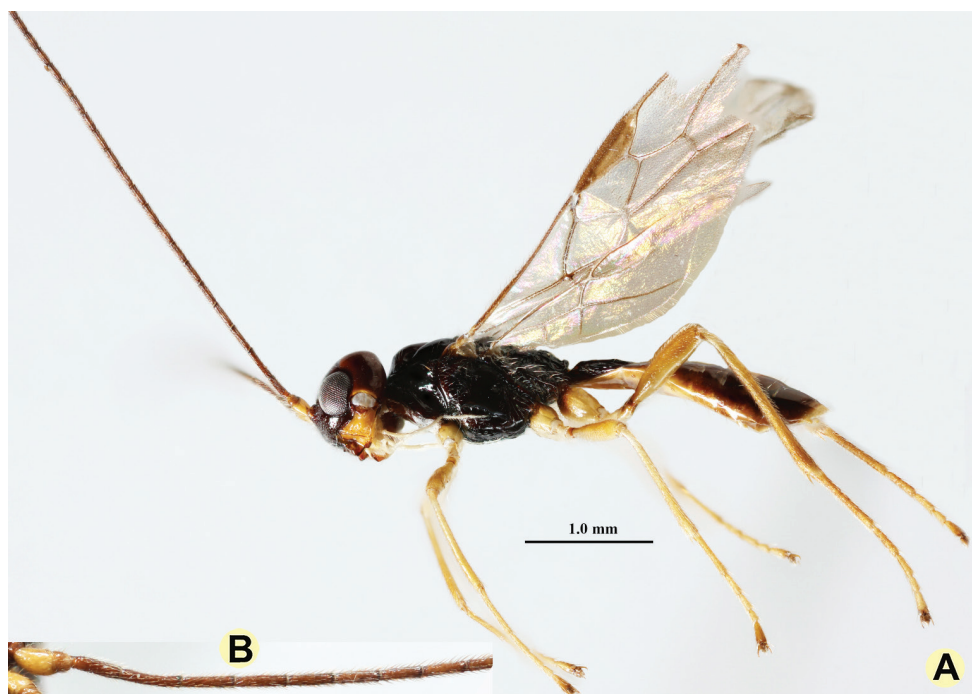


Figure 7. *Anamalsia vanhengstumi* sp. nov., ♂, holotype **A** habitus, lateral aspect **B** detail of basal antennal segments.

as fourth segment, length of third and fourth segments 3.9 and 4.6 times their width, respectively (Fig. 7B); length of maxillary palp 1.2 times height of head; eye in dorsal view 1.1 times as long as temple; temple in dorsal view strongly widened behind eyes (Fig. 8E); OOL:diameter of ocellus: POL = 15:4:3; minimum width of face 0.6 times maximum width of head and 1.8 times its height, coarsely punctate, moderately convex, with long setae and medio-ventrally narrowly smooth (Fig. 8B); with oblique groove from antennal socket to eye; clypeus rather robust and largely smooth (Fig. 8B); vertex strongly shiny and weakly convex and strongly depressed behind stemmaticum; anterior tentorial pit covered by mandible; length of malar space 0.1 times basal width of mandible; mandible strongly widened, 1.4 times as long as wide, middle tooth dorsally connected to wide sinuate and up curved lamella from upper corner of mandible, medially coarsely rugose, first tooth part of apical lamella and third tooth medium-sized (Fig. 8G, H).

Mesosoma. Length of mesosoma 1.7 times its height; pronotum with large pronope; antescutal depression absent; side of pronotum largely crenulate medially (except sub-posteriorly) and posteriorly; epicnemial area with few crenulae; precoxal sulcus absent posteriorly, wide and coarsely crenulate (Fig. 8C); remainder of mesopleuron smooth; episternal scrobe elongate and medium-sized; pleural sulcus finely crenulate dorsally and distinctly crenulate ventrally; mesosternal sulcus wide and coarsely crenulate; metapleuron largely smooth but rugose ventrally; notauli complete, deeply impressed,

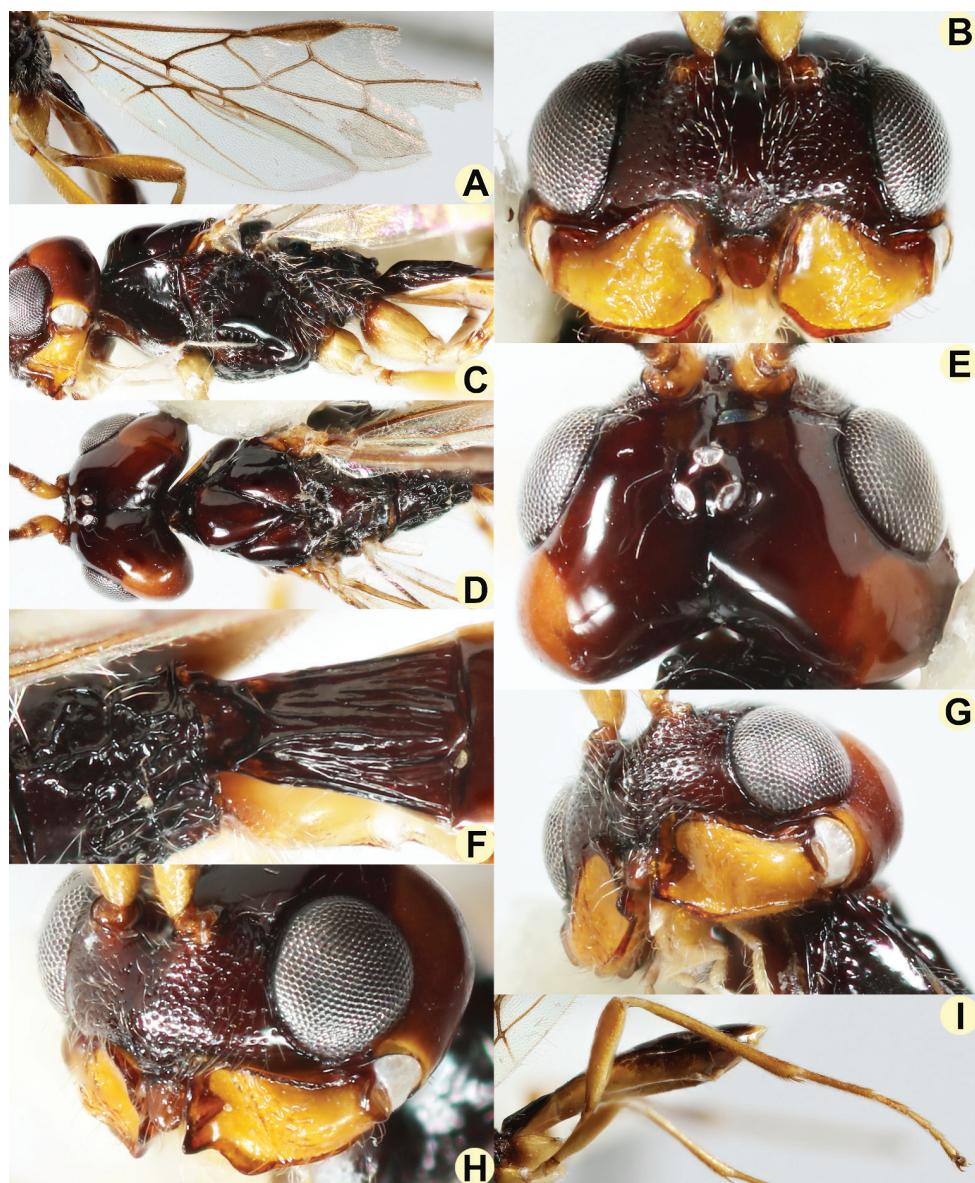


Figure 8. *Anamalsia vanhengstumi* sp. nov., ♂, holotype **A** wings **B** head, anterior aspect **C** mesosoma, lateral aspect **D** head and mesosoma, dorsal aspect **E** head, dorsal aspect **F** propodeum and first metasomal tergite, dorsal aspect **G** mandible, full sight on first tooth **H** mandible, with full sight on third tooth **I** hind leg.

rather narrow, and smooth; medio-posterior depression absent (Fig. 8D); mesoscutum smooth, glabrous, and its lateral carina complete in front of tegulae; scutellar sulcus deep, about 2.5 times as wide as long, with one carina, 0.3 times as long as scutellum; scutellum slightly convex, smooth except a few punctures; metanotum with complete

median carina and rather protruding dorsally; propodeum smooth antero-laterally, reticulate medially and areolate posteriorly, with posteriorly narrowed pentagonal areola medially (Fig. 8F); propodeal spiracle small, round, and submedially in propodeum.

Wings. Pterostigma elongate subtriangular, its posterior margin straight or slightly convex; vein r issued from basal 0.6 of pterostigma and oblique; 1-R1 narrow; r:3-SR:SR1 = 5:22:42; 1-SR+M narrow and nearly straight; SR1 straight; cu-a medium-sized, postfurcal; 1-CU1:2-CU1 = 1:11; 2-SR:3-SR:r-m = 20:22:9; r-m weakly inclivous; m-cu subinterstitial and slightly curved, converging to 1-M; 3-CU1 much longer than CU1b and narrow (Fig. 8A). Hind wing: M+CU:1-M (up to m-cu):1r-m = 20:18:9; m-cu distinct, largely unsclerotised (except basally) and interstitial (Fig. 8A).

Legs. Hind coxa smooth, baso-ventrally rounded, and not protruding; tarsal claws rather robust; length of femur, tibia, and basitarsus of hind leg 4.2, 11.0, and 9.0 times their width, respectively; hind tibia and basitarsus with numerous rather long setae dorsally; hind tibia densely setose and comb at inner apex of tibia absent; fore tarsus 1.4 times as long as fore tibia (Fig. 8I).

Metasoma. Length of first tergite 1.4 times its apical width, its surface longitudinally costate, its dorsal carinae united submedially (Fig. 8F); laterope deep and large; dorsope large, deep, and pointing dorsally; remainder of metasoma smooth and depressed; hypopygium truncate posteriorly (Fig. 7A).

Colour. Black; scapus, pedicellus, mandible, and legs yellow; remainder of antenna dark brown; temple and vertex and metasoma laterally (except first tergite) chestnut brown; palpi ivory; tegulae mainly yellowish brown; pterostigma and most veins brown; wing membrane faintly infuscated.

Distribution. Northern Vietnam.

Etymology. Named after the former director of the National Museum of Natural History (Naturalis) Ronald van Hengstum (1952–2007), who tragically died after a short swim in the North Sea near The Hague. He visited Vietnam during one of the RMNH-IEBR expeditions and was strongly in favour of cooperation with our Vietnamese counterparts.

Acknowledgements

We thank the staff at Queen Sirikit Botanic Garden in Chiang Mai, Thailand (QSBG), for sorting the many hundreds of samples and the QSBG staff for operating Malaise traps and other collection devices. We give a special thanks to Chaweewan Hutacharn for managing the TIGER project in Thailand. We are grateful to Dr Dicky Yu (Ottawa) for making literature available for this study and for creating the Taxapad database, to Dr Frederique Bakker (Leiden) and Prof. Dr Robert Wharton (College Station) for access to the RMNH and TAMU material, respectively. Funding was provided by National Natural Science Foundation of China (32000319), NSF grants DEB-0542864 and EF-0337220, a University of Kentucky Research Activity Award, and Hatch projects KY008041 and KY008065 (to MJS).

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New species and new records of semiaquatic bugs (Arthropoda, Insecta, Hemiptera, Heteroptera, Gerromorpha) from French Guiana

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Abstract

Semiaquatic bugs (Hemiptera: Heteroptera: Gerromorpha) are predatory insects that occupy a wide range of freshwater and marine habitats, with some secondary transitions to terrestrial life. They currently represent more than 2100 species distributed through all continents, except for Antarctica, and are especially rich in the Neotropical and Oriental regions. Although the fauna from the former region is relatively well known, some areas remain almost unexplored. Such is the case of French Guiana, where only a few species have been previously recorded, several of which based on collections made in the 19th and early 20th centuries. As a result of material recently collected in the territory, the descriptions of *Rhagovelia depressa* Rodrigues, Khila & Moreira, **sp. nov.**, *R. tantilloides* Rodrigues, Khila & Moreira, **sp. nov.** and *Steinovelina vittata* Rodrigues, Khila & Moreira, **sp. nov.** (Veliidae) are presented here. New records for 28 species are also provided, of which *Cylindrostethus hungerfordi* Drake & Harris, 1934, *Neogerris magnus* (Kuitert, 1942), *Rheumatobates mangrovensis* (China, 1943), *R. trinitatis* (China, 1943), *Ovatametra obesa* Kenaga, 1942, *Telmatometra fusca* Kenaga, 1941, *T. parva* Kenaga, 1941 (Gerridae), *Mesovelina amoena* Uhler, 1894 (Mesoveliidae), *Rhagovelia brunae* Magalhães & Moreira, 2016, *R. elegans* Uhler, 1894, *R. ephydros* (Drake & Van Doesburg, 1966), *R. equatoria* D. Polhemus, 1997, *R. evidis* Bacon, 1948, *R. guianana* D. Polhemus, 1997, *R. tenuipes* Champion, 1898, *Oiovelina cunucunumana* (Drake & Maldonado-Capriles, 1952), *Stridulivelina alia* (Drake, 1957), *S. stridulata* (Hungerford, 1929), and *S. tersa* (Drake & Harris, 1941) (Veliidae) are reported from French Guiana for the first time.

Keywords

Aquatic insects, faunistics, Neotropical Region, riffle bugs, taxonomy, water striders

Introduction

Semiaquatic bugs (Hemiptera: Heteroptera: Gerromorpha) are an important group of insects commonly found in a wide range of freshwater bodies, with some clades that transitioned to terrestrial life or even to marine habitats (e.g., Andersen 1982). They are predators that can potentially be used in the control of pests or disease vectors, or as bioindicators of environmental quality (Ignacimuthu 2002; Weterings et al. 2018; Cunha et al. 2020).

The Neotropical fauna of Gerromorpha is relatively well known, with more than 290 described species so far, but some areas within South America still remain very poorly explored (J. Polhemus and D. Polhemus 2007, 2008). Such is the case of French Guiana, where only a limited number of were collected in expeditions that took place during the 19th and early 20th centuries, and published in isolated papers until the 1950's (Champion 1898; Kirkaldy 1899a; Esaki 1927; Hungerford 1929a; Drake and Harris 1935a; Hungerford and Matsuda 1957). An exception was the recent description of *Rhagovelia apuruaque* Motta, Moreira, Crumière, Santos & Khila, 2018, which was collected during an expedition to the region in 2014 that exclusively targeted the semiaquatic bugs. The knowledge on the gerromorphan fauna from French Guiana was so poor at the time that the expedition also produced first records of 11 species, almost all of which are very common and widespread in northern South America as a whole, but had not yet been found in the region (Motta et al. 2018).

Here, we report the results of a second expedition to this territory performed in 2016 (Fig. 1), including the descriptions of *Rhagovelia depressa* Rodrigues, Khila & Moreira, sp. nov., *R. tantilloides* Rodrigues, Khila & Moreira, sp. nov., and *Steinovelina vittata* Rodrigues, Khila & Moreira, sp. nov. New records are also presented for 28 species, of which 19 are reported from French Guiana for the first time.

Materials and methods

Material examined for this study was collected as part of the project “Mechanisms underlying the evolution of an exaggerated sex-specific trait” (Laboratory of Excellence, Center for the Study of Biodiversity in Amazonia [Labex CEBA] 2016). The main target was *Microvelia longipes* Uhler, 1894 (Veliidae: Microveliinae), which lives in temporary pools. In addition to these habitats, sampling was also performed in streams, rivers, waterfalls and other types of aquatic habitats, in the surroundings of Cayenne and in the Réserve Naturelle Nationale des Nouragues (Fig. 1). Specimens were preserved in > 96% ethanol, which will allow future molecular studies, and are deposited in the Coleção Entomológica do Instituto Oswaldo Cruz, Fundação Oswaldo Cruz, Rio de Janeiro, Brazil (CEIOC). Photographs of the new species described here were taken under different focal lengths and combined into single images with a Keyence VHX-7000 Digital Microscope. For the newly recorded species and



Figure 1. Map showing previous records (green circles) and new collecting sites (red stars) of Gerromorpha in French Guiana.

the terminalia of the new species, the same process was performed using a Leica M205 C stereomicroscope coupled with a digital camera. All these images were edited and the figure plates organized using Corel Photo-Paint 2020 and Corel Draw 2020, respectively.

All measurements are presented in millimetres. Abbreviations used for measurements are as follows: body length (**BL**), head length (**HL**), head width through eyes (**HW**), length of antennomeres I–IV [without intersegmental pieces] (**ANT I**, **ANT II**, **ANT III**, **ANT IV**), maximum eye width (**EYE**), pronotum length on midline (**PL**), pronotum width (**PW**), length of foreleg segments (**FORELEG**), length of midleg segments (**MIDLEG**), length of hindleg segments (**HIND-LEG**), femoral length (**FEM**), tibial length (**TIB**), length of tarsomeres I–III (**TAR I**, **TAR II**, **TAR III**).

