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Systematics of Reduviidae with Emphases on Reduviinae, Triatominae and Physoderinae

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Systematics of Reduviidae With Emphases on the Subfamilies Reduviinae, Triatominae, and Physoderinae

A Dissertation submitted in partial satisfaction
of the requirements for the degree of

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in

Entomology

by

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ABSTRACT OF THE DISSERTATION

Systematics of Reduviidae With Emphases on the Subfamilies
Reduviinae, Triatominae, and Physoderinae

by

Wei-Song Hwang

Doctor of Philosophy, Graduate Program in Entomology
University of California, Riverside, December 2012
Dr. Christiane Weirauch, Chairperson

Reduviidae (assassin bugs), the largest clade of predatory non-holometabolous insects (~6,800 species), display a range of prey specializations and members of one subfamily, the Triatominae, feed on vertebrate blood and are the vectors of *Trypanosoma cruzi*. A combination of phylogenetic analyses and taxonomic revisions of several target taxa are conducted to improve our knowledge of reduviid systematics. The emphasis is on resolving the highly polyphyletic Reduviinae, shedding light on the prevalence of trypanosomes in a species of endemic Triatominae in Southern California, revising a genus of Malagasy Reduviinae and the Indo-Pacific group of Physoderinae, a group once thought to be sister to the Triatominae.

A higher-level phylogeny of Reduviidae (178 taxa, 18 subfamilies) is reconstructed to investigate the relationships among subfamilies using five gene regions, with extensive sampling of the polyphyletic Reduviinae. Results indicate that Reduviinae fall into 11–14 separate clades and Triatominae may be paraphyletic. The evolution of blood-feeding may thus have occurred once or twice independently among predatory reduviids. Fossil-calibrated divergence time estimates show that Reduviidae originated in the Middle Jurassic (~178Ma), but the majority of extant lineages only emerged in the Late Cretaceous (~97Ma). Ancestral state reconstructions indicate bark-association as the ancestral microhabitat for Higher Reduviidae.

A survey on the infection rate of *Triatoma protracta* with *T. cruzi* in Southern California show relatively high rates (19-36%) with geographical variability but no clear temporal differences. A taxonomic revision of the Malagasy endemic reduviine *Durevius* is provided and 2 new species described.

A phylogenetic analysis of Physoderinae (57 taxa) based on 57 morphological characters (50 discrete, 7 continuous) indicate that the Neotropical Physoderinae are sister to all remaining Physoderinae except *Porcelloderes*. The morphologically diverse Malagasy physoderines are not monophyletic. Physoderine diversity in the Oriental and Australasian regions is here revised based on the most extensive collection of specimens (902) assembled to date. Based on the phylogenetic analysis, the generic classification of Old World Physoderinae is revised. Three new genera are created, 14 new species described, 11 new combinations created, and 17 synonyms established. Diagnoses and identification keys for Old World genera are provided and species illustrated.

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Introduction

Systematics is the field of biology that is charged with documenting global biodiversity and understanding biological phenomena in an evolutionary context. Within systematics, taxonomy is the practice of discovering, describing, classifying, and testing concepts of new and known species in a system that reflects evolution and allows for targeted data retrieval. Systematics is thus a crucial science to address the current biodiversity crisis (Ebach et al., 2011). The other branch of systematics is phylogenetics that attempts to reconstruct the evolutionary relationships of all organisms (phylogeny) and to understand the origins of biological patterns and processes. My research encompasses both aspects of systematics, focusing on three subfamilies of Reduviidae.

Reduviidae (assassin bugs) are a highly speciose group of predatory insects (6,800 described species) that display a wide range of prey specializations along with associated morphological diversity (Maldonado, 1990). Kleptoparasitism on spider-webs (Emesinae), sticky-trap ambush behavior (Harpactorinae), millipede-feeding (Ectrichodiinae) and baited ant-feeding (Holoptilinae) are some of the innovative predatory strategies that have evolved within Reduviidae. Moreover, the evolution of blood-feeding within Reduviidae (subfamily Triatominae) has substantial medical importance due to species being vectors of *Trypanosoma cruzi* Chagas. Understanding how such an assortment of predatory and blood-feeding behaviors has evolved is the underlying rationale for embarking on this research. This dissertation is the result of several research projects that comprise a) testing the phylogenetic relationships of Physoderinae, Reduviinae and Triatominae; b) an investigation into the infection rate of native kissing bugs in Southern California with the Chagas disease etiologic agent *Trypanosoma cruzi* (Chagas), c) revising the taxonomy of the Malagasy reduviine *Durevius* Villiers; as well as d) that of *Physoderes* Westwood and other physoderine genera. These projects are treated in separate taxon-oriented chapters except for the phylogenetic relationships of Reduviinae and Triatominae (Chapter 1) which falls under a more comprehensive analysis of the evolutionary history of the entire Reduviidae.

To improve our understanding of the evolutionary history of Reduviidae (Weirauch, 2008; Weirauch & Munro, 2009), the largest, both in terms of taxa and sequence data, molecular phylogeny of assassin bugs is reconstructed. Further insights into the evolution of assassin bugs can be established by integrating the molecular phylogeny with data on fossils, microhabitats and prey specializations in separate analyses. None of these topics has so far been investigated using cladistic approaches. Together, these results will provide a temporal and ecological pattern of how reduviids have evolved. Such results can be compared with other studies to generate general hypotheses of how insects diversify and also identify unique examples of reduviid evolution worth further investigating.

One group of reduviids that greatly benefits from this large-scale multi-dataset approach is the blood-feeding Triatominae (kissing bugs); their phylogenetic relationships have remained problematic. The increased sampling of triatomine tribes and sister-group taxa in this analysis allows for further testing of controversial relationships. In addition, fossil-calibrated divergence time estimates and ancestral state reconstructions using microhabitat and prey specialization will allow for a better understanding of the timing of the switch to blood-feeding and whether it coincided with microhabitat transitions.

The second chapter surveys the infection rate of *Triatoma protracta* (Uhler) native to Southern California based on two populations. The concern here is the extent to which native Triatominae species found in wilderness areas serve as disease reservoirs (Burkholder *et al*. 1980, Peterson *et al*. 2002, Bradley & Altizer 2006). Such information is currently outdated, based on collections and studies before the 1960s, and in need of review (e.g., Kofoid & Whitaker, 1936; Ryckman, 1962; Wood & Wood, 1967). Several genotypes (also referred to as natural clones or major lineages) of *T. cruzi* are associated with different host lineages across the Western hemisphere. An attempt to identify the genotype of native *T. cruzi* in Southern California is also conducted and their phylogenetic relationship inferred.

Madagascar is well known for its high level of species endemism and new species continue to be discovered (Myers et al., 2000; Goodman & Benstead, 2005). Madagascar is also highlighted as one of the most critical biological hotspots that are experiencing the greatest biodiversity loss due to habitat destruction (Myers et al., 2000; Brooks et al., 2002). A recent island-wide inventory of terrestrial arthropods of Madagascar by the California Academy of Sciences (CAS) yielded more than 3000 reduviid specimens, which provide an excellent opportunity to document the reduviid diversity on this island. *Durevius* Villiers, a relatively small reduviine genus, is here selected to be revised while adding two new species to this taxon.

The third chapter also touches on Malagasy biodiversity, but goes beyond this island and into the Oriental and Australasian regions: Physoderines of Madagascar stand out in being morphologically rather diverse and species were accordingly classified into 11 endemic genera (Villiers, 1968). The genus *Physoderes* Westwood in contrast, is widespread in the Oriental and Australasian regions and fairly speciose, but rather uniform; the monophyly of this genus has not been tested. The remainder of the subfamily comprises two Neotropical genera that were proposed to be basal within Physoderinae (Weirauch, 2006) and one recently described genus from Africa. Phylogenetic relationships within the subfamily are unknown. Here I will test if 1) the Malagasy physoderines are monophyletic, inferring a single colonization event and subsequent radiation, and 2) the most primitive physoderines are Neotropical.

This phylogenetic analysis will also allow revising Physoderinae at the genus level and below. Based on phylogenetic hypotheses, genera will be redefined to represent monophyletic groups and new combinations and synonyms created as necessary. The descriptive, species-level focus of this research goal is on the genus *Physoderes*. This genus is in a poor state, as most species were not described based on modern standards, rendering species identification and the discovery and description of new species problematic. New species are described and the genus *Physoderes* is redefined to comprise a monophyletic clade.

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Chapter 1: Evolutionary history of assassin bugs – insights from divergence dating and ancestral state reconstruction

Abstract

Assassin bugs are one of the most successful clades of predatory animals based on their species numbers (~6,800 spp.) and wide distribution in terrestrial ecosystems. Various novel prey capture strategies and remarkable prey specializations contribute to their appeal as a model to study evolutionary pathways involved in predation. Here, we reconstruct the most comprehensive reduviid phylogeny (178 taxa, 18 subfamilies) to date based on molecular data (5 markers). This phylogeny tests current hypotheses on reduviid relationships emphasizing the polyphyletic Reduviinae and the blood-feeding, disease-vectoring Triatominae, and allows us, for the first time in assassin bugs, to reconstruct ancestral states of prey associations and microhabitats. Using a fossil-calibrated molecular tree, we estimated divergence times for key events in the evolutionary history of Reduviidae. Our results indicate that the polyphyletic Reduviinae fall into 11-14 separate clades. Triatominae are paraphyletic with respect to the reduviine genus *Opisthacidius* in the maximum likelihood anaylses; this result is in contrast to prior hypotheses that found Triatominae to be monophyletic or polyphyletic and may be due to the more comprehensive taxon and character sampling in this study. The evolution of blood-feeding may thus have occurred once or twice independently among predatory assassin bugs. All prey specialists evolved from generalist ancestors, with multiple evolutionary origins of termite and ant specializations. A bark-associated life style on tree trunks is ancestral for most of the lineages of Higher Reduviidae; living on foliage has evolved at least six times independently. Reduviidae originated in the Middle Jurassic (178Ma), but significant lineage diversification only began in the Late Cretaceous (97Ma). The integration of molecular phylogenetics with fossil and life history data as presented in this paper provides insights into the evolutionary history of reduviids

and clears the way for in-depth evolutionary hypothesis testing in one of the most speciose clades of predators.

Introduction

Assassin bugs (Hemiptera: Reduviidae) are the largest clade of predatory non-holometabolous insects (~6,800 described species) (Maldonado, 1990; Froeschner & Kormilev, 1989) and one of the largest clades of predatory animals. In addition, Reduviidae have adapted to a wide range of terrestrial habitats and diversified in their prey choices while developing a wide repertoire of innovative prey capture strategies (Soley et al., 2011; Wignall et al., 2011; Forero et al., 2011; Zhang & Weirauch, 2011; Jacobson, 1911). Some Emesinae, the thread-legged bugs, cut through webs to reach their spider prey (Soley et al., 2011) or lure spiders using aggressive mimicry (Wignall et al., 2011). Apiomerini, Ectinoderini and Diaspidiini (Harpactorinae) coat their fore legs with plant resins for prey capture (Forero et al., 2011), while some members of the Harpactorini have evolved their own sticky secretions for the same purpose (Zhang & Weirauch, 2011). Holoptilinae, the feather-legged bugs, attract ants to imbibe paralyzing secretions before killing their prey (Jacobson, 1911). The most infamous assassin bugs belong to the mostly Neotropical subfamily Triatominae, the kissing bugs, which feed on vertebrate blood. After humans colonized the Americas, several kissing bug species have adapted to blood-feed on humans where they vector *Trypanosoma cruzi* Chagas, the etiologic agent of Chagas disease (Lent & Wygodzinsky, 1979). Due to this range of predatory lifestyles and to the size of the group, assassin bugs offer a unique opportunity to investigate the evolution and diversification of one of the most speciose clades of animal predators. No study has so far addressed the evolutionary history of microhabitat and prey choices or examined the timing of key transitions within assassin bugs. We here present the largest molecular phylogeny of Reduviidae published to date with extensive subfamily representation and dense sampling of the polyphyletic Reduviinae. Based on this phylogeny, we trace the evolution of microhabitat colonizations and prey specialization within the group, but also date important diversification events based on a fossil-calibrated molecular divergence tree.

Assassin bugs are found in many terrestrial ecosystems and microhabitats, ranging from mammal burrows in the Sonoran desert to decomposing logs in the Bornean rainforest (Ryckman, 1954; Miller, 1959). Microhabitats of various assassin bug species are relatively well documented in the literature and are supplemented with our lab's field observations. Interestingly, a large number of species are either found in association with the bark of trees or dwell on foliage of herbs, shrubs, and trees (Readio, 1927; Miller, 1953; Louis, 1974). Several lineages of the Phymatine Complex (Centrocnemidinae, Elasmodeminae, Hammacerinae, Holoptilinae, Phymatinae) (Weirauch, 2008; Weirauch & Munro, 2009; Weirauch et al., 2011), the sister group to a clade that comprises the majority of Reduviidae, the "Higher Reduviidae", are associated with the bark of trees and this association also occurs in various lineages within the Higher Reduviidae, which may infer that this association is ancestral for assassin bugs. Vegetation dwelling as a lifestyle, in contrast, occurs in more derived clades, e.g., the Phymatini among the Phymatinae and the Harpactorini among the Harpactorinae, and might therefore represent a derived microhabitat associations. We here test if bark association may represent the ancestral microhabitat for Reduviidae and trace microhabitat evolution across the group.

Ecological specializations have frequently been postulated to represent evolutionary dead-ends due to higher extinction risks (Futuyma & Moreno, 1988; Kelley & Ferrell, 1998; Labandeira et al., 2002), although this hypothesis has been challenged by some authors (Scheffer & Wiegmann, 2000; Stireman, 2005). According to this theory, specialist predation strategies would be more likely to evolve from generalist strategies, than the reverse transition from specialist to generalist predation. Assassin bugs show a pattern of generalist and specialist species, with some taxa apparently feeding on a wide range of prey species and others being specialized on certain taxonomic groups (Miller, 1953; McMahan, 1983). Some of the most speciose clades within Reduviidae, such as the millipede-feeding Ectrichodiinae (>600 spp.), are specialists, while other specialist clades are much less diverse, e.g., the ant-feeding Holoptilinae (78 spp.) and the termite-specialist Salyavatinae (99 spp.) (Maldonado, 1990; Miller, 1953). Conversely, Harpactorinae (>2,000 spp.), the largest subfamily of Reduviidae, consists predominantly of generalist predators (Readio, 1927; Louis, 1974). We compiled feeding records of Reduviidae from the literature and our own observations to investigate evolutionary patterns across the phylogeny. Compared to the microhabitat dataset, the feeding dataset is less complete due to the scarcity of feeding observations in the laboratory and field. The assembled data together with the phylogeny nevertheless allow us to reconstruct generalist-specialist patterns, test whether reduviids evolved from an ancestral generalist or specialist predator, determine if reversals from specialization to generalist feeding have occurred, but also to predict feeding patterns for taxa with unknown feeding habits.

The phylogenetics of blood-feeding Triatominae has received considerable attention due to the epidemiological significance of certain species as vectors of Chagas disease in Latin America (Schofield & Galvao, 2009; Patterson & Gaunt, 2010; Hypsa et al., 2002). Conflicting hypotheses support Triatominae as monophyletic (Weirauch, 2008; Weirauch & Munro, 2009; Patterson & Gaunt, 2010; Hypsa et al., 2002) or propose polyphyletic origins for the blood-feeders (Schofield & Galvao, 2009; de Paula et al., 2005). These alternative relationships impact interpretations of hematophagy in Reduviidae as a unique evolutionary event or as multiple independent evolutionary transitions. Schofield (2009, 1994) proposed multiple transitions to hematophagy and postulated a step-wise ecological scenario of separate lineages of predatory assassin bugs exploiting nest-dwelling invertebrates as a precursor to feeding on the vertebrate hosts. Almost all published triatomine phylogenies are based only on Triatomini and Rhodniini and exclude the remaining three triatomine tribes Alberproseniini, Bolboderini, and Cavernicolini (Schofield & Galvao, 2009), except Patterson and Gaunt (2010), who reported a sister-group relationship between Bolboderini and Rhodniini. We here test relationships of Triatominae with the predatory Reduviidae by including 13 species of Cavernicolini, Triatomini and Rhodniini in the first multi-gene analysis that includes three triatomine tribes. We exclude Bolboderini and Alberproseniini due to the lack of data. Microhabitat and prey specialization of Triatominae and closely related reduviid species are traced to test if Schofield's ecological scenarios are corroborated by our phylogenetic investigations.

Our current understanding of the evolutionary history of assassin bugs from fossils is based on a relatively small published fossil record that comprises 52 species (EDNA database http://edna.palass-hosting.org/, [Scudder, 1891; Arillo & Ortuno, 2005]). Of these fossils, 31 are of questionable classification due to the lack of illustrations and meaningful descriptions. Reduviidae are relatively old, with one fossil that has been attributed to the Reduvioidea (Reduviidae + Pachynomidae) from the Early Jurassic and three reduviid specimens from the Early Cretaceous (Shcherbakov, 2007). Fossils that can be reliably classified to subfamily, tribe, or genus are predominantly from Dominican and Baltic amber (Miocene – Eocene) and offer little insight into the evolutionary timing of major lineage diversification events within Reduviidae. In order to date some of these key events, we here use, for the first time in assassin bugs, divergence time estimates based on relaxed clock models and model calibration using described fossil taxa (Cardinal et al., 2010; Smith et al., 2010; Wiegmann et al., 2011). The use of fossil-calibrated molecular phylogenies in Hemiptera is in its infancy and currently restricted to agriculturally important Sternorrhyncha (psyllids [Percy et al., 2004], aphids [Kim et al., 2011]), some Auchenorrhyncha (cicadas [Buckley & Simon, 2007], spittlebugs [Cryan & Svenson, 2010]) and one study on heteropteran infraorders (Li et al., 2012). Within Heteroptera, divergence times have so far only been investigated for Cimicoidea (Jung & Lee, 2012). Previous molecular dating work within Reduviidae is restricted to a small data set, in terms of taxa and genes, of Triatominae and has used a strict-clock model (Patterson & Gaunt, 2010; Gaunt & Miles, 2002).

Recent phylogenetic analyses have recovered the monophyly of many, but not all, reduviid subfamilies while the monophyly of Reduviidae is well-established and Reduvioidea (Reduviidae + Pachynomidae) are sister-group to the rest of Cimicomorpha based on morphology (Weirauch, 2008; Weirauch & Munro, 2009; Schuh & Stys, 1991; Schuh et al., 2009). A notable exception are the Reduviinae, the second largest assassin bug subfamily, with worldwide 142 genera and ~1,100 described species (Maldonado, 1990), which have long been suspected to be polyphyletic. Usinger (1943), based on a 'pre-cladistic' phylogeny of Reduviidae, postulated that Reduviinae are 'an unnatural group' due to the fact that several genera were removed from that group to serve as type genera of new reduviid subfamilies, among them the Cetherinae, Vesciinae, and Sphaeridopinae. Due to the limited sampling of Reduviinae in previous analyses (Weirauch, 2008; Weirauch & Munro, 2009), the extent of the reduviinae polyphyly problem remains in the dark. Our current analyses include an extensive sample of Reduviinae, allowing for tests of relationships and determining the major clades of Reduviinae. We regard our results as the first step towards resolving the Reduviinae polyphyly problem that will eventually lead to a re-classification of Reduviidae.

Materials and methods

Taxon sampling

A total of 178 taxa were sampled comprising 170 ingroup (Reduviidae) and 8 outgroup taxa (Nepomorpha: Belostomatidae, Corixidae; Pentatomomorpha: Scutelleridae, Aradidae; Cimicomorpha: Nabidae, Tingidae, Miridae). Ingroup sampling comprised 12 taxa of the Phymatine Complex (Centrocnemidinae, Elasmodeminae, Hammacerinae, Holoptilinae, Phymatinae); the remaining taxa belong to a clade that we here refer to as the 'Higher Reduviidae' (all Reduviidae with the exception of the Phymatine Complex). We recognize 25 subfamilies within the Reduviidae (Maldonado, 1990; Davis, 1969; Putshkov & Putshkov, 1985), 18 of which are represented in our analysis (Table S1.1). Taxa not included due to the lack of DNA quality material are the reduviid sister-group Pachynomidae and the assassin bug subfamilies Bactrodinae, Chryxinae, Elasmodeminae, Manangocorinae, Phimophorinae, Pseudocetherinae, and Sphaeridopinae. We included 75 terminal taxa (31 genera) of Reduviinae to test relationships of clades currently classified within this polyphyletic subfamily. Table S1.1 and Table S1.2 summarizes classification, molecular data, GenBank accession numbers, microhabitat, and prey specialization.

Specimen identification, databasing, and vouchering

Specimens were identified using species descriptions, identification keys e.g., (Lent & Wygodzinsky, 1979; Wygodzinsky & Usinger, 1964; Melo, 2007) and images of type specimens where available. Undescribed species are listed as "n. sp.", while specimens that could not be identified with certainty to species level are referred to as "sp." or denoted as "nr. xxx" to the closest matching species. Inability to identify most species is due to the lack of adequate diagnoses and descriptions, illustrations and keys in historical literature. One hind leg was removed for non-destructive DNA extraction and subsequently mounted with the voucher specimen. Unique specimen identifier matrix bar-code labels (USIs) were associated with each voucher. Specimens were databased using the online specimen database of the Plant Bug Planetary Biodiversity Inventory (PBI) project (https://research.amnh.org/pbi/locality). Geo-referenced localities and other specimen information (e.g., images) are publicly available on the Discover Life website (http://www.discoverlife.org). Voucher specimens depository information is listed in Table S1.1.

Molecular markers and primers

Five molecular markers were amplified comprising four ribosomal gene regions (16S rDNA, 18S rDNA, 28S D2 rDNA, 28S D3-D5 rDNA) and one nuclear protein-coding gene (wingless, Wg). The choice of the wingless gene is based on its utility for higher level phylogenetic studies of insects, especially Hemiptera (Cryan & Svenson, 2010; Urban & Cryan, 2007; Urban et al., 2010; Thao et al., 2000) and variation across Reduviidae is found to be at a suitable level (average 18.43%, range 15.36%-30.96%). For primer information and PCR thermocycling regimes see Weirauch and Munro (2009) for ribosomal genes and Urban and Cryan (2007) for the wingless gene.

DNA extraction, amplification, purification, and sequencing

DNA was extracted using Qiagen DNeasy Blood and Tissue Kit standard protocols (Qiagen, Valencia, CA). Proteinase K digestion for dry specimens (see Table S1.1) was extended to 48hrs. PCR amplification was conducted using Illustra PuReTaq Ready-To-Go PCR beads in an Eppendorf Thermocycler. Amplification results were visualized via gel electrophoresis with SyberSafe gel staining and UV illuminator. PCR products for ribosomal genes were purified using SureClean (Bioline); Wg PCR products encountered lower success rates in overall PCR amplification (see Table S1.1) and required gel extraction using QIAquick Gel Extraction Kit standard protocols. Sanger (BigDye) DNA sequencing was conducted at the UCR Genomics Core facility. Sequences are deposited in GenBank (Table S1.1). Completeness of the molecular data set is 79.78%.

Sequence alignment and phylogenetic analysis

Sequences were edited and concatenated using Sequencher 4.8. Stop codons in open reading frames of Wg were checked in Sequencher. Sequences were aligned individually with MAFFT (Katoh et al., 2005) (E-INS-i, G-INS-i, L-INS-i, Q-INS-i) and MUSCLE (Edgar, 2004) to compare effects of alignment on phylogenetic analyses. SequenceMatrix 1.7.8 (Vaidya et al., 2011) and Mesquite 2.74 (Maddison & Maddison, 2011) were used to concatenate aligned gene regions into a combined molecular dataset. Lengths of the combined, aligned dataset ranged from 3,793bp (E-INS-i) to 4,043bp (Q-INS-i) (Table S1.3).

Phylogenetic analyses were conducted using TNT version 1.1 (Goloboff et al., 2008) (parsimony [P]) on a PC and RAxML-HPC2 (Stamatakis, 2006) (maximum likelihood [ML]) on the teragrid accessible through the CIPRES web portal (http://www.phylo.org). TNT was set at 50, 80 and 100 initial levels to test the robustness of the search. All runs set at 80 and above produced identical results. Heuristic searches were conducted using New Technology Search with ratchet, tree-drifting, sectorial search, and tree-fusing with default settings. Best score hits of 10 times were performed and 500 standard bootstrap replicates were conducted. Internal gaps were treated as fifth character states in parsimony analyses, with terminal gaps converted to missing data. RAxML analyses used a partitioned dataset (i.e., treating the 5 gene regions separately) and rapid bootstrapping with automatic halt and subsequent higher bootstrap iterations (500-1,000). Support values are reported in the text henceforth in parentheses indicating the method of analysis (P for parsimony, ML for Maximum Likelihood). For bootstrap support, we define values >90% as strongly supported, 90 – 70% as well-supported/moderate support, <70% as weakly supported.

The different alignment strategies resulted in largely identical tree topologies in the RAxML analyses (Table S1.4). Bootstrap support values varied slightly between alignments (Table S1.4). Well-supported clades (>70%) were consistently recovered from all alignments. The MAFFT G-INS-i and MAFFT E-INS-i recovered identical topologies and only slight differences in bootstrap support values. The phylogenies discussed in the following are based on the MAFFT G-INS-i algorithm that shows highest congruence with published phylogenies (Weirauch & Munro, 2009). For the MAFFT G-INS-i alignment we report 1,649 parsimony informative characters out of a total of 3,796 characters.

Trait evolution

Ancestral states for prey specializations and microhabitats, as separate characters, were reconstructed in Mesquite 2.74 using a parsimony model with characters treated as unordered and in BayesTraits 1.0 (www.evolution.rdg.ac.uk) for a maximum likelihood model (Pagel et al., 2004). We used the BayesMultistate method within BayesTraits with restrictions of equal probability for all state changes to reflect the one parameter Mk1 model for both microhabitat and prey specialization analyses. We based ancestral state reconstructions on the topology of the best likelihood tree from the RAxML analysis. Sources of data for prey specialization and microhabitat are listed in Table S1.2. We coded terminal taxa based on biological data from congeneric species when observations for the species in the analysis were unavailable. We coded data as missing where genus-level data were unavailable.

Molecular dating

The divergence time estimate analysis was conducted using BEAST 1.6.1 (Drummond & Rambaut, 2007) with a 4-gene partitioned dataset (16S rDNA, 18S rDNA, 28S rDNA, Wg), G-INS-i aligned, unlinked substitution models (GTR+ Γ+I), relaxed clock uncorrelated lognormal, and 11 fossil data points for calibration. The 28S D2 and 28S D3-D5 gene regions were analyzed using the same clock model to reflect their single identity. The fossils were placed using the specimen-based method for placement within taxon groups (Fig. 1.3, Table S1.5; [Parham et al., 2012]). We used the oldest-assigned fossil of the taxon which has unambiguous diagnostic characters to place it within a clade. Based on the geologic age range estimates provided by the fossil literature or updated estimates of the stratigraphy (Table S1.5), fossil ages were incorporated as taxon group priors with a lognormal distribution with a hard-bound minimum age and a soft-bound maximum age that captures the date range within the 95% confidence interval (Ho & Philips, 2009). Ten million generations were performed, sampling every 1,000 generations to produce 10,000 trees. The initial 2,500 trees (25%) were discarded as burn-in using TreeAnnotator 1.6.1 (Drummond & Rambaut, 2007). The remaining 7,500 trees were used to produce the maximum clade credibility tree visualized using FigTree 1.3.1 (http://tree.bio.ed.ac.uk/software/figtree/).

Results

Phylogenetic analyses

Figure 1.1 (ML; habitus images show the diversity in the subfamily Reduviinae) and figure 1.2 (P; habitus images show non-reduviine subfamilies) represent the largest, both in terms of terminals (178 taxa) and subfamily coverage (18 subfamilies), phylogeny of Reduviidae published to date. Although certain relationships above the subfamily level are weakly supported, these results drastically advance our understanding of assassin bug relationships and provide a solid framework for future studies. Most importantly, this analysis shows, for the first time, a glimpse of the true extent of the polyphyly of the large subfamily Reduviinae (lineages highlighted in red in Figs. 1 and 2). Hematophagous and disease vectoring Triatominae (shaded red) are nested within a clade of large predatory Neotropical Reduviinae and are paraphyletic in the ML analysis due to the sister-group relationship of the reduviine *Opisthacidius* Berg and the triatomine Cavernicolini + Rhodniini. We further show that the rather unique big-eyed Cetherinae (red arrowheads in Fig. 1.1) are polyphyletic and split into an Old World and New World clade in the ML analyses. At a higher level, Reduviidae are monophyletic (P 96, ML 100) and the Phymatine Complex (P 95, ML 100) is consistently recovered as the sister to the Higher Reduviidae (P 93, ML 100), which include ~90% of the reduviid species diversity. Sequence alignment data is provided in Table S1.3 with the resulting bootstrap support for clades of interest from topologies based on the different alignment methods summarized in Table S1.4.

Relationships within Reduviidae

Within the Higher Reduviidae, the sister-group relationship between Ectrichodiinae and Tribelocephalinae is well-supported (P 94, ML 99). Similarly, a clade containing Stenopodainae, Triatominae, and the reduviine genera Zelurus Burmeister and *Opisthacidius* was consistently recovered with high support (P 99, ML 94). Most other relationships between subfamilies vary between analyses or receive weak support. We only highlight two of them: the "Emesine Complex" that we here define as comprising Emesinae, Visayanocorinae, and Saicinae, was recovered, with low support (ML 50), only in the ML analysis and is paraphyletic in the P analysis. Physoderinae (asterisk in Fig. 1.1) were grouped with *Microlestria* Stål and Nalata Stål in the ML analysis (ML 78), but are polyphyletic in the P analysis. In the Phymatine Complex, the long branch of *Neocentrocnemis stali* (Reuter) representing Centrocnemidinae is attributed to incomplete data (16S, Wg absent) due to suboptimal preservation of specimen. We retain this taxon in the phylogeny as its placement is consistent with previous analyses based on morphology and molecular datasets (Weirauch, 2008; Weirauch & Munro, 2009). No large insertions, deletions or highly divergent sequences are present in the ribosomal dataset of *N. stali* and therefore no long-branch attraction is suspected.

Monophyly of subfamilies

The monophyly of eight subfamilies was strongly supported in both P and ML analyses (Hammacerinae, Holoptilinae, Peiratinae, Phymatinae, Stenopodainae, Salyavatinae, Tribelocephalinae and Visayanocorinae). Two additional subfamilies were recovered as monophyletic with strong support in ML but not in P (Ectrichodiinae: ML 93, Physoderinae: ML 100). Saicinae were monophyletic only under ML, and merely with weak support (ML 44). Harpactorinae (P 62) and Emesinae (P <50) were monophyletic in the P analysis, but paraphyletic in the ML analyses. Cetherinae are polyphyletic, separating the Old and New World genera Cethera Amyot & Serville and Eupheno Gistel, respectively. Reduviinae are polyphyletic (see below) with all lineages nested within the Higher Reduviidae clade. Triatominae relationships are discussed below. The monophyly of Centrocnemidinae and Vesciinae was not tested due to single taxon representation.

Reduviinae polyphyly

Reduviinae are grouped into 11 (ML, Fig. 1.1) or 14 (P, Fig. 1.2) clades, some of which also include other subfamily-level taxa. Strongly supported clades (see Table S1.1 for definitions of clades defined in this study) regardless of method used are the '*Velitra* clade' (P 94, ML 100) and the '*Zelurus* clade' (P 91, ML 96). We also recovered with strong support in ML but not in P, the

‘*Acanthaspis* clade’ (ML 97) and a more inclusive clade comprising Salyavatinae, the ‘*Acanthaspis* clade’, *Platymeris* Laporte, *Cethera*, and *Varus* Stål (P 59, ML 94). Some additional reduviine clades are recovered with weak support in ML, but are absent in the P analysis. These include the ‘*Psophis* clade’ (ML 59), the ‘*Reduvius* clade’ (ML 37), a clade comprising the *Velitra* clade and two additional reduviine genera, *Durganda* Amyot & Serville and *Tiarodes* Burmeister (ML 60), and the Old World Cetherinae *Cethera* grouping with *Varus* (P 59, ML 94). The monophyly of nine genera of Reduviinae was tested and recovered with strong to moderate support in both ML and P analyses (*Nanokerala* Wygodzinsky & Lent, *Psophis* Stål, *Microlestria*, *Gerbelius* Distant, *Leogorrus* Stål, *Opisthacidius*, *Pseudozelurus* Lent & Wygodzinsky, *Tiarodes*, *Velitra* Stål). *Pasiropsis* Reuter (P 93, ML 65) and *Zelurus* (P 70, ML 53) are weakly to strongly supported as monophyletic. *Nalata* (ML 100) and *Inara* Stål (ML 75) are strongly supported in ML but not in P. *Reduvius* Fabricius is paraphyletic with respect to *Durevius* Villiers. *Acanthaspis* Amyot & Serville is polyphyletic with several other reduviine genera nested within this genus (*Inara*, *Paraplynus* Schouteden, *Plynoides* Schouteden, *Paredocla* Jeannel); the monophyly of this more inclusive clade is strongly supported (see *Acanthaspis* clade above).

Triatominae relationships

Our analyses indicate a close relationship of Triatominae with the reduviine genera *Zelurus* and *Opisthacidius* (Figs. 1, 2). Rhodniini and Cavernicolini are strongly supported as sister taxa (P 98, ML 80) and Triatomini are monophyletic (P 98, ML 94). The subfamily Triatominae is paraphyletic with Triatomini being the sister-group to the *Opisthacidius* + (Rhodniini + Cavernicolini) clade in the ML analysis (Fig. 1.1). Parsimony analysis results in a polytomy of Triatomini, the Rhodniini + Cavernicolini clade and the *Opisthacidius* clade. *Triatoma* is polyphyletic in all our analyses, with *Paratriatoma* Barber, *Panstrongylus* Berg and *Eratyrus* Stål nested within this genus (Figs. 1, 2).

Ancestral state reconstructions of microhabitats and prey specializations

Our analysis shows multiple shifts between microhabitats at higher taxonomic levels, while closely related taxa, with a few exceptions, tend to share the same microhabitats (Fig. 1.3A). The evolutionary scenarios for the two most commonly encountered microhabitats – association with foliage versus tree bark – are quite different. Foliage was invaded at least six times independently by distantly related lineages (Fig. 1.3A; green arrowheads), including Emesinae, Harpactorinae, and Phymatinae. The bark-associated lifestyle in contrast is unambiguously optimized as the ancestral condition for most of the Higher Reduviidae (Higher Reduviidae except Peiratinae and the Emesine Complex; Fig. 1.3A; brown arrowhead) under both parsimony and maximum likelihood (99.21% - 99.9% bark-associated) methods. Many clades within the Higher Reduviidae, especially among the Reduviinae lineages, retain this ancestral association. The maximum likelihood mapping projected bark-association as the most probable state (86.24%) for the ancestral nodes of the Higher Reduviidae including the Emesine Complex but excluding the Peiratinae while parsimony depicted this node as ambiguous between bark-association, living on foliage and ground-dwelling. A similar ambiguity is seen under parsimony for the ancestral state of Higher Reduviidae, while maximum likelihood predicted almost equal probabilities between bark-association (46.98%) and ground-dwelling (44.10%). The ancestral microhabitat for all Reduviidae (Fig. 1.3A; red asterisk) is ambiguous in the parsimony analysis, with possible microhabitats comprising the ground, tree bark or foliage of herbaceous vegetation or trees. The maximum likelihood method however placed bark-association as the most probable (96.39%) ancestral state for Reduviidae. The bark-associated lifestyle in some of the basal Reduviidae, the

Hammacerinae, Centrocnemidinae, and some Holoptilinae, may thus either be homologous to the one in Higher Reduviidae, or may represent a separate colonization event from foliage or the ground, depending on the method used. Ground-dwelling habits (Fig. 1.3A; gray lineages) have evolved multiple times across Reduviidae and are frequently not inhabited exclusively, with taxa also recorded as inhabiting other microhabitats such as tree bark and foliage.

Mammal nests are here recovered as the ancestral microhabitats for blood-feeding Triatominae including the predatory reduviine species of *Opisthacidius* for both methods (96.52% ML). The three bat-feeding Triatominae, *Cavernicola pilosa* Barber, *Triatoma dimidiata* (Latreille) and *Eratyrus mucronatus* Stål, have colonized bat dwellings independently (data not shown, Fig. 1.3A). For the Emesine Complex, spider webs are reconstructed as the more likely ancestral habitat under maximum likelihood (59.42%) compared to foliage (17.68%), palm fronds (9.18%), ground (5.79%) and leaf litter (5.79%), whereas parsimony considered the node as ambiguous among these microhabitats (Fig. 1.3A).

The reconstruction of prey preferences shows that the generalist predatory feeding strategy is ancestral for Reduviidae (84.93% ML; Fig. 1.3B; red asterisk) and that all prey specialists evolved from generalist ancestors (Fig. 1.3B; various cases across phylogeny). Ant specialization (Fig. 1.3B; black arrowheads) occurred twice independently among the included taxa Holoptilinae (75.97% ML), *Acanthaspis* clade (77.30% ML), while termite specialization evolved probably at least three times (Fig. 1.3B; cyan arrowheads) across Reduviidae (well documented in Salyavatinae and *Micrauchenus* Amyot & Serville, less well established in Cetherinae and Leogorrus). Millipede feeding is here shown to have evolved only once and can be traced to the base of the Ectrichodiinae unambiguously, or predicted to have occurred earlier at the Ectrichodiinae + Tribelocephalinae clade (97.13% ML) or even further to include the *Pasiropsis* sister-clade (91.55% ML). Prey preferences for the ectrichodiine sister-group Tribelocephalinae and *Pasiropsis* Reuter are unknown and it remains to be shown if the unique millipede association is shared with Tribelocephalinae and *Pasiropsis*. The reconstruction of spider specialization within Emesinae is ambiguous and either supports two independent origins or a single specialization event at the most recent common ancestor (46.51% ML). The transition from predatory to hematophagous life-style is ambiguous under parsimony, lending equal support to two scenarios on the evolution of blood feeding: 1) the switch to hematophagy may have occurred once at the base of the Triatominae + *Opisthacidius* clade (Fig. 1.3B; larger red arrowhead), with a reversion to generalist feeding behavior in *Opisthacidius*, or 2) Triatomini and Rhodniini + Cavernicolini may have acquired hematophagy independently (Fig. 1.3B; smaller red arrowhead). The maximum likelihood method overwhelmingly supports (99.62%) the first scenario of a single transition to hematophagy at the ancestral node of the Triatominae + *Opisthacidius* clade. The documentation of *Opisthacidius rubropictus* (Herrich-Schaeffer) in bird nests [61], presumably as an arthropod predator, also suggests two possible scenarios for the correlation between habitat switch and the transition from predatory to hematophagous habits: the colonization of vertebrate nests either preceded the evolution of hematophagy or it coincided with the transition to blood-feeding.

Molecular dating

The BEAST analysis produced a phylogeny that is highly congruent with the ML analysis (Fig. 1.4), but somewhat less similar to the topology of the P analysis. The monophyly of all strongly-supported major clades and subfamilies is recovered as well as the paraphyly of Triatominae and the polyphyly of Cetherinae. The origin of Reduviidae is dated to 178Ma [176 – 185Ma] and thus falls within the Middle Jurassic (Fig. 1.4, Table S1.6). The divergence between the Phymatine

Complex and the Higher Reduviidae occurred shortly thereafter, at around 160Ma (137 – 180Ma) during the Late Jurassic. The diversification of the Higher Reduviidae began only in the Late Cretaceous starting at 97Ma [81 – 113Ma] and continued through the Miocene. The origins of all subfamily-level clades within the Phymatine Complex (Hammacerinae, Phymatinae, Centrocnemidinae, Holoptilinae) are comparatively older than all subfamily-level clades in the Higher Reduviidae with the exception of the Peiratinae. The oldest Phymatine Complex subfamily is Hammacerinae at 142Ma (119 – 168Ma) and the youngest is Holoptilinae and Centrocnemidinae at 90Ma (67 – 115Ma). Comparatively, the oldest Higher Reduviidae subfamily is Peiratinae at 97Ma (81 – 113Ma) and the youngest is Triatominae at 32Ma (24 – 38Ma). Chronogram with terminal taxon names and all 95% highest posterior density (HPD) node bars annotated is provided as Figure S1 and age estimates of selected clades are summarized in Table S1.5.

Discussion

Triatominae and the origin of blood-feeding in Reduviidae

With the extensive taxon sampling of Triatominae and related predatory Reduviidae, and the large and relatively complete set of sequence data, we here present the most rigorous test of triatomine monophyly or polyphyly published to date. As opposed to previous analyses (Weirauch, 2008; Weirauch & Munro, 2009; Patterson & Gaunt, 2010), we did not recover a monophyletic Triatominae in any of our analyses, nor did we find support for Triatominae being polyphyletic (Schofield & Galvao, 2009; Schofield, 1994). Instead, Triatominae are paraphyletic with respect to the genus *Opisthacidius* based on the ML analysis (Fig. 1.1) or part of a polytomy that also includes *Opisthacidius* in the P analysis (Fig. 1.2). Short branch lengths between *Opisthacidius*, the Rhodniini + Cavernicolini clade, and the Triatomini indicate that additional data is required to further test relationships among these three well-supported clades. Our results show that Triatominae are nested within the *Zelurus* clade that is restricted to the New World, supporting the hypothesis of a Neotropical origin of Triatominae (Lent & Wygodzinsky, 1979; Hypsa et al., 2002). The existence of Old World triatomines, namely the South Asian *Linshcosteus* Distant and the South-east Asian *rubrofasciata* species complex of *Triatoma* Laporte has intrigued workers for the past two decades (Lent & Wygodzinsky, 1979; Hypsa et al., 2002; Schofield, 2000). This disjunct distribution was even interpreted as support for the hypothesis of a polyphyletic Triatominae (Schofield, 2000). Although not included in our analyses, *Linshcosteus* and *T. rubrofasciata* have been placed within Triatomini (Hypsa et al., 2002) and our dating estimate for Triatomini (~32Ma) suggests that the Old World Triatomini represent a relatively recent dispersal rather than an older vicariant event.

Our divergence time estimates (Fig. 1.4) for Triatomini (32Ma) and for Rhodniini + Cavernicolini (27.5Ma) are much younger than the 107Ma age that Patterson and Gaunt (2010) postulated for Triatominae using a fixed molecular clock model. A strict clock analysis is shown to be accurate only for shallow phylogenies (Miocene and later) but not for cases where rate variation is higher (Brown & Yang; 2011). Our use of a relaxed clock model for dating cladogenetic events among Triatominae is therefore a significant improvement, given that constant rate variation is implausible for deep divergences Kishino et al., 2001). Based on our estimates, Triatominae evolved in the Oligocene when South America was already isolated from Antarctica and migrating towards North America (Veevers, 2004; Verard et al., 2012). Our analysis therefore does not show a link between the evolution of triatomine hematophagy and the break-up of Gondwanaland as hypothesized by Patterson and Gaunt. Instead, we propose that the emergence of hematophagous triatomines in the Oligocene coincided with two other large-scale events: a period of well-documented species radiations among Neotropical mammals and birds (Delsuc et al., 2004; Bininda-Emonds et al., 2007; Ericson et al., 2006) and a period of extensive diversification of ecotypes in South America then and thereafter (Graham, 2011; Antonelli et al., 2009; Werneck, 2011).

The lack of well-defined host specificity between genera and species groups of Triatominae with their respective vertebrate hosts has long puzzled scientists (Lent & Wygodzinsky, 1979; Patterson et al., 2009). Vertebrate host associations are generally much more specific in other blood-feeding insects such as Phthiraptera (lice) (Light & Hafner, 2007), and Cimicidae (bedbugs) (Usinger, 1967), which suggests a co-evolutionary history between the host and parasite. This is not the case for many Triatominae such as certain species of *Panstrongylus* and *Triatoma* that appear to feed indiscriminately on opossums, bats and other mammals (Lent & Wygodzinsky, 1979). Besides ecological factors that may determine host specificity, the relatively younger age of Triatominae (27-32Ma) compared to lice 115-130Ma (Smith et al., 2011) and bedbugs 100Ma (Jung & Lee, 2012) may contribute to this lesser degree of host-parasite specificity observed in kissing bugs. Claims of any correlation between host and habitat diversification and co-speciation within Triatominae will also require denser taxon sampling and host-parasite co-evolutionary analyses.

The colonization of vertebrate nests occurred only once according to our analysis (Fig. 1.3A) and may be interpreted as a precursor for the evolution of hematophagy, although our optimization also allows for the possibility that nest invasion and switch to blood-feeding co-occurred (Fig. 1.3A, B; red arrowheads). The single nest colonization event may indicate that the transition from a free-living predatory to nest-inhabiting hematophagous lifestyle is less easily achieved in evolutionary terms than indicated by Schofield (1994), who proposed multiple of such switches to have given rise to a polyphyletic Triatominae.

Early diversification patterns of Reduviidae

Our divergence time estimates (Fig. 1.4) provide the first glimpses into the timing of evolutionary events in the second largest family of True Bugs, the Reduviidae, and is one of less than a handful of dating analyses for Heteroptera (Patterson & Gaunt, 2010; Li et al., 2012; Jung & Lee, 2012). These estimates allow us to formulate explicit hypotheses on the timing of specific cladogenetic events that can be further investigated. One of these hypotheses is the early and continuous divergence of subfamily-level clades within the Phymatine Complex (Early Cretaceous) as opposed to the apparently delayed diversification (Late Cretaceous) within the Higher Reduviidae, a clade comprising ~90% of the extant species diversity. The Late Cretaceous start of the Higher Reduviidae diversification coincides with two global changes affecting all terrestrial ecosystems, the radiations of angiosperms and phytophagous insects (Wiegmann et al., 2011; Davis et al, 2005; Bell et al., 2005; Moreau et al., 2006; Hunt et al., 2007). Both of these events have likely impacted the evolution of Reduviidae, by supplying increased microhabitat heterogeneity as well as new food sources for these predatory insects. The initial diversification of Higher Reduviidae occurred over a relatively short period of about 31 million years (65-96Ma), which partially accounts for the lack of strong support for subfamily and higher-level clade relationships within Higher Reduviidae.

Microhabitat colonizations

The ability of reduviids to colonize a wide range of microhabitats (Fig. 1.3A) might be one of the factors that have influenced their high species diversity, driven by ecological adaptations. Of the six independent transitions to foliage-dwelling, three clades are noteworthy for their high species numbers: Phymatinae (291 spp. [Froeschner & Kormilev, 1989]), *Zelurus* (132 spp. [Maldonado, 1990]), and Harpactorini (~2,000 spp. [Maldonado, 1990]). High species diversity is however not linked to this particular microhabitat, since Ectrichodiinae (>600 spp.; ground-dwelling/leaf-litter) and Stenopodainae (~732 spp.; ground-dwelling/leaf-litter/on foliage) are both found in various microhabitats and are among the most speciose reduviid subfamilies (Fig. 1.3A). Conversely, some of the clades that have retained the ancestral bark-associated lifestyle among Higher Reduviinae are also speciose, best exemplified by the large *Acanthaspis* and *Velitra* clades. We suspect that factors other than microhabitat association may have driven the diversification of Reduviidae, among them prey specialization and changes in prey capture techniques.

Even though our analyses tend towards bark-association as the ancestral microhabitat of all Reduviidae (Fig. 1.3A, ML 96.39% bark-association, P ambiguous between bark-association, foliage-dwelling, ground-dwelling), this is not conclusive at the moment. The inclusion of members of the rarely collected ground-dwelling (pers. obs.) reduviid sister-group Pachynomidae (Carayon, 1950; Schuh & Slater, 1995; Davis, 1966) that were unavailable for this study will further test, and refine, this hypothesis.

Prey preferences

The hypothesis that specialized taxa are more susceptible to mass extinction events (Labandeira et al., 2002) and therefore more likely to be restricted to the tips of a phylogeny (Kelley & Farrell, 1998) is not entirely corroborated by our analysis of Reduviidae (Fig. 1.3B). Some specialized clades are relatively old (ant specialist Holoptilinae [90Ma], millipede specialist Ectrichodiinae [67.5Ma], spider specialist Emesinae [75Ma]), but others are clearly more recently evolved specializations (blood-feeding Triatominae [32Ma and 27.5Ma], termite specialist Salyavatinae [42Ma] and *Micrauchenus* [20Ma], and the ant specialist *Acanthaspis* clade [25Ma]) (Fig. 1.4). This indicates that specialized predators may not necessarily suffer a higher extinction risk due to a more restricted diet. Likewise, the hypothesis that prey specialization constrained food availability and therefore impacts the ability of specialists to diversify (e.g., [Futuyma & Moreno, 1988]) is not corroborated by Reduviidae (Fig. 1.3B, [Maldonado, 1990]). We do however observe a general trend of specialists to evolve from generalist ancestors rather than the reverse as documented for some insects (Scheffer & Wiegmann, 2000).

Even though reduviids are currently mostly regarded as generalist predators, this observation might mostly be due to the limited number and nature of published observations documenting specialization (Table S1.2). We therefore expect that additional cases of prey specializations will be discovered as more detailed field observations and experiments become available.

Reduviinae polyphyly

Our extensive sampling of Reduviinae generates a phylogeny-informed framework for the eventual re-classification of this polyphyletic assemblage, a somewhat daunting task given the size of the group and the number of included genera. In 1904, Distant proposed a first classification of the group, referred to by him as Acanthaspidinae, and grouped 23 genera into 6 divisions (Distant, 1904) (Table S1.7), unfortunately without identifying diagnostic characters for these divisions. Unsurprisingly, Distant's classification was not adopted by later workers and subsequently described reduviine taxa were not grouped accordingly. We here recognize the reduviine clades derived from our ML phylogenetic analysis (Fig. 1.1, clade membership listed in Table S1.1) and tentatively propose the inclusion of 45 additional genera that were not included in the current analysis based on similar general morphology (Table S1.8), with the remaining 64 unexamined reduviine genera listed as uncertain placement. The membership of these additional 45 taxa remains to be tested by future cladistic analyses that also should include morphological data to eventually generate meaningful diagnoses.

Interestingly, three among the proposed reduviine clades (*Acanthaspis* clade, *Reduvius* clade, *Velitra* clade) together represents 48% (525 spp.) of the entire reduviine diversity (Maldonado, 1990). *Reduvius* and *Acanthaspis* are the most (197 spp.) and second most (110 spp.) speciose genera of Reduviinae, respectively (Maldonado, 1990), but neither one of them is monophyletic. Non-monophyly at the genus-level will complicate a future re-classification, since multiple species will have to be phylogenetically evaluated before a placement for the genus in question (or parts thereof) can be proposed. On a positive note, we believe that the Reduviinae polyphyly problem is now rather well defined, allowing for independent phylogenetic and taxonomic revisions of several smaller, more manageable clades.

Conclusion

Employing molecular, fossil, microhabitat and prey specialization data, we present the first comprehensive hypothesis on the evolutionary history of Reduviidae. The inclusion of multiple Reduviinae taxa has significantly improved our notion of the overall Reduviidae phylogeny. Fossil-calibrated divergence time estimates indicate that the diversification pattern is different between the Phymatine Complex and the Higher Reduviidae, while more focal research on the early diversification of Higher Reduviidae is required to determine the deeper node relationships. We show that bark-associated living is an ancestral condition for most of Higher Reduviidae including all Reduviinae while living on foliage has evolved independently at least six times across Reduviidae. Prey specializations occur in old as well as more recent clades and have coincided with significant diversification in some cases such as the millipede-feeding Ectrichodiinae. More field observations across the family will enhance our understanding of both microhabitat and prey selection and provide a more accurate picture of their evolutionary pattern. Finally, we show a close relationship between the Neotropical reduviine genus *Opisthacidius* and the presumably paraphyletic hematophagous Triatominae and propose that the clade including these taxa has diverged relatively recently (~32Ma).

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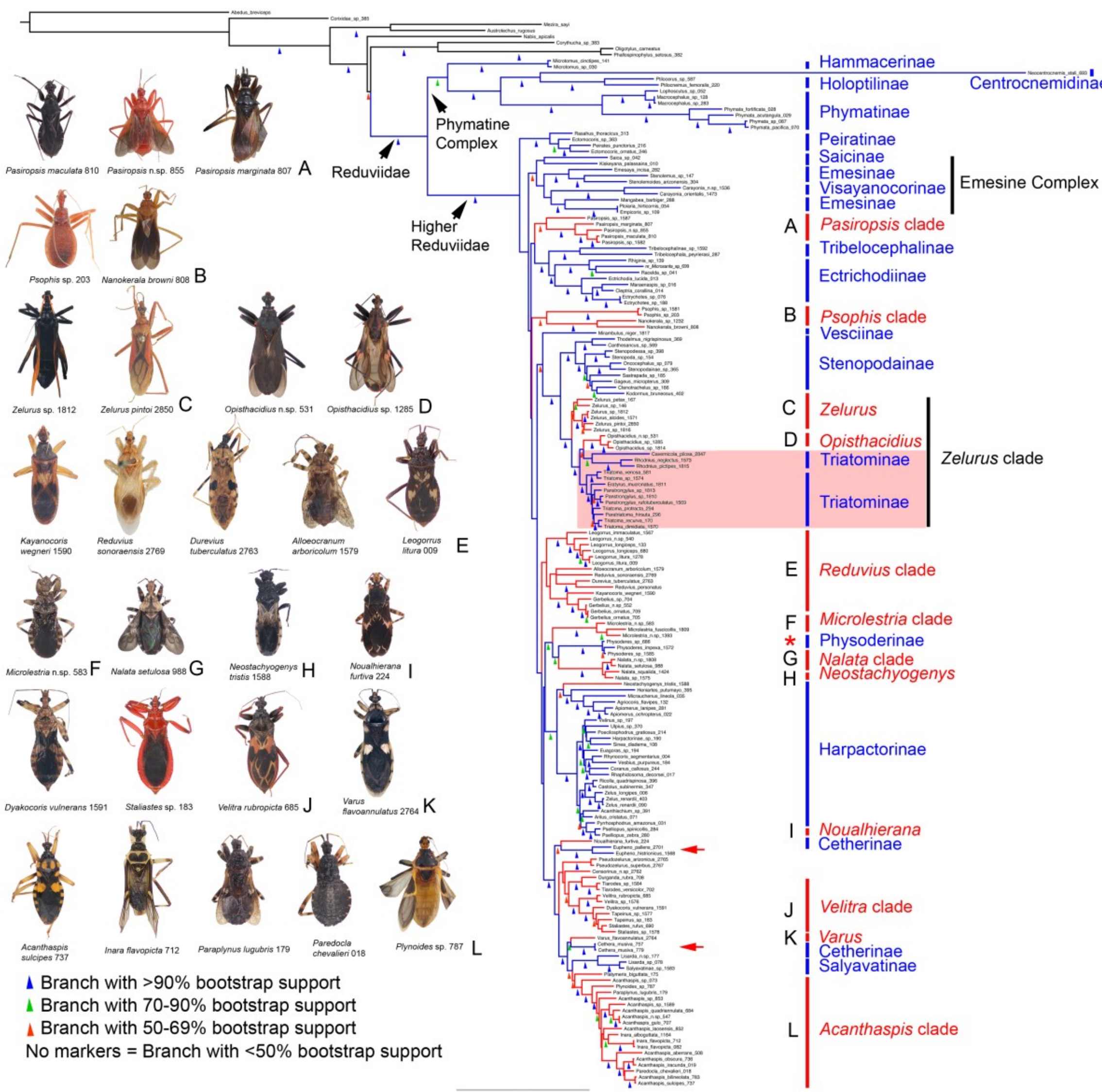
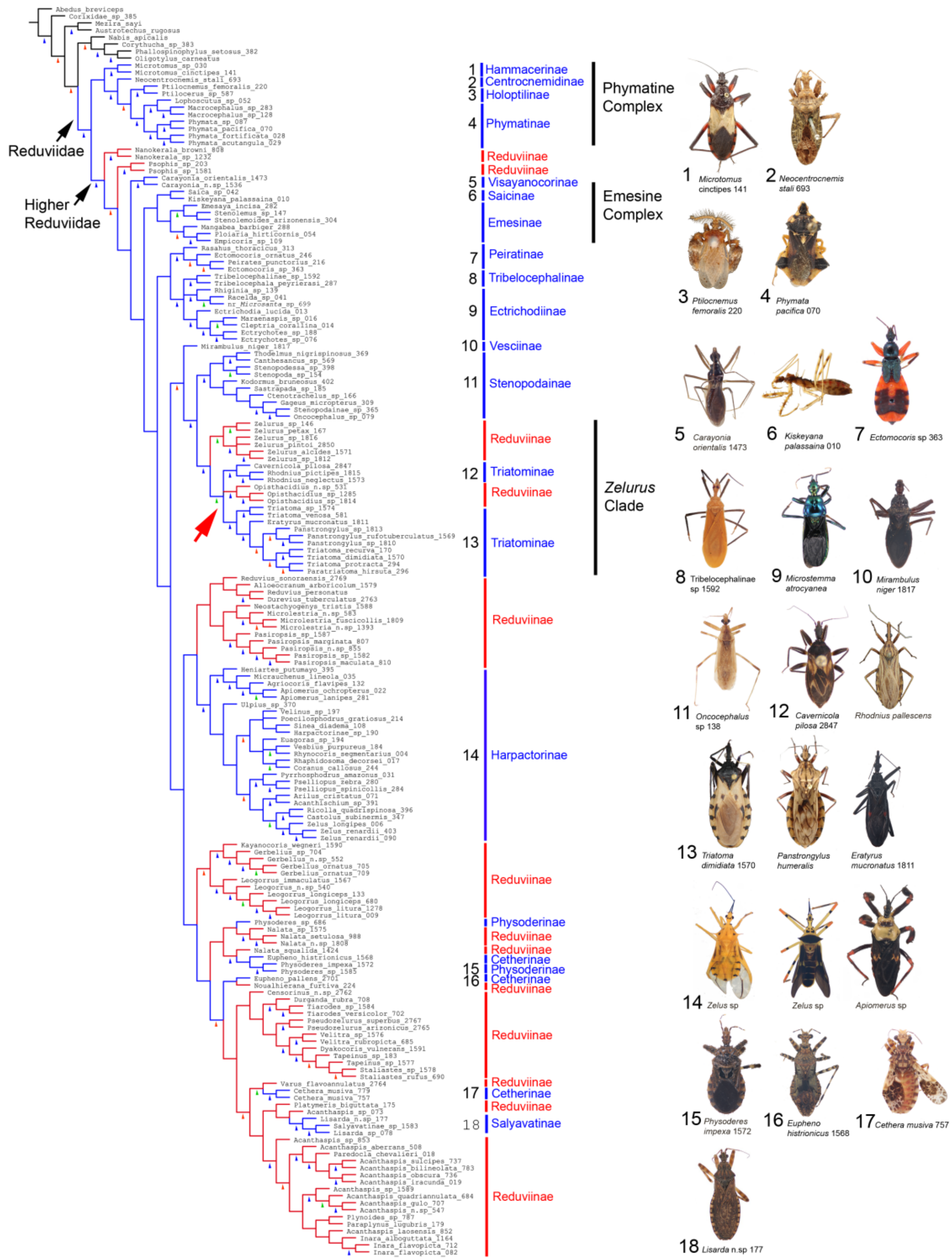


Figure 1.1. Maximum Likelihood phylogram with representative habitus images of reduviine clades. Best tree (score = -83447.290932) based on RAxML analysis of 178 taxa using a partitioned molecular dataset of 5 gene regions (16S, 18S, 28S D2, 28S D3-D5, Wg) aligned with MAFFT G-INS-i. Bootstrap values are indicated on branches by colored triangles according to support strength (explained by inset). Reduviinae lineages are indicated as red branches and remaining reduviids as blue while outgroup taxa are black. Habitus images of Reduviinae species with RCW specimen ID numbers are grouped (A-L) according to the 11 separate reduviine clades. The shaded red box highlights members of the hematophagous Triatominae, here shown

as paraphyletic. Red arrowheads refer to the polyphyletic Cetherinae; the asterisk refers to Physoderinae nested within a reduviine clade.



▲ Branch with >90% bootstrap support
▲ Branch with 70-90% bootstrap support
▲ Branch with 50-69% bootstrap support
No markers = Branch with <50% bootstrap support

Figure 1.2. Strict consensus of 16 equally parsimonious trees with representative habitus images of reduviid subfamilies. Shortest trees (tree length = 23413, C.I.= 0.21, R.I.=0.57) generated by TNT using the same molecular dataset (178 taxa, G-INS-i aligned, 5 gene regions) with bootstrap values indicated by colored triangles on branches (explained by inset). Reduviinae lineages are indicated as red branches and other subfamilies as blue while outgroup taxa are black. Habitus images of reduviids with RCW specimen ID numbers are labeled 1-18 according to subfamily membership indicated beside the phylogeny. Reduviinae are separated into 14 clades here and Triatominae + *Opisthacidius* form an unresolved polytomy (red arrowhead).

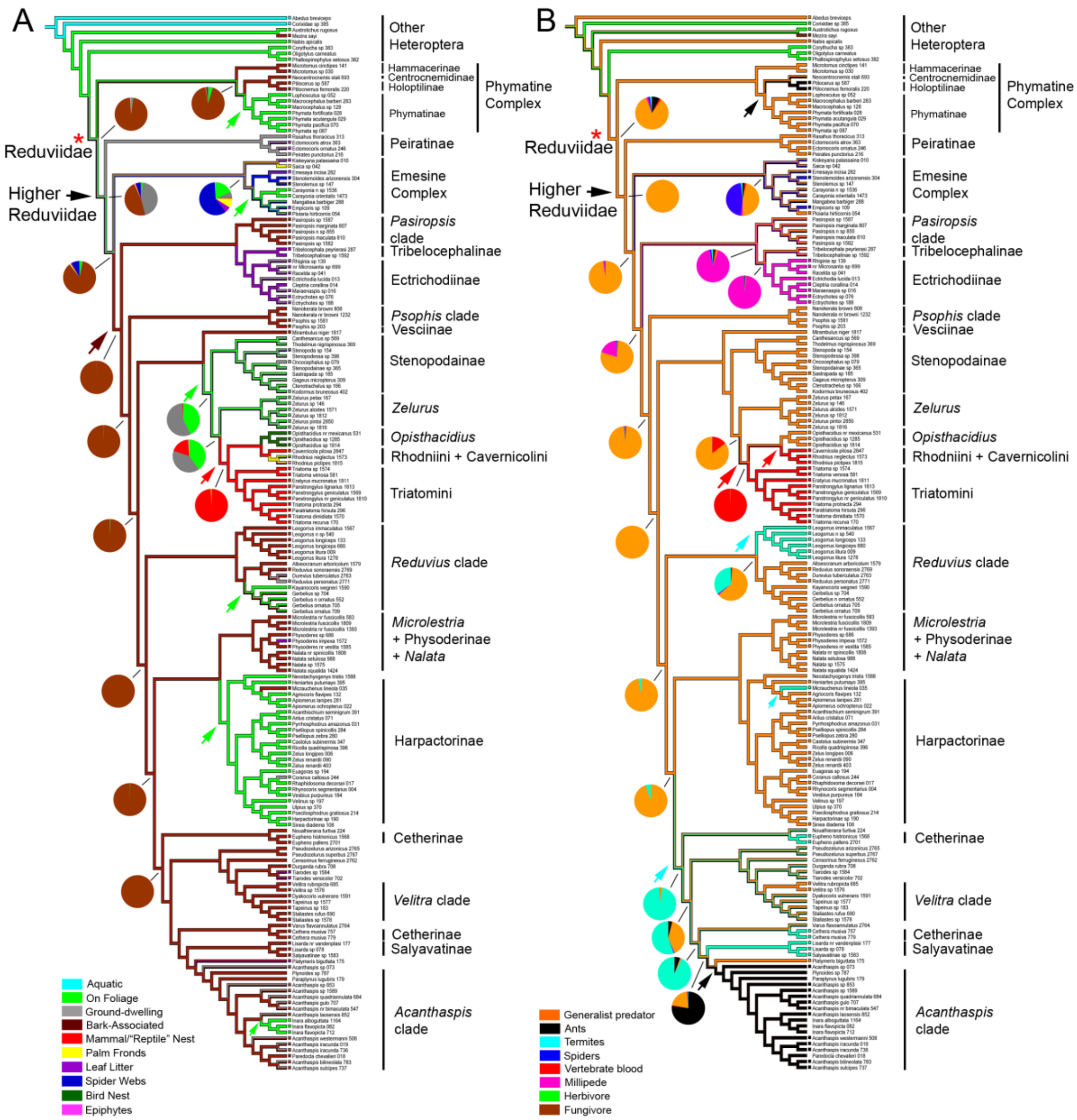


Figure 1.3. Ancestral state reconstructions based on best maximum likelihood tree. A. Microhabitats. Microhabitats of terminal taxa mapped onto ML best tree using Mesquite parsimony (P) model and maximum likelihood (ML) model in BayesTraits. Branches are color coded to represent different microhabitats (see color legends) based on parsimony and similarly-colored pie-charts represent probabilities generated from BayesTraits. Terminals without colored squares indicate unknown microhabitats and are coded as missing information in the matrix. Bark-associated lifestyle (brown arrowhead) is ancestral for all Higher Reduviidae except Peiratinae and Emesinae under both P and ML. Foliage-living (green arrowheads) has evolved at

least six times independently within Reduviidae. Ancestral condition for all reduviids (red asterisk) remains ambiguous (bark associated/ground-dwelling/foliage-living) under P but ML favors bark-association (96.39%). Ancestral condition for Triatominae + *Opisthacidius* is mammal/"reptile" nest dwelling (red arrowhead). **B. Prey Specialization.** Prey specialization of terminal taxa mapped onto ML best tree using Mesquite parsimony (P) model and maximum likelihood (ML) model in BayesTraits. Branches and pie-charts (from ML) are color coded to represent different targeted prey (see color legends). Terminals without colored squares indicate unknown diets and are coded as missing information in the matrix. Ancestral condition for all reduviids is generalist predator (red asterisk). Hematophagy (red arrowheads) may have evolved once or twice independently under P while ML favors a single evolution (99.62%). Termite-specialization (cyan arrowheads) occurred at least three times independently while ant-specialization (black slanted arrowheads) evolved at least twice (Holoptilinae, *Acanthaspis* clade).

