



**Monograph**

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**Uncovering hidden diversity: phylogeny and taxonomy of  
Physoderinae (Reduviidae, Heteroptera), with emphasis on  
*Physoderes* Westwood in the Oriental and Australasian regions**

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**Abstract.** The cryptic assassin bug subfamily Physoderinae is characterized by a distinctly uneven species and genus-level diversity across continents, but the lack of a phylogeny has so far precluded investigations into the biogeographic history of the group. Endemic Madagascan Physoderinae (11 of the 15 genera) exhibit broad morphological diversity, but the large (38 spp.) and seemingly uniform genus *Physoderes* is widely distributed across the Oriental and Australasian regions. The three remaining genera are small or even monotypic and restricted to the Neotropical (*Cryptophysoderes*, *Leptophysoderes*) and Afrotropical (*Porcelloderes*) regions. To investigate relationships among Physoderinae, with emphasis on the monophyly of the Madagascan fauna and the monophyly of *Physoderes*, we conducted a cladistic analysis based on 57 morphological characters and complete genus-level taxon sampling. We found that the Madagascan fauna is not monophyletic, indicating that the island was colonized more than once, although the great majority of Madagascan taxa are part of a single clade. Overall relationships are recovered as Afrotropical *Porcelloderes* + [(Neotropical *Cryptophysoderes*, *Leptophysoderes*) + (Madagascan, Oriental and Australasian taxa)]. *Physoderes* is shown to be polyphyletic and 3 new genera, *Breviphysoderes* gen. nov., *Macrophysoderes* gen. nov. and *Nanophysoderes* gen. nov., are erected to accommodate new species and several species previously classified as *Physoderes*. A taxonomic revision of *Physoderes* and allied genera is conducted. Diagnoses, updated distribution ranges, habitus and genitalic images, and identification keys are provided. A total of 17 synonymies are given, and 15 new species and 3 new genera are described, focusing on the diversity of Physoderinae in the Oriental and Australasian regions. The new species are *Breviphysoderes fulvopicta* gen. et sp. nov., *B. tenebrosa* gen. et sp. nov., *Macrophysoderes cirripilosa* gen. et sp. nov., *M. elongata* gen. et sp. nov., *M. finisterre* gen. et sp. nov., *M. grandis* gen. et sp. nov., *Paraphysoderes popeye* sp. nov., *Physoderes anamalaiensis* sp. nov., *P. brevipennis* sp. nov., *P. minime* sp. nov., *P. muluensis* sp. nov., *P. mysorensis* sp. nov., *P. nigripennis* sp. nov., *P. ractepilosa* sp. nov. and *P. tricolor* sp. nov.

**Keywords.** Assassin bugs, systematics, diversification, radiation, Madagascar.

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## Introduction

The reduviid subfamily Physoderinae is among the lesser-known groups of assassin bugs due to cryptic habits, restriction of most species to apparently small endemic ranges in wet-tropical areas of the Old and New Worlds, and the overall small number of genera and species compared to other reduviid subfamilies (Rédei 2012; Weirauch *et al.* 2014): only 70 species classified into 15 genera are described to date (Maldonado 1990; Weirauch 2006; Davranoglou 2014; Davranoglou *et al.* 2015). All members are small, rarely collected, feature subtle hues of brown and dirty yellow that allow them to blend into leaf litter and decaying wood, and many species share a somewhat dorsoventrally flattened, compact body shape and relatively short, heavily armored legs (Fig. 1). In contrast, the physoderine fauna of Madagascar and the nearby Comoros Islands (11 genera with 29 spp.; Villiers 1962) shows considerable morphological diversity, with some taxa resembling assassin bugs in other subfamilies, such as *Tribelocephaloides* Villiers, 1962 and *Mimoelasmodemima* Villiers, 1962, that superficially resemble Tribelocephalini (in the subfamily Ectrichodiinae) and Elasmodeminae, respectively (Villiers 1962; Weirauch *et al.* 2014; Forthman & Weirauch 2017; Fig. 2). More speciose, but morphologically relatively uniform, the Oriental and Australasian fauna of Physoderinae comprises 38 species currently classified within a single genus – *Physoderes* Westwood, 1845 (Maldonado 1990; Cao *et al.* 2011; Chlund 2011). Only two Neotropical genera of Physoderinae have so far been described, the monotypic *Cryptophysoderes* Wygodzinsky & Maldonado, 1972 from Panama and *Leptophysoderes* Weirauch, 2006 from Costa Rica and Ecuador, with *L. sarapiqui* Davranoglou, Hwang & Weirauch, 2015 showing pronounced sexual dimorphism (Wygodzinsky & Maldonado 1972; Weirauch 2006; Davranoglou *et al.* 2015). The only described continental Afrotropical species of Physoderinae is *Porcelloderes impenetrabilis* Rédei, 2012 from mountain ranges in northeastern Tanzania (Rédei 2012).

The present classification of Physoderinae is largely the result of the studies of two researchers: André Villiers and Norman C.E. Miller. Villiers (e.g., 1962, 1968) described the majority of the physoderine diversity in Madagascar during the 1950s and 1960s, and Miller (e.g., 1940, 1941) described the Oriental and Australasian *Physoderes* species in South-East Asia and the Pacific from the 1940s to the 1960s.



**Fig. 1.** *In situ* images of *Physoderes curculionis* China, 1936 in Singapore on mossy substrate (left) and vegetation debris (right).

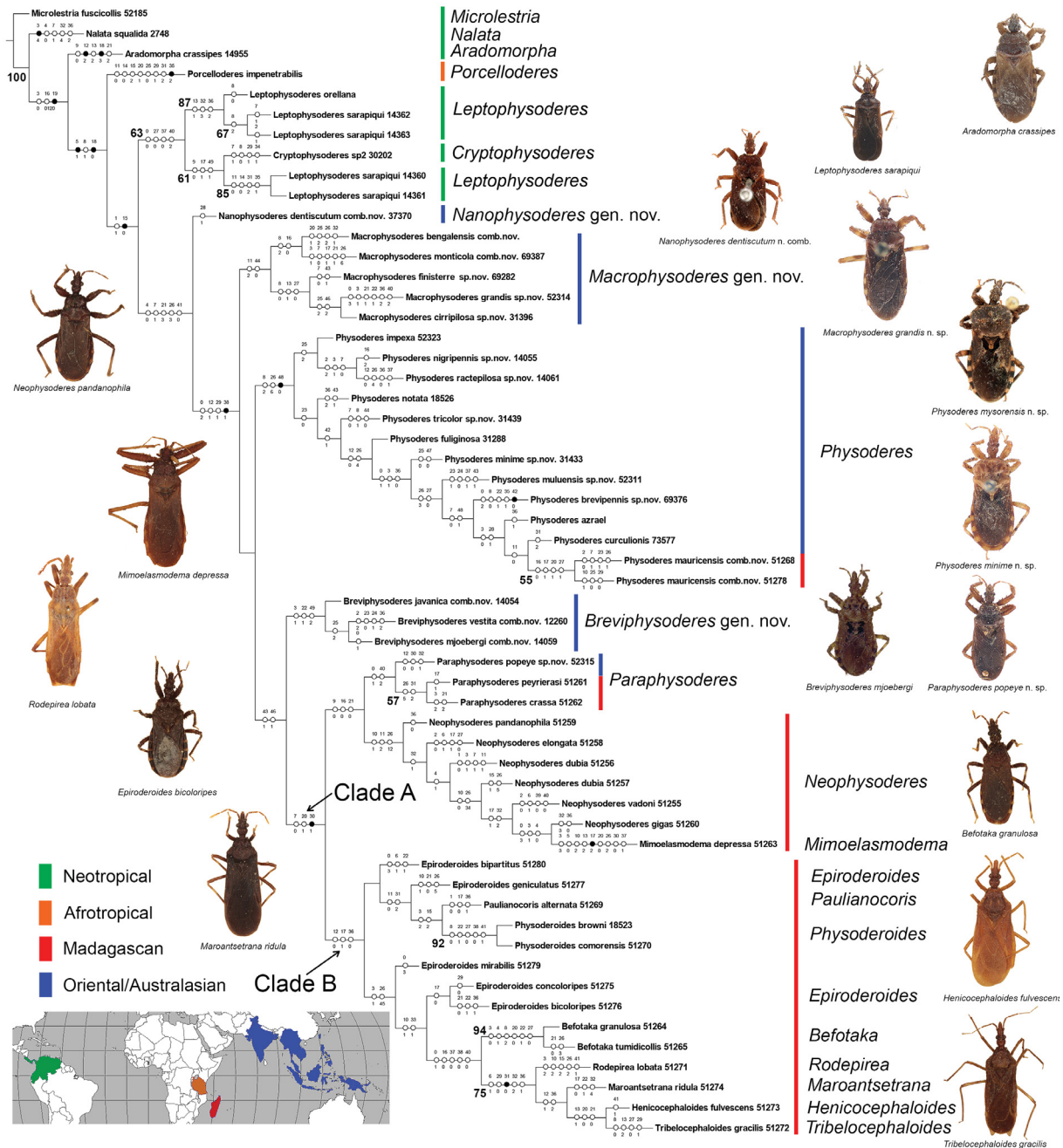
Since then, three Neotropical species (Wygodzinsky & Maldonado 1972; Weirauch 2006; Davranoglou *et al.* 2015) were described as new and Physoderinae were rediagnosed by Weirauch (2006) and Rédei (2012). More recently, new species were described from Madagascar (Chlond 2011; Baňáň *et al.* 2016; Chlond *et al.* 2016), the Oriental (Cao *et al.* 2011) and Australasian regions (Davranoglou 2014), and *Physoderes impexa* (Distant, 1903) was redescribed (Cao *et al.* 2011).

Phylogenetic relationships of Physoderinae, both between genera and species within the group and to other clades of assassin bugs, have largely remained in the dark. Miller (1954) suspected that the Neotropical reduviine *Aradomorpha* Champion, 1899 may be closely related to Physoderinae, whereas Lent & Wygodzinsky (1979) tentatively proposed a relationship with Triatominae, and Weirauch (2008) recovered the African reduviine *Sphedanovarus* Jeannel, 1866 as the sister taxon of the single species of *Physoderes* included in her morphology-based analysis. Molecular analyses found a poorly supported relationship with the Neotropical reduviine genus *Leogorrus* Stål, 1859 as part of an equally poorly supported larger clade also containing other Reduviinae and Salyavatinae (Weirauch & Munro 2009). These hypotheses were either not based on cladistic analyses (Miller 1954; Lent & Wygodzinsky 1979) or hampered by inadequate taxon sampling (Weirauch 2008; Weirauch & Munro 2009). A recent molecular phylogenetic analysis with more comprehensive sampling of Reduviinae (but lacking *Aradomorpha*) found Physoderinae to be closely related to the Neotropical reduviine genera *Microlestria* Stål, 1872 and *Nalata* Stål, 1860 (Hwang & Weirauch 2012). To date, relationships among genera and species of Physoderinae have not been investigated using cladistic methods: molecular data are available for less than a handful of species and morphological characters have not been coded and analyzed across the group. The Neotropical *Leptophysoderes* and *Cryptophysoderes* possess several characters thought to be plesiomorphic among Physoderinae and were suggested to be the putative sister-group of all remaining Physoderinae (Weirauch 2003), but this hypothesis remains to be tested. The aptery and resulting modified morphology somewhat hamper the testing of hypotheses for the phylogenetic placement of the Afrotropical *Porcelloderes* based on morphology. Finally, it also remains to be tested whether the Madagascan Physoderinae are monophyletic, representing a single clade and potentially therefore a radiation in adaptation to different habitats or other biotic or abiotic factors. Alternatively, the Madagascan fauna might represent several unrelated lineages, as recently shown for the assassin bug subfamily Ectrichodiinae (Forthman & Weirauch 2016).

Even though some of the smaller genera are likely monophyletic, this is not necessarily the case for *Physoderes*: examination of specimens from various institutions, including types, has revealed undocumented morphological diversity that may challenge the monophyly of this genus. *Physoderes* currently contains 38 species mostly described by Miller (e.g., 1940, 1941), with additional species contributed by Westwood (1847), Stål (1863, 1870), Horváth (1900), Breddin (1903), Kirkaldy (1905), Bergroth (1906), Distant (1903, 1909), China (1935), Usinger (1946), Cao *et al.* (2011) and Davranoglou (2014). *Physoderes* has never been taxonomically revised, almost all descriptions lack proper diagnoses as well as high-quality habitus and genitalic illustrations, and no identification key for the genus is in existence, resulting in a large number of misidentified museum specimens. In addition, many species descriptions are based on singletons, with either males or females assigned as holotypes, which can be problematic due to the presence of sexual dimorphism in some species. A sizeable number of *Physoderes* specimens have accumulated in various museums (we have located 905 specimens in 13 natural history collections) and we believe that it is timely to produce a modern monograph of the Oriental/Australasian fauna of Physoderinae, while revising generic concepts across the group and recognizing monophyletic groups as genera.

Here we use a morphology-based cladistic analysis that includes representatives of all described physoderine genera, dense species-sampling of *Physoderes* and representatives of *Microlestria*, *Nalata*,

and *Aradomorpha* as outgroups to: 1) investigate phylogenetic relationships within Physoderinae, with emphasis on the position of the Neotropical and Afrotropical genera as well as on the number and composition of monophyletic lineages in Madagascar; 2) test the monophyly of *Physoderes*; and 3) taxonomically revise the Oriental/Australasian fauna of Physoderinae according to the generic concepts derived from this analysis.



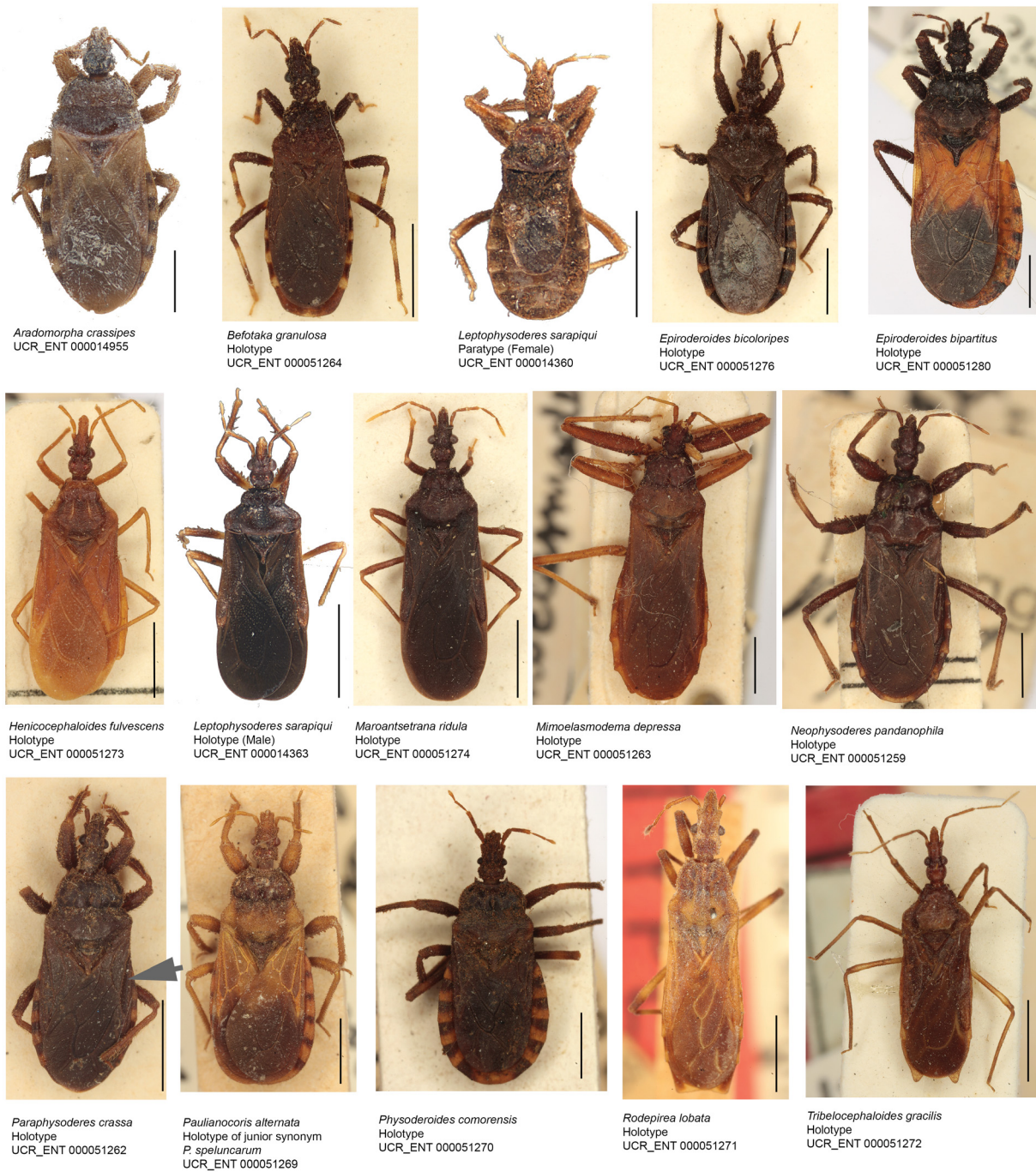
**Fig. 2.** Phylogeny of Physoderinae based on 57 morphological characters for 57 taxa analyzed using parsimony on TNT. Open white circles denote homoplastic characters, black circles denote characters that are not homoplastic. Numbers above the circles refer to character number (Table 1) and numbers below the circles refer to the character states (Table 3). Numbers in bold indicate symmetric resampling values.

## Material and methods

### Phylogenetic analysis

#### Taxon sampling

A total of 57 taxa (3 outgroup taxa: *Aradomorpha*, *Microlestria*, *Nalata*; 54 ingroup taxa) were examined. All 14 genera of Physoderinae were sampled (Fig. 3), with all species represented except in *Physoderes*



**Fig. 3.** Dorsal habitus images of other specimens examined for morphological coding. Images by Jean-Michel Berenger, except *Leptophysoderes sarapiqui* Davranoglou, Hwang & Weirauch, 2015 and *Aradomorpha crassipes* Champion, 1899. Scale bars = 2 mm.

**Table 1.** Morphological matrix for Physoderinae and outgroup taxa.

	0	0	1	1	2	2	3	3	4	4
	0	5	0	5	0	5	0	5	0	5
Microlestria_fuscicollis_52185	01131	00001	01001	13121	01111	10010	01020	01201	10???	?????
Nalata_squalida_2748	10140	00101	01011	13011	00111	10100	01420	02201	11???	??210
Aradomorpha_crassipes_14955	10101	0?000	01221	10130	02011	10100	01020	01201	11?1?	0?0??
Epiroderoides_mauricensis_51268	11000	10121	00001	00100	1301?	11111	01020	00211	10???	?????
Physoderes_mauricensis_51278	11100	1002?	10001	00100	13002	03110	01020	00211	10???	?????
Epiroderoides_concoloripes_51275	21110	10011	11001	01000	12010	15100	11110	00211	10???	?????
Epiroderoides_bicoloripes_51276	21110	10011	11001	01000	1011?	15101	11010	01211	10???	?????
Epiroderoides_geniculatus_51277	21100	10011	10001	01100	1001?	1510?	12020	00211	10???	?????
Epiroderoides_mirabilis_51279	31110	10011	01001	01100	13010	15101	11020	00211	10???	?????
Epiroderoides_bipartitus_51280	31100	11011	01001	01?00	1311?	13101	11020	00211	10???	?????
Befotaka_granulosa_51264	11101	10021	11001	00100	02111	25001	11110	00001	00???	?????
Befotaka_tumidicollis_51265	11101	10021	11001	00100	0011?	23001	11010	00001	00???	?????
Neophysoderes_dubia_51256	20111	10100	11101	00000	1001?	12101	11???	01211	10???	?????
Neophysoderes_dubia_51257	21101	10000	02101	10000	1001?	2510?	11101	01211	10???	?????
Neophysoderes_vadoni_51255	21001	11000	02111	00100	10010	2410?	11201	02210	00???	?????
Neophysoderes_elongata_51258	21000	11000	12101	00100	1001?	11001	11111	01211	10???	?????
Neophysoderes_pandanophila_51259	21100	10000	12101	00000	10010	11101	11001	00211	10???	?????
Neophysoderes_gigas_51260	31110	10000	02101	00100	10010	13101	11301	00211	10???	?????
Henicocephaloides_fulvescens_51273	11110	11011	11111	00100	00010	14100	10210	02000	01???	?????
Tribelocephaloides_gracilis_51272	11010	11001	11121	00100	00010	14001	10210	020??	?0???	?????
Maroantsetrana_ridula_51274	11010	11011	11101	00000	12110	15100	10410	02000	00???	?????
Mimoelasmodemata_depressa_51263	31130	00000	22121	00200	00010	12101	01201	02111	10???	?????
Paraphysoderes_peyrierasi_51261	11100	10000	01101	00100	1011?	1510?	12010	01211	20???	?????
Paraphysoderes_crassa_51262	11120	10000	01101	00000	12010	15101	?2010	01211	20???	?????
Paulianocoris_alternata_51269	20120	10011	00001	21000	12010	13101	12020	01211	10???	?????
Physoderoides_browni_18523	21120	10001	00001	21100	1211?	1300?	12020	00201	11???	?????
Physoderoides_comorensis_51270	21120	10001	00001	21100	12110	13001	12020	00201	11???	?????
Rodepirea_lobata_51271	11120	11011	21001	20100	12010	22100	10210	010??	?1???	?????
Porcelloderes_impenetrabilis	1010?	1001?	00000	20000	1011–	00–1	02020	2–101	11???	?????
Leptophysoderes_sarapiqui_14360	01001	10010	00000	02100	0001?	10000	02020	1–001	21?0?	0?011
Leptophysoderes_sarapiqui_14361	01001	10010	00000	02100	0001?	1000?	02020	1–001	21?0?	0?011
Cryptophysoderes_sp2_30202	01001	10100	01001	02100	0001?	10001	01021	01001	21?0?	0?011
Leptophysoderes_orellana	0100?	1000?	01011	0?000	?0010	10000	01320	0200?	?1?–1	0?010
Leptophysoderes_sarapiqui_14362	01001	10121	01011	02000	00010	10000	01320	02001	21???	?????
Leptophysoderes_sarapiqui_14363	01101	10021	01011	02000	00010	10000	01320	02001	21???	?????
Nanophysoderes_dentiscutum_37370	11000	10111	01001	02000	0301?	13110	01020	01201	10???	?????
Paraphysoderes_popeye_52315	11100	10000	01001	00000	10110	13101	01121	01211	20210	11110
Physoderes_brevipennis_69376	21110	10001	01001	01000	03102	13001	01020	1–211	10001	12110
Physoderes_muluensis_52311	11110	10121	01001	01000	03010	13001	01020	00111	10111	1010–
Breviphysoderes_vestita_12260	21210	10101	01101	01000	03101	23101	01020	02211	10211	11112
Breviphysoderes_javanica_14054	21110	10101	01101	01000	03110	13101	01020	01211	10211	11112
Breviphysoderes_mjobergi_14059	11110	10101	01101	01000	03110	23101	01020	01211	10???	?????
Physoderes_notata_18526	21100	1012?	01101	01000	03002	16101	01020	02211	10211	1010–
Physoderes_fuliginosa_31288	21100	10121	01001	01000	03002	14101	01020	01211	10???	?????
Physoderes_minime_31433	11110	10121	01001	01000	03002	04101	01020	00211	10?01	1200–

**Table 1.** (Continued)

	0	0	1	1	2	2	3	3	4	4
	0	5	0	5	0	5	0	5	0	5
<i>Physoderes_ractepilosa_14061</i>	21210	10021	01001	01000	03010	24101	01020	00111	10201	1020–
<i>Physoderes_nigripennis_14055</i>	21210	10021	01101	02000	03010	26101	01020	01211	10?01	1020–
<i>Physoderes_tricolor_31439</i>	21100	10011	01101	01000	03001	16101	01020	01211	10100	1010–
<i>Physoderes_impexa_52323</i>	21100	10121	01101	01000	03011	26101	01020	01211	10????	?????
<i>Physoderes_curculionis_73577</i>	11100	10021	00001	01000	03001	13011	02020	00211	10100	12210
<i>Physoderes_azrael</i>	11100	10021	01001	01000	03001	13011	01020	01211	10101	12110
<i>Macrophysoderes_finisterre_69282</i>	21100	10001	02111	01000	03010	13001	01020	01211	10110	10210
<i>Macrophysoderes_cirripilosa_31396</i>	21100	10101	02111	01000	03010	23001	01020	01211	10100	120??
<i>Macrophysoderes_grandis_52314</i>	31110	10101	02111	01000	01110	23001	01020	02211	20100	12210
<i>Macrophysoderes_bengalensis</i>	21000	1012?	02101	00000	13010	22101	01120	01211	10100	10012
<i>Macrophysoderes_monticola_69387</i>	21010	10020	02101	00100	01010	16101	01020	01211	10????	?????

(12 of 38 sampled) and *Neophysoderes* Miller, 1955a (5 of 6 sampled). Species of *Physoderes* were selected to represent what we perceive as morphogroups that may not be monophyletic and therefore were important to include in this analysis. Ten newly described species are also included to determine their genus-level placement. Whenever the association between males and females was in doubt, such as when the type specimen and its allotype are morphologically different, both were included in the analysis.

### Morphological dataset

Type specimens for all species were examined at the British Museum of Natural History (BMNH) and the Muséum national d’Histoire naturelle (MNHN). Additional specimens were loaned from different institutions and examined at the University of California, Riverside (UCR) using a Nikon SMZ1500 stereo microscope and recording morphological measurements. Scoring of characters was based on type specimens, plus additional identified material whenever available. A total of 57 morphological characters were coded using MESQUITE (Maddison & Maddison 2011; Tables 1–2), 50 as discrete characters that are either binary (24 characters) or unordered multistate (26 characters). A total of 7 continuous characters based on ratios of body measurements were also included (Table 2).

### Analysis parameters

A cladistic analysis was performed using a TNT (Goloboff *et al.* 2008) new technology search with initial level set at 50, 80 and 100, finding minimum length 10 times, and otherwise default settings. Symmetric resampling was performed using default settings for 500 replicates. Optimization of morphological characters on the resulting most parsimonious tree was performed in WinClada (Nixon 2002).

### Taxonomic revision

#### Specimens examined

A total of 905 specimens were examined during the course of this study. The specimens were loaned from various museums (see list of museum acronyms below). Holotype specimens described by Miller were examined, documented and imaged at BMNH and MNHN. Additional images of type specimens from other institutions were provided by Yvonne van Nierop, Tadashi Ishikawa, Cai Wanzhi, Cao Liangming, and Dávid Rédei. Each specimen was labeled with a Unique Specimen Identifier (USI) and label information recorded and georeferenced in the Plant Bug Planetary Biodiversity Inventory (PBI) locality database (<https://research.amnh.org/pbi/locality/>) located at AMNH. Specimen examined

**Table 2.** Measurements used as continuous characters in matrix. Note: total pronotal length excludes antero-lateral tubercles and paramedian lobes.

	Head length/postocular lobe width	Head width/interocular distance	Head length/anteocular lobe length	Head width/postocular lobe length	Head length/pronotal length	Posterior pronotal width/total pronotal length	Abdomen length/width
Microlestria_fuscicollis_52185	1.429	1.54	0.611	1.222	0.796	1.292	2.982
Nalata_squalida_2748	1.8	1.679	0.603	1.343	0.778	1.235	1.458
Aradomorpha_crassipes_14955	1.529	1.738	0.769	1.074	0.821	1.421	1.408
Paulianocoris_alternata_51269	1.964	1.65	0.727	1.179	0.733	1.2	1.413
Physoderes_mauricensis_51268	1.852	1.5	0.7	1	0.862	1.379	1.255
Epiroderoides_concoloripes_51275	2.133	1.737	0.688	1.1	0.79	1.21	1.585
Epiroderoides_bicoloripes_51276	2.2	1.65	0.682	1.1	0.957	1.232	0.818
Epiroderoides_geniculatus_51277	1.897	1.5	0.691	1.034	0.887	1.323	0.737
Epiroderoides_mauricensis_51278	1.828	1.429	0.679	1.034	0.779	1.309	1.271
Epiroderoides_mirabilis_51279	2.161	1.75	0.672	1.129	0.848	1.316	2.031
Epiroderoides_bipartitus_51280	1.943	1.68	0.662	1.2	0.828	1.363	1.511
Befotaka_granulosa_51264	2.042	1.647	0.673	1.167	1.167	1.31	1.758
Befotaka_tumidicollis_51265	2.143	1.545	0.667	1.214	1.017	1.203	1.363
Neophysoderes_dubia_51256	2.333	1.81	0.757	1.267	0.875	1.225	?
Neophysoderes_dubia_51257	1.71	1.783	0.679	1.323	0.736	1.222	1.489
Neophysoderes_vadoni_51255	1.96	1.7	0.653	1.36	0.69	1.197	1.906
Neophysoderes_elongata_51258	2.143	1.727	0.65	1.357	0.822	1.192	1.612
Neophysoderes_pandanophila_51259	2.25	1.684	0.648	1.333	0.831	1.123	1.53
Neophysoderes_gigas_51260	2.355	1.826	0.685	1.355	0.82	1.27	1.772
Henicocephaloides_fulvescens_51273	2.455	1.786	0.704	1.136	1.038	1.288	1.212
Maroantsetrana_ridula_51274	2.083	2.071	0.68	1.208	0.926	1.241	1.892
Mimoelasmodesma_depressa_51263	1.519	1.947	0.61	1.37	0.506	1.049	1.757
Paraphysoderes_peyrierasi_51261	1.913	1.8	0.614	1.174	0.786	1.268	1.328
Paraphysoderes_crassa_51262	2.143	1.6	0.644	1.143	0.789	1.246	1.356
Rodepirea_lobata_51271	2.333	1.667	0.696	1.25	0.982	1.053	2.07
Tribelocephaloides_gracilis_51272	2.706	2	0.696	1.176	1.243	1.514	2.086
Porcelloderes_impenetrabilis	2.288	1.076	0.7	1.231	?	?	0.98
Physoderoides_browni_18523	2	1.556	0.68	1.12	0.806	1.258	1.245
Physoderoides_comorensis_51270	1.69	1.667	0.673	1.034	0.803	1.328	1.242
Leptophysoderes_sarapiqui_14360	2.116	1.537	0.633	1.125	1.053	1.347	1.475
Leptophysoderes_sarapiqui_14361	2.079	1.477	0.633	1.14	1.026	1.247	1.55
Cryptophysoderes_sp2_30202	2.082	1.6	0.595	1.194	0.93	1.28	1.562
Leptophysoderes_orellana	1.714	2.002	0.6	1.143	1.518	1.404	1.416
Leptophysoderes_sarapiqui_14362	2.036	1.784	0.987	1.179	0.987	1.489	1.69
Leptophysoderes_sarapiqui_14363	1.947	1.789	0.676	1.193	0.925	1.467	1.675
Physoderes_notata_18526	2.067	1.7	0.677	1.133	0.775	1.25	1.792
Physoderes_fuliginosa_31288	2.188	1.545	0.686	1.063	0.795	1.288	1.419
Breviphysoderes_vestita_12260	2.125	1.733	0.686	1.083	0.857	1.303	1.308



**Table 2.** (Continued)

	Head length/postocular lobe width	Head width/interocular distance	Head length/anteocular lobe length	Head width/postocular lobe length	Head length/pronotal length	Posterior pronotal width/total pronotal length	Abdomen length/width
Breviphysoderes_javanica_14054	2.174	1.594	0.69	1.109	0.893	1.339	1.19
Physoderes_azrael	1.867	1.517	0.667	0.978	0.84	1.4	1.449
Physoderes_nigripennis_14055	2.205	1.793	0.68	1.182	0.843	1.326	1.465
Physoderes_ractepilosa_14061	2.326	1.438	0.71	1.07	0.98	1.373	1.528
Physoderes_curculionis_73577	1.897	1.414	0.662	1.051	0.813	1.374	1.393
Paraphysoderes_popeye_52315	1.914	1.64	0.687	1.171	0.87	1.429	1.64
Macrophysoderes_grandis_52314	2.369	2.083	0.69	1.316	0.865	1.423	1.67
Physoderes_brevipennis_69376	2.093	1.679	0.69	1.093	0.857	1.238	1.414
Physoderes_muluensis_52311	2.297	1.615	0.671	1.135	1.012	1.31	1.53
Macrophysoderes_finisterre_69282	2.093	1.677	0.69	1.209	0.874	1.408	1.67
Physoderes_minime_31433	2.563	1.517	0.732	1.1	0.949	1.204	1.581
Physoderes_tricolor_31439	2.049	1.769	0.69	1.122	0.792	1.226	1.655
Macrophysoderes_bengalensis	2.024	2.136	0.699	1.146	0.822	1.361	1.841
Macrophysoderes_monticola_69387	2.174	1.742	0.7	1.174	0.862	1.379	1.525
Physoderes_impexa_52323	2.152	1.559	0.707	1.152	0.825	1.333	1.818
Macrophysoderes_mjoebergi_14059	2.244	1.714	0.707	1.171	0.979	1.33	1.328
Macrophysoderes_cirripilosa_31396	2.125	1.815	0.682	1.225	0.842	1.337	1.613
Nanophysoderes_dentiscutum_37370	2.103	1.593	0.732	1.103	1	1.433	1.574

information for each species was generated from the database and provided the basis for the “material examined” section as part of each species description.

Almost all locality labels lacked geographic coordinates and were therefore subsequently georeferenced using Google Earth. Localities with generic provincial or country information were georeferenced to the center of the least inclusive geographic region provided. Distribution maps were generated based on the georeferenced data and created using the AMNH Simple Mapper online tool linked to the PBI database. The maps are organized according to genus, except for *Physoderes*, which is split into two maps to avoid heavy overlap of specimen points.

### Morphological methods

Habitus images were produced using either a Microoptics-USA imaging system with a Canon EOS 1D camera or an Automontage GT-Vision imaging system. Images are either single exposures or combined from raw images using the Helicon Focus version 4.16 software or Archimed. To remove male genitalia, specimens were relaxed overnight in a hot water bath before soaking the apex of the abdomen in 10% potassium hydroxide (KOH) for 2 hours. Male genitalia were dissected after being heated in a 10% KOH solution for 8 minutes, neutralized in water and transferred into 99% glycerol on a ceramic spot plate. The endosoma remained contracted for all specimens examined as we were unable to completely inflate it. The pygophores, parameres and phallus were dissected and mounted in a glycerin-gelatin mixture for imaging with an Automontage GT-Vision imaging system. Dissected genitalia were stored

in glycerol in a genitalic vial and pinned with the specimen. All images and illustrations were edited and compiled into plates using Adobe Photoshop CS3 version 10.0.

Measurements were made using a dissecting microscope equipped with a 2-axes movable stage (Mitutoyo Corp.), with the aid of two digital micrometers (Boeckeler) which were connected to a Microcode II RS-232 digital readout (Boeckeler). Standardized genus and species descriptions were generated using DELTA (Dallwitz *et al.* 1999) using a customized template for Physoderinae using DELTA editor. This output was modified slightly to accommodate the format of the journal.

- AMNH = American Museum of Natural History, New York, NY, USA  
BMNH = The Natural History Museum, London, UK  
BPBM = Bernice P. Bishop Museum, Honolulu, HI, USA  
CAS = California Academy of Sciences, San Francisco, CA, USA  
DEI = Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany  
HNHM = Hungarian Natural History Museum, Budapest, Hungary  
ISNB = Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium  
MNHN = Muséum national d'Histoire naturelle, Paris, France  
NMPC = National Museum (Natural History), Prague, Czech Republic  
NHRS = Naturhistoriska Riksmuseet, Stockholm, Sweden  
RMNH = Nationaal Natuurhistorisch Museum, Leiden, the Netherlands  
UCR = Entomology Research Museum, University of California, Riverside, Riverside, CA, USA  
USNM = National Museum of Natural History, Washington DC, USA  
ZMAN = Zoological Museum, Amsterdam, the Netherlands

## Terminology

Descriptive terminology of the male genitalia follows Davis (1966) and Forero & Weirauch (2012). The pair of extended lobes projecting from the posterior margin of the posterior pronotal lobe are here referred to as parascutellar lobes. Setigerous tubercles here refer to seta-bearing tubercles found across the body, including on the legs, as used in Davranoglou *et al.* (2015). Body size descriptions here are grouped into four categories based on total body length: small (6–8 mm), medium (8.01–10 mm), large (10.01–11 mm), very large (11.01–13 mm).

## Results

### Results of the phylogenetic analysis

The morphological coding for each taxon is shown in Table 1, measurements used as continuous characters in Table 2, and the list of the morphological character states used in Table 3. The phylogenetic analysis consistently produced a single most parsimonious tree (length = 365, CI = 0.22, RI = 0.61, Fig. 2; symmetric resampling values greater than 50 reported) that identified the Neotropical *Aradomorpha* as the sister-group to Physoderinae, the Afrotropical *Porcelloderes* as sister to all remaining Physoderinae and a monophyletic New World clade containing *Leptophysoderes* and *Cryptophysoderes*. The Madagascan Physoderinae are separated into at least two clades and are therefore not monophyletic (Fig. 2). *Physoderes mauriciensis* (Villiers, 1964) comb. nov., which is only known from Mauritius and is here transferred from *Epiroderoides* Villiers, 1962, is deeply nested within a clade that otherwise only includes Oriental and Australasian species of *Physoderes*, suggesting that *Physoderes* has expanded once into the Madagascan region. Clade A (Fig. 2) almost exclusively consists of Madagascan taxa, with the exception of *Paraphysoderes popeye* sp. nov., which we describe below as a new species from Papua New Guinea and which in our analysis is recovered as the sister taxon to the Madagascan species of *Paraphysoderes* Villiers, 1962. The remaining Madagascan genera (Clade B, Fig. 2) fall into two subclades, one comprised of the paraphyletic genus *Neophysoderes* Miller, 1955a and the

**Table 3.** List of characters and their states.

Char. no.	Character description	States						
		0	1	2	3	4	5	6
0	Overall body size	very small	small	medium	large			
1	Short, fine adpressed setae on body	absent	present					
2	Curved setigerous tubercles on body	absent	present, short	present, long				
3	Head shape	conical	elongate conical	angular conical	ovoid	cuboid		
4	Labrum shape in anterior view	short triangular	elongate triangular					
5	Clypeus length in dorsal view	short	extended					
6	Clypeus apex in lateral view	rounded	subacute					
7	Maxillary plate apex shape	rounded	truncate					
8	Length of scapus	extends beyond clypeus	shorter than clypeus	equal in length to clypeus				
9	Pedicellar trichobothria socket membranous area	absent	present					
10	Head vertex shape	convex	strongly convex	almost flat				
11	Size of eyes relative to head in dorsal view	small	large	very large				
12	Eye shape in dorsal view	hemispherical	distinctly projecting	not projecting				
13	Eye ventral margin to head ventral margin	not reaching	reaching	surpassing				
14	Ocellus	obsolete	present					
15	Shape of postocular lobe	globular	rounded	angular				
16	Pair of straight, long setae at posterior margin of postocular lobe	absent	present	present, position different	present, setigerous tubercles			
17	Height of anteoocular lobe in lateral view	lower than postocular	level with postocular	higher than postocular				
18	Length of second visible labial segment	more than twice that of first segment	shorter than first segment	equal to first segment	slightly longer than first segment			

**Table 3. (Continued)**

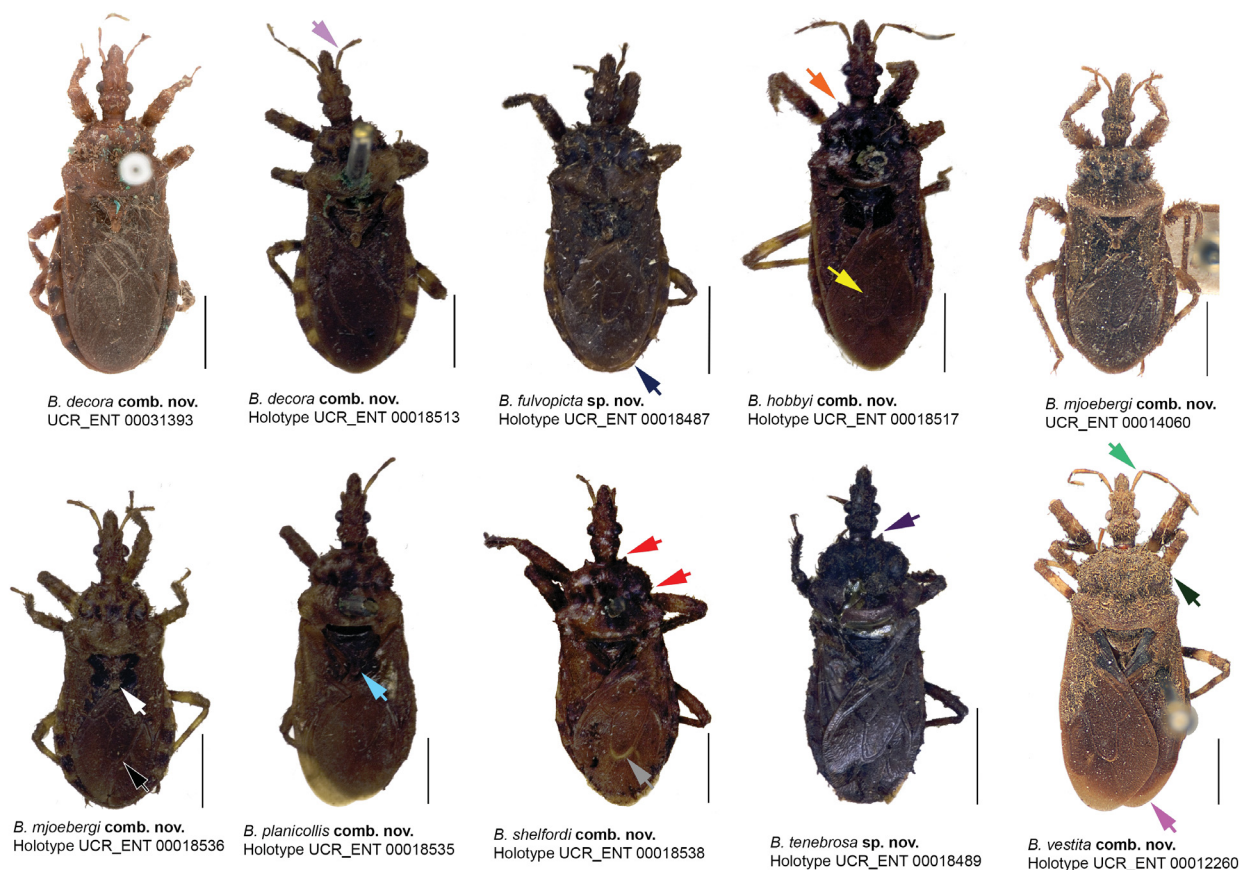
Char. no.	Character description	States						
		0	1	2	3	4	5	6
19	Curvature of second visible labial segment	straight	curved					
20	Head ventrally with row of stout setigerous tubercles	absent	present					
21	Shape of antero-lateral pronotal projections	obsolete	truncate	acute	acute, diverging			
22	Dorsal surface of anterior pronotal lobe	smooth	tuberculated					
23	Median pronotal depression contiguous with transverse sulcus	absent	present					
24	Males with distinctly inflated anterior pronotal lobe wider than posterior pronotal lobe	narrower than	equal to	wider than				
25	Carinae bridging anterior and posterior pronotal lobes	obsolete	slightly carinated	deeply carinated				
26	Shape of parascutellar lobes	obsolete	semicircular	triangular	bell-shaped, skewed towards median	regular rounded lobe	skewed quadrant towards median	regular lobe, skewed towards median
27	Length of scutellar process	short	long					
28	Scutellum shape	rounded triangular	hemispherical					
29	Mesosternite with irregular tuberculated protrusion between fore and mid coxae	absent	present					
30	Ventral antero-lateral angles, adjacent to stridulitrum	absent	present					
31	Abdominal shape in dorsal view	elongate	elongate ovoid	ovoid				
32	Shape of abdominal terminal tergite margin	rounded	straight	with triangular lobes	undulating	notched medially		
33	Body shape in lateral view	distinctly flattened	slightly flattened	not flattened				

**Table 3. (Continued)**

Char. no.	Character description	States							
		0	1	2	3	4	5	6	
34	Position of last two abdominal spiracles	along sternite margin	along connexival margin						
35	Wing form	macropterous	brachypterous	apterous					
36	Hemelytron distance to tip of abdomen	not reaching	reaching	surpassing					
37	Fore femur shape	slender	slightly incrassate	distinctly incrassate					
38	Fore femur armature (spines)	absent	present						
39	Fore femur armature (stout setigerous tubercles)	absent	present						
40	Fore tibia armature	absent	row of setigerous tubercles present	few setigerous tubercles present					
41	Number of tarsal segments	three	two						
42	Shape of anterior margin of abdominal sclerite 8	smooth	undulating	sharp emarginate					
43	Width of transverse bridge of pygophore	narrow	broad						
44	Rim of anterior opening of pygophore in lateral view	rounded	angular						
45	Presence of lateral flap-like prolongations of phallosoma	absent	present						
46	Shape of lateral flap-like prolongations of phallosoma	plate-like	band-like						
47	Arrangement of arms of basal plate	converging	parallel	rounded					
48	Ductifer with sclerotized ring	absent	present						
49	Shape of ductifer sclerotized ring	rounded	angular	elongate					

oddly dorso-ventrally flattened *Mimoelasmodesma depressa* Villiers, 1962, the other containing all other documented Madagascan Physoderinae (Fig. 2). The two largest Madagascan genera, *Neophysoderes* and *Epiroderoides*, are not monophyletic; *Epiroderoides* is rendered paraphyletic by the remaining Madagascan physoderine genera included in Clade B. Similarly, our analysis indicates that *Physoderes* is polyphyletic, such that species that fall into three distinct clades and one single-species lineage are currently classified in this genus. We here propose a revised classification that splits *Physoderes* into four genera, describing three of them as new: *Nanophysoderes* gen. nov. for *N. dentiscutum* (Bergroth, 1906) comb. nov. from Indonesia, which is recovered as the sister species to all Oriental, Australasian, and Madagascan Physoderinae; *Macrophysoderes* gen. nov. for a clade currently comprised of eight previously described or new species with distributions ranging from peninsular Malaysia to Papua New Guinea; and *Breviphysoderes* gen. nov., also with eight species that are widely distributed in Southeast Asia. We refrain from re-classifying the two non-monophyletic Madagascan genera, pending additional character investigation.

The overall morphology of Physoderinae is rather conserved and identifying phylogenetically informative characters proved challenging. Most of the characters that vary between species are found on the head and pronotum. However, our analysis shows that many of these features tend to be homoplastic, either having evolved multiple times across the phylogeny or having been lost on some members of a clade.



**Fig. 4.** Dorsal habitus images for species of *Breviphysoderes* gen. nov. For an explanation of the colored arrows, see key on page 17. Scale bars = 2 mm.

**Key to Oriental/Australasian Physoderinae genera**

1. Scutellum with distinct paired lateral tubercles; mesosternum with three longitudinal rows of setae ..... *Nanophysoderes* gen. nov.  
 – Scutellum without paired lateral tubercles; mesosternum with one or no longitudinal rows of setae ..... 2
2. Antero-lateral pronotal projection obsolete ..... *Paraphysoderes* Villiers, 1962  
 – Antero-lateral pronotal projection acute or truncated ..... 3
3. Eyes very large, distinctly projecting in dorsal view, sometimes attaining ventral margin of head in lateral view; antero-lateral pronotal projection often truncate; pronotum glabrous ..... *Macrophysoderes* gen. nov.  
 – Eyes large, not distinctly projecting in dorsal view, not attaining ventral margin of head in lateral view; antero-lateral pronotal projection acute, not truncate (except *P. nigripennis*); pronotum with various forms of setation ..... 4
4. Scape surpassing apex of clypeus; anterior pronotal lobe narrower than posterior lobe in both sexes; parascutellar lobes semicircular ..... *Breviphysoderes* gen. nov.  
 – Scape not surpassing apex of clypeus; anterior pronotal lobe often wider than posterior lobe in males; parascutellar lobes rounded, often skewed towards median of pronotum ..... *Physoderes* Westwood, 1845

Phylum Arthropoda Latreille, 1829  
 Class Hexapoda Blainville, 1816  
 Order Hemiptera Linnaeus, 1758  
 Suborder Heteroptera Latreille, 1810  
 Family Reduviidae Latreille, 1807  
 Subfamily Physoderinae Miller, 1954

***Breviphysoderes* gen. nov.**

[urn:lsid:zoobank.org:act:083107C2-6EAB-4DC4-BC2E-F5DAAF0F7A43](http://urn:lsid:zoobank.org:act:083107C2-6EAB-4DC4-BC2E-F5DAAF0F7A43)

Figs 4–9, Appendix

**Diagnosis**

Recognized among all other genera of Physoderinae by the head being elongate conical, without a pair of long, straight setae on the posterior margin of the postocular lobe; the scape surpassing the apex of the clypeus; the eye being distinctly projecting in dorsal view; the pronotum with setigerous tubercles bearing short, curved setae; the anterior pronotal lobe always narrower than the posterior lobe in both sexes; the parascutellar lobe being semicircular; the posterior margin of the connexivum often being slightly elevated, with short, curved setae; the anterior margin of the male mediosternite 8 sharply emarginated; the cup-like sclerite of the pygophore apically rounded, with paired sclerotized latero-ventral slight protuberances; the arms of the basal plate parallel to each other; the sclerotized ring of the ductifer elongate; the dorsal phallothecal sclerite subacute, with lateral narrow; and the band-like prolongations of the dorsal phallothecal sclerite extended diagonally towards the basal plate. Most similar to *Physoderes*, but distinguished by the scape surpassing the apex of the clypeus and the anterior pronotal lobe being narrower than the posterior lobe in males.

**Etymology**

Named after *Physoderes*, the type genus of the subfamily Physoderinae, in combination with “brevi” (Latin for “short”) to indicate the shorter body length. The gender is feminine.

### Type species

*Physoderes mjoebergi* Miller, 1940.

### Description

#### Male

**BODY LENGTH.** Ranging from relatively small to medium-sized, 7.49–10.23 mm (Appendix).

**COLORATION** (Fig. 4). Variable, from straw-colored to dark brown. Head, anterior pronotal ridges, posterior pronotal lobe, legs and corium of similar lighter coloration, anterior pronotal lobe, scutellum and claval region with darker coloration.

**VESTITURE.** Densely setose with curved setae, strongly tuberculated on head, along pronotal margin and ridges.

**HEAD.** Elongate conical; maxillary plate truncate apically; scape surpassing apex of clypeus except in *Breviphysoderes decora* comb. nov.; eye distinctly projecting in dorsal view except in *B. decora* comb. nov., not attaining head ventral margin in lateral view; height of anteocular lobe shorter than postocular lobe, ocelli present.