Geographic coordinates of the collecting sites were obtained with a GPS receiver. Maps were produced using ArcGIS v. 10.5 (ESRI Inc., Redlands, CA, USA). In the distribution lists of each species, all known references are cited for French Guiana, while only the first known reference is cited for other countries.

Results and discussion

Family Gerridae

Subfamily Charmatometrinae

Brachymetra lata Shaw, 1933

Figs 2A, 3A

Material examined. FRENCH GUIANA • 1 apterous ♂, 3 apterous ♀; Réserve Naturelle Nationale des Nouragues, Camp Inselberg; 4.0799, –52.6860; 15 Oct. 2016; A.J.J. Crumière, A. Khila, F.F.F. Moreira, W. Toubiana leg.; CEIOC 81279 • 1 apterous ♂, 3 apterous ♀, 3 nymphs; same, except 4.0892, –52.6772; 14 Oct. 2016; CEIOC 81281.

Distribution. Colombia (Aristizábal 2002), Venezuela (Moreira et al. 2016), Suriname (Nieser 1970), French Guiana (Motta et al. 2018; this work), Brazil (Shaw 1933), Ecuador (Aristizábal 2002).

Subfamily Cyldrostethinae

Cylindrostethus hungerfordi Drake & Harris, 1934

Figs 2B, 3A

Material examined. FRENCH GUIANA • 2 apterous ♂; Réserve Naturelle Nationale des Nouragues, Camp Inselberg; 4.0799, –52.6860; 15 Oct. 2016; A.J.J. Crumière, A. Khila, F.F.F. Moreira, W. Toubiana leg.; CEIOC 81287.

Distribution. Guyana (Drake and Harris 1934), Suriname (Nieser 1970), French Guiana (this work), Brazil (Nieser 1970).

Cylindrostethus palmaris Drake & Harris, 1934

Figs 2C, 3A

Material examined. FRENCH GUIANA • 1 apterous ♂, 6 apterous ♀; localities near Cayenne; [4.86, –52.34]; 12–13 Oct. 2016; A.J.J. Crumière, A. Khila, F.F.F. Moreira, W. Toubiana leg.; CEIOC 79997.

Distribution. Trinidad & Tobago (Drake and Harris 1934), Colombia (Aristizábal 2002), Venezuela (Drake and Roze 1954), Guyana (Drake and Harris 1934), Suriname (Nieser 1970), French Guiana (Drake and Harris 1935a; Motta et al. 2018; this work); Brazil (Drake and Harris 1934), Ecuador (Aristizábal 2002), Peru (Peralta-Argomeda 2011), Bolivia (Kuitert 1942), Argentina (Mazzucconi et al. 2009).

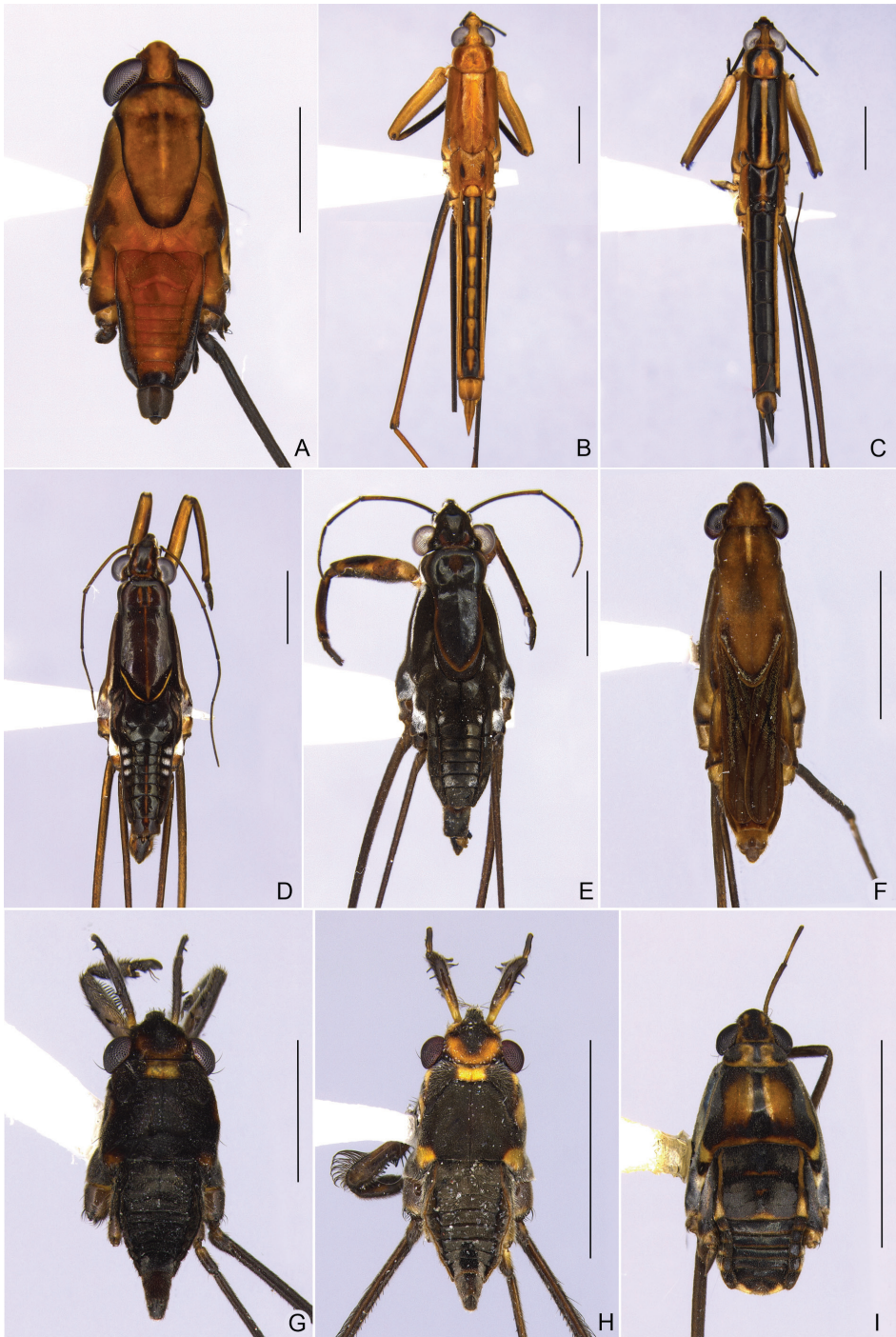


Figure 2. Habitus, dorsal view **A** *Brachymetra lata* **B** *Cylindrostethus hungerfordi* **C** *C. palmaris* **D** *Limnogonus hyalinus* **E** *Neogerris magnus* **F** *Tachygerris adamsoni* **G** *Rheumatobates mangrovensis* **H** *R. trinitatis* **I** *Ovatametra obesa*. Scale bars: 1.0 mm (**G**); 2.0 mm (**A–F, H, I**).

Subfamily Gerrinae**Tribe Gerrini*****Limnogonus hyalinus* (Fabricius, 1803)**

Figs 2D, 3A

Material examined. FRENCH GUIANA • 1 macropterous ♂, 2 macropterous ♀; Réserve Naturelle Nationale des Nouragues, Camp Inselberg; 4.0799, –52.6860; 15 Oct. 2016; A.J.J. Crumière, A. Khila, F.F.F. Moreira, W. Toubiana leg.; CEIOC 79998 • 1 apterous ♂, 3 macropterous ♂, 1 macropterous ♀; same, except 4.0892, –52.6772; 14 Oct. 2016; CEIOC 81284 • 3 apterous ♂, 3 macropterous ♂, 4 apterous ♀, 3 macropterous ♀; localities near Cayenne; [4.86, –52.34]; 12–13 Oct. 2016; A.J.J. Crumière, A. Khila, F.F.F. Moreira, W. Toubiana leg.; CEIOC 79994.

Distribution. Costa Rica (Herrera 2014), Panama (Rodrigues et al. 2021a), Trinidad & Tobago (Hynes 1948), Colombia (Aristizábal 2002), Venezuela (Moreira et al. 2016), Guyana (Kuitert 1942), Suriname (Nieser 1970), French Guiana (Champion 1898; Kirkaldy 1899a; Motta et al. 2018; this work), Brazil (White 1879), Ecuador (Kirkaldy 1899b), Bolivia (Hungerford 1927).

***Neogerris magnus* (Kuitert, 1942)**

Figs 2E, 3A

Material examined. FRENCH GUIANA • 1 apterous ♀; Réserve Naturelle Nationale des Nouragues, Camp Inselberg; 4.0892, –52.6772; 14 Oct. 2016; A.J.J. Crumière, A. Khila, F.F.F. Moreira, W. Toubiana leg.; CEIOC 77290 • 1 macropterous ♂; same, except 4.0799, –52.6860; 15 Oct. 2016; CEIOC 81285 • 1 apterous ♂; localities near Cayenne; [4.86, –52.34]; 12–13 Oct. 2016; A.J.J. Crumière, A. Khila, F.F.F. Moreira, W. Toubiana leg.; CEIOC 77287.

Distribution. Colombia (Roback and Nieser 1974), Venezuela (Hungerford 1944), Guyana (Kuitert 1942), Suriname (Nieser 1994), French Guiana (this work), Brazil (Kuitert 1942), Bolivia (Kuitert 1942).

Tribe Tachygerrini***Tachygerris adamsoni* (Drake, 1942)**

Figs 2F, 3A

Material examined. FRENCH GUIANA • 1 brachypterous ♂; Réserve Naturelle Nationale des Nouragues, Camp Inselberg; 4.0892, –52.6772; 14 Oct. 2016; A.J.J. Crumière, A. Khila, F.F.F. Moreira, W. Toubiana leg.; CEIOC 79988 • 1 macropterous ♀; same, except 4.0799, –52.6860; 15 Oct. 2016; CEIOC 79989.

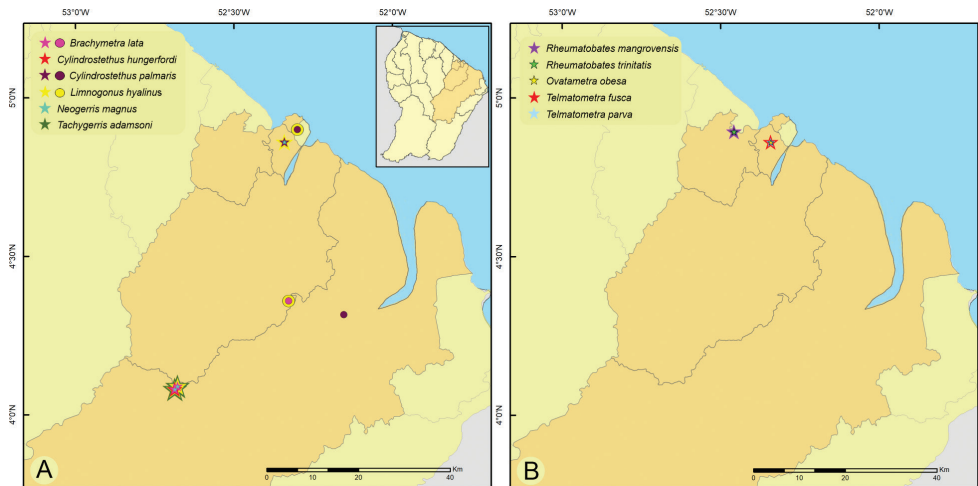


Figure 3. Geographic distribution of Gerridae in French Guiana **A** *Brachymetra lata*, *Cylindrostethus hungerfordi*, *C. palmaris*, *Limnogonus hyalinus*, *Neogerris magnus* and *Tachygerris adamsoni* **B** *Rheumatobates mangrovensis*, *R. trinitatis*, *Ovatametra obesa*, *Telmatometra fusca* and *T. parva*. Circles indicate previous records; stars indicate new records.

Distribution. Trinidad & Tobago (Drake 1942), Colombia (Aristizábal 2002); Venezuela (Hungerford 1944), Suriname (Nieser 1970), French Guiana (Andersen 1995; Motta et al. 2018; this work), Brazil (Drake 1942), Peru (Drake 1942), Bolivia (Kuitert 1942), Paraguay (Kuitert 1942).

Subfamily Rhagadotarsinae

Rheumatobates mangrovensis (China, 1943)

Figs 2G, 3B

Material examined. FRENCH GUIANA • 1 apterous ♂, 2 apterous ♀; Rivière de Montsinéry; 4.8930, -52.4558; [Oct. 2016]; A.J.J. Crumière, A. Khila, F.F.F. Moreira, W. Toubiana leg.; CEIOC 81286.

Distribution. Guadeloupe (Conjard et al. 2021), Trinidad & Tobago (China 1943); French Guiana (this work).

Rheumatobates trinitatis (China, 1943)

Figs 2H, 3B

Material examined. FRENCH GUIANA • 1 apterous ♂, 1 apterous ♀; Rivière de Montsinéry; 4.8930, -52.4558; [Oct. 2016]; A.J.J. Crumière, A. Khila, F.F.F. Moreira, W. Toubiana leg.; CEIOC 79987.

Distribution. Guadeloupe (Nieser 1970), Trinidad & Tobago (China 1943), Suriname (Nieser 1970), French Guiana (this work), Brazil (Rodrigues et al. 2021b).

Subfamily Trepobatinae

Tribe Trepobatini

Ovatametra obesa Kenaga, 1942

Figs 2I, 3B

Material examined. FRENCH GUIANA • 1 apterous ♀; localities near Cayenne; [4.86, –52.34]; 12–13 Oct. 2016; A.J.J. Crumière, A. Khila, F.F.F. Moreira, W. Toubiana leg.; CEIOC 79985.

Distribution. Colombia (Moreno-R et al. 2018), French Guiana (this work), Brazil (Kenaga 1942), Bolivia (Floriano et al. 2017a), Argentina (Mazzucconi et al. 2022).

Telmatometra fusca Kenaga, 1941

Figs 3B, 4A

Material examined. FRENCH GUIANA • 1 apterous ♂; localities near Cayenne; [4.86, –52.34]; 12–13 Oct. 2016; A.J.J. Crumière, A. Khila, F.F.F. Moreira, W. Toubiana leg.; CEIOC 82165.

Distribution. Colombia (Aristizábal 2017), Suriname (Nieser 1970), French Guiana (this work), Brazil (Kenaga 1941).

Telmatometra parva Kenaga, 1941

Figs 3B, 4B

Material examined. FRENCH GUIANA • 1 apterous ♀; Réserve Naturelle Nationale des Nouragues, Camp Inselberg; 4.0892, –52.6772; 16 Oct. 2016; A.J.J. Crumière, A. Khila, F.F.F. Moreira, W. Toubiana leg.; CEIOC 77299 • 1 apterous ♀; localities near Cayenne; [4.86, –52.34]; 12–13 Oct. 2016; A.J.J. Crumière, A. Khila, F.F.F. Moreira, W. Toubiana leg.; CEIOC 79991.

Distribution. French Guiana (this work), Brazil (Kenaga 1941).

Note. This species and the previous two above have been identified based on Kenaga's (1941, 1942) revisions, in which color patterns have been used to delimit species. We believe that there is a good amount of intraspecific variation in this aspect, and that both *Ovatametra* Kenaga, 1942 and *Telmatometra* Bergroth, 1908 are in serious need of more thorough revisions.

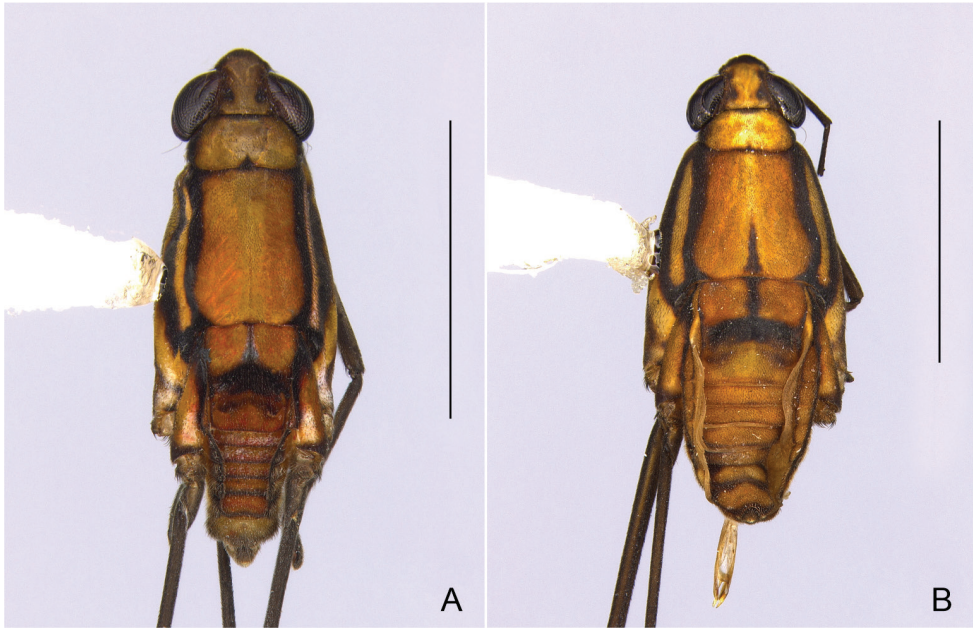


Figure 4. Habitus, dorsal view. **A** *Telmatometra fusca* **B** *Telmatometra parva*. Scale bars: 2.0 mm.