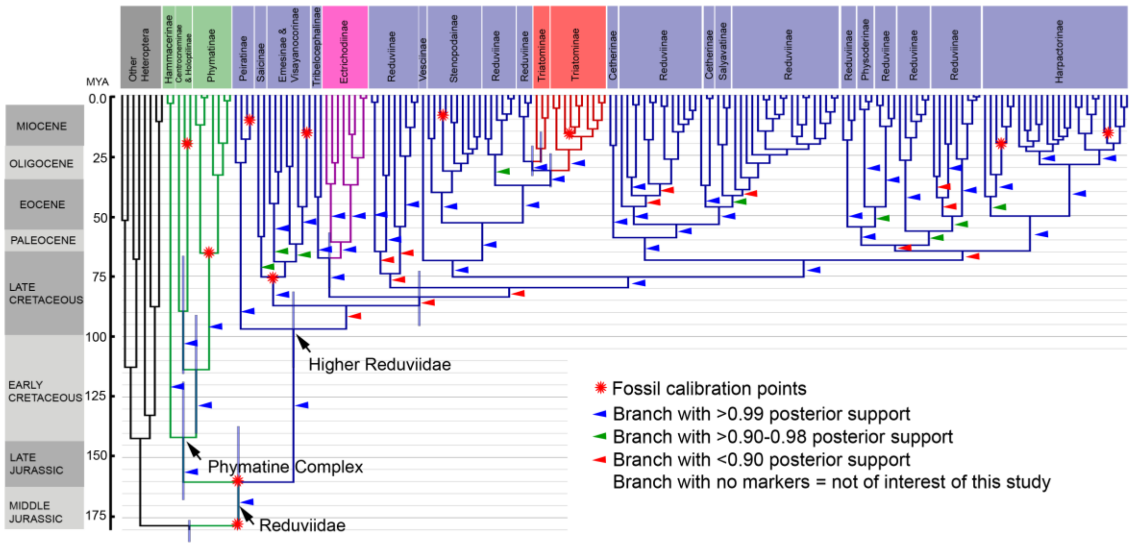


Figure 1.4. Divergence time estimates based on BEAST analysis using relaxed-clock model and 11 fossil calibration points. Chronogram based on same G-INS-i aligned molecular dataset (178 taxa; 5 gene regions: 16S, 18S, 28S D2, 28S D3-D5, Wg), using unlinked substitution models (GTR+ Γ+I), relaxed clock uncorrelated lognormal and 11 fossils as priors. Lineages are colored on the chronogram as follows: Outgroup taxa (black), Phymatine Complex (green), Ectrichodiinae (pink), Triatominae (red), all other reduviid subfamilies (blue). Posterior probabilities are indicated on branches by colored triangles (see inset). Shaded node bars indicate 95% highest posterior density (HPD) credibility intervals for clades of interest only. Placement of fossils as calibration points of clades indicated by red stars.

Supporting Information

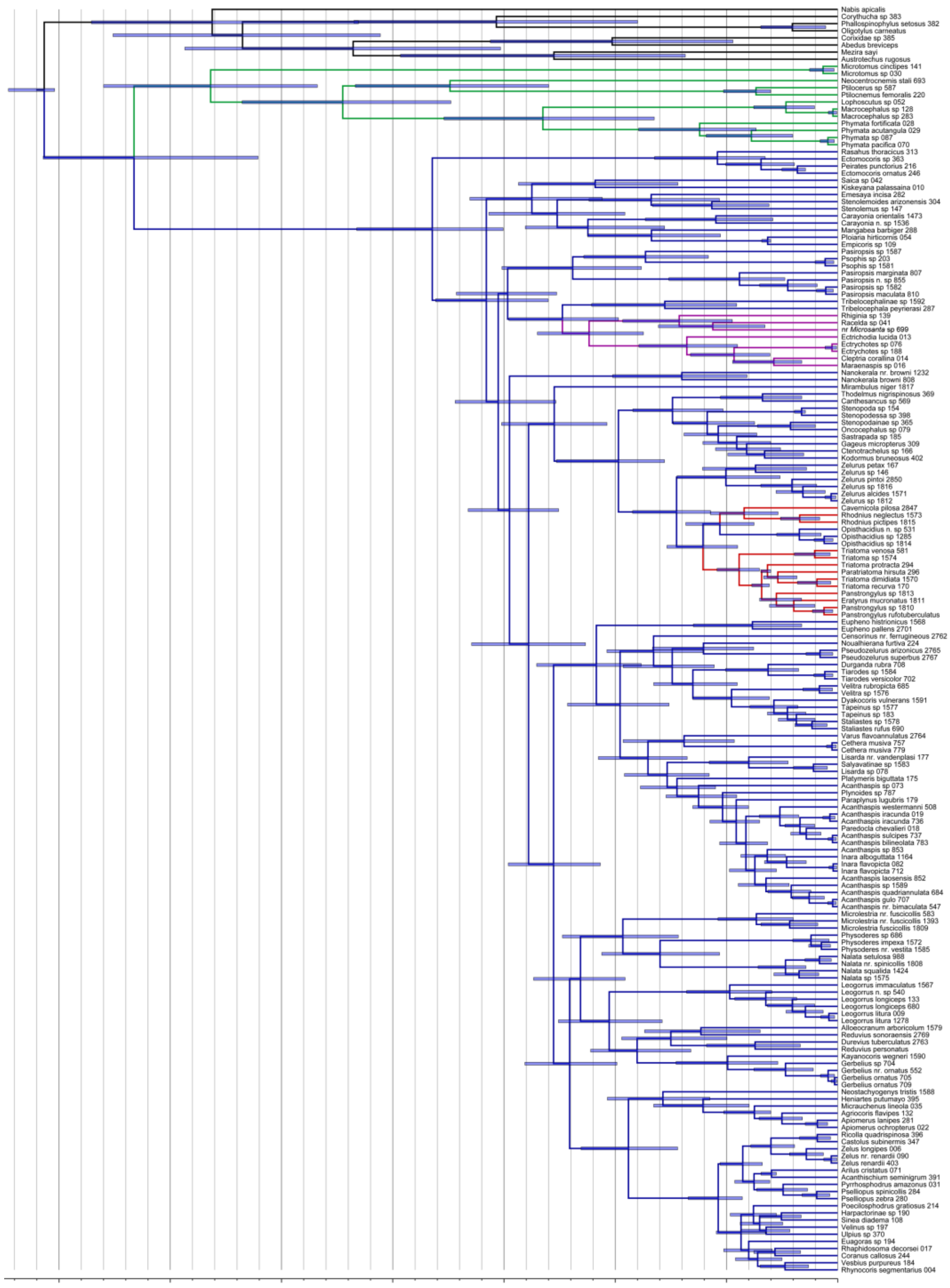


Figure S1.1. Chronogram with terminal taxon names and 95% HPD node bars.

Table S1.1 List of species used for phylogenetic reconstructions with the GenBank accession numbers for each gene region provided and the clade they are assigned to according to Figure 1.1. Abbreviations for the clades are as follows: A=*Acanthaspis*, M=*Microlestria*, N=*Nalata*, Ps=*Psophis*, Pa=*Pasiropsis*, R=*Reduvius*, T=*Tiarodes*, V=*Velitra*, Z=*Zelurus* . Taxon names with * denotes DNA extracted from museum dried specimens.

						GenBank Accession numbers					
Family	**Subfamily**	**Species**	**RC W no.**	**USI**	**Voucher Depository**	**16S**	**18S**	**28S D2**	**28S D3-D5**	**Wg**	**Clade**
Belostomatidae	Belostomatinae	*Abedus breviceps* Stal	N/A	N/A	N/A	AY252676	AY252186		AY252440		
Corixidae		Corixidae sp	385	UCR_ENT 00000183	UCR	FJ230383	FJ230456	FJ230537	FJ230615, FJ230694	JQ897872	
Scutellaridae		*Austrotichus rugosus* Gross	N/A	N/A	N/A	AY252745	AY252171		AY252517		
Aradidae	Mezirinae	*Mezira sayi* Kormilev	N/A	N/A	N/A	EU683100	AY252222		EF641177		
Nabidae	Nabinae	*Nabis apicalis* Matsumura	N/A	N/A	N/A	EF487292	EF487316		EF487339		
Tingidae		*Corythuca* sp	383	UCR_ENT 00000083	UCR	JQ897789	FJ230455	FJ230536	FJ230614, FJ230693		
Miridae	Phylinae	*Oligotylus carneatus* (Knight)	N/A	N/A	N/A	AY252853	AY252377		AY252596		
Miridae	Phylinae	*Phallospinophylus setosus* Weirauch	382	UCR_ENT 00000082	UCR	FJ230382	FJ230454	FJ230535	FJ230613, FJ230692		
Reduviidae	Centrocnemidinae	*Neocentrocnemis stali* (Reuter)	693	UCR_ENT 00001976	UCR		JQ897578	GU188466	GU188447		
Reduviidae	Cetherinae	*Cethera musiva* (Germar)	757	UCR_ENT 00052215	UCR	JQ897787		JQ897629	JQ897706		
Reduviidae	Cetherinae	*Cethera musiva* (Germar)	779	UCR_ENT 00052176	UCR	JQ897788	JQ897552	JQ897630	JQ897707		
Reduviidae	Cetherinae	*Eupheno histrionicus* (Stal)	1568	UCR_ENT 00014326	INBIO	JQ897795	JQ897556	JQ897636	JQ897712	JQ897883	
Reduviidae	Cetherinae	*Eupheno pallens* (Laporte)	2701	UCR_ENT 00052214	UCR	JQ897796	JQ897557	JQ897637	JQ897713		
Reduviidae	Ectrichodiinae	*Cleptria corallina* Villiers	14	AMNH_PBI 00218770	UCR	FJ230388	FJ230462	FJ230543	FJ230621, FJ230700	JQ897871	
Reduviidae	Ectrichodiinae	*Ectrichodia lucida* Lepelletier and Serville	13	AMNH_PBI 00218769	UCR	FJ230387	FJ230461	FJ230542	FJ230620, FJ230699	JQ897878	

Table S1.1 (cont'd).

Family	Subfamily	Species	RCW no.	USI	Voucher Depository	16S	18S	28S D2	28S D3-D5	Wg	Clade
Reduviidae	Ectrichodiinae	nr *Microsanta* sp	699	UCR_ENT 00052213	UCR	JQ897793		JQ897634	JQ897710	JQ897880	
Reduviidae	Ectrichodiinae	*Ectrychotes* sp	76	AMNH_PBI 00218830	UCR		FJ230479	FJ230560	FJ230638, FJ230717		
Reduviidae	Ectrichodiinae	*Ectrychotes* sp	188	AMNH_PBI 00218932	UCR	FJ230424	FJ230503	FJ230584	FJ230661, FJ230740	JQ897879	
Reduviidae	Ectrichodiinae	*Maraenaspis* sp	16	AMNH_PBI 00218772	UCR	FJ230389	FJ230463	FJ230544		JQ897889	
Reduviidae	Ectrichodiinae	*Racelda* sp	41	AMNH_PBI 00218801	UCR	FJ230398	FJ230472	FJ230553	FJ230631, FJ230710	JQ897915	
Reduviidae	Ectrichodiinae	*Rhiginia* sp	139	AMNH_PBI 00218891	UCR	FJ230410	FJ230490	FJ230571	FJ230648, FJ230727	JQ897917	
Reduviidae	Emesinae	*Emesaya incisa* McAtee and Malloch	282	AMNH_PBI 00219017	UCR	FJ230436	FJ230515	FJ230598	FJ230672, FJ230751	JQ897881	
Reduviidae	Emesinae	*Empicoris* sp	109	AMNH_PBI 00218862	UCR		FJ230486	FJ230567			
Reduviidae	Emesinae	*Mangabea barbiger* Weirauch	288	UCR_ENT 00005201	CAS	FJ230441		FJ230602	FJ230674, FJ230753	JQ897888	
Reduviidae	Emesinae	*Ploiaria hirticornis* (N. Banks)	54	AMNH_PBI 00218808	UCR		FJ230475	FJ230556	FJ230634, FJ230713		
Reduviidae	Emesinae	*Stenolemoides arizonensis* (N. Banks)	304	AMNH_PBI 00218753	UCR	FJ230444	FJ230522	FJ230605	FJ230677, FJ230756	JQ897923	
Reduviidae	Emesinae	*Stenolemus* sp	147	AMNH_PBI 00218899	UCR	FJ230413		FJ230573			
Reduviidae	Holoptilinae	*Ptilocerus* sp	587	UCR_ENT 00001974	UCR	GU188453	JQ897599	GU188467	GU188448		
Reduviidae	Holoptilinae	*Ptilocnemus femoralis* Horvath	220	AMNH_PBI 00218963	AMNH	FJ230431	FJ230509	FJ230591	FJ230667, FJ230746		
Reduviidae	Hammacerinae	*Microtomus cinctipes* (Stal)	141	AMNH_PBI 00218893	UCR	FJ230411	FJ230491		FJ230649, FJ230728		

Table S1.1 (cont'd).

Family	Subfamily	Species	RCW no.	USI	Voucher Depository	16S	18S	28S D2	28S D3-D5	Wg	Clade
Reduviidae	Hammacerinae	*Microtomus* sp	30	AMNH_PBI 00218785	UCR	FJ230395	FJ230469		FJ230628, FJ230707		
Reduviidae	Harpactorinae	*Acanthiscium seminigrum* Stal	391	UCR_ENT 00000074	FCAP	FJ230450	FJ230530	FJ230607	FJ230685, FJ230764		
Reduviidae	Harpactorinae	*Agriocoris flavipes* (Fabricius)	132	AMNH_PBI 00218884	UCR		FJ230488	FJ230569	FJ230646, FJ230725		
Reduviidae	Harpactorinae	*Apiomerus lanipes* (Fabricius)	281	AMNH_PBI 00219016	UCR	FJ230435	FJ230514	FJ230597	FJ230671, FJ230750	JQ897868	
Reduviidae	Harpactorinae	*Apiomerus ochropterus* Stal	22	AMNH_PBI 00218777	UCR	FJ230393	FJ230466	FJ230548	FJ230625, FJ230704	JQ897869	
Reduviidae	Harpactorinae	*Arilus cristatus* (Linne)	71	AMNH_PBI 00218826		FJ230402	FJ230477	FJ230558	FJ230636, FJ230715		
Reduviidae	Harpactorinae	*Castolus subinermis* (Stal)	347	UCR_ENT 00000089	UCR	FJ230446	FJ230526		FJ230681, FJ230760		
Reduviidae	Harpactorinae	*Coranus callosus* Stal	244	AMNH_PBI 00218984	UCR	FJ230433	FJ230511	FJ230594	FJ230669, FJ230748		
Reduviidae	Harpactorinae	*Euagoras* sp	194	AMNH_PBI 0021928	UCR	FJ230427	FJ230505	FJ230587	FJ230663, FJ230742		
Reduviidae	Harpactorinae	Harpactorinae sp	190	AMNH_PBI 00218934	UCR	FJ230425	FJ230504	FJ230585	FJ230662, FJ230741		
Reduviidae	Harpactorinae	*Heniartes putumayo* Wygodzinsky	395	UCR_ENT 00000079	FCAP			FJ230609	FJ230686, FJ230766		
Reduviidae	Harpactorinae	*Micrauchenus lineola* (Fabricius)	35	AMNH_PBI 00218790	UCR	FJ230397	FJ230471	FJ230552	FJ230630, FJ230709		
Reduviidae	Harpactorinae	*Poecilosphodrus gratiosus* (Stal)	214	AMNH_PBI 00218958	UCR	FJ230429	FJ230507	FJ230589	FJ230665, FJ230744		

Table S1.1 (cont'd).

Family	Subfamily	Species	RCW no.	USI	Voucher Depository	16S	18S	28S D2	28S D3-D5	Wg	Clade
Reduviidae	Harpactorinae	*Pselliopus spinicollis* (Champion)	284	AMNH_PBI 00219019	UCR	FJ230438	FJ230517	FJ230600			
Reduviidae	Harpactorinae	*Pselliopus zebra* (Stal)	280	AMNH_PBI 00219015	UCR	FJ230434	FJ230513	FJ230596	FJ230670, FJ230749		
Reduviidae	Harpactorinae	*Pyrrhosphodrus amazonus* Stal	31	AMNH_PBI 00218786	UCR	FJ230396	FJ230470	FJ230551	FJ230629, FJ230708		
Reduviidae	Harpactorinae	*Rhaphidosoma decorsei* Jeannel	17	AMNH_PBI 00218773	UCR	FJ230390	FJ230464	FJ230545	FJ230622, FJ230701		
Reduviidae	Harpactorinae	*Rhynocoris segmentarius* (Germar)	4	AMNH_PBI 00218760	UCR	FJ230384	FJ230457	FJ230538	FJ230616, FJ230695		
Reduviidae	Harpactorinae	*Ricolla quadrispinosa* (Linne)	396	UCR_ENT 00000075	FCAP		FJ230531	FJ230610	FJ230687		
Reduviidae	Harpactorinae	*Sinea diadema* Caudell	108	AMNH_PBI 00218861	UCR	FJ230408	FJ230485	FJ230566	FJ230644, FJ230723		
Reduviidae	Harpactorinae	*Ulpius* sp	370	UCR_ENT 00000086	UCR	FJ230449	FJ230529		FJ230684, FJ230763		
Reduviidae	Harpactorinae	*Velinus* sp	197	AMNH_PBI 00218941	UCR	FJ230428	FJ230506	FJ230588	FJ230664, FJ230743		
Reduviidae	Harpactorinae	*Vesbius purpureus* (Thunberg)	184	AMNH_PBI 00218928	UCR	FJ230422	FJ230501	FJ230582	FJ230659, FJ230737		
Reduviidae	Harpactorinae	*Zelus longipes* (Linne)	6	AMNH_PBI 00218762	UCR	FJ230385	FJ230458	FJ230539	FJ230617, FJ230696		
Reduviidae	Harpactorinae	*Zelus* nr *renardii*	90	AMNH_PBI 00218842	UCR		FJ230484	FJ230565	FJ230643, FJ230722		
Reduviidae	Harpactorinae	*Zelus renardii* Kolenati	403	UCR_ENT 00000076	UCR	FJ230453	FJ230534		FJ230691, FJ230770		
Reduviidae	Peiratinae	*Ectomocoris atrox* (Stal)	363	AMNH_PBI 00000088	UCR	FJ230447	FJ230527		FJ230682, FJ230761	JQ897876	
Reduviidae	Peiratinae	*Ectomocoris ornatus* (Stal)	246	AMNH_PBI 00218985	UCR		FJ230512	FJ230595		JQ897877	
Reduviidae	Peiratinae	*Peirates punctorius* (Stal)	216	AMNH_PBI 00218960	UCR	FJ230430	FJ230508	FJ230590	FJ230666, FJ230745	JQ897908	
Reduviidae	Peiratinae	*Rasahus thoracicus* Stal	313	AMNH_PBI 00219025	UCR		FJ230525		FJ230679, FJ230758	JQ897916	

Table S1.1 (cont'd).

Family	Subfamily	Species	RCW no.	USI	Voucher Depository	16S	18S	28S D2	28S D3-D5	Wg	Clade
Reduviidae	Phymatinae	*Lophoscutus* sp	52	AMNH_PBI 00218806	UCR	FJ230400	FJ230474	FJ230555	FJ230633, FJ230712		
Reduviidae	Phymatinae	*Macrocephalus barberi* Evans	283	AMNH_PBI 00219018	UCR	FJ230437	FJ230516	FJ230599	FJ230673, FJ230752		
Reduviidae	Phymatinae	*Macrocephalus* sp	128	AMNH_PBI 00218881	UCR	FJ230409	FJ230487	FJ230568	FJ230645, FJ230724	JQ897887	
Reduviidae	Phymatinae	*Phymata acutangula* Guerin	29	AMNH_PBI 00218783	UCR	FJ230394	FJ230468	FJ230550	FJ230627, FJ230706		
Reduviidae	Phymatinae	*Phymata fortificata* Herrich-Schaeffer	28	AMNH_PBI 00218784	UCR		FJ230467	FJ230549	FJ230626, FJ230705	JQ897909	
Reduviidae	Phymatinae	*Phymata pacifica* Evans	70	AMNH_PBI 00218825	UCR	FJ230401	FJ230476	FJ230557	FJ230635, FJ230714		
Reduviidae	Phymatinae	*Phymata* sp	87	AMNH_PBI 00218851	UCR	FJ230407	FJ230483	FJ230564	FJ230642, FJ230721	JQ897910	
Reduviidae	Physoderinae	*Physoderes impexa* (Distant)	1572	UCR_ENT 00052181	UCR	JQ897830	JQ897591	JQ897662	JQ897748	JQ897911	
Reduviidae	Physoderinae	*Physoderes* nr. *vestita*	1585	UCR_ENT 00052186	UCR	JQ897831	JQ897592	JQ897663	JQ897749	JQ897912	
Reduviidae	Physoderinae	*Physoderes* sp	686	UCR_ENT 00052221	ZMUC	JQ897832	JQ897593	JQ897664		JQ897913	
Reduviidae	Reduviinae	*Acanthaspis bilineolata* (de Beauvois)	783	UCR_ENT 00052224	UCR	JQ897773	JQ897540		JQ897690	JQ897859	*A*
Reduviidae	Reduviinae	*Acanthaspis gulo* Stal	707	UCR_ENT 00052222	ZMUC	JQ897774		JQ897619	JQ897691	JQ897860	*A*
Reduviidae	Reduviinae	*Acanthaspis iracunda* Stal	19	AMNH_PBI 00218775	UCR	FJ230392		FJ230547	FJ230624, FJ230703	JQ897861	*A*
Reduviidae	Reduviinae	*Acanthaspis iracunda* Stal	736	UCR_ENT 00052190	UCR	JQ897775	JQ897541		JQ897692	JQ897862	*A*
Reduviidae	Reduviinae	*Acanthaspis laosensis* Distant	852	UCR_ENT 00052193	TIGER	JQ897776			JQ897693		*A*
Reduviidae	Reduviinae	*Acanthaspis* nr. *bimaculata*	547	UCR_ENT 00052192	TIGER	JQ897777	JQ897542		JQ897694	JQ897863	*A*
Reduviidae	Reduviinae	*Acanthaspis quadriannulata* Stal	684	UCR_ENT 00004575	UCR	JQ897778		JQ897620	JQ897695	JQ897864	*A*

Table S1.1 (cont'd).

Family	Subfamily	Species	RCW no.	USI	Voucher Depository	16S	18S	28S D2	28S D3-D5	Wg	Clade
Reduviidae	Reduviinae	*Acanthaspis sulcipes* Signoret	737	UCR_ENT 00052174	UCR	JQ897781	JQ897545		JQ897698	JQ897866	*A*
Reduviidae	Reduviinae	*Acanthaspis westermanni* Reuter	508	UCR_ENT 00052218	TIGER	JQ897782	JQ897546		JQ897699	JQ897867	*A*
Reduviidae	Reduviinae	*Acanthaspis* sp	1589	UCR_ENT 00052205	UCR	JQ897779	JQ897543	JQ897621	JQ897696		*A*
Reduviidae	Reduviinae	*Acanthaspis* sp	73	AMNH_PBI 00218828	UCR	FJ230403	FJ230478	FJ230559	FJ230637, FJ230716	JQ897865	*A*
Reduviidae	Reduviinae	*Acanthaspis* sp	853	UCR_ENT 00052175	TIGER	JQ897780	JQ897544	JQ897622	JQ897697		*A*
Reduviidae	Reduviinae	*Alloeocranum arboricolum* Miller	1579	UCR_ENT 00052180	UCR	JQ897783	JQ897547	JQ897623	JQ897700		*R*
Reduviidae	Reduviinae	*Censorinus ferrugineous* Distant	2762	UCR_ENT 00046577	CAS	JQ897786	JQ897551	JQ897628	JQ897705		*C*
Reduviidae	Reduviinae	*Durevius tuberculatus* (Villiers)	2763	UCR_ENT 00046578	CAS	JQ897790	JQ897553	JQ897631	JQ897708		*R*
Reduviidae	Reduviinae	*Durganda rubra* Amyot and Serville	708	UCR_ENT 00052223	ZMUC	JQ897791		JQ897632		JQ897874	*T*
Reduviidae	Reduviinae	*Dyakocoris vulnerans* (Amyot and Serville)	1591	UCR_ENT 00052204	UCR	JQ897792	JQ897554	JQ897633	JQ897709	JQ897875	*V*
Reduviidae	Reduviinae	*Gerbelius* nr *ornatus*	552	UCR_ENT 00052225	TIGER	JQ897797	JQ897558		JQ897714		*R*
Reduviidae	Reduviinae	*Gerbelius ornatus* Distant	709	UCR_ENT 00052220	ZMUC	JQ897799	JQ897560		JQ897716		*R*
Reduviidae	Reduviinae	*Gerbelius ornatus* Distant	705	UCR_ENT 00052189	UCR	JQ897798	JQ897559	JQ897638	JQ897715		*R*
Reduviidae	Reduviinae	*Gerbelius* sp	704	UCR_ENT 00052219	UCR	JQ897800		JQ897639	JQ897717		*R*
Reduviidae	Reduviinae	*Inara alboguttata* Stal	1164	UCR_ENT 00002551	TIGER	JQ897801	JQ897561	JQ897640	JQ897718		*A*
Reduviidae	Reduviinae	*Inara flavopicta* Stal	82	UCR_ENT 00052191	UCR	FJ230406	FJ230482	FJ230563	JQ897719		*A*

Table S1.1 (cont'd).

Family	Subfamily	Species	RCW no.	USI	Voucher Depository	16S	18S	28S D2	28S D3-D5	Wg	Clade
Reduviidae	Reduviinae	*Inara flavopicta* Stal	712	UCR_ENT 00052170	UCR	JQ897802	JQ897562	JQ897641	JQ897720		*A*
Reduviidae	Reduviinae	*Kayanocoris wegneri* Miller	1590	UCR_ENT 00052216	UCR	JQ897803	JQ897563	JQ897642	JQ897721	JQ897884	*R*
Reduviidae	Reduviinae	*Leogorrus immaculatus* Champion	1567	UCR_ENT 00014323	INBIO	JQ897804	JQ897564		JQ897722		*R*
Reduviidae	Reduviinae	*Leogorrus litura* (Fabricius)	9	UCR_ENT 00000068	UCR	FJ230386	FJ230459	FJ230540	FJ230618, FJ230697		*R*
Reduviidae	Reduviinae	*Leogorrus litura* (Fabricius)	1278	UCR_ENT 00012955	MUSM	JQ897805	JQ897565		JQ897723	JQ897885	*R*
Reduviidae	Reduviinae	*Leogorrus longiceps* Champion	133	AMNH_PBI 00218886	?		FJ230489	FJ230570	FJ230647, FJ230726		*R*
Reduviidae	Reduviinae	*Leogorrus longiceps* Champion	680	UCR_ENT 00052197	UCR	JQ897806	JQ897566		JQ897724		*R*
Reduviidae	Reduviinae	*Leogorrus* n. sp.	540	UCR_ENT 00052198	UCR	JQ897807	JQ897567		JQ897725	JQ897886	*R*
Reduviidae	Reduviinae	*Microlestria fuscicollis* (Stal)	1809	UCR_ENT 00052185		JQ897808	JQ897568	JQ897643	JQ897726		*M*
Reduviidae	Reduviinae	*Microlestria* nr. *fuscicollis*	1393	UCR_ENT 00052226	UCR	JQ897809	JQ897569	JQ897644	JQ897727		*M*
Reduviidae	Reduviinae	*Microlestria* nr. *fuscicollis*	583	UCR_ENT 00052183	UCR	JQ897810	JQ897570		JQ897728		*M*
Reduviidae	Reduviinae	*Nalata* nr. *spinicollis*	1808	UCR_ENT 00052188	UCR	JQ897812	JQ897572	JQ897646	JQ897730		*N*
Reduviidae	Reduviinae	*Nalata setulosa* Stal	988	UCR_ENT 00003121	UCR	JQ897813	JQ897573		JQ897731	JQ897890	*N*
Reduviidae	Reduviinae	*Nalata squalida* Bergroth	1424	UCR_ENT 00002748	UCR	JQ897815	JQ897575	JQ897648	JQ897733	JQ897892	*N*
Reduviidae	Reduviinae	*Nalata* sp	1575	UCR_ENT 00014325	INBIO	JQ897814	JQ897574	JQ897647	JQ897732	JQ897891	*N*
Reduviidae	Reduviinae	*Nanokerala browni* Wygodzinsky and Lent	808	UCR_ENT 00052179	TIGER	JQ897816	JQ897576	JQ897649	JQ897734		*Ps*
Reduviidae	Reduviinae	*Nanokerala* nr. *browni*	1232	UCR_ENT 00052228	TIGER	JQ897817	JQ897577	JQ897650	JQ897735	JQ897893	*Ps*
Reduviidae	Reduviinae	*Neostachyogenys tristis* Miller	1588	UCR_ENT 00052184		JQ897818	JQ897579	JQ897651	JQ897736		

Table S1.1 (cont'd).

Family	Subfamily	Species	RCW no.	USI	Voucher Depository	16S	18S	28S D2	28S D3-D5	Wg	Clade
Reduviidae	Reduviinae	*Noualhierana furtiva* Miller	224	AMNH_PBI 00218966	UCR	FJ230432	FJ230510	FJ230592	FJ230668, FJ230747	JQ897894	
Reduviidae	Reduviinae	*Opisthacidius chinai* Lent & Wygodzinsky	1285	UCR_ENT 00012957	MUSM	JQ897819	JQ897580	JQ897652	JQ897737	JQ897896	*Z*
Reduviidae	Reduviinae	*Opisthacidius* nr. *mexicanus*	531	UCR_ENT 00004576	UCR	JQ897820	JQ897581	JQ897653	JQ897738	JQ897897	*Z*
Reduviidae	Reduviinae	*Opisthacidius* sp	1814	UCR_ENT 00052199	UCR	JQ897821	JQ897582	JQ897654	JQ897739	JQ897898	*Z*
Reduviidae	Reduviinae	*Paraplynus lugubris* (Stal)	179	AMNH_PBI 00218923	UCR	FJ230420	FJ230499	FJ230580	FJ230657, FJ230736		*A*
Reduviidae	Reduviinae	*Paredocla chevalieri* Jeannel	18	AMNH_PBI 00218774	UCR	FJ230391	FJ230465	FJ230546	FJ230623, FJ230702	JQ897902	*A*
Reduviidae	Reduviinae	*Pasiropsis maculata* Distant	810	UCR_ENT 00052227	TIGER	JQ897825	JQ897586	JQ897658	JQ897743	JQ897903	*Pa*
Reduviidae	Reduviinae	*Pasiropsis marginata* Distant	807	UCR_ENT 00052177	TIGER	JQ897826	JQ897587		JQ897744	JQ897904	*Pa*
Reduviidae	Reduviinae	*Pasiropsis* n. sp	855	UCR_ENT 00052178	TIGER	JQ897827	JQ897588	JQ897659	JQ897745	JQ897905	*Pa*
Reduviidae	Reduviinae	*Pasiropsis* sp	1587	UCR_ENT 00052217	UCR	JQ897829	JQ897590	JQ897661	JQ897747	JQ897907	*Pa*
Reduviidae	Reduviinae	*Pasiropsis* sp	1582	UCR_ENT 00052195	UCR	JQ897828	JQ897589	JQ897660	JQ897746	JQ897906	*Pa*
Reduviidae	Reduviinae	*Platymeris biguttata* (Linne)	175	AMNH_PBI 00218919	UCR	FJ230418	FJ230497	FJ230578	FJ230655, FJ230734		
Reduviidae	Reduviinae	*Plynoides* sp	787	UCR_ENT 00052196	UCR	JQ897833	JQ897594	JQ897665	JQ897750		*A*
Reduviidae	Reduviinae	**Pseudozelurus arizonicus* (N. Banks)	2765	UCR_ENT 00004573	UCR	JQ897834	JQ897595	JQ897666	JQ897751		
Reduviidae	Reduviinae	**Pseudozelurus superbus* (Champion)	2767	UCR_ENT 00004571	UCR	JQ897835	JQ897596	JQ897667	JQ897752		
Reduviidae	Reduviinae	*Psophis* sp	1581	UCR_ENT 00052230	UCR	JQ897836	JQ897597	JQ897668	JQ897753	JQ897914	*Ps*

Table S1.1 (cont'd).

Family	Subfamily	Species	RCW no.	USI	Voucher Depository	16S	18S	28S D2	28S D3-D5	Wg	Clade
Reduviidae	Reduviinae	*Psophis* sp	203	AMNH_PBI 00218947	UCR		JQ897598	JQ897669	JQ897754		*Ps*
Reduviidae	Reduviinae	**Reduvius personatus* (Linne)	2771	UCR_ENT 00004567	UCR	JQ897837	JQ897600				*R*
Reduviidae	Reduviinae	**Reduvius sonoraensis* Usinger	2769	UCR_ENT 00004569	UCR	JQ897838					*R*
Reduviidae	Reduviinae	*Staliastes rufus* (Laporte)	690	UCR_ENT 00052172	UCR	JQ897842	JQ897604	JQ897673	JQ897758	JQ897921	*V*
Reduviidae	Reduviinae	*Staliastes* sp	1578	UCR_ENT 00052231	UCR	JQ897843	JQ897605	JQ897674	JQ897759	JQ897922	*V*
Reduviidae	Reduviinae	*Tiarodes versicolor* (Laporte)	702	UCR_ENT 00052171	UCR	JQ897847	JQ897608	JQ897678	JQ897763	JQ897927	
Reduviidae	Reduviinae	*Tapeinus* sp	1577	UCR_ENT 00052200	UCR	JQ897845	JQ897606	JQ897676	JQ897761	JQ897925	*V*
Reduviidae	Reduviinae	*Tapeinus* sp	183	AMNH_PBI 00218926	UCR	FJ230421	FJ230500		FJ230658, FJ230737	JQ897926	*V*
Reduviidae	Reduviinae	*Tiarodes* sp	1584	UCR_ENT 00052206	UCR	JQ897846	JQ897607	JQ897677	JQ897762		
Reduviidae	Reduviinae	*Varus flavoannulatus* (Stal)	2764	UCR_ENT 00004574	UCR	JQ897852	JQ897613	JQ897683	JQ897768		
Reduviidae	Reduviinae	*Velitra rubropicta* (Amyot and Serville)	685	UCR_ENT 00052173	UCR	JQ897853		JQ897684	JQ897769	JQ897933	*V*
Reduviidae	Reduviinae	*Velitra* sp	1576	UCR_ENT 00052201	UCR	JQ897854	JQ897614	JQ897685	JQ897770	JQ897934	*V*
Reduviidae	Reduviinae	*Zelurus alcides* (Stal)	1571	UCR_ENT 00014324	INBIO	JQ897855	JQ897615	JQ897686	JQ897771	JQ897935	*Z*
Reduviidae	Reduviinae	*Zelurus petax* (Breddin)	167	AMNH_PBI 00218911	UCR	FJ230416	FJ230495		FJ230653, FJ230732		*Z*
Reduviidae	Reduviinae	**Zelurus pintoi* (Costa Lima)	2850	UCR_ENT 00011856	FSCA	JQ897856	JQ897616	JQ897687			*Z*
Reduviidae	Reduviinae	*Zelurus* sp	1812	UCR_ENT 00052209	UCR	JQ897857	JQ897617	JQ897688	JQ897772	JQ897936	*Z*

Table S1.1 (cont'd).

Family	Subfamily	Species	RCW no.	USI	Voucher Depository	16S	18S	28S D2	28S D3-D5	Wg	Clade
Reduviidae	Reduviinae	*Zelurus* sp	1816	UCR_ENT 00052194	UCR	JQ897858	JQ897618	JQ897689		JQ897937	*Z*
Reduviidae	Reduviinae	*Zelurus* sp	146	AMNH_PBI 00218898	UCR	FJ230412	FJ230492		FJ230650, FJ230729		*Z*
Reduviidae	Saicinae	*Kiskeyana palassaina* Weirauch and Forero	10	AMNH_PBI 00190561	USNM		FJ230460	FJ230541	FJ230619, FJ230698		
Reduviidae	Saicinae	*Saica* sp	42	AMNH_PBI 00218796	UCR	FJ230399	FJ230473	FJ230554	FJ230632, FJ230711		
Reduviidae	Salyavatinae	*Lisarda* nr. *vandenplasi*	177	AMNH_PBI 00218921	UCR	FJ230419	FJ230498	FJ230579	FJ230656, FJ230735		
Reduviidae	Salyavatinae	*Lisarda* sp	78	AMNH_PBI 00218832	UCR	FJ230404	FJ230480	FJ230561	FJ230639, FJ230718		
Reduviidae	Salyavatinae	Salyavatinae sp	1583	UCR_ENT 00052207	UCR	JQ897841	JQ897603	JQ897672	JQ897757		
Reduviidae	Stenopodainae	*Canthesancus* sp	569	UCR_ENT 00052211	TIGER	JQ897784		JQ897624	JQ897701	JQ897870	
Reduviidae	Stenopodainae	*Ctenotrachelus* sp	166	UCR_ENT 00000181	UCR	FJ230415	FJ230494	FJ230575	FJ230652, FJ230731	JQ897873	
Reduviidae	Stenopodainae	*Gageus micropterus* Villiers	309	AMNH_PBI 00219021	CAS	FJ230445	FJ230524	FJ230606	FJ230678, FJ230757		
Reduviidae	Stenopodainae	*Kodormus bruneosus* Barber	402	UCR_ENT 00000072	UCR	FJ230452	FJ230533		FJ230690, FJ230769		
Reduviidae	Stenopodainae	*Oncocephalus* sp	79	UCR_ENT 00000182	UCR	FJ230405	FJ230481	FJ230562	FJ230640, FJ230719	JQ897895	
Reduviidae	Stenopodainae	*Sastrapada* sp	185	AMNH_PBI 00218929	UCR	FJ230423	FJ230502		FJ230660, FJ230739	JQ897920	
Reduviidae	Stenopodainae	*Stenopoda* sp	154	AMNH_PBI 00218904	UCR	FJ230414	FJ230493		FJ230651, FJ230730	JQ897924	
Reduviidae	Stenopodainae	*Stenopodessa* sp	398	UCR_ENT 00000078	FCAP	FJ230451	FJ230532		FJ230688, FJ230767		
Reduviidae	Stenopodainae	*Thodelmus nigrispinosus* Villiers	369	UCR_ENT 00000085	CAS	FJ230448	FJ230528		FJ230683, FJ230762		
Reduviidae	Stenopodainae	Stenopodainae sp	365	UCR_ENT 00052212	UCR	JQ897844		JQ897675	JQ897760		

Table S1.1 (cont'd).

Family	Subfamily	Species	RCW no.	USI	Voucher Depository	16S	18S	28S D2	28S D3-D5	Wg	Clade
Reduviidae	Triatominae	**Cavernicola pilosa* Barber	2847	UCR_ENT 00040130	TAMU	JQ897785	JQ897550	JQ897627	JQ897704		*Z*
Reduviidae	Triatominae	*Eratyrus mucronatus* Stal	1811	UCR_ENT 00052168	UCR	JQ897794	JQ897555	JQ897635	JQ897711	JQ897882	*Z*
Reduviidae	Triatominae	*Panstrongylus geniculatus* (Latreille)	1569	UCR_ENT 00052167	UCR	JQ897822	JQ897583	JQ897655	JQ897740	JQ897899	*Z*
Reduviidae	Triatominae	*Panstrongylus* nr. *geniculatus*	1810	UCR_ENT 00052165	UCR	JQ897824	JQ897585	JQ897657	JQ897742	JQ897901	*Z*
Reduviidae	Triatominae	*Panstrongylus lignarius* (Walker)	1813	UCR_ENT 00052166	UCR	JQ897823	JQ897584	JQ897656	JQ897741	JQ897900	*Z*
Reduviidae	Triatominae	*Paratriatoma hirsuta* Barber	296	UCR_ENT 00218745	UCR	FJ230443	FJ230521	FJ230604	FJ230676, FJ230755		*Z*
Reduviidae	Triatominae	*Rhodnius neglectus* Lent	1573	UCR_ENT 00052203	UCR	JQ897839	JQ897601	JQ897670	JQ897755	JQ897918	*Z*
Reduviidae	Triatominae	*Rhodnius pictipes* Stal	1815	UCR_ENT 00052208	UCR	JQ897840	JQ897602	JQ897671	JQ897756	JQ897919	*Z*
Reduviidae	Triatominae	*Triatoma dimidiata* (Latreille)	1570	UCR_ENT 00052169	UCR	JQ897848	JQ897609	JQ897679	JQ897764	JQ897928	*Z*
Reduviidae	Triatominae	*Triatoma protracta* Uhler	294	UCR_ENT 00218742	UCR	FJ230442	FJ230520		FJ230675, FJ230754	JQ897929	*Z*
Reduviidae	Triatominae	*Triatoma recurva* (Stal)	170	AMNH_PB I 00218913	UCR	FJ230417	FJ230496	FJ230577	FJ230654, FJ230733	JQ897930	*Z*
Reduviidae	Triatominae	*Triatoma venosa* (Stal)	581	UCR_ENT 00052210	UCR	JQ897850	JQ897611	JQ897681	JQ897766	JQ897932	*Z*
Reduviidae	Triatominae	*Triatoma* sp	1574	UCR_ENT 00052202	UCR	JQ897849	JQ897610	JQ897680	JQ897765	JQ897931	*Z*
Reduviidae	Tribelocephalina e	*Tribelocephala peyrierasi* Villiers	287	AMNH_PB I 00219033	CAS	FJ230440	FJ230521	FJ230601			
Reduviidae	Tribelocephalina e	Tribelocephalinae sp	1592	UCR_ENT 00052187	UCR	JQ897851	JQ897612	JQ897682	JQ897767		
Reduviidae	Vesciinae	*Mirambulus niger* Breddin	1817	UCR_ENT 00052182	UCR	JQ897811	JQ897571	JQ897645	JQ897729		
Reduviidae	Visayanocorinae	*Carayonia orientalis* Ishikawa and Okajima	1473	UCR_ENT 00052232	TIGER		JQ897549	JQ897626	JQ897703		
Reduviidae	Visayanocorinae	*Carayonia* n. sp.	1536	UCR_ENT 00003627	CAS		JQ897548	JQ897625	JQ897702		

Table S1.2 List of species used for ancestral state reconstructions with the associated microhabitat, prey specialization and references listed. Abbreviations are as follows: Aq: Aquatic, Fo: Foliage, Ba: Bark-associated, Gr: Ground, LL: Leaf Litter, Bn: Bird nest, Mm: Mammal dwelling, Pf: Palm fronds, Ep: Epiphytes; GP: General Predators, Hb: Herbivore, Fg: Fungivore, Tm: Termites, An: Ants, VB: Vertebrate blood, Mp: Millipedes, Sp: Spiders.

Family	Subfamily	Species	USI	Micro-habitat	Reference	Prey specialization	Reference	Locality
Belostomatidae	Belostomatinae	*Abedus breviceps* Stal	N/A	Aq	Schuh and Slater, 1995	GP	Schuh and Slater, 1995	
Corixidae		Corixidae sp	UCR_ENT 00000183	Aq	Schuh and Slater, 1995	Hb	Schuh and Slater, 1995	USA; California
Scutellaridae		*Austrotichus rugosus* Gross	N/A	Fo	Cassis and Loren, 2006	Hb	Cassis and Vanags, 2006; Schuh and Slater, 1995	Australia
Aradidae	Mezirinae	*Mezira sayi* Kormilev	N/A	Ba	Usinger and Matsuda, 1959; Taylor and Gil, 2009	Fg	Usinger and Matsuda, 1959; Nardi et al, 2009	
Nabidae	Nabinae	*Nabis apicalis* Matsumura	N/A	Fo	Lattin, 1989	GP	Lattin, 1989	
Tingidae		*Corythuca* sp	UCR_ENT 00000083	Fo	own obs; Wellhouse, 1919	Hb	Gibson, 1918	USA; California
Miridae	Phylinae	*Oligotylus carneatus* (Knight)	N/A	Fo	Schuh, 2000	Hb	Schuh, 2000	USA; California
Miridae	Phylinae	*Phallospinophylus setosus* Weirauch	UCR_ENT 00000082	Fo	Weirauch 2006, own obs	Hb	Weirauch 2006, own obs	USA; California
Reduviidae	Centrocnemidinae	*Neocentrocnemis stali* (Reuter)	UCR_ENT 00001976	Ba	Miller, 1956	?		Laos
	Cetherinae	*Cethera musiva* (Germar)	UCR_ENT 00052215	Ba	own obs; Louis, 1974	Tm	Miller, 1953	Nigeria; Ondo
	Cetherinae	*Cethera musiva* (Germar)	UCR_ENT 00052176	Ba	own obs; Louis, 1974	Tm	Miller, 1953	Nigeria; Ondo
	Cetherinae	*Eupheno histrionicus* (Stal)	UCR_ENT 00014326	Ba	own obs	Tm	Haviland, 1931 (*Sorglana*)	Costa Rica; Heredia
	Cetherinae	*Eupheno pallens* (Laporte)	UCR_ENT 00052214	Ba	own obs	Tm	Haviland, 1931 (*Sorglana*)	Peru; Madre de Dios
	Ectrichodiinae	*Cleptria corallina* Villiers	AMNH_PBI 00218770	?	?	Mp	Lawrence, 1984	Guinea-Bissau
	Ectrichodiinae	*Ectrichodia lucida* Lepelletier and Serville	AMNH_PBI 00218769	Gr/LL	Louis, 1974	Mp	Miller, 1953	Guinea-Bissau

Table S1.2 (cont'd).

Family	Subfamily	Species	USI	Micro-habitat	Reference	Prey specialization	Reference	Locality
Reduviidae	Ectrichodiinae	nr *Microsanta* sp	UCR_ENT 00052213	Gr/LL	Miller, 1953	Mp	Haridass, 1985	Laos
Reduviidae	Ectrichodiinae	*Ectrychotes* sp	AMNH_PBI 00218830	Gr/LL	Miller, 1953	Mp	Haridass, 1985	Malaysia; Johor
Reduviidae	Ectrichodiinae	*Ectrychotes* sp	AMNH_PBI 00218932	Gr/LL	Miller, 1953	Mp	Haridass, 1985	Malaysia; Selangor
Reduviidae	Ectrichodiinae	*Maraenaspis* sp	AMNH_PBI 00218772	Gr/LL	Miller, 1953	Mp	Miller, 1953	Senegal
Reduviidae	Ectrichodiinae	*Racelda sp*	AMNH_PBI 00218801	Gr/LL	Miller, 1953	?		French Guiana; Approuague-Kaw
Reduviidae	Ectrichodiinae	*Rhiginia sp*	AMNH_PBI 00218891	Gr/LL	own obs	Mp	own obs	Nicaragua; Granada
Reduviidae	Emesinae	*Emesaya incisa McAtee and Malloch*	AMNH_PBI 00219017	Ep/Sp	Wygodzinsky, 1966	Sp/GP	Wygodzinsky, 1966; Readio, 1927	USA; California
Reduviidae	Emesinae	*Empicoris sp*	AMNH_PBI 00218862	Ep/Sp	Wygodzinsky, 1966	?		Mexico; Sonora
Reduviidae	Emesinae	*Mangabea barbiger Weirauch*	UCR_ENT 00005201	?		?		Madagascar; Fianarantsoa
Reduviidae	Emesinae	*Ploiaria hirticornis (N. Banks)*	AMNH_PBI 00218808	Fo/Ba/Gr/LL/Sw	Wygodzinsky, 1966	GP	Wygodzinsky, 1966	Mexico; Sonora
Reduviidae	Emesinae	*Stenolemoides arizonensis (N. Banks)*	AMNH_PBI 00218753	Sw	own obs	Sp	Wygodzinsky, 1966	USA; California
Reduviidae	Emesinae	*Stenolemus sp*	AMNH_PBI 00218899	Sw/Ba/Bn	Wygodzinsky, 1966	?		Ecuador
Reduviidae	Holoptilinae	*Ptilocerus sp*	UCR_ENT 00001974	Ba	Jacobson, 1911	An	Jacobson, 1911	Thailand
Reduviidae	Holoptilinae	*Ptilocnemus femoralis Horvath*	AMNH_PBI 00218963	Ba	own obs; Malipatil, 1985	An	Malipatil, 1985; McKeown, 1944	Australia; South Australia
Reduviidae	Hammacerinae	*Microtomus cinctipes (Stal)*	AMNH_PBI 00218893	Ba	Readio, 1927; Champion, 1899	?		Nicaragua
Reduviidae	Hammacerinae	*Microtomus sp*	AMNH_PBI 00218785	Ba	Readio, 1927; Champion, 1899	?		French Guiana; Maripasoula
Reduviidae	Harpactorinae	*Acanthiscium seminigrum Stal*	UCR_ENT 00000074	Fo	own obs	?		Brazil

Table S1.2 (cont'd).

Family	Subfamily	Species	USI	Micro-habitat	Reference	Prey specialization	Reference	Locality
Reduviidae	Harpactorinae	*Agriocoris flavipes* (Fabricius)	AMNH_PBI 00218884	Fo	own obs	?		French Guiana; Cayenne
Reduviidae	Harpactorinae	*Apiomerus lanipes* (Fabricius)	AMNH_PBI 00219016	Fo	Readio, 1927	GP	Gil-Santana, 2002; Readio, 1927	
Reduviidae	Harpactorinae	*Apiomerus ochropterus* Stal	AMNH_PBI 00218777	Fo	Readio, 1927	GP	Readio, 1927	French Guiana; Cayenne
Reduviidae	Harpactorinae	*Arilus cristatus* (Linne)	AMNH_PBI 00218826	Fo	Readio, 1927	GP	Readio, 1927	USA; Pennsylvania
Reduviidae	Harpactorinae	*Castolus subinermis* (Stal)	UCR_ENT 00000089	Fo	own obs	GP	Koponen, 1988	USA; Arizona
Reduviidae	Harpactorinae	*Coranus callosus* Stal	AMNH_PBI 00218984	Gr	Wachmann et al, 2006	GP	Sahayaraj and Ambrose, 1993; Miller, 1953	Australia; Western Australia
Reduviidae	Harpactorinae	*Euagoras* sp	AMNH_PBI 0021928	Fo	own obs	?		Malaysia; Selangor
Reduviidae	Harpactorinae	Harpactorinae sp	AMNH_PBI 00218934	Fo	own obs	?		Malaysia; Selangor/Pahang border
Reduviidae	Harpactorinae	*Heniartes putumayo* Wygodzinsky	UCR_ENT 00000079	Fo	own obs; Wygodzinsky, 1948	GP	Wygodzinsky, 1948	South America
Reduviidae	Harpactorinae	*Micrauchenus lineola* (Fabricius)	AMNH_PBI 00218790	Ba	Berenger & Pluot-Sigwalt, 2009	Tm	Berenger & Pluot-Sigwalt, 2009	French Guiana
Reduviidae	Harpactorinae	*Poecilosphodrus gratiosus* (Stal)	AMNH_PBI 00218958	Fo	own obs	?		Australia; Western Australia
Reduviidae	Harpactorinae	*Pselliopus spinicollis* (Champion)	AMNH_PBI 00219019	Fo	Readio, 1927	GP	Readio, 1927	USA; California
Reduviidae	Harpactorinae	*Pselliopus zebra* (Stal)	AMNH_PBI 00219015	Fo	Readio, 1927	GP	Readio, 1927	Guatemala; Sacatepequez
Reduviidae	Harpactorinae	*Pyrrhosphodrus amazonus* Stal	AMNH_PBI 00218786	Fo	own obs	?		French Guiana; Montsinery
Reduviidae	Harpactorinae	*Rhaphidosoma decorsei* Jeannel	AMNH_PBI 00218773	Fo (grasses)	Miller, 1953	GP	Haridass, 1985	Senegal; Thies
Reduviidae	Harpactorinae	*Rhynocoris segmentarius* (Germar)	AMNH_PBI 00218760	Fo	Louis, 1974; Miller, 1953	GP	Miller, 1953; Louis, 1974; Haridass, 1985	South Africa; Limpopo
Reduviidae	Harpactorinae	*Ricolla quadrispinosa* (Linne)	UCR_ENT 00000075	Fo	Haviland, 1931	?		Brazil; Mato Grosso
Reduviidae	Harpactorinae	*Sinea diadema* Caudell	AMNH_PBI 00218861	Fo	Readio, 1927; Haviland, 1931	GP	Readio, 1927	Mexico; Chihuahua

Table S1.2 (cont'd).

Family	Subfamily	Species	USI	Micro-habitat	Reference	Prey specialization	Reference	Locality
Reduviidae	Harpactorinae	*Ulpius* sp	UCR_ENT 00000086	?		?		Madagascar; Toliara
Reduviidae	Harpactorinae	*Velinus* sp	AMNH_PBI 00218941	Fo	own obs	?		Malaysia; Pahang
Reduviidae	Harpactorinae	*Vesbius purpureus* (Thunberg)	AMNH_PBI 00218928	Fo	own obs	?		Malaysia; Pahang
Reduviidae	Harpactorinae	*Zelus longipes* (Linne)	AMNH_PBI 00218762	Fo	Haviland, 1931; Readio, 1927; own obs	GP	Readio, 1927; Gil-Santana & Alves 2011; own obs	Dominican Republic; Santiago
Reduviidae	Harpactorinae	*Zelus* nr *renardii*	AMNH_PBI 00218842	Fo	Haviland, 1931; Readio, 1927; own obs	GP	Readio, 1927; Gil-Santana & Alves 2011; own obs	Mexico; Chihuahua
Reduviidae	Harpactorinae	*Zelus renardii* Kolenati	UCR_ENT 00000076	Fo	Haviland, 1931; Readio, 1927; own obs	GP	Readio, 1927; Gil-Santana & Alves 2011; own obs	USA; California
Reduviidae	Peiratinae	*Ectomocoris atrox* (Stal)	AMNH_PBI 00000088	Gr/LL	own obs; Miller, 1956; Louis, 1974; Miller, 1953	GP	Ambrose, 1987	Singapore
Reduviidae	Peiratinae	*Ectomocoris ornatus* (Stal)	AMNH_PBI 00218985	Gr/LL	own obs; Miller, 1956; Louis, 1974; Miller, 1953	GP	Ambrose, 1987	Australia; New South Wales
Reduviidae	Peiratinae	*Peirates punctorius* (Stal)	AMNH_PBI 00218960	Gr	own obs; Miller, 1956	GP	Ambrose, 1987	Australia; New South Wales
Reduviidae	Peiratinae	*Rasahus thoracicus* Stal	AMNH_PBI 00219025	Gr	own obs; Readio, 1927	GP	Readio, 1927	USA; California
Reduviidae	Phymatinae	*Lophoscutus* sp	AMNH_PBI 00218806	Fo	own obs; Kormilev, 1981; Miller, 1956	GP	Kormilev, 1981; Miller, 1956	Mexico; Sonora
Reduviidae	Phymatinae	*Macrocephalus barberi* Evans	AMNH_PBI 00219018	Fo	own obs; Kormilev, 1981; Miller, 1956	GP	Kormilev, 1981; Miller, 1956	USA; California
Reduviidae	Phymatinae	*Macrocephalus* sp	AMNH_PBI 00218881	Fo	own obs; Kormilev, 1981; Miller, 1956	GP	Kormilev, 1981; Miller, 1956	Mexico; Chihuahua
Reduviidae	Phymatinae	*Phymata acutangula* Guerin	AMNH_PBI 00218783	Fo	Haviland, 1931; own obs; Miller, 1956; Balduf, 1941	GP	Balduf, 1943; Balduf, 1948; Miller, 1956	French Guiana; Montsinery
Reduviidae	Phymatinae	*Phymata fortificata* Herrich-Schaeffer	AMNH_PBI 00218784	Fo	Haviland, 1931; own obs; Miller, 1956; Balduf, 1941	GP	Balduf, 1943; Balduf, 1948; Miller, 1956	French Guiana; Montsinery
Reduviidae	Phymatinae	*Phymata pacifica* Evans	AMNH_PBI 00218825	Fo	Haviland, 1931; own obs; Miller, 1956; Balduf, 1941	GP	Balduf, 1943; Balduf, 1948; Miller, 1956	USA; California
Reduviidae	Phymatinae	*Phymata* sp	AMNH_PBI 00218851	Fo	Haviland, 1931; own obs; Miller, 1956; Balduf, 1941	GP	Balduf, 1943; Balduf, 1948; Miller, 1956	Mexico; Sonora

Table S1.2 (cont'd).

Family	Subfamily	Species	USI	Micro-habitat	Reference	Prey specialization	Reference	Locality
Reduviidae	Physoderinae	*Physoderes impexa* (Distant)	UCR_ENT 00052181	LL	Miller, 1953	GP	Miller, 1954	Vietnam; Vinh Phuc
Reduviidae	Physoderinae	*Physoderes* nr. *vestita*	UCR_ENT 00052186	Ba	own obs	GP	Miller, 1954	Brunei; Temburong
Reduviidae	Physoderinae	*Physoderes* sp	UCR_ENT 00052221	Ba	own obs	GP	Miller, 1954	Laos; Champasak
Reduviidae	Reduviinae	*Acanthaspis bilineolata* (de Beauvois)	UCR_ENT 00052224	Gr/Ba	own obs, Louis 1974	An	Haridass, 1985; Odhiambo, 1958	Nigeria; Osun
Reduviidae	Reduviinae	*Acanthaspis gulo* Stal	UCR_ENT 00052222	Gr/Ba	Louis, 1974	An	Haridass, 1985; Odhiambo, 1958	Laos; Vientiane
Reduviidae	Reduviinae	*Acanthaspis iracunda* Stal	AMNH_PBI 00218775	Gr/Ba	Louis, 1974	An	Haridass, 1985; Odhiambo, 1958	Guinea-Bissau
Reduviidae	Reduviinae	*Acanthaspis iracunda* Stal	UCR_ENT 00052190	Gr/Ba	own obs, Louis 1974	An	Haridass, 1985; Odhiambo, 1958	Nigeria; Ondo
Reduviidae	Reduviinae	*Acanthaspis laosensis* Distant	UCR_ENT 00052193	Gr/Ba	Louis, 1974	An	Haridass, 1985; Odhiambo, 1958	Thailand; Suphan Buri
Reduviidae	Reduviinae	*Acanthaspis* nr. *bimaculata*	UCR_ENT 00052192	Gr/Ba	Louis, 1974	An	Haridass, 1985; Odhiambo, 1958	Thailand; Chaiyaphum
Reduviidae	Reduviinae	*Acanthaspis quadriannulata* Stal	UCR_ENT 00004575	Gr/Ba	Louis, 1974	An	Haridass, 1985; Odhiambo, 1958	Laos
Reduviidae	Reduviinae	*Acanthaspis sulcipes* Signoret	UCR_ENT 00052174	Gr/Ba	own obs, Louis 1974	An	Haridass, 1985; Odhiambo, 1958	Nigeria; Osun
Reduviidae	Reduviinae	*Acanthaspis westermanni* Reuter	UCR_ENT 00052218	Gr/Ba	Louis, 1974	An	Haridass, 1985; Odhiambo, 1958	Thailand; Phetchabun
Reduviidae	Reduviinae	*Acanthaspis* sp	UCR_ENT 00052205	Gr/Ba	Odhiambo, 1958; Miller, 1953; Louis, 1974	An	Haridass, 1985; Odhiambo, 1958	Singapore
Reduviidae	Reduviinae	*Acanthaspis* sp	AMNH_PBI 00218828	Gr/Ba	Louis, 1974	An	Haridass, 1985; Odhiambo, 1958	South Africa; Northern Cape
Reduviidae	Reduviinae	*Acanthaspis* sp	UCR_ENT 00052175	Gr/Ba	Louis, 1974	An	Haridass, 1985; Odhiambo, 1958	Thailand; Chanthaburi
Reduviidae	Reduviinae	*Alloeocranum arboricolum* Miller	UCR_ENT 00052180	?		?		Brunei; Temburong
Reduviidae	Reduviinae	*Censorinus ferrugineous* Distant	UCR_ENT 00046577	?		?		Madagascar
Reduviidae	Reduviinae	*Durevius tuberculatus* (Villiers)	UCR_ENT 00046578	?		?		Madagascar; Fianarantsoa
Reduviidae	Reduviinae	*Durganda rubra* Amyot and Serville	UCR_ENT 00052223	Ba	Miller, 1956; own obs.	?		Laos; Champasak
Reduviidae	Reduviinae	*Dyakocoris vulnerans* (Amyot and Serville)	UCR_ENT 00052204	Ba	own obs	?		Brunei; Temburong

Table S1.2 (cont'd).

Family	Subfamily	Species	USI	Micro-habitat	Reference	Prey specialization	Reference	Locality
Reduviidae	Reduviinae	*Gerbelius ornatus* Distant	UCR_ENT 00052220	?		?		Laos; Khammouane
Reduviidae	Reduviinae	*Gerbelius ornatus* Distant	UCR_ENT 00052189	?		?		Laos; Vientiane
Reduviidae	Reduviinae	*Gerbelius* sp	UCR_ENT 00052219	?		?		Laos
Reduviidae	Reduviinae	*Inara alboguttata* Stal	UCR_ENT 00002551	Fo	own obs	?		Thailand; Nakhon Nayok
Reduviidae	Reduviinae	*Inara flavopicta* Stal	UCR_ENT 00052191	Fo	own obs	?		Singapore
Reduviidae	Reduviinae	*Inara flavopicta* Stal	UCR_ENT 00052170	Fo	own obs	?		Thailand
Reduviidae	Reduviinae	*Kayanocoris wegneri* Miller	UCR_ENT 00052216	Fo	own obs	?		Brunei; Belait
Reduviidae	Reduviinae	*Leogorrus immaculatus* Champion	UCR_ENT 00014323	Ba	Haviland, 1931; Champion, 1899; own obs.	Tm	Haviland, 1931; own obs	Costa Rica; Heredia
Reduviidae	Reduviinae	*Leogorrus litura* (Fabricius)	UCR_ENT 00000068	Ba	Haviland, 1931; Champion, 1899; own obs.	Tm	Haviland, 1931; own obs	Dominican Republic
Reduviidae	Reduviinae	*Leogorrus litura* (Fabricius)	UCR_ENT 00012955	Ba	Haviland, 1931; Champion, 1899; own obs.	Tm	Haviland, 1931; own obs	Peru; Loreto
Reduviidae	Reduviinae	*Leogorrus longiceps* Champion	AMNH_PBI 00218886	Ba	Haviland, 1931; Champion, 1899; own obs.	Tm	Haviland, 1931; own obs	French Guiana; Cayenne
Reduviidae	Reduviinae	*Leogorrus longiceps* Champion	UCR_ENT 00052197	Ba	Haviland, 1931; Champion, 1899; own obs.	Tm	Haviland, 1931; own obs	Costa Rica; Guanacaste
Reduviidae	Reduviinae	*Leogorrus* n. sp.	UCR_ENT 00052198	Ba	Haviland, 1931; Champion, 1899; own obs.	Tm	Haviland, 1931; own obs	Costa Rica; Guanacaste
Reduviidae	Reduviinae	*Microlestria fuscicollis* (Stal)	UCR_ENT 00052185	Ba	own obs	?		French Guiana; Regina
Reduviidae	Reduviinae	*Microlestria* nr. *fuscicollis*	UCR_ENT 00052226	Ba	own obs	?		Ecuador
Reduviidae	Reduviinae	*Microlestria* nr. *fuscicollis*	UCR_ENT 00052183	Ba	own obs	?		Costa Rica; Limon

Table S1.2 (cont'd).

Family	Subfamily	Species	USI	Micro-habitat	Reference	Prey specialization	Reference	Locality
Reduviidae	Reduviinae	*Nalata* nr. *spinicollis*	UCR_ENT 00052188	Ba	own obs	?		French Guiana; Regina
Reduviidae	Reduviinae	*Nalata setulosa* Stal	UCR_ENT 00003121	Ba	own obs	?		Mexico; Chiapas
Reduviidae	Reduviinae	*Nalata squalida* Bergroth	UCR_ENT 00002748	Ba	own obs	?		Ecuador; Napo
Reduviidae	Reduviinae	*Nalata* sp	UCR_ENT 00014325	Ba	own obs	?		Costa Rica; Heredia
Reduviidae	Reduviinae	*Nanokerala browni* Wygodzinsky and Lent	UCR_ENT 00052179	?		?		Thailand; Nakhon Si Thammarat
Reduviidae	Reduviinae	*Nanokerala* nr. *browni*	UCR_ENT 00052228	?		?		Thailand; Surat Thani
Reduviidae	Reduviinae	*Neostachyogenys tristis* Miller	UCR_ENT 00052184	Fo	own obs	?		Brunei; Belait
Reduviidae	Reduviinae	*Noualhierana furtiva* Miller	AMNH_PBI 00218966	?		?		Australia; New South Wales
Reduviidae	Reduviinae	*Opisthacidius chinai* Lent & Wygodzinsky	UCR_ENT 00012957	Bn	Lent and Wygodzinsky, 1956	GP	Costa Lima, 1940 (*Spiniger*)	Peru
Reduviidae	Reduviinae	*Opisthacidius* nr. *mexicanus*	UCR_ENT 00004576	Bn	Lent and Wygodzinsky, 1956	GP	Costa Lima, 1940 (*Spiniger*)	Costa Rica; Guanacaste
Reduviidae	Reduviinae	*Opisthacidius* sp	UCR_ENT 00052199	Bn	Lent and Wygodzinsky, 1956	GP	Costa Lima, 1940 (*Spiniger*)	French Guiana; Roura
Reduviidae	Reduviinae	*Paraplynus lugubris* (Stal)	AMNH_PBI 00218923	?		?		Guinea-Bisseau
Reduviidae	Reduviinae	*Paredocla chevalieri* Jeannel	AMNH_PBI 00218774	Ba	own obs	?		Senegal
Reduviidae	Reduviinae	*Pasiropsis maculata* Distant	UCR_ENT 00052227	Ba	own obs	?		Thailand
Reduviidae	Reduviinae	*Pasiropsis marginata* Distant	UCR_ENT 00052177	Ba	own obs	?		Thailand; Chiang Mai
Reduviidae	Reduviinae	*Pasiropsis* n. sp	UCR_ENT 00052178	Ba	own obs	?		Thailand; Suphan Buri
Reduviidae	Reduviinae	*Pasiropsis* sp	UCR_ENT 00052217	Ba	own obs	?		Vietnam; Cat Tien
Reduviidae	Reduviinae	*Pasiropsis* sp	UCR_ENT 00052195	Ba	own obs	?		Brunei; Temburong
Reduviidae	Reduviinae	*Platymeris biguttata* (Linne)	AMNH_PBI 00218919	Ba/LL	Fritzcshe, 2008; Louis, 1974	GP	Miller 1956; Edwards, 1962	Guinea-Bisseau

Table S1.2 (cont'd).