**THORAX.** Antero-lateral paired projections acute, oriented anteriorly or diverging; surface of anterior lobe with low ridges; median pronotal depression contiguous with transverse sulcus in males except in *Breviphysoderes vestita* comb. nov.; paramedian carina strongly defined except in *B. decora* comb. nov.; posterior lobe medially rugose; anterior pronotal lobe of equal length to posterior lobe, narrower than posterior lobe in both sexes, anterior lobe lower than posterior lobe in lateral view except in *B. vestita* comb. nov.; parascutellar lobe semicircular; scutellum rounded triangular, scutellar process long, with rounded apex, except in *B. decora* comb. nov.; mesosternite usually with median irregular tuberculated protrusion between fore and mid coxae.

**HEMELYTRON.** Macropterous, hemelytron length variable.

**LEGS.** Fore femur distinctly incrassate; tarsus three-segmented.

**ABDOMEN.** Elongate ovoid, with rounded or straight terminal margin; connexival margin slightly undulating except in *Breviphysoderes planicollis* comb. nov., posterior margin most often slightly elevated.

**GENITALIA.** Anterior margin of mediosternite 8 sharply emarginate, with or without medial apodeme; transverse bridge of pygophore broad, margin of anterior opening angular, with apodeme present, apical margin of posterior opening smooth; cup-like sclerite apically rounded, with sclerotized paired latero-ventral slight protuberance; arms of basal plate parallel to each other; ductifer with sclerotized, elongate ring; endosomal struts conical, with subacute apex, basally divided into two arms; apex of dorsal phallosclerite subacute or rounded, with lateral narrow band-like prolongations oriented diagonally towards basal plate.

#### Female

Similar in shape and coloration to males but slightly larger or having a wider abdomen or narrower anterior pronotal lobe.

### Ecology

Specimens have been collected from dead plant material, tree bark and in the undergrowth. Different species have been found at different elevations with *B. vestita* comb. nov. collected at the highest altitude of 1955 m.



## Distribution

This genus currently comprises 8 described and new species and is widely distributed across Southeast Asia; found in continental Indochina, peninsular Malaysia, Sumatra, Java and Borneo. The highest species diversity for this genus is in Borneo.

## Key to species of *Breviphysoderes* gen. nov.

1. Apical portion of veins forming external cell of hemelytron (Cu+M) straw-colored or distinctly lighter than remainder of veins (Fig. 4, grey arrow) .....2
  - Veins framing external cell of hemelytron uniformly colored, not straw-colored (Fig. 4, black arrow) .....4
2. Hemelytron short, not reaching tip of abdomen (Fig. 4, blue arrow) ....*B. fulvopicta* gen. et sp. nov.
  - Hemelytron reaching or surpassing tip of abdomen (Fig. 4, pink arrow) .....3
3. Antero-lateral pronotal projections diverging, males with anterior pronotal lobe enlarged, wider than in females, as wide or almost as wide as posterior lobe (Fig. 4, dark green arrow) .....
  - .....*B. vestita* (Horváth, 1900) comb. nov.
  - Antero-lateral pronotal projections oriented anteriorly, males with anterior pronotal lobe as in females, narrower than posterior lobe (Fig. 4, red arrows) .....*B. shelfordi* (Miller, 1940) comb. nov.
4. Head and body uniformly brownish-black, antero-lateral pronotal projections acute, oriented anteriorly (Fig. 4, purple arrow) .....*B. tenebrosa* gen. et sp. nov.
  - Head and body not uniformly brownish black, antero-lateral pronotal projections acute and diverging (Fig. 4, orange arrow) .....5
5. Scape reaching, but not surpassing apex of clypeus (Fig. 4, light purple arrow) .....
  - .....*B. decora* (Miller, 1940) comb. nov.
  - Scape surpassing apex of clypeus (Fig. 4, light green arrow) .....6
6. Ridges of anterior pronotal lobe dark brown, similar in color to remainder of anterior pronotal lobe; external cell of hemelytron (Cu+M) elongated (Fig. 4, yellow arrow) .....
  - .....*B. hobbyi* (Miller, 1940) comb. nov.
  - Ridges of anterior pronotal lobe straw-colored, color contrasting with remainder of anterior pronotal lobe; external cell of hemelytron (Cu+M) not elongated (Fig. 4, black arrow) .....7
7. Apex of scutellar process straw-colored (Fig. 4, white arrow) .....
  - .....*B. mjoebergi* (Miller, 1940) comb. nov.
  - Apex of scutellar process dark brown or uniform color as scutellum (Fig. 4, light blue arrow) ..
    - .....*B. planicollis* (Miller, 1940) comb. nov.

*Breviphysoderes decora* (Miller, 1940) comb. nov.

Figs 4–7; Appendix

*Physoderes decora* Miller, 1940: 551, fig. 91.

*Physoderes ostenta* Miller, 1941: 780, fig. 6. New synonymy.

## Diagnosis

Recognized among other species in the genus by the scape almost reaching or reaching clypeus apex, the dorsal surface of the anterior pronotal lobe tuberculated, the color pattern on the anterior pronotal lobe, the small and semicircular parascutellar lobes, the short and apically straw-colored scutellar process, the

hemelytron attaining the apex of the abdomen, and the anterior half of the connexivum brown and the posterior half straw-colored. It most closely resembles *B. mjoebergi* (Miller 1940) comb. nov., but can be differentiated by the scape not extending beyond the clypeal apex and the shorter scutellar process for *B. mjoebergi* comb. nov.

#### Material examined

##### Holotype

MALAYSIA: ♀, Sarawak, Mt. Poi (Mt. Pueh), 1.8° N, 109.68305° E, 61 m, no date, E. Mjöberg leg. (UCR\_ENT 00018513) (BMNH).

##### Paratype

MALAYSIA: 1 ♀, Sabah, N Borneo, Bettotan, nr. Sandakan, 5.28222° N, 117.59305° E, 6 Aug. 1927, C. Boden Kloss and H.M. Pendlebury leg. (UCR\_ENT 00018510) (BMNH).

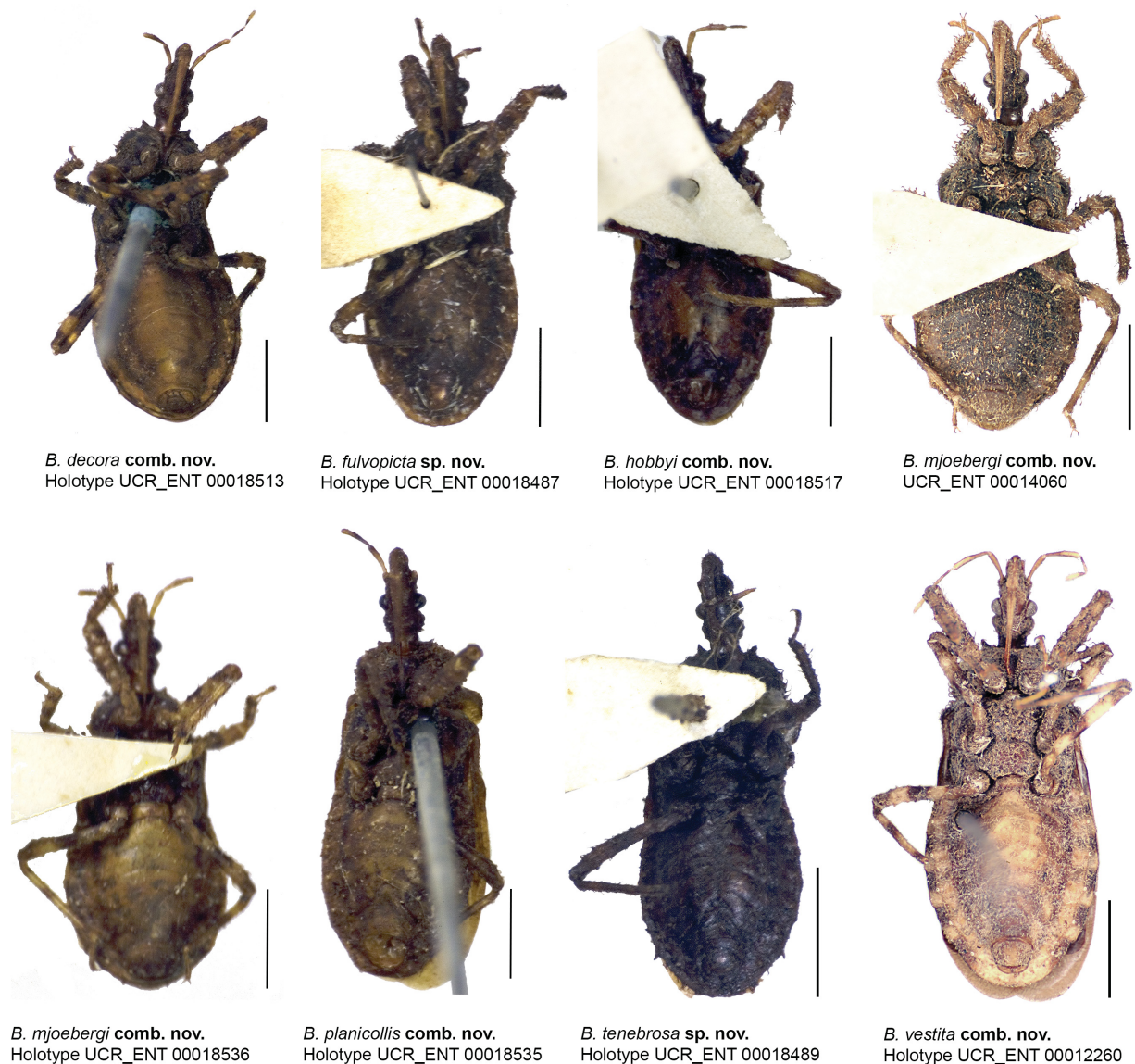


Fig. 5. Ventral habitus images for species of *Breviphysoderes* gen. nov. Scale bars = 2 mm.

### Other material

BRUNEI DARUSSALAM: 1 ♀, Temburong District, Kuala Belalong Field Studies Center, 4.54716° N, 115.15825° E, 82 m, 26 Jun. 2010, C. Weirauch and W. Hwang leg. (UCR\_ENT 00052186) (UCR).

MALAYSIA: Perak: 1 ♀, Batang Padang, Jor Camp, 3.52972° N, 101.55277° E, 549 m, 4 Jun. 1923, H.M. Pendlebury leg., holotype of *P. ostenta* (junior synonym) (UCR\_ENT 00018522) (BMNH). – Sabah: 1 ♀, Mile 50 Lungmanis, 5.42027° N, 116.79638° E, 9 Aug. 1967, F.E. leg. (UCR\_ENT 00014058) (RMNH); 3 ♀♀, Sandakan, 5.8333° N, 118.1167° E, 4 m, no date, Baker leg. (UCR\_ENT 00031391–UCR\_ENT 00031393) (USNM).

### Redescription

#### Female

BODY LENGTH. Medium, total length 9.19 mm, SD ± 0.33 (Appendix).

COLORATION (Figs 4–5, 7). Straw-colored and brown. Head brown with straw-colored suffusion. Scape of antenna straw-colored with brown apex, pedicel brown with straw brown apex, basi-flagellomere brown, distiflagellomere brown with straw brown apex. Labium light brown. Anterior lobe of pronotum dark brown with straw-colored patterns, posterior lobe straw brown, scutellum dark brown with straw-colored apex, pleuron brown with straw brown suffusion, sternum brown. Corium and membrane of hemelytron brown to dark brown. Femora of legs straw-colored with medial and apical brown annulations, tibiae brown with sub-basal and apical straw-colored annulations, tarsus and claw light brown. Abdomen dorsally straw brown with orange suffusion, ventrally light brown with brown suffusion, anterior half of connexivum brown, posterior half straw brown.

VESTITURE. Sparsely setose. Head with widespread curved, setigerous tubercles, ventral surface of postocular lobe with sparse, setigerous tubercles, without pair of long, straight setae on postocular lobe posterior to ocelli. Anterior lobe of thorax with tuberculated, short, curved setae on lateral margins and along dorsal ridges, posterior lobe with short, curved, setigerous tubercles along lateral margins and sparsely distributed on dorsal surface. Corium of hemelytron with short, curved setae. Legs with two rows of spines and setigerous tubercles, tibia with regular rows of tuberculated, stout, sharp setae. Posterior margin of connexivum with short, curved setae.

HEAD. Scape reaching apex of clypeus; eye hemispherical in dorsal view, less than 1/5 length of head, not attaining ventral margin of head in lateral view.

THORAX. Antero-lateral paired projections acute, diverging; median pronotal depression contiguous with transverse sulcus; paramedian carina weakly defined; scutellar process short, apex subacute; mesosternite with setigerous tubercles but no protrusion.

HEMELYTRON. Attaining tip of abdomen.

LEGS. Same as genus description.

ABDOMEN. Elongate ovoid, with rounded terminal margin; connexival margin slightly undulating, posterior margin not elevated.

GENITALIA. Not dissected.

#### Male

Unknown.

### Ecology

Little known, specimens collected from altitude of 82 m to 549 m (1800 ft). Coloration of specimens differs slightly, but it is unclear whether this is due to natural variation or preservation history.

### Distribution

Found across Northern Borneo from east (Bettotan, Sandakan) to west (Mt. Poi), and also one specimen from Peninsular Malaysia (Perak, Jor Camp).

### Remarks

*Physoderes ostenta* is synonymized with *B. decora* comb. nov. as it shares the same diagnostic features, including scape almost reaching or reaching clypeal apex, short scutellar process and straw brown apex, hemelytron attaining the abdominal apex, anterior half of the connexivum brown, and posterior half straw brown. No other specimen of *P. ostenta* exists besides the holotype. *Breviphysoderes decora* comb. nov. is removed from *Physoderes* and transferred to *Breviphysoderes* gen. nov. because it possesses the synapomorphies of the new genus (parascutellar lobes are semicircular and have prominent setigerous tubercles on the dorsal ridges of the anterior pronotal lobe). One specimen originally designated as a *P. hobbyi* paratype (UCR\_ENT00018511) is considered to be misidentified by Miller and is here treated as belonging to *B. decora* comb. nov. This species is known only from female specimens. Currently there are no males that can be associated with these females and hence the redescription is based on females only.

*Breviphysoderes fulvopicta* gen. et sp. nov.

[urn:lsid:zoobank.org:act:27A9078A-D5EB-45B2-A579-5D8F5746288D](https://zoobank.org/act:27A9078A-D5EB-45B2-A579-5D8F5746288D)

Figs 4–6; Appendix

### Diagnosis

Recognized among species of *Breviphysoderes* gen. nov. by having the head and anterior pronotal lobe distinctly covered with dense, short, curved, setigerous tubercles, the pronotal paramedian carina deeply defined, the apical veins of the external cell of the hemelytron (Cu+M) and the apex of the scutellar process with distinct straw-colored marks, and the hemelytron not attaining the tip of the abdomen. This species is most similar to *B. hobbyi* comb. nov. and *B. decora* comb. nov. It can be differentiated from the former species by the hemelytron not attaining the tip of the abdomen, the straw-colored apical veins of the external cell and the shorter external cell length. It differs from *B. decora* comb. nov. in having the scape surpassing the apex of the clypeus and in having the apical veins of the external cell straw-colored. The straw-colored mark on the apical veins of the external cell is also present in *B. vestita* comb. nov. and *B. shelfordi* comb. nov., but the anterior pronotal lobe is wider in *B. vestita* comb. nov. and the hemelytron is longer and surpasses the tip of the abdomen in *B. shelfordi* comb. nov.

### Etymology

The name *fulvopicta* is an adjective derived from Latin “fulvus” meaning reddish yellow and “pictus” meaning decorated to describe the distinctive straw-colored apical veins of the external cell of the hemelytron.

### Material examined

#### Holotype

MALAYSIA: ♂, Sarawak, River Kapah, tributary of River Tinjar, 3.34261° N, 114.30208° E, 174 m, 23 Nov. 1932, B.M. Hobby and A.W. Moore leg. (UCR\_ENT 00018487) (BMNH).

### Paratypes

MALAYSIA: 1 ♂, Sarawak, foot of Mt. Dulit, junction of Rivers Tinjar and Lejok, 3.32388° N, 114.14722° E, 730 m, 28 Aug. 1932, B.M. Hobby and A.W. Moore leg. (UCR\_ENT 00018512) (BMNH); 1 ♂, same collection data as preceding but 5 Sep. 1932 (UCR\_ENT 00018488) (BMNH).

### Description

#### Male

BODY LENGTH. Small size, total length 7.07 mm.

COLORATION (Figs 4–5). Light brown to dark brown. Head light brown to dark brown. Scape of antenna straw-colored, with apex brown, pedicel straw-colored and medially brown, basiflagellomere dark brown, distiflagellomere dark brown with straw-colored apex. First segment of labium brown or dark brown, second segment light brown and basally and apically brown or dark brown entirely, third segment brown or dark brown. Anterior lobe of pronotum dark brown with straw-colored ridges, posterior lobe light brown or brown, scutellum dark brown with straw-colored apex, pleuron dark brown entirely or with brown suffusion, sternum dark brown. Corium of hemelytron brown, membrane brown with apical veins of external cell (Cu+M) straw-colored. Femora of legs straw-colored or light brown with medial and apical dark brown annulations, tibiae straw-colored or brown with basal, medial and apical dark brown annulations, tarsi and claws light-brown or brown. Abdomen not examined dorsally, ventrally light brown medially with lateral suffusion to dark brown or entirely dark brown, anterior half of connexivum dark brown and posterior half straw-colored, or dark brown entirely, exposed part of pygophore variable, light brown to dark brown.

VESTITURE. Densely setose. Head with widespread curved, setigerous tubercles, ventral surface of postocular lobe with sparse, setigerous tubercles, without pair of long, straight setae on postocular lobe posterior to ocelli. Anterior lobe of thorax with tuberculated, short, curved setae on lateral margins and along dorsal ridges, posterior lobe with short, curved, setigerous tubercles along lateral margins and sparsely distributed on dorsal surface. Corium of hemelytron with short, curved setae. Fore femur of legs with two rows of spines and setigerous tubercles, fore tibia with regular rows of tuberculated, stout, sharp setae. On abdomen, posterior margin of connexivum with short, curved setae.

HEAD. Scape surpassing apex of clypeus; eye distinctly projecting in dorsal view, about  $\frac{1}{5}$  length of head, not attaining ventral margin of head in lateral view.

THORAX. Antero-lateral paired projections acute, diverging; median pronotal depression contiguous with transverse sulcus; paramedian carina strongly defined; scutellar process long, with rounded apex; mesosternite with median irregular, tuberculated protrusion between fore and mid coxae.

HEMELYTRON. Not attaining tip of abdomen.

LEGS. Same as genus description.

ABDOMEN. Elongate ovoid, with straight terminal margin; connexival margin slightly undulating, posterior margin slightly elevated.

GENITALIA. Not examined.

#### Female

Unknown.

### Ecology

This species is found in the tropical forest of Borneo and has been collected from the undergrowth, sapwood just under bark, and flood refuse and cut reeds at the junction of rivers.

### Distribution

This species is known only from the type locality of Mt Dulit in Sarawak, north-central Borneo. All three specimens were collected near each other, at the foot of Mt Dulit near the River Tinjar.

### Remarks

This species is described based on three specimens originally designated as paratypes of *B. hobbyi* (Miller, 1940) comb. nov. Even though they share the same collecting event and locality as that of *B. hobbyi*, closer examination shows distinct, consistent, morphological differences and the specimens are therefore described as a separate species. The specimens were collected by B.M. Hobby and A.W. Moore during the Oxford University Expedition in 1932. The darkened scutellum and overlapping distribution shared with *B. hobbyi* comb. nov., *B. decora* comb. nov., *B. planicollis* comb. nov. and *B. tenebrosa* gen. et sp. nov. suggest that they are likely to be closely related.

*Breviphysoderes hobbyi* (Miller, 1940) comb. nov.

Figs 4–6; Appendix

*Physoderes hobbyi* Miller, 1940: 554, fig. 92.

### Diagnosis

This species is recognized among species of *Breviphysoderes* by the head and anterior pronotal lobe being distinctly covered with dense, short, curved, setigerous tubercles, the deeply defined pronotal paramedian carina, the hemelytron surpassing the tip of the abdomen, the medial vein of the hemelytron shaped like an inverted S, and the elongated external cell of the hemelytron (Cu+M). This species is most similar to *B. tenebrosa* gen. et sp. nov. and *B. planicollis* comb. nov. It can be differentiated from the former by the overall coloration, the diverging antero-lateral pronotal projections, and the shape of the external cell. It differs from *B. planicollis* comb. nov. by the overall coloration and the shape of the external cell.

### Material examined

#### Holotype

MALAYSIA: ♂, Sarawak, Mt Dulit, Dulit Trail, 3.32388° N, 114.1475° E, 730 m, 3 Sep. 1932, B.M. Hobby and A.W. Moore leg. (UCR\_ENT 00018517) (BMNH).

### Redescription

#### Male

BODY LENGTH. Medium size, total length 8.7 mm.

COLORATION (Figs 4–5). Light brown with dark brown patterns. Head brown. Scape of antenna straw-colored with light brown apex, basal half of pedicel straw-colored and apical half brown, basiflagellomere brown and distiflagellomere brown with light brown apex. Labium brown. Anterior lobe of pronotum dark brown, posterior lobe brown, scutellum dark brown with brown apex, pleuron dark brown with brown suffusion. Corium and membrane of hemelytron brown. Femora of legs straw-colored with medial dark brown annulation and apical dark brown suffusion, tibiae straw-colored with basal, medial and apical dark brown annulations, tarsi and claws straw-colored. Abdomen not examined dorsally,

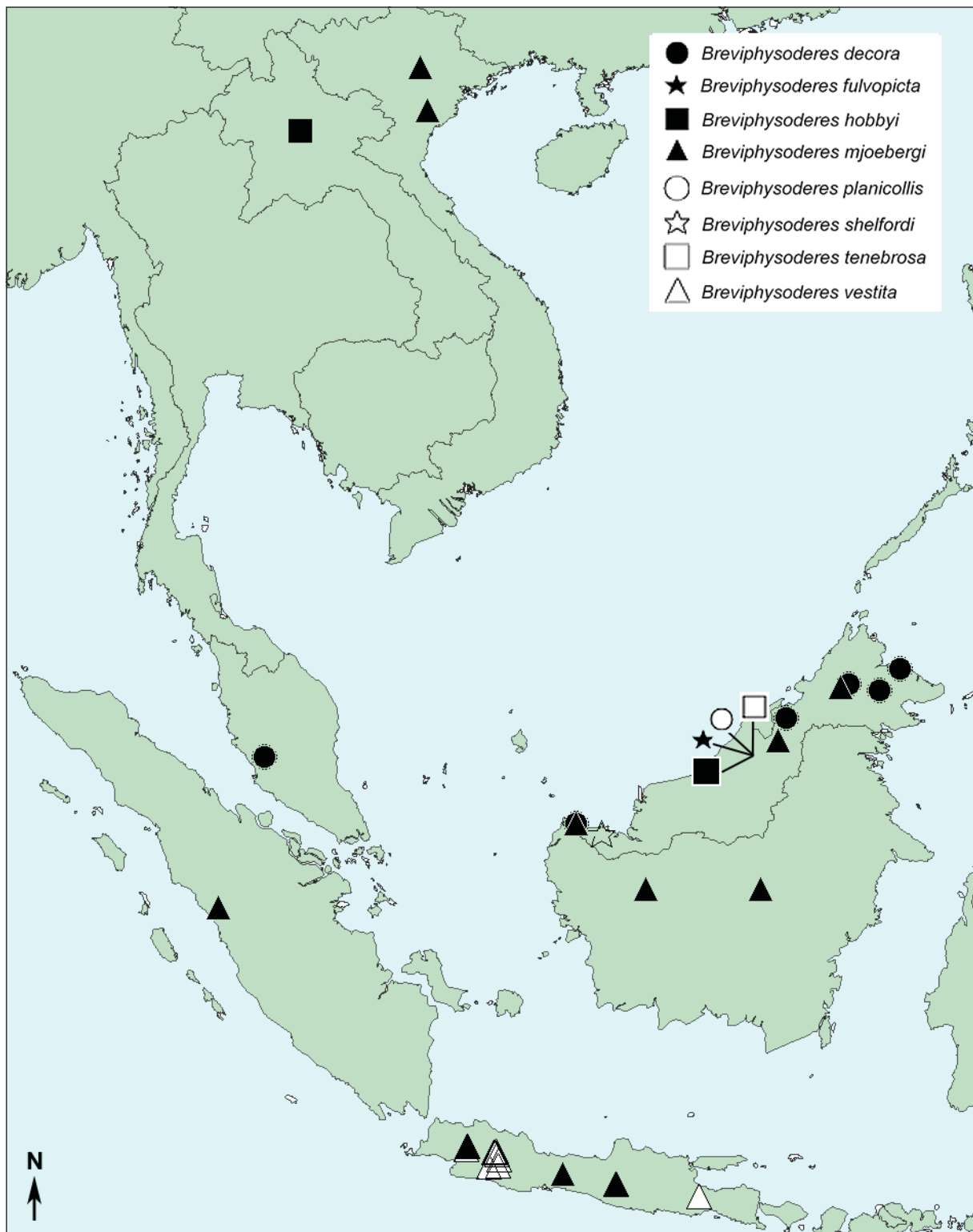


Fig. 6. Distribution map for species of *Breviphysoderes* gen. nov.

ventrally light brown medially with lateral suffusion to dark brown, connexivum dark brown with apex straw-colored, exposed part of pygophore brown.

**VESTITURE.** Sparsely setose. Head with widespread curved, setigerous tubercles, ventral surface of postocular lobe with sparse, setigerous tubercles, without pair of long, straight setae on postocular lobe posterior to ocelli. Anterior lobe of thorax with tuberculated, short, curved setae on lateral margins and along dorsal ridges, posterior lobe with short, curved, setigerous tubercles along lateral margins and sparsely distributed on dorsal surface. Corium of hemelytron with short, curved setae. Legs with two rows of spines and setigerous tubercles, tibiae with regular rows of tuberculated, stout, sharp setae. Posterior margin of connexivum with short, curved setae.

**HEAD.** Scape surpassing apex of clypeus; eye distinctly projecting in dorsal view, about  $\frac{1}{5}$  length of head, not attaining ventral margin of head in lateral view.

**THORAX.** Antero-lateral paired projections acute, diverging; median pronotal depression contiguous with transverse sulcus; paramedian carina strongly defined; posterior lobe damaged/obscured medially by pin; scutellar process long, with rounded apex; mesosternite with median irregular, tuberculated protrusion between fore and mid coxae.

**HEMELYTRON.** Surpassing tip of abdomen.

**LEGS.** Same as genus description.

**ABDOMEN.** Elongate ovoid, with rounded terminal margin; connexival margin slightly undulating, posterior margin slightly elevated.

**GENITALIA.** Not examined.

### **Female**

Unknown.

### **Ecology**

This species is found in old secondary forest of Borneo.

### **Distribution**

This species is only known from the type locality of Mt Dulit in Sarawak, north-central Borneo. The type locality is shared with *B. fulvopicta* gen. et sp. nov., *B. planicollis* comb. nov., *B. decora* comb. nov. and *B. tenebrosa* gen. et sp. nov.

### **Remarks**

This species is redescribed based only on the holotype specimen. Originally, five paratype specimens were associated with the holotype from the same area. Closer examination of these specimens showed that they are not conspecific. We here treat these specimens as the two newly described species *B. fulvopicta* gen. et sp. nov. and *B. tenebrosa* gen. et sp. nov., and also as *B. decora* comb. nov. *Breviphysoderes hobbyi* comb. nov. is removed from *Physoderes* here and transferred to the new genus because it possesses its synapomorphies (semicircular parascutellar lobes, males do not possess an inflated anterior pronotal lobe and have prominent setigerous tubercles on the dorsal ridges of the anterior pronotal lobe). The specimen was collected by B.M. Hobby and A.W. Moore during the Oxford University Expedition in 1932.



*Breviphysoderes mjoebergi* (Miller, 1940), comb. nov.

Figs 4–9; Appendix

*Physoderes mjoebergi* Miller, 1940: 547, fig. 90.

*Physoderes dyak* Miller, 1955b: 59, fig. 4. New synonymy.

**Diagnosis**

Recognized among species of *Breviphysoderes* gen. nov. by the smaller size, the head and anterior pronotal lobe being distinctly covered with dense, short, curved, setigerous tubercles, the deeply defined pronotal paramedian carina, the slightly elevated and setose posterior margin of the connexivum and the ductifer having a sclerotized elongate ring. This species is most similar to *B. vestita* comb. nov. but can be differentiated by its smaller size, the lack of an inflated anterior pronotal lobe in males, the hemelytron not surpassing the tip of the abdomen, and the slightly undulating (vs angularly hooked), sclerotized, flap-like prolongations of the phallosoma.

**Material examined**

**Holotype**

MALAYSIA: ♀, Sarawak, Mt Poi (Mt Pueh), 1.8° N, 109.68333° E, 610 m, no date provided, E. Mjöberg leg. (UCR\_ENT 00018536) (BMNH).

**Other material**

INDONESIA: Borneo: 1 ♀, Melawi, 0.08333° N, 111.48333° E, 43 m, Nov–Dec. 1924, A. Blanche-manche leg. (UCR\_ENT 00014059) (RMNH); 1 ♂, Central Borneo, Malinau, Long Nawang, 0.085° N, 114.48305° E, 762 m, 1925, Mjöberg leg., paratype of *Physoderes dyak* (junior synonym) (UCR\_ENT 00018530) (BMNH); 1 ♂, same collection data as preceding, holotype of *Physoderes dyak* (junior synonym), MacGillavry Collection (ZMAN, ZMA.INS.834307). – Java: 1 ♂, Batoerraden G. Slamet (Baturaden), 7.34083° S, 109.33055° E, 800 m, Feb. 1937, F.C. Drescher leg. (UCR\_ENT 00014060) (RMNH); 1 ♀, 7.61444° S, 110.71222° E, no date provided, Horsfield leg. (UCR\_ENT 00069398) (BMNH); 1 ♂, Megamendung, 6.61861° S, 106.84722° E, 800 m, Oct 1954 (UCR\_ENT 00073851) (NMPC). – Sumatra: 1 ♀, Sumatera Barat (West Sumatra), Gunung Singgalang, 0.39078° S, 100.35682° E, 1800 m, 1926, E. Jacobson leg. (UCR\_ENT 00024039) (RMNH); 1 ♀, Padang, 1° S, 100.5° E, no date provided, Schouteden leg. (UCR\_ENT 00037371) (ISNB).

MALAYSIA: 1 ♀, Sabah, 1 km S of Kundasang, 5.33944° N, 116.57638° E, 1530 m, 27 Aug. 1983, G.F. Hevel and W.E. Steiner leg. (UCR\_ENT 00030981) (USNM); 1 ♂, Sarawak, Mulu National Park, near Base Camp, 4th Division Gn. [= Garrison?], 3.97444° N, 114.93638° E, 100 m, May–Aug. 1978, P.M. Hammond and J.E. Marshall leg. (UCR\_ENT 00069399) (BMNH).

VIETNAM: 1 ♀, Ha Nam, Cuc Phuong, 20.40777° N, 105.79416° E, 86 m, 24–25 May 1986, Jan Horak leg. (UCR\_ENT 00073849) (NMPC); 3 ♂♂, Vinh Phuc, Tam Dao Co., Tam Dao National Park, 21.50694° N, 105.61527° E, 145 m, 6 Sep. 2009, T. Ishikawa leg. (UCR\_ENT 00052181, UCR\_ENT 00073392, UCR\_ENT 00077822) (UCR).

**Redescription**

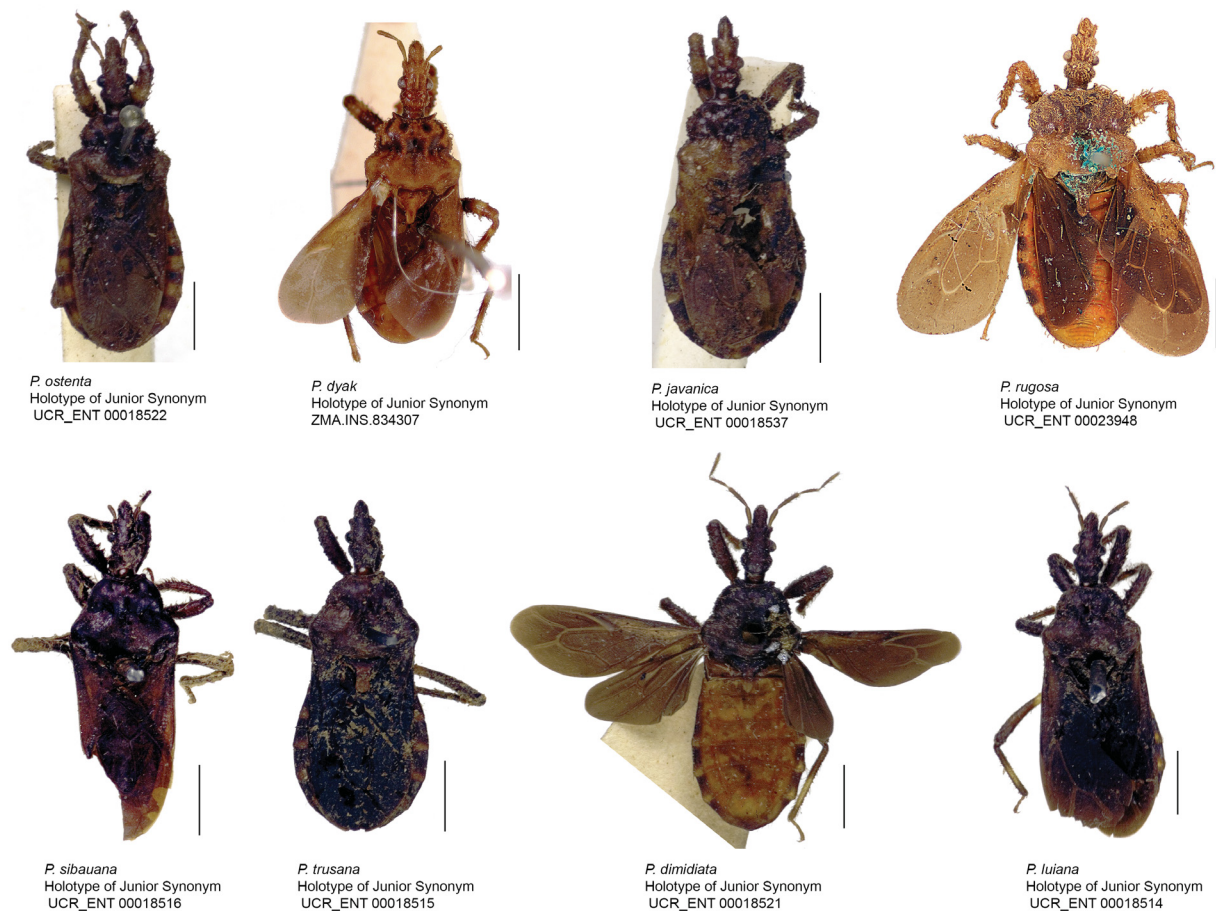
**Male**

BODY LENGTH. Small-medium size, total length 7.91 mm, SD ± 1.62 (Appendix).

COLORATION (Figs 4–5). Straw-colored with dark brown patterns. Head straw-colored to light brown with dark brown suffusion. Scape and pedicel of antenna straw-colored to light brown, with slight apical darkening, basiflagellomere distinctly darker than scape and pedicel, light brown to dark brown,

distiflagellomere straw-colored to light brown with base dark brown. First segment of labium straw-colored to brown, second segment basally and apically dark brown, medially straw-colored or light brown, third segment dark brown. Anterior lobe of pronotum dark brown with straw-colored ridges, posterior lobe straw-colored or light brown, scutellum basally dark brown, progressively lightening towards a straw-colored apex, pleuron straw-colored with dark brown suffusion, sternum straw-colored with dark brown suffusion. Corium of hemelytron straw-colored or light brown, membrane dark brown. Femora of legs straw-colored with medial and apical dark brown annulations, tibiae straw-colored with basal, medial and apical dark brown annulations, tarsi and claws straw-colored. Abdomen dorsally yellowish-orange, ventrally brown with straw-colored lateral margins, sub-lateral and medial spots, and dark brown sub-lateral suffusion, anterior half of connexivum dark brown and posterior half straw-colored, with the color proportions slightly variable, exposed part of pygophore straw-colored.

VESTITURE. Densely setose. Head with widespread curved, setigerous tubercles, ventral surface of postocular lobe with sparse, setigerous tubercles, without pair of long, straight setae on postocular lobe posterior to ocelli. Anterior lobe of thorax with tuberculated, short, curved setae on lateral margins and along dorsal ridges, posterior lobe with short, curved, setigerous tubercles along lateral margins and sparsely distributed on dorsal surface. Corium of hemelytron with short, curved setae. Legs with two rows of spines and setigerous tubercles, tibiae with regular rows of tuberculated, stout, sharp setae. Posterior margin of connexivum with short, curved setae.



**Fig. 7.** Dorsal habitus images for junior synonym holotypes of species in *Breviphysoderes* gen. nov. and *Macrophysoderes* gen. nov. Scale bars = 2 mm.

HEAD. Scape surpassing apex of clypeus; eye distinctly projecting in dorsal view, about  $\frac{1}{5}$  length of head, not attaining ventral margin of head in lateral view.

THORAX. Antero-lateral paired projections acute, diverging; median pronotal depression contiguous with transverse sulcus; paramedian carina strongly defined; scutellar process long, with rounded apex; mesosternite obscured.

HEMELYTRON. Attaining tip of abdomen.

LEGS. Same as genus description.

ABDOMEN. Elongate ovoid, with rounded apical margin; posterior margin slightly elevated.

GENITALIA. Anterior margin of mediosternite 8 sharply emarginate, without medial apodeme; apex of dorsal phallosclerite subacute, with narrow lateral band-like prolongations, oriented diagonally and undulating.

#### **Female**

Similar in shape and coloration as males, but some individuals slightly larger.

#### **Ecology**

Unknown.

#### **Distribution**

Vietnam, Borneo and Java. This species has a relatively wide distribution, with specimens collected from northern Vietnam and Java, which are near the northern- and southern-most limits of the distribution of Oriental physoderine species.

#### **Remarks**

Originally described as *Physoderes mjoeberti* by Miller (1940), this species is transferred to *Breviphysoderes* gen. nov. based on the phylogenetic analysis conducted above. It is most closely related to *B. vestita* (Horváth, 1900) comb. nov. and both species are found on the island of Java. The two female specimens from Vietnam are slightly larger than those from Borneo and Java, but do not have any differential morphological characters and are thus identified as conspecifics. *Physoderes dyak* (Miller, 1955b) is synonymized here with *B. mjoeberti* comb. nov. based on the examination of one paratype at BMNH together with the holotype of *B. mjoeberti* comb. nov. No diagnostic characters were found to separate the two species based on the examination of these two specimens. Conspecificity was further confirmed by examination of habitus images of the *P. dyak* holotype at the ZMAN.

*Breviphysoderes planicollis* (Miller, 1940), comb. nov.

Figs 4–6; Appendix

*Physoderes planicollis* Miller, 1940: 547, fig. 90.

#### **Diagnosis**

This species is recognized among species of *Breviphysoderes* gen. nov. by having the anterior pronotal lobe distinctly covered with dense, short, curved, setigerous tubercles, the deeply defined pronotal paramedian carina, the hemelytron surpassing the tip of the abdomen, and the smooth (not undulating) connexivum. This species is most similar to *B. hobbyi* comb. nov., *B. decora* comb. nov. and *B. fulvopicta* gen. et sp. nov. It can be differentiated from *B. hobbyi* comb. nov. by the overall lighter coloration,

especially the color pattern of the anterior pronotal lobe, and the shorter external cell of the hemelytron (framed by the cubital and medial veins). It differs from *B. decora* comb. nov. and *B. flavopicta* gen. et sp. nov. by having its hemelytron extending beyond the tip of the abdomen, while the apex of the scutellar process and the apex of the external cell of the hemelytron lack the prominent straw color.

### Material examined

#### Holotype

MALAYSIA: ♂, Sarawak, Mt Dulit, 3.33305° N, 114.14972° E, 886 m, no date provided, E. Mjöberg leg. (UCR\_ENT 00018535) (BMNH).

### Redescription

#### Male

BODY LENGTH. Medium size, total length 9.8 mm.

COLORATION (Figs 4–5). Light brown with dark brown patterns. Head brown with dark brown suffusion. Scape of antenna straw-colored with brown apex, pedicel brown with straw brown apex, basi- and distiflagellomeres missing. First segment of labium brown, second segment basally and apically dark brown, medially light brown, third segment dark brown. Anterior lobe of pronotum dark brown with straw-colored patterns, posterior lobe straw brown, scutellum dark brown with brown apex, pleuron light brown with dark brown suffusion, sternum brown with dark brown suffusion. Corium of hemelytron straw-colored to brown, membrane straw brown to brown, slightly translucent. Femora of legs straw-colored with medial and apical light brown annulations, tibiae straw-colored with basal, medial and apical light brown annulations, tarsi and claws straw-colored. Abdomen dorsally yellowish-orange, ventrally brown with dark brown lateral suffusion.

VESTITURE. Densely setose. Head with widespread curved, setigerous tubercles, ventral surface of postocular lobe with sparse, setigerous tubercles, without pair of long, straight setae on postocular lobe posterior to ocelli. Anterior lobe of thorax with tuberculated, short, curved setae on lateral margins and along dorsal ridges, posterior lobe with short, curved, setigerous tubercles along lateral margins and sparsely distributed on dorsal surface. Corium of hemelytron with short, curved setae. Legs with two rows of spines and setigerous tubercles, tibia with regular rows of tuberculated, stout, sharp setae. Posterior margin of connexivum with short, curved setae.

HEAD. Scape surpassing apex of clypeus; eye distinctly projecting in dorsal view, less than  $\frac{1}{5}$  length of head, not attaining ventral margin of head in lateral view.

THORAX. Antero-lateral paired projections acute, diverging; median pronotal depression contiguous with transverse sulcus; paramedian carina strongly defined; scutellar process long with rounded apex; mesosternite with irregular, tuberculated median protrusion between fore and mid coxae.

HEMELYTRON. Surpassing tip of abdomen.

LEGS. Same as genus description.

ABDOMEN. Elongate ovoid, with straight terminal margin; connexival margin smooth, not undulating, posterior margin slightly elevated.

GENITALIA. Previously dissected and genitalia missing.

#### Female

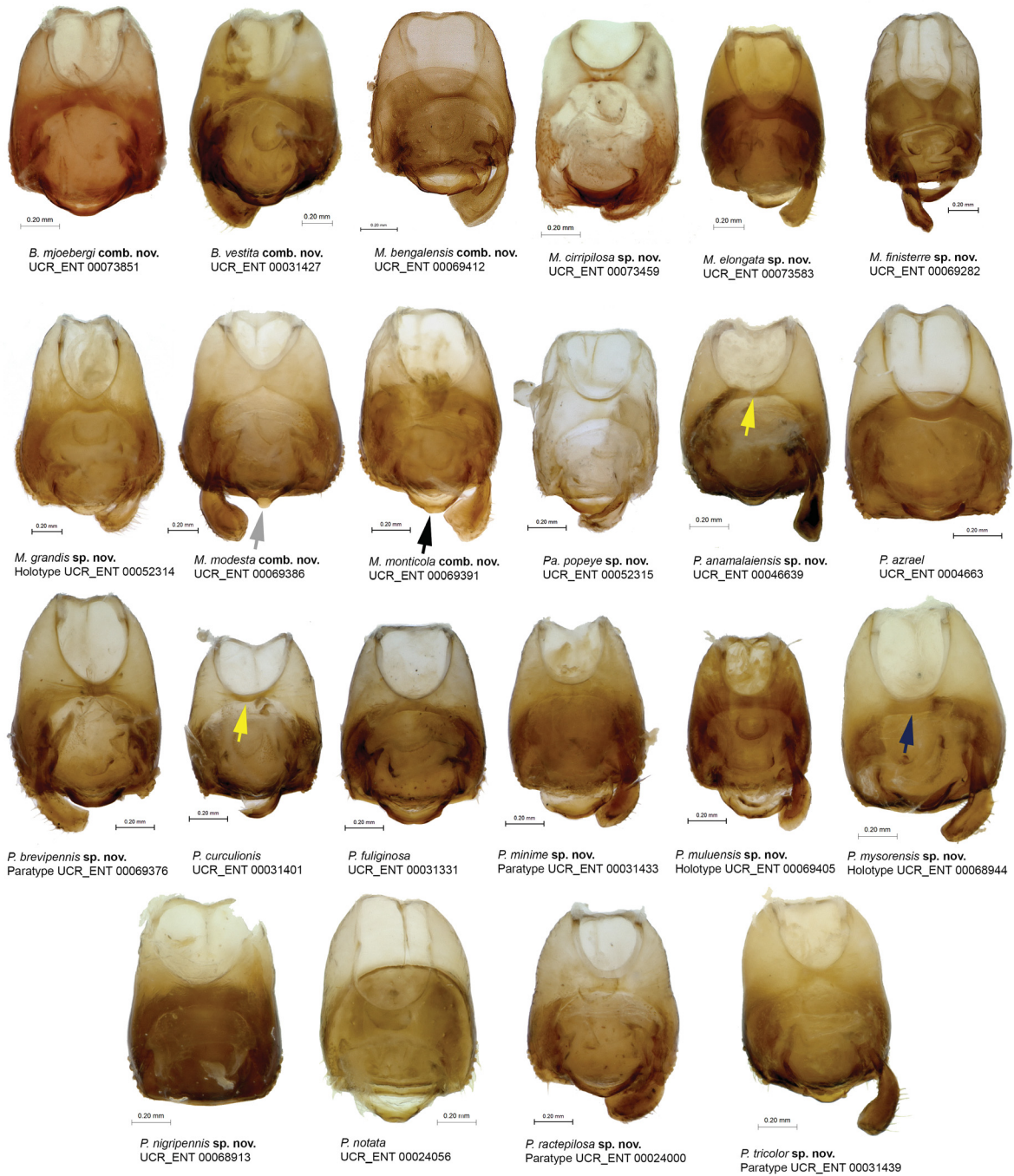
Unknown.

**Ecology**

Nothing is known about the biology of this species.

**Distribution**

This species is only known from the type locality of Mt Dulit in Sarawak, north-central Borneo. The type locality is shared with *B. fulvopicta* gen. et sp. nov., *B. hobbyi* comb. nov., *B. decora* comb. nov. and *B. tenebrosa* gen. et sp. nov.



**Fig. 8.** Dorsal view of the male pygophore in species of *Breviphysoderes* gen. nov., *Macrophysoderes* gen. nov., *Paraphysoderes* Villiers, 1962 and *Physoderes* Westwood, 1845. For an explanation of the colored arrows, see keys on pages 37 and 66.

## Remarks

This species is redescribed based on the holotype specimen. Miller (1940) recognized this specimen as a species different from *B. hobbyi* (Miller, 1940) comb. nov. due to the different anterior pronotal lobe coloration. *Breviphysoderes planicollis* comb. nov. is removed from *Physoderes* and transferred to this genus because it shares its synapomorphies (parascutellar lobes are semicircular, the male specimen does not possess an inflated anterior pronotal lobe and has prominent setigerous tubercles on the dorsal ridges of the anterior pronotal lobe). The specimen was collected by Dr E. Mjöberg during the Kalabit Expedition. The darkened scutellum and overlapping distribution, shared with *B. hobbyi* comb. nov., *B. decora* comb. nov. and *B. tenebrosa* gen. et sp. nov., suggest that they are likely to be closely related.

*Breviphysoderes shelfordi* (Miller, 1940), comb. nov.

Figs 4, 6; Appendix

*Physoderes shelfordi* Miller, 1940: 551, fig. 91.

## Diagnosis

This species is recognized among other species of *Breviphysoderes* gen. nov. by the scape surpassing the apex of the clypeus, the antero-lateral pronotal projection oriented anteriorly, the deeply defined pronotal paramedian carina, the distinct straw-colored mark on the apical veins of the external cell of the hemelytron (Cu+M) and hemelytron surpassing the tip of the abdomen. It is most similar to *B. hobbyi* comb. nov. and *B. planicollis* comb. nov. It can be differentiated from *B. tenebrosa* gen. et sp. nov. by the overall coloration and a narrower postocular lobe. It differs from *B. planicollis* comb. nov. by the orientation of the antero-lateral pronotal projection and the straw-colored mark on the apical veins of the external cell.

## Material examined

### Holotype

MALAYSIA: ♂, Sarawak, Kuching, Capt. [= Capital?], 1.53055° N, 110.34388° E, 12 m, 14 Aug. 1899, Dyak Collection (UCR\_ENT 00018538) (BMNH).

## Redescription

### Male

BODY LENGTH. Medium, total length 9 mm.

COLORATION (Fig. 4). Light brown with dark brown patterns. Head light brown to dark brown. Scape of antenna straw-colored with light brown apex, basal half of pedicel straw-colored and apical half brown, basi- and distiflagellomeres missing. Labium light brown. Pronotum dark brown with brown suffusion, scutellum dark brown with light brown apex. Corium of hemelytron brown, membrane brown with apical veins of external cell (Cu+M) straw-colored. Femora of legs light brown with medial and apical dark brown annulations, tibiae brown with basal, medial and apical dark brown annulations, tarsi and claws light-brown or brown. Abdomen not examined dorsally, ventrally light brown medially with lateral brown suffusion, anterior half of connexivum dark brown and posterior half straw-colored.

VESTITURE. Sparsely setose. Head with some flat, curved setae, without pair of long, straight setae on postocular lobe posterior to ocelli. Anterior lobe of thorax with tuberculated, short, curved setae on lateral margins and along dorsal ridges, posterior lobe with short, curved, setigerous tubercles along lateral margins and sparsely distributed on dorsal surface. Corium of hemelytron with short, curved setae. Legs with two rows of spines and setigerous tubercles, tibiae with regular rows of tuberculated, stout, sharp setae. Posterior margin of connexivum with short, curved setae.

HEAD. Scape surpassing apex of clypeus; eye distinctly projecting in dorsal view, about  $\frac{1}{5}$  length of head, not attaining ventral margin of head in lateral view.

THORAX. Antero-lateral paired projections acute; median pronotal depression contiguous with transverse sulcus; paramedian carina strongly defined; posterior lobe medially rugose (damaged/obscured medially by pin); scutellar process long, with rounded apex; mesosternite obscured.

HEMELYTRON. Surpassing tip of abdomen.

LEGS. Same as genus description.

ABDOMEN. Elongate ovoid, with rounded terminal margin; connexival margin slightly undulating, posterior margin slightly elevated.

GENITALIA. Not examined.

#### **Female**

Unknown.