Family Mesoveliidae
Subfamily Mesoveliinae

***Mesovelia amoena* Uhler, 1894**

Fig. 5A, C

Material examined. FRENCH GUIANA • 3 apterous ♀; Réserve Naturelle Nationale des Nouragues, Camp Inselberg; 4.0892, -52.6772; 16 Oct. 2016; A.J.J. Crumière, A. Khila, F.F.F. Moreira, W. Toubiana leg.; CEIOC 81290 • 9 apterous ♀; same, except, waterfall with moss and litter; [4.09, -52.68]; 17 Oct. 2016; CEIOC 81291 • same, except CEIOC 81292.

Distribution. Canada (Chagnon and Fournier 1948), United States (Hungerford 1924), Mexico (Andersen and J. Polhemus 1980), Belize (Spangler 1990), Cuba (Nieser 1977), Jamaica (Usinger 1968), Dominican Republic (Spangler 1990), Puerto Rico (Harris and Drake 1941), U.S. Virgin Islands (Rogers and Cruz-Rivera 2021), St. Eustatius (Cobben 1960), Martinique (de Kort-Gommers and Nieser 1969), Costa Rica (Spangler 1990), Panama (Harris and Drake 1941), St. Vincent & the Grenadines (Jaczewski 1930), Curaçao (Cobben 1960), Bonaire (Cobben 1960), Grenada (Uhler 1894), Trinidad & Tobago (Hynes 1948), Colombia (Alvarez and Roldán-Pérez 1983), French Guiana (this work), Brazil (Jaczewski 1928), Argentina (Harris and Drake 1941), Galápagos Islands (Peck 2001), Hawaiian Islands (Gagné and Howarth 1975).

Family Veliidae**Subfamily Rhagoveliinae*****Rhagovelia brunae* Magalhães & Moreira, 2016**

Fig. 5B, D

Material examined. FRENCH GUIANA • 4 apterous ♂, 1 apterous ♀, 1 macropterous ♀; near Cayenne; 4.6282, –52.3072; 21 Oct. 2016; A.J.J. Crumière, A. Khila, F.F.F. Moreira, W. Toubiana leg.; CEIOC 82158 • 3 apterous ♂, 3 apterous ♀; [unspecified locality]; [Oct. 2016]; [A.J.J. Crumière, A. Khila, F.F.F. Moreira, W. Toubiana leg.]; CEIOC 82156 • 1 apterous ♂, 1 apterous ♀; same, except CEIOC 82157.

Distribution. Venezuela (Magalhães et al. 2019), French Guiana (this work), Brazil (Magalhães et al. 2016).

Note. We noticed slight divergences in the male hind femoral armature in this species when compared with the types. The degree of intraspecific variation concerning this feature is higher than originally assumed when the species was described.

***Rhagovelia depressa* Rodrigues, Khila & Moreira, sp. nov.**

<https://zoobank.org/5E24B1FA-2914-4D0D-8B7A-35330A97576E>

Figs 6–9

Type material examined. FRENCH GUIANA • apterous ♂ holotype; Réserve Naturelle Nationale des Nouragues, Camp Pararé and surroundings; 4.0386, –52.6728; 17–18 Oct. 2016; A.J.J. Crumière, A. Khila, F.F.F. Moreira, W. Toubiana leg.; CEIOC 82144 • 42 apterous ♂ paratypes, 32 apterous ♀ paratypes; same, except CEIOC 82145.

Description. Apterous male (Figs 6, 7). Holotype (paratypes). BL 2.10 (2.03–2.10); HL 0.22 (0.20–0.22); HW 0.62 (0.61–0.65); INT 0.17 (0.17); ANT I 0.55 (0.55–0.57); ANT II 0.35 (0.32–0.35); ANT III 0.35 (0.32–0.35); ANT IV 0.40 (0.37–0.40); EYE 0.22 (0.21–0.23); PL 0.12 (0.12–0.13); PW 0.70 (0.70–0.75); FORELEG: FEM 0.77 (0.77); TIB 0.75 (0.70–0.75); TAR I 0.02 (0.02); TAR II 0.05 (0.05); TAR III 0.15 (0.15); MIDLEG: FEM 1.20 (1.17–1.20); TIB 0.85 (0.82–0.87); TAR I 0.15 (0.15–0.20); TAR II 0.37 (0.30–0.37); TAR III 0.60 (0.52–0.60); HINDLEG: FEM 0.90 (0.87–0.92); TIB 0.90 (0.85–0.92); TAR I 0.05 (0.05); TAR II 0.07 (0.07); TAR III 0.17 (0.15–0.17).

Head dorsally black, covered by stiff short setae; frons with denser cover of short setae and few long, curved setae; longitudinal midline and a pair of oblique indentations at base impressed and shining; impressed midline fading posteriorly. Eye shining dark red; ocular setae present. Antenniferous tubercle shining dark brown. Antennomeres covered by short and medium setae; antennomere I yellow basally, turning brown, then black towards apex, with four or five thick long black setae on mesal surface and one on lateral surface; antennomeres II–IV dark brown to black; II with some long setae on mesal surface; interarticular pieces shining dark-brown. Buccula and labium shining dark brown. Venter of head black.

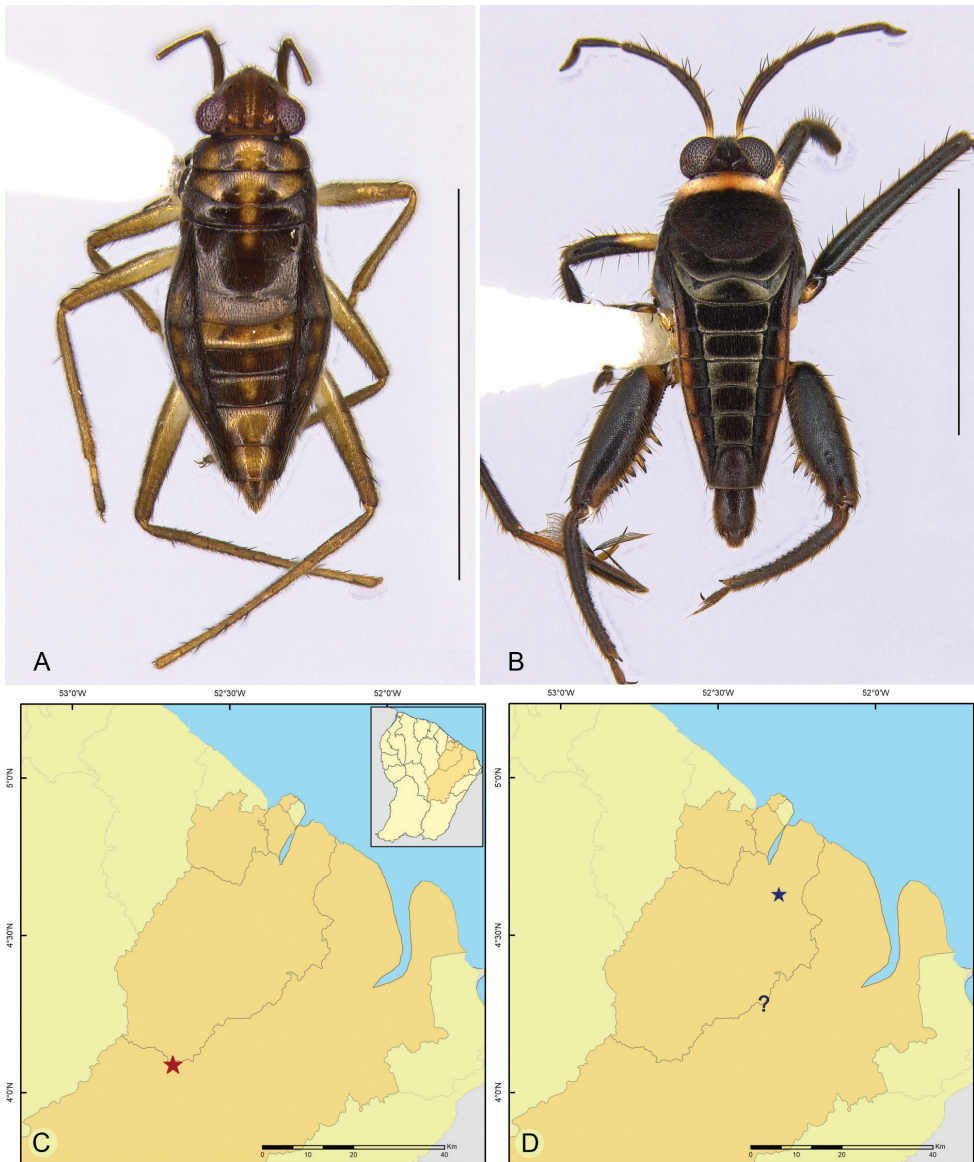


Figure 5. **A, B** habitus, dorsal view **A** *Mesovelia amoena* **B** *Rhagovelia brunae* **C, D** geographic distribution in French Guiana **C** *M. amoena* **D** *R. brunae*. Stars indicate new records; question mark indicates an imprecise record (only the country is known, but not a specific locality). Scale bars: 2.0 mm.

Pronotum black, with dark-orange mark between eyes behind vertex of head, covered by medium-sized dark setae. Meso- and metanota black, covered by medium and long black setae; discreet greyish pubescence posteriorly on mesonotum and on metanotum. Thoracic pleura black with greyish pubescence, covered by medium and long black setae. Proacetabulum mostly yellow, becoming brown, then black laterally and mesally. Mesoacetabulum black with greyish pubescence, becoming brown,

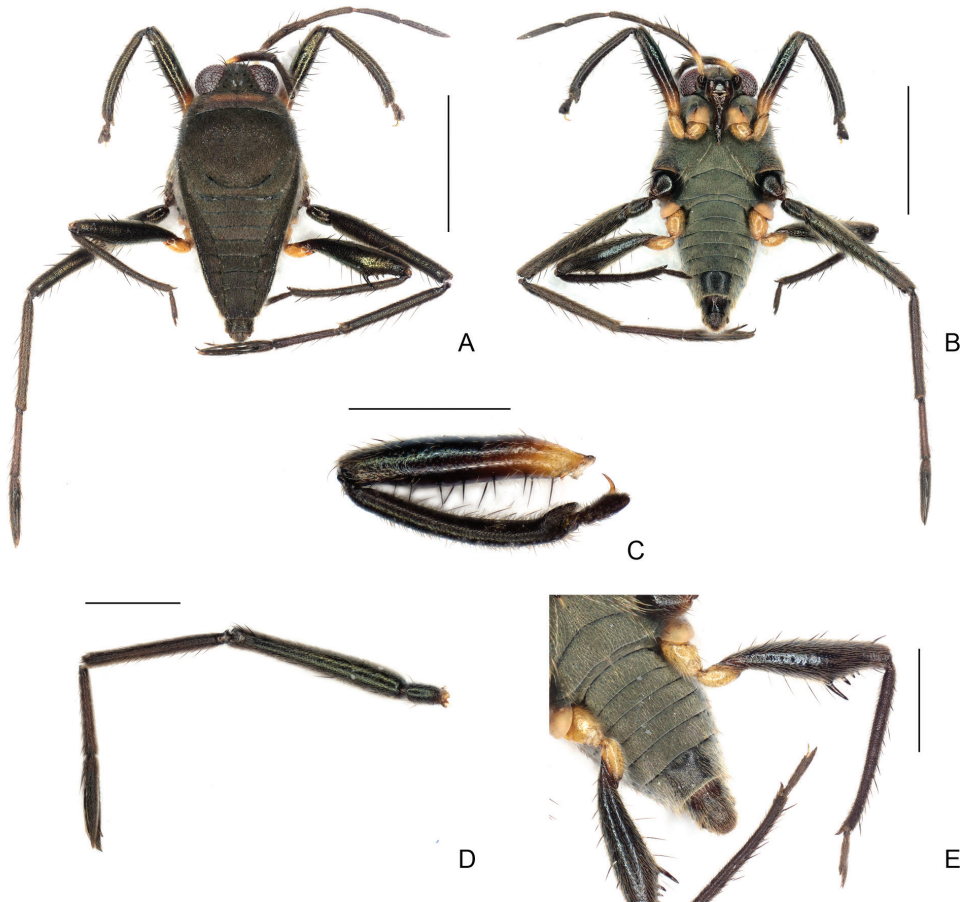


Figure 6. *Rhagovelia depressa* Rodrigues, Khila & Moreira, sp. nov., apterous male **A** habitus, dorsal view **B** habitus, ventral view **C** fore femur, tibia and tarsus, ventral view **D** middle trochanter, femur, tibia and tarsus, ventral view **E** part of thorax, abdomen and hind legs, ventral view.

then yellow on margin surrounding middle coxa. Metacetabulum black with greyish pubescence proximally, becoming brown, then pale yellow towards apex; in ventral view, mostly pale yellow; covered by strong light setae directed laterally. Thoracic sternum black, covered by greyish pubescence, with sparse medium-sized light setae, long brown setae laterally on mesosternum, and two oblique rows of light setae submedially on mesosternum.

Fore and hind coxae and trochanters yellow; distal tip of trochanters, in ventral view, brown; fore coxa with few long light setae marginally; hind coxa with stiff long light setae; fore trochanter with medium and long light setae; hind trochanter with medium setae on mesal surface and longer light setae marginally to tibia. Middle coxa shining, in ventral view, black with dark-brown apex, dark brown to black centrally; covered by medium and long brown setae, with stiffer long brown setae laterally. Middle

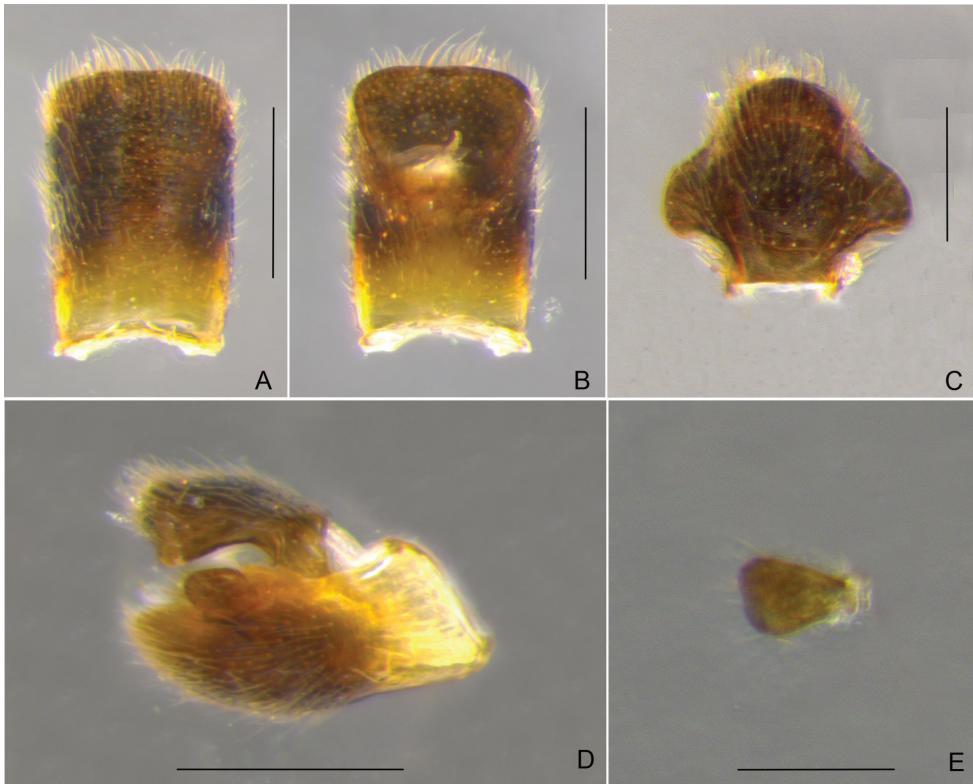


Figure 7. *Rhagovelia depressa* Rodrigues, Khila & Moreira, sp. nov., male terminalia **A, B** abdominal segment VIII, dorsal and ventral views, respectively **C** proctiger, dorsal view **D** genital capsule, lateral view **E** paramere, lateral view. Scale bars: 0.2 mm (**A, B, D**); 0.1 mm (**C, E**).

trochanter dark brown to black, shining dorsally and ventrally, covered by medium and long setae. Fore femur basally yellow, becoming brown, then black towards apex, covered by medium and long light setae, with several stiff long dark setae on posterior surface, and one or two near apex of anterior surface. Fore tibia and tarsus dark brown to black. Fore tibia covered by medium and long curved setae, with a row of stiff longer dark setae on anterior surface; grasping comb evident; grooming comb present. Tarsus with dense cover of short and medium-sized brown setae. Middle femur dark brown to black, covered by medium and long light setae, with rows of longer stiff brown setae on anterior and posterior surfaces, and some longer curved brown setae apically. Middle tibia dark brown to black, densely covered by medium and long brown setae, with a row of stiff longer brown setae on distal 2/3 of anterior surface. Middle tarsus dark brown to black, densely covered by medium and long brown setae, with some longer brown setae on anterior surface. Hind femur, in dorsal view, narrowly shining dark brown on base; in ventral view, narrowly shining lighter brown on base; rest dark brown to black; densely covered by long light setae, with rows of stiffer dark setae on anterior surface, a row of long brown setae on posterior surface basally to spine row, and

two long brown setae distally on posterior surface. Hind tibia dark brown, covered by medium and long brown setae, with a row of longer thicker setae on anterior surface. Hind trochanter dark brown, covered by medium-sized brown setae.