Family	Subfamily	Species	USI	Micro-habitat	Reference	Prey specialization	Reference	Locality
Reduviidae	Reduviinae	*Plynoides* sp	UCR_ENT 00052196	?		?		Nigeria; Ondo
Reduviidae	Reduviinae	**Pseudozelurus arizonicus* (N. Banks)	UCR_ENT 00004573	?		?		USA; Arizona
Reduviidae	Reduviinae	**Pseudozelurus superbus* (Champion)	UCR_ENT 00004571	?		?		Belize; Cayo
Reduviidae	Reduviinae	*Psophis* sp	UCR_ENT 00052230	Ba	own obs	?		Brunei; Temburong
Reduviidae	Reduviinae	*Psophis* sp	AMNH_PBI 00218947	Ba	own obs	?		Brunei; Temburong
Reduviidae	Reduviinae	**Reduvius personatus* (Linne)	UCR_ENT 00004567	Gr	Readio, 1927	GP	Immel, 1954; Readio, 1927	USA; Colorado
Reduviidae	Reduviinae	**Reduvius sonoraensis* Usinger	UCR_ENT 00004569	Mm/Gr	Ryckman, 1954; Wygodzinsky and Usinger, 1964	GP	Wood, 1954; Ryckman, 1954; Wygodzinsky and Usinger 1964	USA; California
Reduviidae	Reduviinae	*Staliastes rufus* (Laporte)	UCR_ENT 00052172	Ba	Miller, 1956	?		Laos
Reduviidae	Reduviinae	*Staliastes* sp	UCR_ENT 00052231	Ba	Miller, 1956	?		Brunei; Temburong
Reduviidae	Reduviinae	*Tiarodes versicolor* (Laporte)	UCR_ENT 00052171	Ba/LL	Miller, 1959	?		Laos
Reduviidae	Reduviinae	*Tapeinus* sp	UCR_ENT 00052200	Ba	Miller, 1956	?		Brunei; Temburong
Reduviidae	Reduviinae	*Tapeinus* sp	AMNH_PBI 00218926	Ba	Miller, 1956	?		Malaysia; Pahang
Reduviidae	Reduviinae	*Tiarodes* sp	UCR_ENT 00052206	Ba/LL	Miller, 1959	?		Brunei; Temburong
Reduviidae	Reduviinae	*Varus flavoannulatus* (Stal)	UCR_ENT 00004574	Ba	Miller, 1953	?		Zambia; Copperbelt
Reduviidae	Reduviinae	*Velitra rubropicta* (Amyot and Serville)	UCR_ENT 00052173	Ba	Miller, 1956	GP	Vennison and Ambrose, 1990	Laos
Reduviidae	Reduviinae	*Velitra* sp	UCR_ENT 00052201	Ba	Miller, 1956	GP	Vennison and Ambrose, 1990	Brunei; Temburong
Reduviidae	Reduviinae	*Zelurus alcides* (Stal)	UCR_ENT 00014324	Fo/Gr	Haviland, 1931	GP	Gnaspini, 1996; Ferreira & Martins, 1999	Costa Rica; Heredia
Reduviidae	Reduviinae	*Zelurus petax* (Breddin)	AMNH_PBI 00218911	Fo/Gr	Haviland, 1931	GP	Gnaspini, 1996; Ferreira & Martins, 1999	Ecuador
Reduviidae	Reduviinae	**Zelurus pintoi* (Costa Lima)	UCR_ENT 00011856	Fo/Gr	Haviland, 1931	GP	Gnaspini, 1996; Ferreira & Martins, 1999	Bolivia; Santa Cruz

Table S1.2 (cont'd).

Family	Subfamily	Species	USI	Micro-habitat	Reference	Prey specialization	Reference	Locality
Reduviidae	Reduviinae	*Zelurus* sp	UCR_ENT 00052209	Fo/Gr	Haviland, 1931	GP	Gnaspini, 1996; Ferreira & Martins, 1999	French Guiana; Roura
Reduviidae	Reduviinae	*Zelurus* sp	UCR_ENT 00052194	Fo/Gr	Haviland, 1931	GP	Gnaspini, 1996; Ferreira & Martins, 1999	French Guiana; Regina
Reduviidae	Reduviinae	*Zelurus* sp	AMNH_PBI 00218898	Fo/Gr	Haviland, 1931	GP	Gnaspini, 1996; Ferreira & Martins, 1999	Ecuador
Reduviidae	Saicinae	*Kiskeyana palassaina* Weirauch and Forero	AMNH_PBI 00190561	Gr/LL	Weirauch and Forero, 2007	?		Dominican Republic
Reduviidae	Saicinae	*Saica* sp	AMNH_PBI 00218796	Pf	Readio, 1927	?		French Guiana; Approuague-Kaw
Reduviidae	Salyavatinae	*Lisarda* nr. *vandenplasi*	AMNH_PBI 00218921	Ba	Louis, 1974	Tm	McMahan, 1983	Guinea-Bissau
Reduviidae	Salyavatinae	*Lisarda* sp	AMNH_PBI 00218832	Ba	Louis, 1974	Tm	McMahan, 1983	Singapore
Reduviidae	Salyavatinae	Salyavatinae sp	UCR_ENT 00052207	Ba	McMahan, 1983	Tm	McMahan, 1983	Brunei; Temburong
Reduviidae	Stenopodainae	*Canthesancus* sp	UCR_ENT 00052211	?		?		Thailand; Phitsanulok
Reduviidae	Stenopodainae	*Ctenotrachelus* sp	UCR_ENT 00000181	?		?		Costa Rica
Reduviidae	Stenopodainae	*Gageus micropterus* Villiers	AMNH_PBI 00219021	?		?		Madagascar; Toamasina
Reduviidae	Stenopodainae	*Kodormus bruneosus* Barber	UCR_ENT 00000072	Gr/Fo	Miller, 1956	?		Costa Rica
Reduviidae	Stenopodainae	*Oncocephalus* sp	UCR_ENT 00000182	Gr	Readio, 1927	GP	Vennison and Ambrose, 1987	Singapore
Reduviidae	Stenopodainae	*Sastrapada* sp	AMNH_PBI 00218929	?		GP	Villiers, 1948	Malaysia; Selangor/Pahang border
Reduviidae	Stenopodainae	*Stenopoda* sp	AMNH_PBI 00218904	LL/Fo	Readio, 1927; Haviland, 1931	?		Nicaragua
Reduviidae	Stenopodainae	*Stenopodessa* sp	UCR_ENT 00000078	?		?		Brazil; Mato Grosso
Reduviidae	Stenopodainae	*Thodelmus nigrispinosus* Villiers	UCR_ENT 00000085	?		?		Madagascar; Antsiranana
Reduviidae	Stenopodainae	Stenopodainae sp	UCR_ENT 00052212	?		?		Singapore
Reduviidae	Triatominae	**Cavernicola pilosa* Barber	UCR_ENT 00040130	Mm	Lent and Wygodzinsky, 1979	VB	Lent and Wygodzinsky, 1979	Nicaragua; Rio San Juan

Table S1.2 (cont'd).

Family	Subfamily	Species	USI	Micro-habitat	Reference	Prey specialization	Reference	Locality
Reduviidae	Triatominae	*Eratyrus mucronatus* Stal	UCR_ENT 00052168	Mm	Lent and Wygodzinsky, 1979	VB	Lent and Wygodzinsky, 1979	French Guiana; Roura
Reduviidae	Triatominae	*Panstrongylus geniculatus* (Latreille)	UCR_ENT 00052167	Mm	Lent and Wygodzinsky, 1979	VB	Lent and Wygodzinsky, 1979	Costa Rica; Heredia
Reduviidae	Triatominae	*Panstrongylus* nr. *geniculatus*	UCR_ENT 00052165	Mm	Lent and Wygodzinsky, 1979	VB	Lent and Wygodzinsky, 1979	French Guiana; Roura
Reduviidae	Triatominae	*Panstrongylus lignarius* (Walker)	UCR_ENT 00052166	Mm	Lent and Wygodzinsky, 1979	VB	Lent and Wygodzinsky, 1979	French Guiana; Roura
Reduviidae	Triatominae	*Paratriatoma hirsuta* Barber	UCR_ENT 00218745	Mm	Lent and Wygodzinsky, 1979	VB	Lent and Wygodzinsky, 1979	USA; California
Reduviidae	Triatominae	*Rhodnius neglectus* Lent	UCR_ENT 00052203	Pf/Bn	Lent and Wygodzinsky, 1979	VB	Lent and Wygodzinsky, 1979	Ecuador; Orellana
Reduviidae	Triatominae	*Rhodnius pictipes* Stal	UCR_ENT 00052208	Pf/Ep	Lent and Wygodzinsky, 1979	VB	Lent and Wygodzinsky, 1979	French Guiana; Roura
Reduviidae	Triatominae	*Triatoma dimidiata* (Latreille)	UCR_ENT 00052169	Mm	Lent and Wygodzinsky, 1979	VB	Lent and Wygodzinsky, 1979	Costa Rica; Heredia
Reduviidae	Triatominae	*Triatoma protracta* Uhler	UCR_ENT 00218742	Mm	Lent and Wygodzinsky, 1979	VB	Lent and Wygodzinsky, 1979	USA; California
Reduviidae	Triatominae	*Triatoma recurva* (Stal)	AMNH_PBI 00218913	Mm	Lent and Wygodzinsky, 1979	VB	Lent and Wygodzinsky, 1979	Mexico; Sonora
Reduviidae	Triatominae	*Triatoma venosa* (Stal)	UCR_ENT 00052210	Mm	Lent and Wygodzinsky, 1979	VB	Lent and Wygodzinsky, 1979	Costa Rica; Alajuela
Reduviidae	Triatominae	*Triatoma* sp	UCR_ENT 00052202	Mm	Lent and Wygodzinsky, 1979	VB	Lent and Wygodzinsky, 1979	Ecuador; Sucumbios
Reduviidae	Tribelocephalinae	*Tribelocephala peyrierasi* Villiers	AMNH_PBI 00219033	LL	Miller, 1956	?		Madagascar; Mahajanga
Reduviidae	Tribelocephalinae	Tribelocephalinae sp	UCR_ENT 00052187	?		?		Brunei; Belait
Reduviidae	Vesciinae	*Mirambulus niger* Breddin	UCR_ENT 00052182	Ba	own obs	?		French Guiana; Regina
Reduviidae	Visayanocorinae	*Carayonia orientalis* Ishikawa and Okajima	UCR_ENT 00052232	Fo	Ishikawa & Okajima, 2004	?		Thailand; Nakhon Nayok
Reduviidae	Visayanocorinae	*Carayonia* n. sp.	UCR_ENT 00003627	Fo	Ishikawa & Okajima, 2004	?		Madagascar; Antsiranana

Table S1.3. Summary of individual gene region and combined sequence lengths of dataset based on different alignment algorithms.

Sequence alignment algorithms	Combined aligned length	16S	18S	28SD2	28SD3-D5	Wg
E-INS-i (MAFFT)	3793bp	634	1065	938	772	384
G-INS-i (MAFFT)	3796bp	631	1083	915	783	384
L-INS-i (MAFFT)	3822bp	636	1083	943	776	384
MUSCLE	3881bp	644	1081	959	813	384
Q-INS-i (MAFFT)	4043bp	654	1076	1082	847	384

Table S1.4. Table for bootstrap values of all subfamilies and Reduviinae clades based on different sequence alignment algorithms.

	RaxML	**TNT**	**RaxML**	**RaxML**	**RaxML**	**RaxML**
Other subfamilies	**GINSI**	**GINSI**	**EINSI**	**LINSI**	**MUSCLE**	**QINSI**
Hammacerinae	100	100	100	100	100	100
Holoptilinae	100	99	100	100	100	100
Phymatinae	100	100	100	100	100	100
Peiratinae	100	91	100	100	100	100
Saicinae	44	NA	74	NA	85	43
Visayanocorinae	100	99	100	100	100	100
Emesinae + Visayanocorinae + Saicinae	50	NA	55	NA	71	75
Ectrichodiinae	93	NA	100	98	92	95
Tribelocephalinae	100	97	100	100	100	100
Stenopodainae	100	98	100	100	100	99
Physoderinae	100	NA	100	100	100	100
Salyavatinae	100	100	100	100	100	100

Table S1.4. Table for bootstrap values of all subfamilies and Reduviinae clades based on different sequence alignment algorithms. (continued)

	RaxML	TNT	RaxML	RaxML	RaxML	RaxML
Reduviinae + others	**GINSI**	**GINSI**	**EINSI**	**LINSI**	**MUSCLE**	**QINSI**
Pasiropsis	65	93	83	86	47	85
Psophis	100	98	100	100	100	100
Nanokerala	100	100	100	100	100	100
Psophis + Nanokerala	59	NA	75	78	32	83
Zelurus	53	70	69	74	NA	77
Opisthacidius	100	100	100	100	100	100
Cavernicola + Rhodnius	80	98	80	77	80	81
Opisthacidius + Cavernicola + Rhodnius	67	NA	67	52	55	51
Triatomini	94	98	94	99	95	100
Triatomini + *Opisthacidius + Cavernicola + Rhodnius*	99	91	100	96	89	93
Zelurus + Opisthacidius + Triatominae	96	91	96	95	97	99
Leogorrus	99	99	100	99	99	100
Alloeocranum + Reduvius + Durevius	32	NA	32	28	30	19
Reduvius + Durevius	100	99	100	100	100	100
Gerbelius + Kayanocoris	100	99	100	100	100	100
Leogorrus + Reduvius + Alloeocranum + Durevius + Gerbelius + Kayanocoris	37	NA	38	36	38	41
Microlestria	100	100	100	100	100	100
Nalata	100	NA	100	100	100	100
Physoderes + Nalata	72	NA	80	91	50	NA
Physoderes + Nalata + Microlestria	78	NA	78	77	82	86
Pseudozelurus	100	100	100	100	100	100
Durganda + Tiarodes	100	100	100	100	100	100

Table S1.4. Table for bootstrap values of all subfamilies and Reduviinae clades based on different sequence alignment algorithms. (continued)

	RaxML	TNT	RaxML	RaxML	RaxML	RaxML
Reduviinae + others	**GINSI**	**GINSI**	**EINSI**	**LINSI**	**MUSCLE**	**QINSI**
Velitra + Dyakocoris + Tapeinus + Staliastes	100	94	100	100	99	99
Durganda + Tiarodes + Velitra + Dyakocoris + Tapeinus + Staliastes	60	NA	82	58	NA	98
Cethera	100	100	100	100	100	100
Eupheno	100	NA	100	100	100	100
Varus + Cethera	74	76	73	64	48	30
Noualhierana + Eupheno	56	NA	61	57	42	54
Censorinus + Durganda + Tiarodes + Velitra + Dyakocoris + Tapeinus + Staliastes	35	NA	NA	42	NA	NA

Table S1.4. Table for bootstrap values of all subfamilies and Reduviinae clades based on different sequence alignment algorithms. (continued)

	RaxML	TNT	RaxML	RaxML	RaxML	RaxML
Reduviinae + others	**GINSI**	**GINSI**	**EINSI**	**LINSI**	**MUSCLE**	**QINSI**
Pseudozelurus + Censorinus + Durganda + Tiarodes + Velitra + Dyakocoris + Tapeinus + Staliastes	43	NA	NA	48	40	NA
Platymeris + Acanthaspis + Plynoides + Paraplynus + Inara + Paredocla	50	NA	82	55	50	NA
Acanthaspis + Plynoides + Paraplynus + Inara + Paredocla	97	NA	92	96	66	95
Salyavatinae + Platymeris + Acanthaspis + Plynoides + Paraplynus + Inara + Paredocla	56	NA	68	28	61	21

Table S1.5. Fossil calibration table with fossil taxonomic information, locality, taphonomy, fossil age and age references.

Family	Subfamily	Genus	Species	Reference	Year	Locality	Taphonomy	Geologic Timescale	Age (Ma)	Age reference
Reduviidae	Emesinae	*Paleoploiariola*	*venosa*	Maldonado Capriles, Santiago-Blay & Poinar	1993a	Dominican	amber	late Early to early Middle Miocene	15-20	Iturralde-Vinent and MacPhee, 1996
Reduviidae	Harpactorinae	*Apicrenus*	*fossilis*	Maldonado Capriles, Santiago-Blay & Poinar	1993b	Dominican	amber	late Early to early Middle Miocene	15-20	Iturralde-Vinent and MacPhee, 1996
Reduviidae	Triatominae	*Triatoma*	*dominicana*	Poiner	2005	Dominican, La Toca Mine	amber	late Early to early Middle Miocene	15-20	Iturralde-Vinent and MacPhee, 1996
Reduviidae	Holoptilinae	*Praecoris*	*dominicana*	Poinar	1991b	Dominican, La Toca Mine	amber	late Early to early Middle Miocene	15-20	Iturralde-Vinent and MacPhee, 1996
Reduviidae	Phymatinae	*Koenigsbergia*	*herczeki*	Popov	2003	Baltic, Yantarnyi, Kaliningrad Region, Samland Peninsula, Russia	amber	Eocene	33.9-55.8	Perkovsky et al., 2007
Reduviidae	Emesinae	*Danzigia*	*christelae*	Popov	2003	Baltic, Yantarnyi, Kaliningrad Region, Samland Peninsula, Russia	amber	Eocene	33.9-55.8	Perkovsky et al., 2007
Reduviidae	Stenopodainae	*Stenopoda*	*oeningensis*	Heer	1861	Oeningen, Baden	compression	Tortonian Horizon	7.2-11.6	Heer, 1861; The Geological Society of America Geologic Time Scale
Reduviidae	Peiratinae	*Pirates*	*oeningensis*	Heer	1853	Oeningen, Baden	compression	Tortonian Horizon	7.2-11.6	Heer, 1853; The Geological Society of America Geologic Time Scale
Reduviidae	Harpactorinae	*Arilus*	*faujasi*	Riou	1998	Montagne d'Andance (Ardeche, France)	compression	Upper Miocene (Lower Turolian)	7.1-7.5	Pastre et al., 2004; Riou, 1998
Ceresopsidae (Reduvioidea)		*Ceresopsis*	*costalis*	Becker-Migdisova	1958	Sogyuty	compression	Early Jurassic	176-201.6	Shcherberkov 2008
Reduviidae				Shcherberkov	2008	unknown	compression	Early Cretaceous	99.6-145.5	Shcherberkov 2008

Table S1.6. Summary table of age estimates of selected reduviid clades with 95% highest probability density intervals.

	Age (Ma)	95% HPD
Reduviidae	178.31	[176, 184.98]
Higher Reduviidae-Phymatine Complex split	160.25	[137.19, 179.59]
Hammacerinae	141.75	[118.73, 167.61]
Phymatinae	113.69	[91.12, 140.1]
Centrocnemidinae-Holoptilinae split	89.5	[66.63, 115.4]
Peiratinae	96.85	[81.44, 112.74]
Tribelocephalinae + Ectrichodiinae	83.61	[72.87, 95.55]
Ectrichodiinae	67.47	[57.03, 79.65]
Zelurus + *Opisthacidius* + Triatominae	52.89	[41.64, 64.56]
Opisthacidius + Triatominae	37.41	[29.74, 45.34]
Triatomini	31.26	[24.23, 38.17]
Rhodniini + Cavernicolini	27.54	[21.05, 33.49]
Rhodniini	22.18	[15.26, 27.97]
Salyavatinae	41.62	[31.35, 56.7]
Acanthaspis	39.16	[29.8, 47.86]
Microlestria + *Physoderes* + *Nalata*	62.18	[53.43, 72.85]
Reduvius + *Alloeocranum* + *Durevius*	50.17	[36.93, 61.35]
Harpactorinae + *Neostachyogenys*	64.56	[54.6, 75.58]
Apiomerini	42.04	[31.09, 52.67]
Harpactorini	50.11	[40.05, 61.03]

Table S1.7. Distant's 1904 classification of Reduviinae (Acanthaspidinae) into six divisions.

Subfamily	Divisions	Genus
Reduviinae (Acanthaspidinae)	1. Psopharia	*Psophis*
		Euvonymus
	2. Epiroderaria	*Centrocnemis*
		Epirodera
		Marbodus
	3. Reduviaria	*Alloeocranum*
		Reduvius
		Gerbelius
	4. Acanthaspisaria	*Pasira*
		Pasiropsis
		Acanthaspis
		Inara
		Edocla
	5. Lenaearia	*Velitra*
		Lenaeus
		Paralenaeus
		Sminthocoris
		Apechtia
	6. Conorhinaria	*Durganda*
		Tiarodes
		Conorhinus
		Linshcosteus
		Cerilocus

Table S1.8. Proposed clade-membership of Reduviinae genera.

***Acanthaspis* clade**	
	***Acanthaspis* Amyot & Serville**
	***Inara* Stål**
	***Paraplynus* Schouteden**
	***Paredocla* Jeannel**
	***Platymeris* Laporte**
	***Plynoides* Schouteden**
	***Varus* Stål**
	Diplosiacanthia Breddin
	Edocla Stål
	Edoclella Miller
	Empyrocoris Miller
	Leptacanthaspis Jeannel
	Neotrichedocla Villiers
	Plynaspoides Miller
	Plynus Stål
	Psytalla Stål
	Raipurocoris Miller
	Stigmonotocoris Miller
	Tetroxia Amyot & Serville
	Trichedocla Jeannel
	Ukambocoris Miller
***Reduvius* clade**	
	***Alloeocranum* Reuter**
	***Durevius* Villiers**
	***Gerbelius* Distant**
	***Kayanocoris* Miller**
	***Leogorrus* Stål**
	***Reduvius* Fabricius**
	Cyclopocoris Miller
	Kobacoris Villiers
	Microvarus Jeannel
	Paragerbelius Miller
	Peregrinator Kirkaldy
	Perissopygocoris Miller
	Pseudoreduvius Villiers
	Stesiochorus Distant

Table S1.8. Proposed clade-membership of Reduviinae genera. (continued)

***Velitra* clade**	
	***Durganda* Amyot & Serville**
	***Dyakocoris* Miller**
	***Staliastes* Kirkaldy**
	***Tapeinus* Laporte**
	***Tiarodes* Burmeister**
	***Velitra* Stål**
	Durgandana Miller
	Lenaeus Stål
	Neotiarodes Miller
	Tiarodurganda Breddin
	Velitroides Miller
***Nalata* clade**	
	***Microlestria* Stål**
	***Nalata* Stål**
	***Physoderes* Westwood (Physoderinae)**
	Aradomorpha Champion
***Zelurus* clade**	
	***Opisthacidius* Berg**
	Triatominae
	***Zelurus* Burmeister**
	Gnistus Stål
	Holotrichius Burmeister
	Zeluroides Lent & Wygodzinsky
***Psophis* clade**	
	***Nanokerala* Wygodzinsky & Lent**
	***Psophis* Stål**
	Hadrokerala Wygodzinsky & Lent
	Namapa Wygodzinsky & Lent

Table S1.8. Proposed clade-membership of Reduviinae genera. (continued)

***Pasiropsis* clade**	
	***Pasira* Stål**
	***Pasiropsis* Reuter**
	Haplonotocoris Miller
	Jacobsonocoris Miller
	Nannolestes Bergroth
***Neostachyogenys* clade**	
	***Neostachyogenys* Miller**
	Marbodus Distant
Pseudozelurus	
	***Pseudozelurus* Lent & Wygodzinsky**
Noualhierana	
	***Noualhierana* Miller**
	Australocleptes Miller
	Dilophocoris Miller
	Horcinia Stål
	Sphedanocoris Stål
	Sphedanovarus Jeannel
	Tympanistocoris Miller
Censorinus	
	***Censorinus* Distant**
	Centrogonus Bergroth
	Neocentrogonus Miller

Table S1.8. Proposed clade-membership of Reduviinae genera. (continued)

Incertae sedis	
	Anacerilocus Miller
	Apechtia Reuter
	Apechtiella Miller
	Apteroreduvius Villiers
	Archilestidium Breddin
	Bergrotheus Schouteden
	Brachytonus China
	Cargasdama Villiers
	Cerilocus Stål
	Cheronea Stål
	Cheronella Miller
	Corupaia Lent & Wygodzinsky
	Crociaeus Breddin
	Croscius Stål
	Drescherocoris Miller
	Ectmetacanthspis Reuter
	Edoclina Jeannel
	Eriopreda Jeannel
	Eriopredoides Miller
	Euvonymys Distant
	Ganesocoris Miller
	Hermilloides Schouteden
	Hermillus Stål
	Heteropinus Breddin
	Hoberlandtia Villiers
	Horciniella Miller
	Iphithereuta Breddin
	Isdegardes Distant
	Junghuhnidia Breddin
	Kalshovenia Miller
	Khafra Distant
	Khafrana Miller
	Kopsteinia Miller
	Korinchocoris Miller
	Lamabokeus Villiers
	Lydenburgia Miller

Table S1.8. Proposed clade-membership of Reduviinae genera. (continued)

Incertae sedis	
	Mankuninga Distant
	Mardania Stål
	Moramanga Villiers
	Neervoortia Miller
	Neivacoris Lent & Wygodzinsky
	Neocerilocus Miller
	Neocheronea Miller
	Neokhafra Miller
	Nyplus Villiers
	Pantopsilus Berg
	Paracerilocus Miller
	Parahermillus Miller
	Paralenaeus Reuter
	Parapechtia Miller
	Patago Bergroth
	Pelurgocoris Miller
	Phaurolestes Bergroth
	Pheletocoris Miller
	Phonergates Stål
	Phyja Distant
	Platymicrus Bergroth
	Poecilopterocoris Miller
	Recicolus Jeannel
	Schoutedenana Miller
	Schultheissidia Breddin
	Stachyogenys Stål
	Timotheus Distant
	Voconia Stål

Footnote: genera in bold font represent genera included in present study, genera in regular font are genera absent here.

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Chapter 2: Infection Rates of *Triatoma protracta* (Uhler) with *Trypanosoma cruzi* (Chagas) in Southern California and Molecular Identification of Trypanosomes

Abstract

We report *Trypanosoma cruzi* infection rates of the native kissing bug *Triatoma protracta* in Southern California. The rates fall within the historically reported range, but differ significantly between the two sites (19% in Escondido [Es] and 36% in Glendora [Gl]). Identification of *T. cruzi* in *T. protracta* was conducted for the first time using partial 18S rRNA and 24Sα rRNA sequences. Incongruence of 24Sα rRNA phylogeny with current *T. cruzi* genotype classification supports non-clonality of some *T. cruzi* genotypes.

Introduction

Chagas disease is caused by the protozoan parasite *Trypanosoma cruzi* (Chagas) transmitted by Triatominae or kissing bugs (Insecta: Hemiptera: Reduviidae). An estimated 9.8 million people are infected with this disease and 40 million are at risk in Latin America (Schofield et al., 2006). Transmission, even though apparently rare, also occurs in the Southwestern US as indicated by 6 autochthonous transmission cases since 1955 including one in California. Surveillance of *T. cruzi* infection rates among local populations of Triatominae is therefore critical for assessing the public health risk.

Several species of Triatominae are native to the United States, with *Triatoma protracta* (Uhler) being the most common of the three endemic species in California. *Triatoma protracta* is widespread in California and host specific to woodrats (*Neotoma* spp.), which nest in middens found in a wide range of natural habitats. Human bites by *T. protracta* in houses occur when *T. protracta* is attracted to lights on warm evenings (Ryckman, 1981). The low incidence of autochthonous *T. cruzi* transmission may be explained by the transmission inefficacy of endemic kissing bugs, especially *T. protracta* (Klotz et al., 2009), but also by limited contact of humans with the vectors, or low infection rates of kissing bugs with *T. cruzi*. Autochthonous transmissions in Southwestern US are rare even though studies based on blood-bank screenings and serosurveys hints of undiagnosed cases (Navin et al., 1985; Bern et al., 2008). Such cases remains unverified but points to the need of constant monitoring. A recent study in Arizona showed that a much higher infection rate was found in *Triatoma rubida* (Uhler) compared with historical surveys, suggesting temporal variability with regards to infection rates (Reisenman et al., 2010).

Large-scale surveys of *T. cruzi* infection rates of local *T. protracta* populations in California have not been conducted since the 1980s. To test for the potential of autochthonous Chagas transmission in Southern California, we measured infection rates with *T. cruzi* among two populations of *T. protracta* bordering the large population centers of Los Angeles and San Diego.

We additionally developed a PCR-based method primarily for identification of *T. cruzi* but also to genotype *T. cruzi* in Triatominae. Several genotypes (also referred to as natural clones or major lineages) of *T. cruzi* are associated with different host lineages. In the US, the genotypes TcI and TcIV occur exclusively in marsupials (opossums) and placental mammals (e.g. raccoons), respectively (Roellig et al., 2008). Different genotypes are also known to result in differences in clinical manifestations of the disease (Llewellyn et al., 2009). Genotyping of trypanosome isolates is therefore an important endeavor and we here follow the latest *T. cruzi* genotype nomenclature (Zingales et al., 2009).

Materials and Methods

Specimens were collected using light traps (UV and MV) in Escondido (Es; San Diego Co., 33°12' 44.9994"N 117° 5' 36.9954"W, 405 m) and Glendora (Gl; Los Angeles Co., 34° 9' 59.364" N 117° 50' 18.204" W, 391 m). The sites are located at (Es) or less than 1 km (Gl) from a suburban residence. A total of 161 specimens (Es:139, Gl: 22) were collected during 8 weeks (Jun--Sep 2008). All specimens were identified as *T. protracta*, databased (collecting and dissection data), and are vouchered in the Entomology Research Museum at UC Riverside. Abdominal contents of live specimens were examined following protocols by Westenberger et al. (2004). The microscopy examination served as the basis for determining the infection rates. The average infection rate of *T. protracta* with *T. cruzi* was found to be 21.1% with significant difference between the two populations (Gl: 36.4%; Es: 18.7%) (Table 2.1).

We used a rapid method to identify *T. cruzi* based on amplification and sequencing of partial 18S and 24Sα ribosomal genes (Souto & Zingales, 1993). Instead of identifying the trypanosomes only on the basis of size polymorphisms of the amplicons, we sequenced the PCR products and phylogenetically analyzed the sequences. DNA was extracted using the QIAGEN DNeasy Blood & Tissue Kit. PCR settings followed those of Souto et al. (1996). PCR amplification using the primer pairs Tcz18Sf: (5'-TTAACGGGAATATCCTCAGC, designed in the course of this work) and TczS829r (Maslov et al., 1996) yielded 440 bp of the 18S rRNA. The primers Tcz24S-D71 and Tcz24S-D72 (Souto et al., 1996) were used to amplify a 110bp fragment of the 24Sα rRNA gene.

Results

Twenty 18S DNA sequences and two 24Sα DNA sequences were analyzed. These sequences were aligned with sequences from GenBank™ (see figure legends) using MAFFT (GINSI default setting) (Katoh et al., 2005). With each set of sequences all phylogenetic approaches used (parsimony, maximum likelihood [ML], Bayesian) identified the parasites from both localities as *T. cruzi* (Figs. 2.1 and 2.2 represent the Bayesian and ML analyses, respectively; trees generated by other methods not shown). The 18S rRNA gene fragment was too conserved to differentiate between *T. cruzi* genotypes (Fig. 2.1), with only seven Single Nucleotide Polymorphisms (SNPs) out of 427 positions (1.64% variability). The 24Sα fragment proved to be more informative for genotyping (63 polymorphisms out of 103 positions, 61.17% variable). The 24Sα gene phylogeny (Fig. 2.2) places the Southern Californian isolates in a clade that comprises members of the TcII and TcVI genotypes, although the relationships within this clade are not resolved.

Discussion

Our study presents an updated report of infection rates of two *T. protracta* populations with *T. cruzi* in Southern California and provides the first molecular identification of *T. cruzi* in this region. Infection rates differ significantly between the two populations, but overall are comparable with historical data. Previous studies of infection rates in California were predominantly conducted by Sherwin F. Wood (1930s--1960s) and ranged typically between 20-30% (Wood, 1975). A recent study of infection rates of *T. protracta* from Escondido (Southern California) was based on only 20 specimens, four (20%) of which tested positive by PCR detection (Klotz et al., 2009). Our study, based on a larger sample size, shows virtually identical prevalence for Escondido (19%), but a much higher infection rate in the Glendora population (36%) indicating that infection levels of *T. protracta* may show significant geographic variation.

All phylogenetic analyses of the 24Sα dataset found the isolates from California to be closely related to the TcII and TcVI group members. This result was unexpected, since neither one of these groups has been previously reported from North America. In addition, none of the TcII, TcIV, TcV and TcVI groups is recovered as monophyletic in our study (Fig. 2.2), indicating that the current classification may not fully reflect relationships of the *T. cruzi* genotypes. Our results lend support to the prevailing view that different *T. cruzi* genotypes may not be strictly clonal especially with the recognition that several genotypes are actually hybrids (Fig. 2.2) or suspected to be hybrids (Zingales et al., 2009). Further investigations are needed to establish the relationships of the Southern California *T. cruzi* with the remaining major lineages of this species. We recommend the use of identification techniques using DNA sequences for the added advantage of providing nucleotide information that is valuable for documenting genetic variation within *T. cruzi* from different geographic regions.

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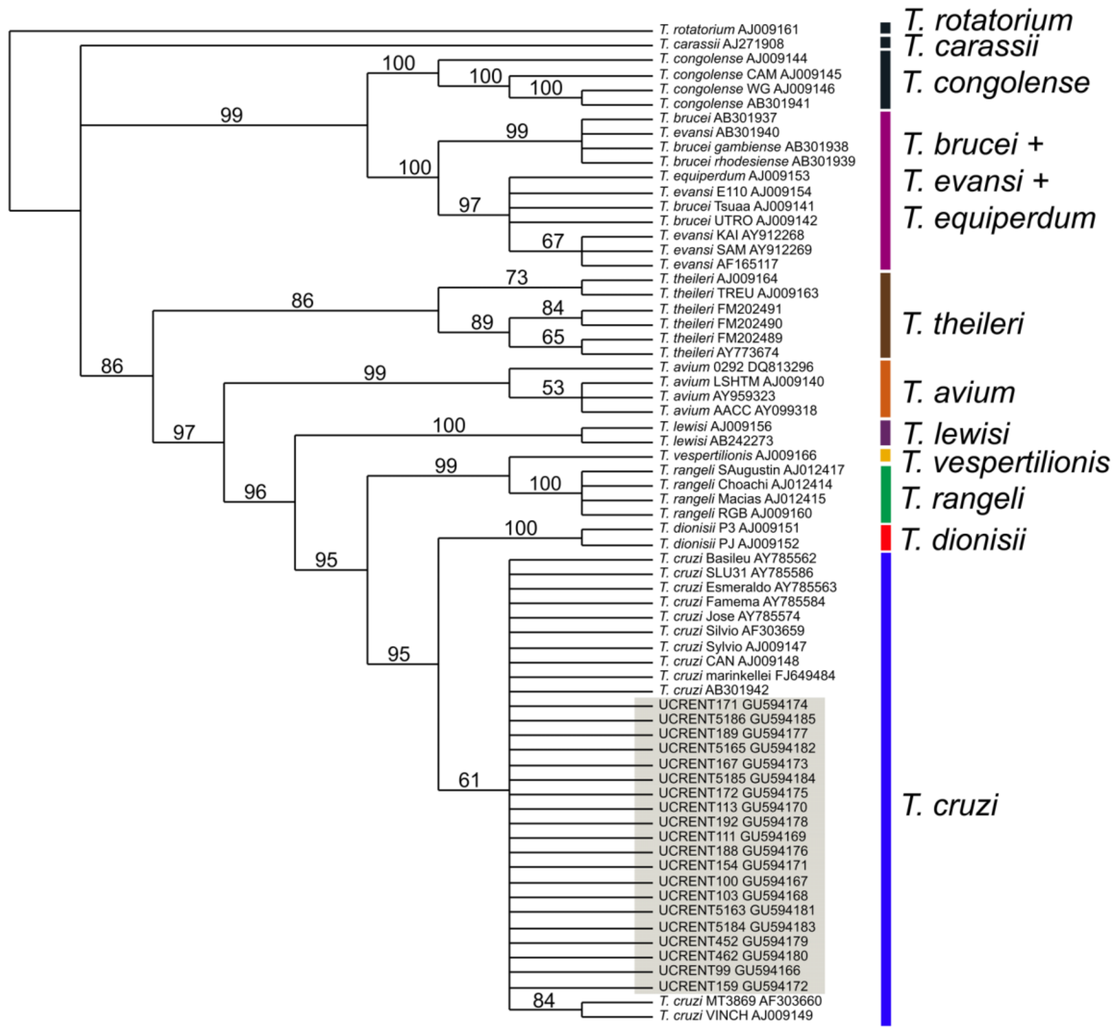

Figure 2.1. Bayesian 50% majority-rule consensus phylogeny of *Trypanosoma cruzi* based on partial 18S rRNA sequences. A total of 20 sequences (GenBank™ accession numbers GU594166--59416685) were obtained in this project. The remaining sequences were retrieved from GenBank™ with accession numbers listed. Numbers above branches indicate posterior probabilities. The analysis was performed using MrBayes (CIPRES portal) with GTR+I+Γ model parameters. A total of 2 million generations were conducted with temperature settings at 0.2. A sampling frequency of 1000 and a burn-in at 25% of the sampled trees were set for final tree production.

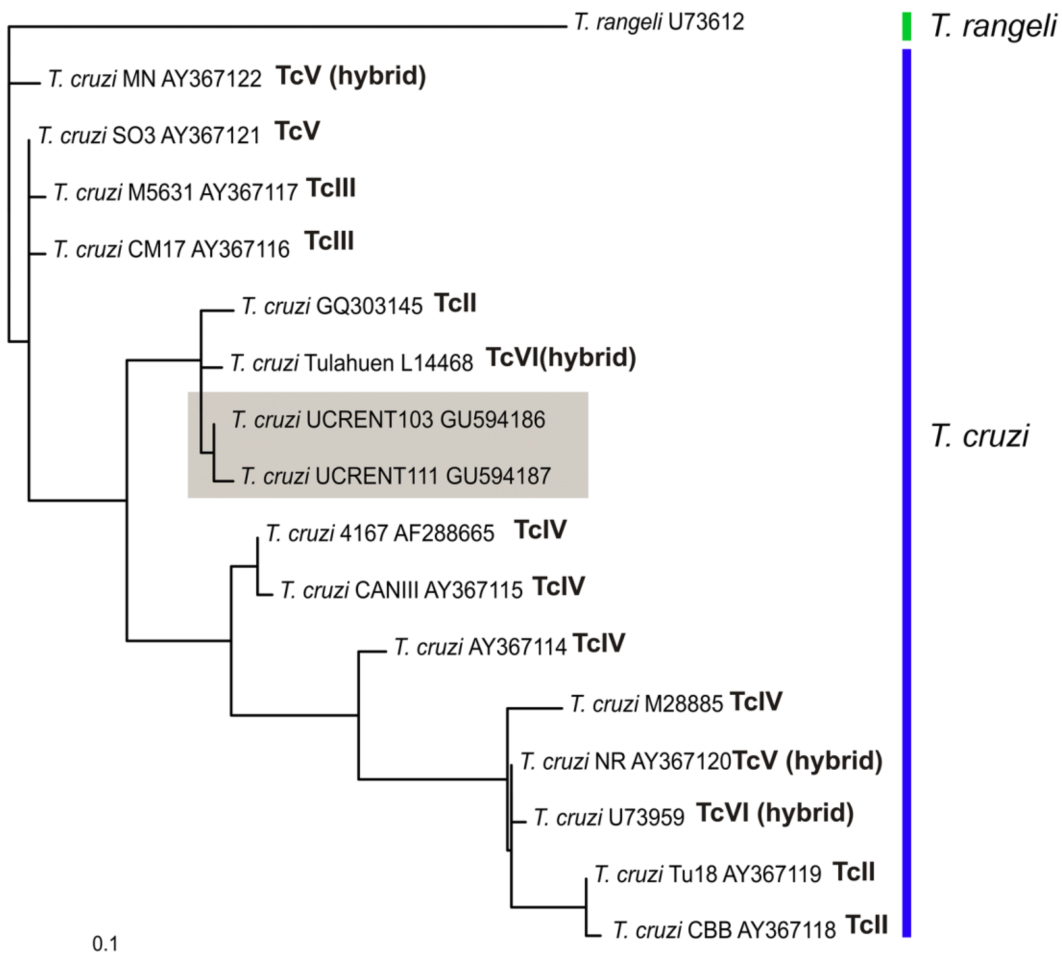

Figure 2.2. 24Sα rRNA phylogram of *Trypanosoma cruzi* generated by RaxML (CIPRES portal) using GTR+I+Γ model parameters (default settings). Abbreviations of current *T. cruzi* genotype classification listed to the right with known hybrids noted. Two sequences were generated in this study (GenBank™ accession numbers GU594186 and GU594187). The remaining 15 sequences were retrieved from GenBank™.

Table 2.1. Infection rates of *T. protracta*

	Glendora	Escondido	p-value
Total number of *T. protracta*	22	139	
T. cruzi infected	8 (36.4%)*	26 (18.7%)	0.000911

*Significantly different with respect to the mean at the 5% level Chi-square test.

Chapter 3 Revision of the Malagasy *Durevius* Villiers with descriptions of two new species (Hemiptera: Reduviidae: Reduviinae)

Abstract

The small genus *Durevius* Villiers, 1962 (Reduviinae) is redescribed and two species are described as new, thus recognizing five species in the genus. *Durevius* is endemic to Madagascar with species found in the inland plateau and coastal lowland regions. Diagnoses for the genus and all species are developed and an identification key, habitus images, and a distribution map are provided.

Introduction

Durevius Villiers, 1962 is a small genus of relatively large and stout-bodied Reduviinae (Hemiptera: Reduviidae) and currently comprises three described species endemic to Madagascar. Villiers (1962) established this genus based on the presence of a pair of small tubercles posteriorly on the posterior pronotal lobe that distinguishes it from the highly speciose genus *Reduvius* Fabricius, 1775 and other reduviine genera occurring in Madagascar. *Reduvius* is a largely Afrotropical and Palaearctic genus with a few species in the Oriental Region and the New World, and altogether containing 197 described species (Maldonado, 1990). Two of the species now treated as being part of the genus *Durevius*, *D. tuberculatus* (Villiers, 1950) and *D. usingeri* (Villiers, 1960), were originally described in *Reduvius*. They were transferred to the new genus *Durevius* upon the description of the third species, *D. piceus* Villiers, 1962. No additional species have been added to *Durevius* since the genus was established. With only 7 genera (27 spp.) recorded from Madagascar, the fauna of Reduviinae on the island is relatively small compared to other subfamily-level groups such as Stenopodainae (76 spp.) and Harpactorinae (77 spp.) (Villiers, 1968; Maldonado, 1990). Most Malagasy Reduviinae were described by Villiers in a series of papers (Villiers 1950, 1962, 1968). Apart from the monotypic genera *Cargadasma*

Villiers, 1950 and *Moramanga* Villiers, 1962, the reduviine fauna of Madagascar comprises the more speciose genera *Censorinus* Distant, 1903, *Hoberlandtia* Villiers, 1950, *Sphedanovarus* Jeannel, 1919 and *Peregrinator* Kirkaldy, 1904. All except *Sphedanovarus* and *Peregrinator* are endemic to Madagascar. *Reduvius* is apparently absent from Madagascar.

Villiers' genus and species descriptions are often brief and lack detailed illustrations, proper diagnoses, and descriptions of male and female genitalia. The description of the genus *Durevius* is identical to the species description of *D. tuberculatus*, even though Villiers had previously included the other two new species in the genus. Intrageneric variation was thus not reflected in his description of the genus. No illustrations were included except for a single dorsal habitus image of *D. tuberculatus.*

A recent island-wide inventory of terrestrial arthropods of Madagascar by the California Academy of Sciences (CAS) yielded more than 3,000 reduviid specimens. This material, together with specimens assembled and studied by Villiers at the Muséum national d'Histoire naturelle Paris, France (MNHN), provide an excellent opportunity to document the reduviid diversity on this island. Several specimens of *Durevius* were present in the CAS material, amongst them specimens representing two new species. We here describe the two new species, redescribe the genus *Durevius* as well as 2 of the described species, and provide habitus images, a key, and distribution maps for all species.

Materials and Methods

Specimens

Eleven previously unidentified specimens and one holotype (*D. usingeri*) from CAS were examined. Type specimens deposited at the Muséum national d'Histoire naturelle (MNHN) could not be physically examined. Instead, Dr. Eric Guilbert (MNHN) supplied us with habitus images of the holotypes of *D. tuberculatus* and *D. piceus*. Six of the CAS specimens were identified as *D. tuberculatus* and were used together with the type image for the redescription of the species. Specimens of *D. piceus* were unavailable for direct study and thus a full redescription of this species is omitted. *Durevius piceus* is very distinct from any other species in the genus (i.e. the only mostly dark-colored species) and it clearly possesses the diagnostic characters of the genus. Hence, *D. piceus* is included in the redescription of the genus and the identification key. Four of the CAS specimens were identified as *D. galbeum* **sp.n.** and a singleton as *D. cacao* **sp.n.**

Specimen locality database

All specimens examined were databased using the online specimen locality database developed by the Planetary Biodiversity Inventory on Plant Bugs (PBI) [http://research.amnh.org/pbi/databases/locality_database.html]. Each specimen was associated with a unique specimen identifier (USI) label consisting of a unique specimen identification number and the prefix "UCR_ENT". The specimen depository is shown on the label as "CAS".

Distribution map

A distribution map of the examined specimens and holotypes was generated using DIVA-GIS [http://www.diva-gis.org/] (Fig. 3.42). Specimen localities were either based on GPS coordinates on the locality labels or estimated using Google Earth for those specimens that were not examined physically and where records are based on literature data (i.e. holotype of *D. usingeri*). Estimated GPS data are denoted by parentheses (e.g. [15.73333°S 49.83333°E, -30 m]).

Morphological methods

Specimens were examined using a stereomicroscope (Nikon SMZ1500). Habitus images, foreleg, scutellar spine and pygophore images were produced using a Microptics-USA imaging system with a Canon EOS 1D camera. Images are either single exposures or combined from raw images using the Helicon Focus version 4.16 software. Male genitalia were dissected after being heated in 10% potassium hydroxide (KOH) solution for 5 – 10 minutes, neutralized in water and transferred into 99% glycerol on a ceramic spot plate. The endosoma remains contracted for all specimens examined. The pygophores, parameres and phallus were dissected and mounted in a glycerin-gelatin mixture for imaging with an Auto-montage GT-Vision imaging system. Dissected body parts were stored in glycerol in a genitalic vial and associated with the specimen. Forelegs, pronotum, hemelytron, pygophores, parameres and phallus were illustrated using a camera lucida mounted on the stereomicroscope. All images and illustrations were edited and compiled into plates using Adobe Photoshop CS3 version 10.0.

Measurements were made using a mounted micrometer in the stereomicroscope calibrated with a micrometer.

Terminology

We adopt the term humeral angles to refer to the postero-lateral protrusions of the posterior pronotal lobe (Fig. 3.22a). This is to avoid confusion with the tubercles projecting from the posterior base of the posterior pronotal lobe, which we refer to as posterior tubercles (Fig. 3.22b). We propose the new term “median furrow protuberances” to refer to a pair of small protuberances extending into the median furrow at the base of the anterior pronotal lobe (Fig. 3.22c). The ponticulus basilaris refers to the basal plate bridge of the male genitalia (Figs 3.30b, 3.31b, 3.32b).

Results

Durevius Villiers, 1962

(Figs 3.1–3.42, Table 3.1)

Type species: *Reduvius tuberculatus* Villiers, 1950, 22:734 (by original designation)

Durevius Villiers, 1962: 242 [n. gen.]

Maldonado 1990: 396 [Systematic Catalogue of the Reduviidae of the World]

Diagnosis: Recognized by the presence of posterior tubercles (Fig. 3.22b), the brown and stramineous swirls on the anterior pronotal lobe (Figs 3.1-5, 3.22), a large brown spot subapically on the corium at mid-length of hemelytron in most species (Figs 3.1, 3.2, 3.4, 3.5, except in *D. piceus* Fig. 3.3), and a pair of median furrow protuberances (Fig. 3.22c). Resembles most closely *Reduvius* Fabricius among Reduviinae, but distinguished by the presence of the pair of posterior tubercles (Fig. 3.22b). Endemic to Madagascar. Differentiated from other Malagasy Reduviinae by the smaller size compared to *Hoberlandtia* and *Censorinus*, but distinctly larger size than *Sphedanovarus* and *Peregrinator*. *Durevius* is further distinguished from other Malagasy Reduviinae by the lack of lateral spines on the anterior pronotal lobe (Fig. 3.22), more slender labial segments, more prominent anterior pronotal lobe (versus *Censorinus*); coloration pattern, pronounced median furrow of anterior pronotal lobe (Figs 3.1–5, 3.22); presence of sculptured anterior pronotal lobe (Fig. 3.22) (versus *Hoberlandtia*); shape of head, lack of tubercles on head and pronotum, fore femora not exceptionally incrassate (versus *Sphedanovarus*); shape of head and narrow interocular distance (versus *Peregrinator*).

Redescription: ♂: (Figs 3.1–3.41, Table 3.1): Total length: 14.08-16.86mm. Coloration: Head: brown suffused with stramineous or completely dark brown. Labium: first visible labial segment stramineous to light brown or uniformly dark brown; second and third segments mostly brown to light brown. Antenna: ranging from uniformly stramineous to uniformly dark brown, intermediates with variable degrees of dark brown suffusion. Thorax: anterior pronotal lobe light to dark brown with stramineous or dark orange swirls; posterior pronotal lobe stramineous to dark orange with brown markings. Scutellum entirely dark brown or brown and stramineous. Hemelytron off-white with light brown suffusion and spot, stramineous with brown suffusion and spot, or uniformly dark brown. Legs: coxae stramineous to dark brown; trochanters stramineous to brown; femora stramineous with variable number of brown transverse bands, or completely dark brown; tibiae uniformly stramineous, stramineous with apex slightly darkened, or uniformly dark brown; tarsi uniformly stramineous or dark brown. Abdomen: tergites uniformly stramineous, light brown or dark brown; dorsal laterotergites with alternating stramineous and dark brown bands or uniformly dark brown; sternites uniformly dark brown or stramineous with lateral dark brown suffusion. Vestiture: Almost entire body covered with medium-length setae. Setae along costal margin of hemelytron denser and much shorter. Setae on corium restricted to single rows of setae along veins; setation on abdominal tergites limited to short, fine setae; fore leg with trochanter to tibia ventrally lined with denser cover of setae. Apical portion of tibiae with dense short, stout setae. Structure: Head: longer than wide with a short neck, separated into two lobes by a shallow transverse furrow posterior to eyes; eyes large and reniform. Ocelli large and raised on a median tubercle. Median longitudinal furrow between eyes sometimes present.

Antenna: antennal insertion anterior to eyes, subdorsal. Scapus long and slender (1.66-2.31mm); pedicellus longer and more slender than scapus (2.62-3.16mm); basiflagellomere about as long as pedicellus (2.5-3.1mm); distiflagellomere almost as long as basiflagellomere (2.21-2.60mm). Labial segments stout; first visible labial segment curved, second segment straight, third segment short (0.30-0.42mm). Thorax: collar with a pair of antero-lateral tubercles; stridulitrium diamond-shaped; anterior pronotal lobe divided by median longitudinal furrow; paired median furrow protuberances present; anterior pronotal lobe prominently sculptured; setation only along stramineous regions, dark regions tuberculated; posterior pronotal lobe trapezoidal, rugose; humeral angle with rounded or conical tubercle; posterior tubercles slight or prominent; scutellum triangular, broad and rugose with a median depression; scutellar spine erect or suberect (Figs 3.18-3.21); mesosternum with median longitudinal ridge perpendicular, connected to anterior and posterior transverse ridges. Legs: long and slender; fore coxa elongate and stout; fore femur slightly incrassate; mid and hind femora slender and elongate; fossula spongiosa present on fore and mid tibiae; fossula spongiosa on mid leg (0.47-0.99mm) shorter than on foreleg (0.78-1.29mm); tibiae slender and elongate; fore tibial comb present; legs with three tarsal segments; fore and mid legs with first tarsomere much shorter than remaining segments, hind leg with longer first (0.3-0.70mm) and second (0.58-0.74mm) tarsomeres; claws simple; parempodia setiform. Wings: hemelytron extending beyond abdomen in males; hemelyton venation provided (Fig. 3.25). Abdomen: elongate ovate, second visible sternite with thickened and raised margins. Male genitalia: pygophore rounded and prominent, median process of pygophore rectangular or bifurcated to varying degrees, relatively short, only slightly exceeding beyond dorsal rim of pygophore; apex of paramere broad or tapering, curvature of apex acute to smooth, setation on apex stout and erect, setae long to medium-length, stout setae in sub-apical to medial position along ‘inner’ margin (Fig. 3.26). Aedeagus: endosomal struts spear-shaped apically, with variable width (Figs 3.30a, 3.31a, 3.32a) and tubular to conical basally (Figs 3.33a, 3.34a, 3.35a); dorsal phallothecal sclerite obsolete to well-sclerotized (Figs 3.30, 3.31, 3.32); well-sclerotized basal plate extension as wide as or narrower than phallotheca (Figs 3.33b, 3.34b, 3.35b); apex of basal plate extension round and smooth or rectangular with distinct angles (Figs 3.33b, 3.34b, 3.35b); curvature of basal plate extension in lateral view variable from smoothly rounded to more angular (Figs 3.39, 3.40, 3.41); shape of basal plates and ponticulus basilaris variable, basal plates slender and diverging (Fig. 3.30) or thick and adjacent (Fig. 3.31); ponticulus basilaris well-defined (Figs 3.30b, 3.32b) or almost inconspicuously short and broad (Fig. 3.31b).

♀: Total length: 14.36-17.54mm. Morphologically similar to males, sometimes slightly larger (see Table 3.1) and darker than males. For specific female descriptions refer to descriptions of *D. galbeum*, *D. tuberculatus* and *D. usingeri*.

Key to species

1. Body and hemelytron uniformly dark brown, pronotum dark orange (Fig. 3.3) .... *D. piceus*

-- Entire body with stramineous and brown patterns, including pronotum and hemelytron (Figs 3.1, 3.2, 3.4, 3.5) ....2.

2. Hemelytron off-white with light brown spot (Fig. 3.2), with single brown band on femora (Fig. 3.15) .... *D. galbeum* **sp.n.**

-- Hemelytron stramineous with prominent brown spot (Figs 3.1, 3.4, 3.5), with 2 or 3 brown bands on femora (Figs 3.14, 3.16, 3.17) ....3.

3. Scutellum including scutellar spine dark brown (Fig. 3.18) .... *D. cacao* **sp.n.**

-- Scutellum including scutellar spine in part pale (Figs 3.19, 3.20, 3.21) ....4.

4. Humeral angles pronounced and sub-conical (Fig. 3.5), scapus brown, stramineous apically, head and labial segments almost uniformly brown, coxae brown (Figs 3.5, 3.9, 3.13) ...... *D. usingeri*

-- Humeral tubercles less pronounced and rounded (Fig. 3.4), scapus brown suffused with stramineous coloration or stramineous, head brown suffused with stramineous coloration, fore coxa brown with stramineous apex, mid and hind coxae stramineous with variable brown suffusion (Figs 3.4, 3.8, 3.12) .... *D. tuberculatus*

Durevius cacao **sp.n.**

(Figs 3.1, 3.6, 3.10, 3.14, 3.18, 3.27, 3.30, 3.33, 3.36, 3.39, 3.42, Table 3.1)

Holotype: ♂: MADAGASCAR: Toliara: Manombo, 22.81222°S 43.73944°E, 165 m, 20-25 May 2004, Frontier Wilderness Project, (UCR_ENT 00005354) (CAS).

Diagnosis: Recognized by the combination of three dark brown bands on the fore-femora (Fig. 3.14), dark brown scapus with stramineous apex (Figs 3.1, 3.6, 3.10), scutellum completely dark brown, scutellar spine erect (Fig. 3.18) and relatively short (0.51mm) (Table 3.1). Fossula spongiosa on fore femur (1.29 mm) long relative to femur length (3.29 mm) (Fig. 3.24, Table 3.1). Median process of pygophore with a narrow stalked base and a wide bifurcated apex (Figs 3.27, 3.36), the ponticulus basilaris is a well-defined arch adjoining two slender and diverging basal plate struts to form a subtriangular basal foramen (Fig. 3.30b). Most similar to *D. tuberculatus* but can be distinguished from this species by the above characters.

Description: ♂: Total length: 14.4mm. Coloration: Head (Figs 3.1, 3.6, 3.10): almost entirely dark brown except gular region stramineous. Labium: first visible labial segment stramineous, second labial segment stramineous suffused with brown on ventral region, third segment light brown, Antenna: antenniferous tubercles light brown; scapus dark brown, stramineous apically; pedicellus stramineous, apically and basally brown; basiflagellomere stramineous, brown basally; distiflagellomere stramineous. Thorax (Figs 3.1, 3.6, 3.10, 3.18, 3.24) as in *D. tuberculatus* (Fig. 3.22): anterior pronotal lobe dark brown with stramineous swirls; posterior pronotal lobe stramineous with brown markings; scutellum entirely dark brown; hemelytron stramineous with brown patterns. Legs (Fig. 3.14): femora stramineous with three brown transverse bands; tibiae stramineous with brown darkening apically and sub-basally; pretarsi stramineous. Abdomen (Figs 3.1, 3.6, 3.10): sternites brown; dorsal laterotergites with alternating stramineous and dark brown bands; sternites with diffusion from stramineous to dark brown from median to lateral sides. Vestiture: as in generic description. Structure: head, eye, antenna and labium: as in generic description. Thorax: as in generic description; humeral angle with rounded tubercles; scutellar spine relatively short (0.51mm) (Table 3.1), erect (Fig. 3.18); legs, wings, and abdomen as in generic description. Male Genitalia: as in generic description; paramere apically broad as in *D. tuberculatus* (Fig. 3.26), setae of medium length; curvature of apex of paramere acute; median process of pygophore with narrow stalked base and a wide bifurcated apex (Figs 3.27, 3.36). Aedeagus: endosomal struts narrowly spear-shaped apically (Fig. 3.30a), dorsal phallothecal sclerite visibly covering entire dorsal surface (Fig. 3.30); well-sclerotized basal plate extension narrower than phallotheca (Fig. 3.33b); apex of basal plate extension round and smooth (Fig. 3.33b); basal endosomal struts tubular (Fig. 3.33a); curvature of basal plate extension more abrupt (Fig. 3.39); ponticulus basilaris well-defined arch adjoining two slender and diverging basal plate struts to form a triangular basal foramen (Fig. 3.30b). ♀: unknown.

Distribution: Only known from the type locality. According to label information, the locality is in the southern coastal area of Madagascar at low elevation (165m) in gallery forest.

Etymology: The name “cacao” refers to the general dark brown coloration patterns especially on the scutellum and scapus of the species.

Notes: The specimen studied is easily distinguished from all other *Durevius* species. The specimen was collected using a malaise trap in gallery forest. Three *D. galbeum* specimens were collected relatively nearby, but closer to the coast and in a different habitat (spiny bush thicket) (Fig. 3.42), suggesting that their distributions may overlap but that each species might inhabit a different habitat.

Durevius galbeum **sp.n.**

(Figs 3.2, 3.7, 3.11, 3.15, 3.19, 3.28, 3.31, 3.34, 3.37, 3.40, Table 3.1)

Holotype: ♂: MADAGASCAR: Toliara: Cap Ste Marie Special Reserve, 74km S of Tsihombe, 25.58766°S 45.163°E, 37 m, 20-31 Aug 2003, M. Irwin, F. Parker, Ra. Harin'Hala, (UCR_ENT 00005352) (CAS)

Diagnosis: Recognized by the overall pale coloration compared to other species in the genus, especially the off-white hemelytron and less prominent brown spot (Figs 3.2, 3.7, 3.11), the stramineous antenna (Figs 3.2, 3.7, 3.11), the more pronounced and anteriorly bifurcated mandibular plates, the single brown band on the femora (Fig. 3.15), and the shorter fore leg fossula spongiosa (0.76-0.87mm).

Description: ♂: Total length: 15.83-16.86mm. Coloration: Head (Figs 3.2, 3.7, 3.11): brown suffused with stramineous regions at the mandibular plates, postocular region, neck, gena and labrum. Labium: first visible labial segment stramineous, second labial segment brown gradation to light brown, third segment light brown, Antenna: antenniferous tubercles light brown to stramineous; scapus, pedicellus, basiflagellomere and distiflagellomere stramineous. Thorax (Figs 3.2, 3.7, 3.11, 3.19): anterior pronotal lobe dark brown with stramineous swirls; posterior pronotal lobe stramineous with brown markings; scutellum brown with stramineous ridges laterally; hemelytron off-white with faint brown spot and patterns. Legs: coxae and trochanters stramineous with brown suffusion; femora stramineous with single brown transverse bands (Figs 3.2, 3.7, 3.11, 3.15); tibiae and tarsi stramineous. Abdomen (Figs 3.2, 3.7, 3.11): tergites brown; dorsal laterotergites with alternating stramineous and dark brown bands; sternites with diffusion from stramineous to dark brown from median to lateral sides. Vestiture: as in generic description. Structure: Head and eyes: as in generic description; median longitudinal furrow between eyes absent. Antenna and labium: as in generic description. Thorax as in generic description; humeral angle with slight protrusion; scutellar spine relatively short (0.50-0.63mm) (Table 3.1), suberect (Fig. 3.19). Legs, wings, and abdomen: as in generic description. Male genitalia: as in generic description; paramere apically broad as in *D. tuberculatus* (Fig. 3.26), setae of medium length; curvature of apex of paramere acute; median process of pygophore with narrow stalked base and a narrow bifurcated apex (Figs 3.28, 3.37). Aedeagus: endosomal struts broadly spear-shaped apically (Fig. 3.31a), conical basally (Fig. 3.34a); dorsal phallothecal sclerite visible as a transverse sclerite (Fig. 3.31); well-sclerotized basal plate extension as broad as phallotheca (Fig.

3.34b); apex of basal plate extension broad with angular corners (Fig. 34b); curvature of basal plate extension rounded (Fig. 3.40); ponticulus basilaris almost insignificant with adjoining basal plate struts fused to form a small rounded basal foramen (Fig. 3.31b).

♀: Total length: 16.69mm. Morphologically similar to males.

Other specimens examined: Paratypes: MADAGASCAR: Toliara: Ranobe, 23.04638°S 43.61028°E, 20 m, 27 Oct 2003, CAS - Frontier Wilderness Project, ♀ (UCR_ENT 00005353) (CAS). Toliara: Cap Ste Marie Special Reserve, 74km S of Tsihombe, 25.58766°S 45.163°E, 37 m, 25 Feb - 07 Mar 2003, M. Irwin, F. Parker, Ra. Harin'Hala, 2♂ (UCR_ENT 00005350, UCR_ENT 00005351) (CAS).

Distribution: All specimens were collected from the southern coastal area of Madagascar at low elevation (20–37m) in spiny forest thickets (Fig. 3.42).

Etymology: The name “galbeum” (noun) means “armband” in Latin and refers to the single brown band on the femora.

Notes: Specimens were collected using Malaise traps. The species occurs close to *D. cacao*, **sp.n**. with differences in elevation and habitat. *Durevius galbeum* is found at coastal lowland spiny thickets while *D. cacao* is found at slightly higher elevation in a gallery forest.

Durevius tuberculatus (Villiers, 1950)

(Figs 3.4, 3.8, 3.12, 3.16, 3.20, 3.22, 3.23, 3.25, 3.29, 3.32, 3.35, 3.38, 3.41, 3.42, Table 3.1)

1950 *Reduvius tuberculatus* Villiers, 22:734 [n. sp.]

1962 *Durevius tuberculatus* Villiers, 29:242

Maldonado 1990: 396

Holotype: ♂: MADAGASCAR: Toamasina: Antongil Bay, unknown date, Mocquerys

Diagnosis: Recognized by the three brown bands on the fore femur (Fig. 3.16), the rounded humeral angles (Figs 3.4, 3.22a), the erect scutellar spine (Fig. 3.20), the antenna of the male entirely stramineous (Figs 3.4, 3.8, 3.12) but females with brown suffusion, the base of the median process of the pygophore broad with crescent-shape apex (Figs 3.29, 3.38), and the ponticulus basilaris forming a well-defined arch connecting the curved basal plate (Fig. 3.32). Most similar to *D. usingeri* in overall coloration and habitus, but clearly distinguished by the rounded humeral angles.