#### **Ecology**

Nothing is known about the biology of this species.

#### **Distribution**

This species is only known from the type locality in north-western Borneo, Kuching.

#### **Remarks**

This species is redescribed based on the holotype specimen. *Breviphysoderes shelfordi* comb. nov. is removed from *Physoderes* and transferred to *Breviphysoderes* gen. nov. because it possesses the synapomorphies of this genus (parascutellar lobes are semicircular, males do not possess an inflated anterior pronotal lobe and have prominent setigerous tubercles on the dorsal ridges of the anterior pronotal lobe). This species is quite similar to other members of the genus found in Sarawak, Borneo, but is recognized as a separate species based on the diagnostic characters listed above. More specimens from this area will be needed to further test the status of these closely related species.

*Breviphysoderes tenebrosa* gen. et sp. nov.

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Figs 4–6; Appendix

#### **Diagnosis**

This species is recognized among other species of *Breviphysoderes* gen. nov. by the entirely brownish-black coloration, the antero-lateral pronotal projection oriented anteriorly, the pronotal paramedian carina being deeply defined and the hemelytron surpassing the tip of the abdomen. This species is most similar to *B. hobbyi* comb. nov. and *B. planicollis* comb. nov. It can be differentiated from both species by the overall coloration, the orientation of the antero-lateral pronotal projection and the shape of the external cell.

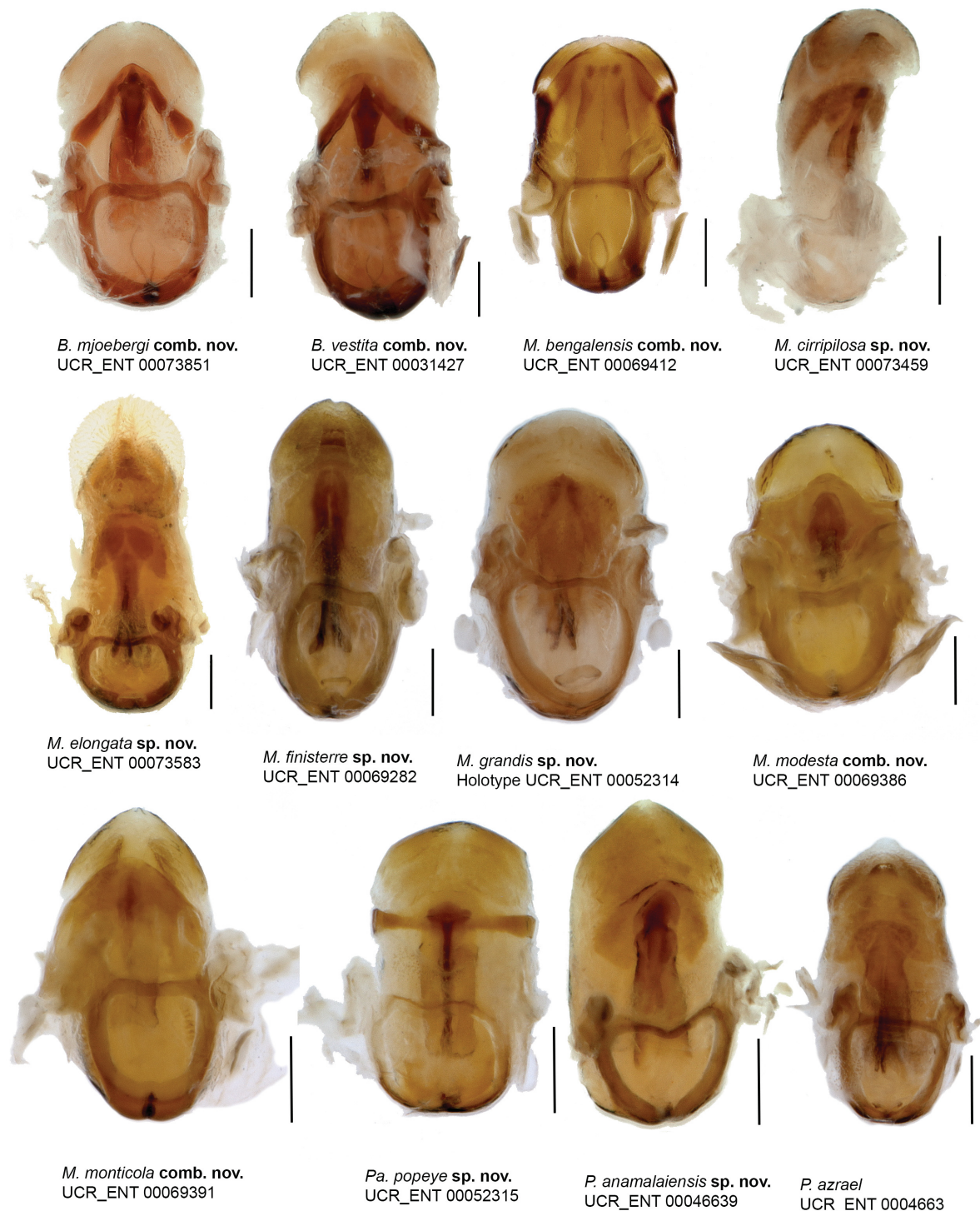
#### **Etymology**

The name *tenebrosa* is selected after the Latin adjective for “tenebrosus”, meaning dark, to describe the distinctive brownish-black coloration of the specimen.

**Material examined**

**Holotype**

MALAYSIA: ♂, Sarawak, foot of Mt Dulit, junction of Rivers Tinjar and Lejok, 3.32388° N, 114.14722° E, 730 m, 24 Aug. 1932, B.M. Hobby and A.W. Moore leg. (UCR\_ENT 00018489) (BMNH).



**Fig. 9.** Dorsal view of the phallus in species of *Breviphysoderes* gen. nov., *Macrophysoderes* gen. nov., *Paraphysoderes* Villiers, 1962 and *Physoderes* Westwood, 1845 (partial). Scale bars = 0.20 mm.



## Description

### Male

BODY LENGTH. Small size, total length 7.07 mm.

COLORATION (Figs 4–5). Entirely brownish-black. Antenna missing. Forelegs missing, mid- and hindlegs brownish black.

VESTITURE. Densely setose. Head with widespread curved, setigerous tubercles, ventral surface of postocular lobe with sparse, setigerous tubercles, without pair of long, straight setae on postocular lobe posterior to ocelli. Anterior lobe of thorax with tuberculated, short, curved setae on lateral margins and along dorsal ridges, posterior lobe with short, curved, setigerous tubercles along lateral margins and sparsely distributed on dorsal surface. Corium of hemelytron with short, curved setae. Tibiae with regular rows of tuberculated, stout, sharp setae. Posterior margin of connexivum with short, curved setae.

HEAD. Eye distinctly projecting in dorsal view, about  $\frac{1}{5}$  length of head, not attaining ventral margin of head in lateral view.

THORAX. Antero-lateral paired projections acute, oriented anteriorly; median pronotal depression contiguous with transverse sulcus; paramedian carina strongly defined (posterior lobe damaged/obscured medially by pin); scutellar process long, with rounded apex; mesosternite with median, irregular, tuberculated protrusion between fore and mid coxae.

HEMELYTRON. Surpassing tip of abdomen.

ABDOMEN. Elongate ovoid, with rounded terminal margin; connexival margin slightly undulating, posterior margin not elevated.

GENITALIA. Not examined.

### Female

Unknown.

## Ecology

The type specimen was found on the bark of a felled tree along the junction of two rivers.

## Distribution

This species is only known from the type locality of Mt Dulit in Sarawak, north-central Borneo. The type locality is shared with *B. fulvopicta* gen. et sp. nov., *B. planicollis* comb. nov., *B. decora* comb. nov. and *B. hobbyi* comb. nov.

## Remarks

This species is described based on a single specimen originally designated as a paratype of *B. hobbyi* (Miller, 1940) comb. nov. Even though it shares the collecting event and locality with specimens of that species, closer examination showed distinct morphological differences and we describe this specimen as a separate species. It was collected by B.M. Hobby and A.W. Moore during the Oxford University Expedition in 1932.

***Breviphysoderes vestita* (Horváth, 1900), comb. nov.**  
Figs 4–9; Appendix

*Epirodera vestita* Horváth, 1900: 639.

*Physoderes serraticollis* Breddin, 1903: 125. New synonymy.

*Physoderes javanica* Miller, 1940: 549, fig. 91. New synonymy.

*Physoderes rugosa* Miller, 1954: 87, fig. 11. New synonymy.

*Physoderes vestita* – Maldonado 1990: 381.

**Diagnosis**

This species is recognized among species of *Breviphysoderes* gen. nov. by having the head and anterior pronotal lobe distinctly covered with dense, short, curved, setigerous tubercles, the scape surpassing the apex of the clypeus, males with the anterior pronotal lobe almost as wide as the posterior pronotal lobe, the apical veins of the external cell of the hemelytron (Cu+M) with distinct straw-colored marks, and the hemelytron surpassing the tip of the abdomen. This species most closely resembles *B. fulvopicta* gen. et sp. nov. but is differentiated by the wider anterior pronotal lobe in males and the length of the hemelytron (i.e., surpassing the tip of the abdomen).

**Material examined**

**Holotype**

INDONESIA: ♂, East Java, Tjibodas (Cibodas), 6.97527° S, 107.6625° E, 614 m, no date provided, R. Semon leg. (UCR\_ENT 00012260) (HNHM).

**Other material**

INDONESIA: Java: 2 ♀♀, E Java, Nongkodjadar (Nonkojajar), 7.91611° S, 112.8875° E, 846 m, 1911, E. Jacobson leg. (UCR\_ENT 00024050, UCR\_ENT 00014054) (RMNH); 1 ♀, Buitenzorg (Bogor), 6.6875° S, 106.81472° E, 447 m, Mar. 1909, Bryant and Palmer leg. (UCR\_ENT 00068910) (AMNH); 1 ♂, Gunung Boerangrang (Burangrang), 6.775° S, 107.55555° E, 1600 m, Dec. 1936, F.C. Drescher leg. (UCR\_ENT 00024043) (RMNH); 1 ♀, Gunung Malabar, 7.13° S, 107.65° E, 1600 m, Jun. 1936, F.C. Drescher leg. (UCR\_ENT 00024038) (RMNH); 1 ♀, 7.61444° S, 110.71222° E, no date provided, Muller leg. (UCR\_ENT 00024049) (RMNH); 1 ♀, unknown date, holotype of *Physoderes javanica* (junior synonym) (UCR\_ENT 00018537) (BMNH); 1 ♀, 7.61444° S, 110.71222° E, 1000 m, Dec. 1951, L.G.E. Kalshoven leg. (UCR\_ENT 00024040) (RMNH); 1 ♂, Lembang, W Java, 6.82166° S, 107.63° E, 1259 m, 1921, L.G.E. Kalshoven leg. (UCR\_ENT 00024061) (RMNH); 1 ♀, Megamedg Mountains, 6.61861° S, 106.84722° E, 1280 m, no date provided, Bryant and Palmer leg. (UCR\_ENT 00068909) (AMNH); 2 ♂♂, same collection data as preceding (UCR\_ENT 00031427, UCR\_ENT 00031428) (USNM); 1 ♀, Mt Patoeha, 7.16138° S, 107.39972° E, 1550 m, Mar. 1937, E. Jacobson leg. (UCR\_ENT 00024037) (RMNH); 1 ♂, Tangkuban Perahu (Tangkoeban Prahoe) volcano, 4000–5000 ft, 6.76305° S, 107.59944° E, 1955 m, Nov. 1936, F.C. Drescher leg. (UCR\_ENT 00024042) (RMNH); 1 ♀, same locality as preceding, Mar. 1937, F.C. Drescher leg. (UCR\_ENT 00024036) (RMNH); 6 ♀♀, same locality as preceding, Feb. 1937, F.C. Drescher (UCR\_ENT 00024034, UCR\_ENT 00024035, UCR\_ENT 00024045–UCR\_ENT 00024048) (RMNH); 1 ♀, W Java, Tjisaroea (Cisarua), 6.78916° S, 107.535° E, 1000 m, 11 Jan. 1931, collector unknown (UCR\_ENT 00024041) (RMNH); 1 ♀, 14 Dec. 1928, L.G.E. Kalshoven leg., holotype of *Physoderes rugosa* (junior synonym) (UCR\_ENT 00023948) (RMNH); 1 ♂, Jawa Barat (West Java), Pangalengan, 7.18988° S, 107.57993° E, 1219 m, 1893, H. Fruhstorfer leg., holotype of *Physoderes serraticollis* (junior synonym) (UCR\_ENT 00040567) (DEI); 1 ♂, unlabeled specimen (UCR\_ENT 00024044) (RMNH).

## Redescription

### Male

**BODY LENGTH.** Medium-large size, total length 10.02 mm, SD  $\pm$  0.24 (Appendix).

**COLORATION** (Figs 4–5, 7). Straw-colored to brown with dark brown patterns. Head brown. Scape of antenna straw-colored with light brown apex, pedicel straw-colored to light brown, basiflagellomere straw-colored with light brown apex, distiflagellomere straw-colored with light brown base. First segment of labium with basal half brown, apical half straw-colored, second segment straw-colored with base and apex brown, third segment brown. Pronotum dark brown with straw-colored setae, scutellum dark brown, pleuron straw-colored to dark brown, sternum brown to dark brown. Corium of hemelytron straw-colored, membrane brown with apical veins of external cell (Cu+M) straw-colored, sometimes including medial vein apex. Femora straw-colored with medial and apical brown annulations, tibiae straw-colored with basal, medial and apical light brown annulations, tarsi and claws straw-colored. Abdomen dorsally yellowish-orange, ventrally light brown, medially with dark brown sub-lateral and posterior suffusion, anterior half of connexivum dark brown and posterior half straw-colored, exposed part of pygophore straw-colored.

**VESTITURE.** Densely setose. Head with widespread setigerous tubercles bearing long, semi-erect, spatulate, curved setae, ventral surface of postocular lobe with sparse, setigerous tubercles, with a pair of long, straight setae on postocular lobe posterior to ocelli. Anterior lobe of thorax with tuberculated, short, curved setae on lateral margins and along dorsal ridges, posterior lobe with short, curved, setigerous tubercles along lateral margins and sparsely distributed on dorsal surface. Corium of hemelytron with short, curved setae. Legs with two rows of spines and setigerous tubercles, tibiae with regular rows of tuberculated, stout, sharp setae. Posterior margin of connexivum with short, curved setae.

**HEAD.** Scape surpassing apex of clypeus; eye distinctly projecting in dorsal view, about  $\frac{1}{3}$  length of head, not attaining ventral margin of head in lateral view.

**THORAX.** Antero-lateral paired projections acute, diverging; surface of anterior lobe with raised ridges; median pronotal depression not contiguous with transverse sulcus; paramedian carina strongly defined; scutellar process long, with rounded apex; mesosternite with median irregular tuberculated protrusion between fore and mid coxae.

**HEMELYTRON.** Surpassing tip of abdomen.

**LEGS.** Same as genus description.

**ABDOMEN.** Elongate ovoid, with rounded terminal margin; connexival margin slightly undulating, posterior margin slightly elevated.

**GENITALIA.** Anterior margin of mediosternite 8 sharply emarginate, with medial apodeme; apex of dorsal phallosomal sclerite rounded, with narrow, lateral, band-like prolongations, oriented diagonally and angularly curved along lateral margins of phallosoma towards basal plate.

### Female

Similar to males except in having a narrower anterior pronotal lobe.

## Ecology

Nothing is known about the biology of this species except that specimens have been collected from mid to high altitudes ranging from 447 m to 1955 m with most specimens collected from elevations higher than 1200 m.

### Distribution

This species is exclusively found on the island of Java (the locality for one of the examined specimens is unknown).

### Remarks

Originally described as *Epirodera vestita* (Horváth, 1900), this species is transferred to *Breviphysoderes* gen. nov. based on the phylogenetic analysis conducted above. It is most similar to *B. mjoebergi* (Miller, 1940) comb. nov., and both species co-occur on the island of Java. *Physoderes serraticollis* Breddin, 1903, *P. javanica* Miller, 1940 and *P. rugosa* Miller, 1954 are here synonymized with *B. vestita* comb. nov. based on the examination of all type specimens. No diagnostic morphological characters can be found to separate these species, except that the holotype of *P. javanica*, which is a female, has a narrower anterior pronotal lobe. Nevertheless, this specimen possesses the raised anterior pronotal ridges with setigerous tubercles, the completely dark brown anterior pronotal lobe, the straw-colored apical veins of the external cell of the hemelytron and the rounded abdominal margin that are diagnostic for *B. vestita* comb. nov. The holotypes of both *P. rugosa* and *P. serraticollis* are males and share the broad anterior pronotal widths of *B. vestita*, which has raised ridges and dense, tuberculated, curved setae, as well as the remaining diagnostic characters. Both were also collected from Java.

*Macrophysoderes* gen. nov.

[urn:lsid:zoobank.org:act:2D4195FE-B54C-42E2-B023-0EE03A15A464](https://zoobank.org/act:2D4195FE-B54C-42E2-B023-0EE03A15A464)

Figs 7–12; Appendix

### Diagnosis

This genus is recognized among genera of Physoderinae by often having a glabrous, sparsely setose pronotum (except for *M. cirripilosa* gen. et sp. nov., *M. elongata* gen. et sp. nov. and *M. finisterre* gen. et sp. nov.), the eyes being very large and distinctly projecting in dorsal view and sometimes attaining the ventral margin of the head in lateral view, the anterior pronotal lobe narrower or slightly narrower than the posterior lobe, the antero-lateral pronotal projection often being truncate, but sometimes acute, and the margin of the anterior opening of the pygophore being rounded in lateral view. *Macrophysoderes* gen. nov. is most similar to *Physoderes*, but is distinguished by the very large and distinctly projecting eyes in most species, the males with the anterior pronotal lobe narrower than the posterior lobe and by the glabrous pronotum.

### Etymology

The name combines *Physoderes* after the type genus of Physoderinae and the Greek adjective “macro” to indicate the large size of the eyes. The gender is feminine.

### Type species

*Physoderes modesta* Miller, 1940.

### Description

#### Male

BODY LENGTH. Ranging from small to very large, 7.80–11.58 mm.

COLORATION (Figs 7, 10–11). Variable, from straw-colored to dark brown. Head, pronotum, legs and corium of similar lighter coloration, annulation patterns of hind femur variable, scutellum and claval region with darker coloration.

VESTITURE. Glabrous or densely setose with tuberculated, curved setae.

HEAD. Elongate or short conical; maxillary plate truncate or rounded apically; scape length variable; eye distinctly projecting in dorsal view except in *M. elongata* gen. et sp. nov., sometimes attaining ventral margin of head in lateral view; height of anteocular lobe shorter or level with postocular lobe, ocelli present.

THORAX. Antero-lateral paired pronotal projection truncate or acute, oriented anteriorly or diverging; surface of anterior lobe smooth, anterior pronotal ridges almost obsolete or low; median pronotal depression contiguous with transverse sulcus in both sexes except in *M. cirripilosa* gen. et sp. nov. and *M. elongata* gen. et sp. nov.; paramedian carina variably defined; posterior lobe medially rugose; anterior pronotal lobe equal to or shorter than posterior lobe, narrower or slightly narrower than posterior lobe in males, anterior lobe lower than or level with posterior lobe in lateral view; parascutellar lobe shape variable, either triangular, bell-shaped or rounded and skewed towards median; scutellum rounded triangular, length of scutellar process variable from very short to long, shape of apex variable; mesosternite with median, irregular, tuberculated protrusion between fore and mid coxae except in *M. elongata* gen. et sp. nov.

HEMELYTRON. Macropterous, length variable.

LEGS. Fore femur distinctly incrassate, tarsi three-segmented.

ABDOMEN. Elongate ovoid, with straight or rounded posterior margin; connexival margin smooth or slightly undulating, posterior margin not elevated.

GENITALIA. Anterior margin of mediosternite 8 undulating or sharply emarginated, with or without medial apodeme; transverse bridge of pygophore of variable width, margin of anterior opening rounded or angular, apodeme present, apical margin of posterior opening smooth; cup-like sclerite apically variable; arms of basal plate converging or curved to form rounded foramen; ductifer with membranous or sclerotized ring of variable shapes; endosomal struts of variable shapes; dorsal phallosomal sclerite subacute, with lateral, broad, plate-like prolongations of variable sizes.

### Female

Most often similar in size, shape and color to male except with wider abdomen.

### Ecology

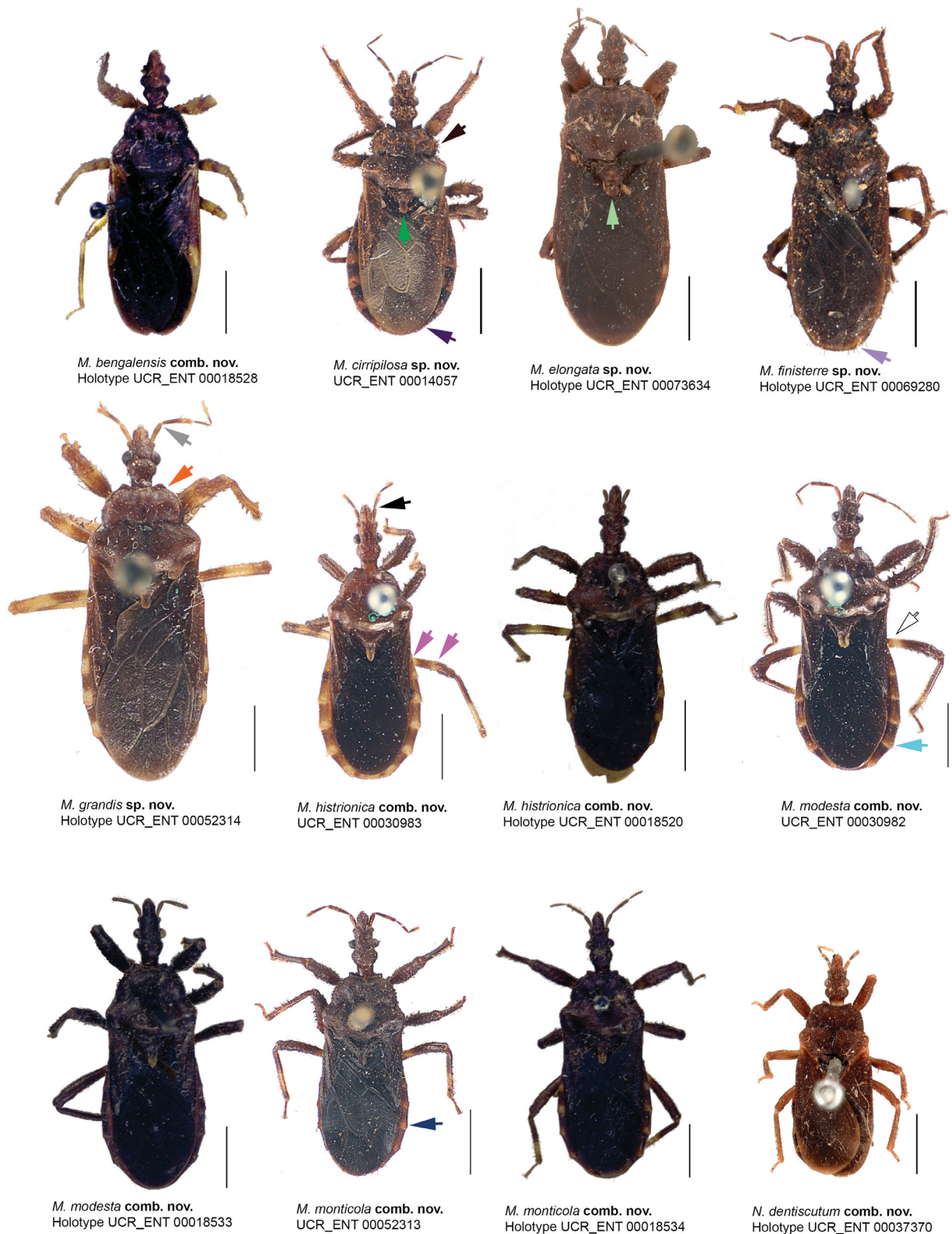
Not much is known about the biology. A few species are known to occur at higher elevations (1000–2000 m). One specimen of *M. cirripilosa* gen. et sp. nov. was collected from a log and another from a light trap.

### Distribution

This genus currently comprises 8 species and is widely distributed across Southeast Asia and Australasia, and can be found in the Bengal region, peninsular Malaysia, Borneo, New Guinea and the Solomon Islands. The highest species diversity for this genus is found on the island of New Guinea.

### Key to species of *Macrophysoderes* gen. nov.

1. Head elongate conical, scape not reaching apex of clypeus (Fig. 10, black arrow) .....2
  - Head short conical, scape reaching or surpassing apex of clypeus (Fig. 10, grey arrow) .....4
2. Hind femur brown, with basal and subapical straw-colored annulations (Fig. 10, pink arrows) ..
  - .....*M. histrionica* (Miller, 1940) comb. nov.
  - Hind femur brown, with single basal straw-colored annulation (Fig. 10, white arrow) .....3



**Fig. 10.** Dorsal habitus images for species of *Macrophysoderes* gen. nov. and *Nanophysoderes* gen. nov. For an explanation of the colored arrows, see key on page 37. Scale bars = 2 mm.

3. Anterior two-thirds of connexivum dark brown, posterior third straw-colored (Fig. 10, dark blue arrow), anterior margin of male mediosternite 8 without apodeme, apical margin of posterior opening of pygophore smooth, without medial process, cup-like sclerite smooth, apically rounded (Fig. 8, black arrow) .....*M. monticola* (Miller, 1940) comb. nov.  
 – Connexivum dark brown, posterior margin straw-colored (Fig. 10, light blue arrow), anterior margin of male mediosternite 8 with apodeme, apical margin of posterior opening of pygophore with small medial process, cup-like sclerite apex with a medial process (Fig. 8, grey arrow) ...  
 .....*M. modesta* (Miller, 1940) comb. nov.
4. Dorsal surface of pronotum glabrous (Fig. 10, orange arrow) .....5  
 – Dorsal surface of pronotum, at least along ridges, with dispersed curved setae (Fig. 10, brown arrow) .....6
5. Very large (11.58–12.66 mm), scape surpassing apex of clypeus, head with pair of long, straight setae along posterior margin of postocular lobe, antero-lateral pronotal projections truncate (Fig. 10, orange arrow) .....*M. grandis* gen. et sp. nov.  
 – Medium (9 mm), scape reaching apex of clypeus, head without pair of long, straight setae along posterior margin of postocular lobe, antero-lateral pronotal projections acute and diverging .....  
 .....*M. bengalensis* (Distant, 1909) comb. nov.
6. Medium to very large (9.47–11.11 mm), scutellar process short and spatulate (Fig. 10, light green arrow), fore femur extremely incrassate, abdomen relatively long .....*M. elongata* gen. et sp. nov.  
 – Small to very large (7.16–11.01 mm), scutellar process subacute or rounded, not spatulate (Fig. 10, green arrow), fore femur not extremely incrassate, abdomen not elongated .....7
7. Body brownish-black, scape just surpassing apex of clypeus, scutellar process very short, connexivum narrow, abdominal apical margin straight (Fig. 10, light purple arrow) .....  
 .....*M. finisterre* gen. et sp. nov.  
 – Body straw-colored and brown, scape reaching apex of clypeus, scutellar process short, connexivum wide, abdominal apical margin rounded (Fig. 10, purple arrow) .....  
 .....*M. cirripilosa* gen. et sp. nov.

*Macrophysoderes bengalensis* (Distant, 1909) comb. nov.  
 Figs 8–10, 12; Appendix

*Epirodera bengalensis* Distant, 1909: 364.

*Physoderes bengalensis* – Maldonado 1990: 379.

**Diagnosis**

This species is recognized among species of *Macrophysoderes* gen. nov. by the dark brown coloration, the scape reaching the apex of the clypeus, the very large eyes relative to the head, the absence of paired long setae at the posterior margin of the postocular lobe, the two rows of small setigerous tubercles on the ventral surface of the postocular lobe, the pronotum with deep paramedian carinae, the triangular pronotal paramedian lobes, the spines on the fore trochanter and the straight margin of the abdominal apex. This species is quite distinct from other members of the genus.

**Material examined**

**Holotype**

INDIA: ♂, Bengal, Pusa, 22.98666° N, 87.855° E, exact locality, date and collector unknown (UCR\_ENT 00018528) (BMNH).

**Other material**

INDIA: 1 ♂, Meghalaya, Khasi Hills, 25.58333° N, 91.63333° E, no date provided, collector unknown (UCR\_ENT 00069412) (BMNH).

**Redescription**

**Male**

BODY LENGTH. Medium size, total length 9 mm.

COLORATION (Fig. 10). Brown. Head brown. Scape of antenna brown, other segments missing. First segment of labium brown, second and third straw brown. Anterior lobe of pronotum dark brown, posterior lobe brown, scutellum dark brown, pleuron brown with light brown margin along acetabulum, sternum brown. Corium of hemelytron brown with straw brown apex, membrane dark brown. Femora straw brown with sub-basal and sub-apical brown annulations, tibiae brown, basally straw brown, tarsi and claws straw brown. Abdomen dorsally straw brown, ventrally straw brown with lateral brown patterns, connexivum yellow brown with anterior indistinct brown spot, exposed part of pygophore straw-colored.

VESTITURE. Sparsely setose. Head with some flat, curved setae, ventral surface of postocular lobe with two rows of small, setigerous tubercles. Anterior lobe of thorax with irregular row of tuberculated, short, curved setae on lateral margins and short, setigerous tubercles dispersed on dorsal surface, posterior lobe with only short, sparse setae. Corium of hemelytron glabrous. Fore trochanter of legs with small process on internal surface, fore femur with two rows of spines and setigerous tubercles, fore tibiae with regular rows of tuberculated, stout, sharp setae. Connexival margin of abdomen without setae.

HEAD. Short conical; maxillary plate rounded apically; scape reaching apex of clypeus; eye about  $\frac{1}{5}$  length of head, not attaining ventral margin of head in lateral view; height of anteocular lobe shorter than postocular lobe.

THORAX. Antero-lateral paired projections acute, diverging; surface of anterior lobe with low ridges; paramedian carina strongly defined; posterior lobe medially weakly rugose; anterior pronotal lobe shorter than posterior lobe, narrower than posterior lobe, anterior lobe lower than posterior lobe in lateral view; parascutellar lobe triangular; scutellar process long, with acute apex.

HEMELYTRON. Attaining tip of abdomen.

LEGS. Same as genus description.

ABDOMEN. Elongate ovoid, with straight terminal margin; connexival margin smooth.

GENITALIA. Anterior margin of mediosternite 8 undulating, without medial apodeme; transverse bridge of pygophore extremely narrow, only consisting of margin of anterior opening of pygophore, margin of anterior opening rounded; cup-like sclerite apically rounded, with sclerotized paired latero-ventral protuberance; arms of basal plate converging; ductifer with sclerotized elongate ring; endosomal struts apically truncate, divided into two arms; shape of dorsal phallosclerite subacute with lateral broad, plate-like prolongations, small acute apex and broad lateral plates with rounded margins extended laterally and curved towards apex.

**Female**

Unknown.



### Ecology

Nothing is known about the biology of this species.

### Distribution

This species is only known from two localities: Pusa, Bengal (type locality) and Khasia Hills, Assam. It appears to be restricted to areas adjoining the Indian subcontinent and Myanmar.

### Remarks

This species is placed in the *Macrophysoderes* gen. nov. clade based on the phylogenetic analysis above. It is most closely related to *M. monticola* comb. nov., as both possess a scape that reaches the apex of the clypeus and lack the paired, long setae at the posterior margin of the postocular lobe. *M. bengalensis* comb. nov. possesses several unique characters, especially on the male genitalia.

#### *Macrophysoderes cirripilosa* sp. nov.

[urn:lsid:zoobank.org:act:9B61EDE2-4732-4BCB-92B7-8C200A34A7BE](https://doi.org/10.3896/abris.urn:lsid:zoobank.org:act:9B61EDE2-4732-4BCB-92B7-8C200A34A7BE)

Figs 8–12; Appendix

### Diagnosis

This species is recognized among species of *Macrophysoderes* gen. nov. by the short conical head that is covered with semi-erect, curved setae, with a distinct concentration of setae on the postocular lobe between the ocelli, the length of the scape reaching the apex of the clypeus, the very large eye that attains the ventral margin of the head in lateral view, the median pronotal depression not contiguous with the transverse sulcus and the short scutellar process. It most closely resembles *M. finisterre* gen. et sp. nov. and *M. elongata* gen. et sp. nov. It is differentiated from the former by the overall coloration, the shape of the antero-lateral pronotal projections, the wider anterior pronotal lobe and the shape of the abdominal apical margin. It is differentiated from *M. elongata* gen. et sp. nov. by the size, the shape of the scutellar process, the relative length of head to body and the less swollen fore femur.

### Etymology

The name combines the Latin noun “cirrus”, meaning curl or hair-tuft, with the Latin adjective “pilosus”, meaning hairy, to describe the abundant, curved setae on the head, especially between the ocelli.

### Material examined

#### Holotype

PAPUA NEW GUINEA: ♂, Western Province, Fly River, Kiunga, 6.11944° S, 141.29194° E, 8–10 Aug. 1957, W.W. Brandt leg. (UCR\_ENT 00073448) (BPBM).

#### Paratypes

PAPUA NEW GUINEA: 4 ♂♂, same collection data as for holotype (UCR\_ENT 00073446, UCR\_ENT 00073447, UCR\_ENT 00073453, UCR\_ENT 00073454) (BPBM).

#### Other material

INDONESIA: Irian Jaya: 1 ♀, Cyclops Mts, Ifar, 2.6° S, 140.61° E, 300 m, 23–25 Jul. 1962, J. Sedlacek leg. (UCR\_ENT 00073499) (BPBM); 1 ♀, Cyclops Mts, 2.8775° S, 140.70333° E, 1067 m, Mar. 1936, L.E. Cheesman leg. (UCR\_ENT 00069271) (BMNH); 1 ♂, Cyclops Mts, Mt Lina, 2.43055° S, 140.45333° E, 1067 m, Mar. 1936, L.E. Cheesman leg. (UCR\_ENT 00069263) (BMNH); 1 ♂, Guega, W of Swart Valley, 3.6° S, 138.41666° E, 1200 m, 15 Nov. 1958, J.L. Gressitt leg. (UCR\_ENT 00073468) (BPBM); 1 ♀, Ifar, Cyclops Mts, 2.83166° S, 140.60555° E, 450 m, 8 Sep. 1962, J. Sedlacek leg. (UCR\_ENT 00073500) (BPBM); 1 ♂, Yapen, 1.79472° S, 136.30361° E, 600 m, 4 Jan. 2007, S. Bily leg.

(UCR\_ENT 00073850) (NMPC). – Papua: 1 ♂, Paniai Division Co., Wisselmeren Enarotadi, 4.205° S, 136.59305° E, 1900 m, 16 Jul. 1962, J. Sedlacek leg. (UCR\_ENT 00073466) (BPBM); 1 ♀, Araboebivak, 2.61527° S, 140.62805° E, 6 Oct. 1939, collector unknown (UCR\_ENT 00024031) (RMNH); 1 ♀, Araucaria Camp, 5.65916° S, 139.13583° E, 800 m, Mar. 1939, L.J. Toxopeus leg. (UCR\_ENT 00024011) (RMNH); 1 ♀, Bernhard Camp, 6.21305° S, 141.54805° E, 50 m, 5 Oct. 1938, J. Olthof leg. (UCR\_ENT 00014057) (RMNH); 2 ♀♀, same collection data as preceding but Aug. 1938 (UCR\_ENT 00024007, UCR\_ENT 00024008) (RMNH); 2 ♀♀, same collection data as preceding but Jul.–Nov. 1938 (UCR\_ENT 00024009, UCR\_ENT 00024010) (RMNH); 1 ♂, Hollandia (Jayapura), 2.61527° S, 140.62805° E, 500 m, Jul. 1938, L.J. Toxopeus leg. (UCR\_ENT 00024005) (RMNH); 1 ♂, Nabire, S Geelwink Bay, 3.36667° S, 135.48333° E, 2–9 Jul. 1962, J.L. Gressitt leg. (UCR\_ENT 00073469) (BPBM); 1 ♂, Sibil, Star Mountain Range, 5.2375° S, 141.14861° E, 1260 m, 18 Apr. 1959, collector unknown (UCR\_ENT 00024028) (RMNH); 1 ♂, same collection data as preceding but 21 Apr. 1959 (UCR\_ENT 00024030) (RMNH); 1 ♂, same collection data as preceding but 25 Apr. 1959 (UCR\_ENT 00024029) (RMNH); 1 ♂, same collection data as preceding but 25 May 1959 (UCR\_ENT 00024006) (RMNH); 1 ♀, Wamena, 4.10055° S, 138.90472° E, 700 m, 10–25 Feb. 1960, T.C. Maa leg. (UCR\_ENT 00073485) (BPBM); 3 ♂♂, same collection data as preceding (UCR\_ENT 00073530–UCR\_ENT 00073532) (BPBM).

PAPUA NEW GUINEA: Bougainville Province: 1 ♂, Mt Nomo, S of Mt Bougainville, 6.05361° S, 155.19055° E, 213 m, Feb. 1936, L.E. Cheesman leg. (UCR\_ENT 00069295) (BMNH). – Central Province: 1 ♂, Daradae Plain, 80 km N of Port Moresby, 8.73665° S, 146.8088° E, 580 m, 6 Sep 1959, T.C. Maa leg. (UCR\_ENT 00073480) (BPBM); 1 ♂, Iriri, near Kerema, 8.98416° S, 146.98944° E, 7 May 1959, C.D. Michener leg. (UCR\_ENT 00073484) (BPBM); 1 ♀, Murua River near Kerema, 8.08361° S, 145.91138° E, 6 May 1959, C.D. Michener leg. (UCR\_ENT 00073492) (BPBM); 1 ♂, Otomata Plantation, 1 mi. E of Moresby, 9.48166° S, 147.10361° E, 2 Nov. 1960, J.L. Gressitt leg. (UCR\_ENT 00073481) (BPBM); 1 ♂, Owen Stanley Range, Goilala, Bome, 9.57666° S, 146.37194° E, 1950 m, 8–15 Mar. 1958, W.W. Brandt leg. (UCR\_ENT 00073483) (BPBM); 1 ♀, Owen Stanley Range, Goilala, Loloipa, 9.23583° S, 147.98444° E, 1–15 Feb. 1958, W.W. Brandt leg. (UCR\_ENT 00073498) (BPBM). – East New Britain Province: 1 ♀, near Rabaul, 4.175° S, 152.24805° E, Feb. 1929, collector unknown (UCR\_ENT 00046667) (CAS). – East Sepik Province: 1 ♀, Amboin Patrol Post, Karawari Lodge, 4.40444° S, 142.98555° E, Feb. 1983, A.C. Messer leg. (UCR\_ENT 00031394) (USNM); 1 ♀, Mar.–Apr. 1983, A.C. Messer leg. (UCR\_ENT 00031395) (USNM); 1 ♀, May River, 4.40694° S, 141.83944° E, 6 Jun. 1963, R. Straatman leg. (UCR\_ENT 00073503) (BPBM). – Madang Province: 1 ♂, Erima, Astrolabe Bay, 5.4225° S, 145.73361° E, 1897, Biro leg. (UCR\_ENT 00069770) (HNHM); 1 ♀, same collection data as preceding (UCR\_ENT 00069777) (HNHM); 1 ♂, same collection data as preceding but 1896 (UCR\_ENT 00069767) (HNHM); 5 ♀♀, same collection data as preceding (UCR\_ENT 00069772–UCR\_ENT 00069776) (HNHM); 1 ♂, Mondo, 5.41666° S, 144.76138° E, 1524 m, Feb. 1934, L.E. Cheesman leg. (UCR\_ENT 00069261) (BMNH); 1 ♂, Stephansort, Astrolabe Bay, 5.43638° S, 145.74138° E, 1897, Biro leg. (UCR\_ENT 00069771) (HNHM). – Morobe Province: 2 ♂♂, Huon Peninsula Co., Finschhafen, 6.55527° S, 147.17361° E, 20 Apr. 1944, E.S. Ross leg. (UCR\_ENT 00046650, UCR\_ENT 00046651) (CAS); 1 ♀, same collection data as preceding (UCR\_ENT 00046654) (CAS); 1 ♀, same locality as preceding, May 1944, F. Skinner leg. (UCR\_ENT 00046655) (CAS); 1 ♂, same locality as preceding, 7 May 1944, E.S. Ross leg. (UCR\_ENT 00046652) (CAS); 1 ♂, same locality as preceding, May 1944, E.S. Ross leg. (UCR\_ENT 00046653) (CAS); 1 ♀, 15 Nov. 1969, J.E. Tobler leg. (UCR\_ENT 00046673) (CAS); 1 ♀, Huon Gulf, Morobe District, 6.55861° S, 147.50805° E, 22 May–19 Jun. 1937, J.L. Froggatt leg. (UCR\_ENT 00069312) (BMNH); 1 ♂, Sattelberg, Huon-Golf, 6.485° S, 147.75861° E, 1899, Biro leg. (UCR\_ENT 00069788) (HNHM); 1 ♂, same collection data as preceding but 1898 (UCR\_ENT 00069787) (HNHM); 1 ♂, Bulolo, 7.20472° S, 146.63166° E, 900 m, 27 Mar. 1968, P. Colman leg. (UCR\_ENT 00073467) (BPBM); 1 ♀, same collection data as preceding (UCR\_ENT 00073501) (BPBM); 1 ♀, Bumayong, 6.63444° S,

147.0025° E, Jul. 1957, R.W. Paine leg. (UCR\_ENT 00069302) (BMNH); 1 ♀, Garaina, 7.88333° S, 147.13333° E, 800 m, 4 Jan. 1968, J. and M. Sedlacek leg. (UCR\_ENT 00073496) (BPBM); 3 ♂♂, same collection data as preceding but 15 Jan. 1968 (UCR\_ENT 00073474–UCR\_ENT 00073476) (BPBM); 1 ♂, same collection data as preceding but 13–15 Jan. 1968 (UCR\_ENT 00073477) (BPBM); 1 ♂, Gewak, Salawaket Range (Saruwaged Range), 6.21694° S, 146.75° E, 1530 m, 6 Sep. 1956, E.J. Ford Jr leg. (UCR\_ENT 00073464) (BPBM); 1 ♂, NE Wau, 7.33805° S, 146.71555° E, 1270 m, 7 May 1962, J. Sedlacek leg. (UCR\_ENT 00073612) (BPBM); 1 ♂, same collection data as preceding but 2–4 Jan. 1963 (UCR\_ENT 00073607) (BPBM); 1 ♀, NE Wau, 7.33166° S, 146.71805° E, 1010 m, 18 Dec. 1968, J. Sedlacek leg. (UCR\_ENT 00073620) (BPBM); 1 ♂, NE Wau, 7.32138° S, 146.71583° E, 1050 m, 5 Jan. 1963, G. Monteith leg. (UCR\_ENT 00073611) (BPBM); 2 ♂♂, same collection data as preceding but 7 Jan. 1963, J. Sedlacek leg. (UCR\_ENT 00073609, UCR\_ENT 00073610) (BPBM); 1 ♀, same collection data as preceding (UCR\_ENT 00073613) (BPBM); 1 ♂, NE Wau, Hospital Creek, 7.33805° S, 146.71555° E, 1300 m, 5 Dec. 1965, J. Sedlacek leg. (UCR\_ENT 00073606) (BPBM); 1 ♂, NE Wau, Mt Missim, 7.1167° S, 146.9167° E, 950–1300 m, Mar. 1965, J. and M. Sedlacek leg. (UCR\_ENT 00073478) (BPBM); 2 ♂♂, Waing, ca 18 mi. (?) of Lae, 6.72444° S, 146.96805° E, 13–14 Apr. 1965, Balogh and Szent-Ivany leg. (UCR\_ENT 00069768, UCR\_ENT 00069769); 1 ♀, same collection data as preceding (UCR\_ENT 00069778) (HNHM); 1 ♀, Wau, 7.33333° S, 146.71667° E, Jan.–Mar. 1982, R.T. Bell leg. (UCR\_ENT 00073618) (BPBM); 2 ♀♀, same collection data as preceding but Feb–May 1982 (UCR\_ENT 00073616, UCR\_ENT 00073617) (BPBM); 1 ♂, Wau, 7.32138° S, 146.71555° E, 1097 m, 11 Sep. 1971, W. Gagne leg. (UCR\_ENT 00046657) (CAS); 1 ♀, Wau, 7.3333° S, 146.71667° E, 1200 m, 27 Jul. 1961, J. and J.H. Sedlacek leg. (UCR\_ENT 00073614) (BPBM); 1 ♂, same collection data as preceding but 23 Dec. 1961, G. Monteith leg. (UCR\_ENT 00073603) (BPBM); 1 ♂, same collection data as preceding but 31 Aug. 1961, J. Sedlacek leg. (UCR\_ENT 00073602) (BPBM); 1 ♂, same collection data as preceding but 18–25 Jun. 1962 (UCR\_ENT 00073599) (BPBM); 1 ♂, same collection data as preceding but 14–24 Mar. 1964 (UCR\_ENT 00073601) (BPBM); 1 ♂, same collection data as preceding but 17–19 Sep. 1964 (UCR\_ENT 00073600) (BPBM); 1 ♂, 8–14 Dec. 1976, G.F. Hevel and R.E. Dietz IV leg. (UCR\_ENT 00031396) (USNM); 1 ♂, Wau, 7.3333° S, 146.71667° E, 1300 m, 24 Nov. 1963, J.L. Gressitt leg. (UCR\_ENT 00073605) (BPBM); 1 ♂, Wau, 7.3333° S, 146.71667° E, 1100 m, 4 Oct. 1962, J. Sedlacek leg. (UCR\_ENT 00073604) (BPBM); 1 ♂, Wau, Hospital Creek, 7.33805° S, 146.71555° E, 1250 m, 10 Apr. 196X [exact year unknown], J. and M. Sedlacek leg. (UCR\_ENT 00073608) (BPBM); 1 ♀, Wau Ecological Institute, 7.33805° S, 146.71555° E, 4 Dec. 1988, R. Holyuski leg. (UCR\_ENT 00069789) (HNHM). – Northern Province: 1 ♂, SE Popondetta, 8.76666° S, 148.23333° E, 25 m, May 1966, P. Shanahan leg. (UCR\_ENT 00073465) (BPBM). – Oro Province: 1 ♀, Kokoda, 8.86083° S, 147.73722° E, 350 m, 21 Mar. 1956, J.L. Gressitt leg. (UCR\_ENT 00073497) (BPBM); 2 ♀♀, Kokoda, 8.87777° S, 147.7375° E, 366 m, Apr. 1933, L.E. Cheesman leg. (UCR\_ENT 00069264, UCR\_ENT 00069265) (BMNH); 2 ♀♀, Kokoda, 8.87722° S, 147.7375° E, 366 m, Jun. 1933, L.E. Cheesman leg. (UCR\_ENT 00069268, UCR\_ENT 00069269) (BMNH); 3 ♂♂, same collection data as preceding but Sep. 1933 (UCR\_ENT 00069258–UCR\_ENT 00069260) (BMNH); 2 ♀♀, same collection data as preceding (UCR\_ENT 00069266, UCR\_ENT 00069267) (BMNH); 3 ♂♂, same collection data as preceding but Apr. 1933 (UCR\_ENT 00069255–UCR\_ENT 00069257) (BMNH); 1 ♂, Kokoda-Pitoki, 8.8775° S, 147.73722° E, 400 m, 24 Mar. 1956, J.L. Gressitt leg. (UCR\_ENT 00073461) (BPBM); 2 ♂♂, same collection data as preceding but 23 Mar. 1956 (UCR\_ENT 00073459, UCR\_ENT 00073460) (BPBM); 1 ♀, same collection data as preceding (UCR\_ENT 00073491) (BPBM); 1 ♂, NE Kokoda, 8.86861° S, 147.74777° E, 400 m, 17–18 Nov. 1965, J. and M. Sedlacek leg. (UCR\_ENT 00073462) (BPBM); 1 ♂, same collection data as preceding but 19 Nov. 1965 (UCR\_ENT 00073463) (BPBM). – Sandaun (West Sepik) Province: 1 ♂, Waris, S of Hollandia, 3.26667° S, 141.05° E, 450–500 m, 16–23 Aug. 1959, T.C. Maa leg. (UCR\_ENT 00073470) (BPBM). – Simbu Province: 1 ♀, Karimui, 6.49611° S, 144.82277° E, 1080 m, 13 Jul. 1963, J. Sedlacek leg. (UCR\_ENT 00073504) (BPBM). – West New Britain Province: 1 ♀, Silanga, Nakanai Mts, 5.5525° S, 150.87° E, 150 m, 31 Jul. 1956, E.J. Ford Jr leg. (UCR\_ENT

00073507) (BPBM). – Western Highlands Province: 1 ♂, Wum, Upper Jimmi Valley, 5.92972° S, 144.26805° E, 840 m, 18 Jul. 1955, J.L. Gressitt leg. (UCR\_ENT 00073482) (BPBM). – Western Province: 1 ♂, Eliptamin Valley, 5.17638° S, 141.54361° E, 1200–1350 m, 16–30 Aug. 1959, W.W. Brandt leg. (UCR\_ENT 00073479) (BPBM); 1 ♀, same collection data as preceding but 1–15 Sep. 1959 (UCR\_ENT 00073502) (BPBM); 1 ♂, Fly River, Kiunga, 6.11944° S, 141.29194° E, 11–14 Jul. 1957, W.W. Brandt leg. (UCR\_ENT 00073458) (BPBM); 2 ♀♀, same collection data as preceding (UCR\_ENT 00073493, UCR\_ENT 00073494) (BPBM); 1 ♂, same collection data as preceding but 23–25 Jul. 1957 (UCR\_ENT 00073457) (BPBM); 1 ♀, same collection data as preceding (UCR\_ENT 00073495) (BPBM); 1 ♂, same collection data as preceding but 5–7 Aug. 1957 (UCR\_ENT 00073456) (BPBM); 5 ♂♂, same collection data as preceding but 8–10 Aug. 1957 (UCR\_ENT 00073449–UCR\_ENT 00073452, UCR\_ENT 00073455); 5 ♀♀, same collection data as preceding (UCR\_ENT 00073486–UCR\_ENT 00073490) (BPBM); 2 ♂♂, Star Mts, Sibil Valley, 5.04823° S, 140.97958° E, 1245 m, 18 Oct.–8 Nov. 1961, S. and L. Quate leg. (UCR\_ENT 00073472, UCR\_ENT 00073473) (BPBM); 1 ♀, Koitaki, 8.92527° S, 147.73861° E, 457 m, Nov.–Dec. 1928, collector unknown (UCR\_ENT 00046656) (CAS); 1 ♂, Maffin Bay, Dutch New Guinea, 2.09222° S, 139.01472° E, Sep. 1944, E.S. Ross leg. (UCR\_ENT 00046658) (CAS); 1 ♂, Peria Creek, Kwagira River, 9.63111° S, 149.38555° E, 50 m, 14 Aug.–6 Sep. 1953, G.M. Tate leg. (UCR\_ENT 00068948) (AMNH); 2 ♀♀, Kalalo, 6.76° S, 147.91027° E, 750 m, 20–30 Aug. 1966, G.A. Samuelson leg. (UCR\_ENT 00073508, UCR\_ENT 00073509) (BPBM); 1 ♂, Mafulu, 8.45388° S, 146.7425° E, 1219 m, Jan. 1934, L.E. Cheesman leg. (UCR\_ENT 00069262) (BMNH). – 1 ♂, unknown locality, no date provided, Saunders leg. (UCR\_ENT 00069270) (BMNH).