Abdominal medio- and laterotergites black, covered by discreet greyish pubescence, except for shining black lateral margins of laterotergites; long dark setae widespread; longer brown setae on apex of last laterotergite. Abdominal sterna II–VI black, covered by greyish pubescence; with medium-sized light setae adjacent to posterior margins; long light setae on sides of sterna III–VI, posteriorly on III and centrally on V–VI. Abdominal sternum shining black on wide subquadrate central area; black with greyish pubescence on sides of shining area; with long light setae laterally. Abdominal segment VIII and pygophore light brown on anterior 1/3, dark brown on posterior 2/3, densely covered by long light setae. Proctiger dark brown, densely covered by long light setae.

Head compact. Eyes not distinctly large, touching pronotum. Antennomere I thickest, curved laterally; II–III cylindrical, subequal in width; IV fusiform, slightly thicker than II–III. Labium robust, reaching mesosternum between fore coxae.

Pronotum laterally, mesonotum, metanotum and abdominal mediotergite I anterolaterally, thoracic pleura and sterna, and abdominal sterna II–VI and sides of VII with minute rounded (mostly) or irregular punctations; punctations shining on mesonotum to mediotergite I, much more sparse and less evident on abdomen. Pronotum shorter than dorsal eye length, with posterior margin slightly concave. Mesonotum slightly elevated centrally, posterior margin widely rounded. Metanotum short at midline, posterior margin slightly concave centrally. Posterior margins of pro- and mesosterna concave medially. Posterior margin of metasternum slightly concave medially.

Fore trochanter unarmed. Fore femur as thick as fore tibia, approximately as thick as middle femur. Fore tibia curved, with a weak preapical concavity on ventral surface, widest on apex + grasping comb. Middle femur without flattening or constriction, thickest subbasally. Hind femur surpassing apex of terminalia, thicker than middle femur, thickest right after middle, with a distally decreasing row of three or four black spines starting after middle of posterior surface and not reaching apex. Hind tibia slightly narrowed and curved distally, without pegs throughout length, with a strong curved spur at apex.

Lengths of abdominal laterotergites on midline slightly increasing from I–IV, IV–VI subequal, VII longest; VII with straight posterior margin. Laterotergites slightly elevated; lateral margins slightly converging anteriorly on first segment, then more strongly and evenly converging up to penultimate segment, then more strongly to apex, ending continuously to posterior margin of mediotergite VII. Lengths of abdominal sterna on midline decreasing from II–IV, IV–V subequal and shorter than VI, VI shorter than I, VII longest. Sternum II slightly laterally compressed, with a concavity each side through which hind coxae move, without distinct median carina; III very weakly compressed laterally, without median carina; IV–VI without median carina; VII without median carina, flattened centrally, with widely concave posterior margin. Abdominal segment VIII cylindrical; dorsal apical margin almost straight (Fig. 7A, B). Proctiger short; lateral lobes large, curved anteriorly, each with approximately half the

distal width of proctiger; apex rounded (Fig. 7C, D). Paramere small, subtrapezoidal, apical margin oblique, almost straight (Fig. 7E).

Apterous female (Fig. 8). BL 2.70–2.82; HL 0.25–0.30; HW 0.72–0.80; INT 0.17–0.20; ANT I 0.65–0.67; ANT II 0.37–0.42; ANT III 0.40–0.42; ANT IV 0.42–0.45; EYE 0.27–0.30; PL 0.16–0.17; PW 0.87–0.90; FORELEG: FEM 0.85–0.90; TIB 0.80–1.00; TAR I 0.02; TAR II 0.05; TAR III 0.20–0.22; MIDLEG: FEM 1.45–1.50; TIB 1.00–1.10; TAR I 0.12–0.20; TAR II 0.37–0.52; TAR III 0.65–0.67; HINDLEG: FEM 1.02–1.12; TIB 1.07–0.20; TAR I 0.05; TAR II 0.10–0.12; TAR III 0.22.

Similar to apterous male in colour and structure, except for: antennomere II with stiff black setae on dorsal surface; mesonotum with a large rounded central depression, with posterior margin concave centrally; posterior margin of metanotum more strongly convex; fore femur approximately as thick as fore tibia, thinner than middle femur, with weaker stiff setae; fore tibia without preapical concavity nor grasping comb; hind femur thinner than middle femur, without spines; hind tibia straight, with weaker and less curved apical spur; abdomen narrowed; abdominal mediotergites with more concave posterior margins; laterotergites reflexed over mediotergites, progressively covering them more from I–VII, then opening throughout tergum VIII; posterior margins of abdominal sterna II–IV more concave; long light setae much scarcer on sterna III–VI, more widespread on VII; VII with posterior margin slightly projecting medially.

Etymology. The specific epithet *depressa* (Latin, feminine) refers to the depressed central portion of the female mesonotum in this species.

Comments. *Rhagovelia depressa* Rodrigues, Khila & Moreira, sp. nov. belongs to the *angustipes* complex based on the pronotum of the apterous form shorter than the dorsal length of the eye, with the posterior margin concave. It displays three articles on each tarsus (although tarsomere I is extremely reduced in the middle leg,



Figure 8. *Rhagovelia depressa* Rodrigues, Khila & Moreira, sp. nov., habitus, apterous female paratype **A** dorsal view **B** ventral view. Scale bars: 1 mm.

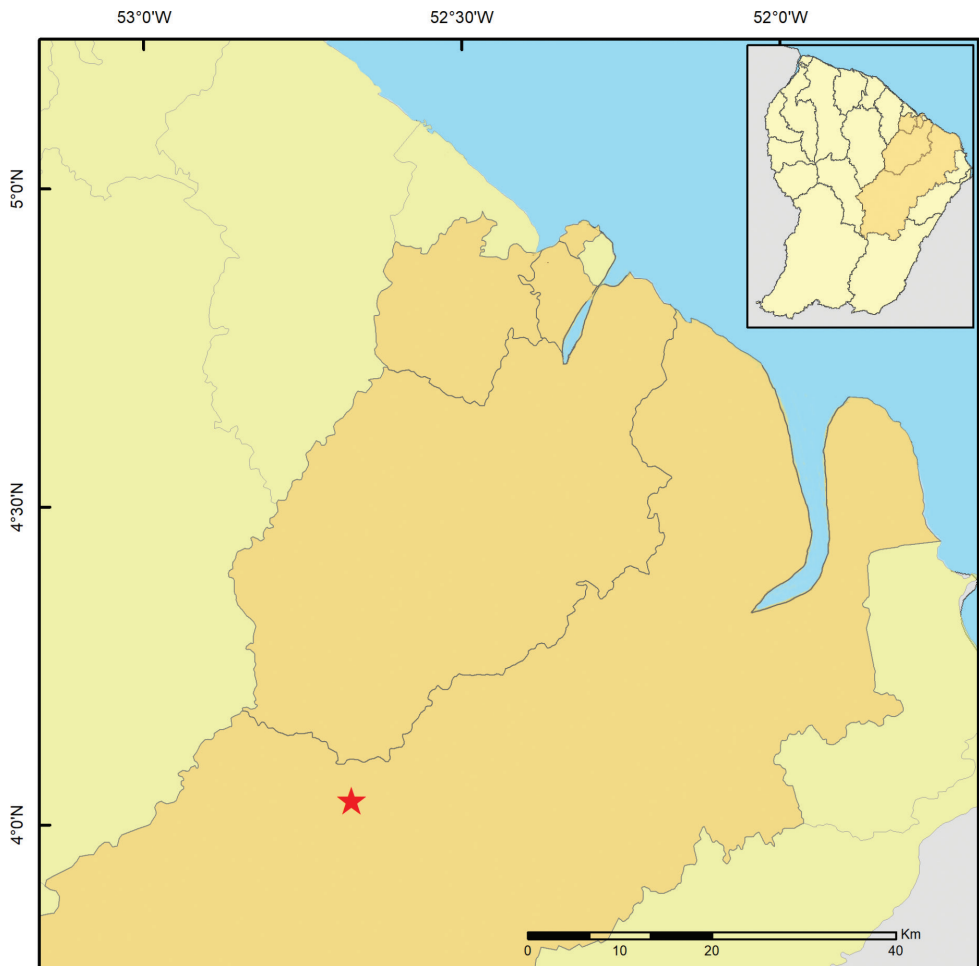


Figure 9. Geographic distribution of *Rhagovelia depressa* Rodrigues, Khila & Moreira, sp. nov. in the Réserve Naturelle Nationale des Nouragues, Camp Pararé and surroundings (4.0386, –52.6728), French Guiana.

especially in the male), so it cannot be part of the *salina* group. Assigning it to either the *bisignata* or *hambletoni* group, however, is not possible due to the absence of macropterous forms (D. Polhemus 1997). The males of this new species are much smaller than the females and displayed piggyback behavior in the field, like that observed in other congeners with the same type of sexual dimorphism for body size (e.g., Moreira et al. 2010: fig. 5H).

Running this species through the keys for the *angustipes* complex provided by Bacon (1956), Nieser and D. Polhemus (1999) and Galindo-Malagón et al. (2021) ended in no possible logical results. The few species of the complex that are absent in these keys due to subsequent description or different geographic distribution also

do not match the specimens at hand. *Rhagovelia depressa* can be diagnosed by the combination of the following features: 1) body length 2.03–2.10 in the male and 2.70–2.82 in the female; 2) antennomere II longer than III; 3) female mesonotum with a large rounded central depression (Fig. 8A); 4) fore and hind coxae and trochanters yellow, middle coxa and trochanter black (Figs 6B, 8B); 5) male fore and hind trochanters without spines (Fig. 6B, E); 6) male fore femur thickened, with strong setae on posterior surface (Fig. 6B, C); 7) male fore tibia curved, with distinct grasping comb (Fig. 6B, C); 8) male hind femur thicker than middle femur, with a decreasing row of three or four spines starting after middle of posterior surface (Fig. 6B, E); 9) female fore and hind femora thinner than in males, without spines (Fig. 8B); 10) male hind tibia slightly narrowed and curved distally, without pegs throughout length, with strong apical spur (Fig. 6E); 11) female hind tibia straight, with apical spur weaker than in male (Fig. 8A); 12) female abdomen narrowed, with laterotergites reflexed over mediotergites, progressively covering them more from I–VII, then opening throughout tergum VIII (Fig. 8A); and 13) shape of the paramere (Fig. 7E).

Rhagovelia elegans Uhler, 1894

Figs 10A, 11

Material examined. FRENCH GUIANA • 2 apterous ♀; Réserve Naturelle Nationale des Nouragues, Camp Inselberg; 4.0892, –52.6772; 14 Oct. 2016; A.J.J. Crumière, A. Khila, F.F.F. Moreira, W. Toubiana leg.; CEIOC 82149 • 1 apterous ♀; same, except 4.0799, –52.6860; 15 Oct. 2016; CEIOC 82148 • 1 apterous ♂; localities near Cayenne; [4.86, –52.34]; 12–13 Oct. 2016; A.J.J. Crumière, A. Khila, F.F.F. Moreira, W. Toubiana leg.; CEIOC 82150.

Distribution. Hispaniola Island (D. Polhemus 1997), St. Kitts & Nevis (Bacon 1956), Dominica (Bacon 1956), Martinique (de Kort-Gommers and Nieser 1969), St. Lucia (D. Polhemus 1997), Costa Rica (D. Polhemus 1997), Panama (Champion 1898), St. Vincent & the Grenadines (Uhler 1893), Grenada (Uhler 1894), Trinidad & Tobago (Gould 1931), Colombia (Gould 1931), Venezuela (Hungerford 1944), French Guiana (this work), Brazil (Gould 1931), Ecuador (D. Polhemus 1997).

Rhagovelia ephydros (Drake & Van Doesburg, 1966)

Figs 10B, 11

Material examined. FRENCH GUIANA • 2 apterous ♂, 3 apterous ♀; Rivière de Montsinéry; 4.8930, –52.4558; [Oct. 2016]; A.J.J. Crumière, A. Khila, F.F.F. Moreira, W. Toubiana leg.; CEIOC 81278.

Distribution. Suriname (Drake and Van Doesburg 1966), French Guiana (this work).

***Rhagovelia equatoria* D. Polhemus, 1997**

Figs 10C, 11

Material examined. FRENCH GUIANA • 1 apterous ♂, 1 apterous ♀; Réserve Naturelle Nationale des Nouragues, Camp Inselberg; 4.0892, –52.6772; 14 Oct. 2016; A.J.J. Crumière, A. Khila, F.F.F. Moreira, W. Toubiana leg.; CEIOC 82146 • 2 apterous ♂; same, except 4.0892, –52.6772; 16 Oct. 2016; CEIOC 82147.

Distribution. Venezuela (D. Polhemus 1997); French Guiana (this work).

Note. The large hind tibial spine is not developed in the first male above.

***Rhagovelia evidis* Bacon, 1948**

Figs 10D, 11

Material examined. FRENCH GUIANA • 2 apterous ♀; Réserve Naturelle Nationale des Nouragues, Camp Inselberg; 4.0892, –52.6772; 14 Oct. 2016; A.J.J. Crumière, A. Khila, F.F.F. Moreira, W. Toubiana leg.; CEIOC 82161 • 4 apterous ♀; same, except 4.0799, –52.6860; 15 Oct. 2016; CEIOC 82162 • 7 apterous ♀; same, except 4.0892, –52.6772; 16 Oct. 2016; CEIOC 82163 • 4 apterous ♀; same, except stream near dam; 4.0799, –52.6838; 17 Oct. 2016; CEIOC 82159 • 11 apterous ♀; localities near Cayenne; [4.86, –52.34]; 12–13 Oct. 2016; A.J.J. Crumière, A. Khila, F.F.F. Moreira, W. Toubiana leg.; CEIOC 82160.

Distribution. French Guiana (this work), Brazil (Bacon 1948), Peru (Bacon 1956).

***Rhagovelia guianana* D. Polhemus, 1997**

Figs 10E, 11

Material examined. FRENCH GUIANA • 2 apterous ♂, 6 apterous ♀; Réserve Naturelle Nationale des Nouragues, Camp Inselberg; 4.0799, –52.6860; 15 Oct. 2016; A.J.J. Crumière, A. Khila, F.F.F. Moreira, W. Toubiana leg.; CEIOC 82153 • 1 apterous ♂, 3 apterous ♀; same, except stream near dam; 4.0799, –52.6838; 17 Oct. 2016; CEIOC 82155 • 8 apterous ♂, 12 apterous ♀; near Cayenne; 4.6282, –52.3072; 21 Oct. 2016; CEIOC 82151 • 3 macropterous ♂; [unspecified locality]; [Oct. 2016]; [A.J.J. Crumière, A. Khila, F.F.F. Moreira, W. Toubiana leg.]; CEIOC 82154 • 4 apterous ♂, 3 apterous ♀; same, except CEIOC 82152.

Distribution. Venezuela (D. Polhemus 1997), Suriname (D. Polhemus 1997), French Guiana (this work), Brazil (D. Polhemus 1997).