Redescription: ♂: Total length: 14.08mm-16.08mm. Coloration: Head (Figs 3.4, 3.8, 3.12): brown suffused with stramineous on mandibular plate, postocular region, neck, gena, and labrum. Labium: first visible labial segment stramineous, second brown grading to light brown, third light brown. Antenna: antenniferous tubercle light brown to stramineous; scapus light brown to stramineous; pedicellus stramineous, distally brown or light brown; basiflagellomere and distiflagellomere light brown. Thorax (Figs 3.4, 3.8, 3.12): anterior pronotal lobe dark brown with stramineous swirls; posterior pronotal lobe stramineous with brown markings; scutellum stramineous with brown suffusion; hemelytron stramineous with brown spot and pattern. Legs: fore coxa brown with stramineous apex; mid and hind coxae stramineous with variable brown suffusion; trochanters stramineous; femora stramineous with two broad brown bands and one narrow subapical brown band (Figs 3.8, 3.16); tibiae stramineous with brown darkening apically and sub-basally (Figs 3.4, 3.8, 3.12); tarsi stramineous (Figs 3.4, 3.8, 3.12). Abdomen (Figs 3.4, 3.8, 3.12): tergites brown; dorsal laterotergites with alternating stramineous and dark brown bands; sternites with diffusion from stramineous to dark brown from median to lateral sides. Vestiture: as in generic description. Structure: head and eyes as in generic description; median longitudinal furrow between eyes present. Antennae and labium as in generic description. Thorax as in generic description; humeral angle with rounded tubercles (Figs 3.4, 3.22a); posterior tubercles with slight protrusion (Figs 3.4, 3.22b); scutellar spine relatively short (0.52-0.82mm) (Table 3.1), erect (Fig. 3.20). Legs, wings, and abdomen: as in generic description. Male genitalia as in generic description, with paramere apically broad, setae of medium length; curvature of apex of paramere acute; median process of pygophore with wide base and apex (Figs 3.29, 3.38). Aedeagus: endosomal struts narrowly spear-shaped apically (Fig. 3.32a); dorsal phallothecal sclerite obsolete (Fig. 3.32); sclerotized basal plate extension narrower than phallotheca (Fig. 3.35b); apex of basal plate extension round and smooth (Fig. 3.35b); endosomal struts tubular (Fig. 3.35a); basal plate extension curvature angular (Fig. 3.41); ponticulus basilaris well-defined arch adjoining slender diverging basal plate to form a subtriangular basal foramen (Fig. 3.32b). ♀: Total length: 17.38-17.54mm. Morphologically similar to males but slightly larger (see table 3.1) and darker. Coloration: Head: as in male. Labium: as in male. Antenna: scapus brown to light brown with stramineous apex; pedicellus brown to stramineous, distally brown or light brown; basiflagellomere and distiflagellomere brown. Thorax: as in male except scutellum stramineous to light brown with brown suffusion. Legs: femora stramineous with three broad brown bands; tibiae stramineous with pronounced brown darkening apically and sub-basally; tarsi light brown. Abdomen: as in male. Vestiture and structure as in male.

Specimens examined: MADAGASCAR**:** Antananarivo**:** Ambohitantely, 18.198°S 47.2815°E, 27 Jan - 06 Feb 2005, M. Irwin, R. Harin'Hala, 1♂ (UCR_ENT 00005344) (CAS). Antsiranana:

Marojejy Nat'l Park, 5 km W Manantenina village, Camp Mantella, 14.43816°S 49.774°E, 490 m, 20 - 25 Dec 2004, M. Irwin, R. Harin'Hala, 1♀ (UCR_ENT 00005349) (CAS); 11 - 18 Sep 2005, M. Irwin, R. Harin'Hala, 1♀ (UCR_ENT 00005348) (CAS). Fianarantsoa: Parc National Ranomafana, Vohiparara, at broken bridge, 21.22616°S 47.36983°E, 1100 m, 12 - 19 Mar 2002, M. Irwin, R. Harin'Hala, 1♂ (UCR_ENT 00005347) (CAS). Parc National Ranomafana, radio tower at forest edge, 21.251°S 47.40716°E, 1130 m, 24 May - 04 Jun 2002, M. Irwin, R. Harin'Hala, 1♂ (UCR_ENT 00005345) (CAS); 25 Jul - 03 Aug 2002, M. Irwin, R. Harin'Hala, 1♂ (UCR_ENT 00005346) (CAS).

Distribution: Specimens were recorded from mid to higher elevations (490m – 1130m) from the north, central and mid-south areas along the highland plateau of Madagascar. Habitat types are subtropical wet rainforest, dry sclerophilous woodland of broadleaf evergreens, and mixed and premontane forests according to label information.

Notes: With a total of six specimens from the CAS Madagascar project, *D. tuberculatus* was more frequently collected in malaise traps compared to its congeners. It is the only species other than *D. usingeri* found in the inland highland plateau of Madagascar and also the species with the widest distribution. The holotype was not examined but a dorsal image was provided by Dr. Guilbert (MNHN).

Durevius usingeri (Villiers, 1960)

(Figs 3.5, 3.9, 3.13, 3.17, 3.21, 3.42, Table 3.1)

1960 *Reduvius usingeri* Villiers, 12:1333 [sp. n.]

1962 *Durevius usingeri* Villiers, 29:242

Maldonado 1990: 396

Holotype, ♀: MADAGASCAR: Antananarivo: Antananarivo, [18.92014°S 47.52371°E, 1263 m], II III 1950, collector unknown, (UCR_ENT 00019020) (CAS).

Diagnosis: Recognized by the combination of the three brown bands on the fore-femora (Fig. 3.17), brown coxae, more pronounced sub-conical humeral angles (Fig. 3.5), and sub-erect scutellar spine (Figs 3.9, 3.21). Head almost uniformly brown, scapus brown with stramineous apical end (Figs 3.5, 3.9, 3.13). Abdomen uniformly brown (Figs 3.9, 3.13). Male genitalia: unknown. Most similar to *D. tuberculatus*, but distinguished by the above characters.

Redescription: ♀: Total length: 14.36mm. Coloration: head (Figs 3.5, 3.9, 3.13): brown suffused with light brown regions at the mandibular plate, postocular region, neck, gena, and labrum. Labium: first visible labial segment light brown, second brown gradation to light brown, third light brown. Antenna: antenniferous tubercle light brown; scapus brown with stramineous apex; pedicellus stramineous, distally brown; basiflagellomere and distiflagellomere broken off. Thorax: anterior pronotal lobe dark brown with stramineous swirls; posterior pronotal lobe stramineous with brown markings; scutellum brown with stramineous ridge; hemelytron stramineous with brown spot and patterns. Legs: coxae brown; trochanters stramineous to light brown; femora stramineous with three thick brown bands (Fig. 3.17); tibiae stramineous with brown darkening distally and sub-proximally; tarsi stramineous (Figs 3.5, 3.9, 3.13). Abdomen (Figs 3.9, 3.13): tergites brown; dorsal laterotergites with alternating stramineous and dark brown bands; sternites brown. Vestiture: as in generic description. Structure: head and eyes: as in generic description; median longitudinal furrow between eyes present. Antenna and labium: as in generic description. Thorax: as in generic description; humeral angle with pronounced sub-conical tubercles (Fig. 3.5); posterior tubercles with slight protuberances (Fig. 3.5); scutellar spine broken (Fig. 3.21), suberect. Legs, wings and abdomen: as in generic description. ♂: unknown.

Distribution: Known from the holotype locality in the northern central region of Madagascar at an elevation of about 1200 meters (as estimated from Google Earth).

Notes: The female holotype is the only known specimen. Females are generally slightly larger in size and slightly darker in coloration in *D. tuberculatus* and *D. galbeum*. Except size and coloration, all other characters are consistent with males in other congeneric species examined. Females of *D. tuberculatus* observed here do not have overlapping characters with the observed *D. usingeri* holotype and thus *D. usingeri* is treated as a distinct species.

References

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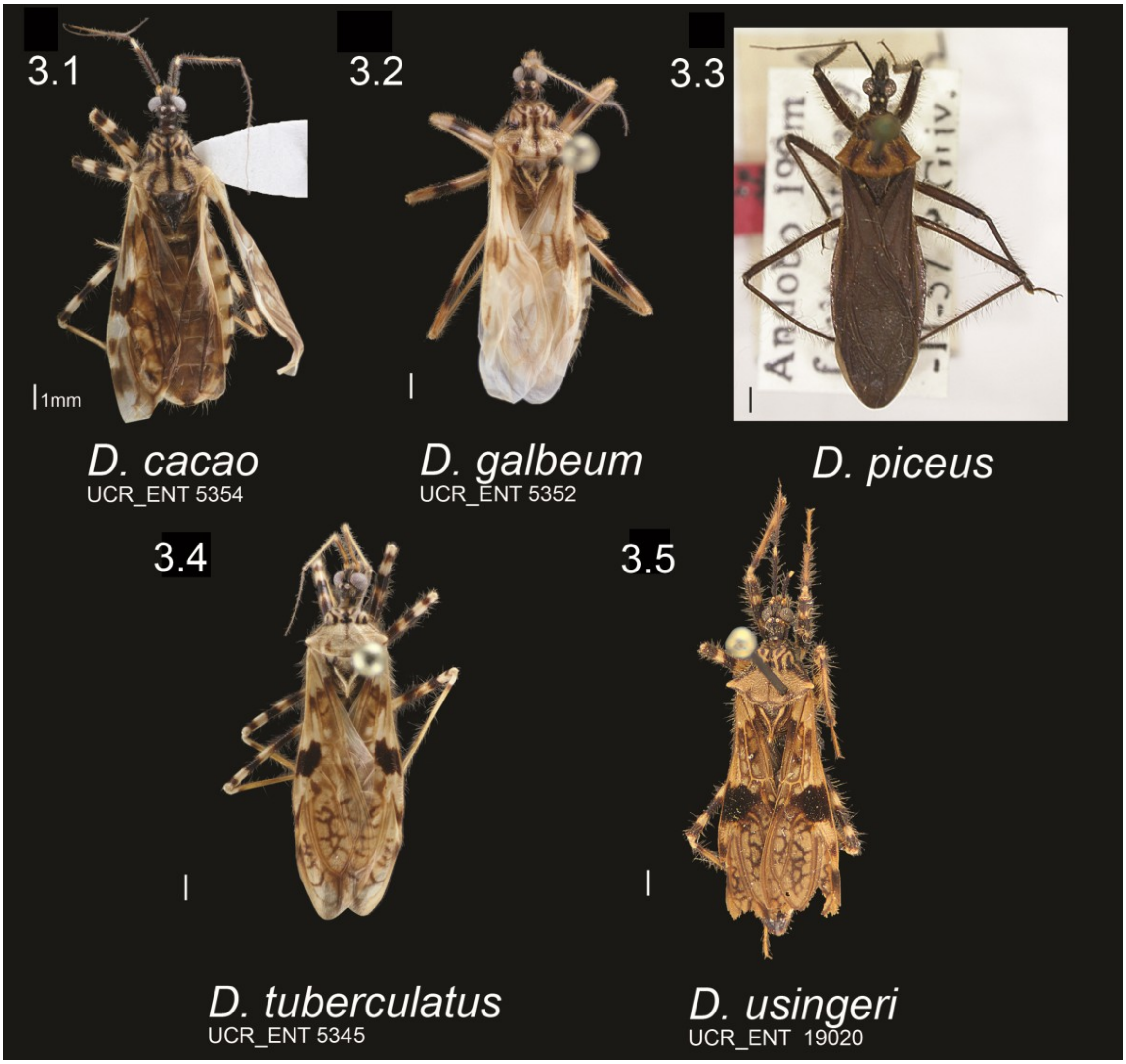
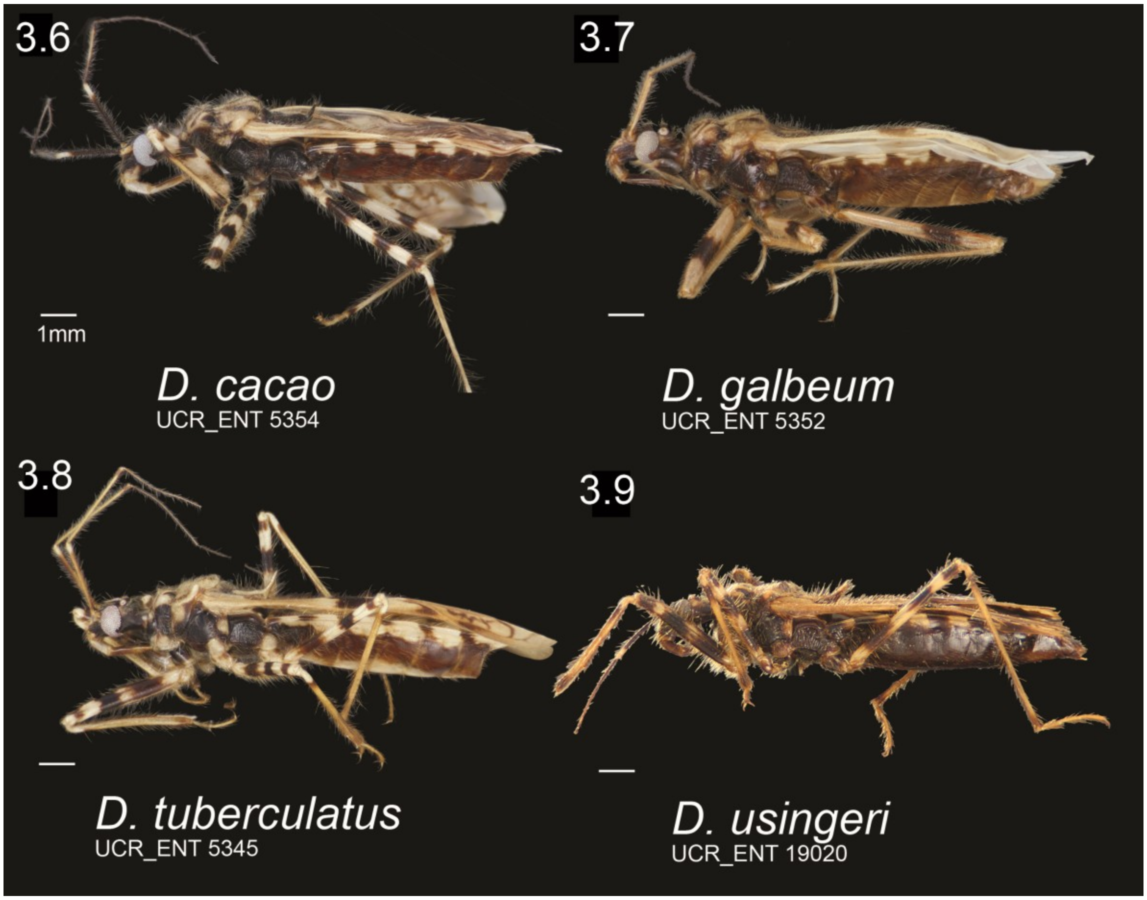
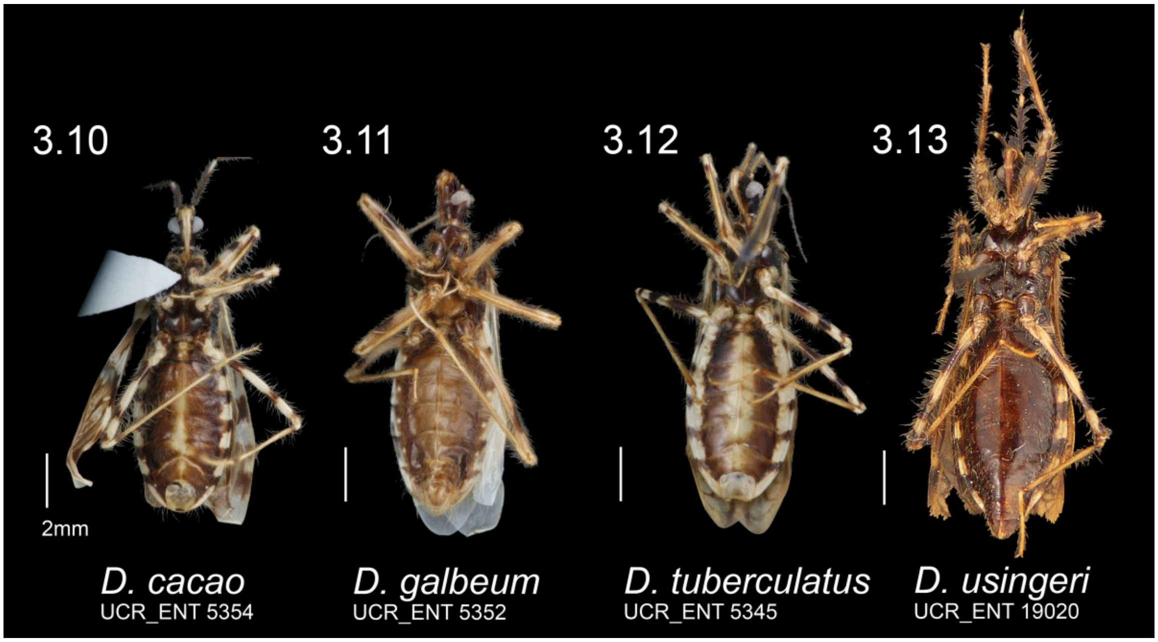


Figures 3.1–5: Dorsal habitus images of *D. cacao* ♂ (1), *D. galbeum* ♂ (2), *D. piceus* ♂ (3), *D. tuberculatus* ♂ (4), *D. usingeri* ♀ (5)

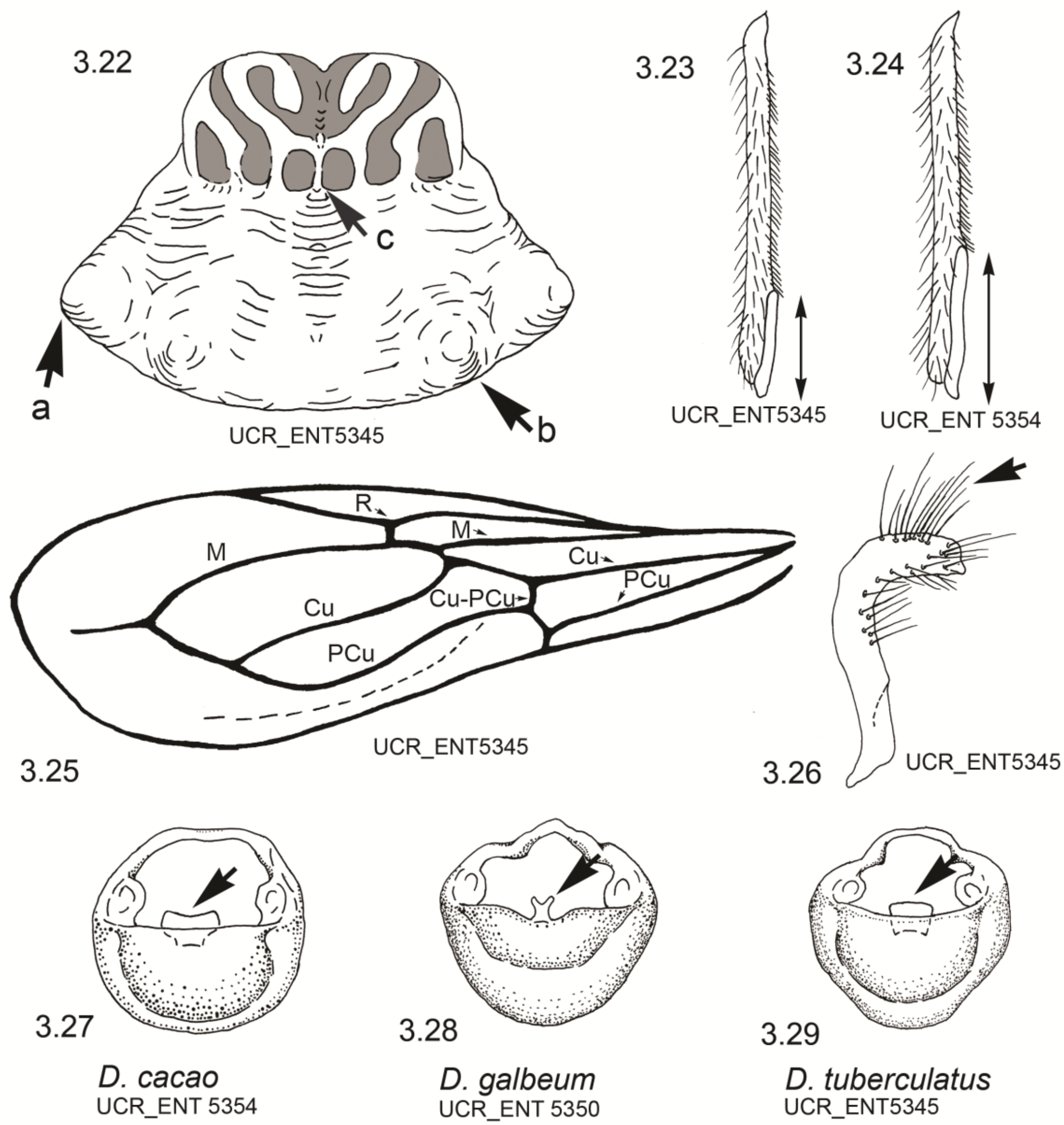


Figures 3.6–9: Lateral habitus images of *D. cacao* ♂ (6), *D. galbeum* ♂ (7), *D. tuberculatus* ♂ (8), *D. usingeri* ♀ (9)

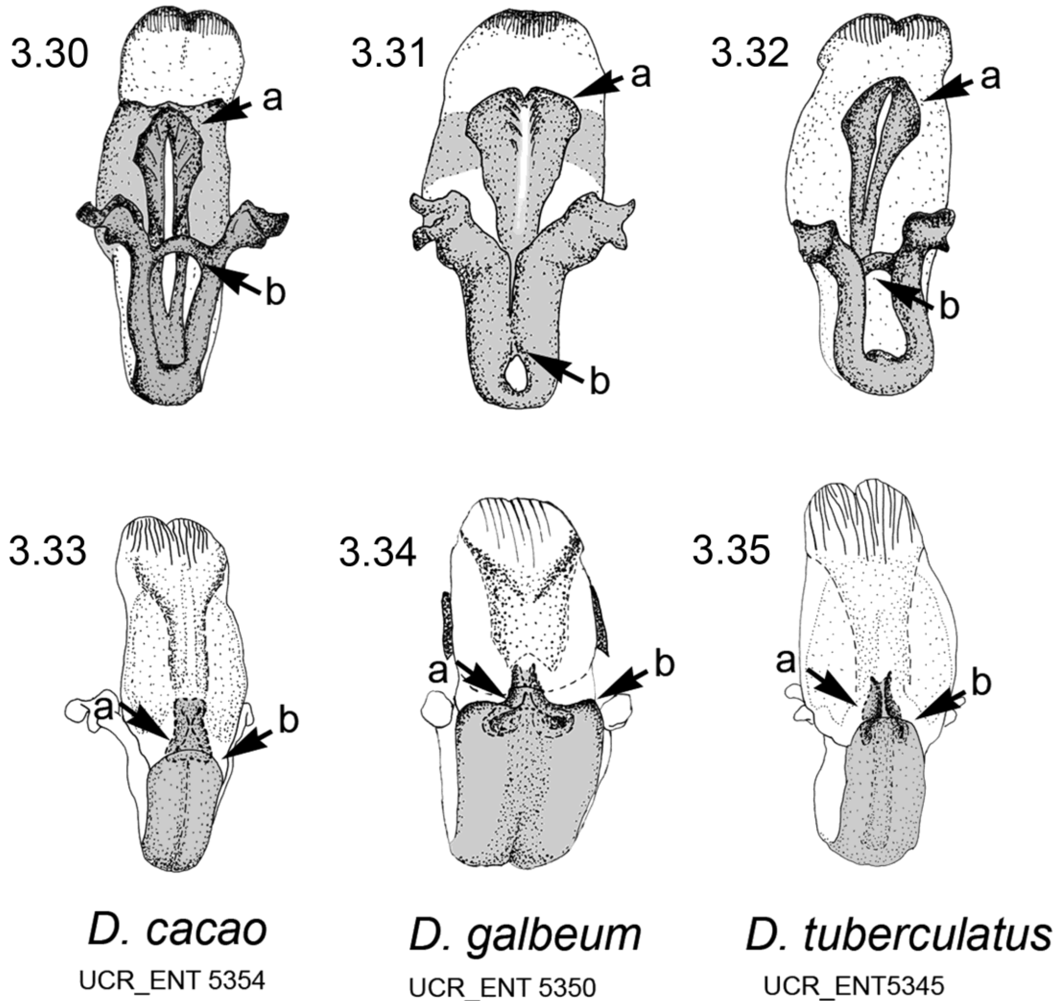


Figures 3.10–13: Ventral habitus images of *D. cacao* ♂ (10), *D. galbeum* ♂ (11), *D. tuberculatus* ♂ (12), *D. usingeri* ♀ (13)

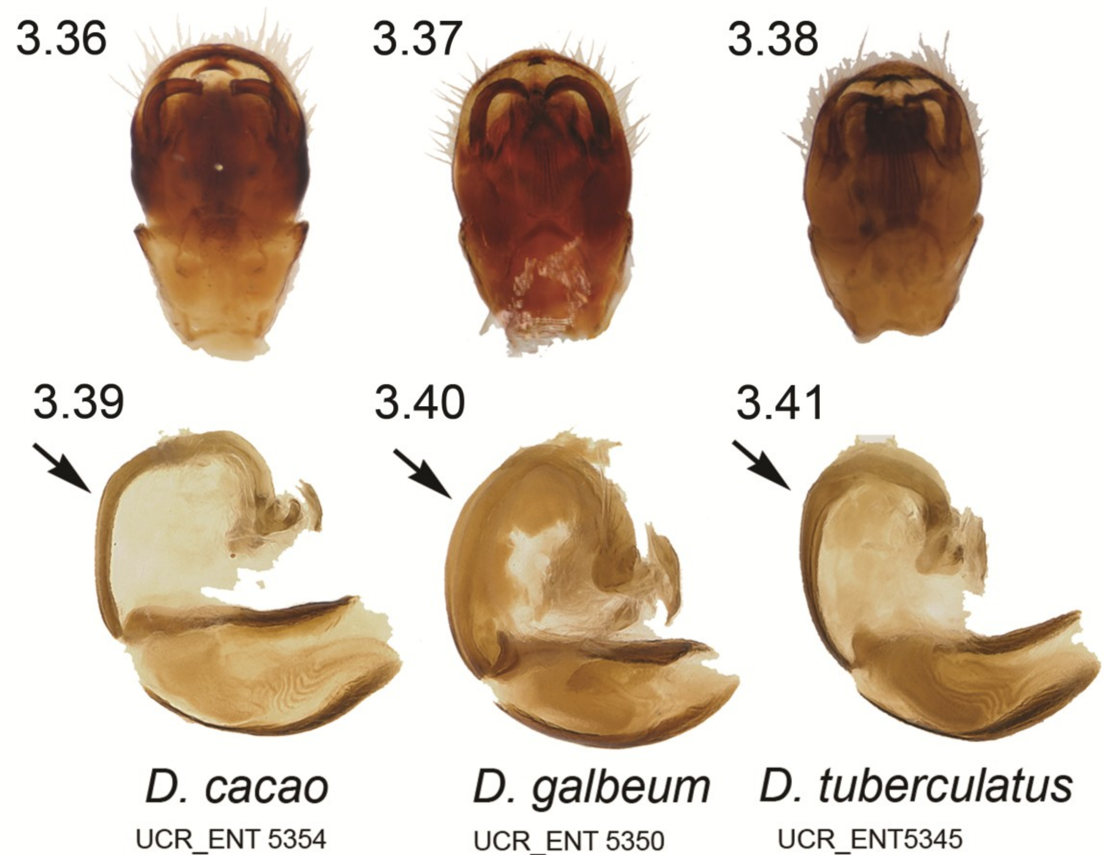
Figures 3.14–21. Fore-femur and scutellum color patterns. Figs 3.14 – 17: Fore-femur color patterns (posterior view) of *D. cacao* ♂ (14), *D. galbeum* ♂ (15), *D. tuberculatus* ♂ (16), *D. usingeri* ♀ (17), Figs 3.18–21: Scutellar spines (left lateral view) of *D. cacao* (18), *D. galbeum* (19), *D. tuberculatus* (20), *D. usingeri* (21)



Figures 3.22–29: Pronotum of *Durevius tuberculatus* (3.22) showing humeral angle (a), posterior tubercles (b), median furrow protuberances (c); Fore-tibia with fossula spongiosa region (arrow) of *D. tuberculatus* (3.23), *D. cacao* (3.24), Venation of hemelytron of *D. tuberculatus* (3.25), Paramere setation of *D. tuberculatus* (3.26), pygophore with median process (arrow) of *D. cacao* (3.27), *D. galbeum* (3.28), *D. tuberculatus* (3.29)



Figs 3.30–35. Aedeagus in dorsal view of *D. cacao* (3.30), *D. galbeum* (31) and *D. tuberculatus* (3.32) with apical endosomal struts (a) and ponticulus basilaris (b). Aedeagus in ventral view of *D. cacao* (3.33), *D. galbeum* (3.34) and *D. tuberculatus* (3.35) with basal endosomal struts (a) and basal plate extension apex (b).



Figures 3.36–41: Dorsal view of pygophores with median process of *D. cacao* (3.36), *D. galbeum* (3.37), *D. tuberculatus* (3.38), lateral view of basal plate extension curvature (arrow) of *D. cacao* (3.39), *D. galbeum* (3.40), *D. tuberculatus* (3.41)

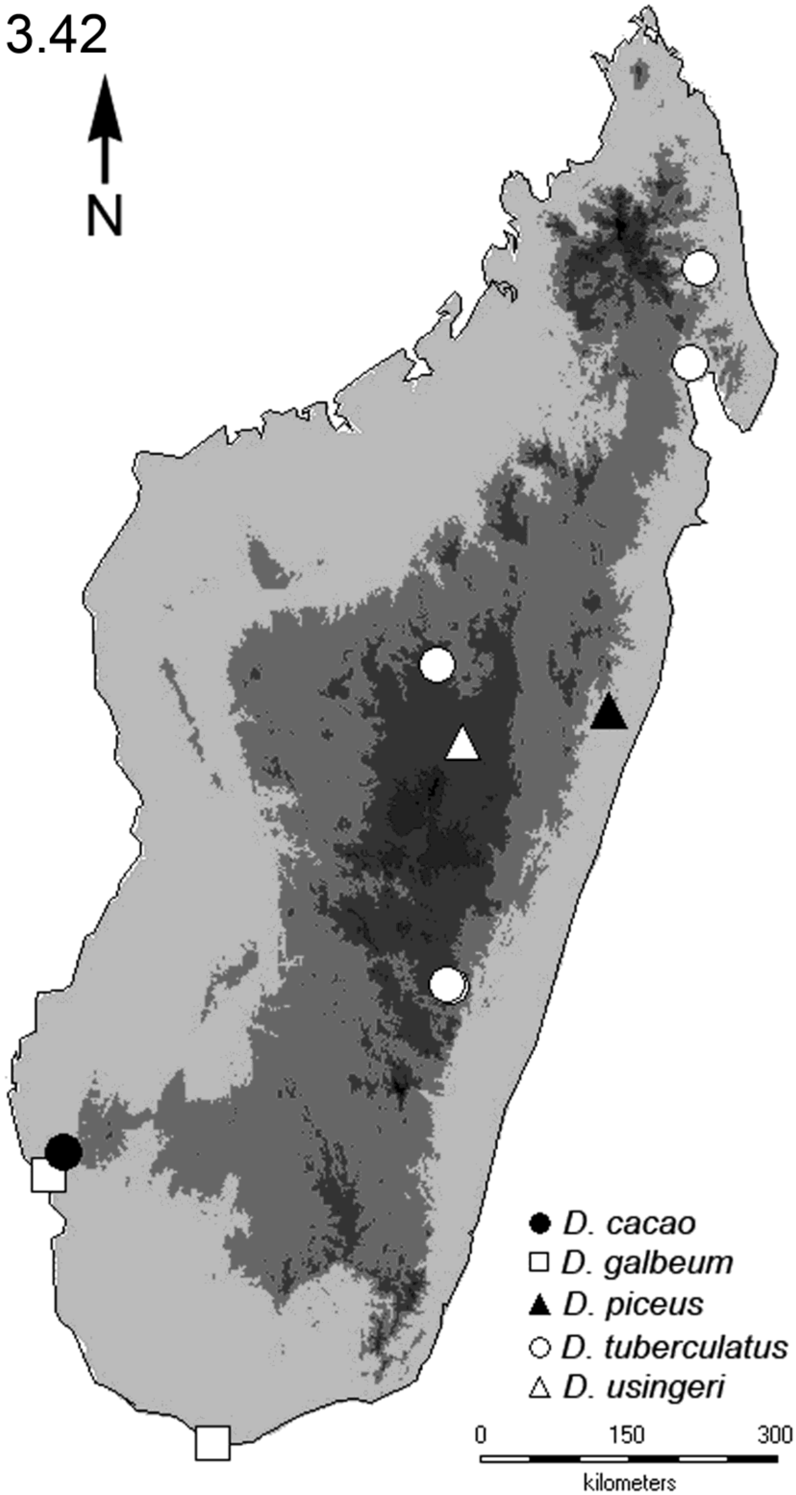


Figure 3.42: Distributions of species of *Durevius*.

Table 3.1. Measurements (in mm) of external morphological structures of *Durevius* spp.

		D. cacao	*D. galbeum*				*D. tuberculatus*						*D. usingeri*
		male 5354	male 5352	male 5351	male 5350	female 5353	male 5346	male 5347	male 5345	male 5244	female 5349	female 5348	female 19020
1st labial segment length		0.64	0.6	0.66	0.64	0.69	0.67	0.67	0.62	0.6	0.74	0.76	0.7
2nd labial segment length		1.04	1.17	1.24	1.16	1.39	1.091	0.98	1	0.82	1.21	1.12	1.16
3rd labial segment length		0.33	0.32	0.3	0.34	0.33	0.37	0.3	0.42	0.4	0.34	0.4	0.34
Head length		2.05	2.03	2.16	2.23	2.59	1.984	1.86	1.92	1.78	2.28	2.69	2.36
Head width		1.34	1.34	1.4	1.33	1.34	1.43	1.26	1.31	1.15	1.44	1.39	1.39
Interocular distance		0.5	0.45	0.55	0.55	0.57	0.32	0.3	0.35	0.31	0.33	0.4	0.4
Eyes dorsal width		0.43	0.42	0.42	0.37	0.37	0.55	0.48	0.5	0.44	0.53	0.52	0.53
Scapus		2.03	1.9	1.66	1.6	1.55	2.31	2.02	2.11	1.92	2.18	2.06	2.28
Pedicellus		2.69	2.89	2.92	2.72	2.72	3.16	2.76	2.99	2.62	2.86	NA	3.19
Basiflagellomere		2.86	3.1	2.5	2.33	NA	3.02	2.69	2.72	2.62	3.5	NA	NA
Distiflagellomere		2.35	NA	2.6	1.89	NA	2.45	2.36	2.48	2.21	2.48	NA	NA
Anterior pronotal lobe width		1.56	1.86	2.08	1.98	1.88	1.7	1.55	1.64	1.48	1.79	1.84	1.85
Posterior pronotal lobe width		2.96	3.33	3.45	3.45	3.5	3.23	2.89	3.02	2.65	3.5	3.5	3.9
Pronotum length		2.15	2.06	2.2	2.45	2.18	1.98	1.78	1.85	1.69	2.45	2.35	2.45
Thorax ventral		3.35	3.9	4.4	4.1	3.9	3.7	3.5	3.5	2.8	4.1	4.05	4.3
Scutellar spine		0.51	0.5	NA	NA	0.63	0.72	NA	0.73	0.52	0.82	0.77	NA
Scutellum		1.34	1.71	1.65	1.48	1.61	1.2	1.1	1.38	1.04	1.4	1.68	1.51
Fore femur length		3.29	3.6	3.4	3.36	3.5	4.1	3.5	3.5	3.36	4.15	3.9	4.15
Fore tibia length		3.23	3.35	3.55	3.36	3.43	4	3.45	3.6	3.39	4	4	4
Fossula spongiosa (foreleg)		1.29	0.87	0.78	0.78	0.75	1.14	1.09	1.12	1.05	1.36	1.36	1.31
Mid femur		3.26	3.5	3.23	3.02	3.36	3.85	3.36	3.25	3.1	3.9	3.75	4
Mid tibia		3.45	3.5	3.65	3.6	3.65	4.25	3.6	3.7	3.5	4.25	4	4.3
Fossula spongiosa (midleg)		0.99	0.68	0.47	0.57	0.49	0.57	0.59	0.66	0.65	1.04	1.05	0.94
Hind femur		4.45	5.2	5	4.6	4.6	5.3	4.65	4.5	4.5	5.5	5	5.5
Hind tibia		5.5	6	6.1	6	5.9	6	5.2	5.6	5.05	6.2	6	6.3
Tarsal segments fore	1st	0.13	0.18	0.17	0.1	0.15	0.24	0.17	0.18	0.18	0.25	0.22	0.25
	2nd	0.37	0.48	0.42	0.25	0.48	0.56	0.55	0.43	0.37	0.57	0.53	0.55
	3rd	0.62	0.83	0.73	0.35	0.67	0.74	0.62	0.75	0.65	0.87	0.85	0.84

Table 3.1. Measurements (in mm) of external morphological structures of *Durevius* spp. (cont'd)

		D. cacao	*D. galbeum*				*D. tuberculatus*						*D. usingeri*
		male 5354	male 5352	male 5351	male 5350	female 5353	male 5346	male 5347	male 5345	male 5244	female 5349	female 5348	female 19020
Tarsal segments mid	1st	0.23	0.1	0.22	0.15	0.2	0.26	0.26	0.18	0.19	0.25	0.3	0.25
	2nd	0.4	0.35	0.38	0.42	0.5	0.57	0.43	0.5	0.41	0.61	0.5	0.45
	3rd	0.56	0.82	0.67	0.67	0.73	0.73	0.67	0.72	0.65	0.89	0.67	0.72
Tarsal segments hind	1st	0.67	0.38	NA	0.3	0.45	0.7	0.56	0.52	0.43	0.74	0.65	0.75
	2nd	0.59	0.71	NA	0.5	0.65	0.74	0.64	0.61	0.58	0.82	0.62	0.63
	3rd	0.67	0.87	NA	0.83	0.84	0.74	0.57	0.83	0.74	0.92	0.75	0.8
Hemelytron length		9	9.9	10.3	10.01	10.2	10.4	9	10	9.5	11	10.8	NA
Abdomen length		6.3	7.3	7	7.7	8	6.6	6.6	6.8	6.2	8	8	7.7
Abdomen width		3.7	4.3	4.4	4.7	3.85	3.75	3.7	4.05	3.2	4.6	4.25	4.2
Body length		14.4	15.83	16.86	16.34	16.69	16.084	14.36	15.42	14.08	17.38	17.54	14.36

Chapter 4 Physoderinae higher-level phylogeny and taxonomic revision of *Physoderes* Westwood and allied genera in the Oriental and Australasian regions

Abstract

Malagasy Physoderinae exhibit broad morphological diversity, a fact that is evidenced by their classification into 11 of the 14 genera in this subfamily. In contrast, the genus *Physoderes* is widely distributed across the Oriental and Australasian regions and has the highest species diversity (37 spp.) among physoderine genera, but relatively limited morphological diversity. I here test the monophyly of the Malagasy physoderine fauna to investigate if it represents a single origin with a subsequent radiation within the island. The putative position of the two Neotropical physoderine genera (*Cryptophysoderes*, *Leptophysoderes*) as sister to all remaining Physoderinae is also tested in this analysis as well as the hypothesis that the Neotropical reduviine genus *Aradomorpha* is the sister-group to the Physoderinae. A cladistic analysis is conducted based on morphological characters and a complete genus-level taxon sample of worldwide Physoderinae. Results indicate that the Malagasy fauna is not monophyletic and that the Neotropical Physoderinae are the sister to all remaining Physoderinae (except the Afrotropical "Porcelloderes" manuscript name). *Physoderes* is polyphyletic and 3 new genera are erected to accommodate several new species and certain species previously classified as *Physoderes*. A taxonomic revision of *Physoderes* and allied genera is conducted to describe new species and re-describe taxa. Diagnoses, updated distribution ranges, habitus and genitalic images, and identification keys are provided. A total of 17 synonymies, 14 new species and 3 new genera are described, focusing on the diversity of Physoderinae in the Oriental and Australasian regions.

Introduction

The assassin bug subfamily Physoderinae, while relatively few in species, have an apparently disjunct biogeographic distribution. All members are small, cryptic in coloration and behavior, and rarely collected. A total of 65 species classified into 15 genera are known, with the highest morphological diversity (11 genera, 27 spp.) endemic to Madagascar (and the nearby Comores islands). In contrast, the Oriental and Australasian regions are populated by a single genus *Physoderes* Westwood consisting of 37 species (Maldonado 1990; Chlond, 2011; Cao, Tomokuni & Cai, 2011). Only two Neotropical monotypic genera have so far been described (Wygodzinsky & Maldonado, 1972; Weirauch, 2006). A monotypic Afrotropical genus was recently described from Tanzania (Redei, in press). Present Physoderinae taxonomy 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 – 1960s and Miller (e.g., 1940, 1955) described the Oriental and Australasian *Physoderes* species in South-East Asia and the Pacific during the 1940s – 1960s. Since then, two new Neotropical species (Wygodzinsky & Maldonado, 1972; Weirauch, 2006) were described and Physoderinae were re-diagnosed by Weirauch (2006). Most recently, one new Malagasy species of *Rodepirea* was described (Chlond, 2011) and one Oriental species with the northern-most record of any Physoderinae including a redescription of *Physoderes impexa* (Distant) was added (Cao, Tomokuni and Cai, 2011). The goal of the present research is to produce a genus-level phylogeny of Physoderinae and a taxonomic revision of the species that fall within the currently defined limits of the nominal and largest genus - *Physoderes*.

The systematics of Physoderinae is largely unstudied. Beyond the alpha-taxonomy of Physoderinae, no phylogenetic relationships between the various genera have been proposed other than the hypothesis that the two Neotropical genera *Leptophysoderes* and *Cryptophysoderes* possess the most plesiomorphic characters and hence are likely the sister-group to the remaining physoderines (Weirauch, 2003). The remarkable morphological diversity (roughly translated to genus diversity) endemic to Madagascar raises the question of whether Physoderinae had undergone similar episodes of species radiation within Madagascar as documented in other endemic, speciose Malagasy fauna (e.g., lemurs, chameleons, palms, orchids). The hypothesis that a radiation of species occurred on Madagascar requires that it was historically a single colonization event (monophyly) that led to a diversification of species thereafter. Miller had proposed that the Neotropical *Aradomorpha* Champion may be closely related to Physoderinae but this has not been tested cladistically. Based on a recent molecular phylogenetic analysis, Physoderinae are also shown to be closely related to the Neotropical reduviines *Microlestria* Stål and *Nalata* Stål, increasing the number of potential candidates as the sister-taxon of Physoderinae (Hwang & Weirauch, 2012). The newly described Afrotropical physoderine is the first species of this subfamily found in continental Africa. Its modified morphology due to aptery makes it difficult to formulate a phylogenetic hypothesis of whether it could be more closely related to the Neotropical or to the Malagasy species (Redei, pers comms.). A genus-level phylogeny based on morphology is conducted here to test the monophyly of the Malagasy Physoderinae, and resolve the phylogenetic hypotheses mentioned above. The inclusion of the Afrotropical "Porcelloderes" (manuscript name) is an attempt to phylogenetically place the afrotropical taxon, and having *Aradomorpha*, *Microlestria* and *Nalata* among the outgroup taxa will help address the Physoderinae sister-group hypothesis.

In addition, examination of *Physoderes* specimens assembled from various institutions and access to type material revealed a level of morphological diversity that puts the monophyly of *Physoderes* into question. In order to proceed with the taxonomic revision of *Physoderes*, the phylogenetic relationships of both described and undescribed species need to be clarified in order to produce a classification that reflects the evolutionary relationships among these species. The decision is thus made to include representative species of *Physoderes* and undescribed species that are difficult to place into the phylogenetic analysis to help inform taxonomic decisions. The result of the phylogenetic analysis will help to re-classify species not belonging to the same clade as *P. notata* Westwood, the type species of *Physoderes*, and a redefinition as well as redescription of *Physoderes* will be based off of the phylogeny.

Physoderes contains 37 species mostly described by Miller (e.g.,1940, 1941). Other workers that also described *Physoderes* species include Bergroth (1906), Breddin (1903), China (1935), Distant (1903, 1909), Horváth (1900), Kirkaldy (1905), Stål (1863, 1870), Usinger (1946) and Westwood (1847). The current state of the taxonomy of *Physoderes* is dismal in contemporary standards and a revision is necessary to improve the condition of the overall taxonomy. Almost all descriptions to date are inadequate due to a lack of a proper diagnosis, with poor or completely no accompanying illustrations, while few morphological characters were documented, and no identification key for the entire genus is in existence. Many species descriptions were based on singletons and both males and females were assigned as holotypes by various authors. This is problematic when no opposite sex was associated due to the presence of sexual dimorphism in Physoderinae. This resulted in problematic species identifications, and many museum specimens were subsequently misidentified. A comprehensive revision based on a large number of specimens was never undertaken for *Physoderes*. Over the years, a sizeable amount of *Physoderes* specimens have accumulated in various museums and it is timely to produce a modern monograph of the Oriental/Australasian Physoderinae.

Materials and methods

Phylogenetic analysis

Taxon sampling

A total of 57 taxa (3 outgroup taxa: *Aradomorpha*, *Microlestria*, *Nalata*; 54 ingroup taxa) were examined. All the 14 genera of Physoderinae were sampled, with all species represented except in the two large genera *Physoderes* (12 of 36 sampled) and *Neophysoderes* Miller (5 of 6 sampled). *Physoderes* specimens were selected to represent morphogroups that may not be monophyletic and required testing. Ten newly described species are included to determine their genus-level membership. Whenever the association between males and females are in doubt, such as when the type specimens and their allotype look morphologically different, both are included into the analysis. Four additional undescribed species of *Leptophysoderes* and *Cryptophysoderes* were also included.

Morphological dataset

Type specimens for all species were examined at the British Museum of Natural History (BMNH) and Muséum National d'Histoire Naturelle (MNHN). Additional specimens were examined at UCR using a Nikon SMZ1500 stereomicroscope and morphological measurements were recorded. Scoring of characters was based on type specimens, plus additional identified material wherever available. A total of 57 morphological characters were coded using MESQUITE (Maddison & Maddison, 2011); 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.

Phylogenetic analysis

A cladistic analysis was performed using a TNT new technology search with initial level set at 50, 80 and 100, and finding minimum length 10 times. 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 902 specimens were examined during the course of this study. The specimens were loaned from various museums and the list of museum acronyms is provided 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 Tadashi Ishikawa, Cai Wanzhi, Cao Liangming, and David Redei. Each specimen is labeled with a Unique Specimen Identifier (USI) and label information is recorded and georeferenced in the Plant Bug Planetary Biodiversity Inventory (PBI) locality database located at the AMNH. Specimen examined information for each species was generated from the database and provided for each species description.

Almost all locality labels lacked geographic coordinates and were georeferenced using Google Earth. Localities with generic provincial or country information were placed at 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 due to limitations of taxa allowed per map and to avoid heavy overlap of specimen points.

Morphological methods

Specimens were examined using a stereomicroscope (Nikon SMZ1500). Habitus images were produced using either a Microptics-USA imaging system with a Canon EOS 1D camera or with 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 having the apex of the abdomen soaked in 10% potassium hydroxide (KOH) for 2 hours. Male genitalia were dissected after being heated in 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 and not completely inflated. The pygophores, parameres and phallus were dissected and mounted in a glycerin-gelatin mixture for imaging with an Automontage GT-Vision imaging system. Dissected body parts were stored in glycerol in a genitalic vial and associated 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 fixed 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).

AMNH	American Museum of Natural History
BMNH	The Natural History Museum, London
BPBM	Bernice P. Bishop Museum
CAS	California Academy of Sciences
DEI	Senckenberg Deutsches Entomologisches Institut
HNHM	Hungarian Natural History Museum

ISNB	Institut Royal des Sciences Naturelles de Belgique
MNHN	Muséum National d'Histoire Naturelle, Paris
NMPC	National Museum (Natural History) Czech Republic, Prague
RMNH	Leiden Nationaal Natuurhistorische Museum
UCR	University of California, Riverside, Entomology Research Museum
USNM	National Museum of Natural History, USA, Washington DC

Terminology

Descriptive terminology of the male genitalia follows Davis (1966) and Forero and Weirauch (2012). The pair of extended lobes projecting from the posterior margin of the posterior pronotal lobe are refered to here as parascutellar lobes.

Results

The scoring of each taxon in the morphological matrix is shown in Table 4.1, measurements used as continuous characters are shown in Table 4.2, and the list of the morphological character states used are in Table 4.3. The overall morphology of Physoderinae is rather conserved and identifying phylogenetically informative characters proved challenging. Most of the variable characters can be found on the head and pronotum. The analysis shows that many of these characters turned out to be homoplastic and have evolved multiple times across the phylogeny.

The phylogenetic analysis consistently produced a single most parsimonious tree (tree length = 366, CI=0.22, RI=0.61, Fig. 4.1) showing *Aradomorpha* as the sister-group to Physoderinae, "*Porcelloderes*" as sister to all remaining Physoderinae and a monophyletic New World clade containing *Leptophysoderes* and *Crytophysoderes.* The Malagasy Physoderinae are not monophyletic (Fig. 4.1). *Epiroderoides mauriciensis* Villiers is nested within a clade containing

Physoderes species, while a new species found in Australasia is most closely related to the Malagasy-restricted *Paraphysoderes* Villiers. The entire Malagasy fauna except *E. mauriciensis* belongs to two monophyletic clades that are sister to each other (Fig. 4.1). The two largest Malagasy genera – *Neophysoderes* and *Epiroderoides* are not monophyletic. The morphologically unique *Mimoelasmodema* Villiers is nested within *Neophysoderes* while *Epiroderoides* is polyphyletic with respect to the remaining physoderine genera except *Paraphysoderes* (Fig. 4.1). Similarly, *Physoderes* is found to be polyphyletic and can be split into 4 clades including one that is a single taxon lineage (*P. dentiscutum* Bergroth).

Discussion

The non-monophyletic nature of the Malagasy Physoderinae suggests a more complex evolutionary history than a single colonization event followed by species radiation. A proper biogeographic analysis will need to be carried out to explain the current relationships reconstructed here. Species radiation within Madagascar cannot yet be completely ruled out, as almost all Madagascar species are still more closely related to each other than other Old World species. The placement of the Afrotropical "Porcelloderes" as sister to all Physoderinae may be a biased interpretation due to the nature of the coding of this morphological dataset due to its strong representation of pronotal structure that is highly modified for "Porcelloderes". The New World clade, showing a monophyletic *Leptophysoderes* and monophyletic *Cryptophysoderes* holds up to the hypothesis that it is sister to all remaining Physoderinae except "Porcelloderes". The polyphyletic *Epiroderoides* and paraphyletic *Neophysoderes* indicate that the classification of the Malagasy fauna requires re-examination and revision to produce a classification that is reflective of their relationships. It is of interest to note that the Malagasy species that are more highly modified morphologically from the typical physoderine habitus such as *Mimoelasmodema*

Villiers and *Tribelocephaloides* Villiers are placed at the more derived positions within their respective clades.

The polyphyletic *Physoderes* requires a redefinition of the genus and the description of new genera based on the remaining clades. One undescribed species that is sister to a monophyletic *Paraphysoderes* is to be classified under *Paraphysoderes* and *Paraphysoderes* is re-defined to accommodate the new species. The synapomorphies of this clade are used to build the diagnosis of the newly defined *Paraphysoderes*. On the other hand, *P. dentiscutum* is morphologically unique relative to other species and does not fall into any other clades (Fig. 4.1). The decision here is thus to recognize it as a new monotypic genus. All remaining *Physoderes* species sampled fall into one of the three clades, of which the clade containing the nominal *P. notata* is the largest. In following the International Commission on Zoological Nomenclature rules, this type species-bearing clade retains the name *Physoderes* and the two other clades are recognized as two new genera (Fig. 4.1). Redescriptions of *Physoderes*, *Paraphysoderes* and descriptions for the new genera are below.

Taxonomy

Breviphysoderes, **new genus** (Figs 4.2, 4.6, 4.7, 4.9, Table 4.4)

Type species: *Physoderes mjoebergi* Miller, 1940

DIAGNOSIS: Recognized among all other genera of Physoderinae by the head being elongate conical, without a pair of long straight setae on postocular lobe posterior margin, the scape surpassing the apex of the clypeus, the eye being distinctly projecting in dorsal view, the pronotum with tuberculated, 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 apically rounded with sclerotized paired latero-ventral slight protuberance, the basal plate arms parallel to each other, the sclerotized ring of the ductifer elongate, the dorsal phallothecal sclerite subacute with lateral narrow, the band-like prolongations extended diagonally towards basal plate. Most similar to *Physoderes*, but distinguished by the scape surpassing the apex of the clypeus, anterior pronotal lobe narrower than posterior lobe in males.

DESCRIPTION: *MALE:* Length ranging from relatively small to medium-sized, 7.49 - 10.23 mm (Table 4.4). COLORATION (Fig. 4.2): Variable, from straw-colored to dark brown. Head, anterior pronotal ridges, posterior pronotal lobe, legs, 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. STRUCTURE: HEAD: Elongate conical; maxillary plate truncate apically; scape surpassing apex of clypeus except in *Breviphysoderes decora* **comb. n.**; eye distinctly projecting in dorsal view except in *B. decora* **comb. n.**, 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. n.**; paramedian carina strongly defined except in *B. decora* **comb. n.**; 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. n.**; parascutellar lobe semicircular; scutellum rounded triangular, scutellar process long with rounded apex except in *B. decora* **comb. n.**; 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. n.**, posterior margin most often slightly elevated. MALE 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; cuplike sclerite apically rounded with sclerotized paired latero-ventral slight protuberance; basal plate arms parallel to each other; ductifer with sclerotized, elongate ring; endosomal struts conical, with subacute apex, basally divided into two arms; shape of dorsal phallothecal sclerite subacute with lateral narrow, band-like prolongations, oriented diagonally towards basal plate.

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

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.

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

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

Key to species of *Breviphysoderes*

1. Apical portion of veins forming external cell of hemelytron (Cu+M) straw-colored or distinctly lighter than remainder of veins (Fig. 4.2)..(2)

- Veins framing external cell of hemelytron uniformly colored, not straw-colored (Fig. 4.2) ....(4)

2. Hemelytron short, not reaching tip of abdomen (Fig. 4.2).....................*B. fulvopicta* **n. sp.**

- Hemelytron reaching or surpassing tip of abdomen (Fig. 4.2) ....(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. 4.2) ....*B. vestita* **comb. n.**

- Antero-lateral pronotal projections oriented anteriorly, males with anterior pronotal lobe as in females, narrower than posterior lobe (Fig. 4.2) ....*B. shelfordi* **comb. n.**

4. Head and body uniformly brownish-black (Fig. 4.2), antero-lateral pronotal projections acute, oriented anteriorly ....*B. tenebrosa* **n. sp.**

- Head and body not uniformly brownish black (Fig. 4.2), antero-lateral pronotal projections acute and diverging ....(5)

5. Scape reaching but not surpassing apex of clypeus (Fig. 4.2) ....*B. decora* **comb. n.**

- Scape surpassing apex of clypeus (Fig. 4.2) ....(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. 4.2) …………………………………………………………………….....*B. hobbyi* **comb. n.**

- Ridges of anterior pronotal lobe straw-colored, color contrasting with remainder of anterior pronotal lobe, external cell of hemelytron (Cu+M) not elongated (Fig.4.2) ....(7)

7. Apex of scutellar process straw-colored (Fig. 4.2)............................*B. mjoebergi* **comb. n.**
8. Apex of scutellar process dark brown or uniform color as scutellum (Fig. 4.2) ....*B. planicollis* **comb. n.**

***Breviphysoderes decora* (Miller), new combination** (Figs 4.2, 4.9, Table 4.4)

Physoderes decora Miller 1940, original combination.

Physoderes ostenta Miller, 1941, **new synonymy.**

Holotype: 1 female; MALAYSIA: Sarawak: Mt. Poi (Mt. Pueh), 1.8°N 109.68305°E, 61 m, no date provided, E. Mjoberg. Holotype specimen deposited at BMNH.

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 distinct 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. n.,** but can be differentiated by the scape not extending beyong the clypeal apex and the shorter scutellar process.

REDESCRIPTION: *FEMALE:* Medium, total length 9.19mm, (SD ± 0.33) mm (Table 4.4). COLORATION (Fig. 4.2): Straw-colored and brown. HEAD: Brown with straw-colored suffusion. ANTENNA: Scape straw-colored with brown apex, pedicel brown with straw brown apex, basi-flagellomere brown, distiflagellomere brown with straw brown apex. LABIUM: Light brown. THORAX: Pronotum anterior lobe 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. *Hemelytron:* Corium and membrane brown to dark brown. *Legs:*

Femora 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, exposed part of pygophore straw brown. VESTITURE: Sparsely setose. HEAD: With widespread curved, tuberculated setae, ventral surface of postocular lobe with sparse, tuberculated setae, without pair of long straight setae on postocular lobe posterior to ocelli. THORAX: Anterior lobe with tuberculated, short, curved setae on lateral margins and along dorsal ridges, posterior lobe with short, curved, tuberculated setae along lateral margins and sparsely distributed on dorsal surface. *Hemelytron:* Corium with short, curved setae. *Legs:* With two rows of spines and tuberculated setae, tibia with regular rows of tuberculated, stout, sharp setae. ABDOMEN: Posterior margin of connexivum with short, curved setae. STRUCTURE: HEAD: Elongate conical; maxillary plate truncate apically; 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; 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 contiguous with transverse sulcus; paramedian carina weakly defined; posterior lobe medially rugose; anterior pronotal lobe equal length to posterior lobe, narrower than posterior lobe, alobe lower than posterior lobe in lateral view; semicircular; scutellum rounded triangular, scutellar process short, apex subacute; mesosternite with tuberculated setae but no protrusion. *Hemelytron:* Attaining tip of abdomen. *Legs:* Fore femur distinctly incrassate. ABDOMEN: Elongate ovoid, with rounded terminal margin; connexival margin slightly undulating, posterior margin not elevated. FEMALE GENITALIA: Not dissected.

BIOLOGY: Little known, specimens collected from altitude of 82m to 549 (1,800 ft). Coloration of specimens differs slightly, unclear if 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).

DISCUSSION: *P. ostenta* is synonymized with *B. decora* as it shares the same diagnostic features including scape almost reaching or reaching clypeus 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 specimens of *P. ostenta* exist except for the holotype specimen. *B. decora* is removed from *Physoderes* and transferred to *Breviphysoderes* because it possesses the synapomorphies of *Breviphysoderes* (parascutellar lobes are semicircular and has prominent tuberculated setae on the anterior pronotal lobe dorsal ridges). One specimen originally designated as a *P. hobbyi* paratype (UCR_ENT 00018511) is considered to be misidentified by Miller and is here treated as belonging to *B. decora*. *B. decora* is known only from female specimens. Currently there are no males that can be associated with these female hence the redescription is based on females only.

Paratype: Sabah: N. Borneo, Bettotan, nr. Sandakan, 5.28222°N 117.59305°E, 06 Aug 1927, C. Boden Kloss and H. M. Pendlebury, Paratype, 1;f (BMNH).

Other specimens examined: BRUNEI DARUSSALAM: Temburong District: Kuala Belalong Field Studies Center, 4.54716°N 115.15825°E, 82 m, 26 Jun 2010, C. Weirauch, W. Hwang, 1;f (UCR). MALAYSIA: Perak: Batang Padang, Jor Camp, 3.52972°N 101.55277°E, 549 m, 04 Jun 1923, H. M. Pendlebury, Holotype of junior synonym, 1;f (BMNH). Sabah: Sabah, Mile 50 Lungmanis, 5.42027°N 116.79638°E, Aug 09 1967, F. E., 1;f (RMNH). Sandakan, 5.8333°N 118.1167°E, 4 m, No date provided, Baker, 3;f (USNM).

***Breviphysoderes fulvopicta* n. sp.** (Figs 4.2, 4.9, Table 4.4)

Holotype 1 male; 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. Holotype specimen deposited at BMNH.

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

DESCRIPTION: *MALE:* Medium, total length 7.07 mm. COLORATION (Fig. 4.2): Light brown to dark brown. HEAD: Light brown to dark brown. ANTENNA: Scape straw-colored, with apex brown, pedicel straw-colored and medially brown, basiflagellomere dark brown, distiflagellomere dark brown with straw-colored apex. LABIUM: First segment brown or dark brown, second segment light brown with basally and apically brown or dark brown entirely, third segment brown or dark brown. THORAX: Pronotum anterior lobe 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. *Hemelytron:* Corium brown, membrane brown with apical veins of external cell (Cu+M) straw-colored. *Legs:* Femora 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, tuberculated setae, ventral surface of postocular lobe with sparse, tuberculated setae, without pair of long straight setae on postocular lobe posterior to ocelli. THORAX: Anterior lobe with tuberculated, short, curved setae on lateral margins and along dorsal ridges, posterior lobe with short, curved, tuberculated setae along lateral margins and sparsely distributed on dorsal surface. *Hemelytron:* Corium with short, curved setae. *Legs:* Fore femur with two rows of spines and tuberculated setae, fore tibia with regular rows of tuberculated, stout, sharp setae. ABDOMEN: Posterior margin of connexivum with short, curved setae. STRUCTURE: HEAD: Elongate conical; maxillary plate truncate apically; scape surpassing apex of clypeus; eye distinctly projecting in dorsal view, about 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; median pronotal depression contiguous with transverse sulcus; paramedian carina strongly defined; posterior lobe medially rugose; anterior pronotal lobe of equal length with posterior lobe, narrower than posterior lobe, anterior lobe lower than posterior lobe in lateral view; semicircular; scutellum rounded triangular, scutellar process long, apex rounded; mesosternite with median irregular tuberculated protrusion between fore and mid coxae.

Hemelytron: Not attaining tip of abdomen. *Legs:* Fore femur distinctly incrassate. ABDOMEN: Elongate ovoid, with straight terminal margin; connexival margin slightly undulating, posterior margin slightly elevated. MALE GENITALIA: Not examined.

FEMALE: Unknown.

ETYMOLOGY: The name *fulvopicta* is a 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.

BIOLOGY: 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 from only 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.

DISCUSSION: This species is described based on three specimens originally designated as paratypes of *B. hobbyi* (Miller, 1940) **comb. n.** Even though they share the same collecting event and locality as that of *B. hobbyi* (Miller, 1940) **comb. n.**, closer examination shows distinct morphological differences and the specimens are therefore here treated 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. n.**, *B. decora* **comb. n.**, *B. planicollis* **n. sp.** and *B. tenebrosa* **n. sp.** suggest that they are likely to be closely related.

Paratypes: MALAYSIA: 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, 1;m (BMNH); 05 Sep 1932, B. M. Hobby and A. W. Moore, Paratype, 1;m (BMNH).

Breviphysoderes hobbyi **(Miller)**, **new combination** (Figs 4.2, 4.9, Table 4.4)

Physoderes hobbyi Miller 1940, original combination.

Holotype 1 male; MALAYSIA: Sarawak: Mt. Dulit, Dulit Trail, 3.32388°N 114.1475°E, 730 m, 03 Sep 1932, B. M. Hobby and A. W. Moore (UCR_ENT 00018517). Holotype deposited at BMNH.

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

REDESCRIPTION: *MALE:* Medium, total length 8.7mm. COLORATION (Fig. 4.2): Light brown with dark brown patterns. HEAD: Brown. ANTENNA: Scape straw-colored with light brown apex, pedicel basal half straw-colored and apical half brown, basiflagellomere brown, and distiflagellomere brown with light brown apex. LABIUM: Brown. THORAX: Anterior lobe of pronotum dark brown, posterior lobe brown, scutellum dark brown with brown apex, pleuron dark brown with brown suffusion. *Hemelytron:* Corium and membrane brown. *Legs:* Femora 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, 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, tuberculated setae, ventral surface of postocular lobe with sparse, tuberculated setae, without pair of long straight setae on postocular lobe posterior to ocelli. THORAX: Anterior lobe with tuberculated, short, curved setae on lateral margins and along dorsal ridges, posterior lobe with short, curved, tuberculated setae along lateral margins and sparsely distributed on dorsal surface. *Hemelytron:* Corium with short, curved setae. *Legs:* With two rows of spines and tuberculated setae, tibiae with regular rows of tuberculated, stout, sharp setae. ABDOMEN: Posterior margin of connexivum with short, curved setae. STRUCTURE: HEAD: Elongate conical; maxillary plate truncate apically; scape surpassing apex of clypeus; eye distinctly projecting in dorsal view, about 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; median pronotal depression contiguous with transverse sulcus; paramedian carina strongly defined; posterior lobe damaged/obscured medially by pin; anterior pronotal lobe equal length to posterior lobe, narrower than posterior lobe, anterior lobe lower than posterior lobe in lateral view; semicircular; scutellum rounded triangular, scutellar process long, apex rounded; 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 rounded apical margin; connexival margin slightly undulating, posterior margin slightly elevated. MALE GENITALIA: Not examined.

FEMALE: Unknown.

BIOLOGY: 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* **n. sp.**, *B. planicollis* **comb. n.**, *B. decora* **comb. n.**, and *B. tenebrosa* **n. sp**.

DISCUSSION: 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* **n. sp.** and *B. tenebrosa* **n. sp.** and as *B. decora* **comb. n.** *B. hobbyi* is removed from *Physoderes* and transferred to *Breviphysoderes* because it possesses the synapomorphies of *Breviphysoderes* (parascutellar lobes are semicircular, males do not possess an inflated anterior pronotal lobe and has prominent tuberculated setae on the anterior pronotal lobe dorsal ridges). The specimen was collected by B. M. Hobby and A. W. Moore during the Oxford University Expedition in 1932.

***Breviphysoderes mjoebergi* (Miller), new combination** (Figs 4.2, 4.6, 4.7, 4.9, Table 4.4)

Physoderes mjoebergi Miller 1940, original combination.

Physoderes dyak Miller 1955, **new synonymy.**

Holotype 1 female; MALAYSIA: Sarawak: Mt. Poi (Mt. Pueh), 1.8°N 109.68333°E, 610 m, no date provided, E. Mjoberg. Holotype specimen deposited at BMNH.

DIAGNOSIS: Recognized among species of *Breviphysoderes* by the small body, the head and anterior pronotal lobe being distinctly covered with dense, short, curved, tuberculated setae, 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* but can be differentiated by the 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 instead of angularly hooked sclerotized flaplike prolongations of the phallosoma.