## Description

### Male

**BODY LENGTH.** Medium size, total length 8.7 mm, SD ± 0.66 (Appendix).

**COLORATION** (Figs 10–11). Straw-colored and brown. Head brown. Scape and pedicel of antenna straw-colored, sometimes with brown suffusion, basiflagellomere brown, distiflagellomere straw-colored with brown base. First segment of labium brown with straw-colored apex, second segment basally and apically brown, medially straw-colored, third segment brown. Anterior lobe of pronotum brown with straw-colored markings, posterior lobe straw-colored to light brown, parascutellar lobe with lighter margin, scutellum basally dark brown, apically including process straw-colored, pleuron mixture of straw-color to dark brown, with straw-colored margin of acetabula, sternum dark brown. Corium of hemelytron light brown to brown, membrane brown. Femora straw-colored with basal and apical brown annulations, tibiae straw-colored with basal, medial and apical brown annulations, tarsi and claws straw-colored. Abdomen dorsally dull yellow, ventrally brown medially, straw-colored laterally, with dark brown sub-lateral markings, anterior half of connexivum dark brown, posterior half straw-colored, exposed part of pygophore dark brown.

**VESTITURE.** Densely setose. Head with widespread curved, setigerous tubercles, ventral surface of postocular lobe with two rows of small, setigerous tubercles, with pair of long, straight setae on postocular lobe posterior to ocelli. Anterior lobe of thorax with tuberculated, short, curved setae on lateral margins and along dorsal ridges, posterior lobe with short, curved setae on humeral angle and sparsely distributed along dorsal surface. Corium of hemelytron with short, curved setae. Legs with two rows of spines and setigerous tubercles, tibiae with regular rows of tuberculated, stout, sharp setae. Connexival margin of abdomen with a few clubbed setae on each segment.

**HEAD.** Short conical; maxillary plate rounded apically; scape reaching apex of clypeus; eye distinctly projecting in dorsal view, about 1/5 length of head, attaining ventral margin of head in lateral view; height of anteocular lobe shorter than postocular lobe.

THORAX. Antero-lateral paired projections acute, diverging; surface of anterior lobe with low ridges; median pronotal depression not contiguous with transverse sulcus; paramedian carina strongly defined; posterior lobe medially weakly rugose; anterior pronotal lobe shorter than posterior lobe, slightly narrower than posterior lobe, anterior lobe lower than posterior lobe in lateral view; parascutellar lobe bell-shaped and skewed towards median; scutellar process short with rounded apex.

HEMELYTRON. Not attaining tip of abdomen.

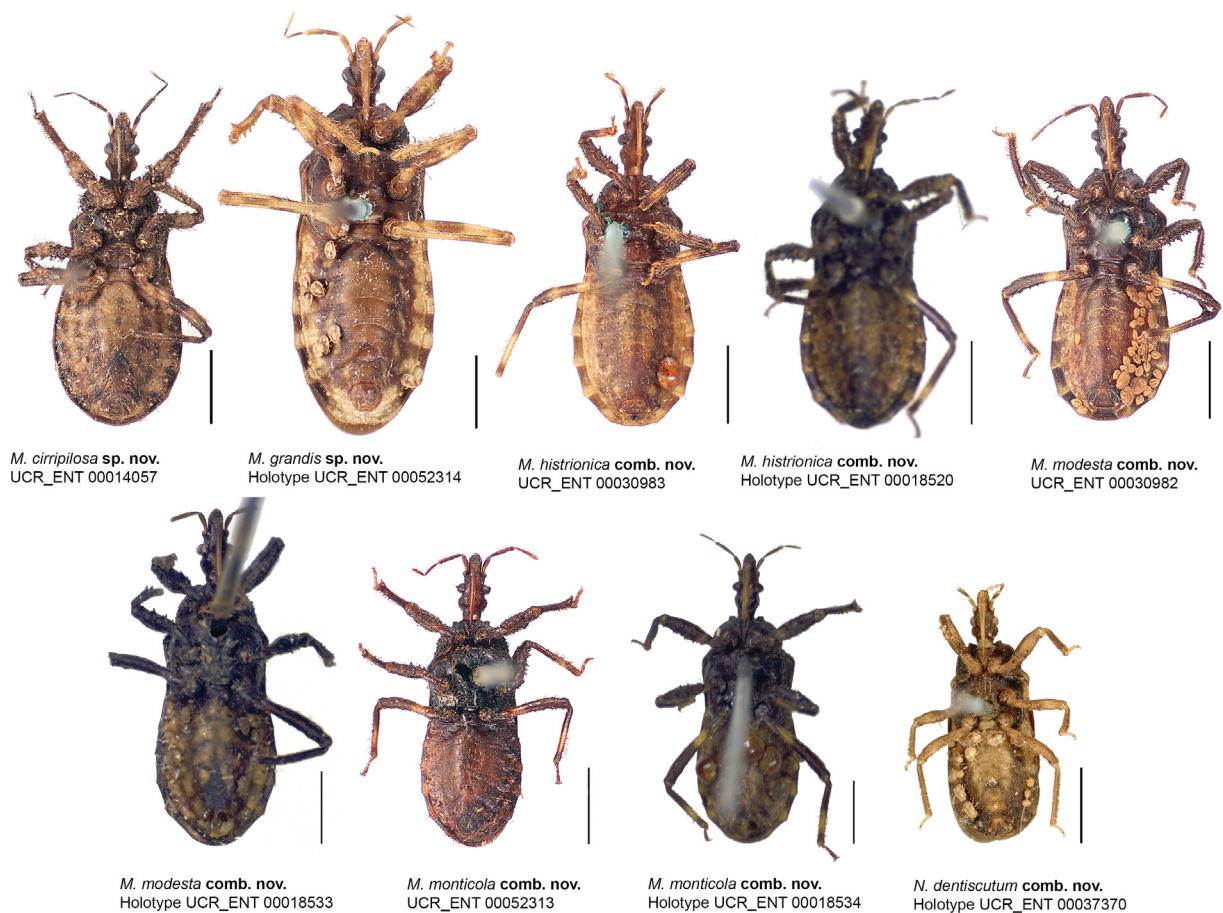
LEGS. Same as genus description.

ABDOMEN. Elongate ovoid, with rounded terminal margin; connexival margin slightly undulating.

GENITALIA. Anterior margin of mediosternite 8 sharply emarginated, with medial apodeme; transverse bridge of pygophore narrow, margin of anterior opening rounded; cup-like sclerite apically rounded and rim ventrally sclerotized; arms of basal plate converging; ductifer with sclerotized rounded ring; endosomal struts conical, with subacute apex, basally divided into two plates; dorsal phallosclerite subacute, with lateral, broad, plate-like prolongations, short triangular.

### Female

Similar in size and shape to males except with rounder or wider abdomen.



**Fig. 11.** Ventral habitus images for species of *Macrophysoderes* gen. nov. and *Nanophysoderes* gen. nov. Scale bars = 2 mm.

### Ecology

One specimen was recorded as having been found in logs and another as caught in a light trap.

### Distribution

Found throughout the island of New Guinea, on the nearby island New Britain, and on Bougainville Island (Solomon Archipelago).

### Remarks

This species is described based on the examination of 147 specimens. It is the most commonly collected physoderine from the island of New Guinea. There are slight differences among specimens collected from different regions, most apparently variation of size and color. These differences include overlapping variation and are therefore not indicative of multiple species. Genitalic dissections of specimens from different regions showed no differences. Based on the phylogenetic analysis above, the species is placed in the newly created *Macrophysoderes* gen. nov. Two other new species, *M. grandis* gen. et sp. nov. and *M. elongata* gen. et sp. nov., share several characters with *M. cirripilosa* gen. et sp. nov., including the setose head, the very large eyes, the shape of the parascutellar lobe and the anterior pronotal lobe being almost as wide as the posterior lobe.

*Macrophysoderes elongata* gen. et sp. nov.

[urn:lsid:zoobank.org:act:B3ACB02E-6EE2-446F-BB49-3B838E3FE625](https://zoobank.org/urn:lsid:zoobank.org:act:B3ACB02E-6EE2-446F-BB49-3B838E3FE625)

Figs 8–10, 12; Appendix

### Diagnosis

This species is recognized among species of *Macrophysoderes* gen. nov. by the large size, the short conical head with semi-erect, curved setae on the postocular lobe between the ocelli, the length of the scape reaching the apex of the clypeus, the very large eye that does not attain the ventral margin of the head in lateral view, the acutely diverging antero-lateral pronotal projections, the wide anterior pronotal lobe that is slightly narrower than the posterior pronotal width, the short and spatulate scutellar process, the extremely incrassate fore femur, the hemelytron surpassing the abdominal tip and the abdominal terminal margin being straight. This species is closest to *M. grandis* gen. et sp. nov., but is differentiated by the body size, head shape, scape length, eye shape and the shape of the anterior pronotal lobe.

### Etymology

The name *elongata* is an adjective based on the Latin participle “elongatus” meaning elongate to describe the elongated abdomen unique to this species.

### Material examined

#### Holotype

PAPUA NEW GUINEA: ♂, Morobe Province, Mt Missim, 7.1167° S, 146.9167° E, 1600 m, 21–24 Sep. 1964, M. Sedlacek leg. (UCR\_ENT 00073634) (BPBM).

#### Paratypes

PAPUA NEW GUINEA: Central Province: 1 ♂, Owen Stanley Range, Goilala, Bome, 8.45567° S, 146.7412° E, 1950 m, 24 Feb.–7 Mar. 1958, W.W. Brandt leg. (UCR\_ENT 00073630) (BPBM). – Eastern Highlands Province: 1 ♂, Goroka-Kabebe, 6.08777° S, 145.38666° E, 1800 m, 24 Jun. 1955, J.L. Gressitt leg. (UCR\_ENT 00073636) (BPBM). – Morobe Province: 1 ♂, South Garaina, 7.88694° S, 147.13277° E, 1800 m, 8–14 Jan. 1968, J. and M. Sedlacek leg. (UCR\_ENT 00073633) (BPBM); 1 ♂, Wau, Big Wau Creek, 7.33416° S, 146.71833° E, 1350 m, Sep. 1965, J. and M. Sedlacek leg. (UCR\_ENT 00073583) (BPBM).

### Other material

PAPUA NEW GUINEA: Eastern Highlands Province: 1 ♀, Okapa District County, 13 km SE of Okapa, 6.30388° S, 145.33666° E, 1650 m, 26 Aug. 1964, J. Sedlacek leg. (UCR\_ENT 00073506) (BPBM); 1 ♀, Purosa, 20–26 km SE of Okapa, 6.64944° S, 145.56972° E, 2000 m, 28 Aug. 1964, J. Sedlacek leg. (UCR\_ENT 00073505) (BPBM); 1 ♀, Kainantu, 6.28972° S, 145.85916° E, 2100 m, 8 Jan. 1965, J. and M. Sedlacek leg. (UCR\_ENT 00073637) (BPBM); 2 ♀♀, Moife, 15 km NW of Okapa, 6.43206° S, 145.49581° E, 2100 m, 11–13 Oct. 1959, T.C. Maa leg. (UCR\_ENT 00073639, UCR\_ENT 00073640) (BPBM). – Gulf Province: 1 ♂, NE Wau, Biaru, 8.4875° S, 146.34444° E, 1225 m, 8 Oct. 1978, J.L. Gressitt leg. (UCR\_ENT 00073635) (BPBM). – Morobe Province: 1 ♂, NE Wau, 7.33805° S, 146.71555° E, 1270 m, 11 Sep. 1964, M. Sedlacek leg. (UCR\_ENT 00073632) (BPBM); 1 ♂, NE Wau, 7.3333° S, 146.71667° E, 1200 m, 7 Sep. 1961, J. Sedlacek leg. (UCR\_ENT 00073631) (BPBM); 1 ♀, NE Wau Creek, Wau, 7.33166° S, 146.71805° E, 1500 m, 16–18 Sep. 1964, M. Sedlacek leg. (UCR\_ENT 00073619) (BPBM).

### Description

#### Male

**BODY LENGTH.** Medium-large size, total length 10.29 mm, SD ± 0.47 (Appendix).

**COLORATION** (Fig. 10). Brown. Head brown. Scape of antenna straw-colored to light brown, sometimes with brown apex, pedicel basally brown and apically straw-colored, basiflagellomere brown, distiflagellomere basally brown, apically straw-colored. First segment of labium basally brown, apically light brown, second segment basally and apically brown, medially straw-colored or light brown, third segment brown. Anterior lobe of pronotum dark brown with light brown markings, posterior lobe brown, scutellum basally dark brown, apically including process light brown, pleuron with mixture of straw-color to dark brown, sternum dark brown. Corium of hemelytron brown to dark brown, membrane dark brown. Femora of legs light-brown with sub-basal and apical dark brown annulations, tibiae light brown with basal, medial and apical dark brown annulations, tarsi and claws brown. Abdomen dorsally yellowish orange, ventrally brown medially with sub-lateral dark and light brown patterns, anterior half of connexivum dark brown, posterior half light brown, exposed part of pygophore brown.

**VESTITURE.** Sparsely setose. Head with widespread curved setae, ventral surface of postocular lobe with two rows of small, setigerous tubercles, with pair of long, straight setae on postocular lobe, posterior to ocelli. Anterior lobe of thorax with irregular row of tuberculated, short, curved setae on lateral margins and short, setigerous tubercles dispersed on dorsal surface, posterior lobe with short, curved, setigerous tubercles along lateral margins and sparsely distributed on dorsal surface. Corium of hemelytron with short, curved setae. Legs with two rows of spines and setigerous tubercles, tibiae with regular rows of tuberculated, stout, sharp setae. Connexival margin of abdomen with no prominent paired setae, or connexival margin with a few clubbed setae on each segment.

**HEAD.** Short conical; maxillary plate rounded apically; scape reaching apex of clypeus, or just surpassing apex of clypeus; eye hemispherical in dorsal view, about 1/5 length of head, not attaining ventral margin of head in lateral view; height of antecular lobe shorter than postocular lobe.

**THORAX.** Antero-lateral paired projections acute, diverging; surface of anterior lobe smooth, ridges almost obsolete; median pronotal depression not contiguous with transverse sulcus; paramedian carina weakly defined; posterior lobe medially weakly rugose; anterior pronotal lobe of equal length to posterior lobe, slightly narrower than posterior lobe, anterior lobe level with posterior lobe in lateral view; parascutellar lobe bell-shaped and skewed towards median; scutellar process short, apex spatulate; mesosternite with setigerous tubercles, but no protrusion.

HEMELYTRON. Surpassing tip of abdomen.

LEGS. Fore femur extremely incrassate.

ABDOMEN. Elongate ovoid, with straight terminal margin; connexival margin smooth.

GENITALIA. Anterior margin of mediosternite 8 sharply emarginated, with medial apodeme; transverse bridge of pygophore narrow, margin of anterior opening angular; cup-like sclerite apically rounded and rim ventrally sclerotized; arms of basal plate rounded; ductifer membranous; endosomal struts apically spatulate, basally divided into two plates; shape of dorsal phallosomal sclerite subacute with lateral broad, plate-like prolongations, short plates extended diagonally.

#### **Female**

Similar in size and coloration to males, with median depression of anterior pronotal lobe contiguous with transverse sulcus.

#### **Ecology**

This species was collected from high altitudes ranging between 1200 and 2100 m.

#### **Distribution**

This species is known to occur in the highlands of eastern Papua New Guinea.

#### **Remarks**

This species shares characters with *M. cirripilosa* gen. et sp. nov., including the setose, short, and conical head, the very large eyes, the shape of the parascutellar lobe and the anterior pronotal lobe being almost as wide as the posterior lobe.

*Macrophysoderes finisterre* gen. et sp. nov.

[urn:lsid:zoobank.org:act:4956E5F1-A185-4DA2-A4BE-119428AD3D42](https://doi.org/10.21203/rs.3.rs-1194284/v1)

Figs 8–10, 12; Appendix

#### **Diagnosis**

This species is recognized among species of *Macrophysoderes* gen. nov. by the overall brownish-black color, the short conical head with semi-erect, curved setae on the postocular lobe between the ocelli, the length of the scape that just surpasses the apex of the clypeus, the very large eye that attains the ventral margin of the head in lateral view, the very short antero-lateral pronotal projections that are acute and diverging, the narrow anterior pronotal lobe, the very short scutellar process, the narrow connexivum, and the straight abdominal terminal margin. It most closely resembles *M. cirripilosa* gen. et sp. nov. and *M. elongata* gen. et sp. nov. It is differentiated from the former by the overall coloration, the shape of the antero-lateral pronotal projections, the narrower anterior pronotal lobe and the shape of the abdominal apical margin. It differs from the latter by the size, the shape of the scutellar process, the relative length of the head versus the body and the only slightly swollen fore femur.

#### **Etymology**

The name *finisterre* is a noun in apposition named after the holotype locality, the Finisterre mountain range in Papua New Guinea.

#### **Material examined**

##### **Holotype**

PAPUA NEW GUINEA: ♂, Madang Province, Finisterre Mts, Damanti, 5.92027° S, 146.22555° E, 1082 m, 2–11 Oct. 1964, collector unknown (UCR\_ENT 00069280) (BMNH).



### Paratypes

PAPUA NEW GUINEA: 1 ♂, Madang Province, Finisterre Mts, Damanti, 5.92027° S, 146.22555° E, 1082 m, 2–11 Oct. 1964, collector unknown (UCR\_ENT 00069278) (BMNH); 1 ♂, same collection data as preceding (UCR\_ENT 00069276) (BMNH); 2 ♂♂, same collection data as preceding (UCR\_ENT 00069274, UCR\_ENT 00069275) (BMNH).

### Other material

PAPUA NEW GUINEA: Madang Province: 1 ♂, Finisterre Mts, Budemu Station no. 52, 5.95222° S, 146.37055° E, 1219 m, 15–24 Oct. 1964, collector unknown (UCR\_ENT 00069279) (BMNH); 2 ♀♀, same collection data as preceding (UCR\_ENT 00069288, UCR\_ENT 00069289) (BMNH); 1 ♂, Finisterre Mts, Damanti Station no. 33, 5.92027° S, 146.22555° E, 1082 m, 2–11 Oct. 1964, collector unknown (UCR\_ENT 00069277) (BMNH); 2 ♂♂, same collection data as preceding (UCR\_ENT 00069272, UCR\_ENT 00069273) (BMNH); 2 ♀♀, same collection data as preceding (UCR\_ENT 00069285, UCR\_ENT 00069286) (BMNH); 1 ♀, same collection data as preceding but Damanti Station no. 34 (UCR\_ENT 00069287) (BMNH). – Morobe Province: 2 ♂♂, Herzog Mts, Vagau C. Station 137, 6.76638° S, 146.8° E, 1219 m, 4–17 Jan. 1965, collector unknown (UCR\_ENT 00069281, UCR\_ENT 00069282) (BMNH); 2 ♀♀, same collection data as preceding (UCR\_ENT 00069283, UCR\_ENT 00069284) (BMNH).

### Redescription

#### Male

BODY LENGTH. Medium size, total length 8.85 mm, SD ± 0.38 (Appendix).

COLORATION (Fig. 10). Brownish-black. Head brownish-black. Scape of antenna straw-colored to light brown with brown apex, pedicel light brown suffused with brown, basiflagellomere brown, distiflagellomere basally brown, apically straw-colored. First segment of labium light brown, second segment basally and apically brown, medially straw-colored or light brown, third segment brown. Pronotum brownish-black, with faint brown ridges, scutellum basally brownish-black, apically including process brown, pleuron mixture of straw-color to dark brown, sternum brownish-black. Corium of hemelytron brownish black, membrane brownish black. Femora light-brown with sub-basal and apical dark brown annulations, tibiae light brown with basal, medial and apical dark brown annulations, tarsi and claws brown. Abdomen dorsally dull yellow, ventrally straw-colored or light brown with dark brown suffusion or patterns, anterior half of connexivum dark brown, posterior half light brown, sometimes indistinct, exposed part of pygophore brown.

VESTITURE. Densely setose. Head with widespread curved, setigerous tubercles, ventral surface of postocular lobe with two rows of small, setigerous tubercles, with pair of long, straight setae on postocular lobe posterior to ocelli. Anterior lobe of thorax with tuberculated, short, curved setae on lateral margins and along dorsal ridges, posterior lobe with short, curved setae on humeral angle and sparsely distributed along dorsal surface. Corium of hemelytron with short, curved setae. Legs with two rows of spines and setigerous tubercles, tibia with regular rows of tuberculated, stout, sharp setae. Connexival margin of abdomen with a few clubbed setae on each segment.

HEAD. Short conical; maxillary plate rounded apically; scape reaching apex of clypeus or surpassing apex of clypeus; eye distinctly projecting in dorsal view, about  $\frac{1}{5}$  length of head, attaining ventral margin of head in lateral view; height of anteocular lobe shorter than that of postocular lobe.

THORAX. Antero-lateral paired projections slightly acute, diverging or obsolete; surface of anterior lobe with low ridges; median pronotal depression contiguous with transverse sulcus; paramedian carina strongly defined; posterior lobe medially rugose; anterior pronotal lobe of equal length to posterior lobe,

narrower than posterior lobe, anterior lobe level with posterior lobe in lateral view; parascutellar lobe bell-shaped and skewed towards median; scutellar process very short, with subacute apex.

HEMELYTRON. Attaining tip of abdomen.

LEGS. Same as genus description.

ABDOMEN. Elongate ovoid, with straight terminal margin; connexival margin slightly undulating.

GENITALIA. Anterior margin of mediosternite 8 sharply emarginated, without medial apodeme; transverse bridge of pygophore broad, margin of anterior opening angular, apodeme present, apical margin of posterior opening smooth; cup-like sclerite apically rounded and rim ventrally sclerotized; arms of basal plate converging; ductifer with sclerotized rounded ring; endosomal struts conical, with subacute apex, basally divided into two plates; dorsal phallothecal sclerite subacute, with lateral broad, plate-like prolongations, elongated longitudinal plates close to dorsal surface.

### **Female**

Similar in size and shape to males except having a wider abdomen and connexivum.

### **Ecology**

This species was collected from an altitude between 1000 and 1200 m.

### **Distribution**

This species is known only from the Finisterre and Herzog mountain ranges in eastern Papua New Guinea.

### **Remarks**

Based on the phylogenetic analysis above, this species forms a monophyletic clade together with two other species from Papua New Guinea within *Macrophysoderes* gen. nov.

*Macrophysoderes grandis* gen. et sp. nov.

[urn:lsid:zoobank.org:act:496917F0-28BC-4B33-B2D6-BBAB58A084C8](https://doi.org/10.21203/rs.3.rs-1711170/v1)

Figs 8–12; Appendix

### **Diagnosis**

This species is recognized among other species of *Macrophysoderes* gen. nov. by its very large size, the elongate conical head, the scape surpassing the apex of the clypeus, the bulbous eye that reaches the ventral margin of the head in lateral view, the truncate antero-lateral pronotal projection, the anterior pronotal lobe being distinctly narrower than the posterior lobe, and the short and spatulate scutellar process. This species is distinctive based on these characters, especially its large size.

### **Etymology**

The name *grandis* is an adjective after the Latin “grandis”, meaning large, to describe the exceptionally large size of this species.

### **Material examined**

#### **Holotype**

PAPUA NEW GUINEA: ♂, Morobe Province, Bulolo, 7.20472° S, 146.63166° E, 1010 m, light trap, 23 Aug. 1956, E.J. Ford Jr. leg. (UCR\_ENT 00052314) (BPBM).

**Paratype**

PAPUA NEW GUINEA: 1 ♀, same collection data as holotype but 28 Aug. 1956 (UCR\_ENT 00073625) (BPBM).

**Description**

**Male**

BODY LENGTH. Very large size, total length 11.58 mm.

COLORATION (Figs 10–11). Brown with straw-colored markings. Head brown. Scape and pedicel of antenna straw-colored with brown suffusion, basiflagellomere brown, distiflagellomere straw-colored with brown base. First segment of labium light brown, second segment basally and apically brown, medially straw-colored, third segment brown. Pronotum brown, scutellum basally brown to dark brown, apically straw-colored or light brown, pleuron brown, sternum brown and straw-colored. Corium and membrane of hemelytron brown. Femora of legs straw-colored with sub-basal and apical brown annulations, tibiae straw-colored with basal, medial and apical brown annulations, tarsi and claws straw-colored. Abdomen dorsally dull yellow, ventrally light brown medially with brown and straw-colored sub-lateral patterns, anterior half of connexivum dark brown, posterior half straw-colored.

VESTITURE. Glabrous. Head with some flat, curved setae, ventral surface of postocular lobe with a few curved setae, with pair of long, straight setae on postocular lobe posterior to ocelli. Anterior lobe of thorax with irregular row of tuberculated, short, curved setae on lateral margins and glabrous dorsal surface, posterior lobe glabrous. Corium of hemelytron glabrous. Legs with two rows of spines and setigerous tubercles, tibiae with a few prominent tuberculated, stout, sharp setae. Connexival margin of abdomen glabrous.

HEAD. Elongate conical; maxillary plate rounded apically; scape surpassing apex of clypeus; eye distinctly projecting in dorsal view, about  $\frac{1}{5}$  length of head, reaching ventral margin of head in lateral view; height of anteocular lobe shorter than postocular lobe.

THORAX. Antero-lateral paired projections truncate; surface of anterior lobe smooth, ridges almost obsolete; paramedian carina strongly defined; posterior lobe medially weakly rugose; anterior pronotal lobe shorter than posterior lobe, narrower than posterior lobe, anterior lobe level with posterior lobe in lateral view; parascutellar lobe bell-shaped, skewed towards median; scutellar process short, apex spatulate; mesosternite with median, irregular, tuberculated protrusion between fore and mid coxae.

HEMELYTRON. Surpassing tip of abdomen.

LEGS. Fore femur distinctly incrassate.

ABDOMEN. Elongate ovoid, with straight terminal margin; connexival margin slightly undulating.

GENITALIA. Anterior margin of mediosternite 8 sharply emarginated, without medial apodeme; transverse bridge of pygophore narrow, margin of anterior opening rounded, apodeme present, apical margin of posterior opening smooth; cup-like sclerite apically rounded and rim ventrally sclerotized; arms of basal plate rounded; ductifer with sclerotized rounded ring; endosomal struts conical, with subacute apex, basally divided into two plates; dorsal phallosomal sclerite subacute, with lateral, broad, plate-like prolongations and short plates extended diagonally.

**Female**

Similar in size, shape and color to male, except with lighter colored scutellum.

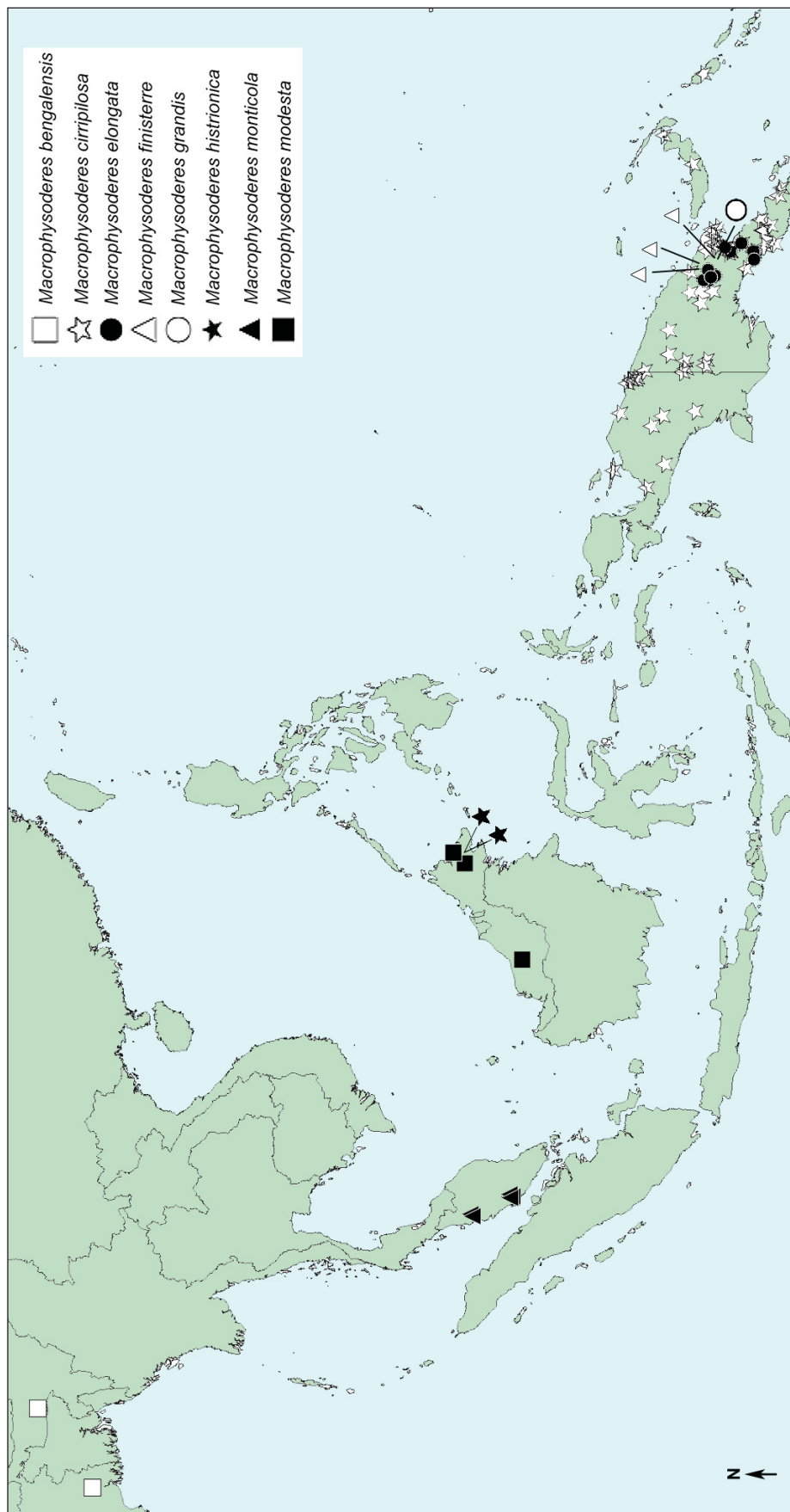


Fig. 12. Distribution map for species of *Macrophysoderes* gen. nov.

### Ecology

This species is only known from two specimens caught in a light trap set at an altitude of 1010 m.

### Distribution

This species is known only from the type locality of Bulolo, northeast Papua New Guinea.

### Remarks

This species shares characters with *M. cirripilosa* gen. et sp. nov., including the setose conical head, the very large eyes and the shape of the parascutellar lobe.

*Macrophysoderes histrionica* (Miller, 1940) comb. nov.  
Figs 10–12; Appendix

*Physoderes histrionica* Miller, 1940: 554, fig. 89.

### Diagnosis

This species is recognized among species of *Macrophysoderes* gen. nov. by the very large eye, the scape almost reaching the apex of the clypeus, the truncate antero-lateral pronotal projection, the glabrous pronotum, the long, subacute, brownish-black scutellar process and the hind femur being brown with two straw-colored annulations at the base and sub-apex. It most closely resembles *M. modesta* comb. nov., but is differentiated by the color pattern on the hind femur and the shape of the scutellar spine.

### Material examined

#### Holotype

MALAYSIA: ♂, Sabah, N Borneo, Bettotan, nr. Sandakan, 5.28222° N, 117.59305° E, 19 Aug. 1927, C. Boden Kloss and H.M. Pendlebury leg. (UCR\_ENT 00018520) (BMNH).

#### Paratypes

MALAYSIA: 1 ♀, same collection data as for holotype but 17 Aug. 1927 (UCR\_ENT 00018506) (BMNH); 1 ♀, same collection data as for holotype but 2 Aug. 1927 (UCR\_ENT 00018502) (BMNH); 1 ♀, same collection data as for holotype but 18 Aug. 1927 (UCR\_ENT 00018505) (BMNH).

#### Other material

MALAYSIA: 1 ♀, Sabah, Sandakan, 5.8333° N, 118.1167° E, 4 m, no date provided, Baker leg. (UCR\_ENT 00030983) (USNM); 1 ♂, same collection data as preceding (UCR\_ENT 00068916) (AMNH).

### Redescription

#### Male

BODY LENGTH. Medium size, total length 8.5 mm.

COLORATION (Figs 10–11). Brown. Head brown. Scape of antenna straw-colored with brown apex, pedicel brown with straw-colored apex, basiflagellomere brown, distiflagellomere basally brown, apically straw-colored. First segment of labium brown, second segment straw-colored with brown base, third segment brown. Pronotum brown or dark brown, scutellum dark brown, pleuron brown or dark brown, sternum brown or dark brown. Corium of hemelytron brown or dark brown, membrane brownish-black. Fore and mid femora of legs brown, fore and mid tibiae brown with sub-basal straw-colored annulation, tarsi and claws light brown, hind femur brown with basal and sub-apical straw-colored annulations, hind

tibia brown with sub-basal straw-colored annulation, tarsus and claw light brown. Abdomen dorsally yellowish-orange, ventrally straw-colored with sub-lateral dark brown suffusion, anterior two-thirds of connexivum dark brown, posterior third straw-colored.

**VESTITURE.** Glabrous. Head with some flat, curved setae, ventral surface of postocular lobe with sparse, setigerous tubercles, with pair of long, straight setae on postocular lobe posterior to ocelli. Anterior lobe of thorax with irregular row of tuberculated, short, curved setae on lateral margins and fine, adpressed setae on dorsal surface, posterior lobe with short, curved setae on humeral angle and sparsely distributed along dorsal surface. Corium of hemelytron glabrous. Legs with two rows of spines and setigerous tubercles, tibiae with regular rows of tuberculated, stout, sharp setae. Connexival margin of abdomen with a few clubbed setae on each segment.

**HEAD.** Elongate conical; maxillary plate rounded apically; scape not reaching apex of clypeus; eye distinctly projecting in dorsal view, less than  $\frac{1}{5}$  length of head, not attaining ventral margin of head in lateral view; height of antecular lobe level with postocular lobe.

**THORAX.** Antero-lateral paired projections truncate; surface of anterior lobe smooth, ridges almost obsolete; median pronotal depression contiguous with transverse sulcus; paramedian carina weakly defined; posterior lobe medially rugose; anterior pronotal lobe shorter than posterior lobe, narrower than posterior lobe, anterior lobe lower than posterior lobe in lateral view; parascutellar lobe rounded, skewed towards median; scutellar process long, with subacute apex; mesosternite with median, irregular, tuberculated protrusion between fore and mid coxae.

**HEMELYTRON.** Surpassing tip of abdomen.

**LEGS.** Same as genus description.

**ABDOMEN.** Elongate ovoid, with rounded terminal margin; connexival margin undulating.

**GENITALIA.** Not examined.

### **Female**

Similar in size, shape and color to male except with wider abdomen.

### **Ecology**

Unknown.

### **Distribution**

This species is only known from two localities in north Borneo, Sabah.

### **Remarks**

*Macrophysoderes histrionica* comb. nov. shares the dark body color, head shape, general vestiture, and the shape of the parascutellar lobe with *M. monticola* comb. nov. and is thus transferred to the new genus to reflect the hypothesized close relationship. Examination of the type series of *M. histrionica* comb. nov. showed that 3 of the paratypes match the holotype of *M. modesta* comb. nov. more closely than *M. histrionica* comb. nov. and these specimens are here treated under *M. modesta* comb. nov.

### ***Macrophysoderes modesta* (Miller, 1940) comb. nov.**

Figs 7–12; Appendix

*Physoderes modesta* Miller, 1940: 543, fig. 88.

*Physoderes sibauana* Miller, 1940: 553, fig. 88. New synonymy.

*Physoderes trusana* Miller, 1940: 553, fig. 89. New synonymy.

### Diagnosis

This species is recognized among species of *Macrophysoderes* gen. nov. by the elongate, conical head, the rounded maxillary plate, the antecular lobe being almost level with the postocular lobe, the truncate antero-lateral rounded pronotal projections, the rounded parascutellar lobes that are skewed towards the median, the dark brown hind femur with a single basal straw-colored annulation, the apex of the scutellar process being straw-colored, the undulating connexivum, the cup-like sclerite with distinct medial process, and the flap-like prolongations of the phallosoma being plate-like and with a uniform basal margin. It is similar to *M. monticola* comb. nov. and *M. histrionica* comb. nov., but can be differentiated by the uniform color of the legs and connexiva, the margin of the pygophore posterior opening having a medial process and cup-like sclerite, and the shape of the plate-like prolongations of the phallosoma.

### Material examined

#### Holotype

MALAYSIA: ♂, Sarawak, N Borneo, 2.56055° N, 113.00555° E, 112 m, 1909, C.J. Brooks leg. (UCR\_ENT 00018533) (BMNH).

#### Other material

MALAYSIA: Sabah: 1 ♀, N Borneo, Bettotan, nr. Sandakan, 5.28222° N, 117.59305° E, 25 Jul. 1927, C. Boden Kloss and H.M. Pendlebury leg. (UCR\_ENT 00018507) (BMNH); 1 ♀, same collection data as preceding but 26 Jul. 1927 (UCR\_ENT 00018503) (BMNH); 1 ♀, same collection data as preceding but 19 Aug. 1927 (UCR\_ENT 00018504) (BMNH); 1 ♀, N Borneo, Sandakan, 5.8333° N, 118.1167° E, 4 m, no date provided, Baker leg. (UCR\_ENT 00030982) (USNM). – Sarawak: 1 ♀, N Borneo, SAR, 2.55722° N, 113.00111° E, 113 m, no date provided, Saunders leg. (UCR\_ENT 00069384) (BMNH); 1 ♂, same collection data as holotype (UCR\_ENT 00069386) (BMNH).

### Redescription

#### Male

BODY LENGTH. Medium, total length 9.45 mm, SD ± 0.05 (Appendix).

COLORATION (Figs 7, 10–11). Dark brown. Head dark brown. Scape of antenna brown, straw brown basally, pedicel brown, basi- and distiflagellomere brown. Labium brown. Pronotum dark brown, scutellum dark brown, pleuron dark brown, sternum dark brown. Corium of hemelytron dark brown, membrane black to dark brown. Fore and mid legs dark brown, hind femur dark brown, hind tibia dark brown with straw-colored apex, hind tarsus and claw straw-colored. Abdomen dorsally orange-brown, ventrally light brown to brown with reddish-brown or dark brown lateral suffusion, connexivum dark brown with straw-colored posterior margin.

VESTITURE. Glabrous. Head with some flat, curved setae, ventral surface of postocular lobe with sparse, setigerous tubercles, without pair of long, straight setae on postocular lobe posterior to ocelli. Anterior lobe of thorax with irregular row of tuberculated, short, curved setae on lateral margins and fine, adpressed setae on dorsal surface, posterior lobe with only short, sparse setae. Corium of hemelytron with short, sparse, adpressed setae. Legs with two rows of spines and setigerous tubercles, tibiae with regular rows of tuberculated, stout, sharp setae. Posterior margin of connexivum on abdomen with short, fine setae.

HEAD. Elongate conical; maxillary plate rounded apically; scape not reaching apex of clypeus; eye distinctly projecting in dorsal view, less than 1/5 length of head, not attaining ventral margin of head in lateral view; height of antecular lobe level with postocular lobe.

THORAX. Antero-lateral paired projections truncate; surface of anterior lobe smooth, ridges almost obsolete; median pronotal depression contiguous with transverse sulcus; paramedian carina weakly defined; posterior lobe medially rugose; anterior pronotal lobe shorter than posterior lobe, narrower than posterior lobe, anterior lobe lower than posterior lobe in lateral view; parascutellar lobe rounded, skewed towards median; scutellar process long, with subacute apex; mesosternite with median irregular tuberculated protrusion between fore and mid coxae.

HEMELYTRON. Attaining tip of abdomen.

LEGS. Same as genus description.

ABDOMEN. Elongate ovoid, with rounded terminal margin; connexival margin undulating.

GENITALIA. Anterior margin of mediosternite 8 undulating, with medial apodeme; transverse bridge of pygophore broad, margin of anterior opening angular, apodeme present, apical margin of posterior opening with small medial process; cup-like sclerite with medial process; arms of basal plate rounded; ductifer membranous; endosomal struts conical, with subacute apex, basally divided into two arms; shape of dorsal phallosomal sclerite subacute, with lateral broad, plate-like prolongations.

#### **Female**

Similar to male.

#### **Ecology**

Nothing is known about the biology of this species.

#### **Distribution**

This species is collected from both Sabah and Sarawak, Malaysia.

#### **Remarks**

This species is transferred to *Macrophysoderes* gen. nov. because of the similarities it shares with *M. monticola* comb. nov. and *M. histrionica* comb. nov. Examination of the type specimens of *P. sibauana* and *P. trusana* shows no morphological differences between them and they are hereby synonymized under *M. modesta* comb. nov.

*Macrophysoderes monticola* (Miller, 1940) comb. nov.

Figs 7–12; Appendix

*Physoderes monticola* Miller, 1940: 545, fig. 89.

*Physoderes dimidiata* Miller, 1940: 556, fig. 92. New synonymy.

*Physoderes luiana* Miller, 1940: 552, fig. 90. New synonymy.

#### **Diagnosis**

This species is recognized among species of *Macrophysoderes* gen. nov. by the elongate conical head, the rounded maxillary plate, the anteocular lobe being almost level with the postocular lobe, the truncate antero-lateral pronotal projections, the rounded parascutellar lobes being skewed towards the median, the dark brown hind femur with a single basal straw-colored annulation, the apex of the scutellar process being straw-colored, the connexivum undulating, and the plate-like and angular flap-like prolongations of the phallosoma. It is similar to *M. modesta* comb. nov. and *M. histrionica* comb. nov., but can be differentiated by the color of the legs, scutellar spine and connexiva, the shape of the margin of the



posterior opening of the pygophore and cup-like sclerite, and the shape of the plate-like prolongations of the phallosoma.

### Material examined

#### Holotype

MALAYSIA: ♂, Perak, Taiping Co., Larut Hills, 5.00° N, 100.88333° E, 1372 m, 21 Feb. 1932, H.M. Pendlebury leg. (UCR\_ENT 00018534) (BMNH).

#### Paratypes

MALAYSIA: 1 ♀, Perak, Batang Padang Co., Jor Camp, 4.89972° N, 100.79055° E, 549 m, 31 May 1923, H.M. Pendlebury leg. (UCR\_ENT 00069389) (BMNH); 1 ♀, Perak, Batang Padang Co., Jor Camp, 4.89972° N, 100.79055° E, 610 m, 25 Aug. 1922, E. Seimund leg. (UCR\_ENT 00069387) (BMNH).

#### Other material

MALAYSIA: 1 ♀, Perak, Batang Padang Co., Jor Camp, 4.89972° N, 100.79055° E, 610 m, 30 Aug. 1922, E. Seimund leg. (UCR\_ENT 00069388) (BMNH); 1 ♂, Selangor, Kuala Lumpur, 17<sup>th</sup> mile Kanching, 3.13888° N, 101.68666° E, 22 Oct. 1922, H.M. Pendlebury leg., holotype of *P. dimidiata* (junior synonym) (UCR\_ENT 00018521) (BMNH); 1 ♀, same collection data as preceding, paratype of *P. dimidiata* (junior synonym) (UCR\_ENT 00018509) (BMNH); 1 ♀, Sungei Lui, Ulu Langat, 3.03805° N, 101.70583° E, 86 m, 13 Aug. 1933, N.C.E. Miller leg., holotype of *P. luiana* (junior synonym) (UCR\_ENT 00018514) (BMNH); 1 ♀, Kuala Sleh, 3.02472° N, 101.71638° E, 17 May 1936, H.M. Pendlebury leg., paratype of *P. dimidiata* (junior synonym) (UCR\_ENT 00018508) (BMNH); 1 ♀, Dusun Tua, 3.14555° N, 101.83888° E, 12 Jan. 1930, H.M. Pendlebury leg. (UCR\_ENT 00069390) (BMNH); 1 ♂, Gombak Valley, 3.13027° N, 101.65777° E, 12 Oct. 1921, H.M. Pendlebury leg. (UCR\_ENT 00069391) (BMNH); 1 ♀, Kepong, in forest, 3.2325° N, 101.6275° E, Aug. 1949, Army Scrub Typhus Unit leg. (UCR\_ENT 00025941) (USNM).

### Redescription

#### Male

BODY LENGTH. Large, total length 10.34 mm.

COLORATION (Figs 7, 10–11). Dark brown. Head dark brown. Scape of antenna brown, straw brown basally, pedicel brown, basi- and distiflagellomere brown. Labium brown. Pronotum dark brown, scutellum dark brown, pleuron dark brown, sternum dark brown. Corium of hemelytron dark brown, membrane black to dark brown. Fore and mid legs dark brown, hind femur dark brown, hind tibia dark brown with straw-colored apex, hind tarsus and claw straw-colored. Abdomen dorsally orange-brown, ventrally light brown with reddish-brown or dark brown suffusion, anterior two-thirds of connexivum dark brown, posterior third straw-colored.

VESTITURE. Glabrous. Head with some flat, curved setae, ventral surface of postocular lobe with sparse, setigerous tubercles, without pair of long, straight setae on postocular lobe posterior to ocelli. Anterior lobe of thorax with irregular row of tuberculated, short, curved setae on lateral margins and fine, adpressed setae on dorsal surface, posterior lobe with short, curved setae on humeral angle and sparsely distributed along dorsal surface. Corium of hemelytron with short, sparse, adpressed setae. Legs with two rows of spines and setigerous tubercles, tibia with regular rows of tuberculated, stout, sharp setae. Connexival margin of abdomen with a few clubbed setae on each segment.

HEAD. Elongate conical; maxillary plate rounded apically; scape not reaching apex of clypeus; eye distinctly projecting in dorsal view, less than 1/5 length of head, not reaching ventral margin of head in lateral view; height of anteocular lobe level with postocular lobe.

THORAX. Antero-lateral paired projections truncate; surface of anterior lobe smooth, ridges almost obsolete; median pronotal depression contiguous with transverse sulcus; paramedian carina weakly defined; posterior lobe medially rugose; anterior pronotal lobe shorter than posterior lobe, narrower than posterior lobe, anterior lobe lower than posterior lobe in lateral view; parascutellar lobe rounded, skewed towards median; scutellar process long, with subacute apex; mesosternite with median irregular tuberculated protrusion between fore and mid coxae.

HEMELYTRON. Attaining tip of abdomen.

LEGS. Same as genus description.

ABDOMEN. Elongate ovoid, with rounded terminal margin; connexival margin undulating.

GENITALIA. Anterior margin of mediosternite 8 undulating, without medial apodeme; transverse bridge of pygophore broad, margin of anterior opening angular, apodeme present, apical margin of posterior opening smooth; cup-like sclerite apically rounded and rim ventrally sclerotized; arms of basal plate parallel to each other; ductifer membranous; endosomal struts conical, with subacute apex, basally divided into two arms; dorsal phallosomal sclerite subacute, with lateral broad, plate-like prolongations, broad plates angularly oriented towards basal plate.

#### **Female**

Similar to male in size, shape and color.

#### **Ecology**

Nothing is known about the biology of this species.

#### **Distribution**

This species is distributed along the western area of peninsular Malaysia. Specimens from the state of Perak are larger than those from Selangor.

#### **Remarks**

Based on the phylogenetic analysis, this species forms a monophyletic clade with *M. bengalensis* comb. nov. as part of the *Macrophysoderes* gen. nov. clade. Other species closely resembling *M. monticola* comb. nov. are also transferred to *Macrophysoderes* gen. nov. based on the hypothesis that they are most closely related, namely *M. modesta* comb. nov. and *M. histrionica* comb. nov. Common characteristics shared among these three species include having an elongate conical head, truncate antero-lateral pronotal projections and a hemelytron with a dark brown membrane. Examination of the type specimens of *P. dimidiata* and *P. luiana* show no morphological differences except for size and are hereby synonymized with *M. monticola* comb. nov. This species and *M. modesta* comb. nov. are highly similar and difficult to distinguish other than based on the morphology of the male genitalia and on distribution.

*Nanophysoderes* gen. nov.

[urn:lsid:zoobank.org:act:B90EE5D9-EDDB-419D-BFC1-141C9E42D4B4](https://doi.org/10.3897/ejt.341.141C9E42D4B4)

Figs 10–11, 13; Appendix

#### **Diagnosis**

This genus is recognized among other genera of Physoderinae by the small size, the pair of prominent setigerous tubercles on the ventral surface of the postocular lobe, the lateral margins of the anterior pronotal lobe being almost straight and not curved, the semicircular shape of the scutellum, the scutellum having distinct paired lateral tubercles, the mesosternum having three longitudinal rows of setae and the

armature of the fore femur consisting of two dense rows of setigerous tubercles. The genus is distinct from any other physoderine genus by the straight lateral margins of the anterior pronotal lobe, small size, uniform coloration, sparse setation over the entire body, paired projections on the scutellum, and the three longitudinal rows of setae on the mesosternum.

### **Etymology**

The name combines *Physoderes* after the type genus of Physoderinae and the Latin noun “nanus”, meaning dwarf, to indicate small body size. The gender is feminine.

### **Type species**

*Physoderes dentiscutum* Bergroth, 1906.

### **Description**

#### **Female**

**BODY LENGTH.** Small, total length 7.66 mm.

**COLORATION** (Figs 10–11; *Nanophysoderes dentiscutum* comb. nov.). Brown to straw brown. Head brown, neck straw brown. Antenna straw brown with brown suffusion. Labium straw brown. Pronotum brown, scutellum brown, pleuron brown, sternum brown. Corium of hemelytron brown, membrane brown. Legs straw brown. Abdomen yellow dorsally, straw brown ventrally with lateral brown suffusion, anterior half of connexivum brown, posterior half straw-colored, margin indistinct.