Note. We noticed a fair amount of variation in hind femoral size among the males above. In addition, specimens with larger femora displayed the typical pilose anterior surface of the segment, whereas those with smaller femora showed less developed pilosity. Furthermore, a few of them showed considerably lighter colour

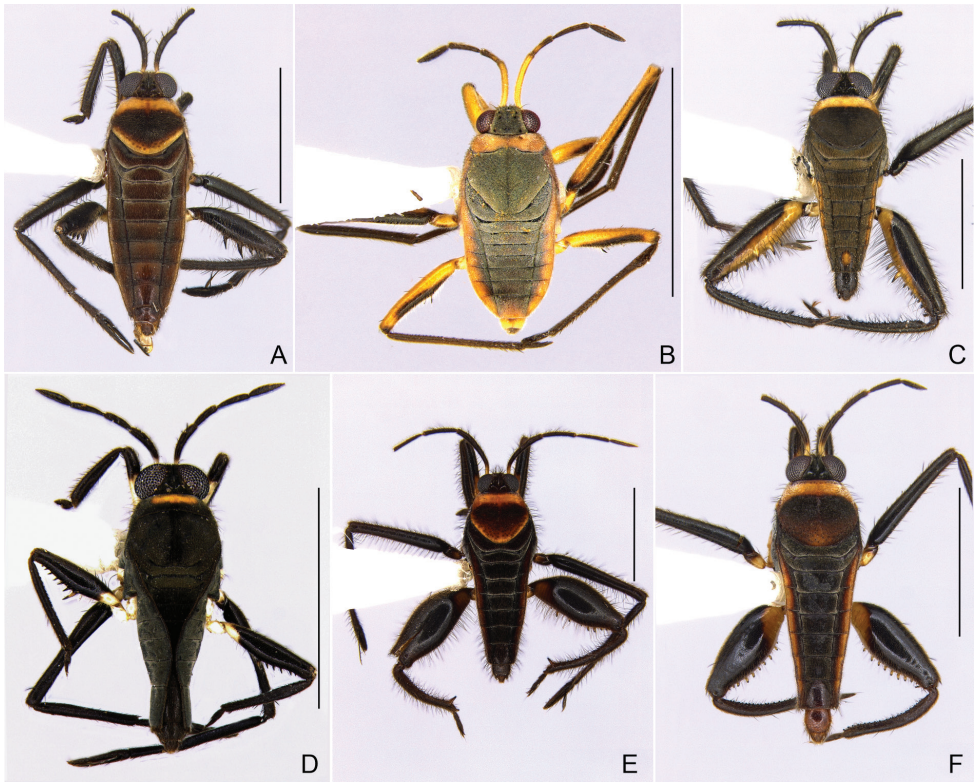


Figure 10. Habitus, dorsal view **A** *Rhagovelia elegans* **B** *R. ephydros* **C** *R. equatoria* **D** *R. evidis* **E** *R. guianana* **F** *R. humboldti*. Scale bars: 2 mm.

than the rest of the series and of the holotype of the species, being yellow/brown instead of brown/black. However, the dense cover of pilose setae on the antennae, sides of the body and over the legs was consistent with the species concept, as well as the spination of the hind trochanter, femur and tibia, and the shape of the paramere.

***Rhagovelia humboldti* D. Polhemus, 1997**

Figs 10F, 11

Material examined. FRENCH GUIANA • 2 apterous ♂, 1 macropterous ♂, 2 apterous ♀, 1 macropterous ♀; [unspecified locality]; [Oct. 2016]; [A.J.J. Crumière, A. Khila, F.F.F. Moreira, W. Toubiana leg.]; CEIOC 82164.

Distribution. Venezuela (D. Polhemus 1997), French Guiana (Motta et al. 2018; Crumière et al. 2019; this work), Brazil (Guterres et al. 2020).

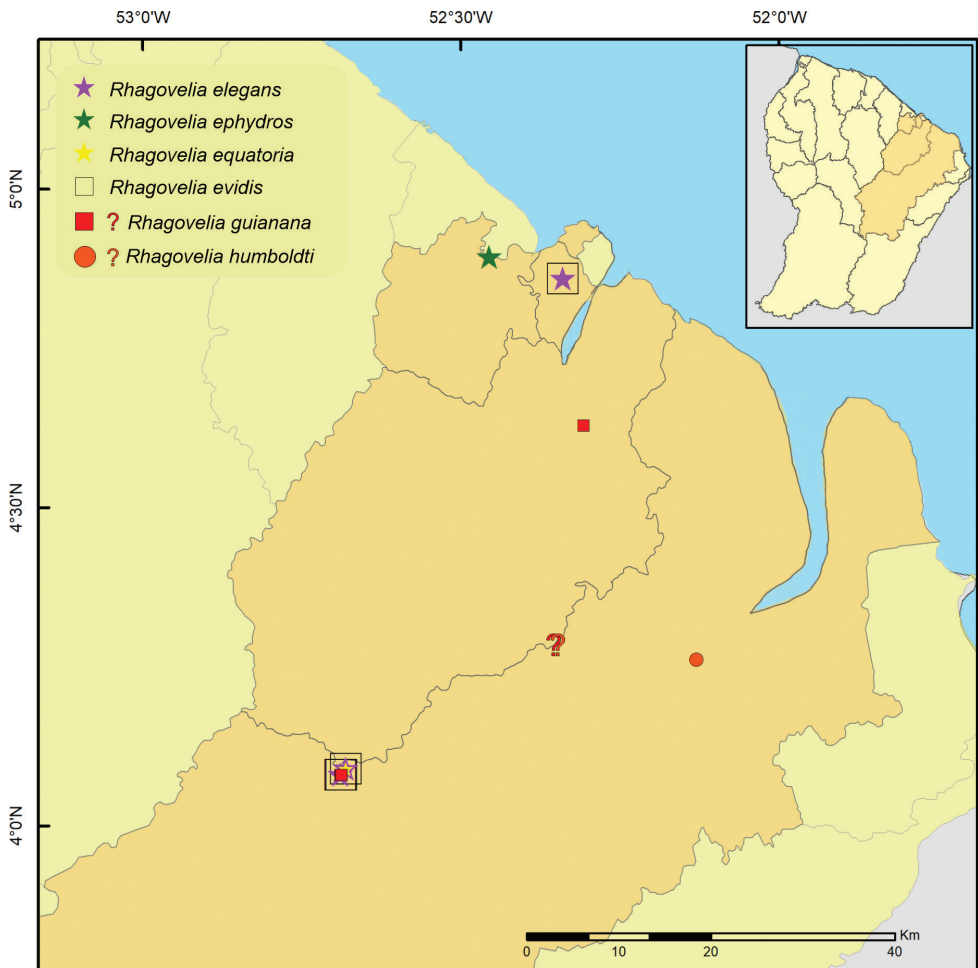


Figure 11. Geographic distribution of *Rhagovelia elegans*, *R. ephydros*, *R. equatoria*, *R. evis*, *R. guianana* and *R. humboldti* in French Guiana. Stars, squares and circle indicate new records; question marks indicate imprecise records (only the country is known, but not a specific locality).

***Rhagovelia tantilloides* Rodrigues, Khila & Moreira, sp. nov.**

<https://zoobank.org/7CE1FCF7-4244-4035-AE9E-E65DB3C731C7>

Figs 12–15

Type material examined. FRENCH GUIANA • apterous ♂ holotype; [unspecified locality]; [Oct. 2016]; [A.J.J. Crumière, A. Khila, F.F.F. Moreira, W. Toubiana leg.]; CEIOC 82141 • 2 apterous ♂ paratypes, 3 apterous ♀ paratypes; same, except CEIOC 82143 • 2 apterous ♀ paratypes; near Cayenne; 4.6282, –52.3072; 21 Oct. 2016; A.J.J. Crumière, A. Khila, F.F.F. Moreira, W. Toubiana leg.; CEIOC 82142.

Description. Apterous male (Figs 12, 13). Holotype (paratypes). BL 2.80 (2.80–2.85); HL 0.30 (0.30); HW 0.72 (0.75); INT 0.15 (0.15); ANT I 0.67 (0.67–0.70); ANT II 0.35 (0.37–0.70); ANT III 0.40 (0.42); ANT IV 0.50 (0.50); EYE 0.30 (0.30); PL 0.17 (0.17); PW 0.80 (0.75–0.80); FORELEG: FEM 0.82 (0.85–0.87); TIB 0.85 (0.87–0.90); TAR I 0.02; TAR II 0.02; TAR III 0.17 (0.15–0.20); MIDLEG: FEM 1.50 (1.50); TIB 1.07 (1.12); TAR I 0.07 (0.05–0.07); TAR II 0.45 (0.52); TAR III 0.65 (0.67–0.70); HINDLEG: FEM 1.15 (1.13–1.20); TIB 1.25 (1.37); TAR I 0.05 (0.05); TAR II 0.10 (0.10); TAR III 0.27 (0.27).

Head dorsally black, covered by stiff short setae; frons with denser cover of short setae and few long, curved setae; longitudinal midline and a pair of oblique indentations at base impressed and shining; impressed midline fading posteriorly. Eye shining dark red; ocular setae present. Antenniferous tubercle shining brown, darker at apex. Antennomeres covered by short and medium setae; antennomere I yellow basally, turning brown, then black towards apex, with four or five thick long black setae on mesal surface; antennomeres II–IV black; II with one thick long black seta; interarticular pieces shining brown. Buccula and labium shining brown; buccula and last labial article darker. Venter of head dark brown to black.

Pronotum black, with dark orange mark between eyes behind vertex of head; with greyish pubescence on sides of mark, covered by medium-sized dark setae, with longer black setae on sides and posterior margin. Meso- and metanota black, covered by medium and long black setae; metanotum with greyish pubescence on posterolateral corners. Thoracic pleura black with greyish pubescence, covered by medium and long black setae. Proacetabulum mostly pale yellow, becoming brown, then black laterally and mesally. Mesoacetabulum black with greyish pubescence; laterally with a brown mark; margin surrounding middle coxa pale yellow. Metacetabulum laterally black with greyish pubescence, becoming brown, then pale yellow towards apex; in ventral view, mostly pale yellow. Thoracic sterna bluish black, covered by greyish pubescence, with long brown setae laterally on mesosternum, two oblique rows of light setae submedially on mesosternum, and medium-sized light setae posteriorly on meso- and metasterna.

Fore and hind coxae and trochanters pale yellow; distal tip of trochanters, in ventral view, brown; fore coxa with medium and long light setae on mesal surface, and few stiffer long brown setae; hind coxa with curved, short, light setae basally and longer more straight light setae apically; fore trochanter with medium and long light setae, and stiffer long brown setae; hind trochanter with medium and long light setae, and few long brown setae. Middle coxa shining, in ventral view, light brown to brown marginally, dark brown to black centrally; covered by medium and long, light and brown, setae; with stiffer long brown setae laterally. Middle trochanter dark brown to black, shining on dorsal apex, covered by medium and long light setae. Fore femur basally light yellow, becoming brown, then black towards apex, covered by medium and long light setae, with rows of stiff long dark setae on anterior and posterior surfaces. Fore tibia and tarsus dark brown to black. Fore tibia covered by medium and long curved light setae, with longer dark setae on anterior and posterior surfaces, those on basal

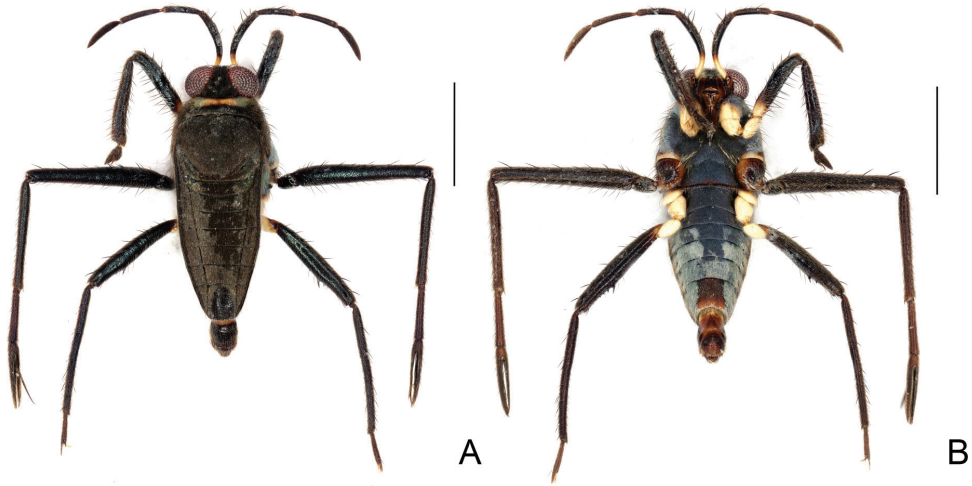


Figure 12. *Rhagovelia tantilloides* Rodrigues, Khila & Moreira, sp. nov., habitus, apterous male **A** dorsal view **B** ventral view. Scale bars: 1 mm.

posterior surface thicker; dense cover of long, almost straight, brown, setae on apex of ventral surface; grasping comb discreet; grooming comb present. Tarsus with dense cover of short and medium-sized brown setae. Middle femur dark brown to black, covered by medium and long light setae, with rows of longer stiff brown setae on anterior and posterior surfaces, and two thicker black setae near apex of anterior surface, the distalmost thickest. Middle tibia dark brown to black, densely covered by medium and long brown setae, with rows of longer brown setae on anterior and posterior surfaces. Middle tarsus brown to black, densely covered by medium and long brown setae, with some longer brown setae on anterior surface. Hind femur, in dorsal view, narrowly dark brown on base; in ventral view, narrowly lighter brown on base; rest dark brown to black; covered by medium-sized brown setae, with rows of longer dark setae on anterior and posterior surfaces, those on anterior surface thicker. Hind tibia dark brown, covered by medium-sized brown setae, with rows of longer thicker setae on anterior and posterior surfaces; those on anterior surface thicker. Hind trochanter dark brown, covered by medium-sized brown setae.

Abdominal medio- and laterotergites black, covered by greyish pubescence, except for large shining black area covering most of mediotegite VII, and shining black lateral margins of laterotergites; long dark setae widespread. Abdominal sterna II–VI bluish black, covered by greyish pubescence; with medium-sized light setae adjacent to posterior margins; long light setae on sides of sterna III–VI and center of VI. Abdominal sternum VII brown to dark brown on wide subrectangular area centrally; bluish black with greyish pubescence on sides of brown area and posterior margin; with long light setae, these are more dense laterally. Abdominal segment VIII light brown on anterior half, dark brown on posterior half, laterally covered by long brown setae and medium-sized light setae. Pygophore and proctiger light brown on anterior 1/3, dark brown on posterior 2/3, densely covered by medium-sized light setae.

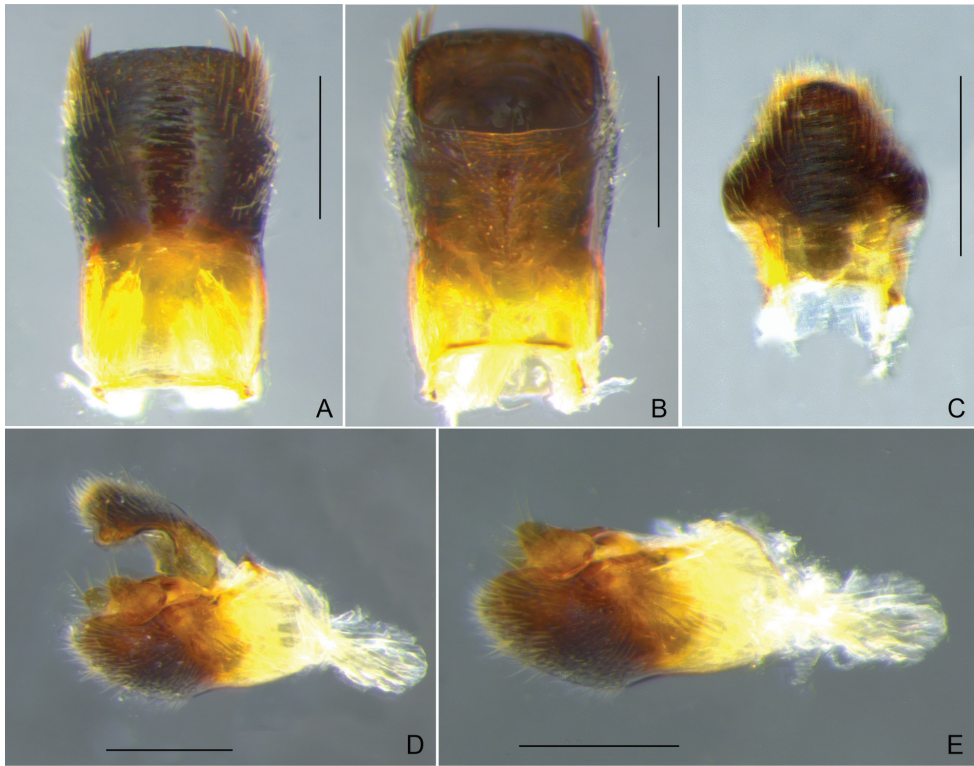


Figure 13. *Rhagovelia tantilloides* Rodrigues, Khila & Moreira, sp. nov., male terminalia **A, B** abdominal segment VIII, dorsal and ventral views, respectively **C** proctiger, dorsal view **D** genital capsule, lateral view **E** pygophore and paramere, lateral view. Scale bars: 0.2 mm.