REDESCRIPTION: *MALE:* Small, total length 7.91mm, (SD ± 1.62) mm (Table 4.4). COLORATION (Fig. 4.2): Straw-colored with dark brown patterns. HEAD: Straw-colored to light brown with dark brown suffusion. ANTENNA: Scape and pedicel 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. LABIUM: First segment straw-colored to brown, second segment basally and apically dark brown, medially straw-colored or light brown, third segment dark brown. THORAX: 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. *Hemelytron:* Corium straw-colored or light brown, membrane dark brown. *Legs:* Femora 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, tuberculated setae, ventral surface of postocular lobe with sparse, tuberculated setae, without pair of long straight setae on postocular lobe posterior to ocelli. THORAX: Anterior lobe with tuberculated, short, curved setae on lateral margins and along dorsal ridges, posterior lobe with short, curved, tuberculated setae along lateral margins and sparsely distributed on dorsal surface. *Hemelytron:* Corium with short, curved setae. *Legs:* With two rows of spines and tuberculated setae, tibiae with regular rows of tuberculated, stout, sharp setae. ABDOMEN: Posterior margin of connexivum with short, curved setae. STRUCTURE: HEAD: Elongate conical; maxillary plate truncate apically; scape surpassing apex of clypeus; eye distinctly projecting in dorsal view, about 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; 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 lower than posterior lobe in lateral view; semicircular; scutellum rounded triangular, scutellar process long, apex rounded; mesosternite obscured. *Hemelytron:* Attaining tip of abdomen. *Legs:* Fore femur distinctly incrassate. ABDOMEN: Elongate ovoid, with rounded apical margin; connexival margin slightly undulating, posterior margin slightly elevated. MALE 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; cuplike sclerite apically rounded with slight, sclerotized, paired, latero-ventral protuberance; basal plate arms parallel to each other; ductifer with sclerotized elongate ring; endosomal struts conical, with subacute apex, divided basally into two arms; shape of dorsal phallothecal sclerite subacute with narrow lateral band-like prolongations, oriented diagonally and undulating.

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

BIOLOGY: Unknown.

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

DISCUSSION: Originally described as *Physoderes mjoebergi* by Miller (1940), this species is transferred to *Breviphysoderes* **n. gen.** based on the phylogenetic analysis conducted above. It is most closely related to *B. vestita* (Horváth) **n. syn**. 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, 1955) is synonymized here with *B. mjoebergi* based on the examination of one *P. dyak* paratype at BMNH together with the *B. mjoebergi* holotype. No diagnostic characters were found to separate the two species based on examination of these two specimens. Conspecificity was further confirmed by examination of habitus images of the *P. dyak* holotype at the ZMA.

Paratypes: MALAYSIA: Sarawak: C. Borneo Long Nawang, 0.085°N 114.48305°E, 762 m, 1925, Mjoberg, 1;m (BMNH).

Other specimens examined: INDONESIA: Borneo: Melawi, 0.08333°N 111.48333°E, 43 m, Nov- Dec. 1924, A. Blanchemanche, 1;f (RMNH). Java: Batoerraden G. Slamet, Java (Baturaden), 7.34083°S 109.33055°E, 800 m, Feb. 1937, F. C. Drescher, 1;m (RMNH). Java, 7.61444°S 110.71222°E, No date provided, Horsfield, 1;f (BMNH). Megamendung, 6.61861°S 106.84722°E, 800 m, Oct 1954, Unknown, 1;m (NMPC). Sumatera Barat (West Sumatra): Gunung Singgalang (Sumatra's Westkust), 1800 m, 1926, E. Jacobson, 1;f (RMNH). MALAYSIA: Sabah: 1 Km S. Kundasang, 5.33944°N 116.57638°E, 1530 m, 27 Aug 1983, G. F. Hevel and W. E. Steiner, 1;f (USNM). Sarawak: Mulu National Park, near Base Camp; 4th division Gn., 3.97444°N 114.93638°E, 100 m, v-viii 1978, P. M. Hammond & J. E. Marshall, 1;m (BMNH). VIETNAM: Ha Nam: Cuc Phuong, 20.40777°N 105.79416°E, 86 m, 24 May 1986 – 25 May 1986, Jan Horak, 1;f (NMPC). Vinh Phuc: Tam Dao Co.: Tam Dao NP, 21.50694°N 105.61527°E, 145 m, 06 Sep 2009, T. Ishikawa, 1;m (UCR).

***Breviphysoderes planicollis* (Miller), new combination** (Figs 4.2, 4.9, Table 4.4)

Physoderes planicollis Miller, 1940, original combination.

Holotype 1 male; MALAYSIA: Sarawak: Mt. Dulit, 3.33305°N 114.14972°E, 886 m, no date provided, E. Mjoberg. The holotype is deposited at the BMNH.

DIAGNOSIS: This species is recognized among *Breviphysoderes* species by having the anterior pronotal lobe distinctly covered with dense, short, curved, tuberculated setae, the deeply defined pronotal paramedian carina, the hemelytron surpassing the tip of the abdomen, and the smooth, not undultating, connexivum. This species is most similar to *B. hobbyi* **comb. n.**, *B. decora* **comb. n.** and *B. fulvopicta* **n. sp.** It can be differentiated from *B. hobbyi* **comb. n.** 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. n.** and *B. flavopicta* **n. sp.** 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.

REDESCRIPTION: *MALE:* Medium, total length 9.8mm. COLORATION (Fig. 4.2): Light brown with dark brown patterns. HEAD: Brown with dark brown suffusion. ANTENNA: Scape straw-colored with brown apex, pedicel brown with straw brown apex, basi- and distiflagellomeres missing. LABIUM: First segment brown, second segment basally and apically dark brown, medially light brown, third segment dark brown. THORAX: 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. *Hemelytron:* Corium straw-colored to brown, membrane straw brown to brown, slightly translucent. *Legs:* Femora 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, tuberculated setae, ventral surface of postocular lobe with sparse, tuberculated setae, without pair of long straight setae on postocular lobe posterior to ocelli. THORAX: Anterior lobe with tuberculated, short, curved setae on lateral margins and along dorsal ridges, posterior lobe with short, curved, tuberculated setae along lateral margins and sparsely distributed on dorsal surface. *Hemelytron:* Corium with short, curved setae. *Legs:* With two rows of spines and tuberculated setae, tibia with regular rows of tuberculated, stout, sharp setae. ABDOMEN: Posterior margin of connexivum with short, curved setae. STRUCTURE: HEAD: Elongate conical; maxillary plate truncate apically; scape surpassing apex of clypeus; eye distinctly projecting in dorsal view, less than 1/5 length of head, not attaining head ventral margin 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 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 lower than posterior lobe in lateral view; semicircular; scutellum rounded triangular, scutellar process long, apex rounded; 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 smooth, not undulating, posterior margin slightly elevated. MALE GENITALIA: Already dissected and dissections missing.

FEMALE: Unknown.

BIOLOGY: 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* **n. sp.**, *B. hobbyi* **comb. n.**, *B. decora* **comb. n.**, and *B. tenebrosa* **n. sp.**

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

***Breviphysoderes shelfordi* (Miller), new combination** (Figs 4.2, 4.9, Table 4.4)

Physoderes shelfordi Miller, 1940, original combination.

Holotype 1 male; MALAYSIA: Sarawak: Kuching, Capt., 1.53055°N 110.34388°E, 12 m, 14 Aug 1899, (Dyak coll.) (UCR_ENT 00018538). The holotype is deposited at the BMNH.

DIAGNOSIS: This species is recognized among other species of *Breviphysoderes* by scape surpassing the apex of the clypeus, antero-lateral pronotal projection oriented anteriorly, deeply defined pronotal paramedian carina, 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. n.** and *B. planicollis* **comb. n.** It can be differentiated from *B. tenebrosa* **n. sp.** by the overall coloration and a narrower postocular lobe. It differs from *B. planicollis* **comb. n.** by the orientation of the antero-lateral pronotal projection and the straw-colored mark on the apical veins of the external cell.

REDESCRIPTION: *MALE:* Medium, total length 9mm. COLORATION (Fig. 4.2): Light brown with dark brown patterns. HEAD: Light brown to dark brown. ANTENNA: Scape straw-colored with light brown apex, basal half of pedicel straw-colored and apical half brown, basi- and distiflagellomeres missing. LABIUM: Light brown. THORAX: Pronotum dark brown with brown suffusion, scutellum dark brown with light brown apex. *Hemelytron:* Corium brown, membrane brown with apical veins of external cell (Cu+M) straw-colored. *Legs:* Femora 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: Dorsally not examined, 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. THORAX: Anterior lobe with tuberculated, short, curved setae on lateral margins and along dorsal ridges, posterior lobe with short, curved, tuberculated setae along lateral margins and sparsely distributed on dorsal surface. *Hemelytron:* Corium with short, curved setae. *Legs:* With two rows of spines and tuberculated setae, tibiae with regular rows of tuberculated, stout, sharp setae. ABDOMEN: Posterior margin of connexivum with short, curved setae. STRUCTURE: HEAD: Elongate conical; maxillary plate truncate apically; scape surpassing apex of clypeus; eye distinctly projecting in dorsal view, about 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; surface of anterior lobe with low ridges; median pronotal depression contiguous with transverse sulcus; paramedian carina strongly defined; posterior lobe medially rugose (damaged/obscured medially by pin); anterior pronotal lobe of equal length to posterior lobe, narrower than posterior lobe, anterior lobe lower than posterior lobe in lateral view; semicircular; scutellum rounded triangular, scutellar process long, apex rounded; mesosternite obscured. *Hemelytron:* Surpassing tip of abdomen. *Legs:* Fore femur distinctly incrassate. ABDOMEN: Elongate ovoid, with rounded terminal margin; connexival margin slightly undulating, posterior margin slightly elevated. MALE GENITALIA: Not examined.

FEMALE: Unknown.

BIOLOGY: Nothing is known about the biology of this species.

DISTRIBUTION: This species is known only from the type locality North-western Borneo, Kuching.

DISCUSSION: This species is redescribed based on the holotype specimen. *B. shelfordi* **comb. n.** is removed from *Physoderes* and transferred to *Breviphysoderes* because it possesses the synapomorphies of *Breviphysoderes* (parascutellar lobes are semicircular, males do not possess an inflated anterior pronotal lobe and has prominent tuberculated setae on the anterior pronotal lobe dorsal ridges). This species is quite similar to other *Breviphysoderes* species found in the 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*, new species** (Figs 4.2, 4.9, Table 4.4)

Holotype 1 male; 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 (UCR_ENT 00018489) (BMNH). The holotype is deposited at the BMNH.

DIAGNOSIS: This species is recognized among other species of *Breviphysoderes* 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. n.** and *B. planicollis* **comb. n.** 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.

DESCRIPTION: *MALE:* Medium, total length 7.07mm. COLORATION (Fig. 4.2): Entirely brownish-black. ANTENNA: Missing. *Legs:* Forelegs missing, mid and hindlegs brownish black. VESTITURE: Densely setose. HEAD: With widespread curved, tuberculated setae, ventral surface of postocular lobe with sparse, tuberculated setae, without pair of long straight setae on postocular lobe posterior to ocelli. THORAX: Anterior lobe with tuberculated, short, curved setae on lateral margins and along dorsal ridges, posterior lobe with short, curved, tuberculated setae along lateral margins and sparsely distributed on dorsal surface. *Hemelytron:* Corium with short, curved setae. *Legs:* Tibiae with regular rows of tuberculated, stout, sharp setae. ABDOMEN: Posterior margin of connexivum with short, curved setae. STRUCTURE: HEAD: Elongate conical; maxillary plate truncate apically; eye distinctly projecting in dorsal view, about 1/5 length of head, not attaining head ventral margin in lateral view; height of anteocular lobe shorter than postocular lobe. THORAX Antero-lateral paired projections acute; surface of anterior lobe with low ridges; median pronotal depression contiguous with transverse sulcus; paramedian carina strongly defined (posterior lobe damaged/obscured medially by pin); anterior pronotal lobe of equal length to posterior lobe, narrower than posterior lobe, anterior lobe lower than posterior lobe in lateral view; semicircular; scutellum rounded triangular, scutellar process long, apex rounded; 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. MALE GENITALIA: Not examined.

FEMALE: Unknown.

ETYMOLOGY: The name *tenebrosa* is selected after the Latin adjective "tenebrosus" meaning dark to describe the distinctive brownish-black coloration of the specimen.

BIOLOGY: This 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* **n. sp.**, *B. planicollis* **comb. n.**, *B. decora* **comb. n.**, and *B. hobbyi* **comb. n.**.

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

***Breviphysoderes vestita* (Horváth), new combination** (Figs 4.2, 4.6, 4.7, 4.9, Table 4.4)

Epirodera vestita Horváth, 1900, original combination.

Physoderes vestita (Horváth), new combination by Maldonado 1990.

Physoderes serraticollis Breddin, 1903, **new synonymy.**

Physoderes javanica Mille, 1940, **new synonymy.**

Physoderes rugosa Miller, 1954, **new synonymy.**

Holotype 1 male; INDONESIA: East Java: Tjibodas (Cibodas), 6.97527°S 107.6625°E, 614 m, No date provided, R. Semon. The holotype is deposited at the HNHM.

DIAGNOSIS: This species is recognized among species of *Breviphysoderes* **n. gen.** by having the head and anterior pronotal lobe distinctly covered with dense, short, curved, tuberculated setae, the scape surpassing 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* **n. sp.** 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).

REDESCRIPTION: *MALE:* Medium, total length 10.02 mm (SD ± 0.24) (Table 4.4). COLORATION (Fig. 4.2): Straw-colored to brown with dark brown patterns. HEAD: Brown. ANTENNA: Scape 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. LABIUM: First segment with basal half brown, apical half straw-colored, second segment straw-colored with base and apex brown, third segment brown. THORAX: Pronotum dark brown with straw-colored setae, scutellum dark brown, pleuron straw-colored to dark brown, sternum brown to dark brown. *Hemelytron:* Corium straw-colored, membrane brown with the apical veins of the external cell (Cu+M) straw-colored, sometimes including the medial vein apex. *Legs:* 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 long, semi-erect, spatulate, curved, tuberculated setae, ventral surface of postocular lobe with sparse, tuberculated setae, with pair of long straight setae on postocular lobe posterior to ocelli. THORAX: Anterior lobe with tuberculated, short, curved setae on lateral margins and along dorsal ridges, posterior lobe with short, curved, tuberculated setae along lateral margins and sparsely distributed on dorsal surface. *Hemelytron:* Corium with short, curved setae. *Legs:* With two rows of spines and tuberculated setae, tibiae with regular rows of tuberculated, stout, sharp setae. ABDOMEN: Posterior margin of connexivum with short, curved setae. STRUCTURE: HEAD: Elongate conical; maxillary plate truncate apically; scape surpassing apex of clypeus; eye distinctly projecting in dorsal view, about 1/5 length of head, not attaining head ventral margin in lateral view; height of anteocular lobe shorter than postocular lobe. 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; posterior lobe medially rugose; anterior pronotal lobe longer than posterior lobe, width equal to posterior lobe or slightly narrower than posterior lobe, anterior lobe higher than posterior lobe in lateral view; semicircular; scutellum rounded triangular, scutellar process long, apex rounded; 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 rounded terminal margin; connexival margin slightly undulating, posterior margin slightly elevated. MALE 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 smooth; cuplike sclerite apically rounded with slight, sclerotized, paired, latero-ventral protuberance; basal plate arms parallel to each other; ductifer with sclerotized elongate ring; endosomal struts conical, with subacute apex, basally divided into two arms; shape of dorsal phallothecal sclerite subacute with narrow, lateral, band-like prolongations, oriented diagonally and angularly curved along lateral margins of phallosoma towards the basal plate.

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

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

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

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

Other specimens examined: INDONESIA: East Java: Nongkodjadjar (Nonkojajar), 7.91611°S 112.8875°E, 846 m, 1911, E. Jacobson, 2;f (RMNH). Java: Buitenzorg (Bogor), 6.6875°S 106.81472°E, 447 m, Mar 1909, Bryant & Palmer, 1;f (AMNH). Gunung Boerangrang (Burangrang), 6.775°S 107.55555°E, 1600 m, Dec. 1936, F. C. Drescher, 1;m (RMNH). Gunung Malabar, 7.13°S 107.65°E, 1600 m, Jun. 1936, F. C. Drescher, 1;f (RMNH). Java, 7.61444°S 110.71222°E, No Date Provided, Muller, 1;f (RMNH); 2999, Unknown, Holotype, 1;f (BMNH). Java, 7.61444°S 110.71222°E, 1000 m, Dec. 1951, L. G. E. Kalshoven, 1;f (RMNH). Lembang, W. Java, 6.82166°S 107.63°E, 1259 m, 1921, L. G. E. Kalshoven, 1;m (RMNH). Megamedg Mountains, 6.61861°S 106.84722°E, 1280 m, No date provided, Bryant & Palmer, 1;f (AMNH), 2;m (USNM). Mt. Patoeha, 7.16138°S 107.39972°E, 1550 m, Mar. 1937, E. Jacobson, 1;f (RMNH). Tangkuban Perahu (Tangkoeban Prahoe) volcano, 4000–5000 ft, 6.76305°S 107.59944°E, 1955 m, Nov. 1936, F. C. Drescher, 1;m (RMNH); Mar. 1937, F. C. Drescher, 1;f (RMNH); Feb. 1937, F. C. Drescher, 6;f (RMNH). Tjisaroea (Cisarua), West Java, 6.78916°S 107.535°E, 1000 m, 11–1–1931, no collector, 1;f (RMNH); 14 Dec 1928, L. G. E. Kalshoven, Holotype, 1;f (RMNH). UNKNOWN: unknown: unknown Co.: none, no date provided, Unknown, 1;m (RMNH).

Macrophysoderes, **new genus** (Figs 4.3, 4.6, 4.7, 4.10, Table 4.4)

Type species: *Physoderes histrionica* Miller, 1940

DIAGNOSIS: This genus is recognized among genera of Physoderinae by often having a glabrous pronotum (except for *M. cirripilosa* **n. sp.,** *M. elongata* **n. sp.** and *M. finisterre* **n. sp.**), the eyes being very large and distinctly projecting in dorsal view and sometimes attaining the ventral margin of the head in lateral view, anterior pronotal lobe narrower or slightly narrower than the posterior lobe, 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. Most similar to *Physoderes*, but 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.

DESCRIPTION: *MALE:* ranging from medium-sized to very large, 7.80 - 11.58 mm. COLORATION (Fig. 4.3): Variable, from straw-colored to dark brown. Head, pronotum, legs, 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. STRUCTURE: HEAD: Elongate or short conical; maxillary plate truncate apically except in *M. bengalensis* **comb. n.** and *M. cirripilosa* **n. sp.**; scape length variable; eye distinctly projecting in dorsal view except in *M. elongata* **n.sp.**, 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 and oriented anteriorly; surface of anterior lobe smooth, ridges almost obsolete or with low ridges; median pronotal depression contiguous with transverse sulcus in both sexes except in *M. cirripilosa* **n. sp.** and *M. elongata* **n.sp.** ; 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* **n.sp.**. *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. MALE GENITALIA: Anterior margin of mediosternite 8 undulating or sharpy 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; cuplike sclerite apically variable; basal plate arms converging or curved to form rounded foramen; ductifer with membranous or sclerotized ring of variable shapes; endosomal struts of variable shapes; dorsal phallothecal 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.

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.

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

DISTRIBUTION: This genus currently comprises 8 described and new species and is widely distributed across Southeast Asia and can be found in peninsular Malaysia, Borneo, Papua New

Guinea and the Solomon Islands. The highest species diversity for this genus is found on Papua New Guinea.

Key to species of *Macrophysoderes*

1. Head elongate conical, scape not reaching apex of clypeus (Fig. 4.3) ....(2)

- Head short conical, scape reaching or surpassing apex of clypeus (Fig. 4.3) ....(4)

2. Hind femur brown with basal and subapical straw-colored annulations (Fig. 4.3) …...*M. histrionica* **comb. n.**

- Hind femur brown with single basal straw-colored annulation (Fig. 4.3) ....(3)

3. Anterior two-thirds of connexivum dark brown, posterior third straw-colored (Fig. 4.3), anterior margin of male mediosternite 8 without apodeme, apical margin of posterior opening of pygophore smooth, without medial process, cuplike sclerite smooth, apically rounded (Fig. 4.6) ....*M. monticola* **comb. n.**

- Connexivum dark brown, posterior margin straw-colored (Fig. 4.3), anterior margin of male mediosternite 8 with apodeme, apical margin of posterior opening of pygophore with small medial process, cuplike sclerite apex with a medial process (Fig. 4.6) ....*M. modesta* **comb. n.**

4. Dorsal surface of pronotum glabrous (Fig. 4.3) ....(5)

- Dorsal surface of pronotum, at least along ridges, with dispersed curved setae (Fig. 4.3) ....(6)

5. Very large (11.58 – 12.66mm), scape surpassing apex of clypeus, head with pair of long, straight setae along posterior margin of postocular lobe, antero-lateral pronotal projections truncate (Fig. 4.3) ....*M. grandis* **n. sp.**

- Large (9mm), 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 (Fig. 4.3) ....*M. bengalensis* **comb. n.**

6. Large (9.47 – 11.11mm), scutellar process short and spatulate, fore femur extremely incrassate, abdomen relatively long (Fig. 4.3) ....*M. elongata* **n. sp.**

   Medium size (7.16 – 11.01mm), scutellar process subacute or rounded, not spatulate, fore femur not extremely incrassate, abdomen not elongated (Fig. 4.3)..................................(7)

7. Body brownish-black, scape just surpassing apex of clypeus, scutellar process very short, connexivum narrow, abdominal apical margin straight (Fig. 4.3) ....*M. finisterre* **n. sp.**

- Body straw-colored and brown, scape reaching apex of clypeus, scutellar process short, connexivum wide, abdominal apical margin rounded (Fig. 4.3) ....*M. cirripilosa* **n. sp.**

***Macrophysoderes bengalensis* (Miller), new combination** (Figs 4.3, Table 4.4)

Epirodera bengalensis Distant, 1909, original combination.

Physoderes bengalensis (Distant), new combination by Maldonado 1990.

Holotype 1 male; INDIA: Bengal: Bengal, 22.98666°N 87.855°E, exact locality, date, and collctor unknown (UCR_ENT 00018528). The holotype is deposited at the BMNH.

DIAGNOSIS: This species is recognized among species of *Macrophysoderes* by the dark brown coloration, the scape reaching the apex of the clypeus, the very large eyes relative to the head, the absence of the paired long setae at the posterior margin of the postocular lobe, the two rows of small tuberculated setae 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 Physoderinae. It is distinguished most easily by its large eyes, the short conical head, and the spine on the fore trochanter.

REDESCRIPTION: *MALE:* Medium, total length 9mm. COLORATION (Fig. 4.3): Brown. HEAD: Brown. ANTENNA: Scape brown, other segments missing. LABIUM: First segment brown, second and third straw brown. THORAX: Anterior lobe of pronotum dark brown, posterior lobe brown, scutellum dark brown, pleuron brown with light brown margin along acetabula, sternum brown. *Hemelytron:* Corium brown with straw brown apex, membrane dark brown. *Legs:* 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, tuberculated setae, without pair of long straight setae on postocular lobe posterior to ocelli. THORAX: Anterior lobe with irregular row of tuberculated, short, curved setae on lateral margins and short, tuberculated setae dispersed on dorsal surface, posterior lobe with only short, sparse setae. *Hemelytron:* Corium glabrous. *Legs:* Fore trochanter with small process on the internal surface, fore femur with two rows of spines and tuberculated setae, fore tibiae with regular rows of tuberculated, stout, sharp setae. ABDOMEN: Connexival margin without setae. STRUCTURE: HEAD: Short conical; maxillary plate truncate apically; scape reaching apex of clypeus; eye distinctly projecting in dorsal view, about 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; median pronotal depression contiguous with transverse sulcus; 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; triangular; scutellum rounded triangular, scutellar process long, apex acute; mesosternite with median irregular tuberculated protrusion between fore and mid coxae. *Hemelytron:* Attaining tip of abdomen. *Legs:* Fore femur distinctly incrassate. ABDOMEN: Elongate ovoid, with straight terminal margin; connexival margin smooth, not undulating, posterior margin not elevated. MALE 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, apodeme present, apical margin of posterior opening smooth; cuplike sclerite apically rounded with sclerotized paired latero-ventral protuberance; basal plate arms converging; ductifer with sclerotized elongate ring; endosomal struts apically truncate, divided into two arms; shape of dorsal phallothecal sclerite subacute with lateral broad, plate-like prolongations, small acute apex and broad lateral plates with rounded margins extended laterally and curved towards the apex.

FEMALE: Unknown.

BIOLOGY: 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 djoining the Indian subcontinent and Myanmar.

DISCUSSION: This species is placed in the *Macrophysoderes* clade based on the phylogenetic analysis above. It is most closely related to *M. monticola* **comb. n.:** 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. n.** possesses several unique characters, especially on the male genitalia.

Other Specimens Examined: INDIA: Meghalaya: Khasi Hills, 25.58333°N 91.63333°E, No date provided, no collector, 1;m (UCR_ENT 00069412) (BMNH).

***Macrophysoderes cirripilosa*, new species** (Figs 4.3, 4.6, 4.7, 4.10, Table 4.4)

Holotype: 1 male; PAPUA NEW GUINEA: Western Province: Fly River, Kiunga, 6.11944°S 141.29194°E, 08 Aug 1957 - 10 Aug 1957, W. W. Brandt (UCR_ENT 00073448). The holotype is deposited at the BPBM.

DIAGNOSIS: This species is recognized among species of *Macrophysoderes* by the short conical head short that is covered with semi-erect, curved setae, with a distinct concentration of setae on the postocular lobe in 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 strongly defined paramedian carina, and the short scutellar process. It resembles most closely *M. finisterre* **n. sp.** and *M. elongata* **n. sp.** It is differentiated from *M. finisterre* **n. sp.** 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* **n. sp.** by the size, the shape of the scutellar process, the relative length of head to body, and the less swollen fore femur.

DESCRIPTION: *MALE:* Medium, total length 8.7 mm, (SD ± 0.66) (Table 4.4). COLORATION (Fig. 4.3): Straw-colored and brown. HEAD: Brown. ANTENNA: Scape and pedicel straw-colored, sometimes with brown suffusion, basiflagellomere brown, distiflagellomere straw-colored with brown base. LABIUM: First segment brown with straw-colored apex, second segment basally and apically brown, medially straw-colored, third segment brown. THORAX: 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 the acetabula, sternum dark brown. *Hemelytron:* Corium light brown to brown, membrane brown. *Legs:* 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, tuberculated setae, ventral surface of postocular lobe with two rows of small, tuberculated setae, with pair of long straight setae on postocular lobe posterior to ocelli. THORAX: Anterior lobe 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. *Hemelytron:* Corium with short, curved setae. *Legs:* With two rows of spines and tuberculated setae, tibiae with regular rows of tuberculated, stout, sharp setae. ABDOMEN: Connexival margin with a few clubbed setae on each segment. STRUCTURE: HEAD: Short conical; maxillary plate truncate apically; scape reaching apex of clypeus; eye distinctly projecting in dorsal view, about 1/5 length of head, attaining head ventral margin 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; bell-shaped skewed towards median; scutellum rounded triangular, scutellar process short, apex rounded; mesosternite with median, irregular, tuberculated protrusion between fore and mid coxae. *Hemelytron:* Not attaining tip of abdomen or attaining tip of abdomen. *Legs:* Fore femur distinctly incrassate. ABDOMEN: Elongate ovoid, with rounded terminal margin; connexival margin slightly undulating, posterior margin not elevated. MALE GENITALIA: Anterior margin of mediosternite 8 sharply emarginate, with medial apodeme; transverse bridge of pygophore narrow, margin of anterior opening rounded, apodeme present, apical margin of posterior opening smooth; cuplike sclerite apically rounded and rim ventrally sclerotized; basal plate arms converging; ductifer with sclerotized rounded ring; endosomal struts conical, with subacute apex, basally divided into two plates; shape of dorsal phallothecal sclerite subacute with lateral broad, plate-like prolongations, short triangular.

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

ETYMOLOGY: The name combines Latin noun "cirrus" meaning curl or hairtuft with Latin adjective "pilosus" meaning hairy to describe the abundant, curved setae on the head especially between the ocelli.

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

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

DISCUSSION: This species is described based on examining 147 specimens. It is the most commonly collected physoderine from the island of Papua 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 indictive 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* **n. gen.** Two other new species, *M. grandis* **n. sp.** and *M. elongata* **n. sp.,** share several characters with *M. cirripilosa* **n. sp.** 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. These species are therefore also placed in *Macrophysoderes* **n. gen.**

Paratypes: PAPUA NEW GUINEA: Western Province: Fly River, Kiunga, 6.11944°S 141.29194°E, 08 Aug 1957 - 10 Aug 1957, W. W. Brandt, 4;m (UCR_ENT 00073446, UCR_ENT 00073447, UCR_ENT 00073453, UCR_ENT 00073454) (BPBM).

Other Specimens Examined: INDONESIA: Irian Jaya: Cyclops Mountains, Ifar, 2.6°S 140.61°E, 300 m, 23 Jul 1962 - 25 Jul 1962, J. Sedlacek, 1;f (UCR_ENT 00073499) (BPBM). Cyclops Mts., 2.8775°S 140.70333°E, 1067 m, Mar. 1936, L. E. Cheesman, 1;f (UCR_ENT 00069271) (BMNH). Cyclops Mts., Mt. Lina, 2.43055°S 140.45333°E, 1067 m, Mar. 1936, L. E. Cheesman, 1;m (UCR_ENT 00069263) (BMNH). Guega, W. of Swart Valley, 3.6°S 138.41666°E, 1200 m, 15 Nov 1958, J. L. Gressitt, 1;m (UCR_ENT 00073468) (BPBM). Ifar, Cyclops Mts., 2.83166°S 140.60555°E, 450 m, 08 Sep 1962, J. Sedlacek, 1;f (UCR_ENT 00073500) (BPBM). Yapen, 1.79472°S 136.30361°E, 600 m, 04 Jan 2007, S. Bily, 1;m (UCR_ENT 00073850) (NMPC). Papua: Paniai Division Co.: Wisselmeren Enarotadi, 4.205°S 136.59305°E, 1900 m, 16 Jul 1962, J. Sedlacek, 1;m (UCR_ENT 00073466) (BPBM). Araboebivak, 2.61527°S 140.62805°E, 06 Oct. 1939, no collector, 1;f (UCR_ENT 00024031) (RMNH). Araucaria Camp, 5.65916°S 139.13583°E, 800 m, Mar 1939, L. J. Toxopeus, 1;f (UCR_ENT 00024011) (RMNH). Bernhard camp, 6.21305°S 141.54805°E, 50 m, 05 Oct 1938, J. Olthof, 1;f (UCR_ENT 00014057) (RMNH); Aug 1938, J. Olthof, 2;f (UCR_ENT 00024007, UCR_ENT 00024008) (RMNH); vii-xi 1938, J. Olthof, 2;f (UCR_ENT 00024009, UCR_ENT 00024010) (RMNH). Hollandia (Jayapura), 2.61527°S 140.62805°E, 500 m, Jul 1938, L. J. Toxopeus, 1;m (UCR_ENT 00024005) (RMNH). Nabire, S. Geelwink Bay, 3.36667°S 135.48333°E, 02 Jul 1962 - 09 Jul 1962, J. L. Gressitt, 1;m (UCR_ENT 00073469) (BPBM). Sibil, Star Mountain Range, 5.2375°S 141.14861°E, 1260 m, 18 Apr 1959, no collector, 1;m (UCR_ENT 00024028) (RMNH); 21 Apr

1959, no collector, 1;m (UCR_ENT 00024030) (RMNH); 25 Apr 1959, no collector, 1;m (UCR_ENT 00024029) (RMNH); 25 May 1959, no collector, 1;m (UCR_ENT 00024006) (RMNH). Wamena, 4.10055°S 138.90472°E, 700 m, 10 Feb 1960 - 25 Feb 1960, T. C. Maa, 1;f (UCR_ENT 00073485), 3;m (UCR_ENT 00073530-UCR_ENT 00073532) (BPBM). PAPUA NEW GUINEA: Bougainville Province: Mt. Nomo, S. of Mt. Bougainville, 6.05361°S 155.19055°E, 213 m, Feb. 1936, L. E. Cheesman, 1;m (UCR_ENT 00069295) (BMNH). Central Province: Iriri, near Kerema, 8.98416°S 146.98944°E, 07 May 1959, C. D. Michener, 1;m (UCR_ENT 00073484) (BPBM). Murua R. near Kerema, 8.08361°S 145.91138°E, 06 May 1959, C. D. Michener, 1;f (UCR_ENT 00073492) (BPBM). Otomata Plantation, 1m E of Moresby, 9.48166°S 147.10361°E, 02 Nov 1960, J. L. Gressitt, 1;m (UCR_ENT 00073481) (BPBM). Owen Stanley Range, Goilala: Bome, 9.57666°S 146.37194°E, 1950 m, 08 Mar 1958 - 15 Mar 1958, W. W. Brandt, 1;m (UCR_ENT 00073483) (BPBM). Owen Stanley range, Goilala: Loloipa, 9.23583°S 147.98444°E, 01 Feb 1958 - 15 Feb 1958, W. W. Brandt, 1;f (UCR_ENT 00073498) (BPBM). East New Britain Province: near Rabaul, 4.175°S 152.24805°E, Feb. 1929, no collector, 1;f (UCR_ENT 00046667) (CAS). East Sepik Province: Amboin Patrol Post, Karawari Lodge, 4.40444°S 142.98555°E, Feb. 1983, A.C Messer, 1;f (UCR_ENT 00031394) (USNM); Mar-Apr 1983, A.C Messer, 1;f (UCR_ENT 00031395) (USNM). May River, 4.40694°S 141.83944°E, 06 Jun 1963, R. Straatman, 1;f (UCR_ENT 00073503) (BPBM). Madang Province: Erima, Astrolabe Bay, 5.4225°S 145.73361°E, 1897, Biro, 1;m (UCR_ENT 00069770), 1;f (UCR_ENT 00069777) (HNHM); 1896, Biro, 1;m (UCR_ENT 00069767), 5;f (UCR_ENT 00069772-UCR_ENT 00069776) (HNHM). Mondo, 5.41666°S 144.76138°E, 1524 m, Feb. 1934, L. E. Cheesman, 1;m (UCR_ENT 00069261) (BMNH). Stephansort, Astrolabe Bay, 5.43638°S 145.74138°E, 1897, Biro, 1;m (UCR_ENT 00069771) (HNHM). Milne Bay Province: Daradae Plain, 80 km N to Port Moresby, 9.78°S 149.76°E, 580 m, 06 Sep 1959, T. C.

Maa, 1;m (UCR_ENT 00073480) (BPBM). Morobe Province: Huon Penninsula Co.: Finschhafen, 6.55527°S 147.17361°E, 20 Apr 1944, E. S. Ross, 2;m (UCR_ENT 00046650, UCR_ENT 00046651), 1;f (UCR_ENT 00046654) (CAS); May 1944, F. Skinner, 1;f (UCR_ENT 00046655) (CAS); 07 May 1944, E. S. Ross, 1;m (UCR_ENT 00046652) (CAS); May 1944, E. S. Ross, 1;m (UCR_ENT 00046653) (CAS); 15 Nov 1969, James E. Tobler, 1;f (UCR_ENT 00046673) (CAS). Huon Gulf, Morobe Disctrict, 6.55861°S 147.50805°E, 22 May- 19 Jun 1937, J. L. Froggatt, 1;f (UCR_ENT 00069312) (BMNH). Sattelberg, Huon-Golf, 6.485°S 147.75861°E, 1899, Biro, 1;m (UCR_ENT 00069788) (HNHM); 1898, Biro, 1;m (UCR_ENT 00069787) (HNHM). Bulolo, 7.20472°S 146.63166°E, 900 m, 27 Mar 1968, P. Colman, 1;m (UCR_ENT 00073467), 1;f (UCR_ENT 00073501) (BPBM). Bumayong, New Guinea, 6.63444°S 147.0025°E, July 1957, R. W. Paine, 1;f (UCR_ENT 00069302) (BMNH). Garaina, 7.88333°S 147.13333°E, 800 m, 04 Jan 1968, J. & M. Sedlacek, 1;f (UCR_ENT 00073496) (BPBM); 15 Jan 1968, J. & M. Sedlacek, 3;m (UCR_ENT 00073474-UCR_ENT 00073476) (BPBM); 13 Jan 1968 - 15 Jan 1968, J. & M. Sedlacek, 1;m (UCR_ENT 00073477) (BPBM). Gewak, Salawaket Range (Saruwaged Range), 6.21694°S 146.75°E, 1530 m, 06 Sep 1956, E.J. Ford, Jr., 1;m (UCR_ENT 00073464) (BPBM). NE Wau, 7.33805°S 146.71555°E, 1270 m, 07 May 1962, J. Sedlacek, 1;m (UCR_ENT 00073612) (BPBM). NE Wau, 7.33805°S 146.71555°E, 02 Jan 1963 - 04 Jan 1963, J. Sedlacek, 1;m (UCR_ENT 00073607) (BPBM). NE Wau, 7.33166°S 146.71805°E, 1010 m, 18 Dec 1968, J. H. Sedlacek, 1;f (UCR_ENT 00073620) (BPBM). NE Wau, 7.32138°S 146.71583°E, 1050 m, 05 Jan 1963, G. Monteith, 1;m (UCR_ENT 00073611) (BPBM); 07 Jan 1963, J. Sedlacek, 2;m (UCR_ENT 00073609, UCR_ENT 00073610), 1;f (UCR_ENT 00073613) (BPBM). NE Wau, Hospital Ck., 7.33805°S 146.71555°E, 1300 m, 05 Dec 1965, J. Sedlacek, 1;m (UCR_ENT 00073606) (BPBM). NE Wau, Mt. Missim 950-1300 m, 7.1167°S 146.9167°E, Mar 1965, J. & M. Sedlacek, 1;m (UCR_ENT

00073478) (BPBM). Waing, Ca 18 mi of Lae, 6.72444°S 146.96805°E, 13 Apr 1965 - 14 Apr 1965, Balogh et. Szent-Ivany, 2;m (UCR_ENT 00069768, UCR_ENT 00069769), 1;f (UCR_ENT 00069778) (HNHM). Wau, 7.33333°S 146.71667°E, Jan-Mar 1982, R.T. Bell, 1;f (UCR_ENT 00073618) (BPBM); Feb-May 1982, R.T. Bell, 2;f (UCR_ENT 00073616, UCR_ENT 00073617) (BPBM). Wau, 7.32138°S 146.71555°E, 1097 m, 11 Sep 1971, W. Gagne, 1;m (UCR_ENT 00046657) (CAS). Wau, 7.3333°S 146.71667°E, 1200 m, 27 Jul 1961, J. & J.H. Sedlacek, 1;f (UCR_ENT 00073614) (BPBM); 23 Dec 1961, G. Monteith, 1;m (UCR_ENT 00073603) (BPBM); 31 Aug 1961, J. Sedlacek, 1;m (UCR_ENT 00073602) (BPBM); 18 Jun 1962 - 25 Jun 1962, J. Sedlacek, 1;m (UCR_ENT 00073599) (BPBM); 14 Mar 1964 - 24 Mar 1964, J. Sedlacek, 1;m (UCR_ENT 00073601) (BPBM); 17 Sep 1964 - 19 Sep 1964, J. Sedlacek, 1;m (UCR_ENT 00073600) (BPBM); 08 Dec 1976 - 14 Dec 1976, G. F. Hevel and R. E. Dietz IV, 1;m (UCR_ENT 00031396) (USNM). Wau, 7.3333°S 146.71667°E, 1300 m, 24 Nov 1963, J. L. Gressitt, 1;m (UCR_ENT 00073605) (BPBM). Wau, 7.3333°S 146.71667°E, 1100 m, 04 Oct 1962, J. Sedlacek, 1;m (UCR_ENT 00073604) (BPBM). Wau, Hospital Ck., 7.33805°S 146.71555°E, 1250 m, 10 Apr 196, J. & M. Sedlacek, 1;m (UCR_ENT 00073608) (BPBM). Wau Ecological Insitute, 7.33805°S 146.71555°E, 04 Dec 1988, R. Holyuski, 1;f (UCR_ENT 00069789) (HNHM). Northern Province: SE Popondetta, 8.76666°S 148.23333°E, 25 m, May 1966, P. Shanahan, 1;m (UCR_ENT 00073465) (BPBM). Oro Province: Kokoda, 8.86083°S 147.73722°E, 350 m, 21 Mar 1956, J. L. Gressitt, 1;f (UCR_ENT 00073497) (BPBM). Kokoda, 8.87777°S 147.7375°E, 366 m, Apr. 1933, L. E. Cheesman, 2;f (UCR_ENT 00069264, UCR_ENT 00069265) (BMNH). Kokoda, 8.87722°S 147.7375°E, 366 m, Jun 1933, L. E. Cheesman, 2;f (UCR_ENT 00069268, UCR_ENT 00069269) (BMNH); Sep 1933, L. E. Cheesman, 3;m (UCR_ENT 00069258-UCR_ENT 00069260), 2;f (UCR_ENT 00069266, UCR_ENT 00069267) (BMNH); Apr. 1933, L. E. Cheesman, 3;m (UCR_ENT 00069255-

UCR_ENT 00069257) (BMNH). Kokoda-Pitoki, 8.8775°S 147.73722°E, 400 m, 24 Mar 1956, J. L. Gressitt, 1;m (UCR_ENT 00073461) (BPBM); 23 Mar 1956, J. L. Gressitt, 2;m (UCR_ENT 00073459, UCR_ENT 00073460), 1;f (UCR_ENT 00073491) (BPBM). NE Kokoda, 8.86861°S 147.74777°E, 400 m, 17 Nov 1965 - 18 Nov 1965, J. & M. Sedlacek, 1;m (UCR_ENT 00073462) (BPBM); 19 Nov 1965, J. & M. Sedlacek, 1;m (UCR_ENT 00073463) (BPBM). Sandaun aka West Sepik Province: Waris, S. of Hollandia, 450-500 m, 3.26667°S 141.05°E, 16 Aug 1959 - 23 Aug 1959, T. C. Maa, 1;m (UCR_ENT 00073470) (BPBM). Simbu Province: Karimui, 6.49611°S 144.82277°E, 1080 m, 13 Jul 1963, J. Sedlacek, 1;f (UCR_ENT 00073504) (BPBM). West New Britain: Silanga, Nakanai Mts., 5.5525°S 150.87°E, 150 m, 31 Jul 1956, E.J. Ford, Jr., 1;f (UCR_ENT 00073507) (BPBM). Western Highlands: Wum, Upper Jimmi V., 5.92972°S 144.26805°E, 840 m, 18 Jul 1955, J. L. Gressitt, 1;m (UCR_ENT 00073482) (BPBM). Western Province: Eliptamin Valley 1200-1350m, 5.17638°S 141.54361°E, 1350 m, 16 Aug 1959 - 30 Aug 1959, W. W. Brandt, 1;m (UCR_ENT 00073479) (BPBM); 01 Sep 1959 - 15 Sep 1959, W. W. Brandt, 1;f (UCR_ENT 00073502) (BPBM). Fly River, Kiunga, 6.11944°S 141.29194°E, 11 Jul 1957 - 14 Jul 1957, W. W. Brandt, 1;m (UCR_ENT 00073458), 2;f (UCR_ENT 00073493, UCR_ENT 00073494) (BPBM); 23 Jul 1957 - 25 Jul 1957, W. W. Brandt, 1;m (UCR_ENT 00073457), 1;f (UCR_ENT 00073495) (BPBM); 05 Aug 1957 - 07 Aug 1957, W. W. Brandt, 1;m (UCR_ENT 00073456) (BPBM); 08 Aug 1957 - 10 Aug 1957, W. W. Brandt, 5;m (UCR_ENT 00073449-UCR_ENT 00073452, UCR_ENT 00073455), 5;f (UCR_ENT 00073486-UCR_ENT 00073490) (BPBM). Star Mts. Sibil Val., 5.04823°S 140.97958°E, 1245 m, 18 Oct 1961 - 08 Nov 1961, S. Quate & L. Quate, 2;m (UCR_ENT 00073472, UCR_ENT 00073473) (BPBM). Koitaki, 8.92527°S 147.73861°E, 457 m, Nov-Dec. 1928, no collector, 1;f (UCR_ENT 00046656) (CAS). Maffin Bay, Dutch New Guinea, 2.09222°S 139.01472°E, Sep 1944, E. S. Ross, 1;m (UCR_ENT 00046658) (CAS). Peria Creek, Kwagira River, 9.63111°S 149.38555°E, 50 m, 14 Aug 1953 - 06 Sep 1953, Geoffrey M. Tate, 1;m (UCR_ENT 00068948) (AMNH). unknown: Kalalo, 6.76°S 147.91027°E, 750 m, 20 Aug 1966 - 30 Aug 1966, G. A. Samuelson, 2;f (UCR_ENT 00073508, UCR_ENT 00073509) (BPBM). Mafulu, 8.45388°S 146.7425°E, 1219 m, Jan. 1934, L. E. Cheesman, 1;m (UCR_ENT 00069262) (BMNH). UNKNOWN: none, No date provided, Saunders, 1;m (UCR_ENT 00069270) (BMNH).

***Macrophysoderes elongata*, new species** (Figs 4.3, 4.6, 4.7, 4.10, Table 4.4)

Holotype 1 male; PAPUA NEW GUINEA: Morobe Province: Mt. Missim, 7.1167°S 146.9167°E, 1600 m, 21 Sep 1964 – 24 Sep 1964, M. Sedlacek (UCR_ENT 00073634). The holotype is deposited at the BPBM.

DIAGNOSIS: This species is recognized among species of *Macrophysoderes* by the large size, the short conical head with semi-erect, curved setae on the postocular lobe in between the ocelli, the length of the scape reaching the apex of the clypeus, the very large eye that is not attaining 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 apical margin straight. This species is closest to *M. grandis* **n. sp.**, but is differentiated by the body size, head shape, scape length, eye shape, and the shape of the anterior pronotal lobe.

DESCRIPTION: *MALE:* Large, total length 10.29 mm, (SD ± 0.47) (Table 4.4). COLORATION (Fig. 4.3): Brown. HEAD: Brown. ANTENNA: Scape straw-colored to light brown sometimes with brown apex, pedicel basally brown and apically straw-colored, basiflagellomere brown, distiflagellomere basally brown, apically straw-colored. LABIUM: First segment basally brown, apically light brown, second segment basally and apically brown, medially straw-colored or light brown, third segment brown. THORAX: 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. *Hemelytron:* Corium brown to dark brown, membrane dark brown. *Legs:* 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 yellowish orange, ventrally brown medially with sub-lateral dark and light brown patterns, connexivum anterior half 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, tuberculated setae, with pair of long straight setae on postocular lobe, posterior to ocelli. THORAX: Anterior lobe with irregular row of tuberculated, short, curved setae on lateral margins and short, tuberculated setae dispersed on dorsal surface, posterior lobe with short, curved, tuberculated setae along lateral margins and sparsely distributed on dorsal surface. *Hemelytron:* Corium with short, curved setae. *Legs:* With two rows of spines and tuberculated setae, tibiae with regular rows of tuberculated, stout, sharp setae. ABDOMEN: Connexival margin with no prominent paired setae, or connexival margin with a few clubbed setae on each segment. STRUCTURE: 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 anteocular 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; bell-shaped skewed towards median; scutellum rounded triangular, scutellar process short, apex spatulate; mesosternite with tuberculated setae, but no protrusion. *Hemelytron:* Surpassing tip of abdomen. *Legs:* Fore femur distinctly incrassate. ABDOMEN: Elongate ovoid, with straight terminal margin; connexival margin smooth, not undulating, posterior margin not elevated. MALE GENITALIA: Anterior margin of mediosternite 8 sharply emarginate, with medial apodeme; transverse bridge of pygophore narrow, margin of anterior opening angular, apodeme present, apical margin of posterior opening smooth; cuplike sclerite apically rounded and rim ventrally sclerotized; basal plate arms rounded; ductifer membranous; endosomal struts apically spatulate, basally divided into two plates; shape of dorsal phallothecal 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.

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

BIOLOGY: This species was collected from high altitudes ranging between 1200m - 2100m.

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

DISCUSSION: This species shares characters with *M. cirripilosa* **n. sp**., including the setose, short, and conical head, the very large eyes, the shape of the parascutellar lobe and the anterior pronotal lobe almost as wide as the posterior lobe. It is thus placed in *Macrophysoderes* **n. gen.**

Paratypes: PAPUA NEW GUINEA: Central Province: Owen Stanley Range, Goilala: Bome, 8.45567°S 146.7412°E, 1950 m, 24 Feb 1958 – 07 Mar 1958, W. W. Brandt, 1;m (UCR_ENT 00073630) (BPBM). Eastern Highlands: Goroka-Kabebe, 6.08777°S 145.38666°E, 1800 m, 24 Jun 1955, J. L. Gressitt, 1;m (UCR_ENT 00073636) (BPBM). Morobe Province: South Garaina, 7.88694°S 147.13277°E, 1800 m, 08 Jan 1968 – 14 Jan 1968, J. & M. Sedlacek, 1;m (UCR_ENT 00073633) (BPBM). Wau, Big Wau Ck., 7.33416°S 146.71833°E, 1350 m, Sep 1965, J. & M. Sedlacek, 1;m (UCR_ENT 00073583) (BPBM).

Other Specimens Examined: PAPUA NEW GUINEA: Eastern Highlands: Okapa District Co.: 13 km SE Okapa, 6.30388°S 145.33666°E, 1650 m, 26 Aug 1964, J. Sedlacek, 1;f (UCR_ENT 00073506) (BPBM). Purosa, 20–26 km SE Okapa, 6.64944°S 145.56972°E, 2000 m, 28 Aug 1964, J. Sedlacek, 1;f (UCR_ENT 00073505) (BPBM). Kainantu, 6.28972°S 145.85916°E, 2100 m, 08 Jan 1965, J. & M. Sedlacek, 1;f (UCR_ENT 00073637) (BPBM). Moife, 15km NW of Okapa, 6.43206°S 145.49581°E, 2100 m, 11 Oct 1959 – 13 Oct 1959, T. C. Maa, 2;f (UCR_ENT 00073639, UCR_ENT 00073640) (BPBM). Gulf province: NE Wau: Biaru, 8.4875°S 146.34444°E, 1225 m, 08 Oct 1978, J. L. Gressitt, 1;m (UCR_ENT 00073635) (BPBM). Morobe Province: NE Wau, 7.33805°S 146.71555°E, 1270 m, 11 Sep 1964, M. Sedlacek, 1;m (UCR_ENT 00073632) (BPBM). NE Wau, 7.3333°S 146.71667°E, 1200 m, 07 Sep 1961, J. Sedlacek, 1;m (UCR_ENT 00073631) (BPBM). NE Wau Ck., Wau, 7.33166°S 146.71805°E, 1500 m, 16 Sep 1964 – 18 Sep 1964, M. Sedlacek, 1;f (UCR_ENT 00073619) (BPBM).

***Macrophysoderes finisterre*, new species** (Figs 4.3, 4.6, 4.7, 4.10, Table 4.4)

Holotype: 1 male; PAPUA NEW GUINEA: Madang Province: Finisterre Mts., Damanti, 5.92027°S 146.22555°E, 1082 m, 2-11 Oct 1964, no collector (UCR_ENT 00069280). The holotype is deposited at the BMNH.

DIAGNOSIS: This species is recognized among species of *Macrophysoderes* by the overall brownish-black color, the short conical head with semi-erect, curved setae on the postocular lobe in between the ocelli, the length of the scape that is just surpassing the apex of the clypeus, the very large eye that is attaining 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* **n. sp.** and *M. elongata* **n. sp.** It is differentiated from *M. cirripilosa* by the overall coloration, shape of the antero-lateral pronotal projections, narrower anterior pronotal lobe, and the shape of the abdominal apical margin. It differs from *M. elongata* by the size, shape of the scutellar process, the relative length of the head versu the body, and the only slightly swollen fore femur.

REDESCRIPTION: *MALE:* Medium, total length 8.85 mm (SD ± 0.38) (Table 4.4). COLORATION (Fig. 4.3): Brownish-black. HEAD: Brownish-black. ANTENNA: Scape straw-colored to light brown with brown apex, pedicel light brown suffused with brown, basiflagellomere brown, distiflagellomere basally brown, apically straw-colored. LABIUM: First segment light brown, second segment basally and apically brown, medially straw-colored or light brown, third segment brown. THORAX: 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. *Hemelytron:* Corium brownish black, membrane brownish black. *Legs:* 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, tuberculated setae, ventral surface of postocular lobe with two rows of small, tuberculated setae, with pair of long straight setae on postocular lobe posterior to ocelli. THORAX: Anterior lobe 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. *Hemelytron:* Corium with short, curved setae. *Legs:* With two rows of spines and tuberculated setae, tibia with regular rows of tuberculated, stout, sharp setae. ABDOMEN: Connexival margin with a few clubbed setae on each segment. STRUCTURE: HEAD: Short conical; maxillary plate rounded apically; scape reaching apex of clypeus, or surpassing apex of clypeus; eye distinctly projecting in dorsal view, about 1/5 length of head, attaining head ventral margin in lateral view; height of anteocular lobe shorter than postocular lobe. THORAX Antero-lateral paired projections 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; bell-shaped skewed towards median; scutellum rounded triangular, scutellar process very short, apex subacute; mesosternite with median irregular tuberculated protrusion between fore and mid coxae. *Hemelytron:* Attaining tip of abdomen. *Legs:* Fore femur distinctly incrassate. ABDOMEN: Elongate ovoid, with straight terminal margin; connexival margin slightly undulating, posterior margin not elevated. MALE 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; cuplike sclerite apically rounded and rim ventrally sclerotized; basal plate arms converging; ductifer with sclerotized rounded ring; endosomal struts conical, subacute apex, divided into two plates basally; shape of dorsal phallothecal sclerite subacute with lateral broad, plate-like prolongations, elongated longitudinal plates close to the dorsal surface.

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

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

BIOLOGY: This species was collected from an altitude between 1000 - 1200m.

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

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

Paratypes: PAPUA NEW GUINEA: Madang Province: Finisterre Mts., Damanti, 5.92027°S 146.22555°E, 1082 m, 2-11 Oct 1964, no collector, 1;m (UCR_ENT 00069278) (BMNH); 2-11 Oct 1964, no collector, 1;m (UCR_ENT 00069276) (BMNH); 2-11 Oct 1964, no collector, 2;m (UCR_ENT 00069274, UCR_ENT 00069275) (BMNH).

Other Specimens Examined: PAPUA NEW GUINEA: Madang Province: Finisterre Mts., Budemu, 5.95222°S 146.37055°E, 1219 m, 15-24 Oct 1964, no collector, 1;m (UCR_ENT 00069279) (BMNH). Finisterre Mts., Budemu Station No. 52, 5.95222°S 146.37055°E, 1219 m, 15-24 Oct 1964, no collector, 2;f (UCR_ENT 00069288, UCR_ENT 00069289) (BMNH). Finisterre Mts., Damanti, 5.92027°S 146.22555°E, 1082 m, 2-11 Oct 1964, no collector, 1;m (UCR_ENT 00069277) (BMNH); 2-11 Oct 1964, no collector, 2;m (UCR_ENT 00069272, UCR_ENT 00069273) (BMNH). Finisterre Mts., Damanti Station No. 33, 5.92027°S 146.22555°E, 1082 m, 2-11 Oct 1964, no collector, 2;f (UCR_ENT 00069285, UCR_ENT 00069286) (BMNH). Finisterre Mts., Damanti Station No. 34, 5.92027°S 146.22555°E, 1082 m, 2-11 Oct 1964, no collector, 1;f (UCR_ENT 00069287) (BMNH). Morobe Province: Herzog Mts, Vagau C. Sation 137, 6.76638°S 146.8°E, 1219 m, 4-17 Jan 1965, no collector, 2;m (UCR_ENT 00069281, UCR_ENT 00069282), 2;f (UCR_ENT 00069283, UCR_ENT 00069284) (BMNH).

***Macrophysoderes grandis*, new species** (Figs 4.3, 4.6, 4.7, 4.10, Table 4.4)

Holotype 1 male; PAPUA NEW GUINEA: Morobe Province: Bulolo, 7.20472°S 146.63166°E, 1010 m, 23 Aug 1956, E.J. Ford, Jr., Light Trap, (UCR_ENT 00052314). Holotype deposited at BPBM.

DIAGNOSIS: This species is recognized among other species of *Macrophysoders* by its very large size, the elongate conical head, the scape surpassing the apex of clypeus, the bulbous eye that is attaining 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 the characters listed above especially its large size.

DESCRIPTION: *MALE:* Very large, total length 11.58mm. COLORATION (Fig. 4.3): Brown with straw-colored markings. HEAD: Brown. ANTENNA: Scape and pedicel straw-colored with brown suffusion, basiflagellomere brown, distiflagellomere straw-colored with brown base. LABIUM: First segment light brown, second segment basally and apically brown, medially straw-colored, third segment brown. THORAX: Pronotum brown, scutellum basally brown to dark brown, apically straw-colored or light brown, pleuron brown, sternum brown and straw-colored. *Hemelytron:* Corium and membrane brown. *Legs:* Femora 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. THORAX: Anterior lobe with irregular row of tuberculated, short, curved setae on lateral margins and glabrous dorsal surface, posterior lobe glabrous. *Hemelytron:* Corium glabrous. *Legs:* With two rows of spines and tuberculated setae, tibiae with a few prominent tuberculated, stout, sharp setae. ABDOMEN: Connexival margin with no setae. STRUCTURE: HEAD: Elongate conical; maxillary plate rounded apically; scape surpassing apex of clypeus; eye distinctly projecting in dorsal view, about 1/5 length of head, attaining head ventral margin 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; median pronotal depression contiguous with transverse sulcus; 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; bell-shaped skewed towards median; scutellum rounded triangular, 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, posterior margin not elevated. MALE GENITALIA: Anterior margin of mediosternite 8 sharply emarginate, without medial apodeme; transverse bridge of pygophore narrow, margin of anterior opening rounded, apodeme present, apical margin of posterior opening smooth; cuplike sclerite apically rounded and rim ventrally sclerotized; basal plate arms rounded; ductifer with sclerotized rounded ring; endosomal struts conical, subacute apex, divided into two plates basally; shape of dorsal phallothecal sclerite subacute with lateral broad, plate-like prolongations, short plates extended diagonally.

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

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

BIOLOGY: This species is known only from two specimens caught from a light trap set at 1010m altitude.

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

DISCUSSION: This species shares characters with *M. cirripilosa* **n. sp.** including the setose conical head, the very large eyes, and the shape of the parascutellar lobe. It is thus placed in *Macrophysoderes* **n. gen.**

Paratypes: PAPUA NEW GUINEA: Morobe Province: Bulolo, 7.20472°S 146.63166°E, 1010 m, 28 Aug 1956, E.J. Ford, Jr., Light Trap, 1;f (UCR_ENT 00073625) (BPBM).

***Macrophysoderes histrionica* (Miller), new combination** (Figs 4.3, 4.10, Table 4.4)

Physoderes histrionica Miller, 1940, original combination.

Holotype 1 male; MALAYSIA: Sabah: N. Borneo, Bettotan, nr. Sandakan, 5.28222°N 117.59305°E, 19 Aug 1927, C. Boden Kloss and H. M. Pendlebury (UCR_ENT 00018520). The holotype is deposited at the BMNH.

DIAGNOSIS: This species is recognized among species of *Macrophysoderes* by the dark brown coloration, 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. n.,** but is differentiated by the color pattern and shape of the scutellar spine and the color pattern on the hind femur.

REDESCRIPTION: *MALE:* Medium, total length 8.5mm. COLORATION (Fig. 4.3): Brown. HEAD: Brown. ANTENNA: Scape straw-colored with brown apex, pedicel brown with straw-colored apex, basiflagellomere brown, distiflagellomere basally brown, apically straw-colored. LABIUM: First segment brown, second segment straw-colored with brown base, third segment brown. THORAX: Pronotum brown or dark brown, scutellum dark brown, pleuron brown or dark brown, sternum brown or dark brown. *Hemelytron:* Corium brown or dark brown, membrane brownish-black. *Legs:* Fore and mid femora 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, tuberculated setae, with pair of long straight setae on postocular lobe posterior to ocelli. THORAX: Anterior lobe 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. *Hemelytron:* Corium glabrous. *Legs:* With two rows of spines and tuberculated setae, tibiae with regular rows of tuberculated, stout, sharp setae. ABDOMEN: Connexival margin with a few clubbed setae on each segment. STRUCTURE: 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 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; rounded lobe skewed towards median; scutellum rounded triangular, scutellar process long, apex subacute; 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 rounded terminal margin; connexival margin undulating, posterior margin not elevated. MALE GENITALIA: Not examined.

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

BIOLOGY: Unknown.

DISTRIBUTION: This species is known only from two localities in North Borneo, Sabah.

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

Paratypes: MALAYSIA: Sabah: N. Borneo, Bettotan, nr. Sandakan, 5.28222°N 117.59305°E, 17 Aug 1927, C. Boden Kloss and H. M. Pendlebury, 1;f (UCR_ENT 00018506) (BMNH); 02 Aug 1927, C. Boden Kloss and H. M. Pendlebury, 1;f (UCR_ENT 00018502) (BMNH); 18 Aug 1927, C. Boden Kloss and H. M. Pendlebury, 1;f (UCR_ENT 00018505) (BMNH).

Other Specimens Examined: MALAYSIA: Sabah: Sandakan, 5.8333°N 118.1167°E, 4 m, No date provided, Baker, 1;f (UCR_ENT 00030983) (USNM).

***Macrophysoderes modesta* (Miller), new combination** (Figs 4.3, 4.6, 4.7, 4.10, Table 4.4)

Physoderes modesta Miller, 1940, original combination.

Physoderes sibauana Miller, 1940, **new synonymy.**

Physoderes trusana Mille, 1940, **new synonymy.**

Holotype 1 male; MALAYSIA: Sarawak: Sarawak, Borneo [2.56055°N 113.00555°E], 112 m, 1909, C. J. Brooks, 1;m (UCR_ENT 00018533). The holotype is deposited at the BMNH.

DIAGNOSIS: This species is recognized among species of *Macrophysoderes* by the elongate conical head, the rounded maxillary plate, the anteocular lobe being almost at 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 scutellar process apex being straw-colored and acute, the undulating connexivum, the cuplike sclerite with distinct medial process, the flaplike prolongations of the phallosoma being plate-like and with a uniform basal margin. It is similar to *M. monticola* **comb. n.** and *M. histrionica* **comb. n.**, but can be differentiated by the uniform color of the legs and connexiva, the margin of the pygophore posterior opening with a medial process and cuplike sclerite, and the shape of the plate-like prolongations of the phallosoma.

REDESCRIPTION: *MALE:* Medium, total length 9.45mm (SD ± 0.05) (Table 4.4). COLORATION (Fig. 4.3): Dark brown. HEAD: Dark brown. ANTENNA: Scape brown, straw brown basally, pedicel brown, basi- and distiflagellomere brown. LABIUM: Brown. THORAX:

Pronotum dark brown, scutellum dark brown, pleuron dark brown, sternum dark brown. *Hemelytron:* Corium dark brown, membrane black to dark brown. *Legs:* 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, tuberculated setae, without pair of long straight setae on postocular lobe posterior to ocelli. THORAX: Anterior lobe 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. *Hemelytron:* Corium with short, sparse, adpressed setae. *Legs:* With two rows of spines and tuberculated setae, tibiae with regular rows of tuberculated, stout, sharp setae. ABDOMEN: Posterior margin of connexivum with short, fine setae. STRUCTURE: 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 head ventral margin 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; rounded lobe skewed towards median; scutellum rounded triangular, scutellar process long, apex subacute; mesosternite with 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 undulating, posterior margin not elevated. MALE 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; cuplike sclerite with medial process; basal plate arms rounded; ductifer membranous; endosomal struts conical, subacute apex, basally divided into two arms; shape of dorsal phallothecal sclerite subacute with lateral broad, plate-like prolongations.

FEMALE: Similar to male.

BIOLOGY: Nothing is known about the biology of this species.

DISTRIBUTION: This species is collected from only two localities within Sarawak, Malaysia: Mt. Sibau and another unknown locality within Sarawak.

DISCUSSION: Based on the phylogenetic analysis above, this species forms a monophyletic clade together with *M. bengalensis* **comb. n.** as part of the *Macrophysoderes* **n. gen.** clade. Examination of the type specimens for *P. sibauana* and *P. trusana* show no morphological differences between them and are hereby synonymized under *M. modesta* **comb. n.**

Other Specimens Examined: MALAYSIA: Sabah: N. Borneo, Bettotan, nr. Sandakan, 5.28222°N 117.59305°E, 25 Jul 1927, C. Boden Kloss and H. M. Pendlebury, 1;f (UCR_ENT 00018507) (BMNH); 26 Jul 1927, C. Boden Kloss and H. M. Pendlebury, 1;f (UCR_ENT 00018503) (BMNH); 19 Aug 1927, C. Boden Kloss and H. M. Pendlebury, 1;f (UCR_ENT 00018504) (BMNH). Sandakan, 5.8333°N 118.1167°E, 4 m, No date provided, Baker, 1;f (UCR_ENT 00030982) (USNM). Sarawak: SAR, 2.55722°N 113.00111°E, 113 m, No date provided, Saunders, 1;f (UCR_ENT 00069384) (BMNH). Sarawak, Borneo, 2.56055°N 113.00555°E, 112 m, 1909, C. J. Brooks, 1;m (UCR_ENT 00069386) (BMNH).

***Macrophysoderes monticola* (Miller), new combination** (Figs 4.3, 4.6, 4.7, 4.10, Table 4.4)

Physoderes monticola Miller, 1940, original combination.

Physoderes dimidiata Miller, 1940, **new synonymy.**

Physoderes luiana Miller, 1940, **new synonymy.**

Holotype 1 male; MALAYSIA: Perak: Taiping Co.: Larut Hills, 5.00°N 100.88333°E, 1372 m, 21 Feb 1932, H. M. Pendlebury (UCR_ENT 00018534). The holotype is deposited at the BMNH.