**VESTITURE.** Sparsely setose. Head with some flat, curved setae or with widespread short, fine, adpressed setae, ventral surface of postocular lobe with only a pair of prominent setigerous tubercles, with pair of long, straight setae wider apart on postocular lobe posterior to ocelli. Anterior lobe of thorax with irregular row of tuberculated, short, curved setae on lateral margins and fine, adpressed setae on dorsal surface, posterior lobe with only short, sparse setae. Corium of hemelytron with short, sparse, adpressed setae. Legs with two rows of setigerous tubercles, tibiae with regular rows of tuberculated, stout, sharp setae. Connexival margin of abdomen glabrous.

**HEAD.** Short conical; maxillary plate apically truncate; scape not reaching apex of clypeus; eye hemispherical in dorsal view, about  $\frac{1}{5}$  length of head, not attaining ventral margin of head in lateral view; height of antocular lobe shorter than postocular lobe.

**THORAX.** Antero-lateral paired projections acute, diverging; surface of anterior lobe with low ridges; median pronotal depression contiguous with transverse sulcus; paramedian carina weakly defined; posterior lobe medially weakly rugose; anterior pronotal lobe shorter than posterior lobe, narrower than posterior lobe, anterior lobe lower than posterior lobe in lateral view; paramedian lobe bell-shaped and skewed towards median; scutellum semicircular, scutellar process long, with subacute apex; mesosternite without median irregular tuberculated protrusion between fore and mid coxae.

**HEMELYTRON.** Attaining tip of abdomen.

**LEGS.** Fore femur distinctly incrassate.

**ABDOMEN.** Elongate ovoid, with rounded terminal margin; connexival margin smooth, posterior margin not elevated.

#### **Male**

Unknown.

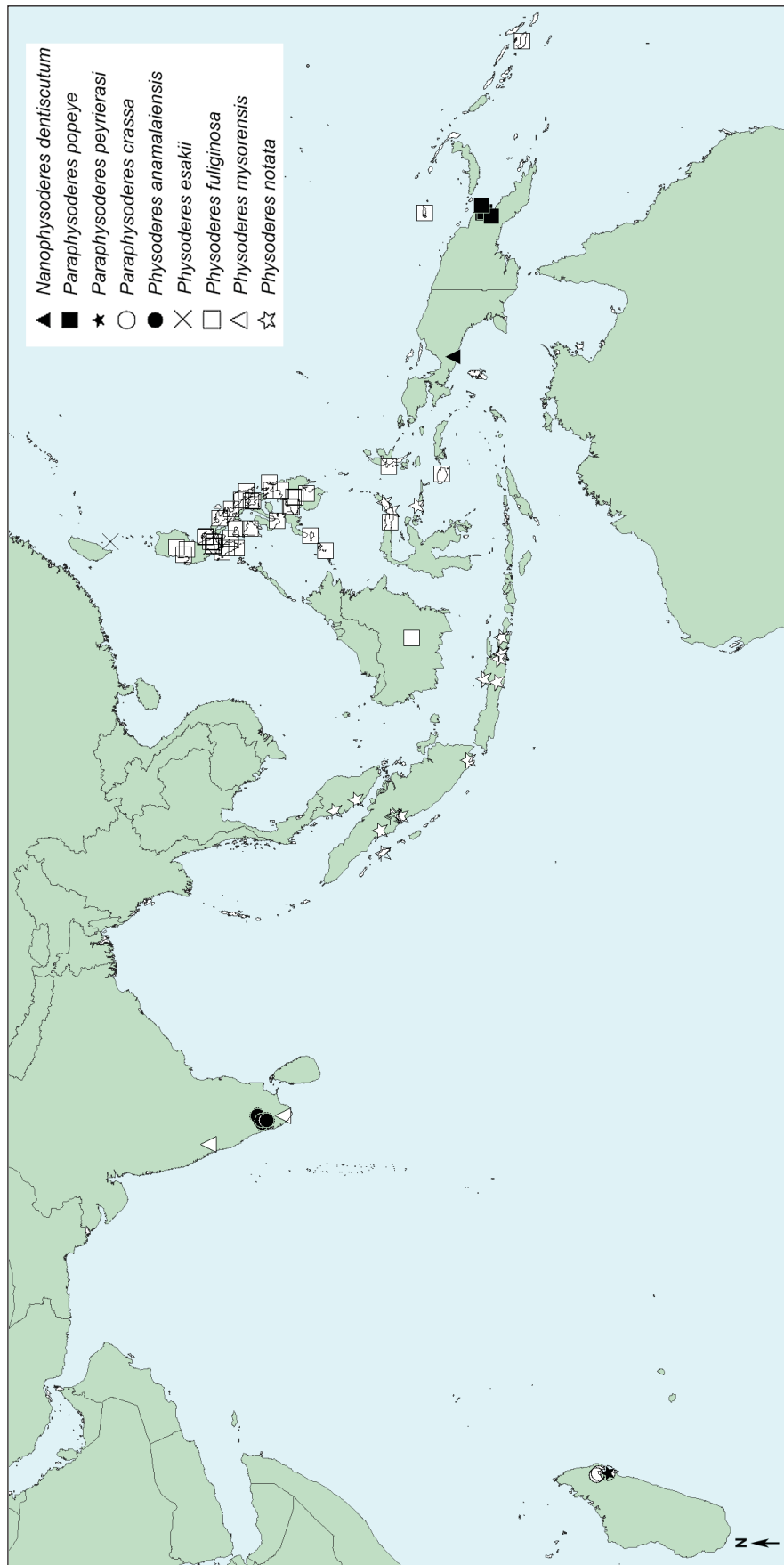


Fig. 13. Distribution map for species of *Nanophysoderes* gen. nov., *Paraphysoderes* Villiers, 1962 and *Physoderes* Westwood, 1845 (in part).

**Ecology**

Unknown.

**Distribution**

Known only from the locality of the holotype of the type species, which was labelled as “New Guinea”.

**Remarks**

Based on the phylogeny, *N. dentiscutum* comb. nov. is sister to all other physoderines except for the Neotropical and Afrotropical species. The isolated placement of *N. dentiscutum* comb. nov. in the phylogeny and its distinct morphology warrant the decision to erect a new genus to accommodate this species. This genus is described based on a female specimen as no males are known.

*Nanophysoderes dentiscutum* (Bergroth, 1906) comb. nov.  
Figs 10–11, 13; Appendix

*Physoderes dentiscutum* Bergroth, 1906: 16.

**Diagnosis**

As in generic description.

**Material examined**

**Holotype**

INDONESIA: ♀, Irian Jaya, W New Guinea, 4.24891° S, 135.79065° E, 285 m, 1869, Higgins leg. (UCR\_ENT 00037370) (ISNB).

**Redescription**

As in generic description.

*Paraphysoderes* Villiers, 1962  
Figs 3, 8–9, 13–14; Appendix

**Diagnosis**

This genus is recognized among other genera of Physoderinae by its small size (6.30–7.09 mm), brown to dark brown coloration, the scape surpassing the apex of the clypeus and being thicker than the remaining antennal segments, the obsolete antero-lateral pronotal projection, the rounded lateral margins of the anterior pronotal lobe, the anterior pronotal lobe being level with the posterior lobe, the acute scutellar spine, and the fore tibia bearing a few prominent processes with sharp, stout, setae. It is most similar to *Physoderoides* Miller (1955a), but is distinguished by the body size, head shape, the maxillary plate not being raised and the lack of antero-lateral pronotal projections.

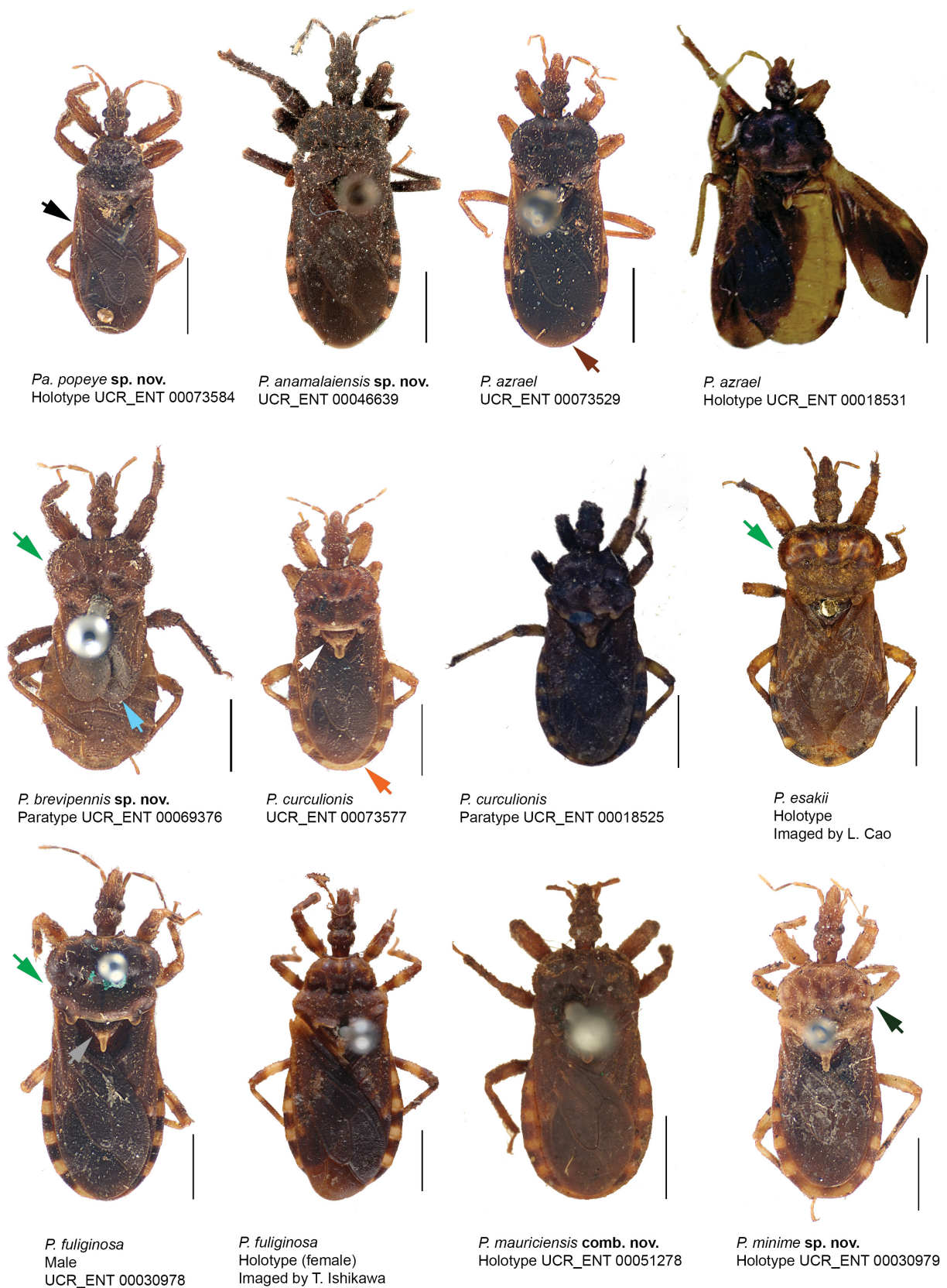
**Type species**

*Paraphysoderes crassa* Villiers, 1962, by original designation.

**Redescription**

**Male**

BODY LENGTH. Small, total length 6.30–7.09 mm.



**Fig. 14.** Dorsal habitus images for species of *Paraphysoderes* Villiers, 1962 and *Physoderes* Westwood, 1845 (partial). For an explanation of the colored arrows, see keys on page 63 and 66. Scale bars = 2 mm.

**COLORATION** (Fig. 13; *Paraphysoderes popeye* sp. nov.). Yellow-brown to dark brown. Head, pronotum, legs, corium of similar coloration, legs with uniform color, no annulation pattern, connexivum sometimes uniformly colored.

**VESTITURE.** Sparsely setose with tuberculated, curved, short, setae. Surface of anterior pronotal lobe smooth or tuberculated.

**HEAD.** Short conical; maxillary plate rounded apically; scape surpassing apex of clypeus; eye relatively large, hemispherical or projecting in dorsal view, not reaching ventral margin of head in lateral view; ocelli present; height of anteocular lobe level or shorter than postocular lobe.

**THORAX.** Antero-lateral paired projections obsolete; ridges of anterior pronotal lobe almost obsolete; median pronotal depression contiguous with transverse sulcus; paramedian carina weakly defined; length of anterior pronotal lobe variable, narrower than posterior lobe in both sexes, level with posterior lobe in lateral view; parascutellar lobe semicircular or quadrant-shaped, skewed towards median; scutellum triangular, scutellar process long, apex variable; mesosternite with median, irregular, tuberculated protrusion between fore and mid coxae.

**HEMELYTRON.** Macropterous, not attaining tip of abdomen.

**LEGS.** Fore femur distinctly incrassate, fore tibia bearing a few prominent processes with sharp, stout setae; tarsi three-segmented.

**ABDOMEN.** Ovoid or elongate ovoid, with straight or rounded terminal margin; connexival margin smooth, posterior margin not elevated.

**GENITALIA.** Only examined for *Pa. popeye* sp. nov. (see species description below).

### **Female**

Similar to males, but larger and with wider abdomen.

### **Ecology**

No information is available for the Madagascan species, while *Pa. popeye* sp. nov. has been recorded on *Pandanus* (Pandanaceae).

### **Distribution**

This genus has a disjunct distribution, with two species occurring in northeastern Madagascar and one species on the eastern edge of Papua New Guinea, on the Huon Peninsula.

### **Remarks**

Based on the phylogenetic analysis, the new species *Paraphysoderes popeye* sp. nov. forms a monophyletic clade with *Pa. peyrierasi* and *Pa. crassa*. It shares the synapomorphies of the small body size and the fore tibia bearing a few prominent setigerous tubercles. Closer examination also revealed similarities in the shape of the head and pronotum, a similar acute scutellar process and the hemelytron not reaching the tip of the abdomen. This evidence led to classifying this new species as *Paraphysoderes*, even though this significantly expands the distribution range of this genus, which was previously restricted to Madagascar.

### Key to species of *Paraphysoderes*

1. Fore femur longer than mid femur, surpassing apex of clypeus, scutellar process acute and tapered, Cu and M veins not parallel, converging basally (Fig. 14, black arrow), Pacific distribution .....*Pa. popeye* sp. nov.
  - Fore femur as long as or shorter than mid femur, not surpassing apex of clypeus, scutellar process subacute, Cu and M veins parallel, not converging (Fig. 3, grey arrow), restricted to Madagascar .....2
2. Body reddish-brown, scutellum apex and scutellar process straw-colored, connexivum uniformly reddish-brown .....*Pa. peyrierasi* Villiers, 1968
  - Body brown, scutellum and scutellar process brown, anterior half of connexivum dark brown, posterior half light brown .....*Pa. crassa* Villiers, 1962

### *Paraphysoderes popeye* sp. nov.

[urn:lsid:zoobank.org:act:533BD1D8-0A74-4197-B7E9-3CD231BC2F61](https://doi.org/10.33321/1D8-0A74-4197-B7E9-3CD231BC2F61)

Figs 7–8, 12–13; Appendix

### Diagnosis

This species is recognized among species of *Paraphysoderes* by its small size, brown to dark brown coloration, the elongate conical head, the scape surpassing the apex of the clypeus, the obsolete antero-lateral pronotal projection, the anterior pronotal lobe being level with the posterior lobe, the scutellar spine being acute and tapered, the parascutellar spine being semicircular, the cubital (Cu) vein being angular at the junction of the connecting vein with the first anal vein (1A), the distinctly incrassate fore femur, which is longer than the mid femur, the fore tibia bearing a few prominent processes with sharp, stout, setae, the mid femur with prominent processes with peg-like setae on the anterior surface, and the abdominal spiracles turreted and being located directly ventral to the connexival margin.

### Etymology

The name *popeye* is a noun in apposition to describe the uniquely enlarged fore-arms of this species that is similar to the fictional cartoon character Popeye the Sailor Man.

### Material examined

#### Holotype

PAPUA NEW GUINEA: ♂, Morobe Province, Didymann's Creek, Lae, 6.72444° S, 146.99083° E, 15 m, 30 Apr. 1963, J. Sedlacek leg. (UCR\_ENT 00073584) (BPBM).

#### Paratypes

PAPUA NEW GUINEA: Morobe Province: 1 ♀, Huon Peninsula Co., Pindiu, 6.44388° S, 147.515° E, 450 m, 19 Apr. 1963, J. Sedlacek leg. (UCR\_ENT 00073624) (BPBM); 1 ♀, Bulolo, 7.20472° S, 146.63166° E, 130 m, 30 Aug. 1956, E.J. Ford Jr. leg. (UCR\_ENT 00073621) (BPBM); 1 ♀, same collection data as for holotype (UCR\_ENT 00073623) (BPBM); 1 ♀, Yalu, Lae, 6.5875° S, 146.87666° E, Dec. 1957, R.W. Paine leg. (UCR\_ENT 00069393) (BMNH).

### Description

#### Male

BODY LENGTH. Small, total length 7.09 mm.

COLORATION (Fig. 14). Brown to dark brown. Head brown or dark brown. Scape and pedicel of antenna light brown with brown suffusion, disti- and basiflagellomeres straw-colored. First segment of labium



brown, second segment basally brown, medially straw-colored, apically brown, third segment brown. Thorax dark brown. Corium of hemelytron dark brown, membrane dark brown. Fore and mid femora and tibiae of legs light brown to brown, tarsi and claws light brown, hind femur dark brown with medial light brown annulation, hind tibia light brown to dark brown, hind tarsus and claw light brown. Abdomen dorsally reddish-orange, ventrally light brown with brown suffusion, connexivum brown with a lighter margin, exposed part of pygophore dark brown.

**VESTITURE.** Sparsely setose. Head with widespread curved setae, ventral surface of postocular lobe with sparse, setigerous tubercles, without pair of long, straight setae on postocular lobe posterior to ocelli. Anterior lobe of thorax with irregular row of tuberculated, short, curved setae on lateral margins and short, setigerous tubercles dispersed on dorsal surface, posterior lobe with short, curved, setigerous tubercles on humeral angle and glabrous on dorsal surface. Corium of hemelytron with short, sparse, adpressed setae. Legs with two rows of spines and setigerous tubercles, tibia with a few prominent tuberculated, stout, sharp setae. Connexival margin of abdomen sparsely setose, without prominent setae.

**HEAD.** Elongate conical; maxillary plate rounded apically; scape surpassing apex of clypeus; eye hemispherical in dorsal view, about  $\frac{1}{5}$  length of head, not attaining ventral margin of head in lateral view; height of anteocular lobe level with postocular lobe.

**THORAX.** Antero-lateral paired projections obsolete; surface of anterior lobe smooth, ridges almost obsolete; median pronotal depression contiguous with transverse sulcus; paramedian carina weakly defined; posterior lobe smooth, dull; anterior pronotal lobe shorter than posterior lobe, narrower than posterior lobe, anterior lobe level with posterior lobe in lateral view, semicircular; scutellum triangular, scutellar process long, apex acute and tapered; mesosternite with median, irregular, tuberculated protrusion between fore and mid coxae.

**HEMELYTRON.** Not reaching tip of abdomen.

**LEGS.** Fore femur distinctly incrassate.

**ABDOMEN.** Elongate ovoid, with straight terminal margin; connexival margin smooth, not undulating, posterior margin not elevated.

**GENITALIA.** Anterior margin of mediosternite 8 sharply emarginate, without medial apodeme; transverse bridge of pygophore broad, margin of anterior opening rounded, apodeme present, apical margin of posterior opening smooth; cup-like sclerite apically rounded, with sclerotized paired latero-ventral slight protuberances; arms of basal plate parallel to each other; ductifer with sclerotized rounded ring; endosomal struts tube-like, with medial sclerotization and with a T-shaped apex; shape of dorsal phallosomal sclerite subacute with narrow, lateral, band-like prolongations, sclerotized band extended horizontally towards ventral surface of phallosoma.

### **Female**

Similar in morphology to males, but much larger (7.89 mm average total length) with wider abdomen (2.56 mm for males, 3.32 mm average width for females). Because one such female was collected in the same collecting event as the holotype male, these females are here treated as the same species.

### **Ecology**

This species has been recorded on *Pandanus* (Pandanaeae).

### Distribution

This species is distributed in the eastern edge of Papua New Guinea around the Huon Peninsula.

### Remarks

A damaged female specimen from Fiji (not described here), that is most likely not the same species as *Pa. popeye* sp. nov. but likely belongs to *Paraphysoderes*, suggests an even more extended and disjunct distribution of this genus and potential undiscovered diversity in the Pacific region. *Note*: The current color of the holotype has been altered and is different from the image provided here due to treatment with KOH solution for dissection of the male genitalia.

*Physoderes* Westwood, 1845

Figs 8–9, 13–20; Appendix

### Diagnosis

This genus is recognized among other genera of Physoderinae by the scape reaching the apex of the clypeus, the parascutellar lobe being rounded and skewed towards the median, the males having an enlarged anterior pronotal lobe, wider than or equal to the width of the posterior lobe (except in *P. nigripennis* sp. nov., *P. ractepilosa* sp. nov. and *P. muluensis* sp. nov.), the median pronotal depression not being contiguous with the transverse sulcus (males) and by males having a membranous ductifer. This genus is most similar to *Epiroderoides* Villiers, 1962, but can be differentiated from it based on the anterior pronotal shape in males and the shape of the parascutellar lobes.

### Type species

*Physoderes notata* Westwood, 1845, by monotypy.

### Redescription

#### Male

**BODY LENGTH.** Size variable, total length 6.08–11.03 mm (Appendix).

**COLORATION** (Figs 14–18). Variable, from straw-colored to dark brown. Head, anterior pronotal ridges, posterior pronotal lobe, legs and corium of similar lighter coloration, anterior pronotal lobe, scutellum and claval region with darker coloration.

**VESTITURE.** Sparsely to densely setose with curved, fine or erect setae, with pair of long, straight setae on posterior margin of postocular lobe (except in *P. nigripennis* sp. nov. and *P. nigroalbus*).

**HEAD.** Elongate or short, conical; maxillary plate most often rounded apically; scape never distinctly surpassing apex of clypeus; eye hemispherical in dorsal view except in *P. nigripennis* sp. nov. and *P. tricolor* sp. nov., less than  $\frac{1}{5}$  length of head and never reaching ventral margin of head in lateral view; ocelli present; height of anteocular lobe shorter than postocular lobe except in *P. anamalaiensis* sp. nov. and *P. mysorensis* sp. nov.

**THORAX.** Shape of antero-lateral paired pronotal projection variable; surface of anterior pronotal lobe most often with low ridges; median pronotal depression not contiguous with transverse sulcus except in species without enlarged anterior pronotum; paramedian carina variable; posterior lobe medially rugose; length of anterior pronotal lobe variable, wider and higher than or equal to posterior lobe except in *P. nigripennis* sp. nov., *P. ractepilosa* sp. nov. and *P. muluensis* sp. nov.; parascutellar lobe rounded and sometimes skewed towards median, except in *P. brevipennis* sp. nov.; scutellum rounded triangular

except in *P. azrael* and *P. curculionis*, length of scutellar process and shape of apex variable; mesosternite with median irregular tuberculated protrusion between fore and mid coxae.

HEMELYTRON. Macropterous, never surpassing tip of abdomen.

LEGS. Fore femur distinctly incrassate, tarsi three-segmented.

ABDOMEN. Elongate ovoid except in *P. brevipennis* sp. nov. and *P. curculionis*, with rounded terminal margin except in *P. ractepilosa* sp. nov.; shape of connexival margin variable, posterior margin only slightly elevated in *P. nigripennis* sp. nov.

GENITALIA. Variable (see species descriptions for details).

### Female

Females with anterior pronotal lobe narrower and lower than posterior lobe, with median pronotal depression contiguous with transverse depression.

### Ecology

Species from this genus are found in a variety of living and dead plant materials and in the undergrowth. Specimens have been collected from pitfall traps and carrion traps and have been found at up to 1200 m elevation.

### Distribution

This genus is the most widespread of the subfamily, and species distributions cover the entire known range of Physoderinae in the Old World except in the Afrotropics. Species can be found in Madagascar, the Indian subcontinent, peninsular Malaysia, Sumatra, Java, Borneo, the Philippine archipelago, Sulawesi, Papua New Guinea, the Solomon Islands and the Fiji Islands.

### Remarks

*Physoderes notata* is the type species of *Physoderes* by monotypy and the clade that includes *P. notata* and *P. nigripennis* sp. nov. derived from the phylogenetic analysis above is recognized as the revised *Physoderes*.

### Key to species of *Physoderes*

1. Scutellum semicircular (Fig. 14, white arrow), transverse bridge of pygophore narrow (Fig. 8, yellow arrow) .....2
  - Scutellum triangular (Fig. 14, grey arrow) transverse bridge of pygophore broad (Fig. 8, dark blue arrow) .....3
2. Small (7.23–7.90 mm), anterior pronotal lobe longer than posterior lobe, hemelytron not reaching tip of abdomen, abdomen ovoid, connexivum slightly undulating (Fig. 14, orange arrow) .....*P. curculionis* China, 1935
  - Of medium size (8.14–8.83 mm), anterior and posterior pronotal lobes equal in length, hemelytron reaching tip of abdomen, abdomen elongate ovoid, connexivum smooth, not undulating (Fig. 14, brown arrow) .....*P. azrael* Kirkaldy, 1905
3. Anterior pronotal lobe narrower than posterior lobe in males (Fig. 15, black arrows) .....4
  - Anterior pronotal lobe wider than posterior lobe in males (Figs 14, 15, green arrows) ....7

- 
4. Fore femur slender, slightly incrassate, hemelytron not reaching tip of abdomen (Fig. 15, orange arrows) .....5  
 – Fore femur distinctly incrassate, hemelytron reaching tip of abdomen (Fig. 15, brown arrow) ....6
5. Small-medium size (6.99–8.21 mm), without long, erect setae (Fig. 15, light purple arrow), scape reaching apex of clypeus, paramedian carina weakly defined, anterior pronotal lobe level with posterior lobe in lateral view, parascutellar lobe rounded and skewed towards median .....  
 .....*P. muluensis* sp. nov.  
 – Medium-large size (8.32–10.19 mm), body covered with long, erect setae (Fig. 15, purple arrow), scape not reaching apex of clypeus, paramedian carina strongly defined, anterior pronotal lobe lower than posterior lobe in lateral view, parascutellar lobe rounded and straight .....  
 .....*P. ractepilosa* sp. nov.
6. Head elongate and conical, maxillary plate truncate apically, scape reaching apex of clypeus, eye distinctly projecting in dorsal view, antero-lateral pronotal projection truncate, hemelytron entirely black (Fig. 15, brown arrow) .....*P. nigripennis* sp. nov.  
 – Head short and conical, maxillary plate rounded apically, scape not reaching apex of clypeus, eye hemispherical in dorsal view, antero-lateral pronotal projection acute and diverging, basal half of hemelytron dark brown, apical half off-white (Fig. 15, red arrow) .....  
 .....*P. nigroalbus* Breddin, 1903
7. Brachypterous (Fig. 14, light blue arrow) .....*P. brevipennis* sp. nov.  
 – Macropterous .....8
8. Parascutellar lobe rounded and skewed towards median (Fig. 15, light blue arrow) .....9  
 – Parascutellar lobe rounded and straight (Fig. 15, dark blue arrow) .....10
9. Anterior pronotal lobe shorter than posterior lobe, lobes level with each other in lateral view, hemelytral membrane basally dark brown, apically off-white .....*P. tricolor* sp. nov.  
 – Length of anterior pronotal lobe equal to that of posterior lobe, anterior lobe higher than posterior lobe in lateral view, membranous portion of hemelytron uniformly brown .....  
 .....*P. notata* Westwood, 1845
10. Height of anteocular lobe shorter than that of postocular lobe, scutellar process long and slender (Fig. 14, grey arrow) .....11  
 – Height of anteocular and postocular lobes equal, scutellar process broad (Fig. 15, white arrow) .....13
11. Hemelytron reaching tip of abdomen .....*P. fuliginosa* (Stål, 1870)  
 – Hemelytron short, not reaching tip of abdomen .....12
12. Large (10.5 mm), scape reaching apex of clypeus, anterior pronotal lobe distinctly wider than posterior lobe (Fig. 14, green arrow) .....*P. esakii* Cao *et al.*, 2011  
 – Of medium size (8.10–9.03 mm), scape not reaching apex of clypeus, anterior pronotal lobe marginally wider than posterior lobe (Fig. 14, dark green arrow) .....*P. minime* sp. nov.
13. Large (10.52–10.96 mm), males with apodeme on mediosternite 8, transverse bridge of pygophore broad (Fig. 8, dark blue arrow), margin of anterior opening of pygophore rounded in lateral view, with sclerotized, angular ductifer .....*P. mysorensis* sp. nov.

- Of medium size (8.91–9.82 mm), males without apodeme on mediosternite 8, transverse bridge of pygophore narrow (Fig. 8, yellow arrow), margin of anterior opening of pygophore angular in lateral view, with membranous ductifer .....*P. anamalaiensis* sp. nov.

*Physoderes anamalaiensis* sp. nov.

[urn:lsid:zoobank.org:act:C302D0E6-40FC-446C-A044-EBFD1A76F7D2](https://doi.org/10.3896/IBID.446C-A044-EBFD1A76F7D2)

Figs 8–9, 13–14, 17; Appendix

**Diagnosis**

This species is recognized among species of *Physoderes* by the scape reaching the apex of the clypeus, the small eye, the acute and anteriorly oriented antero-lateral projection of the anterior pronotal lobe, the wide anterior pronotal lobe, which is equal to or wider than the posterior lobe in males and only slightly narrower than the posterior lobe in females, the rounded parascutellar lobe, the dark brown scutellum with the apex thickened and raised, the straw-colored, rounded and short scutellar process, and the hemelytron reaching the tip of the abdomen. This species is most similar to *P. mysorensis* sp. nov., but is differentiated by the smaller size (8.91–9.82 mm), having no apodeme on mediosclerite 8, the narrow transverse bridge of the pygophore, and the margin of the anterior opening of the pygophore being angular in lateral view and with a membranous ductifer.

**Etymology**

The name *anamalaiensis* is a noun in apposition as a tribute to the type locality Anamalai Hills, Tamil Nadu, India.

**Material examined**

**Holotype**

INDIA: ♂, Tamil Nadu, Madras Co., Anamalai Hills, Cinchona, 10.28228° N, 76.97999° E, 1067 m, Sep. 1959, P.S. Nathan leg. (UCR\_ENT 00046637) (AMNH).

**Paratypes**

INDIA: Tamil Nadu: Madras Co., Anamalai Hills: 1 ♂, 10.74944° N, 77.29888° E, 1067 m, May 1956, P.S. Nathan leg. (UCR\_ENT 00068925) (AMNH); 2 ♂♂, same collection data as preceding but Apr. 1957 (UCR\_ENT 00068923, UCR\_ENT 00068924) (AMNH); 3 ♂♂, Kadamparai, 10.39444° N, 76.97333° E, 1067 m, May 1963, P.S. Nathan leg. (UCR\_ENT 00068918–UCR\_ENT 00068920) (AMNH).

**Other material**

INDIA: Tamil Nadu, Madras Co., Anamalai Hills: 1 ♂, 10.74972° N, 77.29972° E, 344 m, May 1957, P.S. Nathan leg. (UCR\_ENT 00068922) (AMNH); 2 ♂♂, 10.38277° N, 76.92944° E, 1372 m, Sep. 1946, P.S. Nathan leg. (UCR\_ENT 00046638, UCR\_ENT 00046639) (CAS); 1 ♀, same collection data as preceding but 21 Jun. 1946 (UCR\_ENT 00046622) (CAS); 1 ♀, 10.74944° N, 77.29888° E, 1067 m, May 1964, P.S. Nathan leg. (UCR\_ENT 00068934) (AMNH); 2 juvs, same collection data as preceding but May 1957 (UCR\_ENT 00068938, UCR\_ENT 00068939) (AMNH); 1 ♀, same collection data as preceding but Apr. 1957 (UCR\_ENT 00068933) (AMNH); 3 juvs, same collection data as preceding (UCR\_ENT 00068935–UCR\_ENT 00068937) (AMNH); 1 ♂, same collection data as for holotype (UCR\_ENT 00046636) (CAS); 3 ♀♀, same collection data as for holotype (UCR\_ENT 00046642–UCR\_ENT 00046644) (CAS); 1 ♀, same collection data as for holotype but Apr. 1959 (UCR\_ENT 00046645) (CAS); 1 ♀, same collection data as for holotype but May 1957 (UCR\_ENT 00068929) (AMNH); 2 ♀♀, same collection data as preceding (UCR\_ENT 00046640, UCR\_ENT 00046641) (CAS); 1 ♀, Cinchona, 10.74944° N, 77.29861° E, 344 m, May 1957, P.S. Nathan leg. (UCR\_ENT 00068930) (AMNH); 2 ♀♀, same collection data as preceding but Apr. 1956 (UCR\_ENT 00068926, UCR\_ENT 00068927) (AMNH); 1 juv., same collection data as preceding (UCR\_ENT 00068928)

(AMNH); 2 ♀♀, same collection data as preceding but Apr. 1957 (UCR\_ENT 00068931, UCR\_ENT 00068932) (AMNH); 1 ♂, Kadamparai, 10.39444° N, 76.97333° E, 1067 m, May 1965, P.S. Nathan leg. (UCR\_ENT 00068921) (AMNH); 1 ♂, Anamalais, 10.36667° N, 77.125° E, 914 m, 25 Jan. 1912, K. Pandal leg. (UCR\_ENT 00069254) (BMNH).

## **Description**

### **Male**

**BODY LENGTH.** Medium, total length 9.27 mm, SD ± 0.36 (Appendix).

**COLORATION** (Figs 14, 17). Dark brown. Head dark brown. Scape of antenna brown, pedicel brown basally, straw-colored apically, basiflagellomere brown, distiflagellomere basally brown, apically straw-colored. First segment of labium brown, second segment basally brown, medially straw-colored, apically brown, third segment brown. Pronotum of thorax dark brown, scutellum dark brown, scutellar process straw-colored, pleuron dark brown, sternum dark brown. Corium of hemelytron dark brown, membrane dark brown. Legs dark brown. Abdomen dorsally yellowish-orange, ventrally dark brown with suffusion of straw-color and brown, anterior half of connexivum dark brown, posterior half straw-colored, exposed part of pygophore dark brown.

**VESTITURE.** Sparsely setose. Head with widespread curved setae, ventral surface of postocular lobe with sparse, setigerous tubercles, with pair of long, straight setae on postocular lobe posterior to ocelli. Anterior lobe of thorax with irregular row of tuberculated, short, curved setae on lateral margins and short, setigerous tubercles dispersed on dorsal surface, posterior lobe with short, curved setae on humeral angle and sparsely distributed along dorsal surface. Corium of hemelytron with short, curved setae. Legs with two rows of spines and setigerous tubercles, tibiae with regular rows of tuberculated, stout, sharp setae. Connexival margin of abdomen with no prominent setae.

**HEAD.** Elongate conical; maxillary plate rounded apically; scape reaching apex of clypeus; eye hemispherical in dorsal view, less than 1/5 length of head; height of anteocular lobe level with postocular lobe.

**THORAX.** Antero-lateral paired projections acute; surface of anterior lobe with low ridges; median pronotal depression not contiguous with transverse sulcus; paramedian carina weakly defined; anterior pronotal lobe longer than posterior lobe, wider than or equal in width to posterior lobe, higher than posterior lobe in lateral view; parascutellar lobe rounded; scutellar process short, apex rounded.

**HEMELYTRON.** Reaching tip of abdomen.

**LEGS.** Same as genus description.

**ABDOMEN.** Connexival margin slightly undulating, posterior margin not elevated.

**GENITALIA.** Anterior margin of mediosternite 8 undulating, without medial apodeme; transverse bridge of pygophore narrow, margin of anterior opening angular, apodeme present, apical margin of posterior opening smooth; cup-like sclerite apically rounded and rim ventrally sclerotized; arms of basal plate converging; ductifer membranous; endosomal struts conical, with subacute apex, divided into two arms basally; shape of dorsal phallosomal sclerite subacute with lateral broad, plate-like prolongations, short, rounded lateral plates.

### **Female**

Similar to males except with anterior pronotal lobe slightly narrower than posterior lobe and median pronotal depression contiguous with transverse sulcus.

### Ecology

Nothing is known about the biology of this species.

### Distribution

This species is known only from the area around the type locality in the Anamalai Hills, Madras, Tamil Nadu, India.

### Remarks

This species possesses the enlarged anterior pronotal lobe characteristic of *Physoderes* along with the associated pronotal modifications, and is thus placed in this genus. The females possess an enlarged anterior pronotal lobe, although not as exaggerated as that of the males, which is quite unique. The species is most likely closely related to the other *Physoderes* species native to India, *P. mysorensis* sp. nov., described below.

*Physoderes azrael* Kirkaldy, 1905  
Figs 8–9, 14, 17, 20; Appendix

*Physoderus* [sic] *azrael* Kirkaldy, 1905: 339.

### Diagnosis

This species is recognized among other species of *Physoderes* by the head being anteriorly light brown and posteriorly brown, the pronotum dark brown straw-colored or with a light brown humeral tubercle, the posterior margin, parascutellar lobe, scutellar process and base of the corium light brown, the short and conical head, the scape reaching the apex of the clypeus, the anterior pronotal lobe being equal to or slightly narrower than the posterior lobe, the parascutellar lobe being rounded and skewed towards the median, the semicircular scutellum, the spatulate and apically rounded scutellar process, the pronotum flattened in lateral view and the hemelytron reaching the tip of the abdomen. In the male genitalia, the following features are also diagnostic: the extremely narrow transverse bridge of the pygophore and the apically truncate endosomal struts, which are basally divided into two arms converging medially to form basally a ridge. This species is most similar to *P. curculionis* but can be differentiated by the coloration, elevation of the pronotum, shape of the abdomen and shape of the endosomal struts in males.

### Material examined

#### Holotype

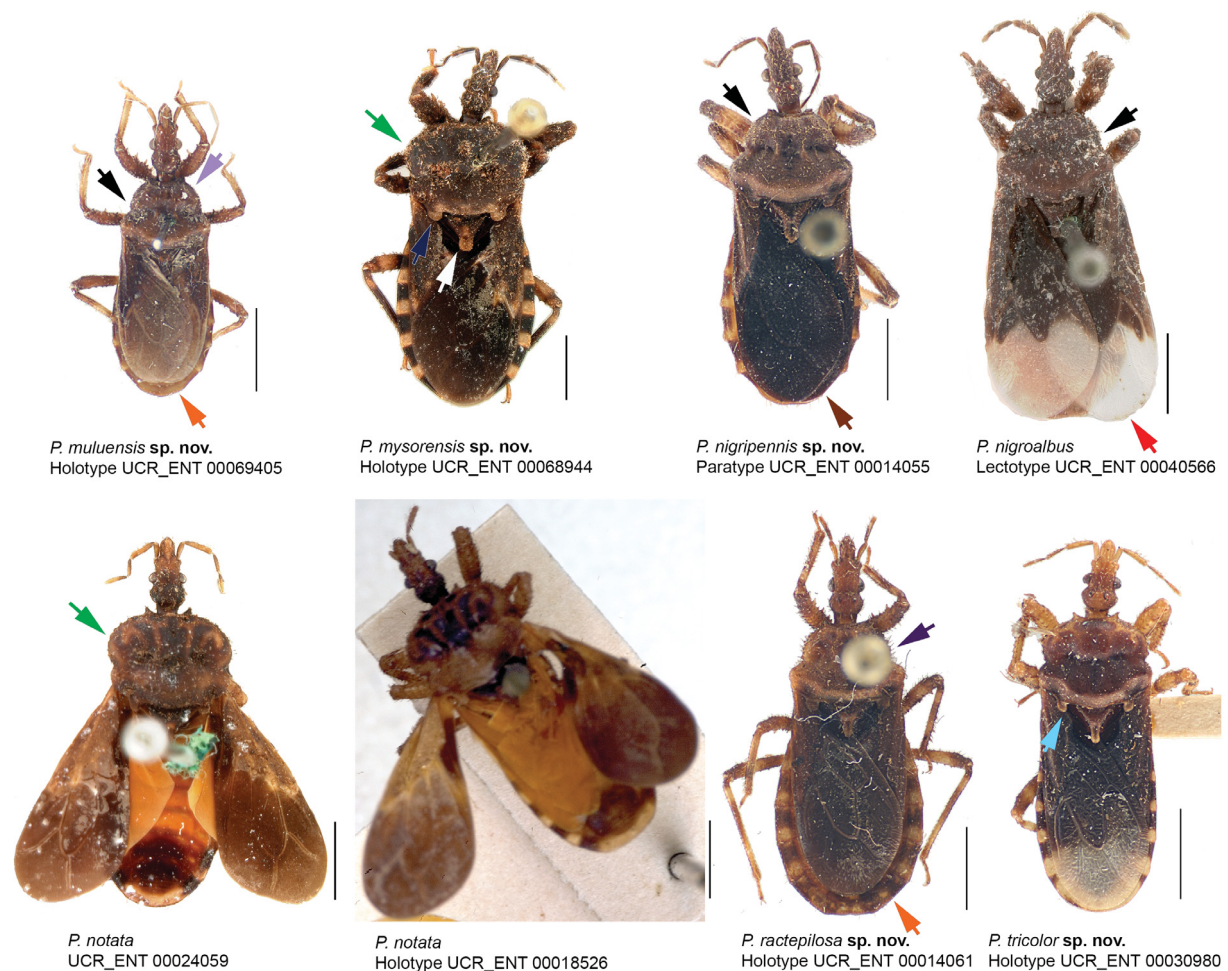
PAPUA NEW GUINEA: ♂, East New Britain Province, 5.76277° S, 151.1375° E, date unknown, Willey leg. (UCR\_ENT 00018531) (BMNH).

#### Other material

FIJI: 1 juv., Ovalau, Andubangda, 17.64277° S, 178.74944° E, 305 m, 18 Jul. 1938, E.C. Zimmerman leg. (UCR\_ENT 00073576) (BPBM); 1 juv., Viti Levu, Nadarivatu Co., 4 mi. S of Nadarivatu, 17.51° S, 177.91888° E, 732 m, 9 Sep. 1938, Y. Kondo leg. (UCR\_ENT 00073569) (BPBM); 2 juvs, Nadarivatu, 17.51° S, 177.91888° E, 1067 m, 5 Sep. 1938, Y. Kondo leg. (UCR\_ENT 00073570, UCR\_ENT 00073572) (BPBM); 1 juv., Nadarivatu, 17.51° S, 177.91888° E, 823 m, 7 Sep. 1938, Y. Kondo leg. (UCR\_ENT 00073571) (BPBM); 1 juv., Viti Levu, 17.84833° S, 178.01194° E, 853 m, 11 Sep. 1938, E.C. Zimmerman leg. (UCR\_ENT 00073568) (BPBM); 1 juv., Belt Road, 16–18 mi. W of Suva, 18.015° S, 178.38388° E, 22 Sep. 1938, Y. Kondo leg. (UCR\_ENT 00073575) (BPBM); 1 juv., Mt Victoria, train from Navai, 17.61638° S, 178.01222° E, 600 m, 2 Jul. 1958, B. Malkin leg. (UCR\_ENT 00073573) (BPBM); 1 juv., Navai, 17.61638° S, 177.97694° E, Jan. 1951, N.L.H. Krauss leg. (UCR\_ENT 00073574) (BPBM).

INDONESIA: Maluku Province: 1 ♀, Larat, 7.14521° S, 131.88479° E, Dec. 1907, collector unknown (UCR\_ENT00046675) (CAS). – Papua Province: 1 ♀, Hollandia, Neth. Ind-Amer. (Jayapura), 2.54138° S, 140.71361° E, Jul. 1938, L.J. Toxopeus leg. (UCR\_ENT00023997) (RMNH); 1 ♀, Maffin Bay, 2.09222° S, 139.01472° E, Jun. 1944, E.S. Ross (UCR\_ENT 00046670) (CAS); 1 ♂, same collection data as preceding but Sep. 1944 (UCR\_ENT 00046659) (CAS). – West Papua Province: 1 ♂, Vogelkop, Sucumi Camo, near head of Ransiki River, 1.5° S, 132.5° E, 300 m, 6 Aug. 1957, D.E. Hardy leg. (UCR\_ENT 00073538) (BPBM).

PAPUA NEW GUINEA: Bougainville Province: 1 ♂, Buin, 6.81361° S, 155.73194° E, 29 m, 31 May 1956, J.L. Gressitt leg. (UCR\_ENT 00073536) (BPBM); 3 ♂♂, Kieta, 6.23638° S, 155.64388° E, 31 May 1960, R.W. Paine leg. (UCR\_ENT 00069325–UCR\_ENT 00069327); 4 ♀♀, same collection data as preceding (UCR\_ENT 00069332–UCR\_ENT 00069335) (BMNH); 1 ♂, Kukugai, 6.05194° S, 155.19194° E, 150 m, Dec. 1960, W.W. Brandt leg. (UCR\_ENT 00073535) (BPBM); 1 ♀, same collection data as preceding (UCR\_ENT 00073553) (BPBM). – East New Britain Province: 3 ♀♀, Gazelle Peninsula, Gaulim, 4.45° S, 152.08333° E, 130 m, 23–28 Oct. 1962, J. Sedlacek leg. (UCR\_ENT 00073542–UCR\_ENT 00073544) (BPBM); 1 ♀, Gazelle Peninsula, Upper Warangoi, Illugi, 4.71472° S, 151.97944° E, 15 Dec. 1962, J. Sedlacek leg. (UCR\_ENT 00073567) (BPBM); 1 ♂, Gazelle Peninsula, Upper Warangoi, Illugi, 4.48333° S, 152.15° E, 230 m, 8–11 Dec. 1962, J. Sedlacek leg. (UCR\_ENT 00073520) (BPBM); 2 ♀♀, same collection data as preceding (UCR\_ENT 00073565,



**Fig. 15.** Dorsal habitus images for species of *Physoderes* Westwood, 1845 (partial). For an explanation of the colored arrows, see key on page 66. Scale bars = 2 mm.



UCR\_ENT 00073566) (BPBM); 1 ♂, Gazelle Peninsula, Gaulim, 4.45° S, 142.08333° E, 23 May 1956, J.L. Gressitt leg. (UCR\_ENT 00073523); 1 ♀, same collection data as preceding (UCR\_ENT 00073541) (BPBM); 1 ♀, Gazelle Peninsula, Gaulim, 4.44472° S, 152.08444° E, 140 m, 21–27 Oct. 1962, J. Sedlacek leg. (UCR\_ENT 00073540) (BPBM); 3 ♂♂, same collection data as preceding but 19–20 Nov. 1962 (UCR\_ENT 00073516–UCR\_ENT 00073518) (BPBM); 1 ♂, Karavat, 4.35194° S, 152.04194° E, Jul. 1957, R.W. Paine leg. (UCR\_ENT 00069324) (BMNH); 1 ♀, Keravat, 4.35° S, 152.03334° E, 30 m, 2 Apr. 1956, E.J. Ford Jr leg. (UCR\_ENT 00073562) (BPBM); 2 ♀♀, Kerawat, Gazelle Peninsula, 4.35194° S, 152.04194° E, 60 m, 27 Aug. 1955, J.L. Gressitt leg. (UCR\_ENT 00073545, UCR\_ENT 00073546) (BPBM); 1 ♂, Rabaul, 4.19611° S, 152.17305° E, 17 Aug. 1930, J.L. Froggatt leg. (UCR\_ENT 00046662) (CAS); 1 ♀, same collection data as preceding but 17 May 1932 (UCR\_ENT 00046669) (CAS); 1 ♂, Rabaul, 4.175° S, 152.23083° E, 4 Jul. 1959, J.L. Gressitt leg. (UCR\_ENT 00073519); 1 ♀, same collection data as preceding (UCR\_ENT 00073559) (BPBM); 1 ♀, near Rabaul, 4.175° S, 152.24805° E, Feb. 1929, collector unknown (UCR\_ENT 00046668) (CAS); 1 ♀, Jaquinot Bay, 5.54638° S, 151.51722° E, 3 Dec. 1969, J.E. Tobler leg. (UCR\_ENT 00046672) (CAS); 1 ♀, Wunung Plains, Jacquinot Bay, 5.56472° S, 151.57111° E, 30 Apr. 1956, J.L. Gressitt leg. (UCR\_ENT 00073560) (BPBM); 1 ♂, Malmalwan-Vunakanau, Gazelle Peninsula, 4.6667° S, 152° E, 17 May 1956, J.L. Gressitt leg. (UCR\_ENT 00073521) (BPBM). – West New Britain Province: 1 ♂, Talasea, Narunageru Road, 5.53916° S, 150.13555° E, 22 Nov. 1969, J.E. Tobler leg. (UCR\_ENT 00046663) (CAS); 1 ♂, Linga Linga Plantation, W of Willaumez Peninsula lm. [?], 5.79944° S, 149.38083° E, 13 Apr. 1956, J.L. Gressitt leg. (UCR\_ENT 00073522) (BPBM); 1 ♀, Volupai, Willaumez Peninsula, 5.26916° S, 149.97638° E, 100 m, 18 Apr. 1956, J.L. Gressitt leg. (UCR\_ENT 00073561) (BPBM). – New Ireland Province: 1 ♀, Camp Bishop, 12 km up Kait River, 240 m, 7 Jul. 1956, E.J. Ford Jr leg. (UCR\_ENT 00073564) (BPBM); 1 ♂, ridge above Camp Bishop, 15 km up Kait River, 4.48744° S, 152.76638° E, 284 m, 9 Jul. 1956, J.L. Gressitt leg. (UCR\_ENT 00073539) (BPBM); 1 ♀, same collection data as preceding (UCR\_ENT 00073563) (BPBM); 2 ♂♂, Wana Wana, 4.52666° S, 152.40555° E, Nov. 1960, R.W. Paine leg. (UCR\_ENT 00069322, UCR\_ENT 00069323) (BMNH). – Madang Province: 1 ♂, Madang, 5.23361° S, 145.78888° E, Sep. 1957, R.W. Paine leg. (UCR\_ENT 00069293) (BMNH). – Milne Bay Province: 1 ♂, Woodlark Island Co., Kulumadai Hill Mar., 9.05° S, 152.71667° E, 25 Feb. 1957, W.W. Brandt leg. (UCR\_ENT 00073537) (BPBM). – Morobe Province: 1 ♀, Huon Peninsula Co., Finschhafen, 6.55527° S, 147.17361° E, 2 May 1944, E.S. Ross leg. (UCR\_ENT 00046671) (CAS); 1 ♂, 18 Nov. 1969, J.E. Tobler leg. (UCR\_ENT 00046661) (CAS); 2 ♂♂, Bumayong, 6.63444° S, 147.0025° E, Jul. 1957, R.W. Paine leg. (UCR\_ENT 00069292, UCR\_ENT 00069316) (BMNH); 1 ♀, same collection data as preceding (UCR\_ENT 00069304) (BMNH); 1 ♀, same collection data as preceding but Sep. 1957 (UCR\_ENT 00069303) (BMNH); 5 ♀♀, Gurakor, 6.73972° S, 146.615° E, 610 m, Jul. 1957, R.W. Paine leg. (UCR\_ENT 00069309, UCR\_ENT 00069310, UCR\_ENT 00069329–UCR\_ENT 00069331) (BMNH); 3 ♂♂, same collection data as preceding (UCR\_ENT 00069317–UCR\_ENT 00069319) (BMNH); 1 ♀, Lae, 6.81444° S, 146.80416° E, Jul. 1957, R.W. Paine leg. (UCR\_ENT 00069301) (BMNH); 5 ♂♂, same collection data as preceding but May 1957 (UCR\_ENT 00069290, UCR\_ENT 00069291, UCR\_ENT 00069294, UCR\_ENT 00069314, UCR\_ENT 00069321) (BMNH); 6 ♀♀, same collection data as preceding (UCR\_ENT 00069296–UCR\_ENT 00069300, UCR\_ENT 00069308) (BMNH); 3 ♀♀, same collection data as preceding but date only as 1957 (UCR\_ENT 00069305–UCR\_ENT 00069307) (BMNH); 1 ♂, same collection data as preceding (UCR\_ENT 00069315) (BMNH); 1 ♂, Sio, N coast, 5.95333° S, 147.3925° E, 600 m, 24 Jul. 1956, E.J. Ford Jr leg. (UCR\_ENT 00073524) (BPBM); 1 ♀, Yalu, Lae, 6.5875° S, 146.87666° E, Apr. 1957, R.W. Paine leg. (UCR\_ENT 00069311); 1 ♂, same collection data as preceding (UCR\_ENT 00069320) (BMNH); 1 ♀, Rooke Island (= Umboi Island), 5.71972° S, 147.71666° E, Jan. 1957, R.W. Paine leg. (UCR\_ENT 00069313) (BMNH).