Head compact. Eyes large, touching pronotum. Antennomere I thickest, curved laterally; II–III cylindrical, subequal in width; IV fusiform, slightly thicker than II–III. Labium robust, reaching middle of mesosternum.

Pronotum shorter than dorsal eye length, with posterior margin slightly concave. Mesonotum slightly elevated centrally, posterior margin widely rounded. Metanotum short at midline, posterior margin almost straight. Thoracic pleura and sterna, and abdominal sterna covered by minute circular punctations on bluish black areas. Posterior margin of mesosternum widely concave. Posterior margin of metasternum slightly concave medially.

Fore trochanter unarmed. Fore femur as thick as fore tibia, thinner than middle femur, with a slight concavity before middle of anterior margin. Fore tibia slightly widened near apex, with a weak preapical concavity on ventral surface. Middle femur without flattening or constriction, thickest subbasally, slightly thicker in this area than hind femur. Hind femur not reaching apex of terminalia, thickest right after middle, with a distally decreasing row of 2–4 black spines starting approximately on apical 1/3 of posterior surface and not reaching apex. Hind tibia slightly curved distally, without pegs throughout length nor apical spur; a tuft of medium-sized brown setae apically.

Abdominal mediotergite I shortest; II–VI of approximately same length, progressively narrower; VII longest, with posterior margin slightly convex. Laterotergites slightly elevated; lateral margins slightly divergent for first two segments, then tapering for one segment, then tapering more strongly towards apex, ending continuously to posterior margin of mediotergite VII. Sternum II laterally compressed, with a concavity each side through which hind coxae move, without distinct median carina; III very weakly compressed laterally, without median carina; IV–VI progressively longer, without median carina; VII longest, without median carina or depression, slightly swollen adjacent to concave posterior margin. Abdominal segment VIII cylindrical; dorsal apical margin straight (Fig. 13A, B). Proctiger short; lateral lobes moderately large, rounded; apex rounded (Fig. 13C, D). Paramere small, slightly curved dorsally near apex; apex rounded (Fig. 13D, E).

Apterous female (Fig. 14). BL 3.00–3.15; HL 0.32–0.37; HW 0.75–0.82; INT 0.15–0.17; ANT I 0.65–0.70; ANT II 0.35–0.40; ANT III 0.37–0.40; ANT IV 0.45; EYE 0.30–0.32; PL 0.17–0.20; PW 0.75–0.85; FORELEG: FEM 0.77–0.85; TIB 0.80–0.90; TAR I 0.02; TAR II 0.02; TAR III 0.20–0.22; MIDLEG: FEM 1.45–1.55; TIB 1.02–1.12; TAR I 0.05–0.07; TAR II 0.45–0.52; TAR III 0.65–0.70; HINDLEG: FEM 1.10–1.20; TIB 1.25–1.40; TAR I 0.05; TAR II 0.10–0.12; TAR III 0.27–0.30.

Similar to apterous male in colour and structure, except for: fore femur lacking slight concavity on anterior surface; fore tibia lacking weak preapical concavity, without grasping comb; hind femur relatively shorter in relation to abdomen, with 1–4 spines; hind tibia not curved; abdominal mediotergite I with stronger greyish pruinosity on posterolateral angles; narrow shining black areas on centre of mediotergites V–VI, larger areas on VII–VIII and on dorsum of proctiger; mediotergite VII shorter, with almost straight posterior margin; tergum VIII wide anteriorly, with lateral margins tapering to almost straight posterior margin; laterotergites slightly more bowed laterally, ending next to tergum VIII, with a tuft of brown setae on apex; abdominal sternum VII swollen anteriorly and not posteriorly, with larger brown area covered by more light setae, and posterior margin slightly projected medially.

Etymology. The specific epithet *tantilloides* refers to the resemblance between this new species and *R. tantilla* Drake & Harris, 1933.

Comments. *Rhagovelia tantilloides* Rodrigues, Khila & Moreira, sp. nov. is part of the *angustipes* complex of species, based on the pronotum of the apterous form shorter than the dorsal eye length, with the posterior margin slightly concave. The tarsal formula 3-3-3 indicates that it is not part of the *salina* group, but an assignment to either the *bisignata* or *hambletoni* group is not possible due to the absence of macropterous individuals (D. Polhemus 1997). This new species displays an elongated abdomen and a relatively short and thick hind femora in both males and females. Running it through Nieser and D. Polhemus (1999) key to species of the *angustipes* complex from south-eastern and southern Brazil ends in no possible logical results. Using the keys provided by Bacon (1956) and Galindo-Malagón et al. (2021), however, results in *R. tantilla*, which is indeed similar to the specimens at hand.



Figure 14. *Rhagovelia tantilloides* Rodrigues, Khila & Moreira, sp. nov., habitus, paratype apterous female **A** dorsal view **B** ventral view. Scale bars: 1 mm.

This new species and *R. tantilla* share the following features: 1) similar body size (2.80–2.90 in the male, 3.00–3.15 in the female); 2) antennomere II shorter than III; 3) fore and hind coxae and trochanters yellow, middle coxa and trochanter dark (Figs 12B, 14B); 4) male fore and hind trochanters without spines (Fig. 12B); 5) male fore tibia not distinctly curved (Fig. 12B); 6) male hind tibia without pegs throughout length nor apical spur (Fig. 12B); 7) abdomen relatively elongated, with laterotergites slightly elevated and lateral margins tapering more or less evenly to apex (Fig. 12A); and 8) male abdominal segment VIII subcylindrical, with lateral margins bowed, shorter dorsally than mediotergite VII (Fig. 12A, 13A).

There are, however, essential differences between them, including: 1) male hind femur surpassing terminalia, thickest at middle, with 6–7 spines on the posterior surface (vs. not reaching terminalia, thickest after middle, with 2–4 spines in the new species; Fig. 12B); 2) male hind tibia straight (vs. slightly curved distally in the new species; Fig. 12B); and 3) shape of the paramere (compare Fig. 13E and Galindo-Malagón et al. 2021: fig. 19T). The distribution of shining black areas on the abdominal dorsum of *R. tantilla* is variable. For males, Bacon (1956) reported them on segments VIII or VII–VIII, while Galindo-Malagón et al. (2021) mentioned VII–VIII and figured a specimen with an additional smaller mark on VI. Females, in turn, reportedly have shining black areas on segments VII–VIII to V–VIII, according to both studies above. In the new species, we found shining black areas occupying most of male abdominal mediotergite VII and tergum VIII, whereas for females there are two narrow marks centrally on V–VI and two larger marks on VII–VIII. Finally, while our new species occurs in French Guiana, *R. tantilla* has a much more western distribution, from Belize (Drake and Harris 1933), through Central America (Bacon 1956; Moreira et al. 2015) and the Colombian Andes (Galindo-Malagón et al. 2021), to northwestern Peru (Bacon 1956).

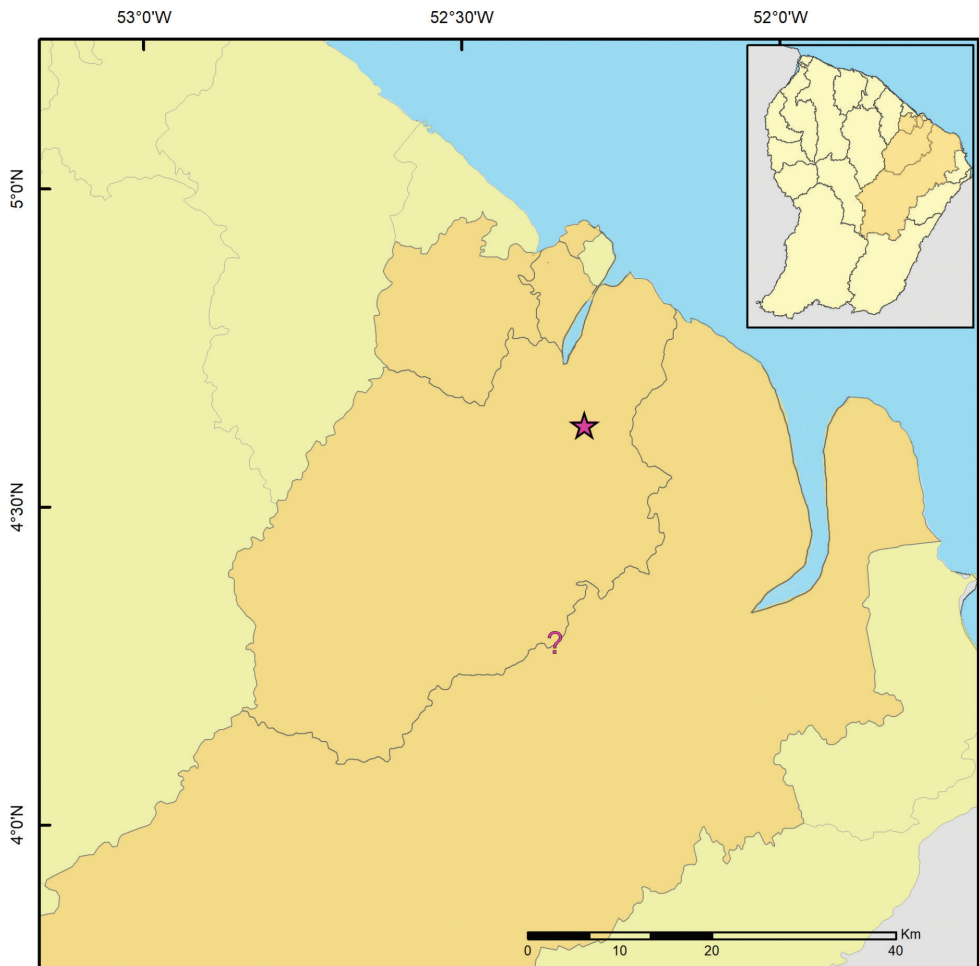


Figure 15. Geographic distribution of *Rhagovelia tantilloides* Rodrigues, Khila & Moreira, sp. nov. in French Guiana. Question mark indicates an imprecise record (only the country is known, but not a specific locality).

Rhagovelia tenuipes Champion, 1898

Fig. 16

Material examined. FRENCH GUIANA • 3 apterous ♂; Réserve Naturelle Nationale des Nouragues, Camp Inselberg, stream near dam; 4.0799, –52.6838; 17 Oct. 2016; A.J.J. Crumière, A. Khila, F.F.F. Moreira, W. Toubiana leg.; CEIOC 77296.

Distribution. Mexico (Champion 1898), Cayman Islands (Hungerford 1940), Belize (Drake and Harris 1935b), Guatemala (Drake and Harris 1935b), Honduras (Drake and Harris 1927), Nicaragua (University of California Berkeley 2009), Costa Rica (Hungerford 1939), Trinidad & Tobago (Hynes 1948), Colombia (Bacon 1956), Venezuela (Hungerford 1944), French Guiana (this work), Brazil (Bacon 1956), Ecuador (Gould 1931), Peru (Drake and Harris 1935b).

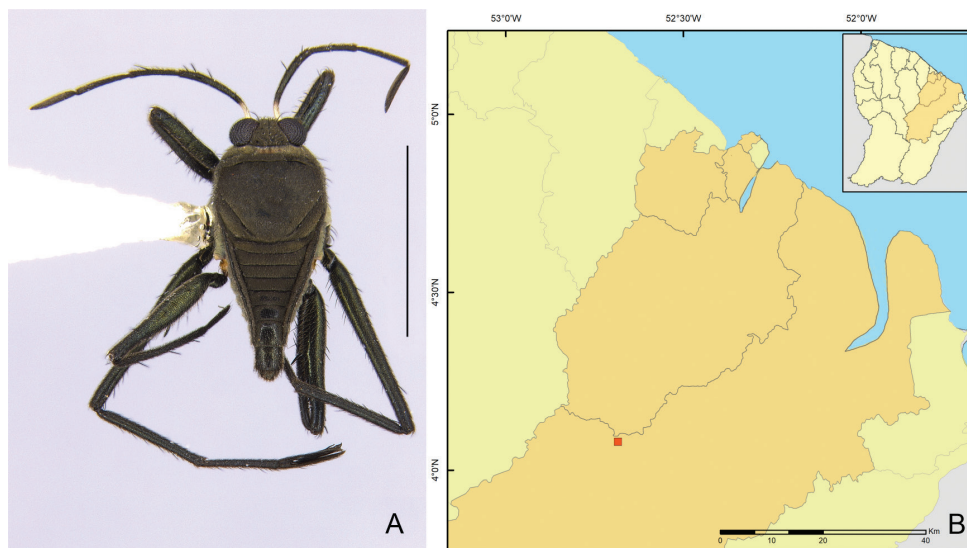


Figure 16. *Rhagovelia tenuipes* from French Guiana **A** habitus, male, dorsal view **B** geographic distribution. Scale bar: 2 mm.

Subfamily Veliinae

Callivelia conata (Hungerford, 1929)

Figs 17A, 18

Material examined. FRENCH GUIANA • 6 macropterous ♂; Réserve Naturelle Nationale des Nouragues, Camp Inselberg; 4.0892, –52.6772; 14 Oct. 2016; A.J.J. Crumière, A. Khila, F.F.F. Moreira, W. Toubiana leg.; CEIOC 79996 • 1 macropterous ♀; same, except Camp Pararé and surroundings; 4.0386, –52.6728; 17–18 Oct. 2016; CEIOC 79986.

Distribution. Trinidad & Tobago (Floriano et al 2017a), Venezuela (Floriano et al. 2017a), Guyana (Floriano et al. 2017a), Suriname (D. Polhemus 2021), French Guiana (Hungerford 1929a; this work), Brazil (Hungerford 1929a), Peru (D. Polhemus 2021).

Oiovelia cunucunumana (Drake & Maldonado-Capriles, 1952)

Figs 17B, C, 18

Material examined. FRENCH GUIANA • 33 macropterous ♂, 17 macropterous ♀; Réserve Naturelle Nationale des Nouragues, Camp Pararé and surroundings; 4.0386, –52.6728; 17–18 Oct. 2016; A.J.J. Crumière, A. Khila, F.F.F. Moreira, W. Toubiana leg.; CEIOC 79999.

Distribution. Colombia (Molano et al. 2016), Venezuela (Drake and Maldonado-Capriles 1952), French Guiana (this work), Brazil (Spangler 1986), Peru (Spangler 1986), Paraguay (Drake and Roze 1955), Argentina (Mazzucconi and Bachmann 1997).



Figure 17. Habitus, dorsal view **A** *Callivelia conata* **B** *Oiovelia cunucunumana*, specimen with approximately v-shaped whitish pruinosity on posterior portion of pronotum **C** *Oiovelia cunucunumana*, specimen without approximately v-shaped whitish pruinosity on posterior portion of pronotum **D** *Paravelia bullialata*. Scale bars: 2 mm.

Note. Most of the specimens above display an approximately V-shaped whitish pruinosity on the posterior lobe of the pronotum, which is not expected for this species (Floriano and Rodrigues 2016). This could lead to a confusion with *O. rivicola*

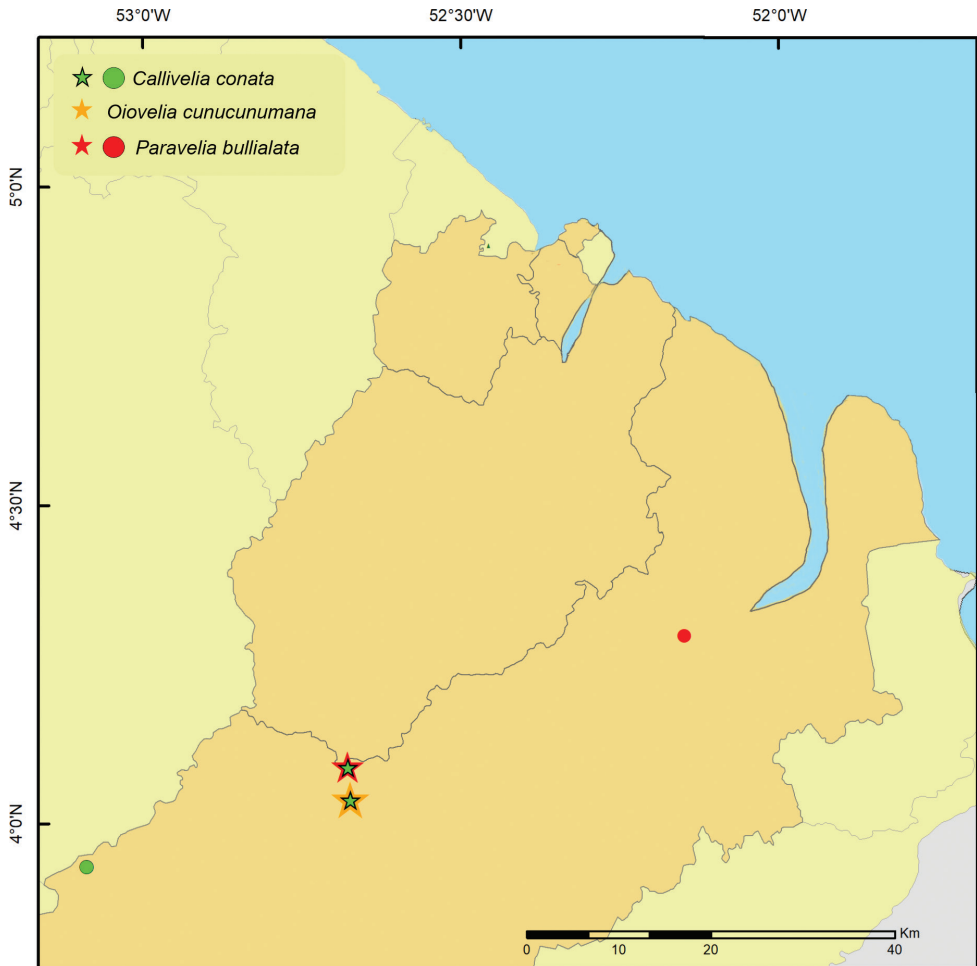


Figure 18. Geographic distribution of *Callivelia conata*, *Oiovelia cunucunumana* and *Paravelia bullialata* in French Guiana. Circles indicate previous records; stars indicate new records.