DIAGNOSIS: This species is recognized among species of *Macrophysoderes* **gen. n.** 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 straw-colored, the connexivum undulating, and the plate-like and angular flaplike prolongations of the phallosoma. It is similar to *M. modesta* **comb. n.** and *M. histrionica* **comb. n.**, but can be differentiated by the color of the legs, scutellar spine and connexiva, the shape of the pygophore posterior opening margin and cuplike sclerite, and the shape of the plate-like prolongations of the phallosoma.

REDESCRIPTION: *MALE:* Medium, total length 10.34mm. COLORATION (Fig. 4.3): Dark brown. HEAD: Dark brown. ANTENNA: Scape brown, straw brown basally, pedicel brown, basi- and distiflagellomere brown. LABIUM: Brown. THORAX: Pronotum dark brown, scutellum dark brown, pleuron dark brown, sternum dark brown. *Hemelytron:* Corium dark brown, membrane black to dark brown. *Legs:* 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, connexivum anterior two-thirds dark brown, posterior third straw-colored. VESTITURE: Glabrous. HEAD: With some flat, curved setae, ventral surface of postocular lobe with sparse, tuberculated setae, without pair of long straight setae on postocular lobe posterior to ocelli. THORAX: Anterior lobe 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. *Hemelytron:* Corium with short, sparse, adpressed setae. *Legs:* With two rows of spines and tuberculated setae, tibia with regular rows of tuberculated, stout, sharp setae. ABDOMEN: Connexival margin with a few clubbed setae on each segment. STRUCTURE: 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 head ventral margin 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; rounded lobe skewed towards median; scutellum rounded triangular, scutellar process long, apex subacute; mesosternite with 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 undulating, posterior margin not elevated. MALE 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; cuplike sclerite apically rounded and rim ventrally sclerotized; basal plate arms parallel to each other; ductifer membranous; endosomal struts conical, subacute apex, divided into two arms basally; shape of dorsal phallothecal sclerite subacute with lateral broad, plate-like prolongations, broad plates angularly oriented towards basal plate.

FEMALE: Similar to male in size, shape and color.

BIOLOGY: 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.

DISCUSSION: Based on the phylogenetic analysis above, this species forms a monophyletic clade with *M. bengalensis* **comb. n.** as part of the *Macrophysoderes* **n. gen.** clade. Other species closely resembling *M. monticola* **comb. n.** are also transfered to *Macrophysoderes* **n. gen.** based on the hypothesis that they are most closely related, namely *M. modesta* **comb. n.** and *M. histrionica* **comb. n.** Examination of the type specimens for *P. dimidiata* and *P. luiana* show no morphological differences except for size and are hereby synonymized with *M. monticola* **comb. n.** *M. modesta* **comb. n. and** *M. monticola* **comb. n.** are highly similar and difficult to distinguish other than based on male genitalia morphology and distribution.

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

Other Specimens Examined: MALAYSIA: Perak: Jor Camp, 4.89972°N 100.79055°E, 610 m, 30 Aug 1922, E. Seimund, 1;f (UCR_ENT 00069388) (BMNH). Selangor: Dusun Tua, 3.14555°N 101.83888°E, Jan 12 1930, H. M. Pendlebury, 1;f (UCR_ENT 00069390) (BMNH). Gombak Valley, 3.13027°N 101.65777°E, Oct 12 1921, H. M. Pendlebury, 1;m (UCR_ENT 00069391) (BMNH). Kuala Lumpur, 17th miles Kanching, 3.13888°N 101.68666°E, 22 Oct 1922, H. M. Pendlebury, 1;m (UCR_ENT 00018521), 1;f (UCR_ENT 00018509) (BMNH). Kuala Sleh, 3.02472°N 101.71638°E, 17 May 1936, H. M. Pendlebury, 1;f (UCR_ENT 00018508) (BMNH). Sungei Lui, Ulu Langat, 3.03805°N 101.70583°E, 86 m, 13 Aug 1933, N.C.E. Miller, 1;f (UCR_ENT 00018514) (BMNH).

Nanophysoderes, **new genus** (Figs 4.3, 4.11, Table 4.4)

Type species: *Physoderes dentiscutum* Bergroth, 1906.

DIAGNOSIS: This genus is recognized among other genera of Physoderinae by the small size, the pair of prominent tuberculated setae on the ventral surface of the postocular lobe, the lateral margins of the anterior pronotal lobe being straight and not curved, the semicircular shape of the scutellum, the scutellum with distinct paired lateral tubercles, the mesosternum with three longitudinal rows of setae, and the armature of the fore femur consisting of two dense rows of tuberculated setae. 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 throughout the body, paired projections on the scutellum, and the three longitudinal rows of setae on the mesosternum.

DESCRIPTION: *FEMALE:* Small, total length 7-8mm. COLORATION (Fig. 4.3): Brown to straw brown. HEAD: Brown, neck straw brown. ANTENNA: Straw brown with brown suffusion. LABIUM: Straw brown. THORAX: Pronotum brown, scutellum brown, pleuron brown, sternum brown. *Hemelytron:* Corium 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 tuberculated setae, with pair of long straight setae wider apart on postocular lobe posterior to ocelli. THORAX: Anterior lobe 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. *Hemelytron:* Corium with short, sparse, adpressed setae. *Legs:* With two rows of tuberculated setae, tibiae with regular rows of tuberculated, stout, sharp setae. ABDOMEN: Connexival margin without setae. STRUCTURE: HEAD: Short conical; maxillary plate apically truncate; scape not reaching 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 anteocular 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 lobes bell-shaped and skewed towards median; scutellum semicircular, scutellar process long, apex subacute; 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, not undulating, posterior margin not elevated.

MALE: Male unknown.

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.

BIOLOGY: Unknown.

DISTRIBUTION: Known only from the locality of the holotype of the type species that on the label is provided as “New Guinea”.

DISCUSSION: Based on the phylogeny, *N. dentiscutum* **comb. n.** is sister to all other physoderines except for the Neotropical and Afrotropical species. The isolated placement of *N. dentiscutum* **comb. n.** 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), new combination** (Figs 4.3, 4.11, Table 4.4)

Physoderes dentiscutum Bergroth, 1906, original combination.

Holotype 1 female; INDONESIA: Irian Jaya: New Guinea (W), 4.24891°S 135.79065°E, 285 m, 1869, Higgins, (UCR_ENT 00037370). The holotype is deposited at the ISNB.

DIAGNOSIS AND REDESCRIPTION: as in generic description.

Paraphysoderes Villiers (Figs 4.4, 4.6, 4.7, 4.11, Table 4.4)

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

DIAGNOSIS: This genus is recognized among other genera of Physoderinae by its small size (6.30 – 7.09mm), 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 scutellar spine being acute, and the fore tibia bearing a few prominent processes with sharp, stout, setae. Most similar to *Physoderoides* Miller (1955), but distinguished by the body size, head shape, the maxillary plate not being raised, and the lack of antero-lateral pronotal projections.

REDESCRIPTION: *MALE:* Small, total length 6.30 - 7.09mm. COLORATION (Fig. 4.4): 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. STRUCTURE: HEAD: Short conical; maxillary plate rounded apically; scape surpassing apex of clypeus; eye relatively large, hemispherical or projecting in dorsal view, not attaining 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, not undulating, posterior margin not elevated. MALE GENITALIA: Only examined for *P. popeye* **n. sp.**, refer to species description.

FEMALE: Similar to males, but larger and with wider abdomen.

BIOLOGY: No information available for the Malagasy species while *P. popeye* **n. sp.** has been recorded on *Pandanus*.

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.

DISCUSSION: Based on the phylogenetic analysis above, the new species *P. popeye* **n. sp.** forms a monophyletic clade with *Paraphysoderes peyrierasi* and *Paraphysoderes crassa*. It shares the synapomorphies of the small body size and the fore tibia bearing a few prominent tuberculated setae. Closer examination also revealed similarities in the shape of the head and pronotum, a similar acute scutellar process, and the hemelytron not attaining the tip of the abdomen. This evidence led to classifying this new species as *Paraphysoderes*, even though this significantly exapands the distribution range of this genus that was previously restricted to Madagascar.

Key to *Paraphysoderes* species

1. Fore femur longer than mid femur, surpassing apex of clypeus, scutellar process acute and tapered, Cu and M veins not parallel, converging basally, Pacific distribution (Fig. 4.4) ....*P. popeye* **n. sp.**

- Fore femur as long as or shorther than mid femur, not surpassing apex of clypeus, scutellar process subacute, Cu and M veins parallel, not converging, restricted to Madagascar..(2)

2. Body reddish-brown, scutellum apex and scutellar process straw-colored, connexivum uniformly reddish-brown ....*P. peyrierasi*

- Body brown, scutellum and scutellar process brown, anterior half of connexivum dark brown, posterior half light brown ....*P. crassa*

***Paraphysoderes popeye*, new species** (Figs 4.4, 4.6, 4.7, 4.11, Table 4.4)

Holotype 1 male; PAPUA NEW GUINEA: Morobe Province: Didymann's Ck., Lae, 6.72444°S 146.99083°E, 15 m, 30 Apr 1963, J. Sedlacek (UCR_ENT 00073584). The holotype is deposited at the BPBM.

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 with the connecting vein with the first anal vein (1A), the hemelytron not attaining the tip of the abdomen, the distinctly incrassate fore femur that is longer than the mid femur, 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.

DESCRIPTION: *MALE:* Small, total length 7.09mm. COLORATION (Fig. 4.4): Brown to dark brown. HEAD: Brown or dark brown. ANTENNA: Scape and pedicel light brown with brown suffusion, disti- and basi-flagellomeres straw-colored. LABIUM: First segment brown, second segment basally brown, medially straw-colored, apically brown, third segment brown. THORAX: Pronotum dark brown, scutellum dark brown, pleuron dark brown, sternum dark brown. *Hemelytron:* Corium dark brown, membrane dark brown. *Legs:* Fore and mid femora and tibiae light brown and brown, tarsi and claws light brown, hind femur dark brown with medial light brown annulation, hind tibia light brown and 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, tuberculated setae, without pair of long straight setae on postocular lobe posterior to ocelli. THORAX: Anterior lobe with irregular row of tuberculated, short, curved setae on lateral margins and short, tuberculated setae dispersed on dorsal surface, posterior lobe with short, curved, tuberculated setae on humeral angle and glabrous on dorsal surface. *Hemelytron:* Corium with short, sparse, adpressed setae. *Legs:* With two rows of spines and tuberculated setae, tibia with a few prominent tuberculated, stout, sharp setae. ABDOMEN: Connexival margin without prominent setae. STRUCTURE: HEAD: Elongate conical; maxillary plate rounded apically; scape 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 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 attaining tip of abdomen. *Legs:* Fore femur distinctly incrassate. ABDOMEN: Elongate ovoid, with straight terminal margin; connexival margin smooth, not undulating, posterior margin not elevated. MALE 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; cuplike sclerite apically rounded with sclerotized paired latero-ventral slight protuberance; basal plate arms parallel to each other; ductifer with sclerotized rounded ring; endosomal struts tube-like, with medial sclerotization with a T-shape apex; shape of dorsal phallothecal 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 (7.89mm average total length) with wider abdomen (2.56mm males, 3.32mm 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.

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.

BIOLOGY: This species has been recorded on *Pandanus*.

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

DISCUSSION: A damaged female specimen from Fiji (not described here) that is most likely not the same species as *P. popeye* **n. sp**., 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 here.

Paratypes: PAPUA NEW GUINEA: Morobe Province: Huon Penninsula Co.: Pindiu, 6.44388°S 147.515°E, 450 m, 19 Apr 1963, J. Sedlacek, 1;f (UCR_ENT 00073624) (BPBM). Bulolo, 7.20472°S 146.63166°E, 130 m, 30 Aug 1956, E.J. Ford, Jr., 1;f (UCR_ENT 00073621) (BPBM). Didymann's Ck., Lae, 6.72444°S 146.99083°E, 15 m, 30 Apr 1963, J. Sedlacek, 1;f (UCR_ENT 00073623) (BPBM). Yalu, Lae, 6.5875°S 146.87666°E, Xii 1957, R. W. Paine, 1;f (UCR_ENT 00069393) (BMNH).

Physoderes Westwood (Figs 4.4 – 4.8, 4.11, 4.12 Table 4.4)

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

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* **n. sp.**, *P. ractepilosa* **n. sp.**, and *P. muluensis* **n. sp.**), 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 based on the anterior pronotal shape in males and the shape of the parascutellar lobes.

REDESCRIPTION: *MALE:* Size variable, total length 6.08 – 11.03mm (Table 4.4). COLORATION (Fig. 4.4, 4.5): Variable, from straw-colored to dark brown. Head, anterior pronotal ridges, posterior pronotal lobe, legs, 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* **n. sp.** and *P. nigroalbus*). STRUCTURE: 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* **n. sp.** and *P. tricolor* **n. sp.**, less than one-fifth length of head, and never attaining ventral margin of head in lateral view; ocelli present; height of anteocular lobe shorter than postocular lobe except in *P. anamalaiensis* **n. sp.** and *P.mysorensis* **n. sp.** 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 species without enlarged anterior pronotum; paramedian carina variable; posterior lobe medially rugose; anterior pronotal lobe length variable, wider and higher than or equal to posterior lobe except in *P. nigripennis* **n. sp.**, *P. ractepilosa* **n. sp.**, and *P. muluensis* **n. sp.**; parascutellar lobe rounded and sometimes skewed towards median, except in *P. brevipennis* **n. sp.**; scutellum rounded triangular except in *P. azrael* and *P. curculionis*, scutellar process length and apex shape 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* **n. sp.** and *P. curculionis*, with rounded terminal margin except in *P. ractepilosa* **n. sp.**; shape of connexival margin variable, posterior margin only slightly elevated in *P. nigripennis* **n. sp.** MALE 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.

BIOLOGY: Species from this genus are found in a variety of living and dead plant materials and the undergrowth. Specimens have been collected from pitfall traps and carrion traps and have been found at up to 1200m 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, Philippines archipelago, Sulawesi, Papua New Guinea, Solomon Islands and Fiji Islands.

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

Key to *Physoderes* species

1. Scutellum semicircular, transverse bridge of pygophore extremely narrow (Fig. 4.4, 4.5) ....(2)

- Scutellum triangular, transverse bridge of pygophore wider (Fig. 4.4 - 4.6) ....(3)

2. Small (7.23 – 7.90mm), anterior pronotal lobe longer than posterior lobe, hemelytron not attaining tip of abdomen, abdomen ovoid, connexivum slightly undulating (Fig. 4.4) ....*P. curculionis*

- Of medium size (8.14 – 8.83mm), anterior and posterior pronotal lobes equal in length, hemelytron attaining tip of abdomen, abdomen elongate ovoid, connexivum smooth, not undulating (Fig. 4.4) ....*P. azrael*

3. Anterior pronotal lobe narrower than posterior lobe in males (Fig. 4.4, 4.5)..................(4)

- Anterior pronotal lobe wider than posterior lobe in males (Fig. 4.4, 4.5).........................(7)

4. Fore femur slender, slightly incrassate, hemelytron not attaining tip of abdomen (Fig. 4.4, 4.5) ....(5)

- Fore femur distinctly incrassate, hemelytron attaining tip of abdomen (Fig. 4.4, 4.5)........ ....(6)

5. Small size (6.99 – 8.21mm), without long, erect setae, 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 (Fig. 4.4) .... *P. muluensis* **n. sp.**

- Medium size (8.32 – 10.19mm), body covered with long, erect setae, 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 (Fig. 4.5) .... *P. ractepilosa* **n. sp.**

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. 4.5) .... *P. nigripennis* **n. sp.**

- 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. 4.5) .... *P. nigroalbus*

7. Brachypterous (Fig. 4.4)... *P. brevipennis* **n. sp.**

- Macropterous ....(8)

8. Parascutellar lobe rounded and skewed towards median ....(9)

- Parascutellar lobe rounded and straight ....(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 (Fig. 4.5) .... *P. tricolor* **n. sp.**

- Length of anterior pronotal lobe equal to posterior lobe, anterior lobe higher than posterior lobe in lateral view, hemelytron membranous portion uniformly brown (Fig. 4.5) ……………………….. *P. notata*

10. Height of anteocular lobe shorter than postocular lobe, scutellar process long and slender (Fig. 4.4) ....(11)

- Height of anteocular and postocular lobes equal, scutellar process short (Fig. 4.4, 4.5) ....(12)

11. Large (9.59 – 11.03mm), scape reaching apex of clypeus, anterior pronotal lobe distinctly wider than posterior lobe, hemelytron attaining tip of abdomen (Fig. 4.4)...... *P. fuliginosa*

- Of medium size (8.10 – 9.03mm), scape not reaching apex of clypeus, anterior pronotal lobe slightly wider than posterior lobe, hemelytron short, not attaining tip of abdomen (Fig. 4.4) .... *P. minime* **n. sp.**

12. Large (10.52 – 10.96mm), males with apodeme on mediosternite 8, broad transverse bridge of pygophore, margin of anterior opening of pygophore rounded in lateral view, sclerotized angular ductifer (Fig. 4.5) .... *P. mysorensis* **n. sp.**

13. Of medium size (8.91 – 9.82mm), males without apodeme on mediosternite 8, transverse bridge of pygophore narrow, margin of anterior opening of pygophore angular in lateral view, membranous ductifer (Fig. 4.4) .... *P. anamalaiensis* **n. sp.**

Physoderes anamalaiensis, **new species** (Figs 4.4, 4.6, 4.7, 4.11 Table 4.4)

Holotype 1 male; INDIA: Tamil Nadu: Madras Co.: Anamalai Hills, Cinchona, 10.39944°N 76.76111°E, 1067 m, Sep 1959, P. S. Nathan, (UCR_ENT 00046637). The holotype is deposited at AMNH.

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 projectionof the anterior pronotal lobe, the wide anterior pronotal lobe that 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 attaining the tip of the abdomen. This species is most similar to *P. mysorensis* **n. sp.**, but is differentiated by the smaller size (8.91–9.82mm), having no apodeme on mediosclerite 8, the narrow transverse bridge of the pygophore, and the margin of the anterior opening of the pygophore angular in lateral view and with a membranous ductifer.

DESCRIPTION: *MALE:* Medium, total length 9.27mm (SD ± 0.36) (Table 4.4). COLORATION (Fig. 4.4): Dark brown. HEAD: Dark brown. ANTENNA: Scape brown, pedicel brown basally, straw-colored apically, basiflagellomere brown, distiflagellomere basally brown, apically straw-colored. LABIUM: First segment brown, second segment basally brown, medially straw-colored, apically brown, third segment brown. THORAX: Pronotum dark brown, scutellum dark brown, scutellar process straw-colored, pleuron dark brown, sternum dark brown. *Hemelytron:* Corium 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, tuberculated setae, with pair of long straight setae on postocular lobe posterior to ocelli. THORAX: Anterior lobe with irregular row of tuberculated, short, curved setae on lateral margins and short, tuberculated setae dispersed on dorsal surface, posterior lobe with short, curved, setae on humeral angle and sparsely distributed along dorsal surface. *Hemelytron:* Corium with short, curved setae. *Legs:* With two rows of spines and tuberculated setae, tibiae with regular rows of tuberculated, stout, sharp setae. ABDOMEN: Connexival margin with no prominent setae. STRUCTURE: HEAD: Elongate conical; maxillary plate rounded apically; scape reaching apex of clypeus; eye hemispherical in dorsal view, less than 1/5 length of head, not attaining head ventral margin in lateral view; 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; posterior lobe medially rugose; anterior pronotal lobe longer than posterior lobe, wider than posterior lobe or equal width to posterior lobe, anterior lobe higher than posterior lobe in lateral view; rounded lobe; scutellum rounded triangular, scutellar process short, apex rounded; mesosternite with 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 slightly undulating, posterior margin not elevated. MALE 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; cuplike sclerite apically rounded and rim ventrally sclerotized; basal plate arms converging; ductifer membranous; endosomal struts conical, subacute apex, divided into two arms basally; shape of dorsal phallothecal 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.

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

BIOLOGY: Nothing is known about the biology of this species.

DISTRIBUTION: This species is known only from the type locality of Anamalai Hills, Madras, Tamil Nadu, India.

DISCUSSION: 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 of which *P. mysorensis* **n. sp.** described here.

Paratypes: INDIA: Tamil Nadu: Madras Co.: Anamalai Hills, 10.74944°N 77.29888°E, 1067 m, May 1956, P.S. Nathan, 1;m (UCR_ENT 00068925) (AMNH); Apr 1957, P. S. Nathan, 2;m (UCR_ENT 00068923, UCR_ENT 00068924) (AMNH). Anamalai Hills, Kadamparai, 10.39444°N 76.97333°E, 1067 m, May 1963, P. S. Nathan, 3;m (UCR_ENT 00068918-UCR_ENT 00068920) (AMNH).

Other Specimens Examined: INDIA: Tamil Nadu: Madras Co.: Anaimalai Hills, 10.74972°N 77.29972°E, 344 m, May 1957, P. S. Nathan, 1;m (UCR_ENT 00068922) (AMNH). Anamalai Hills, 10.38277°N 76.92944°E, 1372 m, Sep. 1946, P.S. Nathan, 2;m (UCR_ENT 00046638, UCR_ENT 00046639) (CAS); 21 Jun 1946, P.S. Nathan, 1;f (UCR_ENT 00046622) (CAS). Anamalai Hills, 10.74944°N 77.29888°E, 1067 m, May 1964, P.S. Nathan, 1;f (UCR_ENT 00068934) (AMNH); May 1957, P.S. Nathan, 2;juvu (UCR_ENT 00068938, UCR_ENT 00068939) (AMNH); Apr 1957, P. S. Nathan, 1;f (UCR_ENT 00068933), 3;juvu (UCR_ENT 00068935-UCR_ENT 00068937) (AMNH). Anamalai Hills, Cinchona, 10.39944°N 76.76111°E, 1067 m, Sep 1959, P. S. Nathan, 1;m (UCR_ENT 00046636), 3;f (UCR_ENT 00046642-UCR_ENT 00046644) (CAS); Apr 1959, P.S. Nathan, 1;f (UCR_ENT 00046645) (CAS); May 1957, P.S. Nathan, 1;f (UCR_ENT 00068929) (AMNH), 2;f (UCR_ENT 00046640, UCR_ENT

00046641) (CAS). Anamalai Hills, Cinchona, 10.74944°N 77.29861°E, 344 m, May 1957, P.S. Nathan, 1;f (UCR_ENT 00068930) (AMNH); Apr 1956, P.S. Nathan, 2;f (UCR_ENT 00068926, UCR_ENT 00068927), 1;juvu (UCR_ENT 00068928) (AMNH); Apr 1957, P.S. Nathan, 2;f (UCR_ENT 00068931, UCR_ENT 00068932) (AMNH). Anamalai Hills, Kadamparai, 10.39444°N 76.97333°E, 1067 m, May 1965, P.S. Nathan, 1;m (UCR_ENT 00068921) (AMNH). Anamalais, 10.06666°N 76.91666°E, 914 m, 25 Jan 1912, Kalyana Pandal, 1;m (UCR_ENT 00069254) (BMNH).

Physoderes azrael Kirkaldy (Figs 4.4, 4.6, 4.7, 4.12, Table 4.4)

Physoderus (sic) *azrael* Kirkaldy, 1905, original description.

Holotype 1 male; PAPUA NEW GUINEA: New Britain Province: unknown, 5.76277°S 151.1375°E, 2999, Willey, (UCR_ENT 00018531). The holotype is deposited at the BMNH.

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 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 attaining the tip of the abdomen. Among the male genitalia, the following features are also diagnosyic: the extremely narrow transverse bridge of the pygophore, the apically truncate endosomal struts that 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 abdomen and shape of the endosomal struts in males.

REDESCRIPTION: *MALE:* Medium, total length 8.58mm, (SD ± 0.16) mm (Table 4.4). COLORATION (Fig. 4.4): Yellowish-brown and dark brown. HEAD: Anteriorly straw-colored, posteriorly brown. ANTENNA: Straw colored or light brown. LABIUM: First and second segment light brown, third segment brown. THORAX: Pronotum 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. *Hemelytron:* Corium base straw-colored, apex dark brown, membrane dark brown. *Legs:* Femora 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, tuberculated setae, with pair of long straight setae on postocular lobe posterior to ocelli. THORAX: Anterior lobe 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. *Hemelytron:* Corium with short, sparse, adpressed setae. *Legs:* With two rows of spines and tuberculated setae, tibia with regular rows of tuberculated, stout, sharp setae. ABDOMEN: Connexival margin with a few clubbed setae on each segment, or connexival margin with no prominent setae. STRUCTURE: HEAD: Short conical; maxillary plate rounded apically; scape reaching apex of clypeus; eye hemispherical in dorsal view, less than 1/5 length of head, not attaining head ventral margin 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 weakly defined; posterior lobe medially rugose; anterior pronotal lobe equal length to posterior lobe, equal width to posterior lobe or slightly narrower than posterior lobe, anterior lobe higher than posterior lobe in lateral view; rounded lobe skewed towards median; scutellum semicircular, scutellar process long, apex rounded or spatulate; mesosternite with 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, not undulating, posterior margin not elevated. MALE 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; cuplike sclerite apically rounded with adjacent paired round protuberances; basal plate arms 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 phallothecal sclerite subacute with lateral broad, plate-like prolongations.

FEMALE: Similar to males.

BIOLOGY: This species has been collected most commonly on or inside *Heliconia* flowers, but also on *Pandanus* in forest, on foliage of *Avocado* pear, in rotting tissue of the trunk of *Oreodoxa regia*, on *Nipa fruticans*, on *Cocos rucifera*, under sacking bands on trees, logs near the coast, in coastal litter, under dead bark, and on *Musa*.

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 on Fiji island.

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

Other Specimens Examined: FIJI: Ovalau: Andubangda, Ovalau, 17.64277°S 178.74944°E, 305 m, 18 Jul 1938, E. C. Zimmerman, 1;juvu (UCR_ENT 00073576) (BPBM). Viti Levu: Nadarivatu Co.: 4 mi S of Nadarivatu, 17.51°S 177.91888°E, 732 m, 09 Sep 1938, Y. Kondo, 1;juvu (UCR_ENT 00073569) (BPBM). Nadarivatu, 17.51°S 177.91888°E, 1067 m, 05 Sep 1938, Y. Kondo, 2;juvu (UCR_ENT 00073570, UCR_ENT 00073572) (BPBM). Nandarivatu, 17.51°S 177.91888°E, 823 m, 07 Sep 1938, Y. Kondo, 1;juvu (UCR_ENT 00073571) (BPBM). Viti Levu, 17.84833°S 178.01194°E, 853 m, 11 Sep 1938, E. C. Zimmerman, 1;juvu (UCR_ENT 00073568) (BPBM). Belt Road, 16-18 mi W of Suva, 18.015°S 178.38388°E, 22 Sep 1938, Y. Kondo, 1;juvu (UCR_ENT 00073575) (BPBM). Mt. Victoria, Train from Navai, 17.61638°S 178.01222°E, 600 m, 02 Jul 1958, B. Malkin, 1;juvu (UCR_ENT 00073573) (BPBM). Navai, 17.61638°S 177.97694°E, Jan 1951, N. L. H. Krauss, 1;juvu (UCR_ENT 00073574) (BPBM). INDONESIA: Maluku: Larat, 7.78777°S 131.81694°E, Dec 1907, no collector, 1;f (UCR_ENT 00046675) (CAS). Papua: Hollandia, Neth. Ind-Amer. (Jayapura), 2.54138°S 140.71361°E, vii 1938, L. J. Toxopeus, 1;f (UCR_ENT 00023997) (RMNH). Maffin Bay, 2.09222°S 139.01472°E, Jun 1944, E. S. Ross, 1;f (UCR_ENT 00046670) (CAS). Vogelkop: Sucumi Camo, near head of Ransiki Rivcer, 1.5°S 132.5°E, 300 m, 06 Aug 1957, D. E. Hardy, 1;m (UCR_ENT 00073538) (BPBM). MALAYSIA: Sabah: Sandakan, 5.8333°N 118.1167°E, 4 m, No date provided, Baker, 1;m (UCR_ENT 00068916) (AMNH). PAPUA NEW GUINEA: Bougainville Province: Buin, 6.81361°S 155.73194°E, 29 m, 31 May 1956, J. L. Gressitt, 1;m (UCR_ENT 00073536) (BPBM). Kieta, 6.23638°S 155.64388°E, 31 May 1960, R. W. Paine, 3;m (UCR_ENT 00069325-UCR_ENT 00069327), 4;f (UCR_ENT 00069332-UCR_ENT 00069335) (BMNH). East New

Britain Province: Gazelle Pen., Gaulim, 4.45°S 152.08333°E, 130 m, 23 Oct 1962 - 28 Oct 1962, J. Sedlacek, 3;f (UCR_ENT 00073542-UCR_ENT 00073544) (BPBM). Gazelle Pen., Upper Warangoi, Illugi, 4.71472°S 151.97944°E, 15 Dec 1962, J. Sedlacek, 1;f (UCR_ENT 00073567) (BPBM). Gazelle Pen., Upper Warangoi, Illugi, 4.48333°S 152.15°E, 230 m, 08 Dec 1962 - 11 Dec 1962, J. Sedlacek, 1;m (UCR_ENT 00073520), 2;f (UCR_ENT 00073565, UCR_ENT 00073566) (BPBM). Gazelle Peninsula, Gaulim, 4.45°S 142.08333°E, 23 May 1956, J. L. Gressitt, 1;m (UCR_ENT 00073523), 1;f (UCR_ENT 00073541) (BPBM). Gazelle Peninsula, Gaulim, 4.44472°S 152.08444°E, 140 m, 21 Oct 1962 - 27 Oct 1962, J. Sedlacek, 1;f (UCR_ENT 00073540) (BPBM); 19 Nov 1962 - 20 Nov 1962, J. Sedlacek, 3;m (UCR_ENT 00073516-UCR_ENT 00073518) (BPBM). Karavat, New Britain, 4.35194°S 152.04194°E, July 1957, R. W. Paine, 1;m (UCR_ENT 00069324) (BMNH). Keravat, 4.35°S 152.03334°E, 30 m, 02 Apr 1956, E.J. Ford, Jr., 1;f (UCR_ENT 00073562) (BPBM). Kerawat, Gazelle Peninsula, 4.35194°S 152.04194°E, 60 m, 27 Aug 1955, J.L Gressitt, 2;f (UCR_ENT 00073545, UCR_ENT 00073546) (BPBM). Rabaul, 4.19611°S 152.17305°E, 17 Aug 1930, J. L. Froggatt, 1;m (UCR_ENT 00046662) (CAS); 17 May 1932, J. L. Froggatt, 1;f (UCR_ENT 00046669) (CAS). Rabaul, 4.175°S 152.23083°E, 04 Jul 1959, J. L. Gressitt, 1;m (UCR_ENT 00073519), 1;f (UCR_ENT 00073559) (BPBM). near Rabaul, 4.175°S 152.24805°E, Feb. 1929, no collector, 1;f (UCR_ENT 00046668) (CAS). Madang Province: Madang, New Guinea, 5.23361°S 145.78888°E, Sep 1957, R. W. Paine, 1;m (UCR_ENT 00069293) (BMNH). Milne Bay Province: Woodlark Island Co.: Kulumadau Hill Mar., 9.05°S 152.71667°E, 25 Feb 1957, W. W. Brandt, 1;m (UCR_ENT 00073537) (BPBM). Morobe Province: Huon Penninsula Co.: Finschhafen, 6.55527°S 147.17361°E, 02 May 1944, E. S. Ross, 1;f (UCR_ENT 00046671) (CAS); 18 Nov 1969, James E. Tobler, 1;m (UCR_ENT 00046661) (CAS). Bumayong, New Guinea, 6.63444°S 147.0025°E, July 1957, R. W. Paine, 2;m (UCR_ENT 00069292, UCR_ENT 00069316), 1;f (UCR_ENT

00069304) (BMNH); Sep 1957, R. W. Paine, 1;f (UCR_ENT 00069303) (BMNH). Gurakor, New Guinea, 6.73972°S 146.615°E, 610 m, July 1957, R. W. Paine, 5;f (UCR_ENT 00069309, UCR_ENT 00069310, UCR_ENT 00069329-UCR_ENT 00069331), 3;m (UCR_ENT 00069317-UCR_ENT 00069319) (BMNH). Lae, New Guinea, 6.81444°S 146.80416°E, July 1957, R. W. Paine, 1;f (UCR_ENT 00069301) (BMNH); May 1957, R. W. Paine, 5;m (UCR_ENT 00069290, UCR_ENT 00069291, UCR_ENT 00069294, UCR_ENT 00069314, UCR_ENT 00069321), 6;f (UCR_ENT 00069296-UCR_ENT 00069300, UCR_ENT 00069308) (BMNH); 1957, R. W. Paine, 3;f (UCR_ENT 00069305-UCR_ENT 00069307), 1;m (UCR_ENT 00069315) (BMNH). Sio, N. Coast, 5.95333°S 147.3925°E, 600 m, 24 Jul 1956, E.J. Ford, Jr., 1;m (UCR_ENT 00073524) (BPBM). Yalu, Lae, 6.5875°S 146.87666°E, Apr 1957, R. W. Paine, 1;f (UCR_ENT 00069311), 1;m (UCR_ENT 00069320) (BMNH). New Britain Province: Jaquinot Bay, Bismarck Archipalago, 5.54638°S 151.51722°E, 03 Dec 1969, James E. Tobler, 1;f (UCR_ENT 00046672) (CAS). Malmalwan-Vunakanau, Gazelle Pen., 4.6667°S 152°E, 17 may 1956, J.L Gressitt, 1;m (UCR_ENT 00073521) (BPBM). Talasea, Narunageru Road, 5.53916°S 150.13555°E, 22 Nov 1969, James E. Tobler, 1;m (UCR_ENT 00046663) (CAS). Wunung Plains, Jacquinot Bay, 5.56472°S 151.57111°E, 30 Apr 1956, J. L. Gressitt, 1;f (UCR_ENT 00073560) (BPBM). New Ireland Province: Camp Bishop, 12 km up Kait River, 240 m, 07 Jul 1956, E.J. Ford, Jr., 1;f (UCR_ENT 00073564) (BPBM). Ridge above "Camp Bishop", 15km up Kait R., 4.48744°S 152.76638°E, 284 m, 09 Jul 1956, J.L Gressitt, 1;m (UCR_ENT 00073539), 1;f (UCR_ENT 00073563) (BPBM). Wana Wana, 4.52666°S 152.40555°E, Nov 1960, R. W. Paine, 2;m (UCR_ENT 00069322, UCR_ENT 00069323) (BMNH). West New Britain: Linga Linga Pl'n W. of Willaumez Pen. lm., 5.79944°S 149.38083°E, 13 Apr 1956, J. L. Gressitt, 1;m (UCR_ENT 00073522) (BPBM). Volupai, Willaumez Peninsula, 5.26916°S 149.97638°E, 100 m, 18 Apr 1956, J. L. Gressitt, 1;f (UCR_ENT 00073561) (BPBM). Maffin Bay, Dutch New

Guinea, 2.09222°S 139.01472°E, Sep 1944, E. S. Ross, 1;m (UCR_ENT 00046659) (CAS). Rooke Island, New Guinea (Umboi Island), 5.71972°S 147.71666°E, Jan 1957, R. W. Paine, 1;f (UCR_ENT 00069313) (BMNH). SOLOMON ISLANDS: Bougainville: Kukugai, 6.05194°S 155.19194°E, 150 m, Dec 1960, W. W. Brandt, 1;m (UCR_ENT 00073535), 1;f (UCR_ENT 00073553) (BPBM). Central Province: Nggela Hagalo, 9.06638°S 160.21138°E, 88 m, 25 May 1936, R. A. Lever, 1;m (UCR_ENT 00069328) (BMNH). Choiseul Island: Choiseul Island, Kolombangara R., 7.05166°S 156.95027°E, 60 m, 20 Mar 1964, P. Shanahan, 1;f (UCR_ENT 00073557) (BPBM). Guadalcanal: Honiara Co.: Kukum, 9.43361°S 159.95111°E, 27 oct 1956, E. S. Brown, 1;m (UCR_ENT 00069349) (BMNH). 9.6 km SE Honiara, Lunga R. (bridge), 9.49471°S 160.01181°E, 02 Jun 1960, C. W. O'Brien, 1;f (UCR_ENT 00073550) (BPBM). Berande, Guadalcanal, 9.49222°S 160.17833°E, Nov 1931, R. Lever, 2;f (UCR_ENT 00046665, UCR_ENT 00046666) (CAS). Bonegi River, 9.435°S 159.98527°E, 213 m, 14 Dec 1934, R. A. Lever, 1;m (UCR_ENT 00069348) (BMNH). Guadalcanal Lavoro, 9.57722°S 160.14555°E, 18 Feb 1934, H. T. Pagden, 1;m (UCR_ENT 00046660) (CAS). Kokum, 9.48916°S 160.16944°E, Nov 1931, R. J. A. W. Lever, 1;f (UCR_ENT 00046674) (CAS). Kukum, 9.48916°S 160.16944°E, 29 Oct 1963, P. Greenslade, 2;m (UCR_ENT 00069345, UCR_ENT 00069351), 4;f (UCR_ENT 00069354-UCR_ENT 00069357) (BMNH). Mt. Austen, 9.61777°S 160.12138°E, 09 Jun 1965, P. Greenslade, 1;m (UCR_ENT 00069344) (BMNH); 09 Jul 1963, P. Greenslade, 1;m (UCR_ENT 00069336) (BMNH). Mt. Austen, 9.55472°S 160.10666°E, 305 m, 25 Feb 1963, P. Greenslade, 3;m (UCR_ENT 00069341-UCR_ENT 00069343), 2;f (UCR_ENT 00069361, UCR_ENT 00069362) (BMNH); 19 Jun 1963, P. Greenslade, 1;f (UCR_ENT 00069367), 1;m (UCR_ENT 00069368) (BMNH); 11 Feb 1963, P. Greenslade, 2;m (UCR_ENT 00069337, UCR_ENT 00069338) (BMNH); 23 Jun 1963, P. Greenslade, 1;m (UCR_ENT 00069339) (BMNH); 04 Mar 1963, P. Greenslade, 1;m (UCR_ENT 00069340) (BMNH); 29 Oct 1963, P.

Greenslade, 2;f (UCR_ENT 00069365, UCR_ENT 00069366) (BMNH). Nr. Tatuve, Kolosulu, 9.65916°S 160.16361°E, 19 May 1960, C. W. O'Brien, 1;m (UCR_ENT 00073534), 1;f (UCR_ENT 00073548) (BPBM). Paripao, 9.56667°S 160.33333°E, 21 May 1960, C. W. O'Brien, 1;m (UCR_ENT 00073525) (BPBM). Tenaru, 9.4475°S 160.07555°E, 11 Aug 1955, E. S. Brown, 2;m (UCR_ENT 00069346, UCR_ENT 00069347), 3;f (UCR_ENT 00069358-UCR_ENT 00069360) (BMNH). Kolombangara: Pepele, 8.05°S 156.96667°E, 30 m, 12 Feb 1964, P. Shanahan, 1;f (UCR_ENT 00073556) (BPBM); 09 Feb 1964, P. Shanahan, 1;m (UCR_ENT 00073528) (BPBM). Malaita: 12 km NE of Dala, 8.6325°S 160.69638°E, 300 m, 12 Jun 1964, J. Sedlacek, 1;f (UCR_ENT 00073555) (BPBM). Dala, Malatia, 8.59027°S 160.68555°E, 50 m, 09 Jun 1964 - 14 Jun 1964, J. & M. Sedlacek, 1;f (UCR_ENT 00073551) (BPBM). Tangtalau-Kwalo, 8.73333°S 160.73333°E, 200 m, 30 Sep 1957, J. L. Gressitt, 1;f (UCR_ENT 00073554) (BPBM). New Georgia Islands: Gizo, Gizo Is, 8.1°S 156.85°E, 100 m, Dec 1976, N. L. H. Krauss, 1;m (UCR_ENT 00073529), 1;f (UCR_ENT 00073547) (BPBM); Feb 1984, N. L. H. Krauss, 1;m (UCR_ENT 00073526) (BPBM). Solomons, 9.64555°S 160.15611°E, No date provided, W. M. Mann, 1;f (UCR_ENT 00068917) (AMNH). Santa Ysabel: Sukapisu, 8.11444°S 159.33638°E, 900 m, 19 Jun 1960, C. W. O'Brien, 1;m (UCR_ENT 00073533) (BPBM); 18 Jun 1960, C. W. O'Brien, 1;f (UCR_ENT 00073558) (BPBM). Western Province: New Georgia Islands Co.: Banga, 11.0425°S 166.68388°E, 12 Oct 1964, E. S. Brown, 1;m (UCR_ENT 00069350) (BMNH). Vella Lavella, Ulo crater, 7.68555°S 156.58472°E, 10 m, 21 Jul 1963, P. Shanahan, 1;f (UCR_ENT 00073552) (BPBM). Guadalcanal, 9.6 km SE Honiara, Lunga, 7.75944°S 156.57694°E, 02 Jun 1960, C. W. O'Brien, 1;m (UCR_ENT 00073527) (BPBM). Lunga, 8.08638°S 156.78083°E, 10 Feb 1958, P. G. Fenemore, 2;m (UCR_ENT 00069352, UCR_ENT 00069353), 1;f (UCR_ENT 00069363) (BMNH); 29 Jul 1955, E. S. Brown, 1;f (UCR_ENT 00069364) (BMNH). Lunga River, 8.08638°S 156.78083°E, 06 Nov

1944, H. E. Milliron, 1;f (UCR_ENT 00073549) (BPBM).

***Physoderes brevipennis*, new species** (Figs 4.4, 4.6, 4.7, 4.12, Table 4.4)

Holotype 1 male; SOLOMON ISLANDS: Guadalcanal: Mt. Austen, 9.55472°S 160.10666°E, 305 m, 11 Feb 1965, P. Greenslade, (UCR_ENT 00069375). The holotype is deposited at the BMNH.

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 featres, 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 phallothecal sclerite thinly shaped like a moustache. This species is distinct by being the only brachypterous *Physoderes* species and it is restricted to Guadacanal of the Solomon Island archipelago.

DESCRIPTION: *MALE:* Small, total length 6.61mm, (SD ± 0.35) mm (Table 4.4). COLORATION (Fig. 4.4): Brown. ABDOMEN: Connexivum brown with posterior margin straw-colored. VESTITURE: Densely setose. HEAD: With widespread curved setae, ventral surface of postocular lobe with sparse, tuberculated setae, with pair of long straight setae on postocular lobe posterior to ocelli. THORAX: Anterior lobe 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. *Hemelytron:* Corium with short, curved setae. *Legs:*

With two rows of spines and tuberculated setae, tibia with regular rows of tuberculated, stout, sharp setae. ABDOMEN: Connexival margin with a few clubbed setae on each segment. STRUCTURE: 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, not attaining head ventral margin 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 rugose; anterior pronotal lobe longer than posterior lobe, wider than posterior lobe, anterior lobe higher than posterior lobe in lateral view; bell-shaped skewed towards median; scutellum rounded triangular, scutellar process short, apex subacute; mesosternite with median, irregular, tuberculated protrusion between fore and mid coxae. *Hemelytron:* Hemelytron not attaining tip of abdomen. *Legs:* Fore femur distinctly incrassate. ABDOMEN: Ovoid, with rounded terminal margin; connexival margin undulating, posterior margin not elevated. MALE 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; cuplike sclerite apically rounded with adjacent paired round protuberances; basal plate arms rounded; ductifer with sclerotized rounded ring; endosomal struts apically bulbous, basally divided into two plates converging to form a ridge medially; shape of dorsal phallothecal sclerite thinly shaped like a moustache.

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

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

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

DISTRIBUTION: This species is restricted to Guadacanal of the Solomon Island archipelago.

DISCUSSION: 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 retained the enlarged anterior pronotum but have a reduced posterior pronotal lobe.

Paratypes: SOLOMON ISLANDS: Guadalcanal: Mt. Austen, 9.55472°S 160.10666°E, 305 m, 20 Apr- 03 May 1965, P. Greenslade, 1;m (UCR_ENT 00069376) (BMNH); 3. vii-24. viii. 1965, P. Greenslade, 1;m (UCR_ENT 00069372) (BMNH); 10.v-23.vi. 1965, P. Greenslade, 1;m (UCR_ENT 00069371) (BMNH). Mt. Austen, 9.61777°S 160.12138°E, xii-i. 1965–66, P. Greenslade, 1;m (UCR_ENT 00069370) (BMNH).

Other Specimens Examined: SOLOMON ISLANDS: Guadalcanal: Gallego Camp 2, 9.5772°S 160.14555°E, 10 Jul 1965, no collector, 1;f (UCR_ENT 00069382) (BMNH). Mt. Austen, 9.55472°S 160.10666°E, 305 m, 3. vii-24. viii. 1965, P. Greenslade, 1;f (UCR_ENT 00069378) (BMNH); x. i. 1966, P. Greenslade, 1;m (UCR_ENT 00069373) (BMNH); 26 Jun 1965, P. Greenslade, 1;f (UCR_ENT 00069381) (BMNH); 20 Mar- 05 Apr 1965, P. Greenslade, 1;m (UCR_ENT 00069374) (BMNH); 12. 10. 1965, P. Greenslade, 1;f (UCR_ENT 00069379) (BMNH). Mt. Austen, 9.61777°S 160.12138°E, xii-i. 1965–66, P. Greenslade, 2;f (UCR_ENT 00069377, UCR_ENT 00069380) (BMNH). Mt. Jonapau (Mt. Chaunapaho), 9.63222°S 160.11638°E, 610 m, 05 Jun 1965, P. Greenslade, 1;f (UCR_ENT 00069383) (BMNH).

***Physoderes curculionis* China** (Figs 4.4, 4.6, 4.8, 4.12, Table 4.4)

Physoderes curculionis China, 1935, original description.

Physoderes insulanus Miller, 1940, **new synonymy.**

Physoderes patagiata Miller, 1941, **new synonymy.**

Physoderes minor Usinger, 1946, **new synonymy.**

Physoderes kalshoveni Miller, 1954, **new synonymy.**

Holotype 1 male; MALAYSIA: Malaya: unknown, 3.11°N 101.72111°E, 2999, Unknown, (UCR_ENT 00018529). The holotype is deposited at the BMNH.

DIAGNOSIS: This species is recognized among species of *Physoderes* by its small size (7.64mm 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 that is skewed towards the median, the semicircular scutellum, the spatulate and apically rounded scutellar process, the hemelytron not attaining the tip of the abdomen, the ovoid abdom of the mediosternite 8 undulating and with apodeme, the extremely narrow transverse bridge of the pygophore, 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.

REDESCRIPTION: *MALE:* Small, total length 7.64mm, (SD ± 0.21) mm (Table 4.4). COLORATION (Fig. 4.4): Brown. HEAD: Brown. ANTENNA: Scape, pedicel and basiflagellomere light brown, distiflagellomere basally light brown, straw-colored apically. LABIUM: First segment light brown, second segment straw-colored, third segment brown.

THORAX: Pronotum anterior lobe light brown to dark brown with straw-colored ridges, posterior lobe lighht 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. *Hemelytron:* Corium light brown to brown, membrane dark brown. *Legs:* Fore femora 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, tuberculated setae, with pair of long straight setae on postocular lobe posterior to ocelli. THORAX: Anterior lobe 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. *Hemelytron:* Corium with short, curved setae. *Legs:* With two rows of spines and tuberculated setae, tibia with regular rows of tuberculated, stout, sharp setae. ABDOMEN: Connexival margin with a few clubbed setae on each segment, or connexival margin with no prominent setae. STRUCTURE: HEAD: Short conical; maxillary plate rounded apically; scape reaching apex of clypeus; eye hemispherical in dorsal view, less than 1/5 length of head, not attaining head ventral margin 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 weakly defined; posterior lobe rugose; anterior pronotal lobe longer than posterior lobe, equal width to posterior lobe or slightly narrower than posterior lobe, anterior lobe higher than posterior lobe in lateral view; rounded lobe skewed towards median; scutellum semicircular, scutellar process long, apex rounded or spatulate; mesosternite with median irregular tuberculated protrusion between fore and mid coxae. *Hemelytron:* Hemelytron not attaining tip of abdomen. *Legs:* Fore femur distinctly incrassate. ABDOMEN: Ovoid, with rounded terminal margin; connexival margin slightly undulating, posterior margin not elevated. MALE 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; cuplike sclerite apically rounded with adjacent paired round protuberances; basal plate arms 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 of the dorsal phallothecal sclerite, short, rounded lateral plates at apex.

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

BIOLOGY: This species has been recorded to feed on curculionid larvae and has been collected on decaying plant material including fallen banana logs, rotten papaya plant, rotten pumpkin, on log, on rotten board on the ground and beneath rotten breadfruit.

DISTRIBUTION: This species has the most widespread distribution of all Oriental physoderine 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.

DISCUSSION: 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 with 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.

Paratypes: MALAYSIA: Selangor: Petaling Co.: Serdang, 3.02277°N 101.71361°E, 14 Jan 1935, G. H. Corbett, 1;f (UCR_ENT 00018525) (BMNH).

Other Specimens Examined: GUAM: Mariana Is.: Mt. Lamlam Co.: Mt. Lalam, 13.33583°N 144.66527°E, 406 m, Dec 1958, N. L. H. Krauss, 1;f (UCR_ENT 00073596) (BPBM). 1 mi. SE of Asan, 13.47305°N 144.71305°E, 244 m, 31 Oct 1947, H.S. Dybas, 1;f (UCR_ENT 00031420) (USNM). Pilgo River, 13.44222°N 144.77416°E, May 26, 1945, J.L Gressitt, 1;f (UCR_ENT 00031421) (USNM); 26 May 1945, G.E. Bohart and J.L. Gressit, 1;f (UCR_ENT 00073595) (BPBM). Port Ajayan, 13.2725°N 144.70444°E, 143 m, 06 June 1945, H. S. Dybas, 2;m (UCR_ENT 00073588, UCR_ENT 00073589) (BPBM). 2 mi W. Piti, 13.45472°N 144.695°E, 61 m, July 20 1937, R. G. Oakley, 1;f (UCR_ENT 00031419) (USNM). Dededo, 13.52°N 144.84°E, Aug 25 1937, R.G Oakley, 2;f (UCR_ENT 00031417, UCR_ENT 00031418) (USNM); Feb. 23 1938, R.G Oakley, 1;m (UCR_ENT 00031412) (USNM); July 13 1937, R.G Oakley, 1;f (UCR_ENT 00031416) (USNM). Harmon Field, 13.50722°N 144.81527°E, 54 m, 21 Jan 1949, no collector, 2;f (UCR_ENT 00031422, UCR_ENT 00031423) (USNM). Mt. Santa Rosa, 13.50805°N 144.91083°E, 182 m, 16 May 1948, G.E. Bohart and J.L. Gressit, 1;f (UCR_ENT 00031425) (USNM). Piti, 13.46°N 144.69166°E, 5 m, 22 May 1936, O. H. Swezey, 1;m (UCR_ENT 00046624) (CAS). Pt. Oca, 13.503°N 144.771°E, 19 May 1945, J. L. Gressitt, 1;m (UCR_ENT 00073587) (BPBM); May 1945, G.E. Bohart and J.L. Gressit, 1;f (UCR_ENT 00073590) (BPBM); 15 May 1945, G.E. Bohart and J.L. Gressit, 1;f (UCR_ENT 00073594) (BPBM). Santa Rita, 13.37416°N 144.70805°E, 69 m, Jan. 25 1948, no collector, 1;f (UCR_ENT

00031424) (USNM). none, 13.44416°N 144.79361°E, 37 m, 1937, R.G Oakley, 2;f (UCR_ENT 00031414, UCR_ENT 00031415) (USNM); No date provided, D.T. Fullaway, 1;m (UCR_ENT 00031413) (USNM). INDONESIA: Java: Ambarawa, 7.25611°S 110.40638°E, No date provided, no collector, 1;m (UCR_ENT 00024014) (RMNH). Bogor, 6.58916°S 106.79305°E, 240 m, 28 Apr 1954, A. H. G. Alston, 1;f (UCR_ENT 00069413) (BMNH). Bogor (Buitenzorg), 6.5897°S 106.7914°E, 02 Jul 1936, J. v. d. Vecht, 1;f (UCR_ENT 00024013) (RMNH). Samarang, Java, 6.96666°S 110.41666°E, 4 m, Jun 1910, E. Jacobson, 1;m (UCR_ENT 00024012) (RMNH). Maluku: Ambon Co.: Waai, Ambon Island, 3.565°S 128.32083°E, 93 m, 10 Mar 1965, A. M. R. Wegner, 1;m (UCR_ENT 00073586) (BPBM). Sumatera Barat (West Sumatra): Sumatra, 0.74°N 100.8°E, No date provided, Muller, 1;subu (UCR_ENT 00024032) (RMNH). MALAYSIA: Penang: Penang Island, 5.37027°N 100.2375°E, 198 m, No date provided, Baker, 6;m (UCR_ENT 00031397-UCR_ENT 00031402), 8;f (UCR_ENT 00031403-UCR_ENT 00031410) (USNM). NORTHERN MARIANA ISLANDS: Saipan: Pagan Island, 18.13555°N 145.79111°E, 155 m, 22 Aug 1954, G. Corwin, 1;f (UCR_ENT 00073591), 2;subu (UCR_ENT 00073597, UCR_ENT 00073598) (BPBM). SINGAPORE: Singapore, 1.27166°N 103.83416°E, 12 m, No date provided, Baker, 1;m (UCR_ENT 00031411) (USNM). Holotype of junior synonym *Physoderes insulanus*: AUSTRALIA: Territory of Christmas Island: Christmas Island, 10.45916°S 105.68972°E, 248 m, 28 Jan 1933, Unknown, 1;f (UCR_ENT 00018532) (BMNH). Holotype of junior synonym *Physoderes kalshoveni*: INDONESIA: Java: Buitenzorg, Java, 6.58916°S 106.79305°E, 250 m, Jan 1926, L. G. E. Kalshoven, 1;m (UCR_ENT 00023947) (RMNH). Paratypes of junior synonym Physoderes minor: GUAM: 3 mi S. of Piti, 13.45444°N 144.70444°E, 98 m, 23 May 1936, O. H. Swezey, 1;m (UCR_ENT 00073581), 1;f (UCR_ENT 00073592) (BPBM). Dededo, 13.52°N 144.84°E, 19 May 1936, R. L. Usinger, 3;f (UCR_ENT 00046627-UCR_ENT 00046629) (CAS). Mt. Alifan, 13.38055°N 144.67138°E, Jun 1936, R. L.

Usinger, 1;m (UCR_ENT 00073579) (BPBM); 26 May 1936, R. L. Usinger, 1;f (UCR_ENT 00068911) (AMNH), 1;m (UCR_ENT 00046625) (CAS). Piti, 13.46°N 144.69166°E, 5 m, 26 May 1936, O. H. Swezey, 1;m (UCR_ENT 00073577) (BPBM); 27 Oct 1936, O. H. Swezey, 1;f (UCR_ENT 00073593) (BPBM), 1;f (UCR_ENT 00046626) (CAS). Yigo, 13.53194°N 144.88027°E, 126 m, 13 Nov 1936, O. H. Swezey, 2;m (UCR_ENT 00073578, UCR_ENT 00073580) (BPBM). NORTHERN MARIANA ISLANDS: Saipan: Pagan Island, 18.13555°N 145.79111°E, 155 m, 22 Aug 1954, G. Corwin, 1;m (UCR_ENT 00073582) (BPBM).

***Physoderes fuliginosa* (Stål, 1870)** (Figs 4.4, 4.6, 4.8, 4.11, Table 4.4)

Epirodera fuliginosa Stål, 1870, original combination.

Physoderes fuliginosa (Stål), new combination by Maldonado 1990.

Physoderes esakii Cao, Tomokuni & Cai 2011, **new synonymy.**

Epirodera latithorax Esaki, 1931, nomen nudum.

Physoderes latithorax (Esaki), new combination by Maldonado 1990.

DIAGNOSIS: This species is recognized among species of *Physoderes* by the elongate head, thee 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 with a short medial process, and the phallosoma without flaplike prolongations.This species is most similar to *P. minime* **n. sp.,** but can be differentiated by the larger size, darker coloration, hemelytron close to or attaining tip of abdomen, the presence of the apical median process on the pygophore posterior opening, and the lack of flaplike prolongations of the phallosoma.

REDESCRIPTION: *MALE:* Medium, total length 10.47mm, (SD ± 0.54) mm (Table 4.4). COLORATION (Fig. 4.4): Dark brown. HEAD: Dark brown. ANTENNA: Scape and pedicel light brown and brown, basiflagellomere brown, distiflagellomere basally brown, apically straw-colored. LABIUM: First segment brown, second segment basally and apically brown, medially straw-colored, third segment brown. THORAX: Pronotum 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. *Hemelytron:* Corium brown to dark brown, membrane dark brown. *Legs:* Femur and tibia straw-colored with medial and apical brown annulations, tarsus and claw light brown, same, same. 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, tuberculated setae, with pair of long straight setae on postocular lobe posterior to ocelli. THORAX: Anterior lobe with irregular row of tuberculated, short, curved setae on lateral margins and short, tuberculated setae dispersed on dorsal surface, posterior lobe with short, curved, setae on humeral angle and sparsely distributed along dorsal surface. *Hemelytron:* Corium with short, curved setae. *Legs:* With two rows of spines and tuberculated setae, tibia with regular rows of tuberculated, stout, sharp setae. ABDOMEN: Connexival margin with no prominent setae. STRUCTURE: HEAD: Elongate conical; maxillary plate rounded apically; scape reaching apex of clypeus; eye hemispherical in dorsal view, less than 1/5 length of head, not attaining head ventral margin 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 weakly defined; posterior lobe medially rugose; anterior pronotal lobe longer than posterior lobe, wider than posterior lobe, anterior lobe higher than posterior lobe in lateral view; rounded lobe; scutellum rounded triangular, scutellar process long, apex subacute; mesosternite with 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 slightly undulating, posterior margin not elevated. MALE 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; cuplike sclerite apically rounded with sclerotized paired latero-ventral slight protuberance; basal plate arms converging; ductifer membranous; endosomal struts conical, subacute apex, divided into two arms basally; shape of dorsal phallothecal sclerite not scleratized.

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

BIOLOGY: Nothing is known about the biology of this species.

DISTRIBUTION: This species is widespread across the Philippines island archipelago and also on Botel Tobago (Orchid Island).

DISCUSSION: 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 corresponding females that match the holotype morphology confirm that the *P. fuliginosa* 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 great variation in overall size and coloration, but do not differ morphologically. Dissections of male genitalia also do not show any variation. Hence, *P. fuliginosa* is here considered to be highly variable in size and general coloration. *P. esakii* is synonymized under *P. fuliginosa* based on the presence of the same enlarged anterior pronotal lobe, 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).

Other Specimens Examined: INDONESIA: Borneo: Borneo, 1.10611°S 114.14388°E, No date provided, Muller, 2;m (UCR_ENT 00024015, UCR_ENT 00024016) (RMNH). Maluku: Buru Island, 3.3925°S 126.78194°E, 1903, no collector, 2;m (UCR_ENT 00069252, UCR_ENT 00069253) (BMNH). Sulawesi: Gorontalo, 0.5525°N 123.06555°E, No date provided, A. Forsten, 1;f (UCR_ENT 00024018) (RMNH). Tidore Island: Kampung Guaepaji, 0.67333°N 127.31166°E, 05 Jul 1981 - 10 Jul 1981, A.C Messer, 1;m (UCR_ENT 00031353) (USNM). PAPUA NEW GUINEA: Manus: Manus Island, N. G., 2.09388°S 146.87583°E, No date provided, no collector, 1;f (UCR_ENT 00069225) (BMNH). PHILIPPINES: Basilan: Basilan Island, 6.69277°N 122.02305°E, No date provided, no collector, 1;m (UCR_ENT 00069249) (BMNH). Bukidnon: Tangcolan, 7.97611°N 125.02583°E, No date provided, Baker, 29;f (UCR_ENT 00030985-UCR_ENT 00030999, UCR_ENT 00031313, UCR_ENT 00031354-UCR_ENT 00031366), 37;m (UCR_ENT 00031278-UCR_ENT 00031312, UCR_ENT 00031314, UCR_ENT 00031435) (USNM). Leyte: Biliran Island, 11.26722°N 124.64833°E, No date provided, Baker, 2;m (UCR_ENT 00031347, UCR_ENT 00031348) (USNM). Leyte, 11.11388°N 124.7375°E, Jan 5 1915, G. Bottcher, 1;f (UCR_ENT 00069223) (BMNH); 03 May 1915, G. Bottcher, 1;m (UCR_ENT 00069247) (BMNH). Luzon: Laguna Co.: Paete, Laguna, 14.3675°N 121.52972°E, No date provided, W. Schultze, 1;f (UCR_ENT 00069224) (BMNH).

Balbalan, N. Luzon, 16.98916°N 121.12111°E, 1219 m, Jul 2 1917, G. Bottcher, 1;m (UCR_ENT 00069204) (BMNH); 30 Jan 1917, G. Bottcher, 2;m (UCR_ENT 00069200, UCR_ENT 00069201) (BMNH); Mar 1918, G. Bottcher, 2;m (UCR_ENT 00069202, UCR_ENT 00069203) (BMNH). Imugan, Nord-Luzon, 16.16166°N 120.93888°E, 1219 m, 30 Jun 1917, G. Bottcher, 1;m (UCR_ENT 00069207) (BMNH); May 1917, G. Bottcher, 2;m (UCR_ENT 00069205, UCR_ENT 00069206) (BMNH). Mt. Banahao, N. Luzon, 14.0675°N 121.4925°E, 610 m, 29 Apr 1914, G. Bottcher, 1;m (UCR_ENT 00069197) (BMNH); 21 Jun 19124, G. Bottcher, 1;m (UCR_ENT 00069198) (BMNH); 01 May 1914, G. Bottcher, 1;m (UCR_ENT 00069196) (BMNH); 10 Jun 1914, G. Bottcher, 1;m (UCR_ENT 00069199) (BMNH); 18 Aug 1914, G. Bottcher, 1;m (UCR_ENT 00069195) (BMNH). Santo Tomas, Luzon, 14.08694°N 121.19444°E, 1924, No Collector on label, 1;u (UCR_ENT 00031390) (USNM). Mindanao: Butuan, 8.9475°N 125.54055°E, No date provided, Baker, 8;m (UCR_ENT 00031315-UCR_ENT 00031322), 5;f (UCR_ENT 00031367-UCR_ENT 00031371) (USNM). Galog River, Mt. Apo, 6.98555°N 125.25972°E, 1829 m, No date provided, C. F. Clagg, 1;m (UCR_ENT 00068947) (AMNH). Iligan, Mindanao, 8.22805°N 124.24527°E, No date provided, Baker, 2;m (UCR_ENT 00031349, UCR_ENT 00031350) (USNM); No date provided, no collector, 1;m (UCR_ENT 00069241) (BMNH). Mamungan, Nord Mindanao, 8.11722°N 124.21861°E, 1272 m, 22 Feb 1915, G. Bottcher, 1;f (UCR_ENT 00069216) (BMNH); 18 Feb 1915, G. Bottcher, 1;m (UCR_ENT 00069227) (BMNH); 19 Feb 1915, G. Bottcher, 1;f (UCR_ENT 00069217), 1;m (UCR_ENT 00069226) (BMNH); No date provided, no collector, 1;f (UCR_ENT 00069220) (BMNH); 03 Mar 1915, G. Bottcher, 1;m (UCR_ENT 00069228) (BMNH). Momungan, Nord Mindanao, 19 Feb 1915, G. Bottcher, 1;m (UCR_ENT 00069209) (BMNH). Siasi Island, Siasi, 5.53388°N 120.86138°E, 300 m, 26 Aug 1958, H. E. Milliron, 1;m (UCR_ENT 00073627) (BPBM). Mindoro: Abra de Llog, 13.45°N 120.73333°E, 9 m, No date provided, W. Schultze, 2;m

(UCR_ENT 00069211, UCR_ENT 00069248) (BMNH). Mindoro, 13.12888°N 121.06611°E, 112 m, No date provided, S. Theodoro, 1;f (UCR_ENT 00014053) (RMNH). Misamis Oriental: Hindangon, 20 km S of Gingoog, 7.81361°N 124.96888°E, 600 m, 09 Apr 1960 - 18 Apr 1960, H. M. Torrevillas, 1;m (UCR_ENT 00073628) (BPBM). Negros Oriental: Mt. Talinas (Mt. Talinis), 9.24416°N 123.1775°E, 1020 m, 28 Jun 1958, H. E. Milliron, 1;f (UCR_ENT 00073626) (BPBM). Nueva Vizcaya: Imugin, 16.16138°N 120.93972°E, 589 m, No date provided, Baker, 1;m (UCR_ENT 00031330) (USNM). Occidental Mindoro: San Jose, 12.35361°N 121.06666°E, 30 Jan 1945, E. S. Ross, 1;m (UCR_ENT 00046630) (CAS). Polillo: Polillo Island, 14.71805°N 121.94583°E, 27 m, No date provided, no collector, 1;f (UCR_ENT 00069219) (BMNH). Polillo Island, 14.77555°N 121.92194°E, 54 m, No date provided, no collector, 1;m (UCR_ENT 00024017) (RMNH); No date provided, W. Schultze, 2;m (UCR_ENT 00069212, UCR_ENT 00069213) (BMNH). Romblon: Island Sibuyan, 12.4125°N 122.55888°E, 1529 m, No date provided, Baker, 1;m (UCR_ENT 00031340) (USNM). Samar: Borongan, Samar, 11.60777°N 125.43277°E, 19 m, No date provided, W. Schultze, 4;m (UCR_ENT 00069214, UCR_ENT 00069244-UCR_ENT 00069246), 1;f (UCR_ENT 00069215) (BMNH). Surigao: Siargao, 9.84805°N 126.04583°E, 57 m, No date provided, no collector, 1;m (UCR_ENT 00069251) (BMNH). Surigao del Norte: Surigao, Mindanao, 9.67138°N 125.52861°E, 130 m, No date provided, Baker, 4;m (UCR_ENT 00031331-UCR_ENT 00031334), 6;f (UCR_ENT 00031335, UCR_ENT 00031372-UCR_ENT 00031376) (USNM); 1700, Baker, 1;m (UCR_ENT 00031436) (USNM). Surigao, Nord Mindanao, 9.67138°N 125.52888°E, 130 m, 01 Nov 1915, G. Bottcher, 1;m (UCR_ENT 00069230) (BMNH); No date provided, no collector, 1;f (UCR_ENT 00069222) (BMNH); 13 Nov 1915, G. Bottcher, 2;m (UCR_ENT 00069208, UCR_ENT 00069229) (BMNH); 20 Oct 1915, G. Bottcher, 1;m (UCR_ENT 00069231) (BMNH). Philippine Islands, 12.82027°N 121.79694°E, 1912, J. J.