SOLOMON ISLANDS: Central Province: 1 ♂, Nggela Hagalo, 9.06638° S, 160.21138° E, 88 m, 25 May 1936, R.A. Lever leg. (UCR\_ENT 00069328) (BMNH). – Choiseul Island: 1 ♀, Kolombangara River, 7.05166° S, 156.95027° E, 60 m, 20 Mar. 1964, P. Shanahan leg. (UCR\_ENT 00073557) (BPBM).

– Guadalcanal: 1 ♂, Honiara Co., Kukum, 9.43361° S, 159.95111° E, 27 Oct. 1956, E.S. Brown leg. (UCR\_ENT 00069349) (BMNH); 1 ♀, 9.6 km SE of Honiara, Lunga River bridge, 9.49471° S, 160.01181° E, 2 Jun. 1960, C.W. O'Brien leg. (UCR\_ENT 00073550) (BPBM); 2 ♀♀, Berande, 9.49222° S, 160.17833° E, Nov. 1931, R. Lever leg. (UCR\_ENT 00046665, UCR\_ENT 00046666) (CAS); 1 ♂, Bonegi River, 9.435° S, 159.98527° E, 213 m, 14 Dec. 1934, R.A. Lever leg. (UCR\_ENT 00069348) (BMNH); 1 ♂, Guadalcanal Lavoro, 9.57722° S, 160.14555° E, 18 Feb. 1934, H.T. Pagden leg. (UCR\_ENT 00046660) (CAS); 1 ♀, Kukum, 9.48916° S, 160.16944° E, Nov. 1931, R.J.A.W. Lever leg. (UCR\_ENT 00046674) (CAS); 2 ♂♂, Kukum, 29 Oct. 1963, P. Greenslade leg. (UCR\_ENT 00069345, UCR\_ENT 00069351); 4 ♀♀, same collection data as preceding (UCR\_ENT 00069354–UCR\_ENT 00069357) (BMNH); 1 ♂, Mt Austen, 9.61777° S, 160.12138° E, 9 Jun. 1965, P. Greenslade leg. (UCR\_ENT 00069344) (BMNH); 1 ♂, same locality as preceding, 9 Jul. 1963, P. Greenslade leg. (UCR\_ENT 00069336) (BMNH); 3 ♂♂, Mt Austen, 9.55472° S, 160.10666° E, 305 m, 25 Feb. 1963, P. Greenslade leg. (UCR\_ENT 00069341–UCR\_ENT 00069343) (BMNH); 2 ♀♀, same collection data as preceding (UCR\_ENT 00069361, UCR\_ENT 00069362) (BMNH); 1 ♀, same collection data as preceding but 19 Jun. 1963 (UCR\_ENT 00069367) (BMNH); 1 ♂, same collection data as preceding (UCR\_ENT 00069368) (BMNH); 2 ♂♂, same collection data as preceding but 11 Feb. 1963 (UCR\_ENT 00069337, UCR\_ENT 00069338) (BMNH); 1 ♂, same collection data as preceding but 23 Jun. 1963 (UCR\_ENT 00069339) (BMNH); 1 ♂, same collection data as preceding but 4 Mar. 1963 (UCR\_ENT 00069340) (BMNH); 2 ♀♀, same collection data as preceding but 29 Oct. 1963 (UCR\_ENT 00069365, UCR\_ENT 00069366) (BMNH); 1 ♂, Nr. Tatuve, Kolosulu, 9.65916° S, 160.16361° E, 19 May 1960, C.W. O'Brien leg. (UCR\_ENT 00073534) (BPBM); 1 ♀, same collection data as preceding (UCR\_ENT 00073548) (BPBM); 1 ♂, Paripao, 9.56667° S, 160.33333° E, 21 May 1960, C.W. O'Brien leg. (UCR\_ENT 00073525) (BPBM); 2 ♂♂, Tenaru, 9.4475° S, 160.07555° E, 11 Aug. 1955, E.S. Brown leg. (UCR\_ENT 00069346, UCR\_ENT 00069347) (BMNH); 3 ♀♀, same collection data as preceding (UCR\_ENT 00069358–UCR\_ENT 00069360) (BMNH); 1 ♀, 9.64555° S, 160.15611° E, date unknown, W.M. Mann leg. (UCR\_ENT 00068917) (AMNH); 2 ♂♂, Lunga, 9.42971° S, 160.04632° E, 10 Feb. 1958, P.G. Fenemore leg. (UCR\_ENT 00069352, UCR\_ENT 00069353) (BMNH); 1 ♀, same collection data as preceding (UCR\_ENT 00069363) (BMNH); 1 ♀, same collection data as preceding but 29 Jul. 1955, E.S. Brown leg. (UCR\_ENT 00069364) (BMNH); 1 ♂, Guadalcanal, 9.6 km SE of Honiara, Lunga, 9.49471° S, 160.01181° E, 2 Jun. 1960, C.W. O'Brien leg. (UCR\_ENT 00073527) (BPBM). – Malaita Province: 1 ♀, Alite Island, 12 km NE of Dala, 8.6325° S, 160.69638° E, 300 m, 12 Jun. 1964, J. Sedlacek leg. (UCR\_ENT 00073555) (BPBM); 1 ♀, Alite Island, Dala, 8.59027° S, 160.68555° E, 50 m, 9–14 Jun. 1964, J. and M. Sedlacek leg. (UCR\_ENT 00073551) (BPBM); 1 ♀, Alite Island, Tangtalau-Kwalo, 8.73333° S, 160.73333° E, 200 m, 30 Sep. 1957, J.L. Gressitt leg. (UCR\_ENT 00073554) (BPBM). – Santa Ysabel: 1 ♂, Sukapisu, 8.11444° S, 159.33638° E, 900 m, 19 Jun. 1960, C.W. O'Brien leg. (UCR\_ENT 00073533) (BPBM); 1 ♀, same collection data as preceding but 18 Jun. 1960 (UCR\_ENT 00073558) (BPBM). – Western Province: 1 ♀, Kolombangara, Pepele, 8.05° S, 156.96667° E, 30 m, 12 Feb. 1964, P. Shanahan leg. (UCR\_ENT 00073556) (BPBM); 1 ♂, same collection data as preceding but 9 Feb. 1964 (UCR\_ENT 00073528) (BPBM); 1 ♂, Gizo Island, Gizo, 8.1° S, 156.85° E, 100 m, Dec. 1976, N.L.H. Krauss leg. (UCR\_ENT 00073529) (BPBM); 1 ♀, same collection data as preceding (UCR\_ENT 00073547) (BPBM); 1 ♂, same collection data as preceding but Feb. 1984 (UCR\_ENT 00073526) (BPBM); 1 ♂, New Georgia Islands Co., Banga, 8.28384° S, 157.21628° E, 12 Oct. 1964, E.S. Brown leg. (UCR\_ENT 00069350) (BMNH); 1 ♀, Vella Lavella Island, Ulo Crater, 7.68555° S, 156.58472° E, 10 m, 21 Jul. 1963, P. Shanahan leg. (UCR\_ENT 00073552) (BPBM); 1 ♀, Lunga River, 8.08638° S, 156.78083° E, 6 Nov. 1944, H.E. Milliron leg. (UCR\_ENT 00073549) (BPBM).

## Redescription

### Male

BODY LENGTH. Medium, total length 8.58 mm, SD ± 0.16 (Appendix).

**COLORATION** (Figs 14, 17). Yellowish-brown and dark brown. Head anteriorly straw-colored, posteriorly brown. Antenna straw colored or light brown. First and second segments of labium light brown, third segment brown. Pronotum of thorax dark brown with straw-colored humeral tubercle, posterior margin and parascutellar lobe, scutellum dark brown basally, straw-colored apically including scutellar apex, pleuron dark brown with straw-colored suffusion, sternum dark brown. Corium of hemelytron base straw-colored, apex dark brown, membrane dark brown. Femora of legs straw-colored with medial and apical darkening, tibiae basally straw-colored and apically brown, tarsi and claws brown. Abdomen dorsally yellowish-orange, ventrally straw-colored with dark brown patterns, anterior half of connexivum dark brown, posterior half straw-colored, exposed part of pygophore dark brown.

**VESTITURE.** Densely setose. Head with some curved setae and short, fine, adpressed setae, ventral surface of postocular lobe with two rows of small, setigerous tubercles, with pair of long, straight setae on postocular lobe posterior to ocelli. Anterior lobe of thorax with irregular row of tuberculated, short, curved setae on lateral margins and fine, adpressed setae on dorsal surface, posterior lobe with short, sparse setae intermixed with short, tuberculated, curved setae. Corium of hemelytron with short, sparse, adpressed setae. Legs with two rows of spines and setigerous tubercles, tibia with regular rows of tuberculated, stout, sharp setae. Connexival margin of abdomen with a few clubbed setae on each segment or connexival margin with no prominent setae.

**HEAD.** Short conical; maxillary plate rounded apically; scape reaching apex of clypeus; eye hemispherical in dorsal view, less than  $\frac{1}{5}$  length of head.

**THORAX.** Antero-lateral paired projections acute, diverging; surface of anterior lobe with low ridges; median pronotal depression not contiguous with transverse sulcus; paramedian carina weakly defined; anterior pronotal lobe equal in length to posterior lobe, equal in width to or slightly narrower than posterior lobe, higher than posterior lobe in lateral view; parascutellar lobe rounded, skewed towards median; scutellum semicircular, scutellar process long, apex rounded or spatulate.

**HEMELYTRON.** Reaching tip of abdomen.

**LEGS.** Same as genus description.

**ABDOMEN.** Connexival margin smooth, not undulating, posterior margin not elevated.

**GENITALIA.** Anterior margin of mediosternite 8 undulating, without medial apodeme; transverse bridge of pygophore extremely narrow, only consisting of margin of anterior opening of pygophore, margin of anterior opening angular, apodeme present, apical margin of posterior opening smooth; cup-like sclerite apically rounded, with adjacent paired round protuberances; arms of basal plate converging; ductifer with sclerotized, rounded ring; endosomal struts apically truncate, basally divided into two arms converging medially to form a tapered ridge basally; shape of dorsal phallosomal sclerite subacute with lateral broad, plate-like prolongations.

### **Female**

Similar to males.

### **Ecology**

This species has been collected most commonly on or inside *Heliconia* flowers (Heliconiaceae), but also on *Pandanus* (Pandanaeae) in forests, on foliage of *Avocado* pear (Lauraceae), in rotting tissue of the trunk of *Roystonea regia* (Arecaceae), on *Nypa fruticans* (Arecaceae), on *Cocos nucifera* (Arecaceae), under sacking bands on trees, logs near the coast, in coastal litter, under dead bark and on *Musa* (Musaceae).

### Distribution

This species is mostly found on New Britain Island and the Solomon Islands archipelago, but is also found on Fiji Island, Papua New Guinea, Sabah (Borneo) and Pulau Larat (Indonesia). This species has the eastern-most distribution of all physoderines with specimens found in Fiji.

### Remarks

This species is placed in the *Physoderes* clade based on the phylogenetic analysis above. It is most closely related to *P. curculionis*, with which it shares the semicircular scutellum and the very narrow transverse bridge on the pygophore.

*Physoderes brevipennis* sp. nov.

[urn:lsid:zoobank.org:act:7184D9A5-EFC9-4128-9578-91C7D9318AFF](https://zoobank.org/act:7184D9A5-EFC9-4128-9578-91C7D9318AFF)

Figs 8, 14, 17, 19–20; Appendix

### Diagnosis

This species is recognized among other species of *Physoderes* by the small size, the head and pronotum being densely covered with long, curved setae, the elongate conical head, the scape reaching the apex of the clypeus, the enlarged anterior pronotal lobe, the wide posterior pronotal lobe (males), the posterior pronotal lobe and parascutellar lobe being reduced in size, the brachypterous wing type and the ovoid abdomen. Among male genitalic features, the following are also diagnostic: the narrow transverse bridge of the pygophore, the endosomal struts being apically bulbous and basally divided into two plates converging to form a ridge medially, and the dorsal phallosomal sclerite shaped like a thin moustache. This species is distinct by being the only brachypterous *Physoderes* species and it is restricted to Guadalcanal of the Solomon Islands archipelago.

### Etymology

The name *brevipennis* is chosen after the Latin adjective “brevipennis”, meaning short-winged, to describe the short wings of this species.

### Material examined

#### Holotype

SOLOMON ISLANDS: ♂, Guadalcanal, Mt Austen, 9.55472° S, 160.10666° E, 305 m, 11 Feb. 1965, P. Greenslade leg. (UCR\_ENT 00069375) (BMNH).

#### Paratypes

SOLOMON ISLANDS: 1 ♂, same collection data as for holotype but 20 Apr.–3 May 1965, P. Greenslade leg. (UCR\_ENT 00069376) (BMNH); 1 ♂, same collection data as preceding but 3 Jul.–24 Aug. 1965 (UCR\_ENT 00069372) (BMNH); 1 ♂, same collection data as preceding but 10 May–23 Jun. 1965 (UCR\_ENT 00069371) (BMNH); 1 ♂, Guadalcanal, Mt Austen, 9.61777° S, 160.12138° E, Dec. 1965–Jan. 1966, P. Greenslade leg. (UCR\_ENT 00069370) (BMNH).

#### Other material

SOLOMON ISLANDS: Guadalcanal: 1 ♀, Gallego Camp 2, 9.5772° S, 160.14555° E, 10 Jul. 1965, collector unknown (UCR\_ENT 00069382) (BMNH); 1 ♀, Mt Austen, 9.55472° S, 160.10666° E, 305 m, 3 Jul.–24 Aug. 1965, P. Greenslade leg. (UCR\_ENT 00069378) (BMNH); 1 ♂, same collection data as preceding but 10 Jan. 1966 (UCR\_ENT 00069373) (BMNH); 1 ♀, same collection data as preceding but 26 Jun 1965 (UCR\_ENT 00069381) (BMNH); 1 ♂, same collection data as preceding but 20 Mar.–5 Apr. 1965 (UCR\_ENT 00069374) (BMNH); 1 ♀, same collection data as preceding but 12 Oct. 1965 (UCR\_ENT 00069379) (BMNH); 2 ♀♀, Mt Austen, 9.61777° S, 160.12138° E, Dec. 1965–Jan. 1966,

P. Greenslade leg. (UCR\_ENT 00069377, UCR\_ENT 00069380) (BMNH); 1 ♀, Mt Jonapau (Mt Chaunapaho), 9.63222° S, 160.11638° E, 610 m, 5 Jun. 1965, P. Greenslade leg. (UCR\_ENT 00069383) (BMNH).

### **Description**

#### **Male**

**BODY LENGTH.** Small, total length 6.61 mm, SD ± 0.35 (Appendix).

**COLORATION** (Figs 14, 17). Brown. Connexivum of abdomen brown with posterior margin straw-colored.

**VESTITURE.** Densely setose. Head with widespread curved setae, ventral surface of postocular lobe with sparse, setigerous tubercles, with pair of long, straight setae on postocular lobe posterior to ocelli. Anterior lobe of thorax with tuberculated, short, curved setae on lateral margins and along dorsal ridges, posterior lobe with short, curved setae on humeral angle and sparsely distributed along dorsal surface. Corium of hemelytron with short, curved setae. Legs with two rows of spines and setigerous tubercles, tibia with regular rows of tuberculated, stout, sharp setae. Connexival margin of abdomen with a few clubbed setae on each segment.

**HEAD.** Elongate conical; maxillary plate rounded apically; scape just surpassing apex of clypeus; eye hemispherical in dorsal view, less than 1/5 length of head.

**THORAX.** Antero-lateral paired projections acute, diverging; surface of anterior lobe with low ridges; median pronotal depression not contiguous with transverse sulcus; paramedian carina strongly defined; anterior pronotal lobe longer and wider than posterior lobe, higher than posterior lobe in lateral view; parascutellar lobe bell-shaped, skewed towards median; scutellum rounded triangular, scutellar process short, apex subacute.

**HEMELYTRON.** Not reaching tip of abdomen.

**LEGS.** Same as genus description.

**ABDOMEN.** Ovoid, with rounded terminal margin; connexival margin undulating, posterior margin not elevated.

**GENITALIA.** Anterior margin of mediosternite 8 undulating, without medial apodeme; transverse bridge of pygophore narrow, margin of anterior opening angular, apodeme present, apical margin of posterior opening smooth; cup-like sclerite apically rounded, with adjacent paired round protuberances; arms of basal plate rounded; ductifer with sclerotized rounded ring; endosomal struts apically bulbous, basally divided into two plates converging to form a ridge medially; shape of dorsal phallosclerite shaped like a thin moustache.

#### **Female**

Similar to males, with abdomen wider (average width 3.80 mm).

### **Ecology**

This species has most often been collected using pitfall and carrion traps and one specimen was found on rotting pawpaw (Caricaceae).

### **Distribution**

This species is restricted to Guadalcanal of the Solomon Islands archipelago.

## Remarks

This species is placed in the *Physoderes* clade based on the phylogenetic analysis above. No other brachypterous physoderine species is found in the Oriental and Australasian region. The brachypterous males retain the enlarged anterior pronotum, but have a reduced posterior pronotal lobe.

*Physoderes curculionis* China, 1935  
Figs 8, 14, 16–17, 19–20; Appendix

*Physoderes curculionis* China, 1935: 497.

*Physoderes insulanus* Miller, 1940: 543, fig. 88. New synonymy.

*Physoderes patagiata* Miller, 1941: 782, fig. 7. New synonymy.

*Physoderes minor* Usinger, 1946: 50, fig. 11. New synonymy.

*Physoderes kalshoveni* Miller, 1954: 86, fig. 10. New synonymy.

## Diagnosis

This species is recognized among species of *Physoderes* by its small size (7.64 mm average length), the short and conical head, the scape reaching the apex of the clypeus, the anterior pronotal lobe being equal to or slightly narrower than the posterior lobe, the posterior pronotal lobe being rugose, the rounded parascutellar lobe, which is skewed towards the median, the semicircular scutellum, the spatulate and apically rounded scutellar process, the hemelytron not reaching the tip of the abdomen, the anterior margin of mediosternite 8 undulating and with an apodeme, the extremely narrow transverse bridge of the pygophore, and the endosomal struts being apically subacute and basally divided into two plates converging medially to form a ridge. This species is most similar to *P. azrael*, but can be differentiated by the elevation of the pronotum, the shorter and more ovoid abdomen, and the shape of the endosomal struts.

## Material examined

### Holotype

MALAYSIA: ♂, Malaya, unknown locality, 3.11° N, 101.72111° E, no date provided, (UCR\_ENT 00018529) (BMNH).

### Paratype

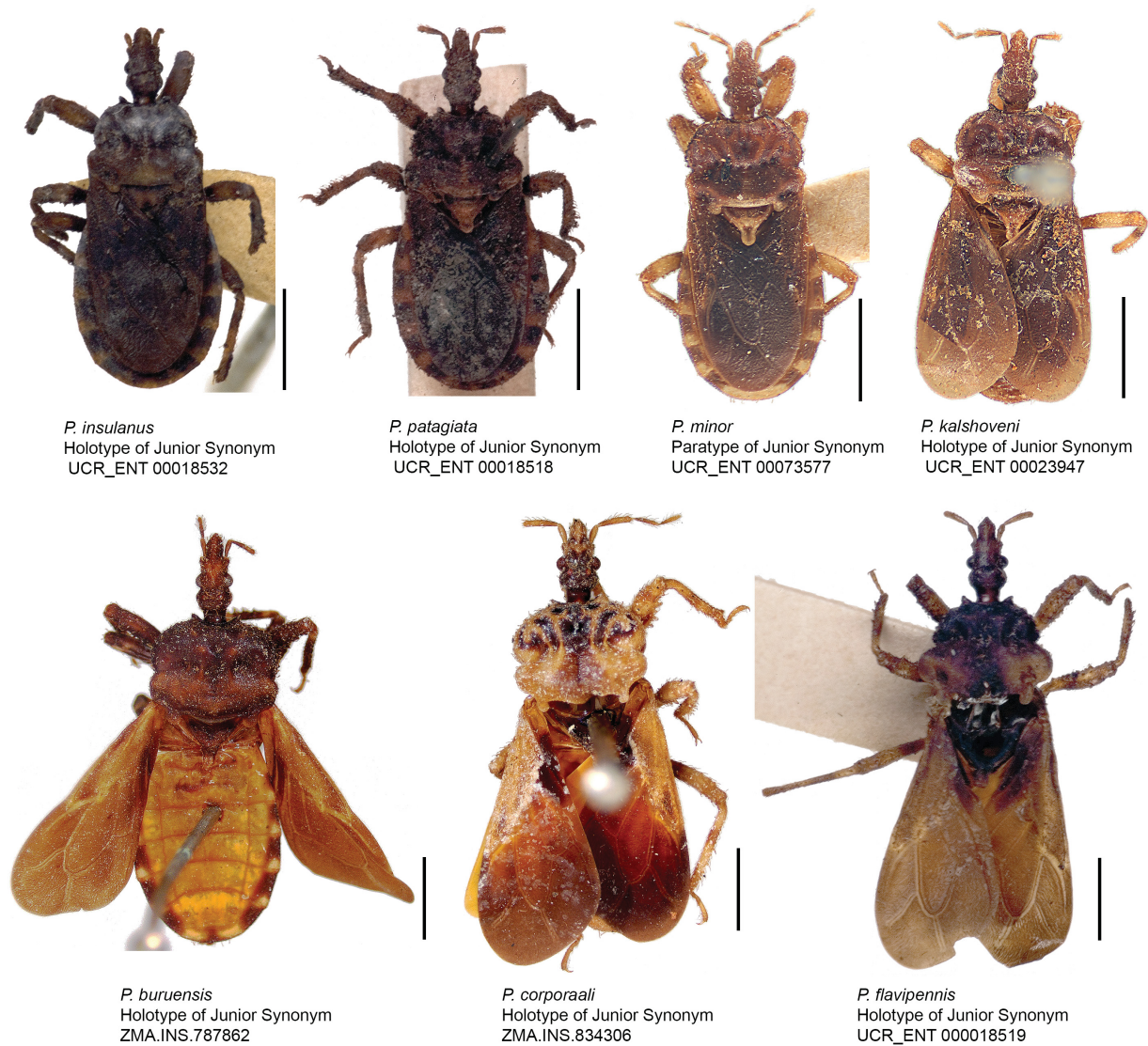
MALAYSIA: 1 ♀, Selangor, Petaling Co., Serdang, 3.02277° N, 101.71361° E, 14 Jan. 1935, G.H. Corbett leg. (UCR\_ENT 00018525) (BMNH).

### Other material

CHRISTMAS ISLAND: 1 ♀, 10.45917° S, 105.68972° E, 248 m, 28 Jan. 1933, unknown collector, holotype of *Physoderes insulanus* (junior synonym) (UCR\_ENT 00018532) (BMNH).

GUAM: 1 ♂, 3 mi. S of Piti, 13.45444° N, 144.70444° E, 98 m, 23 May 1936, O.H. Swezey leg., paratype of *Physoderes minor* (junior synonym) (UCR\_ENT 00073581) (BPBM); 1 ♀, same collection data as preceding (UCR\_ENT 00073592) (BPBM); 1 ♀, Mariana Is., Mt Lamlam Co., Mt Lalam, 13.33583° N, 144.66527° E, 406 m, Dec. 1958, N.L.H. Krauss leg. (UCR\_ENT 00073596) (BPBM); 1 ♀, 1 mi. SE of Asan, 13.47305° N, 144.71305° E, 244 m, 31 Oct. 1947, H.S. Dybas leg. (UCR\_ENT 00031420) (USNM); 1 ♀, Pilgo River, 13.44222° N, 144.77416° E, 26 May 1945, J.L. Gressitt leg. (UCR\_ENT 00031421) (USNM); 1 ♀, same collection data as preceding but G.E. Bohart and J.L. Gressitt leg. (UCR\_ENT 00073595) (BPBM); 2 ♂♂, Port Ajayan, 13.2725° N, 144.70444° E, 143 m, 6 Jun. 1945, H.S. Dybas leg. (UCR\_ENT 00073588, UCR\_ENT 00073589) (BPBM); 1 ♀, 2 mi. W of Piti, 13.45472° N, 144.695° E, 61 m, on *Glycine* sp. (Fabaceae), 20 Jul. 1937, R.G. Oakley leg. (UCR\_ENT 00031419) (USNM); 3 ♀♀, Dededo, 13.52° N, 144.84° E, 19 May 1936, R.L. Usinger leg., paratypes of *Physoderes*

*minor* (junior synonym) (UCR\_ENT 00046627–UCR\_ENT 00046629) (CAS); 1 ♀, Dededo, 13.52° N, 144.84° E, 13 Jul. 1937, R.G. Oakley leg. (UCR\_ENT 00031416) (USNM); 1 ♂, same collection data as preceding but 23 Feb. 1938 (UCR\_ENT 00031412) (USNM); 2 ♀♀, same collection data as preceding but 25 Aug. 1937 (UCR\_ENT 00031417, UCR\_ENT 00031418) (USNM); 2 ♀♀, Harmon Field, 13.50722° N, 144.81527° E, 54 m, on *Carica papaya* L. (Caricaceae), 21 Jan. 1949, collector unknown (UCR\_ENT 00031422, UCR\_ENT 00031423) (USNM); 1 ♂, Mt Alifan, 13.38055° N, 144.67138° E, Jun. 1936, R.L. Usinger leg., paratype of *Physoderes minor* (junior synonym) (UCR\_ENT 00073579) (BPBM); 1 ♀, same collection data as preceding but 26 May 1936, paratype of *Physoderes minor* (junior synonym) (UCR\_ENT 00068911) (AMNH); 1 ♂, same collection data as preceding, paratype of *Physoderes minor* (junior synonym) (UCR\_ENT 00046625) (CAS); 1 ♀, Mt Santa Rosa, 13.50805° N, 144.91083° E, 182 m, 16 May 1948, G.E. Bohart and J.L. Gressitt leg. (UCR\_ENT 00031425) (USNM); 1 ♂, Piti, 13.46° N, 144.69166° E, 5 m, 26 May 1936, O.H. Swezey leg., paratype of *Physoderes minor* (junior synonym) (UCR\_ENT 00073577) (BPBM); 1 ♀, same collection data as preceding but 27 Oct. 1936, paratype of *Physoderes minor* (junior synonym) (UCR\_ENT 00073593) (BPBM); same collection



**Fig. 16.** Dorsal habitus images for junior synonym holotypes of species in *Physoderes* Westwood, 1845 (except *P. minor* = paratype). Scale bars = 2 mm.

data as preceding, paratype of *Physoderes minor* (junior synonym) (UCR\_ENT 00046626) (CAS); 1 juv., Piti, 13.46° N, 144.69166° E, 5 m, 22 May 1936, O.H. Swezey leg. (UCR\_ENT 00046624) (CAS); 1 ♀, Pt Oca, 13.503° N, 144.771° E, May 1945, G.E. Bohart and J.L. Gressitt leg. (UCR\_ENT 00073590) (BPBM); 1 ♂, same collection data as preceding but 19 May 1945 (UCR\_ENT 00073587) (BPBM); 1 ♀, same collection data as preceding but 15 May 1945 (UCR\_ENT 00073594) (BPBM); 1 ♀, Santa Rita, 13.37416° N, 144.70805° E, 69 m, 25 Jan. 1948, collector unknown (UCR\_ENT 00031424) (USNM); 1 ♂, unknown locality, 13.44416° N, 144.79361° E, 37 m, no date provided, D.T. Fullaway leg. (UCR\_ENT 00031413) (USNM); 2 ♀♀, Guam, 1937, R.G. Oakley leg. (UCR\_ENT 00031414, UCR\_ENT 00031415) (USNM); 2 ♂♂, Yigo, 13.53194° N, 144.88027° E, 126 m, 13 Nov. 1936, O.H. Swezey leg., paratypes of *Physoderes minor* (junior synonym) (UCR\_ENT 00073578, UCR\_ENT 00073580) (BPBM).

INDONESIA: Java: 1 ♂, Ambarawa, 7.25611° S, 110.40638° E, no date provided, collector unknown (UCR\_ENT 00024014) (RMNH); 1 ♂, Buitenzorg (Bogor), 6.58916° S, 106.79305° E, 250 m, Jan. 1926, L.G.E. Kalshoven leg., holotype of *Physoderes kalshoveni* (junior synonym) (UCR\_ENT 00023947) (RMNH); 1 ♀, Bogor, 6.58916° S, 106.79305° E, 240 m, 28 Apr. 1954, A.H.G. Alston leg. (UCR\_ENT 00069413) (BMNH); 1 ♀, Bogor, 6.5897° S, 106.7914° E, 2 Jul. 1936, J.v.d. Vecht leg. (UCR\_ENT 00024013) (RMNH); 1 ♂, Samarang, 6.96666° S, 110.41666° E, 4 m, Jun. 1910, E. Jacobson leg. (UCR\_ENT 00024012) (RMNH). – Maluku: 1 ♂, Ambon County, Waai, Ambon Island, 3.565° S, 128.32083° E, 93 m, 10 Mar. 1965, A.M.R. Wegner leg. (UCR\_ENT 00073586) (BPBM). – Larat: 1 ♀, 7.78777° S, 131.81694° E, Dec. 1907, F. Muir leg. (UCR\_ENT 00046621) (CAS). – Sumatra: 1 subadult, Sumatera Barat (West Sumatra), 0.74° N, 100.8° E, no date provided, Muller leg. (UCR\_ENT 00024032) (RMNH).

MALAYSIA: Kuala Lumpur: 1 ♀, 3.13888° N, 101.68694° E, 43 m, 5 Feb. 1940, N.C.E. Miller leg., paratype of *P. patagiata* (junior synonym) (UCR\_ENT 00069396) (BMNH). – Penang: 6 ♂♂, Penang Island, 5.37027° N, 100.2375° E, 198 m, no date provided, Baker leg. (UCR\_ENT 00031397–UCR\_ENT 00031402); 8 ♀♀, same collection data as preceding (UCR\_ENT 00031403–UCR\_ENT 00031410) (USNM). – Sarawak: 1 ♀, Kuching, 1.53111° N, 110.34416° E, 12 m, no date provided, collector unknown (UCR\_ENT 00069397) (BMNH).

NORTHERN MARIANA ISLANDS: 1 ♂, Saipan, Pagan Island, 18.13555° N, 145.79111° E, 155 m, 22 Aug. 1954, G. Corwin leg. (UCR\_ENT 00073582) (BPBM); 1 ♀, same collection data as preceding (UCR\_ENT 00073591) (BPBM); 1 subadult, same collection data as preceding (UCR\_ENT 00073597) (BPBM); 1 juv., same collection data as preceding (UCR\_ENT 00073598) (BPBM).

SINGAPORE: 1 ♂, 1.27166° N, 103.83416° E, 12 m, no date provided, Baker leg. (UCR\_ENT 00031411) (USNM).

## Redescription

### Male

BODY LENGTH. Small, total length 7.64 mm, SD ± 0.21 (Appendix).

COLORATION (Figs 14, 16–17). Brown. Head brown. Scape, pedicel and basiflagellomere of antenna light brown, distiflagellomere basally light brown, straw-colored apically. First segment of labium light brown, second segment straw-colored, third segment brown. Pronotum of thorax anterior lobe light brown to dark brown with straw-colored ridges, posterior lobe light brown to brown, with straw-colored posterior margin including parascutellar lobe, scutellum basally brown, apically straw-colored including scutellar process, pleuron brown to dark brown, sternum brown to dark brown. Corium of hemelytron light brown to brown, membrane dark brown. Fore femora of legs straw-colored, sub-basally and apically



with brown annulations, tibiae straw colored, medially and apically with brown annulations, tarsi and claws straw-colored to brown. Abdomen dorsally yellowish-orange, ventrally straw-colored with brown and dark brown patterns, anterior half of connexivum dark brown, posterior half straw-colored, exposed part of pygophore brown or dark brown.

**VESTITURE.** Sparsely setose. Head with some curved setae and short, fine, adpressed setae, ventral surface of postocular lobe with sparse, setigerous tubercles, with pair of long, straight setae on postocular lobe posterior to ocelli. Anterior lobe of thorax with tuberculated, short, curved setae on lateral margins and along dorsal ridges, posterior lobe with short, curved setae on humeral angle and sparsely distributed along dorsal surface. Corium of hemelytron with short, curved setae. Legs with two rows of spines and setigerous tubercles, tibia with regular rows of tuberculated, stout, sharp setae. Connexival margin of abdomen with a few clubbed setae on each segment, or connexival margin with no prominent setae.

**HEAD.** Short conical; maxillary plate rounded apically; scape reaching apex of clypeus; eye hemispherical in dorsal view, less than  $\frac{1}{5}$  length of head.

**THORAX.** Antero-lateral paired projections acute, diverging; surface of anterior lobe with low ridges; median pronotal depression not contiguous with transverse sulcus; paramedian carina weakly defined; anterior pronotal lobe longer than posterior lobe, equal width to or slightly narrower than posterior lobe, higher than posterior lobe in lateral view; parascutellar lobe rounded, skewed towards median; scutellum semicircular, scutellar process long, apex rounded or spatulate.

**HEMELYTRON.** Not reaching tip of abdomen.

**LEGS.** Same as genus description.

**ABDOMEN.** Ovoid, with rounded terminal margin; connexival margin slightly undulating, posterior margin not elevated.

**GENITALIA.** Anterior margin of mediosternite 8 undulating, with medial apodeme; transverse bridge of pygophore extremely narrow, only consisting of margin of anterior opening of pygophore, margin of anterior opening rounded, apodeme absent, apical margin of posterior opening smooth; cup-like sclerite apically rounded with adjacent paired round protuberances; arms of basal plate rounded; ductifer with sclerotized rounded ring; endosomal struts apically subacute, basally divided into two plates converging medially to form a ridge; shape of dorsal phallothecal sclerite subacute, with short, apical lobes and rounded lateral plates at apex.

### **Female**

Similar to male except slightly narrower anterior pronotal lobe width (2.29 mm average) than posterior lobe width (2.64 mm average).

### **Ecology**

This species has been recorded to feed on curculionid larvae and has been collected on decaying plant material including fallen banana (Musaceae) logs, rotten papaya (Caricaceae) plant, rotten pumpkin (Cucurbitaceae), on logs, on rotten boards on the ground and beneath rotten breadfruit (Moraceae).

### **Distribution**

This species has the most widespread distribution of all Oriental physoderines and can be found in peninsular Malaysia, Sumatra, Singapore, Java, Christmas Island, Ambon Island, Guam and Saipan. The presence of *P. curculionis* in Guam and Saipan is an odd distribution that questions whether this could be

a secondary introduction, considering their association with banana, pumpkin and papaya plant material and curculionid larvae.

### Remarks

This species is confirmed to belong to the *Physoderes* clade based on the phylogenetic analysis above. A number of names have been synonymized under *P. curculionis* based on examination of the type material. These are *P. insulanus*, *P. kalshoveni*, *P. patagiata* and *P. minor*. All share the diagnostic characters of *P. curculionis* listed above including those of the male genitalic morphology (for *P. minor* and *P. kalshoveni*), have no distinct features of their own, and are thus synonymized here.

*Physoderes esakii* Cao *et al.*, 2011

Figs 13–14, 17

*Physoderes esakii* Cao, Tomokuni & Cai, 2011: 23, figs 1–12.

*Epirodera latithorax* Esaki, 1931: 212 (nomen nudum).

*Physoderes latithorax* – Maldonado 1990: 380.

### Re-diagnosis

This species is recognized among species of *Physoderes* by its short hemelytra, not reaching the abdominal apex, the slender scutellar spine, the round parascutellar lobe and the simple phallosoma without lateral prolongations as illustrated in the original description and color images provided by Cao *et al.* (2011). This species is most similar to *P. fuliginosa* but can be differentiated on these characters.

### Description

#### Male

Refer to Cao *et al.* (2011) for full description.

### Distribution

This species is only recorded from Botel Tobago (Orchid Island [Lanyu], Taiwan).

### Remarks

A re-diagnosis is provided here, as the original diagnosis (under Remarks in Cao *et al.* 2011) refers to the sexually dimorphic enlargement of the anterior pronotal lobe also present in other species of *Physoderes*. Two female specimens likely to be conspecifics collected by J.F. Tsai on Botel Tobago island share the same short hemelytron not reaching the abdominal apex, but without an enlarged anterior pronotal lobe and with a rounder abdomen (J.F. Tsai and D. Rédei, pers. comm.; images examined here).

*Physoderes fuliginosa* (Stål, 1870)

Figs 8, 13–14, 17, 19; Appendix

*Epirodera fuliginosa* Stål, 1870: 693.

*Physoderes fuliginosa* – Maldonado 1990: 380.

### Diagnosis

This species is recognized among species of *Physoderes* by the elongate head, the scape reaching the apex of the clypeus, the hemispherical eye that is not distinctly protruding, the acute and diverging antero-lateral projection of the anterior pronotal lobe, the anterior pronotal lobe being wider than the posterior lobe, the rounded parascutellar lobe, the slender and straw-colored scutellar process, the pygophore

apical margin of the posterior opening having a short medial process and the phallosoma lacking flap-like prolongations. This species is most similar to *P. minime* sp. nov., but can be differentiated from it by the larger size, darker coloration, the hemelytron close to or attaining the tip of the abdomen, the presence of an apical median process on the posterior opening of the pygophore, and the lack of flap-like prolongations of the phallosoma.

### Material examined

#### Holotype

PHILIPPINES: ♀, specimen image made available by T. Ishikawa, label information not examined here (NHRS).

#### Other material

INDONESIA: Borneo: 2 ♂♂, 1.10611° S, 114.14388° E, no date provided, Muller leg. (UCR\_ENT 00024015, UCR\_ENT 00024016) (RMNH). – Maluku: 2 ♂♂, Buru Island, 3.3925° S, 126.78194° E, 1903, collector unknown (UCR\_ENT 00069252, UCR\_ENT 00069253) (BMNH). – Sulawesi: 1 ♀, Gorontalo, 0.5525° N, 123.06555° E, no date provided, A. Forsten leg. (UCR\_ENT 00024018) (RMNH). – Tidore Island: 1 ♂, Kampung Guaepaji, 0.67333° N, 127.31166° E, 5–10 Jul. 1981, A.C. Messer leg. (UCR\_ENT 00031353) (USNM).

PAPUA NEW GUINEA: 1 ♀, Manus Province, Manus Island, 2.09388° S, 146.87583° E, no date provided, collector unknown (UCR\_ENT 00069225) (BMNH).

PHILIPPINES: Basilan: 1 ♂, Basilan Island, 6.69277° N, 122.02305° E, no date provided, collector unknown (UCR\_ENT 00069249) (BMNH). – Bukidnon: 29 ♀♀, Tangcolan, 7.97611° N, 125.02583° E, no date provided, Baker leg. (UCR\_ENT 00030985–UCR\_ENT 00030999, UCR\_ENT 00031313, UCR\_ENT 00031354–UCR\_ENT 00031366) (USNM); 37 ♂♂, same collection data as preceding (UCR\_ENT 00031278–UCR\_ENT 00031312, UCR\_ENT 00031314, UCR\_ENT 00031435) (USNM). – Leyte: 2 ♂♂, Biliran Island, 11.26722° N, 124.64833° E, no date provided, Baker leg. (UCR\_ENT 00031347, UCR\_ENT 00031348) (USNM); 1 ♀, 11.11388° N, 124.7375° E, 5 Jan. 1915, G. Bottcher leg. (UCR\_ENT 00069223) (BMNH); 1 ♂, same collection data as preceding but 3 May 1915 (UCR\_ENT 00069247) (BMNH). – Luzon: 1 ♂, Camarines Sur, Mt Isarog, SLuzon, 13.65916° N, 123.37333° E, 1219 m, 13 Apr. 1916, G. Bottcher leg. (UCR\_ENT 00069243) (BMNH); 1 ♀, Laguna, Mt Makiling, 14.13° N, 121.2° E, 1 May 1931, collector unknown (UCR\_ENT 00046632) (CAS); 1 ♂, Laguna County, Los Banos, NLuzon, 14.17° N, 121.24416° E, 23 Dec. 1914, G. Bottcher leg. (UCR\_ENT 00069234) (BMNH); 1 ♀, Mt Makiling, 14.13333° N, 121.2° E, 244 m, 5 May 1932, F.C. Hadden leg. (UCR\_ENT 00046631) (CAS); 1 ♀, Paete, Laguna, 14.3675° N, 121.52972° E, no date provided, W. Schultze leg. (UCR\_ENT 00069224) (BMNH); 4 ♂♂, Balaban, N Luzon, 16.98916° N, 121.12111° E, 1219 m, 30 Jan. 1917, G. Bottcher leg. (UCR\_ENT 00069200, UCR\_ENT 00069201, UCR\_ENT 00069238, UCR\_ENT 00069239) (BMNH); 5 ♂♂, same collection data as preceding but Mar. 1918 (UCR\_ENT 00069202, UCR\_ENT 00069203, UCR\_ENT 00069235–UCR\_ENT 00069237) (BMNH); 1 ♂, same collection data as preceding but 2 Jul. 1917 (UCR\_ENT 00069204) (BMNH); 2 ♂♂, Imugan, N Luzon, 16.16166° N, 120.93888° E, 1219 m, May 1917, G. Bottcher leg. (UCR\_ENT 00069205, UCR\_ENT 00069206) (BMNH); 1 ♂, same collection data as preceding but 30 Jun. 1917 (UCR\_ENT 00069207) (BMNH); 1 ♂, same collection data as preceding but 25 Jun. 1917 (UCR\_ENT 00069240) (BMNH); 1 ♀, Irian, 16.42111° N, 120.56888° E, no date provided, Benguet and McGregor leg. (UCR\_ENT 00031351) (USNM); 6 ♂♂, Mt Banahao, 14.0675° N, 121.4925° E, no date provided, Baker leg. (UCR\_ENT 00031341–UCR\_ENT 00031346) (USNM); 1 ♀, same collection data as preceding (UCR\_ENT 00031386) (USNM); 1 ♂, Mt Banahao, N Luzon, 14.0675° N, 121.4925° E, 610 m, 21 Jun. 1914, G. Bottcher leg. (UCR\_ENT 00069198) (BMNH); 1 ♂, same collection data as preceding but 29 Apr. 1914 (UCR\_ENT 00069197) (BMNH); 1 ♂, same collection data as preceding but 10 Jun. 1914 (UCR\_ENT 00069199) (BMNH);

1 ♂, same collection data as preceding but 17 Apr. 1914 (UCR\_ENT 00069232) (BMNH); 1 ♂, same collection data as preceding but 18 Aug. 1914 (UCR\_ENT 00069195) (BMNH); 1 ♂, same collection data as preceding but 23 Jun. 1914 (UCR\_ENT 00069233) (BMNH); 1 ♂, same collection data as preceding but 1 May 1914 (UCR\_ENT 00069196) (BMNH); 1 ♂, Mt. Bulusan, S Luzon, 12.76916° N, 124.05666° E, 610 m, Sep. 1917, G. Bottcher leg. (UCR\_ENT 00069242) (BMNH); 1 ♀, Mt Maquiling, 14.12444° N, 121.22555° E, 18 Jul. 1936, R.L. Usinger leg. (UCR\_ENT 00046646) (CAS); 1 juv., Santo Tomas, 14.08694° N, 121.19444° E, 1924, collector unknown (UCR\_ENT 00031390) (USNM); 3 ♀♀, Nueva Vizcaya, Imugin, 16.16138° N, 120.93972° E, 589 m, no date provided, Baker leg. (UCR\_ENT 00031323, UCR\_ENT 00031329, UCR\_ENT 00031387); 6 ♂♂, same collection data as preceding (UCR\_ENT 00031324–UCR\_ENT 00031328, UCR\_ENT 00031330) (USNM). – Mindanao: 8 ♂♂, Butuan, 8.9475° N, 125.54055° E, no date provided, Baker leg. (UCR\_ENT 00031315–UCR\_ENT 00031322); 6 ♀♀, same collection data as preceding (UCR\_ENT 00031367–UCR\_ENT 00031371, UCR\_ENT 00026006) (USNM); 1 ♂, Galog River, Mt Apo, 6.98555° N, 125.25972° E, 1829 m, no date provided, C.F. Clagg leg. (UCR\_ENT 00068947) (AMNH); 1 ♂, Iligan, 8.22805° N, 124.24527° E, no date provided, collector unknown (UCR\_ENT 00069241) (BMNH); 2 ♂♂, no date provided, Baker leg. (UCR\_ENT 00031349, UCR\_ENT 00031350) (USNM); 1 ♂, Mamungan, N Mindanao, 8.11722° N, 124.21861° E, 1272 m, 18 Feb. 1915, G. Bottcher leg. (UCR\_ENT 00069227) (BMNH); 1 ♂, same collection data as preceding but 3 Mar. 1915 (UCR\_ENT 00069228) (BMNH); 1 ♀, same collection data as preceding but 22 Feb. 1915 (UCR\_ENT 00069216) (BMNH); 1 ♀, same collection data as preceding but 19 Feb. 1915 (UCR\_ENT 00069217) (BMNH); 1 ♂, same collection data as preceding (UCR\_ENT 00069226) (BMNH); 1 ♂, Momungan, N Mindanao, 19 Feb. 1915, G. Bottcher leg. (UCR\_ENT 00069209) (BMNH); 4 ♂♂, Surigao del Norte, 9.67139° N, 125.52861° E, 130 m, no date provided, Baker leg. (UCR\_ENT 00031331–UCR\_ENT 00031334); 6 ♀♀, same collection data as preceding (UCR\_ENT 00031335, UCR\_ENT 00031372–UCR\_ENT 00031376) (USNM); 1 ♂, no date provided, Baker leg. (UCR\_ENT 00031436) (USNM); 1 ♂, Surigao, N Mindanao, 9.67138° N, 125.52888° E, 130 m, 20 Oct. 1915, G. Bottcher leg. (UCR\_ENT 00069231) (BMNH); 1 ♂, same collection data as preceding but 1 Nov. 1915 (UCR\_ENT 00069230) (BMNH); 2 ♂♂, same collection data as preceding but 13 Nov. 1915 (UCR\_ENT 00069208, UCR\_ENT 00069229) (BMNH); 1 ♂, Misamis Oriental, Hindangon, 20 km S of Gingoog, 7.81361° N, 124.96888° E, 600 m, 9–18 Apr. 1960, H.M. Torre Villas leg. (UCR\_ENT 00073628) (BPBM); 1 ♀, no date provided, collector unknown (UCR\_ENT 00069222) (BMNH); 1 ♀, no date provided, collector unknown (UCR\_ENT 00069220) (BMNH). – Sulu Province: 1 ♂, Siasi Island, Siasi, 5.53388° N, 120.86138° E, 300 m, 26 Aug. 1958, H.E. Milliron leg. (UCR\_ENT 00073627) (BPBM). – Mindoro: 2 ♂♂, Abra de Llog, 13.45° N, 120.73333° E, 9 m, no date provided, W. Schultze leg. (UCR\_ENT 00069211, UCR\_ENT 00069248) (BMNH); 1 ♀, 13.12888° N, 121.06611° E, 112 m, no date provided, S. Theodoro leg. (UCR\_ENT 00014053) (RMNH); 1 ♂, Occidental Mindoro, San Jose, 12.35361° N, 121.06666° E, 30 Jan. 1945, E.S. Ross leg. (UCR\_ENT 00046630) (CAS). – Negros: 1 ♀, Negros Oriental, Mt Talinas (Mt Talinis), 9.24416° N, 123.1775° E, 1020 m, 28 Jun. 1958, H.E. Milliron leg. (UCR\_ENT 00073626) (BPBM). – Polillo: 1 ♂, Polillo Island, 14.77555° N, 121.92194° E, 54 m, no date provided, collector unknown (UCR\_ENT 00024017) (RMNH); 2 ♂♂, no date provided, W. Schultze leg. (UCR\_ENT 00069212, UCR\_ENT 00069213) (BMNH); 1 ♀, Polillo Island, 14.71805° N, 121.94583° E, 27 m, no date provided, collector unknown (UCR\_ENT 00069219) (BMNH). – Romblon: 3 ♂♂, Sibuyan Island, 12.4125° N, 122.55888° E, 1529 m, no date provided, Baker leg. (UCR\_ENT 00031338–UCR\_ENT 00031340); 5 ♀♀, same collection data as preceding (UCR\_ENT 00031381–UCR\_ENT 00031385) (USNM). – Samar: 5 ♂♂, Borongan, 11.60777° N, 125.43277° E, 19 m, no date provided, W. Schultze leg. (UCR\_ENT 00069214, UCR\_ENT 00069215, UCR\_ENT 00069244–UCR\_ENT 00069246) (BMNH); 2 ♂♂, 12.005° N, 124.77416° E, 37 m, no date provided, Baker leg. (UCR\_ENT 00031336, UCR\_ENT 00031337) (USNM); 4 ♀♀, same collection data as preceding (UCR\_ENT 00031377–UCR\_ENT 00031380) (USNM). – Siargao: 1 ♂, 9.84805° N, 126.04583° E, 57 m, no date provided, collector unknown (UCR\_ENT 00069251) (BMNH). – Panay: 1 ♀, NW Panay, 11.32083° N, 122.53722° E, 180 m, no date provided, Baker leg. (UCR\_ENT 00031388) (USNM). – 1 ♂, Philippine

Islands, 12.82027° N, 121.79694° E, 1912, J.J. Mounsey leg. (UCR\_ENT 00069210) (BMNH); 1 ♀, same collection data as preceding (UCR\_ENT 00069218) (BMNH).