Spangler, 1986, but the male parameres examined are not distinctly widened near the apex, and agree with those drawn by Spangler (1986) and Floriano and Rodrigues (2016) for *O. cunucunumana*.

***Paravelia bullialata* J. Polhemus & D. Polhemus, 1984**

Figs 17D, 18

Material examined. FRENCH GUIANA • 2 macropterous ♂, 1 macropterous ♀; Réserve Naturelle Nationale des Nouragues, Camp Inselberg; 4.0892, -52.6772; 14 Oct. 2016; A.J.J. Crumière, A. Khila, F.F.F. Moreira, W. Toubiana leg.; CEIOC 81293.

Distribution. Venezuela (D. Polhemus 2014), Guyana (J. Polhemus and D. Polhemus 1984), Suriname (J. Polhemus and D. Polhemus 1984), French Guiana (Crumière et al. 2016, 2019; Motta et al. 2018; this work), Brazil (J. Polhemus and D. Polhemus 1984), Bolivia (D. Polhemus 2014).

***Steinovelia vittata* Rodrigues, Khila & Moreira, sp. nov.**

<https://zoobank.org/F5D013D2-A985-4E48-AB58-4D2325E71410>

Figs 19–21

Type material examined. FRENCH GUIANA • macropterous ♂ holotype; Réserve Naturelle Nationale des Nouragues, Camp Inselberg; 4.0892, –52.6772; 16 Oct. 2016; A.J.J. Crumière, A. Khila, F.F.F. Moreira, W. Toubiana leg.; CEIOC 82140.

Description. Macropterous male (Figs 19, 20). BL 4.07; HL 0.45; HW 0.60; ANT I 1.15; ANT II partially lost; ANT III–IV lost; EYE 0.15; PL 1.25; PW 1.02; FORELEG: FEM 1.20, TIB 1.05, TAR I–TAR III lost; MIDLEG: FEM 1.80, TIB 1.75, TAR I–TAR III lost; HINDLEG: FEM 1.85, TIB–TARIII lost.

Dorsum of head yellow, darker towards frons, with short dark setae on vertex, and longer setae on frons, along mesal eye margin and posterolateral angles; side brown, darker posterior to eye; venter brown, darker below labium. Antenniferous tubercle brown. Antennomere I brown, darker on short basal ring, densely covered by short curved brown setae, with rows of longer thin setae; remaining portion of antennomere II brown, covered by short curved brown setae only. Eye shining, dark red, without ocular setae. Buccula yellowish brown, densely covered by curved light setae. Jugum and adjacent portion of propisternum without patches of silvery setae or black denticles. Labium yellowish brown up to base of article III; rest of III and base of IV brown; rest of IV dark brown.

Pronotum brown laterally, darker on sides of anterior lobe, yellow on a wide longitudinal stripe that continues over closed forewings; sparsely covered by straight medium setae, with longer setae on sides; without patches of silvery setae. Thoracic pleura brown, with a rough longitudinal yellow stripe above acetabula, covered by sparse long light setae, these more densely concentrated anteriorly on propleura; without patches or stripes of silvery setae. Lateral surface of acetabula brown, with sparse irregular yellowish areas, without patches or stripes of silvery setae. Propisternum and prosternum yellow; a dense cover of long golden setae anteriorly; meso- and metasterna dark brown, with sparse medium-sized golden setae; a fringe of golden setae along posterior margin of metasternum. Mesal surfaces of acetabula yellowish brown, darker on metacetabulum; sparse setae on pro- and mesoacetabulum; a more dense cover on metacetabulum.

Forewings opaque; when closed, dark brown laterally, yellow on wide median stripe that continues from pronotum; with long golden and brown setae on brown areas; a pair of irregular yellow maculae laterally to median stripe close to apex of wings; veins mostly yellow, brown to dark brown basally and anteriorly. Apical portion of hindwings pulled to the side of forewings; translucent brown, with veins darker and a reticular pattern of minute cells with darker margins; margins of wing with fringe of short and medium setae apically.

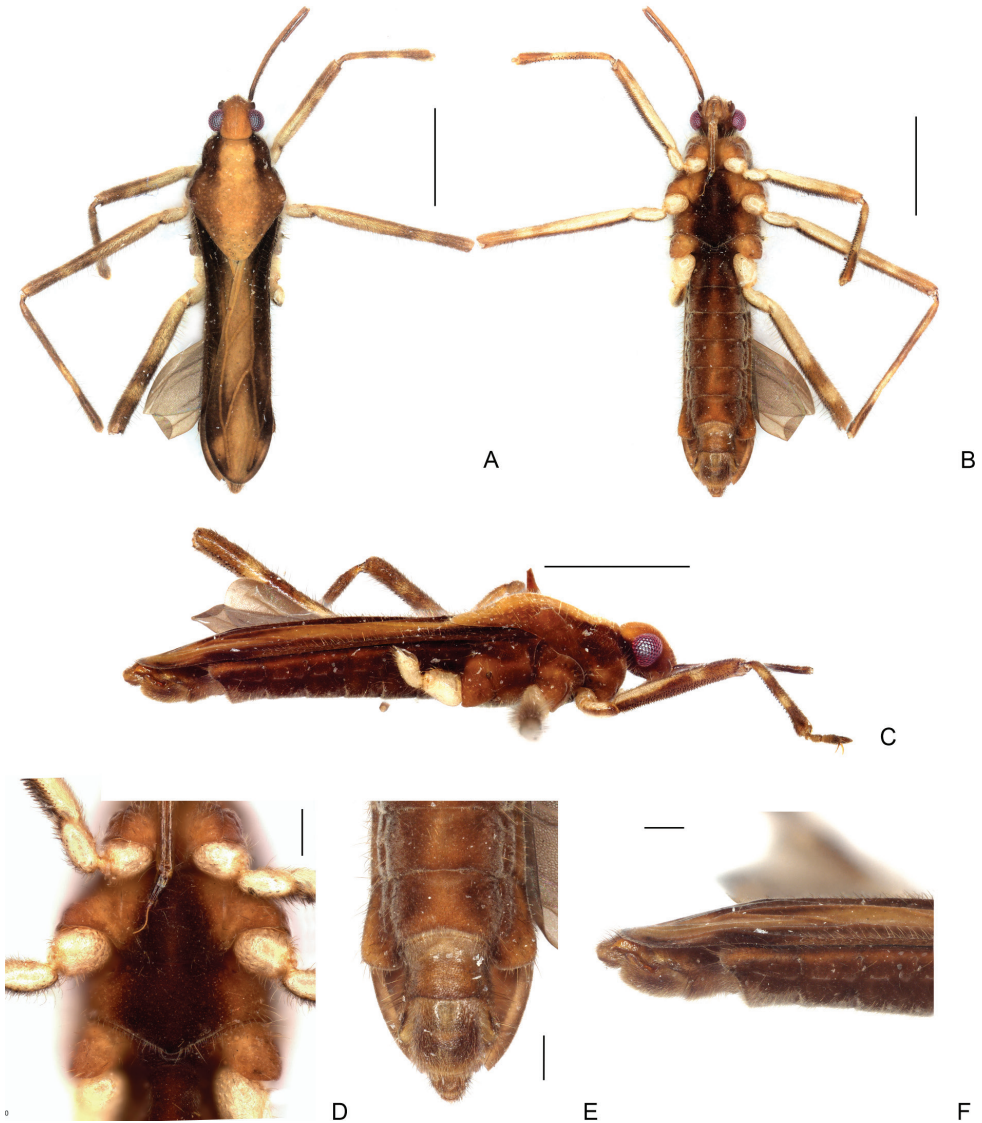


Figure 19. *Steinovelia vittata* Rodrigues, Khila & Moreira, sp. nov., macropterous male holotype **A** habitus, dorsal view **B** habitus, ventral view **C** habitus, lateral view **D** thoracic sternum, coxae, fore and middle trochanters, part of fore femora, and abdominal sternum II, ventral view **E** apex of abdomen, ventral view **F** apex of abdomen, lateral view. Scale bars: 1 mm (**A–C**); 0.2 mm (**D–F**).

Coxae pale yellow, with golden setae on margins. Trochanters pale yellow, with a longitudinal, brown stripe on posterior surface that continues onto femora; fore trochanter with golden setae on margins, and few thick conical black setae near apex of posterior margin; middle trochanter densely margined by curved short setae, with rows of longer, more straight setae; hind trochanter densely covered by setae, these more

numerous close to apex. Femora, viewed dorsally, yellow, with a shorter and a longer preapical brown rings; posterior surface with longitudinal brown stripe continuing from trochanter, preapically interrupted by yellow area; densely covered by short and medium straight brown setae, with rows of long, brown setae on anterior and posterior surfaces; these long setae longer on posterior surface. Fore femur with several thick conical black setae / spinules approximately organized in rows on posterior surface, scarcer towards apex. Middle femur with few of these setae / spinules approximately on distal third. Hind femur with two rows of these setae / spinules along length of posterior surface. Posterior surface of middle femur with dense cover of medium setae curved on apex; distal portion of anterior surface with dense cover of medium-sized black setae. Fore and middle tibiae brown, each with a pair of submedian yellow rings; covered by medium setae curved on apex. Fore tibia with few longer, straighter setae in rows on distal portion of anterior and posterior surfaces; a dense preapical cover of thick, straight setae on ventral surface; without grasping comb; with strong black pegs approximately organized in rows on posterior surface and apical grooming comb. Middle tibia with rows of long straight setae on anterior and posterior surfaces; without conical black setae / spinules, or black pegs.

Abdominal laterotergites covered by wings, except for narrow brown posterolateral corners of last segment. Side of abdomen dark brown, with lighter stripe below wings; stripe wider and lighter posteriorly; sparse medium and long brown setae along segments; last segment with denser cover of long setae on lateral margin and posterolateral corner. Venter of abdomen velvety brown laterally, with a submedian pair of rough longitudinal darker brown stripes, and median line lighter brown; central areas of segments covered by short straight black setae, intermixed with longer lighter more curved setae, these longer setae are more dense submedially and posteriorly on each segment. Terminalia light brown.

Head wide, with shining, shining impressed median line fading posteriorly, and a pair of curved shining indentations between midline and posterior portion of eyes; frons projecting medially. Antennomere I thicker than remaining portion of II, curved laterally; remaining portion of II cylindrical, straight. Antenniferous tubercles swollen, almost half as wide as eye ($\sim 43\%$); anterior margin widely concave. Posterior margin of eye distant from pronotum by $\sim 22\%$ of dorsal eye length. Buccula with a central punctilla. Labium almost reaching middle of mesosternum.

Pronotum convex; in lateral view, higher right after humeri, declining posteriorly; anterior margin slightly concave; lateral margins of anterior lobe swollen, rounded; constriction between anterior and posterior lobes; humeri elevated, conically projected, with apex broken on both sides of body; lateral margins of posterior lobe slightly sinuous anteriorly, then tapering to apex; posterior angle widely rounded; row of subtle circular punctillae adjacent to anterior margin; punctillae unnoticeable on rest of anterior lobe, present on posterior lobe, larger posteriorly. Pleura with a row of circular punctillae posteriorly on prothorax and another anteriorly on mesothorax. Acetabula with scattered circular punctillae. Surfaces of meso- and metasterna with minute circular punctations; intersegmental region between these segments without two pairs of

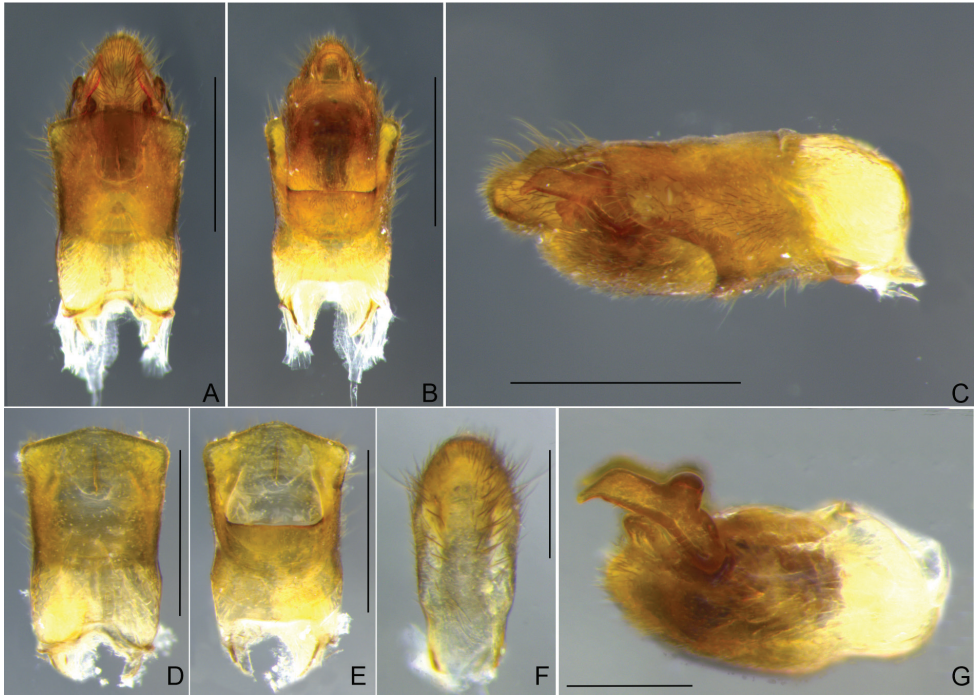


Figure 20. *Steinovelia vittata* Rodrigues, Khila & Moreira, sp. nov., macropterous male holotype, terminalia **A, B, C** genital capsule **A** dorsal view **B** ventral view **C** lateral view **D, E** abdominal segment VIII, dorsal and ventral views, respectively **F** proctiger, dorsal view **G** pygophore and paramere, lateral view. Scale bars: 0.5 mm (**A–E**); 0.2 mm (**F, G**).

small tubercles medially. Mesoacetabula without large circular puncture mesally, not prolonged into a posterior tubercle. Posterior margin of prosternum almost straight. Posterior margin of mesosternum slightly convex. Metasternum with lateral tubercles near middle coxae underdeveloped, almost imperceptible; a circular punctilla near each tubercle; posterior margin almost straight.

Forewings covering abdominal laterotergites except for posterolateral angles of last segment, reaching base of proctiger, with two proximal and two distal closed cells; division between cells on anterior side almost imperceptible.

Fore and middle femora of approximately same width; hind femur slightly wider, without strong spines. Fore tibia slightly clavate, with a weak preapical depression on ventral surface.

In dorsal view, abdomen narrowed between hind coxae and trochanters. Abdominal sterna with longitudinal striae laterally; small transverse regions of differently textured cuticle anteriorly on abdominal sterna IV–VII; sternum II laterally compressed, with a wide smooth median carina; sterna III–VI transversally rectangular, of approximately same length; VII with posterior margin widely concave, and wide rounded posterolateral angles, these angles reaching half of abdominal segment VIII length.

Abdominal segment VIII with dorsal apical margin projecting centrally (Fig. 20D, E). Proctiger elongated; lateral margins irregular; apex rounded (Fig. 20F). Paramere dolphin-shaped; dorsal margin with large, rounded projection almost at middle; apex finger-like, curved mesally, much narrower than rest of paramere (Fig. 20C, G).

Etymology. The specific epithet *vittata* (Latin, feminine) refers to the wide yellow stripe along the dorsum of this new species.