Mounsey, 1;m (UCR_ENT 00069210), 1;f (UCR_ENT 00069218) (BMNH). Samar Island, 12.005°N 124.77416°E, 37 m, No date provided, Baker, 2;m (UCR_ENT 00031336, UCR_ENT 00031337), 4;f (UCR_ENT 00031377-UCR_ENT 00031380) (USNM). SOLOMON ISLANDS: Guadalcanal: Guadalcanal, 9.57722°S 160.14555°E, Nov. 1934, R. J. A. W. Lever, 1;f (UCR_ENT 00046635) (CAS). Guadalcanal Lavoro, 9.57722°S 160.14555°E, 18 Feb 1934, H. T. Pagden, 1;f (UCR_ENT 00046633) (CAS).

***Physoderes minime*, new species** (Figs 4.4, 4.6, 4.8, 4.12, Table 4.4)

Holotype 1 male; PHILIPPINES: Luzon: Mt. Banahao, Luzon, 14.0675°N 121.4925°E, No date provided, Baker (UCR_ENT 00030979). The holotype is deposited at the USNM.

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

DESCRIPTION: *MALE:* Medium, total length 8.64mm, (SD ± 0.28) mm (Table 4.4). COLORATION (Fig. 4.4): Yellowish-brown. HEAD: Yellowish to light brown. ANTENNA: Scape, pedicel and distiflagellomere straw-colored, basiflagellomere basally brown, apically straw-colored. LABIUM: First segment light brown, second segment straw-colored, third segment brown. THORAX: Pronotum brown with straw-colored markings along ridges, scutellum basally brown, apicall straw-colored including scutellar process, pleuron straw-colored with brown suffusion, sternum brown. *Hemelytron:* Corium light brown to brown, membrane light brown to brown. *Legs:* Femora and tibiae 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-coloredbrown. VESTITURE: Sparsely setose. HEAD: With widespread curved setae, ventral surface of postocular lobe with sparse, tuberculated setae, with pair of long straight setae on postocular lobe posterior to ocelli. THORAX: Anterior lobe with irregular row of tuberculated, short, curved setae on lateral margins and fine, adpressed setae on dorsal surface, posterior lobe with short, curved, tuberculated setae on humeral angle and glabrous on dorsal surface. *Hemelytron:* Corium with short, curved setae. *Legs:* With two rows of spines and tuberculated setae, tibia with regular rows of tuberculated, stout, sharp setae. ABDOMEN: Connexival margin with no prominent setae. STRUCTURE: HEAD: Elongate conical; maxillary plate rounded apically; scape not reaching apex of clypeus; eye hemispherical in dorsal view, less than 1/5 length of head, not attaining head ventral margin in lateral view; height of anteocular lobe shorter than postocular lobe. 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; posterior lobe medially rugose; anterior pronotal lobe longer than posterior lobe, wider than posterior lobe, anterior lobe higher than posterior lobe in lateral view; rounded lobe; scutellum rounded triangular, scutellar process long, apex subacute; mesosternite with median irregular tuberculated protrusion between fore and mid coxae. *Hemelytron:* Not attaining tip of abdomen. *Legs:* Fore femur distinctly incrassate. ABDOMEN: Elongate ovoid, with rounded terminal margin; connexival margin slightly undulating, posterior margin not elevated. MALE GENITALIA: Transverse bridge of pygophore broad, margin of anterior opening angular, apodeme present, apical margin of posterior opening smooth; cuplike sclerite apically rounded with sclerotized paired latero-ventral slight protuberance; basal plate arms converging; ductifer membranous; endosomal struts apically spatulate, basally divided into two plates; shape of dorsal phallothecal sclerite subacute with short, apical lobes of the dorsal phallothecal sclerite, short, rounded lateral plates at apex.

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

ETYMOLOGY: The name minime is after the Latin adjective “minime” meaning minimal and the fictional movie character Mini-me from Austin Powers movies to describe the miniaturized resemblance of this species to the co-occuring larger *P. fuliginosa*.

BIOLOGY: Nothing is known about the biology of this species.

DISTRIBUTION: This species is restricted to the Luzon island and Panay island of the Philippines archipelago. Most species were collected from two localities: Mt. Banahao and Mt. Makiling in Luzon.

DISCUSSION: 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.

Paratypes: PHILIPPINES: Capiz: Panay, Capiz Jamindan, 11.44055°N 122.5925°E, No date provided, W. Schultze, 1;m (UCR_ENT 00069250) (BMNH). Luzon: Mt. Banahao, Luzon, 14.0675°N 121.4925°E, No date provided, Baker, 2;m (UCR_ENT 00031432, UCR_ENT 00031433) (USNM). Mt. Makiling, 14.13055°N 121.2°E, 963 m, No date provided, Baker, 1;m

(UCR_ENT 00031434) (USNM).

Other Specimens Examined: PHILIPPINES: Albay Province: Mt. Mayon, 16 km NW of Lagaspi, 13.25666°N 123.685°E, 900 m, 04 May 1962, H. M. Torrevillas, 1;f (UCR_ENT 00073629) (BPBM). Laguna: 4km SE Los Banos: Mt. Makiling, 14.14112°N 121.2097°E, 8-IV-1977, L. Watrous, 1;f (UCR_ENT 00031438) (USNM); 09 Apr 1977, I. Watrous, 1;m (UCR_ENT 00031352) (USNM). Luzon: Laguna Co.: Los Banos, Nord-Luzon, 14.17°N 121.24416°E, 03 Nov 1914, G. Bottcher, 1;f (UCR_ENT 00069221) (BMNH). Mt. Banahao, Luzon, 14.0675°N 121.4925°E, No date provided, Baker, 3;m (UCR_ENT 00031429-UCR_ENT 00031431), 1;f (UCR_ENT 00031437) (USNM). Mt. Maquiling, 14.12444°N 121.22555°E, 18 Jul 1936, R. L. Usinger, 1;f (UCR_ENT 00046647) (CAS).

***Physoderes muluensis*, new species** (Figs 4.4, 4.6, 4.8, 4.12, Table 4.4)

Holotype 1 male; MALAYSIA: Sarawak: Mulu National Park, near Base Camp; 4th division Gn., 3.97444°N 114.93638°E, 100 m, No date provided, No Collector on label (UCR_ENT 00069405). The holotype is deposited at the BMNH.

DIAGNOSIS: This species is recognized among congeners by the males having the anterior pronotal lobe narrower than the posterior lobe, the median pronotal depression contiguous with the transverse sulcus, the fore femur slightly incrassate, and 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 inflated in males.

DESCRIPTION: *MALE:* Small, total length 7.35mm, (SD ± 0.27) mm (Table 4.4). COLORATION (Fig. 4.4): Brown. HEAD: Brown, lighter towards apex. ANTENNA: Scape brown, pedicel brown with apex straw brown, basi- and distiflagellomeres basally brown and apically straw brown or straw brown entirely. LABIUM: First segment brown, second segment gradation from brown to straw-colored, third segment straw-colored. THORAX: Pronotum brown, sometimes posterior pronotal lobe lighter brown, scutellum brown, pleuron brown, sternum brown. *Hemelytron:* Corium brown, membrane brown. *Legs:* Fore femur 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, 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, tuberculated setae, with pair of long straight setae on postocular lobe posterior to ocelli. THORAX: Anterior lobe with irregular row of tuberculated, short, curved setae on lateral margins and short, tuberculated setae dispersed on dorsal surface, posterior lobe with only short, sparse setae. *Hemelytron:* Corium with short, sparse, adpressed setae. *Legs:* With two rows of spines and tuberculated setae, tibia with a few prominent tuberculated, stout, sharp setae. ABDOMEN: Posterior margin of connexivum with long, fine setae. STRUCTURE: HEAD: Elongate conical; maxillary plate truncate apically; scape reaching apex of clypeus; eye hemispherical in dorsal view, less than 1/5 length of head, not attaining head ventral margin 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 contiguous with transverse sulcus; paramedian carina weakly defined; posterior lobe medially weakly rugose; anterior pronotal lobe equal length to posterior lobe, narrower than posterior lobe, anterior lobe level with posterior lobe in lateral view; rounded lobe skewed towards median; scutellum rounded triangular, scutellar process short, apex rounded or subacute; mesosternite with median irregular tuberculated protrusion between fore and mid coxae. *Hemelytron:* Not attaining tip of abdomen. *Legs:* Fore femur slightly incrassate. ABDOMEN: Elongate ovoid, with rounded terminal margin; connexival margin slightly undulating, posterior margin not elevated. MALE 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; cuplike sclerite apically rounded with adjacent paired round protuberances; basal plate arms parallel to each other; ductifer membranous; endosomal struts conical, subacute apex, divided into two arms basally; shape of dorsal phallothecal sclerite subacute with lateral broad, plate-like prolongations, broad plates angularly oriented towards basal plate.

FEMALE: Similar in size and shape to males.

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

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

DISTRIBUTION: Only known from type locality.

Paratypes: MALAYSIA: Sarawak: Gunong Mulu National Park, 3.96638°N 114.78305°E, 215 m, v-viii 1978, P. M. Hammond & J. E. Marshall, 2;m (UCR_ENT 00069401, UCR_ENT 00069403), 2;f (UCR_ENT 00069409, UCR_ENT 00069410) (BMNH). Mulu National Park, near Base Camp; 4th division Gn., 3.97444°N 114.93638°E, 100 m, v-viii 1978, P. M. Hammond & J. E. Marshall, 1;f (UCR_ENT 00069411), 1;m (UCR_ENT 00069400) (BMNH).

Other Specimens Examined: MALAYSIA: Sarawak: Gunong Mulu National Park, 3.96638°N 114.78305°E, 215 m, v-viii 1978, P. M. Hammond & J. E. Marshall, 2;subm (UCR_ENT 00069402, UCR_ENT 00069404) (BMNH).

***Physoderes mysorensis*, new species** (Figs 4.5, 4.6, 4.8, 4.11, Table 4.4)

Holotype 1 male; INDIA: Kerala: Trivandrum Co.: Ponmudi Range, 8.78638°N 77.30361°E, 914 m, No date provided, Susai Nathan (UCR_ENT 00068943). The holotype is deposited at the AMNH.

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 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* **n. sp.** and can be differentiated by the larger size (10.69–10.96mm), 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.

DESCRIPTION: *MALE:* Large, total length 10.82mm, (SD ± 0.14) (Table 4.4). COLORATION

(Fig. 4.5): Dark brown. HEAD: Dark brown. ANTENNA: Scape, pedicel and basiflagellomere brown, distiflagellomere basally brown, apically straw-colored. LABIUM: First segment basally brown, apically straw-colored, second segment straw-colored, third segment brown. THORAX: Pronotum 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. *Hemelytron:* Corium dark brown, membrane dark brown. *Legs:* Femur 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, tuberculated setae, with pair of long straight setae on postocular lobe posterior to ocelli. THORAX: Anterior lobe with irregular row of tuberculated, short, curved setae on lateral margins and short, tuberculated setae dispersed on dorsal surface, posterior lobe with short, curved, setae on humeral angle and sparsely distributed along dorsal surface. *Hemelytron:* Corium with short, curved setae. *Legs:* With two rows of spines and tuberculated setae, tibia with regular rows of tuberculated, stout, sharp setae. ABDOMEN: Connexival margin with no prominent setae. STRUCTURE: HEAD: Elongate conical; maxillary plate rounded apically; scape reaching apex of clypeus; eye hemispherical in dorsal view, less than 1/5 length of head, not attaining head ventral margin in lateral view; 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; posterior lobe medially weakly rugose; anterior pronotal lobe longer than posterior lobe, wider than posterior lobe, anterior lobe higher than posterior lobe in lateral view; rounded lobe; 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:* Fore femur distinctly incrassate. ABDOMEN: Elongate ovoid, with rounded terminal margin; connexival margin slightly undulating, posterior margin not elevated. MALE 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; cuplike sclerite apically rounded and rim ventrally sclerotized; basal plate arms converging; ductifer with sclerotized angular ring; endosomal struts conical, subacute apex, divided into two arms basally; shape of dorsal phallothecal sclerite subacute with lateral broad, plate-like prolongations, 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.

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.

BIOLOGY: Nothing is known about the biology of this species.

DISTRIBUTION: This species is found in two localities in Southwestern India: Agumbe Ghat, Mysore district, Karnataka, and Ponmudi Range, Trivandrum district, Kerala.

DISCUSSION: 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* **n. sp.** described here.

Paratypes: INDIA: Karnataka: Mysore Co.: Agumbe Ghat, 14.49666°N 75.0825°E, 610 m, May 1974, Susai Nathan, 1;m (UCR_ENT 00068945), 2;f (UCR_ENT 00068946, UCR_ENT 00047705) (AMNH). Kerala: Trivandrum Co.: Ponmudi Range, 8.78638°N 77.30361°E, 914 m, No date provided, Susai Nathan, 1;f (UCR_ENT 00068940) (AMNH); May 1971, Susai Nathan, 1;m (UCR_ENT 00068944) (AMNH).

***Physoderes nigripennis*, new species** (Figs 4.5, 4.6, 4.8, 4.12, Table 4.4)

Holotype 1 male; INDONESIA: Sumatera Barat (West Sumatra): Sumatra, 0.74°N 100.8°E, No date provided, E. Jacobson (UCR_ENT 00023968). The holotype is deposited at RMNH.

DIAGNOSIS: This species is recognized among congeners by the elongate conical head that 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 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 basal plate arms of the articulatory apparatus of the male genitalia curved, and the dorsal phallothecal sclerite subacute with lateral rounded plates extending to lateral surface.

DESCRIPTION: *MALE:* Medium, total length 9.12mm, (SD ± 0.29) (Table 4.4). COLORATION (Fig. 4.5): Brown and dark brown. HEAD: Brown with straw-colored setae. ANTENNA: Light brown. LABIUM: First segment brown, second segment straw-colored, apically brown, third segment brown. THORAX: Pronotum anterior lobe dark brown with brown or light brown markings, posterior lobe brown, scutellum basally brown, apically straw-colored including scutellar process, pleuron brown, sternum brown. *Hemelytron:* Corium reddish-brown with black costal margin, membrane brownish-black. *Legs:* Femura 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, connexivum anterior two-thirds brownish-black, posterior third straw-colored, exposed part of pygophore dark brown. VESTITURE: Densely setose. HEAD: With widespread curved setae, ventral surface of postocular lobe with sparse, tuberculated setae, without pair of long straight setae on postocular lobe posterior to ocelli. THORAX: Anterior lobe with irregular row of tuberculated, short, curved setae on lateral margins and curved setae on the anterior portion of the dorsal surface, posterior lobe with short, curved setae widespread. *Hemelytron:* Corium with short, curved setae. *Legs:* With two rows of spines and tuberculated setae, tibia with regular rows of tuberculated, stout, sharp setae. ABDOMEN: Posterior margin of connexivum with short, curved setae. STRUCTURE: 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, not attaining head ventral margin in lateral view; height of anteocular lobe shorter than postocular lobe. THORAX Antero-lateral paired projections truncate; surface of anterior lobe with raised ridges; median pronotal depression contiguous with transverse sulcus; paramedian carina strongly 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; rounded lobe skewed towards median; scutellum rounded triangular, scutellar process long, apex subacute; mesosternite with 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 undulating, posterior margin slightly elevated. MALE GENITALIA: Transverse bridge of pygophore broad, margin of anterior opening angular, apodeme present, apical margin of posterior opening smooth; cuplike sclerite apically rounded with adjacent paired round protuberances; basal plate arms rounded; ductifer membranous; endosomal struts conical, subacute apex, divided into two arms basally; shape of dorsal phallothecal sclerite subacute with lateral broad, plate-like prolongations, short, rounded lateral plates at apex.

FEMALE: Similar to male.

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

BIOLOGY: This specimen is collected from relatively high altitude of 920–1200m.

DISTRIBUTION: This species is found only on the central west Sumatra island, most specimens were collected from Bukit Tinggi, formerly Fort de Kock.

DISCUSSION: This species is the most commonly collected on the island of Sumatra. It is placed within the *Physoderes* clade in the phylogenetic analysis above due to 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.

Paratypes: INDONESIA: Sumatera Barat (West Sumatra): Fort de Kock, 0.26694°N 100.38333°E, 920 m, 1925, E. Jacobson, 1;m (UCR_ENT 00023962) (RMNH); 1926, E. Jacobson, 4;m (UCR_ENT 00023954-UCR_ENT 00023956, UCR_ENT 00014055) (RMNH). Sumatra: Fort de Kock (Bukittinggi), 0.3167°N 100.3667°E, 920 m, Nov. 1920, E. Jacobson, 1;m (UCR_ENT 00068913) (AMNH).

Other Specimens Examined: INDONESIA: Sumatera Barat (West Sumatra): Fort de Kock, 0.26694°N 100.38333°E, 920 m, 1924, E. Jacobson, 1;f (UCR_ENT 00023987) (RMNH); 1926, E. Jacobson, 2;f (UCR_ENT 00023985, UCR_ENT 00023986) (RMNH); 1925, E. Jacobson, 1;f

(UCR_ENT 00069414) (BMNH), 9;m (UCR_ENT 00023957-UCR_ENT 00023961, UCR_ENT 00023963-UCR_ENT 00023966), 8;f (UCR_ENT 00023977-UCR_ENT 00023984) (RMNH). Fort de Kock (=Bukittinggi), 0.26768°S 100.38394°E, Nov 1913, E. Jacobson, 1;m (UCR_ENT 00023975), 1;f (UCR_ENT 00023995) (RMNH). Gunning Singgalang (Sumatra's W Kust), 0.39°N 100.33083°E, 1200 m, 1925, E. Jacobson, 1;m (UCR_ENT 00023974) (RMNH). Gunung Singgalang (Sumatra's Westkust), 1000 m, 1925, E. Jacobson, 1;f (UCR_ENT 00023994) (RMNH). Sumatra, 0.74°N 100.8°E, No date provided, E. Jacobson, 6;m (UCR_ENT 00023967, UCR_ENT 00023969-UCR_ENT 00023973), 7;f (UCR_ENT 00023988-UCR_ENT 00023993, UCR_ENT 00023996) (RMNH). Sumatera Utara (North Sumatra): Lake Toba, 2.59194°N 98.82805°E, 1167 m, No date provided, B. hagen, 1;m (UCR_ENT 00023976) (RMNH). Sumatra: Fort de Kock (Bukittinggi), 0.3167°N 100.3667°E, 920 m, Nov. 1920, E. Jacobson, 1;m (UCR_ENT 00068912), 2;f (UCR_ENT 00068914, UCR_ENT 00068915) (AMNH).

***Physoderes nigroalbus* Breddin** (Figs 4.5, 4.6, 4.8, 4.12, Table 4.4)

Physoderes nigroalbus Breddin, 1903, **lectotype designated.**

Holotype Lectotype designated: 1 female; INDONESIA: Sumatra: Tebing Tinggi, Northeast Sumatra, 3.31944°N 99.15222°E, 21 m, 10 Mar 1884, Dr. Schultheiss (UCR_ENT 00040566). The lectotype is deposited at DEI.

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 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. This species is most similar to *P. tricolor* **n. sp.** but can be differentiated by size, coloration of the head, pronotum and scutellar process, and shape of eye.

REDESCRIPTION: *MALE:* Medium, total length 9.74mm. COLORATION (Fig. 4.5): Brown. HEAD: Brown. ANTENNA: Scape and pedicel light brown to brown, basiflagellomere brown, distiflagellomere basally brown, apically straw-colored. LABIUM: First segment light brown, second segment straw-colored, apically brown, third segment brown. THORAX: Pronotum anterior lobe dark brown, posterior lobe brown, scutellum brown with dark brown scutellar process, pleuron brown with straw-colored suffusion, sternum brown to dark brown. *Hemelytron:* Corium dark brown, membrane basally dark brown, apically off-white. *Legs:* Femur and tibia straw-colored with basal, medial and apical brown annulations, tarsus and claw light brown, same, same. 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, tuberculated setae, without pair of long straight setae on postocular lobe posterior to ocelli. THORAX: Anterior lobe with irregular row of tuberculated, short, curved setae on lateral margins and short, tuberculated setae dispersed on dorsal surface, posterior lobe with short, curved, setae on humeral angle and sparsely distributed along dorsal surface. *Hemelytron:* Corium with short, curved setae. *Legs:* With two rows of spines and tuberculated setae, tibia with regular rows of tuberculated, stout, sharp setae. ABDOMEN: Connexival margin with no prominent setae. STRUCTURE: HEAD: Short conical; maxillary plate rounded apically; scape not reaching apex of clypeus; eye hemispherical in dorsal view, less than 1/5 length of head, not attaining head ventral margin 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 contiguous with transverse sulcus; paramedian carina strongly 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; rounded lobe skewed towards median; scutellum rounded triangular, scutellar process long, apex subacute; mesosternite with 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 slightly undulating, posterior margin not elevated.

FEMALE: Male unknown.

BIOLOGY: Nothing is known about the biology of this species.

DISTRIBUTION: This species is known only from the type locality in Northeast Sumatra, Indonesia.

DISCUSSION: This specimen was found by Stephan Blank at the DEI without 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 are 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 4.5, 4.6, 4.8, 4.11, Table 4.4)

Physoderes notata Westwood 1845, original description.

Epirodera notata (Westwood, 1847), unsanctioned name change

Physoderes notata Miller, 1954

Physoderes corporaali Miller, 1954, **new synonymy.**

Physoderes brunneus Breddin, 1903, **new synonymy.**

Physoderes flavipennis Miller, 1940, **new synonymy.**

Holotype 1 male: INDONESIA: Java: Java, 7.61444°S 110.71222°E, 2999, Unknown, (UCR_ENT 00018526) (BMNH). The holotype is deposited at BMNH.

DIAGNOSIS: This species is recognized among cogeners 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 distinct color patterns on the pronotum, the hemelytron attaining the tip of the abdomen, the hind wings being bright yellow and sometimes apically brown, the cuplike 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* **n. sp.** and *P. impexa* but can be differentiated based on the head and pronotal color patterns, hemelytron color, cuplike sclerite shape and shape of the prolongations of the phallosoma.

REDESCRIPTION: *MALE:* Medium, total length 9.94mm, (SD ± 0.3) mm (Table 4.4). COLORATION (Fig. 4.5): Straw-colored and brown. HEAD: Anteocular lobe straw-colored with brown suffusion, postocular lobe brown. ANTENNA: Straw-colored with brown suffusion.

LABIUM: First segment light brown to brown, second segment straw-colored, third segment brown. THORAX: Pronotum 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. *Hemelytron:* Corium light brown to brown, membrane dark brown. *Legs:* Femur straw-colored with sub-basal and apical brown annulations, tibia brown with straw-colored base, tarsus and claw straw-colored, same, same. 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, tuberculated setae, with pair of long straight setae on postocular lobe posterior to ocelli. THORAX: Anterior lobe with irregular row of tuberculated, short, curved setae on lateral margins and short, tuberculated setae dispersed on dorsal surface, posterior lobe with only short, sparse setae. *Hemelytron:* Corium with short, curved setae. *Legs:* With two rows of spines and tuberculated setae, tibia with regular rows of tuberculated, stout, sharp setae. ABDOMEN: Connexival margin with no prominent setae. STRUCTURE: HEAD: Elongate conical; maxillary plate rounded apically; scape not reaching apex of clypeus; eye hemispherical in dorsal view, less than 1/5 length of head, not attaining head ventral margin 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 weakly defined; posterior lobe medially weakly rugose; anterior pronotal lobe equal length to posterior lobe, wider than posterior lobe, anterior lobe higher than posterior lobe in lateral view; rounded lobe skewed towards median; scutellum rounded triangular, scutellar process long, apex subacute; mesosternite with 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 slightly undulating, posterior margin not elevated. MALE 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; cuplike sclerite apically rounded with adjacent paired round protuberances; basal plate arms parallel to each other; ductifer membranous; endosomal struts 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 lower than the posterior lobe.

BIOLOGY: Not much is recorded about the biology of this species. One specimen was collected from under sheaths of bamboo, 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 227–1496m.

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

DISCUSSION: Examination of the holotypes of *P. corporaali* and *P. flavipennis* and the syntypes of *P. brunneus* indicate that both type specimens for *P. flavipennis* and *P. brunneus* represent females of *P. notata* that have the narrower anterior pronotal lobe. Similarly, *P. corporaali* shares the diagnostic characters and color patterns on the head and pronotum with *P. notata*. All three species are hereby synonymized under *P. notata*.

Other Specimens Examined: INDONESIA: East Java: Blawan, East Java, 7.98805°S

114.17138°E, No Date Provided, H. Lucht, 1;m (UCR_ENT 00024058) (RMNH). Lawang, East Java, 7.77972°S 112.50611°E, 1496 m, 1907, M. Buysman, 4;f (UCR_ENT 00024051-UCR_ENT 00024054) (RMNH). Nongkodjadjar (Nonkojajar), 7.91611°S 112.8875°E, 846 m, 1911, E. Jacobson, 1;f (UCR_ENT 00024055), 1;m (UCR_ENT 00024056) (RMNH). Java: C. N. Java, Moeria Mts., Tjolo (Muria Mts.), 6.61666°S 110.9575°E, 800 m, 20-24 Oct. 1939, M. A. Lieftinck, 1;m (UCR_ENT 00024060) (RMNH). Sulawesi Utara: Dumoga Bone National Park, Barney's Tree, 0.44972°N 123.93305°E, 300 m, 13-22 Nov. 1985, J. Krikken, 1;f (UCR_ENT 00024064) (RMNH). Manado, Cebeles, 1.46361°S 124.31055°E, Jun-Oct. 1926, no collector, 3;f (UCR_ENT 00046623, UCR_ENT 00046648, UCR_ENT 00046649) (CAS). Minahasa, N. Celebes, 1°N 124.58333°E, 550 m, 28 Jul 1941, F. Dupont, 1;m (UCR_ENT 00024062) (RMNH). Sumatera Barat (West Sumatra): Baso (Sumatra's Westkust), 0.27°N 100.46333°E, 800 m, Mar 1926, E. Jacobson, 3;f (UCR_ENT 00024021-UCR_ENT 00024023), 1;m (UCR_ENT 00024057) (RMNH). Fort de Kock, 0.26694°N 100.38333°E, 920 m, 1926, E. Jacobson, 1;f (UCR_ENT 00024020) (RMNH). Fort de Kock (=Bukittinggi), 0.26768°S 100.38394°E, Nov. 1913, E. Jacobson, 1;f (UCR_ENT 00024019) (RMNH); Oct 1913, E. Jacobson, 1;f (UCR_ENT 00014056) (RMNH). Gunning Singgalang (Sumatra's W Kust), 0.39°N 100.33083°E, 1200 m, 1925, E. Jacobson, 1;m (UCR_ENT 00024026) (RMNH). Sumatera Selatan (South Sumatra): S. W. Lampong Dist, Mt. Tanggamoes, 5.41666°S 104.7°E, 700 m, Dec. 1939, M. A. Lieftinck, 1;f (UCR_ENT 00024025) (RMNH). S. W. Lampong Dist, Mt. Tanggamoes, 5.41666°S 104.7°E, 500 m, Dec 1939, M. A. Lieftinck, 1;f (UCR_ENT 00024024) (RMNH). Sumatera Utara (North Sumatra): Nias Island, Goenoeng Sitoli, 1.12527°N 97.52472°E, 227 m, No date provided, Kleiweg de Zwaan, 1;m (UCR_ENT 00024027) (RMNH). Padang Sidempuan, 1.3725°N 99.25527°E, 332 m, No Date Provided, J. D. Pasteur, 1;m (UCR_ENT 00024059) (RMNH). MALAYSIA: Selangor: Kepong, in forest, 3.2325°N 101.6275°E, Aug 1949, none, 1;f

(UCR_ENT 00031389) (USNM). MALAYSIA: Perak: Jor Camp, 4.89972°N 100.79055°E, 610m, 21 Aug 1922, E. Seimund, 1;f (UCR_ENT 00018519) (BMNH).

***Physoderes ractepilosa*, new species** (Figs 4.5, 4.6, 4.8, 4.12, Table 4.4)

Holotype 1 female; INDONESIA: Sulawesi Tengah: Lore Lindu National Park, Marena Forest, 1.51666°N 120.18333°E, 650 m, 14–17 Dec 1985, J. Krikken (UCR_ENT 00014061). The holotype is deposited at the RMNH.

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 attaining the tip of the abdomen, the connexival margin jagged, and the females with wider connexivum than males. Additional diagnosic features are found on the male genitalia: the cuplike sclerite with rounded apex and broad adjacent sclerotized rounded protuberances, the apical margin of the posterior opening of the pygophore with medial process, the basal plate arms curved to form a rounded foramen, and the dorsal phallothecal sclerite apex subacute with broad lateral prolongations that projects angularly towards the apex of the phallosoma. This species most closely resembles *P. fuliginosa*, but can be differentiated by the long, erect setae, shape of the pronotum, parascutellar lobe and connexivum, as well as the hemelytron length.

DESCRIPTION: *MALE:* Medium, total length 9.19mm, (SD ± 0.67) (Table 4.4). COLORATION (Fig. 4.5): Brown. HEAD: Brown. ANTENNA: Scape and pedicel straw-colored with brown suffusion, basiflagellomere brown, distiflagellomere basally brown, apically straw-colored. LABIUM: First and second segment straw-colored, third segment brown. THORAX: Pronotum anterior lobe 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. *Hemelytron:* Corium brown, membrane brown. *Legs:* Femora 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: Densely setose. HEAD: With widespread long, erect, setae, ventral surface of postocular lobe with sparse, tuberculated setae, with pair of long straight setae on postocular lobe posterior to ocelli. THORAX: Anterior lobe 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. *Hemelytron:* Corium with long, erect setae. *Legs:* With two rows of spines and tuberculated setae, tibia with regular rows of tuberculated, stout, sharp setae. ABDOMEN: Posterior margin of connexivum with long, fine setae. STRUCTURE: HEAD: Elongate conical; maxillary plate truncate apically; scape not reaching apex of clypeus; eye hemispherical in dorsal view, less than 1/5 length of head, not attaining head ventral margin in lateral view; height of anteocular lobe shorter than postocular lobe. 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; posterior lobe medially rugose; anterior pronotal lobe shorter than posterior lobe, narrower than posterior lobe, anterior lobe lower than posterior lobe in lateral view; rounded lobe; scutellum rounded triangular, scutellar process long, apex subacute; mesosternite with median irregular tuberculated protrusion between fore and mid coxae. *Hemelytron:* Hemelytron not attaining tip of abdomen. *Legs:* Fore femur slightly incrassate. ABDOMEN: Elongate ovoid, with straight terminal margin; connexival margin jagged, posterior margin not elevated. MALE 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; cuplike sclerite apically rounded with adjacent paired round protuberances; basal plate arms rounded; ductifer membranous; endosomal struts tapered apex and divided into two arms basally; shape of dorsal phallothecal sclerite apex subacute with broad lateral prolongations that projects angularly towards the apex of the phallosoma.

FEMALE: Similar to females except do not seem to have as much long, erect setae and connexivum not as wide.

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

BIOLOGY: Specimens were collected in multistory evergreen forests using fish traps.

DISTRIBUTION: This species is only known from the type locality in Central Sulawesi and another locality in Northern Sulawesi.

DISCUSSION: A female specimen is chosen as the holotype for this species because the long, erected setae throughout 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 male genitalia described here shows that this species is very different from any other *Physoderes* species.

Paratypes: INDONESIA: Sulawesi Tengah: Lore Lindu National Park, Marena Forest, near river, 1.51666°N 120.18333°E, 600 m, 14–17 Dec 1985, J. Krikken, 1;m (UCR_ENT 00023400), 4;f (UCR_ENT 00023401-UCR_ENT 00023404) (RMNH). Sulawesi Utara: Dumoga Bone National Park Mt. Mogogonipa, 0.45°N 123.93305°E, 1000 m, 22–25 Aug 1985, J. Huijbregts, 1;m (UCR_ENT 00023999) (RMNH).

***Physoderes tricolor*, new species** (Figs 4.5, 4.6, 4.8, 4.12, Table 4.4)

Holotype 1 male; MALAYSIA: Sabah: Sandakan, 5.8333°N 118.1167°E, 4 m, No date provided, Baker (UCR_ENT 00030980). This holotype is deposited at the USNM.

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 scutellar process apex 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 pygophore anterior opening apodeme obsolete with the margin rounded, the cuplike sclerite with rounded apex and paired adjacent subacute protuberances, and the dorsal phallothecal sclerite triangular in shape. This species is most similar to *P. nigroalbus* but can be differentiated by size, coloration of the head, pronotum and scutellar process, and shape of eye.

DESCRIPTION: *MALE:* Medium, total length 8.66mm, (SD ± 0.16) (Table 4.4). COLORATION (Fig. 4.5): Brown, brownish black and off-white. HEAD: Anteriorly straw-colored, posteriorly brown. ANTENNA: Straw-colored. LABIUM: First and second segment straw-colored, third segment light brown. THORAX: Pronotum anterior lobe 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. *Hemelytron:* Corium 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. *Legs:* Femora and tibiae 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 od 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, tuberculated setae, with pair of long straight setae on postocular lobe posterior to ocelli. THORAX: anterior lobe with irregular row of tuberculated, short, curved setae on lateral margins and curved setae on the anterior portion of the dorsal surface, posterior lobe with short, curved, setae on humeral angle and sparsely distributed along dorsal surface. *Hemelytron:* Corium with short, curved setae. *Legs:* With two rows of spines and tuberculated setae, tibia with regular rows of tuberculated, stout, sharp setae. ABDOMEN: Connexival margin with a few clubbed setae on each segment, or connexival margin with no prominent setae. STRUCTURE: HEAD: Short 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 head ventral margin in lateral view; height of anteocular 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 rugose; anterior pronotal lobe shorter than posterior lobe, slightly narrower than posterior lobe, anterior lobe level with posterior lobe in lateral view; rounded lobe skewed towards median; scutellum rounded triangular, scutellar process long, apex subacute; mesosternite with 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 slightly undulating, posterior margin not elevated. MALE 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; cuplike sclerite apically rounded with adjacent paired small subacute protuberances; basal plate arms parallel to each other; ductifer membranous; endosomal struts tapered, acute apex, divided into two arms basally; shape of dorsal phallothecal sclerite triangular with angular lateral prolongations.

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

ETYMOLOGY: The name is after Lating adjective “tricolor” meaning three-colored to describe the three colors that are visible dorsally.

BIOLOGY: Nothing is known about the biology of this species.

DISTRIBUTION: This species is known only from the type locality Sandakan, Northeast Borneo.

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

Paratypes: MALAYSIA: Sabah: Sandakan, 5.8333°N 118.1167°E, 4 m, No date provided, Baker, 1;m (UCR_ENT 00031439), 3;f (UCR_ENT 00031440-UCR_ENT 00031442) (USNM).

Revised Classification List

Breviphysoderes, n. gen.

Type species: *Physoderes mjoebergi* Miller, 1940

Breviphysoderes decora (Miller), **new combination**

Physoderes decora Miller, 1940, original combination

Physoderes ostenta Miller, 1941, **new synonymy**

Breviphysoderes fulvopicta, **n. sp.**

Breviphysoderes hobbyi (Miller, 1940), **new combination**

Physoderes hobbyi Miller 1940 original combination

Breviphysoderes mjoebergi (Miller) **new combination**

Physoderes mjoebergi Miller 1940 original combination

Physoderes dyak Miller 1955 **new synonymy**

Breviphysoderes planicollis (Miller) **new combination**

Physoderes planicollis Miller 1940 original combination

Breviphysoderes shelfordi (Miller) 1940 **new combination**

Physoderes shelfordi Miller 1940 original combination

Breviphysoderes tenebrosa **n.sp.**

Breviphysoderes vestita (Horváth) **new combination**

Epirodera vestita Horváth 1900 original combination

Physoderes vestita new combination by Maldonado 1990

Physoderes serraticollis Breddin 1903 **new synonymy**

Physoderes javanica Miller 1940 **new synonymy**

Physoderes rugosa Miller 1954 **new synonymy**

Macrophysoderes n. gen.

Type species: *Physoderes histrionica* Miller 1940

Macrophysoderes bengalensis (Distant)

Epirodera bengalensis Distant 1909 original combination

Physoderes bengalensis new combination by Maldonado 1990

Macrophysoderes cirripilosa **n. sp.**

Macrophysoderes elongata **n. sp**

Macrophysoderes finisterre **n. sp.**

Macrophysoderes grandis **n. sp.**

Macrophysoderes histrionica (Miller) **new combination**

Physoderes histrionica Miller 1940 original combination

Macrophysoderes modesta (Miller) **new combination**

Physoderes modesta Miller 1940 original combination

Physoderes sibauana Miller 1940 **new synonymy**

Physoderes trusana Miller 1940 **new synonymy**

Macrophysoderes monticola (Miller) **new combination**

Physoderes monticola Miller 1940 original combination

Physoderes dimidiata Miller 1940**, new synonymy**

Physoderes luiana Miller 1940 **new synonymy**

Nanophysoderes n. gen.

Type species: *Physoderes dentiscutum* Bergroth 1906

Nanophysoderes dentiscutum (Bergroth) 1906 **new combination**

Physoderes dentiscutum Bergroth 1906 original combination

Paraphysoderes Villiers

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

Paraphysoderes crassa Villiers, 1962

Paraphysoderes peyrierasi Villiers, 1968

Paraphysoderes popeye **n. sp.**

Physoderes Westwood

Type species: *Physoderes notata* Westwood 1844, by monotypy

Physoderes anamalaiensis **n. sp.**

Physoderes azrael Kirkaldy 1905

Physoderes brevipennis **n.sp.**

Physoderes curculionis China 1935

Physoderes insulanus Miller 1940 **new synonymy**

Physoderes patagiata Miller 1941 **new synonymy**

Physoderes minor Usinger 1946 **new synonymy**

Physoderes kalshoveni Miller 1954 **new synonymy**

Physoderes fuliginosa (Stål)

Epirodera fuliginosa Stål 1870 original combination

Physoderes fuliginosa Maldonado 1990

Physoderes esakii Cao, Tomokuni & Cai 2011, **new synonymy**

Epirodera latithorax Esaki 1931 nomen nudum

Physoderes latithorax Maldonado 1990

Physoderes mauriciensis (Villiers), **new combination**

Epiroderoides mauriciensis Villiers 1964 original combination

Physoderes minime **n. sp.**

Physoderes muluensis **n.sp.**

Physoderes mysorensis **n.sp.**

Physoderes nigripennis **n. sp.**

Physoderes nigroalbus Breddin 1903 **Lectotype designated**

Physoderes notata Westwood

Physoderes notata Westwood 1845

Epirodera notata (Westwood 1847) unsanctioned name change

Physoderes notata Miller 1954

Physoderes corporaali Miller 1954, **new synonymy**

Physoderes brunneus Breddin 1903, **new synonymy**

Physoderes flavipennis Miller 1940, **new synonymy**

Physoderes ractepilosa **n.sp.**

Physoderes tricolor **n. sp.**

Incertae sedis

Physoderes brancsiki Bergroth 1906

Physoderes buruensis Miller 1954

Physoderes fuscus Breddin 1903

Physoderes impexa (Distant)

Epirodera impexa Distant 1903 original combination

Physoderes fuscus Breddin 1903 synonymized by Distant 1904

Physoderes impexa Izzard 1936

Physoderes pallidirostris (Stål)

Epirodera pallidirostris Stål 1863

Physoderes pallidirostris Maldonado 1990

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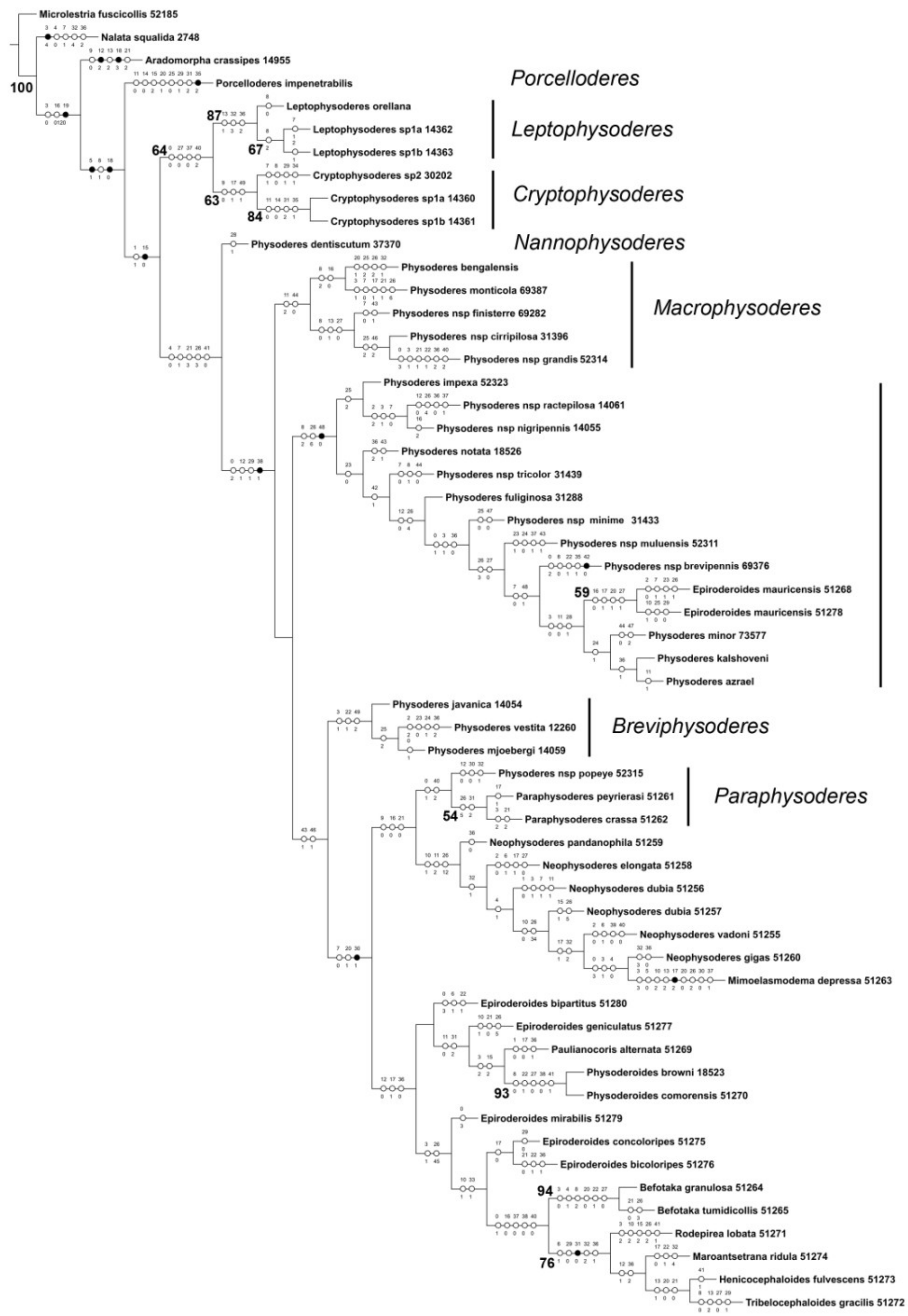

Fig. 4.1. Phylogeny of Physoderinae based on 57 morphological characters for 57 taxa analyzed using parsimony on TNT. Open white circles denote homoplastic characters, black circles denote characters that are not homoplastic. Numbers above the circles refer to character number (Table 4.2) and numbers below the circles refer to the character states (Table 4.3). Numbers in bold indicate symmetric resampling values.

Fig. 4.2 Dorsal habitus images of *Breviphysoderes* gen. n. species. Scale bar = 2mm

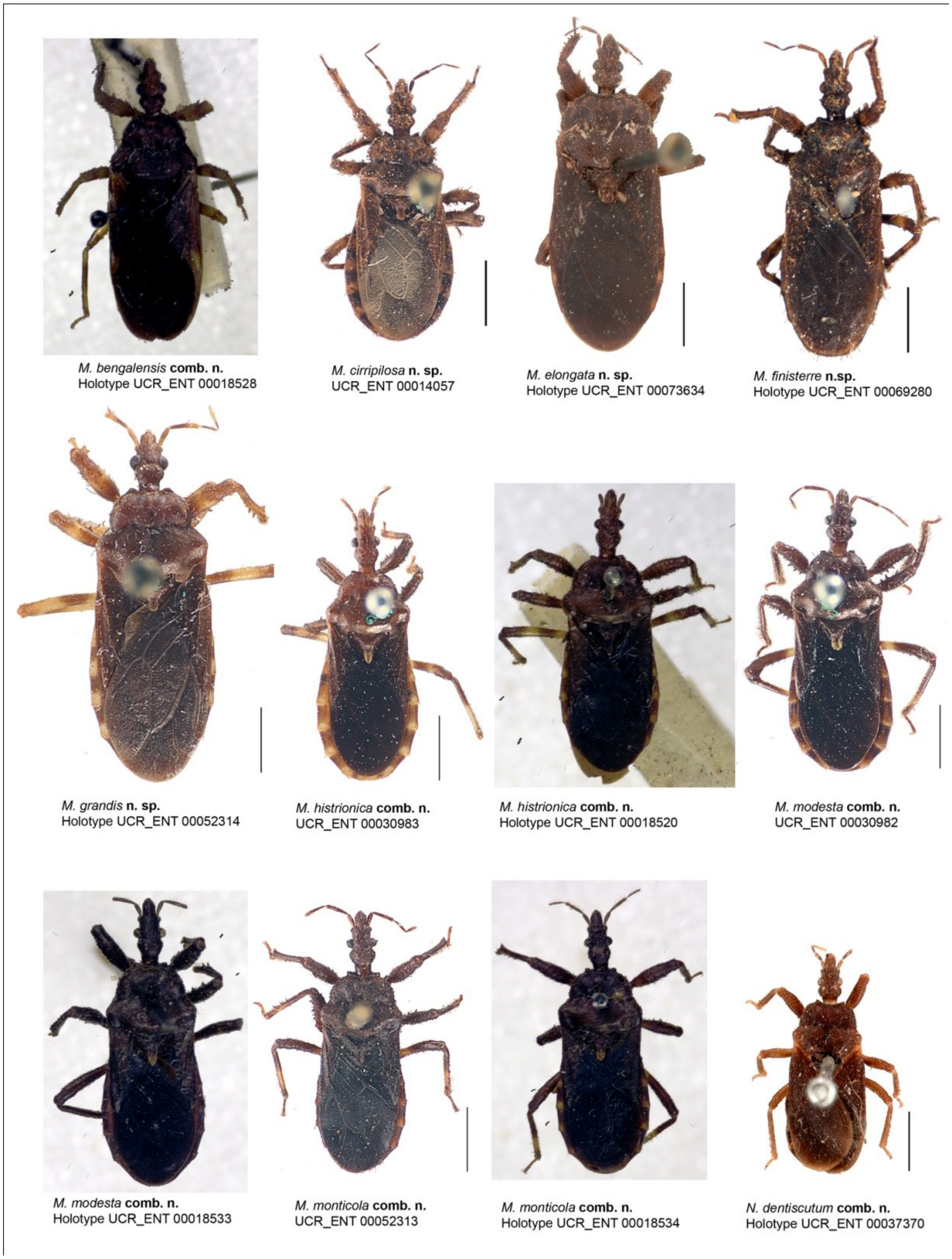

Fig. 4.3 Dorsal habitus images of *Macrophysoderes* gen. n. and *Nanophysoderes* gen. n. species. Scale bar = 2mm

Fig. 4.4 Dorsal habitus images of *Paraphysoderes* and *Physoderes* species (partial). Scale bar = 2mm

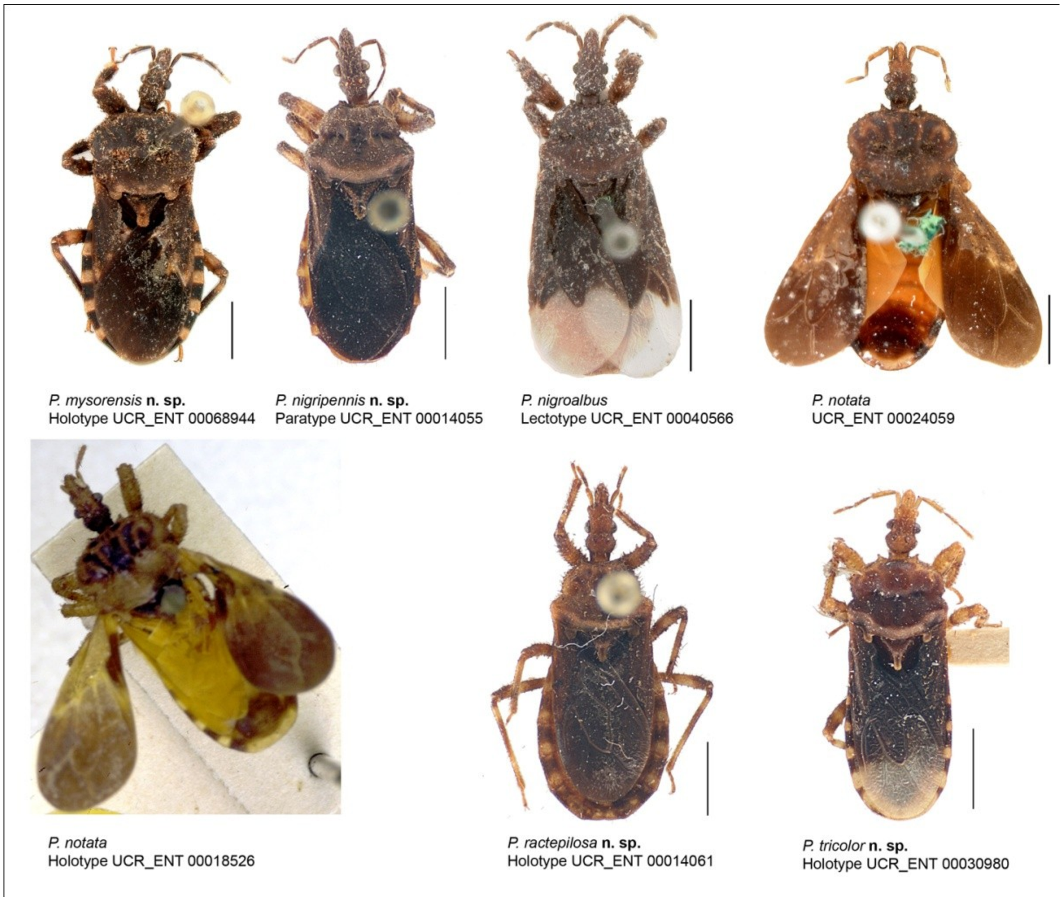

Fig. 4.5 Dorsal habitus images of *Physoderes* species (partial). Scale bar = 2mm

Fig. 4.6 Dorsal view of male pygophore of *Breviphysoderes*, *Macrophysoderes*, *Paraphysoderes* and *Physoderes* species.

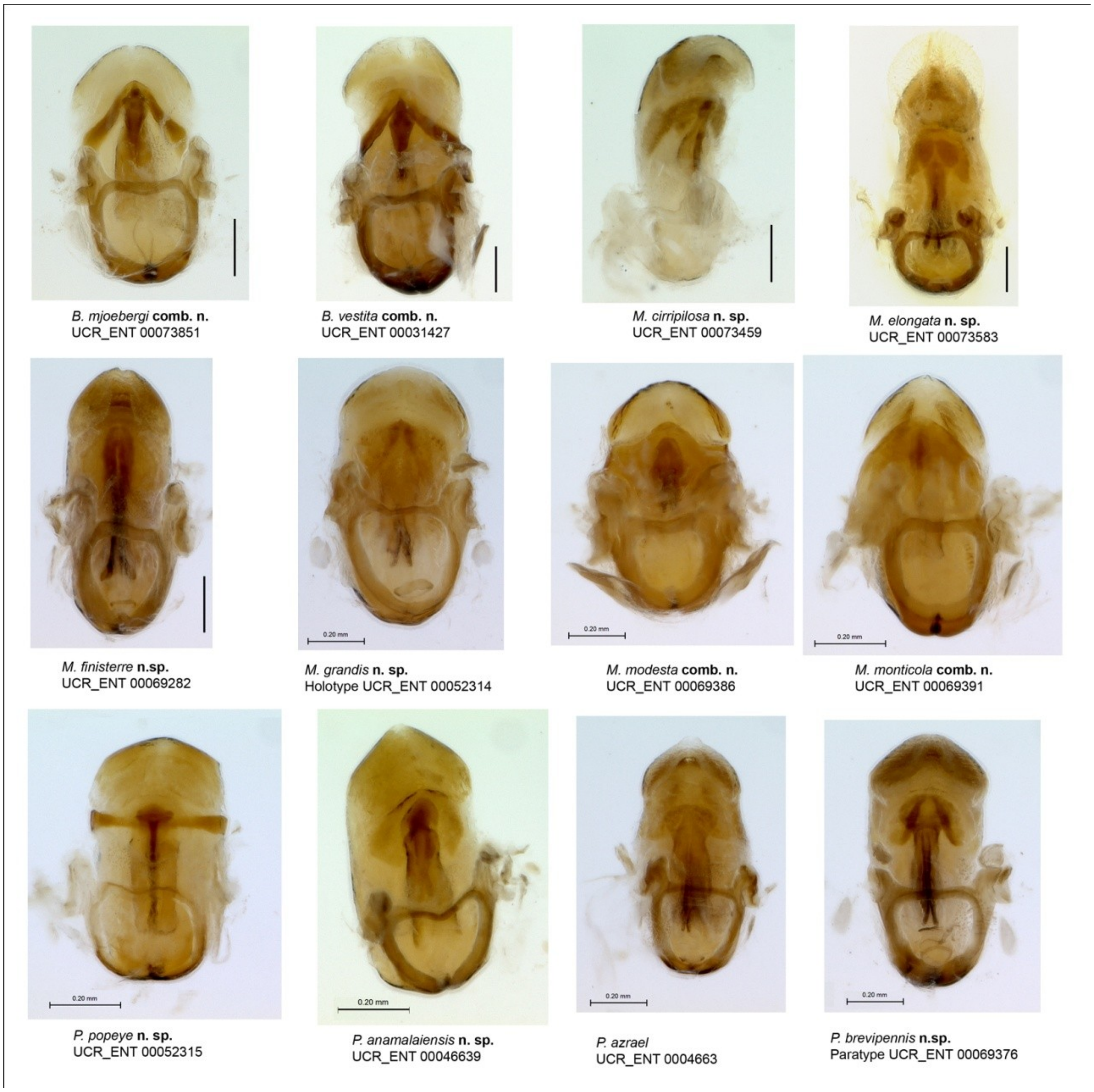

Fig. 4.7 Dorsal view of the phallus (partial). Scale bar = 0.20mm.

Fig. 4.8 Dorsal view of the phallus (partial). Scale bar = 0.20mm.

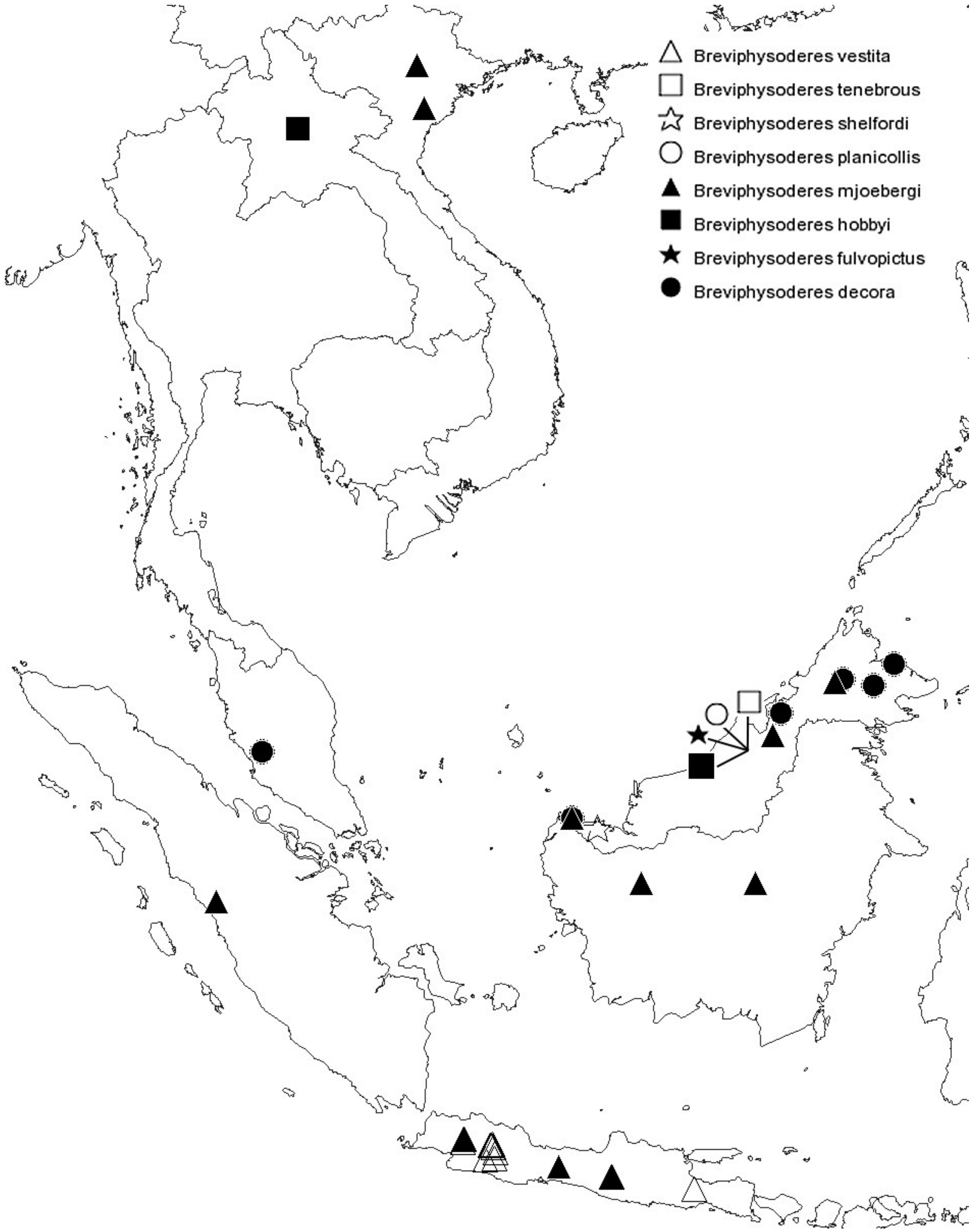

Fig. 4.9. Distribution map for *Breviphysoderes* species.

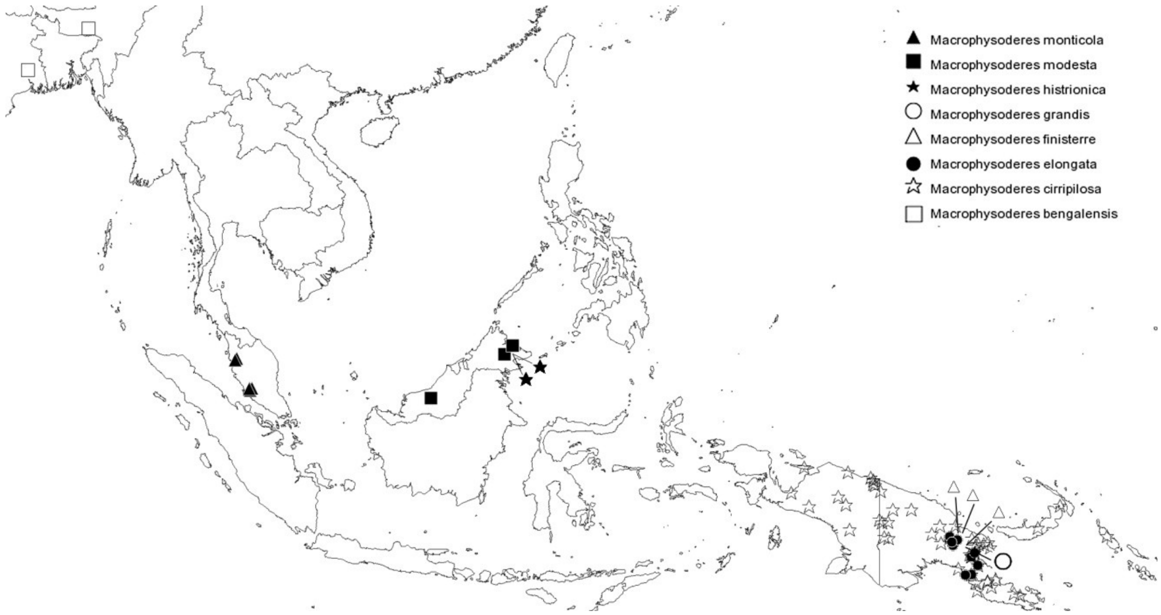

Fig. 4.10. Distribution map for *Macrophysoderes* species.

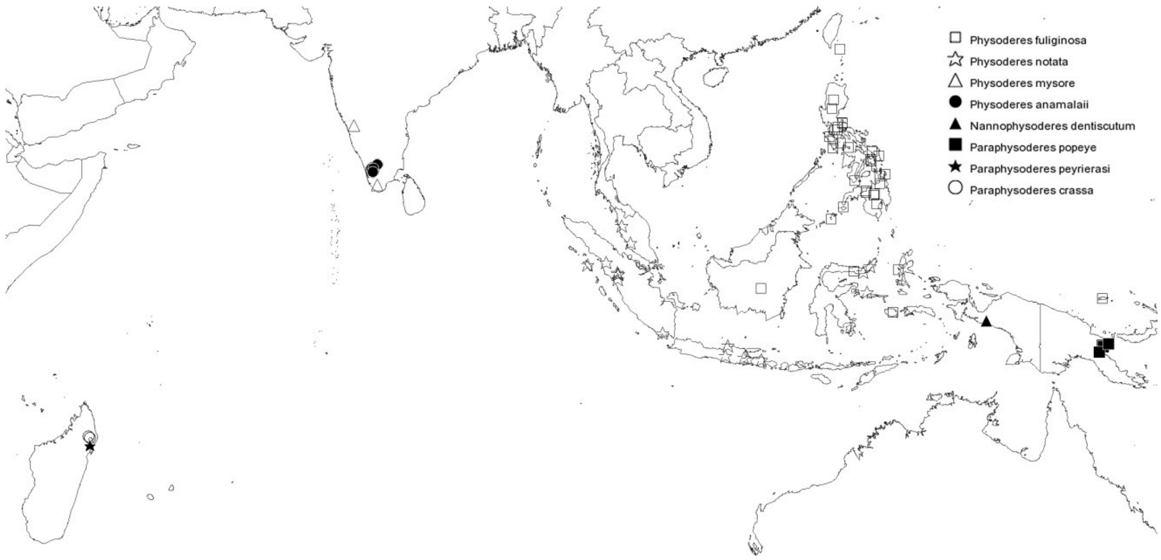

Fig. 4.11. Distribution map of *Paraphysoderes* and *Physoderes* (in part).

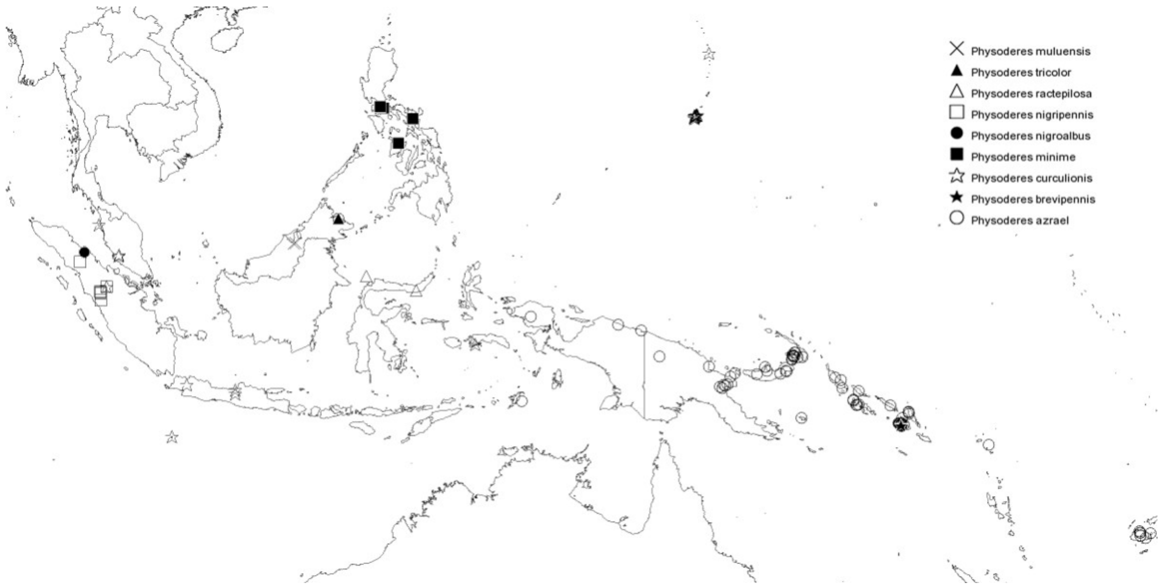

Fig. 4.12. Distribution of *Physoderes* species (in part).

Table 4.1. Morphological matrix for Physoderinae + outgroup taxa.