SOLOMON ISLANDS: 1 ♀, Guadalcanal, Guadalcanal Lavoro, 9.57722° S, 160.14555° E, 18 Feb. 1934, H.T. Pagden leg. (UCR\_ENT 00046633) (CAS).

## Redescription

### Male

BODY LENGTH. Medium, total length 10.47 mm, SD ± 0.54 (Appendix).

COLORATION (Figs 14, 17). Dark brown. Head dark brown. Scape and pedicel of antenna light brown and brown, basiflagellomere brown, distiflagellomere basally brown, apically straw-colored. First segment of labium brown, second segment basally and apically brown, medially straw-colored, third segment brown. Pronotum of thorax dark brown with light brown markings, scutellum basally dark brown with scutellar process straw-colored, pleuron straw-colored with brown and dark brown patterns, sternum dark brown with brown suffusion. Corium of hemelytron brown to dark brown, membrane dark brown. Femur and tibia of legs straw-colored with medial and apical brown annulations, tarsus and claw light brown. Abdomen dorsally yellowish-orange, ventrally straw-colored with sub-lateral dark brown patterns, anterior half of connexivum dark brown, posterior half straw-colored, exposed part of pygophore brown.

VESTITURE. Sparsely setose. Head with widespread curved setae, ventral surface of postocular lobe with sparse, setigerous tubercles, with pair of long, straight setae on postocular lobe posterior to ocelli. Anterior lobe of thorax with irregular row of tuberculated, short, curved setae on lateral margins and short, setigerous tubercles dispersed on dorsal surface, posterior lobe with short, curved setae on humeral angle and sparsely distributed along dorsal surface. Corium of hemelytron with short, curved setae. Legs with two rows of spines and setigerous tubercles, tibia with regular rows of tuberculated, stout, sharp setae. Connexival margin of abdomen with no prominent setae.

HEAD. Elongate conical; maxillary plate rounded apically; scape reaching apex of clypeus; eye hemispherical in dorsal view, less than 1/5 length of head.

THORAX. Antero-lateral paired projections acute, diverging; surface of anterior lobe with low ridges; median pronotal depression not contiguous with transverse sulcus; paramedian carina weakly defined; anterior pronotal lobe longer and wider than posterior lobe, higher than posterior lobe in lateral view; parascutellar lobe rounded; scutellum rounded triangular, scutellar process long, apex subacute.

HEMELYTRON. Reaching tip of abdomen.

LEGS. Same as genus description.

ABDOMEN. Connexival margin slightly undulating, posterior margin not elevated.

GENITALIA. Anterior margin of mediosternite 8 undulating, without medial apodeme; transverse bridge of pygophore narrow, margin of anterior opening angular, apodeme present, apical margin of posterior opening with small medial process; cup-like sclerite apically rounded with sclerotized paired latero-ventral slight protuberance; arms of basal plate converging; ductifer membranous; endosomal struts conical, with subacute apex, divided into two arms basally; dorsal phallosomal sclerite not sclerotized.

### Female

Similar to male, except with anterior pronotal lobe (2.39 mm average) distinctly narrower than posterior lobe (3.20 mm average) and with median pronotal depression contiguous with transverse sulcus.

### Ecology

Nothing is known about the biology of this species.

### Distribution

This species is widespread across the Philippines island archipelago and also recorded from Borneo, parts of the Indonesian archipelago, Papua New Guinea and the Solomon Islands.

### Remarks

The holotype of *P. fuliginosa* is a female with a narrow anterior pronotal lobe and unknown locality, which makes it difficult to associate it with a male. Multiple male specimens found on Mindanao with

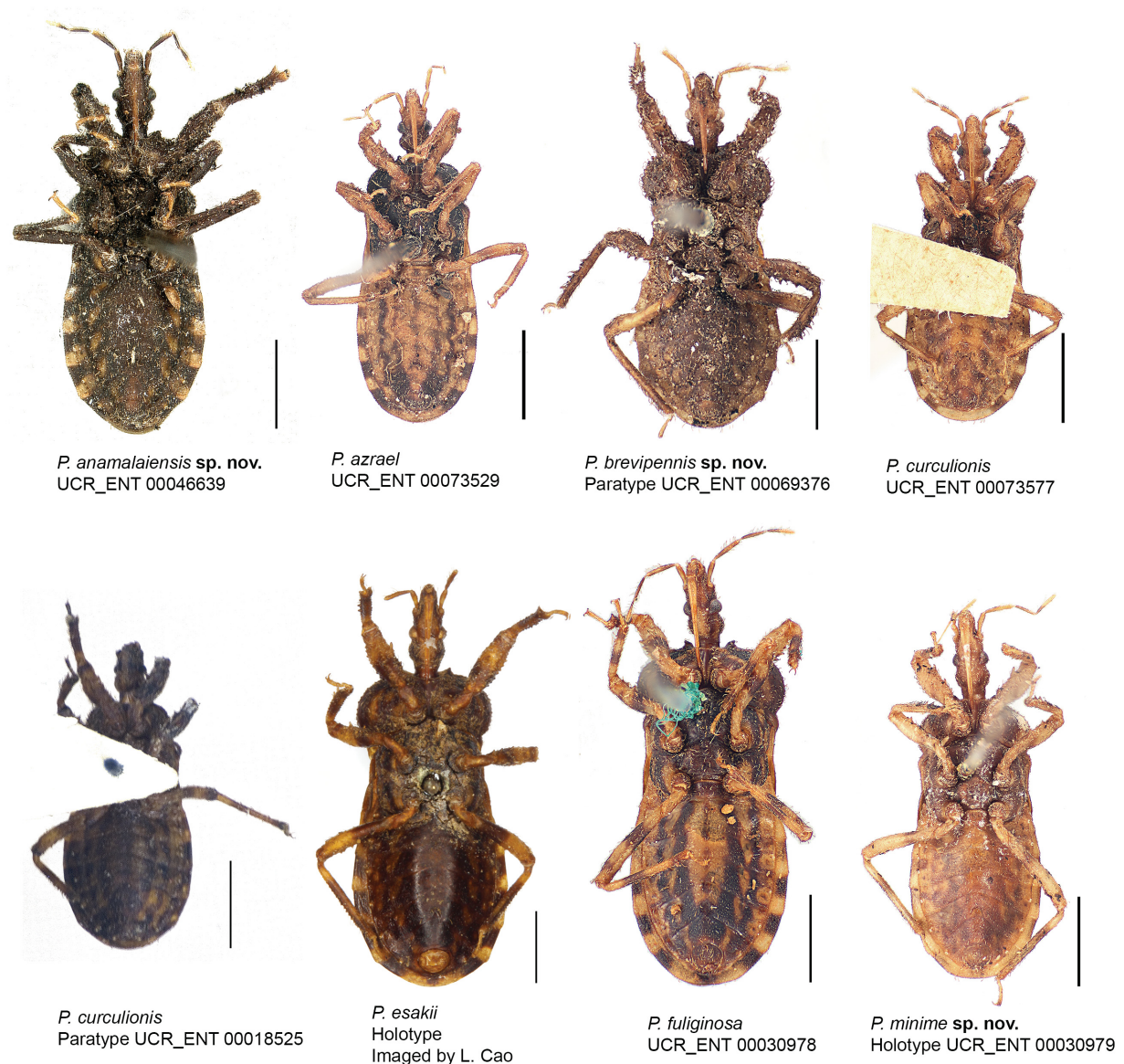


Fig. 17. Ventral habitus images for species of *Physoderes* Westwood, 1845 (partial). Scale bars = 2 mm.

corresponding females that match the holotype morphology confirm that the holotype is most likely from the Philippines region and the redescription here is based on the males from Mindanao. The description of *P. fuliginosa* is difficult, as specimens from the Philippines show variation in overall size and coloration, but do not differ morphologically. Dissections of male genitalia from different geographic localities also do not show any variation. Hence, *P. fuliginosa* is here considered to be highly variable in size and general coloration.

*Physoderes minime* sp. nov.

[urn:lsid:zoobank.org:act:6B773A65-2FB4-4063-8EE6-7CEFA2ADDB5A](https://doi.org/10.3896/abris.6B773A65-2FB4-4063-8EE6-7CEFA2ADDB5A)

Figs 8, 14, 17, 19–20; Appendix

### Diagnosis

This species is recognized among species of *Physoderes* by the elongate head, which is as long as the pronotum, the scape not reaching the apex of the clypeus, the hemispherical eye being slightly flattened, the antero-lateral projection of the anterior pronotal lobe subacute and diverging, the anterior pronotal lobe being wider than the posterior lobe, the rounded parascutellar lobe, the scutellar process being slender and straw-colored and the short hemelytron which does not reach the tip of the abdomen. This species is most similar to *P. fuliginosa*, but can be differentiated from it by the smaller size, yellowish coloration, the short hemelytron and by having a smooth apical margin on the posterior opening of the pygophore, as well as a small apical dorsal phalloshecal sclerite.

### Etymology

The name *minime* is a noun in apposition, after the fictional movie character Mini-Me from the Austin Powers movie series. The name given is to describe the miniaturized resemblance of this species to the co-occurring larger *P. fuliginosa*.

### Material examined

#### Holotype

PHILIPPINES: ♂, Luzon, Mt Banahao, 14.0675° N, 121.4925° E, no date provided, Baker leg. (UCR\_ENT 00030979) (USNM).

#### Paratypes

PHILIPPINES: Panay: 1 ♂, Capiz, Capiz Jamindan, 11.44055° N, 122.5925° E, no date provided, W. Schultze leg. (UCR\_ENT 00069250) (BMNH). – Luzon: 2 ♂♂, Mt Banahao, 14.0675° N, 121.4925° E, no date provided, Baker leg. (UCR\_ENT 00031432, UCR\_ENT 00031433) (USNM); 1 ♂, Mt Makiling, 14.13055° N, 121.2° E, 963 m, no date provided, Baker leg. (UCR\_ENT 00031434) (USNM).

#### Other material

PHILIPPINES: Luzon: 1 ♀, Albay Province, Mt Mayon, 16 km NW of Lagaspi, 13.25666° N, 123.685° E, 900 m, 4 May 1962, H.M. Torrevillas leg. (UCR\_ENT 00073629) (BPBM); 1 ♀, Laguna, 4 km SE of Los Banos, Mt. Makiling, 14.14112° N, 121.2097° E, 8 Apr. 1977, L. Watrous leg. (UCR\_ENT 00031438) (USNM); 1 ♂, same collection data as preceding but 9 Apr. 1977 (UCR\_ENT 00031352) (USNM); 1 ♀, Laguna Co., Los Banos, N Luzon, 14.17° N, 121.24416° E, 3 Nov. 1914, G. Bottcher leg. (UCR\_ENT 00069221) (BMNH); 3 ♂♂, same collection data as for holotype (UCR\_ENT 00031429–UCR\_ENT 00031431) (USNM); 1 ♀, same collection data as preceding (UCR\_ENT 00031437) (USNM); 1 ♀, Mt Maquiling, 14.12444° N, 121.22555° E, 18 Jul. 1936, R.L. Usinger leg. (UCR\_ENT 00046647) (CAS).

## **Description**

### **Male**

**BODY LENGTH.** Medium, total length 8.64 mm, SD  $\pm$  0.28 (Appendix).

**COLORATION** (Figs 14, 17). Yellowish-brown. Head yellowish to light brown. Scape, pedicel and distiflagellomere of antenna straw-colored, basiflagellomere basally brown, apically straw-colored. First segment of labium light brown, second segment straw-colored, third segment brown. Pronotum of thorax brown with straw-colored markings along ridges, scutellum basally brown, apically straw-colored including scutellar process, pleuron straw-colored with brown suffusion, sternum brown. Corium of hemelytron light brown to brown, membrane light brown to brown. Femora and tibiae of legs straw-colored with sub-basal and apical light brown annulations, tarsi and claws straw-colored. Abdomen dorsally yellowish orange, ventrally straw-colored with lateral brown suffusion, anterior half of connexivum dark brown, posterior half straw-colored, exposed part of pygophore straw-colored brown.

**VESTITURE.** Sparsely setose. Head with widespread curved setae, ventral surface of postocular lobe with sparse, setigerous tubercles, with pair of long, straight setae on postocular lobe posterior to ocelli. Anterior lobe of thorax with irregular row of tuberculated, short, curved setae on lateral margins and fine, adpressed setae on dorsal surface, posterior lobe with short, curved, setigerous tubercles on humeral angle and glabrous on dorsal surface. Corium of hemelytron with short, curved setae. Legs with two rows of spines and setigerous tubercles, tibia with regular rows of tuberculated, stout, sharp setae. Connexival margin of abdomen with no prominent setae.

**HEAD.** Elongate conical; maxillary plate rounded apically; scape not reaching apex of clypeus; eye hemispherical in dorsal view.

**THORAX.** Antero-lateral paired projections subacute; surface of anterior lobe with low ridges; median pronotal depression not contiguous with transverse sulcus; paramedian carina weakly defined; anterior pronotal lobe longer and wider than posterior lobe, higher than posterior lobe in lateral view; parascutellar lobe rounded; scutellum rounded triangular, scutellar process long, apex subacute.

**HEMELYTRON.** Not attaining tip of abdomen.

**LEGS.** Same as genus description.

**ABDOMEN.** Connexival margin slightly undulating, posterior margin not elevated.

**GENITALIA.** Transverse bridge of pygophore broad, margin of anterior opening angular, apodeme present, apical margin of posterior opening smooth; cup-like sclerite apically rounded with sclerotized paired latero-ventral slight protuberance; arms of basal plate converging; ductifer membranous; endosomal struts apically spatulate, basally divided into two plates; shape of dorsal phallosclerite subacute with short, apical lobes and rounded lateral plates at apex.

### **Female**

Similar to males except anterior pronotal lobe (2.07 mm average) narrower than posterior lobe (2.60 mm average) and median pronotal depression contiguous with transverse sulcus.

## **Ecology**

Nothing is known about the biology of this species.



### Distribution

This species is recorded from Luzon Island and Panay Island of the Philippines archipelago. Most specimens were collected from two localities: Mt Banahao and Mt Makiling in Luzon.

### Remarks

This species differs from the co-occurring *P. fuliginosa* based on the diagnostic characters listed above and is placed within *Physoderes* based on the phylogenetic analysis conducted above.

### *Physoderes muluensis* sp. nov.

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Figs 8, 15, 19–20; Appendix

### Diagnosis

This species is recognized among congeners by the males having the anterior pronotal lobe narrower than the posterior lobe, the median pronotal depression being contiguous with the transverse sulcus, the fore femur slightly incrassate and by the narrow transverse bridge of the pygophore. This species is distinguished from other species of *Physoderes* by the distinctly small size and the anterior pronotal lobe not being inflated in males.

### Etymology

The name *muluensis* is a noun in apposition derived from the type locality Gunung Mulu National Park, Sarawak.

### Material examined

#### Holotype

MALAYSIA: ♂, Sarawak, Mulu National Park, near Base Camp, 4th division Gn. [= Garrison?], 3.97444° N, 114.93638° E, 100 m, no date provided, collector unknown (UCR\_ENT 00069405) (BMNH).

#### Paratypes

MALAYSIA: Sarawak: 2 ♂♂, Gunong Mulu National Park, 3.96638° N, 114.78305° E, 215 m, May–Aug. 1978, P.M. Hammond and J.E. Marshall leg. (UCR\_ENT 00069401, UCR\_ENT 00069403) (BMNH); 2 ♀♀, same collection data as preceding (UCR\_ENT 00069409, UCR\_ENT 00069410) (BMNH); 1 ♀, Mulu National Park, near Base Camp, 4th division Gn. [= Garrison?], 3.97444° N, 114.93638° E, 100 m, May–Aug. 1978, P.M. Hammond and J.E. Marshall leg. (UCR\_ENT 00069411) (BMNH); 1 ♂, same collection data as preceding (UCR\_ENT 00069400) (BMNH).

#### Other material

MALAYSIA: 2 juvs, Sarawak, Gunong Mulu National Park, 3.96638° N, 114.78305° E, 215 m, May–Aug. 1978, P.M. Hammond and J.E. Marshall leg. (UCR\_ENT 00069402, UCR\_ENT 00069404) (BMNH).

### Description

#### Male

BODY LENGTH. Small, total length 7.35 mm, SD ± 0.27 (Appendix).

COLORATION (Fig. 15). Brown. Head brown, lighter towards apex. Scape of antenna brown, pedicel brown with apex straw brown, basi- and distiflagellomeres basally brown and apically straw brown or straw brown entirely. First segment of labium brown, second segment gradation from brown to straw-colored,

third segment straw-colored. Pronotum of thorax brown, sometimes posterior pronotal lobe lighter brown, scutellum brown, pleuron brown, sternum brown. Corium of hemelytron brown, membrane brown. Fore femur of legs brown entirely or basally dark brown, fore tibia straw-colored, basally brown, tarsus and claws straw-colored, mid femur entirely brown or brown with basally straw brown coloration, mid tibia, tarsus and claws brown and straw-colored, hind femur brown and basally straw-colored or straw-colored with medial brown band, hind tibia brown and straw brown, tarsus and claws straw brown. Abdomen dorsally orange-yellow, ventrally brown, connexivum brown with posterior third light brown, exposed part of pygophore brown.

**VESTITURE.** Sparsely setose. Head with some flat, curved setae or with widespread short, fine, adpressed setae, ventral surface of postocular lobe with sparse, setigerous tubercles, with pair of long, straight setae on postocular lobe posterior to ocelli. Anterior lobe of thorax with irregular row of tuberculated, short, curved setae on lateral margins and short, setigerous tubercles dispersed on dorsal surface, posterior lobe with only short, sparse setae. Corium of hemelytron with short, sparse, adpressed setae. Legs with two rows of spines and setigerous tubercles, tibia with a few prominent tuberculated, stout, sharp setae. Posterior margin of connexivum of abdomen with long, fine setae.

**HEAD.** Elongate conical; maxillary plate truncate apically; scape reaching apex of clypeus; eye hemispherical in dorsal view, less than  $\frac{1}{5}$  length of head.

**THORAX.** Antero-lateral paired projections acute, diverging; surface of anterior lobe with low ridges; median pronotal depression contiguous with transverse sulcus; paramedian carina weakly defined; anterior pronotal lobe of equal length to and narrower than posterior lobe, level with posterior lobe in lateral view; parascutellar lobe rounded, skewed towards median; scutellum rounded triangular, scutellar process short, apex rounded or subacute.

**HEMELYTRON.** Not attaining tip of abdomen.

**LEGS.** Same as genus description.

**ABDOMEN.** Connexival margin slightly undulating, posterior margin not elevated.

**GENITALIA.** Anterior margin of mediosternite 8 undulating, without medial apodeme; transverse bridge of pygophore broad, margin of anterior opening angular, apodeme present, apical margin of posterior opening with slight medial protuberance; cup-like sclerite apically rounded, with adjacent paired round protuberances; arms of basal plate parallel to each other; ductifer membranous; endosomal struts conical, subacute apex, divided into two arms basally; shape of dorsal phallosomal sclerite subacute with lateral broad, plate-like prolongations, broad plates angularly oriented towards basal plate.

### **Female**

Similar in size and shape to males.

### **Ecology**

According to labels, specimens were collected in alluvial forest litter from tropical forests. A few specimens were collected using pitfall traps. Specimens collected are often partially or entirely encrusted with debris.

### **Distribution**

Only known from around the type locality.

*Physoderes mysorensis* sp. nov.

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Figs 8, 13, 15, 18–19; Appendix

**Diagnosis**

This species is recognized among species of *Physoderes* by the scape reaching the apex of the clypeus, the small eye, the antero-lateral projection of the anterior pronotal lobe being acute and oriented anteriorly, the anterior pronotal lobe being wide, wider than the posterior lobe in males, only slightly narrower than the posterior lobe in females, the rounded parascutellar lobe, the dark brown scutellum, the scutellar process being straw-colored, subacute and short, and the hemelytron attaining the tip of the abdomen. This species is most similar to *P. anamalaiensis* sp. nov. and can be differentiated by the larger size (10.69–10.96 mm), by having an apodeme on mediosclerite 8, a broad transverse bridge of the pygophore, and the margin of the anterior opening of the pygophore rounded in lateral view and with a sclerotized, angular ductifer.

**Etymology**

The name *mysorensis* is a noun in apposition as a tribute to the type locality Mysore, Karnataka, India where three out of the six specimens examined here were collected.

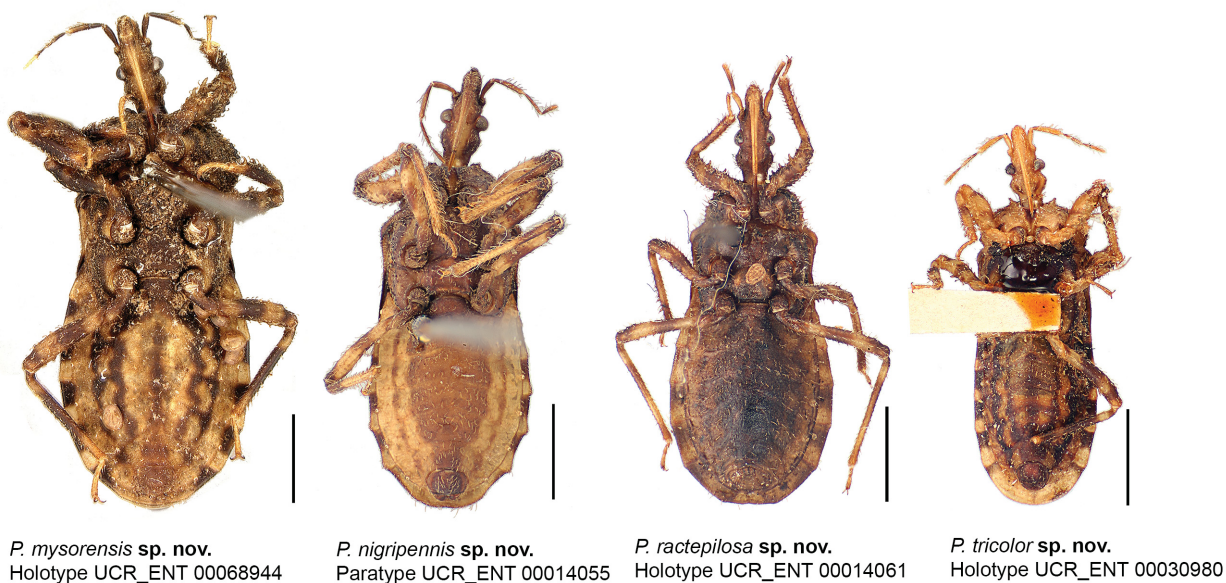
**Material examined**

**Holotype**

INDIA: ♂, Kerala, Trivandrum Co., Ponmudi Range, 8.78638° N, 77.30361° E, 914 m, no date provided, S. Nathan leg. (UCR\_ENT 00068943) (AMNH).

**Paratypes**

INDIA: Kerala: 1 ♀, same collection data as for holotype (UCR\_ENT 00068940) (AMNH); 1 ♂, May 1971, S. Nathan leg. (UCR\_ENT 00068944) (AMNH). – Karnataka: 1 ♂, Mysore Co., Agumbe Ghat, 14.49666° N, 75.0825° E, 610 m, May 1974, S. Nathan leg. (UCR\_ENT 00068945) (AMNH); 2 ♀♀, same collection data as preceding (UCR\_ENT 00068946, UCR\_ENT 00047705) (AMNH).



**Fig. 18.** Ventral habitus images for species of *Physoderes* Westwood, 1845 (partial). Scale bars = 2 mm.

## **Description**

### **Male**

**BODY LENGTH.** Large, total length 10.82 mm, SD  $\pm$  0.14 (Appendix).

**COLORATION** (Figs 15, 18). Dark brown. Head dark brown. Scape, pedicel and basiflagellomere of antenna brown, distiflagellomere basally brown, apically straw-colored. First segment of labium basally brown, apically straw-colored, second segment straw-colored, third segment brown. Pronotum of thorax dark brown, parascutellar lobes lighter in color, scutellum dark brown, scutellar process straw-colored, pleuron dark brown with brown and straw-colored suffusion, sternum dark brown. Corium of hemelytron dark brown, membrane dark brown. Femur of legs straw-colored with medial and apical brown annulations, tibia brown with basal and apical straw-colored brown annulations, tarsus and claw straw-colored. Abdomen dorsally yellowish-orange, ventrally dark brown with suffusion of straw-color and brown, anterior half of connexivum dark brown, posterior half straw-colored, exposed part of pygophore brown.

**VESTITURE.** Sparsely setose. Head with widespread curved setae, ventral surface of postocular lobe with two rows of small, setigerous tubercles, with pair of long, straight setae on postocular lobe posterior to ocelli. Anterior lobe of thorax with irregular row of tuberculated, short, curved setae on lateral margins and short, setigerous tubercles dispersed on dorsal surface, posterior lobe with short, curved setae on humeral angle and sparsely distributed along dorsal surface. Corium of hemelytron with short, curved setae. Legs with two rows of spines and setigerous tubercles, tibia with regular rows of tuberculated, stout, sharp setae. Connexival margin of abdomen with no prominent setae.

**HEAD.** Elongate conical; maxillary plate rounded apically; scape reaching apex of clypeus; eye hemispherical in dorsal view, less than  $\frac{1}{5}$  length of head; height of anteocular lobe level with postocular lobe.

**THORAX.** Antero-lateral paired projections acute; surface of anterior lobe with low ridges; median pronotal depression not contiguous with transverse sulcus; paramedian carina weakly defined; anterior pronotal lobe longer and wider than posterior lobe, higher than posterior lobe in lateral view; parascutellar lobe rounded; scutellum rounded triangular, scutellar process short, apex subacute; mesosternite with median irregular tuberculated protrusion between fore and mid coxae.

**HEMELYTRON.** Attaining tip of abdomen.

**LEGS.** Same as genus description.

**ABDOMEN.** Connexival margin slightly undulating, posterior margin not elevated.

**GENITALIA.** Anterior margin of mediosternite 8 undulating, with medial apodeme; transverse bridge of pygophore broad, margin of anterior opening rounded, apodeme present, apical margin of posterior opening smooth; cup-like sclerite apically rounded and rim ventrally sclerotized; arms of basal plate converging; ductifer with sclerotized angular ring; endosomal struts conical, with subacute apex, divided into two arms basally; shape of dorsal phallosomal sclerite subacute with lateral broad, plate-like prolongations, with short, rounded lateral plates.

### **Female**

Similar to males except anterior pronotal lobe slightly narrower than posterior lobe and median pronotal depression contiguous with transverse sulcus.

## **Ecology**

Nothing is known about the biology of this species.

### Distribution

This species is known from two localities in Southwestern India: Agumbe Ghat, Mysore District, Karnataka and Ponmudi Range, Trivandrum District, Kerala.

### Remarks

This species possesses the enlarged anterior pronotal lobe characteristic of *Physoderes*, along with the associated pronotal modifications, and is thus placed in this genus. The females possess an enlarged anterior pronotal lobe, although not as exaggerated as that of the males, which is quite unique. It is most likely to be closely related to the other *Physoderes* species native to India, *P. anamalaiensis* sp. nov. described above.

### *Physoderes nigripennis* sp. nov.

[urn:lsid:zoobank.org:act:0B62A6F5-805D-41F6-AC29-EB6DDE0144C8](https://doi.org/10.3896/BI.2019.62A6F5-805D-41F6-AC29-EB6DDE0144C8)

Figs 8, 15, 18–20; Appendix

### Diagnosis

This species is recognized among congeners by the elongate conical head, which is densely covered in fine, curved setae, the scape reaching the apex of the clypeus, the eye being distinctly projecting, the antero-lateral pronotal projection being truncate, the anterior pronotal lobe distinctly narrower than the posterior lobe and covered with fine, curved setae along its ridges, the parascutellar lobe rounded and skewed towards median, the apex of the scutellar process straw-colored, the costal margin of the hemelytron black, the connexivum undulating with the posterior margin slightly elevated and beset with short, curved setae, the arms of the basal plate of the articulatory apparatus of the male genitalia being curved and the dorsal phallosclerite being subacute, with lateral rounded plates extending to the lateral surface.

### Etymology

The name *nigripennis* is after the Latin adjective “nigripennis”, meaning with black wings or feathers, to describe the overall black coloration of the hemelytron.

### Material examined

#### Holotype

INDONESIA: ♂, Sumatra, Sumatera Barat (West Sumatra), 0.74° N, 100.8° E, no date provided, E. Jacobson leg. (UCR\_ENT 00023968) (RMNH).

#### Paratypes

INDONESIA: Sumatra, Sumatera Barat (West Sumatra): 1 ♂, Fort de Kock, 0.26694° N, 100.38333° E, 920 m, 1925, E. Jacobson leg. (UCR\_ENT 00023962) (RMNH); 4 ♂♂, same collection data as preceding but 1926 (UCR\_ENT 00023954–UCR\_ENT 00023956, UCR\_ENT 00014055) (RMNH); 1 ♂, Fort de Kock (Bukittinggi), 0.3167° N, 100.3667° E, 920 m, Nov. 1920, E. Jacobson leg. (UCR\_ENT 00068913) (AMNH).

#### Other material

INDONESIA: Sumatra, Sumatera Barat (West Sumatra): Fort de Kock, 0.26694° N, 100.38333° E, 920 m, 1924, E. Jacobson leg. (UCR\_ENT 00023987) (RMNH); 2 ♀♀, same collection data as preceding but 1926 (UCR\_ENT 00023985, UCR\_ENT 00023986) (RMNH); 1 ♀, same collection data as preceding but 1925 (UCR\_ENT 00069414) (BMNH); 9 ♂♂, same collection data as preceding (UCR\_ENT 00023957–UCR\_ENT 00023961, UCR\_ENT 00023963–UCR\_ENT 00023966) (RMNH); 8 ♀♀, same collection data as preceding (UCR\_ENT 00023977–UCR\_ENT 00023984) (RMNH);

1 ♂, Fort de Kock (Bukittinggi), 0.26768° S, 100.38394° E, Nov. 1913, E. Jacobson leg. (UCR\_ENT 00023975) (RMNH); 1 ♀, same collection data as preceding (UCR\_ENT 00023995) (RMNH); 1 ♂, Gunning Singgalang, 0.39° S, 100.33083° E, 1200 m, 1925, E. Jacobson leg. (UCR\_ENT 00023974) (RMNH); 1 ♀, Gunung Singgalang, 1000 m, 1925, E. Jacobson leg. (UCR\_ENT 00023994) (RMNH); 1 ♂, Fort de Kock (Bukittinggi), 0.3167° N, 100.3667° E, 920 m, Nov. 1920, E. Jacobson leg. (UCR\_ENT 00068912) (AMNH); 2 ♀♀, same collection data as preceding (UCR\_ENT 00068914, UCR\_ENT 00068915) (AMNH). – Sumatra, Riau Province: 6 ♂♂, 0.74° N, 100.8° E, no date provided, E. Jacobson leg. (UCR\_ENT 00023967, UCR\_ENT 00023969–UCR\_ENT 00023973); 7 ♀♀, same collection data as preceding (UCR\_ENT 00023988–UCR\_ENT 00023993, UCR\_ENT 00023996) (RMNH). – Sumatra, Sumatera Utara (North Sumatra): 1 ♂, Lake Toba, 2.59194° N, 98.82805° E, 1167 m, no date provided, B. Hagen leg. (UCR\_ENT 00023976) (RMNH).

## Description

### Male

**BODY LENGTH.** Medium, total length 9.12 mm, SD ± 0.29 (Appendix).

**COLORATION** (Figs 15, 18). Brown and dark brown. Head brown with straw-colored setae. Antenna light brown. First segment of labium brown, second segment straw-colored, apically brown, third segment brown. Anterior lobe of pronotum dark brown with brown or light brown markings, posterior lobe brown, scutellum basally brown, apically straw-colored including scutellar process, pleuron brown, sternum brown. Corium of hemelytron reddish-brown with black costal margin, membrane brownish-black. Femora of legs straw-colored with medial and apical brown annulations, tibiae basally brown, apically straw-colored, tarsi and claws light brown. Abdomen dorsally yellowish-orange, ventrally light brown medially and straw-colored laterally with brown suffusion, anterior two-thirds of connexivum brownish-black, posterior third straw-colored, exposed part of pygophore dark brown.

**VESTITURE.** Generally setose. Head with widespread curved setae, ventral surface of postocular lobe with sparse, setigerous tubercles, without pair of long, straight setae on postocular lobe posterior to ocelli. Anterior lobe of thorax with irregular row of tuberculated, short, curved setae on lateral margins and curved setae on anterior portion of dorsal surface, posterior lobe with widespread short, curved setae. Corium of hemelytron with short, curved setae. Legs with two rows of spines and setigerous tubercles, tibia with regular rows of tuberculated, stout, sharp setae. Posterior margin of connexivum of abdomen with short, curved setae.

**HEAD.** Elongate conical; maxillary plate truncate apically; scape reaching apex of clypeus; eye distinctly projecting in dorsal view, less than 1/5 length of head.

**THORAX.** Antero-lateral paired projections truncate; surface of anterior lobe with raised ridges; median pronotal depression contiguous with transverse sulcus; paramedian carina strongly defined; anterior pronotal lobe shorter and narrower than posterior lobe, lower than posterior lobe in lateral view; parascutellar lobe rounded, skewed towards median; scutellum rounded triangular, scutellar process long, apex subacute.

**HEMELYTRON.** Reaching tip of abdomen.

**LEGS.** Same as genus description.

**ABDOMEN.** Connexival margin undulating, posterior margin slightly elevated.

**GENITALIA.** Transverse bridge of pygophore broad, margin of anterior opening angular, apodeme present, apical margin of posterior opening smooth; cup-like sclerite apically rounded, with adjacent paired

round protuberances; arms of basal plate rounded; ductifer membranous; endosomal struts conical, with subacute apex, divided into two arms basally; shape of dorsal phallosclerite subacute with lateral broad, plate-like prolongations, with short, rounded lateral plates at apex.

### Female

Similar to male.

### Ecology

This species was collected at relatively high altitudes of 920–1200 m.

### Distribution

This species is found only in the central west region of Sumatra Island, where most specimens were collected from Bukit Tinggi, formerly Fort de Kock.

### Remarks

This species is the most commonly collected on the island of Sumatra. It is placed within the *Physoderes* clade in the phylogenetic analysis above because of the shared synapomorphies of having the scape reaching the apex of the clypeus, rounded parascutellar lobes skewed toward the median and a membranous ductifer of the male genitalia.

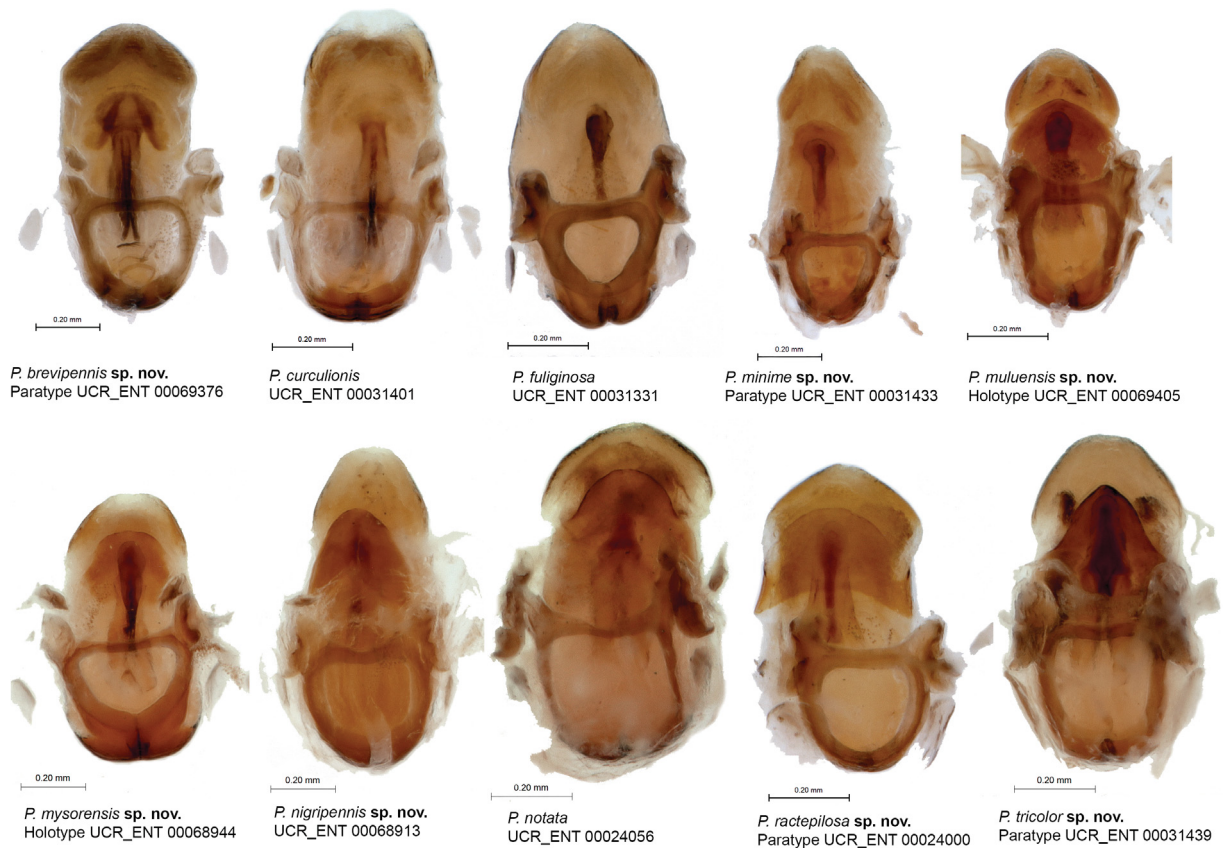


Fig. 19. Dorsal view of the phallus in species of *Physoderes* Westwood, 1845 (partial).

*Physoderes nigroalbus* Breddin, 1903  
Figs 15, 20; Appendix

*Physoderes nigroalbus* Breddin, 1903: 126.

**Diagnosis**

This species is recognized among species of *Physoderes* by the short and conical head, the scape not reaching the apex of the clypeus, the eye hemispherical and slightly flattened, the submedian pronotal carina strongly defined, the scutellum and scutellar process brown, the corium dark brown with the membranous portion basally dark brown including the external cell, and areas directly adjacent to the medial vein apical extension and first anal vein apex with remaining membrane off-white. This species is most similar to *P. tricolor* sp. nov., but can be differentiated from it by its size, coloration of the head, pronotum and scutellar process, and the shape of the eye.

**Material examined**

**Lectotype** (here designated)

INDONESIA: ♀, Sumatra, Tebing Tinggi, NE Sumatra, 3.31944° N, 99.15222° E, 21 m, 10 Mar. 1884, Dr. Schultheiss leg. (UCR\_ENT 00040566) (DEI).

**Redescription**

**Female**

BODY LENGTH. Medium, total length 9.74 mm.

COLORATION (Fig. 15). Brown. Head brown. Scape and pedicel of antenna light brown to brown, basiflagellomere brown, distiflagellomere basally brown, apically straw-colored. First segment of labium light brown, second segment straw-colored, apically brown, third segment brown. Anterior lobe of pronotum dark brown, posterior lobe brown, scutellum brown with dark brown scutellar process, pleuron brown with straw-colored suffusion, sternum brown to dark brown. Corium of hemelytron dark brown, membrane basally dark brown, apically off-white. Femur and tibia of legs straw-colored with basal, medial and apical brown annulations, tarsus and claw light brown. Abdomen dorsally yellowish-orange, basally straw-colored with brown and dark brown patterns, anterior half of connexivum dark brown, posterior half straw-colored.

VESTITURE. Sparsely setose. Head with widespread curved setae, ventral surface of postocular lobe with sparse, setigerous tubercles, without pair of long, straight setae on postocular lobe posterior to ocelli. Anterior lobe of thorax with irregular row of tuberculated, short, curved setae on lateral margins and short, setigerous tubercles dispersed on dorsal surface, posterior lobe with short, curved setae on humeral angle and sparsely distributed along dorsal surface. Corium of hemelytron with short, curved setae. Legs with two rows of spines and setigerous tubercles, tibia with regular rows of tuberculated, stout, sharp setae. Connexival margin of abdomen with no prominent setae.

HEAD. Short conical; maxillary plate rounded apically; scape not reaching apex of clypeus; eye hemispherical in dorsal view, less than  $\frac{1}{5}$  length of head.

THORAX. Antero-lateral paired projections acute, diverging; surface of anterior lobe with low ridges; median pronotal depression contiguous with transverse sulcus; paramedian carina strongly defined; anterior pronotal lobe shorter and narrower than posterior lobe, lower than posterior lobe in lateral view; parascutellar lobe rounded, skewed towards median; scutellum rounded triangular, scutellar process long, apex subacute.



HEMELYTRON. Attaining tip of abdomen.

LEGS. Same as genus description.

ABDOMEN. Connexival margin slightly undulating, posterior margin not elevated.

#### **Male**

Unknown.

#### **Ecology**

Nothing is known about the biology of this species.

#### **Distribution**

This species is only known from the type locality in northeast Sumatra, Indonesia.

#### **Remarks**

This specimen was found by Stephan Blank at the DEI without a type label and labeled as *Epirodera palliderostris* [sic]. It is here interpreted as the type specimen or part of a syntype series that Breddin used to describe *P. nigroalbus*. Because Breddin did not label his types nor mention where they were deposited, this is currently the best assumption. Further evidence is given by the exact match in the locality information provided in Breddin's description and that on the specimen label, the lack of a range of measurements to suggest he examined more than one specimen, and matching description of the black and white hemelytron, measurement and sex. This specimen is thus designated as the lectotype for *P. nigroalbus*. No matching male specimens have been located and the redescription here is based on the single female lectotype specimen.

#### ***Physoderes notata* Westwood, 1845**

Figs 8, 13, 15–16, 19; Appendix

*Physoderes notata* Westwood, 1845: 68.

*Physoderes brunneus* Breddin, 1903: 127. New synonymy.

*Physoderes buruensis* Miller, 1954: 85, fig. 9. New synonymy.

*Physoderes corporaali* Miller, 1954: 88, fig. 12. New synonymy.

*Physoderes flavipennis* Miller, 1940: 556, fig. 92. New synonymy.

*Epirodera notata* – Westwood 1847: 248, pl. 18, fig. 5 (unsanctioned name change).

*Physoderes notata* – Miller 1954: 82, fig. 8.

#### **Diagnosis**

This species is recognized among congeners by the short head, the scape shorter than the apex of the clypeus, the parascutellar lobe being rounded and skewed towards the median, the anterior pronotal lobe wider than the posterior lobe (males only), the median pronotal depression not contiguous with the transverse sulcus (males), the hemelytron reaching the tip of the abdomen, the hind wings being bright yellow and sometimes apically brown, the cup-like sclerite with rounded apex and adjacent paired protuberances, and the plate-like prolongations of the phallosoma with subacute apex and sharp lateral extensions. This species is similar to *P. tricolor* sp. nov. but can be differentiated from it based on the head and pronotal color patterns, hemelytron color, cup-like sclerite shape and the shape of the prolongations of the phallosoma.

## Material examined

### Holotype

INDONESIA: ♂, Java: 7.61444° S, 110.71222° E, no date provided, unknown collector (UCR\_ENT 00018526) (BMNH).

### Other material

INDONESIA: Java, East Java: 1 ♂, Blawan, 7.98805° S, 114.17138° E, no date provided, H. Lucht leg. (UCR\_ENT 00024058) (RMNH); 4 ♀♀, Lawang, 7.77972° S, 112.50611° E, 1496 m, 1907, M. Buysman leg. (UCR\_ENT 00024051–UCR\_ENT 00024054) (RMNH); 3 ♀♀, Mount Tengger, 7.98857° S, 112.9166° E, 1219 m, no date provided, H. Fruhstorfer leg., syntypes of *Physoderes brunneus* (junior synonym) (UCR\_ENT 00040569–UCR\_ENT 00040571) (DEI); 1 ♂, same collection data as preceding, syntype of *Physoderes brunneus* (junior synonym) (UCR\_ENT 00040572) (DEI); 1 ♀, same collection data as preceding but 1890, syntype of *Physoderes brunneus* (junior synonym) (UCR\_ENT 00040568) (DEI); 1 ♀, Nongkodjadar (Nonkojajar), 7.91611° S, 112.8875° E, 846 m, 1911, E. Jacobson leg. (UCR\_ENT 00024055) (RMNH); 1 ♂, same collection data as preceding (UCR\_ENT 00024056) (RMNH). – Java, Central Java: 1 ♂, Moeria Mts, Tjolo (Muria Mts), 6.61666° S, 110.9575° E, 800 m, 20–24 Oct. 1939, M.A. Lieftinck leg. (UCR\_ENT 00024060) (RMNH). – Java, West Java: 1 ♂, Preanger, Pelaburan (Pelabuhan), Jul. 1918 (unclear), J.B. Corporaal leg., holotype of *Physoderes corporaali* (junior synonym), MacGillavry Collection (ZMA.INS.834306) (ZMAN). – Maluku: 1 ♂, Buru Island, station 9, 1–19 Jul. 1921, L.J. Toxopeus leg., holotype of *Physoderes buruensis* (junior synonym), MacGillavry Collection (ZMA.INS.787862) (ZMAN). – Sulawesi, Sulawesi Utara (North Sulawesi): 1 ♀, Dumoga Bone National Park, Barney's Tree, 0.44972° N, 123.93305° E, 300 m, 13–22 Nov. 1985, J. Krikken leg. (UCR\_ENT 00024064) (RMNH); 3 ♀♀, Manado, 1.46361° N, 124.31055° E, Jun.–Oct. 1926, unknown collector (UCR\_ENT 00046623, UCR\_ENT 00046648, UCR\_ENT 00046649) (CAS); 1 ♂, Minahasa, 1° N, 124.58333° E, 550 m, 28 Jul. 1941, F. Dupont leg. (UCR\_ENT 00024062) (RMNH). – Sumatra, Sumatera Barat (West Sumatra): 3 ♀♀, Baso, 0.27° N, 100.46333° E, 800 m, Mar. 1926, E. Jacobson leg. (UCR\_ENT 00024021–UCR\_ENT 00024023); 1 ♂, same collection data as preceding (UCR\_ENT 00024057) (RMNH); 1 ♀, Fort de Kock, 0.26694° N, 100.38333° E, 920 m, 1926, E. Jacobson leg. (UCR\_ENT 00024020) (RMNH); 1 ♀, Fort de Kock (Bukittinggi), 0.26768° S, 100.38394° E, Nov. 1913, E. Jacobson leg. (UCR\_ENT 00024019) (RMNH); 1 ♀, same collection data as preceding but Oct. 1913 (UCR\_ENT 00014056) (RMNH); 1 ♂, Gunning Singgalang, 0.39° N, 100.33083° E, 1200 m, 1925, E. Jacobson leg. (UCR\_ENT 00024026) (RMNH). – Sumatra, Sumatera Selatan (South Sumatra): 1 ♀, SW Lampong District, Mt Tanggamoos, 5.41666° S, 104.7° E, 700 m, Dec. 1939, M.A. Lieftinck leg. (UCR\_ENT 00024025) (RMNH); 1 ♀, same collection data as preceding but at 500 m (UCR\_ENT 00024024) (RMNH). – Sumatra, Sumatera Utara (North Sumatra): 1 ♂, Nias Island, Goenoeng Sitoli, 1.12527° N, 97.52472° E, 227 m, no date provided, Kleiweg de Zwaan leg. (UCR\_ENT 00024027) (RMNH); 1 ♂, Padang Sidempuan, 1.3725° N, 99.25527° E, 332 m, no date provided, J.D. Pasteur leg. (UCR\_ENT 00024059) (RMNH).

MALAYSIA: Selangor: 1 ♀, Kepong, in forest, 3.2325° N, 101.6275° E, Aug. 1949, collector unknown (UCR\_ENT 00031389) (USNM). – Perak: 1 ♀, Jor Camp, 4.89972° N, 100.79055° E, 610 m, 21 Aug. 1922, E. Seimund leg., holotype of *Physoderes flavipennis* (junior synonym) (UCR\_ENT 00018519) (BMNH).

## Redescription

### Male

BODY LENGTH. Medium-large, total length 9.94 mm, SD ± 0.3 (Appendix).

COLORATION (Figs 15–16). Straw-colored and brown. Anteoconular lobe of head straw-colored with brown suffusion, postocconular lobe brown. Antenna straw-colored with brown suffusion. First segment

of labium light brown to brown, second segment straw-colored, third segment brown. Pronotum of thorax dark brown with straw-colored markings along ridges, scutellum basally dark brown, apically straw-colored, pleuron straw-colored with brown and dark brown patterns, sternum dark brown. Corium of hemelytron light brown to brown, membrane dark brown. Femur of legs straw-colored with sub-basal and apical brown annulations, tibia brown with straw-colored base, tarsus and claw straw-colored. Abdomen dorsally yellow, ventrally straw-colored with sub-lateral dark brown patterns, anterior half of connexivum dark brown, posterior half straw-colored, exposed part of pygophore straw-colored.

**VESTITURE.** Sparsely setose. Head with some curved setae and short, fine, adpressed setae, ventral surface of postocular lobe with sparse, setigerous tubercles, with pair of long, straight setae on postocular lobe posterior to ocelli. Anterior lobe of thorax with irregular row of tuberculated, short, curved setae on lateral margins and short, setigerous tubercles dispersed on dorsal surface, posterior lobe with only short, sparse setae. Corium of hemelytron with short, curved setae. Legs with two rows of spines and setigerous tubercles, tibia with regular rows of tuberculated, stout, sharp setae. Connexival margin of abdomen with no prominent setae.

**HEAD.** Elongate conical; maxillary plate rounded apically; scape not reaching apex of clypeus; eye hemispherical in dorsal view, less than  $\frac{1}{5}$  length of head.

**THORAX.** Antero-lateral paired projections acute, diverging; surface of anterior lobe with low ridges; median pronotal depression not contiguous with transverse sulcus; paramedian carina weakly defined; anterior pronotal lobe equal in length to and wider than posterior lobe, higher than posterior lobe in lateral view; parascutellar lobe rounded, skewed towards median; scutellum rounded triangular, scutellar process long, apex subacute.