Comments. *Steinovelina vittata* Rodrigues, Khila & Moreira, sp. nov. diverges from the redescription of the genus provided in its latest revision (Moreira et al. 2020) in the following features: 1) sides of body with many silvery setae, sometimes forming longitudinal rows (vs. patches or stripes of silvery setae completely absent from the new species; Fig. 19C); and 2) paramere elongate and narrow, slightly tapering to apex (vs. dolphin-shaped, with a dorsal projection, abruptly narrowed near apex; Fig. 20C, G). The silvery setae are replaced in *S. vittata* by the more widespread golden setae and, on the sides of the body, by a yellow stripe above the acetabula, and a light brown stripe laterally on the abdominal sterna below the wings (Fig. 19). Additionally, the transverse glabrous areas on the anterior margins of abdominal sterna III–VII mentioned by Moreira et al. (2020) for *Steinovelina* are in fact adjacent to (not on) the anterior margins of sterna IV–VII (not III–VII) (check fig. 2D in the same article). These are represented in the new species by small regions of differently textured cuticle in the corresponding areas, but that are not completely devoid of short setae (Fig. 19B). The presence of short setae in these areas in the other species of *Steinovelina* needs to be verified, perhaps using scanning electron microscopy, for a proper assessment of this character.

Despite of the differences discussed above, this new species fits better in *Steinovelina* than in any other described genus of Neotropical Veliinae, and it seems unreasonable to describe an entire new genus just to allocate it, in face of the many similarities shared with its proposed congeners. Among the features reported in the latest redescription of *Steinovelina*, we can cite: 1) general body shape elongated, widest across humeri (Fig. 19A); 2) ocular setae absent (Fig. 19A, C); 3) black denticles absent from jugum and adjacent portion of proespisternum (Fig. 19D); 4) humeral angles forming projections (Fig. 19C); 5) posterior angle of pronotum broadly rounded (Fig. 19A); 6) forewings without basal maculae, but with distinct color pattern (Fig. 19A); 7) mesoacetabula not prolonged into tubercles, without large, deep puncture on mesal surface (Fig. 19B, D); 8) intersegmental region between the meso- and metasterna without two pairs of small tubercles medially (Fig. 19D); 9) metasternum with a pair of small tubercles laterally (underdeveloped in some cases, such as in the new species) and almost straight posterior margin (Fig. 19D); 10) femora and tibiae annulated in brown and yellow (Fig. 19A–C); 11) black conical setae / spinules / pegs present on posterior surfaces of femora and tibiae (Fig. 19C); 12) abdominal mediotergites II and III each with a prominent pair of submedian longitudinal carinae; and 13) abdominal sternum VII without expansions or projections (Fig. 19E, F).

Heretofore, *Steinovelina* included four valid species: *S. permista* (Drake, 1951); *S. stagnalis* (Burmeister, 1835); *S. vinnula* (Drake, 1951); and *S. virgata* (White, 1879). *Steinovelina vittata* can be immediately distinguished from the others by the wide yellow

median stripe dorsally along the body (Fig. 19A), and by the absence of silvery patches or stripes (Fig. 19A–C). Its congeners bear patches and/or stripes of silvery setae and, when macropterous, show a much more diffuse pattern of light and dark areas on the pronotum and forewings. Additional diagnostic features of this new species include the posterior margin of the eye distant from the pronotum by $\sim 22\%$ of the dorsal eye length (Fig. 19A); the proportionally large conical projections of the humeri (Fig. 19C); the relatively narrow hind femur without strong spines (Fig. 19B); the forewings almost completely covering the abdominal laterotergites, except for the posterolateral angles of the last segment (Fig. 19A, F); the abdomen narrowed between the hind coxae and trochanters (Fig. 19A, B); the posterolateral angles of male abdominal sternum VII reaching approximately half of abdominal segment VIII length (Fig. 19E); the male abdominal segment VIII with the dorsal apical margin projected centrally (Fig. 20D, E); and the shapes of the proctiger (Fig. 20F) and paramere (Fig. 20C, G).

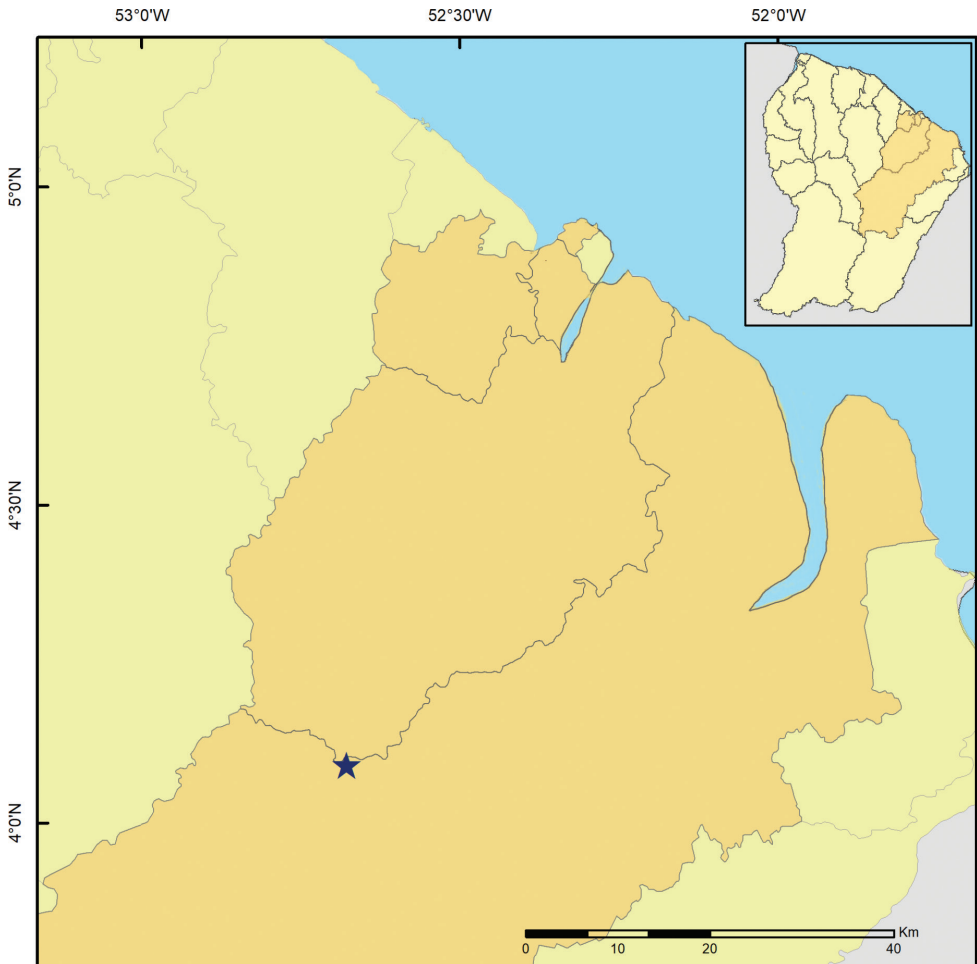


Figure 21. Geographic distribution of *Steinovelina vittata* Rodrigues, Khila & Moreira, sp. nov. in the Réserve Naturelle Nationale des Nouragues, Camp Inselberg (4.0892, –52.6772), French Guiana.

Stridulivelia alia (Drake, 1957)

Figs 22A, 23

Material examined. FRENCH GUIANA • 2 apterous ♂; Réserve Naturelle Nationale des Nouragues, Camp Inselberg; 4.0892, –52.6772; 16 Oct. 2016; A.J.J. Crumière, A. Khila, F.F.F. Moreira, W. Toubiana leg.; CEIOC 77294.

Distribution. Venezuela (J. Polhemus and Spangler 1995), Guyana (Drake 1957), Suriname (J. Polhemus and Spangler 1995), French Guiana (this work), Brazil (J. Polhemus and Spangler 1995).

Stridulivelia stridulata (Hungerford, 1929)

Figs 22B, 23

Material examined. FRENCH GUIANA • 1 apterous ♂; Réserve Naturelle Nationale des Nouragues, Camp Inselberg; 4.0892, –52.6772; 14 Oct. 2016; A.J.J. Crumière, A. Khila, F.F.F. Moreira, W. Toubiana leg.; CEIOC 77288 • 1 apterous ♀; same, except 16 Oct. 2016; CEIOC 77295.

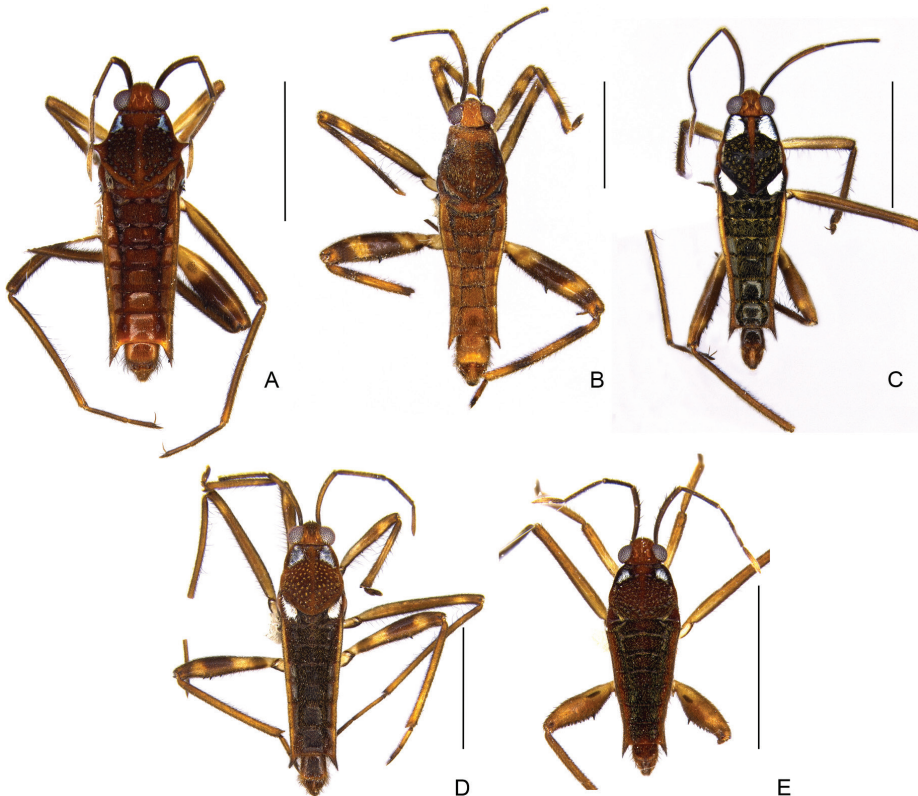


Figure 22. Habitus, dorsal view **A** *Stridulivelia alia* **B** *S. stridulata* **C** *S. strigosa* **D** *S. tersa* **E** *S. transversa*. Scale bars: 2 mm.

Distribution. Colombia (Roback and Nieser 1974), Suriname (J. Polhemus and Spangler 1995), French Guiana (this work), Brazil (Hungerford 1929b).

***Stridulivelia strigosa* (Hungerford, 1929)**

Figs 22C, 23

Material examined. FRENCH GUIANA • 1 micropterous ♂, 6 micropterous ♀; localities near Cayenne; [4.86, -52.34]; 13 Oct. 2016; A.J.J. Crumière, A. Khila, F.F.F. Moreira, W. Toubiana leg.; CEIOC 81282 • 4 micropterous ♂, 1 macropterous ♂, 1 micropterous ♀; Réserve Naturelle Nationale des Nouragues, Camp Inselberg; 4.0892, -52.6772; 14 Oct. 2016; A.J.J. Crumière, A. Khila, F.F.F. Moreira, W. Toubiana leg.; CEIOC 81283 • 6 micropterous ♂, 5 micropterous ♀; same, except 16 Oct. 2016; CEIOC 81288 • 1 micropterous ♂; same, except waterfall with moss and litter; [4.09; -52.68]; 17 Oct. 2016; CEIOC 79995 • 1 apterous ♀; same, except stream near dam; 4.0799, -52.6838; 17 Oct. 2016; CEIOC 81280.

Distribution. Venezuela (J. Polhemus and Spangler 1995), Guyana (J. Polhemus and Spangler 1995), Suriname (J. Polhemus and Spangler 1995), French Guiana (Crumière et al. 2016; Motta et al. 2018; this work), Brazil (Hungerford 1929b), Peru (J. Polhemus and Spangler 1995).

***Stridulivelia tersa* (Drake & Harris, 1941)**

Figs 22D, 23

Material examined. FRENCH GUIANA • 2 micropterous ♂, 1 micropterous ♀; Réserve Naturelle Nationale des Nouragues, Camp Inselberg; 4.0892, -52.6772; 14 Oct. 2016; A.J.J. Crumière, A. Khila, F.F.F. Moreira, W. Toubiana leg.; CEIOC 77291.

Distribution. Trinidad & Tobago (Drake and Harris 1941), Colombia (Molano et al. 2016), Venezuela (Drake and Menke 1962), Guyana (J. Polhemus and Spangler 1995), Suriname (J. Polhemus and Spangler 1995), French Guiana (this work), Brazil (J. Polhemus and Spangler 1995), Peru (J. Polhemus and Spangler 1995), Bolivia (Drake 1957).

***Stridulivelia transversa* (Hungerford, 1929)**

Figs 22E, 23

Material examined. FRENCH GUIANA • 1 apterous ♂, 1 apterous ♀; Réserve Naturelle Nationale des Nouragues, Camp Inselberg; 4.0892, -52.6772; 14 Oct. 2016; A.J.J. Crumière, A. Khila, F.F.F. Moreira, W. Toubiana leg.; CEIOC 77298 • 2 apterous ♂, 3 apterous ♀; same, except 4.0799, -52.6860; 15 Oct. 2016; CEIOC 79992 • 2 apterous ♀; same, except 4.0892, -52.6772; 16 Oct. 2016; CEIOC 77293.

Distribution. Venezuela (Floriano et al. 2017b), Suriname (J. Polhemus and Spangler 1995), French Guiana (Motta et al. 2018; this work), Brazil (Hungerford 1929b).

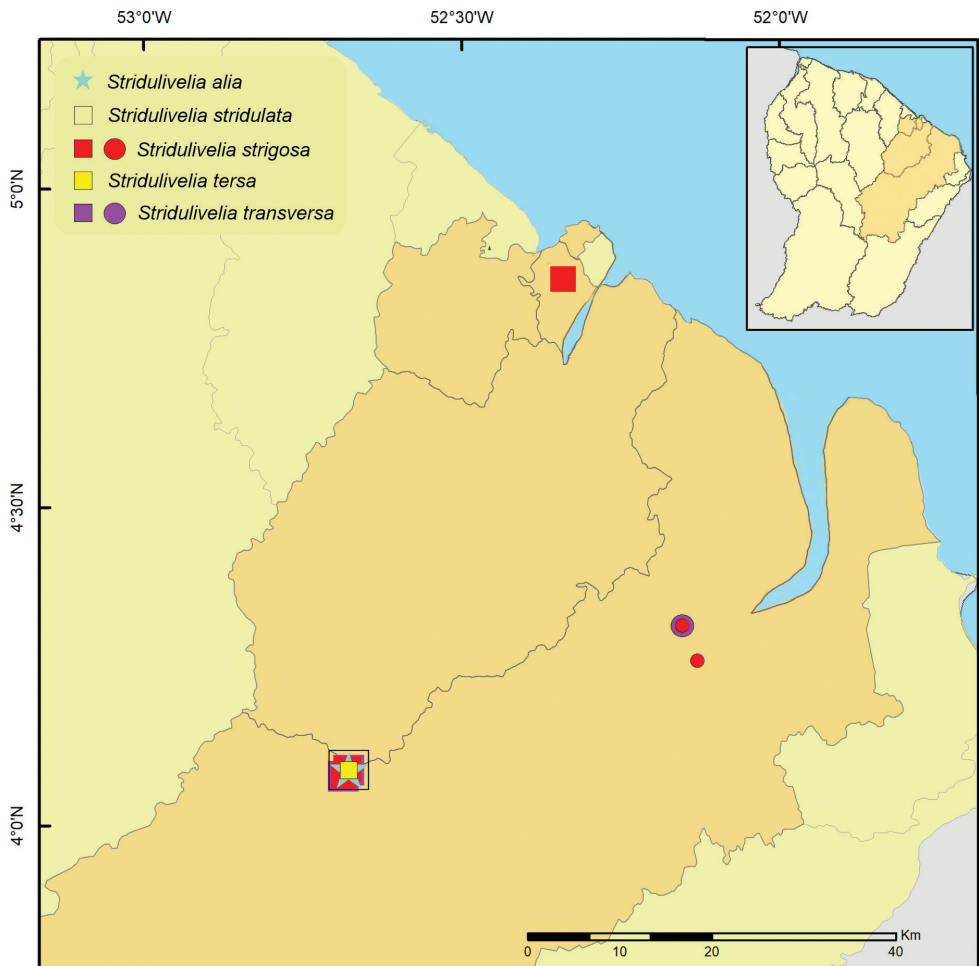


Figure 23. Geographic distribution of *Stridulivelia alia*, *S. stridulata*, *S. strigosa*, *S. tersa*, and *S. transversa* in French Guiana. Circles indicate previous records; star and squares indicate new records.

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