Microlestria_fuscicollis_52185	011310000101001131210111110010010200120110????????
Nalata_squalida_2748	101400010101011130110011110100014200220111?????210
Aradomorpha_crassipes_14955	101010?00001221101300201110100010200120111?1?0?0??
Epiroderoides_mauricensis_51268	110001012100001001001301?11111010200021110????????
Epiroderoides_mauricensis_51278	111001002?10001001001300203110010200021110????????
Epiroderoides_concoloripes_51275	211101001111001010001201015100111100021110????????
Epiroderoides_bicoloripes_51276	211101001111001010001011?15101110100121110????????
Epiroderoides_geniculatus_51277	211001001110001011001001?1510?120200021110????????
Epiroderoides_mirabilis_51279	311101001101001011001301015101110200021110????????
Epiroderoides_bipartitus_51280	31100110110100101?001311?13101110200021110????????
Befotaka_granulosa_51264	111011002111001001000211125001111100000100????????
Befotaka_tumidicollis_51265	111011002111001001000011?23001110100000100????????
Neophysoderes_dubia_51256	201111010011101000001001?1210111???0121110????????
Neophysoderes_dubia_51257	211011000002101100001001?2510?111010121110????????
Neophysoderes_vadoni_51255	21001110000211100100100102410?112010221000????????
Neophysoderes_elongata_51258	210001100012101001001001?11001111110121110????????
Neophysoderes_pandanophila_51259	211001000012101000001001011101110010021110????????
Neophysoderes_gigas_51260	311101000002101001001001013101113010021110????????
Henicocephaloides_fulvescens_51273	111101101111111001000001014100102100200001????????
Tribelocephaloides_gracilis_51272	11010110011112100100000101400110210020???0????????
Maroantsetrana_ridula_51274	1101011011111101000001211015100104100200000????????
Mimoelasmodema_depressa_51263	311300000022121002000001012101012010211110????????
Paraphysoderes_peyrierasi_51261	111001000001101001001011?1510?120100121120????????
Paraphysoderes_crassa_51262	111201000001101000001201015101?20100121120????????
Paulianocoris_alternata_51269	201201001100001210001201013101120200121110????????
Physoderoides_browni_18523	211201000100001211001211?1300?120200020111????????
Physoderoides_comorensis_51270	211201000100001211001211013001120200020111????????
Rodepirea_lobata_51271	11120110112100120100120102210010210010???1????????
Porcelloderes_impenetrabilis	1010?1001?00000200001011-00--1020202-10111????????
Cryptophysoderes_sp1a_14360	010011001000000021000001?10000020201-00121?0?0?011
Cryptophysoderes_sp1b_14361	010011001000000021000001?1000?020201-00121?0?0?011
Cryptophysoderes_sp2_30202	010011010001001021000001?10001010210100121?0?0?011
Leptophysoderes_orellana	0100?1000?010110?000?001010000013200200??1?-10?010
Leptophysoderes_sp1a_14362	010011012101011020000001010000013200200121????????
Leptophysoderes_sp1b_14363	011011002101011020000001010000013200200121????????
Physoderes_dentiscutum_37370	110001011101001020000301?13110010200120110????????
Physoderes_nsp_popeye_52315	11100100000100100000101101310101121012112021011110
Physoderes_nsp_brevipennis_69376	211101000101001010000310213001010201-2111000112110

Table 4.1 Morphological matrix for Physoderinae + outgroup taxa. (cont'd)

Physoderes_nsp_muluensis_52311	11110101210100101000030101300101020001111011111010-
Physoderes_vestita_12260	21210101010110101000031012310101020022111021111112
Physoderes_javanica_14054	21110101010110101000031101310101020012111021111112
Physoderes_mjoebergi_14059	1111010101011010100003110231010102001211110????????
Physoderes_notata_18526	211001012?0110101000030021610101020022111102111010-
Physoderes_fuliginosa_31288	2110010121010010100003002141010102001211110????????
Physoderes_nsp_minime_31433	1111010121010010100003002041010102000021110?011200-
Physoderes_nsp_ractepilosa_14061	21210100210100101000030102410101020001111102011020-
Physoderes_nsp nigripennis_14055	2121010021011010200003010261010102001211110?011020-
Physoderes_nsp_tricolor_31439	21100100110110101000030011610101020012111101001010-
Physoderes_impexa_52323	2110010121011010100003011261010102001211110????????
Physoderes_kalshoveni	1110010021000010100003001130110202001211110????????
Physoderes_minor_73577	11100100210000101000030011301102020002111010012210
Physoderes_azrael	11100100210100101000030011301101020012111010112110
Physoderes_nsp_finisterre_69282	21100100010211101000030101300101020012111011010210
Physoderes_nsp_cirripilosa_31396	211001010102111010000301023001010200121111010012??
Physoderes_nsp_grandis_52314	31110101010211101000011102300101020022112010012210
Physoderes_bengalensis	210001012?021010000013010221010112001211101001012
Physoderes_monticola_69387	2101010020021010010001010161010102001211110????????

Table 4.2. Measurements used as continuous characters in matrix.

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
Epiroderoides_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
Mimoelasmodema_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
Cryptophysoderes_sp1a_14360	2.116	1.537	0.633	1.125	1.053	1.347	1.475
Cryptophysoderes_sp1b_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_sp1a_14362	2.036	1.784	0.987	1.179	0.987	1.489	1.69
Leptophysoderes_sp1b_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
Physoderes_vestita_12260	2.125	1.733	0.686	1.083	0.857	1.303	1.308

Table 4.2. Measurements used as continuous characters in matrix. (cont'd)

Physoderes_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_kalshoveni	2	1.593	0.7	1.075	0.899	1.404	1.579
Physoderes_nigripennis_14055	2.205	1.793	0.68	1.182	0.843	1.326	1.465
Physoderes_nsp_ractepilosa_14061	2.326	1.438	0.71	1.07	0.98	1.373	1.528
Physoderes_minor_73577	1.897	1.414	0.662	1.051	0.813	1.374	1.393
Physoderes_nsp_popeye_52315	1.914	1.64	0.687	1.171	0.87	1.429	1.64
Physoderes_nsp_grandis_52314	2.369	2.083	0.69	1.316	0.865	1.423	1.67
Physoderes_nsp_brevipennis_69376	2.093	1.679	0.69	1.093	0.857	1.238	1.414
Physoderes_nsp_muluensis_52311	2.297	1.615	0.671	1.135	1.012	1.31	1.53
Physoderes_nsp_finisterre_69282	2.093	1.677	0.69	1.209	0.874	1.408	1.67
Physoderes_nsp_minime_31433	2.563	1.517	0.732	1.1	0.949	1.204	1.581
Physoderes_nsp_tricolor_31439	2.049	1.769	0.69	1.122	0.792	1.226	1.655
Physoderes_bengalensis	2.024	2.136	0.699	1.146	0.822	1.361	1.841
Physoderes_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
Physoderes_mjoebergi_14059	2.244	1.714	0.707	1.171	0.979	1.33	1.328
Physoderes_nsp_cirripilosa_31396	2.125	1.815	0.682	1.225	0.842	1.337	1.613
Physoderes_dentiscutum_37370	2.103	1.593	0.732	1.103	1	1.433	1.574

Table 4.3. List of characters and their states.

No.	Character	States				
0	Overall body size	very small	small	medium	large	
1	Short fine adpressed setae on body	absent	present			
2	Curved tuberculated setae on body	absent	present, short	present, long		
3	Head shape	conical	elongate conical	angular conical	ovoid	cuboid
4	Labrum shape anteriad view	short triangular	elongate triangular			
5	Clypeus length dorsal view	short	extended			
6	Clypeus apex lateral view	rounded	subacute			
7	Maxillary plate apex shape	rounded	truncate			
8	Length of scapus	extend beyond clypeus	shorter than clypeus	equal length		
9	Pedicellar trichobothria socket membranous area	absent	present			
10	Head vertex shape	convex	strongly convex	almost flat		
11	Size of eyes relative to head dorsal view	small	large	very large		
12	Eye shape dorsal view	hemispherical	distinctly projecting	not projecting		
13	Eye ventral margin	not attaining	attaining	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, setae tuberculated	
17	Height of anteocular lobe lateral view	lower than postocular	level with postocular	higher than postocular		
18	Length of second visible labial segment	more than twice the length of first segment	shorter than first segment	equal to first segment	slightly longer than first segment	

Table 4.3. List of character and their states (cont'd)

No.	Character	States						
19	Curvature of second visible labial segment	straight	curved					
20	Ventral of head with row of stout tuberculated setae	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	lightly carinated	deeply carinated				
26	Shape of paramedian 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 present, adjacent to stridulitrium	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		

Table 4.3. List of character and their states (cont'd)

No.	Character	States		
33	Body shape in lateral view	distinctly flattened	slightly flattened	not flattened
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 attaining	attaining	surpassing
37	Fore femur shape	slender	slightly incrassate	distinctly incrassate
38	Fore femur armature (spines)	absent	present	
39	Fore femur armature (stout tuberculated setae)	absent	present	
40	Fore tibia armature	absent	row of tuberculated setae present	few tuberculated setae present
41	Number of tarsal segments	three-segmented	two-segmented	
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 lateral view	rounded	angular	
45	Presence of lateral flaplike prolongations of phallosoma	absent	present	
46	Shape of lateral flaplike prolongations of phallosoma	plate-like	band-like	
47	Basal plate arms arrangement	converging	parallel	rounded
48	Ductifer with sclerotized ring	absent	present	
49	Shape of ductifer sclerotized ring	rounded	angular	elongate

Table 4.4 Measurements for species of *Breviphysoderes*, *Macrophysoderes*, *Nanophysoderes*, *Paraphysoderes* and *Physoderes* (in mm).

Species	Sex	USI	Total Length	Head length	Eye length	Eye width	Pronotum Anterior lobe (l)	Pronotum Anterior lobe (w)	Pronotum Posterior lobe (l)	Pronotum Posterior lobe (w)	Hemelytron length	Scape length	Interocular dist.	Postocular lobe width	Abdomen width
Breviphysoderes															
B. decora	F	UCR_ENT 00031393	8.86	1.79	0.38	1.02	0.93	2.10	1.09	2.88	5.47	0.55	0.58	0.86	3.61
	F	UCR_ENT 00031392	9.45	2.17	0.39	1.11	0.95	2.29	1.04	3.12	5.38	0.58	0.64	0.88	4.05
	F	UCR_ENT 00031391	8.81	2.00	0.38	0.99	1.09	2.14	0.89	2.75	5.12	0.55	0.51	0.88	3.56
	F	UCR_ENT 52186	9.53	2.24	0.46	1.10	1.05	2.32	1.13	3.14	5.63	0.51	0.65	0.94	3.86
	F	UCR_ENT 00014058	9.29	1.89	0.38	1.07	0.90	2.06	1.26	2.89	5.42	0.56	0.58	0.85	3.72
		Mean	9.19	2.02	0.40	1.06	0.98	2.18	1.08	2.96	5.41	0.55	0.59	0.88	3.76
		Standard Deviation	0.33	0.19	0.03	0.05	0.09	0.12	0.14	0.17	0.18	0.03	0.06	0.04	0.20
		Minimum	8.81	1.79	0.38	0.99	0.90	2.06	0.89	2.75	5.12	0.51	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	0.65	0.94	4.05
B. mjoebergi	M	UCR_ENT 00014060	8.35	1.82	0.36	0.95	0.92	2.08	1.00	2.74	4.77	0.57	0.56	0.84	3.50
	M	UCR_ENT 00073851	7.89	1.39	0.39	0.95	0.77	2.01	1.38	2.88	4.50	0.50	0.52	0.79	3.37
	M	UCR_ENT 00069399	7.49	1.66	0.36	1.00	0.97	1.96	0.94	2.61	3.96	0.53	0.59	0.85	3.06
		Mean	7.91	1.62	0.37	0.96	0.89	2.02	1.11	2.74	4.41	0.53	0.56	0.83	3.31
		Standard Deviation	0.43	0.21	0.02	0.03	0.11	0.06	0.24	0.14	0.41	0.03	0.04	0.03	0.23
		Minimum	7.49	1.39	0.36	0.95	0.77	1.96	0.94	2.61	3.96	0.50	0.52	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	0.59	0.85	3.50
	F	UCR_ENT 00014059	7.91	1.86	0.87	0.98	0.94	2.08	0.97	2.63	4.36	0.55	0.58	0.84	3.41
	F	UCR_ENT 00069398	8.28	1.90	0.40	1.00	0.87	1.97	1.04	2.77	4.70	0.53	0.57	0.84	3.31
	F	UCR_ENT00030981	8.74	1.96	0.32	1.01	0.90	2.17	1.04	2.87	5.03	0.60	0.62	0.88	3.78
	F	UCR_ENT 52181	9.34	1.71	0.35	1.06	1.25	2.46	1.05	3.14	5.46	0.51	0.64	0.92	4.14
	F	UCR_ENT 00073849	9.54	1.68	0.42	1.12	1.01	2.48	1.32	3.13	5.59	0.63	0.64	0.89	4.17
		Mean	8.76	1.82	0.47	1.03	1.00	2.23	1.08	2.91	5.03	0.56	0.61	0.87	3.76
		Standard Deviation	0.69	0.12	0.23	0.06	0.15	0.23	0.14	0.22	0.52	0.05	0.03	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	0.57	0.84	3.31

Table 4.4 Measurements for species of *Breviphysoderes*, *Macrophysoderes*, *Nanophysoderes*, *Paraphysoderes* and *Physoderes* (cont'd)

							Pronotum								
Species	Sex	USI	Total Length	Head length	Eye length	Eye width	Anterior lobe (l)	Anterior lobe (w)	Posterior lobe (l)	Posterior lobe (w)	Hemelytron length	Scape length	Interocular dist.	Postocular lobe width	Abdomen width
B. vestita (cont'd)		Maximum	10.23	2.08	0.38	1.07	1.50	3.18	1.24	3.35	6.20	0.69	0.65	0.93	4.07
	F	UCR_ENT 00014054	9.16	1.89	0.30	1.00	1.12	2.46	1.11	2.90	5.55	0.59	0.66	0.92	4.15
	F	UCR_ENT 00024040	9.54	2.04	0.38	0.99	1.09	2.22	1.02	2.91	5.54	0.56	0.63	0.89	3.94
	F	UCR_ENT 00024034	8.74	1.57	0.29	0.99	1.03	2.05	1.03	2.73	5.36	0.58	0.61	0.83	3.73
	F	UCR_ENT 00024038	8.99	1.93	0.34	1.01	1.05	2.43	1.10	2.84	5.26	0.64	0.59	0.88	3.87
	F	UCR_ENT 00024035	9.24	1.79	0.34	1.04	1.01	2.30	1.18	3.08	5.58	0.60	0.67	0.89	4.05
		Mean	9.13	1.84	0.33	1.01	1.06	2.29	1.09	2.89	5.46	0.60	0.63	0.88	3.95
		Standard Deviation	0.30	0.18	0.03	0.02	0.04	0.17	0.06	0.13	0.14	0.03	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	0.59	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	0.67	0.92	4.15
Macrophysoderes															
M. cirripilosa	M	UCR_ENT 46653	7.80	1.54	0.32	0.92	0.81	1.88	0.92	2.40	4.71	0.46	0.56	0.83	2.72
	M	UCR_ENT 00069787	7.97	1.68	0.35	0.93	0.89	1.98	0.98	2.54	4.76	0.40	0.57	0.84	2.89
	M	UCR_ENT 00031395	8.38	1.68	0.29	1.05	0.99	2.17	0.88	2.71	5.09	0.48	0.68	0.88	3.52
	M	UCR_ENT 00069770	8.24	1.55	0.36	0.84	0.87	2.11	1.04	2.68	5.17	0.49	0.75	0.91	3.07
	M	UCR_ENT 00073464	8.66	1.65	0.33	0.90	1.02	2.09	0.77	2.86	5.26	0.40	0.56	0.79	3.27
	M	UCR_ENT 46658	8.09	1.45	0.30	0.96	1.07	2.38	0.95	2.79	5.01	0.40	0.64	0.85	3.19
	M	UCR_ENT 00073460	8.88	1.70	0.35	1.04	1.14	2.62	0.94	3.00	5.49	0.49	0.69	0.86	3.38
	M	UCR_ENT 00069257	7.97	1.64	0.32	0.92	0.89	2.09	0.88	2.53	4.74	0.41	0.56	0.84	3.04
	M	UCR_ENT 00073450	8.04	1.57	0.35	0.94	0.92	2.25	0.97	2.75	4.80	0.46	0.56	0.80	3.08
	M	UCR_ENT 00073449	9.03	1.71	0.36	1.05	0.97	2.52	0.97	2.91	5.54	0.46	0.66	0.91	3.22
	M	UCR_ENT 00073448	8.81	1.62	0.34	1.03	0.85	2.41	1.09	2.85	5.48	0.46	0.64	0.84	3.34
	M	UCR_ENT 00031396	9.19	1.76	0.33	0.97	0.95	2.13	1.03	2.87	5.67	0.50	0.59	0.85	3.32
	M	UCR_ENT 00073601	9.62	1.75	0.38	1.01	1.00	2.30	1.12	3.07	6.05	0.46	0.67	0.86	3.62
	M	UCR_ENT 00073479	9.85	1.99	0.39	1.05	0.87	2.31	1.32	3.07	5.93	0.53	0.60	0.90	3.48
	M	UCR_ENT 00073467	8.97	1.60	0.35	1.01	0.94	2.30	1.14	2.91	5.53	0.50	0.64	0.85	3.39
	M	UCR_ENT 00024030	9.67	1.72	0.33	1.02	0.96	2.30	1.21	3.16	5.92	0.49	0.62	0.85	3.43
		Mean	8.70	1.66	0.34	0.98	0.95	2.24	1.01	2.82	5.32	0.46	0.62	0.85	3.25
		Standard Deviation	0.66	0.12	0.03	0.06	0.09	0.19	0.14	0.21	0.45	0.04	0.06	0.03	0.24
		Minimum	7.80	1.45	0.29	0.84	0.81	1.88	0.77	2.40	4.71	0.40	0.56	0.79	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	0.91	3.62

Table 4.4 Measurements for species of *Breviphysoderes*, *Macrophysoderes*, *Nanophysoderes*, *Paraphysoderes* and *Physoderes* (cont'd)

Species	Sex	USI	Total Length	Head length	Eye length	Eye width	Pronotum Anterior lobe (l)	Pronotum Anterior lobe (w)	Pronotum Posterior lobe (l)	Pronotum Posterior lobe (w)	Hemelytron length	Scape length	Interocular dist.	Postocular lobe width	Abdomen width
M. cirripilosa (cont'd)	F	UCR_ENT 00069774	7.45	1.44	0.30	0.89	0.86	1.79	0.79	2.43	4.56	0.44	0.58	0.82	3.06
	F	UCR_ENT 00069775	7.79	1.61	0.31	0.93	0.94	2.04	0.69	2.52	4.99	0.46	0.62	0.87	3.35
	F	UCR_ENT 00069773	7.16	1.37	0.31	0.88	0.75	1.88	0.88	2.47	4.04	0.40	0.55	0.83	3.24
	F	UCR_ENT 00069772	8.12	1.27	0.32	0.89	0.80	1.90	1.10	2.43	4.74	0.44	0.55	0.82	2.91
	F	UCR_ENT 00069776	7.77	1.27	0.23	0.93	0.72	1.96	0.97	2.50	5.06	0.45	0.60	0.84	3.26
	F	UCR_ENT 00073488	8.48	1.66	0.38	1.06	0.83	2.17	1.06	2.82	5.20	0.46	0.59	0.90	3.53
	F	UCR_ENT 00073495	8.64	1.67	0.34	1.04	1.02	2.23	1.03	2.82	5.33	0.44	0.65	0.92	3.59
	F	UCR_ENT 00073494	8.61	1.72	0.46	0.98	0.84	2.05	1.02	2.68	5.14	0.47	0.65	0.82	3.52
	F	UCR_ENT 00073499	8.78	1.66	0.33	1.10	0.91	2.19	1.12	2.88	5.63	0.46	0.79	0.94	3.68
	F	UCR_ENT 00014057	8.71	1.73	0.32	1.02	0.84	2.19	1.10	2.83	5.37	0.45	0.66	0.90	3.64
	F	UCR_ENT 00073618	9.35	1.69	0.39	0.98	0.95	2.11	1.05	2.88	5.77	0.47	0.66	0.81	3.70
	F	UCR_ENT 00073616	9.22	1.63	0.36	1.04	0.88	2.18	1.21	2.98	5.61	0.57	0.67	0.85	3.82
	F	UCR_ENT 00073617	9.71	1.72	0.36	1.10	0.99	2.36	1.13	3.12	5.99	0.51	0.68	0.94	3.91
	F	UCR_ENT 00069271	11.01	1.97	0.38	1.17	1.15	2.79	1.27	3.47	6.97	0.56	0.73	1.04	4.30
	F	UCR_ENT 00073615	8.33	1.67	0.31	0.98	0.99	2.19	0.93	2.76	5.12	0.44	0.69	0.87	3.57
	F	UCR_ENT 00073620	9.37	1.71	0.34	1.04	1.03	2.26	1.12	2.95	5.83	0.52	0.67	0.91	3.82
	F	UCR_ENT 00073613	9.30	1.72	0.35	0.92	0.94	2.24	0.95	2.94	5.93	0.50	0.61	0.83	3.81
	F	UCR_ENT 00073641	10.74	1.85	0.41	1.06	1.09	2.60	1.15	3.33	7.00	0.51	0.60	0.96	4.16
	F	UCR_ENT 00073637	10.79	1.74	0.36	1.06	1.12	2.69	1.28	3.32	7.04	0.54	0.66	0.95	4.14
	F	UCR_ENT 00073638	10.52	1.94	0.34	1.12	1.05	2.55	1.01	3.26	6.59	0.58	0.64	0.93	4.43
	F	UCR_ENT 00024031	10.00	1.96	0.39	1.13	1.05	2.54	1.22	3.15	5.94	0.49	0.69	1.01	4.36
		Mean	9.04	1.67	0.35	1.01	0.94	2.23	1.05	2.88	5.61	0.48	0.65	0.89	3.70
		Standard Deviation	1.12	0.19	0.05	0.09	0.12	0.27	0.15	0.31	0.80	0.05	0.06	0.07	0.42
		Minimum	7.16	1.27	0.23	0.88	0.72	1.79	0.69	2.43	4.04	0.40	0.55	0.81	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	1.04	4.43
M. elongata	M	UCR_ENT 00073630	9.98	1.81	0.37	1.03	0.91	2.49	1.40	3.04	6.49	0.49	0.68	0.93	3.51
	M	UCR_ENT 00073583	10.06	1.57	0.32	1.04	1.04	2.98	1.35	3.39	6.47	0.50	0.64	0.96	3.74
	M	UCR_ENT 00073633	10.07	1.88	0.39	1.02	0.95	2.53	1.32	3.21	6.36	0.57	0.69	0.93	3.59
	M	UCR_ENT 00073634	10.21	1.72	0.35	0.97	1.10	2.97	1.24	3.29	6.59	0.50	0.57	0.95	3.81
	M	UCR_ENT 00073636	11.11	1.87	0.37	1.06	1.29	2.92	1.35	3.49	7.28	0.54	0.69	0.93	4.03
		Mean	10.29	1.77	0.36	1.02	1.06	2.78	1.33	3.28	6.64	0.52	0.65	0.94	3.74
		Standard Deviation	0.47	0.13	0.03	0.03	0.15	0.25	0.06	0.17	0.37	0.03	0.05	0.01	0.20
		Minimum	9.98	1.57	0.32	0.97	0.91	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	1.29	2.98	1.40	3.49	7.28	0.57	0.69	0.96	4.03

Table 4.4 Measurements for species of *Breviphysoderes*, *Macrophysoderes*, *Nanophysoderes*, *Paraphysoderes* and *Physoderes* (cont'd)

Species	Sex	USI	Total Length	Head length	Eye length	Eye width	Pronotum: Anterior lobe (l)	Pronotum: Anterior lobe (w)	Pronotum: Posterior lobe (l)	Pronotum: Posterior lobe (w)	Hemelytron length	Scape length	Interocular dist.	Postocular lobe width	Abdomen width
M. elongata (cont'd)	F	UCR_ENT 00073619	9.47	1.73	0.32	0.98	0.87	2.50	1.14	2.96	6.08	0.37	0.65	0.92	3.51
	F	UCR_ENT 00073506	9.75	1.86	0.38	1.02	0.87	2.34	1.05	2.93	6.20	0.42	0.66	0.85	3.71
	F	UCR_ENT 00073639	10.41	1.84	0.34	0.99	1.13	2.61	1.15	3.21	7.00	0.50	0.66	0.95	3.89
	F	UCR_ENT 00073505	9.94	1.66	0.28	0.98	1.04	2.48	1.14	3.19	6.26	0.49	0.66	0.91	3.91
		Mean	9.89	1.77	0.33	0.99	0.98	2.49	1.12	3.07	6.39	0.45	0.66	0.91	3.76
		Standard Deviation	0.40	0.10	0.04	0.02	0.13	0.11	0.05	0.15	0.42	0.06	0.00	0.04	0.19
		Minimum	9.47	1.66	0.28	0.98	0.87	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	1.13	2.61	1.15	3.21	7.00	0.50	0.66	0.95	3.91
M. finisterre	M	UCR_ENT 00069275	8.66	1.51	0.30	0.99	0.90	2.21	1.15	2.83	4.98	0.50	0.60	0.81	3.33
	M	UCR_ENT 00069274	9.36	1.76	0.38	1.02	0.99	2.29	1.32	2.96	5.61	0.54	0.61	0.90	3.34
	M	UCR_ENT 00069277	8.71	1.63	0.37	0.89	0.89	2.13	1.14	2.80	5.42	0.49	0.62	0.75	3.38
	M	UCR_ENT 00069280	8.40	1.70	0.31	0.95	0.90	1.92	0.94	2.59	4.97	0.43	0.62	0.82	2.92
	M	UCR_ENT 00069281	9.13	1.71	0.30	0.96	0.93	2.13	0.99	2.86	5.84	0.44	0.64	0.82	3.16
		Mean	8.85	1.66	0.33	0.96	0.92	2.14	1.11	2.81	5.36	0.48	0.62	0.82	3.23
		Standard Deviation	0.38	0.10	0.04	0.05	0.04	0.14	0.15	0.14	0.38	0.04	0.01	0.06	0.19
		Minimum	8.40	1.51	0.30	0.89	0.89	1.92	0.94	2.59	4.97	0.43	0.60	0.75	2.92
		Maximum	9.36	1.76	0.38	1.02	0.99	2.29	1.32	2.96	5.84	0.54	0.64	0.90	3.38
	F	UCR_ENT 00069283	9.80	1.71	0.40	1.04	1.08	2.36	1.35	3.18	5.97	0.55	0.67	0.92	4.11
	F	UCR_ENT 00069284	9.23	1.75	0.30	0.98	0.93	2.05	1.07	2.77	5.62	0.43	0.67	0.80	3.43
	F	UCR_ENT 00069285	8.82	1.76	0.35	0.95	0.98	2.08	0.98	2.74	5.37	0.47	0.60	0.84	3.59
	F	UCR_ENT 00069286	8.53	1.76	0.38	0.98	1.01	2.10	1.05	2.79	4.94	0.49	0.67	0.82	3.68
	F	UCR_ENT 00069287	9.21	1.72	0.34	1.00	0.91	2.10	1.15	2.84	5.67	0.46	0.61	0.86	3.67
		Mean	9.12	1.74	0.35	0.99	0.98	2.14	1.12	2.86	5.52	0.48	0.64	0.85	3.70
		Standard Deviation	0.48	0.02	0.04	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	0.30	0.95	0.91	2.05	0.98	2.74	4.94	0.43	0.60	0.80	3.43
		Maximum	9.80	1.76	0.40	1.04	1.08	2.36	1.35	3.18	5.97	0.55	0.67	0.92	4.11
M. histrionica	M	UCR_ENT 00018520	8.50	0.00	0.00	0.00	0.00	0.00	0.00	2.80	5.00	0.00	0.00	0.00	0.00
M. grandis	M	UCR_ENT 52314	11.58	1.59	0.48	1.31	1.03	2.65	1.64	3.74	7.71	0.75	0.62	1.01	4.28
	F	UCR_ENT 00073625	12.66	2.02	0.50	1.33	1.33	2.82	1.69	4.03	8.21	0.75	0.67	1.01	4.86
M. modesta	M	UCR_ENT 00069386	9.45	1.94	0.35	1.06	1.08	2.14	1.27	2.95	5.49	0.52	0.59	0.88	3.46
	F	UCR_ENT 00030982	11.89	2.13	0.36	1.28	1.24	2.56	1.52	3.71	7.37	0.58	0.73	0.96	4.47

Table 4.4 Measurements for species of *Breviphysoderes*, *Macrophysoderes*, *Nanophysoderes*, *Paraphysoderes* and *Physoderes* (cont'd)

Species	Sex	USI	Total Length	Head length	Eye length	Eye width	Pronotum				Hemelytron length	Scape length	Interocular dist.	Postocular lobe width	Abdomen width
							Anterior lobe (l)	Anterior lobe (w)	Posterior lobe (l)	Posterior lobe (w)					
M. monticola	M	UCR_ENT 00069387	10.34	1.81	0.29	1.06	0.96	2.29	1.37	3.36	6.35	0.49	0.63	0.91	4.19
	F	UCR_ENT 00069388	10.01	1.93	0.35	1.09	0.97	2.38	1.23	3.28	6.10	0.46	0.67	0.93	3.97
	F	UCR_ENT 00069389	10.53	2.11	0.37	1.13	1.00	2.48	1.49	3.51	6.21	0.49	0.69	0.96	4.36
	F	UCR_ENT 00069390	9.11	1.89	0.34	1.02	0.84	2.10	1.06	2.93	5.65	0.44	0.62	0.91	3.68
		Mean	9.88	1.98	0.35	1.08	0.93	2.32	1.26	3.24	5.99	0.47	0.66	0.93	4.00
		Standard Deviation	0.72	0.11	0.01	0.06	0.09	0.20	0.22	0.29	0.30	0.02	0.04	0.02	0.34
		Minimum	9.11	1.89	0.34	1.02	0.84	2.10	1.06	2.93	5.65	0.44	0.62	0.91	3.68
		Maximum	10.53	2.11	0.37	1.13	1.00	2.48	1.49	3.51	6.21	0.49	0.69	0.96	4.36
Nanophysoderes															
N. dentiscutum	M	UCR_ENT 00037370	7.66	1.55	0.33	0.89	0.76	1.86	0.86	2.34	4.58	0.42	0.52	0.79	2.80
Paraphysoderes															
P. popeye	M	UCR_ENT 00073584	7.09	1.27	0.26	0.83	0.78	1.57	0.84	2.22	4.35	0.43	0.59	0.69	2.56
	F	UCR_ENT 00069394	8.41	1.83	0.30	0.98	1.10	2.25	0.93	2.77	4.82	0.61	0.69	0.76	3.54
	F	UCR_ENT 00073621	8.33	1.62	0.33	1.01	0.95	1.98	0.90	2.76	5.02	0.53	0.68	0.78	3.34
	F	UCR_ENT 00069393	7.65	1.52	0.27	0.99	1.01	1.85	0.77	2.50	4.54	0.50	0.64	0.76	3.17
	F	UCR_ENT 00073623	7.47	1.25	0.28	0.96	1.00	1.80	0.76	2.50	4.61	0.42	0.63	0.75	3.30
	F	UCR_ENT 00073624	7.60	1.56	0.28	0.95	0.97	1.90	0.82	2.53	4.46	0.49	0.65	0.77	3.27
		Mean	7.89	1.55	0.29	0.98	1.00	1.96	0.84	2.61	4.69	0.51	0.66	0.76	3.32
		Standard Deviation	0.44	0.21	0.02	0.02	0.06	0.18	0.07	0.14	0.23	0.07	0.03	0.01	0.14
		Minimum	7.47	1.25	0.27	0.95	0.95	1.80	0.76	2.50	4.46	0.42	0.63	0.75	3.17
		Maximum	8.41	1.83	0.33	1.01	1.10	2.25	0.93	2.77	5.02	0.61	0.69	0.78	3.54
Physoderes															
P. anamalaiensis	M	UCR_ENT 00068920	9.82	1.97	0.33	1.05	1.32	2.99	1.02	2.94	5.62	0.42	0.64	0.88	3.74
	M	UCR_ENT 46637	9.19	1.87	0.32	0.99	1.34	3.08	0.84	2.94	5.43	0.50	0.66	0.84	3.63
	M	UCR_ENT 00068925	8.91	1.90	0.28	1.02	1.28	2.65	0.84	2.68	5.61	0.48	0.65	0.84	3.41
	M	UCR_ENT 00068924	9.03	1.95	0.35	0.98	1.23	2.45	0.73	2.64	5.37	0.53	0.64	0.82	3.46
	M	UCR_ENT 00068923	9.38	1.95	0.33	1.01	1.46	3.10	0.90	2.96	5.17	0.52	0.67	0.89	3.57
		Mean	9.27	1.93	0.32	1.01	1.33	2.85	0.87	2.83	5.44	0.49	0.65	0.85	3.56
		Standard Deviation	0.36	0.04	0.02	0.03	0.09	0.29	0.11	0.16	0.19	0.04	0.01	0.03	0.13
		Minimum	8.91	1.87	0.28	0.98	1.23	2.45	0.73	2.64	5.17	0.42	0.64	0.82	3.41
		Maximum	9.82	1.97	0.35	1.05	1.46	3.10	1.02	2.96	5.62	0.53	0.67	0.89	3.74

Table 4.4 Measurements for species of *Breviphysoderes*, *Macrophysoderes*, *Nanophysoderes*, *Paraphysoderes* and *Physoderes* (cont'd)

Species	Sex	USI	Total Length	Head length	Eye length	Eye width	Pronotum Anterior lobe (l)	Pronotum Anterior lobe (w)	Pronotum Posterior lobe (l)	Pronotum Posterior lobe (w)	Hemelytron length	Scape length	Interocular dist.	Postocular lobe width	Abdomen width
P. anamalaiensis (cont'd)	F	UCR_ENT 46643	9.59	2.14	0.36	1.03	1.17	2.72	1.10	2.99	5.48	0.49	0.74	0.91	4.07
	F	UCR_ENT 46644	9.08	1.91	0.31	0.99	1.13	2.52	1.01	2.81	5.03	0.47	0.68	0.85	3.71
	F	UCR_ENT 46622	8.96	1.85	0.30	0.94	1.17	2.56	0.77	2.88	5.31	0.48	0.54	0.88	3.74
	F	UCR_ENT 46641	9.12	1.91	0.30	0.96	1.07	2.31	0.83	2.75	5.30	0.47	0.64	0.86	3.55
	F	UCR_ENT 00068934	8.92	2.04	0.36	0.95	1.09	2.44	1.08	2.80	5.07	0.53	0.56	0.85	3.80
	F	Mean	9.13	1.97	0.33	0.97	1.13	2.51	0.96	2.84	5.24	0.49	0.63	0.87	3.77
		Standard Deviation	0.27	0.12	0.03	0.04	0.05	0.15	0.15	0.09	0.18	0.03	0.08	0.02	0.19
		Minimum	8.92	1.85	0.30	0.94	1.07	2.31	0.77	2.75	5.03	0.47	0.54	0.85	3.55
		Maximum	9.59	2.14	0.36	1.03	1.17	2.72	1.10	2.99	5.48	0.53	0.74	0.91	4.07
P. azrael	M	UCR_ENT 00069294	8.39	1.52	0.31	0.91	1.01	2.70	0.92	2.83	5.11	0.40	0.60	0.87	3.15
	M	UCR_ENT 00069319	8.49	1.56	0.32	0.90	0.93	2.33	0.96	2.67	5.23	0.38	0.55	0.82	2.94
	M	UCR_ENT 00073529	8.54	1.69	0.31	0.89	0.90	2.44	0.98	2.60	5.23	0.36	0.57	0.83	2.99
	M	UCR_ENT 00073523	8.76	1.66	0.29	0.86	0.94	2.71	1.00	2.87	5.41	0.41	0.60	0.88	3.20
	M	UCR_ENT 00073526	8.74	1.70	0.27	0.90	1.05	2.70	0.83	2.79	5.49	0.40	0.62	0.85	3.24
		Mean	8.58	1.63	0.30	0.89	0.97	2.58	0.94	2.75	5.29	0.39	0.59	0.85	3.10
		Standard Deviation	0.16	0.08	0.02	0.02	0.06	0.18	0.07	0.11	0.15	0.02	0.03	0.03	0.13
		Minimum	8.39	1.52	0.27	0.86	0.90	2.33	0.83	2.60	5.11	0.36	0.55	0.82	2.94
		Maximum	8.76	1.70	0.32	0.91	1.05	2.71	1.00	2.87	5.49	0.41	0.62	0.88	3.24
	F	UCR_ENT 00069301	8.14	1.51	0.27	0.83	0.87	2.04	0.92	2.55	5.13	0.36	0.55	0.84	3.13
	F	UCR_ENT 00069333	8.67	1.66	0.26	0.88	0.90	2.09	0.94	2.64	5.38	0.40	0.61	0.88	3.23
	F	UCR_ENT 00069335	8.83	1.60	0.29	0.93	0.91	2.18	0.96	2.77	5.64	0.49	0.62	0.87	3.17
	F	UCR_ENT 46672	8.71	1.67	0.29	0.92	0.80	2.22	0.91	2.73	5.50	0.46	0.58	0.86	3.26
	F	UCR_ENT 00073553	8.71	1.63	0.31	0.88	0.83	2.10	0.85	2.70	5.38	0.41	0.62	0.87	3.26
		Mean	8.61	1.61	0.29	0.89	0.86	2.13	0.92	2.68	5.41	0.42	0.60	0.86	3.21
		Standard Deviation	0.27	0.06	0.02	0.04	0.04	0.07	0.04	0.09	0.19	0.05	0.03	0.02	0.06
		Minimum	8.14	1.51	0.26	0.83	0.80	2.04	0.85	2.55	5.13	0.36	0.55	0.84	3.13
		Maximum	8.83	1.67	0.31	0.93	0.91	2.22	0.96	2.77	5.64	0.49	0.62	0.88	3.26
P. brevipennis	M	UCR_ENT 00069376	6.72	1.68	0.27	0.95	1.28	3.13	0.74	2.71	2.86	0.49	0.53	0.88	3.45
	M	UCR_ENT 00069370	6.61	1.76	0.34	0.92	1.22	2.76	0.81	2.53	2.41	0.46	0.59	0.88	3.31
	M	UCR_ENT 00069371	6.08	1.67	0.27	0.88	1.23	2.84	0.71	2.47	2.47	0.47	0.65	0.81	3.19
	M	UCR_ENT 00069372	7.07	2.01	0.32	0.93	1.44	3.25	0.81	2.80	3.05	0.53	0.61	0.91	3.83
	M	UCR_ENT 00069375	6.57	1.73	0.32	0.98	1.21	2.93	0.82	2.51	2.81	0.50	0.64	0.87	3.44
		Mean	6.61	1.77	0.30	0.93	1.28	2.98	0.78	2.60	2.72	0.49	0.60	0.87	3.44
		Standard Deviation	0.35	0.14	0.03	0.04	0.10	0.20	0.05	0.14	0.27	0.03	0.05	0.04	0.24
		Minimum	6.08	1.67	0.27	0.88	1.21	2.76	0.71	2.47	2.41	0.46	0.53	0.81	3.19
		Maximum	7.07	2.01	0.34	0.98	1.44	3.25	0.82	2.80	3.05	0.53	0.65	0.91	3.83

Table 4.4 Measurements for species of *Breviphysoderes*, *Macrophysoderes*, *Nanophysoderes*, *Paraphysoderes* and *Physoderes* (cont'd)

Species	Sex	USI	Total Length	Head length	Eye length	Eye width	Pronotum Anterior lobe (l)	Pronotum Anterior lobe (w)	Pronotum Posterior lobe (l)	Pronotum Posterior lobe (w)	Hemelytron length	Scape length	Interocular dist.	Postocular lobe width	Abdomen width
P. brevipennis (cont'd)	F	UCR_ENT 00069379	6.73	1.78	0.33	0.96	1.18	2.65	0.73	2.66	2.78	0.46	0.68	0.91	4.14
	F	UCR_ENT 00069381	6.29	1.87	0.34	0.98	1.07	2.57	0.86	2.60	2.31	0.46	0.62	0.93	3.42
	F	UCR_ENT 00069382	6.57	1.71	0.31	0.93	1.12	2.50	0.74	2.55	2.97	0.54	0.65	0.87	3.81
	F	UCR_ENT 00069383	6.44	1.58	0.25	0.91	0.98	2.19	0.91	2.31	2.59	0.47	0.64	0.84	3.56
	F	UCR_ENT 00069377	6.60	1.49	0.30	1.01	1.20	2.55	0.79	2.56	2.91	0.48	0.59	0.89	4.09
		Mean	6.53	1.69	0.31	0.96	1.11	2.49	0.81	2.54	2.71	0.49	0.64	0.89	3.80
		Standard Deviation	0.17	0.15	0.04	0.04	0.09	0.18	0.08	0.13	0.27	0.03	0.03	0.03	0.32
		Minimum	6.29	1.49	0.25	0.91	0.98	2.19	0.73	2.31	2.31	0.46	0.59	0.84	3.42
		Maximum	6.73	1.87	0.34	1.01	1.20	2.65	0.91	2.66	2.97	0.54	0.68	0.93	4.14
P. curculionis	M	UCR_ENT 00031397	7.37	1.48	0.28	0.85	1.03	2.37	0.64	2.50	4.60	0.41	0.65	0.80	2.89
	M	UCR_ENT 00031398	7.44	1.58	0.29	0.82	1.04	2.46	0.83	2.60	4.32	0.34	0.59	0.80	2.91
	M	UCR_ENT 00031400	7.76	1.59	0.29	0.86	1.08	2.70	0.82	2.64	4.58	0.44	0.58	0.78	3.35
	M	UCR_ENT 00031402	7.90	1.58	0.27	0.86	0.94	2.74	0.93	2.69	4.62	0.38	0.56	0.83	3.13
	M	UCR_ENT 00031411	7.46	1.53	0.28	0.88	0.96	2.40	0.82	2.50	4.43	0.27	0.54	0.81	2.96
	M	UCR_ENT 00023947	7.70	1.67	0.29	0.87	0.99	2.46	0.74	2.55	4.15	0.40	0.59	0.81	2.68
	M	UCR_ENT 00024014	7.84	1.46	0.28	0.87	1.11	2.59	0.67	2.67	4.63	0.37	0.60	0.82	3.07
		Mean	7.64	1.56	0.28	0.86	1.02	2.53	0.78	2.59	4.48	0.37	0.59	0.81	3.00
		Standard Deviation	0.21	0.07	0.01	0.02	0.06	0.15	0.10	0.08	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	2.50	4.15	0.27	0.54	0.78	2.68
		Maximum	7.90	1.67	0.29	0.88	1.11	2.74	0.93	2.69	4.63	0.44	0.65	0.83	3.35
	F	UCR_ENT 00031403	7.62	1.54	0.29	0.89	1.07	2.29	0.72	2.64	4.58	0.38	0.63	0.85	3.29
	F	UCR_ENT 00031404	7.50	1.59	0.24	0.82	0.86	2.14	0.86	2.49	4.45	0.39	0.54	0.77	3.18
	F	UCR_ENT 00031405	7.45	1.48	0.27	0.85	0.79	2.19	0.93	2.48	4.68	0.39	0.62	0.80	3.13
	F	UCR_ENT 00031406	7.47	1.49	0.23	0.83	0.92	2.11	1.01	2.48	4.43	0.40	0.53	0.78	3.11
	F	UCR_ENT 00031410	7.27	1.61	0.32	0.82	0.87	2.14	0.77	2.46	4.32	0.38	0.56	0.84	3.13
	F	UCR_ENT 00024013	7.67	1.54	0.28	0.92	0.95	2.28	0.90	2.59	4.50	0.44	0.59	0.84	3.39
	F	UCR_ENT 00069413	7.33	1.38	0.25	0.88	0.97	2.36	0.82	2.70	4.57	0.36	0.60	0.85	3.34
	F	UCR_ENT 00069396	7.23	1.48	0.27	0.89	0.88	2.14	0.85	2.53	4.12	0.36	0.58	0.84	2.50
	F	UCR_ENT 00069397	7.68	1.55	0.27	0.82	0.87	2.07	0.83	2.46	4.47	NA	0.59	0.80	3.17
		Mean	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
		Standard Deviation	0.17	0.07	0.03	0.04	0.08	0.10	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	2.50
		Maximum	7.68	1.61	0.32	0.92	1.07	2.36	1.01	2.70	4.68	0.44	0.63	0.85	3.39

Table 4.4 Measurements for species of *Breviphysoderes*, *Macrophysoderes*, *Nanophysoderes*, *Paraphysoderes* and *Physoderes* (cont'd)

Species	Sex	USI	Total Length	Head length	Eye length	Eye width	Pronotum Anterior lobe (l)	Pronotum Anterior lobe (w)	Pronotum Posterior lobe (l)	Pronotum Posterior lobe (w)	Hemelytron length	Scape length	Interocular dist.	Postocular lobe width	Abdomen width
P. fuliginosa	M	UCR_ENT 00031280	10.32	1.89	0.35	1.00	1.48	3.46	1.06	3.26	6.38	0.52	0.69	0.91	3.74
	M	UCR_ENT 00031285	11.03	2.04	0.29	1.04	1.69	3.91	1.17	3.47	6.54	0.56	0.67	1.01	4.02
	M	UCR_ENT 00031290	9.84	1.98	0.36	0.94	1.28	2.85	1.07	3.10	5.84	0.53	0.61	0.91	3.54
	M	UCR_ENT 00031312	11.03	2.08	0.35	1.04	1.57	4.00	1.28	3.63	6.56	0.57	0.74	0.97	4.19
	M	UCR_ENT 00031299	10.11	2.08	0.36	0.93	1.22	2.90	1.18	3.10	5.87	0.55	0.56	0.89	3.59
		Mean	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
		Standard Deviation	0.54	0.08	0.03	0.05	0.20	0.54	0.09	0.23	0.36	0.02	0.07	0.05	0.28
		Minimum	9.84	1.89	0.29	0.93	1.22	2.85	1.06	3.10	5.84	0.52	0.56	0.89	3.54
		Maximum	11.03	2.08	0.36	1.04	1.69	4.00	1.28	3.63	6.56	0.57	0.74	1.01	4.19
	F	UCR_ENT 00031356	10.89	2.01	0.35	1.12	1.10	2.60	1.54	3.40	6.68	0.55	0.74	0.98	4.47
	F	UCR_ENT 00031369	9.59	1.92	0.37	1.04	0.95	2.19	1.22	3.00	5.72	0.50	0.63	0.92	3.80
	F	UCR_ENT 00030995	10.24	2.02	0.44	1.01	1.05	2.55	1.34	3.27	6.36	0.50	0.59	0.93	4.05
	F	UCR_ENT 00030996	9.85	2.03	0.33	0.97	0.90	2.30	1.26	3.12	5.99	0.49	0.61	0.88	4.04
	F	UCR_ENT 00069210	10.11	2.03	0.41	0.93	1.00	2.29	1.35	3.23	6.24	0.49	0.63	0.89	3.85
		Mean	10.14	2.00	0.38	1.01	1.00	2.39	1.34	3.20	6.20	0.50	0.64	0.92	4.04
		Standard Deviation	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	0.90	2.19	1.22	3.00	5.72	0.49	0.59	0.88	3.80
		Maximum	10.89	2.03	0.44	1.12	1.10	2.60	1.54	3.40	6.68	0.55	0.74	0.98	4.47
P. minime	M	UCR_ENT 00030979	8.75	2.03	0.29	0.90	1.28	2.87	0.97	2.82	4.70	0.49	0.62	0.86	3.30
	M	UCR_ENT 00031434	8.31	1.99	0.32	0.90	1.18	2.73	0.93	2.67	4.54	0.52	0.62	0.85	3.31
	M	UCR_ENT 00031433	8.44	1.90	0.30	0.88	1.26	2.83	0.98	2.74	4.63	0.54	0.62	0.84	3.23
	M	UCR_ENT 00031432	9.03	2.12	0.32	0.89	1.18	2.97	1.07	2.81	5.13	0.56	0.62	0.87	3.46
	M	UCR_ENT 00069250	8.67	2.00	0.31	0.90	1.25	2.76	0.94	2.64	4.61	0.51	0.55	0.86	3.19
		Mean	8.64	2.01	0.31	0.89	1.23	2.83	0.98	2.74	4.72	0.52	0.61	0.86	3.30
		Standard Deviation	0.28	0.08	0.01	0.01	0.05	0.09	0.06	0.08	0.23	0.03	0.03	0.01	0.10
		Minimum	8.31	1.90	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	0.90	1.28	2.97	1.07	2.82	5.13	0.56	0.62	0.87	3.46
	F	UCR_ENT 00069221	8.27	1.91	0.25	0.86	0.86	1.99	0.99	2.54	4.70	0.48	0.55	0.85	3.56
	F	UCR_ENT 46647	8.54	1.78	0.34	0.91	0.92	2.08	0.96	2.61	5.11	0.47	0.69	0.89	3.71
	F	UCR_ENT 00031437	8.30	2.05	0.29	0.94	0.98	2.13	1.01	2.70	4.62	0.51	0.61	0.82	3.59
	F	UCR_ENT 00031438	8.10	1.96	0.27	0.79	0.88	1.98	1.02	2.48	4.48	0.47	0.49	0.87	3.31
	F	UCR_ENT 00073629	8.26	1.70	0.38	0.87	0.81	2.15	1.19	2.69	4.96	0.51	0.49	0.94	3.71
		Mean	8.29	1.88	0.30	0.87	0.89	2.07	1.04	2.60	4.77	0.49	0.57	0.87	3.58
		Standard Deviation	0.16	0.14	0.05	0.06	0.06	0.08	0.09	0.10	0.26	0.02	0.09	0.04	0.16
		Minimum	8.10	1.70	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	2.70	5.11	0.51	0.69	0.94	3.71

Table 4.4 Measurements for species of *Breviphysoderes*, *Macrophysoderes*, *Nanophysoderes*, *Paraphysoderes* and *Physoderes* (cont'd)

Species	Sex	USI	Total Length	Head length	Eye length	Eye width	Pronotum: Anterior lobe (l)	Pronotum: Anterior lobe (w)	Pronotum: Posterior lobe (l)	Pronotum: Posterior lobe (w)	Hemelytron length	Scape length	Interocular dist.	Postocular lobe width	Abdomen width
P. muluensis	M	UCR_ENT 00069401	7.30	1.75	0.31	0.95	0.93	1.99	0.99	2.47	3.90	0.49	0.60	0.87	2.94
	M	UCR_ENT 00069403	7.59	1.87	0.27	0.96	1.04	2.08	0.93	2.56	3.98	0.53	0.57	0.93	3.01
	M	UCR_ENT 00069400	7.50	1.46	0.29	0.84	0.86	1.90	0.94	2.44	4.35	0.47	0.53	0.74	2.75
	M	UCR_ENT 00069405	6.99	1.81	0.33	0.87	0.77	1.82	0.93	2.26	3.61	0.46	0.54	0.74	2.61
		Mean	7.35	1.73	0.30	0.91	0.90	1.95	0.95	2.43	3.96	0.49	0.56	0.82	2.83
		Standard Deviation	0.27	0.18	0.03	0.06	0.12	0.11	0.03	0.13	0.30	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	0.60	0.93	3.01
	F	UCR_ENT 00069409	7.89	1.72	0.27	0.89	1.00	1.98	0.90	2.60	4.45	0.45	0.57	0.81	3.32
	F	UCR_ENT 00069410	8.21	1.72	0.32	0.99	1.06	2.15	1.06	2.62	4.50	0.54	0.69	0.86	3.43
	F	UCR_ENT 00069411	7.67	1.83	0.30	0.95	0.95	2.02	0.91	2.55	4.02	0.46	0.66	0.87	3.28
		Mean	7.92	1.75	0.30	0.95	1.00	2.05	0.95	2.59	4.32	0.48	0.64	0.85	3.34
		Standard Deviation	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	0.90	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	4.50	0.54	0.69	0.87	3.43
P. mysorensis	M	UCR_ENT 00068945	10.69	2.10	0.42	1.06	1.71	3.70	1.01	3.58	6.30	0.58	0.73	0.97	NA
	M	UCR_ENT 00068944	10.96	1.92	0.27	1.03	1.64	3.95	1.15	3.63	6.67	0.57	0.72	0.92	4.37
	M	UCR_ENT 00068943	10.83	2.14	0.38	1.12	1.51	3.44	1.21	3.41	6.32	0.58	0.71	0.89	3.92
		Mean	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
		Standard Deviation	0.14	0.11	0.08	0.05	0.10	0.26	0.10	0.12	0.21	0.00	0.01	0.04	0.32
		Minimum	10.69	1.92	0.27	1.03	1.51	3.44	1.01	3.41	6.30	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
	F	UCR_ENT 00068946	10.52	2.00	0.32	1.04	1.56	3.16	1.05	3.61	6.45	0.61	0.58	1.00	NA
	F	UCR_ENT 47705	10.88	2.15	0.36	1.12	1.35	3.05	1.29	3.51	6.52	0.56	0.74	1.01	4.30
		Mean	10.70	2.08	0.34	1.08	1.45	3.11	1.17	3.56	6.48	0.58	0.66	1.00	4.30
		Standard Deviation	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	2.00	0.32	1.04	1.35	3.05	1.05	3.51	6.45	0.56	0.58	1.00	4.30
		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	4.30
P. nigripennis	M	UCR_ENT 00023954	9.22	1.95	0.35	1.09	1.00	2.28	1.26	3.07	5.29	0.49	0.66	0.89	3.46
	M	UCR_ENT 00023955	8.91	1.85	0.29	0.98	0.83	2.04	1.25	2.82	5.09	0.52	0.57	0.85	3.16
	M	UCR_ENT 00023962	9.25	1.94	0.36	0.96	0.91	2.15	1.26	2.92	5.40	0.46	0.53	0.79	3.50
	M	UCR_ENT 00023968	9.48	1.94	0.32	1.02	0.89	2.24	1.32	3.04	5.45	0.51	0.56	0.87	3.72
	M	UCR_ENT 00023956	8.76	1.77	0.36	1.04	0.87	2.13	1.13	2.89	5.11	0.65	0.61	0.87	3.26
		Mean	9.12	1.89	0.34	1.02	0.90	2.17	1.24	2.95	5.27	0.53	0.59	0.85	3.42
		Standard Deviation	0.29	0.08	0.03	0.05	0.07	0.09	0.07	0.10	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	1.00	2.28	1.32	3.07	5.45	0.65	0.66	0.89	3.72

Table 4.4 Measurements for species of *Breviphysoderes*, *Macrophysoderes*, *Nanophysoderes*, *Paraphysoderes* and *Physoderes* (cont'd)

							Pronotum								
Species	Sex	USI	Total Length	Head length	Eye length	Eye width	Anterior lobe (l)	Anterior lobe (w)	Posterior lobe (l)	Posterior lobe (w)	Hemelytron length	Scape length	Interocular dist.	Postocular lobe width	Abdomen width
P. nigripennis (cont'd)	F	UCR_ENT 00023977	9.99	1.97	0.36	1.16	1.05	2.25	1.35	3.20	5.85	0.53	0.62	0.92	4.16
	F	UCR_ENT 00023982	9.80	1.88	0.37	1.11	0.83	2.28	1.32	3.25	5.65	0.71	0.67	0.93	4.09
	F	UCR_ENT 00023985	9.60	1.92	0.33	1.14	0.89	2.22	1.34	3.32	5.79	0.51	0.66	0.93	4.05
	F	UCR_ENT 00023987	10.65	1.88	0.34	1.10	1.00	2.38	1.56	3.49	6.80	0.61	0.62	0.89	4.41
	F	UCR_ENT 00023996	10.22	1.88	0.34	1.13	0.93	2.40	1.43	3.33	6.28	0.65	0.62	0.92	4.16
		Mean	10.05	1.90	0.35	1.13	0.94	2.30	1.40	3.32	6.07	0.60	0.64	0.92	4.17
		Standard Deviation	0.41	0.04	0.02	0.02	0.09	0.08	0.10	0.11	0.47	0.09	0.03	0.02	0.14
		Minimum	9.60	1.88	0.33	1.10	0.83	2.22	1.32	3.20	5.65	0.51	0.62	0.89	4.05
		Maximum	10.65	1.97	0.37	1.16	1.05	2.40	1.56	3.49	6.80	0.71	0.67	0.93	4.41
P. nigroalbus	F	UCR_ENT 00040566	9.74	1.88	0.29	1.00	1.03	2.24	1.17	2.95	6.01	0.41	0.66	0.94	3.66
P. notata	M	UCR_ENT 00024057	10.22	1.70	0.34	1.05	1.35	3.51	1.40	3.26	6.30	0.51	0.57	0.89	3.87
	M	UCR_ENT 00024058	9.97	1.83	0.32	1.08	1.21	3.28	1.23	3.18	6.11	0.45	0.66	1.01	3.50
	M	UCR_ENT 00024060	9.95	1.73	0.29	0.97	1.30	2.89	1.19	3.06	6.15	0.47	0.64	0.93	3.46
	M	UCR_ENT 00024062	10.11	1.99	0.34	0.99	1.12	2.93	1.17	3.09	6.07	0.41	0.63	0.88	3.86
	M	UCR_ENT 00024059	9.44	1.78	0.31	1.00	1.21	3.22	1.24	3.10	5.75	0.41	0.63	0.84	3.34
		Mean	9.94	1.81	0.32	1.02	1.24	3.17	1.25	3.14	6.08	0.45	0.63	0.91	3.61
		Standard Deviation	0.30	0.12	0.02	0.04	0.09	0.26	0.09	0.08	0.20	0.04	0.04	0.06	0.24
		Minimum	9.44	1.70	0.29	0.97	1.12	2.89	1.17	3.06	5.75	0.41	0.57	0.84	3.34
		Maximum	10.22	1.99	0.34	1.08	1.35	3.51	1.40	3.26	6.30	0.51	0.66	1.01	3.87
	F	UCR_ENT 46623	9.54	1.92	0.32	1.10	0.95	2.35	1.06	3.00	5.93	0.47	0.65	0.98	3.38
	F	UCR_ENT 46649	10.08	1.99	0.31	1.03	1.12	2.41	1.22	3.12	6.12	0.51	0.62	0.90	3.90
	F	UCR_ENT 00024053	10.07	1.71	0.32	1.06	0.90	2.53	1.51	3.33	6.42	0.45	0.73	0.92	3.94
	F	UCR_ENT00024051	10.30	1.76	0.37	1.01	0.97	2.57	1.48	3.33	6.51	0.44	0.65	0.94	3.80
	F	UCR_ENT 00024055	9.71	1.62	0.30	1.03	0.84	2.41	1.31	3.09	6.43	0.42	0.64	0.88	3.63
		Mean	9.94	1.80	0.32	1.05	0.96	2.45	1.31	3.17	6.28	0.46	0.66	0.93	3.73
		Standard Deviation	0.31	0.15	0.03	0.04	0.10	0.09	0.18	0.15	0.25	0.04	0.04	0.04	0.23
		Minimum	9.54	1.62	0.30	1.01	0.84	2.35	1.06	3.00	5.93	0.42	0.62	0.88	3.38
		Maximum	10.30	1.99	0.37	1.10	1.12	2.57	1.51	3.33	6.51	0.51	0.73	0.98	3.94

Table 4.4 Measurements for species of *Breviphysoderes*, *Macrophysoderes*, *Nanophysoderes*, *Paraphysoderes* and *Physoderes* (cont'd)

Species	Sex	USI	Total Length	Head length	Eye length	Eye width	Pronotum Anterior lobe (l)	Pronotum Anterior lobe (w)	Pronotum Posterior lobe (l)	Pronotum Posterior lobe (w)	Hemelytron length	Scape length	Interocular dist.	Postocular lobe width	Abdomen width
P. ractepilosa	M	UCR_ENT 00024000	9.27	1.75	0.39	0.86	0.77	2.21	1.21	2.83	5.93	0.44	0.40	0.90	3.57
	M	UCR_ENT 00023999	8.59	1.96	0.34	0.86	1.02	2.04	0.79	2.64	5.09	0.50	0.60	0.80	3.21
		Mean	8.93	1.86	0.37	0.86	0.90	2.13	1.00	2.74	5.51	0.47	0.50	0.85	3.39
		Standard Deviation	0.49	0.15	0.03	0.00	0.17	0.12	0.30	0.14	0.60	0.05	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	0.40	0.80	3.21
		Maximum	9.27	1.96	0.39	0.86	1.02	2.21	1.21	2.83	5.93	0.50	0.60	0.90	3.57
	F	UCR_ENT 00024001	8.32	1.83	0.34	0.89	0.82	2.02	1.02	2.66	4.89	0.44	0.57	0.81	3.44
	F	UCR_ENT 00024002	9.18	2.01	0.40	0.94	0.88	2.32	0.97	3.05	5.46	0.56	0.57	0.84	3.94
	F	UCR_ENT 00024003	9.24	2.08	0.36	0.92	0.95	2.37	1.12	3.05	5.49	0.50	0.58	0.84	4.10
	F	UCR_ENT 00024004	10.19	2.07	0.37	0.93	0.97	2.21	1.27	3.22	6.20	0.53	0.43	0.84	4.04
	F	UCR_ENT 00014061	9.04	1.96	0.36	0.97	0.89	2.21	1.13	2.94	5.29	0.51	0.60	0.85	3.77
		Mean	9.19	1.99	0.37	0.93	0.90	2.23	1.10	2.99	5.47	0.51	0.55	0.84	3.86
		Standard Deviation	0.67	0.10	0.02	0.03	0.06	0.13	0.12	0.21	0.47	0.04	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	0.43	0.81	3.44
		Maximum	10.19	2.08	0.40	0.97	0.97	2.37	1.27	3.22	6.20	0.56	0.60	0.85	4.10
P. tricolor	M	UCR_ENT 00031439	8.77	1.56	0.30	0.95	1.05	2.52	1.17	2.68	5.33	0.42	0.56	0.86	3.04
	M	UCR_ENT 00030980	8.55	1.61	0.29	0.88	0.93	2.42	1.16	2.61	5.26	0.42	0.51	0.82	2.80
		Mean	8.66	1.58	0.29	0.91	0.99	2.47	1.17	2.65	5.30	0.42	0.54	0.84	2.92
		Standard Deviation	0.16	0.04	0.01	0.05	0.09	0.07	0.01	0.05	0.05	0.00	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	0.51	0.82	2.80
		Maximum	8.77	1.61	0.30	0.95	1.05	2.52	1.17	2.68	5.33	0.42	0.56	0.86	3.04
	F	UCR_ENT 00031440	10.15	1.67	0.32	0.93	0.88	2.25	1.28	2.86	NA	0.41	0.60	0.87	3.27
	F	UCR_ENT 00031441	9.15	1.73	0.31	0.92	0.90	2.20	1.10	2.78	5.76	0.42	0.58	0.87	3.34
	F	UCR_ENT 00031442	8.70	1.70	0.29	0.91	0.92	2.07	1.02	2.66	5.44	0.35	0.61	0.80	2.98
		Mean	9.33	1.70	0.31	0.92	0.90	2.17	1.13	2.77	5.60	0.39	0.60	0.85	3.20
		Standard Deviation	0.74	0.03	0.02	0.01	0.02	0.09	0.13	0.10	0.23	0.04	0.02	0.04	0.19
		Minimum	8.70	1.67	0.29	0.91	0.88	2.07	1.02	2.66	5.44	0.35	0.58	0.80	2.98
		Maximum	10.15	1.73	0.32	0.93	0.92	2.25	1.28	2.86	5.76	0.42	0.61	0.87	3.34

Conclusion

The research conducted here has made significant advancements towards our understanding of the systematics of Reduviidae at multiple levels. With respect to the phylogenetics of Reduviidae, the current understanding of higher level relationships has greatly improved with the sizeable representation of the polyphyletic Reduviinae. The resolution of Reduviinae into several clades is the first step towards reclassification of this large subfamily to better reflect their phylogenetic positions. Future research can now build towards improving the resolution and support for higher level relationships within the Higher Reduviidae clade which is currently weakly supported. Ancestral state reconstructions of microhabitats and prey preference, together with divergence time estimates have allowed, for the first time, a temporal and ecological overview of the evolutionary history of Reduviidae. Establishing this framework of reduviid evolution thus paves the way for testing more evolutionary hypotheses to explain for the various biological phenomena of reduviids that make this one of the most successful group of insect predators. Similar but in a smaller scale, the same approaches have greatly improved our understanding of the evolution of the blood-feeding Triatominae. The possibility of a paraphyletic Triatominae with *Opisthacidius* as a closely-related reduviine to Rhodniini and Cavernicolini highlights the need to understand the biology of *Opisthacidius* in order to further understand the biological factors that were involved during the switch to a hematophagous lifestyle. The infection rate of the native kissing bug *Triatoma protracta* with the parasitic *Trypanosoma cruzi* is well established in Southern California and has persisted at a relatively high level over decades as shown here although population level variation is present. Even though the presence of *T. cruzi* is confirmed, the genotype remains unclear. At the taxonomic front, a small revision of the Malagascar endemic *Durevius* added two new species and provided redescriptions of the genus and described species. The larger taxonomic revision of *Physoderes* significantly improved what has been a problematic group to identify and define. Newly described species here show a higher morphological diversity than previously documented and also a wider overall distribution into the Pacific islands. Having a genus-level phylogeny of Physoderinae to test the monophyly of *Physoderes* was a crucial step towards better clarification of the physoderine species found in the Oriental and Australasian regions. The phylogeny also allowed for the testing of several other hypotheses, which includes the Neotropical physoderines shown to be sister to all except the Afrotropical "Porcelloderes" and the Madagascar physoderines, which possess the most remarkable morphological diversity, are shown to be not monophyletic and having a more complex biogeographic history. The contributions here to the taxonomy and phylogenetics of Reduviinae, Triatominae and Physoderinae illustrates the advances in the systematic knowledge of Reduviidae we can make based on current tools and methods and serves as groundwork for future investigations into this most fascinating group of predatory insects.