**HEMELYTRON.** Attaining tip of abdomen.

**LEGS.** Same as genus description.

**ABDOMEN.** Connexival margin slightly undulating, posterior margin not elevated.

**GENITALIA.** Anterior margin of mediosternite 8 sharply emarginate, without medial apodeme; transverse bridge of pygophore broad, margin of anterior opening angular, apodeme present, apical margin of posterior opening smooth; cup-like sclerite apically rounded with adjacent paired round protuberances; arms of basal plate parallel to each other; ductifer membranous; endosomal struts with tapered apex and divided into two arms basally; shape of dorsal phallothecal sclerite subacute with lateral broad, plate-like prolongations, broad plate with a subacute apex and sharp lateral extensions.

### **Female**

Females have a narrower anterior pronotal lobe with median pronotal depression contiguous with transverse sulcus and anterior lobe lower than the posterior lobe.

### **Ecology**

Not much is recorded about the biology of this species. One specimen was collected from under sheaths of bamboo (Poaceae), another one was collected from multi-storey evergreen forest using 'canopy trap fish'. This species has been collected from a range of mid-level elevations from 227 to 1496 m.

### **Distribution**

This species is relatively widespread and can be found on peninsular Malaysia and the islands of Sumatra, Java and Sulawesi.

### Remarks

Examination of the holotype of *P. flavipennis* and the syntypes of *P. brunneus* indicate that both represent females of *P. notata* that have the narrower anterior pronotal lobe. Similarly, the holotype of *P. corporaali* shares the same diagnostic characters and color patterns on the head and pronotum with *P. notata*. Although the holotype of *P. buruensis* has a darker pronotum, all other characters are consistent with those of *P. notata*. The difference in pronotal coloration is hence regarded here as a color variant of the species, possibly unique to the Buru island population. All four species are hereby synonymized under *P. notata*.

### *Physoderes ractepilosa* sp. nov.

[urn:lsid:zoobank.org:act:DFE461F4-658E-45E9-879C-D4747C0D8675](https://zoobank.org/act:DFE461F4-658E-45E9-879C-D4747C0D8675)

Figs 8, 15, 18–20; Appendix

### Diagnosis

This species is recognized among species of *Physoderes* by the body being covered with long, erect setae, the head being elongate conical, the scape not reaching the apex of the clypeus, the anterior pronotal lobe being narrower than the posterior lobe, the anterior pronotal lobe with raised ridges and strongly defined submedian carina, the parascutellar lobe rounded, the scutellar process slender, the fore femur slender and only slightly incrassate, the short hemelytron not reaching the tip of the abdomen, the connexival margin undulating and the females with a wider connexivum than in males. Additional diagnostic features are found on the male genitalia: the cup-like sclerite with rounded apex and broad adjacent sclerotized rounded protuberances, the apical margin of the posterior opening of the pygophore with medial process, the arms of the basal plate curved to form a rounded foramen and the apex of the dorsal phallosomal sclerite subacute, with broad lateral prolongations that project angularly towards the apex of the phallosoma. This species most closely resembles *P. fuliginosa*, but can be differentiated from it by the long, erect setae, the shape of the pronotum, parascutellar lobe and connexivum, as well as the hemelytron length.

### Etymology

The name *ractepilosa* is a noun in apposition to describe the erect setation throughout the body of this species.

### Material examined

#### Holotype

INDONESIA: ♀, Sulawesi Tengah, Lore Lindu National Park, Marena Forest, 1.51666° N, 120.18333° E, 650 m, 14–17 Dec. 1985, J. Krikken leg. (UCR\_ENT 00014061) (RMNH).

#### Paratypes

INDONESIA: Sulawesi Tengah (Central Sulawesi): 1 ♂, Lore Lindu National Park, Marena Forest, near river, 1.51666° S, 120.18333° E, 600 m, 14–17 Dec. 1985, J. Krikken leg. (UCR\_ENT 00023400) (RMNH); 4 ♀♀, same collection data as preceding (UCR\_ENT 00023401–UCR\_ENT 00023404) (RMNH). – Sulawesi Utara (North Sulawesi): 1 ♂, Dumoga Bone National Park, Mt Mogogonipa, 0.45° N, 123.93305° E, 1000 m, 22–25 Aug. 1985, J. Huijbregts leg. (UCR\_ENT 00023999) (RMNH).

### Description

#### Female

BODY LENGTH. Medium, total length 9.19 mm, SD ± 0.67 (Appendix).

COLORATION (Figs 15, 18). Brown. Head brown. Scape and pedicel of antenna straw-colored with brown suffusion, basiflagellomere brown, distiflagellomere basally brown, apically straw-colored. First and

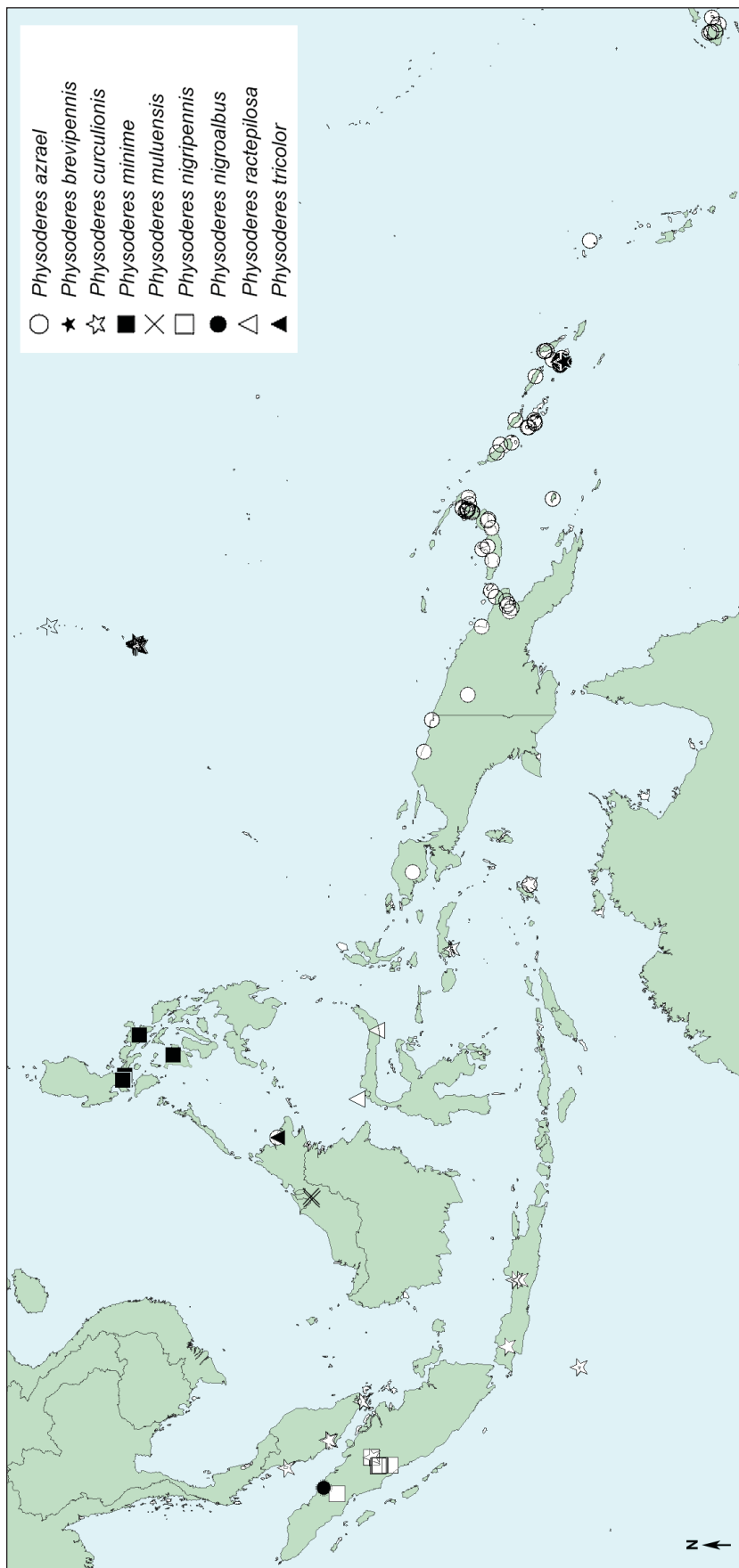


Fig. 20. Distribution map for species of *Physoderes* Westwood, 1845 (partial).

second segment of labium straw-colored, third segment brown. Anterior lobe of pronotum brown with straw-colored ridges, posterior lobe straw-colored, scutellum dark brown basally, straw-colored apically including scutellar apex, pleuron dark brown with straw-colored suffusion, sternum dark brown. Corium of hemelytron brown, membrane brown. Femora of legs straw-colored with medial and apical brown annulations, tibiae brown with basal and apical straw-colored brown annulations, tarsi and claws straw-colored. Abdomen dorsally yellow, ventrally brown with straw-colored suffusion laterally, anterior half of connexivum dark brown, posterior half straw-colored, exposed part of pygophore brown.

**VESTITURE.** Generally densely setose. Head with widespread long, erect setae, ventral surface of postocular lobe with sparse, setigerous tubercles, with pair of long, straight setae on postocular lobe posterior to ocelli. Anterior lobe of thorax with irregular row of tuberculated, long, erect setae on lateral margins and on dorsal ridges, posterior lobe with long, erect setae on humeral angle and sparsely distributed along dorsal surface. Corium of hemelytron with long, erect setae. Legs with two rows of spines and setigerous tubercles, tibia with regular rows of tuberculated, stout, sharp setae. Posterior margin of connexivum of abdomen with long, fine setae.

**HEAD.** Elongate conical; maxillary plate truncate apically; scape not reaching apex of clypeus; eye hemispherical in dorsal view, less than  $\frac{1}{5}$  length of head.

**THORAX.** Antero-lateral paired projections acute, diverging; surface of anterior lobe with raised ridges; median pronotal depression contiguous with transverse sulcus; paramedian carina strongly defined; anterior pronotal lobe shorter and narrower than posterior lobe, lower than posterior lobe in lateral view; parascutellar lobe rounded; scutellum rounded triangular, scutellar process long, apex subacute.

**HEMELYTRON.** Not reaching tip of abdomen.

**LEGS.** Same as genus description.

**ABDOMEN.** Elongate ovoid, with straight terminal margin; connexival margin undulating, posterior margin not elevated.

### **Male**

Similar to females, but do not seem to have as many long, erect setae and connexivum not as wide.

**GENITALIA.** Anterior margin of mediosternite 8 sharply emarginate, with medial apodeme; transverse bridge of pygophore broad, margin of anterior opening angular, apodeme present, apical margin of posterior opening with small medial process; cup-like sclerite apically rounded, with adjacent paired round protuberances; arms of basal plate rounded; ductifer membranous; apex of endosomal struts tapered and divided into two arms basally; shape of apex of dorsal phallothecal sclerite subacute with broad lateral prolongations that project angularly towards apex of phallosoma.

### **Ecology**

Specimens were collected in multistorey evergreen forests using fish traps.

### **Distribution**

This species is only known from the type locality in Central Sulawesi and another locality in northern Sulawesi.

### **Remarks**

A female specimen is chosen as the holotype for this species because the long, erect setae covering the body are not as obvious in the two male specimens available. One of the males was collected from the

same collecting event as the females and shares all other diagnostic characters. The unique setation may be sexually dimorphic. Additional male specimens will be required to determine this. The male was dissected and the genitalia described here show that this species is very different from any other species of *Physoderes*.

*Physoderes tricolor* sp. nov.

[urn:lsid:zoobank.org:act:079BA84D-2C4E-444D-B57F-8555AD38438B](https://doi.org/10.3896/BI.2019.63.1.1)

Figs 8, 15, 18–20; Appendix

### Diagnosis

This species is recognized among congeners by the short and conical head, the scape not reaching the apex of the clypeus, the eye distinctly projecting, the submedian pronotal carina weakly defined, the apex of the scutellar process straw-colored, the parascutellar lobe rounded and skewed towards median, the corium dark brown with the membranous portion basally dark brown, including the external cell, and areas directly adjacent to the medial vein apical extension and first anal vein apex with remaining membrane off-white and translucent, the abdominal dorsal surface dark brown, the apodeme of the anterior opening of the pygophore obsolete with the margin rounded, the cup-like sclerite with rounded apex and paired adjacent subacute protuberances and the dorsal phallosclerite triangular in shape. This species is most similar to *P. nigroalbus* but can be differentiated from it by size, the coloration of the head, pronotum and scutellar process, and the shape of the eye.

### Etymology

The name of this species is based on the Latin adjective “tricolor”, meaning three-colored, to describe the three colors that are visible dorsally.

### Material examined

#### Holotype

MALAYSIA: ♂, Sabah, Sandakan, 5.8333° N, 118.1167° E, 4 m, no date provided, Baker leg. (UCR\_ENT 00030980) (USNM).

#### Paratypes

MALAYSIA: 1 ♂, same collection data as for holotype (UCR\_ENT 00031439) (USNM); 3 ♀♀, same collection data as for holotype (UCR\_ENT 00031440–UCR\_ENT 00031442) (USNM).

### Description

#### Male

BODY LENGTH. Medium, total length 8.66 mm, SD ± 0.16 (Appendix).

COLORATION (Figs 15, 18). Brown, brownish black and off-white. Head anteriorly straw-colored, posteriorly brown. Antenna straw-colored. First and second segment of labium straw-colored, third segment light brown. Anterior lobe of pronotum brown with straw-colored markings, posterior lobe brown, scutellum basally brown, apically straw-colored including scutellar process, pleuron straw-colored with brown patterns, sternum brown to dark brown. Corium of hemelytron dark brown, membrane basally dark brown, including the external cell, and areas directly adjacent to the medial vein apical extension and first anal vein apex with remaining membrane off-white and translucent. Femora and tibiae of legs straw-colored with medial and apical brown annulations, tarsi and claws light brown. Abdomen dorsally dark brown, ventrally straw-colored with brown and dark brown patterns, anterior half of connexivum dark brown, posterior half straw-colored, exposed part of pygophore dark brown.

**VESTITURE.** Sparsely setose. Head with some curved setae and short, fine, adpressed setae, ventral surface of postocular lobe with sparse, setigerous tubercles, with pair of long, straight setae on postocular lobe posterior to ocelli. Anterior lobe of thorax with irregular row of tuberculated, short, curved setae on lateral margins and curved setae on the anterior portion of dorsal surface, posterior lobe with short, curved setae on humeral angle and sparsely distributed along dorsal surface. Corium of hemelytron with short, curved setae. Legs with two rows of spines and setigerous tubercles, tibia with regular rows of tuberculated, stout, sharp setae. Connexival margin of abdomen with a few clubbed setae on each segment, or connexival margin with no prominent setae.

**HEAD.** Short conical; maxillary plate rounded apically; scape not reaching apex of clypeus; eye distinctly projecting in dorsal view, less than  $\frac{1}{5}$  length of head.

**THORAX.** Antero-lateral paired projections acute, diverging; surface of anterior lobe smooth, ridges almost obsolete; median pronotal depression not contiguous with transverse sulcus; paramedian carina weakly defined; anterior pronotal lobe shorter and slightly narrower than posterior lobe, anterior lobe level with posterior lobe in lateral view; parascutellar lobe rounded, skewed towards median; scutellum rounded triangular, scutellar process long, apex subacute.

**HEMELYTRON.** Reaching tip of abdomen.

**LEGS.** Same as genus description.

**ABDOMEN.** Connexival margin slightly undulating, posterior margin not elevated.

**GENITALIA.** Anterior margin of mediosternite 8 undulating, without medial apodeme; transverse bridge of pygophore narrow, margin of anterior opening rounded, apodeme absent, apical margin of posterior opening smooth; cup-like sclerite apically rounded, with adjacent paired small subacute protuberances; arms of basal plate parallel to each other; ductifer membranous; endosomal struts tapered, with acute apex, divided into two arms basally; shape of dorsal phallosomal sclerite triangular with angular lateral prolongations.

### **Female**

Similar to males except anterior pronotal lobe (2.17 mm average) distinctly narrower than posterior lobe (2.77 mm average) and median pronotal depression contiguous with transverse sulcus.

### **Ecology**

Nothing is known about the biology of this species.

### **Distribution**

This species is only known from the type locality of Sandakan, northeast Borneo.

### **Remarks**

This species shares the general head and pronotal morphology of *P. notata* and is placed within the same clade as *P. notata* in the phylogenetic analysis above.



**Revised Classification List**

***Breviphysoderes* gen. nov.**

Type species: *Physoderes mjoebergi* Miller, 1940, by designation.

*Breviphysoderes decora* (Miller, 1940) comb. nov.

*Physoderes decora* Miller, 1940

*Physoderes ostenta* Miller, 1941, syn. nov.

*Breviphysoderes fulvopicta* gen. et sp. nov.

*Breviphysoderes hobbyi* (Miller, 1940) comb. nov.

*Physoderes hobbyi* Miller, 1940

*Breviphysoderes mjoebergi* (Miller, 1940) comb. nov.

*Physoderes mjoebergi* Miller, 1940

*Physoderes dyak* Miller, 1955b, syn. nov.

*Breviphysoderes planicollis* (Miller, 1940) comb. nov.

*Physoderes planicollis* Miller, 1940

*Breviphysoderes shelfordi* (Miller, 1940) comb. nov.

*Physoderes shelfordi* Miller, 1940

*Breviphysoderes tenebrosa* gen. et sp. nov.

*Breviphysoderes vestita* (Horváth, 1900), comb. nov.

*Epirodera vestita* Horváth, 1900

*Physoderes serraticollis* Breddin, 1903, syn. nov.

*Physoderes javanica* Miller, 1940, syn. nov.

*Physoderes rugosa* Miller, 1954, syn. nov.

*Physoderes vestita* – Maldonado 1990

***Macrophysoderes* gen. nov.**

Type species: *Physoderes modesta* Miller, 1940, by designation.

*Macrophysoderes bengalensis* (Distant, 1909) comb. nov.

*Epirodera bengalensis* Distant, 1909

*Physoderes bengalensis* – Maldonado 1990

*Macrophysoderes cirripilosa* gen. et sp. nov.

*Macrophysoderes elongata* gen. et sp. nov.

*Macrophysoderes finisterre* gen. et sp. nov.

*Macrophysoderes grandis* gen. et sp. nov.

*Macrophysoderes histrionica* (Miller, 1940) comb. nov.

*Physoderes histrionica* Miller, 1940

*Macrophysoderes modesta* (Miller, 1940) comb. nov.

*Physoderes modesta* Miller, 1940

*Physoderes sibauana* Miller, 1940, syn. nov.

*Physoderes trusana* Miller, 1940, syn. nov.

*Macrophysoderes monticola* (Miller, 1940) comb. nov.

*Physoderes monticola* Miller, 1940

*Physoderes dimidiata* Miller, 1940, syn. nov.

*Physoderes luiana* Miller, 1940, syn. nov.

***Nanophysoderes*** gen. nov.

Type species: *Physoderes dentiscutum* Bergroth, 1906, by designation.

*Nanophysoderes dentiscutum* (Bergroth, 1906) comb. nov.

*Physoderes dentiscutum* Bergroth, 1906

***Paraphysoderes*** Villiers, 1962

Type species: *Paraphysoderes crassa* Villiers, 1962, by original designation.

*Paraphysoderes crassa* Villiers, 1962

*Paraphysoderes peyrierasi* Villiers, 1968

*Paraphysoderes popeye* sp. nov.

***Physoderes*** Westwood, 1845

Type species: *Physoderes notata* Westwood, 1845, by monotypy.

*Physoderes anamalaiensis* sp. nov.

*Physoderes azrael* Kirkaldy, 1905

*Physoderes brevipennis* sp. nov.

*Physoderes curculionis* China, 1935

*Physoderes insulanus* Miller, 1940, syn. nov.

*Physoderes patagiata* Miller, 1941, syn. nov.

*Physoderes minor* Usinger, 1946, syn. nov.

*Physoderes kalshoveni* Miller, 1954, syn. nov.

*Physoderes esakii* Cao, Tomokuni & Cai, 2011

*Epirodera latithorax* Esaki, 1931, nomen nudum

*Physoderes latithorax* – Maldonado 1990

*Physoderes fuliginosa* (Stål, 1870)

*Epirodera fuliginosa* Stål, 1870

*Physoderes fuliginosa* – Maldonado 1990

*Physoderes manni* Davranoglou, 2014

*Physoderes mauriciensis* (Villiers, 1964), comb. nov.

*Epiroderoides mauriciensis* Villiers, 1964

*Physoderes minime* sp. nov.

*Physoderes muluensis* sp. nov.

*Physoderes mysorensis* sp. nov.

*Physoderes nigripennis* sp. nov.

*Physoderes nigroalbus* Breddin, 1903

*Physoderes notata* Westwood, 1845

*Physoderes brunneus* Breddin, 1903, syn. nov.

*Physoderes flavipennis* Miller, 1940, syn. nov.

*Physoderes buruensis* Miller, 1954, syn. nov.

*Physoderes corporaali* Miller, 1954, syn. nov.

*Epirodera notata* – Westwood 1847, unsanctioned name change

*Physoderes notata* – Miller 1954

*Physoderes ractepilosa* sp. nov.

*Physoderes tricolor* sp. nov.

### ***Incertae sedis***

*Physoderes brancsiki* Bergroth, 1906

*Physoderes impexa* (Distant, 1903)

*Epirodera impexa* Distant, 1903

*Physoderes fuscus* Breddin, 1903 (synonymized in Distant 1904)

*Physoderes impexa* – Izzard 1936

*Physoderes pallidirostris* (Stål, 1863)

*Epirodera pallidirostris* Stål, 1863

*Physoderes pallidirostris* – Maldonado 1990

## **Discussion**

### ***Physoderinae phylogeny: implications for biogeography and character evolution***

Only three representatives of Physoderinae, two species of *Physoderes* and one of *Breviphysoderes* gen. nov., were previously included in a molecular phylogenetic analysis that also investigated divergence dates (Hwang & Weirauch 2012). In that analysis, Physoderinae diverged around 45 Mya from the Neotropical *Nalata* clade, their closest relatives included in that analysis. Divergences within the genus *Physoderes* were hypothesized to be as recent as 5 Mya. Given these timelines, dispersal, not vicariance, is likely the best explanation for the occurrence of Physoderinae in Madagascar. The non-monophyletic nature of the Madagascan Physoderinae indicates that the evolutionary history of this group in the Madagascan region cannot be explained by a single colonization event with subsequent radiation. However, the majority of Madagascan Physoderinae are part of a single evolutionary lineage, Clade A, indicating that the morphological diversity found amongst Madagascan Physoderinae may in fact be due to a radiation in response to different ecological factors on the island. The single Australasian species of *Paraphysoderes* may then represent an “out of Madagascar” dispersal event, while the single Mauritian species of *Physoderes* could represent a second colonization from the Madagascan region. A formal biogeographic analysis based on morphological and molecular data that also includes divergence dating analyses is now the essential next step to test this proposed scenario.

Our analysis partially supports the hypothesis that the Neotropical species of Physoderinae that appear to have retained a number of plesiomorphic features as summarized by Weirauch (2006), are the sister group of all remaining Physoderinae: *Leptophysoderes* and *Cryptophysoderes* do in fact form a clade and are sister to all Australasian, Oriental, and Madagascan Physoderinae, but the Afrotropical

*Porcelloderes* is recovered as the sister group to all remaining Physoderinae. This somewhat puzzling result may in part be derived from the fact that pronotal structures are strongly represented in our morphological dataset and the pronotum is highly modified in the apterous *Porcelloderes*. This result is clearly in need of additional testing, preferably with the addition of molecular data, as is the apparent paraphyly of *Leptophysoderes*, which is likely due to the coding of two male (UCR\_ENT 00014362, UCR\_ENT 00014363) and two female (UCR\_ENT 00014360, UCR\_ENT 00014361) specimens that show significant sexual dimorphism.

Despite being riddled by homoplasy, an examination of morphological characters allows for several observations. As an example, the highly modified physoderines *Tribelocephaloides*, *Henicocephaloides* Villiers, 1962 and *Mimoelasmodema*, which are characterized by derived features including the ventral position of the eye and the lack of armature on the fore femur, are phylogenetically derived within their respective clades. In addition, unarmed and slender forelegs evolved independently from stout and heavily armed forelegs among the Neotropical clade (*Leptophysoderes* + *Cryptophysoderes*) and within a clade nested within the Madagascan Clade B (*Befotaka* Villiers, 1962 + *Rodepirea* Villiers, 1962 + *Maroantsetrana* Villiers, 1962 + *Henicocephaloides* + *Tribelocephaloides*). We speculate that this might be in response to a shift in prey organism or a different predatory strategy.

### **Comments on taxonomy**

Based on findings from our phylogenetic analysis that *Physoderes* is polyphyletic, we here redefine *Physoderes* and erect three new genera to accommodate the remaining species. We retain the name *Physoderes* for the clade that contains the type species of *Physoderes*, *P. notata* (Westwood, 1845), following the International Commission on Zoological Nomenclature. Redescriptions of *Physoderes* and *Paraphysoderes* and descriptions of the new genera are presented above. A summary of the taxonomic changes made in this publication and a list of new taxa described is also presented. A few species of *Physoderes* are placed as *incertae sedis* due to unknown locations of type specimens, leading to uncertainty in their identities. Attempts to locate these type specimens were unsuccessful, as the taxon authors did not specify depository sites and enquiries made to major European museums likely to house these specimens turned out negative.

Our revision of the Oriental and Australasian Physoderinae provides, for the first time, a comprehensive picture of the diversity patterns in these regions. Notably, the highest number of species is found on two islands, Borneo and New Guinea. Borneo had already been identified as a hotspot for physoderine species-level diversity by earlier workers (e.g., Miller 1940), but the addition of new species in the present study has emphasized this observation. Similarly, the addition of seven new species from New Guinea and the surrounding islands highlights the extreme diversity in this region. In contrast, the paucity of species described from the continental Oriental region may be an effect of poor sampling, a hypothesis that is supported by the fact that we discovered two new species from the Indian subcontinent for which we only examined a total of 42 specimens. Additional field work in the continental Oriental region will likely reveal additional undescribed diversity.

Distributional data on physoderine species in the Oriental and Australasian regions do not provide a cohesive pattern with regards to factors that determine species ranges. Some species are widely distributed across island archipelagos, with insignificant morphological variation (see *Physoderes curculionis*, *P. fuliginosa*, *P. notata*). Other species appear to be highly restricted to a small endemic range close to their type locality, despite adequate sampling in surrounding regions and the fact that these species are not isolated on an oceanic island (see *Physoderes muluensis* sp. nov., *P. minime* sp. nov.). Further investigations into the natural history of the various physoderine species will be needed to explain the diversity patterns observed in the Oriental and Australasian regions.

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Measurements for species of *Breviphysoderes* gen. nov., *Macrophysoderes* gen. nov., *Nanophysoderes* gen. nov., *Paraphysoderes* Villiers, 1962 and *Physoderes* Westwood, 1945 (in mm). Numbers in parentheses beside mean values refer to sample size. SD = Standard deviation. In the USI column, UCR\_ENT catalogue numbers are referred to by the number only.

## Appendix

Species	Sex	USI	Total Length	Head length	Eye length	Eye width	Pronotum			Hemelytron length	Scape length	Interocular distance	Postocular lobe width	Abdomen width
							Anterior lobe (l)	Anterior lobe (w)	Posterior lobe (l)					
<b><i>Breviphysoderes</i> gen. nov.</b>														
<i>B. decora</i>	♀	Mean (5)	9.19	2.02	0.40	1.06	0.98	2.18	1.08	2.96	5.41	0.55	0.88	3.76
		SD	0.33	0.19	0.03	0.05	0.09	0.12	0.14	0.17	0.18	0.03	0.06	0.20
		Minimum	8.81	1.79	0.38	0.99	0.90	2.06	0.89	2.75	5.12	0.51	0.85	3.56
		Maximum	9.53	2.24	0.46	1.11	1.09	2.32	1.26	3.14	5.63	0.58	0.94	4.05
<i>B. mjoebergi</i>	♂	Mean (3)	7.91	1.62	0.37	0.96	0.89	2.02	1.11	2.74	4.41	0.53	0.83	3.31
		SD	0.43	0.21	0.02	0.03	0.11	0.06	0.24	0.14	0.41	0.03	0.04	0.23
		Minimum	7.49	1.39	0.36	0.95	0.77	1.96	0.94	2.61	3.96	0.50	0.79	3.06
		Maximum	8.35	1.82	0.39	1.00	0.97	2.08	1.38	2.88	4.77	0.57	0.85	3.50
<i>B. vestita</i>	♀	Mean (5)	8.76	1.82	0.47	1.03	1.00	2.23	1.08	2.91	5.03	0.56	0.87	3.76
		SD	0.69	0.12	0.23	0.06	0.15	0.23	0.14	0.22	0.52	0.05	0.03	0.40
		Minimum	7.91	1.68	0.32	0.98	0.87	1.97	0.97	2.63	4.36	0.51	0.84	3.31
		Maximum	10.23	2.08	0.38	1.07	1.50	3.18	1.24	3.35	6.20	0.69	0.93	4.07
<i>B. vestita</i>	♀	Mean (5)	9.13	1.84	0.33	1.01	1.06	2.29	1.09	2.89	5.46	0.60	0.88	3.95
		SD	0.30	0.18	0.03	0.02	0.04	0.17	0.06	0.13	0.14	0.03	0.03	0.16
		Minimum	8.74	1.57	0.29	0.99	1.01	2.05	1.02	2.73	5.26	0.56	0.83	3.73
		Maximum	9.54	2.04	0.38	1.04	1.12	2.46	1.18	3.08	5.58	0.64	0.92	4.15
<b><i>Macrophysoderes</i> gen. nov.</b>														
<i>M. cirripilosa</i> gen. et sp. nov.	♂	Mean (16)	8.7	1.66	0.34	0.98	0.95	2.24	1.01	2.82	5.32	0.46	0.85	3.25
		SD	0.66	0.12	0.03	0.06	0.09	0.19	0.14	0.21	0.45	0.04	0.06	0.24
		Minimum	7.8	1.45	0.29	0.84	0.81	1.88	0.77	2.4	4.71	0.4	0.56	2.72
		Maximum	9.85	1.99	0.39	1.05	1.14	2.62	1.32	3.16	6.05	0.53	0.75	3.62
<i>M. cirripilosa</i> gen. et sp. nov.	♀	Mean (21)	9.04	1.67	0.35	1.01	0.94	2.23	1.05	2.88	5.61	0.48	0.89	3.7
		SD	1.12	0.19	0.05	0.09	0.12	0.27	0.15	0.31	0.8	0.05	0.07	0.42
		Minimum	7.16	1.27	0.23	0.88	0.72	1.79	0.69	2.43	4.04	0.4	0.55	2.91
		Maximum	11.01	1.97	0.46	1.17	1.15	2.79	1.28	3.47	7.04	0.58	0.79	4.43

Species	Sex	USI	Total Length	Head length	Eye length	Eye width	Pronotum			Hemelytron length	Scape length	Interocular distance	Postocular lobe width	Abdomen width
							Anterior lobe (l)	Anterior lobe (w)	Posterior lobe (w)					
<i>M. elongata</i> gen. et sp. nov.	♂	Mean (5)	10.29	1.77	0.36	1.02	1.06	2.78	1.33	3.28	0.52	0.65	0.94	3.74
		SD	0.47	0.13	0.03	0.15	0.25	0.06	0.17	0.37	0.03	0.05	0.01	0.2
		Minimum	9.98	1.57	0.32	0.97	2.49	1.24	3.04	6.36	0.49	0.57	0.93	3.51
		Maximum	11.11	1.88	0.39	1.06	2.98	1.4	3.49	7.28	0.57	0.69	0.96	4.03
		Mean (4)	9.89	1.77	0.33	0.99	2.49	1.12	3.07	6.39	0.45	0.66	0.91	3.76
	♀	SD	0.4	0.1	0.04	0.13	0.11	0.05	0.15	0.42	0.06	0	0.04	0.19
		Minimum	9.47	1.66	0.28	0.98	2.34	1.05	2.93	6.08	0.37	0.65	0.85	3.51
		Maximum	10.41	1.86	0.38	1.02	2.61	1.15	3.21	7	0.5	0.66	0.95	3.91
		Mean (5)	8.85	1.66	0.33	0.96	2.14	1.11	2.81	5.36	0.48	0.62	0.82	3.23
		SD	0.38	0.1	0.04	0.05	0.14	0.15	0.14	0.38	0.04	0.01	0.06	0.19
<i>M. finisterre</i> gen. et sp. nov.	♂	Minimum	8.4	1.51	0.3	0.89	0.89	1.92	0.94	2.59	0.43	0.6	0.75	2.92
		Maximum	9.36	1.76	0.38	1.02	2.29	1.32	2.96	5.84	0.54	0.64	0.9	3.38
		Mean (5)	9.12	1.74	0.35	0.99	2.14	1.12	2.86	5.52	0.48	0.64	0.85	3.7
		SD	0.48	0.02	0.04	0.07	0.13	0.14	0.18	0.39	0.05	0.04	0.04	0.25
		Minimum	8.53	1.71	0.3	0.95	2.05	0.98	2.74	4.94	0.43	0.6	0.8	3.43
	♀	Maximum	9.8	1.76	0.4	1.04	1.08	1.35	3.18	5.97	0.55	0.67	0.92	4.11
		Mean (5)	8.5	-	-	-	-	-	2.8	5	-	-	-	-
		SD	11.58	1.59	0.48	1.31	2.65	1.64	3.74	7.71	0.75	0.62	1.01	4.28
		Minimum	12.66	2.02	0.5	1.33	2.82	1.69	4.03	8.21	0.75	0.67	1.01	4.86
		Maximum	9.45	1.94	0.35	1.06	2.14	1.27	2.95	5.49	0.52	0.59	0.88	3.46
<i>M. modesta</i>	♂	SD	-1.82	2.13	0.36	1.28	1.24	2.56	1.52	3.71	0.58	0.73	0.96	4.47
		Minimum	10.34	1.81	0.29	1.06	2.29	1.37	3.36	6.35	0.49	0.63	0.91	4.19
		Maximum	9.88	1.98	0.35	1.08	2.32	1.26	3.24	5.99	0.47	0.66	0.93	4
		Mean (3)	0.72	0.11	0.01	0.06	0.2	0.22	0.29	0.3	0.02	0.04	0.02	0.34
		SD	9.11	1.89	0.34	1.02	2.1	1.06	2.93	5.65	0.44	0.62	0.91	3.68
	♀	Minimum	10.53	2.11	0.37	1.13	1	1.49	3.51	6.21	0.49	0.69	0.96	4.36
		Maximum	7.66	1.55	0.33	0.89	1.86	0.86	2.34	4.58	0.42	0.52	0.79	2.8
		Mean (5)	8.5	-	-	-	-	-	2.8	5	-	-	-	-
		SD	11.58	1.59	0.48	1.31	2.65	1.64	3.74	7.71	0.75	0.62	1.01	4.28
		Minimum	12.66	2.02	0.5	1.33	2.82	1.69	4.03	8.21	0.75	0.67	1.01	4.86
<i>Nanophysoderes</i> gen. nov.	♂	Mean (5)	10.29	1.77	0.36	1.02	1.06	2.78	1.33	3.28	0.52	0.65	0.94	3.74
		SD	0.47	0.13	0.03	0.15	0.25	0.06	0.17	0.37	0.03	0.05	0.01	0.2
<i>N. dentiscutum</i>	♂	Minimum	9.98	1.57	0.32	0.97	0.91	2.49	1.24	3.04	0.49	0.57	0.93	3.51
		Maximum	11.11	1.88	0.39	1.06	2.98	1.4	3.49	7.28	0.57	0.69	0.96	4.03

Species	Sex	USI	Total Length	Head length	Eye length	Eye width	Pronotum			Scape length	Interocular distance	Postocular lobe width	Abdomen width
							Anterior lobe (l)	Anterior lobe (w)	Posterior lobe (l)				
<b><i>Paraphysoderes</i></b>													
<i>Pa. popeye</i> sp. nov.	♂	00073584	7.09	1.27	0.26	0.83	0.78	1.57	0.84	2.22	0.59	0.69	2.56
	♀	Mean (5)	7.89	1.55	0.29	0.98	1	1.96	0.84	2.61	0.66	0.76	3.32
		SD	0.44	0.21	0.02	0.02	0.06	0.18	0.07	0.14	0.03	0.01	0.14
		Minimum	7.47	1.25	0.27	0.95	0.95	1.8	0.76	2.5	0.63	0.75	3.17
		Maximum	8.41	1.83	0.33	1.01	1.1	2.25	0.93	2.77	0.69	0.78	3.54
<b><i>Physoderes</i></b>													
<i>P. anamalaiensis</i> sp. nov.	♂	Mean (5)	9.27	1.93	0.32	1.01	1.33	2.85	0.87	2.83	0.65	0.85	3.56
		SD	0.36	0.04	0.02	0.03	0.09	0.29	0.11	0.16	0.01	0.03	0.13
		Minimum	8.91	1.87	0.28	0.98	1.23	2.45	0.73	2.64	0.64	0.82	3.41
		Maximum	9.82	1.97	0.35	1.05	1.46	3.1	1.02	2.96	0.67	0.89	3.74
♀	Mean (5)	9.13	1.97	0.33	0.97	1.13	2.51	0.96	2.84	0.63	0.87	3.77	
	SD	0.27	0.12	0.03	0.04	0.05	0.15	0.15	0.09	0.08	0.02	0.19	
	Minimum	8.92	1.85	0.3	0.94	1.07	2.31	0.77	2.75	0.54	0.85	3.55	
	Maximum	9.59	2.14	0.36	1.03	1.17	2.72	1.1	2.99	0.74	0.91	4.07	
<i>P. azrael</i>	♂	Mean (5)	8.58	1.63	0.3	0.89	0.97	2.58	0.94	2.75	0.59	0.85	3.1
		SD	0.16	0.08	0.02	0.02	0.06	0.18	0.07	0.11	0.03	0.03	0.13
		Minimum	8.39	1.52	0.27	0.86	0.9	2.33	0.83	2.6	0.55	0.82	2.94
		Maximum	8.76	1.7	0.32	0.91	1.05	2.71	1	2.87	0.62	0.88	3.24
♀	Mean (5)	8.61	1.61	0.29	0.89	0.86	2.13	2.68	0.92	2.68	0.6	0.86	3.21
	SD	0.27	0.06	0.02	0.04	0.04	0.07	0.04	0.09	0.03	0.02	0.06	
	Minimum	8.14	1.51	0.26	0.83	0.8	2.04	2.55	5.13	0.55	0.84	3.13	
	Maximum	8.83	1.67	0.31	0.93	0.91	2.22	2.77	5.64	0.62	0.88	3.26	
<i>P. brevipennis</i> sp. nov.	♂	Mean (5)	6.61	1.77	0.3	0.93	1.28	2.98	0.78	2.6	0.6	0.87	3.44
		SD	0.35	0.14	0.03	0.04	0.1	0.2	0.05	0.14	0.05	0.04	0.24
		Minimum	6.08	1.67	0.27	0.88	1.21	2.76	0.71	2.47	0.53	0.81	3.19
		Maximum	7.07	2.01	0.34	0.98	1.44	3.25	0.82	2.8	0.65	0.91	3.83
♀	Mean (5)	6.53	1.69	0.31	0.96	1.11	2.49	0.81	2.54	0.64	0.89	3.8	
	SD	0.17	0.15	0.04	0.04	0.09	0.18	0.08	0.13	0.03	0.03	0.32	
	Minimum	6.29	1.49	0.25	0.91	0.98	2.19	0.73	2.31	0.59	0.84	3.42	
	Maximum	6.73	1.87	0.34	1.01	1.2	2.65	0.91	2.66	0.68	0.93	4.14	

Species	Sex	USI	Total Length	Head length	Eye length	Eye width	Pronotum				Scape length	Interocular distance	Postocular lobe width	Abdomen width	
							Anterior lobe (l)	Anterior lobe (w)	Posterior lobe (l)	Posterior lobe (w)					
<i>P. curvulionis</i>	♂	Mean (7)	7.64	1.56	0.28	0.86	1.02	2.53	0.78	2.59	4.48	0.37	0.59	0.81	3
		SD	0.21	0.07	0.01	0.02	0.06	0.15	0.08	0.03	0.18	0.06	0.03	0.02	0.21
		Minimum	7.37	1.46	0.27	0.82	0.94	2.37	0.64	2.5	4.15	0.27	0.54	0.78	2.68
		Maximum	7.9	1.67	0.29	0.88	1.11	2.74	0.93	2.69	4.63	0.44	0.65	0.83	3.35
		Mean (9)	7.47	1.52	0.27	0.86	0.91	2.19	0.86	2.54	4.46	0.39	0.58	0.82	3.14
	♀	SD	0.17	0.07	0.03	0.04	0.08	0.1	0.08	0.09	0.16	0.03	0.03	0.03	0.26
		Minimum	7.23	1.38	0.23	0.82	0.79	2.07	0.72	2.46	4.12	0.36	0.53	0.77	2.5
		Maximum	7.68	1.61	0.32	0.92	1.07	2.36	1.01	2.7	4.68	0.44	0.63	0.85	3.39
		Mean (5)	10.47	2.01	0.34	0.99	1.45	3.42	1.15	3.31	6.24	0.55	0.65	0.94	3.82
		SD	0.54	0.08	0.03	0.05	0.2	0.54	0.09	0.23	0.36	0.02	0.07	0.05	0.28
<i>P. fuliginosa</i>	♂	Minimum	9.84	1.89	0.29	0.93	1.22	2.85	1.06	3.1	5.84	0.52	0.56	0.89	3.54
		Maximum	11.03	2.08	0.36	1.04	1.69	4	1.28	3.63	6.56	0.57	0.74	1.01	4.19
		Mean (5)	10.14	2	0.38	1.01	1	2.39	1.34	3.2	6.2	0.5	0.64	0.92	4.04
		SD	0.49	0.05	0.04	0.07	0.08	0.18	0.12	0.15	0.37	0.03	0.06	0.04	0.26
		Minimum	9.59	1.92	0.33	0.93	0.9	2.19	1.22	3	5.72	0.49	0.59	0.88	3.8
	♀	Maximum	10.89	2.03	0.44	1.12	1.1	2.6	1.54	3.4	6.68	0.55	0.74	0.98	4.47
		Mean (5)	8.64	2.01	0.31	0.89	1.23	2.83	0.98	2.74	4.72	0.52	0.61	0.86	3.3
		SD	0.28	0.08	0.01	0.01	0.05	0.09	0.06	0.08	0.23	0.03	0.03	0.01	0.1
		Minimum	8.31	1.9	0.29	0.88	1.18	2.73	0.93	2.64	4.54	0.49	0.55	0.84	3.19
		Maximum	9.03	2.12	0.32	0.9	1.28	2.97	1.07	2.82	5.13	0.56	0.62	0.87	3.46
<i>P. minime</i> sp. nov.	♀	Mean (5)	8.29	1.88	0.3	0.87	0.89	2.07	1.04	2.6	4.77	0.49	0.57	0.87	3.58
		SD	0.16	0.14	0.05	0.06	0.08	0.08	0.09	0.1	0.26	0.02	0.09	0.04	0.16
		Minimum	8.1	1.7	0.25	0.79	0.81	1.98	0.96	2.48	4.48	0.47	0.49	0.82	3.31
		Maximum	8.54	2.05	0.38	0.94	0.98	2.15	1.19	2.7	5.11	0.51	0.69	0.94	3.71
		Mean (5)	8.64	2.01	0.31	0.89	1.23	2.83	0.98	2.74	4.72	0.52	0.61	0.86	3.3

Species	Sex	USI	Total Length	Head length	Eye length	Eye width	Pronotum				Hemelytron length	Scape length	Interocular distance	Postocular lobe width	Abdomen width
							Anterior lobe (l)	Anterior lobe (w)	Posterior lobe (l)	Posterior lobe (w)					
<i>P. multiensis</i> sp. nov.	♂	Mean (4)	7.35	1.73	0.3	0.91	0.9	1.95	0.95	2.43	3.96	0.49	0.56	0.82	2.83
		SD	0.27	0.18	0.03	0.06	0.12	0.11	0.03	0.13	0.3	0.03	0.03	0.09	0.18
		Minimum	6.99	1.46	0.27	0.84	0.77	1.82	0.93	2.26	3.61	0.46	0.53	0.74	2.61
		Maximum	7.59	1.87	0.33	0.96	1.04	2.08	0.99	2.56	4.35	0.53	0.6	0.93	3.01
		Mean (3)	7.92	1.75	0.3	0.95	1	2.05	0.95	2.59	4.32	0.48	0.64	0.85	3.34
	SD	0.27	0.07	0.03	0.05	0.05	0.09	0.09	0.04	0.26	0.05	0.06	0.03	0.08	
	Minimum	7.67	1.72	0.27	0.89	0.95	1.98	0.9	2.55	4.02	0.45	0.57	0.81	3.28	
	Maximum	8.21	1.83	0.32	0.99	1.06	2.15	1.06	2.62	4.5	0.54	0.69	0.87	3.43	
	Mean (3)	10.82	2.05	0.36	1.07	1.62	3.69	1.12	3.54	6.43	0.58	0.72	0.93	4.14	
	SD	0.14	0.11	0.08	0.05	0.1	0.26	0.1	0.12	0.21	0	0.01	0.04	0.32	
<i>P. mysorensis</i> sp. nov.	♂	Minimum	10.69	1.92	0.27	1.03	1.51	3.44	1.01	3.41	6.3	0.57	0.71	0.89	3.92
		Maximum	10.96	2.14	0.42	1.12	1.71	3.95	1.21	3.63	6.67	0.58	0.73	0.97	4.37
		Mean (2)	10.7	2.08	0.34	1.08	1.45	3.11	1.17	3.56	6.48	0.58	0.66	1	4.3
		SD	0.25	0.11	0.04	0.06	0.14	0.08	0.17	0.07	0.05	0.03	0.11	0.01	NA
		Minimum	10.52	2	0.32	1.04	1.35	3.05	1.05	3.51	6.45	0.56	0.58	1	4.3
	SD	0.25	0.11	0.04	0.06	0.14	0.08	0.17	0.07	0.05	0.03	0.11	0.01	NA	
	Maximum	10.88	2.15	0.36	1.12	1.56	3.16	1.29	3.61	6.52	0.61	0.74	1.01	4.3	
	Mean (5)	9.12	1.89	0.34	1.02	0.9	2.17	1.24	2.95	5.27	0.53	0.59	0.85	3.42	
	SD	0.29	0.08	0.03	0.05	0.07	0.09	0.07	0.1	0.16	0.07	0.05	0.04	0.22	
	Minimum	8.76	1.77	0.29	0.96	0.83	2.04	1.13	2.82	5.09	0.46	0.53	0.79	3.16	
♀	Maximum	9.48	1.95	0.36	1.09	1	2.28	1.32	3.07	5.45	0.65	0.66	0.89	3.72	
	Mean (5)	10.05	1.9	0.35	1.13	0.94	2.3	1.4	3.32	6.07	0.6	0.64	0.92	4.17	
	SD	0.41	0.04	0.02	0.02	0.09	0.08	0.1	0.11	0.47	0.09	0.03	0.02	0.14	
	Minimum	9.6	1.88	0.33	1.1	0.83	2.22	1.32	3.2	5.65	0.51	0.62	0.89	4.05	
	Maximum	10.65	1.97	0.37	1.16	1.05	2.4	1.56	3.49	6.8	0.71	0.67	0.93	4.41	

Species	Sex	USI	Total Length	Head length	Eye length	Eye width	Pronotum			Hemelytron length	Scape length	Interocular distance	Postocular lobe width	Abdomen width
							Anterior lobe (l)	Anterior lobe (w)	Posterior lobe (l)					
<i>P. nigroalbus</i>	♀	00040566	9.74	1.88	0.29	1	1.03	2.24	1.17	2.95	0.66	0.94	3.66	
	♂	Mean (5)	9.94	1.81	0.32	1.02	1.24	3.17	1.25	3.14	6.08	0.63	0.91	3.61
		SD	0.3	0.12	0.02	0.04	0.09	0.26	0.09	0.08	0.2	0.04	0.06	0.24
	♀	Minimum	9.44	1.7	0.29	0.97	1.12	2.89	1.17	3.06	5.75	0.57	0.84	3.34
		Maximum	10.22	1.99	0.34	1.08	1.35	3.51	1.4	3.26	6.3	0.66	1.01	3.87
	♀	Mean (5)	9.94	1.8	0.32	1.05	0.96	2.45	1.31	3.17	6.28	0.66	0.93	3.73
		SD	0.31	0.15	0.03	0.04	0.1	0.09	0.18	0.15	0.25	0.04	0.04	0.23
		Minimum	9.54	1.62	0.3	1.01	0.84	2.35	1.06	3	5.93	0.42	0.88	3.38
		Maximum	10.3	1.99	0.37	1.1	1.12	2.57	1.51	3.33	6.51	0.51	0.98	3.94
	<i>P. ractepiflosa</i> sp. nov.	♂	Mean (2)	8.93	1.86	0.37	0.86	0.9	2.13	1	2.74	0.5	0.85	3.39
SD		0.49	0.15	0.03	0	0.17	0.12	0.3	0.14	0.6	0.14	0.07	0.25	
Minimum		8.59	1.75	0.34	0.86	0.77	2.04	0.79	2.64	5.09	0.44	0.8	3.21	
Maximum		9.27	1.96	0.39	0.86	1.02	2.21	1.21	2.83	5.93	0.5	0.9	3.57	
♀		Mean (5)	9.19	1.99	0.37	0.93	0.9	2.23	1.1	2.99	5.47	0.55	0.84	3.86
		SD	0.67	0.1	0.02	0.03	0.06	0.13	0.12	0.21	0.47	0.07	0.01	0.26
Minimum		8.32	1.83	0.34	0.89	0.82	2.02	0.97	2.66	4.89	0.44	0.81	3.44	
Maximum		10.19	2.08	0.4	0.97	0.97	2.37	1.27	3.22	6.2	0.56	0.85	4.1	
<i>P. tricolor</i> sp. nov.		♂	Mean (2)	8.66	1.58	0.29	0.91	0.99	2.47	1.17	2.65	0.54	0.84	2.92
		SD	0.16	0.04	0.01	0.05	0.09	0.07	0.01	0.05	0	0.03	0.02	0.17
	Minimum	8.55	1.56	0.29	0.88	0.93	2.42	1.16	2.61	5.26	0.42	0.82	2.8	
	Maximum	8.77	1.61	0.3	0.95	1.05	2.52	1.17	2.68	5.33	0.42	0.86	3.04	
	♀	Mean (3)	9.33	1.7	0.31	0.92	0.9	2.17	1.13	2.77	5.6	0.39	0.85	3.2
		SD	0.74	0.03	0.02	0.01	0.02	0.09	0.13	0.1	0.23	0.04	0.04	0.19
Minimum	8.7	1.67	0.29	0.91	0.88	2.07	1.02	2.66	5.44	0.35	0.8	2.98		
Maximum	10.15	1.73	0.32	0.93	0.92	2.25	1.28	2.86	5.76	0.42	0.87	3.34		